



# A new vertebrate fossil-bearing layer in the Rhætelv Formation (Kap Stewart Group) of central East Greenland: evidence of a Hettangian marine incursion into the continental Jameson Land Basin

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The Kap Stewart Group (Rhaetian–Sinemurian, Triassic–Early Jurassic) of the Jameson Land Basin in central East Greenland has traditionally been regarded as a strictly continental unit with delta and perennial lake sediments. New finds of plesiosaur bone remain in a thin storm deposited sandstone bed in the middle part of the Rhætelv Formation of the Kap Stewart Group, however, indicates a likely period of marine influence. At the study area at the eastern margin of the basin, the Rhætelv Formation is 300-m thick and overlies unconformably the Norian Fleming Fjord Group. The bone-bearing sandstone occurs 190 m above the base of the group and is closely associated with black laminated mudstones; palynological investigation of three samples from these mudstones indicates that they are of a younger Hettangian age. The Hettangian was a relatively short stage (201.3–199.5 Ma) and elsewhere characterized by two episodes of sea-level highstands. Assuming that the marine incursion in the Jameson Land Basin evidenced by the plesiosaur fossil remains took place during the youngest of these sea-level highstands, the bone-bearing bed of the Rhætelv Formation can be dated to 200 Ma and thereby gives the first numerical age constraint of this hitherto poorly dated succession. □ *Hettangian, Jameson Land Basin, Kap Stewart Group, marine incursion, plesiosaur.*

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The Kap Stewart Group (originally defined as the Kap Stewart Formation by Surlyk *et al.* 1973) of the Jameson Land Basin in central East Greenland (Fig. 1) forms a thick succession of interbedded black mudstones and greyish sheet sandstones in large parts of the basin; it is dated to the Rhaetian–Sinemurian (Dam & Surlyk 1993; Surlyk 2003; Surlyk *et al.* 2021). It is divided into the Innakajik and Primulaelv formations in the southernmost part of the basin (type area) and the Rhætelv Formation in the northern and largest part of the basin (Surlyk 2003; Surlyk *et al.* 2021). Early work on this unit was

concentrated on the rich plant-bearing layers in the southernmost part of the basin along Hurry Inlet (see Petersen & Lund 1980 for detailed information on the early history of investigation). Classical palaeobotanical studies (Harris 1937 and references therein) have over the last decades been supported by multiple studies on changes in palaeobotany and palynology across the Triassic–Jurassic boundary of the Astartekløft section (McElwain *et al.* 1999; Hesselbo *et al.* 2002; McElwain *et al.* 2007; Belcher *et al.* 2010; Steinthorsdottir *et al.* 2011, 2018; Mander *et al.* 2013). Studies of stomatal proxies on fossil leaves

from different plant groups suggest extremely elevated atmospheric CO<sub>2</sub> concentrations at the Triassic–Jurassic boundary (Steinthorsdottir *et al.* 2012 and references herein). The sediments in the southernmost part of the basin were interpreted as limnic (Petersen & Lund 1980) or as alluvial plain sediments overlain by delta plain deposits (Dam & Surlyk 1992, 1993).

Less attention was given to the depositional environments in the northernmost part of the basin (the Rhætelv Formation). However, Surlyk *et al.* (1973) gave a brief description of sediments also from this part of the basin. According to them, the sediments were deposited in the non-marine parts of large deltas and rivers perhaps with brackish-marine intercalations in the north-western part of the basin. Clemmensen (1976)

interpreted the sediments in the northernmost part of the basin as deltaic and saw evidence of tidal influence. Later work by Dam & Surlyk (1992, 1993), however, did not find supporting evidence for marine influence and the sediments were interpreted as formed in a land-locked basin with fluvial and deltaic sediments at the basin margin and deep lake sediments in the basin centre.

Marine fossils have not been discovered in the Kap Stewart Group until recently, when Milàn *et al.* (2012) and Hansen *et al.* (2016) described a single shark tooth (the neoselachian shark *Rhomphaiodon minor*, a strictly marine species) from black (supposedly) lacustrine mudstones at the base of the Kap Stewart Group near ‘Track Mountain’ at the eastern margin of the basin (Fig. 1). Marzola *et al.* (2018) reported bone remains of a marine plesiosaur from

