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## End Ordovician extinctions: A coincidence of causes

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### ABSTRACT

The end Ordovician (Hirnantian) extinction was the first of the five big Phanerozoic extinction events, and the first that involved metazoan-based communities. It comprised two discrete pulses, both linked in different ways to an intense but short-lived glaciation at the South Pole. The first, occurring at, or just below, the *Normalograptus extraordinarius* graptolite Biozone, mainly affected nektonic and planktonic species together with those living on the shallow shelf and in deeper water whereas the second, within the *N. persculptus* graptolite Biozone, was less focused, eradicating faunas across a range of water depths. In all about 85% of marine species were removed. Proposed kill mechanisms for the first phase have included glacially-induced cooling, falling sea level and chemical recycling in the oceans, but a general consensus is lacking. The second phase is more clearly linked to near-global anoxia associated with a marked transgression during the Late Hirnantian. Most recently, however, new drivers for the extinctions have been proposed, including widespread euxinia together with habitat destruction caused by plate tectonic movements, suggesting that the end Ordovician mass extinctions were a product of the coincidence of a number of contributing factors. Moreover, when the deteriorating climate intensified, causing widespread glaciation, a tipping point was reached resulting in catastrophe.

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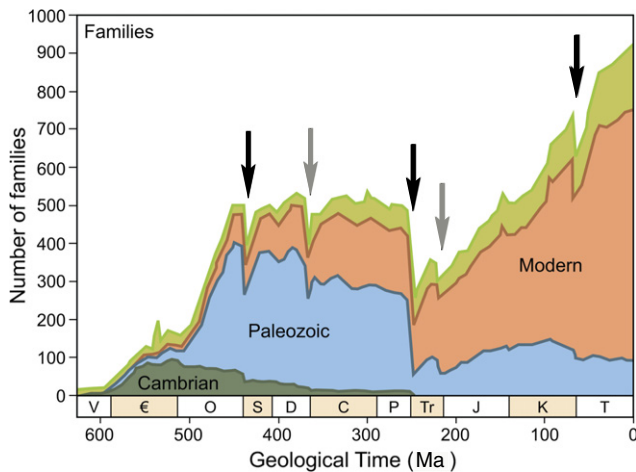
### 1. Introduction

Extinction events have modulated the history of life on our planet. They remove large numbers of species, genera and families, and in varying degrees destroy both marine and terrestrial ecosystems and reset the planet's evolutionary agenda (Jablonski, 1991). Five mass extinctions characterize the Phanerozoic, the end Ordovician, Late Devonian, end Permian, end Triassic and end Cretaceous. The end

Ordovician, generally considered to have occurred in two pulses, was the first of the big five Phanerozoic events and the first to significantly affect animal-based communities (Fig. 1). The end Ordovician extinctions are unusual since they are conventionally related to a short-lived ice age but there is little evidence elsewhere in the Phanerozoic that glaciations have been influential in changing the history of life. One possible exception is the Serpukhovian extinction that had a more substantial effect on biotas than the end Ordovician extinction (McGhee et al., 2012). Moreover the extinctions are characterized by a high proportion of Lazarus taxa, minimal ecological disruption and relatively rapid recoveries in at least parts of the World. In this review we suggest that a coincidence of factors some

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**Fig. 1.** Family diversity of marine animals through the Phanerozoic indicating the three evolutionary faunas (Cambrian [Cm], Paleozoic [Pz] and Modern [Md]) and the major extinction events (end Ordovician, late Devonian, end Permian, end Triassic and end Cretaceous). (After Sepkoski, 1981).

associated with the Hirnantian glaciations, combined to produce a tipping point.

The Early Palaeozoic (Ordovician and Silurian periods) witnessed profound and significant changes in the planet's communities and ecosystems. Marine life was characterized by a major radiation, the Great Ordovician Biodiversification Event (GOBE), a major catastrophe, the end Ordovician extinction event and a subsequent recovery during the Early Silurian. Set in a broader context (Harper, 2011), these events are part of a continuum from the appearance of the first metazoans at latest during the Ediacaran, the skeletalization of animals during the late Neoproterozoic and at the base of the Cambrian, the explosion of body plans during the Early to Mid Cambrian and the massive diversification of benthic marine life during the Ordovician, involving the lower taxonomic levels. Demersal and nektonic organisms radiated subsequently during the Late Silurian and Devonian (Klug et al., 2010). Central to this entire process was the Great Ordovician Biodiversification Event and the end Ordovician extinction. The GOBE was one of the most important and significant events in the history of life (Harper, 2006). The massive escalation in biodiversity at the family, genus, and species levels generated a new, hitherto unknown biocomplexity in marine communities, extending into the deep sea and populating reef and mudmound complexes. These significant changes in marine biodiversity occurred against a background of more modern climatic systems. The trajectory of this diversification was, however, halted by a major extinction at the end of the period when an estimated 85% of marine animal species and 25% of animal families disappeared (Sheehan, 2001a) over a relatively short time span (Brenchley et al., 1994; Finnegan et al., 2011). The GOBE was disrupted, establishing a plateau of marine biodiversity that continued until the end Permian extinction, marking the close of the Palaeozoic Era. Nevertheless this catastrophic taxonomic extinction removed few entire clades, few higher taxa and hosted a range of cryptic refugia for a large number of Lazarus taxa (Rong et al., 2006). There was apparently very minimal disruption to marine ecosystems (Droser et al., 2000). Ecological change in deep time has been defined through a hierarchy of levels. First level changes require the appearance or disappearance of an entire ecosystem whereas second level changes invoke structural changes within an ecosystem for example the appearance or loss of metazoans reefs. Third level changes occur within and between communities, involving the appearance or disappearance of community types; fourth level changes are more subtle signaled by for example taxonomic changes within a major group or within a community (Droser et al., 2000). Changes during the end Ordovician extinctions occurred mainly at the third and

fourth ecological levels, typically involving readjustments, in some cases major, within existing clade and community structures.

The first numerical analysis of fossil range data through deep time (Phillips, 1860) was published a year after Darwin's 'Origin of Species'. Phillips identified with some accuracy and precision the end Permian and end Cretaceous extinction events as boundaries between the Palaeozoic/Mesozoic and Mesozoic/Cenozoic eras, respectively. The end Ordovician event did not feature prominently until the innovative and pioneering studies of Newell (1952, 1962, 1967) whose compilations showed the event as a protracted extinction through the Late Ordovician and Early Silurian. Newell (1967) noted that echinoderms and trilobites, in particular, demonstrated accelerated rates of extinction just prior to the Ordovician–Silurian boundary. Subsequent detailed numerical analyses of the fossil record, using a much larger database and more precise stratigraphic divisions, have identified the end Ordovician events as one of the big five mass extinctions (Raup and Sepkoski, 1982) if not one of the big three (Bambach, 2006), in taxonomic terms. Many more fossil groups have been added to the catalogue of disaster. Growing evidence in the late 1960s and early 1970s of the coincidence of a major, Late Ordovician ice sheet centered on the supercontinent of Gondwana, helped develop some mechanisms for extinction associated with habitat area loss, due to regression and temperature drop (Berry and Boucot, 1973; Sheehan, 1973a). The majority of contemporary models for extinction have continued to involve the waxing and waning of Gondwanan ice sheets in some shape or form, including glacio-eustatic, sea-level drop and cooling in the tropics (see also Finnegan et al., 2012) although elsewhere in the Phanerozoic extinctions have not been directly related to glaciation.

Two end Ordovician extinction phases are known in some detail (e.g., Brenchley, 1984; Brenchley et al., 2006). The initial phase, at the base of, or just below, the *N. extraordinarius* Biozone, is associated with the start of cooler climates generated by the end Ordovician glaciations. These were centered on the supercontinent of Gondwana, located over the South Pole during the Late Ordovician (Brenchley, 1984; Brenchley et al., 2001) and associated with a major drop in sea level (Fig. 2). During this phase, benthic organisms in deep and shallow-water environments were more affected than organisms occupying mid-water depths, and planktonic organisms, particularly graptolites, and nektonic groups, were also particular targets (Rasmussen and Harper, 2011a,b and references herein). The second pulse, initiated at the base of the *Normalograptus persculptus* Biozone, is associated with a strong sea-level rise and widespread anoxia. This extinction generally killed off survivors from the first pulse, and in particular, for example in the case of the conodonts, leaving simpler and cosmopolitan ecosystems behind (Brenchley et al., 2001; Sheehan, 2001a; Rasmussen and Harper, 2011b).

The Ordovician–Silurian boundary is defined at 1.6 m above the base of the Birkhill Shale in the Linn Branch section, Dob's Linn, southern Scotland and is correlated by the first occurrence of the graptolite *Akidograptus ascensus*. The definition agreed in 1985, marked the culmination of some ten years intensive research on this key boundary interval. During the global search for an agreeable boundary, the working group gathered a huge amount of new data regarding faunal distributions through the boundary interval, globally together with preliminary information of environmental changes (Brenchley, 1988). Sections through the boundary are developed across a wide range of facies in different provinces and reflect the changes in biofacies and depositional systems during the glacial events. Nevertheless, challenges remain regarding precise correlations between the marine, mid latitude sections, where stratotypes for the base and top of the Hirnantian are located, and the coeval carbonate sections on Laurentian and glacial sequences on and around parts of Gondwana (Delabroye and Vecoli, 2010).

