Environmental distribution of bryozoans in the Permian of Spitsbergen

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Abstract
Bryozoans are abundant faunal constituents in the shallow water, subtropical through cooler, more open marine Permian succession of Spitsbergen. Trends in preferred habitat for delicate and robust vinculariiform and reteporiform bryozoans, as well as generic distribution through a series of well-known sedimentary facies types, are recorded. The early Permian quiet shallow marine environment contained thin branched vinculariiform trepostomes and cryptostomes, and varied delicate pinnate and fenestrate bryozoans, but only rare colonies in the palaeoaplysinid bioherms. Overlying nearshore high-energy bioclastic barrier deposits contained the richest faunas with thick ramose and encrusting trepostomes and cystoporates and robust fenestrates. More offshore platform spiculitic shales also contained robust trepostomes and delicate fenestrates, whereas open platform carbonates contained varied delicate and robust trepostomes and robust fenestrates. These environmental distributions are generally in accord with previously published patterns.

Keywords: Bryozoa, depositional environments, palaeoecology, Permian, Spitsbergen.

Introduction
Large quantities of bryozoans have been collected during three expeditions to Svalbard, most of them from NW central Spitsbergen. The growth forms and taxonomic compositions of these bryozoan faunas have been analysed in the light of the changing depositional environments interpreted from field observations, laboratory analyses and literature sources. Many outcrops have been analysed, providing a better understanding of the lateral distribution of bryozoan faunas and environmental patterns.

Several papers are devoted to palaeoecological, sedimentological and microfacies analyses of the Permian in Spitsbergen (Siedlecka 1970, Malkowski & Hoffman 1979, Lauritzen 1981, Malkowski 1982, Skaug *et al.* 1982), and there are also several unpublished theses (e.g. Hellem 1981, Lønøy 1981, Skaug 1982, Sundsbø 1982, Dons 1983, Fredriksen 1988, Henriksen 1988); interpretations based on these sources have been used for the depositional reconstructions.

Depositional environments
The Permian succession in western and central Spitsbergen is divided into two major lithostratigraphic units: the Middle Carboniferous–late Early Permian Gipsdalen Group, and the Kungurian(?) to Kazanian(?) Tempelfjorden Group. These two lithological groups were deposited under significantly different conditions, and they are treated separately with regards to bryozoan occurrences. Bryozoans are more common in the upper group and more time has been spent collecting from this unit; this younger fauna is therefore better known. Brief descriptions and comments on the stratigraphical distribution of bryozoans through these units were presented by Nakrem (1991); unit definitions and ages are from Cutbill & Challinor (1965), in part revised in Nakrem *et al.* (1992). Large-scale palaeogeography is adapted from Steel & Worsley (1984). Data from these sources are used subsequently unless otherwise stated.

Environmental controls on bryozoan distribution
Several attempts have been made to describe the correlation between zoarial form and depositional environment, many of them based on the early work by Stach (1936). Faunal models resembling those from Spitsbergen were applied by, for example, Duncan (1969), McKinney & Gault (1980), Kelly & Horowitz (1987) and McKinney & Jackson (1989) for the Carboniferous and Permian of North America. In the present work, vinculariiform (erect sub-cylindrical, with thin and delicate or thick and robust branches), reteporiform (fenestrate), adeoniform (erect bifoliate) and membraniporiform (uni- and multilamellar encrusting) growth forms have been found. Branch diameters of vinculariiform zoaria (cystoporates, trepostomes and cryptostomes), the strength of fenestrate bryozoans (robust forms with small fenestrules and thick branches versus delicate forms with large fenestrules and thin branches), as well as the distribution of bryozoan genera through each depositional unit were recorded. It should be noted that the approach in the current study is to map bryozoans in well-understood depositional sequences, not to infer depositional environments from the bryozoan faunas present.

Rigid statistical analyses could not be carried out as all samples were collected specifically for bryozoans, and the co-existing biota can only be discussed qualitatively.

However, simple calculations, and clustering of depositional units based on presence/absence of bryozoan genera gave some indications of environmental associations. As has been previously suggested (e.g. McKinney & Jackson 1989) water movement ('water energy') is not the only restricting factor; other factors (e.g. nutrients, light, suspended matter) are not, however, considered in the present work.

