Cambro-Ordovician Studies I, Memoir 30 of the Association of Australasian Palaeontologists, J.R. Laurie, ed., 2004, Association of Australasian Palaeontologists, Canberra, 260 p. (Softcover, US $81.75) ISBN: 0-949466-28-X.

DOI 10.2110/palo.2004.P04-79

Our understanding of life's rich history in general, and some key episodes in that history in particular, such as the Cambrian and Ordovician radiations, continues to grow thanks in part to volumes like this one. Laurie, the editor of *Cambro-Ordovician Studies I,* has assembled a fine memoir, including an excellent and well-chosen team of authors. The papers cover a diverse range of topics and organisms, spanning the evolutionarily interesting and geologically important Cambrian and Ordovician periods. This volume, published by the Association of Australasian Palaeontologists, focuses on the faunas of Australia, but these have global relevance because of their scope and diversity in the Ordovician and, especially, the Cambrian. Further, Australian paleontologists have an outstanding tradition of producing important paleontological and stratigraphic studies, and this work is no exception. The book is well illustrated and contains pictures and descriptions of several new and important taxa, especially trilobites, along with detailed stratigraphic sections and geological descriptions. The first paper, by Kruse, Laurie, and Webby, presents a comprehensive overview and analysis of the Cambrian geology and paleontology of the Ord Basin: a region containing an important record of Middle and Upper Cambrian strata. The second paper is a fine one by Edgecombe, Banks, and Banks that focuses on the late Ordovician trilobites of Tasmania; several new and significant taxa are figured and described. Next follows a short paper by Jago and Anderson describing a new bivalved arthropod from the Middle Cambrian of Tasmania; the taxon shows intriguing similarities to *Waptia*, known from various Cambrian soft-bodied faunas including the Burgess Shale. The fourth paper is by Paterson and Laurie and analyzes late Cambrian trilobites from eastern Victoria. Several new taxa are described, a very useful Cambrian correlation chart is presented, and thorough paleoenvironmental and paleoecological analyses are included. Brock and Holmer have a significant paper on the largely endemic lingulate brachiopods from the Ordovician of Western Australia that contains several superb SEMs and summary statistics describing brachiopod morphology. A paper by Engelbretsen rounds out the works focusing on brachiopods with his study of Cambrian paterinids. Three other valuable studies on trilobites also are contained. First, Bentley and Jago have a paper on wuaniid trilobites that presents a phylogenetic analysis of this enigmatic group. Then, Sloan and Laurie are authors on a paper describing some Middle Cambrian trilobites from allochthonous blocks in New South Wales that contained some spectacular specimens with large spines that towered over the trilobites' eyes. Finally, Laurie has a paper on Middle Cambrian trilobites from a corehole taken in the Georgina Basin that has special relevance for Cambrian biostratigraphy.

Brachiopods and trilobites are not the only paleontological subjects of this volume. There are also two well-written papers on Ordovician conodonts: one by Zhen and Percival, the other by Nicoll and Kelman. Further, there is a nice paper by Brock and Paterson describing a new Early Cambrian helcionellid mollusc from South Australia.

This volume will be highly useful to anyone interested in Cambrian or Ordovician geology and paleontology. It also will appeal in particular to trilobite and brachiopod workers, although other groups are represented. In addition, it contains much relevant biostratigraphic information. It is the continued production of quality studies like these that push our paleontological knowledge base forward. The only thing that might have been useful that is lacking would have been an overview of the Cambrian and Ordovician geology of Australia, with emphasis on paleobiogeographic patterns. Still, this omission is not a serious flaw and the authors and the editor are to be commended for producing such a fine volume.

BRUCE S. LIEBERMAN
University of Kansas
Department of Geology
121 Lindley Hall
Lawrence, KS 66044

The Great Ordovician Biodiversification Event, Barry D. Webby, Florentin Paris, Mary L. Droser, and Ian G. Percival, eds., 2004, Columbia University Press, New York, 484 p. (Hardcover, US $99.50) ISBN 0231-12678-6.

DOI 10.2110/palo.2004.P04-49

Have you heard the joke about the time a systematist, a taxon-counter, and a paleoecologist walked into a bar?

It is not surprising that a significant proportion of paleontological attention is focused on the Cambrian Explosion; it indeed marks the rise to dominance of skeletonized metazoans and the emergence of most phyla. But the Cambrian Radiation is inherently difficult to study: the intricacies involved in reconstructing stem-group phylogenies, the lack of a globally correlated time scale, a dearth of paleomagnetic data, often sparsely fossiliferous strata, and significant regional differences in litho- and biofacies all combine to make it difficult to understand the historical underpinnings of this event, despite recent efforts to the contrary (Zhuravlev and Riding, 2000). In contrast, the ensuing Ordovician is nearly unparalleled in its record. The stratigraphic record is significant and nearly complete over broad cratons, fossiliferous strata are abundant and well preserved, there is now a relatively stable and well-constrained time scale for global correlation, and documentation of isotopic and sea-level trends is improving. The interval, sometimes termed the Ordovician Radiation, also is nearly equal to the Cambrian in terms of its evolutionary and ecological consequences. This period witnessed the appearance of dozens of crown-group representatives of taxonomic classes and orders and the first development of communities that would dominate the remainder of the Paleozoic and even the post-Paleozoic. Despite this significance, and the presence of an active global pool of Ordovician workers, very few works have focused extensively on the Ordovician Radiation.

