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Abstract. The Ordovician biodiversification is considered one of the most significant radiations in the marine ecosystems of the entire Phanerozoic. Originally recognized as the 'Ordovician Radiation', a label retained during most of the 1980s and 1990s, the term 'Great Ordovician Biodiversification Event' (GOBE) was coined in the late 1990s and was subsequently adopted by most of the scientific community. The Ordovician biodiversification, has always been considered as a long-term adaptive radiation, resulting in the sum of the different individual diversifications of all groups of marine organisms that occurred diachronously during the entire Ordovician. More recently, based on different palaeontological datasets, comprising data from different palaeogeographical areas, the Ordovician radiation has been interpreted to occur at different times in different places. This is most probably related to the palaeogeography of the Ordovician, when the major palaeocontinents were variously located in low latitudes triggering biodiversity 'hotspots' during different time intervals. In particular, some authors, using the potentially biased dataset of the Paleobiology Database (PBDB), have considered the GOBE to be an early Middle Ordovician global bio-event. Accordingly, the GOBE thus apparently corresponds to a relatively short time interval, with dramatic diversity fluctuations resulting in a profound change in marine environments at a global scale, visible by a major pulse in biodiversification of all fossil groups around the world. A critical analysis of the published biodiversity curves and of our own data confirm the traditional view; the Ordovician radiation is a complex, long-term process of multiple biodiversifications of marine organisms. Rapid increases in diversity can be identified for some fossil groups, at regional or palaeocontinental levels, in particular within limited datasets. However, a short, dramatic event that triggered major biodiversity pulses of all fossil groups at a global level at a particular time interval is an oversimplification.

Key words: biodiversity, Geobiodiversity Database, Great Ordovician Biodiversification Event, Paleobiology Database, radiation

Introduction

Since the dawn of the investigation of biodiversity during the Phanerozoic, i.e., the attempt to understand the evolution of marine and terrestrial ecosystems during Earth history, the idea of the major impact of global, rapid catastrophic events on the evolution of organisms has been repeatedly presented. The question of the abrupt origin of marine life during the Cambrian already puzzled Charles Darwin (1809-1882), for whom the sudden burst or

creation of life was a major dilemma. However, Darwin surmised correctly that there must have been an incredibly long period of evolution prior to the appearance of trilobites and other Cambrian organisms in the fossil record. Mass extinction of Tertiary taxa in the Paris Basin formed the basis for the George Cuvier's (1769-1832) cult of catastrophism.

In the last few decades the extinction of the dinosaurs near the Cretaceous-Paleogene boundary related to a gigantic and catastrophic meteorite impact has gained substantial media attention (Alvarez *et al*., 1980). Following this major discovery and its large impact on the wider public, the search for dramatic triggers for such mass extinctions has been the focus of many palaeontological studies in more recent years (e.g. Bond and Grasby, 2017).

Consequently, are the radiation and diversification of organisms in the fossil record the result of more or less dramatic events in Earth history? In this context, the apparentl sudden appearance of life during the earliest Cambrian, that puzzled Darwin, has been considered by many as corresponding to an 'explosive' process that took place during a very short time-interval. Simplistic scenarios (e.g. Fox, 2016) regularly promote the exciting story of the 'Cambrian Explosion,' although it is now understood that this 'explosion' was not a sudden burst of diversification, but a long-term evolutionary process that started in the late Precambrian and lasted throughout most of the Cambrian (e.g. Briggs, 2015; Zhu *et al*., 2017; Zhuravlev and Wood, 2018; Beasecker *et al*., 2020).

What happened in marine ecosystems after the Cambrian 'explosion'? The Ordovician radiation was first recognized by Sepkoski (1978) based on his fossil compendium of marine invertebrate organisms (Sepkoski, 1982, 1992, 2002). Most authors considered it as a complex, long-term evolutionary radiation following the Cambrian 'explosion' (e.g. Droser *et al*., 1996). The term 'Ordovician Radiation' was largely adopted (e.g. Sepkoski and Sheehan, 1983; Droser and Sheehan, 1997; Harper 2006), although it was clear for most palaeontologists that it was an accumulation of numerous, individual radiations, amply demonstrated by several authors (e.g. Sepkoski and Sheehan, 1983; Sepkoski, 1995; Miller, 2004).

In the frame of the 'International Geological Correlation Programme' (now named 'International Geoscience Programme', IGCP) n° 410, from 1997 to 2002 (Webby *et al*., 2004a), the term 'The Great Ordovician Biodiversification Event' was introduced, and due to the large international success of the project, this term has largely been adopted by the geological and palaeontological community (e.g. Servais *et al.,* 2009). The acronym 'GOBE' similarly became very popular and is commonly used today. However, never was 'The Great Ordovician Biodiversification Event' considered as being related to a single geological 'event' (Servais and Harper, 2018). The origin of the terminology 'The Great Ordovician Biodiversification Event,' proposed in 1996 to the UNESCO and the International Union of Geological Sciences (IUGS) as the title for an IGCP project, can easily be placed in the societal context of (bio-) stratigraphical studies in the late 1990s, that were at that time largely focused on geological events and event stratigraphy (e.g. Walliser, 1996a).

More recently, however, some authors have proposed more restricted time intervals of more or less short durations for the Ordovician radiation, based on biodiversity curves that were produced on the basis of datasets, considered as global by the authors (e.g. Kröger *et al.*, 2019; Rasmussen *et al*., 2019; Fan *et al*., 2020). While the first authors (Kröger *et al.*, 2019; Rasmussen *et al*., 2019) based their interpretation of a short GOBE in the Middle Ordovician on analyses of the Paleobiology Database (PBDB), the last authors (Fan *et al*., 2020) identified a ± 30 myr long GOBE in the late Cambrian and Early Ordovician, in the biodiversity curves generated by the Geobiodiversity Database (GBDB). In addition, in some recent publications, the Ordovician radiation, i.e., the 'Great Ordovician Biodiversification Event,' has been promoted by a few authors (e.g., Rasmussen *et al*., 2019; Stigall *et al*., 2019)

as a very short, global 'event', which is in clear contradiction to the definition and the general understanding of the term.

In the present study, we compare the various biodiversity curves published recently, based on datasets in the PBDB and the GBDB, respectively, and we include our own observations, to understand if sufficient evidence is provided to recognize a short global bio-event, or if, on the other hand, the traditional view of a long-term radiation can be sustained.

Ordovician Radiation or 'Great Ordovician Biodiversification Event?'

Cataclysm or Transformism?

A dispute existed already in the early 1800s between scientists in favour of a 'catastrophism' or 'cataclysm' and those who believed that the evolution of life follows the rules of routine processes, i.e., in some sort of 'transformism.' It was in France, the birthplace of the discipline of palaeontology, that the historical debate started (e.g. Servais *et al*., 2012). Georges Cuvier (Jean Léopold Nicolas Frédéric Cuvier, 1769-1832), who is today generally considered as the founder of palaeontology and of comparative anatomy as a scientific discipline, established the concept of "catastrophism". He presented his first palaeontological studies at the Académie des Sciences in Paris in 1796, and his view of biological events was largely accepted during the first part of the 19th century. Subsequently, Jean-Baptiste Pierre Antoine de Monet de la Marck (Jean-Baptiste Lamarck, 1744-1829), who is considered as one of the founders of biology as a life science and of invertebrate palaeontology as an independent discipline, developed the concept of 'transformative evolution' that is today considered a precursor to Darwinian evolutionary theory.

Today, it is evident that Cuvier's view was strongly biased and influenced by the position of the Christian Church, that generally accepted the undisputed concept of the Deluge, i.e. faunal changes in Earth History must have been the result of catastrophes, as explained in Genesis, the first book of the Christian Old Testament. Following Lamarck's initial studies, it was not until Charles Darwin that the ideas of evolutionary theory became generally accepted, in particular after the major publication '*On the Origin of Species*,' when Darwin (1859) developed the concept of gradualism in the evolution of organisms.

Evolution or revolution?

Were the evolution of marine and terrestrial ecosystems triggered by short-lived geological (or extra-terrestrial) processes, or were they just a consequence of normal geological processes (for example, regular trangressions and regressions), are questions that have been raised many times. The regular presentation of catastrophic events attracts the attention of the scientific community and the wider public. In the context of understanding the increase and decrease of biodiversity over time, extraordinary processes, such as the impact of meteorites, or the dramatic effects of earthquakes with the tsunamis that accompany them, or volcanic explosions, for example, have a much more emotional appeal than more continuous geological processes. A title of a scientific presentation or publication with phrases including 'mass extinction' or 'catastrophic event' clearly attracts more readers than a title that includes ordinary terms such as 'diversity decrease' or 'community change.'

The scientific argumentation about a giant bolide impact at the Cretaceous-Paleogene (K-T) boundary by Alvarez *et al.* (1980) certainly re-animated the long-standing debate

around the existence and significance of mass extinctions. Together with the identification of five major mass extinctions by Raup and Sepkoski (1982) the catastrophic nature of terrestrial (geological) or extraterrestrial processes became very popular and played a major role in the scientific discussions in the last four decades (e.g. Bond and Grasby, 2017). In addition, the potential cyclicity of major mass extinctions, of about 26 million years (Raup and Sepkoski, 1984), also gained traction within the scientific community. Periodicities in fossil-range data have been established by several authors, with cycles of about 60 myr (e.g. Rohde and Muller, 2005; Melott *et al*., 2012; Melott and Bambach, 2014) for which the causes remain unknown. However, Erlykin *et al*. (2017) provided evidence that the periodicities are statistically weak and indicated that the claim of regular astronomical phenomena contributing to mass extinctions is not well founded.

