Early Cretaceous brachiopods from North-East Greenland: Biofacies and biogeography

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Augmentation and revision of the relatively diverse Valanginian brachiopod faunas from North-East Greenland confirm the existence of two mutually exclusive but broadly coeval assemblages, associated with two contrasting facies types. A Boreal, relatively shallow-water assemblage domi-nated by large terebratulids and ribbed rhynchonellids, including *Cyrtothyris*, *Lamellaerhynchia* and *Praelongithyris* characterizes the Falskebugt fauna. By contrast the Albrechts Bugt and Rødryggen fauna contains Tethyan elements, more typical of deeper water, including *Lacunosella*, *Placothyris*, *Pygope* and *Rugitela*. This early Cretaceous Out-of-Tethys migration confirms the early and persist-ent northward track of a proto Gulf Stream current. A new taxon, *Placothyris kegeli*, is described from the Albrechts Bugt and Rødryggen members of the Palnatokes Bjerg Formation.

Key words: Brachiopods, Valanginian, palaeogeography, palaeoenvironments, North-East Greenland.

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Brachiopods were first reported from the Lower Cretaceous rocks of North-East Greenland in the 1940s (Maync 1940, 1949) based on collections made by that author earlier in the late 1930s. Additional material was collected by Donovan (1955, 1957) in the early 1950s on Lauge Koch expeditions, which formed the basis for Owen's (1976) description of the brachiopods from the region. Owen (1976) updated the previous, sparse brachiopod records of Muir-Wood (1953) and Donovan (1955, 1957) from Wollaston Forland and Traill Ø, respectively. The brachiopod fauna is particularly significant. The fauna occupies a key position, geographically, within the Boreal Province, situated at the northern apex of the opening North Atlantic. The region contains a relatively diverse and varied brachiopod assemblage, recorded, to date, from two different facies types. Important is the apparent co-occurrence of elements of both the Boreal and Tethyan provinces within the region (Owen 1976). An assemblage of large terebratulids together with ribbed rhynchonellids characterizes coarse-grained, iron-stained limestones from the Wollaston Forland; this is a typical Boreal biofacies associated with shallow-water, high-energy environments. Tethyan brachiopods, however, have been reported from fine-grained deeper-water limestone from Mols Bjerge on Traill Ø.

The exotic occurrence of Tethyan taxa in the Cretaceous of North-East Greenland has generated two competing models. Tethyan elements entered the region along a proto Gulf Stream current or arrived from deep-water, cooler Tethyan biofacies by upwelling currents (Ager 1971, 1973; Sandy 1991). New collections from North-East Greenland, a modern palaeoenvironmental analysis of the succession (Surlyk 1978, 2003) and a statistical approach to global biogeographical patterns, provide an opportunity to discuss these models further.

Geological Setting

The thick succession of Upper Jurassic – Lower Cretaceous rocks in North-East Greenland is dominated by black mudstones deposited in an anoxic environment, virtually barren of benthic fossils. During a relatively short interval in the Late Ryazanian – Hauterivian light grey, yellowish and red mudstones were deposited over structural highs, containing a rich and diverse fauna, in marked contrast to the under- and overlying black mudstone successions; the benthos includes brachiopods.

The Upper Jurassic – Lower Cretaceous succession was deposited during a major Mid Jurassic – earliest Cretaceous rifting phase, which climaxed in the Volgian, and formed a series of westward-tilted halfgrabens (Surlyk 1978). In the Wollaston Forland area, where the Lower Cretaceous is best exposed, a wide halfgraben basin was filled with a thick succession of submarine conglomerates, sandstones and shales. During the early post-rift phase, in the Valanginian – Early Hauterivian, the halfgraben crests were draped by a few metres of vividly-coloured, light grey, yellowish and red mudstones.

Stratigraphy

The late syn-rift deposits belong to the Palnatokes Bjerg Formation, which comprises the Young Sund, Albrechts Bugt, Rødryggen and Falskebugt members (Surlyk 1978). The western part of the NW flank of Stratumbjerg provides an excellent cross section through a tilted fault block and the relationships between the units are clearly observed (see Surlyk 1978, 2003). The post-rift strata were developed as conglomerates and sandstones of the Young Sund Member to the west, towards the fault scarp. The member gradually becomes finer grained towards the east in a distal direction, towards the block crest, and passes into the Albrechts Bugt Member. Farther to the east, on the crest, the Albrechts Bugt Member is almost wedged out and is overlain by the Rødryggen Member (Surlyk 1978, 2003). The top strata of the Albrechts Bugt Member locally have alternating reddish and grey and yellowish colours reflecting interfingering with or gradual transition into the Rødryggen Member.

