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Substrate affinities of higher taxa and the Ordovician Radiation

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Abstract.—The Ordovician Radiation exhibited a global transition in dominance from the Cambrian evolutionary fauna (e.g., trilobites), to the Paleozoic and Modern faunas (e.g., articulate brachiopods and bivalve molluscs). Although its causes have yet to be determined definitively, the transition coincided with increased global tectonism. Erosion of source areas uplifted during orogenic activity increased the siliciclastic richness of marine substrates in many venues, and it has been hypothesized previously that higher taxa with affinities for siliciclastics diversified in association with these environmental changes, whereas higher taxa not exhibiting such affinities either failed to radiate or declined in diversity. Here, we provide an initial test of this substrate affinity hypothesis by evaluating the Ordovician affinities of trilobites and articulate brachiopods.

Our analyses—at the class level for both trilobites and articulate brachiopods, and at the order level for orthid and strophomenid brachiopods—were based on the affinities of constituent genera for siliciclastic, carbonate, and mixed siliciclastic/carbonate settings. Individual genus affinities are calculated with a database of genus occurrences encompassing nine Ordovician paleocontinents. Using these values, we developed a standardized relative affinity (SRA) metric to compare the propensities of higher taxa, and to assess changes in relative affinities of individual higher taxa from series to series.

A simple comparison of trilobites and articulate brachiopods for the Ordovician in aggregate does not appear to support the substrate affinity hypothesis: articulate brachiopods, which contributed increasingly to overall diversity through the period, exhibit an overall affinity for carbonates and an aversion to siliciclastics. However, a rather different view emerges when we consider the affinity *trajectories* of higher taxa through the period: articulate brachiopods exhibit a growing affinity for siliciclastics and a declining affinity for carbonates, whereas the opposite is the case among trilobites. Among constituent articulate brachiopod orders, the affinity trajectories of orthids and strophomenids mirror that of the class. Thus, the increasing dominance of articulate brachiopods in the Middle and Late Ordovician may have been linked to the affinity for siliciclastics of a diversifying subset of the group, but further investigation will be required to verify this claim.

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Introduction

The Ordovician Period was a time of profound change to the marine benthos. On a global scale, there was an unprecedented increase in the taxonomic richness of marine animal families and genera (Sepkoski 1979, 1997), as well as a transition in dominance among the higher taxonomic components of global diversity, from members of the Cambrian evolutionary fauna (Sepkoski 1981) to those of the Paleozoic and Modern faunas. Collectively, these transitions are referred to as the Ordovician Radiation. Locally, transitions in the overall compositions of benthic communities mirrored the global pattern, although local biotic compositions varied significantly with environment and geography (Sepkoski and Sheehan 1983; Sepkoski and Miller 1985; Miller 1997a,b), and the kinetics of diversity and abundance transitions among evolutionary faunas at the community level are still being investigated (Patzkowsky and Holland 1997, 1999; Adrain et al. 1998; Westrop and Adrain 1998; Li and Droser 1999).

We are engaged in an ongoing study intended to better understand the kinetics and causes of the Ordovician Radiation (e.g., Connolly and Miller 2001a,b). As part of this investigation, we have been evaluating a previous hypothesis (Miller and Mao 1995) that the environmental affinities of Ordovician taxa influenced their propensities to diversify during the period. Following on their recognition that Ordovician taxonomic richness was great-

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est in regions likely to be orogenically active, Miller and Mao (1995) hypothesized that (1) erosion of source areas uplifted during orogeny dramatically increased the siliciclastic richness of marine substrates in several venues around the world; and (2) higher taxa with affinities for siliciclastic substrates diversified as a consequence of increased siliciclastic availability. By contrast, it was hypothesized that taxa not exhibiting an affinity for siliciclastics diversified to a lesser extent, if at all.

However, there has yet to be a definitive, global assessment of the extent to which higher taxa that radiated significantly during the Ordovician differed in their sedimentological affinities relative to taxa that declined in diversity. Here, we provide such an assessment for trilobites and articulate brachiopods by analyzing the siliciclastic and carbonate affinities of their constituent genera, at the class level and among the two brachiopod orders, orthids and strophomenids, that constituted the bulk of brachiopod genus richness during the Ordovician.

