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# Early Eukaryotization of Life: Environmental Driving Forces of Evolution

Mikhail A. Fedonkin*

*Paleontological Institute, Russian Academy of Sciences, Moscow, Russia*

## ABSTRACT

The bottom-up approach (from the origin of life and on) provides deeper causal-historical understanding of the environmental factors that drive the metabolic evolution and the biological complexity growth. The biogenesis in the electron-rich conditions of the Hadean Earth was, probably, inevitable due to the energy flow as a powerful factor of dynamic ordering of the molecular structures. Hydrogen as a primary fuel of life and the metal catalysts, in particular, tungsten, iron and nickel, played a crucial role in the initiation of life. However the physical-chemical parameters of biosphere departed form the initial ones. Subsequent biological evolution was driven in a great degree by competition for access to hydrogen from the primary sources such as the degassing of the Earth interior or radiolysis, and from the simple hydrogen compounds via splitting the molecules of $CH_4$, $NH_3$, $H_2S$, and at last, $H_2O$ in the oxygenic photosynthesis. The archaic metabolic pathways in the cell were superimposed by the new metabolic modules that have been formed due to the interaction with new environmental factors. This process and compartmentalization of the ancient biochemistry in vesicles and organelles etc. were resulted in the growing complexity of the cell. Symbiogenesis based on syntrophy, mutual dependence on the waste products of each other, was a key factor of early eukaryotization of the cell and of the biodiversity growth. Multidisciplinary synthesis of data reveals the timing of the most important events in early biosphere such as the earliest activity of the methanogens, origins of oxygenic photosynthesis, eukaryotic cell, and multicellular animals. New types of physiology related to those evolutionary events strongly affected the global biogeochemical cycles, sedimentogenesis and climate.

**Keywords**: Origin of life, Hydrogen, Metal biocatalysts, Hadean, Archaean, Proterozoic, Prokaryotes, Eukaryotes, Metazoans

## INTRODUCTION

Modern science reveals that the non-equilibrium, the flow of the matter or energy, can be the source of the dynamically ordered structures [1, 2]. This concerns many aspects of nature including the origin and evolution of life. That is why instead of the traditional top-down (biochemical) approach focused on the origin of building blocks of the living cell it is worthwhile to develop the bottom-up (physical) approach to the problem of the initiation of energy flow common for all living organisms [3, 4]. Such universal mechanism of the cell life activity as the electron and proton transport, as the accumulation,

*e-mail: mfedon@paleo.ru

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storage and release of the energy seemed to be formed during the earliest, probably, pre-organic, stages of the biogenesis [5], and persisted through the billons of years in spite of the radical and irreversible change of the environment. The whole biological evolution can be interpreted in terms of protection and upgrade of the mechanisms of the energy metabolism in the factor space of the shifting physical and chemical parameters of biosphere. The origin of immense diversity and complexity of the living systems, improbable for the most of the Universe, not only was possible but apparently inevitable in the changing conditions of early Earth.

## CONDITIONS OF EARLY EARTH

The initial physical-chemical parameters of our planet and of the nearest cosmos over 4 Gyr ago were radically different from the modern ones. The Earth sciences, comparative planetology, and astrophysics shed some light to the factor space of the life's cradle. The Hadean Earth was characterised by the following features: strong radiogenic heat, which was over 10 times more intensive than at present (mostly due to the decay of the short-lived isotopes); high contribution of close Moon into the mechanical heating of the Earth interior; the oceans of lava and intensive volcanism afterwards; rapid formation of the metal core of the planet (during the first 100 Myr); early established magnetic field; full recycling of the primary earth crust; low relief of the surface [6–8]. In spite of the low luminosity of Sun (30% below present) a powerful green-house effect of the dense reducing atmosphere kept high temperature of the planet surface. In the absence of oxygen there was no protective ozone screen. Some authors postulate a global shallow ocean to be established soon after the surface temperature dropped down below the water boiling point. The ocean water was saturated by the ions of the heavy metals and volcanic gases. Those conditions shaped the cradle of life.