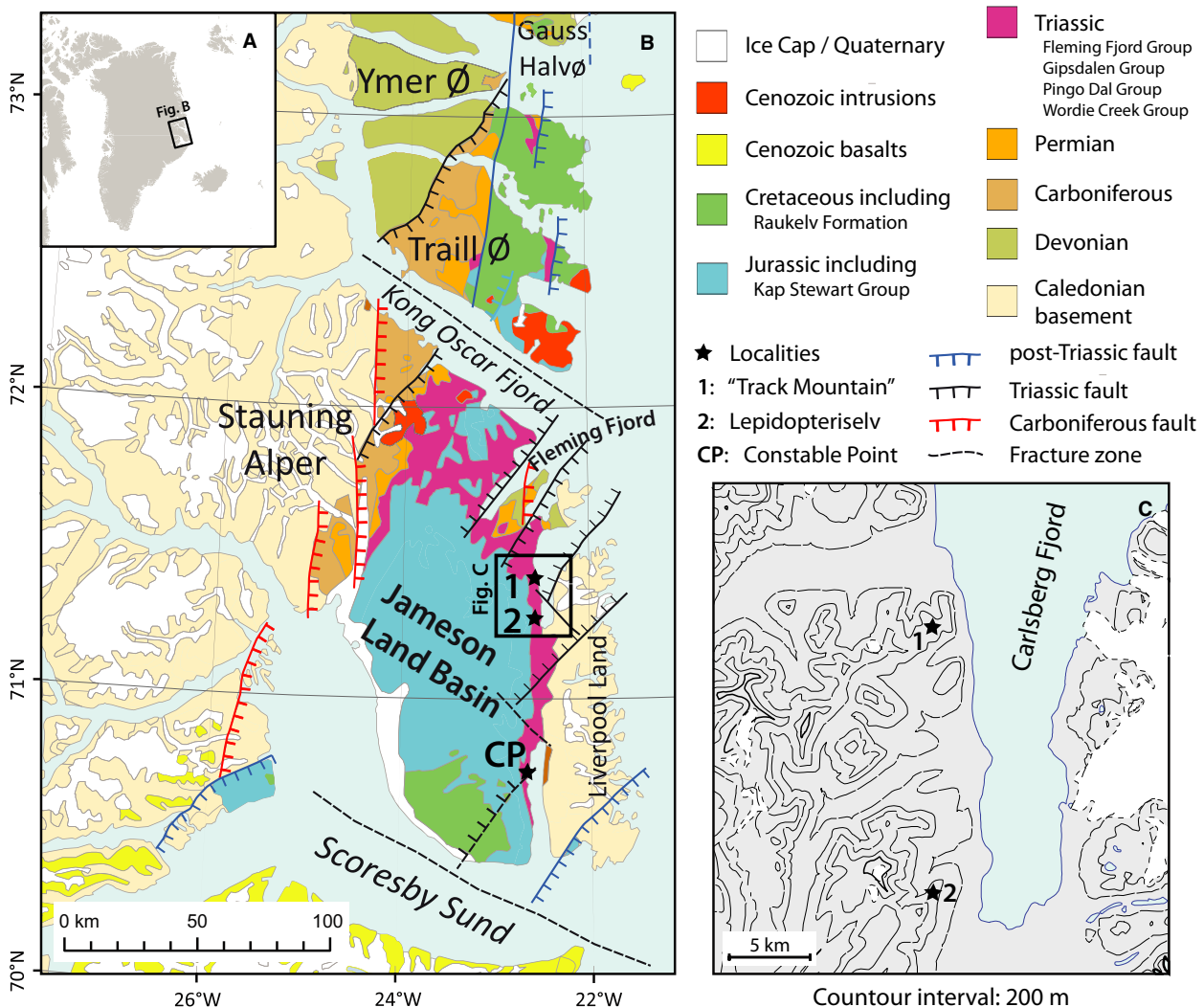


Fig. 1. Location map of the Jameson Land Basin in central East Greenland. Studied sections are indicated. Main section is at Lepidopteriselv; here about 300 m of the Rhætelv Formation of the Kap Stewart Group is exposed. Insert map showing the location of the sections at Lepidopteriselv and immediately west of ‘Track Mountain’.

the middle part of this group at Lepidopterislev, also at the eastern margin of the basin (Fig. 1).

In this paper, we aim to place the new fossil find of plesiosaur bone remains at the Lepidopterislev section in a chronostratigraphical framework, interpret their depositional setting and discuss their palaeoenvironmental implications in relation to Early Jurassic sea-level variation (Surlyk, 1990; Hardenbol *et al.* 1998; Haq 2017).

## Geological setting

The Kap Stewart Group contains the Triassic–Jurassic boundary and is thus at least Rhaetian–Hettangian in age (Dam & Surlyk 1992, 1993; Surlyk 2003; Surlyk *et al.* 2021). In the southern part of the basin along Hurry Inlet, the group has a thickness of about 175-m thick and encompasses the Innakajik and Primulaelv formations (Surlyk 2003; Surlyk *et al.* 2021). In the study area to the northeast at Lepidopterislev and nearby localities Kap Stewart Group sediments are restricted to the Rhætlev Formation, attaining a thickness of about 300 m (Dam & Surlyk 1993; Surlyk 2003). Along Hurry Inlet, the Triassic–Jurassic boundary is situated about 50 m above the base of the group (McElwain *et al.* 1999). However, in the northern part of the basin including the study area, the succession is too poorly dated to allow a clear definition of the Triassic–Jurassic boundary.

The Kap Stewart Group overlies a 350-m-thick Late Triassic (Norian) succession of continental (lacustrine and fluvial) deposits in the Fleming Fjord Group (Clemmensen *et al.* 2020; Kent & Clemmensen 2021). At the study area at Lepidopterislev (Figs 1, 2), an erosional boundary separates the Rhætlev Formation from the underlying Ørsted Dal Formation of the Fleming Fjord Group (Clemmensen *et al.* 2020), and new magnostratigraphical work (Kent & Clemmensen 2021) suggests that this unconformity could have a duration of 8 Myr. Although the Rhætlev Formation overlies the Fleming Fjord Group without visible discontinuity at most other sites in the northern part of the basin a hiatus must also be present at these localities.

Dam & Surlyk (1993) interpreted the Kap Stewart Group sediments to have formed in and around a large wave- and storm-dominated anoxic lake. Coarse-grained sediment was transported to the lake from eastern, western and northern source areas and formed large delta systems. The Kap Stewart lake system displays several short-term lake-level fluctuations many of them probably related to astronomically controlled climate change, while

long-period cycles in the Kap Stewart Group were thought to record eustatic sea-level variation in the Rhaetian, Hettangian and Sinemurian (Dam & Surlyk 1992, 1993). According to this interpretation, the lake system could have had a duration of up to 15–20 Myr before it was transgressed by the sea at the Sinemurian–Pliensbachian transition (Dam & Surlyk 1992, 1993, 1998; Surlyk 2003).

