Space-filling problems in ramose trepostome bryozoans as exemplified in a giant colony from the Permian of Greenland

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In order to maintain branch strength and a confluent outer membrane, trepostome bryozoans had to maintain a continuous colony surface without any structural gaps. This put great constructional demands on colonies with relatively thick exozones to fill the exozonal space while preserving a suitable autozooecial spacing for colony-wide feeding currents. This situation was magnified in a giant colony of the trepostome *Tabulipora* from the Early Permian Kim Fjelde Fm. in eastern North Greenland. This single branch colony fragment had a diameter of 37.5 mm. A block was cut out of the 8-mm thick exozone, and 20 serial tangential peels were made at varying distances from the endozone. Exilazooecial and autozooecial chamber cross-sectional area, packing, spacing, and wall thickness were measured in the maculae and intermacular areas. Results indicate that, in this colony, volumetric space in the exozone was occupied by budding new exilazooecia in the maculae and by exozonal budding: budding of new exilazooecia in the intermacular areas that transform into autozooecia. Exilazooecia played a dominantly space-filling role in the maculae as well as helped to maintain regular spacing of autozooecia in the intermacular areas. □*Bryozoans, functional morphology, Greenland, Permian, space-filling, Tabulipora, trepostomes.*

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There are phylogenetic, functional, and fabricational constraints acting on the evolution of all organisms (Seilacher 1970). The obvious functional demands of resource acquisition, waste disposal, and gamete dispersal must be met within the limitations of the often less obvious phylogenetic and fabricational constraints. This paper deals with the functional demands of volumetric space-filling in a giant ramose trepostome bryozoan. Space-filling in bryozoans with non-unilaminate colonies is often confounded with the better understood surface area filling. The main question addressed was how did a giant ramose trepostome bryozoan colony fill space in a volumetric sense in the exozone as it grew, and the surface area and volume increased acutely through the exozone. When proposing functional hypotheses, it is important to avoid untestable adaptationist stories (Gould & Lewontin 1979), and thus this paper will adopt an approach that permits testing with simple colony- and zooecium-level geometries.

The possible solutions to volumetric space-filling in trepostomes were phylogenetically constrained by the synapomorphies that had evolved in the group. One such constraining synapomorphy was the need for a confluent outer membrane for zooecial budding and interzooecial nutrient exchange (Borg 1926; Boardman 1971, 1998). This eliminated certain space-filling solutions, such as structural gaps, due to the need for a continuous colony surface (Key 1991a). Thus, all space between the feeding zooids at the colony surface had to be occupied. This also would have had an immediate surficial function of eliminating structural gaps that would have provided settlement sites for ebibionts. Another constraining synapomorphy was the small and finite volume of autozooecial chambers (McKinney & Jackson 1989; Jackson & McKinney 1990). This limited how much space an individual autozooecium could occupy. In addition, there was a metabolic cost to secreting carbonate that may have restricted some space-filling solutions (e.g. inordinately thick zooecial walls).

Ramose trepostome colonies generally had radially symmetrical cylindrical branches. The interior of the branch (the endozone; Fig. 1) was occupied by thin-

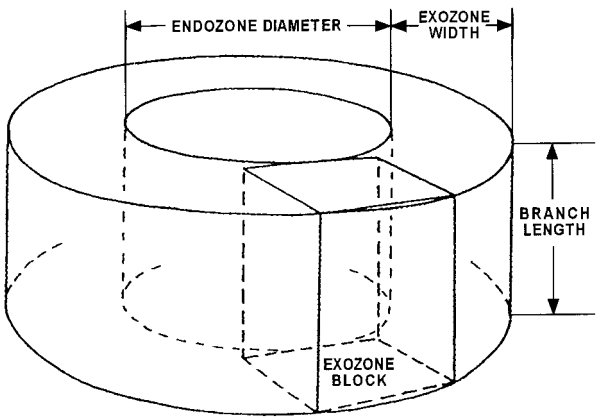

Fig. 1. Diagrammatic representation of a cylindrical trepostome branch showing the block of exozone cut. Modified from Madsen (1991, fig. 9).

walled portions of zooecia that gradually bent outward from a growth trajectory that was parallel to the branch axis to one that was more perpendicular. The exterior of the branch (the exozone; Fig. 1) was occupied by thick-walled portions of zooecia with a growth trajectory that was more perpendicular to the branch axis. This study deals with the question of how ramose trepostomes solved the volumetric space-filling problems associated with relatively wide exozones, since most budding of new autozooecia occurred in the endozone (Boardman & McKinney 1976; McKinney 1975, 1977). Autozooecia are the skeletal walls of the normal feeding zooids with protrusible lophophores (Boardman & Cheetham 1983).

There were a limited number of ways for ramose trepostomes to solve the problem of volumetric space-filling in the exozone (Key 1991a).

(1) Have a large axial ratio. The axial ratio is the endozone diameter divided by the branch diameter (Boardman 1960). Colonies with large axial ratios had relatively wide endozones and narrow exozones. This solution did occur in ramose trepostomes such as *Polycylindricus asphinctus*, which had a mean axial ratio of 0.8 (Boardman 1960, p. 68). A wide endozone permitted sufficient zooecial budding in the endozone to fill a thin exozone. If A = endozone diameter, B = exozone width, and C = branch length (Fig. 1), then branch radius = $A \div 2 + B$, endozone volume = $\pi \times (A \div 2)^2 \times C$, branch volume = $\pi \times (A \div 2 + B)^2 \times C$, and exozone volume = branch volume − endozone volume = $[\pi \times (A \div 2 + B)^2 \times C] - [\pi \times (A \div 2)^2 \times C] = \pi \times C \times (A \times B + B^2)$. This indicates that exozone volume increased linearly with endozone diameter, but exponentially with exozone width. Thus, exozone width affected exozone volume much more than endozone diameter, and colonies with thick exozones had a proportionally greater space-filling problem (Key 1991a).

(2) Maintain a low surface angle through the exozone. The surface angle is the angle made by the colony surface and the axis of the zooecia in the outer exozone. This solution did occur in trepostomes such as *Champlainopora ramusculus*, which has a mean surface angle of 60° (Key 1990a, p. 724). With a low surface angle, each zooecium occupied more space in the exozone by having a longer trajectory through it.

There were also several zooecium-level solutions to the space-filling problem.

(3) The zooecial wall thicknesses could have increased through the exozone. This solution was possible, but it was largely restricted to the basal exozone as zooecia curved from the endozone into the exozone (Key 1990b). If zooecial walls continued to thicken throughout the exozone, it would have increased the spacing between autozooecial chambers (Key 1991a). This would have resulted in widely spaced lophophores which would have prohibited colony-wide feeding currents and decreased feeding efficiency (Grünbaum 1995). This constancy of autozooecial chamber spacing was ubiquitous in the bryozoans. In fact, the lateral spacing of autozooecial chambers on the surface of bryozoan colonies has remained relatively constant throughout the 500 m.y. history of the clade (Jackson & McKinney 1990; McKinney & Jackson 1989).