Our results suggest a more complex relationship between substrate affinity and diversification than envisioned by Miller and Mao (1995). When considering the Ordovician as a whole, we find no relationship between the mean substrate affinities of genera constituting a higher taxon and the taxon's propensity to diversify: taxa that diversified do not exhibit a stronger mean affinity for siliciclastics than those that declined. However, a different impression emerges when we evaluate *changes* in the mean substrate affinities of higher taxa through the Ordovician (*affinity trajectories*): higher taxa that exhibited a growing affinity for siliciclastics over time tended to diversify more extensively than those that exhibited no such trend.

Methods

Our analyses were conducted with a database of Ordovician genus occurrences compiled from the literature (Excel spreadsheet available upon request), first used in a series of papers on the Ordovician Radiation (Miller and Mao 1995, 1998; Miller and Foote 1996; Miller 1997a,b,c). It has since been augmented to include data from several paleocontinents that were underrepresented or not represented in the database previously. For trilobites, inarticulate and articulate brachiopods, bivalves, and gastropods (the core group of major representatives from the three evolutionary faunas used in previous published analyses), the database depicts 9525 occurrences of some 1200 unique genera resolved stratigraphically to the series level, based on the "old" British standard. The following Ordovician paleocontinents and regions are represented: Australia, Avalonia, Baltoscandia, South China, North China, Laurentia, the Mediterranean Province (Bohemia, France, Iberian Peninsula, Morocco), South America "proper," and the Precordillera. Although the database still lacks information from some important Ordovician venues (e.g., Siberia), it was demonstrated that the earlier version successfully cataloged an appreciable percentage of the world's Ordovician genera (Miller and Foote 1996). Given that the number of occurrences in the version used here has increased by nearly 50%, it is assumed that the data are adequate for a study of the global propensities of the higher taxa under investigation.

Substrate Affinities of Individual Genera.— Among the subsidiary data cataloged for each genus occurrence is the *lithology* of the enclosing strata. From this information, the broad substrate regime of each occurrence is categorized simply as *siliciclastic*, *carbonate*, or *mixed*; the latter category includes instances in which siliciclastics and carbonates are mixed within the occurrence horizon or are reported as interbedded. The substrate regime is designated as *unknown* when the lithology is not reported or does not permit a clear categorization. In all, 3944 occurrences are categorized as siliciclastic, 2029 as carbonate, 3312 as mixed, and 170 as unknown (Table 1). On average, the percentage of siliciclastic occurrences increased in the second part of the Ordovician (post-Llanvirnian), reflecting the growing extent of siliciclastic sedimentation in association with increased tectonic activity (Khain and Seslavinsky 1996; see below).

For each genus, we calibrated affinities for each substrate regime on the basis of all occurrences of the genus in the database, using three simple metrics:

TABLE 1. Total number of occurrences categorized within each of the three recognized depositional regimes, series-by-series through the Ordovician. Numbers in parentheses are percentages of the total for the three regimes within the series.

Series	Carbonate	Mixed	Siliciclastic
Tremadocian	180 (15)	566 (48)	432 (37)
Arenigian	550 (28)	567 (28)	878 (44)
Llanvirnian	232 (25)	431 (47)	261 (28)
Llandeilian	180 (19)	315 (34)	443 (47)
Caradocian	819 (27)	924 (31)	1258 (42)
Ashgillian	71 (6)	500 (39)	722 (55)
(Aggregate)	2029 (22)	3312 (35)	3994 (43)

$$A_c = \frac{N_c}{N_c + N_m + N_s},$$

$$A_m = \frac{N_m}{N_c + N_m + N_s}, \qquad (1)$$

$$A_s = \frac{N_s}{N_c + N_m + N_s},$$

where A_c, A_m, and A_s represent affinities for carbonate, mixed, and siliciclastic settings; and N_c, N_m, and N_s are the number of occurrences in each of these settings. Thus, each metric ranges from 0 to 1, and, for a given genus, the sum of the three metrics is unity. The greater the value of the metric, the greater the affinity of the genus for the substrate in question. As an example, if a genus occurs ten times in the database, with five occurrences in siliciclastics, three in carbonates, and two in mixed settings, its siliciclastic affinity is 0.5, its carbonate affinity 0.3, and its mixed affinity 0.2. In cases when the substrate regime of an occurrence is designated as unknown, the occurrence is not included in the calibration for the genus in question; when *all* the occurrences of a genus are from unknown substrate regimes, the genus is removed from subsequent analyses.

Finally, for reasons discussed below, we determined substrate affinities for genera on the basis of data in aggregate for the entire Ordovician, but we also also calibrated them separately for the genera within each of six series of the "old" British standard, using *only* the occurrences within the series in question.

