

New marine reptile fossils from the Oxfordian (Late Jurassic) of Greenland

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Original Article

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Abstract

Knowledge about marine reptile diversity and disparity during the Late Jurassic is increasing. This contribution describes marine reptile skeletal elements (ichthyosaur and plesiosaur) from Kingofjeld mountain in NE Greenland. The assemblage is early Late Oxfordian (Late Jurassic) in age, and consists of *c.* 100 disarticulated skeletal elements. The location is of biogeographic importance as it was at the time situated between the Boreal realm and the Tethys Sea and is promising in terms of future prospecting.

1. Introduction

In the Mesozoic, marine ecosystems were dominated by aquatic reptiles that were descended from terrestrial ancestors, among them plesiosaurs and ichthyosaurs (Kelley & Pyenson, 2015). Ichthyosaur and plesiosaur fossils from the Late Jurassic – Early Cretaceous have been discovered and recovered from localities more or less all around the globe, and have attracted increasing interest in recent years, but several questions remain about their evolution, ecology and geographical distribution (Fischer *et al.* 2016; Foffa *et al.* 2018).

An increasing number of marine reptiles have been described from high-latitude localities (e.g. Fernández & Talevi, 2014; Delsett *et al.* 2016; Zverkov & Efimov, 2019). Although Greenland is a huge island with widespread Jurassic and Cretaceous deposits in the eastern part that have been the subject of research for decades, records of marine reptiles are relatively few (Marzola *et al.* 2018). The study of the Jurassic succession and its fossils in Greenland (Fig. 1) goes back to the report of Madsen (1904), and has since received a lot of attention, so far culminating in the publication of *The Jurassic of Denmark and Greenland* (Ineson & Surlyk, 2003). The first mention of marine reptile fossils was from Milne Land (Aldinger, 1935) (Fig. 1b), of fossils that were later formally described as a plesiosaur (Huene, 1935; redescribed by Smith, 2007). From Milne Land a single Late Jurassic ichthyosaur was collected at Pernaryggen in 1970 (NHMD 74798 at the Natural History Museum of Denmark (Marzola *et al.* 2018)) (Fig. 1b). A single plesiosaur propodial was found in 1998 at Kilen in eastern North Greenland (Fig. 1) (Dypvik *et al.* 2002; Milan, 2009).

Data on marine reptiles from the east coast of Greenland provide significant information from a key area situated between the Boreal areas and the Tethys Sea (present-day Great Britain). Oxfordian marine reptiles are known from the UK, and connected localities in the Tethys, such as Greenland, are important to gain a clearer picture of biogeography and evolution at the time, especially in relation to a suggested climate control over marine reptile distribution (Foffa *et al.* 2018). The objective of this work is to present a short report of Late Jurassic marine reptiles recently discovered in the Uggvik Ravine Member (Bernbjerg Formation) in NE Greenland. The fossils were found on Kuhn Ø during reconnaissance in 2017 (Figs 1, 2). The assemblage includes plesiosauroid, ichthyosaurian and unidentified fossils. Skeletal remains from Wollaston Forland reported by Maync (1947) are possibly from a correlative stratigraphical level as the new material from Kingofjeld (Fig. 1c).

2. Geological setting

The fossil assemblage described in this paper was found in the Upper Jurassic on Kingofjeld mountain, Kuhn Ø, NE Greenland (Figs 1, 2). The Jurassic succession in the area was deposited in the Wollaston Forland Basin (Surlyk, 1977, 1978, 2003). The basin formed during the initial phase of rifting in the Middle Jurassic that reached a maximum in the Volgian. In the Middle Jurassic a peneplaned basement was transgressed by the sea and the first marine deposition took place since the Permian. The westward-tilted fault block controlled the palaeogeographic setting. Peninsulas or islands formed at the emerged block crest towards the east and deposition took place in an embayment with sediment input mainly from the embayment head in the north (Surlyk, 2003). Shallow marine sandstones of the Middle Jurassic Pelion Formation were deposited in high-energy environments directly on the crystalline basement (Maync, 1947; Surlyk, 1977, 2003), though fluvial deposition locally took place in incised valleys (Bastians Dal

Formation, Kuhn Ø; Alsgaard *et al.* 2003). During rising sea level in the Middle and Late Jurassic, deposition forms an overall backstepping pattern.

