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Stream channel network analysis applied to colony-wide feeding structures in a Permian bryozoan from Greenland

Marcus M. Key Jr., Patrick N. Wyse Jackson, and Louis J. Vitiello

Abstract.—Colony-wide feeding currents are a common feature of many bryozoan colonies. These feeding currents are centered on excurrent macular chimneys that expel previously filtered water away from the colony surface. In some bryozoans these macular chimneys consist of a branching channel network that converges at a point in the center of the chimney. The bifurcating channels of the maculae are analogous to a stream channel network in a closed basin with centripetal drainage. The classical methods of stream channel network analysis from geomorphology are here used to quantitatively analyze the number and length of macular channels in bryozoans. This approach is applied to a giant branch of the trepostome bryozoan *Tabulipora* from the Early Permian Kim Fjelde Formation in North Greenland. Its large size allowed 18 serial tangential peels to be made through the 8-mm-thick exozone. The peels intersected two stellate maculae as defined by contiguous exilapores. The lengths of 1460 channels radiating from the maculae were measured and their Horton-Strahler stream order and Shreve magnitude scored.

We hypothesize that if fossil bryozoan maculae function as excurrent water chimneys, then they should conform to Horton's laws of stream networks and behave like closed basins with centripetal drainage. Results indicate that the stellate maculae in this bryozoan behaved liked stream channel networks exhibiting landscape maturation and stream capture. They conformed to the Law of Stream Number. They have a Bifurcation Ratio that falls within the range of natural stream channel networks. They showed a pattern opposite that expected by the Law of Stream Lengths in response to behavior characteristic of a centripetal drainage pattern in a closed basin. Thus, the stellate maculae in this bryozoan probably functioned as excurrent water chimneys with the radiating channels serving to efficiently collect the previously filtered water, conducting it to the central chimney for expulsion away from the colony surface.

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Introduction

One of the challenges for filter-feeding animals is how to maximize feeding by minimizing refiltering previously filtered water. As sessile active filter-feeding animals, bryozoans have evolved colony-wide feeding currents to solve this problem. The colony-wide feeding currents are centered on macular chimneys. Macular chimneys are sites where previously filtered water is expelled from the colony surface. Macular chimneys exhibit centripetal flow, and in some bryozoans they have a stellate branching pattern. The goal of this project is to apply stream channel network analysis to understand water flow in stellate maculae of a Permian bryozoan.

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 outward, 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, autozooids feed simultaneously over large areas of the colony so that when lophophores are protruded, they cover the colony surface as densely as possible

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without overlapping (McKinney 1986a, 1990). In larger encrusting and ramose colonies with their resulting tightly packed canopy of lophophores, the water that is being pumped by the lophophores toward the colony surface cannot be vented from the colony surface between the lophophores (McKinney and Jackson 1989; Taylor 1999). In ramose colonies with smaller diameter branches and inherently more curved branch surfaces, the filtered water can exit between the lophophores because they are more widely spaced, and so chimneys are unnecessary (Banta et al. 1974). In larger encrusting colonies and in ramose colonies with larger diameter branches, the filtered water spreads laterally toward lower-pressure regions caused by the absence of incurrents (Larsen and Riisgård 2001). These regions are called excurrent chimneys because they are sites where filtered water is jetted 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, colony-wide system of feeding currents that effectively separates incurrent (i.e., unfiltered) and excurrent (i.e., filtered) water masses.

Macular Chimneys

An excurrent chimney can form in any region that is less densely packed with or completely lacking 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 tilting their lophophores away from one another (Cook 1977; Winston 1978; Cook and Chimonides 1980; Lidgard 1981). Stenolaemates have lophophores that are situated directly above the autozooecial chambers and cannot 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 this 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). Thus colony-wide feeding currents centered on chimneys can be inferred from skeletal evidence in fossils. Incurrent areas can be identified as aggregations of relatively more densely packed autozooecia, whereas macular chimneys can be identified as areas of lower autozooecial densities or areas devoid of autozooecia (Banta et al. 1974; Taylor 1975, 1979, 1999; Winston 1981). Autozooids are less densely packed or absent in maculae owing to more abundant nonfeeding polymorphs (e.g., larger megazooids or exilapores and mesopores that are smaller than autozooids) and/or buildups of extrazooidal skeleton (McKinney 1986a; Taylor 1999).

Maculae may be depressed below, level with, or elevated above the colony surface (Boardman and Cheetham 1983). Those elevated above the colony surface (i.e., monticules) are analogous to mamelons on stromatoporoid sponges. Some monticules are stellate (e.g., *Constellaria florida*) as stellate structures are a common result of centripetal flow. Such structures can be seen at a variety of spatial scales from star dunes in deserts (Folk 1971; Anstey and Pachut 1976; Nielson and Kocurek 1987) to astrorhizae in sclerosponges (Boyajian and LaBarbera 1987; LaBarbera and Boyajian 1991).

In addition to improved filter-feeding efficiency, 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 filer feeders in the low-velocity fluid boundary layer (Buss 1980, 1981; Lidgard 1981; McKinney 1992). Some if not all of these benefits would be achieved by the centripetal flow inferred for the macular chimneys in this study.

Most of these functions have also been inferred for colony-wide feeding currents associated with maculae in fossils and in particular for monticules in trepostomes. There are several additional inferred functions for maculae in trepostomes. It has been suggested that maculae were centers of zooecial budding (Anstey and Delmet 1972; Delmet and Anstey 1974; Anstey et al. 1976; Pachut and Anstey 1979; Anstey and 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 and Anstey 1979; Podell and Anstey 1979; Patzkowsky 1987; McShea and Venit 2002). As with living colonies, it has been suggested that maculae in fossil colonies served a reproductive role because many maculae contain large polymorphs (i.e., megazooids) similar to reproductive gonozooids in living stenolaemates (Ulrich 1890; Astrova 1973; Anstey et al. 1976).

Flow patterns over the colony surface of fossils can also be inferred from the orientations of autozooecial lunaria and cystiphragms (Anstey 1981, 1987; Patzkowsky 1987). This requires the assumption that these orientations indicate the direction of individual lophophore-generated incurrents. This approach suggests that most (but not all) maculae were areas of centripetal flow, and thus functioned as excurrent chimneys (Anstey 1981, 1987; Patzkowsky 1987; Shunatova and Ostrovsky 2002).

