

# On the Early Stages of the Evolution of the Geosphere and Biosphere

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**Abstract**—The conditions necessary for the existence of nucleic-protein life are as follows: the presence of liquid water, an atmosphere, and a magnetic field (all of which protect from meteorites, abrupt changes in temperature, and a flow of charged particles from space) and the availability of nutrients (macro- and microelements in the form of dissolved compounds). In the evolution of the geosphere, complex interference of irreversible processes (general cooling, gravitational differentiation of the Earth's interior, dissipation of hydrogen, etc.) with cyclic processes of varying natures and periodicities (from the endogenic cycles “from Pangea to Pangea” to Milankovitch cycles), these conditions have repeatedly changed; hence, in the coevolution of the geosphere and biosphere, the vector of irreversible evolution was determined by the geosphere. Only with the appearance of the ocean as a global system of homeostasis, which provided the maintenance and leveling of nutrient concentrations in the hydrosphere, and the conveyor of nutrients from the mantle, “the film of life” could begin its expansion from the source of the nutrients. Life itself is a system of homeostasis, but not due to the global size and a vast buffer capacity, but because of the high rate of reactions and presence of a program (genome) that allowed its development (ontogeny) independent from the outside environment. The early stages of the origin and evolution of the biosphere (from the RNA-world to the development of the prokaryotic ecosystems) were characterized by the domination of chemotrophic ecosystems. The geographical ranges of these ecosystems were directly or indirectly (through the atmosphere and hydrosphere) tied to the sources of nutrients in the geosphere, which were in turn connected to various sources of volcanic and geotectonic activity (geothermal waters, “black smokers” along the rift zones, etc.). This gave the biosphere consisting of chemotrophic ecosystems a mosaic appearance composed of separate local oases of life. The decrease of methane and accumulation of O<sub>2</sub> in the atmosphere in the geological evolution of the Earth caused the extinction of chemotrophic ecosystems and directed evolution of the biosphere toward autotrophy. Autotrophic photosynthesis gave the biosphere an energy source that was not connected to the geosphere, and for the first time allowed its liberation from the geosphere by developing its own vector of evolution. This vector resulted in the biosphere forming a continuous film of life on the planet by capturing the continents and occupying pelagic and abyssal zones, and the appearance of eukaryotes. The geosphere formed biogeochemical cycles in parallel to the geochemical ones, and comparable in the annual balances of participating matter.

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## INTRODUCTION

The geosphere is the habitat of life. Therefore, this paper will primarily focus on the role of the geosphere–biosphere relationships in the evolution of biodiversity from the appearance of the biosphere to the development of major macrotaxa with a note of firmly established facts and unresolved problems.

The conditions necessary for the existence of nucleic-protein life are as follows: the presence of liquid water, an atmosphere, and a magnetic field (all of which protect from meteorites, abrupt changes in temperature, and a flow of charged particles from space) and the availability of nutrients, i.e., macro- (O, C, H, N, Ca, P, S, K, Mg) and microelements (Fe, Ni, Mn, W,

Mo, V, Zn, Cu, Co, Se, Cr) in the form of dissolved compounds. Only after all these conditions were met could the evolution of Earth's biosphere begin (or continue after settlement from space) (Rozanov and Zavarzin, 1997; Dobretsov and Chumakov, 2001; Fedonkin, 2003).

The evolution of Earth for the first few hundred million years from the beginning of accretion continued as a gravitational differentiation of primary material inherited from the solar disk. As a result, the primary material began separating into the crust, enriched with light elements, and the core, to where heavy elements migrated. The internal core, formed by a hard nickel-iron alloy with some diamond content, is surrounded by an external liquid metal core. The presence of a liquid metal core resulted in the appearance of the magnetic field, i.e., the first line of defense for future life. The differentiation also facilitated the warming of the planet and the increased tectonic activity that increased the degassing of the planet's matter (Sorokhtin and Ushakov, 1991, 2002). Whether the main stage of the core formation finished ~2.7–2.5 Ga, as suggested by Sorokhtin and Ushakov (1991, 2002), or earlier is debatable, but as early as ~4.3–4.2 Ga the Earth had a thin, but fairly cool crust (from tens to a few hundred degrees C, compared to thousands degrees C in the core), which enabled the development of the hydrosphere at apparently the same level, 4.3–4.1 Ga (Joyce, 2002), judging from the earliest rounded grains of zircon (de Laeter and Trendall, 2002). The source of this water could be both the degassing of the Earth (Yaroshvskii, 1997), and the flow of small comets (>40 000 tons per day) (Kasting, 2003). The first traces of life (apparently prokaryotic) are recorded from 3.8–3.7 Ga old rocks (Shopf and Parker, 1987; Schidlowski, 1988), whereas the appearance of eukaryotes was not later than 1.9–1.7 Ga (this is also debatable, see Rozanov, 2005 and in this volume) (Rozanov and Fedonkin, 1994; Fedonkin, 2003; Hengeveld and Fedonkin, 2004). In any event, after the appearance of the hydrosphere between 4.2 and 3.8 Ga, archaeobacteria and eubacteria formed a sufficient biosphere (Joyce, 2002) and later there were two coevolving systems, biosphere and geosphere. The irreversibility of the evolution is determined by the geosphere, e.g., gradual cooling and oxidation of the planet.

However, is it possible that the coevolution of the biosphere and geosphere has deeper roots. According to the hypothesis of Parmon and Snytnikov (2004), planets, including the Earth, are formed in protoplanetary disks simultaneously with the abiogenic synthesis of simple organic compounds on particles of space dust, as catalysts, facilitated by ultraviolet radiation and the heat produced by the collisions of the particles. This organic matter, like glue, facilitated the aggregation of

small particles into larger ones, accelerating the process of the planet formation. Indeed, the discovery of new gas-dust disks around stars made astrophysicists reconsider the timing of planetogenesis. The accretion with the origin of planets may be fast in geological terms (less than 1 Myr) (Greaves, 2005). If the hypothesis of the role of organic matter in the origin of planets is correct, the biosphere<sup>1</sup> and geosphere interacted at all stages of the Earth's evolution.

Two aspects of the term “evolution” should be noted. The term “evolution” may be determined as the process of formation of the archetype *de novo* (archetype is a set of features and characters shared by a group of objects “individuals,” which distinguish this group (“species”<sup>2</sup>) from similar objects (Grigor'ev, 1956; Lyubishchev, 1971) and the process of the individual canalized (programmed) evolution of the previously formed archetype. In the first instance, biologists talk about phylogeny, in the second about ontogeny. The relationship between ontogeny and phylogeny was repeatedly discussed in geology, including publications in Russian, beginning from V.I. Vernadsky and E.S. Fedorov (Grigor'ev, 1955), but these discussions have never been accepted as scientific concepts. For instance, the introduction of the term “ontogeny of minerals” was suggested (equal to the genesis of mineral individuals and aggregates) and “phylogeny of minerals” (equal to the genesis of mineral species and associations of minerals) (Zhabin, 1979). Similarly, the ontogeny and phylogeny of ore deposits were recognized; phylogeny being described as geological processes embracing spatial and temporal intervals considerably (by one and more orders of magnitude) exceeding both the time of existence of an individual ore body and the spaces it occupied (Rundkvist, 1968a, 1968b; Rundkvist et al., 1971). Thus, these phylogenetic geological processes formed the environment in which the formation of individual ore bodies could proceed in a particular way. Canalized evolution of geological bodies similar to that in biology is evidently present, but its mechanism is fundamentally distinguished from cana-

<sup>1</sup> Certainly, strictly speaking, the term “biosphere” cannot be used for the prebiological evolution. Bernal (1967) suggested calling the prebiospheric environment, housing prebiological evolution the “equilibrisphere,” emphasizing that this was the place in the universe where the physicochemical environment enables the contact of liquid, solid and/or gaseous phases. Only in this sphere of contact, the exchange of matter could appear and proceed. The contact of heterogeneous-phase matter may appear in the pores of space dust or comet matter (e.g., during the short-term melting of the ice (Vlassov, 2005) in the microchannels of water and organic matter, as a result of the collisions of particles or of proximity to the central star) and occurs on Earth both between the layers of wet montmorillonite (see below) and, for instance, near the membranes of living cells, in the blood vessels, or lung alveoli.

<sup>2</sup> In that case a taxon of the next hierarchical level “genus” may be defined as a combination of shared features of several archetypes (Grigor'ev, 1956; Lyubishchev, 1971).

lized ontogeny in biology.<sup>3</sup> In biological individuals, canalized individual uncoiling of the archetype depends not only on an identical environment, but mostly on the program performed by the genome, a structure the only purpose of which is the storage and reproduction of information (Kolchanov et al., 2003). This mechanism of canalization from within, rather than outside, allowed biological objects to move along the path of independence from the environment (Schmalhausen, 1968), the result of which will be discussed below, to the development of the vector of evolution of the biosphere.

