

# Comparative Taxonomic Richness and Abundance of Late Ordovician Gastropods and Bivalves in Mollusc-rich Strata of the Cincinnati Arch

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*Using a field analysis of Upper Ordovician mollusc-rich faunas of the Cincinnati Arch, this study tests whether the large-scale patterns of Ordovician gastropods and bivalves observed in a companion study are maintained at the finer scales of individual strata and localities, and when utilizing abundance data in addition to taxonomic richness. Non-metric multidimensional scaling and several statistical analyses show that the taxonomic richness and abundance of these classes within samples were significantly negatively correlated, such that bivalve-rich settings were only sparsely inhabited by gastropods and vice versa. There also were important environmental differences between these classes. Gastropods were most dominant in shallow, carbonate-rich, and generally low-turbidity settings. Gastropods also occurred in restricted lagoons, where bivalves were only minor elements. In contrast, bivalves were most dominant in deep subtidal, siliciclastic shales with high levels of turbidity. Both in terms of abundance and taxonomic richness, these results strongly support those observed at the larger scales of paleocontinents and the globe. Taken together, these results argue that, despite similar taxonomical diversification patterns of these classes at the global scale and heterogeneous patterns among paleocontinents and among regions within Laurentia, gastropods and bivalves had quite different, yet unchanging, environmental distributions throughout the Ordovician, and that these classes did not co-occur to a significant degree, either in terms of taxonomic richness or abundance.*

## INTRODUCTION

The advantages of taxonomic data in paleontology are self-evident, whether for documenting first and last stratigraphic occurrences of taxonomic lineages (Sepkoski, 1984; Niklas et al., 1983; Benton, 1985), or as faunal lists detailing the taxonomic richness of a particular stratigraphic unit within a geographically confined region (Miller and Foote, 1996; Miller, 1997; Alroy et al., 2001). Patterns in such data often are used to infer particular ecological processes, whether involving environmental preference (Bretsky, 1969; Bottjer and Jablonski, 1988), competition (Van Valen, 1973; Gould and Calloway, 1980; Thayer, 1983; Rosenzweig and McCord, 1991; Vermeij, 1987), resource utilization (Bambach, 1983, 1985), or mac-

roevolutionary rates (Sepkoski, 1978; Stanley, 1979; Raup and Sepkoski, 1984; Gilinsky, 1994; Foote, 2000). However, while such studies are essential for understanding the ecological underpinnings of evolution, they are limited by their large-scale observational framework. In other words, they cannot be used to test ecological causes of these patterns without using finer-scale data, particularly without using abundance data (see also Lidgard, 2002).

With the exception of terrestrial plant paleoecology where the use of abundance data is commonplace (Pfefferkorn and Thomson, 1982; DiMichele et al., 1985; DiMichele and Wing, 1988; Lupia et al., 1999), use of abundance data in other branches of paleontology historically has been limited. Because of this deficiency, many paleontological hypotheses based on taxonomic richness have assumed implicitly that abundance patterns mirror taxonomic richness in local settings (but see Sepkoski and Miller, 1985; Miller, 1989). However, it is critical that paleontologists test these assumptions, and there are good reasons to be skeptical. For example, Wing et al. (1993) demonstrated that, while several Late Cretaceous terrestrial associations were strongly dominated in terms of taxonomic richness by angiosperms, these plants were only minor components of the preserved fossils when abundance was considered. Lupia et al. (1999) went a step further to demonstrate with richness and abundance data that the ascension of angiosperms during the Cretaceous was accompanied by a major, and presumably competitively driven, decline in free-sporing plants; in contrast, the gymnosperm biota underwent only minor changes, despite traditional expectations guided by richness-only data. Among marine paleontologists, McKinney et al. (1998) showed that, despite only minor changes in taxonomic richness of cheilostome bryozoans following the K/T mass extinction, there was a long-term decline in the percent skeletal mass of cheilostomes in shelf settings over the same interval.

Thus, there are good reasons to question whether taxonomic richness data alone are adequate to identify and explain ecological processes in the fossil record. At the same time, there are ample indications that fossil assemblages can maintain reasonable proxies of the relative abundances of readily preservable taxa, based primarily on analyses of macroscopic molluscan associations (Miller, 1988; Kidwell and Bosence, 1991; Kidwell and Flessa, 1996; Kidwell, 2001). In fact, the preservation of relative abundance has enabled recognition of biologically meaningful faunal

gradients in fossil associations that show similar patterns to those found in living communities (Ziegler, 1965; Whitaker, 1970; Springer and Bambach, 1985; Miller, 1988; Patzkowsky, 1995; Olszewski and Patzkowsky, 2001; Olszewski and Kidwell, 2002).

In a companion study, Novack-Gottshall and Miller (2003) used a literature-derived database of Ordovician fossil occurrences of gastropods and bivalves to determine whether these two molluscan classes, which were prominent members of Sepkoski's (1981) Modern Evolutionary Fauna, displayed similar environmental and geographic diversity dynamics during the Ordovician Radiation at scales ranging from global to regional. At a global scale, both classes displayed similar diversity trajectories. However, at finer scales, their dynamics were more disparate. Bivalves were taxonomically richest in high-latitude paleocontinents dominated by siliciclastic sedimentation, whereas gastropods were taxonomically richest in carbonate-rich, equatorial paleocontinents. Similar patterns also were expressed among regions within Laurentia, with statistically distinct diversity trajectories within regions, in which bivalves dominated deeper, more siliciclastic-rich environments than gastropods.

The database for the companion study, however, did not include relative-abundance data for fossil occurrences because of its scarce documentation in the literature. Furthermore, the database was limited to comparisons at stratigraphic scales larger than individual horizons at a single locality. Thus, the conclusions were limited to patterns of taxonomic richness at scales that could mask important underlying ecological trends. In particular, it could not be determined whether abundance data yielded patterns contrasting with those observed from taxonomic richness. More importantly, in cases where bivalves and gastropods appeared to co-occur at the spatial and temporal resolution of the database, the nature of the data precluded determination whether they actually lived together in an individual assemblage at a given time.

Here, field data are utilized to evaluate the co-occurrence of gastropods and bivalves at the scale of individual strata in the type Cincinnatian (Upper Ordovician). The Cincinnatian Arch is well known for its distinctive, albeit confined, mollusc-dominated strata during this important interval in the diversification of bivalves and gastropods (Pojeta, 1971, 1979; Swadley, 1979; Frey, 1987; Miller, 1989; Dattilo, 1996). Given such representation by molluscs, and the results of a previous study (Novack-Gottshall and Miller, 2003), these strata permit a test of the aforementioned environmental preferences of both classes observed at broader temporal, geographic, and taxonomic scales. Although results demonstrate that both classes tend to co-occur to some extent, the use of abundance data amplifies the earlier conclusion (Novack-Gottshall and Miller, 2003) that these classes had distinct environmental distributions, both within individual Cincinnatian strata as well as throughout the world during the entire Ordovician. Ordovician gastropods were most diverse and abundant in strata representing shallower, more carbonate-rich facies than bivalves, which were ecologically dominant in offshore, siliciclastic-rich facies.

