Evolution, 44(2), 1990, pp. 416–434

THE STRUCTURE OF INDIVIDUAL VARIATION IN MIOCENE *GLOBOROTALIA*

R. ELENA TABACHNICK
Department of Geological Sciences and Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109

AND

FRED L. BOOKSTEIN
Center for Human Growth and Development, University of Michigan, Ann Arbor, MI 48109

Abstract.—Analysis of probability distributions of individual organisms provides a common language to describe synchronic and diachronic diversity. When based on an appropriate quantitative description of morphology, this language can be used to explore the temporal component of diversity embedded in the fossil record.

Miocene *Globorotalia* (planktonic foraminifera) from Deep Sea Drilling Project site 593 are described using two-point registration of landmarks in two views (spiral and apertural) and medial-axis analysis of the shape of the final chamber. The equiangular spiral parameters Θ (the angle of increment), r (the expansion rate), and t (the rate of translation down the spiral axis) appear as principal components of the landmark data. Chamber shape variation is described by three principal components of medial-axis curvature. Partial-least-squares analysis demonstrates that the first components of within-morphospace variation also explain the patterns of correlation between the landmark and chamber-shape morphospaces.

In the landmark morphospaces, the distribution of sampled individuals is continuous and roughly elliptical with few stratigraphic changes. In the chamber-shape morphospace, the distribution is continuous but shows complex features beyond the elliptical; the occupied morphospace changes stratigraphically, but neither strict cladogenesis nor strict anagenesis explains the derivation of new morphologies. Exemplars of named morphospecies are scattered across these spaces with continuous variation among all forms. These names cannot be assumed to represent discrete entities.

Received July 13, 1988. Accepted October 4, 1989

"A fact almost as striking as [organic] diversity itself... is the discontinuity of the variation among organisms."
—Th. G. Dobzhansky (1937 p. 3)

"[Organic] diversity has the very special property that it is not continuous... [Species] are separated from each other by gaps."
—E. Mayr (1963 p. 427)

"The mathematical description of the world depends on a delicate interplay between continuity and discontinuous, discrete phenomena."
—V. I. Arnol'd (1986 p. vii)

The ultimate interpretation of diversity in terms of functioning biologic entities requires information on the relationships among morphology, behavior, interbreeding, and ecology (we employ the term "biologic entity" instead of "species" for reasons that will become clear later in this paper). These sorts of information are available principally from neontologic studies. Yet, since biological processes act through time, all biological entities must have a temporal dimension. The fossil record provides a temporal record of diversity changes, but this information is primarily morphological; therefore, attempts to understand the temporal component of diversity patterns must be founded on descriptions of morphological variation.

Temporal and geographic changes in the pattern of individual variation can be analyzed within multivariate "morphological spaces" (Bookstein et al., 1985). Saunders and Swan (1984) applied such an approach to a study of ammonite variation through time and space, utilizing several typical specimens of each morphospecies to encompass the global pattern of variation. Instead, we advocate sampling individual variation without reference to named morphospecies. In this way, changes in the pattern of individual variation inclusive of the morphospecies can be discerned.

In multivariate space, the structure of variation among organisms generally appears as aggregations which have locations, "shapes" (i.e., variances and sample density functions), and spatial relationships among themselves. These aggregates exist along a

spectrum of diverse topologies. At one extreme are modes in continuous distributions; at the other extreme are discrete clusters. In traditional representations of biological diversity, a range of variation is recognized below the species level, while at the species level and above, specimens are assumed to be organized mainly into discrete groups. For some organisms this range of possible patterns may be exhibited at many levels of an empirical taxonomic hierarchy, not only at the subspecies level (Mishler and Donoghue, 1982). While phylogenetic analyses are primarily concerned with explicating ancestral/descendant relationships among designated taxa, the problem we are approaching here is not "who came first?" (a research program which can be easily applied only to taxa bounded by discontinuities) but, rather, "what is a 'who'?" The answer to our question relies on describing the structure of aggregates in multivariate space, beginning with a minimum of assumptions.

For many fossil taxa, including the planktonic foraminifera, most morphospecies names can be unambiguously applied to at least a few individuals. A closer study of individual variation will not change the application of these names. Calling such named morphologies "species" is often taken to imply that the distribution of individuals is a discrete scatter, approximately normal, and having a centroid near to the type specimen. The distribution of individuals within a morphological space to which a number of species names can be applied is often not addressed explicitly.

Patterns of Morphological Diversity.—One simple expectation for evolution of the pattern of morphological variation of normally distributed groups is that new morphologies arise as a result of cladogenesis, the splitting of an ancestral group into reproductively isolated descendant groups. This reproductive separation may result in morphological divergence between the descendant groups which, once achieved can be maintained or increased. In discussing reproductive divergence Mayr (1963) posed the crucial question: how can a normally distributed group conceivably split? The following discussion concerns the pattern of morphological variation and not necessarily the development of reproductive isolation or the relationship between reproductive isolation and morphological variation, but Mayr's question still applies.

Splitting involves the development of a gap in existing variation. Often there is a concomitant occupation of new morphological space by one or both descendant groups. In that event, there are two alternatives for the history of a particular splitting event: new space may be occupied before or after the development of the gap. In the first alternative, individual variation expands first to occupy new morphological space, and gaps develop in the variation only afterward (as proposed by Rosenzweig [1978]). In the second alternative, gaps develop first in the preexisting variation through loss of intermediate forms, and the now discrete groups move into new morphological space afterward. The two alternatives need not be mutually exclusive: gaps may begin to form (as evidenced by shifts in the modes of the distribution) as individual variation expands into new morphological space.

These alternative modes of splitting can be discriminated only if individual specimens are clustered into discrete groups of similar morphology. However, there are several patterns for the structure of individuals in morphological space other than discrete groups. Distributions of specimens could be uniform over a very large, continuously occupied region of morphospace; peaks of density could occur in morphospace, but with continuous variation between modes; or large, twisting structures could exist in morphospace as continuous variation connects each form to others in some (but not all) directions. In the last case, there are unfilled regions of the space within and between these structures, but continuous variation connects all parts of the structure by some path. Figure 1 illustrates the differences among these patterns of variation.

Many biologists would accept the existence of the three patterns shown in Figure 1A–C below the species level, but the biological species definition of Mayr and Dobzhansky implies that the pattern in Figure 1D is the one normally exhibited at the species level and above. For some organ-

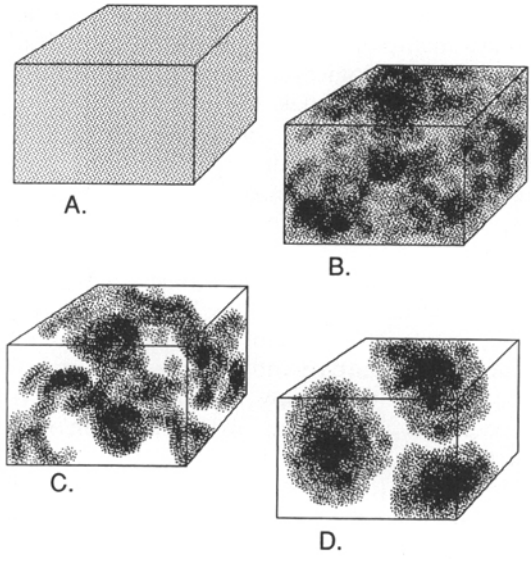

FIG. 1. Diagrammatic representation of diversity patterns in three dimensions: A) uniform over a large region of space; B) density modes in continuously occupied space; C) occupation of large, twisting areas of space (discontinuities are present, but there is some continuous variation linking all individuals); D) discrete groups.

isms, the pattern of synchronous diversity may be of the type in Figure 1C for most morphological characters at a scale of variation that appears to be too great to represent a single species. In some cases, species diagnosis can be based on discrete distributions of nonmorphological data. Such noncoincidence of distributions of genetic, ecological, or morphological data is itself an interesting problem. There may also be some taxa for which none of these data sets exhibits primarily discrete distributions at the magnitude of variation normally attributed to species.

There are also alternatives to cladogenesis as the mode of evolution. The most commonly cited is anagenesis (Bookstein et al., 1978), a net lateral shift in the entire synchronous distribution of a particular character or set of characters without any change in the shape of the distribution. This mode of evolution is exemplified by replacement of forms within a single lineage presumed to be essentially "one species wide," a mode of evolution often cited for morphospecies of planktonic foraminifera. Another possible pattern is reticulation, involving the appearance, disappearance, and reappearance of gaps through evolutionary time. In yet a third possibility, morphological variation could expand into new regions of the morphospace (and density peaks in the variation could move into the new space) but still cover the total space without gaps. If the structure in morphospace consists of density peaks moving within larger, partially gap-bounded structures, then a fourth evolutionary pattern involves the movement of these large, twisting structures through space, as density peaks move within them. Whether evolution typically follows any of these paths is an open question.

