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Patterns and Processes of Stasis in Two Species Lineages of Brachiopods from the Middle Devonian of New York State

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ABSTRACT

More than 17,000 measurements were taken on over 1000 specimens of two species of brachiopods, *Mediospirifer audaculus* and *Athyris spiriferoides* from the Middle Devonian Hamilton Group of New York State. Statistical analyses were performed in order to test patterns and processes of stasis in the morphology of species over several million years. Measurements were taken both to quantify shell shape and organismal ontogeny. Specimens were partitioned by their occurrence in one of many environments and stratigraphic horizons. Stasis could not be refuted, as neither species showed substantial morphological departures between the oldest and youngest samples of the Hamilton Group (a roughly 5-million-year interval). However, oscillations in morphology, allometric heterochrony, and rates of change of single features were discovered in both taxa.

In addition, one of the mechanisms typically held to be responsible for morphological stasis, stabilizing selection in conjunction with habitat persistence, does not appear to be the sole cause of stasis in these taxa. For the two species we studied, groups of organisms occurring in a single environment undergo substantial morphological change through time, suggesting that a stable environment is not producing morphological stability. However, the net sum of changes through time in all the environments these species occur in is essentially zero. Therefore, stasis appears to be partly a property of the organization of species. Species are organized into different environmental populations or demes. Different "environmental populations" may evolve, but they will typically do so in several different "directions" in morphospace, generally producing no net change. As

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long as a species occurs in several different environments it will be resistant to change. The difference between the morphology of species in different environments over the whole interval of the Hamilton Group is also nil, thereby ruling out any major role that ecophenotypic effects could play in the patterns recognized herein.

INTRODUCTION

The pattern and rate of morphological change in evolutionary species lineages over geological time has been a hotly debated topic in paleontology and biology over the last two decades. The traditional, or syntheticist, model of evolutionary change within species, propounded in the work of Haldane (1931), Simpson (1953), Mayr (1963), and others, and referred to as phyletic gradualism, differs significantly from the work of the punctuated equilibrists, most importantly Eldredge and Gould (1972), Gould and Eldredge (1977), Stanley (1979), etc., in the relative importance that the two theories ascribe to the prevalence of morphological stasis in species over long periods of time.

Publication of the punctuated equilibria hypothesis touched off many endeavors to test the rate of change in species through time. Some studies have indicated that over time stasis is the rule (Williamson, 1981; Stanley and Yang, 1987; Gould, 1988; Barnosky, 1990; Lich, 1990; etc.). Others have suggested that gradual trends do occur (Gingerich, 1976, 1985; Sheldon, 1987).

This analysis takes as its starting point the search for a gradualistic pattern of irreversible and orthogenetic morphological change in order to test the hypothesis of stasis. It also assesses the role that the environment plays in mediating stasis and change through time. To attain these goals, two of the most abundant species in the Middle Devonian Hamilton Group of New York State, the brachiopods *Mediospirifer audaculus* (Conrad) and *Athyris spiriferoides* (Eaton) were studied. These species are found in almost all of the stratigraphic units of the Hamilton Group, are plentiful throughout the section, and occur in a range of paleoenvironments.

The Hamilton fauna, and the strata of the Hamilton Group, have been the subject of many detailed stratigraphic and paleoenvironmental studies (e.g., Brett et al., 1990; Grasso, 1986; Miller, 1986; Savarese et al., 1986), and these studies allow fossil specimens collected from the Hamilton Group to be assigned a relatively precise age and to be placed in a distinct paleoenvironment or biofacies. The intensely studied geological system of the Hamilton Group presents a good opportunity to look at the relationship between morphological change, stratigraphic history, and environment in individual species lineages.

Punctuated equilibria and the competing phyletic gradualist model each make clear predictions about the anticipated patterns of morphological change in a single species through time. The former predicts that species will not change morphologically for most of their existence, while the latter argues that morphology will gradually, and in a mostly unidirectional fashion, change over long periods of time (Eldredge and Gould, 1972; Gould and Eldredge, 1977). In both theories the abiotic environment is ascribed an important role as a mechanism either driving or restricting evolutionary change in a species over time.

The environment has been related to patterns we see in species morphology in at least three different ways: 1) it maintains stasis via stabilizing selection, 2) it produces orthogenetic change by initiating a constant selective regime (assumes organisms are not yet adapted to their environment), and 3) environment and morphology are decoupled such that morphology undergoes a random walk regardless of environment (unless environment is severe enough to induce death). The first explanation has typically been touted as one of the main causes of stasis (e.g., Lande, 1980; Charlesworth et al., 1982). (Alberch, 1982; Maynard Smith et al., 1985; and Williamson, 1987 provided excellent discussions of another chiefly cited cause of stasis, developmental constraints/species integrity.)

If stabilizing selection played a prominent role in canalizing the morphology of species, we would predict that species in constant environments would not change, if similar en-

vironments exert similar selective regimes over time. When a brachiopod species from the Hamilton Group is found in the same biofacies or paleoenvironment at two different times, it is held to be occurring in the same environment. If stabilizing selection is a valid explanation of stasis then as long as the members of a species can persist in their preferred environment, they will not change. Thus, in similar environments, populations should not change over time.

We performed a series of multivariate statistical analyses on morphometric data from two of the most abundant brachiopod species restricted in age to the Hamilton Group in order to evaluate the prevalence of stasis. We also conducted analyses on individual morphological variables, to quantify their rates of change through time. In addition, we determined the amount of morphological change in species lineages through time across their entire sampled distributions and within single environments, to assess the role that stabilizing selection within a single biofacies or paleoenvironment may play in mediating stasis. The information on phenotypic evolution within an individual paleoenvironment/biofacies was considered in light of techniques that relate changes in phenotype to minimum selective mortality regimes.

MATERIALS AND METHODS

Geological and Paleoecological Setting Considered

The geological setting we used to test the hypothesis of stasis in species lineages is the Hamilton Group, a package of rocks from New York State that contains around 350 species, and spans 5 million years of the Middle Devonian. Some of these taxa appear to have Armorican and North African affinities (Bailey, 1983; Eldredge, 1985) and their appearance in North America is hypothesized to have been driven by the post-Eifelian (Middle Devonian) reintensification of the Acadian Orogeny (Brett, 1986; Cooper et al., 1942; Ettensohn, 1985). From its inception, the Hamilton Group and its fauna are associated with a drastic increase in the amount of sedimentation from mountains to the east (Brett, 1986; Cooper et al., 1942; Ettensohn, 1985). These mountains formed during the Acadian Orogeny, which was caused either by the collision between Armorica, Laurentia, and the intervening Traveler terrane (Kent, 1985); by oblique convergence of Avalonia and Laurentia (Ettensohn, 1985); or by collision between Armorica-Iberia and Avalonia with subsequent effects on Laurentia (Soper et al., 1992).

The erosional products of this orogenic event imparted a pattern of increasing terrestrialization through time and in a west-to-east gradient in the Hamilton Group rocks. The thickest sections are found in eastern New York at the Catskill front and measure 1000 meters. Near the westernmost extremity of New York State, the Hamilton Group is 100 m thick (Brett, 1986). The bulk of the samples surveyed are from central and western New York, as it is there that the marine facies of the Hamilton Group are prominently developed. Further east, nonmarine environments are found.

The section spans latest Eifelian to middle Givetian and deposition commenced at about 380 Ma and ended around 375 Ma on the basis of Rb-Sr dates (Brett, 1986; Brett and Baird, 1986). Deposition took place in the northern arm of the large, tropical epeiric sea that covered much of eastern North America (Brett et al., 1986) (fig. 1). A stratigraphic section for the Hamilton Group is shown in figure 2, along with bars indicating the geological units from which specimens of *M. audaculus* and *A. spiriferoides* could be obtained. Samples were grouped according to their occurrence in well-circumscribed chrono- and lithostratigraphic units.

Fossil assemblages from the Hamilton Group can be classified into approximately eight generalized biofacies or paleoenvironments which were defined by factor analytic techniques using the presence and abundance of associated species as well as other criteria given in Brett et al. (1990), Grasso (1986), Miller (1986), and Savarese et al. (1986). There is cyclic change in the type of fossil assemblage present, which approximately follows a pattern of lithofacies (rock type) cyclicity (Savarese et al., 1986), and this cyclicity records the upslope and downslope migration of assemblages tracking habitat shifts and changes in water depth (Brett et al., 1990). This, along with other evidence,

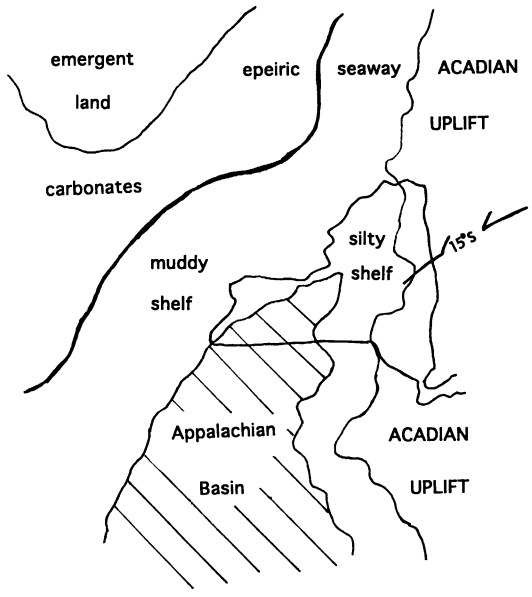

Fig. 1. Schematic diagram of the depositional environment of the Middle Devonian Hamilton Group of New York State, with a generalized sketch of the paleogeography showing the paleolatitude of the North American craton (Laurentia) at this time (380 million years ago). Modified from Brett et al. (1986).

indicates that these biofacies are sound paleoenvironmental indicators. (For more details on the designation of biofacies see Brett et al. [1990].) Locality information was used to assign specimens to one of the Hamilton paleoenvironments/biofacies discussed in Brett et al. (1990) (see fig. 3). The biofacies considered were: the *Athyris-Mediospirifer* biofacies, abbreviated as (B) (where the *Athyris-Mediospirifer* biofacies is taken as equivalent to the *Athyris* biofacies of Brett et al. [1990]), the *Athyris-Mediospirifer* transitional to *Pseudoatrypa* biofacies (C), the *Pseudoatrypa* biofacies (D), the *Tropidoleptus* biofacies (E), the *Pentamerella-Heliophyllum* biofacies (F), and the *Mucrospirifer* transitional to *Ambocoelia* biofacies (G). The number of specimens of *Mediospirifer audaculus* and *Athyris spiriferoides* measured in each paleoenvironment/biofacies is given in figure 3. (There are slightly fewer specimens considered in the analysis by communities because the exact biofacies could not always be determined.)

