PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2006, v. 21, p. 316–324
Research Report
DOI: 10.2110/palo.2005.P05-82e

1926 SEPM Society for Sedimentary Geology

A QUANTITATIVE STUDY OF BENTHIC FAUNAL PATTERNS WITHIN THE PENNSYLVANIAN AND EARLY PERMIAN

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ABSTRACT

Using abundance data, this study explores quantitative patterns from marine benthos, including implications for paleogeography, depositional environment, stratigraphic position, taxonomic groups (brachiopod or mollusc), substrate preferences, and ecological niches. Twenty-nine brachiopod- and bivalve-dominated fossil assemblages from the Pennsylvanian and Early Permian of North and South America, Thailand, and Australia were analyzed from carbonate-platform environments; specifically, Nevada, Kansas, Oklahoma, Texas, Utah, New Mexico, Venezuela, Kanchanaburi (Thailand), and Queensland (Australia). Samples were categorized by paleogeographic location, depositional environment, and age to help differentiate factors controlling the faunal patterns. Pooled from primary and summary literature resources, 336,321 specimens were identified to genus level and classified in terms of taxonomic membership, substrate preference, and ecological niche. Data were analyzed using detrended correspondence analysis (DCA) and multi-response permutation procedure cross-validated *a-priori* categories (e.g., paleogeography, depositional environment, stratigraphic position, and specimen ecology). Multivariate analyses indicate that the separation between genera and the orthogonal trends implies that paleoecological patterns within the studied late Paleozoic faunal associations were influenced strongly by the abundance of sessile versus mobile faunal components.

INTRODUCTION

The late Paleozoic Era has been recognized as a time that global biodiversity plateaued (Sepkoski, 1981, 1991). This plateau is characterized by the Paleozoic Evolutionary Fauna (Sepkoski, 1981), and the consequent ecological stability of the Carboniferous and Permian has been identified as representing a single ~110 million-year-long (Gradstein et al., 2004) Ecological Evolutionary Unit (EEU) by Boucot (1983) and Sheehan (1996). Perhaps due to the perception that this was a relatively long period of evolutionary and ecological stasis, syntheses of paleoecological patterns and processes during this time period have received much less recent attention than periods of change in the Phanerozoic fossil record, such as the Ordovician radiation or the Big Five mass extinctions (Hallam and Wignall, 1997; Webby et al., 2004).

The objectives of this research are to understand paleoecological patterns and processes by comparative quantitative analysis of faunas from the Pennsylvanian through the Early Permian. This time interval provides a good sample from the late Paleozoic period of stasis because it precedes the later Permian times of mass extinction by approximately 10–12 million years, so any direct faunal changes caused by that period of environmental crisis can be avoided. Pennsylvanian–Permian fossils from the United States constitute the main body of data because there are numerous sources of paleoecological data, including abundance data, within the primary literature. Mudge and Yochelson's (1962) monograph describes the stratigraphy and paleontology of the Pennsylvanian–Permian Midcontinent of Kansas using over 300 fossil collections. Yancey and Stevens (1981) studied the Early Permian of Nevada and Utah extensively, recorded abundance data from 55 localities, and identified paleocommunities based on the faunal comparisons and relative abundances within each sample collected. As a result, three groups of commonly occurring communities emerged: (1) nearshore, mollusc-dominated; (2) open-shelf, nonmolluscan; and (3) deeper water, offshore mollusc-dominated. More recently, Olszewski and Patzkowsky (2001) documented the reoccurrence of Pennsylvanian–Permian Midcontinent brachiopod and bivalve associations through time (Olszewski and Patzkowsky, 2001). Using a combination of data from Mudge and Yochelson (1962) and their own data, Olszewski and Patzkowsky's (2001) cluster and ordination analyses revealed two discrete biofacies—one dominated by brachiopods and the other dominated by bivalves. Within these two biofacies, distinct compositional gradients were recognized, which the authors attributed to changes in environmental factors. The particular environmental factors controlling the two gradients remain unclear. This study builds on these previous studies by using multivariate statistics to document late Paleozoic benthic faunal patterns, and a variety of extrinsic and ecological factors were tested to determine underlying processes that influenced faunal distributions during this long interval of evolutionary and ecological stasis.

STUDY AREA AND GEOLOGICAL SETTING

This study focuses on three marine realms that existed along Pangaea throughout the Pennsylvanian to Early Permian: the Northwestern Continental Margin, Northwestern Midcontinent, and Southeastern Tethys (Fig. 1). All realms consist of mixed siliciclastic and carbonate sedimentary sequences. Data sampling concentrated on the Pennsylvanian, Moscovian and Gzhelian stages and the Early Permian Asselian, Sakmarian, and Artinskian stages (Fig. 2). To investigate temporal changes, data were analyzed according to their epoch divisions within the Pennsylvanian and Early Permian (Fig. 2).

All environments were relatively shallow-marine settings. There is abundant evidence suggesting that the early part of the Carboniferous generally was warm. However, through time, pronounced cooling occurred, resulting in a Gondwanan ice sheet covering the South Pole by the end of the Mississippian that persisted into the Permian (Crowley and Baum, 1991; Ziegler et al., 1997). In general, while global temperatures waxed and waned, depositional cyclothems, characteristic of the Pennsylvanian and Permian periods, were deposited in the northwestern Midcontinent. Cyclothems typically contain a sequence of rock layers that indicate a progressive change in depositional environments that appears to be generated by an interaction of tectonic subsidence, sedimentation, and eustasy (Bennington, 2002). More detailed geological information is presented below.

Northwestern Continental Margin Realm

Two studies, one from the Pennsylvanian (Beus and Lane, 1969) and one from the Early Permian (Yancey and Stevens, 1981), document this

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[1] www.sepm.org/archive/index.html

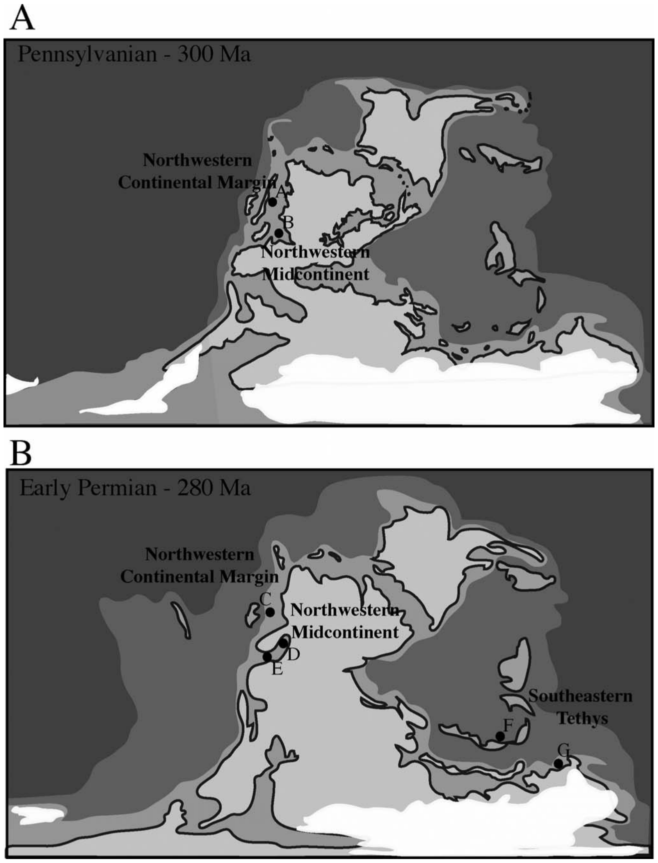

FIGURE 1—Pennsylvanian and Early Permian paleogeography. (A) Pennsylvanian samples; Location A, Northwestern Continental Margin, data from Beus and Lane (1969); Location B, Northwestern Midcontinent, data from Mudge and Yochelson (1962), Olszewski (2000), and West (1970). (B) Early Permian samples; Location C, Northwestern Continental Margin, data from Yancey and Stevens (1981). Location D, data from Kues (1995); and Location E, data from Cooper and Grant (1972), Hoover (1981), and Mudge and Yochelson (1962); Northwestern Midcontinent realm. Location F, data from Grant (1976) and Waterhouse (1983); and Location G, data from Waterhouse (1983); Southeast Tethys realm.

realm (see Supplementary Data 1[1]). During the Moscovian through Artinskian stages, sedimentary deposition within Nevada and Utah occurred near the outer edge of the continental shelf (Stevens, 1977; Yancey and Stevens, 1981). A long-lived, shallow, interior seaway occupied this area adjacent to a deep-marine trough along the western edge of the seaway (Yancey and Stevens, 1981). It should be noted that all faunal information extracted for analyses was obtained from only the interior-seaway environment.