## Material and methods

In 2016, bone remains of a plesiosaur were found in scree from the Rhætlev Formation at Lepidopterislev (Marzola *et al.* 2018). It was possible to locate these bone remains in a thin sandstone horizon in the middle part of the Rhætlev Formation at the adjacent mountain ridge (Fig. 3; 71°15.761'N, 22°34.287'W). In 2018, new examination of this sandstone bed revealed a few more plesiosaur bones as well remains of hybodontid sharks, and a mammal tooth was found in a very thin sandstone interval with burrows immediately above the bone bed. All fossils in this study are part of the collection of the Natural History Museum of Denmark (NHMD for vertebrates). A facies analysis was carried out in the section spanning the bone-bearing bed and three samples of black mudstones were collected for palynological investigation. The three samples were processed according to standard palynological preparation techniques at the Palynological Laboratory at GEUS in Copenhagen. The samples were digested in hydrochloric and hydrofluoric acids in order to remove carbonate and silicate minerals. The organic residues were mildly oxidized in KOH, and filtered on 11 µm mesh filters to remove finely particulate amorphous organic matter. Strew slides were prepared after each preparation step, including two to three additional slides after the final step, and mounted in glycerine gel. A quantitative analysis based on a count of 300 specimens from each sample was carried out on the two of the samples that contained abundant palynomorphs. The third sample only yielded few palynomorphs and was only scanned for identifiable taxa, but no quantitative assessment was performed (Table 1).

## The vertebrate fossil-bearing bed

### Description

The Rhætlev Formation was studied at a mountain ridge near Lepidopterislev (Figs 1, 3). The lowermost 185 m of the formation is nearly completely covered

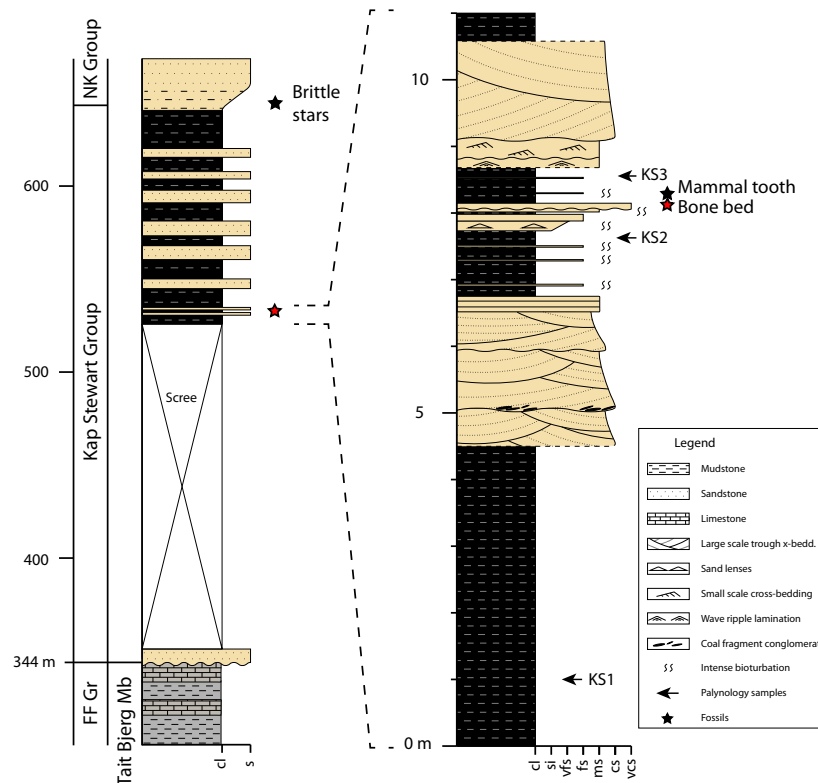


Fig. 2. Simplified stratigraphical section of the Rhætelv Formation (Kap Stewart Group) at Lepidopteriselev (Fig. 1), and sedimentary log of the middle part of the formation with the bone-bearing bed. The Rhætelv Formation is exposed on a mountain ridge between 344 and 633 m above present sea level.



Fig. 3. The middle part of the Rhætelv Formation (Kap Stewart Group) at Lepidopteriselev. Poorly exposed, fine-grained sediments including 'paper shales' at the base of the section are overlain by a strongly disintegrated distributary channel sandstone with an approximate thickness of 2 m. The bone-bearing bed is situated immediately above the sandstone. At the top of the mountain are cliff-forming sandstones in the Neill Klinger Group.

by scree and the uppermost part is apart from few sections not exposed to a degree that enables detailed sedimentological studies. However, at one site between 185 and 200 m above the base of the

formation good exposures are present. In this interval, the bone-bearing bed is situated. About 300 m above the base of the formation, sediments with imprints of brittle stars are seen on top of black mudstones (Fig. 2). Dam & Surlyk (1998) write that fossiliferous sandstones of the Neill Klinger Group overlie black mudstones (paper shales) of the Rhætelv Formation. In agreement with these authors, we therefore include the sediments with brittle star imprints in the basal part of the Neill Klinger Group (Fig. 2).

The bone-bearing bed forms part of succession with units of black laminated mudstones ('paper shales') and 1.5- to 3-m-thick sandstone bodies composed of coarse-grained sand with large-scale trough-formed cross bedding and numerous transported plant and coal fragments (Figs 2, 3). The bone-bearing bed is a thin sandstone about 25-cm thick, over- and underlain by black laminated mudstone. It is a medium- to coarse-grained sandstone with even lamination and some intraformational black wood fragments at the base in association with the bone fragments. The closely associated black mudstones contain several thin (1- to 2-cm thick) sandstone intervals frequently with burrows. One of these burrow fills contained a mammal tooth. The tooth

Table 1. Spores and pollen in three samples from the middle part of the Rhætelv Formation (Kap Stewart Group), Lepidopteriselv, East Greenland.

