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VARIATION OF CARAPACE MORPHOLOGY OF BAIRDIACEAN AND CYTHERACEAN OSTRACODA FROM BERMUDA

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ABSTRACT

Species of the ostracode genus *Bairdia* have been described from all geologic periods from the Ordovician to the Recent, making *Bairdia* one of the longest ranging genera with living representatives in the metazoan subkingdom. Rate of evolutionary change of cytheracean ostracodes has apparently been much more rapid than that of *Bairdia*. The purpose of this research is to test the relationships between evolutionary and geographic variation and specifically the hypothesis that local populations of a species of *Bairdia* are more variable than those of several selected shallow-water cytheracean species. Ostracodes collected from the Bermuda Islands during the summer of 1967 were used in the study. The cytheracean species *Orionina bradyi, Loxocorniculum fischeri,* and *Hemicytherura* sp. and the bairdiacean *Bairdia victrix* were studied. Results of statistical analysis showed *B. victrix* has the most variability among local populations of any of these four species for the characters measured. The findings support the idea that a gene pool rich in variation is a highly adaptable one but not necessarily one rich in evolutionary potential. If analyses of other species of *Bairdia* were to show similar high variability, one might suspect that some of the many species of *Bairdia* described in the literature are geographic variants rather than separate species. It is also possible that variability of Holocene species of *Bairdia* is not representative of species assigned to *Bairdia* in the geologic record.

INTRODUCTION

The genus *Bairdia* (Podocopina: Bairdiacea) has long been regarded as the oldest ostracode genus with living representatives, having a range from Ordovician to Recent. Although there is some argument whether *Bairdia* actually exists over this range, and the Holocene species have recently been revised and separated into different genera within Bairdiinae (Maddocks, 1969), nevertheless in comparison to other ostracode genera *Bairdia* has evolved very slowly.

A possible consequence of slow rate of evolution is a long geologic range. Yet slow evolution may also result in early extinction due to inability to adapt to changing environments. One strategy for maintaining both adaptability and slow rate of evolution is to have a high degree of genetic variability among local populations. Such a gene pool, rich in variation but with a well-balanced epigenotype, should result in great potential for adaptation but little likelihood of evolutionary change (Mayr, 1963). The purpose of this research was to test the hypothesis that species of *Bairdia* have adopted this strategy.

Results of statistical analysis indicate that local

populations of the species of *Bairdia* studied vary more between localities than those of the three cytheracean species. Moreover, for the four species studied, a perfect correlation was found between the amount of variability between populations and the length of the range of the species. We hasten to add that results such as these, based on small sample sizes and study of only a few species, must be regarded as tentative and perhaps fortuitous. Nevertheless, they point the direction for future research and may have implications for understanding the systematics of long-ranged species. Further investigation will, no doubt, reveal instances which contradict our results. Nevertheless, as generalizations they may be valid and useful in the study of evolution. Extensive further study of intraspecific variation is needed to test these relationships.

METHOD OF STUDY

Although the Bermuda platform is isolated from the Bahama Banks, Blake Plateau, and northern Atlantic coast of North America by an abyssal plain, Bermuda has a relatively rich, shallow-water ostracode fauna. Furthermore, this fauna, not yet studied in detail, is a marginal tropical one, the most northern such fauna in the western Atlantic. Brady (1880) described several species collected by the H.M.S. *Challenger* in the Bermuda area. However, all his descriptions were of empty valves collected below 700 meters at the edge of the Bermuda platform. All ostracodes included in our study were collected live at depths of less than 10 meters during the summer of 1967.

Locations of stations where samples were collected are shown in Figure 1 and listed in Table 1. The stations are numbered according to decreasing degree of isolation of the environment and *presumed* isolation of the gene pools of the ostracode species studied. Detailed descriptions of the localities were given by Cadot (1970).

