A PALEOBIOLOGIC TEST FOR DIASTEMS USING THE INTERNAL STRATIGRAPHY OF TREPOSTOME BRYOZOANS[1]

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ABSTRACT

Some hemispherical trepostome bryozoan colonies incorporated remnant growth surfaces as they grew. These growth surfaces mark the past surface of the colony and are caused by environmental perturbations. These growth surfaces produce an internal stratigraphy that can be used to test for the presence and relative duration of diastems. If the internal stratigraphy can be correlated among colonies from a single bedding plane, it should indicate the coexistence of the colonies and a minimal, if any, depositional hiatus. If the internal stratigraphy can not be correlated, it indicates the colonies did no coexist and the possible presence of a longer depositional hiatus. This idea is tested using 24 hemispherical trepostome bryozoan colonies belonging to the genus *Prasopora*. The colonies were collected from a single bedding plane in the Basal Member of the Middle Ordovician Martinsburg Formation of south-central Pennsylvania. The distances between adjacent growth surfaces were measured using digitized video images of acetate peels made of internal longitudinal sections of the colonies. Results reveal poor correlations among colonies. This indicates that the colonies did not coexist for their entire histories, and at least suggests the presence of a depositional hiatus of some minimal duration. [J PA Acad Sci 67(1):32-37, 1993]

INTRODUCTION

What are the temporal durations of depositional hiatuses in the stratigraphic record? This is an important question to sedimentologists, stratigraphers, and paleobiologists. Long-term, depositional hiatuses (paraconformities) are readily recognized using biostratigraphic and chronostratigraphic techniques. For example, paraconformities can be identified using species ranges and/or radiometric dating. Short-term depositional hiatuses (diastems) are much more difficult to identify. As defined by Barrell (1917), diastems are short-term unconformities in which there is no erosional surface and the overlying and underlying beds are parallel. Several sedimentological and geochemical indicators have been developed to identify diastems, the most common being the presence of hardgrounds. The occurrence of a hardground in a stratigraphic section usually indicates missing time (Wilson *et al.* 1989).

This study develops an independent test for determining the presence and relative duration of diastems in the stratigraphic record. The test uses an organismal approach which is independent of any sedimentological and geochemical indicators, but instead is based on the internal stratigraphy of hemispherical trepostome bryozoans.

In some hemispherical trepostome bryozoans, basal diaphragms are occasionally secreted by zooids at or just below the growing surface of the colony. This occurs in response to environmental perturbations and/or zooidal degeneration/regeneration cycles. These diaphragms are useful for marking the three-dimensional growing surface of the colony. In a two-dimensional section longitudinally bisecting this roughly hemispherical surface, the diaphragms form a distally convex band across the colony. As the colony grows distally, successive bands (growth surfaces) can become incorporated into the colony (Figure 1). There can be several such surfaces in a colony, each representing the position of the growing surface at some time during the past growth of the colony. The spacing of these surfaces is generally irregular (Figure 1, Boardman 1960, Gautier 1970, Madsen 1987). It is assumed that these surfaces represent isochronous growth surfaces (sensu Key 1990, Key *et al.* in press). This assumption is in keeping with the two current models for trepostome bryozoan growth (Boardman 1960, Madsen 1987).

These isochronous growth surfaces result in an internal stratigraphy that provides a powerful tool for examining certain paleobiological and paleoenvironmental questions. For example, the growth surfaces have been used to examine relative rates of skeletal secretion among zooids *within colonies* (Key 1990, Key *et al.* in press) as well as to study the cyclicity of zooecial wall thickening *within colonies* (Gautier 1970). The internal stratigraphy within colonies has never been correlated *among colonies*. That is, can the growth surfaces of one colony be correlated with those in

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another? If they can, then it may indicate that the colonies coexisted and that they were impacted similarly by common environmental perturbation(s). If the growth surfaces can not be correlated among colonies, then it may indicate the colonies did not coexist. The ability to correlate the internal stratigraphy among colonies collected from a single bedding plane would suggest the colonies coexisted and that any depositional hiatus at the bedding plane was minimal in duration. The inability to correlate the internal stratigraphy among colonies from a single bedding plane would suggest the colonies did not coexist and that the depositional hiatus at the bedding plane may have been longer in duration.

