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The palaeogeographic impact on the biodiversity of marine faunas during the Ordovician radiations

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ABSTRACT

Diversification is a key property of life. Building on John Phillips' (1860) classic, iconic curve, Phanerozoic biodiversity trajectories have been based, subsequently, on the availability of additional and renewed sets of data and increasingly sophisticated analytical methods. Using a relatively few single sources of data from global databases, the shapes of recent biodiversity curves for Ordovician biotas have predictably converged promoting acceptance of discrete events, aligned with relatively few peaks and discrete drivers. There has been a resistance to investigate under the curves and examine the many and varied causes of biodiversity. The majority of the data available pertains to the most abundant part of the benthos, the brachiopods, and more especially their occurrences in Baltica and Laurentia together with South China. Exploration of a number of regional datasets, deconstructed from global curves, for some key fossil groups indicates the regions that do have distinctive biodiversity signals, but also highlights significant gaps in our knowledge.

1. Introduction

Carl Linnæus (1781), the inspirational Swedish naturalist and scientist, proclaimed that all species originated in Paradise from a single source. There has been substantial progress in understanding biogeography over the last 250 years but Linnæus' observations are not entirely outrageous; modern studies have demonstrated the high diversity of tropical faunas, particularly those occurring in biological hotspots and associated species pumps. There is a strong relationship between biodiversity and latitude in modern marine biotas, where the tropics offer a range of environments in warm waters associated with carbonate mounds and reefs. Moreover, data capture together with management and analysis of large databases for the distribution of fossil ranges has advanced

significantly in the last few decades and the geographic and stratigraphic ranges of organisms and their communities can be tracked with some confidence.

Palaeobiodiversity is based on data from the fossil record (e.g. Benton 1995). During the last 50 years, a succession of global biodiversity curves for the period have been constructed and published from a variety of global databases. In recent years, in palaeontology two databases stand out besides the iconic studies of Sepkoski (e.g. 1988, 1997, 2002). The Paleobiology Database (the PBDB) is a collection-based online resource storing data on the classification and distribution of fossil organisms. The Geobiodiversity Database (GBDB) is a section-based resource. Both databases have captured regional data, whether from collections and sections, and researchers have aggregated and managed these data in a variety of ways to construct global species richness curves.

In addition to these global databases there are a large number on long-tailed inventories, some published and others held by researchers as a less accessible resource. These are, however, generally of higher-quality than those held in the global data repositories.

We test here the hypothesis that global curves reflect global events and thus require global causes and drivers to generate a world-wide biodiversity spike. In this scenario a Court Jester model is applicable to explain the power and reach of factors to initiate a global burst of species richness (Benton 2009). The alternative hypothesis, presented here, is more gradual and relies on the accumulation of biodiversity from the diachronous expansion of species numbers along phylogenies and across the regions of the world; the latter model is preferred.

Here we first explore a number key fossil groups diversifying during the Great Ordovician Biodiversification Events (see Servais and Harper 2018), some of which are not included in the global datasets, the distribution of their biodiversity trajectories across the regions of the globe based on some current literature. Secondly, we interrogate data in the Paleobiology Database for regional patterns, accessing the same dataset utilised in the construction of recently published global curves.

2. A brief modern perspective

Biogeography is the study of the distribution of living organisms. The ranges of bacteria, animals and plants may be as restricted as the digestive system of particular animal or as widespread as the entire globe. Biotic patterns are determined by geographic and the distribution of endemic and cosmopolitan taxa. Endemic taxa are restricted to islands or particular habitats. Studies of modern biodiversity have emphasised a number of key points: Species diversity usually increases towards the equator, islands and mountain summits and other similarly isolated ecosystems exhibit increasing

diversity with larger area and decreasing diversity with increasing isolation; and finally endemism is higher in larger and more isolated areas (Brown and Lomolino 1998). Although there are many more studies on terrestrial floras and faunas and their diversity, marine biotas are best known from studies of coral reefs occupying shallow-water environments in the tropics; deep-water habitats due to relative inaccessibility are less well researched and thought to be species poor and dominated by cosmopolitan taxa. Nevertheless, surveys of deep-water faunas confirm that in these ecosystems too, there is an increase in diversity from the poles to the equator.

The distinctive biogeographies of individual taxonomic groups during much of the early Palaeozoic is now well known (Harper and Servais 2013); they do not always follow global trends. In terms of the Great Ordovician Biodiversification Events (not a single Event, see Servais et al. 2021) the roles of islands, created by magmatic and tectonic processes, as cradles and refugia for species, during the Middle Ordovician are well established. Many authors have invoked a range of scenarios related to magmatism and tectonics, a primary enabler being the disposition of the major continents, their movement, together with the widespread development of island arcs and microcontinents with related volcanisms. The influence of climate and temperature on the diversification of marine faunas has been demonstrated with reference to both living and past biotas. During the Ordovician, high sea levels (Haq and Schutter 2008), the widespread occurrence of large epicratonic seas are associated with global warming particularly during the end of the period (prior to the Hirnantian), contributing to the thalassocratic conditions (Jaanusson 1979) that characterised the later Ordovician. With the movement of the major continents into and around the tropics, marine life expanded (see also Mannion 2020).

