GEOLOGICAL SURVEY OF DENMARK AND GREENLAND BULLETIN 34 · 2015

The ammonites of the Middle Jurassic *Cranocephalites* beds of East Greenland

John H. Callomon, Peter Alsen & Finn Surlyk

With an appendix by Peter Alsen:

Description of a new Bajocian (Middle Jurassic) ammonite species, *Cranocephalites tvaerdalensis* sp.nov., from Geographical Society Ø, North-East Greenland

GEOLOGICAL SURVEY OF DENMARK AND GREENLAND
MINISTRY OF ENERGY, UTILITIES AND CLIMATE

Geological Survey of Denmark and Greenland Bulletin 34

Keywords
Biostratigraphy, Middle Jurassic, Jameson Land Basin, Boreal Realm, Bajocian, Borealis Zone, Indistinctus Zone, Pompeckji Zone, Intermissus Subzone, Carlsbergensis Subzone, Gracilis Subzone, Episcopalis Subzone, *Cranocephalites carolae* sp. nov., *Cranocephalites intermissus* sp. nov., *Cranocephalites episcopalis* sp. nov.

Cover illustration
Jurassic sedimentary strata exposed on the south-western side of the upper Ugleelv valley in eastern Jameson Land. Such exposures along Ugleelv yielded rich Middle Jurassic ammonite faunas that formed the key to the detailed taxonomic and chronostratigraphic results presented in this bulletin. The height of the plateau above the valley floor is about 500 m. Photo: Michael Engkilde.

Frontispiece: facing page
John H. Callomon in the 'Greenland collections' room, at that time on the second floor of the Geological Museum (University of Copenhagen), repository of the material studied in this work. Photo: Peter Alsen.

Scientific editor of this volume: Jon R. Ineson
Editorial secretary: Jane Holst
Referees: Eckhart Mönning (Germany) and Paul L. Smith (Canada)
Illustrations: Jette Halsskov
Digital photographic work: Benny M. Schark
Layout and graphic production: Henrik Klinge Pedersen
Printers: Rosendahls · Schultz Grafisk a/s, Albertslund, Denmark
Manuscript received: 30 April 2014
Final version approved: 19 October 2015
Printed: 28 December 2015

ISSN (print) 1604-8156
ISSN (online) 1904-4666

ISBN (print) 978-87-7871-427-5
ISBN (online) 978-87-7871-428-2

Citation of the name of this series
It is recommended that the name of this series is cited in full, viz. *Geological Survey of Denmark and Greenland Bulletin.*
If abbreviation of this volume is necessary, the following form is suggested: *Geol. Surv. Den. Green. Bulletin 34,* 145 pp.

Available from
Geological Survey of Denmark and Greenland (GEUS)
Øster Voldgade 10, DK-1350 Copenhagen K, Denmark
Phone: +45 38 14 20 00, fax: +45 38 14 20 50, e-mail: geus@geus.dk

or at *www.geus.dk/publications/bull*

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Abstract

Callomon, J.H., Alsen, P. & Surlyk, F. 2015: The ammonites of the Middle Jurassic *Cranocephalites* beds of East Greenland.
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Thick successions of marine Middle Jurassic deposits rich in ammonites occur in the Jameson Land Basin in central East Greenland. The fauna of the so-called *Cranocephalites* beds of this basin, comprising the Borealis–Pompeckji Standard Zones, was until now largely represented by a single collection. This was made by T.M. Harris during a 1927 excursion up the valley of Ugleelv to Katedralen, the type area of *Cranocephalites pompeckji*, which is the oldest named species of this genus. Revisits to this area in 1994 and 1996 by JHC resulted in a large bed-by-bed collection of *Cranocephalites*. The number of faunal horizons that could be distinguished grew from the nine previously recognised to thirty-four today. The zonal stratigraphy of the *Cranocephalites* beds encompasses the Borealis, Indistinctus and Pompeckji Standard Zones. The Pompeckji Zone is subdivided into four new subzones, reflecting four successive basic morphologies of *Cranocephalites* that should be recognisable more widely and are thus useful for subzonal correlations. The detailed zonation that serves as the secondary standard zonation for the Boreal Province in the Middle Jurassic is thus highly improved. The biostratigraphic resolution obtained here is near the achievable limits. It allows a high-resolution study of the evolution of the ammonites which on this timescale appears to be continuous. Three new species are described: *Cranocephalites carolae* sp. nov., *Cranocephalites intermissus* sp. nov. and *Cranocephalites episcopalis* sp. nov.

An additional new species, *Cranocephalites tvaerdalensis* sp. nov., is described in the appendix by P. Alsen based on collections from Tværdal on Geographical Society Ø, North-East Greenland. This species is also recorded in Jameson Land.

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Preface

Professor John H. Callomon died on 1 April 2010. For many years, he had been occupied with resolving the faunal succession of the Middle Jurassic *Cranocephalites* beds in East Greenland. When he died he left an unfinished manuscript, which his family entrusted to Peter Alsen and Finn Surlyk to complete.

John H. Callomon had an interest in geology since childhood, but in his professional career he was a distinguished professor in his field of inorganic chemistry and wrote landmark papers in spectroscopy. His passion for Jurassic ammonite stratigraphy developed during his student years in Oxford where he also met Desmond T. Donovan, through whom John was first introduced to East Greenland as a member of an expedition led by Lauge Koch. He thought he was to assist Donovan during the 1957 field season, but after a few days Donovan flew off to Wollaston Forland and John was left with the responsibility to collect and record the Upper Jurassic sections in Milne Land. He subsequently participated in a number of expeditions to East Greenland and collaborated closely with the late Tove Birkelund and FS. The outcome was a number of papers on Middle and Upper Jurassic ammonite stratigraphy. In 1993, he was awarded the prestigious Steno Medal by the Danish Geological Society in recognition of the influence of his work for the understanding of the Jurassic in East Greenland.

Field camp in the Uglelev valley in the summer of 1971. From left to right: John Callomon, Tove Birkelund, Lise Alkjærsig (field assistant) and Finn Surlyk.

Introduction

Jurassic sedimentary rocks are widely distributed in central East Greenland and North-East Greenland from Jameson Land in the south to Store Koldewey in the north (Fig. 1A). They are commonly beautifully exposed and a comprehensive review was given by Surlyk (2003). Lower Jurassic rocks are restricted to the southern part of the East Greenland rift complex, in the Jameson Land Basin (Fig. 1B). The Kap Stewart Group comprises lacustrine and fluvial deposits of Rhaetian–Sinemurian age overlain by the shallow marine Neill Klinter Group of Pliensbachian – early Bajocian age (Dam & Surlyk 1998). Jurassic rifting was initiated in the late Bajocian and a large area north of the Jameson Land Basin was transgressed for the first time since the Late Permian. Major N–S-trending faults, which sidestepped *en echelon* to the east, controlled the margins of the Jurassic rift complex. The main sedimentary influx took place in the relay-ramp areas between the faults and the rift thus comprised several marine gulfs with their heads towards the north; the main sedimentary transport direction was axial towards the south. Rifting intensified during the Jurassic to reach a climax in mid-Volgian time (Surlyk 2003).

The key area for the study of Middle Jurassic biostratigraphy is Jameson Land where thick successions, commonly rich in ammonites, occur (Fig. 1B). Exposures along Hurry Inlet and around the river of Ugleelv are particularly important in this respect and this is where the ammonite faunas described in the classical monograph of Spath (1932) were collected. Other important, but less accessible areas occur in central and northern Jameson Land; all the localities are shown on the maps in Figs 2–7. The upper Bajocian – middle Callovian part of the early rift succession in Jameson Land is placed in the Pelion and Fossilbjerget Formations, as described below.

The Jurassic in East and North-East Greenland has served as an important analogue for contemporaneous successions in the northern North Sea and along the conjugate Norwegian margin. In addition, the ammonite faunal succession in the Middle Jurassic is the most complete in the Arctic and the zonation serves as a standard of reference for the Boreal Province (Callomon 1993).

History of research

The history of the knowledge of the Middle Jurassic ammonites of East Greenland can be resolved into four phases.

Early days

The first Middle Jurassic ammonites from East Greenland were collected by Nikolaj Hartz, Henrik Deichmann and Otto Nordenskjöld just over a century ago, during the Danish expedition in 1900 led by Georg Carl Amdrup and Hartz. The collections were described by Madsen (1904), who correctly assigned their ages as Middle Jurassic, probably Bathonian–Callovian, although he could not be more precise. He also relayed reports of "innumerable Ammonites scattered about on the plateaux inland", that is, in Jameson Land west of the northern reaches of Hurry Inlet (Madsen 1904, p. 169). This expedition, like others of this era, had been one of general natural science and geographic exploration.

The Koch years, 1926–1957: initial geological exploration

The systematic study of the geology of East Greenland began with the many expeditions led by Lauge Koch in the years 1926–1958. The widespread presence of richly fossiliferous Middle Jurassic marine sediments became apparent during the first of the expeditions in 1926–1927, when large collections of ammonites were made by Alfred Rosenkrantz and Tom Harris in Jameson Land west of Hurry Inlet in central East Greenland. They were described in a classical monograph by Spath (1932), which for many years remained the primary reference as it still is today, at least as concerns the description of species. What was lacking was a detailed stratigraphical framework. This was largely inevitable as the geological observations inland had to be made in the spring on sledge journeys over still largely snow-covered ground. The relative stratigraphic successions of forms found at widely scattered localities had in part to be inferred and the type horizons of most of them were not precisely known. All in all, the succession of ammonites seemed to characterise a series of four biostratigraphical units:

Kepplerites–Cadoceras beds (highest)
Arcticoceras beds
Arctocephalites beds
Cranocephalites beds (lowest)

Callomon and earlier authors informally used the term 'Beds', which in modern lithostratigraphical nomenclature refers to formal subdivisions of members; the term is accordingly given in lower case here.

These four units provide an overall frame of reference that continues to be useful today. The lowest unit rests on a thick succession of dark mudstones with only scattered fossils, and no ammonites, the Sortehat Formation of Dam & Surlyk (1998) and Surlyk (2003), now referred to the Neill Klinter Group (Dam & Surlyk 1998). Within these four Middle Jurassic biostratigraphic units, it seemed possible to distinguish some five ammonite faunal horizons, with indications of perhaps two more – a total of seven (Spath 1932).

Another rich collection from the Middle Jurassic of the coastal cliffs of Neill Klinter, along the western shores of Hurry Inlet, was made in 1933 by Hermann Aldinger, who also produced excellent geological maps and measured the first usable sections (Aldinger 1935). His collections, although also sent to London for analysis by Spath, were however never described. His published account of the succession was fully compatible with the biostratigraphy of Spath (1932) but added nothing of biostratigraphic significance. Further extensive collections were made in central Jameson Land by Stauber (1940) during horseback traverses in 1938 but these, too, were left undescribed; the collections were almost wholly devoid of stratigraphical information. After the Second World War, exploration was resumed north of Kong Oscar Fjord (72°N), on the islands of Traill Ø and Geographical Society Ø (Fig. 1A), but although the Middle Jurassic there is thickly developed and extensive, fossils, including ammonites, are scarce and scattered. Two further ammonite horizons were, however, recognised by Donovan (1955), bringing the total up to perhaps nine. The state of knowledge at the time was comprehensively reviewed by Donovan (1957).

1957–1993: detailed biochronology

A new phase in the study of the Middle Jurassic started with Koch's last two expeditions in 1957 and 1958. It was prompted by a re-examination of some serious unresolved problems posed by the faunas already described, relating to their ages. These problems are reflected in the names given by Spath (1932) to three of his four biostratigraphical units cited above.

The highest of these was named after the genera *Kepplerites*, of the family Kosmoceratidae, and *Cadoceras*, of the family Cardioceratidae. These families are well represented in the classical Jurassic succession of Europe, where as far as was then known, *Kepplerites* and *Cadoceras* made a sudden appearance somewhere in the lower but not lowest part of the Callovian. The Greenland forms, while sim-

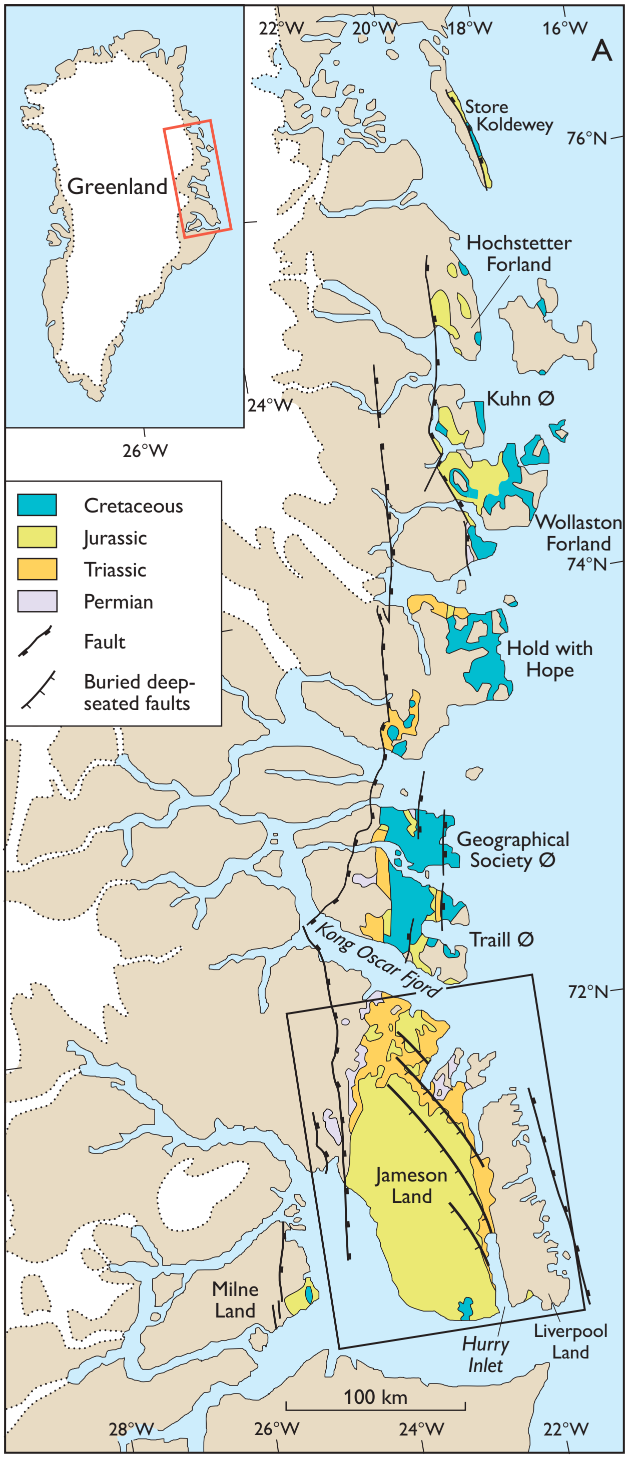
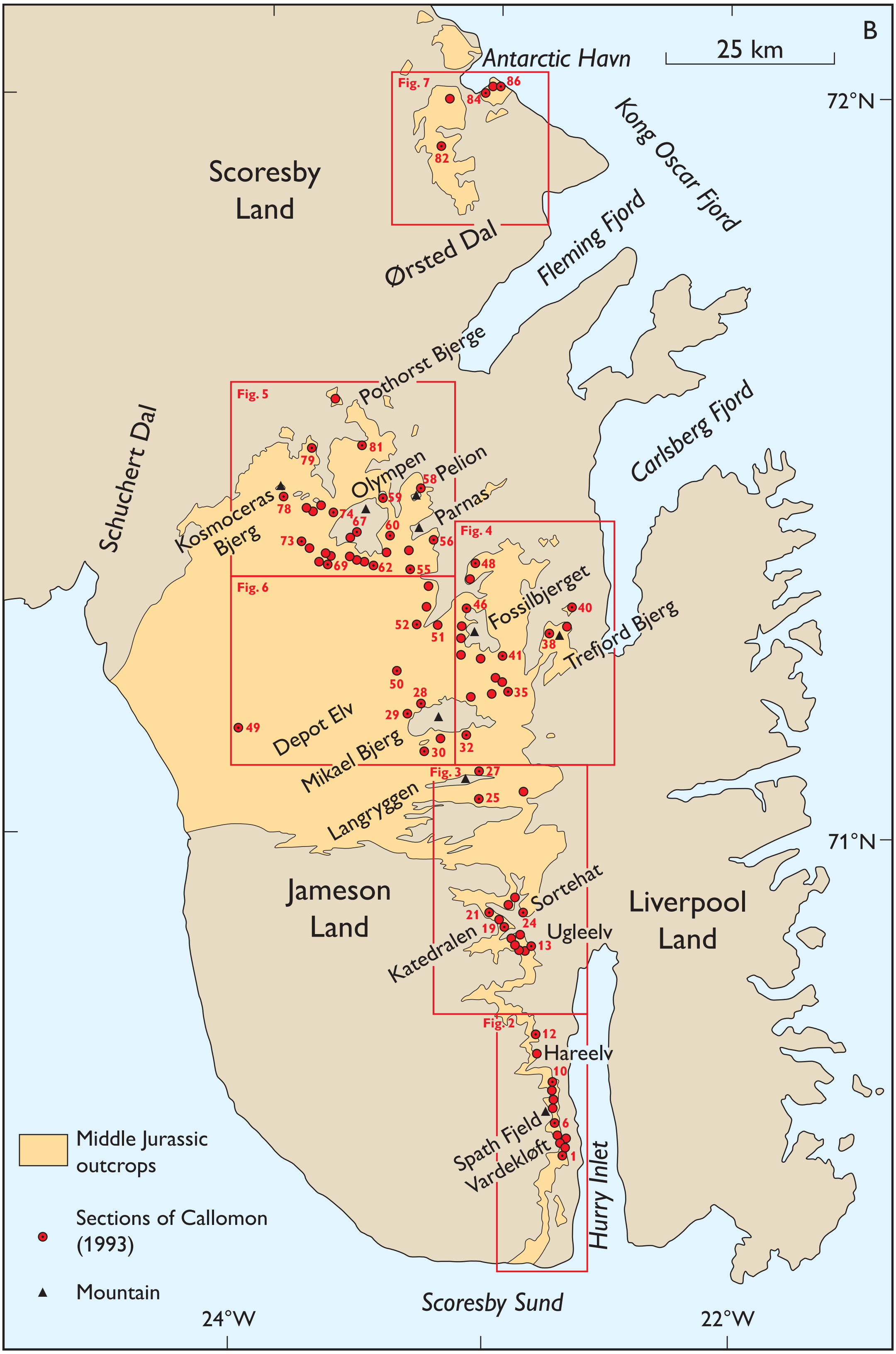


Fig. 1. **A**: Simplified geological map showing the distribution of Permian–Cretaceous sediments in East and North-East Greenland and with the study area of Jameson Land indicated. **B** (Facing page): Map of Jameson Land, showing the outcrops of the Middle Jurassic and the locations of the sections that had been recorded up to 1993, numbered 1–86 from south to north (Callomon 1993). Section numbers are indicated on selected sections; for more detailed positioning of sections see Figs 2–7.


B
25 km
Antarctic Havn
Fig. 7
84
86
82
72°N
Scoresby Land
Kong Oscar Fjord
Ørsted Dal
Fleming Fjord
Pothorst Bjerge
Fig. 5
Schuchert Dal
Carlsberg Fjord
81
79
Olympen
Pelion
58
59
Kosmoceras Bjerg
78
74
67
60
Parnas
73
56
69
62
55
Fig. 4
48
Fig. 6
Fossilbjerget
46
40
52
51
Trefjord Bjerg
38
41
50
35
28
29
Depot Elv
49
Mikael Bjerg
30
32
Fig. 3
27
25
Langryggen
71°N
Jameson Land
Sortehat
Liverpool Land
21
24
19
Ugleelv
13
Katedralen
Fig. 2
12
Hareelv
10
6
Spath Fjeld
Vardekløft
1
Hurry Inlet
Middle Jurassic outcrops
Sections of Callomon (1993)
Mountain
Scoresby Sund
24°W
22°W

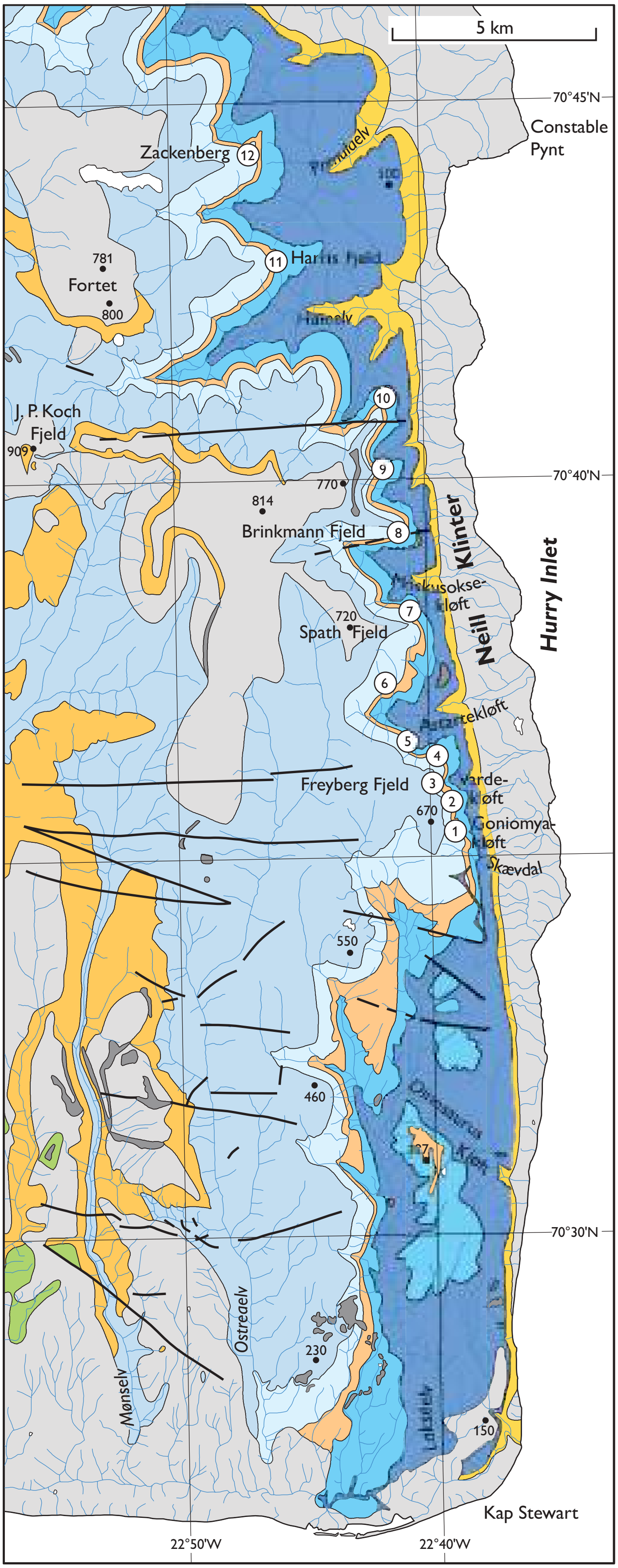


Fig. 2. Geological map showing locations of the sections 1–12 recorded by Callomon (1993) along Neill Klinter on the western shores of Hurry Inlet. Map section from geological map sheets 70 Ø.1 Syd (Bengaard *et al.* 1986) and 70 Ø.1 Nord (Friderichsen & Surlyk 1981). The accompanying legend is applicable to Figs 2–7 and Fig. 9. **N.K. Gp**: Neill Klinter Group.

Legend (Figs 2–7, 9)

⬜	Ice	
■	Recent and Quaternary drift	
	Recent alluvial fans	
■	Hesteelv Fm	Lower Cretaceous
■	Raukelv Fm	Upper Jurassic – Lower Cretaceous
■	Hareelv Fm	Upper Jurassic
■	Olympen Fm	
■	Fossilbjerget Fm	Middle Jurassic
■	Pelion Fm	
■	Sortehat Fm (N.K. Gp)	
■	Neill Klinter Gp (excl. Sortehat Fm)	Rhaetian – Lower Jurassic
■	Kap Stewart Gp	
■	Fleming Fjord Fm	Triassic
■	Gipsdalen Fm	
■	Pingodal Fm	
■	Wordie Creek Fm	
■	Extrusives	
■	Syenite intrusion	
	Sill	
—	Dyke	
•230	Altitude (metres above sea level)	

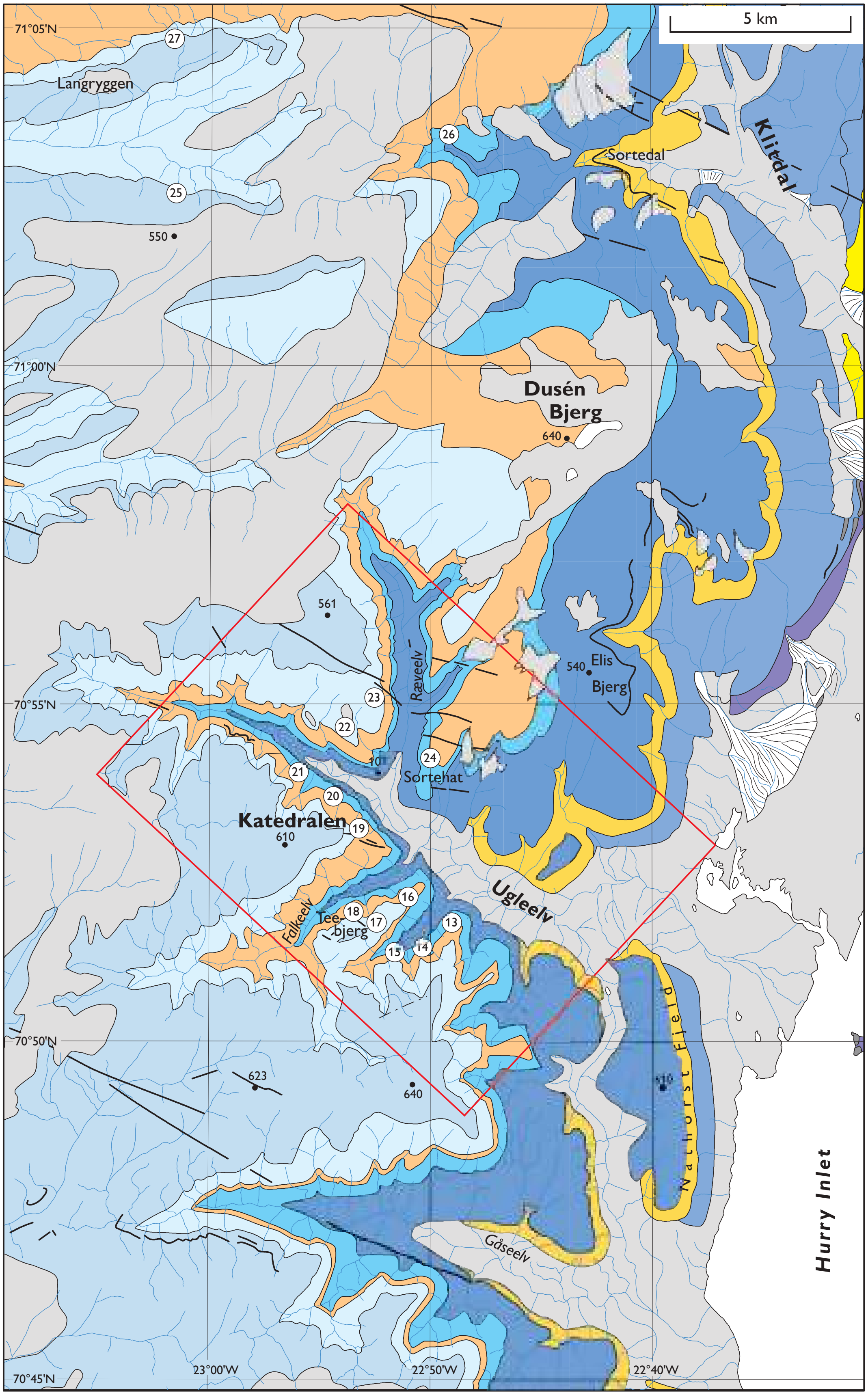


Fig. 3. Geological map of the area around Ugleelv with the names of places and locations of sections 13–27 recorded by Callomon (1993). Map section from geological map sheets 70 Ø.1 Nord (Friderichsen & Surlyk 1981) and 71 Ø.1 Syd (Birkelund & Higgins 1980). For legend, see Fig. 2; red box shows area of Fig. 9.

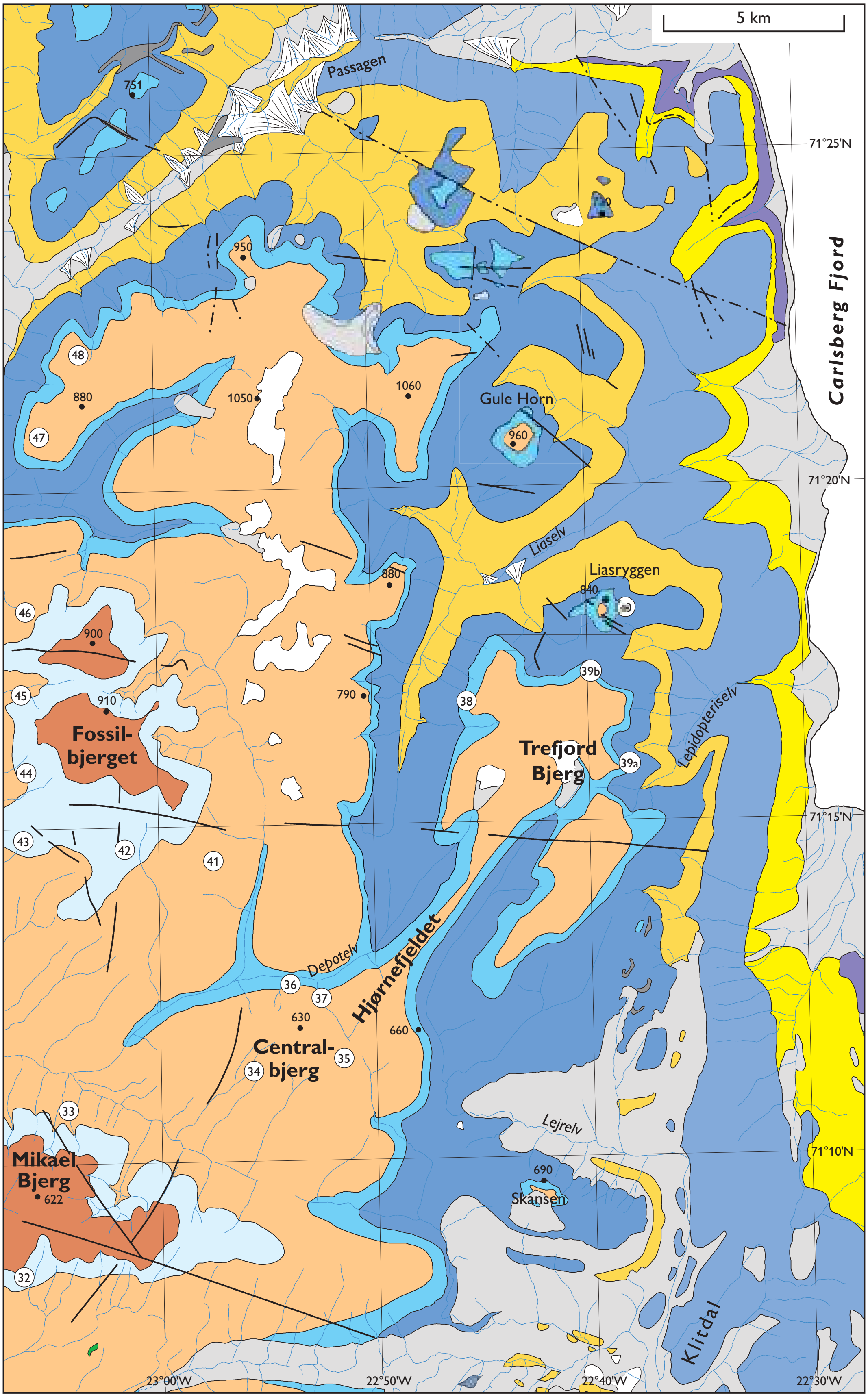


Fig. 4. Geological map of the area around Fossilbjerget and Trefjord Bjerg, showing locations of sections 32–48 recorded by Callomon (1993). Map section from geological map sheet 71 Ø.1 Syd (Birkelund & Higgins 1980). For legend, see Fig. 2.

ilar, were, however, not conspecific with the European forms. Nevertheless, it seemed safe to assign a Callovian age to them also, making them slightly older than the oldest European forms but squeezing them into the small biostratigraphical gap still left in the lower Callovian below their first appearance there (Spath 1932).

The ammonites from the three units below the *Cadoceras–Kepplerites* beds were, however, totally unknown in Europe. This is reflected by the new generic names they were given: *Cranocephalites*, *Arctocephalites* and *Arcticoceras*, in ascending order. They had, however, been previously recorded from elsewhere in the Arctic, for example in Petshora (Keyserling 1846, Sokolov 1912), Franz Josef Land (Newton & Teall 1897; Whitfield 1907) and Novaya Zemlya (Sokolov 1913; Salfeld & Frebold 1924). The evidence from East Greenland therefore suggested the existence of four successive ammonite associations, of which only the highest closely resembled European lower Callovian forms (Spath 1932). While unknown in the underlying European Bathonian, the three lower assemblages did, however, have a certain resemblance to the forms of another European family, the Macrocephalitidae, which dominate the lowest Callovian. The most cautious approach seemed therefore to assume that the morphological differences between the Greenland and European forms were perhaps a reflection of bioprovincial differentiation, making *Arctocephalites*, *Cranocephalites* and *Macrocephalites* but races of the Macrocephalitidae from the lower Callovian, or perhaps uppermost upper Bathonian. The corollary was that there were possibly no Bathonian ammonites in Greenland, nor, by correlation, anywhere else in the Arctic. An implicit assumption that hence there were also no sediments of Bathonian age in the Arctic was not well founded.

Very similar interpretations had meanwhile also been applied to closely analogous – and equally fallacious – observations on the Middle Jurassic ammonites of the whole of the American Cordillera, from the Andes to Alaska. These, too, could be interpreted as bioprovincially differentiated relatives of the Macrocephalitidae. Together, these interpretations did much to cause Arkell, in his influential book (Arkell 1956) to illustrate a more general picture of the Bathonian as a time of world-wide marine sea-level fall leaving no sediments. Attempts to date these Arctic faunas more securely could make no progress without new evidence.

The efforts of Callomon were therefore concentrated in 1957–1958 on the ammonite biostratigraphy of southern Jameson Land, making new in-place collections from carefully recorded sections. It quickly emerged that an immensely rich succession of faunas was to be discovered. After four weeks in the field, the number of faunal horizons characterised by clearly distinguishable ammonite assemblages had risen to nine (Callomon 1959). The resumption of systematic mapping of the sedimentary basins in central East Greenland by the University of Copenhagen in the years 1968–1974 provided access to the remoter interior of Jameson Land, where a wealth of localities and ammonite assemblages was discovered (Birkelund *et al.* 1971).

In all, over 80 sections yielding Middle Jurassic ammonites were recorded (Figs 1–7). The locations of the more important ones relevant to the present discussions are shown in Figs 2–4. The number of well-characterised, time-ordered, stratigraphically precisely located faunal horizons was now raised to thirty-seven. This biostratigraphical framework formed the basis of a standard stratigraphical classification down to zonal level. Callomon (1995) presented his views on the relationships between bio- and chronostratigraphy which are at variance with generally accepted distinctions between the two concepts as he saw his so-called standard zones, which are essentially chronozones, as basic units in chronostratigraphy. The stratigraphic results were reviewed by Callomon (1993, 2003) and are summarised in Fig. 8. The vertical timescale is drawn on an equispaced faunal horizon approximation, the horizons recognised by Callomon (1993) being numbered consecutively upwards as shown on the right in the figure. The species of *Kepplerites* found in the middle of the succession, at horizon 25, is so similar to that found in the *Kepplerites keppleri* horizon defining the base of the Callovian in Europe (Callomon & Dietl 2000) that the Bathonian age of the underlying 24 horizons could no longer be in doubt. There were in fact strong grounds, based on a chain of correlations via the East Pacific, for believing that the lowermost faunal horizon in Greenland, that of *Cranocephalites borealis*, was of early late Bajocian age (Callomon 1985a). Such a correlation has meanwhile received support from strontium stable-isotope stratigraphy based on belemnites (M. Engkilde, personal communication 1998).

It had become clear that the upper Bajocian and Bathonian ammonite succession of central East Greenland was now the best known and nearest to complete anywhere within the clearly delimited Boreal Province, whose ammonites were so strongly endemically confined that precise correlations with their temporal equivalents elsewhere in the world remained impossible: there were no known areas of overlap.

A separate bioprovincial secondary standard chronozonation (in the sense of Callomon 1985b) for the Boreal Province was therefore to be constructed in parallel with the primary standard zonation (Fig. 8). The primary standard zonation has also been drawn on a European equispaced faunal horizon approximation by Callomon & Chandler (1990) for the Bajocian, Westermann & Callomon

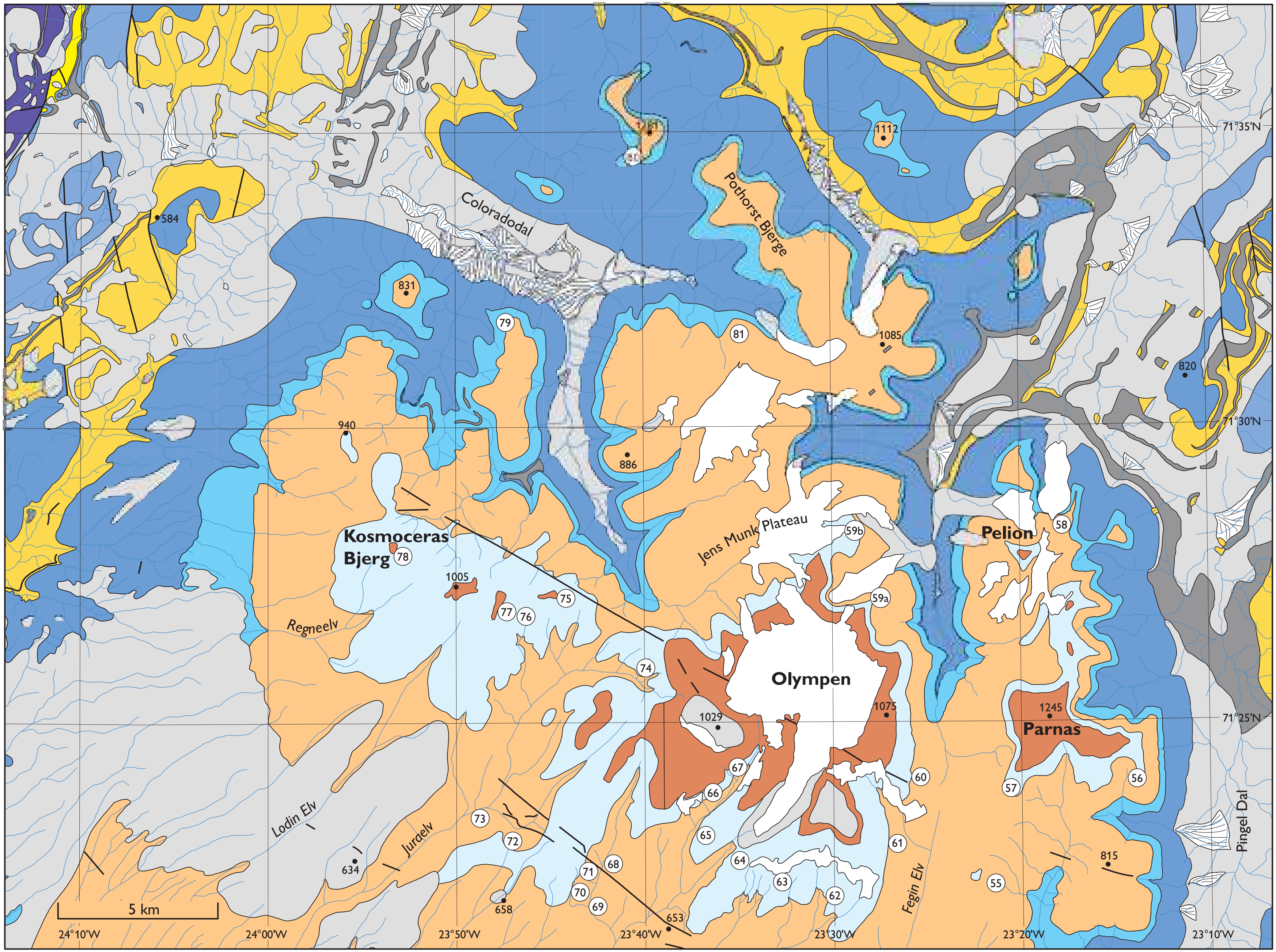


Fig. 5. Geological map of the area around the mountains Olympen, Parnas and Pelion showing locations of sections 55–81 recorded by Callomon (1993). Map section from geological map sheets 71 Ø.1 Syd (Birkelund & Higgins 1980), 71 Ø.2 Syd (Friderichsen & Bromley 1976), 71 Ø.2 Nord (Henriksen & Perch-Nielsen 1977) and 71 Ø.1 Nord (Perch-Nielsen *et al.* 1983). For legend, see Fig. 2.