(4) The cross-sectional areas of autozooecial chambers could have increased through the exozone. This solution did not occur in ramose trepostomes, except for a very short-lived period during early zooecial ontogeny when the newly budding zooecia (e.g. kenozooecia) expanded into autozooecia (Key 1990a, 1991b; Madsen 1994a).

(5) Cystose vesicles could have developed through the exozone. This solution did occur (e.g. *Aostipora*; Bassler 1953, fig. 75.4b), but it was taxonomically restricted among the bryozoans.

(6) New intermacular zooecia could have budded through the exozone. This solution, called exozonal budding, did occur in ramose trepostomes, including *Tabulipora* (Madsen 1994a). Exozonal budding was different from the more common budding, where autozooecia in the exozone were budded in the endozone at the growing tip (Boardman 1983). Exozonal budding involved the budding of small non-feeding polymorphs (i.e. kenozooecia) in the exozone that transformed through ontogeny into full-sized autozooecia in the intermacular areas.

Kenozooecia were generally reduced in size relative to autozooecia, so they lacked protrusible feeding lophophores (Boardman *et al.* 1983; Taylor 1999). This ontogenetic transformation has been recently documented for mesozooecia (Key 1990a, 1991b) and exilazooecia (Madsen 1994a). Mesozooecia and exilazooecia were kenozooecia with and without basal diaphragms, respectively (Taylor 1999). Most kenozooecia in trepostomes were space-fillers, and they regulated the spacing between adjacent autozooecial chambers and their lophophores and occupied channels of excurrent flow (Taylor 1999).

(7) The size and number of maculae could have increased through the exozone. A macula is a small cluster of kenozooecia and/or extrazooecial skeleton surrounded by autozooecia that may be depressed below, level with, or elevated above the colony surface (Boardman & Cheetham 1983). A monticule is simply a macula that is elevated above the colony surface. This paper does not use Anstey's (1981, 1987) definition of a macula as the non-zooecial center of a monticule. Increasing macular size and number through the exozone have been documented in ramose bryozoans (Anstey *et al.* 1976; Pachut & Anstey 1979; Podell & Anstey 1979; Anstey 1981; Patzkowsky 1987; Pachut 1992). On ramose colonies, maculae generally only occurred when the hydrodynamic needs of colony-wide feeding currents required excurrent chimneys. These colonies generally had branch diameters greater than 2 mm (McKinney 1986). It is interesting to note that the larger colonies with maculae tended also to have a greater space-filling problem in the exozone.

When analyzing the functional constraints on an organism, it is important to treat the organism as an integrated entity, not as a collection of independent characters (Gould & Lewontin 1979). To do so would ignore the fact that an organism's characters exist within the constraints imposed by multiple competing functions. In trepostomes, any of these seven space-filling solutions also may have had a very different alternative (and possibly dominant) function. For example, axial ratios also may have evolved to be smaller in response to the need to maintain branch strength (Key 1991a), the number and size of maculae also may have increased as a product of the need to maintain colony-wide feeding currents with excurrent chimneys (Banta *et al.* 1974), and zooecial wall thicknesses were constrained by the need to maintain a sufficient number of feeding lophophores with proper spacing (Taylor 1999). This paper focuses solely on volumetric space-filling, but we realize that these morphologic features may have had other additional functions.

These various solutions to the exozonal space-filling problem were examined in a giant single colony branch fragment of *Tabulipora* with a diameter of 37.5 mm and an axial ratio of 0.57. As the exozone width increased from 0 mm to 8 mm, the branch radius increased from 10.75 mm to 18.75 mm. This caused a 74% increase in the branch's surface area and a 204% increase in the branch's volume. This represented a space-filling problem that was much greater than a typical trepostome bryozoan with a smaller size.

Material

This study was based on a single Geological Survey of Greenland specimen (GGU 196054-1) of the stenoporid trepostome bryozoan *Tabulipora*. This specimen, which was figured by Håkansson & Madsen 1991 (pl. 1, fig. 4), was chosen as it was the largest ramose colony available. The specimen was collected during the 1980 expedition of the regional geological mapping project of eastern North Greenland (Håkansson 1979; Håkansson *et al.* 1981). The sample was collected from Midnatfjeld in the Kim Fjelde area in eastern Peary Land in eastern North Greenland (Stemmerik & Håkansson 1989, fig. 16, locality 11c). It came from the Kim Fjelde Fm. at its type section (Stemmerik & Håkansson 1989; Stemmerik *et al.* 1996). The Kim Fjelde Fm. is part of the Mallemuk Mountain Group, which is part of the Wandel Sea Basin sedimentary sequence (Håkansson 1979; Stemmerik & Håkansson 1989). The Kim Fjelde Fm. is Early Permian (late Artinskian to Kungurian stages) in age (Rasmussen & Håkansson 1996; Stemmerik *et al.* 1996) with an age of 260–255 Ma (Gradstein & Ogg 1996).

The fauna of the Kim Fjelde Fm. was dominated by large robust stenoporid trepostomes (Ross & Ross 1962; Håkansson 1979) with dichotomously branching ramose zoaria with branch fragments that were often more than 20 cm long and up to 7 cm in diameter (Madsen 1987, 1994b; Madsen & Håkansson 1989; Stemmerik 1997). Other giant stenolaemate colonies are known from elsewhere (Taylor & Voigt 1999), but these Greenland colonies were at least twice the size of other Permian trepostomes and an order of magnitude larger than most bryozoans (Madsen 1991). Their large size has been attributed to symbiotic, photosynthetic, zooxanthellae algae living intracellularly within the bryozoan colony (Håkansson & Madsen 1991).

The volume of this colony branch fragment was greater than typical *Tabulipora* colony branch frag-

ments of equal length (Håkansson & Madsen 1991, figs. 1–4). It had a length of 135 mm and a diameter of 37.5 mm with an endozone diameter of 21.5 mm and an exozone width of 8.0 mm. Due to the branch fragment's immense size, it was possible to cut a large block out of the exozone (Fig. 1). The block was 15 mm wide, 15 mm long, and 8 mm deep with a total volume of 1,800 mm^3. From this block, 20 serial tangential acetate peels were made. The remnant of the original specimen and the peels are housed at the Geological Museum in Copenhagen (MGUH 25.988–26.008). The shallowest peel was made at a depth from the surface of 0.62 mm, and the deepest was at the endozone/exozone boundary at a depth of 8.00 mm. The spacing between the serial peels ranged from 0.05 mm to 1.23 mm with a mean of 0.39 mm. These same peels were used in previous studies to document exozonal budding (Madsen 1991, 1994a).

