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The Ordovician biodiversification: Setting an agenda for marine life

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Abstract

Profound changes in the biodiversity and biocomplexity of marine life occurred during the early to mid-Ordovician through an interval of some 25 Myr. The planet's seascapes were changed forever with massive hikes in biodiversity, the installation of a benthos dominated by suspension feeders together with the introduction of many new megaguilds; increased bioturbation, biotic tiering above and below the sediment–water interface, the more widespread prevalence of hard substrates, in a calcite sea, and the development of new reef formers helped drive these changes. The strong and varied regional and taxonomic components of the global signal emphasize the extrinsic controls on the radiation. A model involving the cascading development of γ (inter-provincial), β (inter-community) and α (intra-community) diversity highlights the interplay between ecology, environment, geography and adaptive strategy during the event. Further deconstruction of the event into individual taxonomic and regional components together with the acquisition of more environmental and isotopic data are required to elucidate the causes of this marked and multifaceted biodiversification.

Keywords: Ordovician; Biodiversity; Palaeoecology; Palaeobiogeography

1. Background

During a protracted interval of some 25 Myr, during the mid to late Ordovician, the biological component of the planet's seafloors was irreversibly changed. A massive hike in biodiversity (Sepkoski, 1981) was matched by an increase in the biocomplexity of marine life (Droser and Sheehan, 1997). The Great Ordovician Biodiversification is one of the two most significant evolutionary events in the history of Palaeozoic life. By contrast, however, to the Cambrian explosion, which has been well documented in many books and symposia together with many hundreds of publications, there are relatively few major published studies on the Ordovician diversification; an exception is the recently published compilation by Webby et al. (2004a,b). The Cambrian explosion involved the origins of skeletalization and a range of new body plans together

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with the extinction of the soft-bodied Ediacara fauna and the appearance of the Bilateralia. The Ordovician diversification (Fig. 1), by contrast, generated few new higher taxa, for example phyla, but witnessed a staggering increase in biodiversity at the family, genus and species levels. This taxonomic radiation, which included members of the so-called ‘Cambrian, Paleozoic and Modern’ evolutionary biotas, set the agenda for much of subsequent marine life on the planet against a background of sustained greenhouse climates. Although many taxa counts are available through 45 million years of the Ordovician Period, there are relatively few studies of the ecological and environmental aspects of this diversification (Bottjer et al., 2001). Moreover the causes of the event, and its relationship to both intrinsic (biological) and extrinsic (environmental) factors, are far from clear.

In many ways the Ordovician Period was unique (Jaanusson, 1984). The period was thalassocratic with extensive, epicontinental seas, with virtually flat seabeds, and restricted land areas, many probably represented only by archipelagos. Magmatic and tectonic activity was intense with rapid plate movements and widespread volcanic activity. Island arcs and mountain belts provided sources for clastic sediment in competition with the carbonate belts associated with most of the continents. Biogeographical differentiation was extreme affecting plankton, nekton and benthos and climatic zonation, particularly in the southern hemisphere. Together conditions were ideal for both allopatric and sympatric speciation processes together with opportunities for canalization of ecological niches. Most significant was the diversification of skeletal organisms, including the brachiopods, bryozoans, cephalopods, conodonts, corals, crinoids, graptolites, ostracodes, stromatoporoids and trilobites.

Disassembly of the strong global signal into ecological, taxonomic and regional components has further emphasized the many facets of this complex event. Although the ecological and taxonomic amplitudes of the biodiversification may indeed be decoupled, there are important feedback loops in the process. The hike in biodiversity and marked change in biocomplexity significantly changed the planet’s seafloors and provided a new agenda for much of subsequent marine life.

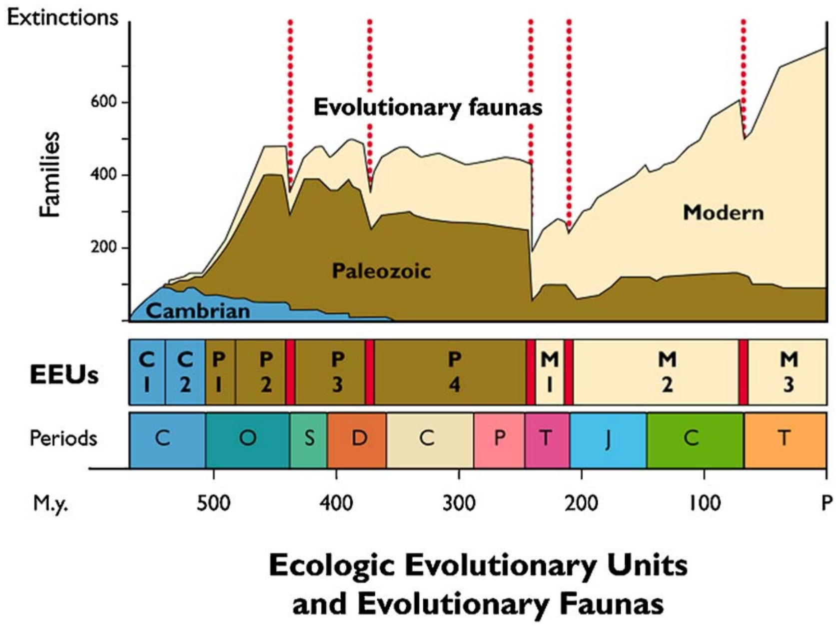


Fig. 1. Family diversity of skeletonized marine invertebrates during the Phanerozoic, together with Sepkoski’s three, statistically based, marine evolutionary faunas; diagram includes Boucot’s evolutionary ecologic units, modified by Sheehan, together with an indication of the five big extinction events (modified from Sheehan, 1996).

2. Timeframe

The chronostratigraphy of the Ordovician System is now well-established, largely through the work of the International Subcommission on Ordovician Stratigraphy (ISOS). Some of the many unique properties of the system have, in fact, made the development of a global timeframe difficult; the intense biogeographical and ecological differentiation of biotas together with a lack of reliable radiometric data have hindered the rapid establishment of a modern chronostratigraphy for the Ordovician System. Nevertheless the definition of three global series (lower, middle and upper) and seven global stages (the Tremadocian, Darriwilian and Hirnantian are already recognized) is far advanced (Ogg, 2004). More precise and highly resolved international chronostratigraphic units have yet be defined, although these exist for many regions (e.g. Fortey et al., 2000). For the purposes of calibration and description of the Ordovician Radiation, Webby et al. (2004b) devised a sequence of shorter time slices, each corresponding to entire or partial, correlatable graptolite, conodont and chitinozoan biozones. These time slices, 19 ranging through 1a–6c, formed the basis for the majority of biodiversity charts in Webby et al. (2004a). The radiation commenced during the late Arenig and continued into the late Ashgill, prior to the end Ordovician extinction event (Sepkoski, 1995). This was a time span of some 25 Myr, relatively short in the overall 3.8 Ga of the history of life.

3. Cambrian roots?

The Cambrian explosion generated a range of new and spectacular body plans together with the extinction of the soft-bodied Ediacara fauna and the appearance of the Bilateralia over a relatively short period of time (Conway Morris, 1998). The rapid appearance of such a wide range of apparently morphologically disparate animals has suggested, however, an interval of cryptic evolution of probable micro and meioscopic organisms, operating beneath the limits of detection prior to the explosion (Cooper and Fortey, 1998). Moreover molecular-clock estimates indicate that animal lineages split some 800 Ma or more before their appearance in the fossil record (Wray et al., 1996). Greater refinement of Cambrian stratigraphy, the taxonomy and phylogeny of key Cambrian taxa and their relative appearance in the fossil record have suggested an alternative hypothesis: The current, lower to middle Cambrian fossil record displays the sequential and orderly appearance, albeit over a short time interval, of successively more complex metazoans (Budd, 2003).

By contrast, with the exception of the bryozoans, no new higher taxa emerged during the Ordovician Radiation, rather the event witnessed a three to four-fold increase at the family level; these clades would dominate marine life for the next 250 Myr. Nevertheless at a taxonomic level the majority of ‘Paleozoic’ taxa were derived from Cambrian stocks. Although an inevitable consequence of the Cambrian explosion, the Ordovician Radiation was quite different and in many ways more dramatic (Droser and Finnegan, 2003).

Much of our knowledge of the Cambrian explosion is derived from three spectacular, intensively studied lägerstatte assemblages: Burgess (Canada), Chengjiang (China) and Sirius Passet (Greenland); the diversities of the Cambrian ‘background’ faunas are generally much lower and arguably contain less morphologically disparate organisms. Ordovician exceptionally preserved biotas are rarer; the Soom Shale (South Africa) contains exquisitely preserved faunas but lacks new higher taxa (Aldridge et al., 1994). Thus whereas the Cambrian explosion provided higher taxa, in some diversity, the Ordovician Radiation generated the sheer biomass, biodiversity and biocomplexity that would fill the world’s oceans.

4. The Ordovician Radiation as an extended multifaceted event

Darwin’s tree of life (Darwin, 1859) predicted the gradual but exponential increase of the diversity and complexity of organisms with time in sympathy with Lyell’s doctrine of uniformitarianism but in contrast to Cuvier’s school of catastrophism. However, within a year of publication of Darwin’s ‘Origin of Species’ Phillips (1860) had provided a semi-quantitative analysis of the biodiversity of Phanerozoic life. His curve was partitioned into Palaeozoic, Mesozoic and Caenozoic divisions separated by supposed extinction events at the end Permian and end Cretaceous (Fig. 2). Interesting, nevertheless, is the clear but gradual Early Palaeozoic climb in diversity.

