

# Colony control over skeletal growth rates in trepostome bryozoans

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## Abstract

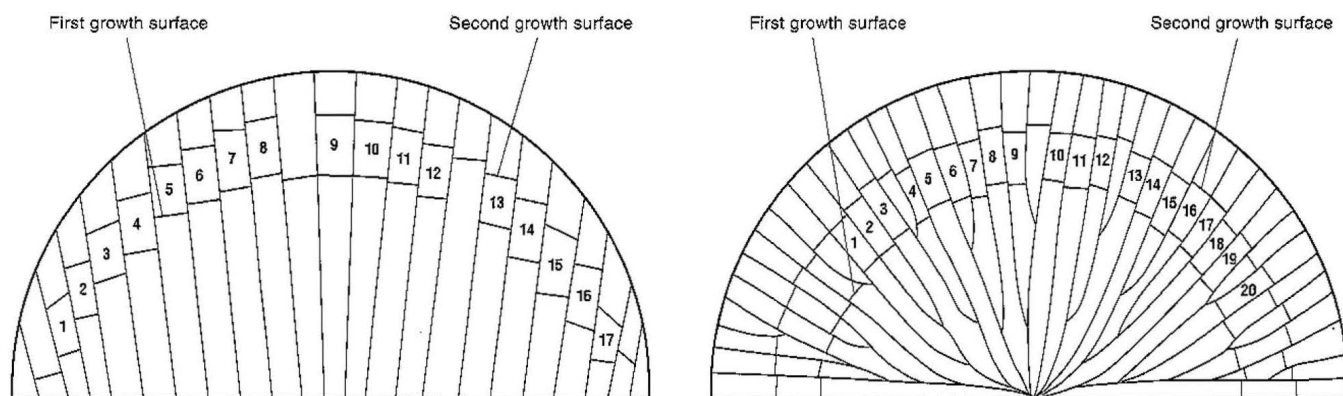
All colonial organisms are characterized by the colony's ability to exert at least some control over the life processes of the individual modules. In the case of bryozoans, the colony dictates to some degree the growth of the individual zooids. Skeletal growth rates among zooids can be used as a proxy for control of the colony over the zooids. A more tightly constrained zooidal growth rate implies a more highly integrated colony with less autonomous zooids. Colonies with isochronous growth surfaces can be used to determine relative skeletal growth rates in fossil bryozoans. This study looks at series of adjacent zooids between consecutive isochronous growth surfaces in nine different species of hemispherical Ordovician trepostome bryozoans. Variation in skeletal volume was analyzed in relation to position across the colony using Pearson correlation coefficients. Results indicate that the rate of skeletal secretion does not systematically vary across the colony. The results support those from ramose colonies in indicating that zooidal morphogenesis is controlled to a certain degree by the colony. This control of the colony over zooidal growth rates regulates the zoarial growth habit of the colony. The rate of skeletal secretion among zooids is more tightly constrained in ramose colonies than in hemispherical ones. This suggests that zooidal morphogenesis is controlled to a greater degree by the colony in ramose forms than in hemispherical forms.

**Keywords:** Bryozoa, trepostomes, Ordovician, skeletal growth, colonial integration.

## Introduction

How is colony growth habit in colonial organisms controlled? How do the individual zooids in the colonies cooperate to produce a unified growth pattern? These questions are addressed in the context of hemispherical trepostomes. Trepostome colonies are typically made up of thousands of zooids, and some colony-wide control of zoarial growth is necessary to produce the uniform growth surfaces common to the order (Boardman & Cheetham 1969).

There are three ways to produce a hemispherical colony. With the first two methods, the hemispherical shape is maintained throughout the colony's history, and it results from an equal rate of distal growth in all of the zooids. In parallel budding (Mannil 1961, figure 1a), the zooids are budded from the entire surface of the basal epitheca (Figure 1). In radial budding (Mannil 1961, figure 1b), the zooids are budded from a single point (Figure 2). Hemispherical colonies may also result fortuitously from repeated zooidal overgrowths of varying widths. This type of hemispherical colony was excluded from this study as the hemispherical shape is not maintained throughout the colony's history.



In some trepostomes, basal diaphragms are occasionally secreted by zooids at or below the growing surface of the colony (Boardman 1960, Madsen 1987). This produces a band of diaphragms across the colony (Figures 1 & 2). The spacing of these bands is generally irregular (Boardman 1960, Gautier 1970, Madsen 1987). The bands represent the past positions of the growing surface of the colony. Using these remnant growing surfaces as isochronous surfaces (*sensu* Key 1990a), the relative rates of skeletal secretion among zooids can be quantified.