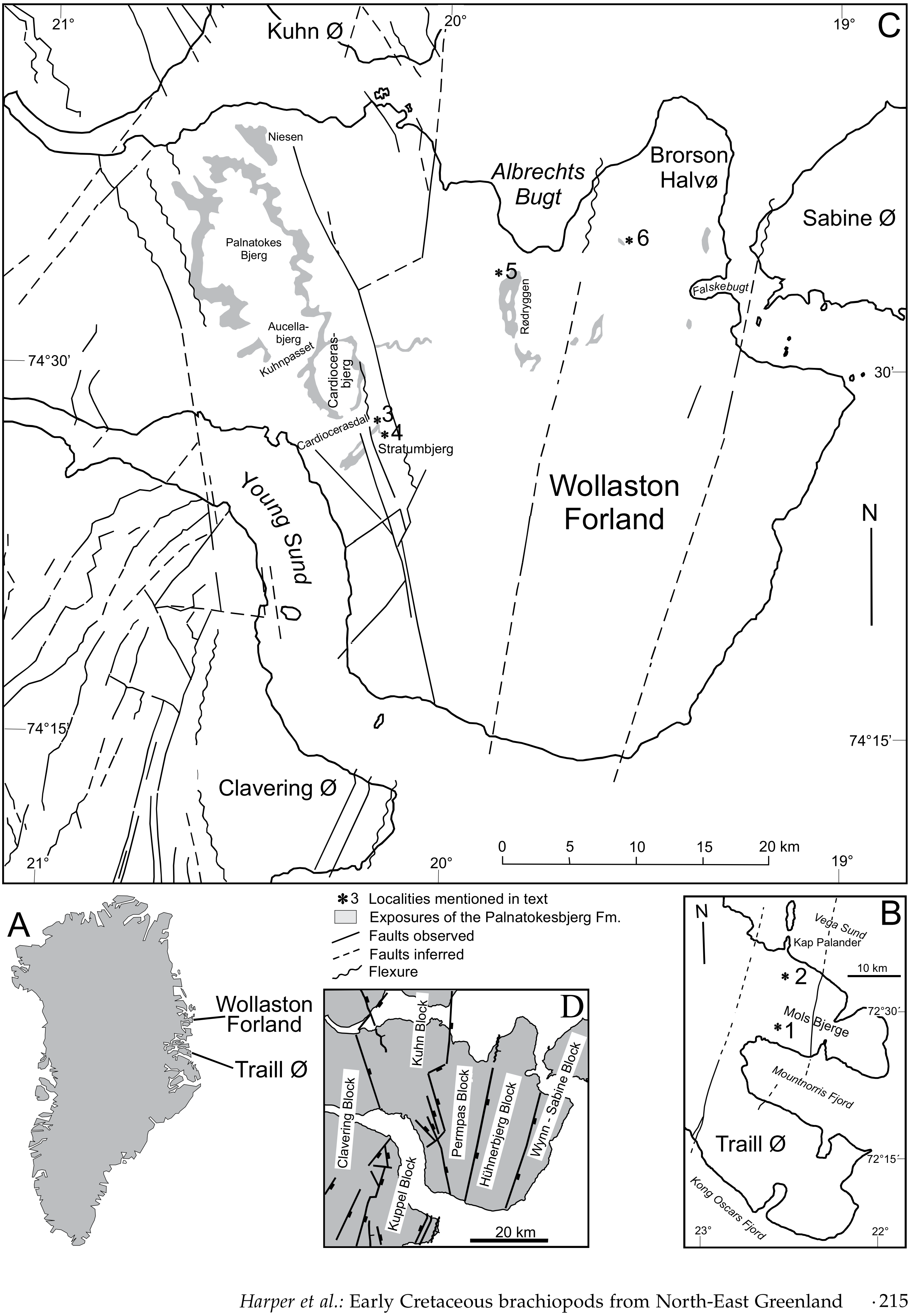
The Young Sund Member is a coarse-grained unit with conglomerates, coarse- and medium-grained sandstones with pebble layers (Surlyk 1978). It contains reworked concretions of the Albrechts Bugt Member. The member is relatively poor in fossils.

The Falskebugt Member is also a coarse grained unit. It is a local facies developed in the easternmost part of Wollaston Forland and represents a setting in the proximity of an emergent block crest, which produced a coarse sandy and conglomeratic facies with a fauna reflecting a near shore environment. A relatively diverse fauna was reported from this facies by Maync (1949) and included a brachiopod fauna, which was described by Owen (1976). Localities within the Young Sund and Falskebugt members were not visited during recent fieldwork, which focused on the younger, more fossiliferous Albrechts Bugt and Rødryggen members.

The southernmost occurrences of Albrechts Bugt and Rødryggen members are within small isolated outliers on northern and southern Mols Bjerge, respectively, on Traill Ø (see descriptions of localities 1 and 2 below), where they are poorly exposed but highly fossiliferous, dominated by *Buchia*-bivalves, belemnites and ammonites. The ammonite fauna includes representatives of the Lower to lower Upper Valanginian of the Russian Platform, Arctic Canada and NW Europe (Alsen & Rawson 2005, this volume), proving the succession to be highly condensed, as was similarly argued by Jeletzky (1965). The units are less-well exposed on Traill Ø compared to localities in the Wollaston Forland area to the north, which, however are not so fossiliferous.

The Albrechts Bugt Member is a light grey, calcareous silty mudstone that weathers to yellowish colours. It interfingers with and is overlain by the Rødryggen Member, which is characterized by claret-coloured mudstones. The Albrechts Bugt Member is generally quite fossiliferous with ammonites of Valanginian age, whereas the Rødryggen Member in the Wollaston Forland almost completely lacks ammonites. Recently, a few fragmentary specimens were retrieved from the Rødryggen Member at Rødryggen (locality 5, see Fig. 1) proving the presence of the Lower Hauterivian (Alsen, unpublished data). Dark grey or black shales everywhere overlie the Rødryggen Member. These were generally correlated with the middle Cretaceous (Aptian–Albian) and the boundary between the Rødryggen Member and the overlying black mudstones was regarded a major hiatus. However, Nøhr-Hansen (1993) demonstrated the oldest sediments of the 'Aptian–Albian series' of Maync (1949) were, in fact, of Barremian age. Mudstones of Barremian age have been since proven from the Hold-with Hope area to the south by Kelly *et al*. (1998). The presence of Hauterivian strata now indicates that sedimentation was more or less continuous during the Early Cretaceous in North-East Greenland interrupted by relatively short intervals of non-deposition.

Facing page:
Fig. 1A. Location of Wollaston Forland and Traill Ø in NE Greenland; B. Localities 1 and 2 on Traill Ø; C. Localities 3–6 on Wollaston Forland; D. Tectonostratigraphic map of Wollaston Forland, identifying the main tectonic blocks.


