



# Paleoecological reconstruction of the Ediacaran benthic macroscopic communities of the White Sea (Russia)



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## ABSTRACT

A number of layers with macroscopic imprints have been discovered in the Ediacaran deposits in the southeastern White Sea region during 40 years of the study. Two fossil assemblages of the Flinders-style preservation are the most abundant and well studied. Comparison of the taxonomic and quantitative composition of biota as well as the characteristics of the microbial surfaces, assumed as the habitation substrate of these Ediacaran organisms, was assessed for these two fossil assemblages. Analysis of size–frequency distribution using a statistical data manipulation program R allows recognition of different size modes, reflecting different stages of sea floor colonization by benthos. On the basis of the received data, the community structure of such fossil assemblages was reconstructed for the White Sea Basin for the first time. The fossil assemblages display the variations of development of similar communities of the benthic Ediacaran organisms, reflecting seasonal colonization of the sea bottom by larvae of mobile and sessile benthos, immigration of the adult individuals of mobile benthos and seasonal conditions of microbial mats associated with these communities.

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## 1. Introduction

The Ediacaran period (575–542 Ma) (Narbonne, 2005) is a time of critical transition between dominant microbial ecosystems of the Precambrian and Phanerozoic eucaryotes. This period has been intensively studied over the past few decades by a number of research groups around the world. However, initial stages of the research were focused on collection and description of morphology to determine the nature of Ediacaran organisms. Less attention was paid to the paleoecology. At present the paleoecological studies are intensively performed at many Ediacaran localities — Newfoundland in Canada (Clapham et al., 2003; Laflamme and Narbonne, 2008; Darroch et al., 2013), the Flinders Ranges of South Australia (Bottjer and Clapham, 2006; Droser et al., 2006) and in southern Namibia (Grazhdankin and Seilacher, 2002; Bottjer and Clapham, 2006; Vickers-Rich et al., 2013). In the White Sea Region such studies have been undertaken by D. Grazhdankin (Grazhdankin and Ivantsov, 1996; Grazhdankin, 2003, 2004). Grazhdankin defined four lithofacies in this sequence of Ediacaran deposits. Each represented specific paleoassemblages: the *Inaria* assemblage, restricted to the lower-shoreface deposits; the *Charnia* assemblage representing the middle-shoreface sediments; the *Dickinsonia–Kimberella* assemblage, a prodelta sequence of alternating sandstones and shales and the *Onegia–Rangea* assemblage, confined to the distributary channels of the mouth bars (Grazhdankin, 2004). Papers by D. Grazhdankin focused on defining the types of

paleoassemblages of separate fossil assemblages without analysis of the population structure of these assemblages. The present paper describes single local assemblages of fossil remains with the purpose to reconstruct an ecological situation for each of these specific communities using statistical methods (Zakrevskaya, 2011, 2012). The paleoecological studies on Ediacaran macroscopic fossil assemblages represent a significant importance for all aspects of Ediacaran paleontology. Statistical methods such as both nearest-neighbor analysis and size frequency distributions can help determine the aspects of reproduction and settling of the organisms (Clapham et al., 2003; Droser and Gehling, 2008; Darroch et al., 2013). The diversity and evenness studies can give information about local levels of productivity, nutrient richness, hydrodynamic conditions, or alternatively indicate stages of ecological succession (Clapham et al., 2003; Wilby et al., 2011). These sorts of studies in future can provide data on behavior, reproduction, nutrient flux, and the nature of biotic interactions without any a priori assumptions about biological or phylogenetic affinity. In this study diversity and evenness studies and also size frequency distribution analysis will help to interpret the ways of organisms' reproduction and settling.

The White Sea material is represented by diversity of unique, perfectly preserved fossil remains. One of the many advantages of this material is that tectonic deformation is absolutely minimal and so specimens do not require retrodeformation, so that lengths/widths and spatial relationships between organisms will be largely unaltered.

Taphonomy of Ediacaran organisms is a very important aspect for paleoecological studies. Ediacaran biota is represented by almost entirely soft-bodied organisms which required exceptional circumstances to be

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preserved. Ediacaran organisms represent a variety of unrelated forms which share a common type of preservation (Narbonne, 2005; Darroch et al., 2012). A critical role in taphonomy of Ediacaran organisms was played by microbial mats which in most cases were their habitation substrate and food source (Gehling, 1999; Seilacher, 1999; Noffke et al., 2001; Noffke, 2009; Darroch et al., 2012). Discovery of a large number of folded and wrinkled structures on the bedding planes of Precambrian sediments has led to the conclusion that microbial mats had wide distribution on the seafloor at that time. Many of these structures are attributed to have microbial origin (Noffke, 2009). They are preserved on bedding planes and within the overlying sandstone layers. Sometimes we observe that the surface together with all wrinkled structures and imprints located on it was rolled up into the sediments, whereas the structure which formed this surface acted as a flexible substance (Ivantsov and Malakhovskaya, 2002; Fedonkin et al., 2007; Ivantsov, 2011a). The fossiliferous surfaces of the White Sea fossil assemblages were examined under the scanning microscope, resulting in the discovery of the fossil remains, representing probable mat makers. The similar remains were found in the deposits of Longmyndian supergroup in England, where they formed large interlaced accumulations, which probably represent the remains of microbial mat (Callow and Brasier, 2009).

