

## The Slottsmøya marine reptile *Lagerstätte*: depositional environments, taphonomy and diagenesis

LENE L. DELSETT<sup>1\*</sup>, LINN K. NOVIS<sup>2</sup>, AUBREY J. ROBERTS<sup>3</sup>,  
MAAYKE J. KOEVOETS<sup>1</sup>, ØYVIND HAMMER<sup>1</sup>,  
PATRICK S. DRUCKENMILLER<sup>4</sup> & JØRN H. HURUM<sup>1</sup>

<sup>1</sup>Natural History Museum, University of Oslo, 0318 Oslo, Norway

<sup>2</sup>Tromsø University Museum, 9037 Tromsø, Norway

<sup>3</sup>Ocean and Earth Science, National Oceanography Centre Southampton,  
University of Southampton, Southampton SO14 3ZH, UK

<sup>4</sup>University of Alaska Museum and Department of Geosciences,  
University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA

\*Corresponding author (e-mail: [l.l.delsett@nhm.uio.no](mailto:l.l.delsett@nhm.uio.no))

**Abstract:** The Late Jurassic Slottsmøya Member *Lagerstätte* on Spitsbergen offers a unique opportunity to study the relationships between vertebrate fossil preservation, invertebrate occurrences and depositional environment. In this study, 21 plesiosaurian and 17 ichthyosaur specimens are described with respect to articulation, landing mode, preservation, and possible predation and scavenging. The stratigraphic distribution of marine reptiles in the Slottsmøya Member is analysed, and a correlation between high total organic content, low oxygen levels, few benthic invertebrates and optimal reptile preservation is observed. A new model for 3D preservation of vertebrates in highly compacted organic shales is explained.

**Supplementary material:** A taphonomic description of each marine reptile specimen is available at <https://doi.org/10.6084/m9.figshare.c.2133549>



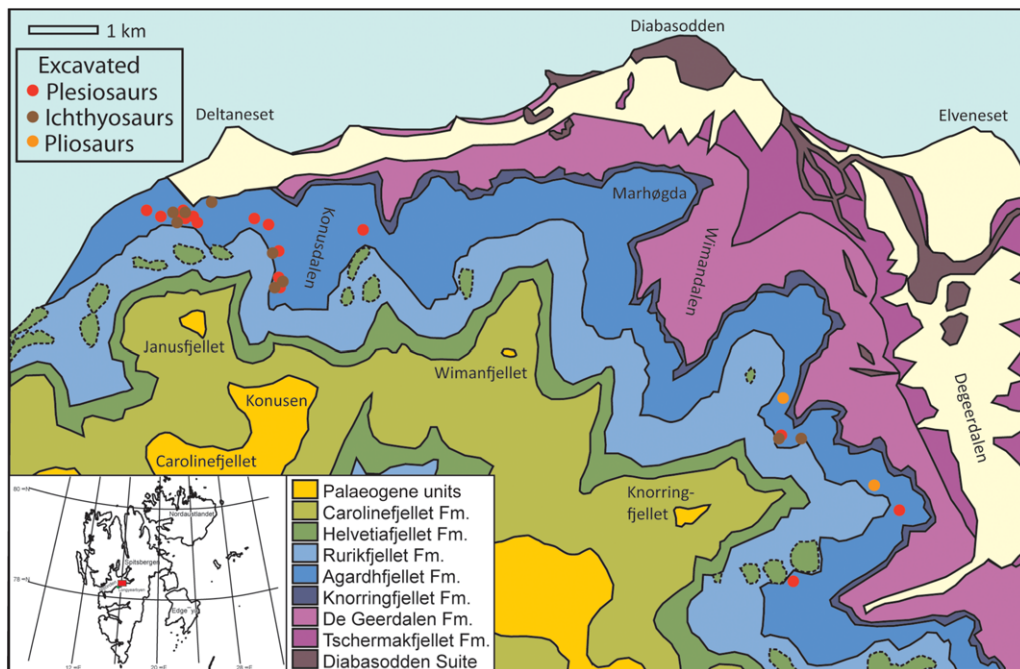
**Gold Open Access:** This article is published under the terms of the CC-BY 3.0 license.

Mesozoic marine reptiles have been known from the Svalbard archipelago for more than 150 years, particularly from Triassic units (Maxwell & Kear 2013; Hurum *et al.* 2014). However, it was not until 1914 that Wiman described the first Jurassic marine reptile, a plesiosaur, from the island of Spitsbergen (Wiman 1914; Kear & Maxwell 2013). Beginning in 2004, an extensive new field survey for Jurassic marine reptiles was undertaken by the Spitsbergen Jurassic Research Group (SJRG), an international team of palaeontologists and geologists. During eight field seasons (2004 and 2006–12) on Spitsbergen, SJRG collected more than 40 marine reptile skeletons from the dark marine shales of the Upper Jurassic–Lower Cretaceous Slottsmøya Member of the Agardhfjellet Formation (Fig. 1). Given the sheer abundance of material and quality of preservation, we have characterized this unit as a *Lagerstätte* (Hurum *et al.* 2012).

In the course of this work, detailed taphonomical data have been collected, permitting a rare insight into plesiosaur and ichthyosaur taphonomy. Previous studies were limited primarily to two other

Jurassic units: the Oxford Clay and the Posidonien-schiefer Formation (Martill 1985, 1986, 1993). However, the material upon which these studies were based was collected decades ago, and the specimens were not adequately stratigraphically constrained or contextualized geologically: thus, taphonomical interpretations presented in these studies are somewhat contentious. Efimov (2001) also analysed the taphonomy of a large number of Upper Jurassic and Lower Cretaceous ichthyosaurs from two parts of the Ulyanovsk Section in the Volga Region.

Here, for the first time, we address plesiosaur and ichthyosaur taphonomy based on a large sample size ( $n = 38$ ) with many articulated specimens from a site where stratigraphic, sedimentological and palaeontological data were collected simultaneously (Table 1; Figs 2 & 3). In this paper, we describe the preservational modes of the skeletons, and attempt to interpret the major physical and biotic factors affecting skeletal preservation. We incorporate new surface and well-log data to document the stratigraphic distribution of skeletons in the unit, especially in relation to the total organic



**Fig. 1.** Geological map of the study area in central Spitsbergen, with the main marine reptile locations marked with red, brown and yellow circles. Redrawn and adapted from Dallmann *et al.* (2001).

content (TOC). The causes for the exceptional abundance of marine reptile skeletons found in the Slottsmøya Member compared to other members is beyond the scope of this paper.

### Geological setting

The Svalbard archipelago is located between latitudes 74–81° N and longitudes 10–35° E, in the northwestern corner of the Barents Sea shelf. The Middle Jurassic–Lower Cretaceous succession forming the Janusfjellet Subgroup comprises the Agardhfjellet and Rurikfjellet formations. The Agardhfjellet Formation consists of black shales and siltstones deposited in an open-marine, oxygen-deficient shelf setting (Dypvik *et al.* 1991; Collignon & Hammer 2012). The Myklagardfjellet bed, a distinct thin marker horizon of weathering clays, marks the boundary between the two formations (Birkenmajer 1980).

The marine reptiles and invertebrates discussed in this study occur in the Slottsmøya Member, the uppermost member of the Agardhfjellet Formation (Figs 1 & 2). The Slottsmøya Member rests on the Oppdalsåta Member and is overlain by the Wimanfjellet Member of the Rurikfjellet Formation (Mørk *et al.* 1999). The Slottsmøya Member was deposited

in an open-marine shelf (Hammer *et al.* 2012). The thickness ranges from 70 to 100 m, and consists of black to grey shales and siltstones with siderite interbeds (Dypvik *et al.* 1991). Shelf conditions were slightly dysoxic with periodical oxygenation of the bottom water, which might have been a result of influx of clastic sediments (Collignon & Hammer 2012). The shales of the mid-section show little alternation in mineralogy, suggesting a stable depositional environment, while the sediments in the silty intervals were transported into the basin by turbidity currents (Collignon & Hammer 2012). This interpretation is supported by taphonomical and ecological evidence. Some crinoids and echinoids were situated in the sediment as if they were transported, while other echinoderms like asteroids and ophiuroids were found *in situ* (Rousseau & Nakrem 2012). TOC values of the Slottsmøya Member show considerable fluctuation, with the largest excursion reaching 9.7% (Hammer *et al.* 2012).

In the uppermost part (39–49 m) of the Slottsmøya Member, several cold-seep communities have been discovered. From these, a diverse and low-dominance invertebrate fauna has been described (Hammer *et al.* 2011, 2013; Wierzbowski *et al.* 2011; Hryniewicz *et al.* 2012, 2014). The non-seep fauna invertebrate diversity was probably also quite high. This assumption is based on a study of the

Slottsmøya Member from East Spitsbergen by Birkenmajer *et al.* (1982), the echinoderm fauna in the section (Rousseau & Nakrem 2012) and field observations in the area.

### Abbreviations

PMO, Natural History Museum, University of Oslo (Palaeontological collection); SJRG, Spitsbergen Jurassic Research Group; SVB, Svalbard Museum, Longyearbyen.

### Materials and methods

The 38 marine reptile skeletons used in this study were excavated during eight field seasons (2004 and 2006–12) by the SJRG. For each skeleton, the locality information, stratigraphic position and taphonomical data (e.g. orientation, nature and degree of articulation, and associated invertebrates) were recorded in the field at the time of collection (Table 1; Figs 2 & 3). During preparation, additional information was obtained concerning the articulation and association of skeletal elements, quality of preservation, completeness and bone modification. Field drawings and photographs before and during preparation were utilized in constructing skeletal maps of 28 of the specimens (Figs 4–8). The remaining specimens were relatively incomplete, poorly preserved or very disarticulated and, consequently, were not illustrated.

The marine-reptile-rich Jurassic deposits in the Oxford Clay Formation and the Posidonienschiefer Formation were used for comparative purposes in this study. The lowermost unit of the Oxford Clay Formation, the Peterborough Member, contains fossiliferous, organic-rich mudstone (Tang 2002). The clay was deposited in a shallow epicontinental seaway, and it is suggested that the seafloor substrate was soupy (Martill *et al.* 1994). The Posidonienschiefer Formation of Holzmaden is known for its well-preserved marine reptiles and fish. The formation comprises finely laminated bituminous shale, and is regarded as the archetype for stagnant deposition (Seilacher *et al.* 1985).

Martill (1985, 1986, 1993) collected vast amounts of information in his descriptions of marine reptiles from the Oxford Clay and the Posidonienschiefer Formation. In his studies of the preservation of the marine reptiles from the Peterborough Member (Martill 1985), he classified five preservation types based on the degree of skeletal articulation and the elements preserved: (1) articulated skeletons; (2) disarticulated skeletons; (3) isolated bones and teeth; (4) rolled and worn skeletal elements; and (5) coprocoenotic accumulations. Two types of disarticulation were observed. In the first type,

bones were disarticulated but associated, and the disarticulation was caused by gravitational collapse of the skeleton. There were no scattered skeletal elements. In the second type, bones were scattered over a considerable distance, and the disarticulation could be a consequence of scavenging, current activity or both (Martill 1993). The five preservational modes of Martill (1985) form the basis for the categorization of the Slottsmøya Member marine reptile skeletons in this study, which we segregate into three different categories:

- **Articulated skeleton:** this definition (Martill 1985, p. 159) is used to describe a specimen with a true bone to bone relationship. However, parts of the skeleton can be missing due to surface erosion.
- **Partly articulated skeleton:** this is a new category based on the definition of the first type of disarticulated skeletons used by Martill (1985), which recognizes that some skeletons found in the Slottsmøya Member are intermediate between articulated and disarticulated (also observed by Martill 1993). A partly articulated specimen consists of two or more skeletal elements in articulation: for example, sections of associated vertebrae, ribs still articulated to vertebrae or partly articulated fins, along with disarticulated elements.
- **Disarticulated skeleton:** the definition (Martill 1985, p. 161) is used to describe a specimen lacking a bone to bone relationship and where the elements are scattered over a limited area. Martill (1985) also included specimens with some articulated elements in the definition, but here we include such specimens in the category of partly articulated skeletons.

To analyse the variation in three-dimensionality of the bones, a computerized tomography (CT) scan of two vertebrae from an ichthyosaur (PMO 222.654: holotype of *Janusaurus lundi* Roberts, Druckenmiller, Sætre & Hurum, 2014) was conducted. The two vertebrae were scanned with a Nikon Metrology XT 225 ST X-ray microtomograph at the Natural History Museum in Oslo, at a voltage of 210 kV, a current of 300  $\mu$ A and an exposure time of 500 ms (Fig. 9).

