Upper Palaeozoic bryozoans from the Wandel Sea Basin, North Greenland

Lena Madsen and Eckart Håkansson

Bryozoans constitute a prolific but poorly known faunal element in most of the Upper Palaeozoic strata in North Greenland. Commonly bryozoans are the dominant fossil group, and occasionally their skeletons are rock-forming. Faunistic and taxonomic investigation has established the presence of at least 21 genera, representing all five Palaeozoic orders of Stenolaemata. However, estimates of species diversity cannot be made until completion of a thorough re-evaluation of species concepts in all the groups present.

L. M. & E. H., Institute of Historical Geology and Palaeontology, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.

The presence of bryozoans in this remote part of the Arctic was already established through the first collections brought back from Holm Land and Amdrup Land early in this century by the Danmarks Ekspedition (cf. Grönwall, 1917). Subsequently E. Nielsen of the Dansk Nordøstgrønlands Ekspedition in 1939 collected additional bryozoans from the same sequences (cf. Ross & Ross, 1962), while J. C. Troelsen of the Danish Pearyland Expeditions in 1950 brought back a few specimens from eastern Peary Land (Peel *et al.*, 1974). These authors reported the presence of *Fenestrellina* and *Polypora* from Kronprins Christian Land. However, it was not established how important and widespread bryozoans are in the Upper Palaeozoic sediments of North Greenland until the large scale investigation initiated by the Geological Survey of Greenland (GGU) in 1978.

Locally bryozoans are rock-forming, and commonly account for a substantial proportion of the sediments. All five orders of Palaeozoic Stenolaemata – Trepostomata, Fenestrata, Cystoporata, Cryptostomata and Cyclostomata – may be present in the strata of the Wandel Sea Basin, but their relative abundance is far from equal. Most limestone intervals containing noticeable amounts of bryozoans are dominated by ramose branching colonies of trepostomes, which here attain colony sizes among the largest ever known. The more delicate colonies of fenestrate bryozoans may also be present in the pure limestones, but are particularly abundant in impure, sometimes shaley limestones. Although some strata and regions have received little more than cursory attention, we feel that sufficient information has now been gathered to present an overview of this important fauna.

Geological framework

Upper Palaeozoic deposits in North Greenland are related to two structural entities, the East Greenland – West Norway Rift Basin and the North Greenland – Svalbard Rift Basin, which governed deposition in the early phases of the somewhat loosely defined Wandel Sea Basin (fig 1; Håkansson & Stemmerik, 1989). Depositional environments in the two rift basins are comparable allowing the erection of a lithostratigraphy applicable to both basins (fig. 2; Stemmerik & Håkansson, 1989). Only centrally in the Wandel Sea Basin, where the two rift basins interfere, has this lithostratigraphic correlation not been possible (Håkansson *et al.*, 1989).

Marine accumulation commenced at various times across the basin, between the Lower Moscovian and the Lower Permian (Håkansson & Stemmerik, 1984). Typically the initial phases are characterised by interbedded red-bed sandstones and carbonates with limited fossil contents, and towards the end of the Upper Carboniferous a carbonate platform was established which in the Lower Permian became essentially Pan-Arctic in extent (Håkansson & Stemmerik, 1989). Prolific faunas flourished at various times on this platform, and most of the bryozoan faunas originate from this stage. Later Per-

