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Intracolony variation in skeletal growth rates in Paleozoic ramose trepostome bryozoans

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Abstract.—All erect, branching (ramose) organisms adhere to the same fundamental geometric growth law: the rate of distal growth decreases away from the branch axis. Regardless of the phylogenetic history of an organism, the formation of cylindrical branches requires adherence to this law. In colonial ramose organisms such as trees, corals, and bryozoans, this law poses a problem. How do colonies coordinate the growth rates of the individual modules to produce an integrated branch? This question is addressed in the context of three Ordovician and three Devonian species of ramose trepostome bryozoans. Using remnant growing tips in the endozone as isochronous surfaces, relative rates of skeletal secretion among zooids were measured. Measurements of skeletal and void spaces across a colony branch enabled calculation of the volume of skeletal material secreted by zooids between successive remnant growing tips. Results indicate that rate of skeletal secretion systematically decreases from the branch axis outward into the exozone. This suggests that zooid morphogenesis is controlled to a certain degree by the colony. Colonial control over zooidal growth rates in turn regulates the shape of the colony.

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Introduction

The morphology of organisms directly affects their ecological and thus their evolutionary success. The ability of sessile, colonial organisms to free themselves from the confines of the substrate provides them with many selective advantages while introducing many structural problems. Erect growth reduces the chance of overgrowth by adjacent organisms competing for substrate space (Jackson 1979). Erect colonies encounter more environments by growing vertically (three-dimensionally) than non-erect ones (Cheetham 1971). This provides access to resources in the water column that are not available to organisms confined to the substrate (Jackson 1979). But there are costs to erect growth. In an aqueous environment with currents, erect growth places greater reliance on the structural integrity of the basal attachment (Cheetham 1971; Cheetham and Thomsen 1981).

In colonial organisms, erect growth poses an additional problem. How can the sometimes autonomous individual modules (e.g., ramets, polyps, or zooids) produce an integrated, erect, branching colony? In this study, I ask how trepostome bryozoans achieve this; does the colony control the growth of zooids to produce an erect, branching colony?

In some ramose trepostomes, basal diaphragms are periodically secreted by zooids at the growing tip of a branch (Boardman 1960: pl. 7, fig. 2; Madsen 1987: fig. 3). These diaphragms are useful in marking the three-dimensional surface of the growing tip, which is basically hemispherical in shape. In a two-dimensional section bisecting this surface longitudinally, the diaphragms form a distally convex band across the endozone that extends laterally into the exozone (Fig. 1). As the branch grows distally, successive bands of diaphragms (remnant growing tips) become incorporated into the branch. There can be several such bands of diaphragms in the endozone, each representing the position of the growing tip at some time during the past growth of the branch. In most cases, the spacing of successive bands of diaphragms through astogeny is irregular (Boardman 1960: pl. 7, fig. 2; Gautier 1970: pl. 6, fig. 1a; Madsen 1987: fig. 3). These bands may reflect environmental fluctuations and/or zooidal degeneration-regeneration cycles.

It is assumed that these bands of diaphragms represent isochronous growth surfaces. This assumption is in keeping with the two current models for trepostome bryozoan growth (Boardman 1960, 1983; Madsen 1987).

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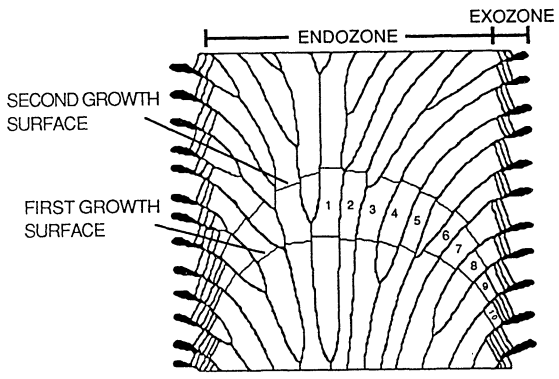

FIGURE 1. Diagrammatic representation of a typical longitudinal section of a ramose trepostome colony showing former growth surfaces in endozone. Numbers refer to zooids measured in a single series. Modified from McKinney (1977).