Do geological bodies have the equivalents of a genome? In crystals, a genome may be considered equivalent to the crystalline lattice (for discussion see Yushkin, 2005; Barskov, 2005; Kostetskii, 2005), but the analogy will be incomplete because the crystalline lattice, in contrast to the genome, not only the carrier of the program, but is also a functional structure. It is possible that in ore and magmatic bodies, the equivalent function is performed by the structure of melted rock (including structures of flow, which determine the resulting structure and properties of the rocks and minerals). The genome is only a carrier of the program defining the functional structures, including organelles, organs, and tissues.<sup>4</sup> The ability of the genome to be the carrier of the program is achieved in living systems due to the code. The code is here interpreted as any of the multidimensional contexts in the polymer, containing information, the importance of which for the performance of a certain function is not determined directly but by certain rules of correspondence. For instance, the coding of the polymer chain in a gene, the correspondence between the codon and amino acid is determined by the adapter rRNA, the mutation in the anticodon of which allows the change in correspondence (Trifonov, 1997; Ratner, 2002). The presence of the rules of correspondence allows the code to become distanced from

the functions in the course of the evolution. For instance, the same function, interruption of translation in genomes of prokaryotes may be performed using different codes: triplet code—three terminal codons, super-triplet codes, various attenuators and riboswitches (Tucker and Breaker, 2005; Winkler, 2005). In eukaryotes the regulation is even more complex. The distancing from the functional structure allows the system using the code to relatively easily change functions, which makes them extremely flexible in the evolutionary sense. For instance, the same transcriptional factor TTF-1 takes part in the regulation of the work of the thyroid and the epithelium of lung alveoli (Lazzaro et al., 1991). An even more complex change in function is observed in the transcriptional factors (central regulators of embryogenesis) (Richardson et al., 1997; Richardson and Keuck, 2002; Raff and Sly, 2002; Gunbin et al., 2004a, 2004b). The entire functional mechanism (interactions between the receptor and ligand, signal transmission, etc.) remains virtually unchanged. Only locations of the sites of connection of transcriptional factors in the regulatory regions of genomes are changed (i.e., recoding takes place).

In most nonbiological systems, even those capable of evolution, all structures are functional (the structure of magma determines the properties of the magmatic body; the structure of the crystalline lattice determines the properties of a crystal, etc.). The first step toward the appearance of the code in the evolution was possibly connected to the development of feedback between two such functional structures, because the feedback determines the rules of correspondence. After the development of feedback one of the structure (the future phenotype) acquires the ability to specialize on the reception of signals from the environment, whereas the other (the future genotype) acquires the ability to produce programmed answers to these signals by changes of the former structure.

Minerals formed by aluminosilicate clays are one of the simplest and widespread nonbiological systems of this type. Structurally they are formed by numerous regularly arranged layers stabilized (as in spirals of DNA and RNA) by stacking interactions. The layers can grow only on the margins, washed by nutritious solution. Distances and interaction forces between the layers may vary depending on the moisture and ionic strength of the solution, which is among other factors, determined in particular by the concentration of ions of metallic elements of biogenic origin (Cairns-Smith, 2005). In the flow system composed of many microchannels with walls overgrown by aluminosilicates, the most long-lived (“adapted”) will be the stacks of layers, the size and structure of those is such that microchannels are not filled (in the opposite case the flow of the nourishing solution will discontinue) and are not washed away with the solution. Ideally the stacks of layers should themselves form the flow of solution optimal for their growth (Cairns-Smith, 2005). The ion-exchange properties will be a “phenotype” of such a

<sup>3</sup> Canalized evolution in biology and geology, despite the fundamental difference in the mechanisms, leads to the performance of the general patterns of evolution, such as the geogenetic principle (parallel evolution on different scales), equivalent to the biogenetic principle (ontogeny briefly repeats phylogeny), and Baer's rule of the embryonic similarity (Rundkvist, 1965, 1968a; Isokh, 1978). At the same time, the higher level of independence of evolution of biological objects from the environment does not allow the biological analogues of the consequences of the geogenetic principle (ontogeny contains predetermination of the future phylogeny to be implemented) (Rundkvist, 1968a). Biology is restricted to the less strict rule of homologous series (Vavilov, 1967) and Cope's Law (on non-specialized ancestors) (Schmalhausen, 1968).

<sup>4</sup> On the other hand, the crystalline structure of such minerals as apatite or opal during the early evolution of life could be used (and sometimes is used until now) as a memory matrix for the formation of biological structures. Biological structures can also induce the formation of specific minerals. This will be discussed in greater details in the papers from Section 2 (Matrix-free synthesis of organic on the biomineral matrices and biomineralogy) see e.g., Barskov, 2005; Alekseeva et al., 2005; Ushatinskaya et al., 2005.

system, which will receive the signal from the environment (saturation of the nourishing solution), a while the stacking structure of the layers retained due to the stacking interaction will be a “genotype.” These two characters are connected by the rules of interactions, allowing their interpretation as a code. Thus, the earliest code was probably nonlinear (sequence of monomers in the polymer), but conforming (stacking of monomers). Apart from stacking interactions in the spirals of DNA and RNA, prions are the relicts of this code in modern organisms (Zhouravleva et al., 2005).

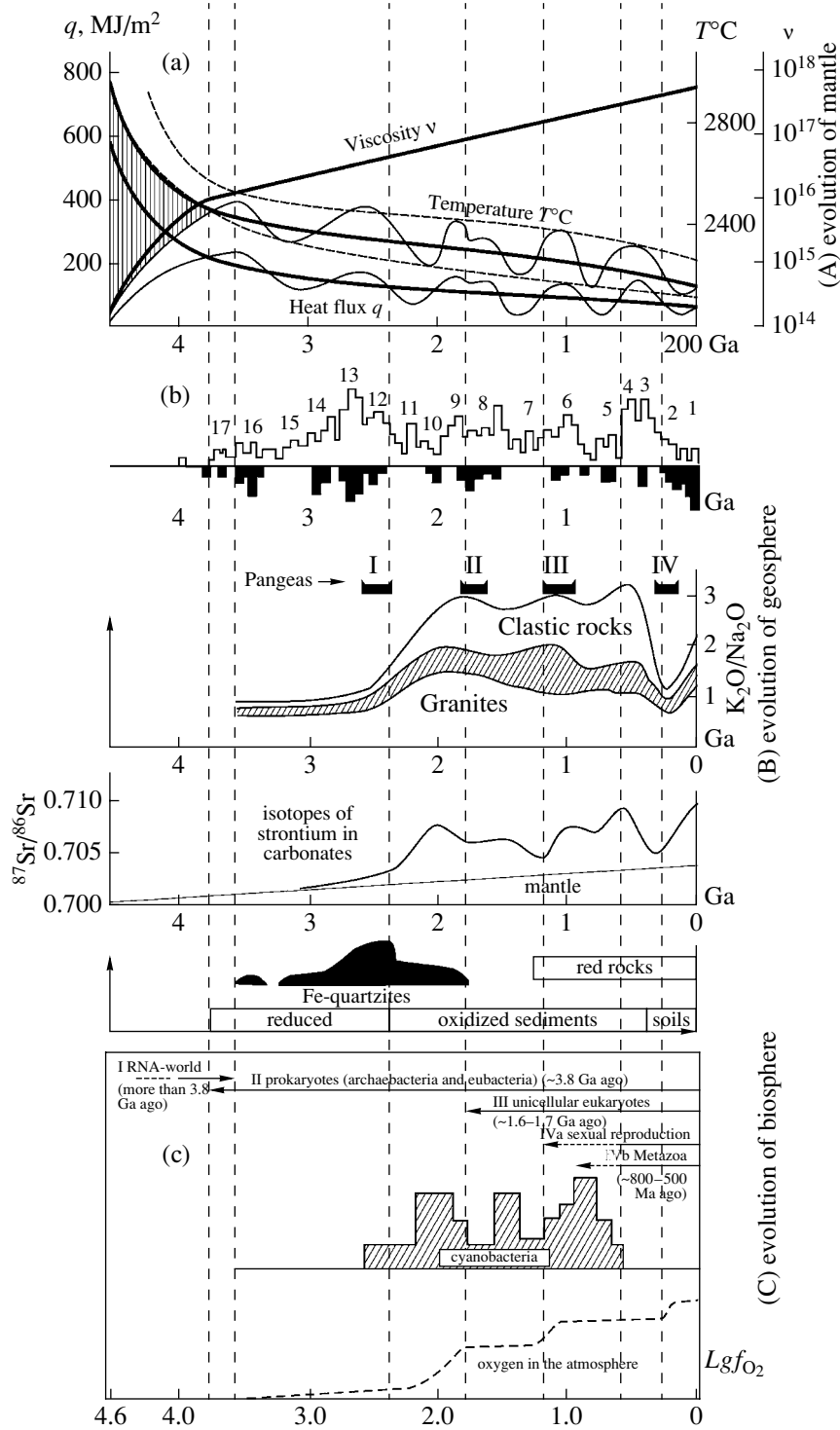
Recently, mainly because of the studies of the coordinator of the Subprogram of the Second Russian Program “Origin and Evolution of the Biosphere,” the recognized Russian microbiologist G.A. Zavarzin and his colleagues, study of the problem of relationships between the mechanisms of canalization of evolution from inside and outside, in particular the correspondence of geosphere and cenotic factors, in the evolution of the biosphere has been resumed. While agreeing with the statement of Zavarzin (1999, 2001, 2003a, 2003b, 2005, and in this volume), that to maintain its existence all new systems should conform already existing systems, and in this sense the evolution of newly appearing species is restricted by geo- and biogeochemical cycles, appeared in the early course of evolution, we cannot completely concur with some conclusions (e.g., the constancy of productivity and biomass of the biosphere throughout its existence) (see also Kanygin, 2001, 2004, 2005).

