

Calibrating the Ordovician Radiation of marine life: implications for Phanerozoic diversity trends

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Abstract.—It has long been suspected that trends in global marine biodiversity calibrated for the Phanerozoic may be affected by sampling problems. However, this possibility has not been evaluated definitively, and raw diversity trends are generally accepted at face value in macroevolutionary investigations. Here, we analyze a global-scale sample of fossil occurrences that allows us to determine directly the effects of sample size on the calibration of what is generally thought to be among the most significant global biodiversity increases in the history of life: the Ordovician Radiation. Utilizing a composite database that includes trilobites, brachiopods, and three classes of molluscs, we conduct rarefaction analyses to demonstrate that the diversification trajectory for the Radiation was considerably different than suggested by raw diversity time-series. Our analyses suggest that a substantial portion of the increase recognized in raw diversity depictions for the last three Ordovician epochs (the Llandeilian, Caradocian, and Ashgillian) is a consequence of increased sample size of the preserved and catalogued fossil record. We also use biometric data for a global sample of Ordovician trilobites, along with methods of measuring morphological diversity that are not biased by sample size, to show that morphological diversification in this major clade had leveled off by the Llanvirnian. The discordance between raw diversity depictions and more robust taxonomic and morphological diversity metrics suggests that sampling effects may strongly influence our perception of biodiversity trends throughout the Phanerozoic.

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Introduction

Because of their significance for interpreting macroevolutionary patterns and processes, Phanerozoic trends in global marine biodiversity have received considerable scrutiny over the past three decades (for a summary of much of this research, see Signor 1990). Some analyses have focused specifically on preservational and statistical artifacts that might bias relative levels of biodiversity over time. Perhaps the best-known of these treatments is Raup's finding of a possible correlation between diversity trends and sedimentary rock volume (Raup 1976a, b), which suggested that increased levels of biodiversity exhibited in the post-Paleozoic might be artifacts of increased sample size of the preserved fossil record. However, subsequent studies, some of which were intended to transcend the rock volume problem (e.g., Bambach 1977; Sepkoski et al. 1981), indicated strong relationships among trends calibrated at several taxonomic levels using a variety of methods. This led to

the widespread view that the general Phanerozoic trend, as depicted directly by the sampled and catalogued fossil record, could be interpreted largely at face value.

Rock volume for a particular stratigraphic interval constitutes only an indirect measure of the number of fossils contained within it; its use as an index of the extent of sampling for this purpose rests on the assumption that a larger sedimentary rock volume contains more fossils. In the present study, to assess global biodiversity trends more definitively, we analyze a global-scale sample of fossil occurrences that allows us to evaluate *directly* the effects of sample size on the calibration of what is generally thought to be among the most significant global biodiversity increases in the history of life: the Ordovician Radiation. We utilize rarefaction analyses of these data, combined with an analysis of morphological diversification exhibited by a major Ordovician group, the trilobites, to demonstrate that the radiation was characterized by a different

diversity trajectory than indicated by raw taxonomic diversity time-series. This, in turn, suggests that sampling effects may well significantly influence our perception of biodiversity trends throughout the Phanerozoic.

Raw Taxonomic Depictions of the Ordovician Radiation

The Ordovician Radiation was characterized by the broadly based proliferation of higher taxa that would come to dominate marine settings through the balance of the Phanerozoic (Sepkoski 1981). It is recognized in published time-series of global marine biodiversity as perhaps the most extensive interval of genus and family diversification in the history of life (Sepkoski 1993, 1995; Benton 1995). The raw, genus-level diversity trend is presented in Figure 1, upper curve (the upper and middle time-series in Fig. 1 were compiled from data contained in an unpublished global compendium of fossil marine genera, August 1994 update, provided by J. J. Sepkoski, Jr.). This relatively coarse, series-level stratigraphic treatment appears to inflate the level of standing diversity during the lengthy Caradocian Series, relative to its depiction at the finer, subseries-level. Nevertheless, the broad Ordovician trend is in substantial agreement with other published compilations at the genus and family levels and indicates a threefold diversity increase.