Northwestern Midcontinent Realm

Most of the data used in this study fall within this realm (Mudge and Yochelson, 1962; West, 1970; Cooper and Grant, 1972, 1974, 1975, 1976, 1977; Hoover, 1981; Kues, 1995; Olszewski, 2000; Olszewski and Patzkowsky, 2001; see Supplementary Data 1[1]). Because of the extensive concentration on, and resulting detailed study of this particular area, the Northwestern Midcontinent Realm provides comparative material that represents a standard for both faunal comparison and stratigraphic correlation within the Pennsylvanian and Early Permian (Hoover, 1981). Within this realm, Mudge and Yochelson (1962), West (1970), and Olszewski (2000) contributed to the Pennsylvanian data. Early Permian data are from the following sources: Mudge and Yochelson (1962), Cooper and Grant (1972), Hoover (1981), and Kues (1995). Cooper and Grant's (1972) work did not record abundance data; however, abundance data

Geochronology			Stratigraphic position of samples according to paleogeographic realm		
Ma	Period	Epoch	NW Cont. Margin	NW Mid-Cont.	SE Tethys
271	Early Permian	Kungurian			
276		Artinskian	Ya1 Ya2 Ya3 Ya4	Co1 Gr1 Gr2 Gr3	Wa3 Ho1 Gr5
284		Sakmarian	Ku2		
295		Asselian		Mu1 Mu4 Mu2	
299	Pennsylvanian	Gzhelian		Mu5 Ol1 Mu6 Ol2 Mu7 Ol3 Mu8 Ol4	
304		Kasimovian			
307		Moscovian	Be1	We1 We2 We3 We4 We5	
312		Bashkirian			
318					

FIGURE 2—Geochronology from Pennsylvanian through the Early Permian (after Gradstein et al., 2004); International Commission on Stratigraphy (ICS) stage names are used. Samples categorized according to stage and paleogeographic realm; samples within stages are not arranged in stratigraphic order. Abbreviations: Be1—Beus and Lane (1969); Mu5, Mu6, Mu7, Mu8—Mudge and Yochelson (1962); Ol1, Ol2, Ol3, Ol4—Olszewski (2000); We1, We2, We3, We4, We5—West (1970); NW—Northwestern.

were collected from their original museum collections housed in the Smithsonian and entered into the paleobiology database.

It is generally agreed that late Paleozoic marine sediments in the Western Hemisphere were deposited in a geosynclinal basin or series of basins (Hoover, 1981). Paleomagnetic research places the southern tip of Mexico near the west coast of South America (Hoover, 1981; Ziegler et al., 1997). This connection produced a more intimate pre-Mesozoic connection between the southern Appalachian, Ouachita, Mexicana–Central American, and northern Andean geosynclinal belts, which helps to explain the faunal similarity between North and South American counterparts (Hoover, 1981). During this time, both North- and South-American areas represented a broad, flat marine platform adjacent to the Anadarko Basin, which was a starved foreland basin associated with the Ouachita thrust belt (Hoover, 1981; Rascoe and Adler, 1983).

Southeastern Tethys Realm

Grant (1976) and Waterhouse (1983) compiled taxonomic and geologic information, including faunal counts, from the Early Permian of Thailand and Australia–New Zealand areas. Compared to the broad, extensive platforms of the Western Hemisphere, the Southeastern Tethys realm represented a similar shelf environment, but a significantly cooler-water setting. Studies indicate that although some paleotropical brachiopod genera are found in these faunas, temperate- to cool-water genera dominate the assemblages (Waterhouse, 1983). In addition, preservation of pebbly mudstones that resemble diamictites of glacial origin indicates that the regional climate was much cooler compared to the Northwestern Midcontinent and the Northwestern Continental Margin realms (Waterhouse, 1982).

METHODS

Sample Collection and Processing

The data used in this study comprise geological, ecological, and taxonomic information from ten regions spanning the Pennsylvanian and Early Permian (Fig. 2). Data were derived primarily from the Paleobiology Database (PBDB)—a public, electronic resource that provides global, collection-based occurrence and taxonomic data for marine animals of any geological age (<http://paleodb.org>). Data were compiled into comprehensive, relative abundance datasets. Samples within this study are defined as closely spaced horizons from the same regional locality, within the same depositional environment. Because samples represent different amounts of time averaging, faunal associations are not considered to represent co-occurrence during life. Instead, these samples represent a long history of information regarding fossil associations and assist in the explanation of faunal compositional differences between different realms and environments. Each sample consists of at least 200 specimens. Two taxonomic levels were used in subsequent analyses: order and genus. Although different authors originally identified these specimens, museum collections and published photographs were utilized to confirm taxonomic identification. Original abundance counts were transformed into percent specimen per sample (i.e., 1–100%). This study analyzed fourteen Pennsylvanian and fifteen Early Permian samples with a total of 366,321 specimens (Fig. 2).

Generally, samples are from two environments: an epeiric sea and a cool-water carbonate platform. Samples were differentiated into appropriate geological stages, paleogeographic realm (see definitions above), and depositional environments within the shelf environment.

Each genus was categorized into it's appropriate group (brachiopod or mollusc), where it lived in relation to the substrate, and feeding habit. Brachiopods were categorized into two guilds: (1) pedunculate suspension feeders, and (2) reclining suspension feeders. Bivalves were categorized into five guilds: (1) burrowing deposit feeders, (2) burrowing suspension feeders, (3) cemented suspension feeders, (4) endobyssate suspension feeders, and (5) epibyssate suspension feeders. Gastropods fell into one guild: epifaunal grazers.

Sampled realms are extremely variable in abundance within the Pennsylvanian; however, within the Early Permian, they roughly correspond in amounts (see Supplementary Data 1[1]). For the Pennsylvanian, the Northwestern Midcontinent realm totals 313,702 specimens (~99%), and the Northwestern Continental Margin realm consists of 237 specimens (~1%). For the Early Permian, the Northwestern Midcontinent realm consists of 9,316 specimens (18%), and the Northwestern Continental Margin realm consists of 23,214 specimens (44%), while the Southeastern Tethys realm comprises 19,852 specimens (38%). In addition, distribution of studied specimens between analyzed facies and sampled stratigraphic intervals is variable. For example, in the Pennsylvanian, the Moscovian stage comprises 96% of the specimens and the Gzhelian 4%, while deep, muddy offshore environments comprise 99% of this time interval. In the Early Permian, the Artinskian stage comprises 91%, the Asselian 6%, and the Sakmarian 3% of studied specimens. Depositional environments have a distribution of ~54% shallow, inner shelf; ~28% middle shelf; and ~18% deep, offshore basin. Despite this substantial variation between particular categories, all comparison categories total to abundances greater than 237—a sufficient sample size for reliable paleoecological comparisons (see Supplementary Data 1[1]).

Analytical Methods

This study takes a two-stage approach to multivariate analyses. First, an investigative stage searched for patterns independent of the grouping variable; second, the confirmatory stage confirmed the statistical significance of patterns seen in stage one. Data matrices are composed of compositional data, with samples described by taxonomic or ecological percents. Because sample abundances vary greatly, relative percentages were calculated per sample; otherwise, an extremely abundant sample would bias statistical analyses strongly (e.g., comparing the Pennsylvanian sample Be1, with 237 specimens, to sample We 2, with 126,596 specimens). Specimens comprising <1% of a sample were deleted to reduce the amount of noise in the datasets and aid in interpreting results. In all analyses, <24% of data were lost as a result of this operation. Since there is a high degree of variation among specimens within samples, data were log transformed before analyses.