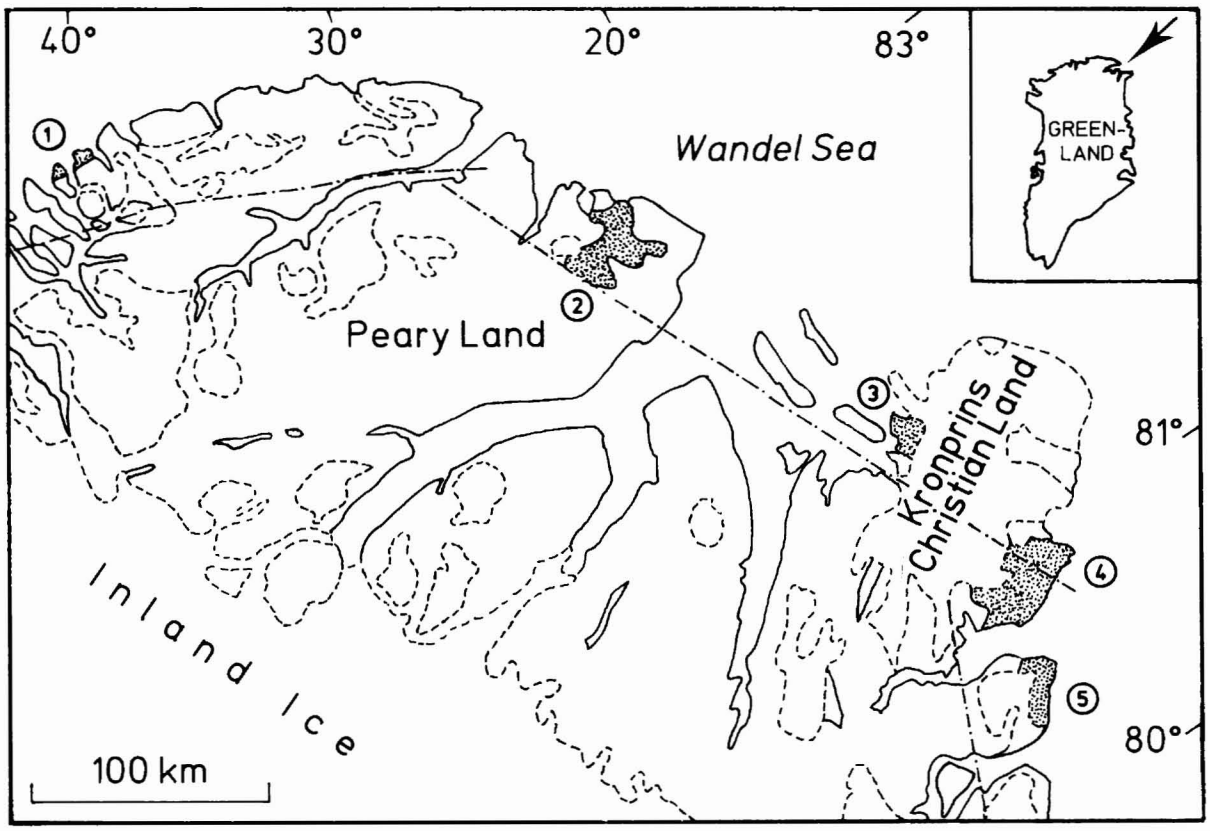

Fig. 1. Distribution of Permo-Carboniferous sediments in the North Greenland Wandel Sea Basin. Fault lines indicate the margins of the rift basins governing deposition during this period. 1, Lockwood Ø area; 2, Kim Fjelde; 3, Prinsesse Ingeborg Halvø; 4, Amdrup Land; 5, Holm Land.

mian deposition has only been preserved in Peary Land and Prinsesse Ingeborg Halvø where a mosaic of carbonate and fine-grained clastic facies contain additional distinctive faunas.

Material and methods

During three GGU expeditions (1978–80) and two subsequent expeditions sponsored by the Carlsberg Foundation (1985 and 1988) large quantities of bryozoan material were collected from Upper Palaeozoic strata throughout eastern North Greenland. In general the bryozoans are well preserved, usually with negligible signs of compression. Diagenetic changes to the skeletons are limited, mostly as irregular chertification in parts of colonies. In a few localities, notably on Prinsesse Ingeborg Halvø, all fossil skeletons have undergone a highly selective diagenesis with light silicification emphasizing colony form and surface features on naturally weathered surfaces.

Determinations of stenolaemate bryozoans are based on a combination of characters derived from both external and internal skeletal features. While determinations at the generic and higher levels are based mainly on qualitative characters, species are typically determined by quantitative methods relying mainly on internal characters (fig. 3). Internal characters are determined from standard petrographic thin sections or acetate peels from polished and etched surfaces, depending on the preservation of the skeleton.

Taxonomic summary

Studies of the North Greenland bryozoan faunas have been very limited; up till now only faunas from Holm Land and Amdrup Land have been subjected to taxonomic treatment where Ross & Ross (1962) described a fauna of 24 taxa including 9 new species in a monograph comprising the following genera: *Rhombotrypella, Tabulipora, Stenopora, Polypora* and *Timanodictya.* The descriptions by Ross & Ross were based entirely on the sparse collections made by dog sledge during the Dan-