In this colony, maculae were practically invisible on the colony surface (Madsen 1991) due to their lack of relief, but in magnified tangential section they were very prominent. The block of exozone contained two maculae (herein referred to as Macula 1 and Macula 2). In *Tabulipora*, maculae were composed of clusters of exilazooecia similar to those in other trepostomes (Boardman 1983, fig. 59.5) and cystoporates (Utgaard 1983, fig. 159e). Macular outlines in the peels were determined by the distribution of contiguous exilazooecia (Fig. 2). Macular outlines were drawn for 18 of the 20 peels. The maculae could not be found in peel 13, because it was of poor quality, and in peel 20, because it was too close to the endozone for the maculae to have developed.

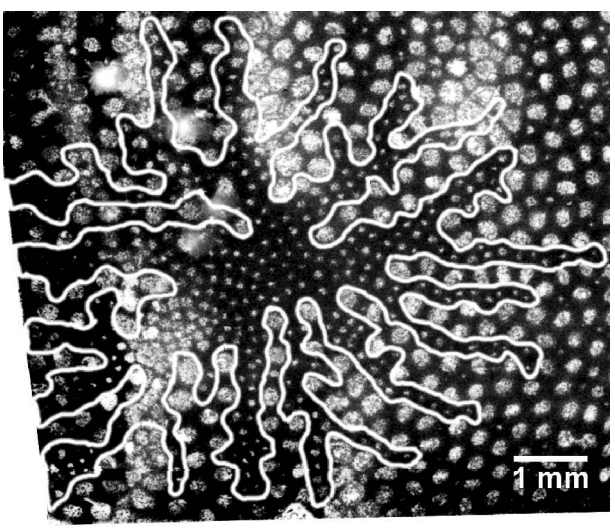

Fig. 2. Photomicrograph of a tangential section of the exozone of *Tabulipora* sp. (GGU 196054-1) showing Macula 1 (outlined in white) at 6.51 mm from endozone. Note the stellate macula defined by contiguous exilazooecia, the truncated macular channels on the left side, and the vertical bands of lighter, thin- and darker, thick-walled zooecia reflecting moniliform wall structure in exozone.

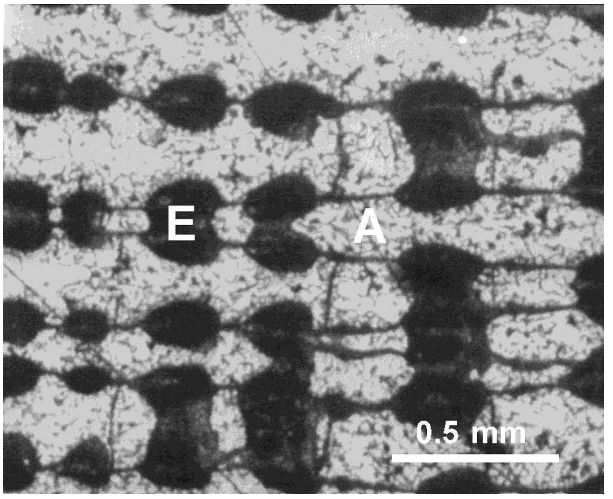

Fig. 3. Photomicrograph of a longitudinal section of the exozone of *Tabulipora* sp. (GGU 196054-1) showing the alterations of thin- and thick-walled zooecia reflecting moniliform wall structure in exozone. Note the sudden transformation of an exilazooecium (E) into an autozooecium (A). Assuming this section runs through the zooecial axis and is not an oblique section, the zooecial chamber went from a diameter of 0.128 mm to 0.225 mm (an increase of 76% in diameter which converts to a 208% in circular cross-sectional area) in only 0.523 mm (6.5% of the total exozone width of 8 mm).

Characters measured

Two basic types of characters were measured: macular and intermacular characters. All of the characters were measured using digitized video images of the tangential serial peels at 50× or 100× magnification. All of the macular characters were measured on each of the 20 peels except for peels 13 and 20, as mentioned previously. The macular characters were measured separately on each of the two maculae. All of the measurements of macular characters were repeated 10 times per macula per peel except for the number of complete exilazooecial chambers which were counted once per macula per peel.

Tabulipora had distinctive moniliform (i.e. alternating thin- and thick-walled) zooecial walls in the exozone (Cuffey 1967; Gautier 1970; Bartley & Anstey 1987) (Fig. 3). Tangential sections intersecting both thin- and thick-walled zones revealed multiple bands of thin- and thick-walled zooecia oriented parallel to the branch axis (vertical bands in Fig. 2). All macular characters were measured in the thick-walled zones.

Five macular characters were determined as follows. Macular area was measured as the area within the macular outline (Fig. 2). The number of exilazooecia

per macula was determined by counting the number of exilazooecial chambers within the macular outline. Exilazooecial chamber cross-sectional area was measured as the area within the exilazooecial walls. Exilazooecial wall thickness was measured as the minimum linear distance between adjacent exilazooecial chambers. Exilazooecial chamber packing was calculated by dividing the number of exilazooecial chambers per macula by the macular area.

Seven different characters were determined in the areas between the maculae. These intermacular measurements were all repeated 10 times per peel. All of the intermacular characters were determined on each of the 20 peels. Each intermacular character was determined separately in both the thin- and thick-walled zones except for autozooecial spacing, which was only measured in the thick-walled zones. The intermacular characters were determined as follows. Autozooecial and exilazooecial chamber cross-sectional areas and zooecial wall thicknesses were measured as mentioned above for macular exilazooecia. Autozooecial and exilazooecial chamber packing were determined by counting the number of complete autozooecial and exilazooecial chambers within a 0.55 mm^2 window and dividing these values by 0.55. Autozooecial spacing was measured as the distance between the centroids of neighboring autozooecial chambers.

Sources of error

A problem with tangential sections of cylindrical colony branches is that the depth of a tangential section below the colony surface increases laterally from the edges of the section (parallel to the growth axis of the branch) to the center along the proximal-distal axis (Fig. 1). At the lateral edges, the section intersects the branch at the colony surface. Along the center, the section intersects the branch deeper in the exozone. As a result, there is a systematic lateral variation in the depth of tangential sections of cylindrical surfaces. This is more of a problem in colonies with small diameters, and less in immense colonies like the one in this study. The amount of this variation depends on both the lateral width of the tangential section and the radius of the branch. In this colony, the tangential peels have a maximum width of 15 mm, and the branch has a radius of 18.75 mm. The maximum variation in depth of the tangential peels was calculated as 1.56 mm. With an exozone width of 8.00 mm, this means there was a maximum of 19.5% variation in the depth of the tangential peels.