The question addressed by this study is whether or not the volume of skeletal carbonate secreted by zooids varies across the colony. The null hypothesis is that the rate of skeletal material secreted by zooids varies randomly among zooids across the colony. Data for ramose colonies have been presented elsewhere (Key 1990a, b). This paper focuses on hemispherical colonies and compares the results with those of ramose colonies.

**Figure 1. (left)** Longitudinal section of a hemispherical trepostome colony with parallel budding. Numbers refer to zooids measured in a single series. Modified from Mannil (1961, figure 1a).

**Figure 2. (right)** Longitudinal section of a hemispherical trepostome colony with radial budding. Numbers refer to zooids measured in a single series. Modified from Mannil (1961, figure 1b).

## Materials and methods

To test the null hypothesis, nine series of zooids were analyzed. A series is a sequence of roughly adjacent zooids that crosses two consecutive isochronous growth surfaces marked by basal diaphragms (Figures 1 & 2). Only zooids having basal diaphragms marking both growth surfaces were included. For example in Figure 1 the zooids between zooids 8 & 9 and 12 & 13, and in Figure 2 the zooids between zooids 3 & 4, 9 & 10, 12 & 13, and 19 & 20 were not used. Series length averaged 14 zooids with a range of 8-20 (Table 1).

Series no.	Species	Mode of budding	USNM no.	No. of zooids measured
1	<i>Diplotrypa cf. westoni</i>	radial	237366	20
2	<i>Esthoniopora communis</i>	parallel	57363-1	12
3	<i>Hallopora? dybowskii</i>	radial	57473-7	17
4	<i>Leptotrypa acervulosa</i>	radial	43189-2	14
5	<i>Mesotrypa angularis</i>	parallel	308406	10
6	<i>M. discoidea orientalis</i>	parallel	57280	10
7	<i>M. favosa</i>	parallel	114616	11
8	<i>Orbignyella sublamellosa</i>	parallel	43174-3	20
9	<i>Prasopora simulatrix</i>	parallel	167688	8

Table 1.  
List of species measured.

This study included nine different species of Ordovician trepotomes with hemispherical zoarial growth habits (Table 1). Six of the nine species exhibited parallel budding, while the others exhibited radial budding (Table 1). Species were selected to maximize the number of different trepotome clades. Specimens came from the thin section type collection in the National Museum of Natural History, Washington, DC (USNM).

Data were collected from a microcomputer-based, digital image analysis system. Through repeatability experiments, measurement error was calculated to be less than 3.7%. Three characters were measured on each zooid within each series. These were interzoecial wall thickness, zoecial chamber width, and zoecial chamber length (Figure 3). Each character was measured five times per zooid. The five measurements per zooid of interzoecial wall thickness and zoecial chamber length were averaged to reduce measurement error. The maximum value of the five measurements per zooid of zoecial chamber width was selected to reduce underestimated chamber widths due to thin sections that did not pass through the axis of the zoecial chamber. To determine the amount of the zoecial wall contributed by each adjacent zooid, the data for interzoecial wall thickness was divided by two. This assumes that the amount contributed was equal.

To determine the relative growth rates among zooids, it was necessary to calculate the volume of skeletal material secreted by each zooid. Defining mean zoecial wall thickness (interzoecial wall thickness/2) as *WT*, maximum zoecial chamber width as *CW*, and mean zoecial chamber length as *CL*, the skeletal volume secreted by each zooid was calculated with the following equation:

$$\left[ CL \times \pi \times \left( \frac{CW}{2} + WT \right)^2 \right] - \left[ CL \times \pi \times \left( \frac{CW}{2} \right)^2 \right]$$

This calculation is based on the approximation that the zooids in these species are cylindrical. Qualitative analysis of tangential and longitudinal sections of these species verifies this assumption.

## Results

Pearson correlation coefficients were calculated to determine the significance of the correlation between the position of the zooid in the colony, as determined by zooid number in a series, and the three measured characters as well as the one calculated character. As expected, there is no systematic variation across the colonies in: 1) zoecial wall thickness (Figure 4) (the only exception is for series 3 which reveals a significant negative relationship), 2) zoecial chamber width (Figure 5) (the only exception is for series 4 & 5 which reveal a significant negative and a positive relationship, respectively), 3) zoecial chamber length (Figure 6) (the only exception is for series 3 which reveals a significant negative relationship, and 4) skeletal volume (Figure 7) (the only exception is for series 3 which reveals a significant negative relationship; Table 2).