3. Global curves and the fossil record

Curiosity about the natural world and its biological diversity was a key theme absorbing 19th Century naturalists (e.g. Wulf 2015). The search to catalogue and understand the Earth's biota was led by a number of iconic 19th Century scientists including Alexander von Humboldt. Fossil data accumulated, concurrently, against the developing stratigraphic column. It was thus possible, using the fossil record and a defined stratigraphical framework, to develop ideas and models for the evolution and extinction of life on Earth (see below). John Phillips (1860) captured range data for the majority of known fossil taxa, compiled in his iconic curve of Phanerozoic life from numerical data gathered from the then-known fossil record, concluding that 'On the whole, it appears that there exist ample materials for testing any hypothesis of the sequence of life which includes the marine races' (op. cit., p. 207).

There has been, however, an explicit and enduring acceptance by palaeontologists that the fossil record is manifestly incomplete, but nonetheless adequate to describe and understand the broad patterns of the history of life on our planet. Charles Darwin considered the 'extreme imperfection' of the fossil record while Thomas Huxley referred to it as 'the skimmings of the pot of life'.

Nevertheless, the record, imperfect as it is, allowed 19th century scientists to develop the concepts of catastrophism and mass extinctions (George Cuvier), the trajectory of life and the Palaeozoic, Mesozoic and Cenozoic eras (Phillips 1860), and evolution itself (Darwin 1859). Subsequent landmark studies during the twentieth and twenty-first centuries have been summarised by Harper et al. (2020) who noted that the studies of Newell (1959), Raup (1972) and Valentine (1973) were incubators for much subsequent research in this space. The concept of time-dependent and time-independent biases (see Raup (1972, 1976a, b), and discussed further by Raup and Stanley (1971), together with observations by Sheehan (1977) and Foote and Miller (2007) paved the way for understanding the strengths and weaknesses of the fossil record in biodiversity studies, based primarily of taxonomic counts. Benton et al. (2000), however, focused on the correspondence of phylogenetic trees with the fossil record, demonstrating that the record was equally across Palaeozoic groups or Cenozoic biotas.

A number of authors have emphasised the close relationship between the fossil and rock records. Smith (2001) noted that, over the last 600Ma, diversity tracked sea level (linked to climate change and ocean ridge spreading); fossil preservation was usually low during regressions and high during transgressions. Peters and Foote (2002) noted the very obvious point that the appearance and disappearance of fossils are linked to the presence and absence of strata. Here, the geology of an area is actually controlling preserved biodiversity, framing the preservation bias hypothesis, but the signal is possibly still real. Peters' (2005) common cause hypothesis posited that during intervals of high sea level biodiversity is actually high and during regression it drops: transgressions provide not only increased habitable areas for marine biotas but also an increased volume of fossiliferous rock. It would not be surprising to discover that during warmer climates, associated with higher sea levels, diversities are high.

Ordovician palaeobiogeography is based on relatively few data points, from only several of the Ordovician continents. Clearly, there are substantial areas of Lower Palaeozoic rocks that remain partly or entirely unexplored; the eastern parts of Gondwana, large parts of palaeocontinents such as Gondwana (e.g., Africa) and Siberia have received little attention in comparison with the palaeocontinents that constitute present-day Europe or North America. In addition, nearshore

environments during some intervals, the probable origin of many clades, are often neglected and deep-water environments, particularly those associated with oceanic crust, are rarely preserved except in obducted slices of mountain belts (Bruton and Harper 1992). A large amount of data has been assembled from Konservat and Konzentrat-Lagerstätten. The preserved rock and fossil record is thus biased. In addition, very little is known about the early diversification of terrestrial ecosystems during the period (e.g., Servais et al. 2019).

Nevertheless, in the last few years there has been an escalation in the management and numerical treatment of big data, notably that in the Paleobiology Database (see following section). Kröger & Lintulaasko (2017), Franeck and Liow (2019), Kröger et al. (2019), Rasmussen et al. (2019) and Stigall et al. (2019) have published some formidable and sophisticated studies at various levels of granularity and resolution, exposing the originations, rates and sites of diversifications for the Phanerozoic (Alroy et al. 2008, Alroy 2010), but especially during the Ordovician. These analyses have relied heavily on the Paleobiology Database as a digital resource but either explicitly (Franeck and Liow 2019) or implicitly (Rasmussen et al. 2019) harvested data from the better-known continents, i.e., Baltica and Laurentia, serving as proxies for entire global diversity. Similar studies based primarily of Chinese data have been generated from the GBDB (e.g. Rong et al. 2007). These studies have encouraged a more global view of Ordovician life and its vicissitudes, one certainly valid for mass extinctions. The case for diversifications requires more nuanced, where many other factors are in play.

4. Bioregionalization under Ordovician global biodiversity curves

The construction of global curves for the Ordovician is the sum of the diversity patterns and trends of individual clades (Harper et al. 2020), but also those of discrete and overlapping biogeographic units. In a much-cited study, correlating vertical range data across most taxonomic groups with global cooling, Trotter et al. (2018) indicated, graphically, the near synchronicity of diversifications across the main mobile and sessile benthos during the Darriwilian, later than the nektonic and planktonic groups; these diversifications were causally linked with a globally cooling event based on a small conodont dataset, yielding temperatures measurements from oxygen isotope analyses. This influential paper has provided a widely-accepted hypothesis and driven much Ordovician research in the quest for a single explanation for the largest increase in marine biodiversity in the Phanerozoic. Nevertheless, doubts have been raised about the restrictive source of the data (mainly from English-speaking countries) and apparent synchronicity of the diversifications (Servais et al. 2010).