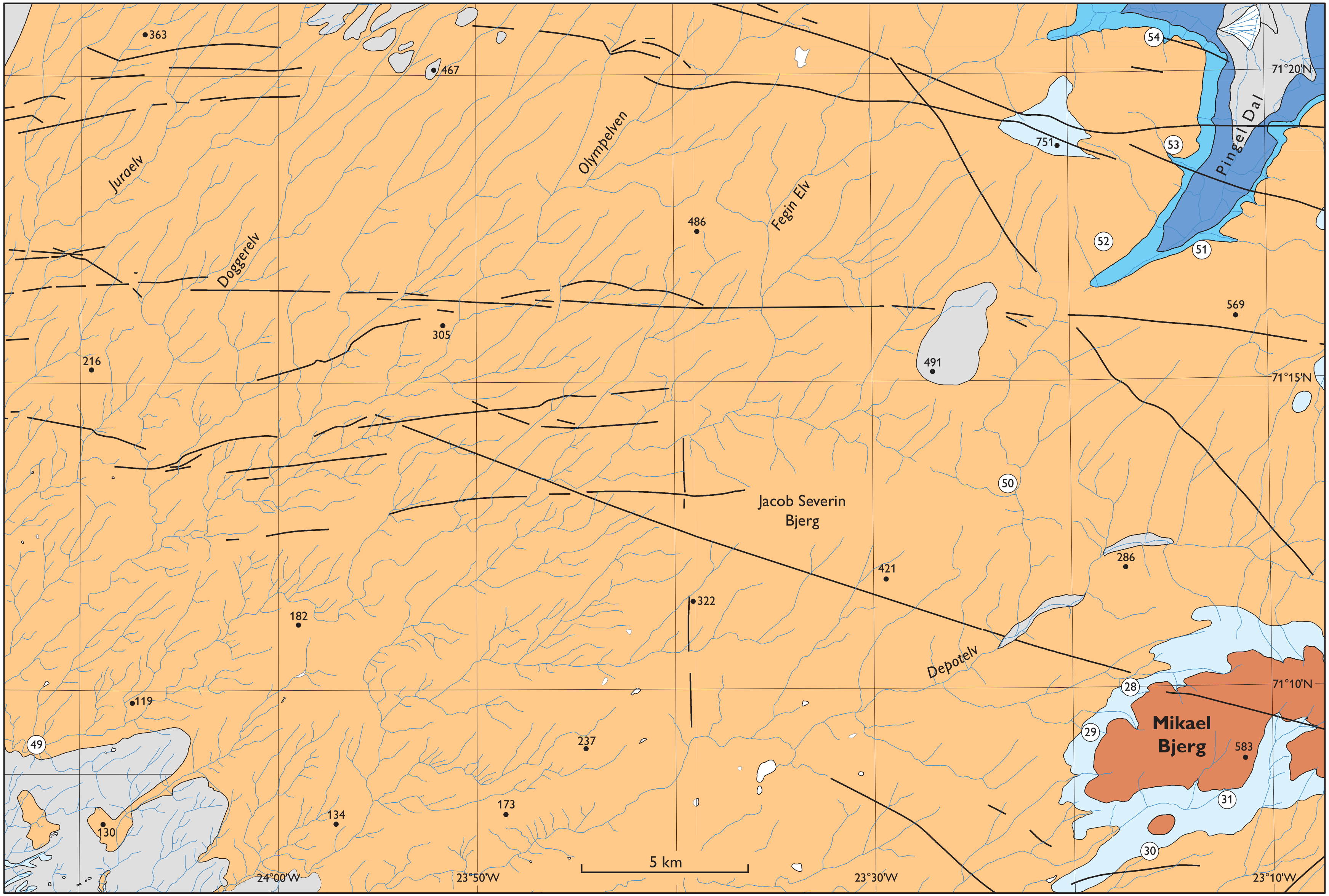


Fig. 6. Geological map of the area around Mikael Bjerg showing locations of sections 28–31 and 49–54 recorded by Callomon (1993). Map section from geological map sheets 71 Ø.1 Syd (Birkelund & Higgins 1980) and 71 Ø.2 Syd (Friderichsen & Bromley 1976). For legend, see Fig. 2

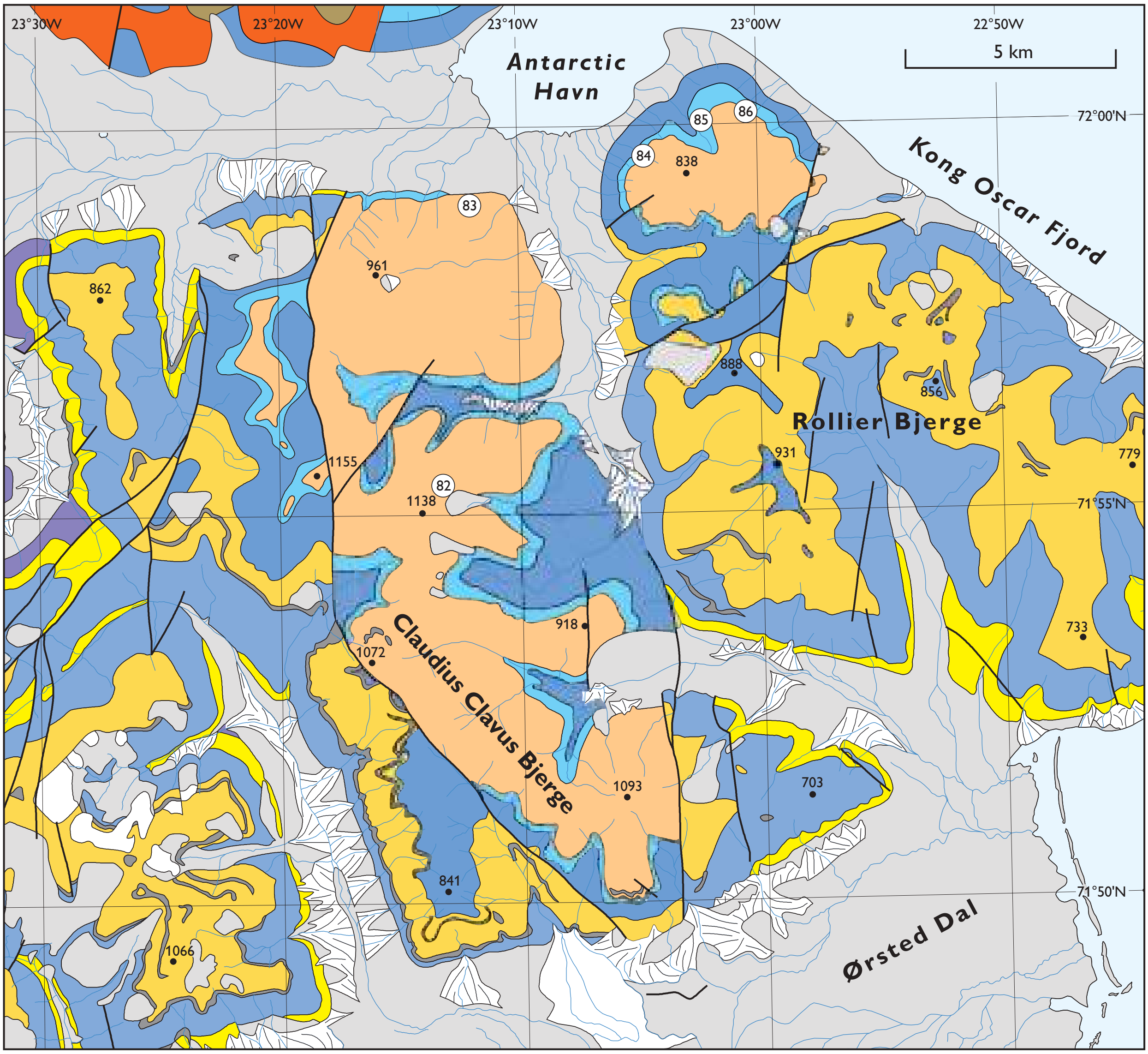
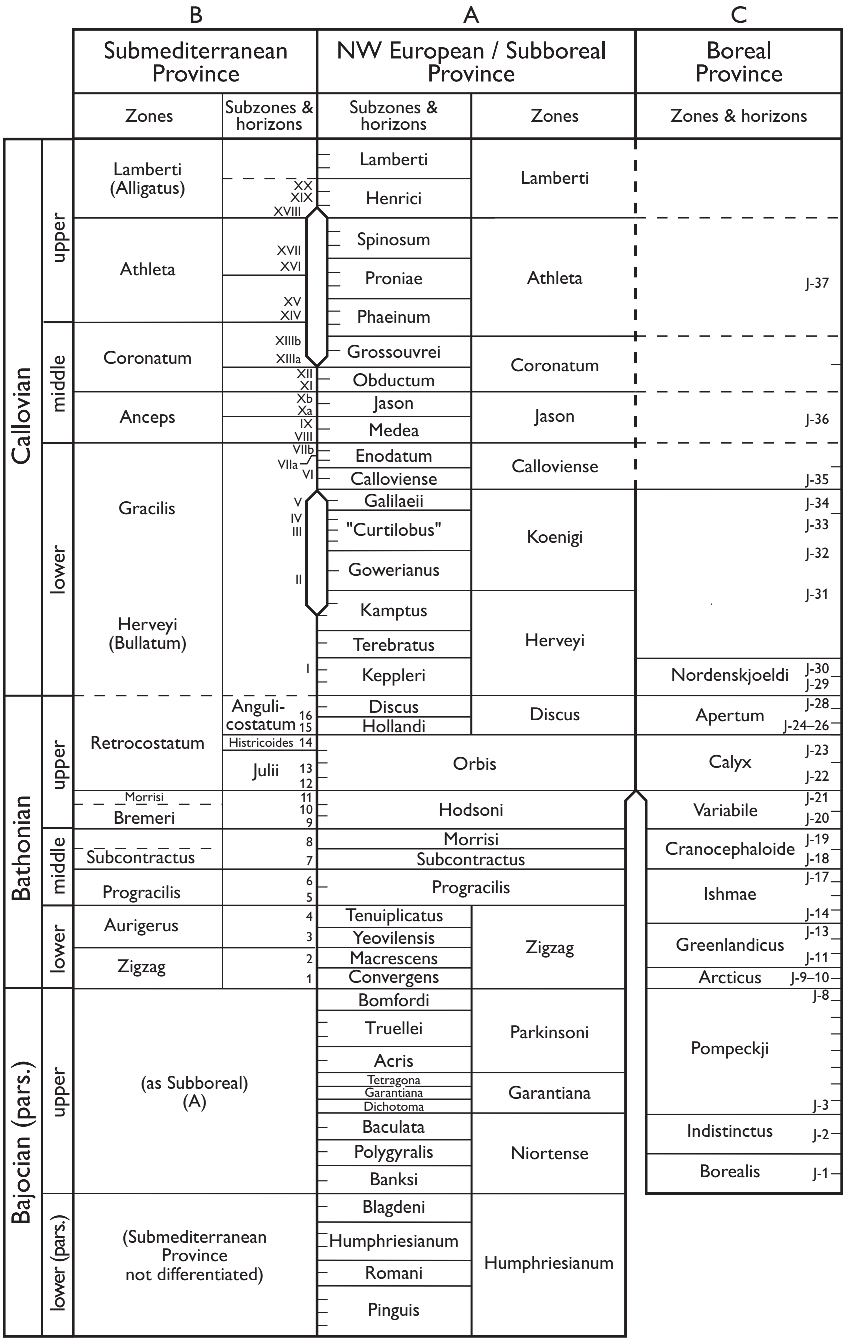


Fig. 7. Geological map of the area around Antarctic Havn showing locations of sections 82–86 of Callomon (1993). Map section from geological map sheets 71 Ø.1 Nord (Perch-Nielsen *et al.* 1983) and 72 Ø.2 (Escher 2001). For legend, see Fig. 2.

(1988) for the Bathonian, and summarised in Callomon (2003). There is no *a priori* reason to believe that the faunal horizon-density, i.e. the reciprocal of the mean time-interval between effectively instantaneous faunal horizons (Callomon 1995, p. 136), is the same in the two scales. It is largely coincidental that the lowest horizon on the right in Fig. 8 falls not far above its probable time equivalent in the left column, in the upper part of the Humphriesianum Standard Zone. It does however suggest that the rate of morphological evolution of the Boreal ammonites was not so very different from that of their cousins (at family-group level in the Linnéan hierarchy of taxonomy) in the sub-Tethyan domains farther south (Callomon 1985a). But it does suggest that the records of the succession in the two domains are now known with comparable completeness.

As knowledge of the Greenland succession grew and there was no way of dating the pre-Callovian part more closely, this part was comprehensively referred to at stage level simply as ‘Boreal Bathonian’ (Callomon 1975, 1979, 1985a, b, 1993). Although it is now certain that the lower part is in fact Bajocian, the Bajocian–Bathonian boundary can still not be precisely located in the Arctic. It cannot however lie far from the boundary between the Pompeckji and Arcticus Standard Zones (horizons 8/9), a boundary marked by an easily and widely recognisable morphological change in the ammonites. Discoveries on the Russian Platform, near

Fig. 8. Ammonite zonal correlation chart with the primary European standard (column **A**, revised), and the secondary Boreal standard (**C**) (Callomon 1993, fig. 2, 2003, fig. 3, revised according to Mangold 1990, 1997; Mitta 2002, 2008, 2009; Mönnig 2010, 2014). Ammonite faunal horizons J1 – J37 recognised in the Middle Jurassic in Jameson Land up to 1993 are shown. They are given the prefix J to clearly distinguish them from the Middle–Upper Jurassic succession of faunal horizons in nearby Milne Land (faunas 1–47 of Callomon & Birkelund 1980, 1982; Birkelund & Callomon 1985) which are accordingly labelled M1 – M47 (e.g. Larsen *et al.* 2003).



Saratov on the Volga River (52°N, 500 km SE of Moscow; Mitta & Seltzer 2002), include *Arcticoceras* of the basal Ishmae Standard Zone (horizon 14) associated with *Parkinsonia* ex gr. *wuerttembergica* characteristic of the top of the European lower Bathonian Zigzag Standard Zone (Fig. 8). No great error is therefore likely to result for general purposes from assigning the Borealis–Pompeckji Zones – the *Cranocephalites* beds – to the upper Bajocian and the Arcticus–Calyx Standard Zones to the Bathonian. More recently, however, Mitta (2009) argued that the Greenlandicus Zone in the Timan–Petchora region correlates with the central Russian (Volga) lowermost Bathonian Besnovi Zone, which would then place the underlying Arcticus Zone in the uppermost Bajocian, but this seems to need further confirmation.

1994–1996: Ugleelv, central Jameson Land

In compiling the faunal succession of Fig. 8, the greatest difficulty lay in the lower part, in the Indistinctus–Pompeckji Standard Zones of the *Cranocephalites* beds. The *Arctocephalites* and *Arcticoceras* beds appeared to be widely rep-

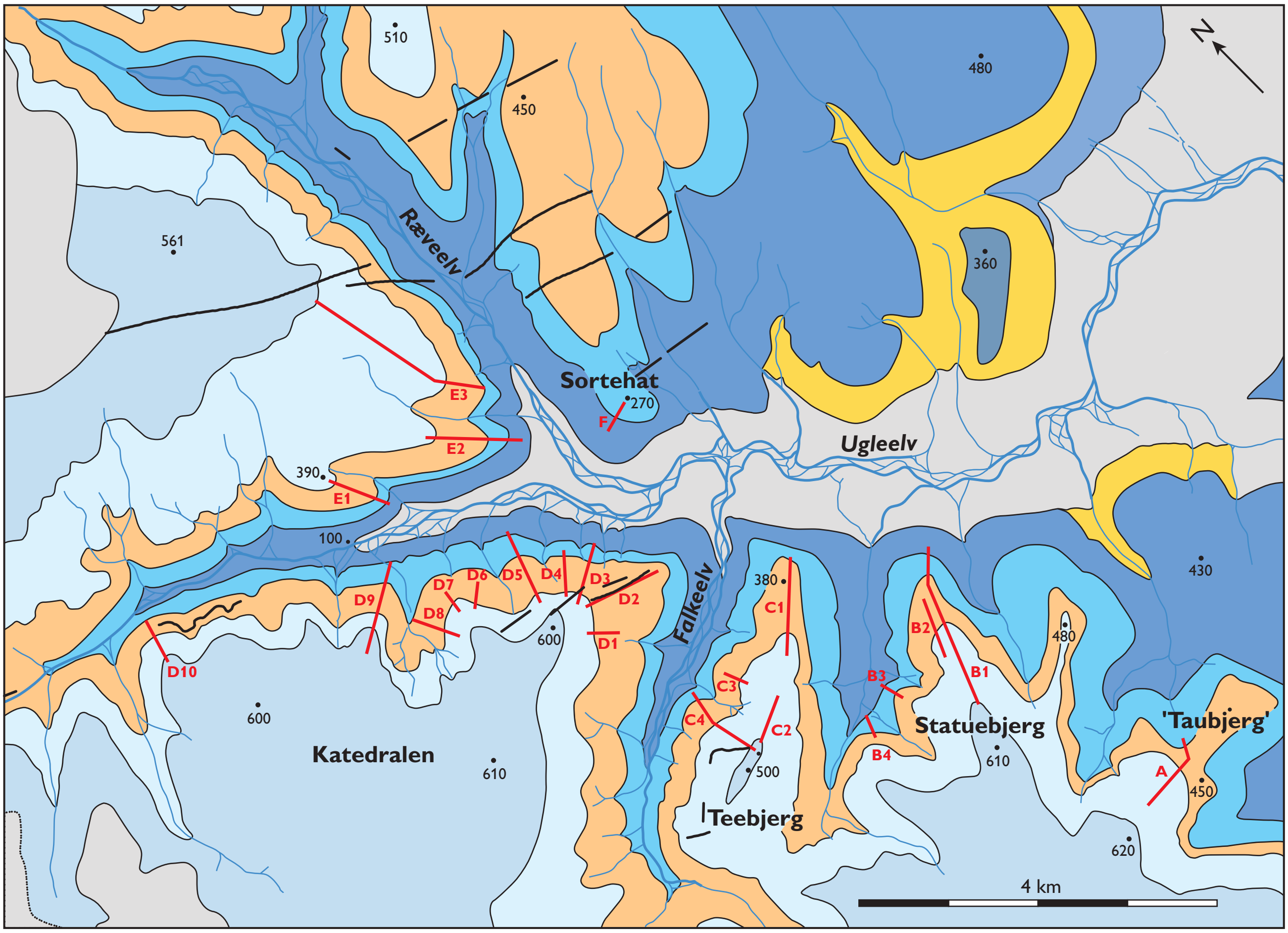


Fig. 9. Geological map of the area around Ugleelv (see Fig. 3), showing the locations of the 23 sections that have been recorded there up to 1996. They include sections 13–24 of Callomon (1993), but they have been collectively newly labelled in six groups A–F as shown. For the correspondence between old and new numbers, see Table 1; for legend, see Fig. 2. Note that 'Taubjerg' is an informal name.

resented in Jameson Land and elsewhere in the Arctic, and their ammonite faunas well sampled in the collections from Hurry Inlet made by Rosenkrantz in 1926–1927 and H. Aldinger and others in later years. However, what was known of the *Cranocephalites* beds was based largely on a single collection made by Harris during an excursion in 1927 up the valley of Ugleelv, west of upper Hurry Inlet, to its headwaters around Katedralen (see map in Rosenkrantz 1934, p. 86, fig. 34). This is also the type area of the oldest named species brought back in 1900, *Cranocephalites pompeckji* (Madsen 1904). Spath's description (1932) of Harris' material revealed a diverse spectrum of forms wholly unknown from Hurry Inlet but also represented in part in the collections made by Rosenkrantz around Mikael Bjerg in north-central Jameson Land (Fig. 4) where a caption to a photograph reads "in the foreground thousands of ammonites lie spread over the ground" (Rosenkrantz 1929, p. 145). Reconnaissance traverses by J.H. Callomon in 1958 and during mapping by the University of Copenhagen in 1970–1974 confirmed the richness of the faunas but could not resolve the stratigraphical uncertainties. Each section seemed to have a specific, but different set of assemblages, the relative temporal relationships of which to each other remaining unclear. The faunal succession in the Indistinctus and Pompeckji Standard Zones was the best that could be done with the available evidence (Callomon 1993; Fig. 8, faunas J-2 – J-8).

Opportunities arose in 1994 and 1996 for Callomon to revisit the area at Ugleelv, in order to concentrate on the ammonite biostratigraphy of the *Cranocephalites* beds. The results obtained exceeded all expectations. Some 750 ammonites were collected bed-by-bed from 23 sections. The number of faunal horizons that could be distinguished grew from the nine recognised in 1993 (Fig. 8) to thirty-four today. It should be stressed however that the assemblages characterising these horizons differ widely in quantity and quality. Even when not sufficiently well-characterised to define a new nominal species, an assemblage may, however, suffice to affirm that it differs from others. The area around Katedralen at Ugleelv now provides the most detailed and complete biostratigraphical record of the ammonites of the *Cranocephalites* beds anywhere and it is the purpose of this paper to describe this record. The Ugleelv sections thus set the standard of reference, and records from other localities will be drawn in as secondary evidence and for comparison.

Further discoveries have also been made in subsequent years from scattered localities to the north of Kong Oscar Fjord (Fig. 1A; Alsen & Surlyk 2004; Piasecki *et al.* 2004a, b) but these have not added to the list of faunal horizons.

Stratigraphy

Localities

Significant information on the *Cranocephalites* beds in Jameson land has come from three areas:

(a) The coastal cliffs of Neill Klinter, along the western shores of Hurry Inlet, sections 1–8 of 1993 (Fig. 2).
(b) Ugleelv, around Katedralen and Sortehat, sections 13–23 (Fig. 3).
(c) East-central Jameson Land, around Centralbjerg, section 35, including Hjørnefjeld of Rosenkrantz (1929) and Spath (1932), and Trefjord Bjerg, section 39 (Fig. 4).

By far the most extensive and detailed information has come from the Ugleelv area, and this is taken to set the standard of reference. Additional information has come from scattered localities to the north, at Antarctic Havn (Figs 1B, 7; sections 82–86 of Callomon 1993), Traill Ø on the northern side of Kong Oscar Fjord (Donovan 1953; Alsen & Surlyk 2004) and Geographical Society Ø (Fig. 1A; Alsen 2015, Appendix 1, this volume), but these will be only briefly alluded to.

The locations of the 23 sections that have been studied in the Ugleelv area are shown on the geological map in Fig. 9. A new and independent section-numbering scheme is introduced for this key region, which prior to the 1994–1996 fieldwork included 12 sections (13–24 on Figs 1B, 3; Callomon 1993). Table 1 illustrates the correspondence between the sections of Callomon (1993) and the section series presented here for the key area of Ugleelv (Fig. 9). The sections lie in clusters, which may be conveniently labelled by a letter as prefix:

A: 'Taubjerg' (field name of Callomon) at the eastern most outcrop. 'Taubjerg' takes its name from the striking resemblance of the Pelion Formation outcrop seen in map view to the Greek letter 'τ'.
B1–B4: Statuebjerg (named by T.M. Harris in Rosenkrantz 1934, fig. 38).
C1–C4: Teebjerg ('tee' as in golf, named by T.M. Harris in Rosenkrantz 1934, fig. 38).
D1–D10: Katedralen (named by T.M. Harris in Rosenkrantz 1934, fig. 38).
E1–E3: Ræveelv (named by T.M. Harris in Rosenkrantz 1934, fig. 38).
F: Sortehat (named by T.M. Harris in Rosenkrantz 1934, fig. 38).

Sections are subdivided into numbered beds with each section having separate bed numbering. The subdivision is based on field-observed surfaces. A bed numbered 1 in a given measured section is the lowest bed in that particular section, with the chosen base of section depending on the topography, outcrop exposure etc. Thus bed 1 in one section does not necessarily, and is rather unlikely to, correlate with bed 1 of other sections. References to bed numbers in sections thus mainly serve to relate observations to a height or interval of those sections, typically the records of a taxon within the study area.

Lithostratigraphy

The Standard Zone concept used by most Jurassic ammonite workers is used throughout this paper also in the descriptions of lithostratigraphic units (see e.g. Callomon 1985b, 1995, 2001; Page 2003). It is important to stress that standard zones are chronozones and not biozones, even if their names are derived from the names of ammonite species. This significant difference, which is commonly overlooked, is indicated by using the non-italicised species name with an upper case first letter (e.g. Borealis Standard Zone and not

Table 1. Previous section labels in relation to this study

Locality	Callomon (1993, fig. 4)		1994 field nos	1996 field nos	This study	
Goniomyakløft		1				Fig. 16
'Taubjerg'				96/4	A	Fig. 17
Statuebjerg	N	13			B1	Fig. 18
				96/1	B2	Fig. 19
	W	14			B3	
	SW	15			B4	
Teebjerg	A	16	94/18		C1	
	B	17	94/18		C2	
		18	94/18		C4, 4'	Fig. 21
				96/13	C3	Fig. 20
Katedralen	E	19			D1	
			94/14	96/11	D2, 2'	Fig. 22
				96/10	D3	
				96/2	D4	Fig. 23
	N	20		96/3	D5	Fig. 24
				96/6	D6	
				96/5	D7	
			94/15		D8	Fig. 25
	NW	21			D9	
				96/7	D10	Fig. 26
Ugleelv–Ræveelv			94/16		E1	Fig. 27
	A	22	94/13		E2	Fig. 28A, B
	B	23	94/17	96/4	E3	Fig. 35A–C
Sortehat		24		96/12	F	
Trefjord Bjerg		39a		96/15		Fig. 29

the *Cranocephalites borealis* Zone or Biozone). A Standard Zone can thus include unfossiliferous strata and its boundaries are isochronous surfaces in contrast to those of biozones. The Middle Jurassic ammonite-based zones of the present study are thus described as Standard Zones following the use of Callomon (1985b, 1995, 2001), even if in the opinion of PA and FS they are biozones.

Jameson Land

The Middle Jurassic of Jameson Land is subdivided into the lithostratigraphical framework figured by Surlyk (2003); formal lithostratigraphic revision of the Jurassic of East Greenland, as figured provisionally in Surlyk (2003), is in progress. The Middle Jurassic succession is placed in the Vardekløft Group which was originally introduced as a formation by Rosenkrantz (1929). It was revised, described and subdivided into the Sortehat, Pelion and Fossilbjerget Members by Surlyk *et al.* (1973) who also gave a historical account. The Sortehat Member was excluded from the formation by Surlyk (1991) and subsequently re-assigned at the status of formation to the newly-defined Neill Klinter Group (Dam & Surlyk 1998). The upgraded Vardekløft Group includes the Bristol Elv, Bastians Dal, Muslingebjerg, Pelion, Charcot Bugt, Fossilbjerget, Payer Dal, Olympen, and Jakobsstigen Formations (Surlyk 2003, fig. 5). In the present context, only those units occurring in Jameson Land are described, viz. the Pelion, Fossilbjerget and Olympen Formations.

The group forms the top unit in most areas of its distribution so the maximum thickness is not well known, but is probably up to about 650 m thick. In Jameson Land, it comprises the sandstone-dominated Pelion Formation and the overlying mudstone-dominated Fossilbjerget Formation.

The *Pelion Formation* overlies black mudstones of the Aalenian – lower Bajocian Sortehat Formation with a sharp boundary (Dam & Surlyk 1998; Koppelhus & Hansen 2003) and is overlain by black mudstones and massive sandstone injectites of the Hareelv Formation (Surlyk *et al.* 2007). It was erected as the middle member of the Vardekløft Formation, which originally included the Sortehat, Pelion and Fossilbjerget Members (Surlyk *et al.* 1973) and was preliminarily elevated to formation rank by Surlyk (2003, fig. 5). Key sections occur at Pelion (type locality), Goniomyakløft, Zackenberg, Katedralen, Mikael Bjerg, Trefjord Bjerg and Olympen (Figs 1–4). The thickness increases northwards from about 10 m in south-eastern Jameson Land to 310 m at the type section at Pelion and 650 m at Antarctic Havn, although the latter section may include the lower part of the Olympen Formation. Cross-bedded, planar-bedded and hummocky cross-stratified medium-grained, micaceous sandstones dominate, with subordinate coarse-grained and pebbly sandstones. The fossil content comprises ammonites, belemnites, bivalves, crinoids and brachiopods and deposition took place in marine shoreface and shallow shelf environments (for details, see Engkilde & Surlyk 2003). The formation spans the upper Bajocian – middle Callovian Borealis–Jason Standard Zones (Faunal horizons 1–36 of Callomon 1993), based on ammonites. The uppermost strata are poorly fossiliferous and the age relations to the overlying Olympen Formation are not always certain.

In Jameson Land, the Pelion Formation is locally subdivided into the Ugleelv and Parnas Members. The Ugleelv Member was named after the river in south-eastern Jameson Land (Figs 1B, 3). The Ugleelv Member of the Pelion Formation overlies dark silty mudstones of the Sortehat Formation and is overlain by grey siltstones of the Fossilbjerget Formation. The upper boundary is a marked ammonite-strewn drowning surface. The member is restricted to an area around inner Ugleelv and Ræveelv, south-eastern Jameson Land (Fig. 3). It belongs to the upper Bajocian Borealis – basal Pompeckji Standard Zones (Faunal horizons 1–4 of Callomon 1993), based on ammonites. The lower part of the member consists of sandstone (Borealis Standard Zone), and the middle part of siltstone (Indistinctus Standard Zone). The member is characterised by one (at Katedralen) or two (at Ræveelv) prominent, cliff-forming, high-angle clinoform-bedded sandstones, which form the upper part of the member (see Surlyk *et al.* 1973, fig. 19; Heinberg & Birkelund 1984, figs 13–14). The lower part of the member at these localities consists of structureless or cross-laminated, cross-bedded and hummocky cross-stratified, very fine-grained to medium-grained sandstones. It contains abundant ammonites and belemnites, bivalves, crinoids, brachiopods, rare gastropods, trace fossils and wood fragments. Fossils are commonly concentrated in distinct layers. Deposition took place in shallow marine shelf and shoreface environments. The upper clinoform-bedded part of the member was deposited in a tidally-influenced shoreface transition zone.

The overlying Parnas Member was first recognised as a sandstone wedge in the top part of the Pelion Formation by Heinberg & Birkelund (1984). The member is named after the mountain Parnas in north-central Jameson Land and the type section is on the north-east slope of the mountain Olympen, also in northern central Jameson Land (Fig. 1B). The member is about 30 m thick and consists of very fine-grained to coarse-grained sandstones forming metre-scale coarsening-upward cycles. It contains abundant ammonites and belemnites, rare bivalves, trace fossils and wood fragments, and deposition took place in a shallow marine shelf to shoreface. It interdigitates with the upper part of the Fossilbjerget Formation, hence temporarily interrupting the general northwards backstepping nature of the Pelion–Fossilbjerget boundary. It overlies very fine-grained silty sandstones of the Fossilbjerget Formation with a gradational transition. The upper boundary is a major drowning surface, which is sharply overlain by very fine-grained silty sandstone of the Fossilbjerget Formation. The Parnas Member is exposed in the mountains of Olympen, Parnas, Pelion and on the north slopes of Fossilbjerget in northern central Jameson Land. It wedges out towards the south and is not present at Mikael Bjerg (Figs 1, 4). It belongs to the lower Callovian Apertum–Nordenskjoeldi Standard Zones (Faunal horizons 24–30 of Callomon 1993), based on ammonites.

The *Fossilbjerget Formation* was erected as a member of the Vardekløft Formation by Surlyk *et al.* (1973) and was preliminarily elevated to formation rank by Surlyk (2003, fig. 5). The type section is at the mountain of Fossilbjerget (Surlyk *et al.* 1973, fig. 23; Fig. 1B) and key sections occur at Goniomyakløft, Zackenberg, Katedralen, Mikael Bjerg, and Pelion (Figs 1–4). The formation is 80–120 m thick and consists of silty, highly micaceous mudstone, with subordinate beds of fine-grained sandstone. Ammonites occur in profusion, and bivalves, belemnites, dinoflagellate cysts, tree trunks and trace fossils are common. Deposition took place in an offshore marine environment. The formation overlies sandstones of the Pelion Formation with a highly diachronous boundary, younging towards the north and is overlain in central Jameson Land by massive sandstones of the Olympen Formation (Athene Member) and in southern Jameson Land by a thin unit of black mudstones of the Olympen Formation (Hades Member). It occurs throughout Jameson Land but appears to have been removed by modern erosion in the northernmost part. As noted above, the sandy Parnas Member of the Pelion Formation forms a southward-tapering wedge in the top part of the formation in northern central Jameson Land (Fig. 1B).The Fossilbjerget Formation belongs to the upper Bajocian – lower upper Callovian, Pompeckji–Athleta Standard Zones (Faunal horizons 3–37 of Callomon 1993), based on ammonites.

The Goniomyakløft Member was recognised as a sharp-based unit of soft light-grey weathering shales, about 20 m thick, forming the top of the Vardekløft Formation in southern Jameson Land (Surlyk *et al.* 1973). The member corresponds roughly to the 'Wood Beds' of Callomon (1993). The type section is at Goniomyakløft, Hurry Inlet (section 6, fig. 14 in Surlyk *et al.* 1973) and good sections occur at Zackenberg and Katedralen (Fig. 2). The member consists of light-grey mudstones with large, greenish, irregular, extremely hard concretions commonly with a nucleus formed by silicified logs. Rare ammonites are found

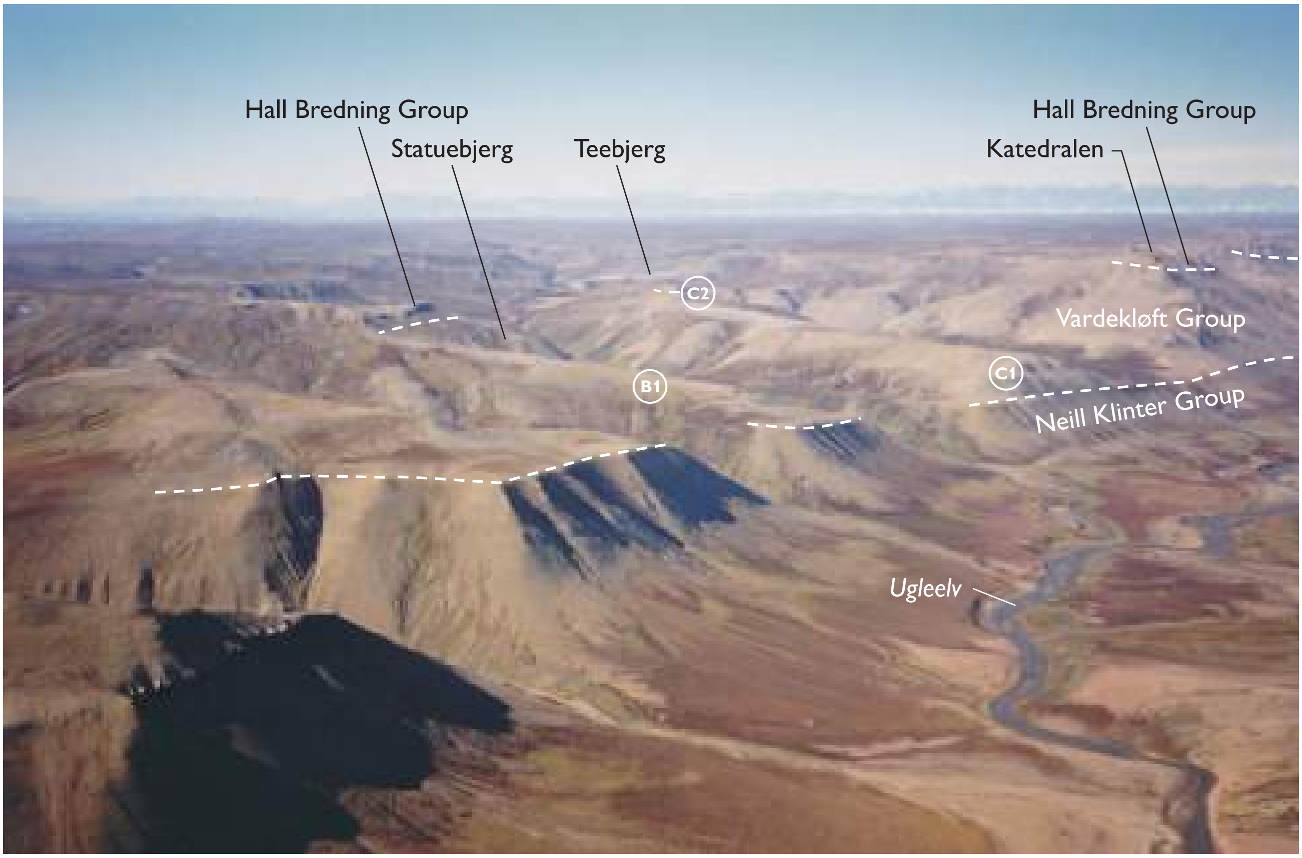


Fig. 10. Aerial view of the southern valley side of Ugleelv, looking almost due west. The highest peak in the far distance on the right is Katedralen. Coming nearer, the two long ridges falling into the valley are Teebjerg and Statuebjerg respectively, rising in the far distance on the left into the regional plateau formed by the resistant Hareelv Formation (Hall Bredning Group). The scarp-edged plateau in the near distance is formed by the top of the resistant sandstones of the Neill Klinter Group, rising via the recessive Sortehat and lower Pelion Formations (Vardekløft Group) to another small plateau, 'Taubjerg' (field name of Callomon), at the foot of the final rise to the Hareelv plateau. Locations of sections B1, C1 and C2 indicated.

in the concretions. Deposition took place in an offshore marine environment. The member is about 20 m thick and overlies silty, dark-grey mudstones with thin fine-grained sandstone intercalations of the lower Fossilbjerget Formation with a sharp contact corresponding to a major hiatus. It is overlain by black mudstones or massive sandstones of the Olympen or Hareelv Formations. It is restricted to south and southern central Jameson Land. The member belongs to the top lower Callovian – lower upper Callovian, Calloviense–Athleta Standard Zones, based on ammonites.