In colonies where it has been measured, the total colony surface area dedicated to incurrents is greater than the area of excurrent macular chimneys (Lidgard 1981; McKinney 1989). This observation and the principle of continuity would suggest that 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 that 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 low-velocity fluid boundary layer created by the colony's surface roughness, through the ambient flow around the colony, and into the overlying flow. Thus, the colony-wide feeding currents keep the incurrents separate from the excurrents, reducing refiltering of water and improving feeding efficiency (Banta et al. 1974; Winston 1978, 1979; Taylor 1979; Lidgard 1981; Dick 1987; Eckman and Okamura 1998; Pratt 2004; Von Dassow 2005a). Empirical data and mathematical modeling of water flow in encrusting bryozoan colonies has shown that currents created by individual zooids may interact deleteriously (Bishop and Bahr 1973; Thorpe and Ryland 1987; Grünbaum 1995). All of these observations thus indicate that colony-wide feeding currents are beneficial to the colony at least in low current velocities where flow remains laminar (Grünbaum 1997; Eckman and Okamura 1998). We hypothesize that if fossil bryozoan maculae function as excurrent water chimneys, then they should conform to Horton's laws of stream channel networks and behave like closed basins with centripetal drainage.

Stream Channel Network Analysis

The first approach used here is the classic system introduced by Horton (1945) and modified by Strahler (1957). Herein it will be referred to as the Horton-Strahler stream order method. This method assigns an order to each branch of the stream. A first-order stream is one that has no tributaries. Where two first-order streams converge, the result is a second-order stream. A third-order stream is the result of two second-order streams merging, and so on. As originally proposed by Horton (1945), each second-order stream arbitrarily extends to the tip of the longest tributary it drains. Strahler (1957) modified this method so that each second-order stream did not extend headward to the tip of the longest tributary it drained. In this way, each segment of the stream was designated an order.

The second approach used is the Shreve (1967) magnitude method. In this method each stream without a tributary is assigned a magnitude of one. When two streams meet, the resulting stream is given a magnitude of the sum of the two connecting streams. This approach is essentially identical to Scheidegger's (1966) equivalent integer method, and it is more informative with respect to the hydrodynamics of fluid flow than the more morphology-based Horton-Strahler stream order method. In this method a lower-order stream can empty into a higher-order stream; however in the Horton-Strahler stream order method, the order of the stream will not change unless it is of equal order. The volume of water entering the higher-order stream is not accounted for in the Horton-Strahler stream order method, whereas the Shreve magnitude method does account for it.

Horton's (1945) pioneering work led to his recognition of several laws of stream morphology. The first is Horton's Law of Stream Number ($N_w = R_b^{\Omega - w}$), which states that the number of streams of the various orders (N_w) in a given basin tends to form a geometric progression, beginning with a single trunk stream of the highest order (Ω), and increasing in number (N) and decreasing in order (w) upstream according to a constant Bifurcation Ratio (R_b). R_b is the dimensionless ratio of the number of segments of any order (w) to the number of segments in the next highest order (w+1).

Horton's Law of Stream Lengths ($L_w = L_1 R_L^{w-1}$) states there is a geometric relationship between the average length of streams (L) of a given order and the corresponding order (w) so that the mean stream length increases with increasing stream order. The parameter of this relationship is the so-called Length Ratio (R_L), which is the dimensionless ratio of the average length of streams of any order (w) to the average length of the next lower order ($w-1$).

What is the basis for these laws? Stream channel networks have similar topologies that follow the principles of maximum entropy (i.e., maximum efficiency in the words of Leopold [1971], thermodynamic optimization in the words of Bejan [2000], or maximum throughput of material with the least resistance in the words of Bejan and Lorente [2008]). According to Leopold's Principle of Economy or Bejan's Constructal Theory, many branching patterns are governed by the opposing tendencies of minimum energy expenditure and uniform energy utilization. The branching systems evolve in a way to provide easier access to the imposed currents that flow through them (Bejan and Lorente 2008).

In contrast, Shreve (1966) and Kirchner (1993) argue that network structures are a statistical inevitability of the topologies of such networks. But their conclusions have subsequently been questioned (Troutman and Karlinger 1994; Dodds and Rothman 2000). Regardless of the causes of these laws, the robustness of Horton's laws has withstood numerous empirical tests in natural stream drainages varying in size, climate, and geologic setting (e.g., Strahler 1952; Leopold et al. 1964; Andah et al. 1987). Stream channel network analysis has also been successfully applied on other planetary systems (e.g., Stepinski and Collier 2003 on Mars; Baugh and Brown 2008 on Titan) as well as to branching networks as varied as limbs in trees (Leopold 1971; Barker et al. 1973), bronchioles in lungs of several species including humans (Horsfield and Cumming 1976; Horsfield et al. 1976; Thurlbeck and Horsfield 1980), as well as maculae in bryozoans (Patzkowksy 1987). Patzkowksy (1987) was the first to argue that maculae are essentially closed circular drainage basins with stream networks converging at the macular chimney.

The application of stream channel network analysis to the dichotomous branching of channels in bryozoan maculae differs in four ways from that of its original use in river drainage systems. First, drainage basins operate between fluids of dissimilar densities (i.e., water flowing in open channels below a gaseous atmosphere). In macular chimneys the fluids are of similar densities (i.e., filtered water in macular channels flowing below unfiltered ambient water above the lophophore canopy). Second, drainage basins are not flat and especially don't slope upward, but the maculae in this study are flat to slightly monticulate. This problem is partly shared with natural streams because their measured lengths are slightly shortened by projection onto the horizontal plane of a map (Morisawa 1957). Third, each macula represents a closed drainage basin with various channels coalescing toward the center of the macula. Such drainage basins are atypical among natural landscapes. Fourth, macular channels are nine orders of magnitude smaller than the longest river. This raises questions of the applicability of physical processes across a range of different scales.

Stream channel network analysis has been successfully applied to systems at a variety of scales from drainage basins, to lungs, to maculae as discussed above. The issue of scaling in drainage basins has been addressed by studies comparing the dynamics of drainage basins of different sizes (Pilgrim et al. 1982; Pilgrim 1983). These studies have demonstrated that any differences seen can be accounted for in terms of geographical location, underlying soils, water infiltration, annual runoff differences, water loss from channels, and likelihood of the basin to be affected by storms. Another recent study of sediment budgets in basins of different spatial scales has suggested that ''scale invariance of sediment budgets is improbable'' (Slaymaker 2006: p. 8). None have discussed possible differences in discharge caused exclusively by rescaling channel lengths and complexity, which in our study we examine. The factors mentioned above that might modify the relationship between basins of different scales do not come into play in maculae of fossil bryozoans.

