

Functional morphology of maculae in a giant ramose bryozoan from the Permian of Greenland

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ABSTRACT: The need for colony-wide feeding currents should be greater in ramose bryozoan colonies with larger diameter branches due to their greater and more planar surface area. This situation was magnified in a giant branch of *Tabulipora* from the Permian of North Greenland. The 8 mm thick exozone allowed the making of 20 serial tangential peels which intersected two maculae. Macular spacing, size, and shape were measured to see how they varied through the exozone in response to increasing branch size. As the branch grew, the spacing and size of the maculae increased, and the maculae became more stellate. These trends continued until the outer exozone, where they reversed, probably in response to the initiation of a new macula. This indicates that macular excurrent chimneys are dynamic in their position, size, and shape in response to changing hydrodynamics of colony-generated, colony-wide currents on a growing branch of a ramose colony.

1 INTRODUCTION

The goals of this project were to quantify the effects of increasing colony branch diameter on macular spacing, size, and shape. These effects should be accentuated in a giant-sized colony. It was hypothesized that as a colony increases its size (i.e. increasing branch diameter) the macular chimneys should become more widely spaced, larger, and more stellate. This is in response to increasing incurrent area as the colony branch expands laterally. For this paper, a macula was defined as a small cluster of non-feeding polymorphs and/or extrazoecial skeleton surrounded by autozoecia that may be depressed below, level with, or elevated above the colony surface (Boardman & Cheetham 1983).

2 COLONY-WIDE FEEDING CURRENTS

Bryozoans are active filter feeders (sensu Jørgensen [1966]) in that their autozooids create their own feeding currents to draw food particles toward their mouths. Autozooids have an inverted cone-shaped lophophore. Lateral cilia on each tentacle of the lophophore beat outwards causing water to be evacuated from the center of the tentacle crown and to pass down toward the mouth and away laterally between the tentacles. This evacuated water is replaced by water flowing into the open end of the lophophore from above. Thus an inhalant current (i.e. incurrent) approaches the autozooid from above and

an exhalent current (i.e. excurrent) departs laterally between the fixed part of the colony surface and the canopy of protruded lophophores.

In extant species polypides feed simultaneously over large areas of the colony so that when lophophores are protruded, they cover the colony surface as densely as possible with minimal overlapping (McKinney 1986a, 1990). In robust ramose colonies with their resulting tightly packed canopy of lophophores, the water that is being pumped by the lophophores toward the colony surface can not be vented from the colony surface between the lophophores (McKinney & Jackson 1989, Taylor 1999). In ramose colonies with small diameter branches with their inherently more curved branch surfaces, the filtered water can exit between the lophophores as they are more widely spaced, and so chimneys are unnecessary (Banta et al. 1974). In ramose colonies with larger diameter branches, the filtered water spreads laterally towards lower pressure regions marked by the absence of incurrents. These regions are called excurrent chimneys as they are sites where filtered water is expelled back out away from the colony surface (Banta et al. 1974, Cook 1977, Winston 1978, 1979, 1981). Chimneys are required to relieve the hydrodynamic resistance to incurrents in larger colonies where surface areas are large relative to peripheral areas (Winston 1979, McKinney 1986b, Dick 1987, McKinney 1990). Thus with an extensive lophophore canopy, efficient performance in food gathering is secured by creating a common, colonial system of feeding currents which effectively

separates incurrent (i.e. unfiltered) and excurrent (i.e. filtered) water masses.

3 MACULAR CHIMNEYS

An excurrent chimney can form in any region that is less densely packed with or completely absent of autozooids with their feeding lophophores (Taylor 1975, 1979), as long as the region is large enough so that the excurrent is unopposed by surrounding incurrents (Boardman 1983). Gymnolaemates can produce a chimney in a group of autozooids simply by titling their lophophores away from one another (Cook 1977, Winston 1978, Cook & Chimonides 1980, Lidgard 1981). Stenolaemates have lophophores that are situated directly above the autozoecial chambers and can not be tilted (McKinney 1988). This may explain why it has never been demonstrated that stenolaemates can form chimneys without involving the skeleton.

