

The onset of the ‘Ordovician Plankton Revolution’ in the late Cambrian



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ABSTRACT

The ‘Great Ordovician Biodiversification Event’ comprises the rapid diversification of marine organisms during the Ordovician Period. It is now clear that this adaptive radiation started for some organisms already in the Cambrian and continued for others beyond the end of the Ordovician, making the ‘Great Ordovician Biodiversification Event’ part of a long-term late Proterozoic and Early Palaeozoic radiation, that in part is expressed by the fossil record as the ‘Cambrian Explosion.’ A significant diversification of different groups of the plankton is observed in the late Cambrian–Early Ordovician interval, leading to the subsequent ‘Ordovician Plankton Revolution.’ The possible causes of this ‘plankton revolution’ are currently debated. They include changes in palaeoclimate, palaeogeography or tectonic and volcanic activity, as well as a modified nutrient supply. In this context, the Steptoean Positive Carbon Isotope Excursion $\delta^{13}\text{C}_{\text{carb}}$ (SPICE) event in the late Cambrian (Paibian Stage, Furongian Series) has been related to a major increase in atmospheric O_2 (from 10–18% to some 20–29%) and to increased oceanic nutrient availability. Here we analyze the diversification of the planktonic groups during the late Cambrian and Early Ordovician, in particular in relation to the SPICE event. Our analyses include the changing diversities of the phytoplankton (acritarchs), diverse groups of zooplankton (e.g., radiolarians, graptolites, chitinozoans) and the switch to a planktonic mode of life of fossil groups (e.g., arthropods, molluscs) that were part of the Cambrian benthos and that later occupied pelagic niches. In addition, we focus also on data indicating evidence for a late Cambrian to Ordovician origin of planktotrophy in invertebrate larvae. It can be concluded that none of the diversifications of the different planktonic organisms can be related directly to the SPICE event. However, a long term (10–20 million years) oxygenation pulse related to the SPICE event might have fuelled the explosion of phytoplankton diversity observed in the latest Cambrian–Early Ordovician that led to completely modified trophic structures permitting an increase in diversity and abundance of plankton-feeding groups during the Ordovician.

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1. Introduction

In a simplified view, marine animal diversity changes during the Phanerozoic include two major radiations (the Early Palaeozoic and the Early Mesozoic radiations) and five mass extinctions, of which the

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Permian/Triassic extinction, considered the most serious in terms of species-diversity loss, clearly stands out. Both the classical Sepkoski-type biodiversity curves of marine faunas (e.g., Sepkoski, 1978, 1979, 1981, 1984, 1988) and the more recent standardized curves provided by the Paleobiology Database (PBDB, e.g., Alroy et al., 2001, 2008) show a clear long-term radiation of marine organisms during the Early Palaeozoic. In the Sepkoski-type biodiversity curves, this major radiation took place in the Cambrian and Ordovician, with a Palaeozoic ‘plateau’ being reached at the end of the Ordovician. In the more recent curves of the PBDB a much longer and continuously increasing diversity trend started already in the late Proterozoic and only ended in the Early Devonian (e.g., Alroy et al., 2008).

The Early Palaeozoic radiation can either be seen as including two separate events, the ‘Cambrian Explosion’ and the ‘Great Ordovician Biodiversification Event’ (GOBE), or as a continuous, stepwise evolution of faunal changes, including the rise of three Evolutionary Faunas, the Cambrian, Palaeozoic and Modern Faunas (e.g., Sepkoski and Miller, 1985). The question of whether the ‘Cambrian Explosion’ and the ‘Great Ordovician Biodiversification Event’ are two separate events or a single one is a current matter of debate.

The ‘Cambrian Explosion’ is considered to be a relatively short period (during the early–middle Cambrian) when most animal phyla that we know today have their first fossil record (e.g., Erwin et al., 2011; Smith and Harper, 2013). The GOBE, on the other hand, is an event that covered most of the Ordovician and that represents an ‘explosion’ in diversity of marine organisms at the family, genus, and species level (e.g., Harper, 2006). Several authors considered the GOBE as a sum of diversification events (e.g., Miller, 2004), because the diversification of individual fossil groups did not take place at the same time, and not on the same palaeocontinents. Other authors pointed out that the Ordovician radiation was clearly a follow-up to the ‘Cambrian Explosion’ (e.g., Droser and Finnegan, 2003).

In terms of ecological shifts, the late Precambrian microbial-dominated ecosystems were replaced during the early Cambrian by benthos dominated communities with most marine groups of the Cambrian biota limited to shallow water environments representing benthic/nekto-benthic communities (e.g., Burzin et al., 2001). It was only during the Ordovician that the water column was more completely filled with planktonic and nektonic organisms and that pelagic habitats were colonized to develop modern marine ecosystems (e.g., Servais et al., 2010).

Bambach (1994) was one of the first to indicate that the biomass of marine consumers increased during the Phanerozoic. Similarly, he considered that expenditure of energy by marine consumers has increased in time as well. Furthermore Bambach (1994) already noted that the great diversification of predators suggests that biomass increased all the way down the food chain to the level of primary production. On the other hand, Bambach et al. (2002) noted that the Early Palaeozoic radiations established stable ecosystem relationships. The term ‘Ordovician Plankton Revolution’ has increasingly been used in the last decade. Signor and Vermeij (1994) already noted that a review of the fossil record suggests that the diversification of the plankton and suspension-feeding marine animals began in the late Cambrian and continued into the Ordovician, pointing out that the ultimate cause of these changes is uncertain, but that it appears likely that the plankton became a refuge from predation and bioturbation. Nützel and Frýda (2003) first coined the term ‘Palaeozoic Plankton Revolution’ to indicate that the plankton was fundamentally restructured during the Palaeozoic. Subsequently, Nützel et al. (2006) provided the first empiric evidence for a late Cambrian to Ordovician switch to planktotrophy in invertebrate larvae, confirming Peterson’s (2005) assumption, based on molecular clock data, that planktotrophy had evolved in several clades during the latest Cambrian to Middle Ordovician. Servais et al. (2008) indicated that the Ordovician Biodiversification represented important changes in the marine trophic chain, with an ‘Ordovician Plankton Revolution’ profoundly modifying the marine food web. They pointed out that after the Steptoean Positive Carbon Isotope Excursion (SPICE) $\delta^{13}\text{C}_{\text{carb}}$ event in the late Cambrian (Paibian Stage of the Furongian Series) the organic-walled phytoplankton (acritarchs) underwent a major change in morphological disparity and taxonomical diversity, triggering the important changes in the marine food webs, with the development of planktotrophy in larval stages and the rise of suspension feeders.

More recently, Saltzman et al. (2011) correlated the late Cambrian Steptoean Positive Carbon Isotope Excursion $\delta^{13}\text{C}_{\text{carb}}$ (SPICE) event with a pulse of atmospheric oxygen that can be correlated with the onset of the GOBE and the plankton and animal radiation that began 40 million years after the so-called ‘Cambrian Explosion.’ Saltzman et al. (2011) argued that it is possible that the oxygenation event during the SPICE led to a promotion of dinoflagellate-like taxa of the organic-

walled microphytoplankton that are the dominant primary producers overall throughout much of the Palaeozoic, triggering the expansion of ecologically diverse plankton groups that provided few food sources for the expanding animal biota.

The main objective of the present paper is to review the literature and to summarize recent results in order to precisely position in time the onset of the ‘Ordovician Plankton Revolution.’ We will attempt to raise and answer several questions. What are the changes that took place in the plankton during the late Cambrian and Early Ordovician? Was there a ‘plankton revolution’ and when may this have occurred precisely? What was the duration of the onset of this ‘plankton revolution?’ Did the SPICE event trigger the plankton revolution and can this event be correlated with the diversification of the different planktonic groups?

In order to examine when the different planktonic groups diversified and when they became an important component of the marine environment, the fossil record of the phytoplankton and of all zooplanktonic groups is here reviewed in detail. In addition, the data on the development of planktotrophic larval stages of marine invertebrates are also reviewed. A major question is the search of the cause(s) of the changes in the marine trophic webs. Might the ‘Ordovician Plankton Revolution’ be the result of a biological escalation or was it triggered by an environmental event, such as a pulse of atmospheric oxygen in the late Cambrian, or both?

2. What is the plankton?

2.1. Definitions – modern plankton

The modern global oceans are dominated in abundance and biomass by the plankton that plays a major role in marine trophic chains (e.g., Le Quééré et al., 2005). The plankton represents all organisms that live in the water column but that cannot freely swim. The term plankton comes from the Greek *πλανκτόν* (*plankton* = drifter) and therefore indicates that the planktonic organisms (plankters) drift, or passively float, with the water currents and within the water column, although some plankton groups are somewhat mobile (most planktonic arthropods, molluscs or cnidarians can swim, but such movements are usually limited to vertical migrations). The nekton, in contrast, represents all organisms that can (freely) swim against a current and move largely independently of water currents.

On the other hand, benthic organisms are those that live close to or are attached to the seafloor, and that are usually not swimming in the water column. Some organisms considered as nekto-benthic live near the seafloor and derive some of their food from the benthos (demersal habitat, see below) but are also able to swim, although usually not in open waters.

Furthermore, some organisms have benthic–planktonic life cycles, with a part of their life in the benthos, and another part in the plankton. Benthic or nekto-benthic organisms that have a planktonic mode at the beginning of their life are classified within the meroplankton, in contrast to the holoplankton that includes all organisms of which the entire lifecycle is planktonic.

In terms of size, the plankton ranges from the bacterioplankton (smaller than 1 μm) and the picoplankton (usually 1–2 μm in diameter) to macro-scale (of a size up to several tens of cm or even meters) zooplankton predators (e.g., jellyfish). Plankton occurs at all depths within the oceans, although such organisms are most common in the photic zone. Plankton distribution is primarily controlled by upwelling zones and by the nutrient supply in the oceans. Plankton is also distributed following temperature and salinity zones, but many species have wide biogeographical distributions.

The plankton is broadly divided into three major trophic categories, the bacterioplankton, the phytoplankton and the zooplankton. The bacterioplankton mainly consists of bacteria, while the phytoplankton is basically composed of prokaryotic and eukaryotic algae. The phytoplankton constitutes the major part of the ‘marine floras’, the

term phytoplankton meaning ‘drifting plants’ (from the Greek φυτόν, *phyton* = plant, and πλαγκτόν, *plankton* = drifter). The phytoplankton is therefore generally considered to represent the autotrophic component of the plankton, in contrast to the zooplankton that constitutes the heterotrophic part of it (although some parts of the phytoplankton can also be heterotrophic, such as dinoflagellates, for example, which are represented by autotrophic, heterotrophic and mixotrophic species). The phytoplankton usually lives in the upper 100 m of the water column.

