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Observed Phenotypic Variation In A Paleozoic Bryozoan

By: **Steven J. Hageman**

Abstract

Documentation of morphologic variation within and among fossil species (and larger clades) provides fundamental data needed for studies of evolution, paleoecology, and the systematic foundation required for most fields of paleobiology. In paleontological (and, frequently, biological) studies, morphologic variation is used as a general proxy for genetic variation. Although the occurrence of ecophenotypic variation is well appreciated in these studies, it is only with the use of colonial (clonal) organisms that the scope and significance of phenotypic variation can be evaluated directly. Systematic evaluation of intracolonial morphologic variation (transects through growth series) can yield insights about ecophenotypic variation in bryozoans and suggest the most appropriate methods for data collection in paleobiologic and taxonomic studies. In this study, morphological conservatism is documented within local segments of bryozoan colonies; each zooid is generally more similar to adjacent zooids than to distant zooids within the same colony. One region of a colony, therefore, can be more similar to a region of a different colony than to a distant region of its own colony. Variation within one colony does not, however, represent the total variation among a group of specimens, indicating a colonial level of morphologic control (genetic or macroenvironmental) over morphogenesis. Directional morphogenetic gradients (associated with successive ontogenetic histories) are not recognized in these specimens, but fluctuating trends within colonies (some cyclic), were observed and are indicative of changing microenvironmental influence during skeletal formation. In order to best document morphologic variation within a population, for any type of paleobiological study, individual measurements should be widely distributed over large colony fragments and (or) a minimal number of measurements collected from each of a large number of smaller fragments. Direct extrapolation of these results to non-colonial organisms is not appropriate at this time. However, additional, related studies with bryozoans and other colonial organisms (e.g., corals, graptolites), should provide a greater, general appreciation of relationships between morphology and genetics.

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Steven J. Hageman

Abstract.—Documentation of morphologic variation within and among fossil species (and larger clades) provides fundamental data needed for studies of evolution, paleoecology, and the systematic foundation required for most fields of paleobiology. In paleontological (and, frequently, biological) studies, morphologic variation is used as a general proxy for genetic variation. Although the occurrence of ecophenotypic variation is well appreciated in these studies, it is only with the use of colonial (clonal) organisms that the scope and significance of phenotypic variation can be evaluated directly. Systematic evaluation of intracolonial morphologic variation (transects through growth series) can yield insights about ecophenotypic variation in bryozoans and suggest the most appropriate methods for data collection in paleobiologic and taxonomic studies.

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Direct extrapolation of these results to non-colonial organisms is not appropriate at this time. However, additional, related studies with bryozoans and other colonial organisms (e.g., corals, graptolites), should provide a greater, general appreciation of relationships between morphology and genetics.

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Introduction

Documentation of phenotypic variation is required for any group of organisms in order to develop sound species concepts and to provide for meaningful ecological and evolutionary inferences. Colonial organisms are comprised of individual units sharing a single genotype (barring mitotic mutations during colony growth). The ability to compare within-colony variation (ultimately limited by the genotype) versus among-colony variation makes colonial organisms excellent candidates for studies of phenotypic variation (Boardman et al. 1970; Abbott 1973; Schopf 1976; Brande and Bretsky 1982).

In previous morphometric studies of some conspecific co-occurring Bryozoa (Hageman 1993, 1994; Holdener in press), it was observed that composite zooids (each comprised of multivariate observations representing a single zooid) could be reassigned to the colony fragment from which they were measured with very high confidence using cluster analysis and discriminant analysis. This strong morphologic conservatism within individual colony fragments suggests some type of control over skeletal formation, whether it be genetic, physiological, microenvironmental or a combination of these. The fact that a few composite zooids can adequately represent a segment of a colony raises questions about how adequately that segment represents colony-wide variation and (or) species-wide variation.

The goal of this study was to document patterns of morphologic variation within and among conspecific bryozoan colony fragments and, where possible, to infer dominant controls over morphogenesis. These features are important when choosing the location

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(distribution) and number of morphometric observations taken from colonial organisms for systematic and evolutionary studies.

Materials and Methods

Analysis of variance (ANOVA) and canonical variates analysis have been employed to evaluate morphological variation in bryozoans (Anstey et al. 1976; Schopf 1976; Taylor and Furness 1978; Pachut 1982; Key 1987) and corals (Foster 1984, 1985). These methods were employed here to evaluate intracolonial versus intercolonial morphologic variation in a Paleozoic bryozoan.

In order to document and compare morphologic variation within and among colonies, a complex of six external characters was measured across continuous transects from five large colony fragments of the rhabdomesine cryptostome *Streblotrypa (Streblascopora) prisca* (Gabb and Horn 1862). The six characters—along branch aperture spacing (AAS), diagonal aperture spacing (ADS), lateral aperture spacing (ALS), aperture length (AAL), aperture width (AAW), and branch diameter (EBW)—were chosen from the 28 characters employed in previous studies based on the fact that they could readily be measured from exterior photographs (fig. 1). These characters, associated with apertural size and spacing, may reflect biological significance of feeding strategies (Winston 1977, 1978, 1981; McKinney and Boardman 1985; Snyder 1991). Although inclusion of interior characters would have been desirable in this study, it would not have been practical (or even possible) to section consecutive zooids throughout an entire colony.

Composite Zooids.—In this study, a composite zooid is the operational unit in numerical analyses rather than a true zooid or a colony. For example, a single composite zooid in this study consists of the observed values for five characters represented by a complete suite of exterior characters measured from a single chamber, plus branch width measured across that zooid. In the operational sense of multivariate numerical methods, a composite zooid is the equivalent of a single specimen of a noncolonial organism.