We will attempt to carry out a comparative analysis of these interpretations in a detailed study of morphological diversity across seven morphospecies of Miocene *Globorotalia*. Our approach differs from the classical multivariate morphometric analyses, such as are reviewed in Reyment et al. (1984). The classical analyses are primarily tests of categories measured or defined in advance (such as species definitions, sex, or survival), with factor and component analyses used to determine whether clusters are distinct enough to deserve species status or to find single dimensions of explanation for subclusters. For example, this analytic approach was taken by Wei (1987) in assembling chronospecies from clusters of samples within a multivariate morphospace.

MATERIALS AND METHODS

Miocene Globorotalia.—Planktonic foraminifera provide an interesting subject for the study of patterns of morphological diversity; these organisms commonly display complicated patterns of morphological variation. Intermediate forms are often present between ancestral and descendant species, with continuous variation between named species in single samples (Stainforth et al., 1975; Tabachnick, 1981; Banner, 1982). We examined a lineage of Early to Middle Miocene *Globorotalia* from a site in the southwest Pacific. The extent of morphological space occupied by this globorotalid lineage increased during the Miocene. The Early Miocene forms *Globorotalia zeal-*

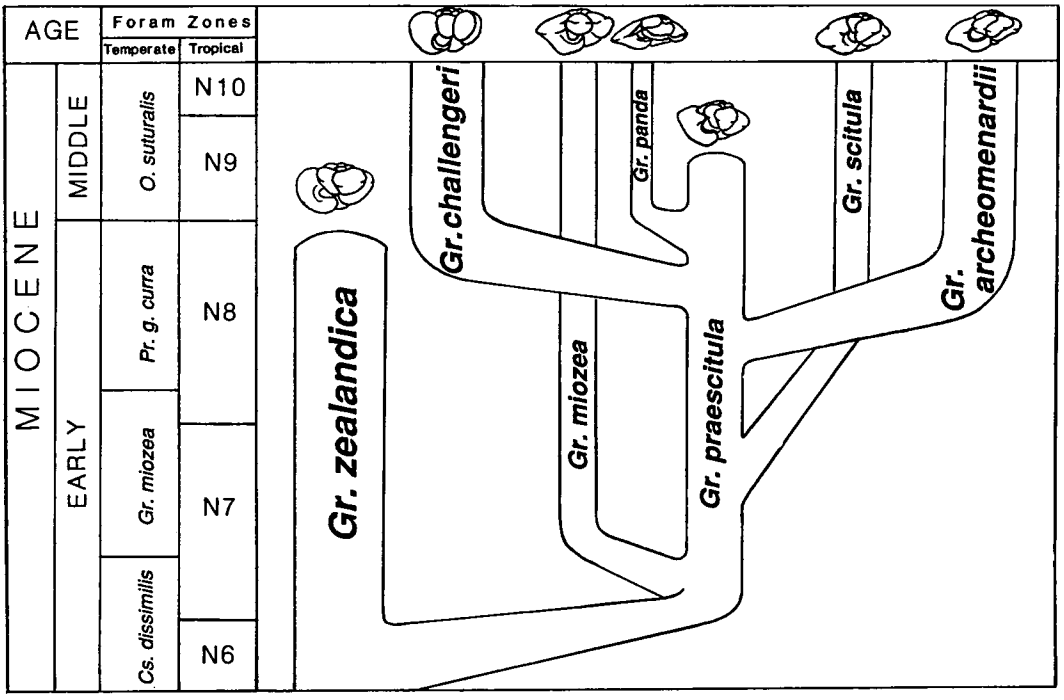

FIG. 2. Phylogenetic hypothesis relating named species of *Globorotalia* (*Gr.*) (from Kennett and Srinivasan [1983]). Note that the derivative species do not constitute a single evolutionary series; each is presumed to represent an independent direction of morphological variation (here presented in three dimensions). *Cs.* = *Catapsydrax, Gr.* = *Globorotalia, Pr. g.* = *Praeorbulina glomerosa,* and *O.* = *Orbulina*; N6–N10 refer to tropical foraminiferal zones 6–10.

andica and *G. praescitula* gave rise, over approximately six million years, to five named species (Fig. 2). For these *Globorotalia,* we can examine changes in the variation of sample populations as morphospecies appear and disappear.

The diagram in Figure 2 exemplifies the simple model of discrete morphological diversity we outlined above. This diagram of ancestral–descendant relationships implies that individual variation is organized into discrete clusters typified by the figured species "type." Yet, actual data on the relationship between individual variation and the higher-order structure of that variation are omitted. We can inquire, then, whether in reality the variation consists of distinct morphospecies as represented in this diagram.

We sampled Deep Sea Drilling Project site 593, which is located between New Zealand and Australia in the southwest Pacific (40°S latitude, 167°E longitude). We used four samples from this site, as indicated in Figure 3; 20–30 individuals of all *Globorotalia* larger than 0.125 mm in diameter with complete, nonkummerform final chambers were randomly chosen from each DSDP sample. Figure 3 also shows the ranges of named forms as presented in the initial report of the Deep Sea Drilling Project (Jenkins and Srinivasan, 1985).

To examine the structure of morphological variation and its relationship with current taxonomy, individuals included in the study were drawn from an "experimental taxon" designed to impose a minimum of preconceptions about that structure on the study samples (Scott, 1966). We have included in the study all individuals of *Globorotalia* present in the samples without reference to species-level designations. From these samples, we can test the structure of variation between and within previously designated species of this genus, but not between this and other genera.

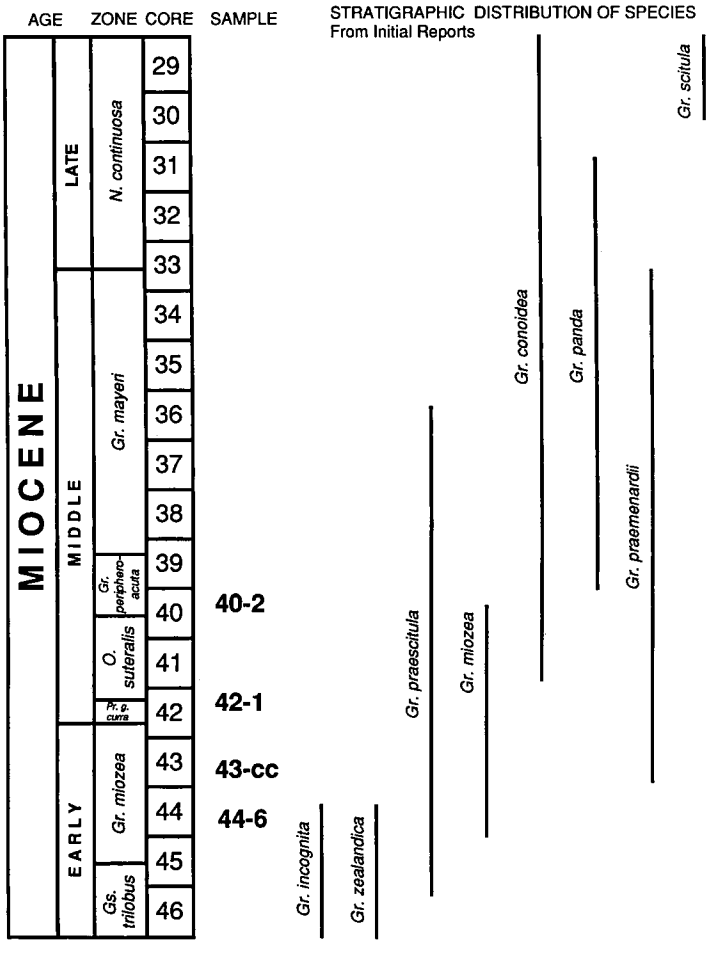

FIG. 3. Stratigraphic section of site 593 showing the position of the samples used in this study: 44-6, 43-cc, 42-1, and 40-2. Range chart of named species is taken from the initial reports of the Deep Sea Drilling Project (Jenkins and Srinivasan, 1985). *Gs.* = *Globigerinoides, Gr.* = *Globorotalia, Pr. g.* = *Praeorbulina glomerosa, O.* = *Orbulina,* and *N.* = *Neogloboquadrina.*

Measurement Techniques

Each numbered individual was mounted on the head of an entomology pin with the axis of coiling perpendicular to the pin axis and the spiral, umbilical, and apertural views free for measurement. The pin was then placed in a pin vise mounted on a universal stage, which was mounted on a vertically placed rotating microscope stage (Tabachnick and Fisher, unpubl.). Specimens could thereby be oriented consistently in a series of views at 90°. Camera-lucida drawings were made of each individual in the spiral, apertural, and umbilical views. Landmark points and outline shapes of the chambers were digitized manually from the drawings.

These forams consist of a series of chambers arranged along an equiangular spiral (see Fig. 4). There are three major components of morphological variation: the parameters of the spiral geometry, the outline shape of the chambers, and the shape of the apertures. Most characters used in the traditional qualitative taxonomy can be decomposed into one or more of these morphological components (Stainforth et al., 1975). The subset of morphological characters measured was based on a qualitative assessment of the magnitude of variation of all characters.

