The origin of the Metazoa in the light of the Proterozoic fossil record

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Abstract. Origin of the eukaryotic organisms (including the multicellular animals or Metazoa) is commonly considered to be related to growing oxygen content in the atmosphere up to a level that allows aerobic metabolism. Here it is suggested that oxygenation of the biosphere was not a permissive condition but rather a forcing factor that drove evolution towards the formation of complex biological systems. Growing concentration of free oxygen in conjunction with other geohistorical trends acted to chemically impoverish the ocean and atmosphere and made many of the chemical elements immobile or unavailable for metabolic processes. Of particular importance in this connection was the decreasing concentration in sea water of the heavy metals that demonstrate high catalytic ability and make an active center in many enzymes. Increasing biological complexity and the eukaryotization of the biosphere (origin of the eukaryotic cell, growing role of heterotrophy, increasing biodiversity, rise of multicellular organisms, lengthening of trophic chains, acceleration of biological recycling of the chemical elements, etc.) can be considered as an evolutionary response to the geochemical deterioration of the environment.

Recent discoveries of the oldest megascopic eukaryotes, such as spiral Grypania (1.9 Ga), the necklace-like colonial organism of tissue-grade organization Horodyskia (1.5 Ga), vermiform Parmia (about 1.0 Ga) and Sinosabellidites (800 Ma ago) are consisitent with the «molecular clock» models on an early origin of animals; metazoans were, however, confined to relatively cold and well oxygenated basins beyond the carbonate belt of the ocean until the end of the Proterozoic. Large and diverse invertebrates of the Vendian Period are known mostly from siliciclastic marine basins. This fauna is characterized by high density of the benthic populations and well established clades both at the diploblastic (e. g., Phylum Trilobozoa) and triploblastic (e. g., Phylum Proarticulata) grades of organization as well as some taxa related to the Paleozoic phyla. An organic skeleton preceded the rise of the mineralized skeleton in some metazoan phyla. Low temperature of the habitats inhibited biomineralization. Almost simultaneous development of the phosphatic, carbonate and siliceous skeletons in different metazoan groups at the beginning of the Cambrian Period some 545 Ma ago could be related to the colonization of the warm carbonate basins by the metazoans. An additional factor for the rapid diversification of the biomineralized phyla could be the growing length of the trophic chains brought about by the rapidly increasing biodiversity and the need for detoxification at the top of the trophic pyramid. Being the byproduct of detoxification, sclerites and spicules, hard mineralized shells and carapaces immediately became an important factor of morphological evolution and growing biodiversity, as well as the object of intensive selection under the growing pressure of predators. Explosive growth of morphophysiological diversity in metazoans during the Vendian and Cambrian had an enormous impact on evolution of other groups of organisms and on the environment.

Key words: biomineralization, evolution, Metazoa, Proterozoic, Vendian, White Sea

Introduction

The origin of multicellular animals has to be considered in the context of the overall increase in biological complexity during the immense time of geological history. The appearance and ecological expansion of the metazoans on the global ecosystem. This rise of biological complexity poses a fundamental problem, which has been tackled by many scientific disciplines because of the growing understanding that the main metabolic pathways and the existing biodiversity have very deep historical causes. The early fossil record, considered in a geohistorical context, provides evidence of the critical importance of the origin and

evolution of complex life forms, and helps to test evolutionary models developed by neontological disciplines. However, biological evolution cannot be understood properly without an appreciation of the numerous geological factors affecting the whole hierarchy of life from metabolic pathways to global cycles of the main biophile elements.

Role of continental growth in history of life

The origin of continental plates must have had an enormous impact on life on the early Earth. Vast, stable continents became a trap for a great volume of sedimentary rocks (and chemical elements), thus removing them from an intense recycling in the biosphere. This factor and the activity of the organisms that inhabited vast epicontinental basins became the main factors driving the chemical evolution of the atmosphere and the oceans.

Continental growth by accretion of smaller fragments into large landmasses went through three major episodes (Lowe, 1994). About 5% of the continental crust was formed 3.3-3.1 billion years ago, 58% was formed later, between 2.7 and 2.3 billion years ago, and 33% of the continental crust was formed 2.1-1.6 billion years ago. Thus, about 96% of the continental crust was in place by the Middle Proterozoic.

This extensive continental crust created an entirely new situation in the ocean ecosystem. Large-scale upwelling became a factor enhancing the recycling of biophilic elements in the biosphere. The vast shallow benthic habitats appearing at that time opened up great ecological opportunities because of their enormous diversification of microenvironments, in contrast to the pelagic realm, which is ecologically more uniform. To appreciate the importance of the shallow marine habitats, one has to remember that in the recent ocean, shallow-water environments (0-200 meter deep) occupy less than 8% of the ocean floor, but the total mass of organisms living there constitutes 82.6% of the total biomass of benthic organisms in the ocean. This disproportion relates to the nutrient supply from the depth of the ocean through upwelling and erosion of the land, as well as to the intense recycling of organic matter in the shallow-water environment.

The intensification of nutrient recycling first of all stimulated the primary production by phytoplankton and phytobenthos (including the stromatolite-forming photosynthesizing cyanobacterial and other prokaryotes), that consumed carbon dioxide and released oxygen into the atmosphere. The removal of carbon dioxide from the geochemical cycle due to the burial of organic matter and the formation of carbonate rocks on vast areas of the continents may have been critical factors for a decreasing greenhouse effect during the Proterozoic.

Already in the Early Proterozoic we see a remarkably small number of the carbonate platforms and the first known extensive glacial event, chronologically coinciding with a maximum accumulation of Banded Iron Formations (BIFs) that fixed enormous amounts of oxygen in the form of iron oxides. Burial of carbon in the sediments of the stable continental plates reduced the greenhouse effect down to a very sensitive balance about 850 Ma ago. From this time onwards, the glacial periods became more or less regular events of geological history.

Deterioration of geochemical basis of life stimulated rise of biological complexity and heterotrophy

The best way to feel the difference between the early Archean atmosphere and the present one can be obtained by comparing the composition of volcanic gas and normal air. These two extremes show the main trend in the evolution of the atmosphere over the last 4 Ga. Living organisms form the principal factor in this dramatic change. Photoautotrophs, in particular, are responsible for decreasing the concentration of carbon dioxide and increasing the concentration of free oxygen in the atmosphere. The concentration of these two gases determines the rate of weathering of rocks and the availability of some chemical elements in the biosphere. The rate of weathering essential for the recycling of the biophilic elements in the biosphere has also been influenced by the increasing rates of erosion and sedimentation due to the increasing contrast of the planetary relief and the shift in composition of the major feeding provinces of the sedimentary basins - from dark basic rocks to the less resistant acidic and sedimentary rocks (Fedonkin 1996a, and references therein).

There are some other examples as well of geochemical trends and events directly or indirectly related to the life activity of biota. There are so-called "extinct sediments", typical for the early geological history only, such as uranium- and gold-bearing conglomerates, Banded Iron Formations, laminated copper deposits in clastic rocks, Pb-Zn ore in shales and carbonates, sedimentary Mn ore, and abundant phosphorites (Schopf and Klein, 1992). Many authors point to a decrease in Mg and an increase of Ca in the composition of carbonate sediments in the Proterozoic-Paleozoic transition, a phenomenon that might be related to a growing biological control over carbonate precipitation in the ocean. In the Precambrian ocean, silica simply precipitated from the seawater and formed layers or nodules in the sediments. The rise of organisms, such as sponges, ra-diolarians, diatoms, and silicoflagellates, capable of sucking up the dissolved silica from the water and using it in the construction of their skeletons, converted the ocean into an almost silica vacuum; the recent seas are undersaturated with regard to this element (Broecker, 1971). This is just

one of many examples of a growing biological control over the geochemical cycles in the biosphere.

The geological record shows that most natural environmental factors (including mutagens) have varied in magnitude throughout the history of life. Thus, the background radiation level changed by nearly an order of magnitude during the last 4 Ga. The role of oxygen as the next mutagenic factor was more complex (Karam and Leslie, 2001). The temperature of the environment is an important factor as well. The rates of most chemical reactions decrease three to four times for every 10° C drop in temperature (Poinar and Paabo, 2001). We know that the primary biosphere was relatively hot, and that it slowly cooled down towards the end of the Proterozoic (Chumakov, 2001). If so, this general cooling trend of the biosphere had to affect the rates of both geochemical and biochemical reactions (including the metabolic pathways) and genomic evolution.

These three factors, although quite heterogeneous, have had a strong impact on the evolution of the environment. Thus, the decrease in radiogenic heat has caused a slow decline in the volcanic supply to the ocean of those chemical elements that were in abundance at the dawn of life. This effect was reinforced by the retreat of the Moon, contributing greatly to the energy balance of early Earth (Touma and Wisdom, 1994). Oxygenation of the ocean and the atmosphere has made chemical elements unavailable through oxidation for metabolism. The temperature decline reduced the rates of biogeochemical reactions including the main metabolic pathways in organisms, the bio-degradation and recycling of metabolites, as well as weathering processes. This triple effect dramatically reduced the former, chemically rich, basis of life and, in a way, created an entirely new world that demanded more complex and efficient enzymatic properties, as well as new sources of energy. Life had to move towards heterotrophy, in particular, to its simplest forms, such as uptake of dissolved organic compounds and predation.

Oxygen and animal life

The origin of eukaryotes including animals is usually considered to be related to the rising oxygen content of the atmosphere up to a level allowing aerobic metabolism (Briant, 1991; Magnum, 1991; Knoll, 1996). Indeed, an oxygen concentration of ca. 5% PAL (present atmospheric level) is the minimum needed to sustain the activity of most eukaryotic microbes. Around 50% PAL of oxygen is the minimum required by animals (Knoll, 1992). Most recent models on the evolution of the Earth's atmosphere suggest a dramatic rise in oxygen content ca. 2 Ga ago. Holland (1994) estimates this change from <0.1% PAL to >15% PAL. Knoll (1996, and later papers) suggests anoth-er rise in the oxygenation of the atmosphere of up to >50% PAL by the end of the Proterozoic, an event that caused the Cambrian explosion.

Recently, Ohmoto (1997) challenged these models, suggesting that the oxygen content rose very quickly to the present atmospheric level more than 3.5 Ga ago and stayed at ± 50% PAL since then. Taking into account the main factors influencing the dynamics of the geochemical cycles of oxygen, Lasaga and Ohmoto (2002) proved that atmospheric oxygen content stayed within a very narrow range of 0.6-2 PAL, and, except for local euxinic basins, the ocean was completely oxygenated 2 Ga ago. The presence of cyanobacterial and eukaryotic biomarkers in rocks 2.7 Ga old is consistent with this, although aerated habitats might have been limited to the topmost part of the water column. Anoxic bottom waters probably persisted well after the deposition of banded iron formations ceased. Canfield (1998) suggested that sulfide, rather than oxygen, was responsible for removing iron from deep ocean water. The sulfur fossil record supports this suggestion, showing that ca. 1.8 Ga ago, the increase in sulfide production was sufficient to precipitate the total flux of iron into the oceans. According to Canfield's scenario, deep-ocean oxygenated waters did not develop until the Neoproterozoic 1.0-0.54 Ga ago in association with a second large oxidation of the surface of the Earth and a number of glacial events accompanied by active ocean ventilation by cold polar currents. The evolution of non-photosynthetic sulfide-oxidizing bacteria coincided with a large shift in isotopic composition of biogenic sedimentary sulfides between 0.64 and 1.05 Ga ago (Canfield and Teske, 1996). Both events were probably driven by a rise in atmospheric oxygen concentration higher than 5-18% PAL, a change that may also have triggered the evolution of animals. But even when this hypothesis would be correct, vast shallow-water and well aerated habitats within the photic zone could still harbor a eukaryotic community since the Late Archean.

The oxygenation of the biosphere was not such a permissive factor, but rather a forcing one driving the formation of complex biological systems. The increasing concentration of free oxygen has dramatically reduced the geochemical basis of life by making many chemical elements either immobile or unavailable for their metabolism. The removal of an enormous amount of metals from the biogeochemical cycle is documented in abundant sedimentary ores, including "extinct deposits" common during some exclusively Precambrian periods. This is particularly true with regard to heavy metals (W, Co, Ni, Mo, Fe etc.) with a great catalytic ability and that take an active part in the operation of many enzymes, real stirrer-ups and accelerators of metabolic processes. The impoverishment of the geochemical basis of life was caused, in addition to oxygenation, by a steady decline in ocean and atmospheric temperatures

during the Precambrian.

The formation of the eukaryotic cell through symbio-genesis of prokaryotes and the subsequent evolution towards biological complexity were their response to the growing oxygenation of the environment in order to protect their metabolic pathways. In this respect, the membranes of the organelles in the eukaryotic cell and multicellularity look like two phases of a single process leading to the creation of a semi-isolated, compartmentalized and controllable internal environment. The rise of biological complexity was the only way to the most economical existence within the conditions of a chemical impoverishment of the environment. The progressive development of heterotrophy during the late Proterozoic and the early Paleozoic eons can be considered as a consequence of the same causal chain (Fedonkin, in press).

The idea that deficiency in the inorganic and organic nutrients can be the driving force in the evolution of eukaryotes is not new (see references in Brasier and Lindsay, 1998), but it should be reconsidered in the light of new data on the very early rise of eukaryotic metabolism.

Eukaryotization as reflected in Proterozoic fossil record

The oldest known rocks containing signs of life are over 3.8 Ga old metasediments in the Itsaq Gneiss complex of Greenland. Rocks of this age are metamorphosed to such a degree that few body fossils, if any, can be preserved; only isotopic geochemistry can provide evidence of life (Mojzsis *et al.,* 1996). Eukaryotic cells (and Cyano-bacteria) appeared before 2.7 Ga, as indicated by hydrocarbon biomarkers that have been preserved in the late Archean rocks of Western Australia (Brocks *et al.,* 1999). It took at least a billion years of evolution to form a complex eukaryotic cell and its numerous genes required for the cytoskeleton, compartmentalization, cell-cycle control, proteolysis, protein phosphorylation and RNA splicing.

