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Microevolutionary Implications Of Clinal Variation In The Paleozoic Bryozoan Streblotrypa

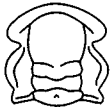By: **Steven J. Hageman**

Abstract

Ideally, studies of microevolution, including those of patterns and rates of speciation, need to account for features of geographic and ecophenotypic morphologic variation. These factors can provide primary sources of variation for evolution to act upon. They can also, however, produce variation among characters that are not directly related to speciation events, thus confounding recognition of larger evolutionary patterns. Because of limitations of geologic settings, features of morphologic variation associated with geographic and ecophenotypic variation are difficult to constrain and are often neglected. Consequences of ignoring potential geographic variation in microevolutionary studies are varied. The likelihood of observing stasis or gradation may increase or decrease depending on initial assumptions. A series of tests that place reasonable limits on potential errors, however, can strengthen conclusions from empirical microevolutionary studies. Late Paleozoic cyclothems of the North American Midcontinent provide an excellent opportunity to study patterns of microevolution and concomitant ecophenotypic and geographic variation.

Microevolutionary implications of clinal variation in the Paleozoic bryozoan *Streblotrypa*

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Ideally, studies of microevolution, including those of patterns and rates of speciation, need to account for features of geographic and ecophenotypic morphologic variation. These factors can provide primary sources of variation for evolution to act upon. They can also, however, produce variation among characters that are not directly related to speciation events, thus confounding recognition of larger evolutionary patterns. Because of limitations of geologic settings, features of morphologic variation associated with geographic and ecophenotypic variation are difficult to constrain and are often neglected. Consequences of ignoring potential geographic variation in microevolutionary studies are varied. The likelihood of observing stasis or gradation may increase or decrease depending on initial assumptions. A series of tests that place reasonable limits on potential errors, however, can strengthen conclusions from empirical microevolutionary studies. Late Paleozoic cyclothems of the North American Midcontinent provide an excellent opportunity to study patterns of microevolution and concomitant ecophenotypic and geographic variation. Based on multivariate analysis of 28 morphometric characters, specimens of the rhabdomesine bryozoan genus *Streblotrypa*, collected from eight coeval localities distributed along a 300 km transect, exhibit a morphologic cline associated with thickening of the skeleton from south to north. Additional specimens were collected from five younger localities to test for temporal and ecologic variation. The range of observed morphologic variation from a single horizon was as great as that observed over the entire stratigraphic sequence from varied lithologies. This indicates a pattern of overall morphological stasis through the interval studied. □*Bryozoa, clines, microevolution, variability, geographic variation, Carboniferous.*

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Mode and tempo of evolutionary character change and speciation remain problematic well over a century after publication of *The Origin of Species*. Because the fossil record is historic and tangible, it provides an ideal venue for studying evolutionary patterns. In recent years, new questions about species and their evolution have been framed, and numerical and microcomputer techniques have been developed that allow rigorous analysis. Documentation of microevolutionary change is accomplished through morphometric studies of fossil clades with samples taken over short intervals through sustained stratigraphic sections. A number of papers treating patterns of evolution have established criteria for study of microevolution, including: wide geographic coverage, a sequence of closely spaced samples, well-defined taxa and rigorous biometric testing of large samples (Gould & Eldredge 1977).

With notable exceptions, conclusions from most empirical studies of microevolution published in the past twenty years are weakened because studies fail to meet all of these criteria. Admittedly, these criteria prove extremely difficult to satisfy simultaneously in natural geologic settings. Most empirical studies have optimized one aspect or another of these criteria (e.g., stratigraphic resolution or temporal duration). Workers cannot be faulted for emphasizing certain aspects of a study based on the favorable characteristics of a given geologic setting, but they should acknowledge clearly the limits of the study with regard to the well-established criteria for microevolutionary studies.

A potentially greater weakness present in most previous empirical studies of microevolution is the attribution of all observed morphologic variation to evolutionary change without consideration of other potential sources of variation (ecophenotypic, geographic, ontogenetic, other?). This arises from the fact that ecophenotypic variation and geographic variation are difficult to constrain in most geologic settings. Kelley (1983) and Wei & Kennett (1988) have, however, directly addressed geographic variation in broader studies of microevolution. Cisne *et al.* (1980) and Wei &
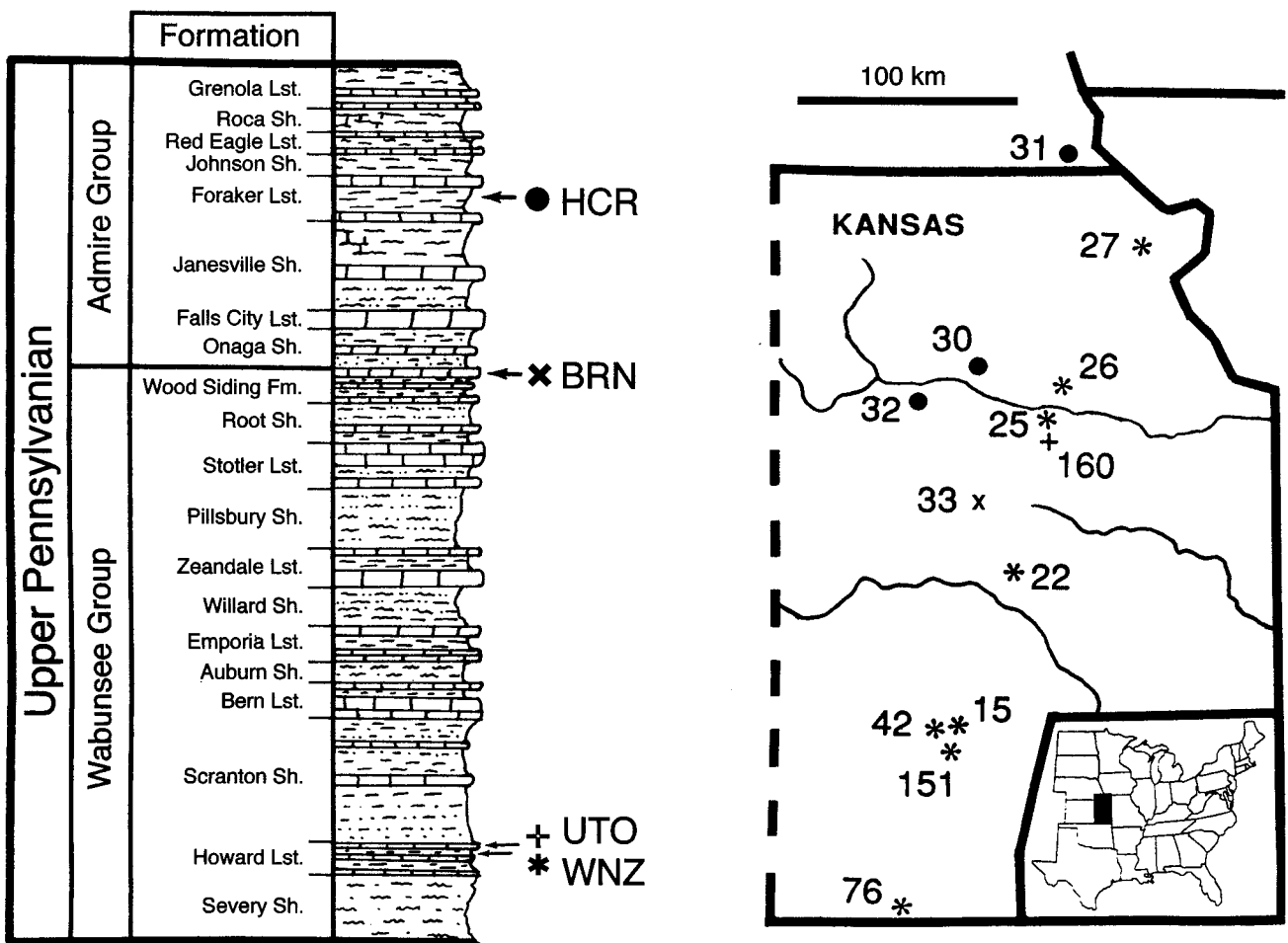
Fig. 1. Stratigraphic and geographic distribution of streblotrypid localities listed in Locality Appendix of Hageman (1993): ✳ WNZ: Winzeler Shale, and + UTO: Utopia Limestone of the Howard Limestone Formation; x BRN: Brownsville Limestone of the Wood Siding Formation; ● HCR: Hughes Creek Shale of the Foraker Limestone Formation.