One of the reasons that Rudwick's (1964) paradigm method for inferring function from form (i.e., functional morphology) works is because the laws of mechanics apply equally to all systems. Rudwick's paradigm applies to the possible functions that a fossil structure served in life, and whether it can possibly work mechanically and biologically (Turner 2000). Rudwick's paradigm applies here because stream channel networks are controlled by the laws of fluid mechanics regardless of whether the system is an extinct organic one on the scale of 10^0 mm (e.g., the bryozoan macular channels in this study) or an extant inorganic one on the scale of 10^3 km (e.g., the Nile River channel). The mathematics and physics of mechanics apply equally to both (Paul 1975; Dodds and Rothman 2000). It is not until smaller scales ($<10^0$ mm) where other processes (e.g., diffusion) because more important.

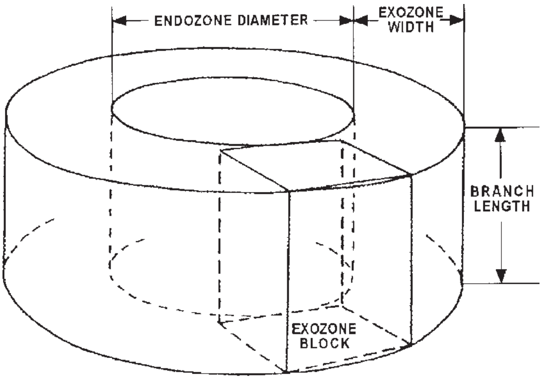

FIGURE 1. Diagrammatic representation of a cylindrical trepostome branch showing the block of exozone cut. Modified from Key et al. (2001: Fig. 1).

Material

This study is based on a single specimen from the Geological Survey of Greenland (GGU 196054-1) of the stenoporid trepostome stenolaemate bryozoan *Tabulipora*. In ramose trepostome bryozoans, the interior of the branch is referred to as the endozone (Fig. 1) and is occupied by thinner-walled portions of zooecia that gradually bend outward from a growth trajectory parallel to the branch axis to one that is more perpendicular. The exterior of the branch (i.e., the exozone; Fig. 1) is occupied by thicker-walled portions of zooecia with a growth trajectory more perpendicular to the branch axis. The branch fragment has 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. Because the colony was so large, it was possible to cut a block out of the exozone (Fig. 1). The block was 15 mm wide, 15 mm long, and 8 mm deep, and has a total volume of 1800 mm^3. From this block, 18 serial tangential acetate peels were made. Smaller branch fragments were available for study, but these were not utilized because their thinner exozones prohibited the making of enough serial peels to draw statistically significant conclusions. The macular patterns described below are known from smaller specimens and other species and are not unique to this giant specimen.

The shallowest peel was made 0.62 mm below the colony surface (i.e., 7.38 mm above the endozone-exozone boundary), and the deepest was 1.02 mm above the endozone-exozone boundary. The spacing between the serial peels ranged from 0.05 mm to 1.23 mm with a mean of 0.39 mm. The peels and remnants are housed in the Geological Museum at the University of Copenhagen (MGUH 25.988–26.008).

The specimen was collected during the 80 expedition of the regional geological mapping project of eastern North Greenland (Håkansson 1979; Håkansson et al. 1981). It was collected from Midnatfjeld in the Kim Fjelde area in eastern Peary Land in eastern North Greenland (Stemmerik and Håkansson 1989: Fig. 16, locality 11c) from the Kim Fjelde Formation at its type section (Stemmerik and Håkansson 1989; Stemmerik et al. 1996). The Kim Fjelde Formation is part of the Mallemuk Mountain Group, which is part of the Wandel Sea Basin sedimentary sequence (Håkansson 1979; Stemmerik and Håkansson 1989). The Kim Fjelde Formation is Early Permian (late Artinskian to Kungurian Stages) in age (Rasmussen and Håkansson 1996; Stemmerik et al. 1996).

The fauna of the Kim Fjelde Formation is dominated by large robust stenoporid trepostomes with dichotomously branching colonies. Branch fragments are often more than 20 cm long and up to 7 cm in diameter (Ross and Ross 1962; Håkansson 1979; Madsen 1987, 1994; Madsen and Håkansson 1989; Håkansson and Madsen 1991; Stemmerik 1997). Similar giant stenolaemate colonies are known from elsewhere (e.g., Taylor and Voigt 1999), but these Greenland colonies are at least an order of magnitude larger than other stenolaemates specifically and other bryozoans in general (Key et al. 2005). Their large size was originally attributed to symbiotic, photosynthetic, zooxanthellae algae living intracellularly within the bryozoan colony (Håkansson and Madsen 1991), but that is no longer considered to be a likely cause (Key et al. 2005).

With a branch diameter or 37.5 mm, this colony of *Tabulipora* is larger than typical *Tabulipora* colony branch fragments of equal length (Håkansson and Madsen 1991: Figs. 1–4) and is classified as having an erect robust maculate radial branch growth form (sensu McKinney 1986a,b, 1990). This growth form usually contains macular chimneys. The maculae in this colony are composed of clusters of contiguous exilapores similar to those in other trepostomes (e.g., Boardman 1983: Fig. 59.5) and cystoporates (e.g., Utgaard 1983: Fig. 159e). In keeping with the terminology introduced by Boardman and Buttler (2005), the term exilapores is used here instead of exilazooecia as previously done by Key et al. (2001, 2002). The intermacular autozooecial chamber cross-sectional areas in this colony are on average ten times larger than the macular exilapore chamber cross-sectional areas (Key et al. 2001). Because the macular exilapores were so small, they probably did not house feeding lophophores as in the intermacular autozooecia. This inability of kenozooecia (e.g., exilapores and mesopores) to feed was suggested by previous workers (Ulrich 1890; Boardman 1983; Boardman et al. 1983a; McKinney and Jackson 1989; Taylor 1999). Without the ability to feed, the exilapores would not have been capable of creating inflow, strengthening the inference that macular clusters of contiguous exilapores acted as excurrent chimneys.

