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A RE-EVALUATION OF EVOLUTIONARY STASIS BETWEEN THE BIVALVE SPECIES *CHIONE EROSA* AND *CHIONE CANCELLATA* (BIVALVIA: VENERIDAE)

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ABSTRACT—Demonstrating stasis in the fossil record has proven to be problematic with respect to both data collection and analysis. A previous approach is morphometric analysis of lineages sampled temporally and geographically. A hypothesis of stasis is apparently supported if morphological distances between descendent species and ancestral species are no greater than those between geographically distant samples of the descendent species. Evidence presented in this paper conflicts with such interpretations for at least one bivalve lineage, *Chione erosa*–*Chione cancellata*, of the late Neogene of tropical America. The direction and magnitude of morphological variance were quantified between two geographically distant groups of *C. cancellata* from the Recent, and compared to Pleistocene samples of *C. cancellata* and Pliocene samples of *C. erosa*. The results indicate that, although the magnitude of intraspecific geographic variation is as great as interspecific temporal variation, the species are morphologically discrete groups. The direction of morphological variance is as important as its magnitude, and interpretations overlooking this point are at best equivocal.

INTRODUCTION

THE REALITY of morphological stasis over geological time as an evolutionary pattern is rarely disputed. More contentious is the empirical demonstration of stasis and the search for an explanation (see Endler, 1986, p. 73–74, for a list of possible explanations) of a static pattern. Two divergent approaches to demonstrating paleontological evolutionary patterns have been employed: detailed stratophenetic analysis (Gingerich, 1974; Williamson, 1981; Kelley, 1984; Geary, 1987; Malmgren and Kennett, 1981) or broad temporal and geographic sampling (Stanley and Yang, 1987). Bookstein (1987 and 1991) has outlined some of the problems inherent in interpreting results from the first method. The present paper demonstrates that results from the second method are sensitive to stratigraphic, morphometric, statistical, and phylogenetic information. Inaccuracies in any of these data invalidate results or lead to inconclusive statements. As described below, for at least one lineage included in Stanley and Yang's (1987) study, *Chione erosa* Dall, 1903–*Chione cancellata* Linnaeus, 1767, an inferred history of morphological stasis over the last 4 million years is inaccurate.

Stratophenetic analyses.—Stratophenetics is the morphologic description of a lineage through time, based on sampling of numerous geographically restricted, consecutive stratigraphic units from a single formation. Bookstein (1987 and 1988) has proven convincingly, using random-walk simulations, that stratophenetic demonstrations of stasis or anagenesis are extremely difficult to accomplish, both statistically and conceptually. The incorporation of statistical rigor into such experiments requires the examination of large numbers of data points, a condition that is often difficult to meet with studies of invertebrates. This condition is more easily met when studying microfossils (e.g., Malmgren and Kennett, 1981; Bookstein and Reyment, 1989). Conceptual difficulties arise when one attempts to reify a morphological pattern by reference to particular ecological and/or selective factors. Time is not a causative factor of evolutionary patterns (McKinney, 1990; Bookstein, 1991), except maybe in the case of random genetic drift. Reification is possible only by direct measurement of exogenous factors and demonstration of causal relationships between the factors and morphological variance (Bookstein, 1991).

Geographic and temporal analysis.—An alternative to detailed stratophenetic analysis involves large-scale temporal and geographic sampling. This is the method adopted by Stanley and Yang (1987). Their method involved describing the mor-

phology of phyletic lineages using multivariate morphometrics and broad geographic sampling over the temporal span of the lineages. They were able to demonstrate, for at least 15 “lineages” of Neogene bivalves, that distributions of morphological distances (as measured by Mahalanobis' D^2) between Recent and fossil species (presumably ancestral) are no greater than distributions of D^2 between geographically separated samples of the Recent species. They concluded that, for the lineages examined, evolution has followed a “weak zigzag course” (Stanley and Yang, 1987, p. 113), with no significant net evolutionary change during the last 4 million years.

Besides the obvious problem of distinguishing biological species in fossil taxa, we must consider the observation that distinct species can sometimes exhibit more intraspecific morphometric differentiation than interspecific differentiation (Levinton, 1988; Boulding et al., 1993). Levinton (1988) also raised the question of whether intraspecific and interspecific variation are continuous. Stanley and Yang's (1987) study, while addressing the magnitude of morphological variation, did not examine, in detail, morphological direction (in “morphospace”) of the variation. To demonstrate, the distance $AB = 5$ units, and $AC = 5$ units, does not necessarily imply that $BC = 0$ units.

This paper presents a morphometric examination of samples of the tropical American venerid bivalve species *Chione cancellata* and *C. erosa* spanning the last 3.5 million years. The results demonstrate that, although there has not been a change in the quantity of morphological variation, there is a definite morphometric discontinuity between Pliocene specimens and post-Pliocene specimens.