Major bio-events were the reasons to subdivide the Phanerozoic into different time units, originally defined as 'Systems,' 'Series' and 'Stages' in order to delimit different stratigraphical units at different scales. Clearly visible changes in the fossil composition of different rock units lead to the first view of three major radiations during the Phanerozoic of Phillips (1860). A major question, over two centuries old, is do rapid worldwide simultaneous changes in the geological and the palaeontological record really exist, or are they just driven by uniform geological processes.

The same question arises when we look at the early Palaeozoic biodiversification that includes the Cambrian 'explosion' and the 'Great' Ordovician Biodiversification 'Event': do we see catastrophic, dramatic 'events' and 'revolutions' in the fossil record, or is there simply an evolution, with a slow expansion of the palaeoecosystems?

Radiation or Event?

A cursory review of the literature reveals that different terms are used to describe the same process. Whereas some authors and editors, for example, Zhuravlev and Riding (2001a) support the 'Cambrian Radiation,' others clearly prefer the term 'Cambrian Explosion' (e.g., Erwin and Valentine, 2013).

Similarly, for the Ordovician, some authors and editors use the 'Ordovician Radiation' (e.g. Droser *et al*., 1996), whereas today terminologies including the words 'Great' and 'Event' attract significant attention: the 'Great Ordovician Biodiversification Event' clearly has dominated the titles of publications related to the Ordovician evolution of ecosystems in the last two decades (see a summary and discussion in Servais and Harper, 2018).

A radiation can be considered as an evolutionary and ecological expansion of life (e.g. Zhuravlev and Riding, 2001b). An adaptive radiation is usually considered as the evolution of an organism into a variety of morphotypes adapted to different life habitats and life modes. The term is common in evolutionary biology to describe the process of diversification from organisms into a multitude of new forms, that are adapted to new environments. It is evident that both the Cambrian and the Ordovician biodiversifications are adaptive radiations (e.g. Droser and Finnegan, 2003), either as separate radiations, or as a single process (e.g. Harper *et al*., 2019). It has, on the other hand, not been demonstrated so far that the early Palaeozoic radiation resulted from a succession of global 'events.'

Bio-event, global events, etc.

In his book 'Global Events and Event Stratigraphy in the Phanerozoic' Walliser (1996a) summarized the results of an international group of experts that focused their research

on various Phanerozoic global events in the frame of another IGCP project, n° 216 'Global Biological Events in Earth History.'

Walliser (1996b) noted that bio-events, often related to significant changes in lithology, were already used by Cuvier and most of the scientists of the 19th Century to subdivide the Phanerozoic. Logically, an international geological correlation programme, such as IGCP n° 216, is in search of such bio-events, that are *de rigueur* for basic research required to establish stratigraphical correlation and the definition of geological boundaries. However, over time it became obvious that many stratigraphical boundaries are diachronous, and thus the global coincidence of many geological events remains an ongoing debate.

Events are caused by short-term changes in the environment that can be the result of terrestrial or extra-terrestrial forces. Classic short-term terrestrial causes for a geological event are earthquakes (and their related tsunamis), or volcanic eruptions. The most obvious extra-terrestrial triggers of short-term events are the impacts on Earth, such as meteorite or planetoid impacts. Among the long-term terrestrial forces the most obvious are plate tectonics, whereas long-term extra-terrestrial forces include astrophysical forces, cosmic radiation, and also simply the planetary parameters of the Earth's motion in the solar system, including excentricity, obliquity and precession. All these forces have an impact on the Earth and the evolution of ecosystems.

It is generally assumed that geological events are short-lived (e.g. Walliser *in* Barnes et al., 1996b). Such events are documented and perceptible in rock successions. Many sudden changes occur as events in stratigraphical sections, including lithological, sedimentological, palaeoecological, and geochemical fluctuations. Their study is the field of event stratigraphy, that can thus be a stratigraphical research field focused on lithology, sedimentology, or geochemistry, respectively. In the late 1980s high resolution event stratigraphy (HIRES) became very popular. It was clearly a combination of several event stratigraphies (Kauffman, 1988).

Global events are those events that can be traced at a global level. Many stratigraphical boundaries, in particular biostratigraphical boundaries are controversial, because the (first) appearance of a fossil taxon is not necessarily a global phenomenon, which generates long debates leading to the definition of boundaries, in particular of many Global Boundary Stratotype Sections and Points (GGSP). This is also the case for the early Palaeozoic, where many of the Cambrian boundaries are debated, and the Cambrian-Ordovician boundary is being rediscussed (e.g., Babcock *et al*., 2015; Miller *et al*., 2018; Wang *et al*., 2019).

Global bio-events are those events that are related to clearly visible faunal or floral changes, and that can be recognized at a global level. For the Ordovician, Barnes et al. (1996a) recognized five major, 'higher order' global bio-events, that were in ascending order, the basal Tremadoc, basal Arenig, basal Llanvirn, basal Caradoc and upper Ashgill Bio-Events, i.e., those bio-events that were placed at some of the boundaries that were used to define the historical standard British Ordovician Series for the Ordovician System, as well as the Late Ordovician extinction 'event.'

Isotopic events have played a significant role in recent years; they include positive or negative excursions in isotope ratios that can be recorded in a sedimentary succession. In simple terms, the fluctuating isotope ratios include those of $\delta^{13}C$, that are usually used as palaeo-productivity proxies, of $\delta^{18}O$, that are interpreted as temperature indicators, of ^{87}Sr / ^{86}Sr, that are an indicator for terrestrial weathering related to orogenies and uplift, or those of $\delta^{14}S$, that can be used to recognize oxygen depletion in the ocean. The latter has been increasingly used for stratigraphical correlation. However, closer scrutiny usually reveals significant inconsistencies and strong interactions between the different proxies (see review in

Munnecke *et al*., 2010). Nevertheless, some isotope ratios have been increasingly used to delimit global stratigraphical horizons (e.g. Cramer et al., 2011a,b).

Ordovician Radiation or 'GOBE?'

Was there a 'cataclysm' during the Ordovician, or can we apply the rules of 'transformism?' Can we observe uniform, gradual change or a spectacular, dramatic revolution in the ecosystems? Are we facing a long-term adaptive radiation or a short-term event?

The significant increase in diversities of marine organisms during the Ordovician (Fig. 1A) was first recognized, numerically, by statistical analyses of the fossil compendium by Sepkoski (e.g. 1978, 1982). Subsequently, the Ordovician biodiversification has been considered by many authors to be the most significant increase of marine biodiversity during the entire Phanerozoic (e.g. Sepkoski, 1995; Harper, 2006, 2010; Algeo *et al.*, 2016).

As indicated in the introduction, since the original studies of Sepkoski, the Ordovician biodiversification was first described as a 'Radiation', and more recently the 'Great Ordovician Biodiversifiation Event.' The latter term was introduced by the co-leaders of IGCP n° 410 and it became very popular, including its suffix 'event.' However, it is obvious that none of the co-leaders of IGCP n° 410 considered the Ordovician radiation as an 'event.' All three co-leaders used the term radiation for the Ordovician biodiversification. In their publications, they never used the term 'event' and they never considered the Ordovician radiation to be a short-lived period (e.g. Droser *et al.*, 1996; Droser and Sheehan, 1997; Webby *et al.,* 2004a; Paris *et al.,* 2004; Achab and Paris, 2007).

Today, the Ordovician radiation is considered by most authors as a long-term, complex adaptive radiation. Servais and Harper (2018) and Goldman *et al.* (2020), for example, follow the traditional concept of the Ordovician radiation, as a long-term, complex mosaic of numerous regional biodiversifications. On the other hand, more dramatic scenarios have been published by other authors who restricted the term of the Ordovician radiation. Trotter *et al.* (2008) provided geochemical evidence for a global cooling that coincided with 'major biodiversity pulses' (Trotter *et al.*, 2008, fig. 3) in the Middle Ordovician, that, although reproduced from the same source (Webby *et al*., 2004b), do not correspond to the analyses of Servais *et al*. (2008, 2010) who clearly indicated that there was no synchroneity in the diversification pulses of the different fossil groups. More recently, Kröger *et al.* (2019, fig. 1) restricted the term GOBE to the Darriwilian, whereas Rasmussen *et al.* (2019) narrowed the concept of the GOBE to the early Darriwilian. Rasmussen *et al.* (2019) noted a particular diversity increase in the PBDB dataset at that time. Not surprisingly, this interval corresponds to the diversification pulses on the palaeocontinent of Baltica (e.g. Hammer, 2003; Hints *et al*., 2010) that moved during this time interval into low latitudes, to form large tropical epicontinental shelf areas, that are optimal for massive biodiversification (e.g. Servais *et al*., 2009). The concept of a restricted GOBE was also followed by Stigall *et al.* (2019). Stigall *et al.* (2017) previously introduced the term, 'Biotic Immigration Events' (BIME), to document regional biodiversification 'events,' such as the Richmondian Invasion (Holland, 1997; Stigall *et al.*, 2010).