The Gipsdalen Group

This group is characterized by carbonates deposited under warm conditions (subtropical, palaeolatitude 30-35°N) with fluctuating sea levels resulting in deposition of nearshore, lagoonal and restricted to open marine shallow platform sediments, including an evaporitic unit (the Gipshuken Formation) as well as palaeoaplysinid biohermal build-ups.

The Late Carboniferous interval consists of carbonates with some minor clastics. The fauna is characterized by abundant brachiopods, corals and fragmented crinoids, with fewer bryozoans. The Carboniferous–Permian transition is considered to represent the shallowest, most nearshore environment (mixed clastic/carbonate, Figure 1B). This nearshore environment was sheltered from the open sea (but probably not closed off) by biohermal build-ups, and water energy was probably not high. Clastics mixed with carbonates here and higher in the unit indicate terrigenous input from sources not far away.

The low diversity bryozoan fauna consists of delicate vinculariiform zoaria (*Ascopora* and *Rhombotrypella*), reteporiform and pinnate fenestrates. Abraded zoaria of *Archimedes*, one specimen encrusted by a trepostome, were found in slightly deeper, yet well-ventilated lagoonal deposits devoid of clastics.

Lagoonal facies developed between several episodes of minor sea-level fluctuations, and at times contact with the open sea was closed off and low oxic or anoxic conditions prevailed (Skaug *et al.* 1982). This superhaline environment contained