More detailed data are now available. The all-taxa curve, compiled from the PBDB (Fig. 2a), exhibits an initial peak during the early Cambrian, coincident with the initiation of Cambrian Explosion, falling before rising again to peak in the Dapingian, with a third more substantial peak in the Sandbian before falling at the end of the Ordovician and continuing on a downward trajectory during the Silurian. The initial peak tracks the rich lower Cambrian faunas in Siberia and South China, researched over many years, whereas the peaks in the Middle and Upper Ordovician mark stages in an extended Great Ordovician Biodiversification. Remarkable, however, is that the amplitude of the global curve is controlled by two continents; Laurentia accounts for c. 50% of the observed and standing biodiversity and Baltica for c. 25% of both measures. There is thus a strong regional signal inherent under the curve.

The geographic diversification patterns for all the main biotic groups have already been summarized in Webby et al. (2004a) and synthesised by Servais et al. (2010) highlighting their diachroneity of appearance, diversification and extinction through a continuum of change. Here we summarise that data and information contained in some more recent publications.

We track first regional changes in elements of the plankton (acritarchs and chitinozoans) that formed the basis for the Ordovician plankton revolution (Servais et al. 2008, 2016) and the benthos and nektobenthos/nekton (brachiopods, bivalves, conodonts and trilobites). Each taxonomic group has a distinctive signal (see also Harper et al. 2020) that expresses varying degrees of regionality.

4.1. Chitinozoans

The chitinozoans comprise an enigmatic group of organic-walled microfossils, traditionally considered as eggs of cryptic extinct marine metazoans, attributed to the zooplankton. However, more recently a protistan affinity has been suggested (Liang et al. 2020). So far, data for the group are not available in the Paleobiology Database, but several biodiversity curves have been published (e.g. Goldman et al. 2020, fig. 20.14).

The chitinozoans were one of the first fossil groups for which an Ordovician global biodiversity curve was dissected to illustrate and understand regional (palaeocontinental) signals. Paris et al. (2004 in Webby et al. 2004a), demonstrated that the global peaks of chitinozoan diversity during the Ordovician are the sum of the peaks of regional diversity. In the same book, Miller (2004) suggested that this example should be followed for all other fossil groups in order to search for the true 'global' biodiversity signal.

In a subsequent publication, Achab and Paris (2007, fig. 2) presented detailed diversity curves for Ordovician chitinozoans from Laurentia, Baltica and the 'northern' Gondwana (North Africa, southern and central Europe) regions, together with the global curve. The curves presented normalized diversity ('balanced total diversity', BTB, following Paris et al. 2004, i.e., the number of species per time-slice, *sensu* Webby et al. 2004b). From this analysis, it became clear that the two 'global' peaks of diversity, in time-slice 4c (late Darriwilian, late Middle Ordovician) and in time-slice VI (5c, early Katian, Late Ordovician), are aggregations of the peaks of diversity in the regional trends. The first 'global' peak highlights the highest diversities of chitinozoans of 'northern' Gondwana and Baltica, whereas the second 'global' peak is clearly the result of the high diversities observed on Laurentia. At a 'global' level, chitinozoan biodiversification, since the appearance of the group during the earliest Tremadocian, was clearly progressive from the Early Ordovician towards the Middle and Late Ordovician, with the global curve being the addition of the three separate regional trends. Significantly, Achab and Paris (2007, fig. 2) also indicated the available samples per time-slice. Not surprisingly, the correlation between the regional diversities and the studied sections is obvious. There was clearly not a 'single' diversification event for the chitinozoans.

Achab and Paris's (2007) investigation also illustrates that chitinozoan research remained mostly focused on three palaeogeographic areas, representing modern day North America, Europe, and North Africa. Data from other large palaeocontinents, such as Siberia, Kazakhstan, but also the Chinese palaeoplates (South China, North China, Tarim, etc.) were unavailable until the 2000s, and they should be included in the datasets in future. However, some of these data remain lacking because none or few chitinozoan studies have been attempted in many areas, including, for example, Australia, where only a few studies have been published, and the stratigraphical coverage is far from being complete.

Hints et al. (2010, fig. 4) presented an updated version of the diversity trends within the chitinozoans from Baltica, illustrating the strong increase of normalised diversity during the Kunda regional stage (lower Darriwilian, Middle Ordovician) and highest diversities on Baltica during the Viru Series, i.e. during the late Darriwilian and early Katian, around the Middle-Late Ordovician boundary, confirming the data from Achab and Paris (2007). The diversity curves produced by Hints et al. (2010) clearly showed a correlation between acritarch and chitinozoan data, confirming also a relationship with the total mean standing diversity of all fossil groups on Baltica in Hammer (2003). The extensively studied component from Baltica thus provides a clear diversity signal that can be observed in the different 'global' curves.