The analyses presented here are limited to an aggregate pool of higher taxa that constitute a significant cross section of major faunal elements from each of Sepkoski's (1981) three evolutionary faunas: (1) trilobites; (2) articulate and inarticulate brachiopods; (3) bivalve, gastropod, and monoplacophoran molluscs. A series-by-series depiction of global genus diversity for these groups (Fig. 1, middle curve) exhibits a trajectory comparable to that recognized for the broader pool of taxa.

The Global Database of Genus Occurrences

The rarefaction analysis of taxonomic diversity described below utilizes a database, compiled from the primary literature, that documents individual occurrences of genera in Ordovician strata around the world. (A bibliography of literature sources is available on

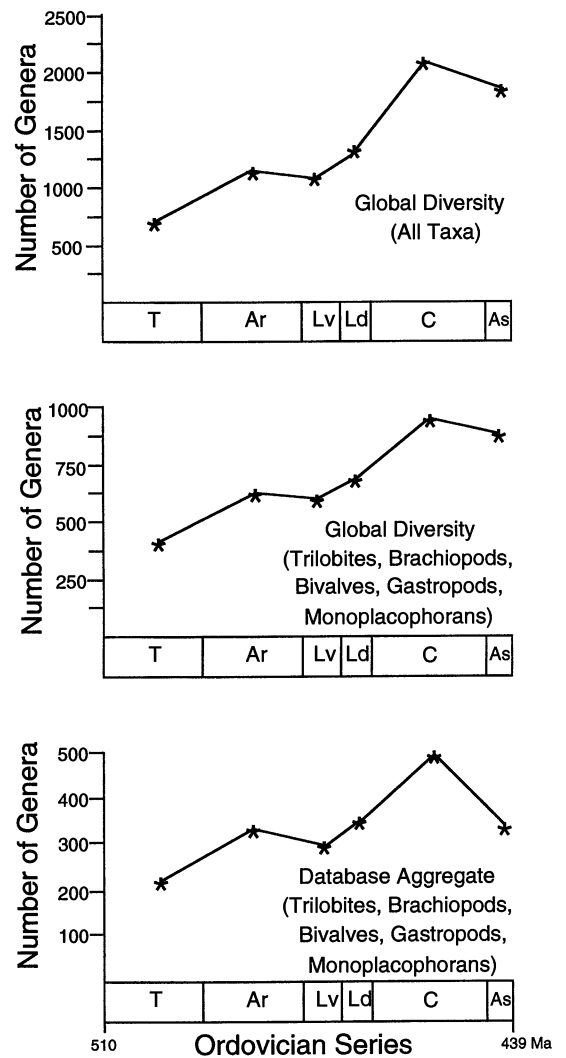


FIGURE 1. Comparisons of genus-level diversity through the Ordovician Period. Abbreviated series designations are the six series of the British Standard: Tremadocian, Arenigian, Llanvirnian, Llandeilian, Caradocian, and Ashgillian. Lengths of series subdivisions reflect their relative durations (Harland et al. 1990); diversity values are plotted at the midpoints of each series. Upper Curve: Global diversity for genera depicted in Sepkoski's unpublished compendium of fossil marine genera. Middle Curve: Global diversity for the pool of Ordovician genera limited to the higher taxa investigated here (see text). Lower Curve: Aggregate Ordovician diversity pattern exhibited by the worldwide database of genus occurrences.

request. Throughout this paper, an individual occurrence of a genus in the rock record is referred to as a *genus occurrence*. This term is synonymous with *genus appearance*, used by Miller and Mao [1995]. It was changed be-

cause of concern that usage of the word *appearance* necessarily implies *first appearance*, which is not its intended meaning.) In contrast to compendia used previously in the construction of global-scale curves (e.g., Sepkoski 1992; Benton 1993), which generally depict only the intervals of first and last appearances of taxa, the database used here records each occurrence encountered in the literature, regardless of stratigraphic level or locality. Thus, genera that are particularly common in Ordovician rocks occur numerous times in the database, whereas less common genera occur less frequently in the data. For example, the strophomenid brachiopod *Sowerbyella* occurs 91 times, whereas the orthid brachiopod *Retrorsirostra* occurs only once.

