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# 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 $\delta^{13}C_{carb}$ (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.



## 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 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).

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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) $\delta^{13}C_{carb}$ 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 $\delta^{13}C_{carb}$ (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 Quéré 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 nektobenthic 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 nektobenthic 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