# Comparative Spatial Variability in Faunal Composition Along Two Middle Devonian Paleoenvironmental Gradients

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*Previous studies of spatial patterns among fossil assemblages have demonstrated the utility of gradient analysis as an investigative tool in paleobiology. However, because lateral samples in these studies have routinely been widely spaced (commonly tens of kilometers apart), there is little sense of the degree to which faunas vary locally, relative to variation observed at larger scales along hypothesized transects. To address this concern, the present study assesses preserved macrofaunal spatial variability in composition among samples collected at both outcrop (small) and basinal (large) scales, along two onshore-offshore transects in the Middle Devonian Hamilton Group within the Appalachian Basin. The horizons sampled are stratigraphically discrete and temporally constrained.*

*Quantitative analyses of faunal composition among samples demonstrate that: 1) Transitions in composition, associated with the onshore-offshore transect, are readily discernible at the basinal scale in both horizons. Along the Browns Creek bed transect, faunal associations vary from an onshore rugose coral-dominated assemblage in a wackestone to an offshore ambocoeliid assemblage in a calcareous mudstone. In the Hills Gulch bed, the faunas range from a rugose coral-meristellid assemblage in a crinoidal packstone/wackestone to a diverse brachiopod/infaunal bivalve assemblage in a calcareous mudstone. 2) In most instances, compositional variation from locality to locality exceeds the degree of variation recognized among samples at individual outcrops. However, there are exceptions, suggesting that it is important to collect multiple samples from each locality. 3) Possible non-random variability at the outcrop-scale is apparent among samples at two of the localities (one in each bed), suggesting that outcrop-scale variability is worth exploring in more detail in future analyses.*

## INTRODUCTION

Analyses of spatial faunal variability along paleoenvironmental gradients (*gradient analyses*) permit the calibration of biological and environmental variability at discrete times in the geologic past (see Cisne and Rabe, 1978; Rabe and Cisne, 1980; Cisne et al., 1982; Springer and Bambach, 1985; Miller, 1988; Miller et al., 1992). To conduct a gradient analysis, samples should be constrained temporally and collection should be methodical, when appropriate and feasible, across the study area. Obviously, studies of spatial variability that utilize samples collected across several horizons risk the possibility of temporal overprint on apparent spatial patterns.

A series of gradient analytic studies conducted by Cisne, Rabe, and others (e.g., Cisne and Rabe, 1978; Cisne et al., 1982; Rabe and Cisne, 1980) involved the collection of bulk samples at several temporally constrained horizons. Transects through the Middle Ordovician Trenton Group of eastern New York State were delineated and samples collected at stratigraphic intervals above and below K-bentonite horizons, as well as along these temporally constrained intervals. However, these studies did not employ lateral sampling at the outcrop scale, and, in most instances, lateral samples were spaced kilometers apart. As a consequence, there is little sense of the degree to which the fauna may have varied locally, relative to variation observed at larger scales along the gradient. Assessment of variability at a more limited, within-outcrop scale, may be useful for two purposes: 1) To ensure that apparent transitions from outcrop to outcrop are generally outside the bounds of "background" variability measured from sample to sample at individual outcrops; 2) To recognize potentially meaningful spatial variability that may be expressed on a relatively confined scale, perhaps not associated directly with the larger-scale gradient.

In this study, preserved macrofaunal variability was as-

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sessed at both the outcrop and basinal scales along two Middle Devonian, onshore-offshore transects in the Appalachian Basin. The horizons sampled, the Hills Gulch and the Browns Creek beds of the Ludlowville Formation, are stratigraphically discrete and temporally constrained (Fig. 1). These two beds differ somewhat in inferred depositional history and were selected to determine whether their contrasting modes of deposition would impart different faunal signatures. Using samples collected from these beds, several interrelated patterns were investigated: 1) The spatial scales at which paleoenvironmental gradients are identifiable based on faunal composition; 2) The variations in environment that produce different spatial faunal transitions at various scales (i.e., within-outcrop versus basinal scale); 3) Similarities and differences among spatial patterns exhibited by the faunas of two separate beds.

Below, we first discuss the inferred depositional histories and lithologies of the two sampled beds and the methodologies for collecting and analyzing data. Then, the analytical results are presented. They reveal systematic spatial variations in macrofaunal assemblages on the basinal scale associated with paleoenvironmental gradients in the Appalachian Basin. Compositional transitions from locality to locality generally transcend the level of faunal variability recognized at single outcrops, even when localities are closely-spaced. However, the degree of compositional variability exhibited at the outcrop scale suggests that, to portray faithfully faunal transitions along the paleoenvironmental gradient, it is essential to collect multiple samples at each locality. At the outcrop scale, where local microenvironments might be expected to vary only randomly, spatial variability generally appears to be random, except for two localities (one in each bed) that exhibit possible, though admittedly questionable, systematic transitions in faunal composition.

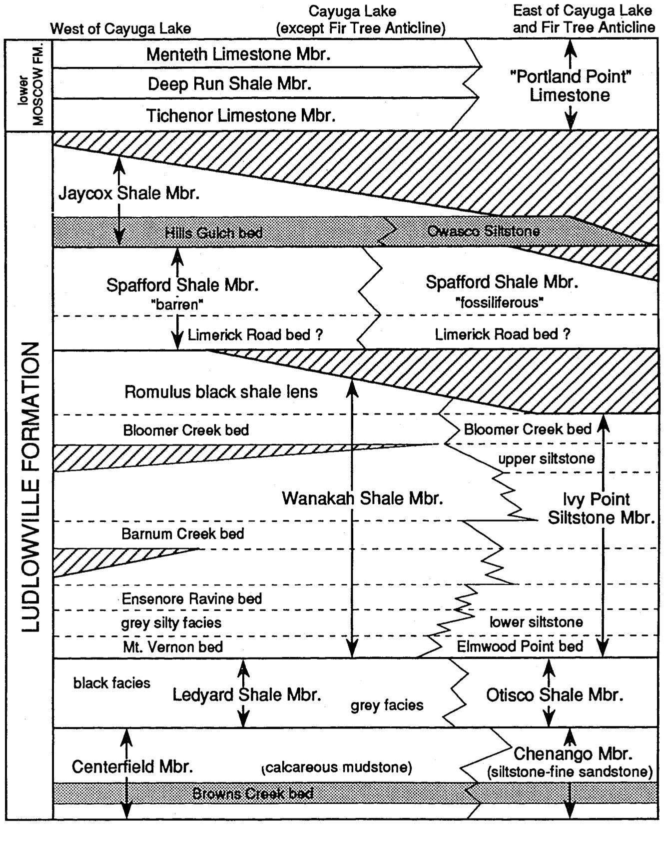

**FIGURE 1**—Generalized stratigraphic column of the Ludlowville Formation (modified from Mayer et al., in press). Study horizons are noted with gray shading.

## GEOLOGIC SETTING

The rocks of the Middle Devonian (Givetian) Hamilton Group of western and central New York State are ideal for this study because they permit a high degree of stratigraphic/temporal constraint: several event beds have been identified and correlated across the outcrop belt (Brett et al., 1986).

During middle Givetian time, fine terrigenous sediments and biogenic carbonate were deposited in the shallow, subtropical waters of the northern Appalachian Foreland Basin (Baird and Brett, 1981; Brett and Baird, 1985; Mayer et al., in press); the study area was a broad, shallow, sediment-starved shelf bounded on the west and northwest by the craton and on the east by a northeast-southwest trending area of active subsidence and deeper water (Baird and Brett, 1981). Further to the east, the Acadian Orogenic Belt shed sediments into the foreland resulting in a large, eastward-thickening clastic wedge (Cooper, 1957; Rickard, 1981; Brett and Baird, 1985).