Characters Measured

In the specimen, maculae are practically invisible on the colony surface owing to their minimal relief, but in magnified tangential section they are very prominent with their stellate shape formed by radiating bifurcating channels (Fig. 2). The block of exozone contains two maculae (herein referred to as Macula 1 and Macula 2). Macular outlines in the peels were identified by mapping the distribution of contiguous exilapores (Fig. 2) and were delineated for each macula in each of the 18 serial peels.

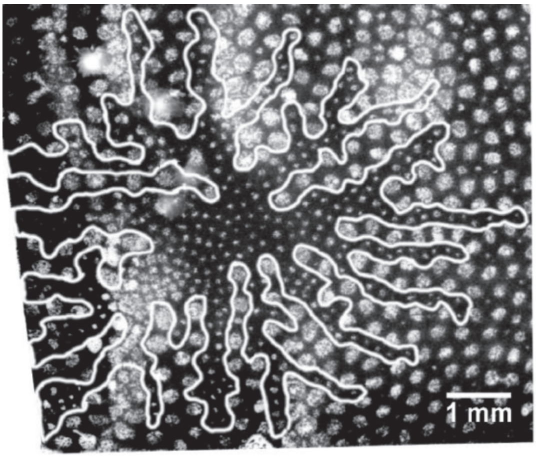

FIGURE 2. Photomicrograph of a tangential section of the exozone of *Tabulipora* sp. (GGU 196054-1) showing Macula 1 (outlined in white) at a distance of 6.51 mm above the endozone-exozone boundary. Note the stellate macula defined by contiguous exilapores, the truncated macular channels on the left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

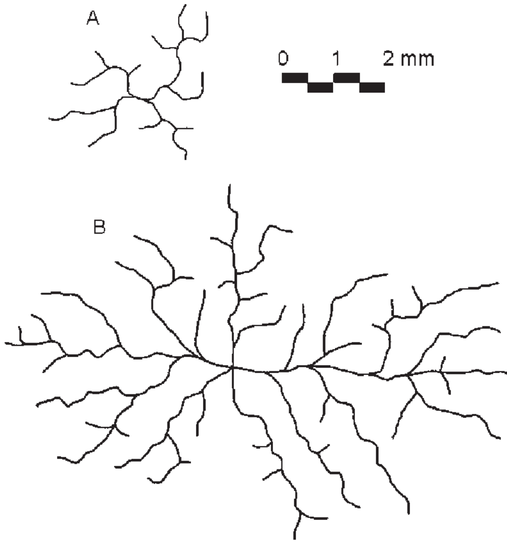

FIGURE 3. Network of Macula 2 channels at a distance of 1.02 mm above the endozone-exozone boundary (A) and at 6.51 mm above the boundary (B) in *Tabulipora*.

Macular outlines were scanned into digital form at a resolution of 600 dpi. Using Adobe Photoshop, a single channel axial line was drawn down the center of every macular channel at high magnification. Channel lines were drawn in such a way that if a perpendicular line were drawn from the sides of the channel toward the center of the channel, the center of the perpendicular line would be the point where it intersects the macular channel line (Fig. 3). The number of channels was counted and their lengths measured by using digitized video images of the channel lines drawn from the macular outlines at 15× magnification. This process was repeated for both maculae on each of the 18 peels, yielding a total of 1640 channels. Each channel was assigned both a Horton-Strahler stream order and a Shreve magnitude.

Our study was conducted at the maximum resolution of the scale of the smallest functional unit controlling macular size and shape (i.e., exilapore chamber cross-sectional area; mean = 0.007 mm^2 [Key et al. 2001]). This avoids the problem of fractal scaling when using digital elevation models to define network topologies in streams (e.g., Pelletier 1999; Lin et al. 2003).

Sources of Error

A problem with a tangential section of a cylindrical colony branch 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. 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 smaller diameters and less problematic in larger colonies like the one in this study. The magnitude of this variation depends on both the lateral width of the tangential section and the radius of the branch. In this colony, the effect of making tangential sections of a cylindrical surface produced a maximum measurement error of 2.3% for channel lengths (Key et al. 2001).

A second source of error for macular characters is caused by the truncation of the lateral margin of maculae in some peels. This error is most noticeable in the nine outermost peels of Macula 1 and in the three outermost peels of Macula 2 (e.g., left side of Fig. 3). An

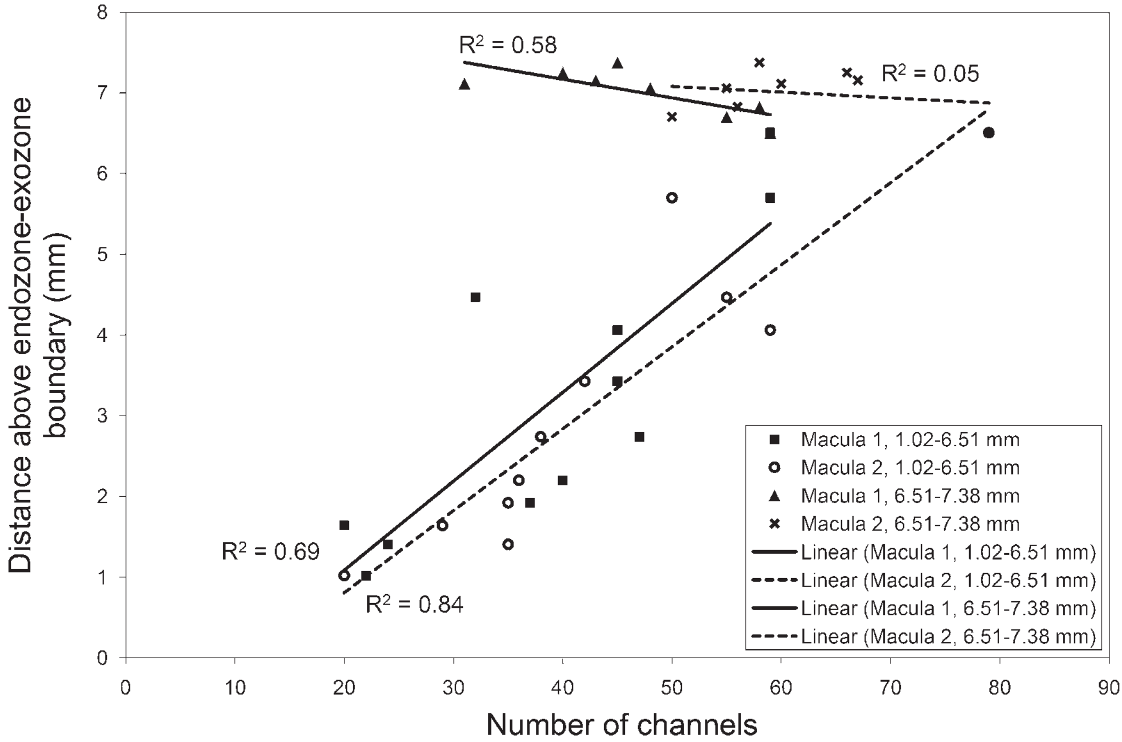

FIGURE 4. Plot of number of channels versus distance above the endozone-exozone boundary in two maculae of *Tabulipora*.