The Pelion Formation is overlain by the heterolithic Jakobsstigen Formation in central Wollaston Forland (Surlyk, 1977; Vosgerau *et al.* 2000; Surlyk, 2003) and by the Payer Dal Formation in northern Wollaston Forland and on Kuhn Ø (Alsgaard *et al.* 2003). The Payer Dal Formation is an overall coarsening-upwards unit with heterolithic offshore transition deposits and shoreface sandstone deposits. Both formations are overlain by the Ugpik Ravine Member of the Bernbjerg Formation (Fig. 3). The Ugpik Ravine Member forms a transitional unit from the underlying sand succession to the black, laminated shales of the Bernbjerg Formation deposited in an offshore environment when the depositional system was totally drowned (Surlyk, 2003).

The age of the assemblage is early late Oxfordian provided by the associated ammonites. Only a few metres above the base of the Ugpik Ravine Member, an imprint of *Decipia lintonensis* indicates the Ilovaikii subzone of the Glosense Zone (Callomon & Birkelund, 1980). An ammonite from the vertebrate-bearing level, and also contained within the sample number 590347, is *Amoeboceras transistorium*, also indicative of the Ilovaikii subzone.

3. Material and methods

Fieldwork on Kuhn Ø in July 2017 included the finding of numerous skeletal elements of marine vertebrates within a limited area on the western slope of Kingofjeld towards Payer Dal in southern Kuhn Ø (N 74°44'46.7", W 20°12'14.3"), NE Greenland (Figs 1, 2). Disarticulated vertebrae have been found by previous workers at the same locality on at least two separate occasions (J Therkelsen and F Surlyk, respectively, pers. comm. 2017). Maync (1947) described the succession at Kingofjeld, but even though his observations are rather detailed he did not find, or at least did not report, any vertebrate fossils.

The assemblage described here was associated with the occurrence of numerous eye-catching, large, belemnite rostra, whereas the vertebrae were less conspicuous. More than 100 skeletal fragments were collected. Most of the material is contained within one sample number (GEUS 590347), and subsequently specimens within that sample were assigned separate subnumbers (e.g. 590347-1). Figured specimens (Fig. 4) are stored in the Natural History Museum of Denmark (NHMD) type collection and have thus been assigned with NHMD numbers.

All specimens were found disarticulated on the surface on a plateau formed by the recessive, relatively fine-grained sandstones of the Ugpik Ravine Member overlying the coarser-grained sandstones of the Payer Dal Formation (Figs 2, 3). Pebbles at the fossiliferous belemnite-vertebrate level indicate some degree of reworking processes during deposition of the Ugpik Ravine Member (Fig. 3). This is also indicated by the fossil assemblage, which contains fragments from numerous specimens suggesting deposition after transport. The material has been subject to long-term weathering, generally resulting in relatively poor preservation. However, most of the skeletal elements are three-dimensional and do not appear compressed. Many elements are too worn or fragmentary to establish any referral, even to animal group. Two of these (GEUS 590347-100 and -101) clearly differ in morphology and microstructure (visible in cross-section) from ichthyosaurs and plesiosaurs, and might represent metacarpals or phalanges from a turtle. However, as there is little and fragmentary material, a formal description and referral is not conducted here. If the fragments originate from a turtle, it might

have biogeographical implications as turtles are found in Late Jurassic localities with ichthyosaurs and/or plesiosaurs in, for example, Poland, Argentina and Mexico (Alvarado-Ortega *et al.* 2014; Gasparini *et al.* 2015; Blazejowski *et al.* 2016), but not in the Late Jurassic – Early Cretaceous Slottsmøya Member Lagerstätte at Spitsbergen (Delsett *et al.* 2016; Fernández *et al.* 2018).

4. Systematic palaeontology

Reptilia Laurenti, 1768

Ichthyopterygia Owen, 1840

Ichthyosauria de Blainville, 1835

Note: All ichthyosaurs known from the Late Jurassic belong to the family Ophthalmosauridae, except the poorly known lineage of *Malawania anachronus* (Fischer *et al.* 2013; Fernández & Campos, 2015). The ichthyosaurian remains from Kingofjeld very likely belong to the former family, but cannot be referred with certainty because skull, fin and girdle material is lacking.

4.a. Referred specimens

Twenty-five complete and 44 incomplete vertebrae (GEUS 590347-1–72, except -26, -27 and -28), rib fragments (GEUS 590347 84–98) and a single distal limb element (GEUS 590347-27) (Fig. 4c–f).

