



Invited review

Phytoplankton dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification Event: A review of Cambrian acritarch diversity



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ABSTRACT

Most early Palaeozoic acritarchs are thought to represent a part of the marine phytoplankton and so constituted a significant element at the base of the marine trophic chain during the 'Cambrian Explosion' and the subsequent 'Great Ordovician Biodiversification Event.' Cambrian acritarch occurrences have been recorded in a great number of studies. In this paper, published data on Cambrian acritarchs are assembled in order to reconstruct taxonomic diversity trends that can be compared with the biodiversity of marine invertebrates. We compile a database and calculate various diversity indices at global and regional (i.e. Gondwana or Baltica) scales. The stratigraphic bins applied are at the level of the ten Cambrian stages, or of fourteen commonly used biozones in a somewhat higher resolved scheme. Our results show marked differences between palaeogeographical regions. They also indicate limitations of the data and a potential sampling bias, as the taxonomic diversity indices of species are significantly correlated with the number of studies per stratigraphic bin. The total and normalized diversities of genera are not affected in the same way. The normalized genus diversity curves show a slow but irregular rise over the course of the Cambrian. These also are the least biased. A radiation of species and to a lesser extent of genera in the 'lower' Cambrian Series 2 appears to mirror the 'Cambrian Explosion' of metazoans. This radiation, not evident on Gondwana, is followed by a prominent low in species diversity in the upper Series 3 and lower Furongian. Highest diversities are reached globally, and on both Baltica and Gondwana, in the uppermost Cambrian Stage 10, more precisely in the *Peltura* trilobite Zone, preceding a substantial phase of acritarch species extinction below and at the Cambrian/Ordovician boundary. Nearly all the genera present in Stage 10 survived into the Ordovician. The forms that emerged during the Cambrian therefore became the foundation for the more rapid radiation of acritarchs during the 'Great Ordovician Biodiversification Event'.

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1. Introduction

The Cambrian fossil record is marked by the well-known ‘Cambrian Explosion’ (or radiation), which is characterized by the appearance of most metazoan phyla in a seemingly short interval (e.g. Conway Morris, 2000). Although molecular clock estimates now indicate a Proterozoic origin for many lineages (Erwin et al., 2011), the Cambrian Explosion is still considered to be one of the most important periods in the history of life. It was followed in the Ordovician by the ‘Great Ordovician Biodiversification Event’ (GOBE), an episode of rising taxonomic diversity in most marine organisms and of increasingly complex ecosystems that were more diverse and differentiated than those of the Cambrian, with a wider range of ecological niches (Webby et al., 2004; Bambach et al., 2007). Whether these two episodes were in fact separate, or should be considered as one long period of diversification, is currently debated (Alroy et al., 2008), as are their possible causes and mechanisms.

Phytoplankton is an important constituent at the base of the food web today and in this capacity may have played a key role in the early Palaeozoic diversification events (Debrenne and Zhuravlev, 1997; Butterfield, 1997). It has been argued that a higher concentration of phytoplankton in the early Palaeozoic oceans triggered the major evolutionary events and had an important impact on metazoan diversification. Butterfield (1997), for example, argued that the interaction between phytoplankton and metazoans fuelled the Cambrian Explosion after the appearance of mesozooplankton. Similarly, Servais et al. (2008, 2010) argued that the evolution of the phytoplankton triggered a ‘plankton revolution’ through the Cambrian–Ordovician boundary interval at the beginning of the GOBE. The expanding and increasingly diverse phytoplankton could have served as food for the developing zooplankton, but also for various clades of suspension feeders and detritus feeding organisms. Detailed knowledge on the development of biomass, taxonomic and morphological diversity of phytoplankton would be useful to test this hypothesis. Here we concentrate on taxonomic diversity.