The apertural view of final chamber outline and the aperture shape were modeled

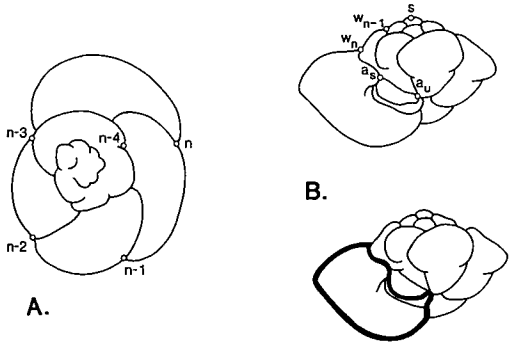

FIG. 4. Landmark and outline data collected on individuals of *Globorotalia*. Small circles represent landmarks used in this study. A) Spiral view: n = intersection of ultimate and penultimate chambers; n-1–4 = intersection of each chamber with the preceding chamber, in sequence. B) Apertural view: s = tip of spiral axis; w_n = intersection of ultimate and penultimate whorls; w_{n-1} = intersection of penultimate and antepenultimate whorls; a_s = spiral end of aperture; a_u = umbilical end of aperture; heavy line = continuous outline of chamber shape.

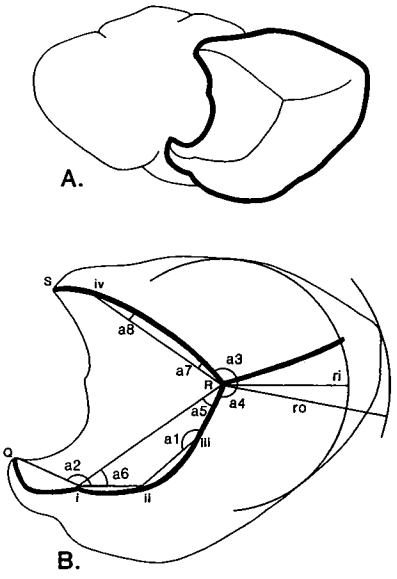

FIG. 5. A) Medial axis for a typical ultimate chamber in apertural view; B) measurements taken on the medial axis. Angles: a_1 and a_2 = curvature of primary axis; a_3 and a_4 = branch angles; a_5 and a_6 = bowing of primary axis; a_7 and a_8 = bowing of upper branch. Points i, ii, and iii are quartiles of arc QR; point iv is the first quartile of arc SR. Radii: r_i = radius of a circle that constructs the triple point; r_o = radius of the circle on the same center that encloses the furthest extension of the shoulder. For multivariate analysis, we use the shape variable $\log(r_i/r_o)$.

together as a single closed curve measured by the technique of medial axes (Bookstein et al., 1985 sect. 4.1). Two-point registration of sets of landmarks in the spiral and apertural views (Bookstein et al., 1985 appendix 4; Bookstein, 1986*b*, 1990) measured the relative arrangement of the chambers. There resulted a description of test variation in three separate morphological spaces. These three groups of measurements are illustrated in Figure 4. The technique of partial least squares (Bookstein, 1982, 1986*a*; Sampson et al., 1989) summarizes the covariation among the three morphological spaces. This paper presents results of analyses of these three morphological spaces separately and then together.

A common approach in multivariate morphometrics has been to measure a number of morphological parameters and then to extract principal components of the entire pool of parameters. When there are subgroupings among the morphological parameters used in an analysis, pooling those parameters obscures the covariation within each group of variables and does not allow quantification of the relationships among the subgroups of variables at all. The sets of measurements used in this study comprise three analytically incommensurate groups: landmarks measured as (*x*, *y*) coordinates projected into two perpendicular planes together with angular measures of curve shape. We therefore construct and analyze three separate morphological spaces, one for each group of variables, before using partial least squares to examine the relationships among them.

The Medial Axis.—The medial axis (Blum, 1973) is a summary of a closed curve by a curve running "up the middle" of the form: the curve of centers of circles that are tangent to the shape in two or more places. Triple points of the medial axis, centers of circles that touch the shape in three places, correspond to bifurcations of the forms into "lobes."

In planktonic foraminifera the "generating curve" (sensu Raup, 1966) of the spiral form is the shape of the chambers (Arnold, 1983). In our initial analysis, we computed medial axes of the final chamber in the apertural view (Fig. 5A), as chamber shape is most variable in this view.

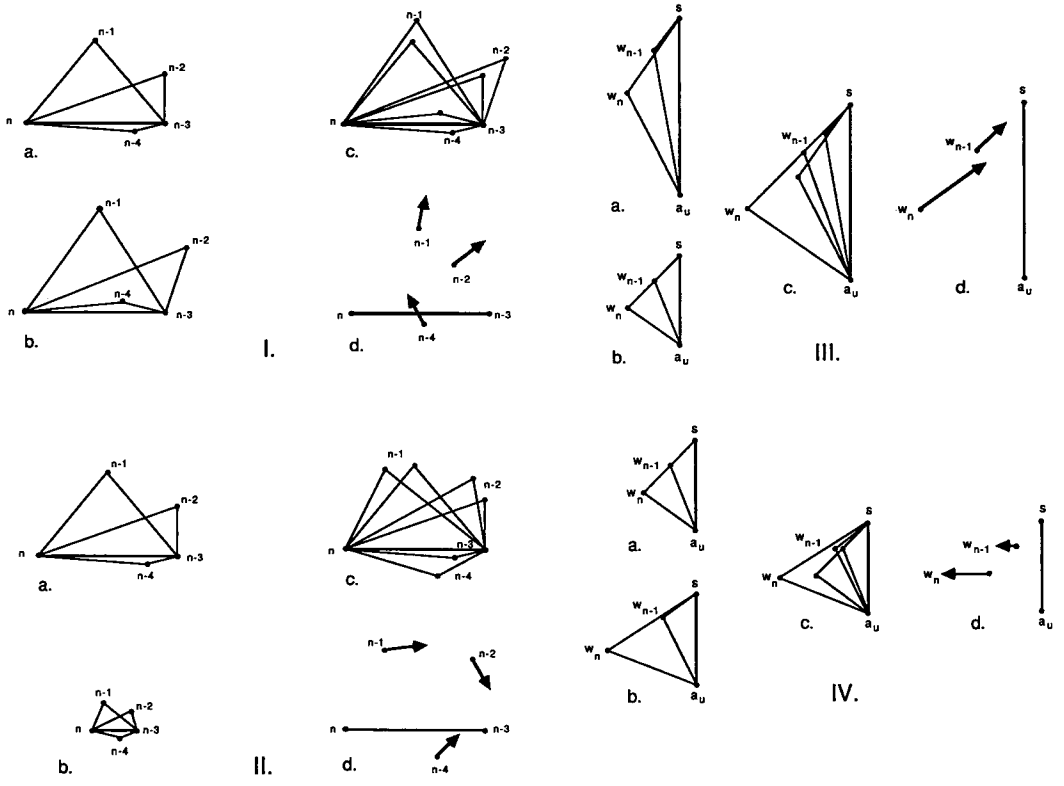

FIG. 6. Vector diagrams produced by a change in each of three spiral parameters. I. Change in Θ: a) Θ = 70°; b) Θ = 80°; c) a and b set to the baseline from n to n-3; d) vectors of landmark movement from a to b. II. Change in spiral-view r: a) $r = 1.5$; b) $r = 1.2$; c) a and b set to the baseline from n to n-3; d) vectors of landmark movement from b to a. III. Change in t: a) $t = 2$; b) $t = 1.5$; c) a and b set to the baseline from s to a_u; d) vectors of landmark movement from b to a. IV. Change in r in apertural view: a) $r = 1.5$; b) $r = 2$; c) a and b set to the baseline from s to a_u; d) vectors of landmark movement from a to b.

The medial-axis analysis reorganizes the information in a curved form without any reduction (Blum, 1973); differences in curve shape among forms may then be measured directly on the medial axis. We used two types of measures of the medial axis: a set of angles measured along the axis and the ratio between two radii, used as a measure of peripheral rounding. Figure 5B illustrates these measurements.

Two-Point Registration of Landmarks.— The shape of a configuration of three or more landmarks can be analyzed by selecting two as a "baseline" fixed in both position and scale. After standardization, all other landmarks may be considered to be "moving" with respect to these two, as illustrated in Figure 6. Each landmark is designated by an (x, y) coordinate pair, called "shape coordinates," relative to the baseline. Multivariate analysis of shape coordinates results in a diagram of vectors of change or correlated effect at each landmark. Properly interpreted, this sort of statistical analysis of effects is nearly independent of the choice of baseline (Bookstein, 1986*b*, 1990).

Most techniques utilizing distance measures confound shape and size variation, which must then be separated in the statistical analysis. Because of the standardization of baselines between forms, the two-point registration allows analysis of shape alone without reference to size information. A size variable can be generated from the same landmarks before standardization for the analysis of size and shape covariance (Bookstein et al., 1985 appendix 4). Correlation of centroid size (the summed squared distance from the centroid) and shape rigorously tests for allometry under a

model for circular measurement noise (Bookstein, 1986*b*, 1988). We have used centroid size as our size variable.

