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Invited Research Article

No (Cambrian) explosion and no (Ordovician) event: A single long-term radiation in the early Palaeozoic

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ABSTRACT

The Cambrian 'Explosion', located by many authors between 540 and 520 million years ago (Ma), is considered to be an abrupt appearance in the fossil record of most animal phyla, with a sudden increase of complex morphologies across metazoan groups. In a few recent papers, the Great Ordovician Biodiversification 'Event' (GOBE) has similarly been restricted to a single dramatic biodiversification 'event' in the Darriwilian Stage of the Middle Ordovician Series, between 470 and 455 Ma, although historically the biodiversification is considered as an aggregation of radiation 'events' capturing a large and complex increase of taxonomic diversity of marine invertebrates covering the entire Ordovician. A review of biodiversity curves of marine organisms during the early Palaeozoic, including some based on data in the Paleobiology Database (PBDB) and the Geobiodiversity Database (GBDB), points towards a single, large-scale, long-term early Palaeozoic radiation of life that already started in the late Precambrian. An abrupt 'explosion' of diversity in the Cambrian or a significant 'event' in the Ordovician are not visible in our biodiversity studies, because they are either regional, or only reflect a single group of organisms. It is evident that the datasets remain incomplete, in particular those for many geographical areas and for several fossil groups, that are not covered by the PBDB and GBDB; also, such areas remain so far poorly or entirely unstudied. Some recently published biodiversity curves have to be considered with care, as the truly global diversity estimates of marine organisms during the early Palaeozoic remain elusive. Here, we argue that published curves of taxonomic richness, which show distinct periods of diversification, cannot sufficiently be disentangled from biases. We therefore question the existence of a distinct Cambrian 'Explosion' and global Ordovician 'Event' in the global datasets. Both terms, Cambrian 'Explosion' and Great Ordovician Biodiversification 'Event should be used as conceptional terms only. The first represents the appearance of almost all animal phyla during the late Precambrian and early Cambrian, whereas the second term embraces the numerous and complex radiations that occurred during the entire Ordovician.

1. Introduction

The early Palaeozoic was a pivotal time for the evolution of marine life and its ecosystems, including major radiations and at least one mass extinction. The Cambrian 'Explosion' and the Great Ordovician Biodiversification 'Event' (GOBE) refer to two different intervals considered to represent two major, discrete biodiversification events during the early Palaeozoic. The Cambrian 'Explosion' is principally known by the wider public through Stephen Jay Gould's popular book *Wonderful Life* (Gould, 1989). This 'explosion' is considered to be a short 'event' when almost simultaneously, nearly all modern animal phyla appeared during a very short time interval during the early Cambrian. The Ordovician radiation has recently been considered by several authors as a similarly rapid 'event' occurring some 40 to 50 myr after the Cambrian

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‘Explosion’ during the Middle Ordovician.

A question arises, are these ‘events’ separate biodiversity pulses that are visible in all or only some biodiversity curves? For several fossil groups, this is the case, as the analyses of different databases show. Nardin and Lefebvre (2010), for example, identified both radiations in the early Palaeozoic diversification of blastozoan echinoderms. Similarly, the brachiopods and the sponges also show distinct Cambrian and Ordovician biodiversification signals in their fossil record. On the other hand, many other groups demonstrate different scenarios, with the two distinct Cambrian and Ordovician radiations largely invisible (Harper et al., 2020).

Global datasets, in particular those based on the Paleobiology Database (PBDB), illustrate more or less clearly both the Cambrian ‘Explosion’ and the Ordovician radiation, but the lack of data available from the interval between these two periods, e.g., from the late Cambrian, in particular the absence of data in the PBDB from the Furongian Series, leads to a marked drop in biodiversity. Such a ‘Furongian Biodiversity Gap’ separating the two ‘events’ has recently been documented by Harper et al. (2019). Those authors noted that few palaeontologists have focused on the late Cambrian interval compared with those below and above. This perfectly illustrates the challenges regarding the varying adequacy of the number of investigations and the quality of the fossil record through time (e.g., Newell, 1959; Benton et al., 2000).

Several authors have considered that the Ordovician radiation has its roots in the Cambrian. Droser and Finnegan (2003), for example, noted that the Cambrian Explosion is clearly more globally mediated, while Ordovician studies were often of a local and regional nature, revealing sharp transitions in timing and magnitudes that vary geographically, suggesting a complex history. Droser and Finnegan (2003) perceptively noted that future studies may possibly resolve the issue of whether the Ordovician radiation was an independent event or if it was the inevitable follow-up to the Cambrian radiation.

In this study, we compare the taxonomic richness estimates based on different datasets published recently, including our own analyses, in order to understand if it is possible to recognize different short-lived ‘events’ or, on the contrary, if a single long-term radiation characterized the early Palaeozoic. For this purpose, we compare some global biodiversity curves recently produced on the basis of datasets from the Paleobiology Database (PBDB) and the Geobiodiversity Database (GBDB), respectively. We also compare the diversity curves of different fossil groups. In addition, it is important to understand if the signals in these biodiversity curves are truly global or rather limited within a specific geographical (i.e., palaeocontinental) context.

2. The early Palaeozoic radiation

2.1. An increasing number of terminologies

The first radiation of marine life during the Palaeozoic had already been recognized in the mid-1800s. Darwin (1859) had observed that the fossil record was incomplete (Chapter 9 ‘On the Imperfection of the Geological Record’ in his landmark book *On The Origin of Species*), but the sudden appearance of fossils in the Cambrian became a key and persistent dilemma for Darwin who did consider that a long evolutionary trajectory must have preceded the first occurrence of organisms visible in the fossil record (see also Conway-Morris, 2003). It was Phillips, 1860, fig. 4) who published the first iconic diversity curve of biodiversity through geological time based on actual fossil range data. He illustrated a Phanerozoic diversity curve, indicating three major radiations of marine organisms (Palaeozoic, Mesozoic, and Cenozoic life), with a gradual increase in numbers of species from the Cambrian to Permian, including a slight decrease during the Devonian, constituting the Palaeozoic radiation.

The two major radiations (Palaeozoic and Mesozoic-Cenozoic) have subsequently been visible in almost all biodiversity curves produced during the last 150 years (e.g., Erwin et al., 1987). Both radiations are usually related to the fragmentation of supercontinents into microcontinents: the Palaeozoic radiation is related to the break-up of the supercontinent Pannotia and the Mesozoic-Cenozoic radiation to that of Pangaea (e.g., Valentine and Moores, 1972; Valentine, 1973).

Besides the Cambrian ‘Explosion’ and the Great Ordovician Biodiversification ‘Event’, a number of further terminologies have been introduced to describe various aspects of the early Palaeozoic radiation (Fig. 1). Bottjer et al. (2000) introduced the term ‘Cambrian Substrate Revolution’ to refer to the evolutionary and ecological effects of substrate changes on benthic metazoans that took place during the Cambrian: the seafloor sediments that had well-developed microbial mats, which sporadically appeared during the Neoproterozoic, were replaced by seafloors with burrowing and grazing organisms and an increased vertically oriented component of bioturbation (see also Buatois et al., 2020).

In a similar way, Wilson and Palmer (2006) coined the term ‘Ordovician Bioerosion Revolution’ to describe the significant diversification of macroboring ichnotaxa during the Middle and Late Ordovician, during a time when the intensity of carbonate substrate bioerosion greatly increased. Wilson and Palmer (2006) related this burst of ichnological diversity directly to the Ordovician ‘Radiation.’

Subsequently, Servais et al. (2008) recognized a revolution in the plankton with important diversifications of different groups observed in the late Cambrian–Early Ordovician interval, including members of both the phytoplankton and zooplankton. The ‘Ordovician Plankton Revolution’ also includes the switch to a planktonic mode of life for several fossil groups (e.g., arthropods and molluscs) that were part of the Cambrian benthos, but also the origin of planktotrophy that occurred in invertebrate larvae within the Cambrian-Ordovician boundary interval. Saltzman et al. (2011) argued that this ‘Ordovician Plankton Revolution’ was possibly triggered by a pulse of atmospheric oxygen during the late Cambrian. Servais et al. (2016) pointed out that new investigations indicated that this ‘plankton revolution’ had already commenced in the late Cambrian, before the first appearance of classic planktonic groups in the fossil record, such as the graptolites. The plankton revolution was clearly a part of the Ordovician radiation, and thus, of the Great Ordovician Biodiversification Event (sensu Webby, 2004). After the initial phase of plankton radiation commencing in the late Cambrian and Early Ordovician, the Ordovician biodiversifications also included a phase of changes in level bottom communities (with strong diversity increases during the Middle Ordovician), and of metazoan reef communities (massively diversifying during the Late Ordovician), making the Ordovician biodiversifications a complex sum of radiations, that does not seem to correspond to a single geological event (see Servais et al., 2021).

Although outside the scope of the early Palaeozoic, an additional concept was introduced by Klug et al. (2010) for the Devonian. These authors coined the term ‘Devonian Nekton Revolution’, illustrating the dramatic increase of nektonic organisms in the Devonian, following the switch to planktonic organisms in the Ordovician. Whalen and Briggs (2018), however, considered that the nekton and eunekton were well established prior to the Devonian and did not diversify dramatically during any particular Palaeozoic interval. The major issue of the reality and the possible onset of the ‘Devonian Nekton Revolution’ lies in the definition and concept of the nekton. Klug et al. (2010) and Whalen and Briggs (2018) place different groups in the different ecological categories. Indeed, very often it is not evident which groups are nektonic, eunektonic, or nektobenthic, and when exactly these life-modes occurred during the life-cycle of the organism (see discussion in Servais et al., 2016). Similar to planktonic groups, including some organisms being holoplanktic (i.e., organisms for which the entire life-cycle is planktonic) and other organisms that have benthic–planktonic life-cycles (with a part of their life in the benthos, and another part in the plankton), some benthic, nektonic, and nektobenthic organisms have complex life-cycles, and it is not easy to assign all taxa of a specific fossil group to a single life-mode. The diversification of the cephalopods can

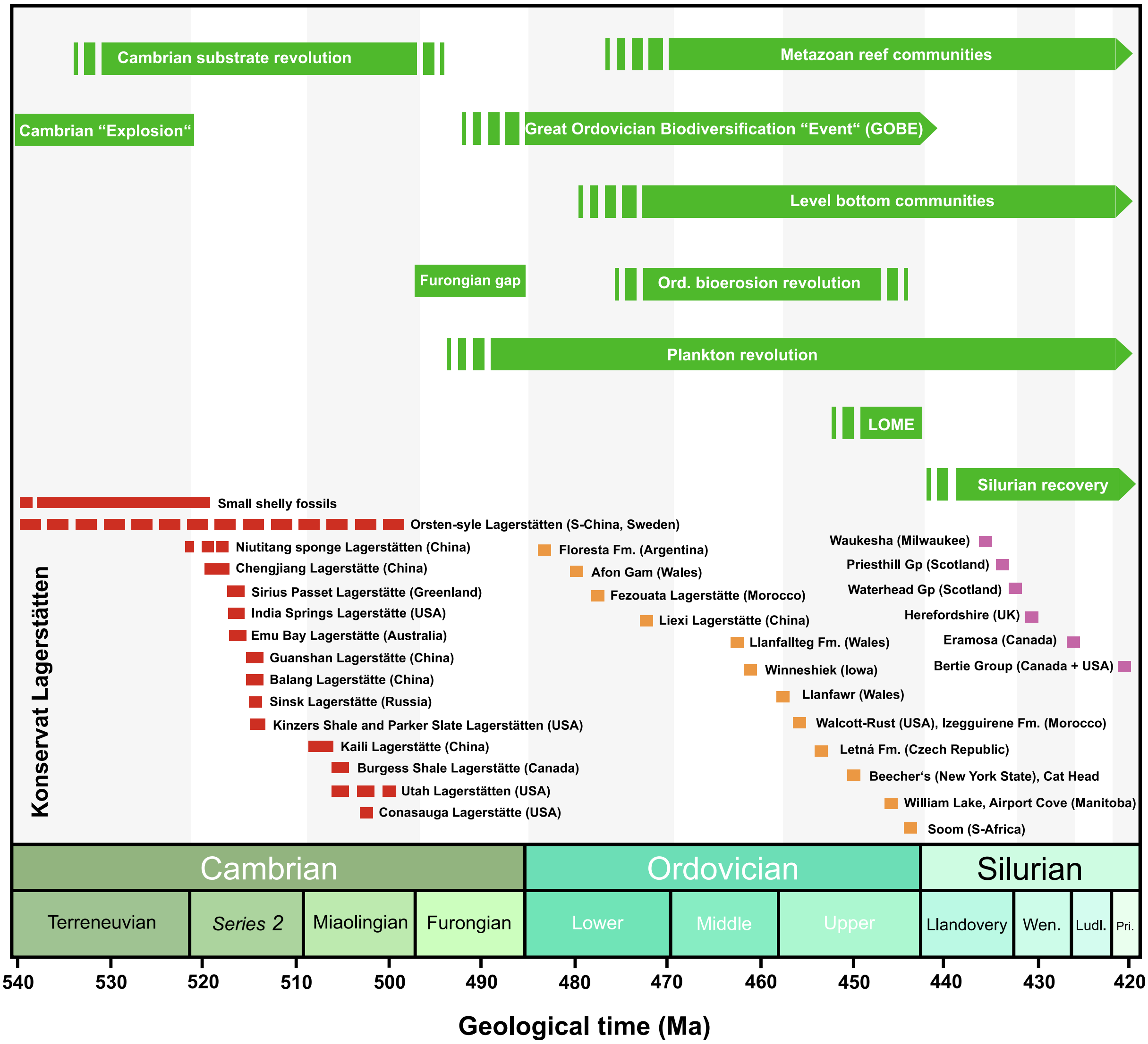

Fig. 1. Overview of the major terminologies used in studies of early Palaeozoic (Cambrian, Ordovician, Silurian) biodiversity, including the Cambrian 'Explosion' and the Great Ordovician Biodiversification 'Event,' and stratigraphical position of some of the most significant *Konservat-Lagerstätten*.

be cited as an example. Although usually considered as free-swimming organisms (thus nektonic), the earliest cephalopods occupied different habitats (from neritic to epipelagic) and adopted different life-modes (benthic, nektobenthic and nektonic) from the late Cambrian onwards; some were truly nektonic, whereas others were only nektonic during a part of their life-cycle (e.g., Kröger et al., 2009; Servais et al., 2016).