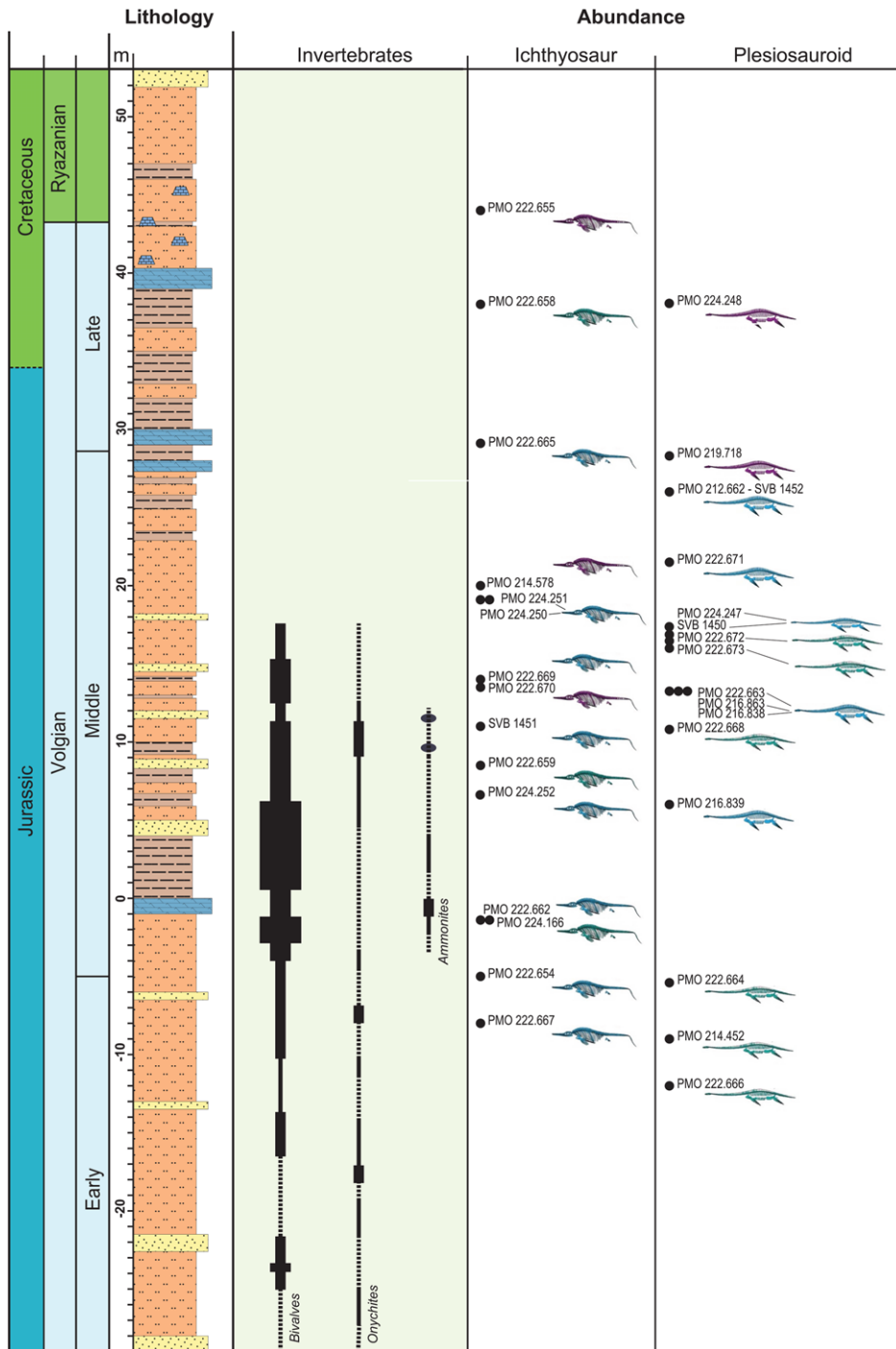
The invertebrate fossils analysed here were discovered while conducting detailed stratigraphic logging of two cores: DH2 and DH5R. These cores were obtained by the Longyearbyen CO<sub>2</sub> Laboratory during a full-core drilling campaign (Larsen 2012). Approximately 70 m of the cores are assigned to be part of the Slottsmøya Member. Invertebrate abundances represent qualitative estimates, as the area covered by the cores is minimal and fossils could only be observed on split surfaces

**Table 1.** *Collected specimens*

Collection No.	Stratigraphic position (m)	Elements preserved	Articulation	Landing mode	References	Taxon	Figure reference
PMO 222.655	44.8	Almost complete	Articulated	Dorsal, then lateral torsion	Under study	I	Figure 4a
PMO 222.658	39.1	Forefin, pectoral girdle, vertebrae	Disarticulated	Unknown	Under study	I	Figure 8d
PMO 224.248	38.5	Skull, forefins, pectoral girdle, vertebrae	Articulated	Ventral	Under study	Pe	Figure 5a
PMO 222.665	30.4	Vertebrae	Partly articulated	Unknown	Knutsen <i>et al.</i> (2012b)	I	Figures 3b and 4e
PMO 219.718	29.3	Almost complete	Articulated	Dorsal		Pe	
PMO 212.662/ SVB 1452	27.0	Partial skull, phalanges, vertebrae	Partly articulated	Dorsal	Druckenmiller <i>et al.</i> (2012)	Pe	Figures 3d and 7c
PMO 222.671	22.5	Forefin, pectoral girdle, vertebrae	Partly articulated	Unknown		I	Figure 5b
PMO 214.578	20.8	Almost complete	Articulated	Anterior, then twisted laterally	Under study	<i>I: Cryopterygius kristiansenae</i>	Figures 3a and 4b
PMO 224.250	19	Forefins, pectoral girdle	Partly articulated	Ventral		I	Figure 5d
PMO 224.251	19	Forefins, girdle elements, vertebrae, hindfin	Partly articulated	Dorsal	Knutsen <i>et al.</i> (2012b)	I	Figure 5c
SVB 1450	17.8	Partial skull, forefin, vertebrae	Partly articulated	Ventral		Pe: <i>Spitrasaurus larseni</i>	Figure 7d
PMO 222.672	17.5	Vertebra, pelvic girdle	Disarticulated	Unknown		Pe	Figure 8e
PMO 222.673	17	Vertebrae	Disarticulated	Unknown		Pe	
PMO 224.247	16.5	Forefins, girdle elements, vertebrae	Partly articulated	Ventral	Under study	Pe	Figure 6d
PMO 222.669	15.5	Skull, vertebrae, pectoral girdle, forefin	Partly articulated	Anterior, then twisted laterally		I	Figures 3c and 7e
PMO 222.670	14.5	Hindfins, vertebrae, pelvic girdle	Articulated	Left lateral	Under study	I	Figure 4c
PMO 222.663	14	Forefins, pectoral girdle, vertebrae, hindfins	Partly articulated	Ventral	Under study	Pe	Figure 7f
PMO 214.135	14	Partial skull, vertebrae, humerus, phalanges, coracoid	Partly articulated	Dorsal	Knutsen <i>et al.</i> (2012d)	<i>Pi: Pliosaurus funkei</i>	Figure 6f
PMO 214.136	14	Partial skull, vertebrae	Disarticulated	Unknown	Knutsen <i>et al.</i> (2012d)	<i>Pi: Pliosaurus funkei</i>	
PMO 216.863	14	Forefin, pectoral girdle, vertebrae, pelvic girdle, hindfin	Partly articulated	Unknown		Pe	

PMO 216.838	14	Hindfins, vertebrae, pelvic girdle, phalanges	Partly articulated	Unknown	Knutsen <i>et al.</i> (2012a); Liebe & Hurum (2012)	<i>Pe: Colymbosaurus svalbardensis</i>	Figure 6c
SVB 1451	11.8	Skull, ribs, vertebrae, phalanges, clavicle	Partly articulated	Dorsal	Druckenmiller <i>et al.</i> (2012)	<i>I: Palvennia hoybergeti</i>	Figure 6e
PMO 222.668	11.8	Vertebrae, pelvic girdle	Disarticulated	Unknown		Pe	Figure 8c
PMO 222.659	9.5	Skull	Disarticulated	Unknown		I	
PMO 216.839	7	Almost complete	Partly articulated	Ventral	Knutsen <i>et al.</i> (2012c); Liebe & Hurum (2012)	<i>Pe: Djupedaliala engeri</i>	Figure 6a
PMO 224.252	7	Partial skull, ribs	Partly articulated	Dorsal	Under study	I	Figure 5e
PMO 222.662	-0.2	Pelvic girdle, femur, tail bend	Partly articulated	Unknown		I	Figure 7b
PMO 224.166	-0.2	Humerus, vertebrae	Disarticulated	Unknown		I	Figures 3e and 8a
PMO 222.654	-4	Partial skull, appendicular skeleton, vertebrae	Partly articulated	Right ventrolateral	Roberts <i>et al.</i> (2014)	<i>I: Janusaurus lundi</i>	Figure 6b
PMO 222.664	-4.4	Propodial, vertebrae	Disarticulated	Unknown		Pe	Figure 8b
PMO 222.667	-7	Partial skull, vertebrae, pectoral girdle, forefin	Partly articulated	Ventral	Roberts <i>et al.</i> (2014); under study	I	Figure 7a
PMO 214.452	-8	Forefins, hindfins, pelvic girdle, vertebrae	Disarticulated	Ventral	Under study	Pe	Figures 3f and 8f
PMO 222.666	-11	Vertebrae	Disarticulated	Unknown		Pe	
PMO 218.377	-31 to -22 or -15 to -11	Propodial, hindfin	Partly articulated	Unknown	Andreassen (2004); Knutsen <i>et al.</i> (2012a)	<i>Pe: Colymbosaurus svalbardensis</i>	
PMO 224.249	-51	Partial skull, vertebrae, partial fin	Disarticulated	Unknown		I	
PMO 222.657	Unknown	Vertebrae	Articulated	Unknown		Pe	
PMO 222.660	Unknown	Vertebrae	Disarticulated	Unknown		I	
PMO A27745	Unknown	Hindfins, pelvic girdle, vertebrae	Articulated	Dorsal	Persson (1962); Andreassen (2004); Knutsen <i>et al.</i> (2012a)	<i>Pe: Colymbosaurus svalbardensis</i>	Figure 4d

Slottsmøya Member marine reptile specimens collected 2004–2012 in stratigraphic order. Stratigraphic position measured above or below (–) the yellow layer (see sedimentary log in Fig. 2). I, ichthyosaur; Pe, plesiosauroid; Pi, pliosauroid. Figure references are to figures in this paper.



**Fig. 2.** Composite log of the marine reptile interval in the Slotsmøya Member in the Janusfjellet–Knorringsfjellet area. Lithology based on Collignon & Hammer (2012); isotope and TOC data from Hammer *et al.* (2012); foraminiferal zones from Hjalmsdóttir (2012) and Nagy & Basov (1998); all from Janusfjellet sections. Invertebrate abundance (qualitative) from the DH2 core, Longyearbyen.

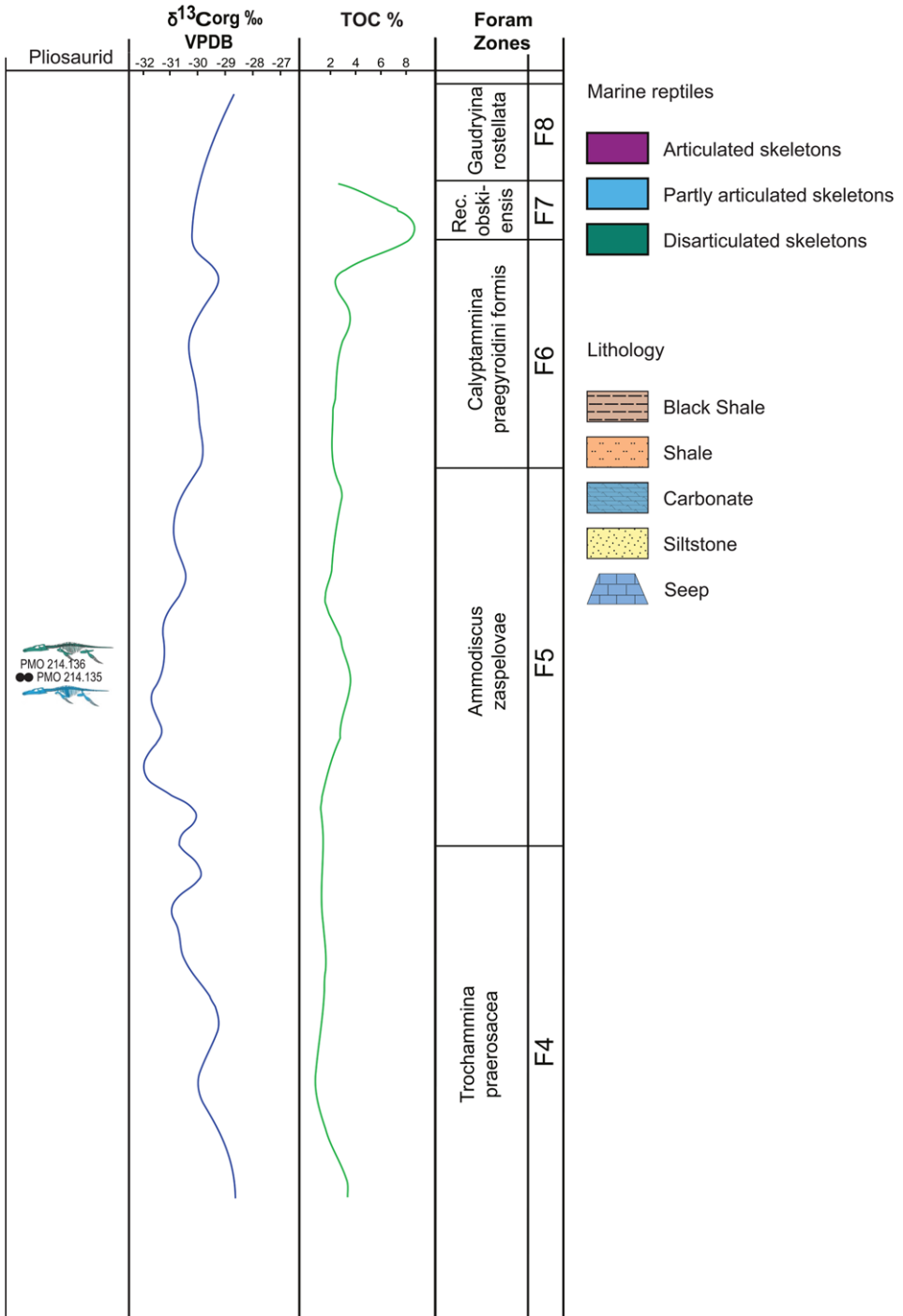
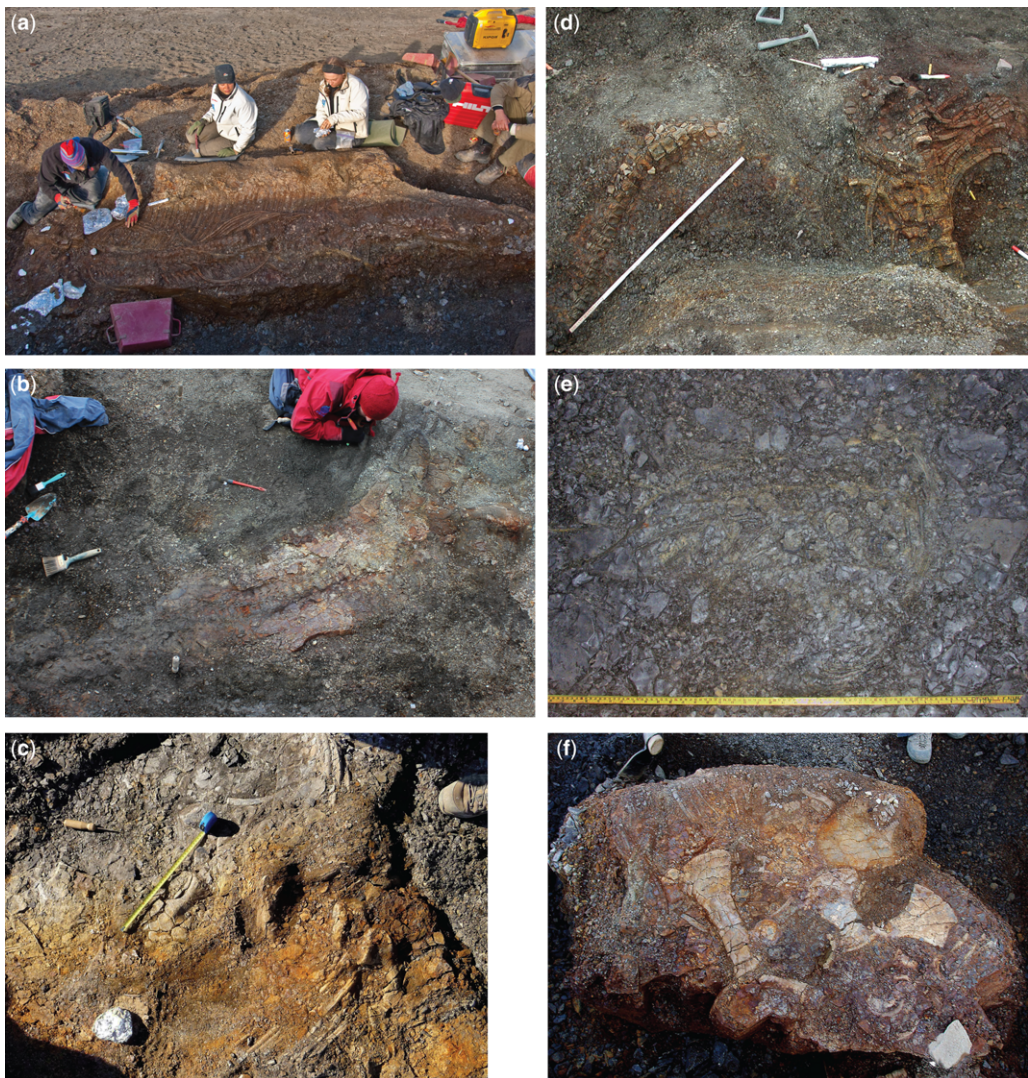