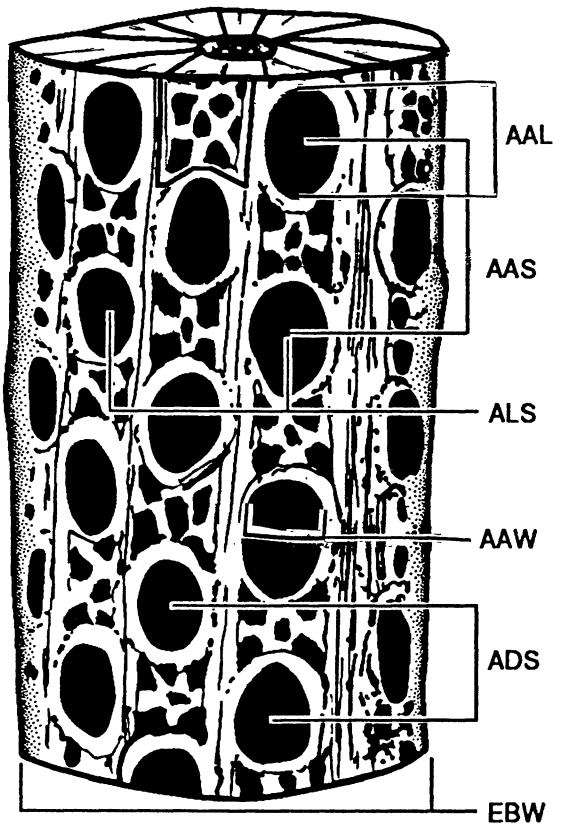


FIGURE 1. Segment of *Streblotrypa (Streblascopora) prisca* illustrating the location of the six exterior characters used in this study: AAS, along branch aperture spacing; ADS, diagonal aperture spacing; ALS, lateral aperture spacing; AAL, aperture length; AAW, aperture width; and EBW, branch diameter.

Data Collection.—Measurements were taken from photographs (75×) using calipers. Adhesive stickers were placed on the photographs over each aperture after a zooecium had been measured in order to document the transect and allow for identification during later comparisons (fig. 2). Five colony fragments were employed. Data from some of these were further subdivided into multiple segments from a single colony fragment, and treated separately. These terms, therefore, have specific meaning throughout this paper. Segments are given subscript numbers in figures and the text (e.g., 398_1, 398_2, and 398_3 are three segments from a single colony fragment 398). Note that fragments were divided into segments based on natural branching events. Long, single branches could have been sub-

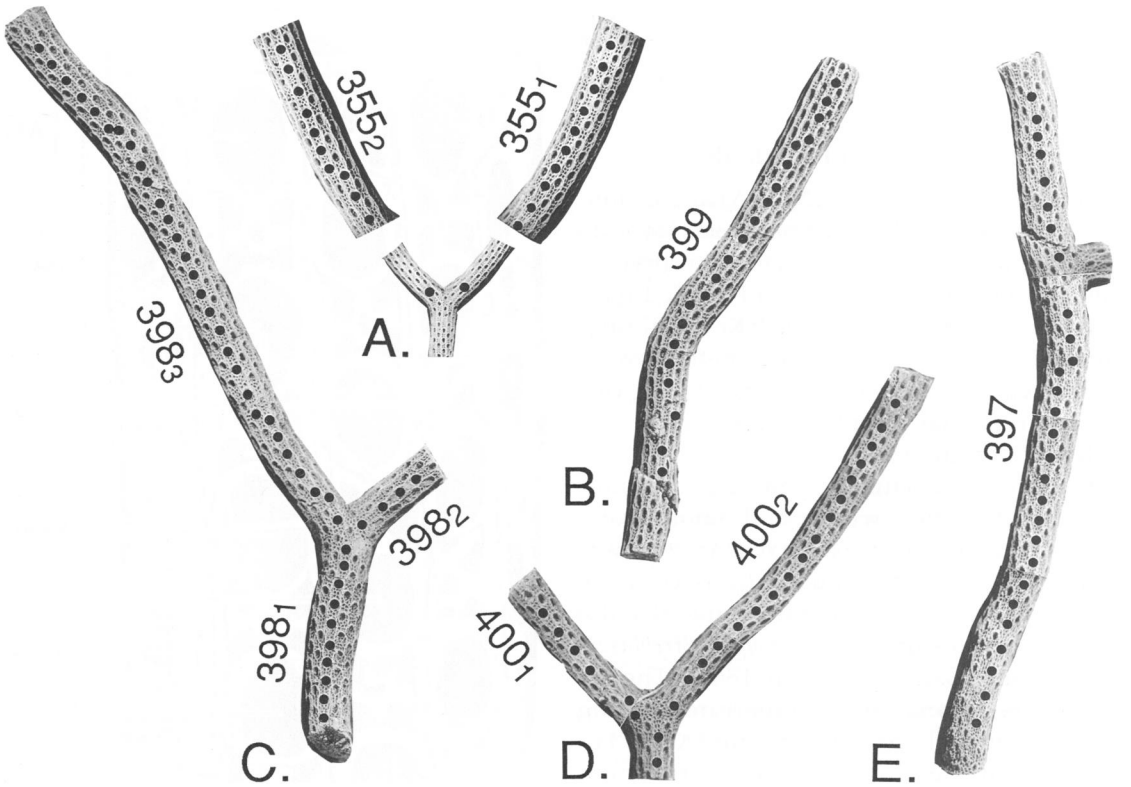


FIGURE 2. Specimens of *Streblotrypa (Streblascopora) prisca* used in this study, with measured transects highlighted by dots. A, Specimen 355 from the Winzeler Shale, Virgilian (NW NW 24-12S-15E), treated as two segments and cataloged as UIX-7084 in the Department of Geology, University of Illinois. B–E, Specimens from the Carboniferous near Fort Belknap, Texas, originally described in Gabb & Horn (1862), all located at Academy of Natural Science of Philadelphia. B, Specimen 399 treated as one segment and cataloged as ANSP 77550 (paralectotype). C, Specimen 398 treated as three segments and cataloged as ANSP 77550 (paralectotype). D, Specimen 400 treated as two segments and cataloged as ANSP 77550 (paralectotype). E, Specimen 397 treated as one segment is the lectotype and cataloged as ANSP 31271 (lectotype).

divided as well, but it is doubtful that further manipulation of these data would have altered conclusions. Data from the five colony fragments can be summarized as follows.

Colony Fragment 355.—Segments 355_1 and 355_2 are the right and left branches, respectively, of a Y bifurcation from a single colony (fig. 2A). Ten composite zooids were measured from each branch. The two dots on the lower figure 2A illustrate the location of the first observations on each of the segments.

Colony Fragment 397.—Specimen 397 is a single, long colony fragment from which 28 consecutive composite zooids were measured (fig. 2E).