Major facies changes associated with the glaciations and major drops in sea level occur in a wide range of settings from high to low latitudes, affecting the glacially-modified supercontinent of Gondwana and its margins, clastic shelves and basins of the high to mid latitudes

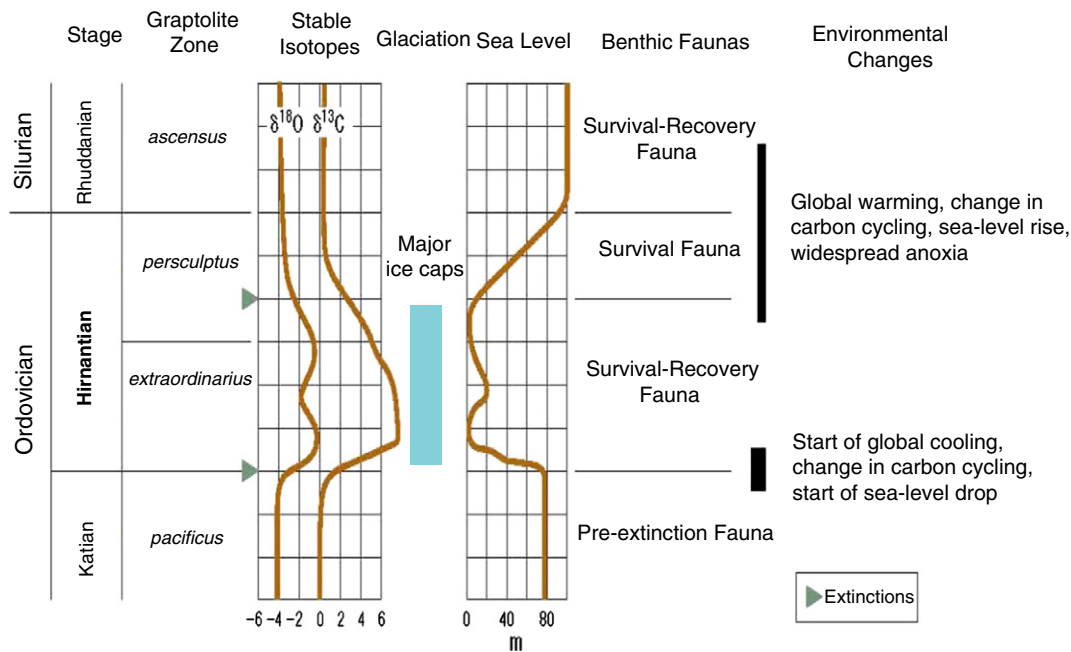


Fig. 2. Stratigraphical window and biotic and environmental events through the Ordovician–Silurian boundary. (After Brenchley et al., 2006).

and the carbonate platforms of the lower latitudes (Brenchley, 1988). An outward-facing belt of glaciomarine deposits linked to floating ice has been identified in, for example, Normandy, Portugal and Spain. In addition the extensive development of glacial features manifest in the terrestrial environments of Gondwana. These glacial deposits include fluvioglacial sandstones, slumped and varved mudstones and a variety of tilloids sometimes resting on karstic surfaces. Many siliciclastic shifal successions, for example on the ancient continents of Avalonia, Baltica, and the Laurentian margins, exhibit regressive, upward-coarsening sequences monitoring the transition from deep shelf to shallower-water biofacies commonly associated with channels; during the subsequent transgression most successions demonstrate an abrupt change to deep-shelf mudstones with a restricted benthos or graptolitic shales. In the basins of Avalonia and the Laurentian margins, coarse clastics entered some otherwise argillaceous depositional environments as mass flow deposits or turbidites, whereas in the deeper basins such influxes provided temporary relief of the anoxic conditions. The carbonate shelves of the lower latitudes are commonly punctuated by gaps, karstic surfaces and patch reefs during the regressive interval and initially high-energy, tidal deposits such as oolites during the subsequent transgression.

The Hirnantian record is, thus, far from complete and biased towards the shallow-water, preservational window and the patterns and trends of extinction and recovery are uneven across continents (Harper and Rong, 2008), providing ghost refugia for Lazarus taxa. Nevertheless over 40 localities with sections through the Hirnantian Stage are now known throughout the World, across a spectrum of latitudinal belts, faunal provinces and through a range of onshore-offshore facies types in both carbonate and clastic facies.

## 2. Taxonomic extinction: winners and losers

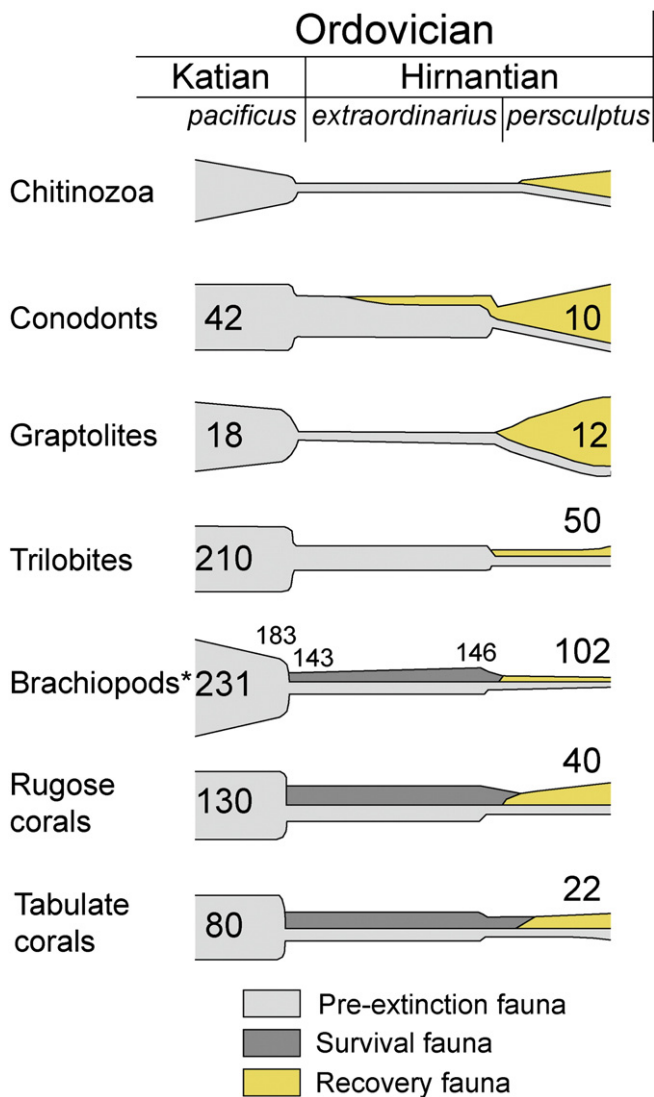
The taxonomic extinction, on the cusp of the GOBE, was substantial with the extinction of some 20% of families, 40% of genera and a maximum estimate of up to 85% of species; the various biotic groups were, however, affected in different manners and to different degrees (Fig. 3). The main ecological groups performed quite differently during the two extinction phases. The phytoplankton and zooplankton, including the acritarchs and chitinozoans, formed the base of the

food chain anchoring the Late Ordovician ecosystem and played a huge role in driving the GOBE (Servais et al., 2008). Both groups declined in diversity during the Late Ordovician, into the Hirnantian. The benthos, both sessile and mobile, suffered dramatic losses in diversity (Brenchley et al., 2001). The sessile benthos of brachiopods, together with rugose and tabulate corals, show a marked two-phase reduction in diversity at the base of the *N. extraordinarius* and *N. persculptus* graptolite biozones, respectively, the first reduction being the more severe. The fixed crinoid and cystoid echinoderms similarly suffered at the base of the Hirnantian together with the main benthic molluscan groups, the bivalves and gastropods. The mobile benthos of conodonts and most trilobites endured a similar two phase extinction, although the conodont extinctions were apparently less pronounced during the first phase. Generally the sessile benthos was most severely hit; the mobile benthos less so. The pelagic fauna, particularly the graptolites, was particularly targeted.

In taxonomic terms there were variable degrees of extinction. Within the Brachiopoda (Fig. 4), nearly 60% of all genera were lost within the most common taxonomic group, the Rhynchonelliformea (Rasmussen, 2009), and overall 40% were wiped out during the first phase of extinction. Taxa were most effectively eradicated in relatively shallow-water environments, particularly those endemic forms inhabiting the epicontinental seas, and in the deep sea the *Foliomena* fauna, an assemblage of low-diversity but widespread, small, thin-shelled, suspension feeders (Sheehan, 1973b; Harper, 1979; Harper and Rong, 1995). The deeper-shelf trilobite assemblages were similarly reduced in diversity together with many members of the deep sea population particularly mesopelagic taxa including those with reduced eyes or lacking vision entirely. In general, the more cosmopolitan species survived this initial phase rather than endemic forms.

Distinctive for the early part of the Hirnantian is the development of a near cosmopolitan *Hirnantia* brachiopod fauna (Temple, 1965) that ranged geographically, in the Bani (high latitude) and Kosov (middle latitudes) provinces (Fig. 5), extending northwards from near the South Pole to subtropical latitudes (Rong and Harper, 1988). These faunas were quite different from those of the generally more diverse Edgewood Province that dominated equatorial and adjacent tropical environments and formed their own distinctive community structures (Rong, 1979; Harper, 1981). A similar pattern is seen with the widely-distributed





**Fig. 3.** Biotic change through the crisis intervals. \*Note also these data indicate the generic loss in brachiopods that appears to have been initiated already within the *pacificus* Biozone. (After Branchley et al., 2001 with modified brachiopod data from Rasmussen and Harper, 2011a).