Deng et al. (2021, fig. 9) also illustrated the varying richness of benthos, plankton and nekton. Although this study recognized neither the 'plankton revolution' nor the 'nekton revolution' (as it is not clear what groups are actually included in these entities), it becomes obvious that the open waters were progressively occupied from the middle Cambrian onwards to the Late Ordovician by planktonic-nektonic organisms (see also Shan et al., 2022). It is thus important to remember that the evolution of early Palaeozoic ecosystems is not just a question of diversity measures, but fundamentally of palaeoecological significance.

As noted by Whalen and Briggs (2018), the metazoan colonization of the water column was considerably more complex and gradual than previously understood. Was it then a succession of dramatic 'explosions,' 'events' or 'revolutions' that occurred, or was the Palaeozoic radiation related to a gradual, step-wise much less spectacular increase in complexity of life in the oceans, initiated near the shoreline and only later filling the entire water column over several tens of million of years?

2.2. *Cambrian 'Explosion'*

The Cambrian Explosion is one of the most iconic research topics in paleontology. Beasecker et al. (2020) tried to find the bibliographic pedigree of the phrase 'Cambrian Explosion' and indicated that its origin has not been clearly established, and that the term has been promoted since the 1960s without an explicit provenance.

The explanation of the sudden burst of diversity of animal life in the fossil record was already a major dilemma for Charles Darwin (1859). Even over 160 years later, and after a multitude of publications, the 'explosion' of life is still one of the most popular research topics, including an extraordinary number of articles in high impact research journals (e.g., Erwin et al., 2011; Smith and Harper, 2013; Briggs, 2015; Mangano and Buatois, 2016; Na and Kiessling, 2015; Fu et al., 2019, just to name but a few). It is obvious today that articles including the words 'Cambrian Explosion' are regularly published in the journals that have a large media attention, also because the terminology 'explosion' attracts readers in search of eye-catching headlines. Probably also partly for this reason, the idea of an abrupt appearance of life has been popular in the media, attracting many readers and followers, similar to the Biblical idea by implying that life on Earth appeared virtually overnight. Occasionally the exact moment of the 'explosion' is even located by some authors precisely at the base of the Cambrian System, about 541 Ma years ago, a gross over-simplification that even appears in articles of high impact research journals (e.g., Fox, 2016). This assumption of a sudden appearance of life, although largely propagated among the wider public, is not generally accepted among most scientists, who consider that the 'explosion' lasted several tens of millions of years (e.g., Erwin and Valentine, 2013; Shu et al., 2014) and was thus not by any means 'explosive.' It is now clear that the Ediacaran biotas of the latest Precambrian were already highly diverse; some authors indicated that the roots of the Cambrian 'Explosion' lie in the Precambrian, and considered that there is possibly no true separation between Ediacaran and Cambrian skeletal biotas (e.g., Zhu et al., 2017). On the other hand, some authors clearly separate both radiations (e.g., Darroch et al., 2018).

Nevertheless, the Cambrian 'Explosion' is today considered to be a relatively abrupt appearance, at least in the context of a geological time frame, of most animal phyla in the fossil record. The arrival of new phyla took place during the latest Precambrian and some parts of the Cambrian, with a sudden increase of complexity of morphologies of diverse metazoan groups (Briggs, 2015). Many publications agree with a time span of about 20 or 30 million years for the duration of the 'explosion' (between 540 and 520 Ma), but the exact timing remains debated. For some authors the 'explosion' had already largely concluded before the typical Cambrian fossil record begins (at around 521 Ma) and that it was followed by a broad-scale evolutionary stasis (e.g., Paterson et al., 2019).

For many other authors the reality of the Cambrian 'Explosion' is massively enhanced by a number of key *Lagerstätten*, and thus is a topic of extreme taxonomic, but also taphonomic interest (e.g., Butterfield, 2003; Briggs, 2015). The famous Cambrian *Lagerstätten*, mostly within the Cambrian Series 2 (Chengjiang, Sirius Passett, Emu Bay, Qingjiang, etc.) and Series 3 (Burgess Shale, Wheeler Formation, etc.) are represented in relatively few formations, with restricted areas of outcrop and thickness, but they resulted in an extraordinary high number of described taxa (e.g., Briggs et al., 1994; Hou et al., 2004, 2017). The well-known 'weird wonders' are only a small part of the many new taxa, and include such iconic forms as *Anomalocaris*, *Halkieria*, and *Hallucigenia*.

The exceptional biotas, including those of Burgess Shale type (BST), are known from a number of palaeocontinents; they are also temporally widespread, covering almost the entire Cambrian (Fig. 1). For many authors, and also for a large part of the wider public, the 'Cambrian Explosion' is related to these famous *Lagerstätten* and their 'weird wonders' present not only in the lower Cambrian, but also in the middle and upper parts of the Cambrian System. More recently, the typical fossils of the Cambrian 'Explosion', including new taxa, are now known in the Lower Ordovician, for example in the Fezouata *Lagerstätte* of southern Morocco (Van Roy et al., 2010; Lefebvre et al., 2018) and in the Middle Ordovician of Central Wales (Hearing et al., 2016), which would suggest that the 'explosion' continues above the Cambrian. Exceptional preservation of diverse fossil groups is now more and more typical of a number of Ordovician *Lagerstätten* (Fig. 1).

The main problem of identifying and fixing in deep time the Cambrian 'Explosion' or 'radiation' is clearly the question of the definition of the term. Whereas for some authors the Cambrian 'Explosion' is limited to the appearance of higher taxonomic ranks, i.e., phyla, and the appearance of different types of body plans (*Baupläne*), for others the radiation is visible by the number of genera and species described. Can the Cambrian 'explosion' be recognized in biodiversity curves? Na and Kiessling (2015) measured the global genus-level diversity of marine animals from the Ediacaran to the earliest Ordovician based on the datasets from the Paleobiology Database (PBDB). These authors clearly observed a peak of genus-level diversity during Cambrian Stage 3. On the other hand, based on a different set of data from the Siberian Platform, Zhuravlev and Wood (2018) noted two phases of the Cambrian 'Explosion,' with a first 'phase' starting in the Ediacaran and continuing during the Terreneuvian, that was interrupted by an extinction during the Cambrian Stage 4, and a second 'phase' much later during the Cambrian Series 3 and 4 and extending into the Ordovician radiation. The precise location of the 'explosion' thus varies according to the datasets used by different authors (see below). In addition, it appears that the Cambrian 'Explosion' is most probably not just a single 'sudden burst' of diversity (that might be visible in a particular dataset) but is an extended event involving Neoproterozoic taxa; Darwin's dilemma is thus no longer a major challenge for palaeontologists and geologists.

2.3. The Great Ordovician Biodiversification 'Event'

After the Cambrian 'Explosion' the fossil record shows another, more numerically important increase in marine diversities during the Ordovician. The Ordovician biodiversification has been considered for many years the most significant and sustained increase of marine biodiversity in Earth history (e.g., Sepkoski, 1995; Harper, 2006, 2010; Algeo et al., 2016; Harper and Servais, 2018). It was first recognized as a major radiation based on the ground-breaking studies of Sepkoski (e.g., 1995) who provided a detailed analysis of diversity based on his global 'compendium' (e.g., Sepkoski, 2002). Today, some authors limit the definition of the biodiversity 'event' to numbers based on taxon counts, i.e., to numerical increases in diversity analyses. However, in addition to the higher numbers of taxa on Ordovician biodiversity curves, the Ordovician radiation firstly introduced significant changes in terms of ecological structuring (e.g., Sepkoski and Sheehan, 1983; Bambach et al., 2007; Servais et al., 2010; Servais and Harper, 2018), substrate change (e.g., Droser and Bottjer, 1989; Miller and Connolly, 2001; Rozhnov, 2017; Buatois et al., 2020) and also biomass production (Payne and Finnegan, 2006; Servais et al., 2016; Pohl et al., 2018).

The Ordovician biodiversification or radiation was recognized under different guises during the last decades. Following the 'explosion' of animal phyla in the fossil record during the Cambrian, the Ordovician displayed a massive diversification at lower taxonomic levels, in particular at the genus and species level. Most authors used the term 'Ordovician Radiation,' but it was clear that Sepkoski and Sheehan (1983) and Sepkoski (1995) had already recognized several Ordovician radiations (in plural), distinguishing different biodiversifications within the different fossil groups. The term 'Radiation' was largely used during the 1990s and early 2000s, as clearly indicated in the seminal publication 'The Ordovician Radiation' by Droser et al. (1996) and also by Droser and Sheehan (1997).

As indicated above, the terminology 'Cambrian Explosion' has no clear bibliographic origin. On the other hand, the term 'Great Ordovician Biodiversification Event' can clearly be traced back through the literature. Following the International Symposium of the Ordovician System in Las Vegas in 1995, three Ordovician palaeontologists and stratigraphers, namely Barry Webby (Sydney, Australia), Mary Droser (Riverside, California, USA) and Florentin Paris (Rennes, France), proposed a new International Geological Correlation Programme (IGCP) project with the title 'The Great Ordovician Biodiversification Event: Implications for Global Correlation and Resources'. This IGCP project n°410 was extremely successful and through this project, the terminology including the suffix 'event' became very popular. The origin and first use of the acronym 'GOBE' has never been clearly established, although it is commonly used today.

The terminology 'event' can clearly be rooted in the societal context of geological studies of the 1990s. Many stratigraphers and palaeontologists were focused during this decade on 'event geology' or 'event stratigraphy,' as is clearly illustrated by the important publication of Walliser (1995). A clear definition of the 'Great Ordovician Biodiversification Event' can also be identified and provenanced. It was Webby (2004), who not only summarized in his introductory chapter the important data compiled by many Ordovician palaeontologists in the Webby et al. (2004a) volume, but also clearly defined the GOBE as capturing biodiversity changes throughout the entire Ordovician, including the different radiations of distinct fossil groups: '… Consequently, all these evolutionary events from the beginning to virtually the end of the Ordovician Period–- through nearly 46 myr of Earth history should be treated as part of the Ordovician Radiation.' It was obvious that for none of the co-leaders of IGCP 410 ('The Great Ordovician Biodiversification Event') the Ordovician radiation was an 'event' (see Servais et al., 2021). They all used the terms radiation or biodiversification (but never 'event') in their publications (e.g., Droser et al., 1996; Droser and Sheehan, 1997; Webby et al., 2004b; Paris et al., 2004; Achab and Paris, 2007).

Although it is considered by most contemporary Ordovician workers that the 'GOBE' was clearly an important increase in biodiversity at the species and genus level during the entire Ordovician, different concepts or interpretations of the 'GOBE' exist. Following Sepkoski's concept (e.g., 1995), Droser et al. (1996) and Webby (2004), Servais and Harper (2018) considered that the Ordovician radiation was long-ranging and complex, with different fossil groups radiating at different geological intervals in different palaeogeographical regions. As indicated above, Servais and Harper (2018) indicated that first some planktonic groups (see also Servais et al., 2016) evolved, mostly during the Early Ordovician, before the majority of the benthic groups that radiated massively during the Middle Ordovician, and that the reef building organisms developed even later during the Late Ordovician (Fig. 1). Similarly, Goldman et al. (2020) considered that the GOBE is not a single event, but the sum of multiple radiations that occurred at different regional and temporal scales, and involving both taxonomic and morphologic diversification, as already noted by Miller (2004).

Like Servais and Harper (2018), Goldman et al. (2020) also considered that the GOBE included different 'Biotic Immigration Events' (BIME), as defined by Stigall et al. (2017). The Richmondian Invasion (e.g., Holland, 1997; Stigall, 2010), that can be considered as a major pulse of Ordovician biodiversification on the Laurentia continent, could be interpreted as one of these 'Biotic Immigration Events' (Servais and Harper, 2018). It can possibly be related to another regional biodiversity increase that was also named 'event', the Boda Event, defined by Fortey and Cocks (2005) as a short-lived warming 'episode' before the Hirnantian glaciation, resulting in the invasion of organisms usually known only from warmer (tropical) water environments into high latitude, cooler waters.