French biologist R. Dubois has left a wonderful metaphor: Life is animated water. The 4.4 Gyr old eroded detrital zircons in Western Australia [9, 10], the elevated $^{18}O/^{16}O$ values of some Hadean zircons [11], and the Ti-in-zircon thermometry [12] are indirect but robust evidence of water on the Hadean Earth. The oldest known banded iron-formations and associated pillow-structures of the basalt lava in some volcano-sedimentary successions in West Greenland and northern Quebec (Canada) directly indicate to the hydrosphere by about 3800 Ma [13]. The main sources of water were the degassing of the Earth interior and small comets [8, 14]. The apatite-hosted isotopically light graphitic inclusions from Akilia supracrustal metasediments (over 3830 Ma) in west Greenland were studied by using Raman confocal spectroscopy and interpreted as possible chemofossils of early life [15].

## ORIGIN OF LIFE

Most of the modern theories of the origin of life are oriented to the problem of the synthesis of the macromolecules that would serve as the predecessors for the biological organic compounds. Advanced direction of research based to a great degree on the laboratory experiment is represented by a group of the so called "mineral hypotheses" of the origin of life (see for example the papers by Bernal, Cairns-Smith, Ferris, Orgel, Wachtershauser, Ricardo, Smith, Hanczyc, Yushkin and many other authors). It is claimed that the minerals could play an important role in the biogenesis as the templates or the catalysts for synthesis of the macromolecules, as a factor of concentration and protection of organic molecules, as a mean of segregation of the molecules in respect of their symmetry (chirality) etc. The most elaborate group of the hypothesis describes the hydrothermal mounds on the ocean floor as a cradle of life's origin [16]. Alkaline fluids from such vents carried hydrogen, sulfide and ammonia as well as the heavy metals such as iron and nickel. Abundant iron and nickel sulfides precipitated around the alkaline vents in the Hadean ocean. The microscopic pores or bubbles in the crust of the sulfide minerals such as greigite provided the space for synthesis of simple organic molecules that formed more complex peptides. The peptides have coated the inside surfaces of the pores, thus representing the first step towards cellular autonomy. The critics of the mineral hypotheses (E.M. Galimov, 2007, personal communication) indicate that the mineral crystal is a relatively stable form in particular conditions and, thus, chemically passive, that at present the minerals do not play the role ascribed to them during the biogenesis, and that all organic molecules are being synthesized by the living cell itself. Additional difficulty is related to the time problem of DNA, protein and lipid synthesis: being tightly interdependent in the living cell how one could appear without the others? The concept of RNA World faces similar difficulty as well.

Similarity between the molecular structures of the sulfide mineral greigite ($Fe_5NiS_8$) and thiocubane

unit of the ferredoxine protein (or between the structure of pyrite and Fe-S clusters in the active centre of many enzymes) indicated by [17] can be considered as an evidence of the ancient hydrothermal environments for the origin of life. Basal position of the hyperthermophilic groups of Archaea and Bacteria on the molecular tree of life [18] is often interpreted in favor of the hydrothermal origin of life [19] though the later adaptation of some prokaryotic taxa to this harsh environment can not be ruled out [20]. Historical continuity of the evolution of the matter from the non-life to life [21] let us look for the formation of the energy aspect of life (as a system of electron transfer) on the prebiotic state of the matter in the environment of the Hadean Earth [5, 22]. From the physical point of view the initiation of life in or by the hydrothermal systems seems to be a plausible hypothesis because of the factors such as an electron-rich environment, electrochemical gradients, and abundance of metal ions and molecular hydrogen.