It follows that the time it takes to grow from one growth surface to the next is the same for all zooids between those successive growth surfaces. However, the linear distance between successive growth surfaces diminishes from the branch axis to branch periphery. For example, in Fig. 1, the distance between the two growth surfaces is greater for zooid 1 than for zooid 10. This means that zooid 1 grew distally farther than zooid 10 during the interval of time between the two growth surfaces. Therefore, rate of distal growth must differ, with zooid 1 growing farther than zooid 10. It is intuitively obvious that the ramose growth habit would not be possible without this disparity in growth rates. This is a fundamental geometric growth law. All ramose organisms (e.g., trees, corals, bryozoans) grow in this way. To permit a cylindrical branch in ramose trepostome branches, the rate of distal zooidal growth must be greatest at the branch axis and least at the outer surface of the exozone. If the rate of distal zooidal growth is equal across the branch, the resulting branch would not be a branch at all, but a hemisphere.

The question addressed by this study is whether or not the volume of skeletal calcite secreted by zooids varies among zooids across a growth interval. This has important implications for colonial integration, especially in regard to colonial versus zooidal control of growth rates. Compared with the variation in length of distal growth among zooids, it is not intuitively obvious whether the volume of skeletal material secreted varies among zooids. The reason is that as the rate of the distal growth of zooids decreases toward the exozone, the zooecial wall thickness of the zooids increases as the zooids pass from the thin-walled endozone into the thick-walled exozone. Do the rates at which these two characters change compensate one another so that the volume of skeleton secreted is the same for all zooids in the branch? The null hypothesis is that the rate of skeletal material secreted by zooids is the same, regardless of the position of the zooid across the width of the branch.

Materials

To test this hypothesis, 12 series of zooids were analyzed as shown in Fig. 1. A series is a sequence of roughly adjacent zooids that cross two successive growth surfaces. Only zooids having diaphragms marking both growth surfaces were included. For example, in Fig. 1, the zooid between numbers 5 and 6 was not included because it lacks a diaphragm for the first growth surface. Because each series is symmetrical on both sides of the endozone, only one side was analyzed. The 12 series were taken from six species that have well-defined bands of diaphragms across the endozone marking previous growth surfaces (Table 1). Three of the species come from the Ordovician Simpson Group fauna of Oklahoma (Loeblich 1942; Key 1988, 1990): *Bimuropora conferta* (Coryell), *Bimuropora dubia* (Loeblich), and *Bimuropora winchelli* (Ulrich). The remaining three species come from the Devonian Hamilton Group fauna of New York (Boardman 1960): *Atactotoechus fruticosus* (Hall), *Leptotrypella asterica* Boardman, and *Leptotrypella multitecta* Boardman.

Except for *L. multitecta*, two colonies from each species were analyzed. One series was measured on each colony, so that two series were measured for each species. For *L. multitecta*, the two series (11 and 12) were measured on the same colony. All colonies are housed in the collections of the United States National Museum of Natural History (USNM). Their USNM numbers are indicated in Table 1.

The species and colonies chosen for mea-

TABLE 1. List of species measured.

Series no.	Species	USNM no.	Age	No. of zooids	
				Endozone	Exozone
1	*Bimuropora conferta*	435421	Ordovician	8	7
2	*B. conferta*	435429	Ordovician	3	10
3	*B. dubia*	100497	Ordovician	11	3
4	*B. dubia*	435404	Ordovician	10	6
5	*B. winchelli*	435436	Ordovician	8	3
6	*B. winchelli*	435443	Ordovician	12	5
7	*Atactotoechus fruticosus*	133940	Devonian	12	5
8	*A. fruticosus*	133943	Devonian	16	0
9	*Leptotrypella asterica*	133893	Devonian	23	6
10	*L. asterica*	133896	Devonian	20	0
11	*L. multitecta*	133884	Devonian	9	4
12	*L. multitecta*	133884	Devonian	10	7

suring were those in which the series are well defined. As a series is followed outward from the branch axis, it becomes difficult to follow in the exozone. At some point in the exozone, the series can no longer be confidently followed. At this point, measurements on the series were stopped. The number of zooids measured per series ranges from 11 to 29 with a mean of 17. The number depends on the width of the endozone and on how well the series could be followed into the exozone. The species with the widest endozone (*L. asterica*) has the most zooids per series (20 and 29).