Species discrimination.—Dall (1903) first recognized the morphological dissimilarity between Pliocene and post-Pliocene specimens of *Chione cancellata* from Florida. He placed middle Pliocene specimens from the Jackson Bluff Formation in a separate species, *C. erosa*, based primarily on differences in lunule size. Since that time, it has become common practice for workers to refer Pliocene specimens from Florida to *C. erosa*. The distinction was rejected by Stanley and Yang (1987), who argued that *C. cancellata* displays a pattern of morphological stasis within its temporal (middle Pliocene to Recent) and geographic (southeast United States to Brazil) ranges. They further suggested that *C. erosa* is the anagenetic forerunner of *C. cancellata* and therefore suggested synonymy of the two species names. This idea can only be supported, however, by the inability to discriminate morphologically between the two taxa. Following

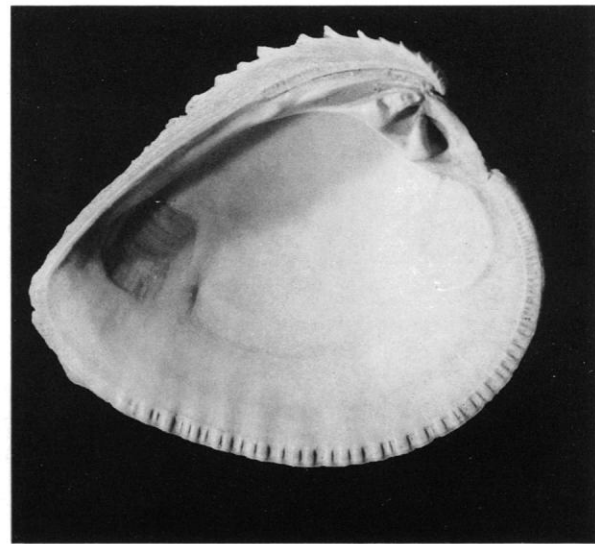
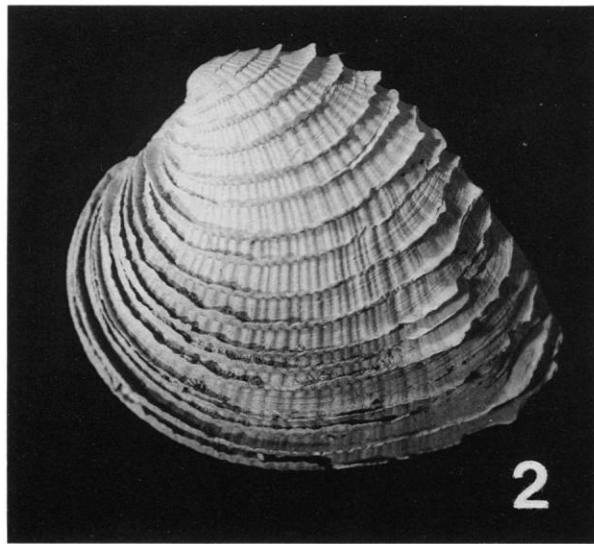
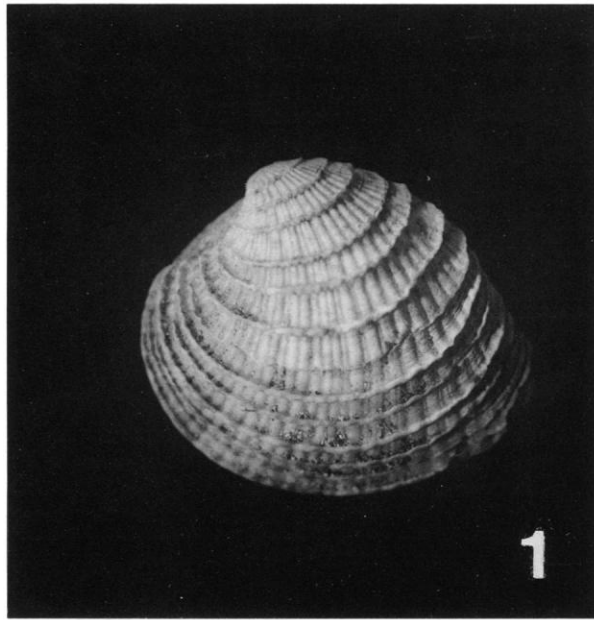


FIGURE 1—1, *Chione cancellata*, FMNH 77122, Recent, Jamaica, $\times 2.25$. 2, *Chione erosa*, middle Pliocene, lower Pinecrest Beds, Florida (author's collection), $\times 1.6$.

is a brief description of *C. cancellata*, the type species of the genus, and a comparison to *C. erosa*.

SYSTEMATIC PALEONTOLOGY

CHIONE CANCELLATA Linnaeus, 1767

Figure 1.1

Description.—Pallial sinus poorly developed. Sculpture consists of prominent concentric and radial ribs. Concentric ribs short, sharp at summits, closely packed on ventral faces, and oriented perpendicular to surface of valve. Radial ribs prominent between concentric ribs. Escutcheon beveled and well defined on left valve; weakly demarcated, but developed and concentrically sculptured on right valve. Lunule concentrically sculptured with subdominant radial ribs present. Anterior cardinal tooth (2a) wide in left valve. Middle cardinal (2b) weakly

grooved on dorsal side of tooth. Posterior cardinal (4b) weakly curved. Hinge plate weakly bowed beneath anterior cardinal. Nymph smooth. Middle cardinal tooth of right valve wide, posterior cardinal tooth smooth. Ventral margins of both valves crenulated.

CHIONE EROSA Dall, 1903

Figure 1.2

Comparison.—*Chione erosa* shares most characteristics with *C. cancellata*, but there are several diagnostic differences. The concentric ribs are more widely spaced in *C. erosa*, and are foliaceous and often recurved, not vertical. Sculpture is a consistent and diagnostic character among species in the subfamily Chioninae (Roopnarine, 1993). The hinge plate of *C. erosa* is more bowed than it is in *C. cancellata*, and the escutcheon of

TABLE 1—Samples of *Chione cancellata* and *C. erosa* used in this study. The abbreviations in the "Sample" column are used in all relevant figures. The "Collection" abbreviations are as follows: A = author's collection; FMNH = Field Museum of Natural History; TU = Tulane University Geological Collections; UF = Florida Museum of Natural History, University of Florida; GJV = collection of G. J. Vermeij.