It is usually accepted that the phytoplankton is an essential part of the modern marine food chain, but the bacterioplankton and picoplankton also play an essential role, with the picoplankton being considered the essential part of the biomass in modern oceans (e.g., Buitenhuis et al., 2012). Although the marine phytoplankton only represents about 1% of the total photosynthetic biomass at a given time, single-celled algae in the oceans are responsible for about 50% of the total primary production (e.g., Falkowski, 2012).

The zooplankton includes both metazoans and unicellular protozoans that are critical intermediaries (primary and secondary consumers) in the flow of energy and biomass through marine ecosystems. Some zooplanktonic organisms have a strictly planktonic lifestyle as they float or drift in the water column during all their life (holozooplankton), while others (merozooplankton) have during their life cycle both a planktonic (usually during their larval stage) and a nektonic lifestyle, because they are able to swim and move independently of currents during one part of their life (as adults).

In terms of marine life habitats, the different zooplanktonic organisms live both in demersal (the zone close to the seafloor) and pelagic (the water column between the demersal zone and the surface, i.e., open waters) environments. The modern marine zooplankton consists of different groups, including arthropods, rhizarians, actinopodes, ciliophores, cnidarians, rotifers and other groups (e.g., CMarZ, 2004).

The definition of the terms plankton and nekton vary. We note that several groups referred to as zooplankton include good swimmers, and in the context of this study these are not treated as planktonic organisms.

2.2. The fossil record of plankton and its significance in Palaeozoic palaeoecology

Understanding ancient food chains and macroevolutionary patterns in the marine realm during geological time is dependent on an analysis of the fossil plankton. However, the fossil record of the plankton is mostly incomplete. The smaller members of the plankton are usually not preserved. At best, some groups can be identified by geochemical biomarkers. The bacterioplankton has almost no fossil record, while the picoplankton is too small to be observed under a light microscope and remains largely unobserved, although very small organic-walled microfossils fall in the size-range of the picoplankton, indicating that the picoplankton was already present during the Early Palaeozoic (see below). Despite these occurrences, the importance of the picoplankton in ancient food chains is far from understood. Moreover, the geological history of virioplankton is almost completely unknown, although viruses are very abundant in modern seawater.

The phytoplankton is considered a major part of the base of modern marine food chains. It can be divided into a calcareous part (e.g., coccolithophores), a siliceous part (e.g., diatoms) and an organic-walled part (e.g., dinoflagellates). However, none of these modern groups of phytoplankton is present in the fossil record before the Mesozoic. The major part of the phytoplankton in the Palaeozoic is represented by the organic-walled fraction, attributed to the ‘acritarchs,’ calcareous and siliceous phytoplankton being usually absent in the fossil record. The analysis of the diversity and abundance of the acritarchs is thus a possible key to understand the presence of Palaeozoic phytoplankton and the functioning of ancient ecosystems.

However, the understanding of phytoplankton diversity does not give any information about the amount of the biomass produced.

The Palaeozoic zooplankton was very different from the modern. Two of the major zooplanktonic groups in the Palaeozoic are the radiolarians and graptolites. Radiolarians are already present in the Cambrian but they only rise in diversity during the Ordovician. Graptolites are very well known as the stratigraphical index fossils in the Ordovician and Silurian, their planktonic life-style making them excellent biostratigraphical markers. They are essentially benthic in the Cambrian and are considered to become planktonic in the Early Ordovician. A further group of Early Palaeozoic microfossils attributed to the plankton are the enigmatic chitinozoans, which rapidly diversified during the Early Ordovician. The diversity changes of all these groups are compiled here in order to understand the timing of the onset of the ‘Ordovician Plankton Revolution.’

The fossil record of arthropod zooplankton is extremely poor for most of the Phanerozoic. The analysis of the fossil record of arthropods indicates that a zooplanktonic lifestyle has arisen independently across several arthropod groups already during the Cambrian. Most probably some groups of the molluscs also belonged to the macrozooplankton during some geological periods. Several groups of Ordovician cephalopods most probably had a planktonic mode of life and need to be integrated in the study of the Early Palaeozoic plankton.

Klug et al. (2010) presented some patterns of the diversity and the proportional abundance of demersal/nektonic organisms, plankton and nekton in the Palaeozoic, based on both Sepkoski’s data resolved to geological stages (Sepkoski, 2002) and on occurrence counts from the Paleobiology Database resolved to 10 million year intervals.

Fig. 1 illustrates the proportional abundance of the different groups, based on the original study of Klug et al. (2010). According to the different datasets, the proportion of the plankton clearly increased significantly in the late Cambrian, and particularly in the Early to Middle Ordovician. The nekton became abundant during the Devonian and was dominant since the Carboniferous, leading Klug et al. (2010) to coin the term ‘Devonian Nekton Revolution.’ Several major palaeoecological shifts thus took place, and it would be interesting to relate these changes to extrinsic or intrinsic parameters.

In addition, many benthic animals have larvae that display a planktonic mode of life and that often feed on phytoplankton. As already indicated in the landmark paper by Signor and Vermeij (1994), the relationships between the plankton and the benthos have changed through geologic time, and most probably in a notable way during the Early Palaeozoic radiation, in particular between the ‘Cambrian Explosion’ and the GOBE, i.e., somewhere during the late Cambrian.

In order to realize the importance of the plankton in the Early Palaeozoic and to establish when the onset of the ‘Ordovician Plankton Revolution’ may have taken place, the data of the first appearance and of the diversifications of the different phytoplanktonic and zooplanktonic groups are reviewed in the following sections, with a focus to the late Cambrian–Early Ordovician interval, when the relative abundance of the plankton significantly increased (Fig. 1; Klug et al., 2010).

3. The fossil record of Early Palaeozoic phytoplankton

3.1. Palaeozoic picoplankton and phytoplankton

The life of the global ocean is fuelled by the microorganisms referred to as phytoplankton, ranging in size from the tiny picoplankton to larger organisms that can be identified under the microscope (e.g., Falkowski et al., 2004). However, determining the net primary production in the oceans of ancient ecosystems is extremely difficult because the fossil record is very incomplete. Nevertheless, some broader trends can be proposed. It is possible to roughly estimate the areas of high versus low productivity in ancient oceans. Models are also proposed to locate oligotrophic versus eutrophic areas. Such estimates can be made both

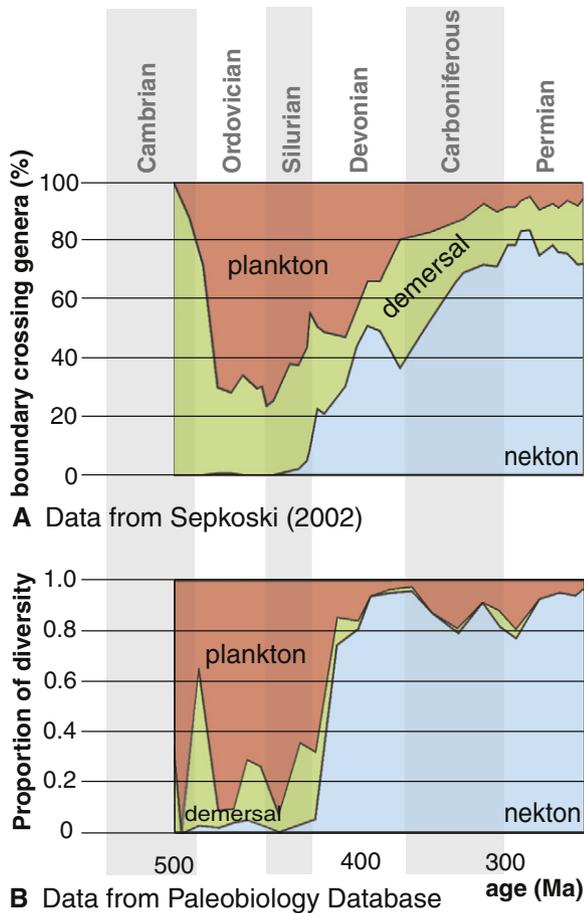


Fig. 1. Macroecological changes in the Palaeozoic (modified after Klug et al., 2010) as reflected in diversity changes as well as the relative abundance of demersal organisms (Cephalopoda: Actinocerida, Ascocerida, Discosorida, Ellesmerocerida, Endocerida, Lituitida, Oncocerida; Arthropoda: Radiodonta, Eurypterida; Vertebrata: Galeaspida, Osteostraci, Pteraspidomorphi, Thelodonti; Cephalochordata), plankton (Graptoloidea, Dacryoconarida, Homoctenida, Orthocerids, Bactritida) and nekton (Ammonoidea, Gnathostomata, most coiled nautiloids) in the Palaeozoic. Note the radical change in diversity in the three macroecological groups. A, curves based on Sepkoski (2002). B, data from the Paleobiology Database (10 myr intervals).

in space (due to the knowledge of palaeocontinental distribution) and in time, in particular by using multiproxy approaches that rely on palaeontological, geochemical, and sedimentological data (e.g., Saltzman, 2005). Moreover, the presence and abundance of consumers such as suspension feeders and planktotrophic larvae also provides indirect evidence for sufficient primary production in the oceans. Furthermore, many organisms clearly increased their size dramatically during the GOBE, as documented, for example in detail for brachiopods (e.g., Zhang et al., 2015).

The knowledge of Palaeozoic picoplankton and phytoplankton is very patchy. Most paleontologists usually consider the phytoplankton (coccolithophorids, diatoms, dinoflagellates in the Mesozoic and Cenozoic) as the main component at the base of the marine trophic chains, but the smaller parts, including the bacterioplankton and the picoplankton, also play an essential role, that is almost impossible to quantify in ancient geological periods.

The tiny picoplankton (0.2 to 2.0 μm in diameter) and even smaller bacterial fraction of the plankton, commonly classified as the bacterioplankton, constitutes an important part of the food source for zooplanktonic organisms (e.g., Hisatugo et al., 2014). The cyanobacteria are another large, heterogeneous group of principally photosynthetic prokaryotic organisms that are widely considered as another major

component of the modern phytoplankton (Blank, 2013; Dagan et al., 2013). The relative proportions of the different groups of bacterioplankton, picoplankton and phytoplankton in the primary production are difficult to estimate, but they undoubtedly changed through geological time, and most probably during the Early Palaeozoic.

