Variation in the Bryozoan *Fistulipora decora* (Moore and Dudley) from the Beil Limestone of Kansas

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ABSTRACT

The study is based on five selected characters, each character being measured on *25* randomly selected zooecia in comparable ontogenetic and astogenetic stages from randomly chosen colonies at each of **four localities. Data are** typically normally distributed **for** four of the five characters, but the colony variances are not homogeneous when data for a **given** character are considered for **all** localities. This failure of **the** assumptions inherent in a nested analysis of variance **would** lead to grossly misleading conclusions if the technique were applied to **the** present data.

Nonparametric tests show that there are significant differences between localities for four of the **five** characters. **These** differences are rather uniformly distributed among localities and characters. They **are** believed to be **caused** by small differences in the average genetic composition of the populations from different localities, but the **effects** of differences in **"gross"** environment **may** have had some influence.

Highly significant differences exist within **all** four localities, ***as*** shown by analysis of variance. Differences are not confined to **one** or two **colonies;** this, **combined with** relative uniformity of **"gross"** environment implied by field evidence, suggests that the differences are caused by **a** high degree of genetic diversity between colonies at **one** locality. Comparison ***of the*** intercolony and intracolony components of variance

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suggests that the **latter typically** accounts for **a** larger proportion *of the total* variance than the former. Thir is believed to reflect the strong influence of microenvironmental factors on the phenetic expression of zooecia within **a** single colony.

INTRODUCTION

In the *past* decade there has been renewed interest in the study of Bryozoa. Numerous authors **have** contributed to our understanding of the paleobiology of these animals, and, although much still remains to be **learned,** various aspects of growth have been **explored** and our conceptual understanding of the causes of variation have been improved (e.g., Boardman and Cheetham, 1969; Boardman. Cheetham, and Cook, 1970). Simultaneously, there has been an increased usage of biometrical techniques in bryozoan investigations, both as descriptive tools and in testing for significant differences between colonies. This field has recently been reviewed by Anstey and Perry (1970).

The principal objective of the present study involves joint consideration of both of t ' above aspects: to assess how variation is distributed in a number of characters of a **particular** species of bryozoan from one horizon over a restricted region, to determine **how** much of the total variation is contributed by variation within **a** colony, how much by variation between colonies at one locality and to ascertain whether significant differences exist between localities. **As** expressed. the problem clearly requires a statistical approach and an ordered sampling plan, but the general conclusions have an equally obvious application in any conventional systematic study of comparable colonial organisms. Related secondary objectives of the investigation are an assessment of character correlation and the degree of redundancy in the data, together with an evaluation of the limitations imposed on this type of investigation by the methods utilized.

MATERIAL AND METHODS

The choice of a species for study was pragmatic; *we* wished to **keep** the model as simple as possible and confine our investigation to zooecia in the **same** ontogenetic and astogenetic *stages.* Individual zooecia of *Fistulipora decora* (originally *Cyclotrypa decora* Moore and Dudley, 1944, **p.** 275) are well suited for this purpose because they rapidly attain a stable adult form in the lenticular to subhemispherical zoaria, thus diminishing the possibility of inadvertently including measurements of ontogenetically immature individuals (Fig. 1).

F. decora is a relatively abundant faunal element of the Beil Limestone Member of the Lecompton Limestone (Virgilian) of northeastern Kansas. In addition, the stratigraphy of the Beil Limestone is known through the work of Brown (1958). Although one could not claim exact correlation from one locality to another, the units sampled are certainly of closely comparable age, since the total thickness of *the* member is usually less than 3 m.

At the outset, consideration must be given to the sampling plan for any study of *this* type, for although differing statistical techniques may have somewhat different underlying assumptions, all are predicated on the. assumption of random sampling. **As** is **well** known in geological situations (Krumbein and Graybill, 1965), very rarely is the target