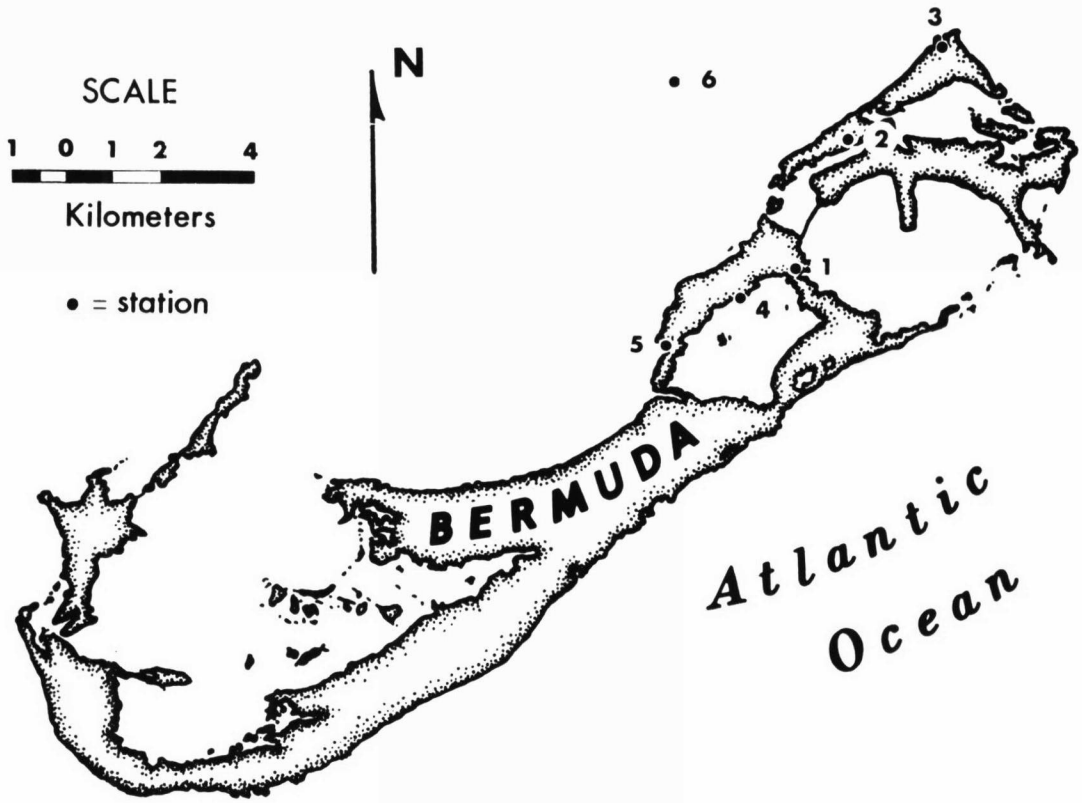

FIG. 1. Bermuda Islands, showing location of stations (modified from Mackenzie, 1964).

TABLE 1.—*Sample Localities, Species Collected, and Depths of Samples.*

	STATION 1 Walsingham Pond	STATION 2 Small cove	STATION 3 Coot Pond	STATION 4 Harrington Sound	STATION 5 Shelly Bay	STATION 6 Three Hill Shoals
LOCALITY DESCRIPTION	submerged sinkhole	small protected cove	small shallow protected bay	large protected nearly enclosed bay	small open bay	open marine environment
MAXIMUM DEPTH OF SAMPLE	2 m	2 m	0.3 m	2 m	1 m	8 m
SPECIES:						
Bairdia victrix	X		X			
Orionina bradyi	X		X	X		
Loxocorniculum fischeri		X	X		X	X
Hemicytherura sp.	X	X			X	X

Ostracodes were collected from several habitats together with the algae *Padina padina, Codium taylori, Codium* sp., *Simopoleum* sp., *Dictyota* sp., and *Colpomenia sinuosa* (?), and the marine grasses *Thalassia testudinum* and *Syringodium filiforme;* the sediments are composed mostly of fine-grained carbonate sand and organic detritus entrapped and held by the grasses and algae. The samples were washed in sea water and sieved while wet. Living ostracodes retained on a 74-micron sieve were preserved in ethyl alcohol and used in the study. Preservation of soft parts permitted determination of sex. Only adult females, which were generally more abundant than males, were studied. Because only one sex was measured, possible effects of sexual dimorphism on the results of the study need not be considered.