The fossil record is usually only documented by the visible part of the phytoplankton. The observation with optical microscopes is generally limited to the investigation of larger phytoplankton, i.e., 20 μm or greater in diameter. The diversity curves of the organic-walled microphytoplankton (both the dinoflagellates since the Mesozoic and the acritarchs in the Palaeozoic) therefore represent only the diversities of the fraction of the phytoplankton that is greater than 20 μm . The smaller fraction (<20 μm) remains mostly unknown, although a few studies document the presence of the tiny microphytoplankton or even picoplankton in the fossil record. With the help of the scanning electron microscope such very small organic-walled microfossils, often between 5 and 10 μm in diameter, have been observed, for example, in the Cretaceous by Schrank (2003) and in the Silurian by Munnecke and Servais (1996). These observations indicate that such specimens may be extremely abundant, and that their importance in the primary production in ancient oceans was probably of great significance. Such organisms, although almost completely absent in the fossil record, were thus most probably a significant part of the food source for the zooplankton or for planktotrophic larvae.

3.2. The Palaeozoic fossil record of calcareous and siliceous phytoplankton

Different phytoplanktonic groups live today in the oceans. Most of these 'modern' groups only evolved during the Mesozoic, and the presence of various phytoplanktonic organisms in the Palaeozoic or Precambrian remains debated. The three major groups today are the coccolithophores (that produce calcareous exoskeletons built up by calcified scales named coccoliths), the diatoms (that produce siliceous tests) and the dinoflagellates (that generally produce organic-walled cysts).

The coccolithophores are the main constituents of modern calcareous microphytoplankton, besides several other microalgal groups. They build calcareous exoskeletons and played an essential role in ancient marine carbonate-forming palaeoenvironments, as they are well known to be a main component of Cretaceous chalk (e.g., Stanley et al., 2005). Coccolithophores appear to have evolved during the early Mesozoic with the first definite specimens in the fossil record found in the Triassic (Gardin et al., 2012). Dinoflagellates usually produce organic-walled resting cysts, but a few taxa also produce calcified exoskeletal structures during their life cycle (e.g., Elbrächter et al., 2008). The presence of calcareous phytoplankton (i.e., of calcareous cysts that have been produced by phytoplanktonic organisms) before the Permian/Triassic extinction event is debated. Munnecke and Servais (2008) and Servais et al. (2009a) reported different types of calcareous microfossils, named calcispheres and nannospheres, from the Silurian carbonate platform of Gotland. The comparison with calcareous microplankton from the Mesozoic and Cenozoic indicated that some morphotypes from the Silurian are comparable with coccospheres, while others show similarities with calcareous dinoflagellates. The observation that many of these calcareous microfossils occur in almost all sedimentary facies indicates that they probably belong to calcareous micro- and nannoplankton. Munnecke and Servais (2008) concluded that calcareous plankton most probably existed already during the Palaeozoic, and even in the Early Palaeozoic, but that it could only be observed if the material was not subject to late stage diagenesis that destroys the microstructures necessary to recognize the morphological parameters typical of calcareous phytoplankton cysts. Versteegh et al. (2009) proposed the term Calcitarcha to include all these calcareous microfossils with unknown biological affinities, in analogy to the Acritarcha, defined by Evitt (1963) who included all organic-walled microfossils of unknown biological affinities (that could not be related with certainty to the dinoflagellates). Calcareous

cysts produced by phytoplanktonic organisms were therefore possibly already present during the Early Palaeozoic, but detailed investigations are mostly absent, and the fossil record of such groups is sparse. To date, calcareous phytoplankton groups have not been reported from the Cambrian and Ordovician, but it is possible that future investigations in well preserved calcareous environments may provide evidence of Calcitarcha in the Early Palaeozoic.

The most common group of phytoplankton producing siliceous tests is the diatoms (the radiolarians being the major group of zooplankton producing siliceous tests). The first occurrence of diatoms in the fossil record is in the Jurassic, but diatoms only became abundant during the Lower Cretaceous (e.g., Sims et al., 2006). A few dinoflagellate taxa produce siliceous cysts, but they are extremely rare (e.g., Harding and Lewis, 1995). So far, there are no records of siliceous phytoplankton from the Palaeozoic and likely they did not exist. But it should be considered that some modern radiolarians have endosymbiotic algae and thus contribute to primary production.

3.3. The fossil record of organic-walled phytoplankton (acritarchs) in the Cambrian and Ordovician

The acritarchs sensu lato provide the most complete fossil record of Palaeozoic phytoplankton, but even this record does not fully document the autotrophic part of the plankton in the Cambrian and Ordovician oceans. Evitt (1963) defined the acritarchs as a 'catch all' entity that groups nearly all organic-walled microfossils of unknown origin. A number of organisms originally classified within the acritarchs now have established affinities with other groups, including prasinophycean and zygnematacean green algae, and cyanobacteria (e.g., Colbath and Grenfell, 1995; Servais, 1996; Servais et al., 1997). However, most of the remaining Palaeozoic acritarchs are considered to be cysts of marine, generally phytoplanktonic unicellular algae. Some acritarchs show greatest similarities with organic-walled cysts of dinoflagellates, displaying some of the typical morphologies of the dinoflagellates (e.g., Lister, 1970; Le Hérisse, 1989) and showing comparable palaeoecological and palaeogeographical distribution patterns (e.g., Li et al., 2004; Molyneux et al., 2013). However, in order to be identified as a fossil dinoflagellate cyst, an organic-walled microfossil must display some characteristic features, such as a paratabulation, a cingulum, a sulcus, and an operculum. Many organic-walled microfossils in the Palaeozoic do not display these features (and even several modern dinoflagellate species do not produce cysts with these morphological criteria). As a consequence, their biological affinity is uncertain and they are classified within the acritarchs. Nevertheless, most Palaeozoic acritarchs are probably the resting cysts of phytoplanktonic organisms, most similar to modern dinoflagellates (e.g., Martin, 1993; Servais et al., 2004a). Such interpretations are also suggested by the discovery of biogeochemical markers typical of dinoflagellates in the Palaeozoic rock record, including the Cambrian (e.g., Moldovan and Talyzina, 1998).

As the precise biological affinities of the acritarchs are (by definition) unknown, acritarch diversity thus only reflects indirectly, and not precisely, phytoplankton cyst diversity. In addition, although most acritarch morphotypes most probably represent the cysts of phytoplanktonic organisms, some Cambrian acritarchs are probably not planktonic, and can be attributed to benthic or nektobenthic organisms (Fig. 2).

Nonetheless, the acritarchs can be interpreted as representing an important part of the marine phytoplankton in the Early Palaeozoic and therefore they constituted a significant element at the base of the marine trophic chain during the 'Cambrian Explosion' and the subsequent GOBE. An increasing phytoplankton biomass would have served as food for the developing zooplankton, but also for various groups of suspension feeders and detritus feeding organisms (e.g., Servais et al., 2010).

Several Palaeozoic acritarch diversity curves are available in the literature. A few studies covering the late Proterozoic and the entire Palaeozoic have been published by Tappan and Loeblich (1973), Strother (1996), Servais et al. (2004b), Katz et al. (2004) and Strother (2008), just to name a few. K5atz et al. (2004) and Strother (2008) created their diversity curves using the Palynodata database (see Palynodata Inc. and White, 2008): Palynodata were compiled by a consortium of oil companies and scientific institutions over the course of three decades, but this process was discontinued in 2006. Mullins et al. (2006) compiled another database (the PhytoPal database) of acritarch occurrences covering the interval from the Cambrian to the Triassic. A common trend in all these diversity curves is a continuous increase of acritarch diversity between the late Precambrian and the Ordovician, with a peak in the Middle Ordovician. Diversities remained high until the Late Devonian, when a relatively rapid acritarch diversity decline took place, associated by some authors as a 'phytoplankton blackout' (e.g., Riegel, 2008; but see also Servais et al., in press).

Several diversity analyses have focused on the late Precambrian to Ordovician evolution of acritarchs. Vidal and Moczyłowska-Vidal (1997) published a species diversity curve from the Neoproterozoic and the Cambrian. Zhuravlev (2001) used acritarch genera to draw a diversity curve of the Cambrian to the earliest Tremadocian, while Huntley et al. (2006a,b) published both taxonomic diversity and morphological disparity curves of Proterozoic to Cambrian acritarch genera. Moczyłowska (2011) published a species diversity curve from the Ediacaran to basal Ordovician, using some of the data of the PhytoPal database. These Cambrian diversity curves show a peak in the early–middle Cambrian, reflecting somehow the numerous studies on levels associated with the 'Cambrian Explosion' and a rapid increase at the end of the Cambrian. Servais et al. (2008) focused on the Cambrian–Ordovician transition, with a species diversity curve from the middle Cambrian to early Silurian (Llandovery), documenting the increase of acritarch diversity during this period.

Nowak et al. (2015) produced the most complete database of acritarch occurrences for the Cambrian, with the aim to analyze acritarch diversity curves using various statistical methods (Fig. 3). The main objective of Nowak et al. (2015) was to address whether the 'Cambrian Explosion' is reflected in acritarch diversity and whether the GOBE was preceded by a diversification of acritarchs, in particular in relation to the SPICE event and the possible global oxygenation of ocean waters during the late Cambrian postulated by Saltzman et al. (2011). A look at the database of Nowak et al. (2015) and the most recent dataset of Na and Kiessling (2015) on the diversity of Cambrian marine invertebrates (based on the Paleobiology Database) shows that a radiation of acritarch species and to a lesser extent of genera in the lower Cambrian Stage 3 appears to mirror the 'Cambrian Explosion' of metazoans. This radiation is followed by a prominent low in species diversity in the upper Series 3 and lower Furongian. Subsequently, the diversity increases, with peak levels reached globally in the uppermost Cambrian Stage 10 (more precisely at the level of the *Peltura* trilobite Biozone), preceding a substantial phase of acritarch species extinction below and at the Cambrian/Ordovician boundary. By contrast, nearly all the genera present in Stage 10 survived into the Ordovician. The diversity maximum in Stage 10 appears globally and for both the Baltica and Gondwana palaeocontinents, suggesting a consistent phenomenon.