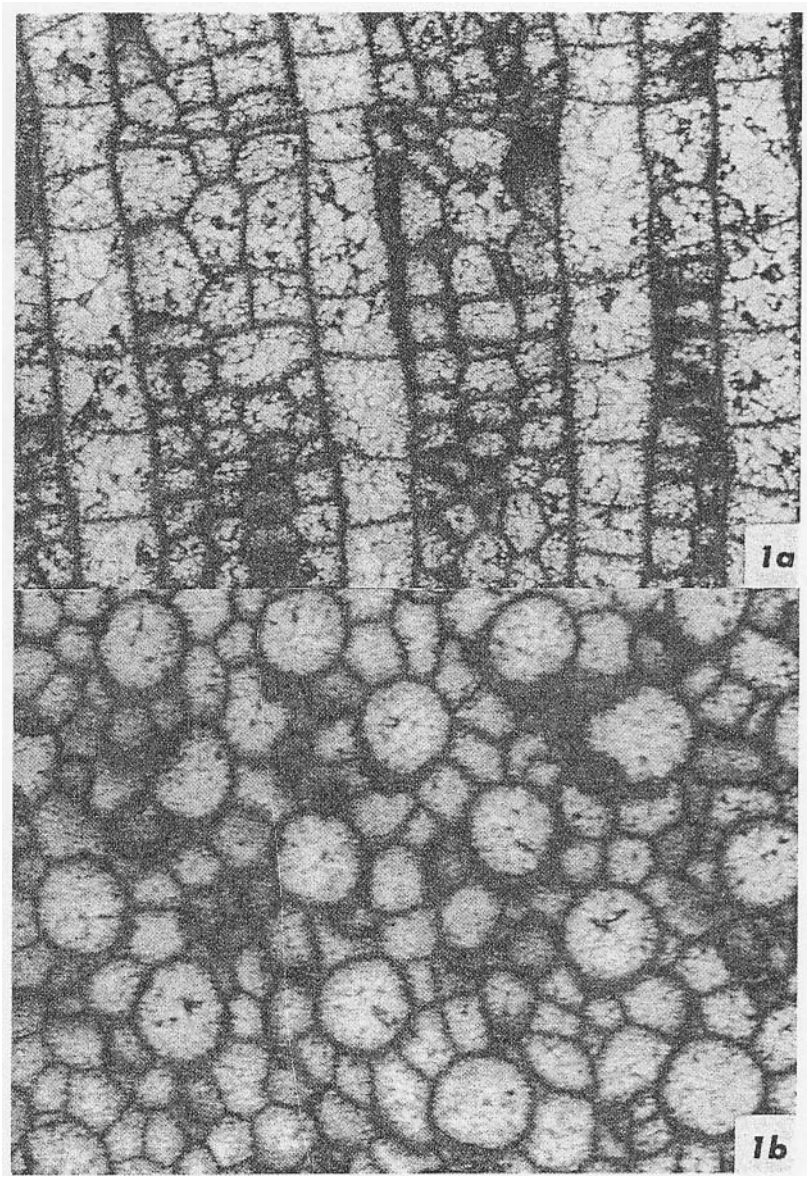


Figure 1

a. Longitudinal acetate peel of *Fistulipora decora*. Beil Limestone Member, Lecompton Formation. Stull locality. KU. 72000. ×35. b. Transverse acetate peel of *F. decora*. Beil Limestone Member, Lecompton Formation. Stull locality. KW. 72686. ×35.

population (in this case, all specimens of *F. decora*) available for sampling. The choice of collecting localities is not random but is determined by the available exposures. Consequently, the statistical inferences apply only *to* the available population, defined as all well-preserved specimens of *F. decora* exposed on selected bedding planes at selected

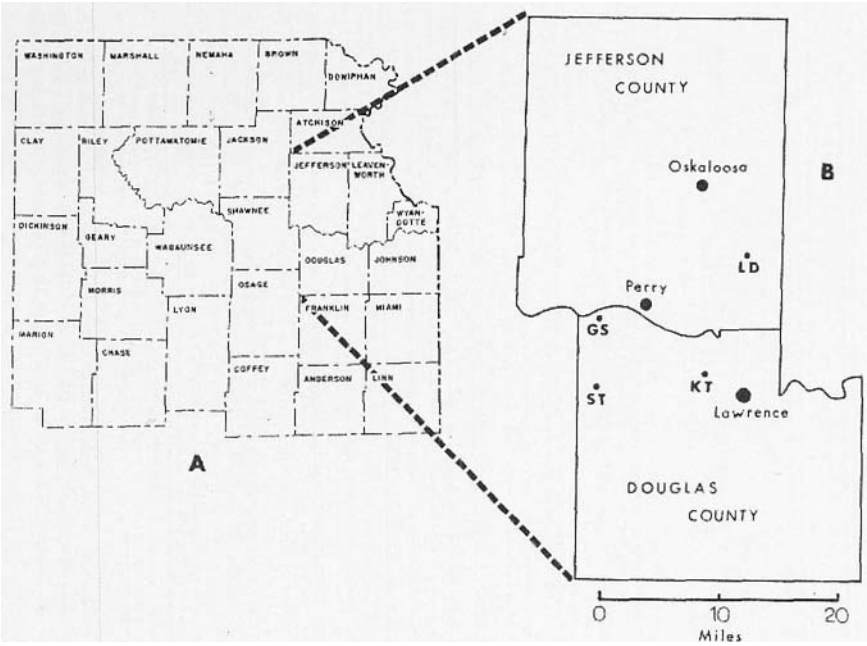


Figure 2

Collection localities in eastern Kansas: LD, Lake Dabinawa; ST, Stull; KT, Kansas Turnpike; GS, Grover Station. These abbreviations are also used in Tables 3 and 5 and Fig. 8.

localities. However, since there is no *a priori* reason for believing that the available population of F. *decora* should be significantly different from the target population, it becomes possible *to* extend the conclusions derived from the available population *to* the target population by substantive geological argument (Krumbein and Graybill, 1965). It must be recognized, however, that the statistical conclusions apply rigorously only to the available population, and their extention, although reasonable, has no statistical basis.