Four species were found living in great enough abundance to be used in the study: *Bairdia victrix* Brady (1869) (*sensu* Benson and Coleman, 1963), *Orionina bradyi* van den Bold (1963), *Loxocorniculum fischeri* (Brady) (Brady, 1869), and an undescribed species of *Hemicytherura,* here called *Hemicytherura* sp. The first ten females of each species found in each sample were measured. Because not all species were found at all stations, the total number of specimens measured was only 130 (Table 1). Each specimen was placed in a glycerin-filled depression-slide, and its image was projected. The outline of each specimen and other features to be measured and studied were traced from the image. The right valve was selected for tracing for purely practical reasons to avoid the optical distortion caused by the greater curvature of the left valve. While it is probably true that most species of *Bairdia* have been erected on the basis of study of the left valve more than the right one, use of the right valve alone should cause no difficulty in a study of *intraspecific variation,* especially since the two valves of any carapace must fit together.

The seven characters discussed below were measured on each specimen. In order to stabilize specimens in the glycerin, it was necessary to place them convex side up. For this reason, the hinges were difficult to see and could not be used for precise orientation to a horizontal position. Cytheracean specimens were oriented by horizontal alignment of two species-specific normal pore canal openings in the central portion of the right valve. In *Bairdia,* the normal pore canal openings are too small and numerous for convenient use in alignment or character definition. Therefore, specimens of *Bairdia* were oriented by the horizontal alignment of the ends of the dorsal flange.

Discussion of statistical tests used and justification of their use are given in Appendix 1.

CHARACTERS

In any study in which the amount of variability of two or more species is compared, it is essential that the characters upon which the comparison is based be homologous ones. Without homologous characters, the investigator is in the position of comparing *apples with oranges,* a practice we are admonished to avoid from the very start of our academic training. One does not, then, compare, for example, *Loxocorniculum*

fischeri with *Orionina bradyi* so much as he compares homologous characters of one species with those of the other one.

The characters we have chosen for study, which are discussed below, are not the kind that are used in taxonomic work. It is important to note that so-called good taxonomic characters, that is, characters that are best for discrimination between taxa, are in many instances the ones that are the most difficult to homologize from one taxon to another. They are likely to be not continuously varying characters but rather binary ones that are either present or absent. Thus it is not only difficult to homologize these characters, but it is also frequently impossible to recognize variability in them. Such characters are often simply either present or absent. For example, in erecting the genus *Loxocorniculum,* Benson and Coleman (1963, p. 38) referred to the presence of a ". . . hornlike protuberance on posterodorsum. . . ." They did not mention the height of the posterodorsal protuberance, nor would it have been appropriate for them to have done so. Similarly, Hazel (1967) did not measure distances between separated muscle scars when discussing them in a taxonomic sense. It is possible to measure height of posterodorsal protuberances and distances between separated muscle scars, but when these characters are studied in this way, especially intraspecifically, they are not the same as diagnostic taxonomic characters.

The characters measured on each of the ostracode species are shown in Figure 2. Characters numbered 1 through 7, hereafter referred to as *common characters,* are regarded as operationally homologous estimators of the shapes of the valves. As was discussed earlier, they are not characters that can be used conveniently for traditional kinds of taxonomic work, and there is no reason to expect them to be good discriminators. They were chosen because they can be easily homologized and because, taken together, they describe fairly well the shape of the carapace. They are 1) length, 2) height, 3-6) length of the four diagonals, and 7) anterior distance.