Fig. 2. Continued.





**Fig. 3.** Field photographs of selected specimens with different articulation status: (a) PMO 214.578, articulated ichthyosaur; (b) PMO 219.718, articulated plesiosauroid; (c) PMO 222.669, partly articulated ichthyosaur; (d) PMO 212.662/SVB 1452, partly articulated plesiosauroid; (e) PMO 224.166, disarticulated ichthyosaur; and (f) PMO 214.452, disarticulated plesiosauroid. Photographs by the SJRG.

that were unevenly distributed. TOC measurements were obtained from the DH2 core samples.

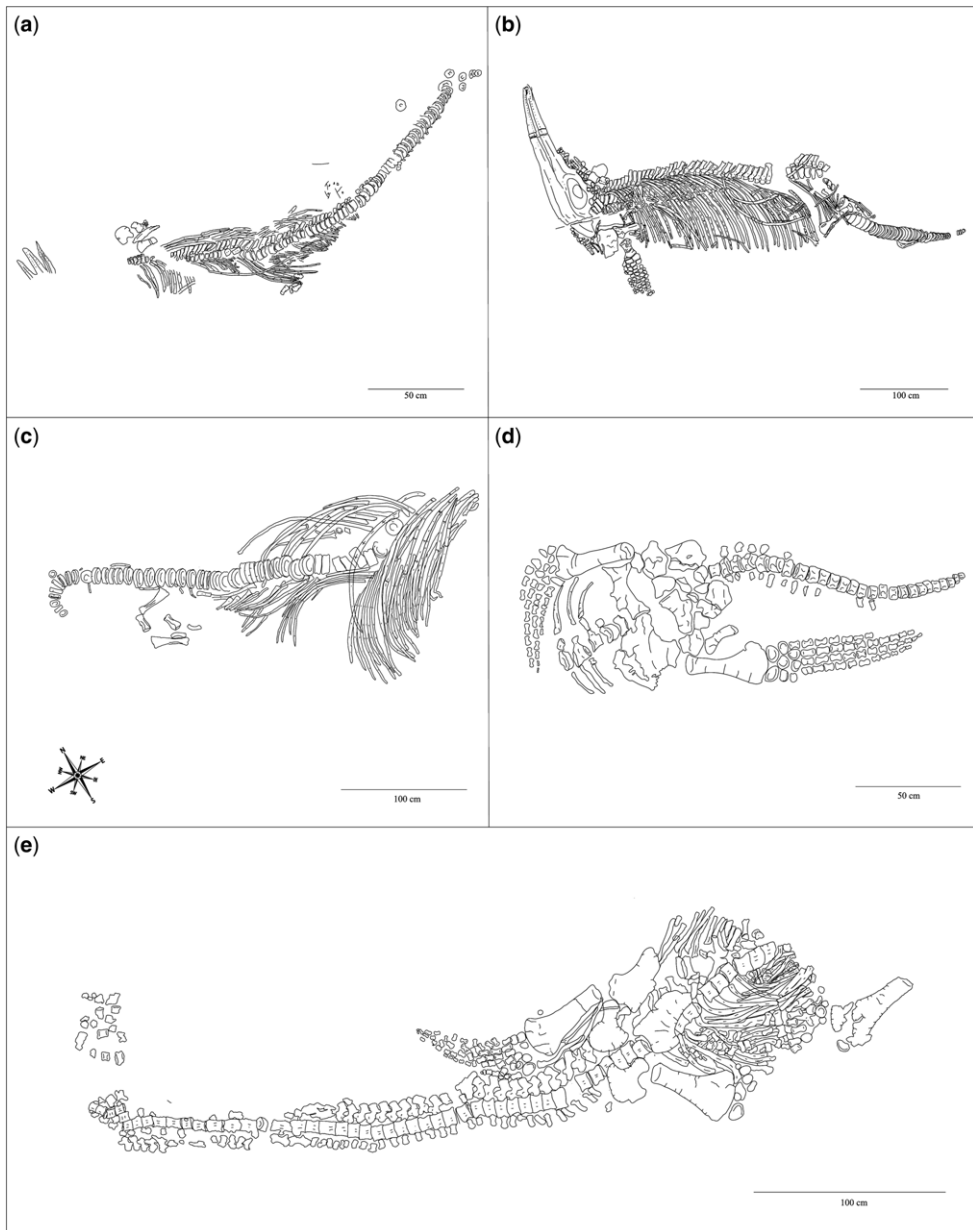
## Results and discussion

### *Articulation of marine reptile specimens*

**Articulated skeletons.** There are seven articulated skeletons among the Slottsmøya marine reptiles: ichthyosaurs ( $n = 3$ ) and plesiosauroids ( $n = 4$ )

(Figs 3a, b, 4 & 5a). Two ichthyosaurs (PMO 214.578, holotype of *Cryptopterygius kristiansenae* Druckenmiller *et al.*, 2012: Figs 3a & 4b; PMO 222.655: Fig. 4a) and one plesiosauroid (PMO 219.718: holotype of *Spitrasaurus wensaasi* Knutsen *et al.*, 2012b: Figs 3b & 4e) are nearly complete. PMO 214.578 lacks only the posterior portion of the tail, while PMO 219.718 lacks the skull in addition to the posterior portion of the skeleton lost to erosion. PMO 222.655 has only a few displaced vertebrae and neural arches, in addition

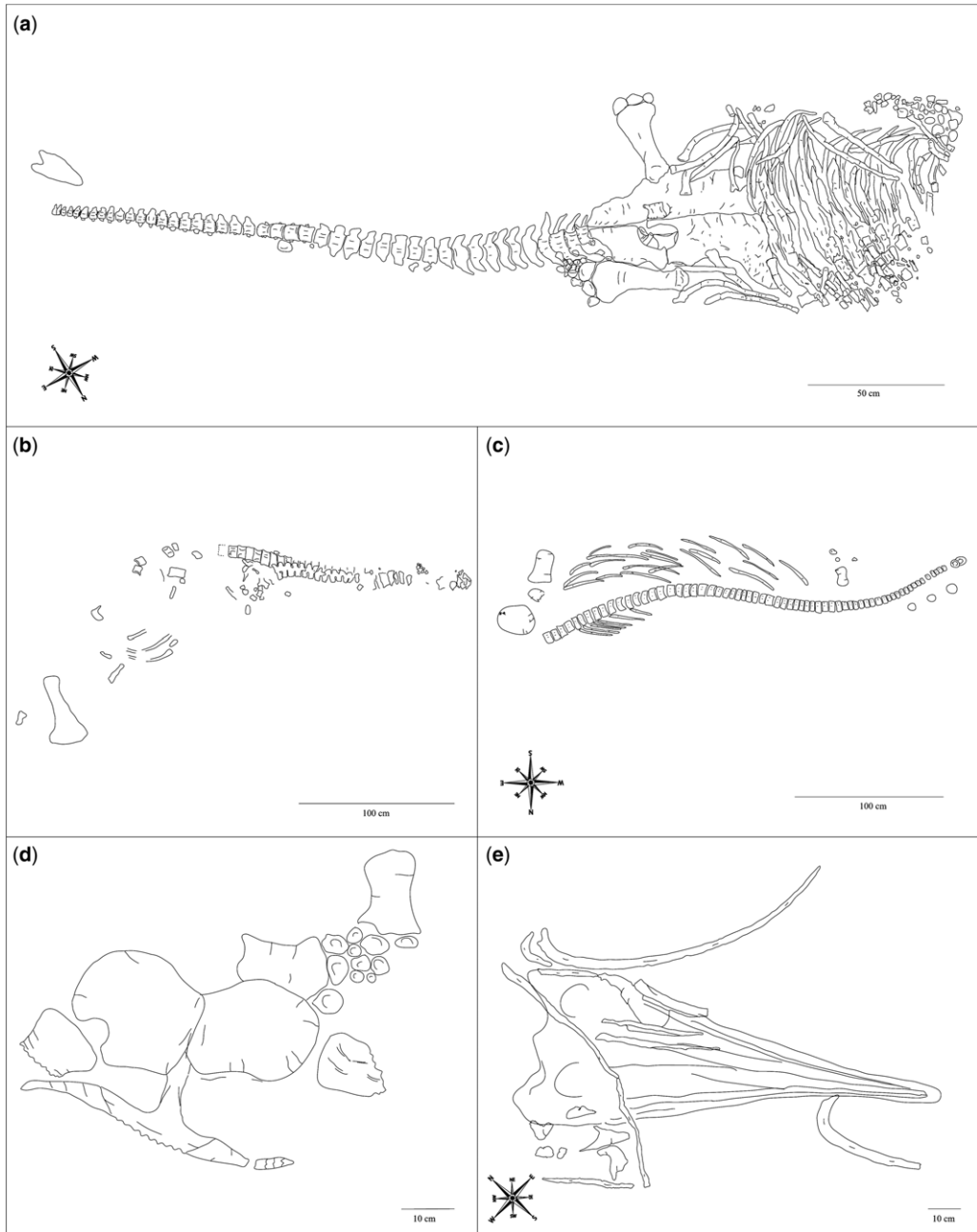




**Fig. 4.** Outlines of articulated marine reptile specimens from the Slottsmøya Member, Agardhfjellet Formation, Svalbard. The specimens are drawn from the side stratigraphically up unless otherwise stated. See Table 1 for more information on each specimen. (a) PMO 222.655, ichthyosaur, drawn from the side stratigraphically down. (b) PMO 214.578, holotype of the ichthyosaur *Cryopterygius kristiansenae*, drawn from the side stratigraphically down. (c) PMO 222.670, ichthyosaur. (d) PMO A27745, holotype of the plesiosauroid *Colymbosaurus svalbardensis*. (e) PMO 219.718, holotype of the plesiosauroid *Spitasaurus wensaasi*.

to the pelvic girdle, which was moved anteriorly from its original position. The rostrum was divided from the body by a fault, and was found about 30 cm