In western and central New York, the Middle Devonian Ludlowville Formation, the third-highest of four formations comprising the Hamilton Group, is composed of calcareous gray to black shales, concretionary limestones, and thin, continuous limestones (Brett and Baird, 1985; Savarese et al., 1986). In western New York, the Ludlowville (Fig. 1) is bounded at the base by the Centerfield Limestone Member and at the top by the Jaycox Shale Member (Baird, 1979; Mayer et al., in press). Further east, the formation becomes more heavily dominated by terrigenous clastics, including siltstones and fine sands (see Clarke, 1903; Kramers, 1970; Baird, 1979; Baird and Brett, 1981; Kloc, 1983; Gray, 1984).

The two laterally continuous beds in the Ludlowville selected for study, the Hills Gulch and the Browns Creek beds (Fig. 1), differ in inferred depositional history. The Browns Creek bed is one of several argillaceous limestones in the lower third of the Centerfield Member. It has been interpreted as preserving a single event, probably a storm (Brett et al., 1986; Speyer and Brett, 1986). The lithology of this bed varies from a crinoid-dominated wackestone at western localities to a calcareous mudstone with localized concentrations of fossil material at eastern localities.

Near the top of the Browns Creek bed, specimens of *Dechenella rowi*, a proetid trilobite, have been observed positioned with the cephalon subhorizontal and the thorax/pygidium oriented at a right angle to the cephalon

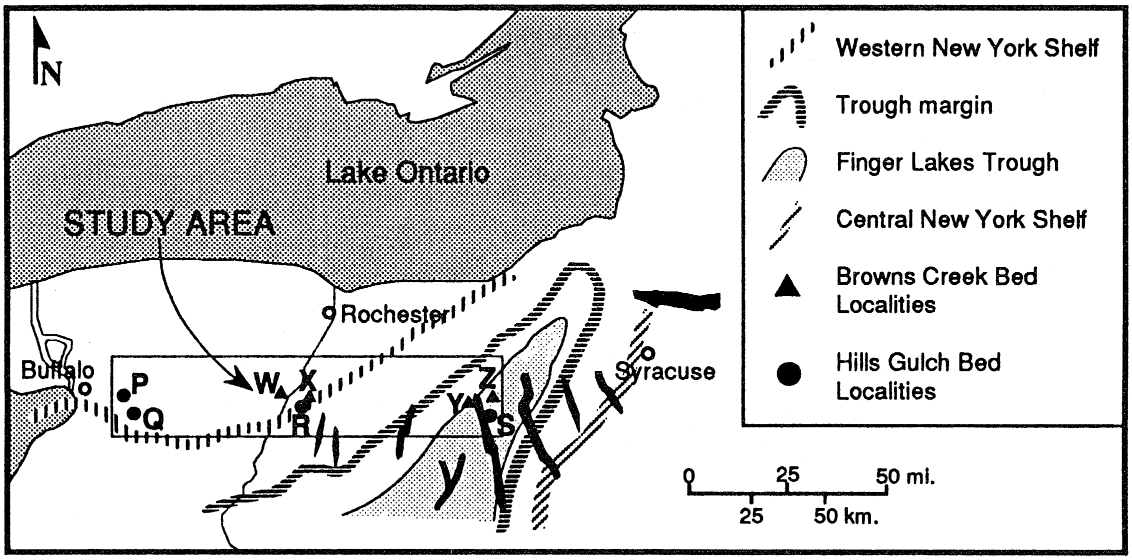

**FIGURE 2**—Generalized paleogeographic map of the study area with sampling localities superimposed (modified from Mayer et al., in press).

**TABLE 1**—Sampling localities of the studied beds. Letters represent sampling localities. The position along the outcrop is the identification number given to the sample.

| Browns Creek bed | | Hills Gulch bed | |
|---|---|---|---|
| W | 0, 1, 5, 7, 8, 9, 10, 15, & 20 m | P | 0, 1, 2, 3, 4, 5, 10, 15, & 20 m |
| X | 0, 1, 2, 3, 4, 5, & 10 m | Q | −5, 0, 10, 15, & 20 m |
| Y | 1, 2, 3, 4, & 5 m | R | 0, 1, 2, 3, 4, 5, & 10 m |
| Z | 0, 3, 5, 15, 20, & 25 m | S | 0, 3, 4, & 5 m |

(Speyer and Brett, 1986; Gray, 1984). This phenomenon has been observed for approximately 80 km along the top of the bed (Gray, 1984; Speyer and Brett, 1986). Rugose corals have been observed with their bases rooted in the top of the bed and their calices extending upward into the overlying Triphammer Falls Coral Beds (pers. obs.). These well-preserved fossils in life position or, in the case of the proetids, possibly in a defensive posture, indicate rapid burial at the top of the Browns Creek bed, possibly within hours to days. Gray (1984) cites the uncompacted nature of shells in this bed as indicative of rapid cementation. As with the Hills Gulch bed, the Browns Creek bed cuts across biofacies and lithofacies boundaries, indicating that it is isochronous (Gray, 1984).

In western New York, the Hills Gulch Bed has been interpreted as an amalgamated storm bed (Brett et al., 1986). Mayer and others (in press) suggest that its thin nature, its slight thickening eastward (troughward), and the presence of biofacies gradients indicate isochroneity. Across the Finger Lakes Trough, the Hills Gulch bed can be correlated with the Owasco Siltstone and has been interpreted as a basinal shoaling event (Mayer et al., in press).

The Hills Gulch bed ranges in thickness from 5 to 20 cm at the outcrops studied. Its lithology changes from highly fossiliferous crinoid-brachiopod packstone/wackestone at western localities to a sparsely fossiliferous calcareous siltstone or mudstone in eastern localities. Large colonies of the tabulate coral *Favosites* sp. are present at the two westernmost localities; many are overturned and encrusted (pers. obs.).

## METHODS

### Sampling Methods

Multiple scales of lateral sampling were utilized to assess spatial variability at different scales throughout the study area. For each of the two beds studied, four sampling localities (P–S for the Hills Gulch bed and W–Z for the Browns Creek bed) were chosen along a hypothesized onshore-offshore, west-east transect extending from the western shelf near present-day Erie County to the Finger Lakes Trough in the vicinity of the modern Finger Lakes (Fig. 2). Sampling localities are described in Appendix 1. At each locality, sampling transects were established and bulk samples collected every five meters for a maximum distance of 25 m, where logistically feasible (Table 1). Moreover, at Browns Creek bed localities W, X and Y and Hills Gulch bed localities P and R, an additional set of bulk samples was collected at one meter intervals between two of the five meter stations.

In the lab, samples were split and faunal abundances tallied. Macrofossil material was identified to genus- or, when possible, species-level, and abundances were recorded. In many studies, abundances of bivalved organisms are counted only for specimens where a beak is present (e.g., Miller, 1988; Miller et al., 1992). However, in many instances the beak was inaccessible because it was positioned obliquely to the exposed bedding surface. Therefore, specimens in which a beak was present or in which more than three-quarters of the original element was present were identified and tallied.

Samples from the western localities were highly indurated and difficult to split without breaking the fossil material. This type of preservation, as well as position in the matrix, impeded identification of some fossil material to generic level, particularly the alate spiriferids (*Delthyris*, *Mediospirifer*, and *Mucrospirifer*).

Left and right or pedicle and brachial valve counts were totaled for bivalve and brachiopod genera, respectively, with the greater value designated as the abundance for a genus in a sample. In some instances, the valves were difficult to distinguish from one another because of breakage or position in the well-indurated samples. In these cases, the total number of valves was halved and rounded to the next highest integer.

At three stratigraphic positions within each bulk sample (top, middle, and bottom), fossil material was point counted. A 32 mm by 70 mm grid of 50 points was placed on the surface of the bed and fossil material under each of the points was tallied. Identifications of skeletal material were very general: e.g., crinoid, bryozoan, trilobite. These counts were then used as proxies of abundance for taxa that were most commonly fragmented, including crinoids and bryozoans. They provide only a general approximation of abundance not available from taxon counts.