unlikely, but potential, source of error is from the moniliform structure of zooecial walls in this species of *Tabulipora* (e.g., Key et al. 2001: Fig. 3; Key et al. 2005: Fig. 2). This is expressed as the vertical bands of lighter, thin-walled and darker, thick-walled exozonal zooecia in Figure 2, reflecting the moniliform wall structure in the exozone. Varying wall thicknesses might lead to misidentification of an exilapore as an autozooecium or vice versa, affecting the identification of inferred boundaries of maculae.

Results and Discussion

In general, the number of channels increased during exozonal growth in both maculae (Fig. 4). In Macula 1, the number of channels increased significantly (linear regression: $r^2 = 0.378$, $p < 0.007$) from 22 channels at 1.02 mm above the endozone-exozone boundary to 45 channels in the outer most peel, 7.38 mm above the boundary. Over the same interval of growth, the number of channels in Macula 2 also increased significantly (linear regression: $r^2 = 0.744$, $p < 0.001$) from 20 to 58. A rapid reversal in this general trend occurs at 6.51 mm above the endozone-exozone boundary, where the slopes change from positive to negative (Fig. 4).

The total channel length also generally increased during exozonal growth in both maculae (Fig. 5). In Macula 1, the total length of channels increased significantly (linear regression: $r^2 = 0.439$, $p < 0.003$) from 18 mm at 1.02 mm above the endozone-exozone boundary to 47 mm in the outer most peel, 7.38 mm above the boundary. Over the same interval of growth, Macula 2 increased in size significantly (linear regression: $r^2 = 0.480$, $p < 0.002$) from 13 to 55 mm. A trend reversal, similar to the one Figure 4, occurs at 6.51 mm above the endozone-exozone boundary (Fig. 5).

Key et al. (2002) measured macular area in these same maculae and showed that the area of Macula 1 begins to contract at 6.51 mm above the endozone-exozone boundary, probably from an adjacent newly initiated macula.

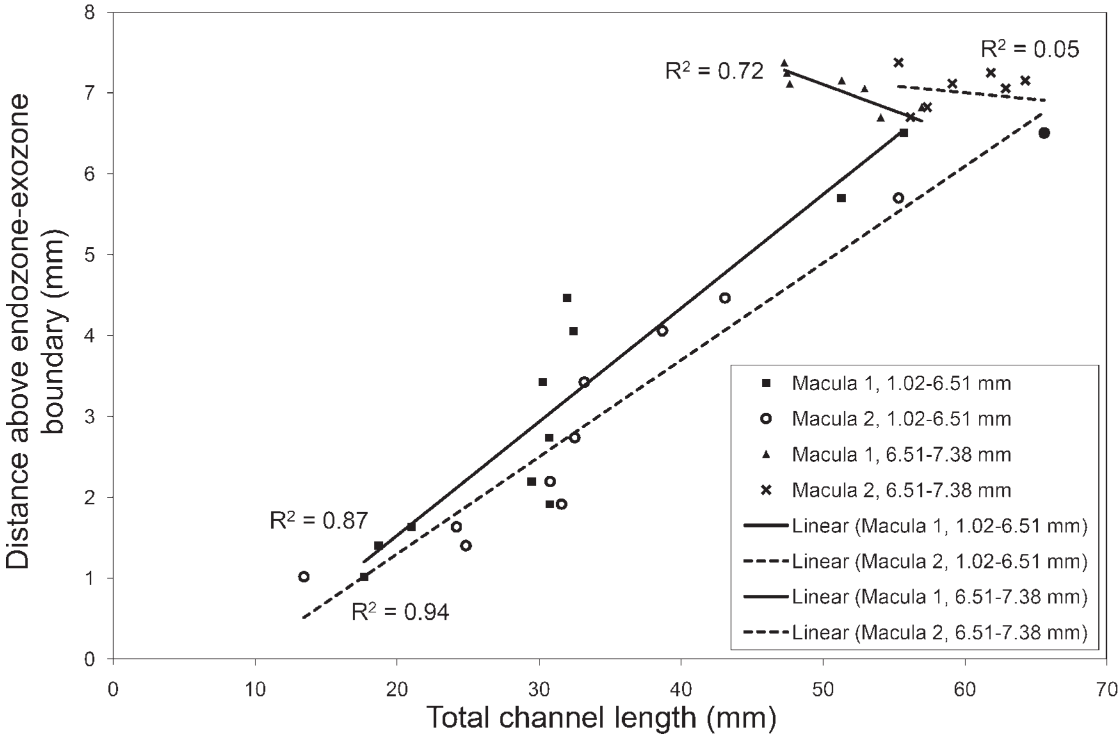

FIGURE 5. Plot of total channel length versus distance above the endozone-exozone boundary in two maculae of *Tabulipora*.

Because the newly formed macula grew by ''stream capture,'' Macula 1 shrank (in total number of channels, total channel length area, and area), whereas the growth in Macula 2 stalled. The new macula is inferred to have formed closer to Macula 1 than 2 because Macula 2 did not shrink significantly after 6.51 mm (Key et al. 2002). Previous workers have shown that new macular chimneys may develop in intermacular areas (Anstey et al. 1976; Pachut 1992; Key et al. 2002), and old ones can shrink and disappear (Pachut and Anstey 1979).

There is no evidence in the peels of a new macula developing in the exozone between 6.51 mm and 7.11 mm above the endozone-exozone boundary. The new macula may have developed in an adjacent part of the exozone not sampled in this study. That macular size is not constant at some optimum (Key et al. 2002) suggests that some incurrent autozooids supplying the preexisting maculae have 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 preexisting ones expand in size, feeding efficiency of the colony will decrease as colony branches grow in circumference.