*Mucronapsis* trilobite fauna (Owen, 1986). Both faunas, however, disappeared almost entirely during the second phase of the extinction, at the very end of the Ordovician, surviving in only a couple of deep-water refugia for a short interval of time. Within the rhynchonelliformeans another 30% of the genera were lost during this phase. Nevertheless, despite the removal of large numbers of taxa, subsequent Silurian brachiopod-dominated communities were not markedly different from those of the Ordovician in general ecological construction but differed in composition, i.e. the types of genera and species occurring within a community.

The trilobites suffered losses in the region of 70% at the generic level, mainly in the benthos, and some interesting ecologic patterns emerge. Of the main feeding strategies, plankton feeders, predators or scavengers, filter chamber feeders and particle feeders, the filter chamber feeders (e.g., the trinucleids) were particularly targeted. No one type of feeding strategy, however, disappeared; these changes had little effect on the overall community structure requiring only within community adjustments and modifications. But in pelagic and planktonic communities, major groups such as the cyclopygid trilobites disappeared entirely and apparently were not replaced in the subsequent

recovery interval, their place in the ecosystem presumably occupied by non-trilobite taxa. The other main group of arthropods, the ostracods, similarly incurred substantial losses during the two phases with at least 30% of families disappearing by the boundary.

A few of elements of the graptolite fauna were already in a state of decline during the Late Katian; however, the group was reduced to a handful of genera and less than 20 species by the first phase of the event (Bapst et al., 2012). The group was particularly diverse in morphologies but during the crisis interval there was a marked reduction in biserial types, for example the dicellograptids, glyptograptids and diplograptids, marking a 65% reduction in species diversity within the Diplograptina. Recovery was surprisingly rapid during the *persculptus* Biozone. Many of the adaptive strategies tested in the Ordovician fauna returned during the Silurian in the successful monograptids to be supplemented by the more bizarre, curved spiral morphologies. Over 200 species have been reported from the Upper Llandovery (Lower Silurian). On a regional scale the extinction and recovery interval is known with great precision from the Yangtze Platform, South China (Chen et al., 2005) where a refugium existed during the extinction providing a locus for the re-diversification of the group. The conodonts suffered a similar major decline with extinction in the order of 80%, with taxa mainly disappearing at the base of the *extraordinarius* Biozone. A range of new taxa appeared, however, during the *persculptus* Biozone, many apparently derived from deeper-water environments.

The two dominant groups of Ordovician bryozoans, the cryptostomes and the trepostomes, together lost about 15% of their familial diversity; these two groups never returned to their former diversity during the subsequent Palaeozoic. The succeeding Llandovery (Early Silurian) faunas are generally less diverse, radiating during the later Llandovery and Early Wenlock (Mid Silurian). Echinoderms were significantly affected by the extinction pulses, for example about 70% of crinoid families disappeared whereas few cystoids and edrioasteroid groups survived the Ordovician. A range of new taxa, however, appeared within the tropical Edgewood Province (see above) and the diversity of the group rapidly recovered during the Llandovery. Rugose and tabulate corals radiated during the GOBE being possibly derived independently from different soft-bodied cnidarian roots. The extinction phases readjusted the relative dominance of the two groups, with the rugosans, both solitary and colonial growth forms, becoming the more dominant group throughout the rest of the Palaeozoic until their demise at the end of the Permian.

The bivalve molluscs suffered substantial losses from their near-shore habitats. The initial offshore migration of the class was sharply curtailed by both extinction phases and recovery was slow. The top predators of the Ordovician, the nautiloid cephalopods, were significantly reduced in diversity during the extinction interval, from nearly 300 species at the height of the GOBE to some 50 during the Hirnantian. This decline in diversity has been correlated with the Early Hirnantian regression, draining many of the epicontinental seas, and destroying habitats for potential prey.

### 3. Ecological dimension: devastation or disruption

Phanerozoic marine life has been described in terms of three great evolutionary faunas (Sepkoski, 1981). These faunas are partitioned stratigraphically but are characterized by distinctive community structures. The Cambrian Evolutionary Fauna is typified by trilobites and various types of early brachiopods, echinoderms and mollusks living in loosely-structured communities. By contrast the Paleozoic evolutionary fauna (Ordovician–Permian) is dominated by suspension feeders such as the brachiopods, bryozoans and corals organized into well-structured communities. The Modern Evolutionary Fauna (Triassic–Recent) is dominated by deposit feeders but participated in an escalated arms race between predators and prey. By the Ordovician radiation, the Paleozoic Evolutionary Fauna was in the ascendancy, co-existing with

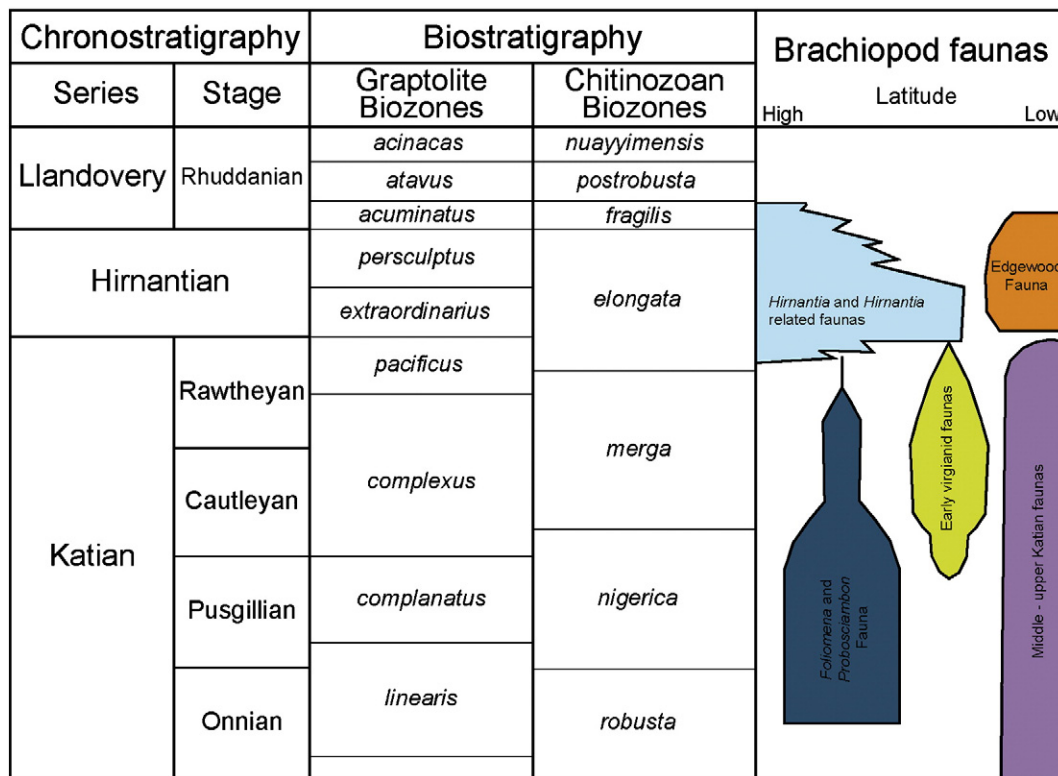


Fig. 4. Changes in the brachiopod faunas through the Ordovician–Silurian boundary interval. (Based on Sutcliffe et al., 2001).