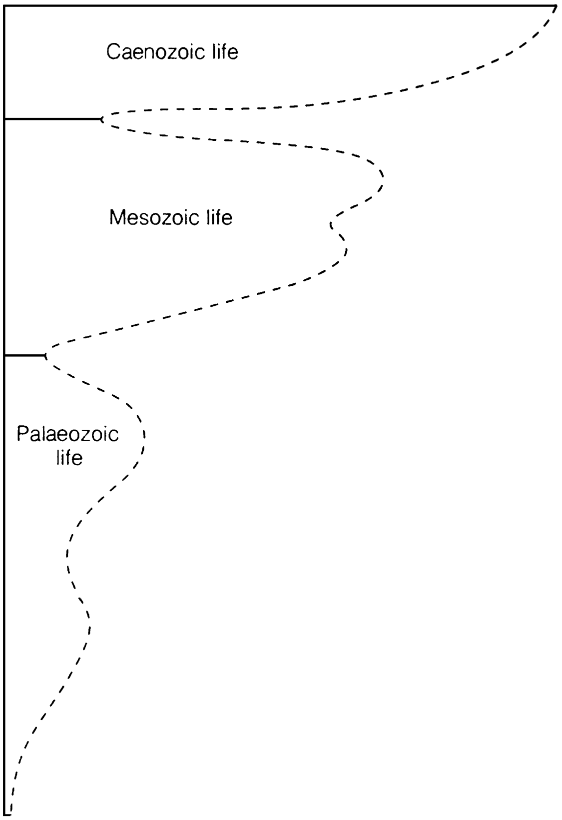


Fig. 2. John Phillip's (1860) division of the Phanerozoic into three stratigraphically based marine faunas.

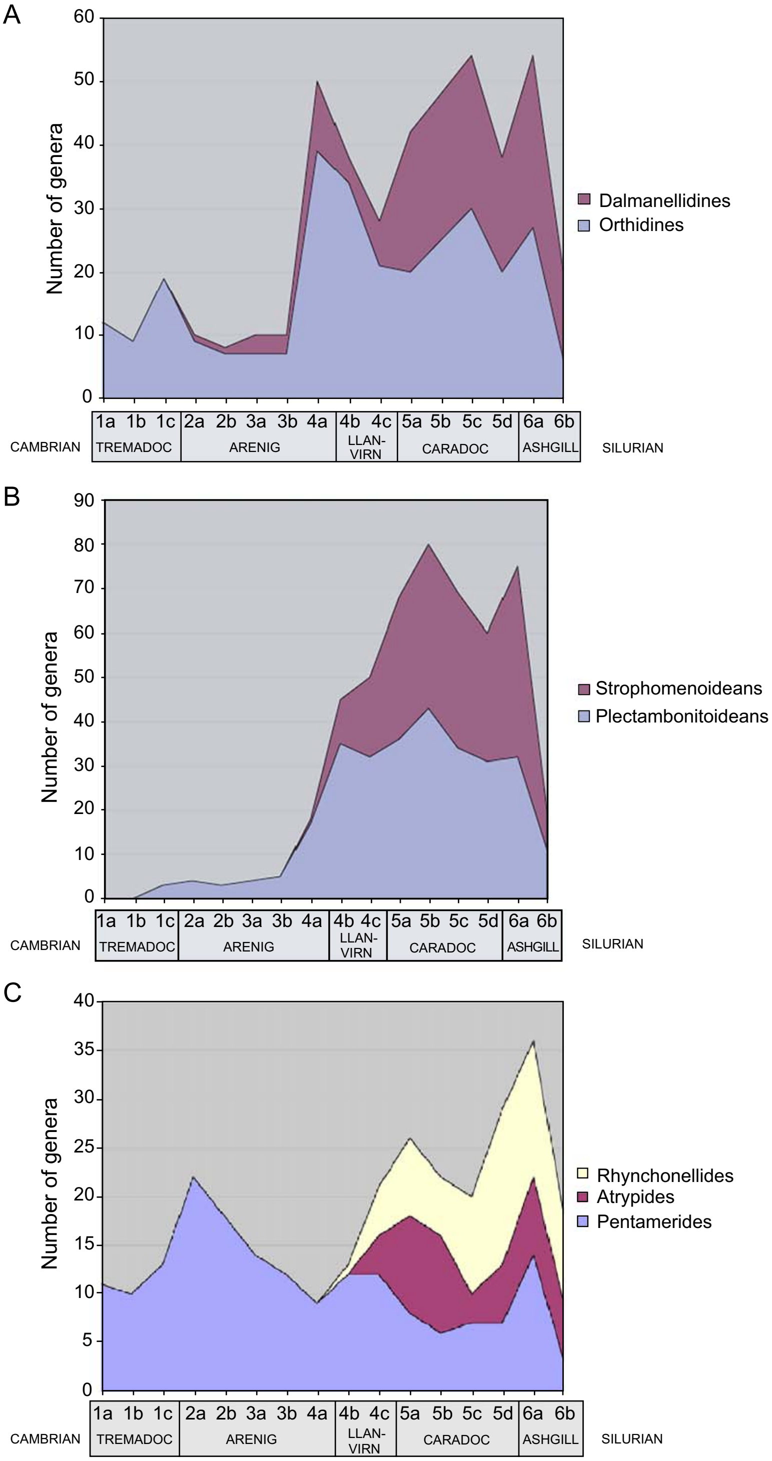
For nearly 100 years relatively little attention was paid to global diversity curves through time. Nevertheless a number of surveys of fossil groups, such as the Brachiopoda (Cooper and Williams, 1952; Williams, 1957), indicated a steep diversification during the early and mid-Ordovician (as then defined). Pivotal, however, was Valentine's work on the biodiversity and ecological structure of the marine biosphere (Valentine, 1973). In a detailed, quantitative investigation of the variation in diversity of higher taxa of marine invertebrates, Valentine (1969) identified a number of clear trends. During the early and mid-Ordovician there was a steep rise in numbers of first classes and then orders; the number of phyla remained stable at eight during these biodiversifications. During the same interval there were a marked number of appearances amongst the classes and orders.

The seminal papers of Sepkoski (1978, 1979, 1981, 1991, 1997) established without doubt the statistical reality of the Ordovician biodiversification; multivariate analyses highlighted the dominance of groups of suspension-feeding organisms through the post-Cambrian, Palaeozoic interval. This theme was developed in some detail by Droser et al. (1997) together with Droser and Sheehan (1997) as the 'Great Ordovician Biodiversification' and three focal points of the event were emphasized: taxonomic diversity, morphological disparity and ecological change. In addition Miller and his colleagues have dissected various aspects of the event based on a series of extensive datasets (Miller, 1997a,b,c, 2001; Miller and Connolly, 2001; Connolly and Miller, 2002; Miller and Foote, 1996; Miller and Mao, 1998; Novack-Gottshall and Miller, 2003a,b). These key studies gave impetus to publication of a comprehensive review of the taxonomic aspects of the event together with aspects of its setting (Webby et al., 2004a).

5. Taxonomic biodiversification

The Ordovician Radiation, in taxonomic terms, marks the greatest and most sustained interval of diversification of life on Earth. Diversification at the family, genus and species levels was staggering (Webby et al., 2004a,b). Approximately 25 taxonomic groups are surveyed in Webby et al., 2004a including, both micro and macrofossil groups, invertebrates and vertebrates, plants and trace fossils. The treatment is as near comprehensive as current levels of knowledge permit and includes approximately 4600 genera. Although a clear and consistent signal emerges, one of consistent and sustained diversification through the period, the radiation was selective; some taxa diversified more than others, some earlier and some later.

The mode and quality of data is necessarily variable. Macrofossil groups such as the brachiopods, trilobites and graptolites, the hallmarks of the system, have been collected for over 200 years from most parts of the world; these form the core of many active and ongoing research programmes. Some less well-known groups, such as the eurypterids are based on relatively small databases and the study of their Ordovician taxa is in its infancy. Accumulation of microfossil data is time-consuming and strongly dependent


A
Number of genera
0
10
20
30
40
50
60
Dalmanellidines
Orthidines
B
Number of genera
0
10
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30
40
50
60
70
80
90
Strophomenoideans
Plectambonitoideans
C
Number of genera
0
5
10
15
20
25
30
35
40
Rhynchonellides
Atrypides
Pentamerides
1a 1b 1c 2a 2b 3a 3b 4a 4b 4c 5a 5b 5c 5d 6a 6b
CAMBRIAN
TREMADOC
ARENIG
LLAN-VIRN
CARADOC
ASHGILL
SILURIAN

on extraction techniques and the availability of processable rocks; these databases are highly focussed but to date, not comprehensive. Some groups were initially discovered by chance, for example vertebrate material in microfossil residues; more focussed investigations are now in progress.

The majority of the diversity trajectories are complex, multipeaked systems. Many groups exhibit stepwise increases through the period suggesting that the global signal is a complex time series curve. The majority of groups show contrasting diversity signals when their component subphyla taxa are isolated; the diversity patterns and trends of the nonarticulated and articulated brachiopods are, not surprisingly, quite different as are the curves for the various classes of gastropod. Within the rhynchonelliformean brachiopods three clear peaks are discernable for the Orthida (Fig. 3A) with the group expanding in the mid-Arenig and fluctuating through the rest of the period; the late Arenig–early Llanvirn, mid-Caradoc and mid-Ashgill peaks correspond to an initial association with the disparate continental and microcontinental configuration of that time, a subsequent move into deeper-water environments and finally a diversification in carbonate buildups. The pattern for the Strophomenida is different (Fig. 3B); the group expanded first in the mid-Arenig but did not peak until the early Caradoc, with a less marked mid-Ashgill spike. The patterns of the other, more minor groups, the atrypides, pentamerides and rhynchonellides differ in detail, radiating later in the upper Arenig with maximum levels in the Ashgill; the mid-Ashgill diversifications may have been associated with carbonate environments during the later Ordovician (Fig. 3C). These groups, in particular, dominated the Silurian benthos following the end Ordovician extinction event (Harper and Rong, 2001).