Biodiversity curves illustrating the Ordovician radiation

Sepkoski's compendium and the Ordovician radiations

Sepkoski (e.g. Sepkoski, 1978, 1979, 1981, 1984, 1988, 1995, 1997) published a series of papers based on a multivariate statistical analysis of his fossil compendium (e.g. Sepkoski, 1982, 1992, 2002). He indicated the ranges of both families and about 37,000 genera of marine invertebrates that formed the basis of his widely-cited diversity curve that has subsequently been reproduced in all major palaeontology text-books. Sepkoski also defined the three 'Great Evolutionary Faunas' in the marine invertebrate fossil record, by including different classes of animals in the three categories that displayed contrasting diversity patterns: the Cambrian, Palaeozoic and Modern Faunas (e.g. Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985). In addition, Raup and Sepkoski (1982) recognized the five major mass extinctions in the marine fossil record, that have subsequently been used by most palaeontologists. Sepkoski's diversity curve (e.g., Sepkoski, 1981) indicated a rapid rise in the Cambrian and the Ordovician 'radiation' that led to a Palaeozoic 'plateau,' with the same levels of diversity until the end of the Permian, when the most severe of all 'mass extinctions' was recognized, the Permian-Triassic crisis.

The Ordovician radiation (Fig. 1A) was clearly visible in Sepkoski's curve who used time bins of approximately 5 myr to depict the biodiversity signals. After the Cambrian, the Ordovician showed a massive increase of the elements of the Palaeozoic Evolutionary Faunas. As indicated above, Sepkoski (1995) clearly considered the Ordovician as a period of numerous, diverse radiations.

The Paleobiology Database and an early Middle Ordovician GOBE 'event'

The Paleobiology Database, or PBDB (www.paleobiodb.org), was created in the late 1990s as a collection-based repository. It is maintained by an international non-governmental group of palaeontologists and is freely accessible. Over 400 scientists from over 20 countries have contributed to the database, with a clear majority of scientists from North America and western and northern Europe leading to a potential bias. A first major article was published by Alroy *et al.* (2008), based on a sampling-standardized analysis of the PBDB. The Phanerozoic biodiversity curve of marine invertebrates of Alroy *et al.* (2008, fig. 1) used 48 temporal bins of roughly equal length (averaging 11 myr), with a genus-level diversity clearly showing a single long-term radiation from the Cambrian to the early Devonian. Another curve without sampling bias correction (Alroy *et al.,* 2008, fig. 4) closely resembled Sepkoski's curve, however.

A large number of biodiversity curves have been generated from the PBDB and have been published, some of them in high-impact journals. A major criticism of some of these studies is the fact that, although including an enormous amount of data (over 400,000 taxa), the dataset remains incomplete, and is mostly concentrated on the 'western' world. Bush and Bambach (2015), for example, noted that the PBDB analyses did not capture the Mesozoic-Cenozoic diversification of marine metazoans, simply because they were based on incomplete data. Similarly, Close *et al.* (2020) used the fossil occurrence data for Phanerozoic tetrapods from the PBDB and noted that a global signal cannot be obtained, because of the incompleteness of the record in the dataset. These authors also indicated that one to two thirds of the variations in 'global' biodiversity curves can be explained by the regional signals in the dataset. In other words, the 'global' signal is not really global. Regarding the Ordovician, most of the data in the PBDB are from North American and European localities, the regional diversity trends from Laurentia and Baltica thus potentially influence strongly the 'global' signal in curves generated from the PBDB.

Rasmussen *et al*. (2019) published a diversity curve for the early Palaeozoic based on the data available in the PBDB. The authors recalculated the data in order to include them in a

set of 53 time slices for the early Palaeozoic. In order to correct sampling and preservation biases, Rasmussen *et al.* (2019) used different statistical methods, including the capture-recapture (CR) technique (Nichols and Pollock, 1983; Connolly and Miller, 2001; Liow and Nichols, 2010), the shareholder quorum subsampling method of Alroy (2010) and the new method of time binning introduced by Kröger and Lintulaakso (2017). Rasmussen *et al.* (2019) presented the curve based on the capture-recapture (CR) modeling, here reproduced in Figure 1C. Kröger *et al.* (2019) used the same dataset and presented a very similar curve (Kröger *et al.,* 2019, fig. 1; Figure 1B). Both curves (Fig. 1B and 1C) indicate very low diversities in Cambrian Series 1, but a strong increase of diversity in Cambrian Series 2 (Cambrian Stage 3), which corresponds to the massive input of data in the PBDB that Na and Kiessling (2015) identified previously. Both Rasmussen *et al.* (2019) and Kröger *et al.* (2019) interpreted this short interval as the Cambrian Explosion. They thus considered the Cambrian 'Explosion' as a diversity signal in their PBDB database, and not as a palaeobiological concept, as suggested by numerous authors (e.g. Erwin *et al*., 2011; Briggs, 2015; Paterson *et al*., 2018), who consider the 'explosion' to be related to the relatively short appearance in the fossil record of all animal phyla, accompanied by the arrival of innovative body plans (*Baupläne*). After this initial rise of diversity in the early Cambrian, the levels remain more or less constant during the remaining parts of the period (Miaolingian and Furongian, i.e., the Cambrian Series 3 and 4) until the Cambrian-Ordovician boundary. The relatively high numbers in the biodiversity curves of Rasmussen *et al.* (2019) and Kröger *et al.* (2019) in Cambrian Series 4 are surprising, clearly due to the recalculations with the capture-recapture (CR) modeling methods, because this interval in the PBDB includes almost no taxa; input of fossil data from the late Cambrian is almost totally absent so far, as discussed by Harper *et al.* (2019) (see below).

At the Cambrian-Ordovician boundary, the curves of both studies (Rasmussen *et al.*, 2019; Kröger *et al.,* 2019) start to show a clear increase, with a step-wise rise of the biodiversity, during the Early, Middle and Late Ordovician. The curves (Fig. 1B and 1C) show a continuous trend of diversity increase between Cambrian Epoch 2 and the Late (but not latest) Ordovician. The Ordovician radiation is thus clearly visible covering the entire Ordovician. Nevertheless, Rasmussen *et al.* (2019) considered the second rapid increase in the Darriwilian to be the 'GOBE.' Although it is not fully documented in that study, but if the 'global' data are derived from restricted continents, it appears evident that this rapid increase in the early Middle Ordovician precisely corresponds to the rapid increase of diversity that has been recorded on Baltica (e.g. Hammer, 2003; Hints *et al*., 2010). Kröger *et al.* (2019) also considered the 'GOBE' to be the interval during the Darriwilian with highest rise in diversity and a decrease in relative diversification rates.

Most surprisingly, in both studies, the authors highlight a particular, rather short interval of diversity increase in the PBDB as the main Ordovician 'event,' although it is clearly visible, even in their published curves (Fig. 1B and 1C), that the diversity increase is continuous, from the late Cambrian to the Late Ordovician, as most previous studies have already indicated.

The Geobiodiversity Database and a 30 myr long 'GOBE'

The Geobiodiversity Database (GBDB – www.geobiodiversity.com) was initiated in 2006 and was first available online in 2007 as an integrated system for the management and analysis of stratigraphic and palaeontological data (e.g., Fan *et al*., 2013, 2014). In comparison to the PBDB that is collection-based, the GBDB is a section-based database that includes not only data from palaeontologists, but also from specialists in sedimentology and

geochemistry and other related disciplines. The GBDB is the formal database of the International Commission on Stratigraphy (ICS); the main objective of the GBDB is to allow stratigraphical correlation and quantitative stratigraphy, developed with the help of several computer programmes, including CONOP (e.g., Sadler, 2001; Sadler *et al.,* 2009). Originally developed at the Nanjing Institute of Geology and Palaeontology, China, where the server and the supercomputer (Tianhe II) are located, the database was designed to compile all data from Chinese sections, although the global coverage is becoming more and more important.

The analyses of the GBDB allowed Fan *et al.* (2020) to produce a high-resolution summary of Cambrian to Early Triassic marine invertebrate biodiversity. The resulting curve, here reproduced in Fig. 2D, has been generated through calculations of billions of iterations per run, to allow the production of precise genus and species level diversity curves for different fossil groups. The total curve, representing the sum of the different fossil groups, indicates a sharp increase in diversity in the early Cambrian (but clearly prior to the onset of the diversity increase in the PBDB), followed by a 'pause' through the remaining parts of the Cambrian. A short diversity increase is visible at the end of Cambrian Series 3 with a short decrease before the Cambrian Series 4. At the base of the late Cambrian Series 4 starts the 'GOBE' of Fan *et al.* (2020): the authors related their 'GOBE' to a diversity increase in their biodiversity curve, which lasted precisely 29.72 myr. It started at 497.05 Ma (i.e. in the late Cambrian, at the base of the Furongian) and lasted until 467.33 Ma (i.e. until the early Middle Ordovician, near the base of the Darriwilian. Most importantly, the diversity increase ceased after this period. In the late Middle Ordovician the diversity even decreases. There is clearly no major diversity pulse observed on the different tectonic blocks and palaeocontinents that constituted China during the Darriwilian during this interval.

Where (and what) is the GOBE?