If the oldest filamentous microfossils that resemble recent Cyanobacteria by their shape, size and habitat, do indeed belong to these rather advanced prokaryotes (Schopf, 1992), one can suppose that all the major metabolic pathways have been formed no later than 3.5 Ga ago. This conclusion can be drawn from the positioning of the Cyanobacteria at the top of the molecular phylogenetic tree of the Eubacteria, as based on the sequencing of bacterial ribosomal RNA (Woese *et al.,* 1990). Recently, doubts have been expressed with respect to the biogenic nature of the oldest known microfossils (Buick, 2001; Brasier *et al.,* 2002) and that of the oldest stromatolites (Grotzinger and Rothman, 1996). However, the critics are unable to prove that all 3.5 Ga old microfossils and stromatolites of roughly the same age ever described are abiogenic, or that the oldest biogeochemical signals of life are doubtful.

The temporal trend in the increase in cell size in Precambrian microfossils is considered as an indication of progressive eukaryotization. The upper size limit of the prokaryotic cell (conventionally accepted near 60 mk) was passed ca. 1.9 Ga ago (Schopf and Klein, 1992). There are, however, some examples of recent giant bacterial cells and very small eukaryotic cells. The lower size limit of eukaryotic cells is ca. 20 um (and, occasionally, may be as low as 1-2 um), and their real history may therefore begin much before 1.9 Ga ago.

In rocks 1.7-1.0 Ga old, eukaryotic microfossils are widespread and well preserved, but their assemblage and global diversities are low and their turnover is slow. Roughly 1.5 Ga ago, eukaryotes already showed a modern cytoskeletal complexity. This may be concluded from the observed ability to remodel their cell morphology dynamically during their lifetime, as well as from a clear capacity for subdividing environments ecologically (Javaux *et al.,* 2001). The early eukaryotic fossil record shows a rise of rhodophytes over 1200 Ma, of dinoflagellates over 1100 Ma, of chlorophytes over 1000 Ma, and of ciliates and testate amoebae over ca. 750 Ma ago (Porter and Knoll, 2000). Observed diversity levels of protistan microfossils increased significantly around 1 Ga ago, as did their turnover rates (Knoll, 1994). Molecular phylogenies suggest that this was part of a broader radiation of "higher" eukaryotic phyla.

Throughout the Proterozoic fossil record we see an increasing abundance and diversity of megascopic fossils. Most fossils consist of carbonaceous material and look like dried and compressed hotdogs or raisins (Hofmann, 1994). These fossils seem to reflect the rise of multicellularity that could have happened independently many times in different kingdoms. Buss (1987) believes that multicellularity arose at least six times: in animals, in several algal taxa, and in fungi. In some taxa, multicellularity may have been genetically preserved as a selective advantage due to large body size and individual biomass, or because of cell specialization.

The oldest megascopic carbonaceous fossils of uncertain nature appear in rocks 1.8-2.1 Ga old. Some of these fossils may represent flattened remains of microbial colonies or fragments of the bacterial mats, while part of them may belong to early eukaryotes. The oldest known megascopic eukaryotic algae are *Grypania* from the Lower Proterozoic iron formation in Michigan (Han and Runnegar, 1992). Originally, the age of these rocks was estimated to be ca. 2.1 Ga, but later only as 1.85 Ga (Porter and Knoll, 2000).

Fossils somewhat resembling cellular structures are extremely rare. Morphologically more complex carbonaceous fossils with some possible anatomical details appear in rocks ca. 1.4 Ga old but they become more complex and
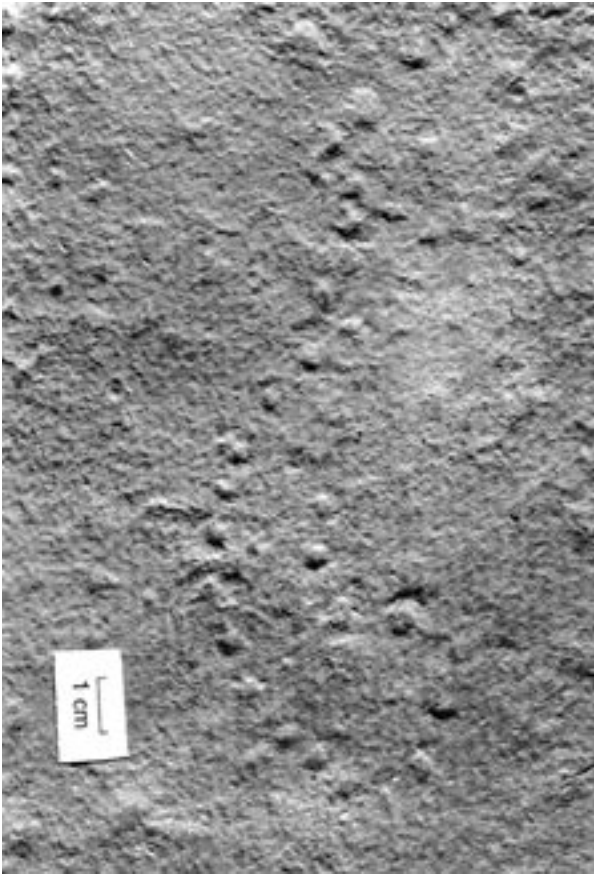
Figure 1. *Horodyskia*, Middle Proterozoic 1.5 Ga old siliciclastic rocks, Belt Supergroup, Montana, USA. Collection of the National Museum of Natural History, Smithsonian Institution, Washington D. C.
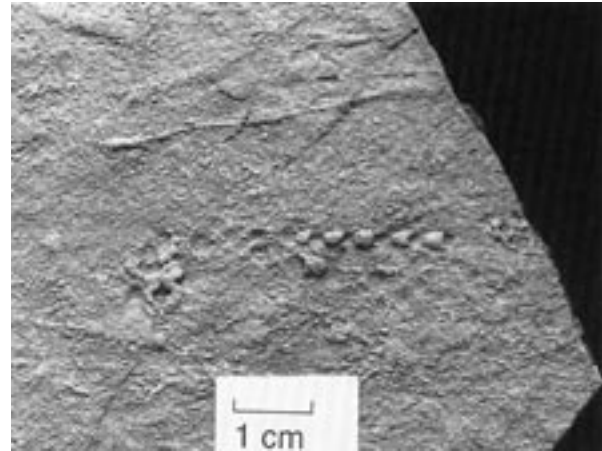
Figure 2. *Horodyskia,* Middle Proterozoic 1.4 Ga old siliciclastic deposits, Manganese Group, Bangemall Supergroup, Western Australia. Conical zooids are tilted along the axis of the colony. Courtesy of K. Grey. Collection of the Geological Survey of Western Australia.

diverse after 0.8-0.9 Ga ago. The larger part of these fossils is interpreted as eukaryotic algae, although some are considered as probable colonial prokaryotes, fungi, or even as metazoans. Knoll (1994) suggests that cellularly preserved microfossils of red, green and brown algae indicate that multicellularity was achieved in these groups by about 1.0 Ga ago. The question is now, where are the first multicellular animals?

An unexpectedly complex life form was recently discovered in old rocks of the Middle Proterozoic age of Montana and Western Australia. The enigmatic bedding-plane impressions, resembling a necklace or string of beads (Figures 1, 2), were initially described from the Belt Supergroup, Montana, USA (Horodyski, 1982) and later also from the Manganese Group, Bangemall Supergroup, Western Australia (Grey and Williams, 1990). These megascopic fossils, recently named *Horodyskia monili-formis* (Yochelson and Fedonkin, 2000), are both prolific

and geographically widespread and appear to be stratigraphically narrowly constrained. A detailed study of the taphonomy, paleoecology and morphology of these fossils resulted in the reconstruction of *Horodyskia* as a colonial benthic eukaryotic organism of tissue-grade organization (Figures 3, 4), most probably, of metazoan nature (Fedonkin and Yochelson, 2002). Wide cones (zooids) growing upward a maximum of 1.0 cm connected with a stolon. The maximum length of the colony reaches 30 cm. The size of the cones and the spacing between them are constant for each colony. The complex mode of growth of the colony (Figure 5), regular arrangement of the zooids, the absence of branching forms, the rigid wall of the cone, and the strong stolon that even survived some transportation of the colony by water currents, all these features suggest a tissue-grade organization and a well established set of regulatory genes. *Horodyskia* marks the first occurrence of complex multicellularity in the history of life as well as the earliest evidence that organismal morphology became an essential factor in the evolutionary process.

If the interpretation of *Horodyskia* as an early metazoan is correct, it almost doubles the time range of the metazoan fossil record. Some associated problematic fossils in Montana and Western Australia suggest a greater diversity of megascopic organisms living 1.5 Ga ago. An important peculiarity of these fossils is that they are preserved in siliciclastic rocks and the same way as the Ediacara fauna of the Vendian Period (600-545 Ma ago).

Recently reported problematic discoidal and trace-like fossils from tidal sandstones 1.2 Ga old from southwestern
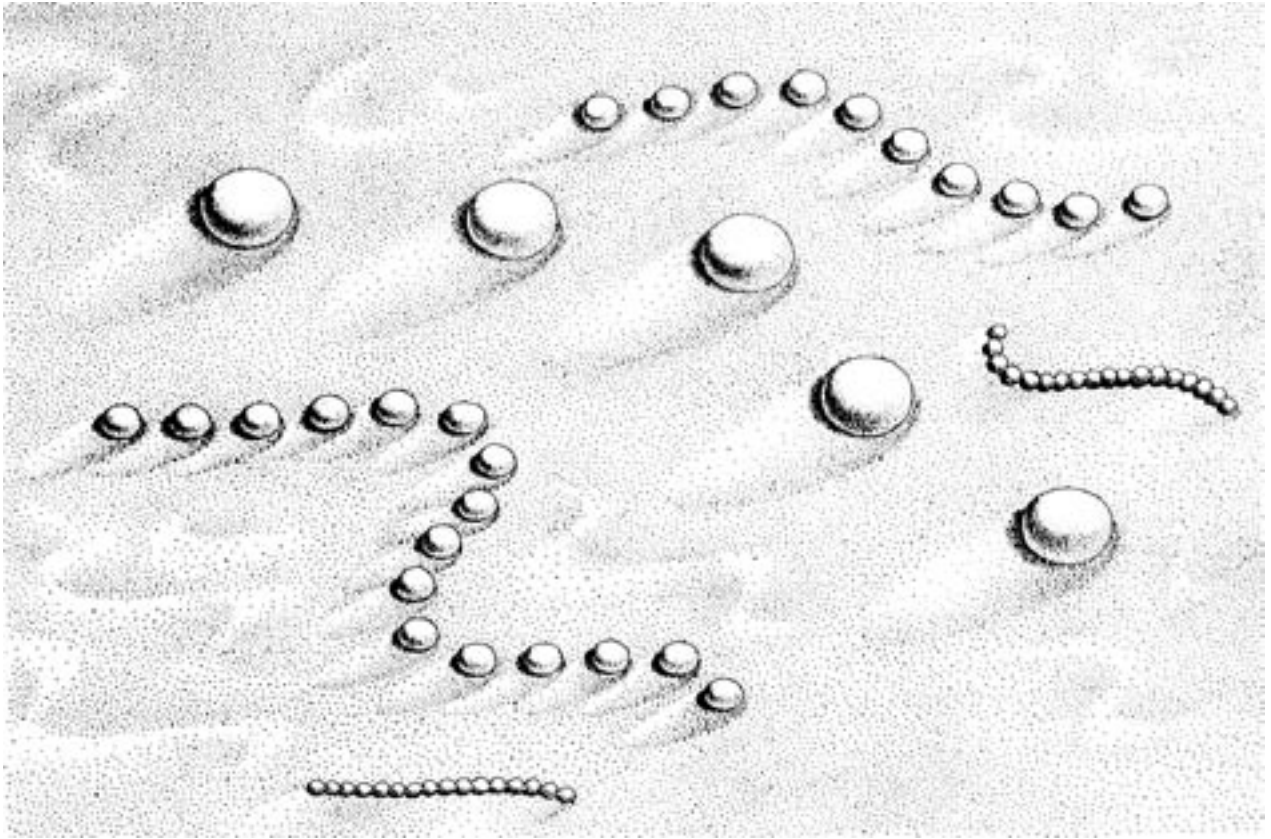
Figure 3. *Horodyskia,* colony in its life position (after Fedonkin and Yochelson, 2002).
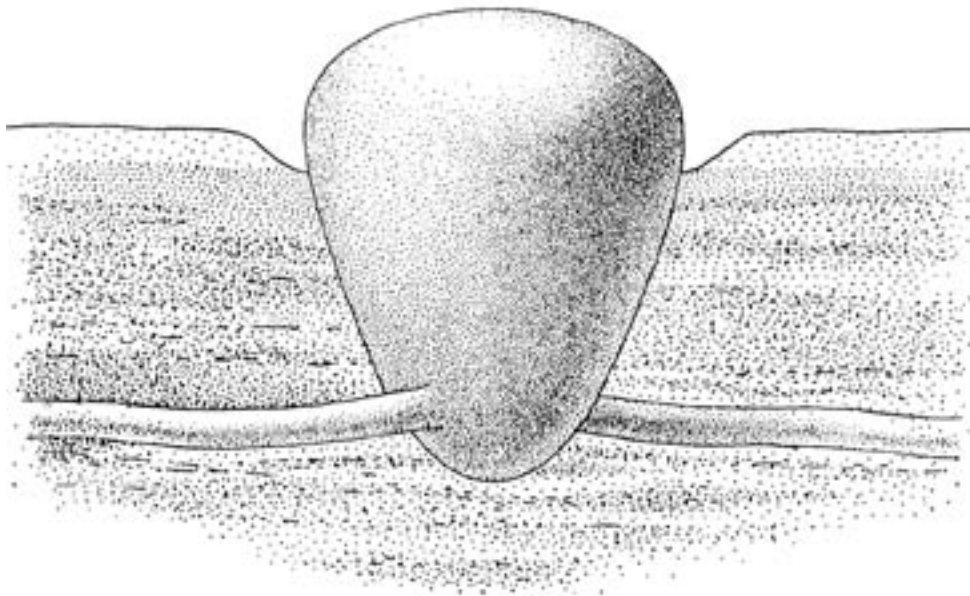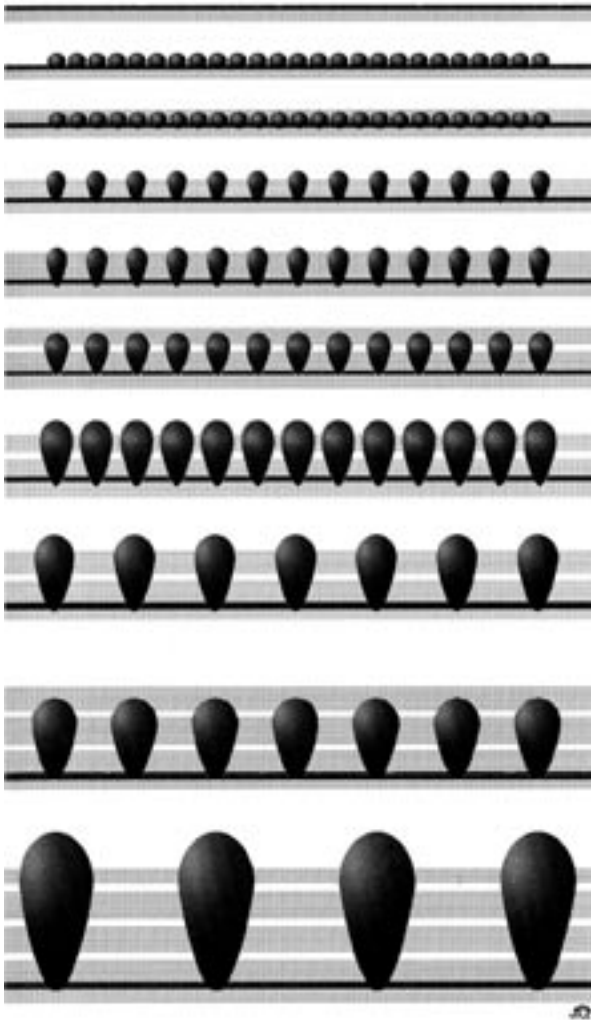

Figure 4. *Horodyskia,* reconstruction of the individual zooid in its life position.