Taxa	Reworked, questionable	KS 1	KS 2	KS 3
Spores and pollen		1.00 m	7.60 m	8.60 m
<i>Alisporites radialis</i>				2
<i>Alisporites robustus</i>		1	X	10
<i>Alisporites thomasi</i>				1
<i>Aratrisporites minimus</i>				2
<i>Aratrisporites</i> spp.				1
<i>Baculatisporites comaumensis</i>		X		
<i>Baculatisporites oppressus</i>		X		
Bisaccate, unidentifiable		15	X	10
<i>Calamospora tener</i>		10	X	
<i>Chasmatosporites apertus</i>		5	X	7
<i>Chasmatosporites hians</i>		10	X	17
<i>Chordasporites</i> spp.				1
<i>Classopollis classoides</i>		1	X	X
<i>Classopollis meyerianus</i>		4	X	10
<i>Conbaculatisporites spinosus</i>		7	X	X
<i>Cordaitina</i> spp.	R			1
<i>Geopollis zwolinkai</i>		1		X
<i>Cyclogranisporites</i> sp.				1
<i>Deltoidospora minor</i>		15	X	8
<i>Deltoidospora toralis</i>		46	X	24
<i>Eucommiidites minor</i>		1		
<i>Eucommiidites granulatus</i>				X
<i>Eucommiidites troedssonii</i>		3		3
<i>Granulatisporites</i> sp.		2		
<i>Granuloperculatipollis rudis</i>		2		
<i>Kraeuselisporites reissingerii</i>				1
<i>Laevigatosporites</i> spp.		1		
<i>Lophotriletes</i> spp.		1		
<i>Lueckisporites virkkiae</i>	R			X
<i>Lunatisporites</i> sp.	R	X		X
<i>Marattisporites scabratus</i>		40	X	4
<i>Monosulcites</i> sp.				1
<i>Monosulcites minimus</i>		8	X	4
<i>Monosulcites punctatus</i>		3	X	8
<i>Osmundacidites wellmannii</i>		25	X	1
<i>Ovalipollis ovalis</i>	?R			1
<i>Perinopollenites elatoides</i>		18	X	76
<i>Pinuspollenites minimus</i>		1	X	35
<i>Platysaccus</i> sp.				1
<i>Podosporites amicus</i>	R			1
<i>Punctatisporites globosus</i>		3	X	4
<i>Quadraeculina anellaformis</i>			X	4
<i>Retisulcites perforatus</i>				1
<i>Skarbysporites crassexina</i>				X
<i>Stereisporites aulosenensis</i>			X	
<i>Stereisporites stereoides</i>				X
<i>Stratella seebergensis</i>		1		
<i>Trachysporites asper</i>		5	X	2
<i>Trachysporites fuscus</i>		X		1
<i>Vitreisporites pallidus</i>		26	X	4
<i>Vittatina</i> spp.	R			
Sum of spores and pollen		266		248
Unidentifiable palynomorphs		34		14
Aquatic palynomorphs				
Dinoflagellate cysts, unidentified	?			2
'Rotundus granulatus'			X	36
<i>Botryococcus braunii</i>			X	
Sum of aquatic palynomorphs		0	0	38

tentatively assigned to a docodont mammal will be the topic of a separate study.

Vertebrate fossils in the bone-bearing bed were found mostly in the form of isolated, broken bone fragments. Two dorsal vertebrae (Fig. 4A, B) and one

dorsal rib (Fig. 4C), show clear plesiosaur affinities in having amphicoelous centra, paired ventral nutritive foramina in the centrum, unfused neurocentral sutures and single-headed ribs. The diameter of the centra is 2 cm indicating a small-sized individual