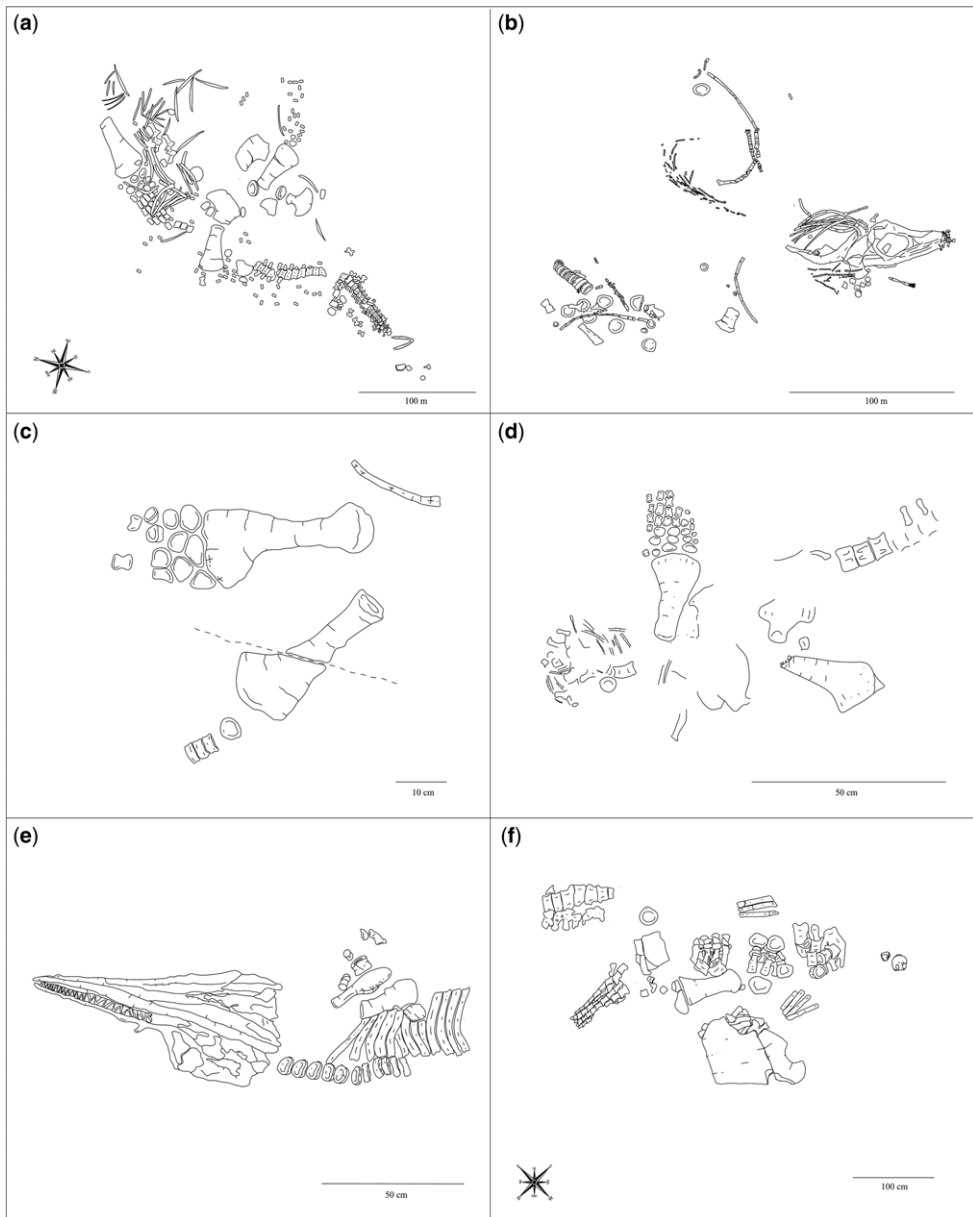
deeper. The preservation of the specimen is poor in the anterior part and improves posteriorly. PMO A27745 (Fig. 4d) is an articulated posterior



**Fig. 5.** Outlines of articulated and partly articulated marine reptile specimens from the Slotsmøya Member, Agardhfjellet Formation, Svalbard. The specimens are drawn from the side stratigraphically up unless otherwise stated. See Table 1 for more information on each specimen. (a) PMO 224.248, plesiosauroid. (b) PMO 222.671, plesiosauroid. (c) PMO 224.251, ichthyosaur. (d) PMO 224.250, ichthyosaur. (e) PMO 224.252, ichthyosaur.

portion of a plesiosauroid, collected in 1931 and described by Persson (1962) as *Tricleidus svalbardensis* and then later redescribed as *Colymbosaurus*

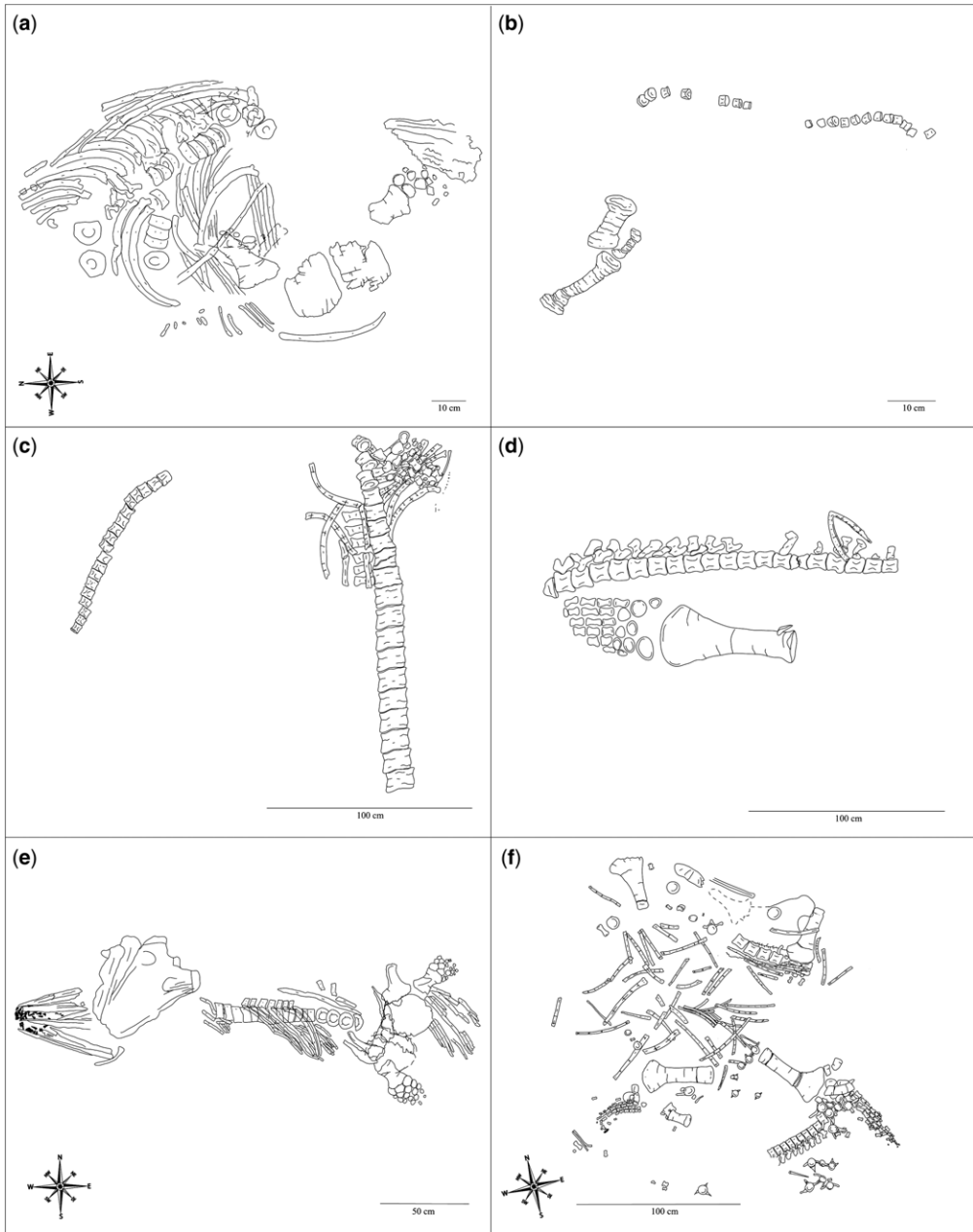
*svalbardensis* by Knutsen *et al.* (2012a). PMO 224.248 (Fig. 5a) is the only plesiosauroid skeleton from the Slotsmøya Member that preserves a



**Fig. 6.** Outlines of partly articulated marine reptile specimens from the Slottsmøya Member, Agardhfjellet Formation, Svalbard. The specimens are drawn from the side stratigraphically up unless otherwise stated. See Table 1 for more information on each specimen. **(a)** PMO 216.839, holotype of the plesiosauroid *Djupedalia engeri*. **(b)** PMO 222.654, holotype of the ichthyosaur *Janusaurus lundi*. **(c)** PMO 216.838, plesiosauroid, referred to *Colymbosaurus svalbardensis*. **(d)** PMO 224.247, plesiosauroid. **(e)** SVB 1451, holotype of the ichthyosaur *Palvemia hoybergeti*. **(f)** PMO 214.135, holotype of the pliosauroid *Pliosaurus funkei*.

complete and articulated skull. It is slightly displaced from the neck. PMO 222.670 (Fig. 4c) is the posterior half of a large ichthyosaur, while PMO 222.657 is an unfigured articulated series of

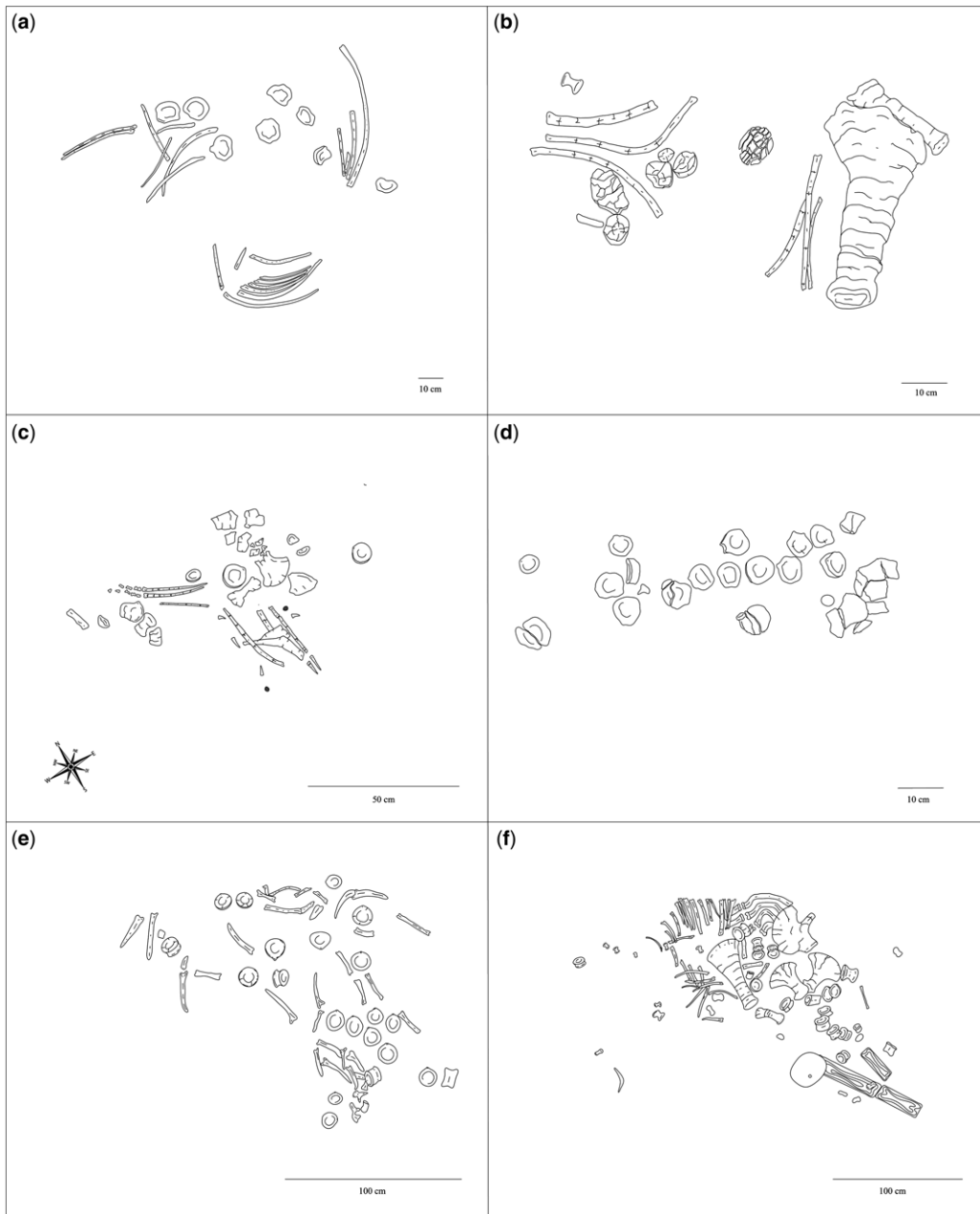
cervical vertebrae from a plesiosauroid. For PMO 222.670, PMO 224.248 and PMO A27745, approximately half of the skeleton is missing, probably due to erosion of the hillside.



**Fig. 7.** Outlines of partly articulated marine reptile specimens from the Slottsmøya Member, Agardhfjellet Formation, Svalbard. The specimens are drawn from the side stratigraphically up unless otherwise stated. See Table 1 for more information on each specimen. (a) PMO 222.667, ichthyosaur. (b) PMO 222.662, ichthyosaur. (c) PMO 212.662/SVB 1452, plesiosauroid. (d) SVB 1450, holotype of the plesiosauroid *Spitasaurus larseni*. (e) PMO 222.669, ichthyosaur. (f) PMO 222.663, plesiosauroid.

Some elements of the articulated skeletons have also undergone other types of post-mortem taphonomical alteration. In the ichthyosaur PMO

214.578, the skull is dorsoflexed at an angle of  $90^\circ$  relative to the long axis of the skeleton. In the pelvic area, there are some crushed vertebrae; in the

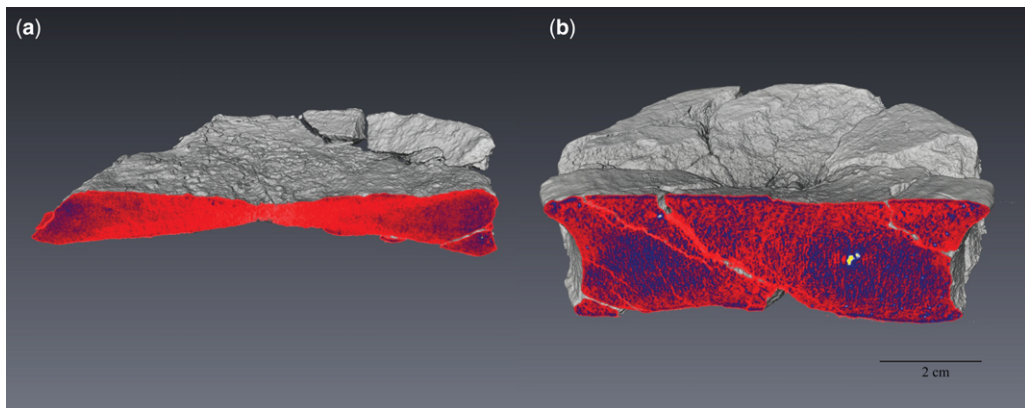


**Fig. 8.** Outlines of disarticulated marine reptile specimens from the Slottsmøya Member, Agardhfjellet Formation, Svalbard. The specimens are drawn from the side stratigraphically up unless otherwise stated. See Table 1 for more information on each specimen. (a) PMO 224.166, ichthyosaur. (b) PMO 222.664, plesiosauroid. (c) PMO 222.668, plesiosauroid. (d) PMO 222.658, ichthyosaur. (e) PMO 222.672, plesiosauroid. (f) PMO 214.452, plesiosauroid.

stomach area, the ribs on the right-hand side are bent inwards. The left forefin is completely articulated, while the right is partly disarticulated and displaced along the dorsal side of the skull. The left hindfin

is articulated, and is flipped posterodorsally on top of the sacral vertebral region. In the plesiosauroid PMO A27745, the right hindfin is articulated and lies parallel to the vertebral column, while the left





**Fig. 9.** Compressed and uncompressed vertebrae from ichthyosaur PMO 222.654, CT scan: (a) compressed vertebra; and (b) uncompressed vertebra. Colours show the X-ray density, with blue (pore-filling) denser than red (bone).

hindfin was rotated 180° and lies articulated in the opposite direction. The left forefin of the plesiosauroid PMO 219.718 is articulated with almost all of the phalanges in life position. In contrast, the right forefin is disarticulated, with the phalanges scattered along the left lateral part of the skeleton. The right femur is found at the posterior end of the specimen, close to the exposed surface, and the phalanges are scattered on top of the left lateral side.