The macular chimneys grew in area and channel length (Key et al. 2002) as the whole colony grew in size in order to accommodate the added incurrent flow of the autozooid lophophores. It is likely that macular area and channel length cannot grow indefinitely. It is reasonable to surmise that at 6.51 mm above the endozone-exozone boundary, in this one small part of the exozone, the macular chimneys reached a maximum size. Beyond this size it became too costly and inefficient to increase the size of the macular chimneys, owing to drag of the water moving along the colony's surface.

Using the Horton-Strahler stream order method, Macula 1 peaked at fourth order at

7.06 mm above the endozone-exozone boundary (0.55 mm above 6.51 mm). Macula 2 peaked at fourth order at 4.47 mm above the boundary (2.04 mm below 6.51 mm). With the Shreve magnitude method, Macula 1 peaked at a magnitude of 14 at 6.83 mm above the endozone-exozone boundary (0.32 mm above 6.51 mm), whereas Macula 2 peaked at a magnitude of 22, 7.11 mm above the boundary (0.60 mm above 6.51 mm). This is an average of 0.14 mm below 6.51 mm, a difference of only 2.2%. Thus, stream orders/magnitudes support the general change in macular morphology at approximately 6.51 mm above the endozone-exozone boundary.

The maximum Horton-Strahler stream order did not significantly increase throughout exozonal growth for either macula (linear regression: Macula 1: $r^2 = 0.024$, $p = 0.537$; Macula 2: $r^2 = 0.102$, $p = 0.197$). This lack of statistical significance is not unexpected because maximum stream order is a discrete variable that varied from 2 to 4 in these maculae, 83% of which had a value of 3. In contrast, Shreve magnitude increased significantly. In Macula 1, the maximum Shreve magnitude increased from 5 to 8 during exozonal growth (linear regression: $r^2 = 0.309$, $p = 0.017$), and the Shreve maximum in Macula 2 increased from 4 to 15 (linear regression: $r^2 = 0.633$, $p < 0.001$).

This general increase in channel order/magnitude is to be expected because maculae enlarge during exozonal growth, similar to rivers cutting upstream in a drainage basin and capturing more ''runoff'' as the ''drainage'' basin expands. This is analogous to the macular chimney increasing its incurrent area as well as the volume of water discharged as the colony grows. A macula on a younger branch with a smaller diameter is analogous to an immature drainage pattern imposed on a recently elevated landscape (Fig. 3A), whereas a macula on an older branch with a larger diameter is similar to the drainage pattern seen on a mature landscape (Fig. 3B).

In various landscapes, drainage basin area is directly proportional to maximum stream order (Chorley 1969; Andah et al. 1987). We did not find a significant correlation for either macula using the Horton-Strahler order. Using the Shreve magnitude method we found a significant correlation for both Macula 1 and 2 between macular area and maximum Shreve magnitude (linear regression: $r^2 = 0.37$, $p = 0.007$ and $r^2 = 0.59$, $p < 0.001$), respectively). This was expected, as discussed above, because Horton-Strahler stream order values vary less and are based primarily on morphology, whereas Shreve magnitude values are more variable and are based more on hydrologic behavior. In natural river basins, drainage basin area is directly proportional to total stream length (Leopold et al. 1964). The same is true for these macular chimneys, where the correlation coefficient for both Macula 1 and 2 for macular area versus total channel length is 0.98 ($p < 0.001$).

In many biological fluid transport systems, there is feedback between the way they function and how they develop, that causes remodeling of the system. This has been documented in the internal fluid transport systems of a variety of diverse organisms. Examples include the veins of plasmodial slime molds (Nakagaki et al. 2001), the gastrovascular canals of hydroids (Buss 2001), and vertebrate circulatory systems (Langille 1995). This function-dependent development has also been suggested in bryozoans, where fluid flow affects the formation of macular chimneys that act as external fluid transport systems (Dick 1987; Grünbaum 1997; Okamura and Partridge 1999; Larsen and Riisgård 2001; Von Dassow 2005a, 2006). Unlike internal fluid transport systems, the external fluid transport systems of macular chimneys interact with the ambient flow environment through conduits that form openings into the external fluid for expelling filtered water (Von Dassow 2005b). Function-dependent development explains the documented changes in macular area, number of channels, and channel order/magnitude. The macular chimneys increased in size and complexity as the colony branch grew. The dynamic change in form and function of the maculae during exozonal growth is function-dependent development.

Horton's Law of Stream Number states that, moving downstream through a given

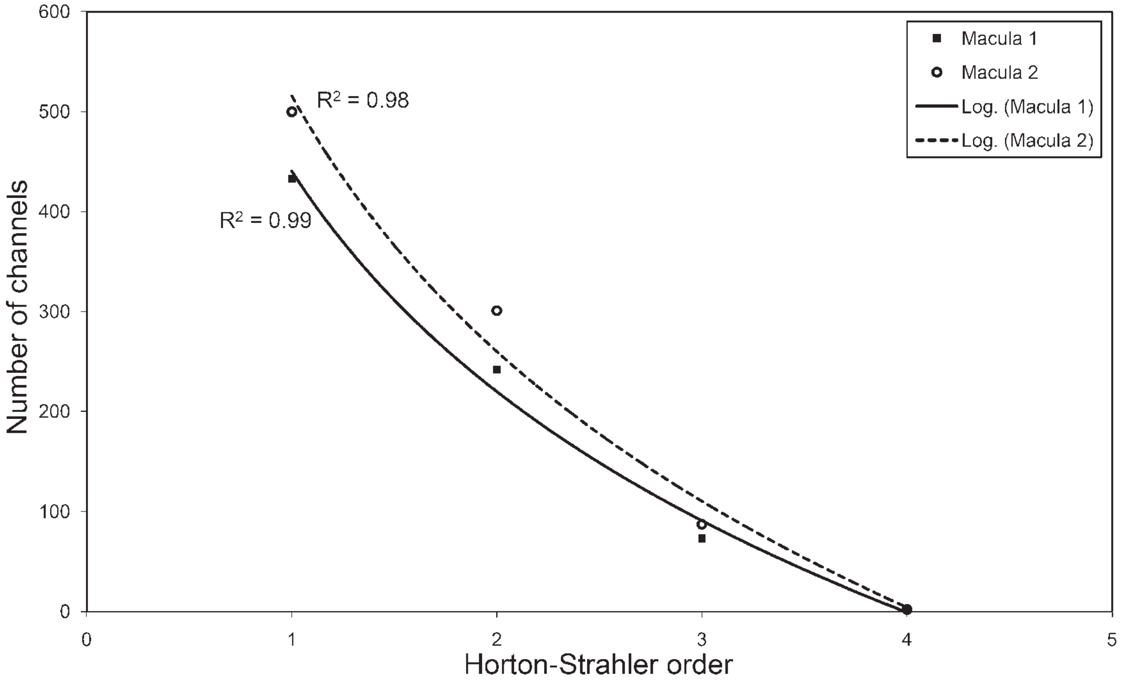

FIGURE 6. Plot of Horton-Strahler order by number of channels in two maculae of *Tabulipora*.

