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PARTITIONING OF MORPHOLOGIC VARIATION ACROSS STABILITY GRADIENTS IN UPPER ORDOVICIAN TREPOSTOMES

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ABSTRACT

The colonial nature of bryozoans allows for the partitioning of morphologic variation into its between- and within-colony components. The relative contributions of these two sources of variation are useful as paleoenvironmental stability indicators. Colonies from more stable environments should exhibit relatively more between-colony variation and/or less within-colony variation. This is demonstrated in three Upper Ordovician trepostome species across well-defined stability gradients.

INTRODUCTION

In colonial organisms such as bryozoans, individual zooids in each colony are genetically identical because of budding from a single larva. Each sexually produced colony represents a single genotype. Therefore, morphologic variation may be partitioned into its between-colony (genetic) and within-colony (extragenetic) sources. Previous workers have utilized this genetic identity of bryozoans to test whether variation partitioning is correlated with environmental stability. Farmer and Rowell (1973) studied the Upper Pennsylvanian Fistulipora decora. Schopf (1976) looked at four extant species of Euginoma. Schopf and Dutton (1976) analyzed the extant species Schizoporella errata. Pachut and Anstey (1979) examined the Upper Ordovician species Peronopora vera, Amplexopora septosa, Hallopora nodulosa and Heterotrypa ulrichi, and Pachut (1982) studied two Upper Devonian species, Leptotrypella pellucida and Nickelsopora renzettiae.

These studies, using both extant and fossil bryozoans, led to the model that in unstable environments within-colony variation dominates whereas in stable environments between-colony variation is greater. This model may be applied in three ways as an indicator of paleoenvironmental stability. The first is by equating within-colony variation with microenvironmental variation. In unstable environments, microenvironmental variation is greater due to more frequent perturbations. This produces within-colony phenotypic variability by causing scattered physical damage to zooids, prolonged lophophore retraction, or stunting. Colonies from more stable environments will exhibit less microenvironmental variation. The second way to apply the model is to equate between-colony variation with genetic variation. Organisms from more stable environments are more genetically variable (Valentine 1976 and references therein). This may reflect heightened adaptation to microecologic conditions in a stable environment or a limit to the number of genotypes that can survive in an unstable environment. Thus, colonies from more stable environments should exhibit

greater between-colony (genetic) variation than those from less stable regimes. The third application of this model lies in the association of morphologic variation with developmental regulation. Pachut and Anstey (1979) documented the occurrence of greater developmental regulation in colonies from stable environments where more canalized development may be adaptive in smaller niches. Conversely, they found more within-genotype developmental deregulation in unstable environments where greater morphologic variation may be selectively advantageous.

This study attempts to apply these three hypotheses in establishing the partitioning of morphologic variation as a paleoenvironmental stability indicator. Whereas previous studies have compared different species from different environments, this study takes a new approach by examining several species across a range of paleoenvironments representing different stability regimes. Only by addressing the problem in this manner can variation partitioning be confidently utilized as a paleostability indicator. Environmental stability refers to the frequency of stress-inducing disturbances. The more stable the environment is, the less frequent are the disturbances (Grime 1977). Stability must be defined in the context of the biology of the organism being studied. In this case, it will refer to the frequency of storm perturbations affecting the bryozoans.

MATERIALS AND METHODS

The species utilized are the trepostome bryozoans Homotrypa obliqua Ulrich, Heterotrypa frondosa (d'Orbigny) and Parvohallopora ramosa (d'Orbigny). They occur in a range of environments with distinctly different paleostabilities from the Maysvillian Stage of the Upper Ordovician Cincinnatian Series. The general environmental setting during the deposition of the Upper Ordovician limestone-shale sequence in the Cincinnati area of Ohio was a storm-dominated, shallow marine carbonate shelf of an epeiric sea (Meyer et al. 1981).

In ascending order, the three stratigraphic units sampled are the Fairmount Member of the Fairview Fm. and the Bellevue and Corryville Members of the McMillan Fm. (for more exact stratigraphic placement, this report employs the traditional classification of Caster et al. 1955). The Bellevue represents a shallow, high energy, unstable environment. The Corryville reflects a much deeper, lower energy, more stable environment. The Fairmount was deposited in an intermediate stability regime. In the shallow unstable environments, as water depth decreased, storm bed frequency increased which caused decreases in both percent shale and average thickness of shale beds (see Table 1). Three transgressive-regressive cycles have been recognized in the Cincinnatian Series (Hay et al. 1981). The Fairmount and Bellevue occur in the late regressive phase of the first cycle while the Corryville is in the early