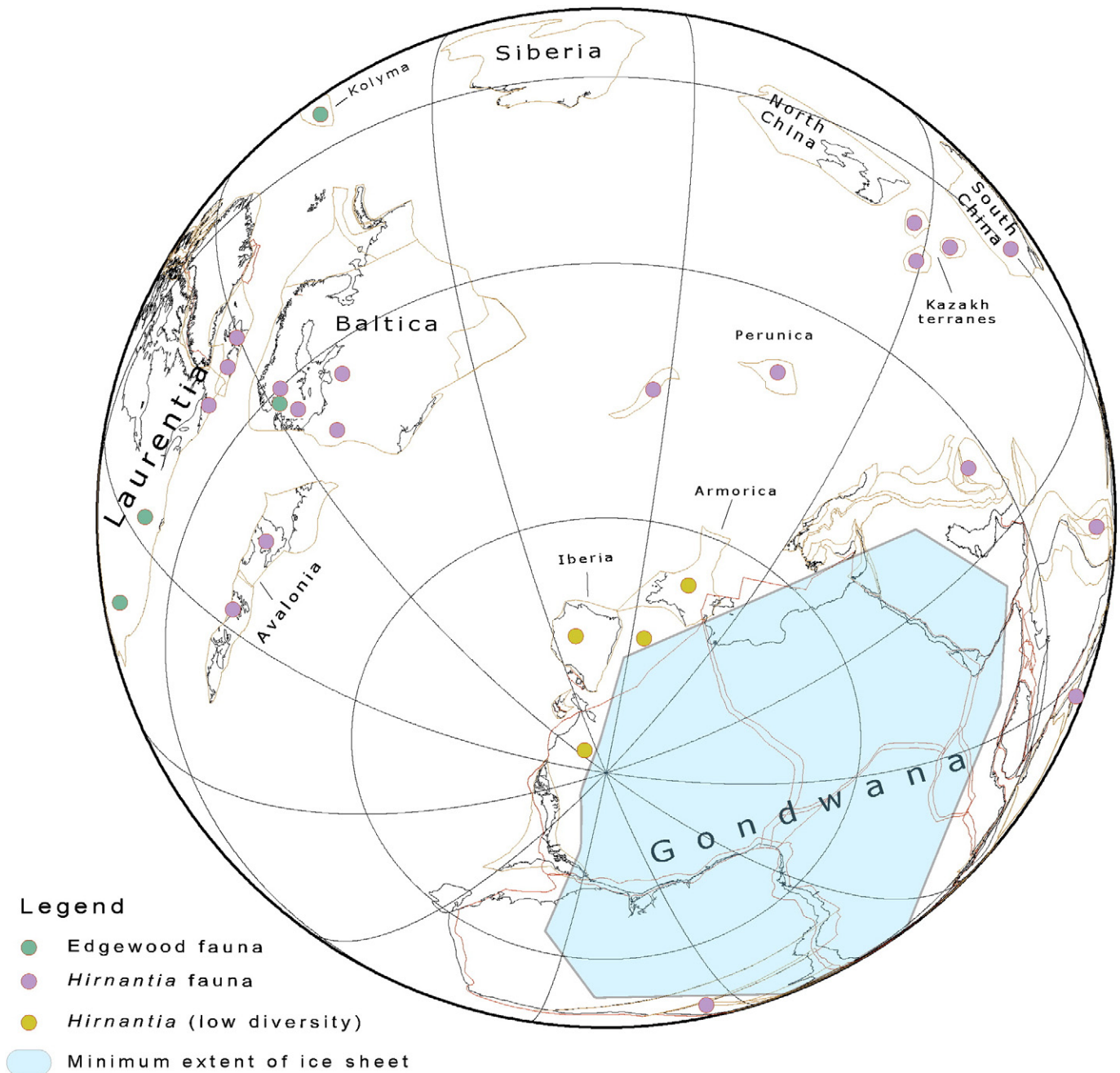
surviving taxa from the Cambrian Evolutionary Fauna and already entraining elements of the Modern Evolutionary Fauna. At a macro-evolutionary level, the discrete patterns in extinctions within the evolutionary faunas are similarly striking. Some 45% of the Cambrian Evolutionary Fauna go extinct compared with 30% and 5% of the Paleozoic and Modern evolutionary faunas, respectively. In ecological terms the extinction marks the end of the Ecological Evolutionary Unit EEU P2, an interval that contained the full force and initial consequences of the GOBE (Sheehan, 2001b). Following the extinction event key elements of the suspension-feeding Paleozoic Evolutionary Fauna expanded while the detritus-feeding cohort of the Modern Evolutionary Fauna continued to diversify, particularly in shallow-water environments.

During the extinction events a number of clear biogeographic and ecologic patterns emerge, firstly regarding the environments that were most severely affected and secondly how the configuration of provinces changed at and around the Ordovician–Silurian boundary. Detailed studies of the loss in alpha (within community) and beta (between community) biodiversity through the events have charted the taxonomic diversity of individual communities and the numbers of actual communities that disappeared during the Hirnantian (Brenchley et al., 2001). During the first phase of extinction there was a relatively small drop in biodiversity in midshelf to outer shelf environments, despite the substantial loss in brachiopod taxa. The diversification and invasion of the *Hirnantia* brachiopod fauna, occupying high to temperate latitudes, helped resuscitate the Early Hirnantian assemblages to levels near to those before the extinction. Nevertheless, outer shelf and upper slope faunas, such as the *Foliomena* brachiopod fauna, were completely eradicated. The second phase, however, removed a substantial part of the mid and outer shelf biotas, removing the widespread *Hirnantia* brachiopod fauna (Rong and Harper, 1988).

Metazoan reef ecosystems may be highly prone to extinction, particularly when subjected to cool temperatures, and take a significant time to recover. Reefs were very rare during the extinction intervals but appeared again in force during the Llandovery with similar taxonomic

compositions, in terms of taxa, and structures to those of the Katian and went on to dominate many Silurian carbonate environments (Copper and Jin, 2012). The reef build-ups remained dominated by the same families of stromatoporoids, a distinctive form of sponge, and tabulate corals, although the latter suffered substantial losses during the events. During the extinction a number of taxa disappeared entirely only to reappear during recovery intervals after the main crisis. Such taxa have been named Lazarus taxa after the biblical character who arose from the dead. Thus the Silurian reef faunas may be interpreted as Lazarus taxa and the reefs, a Lazarus ecosystem. A related concept is that of Elvis taxa, very similar but not identical forms to those that went extinct appearing too in the recovery interval.

The common occurrence of dwarfed individuals following extinction events, the so-called Lilliput Effect, has been related to survival in the miserable conditions after such catastrophes. This effect has been best documented subsequent to the end Permian extinction. Nevertheless, similar trends are apparent during the end Ordovician extinction phases (Huang et al., 2010). Just prior to the extinctions, in the latest part of the Katian Stage, brachiopod taxa within the strophomenide and pentameride groups, experienced gigantism, in which shells grew abnormally large (see, for instance, Jin and Zhan, 2001; Rasmussen et al., 2010). However, during the succeeding extinctions, various brachiopod groups reacted differently. For example, orthide brachiopods within survivor lineages increased their body sizes, but suffered significant losses subsequent to the crisis. This is opposed to surviving pentameride and rhynchonellide brachiopods, which decreased their body size during the crisis, but diversified rapidly after the extinctions during the earliest Silurian. These contrasting trends in body-size change at the ordinal level and dominance, suggest that these two major groups adopted quite different survival strategies, the latter two adopting the more successful direction of travel. Overall these trends did not disturb the general increase in size observed in brachiopod stocks during the Palaeozoic, an illustration of Cope's Law, but provided a short reversal in size trends in a number of key groups.



**Fig. 5.** Palaeogeographical configuration for the Late Ordovician. Key brachiopod faunas, discussed in the text, are indicated, as is the approximate extent of the Gondwanan ice sheet. Palaeoprojection kindly provided by Trond Torsvik, Norwegian Geological Survey. (After Rong and Harper, 1988; Harper and Rong, 1995; Owen et al., 1991.)

Biogeographic provinces are aggregations of communities and clearly their number and individual compositions affect global or gamma biodiversity levels. The number of provinces changed dramatically during the event, with some ten Katian provinces, reduced to nine in the Hirnantian and only five in the Early to Middle Silurian (Sheehan and Coorough, 1990). Clearly, following the first phase there were sufficient endemics to characterize and distinguish nine out of the ten previous provinces although only three provinces are recognized with any clarity (Rong and Harper, 1988). These combined analyses suggest that major losses occurred mainly within communities, as alpha biodiversity (Brenchley et al., 2001), but had significant influences on both beta and gamma diversity levels. Since the causes and severity of the two phases were different, those that survived the first wave of extinction commonly succumbed to the second.

#### 4. Environmental change: from hot-house to ice-house and back

Environmental conditions on the planet were quite unique during the Ordovician, very different from those today (e.g., Jaanusson, 1984; Servais et al., 2010). Most of the continents were aligned along the equator with the exception of the supercontinent of Gondwana that straddled the South Pole; CO<sub>2</sub> levels were much higher, which, to some extent compensated for a 5% dimmer Sun (Sheehan, 2001a).

During the period anoxic bottom waters were common, with dissolved O<sub>2</sub> concentrations at most only half the level of that today (<150 μM compared to the modern ~300 μM); on this basis the ambient concentration of O<sub>2</sub> in the atmosphere was thought to have been 10–50% of present-day levels (PAL) (Dahl et al., 2010). At these low oxygen levels, the ocean was especially inhospitable to metazoans in areas with a vigorous nutrient supply and high rates



of primary production. Additionally, intense magmatic activity associated with rapid plate movements, widespread volcanic eruptions, and the highest eustatic sea level stands of the entire Phanerozoic generated extensive epicontinental seas and restricted land masses that have no modern analogues (Haq and Schutter, 2008; Huff et al., 2010; Lefebvre et al., 2010). During a relatively short interval (less than 1 myr) the Earth experienced the waxing and waning of a major ice sheet on the supercontinent of Gondwana, rapidly modulating climate and environmental conditions. Traditionally, environmental changes associated with these glacial events are cited as the main contributory factors to the extinction events (Brenchley, 1984; Armstrong, 2007).

Substantial isotopic data are currently available through the Ordovician–Silurian boundary interval both at global (see Munnecke et al., 2010) and regional levels (e.g. Schönlaub et al., 2011). Analyses of the Ordovician  $^{13}\text{C}_{\text{carb}}$  curves have mainly focused on the Hirnantian excursion (HICE), which correlates with the mass extinction and the extensive glaciation on Gondwana, associated with a global sea level low stand (see above). The ‘weathering hypothesis’ as a driver for the Hirnantian glaciation and  $^{13}\text{C}$  excursion requires the Taconic Orogeny to have generated a long-term decline in  $\text{CO}_2$  through the increased weathering of silicate rocks, possibly in the intertropical convergence zone, resulting in global cooling and eventually the growth of ice sheets (see below). Increased weathering of carbonate platforms in response to the glacially-induced sea-level drop, on the other hand, was regarded as the driving force for the  $^{13}\text{C}$  excursion.

