Implications Of Intracolonial Variation In A Paleozoic Bryozoan

By: Eric J. Holdener and **Steven J. Hageman**

Abstract

Relative differences between environmentally controlled variation and genetically controlled variation are important when investigating morphologic variation in general, especially when establishing species concepts. The colonial nature of bryozoans provides a means for distinguishing between the two sources; variation can be partitioned into within-colony (microenvironmental) and among-colony (environmental + genetic) components. For the Paleozoic order Cryptostomata, biologically and taxonomically significant morphologic characters are well defined and methods for recognizing morphotaxa are well established. The importance of within-colony variation to the morphometric treatment of fenestrate species was assessed after the discovery of a large specimen of Hemitrypa sp. Variation within the colony was compared to variation among and within two congeneric species. The distribution of study segments across the colony allowed assessment of variation both along the growth axis and laterally between segments of approximately equivalent generational age. Repeatability of methods was assessed using data measured independently from identical segments by three workers. Variation within the large colony is less than variation among congeneric species, indicating that genetic differences among species exceed variation resulting from combined phenotypic and genotypic sources within species. Neither astogenetic nor ontogenetic morphologic gradients are recognized.

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IMPLICATIONS OF INTRACOLONIAL VARIATION IN A PALEOZOIC BRYOZOAN

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ABSTRACT—Relative differences between environmentally controlled variation and genetically controlled variation are important when investigating morphologic variation in general, especially when establishing species concepts. The colonial nature of bryozoans provides a means for distinguishing between the two sources; variation can be partitioned into within-colony (microenvironmental) and among-colony (environmental + genetic) components. For the Paleozoic order Cryptostomata, biologically and taxonomically significant morphologic characters are well defined and methods for recognizing morphotaxa are well established.

The importance of within-colony variation to the morphometric treatment of fenestrate species was assessed after the discovery of a large specimen of *Hemitrypa* sp. Variation within the colony was compared to variation among and within two congeneric species. The distribution of study segments across the colony allowed assessment of variation both along the growth axis and laterally between segments of approximately equivalent generational age. Repeatability of methods was assessed using data measured independently from identical segments by three workers.

Variation within the large colony is less than variation among congeneric species, indicating that genetic differences among species exceed variation resulting from combined phenotypic and genotypic sources within species. Neither astogenetic nor ontogenetic morphologic gradients are recognized. Variation between data collected from identical segments by pairs of workers falls within the range of variation for the entire colony. Thus, multiple workers can reproduce data to the finest level of meaningful resolution. Cryptostome morphospecies concepts are validated.

The potential for partitioning genotypic versus environmental variation in reduced, multidimensional morphospace is reinforced. Studies of microevolution and speciation may be designed that account for these factors.

INTRODUCTION

DISTINGUISHING BETWEEN environmental and genetic components of variation is an elusive goal in paleontological research but one that is critical to establishing meaningful species concepts in fossils. Sound species concepts, in turn, form the basis for paleoecological and evolutionary analyses. Colonial organisms, with colonies comprised of individual units sharing a single genotype, provide a means for comparing within-colony (microenvironmental) variation versus among-colony (environmental + genetic) variation (e.g., Schopf, 1976; Brande and Bretsky, 1982). The relationship between the two is essential, especially when interpreting morphologic variation among statistical populations derived from a limited number of specimens. Furthermore, a connection has been established between among-colony variation and genetic heritability (Cheetham et al., 1993, 1994, 1995).

For bryozoan colonies, several sources of within-colony variation have been identified: 1) subcolonial organization (cormidia of Anstey et al., 1976); 2) ontogeny; 3) polymorphy; 4) microenvironment; and 5) astogeny (latter four sources after Boardman et al., 1983). Of these, astogeny (systematic, related to generational position within a colony) is the least uniformly accepted in terms of process (see e.g., Pachut et al., 1991). Astogenetic variation, however, has been recognized as a potential problem for species concepts, especially among Paleozoic stenolaemates (Anstey and Perry, 1970). For fenestrates (suborder Fenstellina), studies of astogenetic variation within individual characters have addressed this concern (e.g., Elias, 1964; Stratton and Horowitz, 1977; McKinney, 1980; McKinney and Stedman, 1981, Stedman, 1982); the present research assesses fenestrate astogenetic variation using a multivariate approach.

Development of suitable character lists for analysis has relied

FIGURE 1—Obverse surface of *Hemitrypa* sp. specimen with meshwork superstructure, approximately ×1.

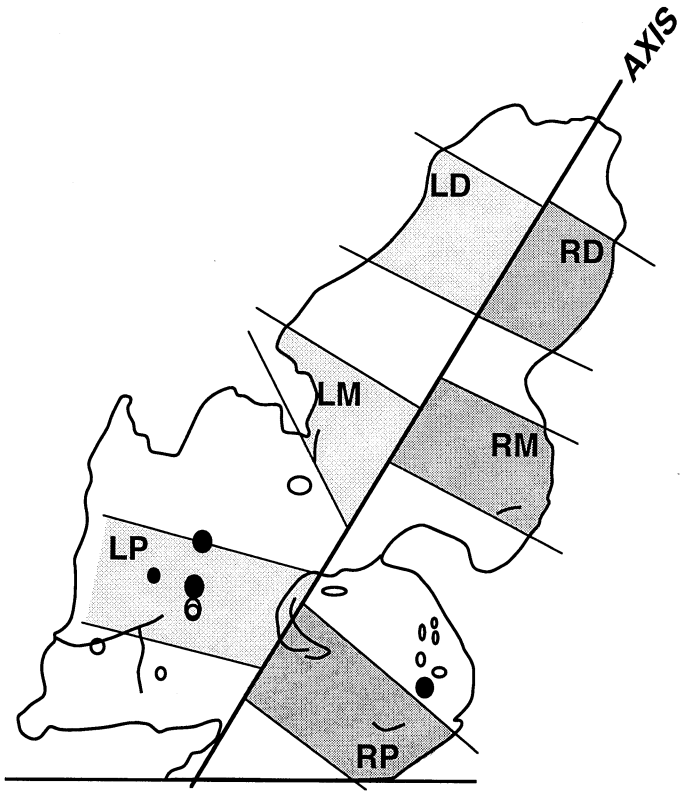


FIGURE 2—Colony map showing division of specimen into segments. Left (L) and right (R) sides of colony were cut into segments, with three chosen per side: LP = left *p*roximal; LM = left *m*edial; LD = left *d*istal; RP = right *p*roximal; RM = right *m*edial; and RD = right *d*istal. Observations are keyed to workers by number: EJH = 1; DBB = 2; SJH = 3. For example: LP2 = observations collected from the *l*eft *p*roximal segment by Worker 2; RM3 = observations collected from the *r*ight *m*edial segment by Worker 3; and LD1 = observations collected from the *l*eft *d*istal segment by Worker 1. Figures and text discussions of observations are coded by this scheme to colony segment and worker.

on both fossil and living bryozoans. For fenestrates, Snyder (1984, 1991; see also McKinney and Kriz, 1986) developed a character list based largely on the autozooecial living chamber and zooidal spacing. Among living analogous cheilostomes, chamber shape and zooidal spacing are intraspecifically constant, correlate closely to biological traits, and strongly reflect features of soft-part zooecial morphology (Winston, 1977; McKinney and Boardman, 1985). Hageman (1991) verified fenestrate species concepts based on a statistical analysis of Snyder's (1984, 1991) data set. Holdener (1994) demonstrated that another worker could collect statistically equivalent data, and he demonstrated that the fenestrate character set was capable of distinguishing between populations of traditionally defined fenestrate species. Hageman (1994) distinguished between populations in a geographic cline for the rhabdomesine *Streblotrypa*. Small-scale intraspecific variation, therefore, can be recognized among Paleozoic cryptostomes.