This could be a problem for the intermacular characters if they were measured on the lateral edge of one peel and on the proximal-distal axis of the next. To minimize this error, all intermacular characters were measured as close as possible to the proximal-distal axis of the peel. This could also be a problem for the macular characters if the position of the maculae moved significantly in the lateral direction. During growth through the exozone, the maculae did migrate apart. At 1.02 mm from the endozone in the deepest peel, the centers of the two maculae were 9.36 mm apart. At 7.38 mm from the endozone in the shallowest peel, they were 10.01 mm apart. But this intermacular distance contains both a lateral and a proximal-distal component. The source of error caused by differences in the depth of the tangential peels was only affected by lateral movement. The amount of lateral (i.e. perpendicular to the proximal-distal axis of the branch and tangential sections) migration of the maculae from peel to peel was determined by measuring the lateral distance between the centroids of the maculae. For Macula 1, this distance ranged from 0.00 mm to 0.36 mm (mean = 0.16 mm). For Macula 2, the range was 0.00 mm to 0.86 mm (mean = 0.21 mm). This lateral migration of the maculae translated into differences in the depth of the tangential sections of 0.00 mm to 0.08 mm (mean = 0.03 mm) for Macula 1 and 0.00 mm to 0.18 mm (mean = 0.04 mm) for Macula 2. With an 8.00 mm exozone, this resulted in a maximum error of 0.9% (mean = 0.4%) for Macula 1 and 2.3% (mean = 0.5%) for Macula 2. Thus, the effect of making tangential sections of a cylindrical surface did not have a 19.5% maximum error on the macular characters, but a 2.3% maximum error.

There was another potential error in the macular characters due to the truncation of the lateral margin of maculae in some peels. This error was noticeable in Macula 1 (e.g. left side of Fig. 2) in the nine outermost peels and in Macula 2 in the three outermost peels.

Results and discussion

All summary data and linear regression statistics for macular characters are listed in Table 1. The surface areas occupied by the two maculae increased significantly through the exozone (Fig. 4). Macula 1 increased from 5.3 mm^2 at 1.02 mm from the endozone to 16.5 mm^2 at 7.38 mm from the endozone. This represented a 206% increase. In this same interval, Macula 2 grew from 3.2 mm^2 to 19.3 mm^2 for a 503% increase in area. These percentage increases were minimums, as the maculae actually increased from a smaller size at the endozone/exozone boundary to a

Table 1. Summary data and linear regression statistics for macular characters measured in exozone of *Tabulipora* specimen GGU 196054-1.

Character	No. of measurements	Range	Mean	Standard deviation	R^2 value for linear regression with distance from endozone (p value)
Macula 1, area (mm^2)	18 × 10	5.3–18.8	12.7	5.0	0.929 (<0.001)
Macula 2, area (mm^2)	18 × 10	3.2–20.2	14.3	5.7	0.945 (<0.001)
Macula 1, no. of exilazooecia	18	91–402	267	116	0.948 (<0.001)
Macula 2, no. of exilazooecia	18	51–454	298	134	0.964 (<0.001)
Macula 1, exilazooecial chamber cross-sectional area (mm^2)	18 × 10	0.004–0.011	0.006	0.002	0.647 (<0.001)
Macula 2, exilazooecial chamber cross-sectional area (mm^2)	18 × 10	0.004–0.012	0.007	0.002	0.339 (0.011)
Macula 1, exilazooecial wall thickness (mm)	18 × 10	0.095–0.116	0.104	0.007	0.064 (0.312)
Macula 2, exilazooecial wall thickness (mm)	18 × 10	0.088–0.141	0.111	0.013	0.281 (0.024)
Macula 1, exilazooecial chamber packing (no./mm^2)	18	17.0–22.9	20.6	1.5	0.687 (<0.001)
Macula 2, exilazooecial chamber packing (no./mm^2)	18	15.7–22.7	20.3	2.1	0.610 (<0.001)

larger size at the colony surface and parts of the maculae were truncated by the edges of the peels in the outer exozone. Other workers have measured macular chimney size in both living and fossil bryozoans. Macular chimney size should be relatively constant in encrusting colonies that grow peripherally. In encrusting colonies, the peripheral growth does not affect the flow dynamics of the pre-existing macular chimneys, which are distant from the colony margin. This is supported by the observations of previous workers who have reported that macular chimneys have a relatively constant diameter of 0.6–2.0 mm (Banta *et al.* 1974; Cook 1977; Cook & Chimonides 1980; Lidgard 1981). This should not be the case in ramose colonies that grow by expansion of the entire branch. As the colony expands in size, previous workers have shown that macular chimneys also increase in size (Anstey *et al.* 1976; Pachut & Anstey 1979; Podell & Anstey 1979; Anstey 1981). As a colony expands by increasing the width of its exozone, more maculae should develop. In fact, maculae rarely occur on colonies with branch diameters less than 2 mm (McKinney 1986).

The maculae increased their size by budding new macular exilazooecia. Thus, as the maculae expanded in size, the number of exilazooecia per macula also increased significantly through the exozone (Fig. 5). The number of exilazooecia in Macula 1 increased from 91 at 1.02 mm from the endozone to 355 at 7.38 mm from the endozone. This represented a 290% increase. In this same interval, Macula 2 grew from 51 exilazooecia to 407 for a 698% increase. This difference in macular size indicates maculae were quite plastic in size at any one astogenetic stage of the colony. Kenozooecia such as exilazooecia were often budded in the maculae of larger colonies (Boardman

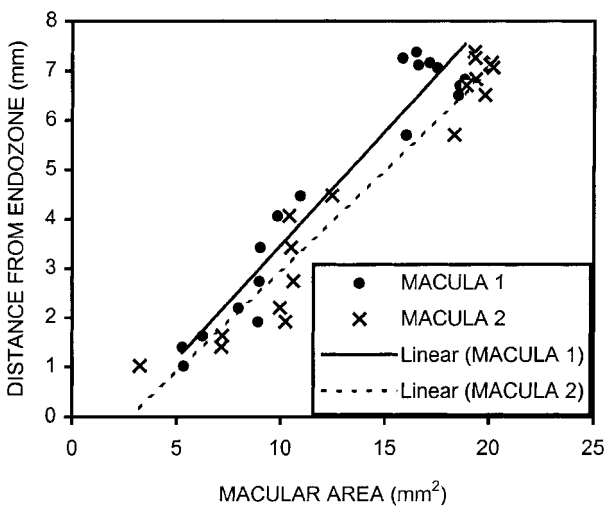

Fig. 4. Plot of macular area versus distance from endozone. See Table 1 for linear regression results.