C
Kuhn Ø
21°
20°
19°
Niesen
Albrechts Bugt
Brorson Halvø
Sabine Ø
Palnatokes Bjerg
*6
*5
Rødryggen
Falskebugt
Aucella-bjerg
Kuhnpasset
Cardioceras-bjerg
74°30'
30'
*3
*4
Cardiocerasdal
Stratumbjerg
Young Sund
Wollaston Forland
N
74°15'
Clavering Ø
0 5 10 15 20 km
A
Wollaston Forland
Traill Ø
*3 Localities mentioned in text
Exposures of the Palnatokesbjerg Fm.
Faults observed
Faults inferred
Flexure
D
Kuhn Block
Clavering Block
Permpas Block
Hühnerbjerg Block
Wynn - Sabine Block
Kuppel Block
20 km
B
N
Vega Sund
Kap Palander
*2
10 km
72°30'
Mols Bjerge
*1
Mountnorris Fjord
Traill Ø
72°15'
Kong Oscars Fjord
23°
22°

Localities and fieldwork

Six Lower Cretaceous localities were investigated by Alsen, in conjunction with a project dealing with ammonites from North-East Greenland (Fig. 1, Table 1). The two localities at Mols Bjerge on Traill Ø, in the southern part of the study area, were discovered in 1950–52 by Donovan (1953, 1955, 1957); these have been revisited in this study.

Donovan's 1950 collection from his locality 92 in southern Mols Bjerge (locality 1 of this study, Fig. 1) comprised a rich fauna of bivalves (*Buchia*), ammonites and belemnites that had weathered out of the red mudstones of the Rødryggen Member (Donovan 1953). The collection lacked brachiopods, but when Donovan revisited the locality in 1952 it yielded 15 brachiopod specimens, and these were later described and figured by Owen (1976). Recent fieldwork, by the second author, (1996–98, 2000), focused on locality 1, added only one more, fragmented, brachiopod, which had also weathered out of its matrix (Table 1).

Donovan's collection from his locality 185 in northern Mols Bjerge (locality 2 of this study, Fig. 1) yielded a similarly rich and diverse fauna of *Buchia*, ammonites and belemnites but it also comprised a single pygopid (*Pygope janitor*, herein) brachiopod (Donovan 1955, 1957). The fauna had weathered out of the hard grey limestone of the Albrechts Bugt Member. The pygopid was described by Owen (1976), as *Pygope janitor* (Pictet) and has attracted much attention due to its palaeobiogeographical and palaeooceanographical significance. The locality was visited recently (during 2000) by PA and many additional fossils were collected; but no further brachiopods were found. However, both *Moutonithyris moutoniana* (d'Orbigny) and *Placothyris kegeli* n. sp. (herein) have been identified from the Donovan collection from this locality (The Natural History Museum, London: BMNH BB 60929-31). Compared to the few and scattered localities on Traill Ø, the Lower Cretaceous succession on the Wollaston Forland area is much better exposed. The succession is not as fossiliferous as that on Traill Ø but brachiopods are fairly common and have been collected at a number of localities during recent fieldwork in 2001 by PA; these new collections supplement those made by Surlyk in 1974 and in the early 1990s.

Strata of the Rødryggen Member are well exposed at locality 3 on a northern ridge of Stratumbjerg

Table 1. Distribution of Lower Cretaceous brachiopod taxa in North-East Greenland

Regional data	Locality	Figure 1	Taxa
Mols Bjerge, Traill Ø	Southern part	Loc. 1	*Lacunosella groenlandica* *Nucleata* sp.
Mols Bjerge, Traill Ø	Northern part	Loc. 2	*Pygope janitor* *Lacunosella groenlandica* *Moutonithyris moutoniana* *Placothyris kegeli*
Wollaston Forland	Falskebugt		*Lamellaerhynchia* cf. *rostriformis* *Praelongithyris borealis* *Cyrtothyris maynci* *Ismenia tricostata* *Zittelina* sp.
Wollaston Forland	North ridge, Stratumbjerg	Loc. 3	*Lacunosella groenlandica* *Placothyris kegeli*
Wollaston Forland	East flank, Stratumbjerg	Loc. 4	*Lacunosella groenlandica*
Wollaston Forland	Rødryggen	Loc. 5	*Rugitela hippopus*
Wollaston Forland	Brorson Halvø	Loc. 6	*Pygope janitor* *Lacunosella groenlandica* *Placothyris kegeli* *Rugitela hippopus* *Nucleata* sp.

mountain in the western Wollaston Forland. Locality 3 represents a crestal position on the fault block. The top of the Upper Jurassic black shales of the Bernbjerg Formation was erosively incised during rifting, but during the Valanginian–Hauterivian the crest was submerged; one metre of the Albrechts Bugt Member, followed by 13.25 m of the Rødryggen Member rest unconformably on older strata. The Rødryggen Member is overlain by middle Cretaceous (Barremian-Aptian-Albian) black mudstones. The red mudstones appear structureless except for *Zoophycos* trace fossils, and imbricated inoceramid shell fragments are found in loose blocks. Macrofossils are common and include the bivalve *Buchia*, belemnites and fragmented inoceramid bivalves. Brachiopods are relatively common, whereas ammonites are absent. All fossils were found in loose blocks derived from the Rødryggen Member.

The Valanginian–Hauterivian succession at locality 4, on the eastern flank of Stratumbjerg, is markedly different although it lies less than one kilometre southeast of locality 3. Here, the Albrechts Bugt Member is expanded and passes gradually upwards into the Rødryggen Member. The whole succession is c. 23 m thick and is overlain by (?Barremian–Albian) middle Cretaceous strata. The succession is mud-dominated but contains numerous thin centimetre thick, silty to fine sand layers and occasional coquina-like shell concentrations. Fossils occur commonly throughout the measured section; the fauna is dominated by *Buchia* and belemnites with less abundant brachiopods and rare, poorly-preserved ammonites. Brachiopods are recorded from five separate levels.