There are, however, problems correlating the  $^{13}\text{C}_{\text{carb}}$  curves from low-latitude carbonate sections both with glacial sediments from (peri-) Gondwana and with  $^{13}\text{C}_{\text{org}}$  curves from elsewhere. Thus, the precise relationship between the sea-level and isotope curves is difficult to assess since the maximum drop in sea level apparently predates the maximum isotope excursions, both for  $^{13}\text{C}$  and  $^{18}\text{O}$  (Fig. 6). A paired analysis of Hirnantian  $^{13}\text{C}_{\text{carb}}$  and  $^{13}\text{C}_{\text{org}}$  from Laurentia indicates enhanced  $p\text{CO}_2$  in the atmosphere possibly as a result of a reduction in silicate weathering. The resulting elevated  $p\text{CO}_2$  values enhanced deglaciation in the Late Hirnantian.

Immediately prior to the Hirnantian, the widespread development of carbonate build-ups, for example the Kildare, Keisley and Boda limestones, and the poleward migration of low-latitude taxa have been used to signpost the climate changes that define the Late Katian Boda Warming Event (Fortey and Cocks, 2005); although most accept the event to be an interval of comparatively warm climates preceding the Hirnantian glaciation some have suggested the Boda Event represents a time of global cooling. These competing hypotheses have yet to be tested by independent  $^{18}\text{O}$  data. A clear correlation between the  $^{18}\text{O}$  and  $^{13}\text{C}$  data curves is, however, documented for the HICE, for example, an approximate 4‰ excursion in  $^{18}\text{O}$  complements a co-eval  $^{13}\text{C}$  excursion reported from brachiopod shells in core material from Estonia and Latvia. The resolution, nonetheless, of reliable  $^{18}\text{O}$  data is much lower than that for  $^{13}\text{C}$ . Nevertheless, there is general agreement that the Hirnantian  $^{18}\text{O}$  excursion reflects the glacial maximum. Two problems remain: firstly, the 4‰ shift measured from brachiopods requires a sea-level fall of > 100 m and a drop of 10 °C in tropical surface water temperatures (Brenchley et al., 1994), the latter seems unrealistically high; and secondly the proposed expansion of the Gondwanan ice sheets does not precisely match the development of the  $^{18}\text{O}$  values.

Osmium isotopic data support the brevity of the glacial event and an initiation mechanism for the glaciation through increased silicate weathering (Finlay et al., 2010), modeling such processes as the driving mechanism behind the Hirnantian glaciation and subsequent mass extinction. The coupling of  $\text{Os}_i$  and  $\delta^{13}\text{C}_{\text{org}}$  proxies provides the most direct evidence for the initiation and cessation of the Hirnantian glaciations. The use of  $^{187}\text{Os}/^{188}\text{Os}$  chemostratigraphy has considerable potential for tracking the Palaeozoic Earth climate system, particularly through palaeoceanography. Nevertheless, new

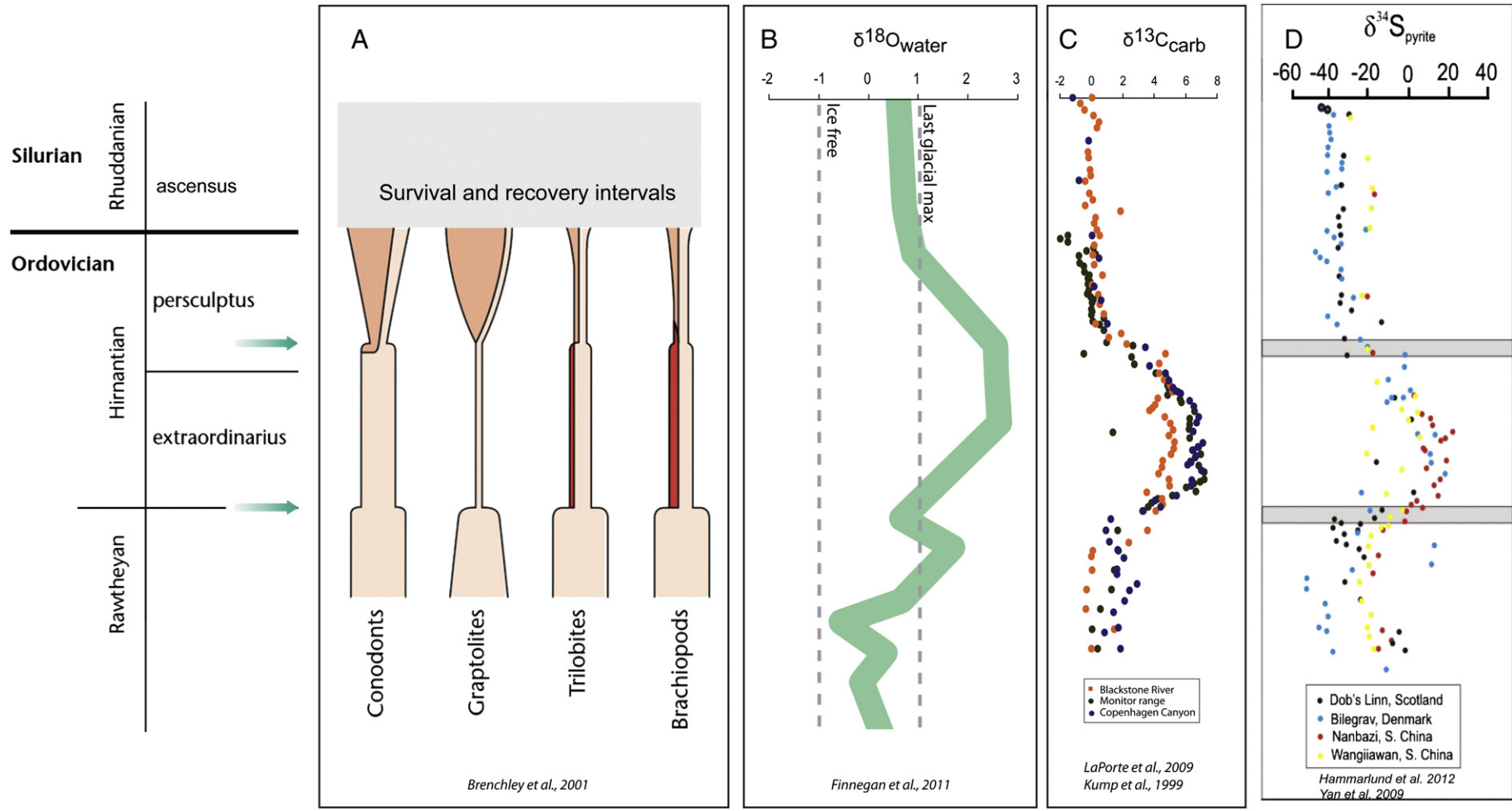
data (see below) from sulphur isotopes support anoxic conditions in the World’s oceans during both pulses of the extinction event (Hammarlund et al., 2012). Additional isotopic proxies will continue to enhance and evolve understanding of these events.

There is no clear consensus on how this short-lived, major and potentially devastating glaciation was initiated. A number of potential causes have been cited: firstly the Monterey Mechanism, first observed in deep-sea canyons off the coast of California, invokes increased primary production of  $\text{CO}_2$  prior to glaciation, especially associated with upwelling zones, and carbon burial to draw down the levels of atmospheric  $\text{CO}_2$ . There is, however, little evidence for such widespread upwelling, extensive carbon burial in the deep sea, or for concomitant decreases in  $\text{CO}_2$  during the latest Ordovician. Secondly a hypothesis involving the rate of silicate weathering in modulating levels of atmospheric  $\text{CO}_2$  (Kump et al., 1999) requires the variable exposure of silicate-dominated terranes, exposed or not, to enhance weathering; the transit of such terranes through the intertropical convergence zone where high rainfall would have aided chemical weathering. Thirdly massive volcanic eruptions prior to the Hirnantian may have primed the climate by direct forcing, an increased albedo assisted by ash particles in the atmosphere and the weathering of volcanic products (Buggisch et al., 2010). The major volcanic eruptions of this interval, however, occurred during the Sandbian some time before the Hirnantian. But the after-effects of these may have formed part of a move towards cooler climates during the later part of the period. Additional tectonic suggestions have included the movement of the supercontinent of Gondwana firmly over the South Pole, providing an albedo effect from land-based ice and snow. The creation of the Taconic Basin, a depression formed on the collapsing Appalachian–Caledonian mountain chain on the edge of ancient North America may have assisted the diversion of cooler currents along the margins of the ancient continent of Laurentia. Finally an elegant model, involving the diversification of land plants, may account for the rapid cooling required to initiate glaciation (Lenton et al., 2012). This new terrestrial flora required nourishment from rock-derived minerals and thus accelerated the release of key nutrients into the oceans, especially phosphorous, by, for example, accelerated silicate weathering. These nutrient pulses assisted carbon burial and enhanced the drawdown of  $\text{CO}_2$ ; ironically the early evolution of land plants may have helped drive the extinction of the marine biota.