Series 3 belonging to *Hallopora? dybowskii* is anomalous. The characters measured and calculated on this colony did not behave like the other eight species. It is possible that this specimen's zoarial growth habit was less hemispherical than the type specimens of this species. Unfortunately, this is impossible to determine from thin sections.

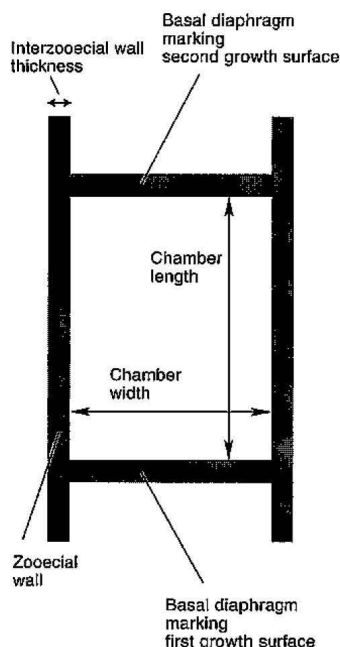
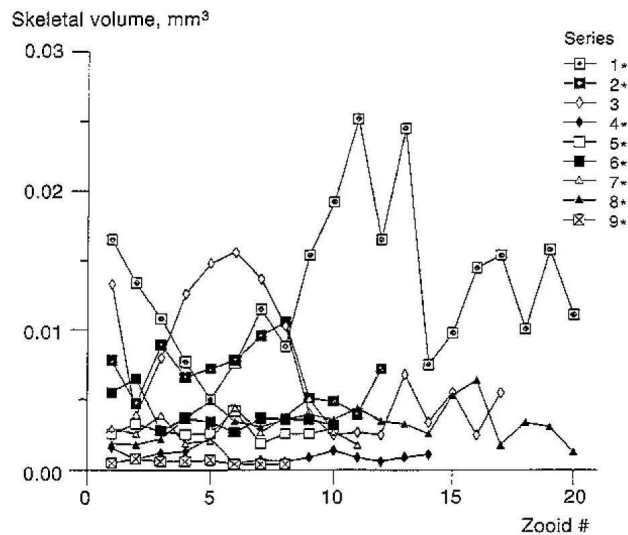
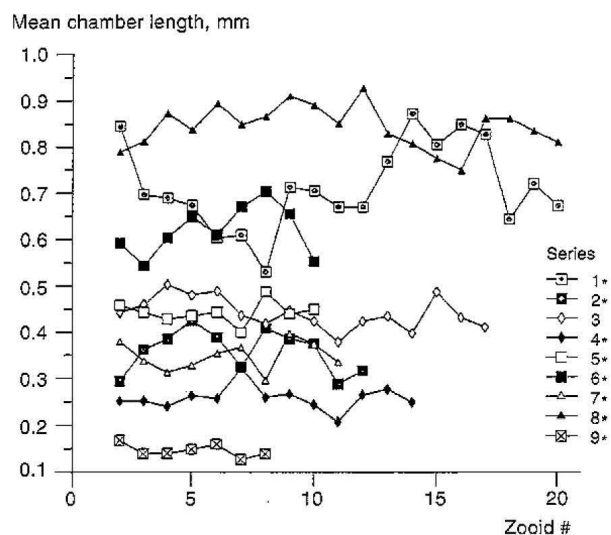
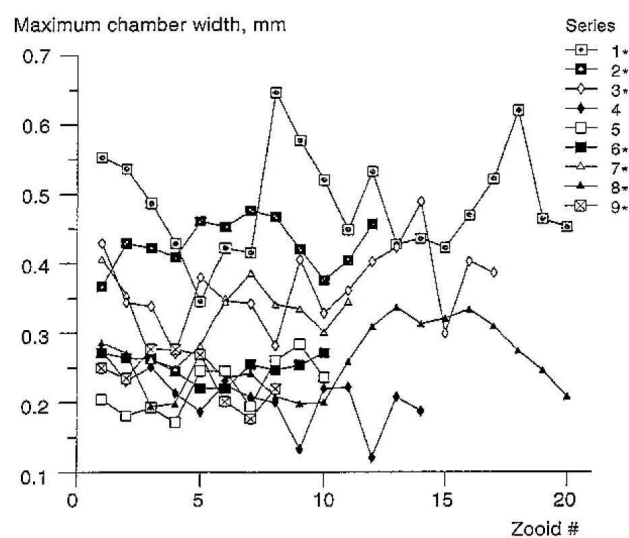
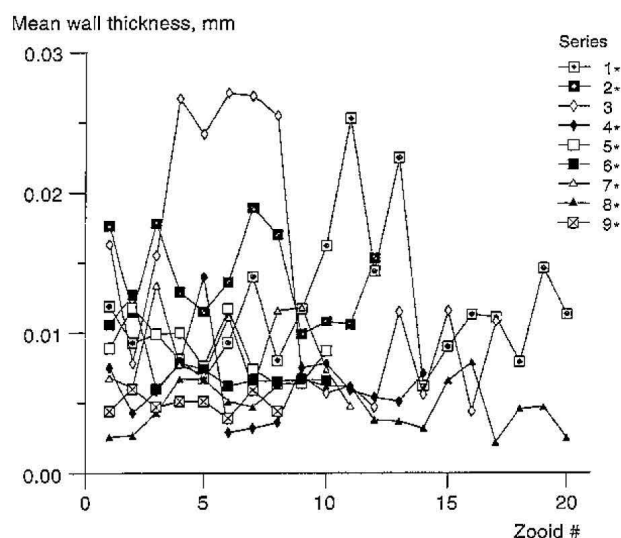


