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VARIATION IN RECENT BRACHIOPOD POPULATIONS

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Abstract. Shape variation in fossil brachiopod assemblages has often aided in the interpretation of paleoenvironments. But few variation studies have been made on Recent brachiopod populations to determine the nature of variation due to environment. The present study is on shape variation in five Recent brachiopod species from three different ecologic situations, a shell and rock substrate with abundant but not crowded *Terebratulina septentrionalis,* a shell and rock substrate crowded with *Magellania venosa* and *Terebratella dorsata,* and an intertidal rocky substrate where *Notosaria nigricans* and *Waltonia inconspicua* lived in confining space, sheltered from the turbulent water.

Asymmetry is primarily caused by environmental conditions. In the Recent samples, asymmetry was measured quantitatively by determining the ratio of the areas of each side of a specimen bisected along the plane of symmetry. A progressive increase in the standard deviation of the samples was found in going from open, uncrowded substrate, to open crowded substrate then to a confining environment under rocks. The number of injured specimens increased also.

A sample of dead *W. inconspicua* had a much greater range of asymmetry than the living sample of this species; there were few specimens that were bilaterally symmetrical in the dead assemblage, and the mean size of the sample was much smaller than the mean size of the living sample. This indicates that although *W. inconspicua* lives in a confining environment, it survives best where size increase is possible in all growth directions.

Five parameters of length, width, thickness, beak angle and symmetry ratio were used for a principal component analysis of the samples. A comparison of total shape variation between samples was possible with a scatter plot of the second and third principal component factor scores. The vectors of shape variation of the costate species *N. nigricans* and *T. dorsata* diverged from the variation vectors of the non-costate species, *W. inconspicua* and *T. septentrionalis* suggesting that inherent shell morphology directs the variation in a species along certain vectors.

A simpler example of shape variation in two morphologically similar costate species was seen in the shape changes described by Du Bois (1916) for *Terebratalia transversa* and found to be similar to shape changes in *Terebratella dorsata.* The genera are in different families and geographically separated. Thus although environment may produce asymmetry in a population, the total shape variation trends are in a direction inherent in the species.

INTRODUCTION

Both intraspecific as well as interspecific variation has been studied quantitatively in fossil assemblages (McKerrow, 1953; Parkinson, 1954; Ochoterena, 1960) and inferences of paleoenvironments have often been made on the basis of shape variation (e.g. Ager, 1965). But almost no comparable studies have been made on living brachiopods. In Recent brachiopods, shape variation and distortion have been noted several times in individuals and in populations of a single species. The present paper is an addition to the limited knowledge of shape variation in Recent brachiopods; it considers variation of more than one species in a particular locality. The environments studied are (1) a rocky substrate where the brachiopods are attached to undersides of rocks, sheltered from turbulent water, (2) a non-turbulent environment, where brachiopods are crowded on shell and rock substrate, and (3) an uncrowded shell and rock substrate.

In studying shell variation in different species, it is understood that inherent variability as well as that induced by environmental factors influences the result. Some species will have a greater potential of variability than others and thus in the same ecological situation one species may show greater observable variation and another little variation although each may be varying over the entire range of which it is capable. However, one aspect of shell variation in brachiopods which can be attributed primarily to effects of environment is asymmetry or distortion. Asymmetry can result from injury during growth of an individual or it can predominate in a population where there is overcrowding or confining space limiting normal growth. Genotypically certain species will be more tolerant of confining and overcrowded conditions whereas others could not survive in this environment. Nonetheless, the amount of asymmetry in a population can give a good indication of environmental conditions as has been illustrated many times in fossil populations (Asgaard, 1968; Ager & Riggs, 1964).

