

The Ordovician Radiation: A Follow-up to the Cambrian Explosion?¹

MARY L. DROSER² AND SETH FINNEGAN

Department of Earth Sciences, University of California, Riverside, California 92521

SYNOPSIS. There was a major diversification known as the Ordovician Radiation, in the period immediately following the Cambrian. This event is unique in taxonomic, ecologic and biogeographic aspects.

While all of the phyla but one were established during the Cambrian explosion, taxonomic increases during the Ordovician were manifest at lower taxonomic levels although ordinal level diversity doubled. Marine family diversity tripled and within clade diversity increases occurred at the genus and species levels. The Ordovician radiation established the Paleozoic Evolutionary Fauna; those taxa which dominated the marine realm for the next 250 million years. Community structure dramatically increased in complexity. New communities were established and there were fundamental shifts in dominance and abundance.

Over the past ten years, there has been an effort to examine this radiation at different scales. In comparison with the Cambrian explosion which appears to be more globally mediated, local and regional studies of Ordovician faunas reveal sharp transitions with timing and magnitudes that vary geographically. These transitions suggest a more episodic and complex history than that revealed through synoptic global studies alone.

Despite its apparent uniqueness, we cannot exclude the possibility that the Ordovician radiation was an extension of Cambrian diversity dynamics. That is, the Ordovician radiation may have been an event independent of the Cambrian radiation and thus requiring a different set of explanations, or it may have been the inevitable follow-up to the Cambrian radiation. Future studies should focus on resolving this issue.

INTRODUCTION

Although commonly overshadowed by the spectacular Cambrian explosion (see rest of volume) the Ordovician radiation was one of the most significant events in the history of life and in fact involved a greater increase at the family and genus level than did the Cambrian. Though obviously a major event, the Cambrian diversification is fraught with largely unresolved and controversial complications. These include issues such as the origin of body plans, the origin of skeletonization, the origin and first appearance of the Bilateria, the affinities of Ediacaran fossils, and the fate of the Ediacaran fauna. In addition, we rely heavily on soft-bodied faunas for our understanding of Cambrian biodiversity and disparity. There are few skeletonized metazoan clades that have an excellent Cambrian fossil record, the trilobites being the obvious exception.

The significant increase in standing diversity began approximately 500 million years ago (Fig. 1). During the Ordovician, marine family diversity tripled and those clades that came to dominate the next 250 million years radiated. The Ordovician radiation included groups as phylogenetically disparate as rynchonelliform brachiopods, echinoderms, trilobites, corals, and bryozoans—the only phylum to have originated in the post-Cambrian. There is a continuous record of skeletonized metazoans through the interval, biostratigraphic control is excellent and there are nearly complete Ordovician sections on most continents repre-

sented a broad range of depositional environments. Thus, the Ordovician radiation provides a far more tractable example than the Cambrian for the study of biodiversification dynamics. Because of the disparate nature of the Ordovician and Cambrian records, it is difficult to make direct comparison between the two events. Ordovician strata do not contain common soft-bodied preservation. So, unlike the Cambrian, our picture of the Ordovician lacks a significant soft-bodied component. On the other hand, the Ordovician fossil record has a diverse range of skeletonized marine animals and plants so that we are able to track patterns and trends at a variety of scales.

ORDOVICIAN DIVERSITY PATTERNS AND DYNAMICS

Evolutionary Faunas

Sepkoski's (1979) compendium of marine families revealed a threefold increase in family-level diversity between the Late Cambrian and the Late Ordovician (Fig. 1). This expansion follows on the heels of an apparent Late Cambrian diversity plateau. The subsequent diversity plateau established in the Ordovician is roughly maintained (despite significant short-term fluctuations) until the catastrophic end Permian extinction.