Of particular interest are the diversity changes of the acritarchs during the SPICE event. Nowak et al. (2015) noted that the Jiangshanian, which follows the SPICE event, is marked by a slight increase in diversity at the regional level (Baltica and Gondwana), but that this rise is not reflected on the global curve, which shows a decline in diversity from the Paibian Stage to the Jiangshanian Stage. Thus, there is no evidence that the Jiangshanian was a time of great innovation, as the number of newly originating genera was low. Importantly, many new genera with new morphologies that progress into the Ordovician first appear late in Stage 10, i.e., post-dating the SPICE event considerably and with no apparent causal mechanism. Although the sudden rise in

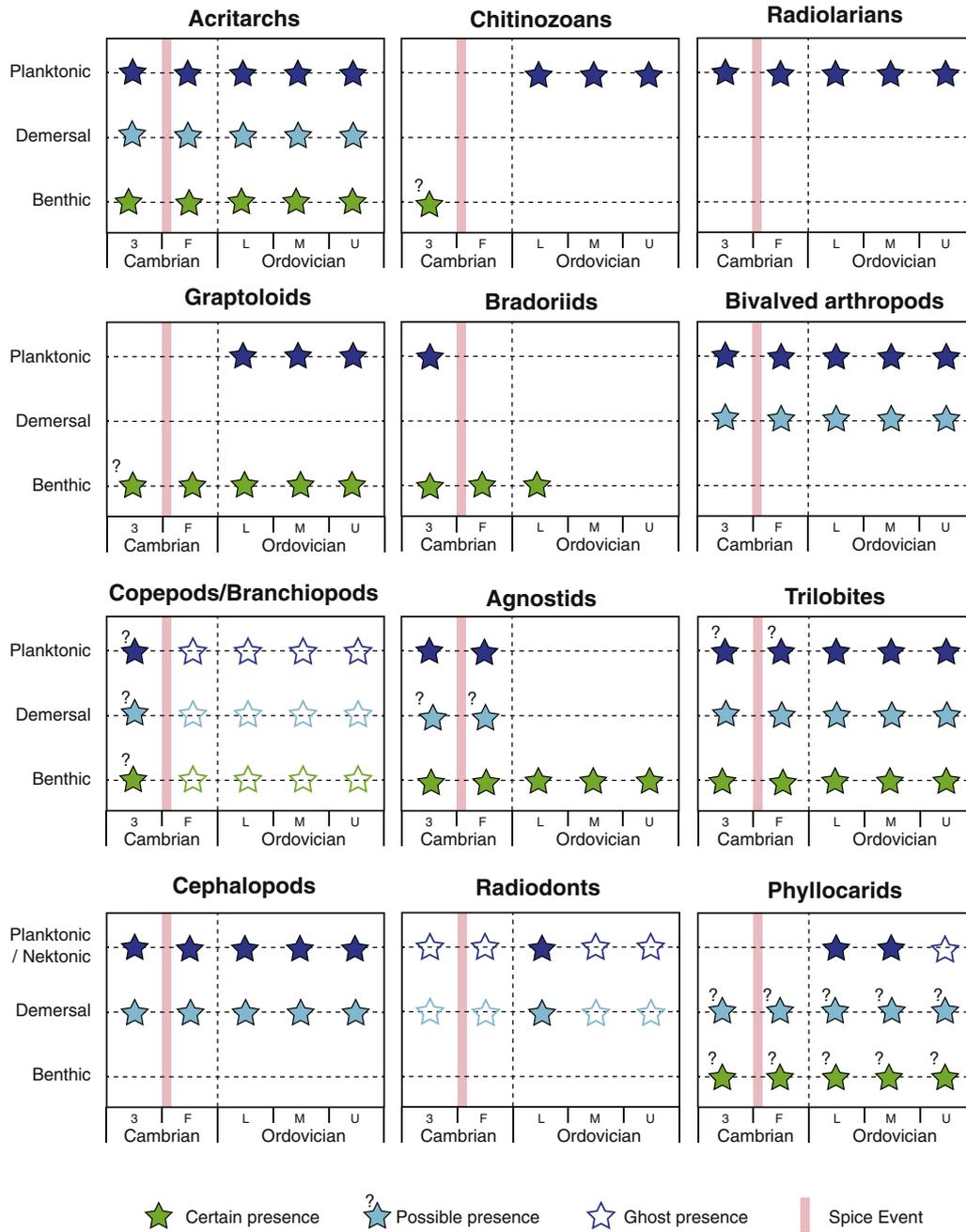


Fig. 2. Qualitative presence/absence data of phytoplankton and zooplanktonic groups in the middle-late Cambrian–Early Ordovician. 3, Cambrian Series 3; F, Furongian; L, M, U, Lower, Middle and Upper Ordovician. For explanation see text.

diversity in Stage 10 might seem like the beginning of the GOBE, the Cambrian appears to end with an extinction of acritarch species. Their diversity drops between the *Peltura* and the *Acerocare* trilobite biozones, and only about half of the species recorded from Stage 10 range into the Tremadocian. On the other hand, many of the typical Early Ordovician acritarch genera find their origin clearly in the late Cambrian, such as the ‘diacromorphs’ or the ‘galeate’ acritarchs (Servais and Eiserhardt, 1995). The latest Cambrian was therefore a time of phytoplankton turnover that preceded and established the foundations for the radiation of acritarchs during the GOBE, but was nevertheless distinct from it (Nowak et al., 2015).

Although the fluctuations in diversity, as well as the origination and extinction of several morphotypes are not completely understood, a general tendency of a marked increase of phytoplankton diversity can be observed between the late Cambrian and the Early Ordovician (Fig. 3).

4. The fossil record of Early Palaeozoic zooplankton

4.1. The fossil record of Radiolaria

Radiolaria (radiolarians) are one of the most important groups of zooplankton in the fossil record (e.g., De Wever et al., 2001). The fossil record of radiolarians dates back to the Cambrian and, because they are usually considered to feed on phytoplankton, it is important to understand if their fossil record shows major changes in diversity in the critical late Cambrian–Early Ordovician interval.

Since Haeckel (1887) three different lineages of protozoans with living representatives are included in the Radiolaria. These are the polycystines, which secrete an esthetically pleasing siliceous skeleton, the Acantharea which secrete a skeleton in celestite (strontium sulfate: SrSO₄), and the Phaeodarea, which produce highly porous siliceous

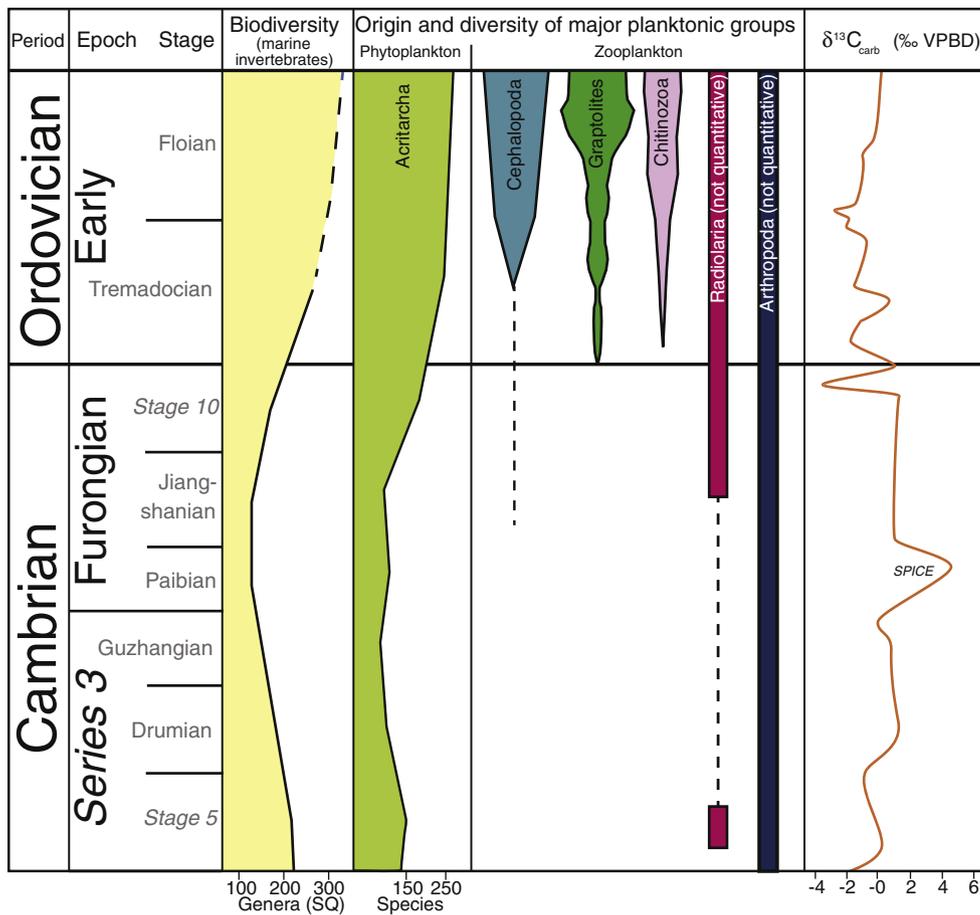


Fig. 3. Middle-late Cambrian–Early Ordovician biodiversity estimates Columns left to right:

- chronological table based on [Gradstein et al. \(2012\)](#);
- biodiversity of marine invertebrate genera based on the shareholder quorum subsampling method ([Na and Kiessling, 2015](#));
- origin and diversity of major planktonic groups (based on published diversity curves; except for radiolarians and arthropods): acritarchs, [Nowak et al. \(2015\)](#) and [Servais et al. \(2008\)](#); cephalopods, [Kröger et al. \(2009, 2011\)](#); graptolites, [Cooper et al. \(2012\)](#); chitinozoans, [Achab and Paris \(2007\)](#).

tests or loosely attached skeletal elements. The single cell of all the above three groups is subdivided in two parts by an organic membrane, called central capsula.

By grazing on the phytoplankton and thus controlling their population size, radiolarians play an important role in modern oceanic food webs. They are locally abundant, depending on the water mass conditions, especially with respect to nutrients. It can be summarized that polycystines are known to be abundant in upwelling areas, both coastal and equatorial (e.g., [Anderson, 1983](#)).

From an ecological point of view, radiolarians live in all depths of the water column, although every species is rather specialized in its trophic strategy. The symbiont-bearing species are usually restricted to the surface waters, while there are other species that prefer to live closer to the nutricline, feeding on picoplankton, while a substantial number of species live in the deeper parts of the water column, feeding on suspended organic particles.

Molecular data confirm the close phylogenetic relationship of polycystines and acantharians, both lineages forming the rhetarian clade, deeply rooted in the recently established monophyletic rhizarian supergroup. However, pheodarians are now included within a diverse cercozoan clade ([Bass et al., 2005](#)).

Acantharians have no fossil record (as their celestite skeleton is not preserved), and pheodarians are only known since the Cretaceous ([Takahashi, 2004](#)). However, the polycystine radiolarians have a much older fossil record, and they allow examination of radiolarian evolution during the Palaeozoic. The oldest currently known fossil polycystine

radiolarians come from a Botomian (lower Cambrian) pelagic sedimentary sequence preserved in the Altai Mountains ([Obut and Iwata, 2000](#); [Pouille et al., 2011](#); [Korovnikov et al., 2013](#)). Polycystines probably diversified and became widespread after their first appearance in the early Cambrian, because by the late Cambrian they were abundant enough to produce deep-water radiolarian oozes ([Tolmacheva et al., 2001](#)).