## GEOGRAPHIC, STRATIGRAPHIC, AND DEPOSITIONAL CONTEXT

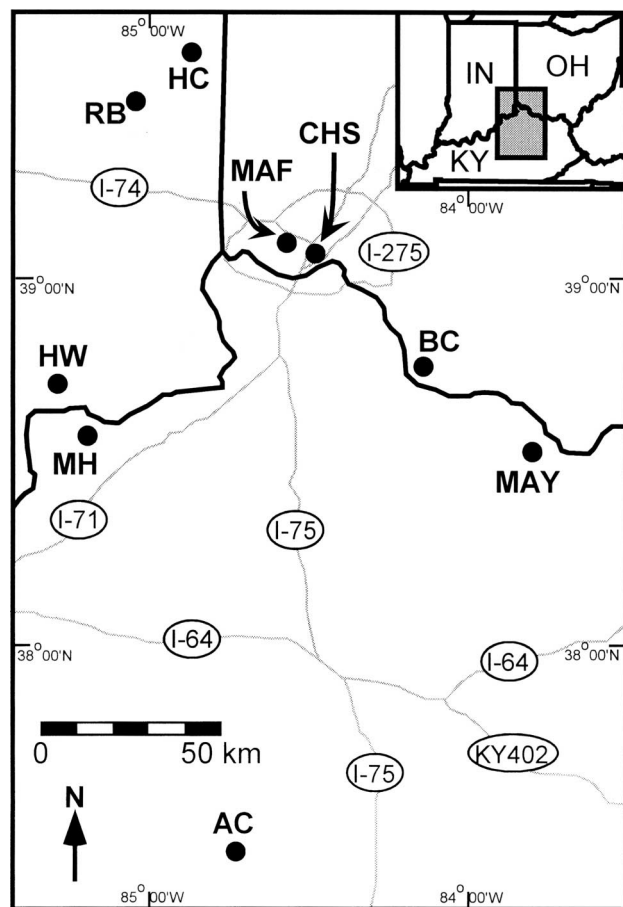
Sedimentation in the Cincinnatian Arch generally consists of mixed carbonate-siliciclastic lithologies in which fine-grained siliciclastics are interbedded with storm-influenced packstones, wackestones, and calcisiltites (Holland, 1993; Jennette and Pryor, 1993; Holland et al., 1997; Webber, 2002). Recent sequence stratigraphic work in the type Cincinnatian confirms that primary controls on sedimentation were eustatic sea-level changes and storm influence in an equatorial epeiric sea with occasional, large pulses of siliciclastic sediments from eastern Taconic sources (Holland, 1993; Dattilo, 1996; Holland and Patzkowsky, 1996; Holland et al., 1997; Webber, 2002). Because of this variability, there is an array of depositional environments in the region, ranging from peritidal and restricted dolomites and limestones, shoal coquinites, and shelf grainstones, to deeper-water packstones, shales, and mudstones, although shelf conditions predominated. In general, shallower-water lithologies are found to the southeast, the presumed upslope direction of a paleoramp (Holland, 1993; Cuffey, 1998; but see Miller et al., 2001) with a maximum depth of 25 to 50 m (Frey, 1987; Cuffey, 1998).

The macrofauna is composed primarily of brachiopods and bryozoans, with less abundant trilobites, molluscs, and echinoderms. Total molluscan fossil abundance in these strata is typically less than 10% throughout the region (Meyer et al., 1981; Goldman, 1993), but there are a variety of strata in which bivalves (Pojeta, 1971; Frey, 1987; Miller, 1989) and gastropods (Swadley, 1979; Frey, 1987; Wahlman, 1992; Dattilo, 1996) exceed 50% of the preserved fossil material. The use of abundance data to compare bivalves and gastropods in such settings is warranted from a taphonomic perspective because these classes share similar preservation potentials (Valentine, 1989; Palmqvist, 1991; Kidwell and Flessa, 1996; Foote and Sepkoski, 1999; Kidwell, 2001). Furthermore, mollusc-rich strata typically tend to be taphonomically autochthonous to parautochthonous (Frey, 1987; Schumacher and Shrake, 1997; Sumrall et al., 2001), although comparative taphonomic studies have not been conducted for all pertinent strata.

## SAMPLING AND ANALYTICAL PROCEDURES

### Field and Data Collection

Twenty-seven bulk samples were collected for this study from ten localities (Fig. 1; Appendix 1); these samples represent eight formations and five of the six stratigraphic sequences composing the type Cincinnatian (Fig. 2; Holland and Patzkowsky, 1996). While not every Cincinnatian formation was sampled, collections reflect the suite of different Cincinnatian facies that are locally mollusc rich. Table 1 details the lithology, inferred depositional environment, and inferred turbidity based on sequence stratigraphic interpretation (Holland, 1993, pers. comm.) for each sample. In most instances, bulk samples were collected and taken to the lab for censusing. Because claystones (locally called "butter shales") from the Waynesville Formation generally were too soft to be transported back to the lab for examination, they were censused in the field, with examples

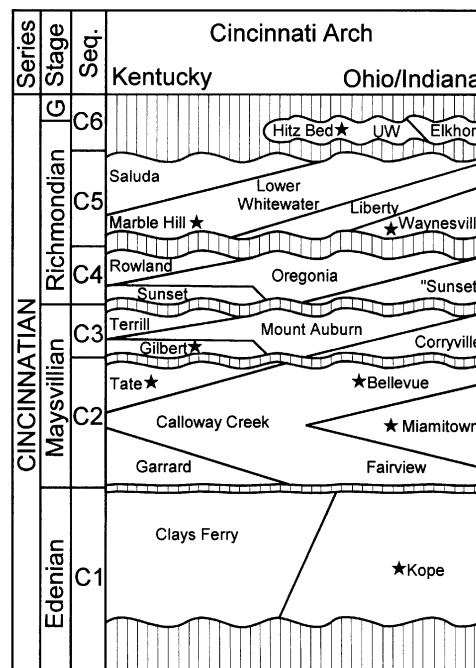


**FIGURE 1**—Location of type Cincinnatian samples. Abbreviations used in the text and formations sampled include: Bear Creek Quarry (BC; Kope Formation), Maysville (MAY; Bellevue Formation), Christ Hospital (CHS; Miamitown Shale), Mount Airy Forest (MAF; Miamitown Shale), Ashlock Cemetery (AC; Tate [AT] and Gilbert [AG] Formations), Hannah Creek (HC; Waynesville Formation), Russell Branch (RB; Waynesville Formation), Bedford (MH; Marble Hill Bed), and Madison (HW; Hitz Bed).

of all sampled species taken to the laboratory to confirm taxonomic identifications. Although formal standardized sampling protocols were not followed, the number of individuals preserved in each sample, the sample area or volume of the samples, and the time expended in collecting the samples were broadly similar. Analyses on the effect of rock area and volume on observed richness and abundance, available in Novack-Gottshall (1999), generally reinforce this conclusion.