The Pelion and Fossilbjerget Formations exhibit major shifts in facies, in some cases associated with non-sequences of considerable magnitude, reflecting important regional changes in relative sea level and sedimentary regime. Characteristically, the succession consists of soft, barely cemented recessive beds of uniform siliciclastic lithology from decimetres to metres thick, punctuated by thin resistant concretionary layers comprising small or medium-sized, hard, calcareous or sideritic concretions and large sandstone 'doggers' (term much used by Callomon to describe ellipsoidally weathering sandstone bodies that are more strongly cemented than the otherwise identical adjacent sandstone). These thin, preferentially cemented beds serve as invaluable markers for correlation. They extend over distances of just hundreds of metres to tens of kilometres. They are commonly marked by concentrations of glauconite and by ferruginous or phosphatic cementation, giving them reddish or brown colours when weathered. They are also the main sources of well-preserved body fossils, particularly ammonites, which can occur in spectacular assemblages of complete, beautifully preserved adults strongly sexually polarised in favour of (female) macroconchs (see, for example, Figs 34, 38, 39, 42, 43; cf. Callomon 1963). Among representatives of the nekton, belemnites can also be abundant. The benthos is represented by sparse faunas of bivalves, gastropods, terebratulid brachiopods and occasional small solitary corals and crinoids.

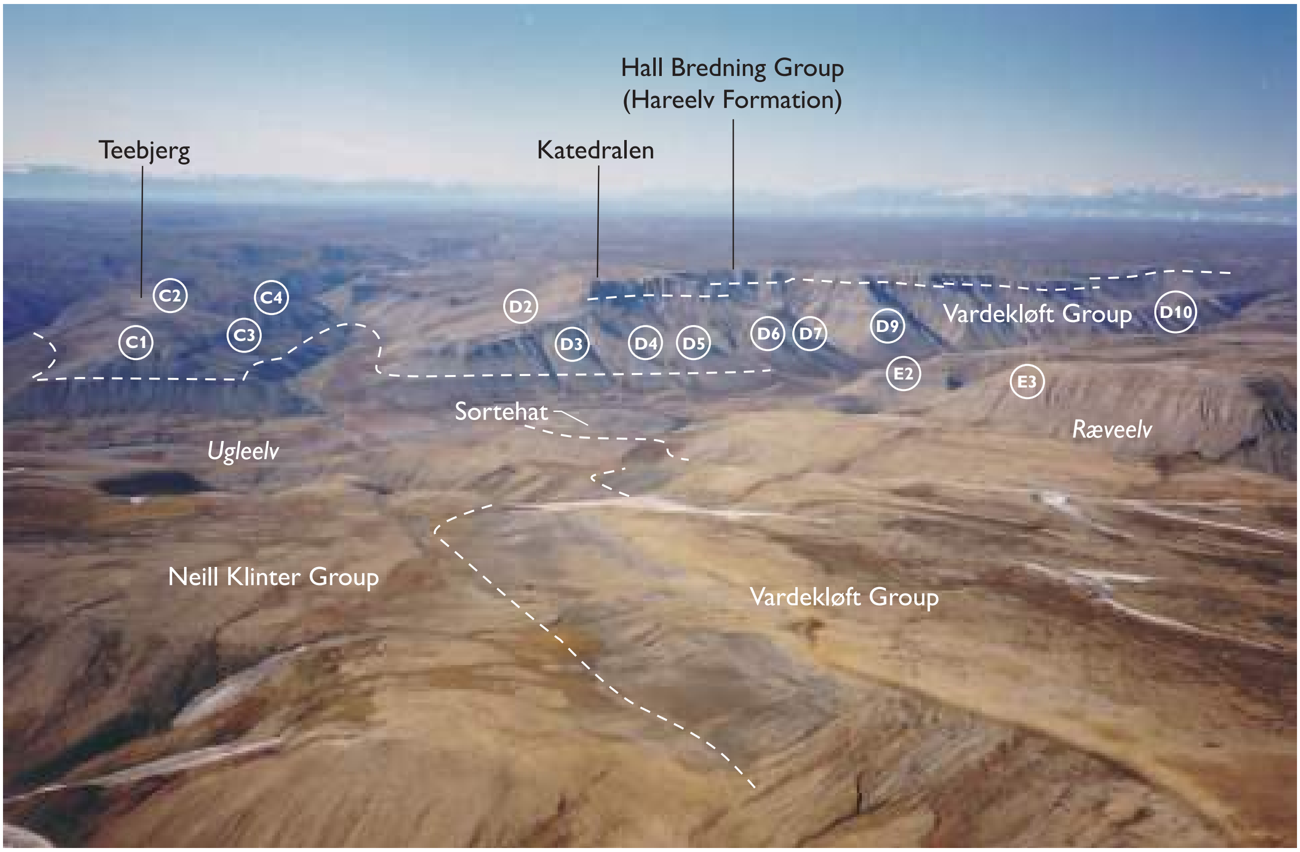


Fig. 11. Aerial view of Ugleelv and Katedralen seen from east-north-east, looking towards the south-west on the horizon to the plateau basalt cliffs on the south side of Scoresby Sund (left) and the Caledonian crystalline basement of Milne Land (right). In the foreground, a thin capping of lower Pelion Formation on Sortehat Formation (steeper slope), resting in turn on the platform top of the Neill Klinter Group (Ostreaelv Formation (Toarcian)). The highest peak in the line of sight is Katedralen, its flat top formed by the Hareelv Formation. The ridge leading from its peak downwards to the left passes through sections D2–D4. The ridge leading downwards to the right, in front of the canyon, is section D5, the most prolific source of *Cranocephalites pompeckji*. This major, deeply incised canyon is flanked by sections D8 (not visible) and D9. The prominent step half-way up marks the clinoforms at the top of the Pelion Formation. The ridge from the plateau at far right, leading into the headwaters of Ugleelv, is section D10. The ridge on the northern (near) side of Ugleelv, facing the Katedralen canyon and topped by the clinoforms, hosts sections E2 and E3. The rounded hill in the far foreground, in direct line to Katedralen, is Sortehat itself, section F (not visible).

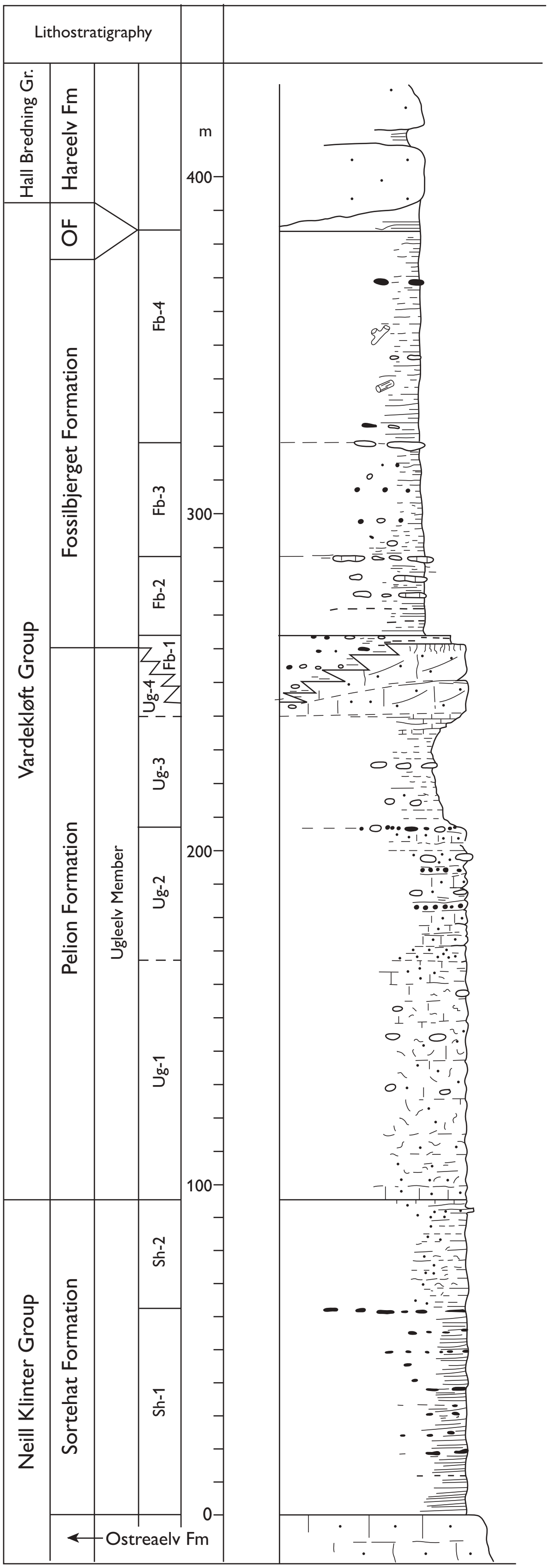
There is a diverse ichnofauna in many beds (Heinberg & Birkelund 1984). Plant remains are abundant, mostly in comminuted form, and large drifted logs of wood are commonly found as cores of siliceous concretions in the higher parts of the Fossilbjerget Formation, notably in the Goniomyakløft Member.

The *Olympen Formation*, which is missing in southern Jameson Land, is first recognised at Langryggen and thickens northwards to 180 m at Olympen (sections 27 and 67 of Callomon 1993, respectively; Fig. 1B). The formation belongs to the lower to middle Oxfordian.

The *Hareelv Formation* comprises black mudstones, and density-flow sandstones which have been remobilised and injected into the surrounding mudstones (Surlyk & Noe-Nygaard 2001, 2003; Surlyk *et al.* 2007). It forms the top plateau of much of southern Jameson Land (Figs 10, 11). The formation belongs to the upper Oxfordian – Kimmeridgian.

Ugleelv – northern Hurry Inlet

The Pelion Formation occurs along the whole length of Jurassic outcrops in central East Greenland, from Hurry Inlet (71°N) to Store Koldewey (76°N). Its age-range varies considerably from place to place. It is subdivided into a succession of members (Surlyk 2003, p. 666, fig. 5), but of these only the lowest, the Ugleelv Member, is of interest here. This encompasses all the beds of the Pelion Formation found in the area around Ugleelv and then southwards along Neill Klinter. The Ugleelv Member can be further



Legend for Figs 12, 16–29, 35

Fossils

- Ammonite
- Belemnite
- Belemnoteuthid cephalopod
- Gastropod
- Pectinid bivalve
- Bivalves, others
- Terebratulid brachiopod
- Plant
- Log

Trace fossils

- *Phoebichnus trochoides*
- *Diplocraterion habichi*

Structures, lithologies

- Massive sandstone
- Clinoform bedded sandstone
- Sandstone with trace fossils
- Siltstone
- Sandstone
- Black mudstone
- ● Phosphatic concretion
- Concretionary sandstone (dogger)
- Carbonate concretion

m a.sl. Metres above sea level

Fig. 12. A synoptic diagram of the development of the Vardekløft Group at Katedralen and its surroundings. The succession is based on weathering profiles drawn by JHC in the field (see Figs 16–29, 35). They mainly illustrate differences in consolidation and cementation of the beds and have less emphasis on the sedimentary structures. The legend also applies to Figs 16–29 and 35. Informal lithostratigraphic units within the Sortehat Formation (Sh-1, Sh-2), the Pelion Formation (Ug-1 – Ug-4) and the Fossilbjerget Formation (Fb-1 – Fb-4) are indicated. Note the diachronous nature of the Pelion–Fossilbjerget boundary. **OF**: Olympen Formation.

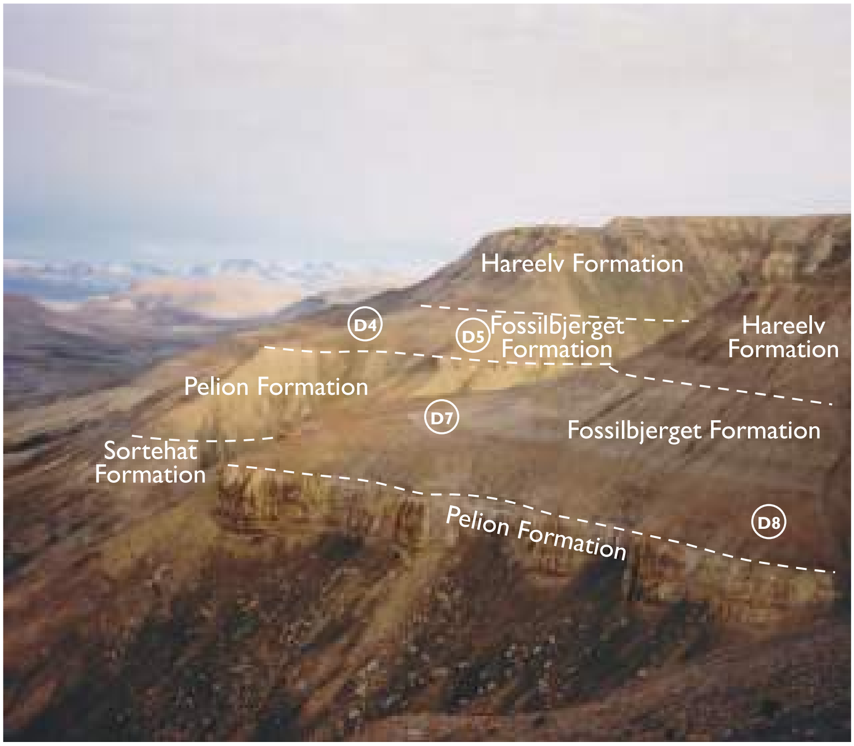
Fig. 13. A belemnite 'battlefield' at a thin interbed with phosphatic concretions near the top of Ug-2 (Pelion Formation), section E3 (Fig. 9, see also Fig. 35B).

subdivided in the region between Ugleelv and Hurry Inlet into roughly four parts that can be widely discerned there. The lithological differences are small, however, and do not merit formal lithostratigraphical status; they are informally labelled Ug-1 to Ug-4 from below (Fig. 12).

Ugleelv unit 1 (Ug-1). Light-coloured quartzose sandstones, heavily burrowed, and rich in plant remains, without marine macrofossils other than rare belemnites throughout. Thicknesses 20–70 m. Strontium isotope dating of the belemnites points to an age around the early/late Bajocian boundary (M. Engkilde, personal communication 1998).

Ug-2. Light-coloured sandstones with subordinate silty shales and thin, lenticular interbeds of ironstone, probably of glauconitic origin, commonly associated with small phosphatic concretions and concentrations of fossils, including ammonites, belemnites (sometimes as 'battlefields', Fig. 13), bivalves and gastropods. The unit is 25–50 m thick

Fig. 14. The northern slopes of Katedralen seen from the north-west, viewed from section D9 (Fig. 9). In sections D7 and D8, the ferruginous *Cranocephalites* beds (Fossilbjerget Formation, Fb-1) are only 2–3 m thick and rest immediately on the clinoforms (Pelion Formation, Ug-4), which are up to 25 m thick. The overlying brown-coloured shales of Fb-2 are essentially the *Arctocephalites* and perhaps lower *Arcticoceras* Beds. The light and darker-coloured shales that follow in the upper Fossilbjerget Formation are Fb-3 and Fb-4 respectively (Fig. 12).



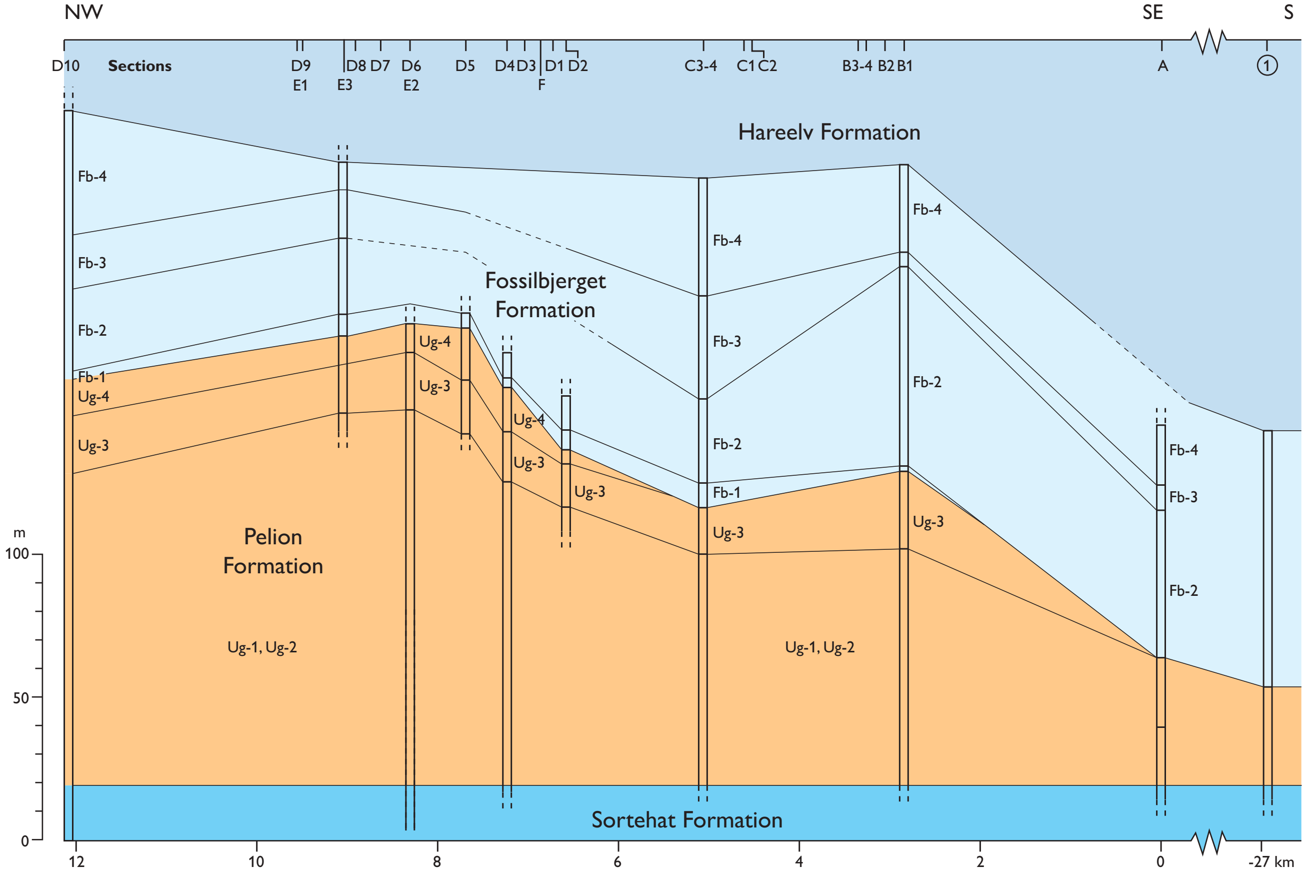


Fig. 15. Regional variations in the development of the Pelion and Fossilbjerget Formations around Ugleelv. Selected sections are projected onto a gently curving arc as baseline from section A in the south-east to Section D10 in the north-west (Fig. 9). Numbers in columns refer to the informal subdivision of the Pelion Formation into Ug-1 – Ug-4 and the Fossilbjerget Formation into Fb-1 – Fb-4. The lower two Pelion units, Ug-1 and Ug-2, are shown undivided. Ug-4: clinoforms. The diagram illustrates that the Pelion Formation becomes thicker and stratigraphically more complete towards the north-west.

and terminates around Katedralen fairly sharply at one of these horizons of ironstone and phosphatic concretions, the latter commonly enclosing a large *Plagiostoma* bivalve, making an excellent marker for local correlation in the Ugleelv area. Ug-2 belongs to the Borealis Standard Zone (all three horizons, Bo-1 – Bo-3, see below).

Ug-3. Siltstones to fine-grained muddy sandstones with occasional thin lenticular concretionary, slightly ferruginous layers containing scattered light-brown weathering doggers, which are the only source of recoverable body fossils. The unit coarsens upwards into sandstone. Ug-3 belongs to the Indistinctus – lower Pompeckji Standard Zones. It is typically about 20 m thick around Katedralen, but thins eastwards to zero at ‘Taubjerg’ (Fig. 9, section A) and grades upwards at Katedralen into the overlying unit Ug-4.

Ug-4. The large-scale, high-angle clinoform sandstone beds at Katedralen (upper part of the Ugleelv Member of Surlyk (2003, fig. 5) which attains thicknesses of up to 30 m (Fig. 14). It is variably divisible into subsets, in some cases separated by softer, muddy interbeds that may yield ammonites. It thins and wedges out eastwards, grading laterally into the upper part of Ug-3. At its thickest, the top surface is sharp and heavily pierced by vertical burrows of *Diplocraterion habichi* and possibly also *Monocraterion*. The unit belongs to a single ammonite biohorizon in the Pompeckji Standard Zone, Po-4. The regional variations in the thickness of the Pelion Formation are illustrated in Fig. 15.

The Pelion Formation is sharply overlain by the Fossilbjerget Formation which consists predominantly of mudstones punctuated by layers of concretions or concretionary induration. The gross lithologies are constant over large distances with relatively small changes in thickness. A subdivision into four parts can again be recognised in the area around Ugleelv and Katedralen. The Fossilbjerget Formation is subdivided into units Fb-1 to Fb-4.

Fossilbjerget unit 1 (Fb-1). A highly condensed succession of thin but sharply bounded ironstones, weathering red-brown, separated by soft muddy interbeds. Westwards from Hurry Inlet, they onlap against and then overlap the clinoforms of Ug-4, so that on top of it the ironstones are in contact. The ironstones are locally highly fossiliferous, especially with ammonites, whose uncrushed body chambers are commonly also somewhat phosphatised. The ammonites have allowed us to establish detailed age relationships, showing that the unit represents a very long period of time with up to 15 ammonite horizons in 5 m of sediment. Individual beds can wedge out over small distances and the succession in any one section can be full of non-sequences. The unit belongs to the Pompeckji Standard Zone, horizons Po-8 to Po-23 at Katedralen, and the lower Arcticus Standard Zone, *A. arcticus* horizon J9, from north of Ugleelv (section E3) as far as Mikael Bjerg and Centralbjerg, 35 km to the north (Fig. 1B). Farther northwards, it interdigitates with the Pelion Formation. The unit as a whole wedges out eastwards and is completely missing in a major non-sequence at section A ('Taubjerg'; Fig. 9), and then southwards along the whole of Neill Klinter. This non-sequence may in part be erosional for it is marked by a sharp contact with the overlying beds. The unit is up to 5 m thick, before grading into the Pelion Formation.

Fb-2. Dark silty mudstones with well-separated thin layers of ferruginous induration or flat concretions in the lower part weathering reddish-brown, changing to lighter mudstones with layers of fine-grained sandstones or fissile concretions in the upper part. These are respectively the *Arctocephalites* and *Arcticoceras* beds (Spath 1932). The slopes of Katedralen mark the type locality of the Greenlandicus Standard Zone. At Neill Klinter, the beds are highly fossiliferous and have yielded large collections of the ammonites giving name to the beds. At Katedralen, they are only sparsely fossiliferous. Some of the beds in the Greenlandicus Standard Zone are marked by spectacular examples of the large, wheel-like burrows *Phoebichnus trochoides.* The unit belongs to the Greenlandicus to Ishmae Standard Zones. It is 50 m thick at Hurry Inlet, thinning westwards to 30 m at Katedralen and merging with the Pelion Formation in the north.

Fb-3. Silty pyritic mudstones, with only a few indurated layers and scattered, hard, sideritic spherical concretions, the *Kepplerites–Cadoceras* beds (Spath 1932). The unit terminates with a widespread bed of concretionary calcareous siltstone or fine-grained sandstone, the Calyx bed at Hurry Inlet, an excellent marker still recognisable in Ugleelv. Two key sections at Fossilbjerget, nos 42 and 43 in Fig. 4, were described by Callomon (2004). The unit belongs to the upper Boreal Bathonian Cranocephaloide–Calyx Standard Zones from Hurry Inlet to Katedralen. It is around 30 m thick, changing little laterally.

Fb-4. This unit has previously been termed the 'Wood Beds' (Callomon 1993) and is now referred to the Goniomyakløft Member (Surlyk 2003, fig. 5). It comprises fine-grained monotonous mudstones, with only sparse concretions and rare macrofossils but abundant silicified wooden logs. The unit belongs to the lower Callovian Calloviense Standard Zone to the upper Callovian. The thickness of *c*. 50 m is very persistent laterally. It terminates in southern Jameson Land in a non-sequence that cuts out the equivalents of the lower Oxfordian part of the Olympen Formation.

The intricate stratigraphic relationships of the ammonite faunal horizons in the Ugleelv region, and their position within the lithostratigraphic framework described above, were determined by detailed collecting linked to stratigraphic logging of 23 sections (Fig. 9). Key sections, mainly from the Ugleelv area, are illustrated here in Figs 16–29.

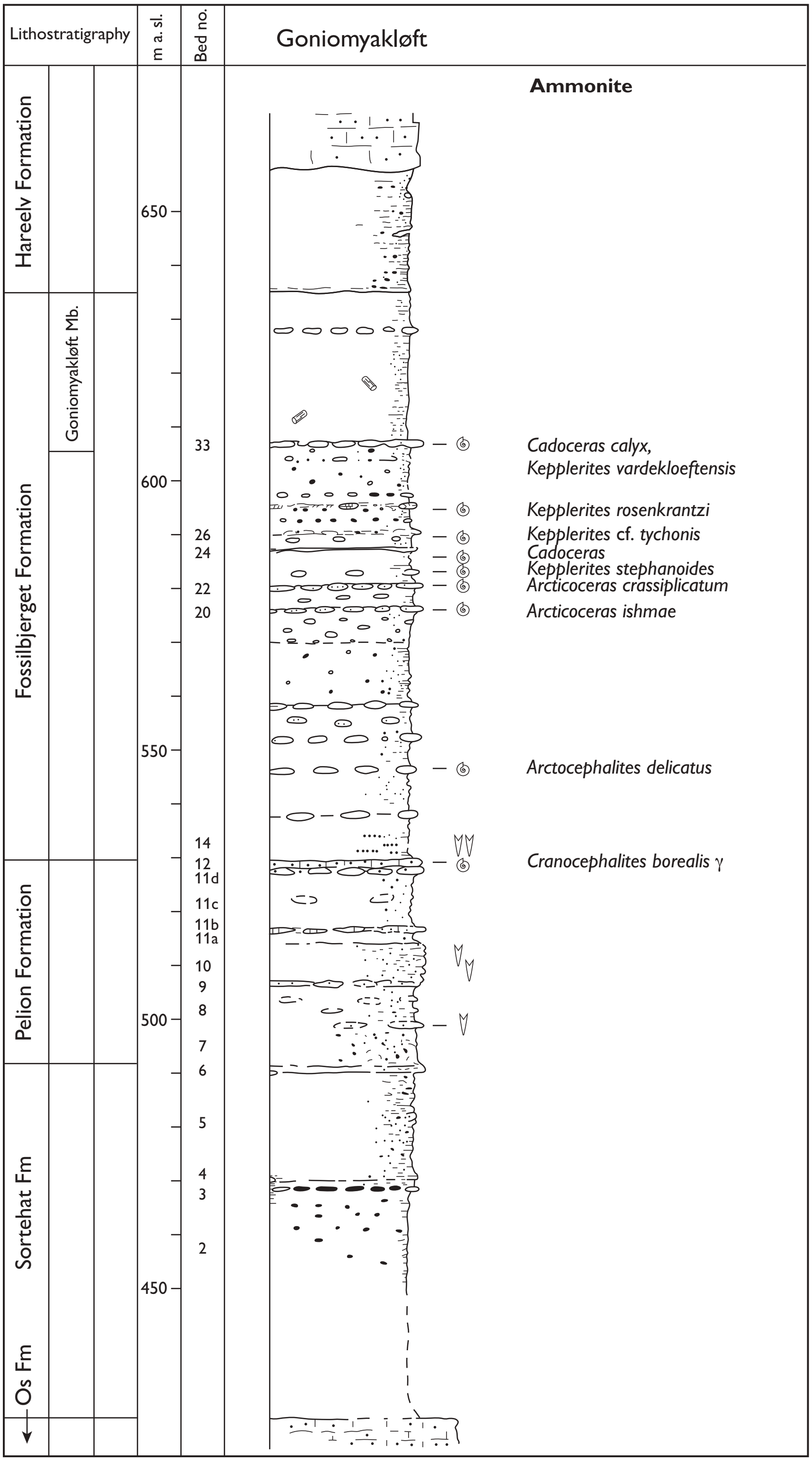


Fig. 16. Section from Goniomyakløft (section 1 of Callomon 1993; for location, see Fig. 2); for legend, see Fig. 12. **Os Fm**: Ostreaelv Formation.

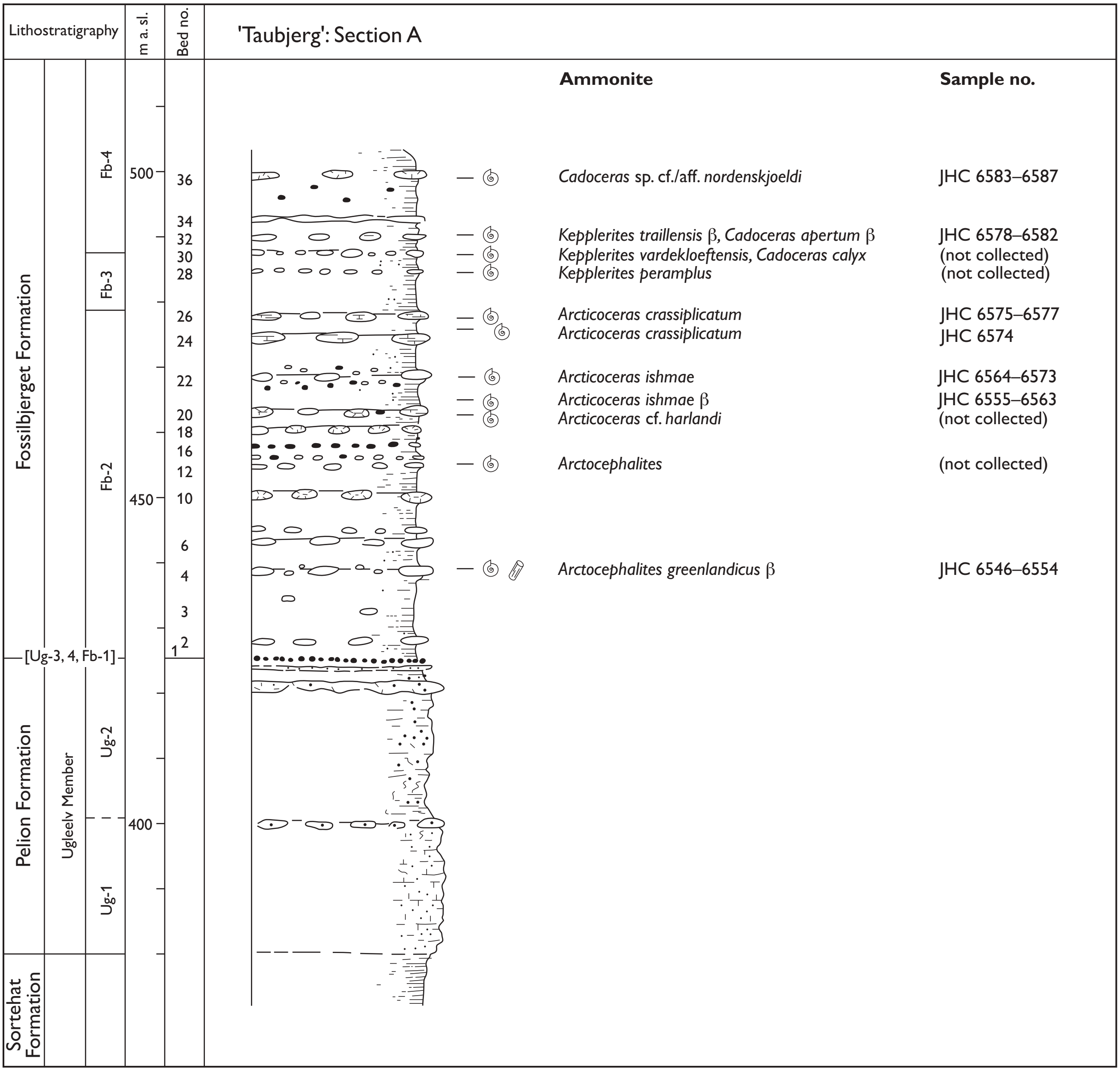


Fig. 17. Section A at 'Taubjerg'. For location, see Fig. 9; for legend, see Fig. 12. Note that the Ug-3, Ug-4 and Fb-1 units are absent at the Pelion–Fossilbjerget boundary.

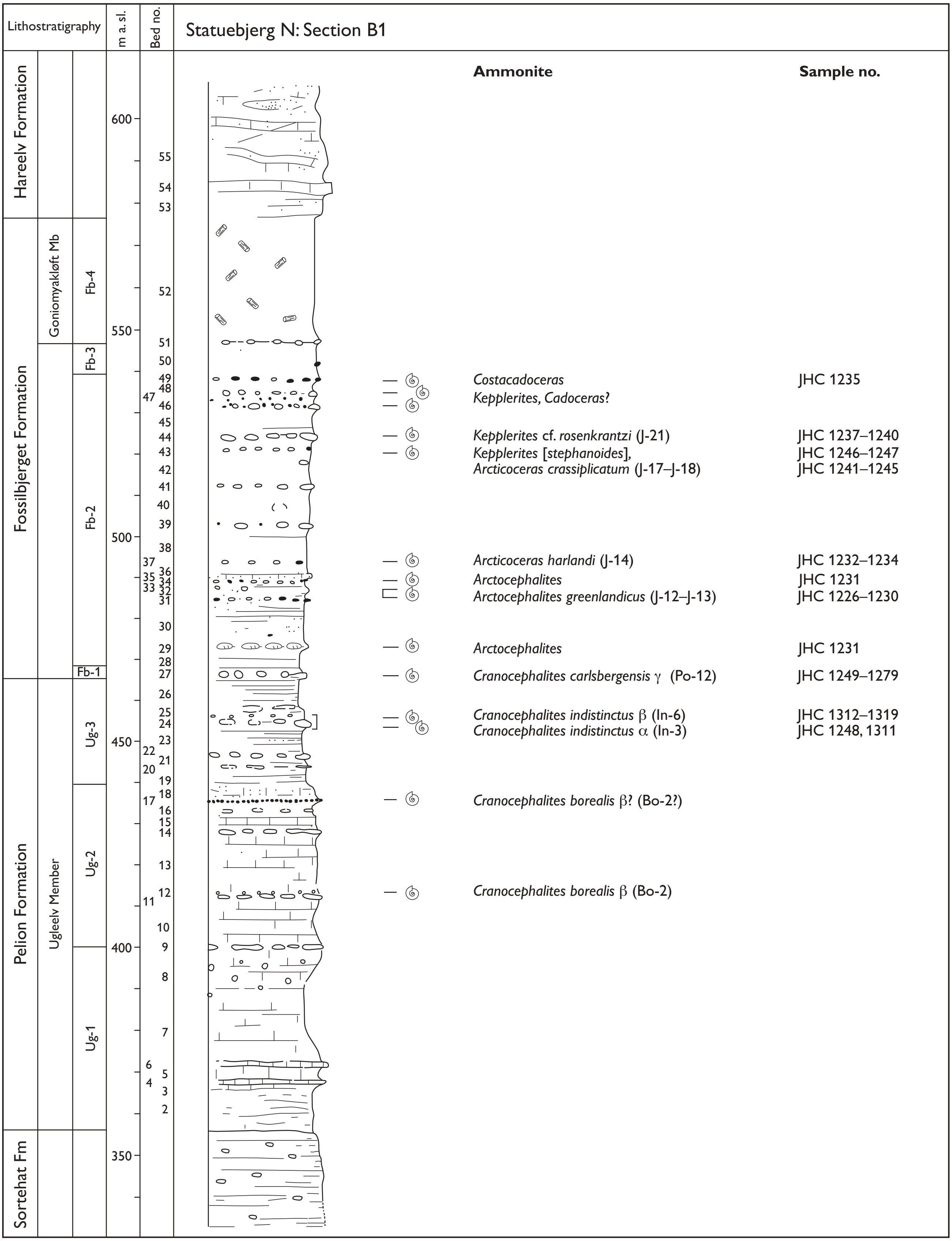


Fig. 18. Section B1 at Statuebjerg N, with samples from before 1994 indicated. For location, see Fig. 9; for legend, see Fig. 12. Note, in comparison to Fig. 17, that only the Ug-4 unit is lacking at the Pelion–Fossilbjerget boundary, but over 10 faunal horizons are absent at this surface (see also Fig. 19).

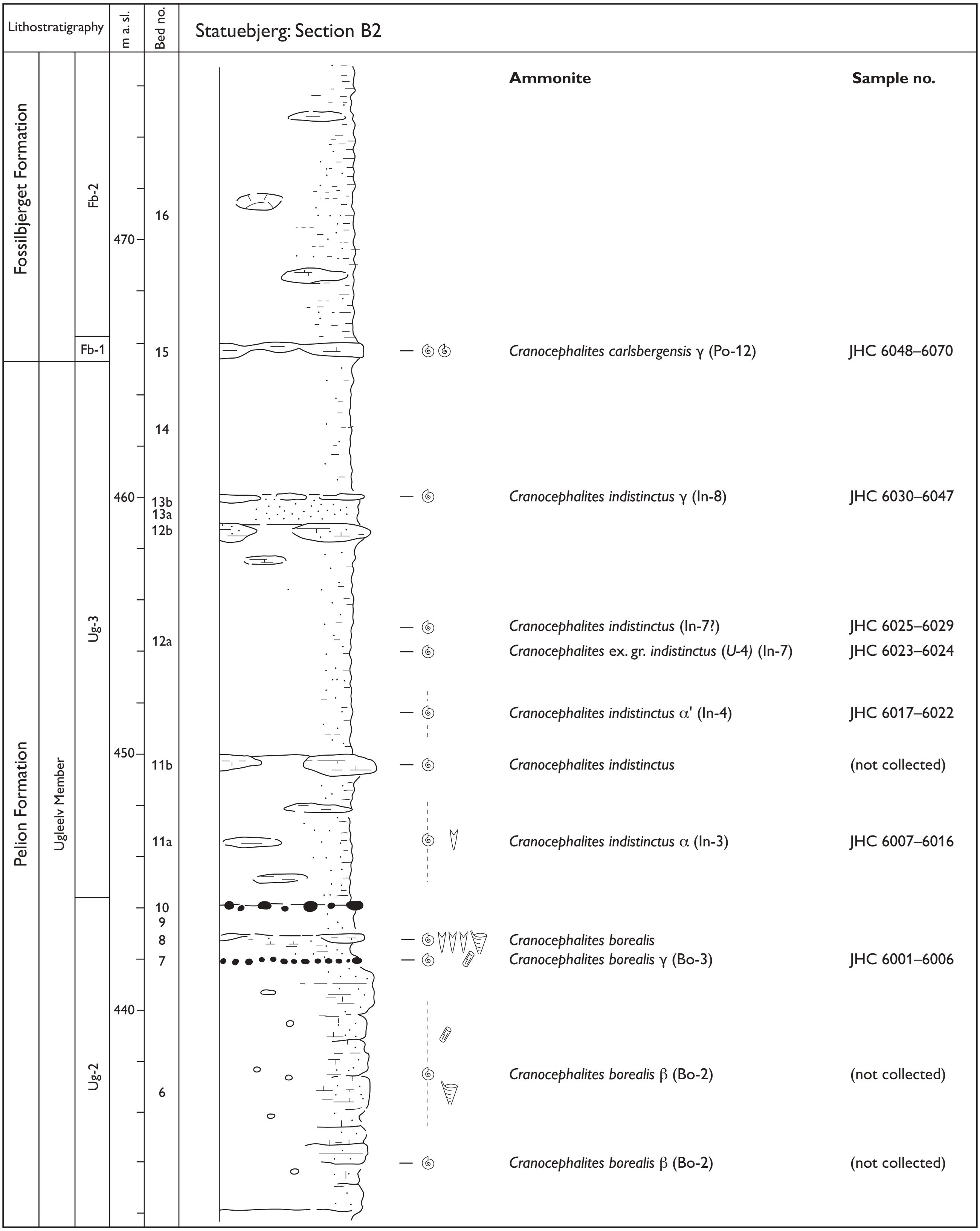


Fig. 19. Section B2 at Statuebjerg; same interval as in nearby section B1 (Fig. 18) but figured in greater detail and showing samples from the J.H. Callomon 1996 collection. For location, see Fig. 9; for legend, see Fig. 12.