4.2. Acritarchs

Acritarchs are organic-walled microfossils of unknown biological affinity, considered to represent mostly the cysts of marine microphytoplankton (e.g. Molyneux et al. 1996). Similar to the chitinozoans, acritarchs have also been studied in detail only since the 1960s, i.e. much later than the classical fossil groups, such as trilobites, brachiopods or graptolites, that have been investigated for over two centuries. Both groups, acritarchs and chitinozoans, were used intensively during the exploration for fossil fuels, with most descriptions published between the 1960s and 1990s (Servais and Paris 2000). In common with chitinozoans, the acritarch dataset is not included in the Paleobiology Database.

A global acritarch biodiversity curve was first produced by Tappan and Loeblich (1973) who counted over 400 species described in the Ordovician. Subsequently, Downie (1984) published a compilation of acritarchs recorded in the British Isles, that was used by Strother (1996) to present an alternative review of Phanerozoic diversity.

Servais et al. (2004) revised the local and regional diversity trends of Ordovician acritarchs, reviewing data from Baltica, Laurentia, South China and North Africa ('northern Gondwana' of Paris et al. 2004). Servais et al. (2004) did not construct a curve in Webby et al. (2004a), because it was already evident, that a 'global' curve could not be truly global; the data were patchy, and global coverage for acritarch investigations covering the entire Ordovician was not possible. For Laurentia, for example, most studies were focused on the Upper Ordovician (with not a single publication available with Lower Ordovician data), and the information from North Africa was clearly related to the intervals investigated, thus leading to a bias in the diversity curves and trends. There were less than a handful of investigations of Australian biotas. Similarly, there was almost a lack of data available in western literature regarding the acritarchs from Siberia, as indicated in the global synthesis of Ordovician acritarch studies, based on about 700 publications, describing ca. 250 genera and over 2000 species (Servais, 1998).

Partly based on the acritarch catalogue constructed by Fensome et al. (1990), a team of experts revised the entire Palaeozoic acritarch record in detail as part of the 'PhytoPal' project (Mullins et al. 2006), covering all intervals, including the Ordovician. This compilation confirmed that the Ordovician stands out as the period with the highest diversities in acritarch taxa of the entire Phanerozoic.

A recent study providing a detailed revision of the palaeobiogeographic distribution of Cambrian and Ordovician acritarchs has been presented by Z Cai et al. (2021). The dataset used,

based essentially on the 'Phytopal' project, consists of over 1500 Cambrian and Ordovician acritarchs species belonging to nearly 300 genera and distributed among over 300 fossil Cambrian and Ordovician localities, at a global scale (Zacai et al. 2021, fig. 2, table S1). The data include all occurrence data published before 2007, and they were filtered and cleaned by removing or reassigning illegitimate, questionable, and synonymous taxa, and by converting local to global chronostratigraphic units. All geographic coordinates of fossil localities were plotted on palaeogeographic maps with the software GPlates (Müller et al. 2018) and the rotation file supplied by Scotese (2016) for each Cambrian series and Ordovician stage (Zacai et al., 2021, table S3). The interpolation map of acritarch genus diversity calculated per 5° latitudinal bands indicated a slight southward drift of peak diversity through the Cambrian and the colonization of intertropical latitudes during the Early Ordovician. Significantly, there is a subsequent duplication of the diversity peak starting in the Middle Ordovician, with clearly at least two 'diversity hotspots' at this time interval. Peak diversity clearly drifts northwards toward the equator during the Middle and Late Ordovician.

Figure 1 is a 'global' curve together with regional (palaeogeographic) trends of Ordovician acritarch biodiversity based on the same dataset (Zacai et al. 2021), designed in a similar way to those of Achab and Paris (2007) in order to compare a direct comparison between both groups. Besides global trends, the regional trends are those from the Gondwanan margin (peri-Gondwana, often referred to 'northern' Gondwana in chitinozoan studies), Baltica, Avalonia (including the detailed Ordovician acritarch investigations on the British Isles based on several PhD theses covering all the classic British series), Laurentia, and South China.

The chitinozoan curves presented by Achab and Paris (2007) are similar to those for the acritarchs; the regional scenarios are very different, and permit deconstruction of the global diversity curve. There are two opposing trends explicit in the South China and the Laurentian data. South China shows a clear peak in the Early Ordovician, whereas Laurentia documents high acritarch diversities only in the Late Ordovician. Peri-Gondwanan localities and Baltica have fluctuating diversities, with peaks in the Middle Ordovician (similar to the chitinozoans). Avalonia has high diversities in the Early and Late Ordovician, partly based on the extensive studies of the British Tremadoc-Arenig, and Caradoc series. The curves presented in Figure 1 are relevant to the investigation of the evolution of the Latitudinal Diversity Gradient (LDG) by Zacai et al. (2021, fig. 2): the two 'hotspots' of diversity that produce the duplication of the diversity peak starting in the Middle Ordovician are derived, respectively, from data from peri-Gondwana (in higher latitudes) and Baltica (in intermediate latitudes).

Similar to the chitinozoans, the 'global' Ordovician acritarch curve is thus an artefact and not truly global, the sum of the regional datasets that display different trends.