*Partly articulated skeletons.* There are a total of 19 partly articulated skeletons including plesiosauroids ( $n = 9$ ), pliosaurid ( $n = 1$ ) and ichthyosaurs ( $n = 9$ ) (Figs 3c, d, 5b–e, 6 & 7). The plesiosauroid PMO 216.839 (holotype of *Djupedalica engeri* Knutsen, Druckenmiller & Hurum, 2012c) (Fig. 6a) is nearly complete, but lacks the skull, left hindfin and caudal vertebral series. The ichthyosaur SVB 1451 (Fig. 6e) is the holotype of *Palvennia hoybergeti* Druckenmiller, Hurum, Knutsen & Nakrem, 2012, and consists of a skull articulated to cervical vertebrae and ribs, associated with a partial clavicle, a partial humerus and some phalanges. SVB 1450 (Fig. 7d) is a plesiosauroid, and the holotype of *Spitrasaurus larseni* Knutsen, Druckenmiller & Hurum, 2012b. The specimen consists of an articulated fin, a partial vertebral series articulated to the neural arches, as well as the lower jaw, teeth and a few skull fragments.

Several of the skeletons were spread over large areas. PMO 222.654 (holotype of the ichthyosaur *Janusaurus lundi*) (Fig. 6b), with an estimated body length of 3–4 m (Roberts *et al.* 2014), had body elements scattered over an area of  $2 \times 2.5$  m, in four distinct clusters. The plesiosauroid PMO 222.663 (Fig. 7f), estimated body length of 6–7 m, was spread over an area of  $2.5 \times 3$  m. PMO 214.135 (holotype of the pliosaurid *Pliosaurus funkei* Knutsen, Druckenmiller & Hurum, 2012d)

(Fig. 6f), with an estimated body length of 10–13 m (Knutsen *et al.* 2012d), had groups of elements scattered over an area of  $4.6 \times 2.7$  m.

PMO 216.838 (Fig. 6c) is a plesiosauroid, referred to *Colymbosaurus svalbardensis* (Persson, 1962) in Knutsen *et al.* (2012a). The specimen had an unusual preservation as it was found in a siderite concretion, and is partially deformed. The plesiosauroid PMO 216.863 (unfigured) was found in a slumped block and tilted nearly vertically.

*Disarticulated skeletons.* Twelve disarticulated skeletons were collected from the Slottsmøya Member, including ichthyosaurs ( $n = 5$ ), a pliosaurid ( $n = 1$ ) and plesiosauroids ( $n = 6$ ) (Figs 3e, f & 8). Vertebrae, ribs and fins are the most frequently preserved body elements, while pelvic girdle elements, teeth and neural arches are less common. The plesiosauroid PMO 214.452 (Figs 3f & 8f) preserves both ischia closely associated with the right pubis, while elements from the body, particularly ribs and vertebrae, have been scattered around the pubis–ischia cluster. PMO 214.136, a referred specimen of *Pliosaurus funkei*, includes cranial remains that were probably articulated prior to burial, but were later displaced by slumping due to solifluction.

### Currents

Bottom currents can be responsible for the disarticulation of skeletons and loss of skeletal elements (Beardmore *et al.* 2012a), and the position of skeletal elements can be used to evaluate water movement and direction of flow (Barnes & Hiller 2010). Small light bones have the highest potential to be moved by currents. For the partly articulated and disarticulated specimens in this study, there is no clear pattern of sorting. Some of the ribs seem

to lie perpendicular to one another, which could indicate changes in current direction. In several of the skeletons, many of the distal phalanges lie scattered around the skeleton, although other phalanges in the same skeleton are articulated, possibly due to stronger ligaments in proximal parts of the fins. This is especially visible in the plesiosauroids PMO 216.839 (Fig. 6a) and PMO 222.663 (Fig. 7f). The phalanges of the plesiosauroid PMO 219.718 (Fig. 4e), all located in the body area of the animal, seem to have been orientated by a dominant current direction crossing the vertebral column. The torso of the plesiosauroid PMO 219.718 most probably hit the seafloor before the rest of the body, and sank down in the sediments. This left the lighter cervical vertebrae and skull on the sea bottom, and they were likely to have been exposed to current activity. Teeth from the skull of the plesiosauroid PMO 224.248 (Fig. 5a) drifted from the skull over the cervical vertebrae in a similar direction, while distal phalanges from one of the forefins were disarticulated in a different direction. This could be indicative of a difference in current direction.

#### *Distribution of the skeletons in the section*

In general terms, the sedimentary environment of the Slottsmøya Member shale is interpreted to be a dysoxic shelf with periods of oxygen influx to the sea bottom when coarser clastic sediments (silt and sand) were deposited as turbidites or by storm events (Collignon & Hammer 2012). TOC content is an important indicator of the environment near the seafloor. Hammer *et al.* (2012) found fluctuating TOC values in the Slottsmøya Member, with a distinct peak at the base of the member (–25 m, TOC value 3.6%), followed by a second peak (12 m, TOC value 4.2%) and a third peak (42 m, TOC value 9.7%) (Fig. 2). The 12 m peak falls within the zone of highest marine reptile abundance in the section, from approximately 10 to 20 m. Two of the seven articulated skeletons are also found in this interval. Nickel–vanadium measurements indicate conditions at the seafloor varying within the dysoxic range throughout the section, with a minimum value at approximately 5–10 m in the section (Collignon & Hammer 2012). No articulated skeletons were found in the interval below 10 m, which is lower in organic carbon content. TOC levels remain relatively high (ranging from 2.7 to 4.4%) from 20 m to the top of the interval prospected for vertebrates. Four articulated skeletons are found in this upper interval, the uppermost (PMO 222.655) close to the maximum TOC value at 42 m.

Figure 2 presents qualitative invertebrate fossil abundance from cores drilled for the CO<sub>2</sub> storage project in Longyearbyen, Svalbard, approximately 12 and 19 km from the excavation sites at

Janusfjellet and Knorringsfjellet, respectively. Correlation between outcrop and core is based on lithostratigraphy, biostratigraphy and organic carbon isotope curves. The majority of the benthic fauna consists of bivalves, but gastropods, brachiopods and scaphopods are also quite common in the Slottsmøya Member. There is a tendency for a negative correlation between bivalve and marine reptile abundance, with relatively few bivalves but some skeletons below 0 m, followed by maximum bivalve abundance and a gap in the vertebrate record from 0 to 6 m, then a gradual reduction in bivalve abundance as the vertebrates become more common around the second TOC peak at 12 m. The benthic faunal record therefore supports the hypothesis of poor oxygenation contributing to the high preservational potential of skeletons.

Hjalmarsdottir (2012) identified foraminiferal morphogroups in the Slottsmøya Member according to the classification scheme of Nagy *et al.* (2009). The main interval of vertebrate finds in the Slottsmøya Member is found between approximately –10 and 30 m in the sections. Hjalmarsdottir (2012) did not extend her study below –1.3 m, but from that level to 30 m she found a dominance of epifaunal species, with subordinate surficial/shallow infauna and occasional deep infauna, indicating a generally dysoxic environment. However, there is considerable stratigraphic variation: for example, Hjalmarsdottir (2012) recorded practically no infauna (i.e. highly dysoxic to anoxic according to Nagy *et al.* 2009) at –1.3, 0.8 and 10.9 m, while at 8.4, 14–18 and 30 m the infauna ranges from 20 to 40% (dysoxic). Together with the stratigraphic variation in lithology and geochemistry (Collignon & Hammer 2012), this indicates that while the seafloor was dysoxic in the vertebrate interval, there was considerable variation throughout the member, with excursions into both highly dysoxic/anoxic and low oxenic conditions at the seafloor.

#### *Floating and sinking*

Whether the marine reptiles floated after death, or sank immediately, is a question under debate (Reisdorf *et al.* 2012). It is density that controls whether a carcass sinks or refloats, but refloating might also be prevented by increased hydrostatic pressure, if the water is sufficiently deep (Allison *et al.* 1991). In modern cetaceans, the drift and refloating pattern varies with fat content: a whale carcass with a high fat content will drift in the surface waters immediately after death, while one with a low fat content will first sink, then possibly refloat as decay gases accumulate. Ichthyosaurs are regarded as sustained high-speed swimmers in the Mesozoic seas, and they were probably negatively buoyant (Holger 1992). Data obtained from studies on Recent cetaceans

show that a carcass may rise from water depths up to 50 m (Reisdorf *et al.* 2012). The Slottsmøya Member is regarded as an open-marine shelf environment (Dallmann 1999), with water depths estimated at between 100 and 150 m (Collignon & Hammer 2012). Similar conditions are also observed in the Posidonienschiefer Formation, with a shelf depth of 50–100 m (Röhl *et al.* 2001). Thus, the ichthyosaur carcasses preserved in these two *Lagerstätten* probably did not resurface.

Schäfer (1972) argued that marine mammals that die by natural causes might, under some circumstances, drift for weeks at the sea surface. When the connective tissue decayed, the skeletal elements would be spread over a large area by ocean currents and finally land on the seafloor as disarticulated bones or groups of bones (Schäfer 1972). Observations of decaying dolphins show that the integument tears first where the mechanical stress is strongest. These areas include the roof of the skull, the margins of the lower jaw, above the scapula and in the tail section. The trachea sometimes supports the connection between the skull and the body for a while (Schäfer 1972). The pliosaurid PMO 214.135 (Fig. 6f) is thought to have been partly disarticulated before it landed on the seabed (Knutsen *et al.* 2012d), and probably decayed whilst floating in the ocean. The porous structure of its vertebrae suggests that they were oil-filled, similar to those of some cetaceans (Kihle *et al.* 2012). This could explain the preservation of only parts of the skeleton, as a longer floating period would advance the decay. The disarticulated specimens PMO 224.166 (Figs 3e & 8a), PMO 222.664 (Fig. 8b), PMO 222.668 (Fig. 8c), PMO 222.658 (Fig. 8d), PMO 222.672 (Fig. 8e) and PMO 214.452 (Figs 3f & 8f) might all represent parts from carcasses that floated for a prolonged period of time post mortem.

Most of the marine reptile skeletons in the Posidonienschiefer Formation are complete but partially disarticulated. The slight disarticulation was for a long time explained by the expansion of internal gases in the gut region, causing the carcass to explode, ejecting bones and internal organs, and leaving a disarticulated carcass (Keller 1976; Martill 1993). However, Reisdorf *et al.* (2012) showed that it is unlikely that skeletal elements from a vertebrate could have been scattered in this way only by the release of putrefaction gases under hydrostatic or atmospheric pressures.

While the ichthyosaur neck and skull resemble those of dolphins, plesiosauroids possess a greatly elongated neck, which narrows towards the skull, so that less connective tissue supports the head. The connection between the atlas–axis complex and the basioccipital was small, and the skull was probably one of the first elements to detach from a decaying animal floating in the water. The majority

of the plesiosauroid skeletons from Slottsmøya were found without cranial material, as is the case for several other localities, such as from the Upper Cretaceous Pembina and Sharon Spring members in the USA (Carpenter 2006). While some of the crania were likely to have been lost due to surface erosion prior to discovery, several skeletons appear to have lost the cranium prior to burial, during the ‘bloat and float’ decompositional phase described by Schäfer (1972). The plesiosauroid PMO 219.718 (Figs 3b & 4e) possesses an articulated skeleton, including all but the anteriormost cervical vertebrae, but lacks a skull. The skull must have been lost during early decay, either in the floating phase or just after settling at the seafloor. The specimen must have had a short post-mortem floating period, since most of the skeletal elements are present. A single plesiosauroid specimen, PMO 224.248 (Fig. 5a), has a complete, articulated skull, while PMO 212.662/SVB 1452 (Figs 3d & 7c) and SVB 1450 (Fig. 7d) retain some skull elements. The skull of PMO 224.248 has disarticulated from the atlas–axis and drifted 10–20 cm away from the anterior cervicals. This is highly unusual and could illustrate the earliest stage of post-mortem skull drifting. An Upper Cretaceous elasmosaurid plesiosauroid from North Canterbury, New Zealand described by Barnes & Hiller (2010) was discovered missing the skull. They suggested that it probably disarticulated prior to the carcass reaching the seafloor, either being removed by a predator or scavenged shortly after death. It could have also been detached during the early stage of the ‘bloat and float’ phase, an interpretation also suggested for the Pembina and Sharon Spring plesiosaurs (Carpenter 2006) and the Triassic sauropterygian *Serpianosaurus* (Beardmore *et al.* 2012b). Barnes & Hiller (2010) also suggested that the head and neck could be transported for a distance after it detached from the torso. This is true for sauropod dinosaurs, where articulated necks are often found without the rest of the skeleton (e.g. Wedel *et al.* 2000), but this is not observed in the Slottsmøya specimens, where the necks are usually associated with the body.