Sepkoski (1981, 1984) proposed that the broad pattern of Phanerozoic marine diversity could be explained by a coupled logistic diversification model involving three "Evolutionary Faunas" (EFs) with distinct phases of diversification and taxonomic dominance in the global oceans (Fig. 1). Each successive fauna is characterized by slower origination rates but higher equilibrium diversity than the preceding fauna. Classes within each fauna have generally similar diversity histories and turnover rates, though there is

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² E-mail: Mary.Droser@ucr.edu

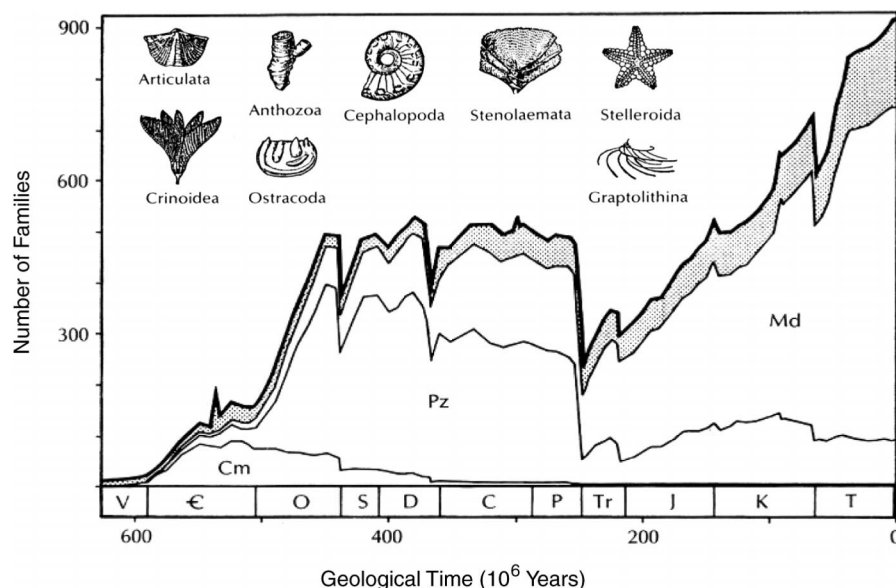


FIG. 1. Sepkoski's (1990) Phanerozoic marine family-level diversity curve, with diversity patterns of Evolutionary faunas delineated and representative members of the Paleozoic Fauna illustrated. The stippled area indicates diversity contributed by poorly preserved groups. Cm, Cambrian evolutionary fauna; Pz, Paleozoic Evolutionary Fauna; Md, Modern Evolutionary Fauna. After Sepkoski, 1990.

considerable variation within them. The three faunas proposed by Sepkoski consist of a Cambrian EF, a Paleozoic EF and a Modern EF.

In this context, Sepkoski viewed the Ordovician radiation as inevitable given the initial appearance of the Paleozoic EF in the Cambrian (Sepkoski, 1979, 1990). The Late Cambrian "plateau" is taken to represent attainment of equilibrium diversity by the Cambrian Fauna, while the Ordovician radiation represents an acceleration of diversification following the initially slow growth of the Paleozoic Fauna in the Cambrian. He suggested that the successively higher equilibrium diversities of the three Evolutionary Faunas could be understood in terms of increasing niche partitioning, with the "generalist" Cambrian EF being replaced by the relatively "specialized" Paleozoic EF in the Ordovician.

Temporal and geographic diversity patterns

Our understanding of the temporal dynamics of Ordovician diversification has been considerably refined by a series of recent investigations. Miller and Foote (1996) conducted a rarefaction analysis on a global database of Ordovician occurrences of a cross-section of representative genera (Fig. 2A). When adjusted to standardized per-series sample size, the shape of the Ordovician diversity curve is significantly altered. Whereas Sepkoski's curve indicates a nearly monotonic increase in diversity throughout the period, Miller and Foote's analysis indicated that diversity increased somewhat through the Early Ordovician, jumped sharply near the base of the Middle Ordovician (mid Arenig and base of the Whiterock Series in North America), and stabilized from the Late mid Ordovician through the Late Ordovician.