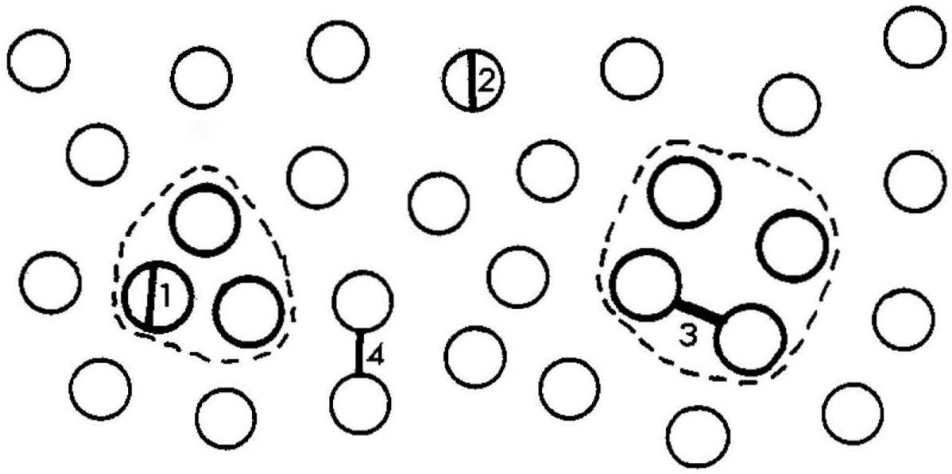
Table 1. Paleoenvironmental stability regimes for the three stratigraphic units included in this study. The units are not in stratigraphic order. Data from Meyer et al. (1981) and Tobin (1986).

UNIT	STABILITY	WATER DEPTH	STORM FREQUENCY	% SHALE	AVG SHALE BED THICKNESS
Corryville	high	deep	low	64	10 cm
Fairmount	intermediate	intermediate	intermediate	49	8 cm
Bellevue	low	shallow	high	17	2 cm

transgressive phase of the second cycle.

Five specimens of each species were selected from each stratigraphic unit within each species range from the Cincinnati area of Ohio. Homotrypa obliqua occurs in all three units so fifteen colonies of this species were studied. Because the remaining two species were found only in two of the three units, they are represented by ten colonies apiece. Each specimen is assumed to represent a separate colony and a separate genotype. The problem of polyembryony in cyclostomes has never been identified in fossil trepostomes, but it could alter the assumed 1 specimen/1 genotype ratio. The assumption of each specimen coming from a separate colony is probably valid because the largest specimens available were chosen for study in order to minimize the potential inclusion of two or more fragments from the same colony. This may be a more critical problem in specimens of Homotrypa obliqua and Parvohallopora ramosa, which have less massive, more fragile colonies. However, both species exhibit the same trends in partitioning morphologic variation as shown in the massive frondose colonies of Heterotrypa frondosa which do not fragment as easily.

Measurements were made on digitized images of tangentially oriented thin sections. This was performed at magnifications of X100 to X200 to the nearest 0.001 mm on the Yale Peabody Museum Morphometrics Lab using a Leitz Laborlux 12 microscope connected to a Spacial Data Systems Eyecom II image analyzer. This study is based on 4 characters diagramatically illustrated in Fig. 1. Maximum megazooecial diameter (MZD) was measured on ten randomly chosen monticular megazooecia per colony. Maximum autozooecial diameter (AZD) was measured on ten randomly selected autozooecia from the intermonticular areas. Interzooecial distance to the nearest neighboring megazooecium (MZID) was measured on ten pairs of randomly chosen megazooecia per colony. Interzooecial distance to the nearest neighboring autozooecium (AZID) was measured on ten pairs of randomly selected autozooecia from the intermonticular areas.



1 = Megazooecial Diameter = MZD
2 = Autozoeecial Diameter = AZD
3 = Megazooecial Interzooecial Distance = MZID
4 = Autozooecial Interzooecial Distance = AZID

Fig. 1. Diagrammatic representation of a tangential section showing the four characters measured. Dashed outlines represent monticular areas.

SOURCES OF VARIATION

Measurement errors can be assigned to two sources. First, the precision of individual measurements is within 3.5% of the mean values of the four characters. Secondly, variation in measurement of all characters is affected by the angle between the tangential section from which the measurements were taken and the zooecial walls in the exozone. Care was taken to grind the thin sections parallel to the branch axis in order to minimize this error.

Four sources of within-colony (extragenetic) variation have been recognized (Boardman et al. 1970), and these represent possible sources of error if not taken into account. The four are ontogeny, astogeny, polymorphism and microenvironment. By eliminating or at least reducing the effects of ontogeny and astogeny and by treating the various zooecial polymorphs separately, microenvironmental variation should remain as the sole source of within-colony variation, barring somatic mutations.