Hageman (1994, for the rhabdomesine *Streblotrypa*) and Holdener and Hageman (this article, for the fenestrate *Hemitrypa*) observed that composite zooids [composed of measurements from several zooids and treated as single individuals (OTUs) in numerical analyses] could be reassigned confidently to the colony segments from which the observations were measured. Furthermore, Hageman (1995) reported the assignment of test composite zooids to conspecific (*Streblotrypa*) colony fragments in analyses that employed additional segments of the colony from which the test observations were measured. Strong morphological conservatism within colonies and among conspecific colonies of cryptostomes raises concerns and questions. Is within-colony variation confusing interpretations of interpopulation variation? How does the scope of within-colony variation compare with that of among-colony variation? Among the stenolaemates, cryptostome morphologic conservatism potentially impacts upon these interpretations and upon species concepts within the order.

The discovery of a large (>10 cm) fenestrate frond offered an opportunity to assess the potential impact of within-colony variation on the morphometric treatment of fenestrate species. Sampling along the colony's growth axis allowed testing of the following questions: 1) Are results reproducible among independent workers? 2) If present, how does the magnitude of between-worker variation compare with that of within-colony variation? 3) What is the impact of within-colony variation on interpretations of variation among colonies, populations, and species? 4) Is astogenetic variation (sensu Pachut et al., 1991) or ontogenetic variation (sensu Boardman et al., 1983) recognizable and could this source of variation adversely affect assessments of variation among colonies or populations? 5) How does the magnitude of microenvironmental variation compare with that of age-related variation, if present?

MATERIALS AND METHODS

This study is based on a single large (>10 cm long), well-preserved frond assigned to *Hemitrypa* sp. (Fig. 1). In order to document and compare within-colony morphological variation, the frond was subdivided into segments (Fig. 2). The midline of the frond was determined visually, and both colony halves were divided into segments along this growth axis. These segments were examined and three were selected from each half to meet the following criteria: 1) To constrain ontogenetic differences

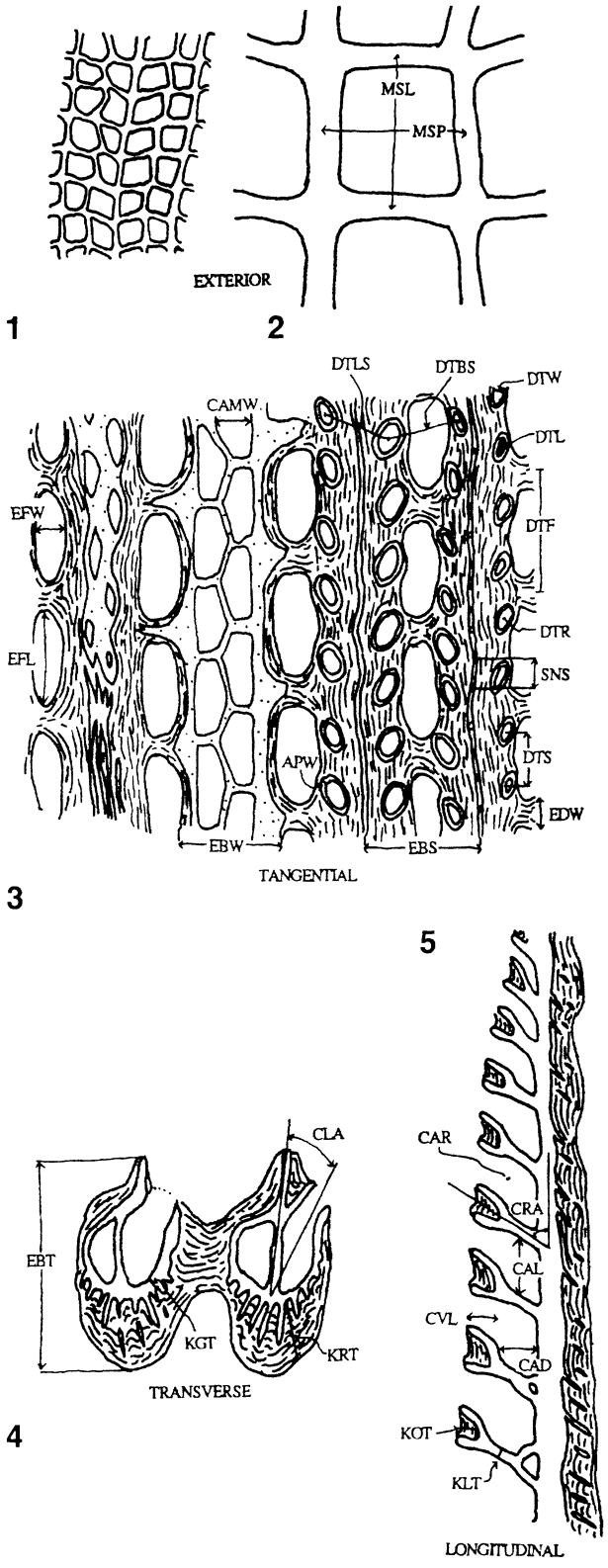


FIGURE 3—Generalized hemitrypid illustrating exterior meshwork superstructure (*1, 2*) and interior (*3, 4, 5*) morphometric characters (1–28) listed in Table 1. All characters except MSL and MSP measured from serial acetate peels. See Snyder (1991) for discussion of characters.

TABLE 1—Morphometric characters used in this study and illustrated in Figure 3. Parenthetic abbreviations are exact or approximate (marked by asterisks) equivalent characters of Snyder (1991) and Hageman (1991). Superscript "e" marks characters used in analyses of characters most likely affected by thickening of extrazooidal skeleton. Superscript "c" marks characters used in analyses of chamber characters.