## Quantitative Methods

### *Construction of Data Matrix*

For multivariate comparisons of sample compositions, a data matrix was constructed at the taxonomic level of family, except for spiriferids which were organized at the level of superfamily. Because abundances of genera within samples were often small, analysis at the family level provided a data set with taxa of sufficient abundance to determine spatial faunal patterns not as easily detectable, paradoxically, when analyses were run at the generic level. In this matrix, raw faunal abundances of each family within a sample were converted to percentages of the total number of fossils in the sample. The percent transformation served to minimize sample size effects in subsequent analyses, which was desirable because sample size differences may simply have been artifacts of post-mortem processes and sampling procedure.

For data analysis, the trilobite, rugose coral, brachiopod, and mollusc abundance data from direct censusing were percent transformed separately from the crinoid and bryozoan point count data. The percent transformed abundances and point counts were then weighted equally in subsequent analyses.

### *Polar Ordination*

A three-dimensional Q-mode polar ordination (i.e., an ordination of samples) was executed on the data matrix using the Quantified Czekanowski's (Dice) similarity coefficient (Sepkoski, 1974) and POLAR II, a computer program written by J.J. Sepkoski, Jr. and J. Sharry and modified by A.I. Miller. For investigation of faunal gradients, ordination may be more appropriate than cluster analysis, which is also commonly used with these kinds of data (e.g., Valentine and Peddicord, 1967; Cisne and Rabe, 1978; McGhee and Sutton, 1981; Springer and Bambach, 1985; Miller, 1988, 1989; Colby and Boardman, 1989). Unlike cluster analysis, it does not force multidimensional data into a two dimensional space, nor does it artifactually distort the relationships among relatively dissimilar samples. There are many polar ordination algorithms described in the literature (e.g., Bray and Curtis, 1957; Beals, 1965); what they all have in common is that two dissimilar samples are chosen as endpoints of the axes and all other samples are plotted along these axes based on their measured dissimilarity from each endpoint. The axes derived from polar ordination do not precisely represent ecological gradients, but they may depict gradational changes in sample composition (see Gauch, 1982) that correspond to ecological or environmental transitions. Moreover, different aspects of variability in the data may be isolated on different axes.

To determine the taxonomic underpinnings of sample transitions, the correlation of each taxon (family/superfamily) with each ordination axis was determined individually. This was accomplished by comparing taxonomic abundances in each sample directly with corresponding sample coordinate values for each axis. If the calculated product-moment correlation coefficient is large and positive, this suggests that the taxon in question is abundant in samples with *large* coordinate values on the axis. Alternatively, if the correlation coefficient is large and negative, then the taxon is most abundant in samples with small coordinate values.

# RESULTS AND DISCUSSION

In all, 27 bulk samples of the Browns Creek bed and 25 bulk samples of the Hills Gulch bed were analyzed. Faunal abundances in samples from the Browns Creek bed varied from five to 48 specimens that, in aggregate, belonged to 36 families; in the Hills Gulch bed, sample faunal abundances varied from six to 34 specimens and belonged to 36 families. Raw data are available upon request. While sample sizes were sometimes small, they were nevertheless sufficient to recognize transitions in faunal composition that were statistically significant (see below).

## Basinal Scale Faunal Variability

### *Hills Gulch Bed*

A two dimensional polar ordination plot (Axes 1 & 2) of the Hills Gulch bed fauna (Fig. 3) reveals a segregation of

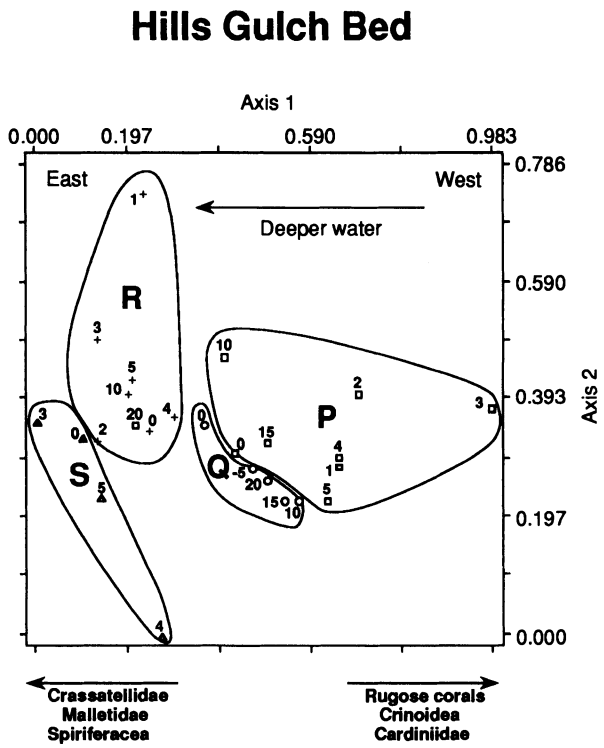

**FIGURE 3**—Q-mode polar ordination plot of Hills Gulch bed samples along Axes 1 and 2. The letters, P–S, correspond to sampling localities. The numbers within the plot are sample numbers. Total cophenetic correlation for Axes 1 through 3 is 0.7575.

samples based on locality. Samples that are geographically proximate tend to plot close together with no overlap among localities. However, despite this general fidelity of localities, there are samples that might be viewed, compositionally, as outliers relative to other samples at the same locality (e.g., sample 3 at HGP, sample 0 at HGQ, sample 1 at HGR, and sample 4 at HGS). This suggests the possibility that, if just one or two samples had been collected at each locality, a misleading picture might have emerged of faunal transitions along the paleoenvironmental gradient (see discussion of these patterns, below). The implication is that, to avoid this possibility, it is important to collect several samples from each locality. Only then can the faunal gradient be diagnosed confidently.

The westernmost localities, P and Q, are positioned to the "right" on Axis 1 with the central locality, R, separating them from the easternmost locality S. Positioning on Axis 1 corresponds roughly to geographic placement in the study area with the "left" side of the axis corresponding to the eastern, basinal paleoenvironments and the "right" side to western, shallower shelf paleoenvironments. Abundances of rugose corals, crinoids, and the bivalve *Cypricardinia* (Family Cardiniidae) are highly positively correlated to Axis 1 (Table 2). Highly negatively correlated to this axis are the spiriferids, as well as the pelecypods *Cypricardella* (Crassatellidae) and *Paleoneilo* (Malletiidae).

**TABLE 2**—Correlation coefficients of taxa with ordination axes for selected families discussed in the text.

| Bed | Family | Correlation coefficients<br>Axis 1 | Axis 2 | Axis 3 |
|---|---|---|---|---|
| Hills Gulch bed | Cardiniidae | 0.593 | −0.317 | −0.245 |
| | Malletidae | −0.504 | 0.124 | −0.584 |
| | Spiriferacea | −0.856 | 0.192 | −0.372 |
| | Rugosans | 0.570 | −0.027 | 0.331 |
| | Crinoidea | 0.818 | −0.340 | 0.598 |
| | Crassatellidae | −0.627 | 0.475 | −0.259 |
| Browns Creek bed | Spiriferacea | 0.609 | −0.567 | −0.240 |
| | Ambocoeliidae | 0.085 | 0.901 | −0.010 |
| | Atrypidae | −0.634 | −0.311 | −0.365 |
| | Rugosans | −0.744 | −0.476 | −0.483 |

A histogram of eight representative families illustrates the primary faunal transitions among the Hills Gulch bed localities (Fig. 4) and confirms the patterns suggested by polar ordination. These eight selected families account for 54% of the total diversity in Hills Gulch bed outcrops. Specimens belonging to the brachiopod family Meristellidae are present in a few samples from localities P and Q, but are conspicuously absent from the other two localities. This is also true, with one exception, of solitary rugose corals. Ambonychiids (solely *Plethomytilus* or *Mytilarca*) are present only in samples from the more basinal locality S. However, *Plethomytilus* can be present in outcrops of this bed further to the west. The family Stropheodontidae is present in most samples at P, Q and R, but is absent from S. It appears that the abundance of this family decreases basinward. *Paleoneilo* and *Nuculites* (Malletiidae) have rare occurrences at localities P and Q, the western localities, while they are very common at the central and eastern collecting localities, R and S. Specimens belonging to the superfamily Spiriferacea and the families Cardiniidae and Tropidoleptidae are nearly ubiquitous across the transect.