Ontogenetic variation was analyzed in two ways: in a growth series across zooecia proximally away from the growing margin; and in a growth sequence within zooecia proximally from the aperture toward the endozone. The first was checked by testing for correlations between the four characters and the distance from the growing margin. The exozone width/endozone width ratio was used as a proxy for the distance from the growing margin because this ratio increases away from the margin (Boardman 1960). For all species, the four characters were significantly independent of the ratio. This suggests ontogenetic variation is minimal. The second method for analyzing ontogenetic variation involved 20 tangentially oriented serial acetate peels taken through the exozone of Heterotrypa obliqua. As expected, MZD and AZD remained conservative in the outer exozone while MZID and AZID generally increased through ontogeny (Cuffey 1967). Applying these ontogenetic traits to all species, thin sections were ground uniformly close to the zoarial surface to minimize these potential sources of within-colony variation.

Astogenetic variation occurs mainly in the primary zone of astogenetic change but may also occur in subsequent zones. The probability of encountering the primary zone of astogenetic change on a branch was eliminated by avoiding any zoarial fragments containing a basal stem. Subsequent zones of astogenetic change stimulated by environmental events such as breakage or overgrowth were avoided by screening all specimens for evidence of branch repairs or overgrowths.

Zooecial polymorphism contributes to within-colony variation through the repeated occurrence of a few different zooecial morphs mainly in the zone of astogenetic repetition. This study precludes the potential problem of polymorphism's contribution to within-colony variation by treating the various polymorphs as distinct characters. Thus, the megazooecia of the monticules and the autozooecia of the intermonticular areas are treated separately.

The final extragenetic component of within-colony variation is microenvironmental differentiation. These are local factors that affect zooecial morphology in one or more regions of the colony but not throughout the colony. Microenvironmental causes of morphologic variation (e.g., turbulence) produce scattered physical damage or stunting in zooids. Microenvironmental factors are expected to play a more important role in the colonies found in the relatively less stable environments where storm perturbations are more frequent.

RESULTS

To determine the contribution of within- and between-colony variation to total morphologic variation, a one-way nested analysis of variance (ANOVA) was utilized. The use of ANOVA F-testing in partitioning total variation requires the fulfillment of several assumptions. Because the following analyses compare the relative values of mean squares but do not utilize confidence limits on their ratios (i.e., F-tests), ANOVA can be used without fulfilling all the assumptions. This is supported by similar results from the nonparametric Kruskal-Wallis test.

Between Formation Analysis Of Variance

To assess the presence of any intraspecific differences in morphologic variation between the stratigraphic units, I applied ANOVA. ANOVA revealed no significant contribution of between-formation variation to total variation (at P=0.05) for all characters for all species except AZID in Heterotrypa frondosa. Based on this analysis, between-formation variation is insignificant and the results indicate all three species show no noteworthy intraspecific morphological differences (for the four characters examined). These results would not support erection of subspecies or ecophenotypic variants for these species in these stratigraphic units.

Within Formation Analysis Of Variance

Mean squares are used to quantify the within-formation variation. Mean squares are the sum of squares adjusted for the degrees of freedom. This method standardizes between-colony mean squares (BMS) and within-colony mean squares (WMS). BMS = BSS/(k-1) and WMS = WSS/(n-k) where BSS is the between-colony sum of squares, WSS is the within-colony sum of squares, k is the number of colonies in each stratigraphic unit, and n is the number of individual zooecia measured per unit. BMS can be compared directly to WMS using the F-value which is defined as BMS/WMS. Thus, larger F-values indicate more between-colony variation and/or less within-colony variation. Table 2 contains these ANOVA results.

As predicted, the Corryville colonies generally exhibit the largest F-values, the Fairmount colonies intermediate and the Bellevue colonies the smallest. Only 3 of the 16 comparisons contradict the model Homotrypa obliqua - MZID - Corryville vs. Fairmount; Homotrypa obliqua - AZID - Fairmount vs. Bellevue; and Heterotrypa frondosa - AZD - Fairmount vs. Bellevue).

The problem of partitioning morphologic variation can also be approached through canonical discriminant analysis. This yields the Mahalanobis distance which is a measure of the difference between the means of multivariate groups. In this analysis, the groups are colonies within stratigraphic units in a multi-dimensional morphospace defined by the four characters measured. The Mahalanobis distance results (Table 3) support the ANOVA results well. Greater between-colony variation in the Corryville causes more dispersed colony centroids in discriminant space than in the Fairmount or Bellevue. This greater between-colony variation is revealed as larger Mahalanobis distances in the more stable environments.

Table 2. ANOVA results using natural log transformed data.
BMS = between-colony mean squares. WMS = within-colony mean squares.
F = F-value. * = F-value not significant (at P=0.05) indicating WMS>BMS.
For character definitions, see figure 1.