Substrate Affinities of Classes and Orders.— One logical way to calibrate the substrate affinities of a higher taxon would simply be to determine the mean affinity of its constituent genera. A higher taxon with a mean siliciclastic affinity, say, of 0.8 might then be judged to have a strong overall affinity for siliciclastics. However, this approach does not account for the possibility that occurrences in a particular sedimentary regime dominate the data. In the case of our Ordovician database, this problem is evident, given the increase in the percentage of siliciclastic occurrences noted earlier. Thus, even a taxon with a biological affinity for carbonates might turn up frequently in siliciclastic settings, assuming that it could subsist there, simply because these sediments are much more plentiful.

What is required is an objective way of assessing whether a higher taxon occurs more frequently in a particular sedimentary regime than other taxa, taking into account the imbalances in availability of strata from these regimes. This is accomplished here using a statistical bootstrapping approach. First, for a given class or order, we determine the mean carbonate, mixed, and siliciclastic affinities of its constituent genera ($\bar{A}_c$, $\bar{A}_m$, and $\bar{A}_s$). Then, using the entire roster of genera (inarticulate and articulate brachiopods, trilobites, bivalves, gastropods), regardless of higher taxonomic membership, we can develop a random set of genera containing the same number of constituents as the higher taxon by resampling randomly with replacement the pool of genus affinities for each of the three regimes; the mean substrate affinities of this random set are then determined ($\overline{Rnd}_c$, $\overline{Rnd}_m$, and $\overline{Rnd}_s$).

The random resampling procedure is repeated multiple times (see below) to generate a frequency distribution of mean affinities expected in a random assembly of genera equal in number to the genus richness of the higher taxon under investigation. The standard deviations of these frequency distributions ($SD_{\overline{Rnd}_c}$, $SD_{\overline{Rnd}_m}$, and $SD_{\overline{Rnd}_m}$), in turn, are used to determine a *standardized relative affinity* (SRA) with a two-step procedure. First, for the depositional regime in question (carbonate, siliciclastic, or mixed), the mean affinity of all genera in the sample pool ($\overline{Atot}_c$, $\overline{Atot}_m$, or $\overline{Atot}_s$) is subtracted from the mean affinity of the genera belonging to the higher taxon ($\bar{A}_c$,

$\bar{A}_m$, or $\bar{A}_s$). Then, this difference is divided by the standard deviation of the bootstrapped frequency distribution of mean affinities for the sample pool in that regime ($SD_{\overline{Rnd}_c}$, $SD_{\overline{Rnd}_m}$, or $SD_{\overline{Rnd}_s}$), yielding the SRA for the higher taxon.

For example, the carbonate SRA for a higher taxon is calculated as

$$SRA = \frac{\bar{A}_c - \overline{Atot_c}}{SD_{\overline{Rnd}_c}} \tag{2}$$

Thus, the SRA measures the number of standard errors by which the mean affinity of a higher taxon differs from the overall average. In calculating the difference for the numerator when determining the SRA, it would have also been appropriate to use the mean of the bootstrapped frequency distribution ($\bar{A}_{\overline{Rnd}_c}$, $\bar{A}_{\overline{Rnd}_m}$, or $\bar{A}_{\overline{Rnd}_s}$) instead of the actual mean for the total genus pool. Because the former simply provides an estimate of the latter, we considered it prudent to use the latter. We found that in practice, however, the bootstrap estimates are consistently within less than 1% of the actual means.

We conducted 2000 bootstrap replicates for each higher taxon. Inspection of the bootstrap results as a function of the number of bootstrap replicates confirmed that this was more than adequate to produce a stable result. The estimated value and standard deviation of mean affinity stabilized well before 2000 replicates were completed, even for higher taxa with relatively few genera (i.e., even for the smallest sample sizes).

The SRA is aptly named in that derived values are contingent on the occurrences included in the database; thus, the SRA measures the propensity for genus-level constituents of a higher taxon to occur in a depositional regime *relative* to those belonging to other higher taxa included in the sampling pool. The implications of using a relative measure, with respect to interpreting the results, are discussed later.

The SRA has two main properties that are useful for interpreting what a particular value signifies:

1. A given value may be positive or negative, depending on whether the mean affinity for the higher taxon exceeds or is less than that of the mean for the entire genus pool. A positive value indicates that the higher taxon has a greater than average propensity to occur in the substrate regime in question, whereas a negative value implies a relative aversion for the substrate.