Kennett (1988) evaluated both evolutionary change through time and ecophenotypic variation through an environmental cline.

Under certain conditions, however, it is possible to recognize presence or absence of environmentally induced phenotypic change in the fossil record (Kues 1989; Pandolfi & Burke 1989; Cuffey & Pachut 1990; Pachut & Cuffey 1991). Documentation of morphologic variation correlated with geographic distribution (whatever the causal factors) requires special settings where coeval sediments can be correlated over great distances. Results from studies that address ecophenotypic and geographic variation need to be considered when developing conclusions for microevolutionary studies, including interpretations of patterns and rates of speciation. For example, a morphologic change originally correlated with a bathymetric gradient could be misinterpreted as an evolutionary trend in a shallowing upward stratigraphic sequence if the ecologic significance is not recognized (Pachut & Cuffey 1991).

This paper employs a morphometric data set (28 characters measured from 450 composite bryozoan zooids) to address factors of ecophenotypic and geographic variation using multivariate numerical methods. This study is part of an ongoing empirical microevolutionary study employing the rhabdomesine bryozoan genus *Streblotrypa*.

Setting

Late Paleozoic sediments of the North American Midcontinent are cyclic deposits of shales, limestones and sandstones representing a depth gradient perpendicular to shore line. Their cyclic nature is a result of multiple transgressions and regressions, possibly related to glacial episodes (Heckel 1986). Much has been published on the paleoenvironments, depositional history, biostratigraphy, and lithostratigraphic correlation of these sediments (Sorensen et al. 1989). Using conodonts, strata as thin as 10–100 cm can be correlated

some 400 km from Oklahoma to Nebraska (Heckel 1986), providing temporal resolution in the order of 10^4–10^5 years, sustained over a period of about twelve million years, from Late Desmoinesan (Westphalian) through Wolfcampian (Sakmarian). Earlier studies of morphologic variation in this setting include works on brachiopods (Spencer 1978), foraminifers (Koepnick & Kaesler 1971), and bryozoans (Cuffey 1967; Farmer & Rowell 1973; Pachut & Cuffey 1991).

Bryozoans, with their many morphologic features (most with known biologic significance), are well suited for studies that require large morphometric data sets. Cryptostome bryozoans are abundant in the cyclothems of the Midcontinent of North America, and their colonial nature means that even small fragments can provide tenable data. An additional benefit of coloniality is that relative proportions of phenotypic versus genotypic variation among large colonies can be tested (Schopf 1976). Numerical analysis of the large, cryptostome bryozoan morphometric data set of Snyder (1991) demonstrated that discrete morphs can be objectively recognized at three hierarchical levels, corresponding to species, genera and families (Hageman 1991). Strong correlation between morphospecies and groupings from protein electrophoresis indicate that at least some cheilostome and scleractinian biological species can be recognized from skeletal characters (Jackson & Cheetham 1990; Potts *et al.*, in press), giving credence to Snyder's (1991) recognition of true biological species, rather than morphotaxa of uncertain biological significance.

The combination of cryptostome bryozoans, with their relative abundance and morphologic complexity, and late Paleozoic cyclic sediments of the Midcontinent, with their fine stratigraphic resolution and varied environments that can be correlated over large geographic distances, provides an excellent opportunity to study patterns of microevolution and concomitant ecophenotypic and geographic variation.

Materials and methods

More than 150 Upper Pennsylvanian and Lower Permian sites were visited in eastern Kansas, and bryozoan faunules were collected where present (Hageman 1992a, Figs. 24, 25 and Appendix I). After a survey of the stratigraphic and geographical distribution of all bryozoan taxa, the rhabdomesine genus *Streblotrypa* was selected for this study. Members of the genus *Streblotrypa* form a morphologically distinct group, separate from related genera. A range of morphologic variability was apparent in available *Streblotrypa* material, and three species had been described previously from the sampled interval. All morphs of *Streblotrypa* present in the study area were employed in these analyses, but species-level taxonomic distinctions were *not* made a priori.

Data were collected for 28 morphometric characters (Table 1) from exteriors and acetate peels prepared from

Table 1. Morphometric characters measured from *Streblotrypa prisca*, with abbreviations. See Hageman (1993) for detailed description and location of characters.

Exterior characters

EBW Branch width (not measured at branch bifurcation, can be measured in transverse section but exterior preferred)

Apertural characters

AAL Aperture length (measured proximo-distally)
AAW Aperture width (measured perpendicular to aperture length)
AAS Aperture spacing along branch (distance between aperture centers along branch)
ALS Lateral aperture spacing (distance between aperture centers across branch)
ADS Diagonal aperture spacing (distance between diagonal aperture centers)
APW Peristome width (measured at distal end of aperture)
AAR Apertural area (including inclined vestibule as needed)
AAA Aperture adjacent angle (acute angle taken from proximo-distal trace adjacent to lateral aperture)

Autozooecial chamber characters

CAL Autozooecial chamber length (maximum length measured down the middle of the chamber from the interior wall to the flexure of the vestibule, measured in longitudinal section)
CVL Vestibule length (measured down the middle of the vestibule from the flexure to the exterior)
CAD Autozooecial chamber depth (measured perpendicular to chamber length in the longitudinal section)
CRA Chamber reverse wall budding angle (acute angle of emplacement measured in longitudinal section)
CPA Autozooecial chamber angle (acute angle measured at flexure in the middle of the maximum chamber length)
CEA Autozooecial exozonal angle (acute angle measured between the chamber length and vestibule)
CAW Autozooecial chamber width (measured across branch at endozone-exozone boundary in transverse section)
CAR Autozooecial chamber area (measured in longitudinal section)

Zoarial skeletal characters

KGT Endozone wall thickness (transverse section)
KXD Diameter of endozone (transverse section)
KXT Thickness of exozone (transverse section)

Polymorph characters

PMD Maximum diameter of polymorphs
PSD Minimum diameter of polymorphs
PMS Spacing of polymorphs
PMN Number of polymorphs (in a rhombic field)

Axial zooecia

XZN Number of zooecia across axial bundle (transverse section)
XZD Axial zooecia diameter (transverse section)
XWT Thickness of axial zooecial wall (transverse section)

Hemisepta

HDL Distance on distal wall (length from reverse all budding site to placement of hemisepta on proximal wall)

oriented sections using Bioscan Optimas image analysis program. (See Hageman 1993 for detailed discussion of morphologic characters, data collection procedures, and locality information.) Specimens were deposited in the Department of Geology, University of Illinois, Urbana.

Stratigraphic distribution

Streblotrypa specimens (colony fragments) were collected from the base of the Winzeler Shale (10 cm interval) from eight localities that span a 300 km transect from southcentral to northeastern Kansas (Fig. 1, Localities 76, 151, 42, 15, 22, 25, 26, 27). The Winzeler Shale Member (WNZ) is a distinctive unit in the Howard Formation, representing a minor transgressive stage in a Kansas-type Pennsylvanian cyclothem (P. Heckel, personal communication, 1988). The Winzeler and the underlying Church Limestone are each only about 50 cm thick, but the sharp interface between them can be traced continuously for 400 km from Oklahoma to Nebraska. The time interval represented between the southern and northern exposures of this contact is far less than the resolution of the most sensitive biostratigraphic markers; for a regional stratigraphic event, the contact is nearly isochronous. Five colony fragments were studied per locality, and seven observations were collected from each fragment for 28 characters (Table 1). The Winzeler samples provide the primary data set for this study.

The Utopia Limestone Member (UTO) of the Howard Formation is the stratigraphically next higher unit above the Winzeler Shale (Fig. 1). Samples were studied from one outcrop, Locality 160. The expression of the Utopia at this locality, lenticular with shaley partings, proved to be unusual for this unit, as it is massive in other areas. Ten samples were prepared from Locality 160 and five observations collected from each sample for 28 characters.