In all, 6576 occurrences of 974 genera were catalogued for the pool of higher taxa analyzed here. These data come from numerous Ordovician paleocontinents: Laurentia (much of present-day North America); several paleocontinents that, today, constitute most of China; East Avalonia (most of present-day England and Wales); Baltoscandia (present-day Scandinavia and the Baltic countries); Bohemia; and, to a limited extent, Australia. Although data have yet to be collected from other paleocontinents that contain appreciable Ordovician strata and fossils (e.g., Siberia, Kazakhstan, and South America), the database is already global in scope, and does not appear to be skewed, relative to Sepkoski's global compendium, with disproportionate inclusion of data from particular paleoecological regimes. This is illustrated in Figure 1, which compares the global time series for the aggregate pool of highlighted taxa (middle curve) to an independent, similarly styled graph generated from the database of genus occurrences (lower curve). The two diversity trajectories are highly comparable, and, during each series, standing diversities in the lower curve are roughly half to two-thirds those in the upper curve, except during the Ashgillian. However, our database of genus occurrences contains no data from the Silurian or later, in contrast to Sepkoski's global compendium. Because estimated global diversity in the Ashgillian depends in part on post-Ordovician data, relative levels of Ashgillian global

diversity (Fig. 1, upper and middle curves) are higher than our estimates (Fig. 1, lower curve), likely reflecting an effect directly analogous to the Pull of the Recent (Raup 1979).

Another version of the middle and lower curves was presented by Miller and Mao (1995); the global diversity levels depicted in the middle curve herein differ slightly from those illustrated by Miller and Mao because Miller and Mao used an earlier version of Sepkoski's global compendium. The diversity trajectories illustrated by the two time-series were virtually identical, however.

Rarefaction Analysis of Taxonomic Data

As described above, for the higher taxa in question, the database already contains an appreciable, representative sample of the genera known from Ordovician rocks worldwide. Because it is a tabulation of the number of occurrences, the database is suitable for direct evaluation of the effects of sample size on perceived levels of global genus diversity throughout the Ordovician. For example, all three curves in Figure 1 depict a small diversity decline from the Arenigian to the Llanvirnian. This may reflect a possible extinction event at the end of the Early Ordovician (Boucot 1990). Alternatively, it may simply reflect differences in the durations of the Arenigian and Llanvirnian Epochs. On standard time scales, the duration of the Arenigian is depicted as more than twice that of the Llanvirnian (Harland et al. 1990). If it followed, therefore, that the volume of sedimentary rock and fossil material preserved in the Arenigian Series were greater than that of the Llanvirnian, then, all else being equal, the Arenigian would be expected to yield a larger sample and, perhaps, a greater genus richness than the Llanvirnian. This possibility, and other comparisons among Ordovician series, can be tested directly with rarefaction (see Hurlbert 1971; Raup 1975), which permits numerical estimates of genus diversity at sample sizes (i.e., the number of genus occurrences) *smaller* than those of the original collection (rarefaction curves *cannot be extrapolated* beyond their endpoints, however, to estimate diversity at sample sizes larger than those of the original samples). In the case of the Arenigian/Llanvirni-

an comparison, the Arenigian sample in the database is larger than that of the Llanvirnian, as expected. The Arenigian sample can be rarefied to the size of the Llanvirnian sample to determine whether the genus richness for the Arenigian would still exceed that of the Llanvirnian if the two series had the same sample size.

Rarefaction curves for all six Ordovician series are presented in Figure 2 (upper graph). A direct comparison of the Arenigian and Llanvirnian curves suggests that the Arenigian-to-Llanvirnian diversity decline is, indeed, an artifact of sampling. In contrast to the raw data, when the Arenigian sample is rarefied to the size of the Llanvirnian sample, the Llanvirnian exhibits a significantly *greater* genus richness. Moreover, the Llanvirnian rarefaction curve stands entirely above the Arenigian curve, a further indication that, after adjusting for sample size differences, the Llanvirnian was actually more genus-rich than the Arenigian.