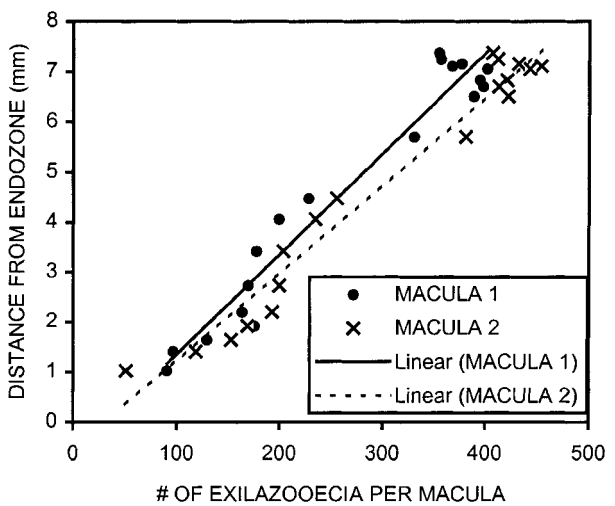

Fig. 5. Plot of no. of exilazooecia per macula versus distance from endozone. See Table 1 for linear regression results.

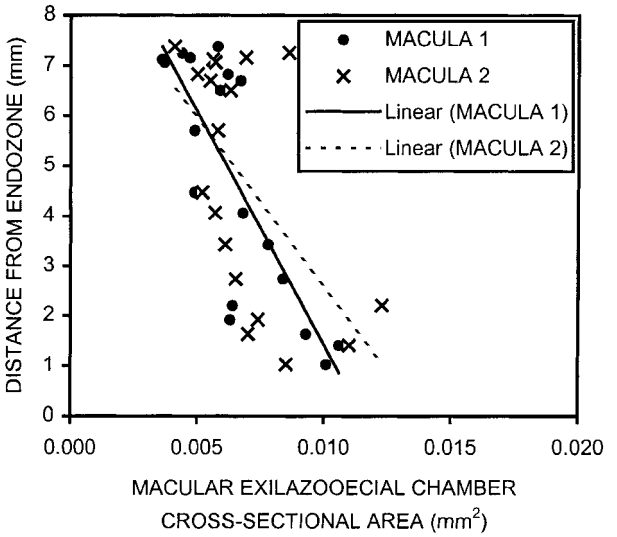

Fig. 6. Plot of macular exilazooecial chamber cross-sectional area versus distance from endozone. See Table 1 for linear regression results.

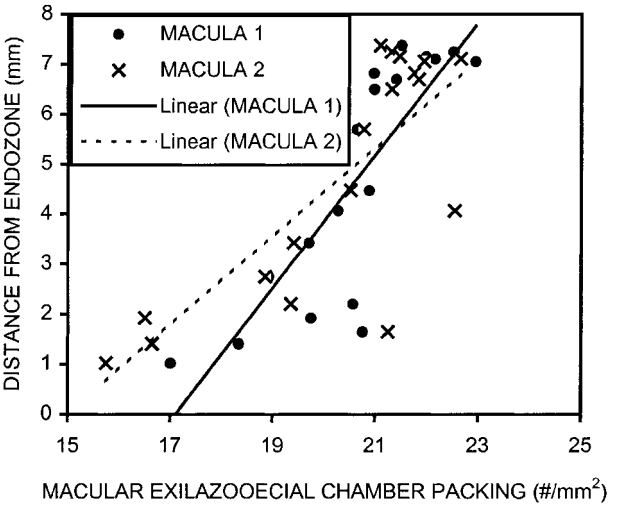

Fig. 7. Plot of macular exilazooecial chamber packing versus distance from endozone. See Table 1 for linear regression results.

1983). Previous workers have suggested that macular kenozooecia gradually expanded in size through ontogeny until they became autozooecia and were pushed into the intermacular areas by new kenozooecia (Anstey *et al.* 1976; Pachut & Anstey 1979). The results from this study indicate that macular exilazooecia also may have remained in the maculae as exilazooecia throughout their ontogeny and contributed to the expansion of the maculae.

As the number of exilazooecia per macula increased, their chamber cross-sectional areas significantly decreased in both maculae (Fig. 6). In Macula 1 the exilazooecial chamber cross-sectional areas decreased from 0.010 mm^2 at 1.02 mm from the endozone to 0.006 mm^2 at 7.38 mm from the endozone. This represented a 40% decrease. In this same interval, the exilazooecial chamber cross-sectional areas in Macula 2 decreased from 0.009 mm^2 to 0.004 mm^2 for a 56% decrease. As the number of exilazooecia per macula increased, the exilazooecial wall thicknesses significantly decreased in Macula 1 but not in Macula 2.

As a result of these changes in the maculae through the exozone, the packing of exilazooecial chambers in both maculae increased significantly (Fig. 7). In Macula 1 the packing increased from 17.0/mm^2 at 1.02 mm from the endozone to 21.5/mm^2 at 7.38 mm from the endozone. This represents a 27% increase. In this same interval, the packing in Macula 2 grew from 15.7/mm^2 to 21.1/mm^2 for a 34% increase. This increase in packing reflected the budding of new macular exilazooecia with smaller chamber cross-sectional areas due to their younger ontogenetic status.

These significant changes through the exozone in the macular characters were in marked contrast to the lack of statistically significant changes through the exozone in most of the intermacular characters. All summary data and linear regression statistics for intermacular characters are listed in Table 2 for the thin-walled zones and Table 3 for the thick-walled zones. The only intermacular character that changed significantly through the exozone was exilazooecial chamber packing, which increased through the exozone in both thin- and thick-walled zones. Autozooecial and exilazooecial chamber cross-sectional areas, autozooecial and exilazooecial wall thicknesses, as well as autozooecial chamber packing and spacing did not change significantly through the intermacular areas of the exozone. The maintenance of uniform packing and spacing of autozooecial chambers in the intermacular areas was probably in response to the need to keep the spacing of lophophores in the canopy constant for the colony-wide feeding currents at the surface (Madsen 1994a).

Volumetrically, exozonal budding was the principal way that space was filled in the exozone of this colony (Madsen 1994b). What was surprising was that these intermacular characters stayed constant despite the exozonal budding documented by Madsen (1994b). Exozonal budding involved the budding of new intermacular exilazooecia which then expanded into autozooecia later in ontogeny. This was determined by following individual zooecia through their ontogeny (i.e. through the series of serial peels) (Madsen 1994a). This ontogenetic transformation occurred quickly (Fig. 3) resulting in two distinct zooecial sizes in tangential section (Fig. 2): the larger autozooecia and the smaller exilazooecia. The rarity of intermediate-sized zooecial chambers confirmed that the transition

Table 2. Summary data and linear regression statistics for intermacular characters measured in thin-walled zones of exozone of *Tabulipora* specimen GGU 196054-1.