Three relatively closely-spaced sections (PAL-3/2001, PAL-4/2001 and PAL-6/2001) were measured at locality 5 on the ridge Rødryggen south of Albrechts Bugt in central north Wollaston Forland. The Lower Cretaceous succession rests on Upper Jurassic black shales of the Bernbjerg Formation. The succession is c. 25 m thick and is overlain by upper Lower Cretaceous black mudstones. The Albrechts Bugt Member is 18 metres thick and contains very early Valanginian ammonites (*Delphinites*) near the base, Early–Late Valanginian ammonites in the middle part, and possible Early Hauterivian *Simbirskites* in the upper part (Alsen & Rawson 2005, this volume; Alsen unpublished data). The member intercalates with the Rødryggen Member and the boundary between the two units thus is transitional. Approximately 7 m of the Rødryggen Member is preserved where thickest, and contains rare Lower Hauterivian ammonites in its middle part (P. Alsen, unpublished data). The succession is thus expanded similar to that at locality 4, Stratumbjerg. Each of the measured sections yielded brachiopods, which extend from near the base to the middle part of the Albrechts Bugt Member.

The Albrechts Bugt and Rødryggen members are also exposed at locality 6 on the peninsula of Brorson Halvø, North Wollaston Forland. The Albrechts Bugt Member, here, also rests on the Upper Jurassic Bernberg Formation and is only 4 m-thick and contains a rich Lower Valanginian fauna with ammonites, bivalves, belemnites and brachiopods (including a complete specimen of *Pygope*). It is overlain by c. 10 m of the Rødryggen Member, which is barren in fossils except for rare echinoids, a few *Buchia* bivalves and some indeterminate ammonite fragments.

Systematic Notes

Type and figured material is reposited in the Geological Museum, University of Copenhagen (MGUH) and The Natural History Museum, London (BMNH BB). Additional material is reposited as follows: Alsen and Surlyk collections (Geological Institute, University of Copenhagen); Donovan and Maync collections (The Natural History Museum, London).

Family Rhynchonellidae Gray, 1848

Genus *Lamellaerhynchia* Burri, 1953

Type species. *Terebratula rostriformis* Roemer, 1836.

Lamellaerhynchia cf. *rostriformis* (Roemer, 1836)

1976 *Lamellaerhynchia* cf. *rostriformis* (Roemer) - Owen, p. 6, pl. 1, figs 1–3, fig. 2.

Remarks. This large, uniplicate, strongly-ribbed rhynchonellid was described originally from mainly mouldic material; key internal features such as the form of the hinge plates, short dental plates and characteristic distal ends of the crura were established by serial sectioning of a single, well-preserved umbonal shell. Owen (1976, p. 7) noted that the Greenland form differed from the type species, recorded from Valanginian–Hauterivian strata in Lincolnshire together with Hannover and Brunswick, North Germany, in being larger with a more consistently oval to subcircular outline.