This study aims to reveal environmental and/or ecological gradients controlling community patterns; therefore, detrended correspondence analysis (DCA; Hill, 1979) is an appropriate exploratory analysis for several reasons (Gauch, 1982). First, DCA, like all ordination techniques, aims to represent specimen and sample relationships in low-dimensional space and typically presents the most important and interpretable underlying environmental gradients. Second, DCA minimizes an arch effect and results in superior conclusions compared to other ordination techniques (Hill and Gauch, 1980; Gauch, 1982). The confirmatory analysis chosen for these datasets is the multi-response permutation procedure (MRPP). MRPP is a non-parametric procedure for testing the hypothesis of no difference between two or more groups of entities. MRPP was chosen because, unlike discriminant analysis and multivariate analysis of variance (MANOVA), MRPP does not assume normality, which is seldom met with ecological data (Biondini et al., 1985). It should be noted that MRPP is closely related to Mantel testing and ANOSIM; all three techniques use a permutation procedure to test for the similarity of *a-priori* groups; therefore, these procedures produce similar results. PC-ORD Version 4 (McCune and Mefford, 1999) was used for both exploratory (DCA) and confirmatory (MMRP) analyses.

RESULTS

Multivariate Taxonomic Analysis

Using detrended correspondence analysis (DCA), four data sets were analyzed independently: Pennsylvanian genera, Pennsylvanian orders, Early Permian genera, and Early Permian orders.

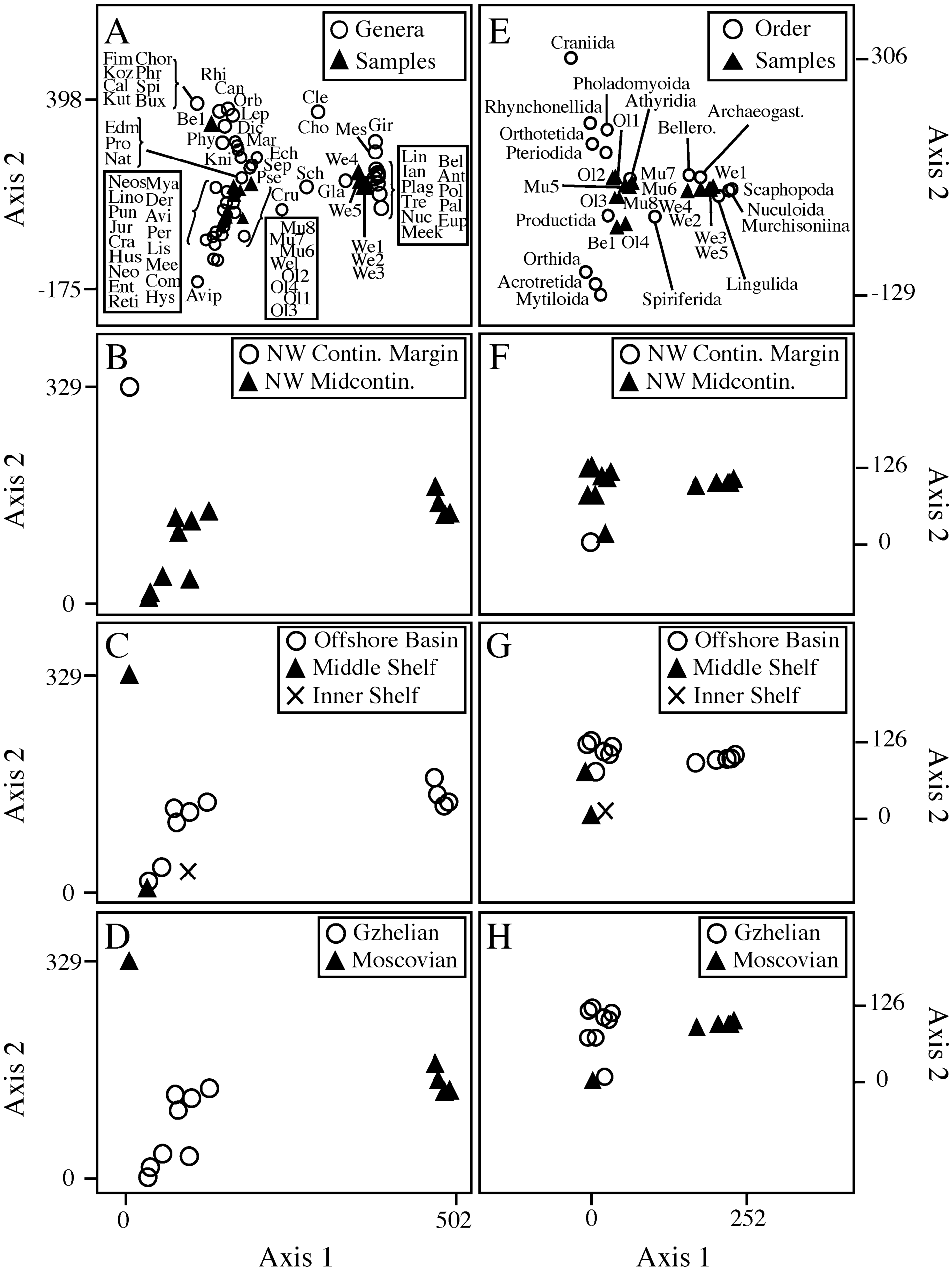

FIGURE 3—Pennsylvanian detrended correspondence analysis of samples. Collection-code abbreviations given in Supplementary Data 1[1]; genera codes are given in Supplementary Data 2[1]. Plots of relative-abundance data for genera (A–D) and orders (E–H). (A) Ordination pattern of samples and genera plotted in ordinal space. (B–D) Genus-level ordination plots for samples grouped by: (B) paleogeography; (C) depositional environment; and (D) stratigraphic stage. (E) Ordination pattern of samples and orders in ordinal space. (F–H) Order-level ordination plots of samples grouped by: (F) paleogeography; (G) depositional environment; and (H) stratigraphic stage.

The Pennsylvanian ordinations indicate that the Northwestern Midcontinent and the Northwestern Continental Margin realms form separate groups with distinct taxonomic compositions. However, the separation tends to be better for the genera than the orders; therefore, this section will focus on results pertaining to generic analyses (Fig. 3). When grouped by depositional environment, samples indicate overlap in each case (Fig. 3C, G). However, when grouped by stage intervals, there is a distinction between Gzhelian and Moscovian faunas (Fig. 3D, H). Since DCA analyzes samples and specimens simultaneously, each genus was coded according to its relation to the substrate (epifaunal or infaunal), guild category, and specific group (brachiopod or mollusc), and plotted in ordinal space. When genera are categorized into their particular substrate relations, infaunal genera plot along the outer limits of the epifaunal cloud of points (Fig. 4A). When genera are grouped according to their taxonomic group, they overlap slightly between groups, but, more distinctly, each group trends differently (Fig. 4B). For example, while axis 1 separates brachiopods from molluscs, it also extracts a compositional gradient in molluscs along axis 1. Perpendicular to this gradient, axis 2 extracts a compositional gradient within the brachiopod genera. Olszewski and Patzkowsky (2001) reported similar compositional gradients for Pennsylvanian brachiopods and bivalves.

Generic patterns of guild structure indicate two distinct groups: sessile and mobile benthos. The left side of the plot contains the majority of pedunculate and reclining suspension-feeding specimens (Fig. 4C). In addition, other sessile benthos exclusively plot on the left side, including epibyssate, endobyssate, and cementing suspension-feeding genera. In contrast, mobile benthos, including all burrowing deposit feeders, the majority of epifaunal grazers, and burrowing suspension feeders, plot on