The pattern of diversification also has a strong and complex biogeographic component. As Miller (1997a, b; Miller and Mao, 1995) has emphasized, the global pattern of Ordovician diversification must be understood as the composite result of processes operating at a variety of taxonomic and geographic levels. Miller and his colleagues have shown that the timing, rate and magnitude of diversification differed considerably among paleocontinents, and among individual basins within continents. Similarly, there is great geographic and temporal variation in the diversity trajectories of the various clades that radiated in the Ordovician. Among the numerous examples: In Laurentia, the diversification of Paleozoic EF elements was accompanied by a significant radiation of mollusks, while in South China the diversity of mollusks remained relatively low (Miller and Mao, 1995). It has been proposed by Miller and others that the differential diversification dynamics among regions and among clades can, in part, be explained by temporal and geographic variation in tectonic activity, which has been tentatively correlated with diversity (Vermeij, 1995; Miller and Mao, 1995; Botting, 2001; but see Miller and Connolly, 2001). Interestingly, despite overall strongly varying geographic and temporal patterns, the base of the Whiterock (mid Arenig) is a globally significant interval, characterized by major diversifications in Laurentia (unpublished data), Baltoscandia (Hammer, 2003) and Argentina (Waisfeld *et al.*, 1999). Thus, the global mid Arenig diversification detected by Miller and Foote (1996) is apparent at regional scales.

Partitioning of diversity: alpha, beta, and gamma

In an evaluation of α and β diversity patterns, Sepkoski (1988) analyzed level-bottom communities both

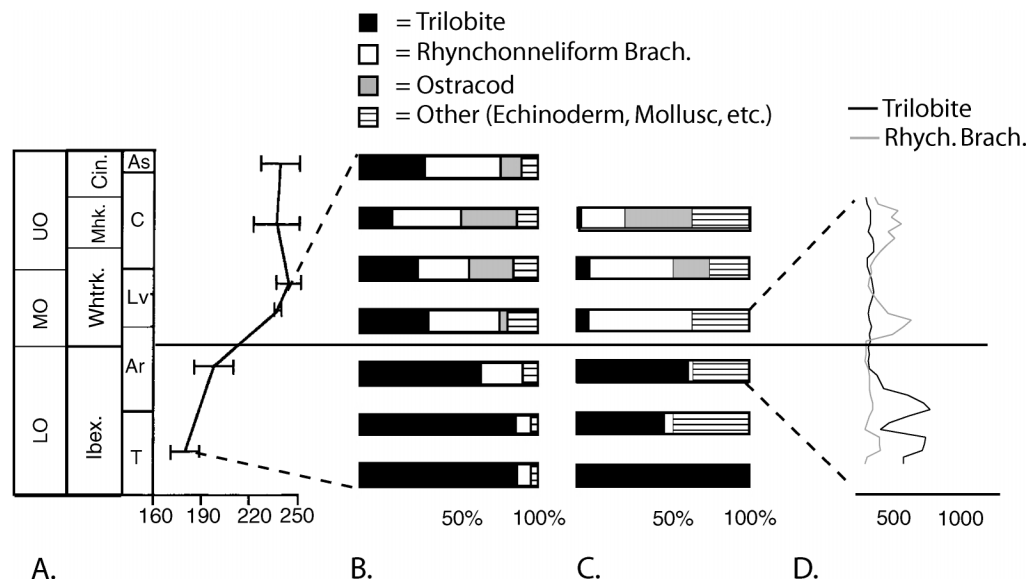


FIG. 2 Significant taxonomic and paleoecological change associated with the Lower/Middle Ordovician boundary. A. A major jump in global standing diversity occurs at this time. After Miller and Foote, 1996. B. In the Great Basin of the western U.S., the mean proportional α diversity of trilobites decreases while that of brachiopods and other groups increases. Data are compiled from literature and exclusive of echinoderms which are difficult to identify and thus rarely included in faunal lists. S.F. and M.L.D., Unpublished data. C. In the Great Basin, the boundary coincides with a dramatic shift in the taxonomic dominance of shell beds: the proportion of trilobite-dominated beds declines abruptly while the proportion of brachiopod-dominated beds increases. After Li and Droser, 1999. D. The sharpness of the transition is apparent in wackestone samples from the boundary interval. T, Tremadocian; Ar, Arenigian; Lv, Llanvirnian; Ld, Llandeilian; C, Caradocian; As, Ashgillian; Ibex., Ibexian; Whtrk., Whiterockian; Mwk., Mohawkian; Cinc., Cincinnati. S.F. and M.L.D., Unpublished data.

within each of the 6 Paleozoic Periods and within 6 environmental zones arrayed from shore to basin. Sepkoski detected an average increase in α diversity of 50–70% between the Cambrian and Ordovician. This is consistent with Bambach’s (1977) analysis of species richness for the same interval. There is also a corresponding increase of ~50% in β diversity.