Banta et al. (1974) were the first to hypothesize that maculae are two-dimensional skeletal representations of a three-dimensional water exchange phenomenon (Anstey 1987). The hypothesized function of maculae as sites of excurrent chimneys is supported by the observation that skeletal maculae in living bryozoans have chimneys centered on them (Cook 1977, Winston 1978, 1979) and by the observation that many may have been areas of converging flow lines (Anstey 1981, 1987, Patzkowsky 1987).

Thus colony-wide feeding currents centered on chimneys can be inferred from skeletal evidence in fossils. Incurrent areas can be identified as aggregations of autozoecia, whereas macular chimneys can be identified as areas of less densely packed autozoecia or areas devoid of autozoecia (Banta et al. 1974, Taylor 1975, 1979, 1999, Winston 1981). Autozooids are less densely packed in maculae due to more abundant nonfeeding polymorphs and/or buildups of extrazooecial skeleton (McKinney 1986a, Taylor 1999).

In colonies where it has been measured, the total colony surface area dedicated to incurrents is greater than the area of excurrent chimneys (Lidgard 1981, McKinney 1989). Based on this and the principle of continuity, excurrent velocities in chimneys are greater than the incurrent velocities of the individual autozooids supplying the chimneys (Lidgard 1981, McKinney 1986b, 1990, Dick 1987). The principle of continuity states that for every volume of fluid which enters a conduit per unit time, an equal volume must leave (Vogel 1981). These enhanced excurrent flow velocities in the chimneys jet the previously filtered water away from the colony surface, through the boundary layer, and into the overlying flow. Thus, the colony-wide feeding currents keep the incurrents separate from the excurrents which reduces re-filtering of water and improves feeding effi-

ciency (Banta et al. 1974, Winston 1978, 1979, Taylor 1979, Lidgard 1981, Dick 1987). Mathematical modeling of water flow in encrusting bryozoan colonies by Grünbaum (1995, 1997) and Eckman and Okamura (1998) has shown that with or without interzooidal feeding interference, colony-wide feeding currents are beneficial to the colony especially in low current velocities where flow remains laminar.

Previous workers have hypothesized several additional benefits of colony-wide feeding currents. Colony-wide currents may: 1) remove waste materials (Cook 1977, Winston 1979), 2) keep sediment from settling on the colony surface (Cook 1977, Taylor 1979, Boardman 1983), 3) aid gamete and larval dispersal especially for those reproductive polymorphs centered in or near the excurrent areas (Taylor 1979), 4) prevent larval recruitment of spatial competitors on the adjacent substrate (Buss 1979), and 5) mediate competition among adjacent benthic filter feeders in the low velocity fluid boundary layer (Buss 1980, 1981, Lidgard 1981, McKinney 1992).

Most of these functions have also been inferred for colony-wide feeding currents associated with maculae in fossils and in particular for maculae in trepostomes that are elevated above the colony surface (i.e. monticules). There are several additional inferred functions for maculae in trepostomes. It has been suggested that maculae were centers of zooecial budding (Anstey & Delmet 1972, Delmet & Anstey 1974, Anstey et al. 1976, Pachut & Anstey 1979, Anstey & Pachut 1980). Maculae may have also been the centers of cormidia (i.e. subcolonies) involved in morphogenetic regulation of the colony (Anstey et al. 1976, Pachut & Anstey 1979, Patzkowsky 1987). As with living colonies, it has been suggested that maculae in fossil colonies served a reproductive role as many maculae contained large polymorphs similar to reproductive gonozooids in living stenolaemates (Ulrich 1890, Astrova 1973, Anstey et al. 1976).