All species in the collections were identified and counted, although the present study is limited to the gastropod and bivalve fractions (Appendix 2). Complete data on the entire fauna and additional paleoecological analyses are available in Novack-Gottshall (1999). Gastropod and bivalve taxa were identified to species level when possible using collections at the Cincinnati Museum of Natural History and descriptions in Pojeta (1966, 1971, 1979, 1997), Frey (1980, 1987), Davis (1992), Wahlman (1992), Feldmann (1996), and Wagner (1999). In some cases, only genus-level identification was possible.

Fossils were counted on all sides of limestone slabs and



**FIGURE 2**—Timescale for the type Cincinnatian. Stars represent formations sampled in this study. UW in the C6 depositional sequence designates the Upper Whitewater formation (Modified from Holland, 1993).

throughout mudstones and softer, wavy-bedded, and nodular limestones. Intact, articulated skeletons, casts and molds were counted individually. All fragmented, disarticulated, or indeterminate skeletons with identifiable parts (e.g., gastropod apices, bivalve left and right valves, etc.) were noted separately and the minimum number of individuals was used as a conservative estimate. Shells that lacked identifiable parts were counted by summing the total number of individual valves and halving that sum. To increase taxonomic accuracy and precision, examples of each fossil were separated as a reference standard. In two cases, when taxa were not identifiable to species level but were notably different from those collected previously, they were given descriptive names based on their morphology (i.e., “short, selenizionate lophospirid”). The data set used here includes 941 individuals within 38 species and 30 genera (Appendix 2).

#### Non-metric Multidimensional Scaling

R-mode ordination of the genus-level abundance data was conducted with non-metric multidimensional scaling (NMS) using PC-ORD version 4 (McCune and Mefford, 1999). As a non-parametric ordination method, NMS is appropriate for ecological studies for many reasons (Minchin, 1987): (1) it does not require a Gaussian assumption to a species response curve along environmental gradients; (2) it can accommodate multiple environmental gradients simultaneously, including those that are discontinuous, non-linear, or arbitrarily measured; (3) unlike detrended correspondence analysis (DCA), it is robust to variations in beta diversity, sampling inhomogeneities, and pattern noise along gradients; and (4) it does not suffer



**TABLE 1**—Lithology (sample and formation), depositional environment, and turbidity of samples used in study. Sample lithology is included, since it is occasionally different than the lithology of the overall formation. Criteria used to infer depositional environments and turbidity are included in text. Parentheses after the depositional environment list the chi-square depth categorization. Sample abbreviations are listed in Appendix 1 and caption for Figure 1.

Samples	Sample lithology	Formation lithology	Depositional environment	Turbidity
HW1	Pyritic wackestone	Irregularly bedded micrite/wackestone	Peritidal lagoon (Shallow)	Low
HW4	Wackestone			
MH1, MH2, MH3, MH4	Dolomitic grainstone/packstone	Massive, dolomitic grainstone	Tidal channel/bar complex (Shallow)	Low
RB1, RB2, RB3, HC1, HC2	Pyritic claystone	Terrigenous claystones interbedded with packstone/wackestone	Deep subtidal (Deep)	High
AG4, AG11, AG15	Irregularly bedded, dark blue-gray, nodular limestone	Gray, tabular, medium-bedded limestone interbedded with silty shale	Peritidal lagoon (Shallow)	Low
AT2, ATB	Irregularly bedded wackestone/mudstone	Glauconitic, crinkly, muddy shale interbedded with nodular and irregularly bedded wackestone/mudstone	Intertidal to shallow subtidal (Shallow)	High
MAY1, MAY2, MAY3	Packstone	Irregularly bedded, fossiliferous packstone and calcarenite	Shoreface (Shallow)	High
CHS1, CHS7, CHS32	Packstone/wackestone	Shale interbedded with packstone/wackestone	Deep subtidal (Deep)	High
MAF1, MAF2, BC3, BC5	Packstone Wackestone/packstone	Shale and mudstone interbedded with lenticular to thin-bedded wackestone/packstone	Deep subtidal (Deep)	High
BC7	Lenticular wackestone/mudstone			

from curvilinear distortion, such as the horseshoe or arch effects, and range truncation, which are found in other parametric ordination techniques (Minchin, 1987; Clarke, 1993). Thus, NMS is widely used for ecological data (Clarke, 1993).

Following the recommendations of methodological studies (Sepkoski, 1974; Faith et al., 1987; Shi, 1993; McCune and Mefford, 1999), the Sørensen dissimilarity coefficient was used here for its ability to maintain monotonic and linear relationships among variables; this property is particularly attractive when using NMS. For R-mode analyses, this coefficient, also known as the Bray-Curtis coefficient, is calculated as:

$$D_{ij} = 1 - \left[ 2 \times \sum \text{MIN}(x_{ij}, x_{hj}) / \left( \sum x_{ij} + \sum x_{hj} \right) \right] \quad (1)$$

where  $x_{ij}$  is the abundance of the  $i^{\text{th}}$  taxon in the  $j^{\text{th}}$  sample and  $x_{hj}$  is the abundance of the  $h^{\text{th}}$  taxon in the same sample. The  $\text{MIN}(x_{ij}, x_{hj})$  function selects the minimum of these two values. When two species share identical abun-

dances in the same sample, the coefficient equals zero; when two species are mutually exclusive, the coefficient equals one. This dissimilarity coefficient is used commonly in paleogeographical, paleoecological, and ecological studies (e.g., Whittaker, 1970; Springer and Bambach, 1985; Faith et al., 1987; Miller, 1989; Patzkowsky, 1995; Olszewski and Patzkowsky, 2001). Additional NMS parameters used in the analysis are listed in Table 2.

For the present analysis, the aim is to evaluate the co-occurrence of gastropods and bivalves and to understand what potential environmental causes account for this pattern. If these classes tend not to co-occur in similar abundances within the same samples, as previous analyses have implied (Novack-Gottshall and Miller, 2003), they should not group together in ordination space.

#### Taxonomic Richness and Abundance Analyses

Despite its value in discerning similarities among taxa and in interpreting environmental causes, NMS is not a statistical test of the correlation, or lack thereof, between these classes. Three statistical analyses were conducted to test this hypothesis more rigorously. The first, between-class analysis tested whether gastropod and bivalve occurrences were negatively correlated with each other within individual samples. This analysis was done using both the one-tailed Pearson product-moment correlation coefficient and a bootstrap correlation (see below for details), and separately for both species richness and numerical abundance data. As in the subsequent statistical test, the abundance and diversity variables were log-transformed prior to analysis after adding 1.0 to allow log-transformation of a value of zero.