Although it was clear from the publications of the co-leaders of IGCP 410 who coined the term 'The Great Ordovician Biodiversification Event,' that the Ordovician radiation is a long-term process and not a short geological 'event,' some other authors, however, restricted the temporal extent of the Ordovician radiation. Kröger and Lintulaakso (2017) used the data from the PBDB to calculate diversity levels and concluded that the Darriwilian (late Middle Ordovician) was the time of a diversification maximum and the Sandbian (early Late Ordovician) the time of the Ordovician diversity climax, before a diversity fall beginning early in the Katian (Late Ordovician). Kröger (2018) subsequently put the Ordovician radiation in the context of changes in the latitudinal diversity gradient (LDG) and the global cooling of Ordovician sea waters (e.g., Trotter et al., 2008; Nardin et al., 2011; Rasmussen et al., 2016). But only more recently the term 'event' was related to a much shorter period of time by a few authors, who based their interpretations on the PBDB. First, Kröger et al. (2019, fig. 1) restricted the term 'Great Ordovician Biodiversification Event' to the Darriwilian (when the diversity levels were the highest). Rasmussen et al. (2019) narrowed the concept of the 'GOBE' even more, considering a particular diversity increase in the PBDB dataset, taking place during an earlier part of the Darriwilian, as the 'event.' This concept was also followed by Stigall et al. (2019), who recommended restricting the term 'GOBE' to this very short interval of diversification in the Darriwilian, while using the term 'Ordovician radiation' when referencing the sum of diversifications that occurred throughout the Ordovician Period. It becomes evident that the terminology 'Great Ordovician Biodiversification Event' needs a more focused redefinition, and consensus within the Ordovician community, by integrating different databases, not just the PBDB.

3. Databases and global biodiversity curves

A number of global biodiversity curves covering the early Palaeozoic have been published. It should be noted that these biodiversity curves are essentially diagrammatic depictions of diversity measures against time, including measurements of fluctuations of taxonomic richness, resulting in diversity change curves (e.g., turnover, temporal alpha or beta diversity). Some of these curves are compared here and illustrated in Fig. 2. These curves have been produced on the basis of datasets of fossil occurrences from all around the world, making them 'global' in the sense that they are not limited to a single country or continent. Nevertheless, none of these datasets provides accurate global coverage (see below).

Furthermore, most of these different datasets are also presented as 'representative' in the sense that they include a wide range of fossil groups. However, some fossil groups have much more 'weight' in a given database than others. In addition, many groups are simply absent in a number of datasets, that are usually limited to some abundant groups of invertebrate fossils, including the well-researched groups such as the brachiopods, trilobites, graptolites and echinoderms. The datasets used for 'global' biodiversity curves are thus neither complete in terms of geographical coverage nor in terms of taxonomic completeness.

3.1. Sepkoski's compendium

Following the studies on diversity counts by Raup and Stanley (1971) and Raup (1972, 1976a, 1976b), Joseph John (Jack) Sepkoski Jr. (1948–1999) published a series of studies (e.g., Sepkoski, 1978, 1979, 1981, 1984, 1988, 1995, 1997) including several biodiversity curves, that were essentially based on his fossil compendia of range data of animal families and genera, of which successive parts were produced (e.g., Sepkoski, 1982, 1992), but remained unpublished at the time of his death (Sepkoski, 2002). Sepkoski also identified the three Great Evolutionary Faunas in the marine invertebrate fossil record, defining, statistically, the Cambrian, Palaeozoic and Modern Faunas, including different classes of animals, showing contrasting diversity patterns (Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985). Sepkoski's database finally listed approximately 37,000 genera, that allowed Raup and Sepkoski (1982) to recognize five major mass extinctions in the marine fossil record.

Sepkoski's famous diversity curve (e.g., Sepkoski, 1981) was based on a simple digital database, where he recorded the first and last appearance of each group of marine invertebrates. The plotting of these occurrences revealed some interesting patterns in the diversity of marine invertebrates, including a rapid rise in the Cambrian and the Ordovician 'radiation' that led to a Palaeozoic 'plateau,' illustrating that between the end of the Ordovician and the end of the Permian, marine diversity remained almost constant, and was only interrupted by two extinction events, at the end of the Ordovician and at the end of the Devonian, before the much more severe Permian-Triassic mass extinction. A similar curve, following the publication of Sepkoski (1981), was published by Raup and Sepkoski (1982) to include the five major mass extinctions.

Sepkoski's work, and especially his diversity curve, was largely accepted and subsequently used and reproduced in almost all palaeontological text-books. Similarly, the concept of the five major mass extinctions in the Phanerozoic fossil record (of marine invertebrates), introduced by Raup and Sepkoski (1982), was widely used, and as the term 'Cambrian Explosion,' became widely known by the public, although often misinterpreted (e.g., Cascales-Miñana et al., 2018).

The highly significant work of Sepkoski inspired many generations of palaeontologists to undertake diversity studies, including those of non-marine fossil groups. More complete studies, including all fossil groups, marine and terrestrial, for example, formed the basis for publication of *The Fossil Record 2*, a compendium edited by Mike Benton

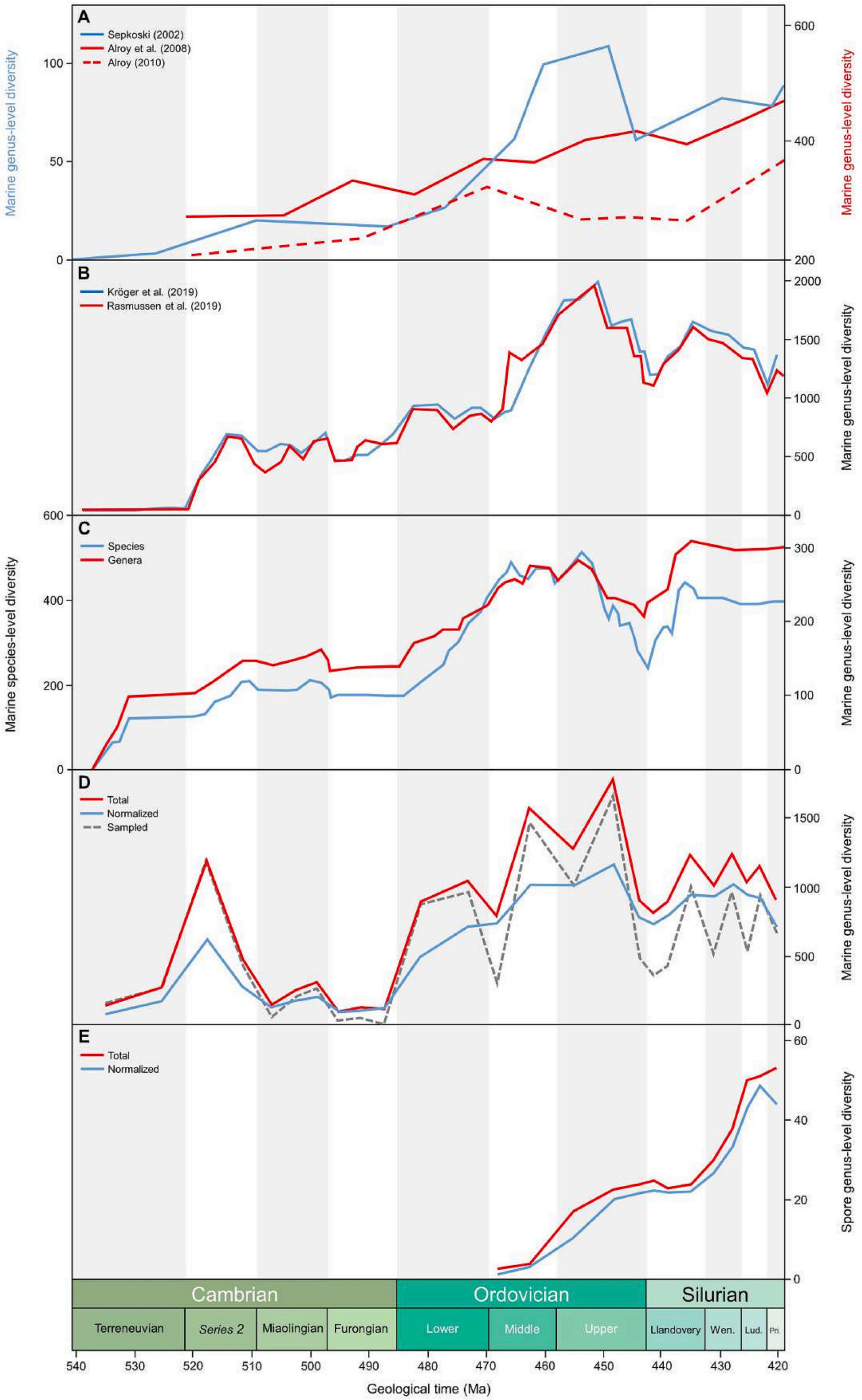

Fig. 2. Trajectory comparison of early Palaeozoic marine (A-D) and terrestrial (E) diversity curves. A, diversity pattern (blue line) of Sepkoski (2002) versus PBDB diversity patterns of Alroy et al. (2008, fig. 1) and Alroy (2010, fig. 3) (solid and dotted red lines, respectively). B, PBDB based diversity patterns of Kröger et al. (2019, fig. 1a) (blue line) versus Rasmussen et al. (2019, fig. 2a) (red line). C, GBDB species- (blue line) versus genus-level (red line) diversity patterns of Fan et al. (2020, fig. 1A). D, total (red line), normalized (sensu Cooper, 2004; blue line) and sampled (dotted line) diversities of marine invertebrates, redrawn from the diversity patterns, based on PBDB data, from Harper et al. (2020, fig. 6a). E, total (red line) and normalized (sensu Cooper, 2004; blue line) land plant derived spore diversity pattern, redrawn from Servais et al. (2019, fig. 4a), based on data from Wellman et al. (2013) and Cascales-Miñana (2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(1993).

The biodiversity curves generated from Sepkoski (2002) compendium show a continuous increase of diversity, with an acceleration of 'global' diversity during the Early and Middle Ordovician (Fig. 2A).

3.2. The Paleobiology Database

Today, one of most frequently used databases for palaeobiodiversity studies (at least in the western world) is the Paleobiology Database, or PBDB (www.paleobiodb.org), created in the late 1990s. This collection-based database is publicly accessible and free for anyone to use. It is maintained by an international non-governmental group of palaeontologists. Currently over 400 scientists from over 130 institutions in over 20 countries have contributed to the database, with clearly the majority of scientists from North America and western and northern Europe. Currently the database includes over 400,000 taxa from over 200,000 collections, and nearly 1.5 million occurrences. The database covers many groups, not only marine invertebrates, but also vertebrate fossils, as well as plants.

Alroy (2000, 2008) initially published several studies introducing new methods for quantifying macroevolutionary patterns. Concurrently, he also presented the first results of the PBDB. Alroy et al. (2001) used subsampling methods developed earlier (e.g., Foote, 1992) to analyze the data of the PBDB, that can help to remove the variations in a biodiversity curve that result from uneven preservation and sampling effects. Alroy et al. (2008) included Phanerozoic biodiversity curves of marine invertebrates, indicating the genus-level diversity, based on a sampling-standardized analysis of the fossil occurrence data compiled within the PBDB. The first curve (Alroy et al., 2008, fig. 1), with 48 temporal bins of roughly equal length (averaging 11 myr), clearly showed a single long-term radiation from the Cambrian to the early Devonian, and removed the Palaeozoic plateau of the Sepkoski curve. Another biodiversity curve, without correction for sampling (Alroy et al., 2008, fig. 4) closely ressembled Sepkoski's curve, however. Alroy et al. (2008) also noted that besides the major mass extinctions of Raup and Sepkoski (1982) several other extinctions were particularly severe, but that a sharp distinction between background information and mass extinctions is sometimes blurred. In addition, Alroy (2010) introduced a new 'shareholder quorum' method of sampling standardization that removes the biases (such as sampling effort). The plots of the curves of Alroy et al. (2008) and Alroy (2010) also indicate a continuous increase of biodiversity throughout the Cambrian and Ordovician (Fig. 2A). Kröger et al. (2019) and Rasmussen et al. (2019) also used the data from the PBDB to produce their global curves (Fig. 2B).

At present, many biodiversity curves have been generated from the PBDB, often published in journals of high-impact in terms of citation biometrics. Some authors have criticized the curves, partly because the dataset is incomplete, but also because of the questionable use of some particular measurement methods. For example, Bush and Bambach (2015) noted that previous standardized analyses (bias-corrected analyses on occurrence-level data in the PBDB) did not capture the Mesozoic-Cenozoic diversification of marine metazoans, simply because they were based on incomplete data. Prothero (2015) also considered that the taxonomic and geographic data in the PBDB for most of the Miocene mammals of North America are so poor that any analysis of such data is premature at best. Close et al. (2020) used the PBDB to analyze fossil occurrence data of Phanerozoic tetrapods. These authors noted that a 'truly global' estimate of tetrapod diversity through geological time remains inaccessible because of the incompleteness of the fossil record. Most importantly, Close et al. (2020) noted that one to two thirds of the variations in 'global' biodiversity curves can be explained by changes in the palaeogeographical extent of sampled fossil localities, or, in short, the 'global' signal is not global. We have to bear in mind these conclusions when focusing on the early Palaeozoic datasets in the PBDB.