Arnold (1983) used three of Raup's (1966) spiral parameters to describe the spiral view of the foraminiferal test: Θ, the angle at which chambers are added; w, the rate of change in chamber radius; and d, the distance of the chambers from the spiral axis. We reduce these to two measures, Θ and r (the expansion rate, incorporating both change in chamber radius and the distance of the chamber from the spiral axis). We also consider two spiral parameters in apertural view: t (the rate of translation down the spiral axis) and, again, r. The landmarks used here incorporate the spiral parameters in both the spiral and the apertural views. That is, if landmarks are taken at points along a spiral, the deformation of shape coordinates incorporates differences in the spiral parameters as well as other morphological changes. Figure 6 illustrates changes in shape coordinates and the resultant vector diagrams for changes in each of three spiral parameters at values typical of *Globorotalia.*

Most morphometric studies involve measurements of predefined parameters of abstract geometry, such as lengths or spiral parameters, or simulations of ideal morphospaces based on varying those parameters. Yet, changes in abstract parameters may not represent most of the actual morphological transformation from one form to another; we cannot know in advance whether these abstract parameters are appropriate for a particular shape comparison. In our approach, the principal factors of morphological transformation are extracted first and then examined to discover whether they are similar to changes in familiar parameters of abstract geometry. This strategy allows us to evaluate the importance of such parameters in characterizing or generating the variation.

Results

The Morphospaces Separately

In separate principal-components analyses, morphological spaces were constructed for the medial axis of the final chamber, the landmark locations in the apertural view, and the landmark locations in the spiral view. Each analysis generated major "dimensions" of variation in the samples and permitted us to examine the arrangement of individuals in the morphological spaces constructed.

Chamber-Shape Morphospace.—We measured eight angular variables upon the medial axis of chamber shape and one ratio (see Fig. 5). Principal-components analysis was carried out on the correlation matrix of the angles together with the log-transformed ratio. The first three principal components of this chamber shape space account for 81% of the variance in the pooled sample (Table 1A). The first component (PC-1, which accounts for 49% of the variance) is a factor for curving of the primary axis (a_1 decreases as a_5 and a_6 increase) and the development of the peripheral "shoulder" indicated by decreases in the radius ratio. Changes in branch angle (a_3 and a_4) are correlated with this primary axis straightening. The second principal component (PC-2, which accounts for 21% of the variance) suggests a factor for change in curvature of the upper branch of the axis (change in a_7 and a_8). The third component (PC-3, which accounts for 11% of the variance) mainly describes the lowest part of the primary axis by the angle a_2. Effects of changes in each of these principal components are illustrated in Figure 7.

The scatter plot of individuals upon the first pair of principal components (Fig. 8) is interesting. Variation in PC-2 has a different morphological meaning when PC-1 is large from that when PC-1 is small. For low values of PC-1 (Fig. 7B), the change in a_7 and a_8 describes the curvature of the upper branch of the axis. However, for high values of PC-1 (Fig. 7C), the change in curvature indicated by PC-2 is the result of migration of the central triple point of this curve. (The morphs shown in Fig. 7 are specimens from extreme ends of the sample-data distributions.)

This statistical structure is very robust as the number of variables representing chamber shape increases or decreases and as the number of individuals in the analysis increases. Although there is continuous variation among all the morphologies in the samples, this variation is not continuous in all directions in the morphospace. There are no morphologies with medial values of PC-1

TABLE 1. Principal components of the three morphological spaces for the Deep Sea Drilling Project (DSDP) sample data: A) chamber-shape space (see Fig. 7); B) apertural-view morphospace (see Fig. 9; baseline points are s and a_u); C) spiral-view morphospace (see Fig. 10; baseline points are n and n-3). Principal components were computed using correlation matrices.

A. Chamber shape: Character	PC-1	PC-2	PC-3
Angles			
a_1	−0.39	0.19	0.11
a_2	−0.17	0.20	−0.82
a_3	−0.36	0.10	0.31
a_4	0.42	0.05	−0.24
a_5	0.42	−0.21	−0.01
a_6	0.37	−0.14	0.33
a_7	0.18	0.65	0.16
a_8	0.17	0.65	0.11
ln(radius ratio)	−0.36	−0.09	0.13
Percentage of variation explained:	49%	21%	11%

B. Apertural view morphology: Landmark	Coordinate	PC-1	PC-2
w_{n-1}	x	0.45	0.13
	y	−0.48	0.14
w_n	x	0.50	0.13
	y	−0.43	0.30
a_u	x	0.34	0.52
	y	−0.14	0.77
Percentage of variation explained:		52%	21%

C. Spiral-view morphology Landmark	Coordinate	PC-1	PC-2
n-1	x	−0.06	−0.85
	y	0.51	−0.07
n-2	x	0.43	0.33
	y	0.45	0.35
n-4	x	−0.28	0.21
	y	0.52	0.05
Percentage of variation explained:		50%	22%

and medial-to-low values of PC-2, creating an upside-down v-shaped scatter. The variation we find is continuous in some directions but discontinuous in others; while the morphospace of chamber shape has unoccupied areas within the scatter, it is not composed of discrete groups. This result is notable, as the samples contain morphologies that would be attributed to several species. We will return to this issue below.

The apparent evenness of "coverage" of a parameter space by a sample varies, in general, when those parameters are subjected to nonlinear transformations among themselves. The heterogeneity of these scatter plots is not attributable to this sort of artifact. Different sets of shape coordinates that exhaust the same set of landmark locations vary only by linear fractional transformations (Bookstein, 1986*b*) and so can only modestly shift the pattern of modes and antimodes and the directions of components in a shape-coordinate morphospace. The same is true of a sufficiently dense set of angles. Linearity is not assumed either for the generation of separate morphospaces by principal-components analysis or for studying their associations by the partial-least-squares technique; instead, linearity is constructed by summing simple regressions over many different degrees of curvature. Thus, we believe that the structure of the scatter in Figure 8 would be likely to be found by any other measurement scheme of equivalent coverage.

Apertural Morphospace.—The five landmarks of the apertural view (Fig. 4B) result in an apertural morphospace of six shape coordinates. Each principal component of the correlation matrix of the shape coordinates is equivalent to the list of x and y components for three vectors of coordinated landmark movement. (We analyze the shape coordinates in terms of their correlations for consistency with the analysis of chamber shape and to simplify the report of the findings of the partial-least-squares analysis.) The first two principal components explain 73% of the variance in those vectors (Table 1B). Figure 9 presents vector diagrams of the components and landmark configurations for sample individuals representing extreme values of the components.

The first principal component, which explains 52% of the total variance, primarily represents variation in coiling of the chambers around the axis; it includes changes in t (the rate of translation down the axis), r (the expansion rate; compare Fig. 9A to Fig. 6 IIId and IVd), and the tilt of the chambers relative to the axis. Variation in chamber tilt affects the angle between the aperture and the spiral axis, as shown by variation in a_s, the spiral end of the aperture. The axis we located from s (the spire tip) to a_u (the

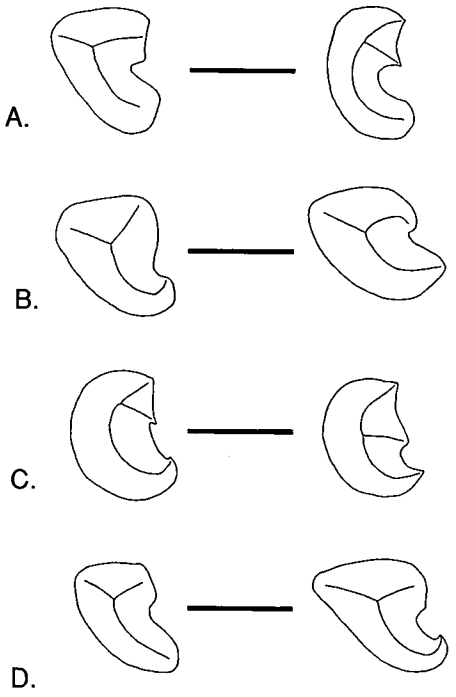

FIG. 7. Principal components of the chamber-shape space. Each pair of medial-axis diagrams exemplifies shapes having extreme values on that component. The illustrated specimens are from the data samples. A) PC-1; B) PC-2 for low values of PC-1; C) PC-2 for high values of PC-1; D) PC-3.

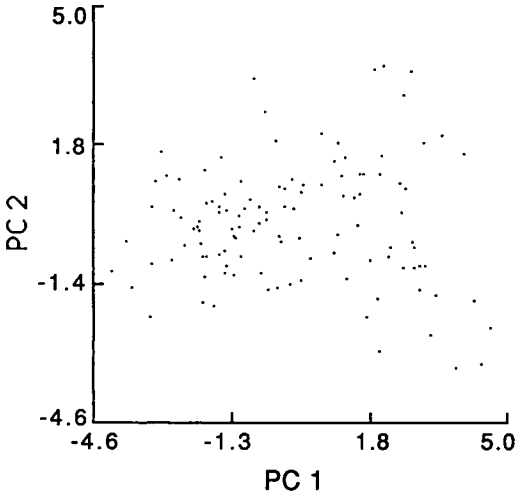

FIG. 8. Scatter plot of individuals in the space of the first two chamber-shape principal components.

umbilical end of the aperture) is an estimate of the spiral axis. PC-1 also reflects variation in the accuracy of this estimate as a_u migrates towards s. The second principal component, representing 21% of the variance, corresponds to changing the width of the aperture. A scatter plot of the first two principal-component scores for this apertural-landmark morphospace shows continuous variation that is roughly elliptical and without apparent gaps, although there are a few isolated outlying individuals (Fig. 10A).