Species	Sample	Formation/Locality	Age	Collection	
<i>Chione cancellata</i>	SC	South Carolina	Recent	A	
	FL1	Lake Worth, Florida	Recent	A	
	FL2	Anclite Key, Florida	Recent	A	
	FL3	Sanibel Island, Florida	Recent	FMNH12136	
	JA	Jamaica	Recent	FMNH77122	
	ST	St. Thomas, U.S. Virgin Islands	Recent	FMNH197286	
	VZ	Venezuela	Recent	GJV	
	WA	Waccamaw Fm., South Carolina	late Pliocene	TU558	
	BM1	Bermont Fm., Florida	e. Pleistocene	TU754	
	BM2	Bermont Fm., Florida	e. Pleistocene	TU815	
	BM3	Bermont Fm., Florida	e. Pleistocene	TU935	
	AN	Anastasia Fm., Florida	l. Pleistocene	TU777	
	<i>Chione erosa</i>	PN1	Pinecrest Beds, Florida	m. Pliocene	TU200
		PN2	Pinecrest Beds, Florida	m. Pliocene	TU203
		PN3	Pinecrest Beds, Florida	m. Pliocene	TU520
		PN4	Pinecrest Beds, Florida	m. Pliocene	TU529
		PN5	Pinecrest Beds, Florida	m. Pliocene	TU532
JB		Jackson Bluff Fm., Florida	m. Pliocene	UF7103	
CA1		Caloosahatchee Fm., Florida	late Pliocene	TU729	
CA2		Caloosahatchee Fm., Florida	late Pliocene	TU755	
CA3		Caloosahatchee Fm., Florida	late Pliocene	TU797	
CA4		Caloosahatchee Fm., Florida	late Pliocene	A	

the right valve is more heavily sculptured. Valve margin crenulations tend to be coarser, though not consistently so. The valves of *C. erosa* are also much flatter than those of *C. cancellata*, which can be very convex in some geographic regions.

The assumption that *C. cancellata* and *C. erosa* represent a phyletic lineage ignores the existence of other "cancellata-like" species in the Pliocene (for example *C. pailasana* Weisbord, 1964) and Recent (for example, *C. mazzykii* Dall, 1902) of the West Atlantic and Caribbean (see Palmer, 1927, for a comprehensive listing). There are also reports that would, if chrono-

logically correct, indicate the presence of *C. cancellata* in the early and middle Pliocene of the southern Caribbean (Jung, 1969; Weisbord, 1964). This would make the stratigraphic descendant contemporaneous with its ancestor. An alternative hypothesis to stasis then, would be the presence, in the late Neogene and the Recent, of several "cancellata-like" taxa in tropical American waters. The elucidation of evolutionary relationships among these taxa must therefore rely upon a phylogenetic framework. This paper demonstrates that the two species can indeed be discriminated, and therefore do not support a hypothesis of stasis.

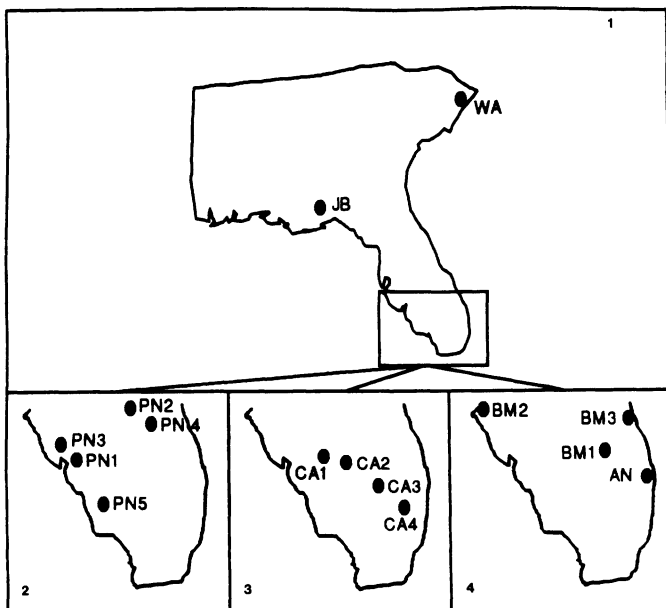


FIGURE 2—Location of fossil sampling localities. 1, Pliocene sample of *Chione cancellata* Linnaeus, 1767; 2, samples of *C. erosa* Dall, 1903, from the Pliocene Pinecrest Beds; 3, samples of *C. erosa* from the late Pliocene Caloosahatchee Formation; 4, Pleistocene samples of *C. cancellata*. Abbreviations explained in Table 1.

METHODS

Samples.—Twelve samples (Table 1) of *Chione cancellata* were collected, covering the Pliocene and Pleistocene of the southeast United States (Figure 2.1, 2.4) and the Recent of the southeast United States and the Caribbean (Figure 3). Recent samples were collected from South Carolina (Florida, Jamaica, St. Thomas (U. S. Virgin Islands), and Venezuela. One sample was obtained from the late Pliocene Waccamaw Formation of South Carolina, three from the early Pleistocene Bermont Formation of Florida, and one from the late Pleistocene Anastasia Formation of Florida. Ten samples of *C. erosa* were collected covering the middle and late Pliocene of Florida (Figure 2.2, 2.3). There is one possible occurrence of *C. erosa* in South Carolina in the early Pliocene Raysor Marl (L. Campbell, personal commun.), but no specimens from this formation were included due to the scarcity and poor preservation of material available. No fossil samples from the Caribbean were available for either species at the time of this study. A total of 534 specimens was used in the study.