MATERIALS AND METHODS

To test this idea, 24 colonies belonging to the trepostome bryozoan genus *Prasopora* were collected from a single bedding plane. The outcrop is in the Basal Member of the Martinsburg Formation in south-central Pennsylvania (Becher and Root 1981). It is located on the south side of Creek Road 13 km west of Carlisle, PA in Cumberland County, Pennsylvania on the Plainfield 7.5 Minute Topographic Quadrangle (Figure 2). The exact location is 0.1 km south of the Conodoguinet Creek, 0.6 km north of the Pennsylvania Turnpike (I-76), 1.4 km east of the Bloserville Road, and 1.0 km west of Township Route 448 (40°12'32" N latitude, 77°20'19" W longitude). In this area, the Martinsburg Formation stratigraphically overlies the Chambersburg Formation (Berg *et al.* 1983). This places the general age of the colonies in the Rocklandian Stage of the Mohawkian Series of the Middle Ordovician (Ross *et al.* 1982).

The lithology at this outcrop is characterized by thin-bedded, platy-weathering, argillaceous limestones (Becher and Root 1981). The colonies were collected from what could best be determined as a single bedding plane. This bedding plane appears to have been an event horizon that was colonized by the bryozoans because the colonies were all oriented convex up (upright). The colonies were identified as belonging to the trepostome bryozoan genus
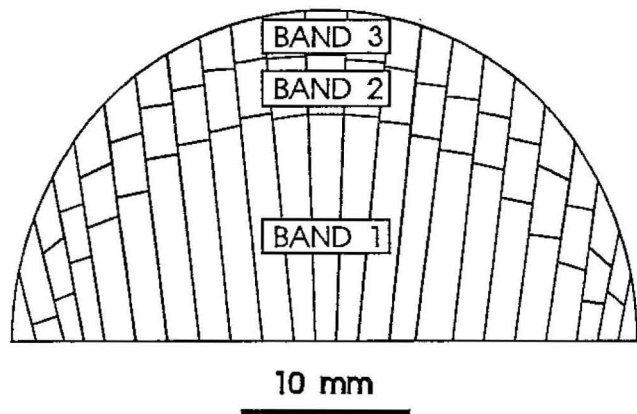
Prasopora based on the abundance of cystiphragms, autozooecia with circular apertures and thin walls, as well as abundant mesozooecia with closely spaced diaphragms (Marintsch 1981). *Prasopora* colonies with the same shape and orientation have been reported from the Middle Ordovician Coburn and Salona Limestones of central Pennsylvania (Arens and Cuffey 1989, 1990). These formations, located roughly 60 km to the northwest of the outcrop examined here, were either roughly contemporaneous with those in this study (Berg *et al.* 1983) or slightly younger (Arens and Cuffey 1989). Arens and Cuffey (1989) hypothesized that the upright hemispherical *Prasopora* colonies grew on top of tempestites (storm deposits).

The colonies were sectioned longitudinally with the cut oriented vertically through the tallest part of the colony. The cuts were made through the tallest part of the colony to reduce potential noise in the data introduced by intracolony differences in zooidal growth rates (sensu Key 1990, Key *et al.* in press) or by intracolony differences in surface abrasion or diagenetic dissolution. Acetate peels were made of the resulting internal surface using the technique of Boardman and Utgaard (1964). Distinctive bands were visible on these surfaces (Figure 1).

The maximum width of each growth band was measured. Maximum band width was measured for the same reasons mentioned above. Measurements were made on digitized video images of the acetate peels. Only those bands that were readily followed completely across a colony were used. These bands were often associated with a distinct clay drape and/or intracolony overgrowth.