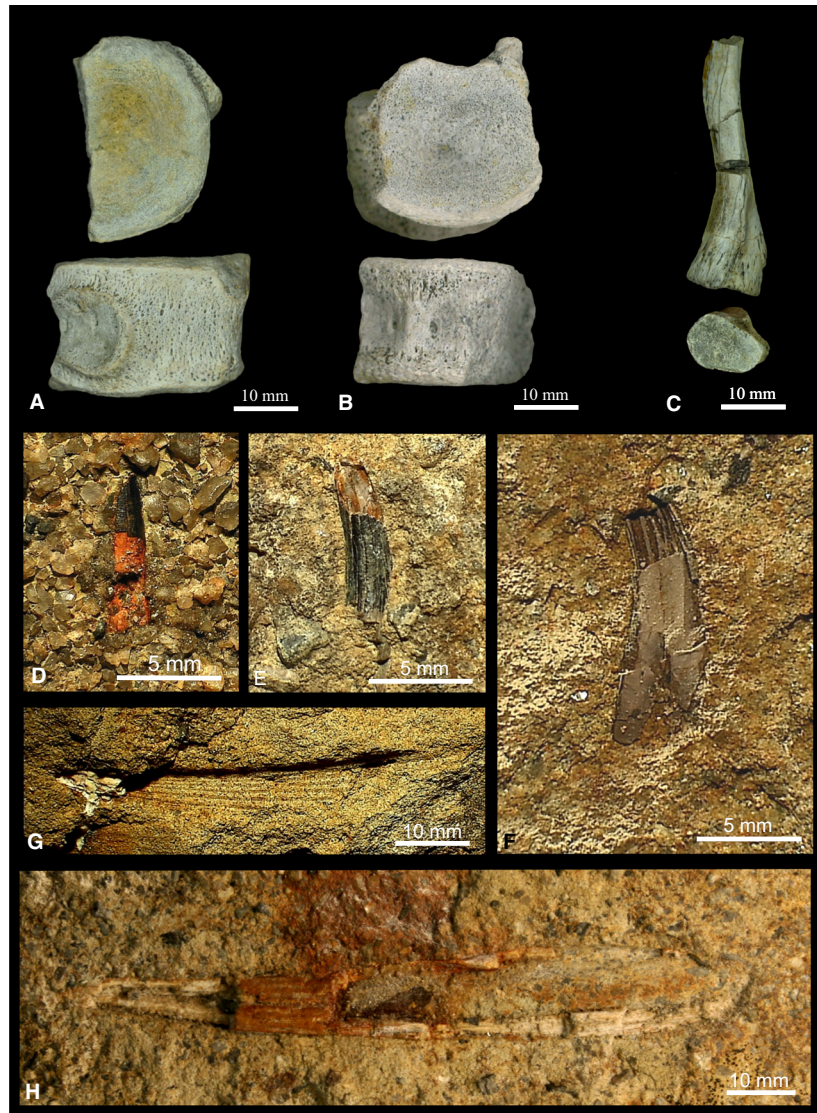


Fig. 4. Vertebrate fossils from the Rhætelv Formation (Kap Steward Group). A, B, plesiosaurian vertebrae centre (NHMD 74795 and 74796). C, plesiosaurian dorsal rib (NHMD 74797). D–F, plesiosaurian teeth (NHMD 872815–872817). G, H, partly preserved hybodontid fin spines of different sizes (NHMD 872818 and 872819).

(Milàn *et al.* 2016, Marzola *et al.* 2018). In addition to the skeletal fragments, three plesiosaur teeth were found in the same unit (Fig. 4D–F). The teeth are all incomplete and relatively small, with sizes of the fragments from 5 to 9 mm, and an estimated total length of up to 18 mm. The teeth are curved, cylindrical in cross-section, and have longitudinal striations in the enamel. Hybodontid sharks are represented by several partly preserved fin spines ranging in lengths from 54 to 114 mm (Fig. 4G, H).

### Interpretation

The coarse-grained sandstone bodies resemble the distributary channel deposits of Dam & Surlyk (1992, 1993), and are interpreted to record clastic input to

delta systems along the shores of the lake/lagoon. The laminated black mudstones ('paper shales') seen at the base of the succession (Fig. 2) are identical to the open lacustrine mudstones of Dam & Surlyk (1993). The mudstones closely associated with the bone-bearing bed are also black and laminated and of paper shale appearance, but they contain a number of very thin sandstone layers (1- to 2-cm thick) with numerous large burrows; they could also represent open lacustrine/lagoonal deposits or alternatively they could represent sediments from a large interdistributary bay. The main bone-bearing sandstone has no apparent facies analogue in Dam & Surlyk (1992, 1993), but it is here interpreted to record an inundation event that brought in sand and bone remains to the interdistributary bay from delta front areas.