How complete are the databases: the input from fossil groups

The PBDB is highly visible, mostly due to several publications in high-impact publications, i.e., in journals of publishers that are generally located in North America and western Europe. But how complete is the PBDB? Several authors have already criticized the problem of incompleteness in the datasets, as indicated above (e.g., Bush and Bambach, 2015; Prothero, 2015; Close *et al*., 2020).

A quick look at the dataset immediately indicates that a particular interval in the Cambrian lacks data in the PBDB: the upper Cambrian Series 4, i.e., the Furongian Series (that includes the three uppermost Cambrian stages Paibian, Jiangshanian and the so far unnamed Stage 10), displays an almost complete lack of data. Two of the three stages actually show no genus-level occurrences at all in the PBDB (Harper *et al*., 2019, fig. 1). The Furongian is a time interval with few sedimentary rocks preserved, but sediments are available from several palaeocontinents. However, the lack of continuous sections in some of the most intensively studied areas most probably contributed to the absence of investigations, and thus also to the absence of data in the PBDB. It can also be hypothesized that few scientists worked in this interval. In summary, it appears evident that a 'Furongian Gap' artificially separates two geological intervals characterised by intense research activity, i.e. the Cambrian and Ordovician radiations (see also Harper *et al*., 2019).

It also rapidly becomes evident that the PBDB does not include data from all fossil groups. Harper *et al.* (2020) have already noted that for many groups the data in the PBDB are either absent, or only partly present. For the enigmatic group of chitinozoans, considered for many years as one of the key-elements for Ordovician biostratigraphy (e.g. Paris *et al*.,

2004) the exact biological affinity is still debated (e.g. Liang *et al*., 2020). Nevertheless, the chitinozoans are a group with a very good fossil record and with an accurate, precise biodiversification trajectory (e.g. Achab and Paris, 2007). Goldman *et al.* (2020) provided a detailed biodiversity curve for the group, based on over 230 taxa from over 1200 sections. However, there are so far no data in the PBDB related to the Chitinozoa. Similarly, the data for the Palaeozoic phytoplankton, represented by the acritarchs, are not in the PBDB. The published biodiversity curves related to this group are so far entirely based on databases that are not included in the PBDB (e.g. Servais *et al*., 2004, 2008; Nowak *et al.*, 2015; Zheng *et al.,* 2020). Another of the groups that is totally absent in the PBDB is the scolecodonts, i.e. the jaws of polychaete annelid worms. Biodiversity curves for this group are available, but no data are present in the PBDB (e.g. Erikssson *et al*., 2013).

For many other important early Palaeozoic fossil groups, the PBDB also lacks precise data (see Harper *et al*., 2020 for a review). Substantially complete datasets have been compiled during several IGCP projects, in particular the projects n° 410 and n° 503 (Webby *et al*., 2004a, Harper *et al*., 2011), with publications of diversity curves and palaeogeographical distribution patterns that are mostly published in specialized book series (e.g., Webby *et al*., 2004b; Harper and Servais, 2013). It becomes evident that only a fraction of the data produced are actually available in the PBDB. This situation is particularly true for the conodonts, graptolites and trilobites. Similar to the chitinozoans, Goldman *et al.* (2020) produced a biodiversity curve for the conodonts, based on over 3750 taxa from over 1200 sections. The same authors also analyze data from the graptolites from nearly 2300 taxa of over 600 sections, that allow construction of a diversity curve similar to that of Crampton *et al.* (2016) who used the same dataset. Similarly, to the three major groups used for biostratigraphy in the early Palaeozoic (i.e. graptolites, conodonts and chitinozoans), the data from the trilobites in the PDBD are also far from complete. Complete datasets used for this last group were prepared by specialists and are not available in the PBDB (e.g., Adrain *et al*., 1998; Adrain, 2013). The situation is the same for many other groups, like the blastozoan echinoderms (e.g. Nardin and Lefebvre, 2010) and bryozoans, for example (e.g. Ernst, 2018).

The GBDB is constructed differently. It is section-based and includes the data from almost all fossil groups. However, the major issue with this database is the fact that it is essentially focused on the data from the different parts of China (see below).

How global are the databases: the input from palaeocontinents

Another major issue with the databases is that they are not complete in terms of global coverage. The curves based on the datasets from both the PBDB and the GBDB attempt to provide a global picture, but it quickly becomes obvious that neither the PBDB (including mainly data from North America and Europe) nor the GBDB (focused on Chinese data) are truly global.

The PBDB aspires to global coverage, but so far most Ordovician data are from North America and western Europe, i.e. from the palaeocontinents of Laurentia, Baltica and Avalonia. This is also the major reason that Franeck and Liow (2019) limited their ‘dissection of the palaeogeographical dynamics’ of the GOBE to the two major continents of Laurentia and Baltica. On the other hand, Fan *et al.* (2020) noted that the Chinese sections that generate most of the data in the GBDB are located on different tectonic blocks (South China including the Yangtze Platform, but also North China, Tarim, etc.) that occupied different palaeolatitudes and thus provide a more global biodiversity pattern. However, it is obvious that the data do not cover the entire Ordovician world, but only a fraction of the available shelf areas present during the Ordovician. For the Silurian and Devonian, some European data

have been added to the GBDB because these intervals were poorly represented in the original (Chinese) dataset.

It is also perfectly well known that many palaeogeographical areas of the Ordovician have not yet been investigated (e.g. Antarctica, but also major parts of Africa, etc.), while for other regions (e.g. Latino-America, Middle East, etc.) the very rich data are not (yet) fully included in the databases.

Both the GBDB and PBDB thus provide signals that are not complete in terms of palaeogeography, although the resulting biodiversity curves have been presented as or are interpreted as 'global.'

To sum up, it is not surprising to see that the two different datasets provide different signals for the 'Cambrian Explosion' and the 'Great Ordovician Biodiversification Event.' The onset of the increase of Cambrian data differs slightly in both datasets, with data from the GBDB appearing earlier in the fossil record than in the PBDB (Fig. 1). For the Ordovician, the patterns are totally different.

Where are the GOBEs?

In Fig. 1, we plot the different 'global' biodiversity curves that have been produced in previous studies: Sepkoski (1995), mostly focused on the Ordovician data presented in his compendium (Fig. 1A), Kröger *et al.* (2019, fig. 1a), based on the PBDB (Fig. 1B), Rasmussen *et al.* (2019, fig. 2a), using basically the same data (Fig. 1C) and Fang *et al.* (2020, fig. 1A), based on the GBDB (Fig. 1D). All these biodiversity curves provide a similar signal, with a long-term radiation from the early Cambrian to the Late Ordovician. Whereas the recognition of the Cambrian 'explosion' differs slightly in the datasets of the PBDB and GBDB, the concept and duration of the GOBE are very different.

Sepkoski (1995) considered that the entire Ordovician Period, from the Tremadocian to the Ashgillian, documented a continuous increase in diversity, that he attributed to several radiations (Fig. 1A). In his curve, representing all groups, three more levels of rapid increase are visible. Sepkoski's dataset and curves were far from complete, but they provided a very good indication, in particular when considering the data available when they were drawn. This curve prompts the question, when did the GOBE, i.e. the Ordovician radiations, start. This was also the main focus of IGCP n° 653 (2016-2020), that attempted to understand the 'onset of the GOBE' (Harper and Servais, 2018). The concept of a complex, long-term, continuous radiation in the Ordovician is one that many Ordovician specialists accept, following Sepkoski (e.g., Droser *et al*., 1996; Webby *et al*., 2004a; Servais *et al*., 2010; Servais and Harper, 2018; Goldman *et al*., 2020): the duration of the GOBE spans the entire Ordovician. The onset of the Ordovician radiations for some groups may have started in the late Cambrian (e.g. Servais et al., 2006), but the 'Furongian Gap' clearly separates the Cambrian and Ordovician radiations, as indicated above.

Kröger *et al.* (2019) defined a short GOBE in the late Middle Ordovician (Darriwilian Stage) (Fig. 1B). They not only used the increase of diversity for their interpretation of the GOBE, but also different diversity measurements (such as varying relative diversification rates or extinction/origination rates). Rasmussen *et al.* (2019), on the other hand (Fig. 1C), considered the rapid increase in their biodiversity curve as the GOBE *sensu stricto*. This interval corresponds to the diversity increase recognized from the palaeocontinent Baltica, at the base of the Darriwilian. Finally, Fan *et al.* (2020), based on the Chinese data, have proposed a longer GOBE, of about 30 myr duration, starting at the base of the Furongian, and finishing before the start of the Middle Ordovician (Fig. 1C).

No 'event' and 'no global diversity pulses'

It is tempting to search for spectacular explanations for an Ordovician 'event' rather than to describe a normal, long-term 'radiation.' This also affected the search in the last decades for more or less spectacular or 'dramatic' triggers of an Ordovician 'event.' Was there a terrestrial or extra-terrestrial event, i.e., a relatively 'short-lived' process, that happened during the Ordovician?