The four diagonals were measured at 45°

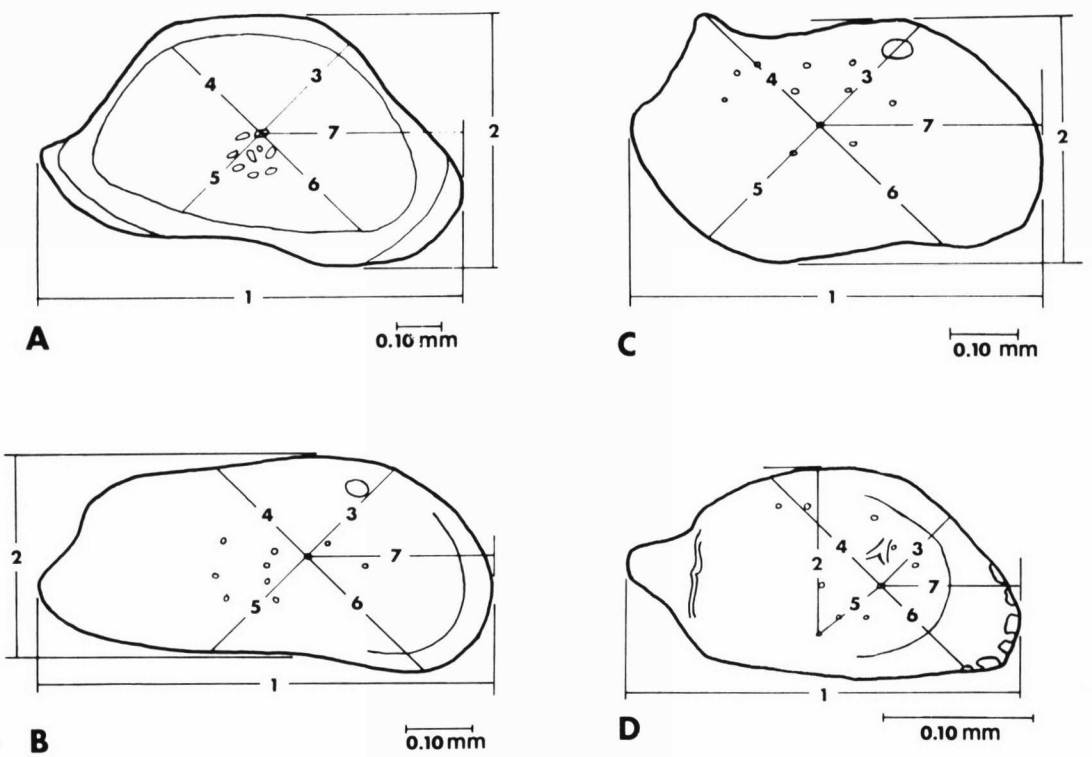

FIG. 2. Species studied showing the seven common characters measured.—A. *Bairdia victrix.*—B. *Orionina bradyi.*—C. *Loxocorniculum fischeri.*—D. *Hemicytherura* sp.

from the muscle scar for the species of *Bairdia* and from a prominent normal pore canal near the dorsal-most adductor muscle scar on all other species. This was necessary because the muscle scars could not always be seen clearly from the outside of the valve.

We have made no attempt to explain the causes of the intraspecific variations observed. It seems unlikely that the common characters themselves are acted upon directly by natural selection. Instead, pleotrophic effects of other genes that are subject to selection pressure are suspected of causing the observed variations in the outline. If so, then measurements of the common characters are merely one indication of the amount of genetic variation in the gene pool. This, of course, is exactly what we hoped to determine in our study.

COMPARISON OF SPECIES

Accessing the amount of variation between local populations is best done using a statistical test such as the analysis of variance or its nonparametric analog the Kruskal-Wallis test (Appendix 1). The reason for using such a test is that the differences observed between populations is very much a function of the amount of variation within each population. For example, if one found that *within* local populations of, say, *Orionina bradyi* there was a great deal of variation, then he would not feel very confident about his measure of the amount of variation *between* populations. Conversely, if he found that variation *within* local populations is almost imperceptible, then even very small differences *between* populations could be accepted as real with a great deal of confidence. The statistical test used here, the Kruskal-Wallis test, is designed to determine the existence of variation between (or among) local populations *in light of* the variation within those same populations (see Appendix 1).