Morphometric measurements.—Eleven variables were measured on left valves (Figure 4). Only left valves were used because left and right valves of *C. cancellata* are morphometrically dissimilar. The 11 measures were selected based on their presumed biomechanical sensitivity to changes in valve shape. All measurements are associated with linear dimensions and relative orientation of either hinge or muscle scar structures, and are defined by nine homologous landmarks. These features are involved in the mechanical operation of the shell and any changes

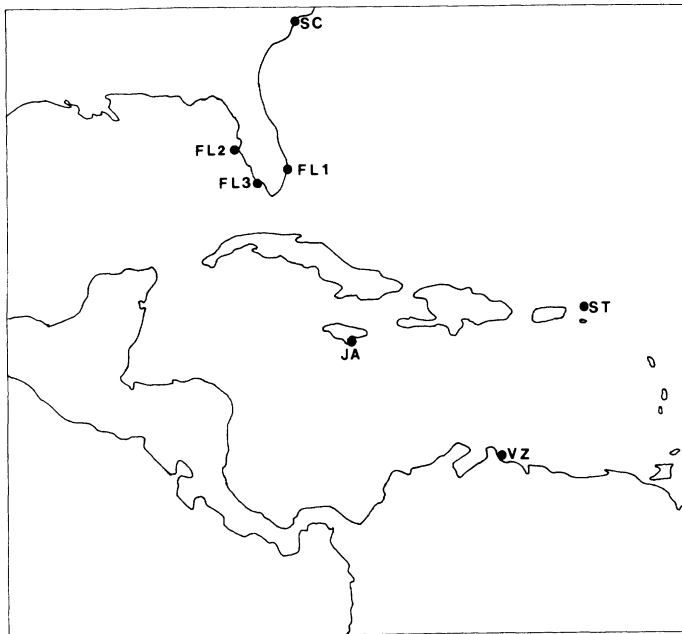


FIGURE 3—Location of Recent sampling localities of *Chione cancellata* Linnaeus, 1767. Abbreviations explained in Table 1.

in valve shape may be assumed to result in appropriate alterations of hinge and muscle morphology. Such alterations would be necessary for maintaining the mechanical integrity of the shell. All measurements were made with dial calipers to the nearest 0.02 mm.

Statistical analyses.—The first step in analyzing the data was to correct for substantial size variability among and within samples. This step is necessary because indeterminate growth in *Chione*, as well as the need for large sample sizes, required use of large size ranges of specimens. The data therefore represent a cross section of a distribution of different sizes and ages. Size correction consisted of calculating an appropriate size variable and removing it from all samples.

A multivariable measure of size was calculated as the logarithm of the geometric mean (Sokal and Rohlf, 1981) of the measurements for each individual:

$$\log GM_Y = 1/n(\sum \log Y_i)$$

where GM_Y = geometric mean of the Y th individual, n = number of variables (=11), and Y_i = value of variable i . Size was removed from a pooled data set of samples, for all variables, by calculating the reduced major axis of each variable when related to geometric mean size (regression coefficient), and then projecting each variable orthogonally to geometric mean size by rotation of the reduced major axis:

$$a = xB$$

where a = size-adjusted variable vector, x = original variable vector, and B = rotation matrix with angle of rotation being angle of reduced major axis with size axis.

The adjusted data matrix A (total of all a_i) was then subjected to canonical variates analysis (CVA) and Mahalanobis distances were computed between all possible pairs of sample means within the data set. The Mahalanobis distance between two points is the Pythagorean distance in canonical variate space. The entire procedure was performed for three data sets consisting of 1) all Recent *Chione cancellata* samples, 2) Recent samples plus

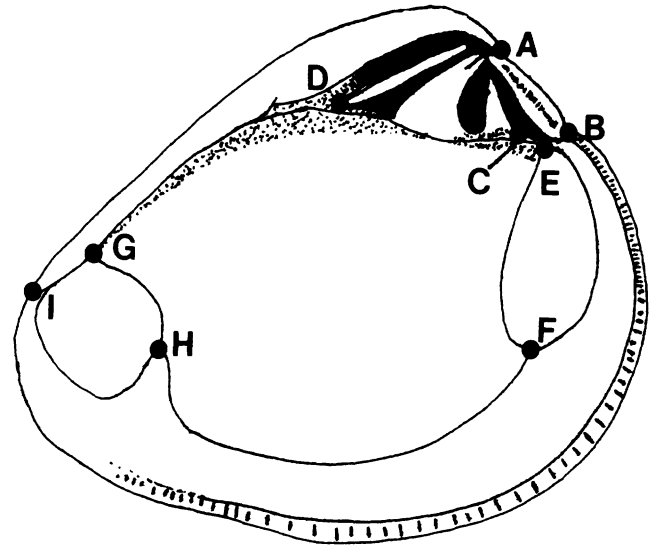


FIGURE 4—Left valve of *Chione cancellata* Linnaeus, 1767. Dark lines indicate morphometric measurements. A, umbo; B, ventral terminal of lunule; C, anterior end of anterior cardinal tooth; D, posterior end of posterior cardinal tooth; E, dorsal junction of anterior muscle scar with pallial cavity; F, ventral junction of anterior muscle scar with pallial line; G, dorsal junction of posterior muscle scar with pallial cavity; H, ventral junction of posterior muscle scar with pallial line; I, ventral terminal of escutcheon. Measures are AB, AC, AD, CD, DG, EF, EG, FH, GH, GI, HI.

the Pliocene and Pleistocene samples of *C. cancellata*, and 3) all *C. cancellata* and *C. erosa* samples.