Figure 5. Mode of growth of *Horodyskia* (modified from Fedonkin and Yochelson, 2002, fig. 19). The sequence of the growth stages is shown from the top down. The colony begins to grow as a horizontal stolon on the surface of the bottom. Next stage shows the regular swellings of the developing zooids on the stolon. As soon as it is buried by the sediment, every second zooid grows upward more actively than its neighbors which supply the growing zooid with their cellular material and experience reverse development. The repeating sedimentation events stimulate the same mode of growth which results in a growing spacing between the growing cones while they sit in the sediment.

Australia (Rasmussen *et al.,* 2002) do not show convincing evidence of their metazoan nature. More promising are the macroscopic worm-like organisms discovered in the lower Neoproterozoic deposits in Huainan District, Anhui Province, of the northern China Platform (Wang, 1982). The age of the rocks is believed to be ca. 740 Ma. These carbonaceous fossils resemble thin dark filaments 15-20 mm long and show a very fine annulation (or segmentation). Known as *Protoarenicola* and *Pararenicola,* these fossils were assigned to the oldest metazoans, probably annelid worms and pogonophorans. In addition to the general worm-like form, size, and kind of segmentation, these organisms show a broad, circular aperture or proboscis-like structure on one, presumably anterior, end of their slender body. The opposite (posterior) end is rounded.

In 1986, this discovery was followed by a report by Sun Weiguo and coauthors on even older worm-like fossils of *Sinosabellidites* from rocks 800-850 Ma old and from the same region (Sun *et al.,* 1986). These fossils show a very fine and regular transverse striation, although without any other features of complexity. Both ends of the band-like fossil are rounded, and, if not with a faint striation, this fossil would look like the associated *Tawuia,* compressed, sausage-like fossils, tentatively interpreted as multicellular eukaryotic algae, or Metaphyta.

More recently Gnilovskaya (1998) published a description of the new genus *Parmia* (Figures 6, 7), which increases the diversity of worm-like creatures inhabiting the ocean during the Late Riphean well before the Ediacara fauna. Over 80 specimens have been collected from a core from a borehole drilled in southern Timan, northeast of the Russian Platform. With a maximum length up to 60 mm and a body width up to 2.5 mm, these organisms show a regular homonomous segmentation (7-11 segments per millimeter of body length). *Parmia* is interpreted as a probable predecessor of the annelid worms. All geological and paleontological evidence (including the representative microfossil assemblage) indicates that the age of *Parmia* may be about 1 Ga (Gnilovskaya *et al.,* 2000). Although the exact age of *Sinosabellidites* and *Parmia* is yet to be determined, these metazoan fossils are certainly much older than the Ediacara-type invertebrates known from the Vendian Period.

Molecular data on origin of metazoans

Gene sequencing supplies evidence that the fungi diverged from plants and animals roughly 1. 6 Ga ago (Heckman *et al.,* 2001), which is the oldest molecular dating of animal life. This conclusion is supported by several earlier molecular data, although calibration problems of molecular clocks cast doubts onto both old and more recent datings of metazoan origins (Lee, 1999). Molecular evidence of an older origin of the metazoan phyla was obtained from analyzing calibrated rates of molecular sequence divergence (Wray *et al.,* 1996). Independent estimates obtained from the analysis of seven gene loci suggest that the invertebrates diverged from the chordates about a billion years ago. Protostomes diverged from chordate lineages well before the echinoderms, which suggests
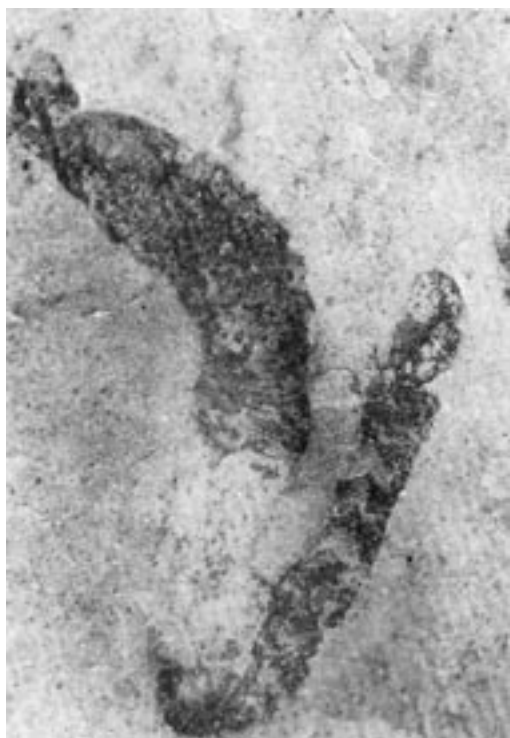
Figure 6. *Parmia,* holotype, Late Riphean (about 1 Ga old) siliciclastic deposits, southern Timan, northeast of the Russian Platform (x 10). Courtesy of M. B. Gnilovskaya. Collection of the Institute of Geology and Geochronology of the Precambrian, Russian Academy of Sciences, Saint-Petersburg.
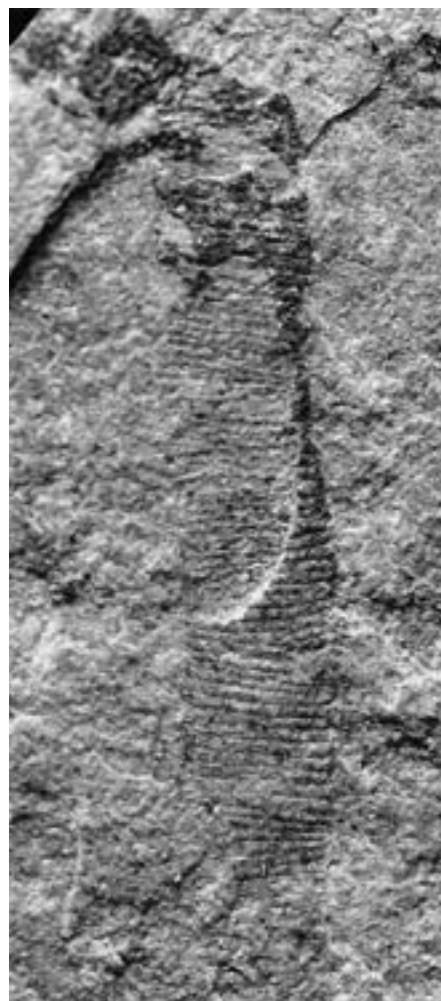
Figure 7. *Parmia,* paratype, (x 10). Locality and age as on Figure 6. Courtesy of M. B. Gnilovskaya. Collection of the Institute of Geology and Geochronology of the Precambrian, Russian Academy of Sciences, Saint-Petersburg.

a prolonged radiation of animal phyla and an origin of animals no later than 1200 Ma ago.

Additional molecular data support this conclusion (Bromham *et al.,* 1998). However, the conflict between these molecular models and the traditional perception of the fossil record (such as a Cambrian evolutionary explosion) makes some specialists wish to reconsider the molecular data. For instance, Ayala *et al.* (1998) analyzed 18 protein-coding gene loci and estimated that the protostomes (arthropods, annelids, and mollusks) diverged from the deuterostomes (echinoderms and chordates) about 670 Ma ago, and the chordates from the echinoderms about 600 Ma ago. Both estimates are still older than the fossil record indicates, but they are close enough to some traditional paleontological estimates. Ayala believes that the results obtained by Wray and coauthors, with corresponding divergence times of 1,200 and 1,000 Ma ago, are imperfect because they extrapolated from slow-evolving vertebrate rates to the faster-evolving invertebrates, with their higher rates of molecular evolution.

In spite of this criticism, a longer Precambrian history of

the metazoans cannot be ruled out. Thus, Cooper and Fortey (1998) pointed to similarities between evolutionary explosions documented by the fossil record. A literal perception of the fossil record gives an impression of a greatly accelerated morphological evolution during some time periods such as the Early Cambrian (545 Ma ago) and the Early Tertiary (c. 65 Ma ago). The Early Cambrian was always considered as the period of appearance of animal phyla, and the Early Tertiary was the time of appearance of modern birds and the orders of placental mammals. These apparent "explosions" are questioned, however, by cladistic and biogeographic studies. Both approaches supported by molecular data expose prolonged periods with evolutionary innovations prior to those "explosions", although the fossil

record tells us very little about those periods.

Recently, molecular biologists (Wood *et al.,* 2002) identified genomic properties related to multicellularity, finding very few genes specific to all multicellular species. This suggests that the transition to multicellularity may not have required the evolution of many new genes absent from unicellular organisms. The metabolic pathways necessary for multicellular organization could already have been in existence in unicellular eukaryotes. This means that the evolution from unicellular protozoans to some multicellular animals could have taken a very short time. The transition from a colonial cell to true multicellularity (that is, to a tissue-grade organization) required that a part of the genome responsible for autonomous cell life is switched off (Zavarzin, 2002). The rise of tissues limited the exchange of genetic information between the cells within the organism and between the multicellular organisms as well. This function was successfully overtaken by sexual reproduction.

The molecular-clock approach is a powerful instrument for revealing cryptic events during biological history. The molecular clock shows ways to uncover the time of origination of metazoans and the time of major bifurcations occurred in the phylogenetic tree. But along with the general methodological difficulties related to problems of homol-ogy and analogy that most comparative methods share, two fundamental assumptions concerning molecular clocks remain uncertain: constant rates and their dependence on generation time. Discrepancies can be expected to occur between various techniques and between various classes of molecules. Attempts to compromise or to average extreme molecular data (Conway Morris, 1997) do not look very promising. Each class of biomolecules tells its own story in its own language, which we have yet to learn. It is now realized that the molecular evolution of life is a very complex process influenced by numerous intrinsic and extrinsic factors.

Stromatolite-forming prokaryotes as ecological antagonists of eukaryotes

One of the most puzzling questions is why, in spite of an early origin of the eukaryotic organisms 2.7 Ga ago, they did not become dominant life forms in the global ecosystem until the end of the Proterozoic, that is ca. 600 Ma ago. Indeed, during the greater part of the Proterozoic, the benthic habitats of the shallow epiplatform basins were dominated by prokaryotic communities, the most widespread of which were the stromatolites.

Stromatolites are biosedimentary structures generated by benthic microbial communities such as bacterial mats and biofilms. They look like mounds, cones, columns, or branching tree-like forms built of thin laminated carbonate rock (simple forms of stromatolites are known from siliciclastic basins as well). The size of these structures ranges from a few millimeters to a few meters high. Microbial mats that today are common in hypersaline marches, lagoons and sabkhas, are considered as stromatolite analogues and as relict ecosystems that once dominated the subaqueous photic realm, or even deeper waters and that were probably widespread on land in lakes throughout most of the Precambrian.

Stromatolites appeared as early as 3.5 Ga ago and became widespread during the Early Proterozoic. The abundance and morphological diversity of the stromatolites increased rapidly during the Late Archean and the Proterozoic and reached their maximum at about 1. 0 Ga ago (Semikhatov and Raaben, 1994, 1996). During the Proterozoic, densely packed and vertically oriented stromatolites covered the bottom of the epiplatform basins and the continental shelf. They formed carbonate platforms, ramps and reefs that seemed to be far more extensive than reefs built by algae and corals during the Phanerozoic. The tremendous morphological diversity of the Precambrian stromatolites and their peculiar micro-structures may reflect the interplay between such factors as the composition of the microbial communities and their environment.

Recent microbial mats do not leave much ecological space for most eukaryotic organisms (Farmer, 1992). Some protists and animals do live in, on and amongst the stromatolites, in spite of the hypersalinity of the water, like the community of Shark Bay, Western Australia (Walter, 1994), but the diversity of these eukaryotic organisms is very low compared to that in the marine environment with a normal salinity, and some invertebrates are represented by dwarf species. A low diversity of eukaryotes is also observed in fresh-water ecosystems dominated by Cyano-bacteria. Recent studies of Cyanobacteria revealed a diversity of toxins (neurotoxins, hepatotoxins, cytotoxins, and several others), which can be directly lethal to small zooplankton and metazoans, or can reduce the size and number of offspring produced by organisms feeding on Cyanobacteria (Carmichael, 1994). These facts bring us back to Vologdin's (1962) hypothesis that Cyanobacteria responsible for stromatolite formation during the Precambrian might, like their recent counterparts, have produced toxins that inhibited early animal evolution. Bacterial toxins as well as marginal marine environments with a high salinity and a fluctuating humidity seem to be major factors controlling the distribution of metazoan grazers at present utilizing Cyanobacteria, and probably to a larger extent also in the past.