	Exterior characters
EBW (WB)[e]	1. Width of branch (not measured at branch bifurcation)
EBS (DBC)	2. Distance between branch centers (not measured at branch bifurcation)
EDW (WD)[e]	3. Width of dissepiment
EFL (LF)[e]	4. Length of fenestrule
EFW (WF)[e]	5. Width of fenestrule
EBT (TB)[e]	6. Thickness of branch
DTF (AF)*	7. Distal tubes per fenestrule (measured between dissepiment centers)
DTL (AL)*	8. Distal tube length (measured proximo-distally)
DTW (AW)*	9. Distal tube width (measured perpendicular to aperture length
DTS (ADB)	10. Distance between distal tube centers along branch
DTLS (AAB)	11. Distance between distal tube centers across branch at closest point
DTBS (ABB)	12. Distance between distal tube centers between branches
APW (WP)*[e]	13. Width of peristome
DTR	14. Distal tube area
SNS (SNB)	15. Distance between keel nodes along obverse branch surface
MSL (LRM)	16. Meshwork spacing parallel to growth axis
MSP (WRM)	17. Meshwork spacing perpendicular to growth axis
	Interior characters
KGT (TRW)	18. Thickness of reverse wall granular layer
KRT (RWT)[e]	19. Thickness of reverse wall laminated layer
KLT (TLW)	20. Thickness of chamber lateral wall granular layer
KOT (FWT)[e]	21. Thickness of obverse wall laminated layer
CAL (CL)[c]	22. Autozooecial chamber length
CAD (CD)[c]	23. Autozooecial chamber depth
CAMW (MAW)[c]	24. Maximum chamber width
CVL (VD)	25. Chamber vestibule length
CRA (RA)[c]	26. Chamber reverse wall budding angle
CLA (LA)[c]	27. Chamber lateral wall budding angle
CAR[c]	28. Maximum area of chamber (in mid-longitudinal section)
	Derived characters
DTLW (AA)*	29. Apertural length * apertural width
CWL (CAMW/CL)[c]	30. Maximum chamber width ÷ chamber length
CLD (CL*CD)[c]	31. Chamber length * chamber depth
CLWD (VOL)[c]	32. Chamber length * chamber depth * maximum chamber width

among zooids, growing tips are excluded. 2) To assess morphological differences related to colony age (e.g., astogeny sensu Pachut et al., 1991 or ontogeny sensu Boardman et al., 1983), segments along the growth axis are spaced (proximal, medial, and distal). 3) To insure equivalent generational age, segments from either side of the colony correspond spatially across the growth axis with regions from the other side. 4) Segments are relatively undamaged and provide readily collectable and adequate data.

Mature portions of hemitrypid colonies possessed a protective meshwork superstructure that formed as an expansion of nodes along the obverse keel and served to protect the feeding zooids (Miller, 1962). This structure obscured the obverse surface of the study specimen and reduced the number of available characters. Characters normally measured from reverse surfaces were unavailable because this surface of the study frond was cemented to underlying matrix. In all, 26 characters of the 43 employed by Snyder (1991) were measured; six additional characters were included in the analyses for a total of 32 (Fig. 3, Table 1).

Data collection.—Data were collected from magnified video images of acetate peels from oriented sections. Holdener (EJH) and Hageman (SJH) prepared peels from opposite sides of the colony. D. B. Blake (DBB) collected data from the left side; SJH collected data from the right; and EJH collected data from both sides (Fig. 2). EJH and SJH have worked extensively with fenestrate material, whereas DBB collected fenestrate data for the first time. Each worker collected data independently after initial discussions of the characters, their meaning, and their proper orientation in section. In figures, tables, and in text discussions below, EJH = Worker 1, DBB = Worker 2, SJH = Worker 3.

Analyses and interpretation.—Canonical discriminant analysis has been used in prior studies of bryozoan morphological variation (e.g., Anstey et al., 1976; Schopf, 1976; Taylor and Furness, 1978; Pachut, 1982; Key, 1987; Hageman 1993, 1994; Holdener, 1994). In essence, characters for which data were collected can be considered axes that define segment regions in multidimensional space (32 dimensions here). Canonical discriminant analysis transforms this space and expresses the total variation among segments using far fewer axes (two dimensions here). Scores for individual composite zooids and segment means (centroids) are calculated in the new axis system, and composite zooids are classified based on their positions relative to all segment means in the analysis (see Neff and Marcus, 1980, and Hageman, 1991, for comprehensive reviews). Results of analyses are presented as percentages of observations assigned correctly to colony segment (by worker) and as plots of observations in the reduced morphospace defined by the first and second canonical discriminant functions. To minimize the confusion of overlapping data points, a second plot may be presented in which the statistical program (StatView II) handles this overlap by enlarging the symbols used in the plots. Text discussions and symbols in plots are coded to correspond to colony segments and workers (Figs. 2 and 4).

Degrees of variability between data collected by pairs of workers from identical colony segments are deduced by comparing the proximity of their respective observation "clouds" or regions in the reduced morphospace. The amount of variation is also indicated by the relative breadth of the morphospace needed to describe the observations; the larger the region occupied by a set of observations, the greater the variation exhibited.

Design of analyses.—Analyses were run using data collected by pairs of workers from identical colony segments (Fig. 2). Reproducibility was measured by the extent to which observations gathered by pairs of workers from identical colony segments plotted together and by comparing between-worker variation with within-colony variation. A discriminant analysis was then run using the combined data set consisting of all observations collected by the three workers. To assess within-colony versus among-colony variation, observations in this combined data set were compared in reduced morphospace with observations from two coeval hemitrypid species.

Data collected by Worker 1 (EJH) was employed to further assess within-colony variation and to test for within-colony trends among subsets of exterior and interior characters. Exterior characters (Table 1) are affected by the addition of laminated skeletal material and are more likely to express within-colony variation resulting from either astogeny (Snyder, 1984, 1991; Pachut et al., 1991), ontogeny (Boardman et al., 1983) or microenvironment. Previous research (Holdener, 1994) has indicated that chamber characters (Table 1) are largely buffered from sources of variation that affect exterior characters. Canonical discriminant analyses were run using exterior and interior characters, and, as a further test, mean values for exterior characters were compared among segments along the growth axis.

ASTOGENY AS A SOURCE OF VARIATION

The extent to which astogeny contributes to within-colony morphologic variation is debated. Boardman et al. (1983, p. 36) defined astogeny as, ". . . the course of development of the sequence of asexual generations of zooids and any extrazooidal parts that together form a colony." For most bryozoans, these authors describe a primary zone of astogenetic change consisting of the ancestrula (primary zooid) and the few succeeding generations of zooids that "show morphologic differences from generation to generation in more or less uniform progression" (Boardman et al., 1983, p. 36). This zone "is followed distally by a primary zone of astogenetic repetition in which large numbers of zooids of repeated morphologies are proliferated" (Boardman et al., 1983, p. 36). Among mature zooids outside of zones of change, morphologic differences are not attributable to astogeny, but rather ontogeny, polymorphism (if present), and microenvironment dominate (Boardman et al., 1983, see, e.g., fig. 24, p. 38). Pachut et al. (1991, p. 213) offered a broader definition: ". . . astogeny (shared changes across multiple zooids during the growth of both the ancestrular zooid and its asexual descendants) includes all coordinated changes in the size, shape, number, and calcification of autozooids, polymorphs, and extrazooidal structures . . . ."