3.3. The Geobiodiversity Database

The Geobiodiversity Database (GBDB – www.geobiodiversity.com), is an integrated system for the management and analysis of stratigraphic and palaeontological data (e.g., Fan et al., 2013, 2014). It was started in 2006 and was first available online in 2007. It is a global, publicly accessible database that is section-based (and not collection-based, as the PBDB). It incorporates data not only from palaeontologists, but also from various disciplines of stratigraphy, including biostratigraphy. It allows regional and global scientific collaborations based on stratigraphical correlation and quantitative stratigraphy, and also on systematics, biodiversity dynamics, palaeogeography and palaeoecology. The GBDB became the formal database of the International Commission on Stratigraphy (ICS) in 2012 (Fan et al., 2013). The database, in addition to stratigraphical and palaeontological data, also started to include geochemical data (Fan et al., 2014).

The rapid growth of data in the GBDB that included by 2012, data from over 35,000 collections with over 90,000 occurrences (Fan et al., 2013), and currently data from about 125,000 collections with over 500,000 occurrences, from over 25,000 sections and over 50,000 formations. The database was originally developed at the Nanjing Institute of Geology and Paleontology, China, one of the major research institutes for stratigraphy and paleontology in the world, that hosts the server and the supercomputer (Tianhe II) to run the analyses. The database was first designed to compile all Chinese data, but the global coverage is an increasingly important facet of the GBDB. The GBDB also includes an integrated GIS-based spatial database, to allow data visualization on maps and palaeogeographical reconstructions. Stratigraphical correlation is developed through different programmes, including CONOP (e.g., Sadler, 2001; Sadler et al., 2009).

The GBDB is increasingly used for analysing stratigraphical research questions and biodiversity studies, mostly from China (e.g., Fan et al., 2014). In the context of the Palaeozoic radiation, Rong et al. (2007) published a comprehensive study of the marine biodiversity patterns of latest Proterozoic-Palaeozoic-early Mesozoic in South China. More recently, Fan et al. (2020) produced a high-resolution summary of Cambrian to Early Triassic marine invertebrate biodiversity, based on the GBDB, whereas Deng et al. (2021) focused specifically on the Ordovician radiation. Here, we plot in Fig. 2C the curves published by Fan et al. (2020) and Deng et al. (2021).

These biodiversity curves based on GBDB data also show the Cambrian and Ordovician radiations, but with different patterns than those observed in the PBDB; this is not unexpected, as both databases cover different palaeogeographical regions (see below). Both databases have a global scope, but differ in regional focus and method of sample collection and pooling.

3.4. Other databases

Although the PBDB is highly visible, mostly due to many publications in high-impact journals (of publishers located in North America and western Europe), and besides the fact that the GBDB is becoming increasingly visible as a potential global player, it is important to note that there are a multitude of other databases that are currently under development, at a global, national, but very often also at a personal level.

For example, Macrostrat (www.macrostrat.org) is an internet platform designed for the integration and distribution of various geological data that are relevant to the spatial and temporal distribution of different rock types. It includes currently over 1500 regional rock columns, from over 35,000 rock units. A major objective is to generate a globally comprehensive stratigraphic database (Peters et al., 2018). Initial results, in relation to Macrostrat, indicate that there is a clear link between continental fragmentation and biodiversity over time (e.g., Zaffos et al., 2017). Macrostrat clearly provides evidence for a need of a quantitative spatio-temporal evaluation of the sedimentary rock record.

However, its coverage is mainly limited to North America so far. Similarly, and as an example, the GeoStrat project (www. Dnr.mo.gov/geology/geostrat.htm), is designed to include all relevant data and metadata for stratigraphic-based data. Many other such initiatives are currently in progress.

The major palaeontological collections, usually housed in national natural history and university museums, also have their own databases. For example, the 'Paleontology Database' of the American History of Natural History (New York, USA) is a dataset from a variety of legacy databases used in the four historical paleontology collections of the institution. Similarly, the Natural History Museum (London, UK) hosts a collection of over 40 million specimens, of which currently over 450,000 are available through the online catalogue. The Musée d'Histoire Naturelle (Paris, France) is also digitizing the data from one of the largest fossil collections in the world, with only a minor part of the collections available in the digital index so far. The French national inventory of all palaeontological collections is also an ongoing project, digitizing the millions of specimens of over 50 French universities and museums (e.g., Servais et al., 2012). But even many much smaller countries have today complete digitized geoscience collections, as, for example, The Netherlands (www.naturalis.nl) with over 3 million fossils, or Estonia (www.geocollections.info), that are also used for biodiversity studies in the early Palaeozoic (e.g., Hints et al., 2010, 2018; Toom et al., 2019)

Such projects of database creation, compilation and digitization of data from public collections are mostly accessible via internet. It will still take a few more decades to complete all datasets, and to allow an interaction between them.

However, in addition to these numerous digital public databases, many collections and databases are not (yet) public, nor publicly available. This highlights the lack of data of some important fossil groups present in the early Palaeozoic. For example, there are so far no data in the PBDB related to the Palaeozoic phytoplankton. The published biodiversity curves related to this group are entirely based on databases that are not included in the PBDB, nor the GBDB (e.g., Nowak et al., 2015; Zheng et al., 2020; Kroeck et al., 2022). Similarly, the datasets on Ordovician and Silurian polychaete worms (e.g., Eriksson et al., 2013) are not available in the PBDB. The data concerning the chitinozoans have also never been integrated with the PBDB, although detailed diversity curves are published for the group (e.g., Paris et al., 2004; Achab and Paris, 2007; Goldman et al., 2020). For many other important early Palaeozoic fossil groups the data available in the global databases are only partly compiled, but compilations of the diversity of these groups have been published, often in special issues resulting from a group effort (e.g., Webby et al., 2004a; Harper and Servais, 2013). The data on graptolites in both the PBDB and the GBDB are only a fraction of the data compiled by the graptolite specialists over the last decades (e.g., Crampton et al., 2016; Goldman et al., 2020). The situation is very similar for other groups, like the bryozoans (e.g., Ernst, 2018), the conodonts (e.g., Goldman et al., 2020), and especially for the trilobites (e.g., Adrain et al., 1998; Adrain, 2013), for which the complete datasets remain in the personal domains of the palaeontologists and principal investigators of the respective fossil group, and only a fraction of the data is available in the PBDB or GBDB.

The sophisticated statistical methods used in producing the diversity curves in the PBDB and GBDB are today not yet able to fully overcome sampling bias. However, if in the future all collected data can be integrated into a single compilation, it would be possible to move towards a truly global signal.

4. Comparing 'global' biodiversity curves

It is very difficult to compare the biodiversity (taxonomic richness) curves of different fossil groups. For the Ordovician radiation, Servais et al. (2010) clearly showed that there are different trends, although it is difficult to compare the different datasets, compilations and biodiversity curves, produced for the different fossil groups in Webby et al. (2004a) or separately. Not only does the taxonomical level vary from one group to another, but also the different methods used to measure (or recalculate and model) biodiversity. Cooper (2004) suggested a common standard for all groups involved in the Ordovician radiation, but the different fossil groups have been treated sometimes in very different ways, and it is difficult, if not impossible to compare the different curves, that therefore logically produce different signals. Nevertheless, for the Ordovician radiation, it becomes obvious that the different fossil groups clearly show different biodiversity 'pulses' (Servais et al., 2010, 2021; Harper et al., 2020, 2021), and not just a single major biodiversity 'pulse' in the Middle Ordovician, as suggested by Trotter et al. (2008), or other authors (e.g., Rasmussen et al., 2016, 2019).

Despite these possible difficulties of comparison, we here attempt to critically analyze and compare the different global biodiversity curves published for the early Palaeozoic. Fig. 2 illustrates several of these global curves published previously, that concern the evolution of the diversity dynamics of the marine invertebrates. The recently published curves of PBDB data concerning the marine invertebrates (Harper et al., 2020, 2021) are also plotted on Fig. 2 (Fig. 2D), as well as the diversity of land-plants (Fig. 2E) as documented by Servais et al. (2019), in order to allow a discussion and comparison of the different curves and their possible interpretation.

4.1. Sepkoski's compendium versus PBDB

Several authors have already compared the diversity curves generated by Sepkoski's compendium (2002) compendium and by the PBDB (e.g., Alroy, 2008, 2010), as for example Servais et al. (2010, fig. 3), Bush and Bambach (2015, fig. 1), Rasmussen et al. (2019, fig. 1), Harper et al. (2020, fig. 1) and Deng et al. (2021, fig. 7).

Here we plot on Fig. 2A the early Palaeozoic part (Cambrian to Silurian) of the biodiversity curves generated by Sepkoski's compendium (2002) and the early Phanerozoic biodiversity curves of the PBDB (Alroy et al., 2008; Alroy, 2010). Both datasets provide a similar signal, with a long-term radiation over the entire early Palaeozoic. Whereas the Late Ordovician Extinction Event (LOME) was clearly visible in Sepkoski's curve (who used time bins of approximately 5 myr), it became invisible in the genus-level diversity curve of Alroy et al. (2008), based on the sampling-standardized analysis of the PBDB, because the curve was limited to time bins of about 11 myr, thus having a relatively low resolution, not revealing short-term fluctuations in the fossil record, such as the LOME. The two main differences, however, between Sepkoski's compendium and the more recent analyses of the PBDB are the different methods used: firstly the estimation of species richness (simple counting versus sampling standardization) and secondly the sample pooling in time bins of different durations.

4.2. Recent PBDB versus GBDB 'global' biodiversity curves

In recent years, several groups of specialists have produced biodiversity curves generated from data available from the PBDB and the GBDB. Both databases, that are global in scope, attempted to compile data from all parts of the world, but it is obvious that neither the PBDB (including mainly data from North America and Europe) nor the GBDB (focused on Chinese data) are truly global. For many palaeogeographical areas the data are not (yet) included in the databases, and for some other regions, the data are simply not yet available (e.g., Antarctica, but also major parts of Africa).

Rasmussen et al. (2019) utilised data available in the PBDB to construct a diversity curve for the early Palaeozoic. To overcome the problem of low temporal resolution (11 myr in Alroy et al., 2008), Rasmussen et al. (2019) established a set of 53 time slices through the entire early Palaeozoic, based on biozones that have been correlated to a global scale of previously published chronostratigraphic schemes. In order to address sampling and preservation biases, Rasmussen et al.

(2019) used a capture-recapture (CR) modeling method that was conceptually transferred from ecology to fossil data (Nichols and Pollock, 1983; Connolly and Miller, 2001; Liow and Nichols, 2010). The shareholder quorum subsampling method (Alroy, 2010) was used for comparison, as well as the new method of time binning introduced by Kröger and Lintulaakso (2017). According to Rasmussen et al. (2019) the three different methods more or less provided identical results. The curve based on the capture-recapture (CR) modeling method published by Rasmussen et al. (2019, fig. 2) is reproduced here in Fig. 2B.

Kröger et al. (2019) used the same dataset to produce an almost identical diversity curve (Kröger et al., 2019, fig. 1; Fig. 2B), that was adapted, but is slightly different from Rasmussen et al. (2019, fig. 2). Kröger et al. (2019) added information about the genus level relative diversification rate, the genus level extinction and origination rates and the duration of the forward and backward survivorship of 50, 70 and 90% of the cohort of genera of each time bin. These different measures allowed Kröger et al. (2019) to divide the early Palaeozoic radiation into different parts.

Both the curves (Fig. 2B) of Rasmussen et al. (2019) and Kröger et al. (2019) indicated a strong increase of diversity in Cambrian Series 2 (Cambrian Stage 3), already observed by Na and Kiessling (2015), and thus illustrating the presence of taxa in the PBDB, resulting mainly from the numerous descriptions of fossils in the major *Lagerstätten.* Similarly, Kröger et al. (2019) interpreted this short interval as the 'CE' (Cambrian Explosion), thus relating the Cambrian 'Explosion' to the number of genera of marine invertebrates in the PBDB, and not to the number of phyla appearing in the fossil record, or to the origin of different types of body plans (*Baupläne*). During the Miaolingian and Furongian series, the diversity curves of Rasmussen et al. (2019) and Kröger et al. (2019) are similar, although the curve of Rasmussen et al. (2019) shows much higher fluctuations, despite the fact that both curves are from the same source and used the same methods. After the initial, dramatic rise in Cambrian Series 2, the two curves generated by the PBDB display some sort of plateau that lasted until the Cambrian-Ordovician boundary. At the Cambrian-Ordovician boundary, the curves start to show a step-wise increase of the biodiversity, with an initial rise in the Early Ordovician, a second rise in the Middle Ordovician, and a final rise in the early part of the Late Ordovician. Whereas Rasmussen et al. (2019) considered the second rapid increase in the Darriwilian to be the 'GOBE' (possibly corresponding to the rapid increase in diversity originating on the Baltic continent, see Hammer, 2003, for example), Kröger et al. (2019) considered the 'GOBE' to be the interval during the Darriwilian with highest rise in diversity and a decrease of relative diversification rates. Both Rasmussen et al. (2019) and Kröger et al. (2019) thus related a particular, rather short interval of diversity increase in the PBDB to the biodiversification 'event.' On the other hand, both curves (Fig. 1B), show a continuous increase of diversity during the Ordovician, from the late Cambrian to the Late Ordovician, similar to most previous studies (Fig. 2A).