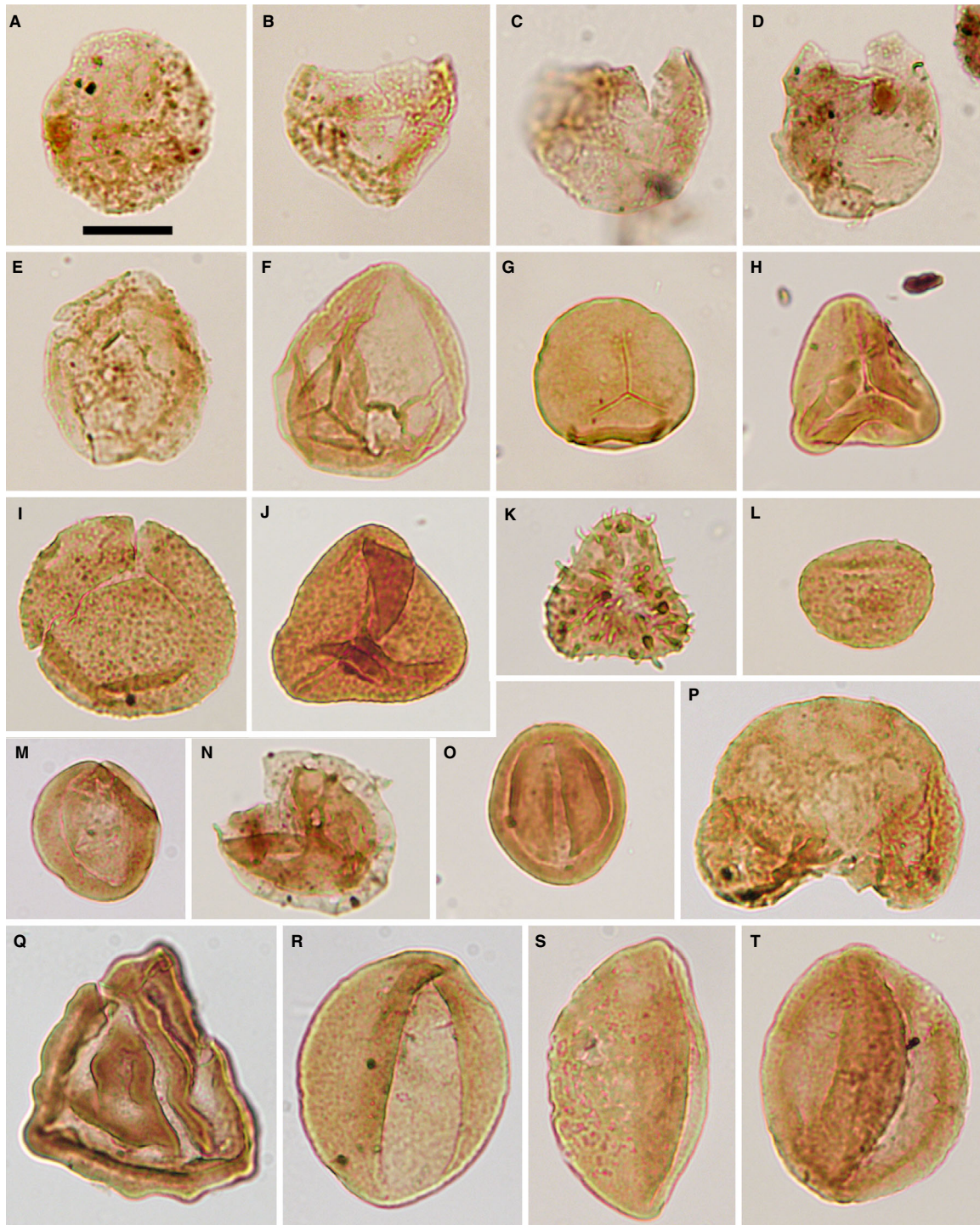


Fig. 5. Selected spores, pollen and dinoflagellate cysts from the middle Rhætelv Formation. All specimens are photographed at the same magnification; scale bar is 20  $\mu\text{m}$ . A, 'Rotundus granulatus', a putative dinoflagellate cyst originally noted by Koppelhus & Nielsen (1994). KS-3: 6, N52/3. B, dinoflagellate cyst with similar ornamentation as in (a), but displaying weak paratabulation. KS-3: 6, E39/2. C, dinoflagellate cyst with similar ornamentation as in (a) and (b) but displaying clear paratabulation on parts of the cyst. KS-3: 7, O37/3. D, dinoflagellate cyst with less ornamentation than in (a)–(c), but with evident epicystal paratabulation. KS-3: 7, M47/3. E, specimen of 'Rotundus granulatus', possibly displaying weak paratabulation. KS-3: 6, W50/2. F, *Calamospora tener*. KS-3: 6, T31/2. G, *Punctatisporites globosus*. KS-3: 7, F25/4. H, *Deltoidospora toralis*. KS-1: 8, H55/4. I, *Osmundacidites wellmanii*. KS-3: 6, J56/4. J, *Trachysporites asper*. KS-1: 8, L38/4. K, *Conbaculatisporites spinosus*. KS-3: 6, G36/2. L, *Marattisporites scabratus*. KS-3: 6, N39/4. M, *Classopollis meyerianus*. KS-3: 7, V45/1. N, *Perinopollenites elatoides*. KS-3: 6, C39/4. O, *Eucommiidites troedsonii* with a circumpolar furrow similar to *Classopollis*. KS-3: 6, N53/3. P, *Pinuspollenites minimus*. KS-3: 7, V30/4. Q, *Striatella seebergensis*. KS-3: 7, U58/3. R, *Chasmatosporites hians*. KS-3: 7, V47/4. S, *Monoalucites punctatus*. KS-3: 7, V32/2. T, *Quadraeculina anellaeformis*. KS-3: 6, T44/3.

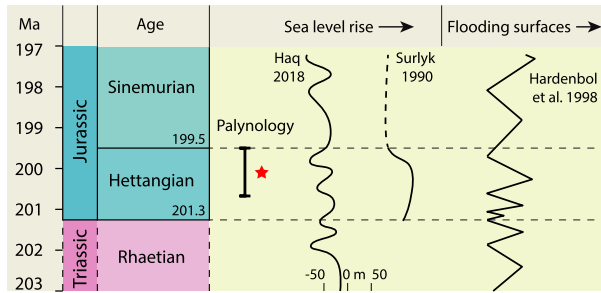


Fig. 6. Age interpretation of the 10-m-thick study section in the middle part of the Rhaetelvf Formation, (Kap Stewart Group), Lepidopteriselv, Jameson Land Basin. The likely age range of the succession given by palynological data (Palynology) is shown by a vertical bar, while the star shows a likely correlation of the marine influenced succession with the second Hettangian highstand in Haq (2017). Ages given for the Hettangian are from Kent *et al.* (2017). The discontinuous lines of the Rhaetian indicate that deposits of this age are not known with certainty in the study area where the Rhaetelvf Formation overlies the Norian Fleming Fjord Group unconformably.

## Palynological data

Black mudstones above and below the bone bed were sampled for palynological investigation. Sample KS1 was taken 7 m below the bone bed (1.0 m height in the measured section), sample KS2 was taken 0.5 m below the bone bed, while sample KS3 was taken 0.5 m above the bone bed (8.60 m in the section) (Fig. 2). The lowermost and uppermost samples contained relatively well-preserved assemblages dominated by spores and pollen (Fig. 5). The middle sample was dominated by amorphous organic matter (AOM) and degraded plant tissue, with very few identifiable palynomorphs. A quantitative assessment was only performed on the lower and upper samples, counting 300 specimens.

### Assemblage KS1

The lowermost assemblage, KS1 from 1.0 m height in the measured section (Fig. 2), is dominated by spores constituting c. 60%. The most dominant spores are *Deltoidospora* spp. and *Marattisporites scabratus* (Table 1). Other spores that are common include the *Osmundacidites wellmannii* and *Calamospora tener*. Among the pollen, *Monosulcites minimus*, *Vitreisporites pallidus*, *Perinopollenites elatoides* and *Chasmatosporites hians* are the most common. This indicates a vegetation dominated by tree ferns and ground ferns, with scattered bennettitaleans, caytonialeans, ginkgoaleans/cycadaleans and cupressacean trees. The cupressacean trees probably preferred wet mire environments, while the other trees most likely preferred more well-drained areas.