This taxon is restricted to the Falskebugt Member

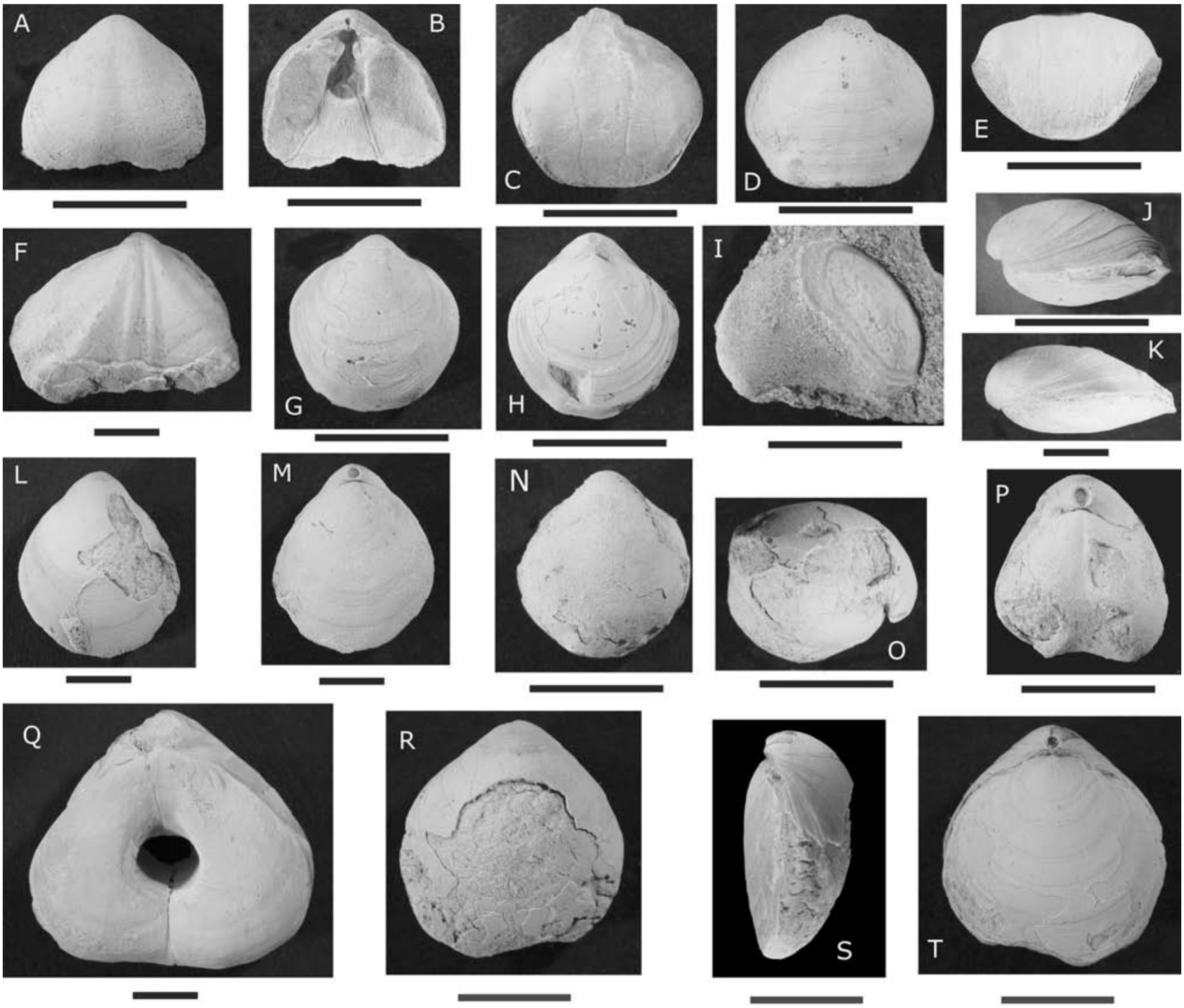


Fig. 2. Early Cretaceous brachiopods from North-East Greenland. A–F, I. *Lacunosella groenlandica* Owen. 1, 2, external and internal views of ventral valve, MGUH 27494 (Alsen colln, locality 4). C–E, ventral, dorsal and anterior views of partly exfoliated conjoined valves, MGUH 27495, (Alsen colln, locality 4). F, ventral exterior, MGUH 27496 (Alsen colln, locality 3). I, exfoliated ventral valve, MGUH 27497 (Alsen colln, locality 4). G, H, J. *Moutonithyris moutoniana* (d'Orbigny), ventral, dorsal and lateral views of conjoined valves, BMNH BB 60930 (Donovan colln, locality 2). K–M, R–T. *Placothyris kegeli* n. sp. K–M, holotype, lateral, ventral and dorsal views of conjoined valves, MGUH 27498 (Surlyk colln, locality 6). R–T Ventral, lateral and dorsal valves, BMNH BB 60929, (Donovan colln, locality 2). N–P. *Rugitela hippopus* (Roemer), ventral, lateral and dorsal views of conjoined valves, MGUH 27499 (Surlyk colln, locality 6). Q. *Pygope janitor* (Pictet), external view of dorsal valve of broken conjoined pair, MGUH 27500 (Surlyk colln, locality 6). Scale bars under each photograph: 1 cm.

and to date is exclusively known from only the Maync collection (see Owen 1976, p. 7).

Genus *Lacunosella* Wiśniewska, 1932

Type species. Rhynchonella arolica Oppel, 1866.

Lacunosella groenlandica Owen, 1976
Fig. 2A–F, I

1953 '*Rhynchonella*' cf. *decipiens* d'Orbigny - Muir-Wood, p. 3, pl. 1, fig. 4.
1957 '*Rhynchonella*' cf. *decipiens* d'Orbigny - Donovan, p. 206.
1973 '*Rhynchonella*' cf. *decipiens* d'Orbigny - Owen, p. 123.
1976 *Lacunosella groenlandica* sp. nov. Owen, p. 7, pl. 2, fig. 4; fig. 4.

Remarks. A significantly larger sample of this taxon is now recorded from a wider range of localities than those available to Owen (1976) within the Albrechts Bugt and Rødryggen members. Moreover the material includes a spectrum of sizes, permitting some discussion on the ontogeny of this variable species. Although samples are still limited this taxon shows marked allometric growth developing a more elongate outline during ontogeny. The younger growth stages are smooth with initially two strong costae developing in the ventral sulcus with about three on each flank. Many of the specimens are exfoliated exaggerating the apparent smooth external ornament.

Family Terebratulidae Gray, 1840

Genus *Praelongithyris* Middlemiss, 1959

Type species. *Praelongithyris praelongiforma* Middlemiss, 1959.

Praelongithyris borealis Owen, 1976
1976 '*Praelongithyris*' *borealis* sp. nov. Owen, p. 11, pl. 2, figs 2a–c; fig. 6.

Remarks. Owen's new species was based on material from the Falskebugt Member in the Maync Collection. Although he identified most of the key characteristics of Middlemiss' genus in serial section, Owen (1976) preferred to cite the generic name within double quotation marks. No further material is available for this species.

Genus *Cyrtothyris* Middlemiss, 1959

Type species. *Terebratula depressa cyrta* Walker, 1868.

Cyrtothyris maynci Owen, 1976

1976 '*Cyrtothyris maynci*' sp. nov. Owen, p. 13, pl. 2, figs 1a–c, pl. 3, figs 4a–c; fig. 7.

Remarks. This taxon was characterized by Owen (1976) on the basis of its subcircular to oval outline, swollen umbo with a large circular foramen and marked concentric growth lines. The species, to date, is known from only the Falskebugt Member.

Genus *Moutonithyris* Middlemiss, 1976

Type species. *Terebratula moutoniana* d'Orbigny, 1849.

Moutonithyris moutoniana (d'Orbigny, 1849)
Fig. 2G, H, J

1979 *Moutonithyris moutoniana* (d'Orbigny) - Middlemiss, p. 63.
1991 *Moutonithyris moutoniana* (d'Orbigny) - Sandy, p. 145.

Remarks. Middlemiss (1979) and later Sandy (1991) noted the presence of this taxon in collections in The Natural History Museum, London (BMNH BB 60930) from a Lauge Koch expedition in 1952. Two specimens have been identified from the same sample collected by D.T. Donovan in 1952 and presented to that museum in 1970.