This volume partially fills this lacuna. It acts as a sort of final report for the IGCP 410 project, with the goal of documenting the global, and in some cases regional, diversity trends for all major taxonomic groups during the Ordovician. In this regard, it is a major success. It is, for the most part, an authoritative compendium of Ordovician taxonomic diversity, although it also summarizes aspects of the physical Ordovician world, including tectonics, oceanography, and climate. Its strengths lie in the vast systematic experience of its 96 compilers, the incredible breadth of its taxonomic coverage (protists, animals, and plants—essentially, fully inclusive), and the generally standardized treatment of these groups using the recently adopted global Ordovician timescale and generally comparable diversity metrics. (Please note I will use the more common term Ordovician Radiation in this review rather than the Great Ordovician Biodiversification Event used in the volume. I just find it less clunky.)

Overall, there are very few errors in this volume; those that exist typically relate to text references of figures. I commend the editors and contributors for extensive documentation of the systematic literature, with a 70-page reference section and a wide-ranging index keyed both to general topics and taxonomy—for the acritarchs alone, this index runs from *Acanthodiacrodium* to the possible link with the Zygnematales.

The volume begins with a thorough introduction by Barry Webby. The review of past research is concise and apt, with a focus on the history and timing of assemblage-wide transitions generally involving evolutionary faunas and floras. The marine radiations are divided further into soft-substrate, reef, and infaunal communities. While useful, this review of assemblage-wide transitions is based largely on past research and does little to synthesize the present findings. The middle portion of the introduction includes an interesting summary of the diversification of all Ordovician pelagic taxa, but again without much synthesis. It appears his goal is to bring additional attention to these organisms that might share similar ecological propensities (and were clearly important for marine productivity), but further discussion is needed. Indeed, the diversity trajectories for many pelagic taxa—including graptolites, acritarchs, and conodonts—closely follow eustatic trends, and a quantitative comparison would be useful. Such a comparison would have made for an interesting stand-alone chapter if further developed with information from the rest of the vol-

 0883-1351/05/0020-0506/$3.00

ume. The remainder of the introduction is a comprehensive summary of the contributions in the volume, with several recommendations for future research, discussed below.

The rest of the volume is divided into four parts. Part One establishes the standardized timescale and diversity metrics used throughout the volume. Barry Webby, Roger Cooper, Stig Bergström, and Florentin Paris present a new, globally correlated time scale for the Ordovician based on global and regional graptolite, conodont, and chitinozoan biostratigraphic zones. This time scale is reminiscent of Webby (1998), with the six-fold division of the Ordovician into the Tremadoc (Time slice 1, TS.1), two as-yet unnamed stages/ages (TS.2–3), Darriwilian (TS.4; including now-obsolete uppermost Arenig, Llanvirn, and Llandeilo), Caradoc (TS.5), and Ashgill (TS.6) stages. Two additional recommendations include adoption of the adjectives Middle for rock units (lithostratigraphic series and stages) and Mid for temporal units (chronostratigraphic epochs and ages). Combined with computer-assisted calibration using well-constrained, global fossil (mostly graptolites) and bentonite ages by Peter Sadler and Roger Cooper, the time scale is subdivided into 19 high-resolution time-slice intervals of roughly 2.5 m.y. duration (1.6–3.0 m.y. range). To allow widespread use of these intervals in later chapters, they are given numbers corresponding to the six Ordovician stages, with letters representing substage-equivalent subdivisions; examples include TS.1a for the lowermost Tremadocian interval and TS.6c for the Hirnantian stage. Although the time scale only has been ratified in part, it is worth becoming familiar with, considering its many merits and the organizational cooperation with the International Subcommission on Ordovician Stratigraphy. To the merits of the editors and the contributors in the rest of the volume, this time scale is used in both the discussion and illustration of diversity dynamics, using regional and global ages when appropriate.

Roger Cooper concludes Part One, comparing the performance of various diversity metrics and recommending that normalized diversity be used as the best metric of standing diversity. Invented by Sepkoski (1975), it is the sum of all taxa ranging through an interval plus half of those with range terminations in the interval, including singletons. Based on simulations with several model data sets displaying a realistic range of diversity parameters, this metric performs better than the traditional total diversity (the simple aggregate of species in an interval) and other metrics. It also has the benefit of implicitly controlling for heterogeneities in interval duration. While more recent sampling-standardized methods may be better still (Alroy et al., 2001), the use of this straightforward metric here seems acceptable given its simplicity. Cooper also recommends standard calculations for various additional diversity metrics, including origination, extinction, and turnover rates. Like the time scale, these metrics are adopted by most contributors in the volume, helping standardize comparisons among taxonomic groups.

Part Two summarizes various physical parameters during the Ordovician. Robin Cocks and Trond Torsvik summarize the changing positions of tectonic plates during the Early, early Late, and latest Ordovician. In addition to Gondwana and the major terranes of Laurentia, Baltica, and Siberia, they also include most of the lesser terranes around Gondwana and throughout the closing Iapetus Ocean, and discuss several island arcs. Graham Shields and Ján Veizer discuss recent isotopic trends for strontium, neodymium, carbon, oxygen, and sulfur. Of these, strontium displays the most impressive trend, with a significant and rapid drop at the Mid–Late Ordovician boundary that, by itself, is greater than any change that has occurred throughout the entire Cenozoic. They interpret this drop as resulting from increased volcanism and seafloor-spreading rates, global transgression, and waning continental runoff.