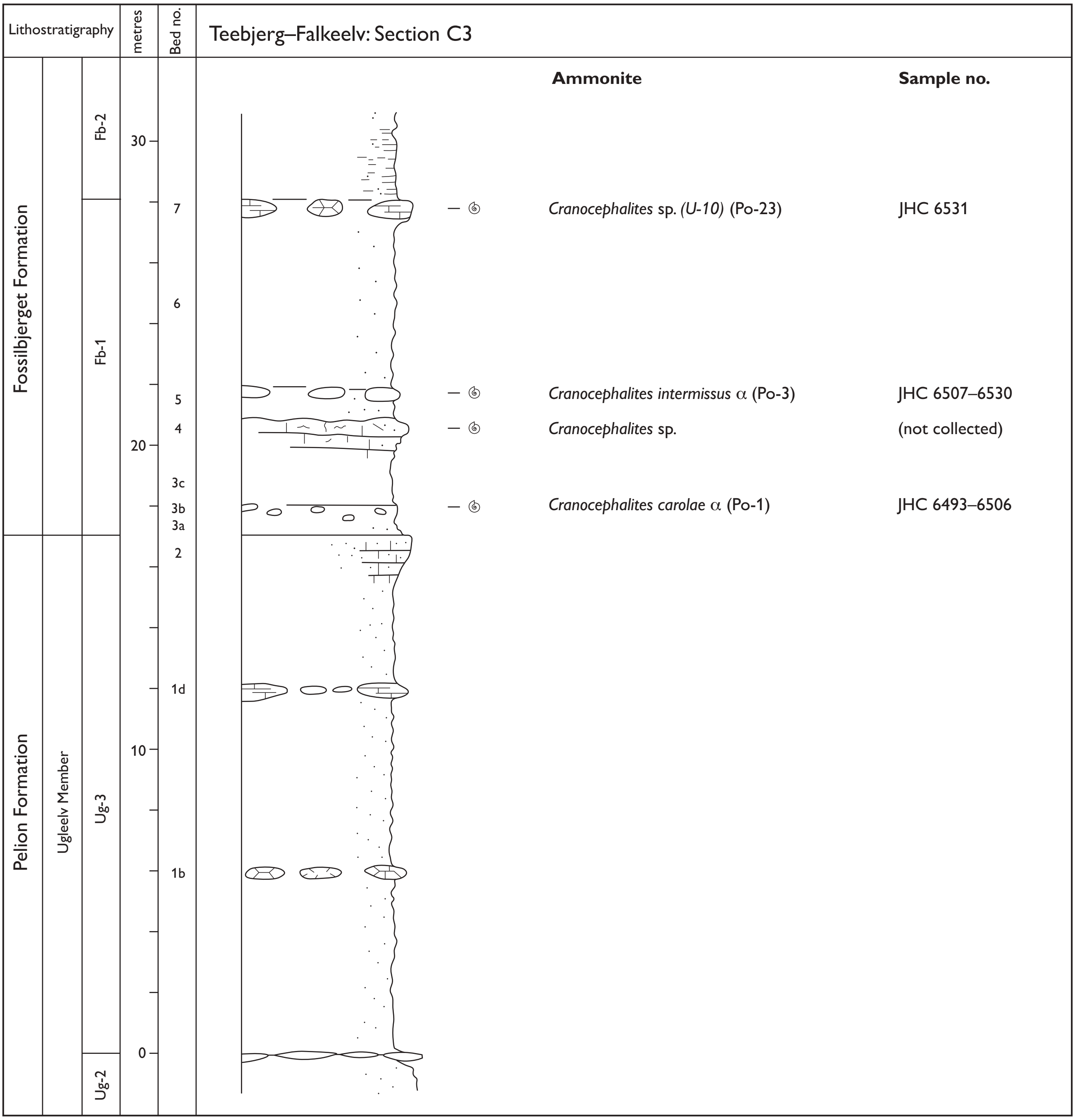


Fig. 20. Section C3 at Teebjerg–Falkeelv. For location, see Fig. 9; for legend, see Fig. 12.

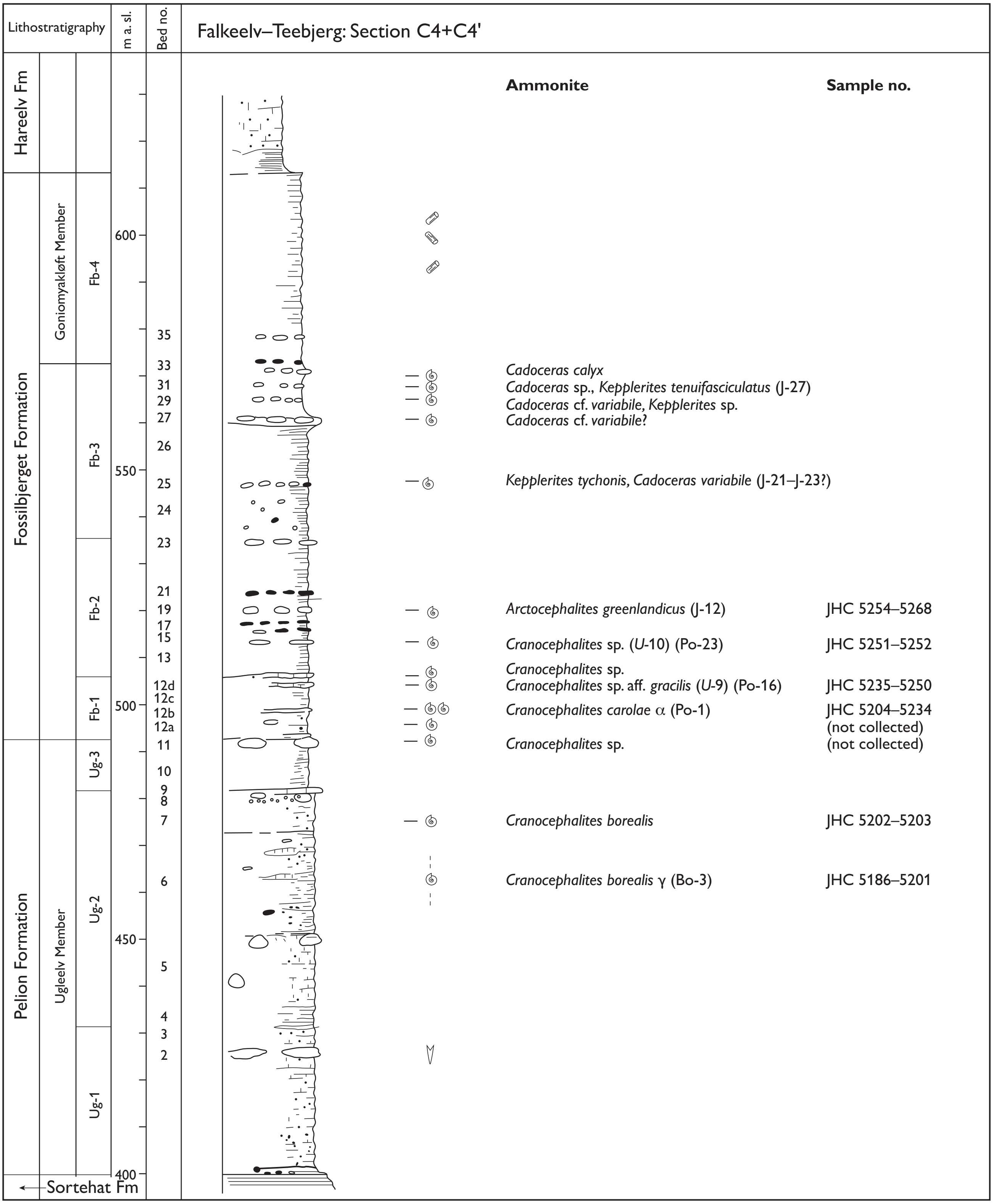


Fig. 21. Section C4, C4´ at Falkeelv–Teebjerg. For location, see Fig. 9; for legend, see Fig. 12.

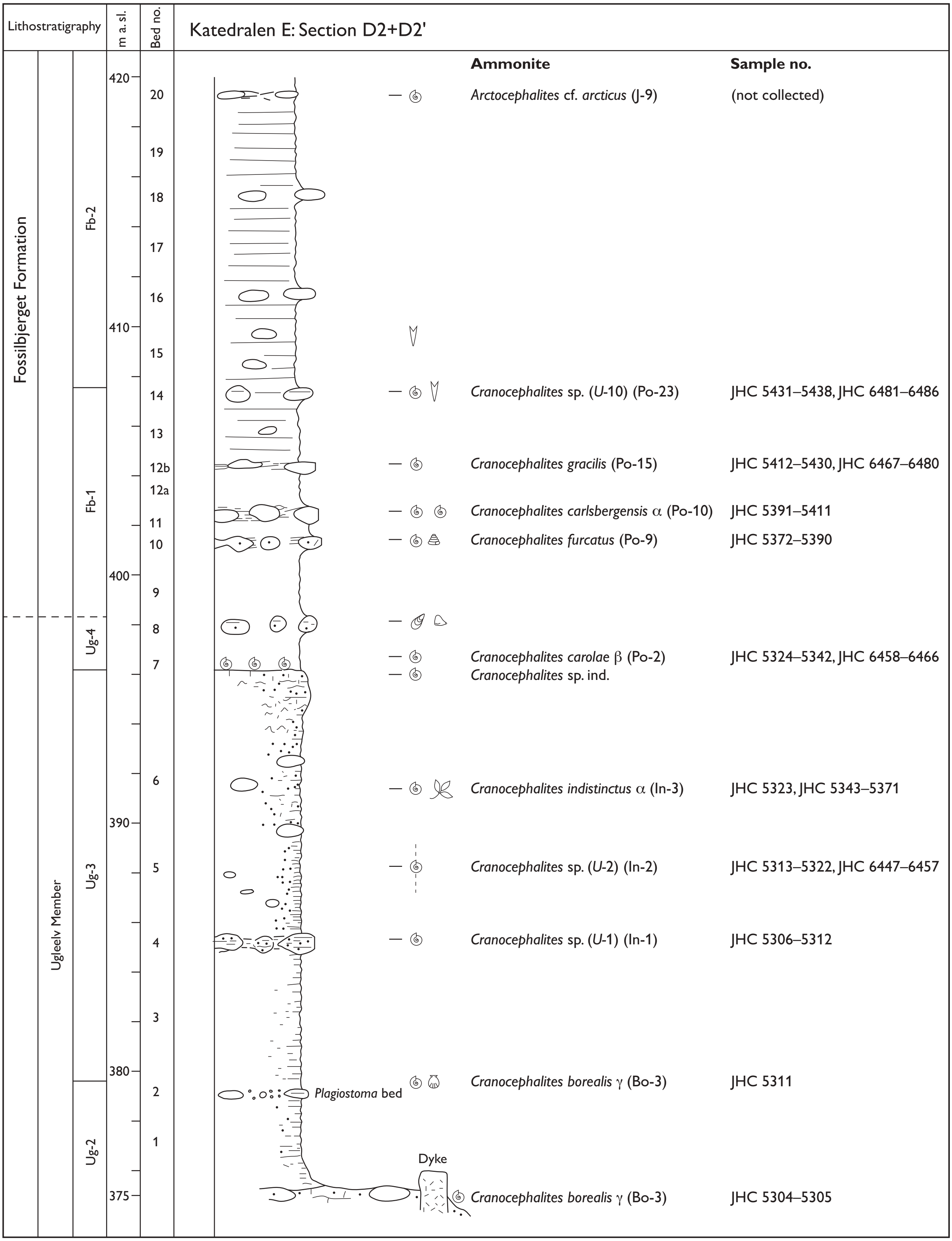


Fig. 22. Section D2, D2´ at Katedralen E. For location, see Fig. 9; for legend, see Fig. 12.

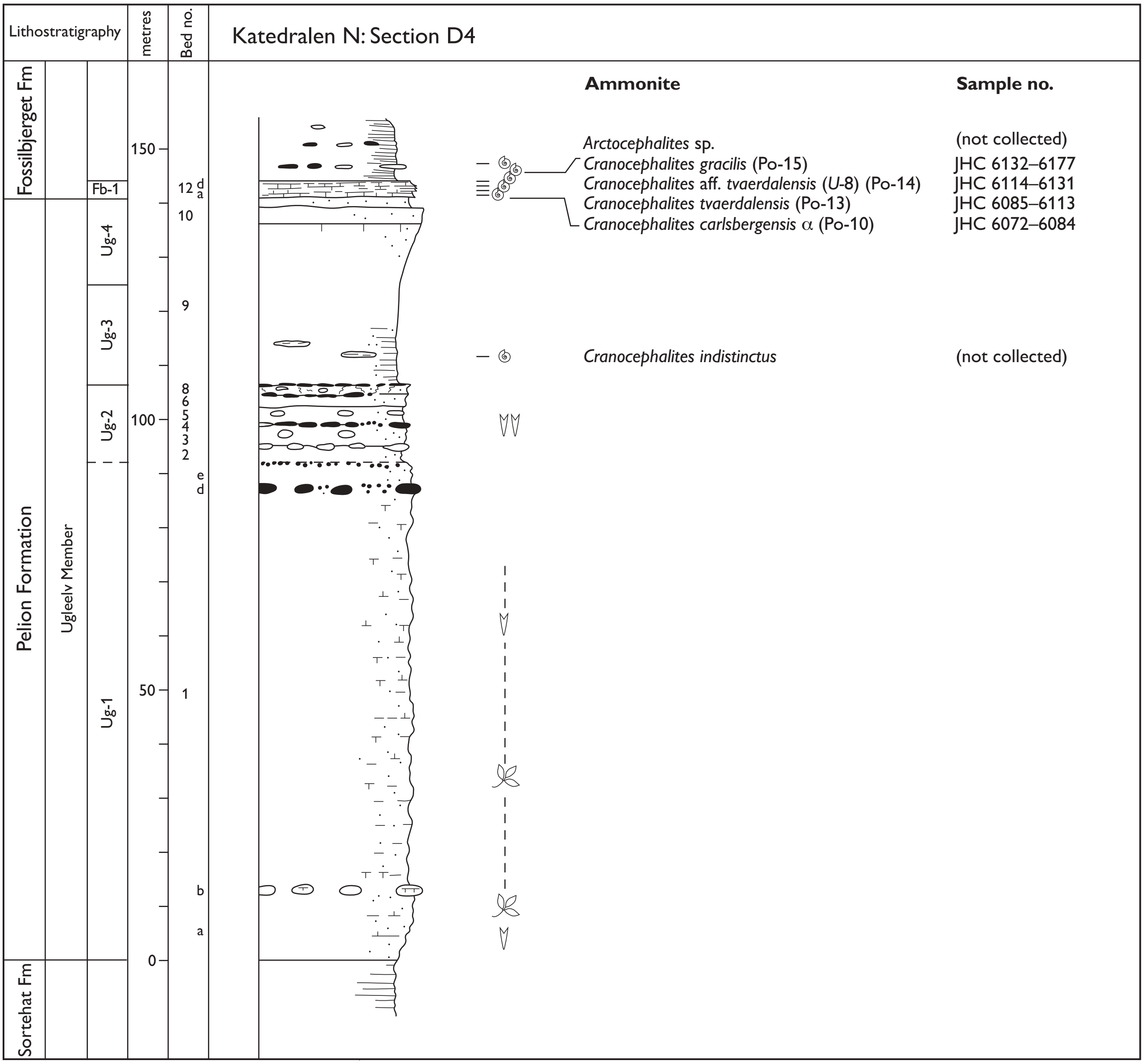


Fig. 23. Section D4 at Katedralen N. For location, see Fig. 9; for legend, see Fig. 12.

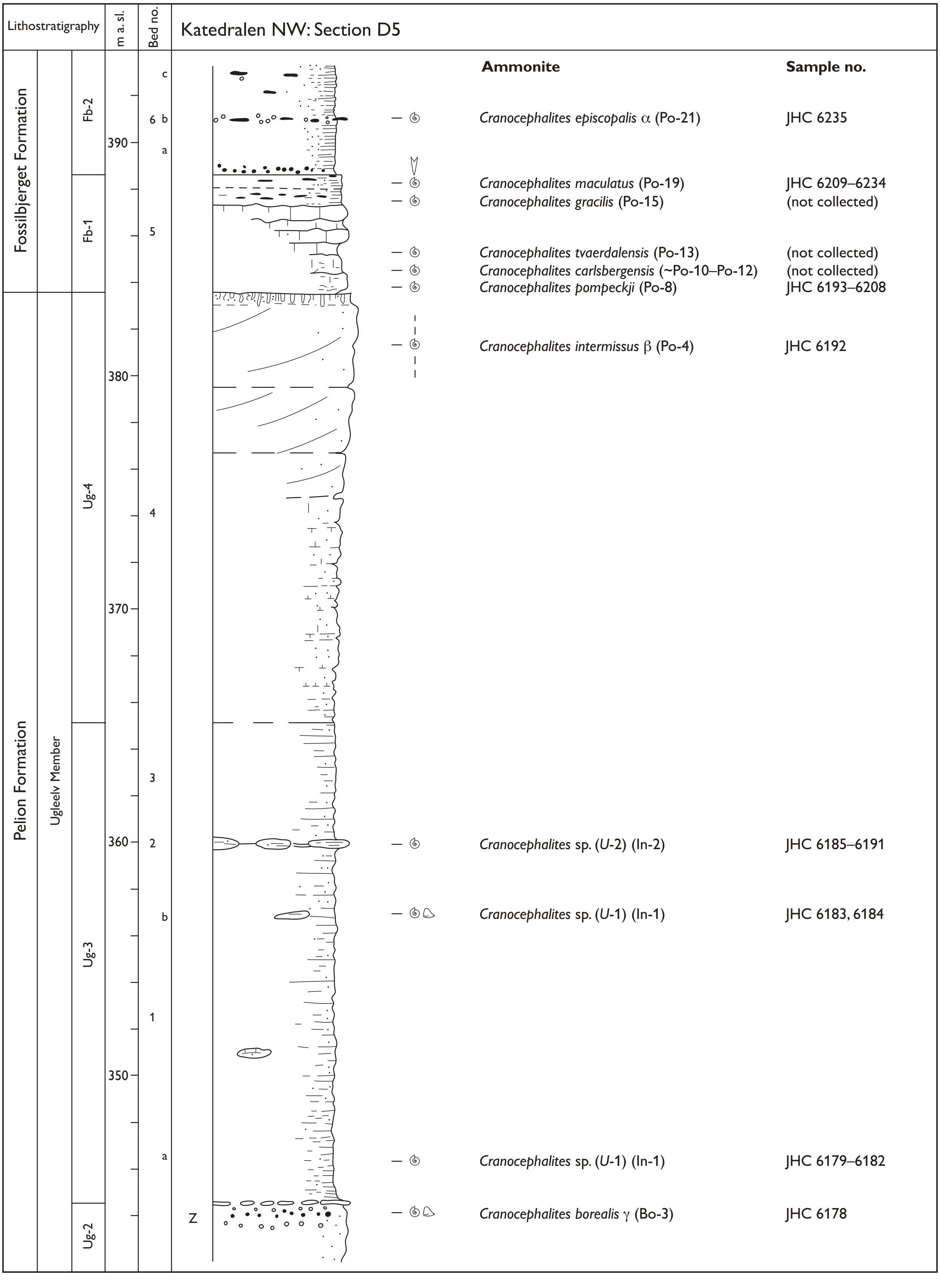


Fig. 24. Section D5 at Katedralen NW. For location, see Fig. 9; for legend, see Fig. 12.

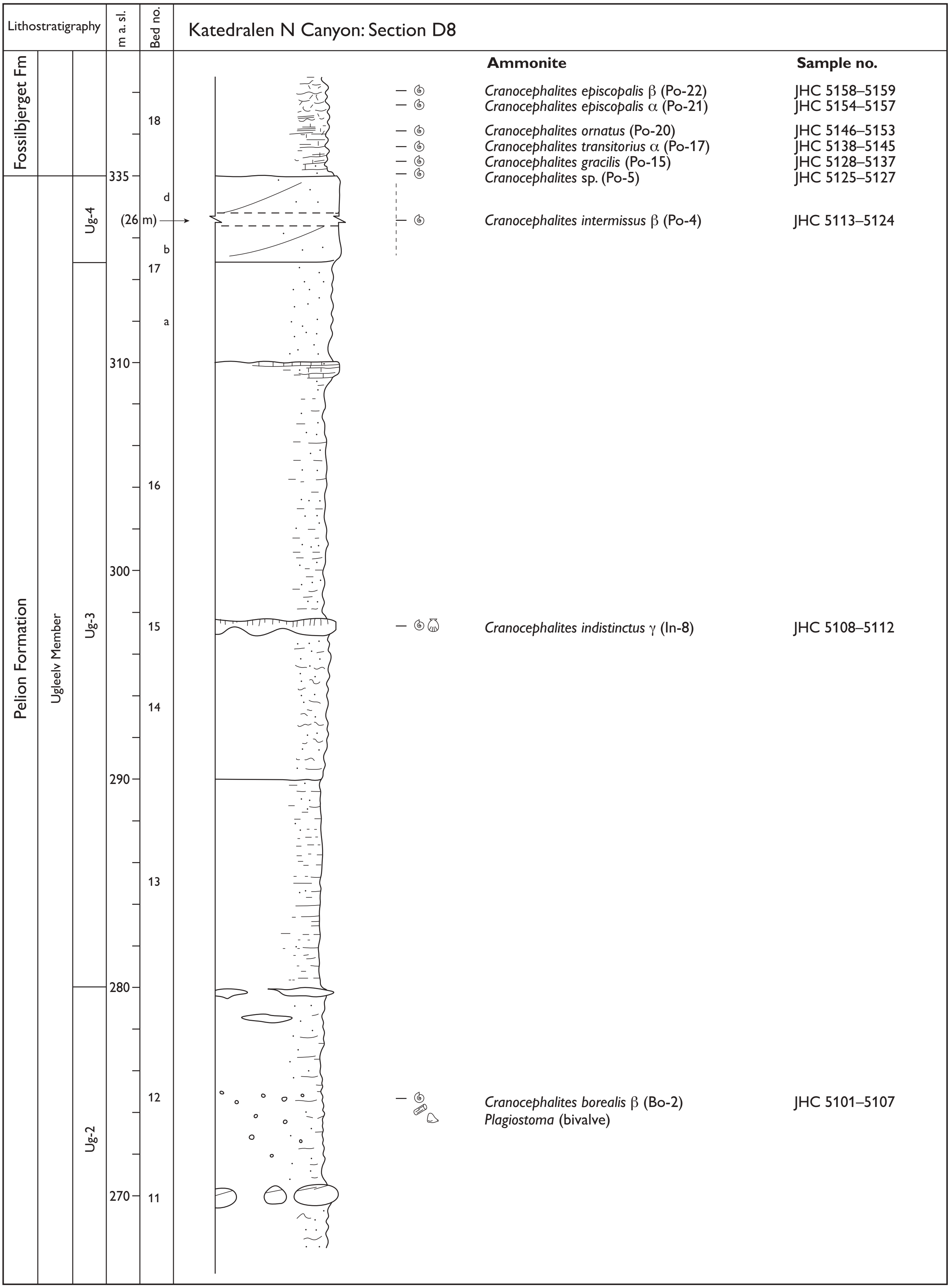


Fig. 25. Section D8 at Katedralen N. For location, see Fig. 9; for legend, see Fig. 12.

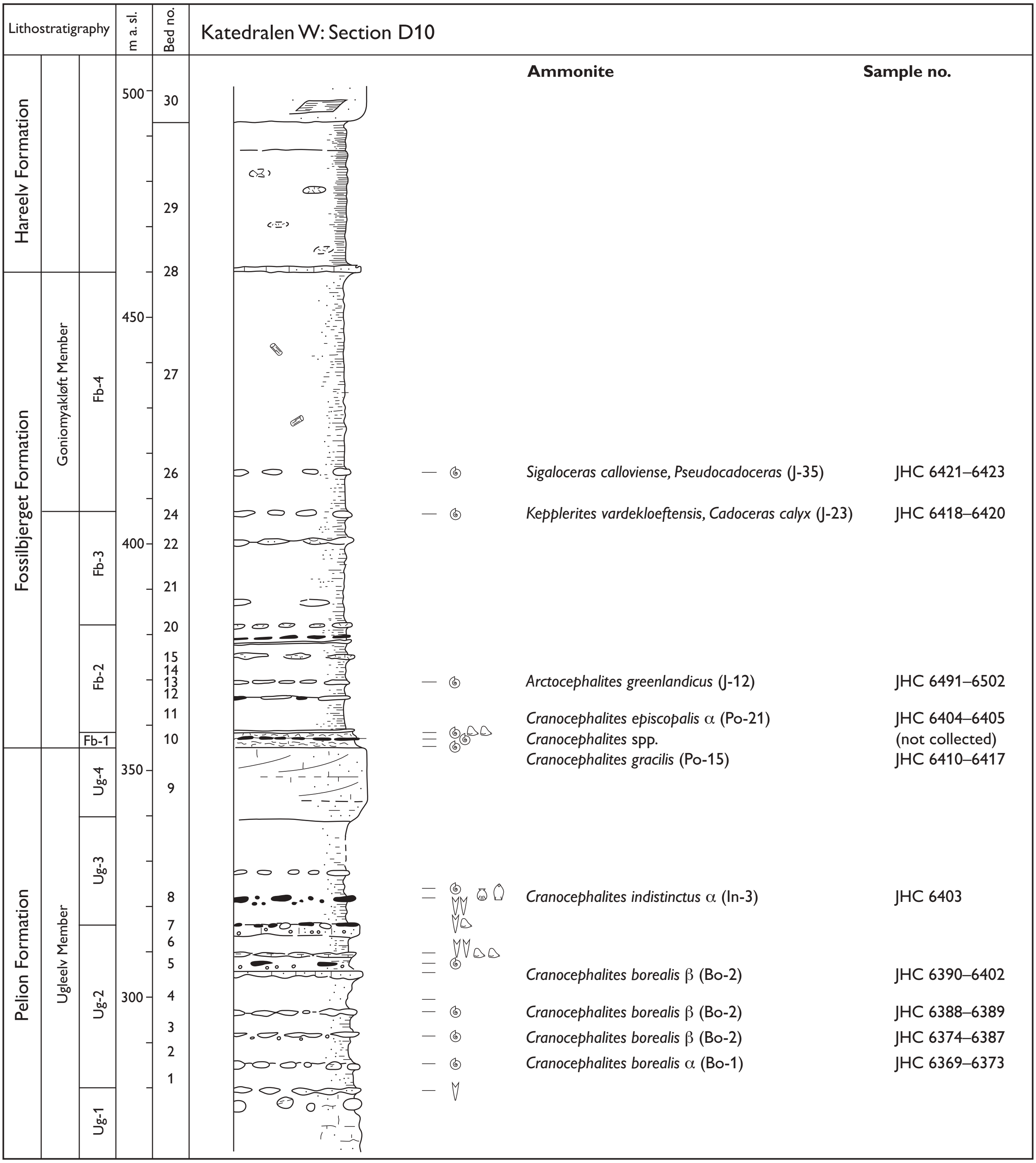


Fig. 26. Section D10 at Katedralen W (upper Ugleelv). For location, see Fig. 9; for legend, see Fig. 12.

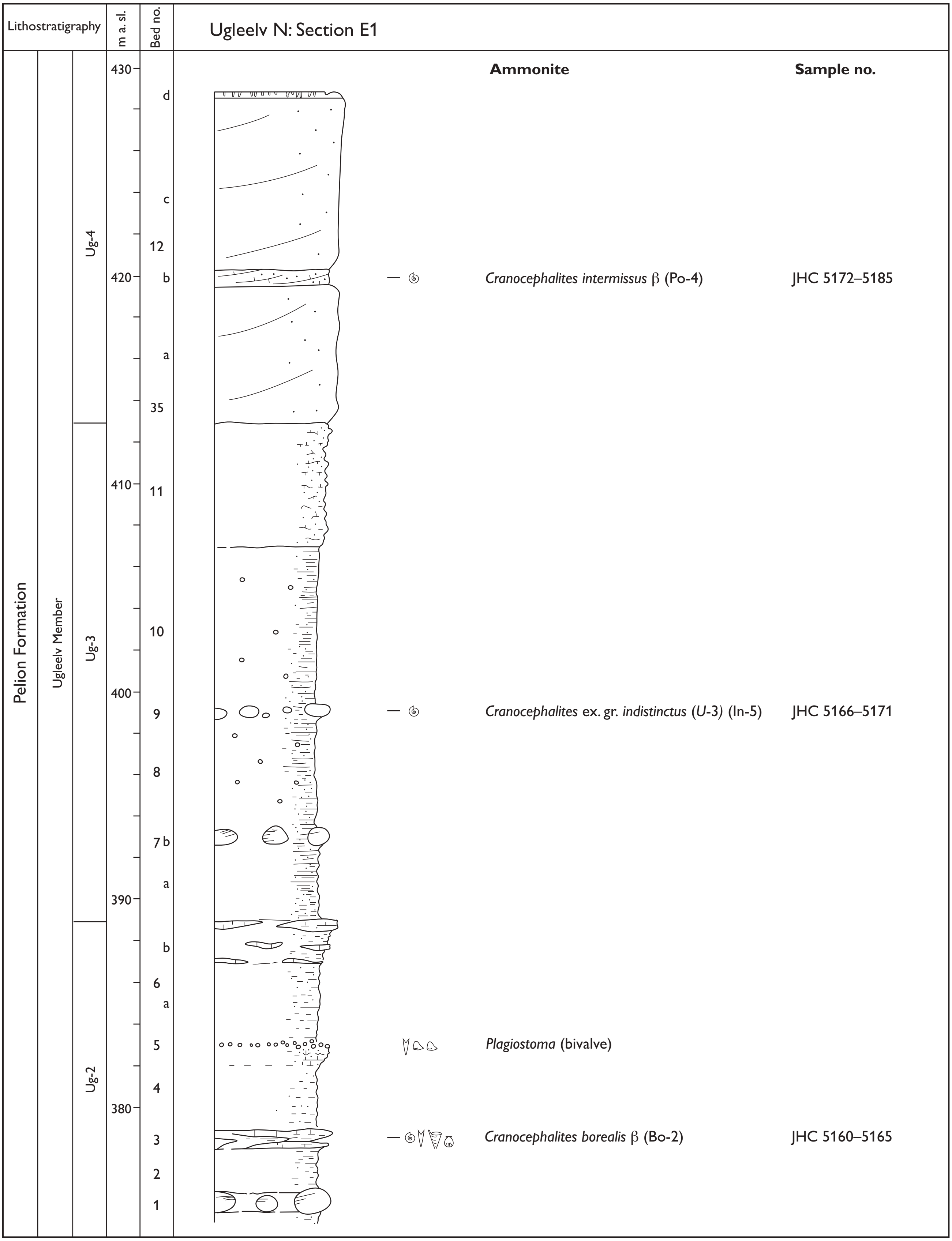


Fig. 27. Section E1 at Ugleelv N. For location, see Fig. 9; for legend, see Fig. 12.

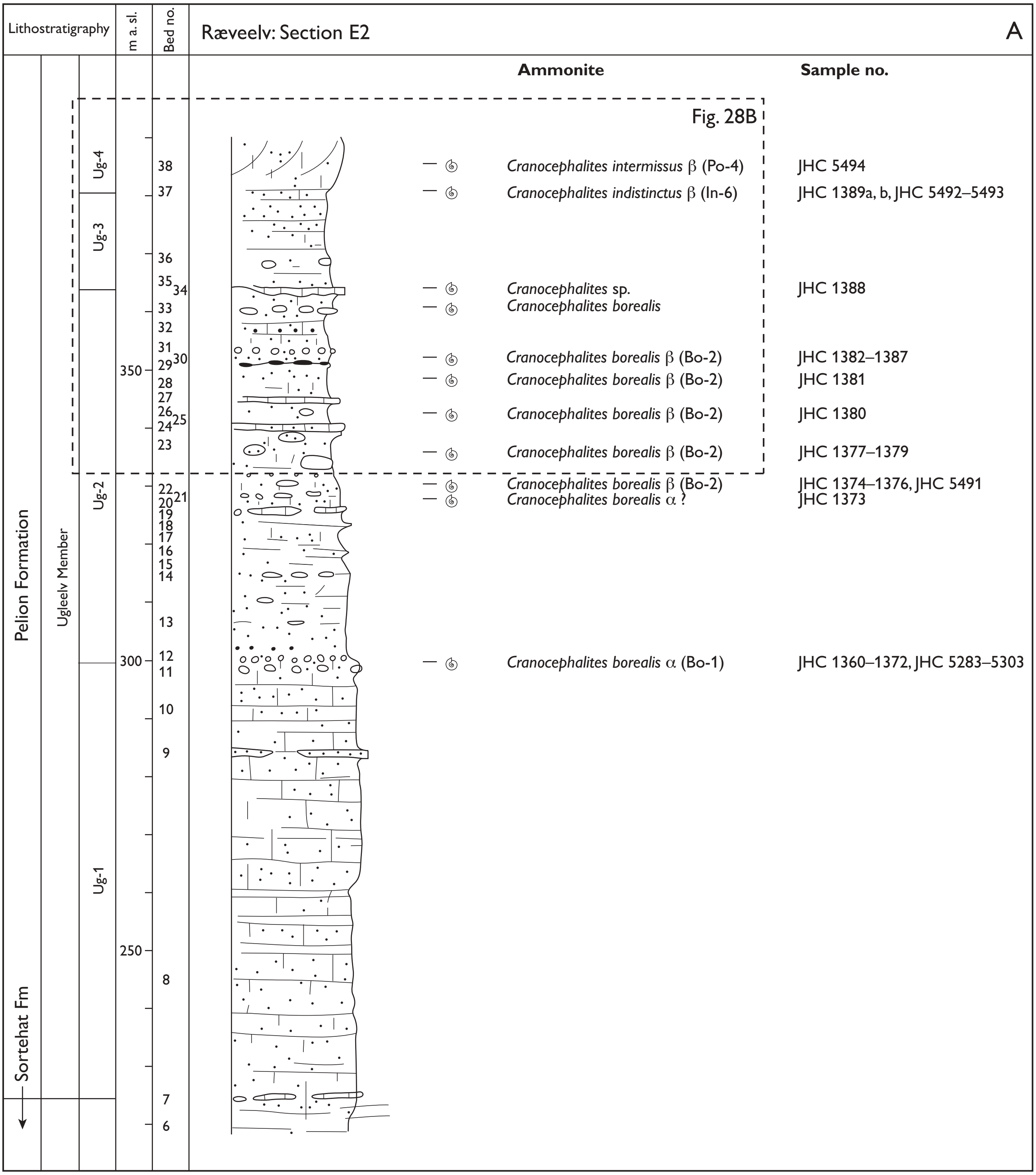
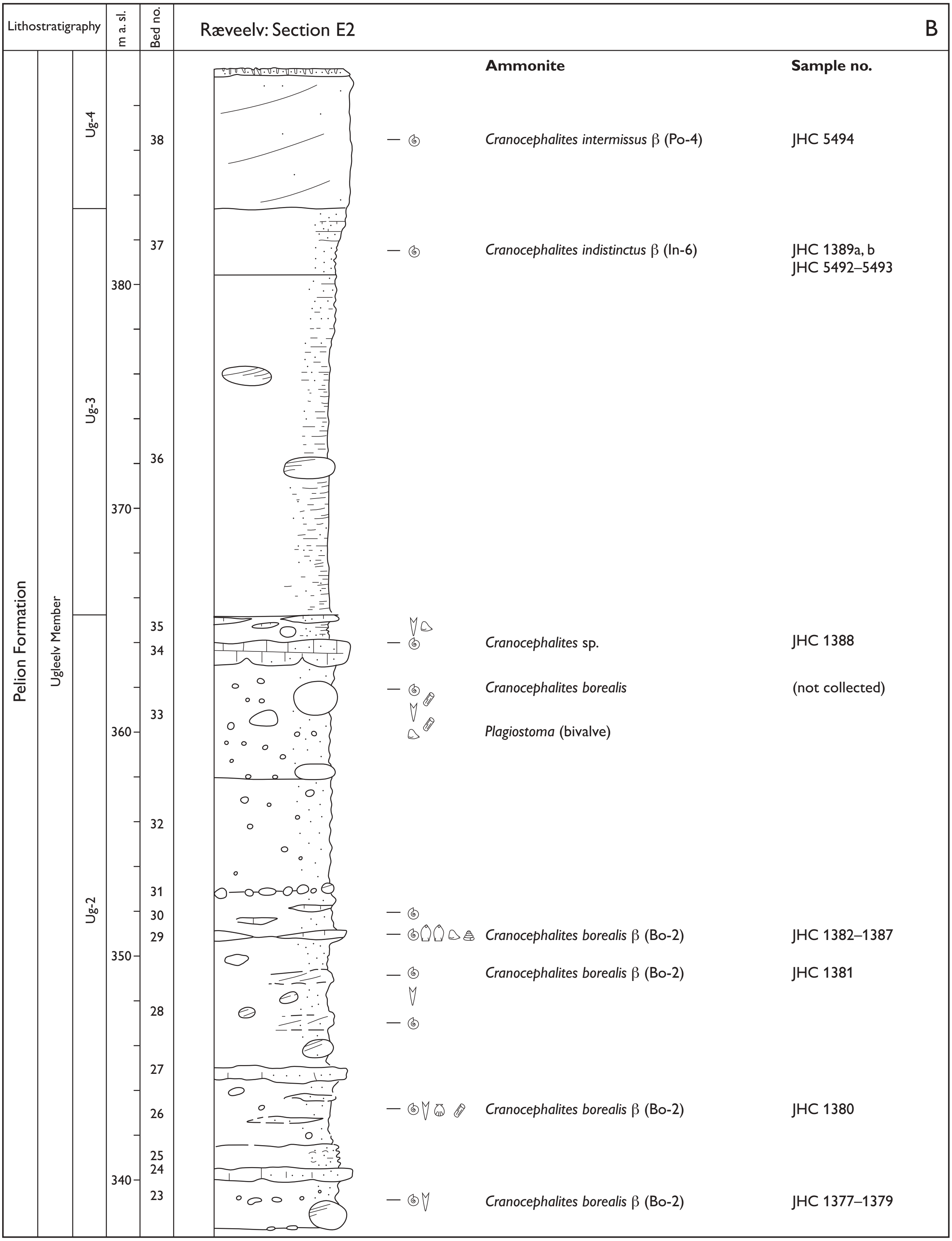


Fig. 28. Section E2 at Ræveelv. For location, see Fig. 9; for legend, see Fig. 12. **A**: General section. **B** (facing page): Detailed section of the upper part shown in **A**.