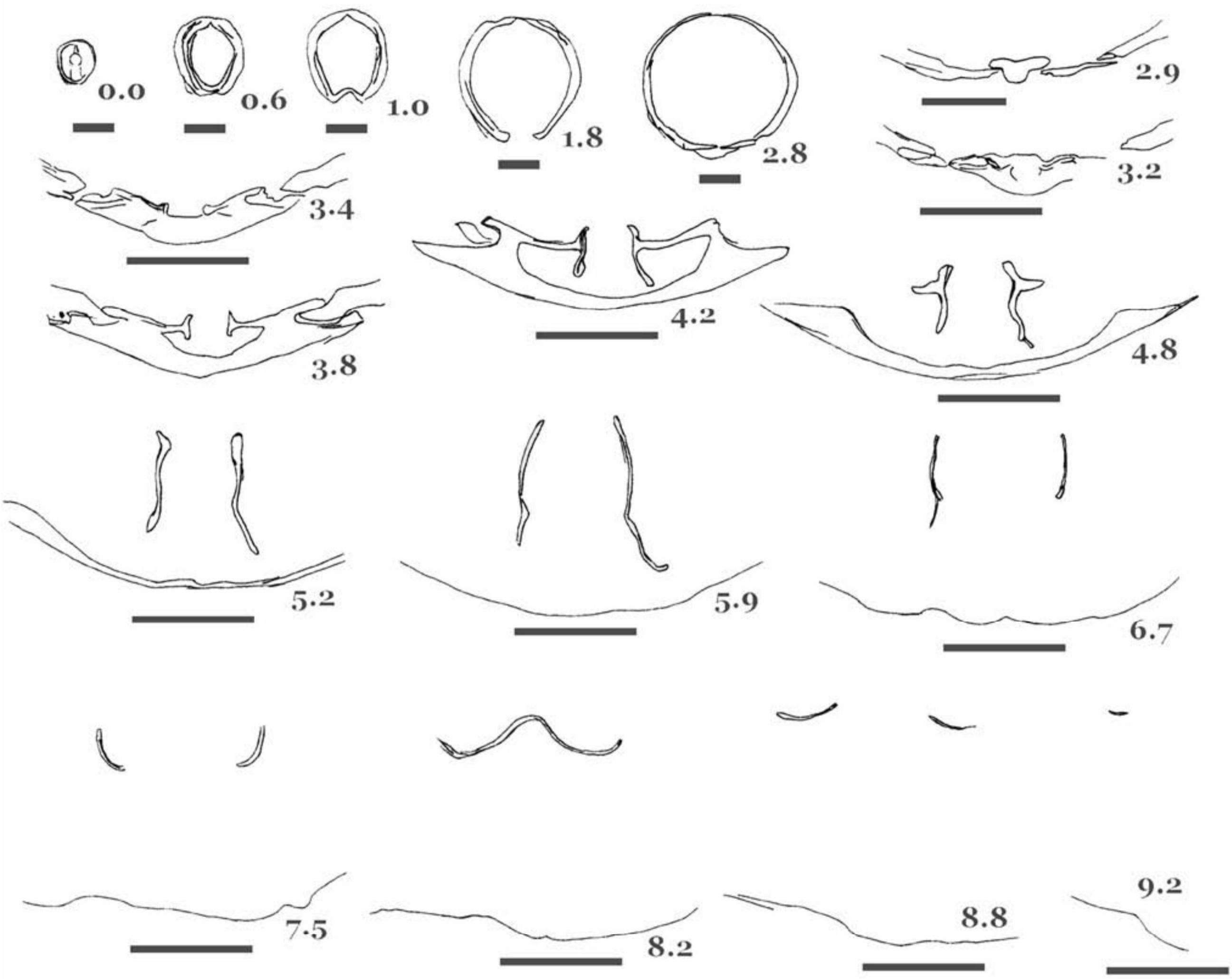


Fig. 3. Serial sections of a specimen of *Placothyris kegeli* n. sp. taken transverse to maximum length. MGUH 27501 (Surlyk colln, locality 6). The following can be seen: pedicle collar (1.0 mm); disjunct deltidial plates (2.8 mm); small, weakly lobed cardinal process (2.9 mm); flat to gently ventrally concave hinge plates (sections 3.4 – 4.2 mm); crura develop approximately at right angles to hinge plates (3.8 mm), dorsal projection becomes greater than ventral (4.2, 4.8 mm); high crural processes (5.9 mm); low-arched transverse band (8.2 mm); flanges of loop traced to 9.2 mm. Dimensions of sectioned specimen: Length 25.0 mm; width 21.8 mm; thickness 13.3 mm. Scale bars under each section: 2 mm.

Genus *Placothyris* Westphal, 1970

Type species. *Terebratula rollieri* Haas, 1893.

Placothyris kegeli n. sp.
Fig. 2K–M, R–T, Fig. 3
Holotype. MGUH 27498, conjoined valves from Brorson Halvø (Surlyk colln).

Type locality. Locality 6, Brorson Halvø, North Wollaston Forland.

Type horizon. Albrechts Bugt Member.

Name. After the late Docent Walter Kegel Christensen in recognition of his significant and substantial contributions to Cretaceous palaeontology and stratigraphy.
Diagnosis. Elongately-oval *Placothyris* species with relatively large pedicle foramen. Internally, crura appear to project both dorsally and ventrally from the earliest growth stages.

Material. 10 specimens (all conjoined valves) from the Albrechts Bugt and Rødryggen members on Stratumbjerg (Alsen and Surlyk collns), Brorson Halvø (Surlyk colln) and Mols Bjerge (Donovan colln).

Description. Exterior. Medium-sized, ventribiconvex valves of elongately oval outline. Anterior commissure rectimarginate. Ventral valve about as wide as long and about 25% as deep as long. Lateral profile weakly convex with maximum curvature at umbones; anterior profile convex medianly with sloping flanks. Dorsal valve about 85% as wide as long and about 15% as deep as long. Both profiles flatly convex. Pedicle foramen, relatively large.

Dorsal interior. A small, weakly lobed cardinal process is present (Fig. 3, section 2.9 mm). Hinge plates are flat to gently ventrally concave (sections 3.4–4.2 mm). The crura develop approximately at right angles to the hinge plates (3.8 mm) and the dorsal projection becomes greater than the ventral (4.2, 4.8 mm). The crural processes are high (5.9 mm) and the W-shape of the transverse band is low-arched (8.2 mm). The flanges of the loop were traced to 9.2 mm.

Ventral interior. Some slight thickening in the extreme posterior of the valve is present (Fig. 3, section 0.0 mm) as part of the pedicle collar (1.0 mm). Deltidial plates are present and are disjunct (2.8 mm). Dental lamellae are absent.

Remarks. The serial sections show dorsally directed crura with small ventral projections, as is typical for *Placothyris*. The related Cretaceous *Gibbithyris* does not show these ventral projections. Dorsally directed crura at the posterior of the loop in *Placothyris* were, however, illustrated by Westphal (1970, fig. 4). In the Greenland specimen this was not observed, the crura appear to project both dorsally and ventrally from the earliest phases. This appears to be the only significant difference between the internal structures of the Greenland and German material and is not considered to be of generic significance.