Measurements Taken and Adjustments for Size

Data were gathered from each brachiopod shell with a digital caliper accurate to 0.01 mm. All measurements were rounded off to the nearest 0.1 mm. Measurements were taken using both homologous landmarks and maximum length/width measurements.

For *M. audaculus,* six measurements were taken on the pedicle valve at its terminal ontogenetic stage. This valve was chosen over the brachial valve because it contains greater amounts of utilizable information and is more resistant to preservational deformation. The measurements taken are illustrated in figure 4.

401 specimens were measured, and these specimens were divided into samples representing 10 different stratigraphic horizons that spanned basal to terminal Hamilton strata. To avoid any biases, all available specimens were measured. The position of the samples in the section is shown by the darkened bars in figure 2, with the number of specimens for each stratigraphic horizon indicated in the figure.

Data were adjusted to remove differences between horizons governed by differences in size using two different methodologies in order to cross-verify their efficacy. This was done to minimize the potential impact size has on the analysis because of the impact ecophenotypic variation has on size, and to correct for possible taphonomic biases relating to size. In the first method, data were log transformed. In the second, magnitudes of the 1 × 6 specimen vector were transformed using the variables *H, IAW,* and *MAXF_SW* which in regressions against each other had slopes equal to 1.0, indicating isometric bivariate slopes (see Somers, 1989; Sundberg, 1989). The correction factor used the square root of the sum of the squares of these variables. After generating derived data in which all variables were adjusted for size using the correction factor, the derived data were plotted against the size factor. For all variables, no association was found between the correction factor and the scores of variables, indicating that for all variables size had been largely adjusted for. Both methods produced congruent results, but for the purposes of

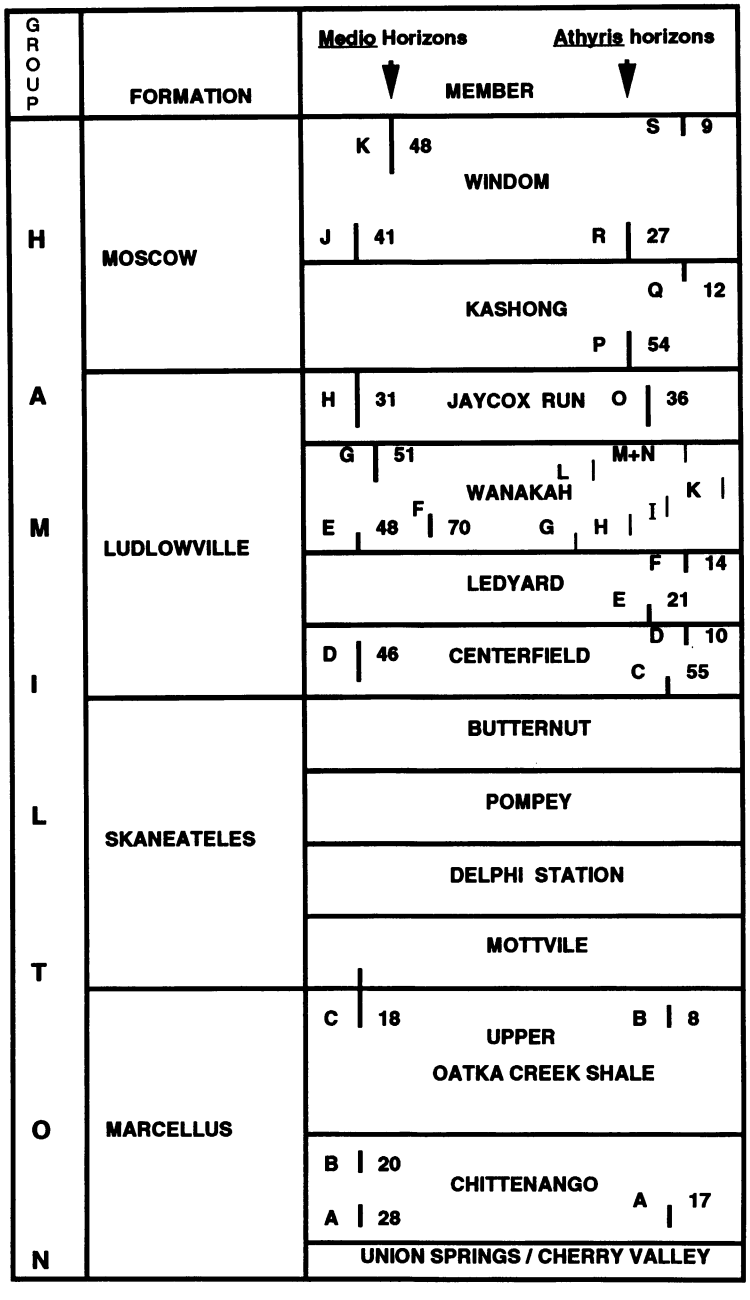

Fig. 2. Idealized stratigraphic column of the Hamilton Group based on Brett et al. (1986) and Cooper et al. (1942), showing the major lithostratigraphic units, the horizons treated for each species, and the number of specimens measured for each of these species. The number of specimens of *Athyris spiriferoides* from the following horizons are: G = 45, H = 52, I = 54, K = 81, L = 35, M = 44, N = 35.

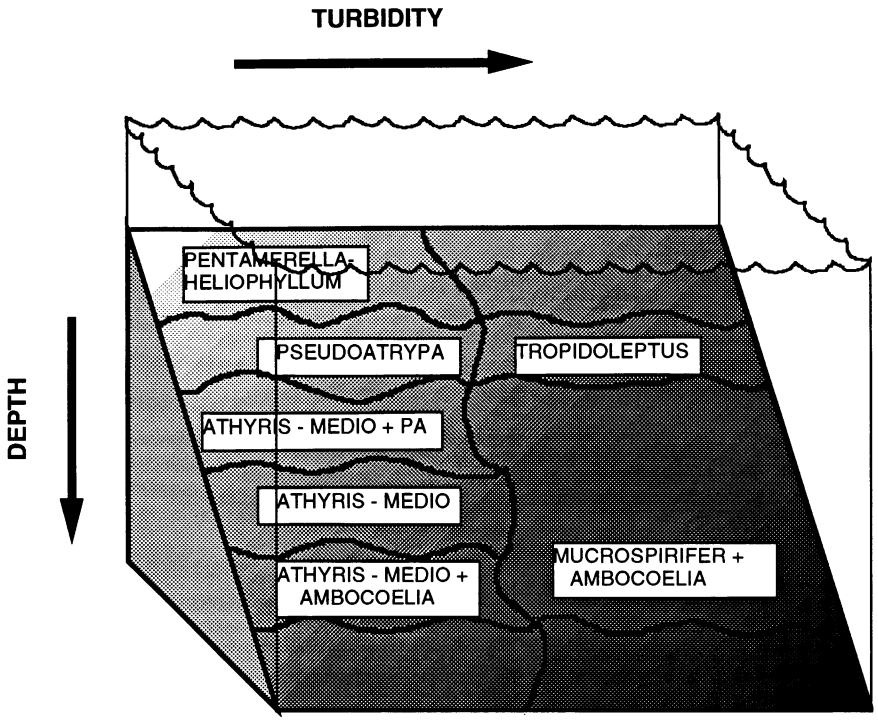

Fig. 3. Diagrammatic depiction of the paleoenvironments/biofacies from the Hamilton Group that were sampled in this analysis (modified from Brett et al. [1990]). The top of the diagram represents the shallowest environments and the right side of the diagram represents increasingly turbid water conditions. The number of specimens of *M. audaculus* analyzed for each biofacies are: from the *Athyris/Mediospirifer* biofacies (abbreviated B in the text) 84, the *Athyris/Mediospirifer* transitional to *Pseudoatrypa* biofacies (abbreviated C in the text) 77, the *Pseudoatrypa* biofacies (D) 152, the *Tropidoleptus* and *Tropidoleptus* transitional to *Pseudoatrypa* biofacies (E) 35, the *Pentamerella/Heliophyllum* and *Pentamerella/Heliophyllum* transitional to *Pseudoatrypa* biofacies (F) 33. The number of specimens of *A. spiriferoides* measured are: (B) 162, (C) 45, (D) 243, (E) 76, (F) 40, and the *Mucrospirifer* transitional to *Ambocoelia* biofacies (G) 35.

brevity and clarity only the results using the second method are presented here.

Four measurements were made on 614 specimens of *Athyris spiriferoides* (see fig. 5) from 18 different stratigraphic horizons. All measurements were taken on the pedicle valve because it is less subject to preservational deformation. Data were scaled to reduce the divergence between horizons caused by size differences by employing the two methodologies used for *M. audaculus*. In the vector magnitude correction method, magnitudes of specimen vectors were adjusted using the variables *MXH* and *MXW* following the criteria presented for *M. audaculus*, and only the results using this method of size correction are presented here. The number of specimens measured for each stratigraphic horizon, and the position of these horizons in the stratigraphic section, is shown in figure 2.

Analyzing Rates of Evolution

Individual morphological variables were analyzed using the technique developed by Haldane (1949) and treated extensively by Gingerich (1985), Stanley (1985), and Stanley and Yang (1987). This technique treats changes in nonmeristic morphological characters as being essentially exponential in nature. Magnitude of change in a variable over time is quantified using darwins. These units represent change in a feature by factors of e ($\sim$2.7) per million years. Rates are calculated

using the formula $(\ln x_2 - \ln x_1)/t$, where x_1 and x_2 are initial and final mean morphologies for a single variable and t is time in millions of years (Stanley and Yang, 1987). Both raw and size-corrected data were analyzed, in recognition that most of the phyletic change that occurs within species lineages is actually size change (Hallam, 1978; Stanley, 1985; Stanley and Yang, 1987).

Because of the paucity of radiometric dates aside from those bracketing the upper and lower horizons of the Hamilton Group, analyses of rates of change in individual shell variables used the following temporal durations: each formation persisted for an equal amount of time (1.25 Ma), and formations were divided up into members of equal duration. These durations are roughly supported by data presented in Brett and Baird (1986).