Characters Measured

Three characters were measured on each zooid within each of the 12 series (Fig. 2). Measurements were made on digitized video images of thin sections at magnifications up to 110×. Through repeatability experiments the measurement error was calculated as 2.82%. Each character was measured five times per zooid at roughly evenly spaced intervals along the zooid. This was done to obtain a better representation of the character being measured. Thin sections are not always oriented exactly parallel to the branch axis and zooids do not grow perfectly straight. Sometimes they pass slightly in and out of the plane of the section. By averaging the five measurements, some of this noise was reduced.

The first character measured was interzooecial wall thickness (Fig. 2). It was measured on the inner zooecial wall (i.e., the zooecial wall closest to the branch axis). The mean interzooecial wall thickness determined for each zooid was divided by two in order to obtain the mean zooecial wall thickness contributed by each of the adjacent zooids.

Zooecial chamber width was the second character, measured as the distance between the inner zooecial wall and the outer zooecial wall (Fig. 2). The zooecial chamber is here defined as the void space in a zooid bounded on the sides by zooecial walls and on the ends by diaphragms. If each zooid is perfectly bisected longitudinally along its length, the true zooecial chamber width will be revealed. In reality, the zooecial chamber width varies as the zooid passes partially in and out of the plane of the thin section. This creates the possibility that the measurements of the zooecial chamber width may be too small. To correct for this, the maximum zooecial chamber width from the five measurements was used. This gives a better representation of the true zooecial chamber width than does mean zooecial chamber width.

The third character measured was zooecial chamber length, the distance between two adjacent diaphragms marking successive growth surfaces (Fig. 2).

Calculation of Skeletal Volume

To determine the relative growth rates among zooids, it is necessary to calculate the volume of skeletal material secreted by each zooid. From the three characters (mean zooecial wall thickness, maximum zooecial chamber width, and mean zooecial chamber length), zooid volume, zooecial chamber vol-

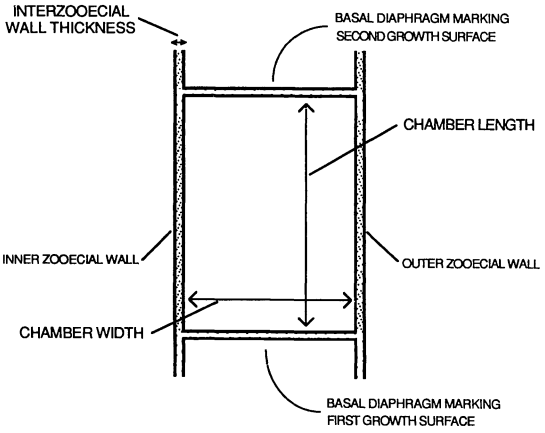

FIGURE 2. Diagrammatic representation of a zooecial chamber in longitudinal section showing characters measured. Stippled areas represent skeletal material secreted by zooid.

ume, skeletal volume, and skeletal area were calculated. The zooid includes the zooecial chamber and its surrounding skeletal walls. All of the calculations assume that the zooid and its corresponding zooecial chamber are cylindrical. In some trepostomes, zooids may be more prismatic than cylindrical, although their zooecial chambers are still essentially cylindrical. The assumption of cylindricity could affect the calculation of skeletal volume if zooid shape varies systematically across the endozone. Zooidal cross-sectional shape was qualitatively examined across the endozones of the colonies using transverse sections. No systematic change in zooidal cross-sectional shape was found. This suggests that there is no systematic variation in zooidal shape (cylindrical or prismatic) in these colonies.