Colony Fragment 398.—Specimen 398 is a large fragment with a bifurcation event (fig. 2C). Data were separated into three groups corresponding to the primary branch (398_1), right branch (398_2), and left branch (398_3). Ten composite zooids were measured from segment 398_1, four from 398_2, and 29 from 398_3. In some cases, specimen was treated as two segments, with the primary section (398_1) included in both the left and right branches (first ten composite zooids included in each).

Colony Fragment 399.—Specimen 399 is a single branch fragment from which 21 consecutive composite zooids were measured (fig. 2B).

Colony Fragment 400.—Specimen 400 also displays a Y bifurcation (fig. 2D). The left branch is designated 400_1 and the right 400_2. The first two measurements on the primary

branch were included with the data for both 400_1 and 400_2, resulting in 8 and 19 consecutive composite zooids respectively.

Data Analysis.—A series of multivariate tests was performed to evaluate the morphologic variation within and among these eight colony segments. These include WPGMA (weighted pair-group method, arithmetic average) cluster analysis (NTSYS-pc [1.60]), discriminant analysis (DISCRIM, SAS[5.18]), and canonical variates analysis (CANDISC, SAS[5.18]). See Hageman (1991: p. 633) for review of these methods.

Allocation of Zooids of Colony Fragments

In previous studies it has been observed that zooids (Cheetham 1986) and composite zooids (Hageman 1993, 1994; Holdener in press) can be objectively allocated to the colony fragment from which they were originally measured with surprisingly high confidence using cluster analysis and discriminant analysis. This phenomenon was tested in the present study using a greater level of morphologic resolution within colonies.

Figure 3 is a phenogram from cluster analysis performed with data from the present study. Composite zooids (equivalent of operational taxonomic unit [OTU] label) were coded based on the colony segment from which they were measured. Note the frequent grouping of composite zooids from the same colony fragments, such as from fragment 399 (fig. 3).

In a previous study (Hageman 1993) in which discriminant analysis was performed with a different data set (380 composite zooids from 76 different colony fragments), 100% of the composite zooids were allocated correctly to the segment from which they were measured. In the present study with eight segments from five colony fragments, 70.3% of the 148 composite zooids were allocated correctly to the colony segment from which they were measured. The second study employed only 6 of the 28 characters used in the original study, which probably accounts for the lower allocation rate (Hageman 1991). An allocation rate of 70.3% is nonetheless convincing for a data set comprised of such similar forms.

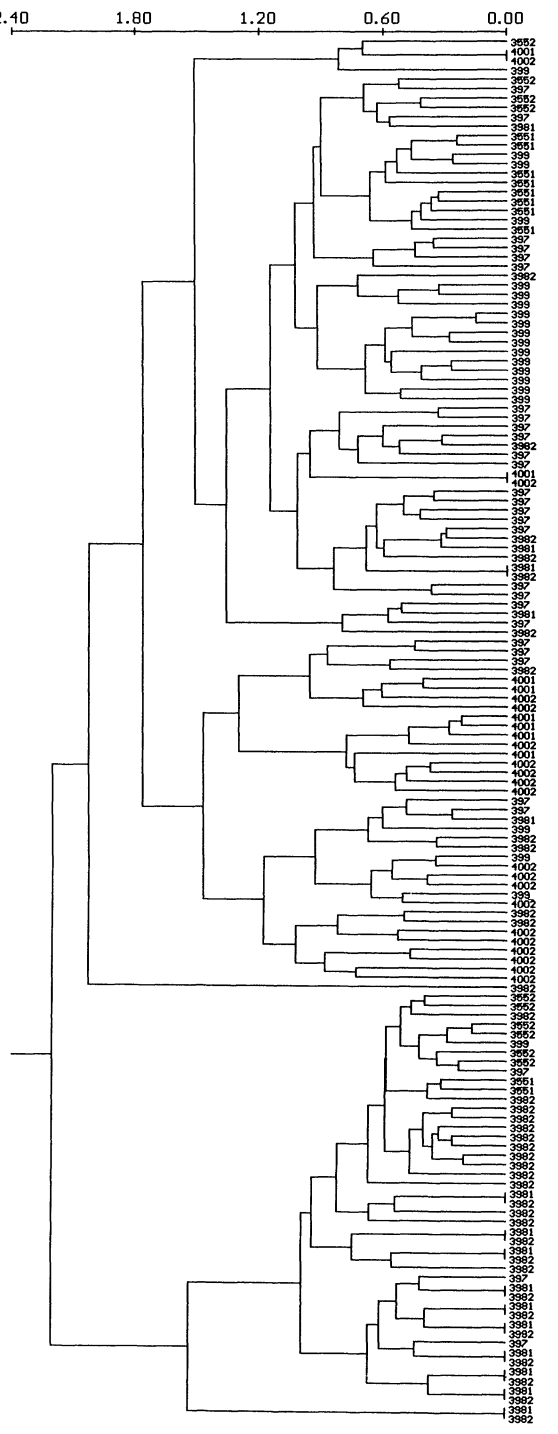


FIGURE 3. Phenogram of WPGMA cluster analysis using composite zooids as the units labeled by the colony segment number. Note the clustering of composite zooids from the same colony fragments (e.g., 399) and in some cases the discrete subgrouping of segments from the same colony (e.g., 355_1 and 355_2).

TABLE 1. Discriminant analysis allocation matrix with data from Hageman 1993 and test composite zooids not included in calculation of the calibration matrix. None of the test composite zooids were allocated to the segments from their original colonial counterparts (— equivalent to zero).

Test segment	Allocated calibration data set													
	355_1	360_1	363_1	364_1	368_1	356	357	358	359	365	366	369	370	371
355_2	0	5	—	—	—	—	—	—	—	—	—	—	—	—
355_3	0	—	—	—	—	—	—	—	—	—	—	—	—	5
360_2	—	0	—	1	—	—	—	2	—	—	—	1	1	—
363_2	—	—	0	1	1	—	—	—	—	—	3	—	—	—
364_2	—	—	—	0	—	—	—	—	—	2	3	—	—	—
368_2	—	—	1	—	0	—	—	—	—	3	1	—	—	—
368_3	—	—	—	—	0	—	—	—	—	—	—	1	2	2

Results from these cluster and discriminant analyses strongly support the idea of morphologic conservatism within segments of colonies that allows for objective allocation of composite zooids to the segment from which they were measured. A minimal number of observations, therefore, can adequately represent a local segment of a colony. However, these results raise a very important question: is the observed morphologic conservatism indicative of colonies as a whole (suggesting a greater genetic control), or is it limited to shorter segments within colonies (suggesting some type of changing influence)?