A total of 55 bands were measured on the 24 colonies. The number of bands measured on a single colony ranged from one to six with a mean of 2.3. The widths of bands ranged from 1.05 mm to 23.16 mm with a mean of 8.37 mm. The total height of colonies ranged from 10.0 mm to 36.2 mm with a mean of 19.2 mm.
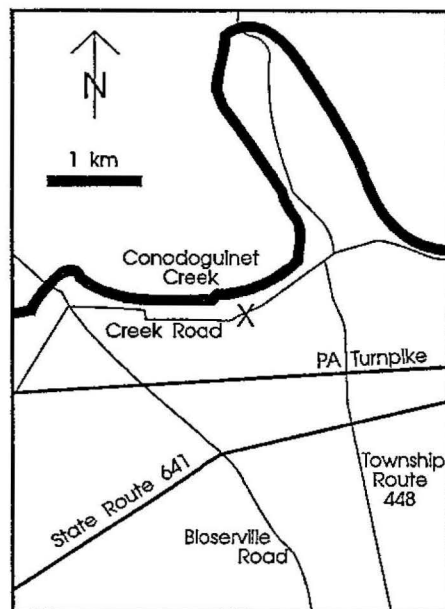

FIGURE 1. Generalized longitudinal section of a *Prasopora* colony showing internal band stratigraphy. Modified from Mannil (1961, fig. 1a).

FIGURE 2. Map showing collection location marked by X.

RESULTS

To determine if the bands in the 24 colonies were induced by common environmental perturbations, correlation of bands among colonies was attempted. All correlations were based on band width, and all correlations assumed that at least one band in each colony was correlatable among all of the colonies. Without this assumption, then the correlations could have been improved by dropping out colonies with bands that were too narrow or wide, but this would have been completely arbitrary. Three different correlation techniques were used.

The first correlation technique assumed that all the colonies began to grow at the same time. That is, the larvae that produced the colonies settled on the substrate simultaneously, and the base of each colony represents an isochronous surface. The results reveal quite a bit of variation in the widths for the first band (Figure 3). The coefficient of variation (standard deviation/mean) for the width of the first band is 0.53. This poor correlation suggests that the assumption of simultaneous larval settlement is invalid or that there are significant intercolony differences in growth rates. As it is impossible to determine the timing of larval settlement, correction for intercolony differences in growth rates was attempted. Some colonies may have wider or narrower bands due to intercolony differences in zooecial growth rates caused by localized environmental differences and/or genetic differences among the colonies. To correct for intercolony differences in growth rates, the band widths were converted into percentages by dividing the band widths by the colony height for each colony. The results show even more variation (Figure 4) with a coefficient of variation of 0.59 for the width of the first band. As this correction for intercolony differences in growth rates did not improve the correlation, the poor correlation is attributed to heterochronous larval settlement.

The second correlation technique assumed that all the colonies died at the same time. That is, the colonies were killed by a common environmental perturbation (e.g., complete burial by sediment), and hence the external surface of each colony represents the same isochronous surface. Compared to the first correlation, the results reveal slightly less variation in the width of the first band (Figure 5) with a still poor coefficient of variation of 0.49. This poor correlation suggests that the assumption of simultaneous colony death is invalid or that there are significant intercolony differences in growth rates. As it is impossible to determine the timing of colony death, correction for intercolony differences in growth rates was attempted. This was achieved as before by converting all of the band widths into percentages by dividing the band widths by the colony height for each colony. The results show still more variation (Figure 6) with a coefficient of variation of 0.54 for the width of the first band. As this correction for intercolony differences in growth rates did not improve the correlation, the poor correlation is attributed to heterochronous colony death.
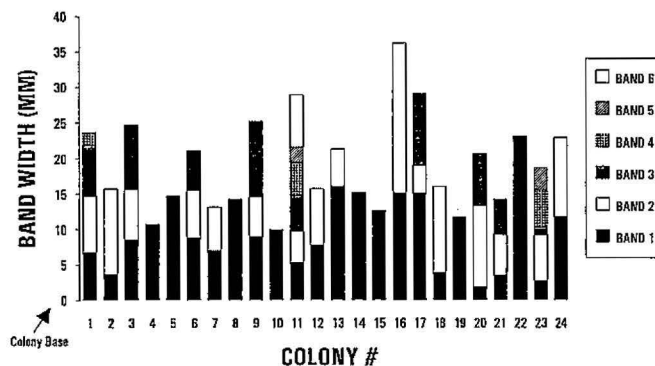