2. The values are standardized, so the probability that an individual SRA differs significantly from zero can be gauged on the basis of the expectations for a standard normal distribution. For example, for an SRA of ±1.96, there is a 95% probability that the true affinity differs from the mean for the sample pool of all genera. However, in the presentation below, no direct assessments are provided of the statistical significance of individual values; doing so would be particularly problematic in cases when a temporal sequence of affinities for a higher taxon is assessed (see below).

As an example, the mean carbonate affinity ($\bar{A}_c$) is 0.28 for all 368 Ordovician articulate brachiopod genera whose individual affinities are determinable. Application of the bootstrapping procedure yields an SRA for articulate brachiopods of 2.64, which stands above the standardized mean (0) of all the genera included in the broader genus pool with 99% confidence. Although this value should be interpreted mainly in comparison to others, it should be clear that the positive standardized value in this case suggests a positive affinity for carbonates.

Variations in Affinity through Time.—The procedure described above was applied to the entire Ordovician database, yielding information about the relative substrate affinities of higher taxa throughout the period, in aggregate. However, as discussed below, it was particularly important to determine whether there were changes in the SRA of individual taxa through time: regardless of their overall propensities to occur in a particular sedimentary regime, did higher taxa exhibit changes in these propensities over the course of the Ordovician? To address this question, we also applied the procedure to the pool of genus occurrences contained individually within each of the six series of the old British standard, yielding SRA time series (trajectories) through the Ordovician for each higher taxon.

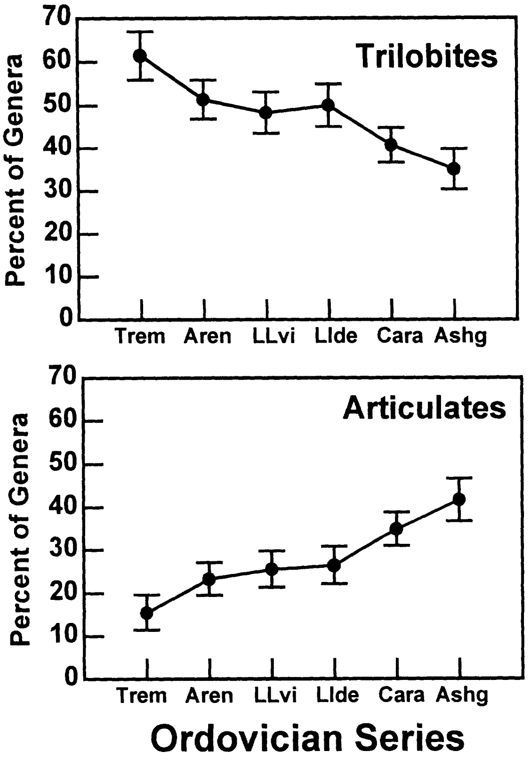

FIGURE 1. Percent diversity trajectories for trilobites and articulate brachiopods through the Ordovician. For each series, the value depicted is the percentage of genera actually occurring in that series that belonged to the taxon in question. Because the database used here was limited to trilobites, brachiopods, bivalves, and gastropods, these percentages should not be taken as an absolute indication of the percentage contributions of the taxon in question to overall marine diversity during the Ordovician. However, the *trajectories* reflect those expected if the analysis were more inclusive taxonomically. As expected, the percent diversity of trilobites declined through the period, whereas that of articulate brachiopods increased. Error bars are 95% confidence intervals about the percentages (Raup 1991). In all figures, values are depicted for the six series of the "old" British standard: Trem = Tremadocian; Aren = Arenigian; Llvi = Llanvirnian; Llde = Llandeilian; Cara = Caradocian; Ashg = Ashgillian. The ordinate is *not* scaled to the absolute durations of individual series.

