

Association of orogenic activity with the Ordovician radiation of marine life

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ABSTRACT

The Ordovician radiation of marine life was among the most substantial pulses of diversification in Earth history and coincided in time with a major increase in the global level of orogenic activity. To investigate a possible causal link between these two patterns, the geographic distributions of 6576 individual appearances of Ordovician genera around the world were evaluated with respect to their proximity to probable centers of orogeny (foreland basins). Results indicate that these genera, which belonged to an array of higher taxa that diversified in the Middle and Late Ordovician (trilobites, brachiopods, bivalves, gastropods, monoplacophorans), were far more diverse in, and adjacent to, foreland basins than they were in areas farther removed from orogenic activity (carbonate platforms). This suggests an association of orogeny with diversification at that time.

INTRODUCTION

The Ordovician increase in global biodiversity, commonly known as the Ordovician radiation, was one of the most significant intervals of diversification in the history of marine animal life. Following on the heels of the Cambrian explosion, during which most fundamental animal designs evolved (Erwin et al., 1987), the Ordovician radiation was marked by the broad-based proliferation of groups that would come to dominate marine settings through the balance of the Phanerozoic (Sepkoski, 1981). During the 71-m.y.-long Ordovician Period, the global diversity of marine families increased from ~160 to 530, and the diversity of genera increased from 470 to 1580 (family data are from Sepkoski, 1993; genus-level data are from an unpublished global-scale compendium of fossil marine genera, compiled by Sepkoski). Despite the importance of the Ordovician radiation, the process or processes responsible for it remain elusive. Although Sepkoski (1984) demonstrated that Phanerozoic global diversity trends have behaved logistically, and were perhaps limited by parameters such as the availability of ecospace, it is not known why diversification should have proceeded in the first place. Links between orogenic activity (mountain building) and biodiversity have been postulated in the past (e.g., Umbgrove, 1947; Henbest, 1952), but little evidence has been provided to support these suggestions, and they must be viewed as mainly speculative. Here, we present new data that suggest a relation between increased levels of orogenic activity and the Ordovician radiation.

Globally, the Ordovician was marked by increasing levels of tectonic activity associated, in part, with the closing of the Iapetus Ocean (see Stillman, 1984; Hain and Seslavinskii, 1991). During the Middle and Late Ordovician, volcanism and orogeny increased substantially, in virtual synchrony with the increase in marine biodiversity. In fact, quantification of the extent of global orogenic activity during the early Paleozoic (Hain and Seslavinskii, 1991) yields a time series that closely resembles that of global biodiversity. However, this temporal association does not, in itself, indicate a causal relation between orogeny and diversification. Rather, a more definitive test involves assessment of the distribution of diversifying taxa in space, with respect to centers of orogenic activity. Specifi-

cally, it is essential to determine whether there was a tendency for such taxa to be located in or near orogenically active regions.

METHODS

We used literature sources to accumulate a global database that includes taxonomic, stratigraphic, lithologic, geographic, and paleoenvironmental information for appearances of Ordovician genera (a genus appearance is defined as an individual appearance of a genus documented from a particular stratigraphic interval at a particular place; a bibliography of literature sources is available on request). Thus far, of some 14 000 genus appearances in our developing database, 6576 belong to groups that are analyzed below: trilobites; inarticulate and articulate brachiopods; and bivalve, gastropod, and monoplacophoran molluscs. These organisms compose a cross section of major representatives from Sepkoski's (1981) three Phanerozoic evolutionary faunas.

Data are from several Ordovician paleocontinents, including Laurentia (much of present-day North America), Baltoscandia (present-day Scandinavia and the Baltic countries), East Avalonia (most of present-day England and Wales), Bohemia, Australia (to a limited degree), and several paleocontinents that, today, compose China (Scotese and McKerrow, 1990). Data have not yet been collected from several other regions that contain significant Ordovician fossil biotas (e.g., Siberia, Kazakhstan, and South America). Nevertheless, there are compelling reasons to believe that the data are now sufficiently extensive to investigate broad-scale issues such as those addressed here. First, global paleogeographic reconstructions (e.g., Scotese and McKerrow, 1990) indicate that the paleocontinents from which data have already been collected extended around the Ordovician world, particularly in low latitudes, and were not limited to a narrow region. Second, as demonstrated in Figure 1, an aggregate diversification pattern through the Ordovician, generated by pooling the data from all sampled paleocontinents for the organisms included in these analyses, is very similar to a global curve constructed independently with data from Sepkoski's unpublished compendium of fossil marine genera. Moreover, on a series-by-series basis, diversities in our database are roughly two-thirds of the levels depicted in the global curve, indicating that the database already contains an appreciable sample of the world's documented Ordovician genera for the higher taxa in question.