It can be demonstrated that these transitions are statistically significant, in several instances, by calculating 95% error bars about the mean percentage abundances of taxa at each locality. This was accomplished using a BASIC program, provided by Raup (1991), which utilizes the binomial distribution and is intended specifically for use with percent abundance data. In the present study, the samples from each locality were combined to form an aggregate sample for the locality. Significance of abundance transitions from locality to locality was assessed by comparing taxonomic abundances among these four integrated samples.

Abundances of the families Cardiniidae and Tropidoleptidae did not vary significantly across the transect (Fig. 5), confirming the observed histogram patterns. In contrast, mean abundances of Malletiidae at P and Q, the nearshore, shallow-water localities, did not significantly

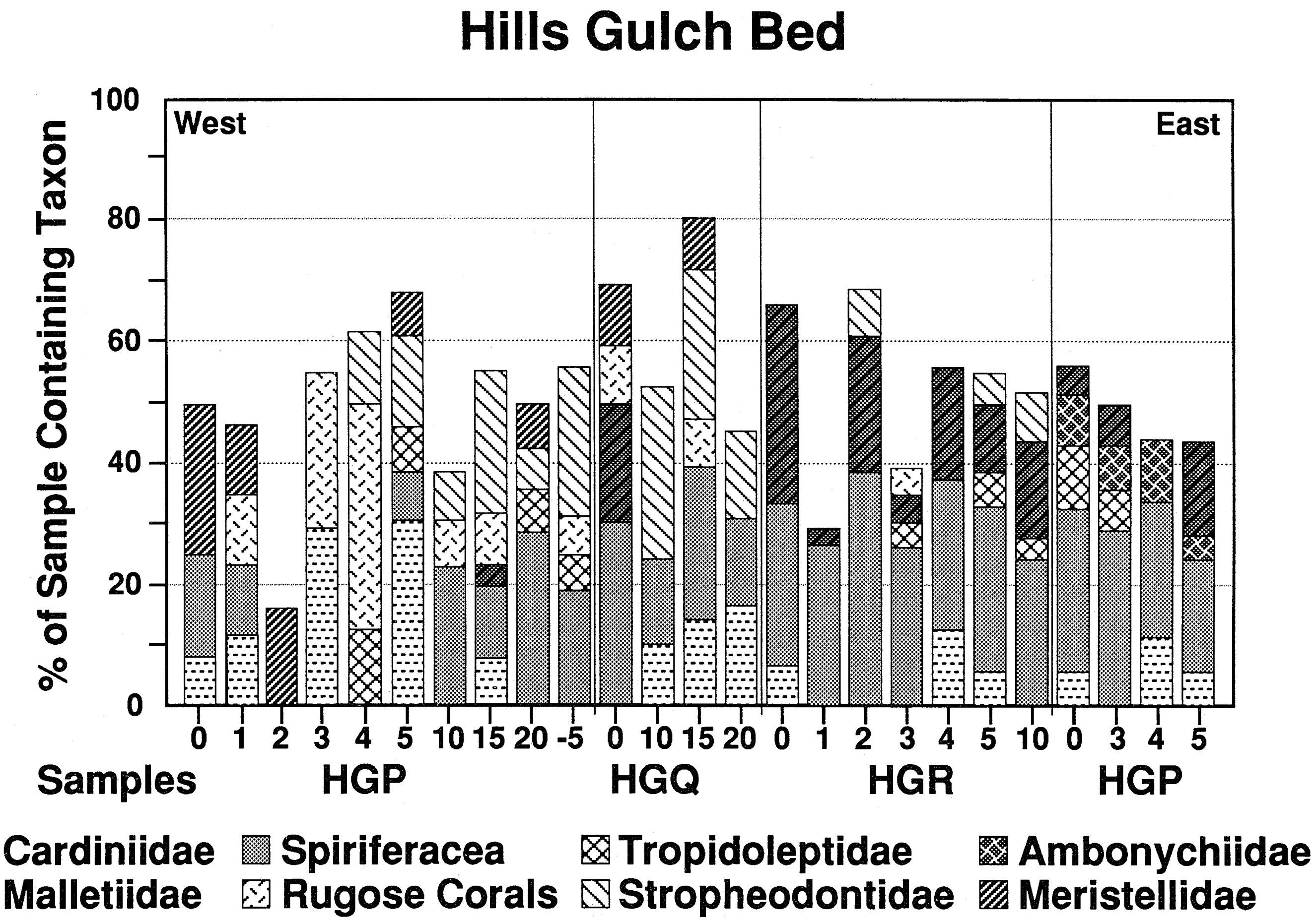

**FIGURE 4**—Histogram of eight representative families for the Hills Gulch bed. Samples are in geographic order from left (west) to right (east). Numbers along X-axis are samples numbers.

exceed zero (suggesting that they might be absent from another "sample" of comparable size collected at either of these localities), whereas at R and S they did (indicating, that they would almost assuredly be present in another "sample" of comparable size collected at either of these localities). Moreover, the mean abundance of rugose corals significantly exceeds zero at nearshore, shallow-water outcrops, P and Q, but not at the troughward outcrops, R and S. Ambonychiidae, present only at S, has an abundance that was significantly above zero at that locality. Interestingly, Spiriferacea are significantly more abundant at R than they are at P and S.

The life habits of the families preserved in the Hills Gulch bed, and the spatial transitions thereof, are consistent with interpreted paleoenvironmental transitions across the Appalachian Basin:

1. The presence of *Plethomytilus* (Ambonychiidae) at S, where the substrate was probably muddy, is not unexpected considering its probable endobyssate, semi-infaunal to infaunal lifestyle (see Kriz, 1984).
2. The common presence of *Paleoneilo* and *Nuculites* (Malletiidae), both mobile infaunal deposit feeders (Lukasik, 1984), indicates that the bottom sediments of central localities R and S were soft muds that were not anoxic. The relative paucity of these two genera in western localities corroborates the sedimentological observations that bottom sediments were coarser, lacking in organics, and not favorable for a mobile, deposit feeding infauna (Lukasik, 1984).
3. The brachiopod *Meristella* (Meristellidae) had an incurved beak on the pedicle valve and may have attached to the substrate with a pedicle (G. Kloc, pers. comm.). Lukasik (1984) suggested that meristellids may have lived positioned among debris and/or were tolerant of minimal wave tumbling. The presence of this brachiopod family at localities P and Q might, therefore, be expected, given the nearshore geographic position of these localities.
4. The presence of solitary rugose corals at western localities, P and Q, and their less common occurrence at eastern localities, R and S, suggests that the turbid water and finer grained substrates of the eastern region provided unfavorable living conditions. Baird and Brett

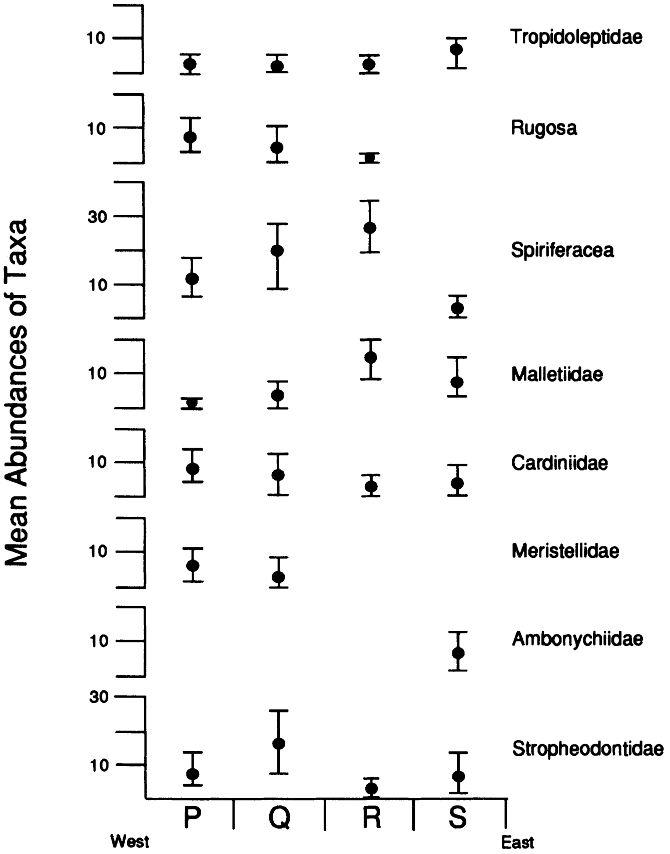

FIGURE 5—Graphs of the mean abundances with 95% error bars for several families present in Hills Gulch bed samples.