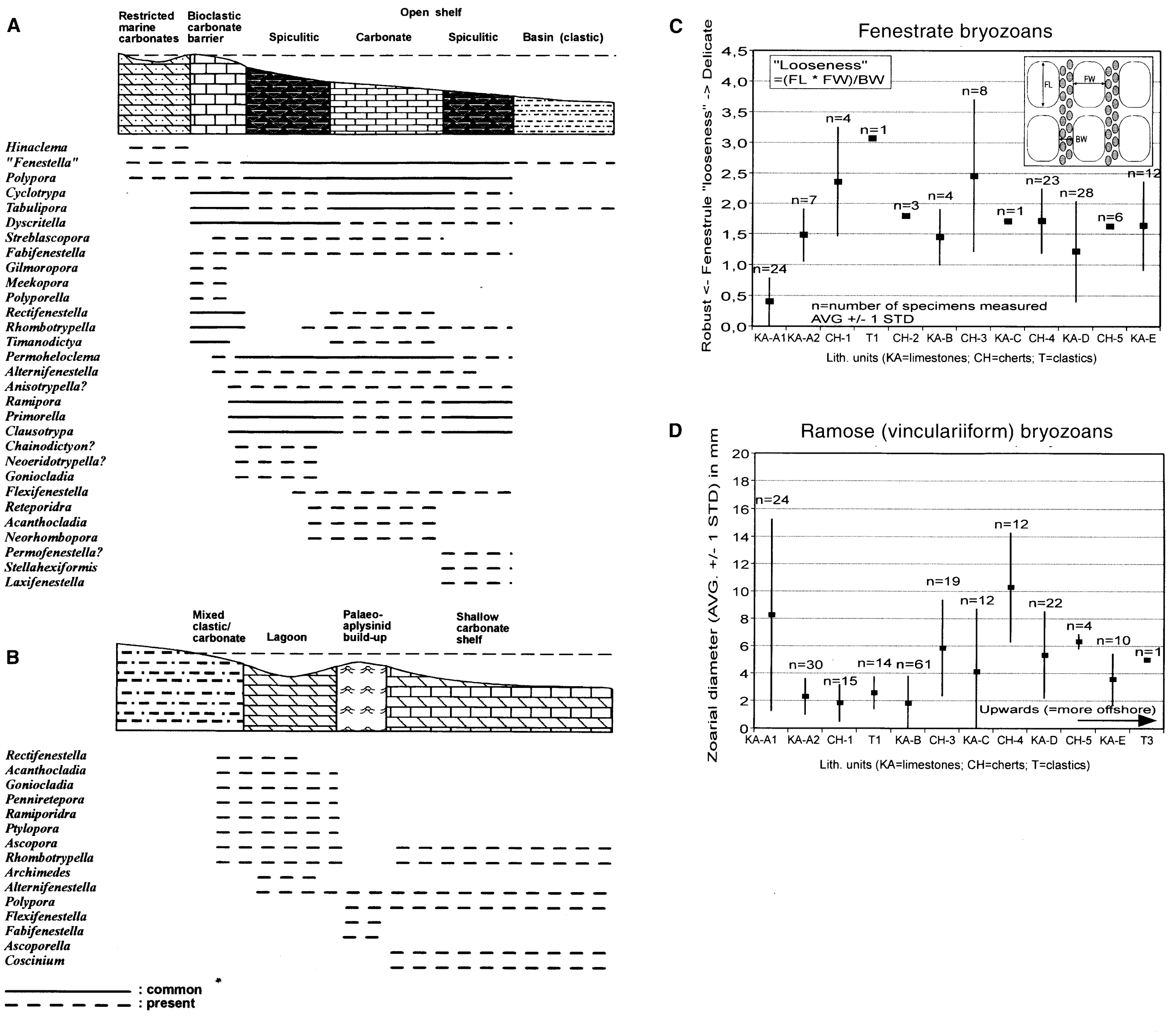

Figure 1.
A, facies belts and distribution of bryozoan genera, uppermost Gipsdalen Group (restricted marine carbonates) and Tempelfjorden Group;
B, facies belts and distribution of bryozoan genera, Gipsdalen Group;
C, calculated fenestrate 'looseness' plotted against lithological units of the Kapp Starostin Formation at Akseløya;
D, branch thickness of vinculariiform bryozoans plotted against lithological units of the Kapp Starostin Formation at Akseløya.