The distribution of distances between samples was plotted as a histogram for each of the three analyses. This procedure follows Stanley and Yang's (1987) method of comparing the distributions. Sample distributions on the first canonical variates axis were compared by drawing box plots of each distribution. Notches, representing nonparametrically derived 95 percent confidence intervals about the median, were placed on each box (McGill et al., 1978). Confidence intervals are calculated as a function of interquartile (25 percent of observations on either side of the median) range (R) and sample size (N):

$$M \pm 1.7(1.25R/1.35\sqrt{N})$$

where M represents the sample median. The formula is a nonparametric approximation of standard deviation. The factor of 1.7 was selected empirically by McGill et al. (1978) to yield a conservative, but not too stringent, test. Other values, for example 1.96, can be substituted. All analyses were performed using SYSTAT (ver. 5.0) for DOS.

RESULTS

All measurements were significantly correlated with geometric mean size for the three data sets (Table 2; Figure 5). Figure 5 also demonstrates the lack of correlation of the rotated variables with size (see Table 2 for P values). The following results can therefore be considered to refer to size-free measurements.

Chione cancellata, Recent.—The first CVA axis for all three analyses is the only axis that discriminates between samples. Mahalanobis distances between sample means of Recent populations of *Chione cancellata* range from 0.682 to 2.066 (Figure 6.1). This range is in relative units, and becomes important only when compared to the results of other analyses. The results of the CVA are summarized for the first canonical axis in Table 2. The range of magnitudes of the variable loadings on this axis

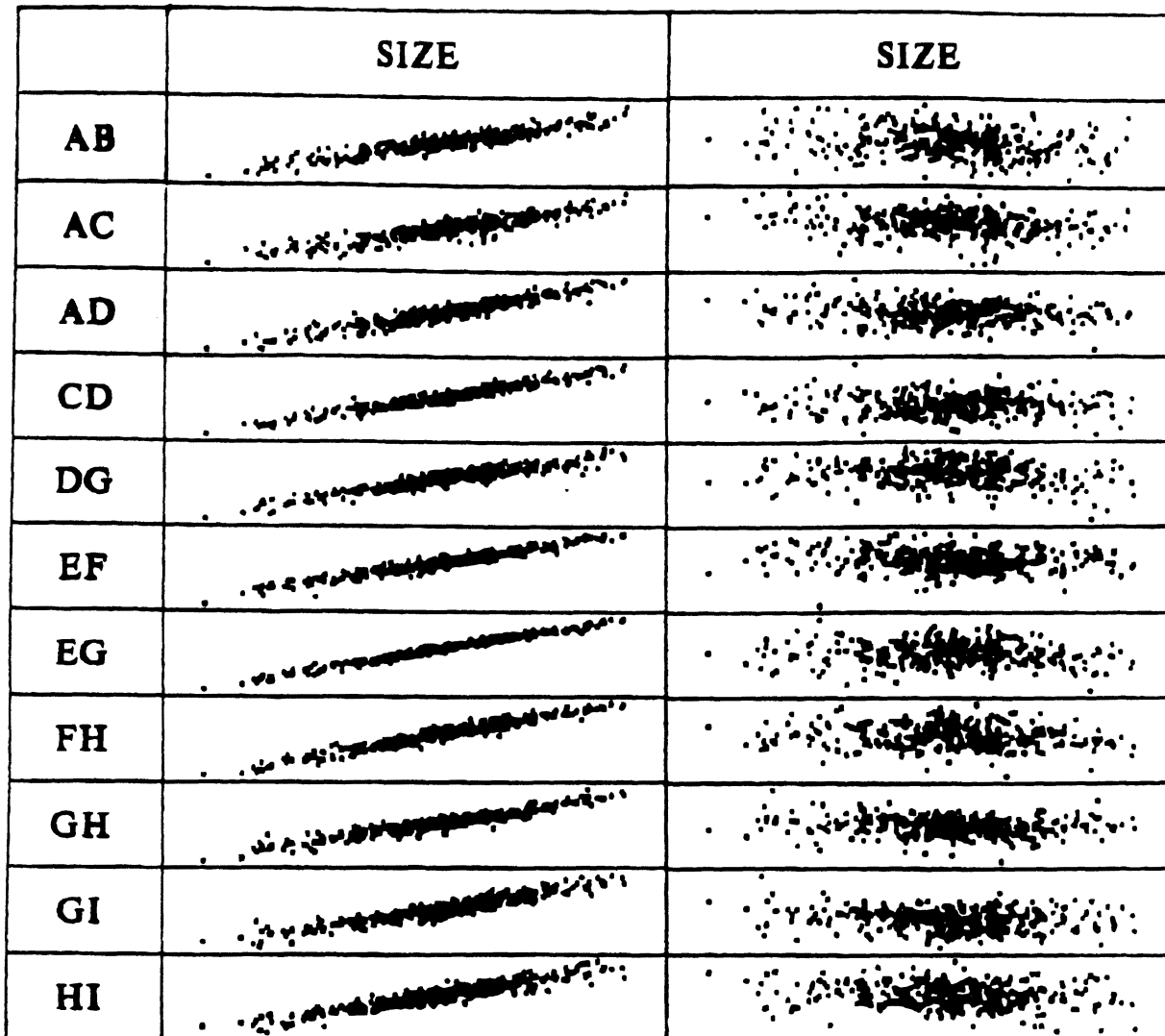


FIGURE 5—Relationship of measurements with geometric size. First column, measurements correlated with size; second column, measurements' correlation with size after reduced major axis regression and axis rotation.

suggests that AB, lunule size, is the main discriminating variable. There appears to be significant discrimination between samples from the southeast United States and samples from the Caribbean. Ordination of the sample distributions on the first

TABLE 2—Pearson correlation coefficients of measured variables with Size. First column lists coefficients before regression, and second column lists correlations of residuals with Size. Coefficients for residuals are all negative, because reduced major axis regression tends to overestimate slopes slightly.