Segment Versus Colony.—Closer examination of cluster analysis indicates that morphologic conservatism does not extend colony wide, but rather is restricted within shorter segments of the colony. In cluster analysis there is a trend for clustering of small groups of composite zooids all from the same colony segment. In some cases, different segments from the same colony fall into distant clusters, as in 355_1 and 355_2 (fig. 3).

Two discriminant analyses were performed on different data sets designed to further address this question. The goal was to determine whether zooids from one colony segment would tend to be preferentially assigned to other segments from the same colony rather than to a segment from a completely different colony. The experimental design of these two tests is slightly different. In the discriminant analysis from the previous study, test composite zooids were not included in calculating the calibration matrix, and in the analysis from the present study, test composite zooids were included in the calibration matrix.

In a previous study (Hageman 1993) fourteen colony fragments were used. Five of the large colony fragments were split into multiple segments. One segment from each of these five, plus the nine other fragments were used in a calibration data set for discriminant analysis. The other seven colony segments (each with a colonial counterpart in the calibration data set) were used in a test data set (table 1). These data sets consisted of five composite zooids per colony segment, measured on 28 morphometric characters (Hageman 1993). Discriminant functions based on the calibration data set were used to allocate composite zooids from the test data set to the colony segments from the calibration data set. In result, none of the test composite zooids were allocated to segments from their original colony counterparts (table 1). Groups of test composite zooids were at times, however, allocated to a single colony fragment (e.g., all

TABLE 2. Discriminant analysis allocation matrix with data set from present study with test composite zooids included in the calibration data matrix. Only misallocated composite zooids are reported (—, equivalent to zero; ●, equivalent to correct allocations).

Test segment	Misallocated calibration data set							
	355_1	355_2	398_1	398_2	400_1	400_2	397	399
355_1	●	0	—	2	—	—	—	1
355_2	0	●	—	3	1	—	—	—
398_1	—	—	●	7	—	—	3	—
398_2	—	1	5	●	1	—	3	—
400_1	—	—	—	—	●	3	1	—
400_2	—	—	—	—	2	●	1	1
397	—	—	1	3	—	—	●	—
399	2	—	—	1	—	2	—	●

five test composite zooids from segment 355_2 were assigned to 360_1)

In the discriminant analysis performed with the data from the present study (eight segments from five colony fragments), all 148 composite zooids were employed in both the test and calibration data sets (table 2). In result, 44 composite zooids from colony fragments with multiple segments were misallocated. Seventeen of these forty-four composite zooids (39%) were allocated to the counterpart segment from the same colony (bold in table 2), and 61% of the misallocated composite zooids were assigned to a segment from a different colony.

Similar patterns were observed by McKinney et al. (1993) using data from an Eocene cyclostome. Some local regions of *Hornera reteramae* colonies were morphologically more similar to regions of other conspecific specimens than they were to different regions of their own colony (McKinney et al. 1993).

Results from these studies indicate that morphologic conservatism does not necessarily extend throughout an entire colony. That is, morphologic expression is not as tightly constrained by genotype as measurements from a local area might indicate. Morphologic conservatism may apparently be restricted to local regions (segments or branches) of colonies. These results demonstrate that as a colony grows through time, different segments of the same colony can occupy slightly different morphospace. In addition, morphospace occupied by one colony can intersect with morphospace occupied by another colony with an independent genotype. That is, in table 1, segment 355_3 is clearly more similar (in this selected morphospace) to segment 371 from a different locality than it is to segment 355_2 from its own colony.

These results document morphologic conservatism within local segments of colonies, overall variation within colonies and overlapping morphologies among colonies, but they provide little insight about how regions of morphologic conservatism change throughout a colony (as a gradient, discretely, cyclic, systematically, randomly) or about controls over this change.

Intracolonial Variation

Presently, disagreement exists among bryozoan workers regarding concepts and terminology for colonial development. The problem arises from uncertainty about the degree of control that individual zooids have over their own development. At one extreme, the colony represents a series of variably integrated zooids, where zooidal units are regarded as individuals with autonomy over their skeletal development. At the other extreme, the colony as a whole is considered the individual, with all skeletal development attributed to the common colonial tissue. In this context, the concept of zooidal ontogeny is blurred. Problems associated with colonial development arise from the fact that different bryozoan groups appear to display different degrees of zooidal autonomy. Additionally, different groups have different degrees and complexity of extrazooidal structures that can not be directly attributed to specific zooids.

A revised terminology is needed to allow for unambiguous communication of the nuances of colonial development in bryozoans. A review of colonial development, however, is beyond the scope of this paper. The terminology of Boardman and Cheetham (1983) is used here (which assumes some degree of zooidal autonomy), but see Pachut et al. (1991) for further discussion.

In bryozoans, several controlling factors for morphologic variation have been recognized. In some cases, these factors can be recognized based on their resultant morphologic expression. Sources of intracolonial variation can be summarized as follows (after Boardman et al. 1983).

Astogeny.—Presently, astogenetic concepts are not recognized uniformly among bryozoan workers, especially as they relate to ontogenetic, extrazooidal, and polymorphic variation (Pachut et al. 1991: p. 213; Boardman et al. 1983: p. 36). Astogeny, as applied here, is restricted to differences between zooidal morphologies of early generations (and associated extrazooidal material) from the time of ancestrula metamorphosis to the generational stage at which a relative morphologic consistency of zooids for the colony is estab-

lished. This region, the traditional zone of astogenetic change (often a gradient [see e.g., Taylor 1988]), is generally restricted to a small part of a colony representing early development. Any other changes throughout the colony, even as gradients, are not astogenetic.

Ontogeny.—Changes arising from the growth histories of individual zooids and associated extrazooidal material are here considered ontogenetic. Because young zooids are generally formed at the distal end of colonies with older zooids at the proximal end, ontogenetic gradients are common in colonies. Gradients may be restricted to a short region of the distal zone, with a mature level of development uniformly throughout the remainder of the colony, or extend as a gradient from one end to the other. Frequently a level of senescence is reached in the proximal end of colonies with extrazooidal skeleton completely covering zooids for skeletal support. This extrazooidal skeleton has been a source of controversy because it is evidently a colonial development that can not be directly associated with a single zooid's ontogeny. However, by the definition in use here, ontogeny includes all associated extrazooidal material adjacent to zooids, and thus, over a local region of a colony all material has an equivalent ontogenetic history.