A second, within-class analysis tested whether taxonomic richness and abundance data are positively corre-

**TABLE 2**—Input parameters and output results for the non-metric multidimensional scaling analysis.

NMS parameter	Setting
Input settings:	
Distance measure	Sørensen
Maximum number of iterations	400
Stability criterion	0.00001
Stability iterations	15
Search algorithm	Global
Output results:	
Dimensionality	3
Final stress	19.01%

lated measures of ecological dominance for each sample. When calculating this relationship, samples lacking the respective class were excluded from analysis to prevent artifactual correlations that could occur when a sample has no individuals, and hence no species, of that class. For example, since bivalves were absent from samples MAY2 and MAY3, they were not included in this bivalve analysis. A correlation coefficient ( $r$ ) was calculated for this set of points, using the product-moment formula (Sokal and Rohlf, 1973):

$$r = \sum xy / (\sqrt{\sum x^2} \times \sqrt{\sum y^2}) \quad (2)$$

Typically,  $r$  ranges from  $-1$  indicating a perfect, negative correlation to  $+1$  indicating a perfect, positive correlation, with  $0$  indicating no relationship between the variables. However, in this case, where there is an inherent relationship between diversity and abundance, it is not appropriate to test against the null hypothesis of  $r=0$ . For example, it is not possible to observe three species when two individuals are sampled. To rectify this constraint, a bootstrap was conducted to determine the correct null hypothesis from which to compare the correlation coefficient through the observed data (Diaconis and Efron, 1983). The bootstrap program, available on request, resampled, with replacement, each species richness and abundance variable independently 27 times, corresponding to the number of samples in the original data set, in essence creating a new data set. To incorporate the dependence of diversity on abundance, each resampled richness value was required to be greater than or equal to the corresponding resampled abundance value. A null estimate of  $r$  was then calculated on this resampled data set using equation 2, and the process was repeated 10,000 times. The  $r$  observed from the actual data was then compared to this null distribution to determine the significance of the actual correlation.

A third, within-class analysis was conducted to test whether the environmental factors implied by the NMS ordination were associated with the actual class occurrences in each sample. Such testing is especially important when using NMS since the ordination axes are not required to be orthogonal to, and thus independent of, one another, and since it is not possible to determine which axis represents the dominant gradient in the ordination (McCune and Mefford, 1999). In order to determine this association, each sample was assigned to discrete depth, sedimentological, and turbidity categories. Samples from peritidal lagoons, shoreface, shallow subtidal, and offshore bar facies were included in the shallow category; deep subtidal facies were included in the deep category. Sedimentological categories followed this same division, with carbonate-rich facies, although of various textures and grain sizes, confined to the shallow category, and with mixed-siliciclastic-carbonate facies limited to the deeper ones. There are no purely siliciclastic facies in the type Cincinnati, but siliciclastics throughout most of the region are generally fine-grained, and siliciclastic-rich strata are indicative of deeper-water deposition relative to most carbonates (Holland, 1993; Cuffey, 1998). To allow for this influence of siliciclastic influx independently of depth, turbidity also was included. Low turbidity, or "clean," was assigned to those samples occurring in early transgressive

systems tracts when terrigenous-poor, tropical carbonates dominated. High turbidity was assigned for the remaining samples that experienced significant siliciclastic influx (Holland, 1993, pers. comm.; Holland and Patzkowsky, 1996). These designations are listed in Table 1.

Because the chi-square statistic was developed for dealing with such discrete, enumerative data (Sokal and Rohlf, 1973), this test is well-suited for comparing taxonomic richness and abundance along shallow-to-deep gradients or among other environmental categories when the absolute, quantitative environmental parameters are not precisely known. Furthermore, chi-square can be used to test single-factor cases (such as depth alone) as well as multi-factor comparisons where several environmental factors are involved, such as depth, turbidity, and sedimentology. To interpret the results and to prevent some species from being counted more than once, it was necessary to restrict analyses to species confined to a single facies. For example, if three species occurred in both shallow and deep depths, it would violate statistical assumptions of independence to count them twice. More importantly, if there were three additional species that occurred only in shallow depths and no species restricted to deep ones, it could be misleading to conclude that there is no preference for this class for shallow depths. Such restrictions allow for the species to be independent of one another, and for the important differences to be diagnosed dependably.

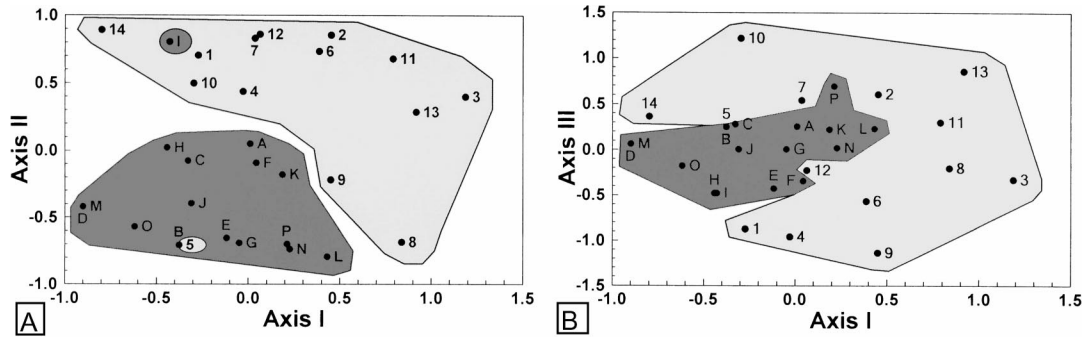
## RESULTS AND DISCUSSION

### Non-metric Multidimensional Scaling

In the NMS figures (Figs. 3–4) and the description that follows, gastropods are designated with numerals and bivalves with capital letters. Additional analyses, including detrended correspondence analysis, reciprocal averaging, and cluster analysis resulted in comparable results to those shown here; details of a cluster analysis, as well as additional paleoecological analyses of the non-molluscan fauna are available in Novack-Gottshall (1999).

NMS axis I (Fig. 3A, B) reflects the biostratigraphic occurrences of these classes, with time generally proceeding from positive to negative values. *Cyclonema* (3), *Sinuities* (11), and *Tetranota* (13) in the high, positive region are dominant Kope Formation gastropods, the oldest-sampled units; additional pre-Richmondian genera, such as *Clathrospira* (2) and *Lophospira* (6) are found with values approximating 0.5. Genera with values generally less than 0.5 represent younger, Richmondian samples. This axis is not a straightforward time gradient, with several species not occurring precisely in temporal order. For example, one might expect *Caritodens* (C) and *Modiolopsis* (K) to occur in more positive locations, reflecting their presence in pre-Richmondian strata; however, their more negative location is largely attributable to their much higher abundance in younger, Richmondian samples. Thus, this axis reflects not only the stratigraphic co-occurrence of genera, but also the interval during which a particular genus was most abundant; in other words, it results from both abundance and taxonomic richness patterns.

Axis II is interpretable as either a depth or lithological gradient (Fig. 3A). Genera in high, positive positions, including *Clathrospira* (2), *Sphenospira* (12), lophospirids



**FIGURE 3**—Two-dimensional graphical results from non-metric multidimensional scaling of genera. Bivalve genera are enclosed in darker shading and designated by letters: A=*Ambonychia*, B=*Anomalodonta*, C=*Caritodens*, D=*Ctenodonta*, E=*Cuneameya*, F=*Cycloconcha*, G=*Cymatonota*, H=*Deceptrix*, I=*Ischyrodonta*, J=*Lyrodessa*, K=*Modiolopsis*, L=*Opisthoptera*, M=*Palaeoconcha*, N=*Pholadomorpha*, O=*Psilooncha*, and P=*Rhytmya*. Gastropod genera are enclosed in lighter shading and designated with numbers: 1=*Bucania*, 2=*Clathrospira*, 3=*Cyclonema*, 4=*Holopea?*, 5=*Liospira*, 6=*Lophospira*, 7=*Paupospira*, 8=*Phragmolites*, 9=*Raphistomina*, 10=*Salpingostoma*, 11=*Sinuities*, 12=*Sphenosphaera*, 13=*Tetranota*, 14=*Tropidodiscus*. (A) Axis 2 versus axis 1. (B) Axis 3 versus axis 1.

(6 and 7), *Tropidodiscus* (14), and the bivalve *Ischyrodonta* (I), are all found in the shallowest and most carbonate-rich samples. In contrast, genera in high, negative regions, including *Liospira* (5) and *Phragmolites* (8) and numerous bivalves, are most abundant in deeper, more siliciclastic-rich samples. Accordingly, genera in the middle of this range, including *Ambonychia* (A), *Caritodens* (C), *Cycloconcha* (F), and *Modiolopsis* (K), are found in both facies. However, this correspondence between shallow carbonates and deep siliciclastics prevents determining whether the gradient is predominantly a depth or sedimentological one. Regardless of the interpretation, the importance of the gradient is strengthened by its persistence throughout the type Cincinnati. In other words, this gradient is essentially independent of axis I, the biostratigraphic succession of genera.

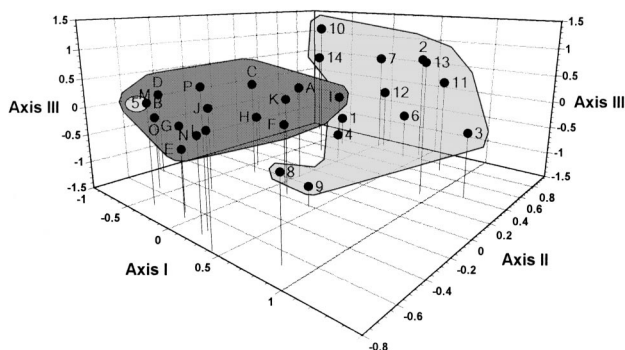
Axis III reflects salinity or a related gradient of environmental restriction (Fig. 3B), with high, negative regions composed mainly of genera, such as *Bucania* (1), *Holopea?* (4), and *Raphistomina* (9), that are dominant in late Cincinnati peritidal lagoons. The most negative bivalves along this axis, *Deceptrix* (H), *Ischyrodonta* (I), and to a lesser extent *Cuneameya* (E) and *Cycloconcha* (F), also are found in these lagoonal facies, although the latter two genera also are found in more open-marine settings. The gastropod *Salpingostoma* (10), found in a high, positive loca-

tion, is also found in lagoonal settings; however, it was only sampled in the older Gilbert Formation and thus does not co-occur with the previous genera. Thus, axis III is consistent with a salinity gradient, from hypersaline facies in both high, positive and high, negative values, with normal marine conditions in the middle. Although such a divided gradient is atypical in most ordination analyses, it is acceptable in NMS where non-linear, arbitrary, and compound gradients can be accommodated by the non-parametric ranking algorithm (Clarke, 1993).

Although bivalves are neither especially diverse nor abundant in pre-Richmondian samples of the Cincinnati Arch, gastropods and bivalves are not segregated along axis I, overlapping significantly at Richmondian values less than 0.5. This invasion of bivalves during the Richmondian also coincides with a recurrence of a typically tropical, carbonate-rich fauna including brachiopods and rugose corals (Patzkowsky and Holland, 1996, 1999). However, unlike these taxa that prospered in more carbonate-rich settings, bivalves were largely confined to the fine-grained siliciclastic mudstones and shales that resulted from the Taconic Orogeny (Novack-Gottshall and Miller, 2003).

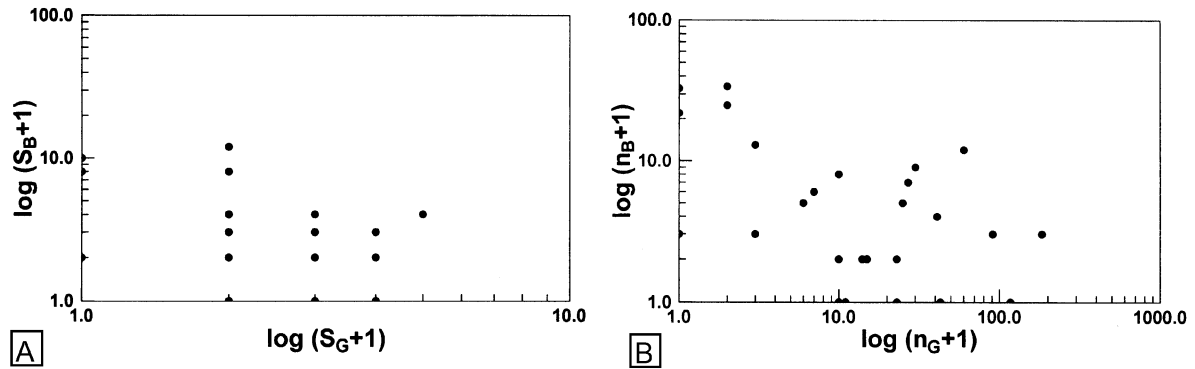
There is much more segregation of these classes along axis II, with most gastropods occurring at positive values and bivalves occurring at negative ones. As noted, this segregation is largely due to a preference of gastropods for shallow, carbonate-rich settings and bivalves for deeper, siliciclastic-rich settings. This pattern, evaluated further below, corroborates the overall environmental distributions of these classes observed at global, paleocontinental, and regional scales throughout the Ordovician (Novack-Gottshall and Miller, 2003). While gastropods occur at both positive and negative high values along axis III, bivalves and gastropods overlap throughout the region defined by low values. Thus, while gastropods are more frequently limited to hypersaline, restricted environments than are bivalves, both classes are most dominant in open marine settings. In contrast, when bivalves occur in such restricted settings (e.g., *Ambonychia* (A) and *Deceptrix* (H); Appendix 2), they tend to be more abundant in open marine settings.