Analyses of rates were also used to relate phenotypic evolution to intensities of selection pressure. Although it is perhaps impossible to discern the actual potency of selective forces acting at the organismal level in the fossil record, Lande (1976) has developed a method for estimating the minimum selective mortality that would produce the observed rate of phenotypic evolution. This method should not be viewed as a way of reconstructing actual selection pressures in the fossil record. However, it does provide a means of quantitatively relating patterns of phenotypic change through time to a hypothetical selection pressure, in order to assess whether those intensities of selection alone are what produced the given trend. If nearly infinitesimal selection pressures are indicated, it suggests that less importance should be ascribed to such processes.

Lande (1976) derived the following formula for estimating the proportion of the population culled each generation:

$$b = \frac{\pm\sqrt{-2\ln(\sqrt{2\pi}\,|z|/\sigma)}}{h^2 t}. \qquad (1)$$

The proportion is obtained using the estimate b and tables of integrals for the standard normal distribution. $|z|$ is the difference between $\ln(x_2) - \ln(x_1)$ where x_2 and x_1 are the means of a population for a single variable at times 2 and 1. σ is the mean of the standard deviation of each variable from those time

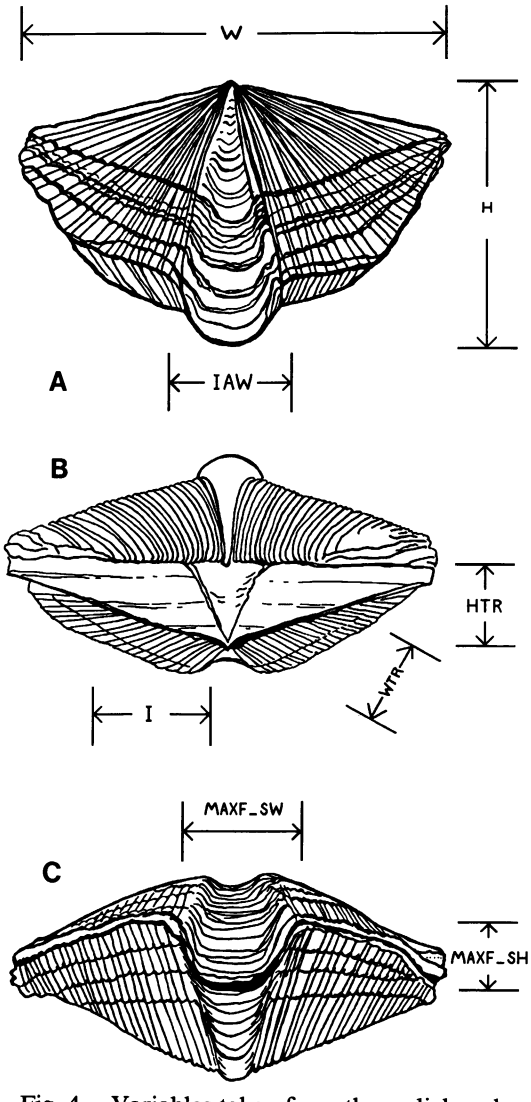

Fig. 4. Variables taken from the pedicle valve of specimens of *Mediospirifer audaculus* (Conrad). **A**, Ventral view: *H*, height of shell or distance from umbone to midline of fold; *W*, total width of shell; *IAW*, distance between the two ribs on each side of fold. **B**, Posterior view: *HTR*, orthogonal distance between umbone and brachial valve, spanning the interarea; *WTR*, distance from umbone to brachial valve, following trace of margin between delthyrium and interarea. **C**, Anterior view: *MAXF_SW*, width of fold; *MAXF_SH*, depth of fold at base of shell. See text for *I*.

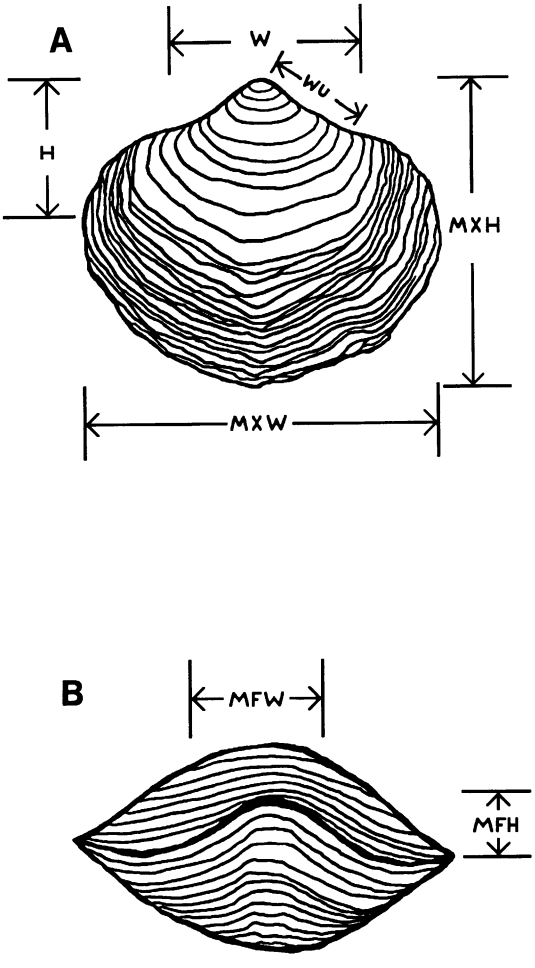

Fig. 5. Measurements taken from the pedicle valve of specimens of *Athyris spiriferoides* (Eaton). **A**, Ventral view: *MXH*, height from umbone to medial portion of fold; *MXW*, maximum width of pedicle valve. **B**, Anterior view: *MFW*, width of fold; *MFH*, depth of fold. See text for *H* and *WU*.

intervals, h^2 is the heritability of the character, and t is the time in generations over the interval of the study. Populations must be checked for homogeneity of variances (Lande, 1976). This requirement was not satisfied for all populations.

Values of heritability of characters (h^2) are difficult to deduce for taxa long extinct whose extant brachiopod relatives have received little study in this area. Thus, the heritability values follow those of Lande (1976) and Jablonski (1987), with $h^2 = 0.5$; however, changes in this variable do not strongly influence the results because this equation is dominated by t, the time variable. t is related to the number of generations over the time interval for which phenotypic evolution is being studied. Again, since establishing generation times for these taxa is impossible, they are treated as having one generation per year.

Statistical Analyses

These data were subjected to a principal components analysis and a canonical discriminant analysis using the PRINCOMP and CANDISC procedures of SAS (1987). These statistical analyses were conducted on samples subdivided both by their occurrence in a particular stratigraphic horizon and in a particular paleoenvironment/biofacies.

For the principal components analysis, only the variance-covariance matrix is shown. When that matrix is used, variables with higher variance are given greater weight in the analysis (Neff and Marcus, 1980). When the correlation matrix is used, the loadings are nearly identical, though the order of the first two principal components obtained is switched in both species.

In order to apply the second statistical technique used, canonical discriminant analysis, all groups must be multivariate normal and have homogeneous variance-covariance structure. Normality for all variables was assessed using PROC UNIVARIATE NORMAL (SAS, 1987). Although univariate normality of all variables does not guarantee multivariate normality, it is a reasonable first-order exploratory technique for its determination (Neff and Marcus, 1980). Across all horizons, variables were normally distributed; however, within certain horizons, the distributions of certain variables departed from normality.

In addition to these two multivariate statistical techniques, analyses using univariate statistics were performed. t-tests (PROC TTEST in SAS [1987]) were performed in pairwise comparisons in conjunction with the Bonferroni inequality to ascertain statistically significant departures between the means of horizons. A value of 0.05 or less was taken to be statistically significant. A series of pairwise comparisons were made using some of

the different variables for some of the key stratigraphic horizons.

Additional statistical analyses were also conducted to take advantage of the fact that these brachiopods were accretionary organisms, and a history of their growth is preserved in their shells. This allowed the measurement of several different ontogenetic stages within a particular organism. Such an analysis made it possible to detect any changes in the ontogenetic trajectory of organisms between stratigraphic horizons and within biofacies.

Data from ontogenetic series of both brachiopod species were analyzed using an analysis of covariance, the PROC GLM of SAS (1987). However, in these organisms it is impossible to determine the age of an individual at any particular ontogenetic stage. McKinney (1986) elaborated the concept of allometric heterochrony, which uses size as a proxy for age/time. This allows the values of certain characters to be calibrated between individuals and across stratigraphic horizons. Ontogenetic stages which occur at the same size are taken to be equivalent. However, this methodology may have problems since trait changes are being compared as a function of size instead of time, and this ignores the fact that size may be a nonlinear function of time (McKinney, 1988).

In addition, Blackstone and Yund (1989) elegantly demonstrated that in analyses searching for heterochrony different results are often produced when either allometry or chronology is used to calibrate the timing of developmental events. Finally, Blackstone (1987) showed that the concept of allometry may not be the best way of looking at evolutionary alterations in development. Therefore, studies based on allometric heterochrony might not be able to illuminate patterns of heterochrony, though they provide the best possible insight into these questions, considering the type of taxa under study. A meaningful analysis of changes in variables with relative or absolute size can still be conducted, and looking at trait change as a function of size can be of interest (Blackstone and Yund, 1989; McKinney, 1986, 1988).

Because measures of absolute size are typically used as calibrations of "time" in allometric ontogeny, this analysis uses the variable *H*, the height of the shell valve, which correlates well with absolute size on the basis of the analysis presented in the section on MEASUREMENTS TAKEN . . . , to determine the "age" of an organism at a particular growth stage. Three different ontogenetic stages were measured for every specimen. At each of these three stages, four measurements, including the measurement calibrating time, were taken. Measurements were taken at roughly one-quarter, one-half, and three-quarters of the shell height to avoid introducing possible biases. Of course, as we are using size to calibrate time, these data were not corrected for size.

Data from ontogenetic series were subjected to an analysis of covariance. This analysis used time as the independent variable, and plotted values of the dependent variables, or morphometric measurements, against time. A regression line was fit to this scatter of data. The goal of this analysis was to compare the changes in variables with age or "time" across different stratigraphic horizons and different biofacies. Differences in the average size of organisms across stratigraphic samples could lead to differences in the slope of regression lines between horizons, if measurements captured different portions of a nonlinear allometric growth curve. However, this is not a problem, because for all horizons the scatter of points is linear.

For *Mediospirifer audaculus,* the ontogenetic trajectory of three measurements was calculated with respect to time (*H*). These measurements are *W,* the width along the interarea from the point where the growth line hits the boundary between the ribs, *IAW,* the width of the fold at the particular stage of ontogeny, and *I,* the distance from the point where the growth line hits the boundary between the ribs and the interarea to the delthyrium, following the trace of the growth line (see fig. 4A–C).