ASYMMETRY IN RECENT POPULATIONS

For a quantitative study of asymmetry in Recent brachiopods, five species were sampled from three different environmental situations. *Notosaria nigricans* (Sowerby) and *Waltonia inconspicua* (Sowerby) were collected in the intertidal zone of Lyttelton Harbor, New Zealand. These species live attached to undersides of rocks, sheltered from strong turbulent currents. A sample of dead *W. inconspicua* was collected in the same locality

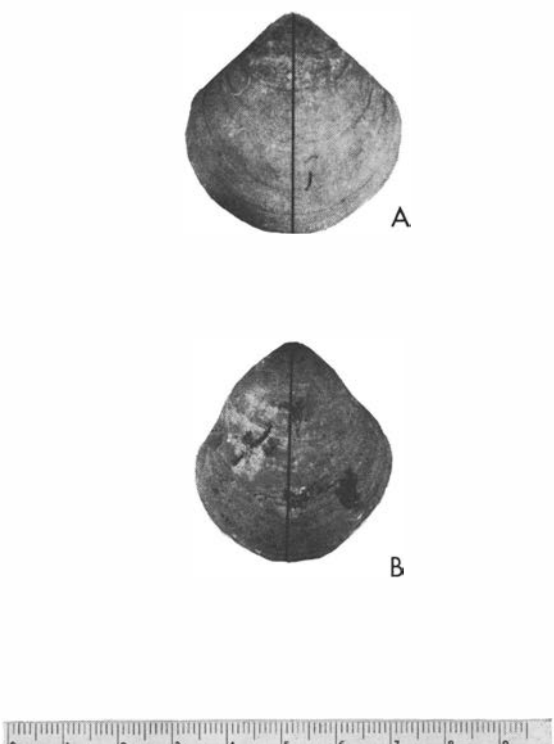

Fig. 1. Magellania venosa with bisecting plane of symmetry, illustrating how the ratio of the left to right areas was measured with a planimeter.

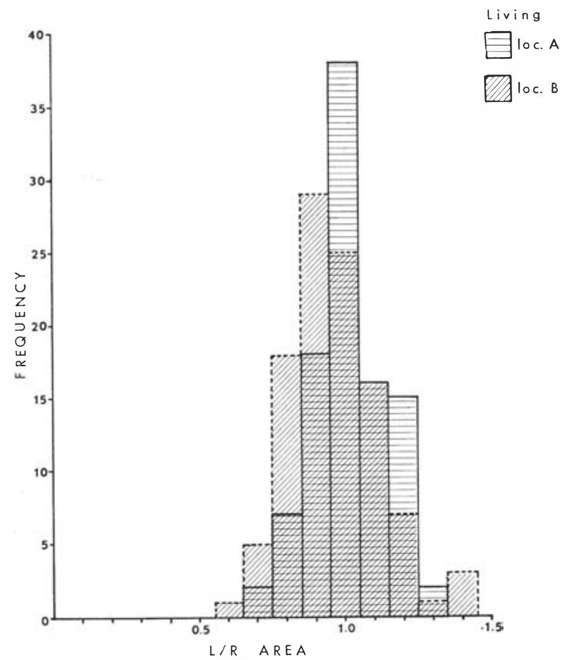

Fig. 2. Frequency distribution of symmetry ratio in two samples of *Terebratulina septentrionalis,* Sample A from 43°00′ N, 67°45′ W, Sample B from 44°00′ N, 68°00′ W.

to determine what difference, if any, there was between the shape of living and dead specimens. *W. inconspicua* and *N. nigricans* extend into the sublittoral zone in other areas of New Zealand, there they reach a larger size but have the same degree of variation.

Magellania venosa (Solander) and *Terebratella dorsata* (Gmelin) were collected in 40 m of water in the Strait of Magellan, South America. The species were attached to shells and pebbles. The depth range of *T. dorsata* extends from 5 to 400 m while *M. venosa* extends from 5 to 900 m depth.