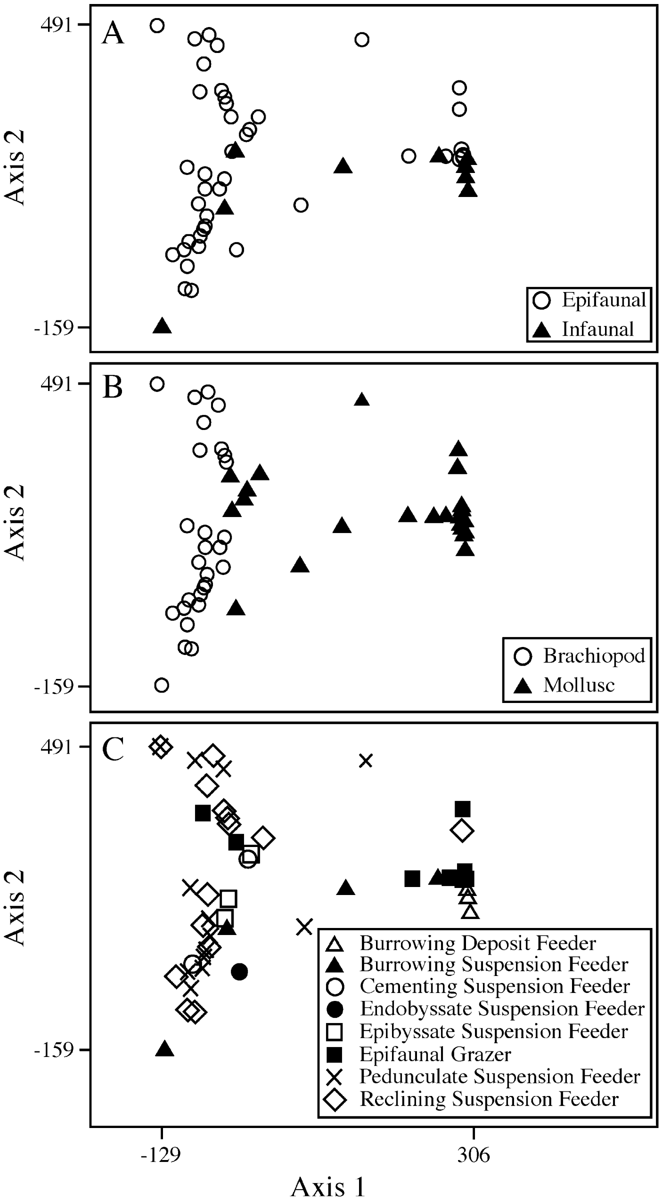

FIGURE 4—Pennsylvanian detrended correspondence analysis of genera. Ordinations grouped by: (A) substrate preference; (B) faunal group (brachiopod or mollusc); and (C) guild structure.

the right (Fig. 4C). In addition to this separation between sessile and mobile benthos, sessile benthos trend differently than mobile benthos (Fig. 4C). As mentioned previously, brachiopods trend along axis 2 and molluscs trend along axis 1 (Fig. 4B). These trends are not limited to taxonomic categories. When genera are coded according to their particular guilds, cementing, epibyssate, pedunculate, and reclining suspension feeders vary along axis 2 (Fig. 4C). However, burrowing suspension feeders and epifaunal grazers trend along axis 1 (Fig. 4C).

Early Permian generic and ordinal ordinations generally overlap, however generic analyses perform better than order analyses in separating *a-priori* categories (Fig. 5). The maximum separation occurs in Figure 5B; only one Northwestern Continental Margin sample overlaps into the Mid-Continental realm (Fig. 5B). In comparison, depositional environments and stratigraphic stages significantly overlap between samples (Fig. 5C, D, G, H). When Early Permian genera are coded according to their taxonomic group, guild structure, and substrate preference, although some specimens overlap, the greatest separation is between brachiopods and molluscs (Fig. 6B). As in the Pennsylvanian, Early Permian taxonomic groupings display similar clustering and trends. For example, most mollusc genera separate from brachiopods with overlap only at the groupings edges; molluscs generally plot along axis 1 and brachiopods range along axis 2 (Fig. 6B). Specifically, burrowing deposit feeders exclusively plot on the left side of the graph with the majority of epifaunal grazers, and their general trend spreads along axis 1 (Fig. 6C). Conversely, pedunculate and reclining suspension feeders plot on the right side of the graph with endobyssate and cementing suspension feeders, with their general trend spreading along axis 2. These results suggest that sessile and mobile genera tend to plot separately from one another, and to display a similar, orthogonal-trending relationship, as do Pennsylvanian genera (Fig. 6C). Although these distinctions among guilds are similar to Pennsylvanian associations, Early Permian genera display weaker orthogonal trends in comparison to the Pennsylvanian genera (Figs. 4C, 6C).

Results from the multi-response permutation procedure (MRPP) confirm some ordination patterns, but not others. Note that the T-statistic describes the separation between groups and is used to quantify the amount of influence a particular factor has on faunal patterns (Tables 1, 2). For example, in the Pennsylvanian, a large degree of separation is present between taxonomic groups (T-statistic=-21.32), indicating that the distinction between brachiopods and molluscs greatly influences faunal pattern. In addition to taxonomic groups, significant factors influencing Pennsylvanian patterns include guild structure and lithologic stages for genera and orders (Table 1). For Early Permian patterns, substrate preference most influences faunal distribution, followed by taxonomic groups, guild structure, generic lithostratigraphic stage intervals, and order-level depositional environments, all of which are significant (Table 2).

Multivariate Ecological Analysis

Percentages of guild categories were calculated per sample, and two ecological data sets were generated: a Pennsylvanian and Early Permian data set. Any guild category comprising less than 1% of the total number of specimens was deleted. As a result, the Pennsylvanian and the Early Permian consist of eight guilds (see Supplementary Data 2 and 3[1]). The ordination plots produced using guild percentages show much poorer separation of *a-priori* categories than the taxonomic-based ordinations (Figs. 7, 8). As with the taxonomic data, similar ecological separation and trends occur between sessile and mobile benthos. The Pennsylvanian ordination (Fig. 7A) indicates that the first axis separates sessile (endobyssate, pedunculate, reclining, epibyssate, and cementing suspension feeders) from mobile (burrowing suspension and deposit feeders and epifaunal grazers) fauna. The second axis, as in the taxonomic data, strings the sessile benthos in a vertical gradient from cementing suspension feeders on the bottom to endobyssate suspension feeders on the top (Fig. 7A). In comparison, Early Permian ecological data show weaker separation and gradients between sessile and mobile benthos (Fig. 8A).

MRPP results indicate that, in the Pennsylvanian stage, intervals affect ecological patterns within samples; however, paleogeographic realms and depositional environments cannot be compared using this technique because more than one sample per category is needed to complete the calculation (Table 3). In contrast, depositional environments affect Early Permian ecological patterns. T-statistic distances between groups tend to be shorter for ecological data and the associated *p* values are less significant (Table 3).

DISCUSSION

Most sample plots for both time intervals display significant overlap, implying that similar taxa are found within the different paleogeographical locations and depositional environments in this study. These results are not surprising, considering the close proximity of the Northwestern Continental Margin and Northwestern Midcontinent (Fig. 1) and the overwhelming number of fossils obtained from these two areas (~99% in Pennsylvanian and 63% in Early Permian). The separation of these sam-