Samples were also studied from four stratigraphically younger localities, representing two horizons. One locality sampled the Brownsville Limestone Member (BRN) of the Wood Siding Formation, which represents a minor transgressive stage in a Kansas-type cyclothem (Heckel *et al.* 1979) and ranges from 30 to 150 cm in thickness (Fig. 1; Locality 33). Samples were studied from three localities of the Hughes Creek Shale Member (HCR) of the Foraker Formation, which represents alternating minor transgressive and regressive stages (Heckel *et al.* 1979), The Hughes Creek is much thicker (6–18 m) than the Winzeler Shale and is more variable lithologically (Fig. 1; Localities 30, 31, 32). The Foraker Formation is here recognized as uppermost Pennsylvanian, based on redefinition of the Pennsylvanian–Permian boundary in Kansas (Baars *et al.* 1990). Five specimens were studied from each of these four younger localities, and when the Winzeler data set was combined with the others, only the first five observations for each character were used in order to achieve equal group sample sizes and optimize quality of data (see Hageman 1993).

Composite zooids and populations

Not all desired characters can be measured from a single zooecium, because the preparation technique is destructive (e.g., chamber length and chamber width require separate perpendicularly oriented sections). In this study, a com-posite zooid (CZ) is the operational unit in numerical analyses rather than a true zooid or a colony. For example, a single CZ in this study consists of the observed values for 28 characters represented by a complete suite of longitudinal characters measured from a single chamber, plus a complete suite of transverse characters measured from a different chamber, plus a complete suite of exterior characters measured from a third chamber. A CZ represents an idealized single zooid but is compiled from the observations (measurements) of three different zooids.

The term 'population' is used here to represent a time-averaged assemblage of potentially conspecific specimens collected from a single lithologic unit (member) from a single geographic locality. The degree of time averaging varies between rock units; it is minimal in the Winzeler and more significant in the Hughes Creek.

A series of numerical tests were performed to evaluate morphologic variability of *Streblotrypa* within and among colonies, populations, morphological variates, lithology (environment), and temporal distribution. Cluster analyses were performed with *NTSYS-pc* (1.60), discriminant and canonical variates analysis with SAS (5.18), descriptive and distribution free statistics with Statview II (1.03), and normal scores test with macros written in Microsoft Excel (Hageman 1992b). See Neff & Marcus (1980) and Hageman (1991, 1992a, 1992b) for review of methods.

Astogenetic variation

Two morphs of *Streblotrypa* are evident in casual observation of available material. End members can be easily distinguished based on exterior appearances alone and consist of a robust form with a greater number of metapores (Fig. 2A) and a thinner form with well-defined longitudinal ridges (Fig. 2C); originally the two were described as *S. striatopora* and *S. ulrichi*, respectively (Rogers 1900). Examination of large populations, however, yields intermediates (Fig. 2B). In fact, some specimens express both morphologies on the same colony, demonstrating an increase in number of metapores, increase in branch size and robustness, and loss of longitudinal ridges with maturity (Fig. 3).

Numerical analyses of the morphs yield mixed results. Discriminant analysis and Mann–Whitney tests (nonparametric equivalent of two-sample t-test) support recognition of discrete morphs, but cluster analysis failed to generate correlative groups. This is not surprising, because end members are well-defined and represent a bimodal frequency distribution, but intermediates are clearly present. In Mann–Whitney tests, all characters that displayed significant differences ($p < 0.01$) between morphs are ones associated with astogenetic effects (sensu Pachut *et al.* 1991).

Based on these observations and analyses and the fact that both morphs co-occur at most localities, it is unlikely that the two morphs represent extremes of environmentally induced
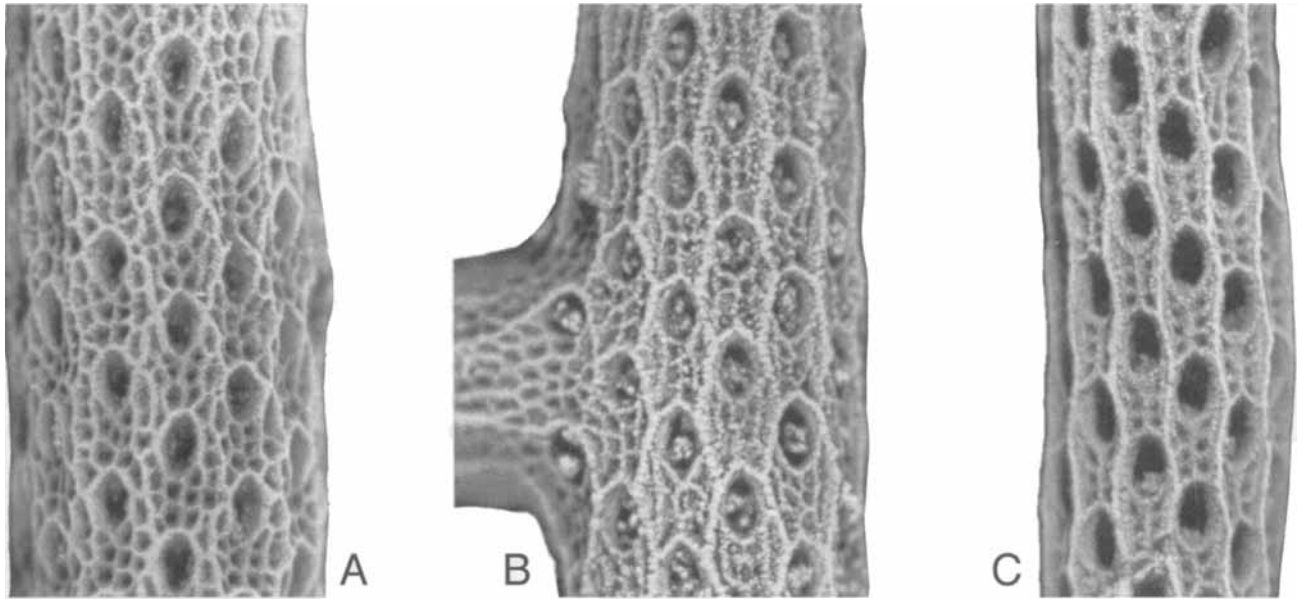
Fig. 2. *Streblotrypa prisca,* ×40. □A. Astogenetically mature morph (UI X-7072). □B. Astogenetically intermediate morph (UI X-7094). □C. Astogenetically immature morph (UI X-7071).
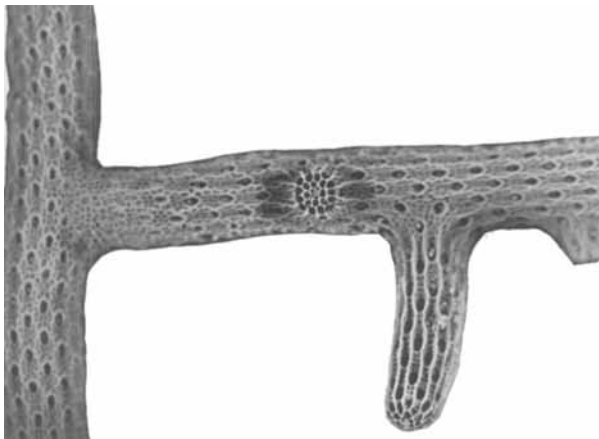

Fig. 3. Single colony of *Streblotrypa prisca,* ×12, expressing both morphs (UI X-7091).

variation. The two morphs apparently represent different astogenetic stages of the same species, *Streblotrypa prisca* (Gabb & Horn) (Hageman 1993). Therefore, specimens were not differentiated by morphs in the following analyses, unless expressly stated.

Geographic variation

Morphologic variation associated with geographic distribution can be a function of differing environmental conditions affecting phenotypes (ecophenotypic), differentiation in

genotypes at distant points along a distribution of interbreeding populations, or a combination of these factors. In any case, geographic variation plays an important role in microevolution and should be documented in microevolutionary studies (Bretsky & Lorenz 1970; Gould & Johnston 1972; Endler 1977). Studies of extant populations, both terrestrial (e.g., Shenbrot *et al.* 1991) and marine (e.g., Miller *et al.* 1982) add to our understanding of geographic and ecophenotypic variation. Although more difficult to constrain, study of geographic variation in paleontologic settings is also viable (e.g., Farmer & Rowell 1973; Kues 1989).