Sepkoski’s analysis shows that, even when increased α and β diversity is taken into account, only about half of the Ordovician increase in genus-level diversity can be accounted for. There are two obvious potential sources of additional generic diversity. One is at the γ level, but at this point, Cambro-Ordovician patterns of provinciality are largely unresolved (Valentine *et al.*, 1978; Harper and MacNiocail, 2002). Secondly, Sepkoski’s (1988) study focused on soft level-bottom communities; clearly the development of reef and

hardground communities during the Ordovician would have impacted generic diversity.

ECOLOGICAL SIGNATURE OF THE ORDOVICIAN RADIATION

Paleoecological levels

Shifts in abundance, dominants, and other features that define ecological structure and complexity cannot be evaluated from taxonomic diversity studies alone. Furthermore, paleoecological shifts, in particular, those that involve structural changes are not easily quantified. However, change in paleoecological systems are scaled in that some changes are far more important than others are. This structuring provides a means to rank paleoecological changes, which can be categorized into four types that are termed paleoecological levels (Droser *et al.*, 1997) (Table 1).

TABLE 1. Definition of paleoecological levels and characteristic signals for each level.*

| FIRST LEVEL Appearance/disappearance of an ecosystem | SECOND LEVEL Structural changes within an ecosystem | THIRD LEVEL Community-level changes within an established ecological structure | FOURTH LEVEL Community changes |
|---|--|---|---|
| <i>Signal</i> 1. initial colonization of an environment | <i>Signals</i> 1. complete ecological shifts in dominance within an environ- ment 2. appearance/disappearance of Bambachian megaguilts 3. loss/appearance of metazoan reefs | <i>Signals</i> 1. appearance/disappearance of community types 2. “filling-in” or “thinning” within Bambachian megaguilts 3. increase/decrease in tiering com- plexity | <i>Signals</i> 1. taxonomic changes within a clade 2. appearance/disappearance of communities |

* After Droser *et al.*, 1997.

During the Precambrian-Cambrian transition, changes occurred at all paleoecological levels as metazoans became established in Earth's oceans. First level changes include the advent of metazoan life on the seafloor and in the water column. With the establishment of these new ecosystems, an associated series of changes by definition, "trickled down." That is, the establishment of a new ecosystem must include new community-types and new communities, etc. During the Cambrian radiation, a series of changes at levels 2, 3 and 4 occurred as communities were in turn dominated by the Ediacaran faunas, Tommotian faunas and typical members of the Cambrian Fauna such as trilobites, linguliform brachiopods and monoplacophorans.

Paleoecological changes associated with the Ordovician radiation of marine invertebrates include second, third and fourth level changes as discussed below. However, evidence from both spores (Gray, 1985) and trace fossils (Retallack and Feakes, 1987) suggests that the initial radiation of complex life onto land occurred in the Ordovician; this constitutes a first level change.

Second level changes

In the marine realm, there were numerous structural changes within established marine soft-substrate as well as reefal and hard-substrate benthic ecosystems.

Bambach (1983) documented an increase in megaguild occupation in the shelfal soft-substrate environment between the Cambrian and the rest of the Paleozoic. Essentially all of the adaptive strategies (Bambach, 1983) used by benthic metazoans for the remainder of the Paleozoic (200 million years) were in place by the end of the Ordovician (Droser and Sheehan, 1995) (Fig. 3).

In this environment, trilobites were the ecologic dominant during the Cambrian and Early Ordovician. As a consequence of the Ordovician radiation, brachiopods, and to a lesser extent echinoderms, became the ecological dominants, a position that they did not give up until the Late Permian mass extinction (Li and Droser, 1999). This constitutes a second level change.