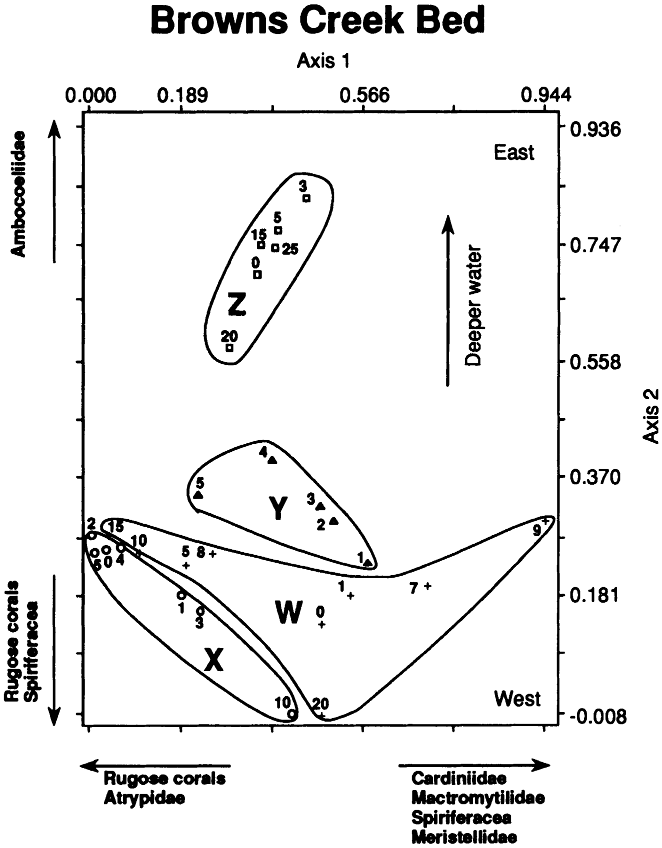

FIGURE 6—Q-mode polar ordination plot of Browns Creek bed samples along Axes 1 and 2. The letters, W–Z, correspond to sampling localities. The numbers within the plot are sample numbers. Total cophenetic correlation for Axes 1 through 3 is 0.8104.

(1983) identified a similar gradient of increased coral abundance away from regions of localized subsidence and sediment accumulation.

5. Stropheodontids persist offshore to locality R, the central sampling locality. Their absence at locality S, in the Finger Lakes Trough, may result from the finer grained substrates and probable turbid water conditions. This environment may have been unfavorable for these small, reclining filter feeders. Within the family Stropheodontidae, there appears to be a segregation of genera. At western localities P and Q, *Protoleptostrophia* is the most common member of this family, while at eastern localities R and S, *Strophodonta* is most common.

### *Browns Creek Bed*

A two dimensional polar ordination plot (Axes 1 & 2) of the Browns Creek bed faunal data is shown in Figure 6. In nearly all cases, samples from individual localities group closely together. Moreover, there is no sample overlap among localities, although, as was the case for the Hills Gulch bed, limitation to just one or two samples from each locality (except locality BCZ) might have generated a misleading picture of faunal transitions along the gradient. As with the Hills Gulch bed, the sample positions in ordination have geographic significance; samples from western localities W, excluding W9, and X group in close proximity along the "bottom" of the Axis 1–Axis 2 plot. Samples from localities Y and Z, the more eastern exposures closer to the trough, are positioned "higher" on Axis 2.

Ambocoeliids are highly positively correlated with Axis 2 (Fig. 6; Table 2), indicating that samples from locality Z are rich in this family. The three other localities, positioned at the lower end of this axis, are rich in rugose corals, spiriferids (negatively correlated with Axis 2), and atrypids (negatively correlated with Axis 1), which are particularly important components of most of the samples from localities W and X.

The histogram of several selected families, which account for 79% of the diversity of the bed, represents graphically the faunal variation along the Browns Creek transect (Fig. 7). Samples from localities W and X have similar faunal contents. Rugose corals and the superfamily Spiriferacea are common in these western localities and rare at the localities near the Finger Lakes Trough, because of environmental factors associated with increasing water