An analysis of covariance was also performed for three variables plus the size or time variable (*H*) taken on specimens of *Athyris spiriferoides.* The variables used were: *W,* the distance between the points where the ontogenetic marker or growth line hits the margins of the pedicle valve; *WU,* the distance from the position of the growth line at the margin to the umbone; and *HTOW,* the

TABLE 1

Principal components analysis using the variance–covariance matrix and data corrected for size showing the eigenvalues (EV) and the proportion of the variance in the data the eigenvectors explain (PROP) for **(A)** *Mediospirifer audaculus* (Conrad) with only the first three eigenvectors shown, and **(B)** *Athyris spiriferoides* (Eaton) with only the first two eigenvectors shown.

(A)	EV	PROP	*H*	*IAW*	*HTR*	*WTR*	*MAXF__SW*	*MAXF__SH*
PRIN1	.0180	.69	−.05	.05	.69	.72	.05	.05
PRIN2	.0037	.15	−.55	.34	−.06	−.07	.68	.34
PRIN3	.0031	.12	.21	−.27	−.01	−.01	−.17	.92
(B)	EV	PROP	*MXH*	*MXW*	*MFW*	*MFH*		
PRIN1	.003	.49	.15	−.12	.87	.46		
PRIN2	.002	.33	−.73	.61	.29	−.15		

distance between the point where the growth line was calibrated using the measurement *H* to the point where the growth line hits the margin of the pedicle valve (see fig. 5A,B; *HTOW* not shown).

All data, and the SAS (1987) programs written to analyze these data, are available from the first author.

Defining Stasis and Recognizing Taxa

The test for stasis in species lineages is restricted to morphological changes accrued from earliest to latest Hamilton times (the stratigraphic ranges of both taxa). If there is no net discernible morphological change between the end members from the bottom and top of the section, then the hypothesis of stasis is not rejected. Change in a species lineage must be irreversible to count as true evolutionary change (see Gould and Eldredge, 1977), and oscillations are held to be equivalent to net evolutionary stability (Wright, 1931; Lande, 1986). This study is predicated on the search for anagenetic change. We do not claim to be able to evaluate Lande's (1986) or Eldredge and Gould's (1972) models of speciation.

Because this study focuses on species-level taxa, it is crucial that we explicitly define a species. We are using the epistemological species concept of Eldredge and Cracraft (1980), which defines a species as the smallest diagnosably distinct cluster of putatively reproductively interacting organisms that can be recognized and defined by at least one apomorphy. For both species, several characters are available to make hypotheses asserting their monophyly. The spiriferid brachiopod *Mediospirifer audaculus* is diagnosed by: large sweeping growth lines of low convexity, large and extensive interarea of the pedicle valve with horizontal striae, large hinge teeth developed as a steep wall, and its micro-ornament which features widely spaced growth lamellae. *Athyris spiriferoides* is diagnosed by: pedicle valve with small pointed teeth with swelling at their dorsal ends, weak dental plates diverging at about a 45° angle, and weak, oval adductor muscle scars. None of the characters used to define taxa were analyzed to avoid logical inconsistency following Lande (1986), for if these characters changed they would no longer indicate the same species.

RESULTS

Analysis of Terminal Ontogenetic Stages Subdivided by Stratigraphic Horizon

Mediospirifer audaculus. — The first exploratory technique used was principal components analysis. The first three principal components account for 95% of the variance in the data (see table 1A). The first principal component has large loadings on *HTR* and *WTR*, indicating that a large portion of the variance in the data set can be attributed to differences in these variables. The other variables have near zero loadings. The second principal component is dominated by *MAXF__SW* and *H*, and the third by *MAXF__SH*.

A canonical discriminant analysis with the

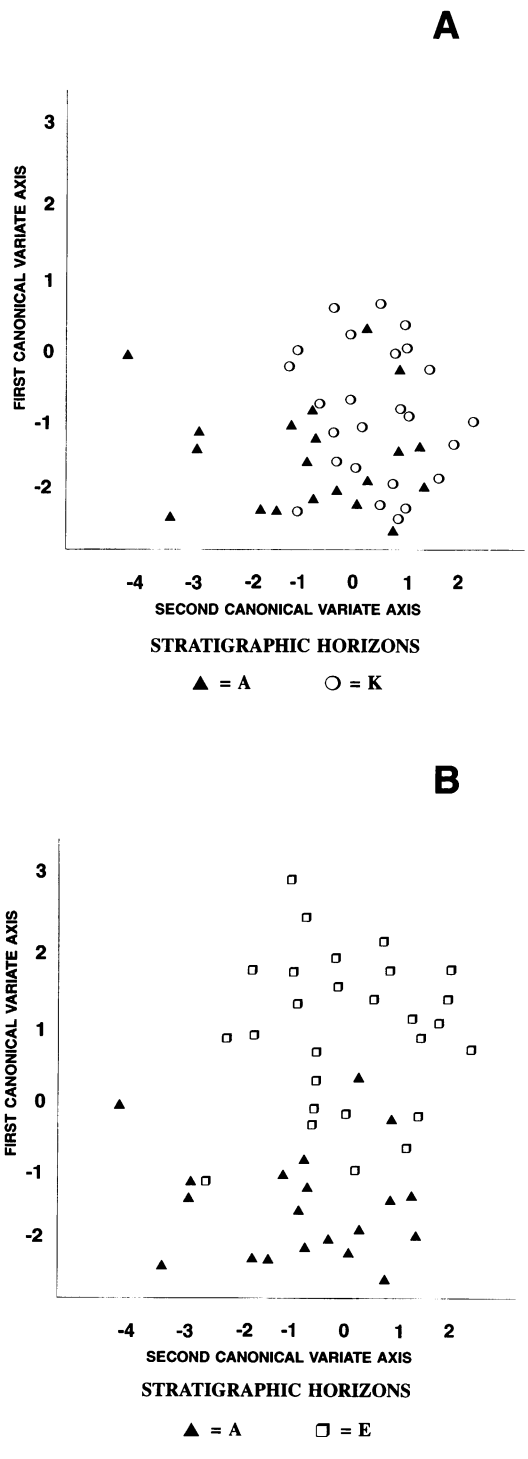

Fig. 6. Results from canonical discriminant analysis of *Mediospirifer audaculus* that employed stratigraphic horizons to discriminate specimens. ← Shown are canonical variate axes 1 and 2 and the scores of specimens from stratigraphic horizons: **A**, from the lowest and uppermost Hamilton Group, stratigraphic horizons A and K. Notice the great degree of overlap, and **B**, stratigraphic horizons A and E. Notice the prominent separation between the specimens from these two horizons.

stratigraphic horizons used as the classes or groups indicates that specimens from the lower and uppermost portion of the Hamilton Group are very similar (see fig. 6A, table 2A), indicating overall net stasis. However, changes in morphology occur within the section. The greatest differences are between the lowest stratigraphic sections, A, B, and C, and the intermediate sections, E, F, and G, with little overlap of the specimens from the Marcellus (horizon A) and Wanakah (horizon E) formations (see table 2A and fig. 6B). Thus, specimens of *M. audaculus* from the oldest sections, the Oatka Creek and Mount Marion shales in the Marcellus Formation, bear a greater resemblance to specimens from the youngest section, the Windom Member of the Moscow Formation than to those from the intermediate Wanakah Shale of the Ludlowville Formation.

There is considerable overlap between samples from successive horizons except in two cases. The first is between C and D, which are quite distinct, with a Mahalanobis distance (D^2) of 4.65. However, samples from the 100 m of rock between sections C and D could not be obtained. One might expect a substantial morphological gap between these sections due to the large interval of time for which no *M. audaculus* specimens were analyzed. The other large morphological gap separates samples H and J. In this case there is no major "sampling unconformity" separating the two horizons.

The similarity between lower Hamilton and upper Hamilton *M. audaculus,* and the divergence of intermediate Hamilton *M. audaculus,* is chiefly governed by the pattern of shifts in the size of the interarea. However, it is impossible to ascribe a cutoff point demarcating those specimens with larger interareas from those with smaller interareas because there is continuous variation between

TABLE 2

(A) Canonical discriminant analysis for *M. audaculus* showing the Mahalanobis distances (D^2) between the different stratigraphic horizons after all vectors were corrected for size. **(B)** The total canonical structure for canonical variates 1–3 and all measured variables, with the proportion of the data explained by each canonical variate designated as PRO.

(A)	B	C	D	E	F	G	H	J	K
A	0.34	2.24	3.11	6.17	5.77	4.54	3.77	2.43	2.19
B	0	1.28	2.04	4.39	4.08	2.84	2.89	1.04	0.95
C		0	4.65	6.74	5.65	3.40	5.64	0.83	1.33
D			0	0.76	0.80	0.99	0.34	2.80	1.75
E				0	0.58	1.31	0.72	4.09	2.53
F					0	0.42	0.73	3.78	2.59
G						0	1.23	2.26	1.67
H							0	3.76	2.44
J								0	0.63

(B)	PRO	*H*	*IAW*	*HTR*	*WTR*	*MAXF_SW*	*MAXF_SH*
CAN1	0.71	−0.35	0.31	0.94	0.90	0.29	0.16
CAN2	0.19	−0.08	0.59	−0.19	−0.26	−0.17	−0.01
CAN3	0.09	0.31	−0.16	−0.01	−0.02	−0.34	0.85

the two end points. The structure of the canonical variates indicates that approximately 70% of the differences of centroids for stratigraphic horizons can be explained by the first canonical variate, and *HTR* and *WTR* have very large loadings on this axis. The second canonical variate summarizes 19% of the variance among centroids of horizons and is controlled mainly by the variable *IAW* (see table 2B).

For the purposes of brevity and clarity, not all of the results obtained from comparisons between stratigraphic horizons using univariate statistics are presented here. However, for those horizons found to differ by substantial D^2 values, *t*-tests demonstrate that the differences in the mean value of *HTR* and *WTR* for horizons A, B, C and E, F, and G were statistically significant differences individually at the 0.0001 level, and thus using the Bonferroni inequality, the differences were significant at the 0.001 level. For those horizons differing by small D^2 values, differences in the mean value of *HTR* for horizons A and B were not statistically significant, and differences between horizons A and K for *HTR* were also not significant. Nonparametric tests mirrored these results.