4 MATERIAL

This study was based on a single Geological Survey of Greenland specimen (GGU 196054-1) of the stenoporid trepostome stenolaemate bryozoan *Tabulipora*. The branch fragment 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 its immense size, it was possible to cut a large (1800 mm³) block out of the exozone that was 15 mm wide, 15 mm long, and 8 mm deep. From this block, 20 serial tangential acetate peels were made. Smaller branch fragments were available for study, but these were not utilized as their thinner exozones prohibited the making of enough serial peels to draw statistically significant conclusions. The macular pat-

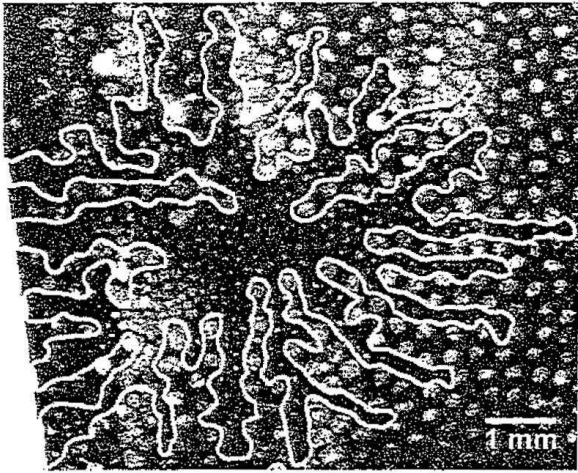


Figure 1. Photomicrograph of a tangential section of the exozone of *Tabulipora* sp. (GGU 196054-1) showing Macula 1 (outlined in white) at 6.51 mm from endozone. Note the stellate macula defined by contiguous exilazooecia. The left side of the macular channels are truncated.

terns described below are known from smaller specimens and other species and are not simply a phenomenon of this giant specimen.

Other giant stenolaemate colonies are known from elsewhere (e.g. Taylor & Voigt 1999), but these Greenland colonies are at least an order of magnitude larger than other stenolaemates specifically and bryozoans in general (Madsen 1991). Their large size has been attributed to symbiotic, photosynthetic, zooxanthellae algae living intracellularly within the zooids (Håkansson & Madsen 1991).

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, 1994) and skeletal space-filling (Key et al. 2001).

The specimen was collected during the 1980 expedition of the regional geological mapping project of eastern North Greenland (Håkansson et al. 1981). The specimen, previously figured by Håkansson & Madsen (1991, Pl. 1, Fig. 4), and its peels are housed in the Geological Museum at the University of Copenhagen (MGUH 25.988-26.008). 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). The Kim Fjelde Formation is Early Permian (late Artinskian to Kungurian stages) in age (Stemmerik et al. 1996).

With a branch diameter of 37.5 mm, this branch fragment is wider than typical *Tabulipora* colony branch fragments of equal length (Håkansson & Madsen 1991: Figs. 1-4) and is classified as having an erect robust maculate radial branch growth form

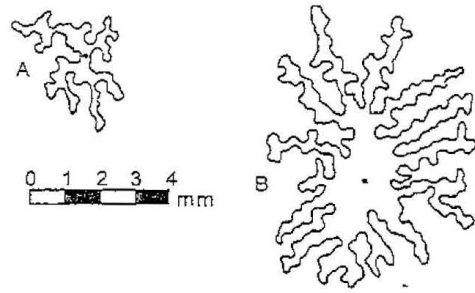


Figure 2. Outlines of Macula 2 of *Tabulipora* sp. (GGU 196054-1) at A) 1.02 mm from endozone and B) 7.38 mm from endozone.

(sensu McKinney 1986a, b, 1990). This growth form usually contains regions of feeding zooids (autozooids) that form incurrent regions that surround regions of excurrent flow (maculae) where autozooids are absent. The maculae in this colony were composed of clusters of contiguous exilazooecia similar to those in cystoporates (e.g. Boardman 1983: Fig. 59.5). The intermacular autozoocial chamber cross-sectional areas in this colony were on average 10 times larger than the macular exilazooecial chamber cross-sectional areas (Key et al. 2001). As the macular exilazooecia were so small, they probably did not house feeding lophophores like the intermacular autozoocia. This inability of kenozoocia (e.g. exilazooecia and mesozoocia) to feed has been suggested by previous workers (Ulrich 1890, Boardman 1983, McKinney & Jackson 1989, Taylor 1999). Without feeding, the exilazooecia would not have been able to create inflow. Without inflow, the macular clusters of contiguous exilazooecia would have acted as excurrent chimneys.