4.b. Description

4.b.1. Distal limb element

The element (GEUS 590347-27) might represent a carpal, distal carpal metacarpal or phalanx (McGowan & Motani, 2003). It is oval as in some ophthalmosaurids such as *Ophthalmosaurus icenicus* (Moon & Kirton, 2016) but in contrast to others, e.g. *Undorosaurus? kristiansenae* (Druckenmiller *et al.* 2012; Zverkov & Efimov, 2019), where distal limb elements are more rectangular. The element is missing parts of its surface and no further description is possible.

4.b.2. Vertebrae (Fig. 4c–f)

The vertebrae are referred to Ichthyosauria because they are deeply biconcave, anteroposteriorly shorter than dorsoventrally tall, with neural arches not fused to the centra. The dorsal surface has facets for the neural arches on each side of the flattened area for the neural canal. The centra bear one or two rib facets on the lateral surface. The morphology of the vertebrae is typical of that seen in Ophthalmosauridae, but no formal criteria are in place for referring single vertebrae to the family. Some of the vertebrae are well preserved, whereas many possess a partly or completely eroded surface and/or margins. Many are broken into two or more pieces, but generally show few signs of compression.

Based on the position of apophyses on the lateral surfaces and the overall shape, 18 of the most complete vertebrae can be assigned to specific regions of the vertebral column (Buchholtz, 2001; McGowan & Motani, 2003) (Table 1). The assemblage includes centra from all regions: cervical (Fig. 4c, d), dorsal (not figured), anterior caudal (Fig. 4e) posterior caudal from the preflexural (Fig. 4f) and anterior fluke regions (not figured). Cervical vertebrae bear two facets on the lateral surface; the dorsalmost one is confluent with the neural arch facet. Two of these centra (GEUS 590347-03 and -06) have a more angled ventral margin in anterior view and appear pentagonal compared to some of the others (GEUS 590347-01 and -08), where the ventral margin is rounded. The vertebra from the dorsal region (GEUS 590347-15) possesses two facets for articulation with the ribs on the lateral surface, in a more ventral position than for the more