To assess the geographic distributions of genus appearances with respect to regions of orogenic activity, we used *Atlas of Lithological Paleogeographical Maps of the World* (Ronov et al., 1984), which depicts, through the Precambrian and Paleozoic, the areal extents, worldwide, of major geologic provinces. By utilizing the maps provided for the Lower, Middle, and Upper Ordovician we developed a simple, tripartite classification of localities with respect to tectonic setting that was intended to reflect proximity to areas of orogenic and other tectonic activity.

1. **Foreland Basins.** These regions were immediately adjacent to the main foci of orogenic activity. Of the foreland basins (geosynclines) depicted on the Ordovician maps, some were not tectonically active at that time. However, the clear majority of the data

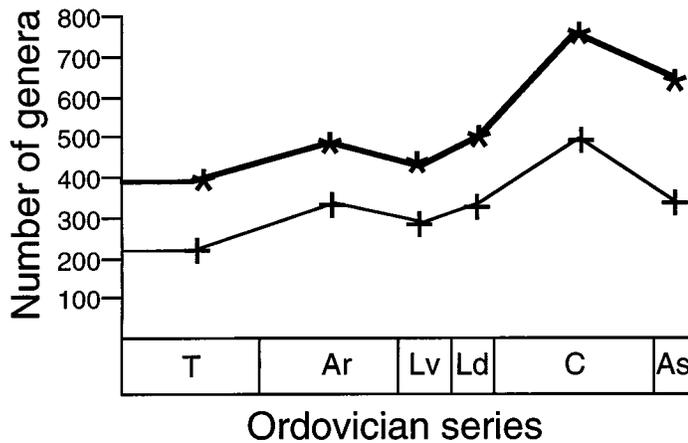


Figure 1. Comparison of genus-level diversification patterns through Ordovician time, in aggregate, for trilobites, inarticulate and articulate brachiopods, bivalves, gastropods, and monoplacophorans. Abbreviated series designations are six series of the British standard: Tremadocian, Arenigian, Llanvirnian, Llandeilan, Caradocian, and Ashgillian. Lengths of series subdivisions reflect their relative time durations (based on Harland et al., 1989); diversity values are plotted at midpoints of each series. Upper curve: Global diversity, based on unpublished compendium of fossil marine genera compiled by J. J. Sepkoski, Jr. Lower curve: Aggregate diversity of all paleocontinents included in the data base.

assigned to foreland basins represent areas that became active in the Middle and Late Ordovician.

2. Transition Zones. With respect to marine organisms, an important effect of orogeny is that uplifted regions typically yield eroded sediments that affect sea floors beyond the bounds of foreland basins; such regions were classified as transitional. For example, during the Late Ordovician, the Cincinnati area, which was west-northwest of the Appalachian foreland basin, received a substantial volume of fine-grained terrigenous sediment derived from uplifted source areas to the east-southeast. Thus, for the Late Ordovician, Cincinnati was considered transitional. Because benthic organisms may respond to terrigenous sedimentation, regardless of its source, any marine area outside of a foreland basin that was receiving appreciable terrigenous sediment was assigned to this category.

3. Carbonate Platforms. Epicontinental regions that received little or no terrigenous sediment and, thus, remained relatively unaffected by orogeny were assigned to this category.

For the organisms included in the analysis, each genus appearance was assigned to one of these three tectonic classes based on its location during the time interval in question; an individual genus may have been present in more than one tectonic province or stratigraphic interval. The appropriate map (Lower, Middle, or Upper Ordovician) for an individual genus appearance was determined on the basis of the stratigraphic subdivision into which the genus appearance fell. For compilation purposes in this study, the Tremadocian and Arenigian series were designated as Lower Ordovician; the Llanvirnian and Llandeilan series; as well as the Costonian through Marshbrookian stages of the Caradocian, were designated as Middle Ordovician; and the Actonian and Onnian stages of the Caradocian, as well as the Ashgillian series, were designated as Upper Ordovician.