Polycystine radiolarians diversified progressively during the Early Palaeozoic, but the fossil record remains particularly poor. Nevertheless, they may have the potential to provide some insights regarding the plankton response to palaeoclimatic, palaeoceanographic and global biogeochemical changes. Only a limited number of studies have attempted to produce biodiversity curves of polycystine radiolarians (e.g., [Danelian and Johnson, 2001](#); [Renaudie and Lazarus, 2013](#)). Most of the previous studies focused on specific time intervals that coincide with either major or minor mass extinction events (e.g., [Erbacher and Thurow, 1997](#); [Hori, 1997](#); [Yao and Kuwahara, 1997](#); [Musavu-Moussavou et al., 2007](#); [Kiessling and Danelian, 2011](#)).

Radiolarian diversity data for the Cambrian–Ordovician interval are patchy, especially for the Cambrian. One of the best-preserved Cambrian polycystine radiolarian assemblages comes from middle Cambrian levels of Australia ([Won and Below, 1999](#)) that can be attributed to Cambrian Stage 5. The diversity of this assemblage is represented by 6 genera and 18 species, all of them being part of the archeontactinid, palaeospiculid and aspiculid families of archaeospicularian radiolarians.

Although some late Cambrian radiolarians are reported from China (Dong et al., 1997) it is the pelagic carbonate sequence of western Newfoundland that provides an observational window on late Cambrian radiolarian diversity and faunal changes during the Cambrian–Ordovician transition. The thorough taxonomic studies conducted initially by Won and Iams (2002) and Won et al. (2005) were more recently supplemented by data from Pouille et al. (2014), who recognized three successive radiolarian assemblages for the late Cambrian–early Tremadocian interval. These studies only cover the interval of the Jiangshanian, Cambrian Stage 10, and the early Tremadocian, but do not report radiolarians from the Paibian, when the SPICE event was recorded. The Jiangshanian *Subechidnina* assemblage is composed of 7 genera and 22 species. The stratigraphically younger *Ramuspiculum* assemblage, known from the Cambrian Stage 10, includes 8 genera and 21 species, while the earliest Tremadocian *Protoentactinia kozuriana* assemblage is composed of 6 genera and 20 species.

There are so far no records of diverse radiolarian assemblages between the middle Cambrian report from Australia (Won and Below, 1999) and the late Cambrian and Early Ordovician report from Newfoundland (Pouille et al., 2014). Although taxonomic richness appears to have remained more or less at the same level as in the middle Cambrian, it is interesting to highlight that only two genera are in common with the middle Cambrian fauna from Australia.

The current knowledge of the polycystine radiolarian record appears to suggest that their taxonomic richness remained at more or less the same level during the middle Cambrian–earliest Ordovician interval. However, a detailed look at the pattern of changes in radiolarian diversity in the latest Cambrian unveils a two-step faunal change, each one of them being approximately correlated with negative excursions of the carbon isotope curve.

As a continuous radiolarian record through the middle and late Cambrian interval, and more particularly from the Paibian, is not yet available, it is not possible to attest if the SPICE event had an impact on radiolarian diversity in late Cambrian planktonic ecosystems. However, in spite of the sparse character of the Cambrian radiolarian record, no ‘explosion’ in diversity is recorded when middle and late Cambrian radiolarian assemblages are compared. The diversity of radiolarian assemblages only increased later, with a continuously increasing number of genera during the Ordovician (Noble and Danelian, 2004). However, the record remains too patchy to draw definite conclusions.

4.2. The fossil record of the Graptoloidea

Graptolites were a major macrozooplanktonic group of the Early Palaeozoic. They include the first abundant, well-preserved fossil record of macrozooplankton in Earth history. They constitute a very well studied fossil group. Although graptolites have a fossil record extending back to the Cambrian, the first planktonic graptoloids are earliest Ordovician. The occurrence of selected planktonic graptoloid species serves for the definition of the Global Boundary Stratotype Section and Point (GSSP) of a number of Ordovician and Silurian series and stages, including the Ordovician–Silurian boundary. Being particularly well studied for biostratigraphical purposes, the graptolites show clear onshore–offshore trends of distribution as well as depth–facies preference, occupying the mesopelagic and epipelagic zones, but also neritic (inshore) biotopes (e.g., Vandenbroucke et al., 2009; Cooper et al., 2012).

The graptoloids were colonial pterobranch hemichordates. By analogy with modern pterobranchs, it is assumed that the graptolites filtered food particles from the ocean waters, probably phytoplankton (or picoplankton). Graptolites may therefore have been primary consumers. The graptolites belong to one of the classes of the Graptolithina, that include several other groups, such as the Dendroidea, that are considered to be benthic and sessile. Maletz (2014) revised the systematic position of the colonial or pseudocolonial Pterobranchia

(Cephalodiscida and Graptolithina) and revised the stratigraphical occurrence of the Pterobranchia with a first occurrence in the middle Cambrian Series 3, although a clonal, colonial organization of the tubaria can only be recognized in the basal Drumian (Stage 6 of the Cambrian). Maletz (2014) indicated that palaeontological data provide evidence that the oldest fossil hemichordates are from the Burgess Shale, but the record of pterobranchs from the Chinese Kaili Formation appears to be slightly older. A possible pterobranch has also been described from the early Cambrian Chengjiang biota of China (Hou et al., 2011).

Graptolites underwent a significant ecological innovation at the beginning of the Ordovician, as planktonic forms were presumably derived from their benthic ancestors. The graptolites are clearly one of the major players in the GOBE, but as the first planktonic graptolites only appear in the earliest Ordovician these diversity changes cannot be linked directly with the late Cambrian SPICE event, that occurred some 8 to 10 million years earlier.

4.3. The fossil record of the chitinozoans

Chitinozoans are an abundant group of organic-walled microfossils that have a well documented fossil record because they have been used in Ordovician and Silurian stratigraphy where they complement graptolites and conodonts, in particular for intercontinental correlation (e.g., Webby et al., 2004).

Chitinozoans are very widespread, but their biological affinity remains unknown. They are considered as reproductive bodies, possibly egg cases, of marine invertebrates, called chitinozoophorans (e.g., Paris and Nölvak, 1999; Grahn and Paris, 2011). Chitinozoans are generally preserved as isolated individuals, but they have also been found in chains of monospecific individuals (sometimes with attachment structures between individuals) or in aggregate masses, sometimes within an organic cocoon-like envelope (e.g., Gabbott et al., 1998). The animals that produced the chitinozoans, the chitinozoophorans, are interpreted as small soft-bodied, probably wormlike organisms, possibly a few millimeters to a few centimeters in length. They most probably occupied marine environments from the Ordovician to the Devonian (e.g., Vandenbroucke et al., 2010). Grahn and Paris (2011) considered that they most likely fed on phytoplankton. Achab and Paris (2007) and Grahn and Paris (2011) revised the biodiversification of the chitinozoans in detail. The chitinozoans occupied the planktonic niche from the Early Ordovician onward, with first occurrences in the fossil record in the early (but not earliest) Tremadocian. Chitinozoans are commonly found together with graptolites, suggesting that graptolites and chitinozoophorans lived in partially overlapping environments, occupying nearshore and offshore habitats. In contrast to the graptolites, the chitinozoans displayed their highest diversity at high palaeolatitudes and in less distal environments (e.g., Vandenbroucke et al., 2010; Grahn and Paris, 2011).

For many years, it was believed that chitinozoans were not present in the Cambrian and that they only occupied their pelagic niche after the Cambrian/Ordovician boundary. A few hypothetical records of older chitinozoans have been published, such as the presence of Precambrian vase-shaped microfossils, tentatively attributed to the chitinozoans by Bloeser et al. (1977). These microorganisms were subsequently attributed to testate amoebae (e.g., Porter et al., 2003). More recently, Shen et al. (2012) reported three phosphatised flask-shaped vesicles recovered from the Duyan fauna of China, attributed to Cambrian Stage 5. They tentatively attributed the specimens to *Eisenackitina?* sp., which would date the oldest occurrence of the chitinozoans some 20 million years earlier. Shen et al. (2012) noted that the exceptional occurrence within an Orsten-type Lagerstätte might imply a benthic mode of life for these organisms. However, both the origin of the chitinozoophorans and the passage from a possible benthic to a planktonic mode of life during the late Cambrian remains uncertain.

Chitinozoophorans clearly were a major component of the Ordovician to Devonian zooplankton. Together with the graptolites, they rapidly diversified during the earliest Ordovician. Chitinozoans disappear at the end of the Famennian (Late Devonian). It has been suggested that their ecological niche was invaded by more efficient organisms and that their usual food supplies disappeared, or were no longer sufficient (Grahn and Paris, 2011). As with the graptolites, they contribute to the 'Ordovician Plankton Revolution,' but they were apparently absent in the late Cambrian and are therefore not directly related to environmental changes associated with the SPICE event. But increased oxygen may have been necessary for their evolution.

4.4. The fossil record of planktonic arthropods

Arthropods are invertebrate animals that have an articulated body, jointed legs and usually a chitinous or calcitic shell that undergoes ecdysis. They have been extremely diverse since the early Cambrian (e.g., Minelli et al., 2013), with trace fossil and body fossil records extending to the early Cambrian.

Trilobites are clearly a species-rich fossil group of the Cambrian, but even when the fossil record is extended to non-biomineralized groups, arthropods are the most numerically abundant and diverse phylum in Early Palaeozoic Lagerstätten (Briggs et al., 1994; Hou et al., 2004). Most of the arthropod groups known at present also have their origin in the Cambrian and these include all major classes of crustaceans that are the only group present in modern plankton (Rota-Stabelli et al., 2013). However, the origin and evolution of planktonic arthropods is not entirely understood, as many arthropods belong to the meroplankton, being present in the plankton for only the first part of their life cycle.

Perrier et al. (2015) reviewed the evolution of the marine arthropod zooplankton, their fossil record, and the palaeoecology of the different groups. Arthropod zooplankton are rare in the fossil record, with virtually no occurrences from post-Carboniferous strata and, except for those groups with mineralized skeletons, most planktonic arthropods are known almost exclusively from Konservat-Lagerstätten, with a majority of these having been described from the Cambrian. Nevertheless, new insights on arthropod evolution are available through the study of the 'Small Carbonaceous Fossils' (SCFs, see Harvey et al., 2012). Some SCFs in the Cambrian represent groups such as branchiopods, copepods or ostracods, but they are so far only known from a few disarticulated appendages, which precludes a detailed reconstruction of their lifestyle. In addition, because studies of SCFs have mostly concentrated on Cambrian material, the Phanerozoic record of these arthropods is strongly biased, with virtually no record of copepods, for example, between the Cambrian and Recent (Selden et al., 2010).