Thus, how could the evolution of the geosphere determine the vector of the evolution of life? Gravitational differentiation led to the separation of elements. Heavier elements permanently moved from the “liquid water” zone to the zone of the core, while the light elements were concentrated in the crust, from where hydrogen permanently dissipated into space, whereas other elements were mainly concentrated in the blocks of the continental crust. The dissipation of hydrogen into the space, intensive at early stages of the “hot Earth,” was a very important factor in the oxidation of the Earth’s surface long before the appearance of the photosynthetic oxidation (Dobretsov and Kovalenko, 1995; Dobretsov and Chumakov 2001; Dobretsov, 2004). The continental rocks dated 4.0–3.9 Ga are found in several places of the Earth’s surface. According to Khain (2003), by the beginning of the Late Archean (3.0 Ga) many stable plates of the continental crust were formed, but these plates were very small. They were separated by numerous basins with the oceanic crust.

By the end of the Archean these small plates were joined into continents and later, possibly ~2.5 Ga for the first time a single supercontinent Pangea was formed. More precise, modern reconstructions register several Pangeas dated 2.5, 1.8, 1.1, and 0.35 Ga. The further evolution of the Earth’s surface could follow a cyclic pattern “from Pangea to Pangea” with a period of

~700 Myr, which were complicated with the interference of shorter periods ca. 210 and 30 Myr. As the evolution of the planet progressed, the zones of volcanism changed their geographic locations, changed in intensity and in properties. For instance, volcanism of the subduction type in the quiet periods was replaced by volcanism of plume type connected with hot flows extending from the core of the planet (Dobretsov et al., 2001). This multiordered endogenic cyclicality was complicated by short-term variations of space origin, such as Milankovitch cycles, with the periods 0.1 Myr and less, related to the variation of the position of the Earth on its solar orbit. The existence of long periods of cyclicality of space origin is possible, but this is debated (Astafieva-Urbaitis and Yasamanov, 1993). In general, the scenario of the Earth’s evolution is now interpreted as a complex interference of irreversible processes (such as general cooling and differentiation and dissipation of hydrogen) with cyclic processes of various natures and periodicity (Dobretsov et al., 2001) (Fig. 1).

It is possible to maintain migrating nutrients in the zone of liquid water and smoothen sharp changes in their concentration caused by this interference by a relatively closed circulation of chemical reactions with a large buffer volume with a continuous exchange of these elements. The world’s ocean became such a system, representing a still-working powerful thermostat and stabilizer of the chemical composition of the atmosphere and upper layers of the crust. The access of the nutrients to the hydrosphere is limited by the rate of weathering of the continental rocks, intensity of volcanism, returning some elements, which migrated to the core and solubility of biogenic compounds in the water, which depends from its temperature and pH. Oceanic volcanism, connected either to spreading (birth of new crust) around the systems of mid-oceanic ridges, or to subduction (submergence) of the crust in the island arcs, is approximately ten times as significant as land volcanism (Lisitsyn, 1980, 2001), whereas its environment is fundamentally different from that of land volcanism. The medium of underwater volcanism is seawater (a natural electrolyte) at temperatures near the sea bottom up to 400°C and pressure of 300–500 atmospheres. The latest studies revealed that almost all water taking part in the high temperature “water–rock” reaction is not juvenile (originating from the mantle), but is seawater. This water, coming through the system of fractures, is heated by the heated rocks to a temperature of 300–400°C and sharply changes its properties becoming a high-temperature, fluid, usually acidic solution (pH up to 2–3) with peroxide oxidation–reduction reaction. This happens when Mg settles (precipitates) from the seawater, addition of  $S_2$  or  $SO_4^{2-}$  and several other elements. The fluid leaches large group of elements from basalts (including Fe, Mn, Zn, and Cu), which are transferred into the solution (Lisitsyn et al., 1990). The total influx of the seawater to the hydrothermal system of the oceans is ~5.7 thousand tons per second, i.e., all water



**Fig. 1.** Evolution of the mantle (A), geosphere (B), and biosphere (C): (A) Calculated mean temperatures of the heat flow and viscosity of the mantle after Tajika and Matsui, 1992 (thick lines), and variations for temperature and heat flow after Dobretsov and Kovalenko, 1995 (thin lines), reflecting processes of the general cooling of the Earth (independent of the original state) and slowing down of the convection as the viscosity grows. Periodic variations of the first order for temperature and heat flow are comparable with max and min of granites (see Fig. 1B). (B) Major figures in the evolution of the geosphere: upper row shows histograms of the age distribution of granites (shown white) and mantle rocks (shown black) in the Earth's crust; figures represent the major endogenic cycles reflected in max of granites; middle row shows the ratio  $\text{K}_2\text{O}/\text{Na}_2\text{O}$  in granites, compared with the appearance of the super-continent Pangea I, II, III, IV; lower row shows variations of the strontium isotope content in carbonate sediments (Condie, 1983 modified after Semikhatov, 1993) against the background of the distribution of iron quartzites, red-bed rocks, reduced and oxidized sediments in the crust, and also of soils (Zavarzin, 2003b). (C) Evolution of biosphere: upper row—major stages of the evolution of the biosphere (Dobretsov, 2005); middle row—geochronological distribution of cyanobacteria (Zavarzin, 2001); lower row—evolution of oxygen in the atmosphere (Rozaov, 2001).

of the world's oceans passes through the hydrothermal vents in a geologically instant time (in 3–8 Myr) (Lisitsyn, 1993). The work of the hydrothermal chemical reactor in combination with precipitation of carbonates and other compounds from the weathered products, washed out by the rivers provides constancy of the chemical composition of the oceanic water. Thus, the world's oceans represent one of the most important systems of exchange between main spheres of the Earth. It is known that the composition of the seawater has not changed for at least one billion years (some data give an estimate of two billion years). This indicates the ancient age of this exchange. This also suggests an ancient age for deep-water oceans, and that the interpretation of early oceans as shallow water (Timofeev et al., 1983) is incorrect. In the shallow waters, because of insufficient pressure, this system cannot work, whereas fresh water cannot become a fluid. In addition, there is also direct evidence of the ancient age of the hydrothermal fields (Maslennikov, 1999).

Only such an exchange system, in combination with a huge, but constant volume of seawater (because the average depth of the world's oceans has not much changed), with a gigantic buffer volume and a global system of currents that appeared because of the latitudinal heating of the water of a single basin, could smoothen abrupt change in the concentrations of nutrients caused by the evolution of volcanism of the Earth and formation of the continents, changing the pattern of nutrient influx in the hydrosphere.

By leveling the concentrations of the nutrients throughout the Earth and having provided their supply to the hydrosphere, straight from the mantle, the world's oceans allowed the "film of life" to spread all over the globe. Until it had appeared the biosphere was apparently a mosaic concentrating near the sources of nutrients (hydrothermal vents, upwelling, outflow cones, etc.).

Could the world's oceans provide the origin of the living organisms? There is no agreement here. From the point of view of biochemistry, life is a relatively closed cycle of chemical reactions, which maintain the stability of concentrations (homeostasis) of the passing flow of elements, but existing in the phase-separated space using enzymes (organic or metal-organic catalysts), which increase the intensity of this circulation by an order of magnitude compared to geochemical processes.

The world's oceans with their vast water mass and leveled chemical composition could provide a suitable surface of the contact between the solid, liquid, and gaseous phases (Bernal's (1967) equilibrisphere) only near the bottom and in the zone of the melting oceanic ice. Could life have arisen near the bottom at very high temperatures and pressure near the mid-oceanic ridges, for instance, in the zones of hydrogen sulfide-methane flows, as in modern black smokers, around which peculiarly highly productive biocenoses are formed? Ores

obtained at latitude 14° N, from the bottom of the Atlantic contained high contents of alcohols, paraffins, olefins, terpenes, waxes, and other organic compounds not related to the lipids of bacterial origin, i.e. apparently synthesized abiogenically (Lein et al., 1998). However, no high concentrations of oligomers of nucleic acid was found there. Experiments show that neither high temperature (Vlassov, 2005) nor chemistry of the seawater (Monnard et al., 2002) facilitate their abiogenic synthesis. Therefore, it is as likely that life originated near the shore of some epicontinental sea, or lake (Zhilina and Zavarzin, 2000; Zavarzin, 2001), or, according to V.V. Vlassov (pers. comm.), in the zones of melting ice in the microcavities within the ice, which provided low temperature favorable for synthesis in the "RNA World."