Collections from the Beil Limestone Member were made at four localities in northeastern Kansas (Fig. 2), the localities forming a rough parallelogram with sides approximately 15 km in length. The four localities are referred to in subsequent discussion as Stull Road, Grover Station, Lake Dabinawa, and Kansas Turnpike. *At* each locality, specimens were collected *in situ* from a single bedding surface in order to avoid the inadvertent mixing of material foreign to the chosen horizon. Specimens embedded in matrix and with the growth surfaces of the lenticular zoaria oriented upward were assumed to be *in situ*. The assumption is at least reasonable, because most of the associated brachiopod fauna is unworn and consists of complete bivalved shells.

As much material as was feasible, within the bounds of reasonable expenditure of time and money, was collected from each locality. Subsequently, it was found that many of the specimens were unusable due to poor preservation, mainly a consequence of dolomitization or secondary recrystallization of calcite. Of the available specimens, five colonies were chosen randomly from each locality, using a random number table.

One of the four localities sampled (Kansas Turnpike) failed to provide the desired number of usable specimens, and in this particular instance only four colonies were analyzed.

Measurements

The acetate peel technique outlined by Boardman and Utgaard (1964) was employed. It was desirable to evaluate the significance of distortion introduced during the process of removing an acetate replica from a specimen. Measurements of an arbitrarily chosen colony dimension were made directly from a specimen and compared to measurements of the same dimension taken from an acetate peel. Statistical analysis of the data using a simple t-test revealed no significant differences between the two sample means at the $\alpha = 0.001$ level of significance.

Measurements were made from the acetate peels by projecting character images at a known scale (×49.3) through a standard petrographic microscope onto a sheet of white tracing paper. Characters were measured directly from the projected image using a pair of Helios calipers (3 and S Precision Scientific Measuring Instrument Company, Brooklyn, N.Y.), graduated to 1/20 mm.

Twenty-five measurements for each character for each colony were taken along randomly chosen traverses utilizing a calibrated mechanical stage, Traverse coordinates were chosen from a random number table, recorded, and each value set on the appropriate scale of the calibrated stage. The traverse was carried out and as many measurements as possible were made. If, after completing a traverse, less than the desired number of measurements had been obtained, a new set of traverse coordinates was chosen in an identical manner, and the process repeated until the required number was recorded. Traverses were consistently carried out in the same direction in order to avoid the possible introduction of bias by making arbitrary choices during the data-gathering process.

Choice of Characters

Owing to the relatively simple structural morphology of fistuliporoid bryozoans, only a modest number of phenetic characters are available for study. This investigation is based upon five characters illustrated diagrammatically in Fig. 3 (cf. Fig. 1a and b).

In tangential sections, zooecial diameter (ZD) in millimeters was determined as the minimum distance between zooecial walls. The interzooecial distance (IZD) is the distance between nearest-neighbor zooecia in millimeters, as measured in tangential section. Related to this character is the number of vesicles between nearest-neighbor zooecia (VCT), also measured in tangential section. In longitudinal section, two characters were obtained: the number of diaphragms in a distance of 1 mm (DC/MM), and she number of complete vesicles enclosed in a circle of radius 0.25 mm (VC/0.25).

RESULTS

Twenty-five measurements were obtained for each of five characters from a total of 19 colonies representing four localities. The raw data are given in Appendix 2 of Farmer (1971), and copies may be obtained as computer tabulation from the authors.

The nature of the principal question posed—how is the variation distributed—suggests

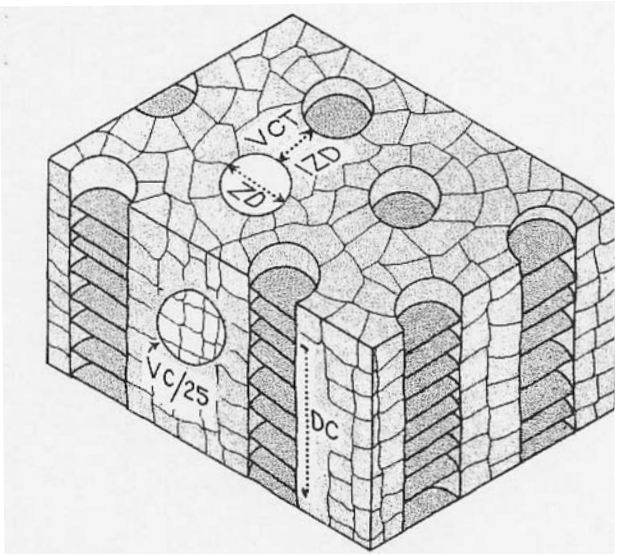


Figure 3

Diagrammatic representation of a fistuliporoid bryozoan showing the five characters utilized in the study. For tangential sections *they* include: zooecial diameter (ZD), interzooecial distance for nearest-neighbor zooecia (IZD), and counts of the number of vesicles between nearest-neighbor zooecia (VCT). For longitudinal *sections* they include diaphragm counts per millimeter (DC/MM) and the number of complete vesicles in circle of radius 0.25 mm (VC/0.25). These abbreviations are also used in Tables 1, 2, 5, and 8

that the data should be analyzed as a *nested* analysis of variance. However, parametric analysis of variance (anova) makes certain assumptions about the data that must be met before its use can be regarded as appropriate or the tests exact. These assumptions *are* discussed in detail by Sokal and Rohlf (1969); they include the need for the error term to be a normally distributed, independent variable, and the variance of the samples to be equal (homoscedastic).