Boardman et al. (1983) developed their definition primarily upon investigations of cheilostomes (class Gymnolaemata). Pachut et al. (1991) limited their scope to stenolaemates (class Stenolaemata), primarily to trepostomes (order Trepostomata) within that clade. Members of the order Cryptostomata are distinctive among stenolaemates, however, in that they possess zooecia that are more boxlike and less tubular, and extrazooidal hard parts, especially among the fenestrates, are well-developed.

If astogenetic variation is only recognized in zones of change (Boardman et al., 1983), changes among characters describing extrazooidal parts in the present study actually fall within their definition of ontogeny that includes ". . . changes in . . . any extrazooidal part . . . during the course of . . . development . . ." (Boardman et al., 1983, p. 34). Such variation should appear as a *proximally* directed gradient of increasing morphologic complexity. According to Pachut et al. (1991), astogenetic variation among characters that describe extrazooidal parts should manifest itself either as coordinated changes in these characters among segments of a colony (cormidia) or as a *distally* directed morphologic gradient. In either direction, a morphologic gradient should be discernible in characters that reflect the growth of extrazooidal skeleton.

RESULTS

Between-worker variation.—Canonical discriminant analyses performed on data collected by Worker 1 and Worker 2 from the left side of the colony (Fig. 4.1) and by Worker 1 and Worker 3 from the right (Fig. 4.2 and 4.3) confirm variation between data sets collected by pairs of workers. For the left side of the colony (Fig. 4.1), observations segregate by worker along the second canonical function (CAN 2); variation along the growth axis is differentiated by the first function (CAN 1). However, the first function accounts for more variation than the second, and, therefore, between-worker variation does not exceed within-colony variation.

For the right side of the colony (Fig. 4.2, 4.3), observations by worker plot essentially on top of one another, and there is considerable overlap among the segments. Observations segregate by worker along the second canonical function (CAN

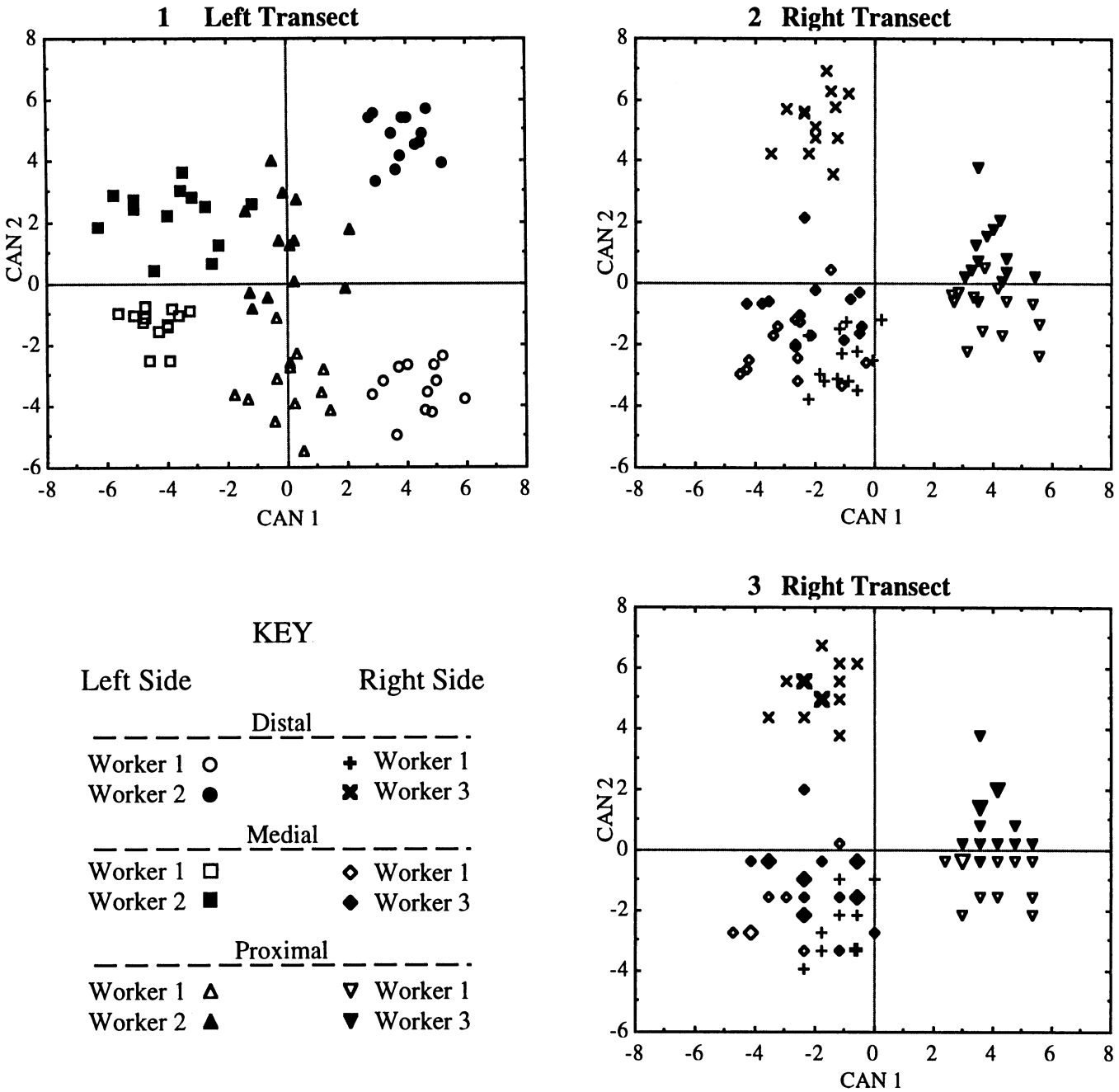


FIGURE 4—Scatterplots produced by discriminant analysis run using data collected by pairs of workers from colony halves. *1*, Worker 1 and Worker 2 observations from left side of hemitrypid frond. Seventy-eight of 78 (100 percent) observations assigned correctly to segment (by worker). *2*, Worker 1 and Worker 3 observations from right side of hemitrypid frond. Seventy-seven of 78 (98.7 percent) observations assigned correctly to segment (by worker). *3*, identical to Figure 4.2 but with overlapping data indicated by enlarged symbols. These and subsequent scatterplots (except Fig. 5) use the labels in the key to identify observations to segment and worker. See Figure 2 for discussion of letter designations.