To summarize the above discussion, it can be said that the geochemical postulates of Vernadsky (1987) about the expansion of the biosphere toward the intensity and closure of the nutrient cycles follow from the facts of the planet's evolution (gravitational differentiation of the Earth's interior and multiorder cyclic fluctuations in the history of the crust. Having appeared as a means of holding the "running away" nutrient elements, the life began its expansion of the planet, as soon as the world's oceans appeared, as a mechanism of global distribution of elements in the upper layers of the crust. Vernadsky's statement of the expansion of the spectrum of nutrient elements follows from the non-closed bio- and geochemical cycles, because of which some elements is buried and become hard to access. The hypothetical sequence of the involvement of minerals in the evolution of enzymes is supported by geological and, to a lesser extent, microbiological data (Fig. 2). In particular, it is known that Mo, V, and W are found in increased concentrations in the old black (bituminous) shale, and some Archean gneiss contain scapolite and scheelite  $\text{CaWO}_4$  (Dobretsov and Chumakov, 2001). In paraffins, vanadium acts as a migrant in the reducing environment (Kontorovich, pers. comm.).

It is not necessary for the entire mass of the nutrient elements to be involved in a biogeochemical cycle. The small amount of elements involved in a cycle is compensated for by the rates impossible for geological cycles. For instance, the mass of organic carbon of the biosphere ( $C_{\text{org}}$ ) is exceeded by three orders of magnitude by the mass of  $C_{\text{org}}$  of the kerogen (dead fossil organic matter left out from the circulation of the biosphere and transformed into oil, bitumen, and others) (Fig. 3) (Zavarzin, 2003b). In other words, a considerable amount of the organic matter is lost by the biosphere and cannot be fully returned.<sup>5</sup> The main mass of

<sup>5</sup> This is another multisided problem of how the matter is taken out of the biosphere circulation, which amount is taken out, and what are the ways of bringing it back into circulation. It is possible that the presence of dead ends is a necessary consequence of the evolutionary mechanism of the closure of the biosphere (Degermendzhi and Gubanov, pers. comm.).

carbon on the Earth is contained in carbonates (CaCO<sub>3</sub>, CaMg(CO<sub>3</sub>)<sub>2</sub>, etc.); hence, the carbon cycle is first of all a carbonate cycle. Carbonates contain 0.6 × 10<sup>23</sup> g of carbon and only 0.5 × 10<sup>18</sup> g of C<sub>org</sub> in the biosphere.

Eventually almost all carbon is accumulated as carbonate sediment (Tajika and Matsui, 1992; Dobretsov and Kovalenko, 1995). Nevertheless, because of the greater rate of the biogeochemical cycle, the annual balance of C<sub>org</sub> is comparable with that in the carbonate cycle, although absolute figures are different by five orders of magnitude (Fig. 3).

What organic molecules were the bases for the first biocatalysts? It is possible that 4.0–3.8 Ga (Joyce, 2002) these were the RNA molecules. The discovery of catalytic RNA-ribozymes and aptamers (RNA, connecting like proteins various ligands), and discovery of the key role of RNA in translation and management of main processes in the cell support this hypothesis (Gilbert, 1986; Spirin, 2002; 2005). Selection experiments showed that by the selection of the pool of random RNA-polymers it is possible to obtain RNA molecules with a spectrum of enzymatic activity, which completely closed the cycle of self-reproduction of the RNA-matrix from the synthesis of nucleotides (Unrau and Bartel, 1998) to matrix synthesis of RNA over RNA (Johnston et al., 2001). Natural abiogenic synthesis of RNA is possible in montmorillonite (Ertem, 2004), one of the most widespread clay minerals, in the shape of molecular colonies (Chetverina and Chetverin, 1993). With periodic drying and moistening of montmorillonite in such colonies, the natural selection of macromolecules of RNA, which could appear by the spontaneous non-enzyme recombination of short oligomers, is possible. (Chetverin, 1999; Spirin, 2005). Apparently, such molecular colonies of RNA were the first coevolutionary acellular ensembles, in which different molecules of RNA played different functions. The evolution of such RNA-ensembles was accelerated because they were not separated from the environment and remote colonies could, for instance, exchange molecules through the air (Chetverina and Chetverin, 1993).

How did the cell membrane appear? The cell membrane created the cell by separating the functional ensembles of molecules from the environment and providing high local concentrations of reagents and some other processes without which the existence of cells is not possible (e.g., Polevoi, 1985; Ratner et al., 1985; Cavalier-Smith, 2001; Martin and Russell, 2003). Experiments showed the possibility of the existence of RNA molecules that are efficiently connected to phospholipid layers organizing those in vesicles and regulating the penetrability of the membranes in these vesicles, which is necessary for their stability. In other words, the appearance of a membrane in the RNA-ensemble could happen as early as the stage of the “RNA world,” which possibly existed on the Earth ~3.8–4 Ga (Spirin, 2005). Perhaps, these events took

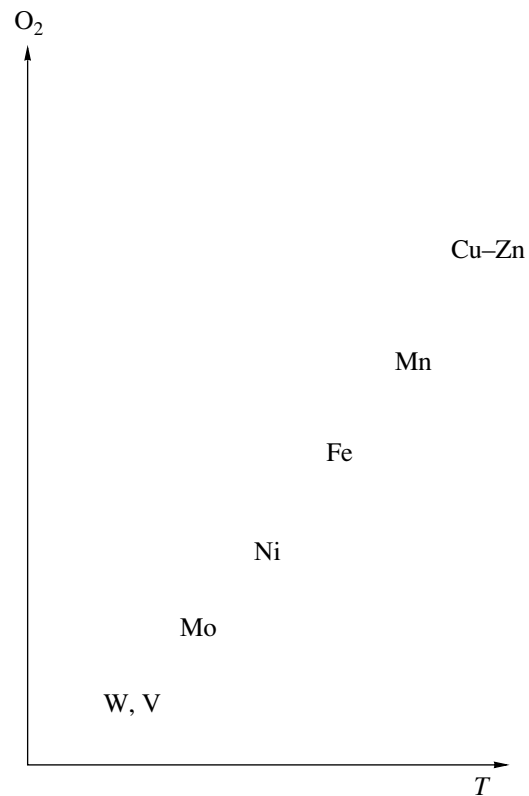


Fig. 2. Hypothetical sequence of the metals involved in the evolution of enzymes in the early evolution of the biosphere (modified after Fedonkin, 2003).

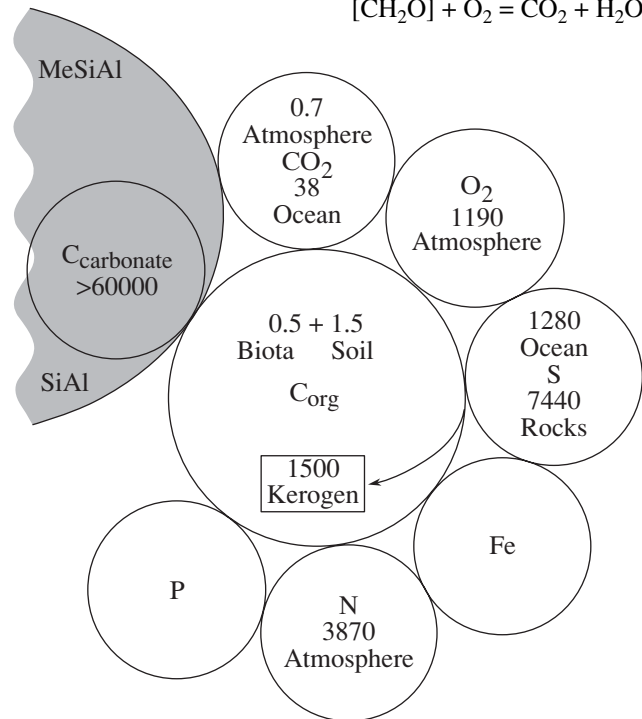
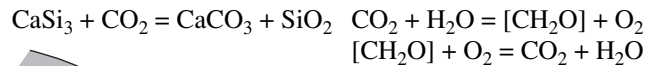
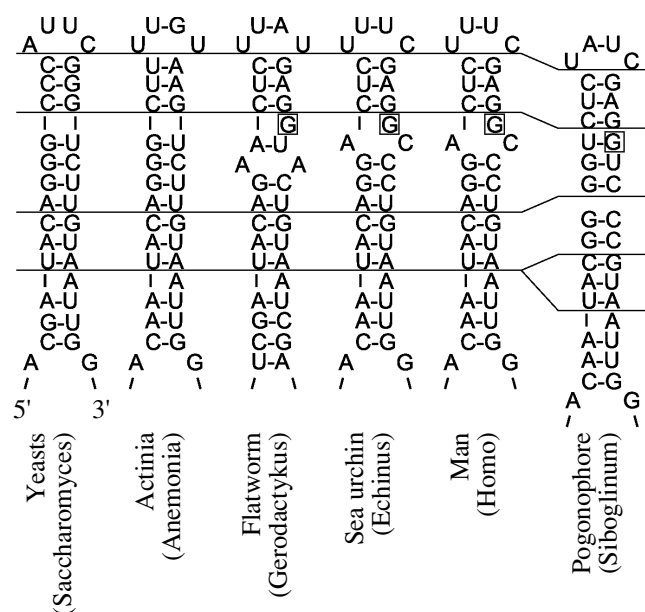