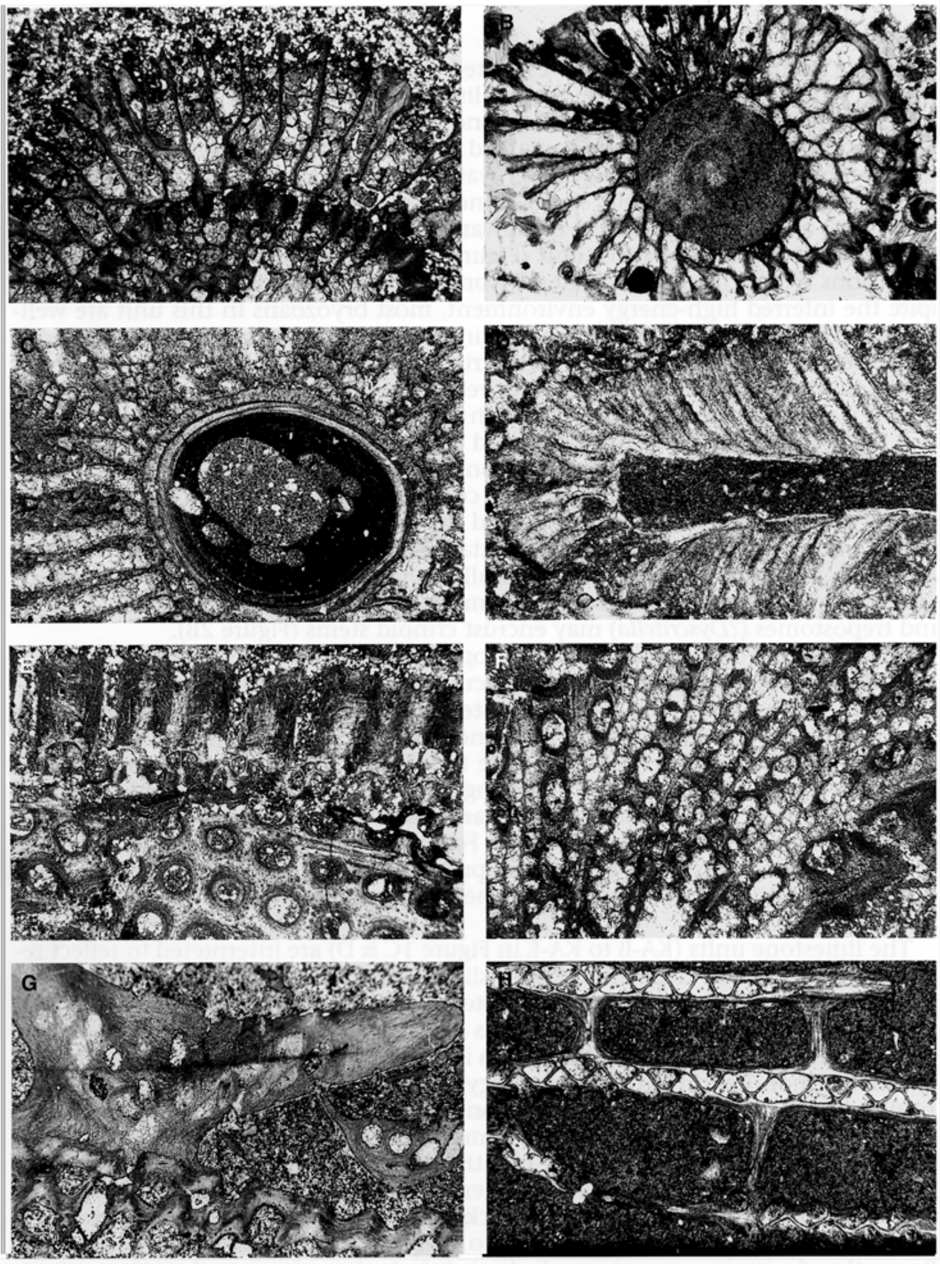

Figure 2.
A, ?*Dyscritella* encrusting *Tabulipora*, Kapp Starostin Formation, Akseløya, unit KA-A2, ×15, PMO 132.063/2;
B, ?*Dyscritella* encrusting crinoid stem, Kapp Starostin Formation, Kapp Wærn, unit KA-A1, ×15, PMO A42271;
C, *Cyclotrypa* encrusting a bored brachiopod spine, Kapp Starostin Formation, Akseløya, unit KA-A1, ×15, PMO 118-081/4A;
D, ?*Hinaclema* encrusting decayed substrate (?algal stem), Gipshuken Formation, Rejmyrefjellet, ×37.5, PMO A42600;
E, robust fenestellid, transverse and reverse tangential section, Kapp Starostin Formation, Akseløya, unit KA-A1, ×15, PMO 118.053;
F, robust *Rectifenestella*, Kapp Starostin Formation, Akseløya, unit KA-A1, ×15, PMO A42658;
G, fenestrate attached to trepostome bryozoan, Kapp Starostin Formation, Akseløya, unit CH-4, ×15, PMO 132.024/2;
H, delicate *Alternifenestella*, Kapp Starostin Formation, Kapp Wijk, unit CH-1, ×15, PMO A42631.
All specimens are in the collections of the Paleontologisk Museum, Oslo (abbreviation: PMO).

abundant fusulinids, but few bryozoans. Only delicate vinculariiform zoaria of *Rhombotrypella* and fenestrates were found associated in the most bituminous deposits, whereas other forms (e.g. pinnates) were recorded in slightly better oxygenated waters (lagoon in Figure 1B). Fenestrates have been found preserved in cavities in the palaeoaplysinid build-ups where they probably lived sheltered from the strong currents which provided them with water of normal salinity.

The late Asselian is characterized by several upwards fining sequences of mixed limestone, dolomite and local sands deposited on a more normal saline and open shallow platform (shallow carbonate shelf in Figure 1B). Bryozoans are locally abundant in this environment, with both robust and delicate vinculariiform *Ascoporella–Ascopora*, fenestrates and 'fenestrated' adeoniform fronds of *Coscinium*. Encrusters, *Archimedes* and pinnate zoaria are absent.

A subsequent regression during the Sakmarian–Artinskian led to the deposition of a thick evaporitic unit with a minor marine incursion known as the Gipshuken Formation (Lauritzen 1981). A typically restricted fauna with gastropods, a few-brachiopods, ostracods and small foraminifers is locally present. Bryozoans are rare; delicate fenestrates are in some places observed as leached voids. Locally, encrusting bryozoans resembling *Hinaclema*, a trepostome previously only known from the Lower Carboniferous of Russia and Japan (Schastlivtseva 1991), are also present in this unit. The zoaria probably encrusted 0.8-1.5 mm thick ?flexible algal or similar stems in shallow water, but the host substrate decayed shortly after burial. The internal void did not collapse and was subsequently infilled with sediment (Figure 2D).

The Tempelfjorden Group

This unit is represented in the investigated area by the Kapp Starostin Formation which is divided into a lower bioclastic limestone (unit KA-A1 in Figures 1C & D) and an upper part of alternating cherts and partly silicified limestones. The transition from the underlying group is marked by a shift from a restricted, shallow marine evaporitic environment to deeper water spiculitic shales and carbonates. The fauna with abundant silicious sponges indicates a shift towards cooler temperate conditions as Spitsbergen drifted northwards to a palaeolatitude of 35-40°N.