Two populations of *Terebratulina septentrionalis* (Couthouy) were sampled off the coast of Maine, in northeastern United States at depths ranging from 25 to 40 m. Sample *A* came from 43°00′ N, 67°45′ W and sample *B* was from 44°00′ N, 68°00′ W. At both localities the brachiopods were attached to pebbles, other brachiopod shells, ascidian stalks, as well as living and dead pelecypod and gastropod shells.

To determine quantitatively the degree of asymmetry in each specimen collected, a photograph was taken of the specimen, with care exercised

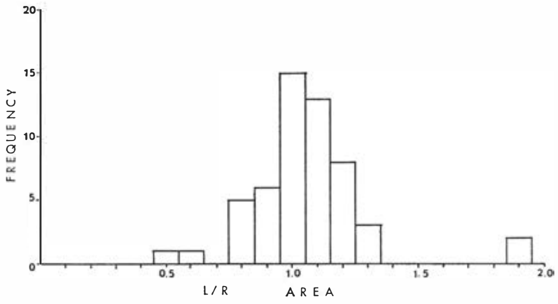

Fig. 3. Frequency distribution of ratio of symmetry in a sample of *Magellania venosa* from the Strait of Magellan.

that the specimen was horizontal. On the photograph, a line was drawn bisecting the beak, perpendicular to the hinge, and extending to the anterior margin. The area of both sections was measured with a planimeter and the ratio of the left to the right area was then determined. A symmetrical specimen would have a value of 1.00 and the more asymmetric the specimen, the greater would be the deviation from unity. In Fig. 1, a ratio of 1.01 is obtained for almost symmetrical specimen *A,* whereas the slightly deformed specimen *B* has a symmetry ratio of 1.20.

The mean and standard deviation of the symmetry ratio for each sample was calculated (Table I) and a histogram constructed from the frequency distribution of the ratios. The mean in all samples is close to unity reflecting the basic bilateral symmetry of the brachiopods, but the dispersion around the mean differs. The two samples of *T. septentrionalis* have the lowest standard deviations of the samples measured. The histogram of the frequency distribution (Fig. 2) illustrates the reason for the slight difference of standard deviation in the two samples, with sample *B* having a

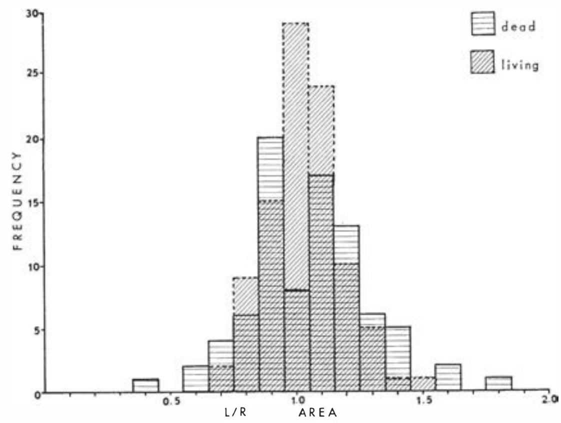

Fig. 5. Histogram of frequency distribution of symmetry ratios in samples of living and dead populations of *Waltonia inconspicua,* Lyttelton Harbor, New Zealand.

broader range and somewhat more asymmetry than sample *A*. In *M. venosa* and *T. dorsata* also living on an open substrate but under more crowded conditions, the standard deviations are considerably higher. As shown on the frequency distribution of these two samples (Figs. 3 and 4 respectively) outliers causing the higher deviation are due to specimens badly disfigured by injury during growth. Elimination of these disfigured specimens would give a range of symmetry similar to that in *T. septentrionalis* for it may be considered that such accidental disfigurement is not a true representation of the species variation, although on the other hand it certainly does tell something of the environment.