Geographic variation in STREBLOTRYPA

The data set consisting of specimens from eight localities of the Winzeler Shale (Fig. 1) was analyzed to recognize potential variation associated with geographic distribution. Cluster analysis failed to generate clear groups corresponding to localities. Discriminant analysis, however, assigned 191 out of 230 (83.0%) observations to their correct locality, and Van der Waerden test (normal scores test equivalent of ANOVA) demonstrated significant differences between localities for all morphometric characters except for Autozooecial Chamber Angle (CPA), Autozooecial Chamber Depth (CAD), Diameter of Endozone (KXD), and Number of Zooecia Across Axial Bundle (XZN) at the $p<0.01$ confidence level. This pattern is even stronger with discriminant analysis performed on subsets of data classified by morph. A subset of specimens recognized as astogenetically immature had an allocation efficiency ratio of $^{153}/_{161}$ (95.0%); that of mature morphs was $^{76}/_{77}$ (98.7%). These results demonstrate that

differences exist between populations from different locali-
ties, which allow for correct allocation under discriminant
analysis. Differences are obscured, however, in unweighted
cluster analysis.

The next important question is whether the localities vary
systematically in a clinal pattern.

Morphologic clines

Morphologic variation correlated with an ecologic gradient,
such as water depth or light intensity in the marine setting
(e.g., Haggerty *et al.* 1980) or altitude or precipitation in
terrestrial settings (e.g., Singh *et al.* 1990), is well known.
Morphologic variation correlated with large-scale latitudinal

gradients has also been documented (Burckle & McLaughlin
1977). Methods of Pachut & Cuffey (1991) and Cuffey &
Pachut (1990) were employed to determine whether a cline
is present in *Streblotrypa* specimens of the Winzeler Shale.

Canonical variates analysis, which is the equivalent of
principal component analysis performed on group means,
provides a set of orthogonal coordinates that maximize
variance between groups (localities here) (Neff & Marcus
1980). Values of group means projected on the first two
canonical variates (accounting for 74.8% of variance) estab-
lishes Locality 25 as an outlier for the Winzeler data (Fig. 4A).
Characters most responsible for distinguishing Locality 25
from the others (heaviest weighted in canonical variate 1 =
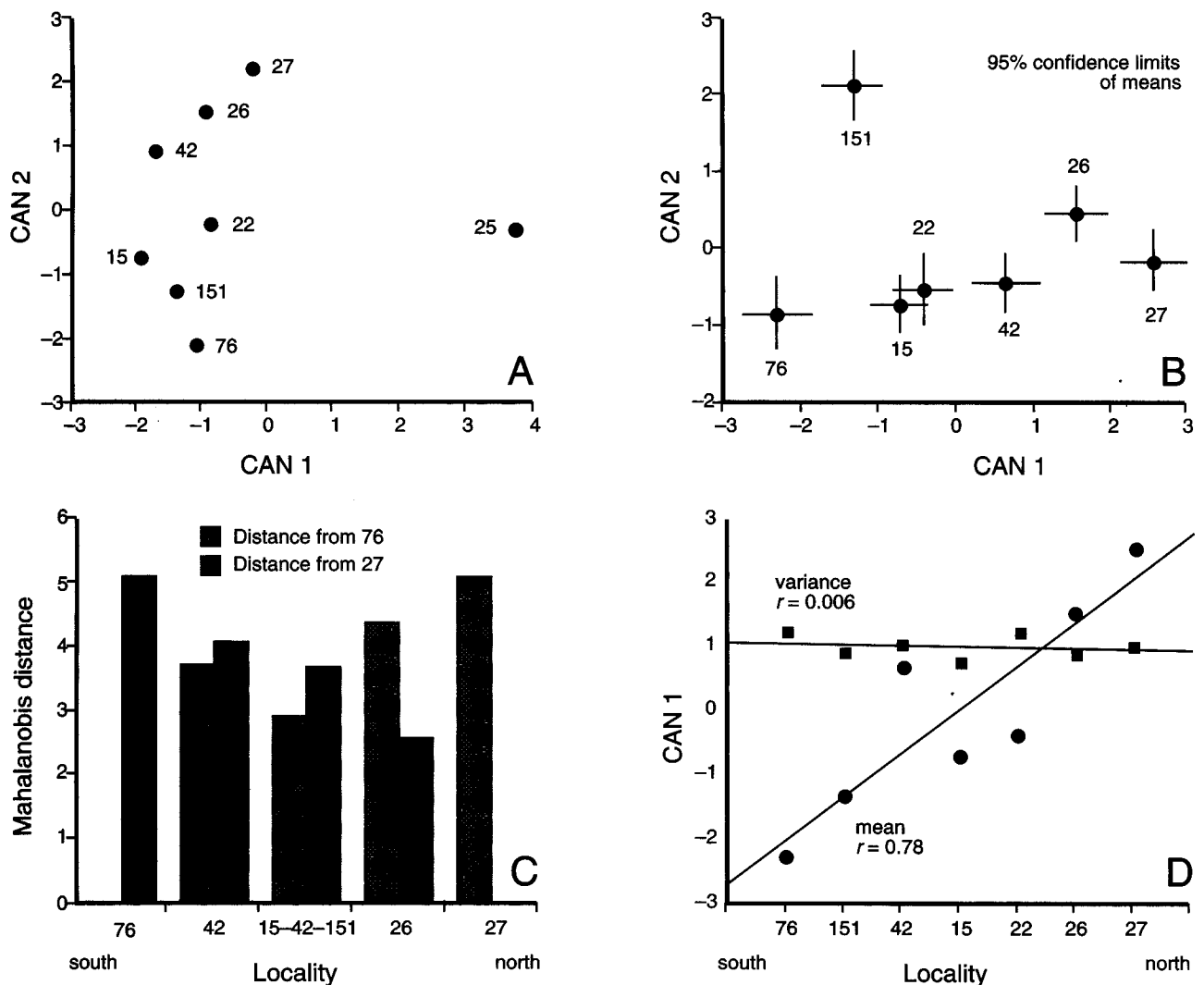CAN 1) are: Minimum Diameter of Polymorphs (PSD),

Fig. 4. □A. Group means for Winzeler Shale localities plotted on canonical discriminant axes 1 and 2. □B. Group means for Winzeler Shale localities, omitting
locality number 25, plotted on canonical discriminant axes 1 and 2. Lines represent 95% confidence limits for means. □C. Mahalanobis distances between
pairwise groupings of Winzeler localities 76 and 27 (end member of geographic distribution) with other localities. □D. Group means for Winzeler Shale
localities (omitting number 25) plotted for geographic distribution versus canonical discriminant axes one, and variance of populations for canonical means.
Linear regression lines through both reveal a correlation between geographic distribution and group means, but not group mean variance.

Aperture Width (AAW), Thickness of Exozone (KXT), Diagonal Aperture Spacing (ADS), Number of Polymorphs (PMN), and Vestibule Length (CVL). These characters, especially number of polymorphs and exozone thickness are indicative of astogenetically mature morphs. Remeasurement of five characters (AAW, ALS, ADS, CAW, and KXT) from Locality 25 verified that there was no systematic measurement error.

When specimens from Locality 25 are omitted from analysis and values of group means projected on the first two canonical variates (accounting for 60.5% of variance), a striking pattern emerges. Groups from northern localities plot high on CAN 1, those from southern localities plot low on CAN 1, and intermediate localities are mixed (Fig. 4B). Only a switch between Localities 22 and 42 keeps the trend from perfect ordination. This is illustrated clearly in a linear regression of group mean scores on CAN 1 versus locality from south to north, which provides a correlation coefficient of $r^2 = 0.78$ (Fig. 4D). This value is somewhat misleading because geographic distance has been standardized to unity between each locality. Nevertheless, the trend is clearly present.

Localities 15, 42, and 151 are in very close proximity relative to others (Fig. 1) and were grouped in some analyses. Mahalanobis distances (standardized distances in multidimensional morphospace) between group means illustrate a correlation between geographic distance and morphologic distance (Fig. 4C). That is, the average morphology of specimens from Locality 27, at one geographic extreme, is more like that of Locality 26 than that of Locality 22, yet less like those of 15–42–151; it is least like that of the most distant, namely Locality 76. The trend is not perfect in the other direction, beginning with Locality 76, but it is strong (Fig. 4C)

Characters associated with cline

Three criteria were used to determine which characters are responsible for the morphologic cline: (1) canonical variate loadings, (2) correlation coefficients between geographic distribution and group means for characters, and (3) relative magnitude of differences between group means at end points of the geographic distribution.