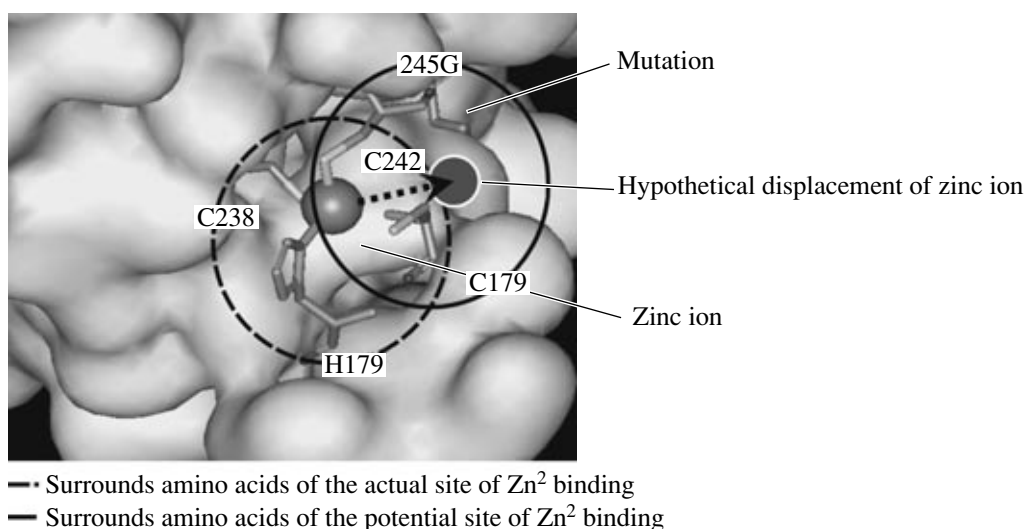
Fig. 3. Correspondence of the geochemical carbonate cycle (purple) and biogeochemical cycles. All values in 10<sup>18</sup> g (after Zavarzin, 2001, modified).



**Fig. 4.** Weak sensitivity of RNA-structures to mutations on the example of spiral 17 (functional element of pRNA). The ancestral spiral; of 13 nucleotide pairs is widespread in algae, higher plants, flagellates, fungi, sponges, and coelenterates. In the ancestors of the bilaterally symmetrical animals die to a mutation, one nucleotide (in a red frame) lost its pair. Nevertheless, the structure of the spiral was distorted so little that this did not influence the synthesis of protein. Green lines show homologous zones (after Aleshin and Petrov, 2003, modified).

places in the microcavities of ice (Vlassov, 2005). It is possible that the descendants of such “ribocytes” still exist, and they can be found when objects of nanometric size are studied (this is discussed in the paper by A.S. Spirin).

Why 3.8–3.6 Ga was the RNA world replaced by the protein-nucleic world that gave rise to prokaryotes (Joyce, 2002)? Possibly, this is also connected to the change in availability of some metals in the course of the evolution of the crust. Loops connected by dozens and even hundreds complementary pairs of nucleotides are the working structures holding ions of metals in the ribozymes. For such a loop to replace one metal by another, fixation of numerous mutations is necessary. This event has a very low probability. Therefore, RNA-structures are not much sensitive to mutations (Fig. 4) (Aleshin and Petrov, 2003). In contrast, in protein enzymes one or two mutations are sufficient to replace one or two amino acid radicals, enabling the enzyme to work with a different metal. In the laboratory of N.A. Kolchanov the group led by V.A. Ivanisenko showed that such mutations are likely events (Ivanisenko et al., 2005) (Fig. 5). In other words, proteins are more efficient in tracing the changes in the environment, whereas ribozymes are much more conservative than proteins. Therefore, it is evolutionary beneficial to use proteins as enzymes, and to perform conservative processes of replication of the genome by ribozyme, the fact that is observed in present life. NA viruses and viroids using the already made protein enzymes of their hosts and ribosome and regulatory RNA of modern organisms are possible remains of the previously existed RNA world. The evolutionary combination of proteins and self-reproducing RNA-ensembles could have been facilitated by that montmorillonite and aluminosilicate derivatives are also capable of the sorption of ions of metallic nutrient elements (see above) and primitive organic compounds (amino acids, peptides, sugars). By absorbing organic molecules, clay minerals can organize them into complex regular molecular ensembles, which being surrounded by enclosed inter-



**Fig. 5.** High sensitivity of protein structures to mutations could accelerate the evolution of the protein-nucleic life compared to RNA-life. A single mutation is sufficient for the appearance of the new site of the tying of the zinc ion (Gly245→Cys) in the functional center of protein (Ivanisenko et al., 2005).

layer water can interact with metal ions (possible ancestors of active centers of enzymes). Finally, being a product of weathering of the erupted rocks, clay minerals may be enriched by phosphorus and sulfur (Smith, 2005; Ferris, 2005; Hazen, 2005). Thus, key chemical compounds of life (nucleic acid, amino acids, metallic and nonmetallic nutrient elements, and water) are spatially combined, which allows the proposal of a clay-siliceous cradle of life.

Could the “RNA world” have begun its evolution in open space? Chemists suggest such a possibility (Goldanskii and Kuz'min, 1989; Nisbet and Sleep, 2001; Parmon and Snytnikov, 2004). It appears to us, irrespectively of where life exists, even if it was transported in space, it could be carried only as short oligonucleotides, which can be frozen into ice of any origin (methane, water) (Anders, 1989; Chyba and McDonald, 1995) and, after reaching a favorable environment, they each time begin the cycle anew, i.e., synthesis on montmorillonite, appearance of RNA, DNA, and protein, appearance of the cell. Therefore, it is not so important where everything began, but it is important that if space transmission is possible, it is not as fully formed living organisms (e.g., bacteria), but as oligonucleotides frozen in ice.

From the beginning of the world of prokaryotes it is possible to discuss the appearance of the Earth's biosphere and beginning of the evolution of biodiversity. The modern biosphere includes representatives of all three macrotaxa (eubacteria and archaeobacteria, both belonging to prokaryotes, and eukaryotes, having a nucleus). While their organization at the cellular and molecular-genetic level is reasonably studied, their origin, phylogeny, evolutionary mechanism, and the roles of each macrotaxon in the functioning and evolution of the biosphere provide more questions than answers.

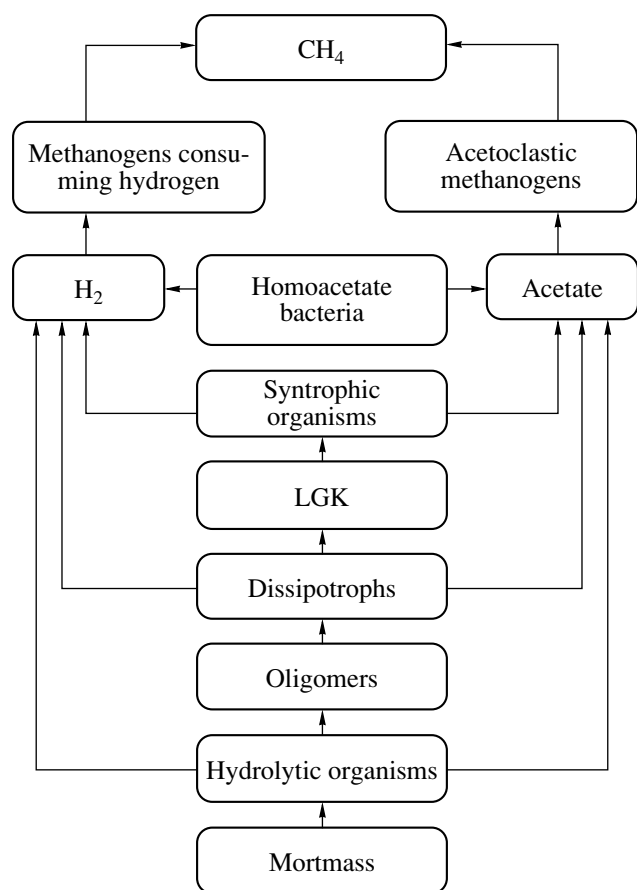
For instance, in the opinion of many experts, e.g., G.A. Zavarzin, the biota always consisted mainly of prokaryotes, whereas all other organisms are only later additions (Sergeev et al., 1996; Zavarzin, 2003a). It is known that 53% of the microbial biomass of the ocean is concentrated in the layer of water up to 100 m deep, 19% in the layer up to 200 m deep, and 28% on the bottom and near bottom (Zavarzin, 2003b). This agrees with the data by the coleader of Subprogram 1 of the Program “Biosphere Origin and Evolution,” M.E. Vinogradov, according to which the oceanic water layer from 0 to 200 m contains  $9.24 \times 10^6$  tons of carbon; of this  $5.28 \times 10^6$  tons are bacteria and phytoplankton (Vinogradov et al., 2000; Vinogradov, 2004). According to Zavarzin (2003b), at least one-third of the entire mass of the biota ( $0.15 \times 10^{18}$  g of  $0.5 \times 10^{18}$  g) is composed of the microbial biomass of the ocean. We do not have similar information for the land, but apparently the microbial biomass of the land is comparable with that of plants. Thus, various estimations of the microbial biomass suggest that it constitutes from 50 to 90% of the total Earth's biomass. It