Defining mean zooecial wall thickness as A, maximum zooecial chamber width as B, and mean zooecial chamber length as C, zooecial chamber volume was calculated as

$$C\pi(B/2)^2.$$

Zooid volume was calculated as

$$C\pi(B/2 + A)^2.$$

Skeletal volume was calculated by subtracting zooecial chamber volume from zooid volume:

$$C\pi(B/2 + A)^2 - C\pi(B/2)^2.$$

Skeletal area in longitudinal section was calculated as a proxy for skeletal volume in the event that skeletal volume is biased by potentially underestimated zooecial chamber widths, as discussed above. Skeletal area was calculated as CA, and should be directly proportional to skeletal volume. If skeletal volume is biased as discussed above, skeletal area could be used. But for all series except 12, skeletal area and skeletal volume are significantly positively correlated ($P < 0.05$). Series 12 reveals a positive but nonsignificant correlation ($P = 0.076$). This general correlation between skeletal volume and skeletal area indicates either that the values obtained for skeletal volume are not systematically biased by underestimating zooecial chamber width, or that zooecial chamber length is the dominant variable in the calculation of both skeletal area and skeletal volume.

Results

The plots of mean zooecial wall thickness are shown in Fig. 3. As expected, zooecial wall thickness systematically increases from the endozone into the exozone. All but two of the series (8 and 10) show statistically significant positive correlations between zooid number and mean zooecial wall thickness (Table 2). Series 8 and 10 do show zooecial wall thickening into the exozone, but it is not significant ($P > 0.05$). This presumably reflects the fact that these series were not followed far enough into the exozone (Table 1). In general, the zooecial wall thicknesses remain at a relatively constant low level through the endozone and begin to increase at the endozone-exozone boundary. They thicken greatly through the exozone. The number of zooids from the beginning of a series to the point at which the zooecial wall thicknesses begin to increase is directly proportional to the radius of the endozone. This varies greatly in these species as can be seen by comparing *L. asterica* (Fig. 3, series 9 and 10) with its wide endozone and *L. multitecta* (Fig. 3, series 11 and 12) with its relatively narrow endozone.

The plots of maximum zooecial chamber width are shown in Fig. 4. As expected, zooecial chamber width does not vary systematically across the branch. All but two of the

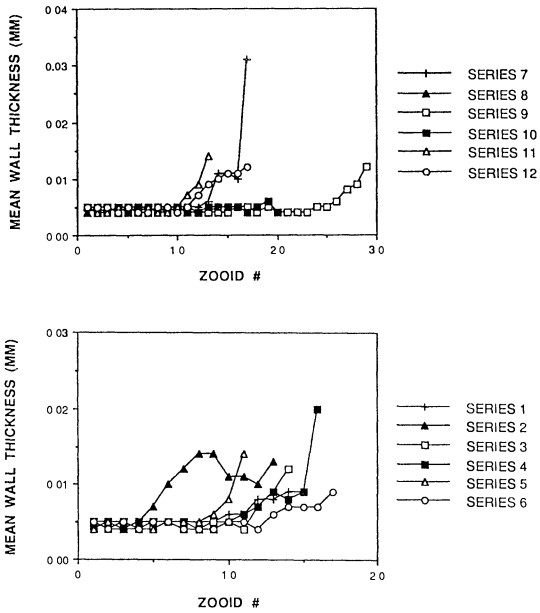

FIGURE 3. Relationship between mean zooecial wall thickness and zooid number for the six Ordovician series (bottom) and the six Devonian species (top). Series numbers refer to Table 1.

series (2 and 6) exhibit no statistically significant correlations between zooid number and maximum zooecial chamber width (Table 2). Series 2 and 6 exhibit a decrease in zooecial chamber width into the exozone.

The plots of mean zooecial chamber length are shown in Fig. 5. As expected, zooecial chamber length systematically decreases from the branch axis into the exozone. All but one of the series (7) reveal statistically significant negative correlations between zooid number and mean zooecial chamber length (Table 2). Series 7 has a negative correlation, but it is statistically insignificant ($P > 0.05$) because the length of distal growth in this series of zooids is the shortest of all the series analyzed in this study. Comparison of the plots of mean zooecial chamber length for all series (Fig. 5; means, 0.29–2.12 mm) reveals that series 7 has the shortest lengths (mean, 0.20 mm). This indicates that for series 7, the two successive growth surfaces marked by the bands of diaphragms are closer together than any of the other series. As a result, the expected pattern of decreasing zooecial chamber length away from the branch axis is only minimally developed.

TABLE 2. Pearson correlation coefficients with zooid number. * Correlation is insignificant ($P > 0.05$).