The sample contains large amounts of black phytoclasts and black wood remains. The composition of the palynoflora, together with the absence of freshwater or marine microalgae, suggests a terrestrial depositional environment. This is somewhat surprising as this sample is from the paper shale, which is presumed to represent an open lacustrine/lagoon environment (Dam & Surlyk 1992, 1993). The dominance of spores suggests a sparsely forested setting, but the abundance of wood fragments and black phytoclasts indicate the presence of forests nearby.

The presence and rare occurrence of *Cerebropollenites thiergartii* suggest an age not older than Hettangian (Hillebrandt *et al.* 2013; Mander *et al.* 2013; Peterffy *et al.* 2016; Vajda *et al.* 2016). The general absence of typical Rhaetian taxa that normally linger on into the earliest Hettangian, suggest an age younger than the earliest Hettangian. Only two questionable typical Rhaetian specimens were registered, one possible *Granulatisporites rudis* and one aberrant specimen of *Lunatisporites rhaeticus*. Both could also be reworked.

### Assemblage KS2

AOM and poorly preserved plant matter dominate the sample. Palynomorphs are generally poorly preserved. *Pinuspollenites minimus* appears to be relatively common (Table 1). A specimen of the putative dinoflagellate cyst 'Rotundus granulatus' was registered.

### Assemblage KS3

The spore-pollen flora of the upper sample, from 8.60 m in the section (Fig. 2), is dominated by *Perinopollenites elatoides* together with abundant *Pinuspollenites minimus* (Table 1). Spores have declined in abundances, making up c. 20% of the spore-pollen flora, with the most abundant taxon being *Deltoidospora* spp. (Table 1). Other spores such as *Trachysporites* spp., *Conbaculatisporites spinosus*, *Punctatisporites globosus*, *Osmundacidites wellmannii* and *Marattisporites scabratus*, are present but not common. Monosulcate pollen assigned to *Chasmatosporites* spp., *Monosulcites punctatus* and *M. minimus* are common, as are *Classopollis meyerianus*. This suggests that a more extensive coastal mire environment had developed, with pinacean conifers occupying drier hinterland areas. Cheirolepidiacean conifers are also believed to have preferred drier habitats, perhaps in the uplands. Tree ferns, bennettitaleans and ginkgoaleans/cycadaleans may have occupied drier patches in the coastal mires.

The putative dinoflagellate cyst 'Rotundus granulatus' comprise >12% of the total assemblage (Table 1).



This taxon has been recorded in Rhaetian to Lower Jurassic strata of the Danish Basin (Koppelhus & Nielsen 1994; Koppelhus & Batten 1996; Lindström *et al.* 2017a). It is a granulate, oval to spherical, and often folded palynomorph, which can be difficult to differentiate from folded specimens of, for example *Osmundacidites wellmannii* in poorly preserved assemblages. In the present samples, the assemblages are well preserved, allowing confident identification of specimens of '*Rotundus granulatus*'. Very rarely specimens exhibit poorly developed paratabulation. It has been recorded in both marine and marginal marine strata (Koppelhus & Nielsen 1994; Koppelhus & Batten 1996; Lindström *et al.* 2017a), hence, it is considered to be a cyst of a dinoflagellate which was tolerant of brackish water conditions. Also, a few dinoflagellate cysts of likely marine origin were observed in this sample (Fig. 6). Apart from this, no other marine or freshwater microalgae were recorded in KS3.

Rare specimens of reworked palynomorphs were also recorded in this sample, and include the Permian taxa *Cordaitina* sp., *Lueckisporites virkkiae* and *Vittatina* sp., and the Middle to Late Triassic taxa *Granuloperculatipollis rudis*, *Lunatisporites rhaeticus*, *Ovalipollis ovalis*, *Podosporites amicus* and *Retisulcites perforatus*.

### Stratigraphical indications

The recorded spore-pollen assemblages are dominated by long-ranging taxa. The palynofloral composition is rather typical for the Hettangian. The general lack of a variety of Rhaetian markers, specifically *Ricciisporites tuberculatus*, *Ovalipollis ovalis*, *Lunatisporites rhaeticus*, *Limboisporites lundbladiae* and *Cingulizonates rhaeticus* that in many NW European sections linger on into the earliest Hettangian (Lindström *et al.* 2017b), may suggest a younger Hettangian age. The few possible typical Rhaetian taxa registered are also present in older Triassic strata, and because they co-occur in KS3 with reworked middle to early late Triassic and Permian taxa, they are herein considered to also be reworked. In comparison to previously described Hettangian palynofloras from the Kap Stewart Group at Astartekløft and several other localities along the Hurry Inlet (Pedersen & Lund 1980; Mander *et al.* 2013), the herein described assemblages are most similar to those reported from Muskusokse-Hareelv by Pedersen & Lund (1980). Pedersen & Lund (1980) subdivided their Hettangian Zone 2 into two, a lower and an upper, subzones. The lower subzone was distinguished from the upper one by lacking *C. thiergartii*, while this taxon is regularly present in the upper

zone. This could possibly indicate that the assemblages investigated herein could correlate with their Upper Zone 2.