5 CHARACTERS MEASURED

In the specimen, maculae were practically invisible on the colony surface due to their lack of relief, but in magnified tangential section they were very prominent with their stellate shape formed by radiating bifurcating channels (Fig. 1). The block of exozone contained two maculae (herein referred to as Macula 1 and Macula 2). Macular outlines in the peels were determined by the distribution of contiguous exilazooecia (Fig. 1). 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.

Five characters were measured as follows: 1) Intermacular distance was measured as the linear distance between macular centers; 2) Macular area was measured as the area within the macular outline; 3) Macular shape was quantified using a stellateness index defined as the macular outline perimeter length squared divided by the product of the macular area

and 4π . This yielded a dimensionless number with a minimum value of 1 for a perfect circle. The macular stellateness index increased with the amount of convolution of a macula's shape; 4) The number of channels (arm-like extensions of the maculae; Fig. 1) per macula was measured by counting the number of separate projections of contiguous exilazooecia out from the macular center. For example Macula 2 in the peel closest to the endozone had 14 channels (Fig. 2A), whereas it had 43 channels in the peel farthest from the endozone (Fig. 2B); 5) Channel length was measured as the mean curvilinear distance from the macular center to the end of the five longest channels.

All of the characters were measured using digitized video images of the tangential serial peels at 50x or 100x magnification. All of the characters were measured on each of the 20 peels except for peels 13 and 20. All of the measurements were repeated ten times per macula per peel except for the number of macular channels which was measured once per peel per macula and the intermacular distance which was measured once per peel.

Tabulipora has distinctive moniliform (i.e. alternating thin-and thick-walled) zooecial walls in the exozone. Tangential sections intersecting both thin-and thick-walled zones reveal multiple bands of thin-and thick-walled zooecia oriented parallel to the branch axis. All macular characters were measured in the thick-walled zones.

6 SOURCES OF ERROR

One problem with tangential sections of cylindrical colony branches is that the depth of the sections 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. 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 giant 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 branch fragment, the effect of making tangential sections of a cylindrical surface had a 2.3 % maximum error on the macular characters (Key et al. 2001).

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 in the nine outermost peels and in Macula 2 in the three outermost peels (e.g. left side Fig. 1).

7 RESULTS AND DISCUSSION

Intermacular distance increased significantly ($R^2 = 0.614$, $p < 0.001$) through the exozone from 9.36 mm at 1.02 mm from the endozone to 10.01 mm at 7.38 mm from the endozone (Fig. 3). If these maculae functioned as excurrent chimneys as originally proposed by Banta et al. (1974), then they may have had a geometric regularity in their spatial distribution. Previous workers have noted the rhombic/hexagonal close-packed array of chimneys over colony surfaces (Banta et al. 1974, Delmet & Anstey 1974, Anstey et al. 1976, Pachut & Anstey 1979, Lidgard 1981, Boardman 1983). Chimney spacing 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 chimneys which are distant from the colony margin. This is supported by the observations of previous workers who have reported that chimneys have a relatively constant spacing of 1-5 mm (Taylor 1975, Cook 1977, Lidgard 1981, McKinney 1986b). This regular spacing may not be the case in ramose colonies that grow by expansion of the entire branch. As the branch expands in size, previous workers have inferred or shown that macular chimneys migrate apart (Taylor 1975, Anstey et al. 1976, Pachut & Anstey 1979, Anstey 1981). Chimney spacing also varies with chimney size as bigger chimneys tend to be more widely spaced (Pachut & Anstey 1979). The only way to maintain constant chimney spacing in ramose colonies is to bud new maculae in the intermacular regions.

The surface areas occupied by the two maculae increased significantly through the exozone (Fig. 4). Macula 1 experienced a three fold increase in area ($R^2 = 0.929$, $p < 0.001$) while Macula 2 grew six fold ($R^2 = 0.945$, $p < 0.001$). These increases are minimums as the maculae actually increased from a smaller size at the endozone/exozone boundary to a larger size at the colony surface. The maculae increased their size by budding new macular exilazooecia (Key et al. 2001).