The following two chapters, both by Christopher Barnes, focus on Ordovician oceanography, climate, and a possible mantle superplume. Distinguishing climatic and oceanographic characteristics include a greenhouse climate with reduced atmospheric oxygen and elevated carbon dioxide and water vapor (relative to today), fluctuating but generally high sea levels resulting in widespread epeiric seas, and poor water circulation between deep and shallow water, resulting in reduced upwelling and extensive deep-water anoxia. The period is also characterized by the Taconic (Laurentia), Benambran, and Delamerian (both in Australia) orogenies; extensive volcanism, among the most extreme in the Phanerozoic; and widespread Hirnantian glaciation, resulting in the end-Ordovician extinction. In combination with these factors, as well as reduced rates of magnetic reversal and the strontium excursion, Barnes raises the possibility for a Mid-Ordovician mantle superplume. Although additional effort is needed to establish such a link more strongly, the timing and consequences for such an event might have provided an important trigger for the Ordovician Radiation.

The Late Ordovician glaciation is the focus of Patrick Brenchley's contribution, noting the two-pronged effects of the South Polar, Gondwanan ice cap: a basal Hirnantian cooling episode linked with global regression and a later Hirnantian transgression linked with warming and oceanic anoxia. Arne Thorshøj Nielsen documents sea-level trends in Baltica that appear to correlate in general with Laurentian trends, further fanning speculation that the major fluctuations and trends during the Ordovician are eustatic in nature. Unfortunately, there are two oversights in the presentation of the data that make evaluation difficult. First, it is difficult to correlate this sea-level trend with later diversity trends because the Baltic trend is presented without the standard time-scale intervals used throughout the volume. Furthermore, the Baltic trend is missing from the figure comparing it to the Laurentian trend. Although crossties are figured, it is not possible to visually evaluate their validity, especially because several are made in question by the author. Of course, it is possible for the interested reader to digitally scan and stretch the Baltic trend to superimpose it for himself, but this is one of very few oversights in the volume that should have been corrected.

In general, these chapters were concise and lucid, but I wanted more. Clearly, the issues of volcanism, orogenies, uplifted highlands and erosional centers, epeiric seas development, lithofacies belts (and especially regions of anoxia), tectonic settings, and biotic provinciality (especially in light of tectonic reconstructions and oceanographic currents) all deserved their own chapters. Furthermore, with the exception of Barnes' intriguing contributions and a short allusion by Brenchley, none addressed the possible biotic consequences of these events.

Part Three is the meat of the volume. It includes summaries of the diversity trajectories for most Ordovician groups, including many groups for which this presentation is a first. Because most are contributed by experts in each group, it is not surprising that the systematics and the diversity trajectories drawn from them are current and authoritative. Given the very patchy record of some of these groups—such as byroniid "tubes" (Lars Holmer), machaeridians (Anette Högström), and phyllocarid arthropods (Patrick Racheboeuf)—it is understandable that chapter length varies, and I am delighted to see that these poorly known suspects are included. Diversity trends typically are presented for genera, although most pelagic and biostratigraphically important taxa—graptolites (Roger Cooper, Jörg Maletz, Lindsey Taylor, and Jan Zalasiewicz), chitinozoans (Florentin Paris, Aïcha Achab, Esther Asselin, Chen Xiao-hong, Yngve Grahn, Jaak Nõlvak, Olga Obut, Joakim Samuelsson, Nikolai Sennikov, Marco Vecoli, Jacques Verniers, Wang Xiao-feng, and Theresa Winchester-Seeto), conodonts (Guillermo Albanesi and Stig Bergström), and radiolarians (Paula Noble and Taniel Danelian)—are presented at the species level. Many chapters give range-data charts for every known genus: radiolarians, corals from various regions (Barry Webby, Robert Elias, Graham Young, Björn Neuman, and Dimitri Kaljo), polyplacophorans (Lesley Cherns), bivalves and rostroconchs (John Cope), hyoliths (John Malinky), cornulitids, coleoloids, and sphenothallids in text (Mark Wilson), palaeoscolecidans and chaetognaths (Petr Kraft and Oliver Lehnert), conodonts, vertebrates (Susan Turner, Alain Blieck, and Godfrey Nowlan), receptaculitids and cyclocrinitids (Matthew Nitecki, Barry Webby, and Nils Spjeldnaes), and important miospore morphotypes (Philippe Steemans and Charles Wellman). This also is sometimes documented for species, including stromatoporoids (Barry Webby), conulariids (Heyo Van Iten and Zdenka Vyhlasová), tentaculitids (Hubert Lardeux), and phyllocarids.

Many chapters give individual treatment to various taxonomic subgroups, ranging from orders to subfamilies. Even more useful for understanding the radiations, many diversity trends are figured at both global and regional scales for the major terranes. This regional documentation is more common in the best-known groups, including sponges (Marcelo Carrera and Keith Rigby), corals, trilobites (Jonathan Adrain, Gregory Edgecombe, Richard Fortey, Øyvind Hammer, John Laurie, Timothy McCormick, Alan Owen, Beatriz Waisfeld, Barry Webby, Stephen Westrop, and Zhou Zhi-yi), graptolites, chitinozoans, and acritarchs (Thomas Servais, Jun Li, Ludovic Stricanne, Marco Vecoli, and Reed Wicander), but also is presented for conulariids, hyoliths, ostracodes (Roger Schallreuter), and vertebrates. Surprisingly, these regional data are not provided for the brachiopods (David Harper, Robin Cocks, Leonid Popov, Peter Sheehan, Michael Bassett, Paul Copper, Lars Holmer, Jisuo Jin, and Rong Jia-yu) and echinoderms (James Sprinkle and Thomas Guensburg), although important regional differences are discussed in the text. Given the standardized time scale and diversity metrics, there is little to disappoint in terms of the data, and I expect the volume will be used by eager, data-crunching taxon-counters.