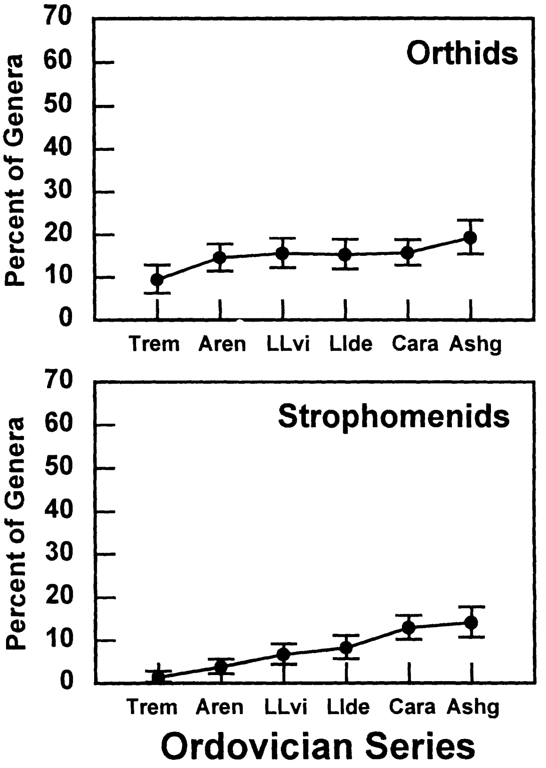

FIGURE 2. Percent diversity trajectories for orthid and strophomenid brachiopods through the Ordovician. Although the trajectory for strophomenids was more continuous, both groups exhibited significant increases during the period. For further explanation, see caption for Figure 1.

Results and Discussion

Percent Diversity Trajectories.—To understand the results of the substrate affinity analyses, it is useful first to consider the Ordovician diversity trajectories of the higher taxa under investigation. To this end, series-to-series diversity trajectories are presented here, with diversity for a taxon calibrated as the percentage of standing genus diversity within each series represented by the taxon; in all cases, total standing diversity is calibrated as the aggregate genus diversity of all higher taxa included in the database. Class-level trajectories for trilobites and articulate brachiopods are presented in Figure 1; order-level trajectories for orthids and strophomenids are presented in Figure 2.

Figure 1 simply conveys one of the fundamental biotic transitions of the Ordovician: the percent diversity of trilobites declined precipitously throughout the period, while that of articulate brachiopods increased nearly continuously. Given that these two taxa constitute such a large overall percentage of the database, these patterns should not be considered indicative of the "real" diversity trajectories of either group, because of closure. That is, the declining percentage diversity of trilobites should not be taken as an indication by itself that the group, overall, was in decline; a declining percentage might reflect an actual diversity decline, but it could be produced even

TABLE 2. Class-level SRAs of trilobites and articulate brachiopods. Aggregate Ordovician values are provided for each of the three recognized depositional regimes. For discussion of standardization procedure, see text.

	Carbonate	Mixed	Siliciclastic
Trilobites	−1.52	3.10	−1.11
Articulates	2.64	0.62	−2.18

TABLE 3. SRAs for orthid and strophomenid brachiopods. Aggregate Ordovician values are provided for each of the three recognized depositional regimes. For discussion of standardization procedure, see text.

	Carbonate	Mixed	Siliciclastic
Orthids	−0.37	−0.59	1.04
Strophomenids	1.20	0.81	−1.45

if trilobite diversity were increasing, provided that articulate brachiopod diversity were increasing at a greater rate (Westrop and Adrain 1998). Nevertheless, these graphs provide a useful indication of the relative fortunes of the two groups through the period. At the least, it can be said that the total genus diversity of articulate brachiopods increased through the Ordovician at a rate significantly exceeding that of trilobites (see Connolly and Miller 2001b).

Among orthids and strophomenids (Fig. 2) percent diversity trajectories broadly mirror those exhibited collectively by all articulate brachiopods, in that both show a significant increase through the Ordovician.

Aggregate Substrate Affinities for the Ordovician.—Aggregate Ordovician SRAs for trilobites and articulate brachiopods are presented in Tables 2 (classes) and 3 (brachiopod orders). At the class level, both groups exhibit clear affinities for different substrates; articulate brachiopods exhibit a substantial positive affinity for carbonates that is nearly matched by their negative affinity for siliciclastics. By contrast, trilobites exhibit a notable negative affinity for carbonates and a positive affinity for mixed substrates.

The two brachiopod orders do not simply mirror the affinities of articulate brachiopods as a class. Strophomenids exhibit a negative affinity for siliciclastics and a positive affinity for carbonates, whereas orthids, if anything, exhibit a positive affinity for siliciclastics, recognizing that the carbonate SRA of strophomenids and the siliciclastic SRA of orthids are relatively weak in comparison to affinity values exhibited at the class level.

Although it may be difficult to determine fully whether there is biological significance to the differences in substrate affinities among these higher taxa, one thing is evident: the suggestion by Miller and Mao (1995) of a relationship between diversification trajectories and substrate affinities does not appear to be borne out. Miller and Mao implied that taxa contributing increasingly to diversity through the period would have affinities for siliciclastic (and perhaps mixed) settings, whereas declining taxa would not have positive affinities for these settings and would, if anything, exhibit affinities for carbonates. However, the opposite appears to be the case: at the class level, articulate brachiopods, which contributed increasingly to biodiversity through the period, exhibit a positive affinity for carbonates and a negative affinity for siliciclastics. Trilobites, the group in decline, exhibit a negative affinity for carbonates.