FIGURE 3. Correlation of bands (in mm) assuming isochronous larval settlement.
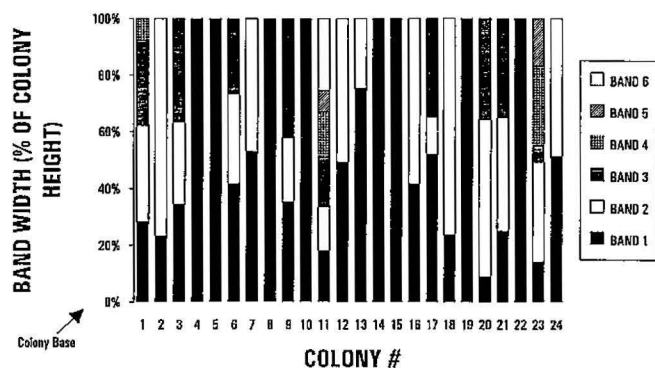

FIGURE 4. Correlation of bands (in % of colony height) assuming isochronous larval settlement.
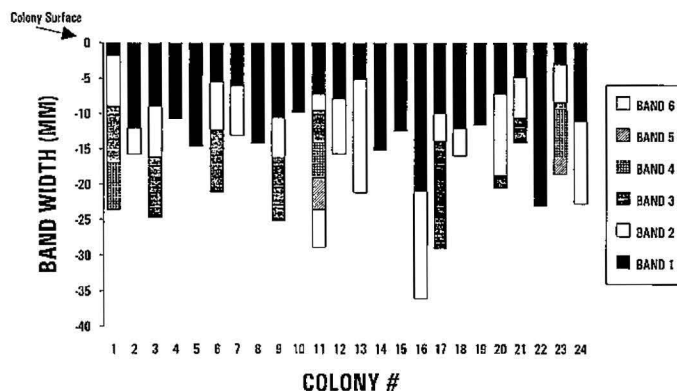

FIGURE 5. Correlation of bands (in mm) assuming isochronous colony death.
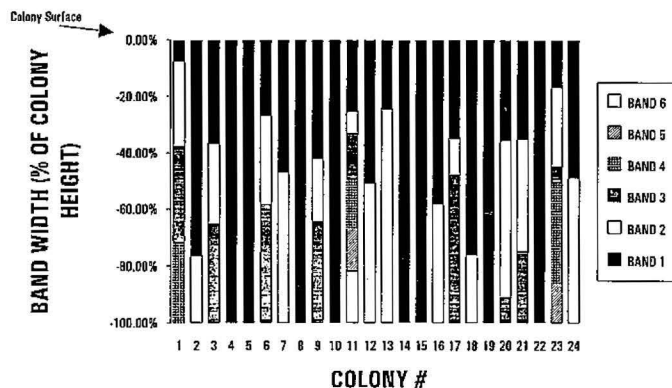

FIGURE 6. Correlation of bands (in % of colony height) assuming isochronous colony death.

The final correlation technique attempted to determine the best correlation. Unfortunately, it was impossible to statistically test the significance of this correlation. The number of possible ways to correlate the bands in the 24 colonies equals $a_1 * b_2 * c_3 * \ldots * x_n$ where a_1 is the number of bands in colony 1, b_2 is the number of bands in colony 2, c_3 is the number of bands in colony 3, and x_n is the number of bands in colony n. In this case with 55 bands ($a + b + c + \ldots + x = 55$) in 24 colonies ($n = 24$), the number of possible ways to correlate the bands is 11,197,440. With this many possible permutations, it is impossible to test the significance of the following correlation due to the limitation of having only 24 colonies.