Many of the other phyla show equally complex patterns amongst their included taxa (see Webby et al., 2004a,b, chapters therein). Whereas the radiolarians display a progressive rise in biodiversity through the period, the sponges accelerated in a step-like manner. In general the global pattern of diversification for the trilobites is quite different from that from many of the regions while the graptolites demonstrate their most marked global radiation during the Tremadocian with the rapid vertical differentiation of faunas; further diversity spikes are associated with latitudinal (geographic) variation in the faunas. Finally some of the key colonial taxonomic groups, the bryozoans and the tabulate corals, diversified later than the other metazoans, suggesting controls on their radiation, availability of specific substrates, may have been different.

The Ordovician Radiation established the so-called Palaeozoic Plateau, bringing sharply into focus competing hypotheses for the diversification of life (Lane and Benton, 2003; see also below). The existence of such an apparent plateau of diversity lends support to equilibrium (Sepkoski, 1984) rather than expansionist (Benton, 1995) models for biodiversification. The former can be displayed as a three-phase coupled-logistic model, predicting that the three evolutionary faunas each, successively, reach equilibrium values for diversity reflecting the carrying capacity of their respective ecosystems. The equilibrium model suggests that clades, after a slow start, diversify rapidly reaching a plateau or equilibrium level, marking the carrying capacity of the habitat, region or in this case the planet. Marine faunas apparently display this pattern with animals in the respective Cambrian, Paleozoic and Modern evolutionary faunas occupying successively wider niches, hence achieving higher diversities. Animals in the Modern fauna burrow deeper, participate in higher and more complex tiers above the sediment–water interface, capture prey more effectively and form more complex reef structures; it could be argued that this fauna is relatively young and yet to reach its equilibrium. By contrast the latter, expansionist model, predicts that life will continue to expand ad infinitum, with current diversity levels increasing by new adaptations and the occupation of new habitats,

Fig. 3. A. Stratigraphical distribution of orthide genera in terms of the two suborders, the orthidines (impunctates) and dalmanellidines (punctates) through the Ordovician (modified from Harper et al., 2004); time bins follow chronostratigraphic divisions defined in Webby et al., 2004a,b. B. Stratigraphical distribution of strophomenide genera in terms of the two superfamilies, the plectambonitoids and strophomenoids through the Ordovician (modified from Harper et al., 2004); time bins follow chronostratigraphic divisions defined in Webby et al., 2004a,b. C. Stratigraphical distribution of atrypide, pentameride and rhynchonellide genera through the Ordovician (modified from Harper et al., 2004); time bins follow chronostratigraphic divisions defined in Webby et al., 2004a,b.

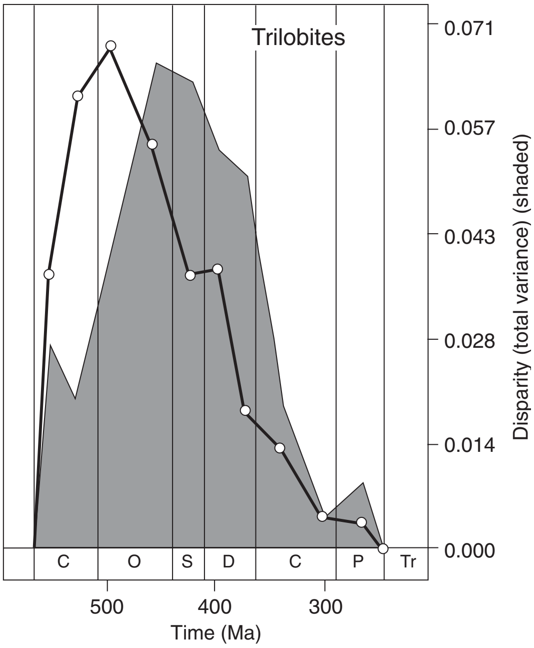

Fig. 4. Trilobite morphological disparity and diversity through the Ordovician Radiation (based on Foote, 1991).

limited only by the availability of organic building blocks such as carbon.

It is clear that the shapes of such curves are markedly affected by the level of taxonomic data analyzed (Lane and Benton, 2003) and moreover significant differences have been demonstrated between the diversity trajectories for marine and nonmarine systems and between those for individual habitats. The Ordovician segment of the curve is overwhelmingly dominated, however, by marine organisms, the majority of which were benthic.

6. Morphological expansion

Morphological disparity, in contrast to diversity, addresses the actual morphological variation amongst groups of taxa. Both are quite different types of measurements: morphologically disparate faunas may be of relatively low diversity, but nevertheless the morphological distances between individual taxa may be large. Morphological disparity has been calculated from cladograms, dendrograms and ordination techniques (Wills, 2001). High-profile studies of morphological disparity on Cambrian-explosion taxa have established that present day disparity amongst certain groups such as the arthropods (Wills et al., 1994) and priapulid worms (Wills, 1998), may be equal to or even exceed Cambrian levels of disparity. During the Ordovician Radiation, however, trilobite morphological disparity apparently accelerated after their peak diversity (Fig. 4) during the early Ordovician (Foote, 1991, 1993), probably when a range of new ecomorphotypes arrived during the later Ordovician (Fortey and Owens, 1990). These new morphologies may not have been the basis for a huge taxonomic diversification, many groups having relatively few families and genera. In some ways the pattern suggests a similarity to the Cambrian explosion, when a range of new body plans, and life modes, was not necessarily associated with a major hike in diversity.

In contrast, however, the orthide brachiopods reached both peak disparity and diversity during the late Ordovician (Harper and Gallagher, 2001). Significantly, another sessile benthic group, the crinoids, exhibited the same pattern (Foote, 1995). Diversity and morphological disparity were clearly decoupled in some groups but not in others. The apparent decoupling of diversity and disparity in some groups is significant and requires investigation.

7. Ecological dimension

The profound changes in biodiversity and morphological disparity were matched by dramatic changes in the planet's marine ecosystems from the apparently less well-organized associations of the Cambrian evolutionary faunas to the more structured palaeocommunities and diverse assemblages of the Palaeozoc evolutionary faunas (Fig. 5). These changes were neither necessarily coincident nor varied in the same way. There is strong evidence to suggest that the many Phanerozoic ecological events were decoupled from major changes in diversity, implying the controls and constraints on diversity trends and ecological structures were not necessarily similar. Ecological structures can be strongly influenced by the abundance or disappearance of keystone species rather than by merely increasing or declining biodiversity (McGhee et al., 2001). For example, intense biologi-

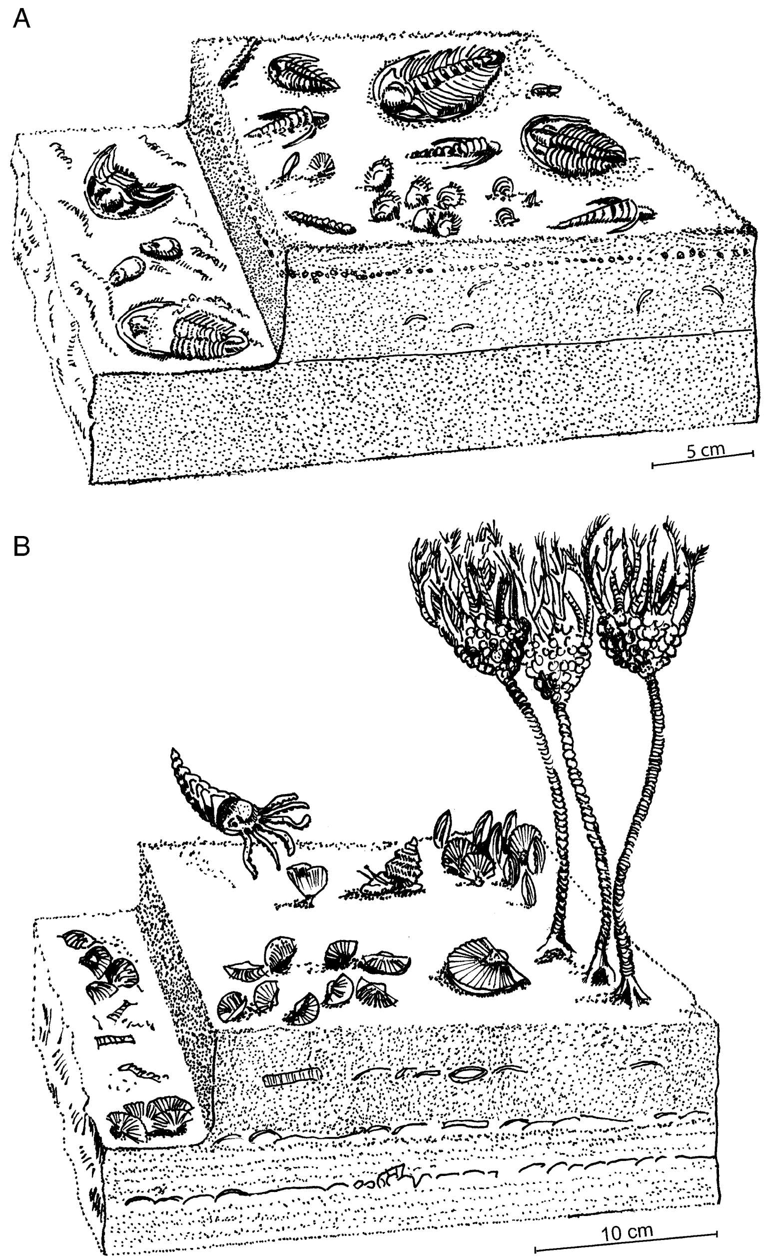

Fig. 5. Transition from the Cambrian evolutionary fauna to that of the suspension-feeding Paleozoic evolutionary fauna (based on an mid Ordovician fauna) (from McKerrow, 1978).

cal activity creating thick shell concentrations, hardgrounds, bioturbation and epifaunal tiers may be limited to a few critical species, rather than a hike in biodiversity; nevertheless their effects on an ecosystem can be profound.