Character	No. of measurements	Range	Mean	Standard deviation	R^2 value for linear regression with distance from endozone (p value)
Autozooecial chamber cross-sectional area (mm^2)	20 × 10	0.082–0.103	0.091	0.006	0.089 (0.201)
Autozooecial wall thickness (mm)	20 × 10	0.010–0.016	0.012	0.002	0.058 (0.306)
Autozooecial chamber packing (no./mm^2)	20 × 10	1.6–3.5	2.7	0.5	0.017 (0.587)
Exilazooecial chamber cross-sectional area (mm^2)	20 × 10	0.020–0.027	0.023	0.002	0.011 (0.659)
Exilazooecial wall thickness (mm)	20 × 10	0.009–0.017	0.012	0.002	0.071 (0.255)
Exilazooecial chamber packing (no./mm^2)	20 × 10	1.8–4.4	2.9	0.6	0.473 (<0.001)

from exilazooecium to autozooecium was very short-lived compared to the entire length of the zooecium, some of which extended for at least 60 mm from the endozone to the exozone (Madsen 1994a).

The relative size of the autozooecia and exilazooecia was also reflected in the autozooecial spacing data. The spacing between the centroids of neighboring autozooecial chambers averaged 0.435 mm, but when the means for the smallest, middle, and largest third of the distribution of autozooecial spacing values were calculated, a different picture emerged. The results indicated the closest autozooecia were on average 0.312 mm apart, the middle third 0.425 mm, and the furthest third 0.569 mm. The spacing of the closest third was 54% of the furthest third. Thus, 0.312 mm was the typical distance between autozooecial centroids at which a new autozooecium became fully developed, and 0.569 mm was the typical distance between autozooecial centroids at which an intervening exilazooecium transformed into an autozooecium.

These intermacular results differ from those of Pachut and others who did similar studies using serial peels through the exozones of other species (Pachut *et al.* 1991; Pachut 1992). Their studies used a different morphometric approach called stereology (Anstey & Bartley 1984) and involved the trepostomes *Heterotrypa ulrichi* and *Tabulipora carbonaria*. They found that in the intermacular areas zooecial chamber cross-sectional area decreased whereas zooecial packing, zooecial wall thickness, and mesozooecium size and abundance increased through the exozone. These different results are not due to the use of different morphometric techniques because when the same characters were analyzed using stereology on the same serial peels used in this study, the results were the same as reported here (Madsen 1994a). The different results must be a function of interspecific variation in how species solve their space-filling problems. The colony in this study was purposely chosen for its extreme space-filling problems, whereas most bryozoans are smaller and can solve their space-filling problems more easily.

Different space-filling demands were placed on the colony in thick-walled versus thin-walled zones in the exozone. The zooecial chamber cross-sectional areas alternated from small (in the thick-walled zones) to large (in the thin-walled zones). The autozooecial chamber cross-sectional areas in the thick-walled zones averaged 0.038 mm^2, and they increased significantly in the thin-walled zones to 0.091 mm^2 (t-test, $p < 0.001$). The same pattern occurred with the exilazooecial chamber cross-sectional areas. In the thick-walled zones, the exilazooecial chambers averaged 0.007 mm^2, and this increased significantly in the thin-walled zones to 0.023 mm^2 (t-test, $p < 0.001$).

This moniliform zooecial morphology in the

Table 3. Summary data and linear regression statistics for intermacular characters measured in thick-walled zones of exozone of *Tabulipora* specimen GGU 196054-1.

Character	No. of measurements	Range	Mean	Standard deviation	R^2 value for linear regression with distance from endozone (p value)
Autozooecial chamber cross-sectional area (mm^2)	20 × 10	0.031–0.046	0.038	0.004	0.003 (0.810)
Autozooecial wall thickness (mm)	20 × 10	0.100–0.154	0.128	0.012	0.001 (0.993)
Autozooecial chamber packing (no./mm^2)	20 × 10	3.3–5.3	4.3	0.6	0.027 (0.490)
Exilazooecial chamber cross-sectional area (mm^2)	20 × 10	0.005–0.009	0.007	0.001	0.187 (0.057)
Exilazooecial wall thickness (mm)	20 × 10	0.085–0.163	0.114	0.021	0.099 (0.177)
Exilazooecial chamber packing (no./mm^2)	20 × 10	1.8–4.9	3.1	0.8	0.220 (0.037)
Autozooecial spacing (mm)	20 × 10	0.248–0.716	0.435	0.114	0.117 (0.147)

exozone was of course also evident in the zooecial wall thicknesses. The autozooecial wall thicknesses in the thick-walled zones averaged 0.128 mm, and they decreased significantly in the thin-walled zones to 0.012 mm (t-test, $p < 0.001$). The exilazooecial wall thicknesses in the thick-walled zones averaged 0.114 mm, and they decreased significantly in the thin-walled zones to 0.012 mm (t-test, $p < 0.001$).

The increasing zooecial chamber cross-sectional areas from the thick- to the thin-walled zones resulted in an artificial decrease in zooecial chamber packing due to the relative size of the sampling window. Exilazooecial chamber packing in the thick-walled zones averaged 3.1/mm^2, and this decreased in the thin-walled zones to 2.9/mm^2. Autozooecial chamber packing in the thick-walled zones averaged 4.3/mm^2, and this decreased in the thin-walled zones to 2.7/mm^2. This decrease was simply due to the small area (0.55 mm^2) of the window used to count the chambers relative to the chamber cross-sectional areas. As only complete chambers were counted, the zooecial packing in the thin-walled zones artificially declined in response to increasing chamber cross-sectional area. This lack of change in autozooecial chamber packing can be seen qualitatively in Fig. 2 by comparing the packing in the thick- and thin-walled zones. This is intuitive, as the packing did not change from the thick- to thin-walled zones; only the zooecial chamber cross-sectional areas changed.

As zooecia grew from a thick-walled zone into a thin-walled zone, the space-filling demands of the colony were heightened. The autozooecial and exilazooecial chamber cross-sectional areas increased, but at different rates. The autozooecial chambers increased in size at a rate of 140%, while the exilazooecia increased in size at a rate of 229%. At the same time, despite the artifact of the relative size of the sampling window, the packing of autozooecial chambers decreased at a rate of 37% versus only 6% for the exilazooecia. While this was occurring, the autozooecial and exilazooecial wall thicknesses decreased at roughly the same rate (91% versus 90%, respectively). This implies that relative to their sizes, more space was being taken up by the exilazooecia than the autozooecia in the thin-walled zones.