In spite of these overwhelming accolades, however, I do not find this part satisfying. Upon reading through the volume, I expected to find updated assessments for the causes of the Ordovician Radiation from those systematists who most closely understand their taxa, their sometimes-subtle morphological evolution, their geographic and facies occurrences, and their autecological characteristics. Yet the chapters were more about presenting data than using them to understand important evolutionary and ecological events. To be sure, several chapters mention relevant issues and how they might help pinpoint a cause (or causes) for their diversifications. But there are few overarching themes that emerge for the radiation as a whole. In part, I can accept my disappointment as unjustified: the explicit goal of the volume was to summarize the taxonomic dynamics of Ordovician taxa, and not the causes of these dynamics. But I think my disappointment points to a general reluctance among Ordovician workers to focus on the larger, synthetic issues of this radiation that, by definition, extend *beyond* single taxonomic groups, and require collaboration among workers of different research backgrounds, methodological tastes, and inherent worldviews. Hopefully the participants of IGCP 503, underway right now, will tackle such issues more directly and synthetically.

In the hope of illuminating several of the many unanswered questions raised by these data, and given the dozens of chapters in Part Three, I will discuss each in the context of overarching patterns I observed rather than critique each chapter separately. There are two dominant themes I observed, and many more exist; Barry Webby and Arnie Miller point to both and several others in their introductory and closing remarks, respectively. The first, the "second facet of why" in Miller's chapter, is that the Ordovician Radiation was not synchronous among all groups. Typical, global descriptions of Ordovician diversity (Sepkoski, 1995, Miller and Foote, 1996) generally point to two major pulses of taxonomic increase, one during TS.3 (roughly equivalent to the lower Middle Ordovician) and a larger one during TS.5 (largely the Caradoc, although really starting during interval TS.4c). While generally true, this simplifies a much more complicated diversification, with several pulses spanning multiple clades, and with even the same taxonomic group displaying multiple pulses of diversification. These pulses are summarized here, at the genus-level unless noted otherwise.

The second important theme, echoed forcefully by Miller, is that there appears to be a strong lithological and biogeographical component to the diversification. In other words, it appears that co-occurring associations in particular environments are undergoing diversifications at similar times, often linked to environmental transitions. These also are summarized here at a larger scale.

Only conodont species and ichnogenera (Gabriela Mángano and Mary Droser) in shallow- and deep-marine settings demonstrate a generally consistent increase throughout the Ordovician. In both cases, the data are compiled at a large temporal resolution; further temporal refinement likely will show additional dynamics. Similarly, only a few groups demonstrate a consistent decline throughout the Ordovician, typically from a Cambrian peak. These include palaeoscolecidans, chaetognaths, the Ibex I trilobite fauna (including olenids and ceratopygids), and cyanophyte (blue-green algae) bacteria. It is important to note here the updated and enlarged analysis of global trilobite faunas by Jonathan Adrain, Stephen Westrop, and Richard Fortey, in which their original Ibex trilobite fauna has been subdivided into two separate faunas, each with their own unique diversity patterns.

The first Late Tremadocian (TS.1c–d) pulse in originations is not apparent in synoptic compilations because it occurred during an interval of appreciable turnover in many groups. It includes sponges (especially orthocladines and hexactinellids), linguliform and rhynchonelliform brachiopods (particularly pentamerides and the first pulse of orthides), polyplacophorans, tryblidiids (monoplacophorans; David Rohr and Jiří Frýda), rostroconchs, chitinozoan species (throughout the Tremadocian in Gondwana, Baltica, and China), conodont species, and the first pulse of soanitid receptaculitid species (continuing through TS.2a).

A more-extensive diversification interval occurs during the now-obsolete Early Arenig (TS.2a–c). It includes radiolarians, esthonioporine and halloporine bryozoan species (Paul Taylor and Andrej Ernst interpret the entire Ordovician history as a single exponential pulse starting in TS.2c during a period of maximal provinciality, continuing through the Caradoc), linguliform brachiopods, euomphaloidean and macluritoidean gastropods (Jiří Frýda and David Rohr), bivalves, nautiloid cephalopods (especially ellesmerocerids; Robert Frey, Matilde Beresi, David Evans, Alan King, and Ian Percival), possibly hyoliths, the Ibex II trilobite fauna and the first pulse of the Whiterock trilobite fauna (especially concentrated in Avalonia, and including asaphids, cheiruroideans, bathyuroideans, trinucleoideans, and cyclopygoideans), Argentinean phyllocarids (in deep waters), ostracode species (especially in Baltic carbonates), blastozoans and homalozoans (confined to TS.2c, with blastozoan diversification continuing through TS.5b), and graptolite species (especially in Australasia, Baltica and Avalonia, although the use of different time intervals makes comparisons difficult).