2). The separation is minimal, but Worker 3 observations, in general, plot higher on the axis. The larger distance between observations collected from the distal segment (RD1, +, and RD3, **X**) results from a slight systematic error in calibration during initial data collection. Less between-worker variation among observations collected from the right side of the colony may reflect greater familiarity with fenestrate morphology for Workers 1 and 3 (relative to Worker 2), or it may result from a growth orientation that was more accommodating for collecting data. The right side of the colony possessed a flatter frond that facilitated the production of peels from properly oriented sections.

Characters that contribute most to the discriminant axes in Figures 4.1 and 4.2 were determined from the absolute values of the coefficients of the standardized canonical functions and are listed in Table 2. For both the left and right sides of the colony, chamber characters top the lists for both the first and second functions. Chamber characters, therefore, are most important for discriminating among segments within the colony (CAN 1) and between workers (CAN 2). The distribution of

TABLE 2—Characters contributing the most to the canonical discriminant functions (CAN 1 and CAN 2) in scatterplots of observations collected by: Column 1 = Workers 1 and 2 from the left side of the colony (Fig. 4.1); Column 2 = Workers 1 and 3 from the right side of the colony (Fig. 4.2, 4.3); and Column 3 = Worker 1 from both sides of the colony (Fig. 7). Relative contributions of characters decrease from top to bottom. See text for discussion.

1 Between workers 1 & 2, left side		2 Between workers 1 & 3, right side		3 Worker 1, both sides, intracolonial	
CAN 1	CAN 2	CAN 1	CAN 2	CAN 1	CAN 2
CLWD	CWL	CAD	CLD	CLD	CWL
DTLW	CAL	DTLW	CAMW	CAL	CAMW
CAMW	CAMW	CLD	CAD	CAD	DTLW
EFL	CLWD	CAL	CAL	CAMW	CAL
DTW	CLD	DTW	CLWD	CLWD	CLD
DTL	KRT	DTL	CWL	CWL	CLWD
CWL	KGT	CWL	DTLW	KRT	DTW
CAD	CAR	CLWD	DTW	KOT	DTL
CLD	CAD	EBT	DTL	DTLW	DTR
APW	KLT	CAR	KRT	DTW	EBT

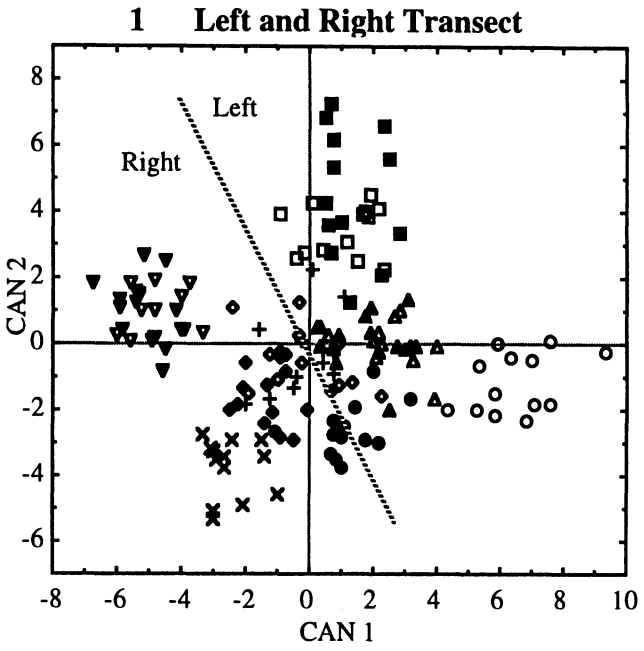
colony segments along the first axis and the segregation by workers along the second axis imply that variation between workers is less than (does not mask) variation among segments within a colony.

Figure 5 presents results of the canonical discriminant analysis performed on the combined data set collected by all three workers. Observations collected by pairs of workers from identical colony segments, in general, occupy relatively tightly defined morphospace regions (e.g., LP1, △, and LP2, ▲; RP1, ▽, and RP3, ▼). Between-worker variation is expressed as distances between observations collected by individual workers from identical colony segments (e.g., LM1, □, and LM2, ■), and this variation is maximal between LD1 (○) and LD2 (●) and between RD1 (+) and RD3 (**X**). Between-worker variation (expressed by distances between groups of observations from identical segments) does not mask patterns of subcolonial morphologic variation. Variation between colony halves is apparent; the dashed line approximately separates observations from the right and left sides of the colony (Fig. 5).

Interspecific comparison of within-colony variation.—In comparison with two coeval hemitrypid species (*Hemitrypa vermifera* and *H. aprilae,* data from Snyder 1991), the range of within-colony variation for the *Hemitrypa* sp. specimen is comparable to among-colony variation for the coeval species (Fig. 6). However, the morphospace region occupied by *Hemitrypa* sp. contains all 156 observations gathered by Workers 1, 2, and 3; the *H. vermifera* and *H. aprilae* regions contain only 12 observations each. The *Hemitrypa* sp. region contains 13 times more observations than those of the other species, and all variation under consideration (within-colony and between-worker) is contained within this region. This result agrees with the findings by Hageman and Blake (1992) and Hageman (1995) that, for the rhabdomesine *Streblotrypa prisca,* within-colony variation can approach that of among-colony (intraspecific) variation. Furthermore, because the *Hemitrypa* sp. observations are known to come from a single specimen (species), similar morphospace dimensions among the three Warsaw species support both the numerical species and morphospecies concepts for fenestrates (Snyder, 1991 ; Hageman, 1994; and Holdener, 1994).

WITHIN-COLONY VARIATION

To avoid possible confusion from between-worker variation, further investigations of within-colony variation were limited to data collected from both colony halves by Worker 1 (Fig. 7). Within-colony variation is clearly expressed by the placement



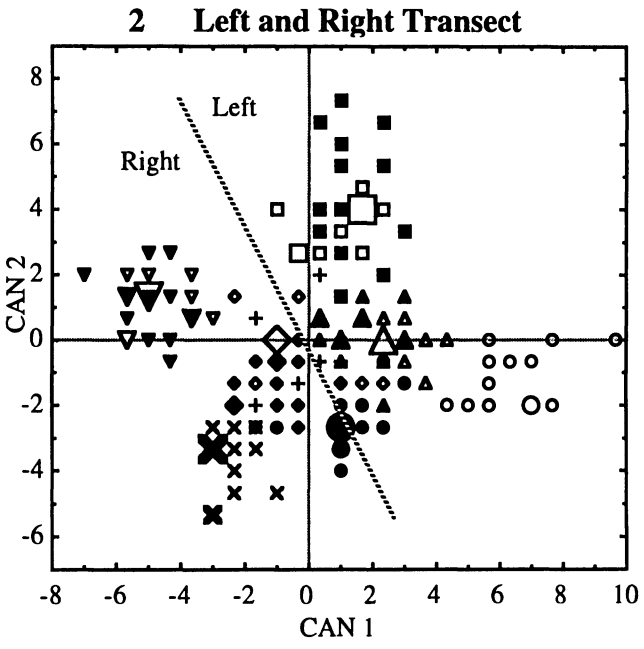


FIGURE 5—*1,* scatterplot produced by discriminant analysis run using combined *Hemitrypa* sp. data set collected by all workers (1, 2, 3) from both sides of hemitrypid frond (key to symbols in Figure 4). Dashed line approximately divided morphospace clouds by left and right sides of frond. *2,* identical to Figure 5.1 but with overlapping data indicated by enlarged symbols.