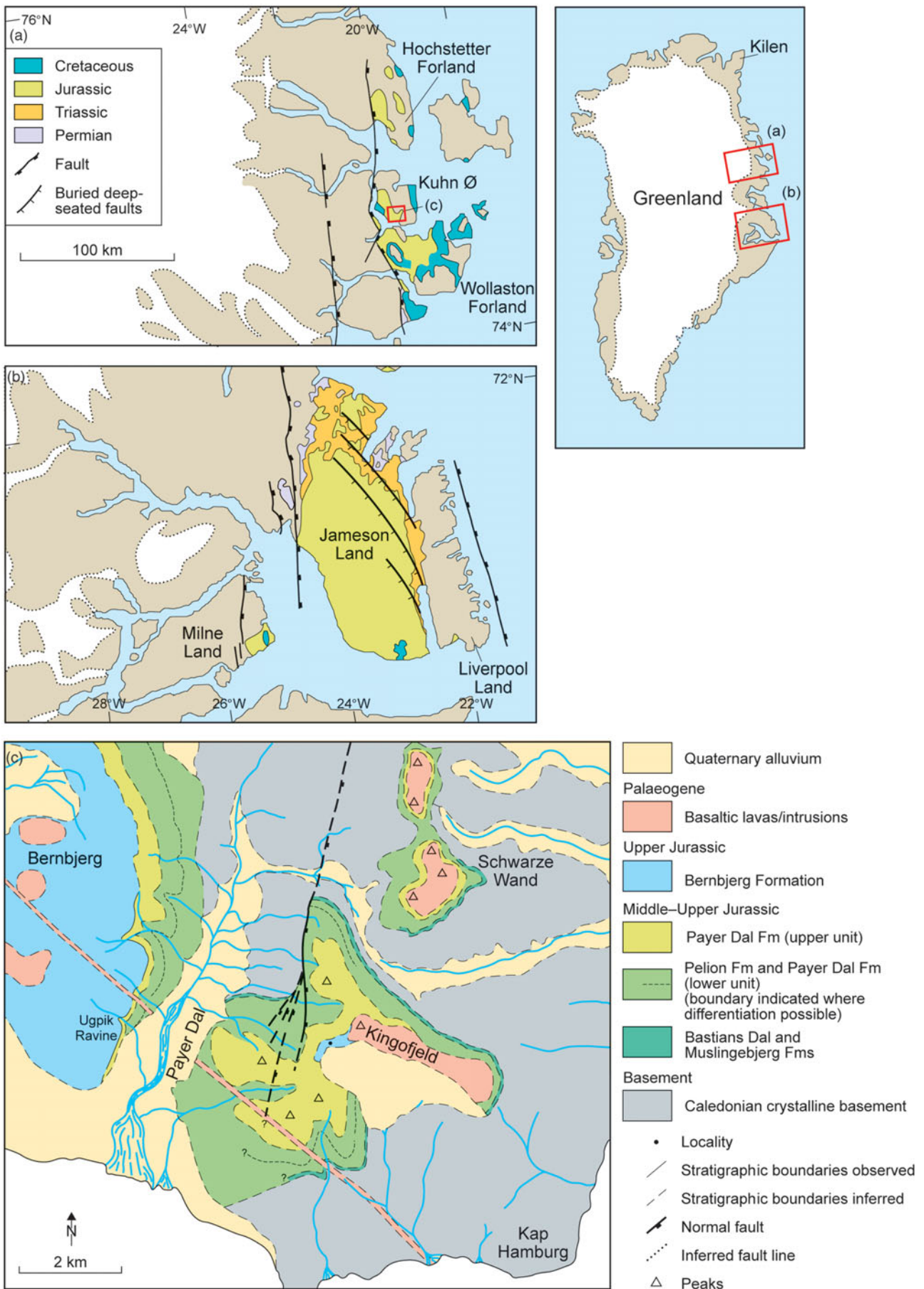


Fig. 1. (a, b) Simplified geological maps of (a) the Wollston Forland - Kuhn Ø area and (b) Jameson Land - Milne Land area in eastern Greenland. (c) Detailed geological map of the Payer Dal area with position of the vertebrate fossil locality at Kingofjeld (modified from Alsgaard *et al.* 2003, fig. 4).

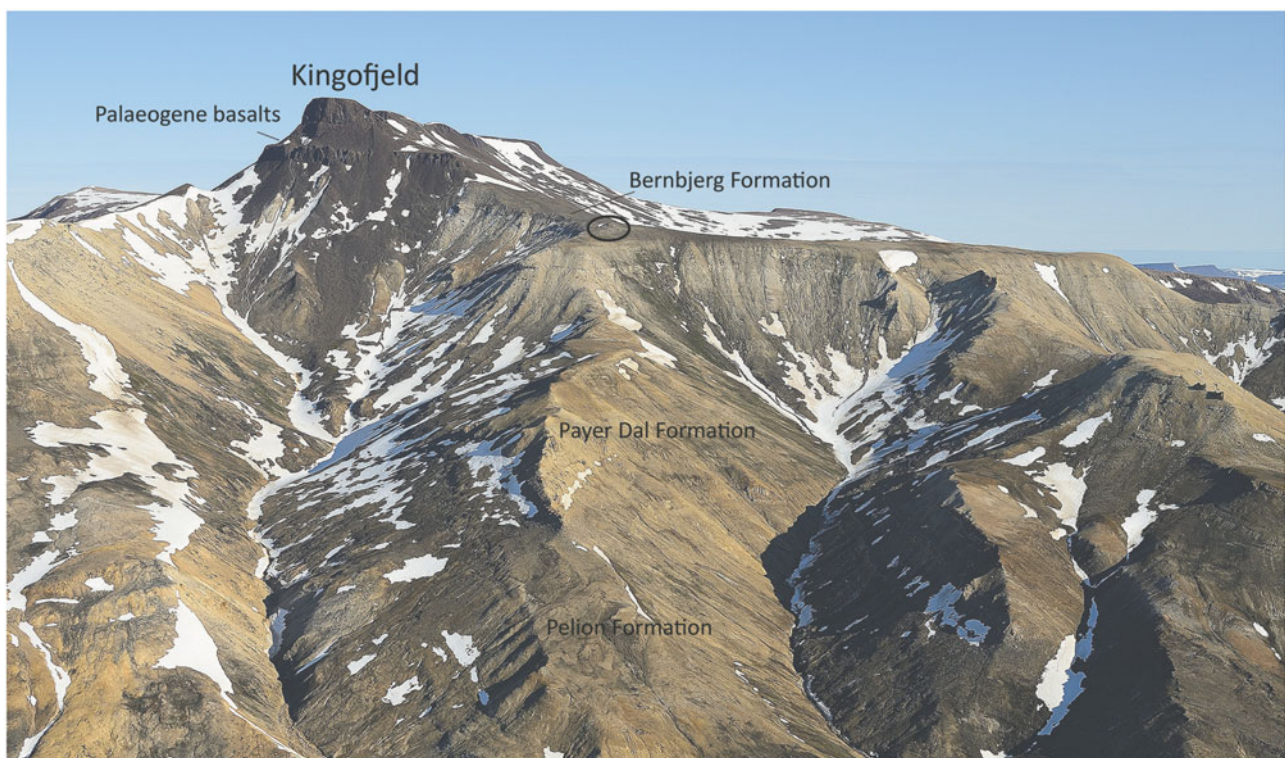


Fig. 2. Oblique view from helicopter towards the east and the eastern flank of Payer Dal and Kingofjeld. Encircled the location of the vertebrate locality.