Ammonite	Sample no.
Cranocephalites intermissus β (Po-4)	JHC 5494
Cranocephalites indistinctus β (In-6)	JHC 1389a, b JHC 5492–5493
Cranocephalites sp.	JHC 1388
Cranocephalites borealis	(not collected)
Plagiostoma (bivalve)	
Cranocephalites borealis β (Bo-2)	JHC 1382–1387
Cranocephalites borealis β (Bo-2)	JHC 1381
Cranocephalites borealis β (Bo-2)	JHC 1380
Cranocephalites borealis β (Bo-2)	JHC 1377–1379

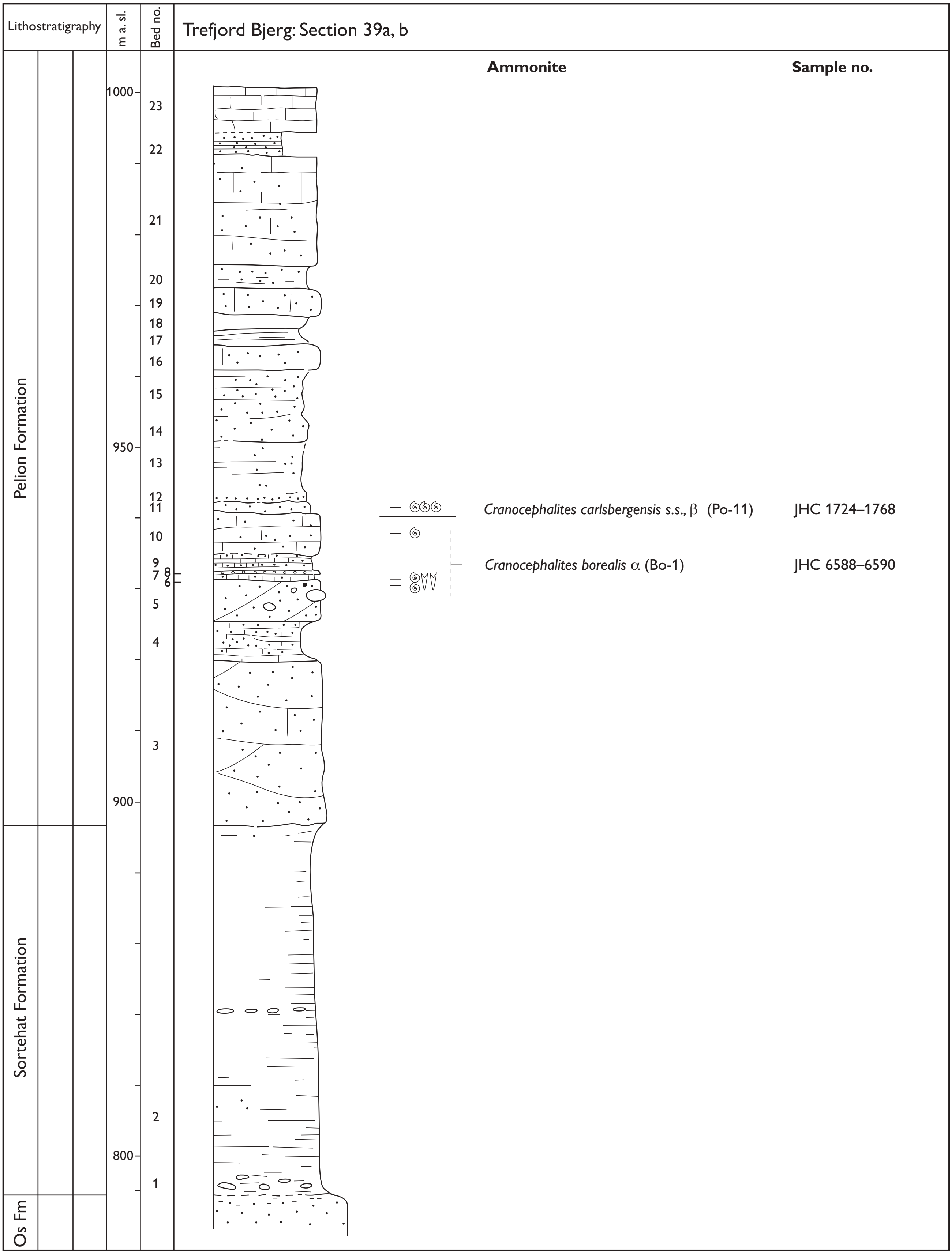


Fig. 29. Section 39a, b at Trefjord Bjerg. For location, see Fig. 4; for legend, see Fig. 12. **Os Fm**: Ostreaelv Formation. The section profile is based on section 39b (Fig. 40); specimens JHC 6588–6590 from section 39a are located by correlation. Note that a significant hiatus is indicated between beds 10 and 11 where 20 faunal horizons are absent (Fig. 30).

Biostratigraphy

The ammonite biostratigraphy of Jameson Land, and indeed of the whole of East Greenland, presents some special features. First, the fossils can, with some exceptions, be collected only from the hard, preferentially cemented beds. In the sandstones of the Pelion Formation, these are almost always well-bounded by clear partings, so that bed-by-bed collecting can be sharply defined. The casts of the shells are well preserved. In the softer mudstones of the upper Pelion and Fossilbjerget Formations, the collectable ammonites are confined to the concretions or otherwise diagenetically indurated horizons that commonly mark the tops of sedimentary cycles. In some cases, the fossils form the nucleus of concretions, particularly in the case of ammonites. Diagenesis was early, for the fossils are generally not distorted by compaction, and one of the striking features of the Greenland collections is their fine state of uncrushed preservation. Phragmocones of ammonites may still be void, or filled with calcite or, as witness perhaps to mild Palaeogene metasomatism, single crystals of barytes. The shells are neither broken nor encrusted with epizoans. Whether fossils also occur in the soft mudstones that separate the levels of concretions is not known, for the beds are either superficially weathered or impenetrable through permafrost.

Assemblages collected from such narrowly-defined stratigraphical horizons approach closely the ideal of what have been termed ‘faunal biohorizons’ (e.g. Callomon 1964, 1985a, b, 1995), viz. assemblages within which no further biostratigraphical differentiation can be resolved and which must therefore be regarded as effectively instantaneously isochronous on the time scale of discernible ammonite evolution. A succession of such assemblages of a group, such as an ammonite genus, therefore gives a time-serial snapshot record of the group and, if its morphology changes with time, of its evolution. These biostratigraphical units recording unknown but brief periods of formation separated by equally unknown intervals of non-recorded time form the basic input of a bottom-upward synthesis of the palaeobiology of an evolving group (more detailed discussions in Callomon 1985a, 1995).

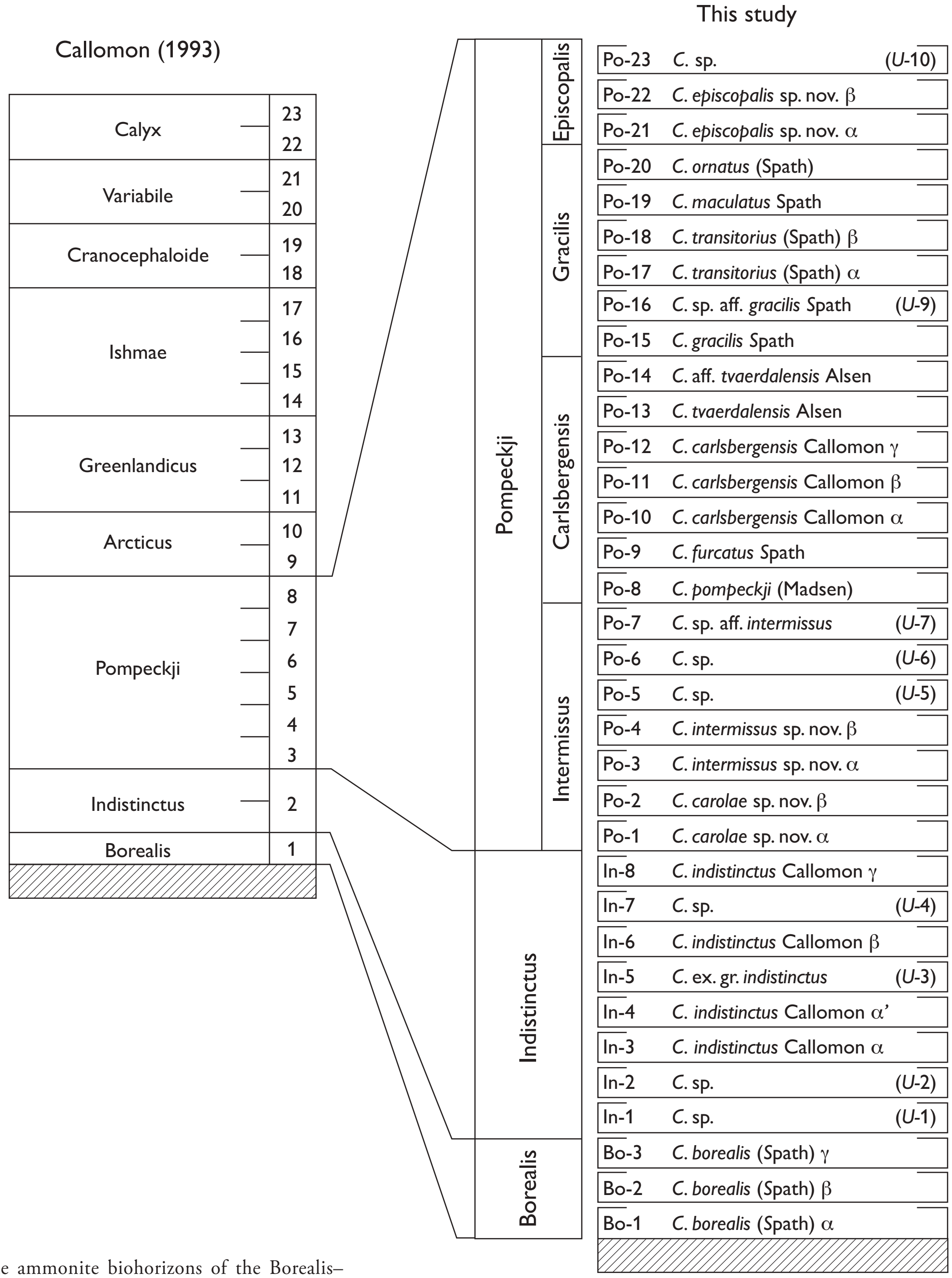
The second point to be noted is that the faunal horizons are highly impersistent. The hard beds come and go, both vertically and horizontally, over distances of as little as a kilometre. Even when beds can be followed over greater distances, their quantitative fossil-content may change drastically. The outcome is that in constructing a correct time-ordered sequence of faunal horizons, recourse has to be made to correlations between sections sufficiently close together geographically for their biohorizons to overlap laterally or in succession. The correlations are then usually lithostratigraphical, relative to selected markers. Even so, uncertainties in relative positions of faunal horizons can remain, for in some cases a well-defined horizon has been found in isolation at only a single locality.

The number of faunal horizons recognised in the *Cranocephalites* beds of Jameson Land prior to 1994 was eight. They were based on material from scattered localities, with little direct evidence of the stratigraphical interrelationships. At that time, they were numbered 1–8, as shown in Fig. 8, but the order in succession of horizons 3–8 had to remain tentative. It was however already clear from the older collections that there were more to be differentiated, given the necessary stratigraphical resolution. As already recounted, this resolution became available in the years 1994–1996, almost wholly in the region of Ugleelv, and the number of faunal horizons in these zones has risen to thirty-four (Fig. 30). They have therefore been given a new system of numbering, with prefixes Bo-, In- and Po- indicating the Standard Zones in which they lie (Borealis, Indistinctus and Pompeckji). Note that uncertainties in the faunal succession in the Pompeckji Zone discussed by Callomon (1993, p. 96) have been eliminated, and the *C. pompeckji*, *C. furcatus*, *C. carlsbergensis* and *C. gracilis* horizons are shown to occur in reverse order compared to the 1993-scheme. The sections and levels in which the 34 faunal horizons have been recognised are shown in Fig. 31. They show large gaps, but this must not be taken to mean that there are no sediments of the relevant ages in the successions. They are biostratigraphical gaps, meaning that the missing organisms were never present at the time or, if present, they left no preserved remains or reflect collection-failure.

To avoid having to renumber the faunal horizons above the *Cranocephalites* beds and the Pompeckji Standard Zone, which would be a cause for confusion, these higher horizons retain their old numbering unchanged, starting with horizon 9 at the base of the Arcticus Standard Zone. They should be prefixed by the letter J (for Jameson Land) to avoid uncertainty (see Fig. 8).

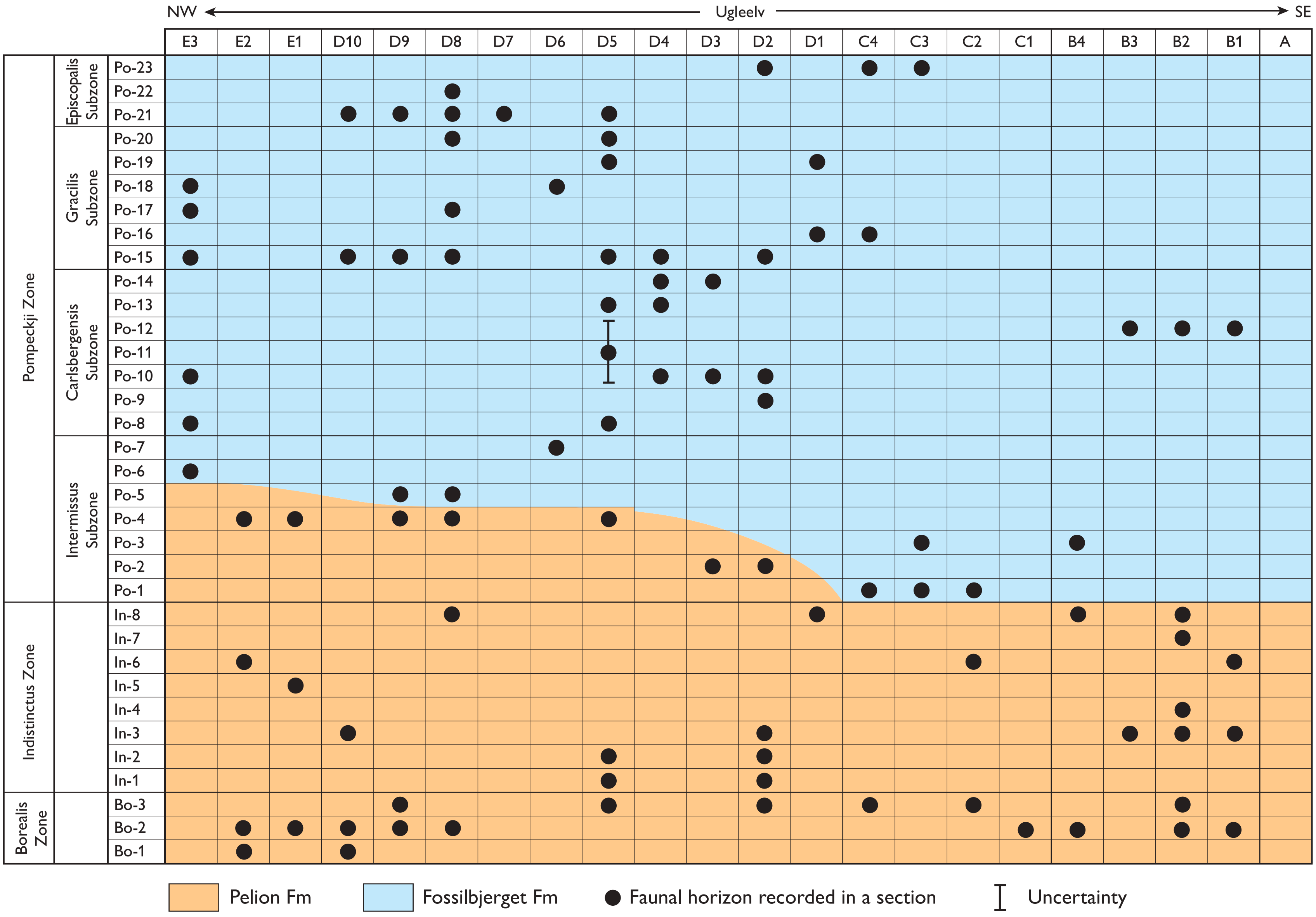
Standard Zone stratigraphy

The zonal stratigraphy of the *Cranocephalites* beds up to 1993 was encompassed by the Borealis, Indistinctus and Pompeckji Standard Zones, based on the then recognised succession of just eight faunal horizons. Of these, five were included in an undifferentiated Pompeckji Standard Zone. These zones form part of the secondary Standard Zonation for the Boreal Province of the biogeographic Boreal Realm of the Middle Jurassic (Callomon 1959, 1993; see above). With the refinement available today, it is possible and useful to subdivide the Pompeckji Standard Zone with its 23



C.: Cranocephalites Spath 1932

Fig. 30. The ammonite biohorizons of the Borealis–Pompeckji Zones and the proposed subzonal subdivision of these zones compared to the zonation of Callomon (1993). Note that faunal horizons 1–23 of Callomon (1993) were subsequently dubbed J-1 – J-23 (see Fig. 8) to differentiate the Jameson Land zonation from that of Milne Land.



NW ← Ugleelv → SE

Zone	Subzone	Horizon	E3	E2	E1	D10	D9	D8	D7	D6	D5	D4	D3	D2	D1	C4	C3	C2	C1	B4	B3	B2	B1	A
Pompeckji Zone	Episcopalis Subzone	Po-23												●		●	●							
		Po-22						●																
		Po-21				●	●	●	●		●													
	Gracilis Subzone	Po-20						●			●													
		Po-19									●				●									
		Po-18	●							●														
		Po-17	●					●																
		Po-16													●	●								
		Po-15	●			●	●	●			●	●		●										
	Carlsbergensis Subzone	Po-14										●	●											
		Po-13									●	●												
		Po-12									I										●	●	●	
		Po-11									●													
		Po-10	●								I	●	●	●										
		Po-9												●										
		Po-8	●								●													
	Intermissus Subzone	Po-7								●														
		Po-6	●																					
		Po-5					●	●																
		Po-4		●	●		●	●			●													
		Po-3															●			●				
		Po-2											●	●										
		Po-1														●	●	●						
Indistinctus Zone		In-8						●							●					●		●		
		In-7																				●		
		In-6		●														●					●	
		In-5			●																			
		In-4																				●		
		In-3				●								●							●	●	●	
		In-2									●			●										
		In-1									●			●										
Borealis Zone		Bo-3					●				●			●		●		●				●		
		Bo-2		●	●	●	●	●											●	●		●	●	
		Bo-1		●		●																		

🟧 Pelion Fm
🟦 Fossilbjerget Fm
● Faunal horizon recorded in a section
I Uncertainty

Fig 31. The ammonite biohorizons of the Borealis–Pompeckji Zones and the sections in the Ugleelv area in which they have been recognised.

faunal horizons into four subzones as shown in Fig. 30. They reflect four successive basic morphologies of *Cranocephalites* that should be recognisable more widely, making possible correlations at subzonal level of precision even when assignment to individual horizons is not possible.

Taxonomy: general principles

The Middle Jurassic ammonites of East Greenland belong predominantly to only two families, the Cardioceratidae and the Kosmoceratidae. There were very minor, short-lived incursions of only two others, the Oppeliidae (*Oxycerites*) in the *Arcticoceras* beds (middle Bathonian) and the Perisphinctidae (*Proplanulites*) in the higher *Cadoceras–Kepplerites* beds (lower Callovian). Those to be described here, from the *Cranocephalites* beds, all belong to the Cardioceratidae and represent the earliest stages in the evolution of that family, which ranges from the late Bajocian to the Kimmeridgian (Callomon 1985a).

The fossil record of these ammonites in Greenland is highly discontinuous, both in time and in space. The faunal succession has been pieced together from many localities and sections and synthesised in the time-ordered sequence of their distinguishable faunal horizons. The material from most of the horizons is abundant and in most cases well-preserved. In planning the taxonomic scheme to be adopted in its description, therefore, the following basic observations have to be taken into account:

(1) From the definition of faunal horizons, it follows that the assemblage of fossils from any one of them must be regarded as isochronous on the time scale of what makes successive assemblages distinguishable: evolutionary change in their morphologies. Fossil horizons may of course be locally 'condensed', i.e. contain mixtures of assemblages that are elsewhere biostratigraphically resolvable, but such condensation can only be recognised through fresh evidence from other localities at which it can be resolved.

(2) The assemblages from single horizons consist overwhelmingly of adults. They show well the characters that are generally of great taxonomic importance in almost all ammonites.

(3) The assemblages each consist of individuals whose morphologies, as far as one can tell, intergrade continuously. The test lies in adding further material, the effect of which is to make the spectrum of morphological variability trend increasingly toward unimodal, rather than accentuating polymodality.

(4) The assemblages may therefore be regarded as monospecific. Individual specimens are therefore treated merely as variants within a single, possibly highly variable biospecies.

(5) Successive faunal horizons yield assemblages that overlap considerably in their ranges of variability, i.e. share some morphological variants. The 'vertical' ranges of individual morphological variants, which were often in the past made into separate (morpho) species, can therefore extend over several faunal horizons and be members of several successive 'horizontal' biospecies.

(6) Such morphological overlapping is observed to greater or lesser degree over the whole range of the 34 faunal horizons. Their biospecies are therefore linked as successive members of a single evolving lineage, the successive slices – transients – of a trunk of a family tree.

Such transients (a term introduced by Bather in 1927) are sometimes referred to as chronospecies or chronosubspecies, but these terms are vulnerable to misinterpretation. The term chronospecies has also been used to label segments of a lineage ranging over several transients that the classifier regards are being still sufficiently similar to each other to be included in the same Linnéan taxon. The boundaries between such successive chronospecies then become entirely subjective. Subspecies are well-defined categories in the context of neontology that are used to label geographically restricted subsets of individuals within a common gene pool. Although phenotypically distinguishable, they retain the potential to interbreed. Such a 'horizontal', biospecific use of the subspecific category can in principle be validly retained in palaeontology if used in a similarly biogeographic sense to label isochronous local fossil races. But such purely biogeographic differentiation is rarely demonstrable in fossil assemblages. Two distinguishable fossil assemblages at two distant localities may differ either because of isochronous genetic, racial differentiation, or because of heterochronous phyletic differentiation, or both. It is rarely if ever possible to decide between them. In an attempt to adopt a natural, phylogenetic classification of a fossil succession, it is therefore best to avoid the use of the subspecific category altogether. A phyletic transient may then be labelled by continuing to use the name of an existing nominal species if, and only if, it can be shown that the type-specimen of the species came from the faunal horizon of that transient, i.e. that the horizon is the type horizon. Other transients may be labelled by means of informal, additional non-Linnéan symbols such as α, β, γ … etc., rather than Linnéan subspecific names. Transients that differ sufficiently from those preceding them may be given new full specific names provided that it is understood that they refer to strictly isochronous 'horizontal' biospecies. The infra-subspecific category of variety, 'var.', should be retained in its strict sense as applied to variants within a biospecies.

A suitable taxonomic category to encompass the successive transients of a monophyletic clade – the segments of a lineage – would then be the one of next higher rank in the Linnéan hierarchy, that of genus. Conventional classifications of ammonites have in the past used the category of the genus-group in a variety of ways. They shared, however, a common feature, again that of perceived purely morphological similarities in the form of selected shared characters. These similarities were now postulated to exist between 'species', but as these species were themselves purely morphological constructs, so were the morphogenera based on them. Classifications oscillated between those of 'splitters' and those of 'lumpers' and differed in the selection of the characters regarded as significant. The proliferation of new nominal taxa generated by the splitters cannot, under the taxonomic rules, be simply annihilated. They continue to swell the lists of synonyms of revisers even if suppressed as invalid taxa. But apart from the burden they impose on the literature, they can and do seriously mislead non-specialist taxonumerologists who take them at their face-value in counts to quantify species diversities and their changes with time in attempts to map the tempo of evolution and to identify its causes.

Thankfully, the number of nominal morphogenera that have been coined for the Arctic pre-Callovian Cardioceratidae is small. It has become clear that with only minor possible exceptions, the 50 or so successive transients of the Cardioceratidae now recognised in the pre-Callovian of Greenland form but a single phyletic strand. It would therefore be possible, following the principles outlined above, to assign them all to but a single genus *Cadoceras*, the oldest available name. But the lineage underwent some very considerable morphological transformations in the course of its evolution over this time-span. These changes have in the past been expressed through the use of the four successive genera of Spath (1932) and used by him to label the four-way major biostratigraphical subdivision cited previously: *Cranocephalites–Arctocephalites–Arcticoceras–Cadoceras*. This usage has become so entrenched internationally that to abandon it now would be confusing. It continues to be useful because of the rough chronostratigraphical connotations that it implies, and it will therefore be retained here. But this is on the understanding that the dividing-lines between these genera are subjective and drawn strictly on grounds of convention and convenience. They do not mark phyletic discontinuities or phylogenetic bifurcation points or major morphological breaks. The faunas of the *Cranocephalites* beds could in fact all be accommodated in the single genus *Cranocephalites*, but the upper boundary is taken to lie at the level at which its successor, *Arctocephalites*, has been conventionally introduced.

Finally, at the level of the family group, no special problems arise. The family Cardioceratidae is used to accommodate a multiply-branching clade of lineages leading back to a single common origin. Arising from this origin, the clade is subdivided both monophyletically and polyphyletically into several subfamilies. Monophyletically, the main stem of the Cardioceratidae has been conventionally subdivided into three successive segments, Arctocephalitinae – Cadoceratinae – Cardioceratinae, to mark major changes of morphology, and this arrangement continues to be convenient. All the forms now to be described fall into the first of these and the subsequent developments of the others therefore need not be considered further here.

The origin of the principal lineage of the Cardioceratidae lies in fact in the earliest of the transients, *Cranocephalites borealis* α, horizon Bo-1 (Callomon 1985a). Its appearance in East Greenland reflects an apparently abrupt re-colonisation by ammonites, after a long absence, of a large circumpolar Boreal Sea covering much of what is now northern Siberia, northern Alaska, Arctic Canada and the Barents Shelf, with an arm southwards to central East Greenland and the Shetland Islands (see Callomon 1985a, text-fig. 6a). The antecedents of the lineage lie most probably in the sphaeroceratid subgenus *Defonticeras* of the upper lower Bajocian of the northern Pacific (Callomon 1985a, text-fig. 7). The main lineage of the Cardioceratidae can then be followed at similar levels of time-resolution upwards to its abrupt termination in the Kimmeridgian (Callomon 1985a, text-fig. 3), in over 100 transients spanning some 20–25 Ma. Its habitat was exclusively Boreal into at least the early Callovian but then expanded somewhat southwards in what Arkell (1956, p. 610) called the 'Boreal spread'. The first indications of a phylogenetic division of the main stem of the Cardioceratidae point to levels no lower than the Cranocephaloide Standard Zone (horizon J-18, Fig. 8) and are indirect, expressed in the appearance at the base of the

Callovian of the genus *Chamoussetia* (*Ch. menzeli* Mönnig 1995, p. 55), if this is taken to be derived from *Arcticoceras ishmae*, horizon J-17 (Callomon & Wright 1989, text-figs 5, 6). The first positive evidence of a split lies in the observed co-occurrence of two biospecies (*sensu* Callomon 1985a) of Cadoceratinae in the Nordenskjoeldi Standard Zone (horizon J-29 in Fig. 8). Others will doubtlessly emerge in the future. All the members of the succession of 34 faunas described here form with little doubt a single phyletic strand.

Systematic taxonomy

Explanation and abbreviations

Collections, specimen abbreviations. Specimens are all housed at the Natural History Museum of Denmark in the Geological Museum section in Copenhagen. Four-digit numbers, prefixed JHC, refer to a catalogue by the first author of material largely collected by him in the years 1957–1996 in association at times with the late Tove Birkelund and the assistance of numerous helpers named in the acknowledgements. MGUH are registration numbers at the Geological Museum, University of Copenhagen. Six-figure numbers, pre-fixed GGU, are serial field numbers from the Geological Survey of Greenland (now merged with the Geological Survey of Denmark into the Geological Survey of Denmark and Greenland, GEUS) that were assigned to material collected by various other workers, largely during the course of mapping in the years 1968–1974 by geologists from the University of Copenhagen. Specimen numbers prefixed CASP were collected by geologists of CASP, Cambridge, UK; specimen numbers prefixed FS were collected by F. Surlyk.

Types. HT: holotype; PT: paratype; LT: lectotype; [M], [m]: macro- and microconch dimorphs respectively; AT: allotype, secondary type, the opposite dimorph – the antidimorph – of the primary type. As the taxonomic differentiations are based on comparisons of assemblages thought to represent isochronous biospecies, the descriptions take into account not only the characters of type specimens but also the variabilities of biospecies as seen in such assemblages. One of these assemblages of specimens found in association in a single bed at a single locality has therefore been selected as a reference collection in each of those species or transients in which material is sufficiently abundant. In most cases, the reference collection includes the types of the species or the representative specimen(s) of the transient it represents. Paratypes have in consequence not generally been explicitly designated as such.

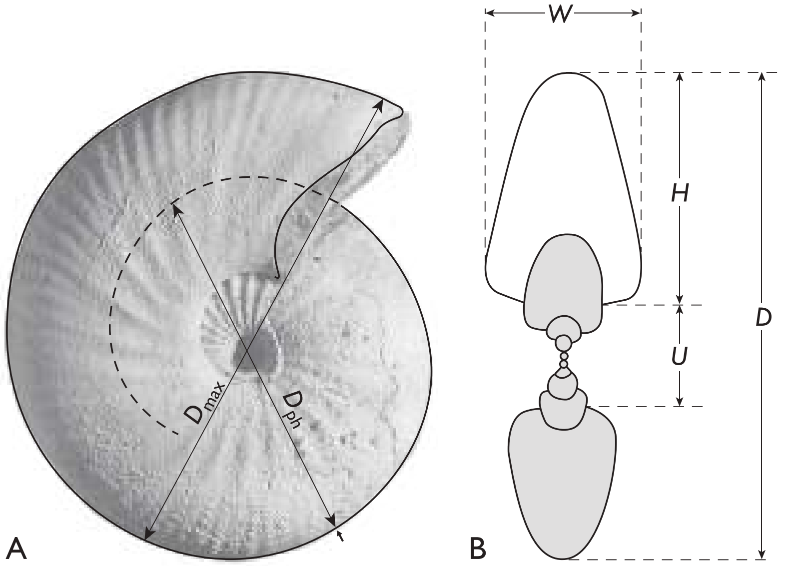


Fig. 32. **A**: Sketch of an adult/mature ammonite (upon photo of *C. pompeckji*, see Plate 11, fig.1a) illustrating the quantitative parameters of largest whorl diameter, $\boldsymbol{D}_{\mathbf{max}}$, and diameter $\boldsymbol{D}_{\mathbf{ph}}$ at the last septum, indicated by the small arrow.
B: Sketch of an ammonite cross-section showing the following parameters: ***H***: whorl-height. ***W***: whorl-width. ***U***: umbilical width, at diameter ***D***.

Dimensions. $D_{\max}$: maximum diameter of adult shell at the peristome; D_{ph}: diameter at the last septum (marked with arrow) of the phragmocone (Fig. 32A). *H*, *W*, *U*: whorl-height, whorl-width and umbilical width at diameter *D* (Fig. 32B); their coefficients *h* (= *H*/*D*), *w* (= *W*/*D*), *u* (= *U*/*D*); < >: mean value in a sample of *n* measurements; σ: their standard deviation from the mean in an assumed simple Gaussian distribution; ρ(π): the logarithmic spiral half-whorl constant, the ratio of shell diameters half a whorl (π) apart.

Taxonomic descriptions. The taxonomic descriptions within the *Cranocephalites* genus that follow are arranged in the temporal order of transients shown in Fig. 30, grouped into standard zones and subzones and referred to their respective faunal horizons; the sources of the material are shown in Fig. 31. The quality and quantity of the material varies widely and in a number of cases is insufficient to justify the creation of a new formal nominal taxon. Such cases are included because they are nevertheless stratigraphically and morphologically sufficiently distinct from their neighbours to show that perceptible evolutionary change has occurred. They are distinguishable transients and are named in open nomenclature and assigned informal labels *U*-1 – *U*-10 (‘*U*’ for Ugleelv).

Order Ammonoidea
Suborder Ammonitina
Superfamily Stephanoceratoidea Neumayr 1875

The names of taxa at superfamily level were not regulated under the International Code of Zoological Nomenclature, until the advent of the current, fourth edition, whose provisions were effective as from January 2000 (International Commission on Zoological Nomenclature 1999, 2012). Article 29.2 now prescribes that names of superfamilies shall end in the suffix -oidea, whereas in previous editions such usage was put forward only as a recommendation (Recommendation 29A). In what had become well-established convention in the taxonomy of ammonites and nautiloids, the *Treatise* (Treatise on Invertebrate Paleontology, Moore 1957, 1964) had the names of superfamilies ending in -aceae, and this usage was continued in the second edition of the ammonite volume of the *Treatise* dealing with Cretaceous taxa (Wright *et al.* 1996), whereas the recent contribution by Howarth (2013) follows Article 29.2.

Family Cardioceratidae Siemiradzki 1891
Subfamily Arctocephalitinae Meledina 1968
Genus Cranocephalites Spath 1932

Type species. C. vulgaris Spath 1932 [incl. *Boreiocephalites* Meledina 1967, type species *B. pseudoborealis* and *C.* (*Pachycephalites*) Meledina 1973, type species *C.* (*P.*) *spathi*].

The generic classification is discussed above. One generic name is regarded here as sufficient, but those wishing to distinguish the earliest forms, *C. borealis*, may retain *Boreiocephalites*, perhaps as a subgenus.

Morphological characters of general taxonomic value. It is a general feature of almost all Jurassic Ammonitina that they grew to an adult stage at which growth stopped. Experience with the Greenland material has shown that the most useful characters for a natural classification of the Arctocephalitinae are those measured at the adult stage: the diameter and whorl-section of the fully grown phragmocone, the modifications in coiling, length and sculpture of the mature body chamber, the form of the final peristome and the size of the fully grown adult. Other morphological characters such as whorl-height, whorl-width and umbilical width have been found to be of lesser significance for they are liable to vary widely within a species. Growth of the shells was logarithmically isometric in the planispiral diameter *D*, in the area of cross-section of the whorls A, and hence more or less in the coupled biometric parameters of whorl-height *(H)*, whorl-width *(W)* and umbilical width *(U)* – the parameters usually cited – up to the end of the adult phragmocone. Onset of the adult body chamber then leads to significant departures from this type of simple growth. Conversely, the observation of such departures is diagnostic of the adult stage. Common features are contraction of the whorl cross-sectional area that is reflected in a number of ways: (1) an uncoiling of the umbilical seam; (2) contraction of the interseptal spacing reflected in crowding-together (approximation) of the last septal sutures; (3) modification of the sculpture of the shell, commonly by the loss of all ribbing (variocostation); and (4) a change in the sweep and structure of the final peristome, in the Arctocephalitinae commonly in the form of a terminal constriction on internal moulds, reflecting a terminal strengthening collar on the shell. The average final adult diameter of a transient assemblage is a quite closely-defined character, particularly significant in the recognition of sexual dimorphism.

Because of the variable modifications of the adult body chamber observed in this material, biometric measurements of the principal parameters of the shell morphology at the maximum shell-diameters have little comparative value. Values of *h*, *w*, *u*, where given, are therefore quoted generally at the end of the adult phragmocone, at D_{ph}. In most transients, the values of *h* and *u* vary so little between subsequent transients that they are hardly worth measuring. The whorl-width, *w*, does, however, vary intraspecifically and from transient to transient, so it is generally given. Ranges of intraspecific variation are indicated in terms of a Gaussian model, standard deviation σ.

All these features are prominently well developed in the faunas described below. The genus *Cranocephalites* is strongly dimorphic. The adult macroconchs are all more or less variocostate, the ribbing modifying and tending to fade, with simple final peristomes preceded by a broad, shallow constriction on the internal moulds. The microconchs are isocostate, with a simple but ventrally projected peristome. The dimorphic size ratio is large, in the range 2.5:1 to 3:1, indicating that the body-chamber volume of macroconchs is much larger than in microconchs.

Palaeoecology. Almost all of the abundant assemblages of ammonites collected in East Greenland consist almost exclusively of fully grown adults and predominantly of macroconchs at that. Microconchs are rare, despite the fact that a special watch was kept out for them in the field. The sex ratio of [M]:[m] is therefore in the range of 10:1 – 100:1. In some of the assemblages to be described, no microconchs have been found at all. The probable reasons for these ontogenetic and sexual polarisations have been discussed previously (Callomon 1985a). They point to a closed life cycle in which the fossil accumulations now mark the breeding, spawning and dying grounds of gregarious nektonic organisms that migrated during their life cycles, with sexual segregation in the final stages. The persistence of such characteristic death-assemblages of mature adults of one genus in a geographically restricted region for such long periods of time, as seen in Jameson Land, points to that region as the 'true home' of that genus for reproductive purposes and hence for its evolution. Such assemblages have been called eudemic and those of East Greenland taken as prototypical (Callomon 1985a).

Juvenile ammonites do occur but in quite different surroundings. The otherwise unfossiliferous, more distal, fine-grained mudstone-dominated successions occasionally yield an isolated concretion packed with completely-preserved small juveniles, too young to identify even as [m] or [M]. The impression is that of a death-assemblage of a migrating school of gregarious juveniles.

Borealis Standard Zone

The Borealis Standard Zone includes three faunal horizons Bo-1 – Bo-3, characterised by transients of *Cranocephalites borealis* (Spath 1932; Fig. 30), and illustrated in Plates 1–3. Three separable transients α, β, γ of these, the earliest forms of *Cranocephalites*, can now be distinguished in Jameson Land. The type of the original species came most probably from trans α. The three transients differ relatively little and some variants are found through the vertical range of all the transients. Conversely, a single specimen found in isolation may not be assignable to any of the transients in particular. The features they have in common are as follows:

General description. Strongly dimorphic. The macroconchs are on the whole smaller than those of younger/succeeding species. They also differ in that maximum diameters within an assemblage can vary much more widely. Mature body chambers occupy *c.* 0.75 whorl and contract strongly, the umbilical seam uncoiling markedly. The final peristome is simple, preceded by a prominent, broad but shallow constriction on the internal mould. The coiling is strongly involute, with minute umbilici on the inner and middle whorls. The whorl-section can range from slightly high oval in compressed variants to rounded, depressed in inflated variants. The umbilical shoulder is always well rounded.

The most characteristic feature lies however in the style of the ribbing: coarse but blunt and subdued on the phragmocone, primaries rising gently on the umbilical shoulder, dividing without accentuation into equally subdued secondaries interspersed with intercalatories that cross the venter without loss of strength. The ribbing tends to fade on the adult body chamber, which becomes wholly smooth in large specimens.

The microconchs are small but otherwise resemble the macroconchs in every respect. Their adult sizes are again very variable and a large microconch may be hard to distinguish from the smallest macroconch. The microconchs remain ribbed to the end, however. The adult stage is seen in the uncoiling of the umbilical seam and in the whorl-width of the body chamber, which ceased to grow isometrically and stayed constant. The peristome is also simple and preceeded by a constriction that is however shallower and broader than in the macroconchs. It is these expressions of the dimorphism that reveal that the origin of *Cranocephalites*, and hence of the whole of the Cardioceratidae, lies in late early Bajocian Sphaeroceratidae of the East Pacific Realm (Callomon 1985a).

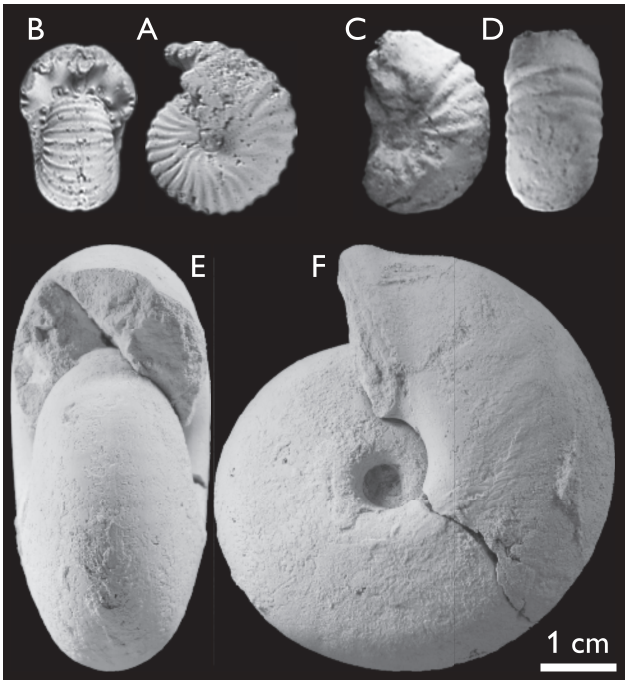


Fig. 33. **A**, **B**: The holotype of *Cranocephalites borealis* [M], MGUH 9235. **C**, **D**: *'Xenocephalites' borealis*, Nordenskjöld collection 1900, near Fossilbjerget. **E**, **F**: Topotype of *C. warreni* Frebold 1961 from Richardson Mountains, Yukon, Canada (JHC collection 1975). All natural size.

Bo-1: *Cranocephalites borealis* (Spath 1932) *sensu stricto*, trans α

Plate 1, figs 1–5 [M], figs 6–7 [m]; Fig. 33A, B

1932 *Xenocephalites borealis* Spath, p. 44, plate 14, fig. 4a–d (HT by monotypy).
1984 *Cranocephalites borealis* (Spath) [M] – Callomon, p. 148, fig. 2B [JHC 1368].
1985a *Cranocephalites borealis* (Spath) [M] – Callomon, p. 64, fig. 7B [*id.*].