Subsequently, Fan et al. (2020) have published a biodiversity curve covering the entire Palaeozoic, based on the GBDB. The section-based database used for drawing the biodiversity curve included over 11,000 species from over 3000 sections. The supercomputer Tianhe II used the CONOP.SAGA (Sadler et al., 2009) programme to construct the composite biodiversity curves. This programme allows comparison of the stratigraphical ranges from many localities in order to assemble them in a global dataset with first and last occurrences. Fan et al. (2020) considered that, although the generated data were largely derived from Chinese sections, the tectonic blocks on which they reside were situated in a large spectrum of palaeolatitudes, and thus reflect global biodiversity patterns. A small amount of data from the European Silurian and Devonian were added, because these intervals were poorly represented in the original (Chinese) dataset. The results allowed the production of genus and species level diversity trajectories for different fossil groups from the Cambrian to the Early Triassic.

The results of Fan et al. (2020, fig. 1A, B; Fig. 2C) revealed a sharp increase in diversity associated with the Cambrian Explosion, followed by a 'pause' (plateau) through the other parts of the Cambrian. A nearly threefold increase in species diversity was observed during the Early Ordovician. Most interestingly, Fan et al. (2020) also related the GOBE to a diversity increase in their biodiversity curve, that according to their calculations lasted precisely 29.72 myr. It started at 497.05 Ma (in the late Cambrian) and lasted until 467.33 Ma, i.e., the Middle Ordovician.

Both studies of the data in the GBDB and PBDB thus provided signals that have the scope to be global and both datasets allowed the authors to define, on the grounds of numbers of diversity measures only, both the 'Cambrian Explosion' and the 'Great Ordovician Biodiversification Event.' It is interesting to note that the timing of the Cambrian 'Explosion' differs slightly in both datasets, but that the definition of the GOBE is totally different: while the GBDB (Fan et al., 2020) indicates a GOBE in the late Cambrian and Early Ordovician, the PBDB related publications by Rasmussen et al. (2019) and Kröger et al. (2019) define a rather short GOBE in the Middle Ordovician (see also Servais et al., 2021).

The different views are possibly reflected by different signals in the 'global' datasets, that seem to originate from differences in the source of data, probably related to palaeogeography.

4.3. *The incompleteness in the 'global' signal*

In the light of understanding the dynamics of the Palaeozoic radiations, Harper et al. (2020) compared previously published datasets that attempted to include all fossil groups and all palaeocontinents. It became obvious that none of the available datasets is complete in terms of palaeocontinental coverage. As indicated above, the PBDB is mostly focused on data published in journals that are listed in the reference database used in western countries, whereas the GBDB is clearly based initially on the large datasets available from China.

Harper et al. (2020) used the raw data to illustrate the presence/absence of fossils occurrences in the PBDB (Fig. 2D). Harper et al. (2020) used three different diversity measures: the total, normalized, and sampled diversities. Total diversity (all taxa observed in a given time interval) differs from the sampled diversity (all taxa recovered in a given time interval) and from normalized diversity sensu Cooper (2004) (all taxa ranging from the interval below to the interval above, plus half the taxa that originate and/or become extinct within the interval, plus half of single-interval taxa). In addition, it has to be taken into account that the data pooling is not the same as in previous studies. The data are plotted in the 26 time-bins that are easily available from the PBDB. However, none of the methods used by Alroy et al. (2008), Rasmussen et al. (2019) and Kröger et al. (2019) have been applied. The diversity curve in Fig. 2D thus provides an indication of the presence of data (as record input in the database), without an attempt to remove biases (such as preservation, sampling effort, taxonomic oversplitting). A look at the raw data in the PBDB indicates that there is a dramatic absence of data in the upper Cambrian, i.e., the Furongian (including three stages: the Paibian, the Jiangshanian and Stage 10). This interval is characterized by a lack of data in the PBDB, illustrating the 'Furongian Gap' (Harper et al., 2019), evidently separating two obvious intervals of high data input in the datasets: the Cambrian and Ordovician radiations, that are logically separated as two distinct parts. It becomes obvious, when comparing the curves generated with correction methods and the raw data, that the Cambrian 'Explosion' (if defined as a strong increase in taxonomic richness) is an artefact and the result of an extraordinary amount of sampling. For the Ordovician radiation, a three-step increase is also obvious, that partly reflects the three phases identified in the Ordovician biodiversification: the plankton revolution in the early part of the Ordovician (although several major planktonic groups are not in the PBDB), the major radiation of bottom-level (benthic) communities in the Middle Ordovician (that were considered by some as the 'major pulses' of the Ordovician radiation (Trotter et al., 2008), and the onset of reef-building communities in the Late Ordovician.

In addition to the absence or incomplete record of several fossil groups, there are also strong discrepancies in the fossil record of the different regions around the world, i.e., from the different palaeocontinental margins.

Similar to the conclusions of Close et al. (2020) who indicated that the 'global' signal of the diversity dynamics of terrestrial tetrapods can largely be explained by the regional input, the 'global' curves of the biodiversity of marine invertebrates of the early Palaeozoic are also impacted by the palaeogeographical context. The PBDB has mostly captured data from a selected part of the world, whereas the GBDB includes data from the different palaeogeographical 'blocks' that formed China during the early Palaeozoic. The Cambrian 'Explosion' thus has different records depending on the datasets used. Similarly, the Ordovician radiation started in some parts of the world (China, Gondwana) in the late Cambrian, when a palaeocontinent such as Baltica was in higher latitudes and far away from tropical waters that are ideal for speciation and diversification (see below, Fig. 6). Logically, when Baltica moved to lower latitudes during the Middle Ordovician, the diversification rates 'exploded' and the numbers of taxa in the PBDB are, not surprisingly, much higher for this interval (e.g., Hammer, 2003), because a large input of data compilation in the PBDB is from Baltica (Harper et al., 2021). The 'BIME' recorded in the Upper Ordovician of Laurentia, i.e., the Richmondian Invasion (Stigall, 2010; Stigall et al., 2019), provided the high number of taxa that, added to the diversification accumulated from the Early and Middle Ordovician, allowed the highest diversities to be attained during the Late Ordovician Katian Age.

Even without sophisticated statistical methods it is obvious that the

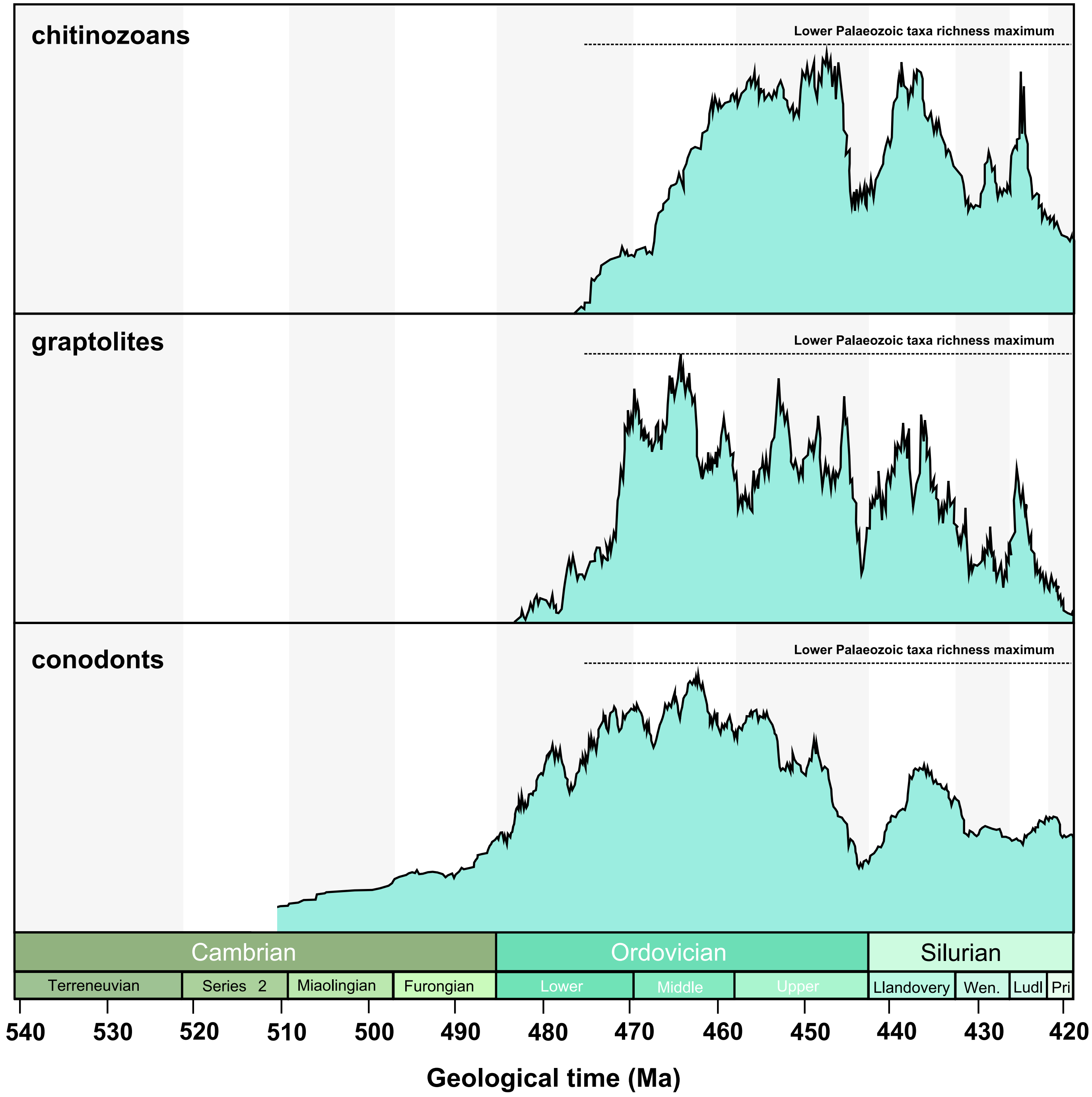

Fig. 3. Early Palaeozoic species richness curves of the three major biostratigraphical groups (after Goldman et al., 2020).

global peaks of diversity are the sums of the peaks of regional diversity, as it has been clearly shown for several fossil groups, such as, for example, the chitinozoans (Paris et al., 2004; Achab and Paris, 2007), an example that should be followed by all other groups in the search for a true 'global' biodiversity signal, as already suggested by Miller (2004) in the 'Webby book' (Webby et al., 2004a). Defining an 'event' on the basis of a single database appears therefore to be an over-simplification.

5. Diachronous radiations of the different fossil groups

After the compilation of datasets during the International Geoscience Programme (IGCP) 410, resulting in the publication of taxonomic richness curves of many Ordovician fossil groups (Webby et al., 2004a), another IGCP project (IGCP 503) attempted to find the triggers of the radiations. In this context, Servais et al. (2010) plotted the diversity curves of different fossil groups and illustrated the divergence of the radiations of the individual groups during the Ordovician. Although there was no uniform technique for all groups, it is obvious that each fossil group provides a different biodiversification scenario: most fossil groups show diachronous radiations, with biodiversifications and peaks of diversity at different time intervals. In this section, we illustrate further examples of divergence of the timing of radiations of the different groups. We do not just limit the comparison to the Ordovician, but compare the datasets of the entire interval of the early Palaeozoic, covering the Cambrian, Ordovician and Silurian.

5.1. Constrained optimization (CONOP) of the three major groups used for biostratigraphy

Fig. 3 illustrates the diversity curves of the three major fossil groups that are traditionally used for biostratigraphical correlation. These groups have been studied intensively, and their stratigraphical distribution has been carefully examined. Complete datasets have been compiled by the specialists of each group, allowing the application of the Constrained Optimization programme (CONOP, Sadler, 2001; Sadler et al., 2009). Goldman et al. (2020) (fig. 20.14) presented the 'taxon richness' trajectories of the three groups, that are redrawn here (Fig. 3). The conodont diversity curve is based on 3788 taxa from 1221 sections, that of the graptolites on 2291 taxa from 619 sections, and the chitinozoan curve was calculated from a database of 231 taxa from 1210 sections. Thus, these diversity (taxonomic richness) curves constitute the most complete global curves of early Palaeozoic fossil groups, with a much higher resolution and a much greater number of data than those available in the PBDB or GBDB. The curves clearly show that these three groups have completely different diversification trajectories. Both the chitinozoans and the graptolites, as part of the zooplankton, show a strong increase of diversity beginning in the Lower Ordovician, reflecting the 'Plankton Revolution' (see also Achab and Paris, 2007; Crampton et al., 2016), with the graptolites clearly diversifying before the chitinozoans, whereas the conodonts show a more continuous, slow increase of diversity between the middle parts of the Cambrian and the upper Middle Ordovician. From this figure alone it becomes evident that there is not a unique diversification, but different radiation scenarios of the three groups at different time intervals. A clear, unique diversification pulse in the Middle Ordovician (Trotter et al., 2008) cannot be distinguished, nor can a 'Darriwilian threshold', interpretated as an origin for the GOBE (sensu Stigall et al., 2019).