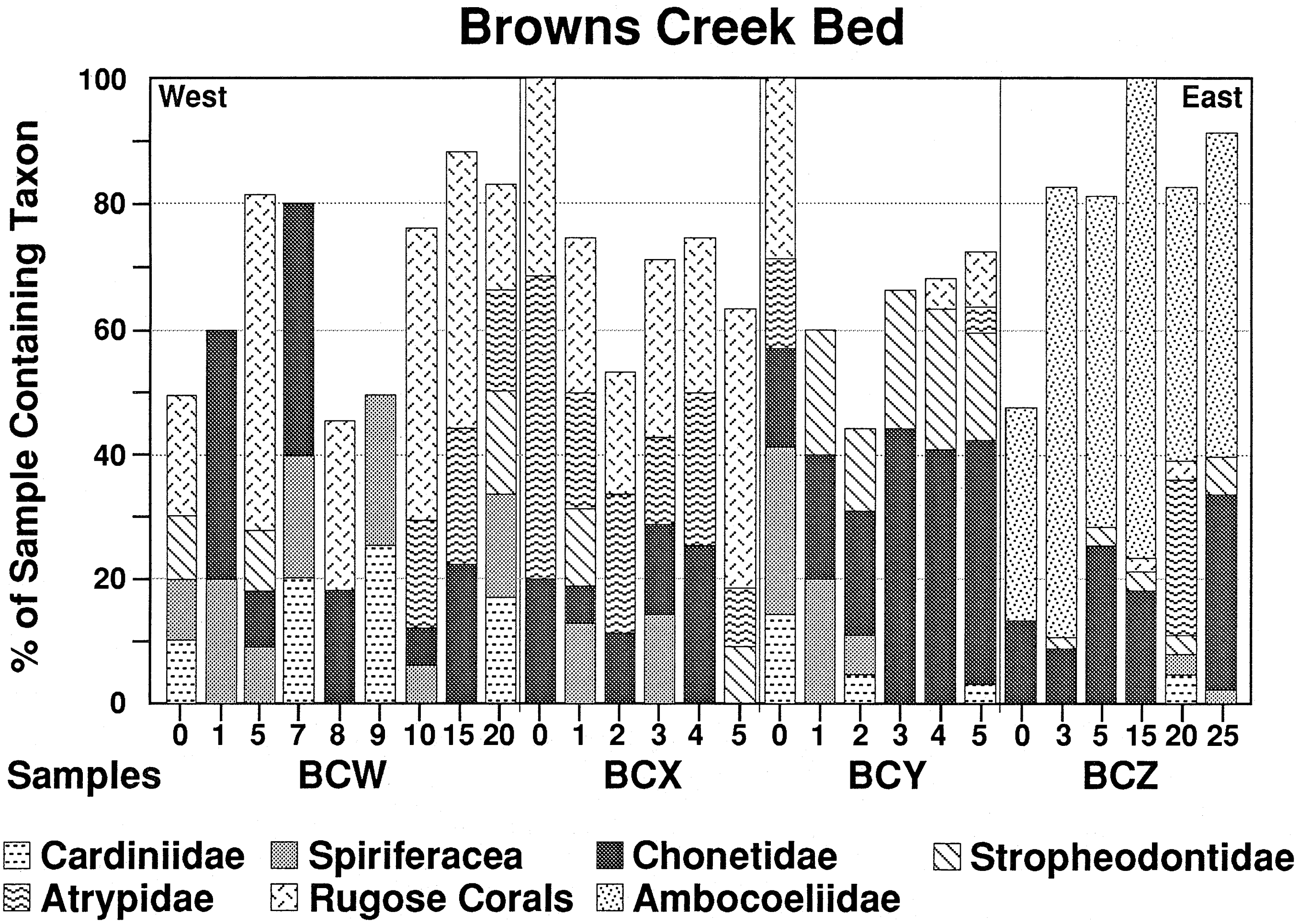

**FIGURE 7**—Histogram of seven representative families for the Browns Creek bed. Samples are in geographic order from left (west) to right (east). Numbers along X-axis are sample numbers.

depth. A similar faunal pattern along the transect is observed for *Pseudatrypa* (Atrypidae). This free-living brachiopod has been interpreted to be a slightly infaunal filter feeder, thereby explaining its absence from the fine muds and concomitant turbid water of the troughward localities (Lukasik, 1984; Brower and Nye, 1991). Ambocoeliids are present only at locality Z, where they are overwhelmingly dominant. Brower and Nye (1991; see also Brett et al., 1991) found that *Ambocoelia umbonata* was similarly dominant in a low diversity, low oxygen, deep water assemblage.

*Devonochonetes* (Chonetidae) and *Strophodonta* (Stropheodontidae) are the most common components of the faunal assemblage at locality Y. *Devonochonetes* lacked a functional adult pedicle, but possessed spines on its convex pedicle valve. It probably lived reclining on the pedicle valve (Brower and Nye, 1991; Lukasik, 1984), as did *Strophodonta,* which has a convex pedicle valve and a concave brachial valve.

A differentiation of strophodeontid genera with respect to environment was identified along the Browns Creek bed transect, similar to that recognized in the Hills Gulch bed. *Strophodonta* and *Prototleptostrophia* are present at eastern localities Y and Z, with other stropheodontids present at western localities.

Abundances of Atrypidae at locality X are significantly greater than those at localities Y and Z (Fig. 8). Not surprisingly, abundances of chonetids at locality Y are significantly greater than at the other localities. Although the 95% confidence interval for strophodontids at locality Y overlaps slightly with that from locality X, this family is significantly more abundant at Y than at W and Z. Finally, mean abundances of rugosans at W and X are significantly greater than at troughward localities Y and Z, whereas Ambocoeliidae are present only at Z, and the percent abundance is significantly greater than zero.

## Comparison of the Browns Creek and Hills Gulch Beds

The faunas of the Browns Creek and the Hills Gulch beds both varied systematically across nearshore-to-trough transects. Spiriferids were common to both transects, but

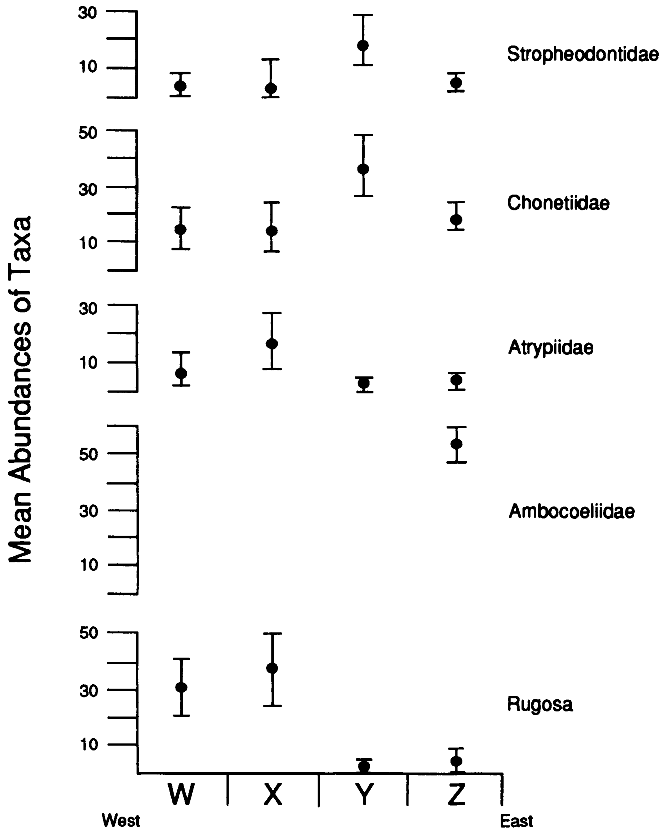

**FIGURE 8**—Graphs of the mean abundances with 95% error bars for several families present in Browns Creek bed samples.

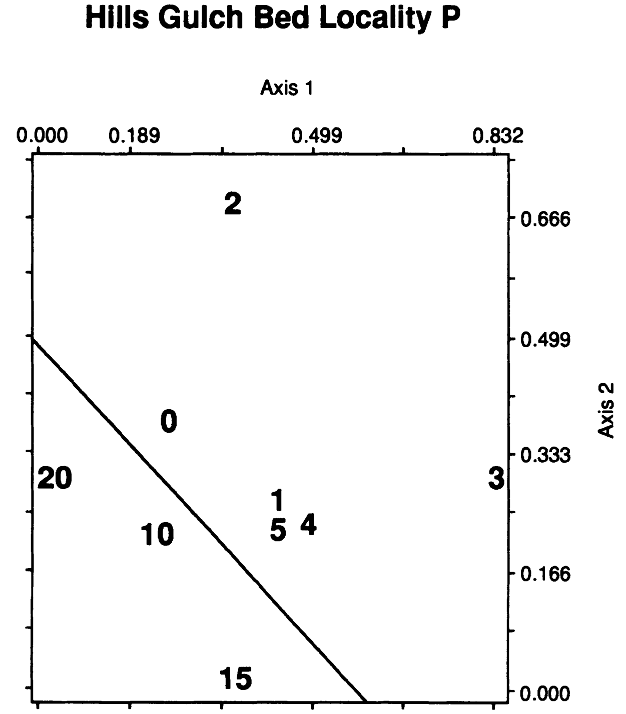

**FIGURE 9**—Two-dimensional, Q-mode polar ordination plot of samples along Axes 1 and 2 from Hills Gulch bed locality P. Numbers are actual sample numbers. Cophenetic correlation is 0.5789.

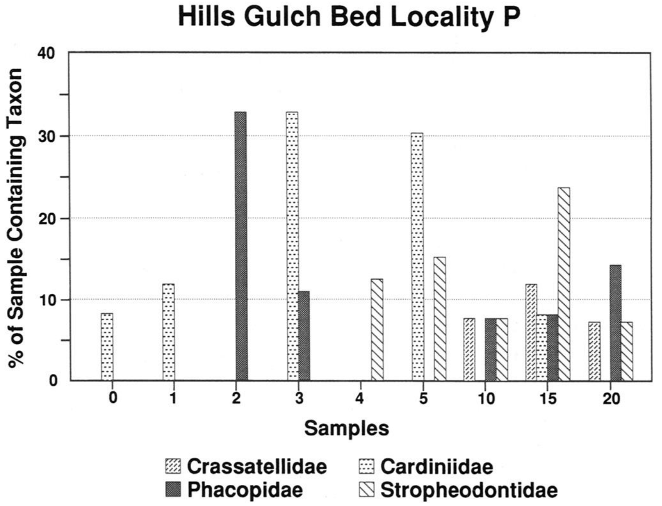

**FIGURE 10**—Histogram of four selected families for the Hills Gulch bed locality P. Numbers along X-axis are sample numbers.

were more abundant in the Hills Gulch bed. Rugose corals were restricted mainly to the western localities of both beds. The faunal gradient identified along the nearshore-to-offshore transect of the Browns Creek bed extended to a relatively deep water ambocoeliid community. While the Hills Gulch bed transect extended to the same geographical area, it does not exhibit these deeper-water faunas. During Hills Gulch time, basinal topography may have been more level because of shallowing in the Finger Lakes trough region, thereby decreasing the extent of the depth gradient.