Carbonate buildups have a more complex history through the early Phanerozoic than level-bottom communities. Stromatolite buildups are a common part of the Precambrian-Cambrian record. Archaeocyathans (an extinct group of sponges) appeared in the Early Cambrian and dominated this setting until the end of the Middle Cambrian when they went extinct. Most Upper Cambrian bioherms reverted to a many-layered stromatolitic or thrombolitic structure with relatively few metazoans present within the buildup itself (Sheehan, 1985).

In the Lower Ordovician, there was a widespread addition of sponges to the structure of reef mounds. Lithistid sponges constituted about 30% to 55% of the reef volume in these Early Ordovician buildups (Cañas and Carrera, 1993; Johns, 1995). Although very similar buildups first occur in the late Middle and Late Cambrian (Hamdi *et al.*, 1995; Wilson, 1950), it was

| | | Suspension | Deposit | Herbivore | Carnivore |
|-----------|-----------------|--|--|---|---|
| Epifaunal | Mobile | Bivalvia | Gastropoda Ostracoda MONOPLACOPHORA TRILOBITA | Echinoidea Gastropoda Ostracoda Malacostraca MONOPLACOPHORA | Cephalopoda Malacostraca Stellerioidea Merostomata |
| | Attached Low | Articulata Edrioasteroidea Bivalvia Anthozoa Stenolaemata Sclerospongia INARTICULATA | Ordovician Adaptive Strategies | | |
| | Attached Erect | Crinoidea Anthozoa Stenolaemata Demospongia Blastoidea Cystoidea Hexactinellida EOCRINOIDEA | | | |
| | Reclining | Articulata Hyolitha Anthozoa Stellerioidea Cricconarida | | | |
| Infaunal | Shallow Passive | Bivalvia Rostroconchia | | | |
| | Shallow Active | Bivalvia INARTICULATA | Bivalvia POLYCHAETA TRILOBITA | | Merostomata POLYCHAETA |
| | Deep Passive | | | | |
| | Deep Active | | Bivalvia ? | | |

FIG. 3. Distribution of Ordovician taxa among primarily skeletonized benthic megaguilds defined by mode of life and feeding type. Cambrian Evolutionary Fauna members are capitalized. See text for further discussion. After Bambach, 1983; Droser and Sheehan, 1997.

not until the Early Ordovician that sponge-microbial buildups became the dominant type of bioherm. Turn-over of dominants in this habitat continued through the Ordovician (Johns, 1995). Middle Ordovician and later Paleozoic reefs associations contain a variety of baffling and encrusting organisms, such as bryozoans, but lithistid sponges retain an accessory role in these younger bioherms. During the Middle Ordovician increasing numbers of framework organisms such as stromatoporoids and corals were added to the reefal community. The Ordovician advent of stromatoporoid reefs, was of considerable significance as these dominated the reef ecosystem through the Devonian.

Hardgrounds were a major factor in the initial Ordovician diversification of crinoids (Guensberg and Sprinkle, 1992). By the Middle Ordovician carbonate shelfal environments were common and hardgrounds were widespread. During this time, encrusters and hardground faunas including, in addition to echinoderms, a variety of bryozoan clades and morphotypes as well as boring sponges and worms diversified (Palmer, 1982). The end result was a complex hardground ecosystem. The Ordovician diversification in this habitat was so pronounced that it could be termed the "hardground revolution."

Third level changes

There were a number of third level paleoecological changes. Bambachian megaguilds were filled up to

their Paleozoic levels, tiering reached levels of 1 meter and depth of bioturbation was up to 1 meter. New community types appeared including a Receptaculites-marcluritid high-energy nearshore community-type, new orthid community-types, and a bivalve-trilobite community-type.

SIGNIFICANCE OF THE EARLY WHITEROCKIAN (MID-ARENIGIAN) INTERVAL

As discussed above, both the Miller and Foote (1996) rarefied global diversity curve and regional diversity studies (Hammer, 2003; Waisfeld *et al.*, 1999) point to the base of the Whiterock (mid Arenig) as a critical time during the Ordovician radiations. We can look at this more closely—from a clade perspective and ecological (regional) perspective.