Series no.	Mean wall thickness	Maximum chamber width	Mean chamber length	Skeletal volume
1	0.869	0.321*	−0.978	−0.842
2	0.807	−0.779	−0.924	−0.815
3	0.663	−0.101*	−0.884	−0.480*
4	0.690	−0.212*	−0.969	−0.914
5	0.704	−0.007*	−0.970	−0.823
6	0.718	−0.510	−0.933	−0.924
7	0.608	0.165*	−0.392*	0.644
8	0.224*	−0.089*	−0.973	−0.863
9	0.493	0.109*	−0.988	−0.776
10	0.238*	0.324*	−0.960	−0.841
11	0.665	−0.016*	−0.946	−0.521*
12	0.824	−0.410*	−0.923	−0.679

The plots of skeletal volume are shown in Fig. 6. These show skeletal volume systematically decreasing from the branch axis into the exozone. All but three of the sereis (3, 7, 11) show statistically significant negative correlations between zooid number and skeletal volume (Table 2). Series 3 and 11 have negative correlations, but they are statistically nonsignificant ($P > 0.05$). The nonsignificant negative correlations in these two series are probably due to small sample sizes. Series 3 and 11 contain only 14 and 13 zooids, respectively, compared with the mean of 17 zooids for all 12 series (Table 1). Series 7 reveals a statistically significant increase in skeletal volume. Series 7 is the series with the least distal growth between successive growth surfaces. As a result of a lack of a significant zooecial chamber-length decrease into the exozone as discussed above, the skeletal volume calculations in series 7 are dominated by the increasing zooecial wall thickness.

Discussion

The strong correlation between zooid number and skeletal volume forces the rejection of the null hypothesis that the volume of skeletal material secreted by zooids per unit of time is the same across a branch tip. Zooids near the branch axis not only have the fastest growth rate distally, they also have the highest rate of skeletal secretion. These results, which are based on actual calculations of the rate of skeletal secretion, corroborate those of Hickey (1987), who measured calcium and

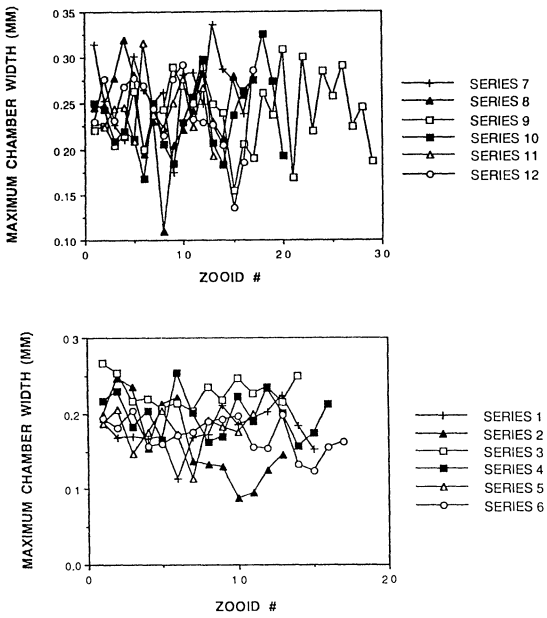

FIGURE 4. Relationship between maximum zooecial chamber width and zooid number for the six Ordovician series (bottom) and the six Devonian species (top). Series numbers refer to Table 1.

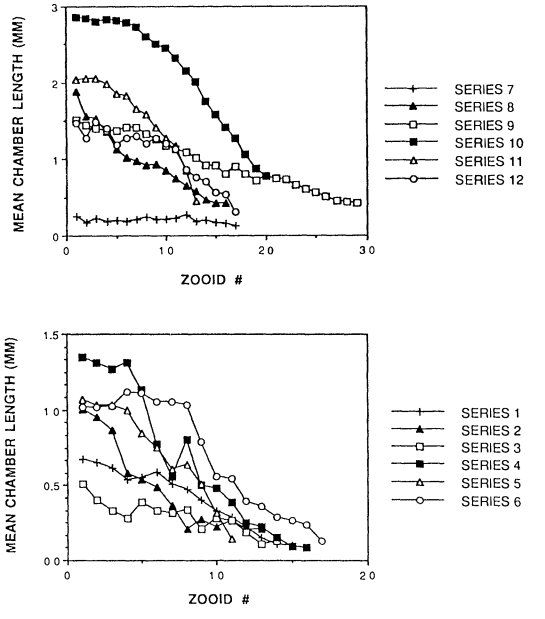

FIGURE 5. Relationship between mean zooecial chamber length and zooid number for the six Ordovician series (bottom) and the six Devonian species (top). Series numbers refer to Table 1.