4.3. Brachiopods

The biogeographic differentiation of Ordovician brachiopods through the period is well documented through a substantial number of both qualitative and quantitative studies. During the latter part of the 20th century. Important contributions included those qualitative studies by Jaanusson (1973, 1979) and Spjeldnæs (1960) whereas Williams (1969, 1973) was in the vanguard of multivariate analysis of brachiopod data through time and space. Later studies (e.g., Neuman and Harper 1992; Harper 1992; Harper et al. 2013) hardened the narrative. Across the provinces different groups thrived developing a distinctive provincial stamp.

The disposition of the Ordovician continents, microcontinents and smaller terranes has been linked to fluctuation in diversity (Servais et al. 2009). The biogeography of the brachiopods has been tracked through the seven Ordovician stages (Harper et al. 2013); more recently the distribution of the Hirnantian brachiopod faunas has been analysed and illustrated in a global survey of these faunas associated with the waxing and waning of a major ice age and the first of the major Phanerozoic extinction events (Rong et al. 2020). That global distribution curve was constructed from range data in the Treatise and the authors' own databases.

An early attempt to compare the regionality of brachiopod diversifications relied on data from a few key published (Harper and MacNiocaill 2002). In the Estonian confacies belt peaks are seen in the Darriwilian and in the lower and upper Katian, whereas in the deeper water of the Livonian Tongue diversities increased from late Darriwilian through to the Katian. Major peaks are present during the Sandbian in Avalonia, Bohemia and western Gondwana.

Since then there have been a number of more regional studies. In a detailed study of the vertical distribution of brachiopod faunas in western Gondwana (principally the Iberian Terrane), Colmenar and Rasmussen (2018) established that during the first wave these high-latitude diversifications involved taxa dominant in the Cambrian Evolutionary fauna, the linguliformeans. The second wave, during the Darriwilian, saw the expansion of the orthidine and dalmanellidine brachiopods, while the third is characterised by the diversification of the plectambonitoids and strophomenoids and other groups such as the pentamerides. High degrees of endemism continued until the Katian when the faunas were more cosmopolitan. To account for the changing diversification patterns, vicariance was invoked to explain the first two waves and dispersal for the

last. Numbers are generally low with less than ten arising during the first wave, 15 during the second and just over 25 in the third. These numbers are not substantial and some increases may be ascribed to a rise in alpha diversity, as communities, across relatively few localities, become more tightly packed.

South China has been a particular focus for brachiopod research over the last five decades; a substantial number of Ordovician sections have been described and their faunas collected against accurate stratigraphic frameworks. Precise figures are available (Zhan in Harper et al. 2015) for the South China plate, indicating an early diversification of the brachiopod fauna during the Tremadocian and Floian (see also Zhan and Harper 2006).

Baltica is characterised by a complex history and rich, well-preserved and extensively documented brachiopod faunas occur across a range of carbonate and siliciclastic environments. The province also generated its own suite of endemic taxa, most notably the clitambonitidines and many groups of orthides such as *Lycophoria*. In a study of brachiopod diversity through the Ordovician successions of the Oslo Region, Harper (1986) combined field and museum collections to generate a biodiversity curve for the region. Major peaks were identified in the Darriwilian, coincident with varied carbonate and siliciclastic, mainly shallow-water facies of the Huk Formation and in the Katian when carbonates were widespread across the region. Detailed studies in western Russia (Rasmussen et al. 2005, Rasmussen et al. 2006) identified a major peak in the Darriwilian that has been tentatively associated with a realignment of oceanic currents driven by global cooling; the breakup and subsequent delivery of a asteroids into the Baltic basin may have affected biodiversities locally (Schmitz et al. 2008).

In a comprehensive and substantial, literature-based census of fossil data from the entire Baltic Province, Hammer (2003) identified four peaks for the brachiopods in increasing magnitude during the Tremadocian, Dapingian, late Darriwilian and the late Katian. The latter two reaching counts of some 120 and nearly 140 species, respectively, based on the 95% percentiles from a 1000 computed replicates (see Hammer 2003 for methodology). More regional studies (e.g. Hints and Harper 2003) were focused on key parts of the Baltoscandian Basin, such as the condensed successions of the East Baltic.

Laurentian data (Candela 2015; Trubovitz and Stigall 2016) indicate a major diversification broadly contemporaneous with the Darriwilian pulse in Baltica, in comparable facies. Data from the Laurentian margin at Girvan, SW Scotland (Harper and Stewart 2008; Candela and Harper 2014) exhibit major spikes during the Sandbian at the end of the Katian, the latter coincident with diverse

fauna of the Lady Burn Starfish Beds (Harper 1982). The data suggest a series of more regional signals combining into the global curve for the phylum (Harper et al. 2004).