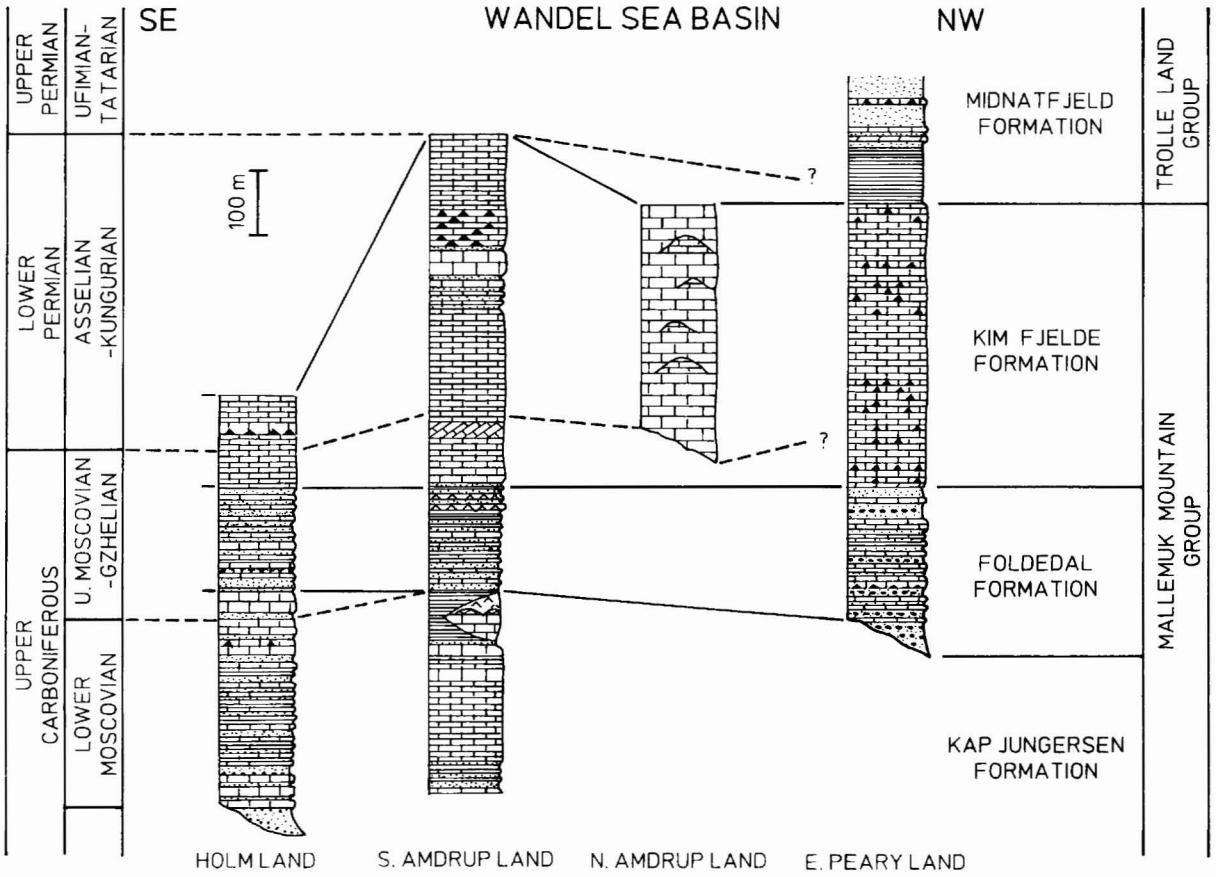

Fig. 2. Stratigraphy and composite lithological sequences from the main regions of the Wandel Sea Basin (based on Stemmerik & Håkansson, 1989).

marks Ekspedition and by the Dansk Nordøstgrønlands Ekspedition. As a result their recognition of taxa is based on very few or, in some cases, only a single specimen. Madsen (1986, 1987) in her studies of the North Greenland faunas has found statistical analysis of quantitative data to be necessary to distinguish at least the trepostome members of these faunas. A thorough investigation of the bryozoan faunas in North Greenland therefore requires a thorough re-evaluation of the fundamental species concepts (Madsen, 1989); hence few taxonomic revisions are attempted here.

Order Trepostomata Ulrich, 1882

Family Stenoporidae Waagen & Wentzel, 1886

Stenoporidae constitutes one of the two most conspicuous bryozoan groups from the Permo-Carboniferous of the Arctic. In North Greenland it is represented by four genera: *Tabulipora* is by far the most widespread and dominant, whereas *Rhombotrypella* and *Amphiporella* are only locally abundant. The nominal genus *Stenopora* Lonsdale, 1844 is rare and has only been identified from the Upper Permian of the Midnatfjeld Formation in eastern Peary Land and the mid-Permian strata of the Kim Fjelde Formation of Amdrup Land.

Tabulipora Young, 1883 (figs 4b, 5b, c) occur most commonly as fragments of ramose colonies (fig. 4 b), while encrusting forms are rare. It is characterized by moniliform exozonal walls, two types of zooids (autozooids and exilazooids), with numerous ringsepta in the autozooidal tubes, and large and small styles in the walls (fig. 5b, c). In transverse section the autozooidal tubes form a polygonal pattern in the endozone (fig. 5b). Branch diameters range between 5 and 35 mm, but specimens up to 70 mm in diameter have been observed in the field, thus ranking these forms among the largest arborescent bryozoans yet known. *Tabulipora* is known from practically all parts of the Mallemuk Mountain Group and the unnamed Permian formations at Prin-

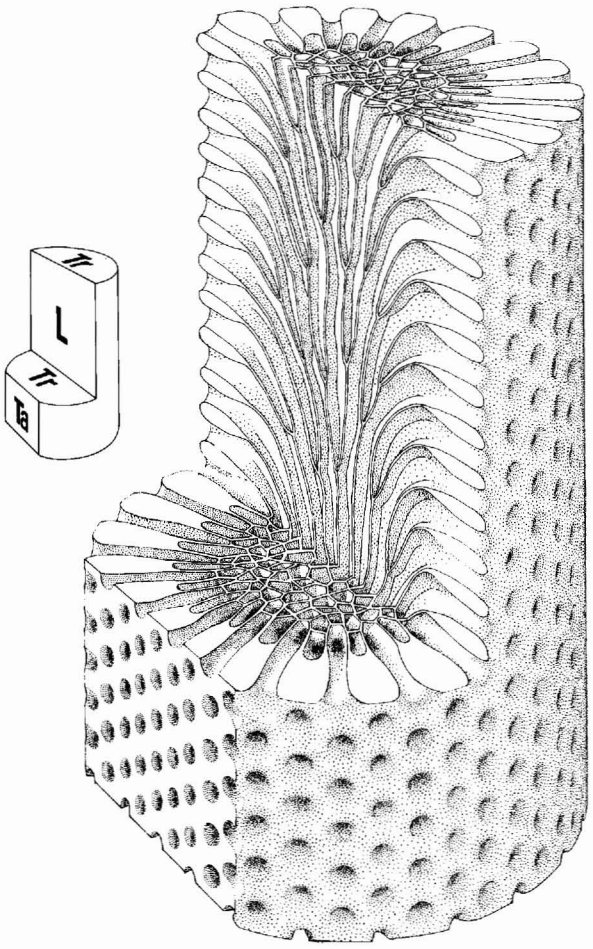

Fig. 3. Cutaway diagram of a ramose trepostome colony showing orientation of standard sections; longitudinal (L) and tangential (Ta) section parallel to the direction of growth, and transverse (Tr) sections perpendicular to this direction.

sesse Ingeborg Halvø. It is particularly abundant and commonly dominant in the higher levels of the Kim Fjelde Formation in Lockwood Ø, eastern Peary Land and southern Amdrup Land.

The similarly branching, very closely related genus *Rhombotrypella* Nikiforova, 1933 was separated from *Tabulipora* solely on the basis of the quadrate to rhombic cross-section of the zooecial tubes in the endozone (fig. 5a). However, investigation of numerous specimens from the North Greenland faunas has indicated that the organization level of the zooecial budding pattern here may show a complete range of patterns from polygonal to quadrate/rhombic within a single colony fragment (Madsen, 1986; 1987). In order to assign a given specimen to the genus *Rhombotrypella* rather than *Tabulipora* it is, therefore, necessary to make repetitive transverse sections within the specimen in order to establish whether its budding pattern is persistent (cf. Boardman & McKinney, 1976).