A hierarchy of severity of palaeoecological events has been developed for Phanerozoic marine life (Droser et al., 1997; Bottjer et al., 2001). The events or levels range from first level (appearance/disappearance of an ecosystem) to fourth level (appearances/disappear-

Table 1
Four palaeoecological levels and their characteristic signals (based on and modified from Bottjer et al., 2001) together with possible events during the Ordovician Radiation

Level	Description	Signals	Ordovician Radiation
First	Appearance/disappearance of an ecosystem	Initial colonization of an environment	1.Colonization of land 2. Deep-water benthos
Second	Structural changes within an ecosystem	1. First appearance of, or changes in ecological dominants of higher taxa 2. Loss/appearance of metazoan reefs 3. Appearance/disappearance of Bambachian megaguilds	1. Brachiopod takeover 2. Development of bryozoan and coral reefs 3. Four new Bambachian megaguilds
Third	Community-type level changes within an established ecological structure	1. Appearance and/or disappearance of community types 2. Increase and/or decrease in tiering complexity 3. ‘Filling-in’ or ‘thinning’ within Bambachian megaguilds	1. New community types associated with deep-water and metazoan reef environments 2. Marked increase in epifaunal tiering and bioturbation 3. Increase in membership of Bambachian megaguilds
Fourth	Community-level changes	1. Appearance and/or disappearance 2. Taxonomic changes within a clade	1. Extensive development of new communities 2. Taxonomic diversity changes at many levels

ances of palaeocommunities); these types of changes had a profound effect on the composition and structure of Phanerozoic life. Bottjer et al. (2001) have emphasized the reality of second, third and fourth level changes through the Ordovician Radiation. For example, changes in dominants, such as transitions from trilobite to brachiopod-dominated communities on soft substrates and echinoderms to bryozoans on hard substrates, the evolution of deep-mobile burrowers and stromatoporoid reefs are cited in support of second level changes. The appearance of new Bambachian megaguilds (groups of organisms with mutually similar adaptive strategies) and the supplementation of existing megaguilds with new taxa together with the arrival of new community types (receptaculitid/macluritid-dominated, orthid-dominated and bivalve–trilobite combinations) together with a marked increase in tiering complexity, signal third level changes whereas the development of many new palaeocommunities is the hallmark of fourth level changes. Key ecological changes, modified from Bottjer et al. (2001), are listed in Table 1.

Five key themes have been emphasized by a number of authors: the increase in numbers of Bambachian megaguilds, tiering complexity (both above and beneath the sediment–water interface), changes in the types of shell concentrations, development of hardgrounds and hardground communities together with the changing composition and structure of carbonate buildups and their associated communities.

During the radiation there was a marked increase in the number of megaguilds (Bambach, 1983). In addition to those already established during the Cambrian, four new megaguilds appeared while a marked increase in numbers of sessile epifaunal (suspension-feeders: attached low, attached erect and reclining) and mobile epifaunal (detritivores, herbivores and carnivores) components occurred. These ecologically organized animals either filled hitherto unoccupied niches or subdivided existing niches (Sheehan, 2001). Such changes were also associated with important changes in tiering complexity both above and below the sediment–water interface (Bambach, 1983; Bottjer and Ausich, 1986).

Although brachiopod shell concentrations are known from the Cambrian, commonly dominated by billingselloids and protorthoids (Bassett et al., 2002), there was clearly a major shift in the composition of Ordovician shell concentrations at the base of the Whiterock in North America (Droser and Sheehan, 1997; Li and Droser, 1999). These shell beds are dominated by orthide brachiopods, such as *Anomalorthis*, *Desmorthis*, *Hesperonomiella*, *Hesperono-*

mia, *Shoshonorthis* and *Orthidiella*. The simplified morphology of variably biconvex, ribbed, pedunculate shells strongly influenced both biological production and the environment in the carbonate ramp settings of California, Nevada and Utah. But there is a strong environmental and geographic component to even the development of shell concentrations. Coeval, but nearshore areas of the Laurentian continent, such as NE Greenland, were in fact dominated by elements of the Modern Evolutionary Fauna, with shell concentrations dominated by gastropods.

The widespread development of hardgrounds during the Ordovician was related to the extensive and pervasive precipitation of low-magnesium calcite on shallow-water marine seafloors (Wilson and Palmer, 1992; Palmer and Wilson, 2004); dissolution of aragonite may have been the source of the calcite cement. The development of such hardgrounds, providing a hard substrate for attachment together with surfaces for cementing and boring organisms, opened up new opportunities for a specialized, yet widespread, set of communities. The 'Ordovician bioerosion revolution' marked the utilization of such hard substrates by adapted boring organisms (Wilson and Palmer, 2002). Moreover aragonite dissolution and calcite precipitation (both organic and inorganic) possibly influenced directly evolution of biomineralization and skeletalization.

The composition and structure of reefs and other carbonate buildups changed during the Ordovician Radiation (Webby, 2002). Critical was the transition from microbial to metazoan-dominated structures at and around the Middle Ordovician–Upper Ordovician boundary. The change from buildups associated with stromatolites, thrombolites, algal mats and various microbes together with sometimes lithistid sponges and stromatoporoids, to the more familiar structures dominated by tabulate corals, stromatoporoids, lithistid sponges, echinoderms and solenoporan algae probably occurred during the Darriwilian. These metazoan buildups were a focus for much biodiversity, creating a plethora of niches around the buildup and its associated marginal facies.

Critical to the stability of the diversification, however, was also the incumbency of key species that can anchor ecosystems at local and regional levels. These have ensured the longevity of ecological units (Sheehan, 1991, 1996, 2001) and the stability of the relationships between predators/prey, buffered/nonbuffered taxa and motile/nonmotile taxa through much of the Palaeozoic (Bambach et al., 2002).

8. Deconstructing global patterns and trends

Current data suggests, that in contrast to the Cambrian explosion, the timing of changes in Ordovician biodiversity and biocomplexity was diachronous across the various taxonomic groups, environments and regions (Webby et al., 2004a), although comparable information is probably lacking for the Cambrian. A focussed study, similar to that on the Ordovician, may serve as a model for more detailed investigations of biodiversity patterns in the Cambrian and other systems. Deconstruction of the global signal into more regional patterns has emphasized the spatial contrasts in the intensity and timing of the event in many groups such as the brachiopods (Fig. 6). Diversity curves are now well-known for the Baltic province (Fig. 6A; Harper and Hints, 2001) and the shape and amplitude of these curves contrast with those for some of the other provinces (Fig. 6B). There is thus a strong extrinsic control on the amplitude and shape of the radiation. Early studies of regional patterns (e.g. Harper, 1986) isolated global trends suggesting regional studies could be used as proxies for more global patterns. However, contrasts in the diversity trajectories for brachiopods (Fig. 6) are now apparent between some of palaeocontinents (Harper and Mac Niocaill, 2002), those for marginal Gondwana being quite different (where the event was apparently delayed) from those of Baltica (Hints and Harper, 2001). Moreover, even across individual brachiopod clades there are partitions (Harper et al., 2004): Within the rhynchonelliformeans, many of the early Ordovician orthide groups were associated with the margins of Gondwana whereas the pentamerides and possibly the plectambonitoids preferred the carbonate environments of Laurentia and its margins.

Regarding individual phyla, most marked is the strong Early Ordovician bivalve radiation around Gondwana, associated with siliciclastic environments (Cope and Babin, 1999); the group diversified outside Gondwana, later during the mid- and late Ordovician. By contrast gastropods were more typical of low-latitude