Thus, statistical analysis of *M. audaculus* indicates net stasis with some oscillation in morphology. The differences in *HTR* and *WTR* seem to be controlling much of the change seen in this species lineage. This pattern may be due to incipient sympatric speciation or it may represent dynamics between two closely related forms. However, because there seems to be continuous variation in the size of the interarea, *M. audaculus* was not split into two separate lineages. If the pattern seen is within one species then we may be seeing changes within different populations. The specimens from the intermediate layers may reflect the increased presence of conspecifics from a different population that evolved elsewhere and migrated in, only to migrate elsewhere or go extinct in the Moscow Formation. As a final possibility, these oscillatory changes may just represent oscillation in morphology producing no net trend and caused by drift or wavering selection pressures.

Athyris spiriferoides. — For the first principal component derived using the variance-covariance matrix *MFW* constitutes the primary loading (see table 1B). The second principal component is most affected by *MXH* and *MXW*. Together these axes explain 82% of the variance in the data.

Canonical discriminant analysis revealed overall net stasis, and specimens from the basal and upper Hamilton Group still overlap in the scores on the canonical axes (see

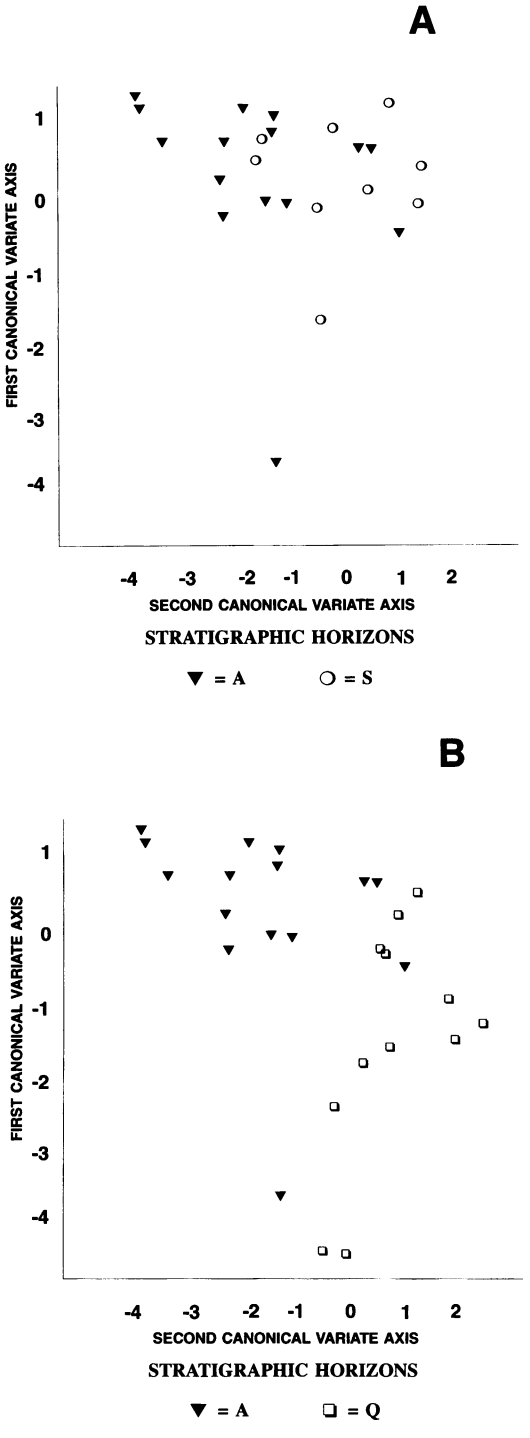

Fig. 7. Results of canonical discriminant analysis of *Athyris spiriferoides* that employed stratigraphic horizons to discriminate specimens. Shown are canonical variate axes 1 and 2 and the scores of specimens from stratigraphic horizons: **A**, A and S. A and S are the lowermost and uppermost horizons, respectively; notice their significant overlap. **B**, A and Q. Notice the prominent separation between specimens from these two horizons.

fig. 7A). The oldest samples, collected from the basal layer of the Oatka Creek Shale, differed most from the samples in horizons O, P, and Q (see table 3 and fig. 7B). These samples represent the Jaycox Shale, the Deep Run Member, and the Kashong Shale, respectively. For this species, unlike *M. audaculus,* there is considerable overlap between Marcellus formation samples and those from the Wanakah Shale. Between successive samples there is considerable overlap, and even samples separated by hundreds of feet of rock, i.e., upper Marcellus (B) and Centerfield (C), are quite similar.

Canonical variate structure suggests that height and negative width predominate on axis 1 and *MFW* and *MFH* predominate on axis 2 (see table 3B).

t-tests on normally distributed data indicate differences in the variables *MXH* and *MFW* between the most divergent horizons A and O significant individually at the 0.0001 level of confidence, which, when used in conjunction with the Bonferroni inequality, imply differences significant at the 0.02 level. When the Bonferroni inequality is applied to differences for *MXW* for these horizons, they are found to be significant at the 0.07 level, i.e., not significant. The nonparametric Wilcoxon test revealed differences between horizons A and O for *MFH* only significant at the 0.81 level. For earliest and latest horizons, A and S, *t*-tests in conjunction with the Bonferroni inequality indicated that the mean values of *MXH, MXW, MFW,* and *MFH* did not significantly differ.

Quantifying Changes in Individual Variables

Rates of change in individual morphological variables were calculated for both the total duration of the species and between the

TABLE 3

(A) Canonical discriminant analysis for *A. spiriferoides* showing the Mahalanobis distances (D^2) between the different stratigraphic horizons after all vectors were corrected for size. **(B)** The total canonical structure for canonical variates 1 and 2, with the proportion of the data explained by each canonical variate designated as PRO.

(A)	B	C	D	E	F	G	H	I	
A	0.58	3.84	4.66	0.25	2.86	4.47	1.97	1.61	
B	0	2.08	2.26	0.41	1.58	2.88	0.95	1.26	
C		0	0.28	3.16	0.41	0.78	0.73	1.14	
D			0	3.76	0.86	1.21	1.18	2.09	
E				0	1.94	3.13	1.23	1.09	
F					0	0.23	0.15	0.38	
G						0	0.63	0.93	
H							0	0.24	
	K	L	M	N	O	P	Q	R	S
A	2.27	3.90	3.54	4.03	6.22	5.76	7.88	2.47	3.09
B	1.96	1.98	2.23	3.31	3.75	3.99	5.50	1.05	2.07
C	1.44	0.24	0.56	1.39	0.45	1.48	1.43	0.43	1.07
D	2.48	0.36	1.05	2.43	0.53	1.98	1.82	0.67	1.75
E	1.51	3.39	2.48	2.96	5.32	5.84	7.53	1.90	2.13
F	0.50	0.80	0.20	0.63	1.17	2.69	2.83	0.37	0.27
G	0.77	1.40	0.24	0.49	1.27	3.60	3.23	1.02	0.43
H	0.59	0.88	0.61	1.10	1.60	2.69	3.25	0.22	0.24
I	0.19	1.53	0.73	0.74	2.38	3.16	3.87	0.72	0.39
K	0	2.24	0.50	0.27	2.89	4.33	4.74	1.35	0.62
L		0	1.36	2.46	0.34	0.78	0.99	0.27	1.27
M			0	0.34	1.57	3.62	3.46	1.01	0.78
N				0	2.55	4.62	4.41	1.87	0.87
O					0	1.07	0.61	0.93	1.58
P						0	0.36	1.54	2.91
Q							0	2.08	3.81
R								0	0.60

(B)	EV	PRO	*MXH*	*MXW*	*MFW*	*MFH*
CAN1	0.48	0.62	0.96	−0.95	−0.20	0.17
CAN2	0.21	0.26	0.22	−0.21	0.98	0.45

most divergent horizons, determined using Mahalanobis D^2 values, to recover the maximum possible rates of change.

Mediospirifer audaculus. — The results from raw data, which include evolutionary changes in size, are presented in table 4A, and indicate modest levels of change. A change of 2.7% per million years represents 10 millidarwins (Stanley and Yang, 1987). These values are comparable with those for changes in size discovered by Hallam (1975) from his studies on Jurassic bivalve lineages. However, when the data are corrected for size the amount of change measured in millidarwins falls precipitously (see table 4A) such that overall changes are very small, and comparable to the minimal changes recovered by Stanley and Yang (1987) from their analysis of changes in Neogene bivalves. Thus, much of the change in these data is related to changes in size. Still, it is important to point out that when only earliest and intermediate sections are considered, significant changes do occur in the variables *HTR* and *WTR,* but these changes are reversible.

Athyris spiriferoides. — The results from raw and size-corrected data are presented in table 4B. Again, very little change transpires from earliest to latest occurrence of the species.

TABLE 4

Rates of change in individual morphological variables in millidarwins (MD) between earliest and latest horizons in the Hamilton Group and also between those horizons which differed the most on the basis of the Canonical Discriminant Analysis. **(A)** *Mediospirifer audaculus,* raw data and data corrected for differences in size. **(B)** *Athyris spiriferoides,* raw data and data corrected for differences in size.

(A)	MD of change between horizons			
	Raw data		Corrected data	
Variables	A–K	A–E	A–K	A–E
H	85	167	2	9
IAW	103	210	14	32
HTR	100	309	17	127
WTR	92	290	9	111
MAXF_SW	87	184	4	6
MAXF_SH	120	240	30	65

(B)	MD of change between horizons					
	Raw data			Corrected data		
Variables	A–S	A–O	A–Q	A–S	A–O	A–Q
MXH	87	100	134	2	21	23
MXW	89	126	170	2	15	15
MFW	143	209	230	55	94	78
MFH	79	144	165	15	29	5

TABLE 5

Canonical discriminant analysis for *M. audaculus* showing the Mahalanobis distances (D^2) **(A)** between different stratigraphic horizons for paleoenvironment/biofacies B, **(B)** the distances between different stratigraphic horizons for paleoenvironment/biofacies D, and **(C)** between the different paleoenvironments/biofacies after all vectors were corrected for size.

(A)	D	E	F	H	
C	9.76	13.28	8.91	7.26	
D	0	1.45	5.54	3.13	
E		0	7.27	6.02	
F			0	5.29	
(B)	F	G	H	J	K
E	0.62	4.13	2.71	14.59	8.64
F	0	2.52	1.66	12.24	6.03
G		0	2.09	5.89	1.32
H			0	9.93	2.98
J				0	5.59
(C)	C	D	E	F	
B	1.80	0.56	0.58	1.61	
C	0	3.21	1.23	2.21	
D		0	0.82	2.02	
E			0	0.91	

Assessing Relationship Between Environment and Stasis

To assess the role environment may play in mediating stasis or change in species morphology, we concentrated on morphological changes through time within a single paleoenvironment/biofacies. This was done to ascertain if there are any morphological shifts through time in any biofacies. If constant environment exerts constant selection pressures, and thus helps mediate stasis via stabilizing selection, then one would predict that through time there would be little morphological change in a species, as long as the environment remained constant. Canonical discriminant analyses were used to assess morphological differences between stratigraphic horizons within a particular biofacies.