A preliminary study of the type specimens of the previously described *Rhombotrypella* species from Holm Land and Amdrup Land (cf. Ross & Ross, 1962) has shown that none of the holotypes possess the basic distinguishing character of having a persistent quadrate/rhombic budding pattern. Accordingly these taxa should be assigned to the genus *Tabulipora*. However, two of the syntypes of *R. mallemukensis* (MMUH nos 9117 and 9145) differ from the holotype in having a consistently rhombic pattern throughout the length of the branches (fig. 5a). Thus they belong to a distinct taxon which is retained within *Rhombotrypella*.

So far the presence of *Rhombotrypella* has been established only in the Upper Carboniferous Foldedal Formation in Holm Land and the unnamed Permian formations on Prinsesse Ingeborg Halvø (cf. Håkansson *et al.*, 1989).

In order to define and distinguish the numerous species referred to the genera *Tabulipora* and *Rhombotrypella* in North Greenland by Ross & Ross (1962), one population from the top of the Kim Fjelde Formation in southern Amdrup Land (GGU 220675) was subjected to a detailed statistical analysis of a series of quantitative characters. This study showed that the variability of the characters traditionally used in species definitions is immense, and in fact the variation found in this single population (39 specimens) encompasses the variation found in most of the new species described by Ross & Ross (1962) (Madsen, 1986, 1987). As pointed out above it is, therefore, imperative to examine a statistically significant population in order to establish any new species within this group; work on additional populations from North Greenland, East Greenland and Svalbard is in progress (Madsen, unpublished).

Amphiporella Girty, 1911 (fig. 4a) by original definition is distinguished from *Tabulipora* only by growth form, with the colonies forming flat, frondose branches and expanses. In general, colony shape or growth form is considered to be of limited use as a taxonomic character in bryozoans. In complete accord with this tradition Astrova (1978) and Morozova & Kruchinina (1986), in the most recent monographic accounts of the Trepostomata, list *Amphiporella* as a junior synonym of *Tabulipora*. Astrova (1978) simply included flat frondose growth forms in the genus description, although this growth form is not otherwise known in *Tabulipora* (cf. Gautier, 1970).

In the North Greenland fauna, however, a large num-

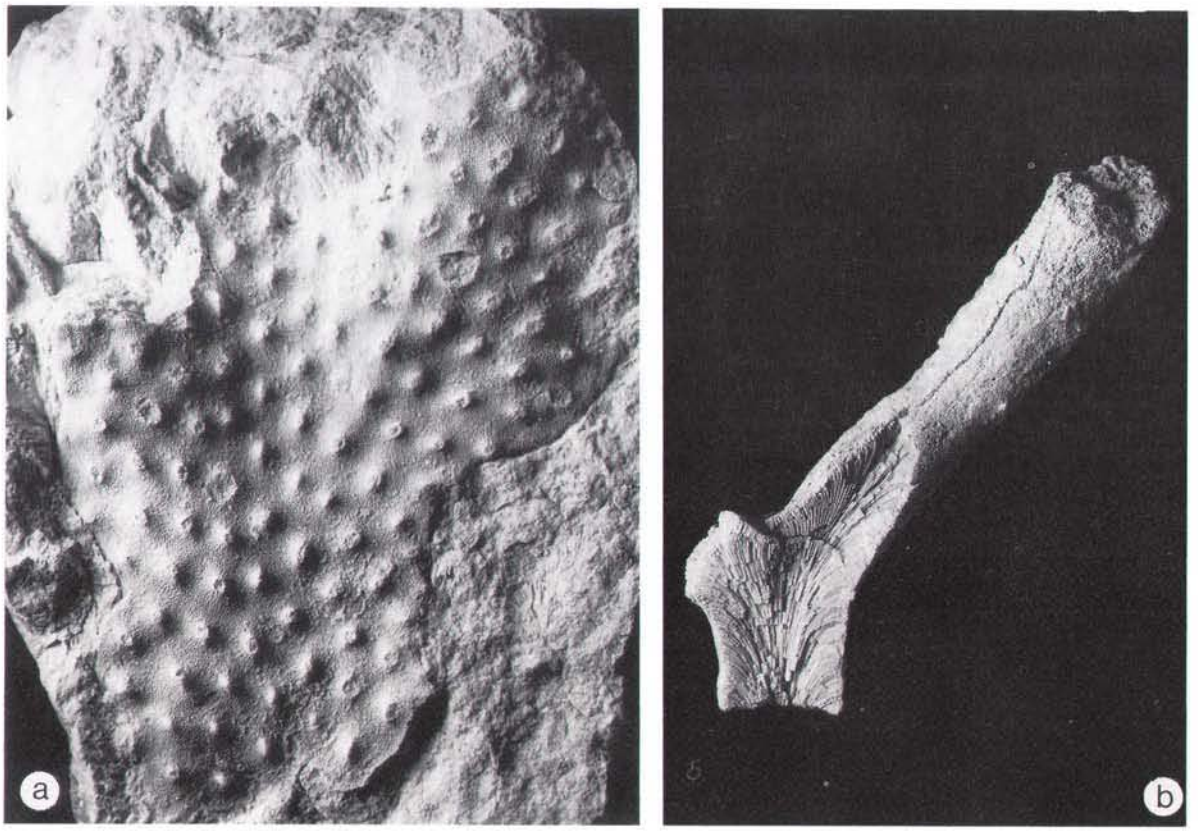

Fig. 4. a. *Amphiporella* sp. Fragment of a flat, frondose colony. Note the regularly spaced maculae. (MGUH 19498 from GGU 220661–1, Kim Fjelde Formation, Amdrup Land.) b. *Tabulipora* sp. Fragment of a ramose colony. In the partly broken proximal region the internal architecture is clearly discernible. (MGUH 19499 from GGU 220667–28, Kim Fjelde Formation, Amdrup Land.) Both specimens nat. size.