magnesium density in zooecial walls as a proxy for the rate of skeletal secretion. Though Hickey's study involved the Ordovician trepostome *Peronopora* with its highly derived bifoliate growth habit, the results are quite similar to those of the current study, based on a wider range of taxa from several different clades and ages. The occurrence of this pattern in all these taxa suggests that it may be common throughout those trepostome clades with erect colonies.

What implications do these findings have for colonial control versus zooidal autonomy of zooid morphogenesis? Randomly varying rates of skeletal secretion among zooids may imply more zooidal autonomy or no colonial control at all. That is, the rate of skeletal secretion would be controlled by the zooid and not by the colony. Consistent rates of skeletal secretion among zooids may imply a certain degree of colonial control over zooid skeletal morphogenesis. Systematically varying rates of skeletal secretion, as found in this study, strongly suggest a certain degree of colonial control over zooid morphogenesis. That is, the rate of deposition of skeletal material is apparently controlled by the colony and not the zooid. This makes sense in light of two facts. First, the zooecial walls in these trepostomes are compound. Adjacent zooids contribute half of the skeletal material for shared zooecial walls. Secretion of skeletal-wall material in this instance would probably be impossible without colonial control. Second, the smooth surfaces of growing tips in trepostomes (Boardman 1960: pl. 7, fig. 2; 1983: fig. 48.4) also reflect apparent colony control over zooidal growth rates. Without such control, growing tips would be uneven.

The results could reflect ontogenetic control and not colonial control if the ontogenetic age of zooids varies systematically across the colony. If this is the case, then the results could simply reflect an ontogenetic trend in the rate of skeletal secretion. For example, if the age of the zooids systematically increases from the branch axis outward, then the results could be explained by a decreasing rate of skeletal secretion through zooidal ontogeny. Qualitative observations in longitudinal sections of the distances from the point of zooidal budding to the growth surfaces indicate that zooid age does not vary system-

atically from the branch axis to the exozone in these six species; zooids are budded throughout the endozone with no apparent order (in the sense of McKinney 1977). At any one growth surface, such as the first growth surface in Fig. 1, zooidal age does not vary systematically from the branch axis to the exozone. Thus, the rate of skeletal secretion of a zooid is dictated by its position within the colony, not by its age.

This discussion of colonial control versus zooid autonomy has relevance to the degree of colonial integration in bryozoans. Species with lower levels of colonial integration may have less tightly constrained or completely unconstrained patterns of skeletal growth rate among zooids. These patterns may be reflected as less significant or nonsignificant correlations between zooid number and skeletal volume in a series of zooids. Species with higher levels of colonial integration may have more tightly constrained patterns of skeletal growth rate among zooids, which may be reflected as more highly significant correlations between zooid number and skeletal volume in a series of zooids.

The results from this study indicate that zooid morphogenesis is controlled at least partly by the colony. The regulation of growth rates (in regard to both skeletal volume and distal length) presumably requires some kind of morphogenetic gradient from the branch axis outward. The decrease in the rate of skeletal secretion away from the branch axis implies that, in these Ordovician and Devonian trepostomes, either the zooids at the growing tip were more successful at feeding than those on the sides of the colony, or the nutrients were being preferentially passed from the autozooids on the sides of the colony through the confluent outer coelomic cavity to the zooids at the growing tip.