The controls on faunal gradients in both the Hills Gulch and Browns Creek beds probably included some combination of depth, turbulence, oxygenation, and sedimentation rate; the transects extended from shallow water in the western, nearshore region and progressed into deeper water in the Finger Lakes Trough. Shallow water organisms, some of which may have possessed zooxanthellae (the corals), as well as those tolerant of or favoring increased turbulence (see earlier discussion), were concentrated closer to shore. Increased sedimentation rates and turbidity in the trough region precluded substantial colonization by light-favoring organisms and those easily fouled by fine-grained sediments, while creating favorable conditions for organisms tolerant of finer-grained substrates and minimal turbulence. Organics concentrated in the sediments of the trough, thereby increasing food for deposit feeding organisms.

There were many faunal differences exhibited among the two beds; in fact, the principal families differ. Clearly, faunal differences were not the consequences of evolutionary turnover, as there is little evidence for such change

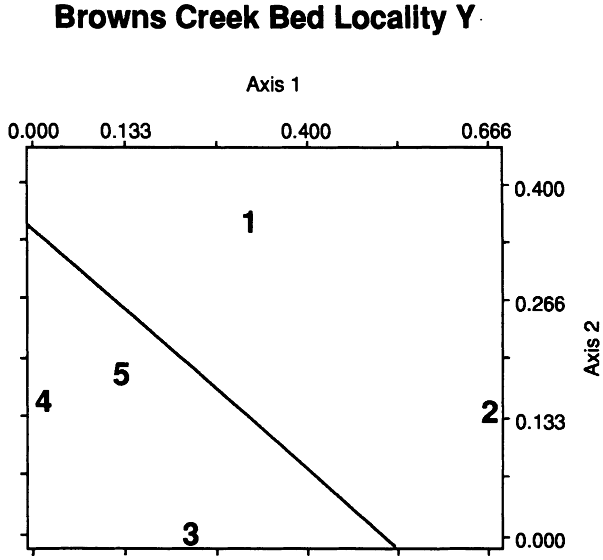

**FIGURE 11**—Two-dimensional, Q-mode polar ordination plot of samples along Axes 1 and 2 from Browns Creek bed locality Y. Numbers are actual sample numbers. Cophenetic correlation is 0.9427.

throughout the entire Hamilton Group (Brett and Baird, 1992).

### Outcrop Scale Faunal Variability

At most localities, outcrop-scale faunal compositions did not appear to vary in any spatially systematic fashion. However, there were two exceptions: Browns Creek bed locality Y (BCY) and Hills Gulch bed locality P (HGP).

On a polar ordination plot of samples from locality HGP, (Fig. 9), a line can be drawn that separates samples 0 through 5 from samples 10 through 20, suggesting a faunal transition along the sampling transect. This is illustrated effectively with a histogram showing the abundances of several families among the samples (Fig. 10). Moreover, samples 0–5 are overwhelmingly dominated by one or two taxa, in contrast to 10–20, suggesting that the former are less diverse than the latter.

The pattern observed at HGP may be illustrative of the two different scales of sampling: meter-scale and five-meter-scale. In this regard, it is telling that samples 1, 4, and 5 grouped very closely on Figure 11, indicating substantial compositional similarity among these closely-spaced samples. However, samples 2 and 3 seemed decidedly dissimilar to all the others.

Among the samples on the polar ordination plot of BCY, there may have been a compositional transition from samples 1 and 2 to samples 3 through 5 (Fig. 11), although, with just five samples, the suggestion that this represents a non-random spatial pattern at the scale of sampling is admittedly tenuous. A histogram of six representative families (Fig. 12) showed that samples 3 through 5 exhibited greater relative abundance of *Devonochonetes* (Chonetidae) and are lacking *Cypricardella* (Crassatellidae) and spiriferids.

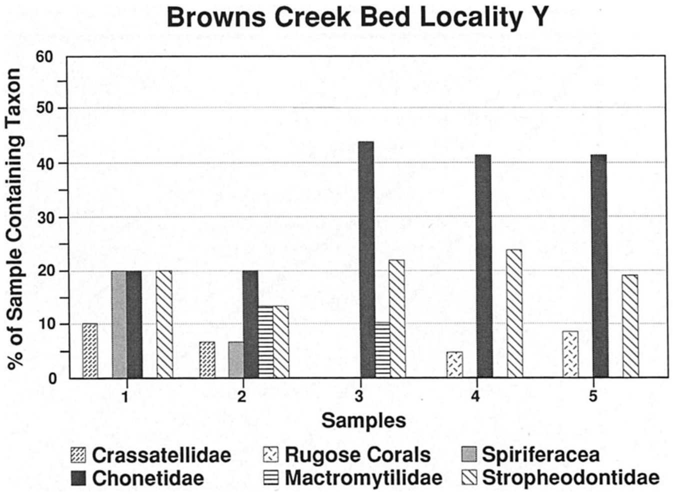

**FIGURE 12**—Histogram of eight selected families for Browns Creek bed locality Y. Numbers along X-axis are sample numbers.

No lithologic transitions are recognized along these transects that correspond to the observed faunal transitions; thus, they may simply reflect compositional patchiness at the outcrop scale. However, the tendency of adjacent samples at HGP to have comparable faunal compositions suggests that faunal composition is not simply varying randomly at the scale of sampling. In any case, these two instances suggest that there is variability at this limited spatial scale that is worth exploring in more detail.

## IMPLICATIONS OF THIS STUDY FOR GRADIENT ANALYSIS

In contrast to the earlier work of Cisne and others (see Introduction), this study involved systematic lateral sampling at the outcrop-scale. Although potentially non-random, within-outcrop variability was identified at one locality for each of the beds studied (see previous discussion), the degree of outcrop-scale compositional variability generally did not exceed that recognized from outcrop to outcrop. However, the recognition of a limited number of compositional outliers at most localities (Figs. 4 and 7) suggests that, to diagnose the gradient confidently, several samples should be collected at each locality.

Studies of the Hamilton Group by Brett and others (1990) have identified faunal changes through time, as well as recurring biofacies. The faunal gradient identified along the transect of the Browns Creek bed, and to some extent that within the Hills Gulch bed, paralleled the community changes predicted by Baird and Brett (1983), Brett et al. (1990), and others (McCollum, 1980; Lukasik, 1984; Savarese et al., 1986) based on studies of vertical (Waltherian) stacking of biofacies and regional variations in communities. Baird and Brett (1983) identified regional faunal gradients in two coral-rich beds. The nearshore-to-deeper water gradient was mirrored by a faunal transition from coral-rich biofacies through a diverse brachiopod biofacies