The consequences of failure to satisfy the assumptions inherent in analysis of variance may be serious (Bradley, 1968), particularly if the variances of the samples are heteroscedastic and only a few degrees of freedom are involved. The data should always be tested *to* see if use of the method is justified.

The Kolmogorov–Smirnov test far goodness of fit showed that for all 19 colonies the data are normally distributed (P = 0.05) for zooecial diameter (ZD), minimum interzooecial distance (IZD), the number of vesicles per unit area (VC/0.25), and the number of diaphragms per millimeter (DC/MM). Only one character, the number of vesicles between nearest-neighbor zooecia (VCT), deviates consistently from normality. Values of d_{max} for this character are all significant at $P<0.01$. This is not surprising due to the small number of classes involved (counts ranged from 0 to 2) and the relatively low frequencies in classes 0 and 2 for moct colonies. For the data as a whole the required equality of variances does not exist; *the* variances are markedly heteroscedastic for the four characters studied (VCT was *not tested* as it had previously failed the

test for normality). None of the transformations employed succeeded in solving this problem of inhomogeneity of variances. Consequently, the nested analysis of variance could not be employed.

Between Locality Variance

The significance of variation between localities was tested using the Kruskal–Wallis nonparametric test (Table 1). For purposes of comparison only, a nested anova was carried out for the four normally distributed characters (Table 2). Comparison of *the* two tables reveals the serious limitations imposed on the parametric analysis of variance of these data by deviations from homoscedascity. At the highest level in the nested anova (Table 2), between-locality effects are all seemingly nonsignificant (at $P = 0.05$) for all characters. Yet the Krusal–Wallis test, which is less powerful than an analysis of variance when all the assumptions of the latter are met, consistently shows highly significant differences between localities ($P<0.005$). This example reemphasizes the importance of testing the assumptions of anova; failure to meet them may give rise to spurious F values and subsequent gross misinterpretations.

The results in Table 1 give no indication how the significant differences between localities are distributed. This may be overcome by performing a Krusal–Wallis test for all possible pairs of localities for each character (Table 3). These tests reveal that the differences arise not by one locality differing consistently from the remainder but by a rather uniform distribution of the differences. The Stull and Kansas Turnpike localities both differ significantly from other localities in eight of a maximum of fifteen character/locality combinations (each locality is compared with three others, for five characters). Grover Station and Lake Dabinawa differ similarly six out of a maximum of fifteen combinations. With the exception of the character "number of vesicles between nearest-neighbor zooecia," all the localities commonly differ significantly from each other. Clearly they do not belong to one statistical population. However, Dice diagrams of the normally distributed characters (Figs. 4–7) show no clearly marked discontinuities between localities. A better overall impression based on simultaneous consideration of all five characters can be obtained using principal-components analysis and projecting the colony means into the reduced character space defined by the first three principal components (Rohlf, 1968). This technique has previously been used in paleontological work by Kaesler (1970) and Rowell (1970), both of whom provide more detailed accounts of the method. Reducing the dimensionality of the data inevitably introduces some distortion: this is often modest and its extent is always known. Moreover, the distortion is not uniformly distributed: the small phenetic distances are more heavily distorted; the larger ones, giving the overall view of phenetic relationships, suffer least. The amount of distortion introduced in the present model is very small (Table 4).

This model (Fig. 8) reveals no marked tendency for colonies to cluster together by locality. The lack of any clearly defined discontinuities suggests that although the colonies from the four localities are not part of a single statistical population, nonetheless they *are* conspecific. Several hypotheses may be advanced to explain the significant differences that exist between the localities. The samples could be from four relatively localized populations, the morphological differences being reflections of differences in average

Table 1
Results for the Nonparametric Kruskal–Wallis **Test,** Between Localities

Character[a]	Kruskal–**Wallis**
ZD	$P < 0.005$
IZD	$P < 0.005$
VCT	Not significant
VC/C.25	$P < 0.005$
DC/MM	$P < 0.005$

[a]Characters abbreviated **as** in **Fig. 3.**

Table 2
Results of **Nested Analysis** *of* Variance for Four Characters

	F ratio for each character[c]			
Source of **Variation**	ZD	IZD	DC/MM	VC/0.25
Among localities	0.6276[b]	0.8588[b]	0.4312[b]	1.3164[b]
Within localities	43.2857[c]	11.0138[c]	16.3007[c]	15.0016[c]

[a]Characters **abbreviated as** in Fig. **3.**
[b]Not significant.
[c]$P < 0.001$.

genetic composition built **up** by t... effects of isolation. The short distances between localities and the presence of the species in most outcrops of *the* Bell Limestone member suggest, however, *that* prolonged isolation of populations is unlikely. Alternatively, small-scale geographic variation in environmental factors **may** be responsible for the differences, either producing differential selection, or acting directly on the phenotype without causing notable changes in the *genetic* composition of the populations. Another explanation may be *that* the differences are primarily genetically controlled and are a reflection: of slight differences in geologic age. It is not, and probably never will be, possible to choose between the latter three potential mechanisms; indeed, all three **may** have operated,