This ecological antagonism of stromatolites and animals was documented in the Phanerozoic fossil record. For instance, Schubert and Bottjer (1992) coined the term «disast-

er forms» for stromatolites and some other microbial structures found in the Lower Triassic strata that dramatically increased in abundance during the recovery interval after a mass extinction event. This fact and observations made in the recent habitats dominated by stromatolites are consistent with the hypothesis that the primary biotope of animals might have existed beyond the prokaryotes-dominated environments (Fedonkin, 1996b, c).

The catastrophic decline in stromatolite diversity and abundance after 850 Ma ago has been interpreted as indirect evidence of metazoan activity. Some authors suggested that grazing and bioturbation by early invertebrates might have caused the decline of stromatolites during the Late Proterozoic (Garret, 1970; Awramik, 1971; Walter and Heys, 1985). However, direct paleontological evidence has never supported this idea, and it seems to be inconsistent with recent observations on the ecology of bacterial mats as well. Arthropods are dominant grazers on recent microbial mats (Farmer, 1992), with a minor role for gastropods and fishes (Walter, 1994), taxa that did not appear as late as 850 Ma ago. Most grazers have a small body size of less than a few millimeters, which is why they do not prevent bacterial mats from developing, but rather coexist with bacterial communities. All these observations cast doubts on the idea that metazoan grazers would have wiped out most Proterozoic stromatolites.

The ecological antagonism between bacterial ecosystems and eukaryotes, which is so obvious at present, may have been even stronger in the Precambrian preventing an early domination of the eukaryotes. That is why it is difficult to accept the idea of a biomat-related lifestyle (Seilacher, 1999). Anoxia beneath the bacterial mat because of the decomposing dead organic material would not allow the metazoans to colonize the space below the mat. Contrast change in oxygen saturation at the top millimeter of the cyanobacterial mat (from 100% in daylight down to zero in the night because of the H_2S rising up) excludes most of the eukaryotes from this microenvironment. There is some evidence that the biotopes of the stable bacterial mats (including stromatolites) and the early metazoans were essentially different (Fedonkin, 1996b, c).

The decline of the stromatolite communities after an almost 2 Ga long global dominance in the benthic realm may have been caused by a combination of heterogeneous factors, such as the appearance of eukaryotic algae that competed with cyanobacteria for nutrients, habitats and light, extremely low seawater levels (in particular, during the glacial periods), negative effects of increasing concentrations of biogenic oxygen on the bacterial stromatolite-building communities, a decreasing carbonate saturation of the sea water during the Late Proterozoic, climate change, particularly during the Neoproterozoic Glacial Era some 850-600 Ma ago with all its paleogeographic and geochemical con-

sequences (for references, see Fedonkin, 1996a, b). In fact, all these hypotheses may complement one another. The positive correlation of water temperatures in the recent oceans with the ratio of bacterial production and the primary production of the phytoplankton (Hoppe *et al.,* 2002) suggests that the cooling Neoproterozoic biosphere favored eukaryotic life rather than prokaryotic life. The dramatic decline of the stromatolite ecosystems as the ecological dominants of the warm marine basins after 850 Ma ago in fact meant their replacement by eukaryote-dominated ecosystems. This process opened the ecospace for the calcareous and other biomineralizing organisms with a high potential of preservation, the main object of classical paleontology.

Climatic trend during the Proterozoic

The climatic history of the Earth does not show any glaciations during most of the Archean eon, rare glacial episodes being found only in the interval from the Late Archean to the Middle Proterozoic, and frequent and periodical glaciations occurring since the late Proterozoic through the Phanerozoic. A cooling mantle, a decrease in radiogenic heat, a lowering intensity of the gravitational differentiation of the mineral substance and of tidal deformations in the subcrustal zones of the Earth are among the factors that will have caused the steady shift from a warm biosphere to a colder one. However, the main causes of cooling were the decrease in concentration of greenhouse gases in the atmosphere and a growing albedo of the planet due to continental growth (Chumakov, 2001). The first extensive glaciation on the planet is documented to have fallen some 2.3 Ga ago, after which there was a long period of warm climates until ca. 800 Ma ago. Since then, glacial periods became more or less regular events in geological history.

Between 800 and 550 Ma ago, the biosphere went through an extremely cold period known as the Snowball Earth period (Hoffman *et al.,* 1998) with at least four (or perhaps five) successive, severe glaciations. The most extensive glaciation was the Varanger glaciation some 650-620 Ma ago, that immediately preceded the first mass appearance and global expansion of animals in the history of the biosphere. The magnitude of this glacial has been inferred from the extensive geographic distribution of tillites, varves and other cold-related evidence from deposits of this age. The proponents of an extreme climatic model suggest that an ice sheet over a mile thick covered the entire planet from the poles to the equator (Hoffman *et al.,* 1998). According to various estimates, this global ice sheet could have stayed in place for a very long time, from 4 up to 35 million years, having tremendous consequences for life (Kaufman *et al.,* 1997). Banded iron formations associat-

ing with glaciogenic rocks are believed to reappear after an absence of 1 Ga long when the ocean, sealed by ice, became anoxic and therefore rich in dissolved ferrous iron. The carbon isotope record shows enormous negative shifts associated with glacial periods, reflecting dramatic changes in the global ecosystem, as well as a presumed collapse of the biological productivity at the ocean surface for millions of years.

This extreme Snowball model is increasingly criticized. No consensus exists about how many extensive glaciations did occur on Earth between 850 and 550 Ma ago. Thus, Kennedy *et al*. (1998) proved that only two glacial periods occurred during that time, the Sturtian and the Marinoan (Varanger) glaciations, both found before 600 Ma and separated by a period of 100 to 150 Ma. This makes them independent events rather than linked ones according to the proposed mechanism of a "Snowball Earth". Hyde *et al.* (2000) suggested a softer scenario for the Cryogenian with an unfrozen band of tropical ocean waters, providing a refugium for the early metazoans. The continuity of the fossil record of eukaryotic organisms (including abundant phytoplankton) throughout the late Proterozoic shows that global ice shields never interrupted photosynthesis, nor eukaryotic life in general.

Remarkably, the time interval of the Cryogenian embraces the minimum age of ca. 700-750 Ma for the first metazoans as predicted by some molecular clock models. Whether we accept this age or chose models that suggest deeper roots for the metazoans, the essential part of early animal life evolved in a cold ocean. In this respect, it is important to know the environmental factors that challenged the oldest metazoans.

Amidst glacial period

Normally, glacial periods are accompanied by strong environmental shifts including radical geographic changes. A shield of ice and snow covered many, though not all, Vendian continents and permafrost was widespread over vast areas of land. The equatorial continents free of ice contained dry deserts. Water erosion of the land and nutrient input into the ocean hardly occurred. Life on frozen continents was reduced to only a few habitats such as hydrotherms and the subsurface realm where liquid ground water could be found. Marine environments were affected by vast shelf glacials and by millions of cubic kilometers of floating ice. The sea level dropped 250-300 meters and strongly fluctuated during the few million years of each glacial period. Most of the shelf was exposed to the air (or was covered with ice) and the area of shallow-water habitats was reduced to a small strip along the edge of continental platforms. Along with the cold climate, vast temperature gradients, changes in atmospheric circulation, and an

increasing storm frequency were found. Thus, the glaciations were accompanied by glacioeustatic dropping sea levels, regressions of the sea, decreasing surface areas of the shelf, increasing terrestrial surface areas, a radical shrinkage of benthic environments, and a shift of life to the pelagic realm. The geographic isolation of species had increased because of the growing surface area of land and because of climatic differentiation. The low content of biophilic elements (nutrients) in the open ocean may have been compensated partly by the input of metabolites from the deeper ocean zone: heavy cold water was sinking, pushing up bottom water rich in dissolved nutrients. The same mechanism caused the "ventilation" of the ocean: sinking waters brought oxygen into the deeper parts of the ocean.

All these phenomena must have affected the biota. The most negative effect of these glaciations will have been the destruction of the shallow-water habitats of the benthos of the shelf that in recent oceans normally supports over 80% of the benthic biomass. During the Varanger glaciation, marine life was concentrated in the nutrient-poor and ecologically homogeneous pelagic waters. Apart from this, a large part of the phytoplankton, being shut off from sunlight by oceanic ice cover, was eliminated. One may presume that organisms living around hot vents in the deep ocean could have survived these glacial periods. But the low oxygen content (if not anoxia) of the deep benthic realm may not have allowed the metazoans to colonize these environments untill the very end of the Vendian, or even later (Crimes and Fedonkin, 1994).

The Neoproterozoic glacial periods beginning ca. 850 Ma ago seemed to have removed the environment from temperatures optimal for prokaryotes, but they may have had advantages for eukaryotic organisms (see below). This formed a prelude to the Vendian radiation of those metazoans that had been able to survive under the severe glacial conditions. The global distribution of the Vendian fauna, together with the nature of the fossiliferous rocks, are evidence of its marine and relatively cold-water environment. The Vendian fauna, and certainly, its predecessors, will have faced all advantages and disadvantages of cold water habitats. It would be worthwhile to look at recent cold-water marine habitats to see the whole spectrum of the environmental factors that might have affected early metazoan evolution.

Recent marine cold-water environments

The extensive literature on cold-water ecosystems of the recent ocean, particularly the Antarctic basins, reveals some peculiarities possibly resembling the Vendian basins that the Ediacara-type fauna inhabited (for references see Fedonkin, 1996 b, c). The recent cold-water communities show a profound difference from tropical ones. These dif-

ferences may hint at the nature of the environment at the dawn of animal life, in particular during the glacial periods of the Cryogenian between 800 ans 600 Ma ago.

The ecological conditions and requirements of recent cold-water basins compared to those of the temperate and equatorial zones of the World Ocean can be summarized in the following tables.

Ecological conditions

Abiotic environmental characteristics of recent cold-water basins includes: 1) extreme climates and temperature fluctuations; 2) siliciclastic sedimentation without carbonates; 3) intense vertical water circulation; 4) high concentration of phosphates, nitrates and other metabolites; 5) better aeration of water; 6) circumpolar basins; 7) high concentration of organic nutrients; 8) seasonality: variability of light regime above the polar (Arctic and Antarctic) circles alternates between continuous darkness in winter and continuous daylight during summer; 9) extensive cloud cover; 10) less transparent water (shorter photic zone); 11) higher water viscosity, (a) making it more difficult for filter feeders to pump sea water in and out, (b) allowing small particles to float longer, and (c) affecting larval and plankton transport (vertical migration); 12) greater gas solubility of cold water (seawater at zero temperature contains ca. 1.6 times more oxygen than at 20 °C, the complexity of CO_2-carbonate-bicarbonate equilibria prevents us from making a similar comparison for the solubility of carbon dioxide); 13) in cold water, the solubility of biogenic calcite and aragonite is higher than in warm water.

Ecological features

1) The poor terrestrial life on continents contrasts with the abundant life in oceans, the productivity of the terrestrial ecosystems is low both in relative and absolute terms; 2) high total biomass of living organisms, especially phytoplankton; 3) higher bioproduction of primary producers; 4) unique short food chains (phytoplankton-krill as main herbivore-seals and whales as higher predators), another food web consists of a very rich and diverse benthic fauna supported by a seasonal detritus rain from the water column above; 4) polar ecosystems are less diverse than tropical ones; 5) low stability of biocoenoses; 6) dominance of herbivorous planktotrophs in planktonic metazoans; 7) low proportion of predators in the plankton which, during some seasons, can show population explosions; 8) a high proportion of coelenterates (medusae and ctenophores) among the predators; 9) dominance of forms with direct development (without a pelagic larval stage); 10) low growth rate; 11) long lifespan; 12) low generation turnover; 13) seasonal resource limitation; 14) low reproductive potential, with few, relatively large and yolk-rich eggs; 15) high incidence of direct development, brooding, and/or vivipary; 16) slow gametogenesis; 17) semelparous reproduction; 18) late reproductive maturity; 19) indeterminate growth and high longevity; 20) slow embryonic development; 21) reduced gonadal volume; 22) low basal metabolic rates with regard to oxygen uptake; 23) low activity levels, lethargy, and vertical orientation; 24) low dispersal rates; 25) low colonization rates; 26) low population densities; 27) low mortality because of low predation pressure; 28) K-strategy species dominating; 29) density dominance of some species; 30) high nutrient concentration at the surface; 31) high neritic primary production; 32) high benthic biomass due to delayed maturation and great longevity; 33) soft bottom sediment supports rich infaunal communities dominated by lamellibranch mollusks, actinarians, scleractinian corals and holothurians; 34) stability of the physical environment coupled with a low growth rate tend to evolution of efficient, stable community structure with low annual turnover rate (this type of community supports a higher biomass or alternatively, a higher number of individuals per unit of organic matter than the less stable, less efficient assemblages characteristic of physically fluctuating environments); 35) rate of microbial carbon degradation through enzyme-catalyzed reactions is temperature-sensitive and should be very low in cold-water environments; 36) polar submergence of shallow-water genera (including eye-bearing species that are commonly known from the photic zone of the intertidal and continental shelf in the temperate-tropical environment; in the polar regions the species belonging to these genera tend to penetrate to the abyssal depth); 37) polar emergence of abyssal genera (including the genera which are known only from the aphotic abyssal depths in the temperate-tropical marine environments); 38) microbes occur both in water and in sediment but their significance in cold marine ecosystem is unknown (that is extremely low!).