Type specimen. The precise level within the range of Bo-1 – Bo-3 from which it came is somewhat uncertain. Its morphology is of little help, for it is a wholly septate macroconch nucleus only 24 mm in diameter (Fig. 33A, B). It is, however, very strongly and coarsely ribbed, suggesting the forms that retain their strong ribbing longest, which are those of trans α. But similar nuclei are equally common in Bo-2, trans β. The place of origin is not much help either. It was collected by Rosenkrantz at 'Mt Hjørnefjæld' (Hjørnefjeldet, Fig. 4) allegedly at a height of 630 m, which, according to the sketch of his section (in Spath 1932, p. 133, text-fig. 14), places it on the slope of the Sortehat Formation. The only associated specimen, a *Crancocephalites* cf. *furcatus* (? Po-9), definitely came from the local '*Cranocephalites* Bed', at 740 m in the section.

There is in fact a further complication. It relates to the precise location of 'Mt Hjørnefjæld' itself. Rosenkrantz's sketch-maps (in Spath 1932, p. 125, text-fig. 9, and Rosenkrantz 1934, plate 1) places it at the 'corner' between the headwaters of Depotelv, running westwards, and Lejrelv, coming from north to south. But here the highest point lies at only 630 m, nothing like the 765 m given in the section. The nearest place corresponding stratigraphically to the section reproduced by Spath lies at Centralbjerg, sections 35–37 in Fig. 1B, about 3 km west of the locality now marked as Hjørnefjeldet on the 1:100 000 geological map of the Geological Survey of Greenland (GGU) (Birkelund & Higgins 1980). Its highest point lies at 660 m, and the succession there can be brought roughly into correspondence with Rosenkrantz's section if all the heights given in the latter are reduced by 100 m. Rosenkrantz and co-workers used aneroid barometers to measure heights, and differences in height indications among authors may thus just reflect differences in atmospheric pressure. The highest beds on Centralbjerg are in typical Pelion Formation and are indeed only a little above a prominent local marker, Rosenkrantz's '*Arctocephalites* Bed', rediscovered in 1971 and now recognised as horizon J-9 (Fig. 8). Rosenkrantz also picked up a second prominent local marker which he called the '*Pecten*-belemnite horizon' (bed (d) in his section, shown in Spath 1932, p. 133 fig. 14), 60 m below the *Arctocephalites* Bed and 50 m above the top of the Sortehat Formation. Spath referred to it as the *Demissus* Grit (after *Entolium demissum* (Phillips), Rosenkrantz's '*Pecten*') and surmised that it was the source of the type of *C. borealis*. This marker bed was also rediscovered in 1971 during mapping and referred to in the field as the 'Brown Bed', *c.* 0.5–1 m thick, for its colour makes it stand out in the otherwise monotonous succession of white or cream-coloured sandstones of the Pelion Formation within which it lies. Also, in contrast to the beds above and below, it is fossiliferous, with abundant belemnites, some oysters and other bivalves. The bed can be seen all round Centralbjerg and followed across to the northern slopes of Mikael Bjerg (section 33, bed 4, 6 km WSW of section 35, Fig. 4.). At Centralbjerg it lies about 100 m above the Sortehat Formation and 100 m below the *Arctocephalites* bed. At Mikael Bjerg, it was estimated to lie about 90 m above the Sortehat Formation and 80 m below the *Arctocephalites* bed; at this locality, it yielded four specimens of *C. borealis* α. The 'Brown Bed' is the only bed in the Pelion Formation in the Mikael Bjerg – Hjørnefjeldet area to have yielded ammonites below the Pompeckji Standard Zone. The conclusion has therefore to be that the type-horizon of *C. borealis* most probably was the '*Pecten*-belemnite horizon/Brown Bed' at or close to Centralbjerg and that it is the lowest of the three ammonite horizons with *C. borealis*, Bo-1, trans α. It seems ironical that the type that was brought back after the extensive surveys of 1926–1927 should have been the sole specimen, and it from the rarest transient, of what is in fact one of the most abundant and widespread species in the whole of Jameson Land.

There was in fact a further specimen that had been brought back by Nordenskjöld in 1900 during the Danish Amdrup expedition, from his 'fossil locality 1', somewhere in the region of Fossil Mountain. It was referred to by Madsen (1904, p. 198, no. 5) but not otherwise described. Spath saw it (1932, p. 45) and gave something of a description, assigning it to his *'Xenocephalites' borealis*, but did not figure it. He noted its small size and that it carried three-quarters of a whorl of body chamber, with rejuvenation of the ribbing at the peristome. It is now figured here, in Fig. 33C, D. Although poorly preserved, it is clearly an adult microconch. Its preservation is in brown sandstone similar to that of the 'Brown Bed' and may well have come from it, hence also trans α.

In view of the inadequacies of the formal type specimen, the one shown on Plate 1, fig. 3a, b (JHC 1368) may be taken as typical stand-in (*typus substituens*) for the macroconchs, and that on Plate 1, fig. 7, (JHC 1363 [m]) as allotype.

Material and distribution. Ugleelv, section E2 (reference collection), bed 12, top of Ug-1, 80 m above Sortehat Formation (Fig. 28A): 30 [M], 3 [m]. Ugleelv, section D10 (Fig. 26): 2 [M], 3 [m]. Mikael Bjerg, section 33, bed 4, 'Brown Bed', *c.* 110 m above base of Pelion Formation: 2 [M], 2 [m]. Trefjord Bjerg, section 39 (Fig. 29): 3, loose, from the basal 20 m of the more massive sandstones of the Pelion Formation (see further discussion below). *Total*: 44 (37 [M] + 7 [m]).

Description. The macroconchs range in size from 40 to 70 mm (Plate 1, figs 4, 5), the microconchs from 20 to 35 mm (Plate 1, fig. 7). The adult body chamber becomes constant in whorl-width (Plate 1, figs 1–3, 6). The whorl-width varies widely, from 0.6 (Plate 1, fig. 2) to 0.8 (Plate 1, fig. 1) of the diameter at the last septum. The shells retain their characteristic strong ribbing to the end, with at times even some strengthening at the final stage (Plate 1, fig. 5).

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 1368 (Plate 1, fig. 3):	57	39	0.50	0.74	0.12
JHC 1789:	53	37	0.50	0.58	0.12

Mean values, reference collection:
$<D_{max}>$ 51.7 ± 1.9 $\sigma = 8.4$ (16%) $n = 21$
$<D_{ph}>$ 31.6 ± 1.8 $\sigma = 9.1$ (29%) $n = 26$
$<w_{ph}>$ 0.66 ± 0.02 $\sigma = 0.11$ (16%) $n = 26$

D_{max}, D_{ph} in mm

Discussion. The species was initially placed in the genus *Xenocephalites* Spath 1928, because of all the Middle Jurassic ammonites then known it was the only one whose type species remotely resembled the Greenland specimen. The figure of the type of the type species, *Macrocephalites neuquenensis* Stehn 1924, is reproduced in the *Treatise* (Arkell *et al.* 1957, fig. 352.13). The interpretation of the genus has since become clear. It represents the microconchs of another sphaeroceratid group, the Eurycephalitinae that is endemic in the East Pacific Realm, extending from Alaska to the Andes and thence to the palaeo-Moluccas of Indonesia (Riccardi & Westermann 1991).

Bo-2: *Cranocephalites borealis* (Spath 1932) trans β

[M]: Plate 1, figs 11–13; Plate 2, figs 1–10
[m]: Plate 1, figs 8–10; Plate 2, figs 11–14

cf 1957 *Xenocephalites kononovaja* Voronets, p. 22, plate 1, fig. 3a, b, v (HT by monotypy).
cf 1957 *Morrisiceras laptinskajana* Voronets, p. 21, plate 1, fig. 2a, b, v (HT by monotypy, [m]?).
?1957 *Morrisiceras sibirica* Voronets, p. 22, plate 1, fig. 1a, b, v, g (HT by monotypy).
1959 *Cranocephalites borealis* (Spath) – Callomon, p. 507, plate 17, figs 1a, b, 2a, b; plate 18, fig. 3a, b.
1961 *Cranocephalites borealis* (Spath) – Frebold, p. 12, plate 1, figs 1–4.
cf 1961 *Cranocephalites warreni* Frebold, p. 14, plate 2, figs 1, 2, 4.
1962 *Xenocephalites kononovae* Voronets, p. 45, plate 9, fig. 3 (= 1957 redescribed).
?1962 *Morrisiceras laptinskajae* Voronets, p. 30, plate 15, fig. 3a, b (= 1957 redescribed).
?1962 *Morrisiceras sibiricum* Voronets, p. 31, plate 15, fig. 2a, b, v (= 1957 redescribed).
1967 *Boreiocephalites pseudoborealis* Meledina, p. 107, plate 1, figs 1a, b, v, 3a (HT), figs 2a–g, 3b (PT).

1973 *Boreiocephalites pseudoborealis* Meledina, p. 35, plate 1, figs 1, 3 (same as 1967), 2a, b.
1982 *Cranocephalites borealis* (Spath) – Poulton *et al.*, p. 84.
1984 *Cranocephalites borealis* (Spath) [m] – Callomon, p. 149, fig. 2b.
1985a *Cranocephalites borealis* (Spath) – Callomon, p. 64, text-figs 7b, 8a; [M]: text-fig. 8A.
1988 *Boreiocephalites borealis* (Spath) – Krymholts *et al.*, p. 22, plate 5, fig. 7a, b (=Meledina 1973, plate 1, fig. 1).

Representative specimen of transient β [M]. MGUH 22255 (ex JHC 1144), Plate 1, fig. 12 (= Callomon 1959, plate 17, fig. 1a, b); in the reference collection from Teebjerg, section C1, bed 18.

Representative specimen of transient β [m]. GGU 135887a, Plate 2, fig. 14; Katedralen, section D9, bed 9.

Material and distribution. This is one of the most abundant and widespread forms in the Ugleelv area. It occurs at several levels in the Ug-2 unit but the abundance at any one of these can change rapidly from place to place. By far the richest occurrence was in a single thin level of slightly phosphatised concretions at Teebjerg, section C1, bed 18, the reference collection, that littered the ground in their hundreds where weathered out, many of them enclosing a beautifully preserved ammonite. Yet at Falkeelv, section C4, 2 km south-west and at Statuebjerg, section B3, 2 km east (Fig. 9), the bed had disappeared.

Reference collection: section C1: 185 [M], 3 [m]. Section B8: 8 [M]. Section C4: 2 [M]. Section D8: 6 [M] (Fig. 25). Section D9: 78 [M], 11 [m]. Section D10 (Fig. 26): 29 [M]. Section E1: 6 [M] (Fig. 27). Section E2 (Fig. 28): 11 [M]. *Total*: 339 (325 [M] + 14 [m]).

Poorly preserved material was often noted but not collected. An important example was on the north ridge of Trefjord Bjerg, section 39b (Fig. 29), where it occurred irrecoverably in beds 5–10 in the Pelion Formation, 80 m above its base and immediately below the main *Cranocephalites* horizon there, that of *C. carlsbergensis*, fauna Po-11.

Description. The range of variability is shown in the plates. In contrast to trans α (Plate 1, figs 1–4), the adult macroconchs of trans β become smooth on the body chamber (Plate 1, figs 11–13). The maximum sizes range from 37 to 83 mm (Plate 2, fig. 2). The whorl-width can range from 0.50 of the diameter (Plate 2, fig. 2) to over 0.90 (Plate 2, figs 1, 10). The whorl-section can be ventrally rounded (Plate 2, figs 6, 8, 10) or arched (Plate 2, fig. 4). The characteristic terminal constriction is well seen on the representative specimen (Plate 1, fig. 12). A slightly immature or precociously aged specimen is shown in Plate 2, fig. 5: the ribbing persists, the body chamber is somewhat longer than usual (0.85 of a whorl, vs. 0.75) and the peristome has not yet modified. A typical nucleus is shown in Plate 2, fig. 3.

Microconchs range in size from c. 15 to 30 mm (Plate 1, figs 8–10; Plate 2, figs 11–14). Their peristomes have typically only a narrow, inconspicuous constriction followed by a slight lateral flaring, well seen in Plate 2, figs 11 and 13a, b.

Dimensions.

	D_{max}	D_{ph}	h	w	u
MGUH 22255:	58	~41			
At $D = 40$			0.50	0.61	0.10
(0.75 whorl body chamber)					

Mean values, reference collection:

$<D_{max}>$	52.0 ± 1.2	$\sigma = 7.4$ (14%)	$n = 36$
$<D_{ph}>$	36.8 ± 0.9	$\sigma = 6.1$ (16%)	$n = 47$
$<w_{ph}>$	0.625 ± 0.01	$\sigma = 0.060$ (9.5%)	$n = 47$

D, D_{max}, D_{ph} in mm

Discussion. The synonymy includes specimens from the Richardson Mountains in the Yukon Territory (Frebold 1961) and Siberia (Voronets 1962; Meledina 1968) described under various new names. The material consists in each case of but a few specimens, insufficient to define an assemblage with a precision comparable to that of those being described here. The specimens match as far as they go the Greenland forms of trans β of comparable sizes, their body chambers becoming wholly smooth and the ribbing exactly as in *C. borealis*. A topotype of *C. warreni* from the Yukon collected in 1975 (Poulton & Callomon 1976; Poulton 1978) is figured here (Fig. 33E–F).

Bo-3: *Cranocephalites borealis* (Spath 1932) trans γ
Plate 3

Representative specimen of trans γ. JHC 1011 (Plate 3, fig. 6a–c), in the reference collection from Hurry Inlet, section 8, Brinkmann Fjeld, bed 3 (Fig. 2).

Material and distribution. The Pelion Formation unit Ug-2 around Ugleelv terminates everywhere with soft sandstones containing a level of small round concretions carrying large *Plagiostoma* bivalves, topped by thin lenticular red ironstones and followed with sharp change of facies by the soft, silty mudstones of unit Ug-3. The top few metres of Ug-2 yield the last *C. borealis*, differing somewhat in aspect from those of trans β below and now differentiated as trans γ. In the region of Hurry Inlet, at Neill Klinter, Ug-2 terminates in similar fashion but is immediately followed there by the mudstones of the Arcticus Standard Zone, horizon J-10, and both the Indistinctus Standard Zone and the Pompeckji Standard Zone are missing. Here, too, the top of Ug-2 carries concretions with *C. borealis γ*. They are particularly abundant around Moskusokseklōft at Brinkmann Fjeld, which produced the best-characterised assemblage, now taken to be the reference collection. Found also at scattered localities elsewhere in Jameson Land while mapping. Hurry Inlet, sections 1–8: 34 [M]. Ugleelv: sections B2 (Fig. 19), C2, C4 (Fig. 21), D2 (Fig. 22), D5 (Fig. 24), D9, E3: 52 [M]. *Total*: 86 (all [M]).

Description. Inner and middle whorls of macroconchs indistinguishable from those of trans β at comparable diameters, except that more inflated variants dominate. The most striking difference lies however in the size (Plate 3). As the ribbing is lost at about the same diameters as in trans β, all that is generally visible in trans γ is entirely smooth.

The microconchs have yet to be found but are expected to be very much like those of trans β, perhaps a little larger.

Dimensions.

	D_{max}	D_{ph}	*h*	*w*	*u*
JHC 1011:	85	61			
At *D*= 60			0.51	0.85	0.13
(0.70 whorl body chamber)					

Mean values, reference collection:

$\langle D_{max} \rangle$	74.5 ± 3.4	$\sigma = 15.7$ (21%)	$n = 22$
$\langle D_{ph} \rangle$	49.7 ± 1.6	$\sigma = 8.2$ (16%)	$n = 27$
$\langle w_{ph} \rangle$	0.63 ± 0.02	$\sigma = 0.12$ (19%)	$n = 28$

D, D_{max}, D_{ph} in mm

An estimate could be made of the logarithmic spiral half-whorl constant from specimens that had been broken diametrically (cf. Plate 3, fig. 6): $\rho(\pi) = 1.29$ (± 0.04), $n = 4$.

The phyletic increases in the sizes of the adult shells of *C. borealis* are reflected in the mean values of the diameter of the phragmocones $\langle D_{ph} \rangle$ in successive transients listed above: α: 32 (± 2) → β: 37 (± 1) → γ: 50 (± 2) mm.

General discussion of the *Cranocephalites borealis* group

Other species. Besides the faunas Bo-1 – Bo-3 there are indications of at least two other species of *Cranocephalites* of the *borealis* group, one from East Greenland, the other from Siberia, each described in terms of two published nominal morphospecies.

East Greenland:

(1) *Cranocephalites kochi* Donovan 1953, (p. 80, plate 15, fig. 8a, b [M], generically as subgenus of *Arctocephalites*), from localities 120 and 104 on Traill Ø, including *Cranocephalites kochi* var. *latus* Donovan (p. 82, plate 16, fig. 6a, b,[M] from locality 137 and *Cranocephalites kochi* var. *pygmaeus* Donovan (p. 81, plate 16, fig. 5a, b [m?]) from localities 120, 137; (2) *Cranocephalites parvus* Donovan 1953 (p. 79, plate 15, fig. 2a, b [M]), also from locality 120.

Stratigraphically, their positions are not very clearly defined. Morphologically, however, they share their style of coiling and ribbing with those of *C. borealis* but are consistently smaller, none of them exceeding 45 mm in diameter. They resemble *C. borealis* α in retaining strong ribbing on the adult body chamber, but the ribbing on *C. parvus* is markedly denser and finer than on any of the transients α–γ of *C. borealis*, recalling perhaps more strongly the putative ancestors of the whole lineage, *Chondroceras* of the early Bajocian. Although the amount of material from Traill Ø is small, it is enough to show that it differs consistently from *C. borealis*.

The only known forms from Jameson Land that could match it are from Trefjord Bjerg, section 39 (Fig. 4), from the basal 20 m of the Pelion Formation (Ug-1), hence presumed to be at least as old as Bo-1, *C. borealis* α. Only three specimens exist, two of them poorly preserved. They are also small, not exceeding 50 mm in diameter, and more densely and finely ribbed than the usual *C. borealis* α. One of them, although crushed, could in this respect be a close match with *C. parvus*. If these indications are correct, they make *C. kochi/parvus* the oldest known species of *Cranocephalites* and the founder of the Cardioceratidae.

Siberia:

(3) *Cranocephalites sibiricus* (Voronets 1957) (p. 22, plate 1, fig. 1a–g, originally as *Morrisiceras*, reproduced and described more fully in Voronets 1962, p. 31, etc.).

(4) *Cranocephalites laptinskajae* (Voronets 1957) (Voronets 1962, fig. 2a–v).

These morphospecies, although still clearly related to *C. borealis* in coiling and the blunt ribbing, differ in retaining strong secondary ribbing long after the primaries have been lost, leaving a wholly smooth umbilical shoulder. Both came from the Uryung–Tumus Peninsula, west of the Anabar estuary in northern Siberia, allegedly from 'bed 5'. The section was reproduced by Meledina (1973, p. 104) but the ammonites are recorded from 'bed 6' (16 m), together with *Cranocephalites* spp. of the *pompeckj–furcatus–maculatus* group, clearly indicating the Pompeckji Standard Zone. At least, beds 5 (21 m) and 6 are above bed 4 (5 m), which yielded *C. borealis* proper, *Boreiocephalites pseudoborealis* Meledina, identified with trans β above, so that *C. sibiricus* must be younger than *C. borealis*. There would be room in the succession in Greenland for additional faunal horizons at the regional facies change from Ug-2 to Ug-3 and additional faunal transients at the marked morphological change at that level, between Bo-3 and In-1.

World-wide distribution. Arctic Canada (Yukon), northern Siberia (Anabar, Lena), central East Greenland.

Indistinctus Standard Zone

The Indistinctus Standard Zone includes eight faunal horizons In-1–In-8, represented by the group of *Cranocephalites indistinctus* Callomon 1959 and *Cranocephalites* spp. (*U*-1) – (*U*-4) (Fig. 30), illustrated in Plates 4–8.

The marked lithological break from Ugleelv units Ug-2 to Ug-3 marks also a fundamental change in the morphology of *Cranocephalites*. Henceforth the shells are more densely and sharply ribbed on the phragmocones, the primaries and secondaries less differentiated, the variabilities of assemblages reduced and the features distinguishing successive transients expressed mainly in the form of the adult macroconch body chamber.

The soft, recessive mudstones of Ug-3 make the biostratigraphy heavily dependent on the relatively uncommon, impersistent and often very poorly fossiliferous layers of doggers or indurated mudstone. The ammonite record in this interval remains patchy. Although eight distinguishable horizons are now recognised, in only a few of them is the material sufficiently abundant and well preserved to be worth describing in any detail. Four of them are labelled in open nomenclature with numerical symbols: (*U*-1) – (*U*-4).

The type material of *C. indistinctus* came from scattered, isolated concretionary levels in Ug-3 between Statuebjerg (sections B1, B2; Figs 18–19) and Ræveelv (section E3) (Callomon 1959). It was clear that more than one faunal horizon was represented, but even after new collecting in 1970–1971, only two could be recognised with any confidence, labelled *C. indistinctus* α and β (Callomon 1993, p. 96, fig. 4). These can now be located in a more extensive succession.

In-1, In-2: *Cranocephalites* spp. (*U*-1), (*U*-2)
(*U*-1): Plate 4, fig 1a, b, [M]
(*U*-2): Plate 4, figs 2–4 [M], figs 5, 6, [m]

Material and distribution. (*U*-1): Representative specimen JHC 5306 (Plate 4, fig. 1, [M]), section D2, 6 m above the *Plagiostoma* bed (Fig. 22): 8 [M], 1 [m]. (*U*-2): Representative specimen JHC 5314 (Plate 4, fig. 2a, b, [M]), section D2, 10 m above the '*Plagiostoma* bed': 18 [M], 2 [m]. *Total*: 29 (26 [M] + 3 [m]).

In sections D2 and D5 (Figs 22, 24), these specimens were found at two levels 3–4 m apart on the particularly featureless lowest 10–15 m of mudstones above the Ug-2 sandstones, on gentle slopes that are usually obscured by scree. Exceptional rainfall in 1994 had, however, provided clean exposures, degraded again already in 1996. The ammonites had originally been embedded freely in the mudstones, acting as their own concretions. Most have now lost their lithified body chambers and all that remains are the partially crystal-infilled phragmocones.

Descriptions. Macroconchs with subcircular whorl-section, slightly depressed (*w/h* = 1.23), with narrow, deep umbilici and rounded umbilical shoulders; ribbing dense, strong and sharp, dividing irregularly with intercalatories at whorl mid-flank, persisting to the end, only mildly variocostate; length of body chamber 0.75 whorl. (*U*-2) more strongly, sharply ribbed than (*U*-1), and the whorl-sides somewhat less rounded. The differences are at the limit of what can be morphologically resolved in assemblages of moderate size, especially when lacking the adult body chambers.

Two microconchs of (*U*-2) are shown in Plate 4, figs 5, 6. They too are complete phragmocones but the uncoiling umbilical seams show the extent of the adult body chambers to be up to 0.75 of a whorl, as in the macroconchs. Estimated complete diameters 32 and 40 mm, respectively, making the average dimorphic size-ratio only 2:1, unusually low for *Cranocephalites*.

Dimensions.

(*U*-1)	D_{max}	D_{ph}	*h*	*w*	*u*
JHC 5306:	63	43			
At *D*= 40			0.51	0.59	0.13
(0.75 whorl body chamber)					

Mean values, reference collection:			
$<D_{max}>$	82 (est.)	σ =	*n* = 10
$<D_{ph}>$	51	σ =	*n* = 9
$<w_{ph}>$	0.63 ± 0.02	σ = 0.038 (6%)	*n* = 8

D, D_{max}, D_{ph} in mm

(*U*-2)	D_{max}	D_{ph}	*h*	*w*	*u*	ρ(π)
JHC 5314: wholly septate		46				
At *D*= 46			0.48	0.69	0.16	1.37
(0.75 whorl body chamber)						

Mean values, reference collection:			
$<D_{max}>$	75 (est.)	σ =	*n* = 10
$<D_{ph}>$	46	σ =	*n* = 10
$<w_{ph}>$	0.59 ± 0.02	σ = 0.063 (11%)	*n* = 10

D, D_{max}, D_{ph} in mm

Discussion. The abrupt change in morphology from that of *C. borealis* is remarkable, particularly in the density and sharpness of the ribbing. The form of the phragmocone remains practically unchanged to the top of the Pompeckji Standard Zone. Inner whorls of many successive transients may be practically indistinguishable.

In-3 – In-8: Cranocephalites indistinctus *Callomon 1959*

1959 *Cranocephalites indistinctus* Callomon, p. 510, plate 17, figs 3, 4; plate 18, figs 1a, b, 2a, b.
?1973 *Cranocephalites indistinctus* Meledina, plate 4, fig. 3a, b.
1985a *Cranocephalites indistinctus* [m] Callomon, fig. 8b (allotype).
1993 *Cranocephalites indistinctus* α, β Callomon, p. 96.

Holotype. *Cranocephalites indistinctus* Callomon, 1959, plate 18, fig. 1a, b, (JHC 1435).

In-3: *Cranocephalites indistinctus* trans α (*sensu* Callomon 1993)

Plate 4, figs 8–13 [M]; figs 7, 14 [m].

1959 *Cranocephalites indistinctus* Callomon, plate 17, fig. 4.
1985a *Cranocephalites indistinctus* [m] Callomon, fig. 8b (allotype).
1993 *Cranocephalites indistinctus* α Callomon, p. 96.

Representative specimen of transient α [M]. MGUH 22258 (ex JHC 1306), Plate 4, fig. 11a, b; section B3, bed 20.

Representative specimen of transient α [m]. JHC 1248 (Plate 4, fig. 14); section B1, bed 24 (Fig. 18).

Material and distribution. Ugleelv sections: B1–B3: 9 [M], 3 [m]. Section D2 (Fig. 22): 23 [M], 7 [m]. Section D10 (Fig. 26): 1 [M]. *Total*: 43 (33 [M] + 10 [m]).

Description. Somewhat more consistently compressed, smaller, more feebly and densely ribbed to the end than the forms below or those in the Pompeckji Standard Zone above.

Dimensions.

[M]	D_{max}	D_{ph}	*h*	*w*	*u*
MGUH 22258 (ex JHC 1306): (0.8 whorl body chamber, crushed, with peristome)	60	37			

Mean values (a collection of 20 specimens from a single concretion)			
$<D_{max}>$	0.54 ± 1.2	σ = 4.1 (8%)	*n* = 13
$<w_{ph}>$	0.56 ± 0.00	σ = 0.035 (6.3%)	*n* = 9

D_{max}, D_{ph} in mm

[m]
JHC 1248: $<D_{max}>$ = 24 mm, *n* = 3; other measurements not possible. Dimorphic size-ratio 2.2

In-4: *Cranocephalites indistinctus* trans α′

Plate 5, figs 1–3 [M]

Representative specimen of transient α′ [M]. JHC 6017 (Plate 5, fig. 1).

Material. From a single locality, section B2, bed 12a, 5 m above In-3 (trans α), 7 m above the top of Ug-2 (Fig. 19): 6 [M].

Description. The main features as in trans α, but differs in a more strongly variocostate adult body chamber, becoming smooth. Umbilicus extremely narrow.

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 6017: (0.70 whorl body chamber)	68	~45			

Mean values:

$\langle D_{max} \rangle$	68	σ =	$n = 6$
$\langle D_{ph} \rangle$	48	σ =	$n = 6$
$\langle w_{ph} \rangle$	0.55	σ =	$n = 3$
$\langle u_{ph} \rangle$	0.05–0.09	σ =	$n = 2$

D_{max}, D_{ph} in mm

In-5: ***Cranocephalites* ex. gr. *indistinctus* (*U*-3)**

(not figured)

Material and distribution. Another distinct assemblage from an isolated locality, section E1, bed 9 (Fig. 27), a layer of sparse doggers in Ug-3 mudstones 10 m above the top ironstone of Ug-2: 6 [M], poorly preserved, crushed.

Description. The smallest of the group, ranging in size from 46 to 60 mm when fully grown ($\langle D_{max} \rangle$ = 50 mm (n = 4)), densely and finely ribbed to the end.

The order of In-4 and In-5 in the succession is conjectural, as both are from single levels in the variably thick Ug-3 mudstones from two localities 6 km apart.

In-6: ***Cranocephalites indistinctus* Callomon 1993 *sensu stricto*, trans ß**

Plate 5, figs 4–6, Plate 8, figs 1, 2 [M]

1959 *Cranocephalites indistinctus* Callomon, p. 510, plate 17, fig. 3; plate 18, figs 1a, b, (HT), 2a, b.
1985a *Cranocephalites indistinctus* [m] Callomon, text-fig. 8B (HT).
1993 *Cranocephalites indistinctus ß* Callomon, p. 96.

Holotype [M]. MGUH 22259 (ex JHC 1435; Plate 5, fig. 4); section C2, bed 28.

Paratypes [m]. JHC 1438 (paratype I), Plate 5, fig 5; JHC 1439 (paratype II), Plate 5, fig. 6.

Material and distribution. The type collection, section C2, 7 m above the top of Ug-2: 17 [M]. Section B1 (Fig. 18), 18 m above top Ug-2 and 2 m above *C. indistinctus* trans α: 8 [M]. Section E2 (Fig. 28), 16 m above the top of Ug-2, immediately below the base of the clinoform bed of Ug-4: 2 [M]. *Total*: 27 [M], microconchs unknown.

Another example of the sporadic local concentration of these ammonite assemblages: so abundant at Teebjerg, section C2, the same still clearly recognisable at Statuebjerg N, section B1 (Fig. 19), but no trace of either the bed or the ammonites at nearby section B2 (Fig. 18).

Description. The macroconchs resemble those of trans α′, In-4 (cf. Plate 5), but are larger, more strongly ribbed and with more open umbilicus through earlier egression of the umbilical seam at maturity. Some variants are homeomorphs of *C. gracilis* in Po-15. The range of variability may be seen in Plate 8, fig. 1a, b, coarsely ribbed to the end; fig. 2a, b, finely ribbed, fading, compressed.

Dimensions.

	D_{max}	D_{ph}	h	w	u
MGUH 22259 (HT): (0.75 whorl body chamber; other measurements not reliable. Rather a small variant.)	60	~40			

Mean values, others:

$\langle D_{max} \rangle$	72 ± 0.9	σ = 6.5 (9%)	$n = 15$
$\langle D_{ph} \rangle$	48 ± 1.5	σ = 5.8 (12%)	$n = 16$
$\langle w_{ph} \rangle$	0.50	σ =	$n = 4$

D_{max}, D_{ph} in mm

In-7: ***Cranocephalites* ex. gr. *indistinctus* (*U*-4)**

(not figured)

Material. Two half-crushed macroconchs only (JHC 6023, 6024), from Statuebjerg, section B2 (Fig. 19), *c*. 12 m above Ug-2, in a single concretion found on a gentle, clean slope of soft mudstones of Ug-3, well separated from other hard beds, so that contamination by downward slippage from higher horizons can be safely ruled out.

Description. Large, whorl-section well rounded, ribbing uniformly fairly dense to the end, fading on the adult body chamber but not disappearing altogether, rejuvenating towards the peristome. General overall resemblance in size and coiling is to the later faunas of Po-1 – Po-4, but in these the ribbing on the adult body chamber is stronger, coarser and more strongly variocostate.

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 6023:	90	55		0.65	
JHC 6024:	100	65		0.72	

D_{max}, D_{ph} in mm

In-8: *Cranocephalites indistinctus* trans γ

(not figured)

Representative specimens of transient γ. JHC 6031 [M]; JHC 6047 [m].

Material and distribution. Statuebjerg, section B2 (Fig. 19), bed 13b, 16 m above Ug-2, another clearly-defined horizon of concretionary sandstone well separated from others; ammonites abundant but mostly poorly preserved, fragmentary or crushed: 14 [M], 1 [m]. Katedralen N Canyon, section D8 (Fig. 25), bed 15, a very similar sandstone 17 m above Ug-2, a prominent marker in an otherwise featureless series of mudstones and sandstones with the long vertical burrows of *Diplocraterion habichi* and containing abundant burrowing razor-shells, *Strimodiolus elongatus* Fürsich: 5 [M]. *Total*: 20 (19 [M] + 1 [m]).

Description. A small species, but the maximum size is unusually variable, ranging from 48 to 75 mm; section sub-circular to depressed; densely and sharply ribbed to the end in small variants, fading on the body chambers of the large variants, which resemble the two large specimens of In-7. Umbilicus slightly more open than in other transients.

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 6031 [M]:	58 (est.)	36	0.51	0.57	0.12
JHC 6047 [m]:	29				

D_{max}, D_{ph} in mm

General discussion. This is the youngest of the series of faunas typified by *C. indistinctus*: rather small, delicately ribbed to the end. It resembles overall the earlier forms, but the inclusion of larger forms presages the change to the subsequent dominant morphology of the faunas of the Pompeckji Standard Zone.

Similar small forms of *Cranocephalites* have also been found in the Canadian Arctic (Prince Patrick Island: Frebold 1958, plate 8, figs 2, 3, closest in resemblance to In-3, *C. indistinctus* α; Richardson Mountains, Yukon: Poulton *et al.* 1982, p. 84). The form described under the name *C. indistinctus* from the Anabar region of northern Siberia (Meledina 1973, p. 51, plate 4, fig. 3) resembles some individual variants of the Greenland faunas in size and coiling, but the style of the ribbing points rather at later forms from the Pompeckji Standard Zone, which occur in the same bed (Meledina 1973, p. 104, bed 6, 0.4–0.7 m).

Pompeckji Standard Zone

The Pompeckji Standard Zone is herein divided into four new subzones: the Intermissus Subzone, the Carlsbergensis Subzone, the Gracilis Subzone and the Episcopalis Subzone (Fig. 30).

Intermissus Subzone

The Intermissus Subzone comprises seven faunal horizons: Po-1–Po-7, forming the group of *Cranocephalites intermissus* sp. nov. This is a succession of transients sharing salient morphological features that mark a significant change from preceding taxa. The macroconchs are larger, more inflated, have depressed whorl-sections, and are strongly ribbed to the end. They have homeomorphs at the levels of Po-11 – Po-13 and again at Po-19 – P-20, but are stratigraphically clearly separated.

Po-1: *Cranocephalites carolae* sp. nov. *sensu stricto*, trans α

Plate 6, figs 1–4; Plate 8, fig. 3 (all [M]); Fig. 34.

Types. Holotype JHC 5205 (Plate 6, fig. 1), paratypes JHC 5215, JHC 5229, JHC 5234 (Plate 6, figs 2–4), all part of the reference collection, section C4, bed 12b (Fig. 21).

Material and distribution. This is another example of an abundant association of adult macroconchs in a beautiful characteristically dark-coloured phosphatic preservation, localised at one thin horizon clearly recognisable over an area of not more than about a square kilometre (sections C2–C4). The reference collection, section C4 (Fig. 21): 31 [M]. Section C3, bed 3b (Fig. 20): 14 [M]. Section C2: 1 [M]. *Total*: 46 (all [M], microconchs not recognised).

Etymology. Named to acknowledge with gratitude the assistance over 30 years, both in the field and in the collections, of Carol St John Payne.

Description. Macroconchs of medium size, section rounded and moderately depressed, umbilici wider and more open than in earlier species. Phragmocone densely, sharply and

Fig 34. A field collection made on a wide exposure of horizon Po-1, *Cranocephalites carolae* sp. nov. Hammers for scale.

finely ribbed (Plate 8, fig. 3) in the style that then remains essentially unchanged over the whole range of successive transients in the Pompeckji Standard Zone. Adult body chamber only mildly variocostate, the primary ribbing persisting to the end, the secondaries passing over the venter with only mild attenuation in strength (Plate 6, figs 2, 4), if any; the finer-ribbed variants (Plate 6, fig. 3) very regularly ribbed, the more coarsely-ribbed ones tending to become somewhat bullate (Plate 6, fig. 4). The variability may be seen in the reference collection photographed in the field and shown in Fig. 25. Microconchs still unknown.

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 5205 (HT):	83	54	0.48	0.59	0.20

Mean values, others:

$\langle D_{max} \rangle$	81 ± 1.8	$\sigma = 9.0$ (11%)	$n = 26$
$\langle D_{ph} \rangle$	55 ± 1.2	$\sigma = 7.0$ (13%)	$n = 26$
$\langle w_{ph} \rangle$	0.59 ± 0.00	$\sigma = 0.06$ (10%)	$n = 26$

D_{max}, D_{ph} in mm

Po-2: *Cranocephalites carolae* sp. nov. trans β

Plate 7, figs 1–9 (all [M])

Primary representative specimen of transient β. JHC 6430, section D3 (Plate 7, fig. 6).

Secondary representative specimens of transient β. JHC 6432 (Plate 7, fig. 1), JHC 5336 (Plate 7, fig. 2).

Material and distribution. Yet a further example of a highly localised (sections D2–D3), sharply-defined horizon with an abundant assemblage of finely-preserved mature macroconchs. In this case, however, it is the phragmocones that are predominantly preserved, in a light orange-coloured calcite, reflecting the concretions in which they occur. Reference collection: section D2 (Fig. 22), on the top of a concretionary, calcareous sandstone *c*. 2 m below the base of the residual wedge of the clinoform bed of the Ugleelv Member at Katedralen: 38 [M]. Section D3, 0.5 km to the west of section D2, in a layer of large, well-separated concretions, the only resistant feature in some 20 m of soft, recessive mudstones, 11 m below the clinoform bed: 17 [M]. *Total*: 55 (all [M], microconchs not recognised).

Description. Macroconchs share the relatively open umbilicus of trans α but are somewhat more compressed, particularly in the inner whorls; adult body chambers more strongly variocostate, the secondaries more strongly differentiated (Plate 7, figs 1, 2, 6).

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 6430:	81*	65	0.48	0.57	0.16

Mean values, reference collection:

$\langle D_{\mathrm{max}}\rangle$	(94) (estimated from $\langle D_{\mathrm{ph}}\rangle \times \rho(\pi)$)		
$\langle D_{\mathrm{ph}}\rangle$	62.3 ± 0.9	$\sigma = 4.0$ (6.4%)	$n = 22$
$\langle w_{\mathrm{ph}}\rangle$	0.54 ± 0.01	$\sigma = 0.053$ (10%)	$n = 39$
$\rho(\pi)$	1.34	$\sigma =$	$n = 6$

*Incomplete body chamber
D_{max}, D_{ph} in mm

Po-3: *Cranocephalites intermissus* sp. nov. trans α

Plate 8, figs 4, 5

Primary representative specimen of transient α. JHC 6510 (Plate 8, fig. 5).

Secondary representative specimen of transient α. JHC 6512 (Plate 8, fig. 5).

Material and distribution. Another highly localised horizon, producing beautifully preserved specimens few of which retain anything of the body chamber. Reference collection: Teebjerg, slopes above Falkeelv, section C3, bed 5, 4 m above Po-1 (Fig. 20): 20 [M]. Statuebjerg, section B4, bed 8: 10 [M]. *Total*: 30 (all [M], microconchs not recognised).

Description. Larger, more round-whorled and inflated than taxa in Po-1 and Po-2, narrower umbilicus; more densely and finely ribbed to greater diameters. The ribbing coarsens and modifies somewhat on the adult body chamber, the primaries becoming more strongly differentiated.

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 6510 (wholly septate but phragmocone complete; Plate 8, fig. 5):		72	0.46	0.56	0.14
JHC 6512 (Plate 8, fig. 4):		69	0.50	0.58	0.11

Mean values, reference collection:

$\langle D_{\mathrm{ph}}\rangle$	65 ± 0.8	$\sigma = 3.7$ (6%)	$n = 21$
$\langle w_{\mathrm{ph}}\rangle$	0.59 ± 0.02	$\sigma = 0.050$ (8.5%)	$n = 21$

D_{ph} in mm

Po-4: *Cranocephalites intermissus* sp. nov. *sensu stricto*, trans β

Plate 9, figs 1–4 [M], fig. 5 [m]

1984 *Cranocephalites intermissus* Heinberg & Birkelund, p. 376, fig. 13.
1993 *Cranocephalites* sp. nov. A [*intermissus* MS], Callomon, p. 96 [fauna 3].