Together, all three NMS ordination axes (Fig. 4) dem-



**FIGURE 4**—Three-dimensional graphical results from non-metric multidimensional scaling of genera. Labels and shading are the same as in Figure 3.





**FIGURE 5**—Log-log plots of gastropod versus bivalve occurrence in 27 samples. A value of one was added to samples prior to log-transformation to plot samples lacking either bivalves or gastropods. Several data points overlap. Using Pearson's product-moment correlation coefficient, both richness and abundance were significantly negatively correlated ( $r = -0.361$ ,  $p < 0.050$  for 5A, and  $r = -0.557$ ,  $p < 0.005$ , for 5B). Similar significance was found using one-tailed bootstrap correlation coefficient (both with  $p < 0.0001$ ). (A) Species richness (S). (B) Numerical abundance (n).

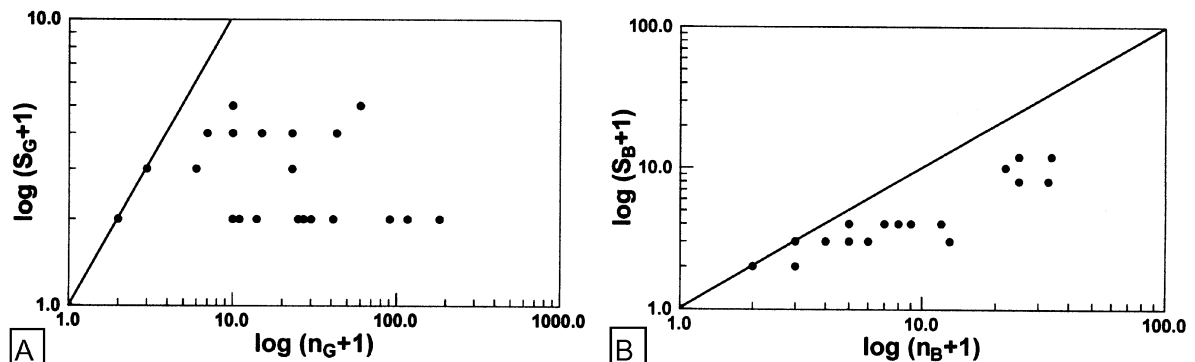
onstrate clearly the largely segregated occurrence of gastropods and bivalves during the type Cincinnati. Gastropods generally group in positive regions of axes I and II and throughout axis III, and bivalves group in negative and low positive regions of axes I and II, and in the central region of axis III. Of the 30 genera, only two, the gastropod *Liospira* (6) and the bivalve *Ischyrodonta* (1), group with the unrelated class. These exceptions are consistent with observations in the field. Although uncommon, *Liospira* is primarily limited to deep subtidal shales and mudstones (Appendix 2; Frey, 1987) in the type Cincinnati, the same setting in which bivalves dominate. *Ischyrodonta*, in contrast, occurs in the type Cincinnati mostly in shallow subtidal and lagoonal, carbonate-rich settings (Appendix 2; Pojeta, 1971; Frey, 1987; Davis, 1992), where gastropods are the dominant mollusc. That these two genera are the only major exceptions to the analytical segregation of bivalves and gastropods is all the more notable given that 19 of the 27 samples included both classes. Abundance data are therefore an essential component in evaluating

the paleoecological distributions of these classes at this regional scale.

#### Taxonomic Richness and Abundance

Figure 5 more directly compares whether gastropods and bivalves are occurring in similar richness and abundance in the 27 samples. Using Pearson's correlation coefficient, both species richness (Fig. 5A) and numerical abundance (Fig. 5B) were significantly negatively correlated for these two groups; these relationships were even more significant using the bootstrap correlation analysis. This confirms the results of NMS: type Cincinnati gastropods and bivalves tended to dominate different samples, both in species richness and abundance. A negative correlation also was exhibited when data from the same formations and same localities were pooled, and with the non-parametric Spearman's rank correlation coefficient.

Figure 6 depicts whether species richness and abundance are correlated measures of ecological dominance for



**FIGURE 6**—Log-log plots of numerical abundance (n) versus species richness (S) in 27 samples. A value of one was added to samples prior to log-transformation to prevent artifactual correlations. However, samples lacking the relevant class were not included in statistical analyses to prevent artifactual correlations. Several data points overlap. The 1:1 line denotes the constraint region above which observations are not possible. (A) Gastropods. Using the bootstrap correlation analysis ( $r_s = 0.172$ ), the measures of gastropod dominance were not significantly correlated ( $n = 24$ ,  $r = -0.035$ ,  $p < 0.855$ ); when the often-dominant *Paupospira* "bowdeni" was removed from analysis, there was a significant, positive correlation ( $n = 15$ ,  $r = 0.713$ ,  $p < 0.0149$ ) against  $r_s = 0.281$ . (B) Bivalves. The measures of bivalve dominance were significantly positively correlated ( $n = 22$ ,  $r = 0.927$ ,  $p < 0.0001$ ) against the bootstrapped null  $r_s = 0.381$ . This significance is maintained when the five very bivalve-rich Waynesville Formation samples are excluded ( $n = 17$ ,  $r = 0.818$ ,  $p < 0.0318$ ) against the bootstrapped null  $r_s = -0.021$ .

**TABLE 3**—Chi-square analyses of species richness (S) and abundance (n) data for species that are confined to a single environmental facies. The contingency table is denoted by observed and expected occurrences, denoted by subscript. Note that there were no samples representing both deep and low turbidity, or clean, facies. Italicized factors denote the factor(s) that is significantly correlated with ecological dominance in each class. (A) Depth/lithology comparison; the depth/lithology comparisons are only presented with the depth categories; deep depths correspond with mixed-siliciclastic-carbonate facies while shallow depths correspond with predominantly carbonate facies. (B) Turbidity comparison; (C) two-factor, depth/lithology and turbidity comparison.

	$S_{obs}$ ( $S_{exp}$ )	Statistic	$n_{obs}$ ( $n_{exp}$ )	Statistic
<b>A. Depth/lithology <math>\chi^2</math>:</b>				
Gastropods				
<i>Shallow</i>	10 (8)	$\chi^2 = 1.000$	86 (51.5)	$\chi^2 = 46.223$
Deep	6 (8)	(N.S.: $p > 0.05$ )	17 (51.5)	( $p < 0.005$ )
Bivalves				
Shallow	4 (7.5)	$\chi^2 = 3.267$	12 (32.5)	$\chi^2 = 25.862$
<i>Deep</i>	11 (7.5)	(N.S.: $p < 0.10$ )	53 (32.5)	( $p < 0.005$ )
<b>B. Turbidity <math>\chi^2</math>:</b>				
Gastropods				
Clean	7 (8.5)	$\chi^2 = 0.529$	63 (61)	$\chi^2 = 0.131$
Turbid	10 (8.5)	(N.S.: $p > 0.05$ )	59 (61)	(N.S.: $p > 0.05$ )
Bivalves				
Clean	3 (7.5)	$\chi^2 = 5.400$	11 (32.5)	$\chi^2 = 28.446$
<i>Turbid</i>	12 (7.5)	( $p < 0.025$ )	54 (32.5)	( $p < 0.005$ )
<b>C. Two-factor, depth/lithology and turbidity <math>\chi^2</math>:</b>				
Gastropods				
<i>Shallow &amp; Clean</i>	7 (5.3)	$\chi^2 = 1.625$	63 (34.3)	$\chi^2 = 36.427$
Shallow & Turbid	3 (5.3)		23 (34.3)	
Deep & Turbid	6 (5.3)	(N.S.: $p > 0.05$ )	17 (34.3)	( $p < 0.005$ )
Bivalves				
Shallow & Clean	3 (5)	$\chi^2 = 11.200$	11 (21.7)	$\chi^2 = 70.277$
Shallow & Turbid	1 (5)		1 (21.7)	
<i>Deep &amp; Turbid</i>	11 (5)	( $p < 0.005$ )	53 (21.7)	( $p < 0.005$ )