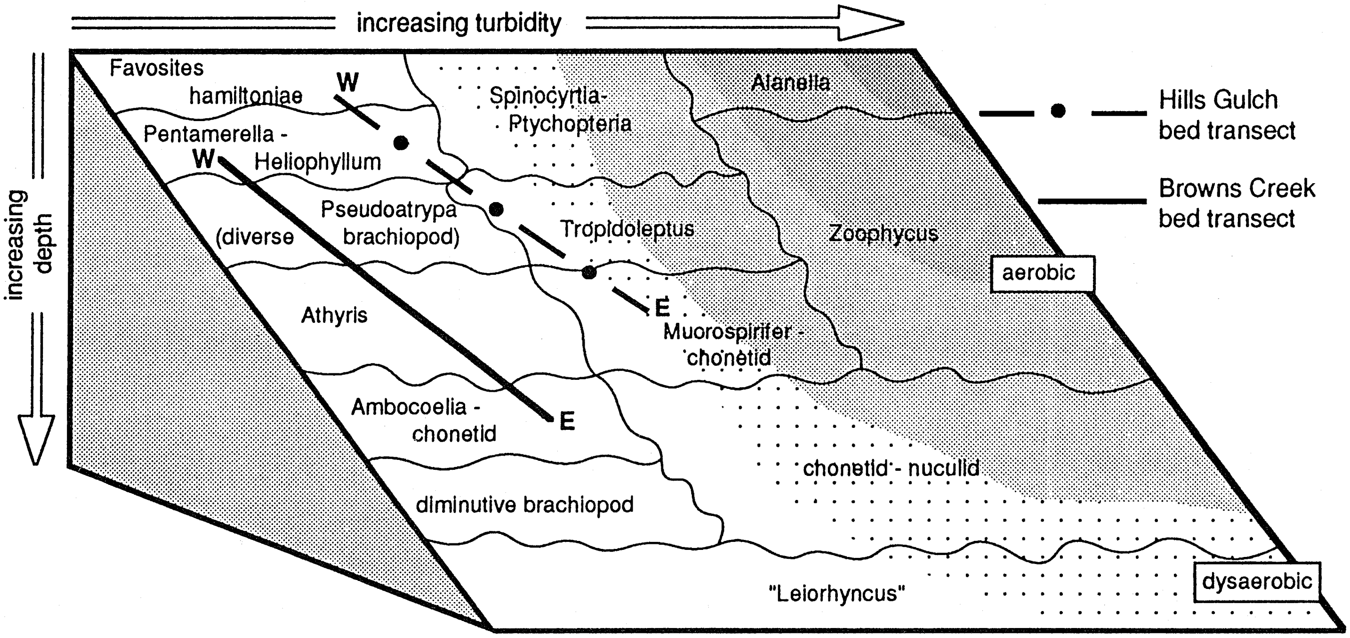

**FIGURE 13**—Biofacies model for the Hamilton Group illustrating relative positions of the Hills Gulch bed and Browns Creek bed transects. (Modified from Brett et al., 1990.)

to an ambocoeliid biofacies. Savarese and others (1986) identified similar faunal transitions in vertically stacked biofacies: *Heliophyllum–Heterophrentis* associations lived in shallow water within storm wave-base; *Pseudoatrypa–Stereolasma* associations lived in low energy areas experiencing periodic times of higher energy; *Ambocoelia*–chonetid associations lived in low-energy, deep water with slow to moderate sedimentation rates. These associations largely parallel the spatial faunal transition identified in the Browns Creek bed.

The transition along the transect of the Hills Gulch bed from a coral-rich–meristellid assemblage through a diverse brachiopod–infaunal bivalve assemblage, also matches with biofacies gradients predicted by the generalized biofacies model of Brett and others (1990). The Hills Gulch gradient begins at a shallower depth than does the Browns Creek bed (Fig. 13), with coral-rich packstones assigned by Brett and others (1990) to the *Favosites hamiltoniae* biofacies (herein referred to as a coral-meristellid assemblage), in western outcrops. It should be noted that *F. hamiltoniae* is represented by large hemispherical coralla that are about as large as entire samples used in this study and were, consequently, not included in the data base. This shallow, near-wave-base assemblage passes eastward into a more rugose coral and brachiopod-rich assemblage, generally lacking large *Favosites,* which is more comparable to the shallowest Browns Creek bed assemblage. However, instead of grading laterally into diverse brachiopod biofacies similar to those seen in the Browns Creek bed transect, the Hills Gulch bed passes into alternative (higher turbidity/sedimentation) association types identified by Brett and others (1990) as the *Tropidoleptus* and *Mucrospirifer* biofacies. To some degree, these biofacies resemble the diverse brachiopod assemblage of intermediate Browns Creek bed samples, but differ in having larger numbers of semi-infaunal brachiopods, spiriferids (especially *Mucrospirifer*), and bivalves, such as *Cypricardella.*

## CONCLUSIONS

1) Spatial faunal transitions can be recognized at a variety of scales from one-meter to basinal in the Middle Devonian Hamilton Group of western and central New York State. Transitions associated with paleoenvironmental gradients were identified along nearshore to trough transects of two beds: the Browns Creek bed of the Centerfield Limestone Mbr. and the Hills Gulch bed of the Jaycox Shale Mbr. (Ludlowville Fm.).
2) Overlap among localities is absent to minimal on Q-mode polar ordination plots of samples from both beds; samples that are geographically proximate plot close together. However, there are exceptions, suggesting that confident assessment of faunal compositions along the transect, and transitions thereof, requires the collection of multiple samples at each locality.
3) Along the Browns Creek bed transect, faunal assemblages vary laterally from a rugose coral assemblage through a diverse brachiopod assemblage to an ambocoeliid assemblage. Along the transect of the Hills Gulch bed, faunal groupings vary from a rugose coral-meristellid assemblage through a diverse brachiopod/infaunal bivalve.
4) At Browns Creek bed locality Y and Hills Gulch bed locality P, there may be systematic patterns of faunal variability exhibited at the outcrop-scale. While the explanation for this variability remains elusive, it does

suggest that systematic variability at this scale may be more common than typically appreciated and is worth exploring in more detail.

## ACKNOWLEDGMENTS

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## APPENDIX 1

### Locality Register
(All Quadrangles USGS 7.5 minute.)

### BROWNS CREEK BED

BCW Exposure along bank of Browns Creek, 0.3 km east of the town of York, Geneseo quadrangle, Livingston Co., NY. Latitude 42°52′42″, Longitude 77°52′30. Trend of collecting transect was N 56° W.

BCX Exposures along bank and in creek bed, Triphammer Falls on Conesus Creek, 0.2 km north of Triphammer Road, 0.2 km east of Rt. 39, South Avon. Geneseo quadrangle, Livingston Co., NY. Latitude 42°51′20″, Longitude 77°45′48″. Trend of collecting transect was N 14° E.

BCY Exposure along bank of Wilson Creek, downstream of intersection of Wilson Creek and Slate Rock Road, 0.3 km north of Billsboro Rd., south of Geneva. Stanley quadrangle, Ontario Co., NY. Latitude 42°48′12″, Longitude 77°00′. Trend of collecting transect was N 50° W.

BCZ Exposure in quarry wall, 0.1 km on Poorman Road, west of Fayette. Romulus quadrangle, Seneca Co., NY. Latitude 42°48′45″, Longitude 76° 49′. Trend of collecting transect was N 85° E.

### HILLS GULCH BED

HGP Exposures in creek bed where Rt. 20 crosses Elevenmile Creek, on south side of road, near Darien Lakes State Park. Corfu Quadrangle, Genesee Co., N.Y. Latitude 42°54′24″, Longitude 78°27′18″. Trend of collecting transect was N 82° E.

HGQ Exposures in creek bed where Bullis Road crosses Buffalo Creek, near Marilla. East Aurora Quadrangle, Erie Co., N.Y. Latitude 42°51′46″, Longitude 76°35′42″. Trend of the collecting transect was N 40° W.

HGR Exposure along Jaycox Creek, 0.4 km south of the intersection of Rt. 39 and Roots Tavern Road, 0.4 km east (through field) of Rt. 39, near Geneseo. Geneseo Quadrangle, Livingston Co., N.Y. Latitude 42°50′, Longitude 77°46′40″.

HGS Exposures along unnamed creek, Sampson State Park, near Wilbur. Dresden Quadrangle, Seneca Co., N.Y. Latitude 42°42′30″, Longitude 76°53′42″. Trend of collecting transect was N 90° E.