Polymorphs.—Controls over the distribution of polymorphs within colonies are highly variable. Their distribution on the colony may be uniform and systematic contributing little to intracolonial variation, or polymorphs may be in discrete patches, or highly variable. Polymorph distribution may be tied to associated zooidal ontogeny, colonial astogeny (sensu strictu), or induced by microenvironmental changes.

Microenvironmental.—Microenvironmental influences are immediate changes in the organism's environment that affect skeletal formation at the time of morphogenesis for each zooid or region of the colony. They also include secondary features such as recovery from predation, breakage or other unrecognized events. They are essentially those features that can not be accounted for by astogeny, ontogeny, and polymorphs (Boardman et al. 1983).

Taylor and Furness (1978) recognized gradients in relative similarity between zooids in a Jurassic cyclostome. That is, adjacent zooids were more similar to each other than to zooids separated by several generations, which in turn, were more similar to each other than to those separated by many generations. Taylor and Furness (1978) attributed this to microenvironmental variation caused by variability of encrusted substrate, and repetition in morphologic gradients within colonies to distinctive substrates encrusted by different parts of the colony. Other potential microenvironmental influences include small changes in temperature, salinity, light intensity or duration, sediment accumulation, substrate availability and obstacles, and nutrient availability (Pachut et al. 1991). Biologic interactions, such as predatory activity, competition for space and self crowding, can also affect morphology (Boardman et al. 1983).

Subcolonial Organization.—Other forms of morphologic variation within bryozoan colonies exist that can not be attributed strictly to those outlined above. Anstey et al. (1976) recognized subcolonial, unified regions (cormidia) in several genera of trepostome bryozoans. In these specimens, cormidia have sharply defined boundaries that can be recognized objectively and are centered on monticules. Cormidia are large groups of zooids cooperating in feeding and water exchange across the colony surface, and may display independent morphogenetic histories within the same colony (Pachut et al. 1991).

Colonial Development.—Morphologic variation observed within a single colony is the result of all of these factors. In some cases the underlying causes can be factored out and recognized, but in other cases not. Therefore, overall changes through a colony (gradational, cyclic, random, etc.) are here referred to as developmental variation.

The term developmental variation is here equivalent to the term astogeny when it is used in the case of a high degree of colonial control over morphogenesis. Pachut et al.'s (1991: p. 213) broad definition of astogeny is appropriate for developmental variation, ". . . shared changes across multiple zooids during the growth of both the ancestrula zooid and

its asexual descendants," including, ". . . all coordinated changes in the size, shape, number and calcification of autozooids, polymorphs, and extrazooidal structures as well as changes within autozooids or polymorphs . . . ." Morphogenetic changes may be expressed as a colony wide gradient from the distal (youngest) to the proximal (oldest) end of the colony, incorporating all of the forms of variation discussed above. In many stenolaemate growth forms, this pattern can also be reflected locally in a series of tangential sections passing through the exozone (oldest at surface and progressively younger in deeper sections). Unidirectional gradients, however, are just one of many potential morphologic expressions of developmental changes.

In summary, five types of morphologic variation have been recognized in Bryozoa, associated with (1) astogeny—changes through early colonial development, (2) ontogeny—changes arising from growth histories of zooids and associated extrazooidal material, (3) polymorphs—distribution of polymorphs within a colony, (4) microenvironmental variation—semi-random changes, directional or abrupt, and (5) subcolonial organization (cormidia)—discrete units with nondirectional change. These forms of variation are all encompassed under the term developmental variation.

Observed Trends Within Colony Fragments

Canonical variates analysis was performed using the entire data set from the present study and colony segments as the class variable. This procedure emphasizes differences between segments, which in some cases belong to the same colony and in others not. This method, therefore, emphasizes neither within nor between colony variation. It simply retains the natural continuity of local segments of colonies. It also allows for simultaneous comparison of multiple segments in canonical discriminant space.

In order to systematically document morphologic change through a colony fragment, composite zooids were plotted in the sequence of their position along the branch (generation) versus the first canonical variate, CAN 1 (figs. 4A,C,E, and 5A,B). To determine the degree of variation between different segments of the same colony fragment, points were plotted on CAN 1 versus CAN 2 for colonies with multiple segments (figs. 4B,D,F). Observations can be summarized as follows.

Colony Fragment 355.—In a plot of generation (transect position number) versus canonical variate one there is no trend (correlation coefficients of 0.19 and 0.14 are too small to be significant). Changes through the two fragments at the same generational stages are uncorrelated, indicating a degree of independent morphogenesis between the two branches of the same colony (fig. 4A).

In a plot of canonical variate one versus two, the two fragments are clearly separated on CAN 2 (fig. 4B). This axis could be used, therefore, to differentiate between two branches at the same astogenetic stage (position in colony development) from this single colony fragment.

Colony Fragment 398.—When generation number is plotted against canonical variate one, a striking difference between trends of the primary branch (398_1) versus the two secondary branches (398_2 and 398_3) is apparent (fig. 4C). The positive slope in the primary branch reflects changes prior to branch bifurcation. There is a great deal of variability in the region after the bifurcation (generation 12–14), and then values stabilize for 398_3.

When CAN 1 is plotted against CAN 2, there is gross differentiation between the primary branch (398_1), and the left secondary branch (398_3), but the right and left branches are not as differentiated as in specimen 355.

Colony Fragment 400.—When the generation number is plotted against CAN 1 (fig. 4E), no trends are apparent, and changes between the two branches are not correlated. Segment 400_2 displays a great degree of variability across the transect. Although only two data points are present in the primary section of the branch (1 and 2) the trend changes direction after the branch bifurcation (fig. 4E). The same change in trend across branch bifurcation is seen in segment 398 (fig. 4C). Unlike the other specimens, when CAN 1 is plotted against CAN 2 (fig. 4F), there is virtually no difference between the branches.