Conclusions

Exilazooecia were important space-filling polymorphs in this colony and quite likely in other stenolaemates as well, as they have similar exilazooecial spatial distributions (Taylor 1999). Even though autozooecia occupied the vast majority of the volume of this colony, relative to their size, exilazooecia seem to be critically important space-fillers in exozones for three reasons. (1) The increase in macular size resulted from budding of more (in both a sense of the gross number as well as in the sense of packing) exilazooecia in the maculae. (2) Relative to their wall thickness and chamber cross-sectional area, more space was taken up by the exilazooecia than by the autozooecia in the thin-walled zones of the exozone. (3) The only intermacular character that changed significantly through the exozone was exilazooecial chamber packing, which increased through the exozone in both thin- and thick-walled zones. Autozooecial chamber packing and spacing remained constant by transformation of a limited number of exilazooecia into autozooecia. This was presumably in order to maintain proper lophophore spacing in the canopy to maintain colony-wide feeding currents.

Of the seven potential solutions outlined previously, only the last two were utilized by this colony of *Tabulipora* to solve its space-filling problem in the exozone. (1) It had a large axial ratio (0.57) which actually made the space-filling problem worse. (2) It had a high surface angle (almost 90°), which also made the space-filling problem worse. (3) The autozooecial wall thicknesses did not increase through the exozone (Tables 2 and 3), so this potential solution was also not utilized. (4) The cross-sectional areas of autozooecial chambers did not increase through the exozone (Tables 2 and 3), so this potential solution was also not utilized. (5) Cystose vesicles were not developed through the exozone, so this potential solution was not utilized. (6) New intermacular zooecia were budded through the exozone, so this was one of the solutions being exploited (Madsen 1994a). (7) The size and possibly the number of maculae were increasing through the exozone (Fig. 4), so this was another solution being exploited.

Thus, this colony solved its enormous space-filling problem in two ways: exozonal budding of new zooecia and increasing macular size and number. These two innovations may have given *Tabulipora* the capacity for essentially unlimited growth. Morphologic characters can and often do have multiple functions. Increasing macular size and number was a space-filling solution but also probably a product of the need for excurrent chimneys.

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References

Anstey, R.L. 1981: Zooid orientation structures and water flow patterns in Paleozoic bryozoan colonies. *Lethaia 14*, 287–302.

Anstey, R.L. 1987: Colony patterning and functional morphology of water flow in Paleozoic stenolaemate bryozoans. *In* Ross, J.R.P. (ed.): *Bryozoa: Present and Past*, 1–8. Western Washington University, Bellingham, Washington.

Anstey, R.L. & Bartley, J.W. 1984: Quantitative stereology: an improved thin section biometry for bryozoans and other colonial organisms. *Journal of Paleontology 58*, 612–625.

Anstey, R.L., Pachut, J.F. & Prezbindowski, D.R. 1976: Morphogenetic gradients in Paleozoic bryozoan colonies. *Paleobiology 2*, 131–146.

Banta, W.C., McKinney, F.K. & Zimmer, R.L. 1974: Bryozoan monticules: excurrent water outlets? *Science 185*, 783–784.

Bartley, J.W. & Anstey, R.L. 1987: Growth of monilae in the Permian trepostome *Tabulipora carbonaria*: evidence for periodicity and a new model of stenolaemate wall calcification. *In* Ross, J.R.P. (ed.): *Bryozoa: Present and Past*, 9–16. Western Washington University, Bellingham, Washington.

Bassler, R.S. 1953: *Treatise on Invertebrate Paleontology, Part G. Bryozoa*. 253 pp. University of Kansas Press and Geological Society of America, Lawrence, Kansas and Boulder, Colorado.

Boardman, R.S. 1960: Trepostomatous bryozoa of the Hamilton Group of New York State. *U.S.G.S. Professional Paper 340*, 1–87.

Boardman, R.S. 1971: Mode of growth and functional morphology of autozooids in some recent and Paleozoic tubular Bryozoa. *Smithsonian Contributions to Paleobiology 9*, 1–51.

Boardman, R.S. 1983: General features of the class Stenolaemata. *In* Robison, R.A. (ed.): *Treatise on Invertebrate Paleontology, Part G. Bryozoa Revised, Volume 1*, 49–137. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas.

Boardman, R.S. 1998: Reflections on the morphology, anatomy, evolution, and classification of the Class Stenolaemata (Bryozoa). *Smithsonian Contributions to Paleobiology 86*, 1–59.

Boardman, R.S. & Cheetham, A.H. 1983: Glossary of morphological terms. *In* Robison, R.A. (ed.): *Treatise on Invertebrate Paleontology, Part G. Bryozoa Revised, Volume 1*, 304–320. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas.

Boardman, R.S., Cheetham, A.H. & Cook, P.L. 1983: Introduction to the Bryozoa. *In* Robison, R.A. (ed.): *Treatise on Invertebrate Paleontology, Part G. Bryozoa Revised, Volume 1*, 3–48. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas.

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

Borg, F. 1926: Studies on recent cyclostomatous Bryozoa. *Zoologiska Bidrag från Uppsala 10*, 181–507.

Cook, P.L. 1977: Colony-wide water currents in living bryozoans. *Cahiers de Biologie Marine 18*, 31–47.

Cook, P.L. & Chimonides, P.J. 1980: Further observations on water current patterns in living Bryozoa. *Cahiers de Biologie Marine 21*, 393–402.

Cuffey, R.J. 1967: Bryozoan *Tabulipora carbonaria* in Wreford megacyclothem (Lower Permian) of Kansas. *University of Kansas Paleontological Contributions, Bryozoa* Article 1, 1–96.

Gautier, T.G. 1970: Interpretive morphology and taxonomy of bryozoan genus *Tabulipora*. *University of Kansas Paleontology Contributions*, Paper 48, 1–21.

Gould, S.J. & Lewontin, R.C. 1979: The spandrels of San Marco and the panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London B 203*, 581–598.

Gradstein, F.M. & Ogg, J. 1996: A Phanerozoic time scale. *Episodes 19*, 3–5.

Grünbaum, D. 1995: A model of feeding currents in encrusting bryozoans shows interference between zooids within a colony. *Journal of Theoretical Biology 174*, 409–425.

Håkansson, E. 1979: Carboniferous to Tertiary Development of the Wandel Sea Basin, Peary Land, eastern North Greenland. *Rapport Grønlands Geologiske Undersøgelse 88*, 73–83.

Håkansson, E., Heinberg, C. & Stemmerik, L. 1981: The Wandel Sea Basin from Holm Land to Lockwood Ø, eastern North Greenland. *Rapport Grønlands Geologiske Undersøgelse 106*, 47–63.

Håkansson, E. & Madsen, L. 1991: Symbiosis – a plausible explanation of gigantism in Permian trepostome bryozoans. *In* Bigey, F.P. & d'Hondt, J.-L. (eds.): *Bryozoa: Living and Fossil*, 151–159. Societe des Sciences Naturalles de l'Ouest de la France. Memoire hors serie. Nantes, France.