The highest order of asymmetry is in samples from the intertidal environment. In a histogram of the frequency distributions of *W. inconspicua* (Fig. 5) and *N. nigricans* (Fig. 6) the accidentally

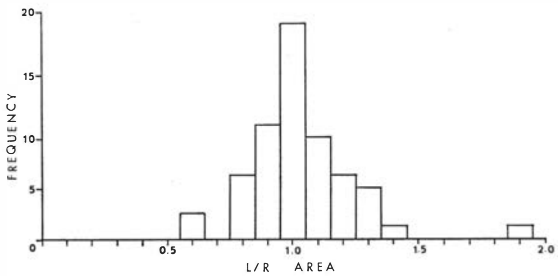

Fig. 4. Frequency distribution of ratio of symmetry in a sample of *Terebratella dorsata* from the Strait of Magellan.

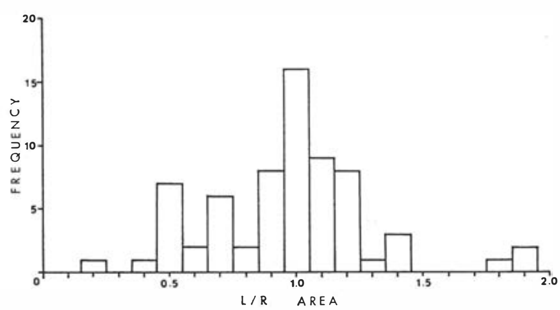

Fig. 6. Histogram of ratio of symmetry in a sample of *Notosaria nigricans,* Lyttelton Harbor, New Zealand

distorted forms merge with the distribution of the main sample, and become part of the symmetry variation except for the ratio approaching 2.0 in *N. nigricans*. The greater degree of asymmetry in *N. nigricans* indicates that this species is genotypically more variable than *W. inconspicua*.

In Fig. 5 a comparison between the distribution of a live sample and a dead sample of *W. inconspicua* is presented. The comparison is notable in that the distribution of the dead population is much broader with very few perfectly symmetrical forms, and the mean size is smaller. This may indicate that specimens died precisely because they were in too confined a space, whereas forms with adequate room for growth could continue to live to a larger size. Both samples were taken in early summer and thus may represent the results of survival ability during the winter and early spring seasons. This distribution is noteworthy in consideration of fossil assemblages, because in a circumstance such as this, the assemblage would consist of an abnormally high proportion of asymmetric valves.

Although the method of asymmetry measurement does not give an absolute criterion for distinguishing between rocky, confining environment, and open substrate, it does permit a quantitative comparison of asymmetry within and between environments and populations.

COMBINED SHAPE VARIATION

Asymmetry is only one parameter of shape variation which can be studied. In fossil studies, combinations of numerous others have been used such as width, length, thickness, number of plications and costae, length of hinge, etc. In none of these studies have all the parameters been combined for study of total variation in the assemblage. A method for studying total variation has been used for several animal groups (Jolicoeur, 1963) as well as for living brachiopods (McCammon & Buchsbaum, 1968). It is the multivariate technique of principal component analysis, where the first principal axis constitutes size variation, and the second and third principal axes represent shape variation. Constructing a scatter diagram from the factor scores of the individuals in the samples allows graphic comparison of total shape variation between samples. This method has been used primarily for comparison of intraspecific samples. But in the present study, a principal

Table I. *Data on Recent species studied for variation*

Substrate ...	Open uncrowded		Open crowded		Confining, rock		
	T. septentrionalis						
Species	*A.* 43°00′ N 67°45′ W	*B.* 44°00′ N 68°00′ W	*M. venosa*	*T. dorsata*	*W. inconspicua* (*live*)	*W. inconspicua* (*dead*)	*N. nigricans*
No. in sample ...	98	98	54	52	95	86	69
Length							
Mean	14.5	16.7	31.7	12.8	13.1	9.0	8.7
S.D.	4.8	4.9	10.6	7.6	3.5	3.2	4.1
Width							
Mean	11.3	12.8	30.0	12.8	11.7	7.9	9.1
S.D.	4.0	4.0	9.1	7.7	3.0	2.9	4.6
Thickness							
Mean	6.0	6.7	16.8	5.3	6.7	4.3	4.4
S.D.	2.5	2.1	6.5	4.1	2.2	1.8	2.2
Beak angle							
Mean	70.4	73.5	89.7	89.2	73.0	70.0	79.6
S.D.	6.0	6.1	7.9	8.8	5.1	5.4	6.9
Symmetry ratio L/R area							
Mean	1.02	0.96	1.03	1.02	1.05	1.10	1.00
S.D.	0.13	0.16	0.27	0.20	0.26	0.33	0.36