4.4. Bivalves

Brachiopods and bivalves are commonly portrayed as competitors, with the former dominant during the Palaeozoic and the latter in the ascendancy during the Mesozoic and Cenozoic, following the end Permian extinction events. Diversity profiles for the bivalves indicate a later peak in the Late Ordovician, in contrast to the Middle Ordovician peaks amongst the brachiopods (Harper et al. 2020). A number of studies (e.g. Cope and Babin 1999; Cope 2002, 2004) have investigated the origins and changing spatial distributions of the group through the Ordovician in detail. During the Tremadocian bivalves are most common associated with high-latitude Gondwana terranes, although the highest diversity faunas were located in the Amadeus Basin in north Central Australia. By the Floian, Avalonia, although close to the Gondwanan margin, hosted diverse bivalve faunas indicating the controls of a climatic gradient controlling bivalve distributions. A clear preference for siliciclastic substrates is apparent. During the Middle Ordovician the class migrated to Baltica and the Laurentian margins, widespread on all continental shelves by the early late Ordovician. Abundant bivalve faunas have been described from the Lower and Middle Ordovician Argentina, when that basin was relatively near to Laurentia. In summary, the first major diversification of the bivalves was restricted to the Gondwanan margins that remained the focus for diversification in the group until the Sandbian when the largest expansion occurred in the low-latitude platform regions of Baltica and Laurentia (Cope 2004).

4.5. Conodonts

Conodonts, the dental apparatuses of eel-like animals, are routinely extracted from carbonates and less commonly from siliciclastic rocks. Thus, conodonts are more likely to be reported from carbonate facies than siliciclastic facies. The group has a near-complete record from the late Cambrian to the end of Triassic.

There are a few studies of conodont diversity through the Palaeozoic and early Mesozoic and those available are dated (e.g. Clark 1987; Sweet 1988). In a recent study, however, Ginot and Goudemand (2020) have tracked conodont biodiversity through time (using data from the Paleobiology database) and identified a major peak of diversity during the Middle Ordovician associated with high sea-surface temperatures. Moreover, the increase in the available shelf area together with the

abundance and diversity of the plankton and the expansion of the group into the open sea, escalated conodont diversity. The palaeobiogeographic evolution of the group indicates the majority of occurrences at low and moderately low latitudes during the Early to Late Ordovician with relatively few faunas at high latitudes. This may of course partly reflect lack of knowledge, sampling and extraction of high latitude terranes.

4.6. Trilobites

Global biodiversity curves for the trilobites demonstrate the dominance of the group throughout much of the Cambrian. Three evolutionary faunas first recognised in Laurentian assemblages (Adrain et al. 1998) include first the Ibex Fauna I, successful during the Tremadocian then rapidly declining; Ibex II radiated during the Arenig then declined rapidly. Within the Ordovician the transition between the Ibex and Whiterock faunas is critical, the Whiterock faunas were the more resilient. The Whiterock fauna radiated during the Middle Ordovician biodiversification and was successful throughout the Ordovician surviving the end Ordovician mass extinction with the exception of the Whiterock clades that diversified at high latitudes which were the least resistant to extinction.

Adrain et al. (2004) broke the curve down to primarily consider diversity patterns across a number of regions while also addressing the development of onshore – offshore trilobite associations and the associated morphological adaptations. Trilobite biodiversity through the Ordovician was analysed with respect to four biogeographic realms (Bathyrud, Reedocalymenine, Megistaspidine and Dalmanitoidean) and their diversity trajectories examined (Adrain et al. 2004). Each is characterised by distinctive elements, the most unique, the Dalmanitoidean Realm populated by cyclopygids, ogygiocarinine as aphids, trinucleids, reedocalymenine calymenids and the early dalmanitids. There is evidence of an Ordovician radiation of trilobites everywhere except the tropical Reedocalymenine Realm which occurred much later. Adrain et al. (2004) demonstrated a strong geographic component to the diversification, high-latitude Gondwana trilobites started to radiate in the early Arenig, but the majority did not survive until the end Ordovician; taxa associated with tropical Laurentia and Siberia radiated during the late Arenig / early Llanvirn and almost all survived the extinction. Regional curves for Australia, South America, Avalonia, Baltica and South China reveal different patterns.

More recent regional studies on trilobite biodiversity display similar cross-province differences. In Avalonia, the major spike occurred during the late Katian, associated with a wide range of palaeoenvironments (McCormick and Owen 2001) and in South China (Yangtze Platform) a first peak

occurs in the early Darriwillian with higher peaks in the early and middle Katian (Song et al. 2021). The peak of trilobite diversity during the Ordovician varies from region to region as a blend of more endemic taxa radiate and the biotas absorb invasive widespread and cosmopolitan elements.

As for the previous groups, it appears evident that there was not a 'single' biodiversification 'event' at a global level for the trilobites.

5. Deconstruction global curves

Global curves are aggregations of regional curves whether geographic or phylogenetic (see Harper et al. 2020). The curves can be deconstructed in different ways for example according to contributions of individual taxonomic groups (Harper et al. 2020) or the contribution of regional biotas. The latter approach is taken here. If the biodiversity spike is in fact truly globally synchronous, not diachronous across environments, geographies and phylogenies, implicit in this scenario is that an apparent global spike should be associated causally with a global event.

Integral in the pursuit for a model for Ordovician biodiversification is the understanding of the significance of gaps and provincialism. Miller (1997, 2004) noted that episodes need not to occur uniformly across the world, highlighting the fact that different mechanisms may be acting at variable environmental and geographic scales.