Although analyses of specific faunal and lithological associations are lacking, it is apparent that these Lower Ordovician diversifications can be sorted into two broad facies-related categories. One generally occurs in carbonate-rich settings in Laurentia and probably Siberia, South China, and the Argentine Precordillera. In his introduction, Barry Webby links these diversifications to the transgression-mediated development of sponge-microbial biostromes and bioherms. Groups participating in this diversification include soanitid receptaculitids, orthocladine sponges, stromatoporoids, and lichenariid tabulate corals, augmented by bryozoans during the Mid-Ordovician. Synchronous diversifications in the same regions, but along carbonate-platform settings, are found among polyplacophorans, euomphaloidean and macluritoidean gastropods, plectorthoid brachiopods, and several Ibexian trilobite groups.

Another major Lower Ordovician diversification is confined to siliciclastic-shelf settings along Gondwana, including the peri-Gondwanan terranes of Avalonia, Perunica, and Armorica. Prominent members of this association include lingulide brachiopods, orthoidean brachiopods, bivalves, hyoliths, several Ibexian trilobite groups, chitinozoans, and probably blastozoans and homalozoans. Adrain, Westrop, and Fortey note that few of these trilobites survived the end-Ordovician extinction. As pointed out in the conclusion by Miller, many of these groups also appear to migrate *en-masse* to Laurentia by the Late Ordovician.

The next important period of diversification is observed in several taxa during the now-obsolete Mid Arenig (TS.3a–b). This diversification is confined largely to members of the Paleozoic Evolutionary Fauna, during which time they became more diverse than the Cambrian EF; most originations are typically second pulses in clades that diversified to varying degrees during previous intervals. Included are the rhynchonelliform brachiopods (especially strophomenides, continuing through TS.5b, and the major pulse of orthides through 4a), bellerophontid gastropods (continuing through TS.4a; David Rohr and Jiří Frýda), second pulses of euomphaloidean and macluritoidean gastropods, numerous nautiloid cephalopod groups, and a second pulse of Whiterock trilobites (especially among illaenids, encrinurids, and odontopleurids, and especially in Laurentia, Baltica, and South China). The diversification of these trilobites occurred first in buildup and marginal deep-subtidal settings before spreading to shallower and deeper settings later in the Ordovician.

Droser et al. (1996) already reported on these biotic changes in the Laurentian Great Basin. This interval was associated with rapid diversification in Whiterock trilobites, brachiopods, ostracodes, bryozoans, nautiloid cephalopods, and ichnofossils. They originally implicated echinoderms in this biotic turnover, but Sprinkle and Guensburg here report no such diversification. Webby discusses a somewhat later (TS.4b), association-wide diversification affecting similar taxa in Siberian platform settings (Kanygin, 2001). Among these diversifying groups, Adrain, Westrop, and Fortey note that these tropical, Whiterock trilobites—especially in the Laurentian Bathyurid Realm—preferentially survived the end-Ordovician extinction, while most other members of this association—especially euomphaloidean and macluritoidean gastropods, many nautiloid cephalopods, receptaculitids, and even Whiterock trilobites diversifying in association in higher latitudes—were less resistant to the extinction.

A general Mid-Ordovician plateau in diversity also is accompanied by diversification during the Early Darriwilian (TS.4a–b, Late Arenig). These diversifications are especially prevalent in Baltica and Laurentia, and are found in several groups, including radiolarians, orthocladine sponges, linguliformean brachiopods (during which most members become infaunal), mimospirinan gastropods (Jiří Frýda and David Rohr), ostracodes, nautiloid cephalopods, possibly hyoliths, and a second pulse of homalozoans.

The greatest Ordovician diversification occurs during the Late Darriwilian through Mid Caradoc (TS.4c–5c), resulting in a tripling of known genera compared to the preceding Cambrian. The diversification is broad and global; it includes members of all three evolutionary faunas, higher taxa making their first-ever occurrence in the fossil record, and groups that had already diversified to some extent previously. Taxa include sponge species, stromatoporoids (continuing to diversify through TS.6b), conulariids, corals (including tetradiid species and tabulate and rugose corals, with the rugose corals making their first-ever occurrence), species in most bryozoan subgroups, lingulide, craniiform, and rhynchonelliform brachiopods (especially atrypides and rhynchonellides through TS.5a), archaeogastropods, bivalves (especially pteriomorphians), the first tube-shaped cornulitids and undoubted tentaculitids, the problematical sphenothallids (which probably diversified during the Cincinnatian, although precise timing is uncertain), polychaete scolecodonts (Olle Hints and Mats Eriksson), the final Ordovician pulse of Whiterock trilobites (dominated by various phacopides, but possibly starting earlier in TS.4b in Australia, New Zealand, South America, and Avalonia), Argentinean phyllocarids (in deep waters, especially in TS.5b), ostracode species (continuing through an Ashgillian peak), all non-homalozoan echinoderms in general (especially during TS.5b–c, with six new clades—coronoids, blastoids, bothriocidarids, echinoids, holothurians, and flexible crinoids—and massive species-level diversification in crinozoans, increasing from 16 to 130 species during TS.5b and setting the stage for their later Paleozoic dominance among echinoderms), Baltic and Avalonian graptolite species (probably during TS.4b–c, chitinozoan species with a variety of pulses at different times in various terranes), vertebrates (especially in TS.5b in Gondwana, Laurentia, Baltica and Siberia), most algae (solenoporans, other red rhodophytes, ischaditid receptaculitides, cyclocrinitids, other green chlorophytes, and brown phaenophytes; Matthew Nitecki, Barry Webby, Nils Spjeldnaes, and Zhen Yong-yi), and miospores (after initial diversification during Darriwilian).