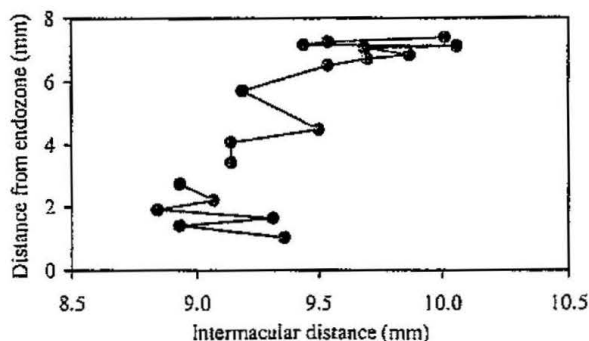


Figure 3. Plot of intermacular distance versus distance from endozone.

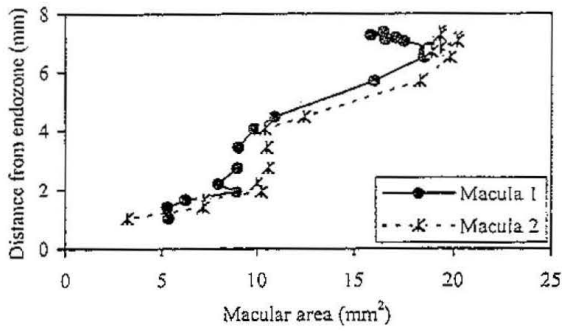


Figure 4: Plot of macular area versus distance from endozone.

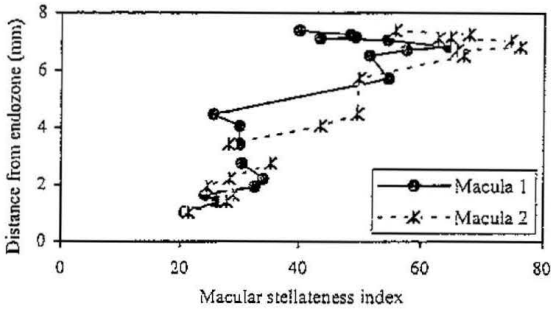


Figure 5. Plot of macular stellateness index versus distance from endozone.

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 established 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 to 2.0 mm (Banta et al. 1974, Cook 1977, Cook & Chimionides 1980, Lidgard 1981). This should not be the case in ramose colonies that grow by expansion of the entire branch. As the colony branch expands in size, previous workers have inferred or shown that macular chimneys increase in size as well (Anstey et al. 1976, Pachut & Anstey 1979, Podell & Anstey 1979, Anstey 1981). This is probably due to increasing incurrent area requiring a larger excurrent flow through the macular chimney (McKinney 1986b). Thus, as a colony branch expands by increasing the width of its exozone, more maculae should develop. In fact, maculae rarely occur on branches with diameters less than 2 mm (McKinney 1986a).

The shape of the maculae in *Tabulipora* became significantly more stellate through the exozone (Macula 1: $R^2 = 0.687$, $p < 0.001$; Macula 2: $R^2 = 0.897$, $p < 0.001$) (Fig. 5). Many excurrent maculae are star-shaped (Anstey 1987), for example those in the cystoporate *Constellaria* (Boardman 1983, Fig.

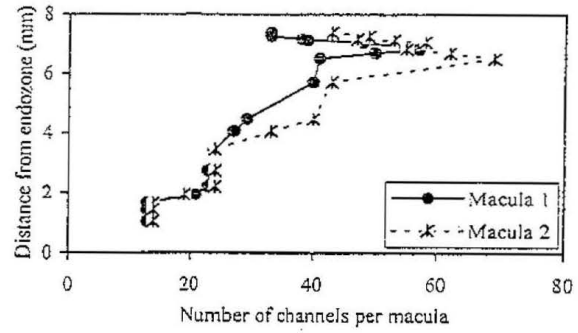


Figure 6. Plot of number of channels per macula versus distance from endozone.