Barnes (2004) correlated a mantle superplume with the GOBE. However, there are no geological traces of such a plume, with no major basalt trap accumulations preserved. Lefebvre *et al.* (2010) tested the hypothesis with a carbon cycle model, and indicated that a scenario including a mantle superplume during the Late Ordovician would generate the Katian warming event, recognized as the 'Boda Event' by Fortey and Cocks (2005), and the subsequent Hirnantian cooling. On the other hand, Schmitz *et al*., (e.g. 2008, 2019) provided evidence that the largest meteorite shower of the entire Earth's history took place at ~466 Ma, i.e. during the early Darriwilian. A possible link between this large breakup of an L-chondrite parent body in an asteroid belt and the GOBE focussed on Baltica has been proposed (Schmitz *et al*., 2008, 2019), but Lindskog *et al*. (2017) pointed out that, in their view, the precise stratigraphical interval of the meteorite showers and the diversification do not match. Even if a link with the 'GOBE' *sensu* Rasmussen *et al.* (2019) is tempting, it must be pointed out that at the same interval, the diversity in the GBDB is falling. We need future, detailed studies to understand the possible influence of the meteorite shower on a possible diversification.

Other short-lived events, i.e., real global events, have not been described in the Ordovician. It is more logical to search for longer-term processes, terrestrial or extra-terrestrial, to understand the Ordovician radiation, and its onset. The long-term, terrestrial drivers that are the most obvious to explain a long-term radiation, that are clearly visible in the biodiversity curves (Fig. 1), are plate tectonic movements, surely with complex multiple triggers. These have also clearly been related to climate change, with a general cooling trend in the Ordovician (e.g., Trotter *et al.,* 2008; Vandenbroucke *et al*., 2010; Nardin *et al.,* 2011; Rasmussen *et al*., 2016). Oxygenation 'events' also played a role, but similarly, they cannot be considered as true, short-lived 'events'. Although different, and sometimes completely opposing interpretations are presented for oxygen levels in the Ordovician (e.g. Munnecke *et al*., 2010), there is now general agreement that oxygenation levels increased during the Ordovician (e.g. Saltzman *et al*., 2011; Algeo *et al*., 2016; Edwards *et al*., 2017).

If it is difficult to find a short-term geological or extraterrestrial event in the Ordovician, do we then see an interval of 'major biodiversity pulses' as postulated by Trotter *et al.* (2008), similarly interpreted in Kröger *et al.* (2019) and Rasmussen *et al.* (2019). In terms of the different fossil groups, it is obvious that the radiations did not take place at the same time: the different groups clearly show different biodiversity 'pulses' (Webby *et al*., 2004b; Servais *et al*., 2010; Harper *et al*., 2020; Goldman *et al*., 2020), and not conflated to indicate a single major biodiversity 'pulse' in the Middle Ordovician, as suggested by Trotter *et al.* (2008). These 'major biodiversity pulses,' clearly visible in some datasets, may correspond to the diversity increases in the palaeocontinents of Baltica and Laurentia, but are not recorded in the tectonic blocks that formed China. The 'global' biodiversity curves presented (Fig. 1) most probably result from the input of data from a selection of the different palaeocontinents, and do not provide a complete picture, in a similar way as Close *et al*. (2020) indicated for the 'global' signal of the diversity dynamics of terrestrial tetrapods, that is just the sum of the regional datasets. This observation has already been made by Paris *et al.* (2004) for Ordovician chitinozoans. We clearly need more detailed studies in future to

distinguish the regional and 'global' signals in our biodiversity curves for the marine invertebrates in the Ordovician.

Conclusion

1. The Ordovician biodiversification is considered as one of the most significant intervals of biodiversity increase in marine ecosystems during the Phanerozoic. It was a long-term adaptive radiation, resulting in the sum of the different individual diversifications across all fossil groups of marine organisms globally, that occurred during different intervals and places during the Ordovician.
2. The 'global' datasets of the PBDB and the GBDB are not really global. The first dataset is mainly focused on the palaeocontinents of Laurentia and Baltica, whereas the second hosts essentially data from China. In addition, the PBDB lacks data from several fossil groups, and for others, the input remains sporadic and/or incomplete.
3. A global bio-event, constituted by a major pulse in biodiversification in all fossil groups at a global level during the early Middle Ordovician, interpreted in some analyses of the PBDB, is not visible in other datasets and cannot be confirmed. On the contrary, the GBDB shows a completely opposite signal for this early Middle Ordovician interval.
4. The interpretation of the Great Ordovician Biodiversification Event (GOBE), as a short 'event' during the early Middle Ordovician recently recognized in the Paleobiology Database (PBDB), and, to a lesser extent, as a biodiversification of ± 30 myr. in a time interval spanning the late Ordovician and the Early Ordovician recognized in the Geobiodiversity Database (GBDB), are in contradiction with the definition and the general understanding of the term. These datasets are neither complete, nor truly global, although they provide significant regional signals.
5. The term 'event' is misleading for the GOBE. Other more classical terminologies, such as 'radiation' or 'biodiversification,' are more suitable to designate the increase of taxonomic diversity during the Ordovician, because they do not imply a dramatic, sudden or catastrophic nature for the long-term Ordovician radiation.

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References

Achab, A. and Paris, F., 2007: The Ordovician chitinozoan biodiversification and its leading factors. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 245, p. 5–19.

Adrain, J. M. 2013: A synopsis of Ordovician trilobite distribution and diversity. *In*: Harper, D.A.T. and Servais, T. *eds*., *Early Palaeozoic Biogeography and Palaeogeography. Geological Society*, *London, Memoirs*, 38, p. 297–336.

Adrain, J. M., Fortey, R. A. and Westrop, S. R., 1998: Post-Cambrian trilobite diversity and evolutionary faunas. *Science*, vol. 280, p. 1922–1925.

Algeo, T. J., Marenco, P. J. and Saltzman, M. R., 2016: Co-evolution of oceans, climate, and the biosphere during the 'Ordovician Revolution'. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 458, p. 1–11.

Alroy, J., 2010: The shifting balance of diversity among major marine animal groups. *Science*, vol. 329, p. 1191–1994.

Alroy, J., Aberhan, M., Bottjer, D. J., Foote, M., Fürsich, F. T., Harries, P. J., Hendy, A. J., Holland, S. M., Ivany, L. C., Kiessling, W., Kosnik, M. A., Marshall, C. R., McGowan, A. I., Miller, A. I., Olszewski, T. D., Patzkowsky, M. E., Peters, S. E., Villier, L., Wagner, P. J., Bonuso, M., Borkow, P. S., Brenneis, B., Clapham, M. E., Fall, L. M., Ferguson, C. A., Hanson, V. L., Krug, A. Z., Layou, K. M., Leckey, E. H., Nürnberg, S., Powers, C. M., Sessa, J. A., Simpson, C., Tomašových, A. and Visaggi, C. C., 2008: Phanerozoic trends in the global diversity of marine invertebrates. *Science*, vol. 321, p. 97–100.

Alvarez, L. W., Alvarez, W., Asaro, F. and Michel, H. V., 1980: Extraterrestrial cause for the Cretaceous–Tertiary extinction. *Science*, vol. 208, p. 1095–1108.

Babcock, L. E., Peng, S. C., Brett, C. E., Zhu, M. Y., Ahlberg, P., Bevis, M. and Robison, R.A., 2015: Global climate, sea-level cycles, and biotic events in the Cambrian Period. *Palaeoworld*, vol. 24, p. 5–15.

Barnes, C., Fortey, R. A and Williams, S. H. 1996: The pattern of global bio-events during the Ordovician Period. *In*: Walliser, O. H. ed., Global Events and Event Stratigraphy, Springer, Berlin. p. 139-172.

Barnes, C., Hallam, A., Kaljo, D., Kauffman, E. G. and Walliser, O. H. 1996b: Global Event Stratigraphy. *In*: Walliser, O. H. ed., Global Events and Event Stratigraphy, Springer, Berlin. p. 319-333.

Barnes, C. R., 2004: Was there an Ordovician superplume event? *In*: Webby, B. D., Paris, F., Droser, M. L. and Percival, I. G. *eds*., *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, p. 77–80.

Beasecker, J., Chamberlin, Z., Lane, N., Reynolds, K., Stack, J., Wahrer, K., Wolff, A., Devilbiss, J., Whar, C., Durbin, D., Garneau, H. and Brandt, D., 2020: It's time to defuse the Cambrian "Explosion". GSA Today, vol. 31, https://doi.org/10.1130/GSATG460GW.1

Bond, D. P. G. and Grasby, S. E. 2017: On the causes of mass extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 478, p. 3-29.

Briggs, D. E. G., 2015: The Cambrian Explosion. *Current Biology*, vol. 25, p. 864–868.

Bush, A. M. and Bambach, R. K., 2015: Sustained Mesozoic-Cenozoic diversification of marine metazoa: a consistent signal from the fossil record. *Geology*, vol. 43, p. 979–982.

Close, R. A., Benson, R. B. J., Alroy, J., Carrano, M. T., Cleary, T. J., Dunne, E. M., Mannion, P. D., Uhen, M. D., Butler, R. J., 2020: The apparent exponential radiation of Phanerozoic land vertebrates is an artefact of spatial sampling bias. *Proceedings Royal Society B*, vol. 287, 20200372.

Connolly, S. R. and Miller, A. I., 2001: Joint estimation of sampling and turnover rates from fossil databases: Capture–mark–recapture methods revisited. *Paleobiology*, vol. 27, p. 751–767.