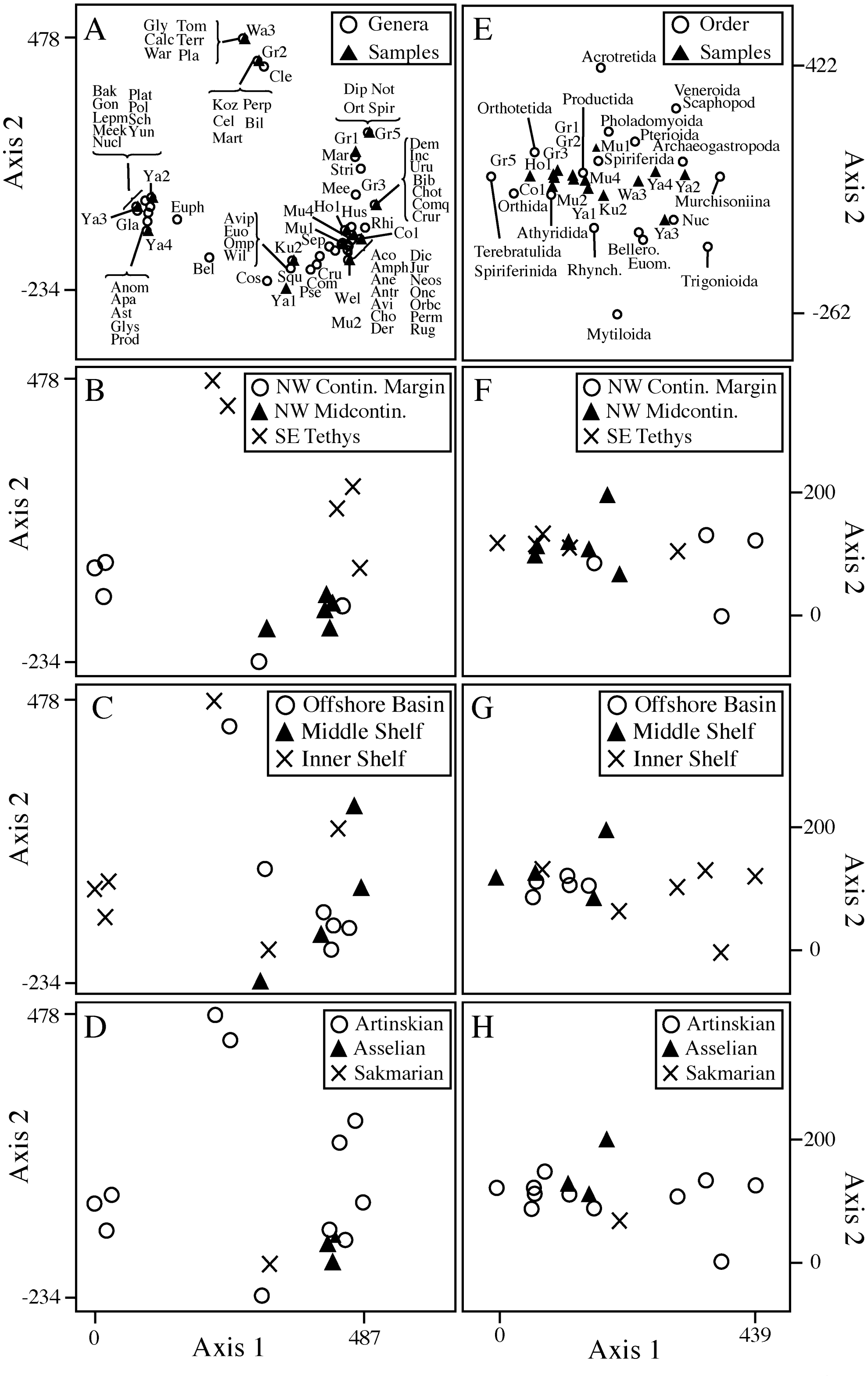

FIGURE 5—Early Permian detrended correspondence analysis of samples. Collection-code abbreviations given in Supplementary Data 1[1]; genera codes are listed in Supplementary Data 3[1]. Plots of relative abundance data for genera (A–D) and orders (E–H). (A) Ordination patterns of samples and genera in ordinal space. (B–D) Genus-level ordination plots for samples grouped by: (B) paleogeography; (C) depositional environment; and (D) stratigraphic stage. (E) Ordination patterns of samples and orders in ordinal space. (F–H) Order-level ordination plots of samples grouped by: (F) paleogeography; (G) depositional environment; and (H) stratigraphic stage.

ples between stratigraphic stages is interpreted as a meaningful signal (Tables 1, 2). This implies that faunal patterns change through time between the Moscovian and Gzhelian stages. This result is not surprising, considering the three-million-year gap between these data (Fig. 2). In addition, 96% of the Pennsylvanian data come from the Moscovian stage. Likewise, Early Permian faunal differences occur through time, but not to the extent revealed in the Pennsylvanian. These results could be explained by the overabundance of Artinskian stage data (97%) in the Early

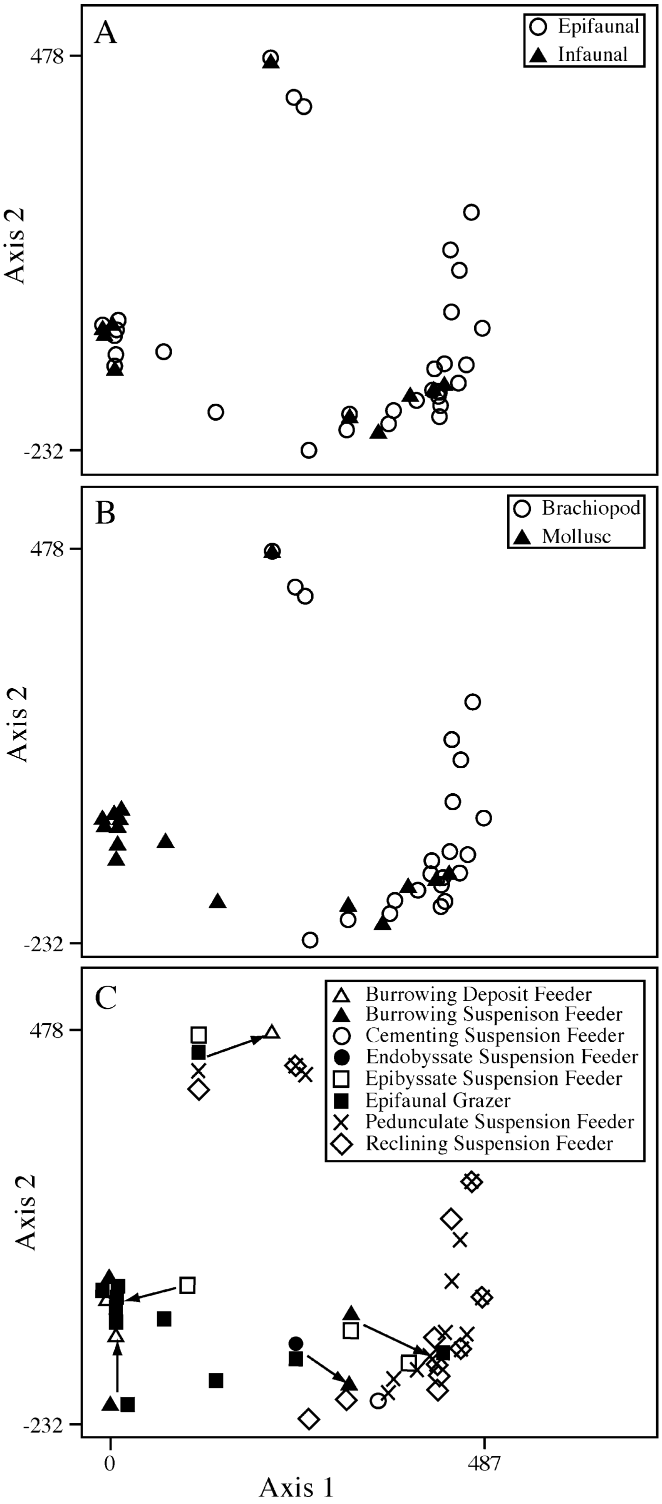

FIGURE 6—Early Permian detrended correspondence analysis of genera. Ordination of genera grouped by: (A) substrate preference; (B) faunal group (brachiopod or mollusc); and (C) guild structure.

TABLE 1—MRPP results for Pennsylvanian taxonomic *a-priori* groups. T-statistic describes the distance (or separation) between analyzed groups of samples categorized according to paleogeographic or lithological criteria and groups of genera according to their ecology and taxonomic groups. N/A—where sample size was ≤2, therefore, group comparison could not be confirmed.

Group comparison	T-statistic	*p* value
Genera		
Substrate (infaunal vs. epifaunal)	−0.68	0.18
Brachiopod vs. Molluscs	−21.32	<0.00001
Taxa Ecology	−8.79	<0.00001
Paleogeographic Realms	N/A	N/A
Lithostratigraphic Stages	−6.74	<0.001
Depositional Environment	N/A	N/A
Orders		
Paleogeographic Realms	N/A	N/A
Lithostratigraphic Stages	−6.11	<0.001
Depositional Environment	N/A	N/A

Permian data. Since these data are biased in terms of paleogeography and stratigraphic age, these factors cannot be ruled out as important contributors to faunal distribution, and they cannot be tested with these particular data. However, ecological patterns within these data still are meaningful and worthwhile to present. The greatest separation, or exhibited differences, lies within taxonomic variation. Both Pennsylvanian and Early Permian analyses indicate that brachiopods trend along a gradient perpendicular to the mollusc compositional gradient. This orthogonal relationship suggests that the two groups are responding to two independent environment factors (Figs. 4, 6–8). MRPP results confirm these results, and suggest that the two taxonomic groups differ significantly.

At this point, these results are similar to the results obtained by Olszewski and Patzkowsky (2001). However, when ecologic information is introduced into the analyses, compositional trends are not restricted to taxonomic membership. The general patterns presented here indicate that pedunculate and reclining suspension-feeding brachiopods tend to plot near cementing, endobyssate, and epibyssate suspension-feeding bivalves, constituting a clustering of sessile benthos. Burrowing deposit and suspension feeders and grazing gastropods cluster near one another, constituting a mobile-benthos group. In addition to this separation among sessile and mobile benthos, the abundant sessile benthos, including cementing, epibyssate, pedunculate, and reclining suspension feeders, trend perpendicular to the abundant mobile benthos (burrowing deposit and suspension feeders, epifaunal grazers). Thus, for these late Paleozoic associations, sessile benthos responded to a different environmental gradient with respect to mobile benthos.