Characters most heavily weighted (absolute value) on CAN 1 are associated with geographic distribution (Fig. 4B), the top ten of which are highlighted in the second column of Table 2. When standardized group means for these ten characters are plotted against geographic distribution, two trends are apparent. Characters KXD and PSD decrease in size from south to north, and all other characters increase in size from south to north (Fig. 5A).

Characters with positive correlations and r^2 greater than 0.50 are illustrated in Fig. 5B and highlighted in column 3 of Table 2. These characters are most strongly correlated with geographic distribution (CEA has a strong negative correla-

Table 2. Changes in morphometric characters from south to north along Winzeler Shale transect (Fig. 1). Column 1: Asterisk to right indicates a character significant in two of the three columns 2, 3 and 4; asterisk to left indicates a character significant in all three columns 2, 3 and 4. Column 2: Standardized loading coefficient for canonical variate one; asterisk indicates the ten with greatest absolute values (characters contributing most to variate). Column 3: Pearson's correlation coefficient for group (locality) mean versus geographic distribution; asterisk indicates those with $r^2 > 0.50$. Column 4: Percent size change of characters from southern localities to northern localities; asterisk indicates percent change greater than 20. Column 5: Pearson's correlation coefficient for group (locality) coefficient of variation (cv) versus geographic distribution; asterisk indicates those greater than 0.40. See Table 1 for explanation of abbreviations.

1 Character	2 CAN 1	3 Group mean r^2	4 Increase (%) south to north	5 Coefficient of variation r^2
EBW	0.4955*	0.29	7.8	0.44*
AAL	0.3189	0.37	5.9	−0.05
AAW	0.2582	0.65*	7.3	−0.15
AAS	0.0820	0.46	4.8	−0.06
ALS	−0.7295*	0.36	7.3	0.63*
ADS	−0.0887	0.65*	8.2	0.05
APW	0.3771	0.49	20.5*	−0.24
AAR*	0.4794*	0.58*	9.8	−0.03
AAA	−0.0435	0.04	3.8	0.03
CAL	0.4332*	0.17	6.9	−0.01
CVL*	−0.2090	0.63*	55.0*	0.45*
CAD	0.0165	0.00	−0.7	−0.27
CRA	0.0018	−0.22	−6.8	0.07
CPA	−0.2043	−0.07	−0.4	−0.41
CEA	−0.1419	−0.81*	−6.2	−0.43*
CAW	0.0847	−0.16	−5.0	0.08
CAR	−0.4255*	0.12	6.6	0.09
KGT	0.9234*	0.66*	43.6*	0.18
KXD	−0.6748*	−0.31	−7.9	0.06
KXT	−0.3958*	0.82*	42.3*	0.03
PMD	0.0334	−0.13	−13.5	0.11
PSD*	−0.5626*	−0.31	−20.7*	0.16
PMS	0.1366	0.04	1.5	0.00
PMN	0.2202	0.32	16.2	0.74*
XZN	−0.0226	0.05	2.1	−.−
XZD	0.0745	−0.07	−5.1	−0.03
XWT	0.5874*	0.57*	21.6*	0.07
HDL	0.0706	0.03	8.7	0.27

tion). Again, absolute values of the correlation coefficients are of little value because distances between localities have been standardized to unity, but it is important that these characters are more highly correlated with geographic distribution than are other characters.

Finally, the relative magnitudes of differences between characters in the north and south were evaluated by calculating mean values for the two southernmost groups (76, 151) and the two northernmost (26, 27). The percentage of change (e.g., size) from south to north was calculated [$(n-s)/s \cdot 100$] for each character. Characters displaying greater than 20% change are highlighted in column 4 of Table 2. These characters show the most significant amount of change between the endpoints of the geographic distribution.
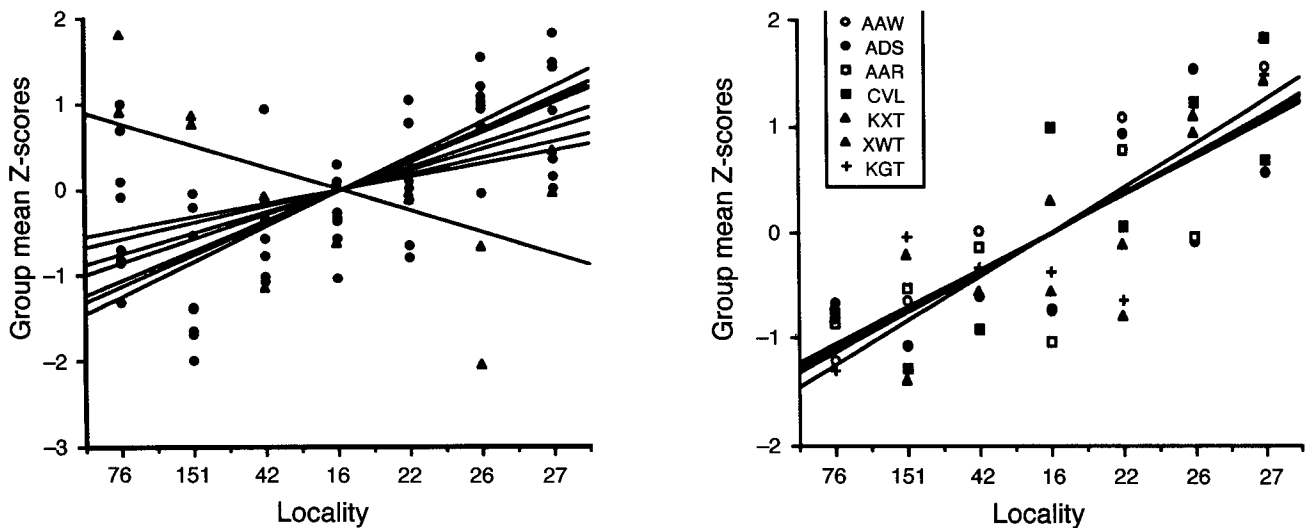
Fig. 5. □A. Standardized group mean scores (by locality) plotted against geographic distribution for ten characters receiving the heaviest loadings on canonical discriminant axis one (Fig. 4B): KGT, ALS, KXD, XWT, PSD, EBW, AAR, CAL, CAR, KXT. Characters KXD and PSD (triangles) both have a negative correlation, all others have positive correlation and are represented by solid circles. □B. Standardized group mean scores (by locality) plotted against geographic distribution for seven characters having the greatest correlation with locality ($r^2 > 0.50$). Pearson's correlation coefficient for each is as follows: AAW = 0.65, ADS = 0.65, AAR = 0.58, CVL = 0.63, KXT = 0.82, XWT = 0.57, KGT = 0.66.

Characters highlighted in all three categories are KGT, KXT, and XWT, which represent the thickness of endozonal, exozonal, and axial walls (Table 2). This demonstrates that the morphologic cline is primarily a function of the thickening of the skeleton, resulting in increased robustness from south to north. Characters highlighted in two categories include AAR – apertural area, CVL – vestibule length and PSD – minimum metapore diameter (Table 2), which are all affected by the thickening of the exozone. In fact, most characters correlated with the cline are related to skeletal thickening (Table 2). Lateral dimensions are affected by the expanding cylinder, but longitudinal spacing is not.

It is noteworthy that characters deemed most important for making species-level distinctions in cryptostome bryozoans (chamber size, shape and orientation, and aperture placement – Snyder 1991; Hageman 1991), are affected minimally by the cline, thus supporting the qualitative interpretations of traditional taxonomists (Ulrich 1890; Karklins 1985; and Snyder 1991).

