

Microbial Biosphere¹

G. A. Zavarzin

Winogradsky Institute of Microbiology, Russian Academy of Sciences

e-mail: zavarzin@inmi.host.ru

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Abstract—Evolution of the prokaryotic biosphere is regarded from the system point of view. It starts with the appearance of the first organisms, the ~3.5 Ga date forming the boundary between the observed and imagined biosphere. The prokaryotic community dominated from the Archean to the Mesoproterozoic. Prokaryotes make a sustainable community due to the cooperative action of specialized forms. The main route for establishing a community is made by trophic links. The structure of the trophic links in the prokaryotic community making a trophic network is an invariant, with secondary adaptive deviations. Material balance is the ultimate requirement for a long living self-supporting system. The system of biogeospheric cycles is dictated by the constancy of biomass composition establishing a quantitative ratio between $C_{org}:N_{org}:P_{org}$. Biospheric processes are driven by the C_{org} -cycle. Carbon assimilation is limited by the size of the illuminated moist surface populated by producers, meaning that C_{org} -production remains within an order of magnitude of 10^2 Gt/yr. Evolution of primary producers forms a basis for the evolution of the biospheric-geospheric system, and cyanobacteria integrated as chloroplasts remain its driving force. Decomposition of organic compounds is performed by organotrophic destructors, anaerobic being less effective. Destructors determine the residual C_{org} accumulation. Recalcitrant C_{org} remaining in the sedimentary record is equilibrated by O_2 and other oxidized compounds as Fe-oxides or sulfates. Geospheric and biotic interactions include both direct and biotically mediated processes; the most important is the weathering-sedimentation pathway. Prokaryotic community makes a sustainable frame into which all other more complex forms of life fit. That makes the prokaryotic biosphere a permanent essence of the whole system. New participants might come in and substitute functional components only when they fit to the existing system. The evolution of a large system is additive rather than substitutive. The message of this is; “we all originated from the cyanobacterial community.”

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INTRODUCTION

The coming-into-being of the biosphere begins with the appearance of the first organisms. All preceding events do not fall into the concept of the biosphere. Habitability precedes habitation. Entering of the Earth in the corridor of habitability depends on both astronomical and planetary factors (Franck, Zavarzin, 2004). This implies the primacy of geospheric conditions. The link between geospheric and biospheric processes is realized by the system of biogeochemical cycles driven by coupling with the cycle of organic carbon. The system of biogeochemical cycles was realized by the activity of prokaryotic microorganisms. The development of the biosphere via cycling mechanisms needs a functional diversity of participants and cannot be reduced to a single common ancestor. Evolution of the biosphere cannot be substituted by the evolution of biota.

The organic carbon cycle is initiated by primary producers and could be quantified in grams of C_{org} . This is the reason why the evolution of the biosphere depends primarily on the evolution of photoautotrophic

organisms, which, in their turn, depend on the availability of sunlight, and to some extent on chemosynthetic microorganisms, which depend on endogenic ox-red reactions in the geosphere. Evolution of the biospheric-geospheric system as a whole might be described as biogeochemical succession, driven by the incomplete balance in the production-destruction cycle and coupled to direct and mediated cycles. Since everything new for its establishment should be installed into the already existing structure, subsequent evolution of biota ought to be based on the prokaryotic biosphere. In this sense evolution is additive, not substitutive. Substitution of components occurs inside the functional niche within the sustainable system. Since the new is installed into the existing, old systems should be retained. The prokaryotic biosphere is a permanent constituent of the biosphere.

The cyanobacterial community represents an entity with almost closed cycles, destructors being responsible for regenerative recycling of biogenic elements. General principles of the functional organization of the biosphere might be studied on the autonomous microbial communities in an extreme environment. That is a reason why it is possible to reveal the functional structure of the prokaryotic biosphere by means of studying

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extant relict microbial communities in extreme habitats, devoid of non-prokaryotic producers and consumers.

Practically, this means that interactions in the primitive biosphere might be studied actualistically with cyanobacterial mats (Matte) as a test system, where cyano- refers to the main primary producers and bacterial—to the prokaryotic destructors. This system might be described chemically by the trophic substrate-product interactions.

The prokaryotic biosphere is complete and sustainable, values confirmed by its being a permanent basis of biotic system throughout geological history. Post-prokaryotic evolution of the biosphere has as its prerequisite successional changes, caused by accumulation of products due to the incomplete destruction, the leading is stoichiometric pair C_{org} of the kerogen and oxygen introduced into the atmosphere, and consumed mainly for the formation of sulfates and iron oxides.