Jackson, J.B.C. & McKinney, F.K. 1990: Ecological processes and progressive macroevolution of marine clonal benthos. *In* Ross R.M. & Allmon, W.D. (eds.): *Causes of Evolution: A Paleontological Perspective*, 173–209. University of Chicago Press, Chicago, Illinois.

Key, M.M., Jr. 1990a: A new family of trepostome bryozoans from the Ordovician Simpson Group of Oklahoma. *Journal of Paleontology 64*, 700–725.

Key, M.M., Jr. 1990b: Intracolony variation in skeletal growth rates in Paleozoic ramose trepostome bryozoans. *Paleobiology 16*, 483–491.

Key, M.M., Jr. 1991a: How to build a ramose trepostome. *In* Bigey, F.P. & d'Hondt, J.-L. (eds.): *Bryozoa: Living and Fossil*, 201–207. Societe des Sciences Naturalles de l'Ouest de la France. Memoire hors serie. Nantes, France.

Key, M.M., Jr. 1991b: The halloporid trepostome bryozoans from the Ordovician Simpson Group of Oklahoma. *Journal of Paleontology 65*, 200–212.

Lidgard, S. 1981: Water flow, feeding, and colony form in an encrusting cheilostome. *In* Larwood, G.P. & Nielsen, C. (eds.): *Recent and Fossil Bryozoa*, 135–142. Olsen & Olsen, Fredensborg, Denmark.

Madsen, L. 1987: Growth and polypide morphology in some ramose trepostome bryozoans from the Permo-Carboniferous of the Arctic. *In* Ross, J.R.P. (ed.): *Bryozoa: Present and Past*, 169–176. Western Washington University, Bellingham, Washington.

Madsen, L. 1991: The species concept in trepostome bryozoans – a study of phenotypical and genotypical variability within the genus *Tabulipora* in North Greenland. 97 pp. Unpublished Ph.D. dissertation, University of Copenhagen, Denmark.

Madsen, L. 1994a: Exozonal budding in trepostome Bryozoa. *In* Hayward, P.J., Ryland, J.S. & Taylor, P.D. (eds.): *Biology and Palaeobiology of Bryozoans*, 113–115. Olsen & Olsen, Fredensborg, Denmark.

Madsen, L. 1994b: *Bryozoans from the Upper Palaeozoic Sequence in the Wandel Sea Basin, North Greenland. Wandel Sea Basin.* 18 pp. Basin Analysis Scientific Report No. 6, University of Copenhagen, Denmark.

Madsen, L. & Håkansson, E. 1989: Upper Paleozoic bryozoans from the Wandel Sea Basin, North Greenland. *Rapport Grønlands Geologiske Undersøgelse* 144, 43–52.

McKinney, F.K. 1975: Autozooecial budding patterns in dendroid stenolaemate bryozoans. *Documents del Laboratoires de Géologie de la Faculté des Sciences de Lyon* Hor Séries 3, 65–76.

McKinney, F.K. 1977: Autozooecial budding patterns in dendroid Paleozoic bryozoans. *Journal of Paleontology 51*, 303–329.

McKinney, F.K. 1986: Historical record of erect bryozoan growth forms. *Proceedings of the Royal Society of London B 228*, 133–148.

McKinney, F.K. & Jackson, J.B.C. 1989: *Bryozoan Evolution*. 238 pp. Unwin-Hyman, London, England.

Pachut, J.F. 1992. Morphological integration and covariance during astogeny of an Ordovician Trepostome bryozoan from communities of different diversities. *Journal of Paleontology 66*, 750–757.

Pachut, J.F. & Anstey, R.L. 1979: A developmental explanation of stability-diversity-variation hypotheses: morphogenetic regulation in Ordovician bryozoan colonies. *Paleobiology 5*, 168–187.

Pachut, J.F., Cuffey, R.J. & Anstey, R.L. 1991: The concepts of astogeny and ontogeny in stenolaemate bryozoans, and their illustration in colonies of *Tabulipora carbonaria* from the Lower Permian of Kansas. *Journal of Paleontology 65*, 213–233.

Patzkowsky, M.E. 1987: Inferred water flow patterns in the fossil *Fistulipora* M'Coy (Cystoporata, Bryozoa). *In* Ross, J.R.P. (ed.): *Bryozoa: Present and Past*, 213–219. Western Washington University, Bellingham, Washington.

Podell, M.E. & Anstey, R.L. 1979: The interrelationship of early colony development, monticules, and branches in Palaeozoic bryozoans. *Palaeontology 22*, 965–982.

Rasmussen, J.A. & Håkansson, E. 1996: First Permo-Carboniferous conodonts from North Greenland. *Geological Magazine 133*, 553–564.

Ross, J.P. & Ross, C.A. 1962: Faunas and correlation of the late Paleozoic rocks of northeast Greenland, part IV, Bryozoa. *Meddelelser Om Grønland 167*, 1–65.

Seilacher, A. 1970: Arbeitskonzept zur konstruktions – morphologie. *Lethaia 3*, 393–396.

Stemmerik, L. 1997: Permian (Artinskian–Kazanian) cool-water carbonates in North Greenland, Svalbard and the western Barents Sea. *In* James, N.P. & Clarke, J.A.D. (eds.): *Cool-Water Carbonates*, 349–364. SEPM Special Publication No. 55. Tulsa, Oklahoma.

Stemmerik, L. & Håkansson, E. 1989: Stratigraphy and depositional history of the Upper Palaeozoic and Triassic sediments in the Wandel Sea Basin, central and eastern North Greenland. *Rapport Grønlands Geologiske Undersøgelse 143*, 21–45.

Stemmerik, L., Håkansson, E., Madsen, L., Nilsson, I., Piasecki, S., Pinard, S. & Rasmussen, J.A. 1996: Stratigraphy and depositional evolution of the Upper Palaeozoic sedimentary succession in eastern Peary Land, North Greenland. *Bulletin Grønlands Geologiske Undersøgelse 171*, 45–71.

Taylor, P.D. 1999: Bryozoans. *In* Savazzi, E. (ed.): *Functional Morphology of the Invertebrate Skeleton*, 623–645. John Wiley & Sons, New York.

Taylor, P.D. & Voigt, E. 1999: An unusually large cyclostome bryozoan (*Pennipora anomalopora*) from the Upper Cretaceous of Maastricht. *Bulletin de l'Institut Royal des Sciences Naturalles de Belgique, Sciences de la Terre 69*, 165–171.

Utgaard, J. 1983: Paleobiology and taxonomy of the order Cystoporata. *In* Robison, R.A. (ed.): *Treatise on Invertebrate Paleontology, Part G. Bryozoa Revised, Volume 1*, 327–357. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas.