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Comparative geographic and environmental diversity dynamics of gastropods and bivalves during the Ordovician Radiation

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Abstract.—Bivalves and gastropods, prominent members of the Modern Evolutionary Fauna, are traditionally noted for sharing remarkably similar global diversity trajectories and environmental distributions throughout the Phanerozoic. By comparing their fossil occurrences at several scales within a finely resolved geographic, environmental, and temporal framework, it is possible to evaluate whether such similarities are caused primarily by intrinsic macroevolutionary factors or extrinsic ecological factors. Using a database of 7779 global gastropod and bivalve genus occurrences, we investigate the geographical and environmental attributes of bivalves and gastropods during the Ordovician Period at scales ranging from global, to a comparison among five paleocontinents, to an intracontinental comparison of four regions within Laurentia. Although both classes shared statistically indistinguishable global diversity trajectories and broadly similar environmental distributions during the Ordovician, their environmental distributions differed in several significant features. Furthermore, the diversity trajectories and environmental distributions of these classes differed significantly among paleocontinents and among regions within Laurentia. Bivalves were consistently most diverse in deeper water, siliciclastic-rich settings in higher-latitude paleocontinents whereas gastropods were consistently most diverse in shallower, carbonate-rich settings in more-equatorial paleocontinents. Notably, these environmental differences were robust to changing physical parameters within paleocontinents, with each class consistently tracking its preferred environmental setting. These results suggest that environmental factors played significant, albeit distinct, roles in the Ordovician diversifications of gastropods and bivalves. However, their similar global diversity trajectories suggest that shared, intrinsic macroevolutionary attributes also may have played an important role in the evolution of these classes during the Ordovician Radiation.

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Introduction

Given the wide variation in diversity trajectories of marine groups through the Phanerozoic, it is remarkable that gastropods and bivalves consistently show similar diversity trajectories (Sepkoski 1981; Bambach 1985), background turnover rates at several taxonomic scales (Stanley 1985; Raup and Boyajian 1988; Valentine et al. 1991), and extinction rates during mass extinctions (Erwin 1990). It is unlikely that such overwhelming similarities are mere coincidence: one may expect an intrinsic or extrinsic cause. With such similarities, however, it is not surprising that the global Phanerozoic diversity histories of these classes correlate when subjected to quantitative analyses (Sepkoski 1981, 1984). Combined with their prominence in the post-Paleozoic, these similarities led to their characterization as dominant members of the Modern Evolutionary Fauna (Sepkoski 1981).

Implicit in Sepkoski's (1984, 1991) kinetic models of Phanerozoic global diversification was the assumption that shared intrinsic macroevolutionary dynamics were the driving force behind the diversity histories and subsequent replacement of each evolutionary fauna, including gastropods and bivalves. Although this model of evolutionary succession was originally formulated from global diversity data, an analysis of Paleozoic fossil communities from Laurentia along an environmental gradient illustrated that the evolutionary faunas, to a large degree, had distinct environmental, as well as temporal, patterns (Sepkoski and Sheehan 1983; Sepkoski and Miller 1985). Furthermore, the faunas displayed a general onshore-offshore pattern in which succeeding evolutionary faunas originated in shallow water and expanded into deeper-water environments during their history (Jablonski et al. 1983; Sepkoski and Shee-

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han 1983; Sepkoski and Miller 1985; Sepkoski 1991; but see Westrop and Adrain 1998). In these onshore-offshore models, the Modern Evolutionary Fauna, and particularly gastropods and bivalves, were characterized primarily as limited to nearshore and lagoonal habitats from their initial radiations until the Devonian, when they also became established in deep-water environments (e.g., Kammer et al. 1986).

Such observations were intended as generalizations about Paleozoic marine community evolution, but their support in other studies (e.g., Bretsky 1968, 1969, 1970a,b; Boucot 1975; Steele-Petroviç 1979; Westrop et al. 1995) created an expectation that early Paleozoic gastropods and bivalves were restricted to nearshore, shallow-water environments. It was not until the more focused work of Frey (1987) and Miller (1988, 1989) that limitations in these models were recognized by demonstrating, for example, that diverse and abundant Late Ordovician bivalve faunas of the Cincinnati Arch also thrived in fine-grained, siliciclastic sediments representing offshore environments. Further limitations included the observation that bivalves and trilobites, members of different evolutionary faunas, commonly overlapped in their environmental distributions (see also Westrop and Adrain 1998).

The greatest limitation, however, of these onshore-offshore models was their reliance on data from the single paleocontinent of Laurentia. For mass extinctions, a limited geographic focus may not necessarily confound studies, as these processes are, by definition, global events of limited temporal duration. For example, Raup and Jablonski (1993; Jablonski and Raup 1995) showed no differential geographic overprint on marine bivalve extinctions during the end-Cretaceous extinction. It is now clear, however, that evolutionary radiations may display significant heterogeneity among paleocontinents. Although much of this work has focused on the Ordovician Radiation (e.g., Miller 1997a, 1998 for global faunas; Cope and Babin 1999 for bivalves; Westrop and Adrain 1998 for trilobites), other research on the recovery from the end-Cretaceous mass extinction (Jablonski 1998 for molluscs) has also suggested differential geographic patterns. For the Ordovician, explanations for such heterogeneity have most often involved local physical factors, such as sedimentology and tectonism (Babin 1993, 1995; Miller and Mao 1995; Miller 1997a,b) or oceanographic and sea level changes (Guensberg and Sprinkle 1992; Patzkowsky and Holland 1996). Jablonski (1998) also stressed that biotas recovering from mass extinctions may also display geographically heterogeneous diversification dynamics for reasons not directly related to ecological features, a compelling extension of the so-called evolutionary founder effect of Raup (1979).

A comparison of the dynamics of individual taxonomic groups has great potential for revealing the causal processes of the Ordovician Radiation and in teasing apart the often subtle distinctions between intrinsic macroevolutionary dynamics and extrinsic ecological factors. However, the usefulness of such a comparison has been realized in only a few studies (Miller 1998). In a series of elegant papers, Babin (1993, 1995; Cope and Babin 1999) proposed that the Ordovician Radiation of bivalves was a two-step process, in which Early Ordovician radiations began in siliciclastic, Gondwanan shallow shelf platforms, whereas later Ordovician radiations of bivalves in other paleocontinents, including Laurentia, Baltica, Siberia, and Kazakhstania, occurred primarily in carbonate settings (but see results below). Similarly, Guensberg and Sprinkle (1992) hypothesized that the Early Ordovician diversification of attached echinoderms in western Laurentia was prompted by the inhibition of siliciclastic influx and the concomitant creation of carbonate hardgrounds caused by global sea level rise. Miller (1997b; Miller and Mao 1995; Miller and Connolly 2001) emphasized the role of tectonically driven sedimentation as a cause of the Ordovician Radiation for several orders of brachiopods, trilobites, and benthic molluscs (but see Connolly and Miller 2002). It is clear that explaining the causes of evolutionary radiations is not a simple endeavor; different causes may be found at different taxonomic levels, different geographic scales, and over different time frames. A fuller understanding requires that these evolutionary phenomena be evaluated at all of these scales. Among the unresolved questions is the extent to which prominent members of the same evolutionary fauna exhibit similar diversification dynamics at all scales: are similarities in global diversity trajectories manifested paleoecologically at more local levels?

Here, we evaluate the extent to which bivalves and gastropods exhibited similar geographic and environmental patterns during the Ordovician at scales ranging from the globe, to paleocontinents, to regions within the paleocontinent of Laurentia. Using a literature-derived database, we demonstrate that the similarity of the Ordovician histories of bivalves and gastropods depends on the scale at which the analysis is conducted. As expected, both gastropods and bivalves show remarkably similar Ordovician diversity trajectories on a global scale, thus lending support to the synoptic model of global evolutionary faunas. However, when these same data are evaluated at the scales of paleocontinents or regions within Laurentia, a more complex picture of gastropod and bivalve evolution during the Ordovician Radiation develops, in which global similarities are the result of the accumulation of different paleoecological and evolutionary histories in different regions and environments throughout the world.

Structure of the Database

The database for this study consists of 8237 Ordovician fossil occurrences compiled from 1090 faunal lists described in 407 paleoecological, systematic, and biostratigraphic works from the global literature. These occurrences represent 364 genera and 1728 species of gastropods, bivalves, and monoplacophorans that were revised to accord with cladistic (e.g., Wagner 1995a, 1999) and traditional phylogenetic relationships (e.g., Cope 1996, 1997; Wahlman 1992). Compiled data also include geography, lithology, inferred depositional environment, mode of preservation, and stratigraphic interval of occurrence (Table 1). All fossil occurrences reported within a single lithological unit representing a single depositional environment at a single geographical coordinate of a distinct age were pooled into a faunal list. In cases where a stratigraphic interval represented more than one depositional environment, the fauna was divided, when possible, into separate lithofacies to represent the immediate surrounding strata of each faunal list. However, although each faunal list is most likely a good representation of the time-averaged fossil assemblage from a particular environmental setting, it is possible that all members of a faunal list did not co-occur simultaneously. A complementary study (Novack-Gottshall and Miller in press) presents the results of a field-based analysis of mollusc-rich strata in the Cincinnati Arch, testing for local co-occurrence in both taxonomic richness and individual abundance at the scale of formations and single bedding planes.

TABLE 1. Sample record in global database of Ordovician gastropods, bivalves, and monoplacophorans. For discussion of the primary data fields, see text.

Genus	*Glyptarca*
Genus synonym	*Hemiprionodonta*
Species	*lusitanica*
Class	Bivalvia
Preservation	Internal mold/steinkern
Formation	Fonte da Horta
Lithology	Mudstone interbedded with sandstone
Lithcode	Siliciclastic
Environment	Deepshelf
Environmental zone	4.5
Country	Portugal
Locality	Bucaco Syncline
Secondary localities	Dornes, Cacemes
Latitude	40°N
Longitude	008°W
Paleocontinent	Iberia (Mediterranean Province)
Harland Subsystem	M-Ord
Harland Series	L/U-Llde
New Standard Subsystem	M-Ord
New Standard Series	U-Darw
Reference	Young 1985
Revision reference	Cope 1996: p. 991
File number	911

Although the focus of this study is on gastropod and bivalve co-occurrence, we included monoplacophorans in the database because of the convoluted historical relationships of many bellerophont molluscs (see review in Harper and Rollins 2000); monoplacophoran results are not presented here. Because these three classes shared similar shell chemistries during the Ordovician and were commonly preserved in the same ways, they serve as taphonomic control groups for one another (sensu Bottjer and Jablonski 1988). Such control groups are helpful when evaluating the environmental distributions of bivalves and gastropods to determine whether the absence of a particular class in a sampled unit is likely caused by non-preservation or by true ecological absence.

We used lithological information to infer a general onshore-offshore environmental zonation for approximately two-thirds of the faunal lists. The remaining lists either lacked lithological information, represented numerous depositional environments, or were ambiguously interpreted. This eight-zone framework is adopted from that of Sepkoski (1988) and is similar to others in the literature (e.g., Sepkoski and Sheehan 1983; Sepkoski and Miller 1985; Miller 1988; Bottjer and Jablonski 1988; Brett et al. 1993; Jablonski et al. 1997). Environmental zones were based on rock type and sedimentary structures rather than the presence of faunal elements, which is typically used when designating Benthic Assemblages (sensu Boucot 1975, 1981). The shallowest setting, zone 1, is indicative of peritidal to shoreface settings characterized by desiccation cracks or large-scale cross-bedding. Zone 2 is characterized by protected, very shallow subtidal settings such as lagoons, that often contain restricted faunas. Zone 3 is characterized by offshore wave-agitated environments including bars and oolitic shoals with tabular or trough cross-bedding. We included reefs and other bioherm-rich settings in this zone, in contrast with Sepkoski (1988) and others who excluded them from study. Open marine shelf and deltaic settings are subdivided into shallow (zone 3.5), middle (zone 4), and deep (zone 4.5) subtidal components on the basis of frequency of storm influence and the ratio of tempestites to fine-grained shales and mudstones (Speyer and Brett 1988), with zone 3.5 dominated by tempestite sandstones, grainstones, and/or packstones and zone 4.5 dominated by shales with fewer tempestite wackestones and/or siltstones. Zone 5 is characterized by deep-shelf, pro-deltaic, and shelf edge settings below storm wave base and generally lacking benthic calcareous algae. The deepest setting, zone 6, is indicative of slope and basinal settings and is characterized by turbidites and by hemipelagic and oxygen-depleted facies.

It is important to note that zones 1 through 5 are all relatively shallow from an oceanographic perspective. The boundary between zone 3 and 3.5 is defined here as fair-weather wave base; likewise, the boundary between zones 4 and 5 is defined here as storm wave base, which can vary between 10 and 50 m in modern settings (Brett et al. 1993). When inferring the depositional environment of faunal lists in this study, we made determinations in consultation with appropriate sequence stratigraphical and sedimentological works (e.g., Crevello et al. 1989; Cope et al. 1992; Witzke et al. 1996).

The database encompasses occurrences from Australasia, Avalonia, Baltica, Laurentia, the Mediterranean Province, Siberia, Kazakhstania, Gondwanan South America, and various oceanic terranes, including the Precordillera. However, because of limited data and monographic biases from several of the latter regions, results of paleocontinental comparisons are illustrated in detail here only for the first five of these paleocontinents. Nevertheless, as the available data in the additional, less studied regions are still concordant with the results from the five better-explored paleocontinents, qualitative summaries of these regions will be presented in the subsequent discussion of paleocontinental trends.

Because of this global coverage, we used the Ordovician timescale of Webby (1998), which more accurately reflects global correlations than previous efforts; 79% of the occurrences were resolvable stratigraphically to the subseries level used in analyses of diversity trajectories and 90% were resolvable to the series level used in analyses of environmental distribution. Webby (1998) does not subdivide the Ordovician series, so we used the following British stages as subseries equivalents: lower Tremadocian is Cressagian, middle Darriwilian is Abereiddian, middle Caradocian is Burrellian/Cheneyan, and middle Ashgillian is Cautleyan/Rawtheyan; the remaining subseries are easily inferred.

The nine paleocontinents in the database encompass the majority of the Ordovician globe, excluding North and South China and portions of South Africa, Antarctica, and the Near and Middle East. Although China had diverse marine biotas throughout the Ordovician (e.g., Wang et al. 1987; BGMRGP 1988; Rigby et al. 1995; Wang and Chen 1999; summarized in Miller 1997a; Miller and Mao 1998), their reported molluscan diversity was relatively minor and composed of cosmopolitan genera. Further systematic studies of the mollusc fauna are encouraged, but the addition of currently published data from these regions to our database is unlikely to change the results presented here.

Because the compilation for Laurentia was the most extensive of any paleocontinent in the database and because there was significant temporal variation in environmental conditions within this paleocontinent during the Ordovician, we analyzed the radiation at finer geographical scales within four regions of this paleocontinent: Appalachian Basin, Cincinnati Arch, Mississippi Valley, and Great Basin. These regions comprise 87% of the occurrences in the Laurentian database and thus likely represent the cumulative dynamics of Laurentia as a whole. Additionally, during the Late Ordovician, they composed a broad transect from predominantly siliciclastic settings in the eastern Appalachian Basin proximal to the Taconic Orogeny, to mixed-siliciclastic-carbonate settings in the Cincinnati Arch and Mississippi Valley showing orogenic influence mainly in the form of fine-grained siliciclastics, and, finally, to predominantly carbonates in the Great Basin at the most distal portion of orogenic influence. This variation in environmental settings serves as a backdrop against which to evaluate the paleoecological characteristics of these classes.

Sampling intensity for data used to compile diversity trajectories and environmental distributions for the various paleocontinents and regions within Laurentia are listed in Appendices 1 and 2; information includes the number of faunal lists; the total number of gastropod, bivalve, and monoplacophoran occurrences; and the number of primary references from which faunal lists were compiled. Differences in tallied data between the two appendices are a result of the different criteria used in compiling each data set. The four Laurentian regions and the paleocontinents, except for Laurentia, are all comparably sampled. The greater sampling intensity in Laurentia likely results from its greater Ordovician rock volume instead of a biased sampling of the literature (Ross et al. 1982).

Despite this overall comparability, the fossil record during certain intervals in some paleocontinents and regions may be less well documented, because of diagenetic alteration, lack of exposed strata, or lack of recent systematic study. The first two biases should affect bivalves and gastropods equally, whereas the last bias is lessened by the relatively stable genus-level taxonomy of these classes and the relatively small number of Ordovician bivalve and gastropod systematists (Schneider 2001; Wagner 2001). Baltica, the Mediterranean Province, and Laurentia contain generally well-studied and well-documented molluscan records throughout the Ordovician. In contrast, Australasia, Avalonia, and the Laurentian Great Basin suffer from one or more of these sampling limitations during at least one interval, the details of which are described below. Although in some cases faunal lists were sufficient to make statistical comparisons for these venues, their interpretation in these limited instances should be considered preliminary pending corroboration from additional field effort. As the primary aim of this study, however, is a comparison, at several scales, of the diversification dynamics of gastropods and bivalves, it is most important that the sampling effort within an interval be comparable for both classes in each region; this aim is satisfied given the comparable preservation of these classes.

Methods

Diversity Trajectories.—Diversity trajectories of taxa through time were calculated on the assumption that taxa range through the interval demarcated by their stratigraphical first and last occurrences. Although this assumption makes sense for global compilations, it may be problematical for smaller geographical scales because of immigration or emigration of taxa (Patzkowsky and Holland 1996).

Lacking evidence to the contrary, we assumed that a taxon was present throughout its stratigraphical range within a region.

To compare quantitatively gastropod and bivalve diversity trajectories while avoiding autocorrelation (McKinney 1990), we calculated proportional changes in diversity over time, or ''first differences'' (Gould and Calloway 1980; Foote 1994; Wagner 1995a):

$$m_{\alpha} = q_{\alpha\max} \bullet (D_{\alpha t} - D_{\alpha t-1}) \qquad (1)$$

where m_{α} is the proportional change in diversity (or slope) between adjacent time intervals t and $t-1$, D_{α} is the diversity in a time interval, and $q_{\alpha\max}$ is the reciprocal of the maximum diversity attained by the class of interest (α) during the Ordovician Period. Once the slopes were calculated for both bivalves and gastropods, the nonparametric Spearman's rank correlation coefficient was calculated to test the significance of the correlation between the two diversity trajectories.

Environmental Distribution.—Environmental distributions were determined by counting the number of unique genera in a specific environmental zone during a time interval; no assumptions were made regarding first and last occurrences. The data were plotted on a time-environment diagram with time arrayed on the vertical dimension and the environmental zonation arrayed along the horizontal dimension. The diversities in each time-environment cell were enclosed by shaded contour lines, with increasingly darker shades denoting greater diversity; unshaded, empty cells contain no known occurrences of either gastropods or bivalves in the database. Taphonomic controls, representing the occurrence of at least one gastropod, bivalve, or monoplacophoran fossil, were symbolized with a filled circle within each cell. Because all three classes exhibited similar preservational potentials during the Ordovician (Valentine 1989; Palmqvist 1991; Foote and Sepkoski 1999), the presence of a taphonomic marker (i.e., monoplacophorans) in an environmental cell lacking both gastropods and bivalves provides greater confidence that the absence has true ecological significance. In contrast, the dual absence of a taphonomic marker and a gastropod or bivalve genus in a zone could be the result of a true absence of all three molluscan classes or non-preservation of such fossils in that setting at that time. Because no attempt was made to determine whether non-molluscan collections are available for these empty cells, no valid conclusions can be made without further information. A comprehensive analysis of the Ordovician benthos is beyond the present study, but our results are evaluated, where possible, by comparison with additional studies.

Because of the limited environmental coverage within most paleocontinents and regions with Laurentia, analyses of environmental distributions at these finer geographic scales were conducted only at the level of Ordovician series rather than subseries; 64% of global fossil occurrences could be categorized within this framework. Although several time-environment cells contain no known record of gastropods, bivalves, or monoplacophorans (Appendix 2), the comparability of sampling effort among the four Laurentian regions and the paleocontinents and the similar preservation potential of these classes allow statistically meaningful comparisons to be made.

Because the environmental framework is a discrete adaptation of a continuous variable, we used the Kolmogorov-Smirnov two-sample test to test the similarity of bivalve and gastropod environmental distributions (Sokal and Rohlf 1995). Distributions were tested at the level of resolvable subseries for the global comparison; data were tested for all geographic scales at the level of Lower (Tremadocian–Latorpian), Middle (Volkhovian–Darriwilian), and Upper Ordovician (Caradocian–Ashgillian) subsystems (Webby 1998). Before testing, data were percent-maximum transformed by dividing the diversity of each class in each time-environmental cell by the maximum diversity attained by that class in any cell during the Ordovician. This transformation ensured that the test among distributions compared the shape of that distribution independently of confounding differences in the diversity of each class.

Although useful as a test for statistically distinct environmental distributions, the Kolmogorov-Smirnov test cannot determine the

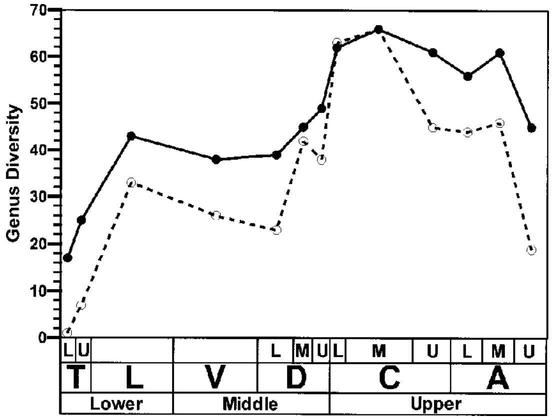


FIGURE 1. Global Ordovician diversity trajectories for gastropod and bivalve genera. In this figure, and in all following diversity charts, solid lines depict the gastropod trajectory and dotted lines depict the bivalve trajectory. The timescale, with time proceeding from left to right, is based on that of Webby (1998), using abbreviations for lower, middle, and upper subseries, where appropriate: (T) Tremadocian, (L) Latorpian, (V) Volkhovian, (D) Darriwilian, (C) Caradocian, and (A) Ashgillian.

basis of such differences. In cases where two distributions were statistically distinct, we used the one-tailed, nonparametric Mann-Whitney *U*-test to test whether the environmental distribution of one class was skewed significantly toward deeper or shallower depths than the other (Sokal and Rohlf 1995). These tests were conducted only at the subsystem level to ensure adequate sample sizes.

Global Results and Discussion

Analyses conducted at each of the three geographic scales are presented separately below, with a summary of scale-transcendent and scale-dependent patterns for all scales in the concluding remarks.

Global Diversity Trajectories.—Figure 1 depicts the global diversity trajectories of gastropod and bivalve genera through the Ordovician Period. Gastropods and bivalves show significantly correlated trajectories based on first differences ($r_s = 0.924$; $p < 0.005$), although gastropods were typically more diverse than bivalves throughout the Ordovician. Both classes shared a dramatic initial rise in diversity through the Lower Ordovician, stability in the Volkhovian, diversification into the Caradocian, and descent through the end of the period.

These trajectories are similar to those plotted by Sepkoski (1995: Fig. 4) for both of these classes and by Wagner (1995a: Fig. 5) for both phylogenetically and taxonomically classified gastropods; minor differences between their results and those in Figure 1 are caused by the different timescale used in this study and the independent compilation of the respective databases. Despite the similarities of these classes, however, it is possible that the raw trajectories may not entirely reflect the true Ordovician biological history of these classes because no attempt was made to standardize sampling biases (e.g., rock volume or sampling intensity) that can substantially alter observed diversity patterns (Miller and Foote 1996; Alroy 2000a,b; Alroy et al. 2001). However, as the focus of the present study is to test for overall similarity in Ordovician trajectories of these classes, and assuming reasonably that the biases are not skewed in favor of an individual class (Foote and Sepkoski 1999), the lack of such standardization does not affect the comparisons presented here.

The Upper Ordovician decrease is in part a sampling artifact caused by an absence of data for Silurian occurrences that eliminates taxa ranging through the Ashgillian, i.e., a lack of the so-called Pull of the Silurian (sensu Miller and Foote 1996). It likely also reflects the initial phase of the Late Ordovician mass extinction that occurred at the end of the middle Ashgillian and is observed in the depleted diversity of upper Ashgillian (Hirnantian) taxa (Brenchley 1990). The low diversity of both classes in the Lower Ordovician is not likely an artifact of range truncation, because only eight gastropod genera have been documented from the Upper Cambrian (Wagner 1995a) and only four of those range into the Ordovician. Similarly, only four unequivocal bivalve genera are known from the Cambrian, and none of those are known in the Ordovician (Cope 1997; Cope and Babin 1999).

Global Environmental Distributions.—Figure 2 displays the global environmental distributions of gastropods and bivalves during the Ordovician Period. Gastropods were relatively widespread throughout most Lower Ordovician environments (zones 1 through 5), with the greatest concentration in shallow offshore

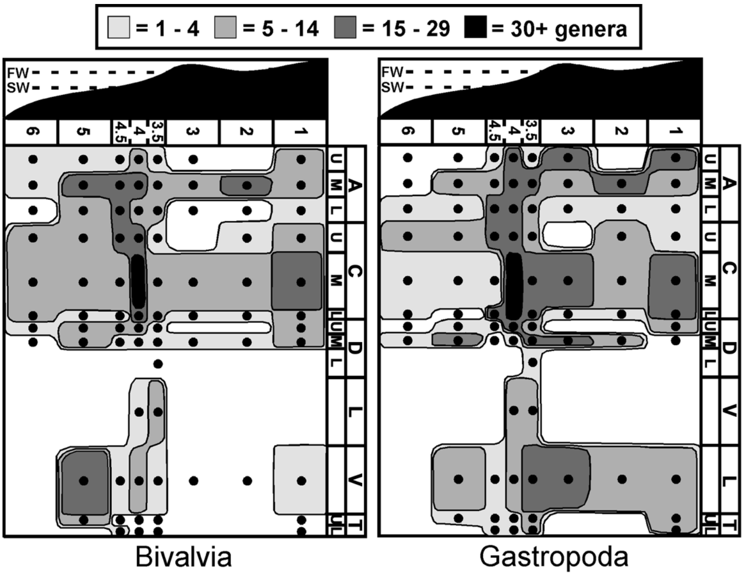


FIGURE 2. Contoured time-environment diagram depicting the global genus diversity of bivalves (left) and gastropods (right) during the Ordovician. The dark circles within some cells are taphonomic markers that represent the occurrence of at least one gastropod, bivalve, or monoplacophoran fossil (see text for details). The timescale is the same as in Figure 1. The key at top depicts the genus diversity of each class within shaded contours.

settings (zones 3 and 3.5); in contrast, bivalves were somewhat more restricted then to shelf settings (zones 4 through 5), with few genera in nearshore settings (zone 1). Thus, although both classes inhabited a similarly wide range of environments, bivalves were generally more diverse in deeper water settings and gastropods in shallower ones.

Given the diverse gastropod assemblages in shallow settings (zones 2 through 3.5) during this time, it is likely that the absence of bivalves in these settings is ecologically significant. Five genera of gastropods are also known from Laurentian lagoonal settings (zone 2) during the Tremadocian (Poulsen 1937; Bass and Northrup 1953; Aitken and Norford 1967), but a lack of precise subseries resolution prevented them from being included in Figure 1; these genera are included in the series-level data from Laurentia below.

The apparent bottleneck exhibited by both classes in the Volkhovian and lower Darriwilian has several possible explanations. Although it may reflect an ecologically or environmentally meaningful restriction, a lack of well-studied faunas from non-shelf environments could also contribute to the pattern observed; indeed, there are few available faunal lists during these time intervals (Appendix 2), although the coverage in zones 3.5 and 4 is comparable to other intervals. Whether real or preservational, the restriction appears to affect more than molluscs; Sepkoski and Sheehan (1983) illustrated a similarly reduced environmental coverage for this time interval among benthic fauna of Laurentia. Erosion during the Sauk-Tippecanoe unconformity that affected Laurentia, Siberia, and possibly Gondwana and other paleocontinents (Ross et al. 1982; Barnes et al. 1996; J. E. Repetski personal communication 2002) also may have played a role. Regardless of the cause, both classes were present in similar diversities in the same environments during these intervals, and paleontological exploration in additional facies could be worthwhile.

In the middle and upper Darriwilian, both gastropods and bivalves ranged throughout most environmental zones with few absences. Throughout the Caradocian and Ashgillian, gastropods continued to display their greatest diversity in nearshore through midshelf settings (zones 1 through 4), withdrawing from deeper water (zones 5 and 6) in the Ashgillian; in contrast, bivalves were most diverse in deeper shelf settings (zones 4 through 5).

TABLE 2. Results of statistical comparisons of environmental distributions of global Ordovician gastropod and bivalve genera during each Ordovician time interval. In the case of the lower Darriwilian, signified with asterisks, data were insufficient to allow a statistical comparison. N.S. signifies a time interval when the environmental distributions of gastropods and bivalves were not statistically distinguishable (i.e., $p > 0.05$); dashes signify that a comparison was not required. The Kolmogorov-Smirnov two-sample test, using percent-maximum transformed data, was used to test whether the two distributions were dissimilar; in cases where dissimilarity was observed, the one-tailed Mann-Whitney *U*-test was then used to test whether one class was displaced toward shallower or deeper water than another. The table gives results from the perspective of bivalves; those of gastropods are opposite.

	Kolmogorov-Smirnov test		Mann-Whitney *U*-test			
	D	Probability	*U*	z	Probability	Bivalves
Subsystem						
U-Ord	0.157	$p < 0.01$	35,365.0	−3.582	$p < 0.005$	Deeper
M-Ord	0.152	$p < 0.05$	5909.5	0.368	N.S.	—
L-Ord	0.690	$p < 0.01$	845.5	−7.304	$p < 0.005$	Deeper
Subseries						
U-Ashg	0.381	$p < 0.01$	570.0	−2.848	$p < 0.005$	Deeper
M-Ashg	0.127	$p < 0.05$	4504.0	−0.954	N.S.	—
L-Ashg	0.194	$p < 0.05$	1108.0	−1.828	$p < 0.05$	Shallower
U-Cara	0.136	N.S.	—	—	—	—
M-Cara	0.243	$p < 0.01$	5543.0	−3.559	$p < 0.005$	Deeper
L-Cara	0.191	$p < 0.01$	2197.0	−1.903	$p < 0.05$	Deeper
U-Darw	0.329	$p < 0.01$	528.0	−2.011	$p < 0.025$	Deeper
M-Darw	0.379	$p < 0.01$	875.0	0.492	N.S.	—
L-Darw	**	**	**	**	**	**
Volk	0.256	N.S.	—	—	—	—
Latp	0.703	$p < 0.01$	476.5	−6.194	$p < 0.005$	Deeper
U-Trem	0.900	$p < 0.01$	9.0	−3.438	$p < 0.005$	Deeper
L-Trem	0.905	$p < 0.05$	1.0	−1.497	N.S.	—

Although there was much environmental overlap, statistical comparisons verify that gastropods and bivalves exhibited significantly different environmental distributions, both in ten of 13 resolvable subseries and in all three pooled Ordovician subsystems (Table 2). The aforementioned lower Darriwilian and Volkhovian suffered from poor sampling, although meaningful ecological similarity within the better-sampled Volkhovian cannot be excluded (Appendix 2). Both classes exhibited similar environmental distributions during the well-sampled upper Caradocian. During intervals when the distributions were different, the Mann-Whitney *U*-test demonstrated that bivalves were typically more diverse in deeper water settings than gastropods (Table 2).

Discussion of Global Patterns.—At a global level, diversity trajectories of gastropod and bivalve genera were not appreciably different. In contrast, their environmental distributions revealed consistent, statistically significant environmental differences: although both classes exhibited broad and overlapping environmental distributions throughout the Ordovician, gastropods were more diverse in shallower-water settings than bivalves, which were most diverse in deeper settings.

These environmental patterns differ from interpretations in earlier studies (Bretsky 1968, 1969, 1970a,b; Sepkoski and Sheehan 1983; Sepkoski and Miller 1985), which characterized both classes as most highly concentrated in nearshore settings. Two explanations may account for this difference. First, the present database comes from an expanded global analysis, whereas the earlier studies were limited primarily to the single paleocontinent of Laurentia; as will be considered below, this paleocontinent presents a biased reading of the Ordovician bivalve diversification. Furthermore, the earlier studies focused on the relative diversity of entire faunas, instead of on the absolute diversities of particular classes of fossils. This distinction is important because diverse taxa can still be perceived as less ecologically dominant when compared with the diversity of the entire assemblage (Miller 1988; Westrop and Adrain 1998). Thus, the generally high diversities of molluscs in Ordovician shelf settings should not imply that these molluscs were the dominant taxa in these settings; it means simply that these classes were generally more diverse in shelf settings than in nearshore ones. The generally held notion of gastropod-dominated nearshore settings could as easily arise from an exclusion of more typically shelf-restricted biotic elements (e.g., brachiopods, bryozoans, and crinoids) from nearshore settings as it could from a propensity of these molluscs to be restricted to nearshore environments (Westrop and Adrain 1998). Several cases are known, however, in which bivalves and gastropods were the dominant faunal elements in Ordovician shelf environments. For example, several studies (Frey 1987; Miller 1989; Patzkowsky and Holland 1999; Novack-Gottshall and Miller in press) have demonstrated Middle and Late Ordovician deep subtidal settings where bivalves constituted more than half of the genera and total number of individuals within single assemblages, and shallow settings where gastropods constituted similar levels of abundance. Regardless of the explanation, the environmental distributions of these classes at a global scale were appreciably different than the nearly identical diversity trajectories might lead one to predict.

Paleocontinental Results and Discussion

Paleocontinental Diversity Trajectories and Environmental Zones

Australasia.—During the Early and Middle Ordovician, Australasia (including present-day Australia, Malaysia, and Thailand) existed as a series of island arcs on the equator along the northeastern Gondwanan coast dominated by siliciclastic and mixed-siliciclastic-carbonate sedimentation (Cocks 2001). As the paleocontinent moved northward during the Late Ordovician, the paleocontinent became more carbonate-rich (Cocks and Fortey 1988, 1997; Scotese and McKerrow 1991; Percival 1995). First differences indicate that gastropod and bivalve diversity trajectories (Fig. 3) were not significantly correlated (Table 3). Gastropods were generally more diverse than bivalves, although both classes exhibited a decline in diversity through the Upper Ordovician; similar diversity trajectories were reported for bivalves by Cope and Babin (1999). Because of poor subseries resolution, the bivalve-rich Darriwilian Stairway Sandstone fauna (Pojeta and Gilbert-Tomlinson 1977) could not be included in these diversity trajectories although it is included in the series-level environmental distributions below. Once a more precise age determination is made of these sediments, the diversity trajectories for Australasian bivalves and gastropods will become even less comparable than presently observed. The Upper Ordovician, and particularly Ashgillian, decline is caused by both reduced available outcrop (Cocks and Fortey 1990) and a lack of recent taxonomic study (Percival 1995; Cocks and Fortey 1997).

Both classes consistently inhabited open-shelf settings (Fig. 4; zones 3.5 to 4), appearing in deeper settings (zone 4.5 to 5) in the Tremadocian, and in shallower settings (zones 1 to 3) in the Latorpian, Darriwilian, and Caradocian. Despite such similarities, the environmental distributions were statistically different throughout the Ordovician (Table 4). Although the data were sufficient to statistically evaluate the environmental displacement of these classes during the Lower and Middle Ordovician, such analyses are difficult to interpret given the patchy nature of the data.

Avalonia.—During the Early Ordovician, Avalonia lay peripheral to northwestern Gondwana in high southern latitudes (Torsvik 1998). This island arc terrane separated from Gondwana by the Middle Ordovician and moved northward toward Laurentia and Baltica, reducing the width of the Iapetus Ocean (Cocks and Fortey 1990; Torsvik 1998). As closing continued into the Late Ordovician, Avalonia, now in subequatorial climates, sutured with Baltica, closing the Thor (Tornquist) Ocean (Berthelsen 1998; Torsvik 1998). Sedimentation throughout the Ordovician was predominantly siliciclastic from prolonged periods of island arc volcanism (Traynor 1988; Scotese and McKerrow 1991). With the exception of two recent collections (Cope 1996, 1999) that significantly elevate the Latorpian and middle Darriwilian bivalve diversities, bivalves showed reduced Lower and Middle Or-

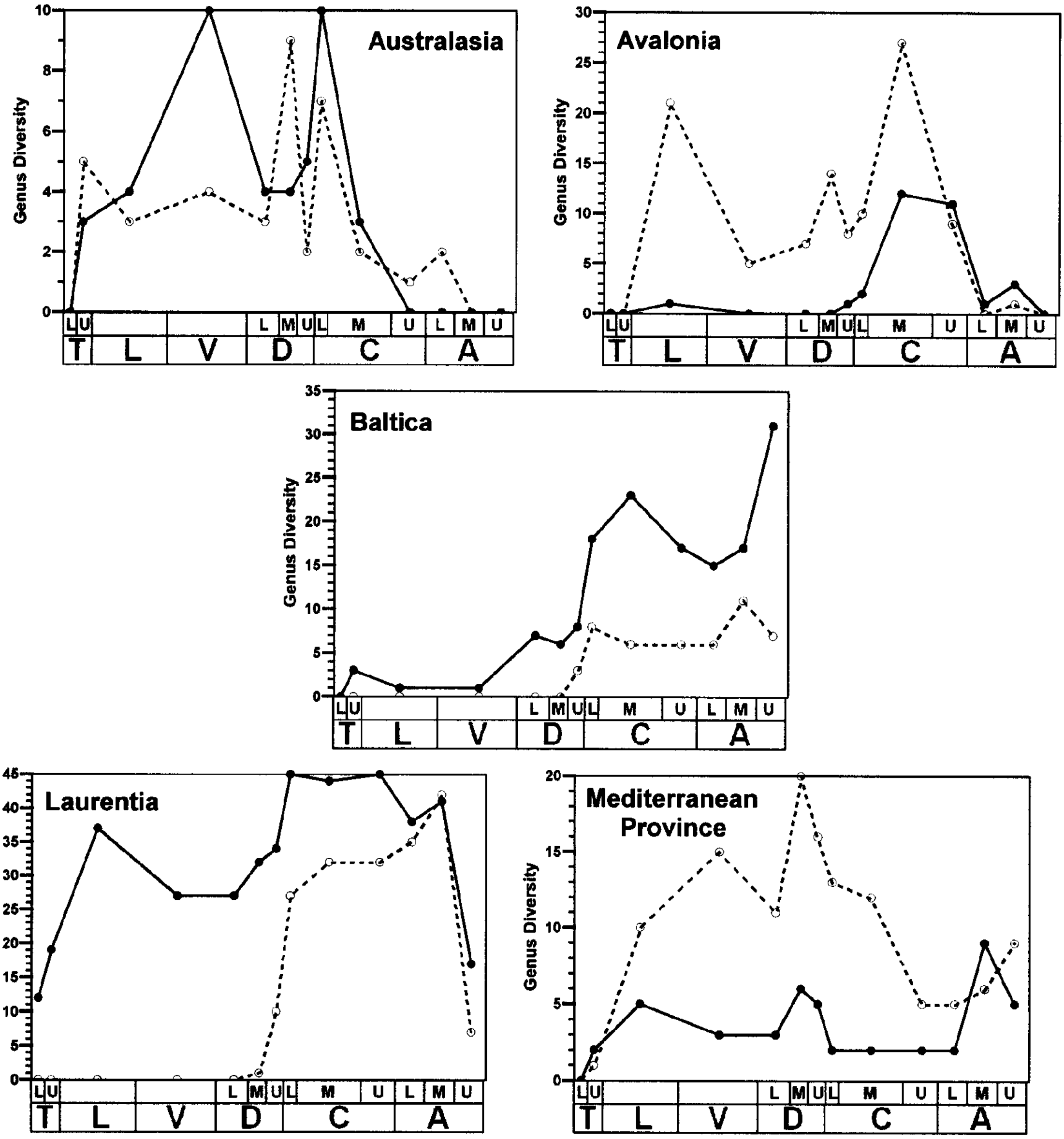


FIGURE 3. Ordovician diversity trajectories for gastropod and bivalve genera in Australasia, Avalonia, Baltica, Laurentia, and the Mediterranean Province. Lines and timescale are the same as in Figure 1.

TABLE 3. Results of the Spearman's rank correlation coefficient comparing gastropod and bivalve diversity trajectories by using first differences within five paleocontinents. N.S. signifies that the trajectories were not significantly correlated (i.e., $p > 0.05$).

Paleocontinents	r_s	Probability
Australasia	0.386	N.S.
Avalonia	0.721	$p < 0.01$
Baltica	−0.082	N.S.
Laurentia	0.334	N.S.
Mediterranean Province	0.310	N.S.

dovician diversities, a Caradocian increase in diversity, and a decrease in the Ashgillian (Fig. 3). Gastropods exhibited a broadly similar pattern that was statistically correlated with the bivalve trajectory (Table 3) despite less diversity, especially in the Lower Ordovician.

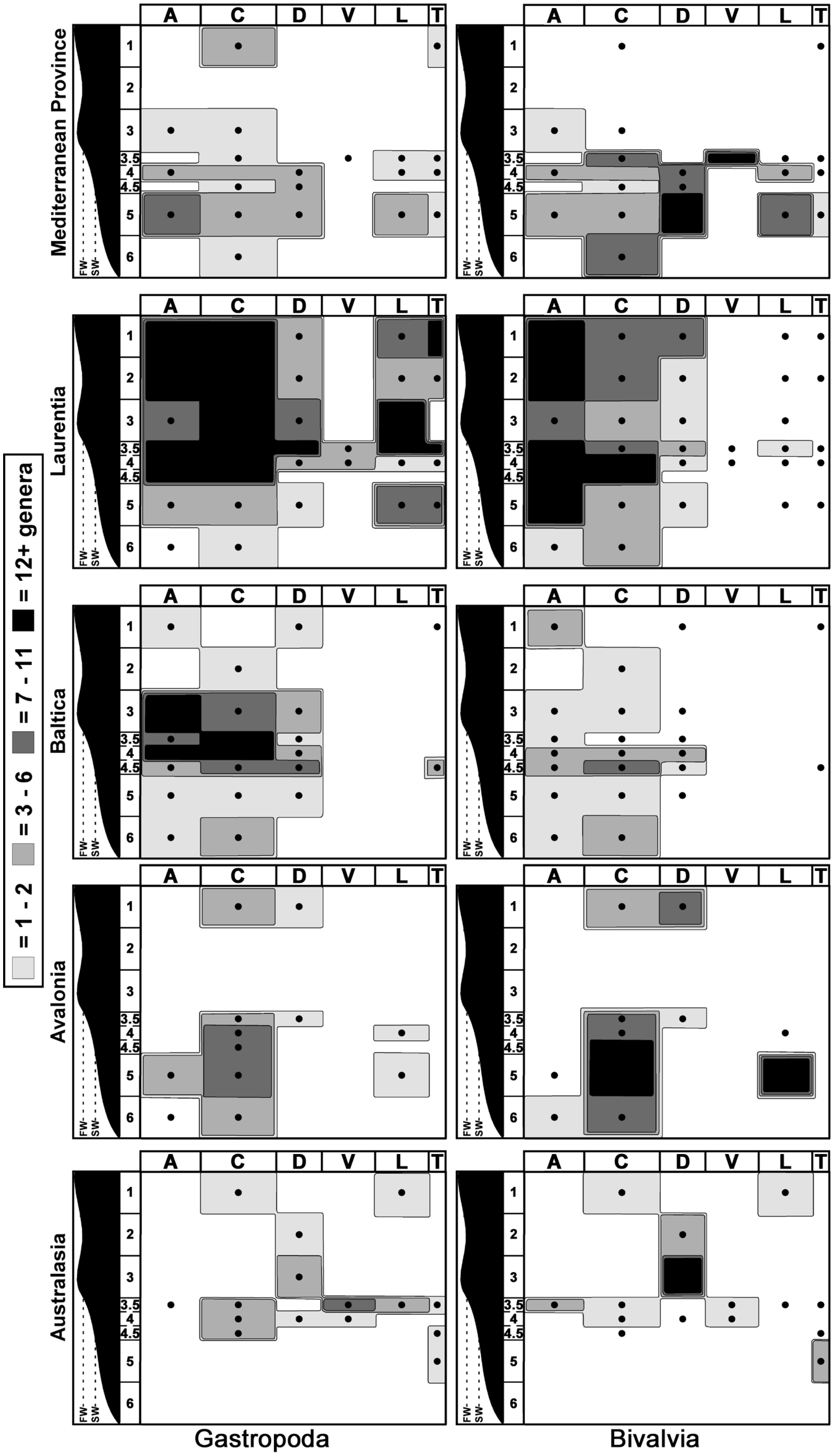
Both classes were most diverse in open-shelf through pro-deltaic and deep-water settings (Fig. 4; zones 3.5 to 6), with several genera of both classes in nearshore, volcaniclastic settings (zone 1) in the Caradocian and a diverse nearshore bivalve fauna (Cope 1999) in the Darriwilian. Despite such overall similarities, the environmental distributions of these classes were statistically different in the Lower and Middle Ordovician, although the limited environmental coverage prevented recognition of significant displacement with the *U*-test (Table 4).

Note that the diverse and important Latorpian bivalve fauna that Cope (1996: p. 980) reported from a ''close inshore'' setting has been reinterpreted here, following several lithofacies analyses of the strata (Traynor 1988; Bevins et al. 1992), as representing a deep-water, fan-delta below storm wave base (zone 5). Although it is possible that this fauna was relatively close to shore given the steep slopes along back-arc basinal deltas (Coleman and Prior 1981), the presence of sediment-gravity debris flows, hemipelagic muds, and the autochthonous nature of the fauna all argue for a zone 5 designation (Traynor 1988).

Baltica.—During the Early Ordovician, Baltica lay in temperate latitudes on the southeastern margin of the Iapetus Ocean (Torsvik 1998). As the Ordovician progressed, Baltica moved equatorward toward Laurentia and Siberia, colliding with Laurentia in the Silurian (Torsvik et al. 1996; Cocks and Fortey 1998; Torsvik 1998). Throughout the Ordovician, condensed sedimentation dominated with cool-water carbonate production and minor siliciclastics (Jaanusson 1973; Podhalanska 1995). Gastropod diversity increased through the period to higher levels than bivalves (Fig. 3), and the trajectories of the two classes were not significantly correlated (Table 3). The absence of gastropods and bivalves in Lower Ordovician sediments in this region possibly reflects ecologically significant patterns, as these sediments bear moderately rich non-molluscan faunas (Tjernvik 1956, 1958). However, the uncertain age determination of several gastropods from the Tremadocian Bjorkäsholmen Formation (Yochelson 1962) and the lack of more recent systematic study are also significant factors, although no Lower Ordovician bivalves have been reported from this richly fossiliferous region. Surprisingly, gastropods seem to have been little affected by the Late Ordovician extinction in this region.

Despite limited data from the Lower Ordovician, environmental distributions of both classes overlapped throughout the remaining Ordovician with greatest diversity of gastropods in shelf settings (Fig. 4; zones 3.5 to 4.5) and Upper Ordovician reefs (zone 3; Sheehan 1979; Harland 1981). Bivalves were rare in these reefs, moderately diverse in nearshore settings (zone 1) in the Ashgillian, and most diverse in deeper shelf environments (zones 4 through 6). Darriwilian bivalves were absent from all except the deeper midshelf (zones 4 to 4.5), despite the presence of moderately diverse gastropods in both deeper and shallower environments; thus, despite limited numbers of faunal lists (Appendix 2), their absence here is likely ecologically significant. There were insufficient data to test the environmental distributions for the Lower Ordovician. Their distributions were significantly different during the Middle Ordovician (Table 4) although limited bivalve data precluded a *U*-test. Despite much overlap in their distributions, Upper Ordovician bivalves were skewed statistically toward deeper water than gastropods.

Laurentia.—Laurentia occupied an equatorial position throughout the Ordovician Period (Scotese and McKerrow 1991). Early and Middle Ordovician sedimentation consisted predominantly of carbonates on passive-margin ramps and relatively shallow cratonic basins with occasional mixed-siliciclastic influx (James et al. 1989; Read 1989; Ross et al. 1989; Holland 1993; Ross and Ross 1995). Siliciclastic sedimentation increased significantly in eastern Laurentia during the Middle to Late Ordovician with initiation of the Taconic Orogeny (Holland and Patzkowsky 1996). Carbonate and mixed regimes, however, still predominated throughout much of the paleocontinent (Holland 1993; Ross and Ross 1995). Although Laurentia produced more faunal lists than all other studied paleocontinents (Appendix 1), identifiable bivalve species are not recorded until the Darriwilian (Fig. 3); sparse Latorpian bivalves from the Smithville Formation of Arkansas remain taxonomically indeterminate (Yochelson and Wise 1972). In


= 1 - 2
= 3 - 6
= 7 - 11
= 12+ genera
Mediterranean Province
Laurentia
Baltica
Avalonia
Australasia
A
C
D
V
L
T
1
2
3
3.5
4
4.5
5
6
FW-
SW-
Gastropoda
Bivalvia

contrast to the bivalve record, the gastropod faunas of Laurentia were the most diverse of any Ordovician paleocontinent (Wagner 1999). Consequently, gastropod and bivalve diversity trajectories were not statistically correlated (Table 3), even when only the Upper Ordovician trajectories were compared ($r_s = 0.700$; $p > 0.05$). Both classes underwent dramatic radiations in the upper Darriwilian that continued into the Caradocian, coincident with the onset of the Taconic Orogeny. Regional dynamics of these classes within Laurentia are described below, as are the implications of the dramatic change in physical environment brought about by this orogenic event.

Laurentian gastropods inhabited a range of Lower and Middle Ordovician environments (Fig. 4; zones 1 through 5), although they were most diverse in nearshore, biohermal, and shallow shelf settings (zones 1 and 3 to 3.5); because of extensive coverage of faunal lists (Appendix 2), the near absence of bivalves in these environments is significant. When bivalves diversified in the Middle to Upper Ordovician, both classes occupied a full range of environments, from nearshore (zone 1) to basinal (zone 6). However, Upper Ordovician gastropods were most diverse in shallow-water and shelf settings (zones 1 through 4.5), with an absence from deep water during the Ashgillian. Upper Ordovician bivalves were consistently most diverse in shelf settings (zones 3.5 through 5), although they were also diverse in nearshore and lagoonal settings (zones 1 through 2) in the Ashgillian. These patterns were corroborated statistically, with Middle Ordovician bivalves skewed toward shallower settings than gastropods, and with the converse pattern in the Upper Ordovician (Table 4).

Mediterranean Province.—The Mediterranean Province denotes the faunas situated on small continental blocks along the western Gondwanan margin found in present-day Portugal, Spain, France, the Czech Republic, and the Moroccan Anti-Atlas (Williams et al. 1995; Cocks and Fortey 1988). During the Ordovician, these blocks bordered the Iapetus Ocean in polar and subpolar latitudes of the Southern Hemisphere (Scotese and McKerrow 1991), dominated by siliciclastic sedimentation in shelf settings (Babin 1993, 1995). The diversity trajectories of gastropods and bivalves throughout the period (Fig. 3) were not significantly correlated (Table 3), with gastropods generally less diverse than bivalves. Although this paleocontinent was the second-most intensively sampled, gastropod diversity was lower than any other paleocontinent or region in Laurentia. Furthermore, gastropod diversity here was relatively stable throughout the Ordovician, with only a minor increase in the middle Ashgillian. Bivalve diversity, in contrast, increased to a Darriwilian peak and decreased to the end of the Ordovician, with a slight increase in the upper Ashgillian.

Throughout the Ordovician, both classes were most diverse in shelf and deep-water settings (Fig. 4; zones 3.5 through 6). Minor occurrences include gastropods in nearshore settings (zone 1) in the Tremadocian and Upper Ordovician to the exclusion of bivalves. Additionally, gastropods also occupied shoal settings (zone 3) throughout the Upper Ordovician, sharing this setting with bivalves in the Ashgillian. Despite the limited number of faunal lists from shallower environments (Appendix 2), the absence of bivalves from moderately gastropod-rich settings in six instances throughout the Ordovician is likely ecologically meaningful. Accordingly, these classes had distinct environmental distributions throughout the Ordovician, although environmental displacement was not distinguishable with the *U*-test (Table 4).

Discussion of Paleocontinental Patterns

Of the five Ordovician paleocontinents discussed above, only Avalonia showed significantly correlated diversity trajectories among gastropod and bivalve genera. Thus, among

←

FIGURE 4. Contoured time-environment diagrams depicting the genus diversity of gastropods (above) and bivalves (below) in Australasia, Avalonia, Baltica, Laurentia, and the Mediterranean Province during the Ordovician. The timescale is the same as in Figure 1. The key at top depicts the genus diversity of each class within shaded contours.

TABLE 4. Results of statistical comparisons of environmental distributions of Ordovician gastropod and bivalve genera for different paleocontinents and Laurentian regions. Comparisons were made at the level of Ordovician subsystems: Lower (or Tremadocian–Latorpian), Middle (or Volkhovian–Darriwilian), and Upper (Caradocian–Ashgillian). Statistical tests and representation of results are the same as in Table 2.

	Lower Ordovician						Middle Ordovician	
	K.-S. test		M.-W. *U*-test				K.-S. test	
	D	Prob.	*U*	z	Prob.	Bivalves	D	Prob.
Paleocontinent								
Australasia	0.633	$p < 0.01$	14.5	-1.681	$p < 0.05$	Deeper	0.376	$p < 0.01$
Avalonia	0.500	$p < 0.01$	10.5	-1.146	N.S.	—	0.846	$p < 0.05$
Baltica	**	**	—	—	—	—	0.286	$p < 0.05$
Laurentia	0.455	N.S.	—	—	—	—	0.416	$p < 0.01$
Mediterranean Province	0.375	$p < 0.01$	43.0	-0.887	N.S.	—	0.273	$p < 0.01$
Regions in Laurentia								
Appalachian Basin	**	**	—	—	—	—	1.000	N.S.
Cincinnati Arch	**	**	—	—	—	—	**	**
Mississippi Valley	**	**	—	—	—	—	0.000	N.S.
Great Basin	**	**	—	—	—	—	0.124	N.S.

these classes, the strong correlation of diversity trajectories observed at the global scale is not maintained at the finer scale of individual paleocontinents. Although the data for other paleocontinents were not presented above because of limited coverage in the database, similar patterns are apparent in the available data (see Appendix 1 for data coverage). Bivalves and gastropods of Siberia and the South American Precordillera exhibited no significant correlations in their diversity trajectories ($r_s = -0.135$ and -0.205, respectively; $p > 0.05$), whereas these classes were significantly correlated in Kazakhstania and Gondwanan South America (in both cases, $r_s = 0.774$; $p < 0.01$). The diversity trajectories for bivalves from several of these regions were reported by Cope and Babin (1999).

A strong distinction is apparent throughout the Ordovician between ''gastropod-rich'' and ''bivalve-rich'' paleocontinents. The former category is exemplified by Baltica and Laurentia, the latter by the Mediterranean Province, South America, Precordillera, and Avalonia. Australasia, Siberia, and Kazakhstania have faunas with approximately equal diversities of both classes. This heterogeneity of diversification patterns amplifies the observations by Babin (1993, 1995; Cope and Babin 1999) and Miller (1997a) that the Ordovician Radiation transpired differently among different paleocontinents.

Given the limitations of smaller data sets at the scale of paleocontinents, the environmental distributions of gastropods and bivalves at these finer scales exhibited trends that were broadly comparable to the global distribution. Despite a pattern of broad environmental overlap between the classes, statistical tests demonstrate quite different environmental distributions; only two in 14 comparisons yielded statistically indistinguishable distributions. Furthermore, bivalves repeatedly were most diverse in deeper settings than gastropods, although this was corroborated statistically in only three instances (Table 4). Given the heterogeneity of diversification patterns found throughout the Ordovician world and the evolution of significant morphologic adaptations in both classes during the Ordovician (Miller 1988; Wagner 1995b, 1996; Cope 1997; Cope and Babin 1999), it is notable that the basic environmental distributions of these classes were consistently maintained.

Dominance of these classes tends to correlate with variation in sedimentological regime, paleoclimate, paleolatitude, and tectonic activity among Ordovician paleocontinents (Table 5). The most-diverse bivalve faunas were found in temperate to polar paleocontinents in fine-grained, deeper environments (zones 3.5 to 5) where the rate of siliciclastic influx was high or where carbonate production was limited. Such regions included west-

TABLE 4. Extended.

Middle Ordovician				Upper Ordovician					
M.-W. *U*-test				K.-S. test		M.-W. *U*-test			
U	z	Prob.	Bivalves	D	Prob.	*U*	z	Prob.	Bivalves
292.5	2.102	$p < 0.05$	Shallower	0.363	$p < 0.01$	56.0	1.321	N.S.	—
12.0	1.364	N.S.	—	0.053	N.S.	—	—	—	—
67.0	0.233	N.S.	—	0.343	$p < 0.01$	1116.0	−3.106	$p < 0.005$	Deeper
525.5	2.188	$p < 0.05$	Shallower	0.172	$p < 0.01$	13,874.5	−3.538	$p < 0.005$	Deeper
350.5	1.227	N.S.	—	0.179	$p < 0.01$	384.0	−0.379	N.S.	—
—	—	—	—	0.217	$p < 0.01$	4804.5	−3.246	$p < 0.005$	Deeper
—	—	—	—	0.191	$p < 0.01$	3289.0	−3.008	$p < 0.005$	Deeper
—	—	—	—	0.175	$p < 0.05$	928.0	−2.233	$p < 0.05$	Deeper
—	—	—	—	**	**	—	—	—	—

ern Gondwana (Mediterranean Province and South America), Avalonia, and the Precordillera (Cope and Babin 1999). Gastropod faunas were negatively correlated with these same factors, showing the greatest diversity in lower-latitude paleocontinents in more carbonate-dominated, shallow environments (zones 1 to 4.5), although representing both tropical and cool-water carbonate deposition. These settings were most characteristic of Laurentia and Baltica. The remaining paleocontinents, Kazakhstania, Australasia, and Siberia, were dominated by neither class and primarily represent low-latitude paleocontinents dominated by mixed-siliciclastic sedimentation and a broad range of environmental settings, although open-shelf settings were most common.

If this proposed ecological connection between physical environment and diversification of these classes is true, one should expect these classes to respond at least as rapidly to changes in environmental conditions *within* a paleocontinent as they did *among* paleocontinents. As noted above, Laurentia was dominated by carbonate environments during the Early and Middle Ordovician; with the onset of the Taconic Orogeny, the sedimentological regime shifted dramatically in several portions of the paleocontinent as a result of siliciclastic sedimentation. Thus, if local environmental regime was an important ecological correlate of bivalve and gastropod diversification during the Ordovician, one should expect their evolutionary dynamics within different regions within Laurentia to reflect these changes in ways similar to those exhibited at the scale of paleocontinents.

Laurentian Results and Discussion

Laurentian Diversity Trajectories and Environmental Zones

Appalachian Basin.—During the Early and Middle Ordovician, the Appalachian Basin was a passive carbonate shelf margin bordering the Iapetus Ocean (James et al. 1989; Read 1989). Middle to Late Ordovician tectonic collision initiated the Taconic Orogeny (Rowley and Kidd 1981), resulting in extensive siliciclastic influx toward the present-day southwest (James et al. 1989; Holland 1993). After accounting for the absence of bivalves until the lower Caradocian in this region, first differences reveal that the trajectories of bivalves and gastropods were still not significantly correlated (Table 6, Fig. 5). Both classes radiated dramatically in the lower Caradocian and waned slightly throughout the remaining Ordovician, with gastropods more diverse than bivalves.

Lower and Middle Ordovician gastropods were most diverse in tidal flat and shallow shelf settings, with minor occurrences in Dar-

TABLE 5. Summary of environmental factors characterizing Ordovician paleocontinents. These regions are arranged by order of dominant molluscan class and paleolatitude. Mixed sedimentation regime refers to mixed-siliciclastic-carbonate facies. Factors describe the interval coinciding with the maximal diversity for the dominant class. See text for explanation of environmental zones.

Paleocontinent	Dominant class	Paleolatitude/ paleoclimate	Primary sedimentologic regime	Primary environmental zones of dominant class
Mediterranean Province	Bivalve	Sub-polar to polar	Siliciclastic	3.5 to 5
South America	Bivalve	Temperate to sub-polar	Siliciclastic	3.5 to 4.5
Avalonia	Bivalve	Temperate to sub-polar	Siliciclastic	4.5 to 5
Precordillera	Bivalve	Subtropical to temperate	Mixed	3.5 to 5
Australasia	Both	Tropical to subtropical	Siliciclastic/Mixed	3.5 to 4
Kazakhstania	Both	Tropical to subtropical	Siliciclastic/Mixed	1 to 4
Siberia	Both	Tropical to subtropical	Mixed	1 and 3.5 to 5
Baltica	Gastropod	Subtropical to temperate	Carbonate	3 to 4.5
Laurentia	Gastropod	Tropical to subtropical	Carbonate/mixed	1 to 4.5

TABLE 6. Results of the Spearman's rank correlation coefficient comparing gastropod and bivalve diversity trajectories using first differences in four regions within Laurentia. N.S. signifies that the trajectories were not significantly correlated (i.e., $p > 0.05$). A single asterisk, for the Cincinnati Arch, designates that the correlation is an artifact of a shared lack of data during the Lower and Middle Ordovician; when only the Upper Ordovician is considered, the results are not significantly correlated. In the case of the Great Basin, a double asterisk indicates insufficient data to allow a meaningful comparison.

Laurentian region	r_s	Probability
Appalachian Basin	0.477	N.S.
Cincinnati Arch	0.616	$p < 0.025$/N.S.*
Mississippi Valley	0.864	$p < 0.005$
Great Basin	**	**

riwilian biostromes (Fig. 6; zones 1 and 3 to 3.5); as is true for all Laurentian regions, bivalves were absent until the Darriwilian. Upper Ordovician gastropods were still present in shallow-water settings but expanded their range in all shelf settings (zones 1 to 4.5), with only sparse Caradocian occurrences in deeper water (zones 5–6). Though bivalves shared generally similar ranges, they were most diverse in shelf settings (zones 3.5 to 4.5), with lesser occurrences in nearshore, lagoonal, and deep-water settings (zones 1 to 2 and 5 to 6). Consequently, bivalves were skewed statistically toward deeper settings than gastropods (Table 4).

Cincinnati Arch.—Despite no outcropping pre-Caradocian rocks in the Cincinnati Arch, subsurface cores are similar to contemporaneous Appalachian Basin strata (Feldman 1996). Late Ordovician sedimentation consisted of mixed-carbonate-siliciclastic lithologies in which orogenically derived shales were interbedded with tempestite packstones, wackestones, and calcisiltites (Holland 1993). Diversity trajectories of gastropod and bivalve genera were significantly correlated (Table 6, Fig. 5). However, this similarity reflects the lack of fossil data within the Lower and Middle Ordovician; when only the Upper Ordovician is considered, the two trajectories are not significantly correlated. Gastropods were very diverse in the Caradocian, but their diversity waned in the Ashgillian whereas bivalve diversity matched that in the Appalachian Basin.

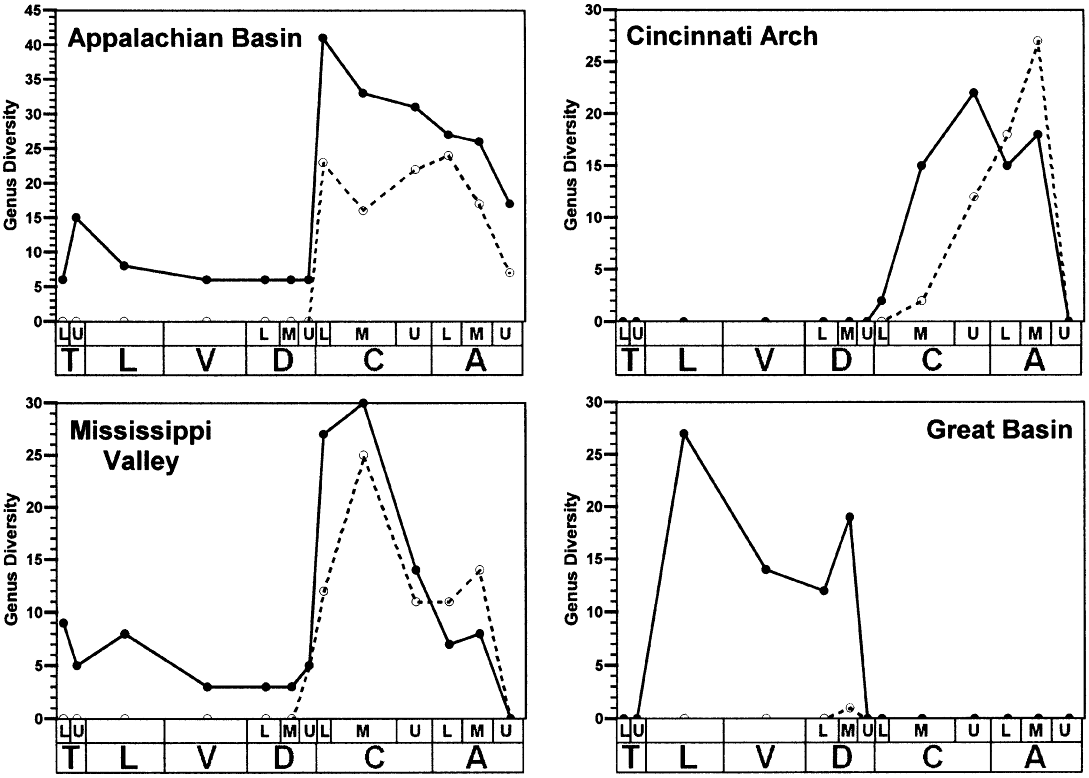
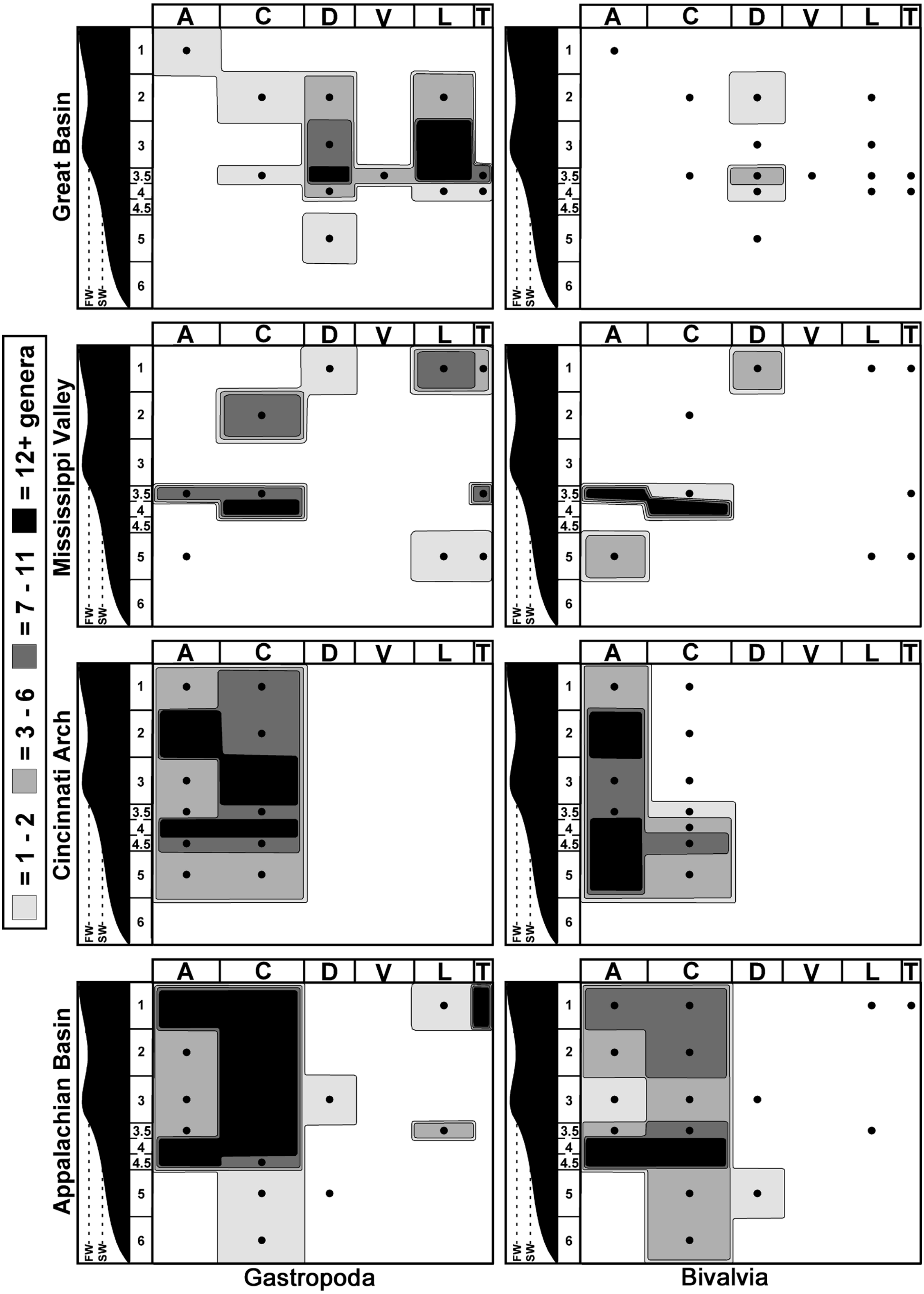


FIGURE 5. Ordovician diversity trajectories for gastropod and bivalve genera in the Appalachian Basin, Cincinnati Arch, Mississippi Valley, and Great Basin. Lines and timescale are the same as in Figure 1.

Caradocian gastropods and bivalves were both found in open-shelf settings (zones 3.5 to 5), although bivalves were absent from peritidal, lagoon, and shoal settings (zones 1 to 3). These absences are significant given the moderate gastropod diversity and intensive sampling in these strata (Pojeta 1971, 1979). Both classes occurred throughout a wide range of Ashgillian settings (Fig. 6; zones 1 to 5), sharing major diversity in lagoonal and midshelf settings (zones 2 and 4). Bivalves, however, were also more diverse than gastropods in deeper shelf settings (zones 4.5 to 5), a difference that was statistically significant (Table 4). This differentiation is further borne out in field studies in the Cincinnati Arch (Novack-Gottshall and Miller in press) that show bivalves were both most diverse *and most abundant* in offshore, siliciclastic-dominated shales with high turbidity, whereas gastropods were most diverse and most abundant in shallower, more carbonate-rich facies generally lacking turbidity.

Mississippi Valley.—Depositional environments in the Mississippi Valley during the Early and Middle Ordovician consisted primarily of relatively shallow, storm-influenced carbonate platforms with occasional siliciclastic influx derived from Precambrian basement rock of the Transcontinental Arch (Raatz and Ludvigson 1996; Barnes et al. 1996). As the basin deepened during the Late Ordovician, the region was inundated with fine-grained, siliciclastic sediments produced by both the Taconic Orogeny and continued erosion of the Transcontinental Arch, resulting in mixed-siliciclastic-carbonate lithologies; however, carbonates still remained locally common. The statistically indistinguishable diversity trajectories of bivalves and gastropods were comparable to those in the Appalachian Basin (Table 6, Fig. 5), with gastropods generally more diverse than bivalves except in the Ashgillian when the diversities of both classes declined.

In the Lower and Middle Ordovician, gastropods were most common in nearshore and


= 1 - 2
= 3 - 6
= 7 - 11
= 12+ genera
Great Basin
Mississippi Valley
Cincinnati Arch
Appalachian Basin
A
C
D
V
L
T
1
2
3
3.5
4
4.5
5
6
FW-
SW-
Gastropoda
Bivalvia

shallow-shelf settings (Fig. 6; zones 1 and 3.5) with sparse occurrences in deep-shelf settings (zone 5); as noted above, bivalves were absent until the Darriwilian when they occurred in nearshore settings (zone 1) with gastropods. In the Upper Ordovician, both classes co-occurred in shallow and midshelf settings (zones 3.5 through 4); however, gastropods also occurred in lagoons (zone 2), whereas bivalves were diverse in deep-shelf settings (zone 5). Given these differences, their environmental distributions were significantly distinct in the Upper Ordovician, with bivalves extending to deeper environments than gastropods (Table 4).

Great Basin.—Located almost directly on the equator for much of the Ordovician, the Great Basin was a vast carbonate platform with a variety of depositional environments (Ross et al. 1989). Sufficient aeolian sands and silts entered the basin to produce mixed-carbonate-siliciclastic lithologies, and cratonic erosion during the latest Middle Ordovician Sauk-Tippecanoe unconformity was sufficient to nearly drown the shelf with coarse-grained siliciclastics (Ross et al. 1989; Keller and Cooper 1995). However, nearly pure carbonate-rich conditions resumed throughout the Late Ordovician (Droser and Sheehan 1995). Gastropods were quite diverse in this region in the Lower and Middle Ordovician (Fig. 5), with Upper Ordovician gastropods either unstudied, poorly preserved, or with poor stratigraphical resolution (Webb 1958; Droser and Sheehan 1995). Because of the rarity of bivalves from this region, statistical comparisons of the diversity trajectories were not possible (Table 4).

Gastropods were distributed throughout a range of environments in the Lower and Middle Ordovician (Fig. 6; zones 2 to 5), attaining greatest diversity in shoal and shallow-shelf settings (zones 3 to 3.5). Upper Ordovician gastropods were locally common in nearshore settings (zone 1; Droser and Sheehan 1995); additional occurrences from a variety of deeper-water settings are also known but unpublished (Sheehan personal communication 2003). Indeterminate bivalves have been noted only rarely and no taxonomic descriptions have been published from this region since Walcott's classic study of the Eureka District (1884). Given the numerous occurrences of gastropods, the rarity of bivalves in the Great Basin is likely ecologically meaningful. Recently, several Middle Ordovician bivalves have been discovered in the Great Basin (Moffat et al. 2001), but these are not sufficiently diverse to change significantly the results presented here. Regardless, statistical comparisons of environmental distributions were not possible (Table 6).

Discussion of Laurentian Patterns

The diversity trajectories of gastropods and bivalves within these four regions were similar to those of Laurentia as a whole, with bivalves absent until the latest Middle Ordovician when both classes diversified dramatically. This diversification was not apparent in the Great Basin, but the lack of well-preserved and recently studied Upper Ordovician molluscs limits further interpretation; the rarity of pre-Caradocian bivalves in this region, however, is not likely to change. Of the four regions studied, only the Mississippi Valley exhibits significant correlations between gastropod and bivalve diversity trajectories. Despite moderately overlapping environmental distributions for both classes in all four regions, these classes had statistically different distributions; gastropods were most diverse in shallower-water settings than bivalves, which were most diverse in deep-shelf, fine-grained, siliciclastic settings.

Although gastropods were quite diverse in each region, bivalves outnumbered them in the Cincinnati Arch and the Mississippi Valley; both of these regions were dominated by storm-influenced sedimentation and mixed-siliciclastic-carbonate lithologies. Notably, bivalve diversification in all four regions coin-

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FIGURE 6. Contoured time-environment diagrams depicting the genus diversity of gastropods (above) and bivalves (below) in the Appalachian Basin, Cincinnati Arch, Mississippi Valley, and Great Basin during the Ordovician. The timescale is the same as in Figure 1. The key at top depicts the genus diversity of each class within shaded contours.

cided with influx of fine-grained sediments from either orogenic activity or erosion of cratonic highlands. Gastropods exhibited similar but reduced patterns in the Upper Ordovician, and they maintained diversity throughout shallow carbonate strata throughout the Ordovician. These environmental patterns parallel observations made at the scales of paleocontinents and the world as a whole, in which gastropods were generally most diverse in shallower water than bivalves. Furthermore, they support the earlier observation from the comparisons among paleocontinents that the nature of the physical environment was intimately related to the diversification of these classes.

General Discussion and Conclusions

The Ordovician Radiation of gastropods and bivalves was a complex but especially important period in the history of these classes, responsible for dramatic increases in the number of genera and the origins of many higher taxonomic groups. Although gastropods and bivalves displayed statistically indistinguishable global diversity dynamics throughout the Ordovician, this study documents more disparate dynamics at the finer scales of five paleocontinents and four regions within Laurentia. Furthermore, there was significant heterogeneity in diversity patterns among paleocontinents, with bivalves diversifying first in the Gondwanan paleocontinents before occurring later in Laurentia and Baltica (see also Babin 1993, 1995 and Cope and Babin 1999), where gastropods were already well established. Among these paleocontinents, only Avalonia exhibited significantly correlated bivalve and gastropod diversity trajectories. These statistical differences were further observed at the finest scale of regions within Laurentia.

This scale-dependence of diversity trajectories contrasts with the scale-independent environmental distributions of these classes. Regardless of whether Ordovician gastropod and bivalve genus occurrences are considered in global aggregate or at the finer scales of paleocontinents or regions within Laurentia, a similar environmental picture emerges in cases where there are sufficient data to permit an analysis. Gastropods were most diverse in shallow water, carbonate-rich platforms in low latitudes; in contrast, bivalves were most diverse in deeper-water, higher-latitude settings in which fine-grained siliciclastics predominated, whether resulting from tectonic activity or a lack of carbonate production.

Although our study supports the conclusions of Babin (1993, 1995; Cope and Babin 1999) regarding the paleocontinental diversification of bivalves, our results concerning environmental trends may appear at first glance to be at odds with those Cope and Babin (1999) in two significant details. First, they argued that Ordovician, and particularly Lower Ordovician, bivalves were generally restricted to nearshore clastic settings. Although it is true that bivalves did inhabit shallow-water settings throughout the Ordovician, our results, and those of several other studies (e.g., Babin et al. 1982; Frey 1987; Miller 1988, 1989) clearly demonstrate that bivalves were neither most diverse nor restricted to these settings at any point during the Ordovician. In fact, with three low-diversity, nearshore exceptions (Harrington 1938; Nikitin et al. 1986; Shergold et al. 1991), most Lower Ordovician bivalves occurred in deeper-water settings, including the diverse Latorpian fauna (Cope 1996) reinterpreted here as representing deep-water, fan-deltaic facies (zone 5). Reconciliation may be found by differences in our definitions of shallow water, as even our zone 5 shelf may be considered ''relatively shallow'' or ''onshore'' compared with slope and basinal deposits (see discussion in Structure of the Database above).

A second, more significant point of difference is their conclusion that Late Ordovician bivalve diversification in Laurentia was spurred on by the presence of carbonate platforms. Although Laurentia was indeed the site of extensive Late Ordovician bivalve diversification (Fig. 3), this radiation was *limited* primarily to settings influenced by siliciclastic sedimentation in a significant part of the central and eastern United States and Canada (Fig. 5). It is possible that Cope and Babin (1999) implied a role for carbonates because of the tropical location of Laurentia during the Ordovician. However, direct assessment of Middle and Upper Ordovician strata makes

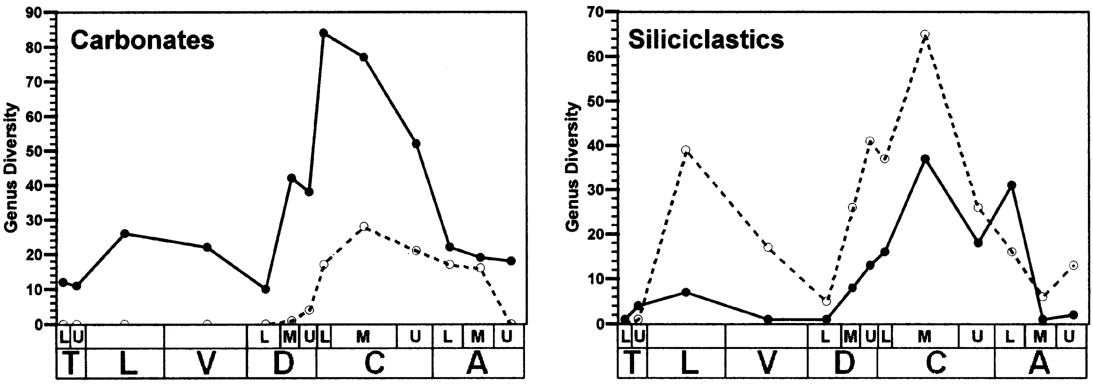

FIGURE 7. Ordovician diversity trajectories for gastropod and bivalve genera in carbonate and siliciclastic sedimentary regimes. Lines and timescale are the same as in Figure 1.

clear the increasing role in Laurentia of siliciclastic sedimentation.

In contrast, gastropods continued to be diverse both in these siliciclastic settings and in the vast carbonate platforms that persisted in other parts of Laurentia. This sedimentological conclusion is further supported at the global scale by plotting the diversity trajectories of gastropods and bivalves in siliciclastic and carbonate environments (Fig. 7). Both classes inhabited both types of sediments, but bivalves were significantly more diverse in siliciclastic settings than they were in carbonate settings throughout the Ordovician, with gastropods exhibiting the opposite pattern.

Although compelling, depth and sedimentation are likely not the sole ecological factors underlying the diversification of these classes. For example, if the presence of deep-water, fine-grained siliciclastics were the sole prerequisites for the establishment of bivalves in Laurentia, one might expect a diverse bivalve fauna in the Lower Ordovician Ninemile Shale in Nevada (Merriam 1963). Clearly, other ecological factors, such as substrate firmness, turbidity, latitude, climate, dispersal histories, microhabitat, or feeding strategies, may also play important roles. For example, using a field-based analysis of Upper Ordovician, mollusc-rich strata in the Cincinnati Arch, Novack-Gottshall and Miller (in press) demonstrated that bivalve dominance, in terms of both species richness and individual abundance, was correlated with high-turbidity settings regardless of lithology, whereas gastropods were generally correlated with low turbidity settings.

What do these patterns reveal about the causes of the radiation of gastropods and bivalves during the Ordovician and the cohesion of evolutionary faunas? Clearly, any answer must resolve the relationship between scale-dependent diversity trajectories and scale-independent environmental distributions. One view, originally formulated by Sepkoski (1991, 1996; Sepkoski and Miller 1985; Miller and Sepkoski 1988; Sepkoski et al. 2000), requires that these classes overlapped in space and time and interacted ecologically in similar ways with other species, either directly through predation, competition, and parasitism or indirectly through decreased availability of resources and habitat. Given the disparate diversity trajectories and environmental distributions of these classes around the Ordovician world, such a hypothesis is not obviously borne out unless these classes were responding similarly to the same stimuli independently of their geographic venues and environmental occurrences.

Another possibility is that the independent, ecological requirements of these classes were negligible relative to the similar, intrinsic turnover dynamics of these classes. This view, proposed by Sepkoski (1981), Gilinsky (1994), and Benton (1995), holds that shared intrinsic macroevolutionary propensities will result in generally similar diversity trajectories as long as both classes originated at approximately the same time. Although this view appears to be borne out at the global scale, it is insufficient, by itself, to explain the rather different dynamics of these classes in different geographic and environmental settings. Furthermore, such a macroevolutionary explanation requires that the strong correlation between the diversification of these classes and the physical setting within these paleocontinents is coincidental, which is unlikely given the general observation that wherever shallow carbonate settings flourished throughout the regions covered in this database, gastropods were diverse. In addition, wherever there was significant influx of or sufficient sedimentological conditions for fine-grained siliciclastic sediments into deep subtidal settings, bivalves were more likely to flourish. These relationships were best exemplified in Laurentia, where the Taconic Orogeny dramatically altered the physical setting of the paleocontinent by introducing large amounts of siliciclastic sedimentation. Only after the advent of widespread siliciclastic sedimentation did bivalves become established there.

Thus, the Ordovician Radiation of gastropods and bivalves appears to be best characterized by a dynamic interaction between the consistent environmental propensities of each class in a world experiencing large-scale physical transitions, including tectonic, climatological, and oceanographic changes (Miller 1997b, 1998). However, given that these classes responded differently to these environmental transitions, and that the composite global diversity trajectories of these classes were statistically indistinguishable, this conclusion does not reject the claim that intrinsic macroevolutionary properties of these classes were also important contributors to their global diversification (see Connolly and Miller 2002). For example, intrinsic factors may have played significant roles in determining the turnover rates, carrying capacities, or other macroevolutionary factors underlying the dynamics of their radiations. However, our results suggest that the initial capacity of these classes to diversify during the Ordovician was affected greatly by their environmental propensities in a physically dynamic Ordovician world.

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Appendix 1

Sampling intensity for data used to compile diversity trajectories. Data are given for the five paleocontinents and four regions within Laurentia for which results are illustrated in the text, as well as the four paleocontinents from which data are only summarized.

	No. of faunal lists	No. of occurrences	No. of primary references
Global	711	6510	267
Paleocontinents from which results are reported:			
Australasia	38	183	15
Avalonia	45	282	16
Baltica	60	287	30
Laurentia	410	5126	132
Mediterranean Province	77	330	26
Paleocontinents from which results are summarized:			
Gondwanan South America	22	58	15
Kazakhstania	8	82	7
Precordillera	11	31	10
Siberia	17	82	13
Regions within Laurentia:			
Appalachian Basin	201	2807	50
Cincinnati Arch	79	570	13
Great Basin	20	117	14
Mississippi Valley	47	926	19

Appendix 2

Sampling intensity for data used to compile environmental distributions. Numbers across the top record the environmental zone. Within each zone, the data record, from left to right, the total number of faunal lists, the number of occurrences, and the number of primary references. Dashes record time-environment cells in which no gastropods, bivalves, or monoplacophorans were available from the published literature.

	1			2			3			3.5			4			4.5			5			6		
Global																								
(Total: 702 faunal lists, 5230 occurrences, 258 primary references)																								
Ashg	17	221	14	14	91	8	10	65	15	29	191	22	34	425	24	25	227	17	15	114	19	4	9	4
Cara	21	203	22	25	128	15	16	108	13	59	350	34	111	1462	70	46	263	20	21	102	21	14	61	12
Darw	11	55	10	5	21	4	13	116	11	23	106	20	15	70	15	16	72	19	24	72	16	2	2	4
Volk	—	—	—	—	—	—	—	—	—	6	48	4	3	12	2	—	—	—	—	—	—	—	—	—
Latp	15	110	9	3	9	1	3	32	5	12	63	13	5	20	7	5	17	5	12	112	7	—	—	—
Trem	21	82	21	3	11	3	—	—	—	15	60	12	9	13	7	4	6	5	16	93	8	—	—	—
Paleocontinents																								
Australasia (Total: 44 faunal lists, 212 occurrences, 10 primary references)																								
Ashg	—	—	—	—	—	—	—	—	—	2	4	2	—	—	—	—	—	—	—	—	—	—	—	—
Cara	2	5	2	—	—	—	—	—	—	6	16	4	8	16	5	1	5	1	—	—	—	—	—	—
Darw	—	—	—	2	9	1	7	62	2	—	—	—	1	3	1	—	—	—	—	—	—	—	—	—
Volk	—	—	—	—	—	—	—	—	—	2	26	2	1	2	1	—	—	—	—	—	—	—	—	—
Latp	3	6	1	—	—	—	—	—	—	1	7	2	—	—	—	—	—	—	—	—	—	—	—	—
Trem	—	—	—	—	—	—	—	—	—	1	3	1	—	—	—	1	1	1	6	47	2	—	—	—
Avalonia (Total: 39 faunal lists, 274 occurrences, 14 primary references)																								
Ashg	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	4	1	1	1	1
Cara	3	21	2	—	—	—	—	—	—	6	41	4	5	42	5	5	52	3	5	47	3	3	19	3
Darw	3	14	1	—	—	—	—	—	—	1	4	1	—	—	—	—	—	—	—	—	—	—	—	—
Volk	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Latp	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	—	—	—	2	28	2	—	—	—
Trem	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Baltica (Total: 81 faunal lists, 345 occurrences, 36 primary references)																								
Ashg	2	8	3	—	—	—	5	38	8	3	16	3	4	35	3	2	17	1	2	4	4	1	3	1
Cara	—	—	—	1	4	2	3	15	5	1	19	1	12	39	9	14	57	3	4	10	6	2	15	2
Darw	1	1	1	—	—	—	1	3	3	1	2	1	4	8	4	11	37	5	2	2	2	—	—	—
Volk	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Latp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Trem	1	4	1	—	—	—	—	—	—	—	—	—	—	—	—	4	8	2	—	—	—	—	—	—
Laurentia (Total: 400 faunal lists, 3716 occurrences, 125 primary references)																								
Ashg	14	201	10	14	91	7	4	24	4	21	161	14	26	363	11	19	208	16	7	73	5	1	2	1
Cara	11	108	9	23	118	12	12	85	6	33	250	17	75	1286	33	25	145	11	6	19	4	5	12	2
Darw	4	36	3	3	12	3	4	28	5	17	82	16	1	6	2	—	—	—	2	6	4	—	—	—
Volk	—	—	—	—	—	—	—	—	—	1	4	1	2	10	1	—	—	—	—	—	—	—	—	—
Latp	11	100	4	3	9	1	3	32	5	10	53	9	2	4	3	—	—	—	3	17	3	—	—	—
Trem	15	61	13	3	11	3	—	—	—	9	52	7	3	5	2	—	—	—	8	42	5	—	—	—

Appendix 2. Continued.

	1			2			3			3.5			4			4.5			5			6		
Mediterranean Province (Total: 69 faunal lists, 332 occurrences, 30 primary references)																								
Ashg	—	—	—	—	—	—	1	3	3	—	—	—	1	13	5	—	—	—	2	29	7	—	—	—
Cara	1	5	2	—	—	—	1	1	1	10	16	4	1	9	3	1	3	1	5	24	9	2	12	2
Darw	—	—	—	—	—	—	—	—	—	—	—	—	3	21	2	4	34	11	18	59	7	—	—	—
Volk	—	—	—	—	—	—	—	—	—	3	18	1	—	—	—	—	—	—	—	—	—	—	—	—
Latp	—	—	—	—	—	—	—	—	—	1	3	1	4	8	1	—	—	—	7	67	3	—	—	—
Trem	1	2	2	—	—	—	—	—	—	1	1	1	1	1	1	—	—	—	1	3	1	—	—	—
Laurentian Regions																								
Appalachian Basin (Total: 161 faunal lists, 1251 occurrences, 44 primary references)																								
Ashg	6	138	3	1	16	1	1	8	1	2	12	2	12	252	5	8	88	8	—	—	—	1	2	1
Cara	8	79	5	20	85	10	7	57	7	15	89	10	40	276	19	16	73	4	5	10	3	5	12	3
Darw	—	—	—	—	—	—	1	1	1	—	—	—	—	—	—	—	—	—	1	1	1	—	—	—
Volk	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Latp	3	5	4	—	—	—	—	—	—	1	4	2	—	—	—	—	—	—	—	—	—	—	—	—
Trem	8	43	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cincinnati Arch (Total: 80 faunal lists, 598 occurrences, 14 primary references)																								
Ashg	2	13	2	11	72	5	2	14	2	9	31	5	13	104	6	13	120	8	5	57	4	—	—	—
Cara	1	12	2	1	10	1	5	28	1	3	34	1	7	44	6	7	50	4	1	9	1	—	—	—
Darw	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Volk	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Latp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Trem	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mississippi Valley (Total: 41 faunal lists, 930 occurrences, 16 primary references)																								
Ashg	—	—	—	—	—	—	—	—	—	2	70	4	—	—	—	—	—	—	2	16	1	—	—	—
Cara	—	—	—	1	22	1	—	—	—	4	38	2	16	664	6	—	—	—	—	—	—	—	—	—
Darw	2	20	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Volk	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Latp	6	70	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	1	—	—	—
Trem	4	12	3	—	—	—	—	—	—	2	15	1	—	—	—	—	—	—	1	1	1	—	—	—
Great Basin (Total: 35 faunal lists, 180 occurrences, 17 primary references)																								
Ashg	4	4	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cara	—	—	—	1	1	1	—	—	—	1	2	1	—	—	—	—	—	—	—	—	—	—	—	—
Darw	—	—	—	1	5	1	2	26	3	9	58	8	1	6	2	—	—	—	1	5	3	—	—	—
Volk	—	—	—	—	—	—	—	—	—	1	4	1	—	—	—	—	—	—	—	—	—	—	—	—
Latp	—	—	—	3	9	1	1	19	3	4	22	6	2	4	3	—	—	—	—	—	—	—	—	—
Trem	—	—	—	—	—	—	—	—	—	2	13	2	2	2	1	—	—	—	—	—	—	—	—	—