Cooper, R., 2004: Measures of diversity. *In*: Webby, B. D., Paris, F., Droser, M. L. and Percival, I. G. *eds*., *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, p. 52–57.

Cramer, B. D., Brett, C. E., Melchin, M. J., Männik, P., Kleffner, M. A., McLaughlin, P. I., Loydell, D. K., Munnecke, A., Jeppsson, L., Corradini, C., Brunton, F. R. and Saltzman, M. R., 2011a: Revised correlation of Silurian Provincial Series of North America with global and regional chronostratigraphic units and $\delta^{13}C_{carb}$ chemostratigraphy. *Lethaia*, vol. 44, p. 185–202.

Cramer, B. D., Munnecke, A., Schofield, D. I., Haase, K. M. and Haase-Schramm, A., 2011b: A revised $^{87}Sr/^{86}Sr$ curve for the Silurian: Implications for global ocean chemistry and the Silurian timescale. *The Journal of Geology*, vol. 119, p. 335–349.

Crampton, J. S., Cooper, R. A., Sadler, P. M. and Foote, M., 2016: Greenhouse-icehouse transition in the Late Ordovician marks a step change in extinction regime in the marine plankton. *Proceedings of the National Academy of Sciences of the USA*, vol. 113, p. 1498–1503.

Darwin, C., 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London.

Droser, M. L. and Sheehan, P. M., 1997: Palaeoecology of the Ordovician radiation: resolution of large-scale patterns with individual clade histories, palaeogeography and environments. *Geobios, Mémoire Spécial*, vol. 20, p. 221– 229.

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

Edwards, C. T., Saltzman, M. R., Royer, D. L. and Fike, D. A., 2017: Oxygenation as a driver of the Great Ordovician Biodiversification Event. *Nature Geoscience*, vol. 10, p. 925–959.

Eriksson, M. E., Hints, O., Paxton, H. and Tonarova, P., 2013: Ordovician and Silurian polychaete diversity and biogeography. *In*: Harper, D.A.T. and Servais, T. *eds*., *Early Palaeozoic Biogeography and Palaeogeography. Geological Society*, *London, Memoirs*, 38, p. 265–272.

Erlykin, A. D., Harper, D. A. T., Sloan, T. and Wolfendale, A.W., 2017. Mass extinctions over the last 500 myr: an astronomical cause? Palaeontology, vol. 60, p. 159-167.

Ernst, A., 2018: Diversity dynamics of Ordovician Bryozoa. *Lethaia,* vol. 51, p. 198–206.

Erwin, D. and Valentine, J., 2013: *The Cambrian Explosion: The Construction of Animal Biodiversity*. W. H. Freeman, p. 1–416.

Erwin, D. H., Laflamme, M., Tweedt, S. M., Sperling, E. A., Pisani, D. and Peterson, K. J., 2011: The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science*, vol. 334, p. 1091–1097.

Fan, J., Chen, Q., Hou, X., Miller, A. I., Melchin, M. J., Shen, S., Wu, S., Goldman, G., Mitchell, C. E., Yang, Q., Zhang, Y., Zhan, R., Wang, J., Leng, Q., Zhang, H. and Zhang, L., 2013: Geobiodiversity Database: a comprehensive section-based integration of stratigraphic and paleontological data. *Newsletters on Stratigraphy*, vol. 46, p. 111–136.

Fan, J., Hou, X., Chen, Q., Melchin, M. J., Goldman, D., Zhang, L. and Chen, Z., 2014: Geobiodiversity Database (GBDB) in stratigraphic, palaeontological and palaeogeographic research: graptolites as an example. *GFF*, vol. 136, p. 70–74.

Fan, J., Shen, S., Erwin, D. H., Sadler, P. M., MacLeod, N., Cheng, Q., Hou, X., Yang, J., Wang, S., Wang, Y., Zhang, H., Chen, X., Li, G., Zhang, Y., Shi, Y., Yuan, D., Chen, Q, Zhang, L., Li, C. and Zhao, Y., 2020: A high resolution summary of Cambrian to Early Triassic marine invertebrate biodiversity. *Science*, vol. 367, p. 272–277

Fortey, R. A. and Cocks, L. R. M., 2005: Late Ordovician global warming—the Boda event. *Geology*, vol. 33, p. 405–408.

Fox, D., 2016: What sparked the Cambrian Explosion? *Nature*, vol. 530, p. 268–270.

Franeck, F. and Liow, L. H., 2019: Dissecting the paleocontinenatl and paleoenvironmental dynamics of the great Ordovician biodiversification. *Paleobiology*, vol. 45, p. 1-14.

Goldman, D., Sadler, P.M. and Leslie, S.A., 2020: The Ordovician Period. *In*: Gradstein, F.M., Ogg, J. M., Schmitz, M. D., Ogg, G. M. *eds*., Geological Time Scale 2020. Elsevier (in print).

Hammer, Ø., 2003: Biodiversity curves for the Ordovician of Baltoscandia. *Lethaia*, vol. 36, p. 305–314.

Harper, D. A. T., 2006: The Ordovician biodiversification: Setting an agenda for marine life. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 232, p. 148–166.

Harper, D. A. T., 2010: The Ordovician Radiation: Roles of alpha, beta and gamma diversity. *Geological Society of America, Special Paper*, vol. 466, p. 69–83.

Harper, D. A. T. and Servais, T., *eds.* 2013: *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoir 38, p. 1–490.

Harper, D. A. T. and Servais, T., 2018: Contextualizing the onset of the Great Ordovician Biodiversification Event. *Lethaia*, vol. 51: 149–323.

Harper, D. A. T., Li, J., Munnecke, A., Owen, A. W., Servais, T. and Sheehan, P. M., 2011: Concluding IGCP 503: towards a holistic view of the Ordovician and Silurian Earth systems. *Episodes*, vol. 34, p. 32-38.

Harper, D. A. T., Topper, T. P., Cascales-Miñana, B., Servais, T., Zhang, Y. D. and Ahlberg, P., 2019: The Furongian (late Cambrian) Biodiversity Gap: Real or apparent? *Palaeoworld*, vol. 28, p. 4–12.

Harper, D. A. T., Cascales-Miñana, B. and Servais, T. 2020: Early Palaeozoic diversifications and extinctions in the marine biosphere: a continuum of change. *Geological Magazine*, vol. 157, p. 5–21.

Hints, O., Delabroye, A., Nolvak, J., Servais, T., Uutela, A. and Wallin, Å., 2010: Biodiversity patterns of Ordovician marine microphytoplankton from Baltica: comparison with other fossil groups and sea-level changes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 294, p. 161–173.

Holland, S.M., 1997: Using time/environment analysis to recognize faunal events in the Upper Ordovician of the Cincinnati Arch. *In*: Brett, C. E. and Baird, G. C., eds. *Palaeontological Event Horizons: ecological and evolutionary implications*. Columbia University Press, New York, p. 309–334.

Kauffmann, E. G. 1988: Concepts and methods of high-resolution event stratigraphy. *Annual Review of Earth and Planetary Sciences*, vol. 16, p. 605-654.

Kröger, B. and Lintulaakso, K., 2017: RNames, a stratigraphical database designed for the statistical analysis of fossil occurrences - the Ordovician diversification as a case study. *Palaeontologica Electronica*, vol. 20.1.1T, p. 1–12.

Kröger, B., Franeck, F. and Rasmussen, C. M. Ø., 2019: The evolutionary dynamics of the early Palaeozoic marine biodiversity accumulation. *Proceedings of the Royal Society B* 286, 20191634.

Lefebvre, V., Servais, T., François, L. and Averbuch, O., 2010: Did a Katian large igneous province trigger the Late Ordovician glaciation? A hypothesis tested with a carbon cycle model. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 296, p. 310–319.

Liang, Y., Hints, O., Tang, P., Cai, C., Goldman, D., Nolvak, J., Tihelka, E., Pang, K., Bernardo, J. and Wang, W., 2020. Fossilized reproductive modes reveal a protistan affinity of Chitinozoa. Geology, vol. 48, p. 47865.1.

Lindskog, A., Costa, M. M., Rasmussen, C. M. Ø., Connelly, J. N. and Eriksson, M. E., 2017: Refined Ordovician timescale reveals no link between asteroid breakup and biodiversification. *Nature Communications*, vol. 8, 14066 (2017).

Liow, L. H. and Nichols, J. D., 2010: Estimating rates and probabilities of origination and extinction using taxonomic occurrence data: Capture–mark–recapture (CMR) approaches. *The Paleontological Society Short Course, October 30th, 2010* (The Paleontological Society, Bethesda), p. 81–94.

Melott, A. L, Bambach, R. K., Petersen, K. D. and McArthus, J. M., 2012. An ~60-million-year periodicity is common to marine $^{87}Sr/^{86}Sr$, fossil biodiversity and large-scale sedimentation: what does the periodicity reflect? *Journal of Geology*, vol. 120, p. 217-226.

Melott, A. L. and Bambach, R. K., 2014: Analysis of periodicity of extinction using the 2012 geological timescale. *Paleobiology*, vol. 40, p. 177-196.

Miller, A.I., 2004: The Ordovician radiation. *In*: Webby, B. D., Paris, F., Droser, M. L. and Percival, I. G. *eds*., *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, p. 72–76.