of observations from the left medial segment (LM1, □). This variation is real as observations collected from this segment by Worker 2 reflect the variation as well (cf. Figs. 4.1, 5). Variation between colony halves is also evident. Observations from the left side of the colony plot above the dashed line; observations from the right side plot below (cf. Fig. 5). Variation does not appear related to age of colony segments, as morphospace

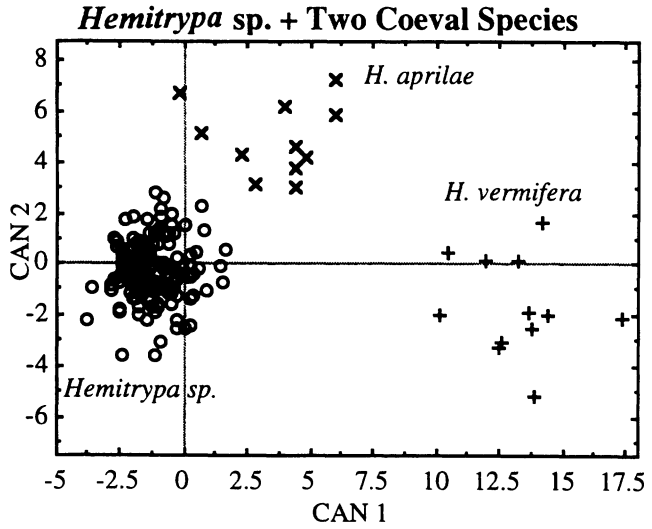
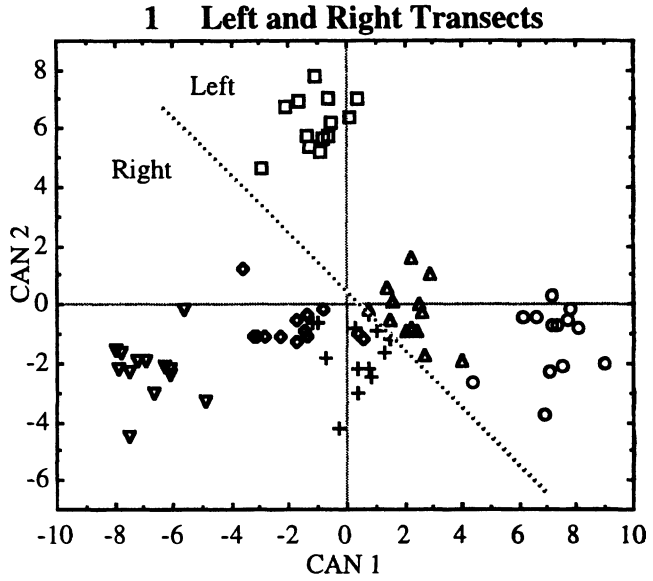


FIGURE 6—Scatterplot produced by canonical discriminant analysis run on combined *Hemitrypa* sp. data collected by all workers (1, 2, 3) from both sides of frond and data collected by Snyder (1991) for two coeval and congeneric species, *H. vermifera* and *H. aprilae*. Symbols for this figure only: *Hemitrypa* sp. (regardless of worker) = **O**; *H. aprilae* = **X**; *H. vermifera* = +.



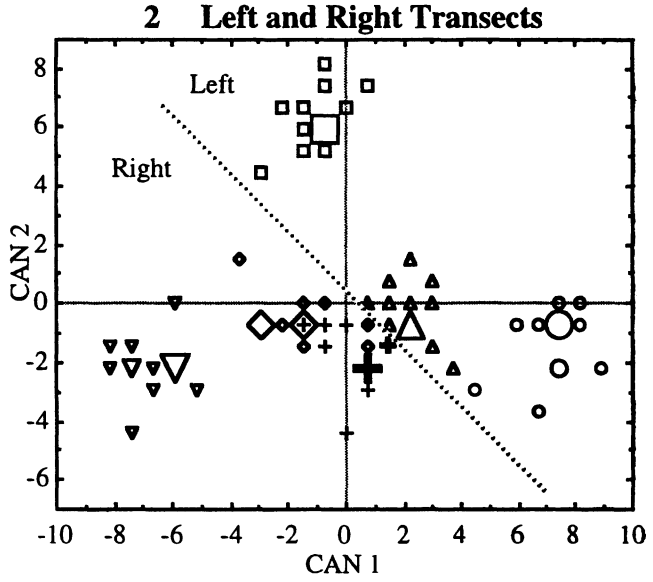


FIGURE 7—*1*, scatterplot produced by discriminant analysis run using combined *Hemitrypa* sp. data set collected by Worker 1 from both sides of frond. Seventy-eight of 78 (100 percent) observations assigned correctly to segment. Dashed line approximately divides morphospace regions by left and right sides of frond. *2*, identical to Figure 7.1 but with overlapping data indicated by enlarged symbols. See Figure 4 key for symbols.

regions representing similar positions along the growth axis do not closely associate with each other (e.g., LP1, △, and RP1, ▽). Some segments are morphologically more similar to distant segments than they are to neighboring segments (e.g., LP1, △, and RD1, +).

Characters that contribute the most to the within-colony canonical discriminant functions (CAN 1 and CAN 2, Fig. 7) are listed in column 3 of Table 2. The distribution of morphospace regions in Figure 7 indicates that both functions contribute to the discrimination of segments and that characters in both functions can be examined concurrently. Characters in column 3 (Table 2) are found in one or both pairs of character sets listed for the left and right sides of the colony (Table 2, columns 1 and 2) with the exception of characters for branch thickness (EBT) and obverse laminated skeletal wall thickness (KOT). Characters important to the discrimination of segments across the entire colony, therefore, are the same as those deemed important for discriminating among segments along the growth axis (Table 2, CAN 1 of columns 1 and 2) and between workers (Table 2, CAN 2 of columns 1 and 2).