anteriorly placed vertebrae. Vertebrae interpreted to belong to the anterior caudal region (five centra) only have one apophysis, positioned in the ventral portion of the lateral surface, whereas the posterior caudal and fluke centra are relatively small. Vertebrae that are mediolaterally wider than tall (GEUS 590347-14, -16 and -23) are interpreted to belong to the posterior portion of preflexural stock whereas two centra that are dorsoventrally taller than mediolaterally wide probably belong to the anterior portion of the fluke (Buchholtz, 2001).

The largest vertebra (diameter 94 mm) is a dorsal half of a centrum. It is interpreted to be a posterior dorsal or an anterior caudal as no facets are preserved in the dorsal half of the lateral surface. The largest centra in the column are found in the anterior caudal region (Buchholtz, 2001), and this specimen is similar in size to large *Ophthalmosaurus icenicus* specimens (Buchholtz, 2001; Moon & Kirton, 2016).

4.b.3. Ribs

There are no complete ribs, and none of the fragments preserve the medial head or the distal tip. Several of the rib fragments (e.g. GEUS 590347-85, -88, -89 and -91) display an eight-shaped cross-section typical of many thunnosaurians (Sander, 2000; McGowan & Motani, 2003). Exceptions to this include ophthalmosaurid specimens from the Slottsmøya Member Lagerstätte on Spitsbergen (Delsett *et al.* 2017, 2018), the Russian *Acamptonectes densus* and the North American *Platypterygius americanus* (Maxwell & Kear, 2010; Fischer *et al.* 2012). Two of the rib fragments, where the inner structure is visible in cross-section, appear to have trabeculae arranged into rings.

Reptilia Laurenti, 1768
 Sauropterygia Owen, 1860
 Plesiosauria de Blainville, 1835

4.c. Referred specimen

GEUS 590347-99, distal limb element (Fig. 4b).

4.d. Description

The surface of the element appears eroded, whereas the element is not compressed to any degree. The element is interpreted to be a metapodial or phalangeal element based on its shape. Its proximal and distal ends are approximately equally anteroposteriorly wide and the middle is constricted. The articular surfaces are convex.

Reptilia Laurenti, 1768
 Sauropterygia Owen, 1860
 Plesiosauria de Blainville, 1835
 Plesiosauroidea Welles, 1943

4.e. Referred specimens

GEUS 590347-83, partial propodial (Fig. 5). GEUS 590347-26, cervical vertebra (Fig. 4a). GEUS 590347-28, caudal vertebra.

4.f. Description

4.f.1. Propodial

GEUS 590347-83 (Fig. 5) represents the distalmost portion of a plesiosauroid propodial and has three distal facets, as in e.g. *Colymbosaurus svalbardensis* (Knutsen *et al.* 2012). In contrast, Pliosauridae propodials are more rounded. The dorsoventral height of the element is approximately similar throughout the element, and it has no dorsal or ventral crests. The element is incomplete and severely eroded. The anteriormost and posterior-most facets are directed anterodistally and posterodistally, respectively, while the middle facet is significantly larger than the two others, both in anteroposterior length and in dorsoventral height.