includes not only land bacteria, symbiotic bacteria of eukaryotes, soil bacteria, nannoplankton, and other bacteria of the ocean, but also prokaryotes of such extreme biotopes as hydrothermal vents, salty and soda lakes, and even nuclear reactors (Dobretsov, 2004).

The next problem is the origin of the major macrotaxa. There are two opposite opinions. According to the first, archaeobacteria is a dead-end branch of evolution originating from eubacteria and inhabiting extreme biotopes with high temperature, acidity, etc. (Cavalier-Smith, 2002a). According to another opinion, archaeobacteria are the earliest organisms and they should be placed at the base of the tree of life (Vorobyeva, 2004). The latter hypothesis is supported by the molecular phylogeny of structures of the ribosomal RNA (Yusupov et al., 2001; Caetano-Anolles, 2002). From the point of view of simple logic archaeobacteria should have been the first to appear, because only these organisms could survive in the extreme conditions of the early Earth: high temperatures, acidic atmosphere, reducing environment, i.e., the environment where archaeobacteria live today.

The hypothesis of the different principles or even of the absence of the evolution in the world of prokaryotes (Zavarzin, 2005, Shestakov, 2005) is particularly interesting. To support biogeochemical cycles and preventing otherwise inevitable migration of nutrients, prokaryotes need energy. Interestingly, molecular phylogeny showed that all known energetic enzyme systems appeared very early in the evolution, from a common ancestor (Castresana and Moreira, 1999), which was almost a miracle. Therefore, it is most likely that there was not a common ancestor represented by an organism. This common ancestor was a biogeocenosis (Zavarzin, 1999, 2001), which was perhaps formed as early as the stage of the “RNA World” where elements formed in enzyme systems in different parts of this biogeocenosis were present in different taxa due to the horizontal transmission widespread in prokaryotes (Shestakov, 2005). A major enzyme system could have developed in combination. This scenario is supported by the surprising fact that among modern prokaryotes mixed communities of archaeobacteria and eubacteria show the highest diversity and balance of biogeochemical cycles, and, hence, stability. Phylogenetically distant groups are often connected by the closest syntrophic relationships. For instance, archaeobacteria-methanogens interact with fermentative bacteria, hydrolytic clostridia interact with spirochetes-dissipothrops, and spirochetes interact with sulfate reducing proteobacteria (Zavarzin, 2001). Figure 6 shows an example of the trophic scheme of one possible model of the primary biosphere of the Earth (methanogenic community of prokaryotes, composed of archaeobacteria and eubacteria) (Zhilina and Zavarzin, 2000; Zavarzin, 2003b).

Although morphologically prokaryotes are relatively simple, their systematics is based on biogeochemical diversity. However, schemes recon-



**Fig. 6.** Trophic scheme of the modern methanogenic community of prokaryotes, possible equivalent of the primary biosphere of the Earth (after Zavarzin, 2001).

structured based on this principle poorly correspond to one another and do not make up entire phylogenetic trees characteristic of eukaryotes (Zavarzin, 1999, 2001, 2003a, 2003b; Zehr et al., 2003), which suggests either lateral transmission or polyphyletic, latticed evolution of bacteria. The horizontal transfer allows rapid changes in the metabolism in an organism in a changing environment, but the general genetic pool of the prokaryotic community does not change (genes are simply redistributed between the cells). Possibly because of this the evolution of a bacterial communities proceeds slowly (Sergeev et al., 1996; Rozanov and Zavarzin, 1997), while an individual organism in this community may change very quickly. It should be said though that in this situation the very term “species of bacterium” is a subject of many debates. Thus, the world of prokaryotes evolves completely differently to the world of metazoans in which we live and to which we are accustomed. One of the central problems of the evolution of the biosphere is when and how photosynthesis first appeared. In the course of the Earth’s evolution, chemotrophic prokaryotes had to migrate after their energy sources, whereas autotrophs are not tied to a particular place. Eventually autotrophs, primarily

cyanobacteria, played the main part in the development of the global biosphere by first of all subordinating the biogeochemical cycle of carbon and providing the development of the oxidizing environment, which prepared geochemical conditions (e.g., appearance of the ozone screen) for the occupation of continents and further expansion of life. With the appearance of photosynthesis, the biosphere by utilizing the source of energy independent from the geosphere began escaping from the dictate of its evolution by forming its own evolutionary vectors.

Some scientists believe that oxygenic photosynthesis could have appeared even earlier than 3.5–3.3 Ga, while some of its enzyme systems are even older. It should be said that the calculation using the molecular clock that uses only isolated key genes of the photosynthetic process does not provide any conclusion. These genes could exist long before the development of the entire photosynthetic apparatus, performing completely different functions, e.g., synthesis of pigments protecting from the solar radiation or from active oxygen of abiogenic origin (photolysis of water). It is necessary to perform the molecular-phylogenetic calculation simultaneously for many key genes of photosynthesis, taking into account their coadaptive evolution. Thus, so far there are more questions than answers in this field, but it is completely clear that only integration of biological, geological, and paleontological evidence may bring more answers.

One of the possible compromise solutions is the existence of the so-called Archean “island” biosphere, where methane environment equivalent to modern black smokers alternated with more oxidative “islands,” produced by the oxygenic photosynthetic organisms (cyanobacteria, or other, extinct, organisms, similar, e.g., to green bacteria). Modern cyanobacteria build bacterial mats composed of several functional layers: (1) the upper layers of autotrophic cyanobacteria and aerobic heterotrophs utilizing oxygen and dead organic matter settled on the mat’s surface; (2) a lining of non-oxygenic photosynthetic organisms (purple bacteria utilizing light quanta not used by cyanobacteria and facultative heterotrophic aerobes; (3) aphotic zone of anaerobes utilizing everything that had remained, i.e., zone of the development of anaerobes is at the bottom, while cyanobacteria live and develop in standard oxygenic environment (Rozanov and Zavarzin, 1997). But this scheme may also be turned upside down! Then in the Archean sulfate reducers and methanotrophs will be contacting the reducing environment, whereas the layer with cyanobacteria will be placed below, and oxygen that they produce is consumed by aerobes at the same place virtually without leaving the layer.

The first maximum of cyanobacterial biological productivity ~2 Ga coincided with the transition from the reduced to oxidized sedimentary rocks, i.e., the process of oxidation in the Earth’s atmosphere already existed by that time, and cyanobacteria developed in a reason-

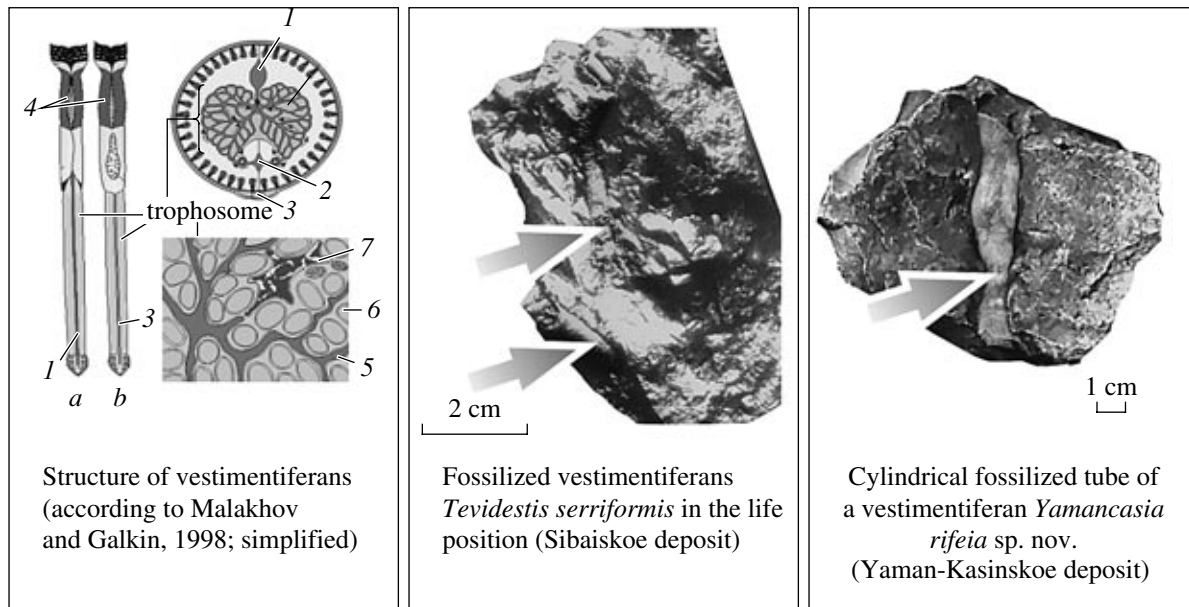


Fig. 7. Morphology of modern Vestimentifera and tubes of their fossil counterparts (age ca. 400 Ma).