Substrate Affinity Trajectories through the Ordovician.—Although the overall Ordovician affinities do not corroborate the suggestion of Miller and Mao (1995), perhaps a simple aggregate comparison misses the point. Arguably, it is more appropriate to ask whether the substrate affinities of these taxa *changed* through the Ordovician, given that the biotic transitions, and the physical changes to substrates hypothesized to be associated with them, exhibited secular transitions during the period. This is tantamount to asking whether and how higher taxa *responded* to changing physical conditions.

Thus, to further evaluate the broader suggestion of Miller and Mao that there was a link between substrate affinity and Ordovician faunal transitions, series-to-series SRA trajectories were constructed for the higher taxa under consideration. Regardless of their aggregate propensities during the Ordovician, it is predicted that higher taxa experiencing an increase in percent diversity through the period exhibited a growing affinity for siliciclastics and a declining affinity for carbonates, where-

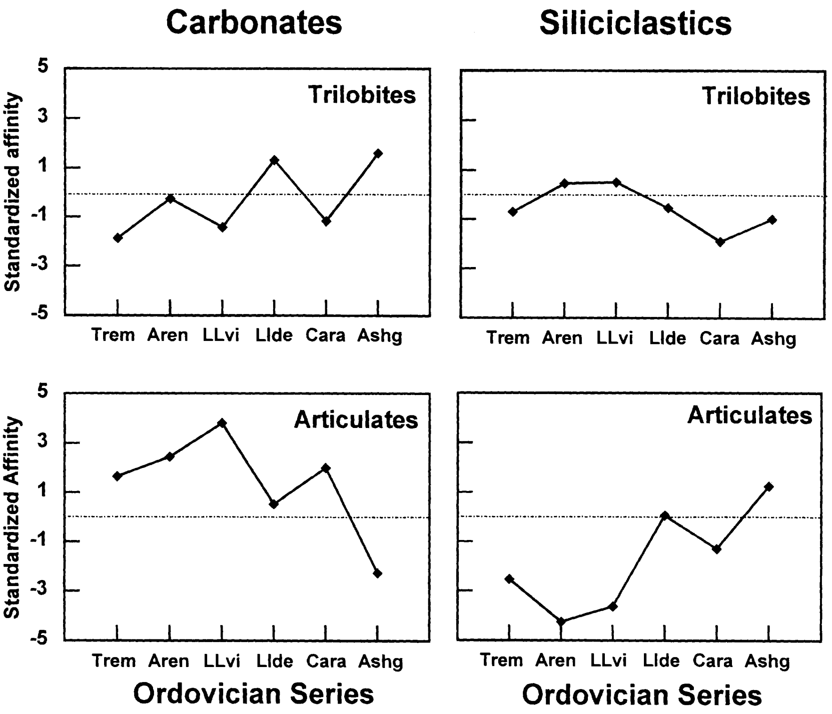

FIGURE 3. Standardized Relative Affinity (SRA) trajectories for trilobites and articulate brachiopods through the Ordovician. Trilobites exhibited a broadly declining siliciclastic SRA in the "second half" of the Ordovician, whereas the siliciclastic SRA of articulate brachiopods increased. The carbonate SRA of articulate brachiopods decreased through the period, whereas that of trilobites suggested a modest increase. For further discussion and explanation, see text.

as higher taxa that were declining in percent diversity did not exhibit these propensities and, in fact, might be expected to show the opposite pattern.

Affinity trajectories at the class level are illustrated in Figure 3. Although the carbonate SRA of articulate brachiopods remained positive and the siliciclastic SRA remained negative for most of the Ordovician, carbonate affinities clearly decreased and siliciclastic affinities increased through the period. Thus, the overall affinity trajectories for articulate brachiopods conform to the prediction for a taxon exhibiting a percent diversity increase. Among the two brachiopod orders (Fig. 4), strophomenids and orthids both maintained salient attributes of the class-level patterns, in that they both exhibited siliciclastic affinity increases through the period. Moreover, the carbonate affinity trajectory of strophomenids exhibit a steep decline, whereas that of orthids is more ambiguous.

The affinity trajectories of articulate brachiopods show several features that warrant further discussion. First, the comparability of trajectories at the class and order levels stand in striking contrast to the aggregate values for the Ordovician as a whole, which vary appreciably both from the class to order level and among strophomenids and orthids at the order level. Thus, the similarities of the trajectories suggest that they transcend the overall propensities of the higher taxa in question, and indicate that genera belonging to the two most genus-rich articulate brachiopod orders of the Middle to Late Ordovician exhibited a pronounced shift toward siliciclastics relative to the fauna as a whole.