drainage basin, the number of streams decreases with increasing stream order, according to a constant Bifurcation Ratio (R_b). Our results from the Horton-Strahler stream order method show just that, with the number of channels, totaled across all 18 peels, decreasing with increasing order in a logarithmic progression with an r^2 of 0.99 for Macula 1 and 0.98 for Macula 2 (Fig. 6). A similar trend is seen with the Shreve magnitudes, with an r^2 of 0.72 for Macula 1 and 0.62 for Macula 2 (Fig. 7). Thus, the channels in the macular chimneys are conforming to the Law of Stream Number just like stream channels.

R_b is the dimensionless ratio of the number of segments of any order to the number of segments in the next highest order. From his study of 246 natural drainage basins, Shreve (1966) showed that R_b ranges from 2 to 6+ with a mode of 3.5. Macula 1 had an R_b of 2.7, whereas for Macula 2 it was 2.5. These values are on the lower end of natural stream basins. Basins with lower R_b values are more prone to flooding because there are relatively fewer channels downstream to accept discharge (Chorley 1969). This is common in closed drainage basins, where the higher order channels are forced to merge as they converge on the center of the basin, like the macular chimneys in this study. Thus, the macular chimneys are behaving like closed drainage basins with small R_b values.

According to Horton's Law of Stream Lengths, as one moves downstream within a drainage basin the mean length of streams increases as stream order increases. Our results found an opposite pattern: the mean length of channels decreased in a logarithmic progression, with an r^2 of 0.95 for Macula 1 and 0.84 for Macula 2 (Fig. 8). A similar trend is seen in the Shreve magnitudes, with an r^2 of 0.92 for Macula 1 and an r^2 of 0.80 for Macula 2 (Fig. 9).

Why have we found this inverse relationship? In part it is an artifact of using the Strahler method of ordering rather than the original Horton method (Morisawa 1968). Horton considered the length of a higher-order stream to extend from its headwaters to its mouth. In contrast, the Strahler method breaks up each stream into segments. The inverse relationship also occurs because maculae behave as closed basins with centripetal flow. As a result there is less interchannel

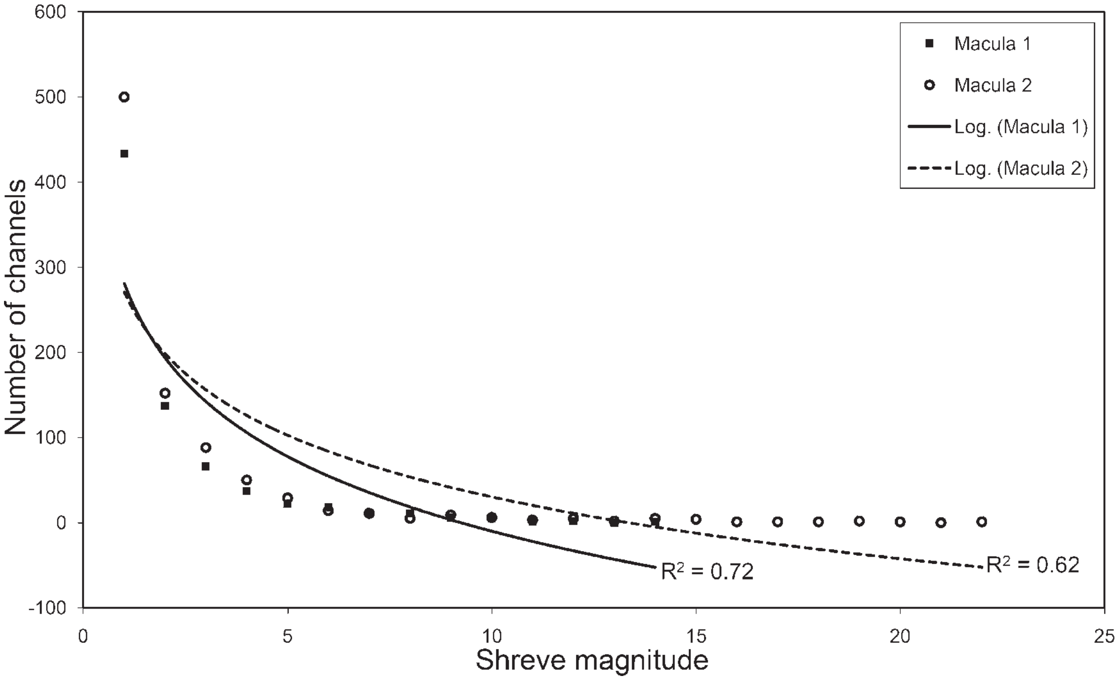

FIGURE 7. Plot of Shreve magnitude by number of channels in two maculae of *Tabulipora*.

space as the channels converge toward the center of the macula, and the excurrent channel at the center of each macula truncates the highest-order channels, analogous to what happens to inflowing streams in closed lake basins. Morisawa (1968) noted that higher-order stream lengths are shorter than they should be in some watersheds. Thus, macular