Within-Locality Analysis of Variance

Although the assumptions for a nested analysis of variance *are* not met, the conditions for a single-way analysis of variance are satisfied at some localities fur all characters except "number of vesicles between nearest-neighbor zooecia." This analysis was performed for each character/locality combination where appropriate (Table S), and both the Kruskal–Wallis anova analog and modified Snedecor test fur the equality of means (Sokal and Rohlf, 1969, p. 376) were employed for all character/locality combinations. The three methods consistently reveal highly significant differences between colonies **at** each locality for the four characters examined.

In the 11 cases for which it was possible to run a single-way analysis of variance,

Table 3
Kruskal–Wallis Test Between All Possible Pairs of Localities[a]

Character: Zooecial Diameter (ZD)

	ST	GS	LD	KT
ST	ns[b]			
GS	[c]	ns		
LD	ns	[c]	ns	
KT		ns	[c]	ns

Character: Interzooecial Distance (IZD)

	ST	GS	LD	KT
ST	ns			
GS	[d]	ns		
LD	[c]	ns	ns	
KT	[c]	ns	ns	ns

Character: No. Diaphragms/mm (DC/MM)

	ST	GS	LD	KT
ST	ns			
GS	ns	ns		
LD	ns	ns	ns	
KT	[c]	[e]	[d]	ns

Character: No. Vesicles/Unit Area *(VC10.25)*

	ST	GS	LD	KT
ST	ns			
GS	ns	ns		
LD		[c]	ns	
KT	[c]	[e]	ns	ns

Character: No Vesicles Between Nearest-Neighbor Zooecia (VCT)

	ST	GS	LD	KT
ST	ns			
GS	ns	ns		
LD	ns	ns	ns	
KT	ns	ns	ns	ns

[a] Localities abbreviated as in Fig. 2.
[b] Not significant.
[c] $0.005 > P$.
[d] $0.01 > P > 0.005$.
[e] $0.05 > P > 0.01$.

one may analyze the data still Further. Recall that this technique enables the variance to be partitioned into two parts, that due to variation within colonies and a component caused by variation between colonies at one locality. In all cases but one, the estimate of the within-colony variance is greater than the estimate of the between-colony variance (Table 6). One can claim only that the unbiased estimates of these variances *are* so related, their real values are unknown. Because 10 of the 11 pairs of variances have this relationship, one may feel some confidence in making the generalization that in

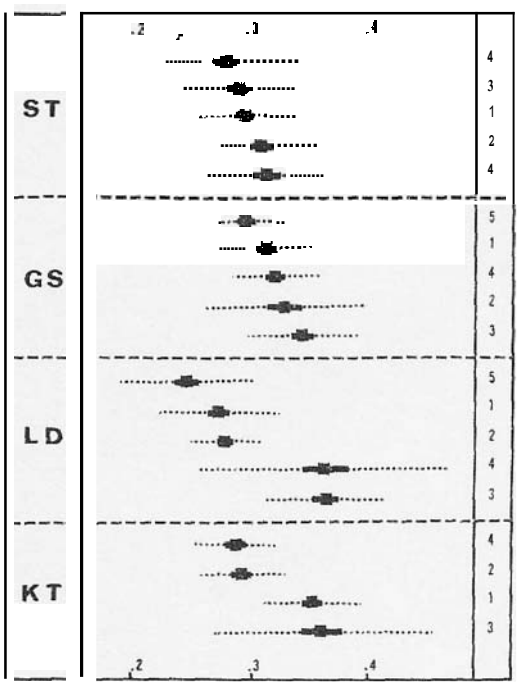


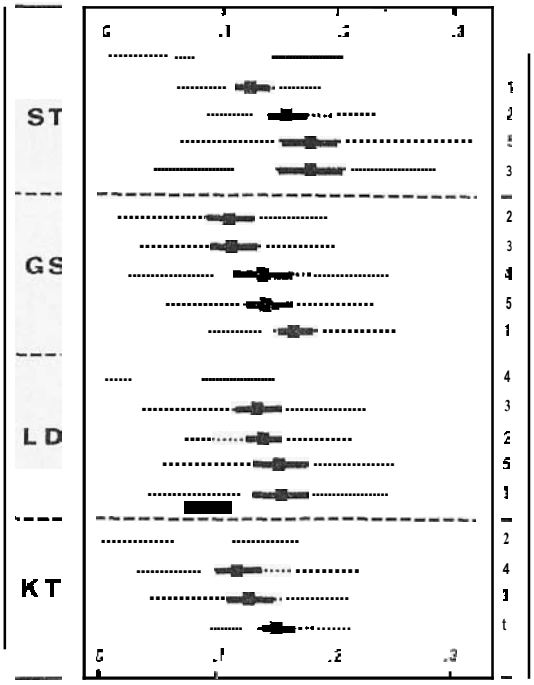
Figure 4

Dice diagrams for zooecial diameter for each colony, dimensions in millimeters. Black square is location of mean, black bar is 95 percent confidence limit of mean, and broken bar is 95 percent confidence limit of character for colony.