Table 2 shows the seven common characters and the probability that the differences observed are the result of chance alone due to sampling. For example, a probability of 0.05, the commonly accepted upper limit in most biological work, means that in only five instances out of 100 of sampling from a normally distributed population, differences as great as or greater than those observed would be obtained by chance alone. If the probability is greater than 0.05, there is said to be no significant difference between the two populations. In Table 2 most of the probability levels are less than 0.01 and are regarded as highly significant.

For *Bairdia victrix,* all seven characters show significant variation between local populations at the 0.01 level. Only six common characters of *Orionina bradyi* show differences among populations at that level of statistical significance. Four common characters of *Loxocorniculum fischeri* and none of the characters of *Hemicytherura* sp. are statistically significant at $P<0.01$. The rank correlation coefficient between number of characters that are statistically significant at the $P<0.01$ and ranked longevity of range is a perfect correlation, and it is statistically significant itself, in spite of the small sample size (Siegel, 1956).

The evidence suggests, then, that, in comparison to the cytheracean ostracodes, *Bairdia victrix* has adopted the hypothesized strategy of maintaining a high degree of genetic variability among local populations while keeping a very stable epigenotype within populations. If we look at

TABLE 2.—*Significance Levels of Kruskal-Wallis Test among Local Populations.*

CHARACTER	*Bairdia victrix*	*Orionina bradyi*	*Loxocorniculum fischeri*	*Hemicytherura* sp.
1	0.01	0.01	0.01	n.s.
2	0.01	0.01	0.05	n.s.
3	0.01	0.01	n.s.	n.s.
4	0.01	n.s.	0.01	0.05
5	0.01	0.01	0.01	n.s.
6	0.01	0.01	0.05	0.05
7	0.01	0.01	0.01	n.s.
TOTAL WITH $P<0.01$	7	6	4	0
RANGE OF GENERA	Ordovician to Recent	Eocene to Recent	Oligocene ? Miocene to Recent	Pliocene to Recent

the analysis of variance test itself rather than the Kruskal-Wallis test we find a useful means of further testing this idea. As was mentioned earlier, the analysis of variance partitions the variance so that it is possible to determine the component of variance due to variation within samples and the proportion due to variances among samples. The *coefficient of intraclass correlations* is the ratio of variance among samples to the total variance (Osborne and Patterson, 1952). Table 3 shows the coefficient of intraclass correlation for the seven common characters, their means, and 95 percent confidence limits for each of the four species studied. On the average, 55 percent of the variance of the morphologic characters studied was variance among samples; the component of variance within samples accounted for only 45 percent. On the other hand, only ten percent of the variance observed for *Hemicytherura* sp. was variance among samples, and 90 percent of the variance could be ascribed to variance within samples. Clearly local populations of *B. victrix* are more different from each other *for the character studied* than local populations of *Hemicytherura* sp.

TABLE 3.—*Coefficients of Intraclass Correlation for the Seven Common Characters, 95 Percent Confidence Intervals, and Means.*

SPECIES	CHARACTERS	COEFFICIENT OF INTRACLASS CORRELATION
Bairdia victrix	1	0.38±0.65
	2	0.64±0.58
	3	0.00±0.04
	4	0.63±0.59
	5	0.53±0.65
	6	0.89±0.24
	7	0.75±0.46
	mean	0.58
Orionina bradyi	1	0.40±0.54
	2	0.36±0.53
	3	0.36±0.53
	4	0.04±0.25
	5	0.41±0.54
	6	0.51±0.53
	7	0.59±0.50
	mean	0.38
Loxocorniculum fischeri	1	0.29±0.44
	2	0.19±0.37
	3	0.00±0.05
	4	0.36±0.46
	5	0.24±0.40
	6	0.17±0.35
	7	0.36±0.46
	mean	0.23
Hemicytherura sp.	1	0.14±0.33
	2	0.06±0.24
	3	0.00±0.12
	4	0.22±0.39
	5	0.10±0.29
	6	0.15±0.34
	7	0.00±0.11
	mean	0.10