Miller, J. F., Evans, K. R., Freeman, R. L., Loch, J. D., Ripperdan, R. L. and Taylor, J. F., 2018: Combining biostratigraphy, carbon isotope stratigraphy and sequence stratigraphy to define the base of Cambrian Stage 10. *Australasian Palaeontological Memoirs*, vol. 51, p. 19-64.

Munnecke, A., Calner, M., Harper, D. A. T. and Servais, T., 2010: Ordovician and Silurian sea–water chemistry, sea level, and climate: A synopsis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 296, p. 389–413.

Na, L. and Kiessling, W., 2015: Diversity partitioning during the Cambrian radiation. *Proceedings of the National Academy of Sciences of the USA*, vol. 112, p. 4702–4706.

Nardin, E. and Lefebvre, B., 2010: Unravelling extrinsic and intrinsic factors of the early Palaeozoic diversification of the blastozoan echinoderms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 294, 142–160.

Nardin, E., Goddéris, Y., Donnadieu, Y., Le Hir, G., Blakey, R. C., Pucéat, E. and Aretz, M., 2011: Modeling the early Paleozoic long-term climatic trend. *Geological Society America Bulletin*, vol. 123, p. 1181–1192.

Nichols, J.D. and Pollock, K. H., 1983: Estimating taxonomic diversity, extinction rates, and speciation rates from fossil data using capture–recapture models. *Paleobiology*, vol. 9, p. 150–163.

Nowak, H., Servais, T., Monnet, C., Molyneux, S. G. and Vandenbroucke, T. R. A., 2015: Phytoplankton dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification Event: a review of Cambrian acritarch diversity. *Earth-Science Review*, vol. 151, p. 117–131.

Paris, F., Achab, A., Asselin, E., Chen, X. H., Grahn, Y., Nolvak, J., Obut, O., Samuelsson, J., Sennikof, N., Vecoli, M., Verniers, J., Wang, X. F. and Winchester-Seeto, T. 2004: Chitinozoa. *In*: Webby, B. D., Paris, F., Droser, M. L. and Percival, I. G. *eds*., *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, p. 294–311.

Paterson, J. R., Edgecombe, G. D. and Lee, M. S. Y., 2019: Trilobite evolutionary rates constrain the duration of the Cambrian explosion. *Proceedings of the National Academy of Sciences of the USA*, vol. 116, p. 4394–4399.

Phillips, J., 1860: *Life on Earth: its origin and succession*. University Press, Cambridge.

Prothero, D. R., 2015: Garbage in, garbage out: the effect of immature taxonomy on database compilations of North American fossil mammals. *New Mexico Museum of Natural History and Science Bulletin*, vol. 67, p. 257–264.

Rasmussen, C. M. Ø., Ullmann, C. V., Jakobsen, K. G., Lindskog, A., Hansen, J., Hansen, T., Eriksson, M. E., Dronov, A., Frei, R., Korte, C., Nielsen, A. T. and Harper, D. A. T., 2016: Onset of main Phanerozoic marine radiation sparked by emerging Mid Ordovician icehouse. *Scientific Reports*, vol. 6, 18884.

Rasmussen, C. M. Ø., Kröger, B., Nielsen, M. L. and Colmenar, J. 2019: Cascading trend of Early Paleozoic marine radiations paused by Late Ordovician extinctions. *Proceedings of the National Academy of Sciences of the USA,* vol. 116, 7207–7213.

Raup, D. M and Sepkoski Jr, J.J., 1982: Mass extinctions in the marine fossil record. *Science,* vol. 215, p. 1501–1503.

Raup, D. M and Sepkoski Jr, J.J., 1984: Periodicity of extinctions in the geological past. *Proceedings of the National Academy of Sciences of the USA,* vol. 81, 801-805.
Roberts, G. G. and Mannion, P. D., 2019: Timing and periodicity of Phanerozoic marine biodiversity and environmental change. *Scientific Reports,* vol. 9, 6116.
Rohde, R. A. and Muller, R. A., 2005: Cycles in fossil diversity. *Nature*, vol. 434, p. 208-210.
Sadler, P. M., 2001: *Constrained Optimization Approaches to the Paleobiologic Correlation and Seriation Problems: A User's Guide and Reference Manual to the CONOP Program Family*. University of California, Riverside.
Sadler, P. M., Cooper, R. A. and Melchin, M. J., 2009: High-resolution, early Paleozoic (Ordovician-Silurian) timescales. *Geological Society of America, Bulletin*, vol. 121, p. 887–906.
Saltzman, M. R., Young, S. A., Kump, L. R., Gill, B. C., Lyons, T. W. and Runnegar, B., 2011: A pulse of atmospheric oxygen during the late Cambrian. *Proceedings of the National Academy of Sciences of the USA,* vol. 108, 3876–3881.
Schmitz, B., Harper, D. A. T., Peucker-Ehrenbrink, B., Stouge, S., Alwmark, C., Cronholm, A., Bergström, S. M., Tassinari, M. and Wang, X. F., 2007: Asteroid breakup linked to the Great Ordovician Biodiversification Event. *Nature Geoscience,* vol. 1, p. 49–53.
Schmitz, B., Farley, K. A., Goderis, S., Heck, P. R., Bergström, S. M., Boschi, A., Claeys, P., Debaille, V., Dronov, A., van Ginneken, M., Harper, D. A. T., Iqbal, F., Friberg, J., Liao, S., Martin, E., Meier, M. M. M., Peucker-Ehrenbrink, B., Soens, B., Wieler, R. and Terfelt, F., 2019: An extraterrestrial trigger for the mid-Ordovician ice age: Dust from the breakup of the L-chondrite parent body. *Science Advances*, vol. 5, eaax4184.
Sepkoski Jr., J.J., 1978: A kinetic model for Phanerozoic taxonomic diversity: I. Analysis of marine orders. *Paleobiology,* vol. 4, p. 223–251.
Sepkoski Jr., J.J., 1979: A kinetic model for Phanerozoic taxonomic diversity: II. Early Phanerozoic families and multiple equilibria. *Paleobiology*, vol. 5, p. 222–251.
Sepkoski Jr., J.J., 1981: A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology*, vol. 7, 36–53.
Sepkoski Jr., J.J., 1982: A compendium of fossil marine animal families. Milwaukee Public Museum Contributions in Biology and Geology, vol. 51, p. 1–125.
Sepkoski Jr., J.J., 1984: A kinetic model for Phanerozoic taxonomic diversity: part 3.Post-Paleozoic families and multiple equilibria. *Paleobiology*, vol. 10, p. 246–267.
Sepkoski Jr., J.J., 1988: Alpha, beta, or gamma: where does all the diversity go? *Paleobiology*, vol. 14, p. 221–234.
Sepkoski Jr., J.J., 1992: A compendium of fossil marine animal families. 2nd edition. Milwaukee Public Museum Contributions in Biology and Geology, vol. 83, p. 1–156.
Sepkoski Jr., J.J., 1995: The Ordovician Radiations: Diversification and extinction shown by global genus level taxonomic data. *In*: Cooper, J. D., Droser, M. L. and Finney, S. C., *eds*., *Ordovician Odyssey: Short Papers, 7th International Symposium on the Ordovician System* Pacific Section Society for Sedimentary Geology (SEPM), Book 77, p. 393–396.
Sepkoski Jr., J.J., 1997: Biodiversity: past, present and future. *Journal of Paleontology,* vol. 71, p. 533– 539.
Sepkoski Jr., J.J., 2002: A compendium of fossil marine animal genera. *In*: Jablonski, D. and Foote, M., *eds*., *Bulletins of American Paleontology,* vol. 363, 10– 560.
Sepkoski Jr., J.J. and Sheehan, P. M., 1983: Diversification, faunal change, and community replacement during the Ordovician radiations. *In*: Biotic Interactions in Recent and Fossil Benthic Communities, Plenum Press, New York, p. 673–717.
Sepkoski Jr., J.J. and Miller, A. I., 1985: Evolutionary faunas and the distribution of benthic communities in space and time. *In*: Valentine, J. W., ed., Phanerozoic Diversity Patterns: Profiles in Macroevolution. Princeton University Press and Pacific Division, American Association for the Advancement of Science, Princeton, New Jersey.