## BIOLOGICAL ROLE OF HYDROGEN

Speaking of energy, there are serious reasons to consider hydrogen as the primary fuel for early life. This, the most abundant chemical element in the Universe, was and still remains the major substrate of the microbial life and the very core of the energy metabolism [23]. Biological role of hydrogen is related to the domination of $H_2O$ in the mass of the living cell. The soft hydrogen bonds provide stability and versatility of the macromolecules. Various microbial enzymes perform the $H^+$ transfer. The $H^+$ gradients are used in the process of ATP generation. Negative ion of hydrogen $H^-$ is known as an energy currency of the cell (an equivalent of two electrons). $H_2$ as a key intermediate product of anaerobic metabolism makes a universal trophic (energy) connection between the microorganisms that live on different substrates, –very important ecosystem factor since the origin of life. The potential for the molecular hydrogen to serve as a reducing power and source of energy and to form the proton gradients as a means of energy storage should make a hydrogen availability a key factor of the earliest metabolic chemistry [24]. The proton gradients and electron transfer from the donor to acceptor is an essence of life if to consider it as a process of energy transformation. Most of the cell chemistry is in fact the electrochemistry, and the prokaryotic cells are particularly good in that. The dependence of all microbes on electrochemistry may indicate to the conditions of life's origin on early Earth [25]. Fundamental difference between prokaryotic and eukaryotic physiology from the standpoint of energy metabolism may indicate the chemoautotrophic origin of life [26]. Large part of the reactions in the prokaryotes involves molecular hydrogen and its simple volatile compounds as a source of energy. Molecular hydrogen could have been reacting with oxidants such as carbon dioxide and sulfur dioxide on early Earth. The hydrogen/carbon dioxide metabolism of the methane producers, as well as the hydrogen/sulfite metabolism in other prokaryotic groups are common for the microbial communities of the modern seafloor hydrothermal vents [27]. Is there any firm evidence of hydrogen in the early Earth atmosphere?

## HYDROGEN ON EARLY EARTH

The chondrite model of the Earth formation suggests that the early volcanic gases were enriched with $CH_4$ and $H_2$ [28]. This model is proved experimentally–the chondrite meteorites under the high temperature and pressure release predominantly $H_2$, $CH_4$ and $NH_3$ so these gases made a large part of the earliest atmosphere on Earth [29]. The first stages of the metal core growth took place under reduced conditions imposed by the pristine terrestrial materials and was accompanied by the emission of $CH_4$, $H_2$, $NH_3$ and minor $H_2O$ into the atmosphere [30]. Having in mind that a great bulk (95%) of the metal core was formed during the first 100 Myr after the accretion of the planet [31], the emission of hydrogen and its gaseous compounds from the indicated source could be very high though for a relatively short period of time. The concentration of $H_2$ in the prebiotic atmosphere could be 3–4 orders of magnitude higher than at present [24]. According to [32] hydrogen could make up to 30% of ancient atmosphere in spite of its fast escape. Concentration of hydrogen could be even greater in the fluids inside the Earth crust and in the sediments due to lower rate of migration.

The major sources of hydrogen on early Earth were: 1) the degassing of the mantle that released the neutral or slightly acidic fluids saturated with $H_2$, $CH_4$, $H_2S$, and $CO_2$; 2) the serpentinization, a low temperature reaction of the rocks, rich with olivine and pyroxene, with water; 3) photolysis of water by UV light; 4) radiolysis, radiation-induced dissociation of $H_2O$. All four sources should be more powerful at the dawn of life than at present. Today the serpentinization of the rocks at tempera-

ture (90–400°C) and high pH remains an important source of hydrogen. This widespread process produces magnetite, hydroxide, and serpentine minerals, and liberates molecular hydrogen, which is utilized by a variety of chemosynthetic organisms [33]. The magma-hosted systems at high temperature and low pH also contribute to the hydrogen budget.

Due to decline of all sources of hydrogen in time the biological evolution was to a great extent driven by the competition for access to hydrogen. In addition to $H_2$, life had to involve the hydrogen compounds such as $H_2S$, $CH_4$ $NH_3$ and at last, $H_2O$ in the oxygenic photosynthesis. The succession and degree of involvement of these simple molecules into early metabolic evolution is yet to be recovered but it could correlate to the energy required for breaking the chemical bonds of those molecules in the conditions of early Earth. If this supposition is correct then we may reconstruct the evolutionary succession of the hydrogen-related metabolic types as follows: methanogenesis, anaerobic methane oxidation, annamox reaction, and oxygenic photosynthesis. In the light of this hypothesis we can suppose that the by-products of the biochemical reactions related to the hydrogen uptake could be the factor of historical change in the atmosphere chemistry, in particular, the rising content of nitrogen and oxygen.

## METAL CATALYSTS: PRIMARY ROLE IN BIOGENESIS

Biochemical reactions that involve hydrogen are catalyzed by the hydrogenases, enzymes, which are predominantly the Fe-only and Fe-Ni proteins. The active sites that bind the metals are generally highly selective and highly conserved. The hydrogenases catalyze the simplest of chemical reactions that is the reversible reductive formation of hydrogen from protons and electrons ($2H^+ + 2e^- \leftrightarrow H_2$).