RESULTS AND DISCUSSION

The diversification (Fig. 1) was reassessed with respect to the tectonic classification scheme (Fig. 2). Clearly, the majority of the

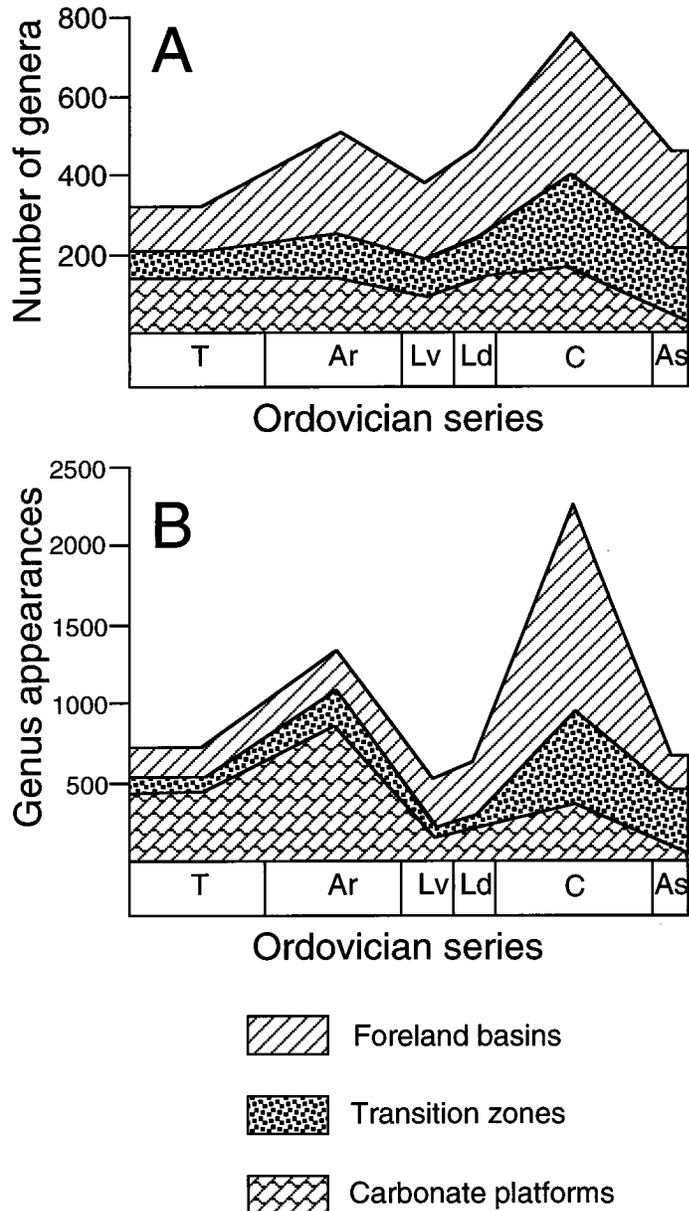


Figure 2. Diversity trends through Ordovician time for each of three designated tectonic settings. Widths of shaded bands directly depict numerical values, and each curve is cumulative for settings beneath it. A: Genus diversity. B: Number of genus appearances. Cumulative diversity values in upper curve in A are not identical to lower curve in Figure 1 because several genera appeared in more than one tectonic setting.

Ordovician diversity increase depicted by these data took place in foreland basins and transition zones (Fig. 2A). Whereas the genus richness of carbonate platforms remained fairly stable from the Tremadocian through the Caradocian, that of transition zones increased nearly threefold, from 63 to 229, and the genus richness of foreland basins grew at a comparable rate, from 118 to 371. To some degree, this simply reflects where the data came from. As illustrated in Figure 2B, the great majority of individual genus appearances in the last two series of the Ordovician were derived from foreland basins and transition zones. However, this does not negate the potential biological significance of the diversification pattern for two reasons. First, rarefaction analyses (see Hurlbert, 1971; Raup, 1975), which permit numerical estimations of genus diversity at sam-

ple sizes smaller than those of the original collections, were conducted individually for the Lower, Middle, and Upper Ordovician. The analyses demonstrated that, in the Lower and Middle Ordovician (Fig. 3, A and B), comparable numbers of genus appearances would yield substantially greater genus-richness values in foreland basins than on carbonate platforms (such a comparison was not possible for the Upper Ordovician because carbonate-platform data from that interval were insufficient for numerical analysis). Rarefaction analyses also indicated that transition zones exhibited genus-diversity levels that were barely distinguishable from carbonate platforms and were well below those of foreland basins until the Late Ordovician, when transition zones and foreland basins exhibited nearly comparable diversities (Fig. 2C).

