



Biodiversity patterns of Ordovician marine microphytoplankton from Baltica: Comparison with other fossil groups and sea-level changes

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ABSTRACT

Based on the extensive literature on Ordovician acritarchs, biodiversity curves of marine microphytoplankton of the palaeocontinent Baltica have been compiled. The dataset is derived from more than 100 publications and includes over 600 species whose ranges can be used in diversity analysis. Stratigraphically well-constrained data from the Rapla and Männamaa boreholes, northern Estonia, are analysed separately in order to provide additional information on the Middle to Late Ordovician microphytoplankton evolution on shallow shelf settings.

The total species diversity and normalised diversity curves based on range-through data show a slight decrease from the Tremadocian to Floian, which may partly be attributed to limited data available. A continuous increase in diversity from the base of the Dapingian to late Darriwilian – early Katian can be observed, with highest total diversity approaching 250 species in the Keila Regional Stage. The highest appearance rates are recorded in the Dapingian and Darriwilian. Diversity progressively diminished after the early Katian with a more pronounced decrease in the upper Ordovician Porkuni Regional Stage, corresponding to the Hirnantian. A significant faunal turnover took place in the uppermost Ordovician Pinguiculate and Porkuni stages, with high extinction rates as well as the appearance of many acritarch taxa that are typical of the Silurian floras.

The phytoplankton diversity curves match rather well with those of several other fossil groups in Baltica, notably brachiopods and ostracods. Comparison with other palynomorphs reveals both similarities and differences. The chitinozoans show the highest diversities in the upper Darriwilian, but their later decline predates that of acritarchs. A rapid diversification of scolecodonts (jawed polychaetes) can also be observed in the upper Darriwilian. However, unlike acritarchs or chitinozoans, their diversity continues to increase until the uppermost Katian.

The acritarch diversity changes are analysed and discussed in the context of palaeogeographic (northwards drifting of Baltica) and palaeoclimatologic changes (rising sea levels up to the middle part of the Upper Ordovician). The increasing diversity of the phytoplankton not only roughly correlates with the Baltic and global sea-level changes, but also with the diversification of marine invertebrate groups.

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1. Introduction

The Great Ordovician Biodiversification Event (GOBE) is known as one of the most important radiations of life on Earth, with a rapid increase in the number of families, genera and species of marine organisms and important changes in biocomplexity of marine life

(Harper, 2006; Servais et al., 2009). Webby et al. (2004a) published a comprehensive set of biodiversity curves of almost all Ordovician fossil groups, documenting the evolution of marine organisms and the radiation of the 'Palaeozoic evolutionary fauna' during the 'Great Ordovician Biodiversification Event'.

Acritarchs are an artificial, utilitarian group used to classify organic-walled microfossils of unknown, but probably varied biological affinities (Evitt, 1963). A consensus exists today that most Ordovician acritarchs represent the cysts of diverse marine microphytoplankton groups, and that as primary producers they occupied an important role in Proterozoic and Palaeozoic trophic chains. Many acritarchs were probably 'pre-dinoflagellates' (Servais, 1996; Servais

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et al., 1997), although some authors argue for green algal lineage (Martin et al., 2008). The acritarch diversity changes therefore do not reflect the evolution of a single biologic group but rather the whole organic-walled phytoplankton. In this paper a few species of prasinophyte algae are also included in the Baltic Ordovician microphytoplankton dataset.

In order to understand the functioning and evolution of the Palaeozoic marine ecosystems, and in particular the Ordovician biodiversification, it is thus essential to understand the evolution and radiation of the marine phytoplankton. Vecoli et al. (2005) considered the evolution of the phytoplankton to be a possible trigger of the Ordovician biodiversification. Servais et al. (2008) pointed out that the evolution of marine phytoplankton during the Ordovician coincided with an important revolution in the trophic chains, including the radiation of planktonic organisms and suspension feeders, which developed due to the presence of phytoplankton in the water column.

Biodiversity curves of the Ordovician microphytoplankton are far from complete, because intensive acritarch research only started in the 1960s, whereas the classical Ordovician fossil groups, such as graptolites, trilobites and brachiopods, have been extensively investigated for more than two centuries. Several palaeocontinents are poorly covered so far, and data on Ordovician acritarchs from many regions, including Australia, South America, Siberia and North China, remain sporadic (Servais and Paris, 2000; Servais et al., 2004). The latter authors presented two preliminary regional biodiversity curves for Ordovician acritarchs: the first curve illustrated the acritarch diversity of South China (Yangtze Platform) and the second concerned the peri-Gondwanan regions of North Africa (and other 'northern Gondwanan' areas). More detailed biodiversity curves for these two areas have subsequently been presented by Li et al. (2007) and Vecoli and Le Hérisse (2004), respectively. However, the curves from these two regions cannot easily be compared and biodiversity peaks observed on 'northern Gondwana' are not directly correlatable with those from China that was divided into at least three different palaeocontinents during the Ordovician. The problems of correlation of the different diversity curves are partly the result of the pronounced provincialism of the acritarch microfloras that have been recognised since the early 1970s (Vavrdová, 1974; Li, 1989; Servais et al., 2003).