So it makes sense to pay attention to these enzymes as a source of information on the earliest stages of the biogenesis. Most of the hydrogenases are found in Archaea and Bacteria, but a few are present in Eukarya. Fe-hydrogenases are restricted to Bacteria and Eukarya while Ni-Fe-hydrogenases are present only in Archaea and Bacteria [34]. Are the Ni-Fe proteins a relic of the Hadean time?

Iron, nickel and some other metals could be abundant and bioavailable on early Earth. Having in mind that early Earth was heavily bombarded by the meteorites and that the iron meteorites may contain over 5–20% of nickel one can suggest that Fe and Ni played a key role in the origin of hydrogen metabolism, presumably the oldest one on Earth. According to A.P. Vinogradov [35] some metals demonstrate a stable decline vector for their concentration in the row ultrabasic rocks → basic rocks → intermediate rocks → granites. The ratio of the elemental content for some metals in ultrabasic rocks versus granites looks as follows: Fe 98500/27000; Ni 2000/8; Co 200/5; Cr 2000/25, and Mg 259000/5600. Thus, early volcanic rocks and fluids were rich in the heavy metals.

The metals play a fundamental role in the biocatalysis. Most of known enzymes contain the transition metal ions as a cofactor of their active sites. The metalloenzymes lose their catalytic activity when the metal ions are being removed from the protein molecule. These facts may indicate to the primary role of the metals in the origin of biocatalysis. Taxonomic distribution of the metalloproteins gives a hint on the biogenesis as well. For example, the tungsten enzymes are discovered so far in prokaryotes only. However, obligatory dependence on tungsten is documented merely for hyperthermophylic Archaea. Their basal position on the molecular tree of life points to the W-rich hydrothermal systems as a cradle of life. The relatively recent discovery of the important biological roles of nickel and tungsten [36–38] illustrates that the list of heavy-metal cofactors of active centers of enzymes may expand. Synthesis of data from geochemistry of early Earth and data on the taxonomic distribution of the metalloproteins looks fruitful for the reconstruction of the evolution of metabolism.

On early Earth iron was far more abundant and available than any other of the transition metals. This explains its almost universal role in the biochemistry of the living cells. Iron sulfur proteins occur in all organisms and perform diverse functions such as electron transfer and catalytic action; they maintain structural integrity [39] as well the biosensing of oxidative stress and redox-dependent gene regulation in prokaryotes and, potentially, eukaryotes [40]. Of a particular importance are the [2Fe–2S], [3Fe–4S] and [4Fe–4S] clusters in the active centers of the proteins that catalyze the redox reactions [41]. These multinuclear combinations of iron and sulphur atoms inside the protein molecule are the most universal cofactors of enzymes and are common for all living organisms. The Fe-proteins seem to be the oldest on Earth. Interesting is that [2Fe–2S] and [3Fe–4S] clusters take part in the catalysis of reaction involving the transfer of one electron while more complex [4Fe–4S] clusters catalyse

much wider diversity of the biochemical reactions. This difference may gain a geohistorical interpretation. But so far it seems certain that iron as the most abundant transition metal readily available in the conditions of early Earth could play a key role in the initiation of life. The primary environment of life could be related to the places of the metal sulphide precipitation. However, contrary to the "minerals hypotheses" of the biogenesis, for instance, one on the primary role of pyrite as a source of energy in the biogenesis [42] I would suggest the metal ions as primary catalysts and the initiators of life [22]. Interesting enough is the overlapping of the redox potential span of iron respiration and the redox potential of the biochemical reactions involving $H_2$, $H_2S$, $CH_4$ and $NH_4^+$ [43]. This coincidence may indicate to the primary role of iron in starting the hydrogen metabolism.