The phytoplankton of early Palaeozoic oceans is generally considered to be present among the acritarchs, which are defined as organic-walled microfossils of uncertain biological affinity (Eviitt, 1963). Consequently, the acritarchs are a polyphyletic group and have a long stratigraphical range. A number of organisms originally considered to be acritarchs now have established affinities with other groups, including prasinophycean and zygnematacean green algae, cyanobacteria, dinoflagellates, multicellular algae (Butterfield, 2004; Mendelson, 1987), fungi (Butterfield, 2005) and even metazoans (e.g. schizomorphae: Van Waveren, 1992; Van Waveren and Marcus, 1993; *Ceratophyton*: Fatka and Konzalová, 1995; large spinose Ediacaran microfossils: Cohen et al., 2009). Although technically no longer acritarchs (Eviitt, 1963), they are still occasionally referred to as such. Nevertheless, most of the remaining Palaeozoic acritarchs are considered to be cysts of marine, generally planktonic unicellular algae, which are often globally distributed. We here use the term ‘acritarchs’ to include all organic-walled microfossils of possible phytoplankton origin, including acritarchs s.s. and organic microfossils that are now attributed to the

green algae and cyanobacteria. Where preserved, they are often recovered in large numbers, even from small samples, resulting in an abundant record and frequent application in biostratigraphy (e.g. Martin and Dean, 1981, 1988; Moczyłowska, 1991, 1998; Vanguetaine and Van Looy, 1983).

Biomarker evidence suggests that Palaeozoic acritarchs may include forms that have a close biological affinity with (or be evolutionary precursors of) dinoflagellates (Moldowan and Talyzina, 1998; Talyzina et al., 2000). However, the oldest unambiguous dinoflagellates in the fossil record are from the Triassic (e.g. Fensome et al., 1996a) and an alternative view is that the Palaeozoic acritarchs represent a “green” phytoplankton lineage (Martin et al., 2008). Observations of recent dinoflagellates have shown that only some species form organic-walled cysts with the potential to fossilize (Dale, 1976), and may do so at more than one stage in their life cycle (Fensome et al., 1996a). If, by analogy, Palaeozoic acritarchs are also cysts, perhaps of various algal groups, there is a clear implication that they only represent a part of the phytoplankton.

A further difficulty is that acritarch taxa are morphospecies rather than true biological species. In some instances, morphological gradations from one Palaeozoic acritarch taxon to another have been demonstrated, suggesting ecophenotypic variation rather than speciation (Servais et al., 2004b). If so, the number of taxa recorded would overestimate the number of biological species. Conversely, for the rather featureless sphaeromorph acritarchs, often identified simply as ‘sphaeromorphs’ or ‘*Leiosphaeridia* spp.’, the number of taxa recorded probably underestimates biological diversity. Despite these limitations, acritarchs remain the main source of information for phytoplankton in the Cambrian, long before the appearance of planktonic algae forming calcitic and siliceous skeletons during the Mesozoic (Bown, 2005).

Various Palaeozoic acritarch diversity curves have been published previously. Detailed global curves are available for the Carboniferous (Mullins and Servais, 2008), Lochkovian to Tournaisian (Klug et al., 2010) and the Permian (Lei et al., 2013). Regional diversity curves have been published for the Ordovician on the Yangtze Platform (South China) and North Africa (Algeria, Tunisia and Libya; also including the latest Cambrian; Servais et al., 2004a), for ‘northern Gondwana’ (including North Africa, Turkey, Saudi Arabia and several peri-Gondwanan microcontinents; Vecoli and Le Hérisse, 2004) and for Baltica (Hints et al., 2010). Li et al. (2007) published a diversity curve for genera in the Ordovician of South China, North China and Tarim.

Acritarch diversity curves that include the Cambrian have been published by Tappan and Loeblich (1972, 1973; genera, Precambrian to present); Vidal and Knoll (1982; species, upper Riphean to lower Cambrian); Knoll (1994; species, Proterozoic to lower Cambrian); Strother (1996; Precambrian and Phanerozoic, using data of Downie, 1984, and Fensome et al., 1990), Vidal and Moczyłowska-Vidal (1997; species, Proterozoic to Cambrian), Moczyłowska (1998; species, Cambrian in Upper Silesia; and 2011; species, Ediacaran to basal Ordovician, global and Baltica); Zhuravlev (2001; genera, Cambrian to Tremadocian); Katz et al. (2004; species, Proterozoic to Neogene, and genera, Cambrian to Neogene); Huntley et al. (2006a, 2006b; genera, Proterozoic to Cambrian), Strother (2008; genera, Phanerozoic), and

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