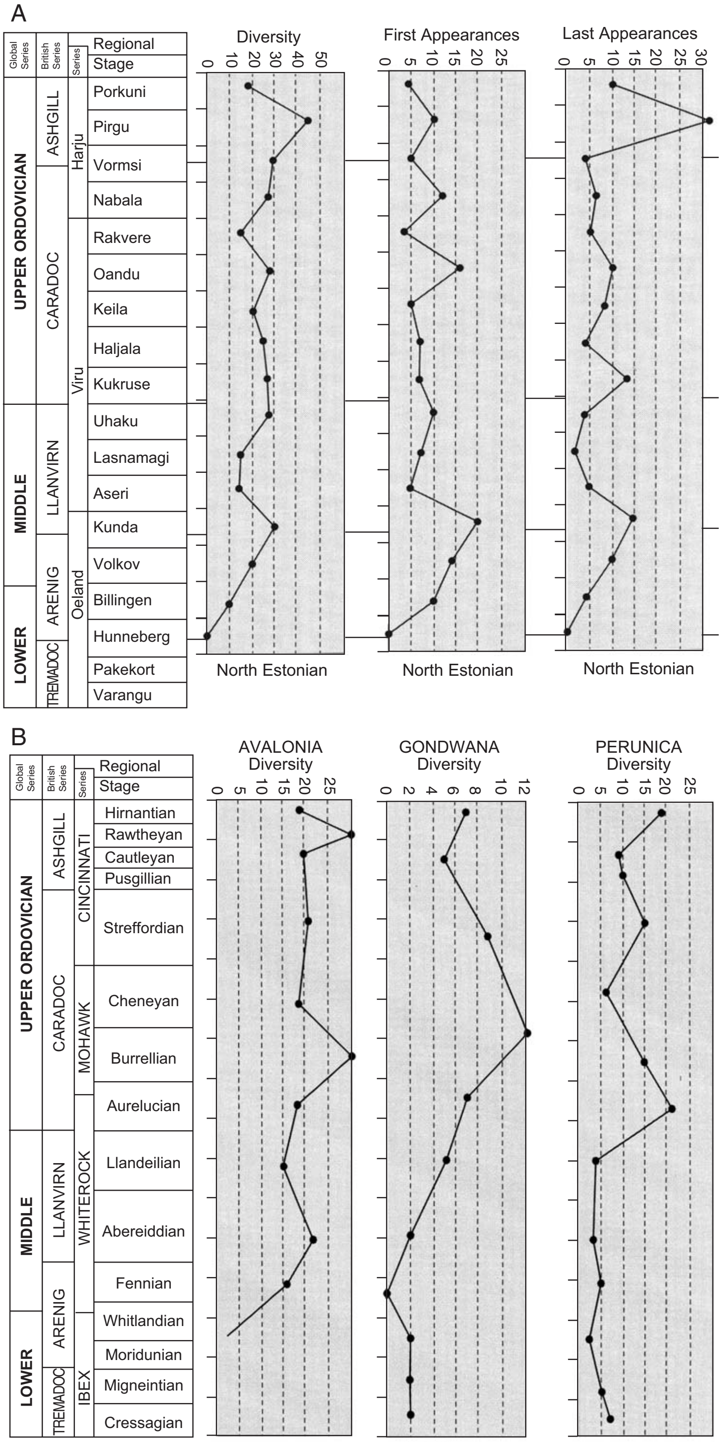

Fig. 6. A. Brachiopod diversity curves through the Ordovician of North Estonia (from Hints and Harper, 2001). B. Brachiopod diversity curves through the Ordovician of Avalonia, Gondwana (North Africa) and Perunica (from Harper and Mac Niocaill, 2002).

carbonate environments in contrast to the high-latitude, siliciclastic settings of the Ordovician bivalve fauna (Novack-Gottshall and Miller, 2003a,b). The interdigitation of bivalve and gastropod faunas, with respect to siliciclastic versus carbonate environments, is also exemplified on a regional scale in the type Cincinnatian (Miller, 2004). Moreover bivalve-dominated faunas appear sporadically in the Ordovician successions of Avalonia where predominantly siliciclastic environments are dominated by brachiopods.

Clearly intimately related clades, taxonomically, may show quite different geographical diversity patterns whereas taxonomically disparate groups may well have similar regional trajectories (Miller, 2004). Such differences and similarities may relate more to morphological adaptations than to phylogeny and suggests again that the taxonomic diversification has controls that depend on factors other than the history of the clade. The geographical dimension of the radiation is real but to date poorly understood. More field based regional studies across critical sections are required to explain more local yet nevertheless significant biodiversity patterns (Droser and Finnegan, 2003).

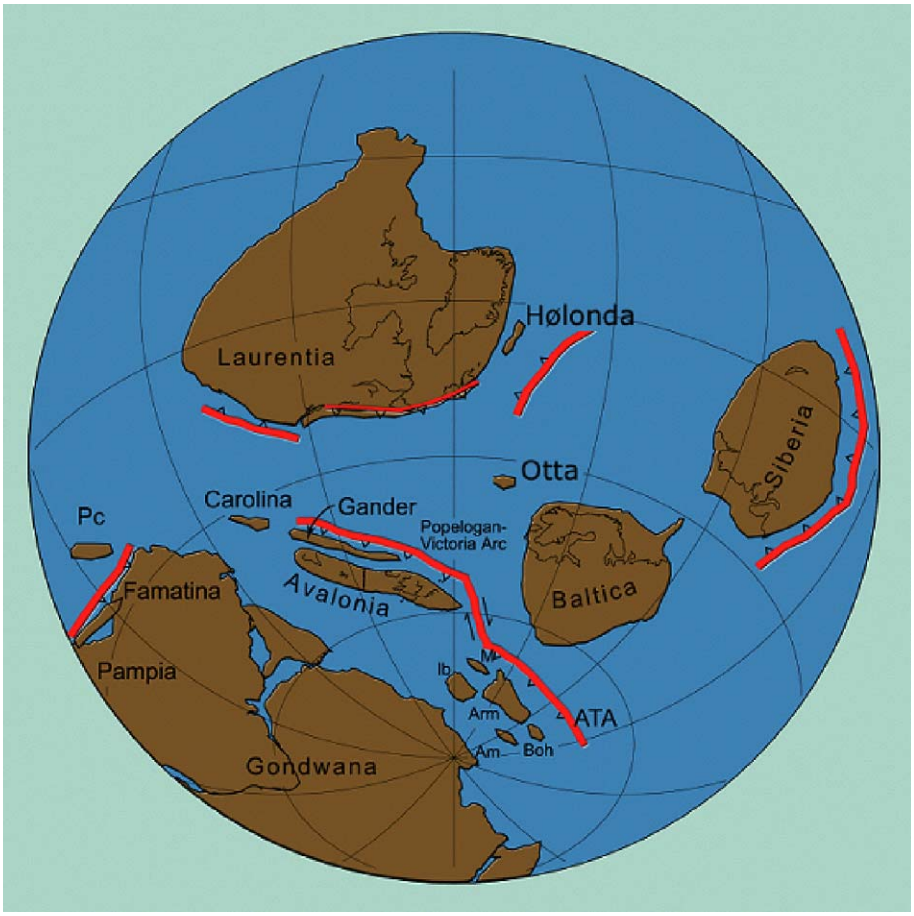

Fig. 7. Early Ordovician palaeogeography of the greater Iapetus region (based on Harper and Mac Niocaill, 2002). The low-latitude Laurentian (1) fauna (see also Fig. 8) occupied the American mid-Continent but included sites in NE Greenland and Siberia; the high-latitude Baltic-Gondwanan (2) fauna included sites around the northern margins of Africa, Bohemia (Perunica), Poland and Baltoscandia; the Toquima-Table Head fauna (3) was developed marginal to Laurentia but included parts of Scotland, western Ireland and Norway together with the Argentinian Precordillera; and the Celtic fauna (4) contained a group of faunas developed around the margins of the high-latitude continents.

9. Sources for the biodiversification and biocomplexity

Careful deconstruction of the global signal, in terms of types of diversity, may also provide a key to the generation of Ordovician biodiversity. Global biodiversity can be resolved into three components: α-diversity (intra-community), β-diversity (inter-community) and γ-diversity (inter-province) (Sepkoski, 1988). The radiation can be modelled in terms of its strong association with the dispersal of the Early Ordovician continents and terranes (γ-diversity), the occupation of new ecospace (β-diversity) and the closer packing of species within existing communities (α-diversity). Sepkoski (1988) noted that increased α- and β-diversity only accounted for about 50% of the observed genus-level diversity. Clearly the surplus may be hidden within γ-diversity and diversities associated with hardground and reef communities, not originally investigated by Sepkoski (Droser and Finnegan, 2003). Nevertheless a model involving the sequential and overlapping increase in these three component diversities can elegantly explain many aspects of the event (Harper and Mac Niocaill, 2002) and provide a number of testable hypotheses.

During the Early Ordovician the continental and terrane assembly in the southern hemisphere was dispersed (Fortey and Cocks, 2003); virtually nothing is known about continental assembly in the northern hemisphere. Neuman (1972) first noted the importance of island arcs as centres for endemism and migration; moreover such arcs during the early Ordovician developed their own biogeographically distinct units, quite separate from the platform provinces (Neuman, 1984; Neuman and