Physiological features of cold-water metazoans

Antarctic poikilotherm animals share several features, such as: 1) slow and seasonal growth; 2) delayed maturation; 3) great longevity; 4) large body size (gigantism in pycnogonids, isopods, sponges, amphipods, free-living nematodes), that reduces potential predation and increase individual fecundity, enhancing population recruitment; 5) low overall fecundity; 6) large, yolky eggs; 7) non-pelagic larval development; 8) seasonal reproduction; 9) low basal metabolic rate; 10) reduced physical activity; 11) seasonal response of growth rates, development and reproduction cycle to seasonal environment; 12) advanced newly hatched juvenile stages; 13) asexuals also tend to occur at high altitudes, and in marginal, nutrient-poor environments compared to their close relatives and sexual species; 14) deferred maturity; 15) energy cost of thermodynamic work, necessary for removing calcium carbonate from sea

water for constructing skeletal carbonate, increases in cold water; 16) enzyme-catalyzed reactions proceed more slowly at low temperature; 17) pH of body fluids increases with low temperature; 18) periodical starvation resulting in body mass decrease causes reduction of endogenous respiration sometimes by 99% which allows the cell to conserve carbon and energy, and stabilizes viability in a very small part of the initial population; 19) higher viscosity of body fluids affects some physiological and biomechanical aspects of the activity of the life of invertebrates.

Morphological features of cold-water metazoans

1) Large number of aberrant morphologies; 2) large size (gigantism in pycnogonids, isopods, sponges, amphipods, free-living nematodes), which reduces potential predation and increases individual fecundity, enhancing population recruitment; 3) dominance of attached forms among benthonic invertebrates; 4) dominance of soft-bodied forms in benthic communities; 5) larger body size than in the forms of the same species living in warm water. Lipps and Hickman (1982) give six mechanisms for attaining and maintaining a large body size that recur in shallow Antarctic biotas: 1) the elongation of appendages and sense organs, 2) extreme flattening, 3) a lattice construction of slightly mineralized skeleton, 4) stalk elongation, especially common in the passive suspension-feeding organisms, 5) agglutination, and 6) big-bag construction.

Not all of the characteristics mentioned above can be identified in the geological and fossil record of the Neoproterozoic, and even more, not all of them could have existed during a time as remote from the present day as 600-800 Ma. However, with these data in mind, we may get a deeper insight into the early history of animal life.

General characteristics of Vendian fauna

Remarkably many of the features typical for recent cold-water invertebrates can be recognized in the Precambrian metazoans and their habitats, in particular: 1) large body size or even gigantism (when compared with the small, shelly fossils of the Cambrian); 2) dominance of soft-bodied forms; 3) extremely rare organisms with a mineralized skeleton (observed in carbonate basins only); 4) a weak sclerotization of the cover tissues; 5) a low biotic diversity; 6) a high proportion of body plans considered as unusual (or aberrant) in the later fossil record; 7) dominance of sedentary and benthic vagile life forms (which may actually have a taphonomic cause); 8) small percentage of infaunal metazoans, active filterers and scavengers, which may partially be explained by the difficulty of performing a high level of physical activity in cold-water conditions; 9) dominance of seston feeding sedimentators, microphagous and detrivorous organisms; 10) main macro-

phagous predators are coelenterate polyps (sea anemones) and medusae; 11) no indication of other predators (no bite marks or regeneration structures in the body of fossils which may indicate a low predator activity); 12) maximum population density in the upper sublittoral zone; 13) very short trophic chains; 14) high portion of cosmopolitan species; 15) low diversity at the species level; 16) dominance of the coelenterate grade or diploblastic forms over triploblastic organisms both in number of species and in the number of individuals; 17) high population density of only a few species; 18) vulnerability of communities (reflected in the very short, though recurring, intervals of the stratigraphic distribution of fossil assemblages, which could often be explained by a high seasonal mortality and a low recolonization rate); 19) mass preservation of the Vendian fauna is typically caused by storms that at present are more frequent in the cold-water zones than in the temperate and tropical zones of the ocean; 20) many of the Vendian animals show features of impulse growth (concentric zones, modularity, segments and other characters of serial homology) that may be related to seasonal variability in the light regime, temperature, bloom of the primary producers, activity and reproduction of algal endosymbionts in the Vendian soft-bodied metazoans.

Low diversity and slow radiation of Vendian fauna

Although the number of collected specimens of Vendian animals on Earth is nearly 10,000, their taxonomic diversity remains very low. Over 220 fossil species of Vendian animals have been described, but less than half of them have proven to be valid. A few distinct grades and clades can be recognized in the fauna. Paradoxically, sponges, which are expected to be abundant in the oldest communities, are represented by just two taxa *Palaeophragmodictia* (Gehling and Rigby, 1996) and *Ausia* (Fedonkin, 1996d). By contrast with Recent coelenterates, which make just two of thirty-five generally recognised phyla of the Animal Kingdom and less than 0.001% of overall species diversity, the Vendian fossil assemblages show a much higher proportion or even domination of the diploblastic organisms and a few well established clades. The most remarkable of the latter is Phylum Trilobozoa (Fedonkin, 1987) which includes genera *Tribrachidium, Albumares, Anfesta, Ventody-rus, Skinnera, Vendoconularia* and a few other tubular forms, such as *Pteridinium,* and demonstrates vast morphological diversity, high complexity and physiological and ecological specialization. The most rich clade of the triploblastic grade (or Bilateria) is represented by the Phylum Proarticulata (Fedonkin, 1987, 2002) which includes genera *Dickinsonia, Yorgia, Vendia, Archaeaspis, Andiva, Ovatoscutum* and some other taxa which demonstrate an unusual kind of alternating segmentation described as the symmetry of gliding reflection (Fedonkin,

1985).

With rare exception, most of the Vendian metazoan genera are represented by a single species. Low diversity at the species level may indicate the stage of initial radiation within most of the known clades and a rather low evolutionary rate during the Vendian Period. The latter assumption can be drawn from the relatively short time interval of the Vendian fossil record which hardly exceeds 30 Ma and from the long time range of many Ediacara taxa.

The absence of a mineralized skeleton may be the cause of the low preservation potential of most of the Pre-cambrian metazoans. However, about 25 forms of trace fossils, which are usually preserved together with imprints of soft-bodied animals, give additional evidence for the idea that both the diversity and the activity of the Vendian metazoans in the benthic realm were low indeed when compared with the Cambrian and later Phanerozoic fossil record. So, the taphonomic and ecological conditions can only partially explain low biodiversity of the Vendian invertebrates, and initial radiation of the macroscopic invertebrate clades seems to be the major cause. We also have always to bear in mind that the overwhelming majority of the recent invertebrates are represented by microscopic forms which have very low preservation potential and virtually no fossil record.

The bulk of the literature dealing with the Antarctic basin shows that slightly more than 3,100 animal species have been described from the Antarctic Ocean, while just over 1,300 species are known from the Arctic Ocean. Compared with the Vendian, this looks like a lot but compared with the faunal diversity from the tropical zone of the recent ocean it is extremely low. Thus, this low diversity may be a primary feature of the cold-water basins, and at the dawn of animal life, especially during glacial periods, this diversity could have been so low that even minor changes in population structure could have had tremendous evolutionary consequences.

Taphonomic evidence for cold-water nature of Vendian fauna

Unusual preservation of the Ediacaran fauna (the abundance of fossil soft-bodied organisms) is explained by cumulative effect of many biotic and abiotic factors (Fedonkin, 1985a) and is consistent with the model of the Cold Cradle of Animal Life (Fedonkin, 1996 b, c). The functional temperature optima of some enzymes that take part in the bacterial degradation of complex organic compounds are essentially higher than those dominating the recent Antarctic waters. The low rates of biological degradation result in the accumulation of living and dead organic material in sediments at ca. 17gC per m^2 per year, that is between 9 and 28% of the primary productivity of the surface waters. These estimates are extremely high compared with those of the temperate zone of the oceanic

regions (Stanley and Herwig, 1993). A practical aspect of this may be found in the prospectiing of cold-water paleobasins for source rocks of hydrocarbons.

Kidwell and Baumiller (1990) demonstrated that low temperatures are far more effective inhibitors of decay than anoxia. In cold siliciclastic basins of the Vendian the inhibition of biodegradation could have been even stronger than that for recent counterparts because of the supposed relatively low oxygen concentration in the Late Proterozoic atmosphere and stratification of the paleobasins due to the thermal gradient caused by the constant water turbidity in the absence of active filter-feeders, as well as because of low aeration of the weakly or non-bioturbated sediment (Fedonkin, 1996b). These are additional arguments in favor of the special taphonomic window that was widely opened in the late Proterozoic and closed again with the change in physical and biotic conditions of the biosphere.

Cold cradle of animal life

The most diverse fossil assemblages of the Vendian metazoans, as well as those even older metazoan fossils (see above), are known from siliciclastic basins. This fact as well as some morphological, paleoecological and taphonomic features of the oldest invertebrates suggests that the cradle of animal life may have been the environments of relatively cold-water basins (Fedonkin, 1996 b, c). The very first metazoans did not appear in warm carbonate basins occupied by stromatolite cyanobacterial communities, but rather beyond the carbonate belt of the planet in siliciclastic basins of the temperate or even the polar zones. Well-oxidized and nutrient-rich environments of the cold basins provided an essential advantage to the animals as aerobic heterotrophs and disfavored their ecological antagonists, rokaryotic communities, just as takes place today.

During the Neoproterozoic glacial periods, the Cryogenian, the ocean could have been a hostile environment. The variability of the light regime, related to the thickness of ice cover, could have affected the primary productivity of the phytoplankton, which could have dropped during winter. One could expect annual periods of starvation in the cold, Vendian water ecosystems as well. These starvation periods resulted in a decrease in the initial population down to small numbers of individuals, in morphological change, and in a reduction of 99% of the endogenous respiration, which allows the cell to conserve carbon and energy (Novitsky and Morita, 1978).

Relatively high concentration of dissolved oxygen allowed the first metazoans to gain large size and individual mass (that seem to be a common adaptation to the conditions of unstable, seasonal food supply) without the development of complex respiratory systems or efficient blood

pigments related to oxygen transport such as haemoglobin. The latter supposition is based on a fascinating example of modern Antarctic ice fish, which lack haemoglobin. The cold climate of the Cryogenian Era of 750-600 Ma ago (the "Snowball Earth") provided heterotrophic aerobic megascopic organisms with a unique opportunity to colonize geographically new and vast habitats.

Vendian metazoans after Ice Age

The oldest known metazoans of the Vendian Period (550-620 Ma ago) are represented by megascopic body fossils and trace fossils. The species diversity of the Vendian fauna looks very limited although the population densities in the shallow-water environments may have been comparable to recent ones. There is no general consensus regarding the nature and systematic position of the fossils. The Vendian fauna seemed to have included both relict species adapted to essentially different environments of earlier periods of the Neoproterozoic and those taxa ancestral to the Phanerozoic phyla. A number of metazoan body plans and physiologies seemed to have gone extinct very early in the Vendian without leaving recent analogues.

So far, among the more than 30 fossil localities from various parts of the world, the White Sea region in the north of the Russian Platform seems to contain the most representative fossil record of the pre-Cambrian metazoans. Here, the faunal elements also known separately from the Terminal Proterozoic of Newfoundland, Namibia, South Australia and other regions have been discovered forming a succession. The extraordinary preservation, including complex three-dimensional fossils, the abundance and diversity of both body and trace fossils make the White Sea region a true window to the world of the most ancient animals.

The more than 25 years of systematic excavations show: a) a growth in taxonomic diversity of body fossils and trace fossils upward in the Vendian succession; b) a stepwise pattern in the increase in biodiversity; c) a variety of species ranges over time; d) a historical change in paleofaunistic connection of the paleobasin; and e) a disappearance of metazoan body fossils and bioturbations in the sediments of the brackish paleobasins. At least six faunal assemblages named after dominant fossils are identified in the sequence: *Calyptrina-Beltanelloides, Ventogyrus, Inaria, Pteridinium, Charnia, Yorgia-Dickinsonia lissa* (Fedonkin and Ivantsov, 2001). Biostratigraphic units (biozones and stages) with a high potential for global correlation can be established. A uranium-lead age of zircon of ca. 555.3 Ma for a volcanic ash at the top of the *Charnia* fossil assemblage in the sea cliffs of Zymnie Gory suggests a minimum age for the triploblastic metazoans as their bilaterian body fossils and trace fossils occur strati-

graphically underneath it (Martin *et al.,* 2000). The dynamics in biodiversity seem to have no direct connection with the carbon isotope excursions in the Vendian ocean.

Although the majority of the Vendian body fossils have been interpreted as soft-bodied coelenterates (solitary and colonial polyps and medusas), there is also a large group of complex body fossils that represent a higher, bilaterian or triploblastic grade of organization. Many bilaterian fossils have several features in common, particularly their shield-like shape, their bipolarity, and their complete and homonomous metamerism combined with the symmetry of gliding reflection. This group includes *Dickinsonia, Ovatoscutum, Chondroplon, Yorgia, Vendia, Archaeaspis, Andiva* and other life forms, collectively assigned to the Phylum Proarticulata (Fedonkin, 1985a, b, 1987). Modes of deformation, of growth pattern and of regeneration marks, although rare, indicate that these fossils have a convex, thin and flexible dorsal carapace composed of an organic, non-mineralized, but slowly degradable substance (Fedonkin, 2002). The high relief of the imprints proves that the soft body of these animals was thick. The interpretation of these fossils as triploblastic invertebrates is based on some preserved features of their internal anatomy as well as on their trails and tracks found in direct association with body fossils.

Priority of predation in animal evolution

Comparative analysis of the metazoan evolutionary models shows that marine macrophagous consumers of living multicellular attached plants always occupy the terminal position on the phylogenetic tree (Vermeij and Lindberg, 2000). Most recent marine herbivores are derived from microphages, detritivores, or predators, and have a post-Paleozoic origin. The pre-bilaterian metazoan clades at the base of the tree, such as Porifera, Cnidaria and Ctenophora often considered as relict phyla of the Proterozoic era, contain carnivores and suspension feeders, but no herbivores. The reason why the Cnidaria and Ctenophora (and almost all other metazoan clades) are all carnivorous is that this way of feeding was the primary feature of their ancestors.

The historical priority of carnivore heterotrophy in animal evolution may be related to the late development of enzymes enabling them to digest plant material. Many metazoan herbivores are themselves unable to digest plant material without the assistance of endosymbiotic bacteria and fungi. Animal proteins can far more easily be decomposed even without special ferments after lysis or denaturation when isolated in the gastric pouch.