Mediospirifer audaculus. — Analyses of morphological change within single paleoenvironments/biofacies were conducted for biofacies B, C, and D. (The other biofacies were present in less than three of the stratigraphic horizons considered herein, and thus could not be subjected to a canonical discriminant analysis.) There are significant shifts in morphology within all of these biofacies through time (see table 5A, B). For example, consider the Mahalanobis distance between stratigraphic horizons E and J from all biofacies (table 2A, fig. 8A), and the distance between stratigraphic horizons E and J solely for specimens from biofacies D (table 5B, fig. 8B). There has been more change through time within a single paleoenvironment/biofacies than across all biofacies. These results are reinforced when patterns of change in individual variables are examined. For instance, the changes in all variables, particularly *HTR* and *WTR*, that transpired between the interval of time in which horizon E and horizon J was deposited (approximately 1.5 Ma) is smaller when all paleoenvironments/biofacies are considered than when only a single biofacies is considered (see table 6A, B).

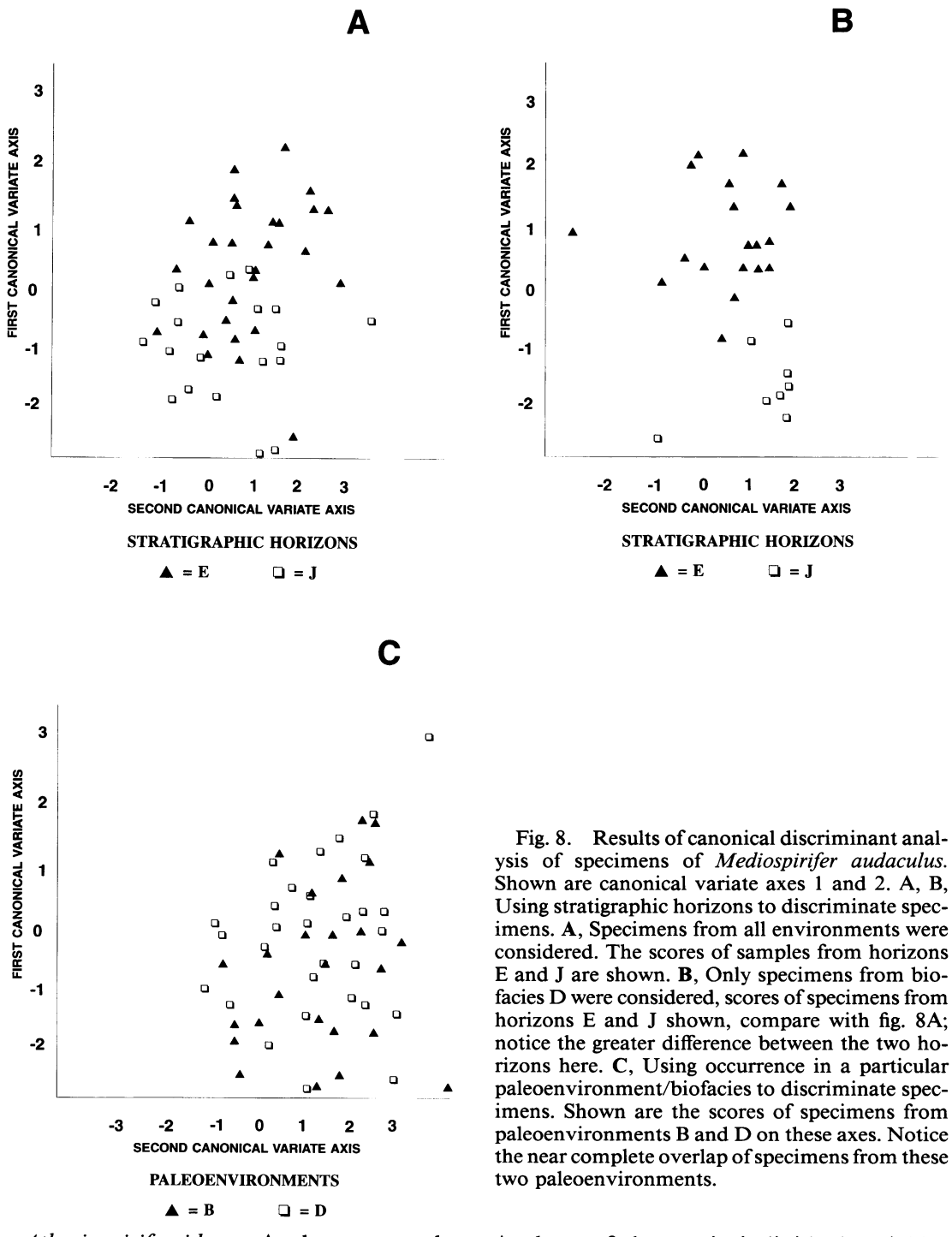

Fig. 8. Results of canonical discriminant analysis of specimens of *Mediospirifer audaculus*. Shown are canonical variate axes 1 and 2. A, B, Using stratigraphic horizons to discriminate specimens. **A**, Specimens from all environments were considered. The scores of samples from horizons E and J are shown. **B**, Only specimens from biofacies D were considered, scores of specimens from horizons E and J shown, compare with fig. 8A; notice the greater difference between the two horizons here. **C**, Using occurrence in a particular paleoenvironment/biofacies to discriminate specimens. Shown are the scores of specimens from paleoenvironments B and D on these axes. Notice the near complete overlap of specimens from these two paleoenvironments.

Athyris spiriferoides. — Analyses to sample temporal variation again show that there are larger differences manifested within a single biofacies through time than when all biofacies are considered together (see table 7A). Analyses of changes in individual variables are comparable to those from *M. audaculus* and are not presented here for the purposes of brevity and clarity.

These results from both taxa suggest that

TABLE 6

Rates of change in individual morphological variables in millidarwins (MD) for *Mediospirifer audaculus* between stratigraphic horizons E, the lower Wanakah Shale, and J, the lower Windom Shale, a 1.5 Ma interval, **(A)** when all paleoenvironments/biofacies are considered and **(B)** when only patterns of change in the *Pseudoatrypa* paleoenvironment/biofacies (biofacies D) are considered.

(A)	MD of change	(B)	MD of change
H	0	*H*	7
IAW	30	*IAW*	0
HTR	46	*HTR*	406
WTR	40	*WTR*	560
MAXF_SW	7	*MAXF_SW*	20
MAXF_SH	53	*MAXF_SH*	133

TABLE 7

Canonical discriminant analysis for *A. spiriferoides* showing the Mahalanobis distances (D^2) after all specimens were corrected for size between samples from **(A)** the different stratigraphic horizons from paleoenvironment/biofaces B and **(B)** different paleoenvironments/biofacies.

(A)	E	F	H	K	
C	4.42	2.12	3.58	3.69	
E	0	2.03	2.20	1.47	
F		0	0.77	0.44	
H			0	1.16	
(B)	C	D	E	F	G
B	0.22	0.25	2.97	0.55	1.25
C	0	0.48	1.95	0.64	0.65
D		0	2.43	0.12	0.85
E			0	2.07	0.65
F				0	0.57

the environment alone may not play a prominent role in maintaining morphological stability. In each case we are seeing moderate morphological changes through time within paleoenvironments/biofacies. However, when all biofacies are lumped together, we see little directed net change. This argues against the notion that morphologically stable populations occupy the same environment through time, and therefore questions the exclusive role that stabilizing selection plays in mediating stasis. It suggests that, for the limits of resolution of this analysis, in these taxa the argument for stasis elaborated by Stanley (1979) and Eldredge (1989) and based on Wright's (1931) view of species is supported. Wright (1931) recognized that species are generally broken up into different groups or demes that live in different environments. Stanley (1979) and Eldredge (1989) suggested that each of these demes will undergo largely independent adaptive histories in reaction to local environmental conditions so that the net sum of these different histories will generally lead to no net change.

We do not claim to be analyzing actually reproducing populations or demes in the Hamilton Group. However, we are considering statistical populations of organisms occurring in similar environments. We refer to these samples as *environmental populations* (see DISCUSSION). In the Hamilton Group these environmental populations appear to undergo significant changes in morphology through time. However, the net sum of these morphological changes across all environmental populations leads to no net shift in species morphology.

No prominent geological features have been recognized in the Middle Devonian of New York State that would have divided the ranges of the species being studied into different geographic subregions. Therefore, this variation may be independent of geographic isolation. However, different environments were in relatively different positions on the sloping profile of the shoreline shown in figure 3.

These differences in patterns of phenotypic evolution in single paleoenvironments and across all paleoenvironments can be quantified using Lande's (1976) procedure for calculating minimum selective mortalities using equation (1) (see table 8A, B). The values of *b* correspond to the truncation point for morphologies, scaled as the number of standard deviations from the average phenotype. The number of selective deaths per individual per generation is also given. This is shown only for *M. audaculus* here, but a similar picture emerges for *A. spiriferoides*. Minimum selective mortalities were calculated for the morphological variables that differed most between horizons E and J. Mortalities are presented both across all paleoenvironment/biofacies and only in biofacies D. These results indicate that selective mortality in re-

TABLE 8

Differences in patterns of phenotypic evolution in *Mediospirifer audaculus* between stratigraphic horizons E, the lower Wanakah Shale, and J, the lower Windom Shale related to minimum selective mortalities using equation (1) in the text, **(A)** across all paleoenvironments/biofacies, and **(B)** only for the *Pseudoatrypa* biofacies (biofacies D). Shown are values for $|z|$, σ, b, and approximate minimum selective mortalities (MSM), all defined in the text. Only the most divergent morphological variables are presented.

(A)	$\|z\|$	σ	b	MSM rates
HTR	0.07	0.06	4.99	3×10^{-7}
WTR	0.06	0.06	5.02	3×10^{-7}
MAXF_SH	0.08	0.06	4.96	3×10^{-7}
(B)	$\|z\|$	σ	b	MSM rates
HTR	0.61	0.046	4.48	3.4×10^{-6}
WTR	0.56	0.047	4.50	3.4×10^{-6}
MAXF_SH	0.08	0.065	4.80	8×10^{-7}

lation to the characters studied is extremely low in this species lineage, and this level of selection could probably not be distinguished from drift. For instance, across all paleoenvironments considered, only three selective deaths per 10 million organisms occurred. These values are comparable to those recovered by Lande (1976) from a series of other fossil taxa, and suggest that across all paleoenvironments only those phenotypes 5 SD from the mean would be eliminated. As Haldane (1949) recognized, fossil specimens that differed this much from mean morphology would probably be assigned to a separate species.