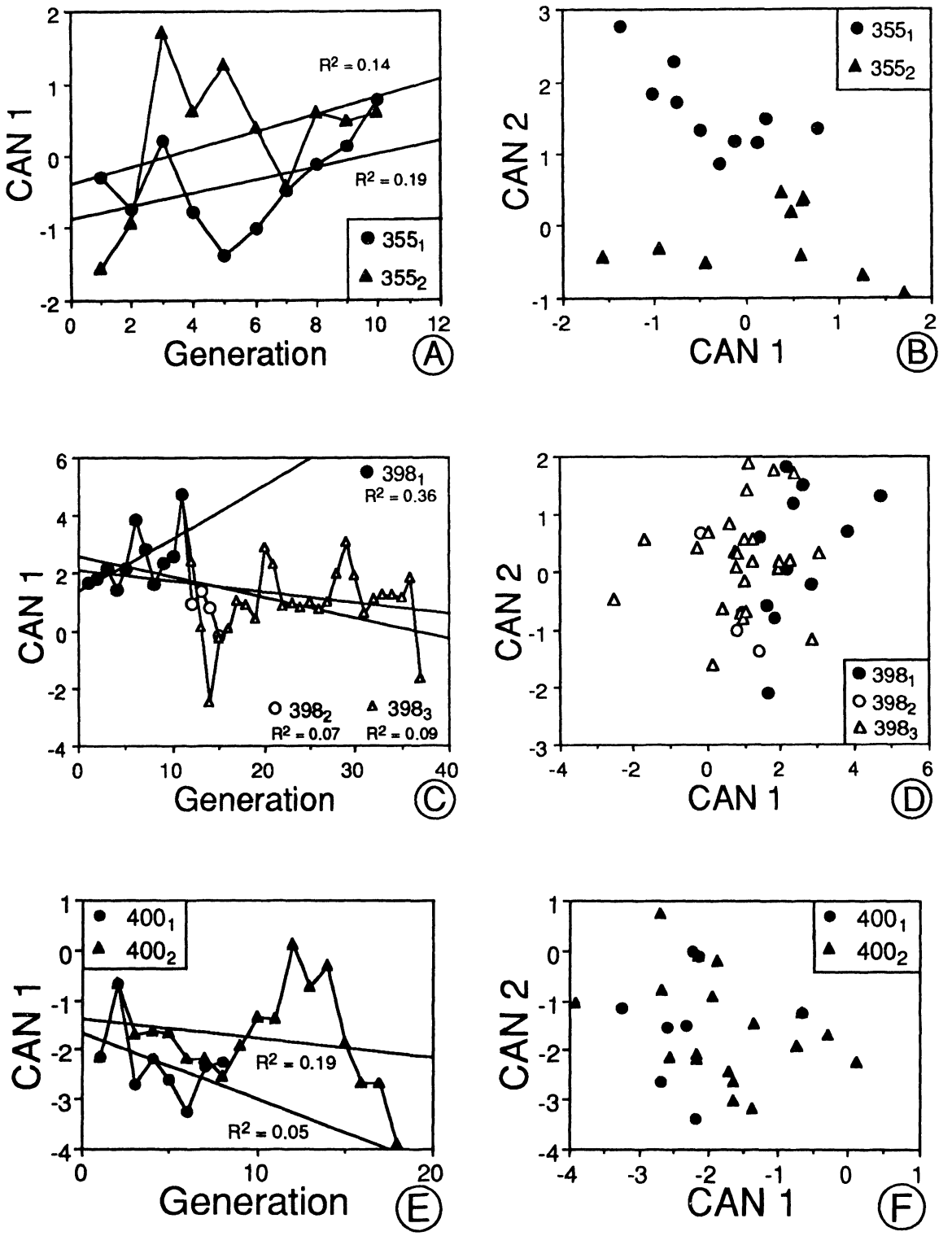


FIGURE 4. A, C, and E, Composite zooids for colony fragments 355, 398, and 400 plotted in the sequence of their position along the branch (generation) versus the first canonical variate (CAN 1). B, D, and F, Composite zooids plotted on canonical variates one versus two (CAN 1 vs. CAN 2) for colony fragments 355, 398, and 400.

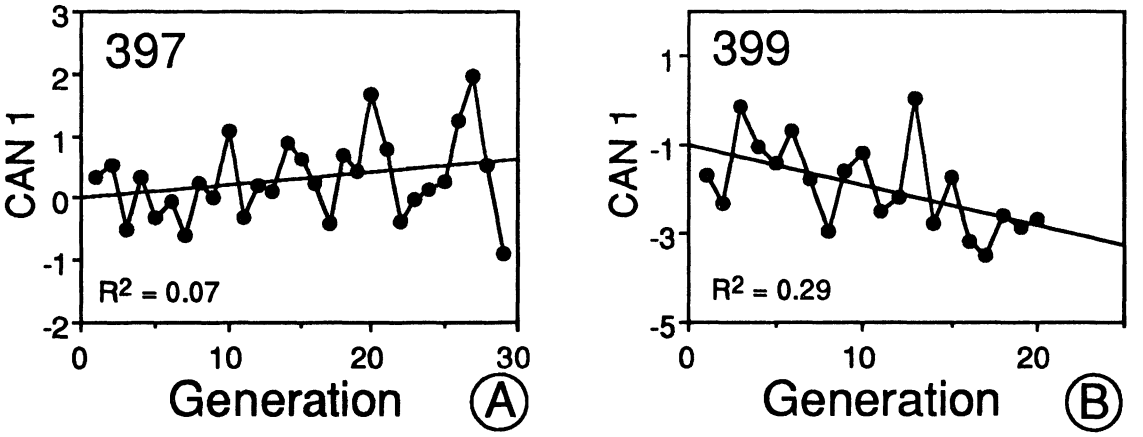


FIGURE 5. Composite zooids for colony fragments 397 and 399 plotted in the sequence of their position along the branch (generation) versus the first canonical variate (CAN 1).

Colony Fragment 397.—In a plot of generation versus canonical variate one (fig. 5A), there is virtually no trend (correlation coefficient of 0.07), but colonial morphology is constrained within relatively narrow bounds that gradually expand.

Colony Fragment 399.—When generation number is plotted against CAN 1 (fig. 5B), trends are stronger than in other specimens (correlation coefficient of 0.29). The scatter, however, still prevents definitive recognition of a unidirectional morphogenetic trend.