Spiral Morphospace.—The five landmarks of the spiral view result in a spiral morphospace again having six shape coordinates. The first two principal components account for 72% of the variance of these six shape coordinates (Table 1C). Vector diagrams for these components are shown in Figure 11, along with landmark configurations for sample individuals representing extreme values of the components. The first principal component, which explains 50% of total variance, corresponds to variation in Θ, the angle of increment of the spiral. This dominance of Θ is very robust, persisting through incremental analyses from 30 to 112 individuals, at a single stratigraphic level, and in analyses progressively adding samples up the section. The second principal component, comprising 22% of the variance, corresponds to changes in the spiral parameter r (rate of increase from the spiral center). The scatter of these principal component scores from the spiral view is primarily continuous in all directions, with a few outlying individuals (Fig. 10B).

The emergence of two of the spiral parameters as separate principal components of the landmark data is remarkable; we did not set out to measure change in the spiral parameters as separate components. In effect, the data themselves are instructing us to measure these parameters.

Relationships Among the Morphospaces

Partial Least Squares.—Partial-least-squares analysis (Bookstein, 1982, 1986*a*; Sampson et al., 1989) is a method for modeling a correlation matrix relating two or more sets of variables. We apply it three times to compare our morphologic spaces in pairs. In two-block partial-least-squares analysis, one factor or latent variable is extracted for each block of variables to be

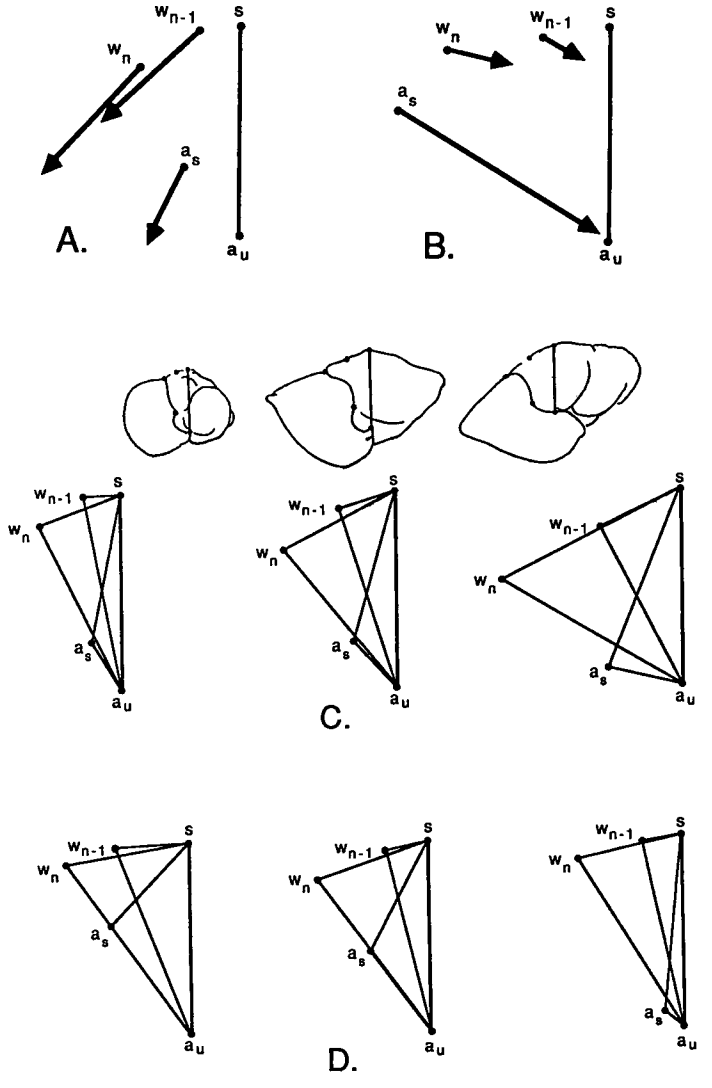

FIG. 9. Vector diagrams for the apertural-landmark shape coordinates showing the movement of landmarks relative to fixed baselines: A) PC-1 (reflects change in t and aperture angle); B) PC-2 (change in aperture width); C) landmarks measured on sample individuals shown, representing mean and extreme values for PC-1 (PC-2 constant); D) landmarks measured on sample individuals (not shown) representing mean and extreme values for PC-2 (PC-1 constant).

compared such that the pair of latent variables together gives the best rank-one fit to all the interblock correlations. Partial-least-squares analysis may be thought of as a compromise between regression analysis and factor analysis. In this application, our goal is to explain the importance of one morphospace for another using the minimal number of factors. The correlation between each variable of one block and the latent variable of the other block is its associated coefficient in the latent variable of its own block. This coefficient expresses the "salience" of the variable in accounting for the other block. The pairs of latent variables extracted by partial least squares are those factors of morphology found to be most parsimonious for explaining correlations between morphospaces. In contrast, conventional canonical-correlation analysis finds the "best-correlating" linear combinations, the coefficients of which cannot be inter-

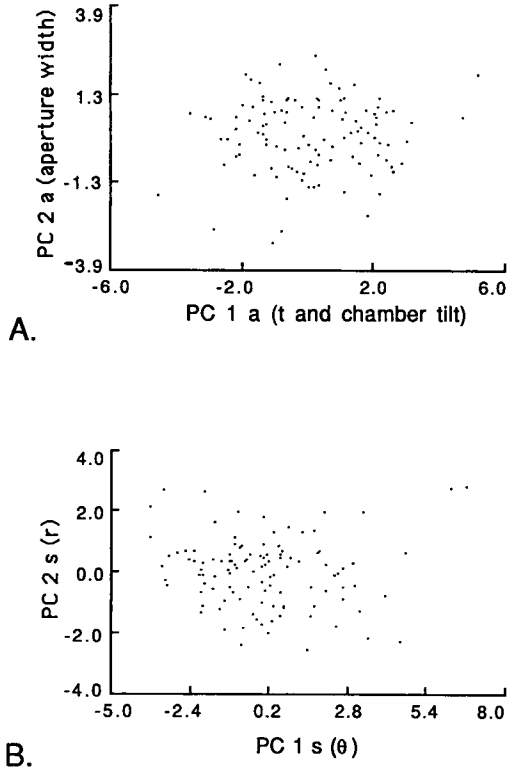

FIG. 10. Scatter plot of individuals in the spaces of the first two apertural principal components and the first two spiral principal components: A) apertural view (indicated by "a"); B) spiral view (indicated by "s").

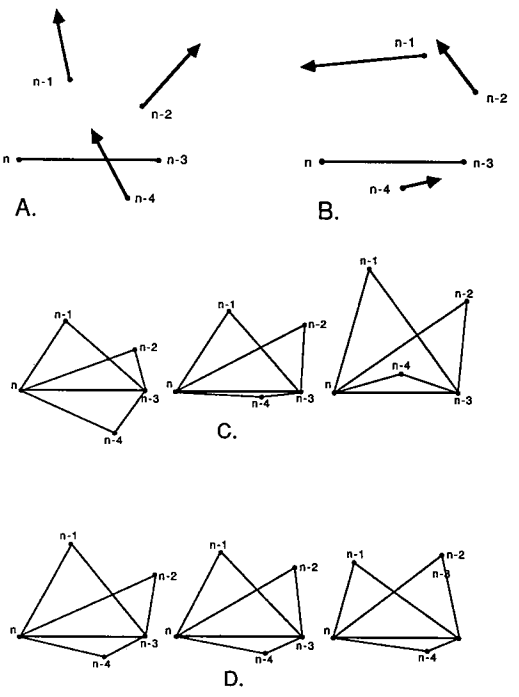

FIG. 11. Vector diagrams for the spiral-landmark shape coordinates showing the movement of landmarks relative to fixed baselines: A) PC-1 (change in θ); B) PC-2 (change in *r*); C) landmarks measured on sample individuals representing mean and extreme values for PC-1 (PC-2 constant); D) landmarks measured on sample individuals representing mean and extreme values for PC-2 (PC-1 constant).

preted in this way (Reyment et al., 1988). In essence, canonical-correlation analysis produces pairs of scores having the highest correlation, while partial-least-squares analysis produces pairs having the highest covariance.

Chamber Shape and Apertural Landmarks.—The component that provides the best explanation of variance in shape coordinates of apertural landmarks also best explains the correlation between the apertural landmarks and chamber shape (Table 2A). The factor of chamber shape correlated with the apertural landmarks is very similar to the first component of chamber-shape variation, differing only in the weights of the radius ratio and upper-branch curvature. The correlation between these factors (i.e., the correlation between the first principal component of the apertural landmark space and the straightening of the primary medial axis) is −0.49, which is large enough to be interesting. This correlation reflects a tendency for the more angular chambers to have high translation rates and to be tilted relative to the spiral axis (Fig. 12). There is no reason a priori for partial least squares to settle on principal components: this finding is an aspect of the data, not an artifact of the method. In fact, the within-block correlation matrices underlying principal-components analysis are ignored completely in partial-least-squares analysis.