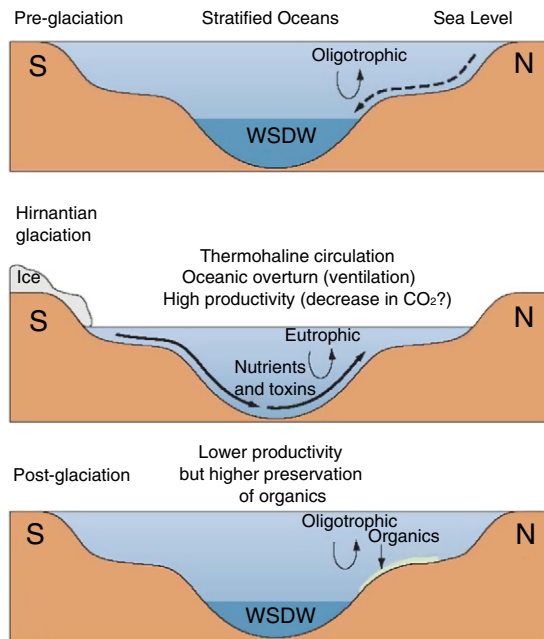
## 5. A multicausal catastrophe: new insights

The complex mosaic of end Ordovician environments and the conflicting patterns of extinctions have led to a range of suggested kill mechanisms for the extinctions. The first extinction phase, at the base of the *N. extraordinarius* Biozone, has been linked by a number of authors to cooling, habitat loss as a result of sea-level drop, as well as to globally increased ventilation of the oceans (Berry and Wilde, 1978; Brenchley et al., 1995) and the amalgamation of the continents (Rasmussen and Harper, 2011a,b). Increased ventilation and, hence, oxygenation of the water column is largely inferred from a widespread shift from deposition of black shales to deposition of gray, sometimes bioturbated, shales (Fig. 7). On the other hand, a few studies have discussed how expanded anoxia could be associated with this first phase of the Hirnantian extinction (Goodfellow and Jonasson, 1984; Briggs et al., 1988; Fortey, 1989; Zhang et al., 2009). For example, the preferential extinction of pelagic species like graptolites as well as key benthic taxa, such as trilobites that had pelagic larval stages, are explained by expansion of water column anoxia (Fortey, 1989). For the second phase of the extinction, anoxia is commonly discussed as indicated by the widespread deposition of black shales following the *N. persculptus* Biozone rise in sea level (Rong and Harper, 1988; Brenchley et al., 2001).





**Fig. 6.** The end-Ordovician mass extinction, glaciation and isotope excursions (from Hammarlund et al., 2012). A) Four marine groups affected by the two-phased end Ordovician extinction (Brenchley et al., 1994), where colors indicate the pre-Hirnantian (beige), Hirnantian (red) and post-Hirnantian (pink) fauna. B) Interpolated  $\delta^{18}\text{O}$  reflect several fluctuations of the pre-Hirnantian sea level and subsequently a major drop and rise during the Hirnantian (Finnegan et al., 2011). C) A compilation of three profiles of inorganic  $\delta^{13}\text{C}$  visualize a significant perturbation of oceanic carbon dynamics during the lower Hirnantian *N. extraordinarius* Biozone (Kump et al., 1999; LaPorte et al., 2009). D) Compiled sulphur isotope curve (Yan et al., 2009 and Hammarlund et al., 2012).

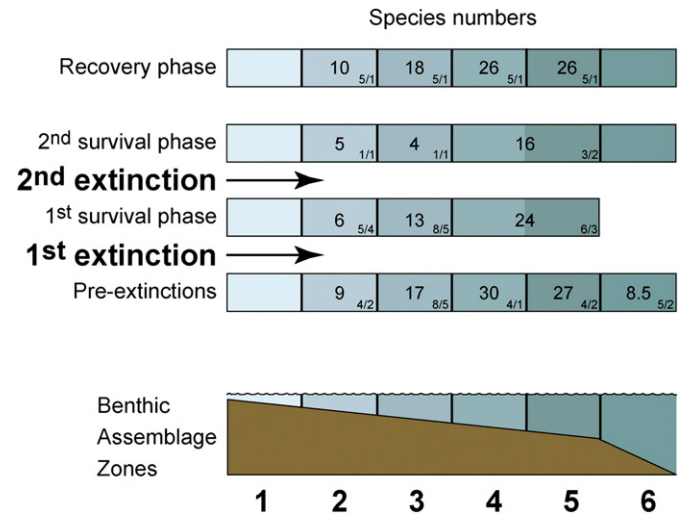


**Fig. 7.** Illustration of differences in oceanic circulation and productivity between glacial and nonglacial phases. Pre- and post-Hirnantian oceans shown with sluggish circulation and warm, saline waters at depth derived from low-latitude evaporation. Hirnantian characterized by strong thermohaline circulation that initiated the change from oligotrophic to eutrophic oceans.

(After [Brenchley et al., 1995](#)).

Temperature change, during a short-lived ice age, is difficult to test as a kill mechanism, even though the link has been claimed for decades ([Stehli and Wells, 1971](#); [Stanley, 2010](#)). A change in the order of a few degrees over hundreds of thousands of years cannot simply be explained to sustain extinctions; however it can destroy and restrict habitats over time. Today, temperature has a major control on the distributions of marine biotas, defining geographic provinces that generally follow climatic belts, although across the globe there is a substantial temperature range from the poles to the equator of about 35 °C. Nevertheless, latitudinal diversity gradients are occasionally interrupted by local biodiversity hot spots. Moreover, diversity gradients also follow longitudinal patterns without associated temperature changes ([Willig et al., 2003](#); [Bellwood and Meyer, 2009](#)). During cooling events organisms can migrate towards the equatorial belt, with major extinctions associated with the contractions or eliminations of climate zones associated with severe range restriction or removal. Shallow-water benthos, above the thermocline would be most exposed. Cooling scenarios were first suggested some 40 years ago but it is difficult, however, to apply this kill mechanism to many of the high-latitude, cool-water taxa (e.g., many conodont, graptolite, and trilobite species), and particularly those living beneath the thermocline. This mechanism is clearly more appropriate to lower-latitude taxa, particularly those dwelling in the large and unusual epicontinental seas of the period. During the end Ordovician glaciation the tropical belt contracted, being restricted to the rather narrow Edgewood Province while the *Hirnantia* brachiopod fauna, dispersed from polar to subtropical latitudes in the Bani and Kosov provinces (see above). The Edgewood Province, the tropical belt of carbonates stretching across equatorial Laurentia into parts of Baltica and Siberia, contained its own distinctive endemic fauna.

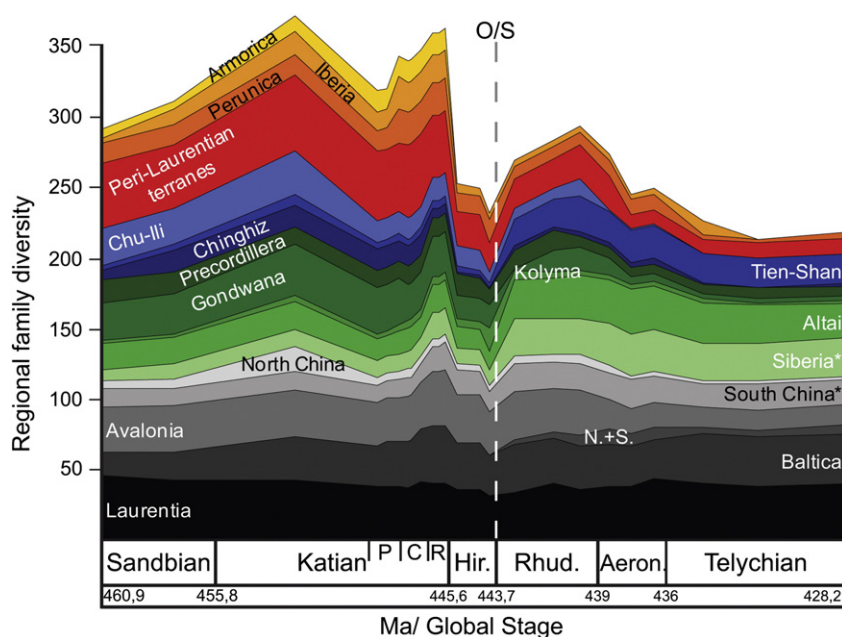
Two main mechanisms have been invoked to restrict or destroy habitat space during the extinction. Firstly a major eustatic sea-level drop, in the region of 100 m, during the first phase removed significant habitable belts of the shelf, presumably bunching up the benthic assemblage depth zones on the previously deeper parts of the shelf. Increased competition for space ([Valentine, 1969](#); [Sheehan, 1975](#);



**Fig. 8.** The change in 'within-community' (alpha) diversity in five of the six benthic assemblages spanning the shelf to upper slope. Alpha diversity was measured as the average diversity of communities in each of four benthic assemblage zones (BA 2 to BA 5). There are no data for BA 1. The numbers separated by a slash in each box are the number of assemblages and the number of palaeogeographic provinces from whence the assemblages are derived. The unexpectedly small fall in alpha diversity after the first phase of extinction results from the addition of new taxa belonging to the Hirnantian recovery fauna; no similar recovery fauna immediately buffers the effect of the second phase of extinction. (Modified from [Brenchley et al., 2001](#)).

[Brenchley, 1984](#)) would drive local extinctions where the carrying capacities of particular ecological niches were exceeded ([Fig. 8](#)). This mechanism was most applicable to the extensive, shallow-water epicontinental seas and their specialized faunas (e.g. [Jin, 2001](#)), so distinctive for the period. A drop in sea level in the order of 100 m would displace taxa seaward to a narrow rim on the platform edge, with less available space; moreover they risked elimination by competition with incumbent and better-adapted species already living on the platform rims ([Sheehan, 1975, 2008](#)). This process may have been of less significance in more open marine, oceanic environments; here emerging cone-shaped islands and archipelagos provided increased habitable shelf space.