Evolution of biota proceeded within the meta-sustainable biosphere due to the rise of organism complexity with reduction of their metabolic versatility. The primary photosynthetic unit—cyanobacterium—was integrated into new entities and reductively transformed into chloroplasts. The subsequent evolution of primary producers occurred in the framework of cyto-morphological complication aimed at creation of an appropriate physical environment for photosynthetic units. The deformation of the entirely prokaryotic biosphere is manifested by the appearance of phagotrophy—nutrition by particles—based on the cytology of protists and then multicellular metazoans like conspicuously symbiotic parazoans as spongy or, probably, archaeociates. The next step, zootrophy, represents variations on the “bowel with gonads” theme based on intestinal microbiota in a tubular chemostate-like structure.

The trophic approach to the evolution of the biota unifies biological and geological concepts in terms of chemical units. It gives the possibility for a system approach to the Earth's biosphere, which evolves from its pioneering state by the coupled interactions in serial quasistable states. This approach requires understanding of the system of interlinked events within the unity of time and space rather than their order. In spite of the claims of evolutionists, evolution, understood as a sequential order, does not explain everything. The philosophical reason for persistent miscomprehension is the introduction of singular instead of multiple in the “Abendlandische Philosophie” (Heidegger, 1984). The interaction of bio- and geospheric systems is better understood with landscape in mind, as A. Humboldt suggested in the 19th century and V. N. Sukachev in the 20th (biogeocoenosis principle). The aim of this paper is not a comprehensive review but an attempt to provide a frame for the system approach based on balances. Priorities in the study are dictated by masses of material involved in processes and turnover rates for reservoirs.

For the geospheric-biospheric system the functional traits of its components are of primary importance. As

a consequence, the virtual world of ribosomal phylogeny remains out of scope as well as the “RNA-world.” The present-day ‘sunflower’ topology of prokaryotic phylogeny makes it difficult to represent evolution in old-fashioned ‘order’ (Woese, 2004). Functional morpho-physiological traits, which are needed for system analysis, do not correlate with phylogenetic position and representatives of various phylogenetic lineages might have similar functions. The empirical rule, as I found, is that distantly related organisms interact, constructing a cooperative functional entity.

LIMITS FOR ACTUALISTIC PRINCIPLE

To what extent is the actualistic principle applicable to the study of the Early Proterozoic and Archean biosphere? This is a question, which should be taken into consideration each time. The greatest limitation is the composition of the present day atmosphere and the ocean equilibrated with it. Both of them are products of the biosphere. The simplest approach is that atmosphere was formed by endogenic degazation and transformed by bacteria and photochemical processes. The bacterial community is particularly specialized in the transformation of gaseous compounds and its cooperative action suffices the chemical composition of the atmosphere with the exception of inert gases (Zavarzin, 1984). It can be stated as empirical evidence that the atmosphere of contemporaneous type was formed by cooperative action of prokaryotic biota already in existence much earlier than 2 Ga. There was no significant accumulation of oxygen until 2.4 Ga, as has been concluded from various geochemical indicators, which does not exclude acting sources of oxygen, which scavenged from the atmosphere. That is the approximate date when the actualistic principle could be applied with some degree of certainty. Reconstruction of Archean environment is more problematic. Did iron-dominated cycles characterize it? What was the form of sulfur?

The history of the biosphere is the history of organic carbon. There is firm evidence that sedimentary organic carbon has biotic origin. Biologically mediated carbon isotope fractionation persisted over 3.5 if not 3.8 Ga, early deviation of $^{13}C/^{12}C$ ratio in Isua is interpreted as the result of high temperature metamorphism (Schidlowsky, 2002). The history of the biota remains uninterrupted from that time, with autotrophic assimilation of CO_2 as the main income into the system. Organic carbon in the biomass makes a minor dynamic reservoir leading to recalcitrant forms from humus to kerogen and dispersed reduced carbon of sedimentary rocks. Kerogen was balanced by oxygen in the Earth system.

Origin of Archean atmosphere supposes two sources: a remnant of the primordial atmosphere, as it is indicated by depletion of rare gases from the cosmic ratio, and continuous degazation, as volcanic exhalations indicate. The source of water remains enigmatic, including supposed transport by comets. It is assumed

that prebiotic atmosphere was neither reductive, nor oxidative with N_2 , H_2O , and some CH_4 . It should also contain products of photochemical reactions. The two main sources of photochemical transformation should be considered: photochemical reactions of water vapor with production of hydroxy radicals and photochemical reactions of methane with possible production of various C-compounds. Could they serve as a source for organotrophic bacteria? It should be noted that fears about lethal UV are not in accordance with presumed high iron content in Archean waters since iron serves as a perfect shield for 220–270 nm UV (Phoenix et al., 2001).