The microbial “death mask” model is the most common and widely accepted explanation of the Ediacaran taphonomic scenario (Gehling, 1999; Gehling, 2005; Darroch et al., 2012), especially concerning the Flinders-style preservation of the Ediacaran organism (i.e. imprints on the bottom surfaces of the sandstone beds; Narbonne, 2005). According to this model the organisms living on substrate-binding mats become buried during slump or storm events. Then the carcasses begin to decay, the aerobic microbes use up available oxygen, and in this localized anoxic environment reduced iron reacts with hydrogen sulfide (produced from reduction of seawater sulfate) to produce iron monosulfides and other pyrite precursors. These iron sulfide minerals formed mineralized, pyritic death mask around the carcasses, thereby the imprints were preserved. The experimental verification of this model was given by Darroch et al., 2012.

The microbial mat also had great significance for preserving Ediacaran Vendian traces, which are rare in comparison with the body fossils. This is due to the fact that animals simply crawling on the microbial mat did not leave traces on it. Only a strong mechanical influence, leading to a partial destruction of the mat, could be preserved in future, for example as a feeding trace (Ivantsov and Malakhovskaya, 2002; Ivantsov, 2009). The microbial structures commonly occur together with the sedimentary structures, syneresis cracks, plucking grooves, casts from ripple marks and others. Part of these sedimentary structures presumably represents the topography of the seafloor, underlying the microbial mat; this fact allows us to talk about a relatively small thickness of the mat.

The Ediacaran deposits of the White Sea represent a thick section (~500 m), which contains fossil assemblages with uniquely preserved fossils. The term “fossil assemblage” is used to describe the fossiliferous beds in which a concentration of fossils occurs. These fossiliferous layers in the White Sea area are most often represented by limited occurrence in lenses. In addition, the fossils throughout the fossiliferous surface occur as concentrations only on the limited areas. These fossiliferous layers alternate with the others completely lacking fossils, although they are characterized by the presence of the same microbial surface.

In the southeastern White Sea region about 3 dozen local fossil assemblages, represented by different types of preservation, have been discovered and documented over the last 40 years (Fendonkin, 1981; Grazhdankin and Bronnikov, 1997; Stankovsky and Fedonkin, 2000; Fedonkin, 2003) since the excavation of the first fossil locality of Ediacaran fossils (1972). Most fossil assemblages occur in small areas. Many of them can only be traced along the strike for less than 1–10 m. The largest concentrations may extend for hundreds of meters but are rare. All fossil assemblages, even if separated by only a few

centimeters of the outcrop, are characterized by a unique assemblage of fossils, which can be quite different from the next assemblage. The richest of these fossil assemblages are those of Flinders-style preservation (imprints on the bottom surfaces of sandstone beds; Narbonne, 2005; see above). The exceptional taphonomic conditions of these assemblages allow them to represent a faithful snapshot of the seafloor communities, suggesting that the organisms were preserved in the position closest to in situ (Seilacher, 1999; Droser et al., 2006). Therefore, two fossil assemblages of Flinders-style preservation (fossil assemblages Z11 (XXII) and SL1 (VII), the richest and the best studied in the White Sea region) were singled out for this project reported here.

## 2. Geological settings

Studied communities of local assemblages come from two localities within the Arkhangelsk region of the southeastern White Sea area: Zimnie Gory and Solza (Stankovsky and Fedonkin, 2000) (Fig. 1).

Fossil assemblages occur at two different stratigraphic levels (Zimnie Gory and Verkhovka formations (Grazhdankin, 2003, 2004, Fig. 1)). Their extent are larger than any fossil assemblages yet discovered in the White Sea area. The fossil assemblages Z11 (XXII) and SL1 (VII) were followed along the strike for 1 km and 0.5 km, respectively. And the surveyed areas equal 29.4 m<sup>2</sup> in assemblage Z11 (XXII) and 14.4 m<sup>2</sup> in assemblage SL1 (VII). The fossil assemblages themselves represent the surface's areas where the higher concentration of fossils in comparison with surrounding areas occurs. However, within the both fossil assemblages the concentration of fossils remains consistently high, and no patchiness was observed. The proportion of potentially missing community is very hard to estimate, but we can conclude that this proportion was rather similar in the two studied assemblages.

Ediacaran sediments containing the fossil assemblages reported here were deposited in a relatively shallow basin on the continental slope. Rapid flooding of the shelf at the beginning of the accumulation of these deposits, resulted from the development of alluvial fans and delta fronts developed in relatively calm hydrodynamic conditions (Grazhdankin, 2004). The environmental conditions of these coastal plains were characterized by episodic avalanches of suspended detrital material associated with the seasonal precipitation and storm events. These down slope movement produced deep erosion, which changed the sea-floor relief and caused a catastrophic sedimentation, which resulted in mass burial of the benthic population close to in situ position (Fendonkin et al., 2007).

Ediacaran fossils in the local assemblages studied with Flinders-style preservation have not been transported after death (Grazhdankin, 2004). The imprints are preserved on the bottom surfaces of sandstone. Thus, the two studied fossil assemblages reflect the structure of the original living communities of the benthic macroorganisms. However, the fossils represent only the part of the living community, those organisms which could firmly attach to the substrate either permanently, throughout their lives or temporarily, under stressful situations (Ivantsov, 2011a). Unfixed bodies would have been swept away by the down slope avalanche, where they then became part of the Nama-style preservational communities (Narbonne, 2005). These are preserved as the three-dimensional molds within the layers (Ivantsov and Grazhdankin, 1997; Fedonkin and Ivantsov, 2007). Only holdfast structures are usually preserved of sessile, frond-like organisms (Petalonamae), as the fronds were ripped away by the flow.

## 3. Material and methods

The material for this paper are in the collection of the Paleontological Institute including mobile benthic organisms and the attachment disks of the sedentary organisms from two the richest fossil local assemblages with Flinders-style preservation, with numbers Z11 (XXII) and SL1 (VII) noted in the PIN Catalog of fossil assemblages of Ediacaran fossils in southeastern White Sea area, in the Laboratory of Precambrian

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