Boullier (1976) illustrated serial sections of the type species *P. rollieri* and a new species *P. welschi*. The sections of the type species from Oxfordian-age localities in Switzerland (Boullier 1976, fig. 163) and France (Boullier 1976, fig. 165) clearly show the dorsal and ventral projections of the crura from the hinge plates. Serial sections though a specimen of *Placothyris welschi* from the Oxfordian of France (Boullier 1976, fig. 166) shows that the crural plates project dorsally at the posterior of the valve, then project both dorsally and ventrally. This is much in the manner of the sections of *P. rollieri* in Westphal (1970, fig. 4).

It would therefore appear there is some variability in the development of the crura in *Placothyris*, posteriorly they may project dorsally or both ventrally and dorsally; but they do project both ventrally and dorsally through the rest of the loop.

Cooper (1983) discussed the relationship of *Placothyris* to other genera and reiterated Boullier's (1976) contention that *Argovithyris* is closely allied. Sulser (1999) has summarized records of *Placothyris* from the Jurassic.

Range. This new species extends the range of *Placothyris* from the Bathonian–Kimmeridgian of Germany, Switzerland, and France into the Cretaceous of Greenland. It is certainly likely to be ancestral to *Gibbithyris* (Sulser 1999).

Family Pygopidae Muir-Wood, 1965

Genus *Pygope* Link, 1830

Type species. Terebratula antinomia Catullo, 1827.

Pygope janitor (Pictet, 1867)
Fig 2Q

1955 *Pygope* sp. Donovan, p. 21.
1957 *Pygope* sp. Donovan, p. 208.
1967 *Pygope* sp. Ager, p. 137.
1976 *Pygope janitor* (Pictet) - Owen, p. 14, pl. 3, fig. 3.

Remarks. This taxon, one of the most distinctive and remarkable brachiopods, has a widespread distribution within the Tethyan Realm. Donovan's material (see Owen 1976) is supplemented by a near complete dorsal and partial ventral valve from the Albrechts Bugt Member (Surlyk colln, loc. 6, Brorson Halvø).

Genus *Nucleata* Quenstedt, 1868

Type species. Nucleata collina Quenstedt, 1868.

Nucleata sp.

1976 *Nucleata* sp. Owen, p. 15, pl. 1, figs 4a–c.

Remarks. One specimen from Mols Bjerge, Traill Ø was assigned to *Nucleata*. Owen (1976) noted similarities with Upper Jurassic species from France and Austria. Further material was collected in the early 1990s (Surlyk colln) from the Rødryggen Member on Brorson Halvø (locality 6).

Family Dallinidae Beecher, 1893

Genus *Ismenia* King, 1850

Type species. *Terebratulites pectunculoides* von Schlotheim, 1820.

Ismenia tricostata Owen, 1976

1976 *Ismenia tricostata* sp. nov. Owen, p. 16, pl. 3, figs 5a–c.

Remarks. This distinctive taxon is characterized by three strong, deeply-incised dorsal costae together with marked and numerous concentric growth lines. *Ismenia* is rare in Lower Cretaceous rocks; Owen (1976, p. 16) recorded the presence of similar shells in the Barremian rocks of Hildesheim, north Germany.

Genus *Zittelina* Rollier, 1919

Type species. Terebratula orbis Quenstedt, 1858.

Zittelina sp.
1976 '*Zittelina*' sp. Owen, p. 16, pl. 3, figs 1a–c.

Remarks. One damaged specimen from the Falskebugt Member was tentatively assigned to *Zittelina* by Owen (1976) on the basis of its similarities to material, possibly belonging to that genus from France and Austria but previously assigned to *Waldheimia*. No further material of this rare taxon is available.

Genus *Rugitela* Muir-Wood, 1936

Type species. Terebratula bullata J. de C. Sowerby, 1823.

Rugitela hippopus (Roemer, 1840)
Figs 2N–P

1976 ?*Rugitela* sp. Owen, p. 17, pl. 2, fig. 3a–c.

Remarks. Owen (1976) tentatively recorded this genus on the basis of a single specimen from the Wollaston Forland. Several specimens of this distinctive species are now known from Rødryggen (Alsen colln) and Brorson Halvø (Surlyk colln). The features of the umbones and a characteristic concentric ornament together with its similarity to species from the near-coeval Speeton Clay and Claxby Ironstone suggests an assignment to *Rugitela hippopus*.

Biofacies and biogeography

Two mutually exclusive sets of brachiopod assemblages occur in the Lower Cretaceous (Valanginian) strata of North-East Greenland associated with two very different facies. The Falskebugt Member of the Palnatokes Bjerg Formation is dominated by conglomerates and coarse sandstones (Surlyk 1978) and is restricted to the western flank of the Hühnerbjerg Block. These sediments, interpreted as fan deposits (Surlyk 1978), were derived from the crest of the emergent parts of the Hühnerbjerg Block, presumably originating in shallow water. The fauna is dominated by *Lamellaerhynchia rostriformis*, *Praelongithyris borealis* and *Cyrtothyris maynci* (Table 1) and is exclusive to the shallow-water facies of the Falskebugt Member. By contrast the fauna of the Albrechts Bugt and Rødryggen members is dominated by *Lacunosella groenlandica*, *Placothyris kegeli* and *Rugitela hippopus* together with *Pygope janitor*. The brachiopods occur within red and yellow sandy mudstones commonly