5.2. Diachronous radiations of fossil groups

Most of the diversity analyses during the early Palaeozoic produced 'global' curves, i.e., mixing all information from different palaeocontinents, of all fossil groups. These allowed some authors to see 'global' radiations, based on PBDB datasets, including a curve that is widely used today to explain the 'global' picture of the early Palaeozoic radiations, including the Cambrian 'Explosion' and the GOBE (e.g., Kröger et al., 2019, fig. 1; Rasmussen et al., 2019, fig. 2; Stigall et al. (2020), fig. 1).

However, it is important to see what is actually behind these curves, and what are the data that are used to produce these compilations. For this reason, Harper et al. (2020) had a closer look at the data from the different fossil groups, not only in the PBDB, but also of other fossil groups, that are not present in this database. Additionally, Harper et al. (2021) dissected the 'global curve' into regional curves, in order to obtain the radiations on each continent. In the latter study, it became clear that the PBDB is not only biased, with a large majority of data from the western world, but also that the data from North America (palaeocontinent Laurentia) largely dominate the 'global' database, followed by the data from northern Europe (Baltica and Avalonia), with the 'global' PBDB curve reflecting actually the evolution of marine life during the early Palaeozoic of the 'western' world.

Here, we review the biodiversity signals of the different fossil groups of the PBDB, based on the investigation of Harper et al. (2020) (Fig. 4). The data in the PBDB are for some groups very abundant (the data from the echinoderms are almost complete in the PBDB, and corresponding to the unpublished datasets of the specialists of the group), for others they are sporadic (trilobite and graptolite data, for example), whereas some other groups are so far totally absent in the dataset. Among the groups that are not present in the PBDB are the palynomorphs, including the acritarchs (phytoplankton), the chitinozoans (zooplankton) and the scolecodonts (jaws of polychaete annelid worms).

For a few groups, the presence of data in Cambrian Series 2 and the Miaolingian records the coverage for the Cambrian radiation in the PBDB: brachiopods, sponges, archaeocyaths, echinoderms, and trilobites are among the groups that are well represented. The dataset of the trilobites (Fig. 4F) in the PBDB is not complete, in comparison to the datasets that remain partly unpublished; they are a very complex group, with changing life habitats and life modes, and several mass extinctions recorded (Adrain, 2013). The absence of data in the Furongian separates the Cambrian and Ordovician biotas. After their massive diversification in the early-middle Cambrian, diversity strongly increases again during the Early Ordovician, according to the data in the PBDB. Brachiopods (Fig. 4L) clearly show important Ordovician radiations, similar to the gastropods (Fig. 4E) and bivalves (Fig. 4J). The conodont diversification in the PBDB roughly reflects that of the CONOP-based studies by Goldman et al. (2020) (Fig. 4K), but with less detail. The echinoderms show both a Cambrian and an Ordovician biodiversification, apparently separated by a Furongian gap (Fig. 4D). The graptolites clearly reflect the evolution of the plankton in the Early Ordovician, and reflect the CONOP-based curve (Fig. 3), but with less resolution (Fig. 4C). Ostracods (Fig. 4I) also show an obvious Ordovician radiation, with strongest increases of taxonomic richness in the Early-Middle Ordovician. The reef-building organisms all develop strongly during the Late Ordovician: cnidarians (Fig. 4A), bryozoans (Fig. 4G; but see also Ernst, 2018), stromatoporoids (Fig. 4B), and also the sponges (Fig. 4H), that already had a first peak of diversity during the early-middle Cambrian.

Harper et al. (2020) also provisionally placed the different fossil groups in macroecological entities (zooplankton, nekton, mobile benthos, mobile nektobenthos, fixed benthos and reef builders), but the affiliation of some fossil groups to these entities remains problematic (see above). Nevertheless, after the Cambrian marine invertebrate faunas being essentially benthic, a three-fold diversification in the Ordovician can be observed, with three major steps of increases of taxonomic richness during the Early, Middle and Late Ordovician. Once the 'global' signal of the PBDB is dissected, it is clear that the different groups show different signals. The diversity dynamics of the different groups show diachronous 'peaks' or 'events' as already noted by Servais et al. (2010): the specialists of every individual fossil group may identify a 'GOBE' that corresponds to their group.

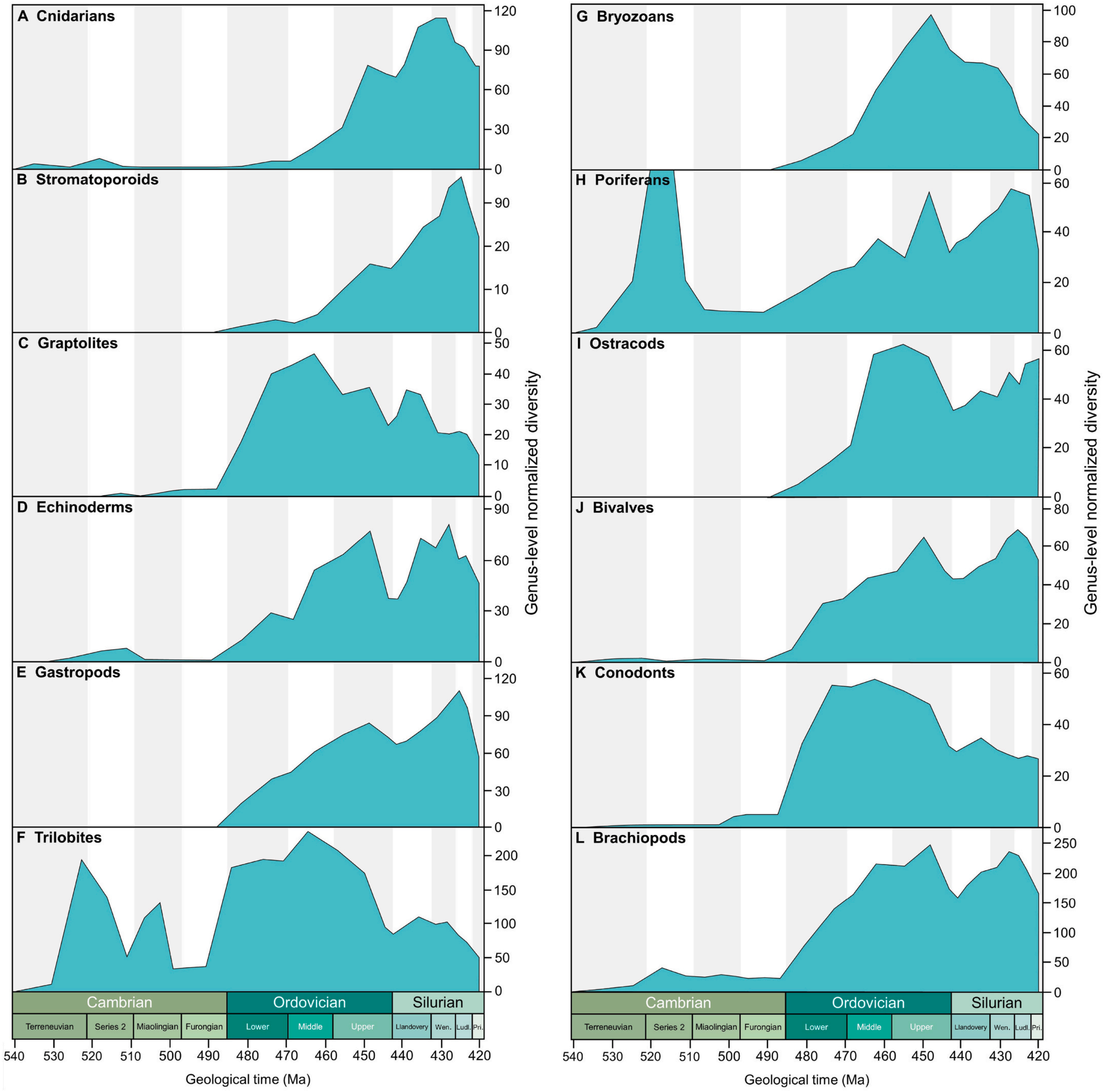

Fig. 4. Early Palaeozoic genus-level biodiversity curves of selected fossil groups based on the PBDB (after Harper et al., 2020).

5.3. Diachronous radiations of fossil groups in the GBDB

In a similar way as for the PBDB, the species richness curves generated by the GBDB also produce signals mixing all fossil groups integrated in the datasets. Fan et al. (2020) produced a curve with the general trajectories of Palaeozoic species diversity (Fan et al., 2020, fig. 1A), but also split these trajectories into that of ten major fossil groups: trilobites, graptolites, conodonts, cephalopods, anthozoans, foraminiferans, bivalves, crustaceans, brachiopods, and others (Fan et al., 2020, fig. 1B). In the supplementary materials, the authors publish, most interestingly, the species-level diversity curves for the three marine evolutionary faunas (Fan et al., 2020, fig. S8), but also the curves of the ten major fossil groups separately (Fan et al., 2020, fig. S10). Deng et al. (2021, fig. 8) also dissect their general curve into curves of the richness of some major marine groups from the middle-late Cambrian to the early Silurian. Some of these taxonomic richness curves are redrawn in Fig. 5.

In the GBDB, the trilobites (Fig. 5) show a first massive diversification in the middle part of the Cambrian (Miaolingian). Most interestingly, their diversity declines strongly in the Darriwilian. Conodonts appear in the middle-late Cambrian, and show a continuous diversification up to the late parts of the Early Ordovician, with a decrease starting in the Middle Ordovician, similar to that of the trilobites. Brachiopods, on the other hand diversify only strongly in the Early Ordovician, with a peak in the early part of the Middle Ordovician, i.e., exactly before the time interval when brachiopods evolve on other continents like Baltica or Laurentia. The 'GOBE' of Rasmussen et al.

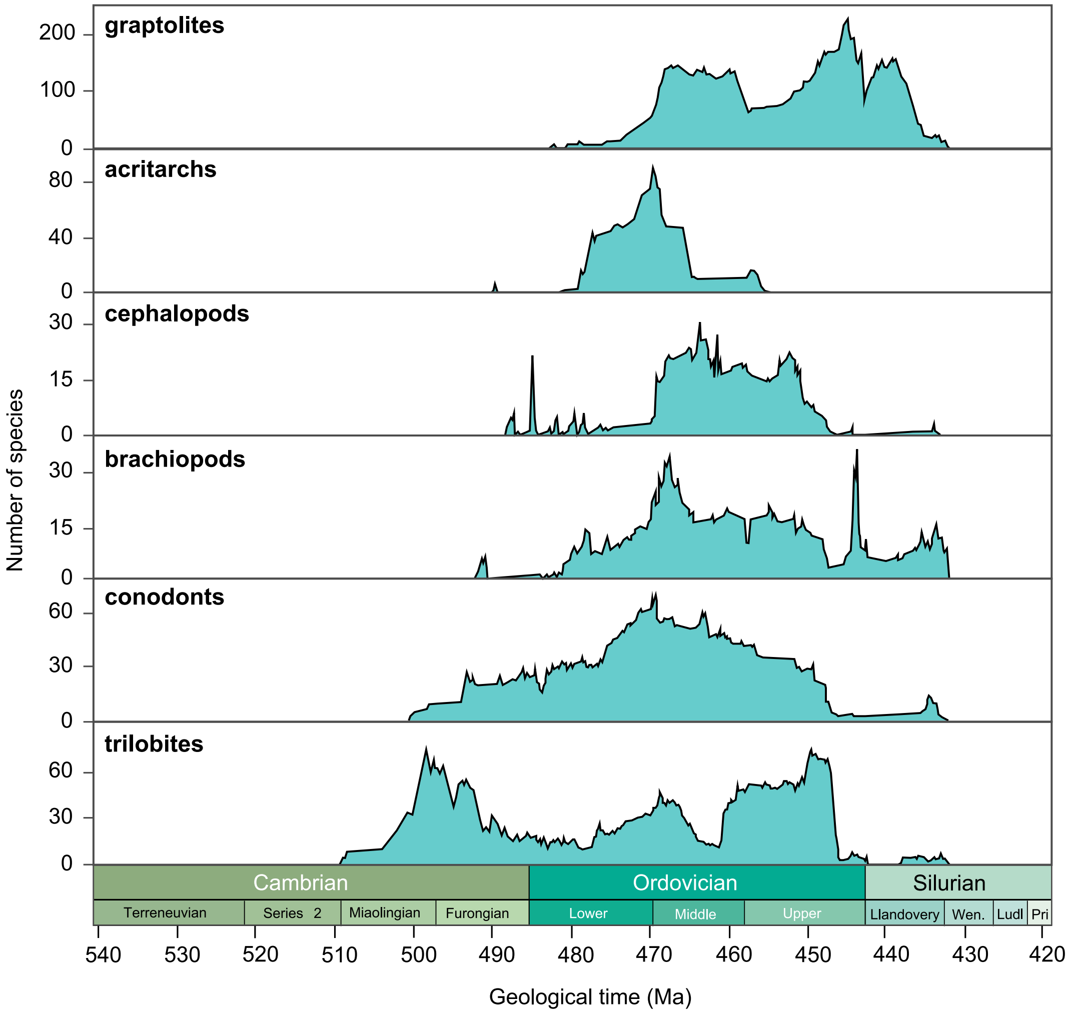

Fig. 5. Species-level biodiversity curves of selected fossil groups in the GBDB (after Deng et al., 2021).