Servais, T. and Harper, D. A. T., 2018: The Great Ordovician Biodiversification Event (GOBE): definition, concept and duration. *Lethaia,* vol. 51, p. 151–164.
Servais, T., Li, J., Stricanne, L., Vecoli, M. and Wicander, R., 2004: Acritarchs. *In*: Webby, B. D., Paris, F., Droser, M. L. and Percival, I. G. *eds*., *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, p. 348-360.
Servais, T., Lehnert, O., Li, J., Mullins, G. L., Munnecke, A., Nützel, A. and Vecoli, M., 2008: The Ordovician Biodiversification: revolution in the oceanic trophic chain. *Lethaia*, vol. 41, p. 99–109.
Servais, T., Harper, D. A. T., Li, J., Munnecke, A., Owen, A. W., Sheehan, P. M., 2009: Understanding the Great Ordovician Biodiversification Event (GOBE): influences of paleogeography, paleoclimate, or paleoecology? *GSA Today*, vol. 19, p. 4–10.
Servais, T., Owen, A. W., Harper, D. A. T., Kröger, B. and Munnecke, A., 2010: The Great Ordovician Biodiversification Event (GOBE): the palaeoecological dimension. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 294, p. 99–119.
Servais, T., Antoine, P. O., Danelian, T., Lefebvre, B. and Meyer-Berthaud, B., 2012: Paleontology in France: 200 years in the footsteps of Cuvier and Lamarck. *Palaeontologia Electronica*, vol. 15, p. 1–12.
Servais, T., Perrier, V., Danelian, T., Klug, C., Martin, R., Munnecke, A., Nowak, H., Nützel, A., Vandenbroucke, T. R. A., Williams, M. and Rasmussen, C. M. Ø., 2016: The onset of the 'Ordovician Plankton Revolution' in the late Cambrian. *Palaeogeography, Palaeoclimatology, Palaeoecology* 458, 12–28.
Stigall, A. L., 2010: Using GIS to assess the biogeographic impact of species invasions on native brachiopods during the Richmondian Invasion in the Type-Cincinnatian (Late Ordovician, Cincinnati Region). *Palaeontologia Electronica* 13, 5A, p. 1–19.
Stigall, A. L., Bauer, J. E., Lam, A. R. and Wright, D. F., 2017: Biotic immigration events, speciation, and the accumulation of biodiversity in the fossil record. *Global and Planetary Change*, vol. 148, p. 242–257.
Stigall, A. L., Edwards, C. T., Freeman, R. L. and Rasmussen, C. M. Ø., 2019: Coordinated biotic and abiotic change during the Great Ordovician Biodiversification Event: Darriwilian assembly of early Palaeozoic building blocks. *Palaeogeography, Palaeoclimatology, Palaeoecology,* vol. 530, p. 249–270.
Trotter, J. A., Williams, I. S., Barnes, C. R., Lécuyer, C. and Nicol, R. S., 2008: Did cooling oceans trigger Ordovician biodiversification? Evidence from conodont thermometry. *Science*, vol. 321, p. 550–554.
Vandenbroucke, T. R. A., Armstrong, H. A., Williams, M., Paris, F., Zalasiewicz, J. A., Sabbe, K., Nolvak, J., Challands, T. J., Verniers, J. and Servais, T., 2010: Polar front shift and atmospheric CO2 during the glacial maximum of the Early Paleozoic Icehouse. *Proceedings of the National Academy of Sciences of the USA,* vol. 107, 14983–14986.
Walliser, O. H., *ed*., 1996a: Global Events and Event Stratigraphy, Springer, Berlin. p. 1–348.
Walliser, O. H. 1996b: The idea of global events: a prologue. *In*: Walliser, O. H. ed., Global Events and Event Stratigraphy, Springer, Berlin. p. 7-19.
Wang, X. F., Stouge, S., Maletz, J., Bagnoli, G., Qi, Y. P., Raevskaya, E. G., Wang, C. S. and Yan, C. B., 2019. Correlating the global Cambrian-Ordovician boundary: precise comparision of the Xiaoyangqiao section, Dayangcha, North China with the Green Point GSSP section, Newfoundland, Canada. *Palaeoworld*, vol. 28, p. 243-275.
Webby, B.D., 2004: Introduction. *In*: Webby, B. D., Paris, F., Droser, M. L. and Percival, I. G. *eds*., *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, p. 1–37.
Webby, B. D., Paris, F., Droser, M. L. and Percival, I. G. *eds*., 2004a: *The Great Ordovician Biodiversification Event*. Columbia University Press, 1–496.

Webby, B. D., Paris, F., Droser, M. L., 2004b: Final report of the IGCP Project 410 (1997-2002) - The Great Ordovician Biodiversification Event. *Episodes*, vol. 27, p. 203–208.
Zheng, S., Clausen, S., Feng, Q. and Servais, T., 2020: Review of organic-walled microfossils research from the Cambrian of China: Implications for global phytoplankton diversity. *Review of Palaeobotany and Palynology*, vol. 534, 104191.
Zhu, M., Zhuravlev, A. Y., Wood, R. A., Zhao, F. and Sukhov, S. S., 2017: A deep root for the Cambrian explosion: Implications of new bio- and chemostratigraphy from the Siberian Platform. *Geology*, vol. 45, p. 459-462
Zhuravlev, A. Y. and Riding, R., *eds*., 2011a. *Ecology of the Cambrian Radiation*. Columbia University Press, 1-525.
Zhuravlev, A. Y. and Riding, R., 2011b. Introduction. In: Zhuravlev, A. Y. and Riding, R., eds., *Ecology of the Cambrian Radiation*. Columbia University Press, 1-8.
Zhuravlev, A. Y. and Wood, R. A., 2018: The two phases of the Cambrian Explosion. *Scientific Reports,* vol. 8, 16656.

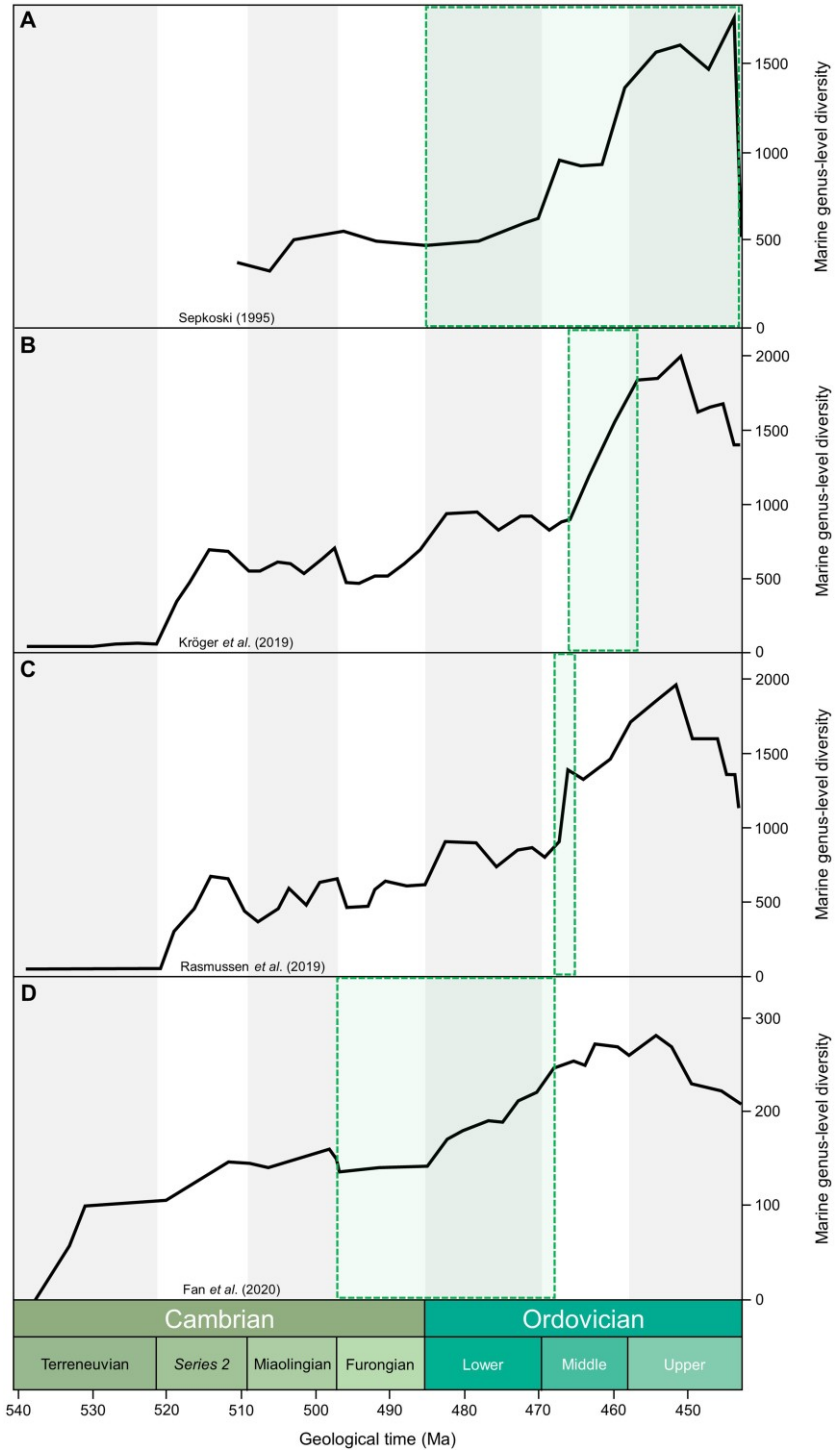

Figure 1. Trajectory comparison of Cambrian-Ordovician marine genus-level diversity curves and the different concepts of the Ordovician radiation. **A,** diversity curve of Sepkoski (1995): the Ordovician radiations span the entire Ordovician Period. **B,** PBDB based diversity curve of Kröger *et al.* (2019): the 'GOBE' spans the major parts of the Middle Ordovician. **C,** PBDB based diversity curve of Rasmussen *et al.* (2019): the 'GOBE' is considered to correspond to a short interval in the early Middle Ordovician. **D,** GBDB based diversity curve of Fang *et al.* (2020, fig. 1A): the 'GOBE' starts at the base of the Furongian (upper Cambrian Series 4) and lasts until the end of the Early Ordovician.