CONCLUSIONS

Various aspects of marine benthic faunas from the late Paleozoic have been studied over the past several decades, including taxonomy (e.g., Mudge and Yochelson, 1962), paleoecology (e.g., Yancey and Stevens, 1981), and evolutionary paleoecology (e.g., Olszewski and Patzkowsky, 2001). However, rigorous quantitative analyses of benthic assemblages

TABLE 2—MRPP results for Early Permian taxonomic *a-priori* groups. T-statistic describes the distance (or separation) between analyzed groups of samples categorized according to paleogeographic or lithological criteria and groups of genera according to their ecology and taxonomic groups.

Group comparison	T-statistic	*p* value
Genera		
Substrate (infaunal vs. epifaunal)	−33.98	<0.00001
Brachiopod vs. Molluscs	−30.67	<0.00001
Taxa Ecology	−14.60	<0.00001
Paleogeographic Realms	−1.23	0.11
Lithostratigraphic Stages	−4.84	<0.001
Depositional Environment	−1.11	0.13
Orders		
Paleogeographic Realms	0.046	0.41
Lithostratigraphic Stages	−1.49	0.08
Depositional Environment	−2.24	0.03

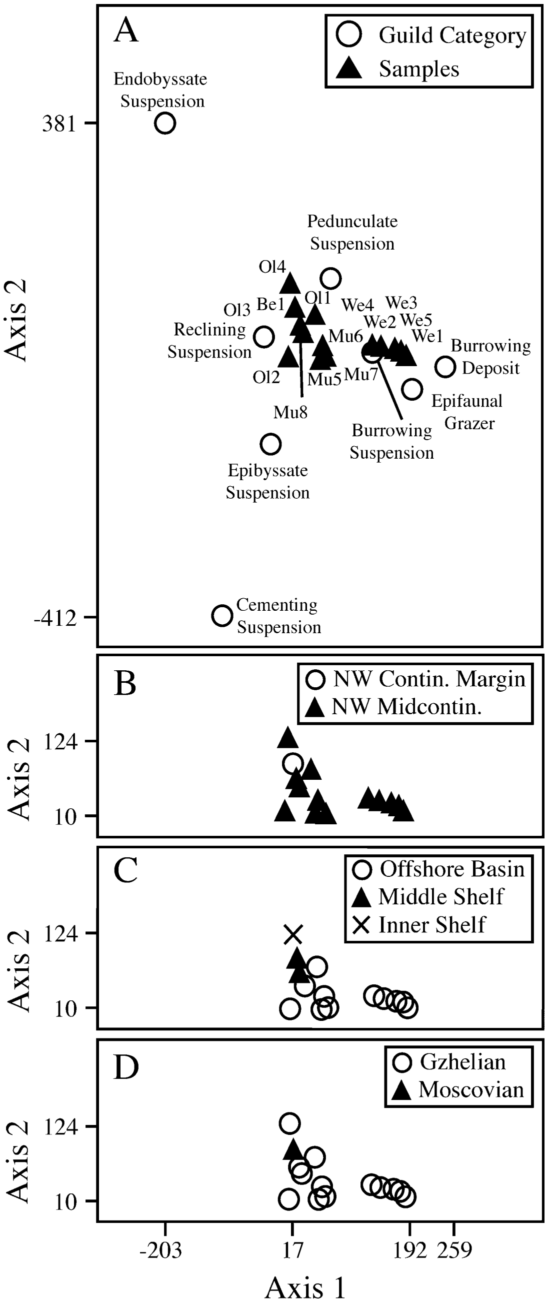

FIGURE 7—Pennsylvanian detrended correspondence analysis of samples described by the relative abundance of guild categories. (A) Guild categories and samples plotted in ordinal space. (B–D) Genera-ecotype ordination plots for samples grouped by: (B) paleogeography; (C) depositional environment; and (D) stratigraphic stage.

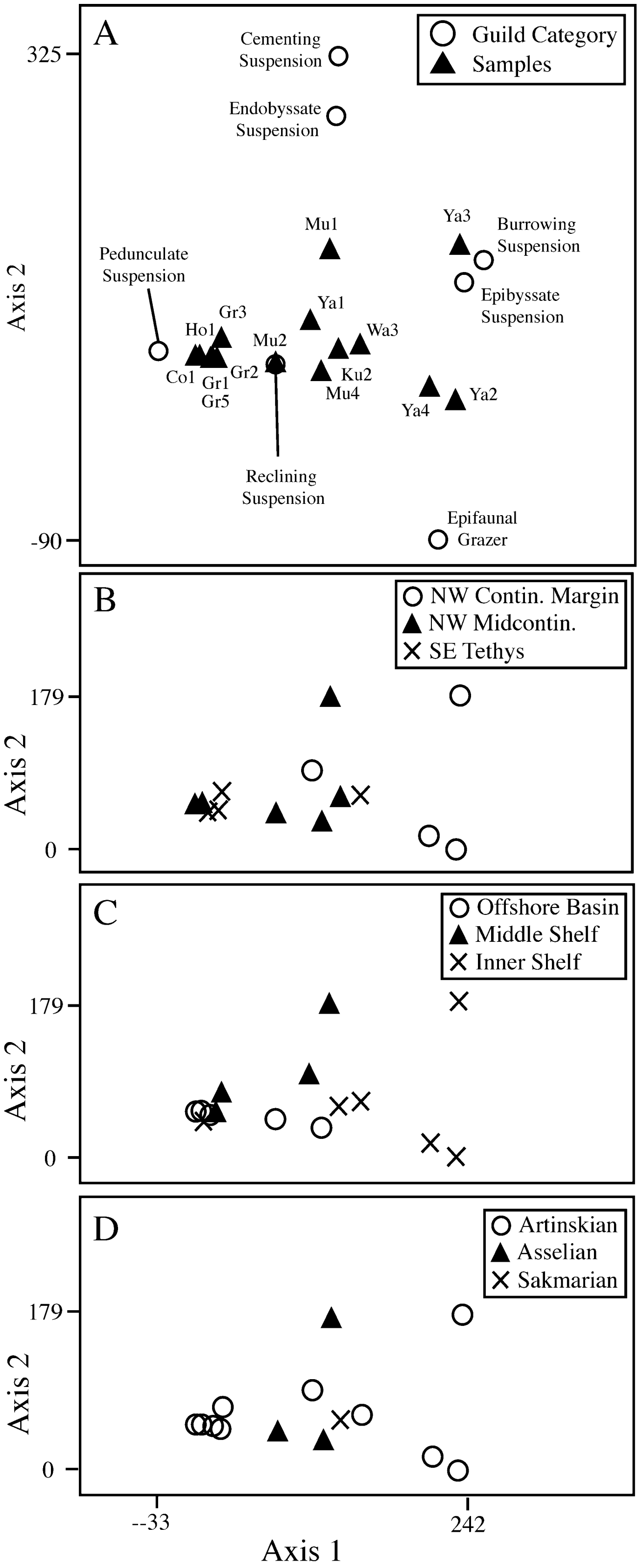

FIGURE 8—Early Permian detrended correspondence analysis of samples described by the relative abundance of guild categories. (A) Guild categories and samples plotted in ordinal space. (B–D) Genera-ecotype ordination plots for samples grouped by: (B) paleogeography; (C) depositional environment; and (D) stratigraphic stage.

primarily have been restricted to local paleoecological studies (e.g., Olszewski and Patzkowsky, 2001), and comparative multivariate studies of benthic assemblages across paleogeographic regions or stratigraphic stages have not been conducted previously. The analyses presented provide new data on patterns of taxonomic and ecologic variation within marine benthic associations. These patterns provide new insight into the possible factors involved in controlling Late Paleozoic faunal patterns.

Ecological variation, specifically the abundance of sessile and mobile benthos, plays an important role in faunal distributions within these Pennsylvanian and Early Permian data sets. For both time periods, faunal patterns indicate that pedunculate, reclining, endobyssate, epibyssate, and cementing suspension-feeders (i.e., sessile benthos) tend to cluster to-

TABLE 3—MRPP results for the Pennsylvanian and Early Permian ecological *a-priori* groups. T-statistic describes the distance (or separation) between analyzed groups of samples categorized according to paleogeographic or lithological criteria and groups of genera according to their ecology and taxonomic groups. N/A—where sample size was ≤ 2, therefore, group comparison could not be confirmed.