This correlation was based on the presence of a distinctive clay drape that occurred in all colonies with two or more bands. In this correlation, it was assumed that the clay drape reflects a common environmental perturbation that affected all colonies simultaneously. In colonies with no clay drapes (i.e., colonies with a single band), the top of the colony was correlated with the clay drape. The top of the colony was chosen assuming that the clay drape killed these colonies by smothering the zooids with mud. In colonies with multiple clay drapes, the chosen clay drape was the one above the band with a width closest to the mean width of the bands immediately below the clay drape in the other colonies with a single clay drape. The results from this approach show the least variation (Figure 7). The band widths for this correlation have a lower coefficient of variation (0.41) than the previous four correlations. A similar correlation was performed using band widths as percentages of colony height instead of the actual widths. The results show more variation (Figure 8) with a coefficient of variation of 0.51.

DISCUSSION

The results would have been less ambiguous if there had been more colonies available for study. With many more colonies, a more rigorous statistical test could have been performed to determine the significance of the patterns. Qualitatively, the results suggest at least some possibility that the 24 colonies may have responded simultaneously to a common environmental perturbation at some point in their histories. That is, most of the colonies would probably have coexisted for part of their history. This is supported by the lower coefficient of variation for the clay drape correlation. The colonies probably did not coexist for their entire histories as evidenced by the higher coefficients of variation for the isochronous larval settlement and isochronous colony death correlations. This suggests that the bedding plane from which the colonies were collected represents a depositional hiatus of at least minimal duration.

It is possible that none of the bands are actually correlated. If none of the bands are correlated, then it would indicate none of the 24 colonies coexisted. This could have resulted from three different scenarios. First, the colonies' larvae may have all settled and/or died on different bedding planes at different times. This would have been possible if the sedimentation rate was very slow but continuous (i.e., no diastem present at all). In this scenario, the colonies did not coexist, they just appeared to occur on the same bedding plane but were actually separated by thin bands of sediment that were indistinguishable after post-depositional compaction.

Second, the colonies' larvae may have all settled and/or died on the same bedding plane but at different times. This would have been possible if there was no sedimentation during the time it took all the 24 colonies to grow and die. In this scenario, the colonies did not coexist, and the bedding plane remained exposed during the time it took all the 24 colonies to grow and die. If this was the case, the bedding plane from which the 24 colonies were collected may represent a depositional hiatus of longer duration.

Third, the bedding plane from which the 24 colonies were collected may represent a time-averaged bedding plane. It is possible that the colonies lived at different times and even in different places. They could have been deposited together simply as a result of a storm-lag deposit (e.g., Specht and Brenner 1979, Meyer et al. 1981, Jennette and Pryor 1993). If this was the case, the orientation of the colonies should have been random (Arens and Cuffey 1989). This scenario is unlikely because the colonies were not randomly oriented. They were all oriented convex up (upright).
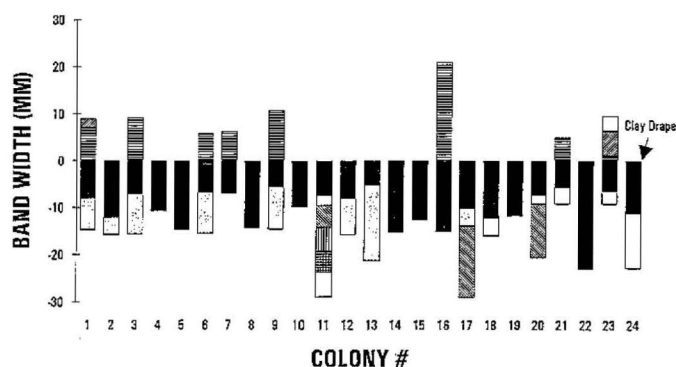