Interestingly, despite first appearing in the Cambrian and having variable patterns of diversification through the Cambrian and Early Ordovician, many phylogenetically disparate groups undergo geologically simultaneous pulses of diversification at this time. These include rynchonelliform brachiopods, nautiloids and ostracodes. Bryozoa first appear in the Early Ordovician and diversify in the mid-Arenig. Echinoderms begin to radiate in the Late Cambrian but diversify onto to soft-substrates in the Middle Ordovician. Bivalves (members of the Modern EF) and trilobites (Members of the Cambrian EF) both diversify amidst global geographic expansions at this time.

Trilobites represent a particularly instructive example. Although they are the principal constituents of the Cambrian EF, Adrain *et al.* (1998) demonstrated that numerous trilobite lineages radiate at the base of the Whiterock (see Fig. 2). The diversifying groups account for all post-Ordovician trilobite diversity. Their fate contrasts sharply with that of a separate cohort, which is dominant in the Lower Ordovician but fails to diversify and undergoes a steady decay in diversity before disappearing entirely at the end of the period. The work of Adrain *et al.* interestingly complements that of Miller and Foote (1996) who showed that the morphological diversity (disparity) trajectory of Ordovician trilobites shows an Ibexian/Whiterockian increase that closely parallels the macrofaunal taxic diversity curve.

Paleoecological patterns

The demonstrable geographic variability and diachroneity of the Ordovician diversifications (Miller, 1997a, b; Miller and Mao, 1995; Droser *et al.*, 1996) imposes limitations on the level of analysis possible with synoptic databases. Moreover very few published sources include abundance data. A program of detailed field paleoecological studies is thus critical to understanding changes in ecological structure through this radiation.

While it is usually impossible to identify keystone taxa from the fossil record, dominance by skeletonized metazoans can easily be determined. Cambrian assemblages are dominated by trilobites, although in Upper

Cambrian strata, echinoderms dominate certain near-shore high energy facies. This pattern continues into the Early Ordovician. However, studies of a variety of depositional environments in the Western U.S. indicate that at the base of the Whiterock, there is a geologically abrupt shift to rynchonelliform brachiopod-dominated assemblages across the shelf (Li and Droser, 1996, 1999; Finnegan, unpublished MS thesis). This corresponds to a global diversification of rynchonelliform brachiopods (Harper and MacNiocaill, 2002). Bivalves and gastropods locally dominated nearshore and restricted environments beginning at the base of the Whiterock.

Many unrelated studies are thus pointing to the transition from the Early to Mid Ordovician as pivotal for this radiation. These results are not mutually dependent, and are suggestive of the possibility of extrinsic controls. This pattern of simultaneous diversification and ecological restructuring after, in most cases long after the origin of radiating clades, contrasts sharply with Cambrian patterns of diversification.

POTENTIAL CAUSAL MECHANISMS

Compared to the Cambrian radiations, relatively little work has been done to explore the causal factors that may underlie the Ordovician diversifications. As previously discussed, Sepkoski (1979) regarded them as inherently intrinsic, the predictable outcome of diversity-dependent interactions between the already-diverse Cambrian EF and the diversifying Paleozoic EF. This model cannot be ruled with our current understanding of patterns of diversification. Other workers have, however, tended to view the diversifications as resulting from a complex mix of intrinsic biological and extrinsic physical factors.

Zhuravlev (2001) noted that Cambrian oceans appear to have been characterized by mesotrophic-eutrophic conditions and that many Cambrian taxa were sessile passive suspension feeders well-adapted for non-nutrient-limited conditions. He argues that the diversification of the Cambrian EF created more oligotrophic conditions, thus leading to their own demise and spurring on the diversification of the dominantly active-filtering Paleozoic Fauna. A shift towards oligotrophic conditions may also have been key in setting the stage for the radiation of calcified algae and photosymbiont-bearing stromatoporoid-chaetid sponges and tabulate corals.