gastropods (Fig. 6A) and bivalves (Fig. 6B) within samples. Due to the inherent constraint of richness on abundance, bootstrap correlation analysis was the only suitable method to ascertain the significance of the relationship. The measures of gastropod dominance were not significantly correlated. This lack of correlation is primarily attributable to *Paupospira* “*bowdeni*” (Wagner, 1999), which often occurs in vast numbers as the only gastropod (Appendix 2). Although this is potentially attributable to post-mortem sorting in the offshore channel/bar complex of the Marble Hill bed (Swadley, 1979; Morton et al., 1996), such taphonomic processes are unlikely in other Cincinnati strata, such as the deep subtidal Miami Shale and the shallow subtidal Bellevue Formation, in which *P. “bowdeni”* also occurs in great numbers. Similar dominance of this gastropod in a variety of environmental settings is observed in contemporaneous and Middle Ordovician strata of the Nashville Dome (Patzkowsky and Holland, 1999). When this species is removed from the analyses, the correlation becomes positively significant. Therefore, with the exception of a single species, richness and abundance data both reflect comparable measures of ecological dominance for type Cincinnati gastropods.

Among bivalves, the measures of dominance were also significantly positively correlated (Fig. 6B). This relationship remained when the five most diverse samples from the Waynesville Formation were removed. This relationship is therefore not the result of a single, exceptionally bi-

valve-rich assemblage, and supports the conclusion that taxonomic richness and abundance are also comparable measures for type Cincinnati bivalves.

Following the results of the NMS ordination, chi-square analyses were conducted to test statistically whether the occurrences of these classes were related to several environmental factors: depth, lithology, and turbidity (Table 3). Since depth and lithological designations correlated with one another in these samples, the results are identical for each: deep depths correspond with mixed-siliciclastic-carbonate facies while shallow depths correspond with predominantly carbonate facies. Turbidity was not recognized as an important factor in the NMS analysis, but is an important environmental factor in these settings (Holland and Patzkowsky, 1996).

When depth/lithology was compared as a single factor (Table 3A), gastropod abundances were significantly associated with shallow, carbonate-rich settings, while bivalve abundances were similarly associated with deep, more siliciclastic-rich settings. In terms of taxonomic richness, neither class was significantly associated with these factors, although bivalves were nearly significant, and gastropods were more diverse in shallower, carbonate-rich settings than in deeper, more siliciclastic-rich ones. Thus, while the comparisons were only significant in terms of abundance, the patterns exhibited by species richness were consistent with these results. When turbidity was compared regardless of depth or lithological facies (Table



3B), bivalves were significantly associated with high turbidity, both in species richness and abundance. In contrast, gastropods were not significant with respect to either measure of dominance, with slightly greater species richness in turbid settings and greater abundance in clean ones.

A more resolved picture emerged when all these environmental factors were combined for a two-factor chi-square analysis. Gastropods were significantly most abundant in shallow, carbonate-rich settings lacking turbidity; while they were also most species-rich in such settings, their presence was not statistically significant. In contrast, bivalves were most species-rich and abundant in deep, siliciclastic-rich, high turbidity settings. Because two-factor chi-square analyses are often more significant than single-factor analyses due to the additive effects of multiple comparisons, and because the results are congruent with those in the single-factor analyses, it is most parsimonious to accept the single, depth/lithology factor as the dominant gradient explaining the occurrence of gastropods and bivalves in type Cincinnati strata.

#### Summary

The analytical results suggest that gastropods and bivalves exhibited different distributional patterns relative to one another in the type Cincinnati. In NMS (Figs. 3–4), these differences were apparent by the grouping of most bivalves in negative regions of axes I and II and central regions of axis III, and gastropods generally in positive regions of axes I and II. This segregation was especially clear given that only two species grouped with the other class. The axes can be explained as depth (or lithology), salinity, and biostratigraphic age gradients. Specifically, Cincinnati gastropods were taxonomically richest and most abundant in shallower, more carbonate-rich strata, while bivalves were taxonomically richest and most abundant in deeper, more siliciclastic-rich strata.

That these classes were largely segregated and that the cause of these disparate distributions was primarily attributable to environmental preferences also was supported with statistical analyses of taxonomic richness and abundance (Fig. 5; Table 3). Furthermore, both of these ecological measures were correlated within each class (Fig. 6). Taken together, type Cincinnati gastropods generally were most diverse and abundant in shallower, more carbonate-rich, and perhaps less turbid settings. In contrast, the most bivalve-rich faunas of the Cincinnati Arch consistently occurred in deep subtidal, fine-grained, siliciclastic-rich, and turbid settings.

This conclusion contrasts with Cope and Babin (1999), who posited that Late Ordovician bivalve diversification in Laurentia, especially among epibyssate pteriods and modiomorphoids, was related to the presence of carbonate platforms. In fact, with a single exception (the restricted, lagoonal, Hitz Bed fauna: Appendix 2), Cincinnati bivalves largely were absent from carbonate-dominated strata throughout the region. Their presence in Cincinnati limestones largely was a result of the availability of intermittent fine-grained siliciclastic sediments eroded from the Taconic Orogeny (Holland, 1993; Holland and Patzkowsky, 1996). More proximal sediments of this predominantly siliciclastic influx in the eastern Appalachian

Basin (Bretsky, 1969, 1970a, 1970b; Miller, 1989) also contain diverse and abundant bivalve faunas with wide areal distributions.

Broadly similar patterns for these classes also were documented by Patzkowsky and Holland (1999) in Middle and Upper Ordovician strata of the Nashville Dome. While their samples were typically dominated by brachiopods, they observed that gastropods were typically most abundant in shallow subtidal settings, while bivalves were most abundant in deep subtidal settings. These patterns were most obvious in later Mohawkian (M5 and M6) depositional sequences, but similar patterns occurred throughout the Middle and Upper Ordovician in this region. Furthermore, they observed that the gastropod *Lophospira*, closely related to and often synonymous with *Paupospira* (Wagner, 1999), occurs in similarly high abundance and in a similarly wide range of environments. Thus, the abundance and environmental distribution patterns presented here are consistent with those from an adjacent region spanning a greater temporal duration.