The absence of bite marks or regeneration signs in the Vendian metazoans has been interpreted as evidence that before the Cambrian explosion there were no predators of invertebrates with hard parts (Glaessner, 1984). Later, the

Ediacaran biota was described as having been dominated by organisms that took up dissolved organic compounds or that were photosynthetically assisted by algal endosym-bionts. In addition, there were herbivores grazing on bacterial mats. The Vendian biota was thus depicted as a peaceful garden in contrast to the more recent marine biota full of predators (McMenamin, 1986; Seilacher, 1989).

These interpretations do not seem justified as they ignore important fossil evidence of predation in the Vendian fossil record. The Ediacara-type communities include large solitary polyps (sea anemones) with a voluminous gastric cavity *(Nemiana, Bonata),* tentaculate medusae *(Ediacaria, Hiemalora),* and a variety of other forms that were certainly predating actively on each other and on smaller invertebrate and their larvae. The absence of bite marks can easily be explained by their way of feeding: the largest part of the predatory lower invertebrates (cnidarians, ctenophorans, flat worms) cannot leave any predation marks on their prey as they have no hard biting organs like teeth, and they swallow and digest their prey whole. The same must be expected of their Vendian ancestors. The earliest evidence of teeth-like structures in metazoans is some comb-like chitinous fossil *Redkinia* from the Vendian of the Russian Platform (Sokolov, 1997). The long spikes show a size gradient along the base (jaw?) and tiny regular spikes between the long ones. This structure could be part of a filtering apparatus which served to catch and retain prey rather than bite pieces from it.

There is no evidence supporting photoendosymbiosis or the utilization of dissolved organic material, although those trophic methods could have been present in the Vendian invertebrates. Modern cnidarian-dominated communities provide an analogue for understanding the trophic roles of ancient gelatinous organisms (Lipps *et al.,* 2000). Anemones capture and devour medusae, as well as many other animals and plants. Medusae eat everything from minute to large plankton and nekton (including, vertebrates) and, in some cases, probe the benthos or ingest detritus. In addition, they commonly prey on one another, some selectively (Madin, 1988; Purcell, 1991; Arai, 1997). The large variety of life forms in the Vendian metazoans indicates that they too were trophically structured, much like similar modern biotas dominated by anemones and medusae. Predation was likely very common right from the very beginning of animal life, and, in a way, may have created the metazoans.

Modularity in Vendian metazoans: key to origin of Hox-type genes

Vendian body fossils show widespread modular growth patterns. Many metazoan taxa from the Vendian have a bipolar bilateral shape and a regular serial homology (Fedonkin, 1998). However, this repetition of homologous parts along the axis of their body cannot be classified as true segmentation (or metamerism *sensu stricto*) because of the unusual arrangement of the left and right half-segments of the body. Instead of being placed opposite to each other, these body parts alternate. In geometric terms, we can describe this pattern as a symmetry of gliding reflection, instead of a mirror symmetry that is commonest among the metazoans. These unusual segmented bilateral forms are united in the Phylum Proarticulata (Fedonkin, 1987).

Forms with a polymeric homonomic segmentation dominate among the body fossils interpreted as Bilateria (Triploblastica). Oligomeric homonomic forms are less abundant, and nonsegmented forms are extremely rare. There are no examples of heteronomic segmentation among the Vendian Bilateria. Although true metamerism can be suspected to occur in some Vendian bilaterians (for instance, in arthropod-like animals), it is hard to prove it for most segmented forms.

The absolute dominance of segmented forms among the Vendian Bilateria can indicate that the evolutionary development of bilateral symmetry and metamerism in many lineages of the earliest Metazoa might have been related processes although this did not always lead to coelomates. An analysis of the promorphology of the Vendian invertebrates, carried out by the author, shows evidence in favor of "cyclomeric" models that derive metamerism from the cyclomerism (or antimerism) of the Coelenterata, as suggested by Sedgwick (1884), Remane (1950), Lemche (1959), and Melnikov (1977) (for further references, see Fedonkin, 1985a, b). However, this analysis reveals essentially new aspects that have not been part of theoretical predictions by neontologists.

The symmetry of gliding reflection in the Vendian metazoans may result from a spiral way of growth. In recent eukaryotic organisms, this symmetry related to a spiral way of growing is especially common among plants. The bilateral pattern and offset (alternating) arrangement of the leaves on the stem can be derived from a spiral shift of the growth point along the axis: a signal to grow is given when the growth point gets to the lateral side of the stem. In some colonial metazoans, such as hydrozoan and anthozoan polyps, the offset pattern of the colony is common as well. We can assume that an arrangement of the leaves in plants and polyp branches in cnidarian colonies may be a morpho-physiological adaptation to an environmental gradient related to light direction for plants and to water current for the polyps. But what about solitary bilateral creeping forms such as *Yorgia* (Figures 8-12)? A hypothesis on the origin of the Eumetazoa from a colonial organism (Dewel, 2000) deserves attention and further development in the

Figure 8. *Yorgia,* body fossil preserved in a negative relief on the undersurface of the Vendian sandstone about 555 Ma old, Zimnii Bereg (Winter Coast) of the White Sea, Russia. Courtesy of A. Yu. Ivantsov. Collection of the Paleontological Institute, Russian Academy of Sciences. White and dark scale bars represent 1 cm.

light of the Vendian fossil record.

An alternative hypothesis here suggested may hold that the spiral cleavage of the egg could develop directly in a spiral way of growth at one pole of the embryo and subsequently in an adult organism. An epibenthic lifestyle with the body axis oriented parallel to the bottom surface seemed to promote the transformation of spiral into bilateral growth with the characteristic offset (alternating) pattern of the homologous parts. This hypothesis may be tested by the observations of the embryonic development of recent invertebrates.

The unusual growth patterns among Vendian bilaterians, such as the Proarticulata, may reveal unknown steps in the early evolution of the metazoan genome particularly, in the Homeobox gene complex. The author has suggested earlier that the genetic control of serial homology or "segmentation" among presumably diploblastic Vendian animals may be similar to that found in bilaterians (Fedonkin, 1988). The discovery of Hox-type gene clusters within crown diploblasts certainly lends credence to this hypothesis. The serial homology of many Vendian bilaterians suggests a compartmentalization of gene expression events, commonly found in Hox-type gene regulation in metazoans through cis-regulatory elements (Valentine, 2001). Recent advances in developmental biology provide convincing evidence of a causal link between the activation of Hox-genes
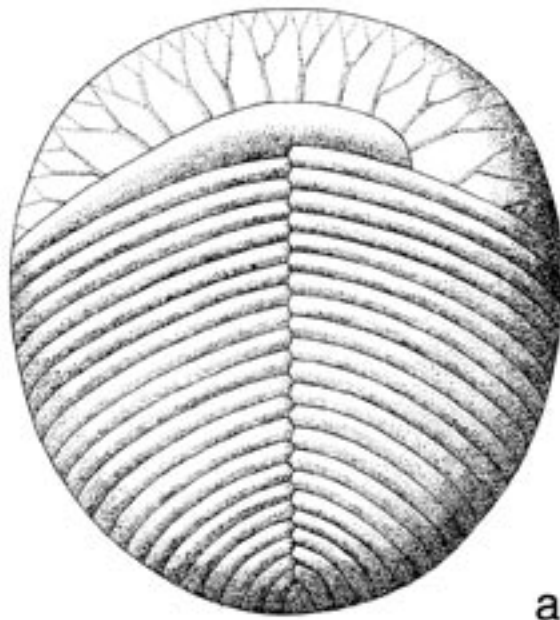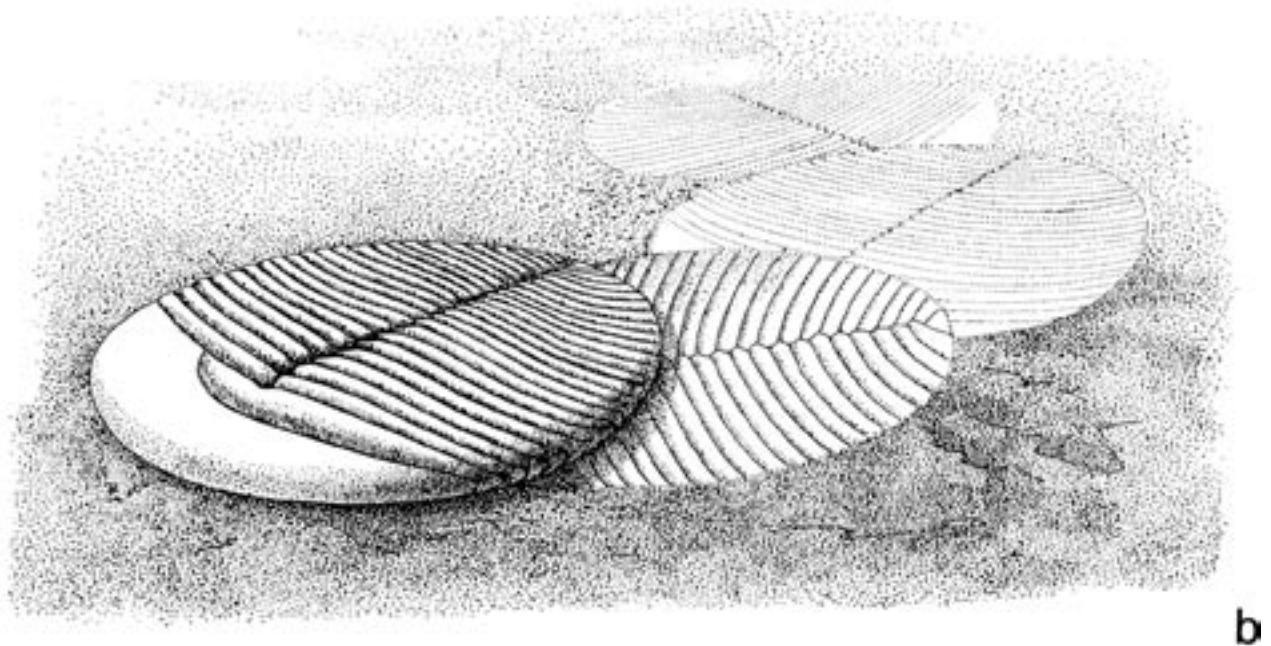
Figure 9. Schematic reconstruction of *Yorgia*. **a:** dorsal view, **b:** life position.

and segmentation (Tabin and Johnson, 2001 and references therein). Analysis of the body plan of Vendian fossils may give clues to the evolution of Hox-type genes, and, conversely, advances in developmental genetics may help interpret the most ancient metazoan fossil record.

Alternating left and right segments and asymmetry of the anterior part, which is so obvious in *Yorgia* and *Archae-*

aspis, remind one of the offset arrangement of the muscle myomeres on the lateral side of modern cephalochordate *Amphioxus.* This similarity returns us to an old theory by Geoffroy Saint-Hilaire on the origin of the chordates from the arthropod-like invertebrates via inversion of the dorsal side to the ventral one. Since the first half of the 19th century this theory experienced acceptance and rejection, and at present new data revive interest in this theory (Malakhov, 1982). Presence of chordates *(Pikaia* and *Yunnanozoon)* in the Cambrian shows that this group might have originated in the Vendian, and the Proarticulata might be considered among the possible ancestors of the chordates.

Bioturbations: from mucociliary creeping to peristaltic crawling

A careful study of trace fossils provides information on the activity of metazoan life and environmental variables. The mode of locomotion, feeding habits, behavioral patterns, body morphology, taxis sensitivity, and some physiological functions can all be derived from bioturbations. Normally, it is rather difficult to identify the nature of the producer unless it is a kind of simple dwelling, such as the burrow of a sea anemone. However, our knowledge on the oldest metazoans is too limited to ignore this group of fossils.

Among over 25 forms of Vendian bioturbations, grazing and crawling trails, feeding and dwelling burrows (in order of descending abundance) form the oldest assemblages of

Figure 10. *Yorgia,* body fossil (on the right below) is preserved in a negative relief on the undersurface of the sandstone bed while the resting tracks (platforms) are preserved in positive relief. Locality and age as on Figure 8. Courtesy of A. Yu. Ivantsov. Collection of the Paleontological Institute, Russian Academy of Sciences. White scale bar represents 1 cm.

trace fossils. Basically «two-dimensional» horizontal behavioral stereotypes dominate, particularly meandering patterns, although vertically oriented dwelling burrows and locomotion tunnels that cross the sediment-water interface are known as well. Normally, penetration into sediment did not go 5 cm below the bottom surface that, along with a limited degree of biological processing of the sediment, might be related to a limited oxidation of the sediment, even in relatively shallow-water habitats. The decreasing diversity and extent of bioturbations in the offshore sedimentary facies may reflect a limited aeration of the deeper benthic realm as well. On average, the body size of the burrowing infaunal animals in the Vendian was less than that of their Cambrian counterparts. A dramatic increase in size, diversity and depth of the bioturbations has been documented for the very end of the Vendian, that is, for the Rovno Regional Stage of the Russian Platform, or for the Nemakit-Daldyn Horizon of the north Siberian Platform (Fedonkin, 1990).

Peristaltic modes of locomotion by means of a pedal wave seem to have dominated over crawling and burrowing by means of a hydrostatic skeleton or by that of the peristaltics of the whole body. Its proportional occurrence may reflect the evolution of the locomotory diversity from muco-ciliary creeping to pedal peristaltic waves (Collins *et al.,* 2000), and further to whole body peristaltics, to wave-like lateral body bending and the usage of appendages. The two latter kinds of locomotion, common in recent invertebrates are not yet documented for the Vendian.

Until very recently, one could not find any correlation between the body fossils and the trace fossils of the Vendian fauna. This situation has changed after a series of

Figure 11. Well preserved resting track of *Yorgia* showing fine morphological features of the ventral side of the animal. Locality and age as on Figure 8. Courtesy of A. Yu. Ivantsov. Collection of the Paleontological Institute, Russian Academy of Sciences. White scale bar represents 1 cm.

important discoveries of locomotion trails and tracks preserved in direct association with Ediacara-type body fossils in Vendian siliciclastic deposits in the White Sea Region, north of the Russian Platform (Fedonkin, 2001; Ivantsov and Fedonkin, 2001a, b; Ivantsov and Malakhovskaya, 2002). These fossil associations were formed under the conditions of fast sedimentation of fine sand lying on top of a muddy bottom plane densely inhabited by a benthic fauna. A sedimentation event stopped the activity of scavengers and bioturbators and thus promoted the preservation of body imprints and trace fossils. Probably, due to bacterial mucilage, the muddy bottom was dense enough to retain its primary microrelief under the conditions of stronger water currents. The sedimentation event did not destroy the trails because the mucus produced by the animals glued and sealed the bottom sediment. Fossil animals of two species are especially common at the end of their trails, *Yorgia* and *Kimberella* (Ivantsov and Fedonkin, 2001 a, b; Fedonkin, 2001).