Global species richness curves are thus strongly dependent on local and regional conditions, for example ambient climate and environmental controls. There are also ecological controls (Droser and Sheehan 1997). Sepkoski (1988) interrogated the concepts of alpha, beta and gamma diversity and their relevance to global biodiversity curves through time. In posing the question 'Where does all the diversity go?' Sepkoski opened a key conversation around the construction and composition of global biodiversity curves. Alpha (within-community) diversity probably contributed insufficiently (see Bambach 1977) to the global curve, the most important element being beta (between-community) diversity. But together alpha and beta counts do not approach the total diversity of the evolving Phanerozoic ecosystem (see also Harper 2010 for a focus on the Ordovician brachiopods). Ecological factors such as the origin and expansion of organic reefs, hardground communities, bryozoan thickets, and crinoid gardens during the Ordovician (Sepkoski 1988) must be invoked. Such ecosystem change is generally related to increased temperate that may itself enable biodiversity (Mayhew et al. 2012) and promote the development of carbonate platforms, mounds and reefs that provide a multiplicity of niches and opportunities for organisms (Kiessling et al. 2003).

In an elegant analysis of global diversity curves, Holland (2010) reiterated that alpha biodiversity contributes only a minute fraction to gamma or global diversity. The major contribution to the global curve must be sought in increases in beta diversity, where geographic distance between communities (with limited dispersal opportunities), the heterogeneity of their environments and niche differentiation within them are key enablers. Thus, environmental patterns and geographic isolation are significant factors. In a series of papers, Valentine (e.g. 1973; Valentine and Moores 1972) focussed on the relationship between the dispersal and proximity of the continents with gamma diversity, a theme pursued by a number of subsequent authors (e.g. Servais et al. 2009) to explain the Ordovician radiation. While Miller targeted more regional factors associated with orogenic activity (Miller and Mao 1995) and substrate preferences (Miller and Connolly 2001).

Implicit in these narratives is that biodiversity change is driven by local speciation events, based around the Darwinian paradigm of migrate, isolate and speciate. In addition, since the longevity of species may have increased during the Ordovician (Miller 1997) there will also be a cumulative effect as species remain on the diversity curve for longer.

To test our hypothesis further, data are downloaded from the PBDB using Fossilworks for the global tally of taxon counts, deconstructed into a series of regions for the brachiopods, bivalves, conodonts and trilobites, relatively abundant groups with a good stratigraphic record and a contract of life styles.

Several rounds of data analysis were performed using Paleobiology Database data via Fossilworks (<http://fossilworks.org/>). In particular, raw parameters were obtained from the diversity curve data analytical tool. The data were downloaded on 2 April 2021. Raw data included diversity information of Cambrian-Silurian marine animals at the genus-level only. Generic data were used because although species diversity is recorded, genus-level allows specifically indeterminate occurrences to be included and ensures comparability with already established patterns (Alroy et al. 2008). Likewise, multiple occurrences of the same genus in a single collection were treated as a single occurrence. Re-identifications of individual appearances and synonymies were employed and subgenera were treated as separate genera. Generically indeterminate occurrences were excluded. Abundance data were based on all collections. The rest of the default parameters were maintained.

Only the fields required for analyses were downloaded, i.e., the class, order and genus name and the abundance value. Raw data were prepared following a stepwise strategy including palaeogeographic units, namely, Laurentia, Baltica, South China, Eastern Avalonia and Siberia. Furthermore, the data analysis also includes largest biodiversity groups of involved time interval such as brachiopods, trilobites, conodonts and bivalves, which ensures a comprehensive representation of

major diversity changes. In each case, total marine diversity was also included for comparison. Moreover, after testing different options concerning time units, we used the Fossil Record 2 time intervals for plotting diversity. This is a unique available option to ensure a full representation of Cambrian-Silurian diversity from the Fossilworks analytical tools.

Following Alroy (2010), two descriptive diversity count approaches were used. Firstly, we traced the range-through diversity. This parameter (RT diversity) shows every taxon ranging into a given time unit so it reflects total diversity changes. RT diversity responds to the equation $N_{r+} + N_{r-} + N_b + N_t + N_1$. Where, N_{r+} represents the taxa ranging across the time interval and sampled within it, N_{r-} the taxa ranging across the time interval but not sampled, N_b and N_t , the bottom-only and top-only boundary crossers, respectively and N_1 the taxa sampled into the interval but not after or before (the so-called one timers). Secondly, we plotted the boundary-crossers (BC) diversity, which responds to the equation $N_{r+} + N_{r-} + N_b$ and shows the diversity changes at the base of each time interval. Interestingly, the boundary-crossing diversity is a direct measure of standing diversity at interval boundaries and it shows better the diversity changes by comparing diversity at the start of different time units (Bambach et al. 2004).

Brachiopods (Fig. 2b), for example, display an initial climb in diversity during the Tremadocian and Floian, following the Furongian Gap (Harper et al. 2009) supported by data from South China (see above). The Dapingian and Darriwilian spike is generated by data from Baltica, Laurentia and South China but Siberia remains largely dormant until the Sandbian when there is an increase across all the regions, most notably Baltica and Laurentia. Interestingly if the data from Baltica and North America are removed the total curve will all but collapse. Conversely data from many areas of the world, e.g. Siberia, are not yet complete and some, e.g. Africa, require a new and more expanded focus.