Webby associates this diversification with the development of Late Ordovician reefs, but it is more so the broad carbonate-dominated shelf that is the dominant facies, especially in Laurentia, Baltica, and perhaps Australia. This association—compositionally similar to the Arctic Ordovician Fauna of Nelson (1959), with its reef and level-bottom members—includes sponges (primarily in Baltica), stromatoporoids, tabulate and rugose corals, bryozoans, craniiform and rhynchonelliform brachiopods, trilobites, nautiloid cephalopods, and algae (ischaditid receptaculitids, brown phaenophytes, and solenoporans).

But there also are a variety of groups that diversified in other facies. Take, for example, the deep-subtidal, siliciclastic, and mixed-siliciclastic-carbonate muddy habitat, typically influenced by orogenic or other tectonic events. In eastern Laurentia, and perhaps in Avalonia and Perunica as well, these associations underwent diversifications of sponges, rugose corals, conulariids, linguliformeans, bivalves (especially infaunal and semi-infaunal pteriomorphians), Whiterock trilobites, and possibly several echinoderm groups. Similar examples of association-wide diversifications can be found in nearly every environment—oceanic, deep marine, shallow marine, marginal, and continental.

This TS.4c–5b diversification also witnessed the origination or proliferation of important ecological strategies. Among bioeroders, encrusters, and cementers, there are stromatoporoids, tabulate corals, members of all brachiopod subphyla, cornulitids, byroniids, tentaculitids, pteriomorphian bivalves, and many pelmatozoans. Within the echinoderms alone, there are new grazing algivores (bothriocidaroids and echinoids), more thorough surface-deposit feeders (holothurians), higher-tiering blastoids, crinoids, and coronoids, and more widespread diversification of predatory asteroids. Similar expansion can be found among other predators (scolecodonts), infaunalization and foraging patterns (as evidenced by trace fossils), and other functional categories.

These diversifications wane during the remaining, high-diversity Caradoc, followed by another, minor increase in most groups producing a second diversity maximum during the Early to Mid Ashgill (TS.6a–b). This final pulse is most apparent in sponge species, stromatoporoids, all coral groups, some bryozoans, craniiform and many rhynchonelliform brachiopods, archaeogastropods, pteriomorph bivalves, Baltic ostracode species, Laurentian chitinozoan species, and possibly miospores.

The record for several taxa makes it difficult to draw conclusions about Ordovician diversity, including several tube-shaped groups (coleoloids and byroniids), machaeridians (with indications of pulses in TS.2 and TS.6), eurypterids (with increased occurrences in the Late Ordovician; Simon Braddy and Victor Tollerton), and acritarchs (with a Middle Ordovician pulse).

Many taxa display significant reductions during the Hirnantian stage (TS.6d) in response to the two phases of the Late Ordovician glaciation. Most authors discuss the effect of the extinction to some degree. For example, stromatoporoids underwent approximately 70% extinction during the initial regressive phase. However, with the Hirnantian treated generally as a single time slice and with the lack of corresponding data for the Silurian, it is difficult to evaluate selectivity for most groups.

Additional highlights are peppered throughout the volume. For example, Heyo Van Iten and Zdenka Vyhlosová note the possibility of a latitudinal diversity gradient in Upper Ordovician conulariids. James Sprinkle and Thomas Guensburg proclaim boldly that the echinoderm record is so substantial, no bothriocidaroid or echinoid older than TS.4c (latest Middle Ordovician) will be discovered. Provinciality and degree of endemism decrease throughout the Ordovician in many groups (bryozoans, echinoderms, and to a lesser degree nautiloids), increase for others (sponges), and remain consistently high for yet others (conulariids and chitinozoans).

Morphological key innovations often are linked with diversifications in several chapters. Paul Taylor and Andrej Ernst link bryozoans with the evolution of a calcitic zooecium. John Cope links bivalves with the development of the feeding gill. Florentin Paris and colleagues link chitinozoans with plasticity of the genome of their enigmatic metazoan producers. And Peter Sheehan and David Harper link brachiopods with the development of planar shells to allow reclining lifestyles, and cyrtomatodont dentition, allowing stronger ball-and-socket hinges. In addition to these morphological adaptations, they also discuss three possible paleoecological causes for brachiopod diversification during the Ordovician, including: (1) lower metabolic rate allowing a competitive advantage during lower nutrient levels of the Early Paleozoic; (2) the opportunity offered calcite-shelled animals during an interval of calcite seas; and (3) wholesale increases in community complexity, causing stabilization of local nutrient levels. They add that these factors are not necessarily unique to the brachiopods and probably affected most members of the diversifying Paleozoic fauna. Additional evidence for an increase in nutrient levels is offered by the compelling pattern of a doubling of median and maximum size of plectorthoidean and orthoidean brachiopods during the Ordovician.