Table II. *Summary of principal component analysis*

Principal axis	% of total variance	Factor loading				
		Length	Width	Thickness	Angle	S. ratio
1	64	.52	.54	.54	.36	.07
2	22	−.07	−.04	−.05	.42	−.90
3	11	−.28	−.15	−.18	.83	.42

component analysis was made for interspecific comparison.

Five variables were used for the multivariate analysis. On each specimen, parameters determined were: length, width, and thickness measured with vernier calipers having an accuracy of ±0.05 mm and the result rounded to the nearest 0.1 mm; the beak angle of the pedicle valve along the break ridges measured with a contact goniometer; and the symmetry ratio by the method described in the previous section.

The means and standard deviations of the five parameters for the samples measured are given in Table I. A logarithmic transformation was made on the measurements for optimum presentation of the data. Calculation of the principal components was on a covariance matrix. The results of the analysis on the data is summarized in Table II. Ninety-seven percent of the total variation is present in the first three components; of this variation, 64% is attributable to size or growth trend since all direction cosines of the major axis are positive and increasing simultaneously. The second principal axis contrasts variation of symmetry ratio with beak angle. The third principal axis compares primarily variation of beak angle which is increasing to length, width and thickness which are decreasing.

The scatter plots of the samples were outlined as shown in Fig. 7. The two samples of *T. septentrionalis* were included in the same areal distribution because of similar scatter of points. Also the dead and living populations of *W. inconspicua* were combined under the one distribution. The plot of *M. venosa* is not shown because of the diffuse points in the lower quadrants ranging well beyond the concentrated points of the other species.

The scatter plot of Fig. 7 shows that the two

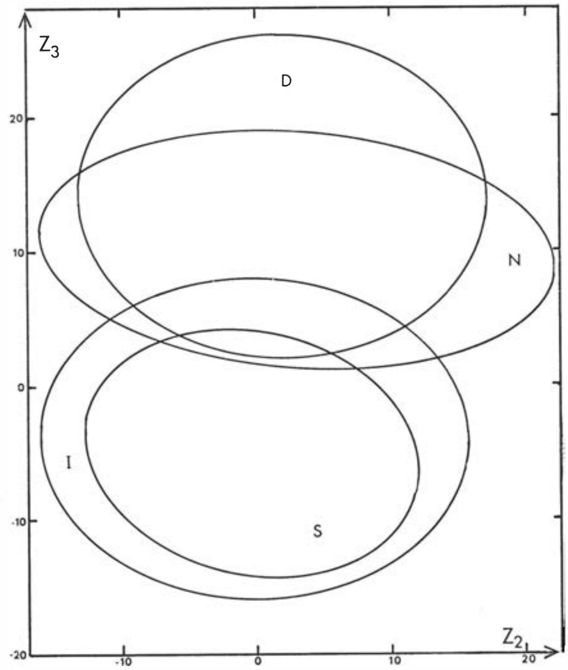

Fig. 7. Ellipses drawn around the scatter plots of the second and third principal components for D–*T. dorsata,* N–*N.* nigricans, I–*W. inconspicua,* S–*T. septentrionalis.*

species with costate shell ornamentation, *N. nigricans* and *T. dorsata* have shape variation tending in the upper quadrants while the smooth shelled species, *W. inconspicua* and *T. septentrionalis* have shape variation trending primarily in the lower quadrants. From this figure it appears that shape variation in costate and smooth shelled species tends to be different. Much of this difference in variation direction is the contrast of ratio of symmetry to the beak angle, and the contrast of the beak angle to the length, width and thickness of the shell. The plot does suggest the possibility that the inherent shell morphology directs the total shape variation along certain vectors.