Group comparison	T-statistic	*p* value
Pennsylvanian		
Paleogeographic Realms	N/A	N/A
Lithostratigraphic Stages	-5.66	<0.001
Depositional Environment	N/A	N/A
Early Permian		
Paleogeographic Realms	-1.36	0.10
Lithostratigraphic Stages	-0.49	0.25
Depositional Environment	-2.26	0.03

gether and trend along a vertical compositional gradient. In contrast, burrowing deposit feeders and epifaunal grazers (i.e., mobile fauna) plot together and trend perpendicular to the sessile benthos.

This study concludes that taxonomic differences between brachiopods and bivalves segregate late Paleozoic faunal distributions, but, more importantly, the cause of this separation is due to a difference in the modes of life exhibited by the two groups. That is, late Paleozoic bivalves that have similar modes of life, particularly epifaunal bivalves, occur in regions otherwise dominated by epifaunal brachiopods. The majority of the differences between these late Paleozoic faunal patterns occur only when burrowing deposit feeders and epifaunal grazers appear in these samples.

ACKNOWLEDGMENTS

Funding for this research was provided by grants to NB from the Geological Society of America, the American Museum of Natural History, and the USC Department of Earth Sciences graduate student research fund, as well as a grant to DJB from the USC Women in Science and Engineering program (WISE). We thank A.G. Fischer, F.A. Corsetti, and C.M. Jamet for useful comments and discussion. We would like to thank M.E. Clapham for collecting abundance data from the Cooper and Grant (1972) collections. Lastly, we would like to thank Thomas Olszewski and Matthew Powell for their thoughtful and helpful reviews. This is Paleobiology Database publication #41.

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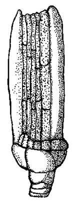
ACCEPTED JANUARY 6, 2006



SUPPLEMENTARY DATA 1—Sample localities, geology, age, and abundance. Abbreviations: Be1—Beus and Lane (1969); Mu5, Mu6, Mu7, Mu8—Mudge and Yochelson (1962); Ol1, Ol2, Ol3, Ol4—Olszewski (2000); We1, We2, We3, We4, We5—West (1970); NW—Northwestern.

Locality	Sample code	Primary lithology	Realm	Depositional environment	Regional stage	Abundance
Nevada, USA	Be1	Packstone	NW Continental Margin	Middle-carbonate shelf	Moscovian	237
Kansas, USA	Mu5	Limestone	Northwestern Midcontinent	Basin	Gzhelian	2558
Kansas, USA	Mu6	Shale	Northwestern Midcontinent	Basin	Gzhelian	696
Kansas, USA	Mu7	Limestone	Northwestern Midcontinent	Basin	Gzhelian	520
Kansas, USA	Mu8	Shale	Northwestern Midcontinent	Basin	Gzhelian	4097
Kansas, USA	Ol1	Limestone	Northwestern Midcontinent	Basin	Gzhelian	327
Kansas, USA	Ol2	Shale	Northwestern Midcontinent	Basin	Gzhelian	2041
Kansas, USA	Ol3	Packstone	Northwestern Midcontinent	Middle-carbonate shelf	Gzhelian	566
Kansas, USA	Ol4	Argillaceous wackestone	Northwestern Midcontinent	Inner-carbonate shelf	Gzhelian	542
Oklahoma, USA	We1	Shale	Northwestern Midcontinent	Basin	Moscovian	60046
Oklahoma, USA	We2	Shale	Northwestern Midcontinent	Basin	Moscovian	126596
Oklahoma, USA	We3	Shale	Northwestern Midcontinent	Basin	Moscovian	74762
Oklahoma, USA	We4	Shale	Northwestern Midcontinent	Basin	Moscovian	25287
Oklahoma, USA	We5	Shale	Northwestern Midcontinent	Basin	Moscovian	15664
Texas, USA	Co1	Wackestone	Northwestern Midcontinent	Basin	Artinskian	4380
Kanchanaburi, Thailand	Gr1	Argillaceous Limestone	Southeastern Tethys	Inner-carbonate shelf	Artinskian	3444
Kanchanaburi, Thailand	Gr2	Limestone	Southeastern Tethys	Basin	Artinskian	1915
Kanchanaburi, Thailand	Gr3	Limestone	Southeastern Tethys	Middle-carbonate shelf	Artinskian	13403
Kanchanaburi, Thailand	Gr5	Limestone	Southeastern Tethys	Middle-carbonate shelf	Artinskian	512
Merida, Venezuela	Ho1	Wackestone	Northwestern Midcontinent	Basin	Artinskian	398
New Mexico, USA	Ku2	Argillaceous shale	Northwestern Midcontinent	Inner-carbonate shelf	Sakmarian	1360
Kansas, USA	Mu1	Limestone	Northwestern Midcontinent	Middle-carbonate shelf	Asselian	459
Kansas, USA	Mu2	Shale	Northwestern Midcontinent	Basin	Asselian	1816
Kansas, USA	Mu4	Siltstone	Northwestern Midcontinent	Basin	Asselian	903
Queensland, Australia	Wa3	Sandstone	Southeastern Tethys	Inner-carbonate shelf	Artinskian	578
Nevada/Utah, USA	Ya1	Limestone	NW Continental Margin	Middle-carbonate shelf	Artinskian	260
Nevada/Utah, USA	Ya2	Calcareous shale	NW Continental Margin	Inner-carbonate shelf	Artinskian	2262
Nevada/Utah, USA	Ya3	Argillaceous Wackestone	NW Continental Margin	Inner-carbonate shelf	Artinskian	15091
Nevada/Utah, USA	Ya4	Wackestone	NW Continental Margin	Inner-carbonate shelf	Artinskian	5601

SUPPLEMENTARY DATA 2—Specimen information for the Pennsylvanian; abbreviations: Bur Dep—burrowing deposit feeders; Bur Susp—burrowing suspension feeder; Cem Susp—cementing suspension feeder; Epib Susp—epibyssate suspension feeder; Epif Graz—epifaunal grazer; Ped Susp—pedunculate suspension feeders.