### Landing

The original body shape and the decompositional state of the carcass upon hitting the seafloor affect the orientation of the preserved skeleton (Martill 1986). Complete or near-complete carcasses land in five different positions: dorsally, laterally, ventrally, anteriorly and posteriorly (Martill 1993). Esperante *et al.* (2002) studied fossil whales from the Miocene–Pliocene Pisco Formation in Peru, and found an equal number of dorsally and ventrally landed skeletons. Of more than 500 specimens, only

two skeletons were found in a lateral position, which could be related to the instability of the whale carcass on the seafloor (Esperante *et al.* 2009). Skeletons may also land laterally and secondarily be moved into a dorsal or ventral position. Martill (1993) observed that ichthyosaurs from the Posidonienschiefer Formation more often had lateral than dorsal landings, and suggested that specimens landing dorsally often rolled over to a lateral position.

**Dorsal landings.** Specimens landing dorsally often possess a perfectly articulated vertebral column (Martill 1993). Decaying whales floating in the water tend to rotate, leaving the heavier dorsal side down due to intestinal gas build-up in the abdominal cavity (Schäfer 1972), but whether this affects the final mode of deposition is difficult to predict. Three plesiosauroids (PMO 219.718: Figs 3b & 4e; PMO 212.662/SVB 1452: Figs 3d & 7c; PMO A27745: Fig. 4d), one pliosaurid (PMO 214.135: Fig. 6f), and four ichthyosaurs (PMO 222.655: Fig. 4a; PMO 224.251: Fig. 5c; SVB 1451: Fig. 6e; PMO 224.252: Fig. 5e) from the Slottsmøya Member are interpreted to have landed dorsally. The ichthyosaur PMO 222.655 probably landed dorsally, and later experienced lateral torsion.

**Lateral landings.** Two ichthyosaur specimens (PMO 222.670: Fig. 4c; PMO 222.654: Fig. 6b) from the Slottsmøya Member are preserved laterally. PMO 222.654 had a ventrolateral landing. In a lateral landing, there is often a distinct preservation difference between the upper and lower surface of the skeleton, and the preservation of the limbs on the stratigraphically down side is usually better preserved than on the opposite side (Martill 1993). This is seen in the ichthyosaur PMO 222.654 (Fig. 10b–d).

**Ventral landings.** In a ventral landing, the skeleton often shows all four limbs articulated. Because of decomposition of the ligament of the vertebral column, the vertebral centra will drop to the seabed, often resulting in a partly or completely disarticulated vertebral column (Martill 1993). Six plesiosauroids (PMO 224.248: Fig. 5a; SVB 1450: Fig. 7d; PMO 224.247: Fig. 6d; PMO 222.663: Fig. 7f; PMO 216.839: Fig. 6a; PMO 214.452: Figs 3f & 8f) and two ichthyosaurs (PMO 224.250: Fig. 5d; PMO 222.667: Fig. 7a) from the Slottsmøya Member show this mode of preservation.

**Anterior landings.** In an anterior landing, the skull lands first and can penetrate into the sediment. Two ichthyosaur specimens (PMO 214.578: Figs 3a & 4b; PMO 222.669: Figs 3c & 7e) in this study are interpreted to have had an anterior landing. The anterior part of the rostrum of PMO 222.669 is damaged and filled with more than 50 teeth, most of which have been displaced. This specimen

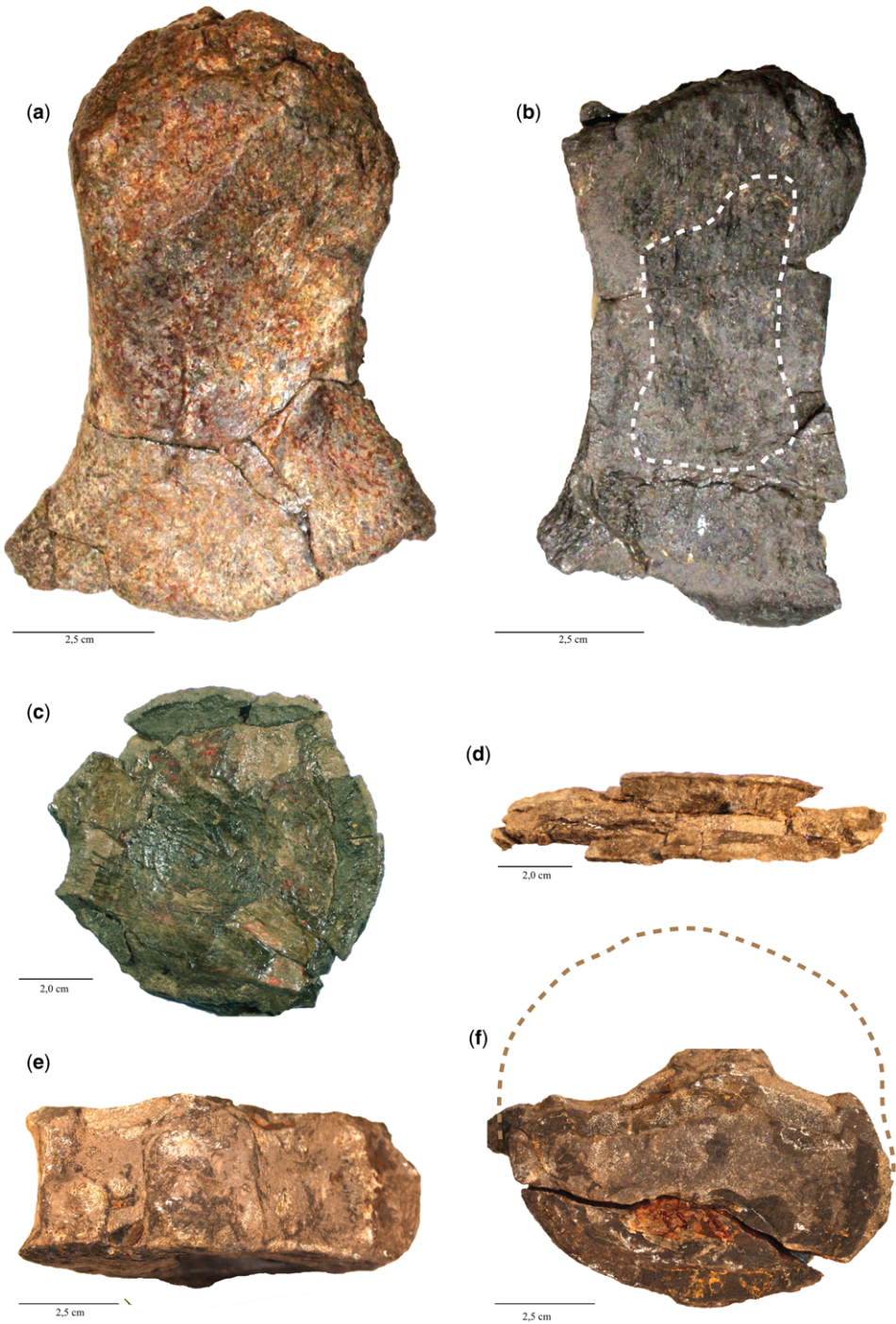
probably experienced a head-first landing, where the rostrum penetrated the sediment and broke, and its pieces and teeth were pressed posteriorly into the remaining parts of the jaw. An anterior landing was also found in an *Ophthalmosaurus* specimen from the Redwater Shale Member, with its skull at a 90° angle to the bedding. The rostrum was split open and broken (Wahl 2009), in contrast to the specimens in this study. In the Lower Jurassic of the Jura Mountains in Switzerland, a vertically emplaced skull was found connected to the postcranial skeleton. The fins restricted further penetration of the animal into the sediment (Wetzel & Reisdorf 2007).

For most of the specimens collected from the Slottsmøya Member, the landing mode cannot be easily assessed owing to a high degree of disarticulation. In specimens where this can be analysed, dorsal ( $n = 8$ ) and ventral ( $n = 8$ ) landings are the most common modes. For plesiosauroids, dorsal ( $n = 4$ ) and ventral ( $n = 6$ ) landings are the only types experienced. The reason for this is probably the plesiosauroid body shape, with large flat fins on the sides of the body, a torso that is broader than high and a small head. Ichthyosaurs, however, in addition to ventral and dorsal landings, experienced lateral ( $n = 2$ ) and anterior ( $n = 2$ ) landings. This is also thought to be related to a large head, taller body, fewer large fins and a dorsoventrally expanded tail. None of the specimens landed posteriorly, nor are such landings known for ichthyosaurs (Martill 1993), nor, to our knowledge, for plesiosauroids. The cause for this, presumably, is the heavier anterior part in ichthyosaurs and the above-explained body shape for plesiosauroids.

#### *Predation, scavengers and associated invertebrates*

The cause of death of any fossil organism is often difficult to assess. Normal causes of death for whales and dolphins are related to predators, parasites and hazards at birth. Death by old age or illness is rare (Schäfer 1972). Evident bite marks, scars on the bones or missing skeletal elements are observed in many of the Oxford Clay Formation specimens, and this could indicate predation or scavenging (Martill 1986). Evidence for predation or scavenging is also seen in whales: for example, in the occurrence of bite marks on the skull of a baleen whale skeleton in the Lower Pliocene Huelva Sands Formation (Corral *et al.* 2004). Most ichthyosaurs and plesiosauroids were not predators of large-bodied vertebrates in the Mesozoic seas, and were certainly a target for predation by pliosaurids and chondrichthyans (Martill 1996). In the Upper Jurassic Kimmeridge Clay, ichthyosaur vertebrae are





**Fig. 10.** Compaction and erosion of bones: (a) lateral view of the left femur of PMO 214.578; (b) lateral view of the left femur of PMO 222.654 with the outline of the eroded area; (c) anterior surface of the compressed vertebra of PMO 222.654; (d) ventral side of the compressed vertebra of PMO 222.654; (e) right lateral side of the eroded vertebra from PMO 214.578; and (f) anterior side of vertebra of PMO 214.578 with the outline of the eroded bone mass.



frequently found with bite marks, some of which are thought to be from pliosaurids (Martill 1996), as is the case for one skull of the Early Cretaceous elasmosaur *Eromangasaurus australis* (Sachs, 2005) (Thulborn & Turner 1993). Interestingly, chondrichthyans have not been found in the Slottsmøya Member.

To predict whether elements are missing as a result of scavenging or predation is difficult (Martill 1986). Most of the *Lagerstätten* with marine vertebrates were deposited in anoxic seafloor environments, which potentially limit the ability for macro-organisms to scavenge carcasses (Allison 1988). Whether the carcass is floating or settled on the seabed, scavengers are often responsible for its disarticulation (Martill 1986). Fragmented remains found near articulated specimens are believed to be the result of scavenging, and some of the marine reptile specimens from the Oxford Clay are possible examples (Martill 1985).

Few of the Slottsmøya marine reptiles show traces of predation or scavenging. In the plesiosauroid PMO 222.663, a belemnite was observed beside its articulated vertebral column, and an ammonite was found in the stomach area of the ichthyosaur PMO 214.578. Both of these findings could indicate scavenging by invertebrates during the 'mobile scavenger stage' (Smith & Baco 2003). The plesiosauroid SVB 1450 had an ichthyosaur tooth lying on top of a neural arch in the cervical region. The plesiosauroid PMO 224.248 had several ichthyosaur teeth located on top of and next to the cervical vertebrae, but the vertebrae were not displaced in any way. In the ichthyosaur PMO 222.654, a gracile plesiosauroid tooth was found close to the disarticulated humerus, but no obvious bite marks are visible, and the observed tooth is more adapted for feeding on soft-bodied organisms such as cephalopods (Roberts *et al.* 2014).

The bivalve *Buchia* is by far the most common invertebrate found close to the skeletons. It is found on the plesiosauroids PMO 212.662/SVB 1452, PMO 224.248 and PMO 222.663, and the ichthyosaurs PMO 222.670 and PMO 222.669. On PMO 222.670, some serpulids were also found. In the plesiosauroid PMO 219.718 and in the pliosaurid PMO 214.135, segments of ophiuroids were lying close to the bones. These associations could indicate part of the enrichment/opportunist stage, which often involves smaller organisms such as invertebrates and bacteria (Smith & Baco 2003), but it is uncertain as we do not know whether the organisms used the bones as a substrate.

### Oxygenation

When a carcass lands on the seabed, sediment firmness, sedimentation rate, presence of currents,

scavengers, epifauna and the oxygen level at the seafloor affect the preservation of the carcass. Rapid burial and low oxygen levels are often regarded as key elements for excellent preservation of skeletons (Seilacher *et al.* 1985; Brett & Baird 1986; Allison 1989).

The Posidonienschiefer Formation contains many well-preserved marine reptiles, together with more disarticulated specimens (Martill 1993). The sediment is described as a laminated organic-rich mud rock with a TOC ranging from 2 to 15% (Littke *et al.* 1991; Martill 1993). The marine reptiles preserved with soft tissue and body outlines are thought to have been exposed to rapid burial, either in soupy sediments or by episodic sedimentation followed by early diagenesis (Allison 1989; Martill 1993). Whether the Posidonienschiefer Formation was oxic or anoxic is debated. Kaufmann (1981) argued that the seafloor and the first few centimetres of the water column were anoxic, and only the part of the animal reaching above this anoxic level would be fed on. In contrast, Seilacher (1982) believed that the seafloor was occasionally oxic, with an anoxic water column.

The Oxford Clay Formation shows excellent preservation of marine reptiles. Most of the specimens were deposited in the Peterborough Member, described as an organic-rich mudstone (Tang 2002) with a TOC of 0.5–16% (Kenig *et al.* 1994). The Peterborough Member is thought to represent a soupy sediment, owing to the lack of burrowing organisms (Tang 2002), and this has been invoked to explain the preservation of soft parts (Martill 1985).