Interrogation of the PBDB data for bivalves (Fig. 2c) indicates some clear trends. Those regions that have a sufficiency of data illustrate that the Late Ordovician diversifications on Laurentia account for a substantial part of the global diversity signal. Diversity on Siberia remains low, while on Avalonia the peak is coincident with the early Katian and that for Laurentia, late Katian. The patterns are different to those of the other key member of the benthos, notably the brachiopods.

Conodont data (Fig. 2d) from the PBDB illustrate a more complex picture, with the total being an aggregate of data from Baltica, Laurentia, Siberia and South China, presumably dominated by carbonate facies with increasing diversities during the Middle and Late Ordovician.

Trilobite data (Fig. 2e) plotted from the PBDB display the very clear late Cambrian spike based on contributions from Laurentia and South China to a lesser extent Baltica. Within the

Ordovician trilobites appear numerically less diverse and the curve is dominated by data from Laurentia. Peaks however are dominated by data from Laurentia particularly in the Katian and from South China in the Sandbian, reflecting a dominance of carbonate environments but also the strong focus on research on these intervals in these key areas.

6. Ordovician biodiversifications and changing geography

The Ordovician Period is characterized by vigorous magmatic and volcanic activity together with rapid plate movements. Regional diversity patterns changed during the period; plate movements had a significant influence on these patterns. Within a Phanerozoic context the high sea levels, high temperatures and plate tectonic activity are matched only by those in the Cretaceous (Crame and Owen 2002).

Regional diversifications have already been demonstrated at mid to high latitudes during the Middle Ordovician associated with the proliferation of island arcs and microcontinents (Harper et al. 2008, 2009). These diversifications are commonly associated with elements of the Celtic province. High sea levels (Haq and Schutter 2008) and the widespread occurrence of large carbonate platforms, associated with global warming characterised the later parts of the period (prior to the Hirnantian), contributing to the thalassocratic world (Jaanusson 1979) that characterised much of the Middle and Late Ordovician. With the movement of the major continents into and around the tropics, marine life expanded. During the period Avalonia, Baltica and Siberia moved from high to low latitudes, Laurentia rotated anticlockwise and South China moved to equatorial latitudes (Fig. 3; Nardin et al. 2010). The northward movement and anticlockwise rotation of Baltica is well established; Avalonia rifted off Gondwana and moved northward during much of the period while Laurentia straddled the equator, rotating anticlockwise. It would be naive not expect these continental movements across the latitudes not have affected the diversity patterns amongst their biotas, particularly when continents arrive in tropical latitudes. The widespread development of warm-water carbonate facies across these continents is aligned with a massive increase in biodiversity during the Katian (see also Mannion 2020). Nevertheless, here is much to be learnt about the latitudinal diversity gradients.

This of course does not rule out other enabling factors such as changes in oceanic circulation patterns, the increasing oxygenation of the World's oceans and the delivery of nutrients into marine

environments during transgressions but unlike catastrophic extinction events where devastation is truly global, biodiversifications are apparently assembled from more regional datasets.

7. Conclusions

Ordovician biotic radiations initially identified in detail by Sepkoski (1995) are complex. Most research has focused on taxon counts using increasingly sophisticated methods to develop a global curve from global databases. Under the curve, there are many enablers (Harper 2006; Harper et al. 2015) including ecologic controls involving the mutual relationships between organisms and between their ambient environment (Droser and Sheehan 1997), their respective phylogenetic histories (Harper et al. 2020) and the distribution of biodiversity across the continents and latitudes (this paper).

A few conclusions can be drawn:

1. Putative global diversity spikes have encouraged the search for global causal factors.
2. Deconstructing the global curve reveals much information on Ordovician biodiversifications across palaeogeographies and phylogenies otherwise hidden beneath the global curve.
3. Gaps in the fossil record that also exercise a control of the shape of a global curve at exposed at a regional level.
4. Contrasting regional curves indicates that firstly the amplitude of the taxon occurrences across different geographies influences the amplitudes of the global curve. For example, the dominance of brachiopods and data from Baltica and Laurentia are sufficiently significant and substantial to dictate the global curve.
5. The major spike in total Ordovician marine biodiversity, in the Late Ordovician is associated with the convergence of principally Baltica and Laurentia in the tropics.
6. The curves highlight the influence of data from Baltica and Laurentia whether real or an artefact of more extensive study and database entry.
7. More focused research on less well-known regions of the world and the better integration of the many 'long-tailed' databases may indicate that biodiversifications occurred throughout the Ordovician, presenting a more continuous and gradual model for global diversification.

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Figures

Figure 1. Acritarch genus-level biodiversity curves, with global data, and palaeocontinental data from South China, Laurentia, Avalonia, Baltica and peri-Gondwana. SIB: sampled in bin taxa; RT: range through taxa; BT: boundary crosser taxa.

Figure 2. Diversity curves derived from data in the Paleobiology Database using Fossilworks (see text for explanation). (a) Total diversity, (b) brachiopod, (c) bivalve, (d) conodont and (e) trilobite diversities through the Early Palaeozoic.

Figure 3. Changing Ordovician palaeogeography demonstrating the equatorial movement of the key continents of Avalonia and Baltica during the period, the equatorial position of South China and the path of Siberia (modified from Nardin et al. 2010).