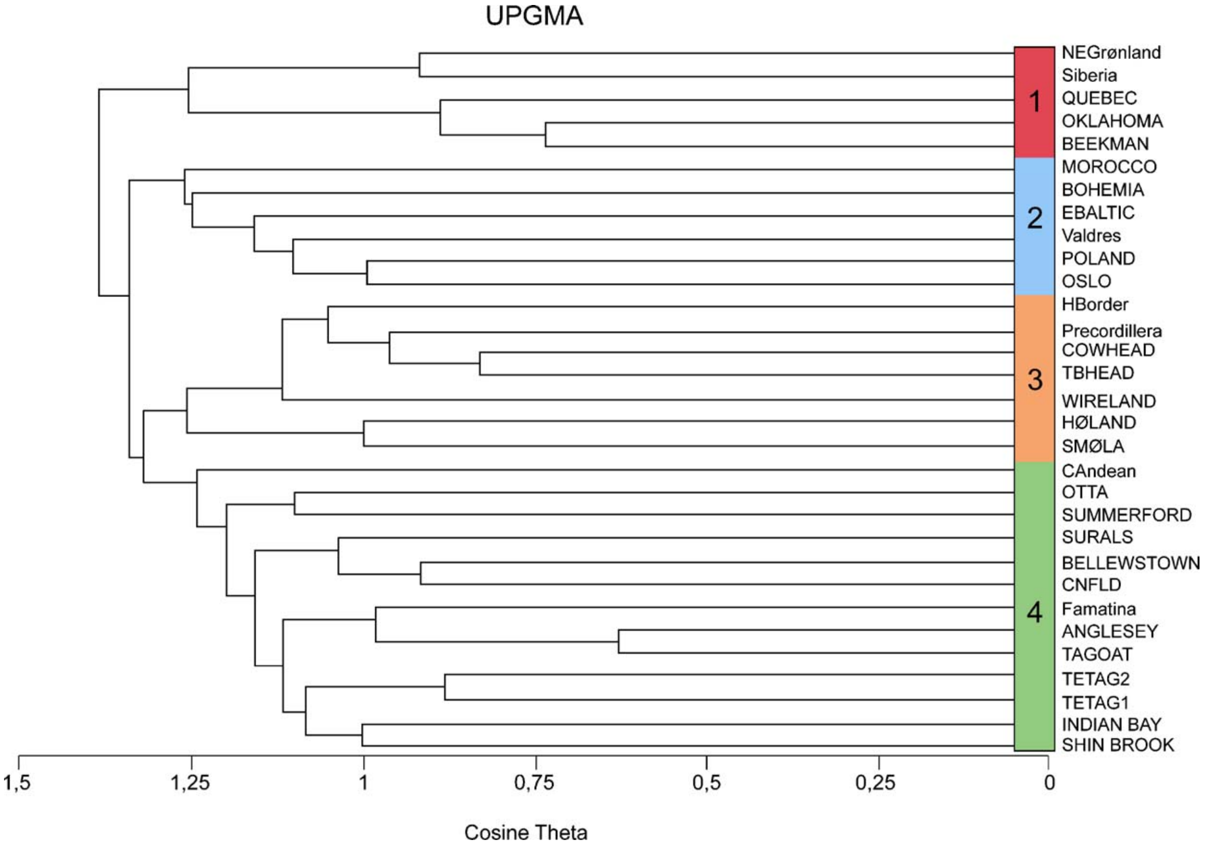

Fig. 8. Cluster analysis of selected Early Ordovician localities based on the occurrences of brachiopod genera: The low latitude Laurentian fauna (1) is recognized together with a high latitude Baltic-Gondwanan (2) fauna; the Toquima-Table fauna (3) was marginal to Laurentia whereas the Celtic fauna (4) was marginal to the Baltic-Gondwanan faunas. Majority of sites taken from Neuman and Harper (1992).

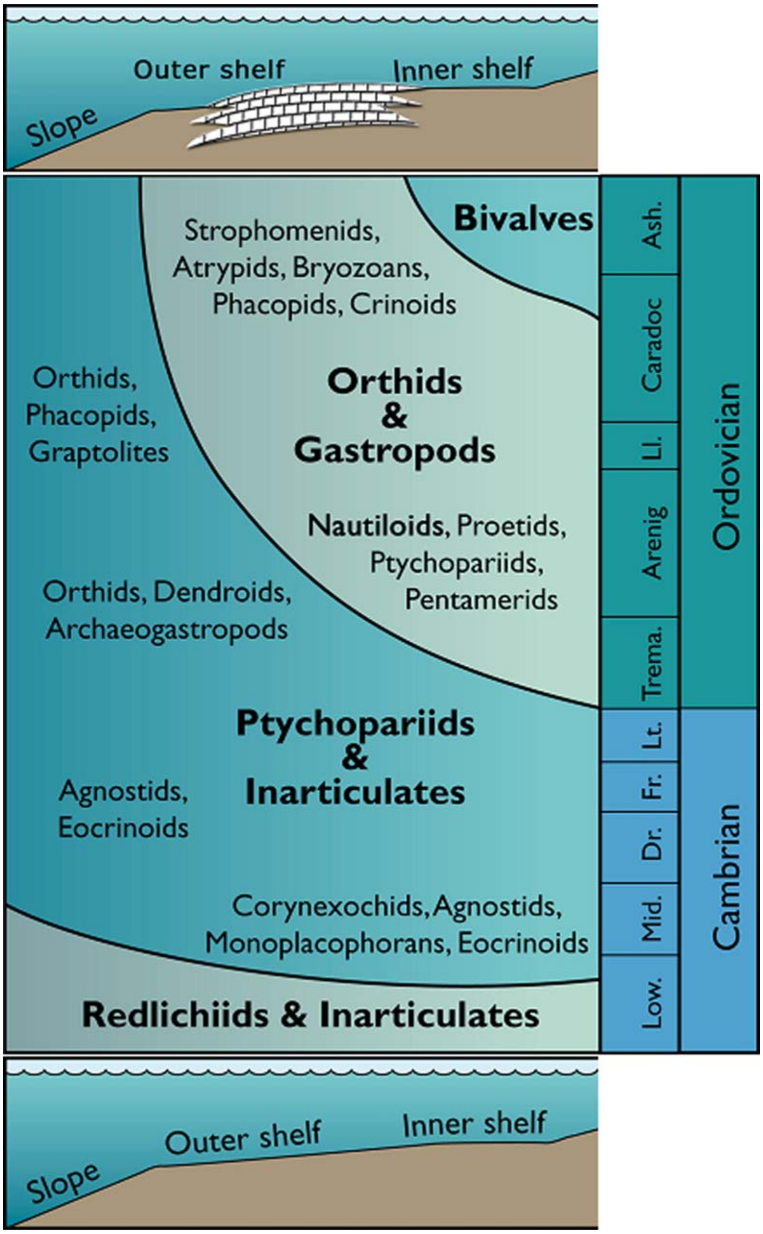

Fig. 9. Onshore–offshore development of taxa during the Cambrian and Ordovician (modified after Sepkoski and Sheehan, 1983). Below the classic onshore–offshore gradient, above the same gradient modified with the addition of midshelf carbonate buildups.

Harper, 1992). The low-latitude Toquima-Table Head province was quite separate from the Celtic province (Harper et al., 1996); these units were characterized not only by their own endemics but also by mixtures of taxa from adjacent continental provinces (Fig. 7). Such marginal and ocean terranes in the greater Iapetus region probably acted both as cradles and museums, the cradles providing taxa to drive subsequent radiations on adjacent platforms. Similar processes were in force at the same time in the central Asian terranes (Holmer et al., 2000, 2001) and later in the Ordovician in eastern Australia

(Webby et al., 1997). Global statistical analyses of the early Ordovician brachiopod faunas demonstrates a range of disparate faunas that can, however, be grouped into continental and marginal provinces (Fig. 8). Endemism was widespread particularly within the Celtic group of faunas. Moreover, Miller and Mao (1995) and Botting (2002) have related directly tectonism and volcanism to diversification within the context of the Ordovician Radiation.

The onshore–offshore expansion of the Ordovician marine fauna (Fig. 9) is well-established (Sepkoski and Sheehan, 1983) and probably occurred as a stepwise process (Sheehan, 2001). It can be demonstrated in detail at regional (Bassett et al., 2002) and local levels (Mergl, 1999) amongst brachiopod faunas. This expansion exploited vacant ecospace creating a range of new communities culminating, during the late Ordovician, with the well-established deep-water brachiopod *Foliomena* fauna (Harper et al., 1999) and trilobite cyclopygid fauna occupying Benthic Assemblage Zone 5 and beyond. Such deep-water faunas attained a relative stability and longevity, with, for example, the *Dicoelosia*-type community ranging from the late Ordovician to the early Devonian (Watkins et al., 2000). These new community types potentially generated β-diversity; nevertheless some authors have challenged this (e.g. Miller and Mao 1998), pointing out that the marked environmental and geographic-range extension of taxa during the later Ordovician may have buffered this effect. However, it was not only the offshore movement of taxa that created new communities; both microbial and metazoan buildups provided a wide range of ecological opportunities for taxa. For example during the mid-Ordovician, carbo-

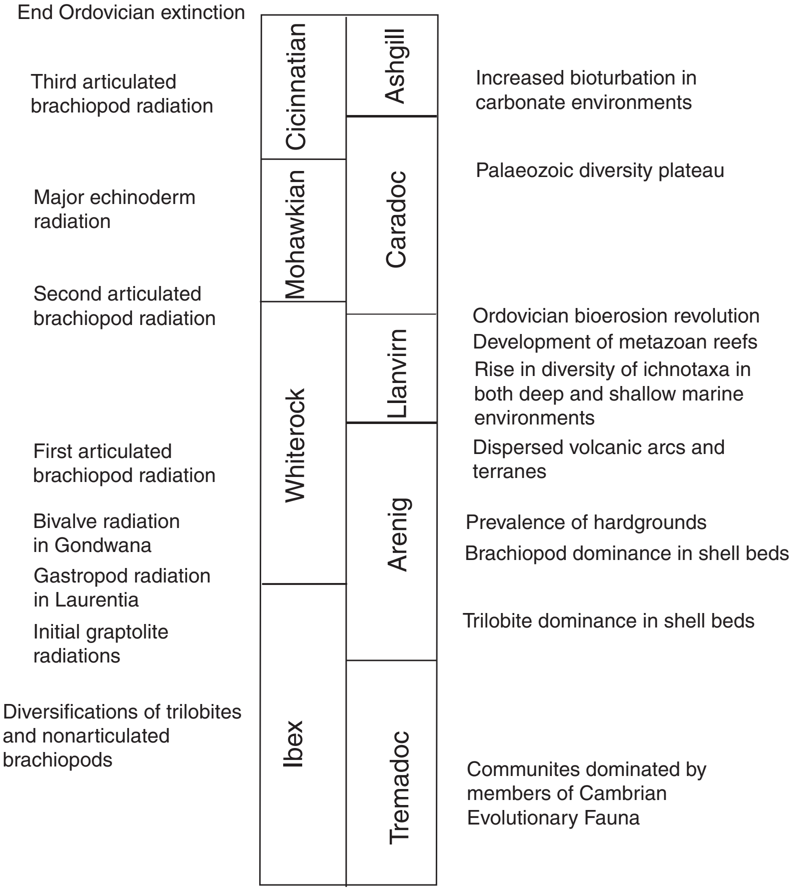

Fig. 10. Synthesis of the Ordovician Radiation based on a time line of taxonomic (left) and ecological (right) events (modified from Droser and Sheehan, 1997).

nate buildups provided the focus for the origin and diversification of a range of rhynchonelliformean brachiopod taxa (Bassett et al., 1999).