Easier to visualize is the following example of two species with similar external shell morphology reacting to environment in a similar manner although they are in different families and geographically separated. The variation described by Du Bois (1916) in the brachiopod *Terebratalia transversa* (Sowerby) from Puget Sound, in northwest United States, is similar to that found in the species *Terebratella dorsata* from the Strait of Magellan. Du Bois found specimens varying "from wide spirifer-like to round, almost smooth forms . . .

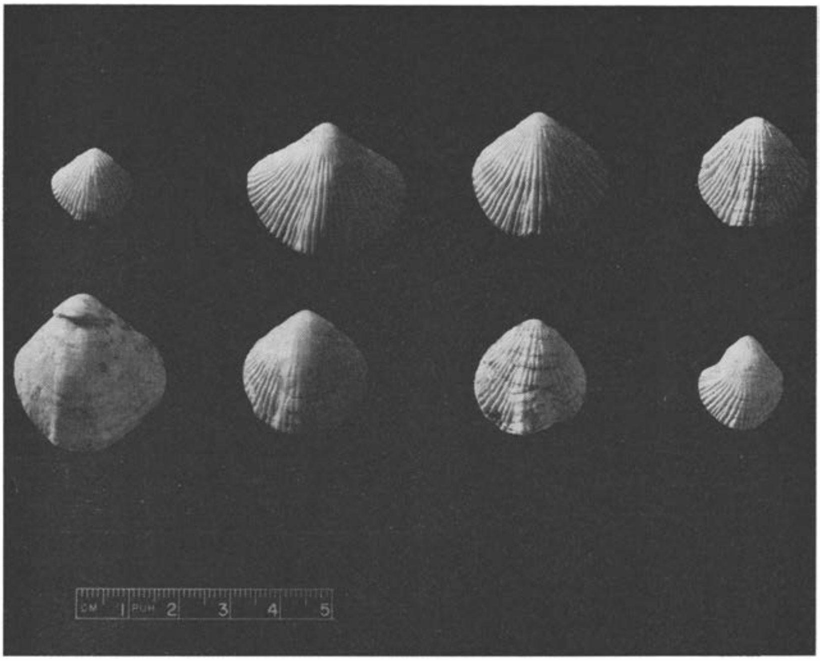

Fig. 8. Specimens of *Terebratella dorsata* taken from one sample in the Strait of Magellan.

The marked tendencies of the variation seemed to be a shortering of the shell and a rounding of the anterior angle." Normal alate shaped specimens from quiet water were figured by Du Bois. Those specimens closely resemble the two upper left hand specimens illustrated in Fig. 8, while the upper right hand specimens in this figure show a rounding of the valves previously mentioned by Du Bois. He also illustrated specimens showing "Effect of local injury. The growth lines have a puckered appearance", then, "specimen with such an injury healed. The growth lines have gradually resumed their regularity", and finally "effect of injury to one side of the mantle". These examples can be closely duplicated in *T. dorsata* and are illustrated in the second row of Fig. 8, except for the far left specimen which grew with a smooth shell, having only faint costae developed. This smooth condition is similar to one mentioned for *T. transversa* by Du Bois.

Recovery from injury may be similar in most brachiopods, but it is striking that many of the shape variations and the loss of costae reported by Du Bois are also duplicated in the species from the Strait of Magellan, Thus it would appear that some species with similar shell morphology react to environmental differences in a similar manner.

SUMMARY

Many excellent studies have been made on size and shape variation of fossil brachiopods. What has been lacking are similar studies on Recent brachiopods, for in studies of Recent brachiopod populations, there are far fewer unknown environmental variables and samples are without doubt contemporaneous. The present study considers examples of variation resulting from environment and shell morphology in extant brachiopods.