Relative movement of the points that are shared between these two measurement systems could result in some of the observed covariation between them. However, the latent vectors found for deformation of apertural landmarks that are correlated with changes in chamber shape are not the same as the vectors of shape change that would result from changes in these shared points alone.

Apertural-View Landmarks and Spiral-

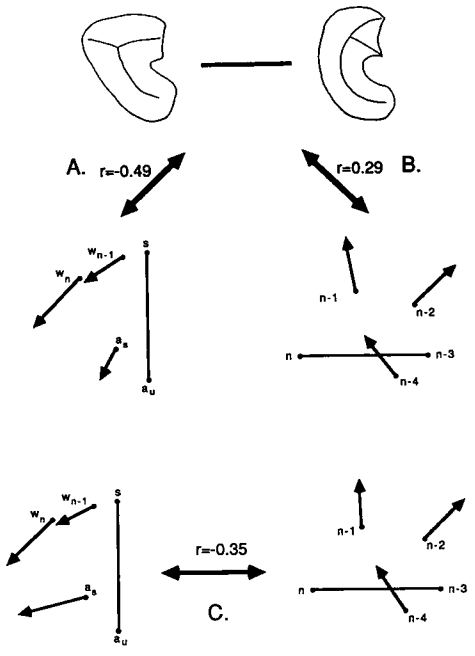

FIG. 12. Latent variables of between-space correlation: A) apertural morphospace and chamber shape ($r = -0.49$); B) spiral morphospace and chamber shape ($r = 0.29$); C) apertural morphospace and spiral morphospace ($r = -0.35$).

View Landmarks.—Again we find that the principal components of the separate morphospaces also serve as the factors explaining covariation between the spaces (Table 2B). Change in Θ (spiral view) is the best summary of the spiral view for explaining the apertural-view variation. The apertural factor it accounts for combines effects of the first and second principal components. Change in aperture width has the largest salience for this correlation, but changes in t and tilt contribute some effect (Fig. 12). The partial-least-squares correlation between the morphospaces is -0.35, which is significant but not strongly so. This correlation represents the extent of three-dimensional variation in spiral parameters beyond that accessible from the separate two-dimensional views.

Spiral Landmarks and Chamber Shape.—We find once again that change in Θ is the best summary of spiral-view variation for explaining chamber-shape variation (Table 2C). The chamber-shape factor it accounts for is similar to the chamber-shape factor that is correlated with the apertural landmarks (Fig. 12). The correlation between the

TABLE 2. Pairs of latent variables from partial-least-squares analysis (see Fig. 12). The salience of each coordinate is its correlation with the latent variable of the other block of variables, not with the latent variable of its own block. A) Chamber shape and spiral view ($r = 0.29$); B) chamber shape and apertural view ($r = -0.49$); C) spiral view and apertural view ($r = -0.35$).

A.		B.		C.	
Character or landmark coordinate	Latent-variable coefficient	Character or landmark coordinate	Latent-variable coefficient	Character or landmark coordinate	Latent-variable coefficient
Chamber shape:		Chamber shape:		Spiral view:	
a_1	−0.12	a_1	−0.16	n-1 x	−0.00
a_2	0.09	a_2	0.06	n-1 y	0.26
a_3	−0.21	a_3	−0.17	n-2 x	0.28
a_4	0.23	a_4	0.19	n-2 y	0.22
a_5	0.11	a_5	0.14	n-4 x	−0.15
a_6	0.06	a_6	0.11	n-4 y	0.26
a_7	0.16	a_7	0.17		
a_8	0.20	a_8	0.31		
ln(radius ratio)	−0.30	ln(radius ratio)	−0.30		
Spiral view:		Apertural view:		Apertural view:	
n-1 x	−0.07	w_{n-1} x	0.16	w_{n-1} x	0.09
n-1 y	0.29	w_{n-1} y	−0.28	w_{n-1} y	−0.25
n-2 x	0.24	w_n x	0.31	w_n x	0.27
n-2 y	0.24	w_n y	−0.33	w_n y	−0.31
n-4 x	−0.25	a_s x	0.15	a_s x	0.13
n-4 y	0.22	a_s y	−0.05	a_s y	−0.41

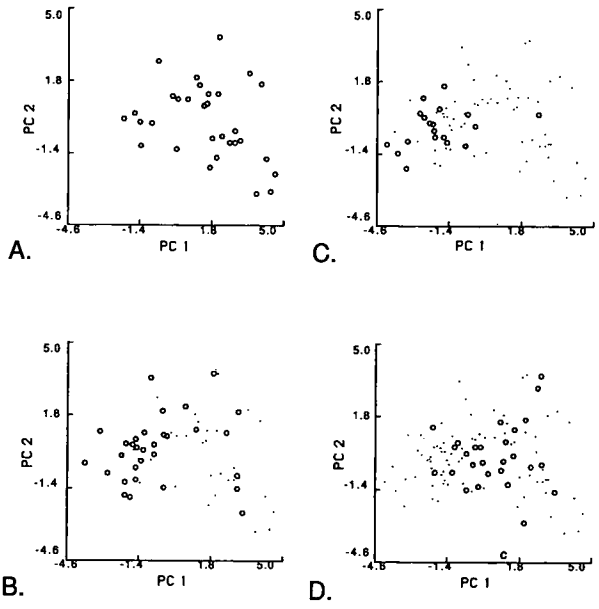

FIG. 13. Distribution of stratigraphic samples in the chamber-shape morphospace. For successive samples, the individuals of that sample are designated by open circles, and the individuals of all previous samples are designated by dots. A) 44-6 (oldest sample); B) 43-cc; C) 42-1; D) 40-2 (youngest sample). For the stratigraphic position of the samples see Figure 3.

factors is fairly weak ($r = 0.29$), but this relationship between chamber shape and parameters that are functions of Θ (such as the number of chambers in the final whorl) is often utilized in qualitative taxonomy.

Size and Shape.—The correlation between size and the variables of chamber shape is moderate ($r = 0.25$). This primarily reflects some tendency for rounded chambers to be small. There is no correlation between size and the principal components of either set of landmarks. Although shape and size are both highly variable, covariation between shape and size is not an important aspect of these data.

Stratigraphic Distribution of the Samples

Figures 13 and 14 show scatter plots for the four samples as in the chamber-shape morphospace and the morphospace of landmarks in apertural view. Clearly, it is in the morphological space of chamber shape that most sorting of stratigraphic samples occurs (Fig. 13); there is less sorting out of stratigraphic samples in the space of apertural landmarks (Fig. 14), and there appears to be none in the space of spiral landmarks (not shown). Morphological variation shows the most structure in the chamber-shape space, which also changes stratigraphically. Scott (1980) showed that much of the discrimination involved in foraminiferal taxonomy is based on the test outline. Although that outline would appear to be a composite of chamber-shape and spiral parameters, our data for *Globorotalia* suggest that it is mainly chamber shape that underlies the utility of the test outline as a discriminator.

In the space of chamber shape, for the four stratigraphic samples in the present study (see Fig. 3), the centroid of sample 44-6 is significantly different from those of samples 43-cc and 42-1 (see Fig. 13); sample 44-6 dominates the high end of PC-1. The structure of this morphospace is both morphological and stratigraphic: occupation of morphospace moves along PC-1 as the stratigraphic position of the samples increases. The fourth sample in the sequence, 40-2, is positioned over the middle of the scatter, partially filling in the upside-down v. Extensive stratigraphic sampling will be required to delimit the temporal persistence of these changes in occupied morphospace.

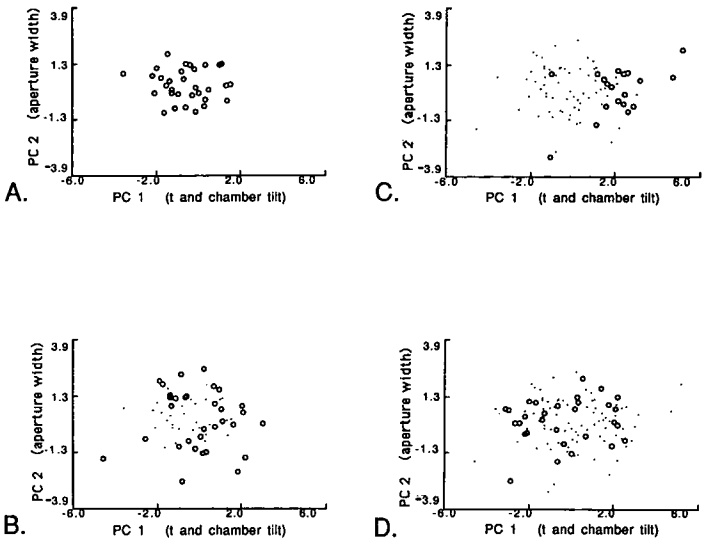

FIG. 14. Distribution of stratigraphic samples in the apertural morphospace. For successive samples, the individuals of that sample are designated by open circles, and the individuals of all previous samples are designated by dots. A) 44-6 (oldest sample); B) 43-cc; C) 42-1; D) 40-2 (youngest sample). For the stratigraphic position of the samples see Figure 3.