During the radiation it is clear that communities became more tightly packed; α-diversity increased. For example the majority of Late Cambrian brachiopod-dominated assemblages contain fewer than 10 taxa whereas by the Late Ordovician such assemblages contain about 30 genera. On a regional scale, Lockley (1983) provided a review of the brachiopod-dominated palaeocommunitites of the Anglo-Welsh basin through time. The palaeocommunities developed in progressively deeper water through time but individual associations attained higher diversities through the period. A possible explanation is the increasing canalization within community structures (Valentine, 1969). Increased specialization was matched with narrower niches in communities experiencing greater competition and interaction amongst their taxa. An alternative approach (Waisfeld et al., 2003) addresses the expansion of guilds within community structures. For example, 11 separate brachiopod guilds are recognised across the three main early Ordovician basins in Argentina; each guild served to further subdivide ecological space providing additional opportunities for diversification.

10. Phanerozoic seafloor

The marine world emerged from the Ordovician Radiation a very different place. All three marine evolutionary faunas were already developed and interacting in more complex but generally well-structured benthic communities. Droser and Sheehan (1997, Fig. 6) developed a time line for events through the Ordovician radiation, which can now be supplemented with new data (Fig. 10). Although ecological and taxonomic events were not necessarily directly related, the former depending more on the abundance and dominance of key taxa, both characterize the mid- and late Ordovician radiations.

Many features established during the Ordovician Radiation remained an integral part of marine life throughout the rest of the Phanerozoic. The development of intense and tiered bioturbation in both shallow and deep-water environments, the initiation of metazoan reef complexes, multi-storied epifaunal tiering, the prevalence of hard grounds and hardground faunas associated with the bioerosion revolution were to be lasting features of marine life. Communities were more complex with a greater number of megaguilds probably associated with increased competition and predation pressures. Increased specialization and decreasing niche width, indicated by guild partitioning and rising α diversity, provided for more varied and tightly packed communities.

Nevertheless the causes for this remarkable event remain far from clear. The deconstruction of the global signal into more discrete taxonomic and regional patterns has demonstrated these trends to be at best diachronous and at worst serendipitous. Further field-based investigations of key sections are essential to target particular problems at a higher resolution than possible at present with global data (Miller, 2004). Critical, however, is the integration of non-biological data, for example isotopic signatures, into models for changing biodiversity, disparity and ecology through these 25 Myr of near unrivalled biological change.

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References

Aldridge, R.J., Theron, J.N., Gabbott, S.E., 1994. The Soom Shale: a unique Ordovician fossil horizon in South Africa. Geology Today 10, 218–221.

Bambach, R.K., 1983. Ecospace utilization and guilds in marine communities through the Phanerozoic. In: Tevesz, M.J.S., McCall, P.L. (Eds.), Biotic Interactions in Recent and Fossil Benthic Communities. Plenum Press, New York, pp. 719–746.

Bambach, R.K., Knoll, A.H., Sepkoski Jr., J.J., 2002. Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm. Proceedings of the National Academy of Sciences, Washington 99, 6854–6859.

Bassett, M.G., Popov, L.E., Sokirin, E.V., 1999. Patterns of diversification in Ordovician cyrtomatodont rhynchonellate brachiopods. Acta Universitatis Carolinae, Geologica 43, 329–332.

Bassett, M.G., Popov, L.E., Holmer, L.E., 2002. Brachiopods: Cambrian-Tremadoc precursors to Ordovician radiation events. In: Crame, J.A., Owen, A.W. (Eds.), Palaeobiogeography and Biodiversity Change: The Ordovician and Mesozoic–Cenozoic radiations, Special Publication, Geological Society, London, vol. 194, pp. 13–23.

Benton, M.J., 1995. Diversification and extinction in the history of life. Science 268, 52–58.

Botting, J., 2002. The relationship between pyroclastic volcanism and Ordovician diversification. In: Crame, J.A., Owen, A.W. (Eds.), Palaeobiogeography and Biodiversity Change: The Ordovician and Mesozoic–Cenozoic radiations. Special Publication, Geological Society, London, vol. 194.

Bottjer, D.J., Ausich, W.I., 1986. Phanerozoic development of tiering in soft substrata suspension-feeding communities. Paleobiology 12, 400–420.

Bottjer, D.J., Droser, M.L., Sheehan, P.M., McGhee Jr., G.R., 2001. The ecological architecture of major events in the Phanerozoic history of marine life. In: Allmon, W.D., Bottjer, D.J. (Eds.), Evolutionary Paleoecology. The Ecological Context of Macroevolutionary Change. Columbia University Press, pp. 35–61.

Budd, G.E., 2003. The Cambrian Fossil record and the Origin of the Phyla. Integrative Comparative Biology 43, 157–165.

Connolly, S.R., Miller, A.I., 2002. Global Ordovician faunal transitions in the marine benthos: ultimate causes. Paleobiology 28, 26–40.

Conway Morris, S., 1998. The evolution of diversity in ancient ecosystems: a review. Philosophical Transactions Royal Society of London B353, 327–345.

Cooper, A., Fortey, R.A., 1998. Evolutionary explosions and the phylogenetic fuse. TREE 13, 151–156.

Cooper, G.A., Williams, A., 1952. Significance of the stratigraphic distribution of brachiopods. Journal of Paleontology 26, 326–337.

Cope, J.C.W., Babin, C., 1999. Diversification of bivalves in the Ordovician. Geobios 32, 175–185.

Darwin, C., 1859. The Origin of Species by Means of Natural Selection. John Murray, London.

Droser, M.L., Finnegan, S., 2003. The Ordovician radiation: a follow-up to the Cambrian explosion. Integrative Comparative Biology 43, 178–184.

Droser, M.L., Sheehan, P.M., 1997. Palaeoecology of the Ordovician Radiation; resolution of large-scale patterns with individual clade histories, palaeogeography and environments. Geobios 20, 221–229.

Droser, M.L., Bottjer, D.J., Sheehan, P.M., 1997. Evaluating the ecological architecture of major events in the Phanerozoic history of marine invertebrate life. Geology 25, 167–170.

Foote, M., 1991. Morphological patterns of diversification: examples from trilobites. Palaeontology 34, 461–485.

Foote, M., 1993. Discordance and concordance between morphological and taxonomic diversity. Paleobiology 19, 185–204.

Foote, M., 1995. Morphological diversification of Palaeozoic crinoids. Paleobiology 21, 273–299.

Fortey, R.A., Cocks, L.R.M., 2003. Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions. Earth-Science Reviews 61, 245–307.

Fortey, R.A., Owens, R.M., 1990. Trilobites. In: McNamara, K.J. (Ed.), Evolutionary Trends. Belhaven Press, London, pp. 121–142.

Fortey, R.A., Harper, D.A.T., Ingham, J.K., Owen, A.W., Parkes, M.A., Rushton, A.W.A., Woodcock, N.H., 2000. A revised correlation of the Ordovician rocks in the British Isles. Special Report, Geological Society, London, vol. 24, pp. 1–83.

Harper, D.A.T., 1986. Distributional trends within the Ordovician brachiopod faunas of the Oslo region, south Norway. In: Racheboeuf, P.R., Emig, C.C. (Eds.), Les Brachiopodes Fossiles et Actuels. Biostratigraphie du Paleozoique, vol. 4, pp. 465–475.

Harper, D.A.T., Gallagher, E., 2001. Diversity, disparity and distributional patterns amongst the orthide brachiopod groups. Journal of the Czech Geological Society 46, 87–93.

Harper, D.A.T., Hints, L., 2001. Distribution and diversity of Ordovician articulated brachiopods in the East Baltic. In: Cocks, L.R.M., Brunton, C.H.C., Long, S.L. (Eds.), Brachiopods, past and present. Systematics Association and Taylor & Francis, pp. 315–326.

Harper, D.A.T., Mac Niocaill, C., 2002. Early Ordovician rhynchonelliformean brachiopod diversity: comparing some platforms, margins and intra-oceanic sites around the Iapetus Ocean. In: Crame, J.A., Owen, A.W. (Eds.), Palaeobiogeography and Biodiversity Change: The Ordovician and Mesozoic–Cenozoic Radiations. Special Publication, Geological Society, London, vol. 194, pp. 25–34.

Harper, D.A.T., Rong, Jia-yu, 2001. Palaeozoic brachiopod extinctions, survival and recovery: patterns within the rhynchonelliformeans. Geological Journal 36, 317–328.

Harper, D.A.T., Mac Niocaill, C., Williams, S.H., 1996. The paleogeography of early Ordovician Iapetus terranes: an integration of faunal and palaeomagnetic constraints. Palaeogeography, Palaeoclimatology, Palaeoecology 121, 297–312.

Harper, D.A.T., Rong, Jia-yu, Zhan, Ren-bin, 1999. Late Ordovician development of deep-water brachiopod faunas. Acta Universitatis Carolinae, Geologica 43, 351–353.

Harper, D.A.T., Cocks, L.R.M., Popov, L.E., Sheehan, P.M., Bassett, M.G., Copper, P., Holmer, L.E., Jisuo, Jin, Rong, Jia-yu, 2004. Brachiopods. In: Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (Eds.), The Great Ordovician Biodiversification. Columbia University Press, New York, pp. 157–178.

Hints, L., Harper, D.A.T., 2001. Review of the Ordovician rhynchonelliformean brachiopoda of the East Baltic: their distribution and biofacies. Bulletin of the Geological Society of Denmark 50, 29–43.

Holmer, L.E., Popov, L.E., Bassett, M.G., 2000. Early Ordovician organophosphatic brachiopods with Baltoscandian affinities from the Alay Range, southern Kyrgystan. GFF 122, 367–375.