Second, at both the class and order levels, a substantial shift in articulate brachiopod affinity toward siliciclastics and away from carbonates occurred during the transition from the Llanvirnian to the Llandeilian. Interestingly, this transition coincides with Ordovician peaks in the genus origination and extinction probabilities of articulate brachiopods

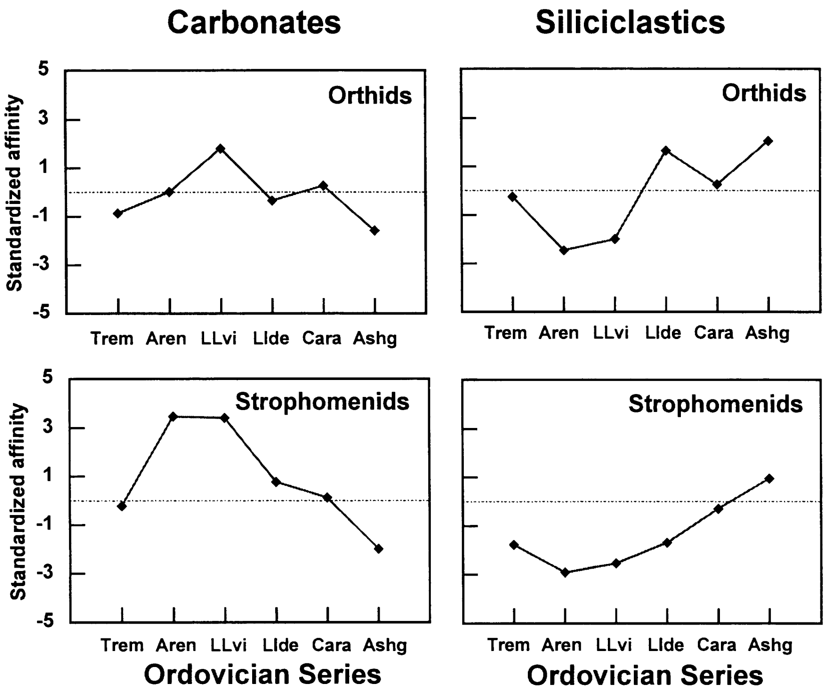

FIGURE 4. SRA trajectories for orthid and strophomenid brachiopods. Despite their rather different SRAs for the Ordovician as a whole (Table 3), the major features of their SRA trajectories were broadly similar and mirrored those of articulate brachiopods in aggregate. For further discussion and explanation, see text.

(Connolly and Miller 2001b), suggesting a link between a major turnover event in articulate brachiopods and the shift to siliciclastics (see below).

Finally, several of these trajectories exhibit an Early Ordovician (Tremadocian to Arenigian or Llanvirnian) pattern opposite to that observed thereafter. Although one should be careful to not read too much into these relatively coarse patterns, it is worth noting that there is indication of an Early Ordovician decline in orogenic activity on a global scale, prior to the longer-term increase that dominates the remainder of the period (Connolly and Miller 2002; Khain and Seslavinsky 1996).

Among trilobites, there was a *decline* at the class level (Fig. 3) in the siliciclastic SRA during the second half of the period, as predicted here for a higher taxon exhibiting a decline in percent diversity. The class-level carbonate SRA trajectory was more irregular; nevertheless, two of the three series in the "second half" of the Ordovician exhibited positive carbonate affinities for trilobites, whereas all three affinities in the "first half" were negative.

The Meaning of SRA Trajectories and an Agenda for Future Research.—Collectively, the affinity trajectories highlighted here suggest linkages in several instances between the changing substrate affinities of taxa and their diversification trajectories during the Ordovician. This possibility speaks to an emerging theme in evolutionary biology: that biodiversity transitions may be influenced strongly by the relative genetic capacities of taxa to evolve phenotypically in the face of novel selective pressures ("evolvability," in the sense of Kirschner and Gerhart [1998] and others). In a study that dovetails on the changing substrate affinities described herein, Foote (2000) focused on the role of changes in taxonomic rates, rather than the actual magnitudes of these rates, in regulating the trajectory of global genus diversity. He found that changes in diversity were associated more strongly with changes in extinction rates during the Paleozoic and changes in origination rates during the post-Paleozoic. Ultimately, there may be genetic bases for the relative propensities of higher taxa to respond to changing selective pressures expressed through geological time by modifying their evolutionary rates, affinities for particular environments, or other attributes. From a paleontological perspective, a first step in demonstrating these propensities is to show that there were, indeed, direct linkages between the apparent modification of evolutionary attributes and changing selective pressures, the latter of which are most easily measured in the stratigraphic record as physical transitions. This is an approach advocated herein, as well as by Foote (2000) to help explain the differences he observed between the Paleozoic and post-Paleozoic.