By contrast, another body of speculation holds that the Ordovician radiations may be related to increasing continental nutrient flux as a consequence of increasing tectonism and volcanism. Vermeij (1995) suggested that the two major phases of diversification in the Phanerozoic oceans (Cambro-Ordovician and Mesozoic-Cenozoic) were generally correlated with intervals of elevated tectonism. The potential correlates of increased tectonism include changes in substrate, greater primary productivity, and increased habitat partitioning. Miller and Mao (1995) found a tentative correlation between diversity and proximity to orogen-

ic belts in a comparison of the Ordovician records of Laurentia and South China, though this correlation has subsequently been called into question (Miller and Connelly, 2001). Botting (2002) has hypothesized that oceanic overturn associated with episodes of pyroclastic volcanism led to creation of temporary "benthic islands" with increased genetic heterogeneity and enhanced speciation rates. Some support for this idea can be found in an apparent correlation between major tuff units and ostracod diversity in Middle and Upper Ordovician sediments of the Welsh Basin.

CONCLUSIONS

We are gaining an increased understanding of global patterns through the Ordovician and there is a large-scale effort at compiling data at the clade level (IGCP 410). However, in order to truly test possible extrinsic controls a number of data still need to be collected. Regional patterns, such as those preliminarily identified for the Great Basin, are needed for variety of areas. We have only limited geochemical data for the Ordovician (excluding the end Ordovician mass extinction). Geochemical data has proven to be instrumental to our understanding of the events surrounding the Precambrian-Cambrian explosion and may yield important insight to possible extrinsic controls of the Ordovician radiation. Finally, a better understanding of the biogeographic and paleogeographic patterns will provide a perspective on the global nature of the event. How global is the pattern and how much of the pattern is a compilation of individual clades and regions (e.g., Miller and Mao, 1995). Studies are underway in all three areas. Data from all of these types of studies will bear on the issue of whether the Ordovician radiation is indeed, simply a follow-up to the Cambrian explosion or represents a unique and independent biodiversification event. Regardless, the Ordovician radiation was an event of singular importance in the history of metazoan life.