Observations of living bryozoans indicate that the zooids at the growing tip were not likely to be more successful feeders. The descendants of Paleozoic trepostomes, modern cyclostomes, have smaller polypides at the growing tip (McKinney and Boardman 1985; McKinney 1988), suggesting that, in the trepostomes, the zooids at the growing tip were less successful feeders because they had

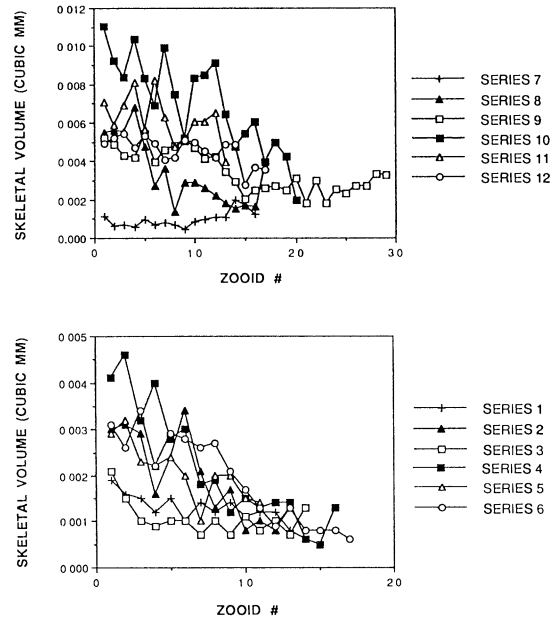

FIGURE 6. Relationship between skeletal volume and zooid number for the six Ordovician series (bottom) and the six Devonian species (top). Series numbers refer to Table 1.

smaller mouths (Winston 1981; McKinney and Boardman 1985) and were more restricted in the size of food particles they could ingest (Winston 1981).

If the zooids at the growing tip were not growing faster because they were more successful feeders, then nutrients must have been passed from the autozooids on the sides of the colony through the confluent outer coelomic cavity to the zooids at the growing tip. Recent studies on living bryozoans support this. Metabolic transport between zooids in cheilostome bryozoans permits locally increased rates of zooidal growth in colonies (Best and Thorpe 1985; Hughes and Hughes 1986). Funicular connections capable of similar metabolic transport may also exist in stenolaemate bryozoans (Carle and Ruppert 1983).

The morphogenetic gradient from the branch axis outward reflects the colonial control of zooidal growth rate across the branch. This control of zooidal growth rate across the branch directs the rate of extension of the endozone and exozone. It is not simply the turning of the zooids away from the branch axis and toward the branch periphery that

differentiates the endozone and exozone. This change occurs simultaneously with a decrease in the rate of skeletal secretion toward the branch periphery. As the zooids are being physically displaced from the endozone by newly budded zooids, their rate of growth is decreasing. The apparent control of zooidal growth rate by the colony regulates the colony's shape and permits the ramose growth habit by allowing the zooids in the endozone to grow faster than those in the exozone. A colony's growth habit is at least partially dictated by the morphogenetic gradients among zooids within the colony.

Conclusions

The slopes and intercepts of Fig. 3 (mean zooecial wall thickness) could possibly be used as new taxonomic characters. They should be as species-specific as the closely related yet more traditional character of zooecial wall thickness measured in tangential section. The slopes of Fig. 6 (skeletal volume) may also prove useful as new characters for bryozoan systematics. Both will require quantification of intraspecific variability.

The results of this study indicate that rates of skeletal secretion among zooids systematically decrease from the branch axis to the branch periphery. The cause of this decrease is attributed to colonial control as opposed to zooid control. This is the case for ramose trepostomes, but do species with hemispherical colonies exhibit the same pattern? It is predicted that they do not. The rate of skeletal secretion should be the same for all zooids in a hemispherical colony. This difference may be associated with a lack of distinction between the endozone and exozone in hemispherical colonies. This line of research raises the question of whether the evolution of the differentiation of endozone and exozone is a crucial apomorphy permitting the development of the ramose colony growth habit in trepostomes.

As discussed previously, the ramose growth habit permits many ecological advantages (Cheetham 1971; Jackson 1979). Recent studies on colonial animals have documented the presence of adaptive macroevolutionary trends in the fossil record (Coates and Jackson 1985; Cheetham 1986; Lidgard 1986; McKinney 1986; McKinney and Jackson 1988; Lidgard and Jackson 1989). If these macroevolutionary patterns are produced by ecological processes (McKinney and Jackson 1988; Lidgard and Jackson 1989), then the evolution of colonial control over zooid morphogenesis, which permitted ramose growth, may have produced adaptive macroevolutionary trends among ramose trepostomes.

Acknowledgments

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