Exterior versus interior character subsets.—Characters describing colony exteriors are more likely to express within-colony variation due to astogeny (Snyder, 1984, 1991; Pachut et al., 1991), ontogeny (Boardman et al., 1983), or microenvironment. Characters describing chambers are largely buffered from these sources of variation (Holdener, 1994). To examine within-colony variation and to search for morphologic trends, canonical discriminant analyses were run using subsets of exterior and interior characters (Table 1). Employing the subset of exterior characters, canonical discriminant analysis correctly assigned all observations from both the left (Fig. 8.1) and right (Fig. 8.2) sides of the colony to their proper region. Spatial distribution of morphospace regions closely resembles the distribution seen in Figure 7. Employing the subset of internal chamber characters, discriminant analysis allocation success was reduced and morphospace regions exhibit considerable degrees of overlapping (Fig. 8.3, 8.4). For the left side, 34 of 39 observations (87.2 percent) were assigned correctly; for the right side, 30 of 39 observations (76.9 percent) were assigned correctly. The morphologically conservative nature of these interior characters and the taxonomic significance of chamber dimensions are reconfirmed.

Search for a morphological gradient.—The perfect discrimination among segments along the growth axis using exterior characters (Fig. 8.1, 8.2) suggests a possible morphological trend that might fit either the Boardman et al. (1983) definition of

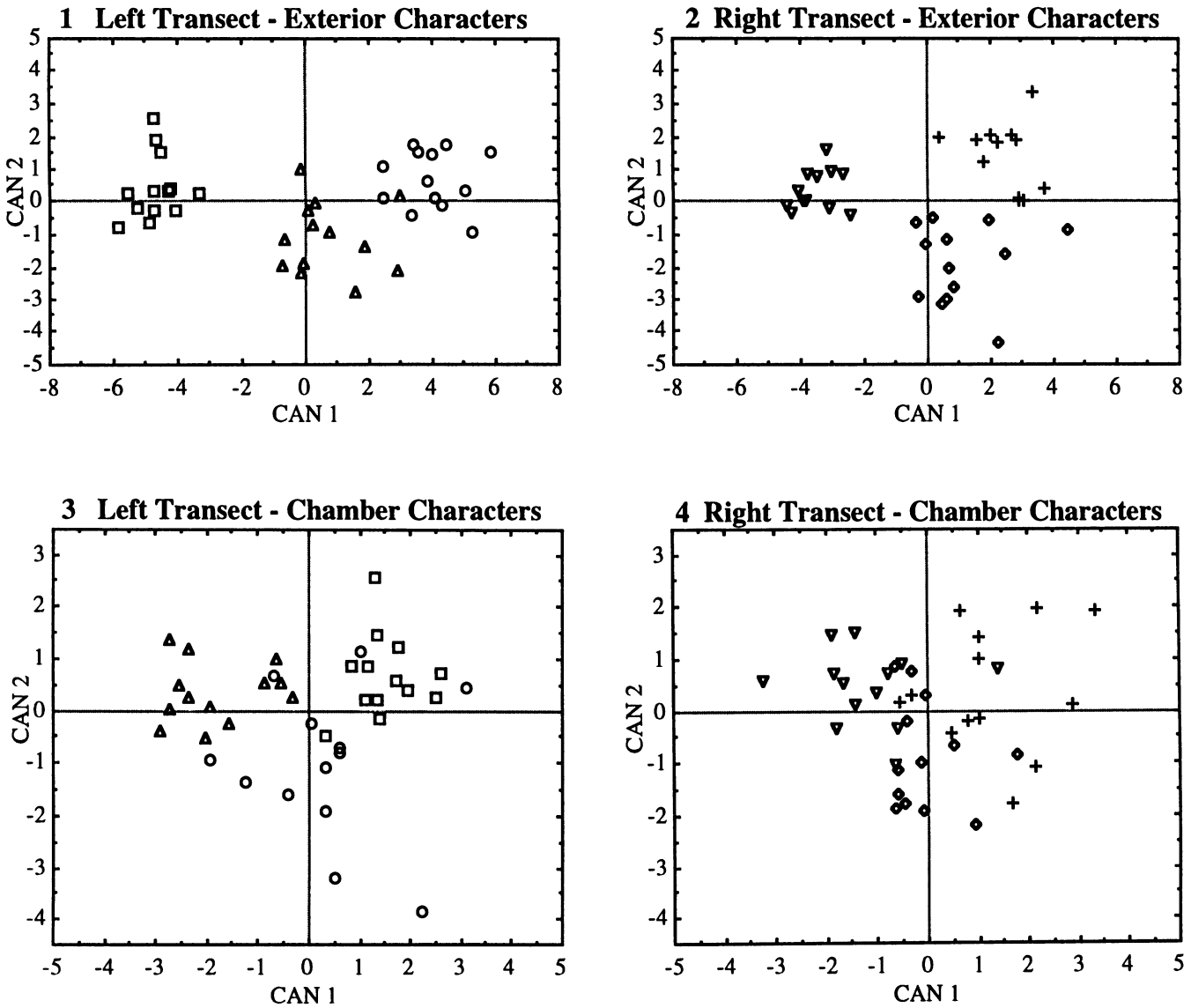


FIGURE 8—*1–4*, scatterplots produced by discriminant analysis run using selected exterior and chamber character data (see text and Table 1) collected by Worker 1 from left and right sides of hemitrypid frond. *1*, left side of frond, exterior characters. Thirty-nine of 39 (100 percent) observations assigned correctly to segment; *2*, right side of frond, exterior characters. Thirty-nine of 39 (100 percent) observations assigned correctly to segment; *3*, left side of frond, chamber characters. Thirty-four of 39 (87.2 percent) observations assigned correctly to segment; *4*, right side of frond, chamber characters. Thirty of 39 (76.9 percent) of observations assigned correctly to segment. See Figure 4 key for symbols.

ontogeny or the Pachut et al. (1991) definition of astogeny. To test for such a trend, mean values of characters that reflect or respond to changes in thickness of the external laminated skeleton were compared between segments (Tables 3 and 4). Neither side exhibits a trend among these characters, and similar comparisons made with the Worker 2 and Worker 3 data produced comparable results. The lack of a defined morphological gradient within a frond of this size argues against an astogenetic overprint (sensu Pachut et al., 1991) or an ontogenetic overprint (sensu Boardman et al., 1983). These findings suggest microenvironmental variation throughout growth of the colony (see Elias, 1964, for similar results).

DISCUSSION

A combination of environmental and genetic factors controls the overall morphogenesis of a bryozoan colony. Results of this and other studies demonstrate that members of the Paleozoic order Cryptostomata exhibit morphologic conservatism (this study for fenestrates; Hageman and Blake, 1992, and Hageman, 1995, for rhabdomesines). Morphologic variation, however, is distinguishable at various levels within cryptostome colonies, populations, and species.