Table 4

Number of characters	% Variance explained by *first* three principal components	Correlation between distances of all possible pairs of OTUs *in* space *and* three-principal-componentspace
5	93.84	0.993

F. decora the within-colony variance is typically greater than the between-colony variance for any me locality. However, for our data, even statements of this nature should be handled with caution. This is readily seen by calculating 95 percent confidence limits for the variance components of the most extreme *case* in Table 6, the interzooecial distances *at* Grover Station {Table 7). Confidence limits for variance components are skewed and the upper 95 percent limit for a between-colony variance overlaps the lower limit of the within-colony variance. Clearly, *if* the parametric value of s_A lay close to the upper 95 percent confidence limit of s_A, then the intercolony variance component



, gure 5

Dice diagrams for interzooecial distance **for** each colony. Dimensions in millimeters. Black square is Location of mean. black bar is 95 **percent** confidence limit of mean, and broken bar **is** 95 **percent** confidence limit of character for colony.

would exceed the intracolony component, the converse of the relationship suggested by the unbiased estimates of these statistics.

Comparable methodological limitations apply in utilizing the coefficient of variation to examine the relative magnitude of **within-** and between-colony variation, a technique that has been used in some earlier studies of colonial animals, This approach, although having the advantage of simplicity, suffers from twc difficulties. If the original measurements **are** markedly nonnormal, the coefficient of variation is not a **very** meaningful statistic, being based on the standard deviation and mean, both inapproporate statistics for nonnormal distributions. The second difficulty is comparable to that experienced in examining the relative size of the partitioned variance components. It is desirable to ascertain whether observed differences between the estimated intra- and intercolony coefficients of variation are indeed significant; they may be more apparent than real. It is necessary that confidence limits for the estimates of coefficients of variation be calculated tc give some control *to* subsequent paleobiological speculation. The appropriate statistics are discussed by Sokal and Rohlf (1969, p. **137).**

The biological explanation of the within- and between-colony variances may be examined further. The within-colony variance is an **expression** of microenvironmentally induced variations (Boardman, Cheetham, and **Cook,** 1970). As is well **known,** genetically

Tabla 5
Comparison of **Results for** Parametric and Nonparametric **Tests** Between **Colonies, Within Localities"**

Character[a]	Locality[b]	Anava	Kruskal–Wallis	Snedecor
ZD	ST	c		c
	GS	na[c]		c
	LD	na	c	c
	KT	na		c
IZD	ST	na	c	c
	GS	c	c	c
	LD	c	c	c
	KT	c	c	c
DC/MM	ST	na[c]	c	c
	FS	na	c	c
	LD	c	c	c
	KT	c	c	c
VC/0.25	ST	c	c	c
	GS	c	c	c
	LD	na[c]	c	c
	KT		c	c

[a]Characters **abbreviated as** in Fig. **3.**
[b]Localities **abbreviated as in** Fig. **2.**
[c]$P < 0.001$; [c], **brackets enclose** results **for** $\log_{10}Y$ **transformed data.**
[d]Test **not applicable.**

the ividual zooids of a colony were identical (barring mutations), having originated by vegetative budding from a single larvae. In detail, however, the individuals were not exposed to identical microenvironmental situations. The animals responded phenetically to these differences, *but* the response to a given microenvironmental situation will have been governed by the genetic features of the colony, which differ from colony *to* colony. Thus, the within-colony variance may be thought *of* statistically as consisting of two components—a "nongenetic (microenvironmental)" effect and a "nongenetic–genetic" interaction term. Unfortunately, with fossil material, it **is** not possible *to* isolate these components **and we** can only group them **under** the accepted term of "extragenetic" effects, as defined by Boardman, Cheetham, and Cook (1970).

Field evidence suggests that *the* environment at any one collecting locality was relatively uniform. Consequently, the between-colony variance at any one locality **is** probably best regarded as a measure **of** *genetic* diversity between individual colonies of the type found in any **population.**

Correlations Between Characters

In preceding discussions, characters have been treated as though they were independent variables. However, it can be argued on geometrical grounds that some characters (for

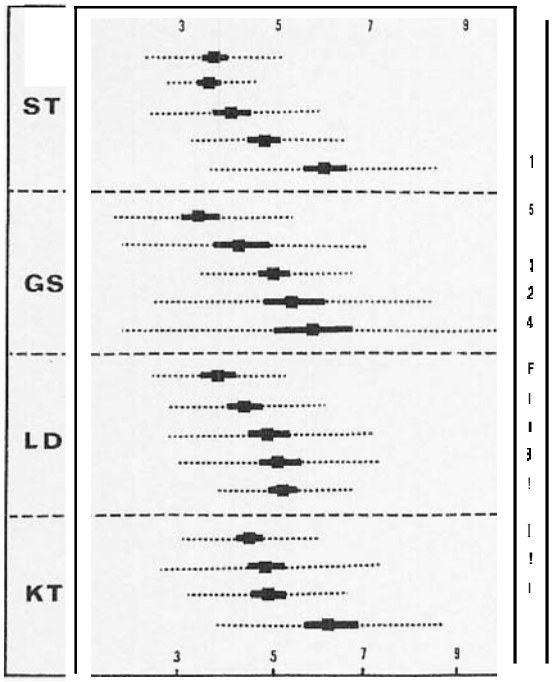


Figure 6

Dice diagrams for **the** number **of** diaphragms in **a** I-mm distance. Black square is location of mean, black **har** is **95** percent confidence: limit *of* mean, **and** broken bar is 95 percent confidence limit of character for colony.