ber of ordinary cylindrical fragments of *Tabulipora* coexist with flat frondose fragments without intermediate growth forms in a fairly narrow stratigraphic interval in the top of the Kim Fjelde Formation in eastern Peary Land and southern Amdrup Land. It therefore seems warranted to attach some taxonomic significance to the growth form in this particular instance. Whether growth form by itself is sufficient to justify a distinction at the generic level is less obvious. Inspection of thin sections prepared from the original type suite of *Amphiporella* (kept in the National Museum of Natural History, Washington, D.C. under the numbers USNM 153110, 153111 & 153115) reveals a high degree of similarity in the internal structure between *A. maculosa* Girty, the type species, and the North Greenland specimens. For the time being, we therefore feel it justifiable to maintain the genus *Amphiporella* as a seperate entity. Further work is necessary in order to ascertain whether the internal characters are indeed distinctive.

Amphiporella from North Greenland is characterized by having well developed maculae (fig. 4a), and specimens from Peary Land, in particular, form very large flat frondose expanses, with fragments up to 11 × 17 cm present in the collections.

Family Dyscritellidae Dunaeva & Morozova, 1967

Only one genus, *Dyscritella* Girty, 1911 (fig. 6), has been determined from North Greenland. It consistently forms arborescent colonies, with branch diameters ranging between 6 and 16 mm. The genus is characterized by having evenly thickened walls in the exozone with very few diaphragms, numerous exilazooecia, and large styles (fig. 6b). A transverse section of the endozone shows a very characteristic polygonal stellate pattern (fig. 6a). *Dyscritella* is common in many parts of the Kim Fjelde Formation, where it is usually associated with other trepostome colonies, but in the unnamed Permian formations at Prinsesse Ingeborg Halvø *Dys-*