The present study also corroborates that of Novack-Gottshall and Miller (2003) regarding the environmental distributions of these classes throughout the Ordovician world, which showed that bivalves were taxonomically richest in deeper water, siliciclastic-rich settings, while gastropods were taxonomically richest in nearshore to shallow shelf, carbonate-rich settings. This environmental distinction contrasts with the similarity of global diversity trajectories of these classes throughout the Ordovician (Novack-Gottshall and Miller, 2003). At the finer scales of paleocontinents and regions within the single paleocontinent of Laurentia, genus diversity trajectories of these classes were much less correlated. Hence, while Ordovician gastropod and bivalve diversity dynamics varied independently among these classes through space and time, the environmental distributions of these classes were relatively constant and, therefore, scale-independent characteristics that could be observed in whatever geographic venues these classes were present, down to the local and regional level of the type Cincinnati.

#### CONCLUSIONS

There typically is an assumption among paleontologists that abundance and taxonomic richness are equivalent measures of ecological dominance. However, more recent studies have questioned the validity of this relationship (Wing et al., 1993; McKinney et al., 1998; Lupia et al., 1999). This assumption was investigated here by evaluating the fine-scale co-occurrence of Cincinnati gastropods and bivalves that had previously only been analyzed using taxonomic richness (Novack-Gottshall and Miller, 2003).

- (1) With few exceptions, settings in which gastropods or bivalves were most abundant generally were the same settings in which they were taxonomically richest. Assuming that abundance reflects ecological or environmental preference, this result demonstrates that, with few exceptions, each class displayed environmental preferences shared among constituent species of that class. Whether this similarity reflects similar ecological adaptations or evolutionary constraints requires further study.

- (2) When gastropod dominance within individual samples was compared to bivalve dominance, either in terms of taxonomic richness or abundance, there was a significant negative correlation. This relationship also was observed using NMS ordination. Thus, Ordovician gastropods and bivalves tended not to co-occur at the local scale, even in the most mollusc-rich settings.
- (3) Both NMS ordination and chi-square analyses implicated depth and sedimentology, and, to a lesser extent, turbidity and salinity as important environmental factors in the ecological dominance of these classes in local settings. In particular, gastropods were most dominant in shallow, carbonate-rich settings. Gastropods also tended to occur in low turbidity and hypersaline environments where bivalves were generally only secondary components. Bivalves, in contrast, were most dominant in deep subtidal settings with high turbidity and significant amounts of fine-grained siliciclastics.
- (4) Combined with analyses conducted at larger geographic and temporal scales (Novack-Gottshall and Miller, 2003), these results indicate that bivalves and gastropods maintained distinct and generally stable environmental distributions throughout their Ordovician histories. Whether viewed at the scale of individual beds or at the scale of the world, Ordovician gastropods were taxonomically richest (and likely most abundant) in carbonate-rich, nearshore, shallow-shelf and midshelf settings. Bivalves, in contrast, were consistently taxonomically richest and abundant in siliciclastic-rich, nearshore, midshelf and deep-shelf settings from their earliest appearance in the Lower Ordovician fossil record to their Ordovician apex late in the period. Therefore, while their diversity trajectories were variable in different paleogeographic settings throughout the Ordovician (Novack-Gottshall and Miller, 2003), the environmental distributions of bivalves and gastropods were appreciably less variable, exhibiting broadly unchanging distributions wherever each of these classes was living. In fact, the variable nature of their diversity trajectories among Ordovician paleocontinents and regions within Laurentia largely reflects variations in the availability of carbonate- and siliciclastic-dominated settings.

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## APPENDIX 1

## Locality Descriptions and Formations Sampled

- ASHLOCK CEMETERY (AG)—Second of three roadcuts on Route I-27, 1.3 km south of Garrard/Lincoln County line. Lancaster, Kentucky 7.5 minute quadrangle. (Source: Weir et al., 1965, 1984; Holland, 1993). [Gilbert Formation]
- ASHLOCK CEMETERY (AT)—Southernmost of three roadcuts on Route I-27, 1.5 km south of Garrard/Lincoln County line. Lancaster, Kentucky 7.5 minute quadrangle. (Source: Weir et al., 1984; Holland, 1993). [Tate Formation]
- BEAR CREEK QUARRY (BC)—Abandoned quarry along the Ohio River, at the intersection of Bear Creek Road and Route I-52, 4.8 km east of Neville and 1.8 km west of Chilo, Washington County, Ohio. Moscow, Ohio–Kentucky 7.5 minute quadrangle. (Source: Wahlman, 1992). [Kope Formation]
- BEDFORD (MH)—Roadcuts on Route I-42, 4.0 km east of intersection with Route I-421 in Bedford, Kentucky. Bedford, Kentucky 7.5 minute quadrangle. (Source: Weir et al., 1984; Holland, 1993). [Marble Hill Bed, Lower Whitewater Formation]
- HANNAH CREEK (HC)—Outcrop on Hannah Creek off Indiana Route 101, 16.1 km north of Brookville. Fairfield, Indiana 7.5 minute quadrangle. (Source: Rosenkrantz, 1999). [Waynesville Shale]
- MADISON (HW)—Roadcut on west side of Route I-421, 5.0 km north of intersection with Indiana State Route 56 in Madison, Indiana. Madison West, Indiana–Kentucky 7.5 minute quadrangle. (Source: Holland, 1993). [Hitz Bed, Upper Whitewater Formation]
- MAYSVILLE (MAY)—Westernmost of two large roadcuts along Kentucky Route 3071, 2.3 km west of intersection with Kentucky Route 8, 2.9 km north of Maysville city line. Maysville West, Kentucky–Ohio 7.5 minute quadrangle. [Bellevue Formation]
- MOUNT AIRY FOREST (MAF)—Loose slabs from bottom of roadcut on I-74 at “mile 15.6” where it enters Mount Airy Forest. Cincinnati West, Ohio 7.5 minute quadrangle. (Source: Dattilo, 1996). [Miami town Shale]
- RICE AND GAGE STREETS (CHS)—Road cut at the intersection of Rice and Gage Streets, Cincinnati, Ohio, on the grounds of Christ Hospital; opposite 2227 Gage Street, Cincinnati, Ohio. Covington, Kentucky–Ohio 7.5 minute quadrangle. (Source: Dattilo, 1996). [Miami town Shale]
- RUSSELL BRANCH (RB)—Series of road cuts along private driveway to farm belonging to Larry Campbell. Driveway located on east side of St. Mary’s Road (Sixth Street), 14.5 km west of Brookville. Spades, Indiana 7.5 minute quadrangle. (Source: Rosenkrantz, 1999). [Waynesville Shale]

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