Part Four includes two additional issues, including a summary of the ichnological record and useful guidance for how future progress can be made in understanding the radiation. Gabriela Mángano and Mary Droser present a broad overview of Ordovician ichnological trends from a variety of environments. The general theme is increasing diversity throughout the period in concert with increased tiering depth, architectural and behavioral complexity, and environmental colonization. The diversity increase in shallow-siliciclastic settings is largely caused by the diminishing dominance of trilobite traces; in both siliciclastic and carbonate environments, more-extensive development of infaunal burrows is an important ecological change. Diversity increase in carbonate settings is due primarily to the advent of bioeroders and development of hard-substrate associations. Environments prone to frequent volcanic disturbance remained relatively simple throughout the Ordovician. The dominant change in deep-marine environments is the establishment of essentially modern types of behavioral complexity, including spiral, meandering, rosette, and boxwork grazing traces. Many of the trace makers probably migrated from shallower environments during the Ordovician, although the colonization histories are not straightforward. Although brackish marginal-marine settings were invaded during the Early Cambrian, such traces generally are rare. However, putative trilobite traces recently have been found in Argentina, demonstrating they were also the dominant brackish-water tracemakers during the Early to Mid Ordovician, with other arthropods and soft-bodied animals becoming more important by the Late Ordovician. The first terrestrial trace fossils, probably made by amphibious animals, are Late Cambrian to Early Ordovician in age. The first fully terrestrial traces, made by arthropods, are found in the Late Ordovician.

In his final comments for the volume, Miller recommends a broad, comparative framework for understanding the causes of the Ordovician Radiation. In particular, he focuses on two, interdependent questions that are still largely unanswered—his "two facets of why." Why is this event one of global reach, and what explains the broad heterogeneity in the timing and nature of diversifications of individual clades? The answer, he suggests, lies in a careful, comparative analysis of the geographic, environmental, and ecological propensities of diversifying clades. Such comparisons can be made in two ways, each pointing to important answers for the Ordovician Radiation, and, by extension, other evolutionary radiations as well. First, what similarities are shared by unrelated or ecologically distinct clades displaying similar diversification trajectories within the same geographic venues? Presumably, such dynamics have a common environmental trigger, but we also might discover emergent similarities related to ecological or macroevolutionary characteristics. For example, Frýda and Rohr note euomphaloidean and macluritoidean gastropods both share similar global diversity trajectories. Assuming these similarities are found at more finely resolved geographic and environmental scales, might this add further fodder for their presumed filter-feeding foraging habit? At a larger scale, this is the type of analysis that would focus on entire biogeographical associations sharing similar diversity dynamics, such as Early Ordovician associations in Gondwanan siliciclastics and in Laurentian carbonates. Second, how comparable are the diversification histories of ecologically similar (or potentially competing) taxa? This is the type of analysis that Webby seems to suggest when focusing on pelagic taxa, or in noting that level-bottom and reef communities sometimes do not diversify in concert. Continuing with the possible filter-feeding gastropod example from above, how might their diversifications compare with sedentary brachiopods, bryozoans, and pelmatozoans in the same geographic and environmental venues?

Both Webby and Miller end their contributions with recommendations for future research on the Ordovician Radiation. Miller emphasizes the continued need for sampling standardization, understanding the geographic basis for diversifications, undertaking comparative analyses such as those mentioned above, conducting similar analyses in the field (especially during critical intervals during which abundance data might be important), and assessing morphological (and I would add ecological) disparity during the radiation. Both he and Webby also point to a greater need to connect the diversification to physical parameters related to orogenesis, paleogeography, and geochemistry.

Webby focuses primarily on the need for improved raw data. For example, although our knowledge of Ordovician island-arc geography is in its infancy, the Iapetus, and in some cases Panthalassic, island arcs clearly were important centers of diversification throughout the period. Chapters specifically mentioning them include sponges, stromatoporoids, micromorphic linguliformeans, trimerellide craniiformeans, and several rhynchonelliformeans (plectambonitoideans, atrypides, spiriferides, and athyridides). He also recommends additional study of microbial biotas, broader cratonic analyses of Baltica and South China, and greater integration of Ordovician ecosystems—especially related to productivity and nutrient levels.

Most emphasis, however, Webby states, should be on finishing the basic description of taxonomic diversity documented in this book. While I agree with this thought, I do not think it should deter from the already exemplary data documented in this volume. Sufficient data exist to start tackling the many important questions above. The rallying cry of "we need more data!" is infinitely defeatist—there never will be a time when all the data are in place, and such a prerequisite is rarely needed. Unlike many ventures, scientific progress can occur—at least preliminarily—with the army of data we have, not the army of data we want.

At the beginning of this review, I mentioned a joke about paleontologists of different ilk, who often grumble about their disparate schools of thought. We all have our own predispositions, and there is only so much time available to specialize on different clades, on different methodologies, and on different sedimentary units. But the synthetic analyses proposed above really do require that we call on additional resources to answer them, including those with skills different than our own. We obviously continue to need well-trained and competent systematists for discovering and documenting the basic data of paleontology and for understanding their evolutionary relationships. This volume attests to the enormous benefits of such endeavors. But we also need critical, analytical paleobiologists who can focus on the larger issues using the appropriate quantitative methodologies to frame important questions; and we need paleoecologists—including community paleoecologists, biomechanicists, biogeographers, climatologists, and numerous soft-rock geologists—to connect the evolutionary histories of clades with their physical and biological environments. This volume, for various reasons, does not deal sufficiently with the latter two needs.