Holotype [M]. GGU 139115a, Birkelund and Heinberg collection 1974, Katedralen, section D9, bed 15.

Allotype [m]. JHC 5119, section D8, bed 17d (Fig. 25), clinoform bed of the Ugleelv Member at Katedralen, highest part.

Material and distribution. The name was introduced at a time when this was the only fauna, then newly discovered, lying between those of the *C. indistinctus* group below and those of the *C. pompeckji/gracilis/maculatus* horizons above.

The type, the reference and largest collection came from a more recessive, mudstone interbed in the middle of the clinoform bed on the west side of the Katedralen canyon, section D9, 9 m above its base and 16 m below its top: 14 [M]. Found also on the opposite side of the canyon, to the east, section D8 (Fig. 25), similar stratigraphic level: 1 [M], 1 [m]; on the opposite side, to the north, of Ugleelv, section E1 (Fig. 27): 14 [M]. There are further scattered records, all within the clinoform bed, serving to confirm that the time needed to build this unit was relatively short, within the typical time interval between successive faunal horizons. The state of preservation is generally rather poor. *Total*: 41 (*c*. 40 [M] + 1 [m]).

Description. Typically depressed, round-whorled macroconchs, with fine, dense ribbing, the primaries rising on well-rounded umbilical shoulders; sculpture of the adult body chambers only moderately modified, although the variability of all characters is considerable.

Dimensions.

[M]	D_{max}	D_{ph}	*h*	*w*	*u*
GGU 139115a (HT; incomplete, 0.6 whorl body chamber preserved; Plate 9, fig. 1):	68	55	0.42	0.65	0.17

Mean values, reference collection:
$\langle D_{ph} \rangle$ 57 ± 2 $\sigma = 7$ (12%) $n = 12$
$\langle w_{ph} \rangle$ 0.66 ± 0.02 $\sigma = 0.06$ (9%) $n = 13$

D_{max}, D_{ph} in mm

[m]	D_{max}	D_{ph}	*h*	*w*	*u*
JHC 5119 (AT; 0.75 whorl body chamber, complete; Plate 9, fig. 5):	35	20			
At $D = 25$:			0.51	0.58	0.16

D, D_{max}, D_{ph} in mm

Po-5: *Cranocephalites* sp. (*U*-5)
(not figured)

This is the lowest of the biospecific transients of *Cranocephalites* that has been identified in the highly condensed succession of ironstone that lie above the clinoform bed on the NE slopes of Katedralen, along the SW side of Ugleelv above its junction with Ræveelv, sections D2–D10 and sections E1–E3. The development of these lenticles is shown on Fig. 35.

Material. The fauna has been found at only a single locality, section D8 (Fig. 25) in the Katedralen canyon and the recoverable assemblage of moderately well-preserved material consists of only three macroconchs. These are somewhat phosphatised and crushed, only the body chambers being preserved. The bed was fairly fossiliferous and fragments of ammonites quite abundant. The forms are, however, so different from those below and above, and their positions immediately on top of the clinoform bed so secure, that their differentiation into a separate faunal horizon seems justified. Nevertheless, its position in the succession must remain somewhat tentative.

Description. A relatively small form, the more evolute variants tending to a depressed but subquadrate whorl-section, the more involute forms inflated and depressed as in *C. intermissus.* Strongly ribbed to the end, with some mid-ventral weakening of the secondary ribbing on the body chamber.

Dimensions.

	D_{max}	D_{ph}	*h*	*w*	*u*
JHC 5125 (a complete adult body chamber, evolute variant with peristomal constriction):	75	50			
At $D = 55$:				~0.55	

D, D_{max}, D_{ph} in mm

Po-6: *Cranocephalites* sp. aff. *intermissus* (*U*-6)
(not figured)

Material. Another assemblage from a well-characterised stratigraphical level at a single locality, section E3, bed 2, in an ironstone band in soft mudstones 0.5 m above the *Diplocraterion habichi* burrowed top of the clinoform bed of the Ugleelv Member (Fig. 35B). The material is plentiful but consists mainly of phragmocones. *Total*: 19 (all [M]).

Description. Similar to *C. intermissus* but markedly more evolute and compressed in the inner whorls, foreshadowing the later forms of the *C. pompeckji* group, its main component, Po-8, occurring in the same section only 0.5 m higher. The variability has also increased.

Dimensions.

	D_{max}	D_{ph}	*h*	*w*	*u*
JHC 5447 (inflated):		64	0.48	0.70	0.14
JHC 5444 (compressed):		58	0.47	0.50	0.15

Mean values:
$\langle D_{ph} \rangle$ 57.2 $\sigma = 8.2$ (14%) $n = 12$
$\langle w_{ph} \rangle$ 0.58 $\sigma = 0.082$ (14%) $n = 12$

D_{ph} in mm

Po-7: *Cranocephalites* sp. aff. *intermissus* (*U*-7)
(Fig. 36)

Material. Another assemblage from a single locality, section D6, in the lowest 0.4 m of non-ferruginous sandy mudstones or soft fine-grained sandstone resting directly on the clinoform bed of the Ugleelv Member at Katedralen. These mudstones have a total thickness of 1.9 m. No other ammonites were found in the higher part of the bed. *Total*: 17 (all [M]).

Description. The collection consists of well-preserved moulds of the adult body chamber, complete with peristome, providing an unusually good insight into the mature stages of

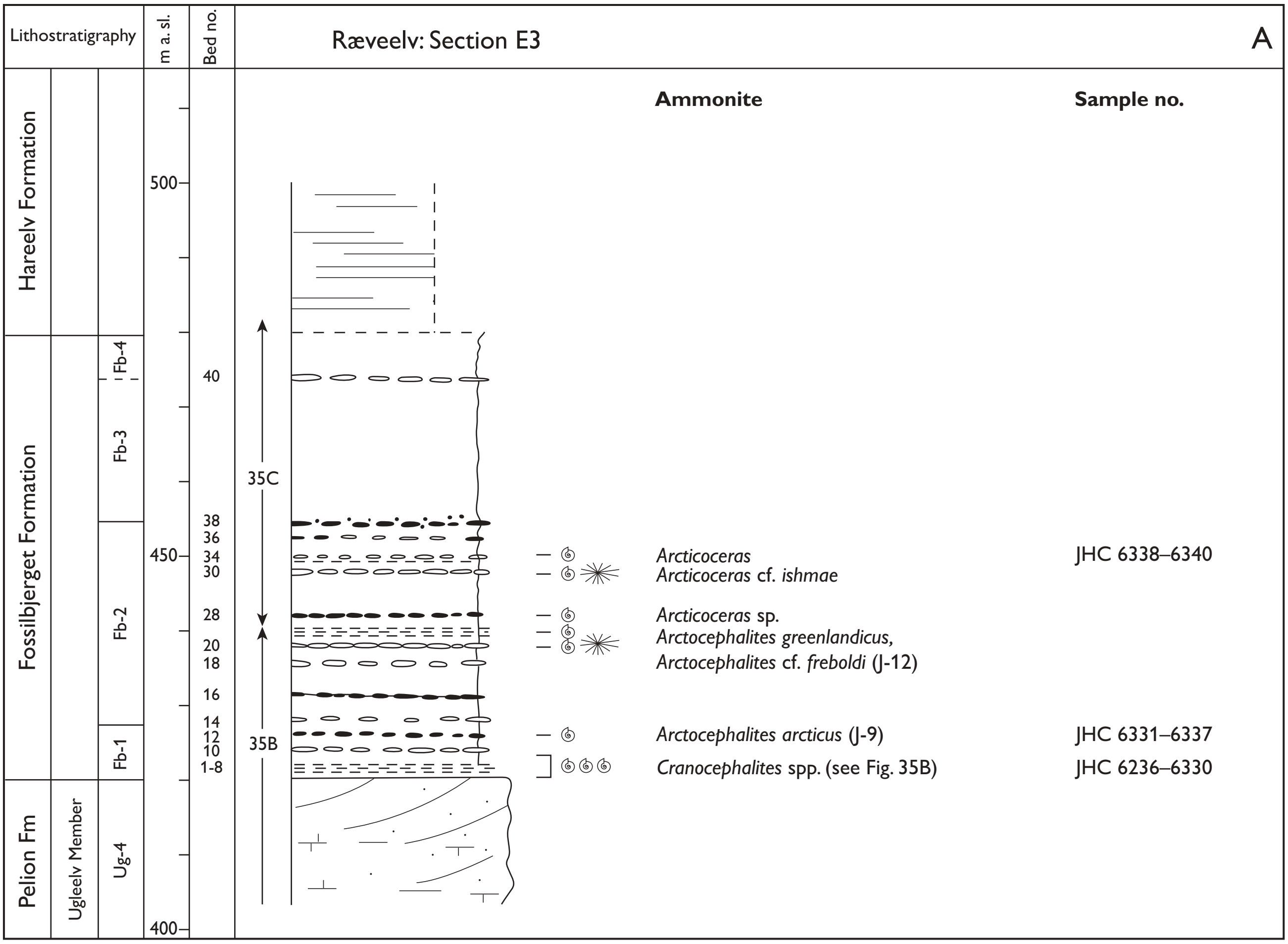


Fig 35. Section E3 at Ræveelv, the origin of the reference collection of *C. carlsbergensis* trans α (Po-10), and C. transitorius trans α (Po-17), shown in a generalised log (**A**) and in a detailed log (**B**: Lower part. **C**: Upper part), see facing page and following page. For location, see Fig. 9; for legend, see Fig. 12.

ontogeny. The phragmocone tends to be lost by crushing in the compressed variants but may be retained in the inflated ones. The assemblage is marked by a high variability in the inflation of the shell, with more compressed variants now dominating. It illustrates yet another example of the pattern of phyletic change of morphology widely observed in ammonites, here the change from inflated to compressed whorl-section of the shell by proterogenesis, the appearance of new characters in the young, subsequently spreading to the later stages of ontogeny (Schindewolf 1925).

The assemblage is marked by high variability in the inflation of the shell, with more compressed variants now dominating (Fig. 36A, B). The average diameter of the adults continues, however, to be closely constrained. The ribbing persists strongly to the end, the secondaries crossing the venter on the adult body chamber in undiminished strength in inflated variants, or fading to smoothness mid-ventrally on the early part of the body chamber. This range of variability generates variants that are close homeomorphs of almost all the other transients of *Cranocephalites*, including *C. intermissus, maculatus, pompeckji*, and even *indistinctus* as an extreme. Conversely, no single specimen characterises the assemblage as a whole. It seems to epitomise the genetic, phenotypic plasticity in expressions of the genome of ammonites as a whole. Yet the stratigraphic ‘purity’ of the biohorizon seems in no doubt; this is not a heterogeneously condensed assemblage.

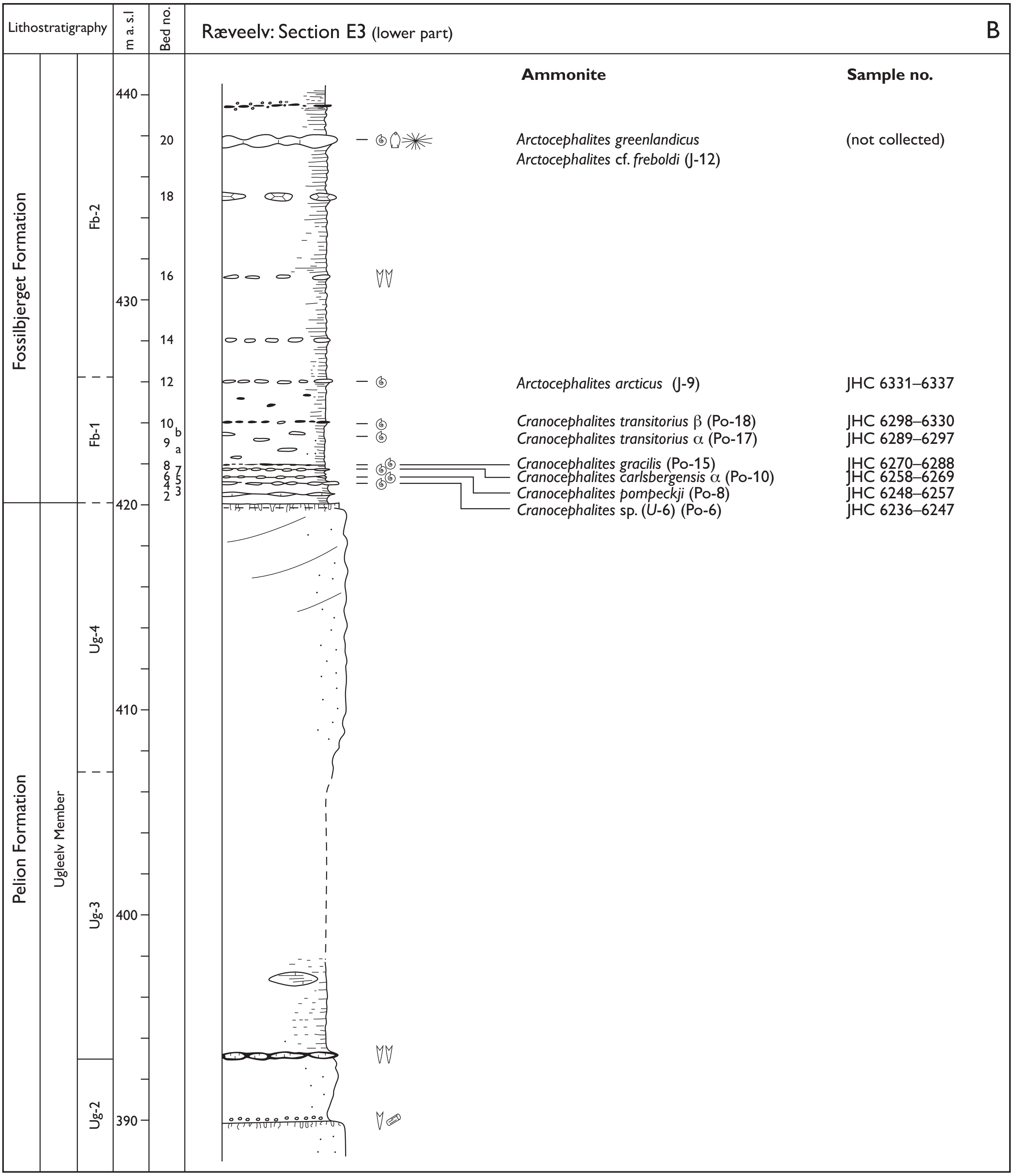
Dimensions.

	D_{max}	D_{ph}	*h*	*w*	*u*
JHC 6351 (cf. *C. intermissus*):	80	64	0.47	0.67	0.14
JHC 6348 (cf. *C. pompeckji*):	81	55	0.49	0.47	0.17

Mean values, reference collection:

$\langle D_{max} \rangle$	81.0	σ =	*n* = 12	
$\langle D_{ph} \rangle$	56.0	σ = 4.2 (7.6%)	*n* = 12	
$\langle w_{ph} \rangle$	0.50	σ = 0.091 (18%)	*n* = 12	(0.42 < *w* < 0.67)

D_{max}, D_{ph} in mm


Lithostratigraphy
m a.s.l
Bed no.
Ræveelv: Section E3 (lower part)
B
Ammonite
Sample no.
Fossilbjerget Formation
Pelion Formation
Ugleelv Member
Fb-2
Fb-1
Ug-4
Ug-3
Ug-2
440
430
420
410
400
390
20
18
16
14
12
10 b
9 a
8 7
6 5
4 3
2
Arctocephalites greenlandicus
Arctocephalites cf. *freboldi* (J-12)
(not collected)
Arctocephalites arcticus (J-9)
JHC 6331–6337
Cranocephalites transitorius β (Po-18)
JHC 6298–6330
Cranocephalites transitorius α (Po-17)
JHC 6289–6297
Cranocephalites gracilis (Po-15)
JHC 6270–6288
Cranocephalites carlsbergensis α (Po-10)
JHC 6258–6269
Cranocephalites pompeckji (Po-8)
JHC 6248–6257
Cranocephalites sp. (*U*-6) (Po-6)
JHC 6236–6247

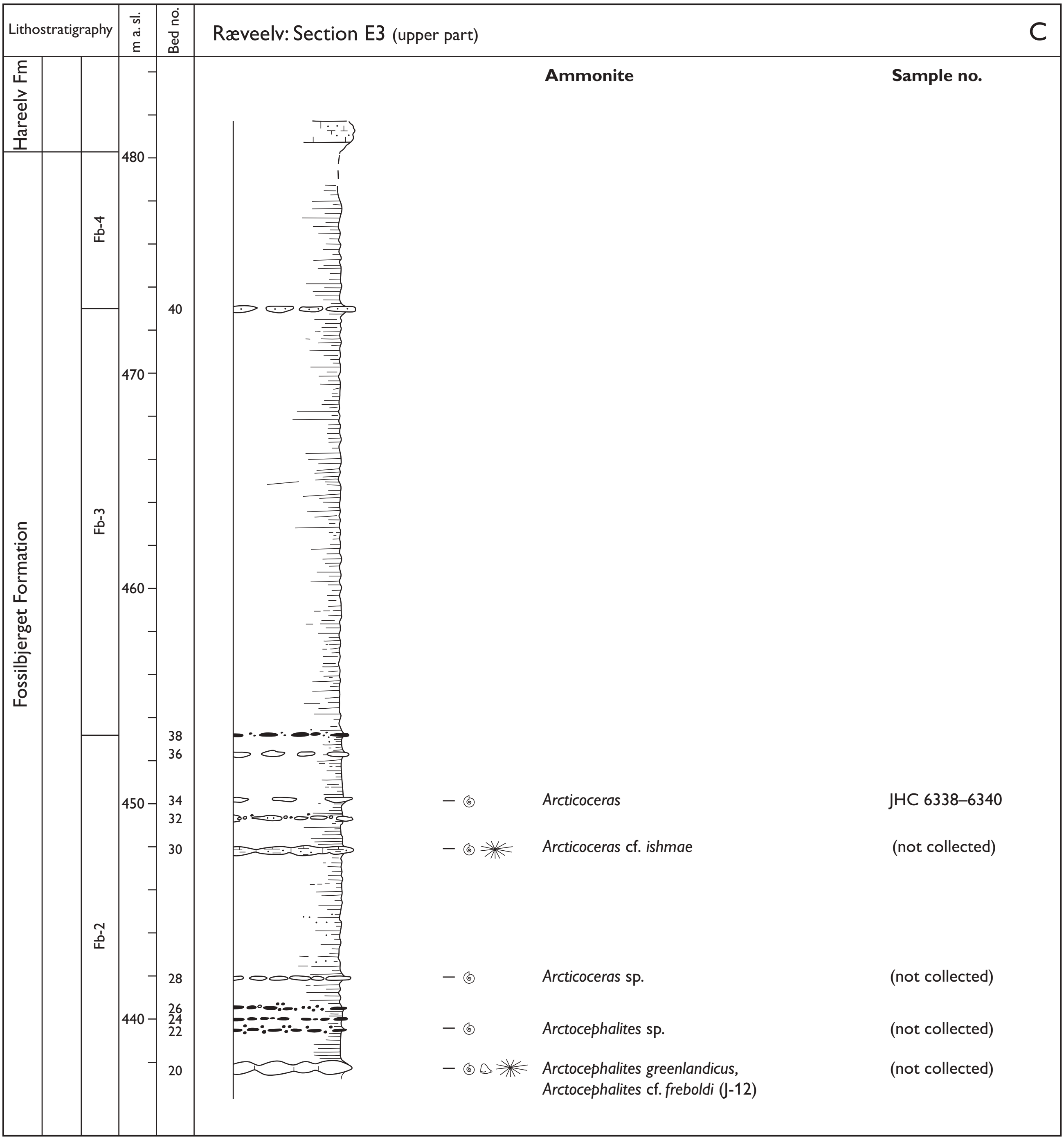


Fig 35. For caption see previous pages.

Fig. 36. *Cranocephalites* sp. aff. *intermissus* (*U*-7), section D6, bed 1a, faunal horizon Po-7. **A**, **B**: Side view and ventral view of JHC 6348, a typical slender variant. **C**, **D**: Side view and apertural view of JHC 6351, the most inflated variant. All natural size.

Carlsbergensis Subzone

The Carlsbergensis Subzone of the Pompeckji Standard Zone includes seven faunal horizons, Po-8 – Po-14 (Fig. 30), described below under two groups, Po-8 – Po-9 and Po-10 – Po-14.

Po-8 – Po-9: the group of Cranocephalites pompeckji *Madsen –* furcatus *Spath*

Po-8: *Cranocephalites pompeckji* (Madsen 1904)
Plate 10, figs 1–6; Plate 11, figs 1, 2 [M]; Plate 11, fig. 3 [m]

1904	*Macrocephalites pompeckji* Madsen, p. 189, plate 8, figs 5, 6 (LT).
?1913	*Macrocephalites pompeckji* Madsen – Sokolov, p. 61, plate 1, figs 1, 2 (Novaya Zemlya).
1929	*Macrocephalites pompeckji* Madsen – Rosenkrantz, p. 146.
1930	*Macrocephalites pompeckji* Madsen – Frebold, p. 111.
1932	*Cranocephalites pompeckji* (Madsen) – Spath, p.16, *non* vars. *laevis* (plate 5, fig. 3, = *Arctocephalites* sp.), *rustica* (plate 4, figs 9, 10; plate 13, fig. 1, = *C. furcatus*), *intermedia*

(plate 5 - fig. 7, = *C. furcatus*), *costata* (plate 5, fig. 6; plate 13, fig. 1, = *C. furcatus*).
1932 *Cranocephalites vulgaris* Spath, p. 20, plate 1, figs 2, 3 (HT), 6 (suture only).
Cranocephalites vulgaris Spath var. *robusta* Spath, p. 22, plate 2, fig. 1.
Cranocephalites vulgaris Spath var. *densicostata* Spath, p. 21, plate 4, fig. 1.
Cranocephalites vulgaris Spath var. *compressa* Spath, p. 21, plate 5, fig. 1.
Cranocephalites aff. *vulgaris* Spath, plate 2, fig. 4.
cf 1962 *Cranocephalites pompeckji* (Madsen) – Voronets, p. 33, plate 7, fig. 1a, b; plate 23, fig. 3.
cf 1962 *Cranocephalites vulgaris* Spath – Voronets, p. 32, plate 22, fig. 2a, b, (northern Siberia, Anabar).
?1973 *Cranocephalites pompeckji* (Madsen) – Meledina, p. 43; *non* plate 2, figs 3a, b, 4a, b; plate 3, fig. 3a, b (northern Siberia, Anabar).
cf 1973 *Cranocephalites pseudogracilis* Meledina, p. 48, plate 5, fig. 3a, b (HT).
1985a *Cranocephalites pompeckji* (Madsen) – Callomon, p. 56, text-figs 4, 8D [M], 8d [m].
1993 *Cranocephalites pompeckji* (Madsen) – Callomon, p. 98 (fauna 7).

Lectotype. MGUH 297; Madsen (1904), plate 8, fig. 6a, b, designated Spath (1932), p. 17; refigured here; Plate 10, fig. 2a, b.

Material and distribution. The material of Madsen (1904) from 'Ammonite Mountain', presumed to be the rising plateau north of Sortehat (i.e. south-west slope of Dusén Bjerg, Fig. 3; Higgins 2010, see Figs 3, 11 foreground): the type and three other identifiable former syntypes (Madsen 1904, plate 8, fig. 5 and two others in MGUH, not numbered); section 23, = section E3 (Figs 3, 9, 35B) on the opposite side of Ræveelv to the west, 14 [M], 2 [m]; the north slopes of Katedralen, section 20 = section D5 (Figs 3, 9, 24), several collections including ones made by T.M. Harris (*C. vulgaris* in Spath 1932), F. Surlyk (in 1970), T. Birkelund and J.H. Callomon (in 1971), T. Birkelund and C. Heinberg (in 1974): *c.* 90 [M], 7 [m]. *Total*: >100 [M] + 7 [m].

Yet another species found in abundance over only a very restricted area, and it is ironic that the only four identifiable specimens brought back by Nordenskjöld should have been from just this stratigraphically highly localised biozone. At section E3, perhaps only 3 km to the south-west of 'Ammonite Mountain' (Fig. 9), well-preserved ammonites from other biohorizons spread over the ground greatly outnumber those of *C. pompeckji*.

What appears to be the fauna characterising the Po-8 faunal horizon has been found at only one other locality in East Greenland, Antarctic Havn. The material is, however, poorly preserved and the identifications must be tentative.

Description. The intraspecific variability among the macroconchs is relatively low and its range is illustrated in the plates and in Callomon (1985a, text-fig. 4). Compared with the older forms, the size is reduced, the coiling is less depressed in whorl-section, the whorl-sides tending to be flatter, the umbilicus opening at an earlier stage. The ribbing is dense and subdued, both the primaries and secondaries persisting with little modification to the end of the adult body chamber but tending to weaken and, in extreme variants, to fade mid-ventrally. A microconch with nearly complete body chamber is shown in Plate 10, fig. 4, and apart from a markedly flexuous, forward-projected ribbing, it differs little from the nuclei of macroconchs at comparable diameters. Not enough specimens of the microconchs of any species of *Cranocephalites* have been found to map out their variabilities.

Dimensions.

	D_{max}	D_{ph}	*h*	*w*	*u*
MGUH 297 (LT; only 0.3 whorl body chamber preserved; Plate 10, fig. 2):	69	60	0.50	0.48	0.13
cf. JHC 4087 (complete adult, large variant; Plate 10, fig. 1):	85	58	0.50	0.50	0.13

Mean values, reference collection:

$<D_{max}>$	73.5 ± 1.8	$\sigma = 11.5$ (16%)	$n = 40$
$<D_{ph}>$	50.1 ± 0.1	$\sigma = 5.0$ (10%)	$n = 45$
$<w_{ph}>$	0.54 ± 0.01	$\sigma = 0.043$ (8%)	$n = 46$
$\rho(\pi)$	1.35		

D_{max}, D_{ph} in mm

Discussion. The discrepancy between the present interpretation of the species of Madsen (1904) and that of Spath (1932) brings out in acute form the conflicts that can arise between morphospecific and biospecific classifications, between comparisons of single specimens as opposed to internally isochronous but variable assemblages. On the one hand, Spath (1932) picked out very successfully a coherent assemblage from the only material at all localised both in place and horizon at his disposal, that collected by T.M. Harris from Katedralen at 370 m. His sketch of the section was reproduced by Spath (1932, p. 128, text-fig. 12). To this assemblage of 11 specimens, which is now unambiguously in assemblage Po-8, he gave the name *C. vulgaris*. On the other hand, he had also to accommodate the only two or three identifiable specimens in the old collections, essentially without provenance, that also carried the oldest name, the syntypes of *C. pompeckji* (Madsen 1904). In this, he saw a closer resemblance of these syntypes to a number of other poorly-preserved specimens collected by A. Rosenkrantz at Hjørnefjeldet located considerably farther north (Figs 1B, 4) than to his *C. vulgaris*.

With the stratigraphic information now available, the matter can be clearly resolved. The assemblage from Hjørnefjeldet is quite distinct from that of *C. vulgaris* at Katedralen. It belongs to fauna Po-9, that of *C. furcatus* Spath 1932, discussed further below. Regarded as an isolated variant, the type of *C. pompeckji* could probably be fitted equally well into either *C. vulgaris* (Po-8) or *C. furcatus* (Po-9), although Spath himself admitted that there was not a single specimen in the new collections before him that showed perfect agreement with the type (Spath 1932, p. 17). The specimen from Katedralen shown here in Plate 10, fig. 1, fits the type of *C. pompeckji* almost exactly. Furthermore, the assemblage of Po-8 has not been found again anywhere around Hjørnefjeldet and that of Po-9 is missing at Katedralen. And whereas the type-locality of *C. pompeckji*, 'Ammonite Mountain', is at most 5 km from Katedralen, it is 35 km from Hjørnefjeldet. The biospecific assemblages Po-8 and Po-9 are both well characterised, but which should carry the morphospecific name *C. pompeckji?* Both morphological and stratigraphical evidence point now overwhelmingly to Po-8, the type assemblage also of *C. vulgaris* – which makes this junior synonym of *C. pompeckji*.

Some of the specimens referred to *C. pompeckji* or *C. vulgaris* by Meledina (1973) agree with the types in size and coiling but not in the style of ribbing, which is consistently too coarse and strong, especially on the venter. Some 34 specimens of *Cranocephalites* were figured by Meledina (1973), all but two of which came from two areas in the region of the Anabar River in northern Siberia (Uryung –Tumus and Anabar Bay) about 50 km apart. The successions are summarised in two sections (Meledina 1973, p. 102–105) which overall are very similar (Meledina 1973, fig. 35). The specimens appear to have come mostly from a layer of concretions in a bed of clay or silt (bed 6) that is 16 and 10 m thick at the two localities, respectively. Their stratigraphic positions are given as *Cranocephalites vulgaris* Zone. The 34 specimens are assigned to 14 nominal species, of which four are new and eight are based on the types of species from East Greenland described by Spath (1932). From what is now known for their type horizons, these Greenland species range in age over a time span of 20 biohorizons, from In-6 (*C. indistinctus*) to Po-19 (*C. maculatus*). It would be tempting, therefore, to conclude that the *Cranocephalites* bed of Spath (1932) is condensed, containing a mixture of fossils of many ages. But with again the experience in Greenland of the variability encountered in the assemblages from single biohorizons, that of isochronous biospecies, it is equally possible to suggest a contrary interpretation. Of the 34 specimens illustrated by Meledina (1973), 26 would fit comfortably into the variability-distribution expected in but a single biospecies, say *C.* sp. *A*. All these specimens share a characteristic style of ribbing, no matter how large or inflated. (The exceptions are Meledina's (1973) plate 2, fig. 2, plate 3, fig. 2: "*C. furcatus*", say sp. *B*; plate 4, fig. 1 from the Lena River, "*C. nordvikensis*"; plate 5, fig. 2, "*C.* aff. *costidensus*"; plate 7, fig. 4; plate 8, figs 2, 4 from the Lena River, "*C. gracilis*", say sp. *C*).

Taken, then, as a single biospecies, the 26 specimens of species *A* do not together match precisely any of the biospecific transients from Jameson Land, neither in the macroconchs nor in the (single) microconch (Meledina 1973, plate 2, fig. 4). The closest resemblance is to the stout, coarsely-ribbed forms of *C. carlsbergensis* (Po-11), or *C. tvaerdalensis* (Po-13). The Siberian assemblage contains variants showing an extreme degree of bullate variocostation on the adult body chamber (Meledina 1973, plate 4, fig. 2, "*C. laevis*" and plate 9, fig. 2a, b, "*C. maculatus*") unknown in Greenland. It would be safest, therefore, to regard this Siberian biospecies *A* as a distinct transient fitting into the succession somewhere in the upper Carlsbergensis Subzone of the Pompeckji Standard Zone. To name it, there is an available choice of four new species of Meledina (1973), of which *C. spathi* Meledina 1973, the type species of *Pachycephalites* Meledina would be the most typical.

Another distinct biospecies of *Cranocephalites* from northern Siberia has been described by Voronets (1962) as *C. nordvikensis* (p. 39; LT plate 6, fig. 1a, b, designated by Meledina 1973). It probably includes other specimens described under a variety of names in plate 4, figs 2a, b, 3a, b; plate 6, fig. 2; plate 9, fig. 1; plate 12, fig. 3 and plate 13, figs 2a, b, 3a,b (Voronets 1962). Taken together, they have no close match in East Greenland.

Po-9: *Cranocephalites furcatus* Spath 1932

Plate 11, figs 4, 5; Plate 12, figs 1–4 [M];
Plate 11, fig. 6; Plate 12, fig. 6 [m]

1932 *Cranocephalites furcatus* Spath, p. 30, plate 6, fig. 1 (HT).
Cranocephalites furcatus Spath var. *pygmaeus* Spath, p. 30, plate 6, fig. 2 [m?].

Cranocephalites pompeckji (Madsen) – Spath, p. 16, plate 4 fig. 10, plate 13, fig. 1[M].
Cranocephalites cf. *pompeckji* (Madsen) – Spath, p. 19, plate 3, fig. 3 [?m].
Cranocephalites pompeckji (Madsen) var. *costata* – Spath, p. 18, plate 5, fig. 6.
Cranocephalites pompeckji (Madsen) var. *intermedia* – Spath, p. 18, plate 5, fig. 7a, b.
Cranocephalites pompeckji (Madsen) var. *rustica* – Spath, p. 18, plate 4, fig. 9a, b.
cf 1953 *Arctocephalites* (*Cranocephalites*) *maculatus* Spath var. *rusticus* nov., Donovan, p. 83, plate 16, figs 1–3.
1993 *Cranocephalites furcatus* Spath – Callomon, p. 98.
non 1973 *Cranocephalites furcatus* Spath: Meledina, plate 2, fig. 2; plate 3, fig. 2.

Holotype. MGUH 9191, refigured here (Plate 11, fig. 4).

Type locality and distribution. The type collection and the other specimens described by Spath (1932, see synonymy) were spot collections brought back by A. Rosenkrantz from his 'Mt. Hjørnefjeld', 'locality 2b, 740 m'. A sketch of the section is shown in Rosenkrantz (1934, p. 92, fig. 45) and in Spath (1932, p. 133, text-fig. 14). Attempts to find this precise locality again during mapping in 1971 were unsuccessful. The highest point in the area does not rise above 660 m. But the Po-9 beds are widely exposed in the region, particularly around Centralbjerg to the west of Hjørnefjeldet (Fig. 4, section 35) and thence further north, and the two levels 20 m apart with ammonites recognised by Rosenkrantz were readily found again and new collections made. The lower is the type-horizon of *C. furcatus*, the higher that of *Arctocephalites arcticus* (Newton 1897) and *A. nudus* Spath 1932, fauna 9 in Callomon (1993, p. 99).

At the time the Callomon (1993) review was written, the relative positions of *C. furcatus* and *C. pompeckji* were not definitely known, for whereas *C. furcatus* had at that time not been found in the region of Katedralen and Ugleelv, *C. pompeckji* was unknown in the region around Hjørnefjeldet and Centralbjerg. After much searching, *C. furcatus*, now horizon Po-9, was found in 1994 on the eastern slopes of Katedralen, in section D2, bed 10 (Fig. 22), at a level of a thin ironstone bed immediately above the clinoform bed, horizon Po-2 of the Ugleelv Member, and directly overlain by another ironstone with the fauna of Po-10. There was no sign of the horizons Po-3 – Po-8, so the succession at section D2 is here highly incomplete, but Po-9 must lie above Po-8.

Material. Centralbjerg region: *c*. 60 [M], 9 [m]; Katedralen, 18 (all [M]).

Description. The photographs of the holotype belie its description. The specimen essentially shows only one side of a macroconch body chamber. It shows, however, the characteristic features of the species: the regular, strong but blunt well-spaced ribbing, the primaries dividing mostly into pairs of secondaries of comparable strength. A specimen that closely matches the type is shown for comparison in Plate 11, fig. 5, with part of the body chamber removed to reveal the similarly coarse but sharp ribbing on the inner whorls. These characters are also evident in the four specimens shown on Plate 12, figs 1–4. Of these, Plate 12, fig. 2 illustrates also the rather flat-sided, subquadrate whorl-section of typical variants and the loss of ribbing on the venter of the adult body chamber. The range of inflation is reflected in Plate 12, fig. 1, which illustrates the extreme. One of the smallest variants, diameter 65 mm, was figured as var. *pygmaeus* by Spath (1932); the maximum size can reach 95 mm. Overall, the size and coiling resemble those of the immediately underlying *C. pompeckji* as discussed above, but the style of ribbing is quite distinct.

A microconch is shown in Plate 11, fig. 6a, b; the specimen figured by Spath (1932, plate 3, fig. 3) is probably another microconch.

Dimensions.

	D_{max}	D_{ph}	*h*	*w*	*u*
MGUH 9191 (HT):	86	~59	~0.49		~0.15
cf JHC4172:	74	50	0.49	0.56	0.14

Mean values, reference collection:
$\langle D_{max} \rangle$ 75 ± 1.5 $\sigma = 6.0$ (8%) $n = 17$
$\langle D_{ph} \rangle$ 48 ± 1.3 $\sigma = 5.4$ (11%) $n = 15$

D_{max}, D_{ph} in mm

Po-10 – Po-14: the group of Cranocephalites carlsbergensis *Callomon*

The lower three faunal horizons of this group (P-10 – Po-12) are defined by three transients (α , β, γ) of the taxon (*Cranocephalites carlsbergensis*), the type of which is represented by transient β.

Po-10 – Po-12: Cranocephalites carlsbergensis *Callomon*

1975 *Cranocephalites carlsbergensis* (sp. nov. MS) Callomon, p. 383, fig. 6A, B; 6C [M].
1985a *Cranocephalites* sp. nov. A, Callomon, text-fig. 8C [M], 8c [m].

1993 *Cranocephalites* sp. nov. B [*carlsbergensis* MS], Callomon, p. 97 [fauna 5].

Holotype. JHC 1751 (in Callomon 1975, fig. 6C), by monotypy. The type comes from the faunal horizon of transient β (Po-11), see below.

These three faunal horizons contain very similar forms but are found so far only in three non-overlapping areas. Their relative succession is therefore surmised indirectly on the basis of lateral lithostratigraphical correlations rather than on direct sequential observation in a single section.

Po-12 (highest): Ugleelv, east of Katedralen, around Statuebjerg, sections B1–B3 (Figs 9, 18, 19): *C. carlsbergensis* transient γ.
Po-11: Trefjord Bjerg, sections 39a and 39b (Figs 4, 29): *C. carlsbergensis* transient β.
Po-10 (lowest): Katedralen and Ræveelv, sections D2–D4, E3 (Figs 9, 35B): *C. carlsbergensis* transient α.

The position of Po-12 above Po-10 seems assured, but the position of Po-11 relative to these is still conjectural. It is placed here in the middle for convenience. Up to 1994, even the position relative to *C. pompeckji*, Po-8, was uncertain, and Po-8 was then still placed above Po-10 – Po-12. The three transients are so similar that only large collections allow distinction. It would suffice for most problems of correlation with material from other localities, therefore, simply to refer to the three transients collectively as *C. carlsbergensis*. The type horizon of the species *sensu stricto* is Po-11 (trans β).

Po-10: *Cranocephalites carlsbergensis* trans α

Figs 37–38

Representative specimens of trans α. JHC 6263, [M], from the reference collection, section E3; JHC 5411, [m], from section D2, bed 11 (Fig. 22).

Material and distribution. Ugleelv (Fig. 9), section D2, bed 11: 20 [M], 1 [m] (Figs 22, 37). Further Ugleelv setions: D3: 4 [M]; D4 (Fig. 23): 13 [M]; E3, reference locality and horizon (Fig. 3, section 23; Figs 9, 37), bed 7: 23 [M]. *Total*: 61 (60 [M] + 1 [m]).

The exposures in sections D2 – D4 were somewhat scree-covered, so that it was not always easy to collect the material precisely *in situ*. The ammonites of Po-10 were abundant, however, and could be easily recognised again even in sections in which the thin ironstones in which they occurred were barely recognisable. In section E3, the bed crops out on a gently rising slope and the ammonites were lying in a narrow strip well separated from those of the fauna below (Po-8) and above (Po-15). The preservation has conserved mostly the mature body chambers, with peristome; the phragmocones tend to be crushed.

Description. Slightly smaller than trans β and more strongly and persistently ribbed, the venter more highly arched, but the styles of ribbing and its variability match those of trans β in almost all respects. The differences lie at the extremes: no single specimen epitomises the differences between trans α and trans β. The microconchs continue to be extremely rare, as are specimens that were demonstrably juvenile.