		MZD	AZD	MZID	AZID
Homotrypa obliqua					
	BMS	.2864	.3045	.6510	.4884
CORRYVILLE	WMS	.0198	.0132	.1519	.0604
(most stable)	F	14.47	23.11	4.29	8.09
	BMS	.1379	.1057	1.258	.0748
FAIRMOUNT	WMS	.0187	.0220	.1446	.0789
(intermediate)	F	7.37	4.80	8.70	0.45*
	BMS	.0767	.0895	.0209	.2438
BELLEVUE	WMS	.0258	.0321	.1140	.1315
(least stable)	F	2.97	2.79	0.18*	1.85*
Heterotrypa frondosa					
	BMS	.1118	.0129	.9465	.1134
FAIRMOUNT	WMS	.0081	.0048	.0663	.0234
	F	13.74	2.72	14.27	4.85
	BMS	.0183	.0452	.1087	.0229
BELLEVUE	WMS	.0109	.0091	.0414	.0119
	F	1.68*	4.99	2.63	1.93*
Parvohallopora ramosa					
	BMS	.0214	.0605	.2320	.1707
CORRYVILLE	WMS	.0060	.0045	.0766	.0435
	F	3.59	13.36	3.03	3.92
	BMS	.0047	.0065	.0432	.1573
BELLEVUE	WMS	.0051	.0044	.0477	.0667
	F	0.92*	1.47*	0.91*	2.36*

DISCUSSION

After controlling for the contributions to within-colony variation by ontogeny, astogeny, and polymorphism as previously discussed, the microenvironmental effect can be determined from ANOVA. The model predicts greater within-colony (i.e., microenvironmental) variation in the less stable environments. Microenvironmentally induced variation is more prevalent (i.e., larger WMS values) in the colonies from the less stable environments in only 8 of the 16 comparisons. Microenvironmental variation does not clearly exhibit the expected inverse relationship with environmental stability.

To test for any genetic or developmental differences among the colonies from the three stratigraphic units, between-colony variation can be compared using BMS. Between-colony variation has genetic, macroenvironmental and extragenetic components. The macroenvironmental component was minimized by restricting specimen collecting to small outcrop areas. Since postmortem transport of material in these deposits was minimal (MacDaniel 1976), the colonies are probably from the same environments. Extragenetic variation has been eliminated except for microenvironmental contributions leaving the genetic (between-colonies)

Table 3. Average Mahalanobis distances between colonies within stratigraphic units using natural log transformed data.

Homotrypa obliqua	MAHALANOBIS DISTANCE
CORRYVILLE	2.487
FAIRMOUNT	1.960
BELLEVUE	1.406
Heterotrypa obliqua	
FAIRMOUNT	2.689
BELLEVUE	1.470
Parvohallopora ramosa	
CORRYVILLE	2.030
BELLEVUE	1.028

and microenvironmental (within-colonies) factors contributing to between-colony variation. In 13 of the 16 comparisons, between-colony variation is greater in the more stable environments as expected.

These results may have several causes. Possibly the colonies from the more stable environments are more genetically variable. As previously discussed, the greater between-colony variation in the Corryville colonies may reflect greater genetic variability than the Fairmount or Bellevue colonies. The same applies to the Fairmount colonies relative to those of the Bellevue. Another possible explanation for the greater between-colony variation in the more stable environments lies in developmental regulation. As discussed previously, the greater between-colony variation in the colonies from the more stable environments may be attributed to greater within-genotype regulation. This regulation in the Corryville colonies is revealed by a correlation matrix of the measured characters. In *Homotrypa obliqua*, the Corryville colonies show a significant correlation between AZD and AZID. The negative correlation of this interaction indicates that as zooecial diameter increases in the intermonticular areas, interzooecial distance decreases as a form of space regulation. The detection of this interaction in only the Corryville colonies may reflect greater within-genotype regulation than in those from the Fairmount or Bellevue where canalization may be less effective in the face of environmental instability.

CONCLUSIONS

By partitioning bryozoan morphologic variation into its within- and between-colony components, this study successfully differentiates between three stratigraphic units with varying degrees of paleoenvironmental stability. Results show that genetic variability and/or developmental regulation dominates in the more stable environments. The analysis shows how to separate the genetic and environmental inputs to a colonial organism's phenotype. This has far-reaching potential in many paleontological problems where solitary organisms fall short. A similar paleoenvironmental analysis can be performed along with any faunal study, because quantitative taxonomic data can be used directly. With the few statistical analyses described here, an investigator can obtain paleoenvironmental stability information useful in testing for homoplasy. Thus, a more complete taxonomic and evolutionary analysis is possible by routinely using variation partitioning.

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