Perhaps more striking is the overall diversity trajectory for the Ordovician, as depicted in Figure 2. Remarkably, the four rarefaction curves for the Llanvirnian through Ashgillian Series virtually coincide, differing only in length (a reflection of differences among the series in sample sizes). For the pool of higher taxa included in this analysis, these results imply that raw diversity differences among post-Arenigian series reflect primarily differences in sample size, and that the Ordovician Radiation was considerably more limited in duration than indicated by the raw diversity trajectories (Fig. 1). This is illustrated further by the lower graph in Figure 2. There, the Ordovician diversity trajectory was recast on the basis of rarefaction estimates of genus richness for each series at a sample size of 510 genus occurrences (slightly less than the 521 genus occurrences recorded for the series with the smallest sample size, the Llanvirnian); in contrast to the raw trajectories in Figure 1, this time-series indicates that a plateau in diversity was reached in the Llanvirnian.

Analysis of Trilobite Morphological Diversification

In addition to addressing the limitations of raw taxonomic data, assessment of diversifi-

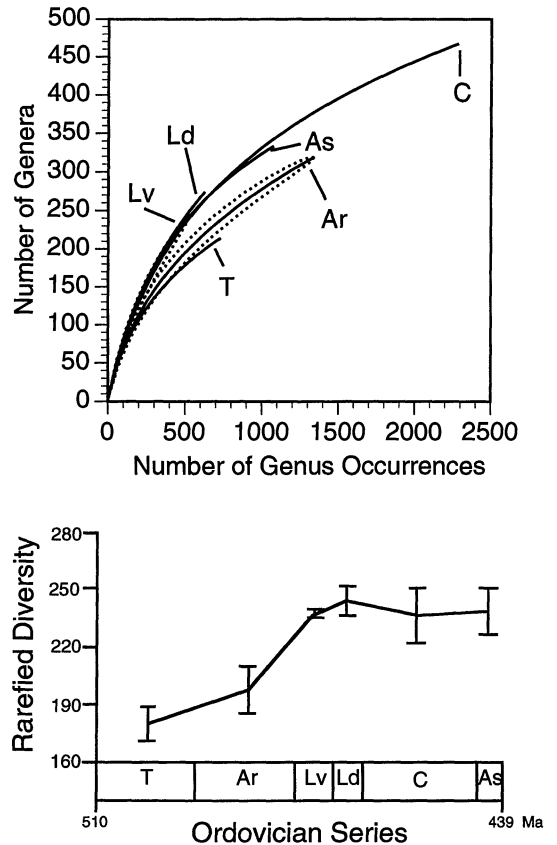


FIGURE 2. Upper Graph: Comparative rarefaction curves for the six Ordovician series, based on analysis of the worldwide database of genus occurrences. Dotted lines depict 95% confidence bands around the curves for Llanvirnian and Arenigian (see Raup 1975); the Llanvirnian curve and confidence bands are barely visible because of the overlap among curves for the Llanvirnian, Llandeilian, Caradocian, and Ashgillian. Additional confidence bands were not included in the figure to avoid further obscuring the curves. Calculated confidence intervals for the other curves were comparable in width to those illustrated and indicate that the rarefaction curves for the Tremadocian and Arenigian were significantly different from those for the Llanvirnian, Llandeilian, Caradocian, and Ashgillian. Lower Graph: Ordovician diversity trajectory based on rarefaction estimates of genus richness for each series at a sample size of 510 genus occurrences (slightly less than the 521 genus occurrences recorded for the Llanvirnian). Error bars depict 95% confidence intervals around the estimates.

cation should also include morphological data (Briggs et al. 1992; Wills et al. 1994). In some instances (e.g., long-term trends among trilobites through the Paleozoic Era), temporal trajectories of morphological and taxonomic diversification for particular groups are not in accord with one another (Foote 1993). Thus, to