example, IZD and VCT) must be correlated to some degree. Particularly for studies limited to only a few characters, it is desirable to reduce the amount of redundancy (in the fc of highly correlated characters) to a minimum in order to obtain a maximum amount of meaningful information. **A** matrix of Pearson product-moment correlation coefficients (r) **was** calculated for all possible pairs of character means and variances (Table 8). **The** variance of VCT (number of vesicles between nearest-neighbor zooecia) was not used because of the pronounced deviation of the data from normality.

Two characters stand out in displaying a high degree of independence from the other variables. Correlation coefficients for DC/MM (diaphragms per millimeter) and VC/0.25 (vesicles per unit area) are not significantly correlated with any of the other four principal characters. Both are count data, rather easily obtained and, for this study, normally distributed.

It is interesting to examine the probable cause of the negative carrelations of ZD (zooecial diameter) with IZD (interzooecial distance) and VCT (vesicles between nearest neighbors). Biologically, these correlations are not entirely unexpected. **As** zooecial diameter increases, crowding occurs with a decrease in the interzooecial distance, also reflected by a decrease in number of vesicles between zooecia. The high **positive** correlation

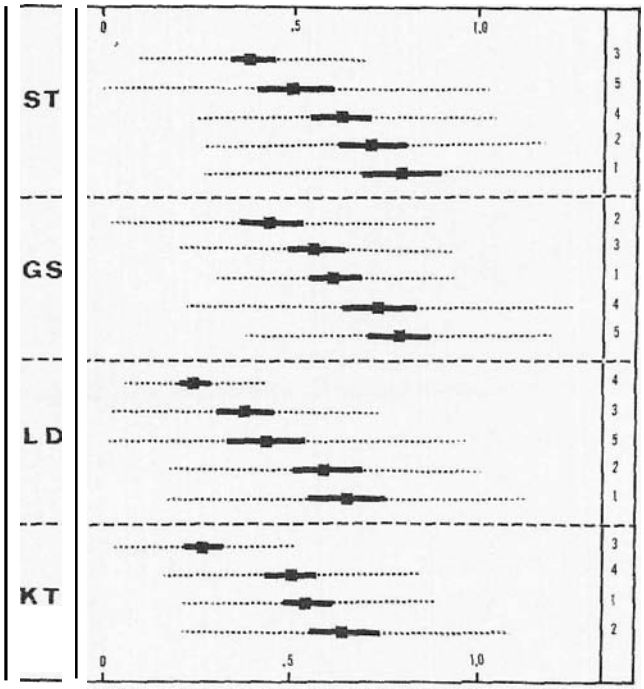


Figure 7

Dice diagrams for the number **of** complete **vesicles** in a circle **of radius** *0.25* mm, **as** measured in longitudinal section. Black square **is** location of mean, **black bar is** 95 percent confidence limit of mean, and broken bar is *95* percent confidence **limit** of **character** for colony

between IZD and VCT (r = .811) seemingly reflects some uniformity in the size of vesicles, although this is not apparent through cursory observation. The relatively high negative correlation *(−0.47)* of VC/0.25 and the variance of ZD is also notable. This can seemingly be interpreted as an increase in the average vesicle *size* as the variance of zooecial diameters increases. Perhaps related to this **is** the positive correlation between VCT a d the variance of VC/0.25, interpreted as an increase in the number of vesicles between zooecia with an increased variation in the size **of** the vesicles. **A** clear-cut biological explanation for these correlations *is* not apparent, but they may possibly reflect the influence of monticular areas on those characters.

Although most characters are correlated to some extent **with** one another, the *fact* that no r value *is* 1.0 indicates that varying degrees of independence exist; thus, varying amounts of information are obtainable from all characters. However, in evaluating the usefulness of **a** particular character it is important to consider not only the degree of independence but also the nature of the data obtained. The data obtained for VCT, as discussed earlier, could not be handled well statistically because of the lack of normality of the data and the limited number of **size** classes. This, coupled with the fact that

Table 6
Partitioning of Variance Components by Single-Classification Anova[a]

		ST[b]	GS	LD	KT
	Zooecial Diameter (ZD)				
s_A^2	Between colonies	24.96	na[c]	na	na
s^2	Within colonies	75.04	na	na	na
	Interzooecial Distance (IZD)				
s_A^2	Between	na	17.47	41.46	25.82
s^2	Within	na	82.53	58.53	74.18
	Diaphragm Counts per Millimeter (DC/MM)				
s_A^2	Between	[50.43][d]	na	28.36	35.30
s^2	Within	[49.57][d]	na	71.64	64.70
	Vesicle Counts per Area (VC/0.25)				
s_A^2	Between	31.82	29.54	42.41	45.78
s^2	Within	68.18	70.46	[57.59][d]	54.22

[a] Values are expressed as a percentage of the sum of the variance components.
[b] Localities abbreviated as in fig. 2.
[c] Anova not applicable due to failure of assumptions.
[d] Values given in brackets are for $\log_{10} Y$ transformed data.