Group	Order	Genus	Genus code	Ecological category
Brachiopod	Productida	*Buxtonia*	Bux	Rec Susp
Brachiopod	Productida	*Calliprotonia*	Cal	Rec Susp
Brachiopod	Productida	*Cancrinella*	Can	Rec Susp
Brachiopod	Productida	*Chonetes*	Cho	Rec Susp
Brachiopod	Spiriferida	*Choristites*	Chor	Ped Susp
Brachiopod	Athyridida	*Cleiothyridina*	Cle	Ped Susp
Brachiopod	Athyridida	*Composita*	Com	Ped Susp
Brachiopod	Craniida	*Crania*	Cra	Cem Susp
Brachiopod	Spiriferida	*Crurithyris*	Cru	Ped Susp
Brachiopod	Orthotetida	*Derbyia*	Der	Ped Susp
Brachiopod	Productida	*Dictyoclostus*	Dic	Rec Susp
Brachiopod	Productida	*Echinoconchus*	Ech	Rec Susp
Brachiopod	Orthida	*Enteletes*	Ent	Ped Susp
Brachiopod	Productida	*Fimbrinia*	Fim	Rec Susp
Brachiopod	Athyridida	*Hustedia*	Hus	Ped Susp
Brachiopod	Productida	*Hystriculina*	Hys	Rec Susp
Brachiopod	Productida	*Juresania*	Jur	Rec Susp
Brachiopod	Productida	*Kozlowskia*	Koz	Rec Susp
Brachiopod	Productida	*Kutorginella*	Kut	Rec Susp
Brachiopod	Productida	*Leptalosia*	Lep	Rec Susp
Brachiopod	Lingulida	*Lingula*	Lin	Bur Susp
Brachiopod	Productida	*Linoproductus*	Lino	Rec Susp
Brachiopod	Productida	*Lissochonetes*	Lis	Rec Susp
Brachiopod	Productida	*Marginifera*	Mar	Rec Susp
Brachiopod	Orthotetida	*Meekella*	Mee	Ped Susp
Brachiopod	Productida	*Mesolobus*	Mes	Rec Susp
Brachiopod	Productida	*Neochonetes*	Neo	Rec Susp
Brachiopod	Spiriferida	*Neospirifer*	Neos	Ped Susp
Brachiopod	Acrotretida	*Orbiculoidea*	Orb	Ped Susp
Brachiopod	Spiriferida	*Phricodothyris*	Phr	Ped Susp
Brachiopod	Spiriferinida	*Punctospirifer*	Pun	Ped Susp
Brachiopod	Productida	*Reticulatia*	Reti	Rec Susp
Brachiopod	Orthida	*Rhipidomella*	Rhi	Ped Susp
Brachiopod	Spiriferinida	*Spiriferellina*	Spir	Ped Susp
Brachiopod	Rhynchonellida	*Wellerella*	Wel	Ped Susp
Mollusc	Nuculoida	*Anthraconeilo*	Ant	Bur Dep
Mollusc	Pterioida	*Aviculopecten*	Avi	Epib Susp
Mollusc	Mytiloida	*Aviculopinna*	Avip	End Susp
Mollusc	Bellerophontida	*Bellerophon*	Bel	Epif graz
Mollusc	Pholadomyoida	*Edmondia*	Edm	Bur Susp
Mollusc	Bellerophontida	*Euphemites*	Eup	Epif graz
Mollusc	Murchisoniina	*Girtyspira*	Gir	Epif graz
Mollusc	Archaeogastropoda	*Glabrocingulum*	Gla	Epif graz
Mollusc	Murchisoniina	*Ianthinopsis*	Ian	Epif graz
Mollusc	Bellerophontida	*Knightites*	Kni	Epif graz
Mollusc	Murchisoniina	*Meekospira*	Meek	Epif graz
Mollusc	Pterioida	*Myalina*	Mya	Epib Susp
Mollusc	Archaeogastropoda	*Naticopsis*	Nat	Epif graz
Mollusc	Nuculoida	*Nuculopsis*	Nucu	Bur Dep
Mollusc	Nuculoida	*Paleyoldia*	Pal	Bur Dep
Mollusc	Pholadomyoida	*Permophorus*	Per	Bur Susp
Mollusc	Archaeogastropoda	*Phymatopleura*	Phy	Epif graz
Mollusc	Scaphopoda	*Plagioglypta*	Plag	Bur Dep
Mollusc	Nuculoida	*Polidevcia*	Pol	Bur Dep
Mollusc	Mytiloida	*Promytilus*	Pro	Epib Susp
Mollusc	Pterioida	*Pseudomonotis*	Pse	Cem Susp
Mollusc	Trigonioida	*Schizodus*	Sch	Bur Susp
Mollusc	Pterioida	*Septimyalina*	Sep	Epib Susp
Mollusc	Archaeogastropoda	*Trepospira*	Tre	Epif graz
Mollusc	Pholadomyoida	*Wilkingia*	Wil	Bur Susp

SUPPLEMENTARY DATA 3—Specimen information for the Early Permian. Abbreviations given in Appendix 2.

Group	Order	Genus	Genus code	Ecological category
Brachiopod	Orthida	*Acosarina*	Aco	Ped susp
Brachiopod	Productida	*Anemonaria*	Ane	Rec susp
Brachiopod	Rhynchonellida	*Antronaria*	Antr	Ped susp
Brachiopod	Productida	*Bibatiola*	Bib	Rec susp
Brachiopod	Productida	*Bilotina*	Bil	Rec susp
Brachiopod	Productida	*Celebetes*	Cel	Rec susp
Brachiopod	Productida	*Chonetes*	Cho	Rec susp
Brachiopod	Productida	*Chonetinella*	Chot	Rec susp
Brachiopod	Athyridida	*Cleiothyridina*	Cle	Ped susp
Brachiopod	Athyridida	*Composita*	Com	Ped susp
Brachiopod	Productida	*Comuquia*	Comq	Rec susp
Brachiopod	Productida	*Costellarina*	Cost	Rec susp
Brachiopod	Spiriferida	*Cruricella*	Crur	Ped susp
Brachiopod	Spiriferida	*Crurithyris*	Cru	Ped susp
Brachiopod	Productida	*Demonedys*	Dem	Rec susp
Brachiopod	Orthotetida	*Derbyia*	Der	Ped susp
Brachiopod	Productida	*Dictyoclostus*	Dic	Rec susp
Brachiopod	Orthotetida	*Diplanus*	Dip	Ped susp
Brachiopod	Athyridida	*Hustedia*	Hus	Ped susp
Brachiopod	Productida	*Incisius*	Inc	Rec susp
Brachiopod	Productida	*Juresania*	Jur	Rec susp
Brachiopod	Productida	*Kozlowskia*	Koz	Rec susp
Brachiopod	Productida	*Marginifera*	Mar	Rec susp
Brachiopod	Spiriferida	*Martiniopsis*	Mart	Ped susp
Brachiopod	Orthotetida	*Meekella*	Mee	Ped susp
Brachiopod	Spiriferida	*Neospirifer*	Neos	Ped susp
Brachiopod	Terebratulida	*Notothyris*	Noto	Ped susp
Brachiopod	Productida	*Oncosarina*	Onc	Rec susp
Brachiopod	Spiriferida	*Orbicoelia*	Orbc	Ped susp
Brachiopod	Orthida	*Orthotichia*	Ort	Ped susp
Brachiopod	Acrotretida	*Orbiculoidea*	Orb	Ped Susp
Brachiopod	Spiriferida	*Permophricodothyris*	Perp	Ped susp
Brachiopod	Orthida	*Rhipidomella*	Rhi	Ped susp
Brachiopod	Productida	*Rugaria*	Rug	Rec susp
Brachiopod	Spiriferinida	*Spiriferellina*	Spir	Ped susp
Brachiopod	Productida	*Squamaria*	Squ	Rec susp
Brachiopod	Orthotetida	*Streptorhynchus*	Str	Ped susp
Brachiopod	Productida	*Striochonetes*	Stri	Rec susp
Brachiopod	Productida	*Terrakea*	Terr	Rec susp
Brachiopod	Spiriferida	*Tomiopsis*	Tom	Ped susp
Brachiopod	Productida	*Urushtenia*	Uru	Rec susp
Brachiopod	Productida	*Waagenites*	Waa	Rec susp
Brachiopod	Rhynchonellida	*Wellerella*	Wel	Ped susp
Mollusc	Euomphalida	*Amphiscapha*	Amph	Epif graz
Mollusc	Euomphalida	*Anomphalus*	Anom	Epif graz
Mollusc	Archaeogastropoda	*Apachella*	Apa	Epif graz
Mollusc	Veneroida	*Astartella*	Ast	Bur susp
Mollusc	Pterioida	*Aviculopecten*	Avi	Epib susp
Mollusc	Mytiloida	*Aviculopinna*	Avip	End susp
Mollusc	Pterioida	*Bakevellia*	Bak	Epib susp
Mollusc	Bellerophontida	*Bellerophon*	Bel	Epif graz
Mollusc	Pterioida	*Calcicanicularia*	Calc	Epib susp
Mollusc	Euomphalida	*Euomphalus*	Euo	Epif graz
Mollusc	Bellerophontida	*Euphemitopsis*	Euph	Epif graz
Mollusc	Archaeogastropoda	*Glabrocingulum*	Gla	Epif graz
Mollusc	Nuculoida	*Glyptoleda*	Gly	Bur dep
Mollusc	Archaeogastropoda	*Glyptospira*	Glys	Epif graz
Mollusc	Archaeogastropoda	*Goniasma*	Gon	Epif graz
Mollusc	Euomphalida	*Leptomphalus*	Lepm	Epif graz
Mollusc	Murchisoniina	*Meekospira*	Meek	Epif graz
Mollusc	Nuculoida	*Nuculavus*	Nucl	Bur dep
Mollusc	Euomphalida	*Omphalotrochus*	Omp	Epif graz
Mollusc	Pholadomyoida	*Permophorus*	Perm	Bur susp
Mollusc	Archaeogastropoda	*Platyteichum*	Pla	Epif graz
Mollusc	Archaeogastropoda	*Platyworthenia*	Plat	Epif graz
Mollusc	Nuculoida	*Polidevcia*	Pol	Bur dep
Mollusc	Pterioida	*Pseudomonotis*	Pse	Cem susp
Mollusc	Trigonioida	*Schizodus*	Sch	Bur susp
Mollusc	Pterioida	*Septimyalina*	Sep	Epib susp
Mollusc	Bellerophontida	*Warthia*	War	Epif graz
Mollusc	Pholadomyoida	*Wilkingia*	Wil	Bur susp
Mollusc	Archaeogastropoda	*Yunnania*	Yun	Epif graz