Factors controlling the cline

By definition, a morphologic cline results from systematic changes in the average genotype or average phenotype of a species throughout a geographic distribution (Levinton 1988). Both genotypic and phenotypic factors are partially governed by local environmental pressures, such as water depth, temperature, salinity, turbidity, and nutrient availability. Organisms from environmentally stable environments display less morphologic variation than those from unstable environments (Bretsky & Lorenz 1970; Eldredge 1974). This relationship has been demonstrated in Paleozoic

bryozoans (Pachut & Anstey 1979; Pachut 1982; Key 1987; Pachut & Cuffey 1991). Pachut & Cuffey (1991) recognized an increase in morphologic variance and canalization of development from offshore (deeper, stable) to onshore (shallow, variable) environments in the trepostome bryozoan *Tabulipora carbonaria.*

The morphologic cline in Winzeler *Streblotrypa* specimens is apparently not controlled by these same factors, because morphologic variability does not change systematically. This is seen in (1) relatively uniform spans for 95% confidence limits for locality group means on CAN 1 (Fig. 4B); (2) lack of correlation between locality group mean variation on CAN 1 and geographic distribution (Fig. 4D); and (3) relatively low correlations between coefficients of variation (cv) for individual characters at each locality, versus geographic distribution (Table 2, column 5). In addition, there is no evidence for lithologic change from south to north.

The cline observed in *Streblotrypa* is characterized by a thickening of exozonal, endozonal, and axial walls and an increased number of metapores. This results in more robust colonies in northern (shoreward) localities. This would be beneficial in higher-energy environments, but such settings should result in predicted increased morphologic variability. It is more likely that this cline is related to water depth and nutrient availability. Schopf *et al.* (1980) documented a cline in branch diameter of a living stick-like cyclostome bryozoan along a depth gradient of 8–30 m. They believed that branch thickness was a function of light (and therefore food) and were able to rule out factors of current and suspended matter. The depth gradient of the Winzeler Shale, although minimal on a broad epicontinental shelf, may have been

sufficient to establish a morphologic cline. Effects of nutrient supply from the continent and other sources of environmental variations cannot be ruled out, however.

Lithologic and temporal variation

Winzeler Shale Locality 25 and Utopia Limestone Locality 160, located 12 km apart, were used to evaluate ecologic and small-scale temporal differences (Fig. 1).

When mean values for specimens (average of 5 observations per colony fragment) were plotted on canonical variate axes 1 and 2, specimens from Winzeler Shale Locality 25 tended to plot low on canonical discriminant axis 1 (CAN 1) and Utopia Limestone specimens high on CAN 1 (Fig. 6A). Groups are not distinct, however, and 95% confidence limits for group means overlap considerably (Fig. 6A). This mixing is also reflected in discriminant analysis, which produced an allocation efficiency ratio of $^{87}/_{105}$ (82.9%). In cluster analysis, two groups could be recognized, plausibly representing localities, but with many misclassified composite zooids (CZs), and a remaining large third group, a mixture of both. Further, when one random observation from each specimen (colony fragment) was removed from the calibration data set and placed in a test data set, the average allocation efficiency ratio of CZs to localities for five runs was $^{8}/_{21}$(38.1%). These results demonstrate that relatively little morphological differentiation exists between populations of *Streblotrypa prisca* at the Winzeler Locality 25 and the Utopia Locality 160.

The results are somewhat surprising because a greater degree of differentiation was present in samples from three closely spaced Winzeler localities. Samples from Localities 15, 42 and 151, all within 13 km of each other, had discriminant allocation efficiency ratios of $^{74}/_{75}$ (98.7%) for CZs to locality. In contrast, analysis employing only specimens from Localities 22, 27 and 76, distributed evenly over the 300 km transect, produced an allocation efficiency ratio of $^{73}/_{75}$ (97.3%). Thus, the allocation efficiency ratio (distinctiveness

of populations) for Winzeler localities is relatively high, regardless of distance between localities.

The smaller degree of differentiation between specimens of *Streblotrypa* between the Winzeler 25 and Utopia 160 localities is even more noteworthy given the results of Holdener (1991). Holdener demonstrated that significant morphological differences exist between populations of fenestrate bryozoan species, *Fenestella geminanoda* and *Rectifenestella limbata*, between these same two localities, using discriminant analysis and cluster analysis. Differences, however, were imperceptible by visual inspection (Holdener 1991). From canonical variates analysis (Fig. 4A), it is apparent that Winzeler Shale Locality 25 is anomalous for *Streblotrypa*, represented by more mature morphs. This may partially explain its similarity to Utopia Locality 160 but does not satisfactorily explain differences between Holdener's (1991) findings for fenestrates and those for *Streblotrypa* here.

Larger temporal differences

Although the data set is too sparse to provide definitive conclusions about temporal trends (four stratigraphic horizons), results are considered guides for further research. Canonical and discriminant analyses were performed with stratigraphic position as the class-variable. Winzeler Locality 25 was omitted from initial analyses because of its anomalous characteristics (Fig. 4A). It is clear that Winzeler Locality 25 is much more like the Utopia Locality 160. For a detailed discussion of the effects of Locality 25 on analyses, see Hageman (1992a, p. 134).

When stratigraphic group means were plotted on the first and second canonical variate axes (Fig. 6B), CAN 1 serves to separate Utopia Limestone from other stratigraphic horizons. Characters most heavily loaded on CAN 1 and therefore responsible for this trend are: polymorph size and number (PMN, PSD, PMD), aperture width (AAW) and vestibule depth (CVL). These characters are similar to those of Fig. 4A, which separated anomalous Locality 25 from the other Winzeler localities.
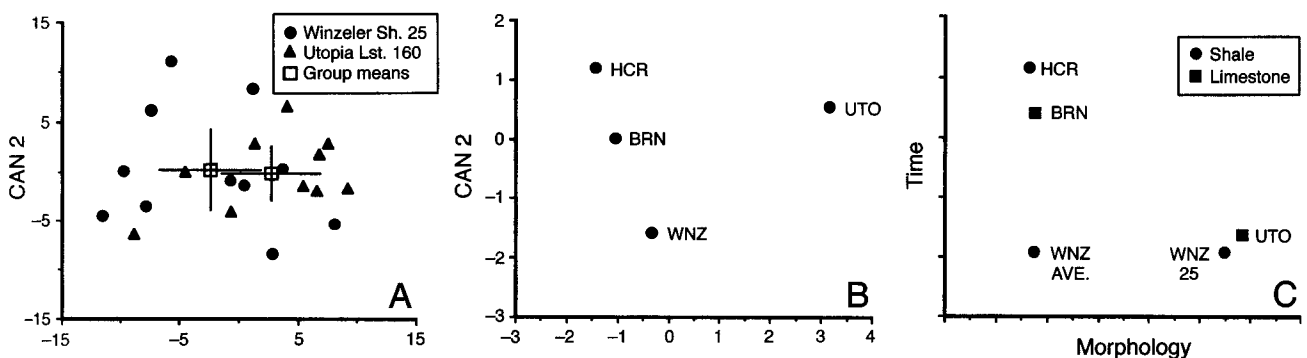

Fig. 6. □A. Mean scores for specimens from Winzeler Shale Locality 25 and Utopia Limestone Locality 160 plotted on canonical variate axes 1 and 2. Lines represent 95% confidence intervals for group means. □B. Group mean scores (by stratigraphic horizon) plotted on canonical variate axes 1 and 2. □C. Generalized summary of potential morphologic variation versus time.

If a stratigraphic trend exists, it is expressed along CAN 2 (Fig. 6B). Characters responsible for separating groups on CAN 2 include PMN–number of metapores, KXT–thickness of exozone, CAL–autozooecial chamber length, PMS–metapore spacing, XZN–number of axial zooecia.

One could begin to draw conclusions about parallels between the reduction of exozonal thickness and associated characters from north to south in the morphologic cline, and reductions in the same characters through time and their heterochronic implications (see Anstey 1987; Pachut 1989; Pachut & Cuffey 1991; and examples therein). However, specimens from the Utopia Limestone Locality 160 and Winzeler Shale Locality 25 do not fit with either temporal or geographic trends. Geographic variation within temporal trends needs to be better constrained before such models can be proposed.

Discussion of *Streblotrypa* data

Several important conclusions can be derived from these data. (1) Small-scale intraspecific morphologic variation, including subtle patterns of geographic variation, can be documented in Paleozoic fossils. (2) In the material studied, characters associated with patterns of intraspecific variation are not those deemed most useful for making species-level distinctions. (3) The range of observed morphologic variation from a single horizon is as great as that observed over the entire stratigraphic sequence from varied lithologies. (4) These data indicate a strong pattern of overall morphological stasis (bounded range) through the stratigraphic interval studied.