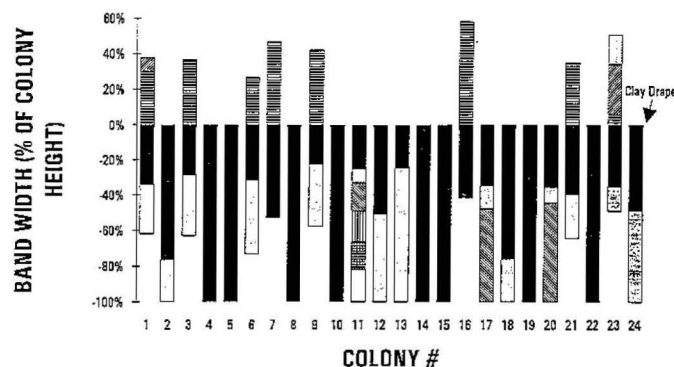FIGURE 7. Correlation of bands (in mm) assuming an isochronous clay drape.

FIGURE 8. Correlation of bands (in % of colony height) assuming an isochronous clay drape.

The correlations of the band widths based on percentage of colony height were consistently poorer than those using the actual band widths. All three correlations based on percentages had higher coefficients of variation for the band widths. Part of this is due to the fact that colonies with a single band had band width percentages of 100. This may be partly responsible for the higher coefficients of variation. To eliminate this potential effect, the eight colonies with single bands were eliminated from the correlations, and new coefficients of variation were calculated. For the correlations of the band widths based on percentage of colony height, the coefficients of variation in band width were reduced when colonies with single bands were excluded. The coefficient of variation for the correlation assuming isochronous larval settlement decreased from 0.59 to 0.49. The coefficient of variation for the correlation assuming isochronous colony death decreased from 0.54 to 0.48. The coefficient of variation for the correlation assuming an isochronous clay drape decreased from 0.51 to 0.40.

The effect on the correlations for the actual band widths was mixed when colonies with single bands were excluded. The coefficient of variation for the correlation assuming isochronous larval settlement did not change from 0.53. The coefficient of variation for the correlation assuming isochronous colony death increased from 0.49 to 0.58. The coefficient of variation for the correlation assuming an isochronous clay drape decreased from 0.41 to 0.34.

What type of environmental perturbation produced the growth surfaces and clay drapes? Kissling and Turonis (1977) attribtued some remnant growth surfaces in bryozoans to temporary cessation of growth due to flipping of the colonies during growth. Gyllenhaal and Kidwell (1989) attributed remnant growth surfaces in bryozoans to periods of episodic turbulence on the sea floor which resulted in flipping and/or partial burial of colonies. The colonies examined in this study do not show evidence of flipping for two reasons. First, the colonies were not randomly oriented. They were all oriented convex up (upright). Arens and Cuffey (1989) attributed the random orientation of *Prasopora* colonies to storm events that overturned and redeposited the colonies in random orientation. Second, the colonies do not have a spherical shape that results from repeated flipping and reorientation of the colonies (Kissling and Turonis 1977, Gyllenhaal and Kidwell 1989). The hemispherical shape of the colonies used in this study suggests the colonies maintained their upright growth orientation throughout their histories.

If the growth surfaces and clay drapes observed here were not caused by flipping of the colonies, then what caused them? Kissling and Turonis (1977) attributed some remnant growth surfaces in bryozoans to temporary cessation of growth due to siltation. Episodic periods of turbidity may have been the source of the sediment. Turbidity may have increased in response to increased water turbulence during storm events. The evidence for this can be found with the remnant growth surfaces which were accompanied by a clay drape and/or an intracolony overgrowth. The clay drapes may indicate smothering of the colony by fine-grained particles settling out of suspension on top of the colony. The intracolony overgrowth may indicate regeneration of zooids following the turbidity perturbation.

In summary, the internal stratigraphy of hemispherical trepostome bryozoans from single bedding planes provides an independent tool to determine the presence and relative duration of diastems. When the internal stratigraphy is easily correlated among colonies, it indicates a shorter duration hiatus. When the internal stratigraphy is not easily correlated among colonies, it may indicate a longer duration hiatus. This approach can be used with any modular organism such as corals, sponges, or other types of bryozoans.

ACKNOWLEDGEMENTS

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