Figure 3 shows this result graphically. The coefficients of intraclass correlations for each common character are plotted along the ordinate, and along the abscissa are plotted the four species in order of decreasing generic longevity. The mean values for each species are connected by a dashed line in Figure 3. The Spearman's rank correlation coefficient between generic longevity and mean of the coefficients of intraclass correlations is 0.658, a highly statistically significant correlation ($P<0.001$). This high correlation provides further support for our hypothesis. It is important to note, however, that not all the data

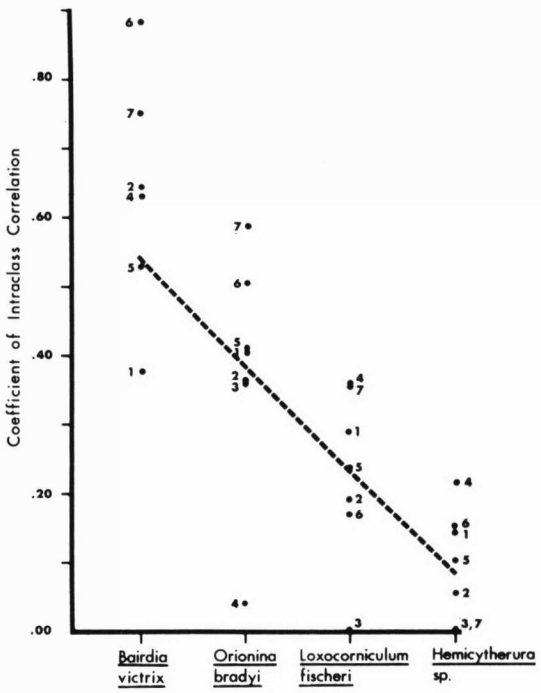

FIG. 3. Coefficients of intraclass correlation for each common character of each species studied. Broken line connects mean coefficients of each species.

TABLE 4.—*Matrix of Correlation Coefficients between Common Characters 4, 5, and 7.* [*B, O, L,* and *H* stand for the four species in the study; the double asterisk (**) indicates a coefficient significant at the 0.01 level.]

	CHARACTERS							
	5				7			
	B	O	L	H	B	O	L	H
4	0.43	0.17	0.04	0.51**	0.46	0.70**	0.07	0.01
5	....	....	....	....	0.57**	0.41	0.18	−0.06

met the assumptions of the analysis of variance, so that some possibility exists for erroneous interpretation. Of perhaps greater importance are the very broad confidence limits of the coefficients of intraclass correlation. Many of the coefficients are not significantly different from zero, and in general they are too broad to permit confident ranking of the coefficients for computation of Spearman's rank correlation coefficient.

A factor that complicates a study of this type is the amount of correlation among characters of a species. It is difficult to find measurable characters on the carapace, especially ones homologous to those of other species, which are not correlated with size. In this study the correlations among characters range from large, highly significant values to very small ones not significant even at low probability levels (Cadot, 1969, appendix 3). However, if three of the common characters which show relatively low intracorrelations are used for comparison, the same relationships between superfamilies and among genera appear to hold true (Tables 4 and 5). *Bairdia victrix* is the most variable, followed by the three cytheracean species of *Orionina, Loxocorniculum,* and *Hemicytherura.*

An attempt was made to discover which localities were the major sources of among-group variance for each character of each species. This was done by the Student-Newman-Keuls multiple range test based on the same assumptions as analysis of variance (Sokal and Rohlf, 1969). Results are reported in Table 6 for all characters including those which may not have met all the assumptions. The results are inconclusive despite the sensitivity of this parametric test. Less sensitive, nonparametric tests were not made. The differences one might have expected to find in samples from Walsingham Pond (Station 1) were not found, perhaps indicating free exchange of instars between nearby Walsingham Bay or

