

**Astogenetic Variability in a Frond of *Polypora laevinodata*
(Hall) (Bryozoa)**

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Abstract

Evaluation of seven characters does not reveal any systematic differences between the oldest and the youngest parts of a large frond of *Polypora laevinodata* (Hall) from the Middle Devonian Speed Member of the North Vernon Formation. Consequently, studies of fragments of fronds will not necessarily produce biased zoarial measurements or provide the basis for excessive taxonomic splitting. Future work should test the hypothesis of rhythmic banding in large fronds of fenestrate bryozoans.

Fragments of fenestrate bryozoans are much more common in the fossil record than complete fronds and fragments commonly are the subject of taxonomic descriptions in the paleontological literature. Quantitative studies of the variability within individual fenestrate fronds are almost lacking. Consequently the availability of a nearly complete frond of *Polypora laevinodata* (Hall) provided the stimulus for a study in astogenetic variability.

Cumings (1, p. 70-74) discussed the earliest development of colonies of *Polypora* M'Coy, but discussions of the later stages of colonial growth in *Polypora* or other fenestellid genera do not appear generally in the literature. Cumings (1, p. 66) noted that in *Fenestella* Lonsdale little or no change in characters could be observed in early to later stages of colonial growth.

Elias (2) prepared a color scheme for illustrating the changes from early to late stages of growth in a single character (fenestrule length) in large fronds of *Fenestella*. The colors generally displayed a banded pattern related to stages of growth in a colony as discussed by Elias. However, no tests were made to determine the significance of the differences nor were any special edge features described to indicate the criteria for late versus early growth stages. Elias (2, p. 375) suggested that some of the concentric banding in the pattern of fenestrule length was seasonal. We have not examined our data from the standpoint of rhythmic banding because it requires a different experimental approach than reported herein. However, future studies should be designed to test this hypothesis in other fenestrate bryozoan fronds.

An exceptional specimen of *P. laevinodata* (Hall) (IU15106-200) from the Speed Member of the North Vernon Limestone exhibited a nearly complete frond displaying lateral edge features and a distal growth margin and lacked only the earliest basal portion of the frond. The specimen, which is 12 cm high and 10 cm wide, was divided into seven 15 mm intervals perpendicular to growth. The proximal level represents, most probably, a part of the colony just above the basal structure as inferred from the width and general geometry of the flabellate frond. The distalmost level contains edge features and also the growing edge, which confirms that this is the position of the youngest part of the colony.

Seven external characters (number of apertures in 5 mm, branch width, number of branches in 10 mm, dissepiment width, fenestrule length, fenestrule width, number of fenestrules in 10 mm) used for differentiating species of *Polypora* within the Speed Member and Jeffersonville Limestone (4) were used in the astogenetic study. No internal sections were made because of some alteration and surface silicification; however, chamber shape was observed on partially weathered areas of the frond and was consistently box-like (quadrangular) wherever observed.

Although the data sets of most measured characters of *Polypora* from the Speed Member and the type suites of the polyporans from the Jeffersonville Limestone were not normally distributed (4), the data sets for each measured character from the different levels of the specimen chosen for the astogeny study approached normality more closely than other sets of measurements from the population. The reason for this is probably due to the small number of measurements involved in the analysis, which decreases the power of the test (i.e. the test results are affected by the small sample size). The different measured intervals on the specimen used in the astogeny study were tested with nonparametric and parametric methods.

A Mann-Whitney U test, a nonparametric test using rank order of the original data, was used to test for association between levels of the specimen. Because of the large number of ranking ties between various levels on each measured character the results of this test suggested no difference between levels, proximally to distally on the frond. All characters tested nonsignificant at a probability level of 0.05. Because the failure of this test to show differences between levels might be caused by the large number of ties between data sets, a parametric test was also performed by applying the central limit theorem to the means of each measured character from each of the intervals. Sokal and Rohlf (3, p. 130) suggest in a discussion of the distribution and variance of means that means of samples drawn from any distribution will approach the normal distribution; this is known as the central limit theorem. A Kolmogorov-Smirnov test (3, p. 571) on the means from composite data of fenestrule width of the astogenetic specimen *P. laevinodata* revealed that the means were normally distributed; the null hypothesis was accepted a probability level of 0.05.

A one-way analysis of variance, using the Student-Newman-Keuls (SNK) test, repeated t-tests, and Tukey's test, tested the associations between all characters for all levels in all combinations of levels; the rejection level for the null hypothesis was set at $p=0.05$. These tests of analysis of variance revealed little difference between the proximal and distal intervals of the frond. Dissepiment width changed significantly but this is not considered the best diagnostic character in discriminating taxa and it did not change systematically within the frond, e.g. smaller to larger as the frond matured or vice-versa. In most cases involving comparisons of the same character between levels, the repeated t-test was more powerful in showing lack of association. Even this test revealed lack of association between intervals in only a few cases, i.e.

discounting dissepiment width, only 25 out of 126 comparisons were significantly different. Complete tables of results can be found in Stratton (4).

The variation observed in the astogenetic study was similar to that observed within other populations of *P. laevinodata* to which this specimen was taxonomically assigned. This suggests that the differentiation of taxa within the polyporans based on the measured characters from zoarial fragments is valid because of the demonstrated minor variation within characters as the colony grows.

At the distal extremities of the astogenetically studied specimen and in other specimens showing a lateral margin, the overall characters change within 5 to 10 mm of the edge of the frond, excluding the growing tip. These changes are due to the secretion of additional calcite at the lateral distal edge, which is presumably involved in structural support of the frond. At the lateral extremities of the colony, excluding the growing tip, the fenestrule length and fenestrule width decrease rapidly and a correspondingly significant increase in branch width and dissepiment width is present; ultimately the dissepiments fuse into a massive structural support along the edge that extends from near the base to an area near the growing tip to the proximal part of the colony. This structural support appears to migrate toward the growing tip as the colony increases the size. When this marginal thickening spreads across the growing edge, it signals the end of growth for the colony.

We conclude that fragments of fronds will not necessarily yield biased measures of characters provided the fragments are sufficiently large (not less than 1 cm square) to permit complete meshwork measurements.

Literature Cited

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