Even if the observed morphologic cline represents actual genetic differentiation rather than just phenotypic expression from a common gene pool, the level of differentiation throughout the cline is still demonstrably intraspecific. In this scenario, multiple, intergraded, gene pools of *Streblotrypa prisca* shifted through space and time, all of which were constrained by boundaries that define the species. This, however, results in the same conclusion of overall stasis.

Because ancestor–descendant relationships for *Streblotrypa prisca* were not established in this study, further inferences about rates of evolution across the species boundaries cannot be made from these data.

Implications for microevolutionary studies

Cheetham's (1986) study of evolutionary change in the Neogene bryozoan *Metrarabdotos* is one of the most comprehensive and cited works to date and is here used as a standard for comparison. Cheetham (1986) employed methods from Charlesworth (1984) that test whether the rate of change within an ancestral species (trajectory *a–a'* in Fig. 7A) is

sufficient to account for change across ancestor–descendant boundaries (trajectory *a–b* in Fig. 7A). Cheetham (1986) provides an in-depth discussion and evaluation of this methodology, for which the null hypothesis is gradual change.

In any microevolutionary study, two questions can be raised: (1) For each time horizon sampled, how completely does the observed range of variation account for the total variation at that time (taphonomic bias)? (2) How much of the observed change through time is due to shifting mean genotypic frequencies and how much due to changes in means of sampled phenotypes? Effects arising from these factors can be evaluated from their four extremes.

No unobserved variation, group mean = genotype

This is the hypothesis used in most previous microevolutionary studies, where each absolute shift in group mean through time represents true evolutionary change in the genotype. Rates of change are calculated from the group means (Fig. 7A). This hypothesis resulted in a conclusion of stasis and punctuated change for *Metrarabdotos* species (Cheetham 1986).

Unobserved variation, group mean = genotype

In this hypothesis, group means still represent shifts in average genotype, but calculations differ from the previous hypothesis in that (1) extremes of potential morphologic variation are used rather than the group means and (2) the mean morphologic trajectory is based on the overall variation rather than on group means. This hypothesis assumes that the extremes of a phenotypic expression are just as valid a testing point as the mean. Although doubtfully true in nature, this methodology allows one to test the extremes of morphologic variation and place relative boundaries on errors at their extremes. If conclusions based on this hypothesis are the same as those from the previous hypothesis, then original conclusions based on mean morphologies are strengthened. If results disagree, conclusions based on mean morphology are not necessarily nullified, but they should be interpreted with greater caution.

In the studies by Charlesworth (1984) and Cheetham (1986), a line of mean morphologic change is drawn directly from first to last appearance (trajectory *a–a'* in Fig. 7A). If a potential range of variation is applied to each group, there is no reason to suspect that the means of these two observations represent the mean genotype more exactly than any of the other observed data points. Therefore, a regression line through all of the data is employed in this hypothesis. Assuming that this hypothesis represents the real world, if *the regression line is shallower than the mean trajectory from the previous hypothesis, the observed pattern from hypothesis one has the potential to suggest greater punctuation than*
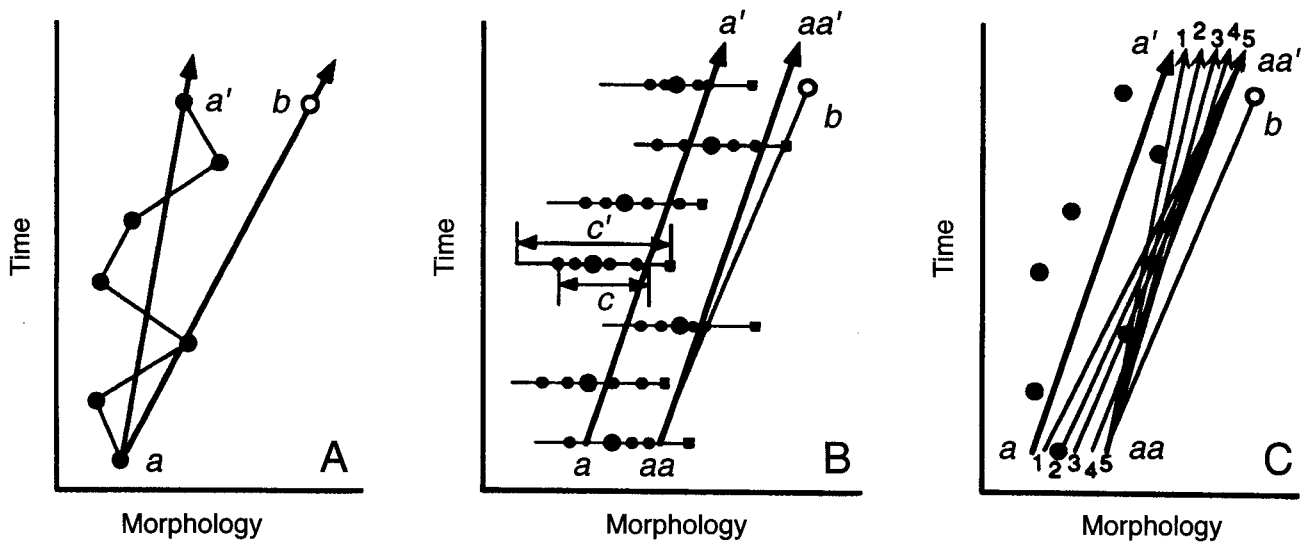
Fig. 7. □A. Model of evolutionary change within ancestor species A; dots represent mean genotype, with trajectories from first to last appearance of ancestor (*a–a'*) and first appearance of ancestor to first appearance of descendant (*a–b*). □B. Evolutionary model illustrating the observed ancestors (small dots) and phenotypic means (large dots), with mean ancestral trajectory (*a–a'*) derived as regression line through the species *a* data cloud. The maximum deviation of observed datum from the regression line is span *c*, and the potential range of variation is span *c'* (twice *c*, centered on mean). Evolutionary trends are tested using the extreme values of the range (squares) through which a regression line, *aa–aa'*, is drawn. □C. The effect of having a smaller range for the first appearance of species *a* (5, 4, 3, 2, 1) while fixing the last appearance (*aa'*) is to increase the likelihood of a gradational pattern. The effect of having a smaller range for the last appearance of species *a'* (5, 4, 3, 2, 1) while fixing the first appearance (*aa*) is to increase the likelihood of a punctuated pattern.

the real world. If the regression line is steeper than the mean trajectory from the previous hypothesis, the observed pattern from *hypothesis one* has the potential to suggest greater *gradation* than the real world. As will be shown, the relative starting point of the line is important as well.

An estimate of potential morphologic variation can be obtained by assuming that at each horizon the range is equivalent to the maximum observed deviation from a regression line through the entire data cloud over the complete stratigraphic interval (Fig. 7B, span *c*). Equidistant potential range bars, which are simply twice the length of the greatest single deviation, can then be drawn onto each observed mean (Fig. 7B, span *c'*). This range provides reasonable, objective bounds with which to test the concepts. One could test other values for potential ranges as well, such as the maximum range observed within any single horizon or even the extreme of the total range observed over the interval studied.

The test employing the group means to evaluate rates of change within and across species boundaries (Cheetham 1986, equations 5 and 6) can be performed on the extreme ranges toward the descendant morphology (Fig. 7B, span *aa–aa'* and solid squares). The within-species trajectory of the ancestor species remains the same, but the shift toward the descendant (employing the end points of the ranges) results in an *increase* of the potential for gradual change (Fig. 7B). This effect is even greater if a potential range of variation for the first observed descendant is included in the calculations as well. In this scenario, therefore, if geographic variation was omitted from the original calculation (hypothesis

one), the observed pattern could be more punctuated than reality. Thus, if the resultant pattern (using the relatively unlikely extremes) is punctuated, then one can be even more confident of the original conclusion of stasis.