## BIOAVAILABILITY OF THE METALS: HISTORICAL TRENDS

The early ocean was saturated with such ions as $Fe^{2+}$, $Mn^{2+}$, $Mo^{6+}$, $V^{4+}$, $W^{6+}$ etc. [44]. These metal ions seemed to form the primary catalytic arsenal of life. However, the chemical and physical parameters of biosphere irreversibly departed from the initial conditions that influenced the abundance and bioavailability of the metals in biosphere. Rise of oxygenic photosynthesis by the end of Archaean aeon about 2.7 Ga ago caused dramatic change in the global geochemistry. First of all it concerned the transition metals, the major biocatalysts. But there were other processes that influenced abundance of the metals:

1) Gravitational migration of the heavier metals towards the center of the planet. Formation of about 90% of its Fe-Ni core occurred during the first 100 Myr after accretion of the planet [31];

2) Dramatic decrease in the metal supply from the space after 3.9 Gyr ago;

3) Volcanic activity decline was related to the radiogenic heat reduction and decreasing contribution of the Moon to the mechanical heating of the Earth, as a result of the Moon's retreat [8];

4) Change in chemical composition of igneous rocks from basic ones (such as ultramafic komatiites rich with Mg, Fe, and Ni) to the acidic ones;

5) Chemical weathering slowed down due to a decrease in the concentration of $CO_2$ and other volcanic gases in the ancient atmosphere, which lowered aggression of the meteoric waters and their effect as the weathering agents;

6) The chemical composition of the weathering objects (feeding provinces of the sedimentary basins) changed over time: from ultrabasic volcanic rocks to acidic ones and then to sedimentary rocks;

7) Growing area of the stable continents served as a trap for an enormous volume of various metals that were isolated from the biological recycling in the ocean;

8) Growing role of biota in the mobilization, transport and isolation of the metals;

9) Global temperature decline that reduced the rate of the chemical weathering and the transport of the nutrients to the ocean, and simultaneously increased the solubility of oxygen in the sea water.

The timing and dynamics of these processes are critical for understanding the early evolution of metabolism. The time of origin of Cyanobacteria, the major producers of the oxygen on early Earth, is debated. The Archaean fossil record is still very poor: less than 30 taxa are known from about 40 localities. First microfossils and stromatolites are 3.5–3.46 Gyr old, possible oldest cyanobacteria are 2.76–2.69 Gyr old, and certain cyanobacteria are identified by the end of Archaean 2.55–2.52 Ga (see review by [45]). Having in mind that Cyanobacteria occupy the terminal branch of the Bacteria Domain of the molecular phylogenetic tree, we can conclude that all basic types of the bacterial physiology were formed before 2.5 Gyr ago. Strong magnesium preference in the growth medium for cyanobacteria [3] may indicate that the environment of their origin was Mg-rich, partially due to the chemical composition of the oldest volcanic rocks such as ultramafic highly magnesial komatiite lava common for the Archaean aeon.

Synthesis of data from geology, paleontology, biochemistry and genomics reveals the timing and causes of the most important events of the biological evolution such as origins of the oxygenic photosynthesis, eukaryotic cell, and the multicellular animals [46]. Molecular clock models show the origin of Cyanobacteria about 2.4 Gyr ago [47]. Discovery of the cyanobacterail biomarkers in the deposits 2.7 Gyr old [48] may shift the origin date of the oxygenic photosynthesis back to the late Archaean if not earlier. However, the geochemical evidences such as the largest ore deposits of Mn and Fe in Early Proterozoic or sulfur isotope fractionation are indicative of active oxygenation of ocean water due to the photosynthesis of cyanobacteria and increasing circulation of cooling waters about 2.2 Gyr ago [49].

The growing uptake of larger volumes of $CO_2$ by

the photosynthesizing organisms and the oxygenation of biosphere caused the reduction of greenhouse effect of atmosphere, cooling climate, oxidation stress upon the archaic, primarily anaerobic kinds of biochemistry, geochemical impoverishment of habitats in respect of some transition metals and eukaryotization of the living systems. To appreciate the magnitude of the global change related to the rise of the oxygenic photosynthesis one can compare the modern global production of $C_{org}$ by hydrothermal biota of the ocean via chemosynthesis (about 200 million ton/year) versus 1000 000 million ton/year via oxygenic photosynthesis [50]. The rise of oxygenic photosynthesis increased global production of organic matter in 2–3 orders of magnitude. Weak role of the heterotrophs (in particular, the decomposers), low rate of the biological recycling of the organic matter, stratification of the ocean and its low oxygenation in the Early Proterozoic let the most of $C_{org}$ be buried in the sediment and thus be saved from oxidation. This was the major factor of the oxygenation of the biosphere.