The excision and limitation of ecospace may also have been provided by the destruction of terranes and microcontinents themselves. A key factor controlling the duration and magnitude of the drop in species diversity during the end Ordovician crisis interval was the configuration of the palaeoplates. Analysis of a global database for rhynchonelliformean brachiopods shows major regional differences in the distribution of brachiopod diversity at the Ordovician–Silurian interface and further that the disparity continues through diachronous recovery intervals from one palaeogeographic unit to the next ([Rasmussen and Harper, 2011a](#)). The extinction event proved to be catastrophic, especially within the peri-Laurentian terranes ([Fig. 9](#)). Detailed analyses of locality-based databases for the key interval suggest that the diverse habitats of the island arcs of the Iapetus Ocean, that had been one of the focal points in diversity prior to the extinctions, particularly during the GOBE, could not be sustained during the survival and recovery intervals. These terranes were accreted to the Laurentian craton during the Appalachian–Caledonian orogeny within the window of the extinction and recovery intervals. Terrane accretion was already underway during the Hirnantian and in the early part of the Llandovery when continued glacially induced sea-level fluctuations made it difficult to adapt to rapidly changing environments. On a global scale, the loss of habitats considerably extended the recovery interval as survivors were forced to re-adapt to continuously changing, new environments. On a regional level the continent of Laurentia benefitted from the terrane accretion by hosting exotic,



**Fig. 9.** Diversity at the family level split into separate geographic entities. Note that virtually no drop in diversity is seen for the large, well-sampled continents (dark colors at the bottom of diagram), whereas smaller terranes exhibit a large taxonomic loss (warm colors at top of diagram). The diagram is based on range-through data. Abbreviations: N. + S.—Novaya + Severnaya Zemlya, South China\* includes Sibumasu, Siberia\* includes Mongolia, Taimyr and Tuva.

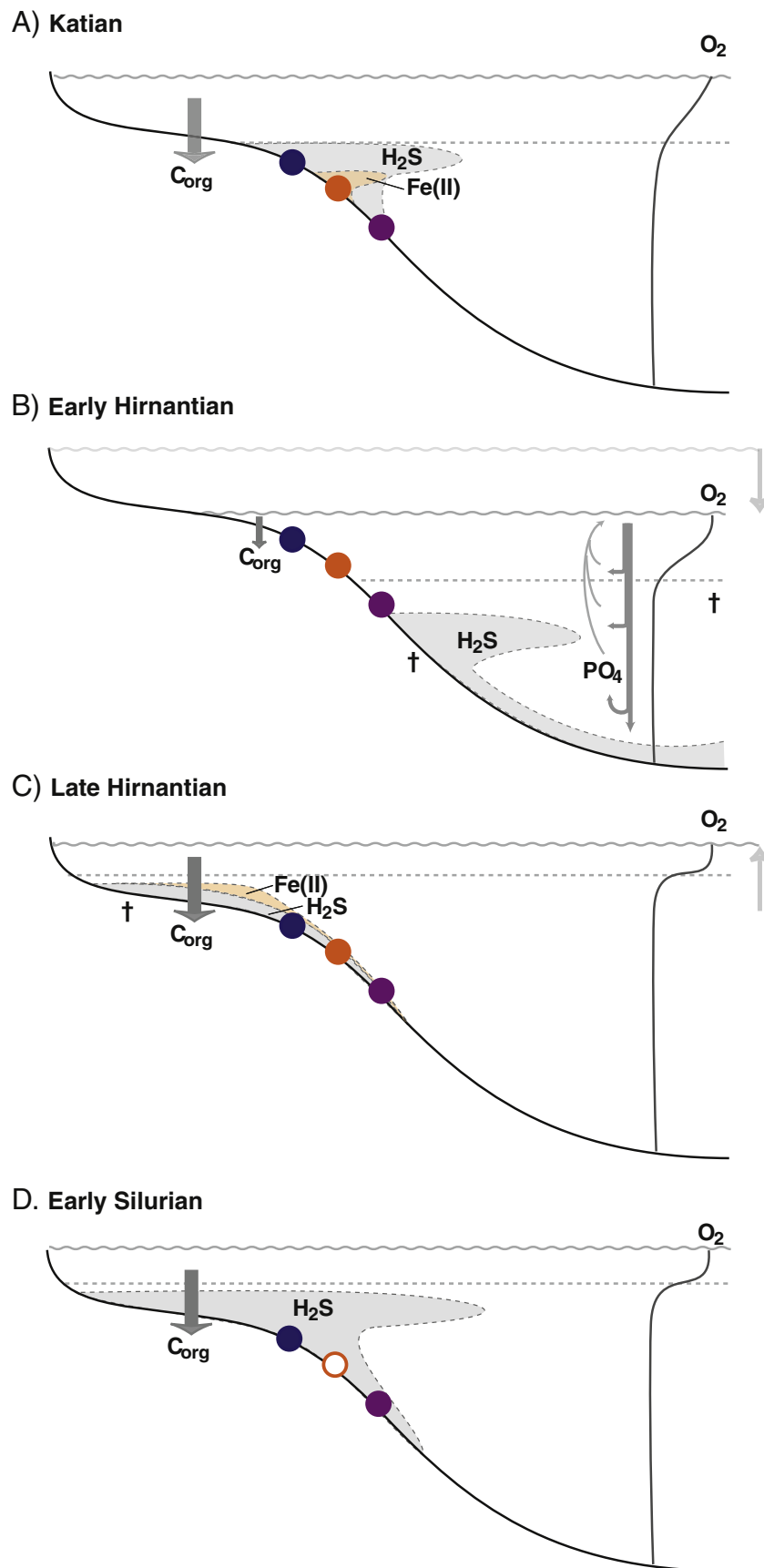
invasive taxa during the crisis and the initial recovery intervals. Here, the recovery interval was delayed some millions of years, compared to other regions of the world. These invaders, however, evolved into assemblages of new taxa that initiated successful radiations fuelling the end Llandovery faunas that were significantly more diverse than those brachiopod faunas evolving on Avalonia and Baltica.

A number of possible extinction mechanisms are associated with changes in ocean chemistry and circulation. During the first phase of the event, planktonic and pelagic groups together with the deep-sea benthos were particularly hard hit. Clearly these crises were related to fundamental changes in oceanic chemistry and circulation patterns rather than due to temperature changes and restriction of habitat space. Models follow three main strands: ventilation of deep water, upwelling of toxic deep water and more recently widespread euxinia. Assuming a generally anoxic deep sea, during the initial stages of the glaciations cold, dense, oxygen-rich waters, generated around the margins of Gondwana sank and ventilated the deep sea, removing black shales from the world's oceans. Although not a direct kill mechanism, and perhaps overly simplistic, oxygenated oceans would remove phosphorous from the nutrient reservoir driving oligotrophy and a collapse of trophic structures (Berry and Wilde, 1978). This lack of primary productivity would have a drastic effect on pelagic and planktonic organisms with presumably a knock-on effect for the filter-feeding, deep-water benthos. Moreover, it is assumed that the loss of dysaerobic habitats had an adverse effect on the deep-sea benthos such as the *Foliomena* brachiopod fauna. The extinction mechanism by the upwelling of poisonous, toxic waters containing large quantities of  $H_2S$  is also associated with the deep-sea circulation of cold water derived from the poles. Nevertheless  $H_2S$  can be rapidly oxidized in the water column during its ascent to the surface. Some extraterrestrial causes have been cited for the event. Although high Iridium values have been reported from some Ordovician–Silurian boundary sections, low rates of sedimentation or erosion of adjacent basement or ophiolite complexes have been cited as probable sources for these anomalies rather than asteroid impacts.

Building on this apparent lack of consensus regarding the causes of the end Ordovician extinction, a more in-depth interpretation of the geochemistry of Hirnantian sediments has provided some

important clues (Hammarlund et al., 2012). Complimentary geochemical redox indicators, such as iron speciation, molybdenum concentration, pyrite framboid size distribution, and sulphur isotopes, analyzed at three key Hirnantian sections: Dob's Linn (Scotland), Billegrav (Denmark) and the Carnic Alps (Austria) revealed that reducing conditions were occasionally present at all three sites before the first pulse of the end Ordovician extinction, and that these conditions expanded during the second pulse.