That said, the results of the present study are not entirely unambiguous. It must be kept in mind that *relative* propensities are measured here, which is important when comparing SRAs among taxa, as well as among substrates for any given higher taxon. For example, the declining carbonate SRA through the Ordovician among articulate brachiopods does not demonstrate that the *absolute* diversity of articulate brachiopods necessarily became depressed in carbonate sediments. It is also plausible that the diversity in carbonates of articulate brachiopods remained constant or even increased through the period, but that any such increase was outpaced by a greater increase within siliciclastics.

This and related issues could be evaluated further through the direct comparison of diversification, origination, and extinction rates in different substrates. With the approach developed by Connolly and Miller (2001a), for example, it should be possible to verify directly whether the net diversification rate of articulate brachiopods actually became elevated in siliciclastics, relative to carbonates, as the Ordovician unfolded, and whether any such diversification increase was a consequence of elevated origination rates, declining extinction rates, or both.

Dovetailing on the assessment of evolutionary rates, there should be a more extensive consideration of the data in phylogenetic and morphological contexts. For example, in the case of strophomenids or orthids, it would be valuable to know whether their increased siliciclastic SRAs in the Middle and Late Ordovician were linked directly to the radiation of a limited set of clades within either group or, alternatively, whether diversification in siliciclastics occurred diffusely—from a phylogenetic standpoint—throughout both groups. With respect to morphology, it could be asked, for example, whether notable changes in the morphological diversity of trilobites (Foote 1991, 1993) or articulate brachiopods were associated with transitions in their SRAs.

In subsequent analyses, it would also be appropriate to consider the affinities and trajectories of genera grouped in ways that transcend traditional higher taxonomic categorization and, instead, are linked by propensities to diversify similarly in space and time. Among the clear candidates for these kinds of assessment are the Ibexian and Whiterockian trilobite faunas recognized by Adrain et al. (1998).

Because diversification patterns varied during the Ordovician among different geographic and environmental regimes (Miller 1997a,b), it is also important to consider whether there are geographic or environmental components to the siliciclastic versus carbonate patterns observed here. Indeed, irrespective of tectonic activity, several researchers have suggested that there were significant latitudinal components to Ordovician diversification that almost assuredly were associated with pole-to-equator differences in the extent of siliciclastic versus carbonate sedimentation (e.g., Babin 1993, 2000; Adrain et al. 1998).

Moreover, during the Ordovician, several geographic regimes that were initially carbonate rich were subjected subsequently to increased siliciclastic influx (e.g., much of eastern Laurentia in association with the Taconic orogeny). If articulate brachiopods already dominated these regions prior to the sedimentological transition, one plausible explanation for the observed class-level patterns is that, simply by surviving the transition, articulate brachiopods became passive "invaders" of siliciclastics. There is already some indication that this hypothesis is implausible in that the regional physical effects of the Taconic orogeny appear to have been detrimental to incumbent taxa (Patzkowsky and Holland 1993, 1999), and, moreover, trilobites, too, were significant contributors to diversity in Ordovician carbonate settings (Westrop and Adrain 1998). Nevertheless, the hypothesis is testable.

Finally, these analyses should be extended to a much broader group of higher taxa than those constituting the core groups subjected to detailed dissection over the past several years (mainly trilobites, brachiopods, and benthic mollusks). If substrate affinity trajectories are, indeed, linked to diversification, then increasing affinities for siliciclastics should be evident among the wide variety of faunal elements that contributed increasingly to global diversity as the Ordovician progressed.

In retrospect, it was naive to expect a simple relationship between the aggregate mean sedimentological affinity of a higher taxon and its propensity to diversify during the Ordovician. Rather, it is more appropriate to evaluate whether the affinities of higher taxa evolved in concert with changing physical conditions. Initial indications are that this was the case for a major taxonomic contributor to the Ordovician Radiation, the articulate brachiopods. However, a series of additional analyses are required that, among other things, directly evaluate the behavior of diversification metrics in a world of changing sedimentation.

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