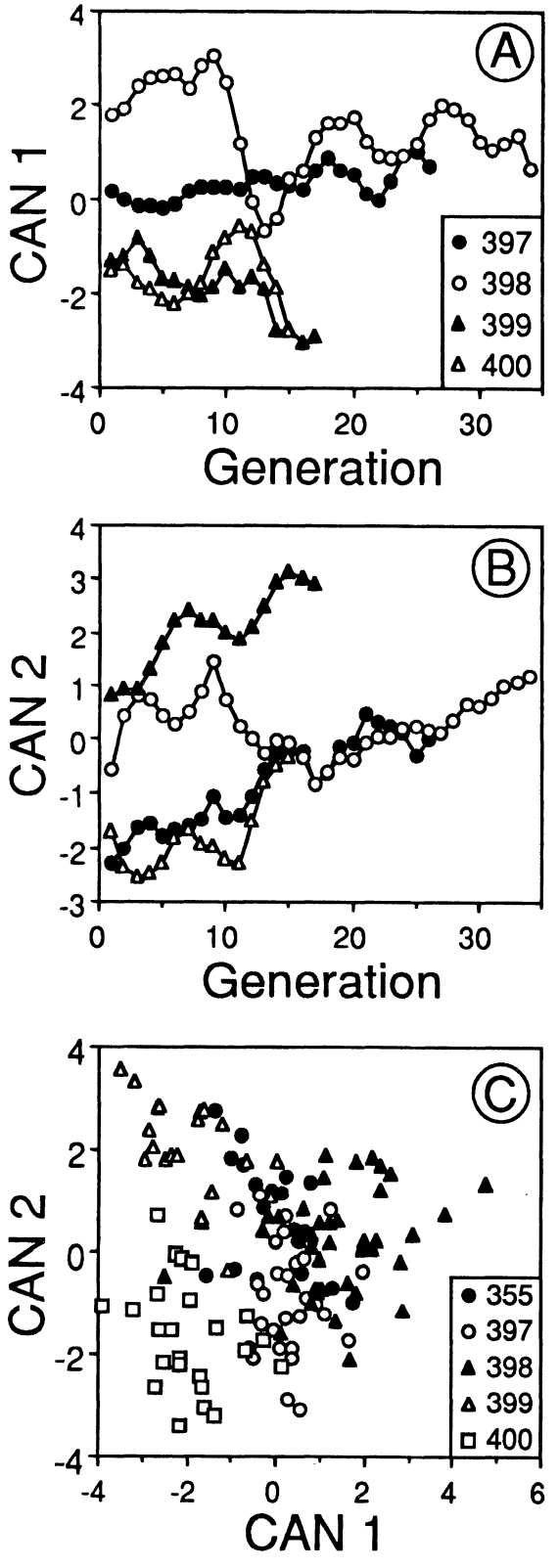
Discussion of Morphogenetic Trends.—The transects from the five colony fragments produce patterns that each invite individual interpretation, but as a whole do not provide a unified model of variation (e.g., no features of consistent directional astogenetic or ontogenetic change can be recognized.) This is, however, consistent with patterns expected from microenvironmental influences. That is, each segment of a colony has a morphology influenced by the specific environmental conditions at the time of its development. Conditions, and resultant morphologies, may change gradually or abruptly, unidirectionally or irregularly.

In general, each successive zooid is more similar to the adjacent zooids than to zooids from progressively more distant generations. Change is generally gradual, being most pronounced at branch bifurcation events. This allows for allocation of composite zooids to local segments from which they were measured.

Intracolonial Versus Intercolonial Variation

In order to evaluate trends within sub-units of colony fragments and to compare overall variation among colonies, average values for each of four successive composite zooids were calculated through a transect. This four-point moving average smooths noise out of the plot. Four colony fragments were plotted with four-point moving average of composite zooids against canonical variate one (fig. 6A) and canonical variate two (fig. 6B). Note that generations are not equivalent between segments (each arbitrarily starting at the first observation).

Variation Among Colonies.—Overall differences do exist between some of these fragments. For example, fragments 397 and 399 do not overlap on either canonical axes one or two (figs. 6A,B). There is also a degree of morphologic conservatism in all colonies. Note that most variation within colonies (four-point means), is contained in about ⅓ of the total observed variation (figs. 6A,B). This indicates that with these specimens, there is another level of morphological control beyond microenvironmental, which is either genetic or macroenvironmental. Paleoecological information for these particular specimens does not provide resolution of this



question. In a more controlled setting, possibly with living specimens, the limits of genetic versus macroenvironmental controls on morphology could be addressed using these same methods.

Cyclic Trends Within Colonies.—Four-point moving averages of the four colony fragments all exhibit alternating trends (figs. 6A,B). These trends inflect about every three to five zooids. Although alternating trends are not present throughout entire fragments, when expressed they are regular enough to suggest cyclic microenvironmental influence(s).

These trends were tested for cyclicity using the nonparametric runs test, which evaluates serial randomness of nominal categories. The categories here were positive (+) and negative (−) changes in successive four-point moving averages. Patterns are varied but are regular enough to suggest cyclicity (table 3). In fact, only segment 399 and the trace of 397 on CAN 1, do not have probabilities of $p \leq 0.20$ of being nonrandom. When the last observation(s) of sequences are omitted (removing artificial truncations of natural sequences), colony fragments 397 (CAN 1) and 400 (CAN 1 and CAN 2), are actually nonrandom at a probability level of $p \leq 0.05$ (table 3). Although, individually, these probability levels are not significant enough to be definitive, the consistent occurrence of low probability values merits serious consideration of cyclic influences.

Absence of growth hiatuses in rhabdomesine bryozoans suggests that colonies reflect a relatively continuous record of growth and microenvironmental changes. Inferred growth rates for this extinct suborder of bryozoans can only be speculated upon, but the preserved cycles are presumably moderately short-term, being in the magnitude of tidal (lunar cycles) or seasonal, rather than diurnal or annual.

←

FIGURE 6. A, Four-point moving average for multi-segment fragments on canonical variate one. B, Four-point moving average for multi-segment fragments on canonical variate two (key same as 6A). C, Composite zooids for all segments plotted on canonical axis one versus two.

TABLE 3. Nonparametric runs test of serial randomness in four-point moving averages through bryozoan colonies. Successive positive and negative change between generations are represented by + and −. Results are summarized as (n_1, n_2, μ), where n_1 is number of observations in the smaller category, n_2 is the number of observations in the larger category, μ is the number of groups and p = probability of random sequence. Critical values for μ are given in Zar (1984: table D.34). First probability includes all data; second probability, last observation(s) omitted to correct for artificial truncation of natural sequence.