All enzyme-mediated processes slow down when organism's temperature declines. Compensatory responses of the cell to the lowering temperature are the increase in the number of enzyme molecules, the change in the type of enzyme (s), and the modulation in the activity of pre-existing enzymes [51]. Cooling down of the global climate during the Proterozoic should influence evolution of enzymes. But probably more important is the increase in the solubility of oxygen in water due to the temperature decline and the resulting growth of the oxygenation stress upon the archaic parts of the metabolic pathways of the cell. More active circulation of the ocean during the glacial periods expanded the aerobic environment down to the ocean floor and the bottom sediments that was far more powerful factor for metabolic evolution. Fast oxygenation of atmosphere began in Early Proterozoic, after the major glaciation at 2.2 Ga. This conclusion is supported by a number of independent data such as time distribution of non-oxidized pyrite and some other oxygen sensitive minerals, red soils, sulfur isotope record etc. [52].

## TRANSITION METALS AS A KEY FACTOR OF EVOLUTION

Different solubility of some metal sulfides *versus* metal hydroxides [53] or metal sulfates in the modern ocean can give an idea of that dramatic change related to the oxygenation of the environments. The rise of free oxygen reduced availability of some metals (such as W, V, Ni, Fe), while others (such as Mo, Cu, Zn) became more readily available [44]. Hypothetical sequence of the incorporation of the metals into the enzymatic evolution in the early history of the biosphere [54, 55] should affect the metabolic evolution and domination of the particular physiology types. Replacement of the unavailable metals with those which were available seemed to be one of the major ways in early evolution of enzymes.

Change in availability of metals in Archaean-Proterozoic oceans was a driving force for the evolution of enzymes and rise of biological complexity of the cell due to:

1) Compartmentalization of internal environment in the cell (membranes, vesicles, organelles) that keeps the Archean biochemistry intact;

2) Mechanisms of scavenging, concentration and storage of the metals internally;

3) Integration of the complementary metabolic types in the cell;

4) Symbiosis of the prokaryotic cells mutually dependent on each others' waste products resulting in the rise of the eukaryotes;

5) Shift towards the heterotrophy because of need to acquire nutrients in chemically impoverished environment;

6) Increasing rates of the biological recycling of nutrients in the ecosystems.

Symbiogenetic theory (origin of a complex eukaryotic cell via symbiosis of the prokaryotic cells) has over 100 years of its history since the pioneering paper by K.S. Merezhkovsky in 1905 [56-58]. Modern approach to the symbiogenesis problem follows the principles of ecosystem ecology and syntrophy [59, 60]. The "hydrogen hypothesis" for the origin of eukaryotic cell [59] deserves further development in the aspect of earlier and multiple events of symbiogenesis, having in mind the central and almost universal role of hydrogen in the prokaryotic energy metabolism. Symbiogenetic origin of the eukaryotic cell was a long process of a functional optimization and structural miniaturization of the primary prokaryotic ecosystems in response to the irreversible change of the environmental parameters [54]. Compartmentalization of the reaction systems in the cell and the addition of new metabolic modules adapted to the changed conditions protected the valuable archaic biochemistry, and, simultaneously, led to the increased complexity [61]. The cascades of the metabolic reactions and the hierarchy of the metabolic modules in the cell may recapitulate the

biogenesis [3] and the succession of the geobiological events in early biosphere [55]. The succession and the timing of those events can be restored by the geological and paleobiological data, and more recently, by the methods of the molecular biology [62]. Eukaryotization of the biosphere resulted in taking the dominating role in the global primary production, increasing biodiversity and ecological expansion of the eukaryotic organisms, growing role of heterotrophy, rising complexity of the trophic chains, increasing rate of recycling of nutrients etc.