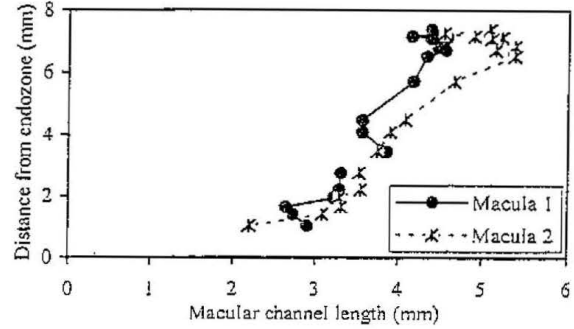


Figure 7. Plot of macular channel length versus distance from endozone.

59.1) and the trepostome *Heterotrypa* (Anstey & Perry 1973, Plate 17). As first noticed by Anstey & Pachut (1976) and Anstey et al. (1976), stellate maculae are similar to centripetal flow structures in other organisms such as astrophorae in living sclerosponges (e.g. Hartman & Goreau 1970: Fig. 5) and fossil stromatoporoids (e.g. LaBarbera & Boyajian 1991: Fig. 1) as well as inorganic centripetal flow structures such as star dunes (e.g. Nielson & Kocurek 1987: Fig. 2A).

The number of channels per macula and the length of the channels also increased significantly through the exozone (Figs. 6 and 7, respectively). The number of channels in Macula 1 more than doubled ($R^2 = 0.761$, $p < 0.001$), while the number in Macula 2 tripled ($R^2 = 0.848$, $p < 0.001$). Macula 1's mean channel length increased 52% ($R^2 = 0.916$, $p < 0.001$), while Macula 2's mean channel length increased 132% ($R^2 = 0.904$, $p < 0.001$).

These last three characters, stellateness index, number of channels, and channel length all increased in response to increasing colony branch size. This probably reflects the need for the macular chimneys to handle more water flow as the incurrent surface area increases. With a more complex stellate shape with more and longer channels, the more efficiently the maculae can collect filtered water into the center of the maculae for ultimate expulsion from the colony surface. This is supported by the work of Patzkowsky (1987) that showed that in some bryozoans as the maculae increase in size, the water flow

into the maculae becomes more centripetal around the maculae. As the colony branch increases in circumference, the macular channels act as rivers cutting upstream in a drainage basin and capturing more and more "runoff" as the "drainage" basin grows. Macular shape could also be affected by ambient flow through the branches of the colony in a way similar to the effect seen in elongate maculae in colonies epizoic on nektonic hosts (Baird et al. 1989).

The general pattern of increasing macular spacing, size, and stellateness through the exozone masks some smaller scale changes. All five of the macular characters measured reached a maximum value in both maculae from 6.51 mm to 7.11 mm from the endozone; then they generally decreased toward the colony surface (Figs. 3-7). This indicates something fundamental changed in the exozone in this depth range. It is probable that the initiation of a new macula caused this effect, as the sizes of both maculae peaked and then declined toward the colony surface. Previous workers have shown that new macular chimneys may develop in the intermacular areas (Anstey et al. 1976), and old ones can shrink and disappear (Pachut & Anstey 1979). What happens to the exilazooecia in a macula when it decreases in size? They transform ontogenetically into autozooecia, pass into the intermacular areas, and are not replaced by new exilazooecia.

The decrease in macular size was more pronounced in Macula 1 than Macula 2. Macula 1's size definitely decreased while Macula 2's remained relatively constant (Fig. 4). This suggests a new macula had been initiated closer to Macula 1 than Macula 2. There was no evidence in the peels of a new macula developing in the exozone from 6.51 mm to 7.11 mm from the endozone. This may reflect that the new macula was on an adjacent part of the exozone and not in the block of exozone sampled in this study. The fact that macular size decreased and did not stay constant at some optimum size suggests that some of the incurrent autozooecia supplying the previous maculae had been pirated by the new macula (sensu stream piracy). Taylor (1975) argued that as a colony branch grows and its circumference increases, there will be an increase in the spacing between adjacent macular chimneys and a deviation from the optimum spacing. Hence, unless new macular chimneys are added and/or pre-existing ones expand in size, the feeding efficiency of the colony will decrease as the colony branch grows in circumference.