The Posidonienschiefer Formation and the Oxford Clay Formation in many ways resemble the Slottsmøya Member in being deposited on a dys-oxic shelf with some beds consisting of reworked sediments such as siltstones to very-fine-grained sandstones with a low sedimentation rate (Collignon 2011). In the Oxford Clay Formation, a positive correlation between the articulation of marine reptiles and the TOC content in the sediments is observed, as in the Slottsmøya Member. It was suggested that high productivity in the water column and low oxygenation levels at depth in the Oxford Clay Formation prevented scavenging and decay (Martill 1985). Except for a thin coal seam observed around some parts of the pliosaurid PMO 214.135, and possible stomach content in the plesiosauroids PMO 214.452 and PMO 222.663, no soft tissue or body outline has been observed on the Slottsmøya Member marine reptiles.

### Bone preservation

The stratigraphic up and down sides of marine reptile specimens from the Posidonienschiefer

Formation demonstrate two very different preservation styles. While the down side (typically the visible prepared surface) is well preserved, the upper side is comparatively eroded by sediment particles in suspension and partly disarticulated by currents (Martill 1993; Reisdorf *et al.* 2012, 2014). The same pattern is also shown in a mysticete cetacean carcass from the Lower Pliocene (Esperante *et al.* 2009).

For the ichthyosaur PMO 222.654, a similar distinct difference in preservation can be seen. The lower side of the bones is better preserved than the upper surface. For example, the left femur is eroded with a flattened upper surface and, when comparing it to that of a well-preserved femur of the ichthyosaur PMO 214.578 (Fig. 10a), the damage is clearly evident. A vertebra from PMO 214.578 is eroded on its right lateral side, the one stratigraphically up (Fig. 10e, f). These specimens indicate soupy sediment where the skeleton partly sank into the sea bottom, but the reason for the erosion is not known.

### *Burial, compaction and diagenesis*

The deformation and flattening of the bones of marine reptiles from the Posidonienschiefer Formation has been studied by several authors (e.g. Martill 1993). This shale has a high organic content and a sedimentation rate of  $4 \text{ mm ka}^{-1}$  (compacted state: Reisdorf *et al.* 2014). The specimens are usually severely flattened during the compaction of the sediment, but early formations of calcareous concretions around fossils prevent the compaction in rare cases (Martill 1993; Reisdorf *et al.* 2012).

Some compaction is observed in the skeletons from the Slottsmøya Member, but to a lesser extent than in the Posidonienschiefer. Within the same specimen, the skeletal elements range from some being almost completely flattened to others retaining their original 3D shape. This is clearly evident in the plesiosauroid PMO 219.718, in which the skeleton has undergone dorsoventral compression: some neck vertebrae are flattened, whereas others are elongated to more than twice the normal length through brittle deformation and regrowth of barite in the cracks. Several of the compacted vertebrae of the ichthyosaur PMO 222.654 were deposited flat on the bedding plane, with one of their articular surfaces facing stratigraphically down, and experienced strong anteroposterior compaction (Figs 9 & 10c, d). This is also present in the plesiosauroid PMO 222.663, where areas of the pectoral girdle and vertebrae are significantly compacted, whereas other regions are completely uncompact. CT scans of vertebrae from PMO 222.654 (Fig. 9) indicate that the 3D vertebrae contain early precipitated

minerals like calcite and barite in the pores, while the compressed vertebrae lack this.

A study of three-dimensionally preserved bones of *Pliosaurus funkei* (PMO 214.135 and PMO 214.136) in thin sections revealed that the pore structures of the bones are mineralized mainly by barite, and to a lesser extent by calcite (Kihle *et al.* 2012). The earliest phase of permineralization is calcite followed by barite in these specimens. The unusually large amount of early diagenetic barite in the pore structure of bones from Slottsmøya Member seems to be crucial for their 3D preservation. Barite in the ocean is known to precipitate in the water column, on the seafloor or within marine sediments. The barite solubility increases with pressure and temperature up to  $100^\circ\text{C}$  (Griffith & Paytan 2012). Fluids enriched in barite may be driven out of the sediment and into the pore structure of the buried bones during compaction or tectonic processes. Large volumes of remobilized barite in highly reducing, organic-rich sediments are mostly related to cold fluid seepage (Torres *et al.* 2003). The presence of cold-seep carbonates *in situ* at the top of Slottsmøya Member (Hryniewicz *et al.* 2012) is evidence for methanogenesis, which could be the mechanism for the remobilization of barite by lowering of porewater sulphate concentration.

Collignon & Hammer (2012) published inductively coupled plasma mass spectrometry (ICP-MS) results that revealed two stratigraphic levels with a high content of barium in the Slottsmøya Member. The first one at the base level (0 m) occurs as a white to yellowish coating of barite on macroinvertebrate fossils. The second is in the uppermost part of the section at approximately 48 m. Collignon & Hammer (2012) interpreted this as either an indicator of a high influx of biogenic material into the sediments or, alternatively, due to cold-seep venting.

Evidence for a very early precipitation of barite in the bones of PMO 214.135 and PMO 214.136 are the major sections of recrystallization of the barite showing weak autofluorescence due to tension or stress from deep burial and tectonics on the skeleton after mineralization (Kihle *et al.* 2012). Aqueous and hydrocarbon-bearing fluid inclusions (HCFI) occur in both calcite and barite, and provide information on burial depth and temperature. Kihle *et al.* (2012) performed microthermometry on 115 inclusions, of which 65 were HCFI. Most primary aqueous inclusions in barite homogenize within a temperature of homogenization ( $T_h$ ) of  $105\text{--}107^\circ\text{C}$ , with Gaussian tails in the range of  $T_h$   $101\text{--}115^\circ\text{C}$ . This is exactly the temperature where barite solubility starts to decrease, following Griffith & Paytan (2012). The secondary aqueous inclusions tend to homogenize at somewhat lower temperatures than their primary counterpart, at a  $T_h$

range of 89–91°C. Later trains of hydrocarbon-bearing fluid inclusions were found to homogenize within 47–71°C (Kihle *et al.* 2012) and are formed during the brittle deformation of the primary barite crystals during the uplift. The primary aqueous inclusions and the hydrocarbon-bearing fluid inclusions revealed a continuous lowering of the minimum trapping temperature, indicative of an uplift scenario with a maximum burial of 2800–3000 m (Kihle *et al.* 2012).

## Conclusions

This paper provides a description of the taphonomy of marine reptiles found in the Slottsmøya Member from the Upper Jurassic on Svalbard. The taphonomical descriptions of the specimens were divided into three preservation categories, where seven skeletons were categorized as articulated, 19 skeletons as partly articulated and 12 skeletons categorized as disarticulated. Eight of the marine reptiles landed dorsally, eight ventrally, two anteriorly and two laterally.

The distribution of marine reptiles in the section is analysed, and a correlation between high total organic content, low oxygen levels, few benthic invertebrates and good reptile preservation is observed. A TOC peak centred at 12 m (TOC value of 4.2%) correlates with the highest abundance of marine reptiles, from approximately 10 to 20 m in the section (Fig. 2).

The Slottsmøya Member preserves the marine vertebrates with a high degree of three-dimensionality, in contrast to several other *Lagerstätten*. In this paper, we suggest a new explanatory model for vertebrates in shale with a high compaction rate under the influence of cold-seep venting:

- (1) landing of marine reptiles at the dysoxic sea bottom at a water depth of about 150 m (Collignon & Hammer 2012);
- (2) slow burial with a sedimentation rate of 11 mm ka<sup>-1</sup> (compacted state: Hammer *et al.* 2012), with erosion of exposed parts and partial disarticulation by currents;
- (3) large accumulation of organic-rich mud leading to microbial degradation of organic carbon and, hence, methanogenesis (Torres *et al.* 2003). Cold seepage starts;
- (4) porewater sulphate is consumed by oxidation of methane and organic carbon (Suess & Whiticar 1989);
- (5) barite dissolves owing to sulphate depletion;
- (6) fluid migration and dissolution of calcite/aragonite due to the early compaction of sediments, with some calcite precipitated in the pores of the bones;
- (7) barite precipitated in the pore structure of the bones;
- (8) the seepage ends;
- (9) the formation of siderite nodules in layers with more sand (Collignon & Hammer 2012);
- (10) large amounts of sediments from the Cretaceous and Lower Cenozoic bury the skeletons to a maximum depth of 3000 m;
- (11) secondary trains of fluid inclusions formed during the uplift state. Brittle deformation of the bones and recrystallization of the barite and calcite occurs.

May-Liss Knudsen Funke, Bjørn Lund, Lena Kristiansen and Victoria Engelschön Nash are thanked for their assistance in the preparation of the specimens. Sincere thanks are also due to the Spitsbergen Jurassic Research Group, which aided in the excavation of the specimens, with a special thanks to the volunteers Magne Høyberget, Øyvind Enger, Stig Larsen, Tommy Wensås and Bjørn Funke. Grants for the excavations were provided by the Polar Institute, the Norwegian Research Council, the Ministry of Education and Research, and National Geographic (EC-0435-9 and EC-0425-09). The sponsors for the excavations are thanked: Spitsbergen Travel, ExxonMobil, Fugro, the Norwegian Petroleum Directorate, Statoil, Bultas, PowerShop, OMV, Helseport, Nexen, Bayerngas, Lividi, Telenor, Simula, forskning.no, Directconnect and livestream.com. This study is, in part, based on a Master thesis by Linn K. Novis. LLD and MJK are supported by PhD grants from the Ministry of Education and Research via the Natural History Museum, University of Oslo. LKN is supported by a PhD grant from the University in Tromsø. AJR is supported by PhD grants from Tullow Oil, NERC and the University of Southampton. Two anonymous reviewers added valuable comments that helped to improve the manuscript.

## References

- ALLISON, P. A. 1988. The role of anoxia in decay and mineralization of proteinaceous microfossils. *Paleobiology*, **14**, 139–154.
- ALLISON, P. A. 1989. Konservat-Lagerstätten: cause and classification. *Paleobiology*, **14**, 331–334.
- ALLISON, P. A., SMITH, C. R., KUKERT, H., DEMING, J. W. & BENNETT, B. A. 1991. Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the bathyal Santa Catalina basin. *Paleobiology*, **17**, 78–89.
- ANDREASSEN, B. H. 2004. *Plesiosaurs from Svalbard*. Master thesis, University of Oslo.
- BARNES, K. M. & HILLER, N. 2010. The taphonomic attributes of a Late Cretaceous plesiosaur skeleton from New Zealand. *Alcheringa*, **34**, 333–344.
- BEARDMORE, S. R., ORR, P. J., MANZOCCHI, T. & FURRER, H. 2012a. Float or sink: modelling the taphonomic pathway of marine crocodiles (Mesoeucrocodylia, Thalattosuchia) during the death–burial interval. *Palaeobiodiversity and Palaeoenvironments*, **92**, 83–98.