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 6263 (Fig. 37A, B):	89	62	0.48	0.55	

Mean values, reference collection:

$<D_{max}>$	83.9 ± 1.9	$\sigma = 7.7$ (9.2%)	$n = 18$
$<D_{ph}>$	59.3 ± 1.2	$\sigma = 5.4$ (9.1%)	$n = 20$
$<w_{ph}>$	0.55 ± 0.02	$\sigma = 0.084$ (15%)	$n = 17$

D_{max}, D_{ph} in mm

Po-11: *Cranocephalites carlsbergensis sensu stricto*, trans β

Plate 12, fig. 5; Plate 13, figs 1–4 [M], 5 [m]; Fig. 39

Types. Holotype, JHC 1751 (in Callomon 1975, see above); paratype I, JHC 1754 [M], Plate 13, fig. 1; paratype II, JHC 1756; allotype [m], JHC 1768 (Plate 13, fig. 5).

Material and distribution. Almost the whole of the material on which this transient is based came from two adjacent localities on the north and north-east ridges of Trefjord Bjerg (Figs 4, 29). The first collection was made in 1958 on the north ridge, section 39b (Figs 29, 40), and is the reference collection that includes the types: 47 [M], 1 [m]. Its appearance at the time of collection is shown in Fig. 39. A second collection was made in 1974 by C. Heinberg and T. Birkelund in section 39a, above Lepidopteris Elv, only 1.3 km to the south-east of 39b: 15 [M]. Scattered finds were made elsewhere in the region during mapping.

Description. A large species, the inner whorls involute with rounded, depressed section and tight umbilicus (Plate 12, fig. 6; Plate 13, figs 3, 4), much as in the other species of *Cranocephalites*. The adult body chambers contract with marked uncoiling of the umbilical seam; ribbing moderately variocostate, characterised by coarse, blunt primary ribbing tending to circumbilical bullae and secondary rib-

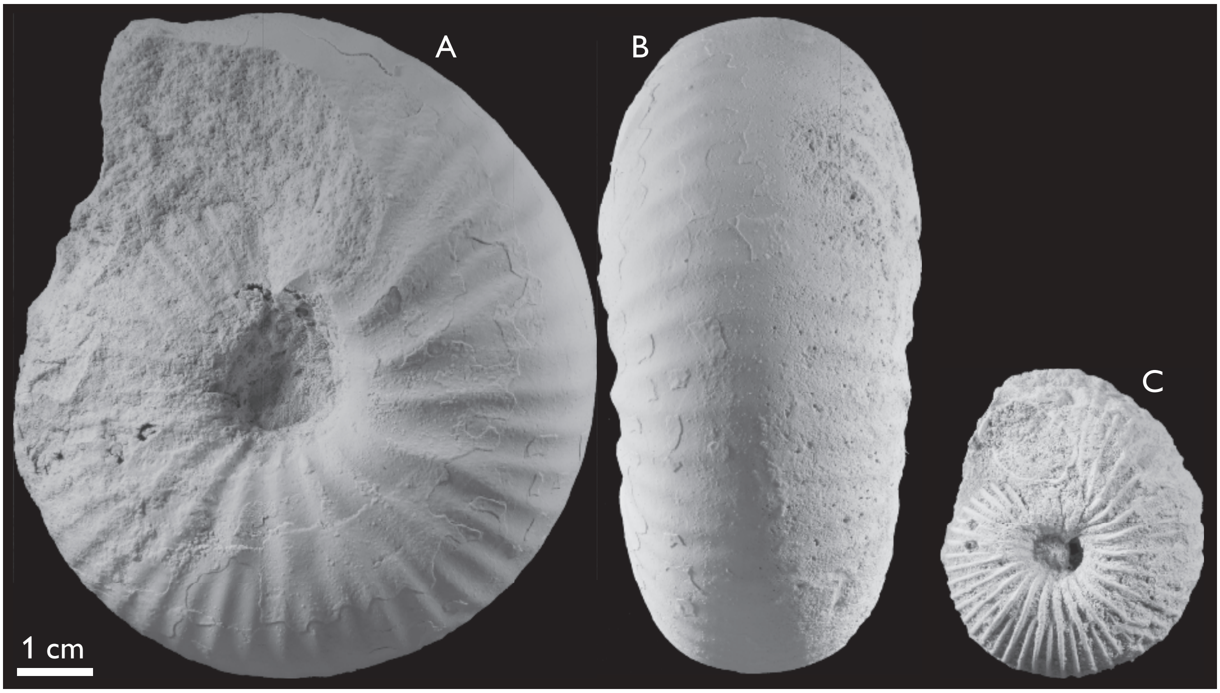


Fig. 37. *Cranocephalites carlsbergensis* trans α (Po-10), representative specimens. **A**, **B**: Side view and ventral view of the primary representative specimen, JHC 6263 [M], Ræveelv, section E3. **C**: Secondary representative specimen, JHC 5411 [m], Katedralen E, section D2. All natural size.

Fig. 38. A field collection of *Cranocephalites carlsbergensis* trans α (Po-10) from Ræveelv, section E3, bed 7 (Fig. 35B). Hammers for scale.

Fig. 39. Part of the type collection of *Cranocephalites carlsbergensis sensu stricto* trans β (Po-11), as collected in section 39b, bed 11 (Fig. 29), on the north ridge of Trefjord Bjerg (Fig. 40) on display on the snow.

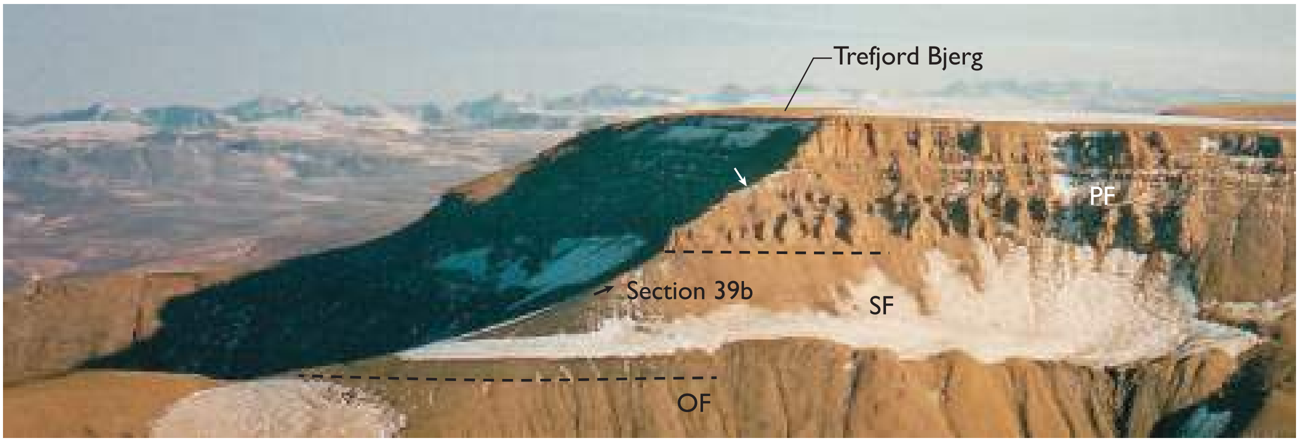


Fig. 40. The northern slopes of Trefjord Bjerg, showing section 39b (Fig. 29), the sunlit ridge rising from the col at the left to the summit. The resistant formation forming the saddle of the col and running to the right under the snow-field is the Ostreaelv Formation (**OF**) of the Neill Klinter Group (Toarcian). Above it, the recessive Sortehat Formation (**SF**, *c.* 105 m thick), largely covered by snow running up to the base of the first massive bluff which marks the lower part of the Pelion Formation (**PF**). The type-horizon of *Cranocephalites carlsbergensis* (Po-11) lies about half-way between this bluff and the summit (white arrow). The highest sandstones, forming the plateau, are probably in the Ishmae Zone, horizons J15 – J16 (Figs 8, 30).

bing that fades, leaving the ventral side of the body chamber smooth. Quite close homeomorphy with Po-1, *C. carolae* in the coarser-ribbed variants, and with Po-19, *C. maculatus*, in the finer-ribbed forms.

Dimensions.

	D_{max}	D_{ph}	*h*	*w*	*u*
JHC 1754 (Plate 13, fig. 1):	92	60	0.52	0.60	0.13
JHC 1731 (Plate 13, fig. 3):	79	56	0.52	0.70	0.10

Mean values, reference collection:

$<D_{max}>$	88.5 ± 1.4	σ = 8.1 (9.2%)	n = 35
$<D_{ph}>$	62.7 ± 0.80	σ = 5.7 (9.0%)	n = 53
$<w_{ph}>$	0.59 ± 0.009	σ = 0.064 (11%)	n = 52
$\rho(\pi)$	1.33 (± 0.015)		n = 2

D_{max}, D_{ph} in mm

Discussion. Some other nominal species created by Spath (1932) bear some resemblance to *C. carlsbergensis*. Three of them (*C. inversus, C. inconstans* and *C. subbullatus*) are based on material from Antarctic Havn that is so poorly preserved that the names are best set aside as *nomina dubia*.

Po-12: *Cranocephalites carlsbergensis* trans γ

Plate 16, fig. 6

Representative specimens of transient γ. GGU 137939.1, from Statuebjerg, section 13/B1, bed 27; GGU 137973.1, Teebjerg, loose.

Material and distribution. This fauna characterises a sharply-defined thin concretionary bed of soft sandstone lying at the top of some 5 m of silty mudstones. The weathered out ammonites were lying in profusion on the gentle slopes but their preservation in a characteristic hard, grey-weathering, somewhat phosphatic very fine-grained rock reveals their source. In most cases only the body chambers have survived more or less undistorted, the phragmocones having been crushed. It was difficult to find a single specimen with both uncrushed body chamber and phragmocone to act as type. Uncrushed phragmocones do occur but then lack the body chambers (Plate 16, fig. 6). Such inner whorls are however so similar to those of other species that they contribute little to the characterisation of the assemblage. Section B1: *c*. 100 [M]; section C1: 16 [M] + 1 [m].

The bed makes an excellent marker in the area of Statuebjerg, sections B1 – B3 (Figs 9, 18, 19). It can just be recognised on Teebjerg, section C1, 2 km to the north-west, but no further. Together with the whole of the Indistinctus Standard Zone and the rest of the Pompeckji Standard Zone, it has been totally lost at Taubjerg, only 3 km to the south-east (Fig. 9). At Statuebjerg, it marks the top of the unit Fb-1 of the Fossilbjerget Member and is there followed immediately by the mudstones of Fb-2, probably Greenlandicus Standard Zone horizon J-11.

Description. Somewhat smaller than trans β, (*C. carlsbergensis sensu stricto*), body chambers more evolute, more densely and finely ribbed, fading earlier, leaving the ventral side more commonly smooth. Some variants are homeomorphs of *C. gracilis* in Po-15.

Dimensions.

	D_{max}	D_{ph}	*h*	*w*	*u*
GGU 137939.1:	81	~55*			
At D = 60:				0.52	
GGU 137973.1:	83	55	0.50	0.50	0.18

Mean values, reference collection:

$<D_{max}>$	91.2 ± 2.9	σ = 9.3 (14%)	n = 11
$<D_{ph}>$	66.6 ± 1.2	σ = 8.4 (13%)	n = 12
$<w_{ph}>$	0.55 (±0.02)	σ = 0.083 (15%)	n = 15

*Inner whorls crushed

D, D_{max}, D_{ph} in mm

The variability distributions have some unusual tails. On the one hand, there are a few variants at the top end of the scale that have very large, inflated phragmocones, D_{ph} *c*. 70 mm, w = 0.61–0.68. At the other end, there are small forms, D_{max} *c*. 55–60 mm, also mature adults, in which the length of the body chamber is reduced from its otherwise ubiquitous 0.75 of a whorl to 0.55–0.60 of a whorl.

Po-13 – Po-14 faunal horizons

Po-13: *Cranocephalites tvaerdalensis* Alsen 2015

Plate 14, figs 1–4 [M], Fig. 41 [m]

cf 1962	*Cranocephalites* (?) *nordvikensis* (pars), Voronets, plate 4, fig. 3a, b.
2015	*Cranocephalites tvaerdalensis* Alsen, plates 1–5 (Appendix 1).

Types. Holotype MGUH 31377 (ex GGU 522023a); allotype MGUH 31378 (ex GGU 444903). Type material from Tværdal, Geographical Society Ø (Appendix 1).

Material and distribution. Known in Jameson Land only from two closely adjacent sections at Katedralen, section D4 (bed 12b; Fig. 23) and section D5 (bed 5c; Fig. 24),

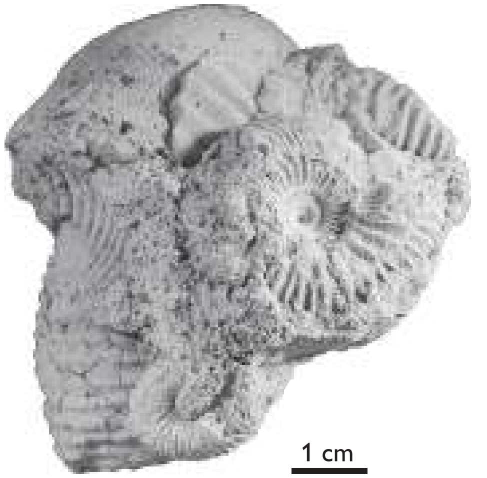


Fig. 41. A slab of sandstone (JHC 4165) with a cluster of a fragment of a macroconch and two microconchs of *Cranocephalites tvaerdalensis* Alsen 2015 (see Appendix 1).

restricted in the latter to a single bed of ironstone 0.5 m thick, separated only by partings from similar ironstones of Po-10 below and Po-15 above. In parts of the bed the ammonites are clustered together. Mature macroconchs dominate as usual, but in one case a macroconch has attached to it a cluster of two microconchs, with imprints of more (Fig. 41). Section D4 (Fig. 23): 29 [M]; section D5 (Fig. 24): 22 [M], 2 [m]. *Total*: 53 (51 [M] + 2 [m]).

Description. This is probably the most strongly-sculptured, strongly-ribbed transient of all the *Cranocephalites* of the Pompeckji Standard Zone, particularly on the middle whorls (Plate 14, figs 2, 4), although extreme variants in other transients can be similar. The adult size is average but the whorl-section markedly inflated and depressed.

Dimensions.

Mean values, reference collection:			
$<D_{max}>$	82.0 ± 1.7	σ = 6.5 (8.1%)	n = 15
$<D_{ph}>$	61.1 ± 0.7	σ = 4.9 (8.0%)	n = 46
$<w_{ph}>$	0.58 ± 0.01	σ = 0.05 (8.5%)	n = 46

D_{max}, D_{ph} in mm

Comparisons. Given the size of the available collections, there can be little doubt about the close synchroneity of the assemblages from Geographical Society Ø and Jameson Land, the only localities at which they have so far been found, some 200 km apart. Yet at both localities the occurrences are restricted to very small areas, of the order of a few square kilometres. And at both localities, the assemblages consist exclusively of mature adults, the dimorphic ratios heavily balanced in favour of the macroconchs. In Jameson Land they are found in thin, highly condensed facies. On Geographical Society Ø, they occur in a thin bed in a sandy succession. The quality of the fossils indicates that the shells had a high preservation potential. The highly disjunct distributions of the ammonites seem therefore once again to point to ecological rather than taphonomic ones as the main factors determining the observed distributions.

Po-14: *Cranocephalites* sp. aff. *tvaerdalensis* (*U*-8)
(not figured)

Representative specimens of (U-8). Section D4, bed 12c (Fig. 23): primary representative specimen, JHC 6117 [M]; secondary representative specimens, JHC 6116, JHC 6114.

Material. Another small collection found in a very restricted area, in sections D4 and D3 on the north slopes of Katedralen (Fig. 9), but in a sharply defined stratigraphical unit, an ironstone 0.3 m thick bounded by clay partings, bed 12c, underlain by Po-13 (*C. tvaerdalensis*) and overlain directly by Po-15, *C. gracilis* (Fig. 23). The lithologies and preservations are also distinct. The specimens of Po-14 are mostly fragmentary or distorted, the phragmocones either crushed or lost through bioturbation by large burrowers. The onset of the body chamber is in many cases not clear. Sections D3, D4: 8 [M], tolerably complete, and *c*. 12 [M] more fragmentary.

Description. A relatively small species, resembling in coiling and compression *C. indistinctus* of In-6, but retaining the coarseness, strength and style of ribbing of *C. tvaerdalensis*, Po-13. Most of the forms cluster around a fairly compressed, small mean, but there are occasional variants that are larger and more inflated. The distribution appears to be skewed, but there is not enough material to test this. The primary representative specimen (JHC 6117) has been chosen to be average in size and compression with strong, coarse ribbing; JHC 6116 is similar but with denser ribbing fading on the venter, presaging *C. gracilis* of Po-15; JHC 6114 represents the larger inflated forms. The length of the adult body chamber is typically only 0.65 of a whorl, shorter than in earlier forms.

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 6117:	76	50	0.50	0.50	
JHC 6116:	73	49		0.49	
JHC 6114:	95	57		0.74	

Mean values, reference collection:
$\langle D_{max} \rangle$ 76.0 ± 2.4 $\sigma = 5.9$ (8%) $n = 7$
$\langle D_{ph} \rangle$ 52.5 ± 1.9 $\sigma = 4.7$ (9%) $n = 8$
$\langle w_{ph} \rangle$ 0.55 ± 0.03 $\sigma = 0.09$ (16%) $n = 8$

D_{max}, D_{ph} in mm

Gracilis Subzone

The Gracilis Subzone of the Pompeckji Standard Zone includes six faunal horizons, Po-15 – Po-20, representing the group of *C. gracilis* Spath 1932 – *ornatus* (Spath 1932). These faunas from the higher part of the Pompeckji Standard Zone largely share some common features: more planulate forms dominate and the ribbing is denser, finer, less differentiated, and less bullate on the adult macroconch body chamber. Spath (1932) introduced two new specific names to mark what he regarded as the most striking features among the very limited selection of specimens he had before him in T.M. Harris' collection from Katedralen: *C. gracilis* and *C. maculatus*. He appended separate varietal names to some of the specimens:

C. gracilis	var. *ornata*
	var. *rotunda*
C. maculatus	var. *transitoria*
	var. *tenuis*

The determinations of Spath (1932) had to be based purely on morphology for he had no further stratigraphical details. With the information now available, it becomes immediately clear that some of the taxonomic distinctions reflect differences of age: that the types came from different horizons. The problem then became the same as that in the case of *C. pompeckji*, viz. to see whether the types could be matched with topotypes from among the successive transients now recognised and hence their names used to label these transients. This was successful in all of the taxa, although in some cases the named types were by no means the most typical of their species. In stratigraphical order:

Po-20 (highest)	*C. gracilis* var. *ornata*
Po-19	*C. maculatus sensu stricto*
Po-18	*C. maculatus* var. *transitoria* and var. *tenuis*
Po-15 (lowest)	*C. gracilis sensu stricto* and var. *rotunda*

Two of the transients, Po-15 and Po-19, can therefore bear the names of full existing species. But the other two, Po-20 and Po-18, contain previously described taxa that carry only varietal names: Po-20, var. *ornata* and Po-18, var. *transitoria*. It would be convenient to retain these names by promoting them to specific rank. This should here be possible within the rules under the provisions of article 45.6.4 of the International Code of Zoological Nomenclature, which allows varietal names introduced between 1930 and 1961 to be construed subsequently as either of varietal or subspecific status even if called 'var.', unless the author explicitly stated 'var.' to be strictly that, an infraspecific category not of specific or subspecific taxonomic meaning in a biological sense. Although Spath (1932) carefully labelled his specimens as 'var.' he never gave an explicit account of what he meant by 'species'. In numerous other cases he referred specimens to be 'transitional' from one 'species' to another, or 'intermediate' between one or another. It seems clear that he regarded his 'species' as little more than descriptive artefacts, and hence the distinction between 'sp.' and 'var.' to be one of degree rather than of principle. The names '*ornata*' and '*transitoria*' will therefore be used here as of species-group rank with authorship and date going back to Spath (1932).

Po-15: *Cranocephalites gracilis* Spath 1932

Plate 14, fig. 5; Plate 15, figs 1–5; Fig. 42

1932 *Cranocephalites gracilis* Spath, p. 22, plate 2, fig. 6; plate 3, fig. 1 (HT); *non* var. *ornata*, plate 2, fig. 6a, b (= *C. maculatus*).

Holotype. MGUH 9166, collected from the north slopes of Katedralen by T.M. Harris, refigured here on Plate 15, fig. 1a, b after some cleaning.

Material and distribution. This is perhaps the commonest and most widespread species in East Greenland. The preservation is, however, everywhere poor. Only the body chambers are preserved in slightly phosphatised, fine-grained, non-ferruginous indurated shale, lying free in the soft mudstones when weathered, the phragmocones having been lost by crushing (Fig. 42).

Ugleelv, two reference collections: (1) Section D4 (Fig. 23), type-locality, bed 12d: 45 [M]; (2): section E3, west of Ræveelv, bed 8: 19 [M]. Others sections: D2 (Fig. 22), D6, D8–10: 82 [M]. *Total*: 149 (all [M]). Other spot collections from Mikael Bjerg, section 33 (Fig. 4), Trefjord Bjerg, section 38 (M. Engkilde 1993 collection). Traill Ø:

Svinhufvud Bjerge (P. Alsen 1996, 1997 collections, CASP collection); Geographical Society Ø: Tværdal (P. Alsen 1998, 2011 collections).

Description. Markedly more evolute than most other forms of *Cranocephalites*, the ribbing more delicate, denser, tending to fade, especially on the venters of the adult body chambers. The type is perhaps close to one end of the range of variability, probably picked out by T.M. Harris because of its relatively good preservation. It bears some resemblance to the younger *C. ornatus* (Po-20, cf. Plate 18, fig. 3a, b) but both the stratigraphical position and the preservation support the difference of horizons. The other end of the range of variability is seen in Plate 14, fig. 5.

Dimensions. In view of the poor preservation, not many measurements have significance. Most of the specimens are complete up to or close to the peristome, so that the maximum shell-diameter remains reliable. The length of the adult body chamber is close to 0.75 of a whorl. The crushing of the shells goes up to the onset of the body chambers, however, so that estimates of whorl-width were made at a point half a whorl back before the peristome. The mean value of the shell-diameter at the last septum could then be estimated from the mean maximum diameter and a spiral half-whorl constant $\rho(\pi) = 1.30$, the value typical of the genus as a whole.

	D_{max}	D_{ph}	h	w	u
MGUH 9166 (HT):	88	60	0.45	0.46	0.25
JHC 6142:	75	53	0.49	0.44	0.15
JHC 6128:	75	53	0.48	0.49	0.13

Mean values, reference collection (1):
$\langle D_{max} \rangle$ 79.2 ± 1.1 $\sigma = 6.6$ (8.4%) $n = 35$
$\langle D_{ph} \rangle$ 59.5 (est.) $\sigma =$
$\langle w_{max-\pi} \rangle$ 0.33 ± 0.006 $\sigma = 0.033$ (10%) $n = 35$

Mean values, reference collection (2):
$\langle D_{max} \rangle$ 80.5 ± 1.5 $\sigma = 6.4$ (7.8%) $n = 18$
$\langle w_{max-\pi} \rangle$ 0.30 ± 0.004 $\sigma = 0.015$ (5%) $n = 18$

D_{max}, D_{ph} in mm

Fig. 42. A field collection of *Cranocephalites gracilis* (Po-15), at section E3, bed 8 (Fig. 35B), made in 1996. Hammers for scale.

Po-16: *Cranocephalites* sp. aff. *gracilis* Spath 1932 (*U*-9)

Plate 16, figs 1–5

?1932 *Cranocephalites maculatus* var. *tenuis* Spath, p. 24, plate 4, fig. 2.

Representative specimen of (U-9). Secion D1, bed 6: primary representative specimen, JHC 1328; secondary representative specimen, JHC 1340.

Material and distribution. Two assemblages. One (JHC 5235–5250) from section C4, bed 12d (Fig. 21) (immediately below the first ironstone of the *Arctocephalites* beds, Fb-2): 16 [M] and the other (JHC 1320–59) from section D1, bed 6: 19 [M]. *Total*: 35 (all [M]).

Description. The inner whorls involute, compressed as in other species. Evolute, serpenticone last whorl, umbilicus shallow, gently rounded umbilical shoulder and wall. Primary ribbing subdued, rising slowly from the umbilical shoulder to maximum strength in lower flank, coarse, persisting to the end in full strength; there are typically 9–10 primary ribs on the final body chamber; bifurcating with intercalatories into coarse, subdued secondaries, fading mid-ventrally on the body chamber; prominent broad terminal constrictions. Body chamber occupies between 0.6–0.65 of the last whorl.

It differs from *C. maculatus* var. *tenuis* which is more involute, ribbing that is denser and finer, primaries that are stronger on the umbilical shoulder, lower level of bifurcation and sharper secondaries. It differs from *C. gracilis* (Po-15) which has similar coiling and size, but on average is more densely and finely ribbed; there is some overlap in variability, however, so close affinity is assured.

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 1328:	78	53	0.47	0.49	

Mean values, reference collection (1), section D1:

$<D_{max}>$	78.5 ± 1.5	$\sigma = 4.7$ (6.1%)	$n = 10$
$<D_{ph}>$	53.1 ± 1.3 (est.)	$\sigma = 4.1$ (7.7%)	$n = 10$
$<w_{ph}>$	0.44 ± 0.077	$\sigma = 0.051$ (11.7%)	$n = 10$

Mean values, reference collection (2), section C4´:

$<D_{max}>$	85.1 ± 3.5	$\sigma = 11.2$ (13.2%)	$n = 10$
$<D_{ph}>$	59.4 ± 2.2 (est.)	$\sigma = 7.0$ (11.7%)	$n = 10$

D_{max}, D_{ph} in mm

Po-17: *Cranocephalites transitorius* (Spath 1932) *trans α*

Plate 15, fig. 6

Representative specimen of transient α. JHC 6294 (Plate 15, fig. 6), section E3, bed 9.

Material and distribution. Collections at section D8, bed 18 (Fig. 25): 8 [M] and section E3, bed 9b, (Fig. 25): 9 [M]. *Total*: 17 (all [M]).

Description. The material includes relatively few and poorly preserved specimens. They show a tendency toward flattened sides giving an almost subrectangular whorl cross section. The whorl is markedly involute until onset of the final body chamber where uncoiling then becomes marked. The final body chamber occupies *c*. 0.65 of the whorl. The ribbing density is similar to the smaller and slender variants of *C. gracilis* but slightly more subdued. The ventral weakening of ribbing on final body chamber commonly results in smooth or near smooth venters, but also commonly ribbing reappears in the last quarter of the body chamber before the peristome. Broad shallow peristomal constrictions may occur.

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 6294:	80	58	0.43	0.39	0.16

Mean values, reference collection:

$<D_{max}>$	82.4 ± 2.3	$\sigma = 6.4$ (7.8%)	$n = 8$
$<D_{ph}>$	55.3 ± 1.5	$\sigma = 4.3$ (7.8%)	$n = 8$
$<w_{ph}>$	0.42 ± 0.01	$\sigma = 0.021$ (5.9%)	$n = 7$

D_{max}, D_{ph} in mm

Po-18: *Cranocephalites transitorius* (Spath 1932) ***sensu stricto*, trans β**

Plate 17, figs 1–3; Fig. 43

1932 *Cranocephalites maculatus* sp. nov. var. *transitoria* Spath, p. 24, plate 3, fig. 6a, b.

Holotype. MGUH 9170, the specimen figured by Spath (1932), collected by T.M. Harris at Katedralen. Refigured here in Plate 17, fig. 2a, b.

Material and distribution. Collections at section D6, bed 1b: 8 [M], section E3, bed 10 (Fig. 35B): 33 [M]; and section D9, bed 19: 2 [M]. *Total*: 43 (all [M]).

Fig. 43. A field collection of ammonites of horizon Po-18, *Cranocephalites transitorius* trans β, section E3, bed 10 (Fig. 35B). Hammers for scale.

Description. The large material shows a large variation in size. The smaller variants overlap with the preceeding horizon Po-17, having flat sides and dense, but somewhat stronger, ribbing. The larger forms develop a somewhat low oval whorl cross section with the maximum width low on the sides, close to the umbilical shoulder. The largest variants are also the thickest ones. The body chamber occupies 0.7–0.75 of the last whorl. The ribbing is generally stronger and coarser. Weakening in a narrow ventral band occurs but consistent ribbing until final peristome seems to be commonest, perhaps giving the first indications of the ribbing in early whorls of the succeeding genus *Arctocephalites*.

Dimensions.

	D_{max}	D_{ph}	h	w	u
MGUH 9170 (HT):	87	60	0.50	0.48	0.20

Mean values, collection from section E3, bed 10:

$\langle D_{max} \rangle$	84.3 ± 1.6	σ = 8.3 (9.8%)	n = 28
$\langle D_{ph} \rangle$	60.0 ± 1.3	σ = 6.4 (10.1%)	n = 26
$\langle w_{ph} \rangle$	0.48 ± 0.02	σ = 0.078 (16.2%)	n = 25

D_{max}, D_{ph} in mm

Po-19: *Cranocephalites maculatus* Spath 1932

Plate 17, fig. 4; Plate 18, figs 1, 2

1932 *Cranocephalites maculatus* Spath, p. 24, plate 1, fig. 1a, b; ? plate 2, fig. 3a, b (a not closely identifiable phragmocone); *non* plate 3, fig. 6a, b (= *C. transitorius*), *non* plate 4, fig. 2.

Holotype. MGUH 9154, T.M. Harris collection 1926 from Katedralen (Spath 1932, plate 1, fig. 1a, b; refigured here in Plate 18, fig. 1a, b).

Material and distribution. Collections from section D1, bed 7: 16 [M], section D5, bed 5 (Fig. 24): 24 [M] and 2 [m]. Further 1 [M] from T. Birkelund and J.H. Callomon 1971 collection, 4 [M] from T. Birkelund and C. Heinberg 1974 collection, and 8 [M] from F. Surlyk 1970 collection, loose from section D5. *Total*: 55 (53 [M] + 2 [m]).

Description. Compared with the previous horizon this fauna is larger and more inflated. The side is thickest on the midside and the venter is broad and rounded. The lower part of the umbilical wall is steep, but then becomes gently curved in the upper part. The inner whorls are serpenticone. The species is generally strongly ribbed. The venter commonly becomes smooth in inflated varieties, some specimens almost being wholly smooth except for bullate primaries low on the sides. Others have strong persistent ribbing until final peristome. The final body chamber occupies about three-quarters of the last whorl.

Dimensions.

	D_{max}	D_{ph}	*h*	*w*	*u*
MGUH 9154 (HT):	89	~56	0.51	0.68	0.16

Mean values:

$<D_{max}>$	89.1 ± 1.1	σ = 6.3 (7.0%)	*n* = 33
$<D_{ph}>$	63.2 ± 0.9	σ = 5.0 (7.9%)	*n* = 33
$<w_{ph}>$	0.56 ± 0.02	σ = 0.098 (17.5%)	*n* = 30

D_{max}, D_{ph} in mm

Po-20: *Cranocephalites ornatus* (Spath 1932)

Plate 18, figs 3, 4; Plate 20, fig. 4

1932 *Cranocephalites gracilis* var. *ornata* Spath, p. 23, plate 2, fig. 6a, b (HT).

Holotype. MGUH 9165, T.M. Harris collection 1926, Katedralen (Spath 1932, plate 2, fig. 6a, b).

Material and distribution. Collections from section D5 (Fig. 24): 2 [M] loose, and section D8, bed 18 (Fig. 25): 8 [M]. *Total*: 10 (all [M]).

Description. The size variation almost similar to the previous faunal horizon (Po-18), but much smaller than the overlying one (Po-20). Contains quite characteristic variants with narrow umbilicus, high gently sloping flanks and narrow rounded venter resulting in an arched whorl section perhaps giving an early indication of the evolution towards the disc-like *Arctocephalites*. The fauna, however, still also contains forms with the broad, rounded venter typical of *Cranocephalites*.

Dimensions.

	D_{max}	D_{ph}	*h*	*w*	*u*
MGUH 9165 (HT):	81	59	0.45	0.53	0.17

Mean values:

$<D_{max}>$	88.7 ± 3.09	σ = 8.17 (9.2%)	*n* = 7
$<D_{ph}>$	71.1 ± 4.04	σ = 10.7 (15.0%)	*n* = 7
$<w_{ph}>$	0.52 ± 0.015	σ = 0.039 (7.5%)	*n* = 7

D_{max}, D_{ph} in mm

Episcopalis Subzone

The Episcopalis Subzone of the Pompeckji Standard Zone includes three faunal horizons, Po-21 – Po-23 (Fig. 30).

Po-21: *Cranocephalites episcopalis* sp. nov. *sensu stricto*, trans α

Plate 18, fig. 5; Plate 19, figs 1, 2; Plate 20, figs 1–3

Holotype. JHC 4061 section D9, bed 22 at Katedralen.

Material and distribution. Collections from section D5 (Fig. 24): 1 [M] in bed 6b and 2 [M] loose, section D7: 3 [M], section D8 (Fig. 25): 4 [M], section D9, bed 22: 7 [M], section D10, bed 10: 2 [M], section 58, bed 35 in northern Jameson Land: 8 specimens. Additionally 7 from F. Surlyk 1991 collection, 3 specimens from M. Engkilde 1993 collection. *Total*: 35 (all [M]).

Description. Very variable and characterised by very large, inflated *Megasphaeroceras*-like forms (Plate 19, fig. 1a, b), becoming relatively smooth on the body chamber, rejuvenation of the secondaries near peristome. Includes coarse, large variants, retaining ribbing in full throughout. Also compressed forms commonly finely and densely ribbed. The body chamber is slightly larger than previous species and now occupies from 0.8 up to a full whorl.

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 4061 (HT):	110	72	0.51	0.50	0.11

Mean values:

$<D_{max}>$	114.3 ± 3.60	σ = 9.53 (8.3%)	n = 7
$<D_{ph}>$	70.3 ± 2.28	σ = 8.22 (11.7%)	n = 13
$<w_{ph}>$	0.72 ± 0.040	σ = 0.144 (20.0%)	n = 13

D_{max}, D_{ph} in mm

Stratigraphy. The morphological affinities are still within *Cranocephalites* rather than *Arctocephalites*: the rounded, inflated sections, dense ribbing retained, no compressed, high-whorled variant. But size and variability indicate affinities with *A. arcticus*.

Po-22: *Cranocephalites episcopalis* sp. nov. trans β

(not figured)

Material and distribution. Only two specimens, fragmentary, JHC 5158, 5159, both [M], from section D8, bed 18 (Fig. 25).

Description. Resembles closely Po-21 with persisting ribbing on adult body chamber with dense ribs that do not fade on the venter. It differs in being smaller and slightly less inflated.

Dimensions.

	D_{max}	D_{ph}	h	w	u
JHC 5158:	95	~69	~0.36	0.36	0.18
JHC 5159:	85	59	0.49	~0.88	

Po-23: *Cranocephalites* sp. (*U*-10)

(not figured)

Material and distribution. Collections from section C3 (Fig. 20), bed 7: 11 [M], section C4 (Fig. 21), bed 13: 3 [M]. Section D2 (Fig. 22), bed 14: 6 [M] from J.H. Callomon 1994 collection and 8 [M] from his 1996 collection. *Total*: 30 (all [M]). All specimens are crushed.

Description. Involute even on body chamber, cross-section difficult to describe due to the preservation but probably originally rounded, mostly high oval, venter mainly rounded, subquadratic in some specimens. Ribbing is strong until late stages, dense, no bullates, and the ribs fade only slightly or more commonly not at all on the venter.

Dimensions.

Mean values:

$<D_{max}>$	81.2 ± 1.56	σ = 5.84 (7.18%)	n = 14
$<D_{ph}>$	55.67 ± 1.40	σ = 4.85 (8.71%)	n = 12

D_{max}, D_{ph} in mm

Stratigraphy. In the sections where Po-23 is recorded, the youngest underlying ammonites belong to Po-15, *C. gracilis* (Fig. 22). The ribbing with strong ribs on the body chamber and commonly no weakening on the venter indicate it to be a very late *Cranocephalites. C. gracilis* is represented in section D8, where it is overlain by Po-17 and the faunal horizons Po-20 – Po-22, in rapid succession. Po-23 is somewhat smaller and less inflated than Po-22, the latter being transient from the underlying larger and more inflated *C. episcopalis sensu stricto* (trans α).

Conclusions

1. The rapidity with which the *Cranocephalites* evolved allows following the microevolution of the ammonites at a level of time-resolution with few rivals in the geological record. The 34 transients, Bo-1 to Po-23, represent evolution over the duration of the late Bajocian, which according to the latest Geological Time Scale (Gradstein *et al.* 2012, table 26.3) had an estimated duration of 1.17 myr providing a time resolution here of *c.* 34 kyr and is close to the achievable limit, set by the ability to recognise morphological changes in successive assemblages. Hence, on this time scale, evolution appears to be continuous.

2. The observed record in the rocks continues to be highly discontinuous: the ammonites are found concentrated in thin beds separated by beds that are devoid of them. The biostratigraphic record is therefore almost entirely composed of snap-shots of faunas in time – some beds with ammonites, most beds without. This is in marked contrast to other marine organisms e.g. dinoflagellates, coccoliths, calpionellids, or planktonic foraminifers whose evolutions have been studied biostratigraphically or used for age determinations.

3. Discontinuities in the vertical sequences of ammonites are caused by stratigraphic discontinuities rather than by punctuated evolution. Geologically, the lithostratigraphic record – the surviving record of sedimentary dynamics, both of input and erosion – is highly incomplete, both vertically and horizontally. As the present account shows, the ammonites reveal the existence of some spectacular non-sequences in the Middle Jurassic sediments of Jameson Land whose presence in the rocks is reflected in nothing more than a parting between beds looking like any other. Thus, vertically, at Trefjord Bjerg, the sandstone of horizon Po-11 sits directly on the sandstone of Bo-1: sediments of ages Bo-2 up to a level of Po-10 are missing. At Hurry Inlet, sediments of In-1 – J-10 (33 transients) are missing. Horizontally, many of the sediments of Po-1 – Po-3, Po-5 – Po-9 are lenticular or lost in the region of Katedralen in the overlap onto the clinoform unit on a distance scale of kilometres or less. As Buckmann (1881) noted, the more complete the biostratigraphical record becomes, the less complete the lithostratigraphic record turns out to be (see Callomon 1995, pp. 140, 147).

4. Almost all of the ammonite assemblages consist almost exclusively of fully-grown adults and predominantly of macroconchs at that. Microconchs are rare. The probable reasons for this point to a closed life cycle in which the fossil accumulations now mark the breeding, spawning and dying grounds of gregarious nektonic organisms that migrated during their life cycles, with sexual segregation in the final stages.

Acknowledgements

The Geological Institute (University of Copenhagen), the Geological Survey of Greenland (GGU, now part of GEUS, the Geological Survey of Denmark and Greenland), the Carlsberg Foundation, the Danish Natural Research Science Council, are thanked for support and the opportunity to make the new collections in the Ugleelv area. JHC's field work in Jameson Land in 1994–1996 was partly funded by Norsk Hydro and by grants from the Danish Natural Science Research Council. The visits of JHC to the Geological Museum in Copenhagen were organised by David A.T. Harper and funded by EU's COBICE and SYNTHESYS museum visitor programmes. Carol St. John Payne, Michael Engkilde and Michael Larsen are thanked for help in the field. Paul and Peter Callomon are thanked for entrusting PAL and FS with the material for preparation for publication. Carol St. John Payne assisted JHC during curation of the collection (in Copenhagen) and with photographing fossils for plates. After the death of JHC, Carol located notes, electronic files and other material which were invaluable for PAL and FS in completing the manuscript. Her help is highly appreciated. Jette Halskov drafted the figures. The referees Eckhard Mönnig (Naturkunde Museum, Coburg) and Paul L. Smith (University of British Columbia) provided valuable comments on the manuscript. Preparation of the manuscript for publication was supported by Geocenter Denmark.

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