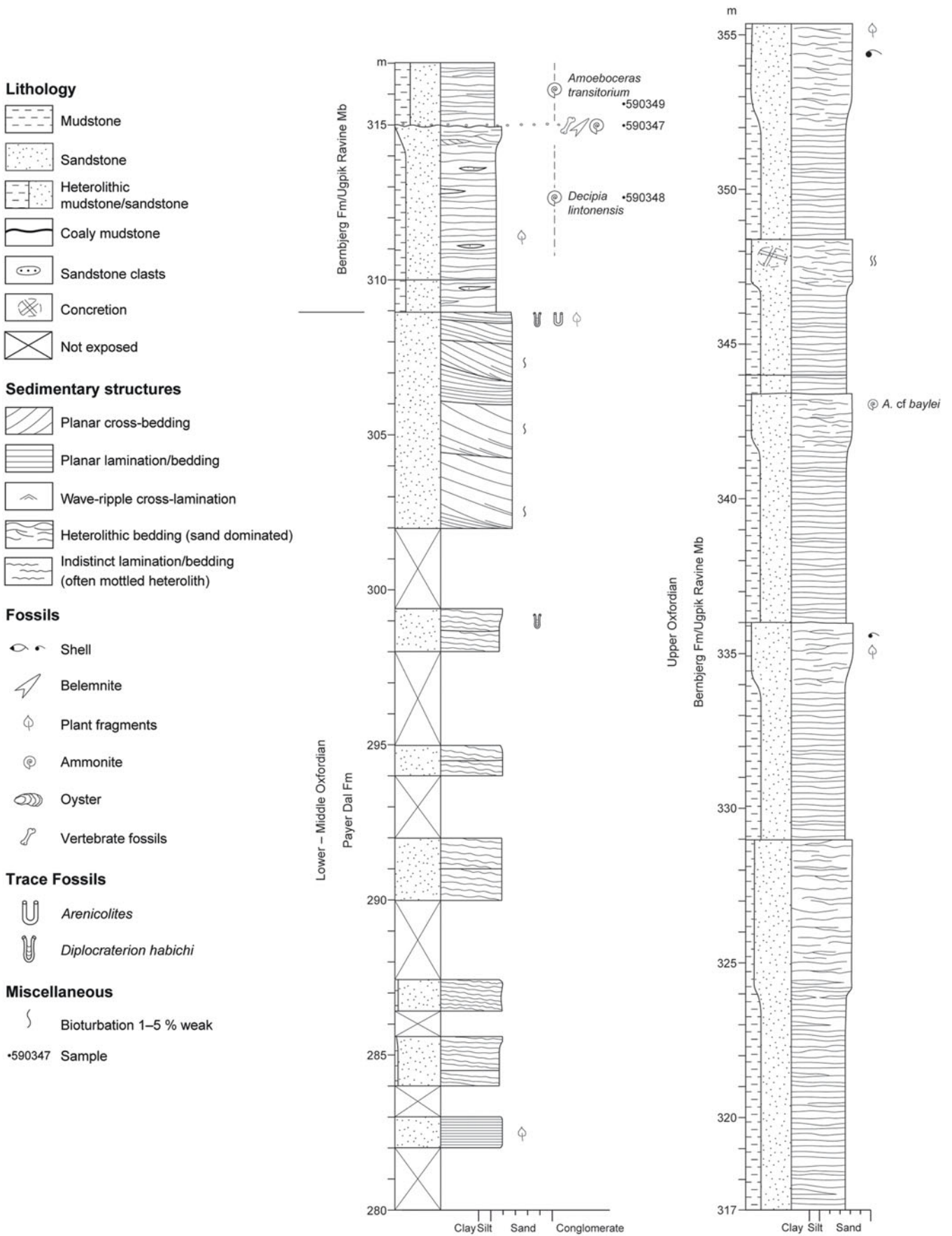


Fig. 3. Sedimentological log of the Jurassic succession at Kingofjeld (measured by H Vosgerau in 1994).



Fig. 4. Selected illustrated plesiosaur (a, b) and ichthyosaur (c–f) specimens. Cervical vertebra (NHMD 608568) in (a1) anterior or posterior and (a2) ventral view. Distal limb element (NHMD 608570) in (b). Cervical vertebrae (NHMD 608564) in (c1) lateral, (c2) anterior and (c3) dorsal view, and (NHMD 608565) in (d1) lateral, (d2) anterior and (d3) dorsal view. Anterior caudal vertebra (NHMD 608566) in (e1) dorsal, (e2) anterior and (e3) lateral view. Posterior caudal vertebra (NHMD 608567) in (f1) lateral, (f2) anterior and (f3) dorsal view.

4.f.2. Vertebrae

The two vertebrae are assigned to Plesiosauroidea based on their relative dimensions and shape (Knutsen *et al.* 2012; Roberts *et al.* 2017). The surface of the plesiosauroid vertebrae is eroded, most severely the surface of the caudal centrum. The cervical vertebra (Fig. 4a) is biconcave and mediolaterally widest in the dorsal half. It bears the broken remains of two neural arches, directed dorso-laterally. The ventral surface shows two small foramina. The caudal vertebra is mediolaterally wider than dorsoventrally tall.