- BEARDMORE, S. R., ORR, P. J., MANZOCCHI, T., FURRER, H. & JOHNSON, C. 2012*b*. Death, decay and disarticulation: modelling the skeletal taphonomy of marine reptiles demonstrated using *Serpianosaurus* (Reptilia; Sauropterygia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **337–338**, 1–13.
- BIRKENMAJER, K. 1980. Jurassic–Lower Cretaceous succession at Agardhbukta, East Spitsbergen. *Studia Geologica Polonica*, **66**, 35–52.
- BIRKENMAJER, K., PUGACZEWSKA, H. & WIERZBOWSKI, A. 1982. The Janusfjellet Formation (Jurassic–Lower Cretaceous) at Myklegardfjellet, East Spitsbergen. *Palaeontologica Polonica*, **43**, 107–140.
- BRETT, C. E. & BAIRD, G. C. 1986. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. *Palaios*, **1**, 207–227.
- CARPENTER, K. 2006. Comparative vertebrate taphonomy of the Pembina and Sharon Springs Members (Middle Campanian) of the Pierre Shale, Western Interior. *Paludicola*, **5**, 125–149.
- COLLIGNON, M. 2011. *Sedimentological analysis of the Slottsmøya Member, Agardhfjellet Formation (Late Jurassic–Early Cretaceous) in the Janusfjellet area, Spitsbergen*. Master thesis, University of Oslo.
- COLLIGNON, M. & HAMMER, Ø. 2012. Lithostratigraphy and sedimentology of the Slottsmøya Member at Janusfjellet, central Spitsbergen: evidence for a condensed section. *Norwegian Journal of Geology*, **92**, 89–101.
- CORRAL, J. C., PEREDA-SUBERBIOLA, X. & BARDET, N. 2004. Shark bite marks in a mosasaur vertebra from the Late Cretaceous of Álava (Basque–Cantabrian Region). *Revista Española de Paleontología*, **19**, 23–32.
- DALLMANN, W. K. 1999. Outline of the geological history of Svalbard. In: DALLMANN, W. K. (ed.) *Lithostratigraphic Lexicon of Svalbard. Upper Palaeozoic to Quaternary Bedrock. Review and Recommendations for Nomenclature Use*. Norwegian Polar Institute, Tromsø, 17–24.
- DALLMANN, W. K., MAJOR, H., HAREMO, P., ANDERSEN, A., KLÆRNET, T. & NØTTVEDT, A. 2001. *Geological Map of Svalbard 1:100,000, Sheet C9G Adventdalen*. Norwegian Polar Institute, Temakart, **31/32**, 4–55.
- DRUCKENMILLER, P. S., HURUM, J. H., KNUTSEN, E. M. & NAKREM, H. A. 2012. Two new ichthyosaurs (Ichthyosauria: Ophthalmosauridae) from the Agardhfjellet Formation (Upper Jurassic: Volgian), Svalbard, Norway. *Norwegian Journal of Geology*, **92**, 311–339.
- DYPVIK, H., NAGY, J. *ET AL.* 1991. The Janusfjellet Subgroup (Bathonian to Hauterivian) on Central Spitsbergen: a revised lithostratigraphy. *Polar Research*, **9**, 21–43.
- EFIMOV, V. M. 2001. On the taphonomy of Late Jurassic and Early Cretaceous Ichthyosaurs from the Volga Region near Ulyanovsk. *Paleontological Journal*, **35**, 188–190.
- ESPERANTE, R., BRAND, L. R., CHADWICK, A. & POMA, O. 2002. Taphonomy of fossil whales in the diatomaceous sediments of the Miocene/Pliocene Pisco Formation, Peru. In: DE RENZI, M., PARDO ALONSO, M. V., BELINCHÓN, M., PEÑALVER, E., MONTOYA, P. & MÁRQUEZ-ALIAGA, A. (eds) *Current Topics on Taphonomy*. Ayuntamiento de Valencia, Valencia, 337–343.
- ESPERANTE, R., GUINEA MUNIZ, F. & NICK, K. E. 2009. Taphonomy of a mysticeti whale in the Lower Pliocene Huelva Sands Formation (southern Spain). *Geologica Acta*, **4**, 489–505.
- GRIFFITH, E. M. & PAYTAN, A. 2012. Barite in the ocean – occurrence, geochemistry and palaeoceanographic applications. *Sedimentology*, **59**, 1817–1835.
- HAMMER, O., NAKREM, H. A. *ET AL.* 2011. Hydrocarbon seeps close to the Jurassic–Cretaceous boundary, Svalbard. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **306**, 15–26.
- HAMMER, Ø., COLLIGNON, M. & NAKREM, H. A. 2012. Organic carbon isotope chemostratigraphy and cyclostratigraphy in the Volgian of central Spitsbergen. *Norwegian Journal of Geology*, **92**, 103–112.
- HAMMER, Ø., HRYNIEWICZ, K., HURUM, J. H., HØYBERGET, M., KNUTSEN, E. M. & NAKREM, H. A. 2013. Large onychites (cephalopod hooks) from the Upper Jurassic of the Boreal Realm. *Acta Palaeontologica Polonica*, **58**, 827–835.
- HJALMARSOTTIR, H. R. 2012. *Foraminifera from Upper Jurassic–Lower Cretaceous hydrocarbon seep carbonates and adjacent shales in the Slottsmøya Member, central Spitsbergen*. Master thesis, University of Oslo.
- HOLGER, J. A. 1992. Taphonomy and paleoecology of *Shonisaurus popularis* (Reptilia: Ichthyosauria). *Palaios*, **7**, 108–117.
- HRYNIEWICZ, K., HAMMER, Ø., NAKREM, H. A. & LITTLE, C. T. S. 2012. Microfacies of the Volgian–Ryazanian (Jurassic–Cretaceous) hydrocarbon seep carbonates from Sassenfjorden, central Spitsbergen, Svalbard. *Norwegian Journal of Geology*, **92**, 113–131.
- HRYNIEWICZ, K., NAKREM, H. A., HAMMER, Ø., LITTLE, C. T. S., KAIM, A., SANDY, M. R. & HURUM, J. H. 2014. The palaeoecology of the latest Jurassic–earliest Cretaceous hydrocarbon seep carbonates from Spitsbergen, Svalbard. *Lethaia*, **48**, 353–374, <http://doi.org/10.1111/let.12112>
- HURUM, J. H., NAKREM, H. A., HAMMER, Ø., KNUTSEN, E. M., DRUCKENMILLER, P. S., HRYNIEWICZ, K. & NOVIS, L. K. 2012. An Arctic Lagerstätte – the Slottsmøya Member of the Agardhfjellet Formation (Upper Jurassic–Lower Cretaceous) of Spitsbergen. *Norwegian Journal of Geology*, **92**, 55–64.
- HURUM, J. H., ROBERTS, A. J., NAKREM, H. A., STENLØKK, J. A. & MØRK, A. 2014. The first recovered ichthyosaur from the Middle Triassic of Edgeøya, Svalbard. *Norwegian Petroleum Directorate Bulletin*, **11**, 97–110.
- KAUFMANN, E. G. 1981. Ecological reappraisal of the Posidonienschiefer (Toarcian) and the stagnant basin model. In: GRAY, J. (ed.) *Communities of the Past*. Hutchinson Ross Publishing, Stroudsburg, PA, 311–381.
- KEAR, B. & MAXWELL, E. E. 2013. Wiman's forgotten plesiosaurs: the earliest recorded sauropterygian fossils from the High Arctic. *GFF*, **135**, 95–103.
- KELLER, T. 1976. Magen- und Darminhalte von Ichthyosauriern des süddeutschen Posidonienschiefers. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **5**, 266–283.
- KENIG, F., HAYES, J. M., POPP, B. N. & SUMMONS, R. E. 1994. Isotopic biogeochemistry of the Oxford Clay Formation (Jurassic), UK. *Journal of the Geological*



- Society, London*, **151**, 139–152, <http://doi.org/10.1144/gsjgs.151.1.0139>
- KIHLE, J., HURUM, J. H. & LIEBE, L. 2012. Preliminary results on liquid hydrocarbons occurring as fluid inclusions in intracellular mineral precipitates in bones of the Late Jurassic *Pliosaurus funkei*, central Spitsbergen. *Norwegian Journal of Geology*, **92**, 341–352.
- KNUTSEN, E. M., DRUCKENMILLER, P. S. & HURUM, J. H. 2012a. Redescription and taxonomic clarification of ‘*Tricleidus svalbardensis*’ based on new material from the Agardhfjellet Formation (Middle Volgian), central Spitsbergen, Norway. *Norwegian Journal of Geology*, **92**, 175–186.
- KNUTSEN, E. M., DRUCKENMILLER, P. S. & HURUM, J. H. 2012b. Two species of long-necked plesiosaurians (Reptilia-Sauropterygia) from the Upper Jurassic (Middle Volgian) Agardhfjellet Formation of central Spitsbergen, Norway. *Norwegian Journal of Geology*, **92**, 187–212.
- KNUTSEN, E. M., DRUCKENMILLER, P. S. & HURUM, J. H. 2012c. A new plesiosauroid (Reptilia–Sauropterygia) from the Agardhfjellet Formation (Middle Volgian) of central Spitsbergen, Norway. *Norwegian Journal of Geology*, **92**, 213–234.
- KNUTSEN, E. M., DRUCKENMILLER, P. S. & HURUM, J. H. 2012d. A new species of *Pliosaurus* (Sauropterygia: Plesiosauria) from the Middle Volgian, central Spitsbergen, Norway. *Norwegian Journal of Geology*, **92**, 234–258.
- LARSEN, L. 2012. Summary of well test results from DH4, DH5, DH6, DH5R and DH7a. Paper presented at the Longyearbyen CO<sub>2</sub> Lab International Workshop, 17–20 September 2012, Longyearbyen, Norway.
- LIEBE, L. & HURUM, J. H. 2012. Gross internal structure and microstructure of Late Jurassic plesiosaur limb bones, central Spitsbergen. *Norwegian Journal of Geology*, **92**, 285–310.
- LITKE, R., LEYTHAEUSER, D., RULLKÖTTER, J. & BAKER, D. R. 1991. Keys to the depositional history of the Posidonia Shale (Toarcian) in the Hills Syncline, Northern Germany. In: TYSON, R. V. & PEARSON, T. H. (eds) *Modern and Ancient Continental Shelf Anoxia*. Geological Society, London, Special Publications, **58**, 311–333, <http://doi.org/10.1144/GSL.SP.1991.058.01.20>
- MARTILL, D. M. 1985. The preservation of marine vertebrates in the Lower Oxford Clay (Jurassic) of central England. *Philosophical Transactions of the Royal Society of London*, **311**, 155–165.
- MARTILL, D. M. 1986. The stratigraphic distribution and preservation of fossil vertebrates in the Oxford Clay of England. *Mercian Geologist*, **10**, 161–186.
- MARTILL, D. M. 1993. Soupy substrates: a medium for the exceptional preservation of ichthyosaurs of the Posidonia Shale (Lower Jurassic) of Germany. *Kaupia: Darmstädter Beiträge zur Naturgeschichte*, **2**, 77–97.
- MARTILL, D. M. 1996. Fossils explained 17: ichthyosaurs. *Geology Today*, **12**, 194–196.
- MARTILL, D. M., TAYLOR, M. A., DUFF, K. L., RIDING, J. B. & BOWN, P. R. 1994. The trophic structure of the biota of the Peterborough Member, Oxford Clay Formation (Jurassic), U.K. *Journal of the Geological Society, London*, **151**, 173–194, <http://doi.org/10.1144/gsjgs.151.1.0173>
- MAXWELL, E. E. & KEAR, B. P. 2013. Triassic ichthyopterygian assemblages of the Svalbard archipelago: a reassessment of taxonomy and distribution. *GFF*, **135**, 85–94.
- MØRK, A., DALLMANN, W. K. ET AL. 1999. Mesozoic lithostratigraphy. In: DALLMANN, W. K. (ed.) *Lithostratigraphic Lexicon of Svalbard. Upper Palaeozoic to Quaternary Bedrock. Review and Recommendations for Nomenclature Use*. Norwegian Polar Institute, Tromsø, 127–214.
- NAGY, J. & BASOV, V. A. 1998. Revised foraminiferal taxa and biostratigraphy of Bathonian to Ryazanian deposits in Spitsbergen. *Micropaleontology*, **44**, 217–255.
- NAGY, J., REOLID, M. & RODRÍGUEZ-TOVAR, F. J. 2009. Foraminiferal morphogroups in dysoxic shelf deposits from the Jurassic of Spitsbergen. *Polar Research*, **28**, 214–221.
- PERSSON, P. O. 1962. Plesiosaurians from Spitsbergen. In: *Norwegian Polar Institute Yearbook 1961*. Tromsø, 62–68.
- REISDORF, A. G., BUX, R. ET AL. 2012. Float, explode or sink: postmortem fate of lung-breathing marine vertebrates. *Palaeobiodiversity and Palaeoenvironments*, **92**, 67–81.
- REISDORF, A., ANDERSON, G. ET AL. 2014. Reply to ‘Ichthyosaur embryos outside the mother body: not due to carcass explosion but to carcass implosion’ by van Loon (2013). *Palaeobiodiversity and Palaeoenvironments*, **94**, 487–494, <http://doi.org/10.1007/s12549-014-0162-z>
- ROBERTS, A. J., DRUCKENMILLER, P. S., SÆTRE, G.-P. & HURUM, J. H. 2014. A New Upper Jurassic Ophthalmosaurid Ichthyosaur from the Slottsmøya Member, Agardhfjellet Formation of Central Spitsbergen. *PLoS ONE*, **9**, e103152, <http://doi.org/10.1371/journal.pone.0103152>
- ROUSSEAU, J. & NAKREM, H. A. 2012. An Upper Jurassic boreal echinoderm Lagerstätte from Janusfjellet, central Spitsbergen. *Norwegian Journal of Geology*, **92**, 133–148.
- RÖHL, H.-J., SCHMID-RÖHL, A., OSCHMANN, W., FRIMMEL, A. & SCHWARK, L. 2001. Erratum to ‘The Posidonia Shale (Lower Toarcian) of SW-Germany: an oxygen-depleted ecosystem controlled by sea level and palaeoclimate’. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **169**, 273–299.
- SACHS, S. 2005. *Tuarangisaurus australis* sp. nov. (Plesiosauria: Elasmosauridae) from the Lower Cretaceous of northeastern Queensland, with additional notes on the phylogeny of the Elasmosauridae. *Memoirs of the Queensland Museum*, **50**, 425–440.
- SCHÄFER, W. 1972. *Ecology and Paleocology of Marine Environments*. Oliver & Boyd, Edinburgh.
- SEILACHER, A. 1982. Ammonite shells as habitats in the Posidonia Shale of Holzmaden-floats or benthic islands? *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **2**, 98–114.
- SEILACHER, A., REIF, W. E. & WESTPHAL, F. 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten. In: WHITTINGTON, H. B. & CONWAY MORRIS, S. (eds) *Extraordinary Fossil Biotas: Their Ecological and Evolutionary Significance*. Cambridge University Press, Cambridge, 5–23.



- SMITH, C. R. & BACO, A. R. 2003. Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology*, **41**, 311–354.
- Suess, E. & WHITICAR, M. J. 1989. Methane-derived CO<sub>2</sub> in pore fluids expelled from the Oregon subduction zone. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **71**, 119–136.
- TANG, C. M. 2002. Oxford Clay: England's Jurassic marine park. In: BOTTJER, D. J., ETTER, W., HAGADORN, J. W. & TANG, C. M. (eds) *Exceptional Fossil Preservation. A unique View on the Evolution of Marine Life*. Columbia University Press, New York, 307–325.
- THULBORN, T. & TURNER, S. 1993. An elasmosaur bitten by a pliosaur. *Modern Geology*, **18**, 489–501.
- TORRES, M. E., BOHRMANN, G., DUBRÉ, T. E. & POOLE, F. G. 2003. Formation of modern and Paleozoic stratiform barite at cold methane seeps on continental margins. *Geology*, **31**, 897–900, <http://doi.org/10.1130/G19652.1>
- WAHL, W. R. 2009. Taphonomy of a nose dive: bone and tooth displacement and mineral accretion in an ichthyosaur skull. *Paludicola*, **7**, 107–116.
- WEDEL, M. J., CIFELLI, R. L. & SANDERS, R. K. 2000. Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*. *Acta Palaeontologica Polonica*, **45**, 343–388.
- WETZEL, A. & REISDORF, A. G. 2007. Ichnofabrics elucidate the accumulation history of a condensed interval containing a vertically emplaced ichthyosaur skull. In: BROMLEY, R. G., BUATOIS, L. A., MÁNGANO, G., GENISE, J. F. & MELCHOR, R. N. (eds) *Sediment–Organism Interactions: Multifaceted Ichnology*. SEPM Special Publications, **88**, 241–251.
- WIERZBOWSKI, A., HRYNIEWICZ, K., HAMMER, Ø., NAKREM, H. A. & LITTLE, C. T. S. 2011. Ammonites from hydrocarbon seep carbonate bodies from the Uppermost Jurassic–Lowermost Cretaceous of Spitsbergen and their biostratigraphical importance. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **262**, 267–288.
- WIMAN, C. 1914. Ein Plesiosaurierwirbel aus dem jüngeren Mesozoicum Spitzbergens. *Bulletin of the Geological Institute, Upsala*, **12**, 201–204.