Figure 3.  
Zooid in longitudinal section showing characters measured. Grey areas represent material secreted by zooids.



The correlation coefficients cannot determine if the rate of skeletal secretion across the colony is constant (i.e. a line of slope zero) or varies randomly. A constant rate of skeletal secretion may indicate control of the colony over zooidal growth rates. Randomly varying rates may indicate more zooidal control. To distinguish between a line with a slope of zero and a random distribution, the data were rotated 45° counter-clockwise using a standard matrix transformation (Davis 1973). Pearson correlation coefficients were then calculated for this transformed data set (Table 2). The results reveal that five of the nine series showed significant correlations. For these five series, skeletal material was secreted at a constant rate across the colony. The other four series support the null hypothesis as they reveal a random rate of skeletal secretion across the colony. Three of these four series exhibited radial budding. Perhaps hemispherical colonies with radial budding are not as hemispherically-shaped as colonies with parallel budding. Perhaps these four colonies had more bell-shaped colonies caused by differential rates of distal growth among the zooids.

Series no.	Ramose untransformed	Hemispherical untransformed	Hemispherical transformed
1	-0.842	0.173*	0.314*
2	-0.815	-0.221*	0.572
3	-0.480*	-0.596	-0.167*
4	-0.914	-0.324*	0.206*
5	-0.823	-0.064*	0.729
6	-0.924	-0.573*	0.589
7	0.644	0.055*	0.434*
8	-0.863	0.113*	0.394
9	-0.776	-0.621*	0.773
10	-0.841		
11	-0.521*		
12	-0.679		

Figure 4. (upper, left)  
Plot of mean zooecial wall thickness versus zooid number. Series numbers refer to Table 1. Asterisk indicates correlation is insignificant ( $p > 0.05$ ).

Figure 5. (upper, right)  
Plot of maximum zooecial chamber width versus zooid number. Symbols as in Figure 4.

Figure 6. (lower, left)  
Plot of mean zooecial chamber length versus zooid number. Symbols as in Figure 4.

Figure 7. (lower, right)  
Plot of skeletal volume versus zooid number. Symbols as in Figure 4.

Table 2.  
Pearson correlation coefficients between skeletal volume and zooid number. Data from ramose colonies are from Key (1990a). Data from hemispherical colonies are from this study. Asterisk indicates correlation is insignificant ( $p > 0.05$ ). For transformation see text above table.

## Discussion

The fact that with the transformed data only five of the nine colonies exhibited constant rates of skeletal secretion across the colony suggests that not all of the hemispherical colonies exhibit control of the colony over zooidal growth rates. This is in stark contrast to results from ramose colonies from a similar study (Key 1990a). The data were collected similarly, but the results were quite different (Table 2). In the ramose colonies with an untransformed data matrix, skeletal growth rates systematically decreased from the axis of the colony toward the exozone (in 9 of the 12 colonies analyzed). This was interpreted by Key (1990a, b) as reflecting strong control of the colony over zooidal growth rates.

The geometric requirement of ramose growth is such that the zooids must grow fastest near the axis of the branches and slowest near the periphery of the branches. In hemispherical colonies, the zooids must all grow at the same rate regardless of their position in the colony. This difference in zooidal growth rates across the colony is the source of the different zoarial growth habits exhibited by trepostomes. Based on the robustness of correlation coefficients, the control of the colonies over these growth rates seems to be greater in the ramose colonies than in the hemispherical ones. In regards to skeletal growth rates, ramose colonies are more integrated than hemispherical ones. The growth of zooids and thus of the colony as well appears to be more constrained in ramose colonies than in hemispherical ones. As a result, the zoarial growth habits of ramose colonies are more regular than those of hemispherical colonies.

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