5. Discussion

The marine reptile assemblage found at Kingofjeld occurs at a narrow interval close to the base of the Uggvik Ravine Member of the Bernbjerg Formation. It thus appear to be from the same or approximately the same stratigraphic level as the marine vertebrate fossils reported from northern Wollaston Forland, which gave rise to the place name Sauruspasset (Maync, 1947). The fossiliferous level was described as a 0.2 m thick ‘bone bed’ with vertebrae, bones, petrified logs, plant remains and ammonites and bivalves

Table 1. The 18 ichthyosaur vertebral centra that could be referred to a section of the vertebral column

Vertebral region	Museum no.
Cervical	GEUS 590347-1
Cervical	NHMD 608565
Cervical	GEUS 590347-8
Cervical	GEUS 590347-3
Cervical	NHMD 608564
Cervical	GEUS 590347-5
Cervical	GEUS 590347-9
Dorsal	GEUS 590347-15
Anterior caudal	NHMD 608566
Anterior caudal	GEUS 590347-18
Anterior caudal	GEUS 590347-19
Anterior caudal	GEUS 590347-21
Anterior caudal	GEUS 590347-22
Posterior caudal	GEUS 590347-14
Posterior caudal	GEUS 590347-16
Posterior caudal	NHMD 608567
Anterior portion of fluke	GEUS 590347-24
Anterior portion of fluke	GEUS 590347-25

(Maync, 1947). It would be desirable to locate Maync's locality in Sauruspasset, and an attempt was made in 2018. It was unsuccessful due to an unusual extensive snow cover (~90–95%) even in the late summer. It is obvious, however, that the Sauruspasset is positioned in an area where the sand-dominated Payer Dal Formation is overlain by the Bernbjerg Formation, similar to the situation at Kingofjeld.

The sand-dominated Middle to lowermost Upper Jurassic Pelion and Payer Dal Formations are relatively rich in fossils, especially in bivalves, fossil wood and occasional ammonites, whereas no vertebrates have previously been reported. The occurrence of vertebrates at two localities at apparently the same stratigraphic level in the overlying Ugpik Ravine Member (Bernbjerg Formation) suggests a possible enrichment of marine reptiles in the upper Oxfordian. This can be due to generally favourable palaeoenvironmental conditions where marine reptiles thrived, or favourable preservation potential of vertebrate fossils in this narrow interval.

Sedimentologically, the reptile finds from Kingofjeld are associated with a conglomerate with rather large pebbles. The conglomerate represents winnowing during transgression subsequent to a sequence boundary. The conglomerate and enrichment of fossils thus apparently represent a transgressive lag removing finer-grained particles and concentrating larger grain sizes including fossils.

The ichthyosaur vertebrae described here are interpreted as the remains of several specimens. Based on their morphology, 18 of them can be placed with confidence in a specific region of the vertebral column. Within the anterior dorsal and anterior caudal regions, the size variation between the single vertebrae is significantly larger than what is observed in other ophthalmosaurids (Buchholtz, 2001; Moon & Kirton, 2016; Delsett *et al.* 2017), and larger than possible for one individual. Future exploration

for further discoveries of marine reptiles can probably benefit from specifically searching in strata correlative to the assemblages at Kingofjeld and Sauruspasset.

A Late Oxfordian age makes the plesiosaurian fossils contemporaneous with some cryptoclidid plesiosaurioids with small skulls and long necks, taxa mainly from the northern hemisphere, but older than the Tithonian specimens from the Slottsmøya Member Lagerstätte on Spitsbergen (Knutsen *et al.* 2012; Roberts *et al.* 2017). Plesiosaur fossils from Ellesmere Island mentioned by Troelsen (1952) are not formally described, but based on his description of the locality, they probably originate from the Tithonian – early Valanginian Deer Bay Formation (S Schneider, pers. comm. 2019).

The ichthyosaur specimens are of the same age as occurrences of the very long-lived and abundant *Ophthalmosaurus icencus* as well as the earliest records of *Arthropterygius chrisorum* and an *Ophthalmosauria* indet. specimen from Cuba (Fernández & Iturralde-Vinent, 2000; Maxwell, 2010; Moon & Kirton, 2016), whereas they are younger than the Bajocian species *Mollesaurus periallus* from Argentina (Fernández, 1999). The ichthyosaur specimens from Kingofjeld are older than the Jurassic ophthalmosaurids found in Solnhofen, Slottsmøya Member Lagerstätte, and the area around Undory in Russia, as well as *Caypullisaurus bonapartei* from the Vaca Muerta Formation in Argentina (Bardet & Fernández, 2000; Fernández, 2007; Zverkov *et al.* 2015; Delsett *et al.* 2016).