There is now sufficient evidence to suggest that the zooplankton food web was already well developed by the early Cambrian, and arthropods are likely to have been present within the plankton from that time onwards (e.g., Signor and Vermeij, 1994; Rigby and Milsom, 2000; Butterfield, 2001; Peterson et al., 2004; Vannier, 2007; Vannier et al., 2009). However, most of these arthropods probably never occupied pelagic niches and only lived in the lower levels of the water column (and therefore likely occupied demersal habitats).

Other small putative mesozooplankton in the Cambrian include species of the bradoriids that probably originated in benthic shelf settings in the early and middle Cambrian (Siveter and Williams, 1997; Williams and Siveter, 1998), possibly migrating into the water column during intervals of widespread shelf dysoxia in the Drumian and Guzhangian stages of Cambrian Series 3 (Collette et al., 2011; Williams et al., 2015).

Other records of arthropod macrozooplankton in the Cambrian are meager. *Isoxys*, with its light carapace, appendages adapted for swimming, a flap-like telson, powerful prehensile frontal appendages, a well-developed digestive system and large spherical eyes, is probably one of the best candidates as a macrozooplankton predator (Vannier

and Chen, 2000; Vannier et al., 2009). Although *Isoxys* is not cosmopolitan at the species level like some Cambrian bradoriids, evidence from functional morphology, taphonomy and palaeogeographic distribution suggests that it may have been a widespread predator, living near the seafloor (Vannier et al., 2009).

The presence of pan-arthropod top predators (e.g., Radiodonta) in the early Cambrian (Series 2) water column is well documented. These animals reached meter-scale lengths in the Cambrian and Ordovician (e.g., Van Roy and Briggs, 2011) and were present until at least the Early Devonian (Kühl et al., 2009). The functional morphology of the frontal appendages suggests that some anomalocaridid taxa were durophagous predators, while others fed on soft-bodied organisms (Daley et al., 2013). Two species from the early Cambrian (Vinther et al., 2014) and Early Ordovician (Van Roy et al., 2015) most probably were microphagous suspension feeders. The appendages of these large (up to 2 m long) anomalocaridids were probably used for sweep-net capture of food items down to 0.5 mm, which is within the size range of mesozooplankton such as copepods and branchiopods.

The first putative malacostracan crustaceans entered the water column only during the Early Ordovician. Based on its cosmopolitan palaeogeographic distribution and its associated faunas, the putative phyllocarid *Caryocaris*, recorded from the Tremadocian onward, has been interpreted as a microphagous/opportunistic mid-water zooplankton animal that probably occupied the same niches as Ordovician pelagic trilobites (Vannier et al., 2003).

Although trilobites were already diverse during the Cambrian (e.g., Fortey and Owens, 1997), there are only a few adult forms that have been interpreted as pelagic. On the contrary, the Ordovician bears a wider range of what are generally agreed to be pelagic trilobite species (e.g., Fortey, 1974, 1975, 1985; Fortey and Owens, 1999). Some of these occur across inner and outer shelf facies.

The presence of a great diversity of lifestyles and feeding strategies in Early Palaeozoic arthropods suggests that the planktonic food web was already complex perhaps as early as the early-middle Cambrian, implying that arthropods were present at several trophic levels from primary consumer to tertiary predator. However, it appears also that during the Cambrian many planktonic niches remained unoccupied, at least until the late Cambrian. The arthropods only filled these niches progressively during the Ordovician.

The review of the literature clearly indicates that radical changes in arthropod zooplankton evolution cannot be related directly to the SPICE event. Several zooplanktonic groups are present in the fossil record since the early-middle Cambrian. Bradoriids, bivalved arthropods, copepods and branchiopods, as well as agnostids were clearly present in the water column of the Cambrian ocean before the SPICE event. Pelagic trilobites and phyllocarids, however, only strongly diversify in the Ordovician (see also Fig. 2).

4.5. The fossil record of planktonic (pelagic) cephalopods

Modern cephalopods are swimming animals and are therefore considered as living freely in the water column (i.e., numerous species clearly belong to the nekton, especially Decabrachia). Today they occupy nearly the entire spectrum of marine environments, with different life habits corresponding to the different habitats. Being mobile, cephalopods have commonly played the consumer-role, similar to some of the larger arthropods described from Cambrian Lagerstätten. For this reason, cephalopods and arthropods were probably the largest animals in Cambrian and Ordovician oceans, although arthropods (e.g., Butterfield, 2001; Van Roy and Briggs, 2011; Vinther et al., 2014; Van Roy et al., 2015) and cephalopods (e.g., Dzik, 1981; Holland, 1987; Kröger, 2003, 2005, 2007; Mutvei et al., 2007; Klug et al., 2010) occupied different niches that changed over time. Both groups also produced relatively gigantic (meter-scale) forms in the Cambrian and Ordovician (e.g., Teichert and Kummel, 1960; Braddy et al., 2007; Van Roy and Briggs, 2011; Vinther et al., 2014; Klug et al., 2015; Van Roy et al., 2015).

The precise moment of the first occurrence of cephalopods in the fossil record has been disputed (e.g., Kröger et al., 2011; Kröger, 2013). Currently, the majority of specialists agree that the sister group of the cephalopods has to be sought in the monoplacophorans (e.g., Kröger et al., 2011). Although the origin of the group is not fully understood, cephalopods are clearly present in the latest Cambrian. They displayed cm-long breviconic shells with several simple chambers and a narrow siphuncle (e.g., Dzik, 1981; Holland, 1987; Kröger, 2007). These early forms are known from the late Cambrian of North America and China (Holland, 1987), from two distinct regions located in tropical palaeolatitudes. The combination of shell characters and their early wide distribution underlines the plausibility that these forms were indeed planktonic drifters, most likely feeding on planktonic organisms of smaller size. Occurrences in South China indicate the presence of late Cambrian and early Tremadocian cephalopods in off-shore shelf carbonates, interpreted as deposited below normal storm wave base, representing in some cases clearly neritic habitats (e.g., Chen and Qi, 1982; Zou, 1987). However, late Cambrian cephalopods are not known from deeper water settings, and the oldest cephalopods from deeper water environments are from the middle Tremadocian (Kröger et al., 2009).

A planktonic mode of life of Ordovician cephalopods with orthoconic or cyrtoconic shells appears likely. Based on the fact that many Ordovician cephalopods with orthoconic shells had thick siphuncles, Kröger (2003) suggested that these may have been vertical migrants in the water column. The presence of apical endosiphuncular or endocameral deposits has been considered as an aid to move the shell into a position to facilitate horizontal swimming (e.g., Holland, 1987), but this hypothesis needs further testing. Simultaneously with the increase in siphuncular disparity, from the late Cambrian to the Late Ordovician (see Kröger, 2003), cephalopod shell disparity also increased. The independent evolution of coiled shells in several Ordovician cephalopod clades documents an ecological transition from an essentially planktonic to a nektonic habit (Kröger, 2005), anticipating similar coiling events in the 'Devonian Nekton Revolution' (Klug and Korn, 2004; Klug et al., 2010).

The probable change in the mode of life from benthic to planktonic in the late Cambrian at the monoplacophoran–cephalopod–transition and from planktonic to nektonic lifestyles early in the Ordovician within several cephalopod clades, may reflect the rich supply of planktonic food sources developing in the later part of the Cambrian. Kröger et al. (2009) summarized data that suggest that the exploitation of the pelagic realm by several independent invertebrate clades began synchronously during the latest Cambrian to Middle Ordovician. Possibly this might be linked to new food supplies from primary producers.

The origin of planktonic/nektonic cephalopods occupying pelagic niches and offshore environments occurs during the time interval of the late Cambrian to Early Ordovician, although a direct link with the SPICE event cannot be demonstrated.

5. The development of planktotrophy in marine invertebrate larvae

Several marine invertebrate organisms begin their lifecycle with a planktonic phase (meroplankton) and several marine invertebrate clades produce free-swimming larvae or hatchlings that feed on the smaller members of the plankton. Such larvae and hatchlings play an important role in the study of the evolution of the Early Palaeozoic plankton. They clearly form a significant part of the plankton, and, on the other hand, if they are plankton feeding (planktotrophic), they are among the primary consumers grazing the phytoplankton.

Marine invertebrates may hatch from the fertilized egg (direct development) or they may have biphasic life cycles and hatch as a larva (indirect development). The definition of larvae is basically the presence of a profound morphological and ecological transformation (metamorphosis) of a hatchling into a larger juvenile animal (Strathmann, 1986). Planktonic larvae and other hatchlings that do

not undergo metamorphosis enhance dispersal and gene flow between populations. They either feed on plankton (planktotrophic larvae) or do not feed but live on yolk or other parental energy resources (lecithotrophic larvae). These ontogenetic pathways vary from clade to clade. For instance, planktotrophic larval development is unknown in modern brachiopods (e.g., Lüter, 2001), although it is common in higher gastropods and bivalves, but absent in other mollusk classes (e.g., Nützel, 2014). Planktotrophic larval development is most common in modern tropical and subtropical shallow waters but rare in species from higher latitudes and deep water (e.g., Thorson, 1950; Jablonski and Lutz, 1980, 1983).

There is currently a detailed debate about the time periods when planktotrophic larval development evolved and whether it is ancestral in Eumetazoa or Bilateria or not (e.g., Nützel, 2014). This is also relevant for the discussion about the onset of the 'Ordovician Plankton Revolution' because the timing of the evolution of planktotrophic larval development has implications for the overall evolution of primary productivity and food chains in the plankton. Planktotrophic larvae are mostly primary consumers of phytoplankton although larvae may also feed on zooplankton (e.g., Richter, 1987). Sufficient and continuous primary production by phytoplankton is therefore a prerequisite for planktotrophic larval development. The question is whether planktotrophic larval development was present as early as the early Cambrian or even the late Proterozoic (e.g., Nielsen, 2013) or whether it evolved later and independently in several evolutionary lineages.

The notion that larval planktotrophy is an original trait of eumetazoans or bilaterians has previously been rejected based on the phylogenetic distribution of planktotrophy (Signor and Vermeij, 1994; Haszprunar, 1995; Haszprunar et al., 1995; Peterson, 2005). Thus, basal clades lack planktotrophic larvae, including basal mollusk clades. Chaffee and Lindberg (1986) also argued that Cambrian molluscs were too small to produce large numbers of planktonic larvae, which suffer high mortality rates (but see also, Mus et al., 2008 and discussion by Nützel, 2014). Therefore, Chaffee and Lindberg (1986) concluded that planktotrophy in molluscs evolved during the late Cambrian/Ordovician transition.