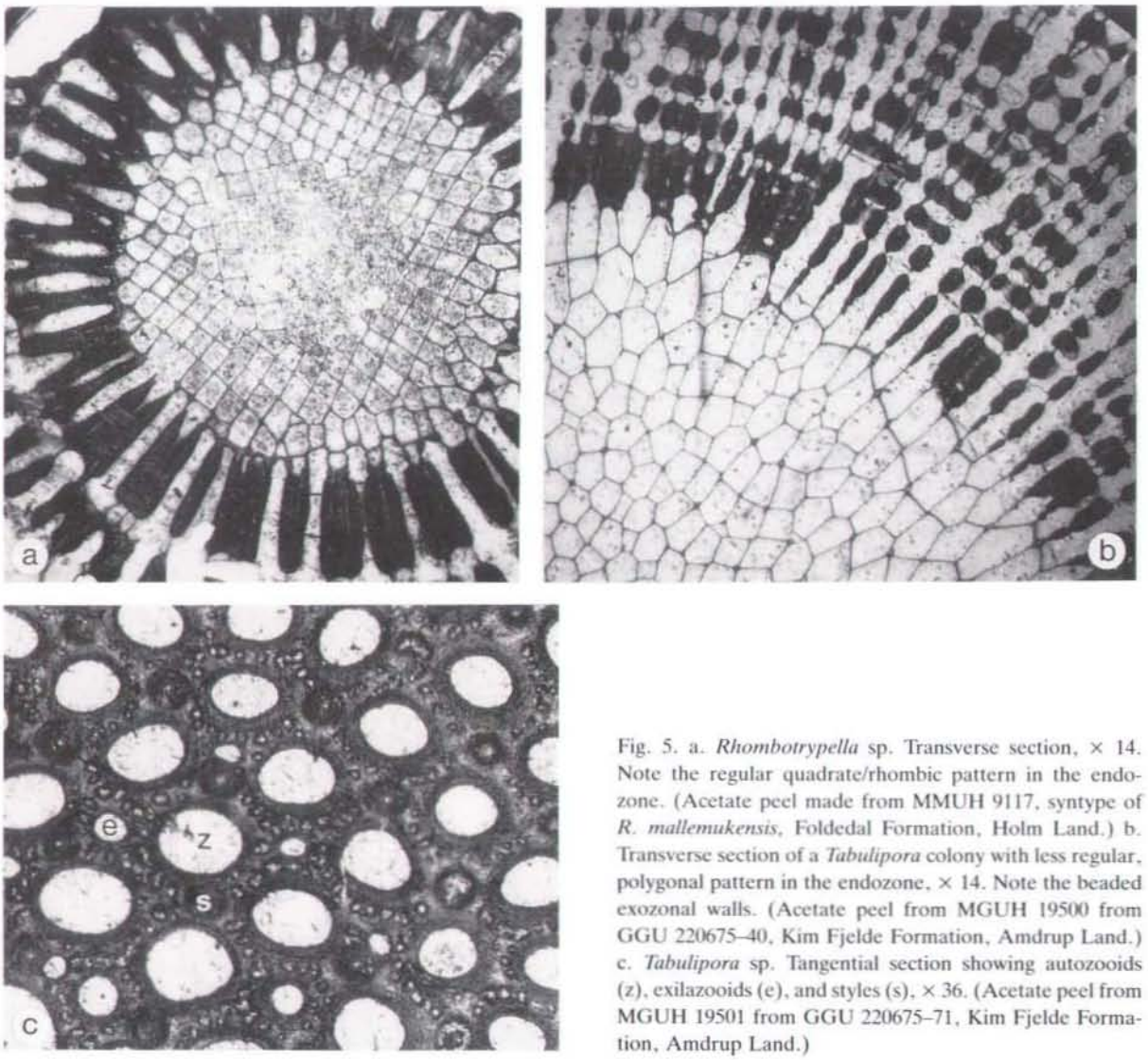

Fig. 5. a. *Rhombotrypella* sp. Transverse section, × 14. Note the regular quadrate/rhombic pattern in the endozone. (Acetate peel made from MMUH 9117, syntype of *R. mallemukensis*, Foldedal Formation, Holm Land.) b. Transverse section of a *Tabulipora* colony with less regular, polygonal pattern in the endozone, × 14. Note the beaded exozonal walls. (Acetate peel from MGUH 19500 from GGU 220675–40, Kim Fjelde Formation, Amdrup Land.) c. *Tabulipora* sp. Tangential section showing autozooids (z), exilazooids (e), and styles (s), × 36. (Acetate peel from MGUH 19501 from GGU 220675–71, Kim Fjelde Formation, Amdrup Land.)

critella is the only bryozoan present in some of the shaley intervals (Håkansson *et al.*, 1989).

Order Cystoporata Astrova, 1964

The order is recognized mainly by the very characteristic vesiculate internal structure of the skeleton. Four genera have so far been identified from North Greenland.

Family Fistuliporidae Ulrich, 1882

Fistulipora McCoy, 1850 (fig. 7) forms fairly irregular ramose branching colonies of considerable size, or encrusting colonies on some of the large trepostome colonies. Characteristic of this genus is that the autozooecia, which contain lunaria and abundant diaphragms, are separated completely by vesicular tissue both in exozone and endozone. All colonies have well developed maculae. *Fistulipora* is particularly abundant in the highest levels of the Kim Fjelde Formation in southern Amdrup Land.

Family Goniocladiidae Waagen & Pichl, 1885

Goniocladia Etheridge, 1876 (fig. 8) is readily recognized by its very characteristic growth form, with irregularly anastomosing to coarsly reticulate branches forming large polygonal fenestrules. The branches have a bifoliate symmetry with autozooids opening on both

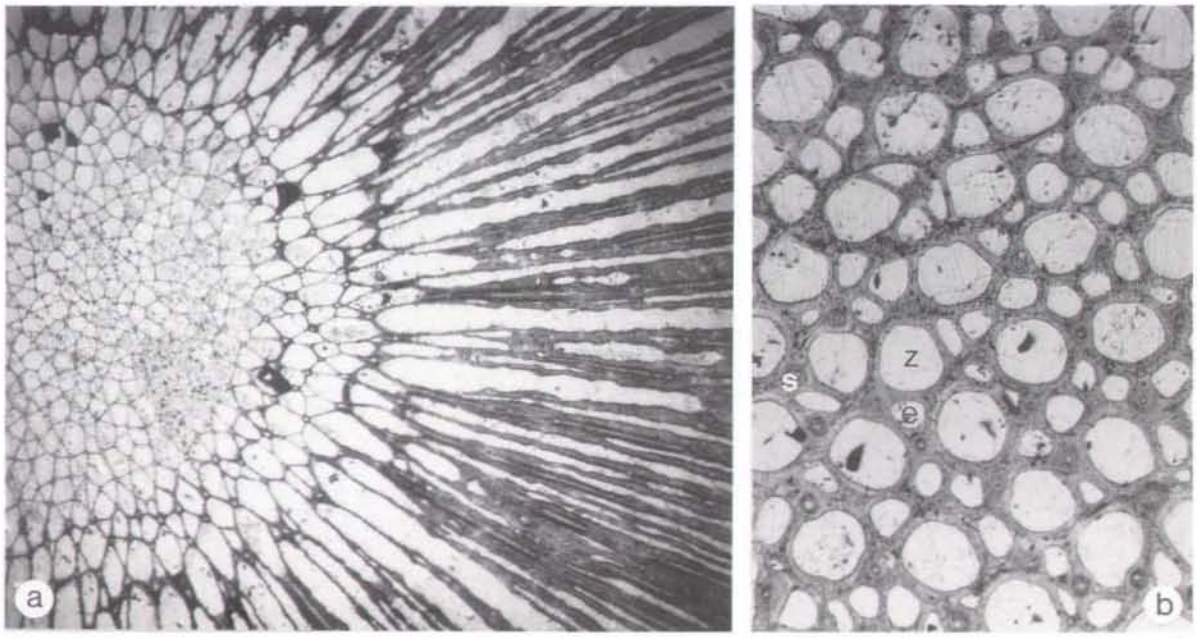

Fig. 6. *Dyscritella* sp. a. Transverse section with characteristic stellate pattern in the endozone and a very prominent, even-walled exozone, × 14. (Acetate peel from MGUH 19502 from GGU 220675–9, Kim Fjelde Formation, Amdrup Land.) b. Tangential section showing autozooids (z), exilazooids (e), and styles (s), × 36. (Acetate peel from MGUH 19503 from GGU 220675–29, Kim Fjelde Formation, Amdrup Land.)