Second, measurements of map areas (Table 1) indicated that the diversity trends exhibited in Figure 2 were not associated with changes in the areal extents of the three kinds of settings, except perhaps for the Late Ordovician areal increase exhibited by transition zones (the data-rich upper Caradocian is part of the Upper Ordovician). In fact, foreland basinal areas, which were rather stable throughout the period, actually decreased somewhat following the Early Ordovician. Thus, the observed pattern cannot be viewed as a simple reflection of changing areas or volumes available to be sampled, but the possibility of artificial bias still remains. For example, it is arguable that, because of increased sedimentation rates associated with erosion of uplifted source areas, rapid burial and, thus, preservation of skeletal material would have been favored in foreland basins and transition zones. Moreover, it may be easier to physically extract fossils from certain kinds of terrigenous rocks (e.g., shales) that are more significant lithologic components in foreland basins and transition zones than on carbonate platforms. However, any such effect might well have been countered by the greater propensity of carbonate skeletons to dissolve in terrigenous settings because pore waters in terrigenous environments were less likely to be saturated with respect to calcium carbonate (for a discussion of principles governing carbonate dissolution, particularly with respect to terrigenous environments, see Aller, 1982). In addition, the greater likelihood of postdepositional fossil distortion in terrigenous rocks (see Foote, 1991), combined with the possibility of chemically extracting significant silicified fossil biotas from limestones (e.g., the Middle Ordovician of Kentucky; see Pojeta, 1979), would argue for greater ease of taxonomic delineation in carbonates. In any case, it is evident that the possibility of taphonomic bias, although potentially important, is not straightforward.

It might also be argued that the observed pattern was a reflection not of location with respect to orogenic activity but of environmental diversity within each of the three kinds of regions. For example, it is possible that foreland basins exhibited a greater diversity of habitats, particularly in deep-water settings, than carbonate platforms and that the greater genus diversity of foreland basins simply reflected this wider environmental spectrum; this possibility is currently being analyzed. However, during the Ordovician, taxa tended to diversify in shallow-water settings (Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985), which were well represented on carbonate platforms. Moreover, the habitat diversity exhibited by foreland basins might, itself, have been a partial consequence of orogenic activity.

Finally, with respect to shortcomings in the data, we suspect that carbonate settings are underrepresented in the database for the Ashgillian series. As the database continues to be augmented, it is anticipated that the measured genus richness of Ashgillian carbonate platforms will increase. However, carbonate-dominated settings were not purposefully avoided thus far, and it is highly unlikely that