Deep ocean remained anoxic and sulfidic till the Late Neoproterozoic that limited the size of the habitats favorable for the eukaryotes [63]. Glaciations periods (between 740 and 545 Myr ago) promoted the "ventilation" of the ocean body and simultaneously influenced the distribution of some particular groups of the physiology. Late ocean chemistry gave physiological advantage to the green algae over the red algae that are dependent from different metal micronutrients [64]. The growing 87Sr/86Sr ratio in seawater during the Neoproterozoic and Cambrian periods indicates the greater weathering inputs to the oceans [65] which might be related to the increasing colonization of the land by the decomposers. The weathered clays have a high surface area facilitate increased burial of organic carbon in marine sediments, which in turn could lead to more oxygen in the atmosphere. Oxygenation stress could be the key factor of the eukaryotic radiation in Early Paleozoic, including the physiological and morphological innovations related to the colonization of the sediment and an active invasion into the carbonate basins.

The major biotic events of the Late Neoproterozoic were the decline of the stromatolites, the diversification of the eukaryotes, the change in the dominating primary producers in favour of eukaryotic plankton, growing heterotrophy, global expansion of the metazoans, acceleration of the evolutionary processes, in particular at the lower trophic levels. Diversification and ecological expansion of animals have dramatically intensified the recycling of the nutrients in the global ecosystem due to predation, biofiltration, pellet transport, and bioturbation [66]. Increasing eukaryotic biomineralization promoted the creation of the stable habitats like reefs and hard grounds that became important factors of the speciation. Still underappreciated is the fact that the heterotrophic eukaryotes with their aerobic respiration, in particular animals, became an enormous sink for the oxygen and thus an important regulating factor of the atmosphere chemistry.

Diversity and abundance of the stromatolites grow through the Archaean and particularly during the Proterozoic aeons and decline abruptly after 850 Ma [67], presumably, because of the following causes: the fall of carbonate saturation of the ocean, competition with the eukaryotic algae, cooling global climate and Neoproterozoic glacial periods, and at last, the metazoan grazing and bioturbation. The distribution of the metazoan taxa in the Vendian siliciclastic successions of the White Sea region demonstrates the dynamics of the biodiversity of the Ediacara-type invertebrates: the phase of initial radiation was followed by a period of stasis and then by a phase of decline of the overall diversity that may indicate the extinction of some taxa. Another clear trend is increasing proportion of the bilaterian taxa in the fossil assemblages [68]. In addition, one can observe growing diversity of the bioturbations including the oldest direct evidences of the metazoan grazing activity that are the scratch marks produced by the Vendian mollusk *Kimberella* [66, 69].

The origin of the metazoans and their global expansion might be related to the growing oxygenation of the ocean, especially during the Neoproterozoic glacial periods. Cold ocean was characterized by an active water circulation, effective supply of the photic zone with the nutrients, and high production of the phytoplankton. Due to better solubility of oxygen in cold water, the oxidation stress upon the anaerobic parts of the cellular biochemistry risen up. This negative factor could promote the multicellularity and colonization of the environments with the relatively low oxygenation level (such as the sediment of the ocean floor or the warm carbonate basins).

## CONCLUSION

Hydrogen as a primary fuel of life and the transition metals as initial catalysts retained their fundamental roles since the biogenesis till present. Historical changes of availability of hydrogen and of those metals in biosphere determined to a great degree the ways of the metabolic evolution, particularly, for the authotrophic part of the biota. The biological complexity growth was related to the additive mode of evolution. The oldest metabolic modules that have been evolved in the conditions of early Earth were overbuilt by the modules capable to cope with new environmental factors. Origin of the eukaryotic organisms imparted new vectors of evolution, in particularly, those that are related to multicellularity and heterotrophy. The Vendian (Edi-

acaran) period was a turning point on the way from the archaic world to the modern style biosphere. The oldest invertebrates have contributed a lot into this change via predation and related increase of the evolutionary innovations at the lower levels of the tropic pyramid. The suspension feeding (including active filtration) and the fast "pellet transport" of the non-digested material down to the sediment dramatically changed the ocean chemistry. Bioturbation of the sediments promoted the recycling of the nutrients. Biomineralization created new stable habitats such as reefs and hard grounds that provided a vast diversity of microenvironments, a key factor of speciation. Animals along with the other eukaryotes became an enormous and growing sink for oxygen. Since then the biota itself was becoming more and more powerful and dynamic factor of regulation of the global biogeochemical cycling, sedimentogenesis and climate of our planet, as well as a key factor of growing biodiversity.

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