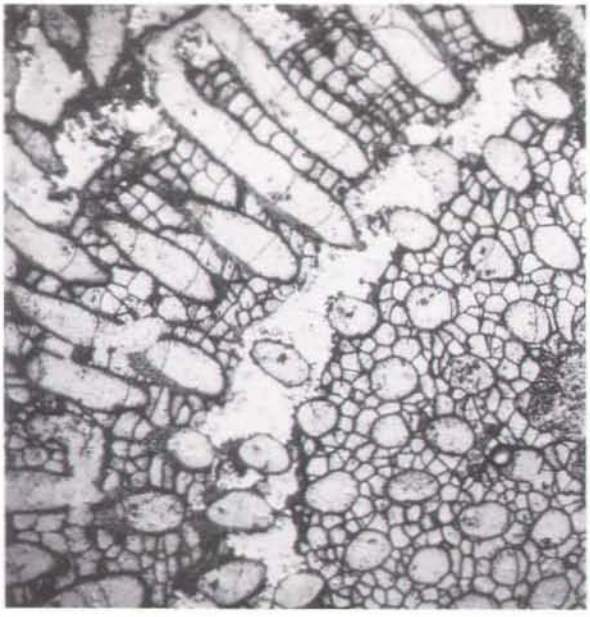

Fig. 7. *Fistulipora* sp. Transverse section with the characteristic vesiculate structure between autozooids in both endo- and exozone, × 14. The structureless area across the center represents chertified skeleton. (Acetate peel from MGUH 19504 from GGU 220675–33, Kim Fjelde Formation, Amdrup Land.)

sides of the branches into the fenestrules. The genus is a very conspicuous faunal element at some levels in the higher parts of the unnamed Permian formations at Prinsesse Ingeborg Halvø (Håkansson *et al.*, 1989), and has been recognized from the uppermost part of Kim Fjelde Formation of southern Amdrup Land and Peary Land.

Colonies with strong affinity to *Goniocladiella* Nekhoroshev, 1953 (fig. 9) are abundant in the uppermost part of the unnamed Permian formations of Prinsesse Ingeborg Halvø. The colonies have main branches with oblique side branches fusing to form fronds with polygonal fenestrules. Each branch has a bifoliate symmetry with several rows of autozooecial openings on both sides of the branch.

Ramipora Toula, 1875 has a similar bifoliate symmetry, but has main branches with second and third order branches which occasionally fuse and thereby form large polygonal fenestrules. So far it has only been reported from thin sections.

Order Cryptostomata Vine, 1884

Bryozoans belonging to this order are mainly very delicate ramose colonies. Most specimens can be assigned to the suborder Rhabdomesina Astrova & Moro-

Fig. 8. *Goniocladia* sp. Fragment of a lightly silicified colony on a naturally weathered rock surface, × 1.8. (From MGUH 19505 from GCI 72101, unnamed Permian formation, Prinsesse Ingeborg Halvø.)

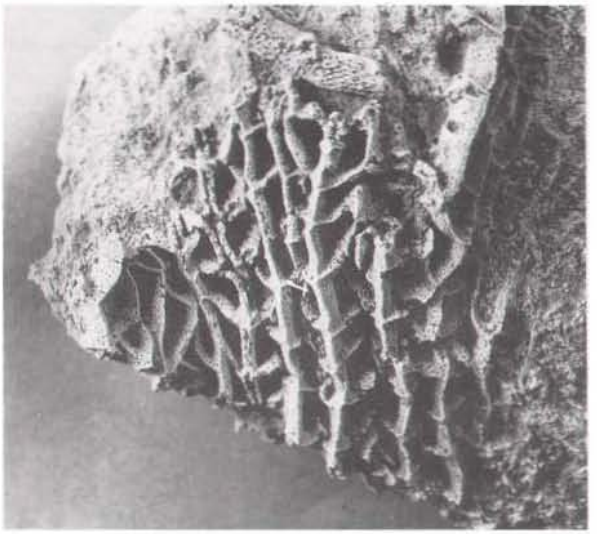

Fig. 9. *Goniocladiella* sp. Fragment of a lightly silicified colony on a naturally weathered rock surface, × 1.8. (From MGUH 19506 from GCI 72178, unnamed Permian formation, Prinsesse Ingeborg Halvø.)

zova, 1956, but due to the minute colony size in most of these taxa, this part of the fauna has so far not been studied in any detail.

Family Timanodictyidae Morozova, 1966

One genus, *Timanodictya* Nikiforova, 1938 has been identified from the higher parts of the unnamed Permian formations of Prinsesse Ingeborg Halvø. Unlike most cryptostomes these forms have fairly large ramose colonies with cross sections of branches showing lenticular outline and bifoliate symmetry.

Order Fenestrata Elias & Condra, 1957

Fenestrate colonies constitute the second important faunal element among the North Greenland bryozoans. They are seen to be rock-forming in the higher parts of the sequence at Prinsesse Ingeborg Halvø (fig. 10) and at some levels of the Midnatfjeld Formation in Peary Land. Bryozoans of the order Fenestrata form delicate, often funnel-shaped colonies, either reticulate or pinnate, where branches are commonly joined by dissepiments leaving open spaces (fenestrules). All types are characterized by having an obverse surface with autozooidal apertures and a reverse surface without apertures. The majority of the North Greenland fenestrate bryozoans probably belong to the genera *Polypora* McCoy, 1844 and *Fenestella* Lonsdale, 1839. Both genera form colonies where the branches have rows of autozooecia, in *Fenestella* 2 rows and in *Polypora* 3 or more, joined by dissepiments without zooecia. Other genera identified are *Ptylopora* McCoy, 1844 which has a strong main stem and long oblique side branches joined by thin dissepiments, and *Penniretepora* d'Orbigny, 1849 with a slender main stem, short oblique side branches without dissepiments and only 2 rows of autozooecia on the branches. *Fenestrellina* d'Orbigny, 1849 has an open meshwork like *Fenestella* but with very long fenestrules. *Acanthocladia* King, 1849 has coarse branches with closely spaced short oblique side branches and 3 or more rows of autozooecia on each branch. *Lyropora* Hall, 1857 forms incomplete funnel-shaped colonies with thickened edges.