Variables	Correlation of variables with size	
	Before	After
AB	0.922	-0.186
AC	0.899	-0.212
AD	0.953	-0.155
CD	0.962	-0.140
DG	0.951	-0.157
EF	0.962	-0.130
EG	0.975	-0.107
FH	0.943	-0.166
GH	0.949	-0.163
GI	0.933	-0.172
HI	0.941	-0.132

canonical axis illustrates the distance distributions (Figure 7). Each sample is represented as a box plot.

Chione cancellata, Recent and Neogene.—These results pertain to a data set comprising samples analyzed above, plus Pleistocene samples from Florida and one late Pliocene sample from South Carolina. The results of the CVA are summarized for the

TABLE 3—First latent vector of canonical variates analysis of Recent samples of *Chione cancellata* Linnaeus, 1767.

Variable	Vector I
AB	0.519
AC	0.325
AD	-0.429
CD	-0.353
DG	0.087
EF	0.118
EG	-0.169
FH	0.368
GH	0.328
GI	-0.184
HI	-0.206
Latent root	0.792

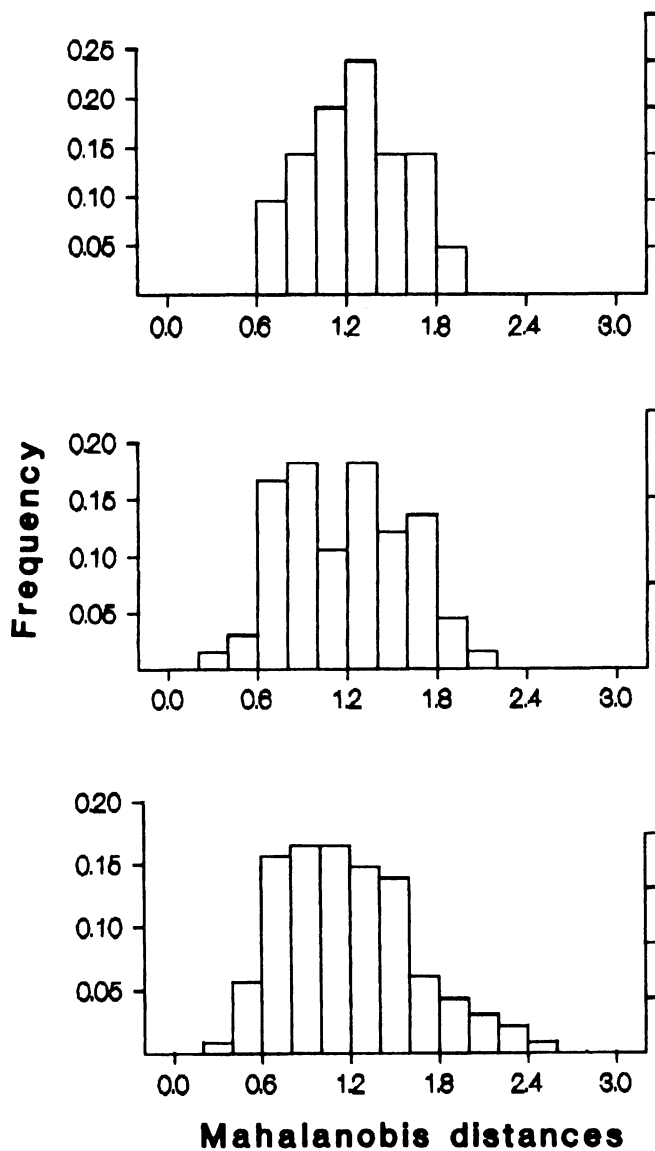


FIGURE 6—Distributions of inter-sample Mahalanobis distances. 1, Recent samples of *Chione cancellata* Linnaeus, 1767; 2, Recent and fossil samples of *C. cancellata*; 3, all samples of *C. cancellata* and *C. erosa* Dall, 1903.

first canonical axis in Table 3. Once again, AB, relative lunule size, is the dominant discriminating variable. The Mahalanobis distance range for this data set (0.332 to 2.19) is summarized in Figure 6.2. The range increased slightly in both directions, which can be explained by observing the ordination of sample distributions on the first canonical axis (Figure 8). Discrimination between samples from Florida and South Carolina and samples from the Caribbean is maintained. The range of distances increases because all the fossil samples cluster with their Recent geographic counterparts; this increases the number of small Mahalanobis distances in the distribution, while also increasing slightly the number of large distances to the Caribbean samples.