397 CAN 1 (11, 14, 11) (11, 13, 10)		
−−−+++−+−++−−−++−−−−+++−	$p = 0.50$	$p = 0.50$
397 CAN 2 (9, 17, 9) (9, 16, 8)		
+++−++++−+++++−−++++−−−−+	$p = 0.20$	$p = 0.10$
398 CAN 1 (14, 19, 12) (13, 17, 10)		
+++++−++−−−−++++++−+−−−++++−−−−++−	$p = 0.10$	$p = 0.05$
398 CAN 2 (4, 19, 13) (14, 17, 12)		
++−−−+++−−−−+−−−++−++++++−−++−++++	$p = 0.20$	$p = 0.20$
399 CAN 1 (7, 9, 9)		
++−−−−−++−+−−+−+	$p = 0.50$	
399 CAN 2 (6, 10, 8)		
+−++++−+−−++++−−	$p = 0.50$	
400 CAN 1 (6, 8, 4) (5, 8, 3)		
+−−−−++++−−−−	$p = 0.10$	$p = 0.05$
400 CAN 2 (6, 8, 4) (4, 8, 3)		
−−++++−−−−++++	$p = 0.10$	$p = 0.05$

Characters Associated with Trends

Absolute values of coefficients from standardized canonical discriminant functions indicate the relative contribution of each of the original variables to a canonical variate. With these data, lateral aperture spacing (ASL) is most important in the first and branch width (EBW) in the second variate, but the variates are generally a mix of all original variables (table 4). This indicates that all of the characters used here are important in defining the recognized patterns. These findings are not particularly enlightening in this case, but this information can provide important information about the relative importance of chosen characters and potentially their biologic significance (Hageman 1991, 1994).

Implications for Systematic and Evolutionary Studies

Sound species concepts depend on accurate documentation of morphologic variation. Colonial organisms have the additional requirement of adequate documentation of intracolonial variation, lest separate "species" be based on disassociated colony fragments from a single genet (Boardman 1954).

Typical taphonomic histories for bryozoan specimens result in breakage of colonies. Workers, therefore, frequently must rely on fragments of colonies for systematic and evolutionary studies. However, bryozoans' colonial nature means that, unlike noncolonial organisms, viable data can be collected from a wide range of fragmented material. Results from this study of intracolonial versus intercolonial morphologic variation provide a strategy for data collection for systematic and microevolutionary studies, which require documentation of morphologic variation within a population.

This work has demonstrated that a small number of observations can adequately represent a local region of a colony. It has been determined that the optimal number of observations is five per segment for this taxon (Hageman 1993). Other workers have effectively employed three to six observations per segment in morphometric studies of cheilo-

TABLE 4. Coefficients from canonical variates analysis performed with 148 composite with colony segment number as class variable. A mix of all characters contributes to defining observed patterns.

Character	CAN 1	CAN 2
AAL	−0.50	0.41
AAW	0.38	0.46
ASL	0.79	−0.60
ASD	−0.34	0.15
ASA	0.11	−0.32
EBW	0.14	0.76

stomes (Cheetham 1986; Lidgard and Buckley 1994).

Because morphologic variation within a local region is not necessarily representative of an entire colony, small fragments should not be used as a proxy for colonial variation (complete genotype). In addition, morphologic variation within one colony does not represent an entire population.

In order to best document morphologic variation within a population, individual measurements should be widely distributed over large colony fragments in clusters of three to five zooids and (or) observations collected from three to five zooids from a large number of smaller fragments. Little additional information is gained from collecting large numbers of observations from a small area or fragment of a colony.

These observations and suggestions may seem inherently logical, but given our very heavy reliance on fragmentary material, their importance for systematic and evolutionary studies has not been adequately tested. Other studies indicate that these guidelines for data collection apply to rhabdomesines (Hageman 1993), fenestellids (Holdener in press), trepostomes (Pachut et al. 1991), cystoporates (Anstey et al. 1976), cyclostomes (Taylor and Furness 1978; McKinney et al. 1993), and cheilostomes (Cheetham 1986).

Broader Applications.—The broader applicability of the principles suggested here can be determined through application of similar methods to corals and graptolites. In addition, great promise exists for studies using modern colonial organisms in experimental designs that incorporate hard-part morphology, genetics and ecology (see e.g., Jackson and Cheetham 1990; Cheetham et al. 1993, 1994, in press).

Observations of morphologic variation in a specific bryozoan and the implications that they carry for systematic studies cannot be extrapolated directly to non-colonial organisms. However, insights gained through further, related studies of morphologic variation in colonial organisms will undoubtedly broaden our understanding of phenotypic plasticity and relationships between morphology and genetics in general.

Conclusions

1. Bryozoan skeletal morphology is conservative over local regions of a colony. Each successive zooid is (generally) more similar to adjacent zooids than to ones further away. This allows for composite zooids (multivariate observations) to be objectively reassigned to the fragment from which they were measured. Measurements from three to five adjacent composite zooids, therefore, adequately represent a local region of a colony.

2. Morphologic conservatism does not necessarily extend throughout an entire colony. A local segment, therefore, may not represent the total morphologic variation within a colony as a whole.

3. Morphologic overlap between segments of different colonies is common. One segment of a colony can be more similar to a region of a different colony than it is to a distant part of its own colony. One colony does not, however, represent the total morphologic variation among several colonies, indicating a genetic or microenvironmental colonial level of control.

4. Unidirectional morphogenetic gradients are not recognized in the specimens studied. Varied patterns of morphologic variation within the observed colony fragments are, however, consistent with those expected from changing microenvironmental influences.

5. Microenvironmental influences in some specimens appear to be cyclic, with a periodicity of three to five zooids. Specific causes of microenvironmental fluctuations are not clear, but appear to be moderately short term.

6. Although differences between genotypic and macroenvironmental constraints over morphology cannot be determined from the present data, these factors could be recognized using the same methods in a more controlled setting.

7. To best document morphologic variation within a population for systematic and evolutionary studies, individual measurements should be widely distributed over large colony fragments and (or) a minimal number of measurements collected from a large number of smaller fragments.

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