Yorgia waggoneri is a large (up to 25 cm) segmented bilateral organism (Figures 8-12) of the triploblastic grade of organization (Ivantsov, 1999; Dzik and Ivantsov, 1999) belonging to the Family Dickinsoniidae, Class Dipleurozoa, Phylum Proarticulata. Its trail consists of a series of similar elements ("platforms") that repeat the oval shape of the body and segmented pattern of the ventral side (Figures 8, 9). Maximum observed length of the trail is 4.3 meters. The «platforms» are arranged as a chain or a cluster and they may overlap each other. Being the cast of the ventral surface of the animal, each element of the trail contains the finest details of external morphology of the animal. The smooth surface of the trail, its preservation in a positive relief on the sole of the sandstone bed, absence of a sharp borderline between the trail and the irregular microrelief of the surrounding bedding plane and the uniform morphology of the "platforms" make a fundamental difference between the ichnofossil and the associated body imprint. Body fossils normally show a broad spectrum of deformations and preservation forms in a deep negative hyporelief (concave imprint on the sole of the sandstone bed).

Whilst crawling or gliding over the mud and staying in a resting phase, *Yorgia* produced abundant mucus similar to recent flatworms or gastropods. This mucus impregnated, glued and sealed the sediment and thus protected the trail from erosion during the sedimentation event. Short pulses of locomotion (gliding over the bottom surface) alternated with long resting phases, during which more mucus was produced and an exact imprint was fixed of the ventral side in the sediment. This study of *Yorgia* and its locomotion trails directs our attention to some other segmented fossils preserved in positive relief, particularly those documented in the same bedding plane of the specimens just mentioned. These long segmented fossils, preserved in a very low

positive relief may well be candidates for the locomotion trails of another dickinsoniid taxon. This was recently confirmed by the discovery of long crawling trails produced by *Dickinsonia tenuis* and, *D. costata,* as well as by a bilaterian *Epibaion* (Dickinsoniidae) recently described by Ivantsov and Malakhovskaya (2002). The body size of *Epibaion* reaches 45 cm, and the documented trail length is over 2.5 meters. These giant trails are indicative of a well developed nervous system for the coordination of work done by a strong and complex musculature. The mode of feeding and the diet of these animals are not known yet, although some evidence suggests their selective microphagy: the numerous transverse grooves on their ventral side could have been lined with cilia transporting food particles to the medial grove and from there to the slit-like mouth.

Kimberella quadrata Glaessner and Wade, 1966 was originally described as a cubomedusa (see also Jenkins, 1984). New fossil material from the Vendian of the White Sea region (Figures 13, 14, 16) led to a new interpretation of *Kimberella* as a mollusk-like triploblastic animal with a high dorsal, non-mineralized shell (Fedonkin and Waggoner, 1997). In the course of recent excavations in the valley of the Solza River, Onega Peninsula, short trails have been found behind a few small (1 cm long) specimens of *Kimberella* (Figure 14). These animals were buried alive by a sand blast in the place of their habitation. While *Kimberella* was trying to crawl out of the sand cover, its dorsal shell was plunging in an arch-like cross section of the space above the animal, which is preserved in negative hyporelief (concave furrows on the sole of the sandstone bed). The sand layer was saturated with water, and it was thin enough to let these animals continue crawling under conditions of relatively low sedimentation rates. At Winter Coast on the White Sea more common are thick lenses of sandstone corresponding to fast, catastrophic sedimentation which preserved the body imprints of several individuals of *Kimberella* of various sizes, but no locomotion trace fossils because of instant burial under the heavy load of sediment (Grazhdankin and Ivantsov, 1996).

Scratch marks arranged in a fan-shape pattern represented another kind of ichnofossil of *Kimberella* (Figures 15, 16). These scratch marks, reported from the Neoproterozoic of South Australia (Glaessner and Wade, 1966), were originally interpreted as imprints of spicules. Jenkins (1992) reconstructed these scratch marks as tracks produced by Ediacaran arthropod-like organisms known from rare body fossils, that are, however, still to be described formally. Gehling (1991) documented fine details of the morphology and taphonomy of these fossils from his collection. Recently, these ichnofossils were interpreted as scratches made by the radula of a mollusk (Gehling *et al.,* 1996). Seilacher (personal communication, 1997) suggested that the trace fossils should be considered graz-
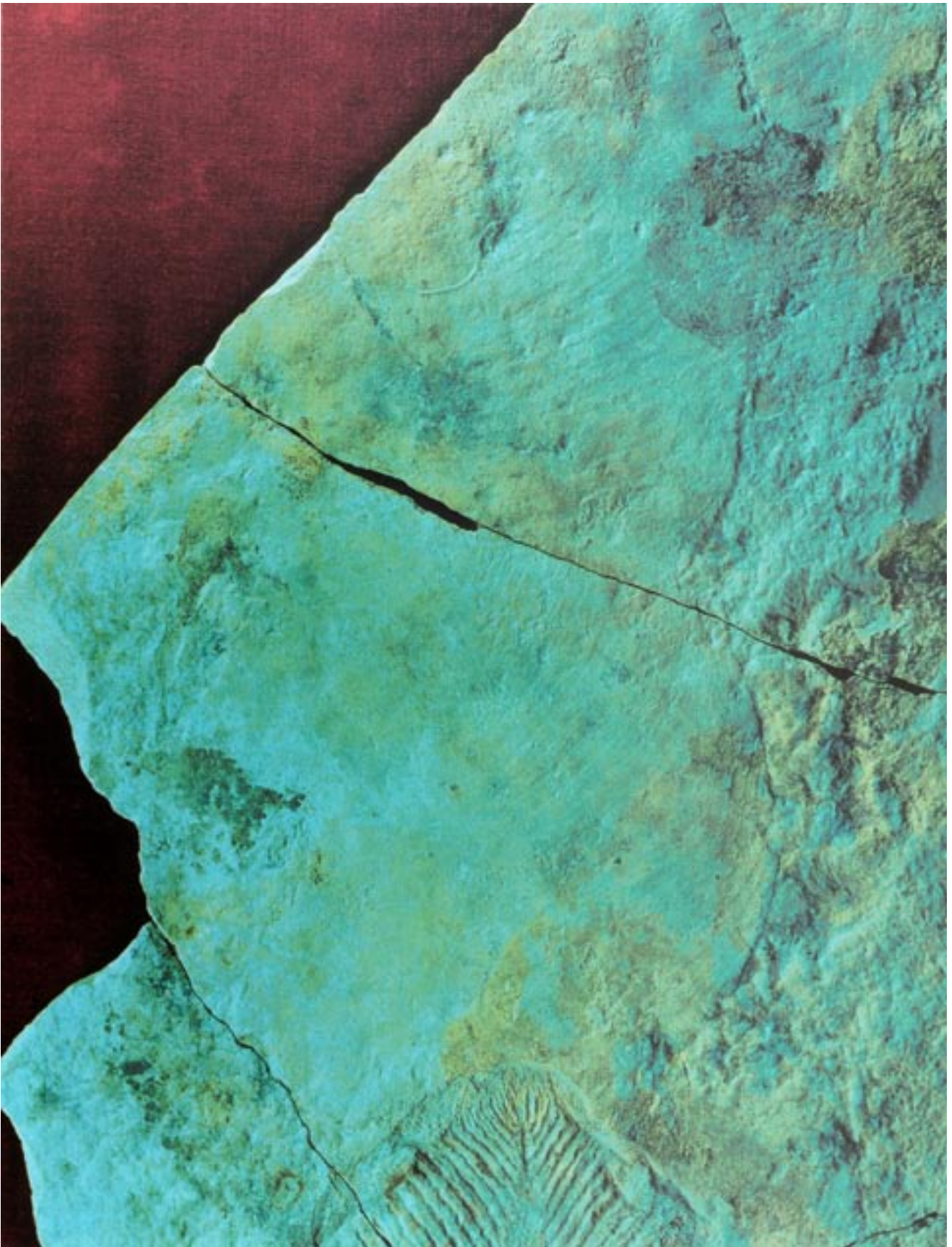
Figure 13. *Kimberella,* body fossil preserved in a negative relief on the undersurface of the Vendian sandstone. Locality and age as on Figure 8. Collection of the Paleontological Institute, Russian Academy of Sciences.

ing marks of *Kimberella.*

Scratch marks arranged in a fan-like pattern are a common element of fossil assemblages in the Vendian deposits of the White Sea region. These ichnofossils are preserved in positive relief on the sole of the accompanying bed (sandstone). The stratigraphic and taphonomic cooccurrence of the scratch marks and body fossils of *Kimberella* is well documented from the Upper Vendian of the White Sea. However, only recently, a few specimens have been collected with the body fossil and scratch marks preserved jointly (Figure 16). These feeding tracks may reflect the repeated functioning of the proboscis carrying two hook-like teeth at its end. Although this bilateral organ might be considered as a predecessor of a true radula, it worked differently: as the animal could stretch and

contract the proboscis, it was able to search a vast area of the bottom surface (and 1-2 mm below it) and to rake the food particles (meiofauna and/or algae) and ingest them. Comparison of the body size and the size of the feeding tracks shows that the length of the proboscis could be comparable to that of the body of *Kimberella.*

The discovery of locomotion and feeding trace fossils preserved together with the body fossils of their producers finally proves that the Ediacara-type organisms are metazo-ans, which puts the Vendian fossils into their phylogenetic and evolutionary context. The new data represented here leave no space for any non-metazoan interpretations (Seilacher, 1989; Zhuravlev, 1993; Retalack, 1994) of the Ediacara fossils.

Organic predecessor of mineralized skeletons

The Ediacara fauna of the Vendian is traditionally characterized as consisting of non-skeletal or soft-bodied animals. This is generally true insofar as this concerns heavy mineral skeletons like a mollusk shell or corallite. Most Ediacara-type fossils are preserved as casts and molds of soft-bodied invertebrates without traces of biomineralization (Glaessner, 1984; Fedonkin, 1987, 1992). The great majority of the Vendian animals did not possess large mineralized parts, like their recent counterparts do, such as in a few phyla of worms. Nevertheless, there is a growing body of evidence that some forms of Ediacara animals had rather rigid organic structures, both internal and external. These skeletal elements include a dorsal carapace, a shell, teeth-like organs, spicules, and sclerites.

Late Riphean tubular fossils *Pararenicola, Proto-arenicola* (Sun *et al.,* 1986) and *Parmia* (Gnilovskaya, 1998), as well as the Vendian *Saarina* (Gnilovskaya, 1996), *Calyptrina* (Sokolov, 1997) and related forms originally interpreted as annelidomorph metazoans, may well be compared to the theca-like exoskeleton of coelenterate polyps similar to the chitinous periderm tubes of the polyps of some recent coronate (Coronata, Scyphozoa) medusa (Jarms, 1991). One can attribute the slender conical and slightly calcified *Cloudina* (Grant, 1990) and poppy-like *Namacalathus* (Grotzinger *et al.,* 2000), and the recently discovered conulariid *Vendoconularia* (Ivantsov and Fedonkin, 2002), to the same group of external tubular skeletons. Another Ediacara species with a preserved exoskeleton is *Conomedusites,* which shows a hard part (theca) supporting a cup-like soft body with marginal tentacles

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⬅ **Figure 12.** Crawling trail of *Yorgia* with the body imprint preserved at the end of the trail. By contrast to the body fossil that is preserved in a deep concave relief (below on the photo), the trail is preserved in the low convex (positive) relief on the sole of the sandstone bed (x 0.35). Surface of the trail (though reflecting the ventral morphology of the body, see the regular arch-like ribs) is smooth is comparison with the irregular knobbly, and probably bioturbated, surface of the bottom on both sides of the trail. Age and locality as on Figure 8. Courtessy of A. Yu. Ivantsov. Collection of the Paleontological Institute. Russian Academy of Sciences.

Figure 14. *Kimberella,* imprints of three juvenile individuals and their trails of crawling under the layer of fine sand that buried the animals, segmented fossil of juvenile *Dickinsonia* is preserved on the same bedding plane (x 2). All fossils are preserved in negative relief on the sole of the sandstone bed. Summer Coast (Letnii Bereg) of the White Sea, Solza River, Ust-Pinega Formation, Upper Vendian. Courtesy of A. Yu. Ivantsov. Collection of the Paleontological Institute, Russian Academy of Sciences. White scale bar represents 1 cm.

(Glaessner, 1971). Long tubular *Sabellidites* that appears in the uppermost part of the Vendian (Sokolov, 1997) has a complex wall structure (Ivantsov, 1990) and may represent a higher grade of metazoan organization. Gehling and Rigby (1996) described imprints of spicules in an Ediacara sponge.