Table 7
Anova Table—Interzooecial Distance (IZD), Grover Station[a]

	d.f.	Mean Square	Expected Mean Square
Between colonies	4	0.3388	$s^2 + 5s_A^2$
Within colonies	120	0.0538	s^2

$s^2 = 0.0538$ $s_A^2 = 0.0114$

95% confidence interval for $s^2 = 0.041 - 0.072$
95% confidence interval for $s_A^2 = 0.003 - 0.110$

[a] Five colonies each with 25 measurements.

it has a moderately high correlation with ZD (−0.633) and IZD (0.811), makes it a relatively undesirable character, It is clear that the potential usefulness of IZD is much greater because it is a continuous variable; moreover, it can be more effectively handled statistically.

Table 8
Matrix of Correlation Coefficients Between Characters[a]

	ZD	VAR/ZD	IZD	VAR/IZD	VCT	VC/0.25	VAR/VC/0.25	DC/MM	VAR/DC/MM
VAR/ZD	**0.51**	**1.00**							
IZD	**−0.55**	**0.46**	**1.00**						
VAR/IZD	−0.12	0.33	0.02	**1.00**					
VCT	**−0.63**	**−0.59**	**0.81**	0.05	**1.00**				
VC/.25	−0.42	−0.77	0.30	−0.36	0.42	**1.00**			
VAR/VC/.25	**−0.64**	**−0.50**	0.36	−0.00	**0.55**	**0.59**	**1.00**		
DC/MM	0.40	−0.07	−0.27	**−0.47**	−0.13	0.14	0.01	**1.00**	
VAR/DC/MM	0.33	−0.06	−0.29	0.03	−0.10	0.25	0.27	**0.55**	**1.00**

[a]Characters abbreviated as in Fig. 3.
[b]Values in boldface significantly different from 0 at $P = 0.05$.

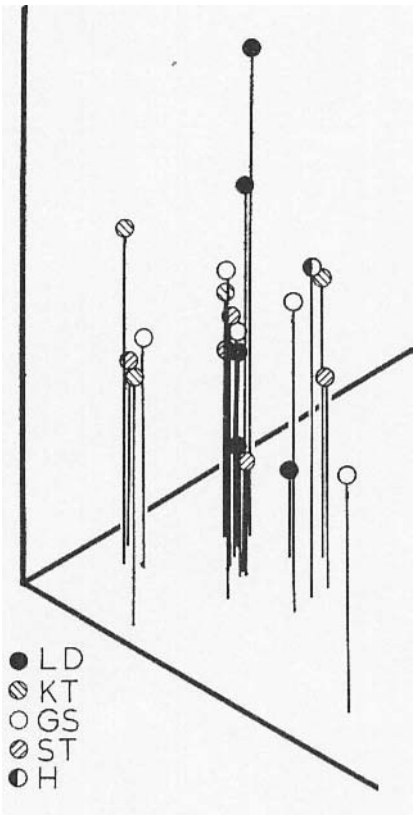


Figure 8

Projection of colony mean value.; into first three principal component **space** based on **five** characters. Holotype of *F. decora* shown **by** half-hollow **circle** labeled H. Other colonies labeled by locality, abbreviated as in **Fig. 2.**

CONCLUSIONS

In this study *(as* in most previous studies of Paleozoic Bryozoa) data are found to be normally distributed for the majority of characters utilized, thus fulfilling one fundamental assumption of analysis of variance. However, **when** data from all 19 colonies were considered together, the variances **of** the selected characters were not homogeneous, It is not *yet* known **how** widespread deviation **from** homoscedasticity is among Bryozoa; **Anstey** and Perry (1969) found that it occurred in two **out** of seven characters, but **their** study **was** based on a smaller number of colonies. The need to test for the assumptions of anova is emphasized; **with** the present data, any interpretation based on **a** nested analysis of variance would be grossly misleading.

The available population **of** *Fistulipora decora* is characterized by extensive and significant variation between individuals within **a** colony, between colonies at one locality,

and between localities. Phenetically the group is quite flexible, responding readily to differences in environment and genetic makeup. The extent of variation between colonies at each **locality** implies that the population exhibited a high degree of genetic diversity. The available data also suggest, but do not conclusively prove, that microenvironmental effects typically account for more than half of the observable variation at a locality.

The extent of morphological variation, and more particularly its distribution, poses problems for the systematist. These are not insurmountable problems; *they* can he overcome by utilization of a logical sampling plan.

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