The greatest number of Ordovician acritarch species has been described from the palaeocontinent Baltica. The Baltic acritarch floras generally differ from those of China and Gondwana, which include palaeobiogeographically diagnostic taxa (e.g., Servais and Fatka, 1997; Servais et al., 2003; Vecoli and Le Hérisse, 2004). However, many species from acritarch assemblages of Baltica, which was located at low to intermediate latitudes during the Ordovician, are also present in areas on the periphery of Gondwana that were located at similar latitudes, such as Argentina and South China (Rubinstein and Toro, 2001; Li et al., 2002; Li and Servais, 2002; Tongiorgi et al., 2003; Molyneux et al., 2007).

The Ordovician fossils of the Baltica palaeocontinent are generally well analysed. For several centuries numerous palaeontologists have worked on the highly fossiliferous and well preserved Lower Palaeozoic sequences of Scandinavia, the Baltic States and western Russia, that all belong to Baltica. Based on these intensive studies, detailed diversity curves of most fossil groups have been presented in recent years, many of them in individual chapters of the compilation of Webby et al. (2004a). In addition, Hammer (2003) analysed a dataset of more than 10,000 species of marine invertebrates of the Ordovician of Baltica to draw diversity curves for different organisms and different regions of Baltica. Whereas diversity curves for other common palynomorphs, such as scolecodonts (Hints, 2000; Hints et al., 2004) and chitinozoans (Nölvak in Paris et al., 2004), have been published, comprehensive diversity curves of Ordovician acritarchs from Baltica are still missing. Biodiversification trends of the

acritarchs from the Ordovician of Baltica remain thus unknown, apart from a regional diversity analysis of the Middle and Upper Ordovician succession of the Rapla borehole, northern Estonia (Kaljo et al., 1995, 1996; studying material of Uutela and Tynni, 1991).

This study documents for the first time a complete diversity curve for the Ordovician marine microphytoplankton of Baltica, based on published ranges of acritarch species. In addition to the compiled literature database, detailed acritarch diversity patterns in Middle and Upper Ordovician successions of the Rapla and Männamaa boreholes, northern Estonia, are discussed (data from Uutela and Tynni, 1991 and Uutela, 2008).

The compiled phytoplankton diversity curves can then be compared to diversification histories of other groups of organisms in Baltica as well as to diversity patterns of acritarchs on other palaeocontinents. Moreover, the new Baltic curves can be discussed and interpreted in relation to geological and environmental changes, in particular the evolving palaeogeography and palaeoclimate, but also in the context of the profound changes of the marine trophic web that took place during the Ordovician, in order to better understand the impact of changing phytoplankton diversity on the Great Ordovician Biodiversification Event.

2. Materials and methods

As indicated by Servais et al. (2004) the available data on Ordovician acritarchs from Baltica make this continent the region with the greatest number of new acritarch species described. Acritarchs from Baltica (Fig. 1) have been described from different marine settings around the continent. Most data come from Sweden (Scania, Öland, etc.), Norway (Oslo region, Finnmark, etc.) and the Baltic States (mostly from Estonia), but numerous data are also available from Russia, including the St. Petersburg area and the Moscow Basin, and from drillcores of north-eastern Poland and Lithuania. Fewer data are available from Belorussia, the Ukraine and from the north-eastern part of European Russia (Timan – northern Ural region). In addition, several investigations were based on erratic boulders of Baltic provenance that have been collected in south-western Finland, northern Poland and northern Germany. These studies, however, commonly lack accurate stratigraphic background and hence add little to the diversity curves presented herein.

In order to present a biodiversity curve as complete as possible, more than 100 papers on Ordovician acritarchs of Baltica have been reviewed, initially in the course of a PhD project by one of us (AW). The now updated database includes taxonomic information (species and genus name, author, year of description) and the stratigraphical ranges of all formally described or fully identified species. The data are thus range- rather than occurrence-based and do not include tentative identifications and names under open nomenclature.

Most of the information comes from papers published before the year 2000, with only a few additional papers having been published after this year complementing the dataset. Altogether the database lists more than 800 species names, but not all could be used in the diversity analysis. This is particularly due to poor stratigraphic information, as, for instance, in the case of material collected from erratic boulders. In some cases, the indicated stratigraphic range is given at the level of regional series (Öland, Viru, Harju), or only vaguely attributed to the 'Lower', 'Middle' or 'Upper Ordovician'. The percentage of stratigraphically well-constrained taxa thus ranges from less than 20% in some intervals of the Lower Ordovician to ca 70–80% in the Middle and Upper Ordovician (see graph in Fig. 2).

Most of the previous studies on Ordovician acritarchs from Baltica concerned taxonomy and biostratigraphy, with only a few complete monographs having been published. They include the works of Gorka (1969) from Poland, Welsch (1986) from Norway, Uutela and Tynni (1991) from the Estonian Rapla section, Eiserhardt (1992), who worked on erratic boulders collected in northern Germany, and Uutela

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