The bilateral metazoan *Andiva* (Fedonkin, 2002), described from the siliciclastic deposits of the Vendian deposits of the Winter Coast, White Sea region, Russia, shows bipolarity in its shield-like imprints. Its modes of deformation, growth pattern, and the regeneration marks, though rare, indicate that the animal had a convex dorsal carapace of a triploblastic invertebrate, but the anatomy of which is yet to be discovered. Its thin and flexible cara-

pace was composed of an organic, non-mineralized, and slowly degradeable substance. The fossil *Andiva* has much in common in its overall body plan, fine structure, and mode of preservation with the well-known Ediacara taxa *Ovatoscutum* and *Chondroplon* which Wade (1971) originally interpreted as the bilateral chitinous pneumatophores of the oldest Chondroplidae (Hydrozoa, Coelenterata). According to this interpretation, these two forms have to be considered skeletal remains rather than imprints of soft tissues, similar to the Early Devonian chondrophorine *Plectodiscus* (Yochelson *et al.,* 1983). However, in the light of new morphological and taphonomic data related to *Andiva,* the nature of *Ovatoscutum, Chondroplon,* and *Dickinsonia* (Figure 17) is reconsidered (Fedonkin, 2002).
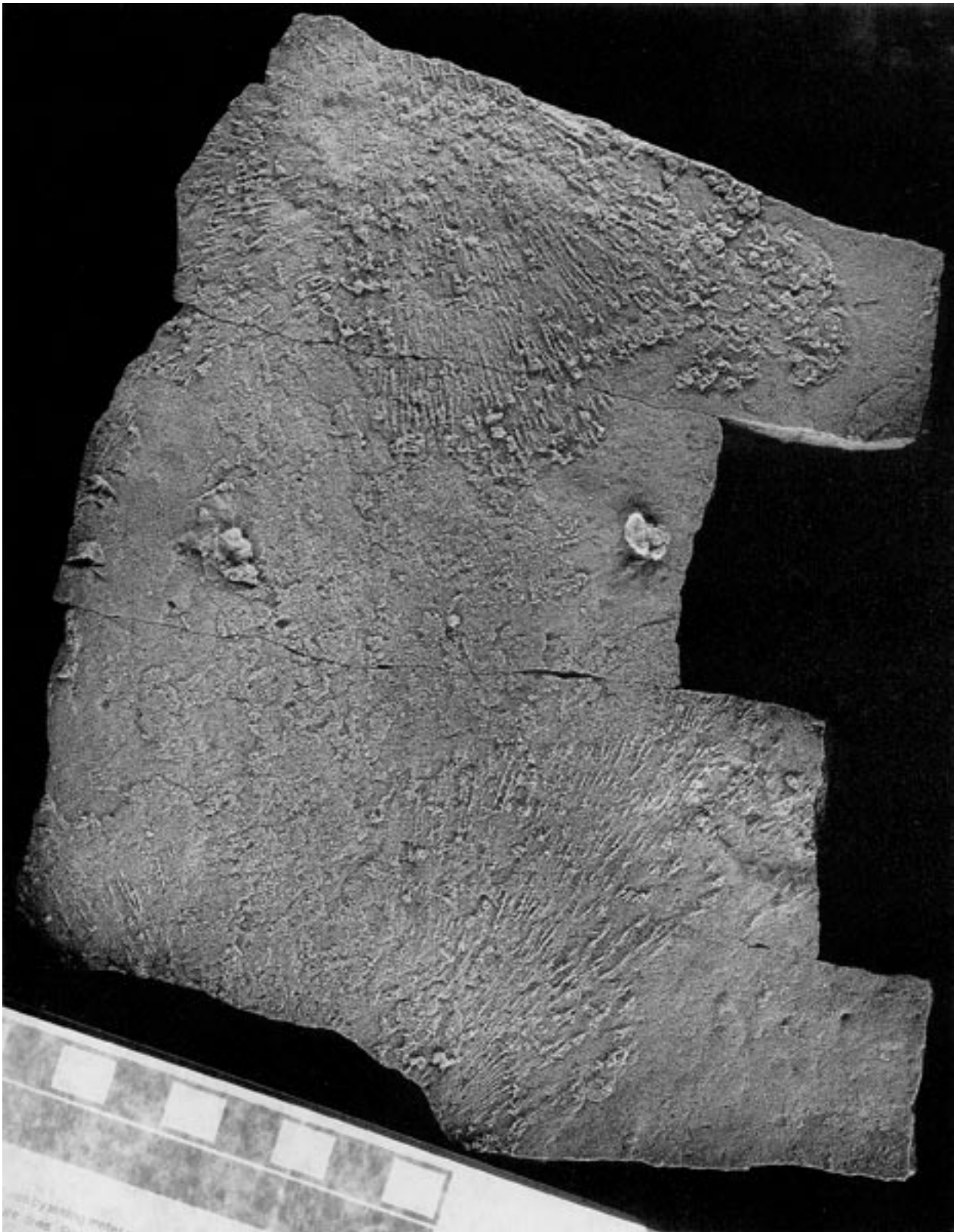
Figure 15. Enigmatic scratch marks on the undersurface of the Vendian sandstone. Locality and age as on Figure 8. Collection of the Paleontological Institute, Russian Academy of Sciences. White and dark scale bars represent 1 cm.

Figure 16. Rather common co-occurrence of the *Kimberella* body fossil preserved along with the grazing tracks of the animal. Locality and age as on Figure 14. Collection of the Paleontological Institute, Russian Academy of Sciences. Black scale bar represents 1 cm.

Figure 17. *Dickinsonia (D. lissa)* and *Archaeaspis* (on the right below) preserved in negative relief on the lower bedding plane of the sandstone (x 0.8). Locality and age as on Figure 8. Courtesy of A. Yu. Ivantsov. Collection of the Paleontological Institute, Russian Academy of Sciences.

These taxa form a clade of vagile epibenthic bilaterians with a thin and flexible dorsal carapace.

A rigid dorsal carapace inferred from the high relief of their fossils is also found in *Parvancorina, Vendomia,* and *Onega* as well as in some other arthropod-like forms (e. g., *"Archaeaspis",* Figure 17). The elongated and high dorsal shell made of flexible and rigid organic material is documented in the Vendian mollusk-like *Kimberella* (Fedonkin and Waggoner, 1997). In the absence of mineralized hard parts, a thin organic skeleton, such as a shell or carapace, is often preserved as an imprint comparable to that of the soft body. Both the carapace and soft body decomposed completely, leaving no primary substance, but it is possible to distinguish one from the another by comparing deformations of various parts of the fossil. In addition, the carapace always keeps its fine sculpture (ribs, suturae) intact even under severe deformation of the body.

The comb-like chitinous *Redkinia* from the Vendian of the Russian Platform (Sokolov, 1990) is an example of complex teeth-like structures that resemble scolecodonts or even parts of a sophisticated conodont apparatus. Fan-like sets of scratch marks (Figures 15, 16), associated with and attributed to the grazing activity of *Kimberella,* have been produced by its proboscis with two sharp teeth at its end. This hook-like tooth made deep, narrow cuts in the muddy sediment or in the bacterial film (Ivantsov and Fedonkin, 2001; Fedonkin, 2001).

Thus, there is strong evidence for the presence of skeleton and hard parts in the metazoans of the Vendian siliciclastic basins. However, there is no evidence of active biomineralization, or more in particular, of carbonate biomineralization, the most widespread in the Animal Kingdom. This absence of carbonate biomineralization could be explained by analogy to recent cold-water marine basins where carbonate skeletons are rather exceptional. If the organism does have carbonate biominerals, its skeleton is usually extremely thin and is very often protected from the external environment by layers of organic compounds (conchiolin etc.). Arnaud (1977) showed that shallow-water Antarctic calcareous organisms as a group are always extremely fragile. This group, including rare calcareous foraminifera, prosobranch gastropods, bivalves, scaphopods, and brachiopods, shows dwarfing, that may be reminiscent of the small shelly fossils (SSF) of the Late Vendian and Early Cambrian, though an essential part of those were sclerites of larger invertebrates.

The very slow growth of calcareous organisms and their small size is indicative of the high-energy cost of calcium biomineralization in cold-water environments. The problem of cold-water biochemistry of invertebrates is well beyond the aim of this paper, but it is suggested that calcium biomineralization for the metazoans of the Precambrian cold-water basins was as difficult as for recent ones.

Some recent calcareous groups may not even have been able to exist in the Vendian, and if they had, those forms should have been of very small size and have had extremely fragile skeletons subjected to quick dissolution in diagenetic and/or postgenetic sedimentary processes. We may therefore never be able to identify any remains of their mineralized skeletons, but we have now firm evidence that skeletonization in the Precambrian invertebrates took place well before the metazoan biomineralization.

From skeletonization to biomineralization

An organic skeleton preceded the rise of the mineralized skeleton in most of the existing animal phyla. The oldest known kinds of non-mineralized external skeletons in metazoans are peridermal tubes with very thin, chitin-like walls that might belong to solitary cnidarian-grade polyps (comparable to *Vendoconularia)*. As several authors showed, the present rise in atmospheric CO_2 levels causes significant changes in surface ocean pH and carbonate chemistry that slow down calcification in planktonic organisms, corals and coralline macroalgae (Riebesel *et al.,* 2000 and references therein). This may explain the absence of calcified eukaryotic organisms through the largest part of the Proterozoic marked by high CO_2 levels in the atmosphere. The low temperatures of the Neoproterozoic glacial periods inhibited biomineralization as well. The Vendian fossil record shows a large variety of organic hard parts (see above) in both cold and temperate climatic zones, and a weak biomineralization in carbonate basins.

The almost simultaneous development of phosphate, carbonate and silicate biomineralization in metazoans at the beginning of the Cambrian Period some 545 Ma suggests ecological causes for this phenomenon. Taking into account that the enzymes responsible for the biomineralization are temperature-sensitive, one can suppose that the sudden appearance of invertebrates with a mineralized skeleton was related to global warming or to the colonization of the warm carbonate basins by the early metazoans. Metazoan colonization of the warm carbonate basins and the low-paleolatitude environments might be assisted by the acquisition of endosymbiotic photosynthesizing algae that, in turn, promoted biomineralization through the supply of additional oxygen.

Another cause of the rapid diversification of biomineralized phyla at the beginning of the Cambrian may be related to the growing length of trophic chains, due to the rapidly increasing biodiversity. The concentration of some ions (in particular, Ca, Mg, P and Si) in their cells increased exponentially up the trophic chain. Being byproducts of detoxification, sclerites and spicules, hard mineralized shells and carapaces immediately became important in morphological evolution, in the growing biodiversity, and as well as a factor of intense selection under the growing pressure predators made.

Also taking into account the low solubility of oxygen in warm water, one can suppose that the metazoans could not colonize the warm carbonate basins until the oxygen level in the atmosphere rose significantly. The lower heat tolerance of metazoans compared with unicellular eukaryotes and bacteria proves to relate to a decrease in oxygen levels in their body fluids, reflecting an excessive oxygen demand at higher temperatures (Portner, 2001).

Conclusion: impact of early metazoans on global ecosystem

The early diversification of the Metazoa strongly influenced their evolutionary rates within the clades already present in marine communities. This implies an important role for ecology in fueling the Cambrian explosion extending across many existing kingdoms. Coincident with the Cambrian radiation of marine invertebrates, protistan microfossils doubled in diversity and turnover rates increased by one order of magnitude (Knoll, 1994). The appearance of new kinds of physiology and feeding habits (see below) greatly affecting both the biota and the environments accompanied the explosive radiations of invertebrates during the Vendian and Early Cambrian.

The bioturbation of the sediment resulted in its better aeration, which, in turn, allowed its progressive colonization underneath its surface by a broad variety of aerobic organisms. Both this aeration and increasing life activity within the sediment promoted the recycling of metabolites in the marine ecosystems. Yet, bioturbation disrupted the stability of the substrate necessary for the formation of bacterial mats and biogenic structures such as stromatolites.

The rise of biomineralization in the invertebrate phyla resulted in the vertical expansion of benthic animal life above the sediment/water interface, and in the creation (with other non-metazoan groups of eukaryotes) of reefs as a mechanically stable biotope and a very special ecosystem of considerable habitat diversity. The biomineralization of the metazoans formed new kinds of bioclastic deposits and hardgrounds.

The filtration of ocean water by actively filtering organisms had a great impact on the global ocean ecosystem. The feeding habits of recent crustaceans show that during 24 hours 1 milligram of living weight of the filterers can filter 360 milliliters of water (Vinberg, 1967). A volume of water equal to the world's ocean is filtered in half a year, and the largest part of the inhabited ocean (0-500 meter depth) is filtered in only 20 days (Bogorov, 1974). These data, together with more recent results (see Dankers, 1993), suggest that the rise of active suspension feeding or filtering in metazoans in the Vendian and Cambrian changed the

sediment and water habitats radically (Fedonkin, 1987, 1992; Logan *et al.,* 1995).

The rise of active filter-feeding organisms such as sponges, some coelenterates, brachiopods, mollusks, arthropods and echinoderms in the Early Cambrian made the ocean water clear and the photic zone deeper. It thus provided additional opportunities for photosynthesizing organisms to occupy lower levels of the water column and deeper benthic environments. The expansion of the photic zone could thus have resulted in better oxygenation of the pelagic and bottom habitats through the activity of chlorophyll-containing organisms. The removal of fine particles from the sea water and their assemblage into pellets must have increased the permeability of the sediment, leading to better aeration and colonization of the subsurface bottom environments and to more rapid oxidation of the buried organic carbon. Pellet transport increased the rate of food supply for the benthic communities.

The increasing length of trophic chains during the Vendian, and more particularly in the Cambrian, decreased the loss of the main biophile elements and of energy from the ecosystems because of more efficient biological recycling. That, in turn, could have led to the global oligotrophication of the ocean waters. This is consistent with the general decrease in buried organic carbon during the Early Cambrian (Knoll, 1992), as well as with the radiation of the Early Cambrian phytoplankton with external processes, spines, ornamentation and a very small cell size (Jankauskas, 1989). All these morphological peculiarities of the Early Cambrian phytoplankton can be interpreted as a means to develop a very large surface-volume ratio with its advantages in an oligotrophic environment (Fedonkin, 1987, 1996). This agrees with the fact that 70% of the biomass and 80% of the chlorophyll belongs to the picoplankton in the oligotrophic waters of the modern ocean. The oligotrophication of the Early Cambrian ocean made some of the feeding habits so common among the Vendian metazoans inefficient (for instance, passive trapping of the food particles by the sedentary suspension feeders). This may have caused the elimination of some Ediacara species from the shallow marine habitats in the Early Cambrian or even slightly earlier.

The colonization of the terrestrial environments could well have began with the rise of triploblastic animals capable of active locomotion over or in the sediment. The acquisition of a dorsal carapace promoted this by strengthening the body structure, making muscles work more efficiently and protecting the animals (especially its respiratory organs) from desiccation, and from the deadly ultraviolet light. Evidence of the oldest known grazing under subaerial conditions on tidal flats is the giant trail *Climactichnites* from the Late Cambrian siliciclastic deposits of North America (Yochelson and Fedonkin, 1993).

Recent discoveries of large carapace-bearing Vendian bilaterians able to crawl may extend the history of the colonization of the land far back into the late Proterozoic.

Acknowledgements

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