Nützel et al. (2006) found that the early (Cambrian) ontogenetic parts of univalved mollusk shells, among them probably early gastropods, are clumsy and large at a defined shell length at 100 µm. They suggested that this reflects yolk-rich early ontogeny and thus either direct or non-planktotrophic larval development. By contrast, Ordovician/Silurian shelly assemblages yield numerous molds of gastropod protoconchs with small initial parts suggesting the presence of planktotrophic larvae. Nützel et al. (2006, 2007) concluded that in molluscs, including gastropods, planktotrophic larval development evolved at the Cambrian/Ordovician transition (for a contrasting opinion see Freeman and Lundelius, 2007). Based on the study of relatively well-preserved helcionellids, Parkhaev (2014) corroborated the assumption that planktotrophic larval development is absent in Cambrian molluscs and concluded that Cambrian univalved molluscs (helcionellids) had either direct or lecithotrophic larval development. Similarly, the oldest known bivalve, *Pojetaja runnegari*, likely had a non-planktotrophic (lecithotrophic) larval development according to Runnegar and Bentley (1983) (but see Freeman and Lundelius, 2007, postscript, for a different opinion).

Freeman and Lundelius (1999, 2005, 2007) proposed that a planktotrophic larval development is common in Early Palaeozoic brachiopods and that the presence of planktotrophic larva is probably a basal and universal character across brachiopod groups. However, seemingly all living brachiopods have a non-planktotrophic early ontogeny, either a lecithotrophic larva or a direct (Lüter, 2001, and references therein). The proposed plesiomorphic presence of a planktotrophic larval development in Brachiopoda is in conflict with the fact that all living members (or at least articulate brachiopods) lack planktotrophic larvae. The presence of exclusively lecithotrophic early ontogenetic stages in all recent representatives of craniiform and

rhynchonelliform brachiopods suggests that the stem species of both groups had a lecithotrophic early ontogeny although the ontogeny of the numerous fossil representatives is either unknown or insufficiently known (Lüter, written communication 2015).

In conclusion, there is no evidence for Cambrian molluscs with planktotrophic larval development. This is also suggested by the phylogenetic distribution of planktotrophic larval development in molluscs and also in other invertebrates and in Eumetazoa as a whole. Planktotrophic larvae evolved independently in several evolutionary lineages during the late Cambrian and Ordovician (see also Signor and Vermeij, 1994; Haszprunar et al., 1995; Haszprunar, 1995; Peterson, 2005; Nützel et al., 2006, 2007; Nützel, 2014). However, more observations on well-preserved early ontogenetic hard parts are needed to corroborate this assumption.

It is evident that the evolution of larval planktotrophy is an important part of the establishment of planktonic food chains. Palaeozoic morphological trends in gastropod larval shells, i.e., the change from open coiling to tight coiling and increasing larval ornament, suggest an increasing predation pressure in the plankton and this was originally termed the 'Palaeozoic Plankton Revolution' in analogy with Vermeij's (1977) 'Mesozoic Marine Revolution' (Nützel and Frýda, 2003; Nützel et al., 2006; Seuss et al., 2012; Nützel, 2014).

An explanation for the convergent evolution of planktotrophy in the larva of several different invertebrate groups remains debatable. Increasing primary production could have triggered this, as well as increasing predation pressure in the benthos by burrowers and suspension feeders, which forced hatchlings to escape to the plankton (see Strathmann, 1986; Signor and Vermeij, 1994; Nützel et al., 2006).

In conclusion, it appears evident that an important ecological shift took place with the development of planktotrophy. This significant additional step took place during the late Cambrian–Early Ordovician interval (see also Peterson, 2005), i.e., it clearly is part of the 'Ordovician Plankton Revolution.' However, the exact timing when these changes took place is imprecisely known.

6. Nutrients and the trophic structure of the oceans between the 'Cambrian Explosion' and the 'Great Ordovician Biodiversification Event'

The objective of this section is to place the late Cambrian and Ordovician in a general context of nutrient availability in the oceans, though noting at present that there is only limited data available to assess this.

The Palaeozoic positive carbon isotope excursions of which some shifted $\delta^{13}\text{C}_{\text{carb}}$ by $\geq 3\text{‰}$, each having a duration of a few million years, are considered to represent significant palaeoceanographic events, commonly modeled as episodes of increases in oceanic nutrient availability (e.g., Kump and Arthur, 1999; Godd ris and Joachimski, 2004). Analyses of the geological processes that took place during the SPICE event are therefore important to assess whether an increased nutrient availability in the late Cambrian oceans fuelled the 'Ordovician Plankton Revolution' and ultimately the GOBE.

The proliferation of phytoplankton that serves as the food supply for both planktotrophic larvae and planktotrophic (heterotrophic) zooplankton, depends on the availability of nutrients. Phytoplankton obtains energy through photosynthesis and primarily needs macronutrients such as nitrogen, phosphate and silicic acid and the 'secondary' micronutrient iron. The abundances of these nutrients in the oceans change in time and space. Phytoplankton usually blooms in spring and summer, and is abundant in upwelling zones where nutrient supply is usually high.

The huge increase of biodiversity during the GOBE, including the 'Ordovician Plankton Revolution,' may ultimately have been fuelled by tectonism, as evidenced by strontium isotope ratios that indicate increased continental weathering or changes in the rock type being weathered. Strontium isotope ratios have been used as a qualitative indicator of nutrient runoff from the continents: increasing strontium

isotope ratios reflect orogeny and enhanced continental weathering, which inputs the heavier isotope ^{87}Sr to the oceans, as opposed to ^{86}Sr input, which is associated with increased rates of seafloor spreading and hydrothermal weathering (e.g., C rdenas and Harries, 2010). Strontium isotopes exhibit strong changes during the Pan-African Orogeny (Neoproterozoic–Cambrian) (e.g., McKenzie et al., 2011). Some of the highest, if not the very highest strontium isotope ratios of the Phanerozoic also occur during the Cambrian, presumably in response to widespread tectonism and orogeny associated with the Pan-African Orogeny and the rifting of Rodinia/Pannotia (Monta nez et al., 2000). Recently, more precise Sr ratios have been published for the late Cambrian–Early Ordovician interval (e.g., McArthur et al., 2012; Saltzman et al., 2014) with a general trend of decreasing values between the late Cambrian and the Middle–Late Ordovician boundary.

Nutrient input in the oceans is also related to volcanism. Some of the greatest volumes of volcanic rocks of the entire Phanerozoic erupted in the Middle Ordovician, possibly in response to a mantle plume (e.g., Barnes, 2004; Servais et al., 2009b; Lef bvre et al., 2010). Mafic volcanic rocks are associated with higher phosphorus concentrations (Hartmann et al., 2014) and satellite data indicate that phytoplankton blooms are stimulated by ash outfall (Duggen et al., 2007; see also Botting, 2002). Models indicate that silicate weathering rates are similar to out-gassing rates of volcanic and metamorphic CO_2 and that intervals of continental dispersion are characterized by high rates of out-gassing and runoff due to intensification of the hydrologic cycle, whereas supercontinent stasis is associated with low out-gassing rates, high aridity resulting from the development of supercontinents, and low chemical weathering fluxes (Tardy et al., 1989; Gibbs et al., 1999; see also Baldwin et al., 2004).

Since about 470 million years ago during the Ordovician, the origin and diversification of land plants and their consequences may also have played a critical role in the weathering of the continents, nutrient runoff, and the evolution of the marine biosphere. Spores and cryptospores provide evidence of land plants at least as early as the Mid Ordovician–Silurian, and likely produced widespread rudimentary soils in place of microbial soil crusts (e.g., Boucot and Gray, 2001; Wellman et al., 2013; Gerrienne et al., submitted for publication). Lenton et al. (2012) also argued that the terrestrialization by land plants cooled the Ordovician oceans. However, the impact of the land plants most probably did not influence the onset of the 'Ordovician Plankton Revolution,' as the first land plants appeared only several tens of million years after the massive occurrence of plankton in the fossil record.

During the late Cambrian–Early Ordovician interval, presumably accelerated nutrient runoff could have supported greater primary productivity. Increased tiering above and below the sea bottom, as evidenced by the fossil record, and the presence of abundant planktotrophic larvae could suggest greater food availability in the marine realm (Droser and Bottjer, 1988, 1989; Bottjer et al., 2000). Increased nutrient availability may have contributed to the alteration of life history traits and the initial evolution of the benthos into the plankton (Elser et al., 1996; Main et al., 1997; Sterner and Elser, 2002; Nützel et al., 2006). All of these conditions together possibly provided optimal conditions for metazoan evolution and diversification. Greater food availability above (in the form of plankton) and below (in the form of dead organic matter at the sea bottom) could have supported expanding populations, potentially leading to their migration and genetic isolation (see also Allmon and Martin, 2014). Other energy-based mechanisms may have also driven biodiversification (Brown, 1995; Maurer, 1999; Evans et al., 2005a,b, 2006).

In conclusion, there is evidence to suggest that there may have been an increase of nutrients available in the global oceans during the Cambrian and Ordovician (see also Miller and Mao, 1995; C rdenas and Harries, 2010; Allmon and Martin, 2014). However, future research is needed, including models of oceanic current distribution and upwelling zones and climate (e.g., Nardin et al., 2011; Servais et al., 2014; Pohl

et al., 2014, 2016), to fully understand the development of trophic webs during the Early Palaeozoic radiation.

7. Isotope geochemistry and oxygen evolution in the Cambrian–Ordovician

Saltzman et al. (2011) related a pulse of oxygenation to the SPICE event and correlated this to the GOBE and the ‘Ordovician Plankton Revolution.’ What might the SPICE event mean in terms of plankton evolution?

The middle-late Cambrian and Early and Middle Ordovician interval is associated with several $\delta^{13}\text{C}_{\text{carb}}$ isotope excursions, though these are of relatively small magnitude, with values varying typically between -1.5% and $+1.5\%$ through this interval (Saltzman, 2005; Bergström et al., 2009; Munnecke et al., 2010). The chief exception is the SPICE event in the late Cambrian (Paibian Stage, Furongian Series). This excursion, with a $\delta^{13}\text{C}_{\text{carb}}$ amplitude of up to 5% , is known from sections in Australia, China, Kazakhstan, North America, and Siberia (Glumac and Walker, 1998; Saltzman et al., 1998, 2000, 2004; Kouchinsky et al., 2008; Gill et al., 2011). Coeval positive excursions in organic matter ($\delta^{13}\text{C}_{\text{org}}$) have been reported from Baltica (Ahlberg et al., 2009) and Avalonia (Woods et al., 2011). The onset of the excursion coincides more or less with the FAD of the cosmopolitan agnostid *Glyptagnostus reticulatus* and with a time of significant faunal changes on different palaeocontinents, among these being the extinction of the marjumiid trilobites (see summary in Gradstein et al., 2012). The early Furongian is characterized by an initial global transgression which led to the deposition of black shales in Avalonia, Baltica, and Argentina (Álvarez et al., 2013), followed by a major glacio-eustatic regression and the deposition of sand- and siltstones or quartz-rich carbonates (Sauk II–Sauk III event; Saltzman et al., 2004; Lindsay et al., 2005; Buggisch, 2008).