The study was made on five species, consisting of living and dead populations of two intertidal species from New Zealand, two shallow-water species from the Strait of Magellan and one shallow-water species from two different localities off the coast of Maine, northeastern United States. The primary parameters used for quantitative studies of living and fossil brachiopods have been length, width and thickness. Along with these three variables, two others were used for the present study; the angle between beak ridges and the ratio of the left area to right area of the pedicle valve. The ratio of the two areas reflects asymmetry of an individual, and a frequency distribution of ratios obtained from a sampled population reflects the variation in shape of the sample.

An obvious variant in a population is a specimen severely injured during growth. These deformed specimens are obvious both to the eye and in quantitative analysis. In frequency distributions of the ratio of symmetry, these individuals are often isolated from the main population. Recognizing less severe deformities may be a problem when the deformities blend in with the extremes of variation in a population. In fact, excessive damage to valves can give an indication of ecological conditions such as overcrowding or wave action.

Some species more than others are restricted genetically to certain environments. The chosen environment is reflected in the degree of variation which is apparent in all species co-inhabiting that area, even though one species may be genotypically less variable than another. For example, populations of both *Waltonia inconspicua* and *Notosaria nigricans* are found living together along the lower sides and beneath rocks of the intertidal zone in New Zealand; both species are highly variable in shape, the variation being reflected in the broad distribution of the frequencies of the ratio of symmetry and the high deviation valves. *N. nigricans* is considered genotypically more variable as evidenced by the higher deviation. From a comparison of dead and living samples of *W. inconspicua,* it would appear that this species is not completely adapted to a confining environment since there is a high mortality of young deformed specimens while the more symmetrical forms reach a larger size.

Species on more open substrates, such as on shell or on rock bottom, not only tend to be genetically larger, but they are more symmetrical as well. *Magellania venosa* and *Terebratella dorsata* are found together on shelly substrates in the Strait of Magellan at depths ranging from 5 m to 400 m with *M. venosa* extending to 900 m. Samples of both species have similar means of the ratio of symmetry and the standard deviations are comparable within statistical limits. The fewer numbers of deformed valves and a lower degree of deviation from the mean indicates that this environment is less rigorous than the one in New Zealand, but it is much more rigorous than the one in which *Terebratulina septentrionalis* is found. *T. septentrionalis* also lives in shallow water, attached to pebbles and other bottom material, but it grows with the least deviation from the symmetry mean of all the species studied.

Although environmental conditions are a primary cause of shape variation, the direction of variation depends upon the inherent characters of a species. By plotting the factor scores of the second and third principal components using the five variables of the samples studied, an analysis of shape trends is determined. Separation of shape trend is immediately apparent between the costate species, and the non-costate species. The two costate species are not related genetically, *Notosaria* is a rhynchonellid, *Terebratella* is a terebratellid, yet the similarity of their morphology causes them to vary in a similar direction.

A further example of variation in morphologically similar species, may be seen when specimens of *T. dorsata* are compared with specimens of the costate *Terebratalia transversa* figured by Du Bois (1916). The same type of shape variation is found in *T. dorsata* as was found in *T. transversa,* although the former is from the Strait of Magellan and the latter is from Puget Sound, in northwestern U.S. Here again, environment plus the inherent trends produce the result of shape variation.

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Sommaire On s'est souvent servi des variations de forme dans les associations de brachiopodes fossiles pour l'interprétation du milieu ancien, mais peu d'études ont été faites sur ces variations en des populations récentes de brachiopodes dans le but de déterminer le nature des variations dépendentes du milieu. Cet article traite des variations de forme en cinq espèces de brachiopodes récents, provenant de trois situations écologiques différentes, à savoir un fond de têts et de roches avec des *Terebratulina septentrionalis* nombreuses mais pas trop serrées, un fond de têts et de roches avec une population de

Magellania venosa et *Terebratella dorsata* très serrée et un fond rocheux dans l'espace entre la marée haute et la marée basse où vivaient des *Notosaria nigricans* et des *Waltonia inconspicua* à l'abri de l'eau en mouvement.