(2019) thus appears actually to be a peak of brachiopod diversity only recorded in the PBDB (see also Harper et al., 2021), that cannot be confirmed by data in the GBDB. Cephalopods show a dramatic increase in species-level diversity at the base of the Middle Ordovician in the GBDB. The graptolite species richness curve from the GBDB is also very interesting, as it does not reflect entirely the patterns in the global curve (Fig. 3). The diversity of the acritarchs from the GBDB (Fig. 5) cannot be used for any wider scenarios, as the dataset in the GBDB (Li et al., 2008) is far from being complete, in comparison with the global dataset (Kroeck et al., 2022).

5.4. Potential sources of multiple 'events'

Here we only provide a few examples, and the compilations are not complete, of diversity (species richness) curves of different fossil groups during the early Palaeozoic. The diversification trends, and the peaks of species (or genus) richness, are clearly diachronous between the different groups, but also from one dataset to another. It becomes obvious from this rapid assessment of the compilations in the PBDB, in the GBDB, and in other databases that are partly published separately (see compilations in Webby et al., 2004a, for example), that every specialist of a fossil group may find an individual diversity trajectory for the group analysed, with specific peaks of diversity at particular intervals. On the other hand, palaeontologists from one continent see different diversification scenarios compared to their colleagues working on another (palaeo-) continent. Logically, this raises the question about the triggers of these diversity changes, and every palaeontologist is confronted with this question: does the diversity pattern, and the diversity peak correspond to an 'event' and was this 'event' possibly of larger significance, if not of 'global' importance?

6. A single long-term marine radiation: relation to geological 'events'

6.1. The complex research for triggers

There are numerous papers discussing the triggers, including extrinsic (abiotic, i.e., geological, extraterrestrial) and intrinsic (biotic, ecological) parameters that enabled the early Palaeozoic radiation. It is impossible to cite even a small fraction of the papers related to this question published in the last 150 years, after Darwin's and Phillips's initial investigations.

In recent years, more 'dramatic' extrinsic triggers have been presented, to explain the Cambrian 'Explosion' or an Ordovician 'event'. For the Ordovician, such possible triggers of a sudden radiation in the marine realm include the presence of a mantle superplume (e.g., Barnes, 2004; but see Lefebvre et al., 2010), a spectacular temperature decrease (Trotter et al., 2008), a meteorite shower following the breakup of an L-chondrite parent body in an asteroid belt (e.g., Schmitz et al., 2008 Schmitz et al., 2019; but see Lindskog et al., 2017, Schmitz and Terfelt, 2022), rapid oxygenation events (e.g., Saltzman et al., 2011; Edwards et al., 2017) or a drastic change of direction in the ocean conveyor belts (e.g., Rasmussen et al., 2016; but see Servais et al., 2014; Pohl et al., 2014, 2016, 2018).

In addition to the different biodiversity curves for marine invertebrates, Fig. 2E also displays the diversification of the earliest land plants, illustrated by the genus-level diversity of fossil land-plant derived spores (Servais et al., 2019, based on data from Wellman et al., 2013 and Cascales-Miñana, 2016). The radiation of land-plants occurred about 100 myr after the initial radiation of marine invertebrates, with an Ordovician 'explosion' of miospore diversity, that resembles a rather normal, progressive radiation (e.g., Gerrienne et al., 2016). The link between the marine and terrestrial realm has also been intensively discussed (e.g., Masuda and Ezaki, 2009; Algeo et al., 2016; Servais et al., 2019) and it appears evident that the radiation of land plants must have had an impact on weathering processes and global chemical fluxes (e.g., Algeo et al., 2001; Porada et al., 2016) and subsequently on the $p\mathrm{CO}_2$ and $p\mathrm{O}_2$ values in the early Palaeozoic (e.g., Lenton et al., 2012, 2018; Edwards et al., 2017).

Fig. 6 illustrates the early Palaeozoic curves of biodiversity for both the marine and terrestrial realm (Fig. 6A), together with the global ichnodiversity calculated during the Cambrian and Ordovician (Buatois et al., 2020, Fig. 6B), plotted against a series of parameters that might indicate the possible triggers of the radiations, the Cambrian 'Explosion' and a short-lived Ordovician 'event.'

Oxygenation has been considered by some authors (see review by Edwards, 2019) as a possible trigger for the Cambrian 'Explosion' or the GOBE. Fig. 6C illustrates two more recent examples of $p\mathrm{O}_2$ curves for the Cambrian and Ordovician (Krause et al., 2018) and the Ordovician (Edwards, 2019) that show contrasting models of oxygenations. Munnecke et al. (2010, fig. 5) already illustrated three different $p\mathrm{O}_2$ curves with completely different interpretations. As a result contrasting models have been presented and are now available, so far a consensus scenario is lacking, that is generally acknowledged.

In terms of palaeotemperature, a number of publications have presented varying models in the last decades. Munnecke et al. (2010, fig. 5) illustrated various curves with modelized levels of $p\mathrm{CO}_2$, that have usually been considered to be a possible indicator of climate change. There is a general agreement of a decrease of $p\mathrm{CO}_2$ during the early Palaeozoic (Fig. 6E). Similarly, there is also a general consensus of decreasing sea-surface temperatures (Fig. 6D), although with varying ranges of temperature shifts. The drastic decrease modeled by Trotter et al. (2008) from very high sea-surface temperatures (> 40 °C) during the Early Ordovician has resulted in an ongoing discussion (see below). Fig. 6F illustrates the changing $^{87}\mathrm{Sr}/^{86}\mathrm{Sr}$ ratios of early Palaeozoic seawaters, that can be used to detect changes on the continental surfaces, whereas the varying $\delta^{13}\mathrm{C}$ is usually used as a palaeo-productivity proxy (Fig. 6G). We also plot here the generally accepted global sea-level curve (Fig. 6H).

It is very important to note that, similar to the diversity curves, the different geochemical proxies, as well as the sea-level curve, are also based on different datasets, including numerous biases, and they often represent models that must be critically and carefully scrutinized. Evidently, it is beyond the scope of this paper to critically analyze all these models, or to numerically compare the proxies against the taxonomic richness curves, with sophisticated statistical cross correlations.

Changing palaeoclimate was very often related to the early Palaeozoic radiation. Past climatic processes can be reflected indirectly in the composition of the specific geochemical proxies illustrated in Fig. 6. It is generally acknowledged that the climate cooled during the Ordovician (e.g., Trotter et al., 2008; Vandenbroucke et al., 2010; Nardin et al., 2011; Rasmussen et al., 2016; Scotese et al., 2021; Marcilly et al., 2022). However, the palaeoenvironmental conditions in the early Palaeozoic were completely different from those we have today, hampering actualistic explanations. For example, we know very little about the seafloor spreading rates, the stratification and oxygen content of water masses in the open ocean, and we completely ignore the currents in the deep oceans at this time (the position and movement of ancient ocean conveyor belts are totally unknown, despite a hypothetical scenario proposed by Rasmussen et al., 2016), although these processes provide a reliable explanation of the chemical proxies. In addition, during the early Palaeozoic, at least during the Cambrian and Early Ordovician, the continents were largely devoid of vegetation, i.e., there was probably hardly any soil, and the weathering was mainly physical. We have very few models regarding the elevation of continents. It is still debated how continental cover by vegetation, for example, influenced the Sr isotopic composition of the sea water, which today is considered as a proxy for global tectonic evolution, because $^{87}\mathrm{Sr}/^{86}\mathrm{Sr}$ variations reflect principally the ratio between Sr input from rivers (continental input) and submarine hydrothermal systems. In addition, a proxy rarely permits monocausal conclusions. Almost all proxies are influenced by various environmental factors, and are often highly altered by diagenetic processes. For example, even if $\delta^{18}\mathrm{O}$ curves are interpreted as temperature curves, $\delta^{13}\mathrm{C}$ curves as palaeo-productivity indicators, or $^{87}\mathrm{Sr}$ / $^{86}\mathrm{Sr}$ curves as an indicator for terrestrial weathering related to orogenies, a closer look usually reveals significant inconsistencies (see review in Munnecke et al., 2010).

The interval from the Cambrian to the Silurian is characterized by strong fluctuations in marine oxygen and carbon isotopes, with the Late Ordovician and Silurian periods in particular being characterized by very strong and obviously very rapid isotopic changes, suggesting that dramatic perturbations in the carbon cycle took place (Fig. 6). Since these excursions have been recognized globally, climatic control is assumed. However, the published models for this differ greatly from one author to another, and the relationships are still puzzling despite better-quality data sets. For example, a direct connection is postulated between the deposition of organically-rich ($^{12}\mathrm{C}$-rich) sediments and the $\delta^{13}\mathrm{C}$ curve. But the gigantic black shale deposits ("hot shales") deposited in the lowermost Silurian (Rhuddanian) in present-day North Africa, which contain around 80 to 90% of all Palaeozoic hydrocarbons in North Africa (Lüning et al., 2000; Soua, 2014), are surprisingly not reflected in the $\delta^{13}\mathrm{C}$ curve (Cramer et al., 2011a). But regardless of which climate model is correct (if any), it is noticeable that there are surprisingly few obvious relationships between isotope curves and the paleobiodiversity curves, as shown in Fig. 6. And if there are any, it seems that the short-term isotope excursions are related to a decrease rather than an increase in biodiversity. The two particularly strong positive carbon isotope excursions in the Hirnantian and in the Ludlow are associated with a decrease in diversity, which, however, begins well before the actual excursions. That leads to two conclusions. Either the environmental changes associated with the rapid isotope fluctuations did not have a strong effect on biodiversity, or the data sets available are not yet sufficient in terms of quantity and/or temporal resolution to demonstrate a possible connection. But, even if the short-term perturbations of the global $\delta^{13}\mathrm{C}$ curves are not directly reflected in the biodiversity data, it is noticeable that the high biodiversity in the Late Ordovician and the Silurian coincides with a time when the global carbon cycle was highly volatile.

The $^{87}\mathrm{Sr}/^{86}\mathrm{Sr}$ curve is also problematic. While the increase in values in the Silurian may be related to the Caledonian orogeny and the increased input of terrestrial weathering products (see Cramer et al., 2011b), the apparently rapid increase in Cambrian Stage 2 and the decrease in the Ordovician (especially in the Darriwilian) have been less well studied (Veizer et al., 1999; Shields and Veizer, 2004; Young et al., 2009; Saltzman et al., 2014). It is unclear, for example, what role the evolution of land plants and the associated changes in terrestrial weathering had on the Sr isotopic composition of the oceans (Servais et al., 2019), although some authors implicate a clear and direct link (e.g., Lenton et al., 2012).

Even though the quality and the amount of chemical and isotopic data have increased significantly in the last few decades, our picture of the early Palaeozoic Era is based almost entirely on the interpretation of data from low-latitude shelf deposits; thus, they remain strongly biased (see also Jones and Eichenseer, 2022). Abyssal deep-sea sediments are