Morphologic gradients that could be attributed to either astogeny (sensu Pachut et al., 1991) or ontogeny (sensu Boardman et al., 1983) are not recognized, and colony segments may be morphologically more similar to distant rather than neighboring segments of the same colony (cf. Fig. 7). For the rhabdomesine, *Streblotrypa prisca,* Hageman and Blake (1992) and Hageman (1995) demonstrated that segments of individual colonies may be morphologically more similar to portions of other, conspecific colonies, and McKinney et al. (1993) reported similar results for the cyclostome

TABLE 3—Comparisons between adjacent colony segments of mean values for characters most likely affected by thickening of laminated skeletal wall, left side of colony. Characters above the dotted line are skeletal characters and are expected to decrease (−) by either astogeny (sensu Pachut et al., 1991) or ontogeny (sensu Boardman et al., 1983) from proximal to medial to distal segments. Characters below the dotted line are nonskeletal characters and are expected to increase (+). Comparisons between segments that yield results other than the expected are blank; expected results are checked (√).

Character	Proximal to medial	Exp	Medial to distal
Aperture width	√	−	
Vestibule length		−	√
Branch thickness		−	√
Branch width		−	
Dissepiment width		−	√
Obv wall thickness		−	
Rev wall thickness	√	−	
Fenestrule length	√	+	
Fenestrule width	√	+	

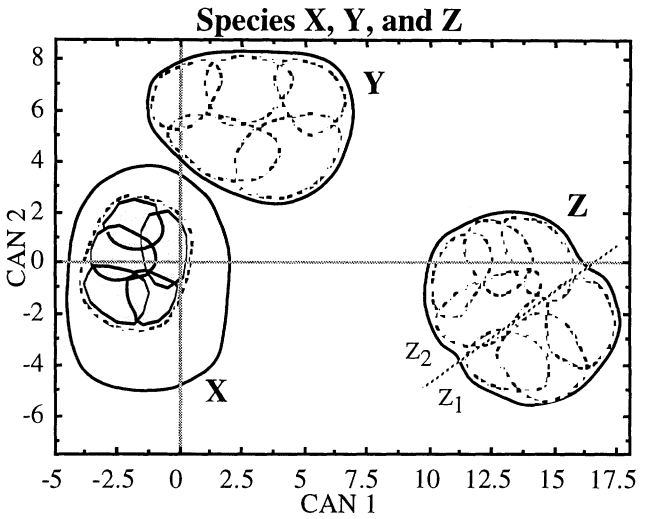


FIGURE 9—Diagrammatic summary of morphologic variation recognizable within and among fenestrate colonies and species. See text for discussion.

Hornera reteramae. For the *Hemitrypa* sp. colony under analysis, within-colony variation approaches among-colony variation for two congeneric species (cf. Fig. 6). Among cheilostomes, Jackson and Cheetham (1990) and Cheetham et al. (1993, 1994) partitioned variance within living and fossil species via single-classification ANOVA and found that the within-colony component of variance far exceeded the among-colony component of the same species. Cheetham et al. (1995) analyzed breeding colonies of two cheilostome species grown under differing conditions and found that such within-colony plasticity could play a significant part in maintaining genetic diversity.

Holdener (1994) detailed small-scale morphologic variation between pairs of populations of two fenestrate species. Hageman (1994) differentiated among multiple populations of a rhabdomesine species when describing a 300 km-long morphologic cline. Both studies detected populations with minimally overlapping or nonoverlapping morphologies. Given the morphologic conservatism of cryptostomes, the recognition of such discrete morphologies is even more significant. The populations in these studies were most likely genetic isolates in only slightly differing environments. The delimiting factor was probably genetic, but environment, or a combination of the two can not be ruled out.

Figure 9 is a diagrammatic summary of the levels of morphologic variation recognized by these studies. Segments within a colony overlap among themselves (shaded regions of X) and whole colonies overlap portions of other colonies (stipled borders within Y and Z). Regions bounding multiple overlapping colonies define species (Y and Z). Within species, populations are recognized as subsets of the colonies that comprise the species as a whole (Z_1 and Z_2 within Z). In the present analysis, all species are congeneric, but morphometric analysis is not restricted to this level. Homeoplasy may make generic distinctions difficult (Hageman, 1991), but a morphometric approach can both draw attention to and point out important differences that may otherwise go unnoticed.

The ability to distinguish among segments within a colony, among colonies within a population, and among populations within a species are powerful accomplishments. Future studies should be capable of evaluating morphologic changes across a species' geographic range and through geologic time. With controlled sampling and detailed analysis, the cause and effect relationships among environment, genotype, and phenotype may become clear, and microevolutionary change and speciation events may be observable in detail.

TABLE 4—Comparisons between adjacent colony segments of mean values for characters most likely affected by thickening of laminated skeletal wall, right side of colony. Characters above the dotted line are skeletal characters and are expected to decrease (−) by either astogeny (sensu Pachut et al., 1991) or ontogeny (sensu Boardman et al. 1983) from proximal to medial to distal segments. Characters below the dotted line are nonskeletal characters and are expected to increase (+). Comparisons between segments that yield results other than the expected are blank; expected results are checked (√).

Character	Proximal to medial	Exp	Medial to distal
Aperture width	√	−	√
Vestibule length		−	
Branch thickness		−	√
Branch width	√	−	
Dissepiment width		−	
Obv wall thickness		−	
Rev wall thickness		−	
Fenestrule length		+	√
Fenestrule width		+	

CONCLUSIONS

1. Fenestrate skeletal morphology is conservative within local segments of a colony. Composite zooids (multivariate constructed observations) generally can be objectively assigned to the segment from which they were measured. A few observations can sufficiently represent a small portion of a colony.

2. Morphologic conservatism is not restricted across an entire colony, and the morphology of a small segment does not represent a colony's total morphologic variation. Within a colony, though, morphologies may repeat. One segment may more closely resemble a distant segment of the same colony than neighboring regions.

3. For large colonies, total within-colony variation may approach among-colony variation within populations of related species. Provided that sufficient observations are gathered from across an adequately large area of such a colony, that colony's within-colony variation may approximate the total morphological variation among several colonies.

4. Morphospecies concepts in general and fenestrate numerical species concepts in particular appear to represent natural taxonomic units.

5. Given the morphologic conservatism of cryptostomes and

the tendency for colonies to overlap in morphospace with portions of other colonies from the same population, the recognition of variation among populations of a species sampled from closely similar environments suggests genetic differences among those populations.

6. There is no suggestion of a directional morphologic gradient as expected from either astogeny (sensu Pachut et al., 1991) nor ontogeny (sensu Boardman et al., 1983). Microenvironmental influences appear to overwhelm these postulated sources of variation.

7. Within-colony variation is greater among exterior characters than interior characters. Exterior characters are more likely affected by microenvironmental fluctuations. Due to inferred biologic significance and strong genetic control, interior characters are buffered from these influences and are less variable.

8. All stages of fenestrate morphometric analyses are repeatable, from production of peels, to measurement of data, to multivariate treatment of that data. Variation between data sets gathered independently by multiple workers from identical colony segments is less than within-colony variation.

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