TABLE 5.—*Coefficients of Intraclass Correlation for Common Characters 4, 5, and 7 Where Shown to Have Significant Differences among Samples at 0.05 Level by the Kruskal-Wallis Test.*

CHARACTER	*Bairdia victrix*	*Orionina bradyi*	*Loxocorniculum fischeri*	*Hemicytherura* sp.
4	0.63	n.s.	0.36	n.s.
5	0.53	0.41	0.24	n.s.
7	0.75	0.59	n.s.	0.22

TABLE 6.—*Results of the Student-Newman-Keuls Test.* [Numbers (col. 2-5) refer to station numbers (Figure 1 and Table 1). Where stations are underlined, they are members of maximum nonsignificant subsets. Single stations or other subsets not underlined by the same line have significantly different means or ranges of means at the 0.05 level. *Loxocorniculum fischeri* character 4, for example, shows that Station 3 is significantly different from a subset of Station 2 plus Station 5 but is not significantly different from Station 6.]

CHARACTER	*Bairdia victrix*	*Orionina bradyi*	*Loxocorniculum fischeri*	*Hemicytherura* sp.
1	1 4	1 3 4	2 3 5 6	1 2 5 6
2	1 4	1 3 4	2 3 5 6	1 2 5 6
3	1 4	3 1 4	2 3 5 6	1 2 5 6
4	1 4	1 3 4	2 5 6 3	1 2 5 6
5	1 4	1 3 4	2 3 5 6	1 2 5 6
6	1 4	1 3 4	2 3 5 6	1 2 5 6
7	1 4	1 3 4	2 5 3 6	1 2 5 6

Harrington Sound and Walsingham Pond. However, significant differences caused by isolation may possibly be present in populations of Harrington Sound (Station 4). *Orionina bradyi* sampled from Harrington Sound are significantly different at the 0.05 level from the *O. bradyi* sampled from Coot Pond (Station 3) and Walsingham Pond, for five of the seven common characters. Of course, the analysis of a single species is hardly conclusive, but there is some evidence that populations of other invertebrates in Harrington Sound are also different from those outside. A study made in the summer of 1967 showed the population profile of the echinoid *Lytechinus variegatus* in Harrington Sound to be different from the profiles of those outside the sound in test diameter (Janssen, unpublished report, Bermuda Biological Station). This may be the result of warmer summer water temperatures. A detailed study of the Harrington Sound Ostracoda might contribute significantly to an understanding of ostracode speciation.

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APPENDIX I

METHODS OF STATISTICAL ANALYSIS

The statistical analysis was designed to determine for each of the four species studied whether significant differences exist among two or more geographically separated populations of the same species. The analysis of variance is well suited for such a task (Sokal, 1952, 1962, 1965; Sokal and Rinkel, 1963; Sokal and Thomas, 1965). It is a parametric and highly sensitive test and one which requires that data meet the following conditions: 1) that sampling is random, 2) that main effects are additive, 3) that there is independence of experimental error, 4) that the variances are homogeneous (homoscedasticity), and 5) that the distribution of each character is normal and therefore continuous.

Although sampling was biased as to habitat, it was probably random as to individuals collected because ostracodes could not be seen while being collected. It is hoped that random subsampling was approximated in the laboratory by measuring the first 10 adult females of a species picked from each sample. The other untested assumption was independence of experimental error. A possible source of error dependence was bias during the measuring procedure. However, because there were no previous results or other suggestions as to outcome, any errors in measurement were probably randomly distributed.

Homogeneity of variance of each of the 55 sets of data was tested by both the F-max test and the Bartlett's chi-square test, which is sensitive to both heterogeneity and non-normality. The results show that 42 sets (76 percent) according to chi-square and 52 sets (95 percent) according to F-max meet the assumption at the 0.05 level (Table 2). For those characters showing heterogeneous variances, it is possible to approximate an analysis of variance by substitution of a special estimation of the within sample variance and proceeding with the F-ratio test as in the analysis of variance (Sokal and Rohlf, 1969). This constructed F-ratio test was completed for all 55 sets, and results agreed with results of the analyses of variance in every case where the variance was heterogeneous (Table 7, ANOVA Approx. column).