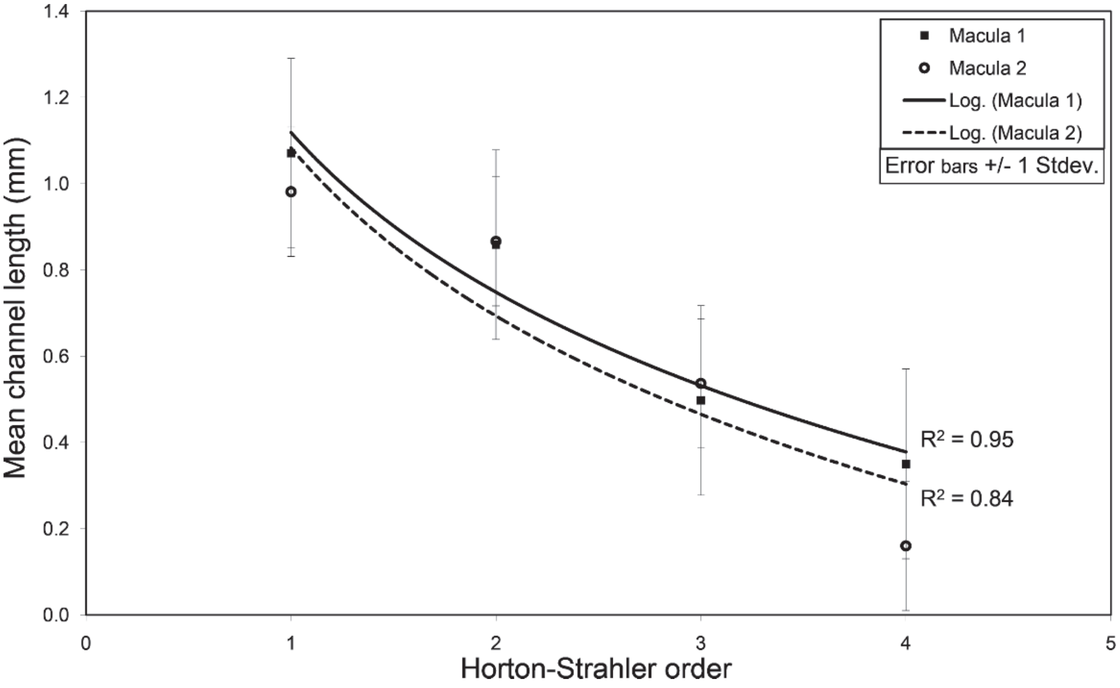

FIGURE 8. Plot of Horton-Strahler order by mean channel length in two maculae of *Tabulipora*.

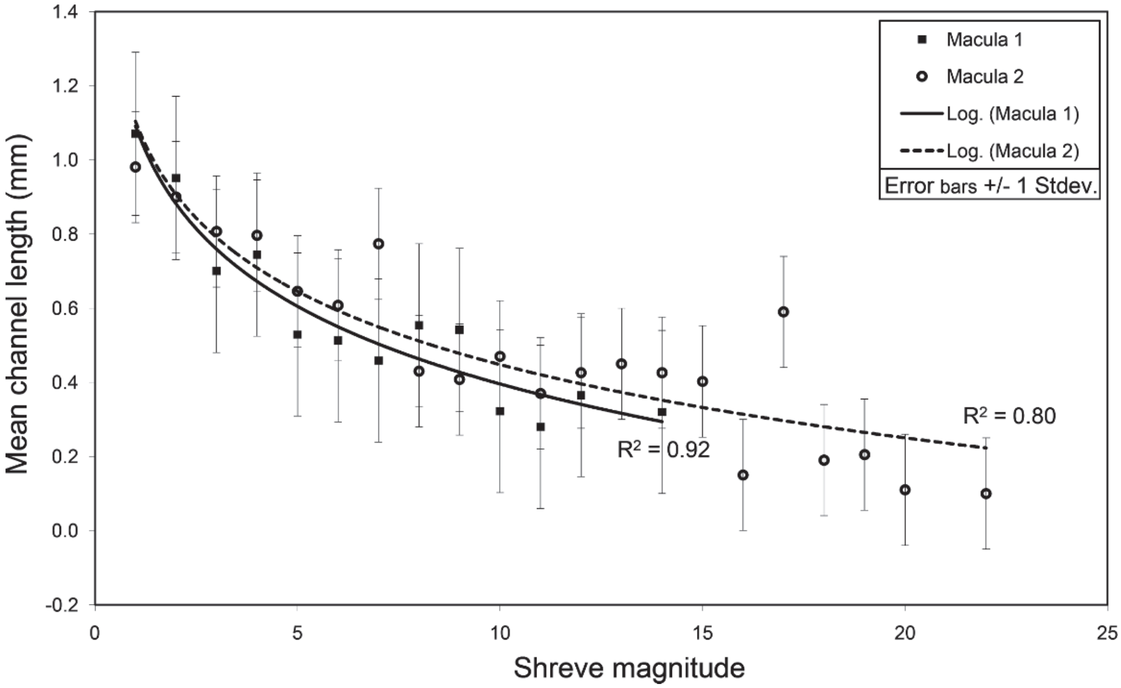

FIGURE 9. Plot of Shreve magnitude by mean channel length in two maculae of *Tabulipora*.

chimneys behave like closed drainage basins with shorter higher-order streams.

Conclusions

This study has applied stream channel network analysis to stellate maculae in a bryozoan to determine if its macular channels behave like natural stream networks. We hypothesize that if fossil bryozoan maculae function as excurrent water chimneys, then they should conform to Horton's laws of stream networks and behave like closed basins with centripetal drainage. Our results fail to reject the hypothesis that the stellate maculae did behave like excurrent water chimneys with centripetal flow.

The stellate macular chimneys in this bryozoan (1) behaved like stream channel networks exhibiting landscape maturation, (2) behaved like stream channel networks exhibiting stream capture, (3) conformed to the Law of Stream Number, (4) had a Bifurcation Ratio that fell within the range of natural stream channel networks, and (5) exhibited the opposite of what the Law of Stream Lengths predicted, because they behave like centripetal stream drainage in a closed basin. Thus, the stellate maculae in this bryozoan probably functioned as excurrent water chimneys, with the radiating channels serving to efficiently collect previously filtered water, conducting it to the central chimney for expulsion away from the colony surface. Improved filtering efficiency for feeding zooids must have compensated calorically for the reduction in feeding zooids required to create the macular channels.

The number of channels, the total length of channels, as well as stream order and magnitude all increased with increasing branch size. This appears to reflect the need for macular chimneys to handle increased water flow as incurrent surface area increases. Increased number of channels, longer channels, and more complex drainage networks increased the efficiency of maculae in collecting filtered water and expelling it from the colony surface. As the colony branch increased in circumference, macular channels responded like rivers cutting upstream in a drainage basin, capturing increasing volumes of ''run-off'' as the ''drainage'' basin enlarged.

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