It is interesting to note that selective mortality is a factor of 10 higher in a single paleoenvironment/biofacies than across all paleoenvironments/biofacies. These selective mortalities are still very low, but this information argues against the conclusion that stabilizing selection is preserving stasis. If anything, selection pressures are stronger within a single environment than across all environments.

It is important to note that in these analyses, environments were constant only for the range of variables we recognized. There are several other variables that we could not or did not measure but which may have varied.

Assessing Ecophenotypic Variation

In order to assess how ecophenotypic effects may have influenced morphology, a canonical discriminant analysis was used to partition specimens according to the paleoenvironment/biofacies they occurred in. If ecophenotypic effects strongly influenced species morphology in these brachiopod taxa, then the scores of specimens on canonical variates axes should significantly differ if specimens hail from different biofacies. However, for both *M. audaculus* and *A. spiriferoides* the opposite result was found. Scores of specimens from different paleoenvironments/biofacies completely overlapped on canonical variate axes (fig. 8C), and there was little difference between biofacies (tables 5C, 7B). Thus ecophenotypic effects do not play a prominent role in these data.

Statistical Analysis of Ontogenetic Trajectories

Mediospirifer audaculus. — An analysis of covariance, when conducted to test for heterogeneities of slope in plots of the variable W versus time (H) across different stratigraphic horizons gave the slopes in table 9A. When regression lines are fit to specimens from different stratigraphic horizons, slopes from the uppermost and lowermost sections do not differ significantly, indicating stasis in allometric heterochrony. However, sections E and H do differ significantly from both horizons A and B and J and K (see fig. 9A). These differences in slope, although statistically significant, are not large. For example, according to table 9A, the slope fitted to the regression line for stratigraphic horizon K is $1.79 \pm$ SE. For horizon H it is $2.16 \pm$ SE. (No units are given for these slopes because both axes depict distance measurements.)

Some statistically significant differences are also found for the y-intercepts of these different regression lines. Stratigraphic horizons that show significant differences in intercepts from the calibrating, uppermost horizon, are not always the same as those which tend to differ in slope.

When the covariance analysis was conducted for the variables IAW and I, patterns similar to those discovered for the variable W emerged, but the heterogeneities of slope

were of lesser magnitude. For the purposes of brevity and clarity these results are not presented here.

The results of the analysis of covariance for ontogenies of *M. audaculus* suggest two broad patterns: 1) there is concordance between the allometric ontogenies of specimens from the lowermost and uppermost stratigraphic horizons, with varying differences in samples from the middle horizons; 2) a 15% difference in slopes is found between those samples that significantly differ. Thus, some oscillatory change does occur in the allometric ontogeny of this species. However, no net change is accrued over earliest to latest Hamilton time (5 million years). The concordance between uppermost and lowermost stratigraphic samples with differences emerging in the middle sections roughly mirrors the results from the canonical discriminant analysis.

Athyris spiriferoides. — Analysis of covariance to test for heterogeneities of slope in plots of the variable *W* versus time (*H*) across different stratigraphic horizons indicates significant differences in slope between the lowermost and uppermost horizons, A and S. In addition, horizons E, P, and Q differ significantly from S. Horizons P and Q differ most significantly from horizon A (see table 9B and fig. 9B). There is a significant shift in allometric ontogeny through time in *A. spiriferoides,* with differences in slope of about 20% between uppermost and lowermost sections. However, oscillation in this trend appears to be present, with a subtle reversion back to the earlier pattern of allometric heterochrony in the latest horizons after 30% differences in slope were manifested between horizon A and horizons P and Q.

The patterns retrieved when ontogenetic trajectories for the variables *WU* and *HW* were considered do not differ from those found for the variable *W,* except that the magnitudes of the greatest differences in slope are smaller, only 15%. For the purposes of brevity and clarity these results are not presented here.

TABLE 9

The slopes obtained by an analysis of covariance used to assess allometric heterochrony in the Hamilton Group. This analysis was performed to test for heterogeneity of slopes for values of the variable *W* vs. time (*H*) from different stratigraphic horizons for **(A)** specimens of *M. audaculus,* and **(B)** for specimens of *A. spiriferoides.* The significance of the departures in slope relative to the reference sections (stratigraphic horizons K and S respectively) is shown along with the standard error of estimate of the slope.

(A)	Slope	Signif	SE
A	1.81	0.88	0.15
B	1.72	0.72	0.21
C	2.03	0.14	0.16
D	1.87	0.47	0.11
E	2.05	0.01	0.10
F	1.96	0.07	0.09
G	1.99	0.07	0.11
H	2.16	0.003	0.12
J	1.84	0.66	0.10
K	1.79		0.07
(B)	Slope	Signif	SE
A	0.99	0.001	0.08
B	1.13	0.11	0.07
C	1.23	0.70	0.06
D	1.27	0.75	0.08
E	1.13	0.04	0.06
F	1.23	0.72	0.06
G	1.22	0.51	0.06
H	1.21	0.42	0.06
I	1.19	0.25	0.06
K	1.16	0.08	0.05
L	1.27	0.81	0.06
M	1.24	0.74	0.06
N	1.18	0.20	0.06
O	1.32	0.27	0.06
P	1.39	0.01	0.06
Q	1.40	0.03	0.07
R	1.34	0.17	0.06
S	1.26		0.05

DISCUSSION

Over 1000 specimens of two species of brachiopods from Middle Devonian rocks of New York State were subjected to morphometric analysis over a variety of environments and stratigraphic horizons. Measurements were taken to capture information both on overall shell shape and organismal ontogeny. The results from multivariate statistical analysis of morphometric data and rates of change of individual variables from *Mediospirifer audaculus* indicate net stasis during its 5 million year history. However, shifts in morphology and allometric heterochrony did occur during this time. The greatest morpho-

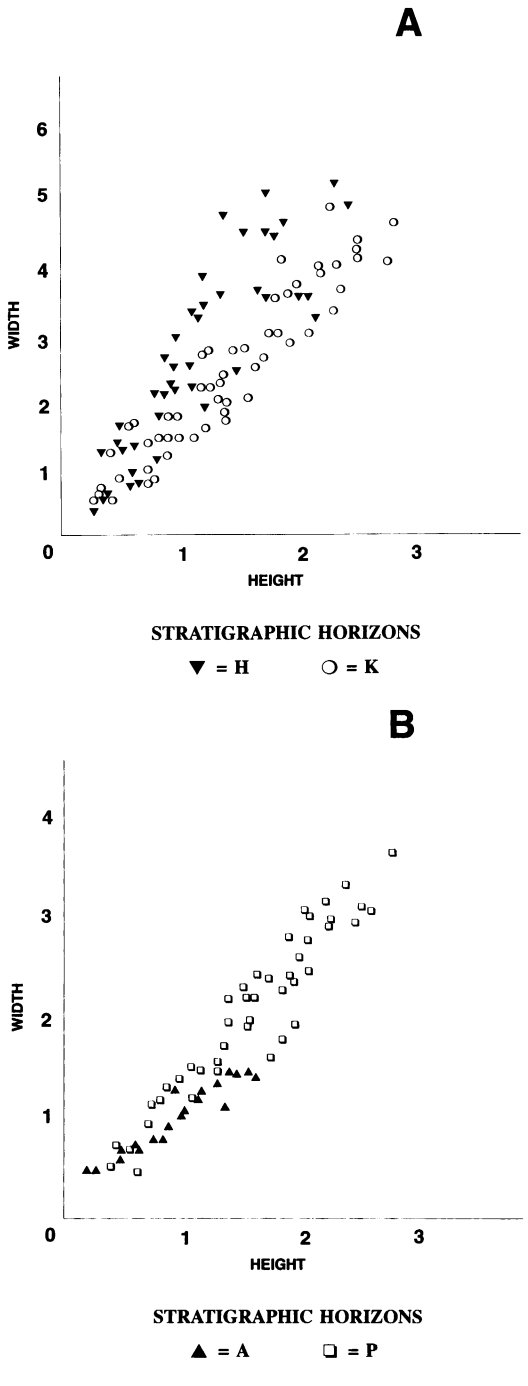

Fig. 9. Scatter plot summarizing the analysis of covariance which tested for heterogeneity of slopes of the variable *W* versus time (*H*) calibrated allometrically, for **A**, *Mediospirifer audaculus* and **B**, *Athyris spiriferoides* from different stratigraphic horizons. **A**, Horizons H and K. Notice the steeper slope of H. **B**, Horizons A and P. Notice the steeper slope of P.

logical excursions were found between samples from the lowest and intermediate sections of the Hamilton Group.

The same largely holds true for *Athyris spiriferoides,* with overall net stasis in morphology, though not in allometric heterochrony. The changes in allometric heterochrony in this species fits Hallam's (1978) suggestion that they may display phyletic trends. Oscillations do occur within the section, with the greatest departures in morphology and allometric heterochrony between oldest and intermediate horizons, though these intermediate horizons are younger than those that encompassed the greatest departures in *M. audaculus.*

Analyses also indicate that ecophenotypic effects do not have an important influence on the morphology of either species. In addition, the morphology of both *Mediospirifer audaculus* and *Athyris spiriferoides,* when quantified using multivariate morphometrics and rates of change of individual characters, was found to change more through time within a single paleoenvironment/biofacies than when all biofacies are considered, and this may have implications for the way we view stasis. It suggests that populations are not morphologically stable in the same paleoenvironment/biofacies over long intervals of time. Typically the environment, via stabilizing selection, has been viewed as an important force contributing to stasis of species lineages. However, these changes in the face of a constant environment (though not necessarily a constant selective regime, but assuming the two are related) suggest that environmental stability does not necessarily preserve species morphology. Amounts of phenotypic selection on the variables studied were found to be a factor of ten stronger in a single paleoenvironment than when all paleoenvironments were considered. This suggests that stabilizing selection is not the sole factor contributing to stasis in these taxa.

An additional mechanism for stasis emerges from the way in which species are orga-

nized. Wright (1931) recognized that species are typically broken up into reproductive groups occurring in separate environments, and these groups, referred to as demes, will undergo partly separate adaptive histories. The morphology of organisms in these demes may change through time as they adapt to local conditions. However, the net sum of these changes will often cancel out such that the overall morphology of the species remains constant (Stanley, 1979; Eldredge, 1989). This is intuitively obvious, since only if all morphological changes in all environments were in the same direction would net change in species morphology be significant.