The standard F-table shows the expected distribution of variance ratios but only for normally distributed variables. Therefore, both the analysis of variance and its above mentioned approximation require the assumption that the characters tested be normally distributed. Skewness (g_1) and kurtosis (g_2) both have values of zero for normal distributions, thus serving as a test of normality among characters. Both statistics were determined for each character at each station, a total of 178 sets of data. Only thirteen g_1 values (7 percent) and seven g_2 values (4 percent) showed a lack of normality at the 95 percent confidence level (Table 2). Sokal and Rohlf (1969, p. 377) stated that the consequences of non-normality are not very serious; "Only very skewed distribution would have a marked effect on the significance level of an F-test or on the efficiency of the design." None of the 178 distributions was highly skewed. Another test for normality is the nonparametric Kolmogorov-Smirnov statistic (d-max). This test of goodness-of-fit of the data to a normal distribution requires only the assumption that the variables tested be continuously distributed. The test showed that only five of the 178 data sets (3 percent) deviate significantly from the expected normal distribution at the 0.05 level (Table 2).

Although 33 of the 55 analyses of variance met all the tested assumptions, 22 did not. Therefore, conclusions concerning significance of differences were based on results of the Kruskal-Wallis test, a nonparametric analog of the analysis of variance, which was computed for all sets of data. This distribution-free test assumes only random sampling, is less sensitive to small differences between populations, and consequently is more conservative. Differences shown to be significant by this analogue of the analysis of variance are usually significant by the analysis of variance, but the converse is not necessarily true. Results of 52 of the 55 analyses of variance were supported by results of the Kruskal-Wallis test at the 0.05 level.

TABLE 7.—*Results of Tests for Normality and Homoscedasticity of Characters and Tests for Significant Differences among Local Population Sample Means.* [The x indicates probable departure from normality. Parentheses enclose results of analyses of data which probably do not meet all requisite assumptions.]

CHARACTER	d-max	g_1 or g_2	F-max	BARTLETT'S CHI-SQUARE	KRUSKAL-WALLIS	ANAL. OF VARIANCE	ANOVA APPROX.
Bairdia victrix							
1		x	....	....	<0.01	<(0.05)	<(0.01)
2			....	....	<0.01	< 0.01	< 0.01
3			....	....	<0.01	....	< 0.01
4	x	x	....	....	<0.01	<(0.01)	<(0.01)
5			....	....	<0.01	< 0.01	< 0.01
6			....	....	<0.01	< 0.01	< 0.01
7	x	x	....	<0.05	<0.01	<(0.01)	<(0.01)
Orionina bradyi							
1			<0.01	<0.01	<0.01	<(0.01)	< 0.01
2			....	<0.05	<0.01	<(0.01)	< 0.01
3			....	<0.05	<0.01	<(0.01)	< 0.01
4			....	<0.01	....	(....)	....
5			....	<0.05	<0.01	<(0.01)	< 0.01
6			....	....	<0.01	< 0.01	< 0.01
7			....	<0.05	<0.01	<(0.01)	< 0.01
Loxocorniculum fischeri							
1			....	<0.05	<0.01	<(0.01)	< 0.01
2			....	....	<0.05	< 0.05	< 0.01
3			....	....	....	....	....
4			....	....	<0.01	< 0.01	< 0.01
5		x	....	....	<0.01	<(0.05)	<(0.05)
6		x	....	....	<0.05	<(0.05)	<(0.05)
7	x		<0.05	<0.01	<0.01	<(0.01)	<(0.01)
Hemicytherura sp.							
1			....	....	....	....	< 0.05
2		x	....	....	....	(....)	(....)
3			....	....	....	....	....
4			....	....	<0.05	< 0.05	< 0.01
5		x	....	....	....	(....)	(....)
6			....	....	<0.05	....	< 0.05
7			....	....	....	....	....