I do not want to give the impression that no chapters delve into these more subtle manifestations of the radiation. The trilobite chapter by John Adrain and colleagues is exemplary in this regard in teasing apart the different dynamics of the Whiterock and two Ibex trilobite faunas in various geographic terranes. This pattern is further evaluated with regard to biogeographic realms, environmental zonation, ecological strategies, and extinction selectivity. Other chapters address some of these issues to a lesser degree. And in many cases—such as machaeridians, polyplacophorans, and others—such developments clearly are not possible at this stage. But they clearly are possible in many, if not most, groups, making this lack of analysis disappointing.

In the end, I am missing still a general consensus for the dominant causes of the Ordovician Radiation. Is it the result of a diversification of facies due to climatic or tectonic changes (Miller and Mao, 1995), of physical transitions in local settings (Miller, 2000), of biogeographic provinciality due to tectonic changes (Crame and Owen, 2002), of mantle plumes (Barnes, this volume), of the advent of calcite seas and development of hardgrounds (Guensburg and Thomas, 1992), of biotically driven changes among associations (Peters, 2004), or of ecological innovation within associations, possibly driven by metazoan reefs (Webby, 2002)? The list of outstanding culprits is much larger than this list. Because they are obviously interrelated in complex ways, testing among these influences will be difficult. But the Ordovician is a perfect period to develop these tests.

This volume will appeal most to Ordovicianados, and it ought to have a presence in every research library. It is sound data, presented openly and by well-informed experts; in this manner, it should be a boon to those interested in explaining these patterns. Yet I would not recommend it for graduate seminars or casual reading unless you wanted to supplement the volume with literature focused on particular causes for the radiation. There is much recent literature to choose from in this vein. These reservations aside, it is an ample and serious compendium and will be useful for those interested in evolutionary radiations in general, and especially those interested in understanding the geographical, ecological, and evolutionary interrelationships for this radiation in particular. I hope it helps motivate researchers during other intervals to build such a strong foundation.

The data clearly are ample enough to begin synthetic research on the causes of the radiation. And I look forward to the punchline.

REFERENCES

Alroy, J., Marshall, C.R., Bambach, R.K., Bezusko, K., Foote, M., Fürsich, F.T., Hansen, T.A., Holland, S.M., Ivany, L.C., Jablonski, D., Jacobs, D.K., Jones, D.C., Kosnik, M.A., Lidgard, S., Low, S., Miller, A.I., Novack-Gottshall, P.M., Olszewski, T.D., Patzkowsky, M.E., Raup, D.M., Roy, K., Sepkoski, J.J., Jr., Sommers, M.G., Wagner, P.J., and Webber, A., 2001, Effects of sampling standardization on estimates of Phanerozoic marine diversification: Proceedings of the National Academy of Sciences, v. 98, p. 6261–6266.

Crame, J.A., and Owen, A.W., eds., 2002, Palaeobiogeography and Biodiversity Change: The Ordovician and Mesozoic–Cenozoic Radiations: Geological Society of London Special Publication 194, 212 p.

Droser, M.L., Fortey, R.A., and Li, X., 1996, The Ordovician Radiation: American Scientist, v. 84, p. 122–131.

Guensburg, T.E., and Sprinkle, J.S., 1992, Rise of echinoderms in the Paleozoic evolutionary fauna: significance of paleoenvironmental controls: Geology, v. 20, p. 407–410.

Kanygin, A.V., 2001, The Ordovician explosive divergence of the earth's organic realm: causes and effects of the biosphere evolution: Russian Geology and Geophysics, v. 42, p. 599–633.

Miller, A.I., 1998, Biotic transitions in global marine diversity: Science, v. 281, p. 1157–1160.

Miller, A.I., and Foote, M., 1996, Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends: Paleobiology, v. 22, p. 304–309.

Miller, A.I., and Mao, S., 1995, Association of orogenic activity with the Ordovician Radiation of marine life: Geology, v. 23, p. 305–308.

Nelson, S.J., 1959, Arctic Ordovician fauna: an equatorial assemblage: Journal of the Alberta Society of Petroleum Geologists, v. 7, p. 45–47.

Peters, S.E., 2004, Relative abundance of Sepkoski's evolutionary faunas in Cambrian–Ordovician deep subtidal environments in North America: Paleobiology, v. 30, p. 543–560.

Sepkoski, J.J., Jr., 1975, Stratigraphic biases in the analysis of taxonomic survivorship: Paleobiology, v. 1, p. 343–355.

Sepkoski, J.J., Jr., 1995, The Ordovician radiations: diversification and extinction shown by global genus-level taxonomic data: *in* Cooper, J.D., Droser, M.L., and Finney, S.C., eds., Ordovician Odyssey: Short Papers for the Seventh Symposium on the Ordovician System: SEPM Pacific Section, Fullerton, CA, p. 393–396.

Webby, B.D., 1998, Steps toward a global standard for Ordovician stratigraphy: Newsletters in Stratigraphy, v. 36, p. 1–33.

Webby, B.D., 2002, Patterns of Ordovician reef development: *in* Kiessling, W., Flügel, E., and Golonka, J., eds., Phanerozoic Reef Patterns: SEPM Special Publication 72, SEPM (Society for Sedimentary Geology), Tulsa, p. 129–179.

Zhuravlev, A.Y., and Riding, R., 2000, The Ecology of the Cambrian Radiation: Columbia University Press, New York, 525 p.

PHIL NOVACK-GOTTSHALL
Department of Geosciences
University of West Georgia
1601 Maple Street
Carrollton, GA 30118