The sandy bioclastic barrier unit (Figure 1A) was deposited under high-energy conditions with a fauna dominated by brachiopods, bryozoans and crinoids. Despite the inferred high-energy environment, most bryozoans in this unit are well-preserved (e.g. trepostomes with protruding acanthostyles) and some brachiopods are preserved with long spines. The matrix consists, however, of well-washed crinoidal detritus. The bryozoan fauna is very rich, with at least 12 genera present. Robust vinculariiform zoaria occur in high numbers, with branch diameters of 5-12 mm being most common (*Tabulipora* and *Cyclotrypa*) (Figure 1D). Thick (>10 mm) and wide (50-70 mm) specimens of adeoniform *Meekopora* are also present.

Fenestrates are dominated by robust colonies of *Polyporella* and *Rectifenestella* (Figure 1A & C) with branches thickened on the reverse (Figure 2E & F) and commonly a low conical shape, some being attached to brachiopod shells. Pinnate fenestrates are absent. Encrusters are also locally common: multilamellar *Cyclotrypa* encrust other bryozoans (*Tabulipora*) and completely envelop brachiopods (Figure 2C), and trepostomes (?*Dyscritella*) may encrust crinoid stems (Figure 2B).

A transition to deeper water, spiculitic open marine shelf facies followed in which are found significantly more delicate vinculariiform zoaria (*Rhombotrypella, Dyscritella* and *Streblascopora*), delicate fenestrates, and an abundance of inter- and intra zoarial overgrowths (Figure 2A). This trend is more clear in the spiculitic deposits (CH-units in Figure 1C & D), where large fronds of *Ramipora* and delicate *Alternifenestella* (Figure 2H) occur. The co-existing fauna is dominated by brachiopods and lithistid sponges. Trepostome bryozoans are observed encrusting brachiopod shells as well as the upper surfaces of sponges. Fenestellid root appendages are common in many thin sections; such forms were probably anchored in soft sediment (Bancroft 1988). Other fenestrates started their growth attached to other bryozoans (Figure 2G).

The limestone units (KA-B to KA-E in Figure 1C & D) are interpreted to reflect regressive episodes and deposition under slightly shallower (more energetic) conditions than the chert units. A simple cluster analysis based on presence/absence of genera showed that the bryozoan faunas are generally different in the chert and limestone lithologies, but that the pattern is not straightforward. The fenestrates are commonly more delicate in the low-energy cherty units, with pinnate *Acanthocladia* locally abundant; vinculariiform zoaria on the other hand show a more mixed distribution, including some thick trepostomes in the low-energy deposits. This contrasts with the abundant occurrence of rather thick colonies in the highly energetic KA-A1 unit. Variations in branch diameter are usually more common in the limestone units. It seems possible that the thicker vinculariiform bryozoans shifted preferences from shallow water, high energy to deeper and more quiet water conditions. Encrusting forms are uncommon in both lithologies, whereas adeoniform zoaria (*Timanodictya*) are locally present.

Conclusions

Based on rich bryozoan faunas in the well-known, varied depositional environments, it is possible to conclude that particular bryozoan growth forms preferred particular environments. Few single growth forms and taxa are specific to an environment; rather each environment is characterized by its total faunal composition. In the early Permian, the warm, nearshore protected shallow waters were inhabited by delicate vinculariiform colonies, delicate fenestrates, *Archimedes* and pinnate forms. Palaeoaplysinid bioherms contained few fenestrates, whereas the shallow open shelf supported richer faunas, including some more robust vinculariiform and adeoniform colonies. Patches in tidal flats contained delicate fenestrates and a few trepostomes encrusting perishable substrates (?algae). A much richer bryozoan fauna developed in the ?Kungurian–late Permian. The nearshore barrier community contained low, robust fenestrates with thickened branches and small fenestrules. Several bryozoans encrusted brachiopods and crinoid stems, and thick vinculariiform zoaria are common. The open shelf spiculitic and carbonate environments were characterized by different faunas, with delicate fenestrates, robust trepostomes and rare encrusters in the spiculitic deposits, and more varied trepostomes and cryptostomes, and robust fenestrates in the carbonate units.

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