Chione cancellata and *C. erosa*.—This step analyzed a data set comprising all *C. cancellata* samples, plus 10 *C. erosa* samples. The results of the CVA are summarized in Table 4. The Mahalanobis distance range for this analysis is 0.2 to 2.1 (Figure

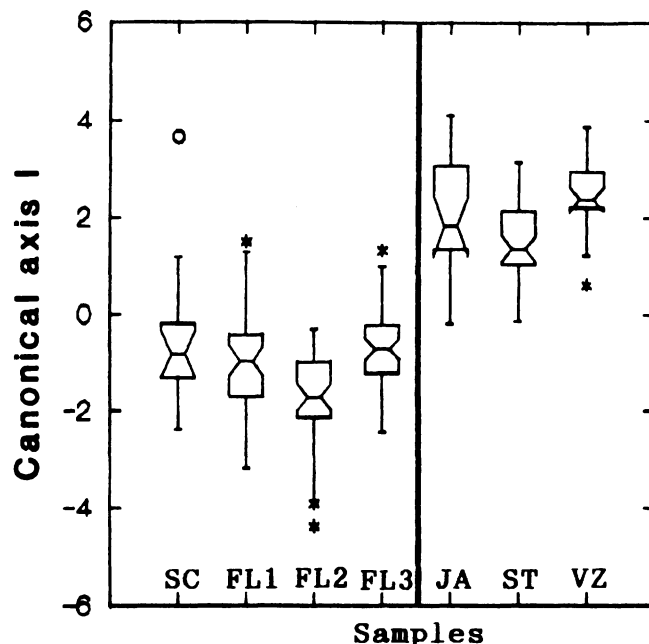


FIGURE 7—Distribution of Recent samples of *Chione cancellata* Linnaeus, 1767, on first canonical axis. Abbreviations on lower axis explained in Table 1. Vertical line separates Caribbean samples from United States samples. Asterisks represent values that are beyond the 75 percent interquartile of each range by a factor of at least 1.5, and circles, values distant by a factor of at least 3.

6.3). In accordance with Stanley and Yang's (1987) results, the distance range is not significantly different from the distance ranges computed for *C. cancellata* alone (F-test, $P = 0.673$). Ordination of sample distributions on the first canonical axis, however, indicates that while the discrimination between the United States and Caribbean samples of *C. cancellata* is preserved, there is also discrimination between both groups of *C. cancellata* and the samples of *C. erosa* (Figure 9). There is very little overlap between samples of *C. cancellata* and samples of *C. erosa*, contrary to the results of Stanley and Yang (1987). The CVA correctly assigned 87.35 percent of the specimens to the correct species.

The mean absolute loading of the measurements on the first canonical vector is 0.237. There are four measurements with loadings higher than this value: AB, AC, AD, and FH (see Figure 4 for explanation). The magnitudes and signs of these loadings explain the orientation of the samples in canonical morphospace relative to each other. AB and FH are relatively larger in *Chione*

TABLE 4—First latent vector of canonical variates analysis of Recent and fossil samples of *Chione cancellata* Linnaeus, 1767.

Variable	Vector I
AB	0.645
AC	0.304
AD	-0.501
CD	-0.404
DG	0.019
EF	0.253
EG	-0.261
FH	0.191
GH	0.356
GI	-0.221
HI	-0.167
Latent root	0.803

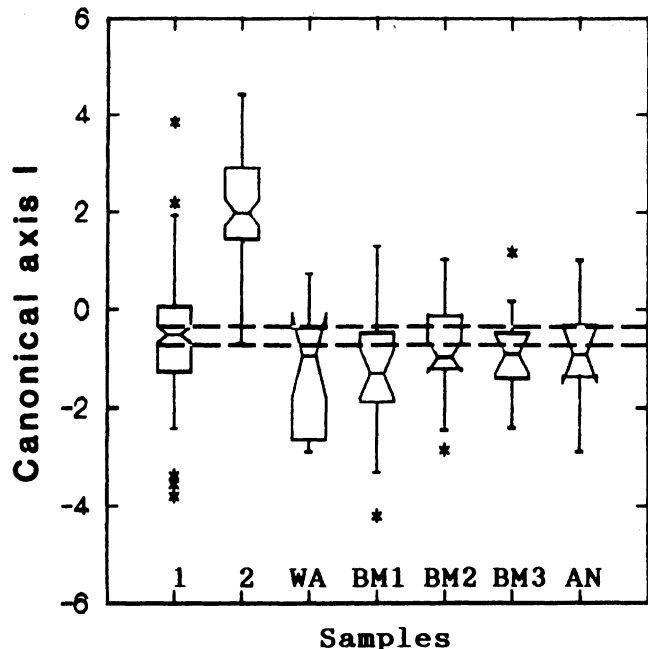


FIGURE 8—Distribution of Recent and fossil samples of *Chione cancellata* Linnaeus, 1767, on first canonical axis. On lower axis: 1, Recent samples from the United States combined; 2, Recent samples from the Caribbean combined. Other abbreviations on lower horizontal axis explained in Table 1, and Figures 2 and 3. Horizontal dashed line demarks the 95 percent confidence boundaries for the first box.

erosa, and AC and AD, both hinge characters, are relatively shorter. *Chione erosa* has a relatively larger lunule than does *C. cancellata*, and is a longer shell (as indicated by the loading of FH). Its hinge is relatively higher than that of *C. cancellata*, as suggested by the loadings of AC and AD and the position of *C. erosa* on the first canonical axis. It is interesting to note that the length of the lunule is the character used originally by Dall (1903) to separate the two species.

DISCUSSION

The apparent distinction of Floridian and South Carolinian samples of *Chione cancellata* from their more southerly Caribbean counterparts should be interpreted with caution. The distinction does not necessarily mean that they are different species, nor that the northern samples are more closely related phylogenetically to *C. erosa*. It is difficult to draw species boundaries based

TABLE 5—First latent vector of canonical variates analysis of Recent and fossil samples of *Chione cancellata* Linnaeus, 1767, and samples of *C. erosa* Dall, 1903.