We do not claim to be studying actual demes or reproductive populations, in the restrictive sense of Wright (1931). Instead, we are studying statistical populations of organisms occurring in similar paleoenvironments through time. We refer to these groups as "environmental populations," and they represent lineages in constant environments in the sense of Eldredge (1989) and in the broad sense of Wright (1931). Study of such groups provides a way of assessing the relationship between organismal morphology and environment. Statistical analyses suggest that these "environmental populations" do change significantly through time. These morphological changes may be due to adaptation, random effects, or the invasion of populations from unsampled geographic regions. However, the latter seems least likely as there are no prominent morphological breaks between successive stratigraphic horizons for either species except in one instance for *M. audaculus,* and in this case the two horizons were separated by a body of rock that could not be sampled.

Because a species is a unit in nature broken up into different subparts, the net change in a species is equal to the sum of the morphological changes in all the different "environmental populations." Each of these parts undergoes an independent history, and thus as long as a species occurs in several different environments one would predict overall that it would resist change.

CONCLUSIONS

For the two brachiopod species studied, *Mediospirifer audaculus* and *Athyris spiriferoides,* the hypothesis of morphological stasis could not be refuted. Samples from the first and last occurrences of the two species, from the lowermost and uppermost stratigraphic horizons of the Hamilton Group, still show considerable morphological overlap. Changes in morphology do occur within the Hamilton, but these changes are reversible and therefore do not count as evolutionarily significant in the sense of Gould and Eldredge (1977) and Lande (1986).

When single paleoenvironments/biofacies are studied using terminal ontogenetic stages, morphological changes are found to occur through time. These changes are larger than the changes that occur through time when the entire range of environments from which a species is known are considered. This implies that persistence in environments through time in conjunction with stabilizing selection is not the only cause of morphological stability. Instead, stasis may also be the result of the organization of species. Separate environmental populations of a species will change through time, but the changes in all these different environmental populations will generally produce no net morphological change.

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REFERENCES

Alberch, P.
1982. Developmental constraints in evolutionary processes. *In* J. T. Bonner (ed.), Evolution and development, pp. 313–332. New York: Springer.

Bailey, J. B.
1983. Middle Devonian Bivalvia from the Solsville Member (Marcellus Formation), central New York State. Bull. Am. Mus. Nat. Hist. 174: 193–326.

Barnosky, A. D.
1990. Evolution of dental traits since latest Pleistocene in meadow voles from Virginia. Paleobiology 16: 370–383.

Blackstone, N. W.
1987. Allometry and relative growth: pattern process in evolutionary studies. Syst. Zool. 36: 76–78.

Blackstone, N. W., and P. O. Yund
1989. Morphological variation in a colonial marine hydroid: a comparison of size-based and age-based heterochrony. Paleobiology 15: 1–10.

Brett, C. E.
1986. The Middle Devonian Hamilton group of New York: an overview. *In* C. Brett (ed.), Dynamic stratigraphy and depositional environments of the Hamilton Group (Middle Devonian) in New York State, Part 1. New York State Mus. Bull. 457: 1–4.

Brett, C. E., and G. C. Baird
1986. Symmetrical and upward shallowing cycles in the Middle Devonian of New York State and their implications for the punctuated aggradational cycle hypothesis. Paleoceanography 1: 431–445.

Brett, C. E., K. B. Miller, and G. C. Baird
1990. A temporal hierarchy of paleoecologic processes within a Middle Devonian epeiric sea. *In* W. Miller, III (ed.), Paleocommunity temporal dynamics: the long-term development of multispecies assemblies. Paleontol. Soc. Spec. Publ. 5: 178–209.

Brett, C. E., S. E. Speyer, and G. C. Baird
1986. Storm-generated sedimentary units: tempestite proximality and event stratification in the Middle Devonian Hamilton Group of New York. *In* C. Brett (ed.), Dynamic stratigraphy and depositional environments of the Hamilton Group (Middle Devonian) in New York State, Part 1. New York State Mus. Bull. 457: 129–156.

Charlesworth, B. R., R. Lande, and M. Slatkin
1982. A Neo-Darwinian commentary on macroevolution. Evolution 36: 474–498.

Cooper, G. A., C. Butts, K. E. Caster, G. H. Chadwick, W. Goldring, E. M. Kindle, E. Kirk, C. W. Merriam, F. M. Swartz, P. S. Warren, A. S. Warthin, and B. Willard
1942. Correlation of the Devonian sedimentary formations of North America. Bull. Geol. Soc. Am. 53: 1729–1794.

Eldredge, N.
1985. Time frames. New York: Simon and Schuster.
1989. Macroevolutionary dynamics. New York: McGraw Hill.

Eldredge, N., and J. Cracraft
1980. Phylogenetic patterns and the evolutionary process. New York: Columbia Univ. Press.

Eldredge, N., and S. J. Gould
1972. Punctuated equilibria: an alternative to phyletic gradualism. *In* T. J. Schopf (ed.), Models in paleobiology, pp. 82–115. San Francisco: Freeman, Cooper.

Ettensohn, F. R.
1985. The Catskill Delta complex and the Acadian orogeny: a model. *In* D. L. Woodrow and W. D. Sevon (eds.), The Catskill Delta. Geol. Soc. Am. Spec. Pap. 201: 39–50. Boulder, CO: Geological Society of America.

Gingerich, P. D.
1976. Paleontology and phylogeny: patterns of evolution at the species level in early tertiary mammals. Am. J. Sci. 276: 1–28.
1985. Species in the fossil record: concepts, trends and transitions. Paleobiology 11: 27–41.

Gould, S. J.
1988. Prolonged stability in local populations of *Cerion agassizi* on Great Bahama bank. Paleobiology 14: 1–18.

Gould, S. J., and N. Eldredge
1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology 3: 115–151.

Grasso, T. X.
1986. Redefinition, stratigraphy and depositional environments of the Mottville Member (Hamilton Group) in central and eastern New York. *In* C. E. Brett (ed.), Dynamic stratigraphy and depositional environments of the Hamilton Group (Middle Devonian) in New York State, Part 1. New York State Mus. Bull. 457: 5–31.

Haldane, J. B. S.
1931. The causes of evolution. New York: Harpers.
1949. Suggestions as to quantitative measurement of rates of evolution. Evolution 3: 51–56.

Hallam, A.
1975. Evolutionary size increase and longev-

ity in Jurassic bivalves and ammonites. Nature 285: 493–496.
1978. How rare is phyletic gradualism and what is its evolutionary significance? Evidence from Jurassic bivalves. Paleobiology 4: 16–25.
Jablonski, D.
1987. Heritability at the species level: analysis of geographic ranges of cretaceous mollusks. Science 238: 360–363.
Kent, D. V.
1985. Paleocontinental setting for the Catskill Delta. *In* D. L. Woodrow and W. D. Sevon (eds.), The Catskill Delta. Geol. Soc. Am. Spec. Pap. 201: 9–14. Boulder, CO: Geological Society of America.
Lande, R.
1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30: 314–334.
1980. Genetic variation and phenotypic evolution during allopatric speciation. Am. Nat. 116: 463–478.
1986. The dynamics of peak shifts and the pattern of morphological evolution. Paleobiology 12: 343–354.
Lich, D.
1990. *Cosomys primus*: a case for stasis. Paleobiology 16: 384–395.
Maynard Smith, J., R. Burian, S. Kauffman, P. Alberch, J. Campbell, B. Goodwin, R. Lande, D. Raup, and L. Wolpert
1985. Developmental constraints and evolution. Q. Rev. Biol. 60: 265–287.
Mayr, E.
1963. Animal species and evolution. Cambridge, MA: Harvard Univ. Press.
McKinney, M. L.
1986. Ecological causation of heterochrony: a test and implications for evolutionary theory. Paleobiology 12: 282–289.
1988. Classifying heterochrony: allometry, size and time. *In* M. McKinney (ed.), Heterochrony in evolution, pp. 17–34. New York: Plenum.
Miller, K.
1986. Depositional environments and sequences, "*Pleurodictyum* Zone", Ludlowville formation of western New York. *In* C. E. Brett (ed.), Dynamic stratigraphy and depositional environments of the Hamilton Group (Middle Devonian) in New York State, Part 1. New York State Mus. Bull. 457: 57–77.
Neff, N. A., and L. F. Marcus
1980. A survey of multivariate methods for systematics. Workshop on Numerical Methods in Syst. Mammal., Annual Meeting of the Am. Soc. of Mammal.
SAS.
1987. SAS Institute Inc. Cary, NC.
Savarese, M., L. M. Gray, and C. E. Brett
1986. Faunal and lithologic cyclicity in the Centerfield Member (Middle Devonian: Hamilton Group) of western New York: a reinterpretation of depositional history. *In* C. Brett (ed.), Dynamic stratigraphy and depositional environments of the Hamilton Group (Middle Devonian) in New York State, Part 1. New York State Mus. Bull. 457: 32–56.
Sheldon, P. R.
1987. Parallel gradualistic evolution of Ordovician trilobites. Nature 330: 561–563.
Simpson, G. G.
1953. The major features of evolution. New York: Columbia Univ. Press.
Somers, K. M.
1989. Allometry, isometry and shape in principal components analysis. Syst. Zool. 38: 169–172.
Soper, N. J., R. A. Strachan, R. E. Holdsworth, R. A. Gayer, and R. O. Greiling
1992. Sinistral transpression and the Silurian closure of Iapetus. J. Geol. Soc. 149: 871–880.
Stanley, S. M.
1979. Macroevolution. San Francisco, CA: W. H. Freeman.
1985. Rates of evolution. Paleobiology 11: 13–26.
Stanley, S. M., and X. Yang
1987. Approximate evolutionary stasis for bivalve morphology over millions of years: a multivariate, multilineage study. Paleobiology 13: 113–139.
Sundberg, P.
1989. Shape and size-constrained principal components analysis. Syst. Zool. 38: 166–168.
Williamson, P. G.
1981. Paleontological documentation of speciation in Cenozoic molluscs from Turkana Basin. Nature 293: 437–443.
1987. Selection or constraint? a proposal on the mechanism for stasis. *In* K. S. W. Campbell and M. F. Day (eds.), Rates of evolution, pp. 129–142. London: Allen and Unwin.
Wright, S.
1931. Evolution in mendelian populations. Genetics 16: 97–159.

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