In the apertural morphospace, there is some sorting of samples (Fig. 14). The centroid of sample 42-1 is significantly different from those of all the other samples. Of course, this may reflect only a temporary response to environmental change.

Named Species

To examine the location of named species in these morphospaces, we can apply our measurements to published photographs of foraminifera. We have done this for *Globorotalia zealandica, G. praescitula, G. scitula, G. miozea, G. archeomenardii, G. panda,* and *G. challengeri,* using photographs of the species taken from Kennett and Srinivasan (1983). We ran principal-components analyses for the three sets of variables on the named specimens. Table 3 lists the results of these analyses.

The loadings of the principal components of chamber shape for the named individuals resemble those from our original analysis, although the separation of upper- from lower-axis curvature is not as clear. The components of the spiral-view landmark morphospace are also similar. Those for the apertural-view morphospace show some similarities to our original components but also some differences. PC-1 primarily reflects variation in coiling of the chambers around the axis, but with some correlated changes in aperture; PC-2 reflects some change in apertural-view morphology, but also a change in spiral parameters expressed between the spiral axis and the penultimate whorl that is not correlated with change in the ultimate whorl. These differences might result from the limited number of individuals (seven) represented by the named forms. Except for these minor deviations, the parameters that we have measured capture most of the variation perceived by previous workers and represented by the application of species names.

We can also examine the location of the named specimens in our three morphospaces. Figure 15 shows the location of specimens of the named species in each morphospace. Although they fall in different areas of the morphospaces, there is, by and large, continuous variation among them. With a few exceptions, the named specimens fall within the spaces occupied by the scatters from site 593 of the Deep Sea Drilling Project. *G. archeomenardii* occurs in an area of the apertural morphospace that is otherwise unoccupied, and *G. scitula* occurs in an area of the spiral morphospace that is otherwise unoccupied. Such deviations in-

dicate morphological variation not present at the stratigraphic and geographic positions of the four drilling-site samples. In each case, the deviation is limited to only one of the three morphological spaces. For example, the value of *r* of the photographed specimen of *G. scitula* is not present in the site-593 samples, but the chamber shape associated with that named morphology is present.

We can evaluate phylogenies of named forms in light of these results. In the chamber-shape space, *G. zealandica* is in the area with high values of PC-1, *G. challengeri* and *G. praescitula* are in areas with progressively lower values of PC-1, and the other four species are in areas with low values of PC-1. There is also a stratigraphic pattern: the *G. zealandica* and *G. praescitula* areas of the space were occupied first, followed by gradual, simultaneous expansion into the spaces corresponding to the other named species. This finding is consistent with the interpretation of *G. zealandica* as the ancestor of the other species.

Discussion

A common assumption in evolutionary theory is that of discrete species. Yet discontinuity is not always the pre-eminent aspect of organic diversity, especially for taxa with facultative sexual reproduction, such as protists and plants. The complex nature of organic diversity requires that we explore the "delicate interplay" (Arnol'd, 1986) between continuity and discontinuity at the outset of any quantitative analysis of that diversity.

Deviations from discrete distributions may be temporally stable (Endler, 1977). Special terms such as "hybrid zone," "cline," or "Rassenkreis" are used to designate these types of patterns. Rather than relying on categorizations of types of diversity pattern by special names, it would be useful to compare all possible patterns within a single, quantitative, descriptive system. It is also important to describe the diversity pattern of individual organisms at a single time (synchronic diversity) using the same language as that used for the pattern through time (diachronic diversity), and to describe the variation at a single location using the same language as for geographic variation. The analysis of probability distributions of individual organisms in character space, whether those characters are behavioral, morphological or ecological, supplies such a language. In this way we go beyond asking whether or not the observed variation represents gap-bounded groups and ask instead what the structure of variation appears to be. The approach we have used in this study will ultimately support such comparisons.

The pattern of morphological diversity of these foraminifera in morphological space is complicated. Just as we find no simple

TABLE 3. Principal components of the three morphological spaces for seven named species exemplars from Kennett and Srinivasan (1983): A) chamber-shape space; B) apertural-view morphospace (baseline points are s and a_u); C) spiral-view morphospace (baseline points are n and n-3). Principal components were computed using correlation matrices.

A. Chamber shape: Character	PC-1	PC-2	PC-3
Angles			
a_1	−0.41	−0.03	0.09
a_2	−0.03	0.49	−0.68
a_3	−0.34	0.12	−0.41
a_4	0.41	−0.15	0.15
a_5	0.41	−0.01	−0.11
a_6	0.40	−0.19	−0.22
a_7	0.25	0.54	0.08
a_8	0.24	0.55	0.36
ln(radius ratio)	−0.33	0.31	0.40
Percentage of variation explained:	62%	19%	12%

B. Apertural-view morphology: Landmark	Coordinate	PC-1	PC-2
w_{n-1}	*x*	0.20	−0.60
	y	−0.38	0.53
w_n	*x*	0.49	0.25
	y	−0.54	−0.08
a_u	*x*	0.14	0.53
	y	−0.51	−0.14
Percentage of variation explained:		49%	33%

C. Spiral-view morphology: Landmark	Coordinate	PC-1	PC-2
n-1	*x*	0.32	0.58
	y	0.49	0.15
n-2	*x*	0.44	0.34
	y	0.41	−0.30
n-4	*x*	−0.29	0.62
	y	0.46	−0.23
Percentage of variation explained:		65%	25%

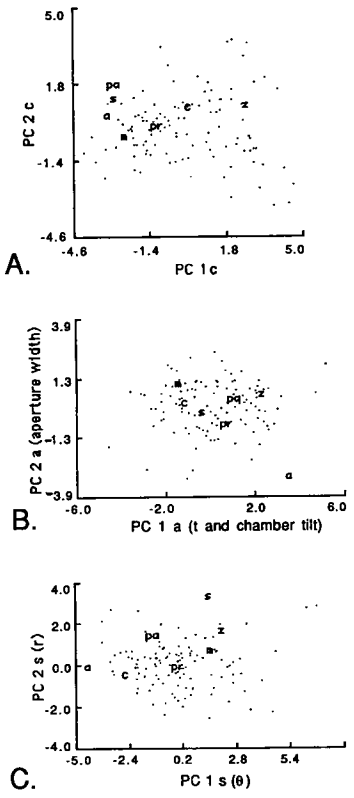

FIG. 15. Distribution of named-species exemplars of Kennett and Srinivasan (1983) in each of the morphospaces: z = *G. zealandica*; pr = *G. praescitula*; m = *G. miozea*; s = *G. scitula*; a = *G. archeomenardii*; pa = *G. panda*; c = *G. challengeri*. A) Chamber-shape morphospace (indicated by "c"); B) apertural-view morphospace (indicated by "a"); C) spiral-view morphospace (indicated by "s").

discrete groups, we also find no evidence for the branching of one entity into two or for gradual change of the central tendency of a single entity at the level of the named morphospecies. The measured pattern varies with the morphological variables involved. The spiral and apertural landmark spaces are both continuously occupied. The distribution of spiral-view parameters is not a function of stratigraphic position, while that of the apertural-view parameters does vary stratigraphically to some extent. Discontinuities occur in chamber-shape space (the most complex space), but there are no complete gaps. There are large changes in the area of chamber-shape space occupied as a function of stratigraphic position. Clearly the pattern of diversity for these data is other than one of discrete groups originating by splitting. Of course, more work will be necessary to discover the scale of persistence of these patterns, both stratigraphically and geographically.

The medial-axis description of chamber shape allows us to describe these shapes as coherent wholes. The most important component of variation of chamber shape is a general elongation and straightening of the body of the chamber. Elongation and increased angularity of the periphery are consequences of this general shape change (involving both chamber outline and apertural-view shape) and not the result of independent variation.

We have explicated the relationships among various aspects of shape, in particular the relationship between chamber-shape variation and the spiral parameters. We have also discovered the extent to which the spiral geometry accounts for morphological variation in these samples and how parameters measured in different views relate to each other. The strongest relationship is between chamber shape and coiling down the spiral axis. There is correlation between the angle of increment and chamber shape, but this is a far weaker relationship than the qualitative taxonomy suggests. Named individuals with distinct values for chamber shape and spiral parameters do not appear to be discrete entities in all spaces. In this situation, classifications that rely on both outline and spiral parameters must actually be emphasizing one set of parameters, as the other apparently cannot help in the sorting of individuals.