L'asymétrie est causée en premier lieu par les conditions du milieu. Dans les échantillons récents, on a mesuré l'asymétrie en déterminant le quotient entre les superficies des deux parts d'un spécimen coupé au plan de symétrie. Les déviations moyennes des échantillons augmentaient successivement du fond ouvert, à population pas très serrée, au fond ouvert surpeuplé, ayant son maximum dans les milieux confinés sous les roches. Le nombre des spéciment lésés augmentaient aussi.

Un échantillon de *W. inconspicua* mortes présentait des cas asymétrique beaucoup plus nombreux que l'échantillon vivant de cette espèce; peu de spécimens dans l'échantillon mort étaient symétriques, et la grandeur moyenne était moindre que la grandeur moyenne de l'echantillon vivant. Ceci montre que *W. inconspicua,* tout en vivant en un milieu confiné, survit mieux là où l'accroissement lui est permis dans toutes les directions.

Cinq paramètres de longueur, largeur, épaisseur, d'angle apical et de symétrie ont été employés dans une analyse des composantes principales des chantillons. Une comparaison des variation totales de forme entre les échantillons a été faite par moyen d'une représentation graphique des deuxième et troisième composantes. Le vecteur de la variation de forme de l'espèce avec têts à côtes *N. nigricans* et *T. dorsata* a différé du vecteur de variation des espèces á têts sans côtes *W. inconspicua* et *T. septentrionalis,* ce qui laisse supposer que des qualités morphologiques inhérentes du têt dirigent les variations d'une espèce le long de certains vecteurs.

Un exèmple plus simple de variations de forme dans deux espèces de morphologie semblable a été noté dans les changements de forme décrits par Du Bois (1916) pour *Terebratalia transversa*; ces changements ont été retrouvés chez *Terebratella dorsata*. Les genres appartiennent à des familles différentes et sont séparés géographiquement. Donc, quoique le milieu puisse donner lieu à l'asymétrie dans une population, les tendances des variations totales de forme sont inhérentes à l'espèce.

REFERENCES

Ager, D. V. 1965. The adaptation of Mesozoic brachiopods to different environments. *Palaeogeog. Palaeoclim., Palaeoecol.* 1, 143–172.

Ager, D. V. and Riggs, E. A. 1964. The internal anatomy, shell growth and asymmetry of a Devonian spiriferid. *J. Paleont.* 38, 749–760.

Asgaard, U. 1968. Brachiopod palaeoecology in middle Danian limestones at Fakse, Denmark. *Lethaia* 1, 103–121.

Du Bois, H. M. 1916. Variation induced in brachiopods by environmental conditions. *Puget Sound Mar. Sta.* 1, 177–183.

Jolicoeur, P. 1963. The degree of generality of robustness in *Martes americana. Growth* 27, 1–27.

McCammon, H. and Buchsbaum, R. 1968. Size and shape variation of three Recent brachiopods from the Strait of Magellan. *Antarctic Research Series,* II, Biol. of Antarctic Seas III, 215–225.

McKerrow, W. S. 1953. Variation in the Terebratulacea of the Fuller's earth rock. *Quart. J. geol. Soc. Lond.* 109, 97–124.

Ochoterena, H 1960. Variacion intraespecifica en *Parathyridina mexicana* n.sp., Terebratulido del Oxfordiano de Mexico. *Paleont. mex.* 9, 1–40.

Parkinson, D. 1954. Quantitative studies of brachiopods from the lower Carboniferous reef limestones of England I. *Schizophoria resupinata* (Martin). *J. Paleont.* 28, 367–381.