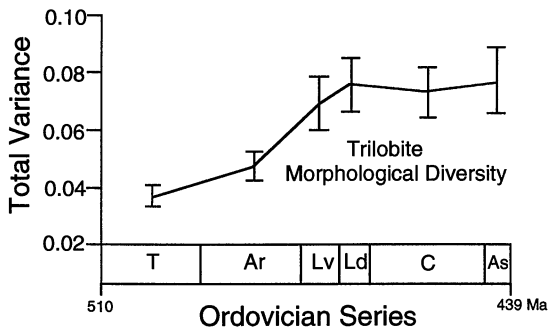


FIGURE 3. Comparisons of total morphological variance (morphological diversity) among trilobites through the Ordovician Period. Error bars are ± 1 standard error (see Foote 1993).

provide an initial assessment of the degree to which morphological data exhibit patterns comparable to the rarefied taxonomic data, we conducted a series-by-series analysis of morphological diversity in a global sample of Ordovician trilobites. This analysis is similar in design to previous analyses of this kind (Foote 1993), but uses a finer degree of stratigraphic resolution. First, for specimens belonging to each of 162 Ordovician trilobite genera, average values were determined for 12 biometric variables generated through previous Fourier analyses of trilobite cranidia (Foote 1991, 1993; these data are available on request). Then, for each Ordovician series, a variance among the genera extant during the series was determined for each variable (the number of sampled genera extant for each series were: Tremadocian—48; Arenigian—60; Llanvirnian—64; Llandeilian—77; Caradocian—92; Ashgillian—68). Finally, total variance (Van Valen 1974) was determined for each series by summing the 12 individual variances; this value, which is not biased by sample size (Foote 1992, 1993), serves as a metric of trilobite morphological diversity during the series.

Results of the morphological analysis are presented in Figure 3; they suggest a significant increase in morphological diversity (total variance) among trilobites from the Tremadocian through the Llanvirnian, followed by little or no increase for the remainder of the Period. Thus, the morphological pattern, which is nearly identical to that illustrated in Figure 2 (lower graph), corroborates the taxonomic analyses described earlier, in that both

suggest a Llanvirnian stabilization. Given that the morphological investigation was limited to trilobites, whereas the taxonomic analysis included a broader pool of taxa, the close similarity, throughout the Ordovician, between the two time-series trajectories should be viewed with some caution (we will provide a direct comparison of trilobite morphologic and taxonomic diversity in a future paper). For present purposes, the important point is that both analyses indicate that diversity stabilized in the Llanvirnian.

Discussion

Thus, the results of the taxonomic and morphologic analyses suggest clearly that, for the composite set of taxa evaluated here, the Ordovician Radiation took place over a shorter time span than suggested by raw diversity compilations. Because only a limited set of higher taxa were evaluated, however, these analyses need not imply that the Ordovician Radiation was over entirely by the end of the Llanvirnian. Although these taxa represent important components of the three Phanerozoic evolutionary faunas, and their combined *raw* diversity signal suggests a substantial Middle and Late Ordovician diversity increase, they are far from an exhaustive list of higher taxa that diversified during the radiation. In fact, a perusal of Ordovician genus diversity curves (Sepkoski 1995) indicates that some higher taxa (e.g., Anthozoa and Bryozoa) must have diversified in the Middle and Late Ordovician, given their very limited diversities earlier in the period. However, we would caution that, even in those instances, the rate and extent of diversification may have been substantially different than suggested by the raw diversity curves.

More importantly, the results of this study transcend the Ordovician Radiation, and suggest that sampling effects may well influence the raw diversity signal throughout the Phanerozoic. For example, the apparent diversity decline during the Late Permian mass extinction may be exaggerated because of a sparse Upper Permian record, relative to that of the Lower Permian (for discussions of Permian/Triassic boundary sections and calibration of the Late Permian mass extinction, see Erwin

1993). The development of a Permian taxonomic database analogous to the Ordovician database evaluated here would provide an opportunity to determine the extent to which raw diversity differences among Lower and Upper Permian series are biased by sample size. More generally, analyses of this kind conducted for all Phanerozoic Systems might well affect long- and short-term trends in apparent global biodiversity as well as the macroevolutionary interpretations drawn from them.

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