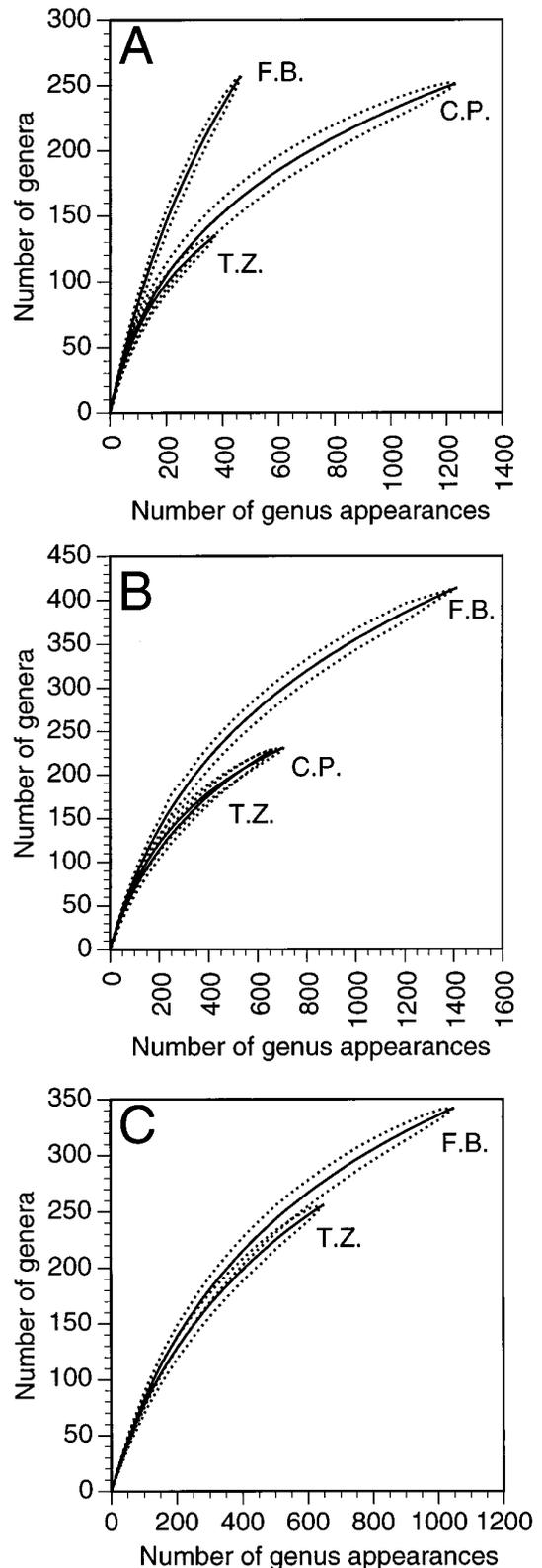


Figure 3. Comparative rarefaction curves for three designated tectonic settings. Dotted lines depict 95% confidence bands around curves (see Raup, 1975). A: Lower Ordovician. B: Middle Ordovician. C: Upper Ordovician. Abbreviations of tectonic settings: F.B.—foreland basins, T.Z.—transition zones, C.P.—carbonate platforms. In B, curves for transition zone and carbonate platform are difficult to distinguish because they nearly overlap.

TABLE 1. AGGREGATE MAP AREAS OF THE THREE KINDS OF TECTONIC PROVINCES FOR THE PALEOCONTINENTS INCLUDED IN THIS STUDY (ORDOVICIAN)

	Early	Middle	Late
Carbonate platform	5.29	8.37	5.99
Transition zone	4.85	2.99	6.58
Foreland basin	9.30	7.61	8.26

Note: Map areas (millions of square kilometres) were determined by using the program Arc/info 6.1.1.

additional data will neutralize the current tendency for diversity to be concentrated in foreland basins and transition zones.

Thus, despite the possibility of preservational and other biases, the data indicate that, for the groups analyzed, the Ordovician radiation was concentrated most heavily in regions associated with orogenic activity. Any biological explanation(s) for this pattern must take into account the broad-based taxonomic character of the diversification, which included such disparate elements as phacopid trilobites, strophomenid brachiopods, and bivalve molluscs. Although we have yet to isolate a singular explanation for the linkage of increased orogenic activity to the radiation, we note three likely effects of orogenic activity, which may have fomented diversification.

1. **Substrate.** An important effect of the uplift and erosion that characterized many regions around the world during the Middle and Late Ordovician would have been a major change in substrate on sea floors, as many areas became inundated with sand and, to a greater areal extent, mud. It is possible that this change in substrate fueled the radiations of higher taxa that flourished on or in mud-covered sea floors (e.g., strophomenid brachiopods and certain kinds of bivalve molluscs).

2. **Food.** The heightened influx of terrigenous material may have introduced increased abundances of nutrients that fueled an early Paleozoic increase in primary productivity, which, in turn, may have promoted the diversification of taxa for which food availability had previously been a limiting factor (Bambach, 1993). Among other things, this would explain observations that, during the Ordovician, bivalve molluscs were more abundant and diverse in terrigenous settings than in carbonate environments (Miller, 1988, 1989; Babin, 1993).

3. **Habitat Partitioning.** The tectonic activity associated with orogenically active regions may have led to increased fracturing of habitats, thereby increasing the likelihood of speciation (Cracraft, 1985).

Before a definitive determination of mechanistic linkages between orogeny and diversification is possible, a more careful assessment of the physical effects of orogeny in a biological context, and an examination of the paleobiology of the major diversifying taxa in the face of changing physical conditions, will be required. In any case, the apparent association described here serves as a reminder of the fundamental role that physical transitions of global significance have played in the history of life.

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