ably oxidized world (Zavarzin, 2001, 2003a). Where did oxygen come from if the atmosphere had previously contained mainly methane, possibly hydrogen, with admixtures of ammonium and hydrogen sulfide, while life on Earth was represented mainly by methanotrophic bacteria? In the geosphere, this event corresponds to the deposition of vast ores of  $\text{Fe}_3\text{O}_4$ , indicated by unique mass accumulation of iron quartzite deposits with magnetite (Fig. 1). In the prokaryotic biosphere, the iron cycle was replaced by the sulfur cycle. These cycles are incompatible because in the process of sulfate reduction all free iron becomes bound up in sulfides. Prior to that, sulfur was apparently concentrated in the crust, e.g., as sulfides in Precambrian volcanites. As a result of the interactions of two events, both in the geosphere and the biosphere, a huge iron reservoir that had previously bound oxygen disappeared from the Earth, resulting in the accumulation of oxygen in the atmosphere (Fig. 1). As a result of oxidation, the atmosphere was, figuratively speaking, turned upside down: anaerobic pockets in places with abundant organic compounds replaced oxygen pockets in the cyanobacterial mats (Zavarzin, 2001, 2003a).

Mineral remains of cyanobacterial mats (stromatolites) compose huge series of rocks suggesting that the biomass of the prokaryotic world was at least one or two orders of magnitude greater than the biomass of the modern biosphere. This conclusion follows from the calculation of the mass of the stromatolite buildups in relation to the length of time required for their accumulation. Thus, the biomass of the biosphere changed in the Earth's history by at least one order of magnitude (Zakrutkin, 1993; Rozanov and Zavarzin, 1997). The same conclusion can be derived from data on the maxima

of oil accumulation, the first of which was ~1.5–1.3 Ga (Vyshemirskii, 1995).

The ecosystems formed in the reducing atmosphere should have escaped from the poisoning effect of oxygen in a refugium (first the depths of the ocean, which until the Ordovician was anoxic, and later other refugia, where they have survived to this day. No equivalents to such ecosystems are known in modern world, but Zavarzin (2001) suggested that the methanotrophic bacterial communities of modern swamps are possibly similar. Perhaps this is true for shallow-water ecosystems, but in the ocean, the biota composed of archaeobacteria and methanotrophs was most likely the equivalent of the biota inhabiting the zone of black smokers. The black smokers are formed in rift zones, where hot gases of ~+300–400°C penetrate through crevices in the oceanic crust and heat the water. This water contains high levels of dissolved hydrogen sulfide, methane, and metal sulfides. Rich communities of life arising and existing at black smokers are based on bacterial chemosynthesis. The biomass of these ecosystems is one or two orders of magnitude greater than the biomass of the ecosystem on the surface. Hence, chemosynthesis dominated the early evolution of the Earth, and was more efficient than photosynthesis by two orders of magnitude. It can be suggested that when prokaryotes consumed all available methane and hydrogen sulfide they turned to photosynthesis to survive (Dobretsov, 2004).

In this connection, it is necessary to mention Vestimentifera (Fig. 7), the most characteristic inhabitants of such biocenoses. The most mysterious thing about them is their structure. Their wormlike body is enclosed in a protein-chitinous tube produced by specific glands. The main part of the body is occupied by a trophosome,

Comparative characterization of the genomes of prokaryotes and eukaryotes (after Carroll, 2001; Taft and Mattick, 2003, modified)

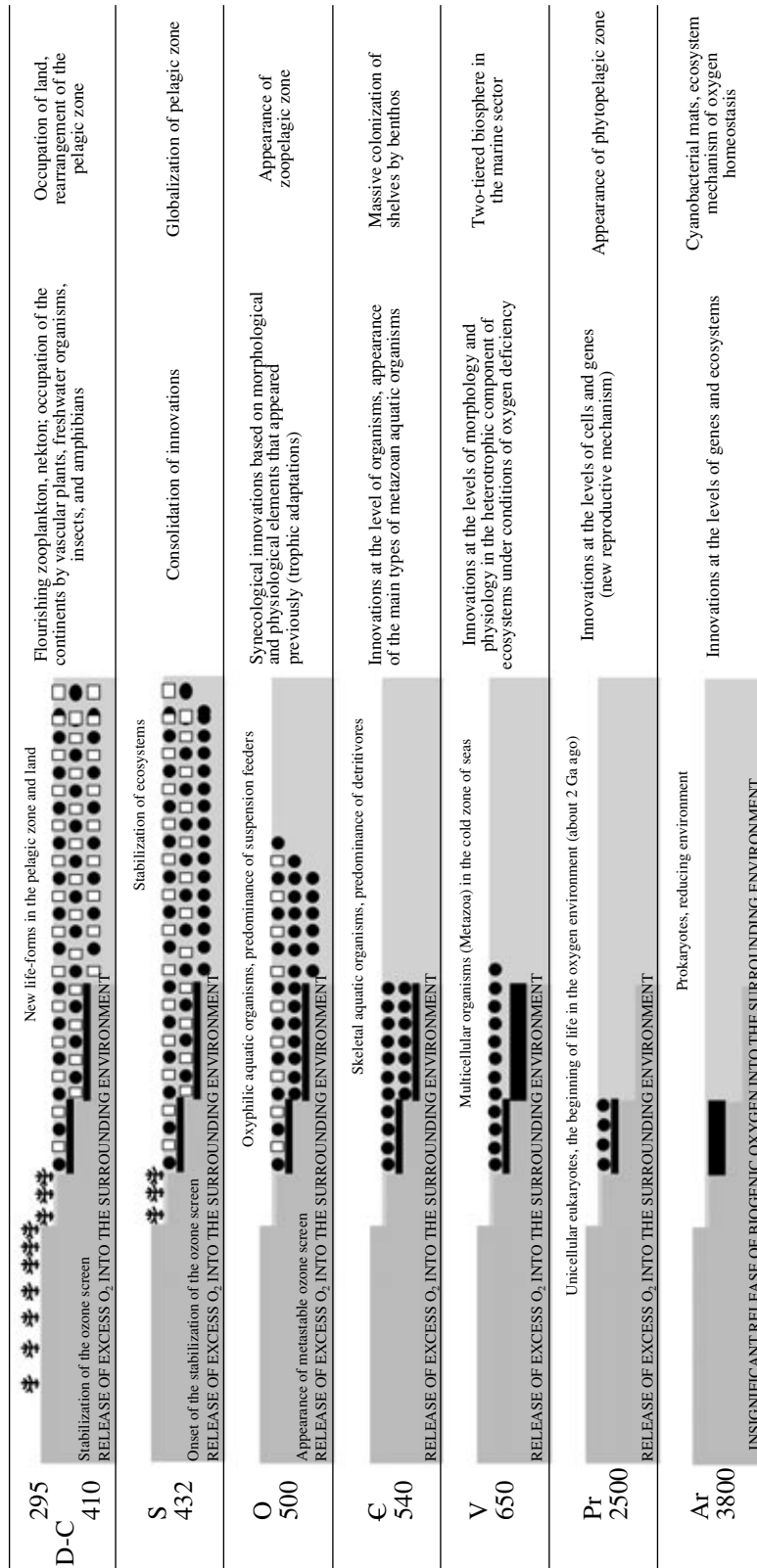
Taxon	Species	Haploid genome (millions pairs of nucleotides)	Number of genes in the genome
Prokaryotes			
Mikoplasma	<i>Mycoplasma genitalium</i>	0.58	470
	<i>Mycoplasma pneumoniae</i>	0.82	~670
Rickettsia	<i>Rickettsia prowazekii</i>	1.1	834
Archaeobacteria	<i>Archaeoglobus fulgidus</i>	2.18	2436
	<i>Methanopyrus kandleri</i>	1.69	1738
Cyanobacteria	<i>Synechocystis</i> sp.	3.57	3168
Eubacteria	<i>Escherichia coli</i>	4.6–5.5	4288
	<i>Campylobacter jejuni</i>	1.64	1654
	<i>Aquifex aeolicus</i>	1.55	1512
	<i>Neisseria meningitidis</i>	2.27	2121
	<i>Bacillus subtilis</i>	4.2	4100
Lower eukaryotes			
Fungi	<i>Saccharomyces cerevisiae</i>	11.4	6241
	<i>Schizosaccharomyces pombe</i>	13.8	4824
	<i>Aspergillus nidulans</i>	31	
Protists	<i>Amoeba dubia</i>	670000	
	<i>Entamoeba histolytica</i>	20	
	<i>Dictyostelium discoideum</i>	32	11000
Higher eukaryotes			
Higher plants	<i>Lilium longiflorum</i>	90000	
	<i>Arabidopsis thaliana</i>	115.7	27540
	<i>Oryza sativa</i>	466	46022–55615
Protostomia	<i>Caenorhabditis elegans</i>	97	19049
	<i>Drosophila melanogaster</i>	120	13600
Deuterostomia	<i>Protopterus aethiopicus</i>	139000	
	<i>Fugu rubriceps</i>	365–400	30000–40000
	<i>Homo sapiens</i>	3000	30000
	<i>Mus musculus</i>	2500	37000