## Discussion

The studied succession represents a deltaic system that flanked a large lake (Dam & Surlyk 1992, 1993). The delta plain was characterized by distributary channels as well as interdistributary bays. The lake basin was probably low-lying and close to the open sea (Dam & Surlyk 1993), and the presence of plesiosaur bones as well as putative dinoflagellate cysts and 'true' dinoflagellate cysts in the studied succession suggest marine influence. Plesiosaurs are predominantly marine animals, but they have on rare occasions been reported in non-marine settings suggesting they could occasionally venture from the ocean into brackish to fresh-water environments (Gao *et al.* 2019). The presence of plesiosaur skeletal remains and teeth thus represents a marine signal in the middle part of Rhætelv Formation of the Kap Stewart Group. It is possible that the Kap Stewart plesiosaurs migrated seasonally between the sea and the inland lake (cf. Goa *et al.* 2019). Alternatively, the plesiosaurs could have entered the lake basin during a period of sea-level highstand. Reports of non-marine plesiosaurs are scarce and most of them originate from Cretaceous deposits closely associated with near-shore marine and estuary settings (e.g. Russell 1931; Kear 2006, 2012; Vajda & Raine 2010; Benson *et al.* 2013; Sachs *et al.* 2016, 2017; Gao *et al.* 2019). Jurassic records of plesiosaurs in non-marine settings are reported from the Middle Jurassic of China (Gao *et al.* 2019), and from fragmentary material from the lower Jurassic (Sinemurian and Toarcian) of Australia (Thulborn & Warren 1980; Kear 2012). Hybodont sharks are relatively common in the Jurassic (e.g. Rees 1998; Rees & Underwood 2008). They inhabited rivers, estuaries and lagoons as well as coastal marine environments (Rees 1998). Their presence in the vertebrate-bearing fossil bed therefore cannot be used to support marine influence.

The episode of likely marine influence took place in the middle of the deposits covered by the lake system. The age of this marine incursion has been constrained by palynological evidence to the Hettangian, probably middle to late Hettangian age. According to Haq (2017) and Kent *et al.* (2017) the Hettangian lasted from 201.3 to 199.5 Ma and thus had a duration of about 2 Ma.

It is suggested here that the plesiosaur arrived in the basin during a sea-level highstand. Surlyk (1990)

recorded a middle Hettangian sea-level rise event in the basin (Fig. 6). Hardenbol *et al.* (1998) define three global highstands (marine flooding surfaces), a minor one in the early Hettangian, followed by a medium and major highstand later in the Hettangian. Haq (2017) describes two highstands during the Hettangian both followed by sea-level drops; amplitudes of these sea-level variations were between 25 and 75 m (medium scale) or below 25 m (minor scale). According to Haq (2017), the first highstand occurred immediately before 200.8 Ma, while the second highstand occurred immediately before 200 Ma (Fig. 6).

Haq (2017) writes that the identified Jurassic sea-level variations are Eurocentric as they primarily are based on ammonite biostratigraphy in sections of central and northern Europe. Certain identification of contemporaneous highstands in the lowermost Jurassic deposits of central East Greenland is not possible due to the lack of ammonites. With assumed sea-level variation up to 75 m during the Hettangian it is considered likely, however, that the plesiosaurs arrived in the Jameson Land Basin during one of the two highstands of Haq (2017). As the palynological date indicates a middle to late Hettangian age, it seems likely that the marine incursion in the Jameson Land Basin can be correlated with the highstand that took place immediately before 200 Ma (Fig. 5). Surlyk (1990) also finds a middle Hettangian sea-level rise event. This interpretation of marine-influenced deposits occurring 185–200 m above the base of the Rhætelv Formation provides an important new numerical age control of this hitherto poorly age-constrained succession.

An additional, and early, episode of marine influence is suggested by the presence of a tooth from a marine shark, *Rhomphaiodon minor*, approximately 30 m above the base of the Rhætelv Formation near 'Track Mountain' (Hansen *et al.* 2016). This shark is known from marine deposits in the Rhaetian of NW Europe (Hansen *et al.* 2016). It is likely therefore that the Rhaetian-Hettangian (Triassic-Jurassic boundary) is situated somewhere between 30 and 185 m above the base of the formation. Additional palynological investigation of samples from this interval is required to place the boundary more accurately.

Imprints of brittle stars at the base of the overlying Neill Klint Group indicate a more permanent connection to the sea. According to Dam & Surlyk (1998) this transgression was gradual and took place at the Late Sinemurian–Pliensbachian transition, and the basin was flooded though a south-eastern entrance along the present day Scoresby Sund.

Offshore mid-Norway (Håltan Terrace) contemporaneous sediments in the Åre Formation (Rhaetian to Early Pliensbachian) formed during an overall

transgression (Thrana *et al.* 2014). The transgression in this area is witnessed by a succession that comprises lowermost non-marine coastal (delta) plain deposits followed by coastal plain deposits with marine influence, estuarine deposits, and at the top open marine shoreface deposits. The transgression was related to the establishment of a seaway between the Tethys Sea in the south and the Boreal Sea in the north (Thrana *et al.* 2014).

## Conclusions

The sediments of the Rhætelv Formation in the Kap Stewart Group (Rhaetian-Sinemurian) formed in a lake basin flanked by deltas. However, the discovery of plesiosaur bone remains in a thin sandstone bed in the middle part of the Rhætelv Formation at the eastern margin of the Jameson Land Basin suggests a period of marine influence in this otherwise strictly continental basin. A plesiosaur entered the basin during this period and bone remains of this animal were eroded from delta front sediments during a storm and probably transported onshore during an inundation event and deposited in a large interdistributary bay on the delta plain. Palynological data indicates that the marine incursion is of middle to late Hettangian age. By comparison with data on global sea-level variation, it is suggested that the marine incursion took place immediately before 200 Ma, and thereby gives a well-constrained age of the vertebrate-bearing fossil layer in the Rhætelv Formation.

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