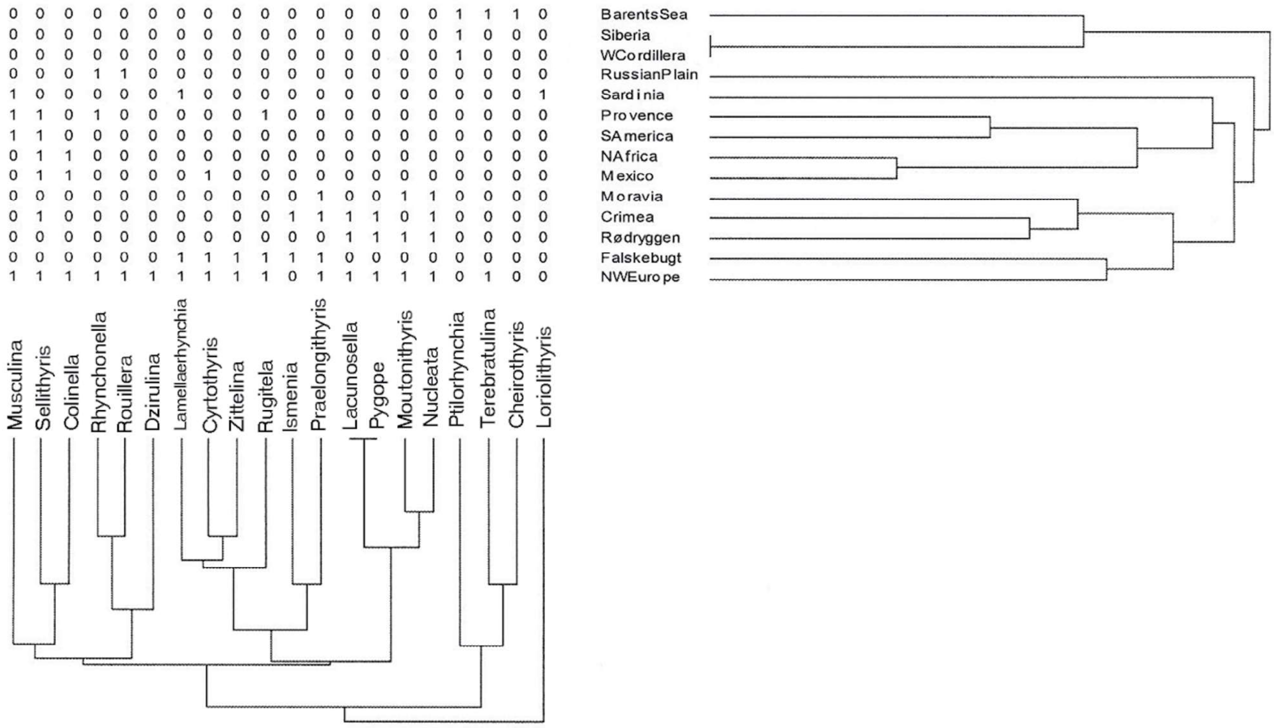


Fig. 4. Q and R-mode dendrogram plot for Early Cretaceous brachiopods generated from the Jaccard index using PAST (Hammer *et al.* 2001). Based on data in Sandy 1991 [Mexico, S and N America, NW Europe, Barents Sea, Siberia, Russian Plain and the W Cordillera] together with Sandy 1986 [Provence, France], Nekvasilova 1980 [Moravia, Czech Republic], Dieni *et al.* 1973 [Sardinia, Italy] and Smirnova 1972 [Crimea, Ukraine].

forming minor shell concentrations in deeper-water environments.

Data have been assembled from a range of Lower Cretaceous localities, globally. The data matrix has been updated from information presented in Sandy (1991). Q and R-mode cluster analysis based on the Jaccard coefficient and generated by PAST (Hammer *et al.* 2001) displays a number of loosely-defined clusters (Fig. 4), suggesting that biogeographical patterns at this time were poorly delineated and a number of sites have inadequate data. Nevertheless a Tethyan cluster comprising, Mexico, North Africa, Sardinia, Provence and South America is clear. The two Greenland faunas have different associates. The Falskebugt fauna is tied to those from NW Europe, whereas Rødryggen is linked to the assemblages from Crimea (Ukraine) and Moravia (Czech Republic). Nonetheless all five form part of the same supercluster suggesting some similarities.

Palaeoecology

Ager (1965) developed a model for the ecological distribution of Mesozoic brachiopods based on the relationship of morphology to environment. In contrast to contemporary models for the distribution of early Palaeozoic brachiopods (e.g. Ziegler 1965), substrate type rather than depth of water was considered a primary controlling factor in the distribution of this part of the post-Palaeozoic epifaunal benthos. The model has been modified, most recently to add seamount (Ager 1993) and chemosynthetic faunas (Sandy 1994). The Falskebugt fauna, dominated by large terebratulids and ribbed rhynchonellids is typical of Ager's shallow-water associations, particularly those on shallow non-depositional seafloors. This type of assemblage is also typical of the Boreal province (Sandy 1991) emphasising the relationship between biogeography and biofacies. By contrast the Albrechts Bugt – Rødryggen fauna contains pygopids together with *Lacunosella* (sulcate, costate in later ontogenetic stages) and *Placothyris* (smooth, rectimarginate), associations more typical of deeper-water environments.

Conclusions

Two distinctive and mutually exclusive brachiopod faunas are confirmed from the Lower Cretaceous rocks of North-East Greenland. The Falskebugt fauna is associated with shallow-water facies and has a Boreal aspect. The Albrechts Bugt - Rødryggen fauna, however, is from deeper-water facies and contains more Tethyan elements. The occurrence of Tethyan elements in North-East Greenland, within the core of the Boreal Province, requires the migration of, presumably, larvae over long distances and suitable environmental conditions to sustain living populations. The migration of these taxa confirms the track of a proto Gulf Stream; their passage north may have been facilitated initially by the presence of seamounts (Ager 1993) along the ridge systems of the low-latitude parts of the North Atlantic. This current together with changing oceanographic conditions (Alsen & Surlyk 2004) provided the means for a significant Out-of-Tethys migration of early Cretaceous brachiopod taxa. Moreover a number of genera, e.g. *Placothyris* and *Pygope*, extended their stratigraphical ranges into these higher latitudes within the Lower Cretaceous, surviving in cooler, partially oligotrophic environments. Such migrations, range extensions and facies shifts add confusion to biogeographical signals during, apparently, an interval of dynamic readjustment of provincial patterns.

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