The pattern of individual variation in morphological space is relevant to questions of phylogeny, as well as to questions concerning the mode of evolution. One theory advanced in support of the sequence of named forms is that *G. zealandica* gave rise to *G. praescitula*, from which *G. miozea* and *G. scitula* split off (Srinivasan and Kennett, 1981). Another theory is that *G. miozea* split off from *G. zealandica*, with *G. praescitula* developing from *G. miozea* and, subsequently, developing into *G. scitula* (Keller, 1981). The relationship between the distribution of species names in the morphologic spaces and the stratigraphic ordering of those spaces suggests that, at Deep Sea Drilling

Project site 593, the *Globorotalia miozea* and *G. scitula* areas of morphological space were simultaneously occupied after the occupation of the *G. praescitula* area of space. If this pattern reflects the evolutionary first appearance of new forms and if the species are assumed to be discrete, the pattern we have found is consistent with the speciation series described by Srinivasan and Kennett (1981). It would be more accurate, however, to describe the evolutionary event as expansion into new space concomitant with a density shift. Discontinuities in the variation appear, but without the development of complete gaps. Areas of morphological space represented by these names are also occupied, vacated and reoccupied over a short stratigraphic interval. The species names, while useful as designations of areas within continuous distributions, do not seem to correspond to discrete gap-bounded parts of the variation. Hence, the appearance and disappearance of named forms cannot be taken to imply cladogenesis.

For studies of evolutionary rates that do not rely on identification of species in advance, one must first determine which changing aspect of the data will be considered. Modes of distributions and covariance structure could both be evolving. As in any other study of evolutionary rates, their changes must be considered in relationship to some variable that can be an explanation of the change, not simply relative to time (Bookstein, 1987, 1988). Supposing an exogenous covariate, such as δO^{18} (the ratio of heavy to light oxygen), is changing its mean in the vicinity of a mode in the distribution, then the (vector) regression coefficient of modal morphology on the covariate might be considered to represent the evolutionary rate of modal form with respect to the covariate. The absence of discrete clusters of morphologies does not preclude analysis of evolutionary mode or rate.

Conclusions

This study demonstrates the feasibility and utility of relatively complete descriptions of individual variation for microfossil data. While named morphospecies provide some information on the regions of morphospace occupied in particular samples, a description of individual variation is necessary to understand the actual diversity pattern. Such descriptions are particularly important for organisms that deviate significantly from the model of discrete morphospecies. At this scale of description, we can explicate the relationship between synchronic diversity and diachronic diversity using a single coherent descriptive language. As a result, we can discriminate among a variety of possible diversity patterns. Expansion of the geographic and stratigraphic range studied, as well as incorporation of isotope data, will allow us to describe the evolutionary relationships among these morphologies more rigorously than is presently possible.

We found that the spiral parameters of four fossil foraminifera samples vary roughly elliptically and that occupied regions of the spiral-parameter morphospaces do not vary much stratigraphically. In contrast, chamber-shape variation is continuous but not elliptical. Features of distributions in the morphospace beyond the elliptical are those that vary stratigraphically. The correlation between variation in spiral parameters and chamber shape is weaker than the qualitative taxonomy had led us to expect.

At Deep Sea Drilling Project site 593, areas of chamber-shape morphospace corresponding to named specimens of *Globorotalia zealandica* and *G. praescitula* predate areas of morphospace corresponding to *G. miozea, G. scitula,* and *G. archeomenardii* and so suggest that *G. zealandica* and *G. praescitula* are ancestral to the others. The stratigraphic changes in this lineage involve changes in the shape and position of occupied morphospace without the appearance of gaps in the variation. This fits neither a model of strict anagenesis nor one of strict cladogenesis.

Acknowledgments

We thank G. R. Smith for many stimulating discussions involved in the inception of this work and D. C. Fisher for generous technical advice and for constructing the measuring stage. G. R. Smith, J. A. Kitchell, D. J. Eernisse, and two anonymous reviewers provided helpful comments on the manuscript. An earlier version of this paper served as a chapter in R. E. Tabachnick's Ph.D. dissertation. The research was sup-

ported in part by NSF Grant BSR-8708563 to J. A. Kitchell and N. MacLeod. Development of the methods of analysis by shape coordinates was partially underwritten by USPHS Grant GM-37251.

Literature Cited

Arnold, A. J. 1983. Phyletic evolution in the *Globorotalia crassiformis* (Galloway and Wissler) lineage: A preliminary report. Paleobiology 9:390–397.

Arnol'd, V. I. 1986. Catastrophe Theory. [Translated from the Russian by G. S. Wasserman based on a translation by R. V. Thomas.] Springer-Verlag, Berlin, W. Ger.

Banner, F. T. 1982. A classification and introduction to the Globigerinacea, pp. 142–239. *In* F. T. Banner and A. R. Lord (eds.), Aspects of Micropaleontology. Allen and Unwin, London, U.K.

Blum, H. 1973. Biological shape and visual science. J. Theoret. Biol. 38:205–287.

Bookstein, F. L. 1982. The geometric meaning of soft modeling, with some generalizations, pp. 55–74. *In* H. Wold and K. Joreskog (eds.), Systems under Indirect Observation, Vol. II. Causality, Structure, Prediction. Elsevier, Amsterdam, Neth.

———. 1986*a*. The elements of latent variable models: A cautionary lecture, pp. 204–230. *In* M. E. Lamb (ed.), Advances in Developmental Psychology, Vol. 4. Erlbaum, Hillsdale, NJ.

———. 1986*b*. Size and shape spaces for landmark data in two dimensions. Stat. Sci. 1:181–242.

———. 1987. Random walk and the existence of evolutionary rates. Paleobiology 13:446–464.

———. 1988. Random walk and the biometrics of morphological characters. Evol. Biol. 23:369–398.

———. 1990. Morphometric Tools for Landmark Data: Geometry and Biology. Cambridge Univ. Press, N.Y. *In press.*

Bookstein, F., B. Chernoff, R. Elder, J. Humphries, G. Smith, and R. Strauss. 1985. Morphometrics in Evolutionary Biology: The Geometry of Size and Shape Change, with Examples from Fishes. Acad. Natural Sciences, Philadelphia, PA.

Bookstein, F. L., P. D. Gingerich, and A. R. Kluge. 1978. Hierarchical linear modeling of the tempo and mode of evolution. Paleobiology 4:120–134.

Dobzhansky, Th. 1937. Genetics and the Origin of Species. Columbia Univ. Press, N.Y.

Endler, J. A. 1977. Geographic Variation, Speciation and Clines. Princeton Univ. Press, Princeton, NJ.

Jenkins, D. G., and M. S. Srinivasan. 1985. Cenozoic planktonic foraminifers from the equator to the subantarctic of the southwest Pacific, pp. 795–834. *In* J. H. Blakeslee (ed.), Initial Reports of the Deep Sea Drilling Project, Vol. 90. U.S. Government Printing Office, Wash., DC.

Keller, G. 1981. The genus *Globorotalia* in the early Miocene of the equatorial and northwest Pacific. J. Foram. Res. 11:118–132.

Kennett, J. P., and M. S. Srinivasan. 1983. Neogene Planktonic Foraminifera: A Phylogenetic Atlas. Hutchinson Ross, Stroudsburg, PA.

Mayr, E. 1963. Animal Species and Evolution. Belknap, Cambridge, MA.

Mishler, B. D., and M. J. Donoghue. 1982. Species concepts: A case for pluralism. Syst. Zool. 31:491–503.

Raup, D. M. 1966. Geometric analysis of shell coiling: General problems. J. Paleontol. 40:1178–1190.

Reyment, R. A., R. E. Blackith, and N. A. Campbell. 1984. Multivariate Morphometrics. Academic Press, London, U.K.

Reyment, R. A., F. L. Bookstein, K. G. McKenzie, and S. Marjoran. 1988. Ecophenotypic variation in *Mutilus pumilus* (Ostracoda) from Australia, studied by canonical variate analysis and tensor biometrics. J. Micropalaeontol. 7:11–20.

Rosenzweig, M. L. 1978. Competitive speciation. Biol. J. Linn. Soc. 10:275–289.

Sampson, P. D., A. P. Streissguth, H. M. Barr, and F. L. Bookstein. 1989. Neurobehavioral effects of prenatal alcohol, part II: Partial least squares analysis. Neurotoxicol. Teratol. 11:477–491.

Saunders, W. B., and A. R. H. Swan. 1984. Morphology and morphologic diversity of mid-Carboniferous (Namurian) ammonoids in time and space. Paleobiology 10:195–228.

Scott, G. H. 1966. Description of an experimental class in the Globigerinidae (Foraminifera), part 1. New Zeal. J. Geol. Geophys. 9:513–540.

———. 1980. The value of outline processing in biometry and systematics of fossils. J. Paleontol. 23:757–768.

Srinivasan, M. S., and J. P. Kennett. 1981. Neogene planktonic foraminiferal biostratigraphy and evolution: Equatorial to subantarctic, south Pacific. Mar. Micropaleontol. 6:499–533.

Stainforth, R. M., J. L. Lamb, H. Luterbacher, J. H. Beard, and R. M. Jeffords. 1975. Cenozoic planktonic foraminiferal zonation and characteristics of index forms. Univ. Kans. Paleontol. Contrib. 62:1–425.

Tabachnick, R. E. 1981. Morphologic variation in Miocene *Globigerina bulloides,* D'Orbigny, New Port Bay, California. M.S. Thesis. Univ. California, Los Angeles, CA.

Wei, K.-Y. 1987. Multivariate morphometric differentiation of chronospecies in the late Neogene planktonic foraminiferal lineage *Globoconella.* Mar. Micropaleontol. 12:183–202.

Corresponding Editor: K. W. Flessa