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 the intermacular regions of this colony (Madsen 1994, Key et al. 2001). Autozooecial packing did not change significantly through the exozone in the incurrent areas. Consistent packing of autozooecia in the intermacular areas was needed to keep the optimal spacing of lophophores in the can-

opy so as to not disrupt the colony-wide feeding currents. This fixed spacing of intermacular autozooecia was regulated by the exilazooecia which were randomly distributed between the autozooecia (Madsen 1991, Key et al. 2001).

8 CONCLUSIONS

This study represents the first time the dynamic nature of macular spacing, size, and shape has been documented serially through the exozone of a ramose bryozoan colony. It was shown that maculae significantly increased in spacing, size, and stellateness through the exozone. This trend continued until roughly 6.81 mm from the endozone when it reversed, and macular spacing, size, and stellateness began to decrease probably in response to the intercalation of a new macula. In this colony of *Tabulipora*, the growth in branch diameter directly affected the hydrodynamics of the colony-wide feeding currents. As the branch diameter increased, the overall branch surface area increased, and most importantly the area of intermacular autozooecia increased. This increased the area of incurrent flow. As a result of the principle of continuity, the macular chimneys increased in spacing, size, and stellateness presumably to accommodate the increasing incurrent flow with a higher excurrent flow rate. The distance between the maculae increased as the branch grew so the maculae had to increase in size and stellateness to maintain their functionality until a new macula budded, and they began to decrease in size. If maculae did not increase in spacing, size, and stellateness and/or if new maculae did not develop, the feeding efficiency of the colony would have decreased as the branch diameter increased.

In smaller colonies of *Tabulipora* with 3-4 mm diameters, macular chimneys may have functioned with only a cluster of three exilazooecia. In this large colony branch, larger more stellate maculae were needed to create functional excurrent chimneys. This type of excurrent chimney which can change size and shape by adding or removing exilazooecia (Key et al. 2001) may be very flexible to accommodate a range of colony branch sizes.

Do macular chimneys have an optimal spacing, size, and shape? These results suggest not, because intermacular distance, macular area, and stellateness index never reached stasis. Macular position in ramose colonies is not fixed in an absolute sense as maculae migrate away from one another as branch diameter increases and toward one another as the number of adjacent maculae increases. Maculae are fixed in their position relative to one another in a radial growth trajectory sense. The spacing, size, and stellateness of maculae increase with increasing branch diameter and then decrease when an adjacent macula is budded. Macular spacing appears to be a function

of macular size, and size appears to be a function of incurrent area. In contrast, maculae may have an optimal spacing, size, and shape in encrusting colonies where colony growth is restricted to the colony margins.

Efficient colony-wide feeding currents centered on macular chimneys may be an intrinsic part of bryozoan colony function and shape, but they have a cost to the colony. These currents are maintained at some metabolic expense to the colony as the chimneys occupy colony surface area which could be filled with feeding zooids (Lidgard 1981, Taylor 1999). In this colony, the combined mean macular areas of 12.7 mm² and 14.3 mm² occupied 12 % of the area of the peel. This number was representative of the entire colony only if the packing of maculae in this block of exozone was representative of the general surface of the colony. McKinney (1986b) measured the sizes of macular chimneys in Paleozoic bryozoans and found 5-25 % of the colony surface area being occupied with most estimates being 10-15 %. Our value of 12 % supports these estimates.

Despite the loss of feeding zooids to macular area, colony-wide feeding currents have evolved independently in numerous bryozoan clades (Banta et al. 1974). This suggests there must be a metabolic energy gain in colonies that have colony-wide feeding currents. In fact, maculae become a virtual necessity in large colonies to provide a flow rate sufficient to sustain the colony (McKinney 1991). The generation and maintenance of efficient colony-wide feeding currents and their resulting decrease in metabolic cost of expelling filtered water has had an evolutionary impact throughout the history of the phylum (Banta et al. 1974, McKinney 1986a, b, Jackson & McKinney 1990). The development of chimneys for outflow of filtered water was critical in the evolution of the bryozoans as chimneys removed the hydrodynamic constraint on branch width in ramose bryozoans (McKinney 1986a), and branch width in turn affected the structural strength of bryozoan colony branches (Key 1991).

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