A narrow seaway (NE Atlantic seaway / Greenland–Norwegian Seaway) connected the Boreal areas to the Tethys Sea for parts of the Late Jurassic (Mutterlose *et al.* 2003) (Fig. 6). Present-day Greenland and Norway were partly land, and their main separation did not occur until 58 Ma. Tectonic movement and a sea level fall caused a characteristic provincialism and endemism for many marine taxa, with a clear separation of the Tethys and Boreal fauna, whereas sea level rise in the Valanginian gave more cosmopolitan distributions (Mutterlose *et al.* 2003; Hammer *et al.* 2013). Close skeletal similarities have been observed between Boreal ichthyosaur taxa, and to some extent South American taxa, and a possible differentiation between low- and high-latitude taxa has been suggested (Maxwell, 2010; Roberts *et al.* 2014; Zverkov *et al.* 2015). Two Late Jurassic seaways might have connected these localities: an Oxfordian–Kimmeridgian route along the Eastern Pacific / Western America (Fernández & Maxwell, 2012) and a Tithonian route through the Russian areas and the newly established Hispanic corridor between the Eastern Pacific and Tethys (Zverkov *et al.* 2015).

The now-abandoned hypothesis that the Late Jurassic saw a decline in Ichthyosauria (Bardet, 1994; Sander, 2000; Lingham-Soliar, 2003; Benson *et al.* 2010) was probably a result of a small number of fossiliferous locations yielding ichthyosaurs, few articulated and/or complete specimens and small datasets for phylogenetic analyses (Maxwell, 2010). Since 2000, ichthyosaurs from the Late Jurassic have been reported from many new localities in France, Germany, Argentina, Russia, UK, Colombia, Italy, Poland, Mexico, Cuba, Canada, India and Spitsbergen (Buffetaut *et al.* 2003; Buchy, 2010; Gasparini *et al.* 2015; Delsett *et al.* 2016; Paparella *et al.* 2016; Tyborowski, 2016; Prasad *et al.* 2017) (Fig. 6). Raw numbers and diversity analyses indicate that Late Jurassic ichthyosaur diversity was high, and that the clade was not severely affected by an extinction event at the Jurassic–Cretaceous boundary (Zammit, 2012; Fischer *et al.* 2016).



Fig. 5. Partial plesiosaur propodial (NHMD 608569) in (a) anterior and (b) dorsal view.

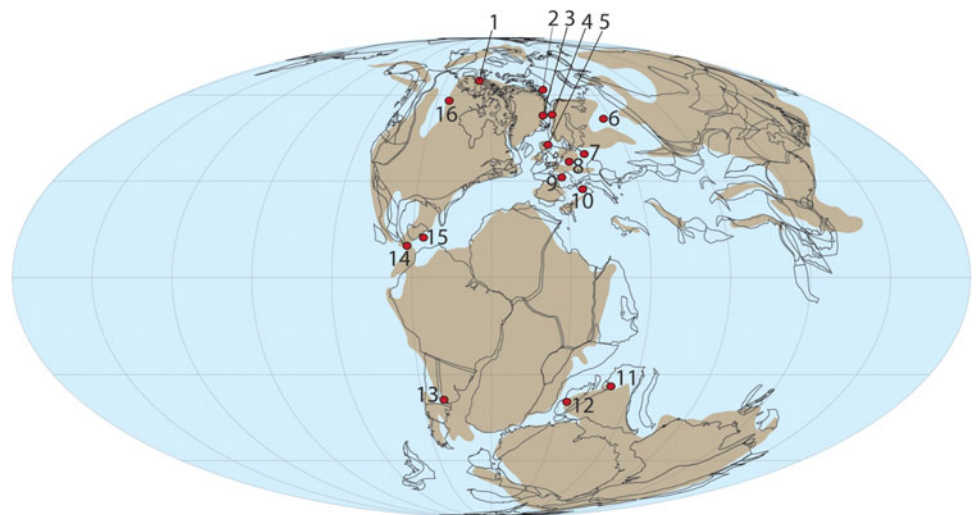



Fig. 6. Late Jurassic palaeogeographic map showing localities with Ophthalmosauridae specimens. 1. Canada; 2. Spitsbergen; 3. Greenland; 4. Norway; 5. UK; 6. Russia (Volga river); 7. Poland; 8. Germany; 9. France; 10. Italy; 11. India; 12. Madagascar; 13. Argentina; 14. Mexico; 15. Cuba; 16. USA. Modified from Rees *et al.* (2000).

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Conflict of interest. The authors declare that there is no conflict of interest.

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