By definition, one can never know the extremes of unobserved variation. However, the only direction of uncertainty that is of importance is the morphologic distance between the ancestor and descendant (extremes of variation in other directions have no bearing on these models). If the morphologic range of the last appearance of the ancestor is fixed, the *narrower* the range of the first appearance becomes, the greater the potential for unobserved *gradualism* (Fig. 7C). If the morphologic range of the first appearance of the ancestor is fixed, the *narrower* the range of the last appearance becomes, the greater the potential for unobserved *stasis* (Fig. 7C). Because the opposite is true as well, this can be summarized as: a net *increase* in unobserved variation (in the morphological direction of ancestor) through the series will result in a greater potential for unobserved gradualism, and a net *decrease* in unobserved variation will result in a greater potential for unobserved *stasis*.

Note that in the scenario where potential ranges are equivalent, the closer the first appearance of the ancestor is to the first appearance of the descendant, the greater the potential for unobserved *gradualism*. Whereas, in the case of changing ranges of morphologic variation, the wider the range of the first ancestor (closer to descendant), the greater the potential for unobserved *stasis*. Therefore, the starting point of the mean trajectory may be as important as any other factor.

The calculations proposed here have not been performed on Cheetham's (1986) data, but inspection of his stratophenetic tree with scaled morphologic distance between ancestors and descendants shows clearly that calculation of trajectories from even large morphologic extremes within species would not alter the conclusion of stasis and punctuated change based on group means.

No unobserved variation, group mean = phenotype

In this hypothesis the entire range of observed variation represents the common gene pool, and each shift in group mean through time represents differential sampling (either restricted phenotypic expression or collecting bias) of the gene pool. This obviously is not to suggest that all samples actually represent an identical genotype through time, but that is the theoretical extreme of the hypothesis.

In all cases, neglecting aspects of this hypothesis results in observed patterns having a greater potential for *gradualism* than reality. Once the assumption of a single gene pool is made, the within-species trajectory becomes a vertical line. At first glance this seems improbable, but indeed this is the pattern suggested in the study of *Streblotrypa* presented here.

Because the entire range of morphologic variation for *Streblotrypa* observed was present within a single horizon, it is not likely that subsequent generations had a more restricted morphological range and evolved the similar genotypes iteratively. Even if the range from a single horizon represents a series of overlapping gene pools with differentiation at the ends, as stated before, this would all still be considered intraspecific variation and the conclusions would remain unchanged.

Inspection of Cheetham's stratophenetic tree scaled to morphologic distance (1986, Fig. 5) suggests that this interpretation for *Metrarabdotos* is plausible as well. The relatively narrow range of intraspecific variation, with observed means that shift back and forth across a range, are not incompatible with the interpretation of sampling of phenotypic expressions from a common gene pool through time. In this case, the conclusions of stasis and punctuated change are ever more justified.

In this hypothesis, if a stratigraphic section represents an environmental gradient, an ecophenotypic cline such as the one documented in *Streblotrypa prisca* could be misinterpreted as evolutionary change (see also Cisne *et al.* 1980; Cuffey & Pachut 1990). Although the potential for this is real, it would require special circumstances of preservation and/or collection bias to go unrecognized.

Unobserved variation, group mean = phenotype

In this hypothesis, the greater the unobserved variation is in the direction toward the descendent species, the greater the potential that the two are conspecific. Because both factors

are unconstrained, we cannot evaluate the validity of this hypothesis.

Suggestions for future studies

Natural events most likely are comprised of some combination of these four models. This exercise seeks to document reasonable end points to unobserved morphology and thus place testable limits on unknown factors. It is impractical to study systematic changes in morphologic variation within every horizon sampled; however, one should document geographic variation from a least one horizon in order to suggest potential limits for others. In cases such as that of Cheetham (1986) where it is not possible to correlate a single horizon over a large distance, collection from a variety of locations and lithologies within a basin or region of study is as acceptable, if one considers the overall range as potential limits for each horizon. In a single stratigraphic section (e.g., a core) the overall range in morphology through time can serve as a guide to limits of potential variation within each horizon as well.

All available characters should be employed in microevolutionary studies, but relative differences between the contribution of characters to patterns within and between species must be recognized. For example, the pattern of clinal variation affected by heterochronic processes through time (Anstey 1987) that has proven important in studies of other bryozoans in similar settings (Cuffey 1967; Pachut et al. 1991) does not appear to be significant in *Streblotrypa prisca*. Methods for evaluating the relative importance of characters for making taxonomic distinctions are discussed by Foster (1984, 1985), Wei (1988), Cheetham (1986) and Hageman (1991).

Conclusions

1 Specimens of *Streblotrypa* demonstrate a degree of morphologic variability that is consistent with astogenetic variation within a single species, *Streblotrypa prisca*. That is, multivariate numerical methods did not demonstrate the presence of smaller subgroupings of specimens that could be objectively and consistently recognized.

2 A morphologic cline in specimens of *Streblotrypa prisca* collected from seven localities of the Winzeler Shale along a 300 km north–south transect is characterized by thickening of the exozonal, endozonal, and axial walls and by correlated characters.

3 Characters deemed most important for species-level distinction in cryptostome bryozoans (chamber size, shape, and orientation and apertural placement; Hageman 1991), display little correlation with the morphologic cline. This supports traditional systematic approaches to

species recognition in cryptostome bryozoans of Ulrich (1890), Karklins (1985), and Snyder (1991).

4 Populations along the cline do not show a systematic increase in morphologic variability, observed by other authors from a gradient of presumably stable (deep-water) to a presumed less stable (shallow-water) environment. The cause of the cline cannot be determined but may be related to water-depth gradient (light availability, temperature), water chemistry and/or a decrease in nutrient availability.

5 In *Streblotrypa prisca*, the range of observed morphologic variation from a single horizon was as great as that observed over the entire stratigraphic sequence from varied lithologies. This indicates a pattern of overall morphological stasis through the interval studied.

6 Conclusions from microevolutionary studies are biased by assumptions made about the significance of group means (representing genotypes or phenotypes) and the importance of morphologic variation within each sampled horizon. Conclusions are strengthened when they are summarized from multiple hypotheses (a series of tests that place reasonable limits on potential errors).

7 Results from this and similar studies demonstrate that documentation of patterns of subspecific morphologic variation in fossils is viable and can contribute to our understanding of evolutionary processes.

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Erratum

In the article by Rong *et al.* (*Lethaia*, Vol. 27, No. 1) the explanations for Fig. 4D, E and F (p. 23, caption to Fig. 4) have been mixed up. For clarity, the full corrected caption is reproduced below.

Fig. 4. Key taxa of the *Kassinella–Christiania* Association from the Linhsiang Formation of Haitupo, Yanzikou, Bijie, NW Guizhou (R2) and from Chientsaokou Formation of Jiancaohe, Donggongsi, Zunyi, N Guizhou (R50): □A–C. *Kassinella* sp. 1, A, C. internal moulds of two pedicle valves, ×7, NIGP 119422 and NIGP 119423, respectively. □B. Internal mould of a brachial valve, ×9, NIGP 119424, R50. □D. *Leptestiina* cf. *prantli*, internal mould of a brachial valve, ×16, NIGP 119426, R2. □E. *Foliomena folium* (Barrande), external mould of a pedicle valve, ×5, NIGP 119427, R50 (also see Cocks & Rong 1988, p. 53, Pl. 9:1). □F. *Kassinella* sp. 2 [= *Kassinella incerta* (Xu, Rong & Liu) of Cocks & Rong 1988, Pl. 9:4], internal mould of a pedicle valve, ×9, NIGP 119425, R2. □G, H. *Christiania* sp. (= *Christiania nilssoni* Sheehan of Cocks & Rong 1988, Pl. 9:9, 10), internal mould of a pedicle valve and exfoliated external mould of a brachial valve showing some impressions of the dorsal interior, both ×7, NIGP 119428 and NIGP 119429, respectively, R50. □I, J. *Glyptorthis* sp. external mould and internal mould of the same pedicle valve, ×16, NIGP 119430 a and b, respectively, R50. □K. *Orbiculoidea* sp. external mould of a pedicle valve, ×16, NIGP 119431, R50. □L. *Paterula* sp., exfoliated external mould of a pedicle(?) valve, ×16, NIGP 119432, R50. □M. *Kozlowskites* sp. internal mould of an incomplete brachial valve, ×16, NIGP 119433, R2. □N. *Dedzetina* sp. internal mould of a pedicle valve, ×7, NIGP 11934, R2. The figured material has been reposited in the Institute of Geology and Palaeontology, Nanjing (NIGP).