Although the *N. extraordinarius* Biozone was characterized by oxic deposition in these sections, pyrite is significantly enriched in  $^{34}S$  in all three sections and in sections in South China (Yan et al., 2009; Zhang et al., 2009). The pyrite signal points to a widespread reduction in sulphate concentration attributable to an increase in pyrite burial ratios during the Early Hirnantian. This S isotope excursion coincides with the major positive carbon isotope excursion indicating globally elevated burial rates of organic carbon. From these data, euxinic conditions probably prevailed during this interval and intensified in the Early Hirnantian oceans; the concomitant global sea-level drop deflecting the chemocline deeper than the depositional setting of these sections. In fact the sea-level drop itself would also be a primary driver for the anoxic conditions, linked to the increased cycling of organic carbon and phosphorous, and modeling suggests that the sea-level drop would result in a reduction of dissolved oxygen that is at least twice as large as that generated by cooling (Bjerrum and Bendtsen, 2002; Wallmann, 2003; Bjerrum et al., 2006). In addition, analyses of Chinese and Canadian sediments from the same, presumably oxic, interval of the Early Hirnantian, have also been interpreted to reflect the presence of local, stratified water columns and anoxic conditions based on sulfur isotope mechanisms (Goodfellow and Jonasson, 1984; Zhang et al., 2009). Later, during the strong and sustained *N. persculptus* Biozone transgression, euxinic conditions invaded the continental shelves, based on data from iron speciation and molybdenum concentrations. In this model (Fig. 10), anoxia in the water column played a critical role in the initial stages of the end Ordovician extinction, despite the apparently oxic environments of the Early Hirnantian that primarily are preserved. In the first pulse, regression, euxinia and a steepened oxygen gradient in the water column caused habitat loss for deep-water benthic and for nektonic and pelagic organisms. In the second pulse, the transgression of anoxic and weakly



**Fig. 10.** A conceptual model of the evolution of ocean chemistry prior to, during and after the Hirnantian. (A) Intermittent euxinia is present in the Katian; here and below the dashed line represents the chemocline. (B) During the Early Hirnantian shelf area is reduced, phosphorous recycling increased and anoxic conditions expanded. The fraction of pyrite burial increases and depletes sulphate concentrations. Extinctions (†) occur among marine animal groups in the water column and at depth. (C) During transgression in the Late Hirnantian, sulphate is low and anoxic conditions reach the shelf, affecting shallow benthos. (D) In the Silurian sulphate availability is re-established, resulting in widespread anoxic and sulphidic water column conditions. (After Hammarlund et al. 2012).



sulphidic water onto the continental shelves, during a marked and sustained transgression, caused widespread extinction across the shelves particularly in shallower habitats.

## 6. The planet recovers

The recovery following the end Ordovician extinctions had many significant dimensions, including the recovery of biodiversity and the marine ecosystem itself, together with readjustments within the animal clades. The process of ecosystem renewal following the event took several million years, but the resulting fauna, broadly speaking, had ecologic patterns similar to the faunas that had become extinct. Intriguingly, other extinction events that eliminated similar or even smaller percentages of species had greater long-term ecological effects, suggesting that many keystone species survived the end Ordovician extinction explicitly or cryptically in refugia (Rasmussen and Harper, 2011a,b). One possible route to recovery involved the origination of taxa in shallow-water environments (Owen et al., 2008) and their subsequent movement into deeper-water habitats with time, a recurring theme during the Palaeozoic (Sepkoski, 1991; Sepkoski and Sheehan, 1983).

Three of the major Palaeozoic groups, the brachiopods, graptolites, and trilobites participated in intra clade renewal. Within the nonarticulate brachiopods, nearly 20 families survived the extinction while some ten families succumbed. Many of the more specialized groups, such as the Eoconulidae and Siphonotretidae went extinct whereas many of the more diverse clades such as the Acrotetidae, Craniidae, Discinidae, and Lingulidae survived to diversify during the Silurian. Within the rhynchonelliformeans, the two dominant groups of the Ordovician, the orthide and strophomenide brachiopods showed substantial casualties. Nearly ten orthide families perished, including many of the well-established Ordovician clades, for example the Cremnorthidae, Orthidae and Plaesiomyidae; only three impunctate orthide families, the Hesperorthidae, Plectrothidae and Skenidiidae survived, survivorship and subsequent diversification being focused in the punctate groups such as the dalmanellids, draboviids and rhipidomellids. Within the strophomenides, some 50% of families survived including the Leptaenidae, Sowerbyellidae and Pholidostrophiidae; these were generally widespread taxa in diverse clades. The most marked expansion occurred within atrypide, athyridide and pentameride brachiopods, with these groups invading many of the niches previously occupied by the orthide–strophomenide-based communities of the Ordovician (Harper and Rong, 2001).

The trilobites showed similar fatalities with some 20 families disappearing at the boundary and some 20 surviving. The survivors included the long-ranging families within the Proetidae, some continuing into the Upper Permian. Some of the more specialized forms such as the Lichidae and the Odontopleuridae also survived together with a number of groups of Phacopida.

Within the Graptolithina approximately 75% of the dendroid families survived the extinction but less than 15% of the more-familiar graptoloids continued into the Llandovery, where they enjoyed a massive diversification, and ecologically and taxonomically recovered their previous abundance and diversity (Brenchley et al., 2001; Bapst et al., 2012). Substantial diversifications characterized the monograptoids (early Rhuddanian), normalograptids (late Hirnantian and early Rhuddanian) and the retiolitoids (late Hirnantian and early Rhuddanian). Other groups such as the top predators of the Ordovician, the nautiloids, that suffered during the extinction with diversity levels falling to values near those during the origination of the group had by the mid-Silurian regained their ecologically-dominant position in both diversity and within Silurian food chains.

Many compilations indicate that diversity recovered slowly during the early and mid Silurian; however, recovery may have been much more rapid, the relevant range data being subject to the Lipps–Signor effect (mirror image of the Signor–Lipps effect) presenting the relatively

sudden diversification as a more delayed and gradual event (Sheehan, 2001a) and possibly due to the use of very broad time bins for the data capture, analysis and display. For example during the recovery interval many surviving clades had radiated within five million years with newly established incumbents displaying relatively few, new modes of life, the large gregarious pentameride brachiopods being an exception. In shallow-water and high-energy environments, these taxa assumed the roles of some groups rooted in the Ordovician, such as the trimerellids, and dominated carbonate shelf environments for much of the Silurian. In the deeper seas the *Dicoelosis* communities remained stable for much of the Silurian and a significant part of the Devonian, derived from shallower-water facies rather than the extinct *Foliomena* fauna of the Ordovician.

The Early Silurian ecosystem rapidly reconstituted many of the ecological structures destroyed by the extinction event. The diverse communities of the Ordovician, characterizing the unique epicontinental seas of the period together with the shelf and slopes of all the continental plates, were largely removed. For example, the first phase of extinction removed, specifically, many of the epicontinental sea communities but also those deep-water assemblages, such as the brachiopod *Foliomena* and trilobite cyclopygid faunas, to be replaced by distinctive community structures in the Hirnantian, for example the *Hirnantia* and *Mucronaspis* faunas (Owen et al., 1991). The second phase of extinction removed these Hirnantian communities, in favor of a generally poorly-diverse Rhuddanian fauna in most parts of the World (Rasmussen and Harper, 2011b). These near-cosmopolitan, low-diversity communities formed the basis for a massive recovery of the shelly fauna during the later Silurian first in the much-depleted epicontinental seas. Seaward in the open marine faunas, especially in deeper shelf and slope settings, more survivors were available to seed the revival and not surprisingly, communities here were not too dissimilar to Ordovician communities, dominated by orthide–strophomenide members in contrast to the atrypides–athyridides–pentamerides of the commonly shallower, carbonate platforms.

## 7. Conclusions and consequences

The end Ordovician extinction comprises two pulses of extinction corresponding to the start and end of the Late Ordovician glaciation. During the first, global sea level dropped nearly 100 m during a marked marine drop in sea level, and steep temperature gradients were established between the poles and the equator. Icy waters spilling off the margins of Gondwana generated thermally-driven deep-water circulation; cold, oxygenated water moved into the deeper ocean, which had hitherto been warm and stratified, suffering little turnover. At the end of the glaciation, sea levels rapidly rose, the temperature gradient was re-equilibrated to pre-Hirnantian conditions, and deep oceanic circulation became sluggish. The glaciation had a very short duration, perhaps only half a million years (Brenchley et al., 1994). The rapid velocity of the onset and decline of the glaciation probably contributed to the extinction by limiting the time available for evolutionary accommodation to the new environments, not least during an interval where habitats were destroyed as a consequence of continental amalgamations that coincided with the glaciations. At the start of the glaciation, while the epicontinental seas were drained, the initial extinction pulse hit the shallow-water inhabitants of these seas particularly hard. Cool temperatures in the open ocean contributed to the incursion of cool-water, and near-cosmopolitan communities collectively known as the *Hirnantia* fauna. When the glaciation ceased, sea-level rise and global warming together with a lack of oceanic mixing, associated with widespread anoxia, caused the second pulse of extinction, during which the *Hirnantia* fauna became extinct together with many other open marine faunas. Following such a major loss of diversity, Silurian communities were initially less complex and broader niched. Highly endemic faunas, which characterized the Late Ordovician, were replaced by faunas that were amongst the most cosmopolitan in the

Phanerozoic, biogeographic patterns that persisted throughout most of the Silurian. The recovery of taxonomic diversity and ecologic complexity took several million years, and was probably to a large extent driven by large scale plate tectonic movements.

These end Ordovician events probably had nothing like the long-term impact of the end Permian and end Cretaceous extinctions. Nevertheless, a large number of taxa disappeared from the Earth over a short time interval. A multicausal hypothesis involving a series of coincident and contributory factors combining to reach a tipping point could simulate a major catastrophe. None on their own was sufficiently destructive or extensive to ignite an Armageddon, but each selectively removed taxa while providing opportunities for the survival of Lazarus taxa. Heterogeneities during the extinction and recovery phases emphasize this selective process (e.g., Harper and Rong, 2008). Major readjustments took place within both clades and community structures, anchoring the longevity and resilience of the Paleozoic Evolutionary Fauna. And many communities and taxa hitherto confined to the narrow, Hirnantian tropics of the Edgewood Province, expanded across the range of carbonate environments during the Silurian and Devonian continuing the suspension-feeding and metazoan-reef ecosystems established during the GOBE.

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