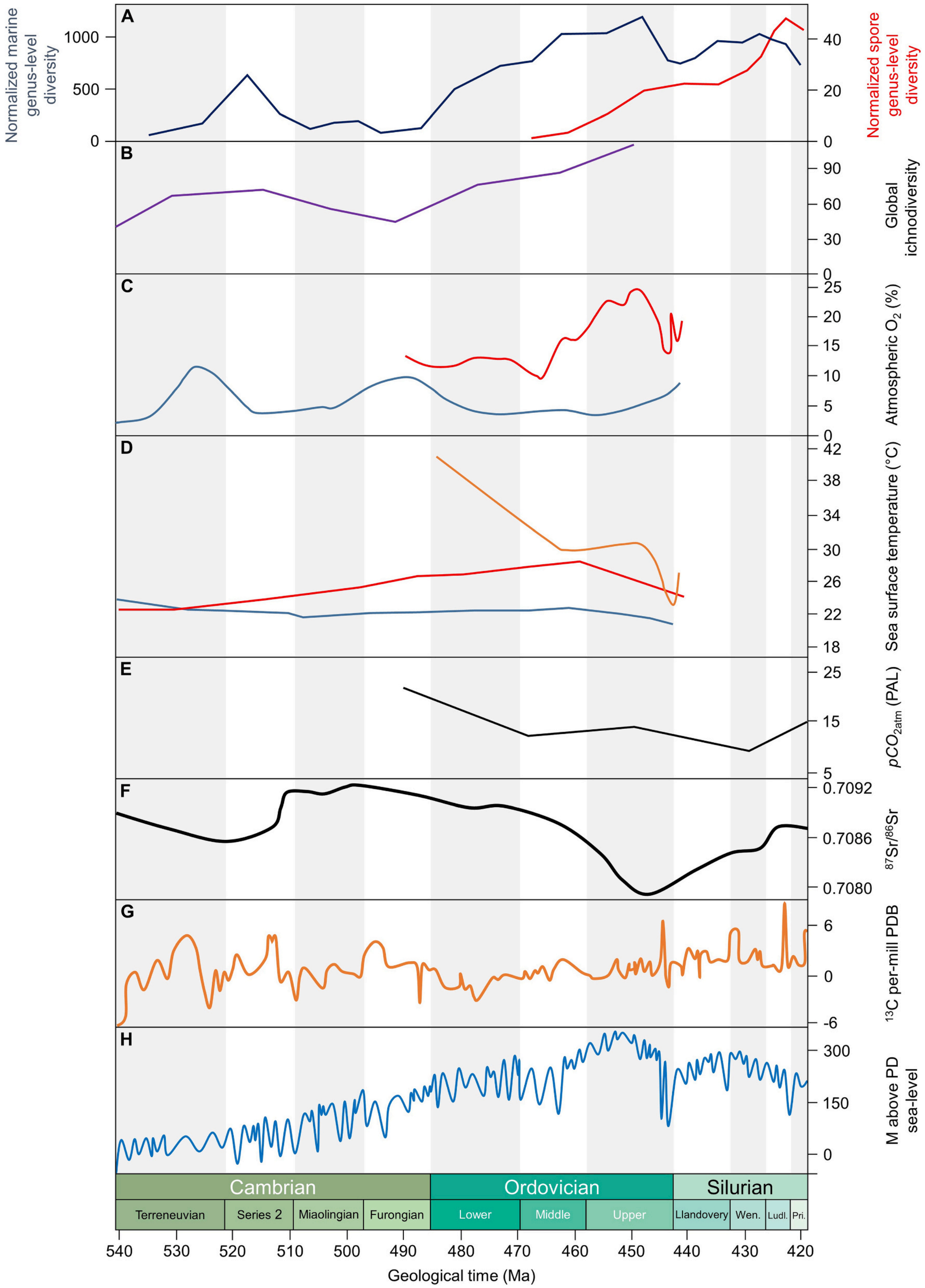

Fig. 6. Comparison of early Palaeozoic biodiversity curves and abiotic parameters. A, Normalized genus-level diversity curves of marine invertebrates (blue line) and land plant derived spores (red line), from Fig. 1D-E, plotted against: B, Global ichnodiversity (number of ichnogenera) during the Cambrian and Ordovician (Buatois et al., 2020, fig. 3); C, modelled pO_2 values during the Cambrian and Ordovician (Krause et al., 2018, blue line; Edwards, 2019, red line); D, Cambrian and Ordovician sea-surface temperature calculations from Mills et al. (2019), red and blue lines: updated GEOCARBSULF and COPSE models, versus Ordovician sea-surface temperature calculated by Trotter et al. (2008), orange line; E, modelled pCO_2 values (PAL) based on the GEOCLIM model (Nardin et al., 2011); F, $^{87}Sr/^{86}Sr$ ratios after McArthur et al. (2012); G, $\delta^{13}C$ curve after Ogg et al. (2016) (C) isotopes; H, global sea-level fluctuations after Haq and Schutter (2008). Modified and updated from Harper et al. (2020, fig. 6). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rarely preserved (e.g., in highly altered ophiolites) and reliable information about terrestrial biological and climatic processes are also extremely scarce. Most chemical proxies are extracted from only a small fraction of the ancient world, namely the shells of carbonate or phosphatic organisms of tropical and subtropical shelf-dwelling invertebrates.

It is thus extremely difficult to establish a (single) trigger, geological or extraterrestrial, for particular high levels of taxonomical richness, i.e., biodiversity, that have been recognized in some curves, in particular intervals considered short and of global impact, such as the Cambrian ‘Explosion’ or an Ordovician ‘event.’

6.2. A single radiation with a single, general trigger?

Fig. 6H illustrates the evolution of global sea-level changes, as modeled by Haq and Schutter (2008). Although sea-level curves must also be regarded carefully, there is today a general agreement about a continuous, slow, long-term increase of the early Palaeozoic sea levels from the early Cambrian towards the Late Ordovician. Servais et al. (2009), for example, noted that the presence of large tropical epicontinental seas, together with high sea-levels favoured a long-term radiation in the early Palaeozoic. It is indeed plausible that the long-term sea-level rise also influenced the single, long-term radiation that is observed in the fossil record of marine invertebrates. This interpretation is not new, and confirms previous studies. For example, Peters (2005) argued that during intervals of high sea level, biodiversity is high and during regression it decreases: transgressions provide increased habitable areas for marine biotas and thus an increased number of fossilizable organisms. McGowan and Smith (2008) together with Smith and McGowan (2011) confirmed the presence of a correlation between the quality of the rock record and the diversity of fossils. Smith et al. (2012), subsequently, provided evidence to indicate that large-scale cycles, which are in the order of about 100–150 myr, are the primary drivers of Phanerozoic marine diversity. Using the same line of evidence, Zaffos et al. (2017) confirmed the view of Valentine and Moores (1972) that plate tectonics regulate biodiversity, by using global databases to test an old model developed half a century ago. Zaffos et al. (2017) observed a positive correlation between global biodiversity and continental fragmentation, indicating that, at least for the Mesozoic breakup of the supercontinent Pangaea, the continental fragmentation has exerted a first-order control on the long-term trajectory of Phanerozoic marine animal diversity. Similarly, Roberts and Mannion (2019) indicated that fluctuations in sea level play an important role in driving Phanerozoic biodiversity at timescales >50 myr. They suggest that long timescale processes (e.g., plate kinematics) are the primary drivers of biodiversity, whereas the processes with significant variability at shorter intervals, such as glacioeustasy, continental uplift and erosion, volcanism, asteroid impact, may play a moderating role.

The continental configuration during the early Palaeozoic could indeed be the main trigger of a long-term radiation. The position of the major palaeocontinents and oceans is today widely accepted, and most recent early Palaeozoic palaeogeographical reconstructions all provide similar configurations. Fig. 7 includes maps for the Cambrian, Ordovician and Silurian (Fig. 7A-C), that allow recognition of the major continental movements. Of greatest importance is the increase during the early Palaeozoic of the extent of flooded epi-continental seas, in particular of tropical shelves, i.e., the areas where highest diversities and diversifications are recorded (Fig. 7D). As already indicated by Servais

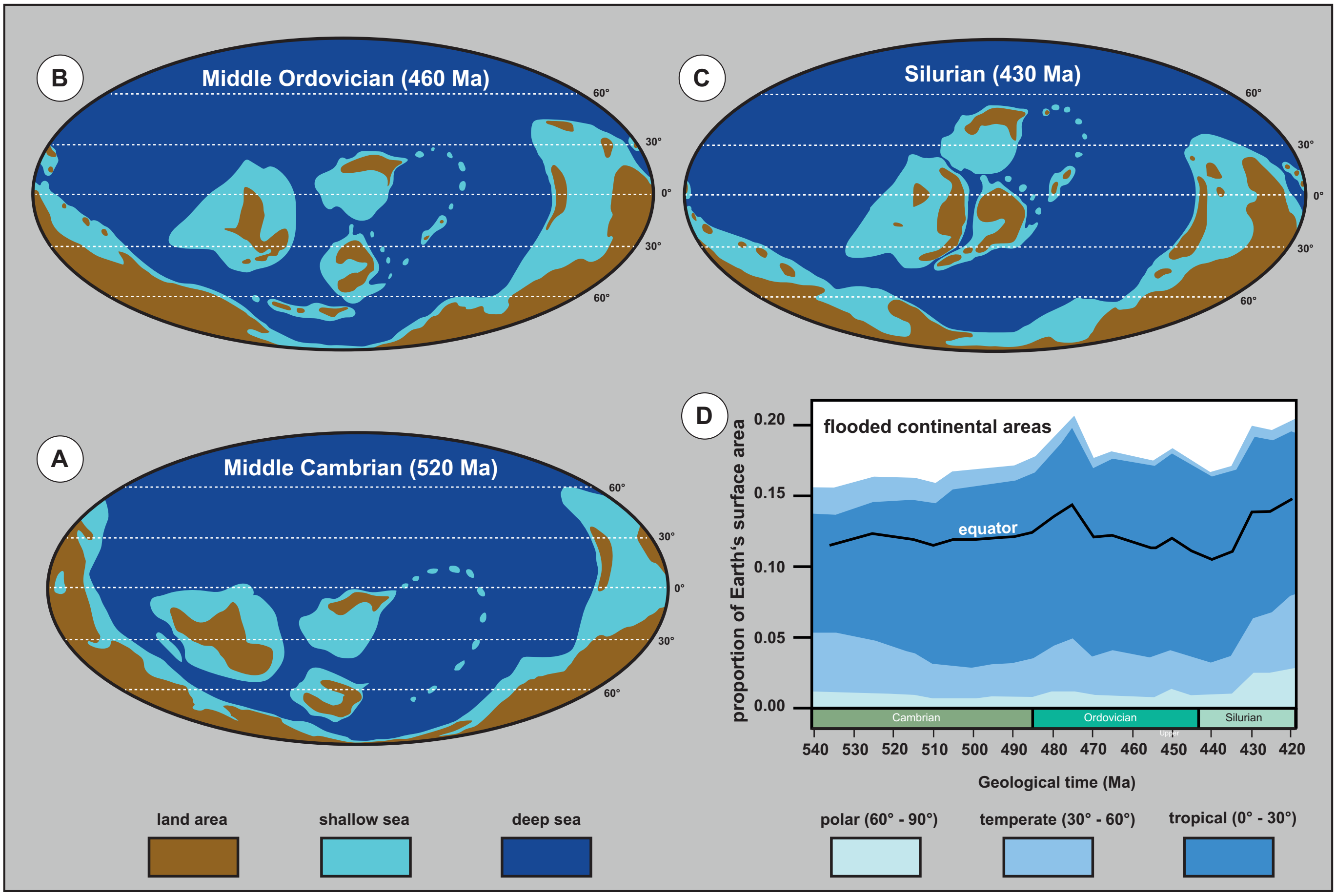

Fig. 7. Palaeobiogeography (A, middle Cambrian; B, Middle Ordovician; C, Silurian) and extent of tropical shelves (D) illustrating the proportion of flooded continental areas of Earth's surface (after Kocsis and Scotese, 2021).

et al. (2009, fig. 1), based on the studies of Walker et al. (2002), the abundance of tropical shelf areas reached a maximum during the Ordovician. Kocsis and Scotese (2021) confirmed this observation. Not only did the Ordovician represent the period with highest continental spreading of the entire Phanerozoic, it was also the geological interval with the largest areas of tropical shelves. The continental configuration during the early Palaeozoic is also the main trigger for the changing climate, with decreasing temperature from the early Cambrian to the middle Silurian (Nardin et al., 2011, fig. 4). In addition, it is now also assumed that the continental configuration controls ocean oxygenation during the Phanerozoic (Pohl et al., 2022). Changing climate, changing sea levels, increasing ocean oxygenation, and an increasing number of tropical shelf areas have all been considered as triggers of the early Palaeozoic radiations. All these parameters are directly linked to the evolution of the continental configuration. The ultimate (and possibly single) trigger for a long-term, continuous, and rather normal radiation, or biodiversification, during the early Palaeozoic could thus simply be the changing palaeogeography. This observation is neither spectacular, nor new, as it has been proposed as a potential scenario for large-scale radiations already many years ago, as described above.

7. Conclusion

1. Even if the fossil record in the marine realm includes some phases of rapid diversity fluctuation, our review of biodiversity patterns and trends indicates that the early Palaeozoic accommodated a single long-term radiation, of which the currently available datasets record only a fraction.
2. The continental fragmentation after the breakup of the supercontinent Pannotia and ensuing continuous drifting, represents a part of a large-scale cycle that most probably exerted a first-order control on this long-term early Palaeozoic radiation.
3. The available palaeontological datasets are incomplete, and none is truly global. The PBDB, although including ‘global’ data, is mostly based on sources from North America and Europe, whereas the GBDB captures and analyses data mainly from the different continental blocks belonging to China. The ‘global’ biodiversity curves are thus not truly global, but are most probably the sum of regional diversity and taxonomic trends.
4. The single long-term early Palaeozoic radiation has been partitioned, partly due to the absence of data in the fossil record from the upper Cambrian (the ‘Furongian Biodiversity Gap’), into two different radiations, the Cambrian ‘Explosion’ and the Great Ordovician Biodiversification ‘Event.’ However, it is impossible to identify a geological, ecological or extraterrestrial ‘event’ throughout the early Palaeozoic that altered profoundly the trajectory of the early Palaeozoic radiation. The Cambrian biodiversification was not a sudden burst (‘explosion’) of diversity, and the Ordovician biodiversification ‘event’ was not a real event.
5. Although defined by most authors as representing the first appearance of all animal phyla and of the different types of body plans - *Baupläne*, that took place during the late Precambrian and the earliest Cambrian, the Cambrian ‘Explosion’ has been restricted in the most recent datasets to specific intervals in Cambrian Series 2, presenting high recordings of taxa from the Cambrian *Lagerstätten*. An ‘explosion’ never took place.
6. Similarly, depending on the datasets interrogated, the Great Ordovician Biodiversification ‘Event’ has been interpreted as a phase of diversity increase, and has been located on published diversity curves at different intervals. Interpretations of the GBDB dataset place the GOBE in a late Cambrian to Early Ordovician interval, whereas interpretations of the PBDB dataset indicate the GOBE to a restricted interval in the early Middle Ordovician, which is in clear contradiction with the definition and the general understanding of the term.
7. Terms such as ‘radiation’ or ‘biodiversification’ are the most suitable to designate increases of taxonomic diversity, reflecting simple, normal fluctuations, without implying a dramatic or catastrophic nature of more emotive terms, such as ‘explosion,’ ‘revolution,’ or ‘event.’

Declaration of Competing Interest

We have no conflict of interest.

Data availability

No data was used for the research described in the article.

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