Holmer, L.E., Popov, L.E., Koneva, S.P., Bassett, M.G., 2001. Cambrian–early Ordovician brachiopods from Malyi Karatau, the Western Balkash region, and Tien Shan Central Asia. Special Papers in Palaeontology 65, 1–180.

Jaanusson, V., 1984. What is so special about the Ordovician? In: Bruton, D.L. (Ed.), Aspects of the Ordovician System. Universitetsforlaget, Oslo, pp. 1–3.

Lane, A., Benton, M.J., 2003. Taxonomic level as a determinant of the shape of the Phanerozoic marine biodiversity curve. American Naturalist 162, 265–276.

Li, Xing, Droser, M.L., 1999. Lower and Middle Ordovician shell beds from the Basin and Range Province of the Western United States (California, Nevada, and Utah). Palaios 14, 215–233.

Lockley, M.G., 1983. A review of brachiopod dominated palaeocommunities from the type Ordovician. Palaeontology 26, 111–145.

McGhee Jr., G.R., Sheehan, P.M., Bottjer, D.J., Droser, M.L., 2001. Ecological ranking of Phanerozoic biodiversity crises: ecological and taxonomic severities are decoupled. Palaeogeography, Palaeoclimatology, Palaeoecology 211, 289–297.

McKerrow, W.S. (Ed.), 1978. Ecology of Fossils. Duckworth Press, London. 383 pp.

Mergl, M., 1999. Inarticulated brachiopod communities in Tremadoc–Arenig of Prague Basin: a review. Acta Universitatis Carolinae, Geologica 43, 337–340.

Miller, A.I., 1997a. Comparative diversification dynamics among palaeocontinents during the Ordovician Radiation. Geobios, Mémoire Spécial 20, 397–406.

Miller, A.I., 1997b. Dissecting global diversity trends: examples from the Ordovician radiation. Annual Review of Ecology and Systematics 28, 85–104.

Miller, A.I., 1997c. A new look at age and area: The geographic and environmental expansion of genera during the Ordovician radiation. Paleobiology 23, 410–419.

Miller, A.I., 2001. Substrate affinities of higher taxa and the Ordovician Radiation. Paleobiology 27, 768–778.

Miller, A.I., 2004. The Ordovician Radiation: towards a new global synthesis. In: Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (Eds.), The Great Ordovician Biodiversification. Columbia University Press, New York, pp. 380–388.

Miller, A.I., Connolly, S.R., 2001. Substrate affinities of higher taxa and the Ordovician Radiation. Paleobiology 27, 768–778.

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

Miller, A.I., Mao, S., 1998. Scales of diversification and the Ordovician radiation. In: McKinney, M.L., Drake, J.A. (Eds.), Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities. Columbia University Press, pp. 288–310.

Miller, A.I., Shuguang, Mao, 1995. Association of orogenic activity with the Ordovician Radiation of marine life. Geology 23, 305–308.

Neuman, R.B., 1972. Brachiopods of early Ordovician volcanic islands. Proceedings of the 24th International Geological Congress, Montreal, vol. 7, pp. 297–302.

Neuman, R.B., 1984. Geology and paleobiology of islands in the Iapetus Ocean: review and implications. Bulletin of the Geological Society of America 95, 1188–1201.

Neuman, R.B., Harper, D.A.T., 1992. Paleogeographic significance of Arenig–Llanvirn Toquima-Table Head and Celtic brachiopod assemblages. In: Webby, B.D., Laurie, J.R. (Eds.), Global Perspectives on Ordovician Geology. Balkema, Rotterdam, pp. 241–254.

Novack-Gottshall, P.M., Miller, A.I., 2003a. Comparative geographic and environmental diversity dynamics of gastropods and bivalves during the Ordovician Radiation. Paleobiology 29, 576–604.

Novack-Gottshall, P.M., Miller, A.I., 2003b. Comparartive taxonomic richness and abundances of the Late Ordovician gastropods and bivalves in the mollusc-rich strata of the Cincinnati Arch. Palaios 18, 559–571.

Ogg, J., 2004. Status of divisions of the International Geologic Timescale. Lethaia 37, 183–200.

Palmer, T.J., Wilson, M., 2004. Calcite precipitation and dissolution of biogenic aragonite in shallow Ordovician calcite seas. Lethaia 37, 417–427.

Phillips, J., 1860. Life on Earth: Its Origin and Succession. Cambridge and London.

Sepkoski Jr., J.J., 1978. A kinetic model for Phanerozoic taxonomic diversity: I. Analysis of marine orders. Paleobiology 4, 223–251.

Sepkoski Jr., J.J., 1979. A kinetic model for Phanerozoic taxonomic diversity: II. Early Phanerozoic families and multiple equilibria. Paleobiology 5, 222–251.

Sepkoski Jr., J.J., 1981. A factor analytical description of the Phanerozoic marine fossil record. Paleobiology 7, 36–53.

Sepkoski Jr., J.J., 1984. A kinetic model for Phanerozoic taxonomic diversity: Part 3. Post-Paleozoic families and multiple equilibria. Paleobiology 10, 246–267.

Sepkoski Jr., J.J., 1988. Alpha, beta or gamma: where does all the biodiversity go? Paleobiology 14, 221–234.

Sepkoski Jr., J.J., 1991. A model for onshore–offshore change in faunal diversity. Paleobiology 17, 157–176.

Sepkoski Jr., J.J., 1995. The Ordovician radiations: diversification and extinction shown by global genus-level taxonomic data. In: Cooper, J.D., Droser, M.L., Finney, S.C. (Eds.), Ordovician Odyssey: Short papers for the Seventh International Symposium on the Ordovician System. Pacific Section Society for Sedimentary Geology (SEPM), Fullerton, California, pp. 393–396.

Sepkoski Jr., J.J., 1997. Biodiversity: past, present and future. Journal of Paleontology 71, 533–539.

Sepkoski Jr., J.J., Sheehan, P.M., 1983. Diversification, faunal change, and community replacement during the Ordovician radiations. In: Tevesz, M.J.S., McCall, P.L. (Eds.), Biotic Interactions in Recent and Fossil Benthic Communities. Plenum Press, New York, pp. 673–718.

Sheehan, P.M., 1991. Patterns of synecology during the Phanerozoic. In: Dudley, E.C. (Ed.), The Unity of Evolutionary Biology. Dioscorides Press, Portland, Oregon, pp. 113–118.

Sheehan, P.M., 1996. A new look at Ecological Evolutionary Units (EEUs). Palaeogeography, Palaeoclimatology, Palaeoecology 127, 21–32.

Sheehan, P.M., 2001. History of marine biodiversity. Geological Journal 36, 231–249.

Valentine, J.M., 1969. Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time. Palaeontology 12, 684–709.

Valentine, J.M., 1973. Evolutionary Paleoecology of the Marine Biosphere. Prentice Hall, Englewood Cliffs, New Jersey.

Waisfeld, B.G., Sánchez, T.M., Benedetto, J.L., Carrera, M.G., 2003. Early Ordovician (Arenig) faunal assemblages from western Argentina: biodiversification trends in different geodynamic and palaeogeographic settings. Palaeogeography, Palaeoclimatology, Palaeoecology 196, 343–373.

Watkins, R., Coorough, P.J., Mayer, P.S., 2000. The Silurian Dicoelosia communities: temporal stability within an Ecological Evolutionary Unit. Palaeogeography, Palaeoclimatology, Palaeoecology 162, 225–237.

Webby, B.D., 2002. Patterns of Ordovician reef development. In: Kiessling, W., Flügel, E., Golonka, J. (Eds.), Phanerozoic Reef Patterns. Society for Sedimentary Geology (SEPM), Special Publication, vol. 72, pp. 129–179.

Webby, B.D., Zhen, Y.-y., Percival, I.G., 1997. Ordovician coral- and sponge-bearing associations: distribution and significance in volcanic shelf to slope habitats, eastern Australia. Boletín de la Sociedad Española de Historia Natural (Sección Geológia) 92, 163–175.

Webby, B.D., Droser, M.L., Paris, F., Percival, I.G. (Eds.), 2004a. The Great Ordovician Biodiversification Event. Columbia University Press, pp. 484.

Webby, B.D., Cooper, R.A., Bergström, S.G., Paris, F., 2004b. Stratigraphic timeframe and time slices. In: Webby, B.D., Droser, M.L., Paris, F., Percival, I.G. (Eds.), The Great Ordovician Biodiversification Event. Columbia University Press, pp. 41–47. 484 pp.

Williams, A., 1957. Evolutionary rates in brachiopods. Geological Magazine 94, 201–211.

Wills, M.A., 1998. Crustacean disparity through the Phanerozoic: comparing morphological and stratigraphical data. Biological Journal of the Linnean Society 65, 455–500.

Wills, M., 2001. How good is the fossil record of arthropods? An assessment using the stratigraphic congruence of cladograms. Geological Journal 36, 187–210.

Wilson, M.A., Palmer, T.J., 1992. Hardgrounds and hardground faunas. Institute of Earth Studies Publications, vol. 9. University of Wales, Aberystwyth, pp. 1–131.

Wilson, M.A., Palmer, T.J., 2002. The Ordovician bioerosion revolution. Geological Abstracts with Programs 33, 248.

Wills, M.A., Briggs, D.E.G., Fortey, R.A., 1994. Disparity as an evolutionary index: a comparison of Cambrian and Recent arthropods. Paleobiology 20, 93–130.

Wray, G.A., Levinton, J.S., Shapiro, L.M., 1996. Molecular evidence for deep pre-Cambrian divergences amongst metazoan phyla. Science 214, 568–573.