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REFERENCES

- Adrain, J. M., R. A. Fortey, and S. R. Westrop. 1998. Post-Cambrian trilobite diversity and evolutionary faunas. *Science* 280:1922–1925.
- Bambach, R. K. 1977. Species richness in marine benthic habitats through the Paleozoic. *Paleobiology* 3:152–167.
- Bambach, R. K. 1983. Ecospace utilization and guilds in marine communities through the Phanerozoic. In M. J. S. Tevesz and P. L. McCall (eds.), *Biotic interactions in recent and fossil benthic communities*, pp. 719–746. Plenum Press, New York.
- Botting, J. 2002. The relationship between pyroclastic volcanism and Ordovician diversification. In J. A. Crame and A. W. Owen (eds.), *Palaeobiogeography and biodiversity change: The Ordovician and Mesozoic-Cenozoic radiations*. Geological Society, London, Special Publications, 194.
- Cañas, F. and M. Carrera. 1993. Early Ordovician microbial-sponge-receptaculitid bioherms of the Precordillera, western Argentina. *Facies* 29:169–178.
- Droser, M. L., D. J. Bottjer, and P. M. Sheehan. 1997. Evaluating the ecological architecture of major events in the Phanerozoic history of marine invertebrate life. *Geology* 25:167–170.
- Droser, M. L., R. A. Fortey, and X. Li. 1996. The Ordovician radiation. *Am. Sci.* 84:122–131.
- Droser, M. L. and P. M. Sheehan. 1995. Paleocology of the Ordovician radiation and the Late Ordovician extinction event. Ordovician of the Great Basin: Fieldtrip and guidebook volume for the seventh international symposium on the Ordovician System, Las Vegas, NV, Pacific Section SEPM.
- Finnegan, S. and M. L. Droser. In Prep. Geologically abrupt shift in clade dominance at the Ibexian-Whiterockian boundary, western Utah.
- Gray, J. 1985. The microfossil record of early land plants: Advances in understanding of early terrestrialization. *Philosophical Transactions of the Royal Society of London B* 309:167–195.
- Guensburg, T. E. and J. Sprinkle. 1992. Rise of echinoderms in the Paleozoic fauna: Significance of paleoenvironmental controls. *Geology* 20:407–410.
- Hamdi, B., A. Y. Rozanov, and A. Y. Zhuravlev. 1995. Latest Middle Cambrian metazoan reef from northern Iran. *Geology Magazine* 132:367–373.
- Hammer, O. 2003. Biodiversity curves for the Ordovician of Baltoscandia. *Lethaia*. (In press)
- Harper, D. A. T. and C. MacNiocaill. 2002. Early Ordovician brachiopod biodiversity: Comparing some platforms, margins and intra-oceanic sites around the Iapetus ocean. In J. A. Crame and A. W. Owen (eds.), *Palaeobiogeography and biodiversity change: The Ordovician and Mesozoic-Cenozoic radiations*, pp. 25–34. Geological Society, London, Special Publications, 194.
- Johns, R. A. 1995. The good, the bad, and the ugly: The paleoecology of Ordovician sponge/algal reef mounds. In J. D. Cooper, M. L. Droser, and S. C. Finney (eds.), *Ordovician Odyssey: Short Papers for the Seventh International Symposium on the Ordovician System*, pp. 429–432. Pacific Section, Society for Sedimentary Geology (SEPM), Fullerton, California.
- Li, X. and M. L. Droser. 1999. Lower and Middle Ordovician shell beds from the Basin and Range province of the western United States (California, Nevada, and Utah). *Palaaios* 14: 215–233.
- Miller, A. I. 1997a. Dissecting global diversity patterns: Examples from the Ordovician Radiation. *Ann. Rev. Ecol. Syst.* 28:85–104.
- Miller, A. I. 1997b. Comparative diversification dynamics among paleocontinents during the Ordovician Radiation. *Geobios M.S.* n 20:397–406.
- Miller, A. I. and S. R. Connolly. 2001. Substrate affinities of higher taxa and the Ordovician Radiation. *Paleobiology* 27:768–778.
- Miller, A. I. and M. Foote. 1996. Calibrating the Ordovician radiation of marine life—implications for Phanerozoic diversity trends. *Paleobiology* 22:304–309.
- Miller, A. I. and S. G. Mao. 1995. Association of orogenic activity with the Ordovician radiation of marine life. *Geology* 23:305–308.
- Palmer, T. 1982. Cambrian to Cretaceous changes in hardground communities. *Lethaia* 15:309–323.
- Retallack, G. J. and C. R. Feakes. 1987. Trace fossil evidence for Late Ordovician animals on land. *Science* 235:61–63.
- Sepkoski, J. J., Jr. 1979. A kinetic model of Phanerozoic taxonomic diversity, II: Early Phanerozoic families and multiple equilibria. *Paleobiology* 5:222–252.
- Sepkoski, J. J., Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7:36–53.
- Sepkoski, J. J., Jr. 1984. A kinetic model of Phanerozoic taxonomic

- diversity, III: Post-Paleozoic families and mass extinctions. *Paleobiology* 10:246–267.
- Sepkoski, J. J., Jr. 1988. Alpha, beta, or gamma: Where does all the diversity go? *Paleobiology* 14:221–234.
- Sepkoski, J. J., Jr. 1990. Evolutionary faunas. In D. E. G. Briggs and P. R. Crowther (eds.), *Palaeobiology: A synthesis*, pp. 37–41. Blackwell Scientific Publications, Oxford.
- Sheehan, P. M. 1985. Reefs are not so different—they follow the evolutionary pattern of the level bottom communities. *Geology* 13:46–49.
- Valentine, J. W., T. C. Foin, and D. Peart. 1978. A provincial model of Phanerozoic marine diversity. *Paleobiology* 4:55–66.
- Vermeij, G. J. 1995. Economics, volcanoes, and Phanerozoic revolutions. *Paleobiology* 21:125–152.
- Waisfeld, B. G., T. M. Sanchez, and M. G. Carrera. 1999. Biodiversification patterns in the Early Ordovician of Argentina. *Palaaios* 14:198–214.
- Wilson, J. L. 1950. An Upper Cambrian pleospongid (?). *J. Paleontol.* 24:591–593.
- Zhuravlev, A. Y. 2001. Biotic diversity and structure during the Neoproterozoic-Ordovician transition. In A. Y. Zhuravlev and R. Riding (eds.), *The ecology of the Cambrian*, pp. 173–199. Columbia University Press, New York.