Variable	Vector I
AB	0.663
AC	-0.253
AD	-0.360
CD	-0.172
DG	0.040
EF	0.005
EG	0.075
FH	0.550
GH	0.127
GI	-0.147
HI	-0.215
Latent root	0.840

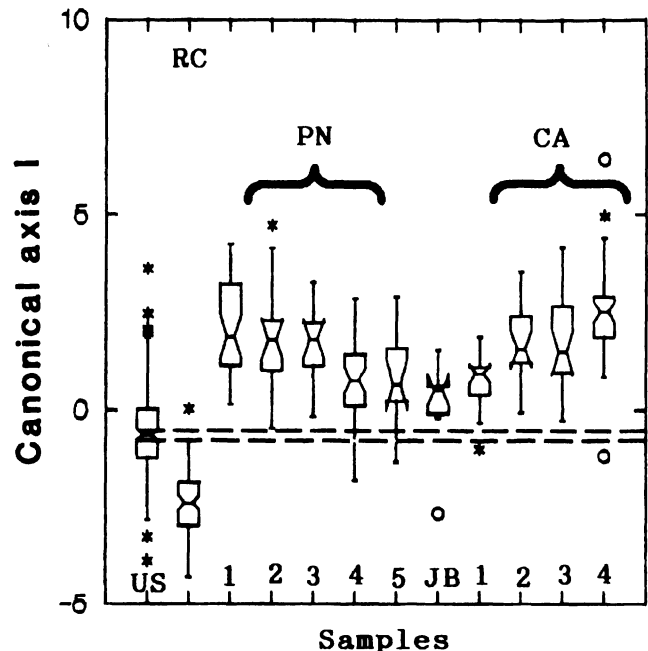


FIGURE 9—Distribution of *Chione cancellata* Linnaeus, 1767, and *C. erosa* Dall, 1903, on first canonical axis. Abbreviations: US, Recent and fossil samples of *C. cancellata* from the United States combined; RC, Recent samples of *C. cancellata* from the Caribbean combined; PN, samples of *C. erosa* from the Pinecrest Beds; CA, samples of *C. erosa* from the Caloosahatchee Formation; JB, samples of *C. erosa* from the Jackson Bluff Formation. Numbers on horizontal axis below PN and CA explained in Figure 3. Horizontal dashed line represents 95 percent confidence boundaries for US.

solely on morphometric data when the extent of ecophenotypic variation or intraspecific differentiation is unknown. There is the possibility, of course, that *C. cancellata* in the Caribbean is indeed taxonomically distinct from its northern counterpart. The present results cannot differentiate between the two alternatives, that the two groups represent geographic "morphs" of the same species, or indeed represent two separate species.

Multivariate morphometric analyses support a morphological dissimilarity between the species *Chione erosa* and *C. cancellata*. Although the two species do not seem morphologically distant in the multivariate morphological space defined by my analyses, there is no overlap between sample medians (Figure 9). The ability to discriminate morphologically between the two species, and within *C. cancellata*, does not support a hypothesis of stasis, or no net evolution, within this pair of species over the last 4 million years. Even though *C. cancellata* does exhibit substantial variation over its Recent geographic range, and the corresponding range of statistical distances is equal in magnitude to the range of distances between *C. cancellata* and *C. erosa*, these distances are oriented differently in morphological space.

It is unclear why the results of this study should differ so significantly from those presented by Stanley and Yang (1987). The CVA ordination of sample distributions in this study, however, is also different from that presented by Stanley and Yang (1987). The sources of difference probably lie in the methods of data collection and analysis. Stanley and Yang (1987) collected their measurements by digitizing two-dimensional images of valves. This "flattening" of concave bivalves introduces a systematic size-related error into the data, because distortion due to flattening, even if minimal, increases with increasing valve size (and therefore concavity).

Stanley and Yang (1987) used a different set of measurements from those used in this study. Seven homologous landmarks are common to both analyses, but Stanley and Yang generated 24 measurements from 20 points. Eight of their 20 points are homologous between different valves. The remaining 12 are defined by the position of at least one of the previous eight, and are termed pseudohomologous points. One probably cannot equate one set of external morphological measurements with another (Levinton, 1988), even if both are attempting to describe the same object. Both Stanley and Yang's (1987) data and the present data, however, proceed from similar homologous points and attempt to archive the same taxa. Additional differences probably arise in the treatment of the collected data.

Stanley and Yang (1987) acknowledged the problem of size variability in their data set, and attempted to account for it by dividing all the measures of an individual by the square root of valve area. The generation of such size-adjusted ratios does not necessarily remove size from the data set. Size can still be present significantly in data as allometrically size-correlated ratio magnitudes. Size adjustment with ratios does not necessarily equal size removal from the data set. It is therefore possible that Stanley and Yang (1987) did not remove all size variability, which then may constitute a large portion of their latent axes. Size differences are difficult to interpret in an evolutionary context unless sampling is designed not to bias any particular size class, or unless one is studying organisms with determinate growth.

An important observation is that there are no temporal discriminations, or trends, within either species. If samples of *Chione cancellata* from the United States are considered taxonomically distinct from those of the Caribbean, then neither group exhibits temporally dependent discrimination. The three morphological groups (*C. cancellata*, United States; *C. cancellata*, Caribbean; and *C. erosa*) therefore may exhibit internal patterns of stasis. Patterns of stasis spanning the middle-late Pliocene (approximately 1.75 million years), or Pleistocene to the Recent (1.64 million years), however, may be of arguable importance to the understanding of long-term evolutionary patterns and mechanisms within species with durations approaching 11–14 million years (Stanley, 1985).

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