Note: *Dictyostelium discoideum* is a protist with a multicellular stage of its life cycle (fruiting body).

an organ with large cells full of chemosynthetic bacteria consuming methane and hydrogen sulfide carried by the blood system, which also carries oxygen: the hemoglobin of Vestimentifera binds both oxygen and hydrogen sulfide. Oxygen is bound by heme, whereas hydrogen sulfide is tied by the protein part of the molecule of hemoglobin (Malakhov et al., 1997; Malakhov and Galkin, 1998). It is not clear why such a complex system of exchange by energy and matter is needed because the ecosystems of “black smokers” contain many other organisms also in symbiosis with chemotrophic bacteria. For instance, shrimps brought by the currents. In the hydrogen sulfide environment they lose their gills retrieving oxygen from water after one or two generations become reduced, while the gill

cavities become inhabited by the chemosynthetic bacteria, which consume oxygen directly. Similar, or even simpler mechanisms of symbiosis with chemosynthetic bacteria were developed in other organisms (mollusks, worms) (Lisitsyn and Sagalevich, 2000; Dobretsov, 2004).

A complex dual system of the exchange of the matter and energy in Vestimentifera may be related to their ancient origin. The systematic position of Vestimentifera is not precisely identified, but they have existed for at least 400 Myr without change, which is supported by the finds of the fossil Vestimentifera tubes in the Urals (Fig. 7) (Malakhov and Galkin, 1998; Maslennikov, 1999, 1997). The conservatism of the Vestimentifera morphology is apparently connected to the con-



**Fig. 8.** Cardinal biological innovations and changes in the spatial parameters of the biosphere (Precambrian–Paleozoic) (after Kanygin, 2001, 2003).

servatism of their habitats that has remained unchanged. Apparently, Vestimentifera were one of the earliest eukaryotes inhabiting the zone of “black smokers,” by developing symbiotic relationships with chemosynthetic bacteria. Originally, they did not experience competition and used a simple adaptation retaining a complex digestive system. Further specialization closed other evolutionary possibilities for them. Over millions years the zone of “black smokers” was gradually occupied by other organisms. Having encountered Vestimentifera, they had to search for other ecological niches of the black smokers, by acquiring adaptations, and more fundamentally restructuring metabolism.

The oxygenation of the atmosphere and, later, of the hydrosphere was the first evolutionary vector, in which the biosphere acted if not independently, at least on equal terms with the geosphere. Before that the vector of the evolution was always dictated by the geosphere. Very importantly, the eukaryotic layer was developed in the biosphere as a result of oxygenation. This apparently happened 1.7–1.9 Ga (Schopf, 1983; Knoll, 1994; Sergeev et al., 1996; Cavalier-Smith, 2002b). The oxygenation of the atmosphere made many nutrients less available by transforming them into oxides and silicates. The productivity of the biosphere fell at that time, which is seen from the changes in the dynamics of sedimentation (Fig. 1). By including a previously missing layer of consumers in the ecosystems eukaryotes considerably elongated food chains by that increasing the closeness and efficiency of biogeochemical cycles (Zakrutkin, 1993). This should have especially been reflected in the cold-water ecosystems due to the greater solubility of oxygen in cold water (Hengeveld and Fedonkin, 2004). However, eukaryotes with nuclei could appear even earlier, simultaneously producing both heterotrophs and autotrophs, i.e., the simplest phytoplankton (a review of the newest data on this problem is published in the article by A. Yu. Rozanov), but they did not play a significant role in the biosphere. Only oxygenation allowed their wider distribution by creating a new mode of evolution.

The main method of reproduction of prokaryotes is division, although they also have equivalents of the sexual process (conjugation, transformation, transduction). But these processes are not necessary conditions for reproduction, often beginning in the population under extreme conditions (Prozorov, 2002). Usually, division in prokaryotes proceeds well even without exchange of parts of the DNA between different individuals. In means that “the sexual process” of prokaryotes is not compulsory and they do not have sexual reproduction in the same sense as eukaryotes. The equivalents of the sexual process in prokaryotes serve only as an auxiliary method of increasing variability in populations. In contrast, in most eukaryotes reproduction is always preceded by the exchange of parts of the DNA (Cavalier-Smith 2002c; Solari, 2002). Thus, for eukaryotes the sexual process and, hence, sexual reproduction is the main way of generating variability. Asex-

ual reproduction known in some eukaryotes is non compulsory and is used either for rapid growth of the biomass (parthenogenesis of green flies, vegetative reproduction of plants) or for reproduction when the chances to meet a partner are minimal (parthenogenesis in lizards, apomixis in plants) (Vasil'ev et al., 1983; Ruvinskii, 1991).

Thus, beginning from a certain moment, the sexual process became not only the leading reproductive strategy in eukaryotes, but also one of the leading factors of speciation, i.e., endogamous species appeared (Starobogatov, 1985; Ruvinskii, 1991). Possibly, this enabled the appearance of multicellular eukaryotes, most of which were represented by endogamous species (Starobogatov, 1985). Multicellular plants, in contrast to cyanobacteria, use lit space more efficiently due to the vertical thalli. The efficiency of photosynthesis increased. By the Ordovician the ozone layer, second line of defense, was formed. This allowed life to begin move to the land, by which the area of the biosphere was enlarged, and the intensity of processes in the biosphere increased (Buzin, 1998).

Thus, 1.7–1.9 Ga is a crucial period in the evolution of biodiversity. If eukaryotes did not appear, we would still be living in the bacterial world with its own evolutionary rules. Table 1 shows the change in the size of a genome as a result of the evolution. The transition from prokaryotes to eukaryotes led to the increased size of a genome from  $10^4$ – $10^5$  to  $10^9$ – $10^{10}$  base pairs, while the number of genes increased from 470 (in *Mycoplasma genitalium*) to 30–40 thousand (in multicellular eukaryotes). However, in bacteria the complexity of organization correlates with the size of the genome and number of genes in it, whereas in eukaryotes there are no correlations between the complexity of organization, size of genomes, and number of genes. For instance, among insects, showing the highest biodiversity on our planet, and among amphibians, which have the lowest diversity among vertebrates, the size of the genome fluctuates only by two orders of magnitude. At the same time, in *Drosophila melanogaster* there are 13600 genes, whereas the simpler round worm *Caenorhabditis elegans* has 19000 genes. It is surprising that man and the puffer fish have almost the same number of genes (30000–40000) (Carroll, 2001; Taft and Mattick, 2003). Apparently, here we are dealing with a fundamental biological rule which is rigidly determined in the future evolutionary pathways of prokaryotes, which rigidly connected their progress with the size of the genome, and eukaryotes, in which this connection at some stage almost disappears, perhaps because of the complex organization and regulation of the genome.

## CONCLUSIONS

As a conclusion we are placing here a general scheme of the evolution of the biosphere and cardinal biological innovations in the Precambrian–Paleozoic (modified after Kanygin, 2001, 2003) (Fig. 8) depend-

ing on the directed changes in the environment. The most important here are the first six stages. (1) Archean, dominated by prokaryotes and reductive environment ("island" variations of oxidation are possible); (2) Proterozoic, when unicellular eukaryotes appeared and life began in the oxygen environment (ca. 2.1–2.0 Ga); (3) Vendian when multicellular Metazoa flourished; (4) Cambrian (appearing of the skeleton, appearance and rapid diversification of all major stems of marine invertebrates, development of almost all phyla and major classes); (5) Ordovician (appearance and explosive growth of biodiversity of new group of oxyphilic aquatic life in the benthic and pelagic zones, the development of almost all classes and major families on the basis of which coherent ecosystems of the modern type are formed in the marine environment); (6) Silurian–Devonian (the beginning of the active occupation of the land by vascular plants, freshwater aquatic organisms, amphibians, and land animals).

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