As for most other Palaeozoic $\delta^{13}\text{C}_{\text{carb}}$ excursions the ultimate cause of the SPICE is a matter of debate. Saltzman et al. (2000) highlighted the fact that sedimentological evidence for glaciation is lacking, and proposed thermal contraction of the deep-ocean water coupled with increased storage of groundwater in continental reservoirs as a cause for the global regression. The lack of large ice sheets that could have changed the ratio of silica to carbonate weathering rates by covering up silicate terranes containing organic matter at high latitudes, suggests that burial of organic carbon in black shales was the likely cause of the $\delta^{13}\text{C}_{\text{carb}}$ excursion (Saltzman et al., 2004). There is, however, no indication of enhanced deposition of black shales during the SPICE (Saltzman, 2005; Ahlberg et al., 2009). Munnecke et al. (2003) pointed out that the SPICE shared many similarities with Late Ordovician and Silurian $\delta^{13}\text{C}_{\text{carb}}$ excursions, and argued that a change from humid to arid climate in low latitudes and thus a change from chemical to physical continental weathering might have increased the availability of quartz grains (see also Bickert et al., 1997, and Kozłowski and Sobieć, 2012).

Gill et al. (2007, 2011) document a positive sulfur isotope excursion both from carbonate-associated sulfate ($\delta^{34}\text{S}_{\text{CAS}}$) and pyrite ($\delta^{34}\text{S}_{\text{pyrite}}$) in phase with the $\delta^{13}\text{C}_{\text{carb}}$ excursion. This is interpreted as indicating enhanced pyrite burial (with preferential removal of ^{32}S) stimulated by large-scale marine organic carbon burial during the SPICE. A decrease and minimum in molybdenum (Mo) and Mo/TOC ratios in the Andrarum 3 core of Scandinavia corresponding to the initiation and peak of the carbon and sulfur isotope excursions, respectively, indicate the transient spread of marine anoxia (Gill et al., 2011). Based on a carbon and sulfur mass balance model Saltzman et al. (2011) interpreted the coeval carbon and sulfur isotope excursions as an indicator of a major increase in atmospheric O_2 . This major increase in atmospheric O_2 is estimated to shift values from 10–18% to some 20 to 29%. On a first view, oceanic anoxia seems to contradict an atmospheric oxygenation event, but deposition and burial of organic matter can plausibly be linked to both increase and decrease in marine oxygenation (Thompson and Kah, 2012). Because the bacterial decomposition of organic matter in the water column removes O_2 from sea-water and,

consequently, from the atmosphere, the non-decomposition and burial of organic matter acts in the opposite direction, and oxygen becomes available to build up in the atmosphere. On the other hand, if black shale deposition is triggered by ocean stratification, i.e., by effective decoupling of the ocean–atmosphere system, the long-term effect would include an increase in global anoxia (Thompson and Kah, 2012).

The most prominent feature of the immediate aftermath of the end-Ordovician (e.g., Delabroye et al., 2011), end-Devonian (e.g., Buggisch and Joachimski, 2006), end-Permian (e.g., Payne et al., 2004), and end-Triassic extinction events (e.g., van de Schootbrugge et al., 2009) is the occurrence of large ($>+3\%$) to very large ($>+5\%$) positive carbon isotope excursions measured from carbonates and organic carbon. Some of these positive excursions have been invariably associated with anoxic conditions in the oceans, and are most readily explained as the result of massive carbon burial during times of enhanced primary productivity (Kump and Arthur, 1999).

8. Discussion

The analysis of early–middle Cambrian (Series 2 and 3) Lagerstätten indicates that formerly benthic organisms began to enter the plankton (e.g., Butterfield, 2001). The exceptionally preserved assemblages in these ecosystems were characteristic of shallow-water shelf communities. It is evident that some arthropods from these communities were able to swim (see Perrier et al., 2015, for a review), and they could thus be attributed to the nekton (or to nekto-benthic organisms), or at least to the plankton (unable to swim against currents). However, these arthropods did not leave shallow shelf environments, although a few organisms probably started to live in deeper shelf and slope environments (e.g., Burzin et al., 2001). The pelagic zones were probably not fully occupied during the ‘Cambrian Explosion,’ but only much later. The main zooplankton captured by the fossil record during the early and middle Cambrian was thus composed of arthropods, together with a first sporadic record of radiolarians.

Fig. 2 summarizes the evolution of the most important fossil groups belonging (partly or entirely) to the plankton. This figure includes some qualitative data on the presence or absence of selected groups of organisms. Between the benthic (at the sea-floor) and planktonic (drifting, with limited swimming capacities), the demersal category includes organisms living in the water column near the sea floor.

The acritarchs include various microorganisms present in the fossil record as organic-walled microfossils. As a polyphyletic group, they include (for all geological periods) several kinds of small organisms, living in benthic, demersal and pelagic habitats, and including cysts of phytoplanktonic organisms. The chitinozoans were possibly already present in the Cambrian Series 3, but the organisms producing them clearly are planktonic after the Cambrian–Ordovician boundary. The zooplanktonic radiolarians first appear in the early Cambrian, and they become common in the late Cambrian, before diversifying progressively in the Ordovician. The graptolites were entirely benthic during the Cambrian; but many Ordovician graptoloids were clearly planktonic. Among the arthropods, a number of groups are considered to belong to the zooplankton. The bradoriids are one of the few groups of which some taxa appear to have adopted a planktonic lifestyle during Cambrian Series 3, while other bradoriids are benthic. The recent findings as SCFs of copepods and branchiopods indicate that these crustaceans already existed in the early and middle Cambrian, though their lifestyles cannot be precisely constrained for this time period. The agnostids include taxa that may have been planktonic during Cambrian Series 3 and the Furongian, but not later. Trilobites were clearly benthic in the Cambrian, but a few taxa moved into the plankton during the late Cambrian, and pelagic taxa became common in the Ordovician. The phyllocarids are a group of crustacean arthropods that may have occupied pelagic niches from the Tremadocian onward. The cephalopods entered the pelagic realm during the late Cambrian. Originally

living near the sea floor they became active swimmers and predators at the top of the Ordovician food chain.

Fig. 3 attempts to quantify the presence of different marine organisms with a planktonic lifestyle from Cambrian Series 3 to the Early Ordovician. The quantitative data (based on published diversity counts, see Legend of Fig. 3) of several groups are plotted against the chronostratigraphical scheme, the values of $\delta^{13}\text{C}_{\text{carb}}$, as well as against the most recent biodiversity curve of marine invertebrate genera recently published by Na and Kiessling (2015). In addition, radiolarians and planktonic arthropods are plotted here, based on qualitative data only, based on the review presented above.

At a geological scale, in the context of the Palaeozoic or the entire Phanerozoic, the increase of the plankton during the late Cambrian–Early Ordovician might be viewed as a relatively short ‘event’ (see also Fig. 1). It appears to have developed over several (tens of) millions of years, assuming that this record is not distorted by an absence of fossil data for the plankton. At a smaller scale, with a focus on the interval of the late Cambrian and Early Ordovician (Fig. 3), the onset of the ‘Ordovician Plankton Revolution’ appears to have been stepwise, and not a sudden event triggered by a single geological or palaeoecological parameter. Between the rapid increase of acritarch (phytoplankton) diversity starting in the Jiangshanian, and the rapid onset of the diversification of the cephalopods, graptolites and chitinozoans in the Tremadocian, it appears that a few million years elapsed.

Of particular interest is the lack of direct correlation between the different planktonic groups and the SPICE $\delta^{13}\text{C}_{\text{carb}}$ event. Saltzman et al. (2011, fig. 6) suggested that the SPICE event triggered the ‘Great Ordovician Biodiversification Event’ (GOBE). They correlated the SPICE event with the onset of the GOBE, based on both the global compilation of marine invertebrate genus level diversity of Alroy (2010) and the diversity compilation of South China by Rong et al. (2007). Our compilation of data shows that the SPICE event does not closely correlate with the diversifications of the planktonic groups examined, nor with a dramatic change in the most recent diversity curve calculated for all marine invertebrates. Based on Na and Kiessling’s (2015) dataset, it would be possible to consider the Jiangshanian Age as the time of the onset of the GOBE, but not the Paibian Age, when the SPICE event took place. In conclusion, there seems to be no clear correlation between the SPICE event and the fossil record of plankton colonization.

An alternative explanation can be considered, with the gap between the SPICE event (its related oxygenation) and the appearance of new planktonic groups being the result of the establishment of complex food webs that surely took some time. The evolution of the zooplankton feeding on the phytoplankton and then larger animals feeding on the zooplankton could reasonably have taken 3 to 5 myr or more, making the hypothesis of Saltzman et al. (2011) plausible.

However, oxygen levels during the SPICE event likely increased in response to enhanced photosynthesis. If so, the question then becomes: What triggered the increase of photosynthesis? One possible cause is increased nutrient availability, as reflected by the broad rise of strontium isotope ratios during the late Proterozoic and into the Cambrian (Fig. 3) and which surpassed values for the Cenozoic, when orogenic uplift of major mountain chains was quite pronounced (Montañez et al., 2000). Rising inorganic nutrient levels may have also enriched food sources (plankton and the pelagic rain of dead organic matter) with inorganic nutrients such as phosphorus and trace elements necessary for nucleic acid synthesis (DNA and especially the ribonucleic acids of ribosomes involved in protein synthesis) and biochemical pathways, including those of photosynthesis. The subsequent rise of sea level into the Cambrian would have produced a much more widespread photic zone on the shelf into which nutrients continued to be added (as indicated by strontium isotopes). Depths of bioturbation also began to increase, possibly in response to both oxygen and the pelagic rain of dead organic matter.

As noted previously, the positive carbon isotope excursion ($\delta^{13}\text{C}_{\text{carb}}$) of the SPICE event may also be associated with oceanic nutrient

availability (e.g., Kump and Arthur, 1999; Godd eris and Joachimski, 2004). Increasing nutrient and food availability in the water column may therefore have provided conditions that produced a refuge from bioturbation and benthic predation. These trends may have been further stimulated by volcanic and tectonic activity later in the Ordovician, as discussed above. Furthermore, biodiversification may have experienced a significant lag following one or both of the SPICE and volcanic/tectonic events. Analyses of the geological processes that took place during the SPICE and subsequent volcanic events may therefore be critical to understanding the ‘Ordovician Plankton Revolution’, and the GOBE.

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