Order Cyclostomata Busk, 1852

So far only a few specimens of an encrusting form with possible cyclostome affinity (fig. 11) have been found in the uppermost, mid-Permian part of the Kim Fjelde Formation in southern Amdrup Land. From the growth form and other external characters these specimens could be related to both the Devonian cystoporate family Botrylloporidae and the otherwise entirely post-Palaeozoic cyclostome family Lichenoporidae. In the apparent lack of the most distinctive internal cystoporate characters – vesicles and lunaria – a cyclostome

Fig. 10. Fragments of various lightly silicified fenestrate colonies covering a naturally weathered rock surface, × 1.2. (From MGUH 19507 from GCI 72196, unnamed Permian formation, Prinsesse Ingeborg Halvø.)

affinity is considered more likely. However, in view of the probable polyphyletic nature of the Cyclostomata (Boardman, 1984) limited conclusions can be drawn from the very restricted material available. Cyclostome bryozoans are altogether exceedingly rare in Late Palaeozoic strata with only a few species formally described (Taylor, 1985).

Fig. 11. Discoid (?) cyclostome colonies encrusting a *Tabulipora* colony, × 4.7. (On MGUH 19508 from GGU 220675–66, Kim Fjelde Formation, Amdrup Land.)

Acknowledgements. The Geological Survey of Greenland and the Carlsberg Foundation surported the field work during several expeditions to North Greenland, and we are grateful to our colleagues from these expeditions who have helped collect the material. Jan Aagaard, Henrik Egelund and René Madsen are thanked for technical assistance. Specimen and collection numbers refer to the following institutions: GGU, Geological Survey of Greenland; GCI, Geological Central Institute, University of Copenhagen; MMUH, MGUH, Geological Museum Copenhagen.

References

Astrova, G. G. 1978: History and development, system, and phylogeny of Bryozoa. Order Trepostomata. *Trudy Paleont. Inst.* **169,** 193 pp. (in Russian).

Boardman, R. S. 1984: Origin of the post-Triassic Stenolaemata (Bryozoa): A taxonomic oversight. *J. Paleont.* **58,** 19–39.

Boardman, R. S. & McKinney, F. K. 1976: Skeletal architecture and preserved organs of four-sided zooids in convergent genera of Paleozoic Trepostomata (Bryozoa). *J. Paleont.* **50,** 25–78.

Gautier, T. G. 1970: Interpretive morphology and taxonomy of bryozoan genus *Tabulipora*. *Kansas University Paleont. Contr. Pap.* **48,** 21 pp.

Grönwall, K. G. 1917: The marine Carboniferous of North-East Greenland and its brachiopod fauna. *Meddr Grønland* **43**(20), 110 pp.

Håkansson, E. & Stemmerik, L. 1984: Wandel Sea Basin – the North Greenland equivalent to Svalbard and the Barents Shelf. *In* Spencer, A. M. *et al.* (edit.) *Petroleum geology of the North European margin,* 97–107. Graham & Trotman, Norwegian Petroleum Society.

Håkansson, E. & Stemmerik, L. 1989: Wandel Sea Basin – a new synthesis of the Late Paleozoic to Tertiary accumulation in North Greenland. *Geology* **17,** 683–686.

Håkansson, E., Madsen, L. & Pedersen, S. A. S., 1989: Geological investigations of Prinsesse Ingeborg Halvø, eastern North Greenland. *Rapp. Grønlands Geol. Unders.* **145,** 113–118.

Madsen, L. 1986: Variational range of some trepostome bryozoans. International Bryozoology Association, 7th International Conference. Abstracts, 1p.

Madsen, L. 1987: Taxonomy, variability and functional morphology of the Tabulipora group from the Late Paleozoic of North Greenland. Unpublished thesis, University of Copenhagen, 111 pp.

Madsen, L. 1989: The species concept in trepostome bryozoans – a discussion based on the variability of morphological characters. International Bryozoology Association, 8th Int. Conf., Paris, Abstracts Volume, 30 only.

Morozova, I. P. & Kruchinina, O. N. 1986: *[The Permian bryozoans of the Arctic region (Western sector).]* Moscow: Nauka. Press, 144 pp. (in Russian).

Peel, J. S., Dawes, P. R. & Troelsen, J. C. 1974: Notes on some Lower Palaeozoic to Tertiary faunas from eastern North Greenland. *Rapp. Grønlands geol. Unders.* **65,** 18–23.

Ross, J. P. & Ross, C. A. 1962: Faunas and correlation of the Late Paleozoic rocks of Northeast Greenland. Part 4, Bryozoa. *Meddr Grønland* **167**(7), 65 pp.

Stemmerik, L. & Håkansson, E. 1989: Stratigraphy and depositional history of the Upper Palaeozoic and Triassic sediments in the Wandel Sea Basin, eastern North Greenland. *Rapp. Grønlands geol. Unders.* **143.**

Taylor, P. D. 1985: Carboniferous and Permian species of the cyclostome bryozoan *Corynotrypa* Bassler, 1911 and their clonal propagation. *Bull. Br. Mus. nat. Hist. (Geol.)* **38**(5), 359–372.