The traditional view on the early atmosphere is based on the CO_2 dominated atmosphere and the wollastonite equilibrium $CaSiO_3 + CO_2 \leftrightarrow CaCO_3 + SiO_2$ as geologically most important CO_2 -sink (e.g. Schwartzman, 1999 and literature there). Calcium and magnesium carbonate deposits in conjunction with weathering and remnant clay mineral formation provide evidence for the main route of mineral deposit evolution in sedimentary record. Carbonates are obvious reservoirs for the atmospheric CO_2 sink produced in an essentially subaerial process. The other pathway is subaqueous carbonatization of basalts, which was characteristic for the ancient ocean hydrochemistry (for review see Westall, 2003). Salinity and sulfate content of the Archean ocean might be most different from the recent waters (Melezhik et al., 2005). Carbonates are responsible for the neutral environment on the Earth's surface. The geological context for early life should be based on the paleogeographic mosaic, as large portions of protocontinental blocks were actually submerged.

Biota—geosphere feedback was expressed first of all by the change of the chemical composition of the atmosphere as the small dynamic reservoir with the substitution of CO_2 by O_2 and transition to oxidative state. Presently it is supposed that there was a methane rich atmosphere during 2.8–2.6 Ga and at the same period oxygenic photosynthesis evolved. Great oxidation occurred during 2.2–2.0 period as is represented by Jatuliian deposits in Karelia (Melezhik et al., 1988). At 1.8 Ga BIF ceased after their presence since 3.5 Ga. About 1.9 Ga eukaryotes appeared, coming to dominance around 1.2–1 Ga.

RELICT MICROBIAL COMMUNITIES

The pragmatic assumption is that the prebiotic atmosphere was like gas streams from volcanoes. However, which kind of volcano? Gaseous emissions from volcanoes of border islands like the Kurils and Kamchatka coming to the surface are influenced by thermal transformation of overlaying sedimentary deposits with injection of meteoric water and air in gas stream. The composition of emissions is close to thermodynamic equilibrium. Submarine vents undergo even stronger influence of convective exchange with the deep waters of modern sulfate-rich ocean. Maybe a better example

is the deep subterranean habitat where water comes into equilibrium with porous rocks. The presence of prokaryotic life in the hydrothermal environment is stated to 3.3–3.5 Barberton sediments (Westall et al., 2001). Two types of extant microbial biogeocenoses are related to endogenous exhalations.

Hydrogenotrophic chemosynthetic microbes represent the first type. These microbes use H_2 produced by the reduction of water by superheated iron of igneous rocks with the partial oxidation of iron. The immediate consequence is that these organisms include hyperthermophiles that develop over the zone of condensation of the vapors of fluids at approximately 100°C. The trophic problem in the H_2 -rich environment is the availability of an oxidant. There are two possible oxidants: CO_2 and S_0 . That gives trophic niche for methanogenic archaea by reaction $4H_2 + CO_2 = CH_4 + 2H_2O$ and sulfur reducing sulfidogenic archaea: $H_2 + S_0 = H_2S$. Large number of hyperthermophiles of these types was described by group of C. Stetter and other workers (for review see Bonch-Osmolovskaya et al., 2004). Sulfate-reducing *Archaeoglobus* could acquire this ability in sulfate-rich environment of recent hydrotherms. Another possibility is fermentation of organic substances by *Desulfurococcus*-type organotrophs, which need elimination of excessive H_2 by reaction with S_0 (“S-dependent archaea”) or simply by the gas stream. At present the source of organic compounds seems to be boiled biomass transported by convective stream in shallow-water hydrotherms. Product of incomplete reduction of CO_2 —carbon monoxide—might be oxidized by water: $CO + H_2O = CO_2 + H_2$ by the now extensively studied *Carboxydotherrmus*, which was the first representative of a new group of anaerobic lithotrophic eubacteria (Svetlichny et al., 1991). Of course, H_2 escaping to the surface is oxidized by thermophiles with different growth temperature ranges (Miroshnichenko, 2004). In the modern O_2 -rich environment H_2 can be oxidized by extremely thermophilic “Knallgasbakterien” like *Hydrogenobacter*, *Calderobacterium*, and *Aquifex* and it should be noted that, phylogenetically, they are the most deep-branching eubacteria. The question is, what if the “molecular clock” for thermophiles is adjusted to the same path of time as for other creatures? Below-the-ground biogeocoenosis might be considered as the oldest persisting relict, especially in the porous spaces of cratons because of the presumably changing composition of oceanic water. The problem for up scaling activity of methanogenic and sulfidogenic ancient microbes comes from the need to close the biogeochemical cycle by oxidation of CH_4 with its strong greenhouse effect. Large-scale photochemical production of organic compounds in the anoxic atmosphere washed out from the atmosphere could make a source of nutrition for the anaerobic microbial community, a possibility which, as far as I know, has not yet been explored. Excessive H_2S does not make such a problem for the atmosphere since it might be bound by iron, presumably present in the

ancient ocean; however no geological evidence for such a type of ancient sedimentary iron sulfide deposits are reported—iron remains as oxides. Studies of microbiota from deep drills to about 3 km until now gave the same types of microbes, which are known from volcanic regions and thermal vents (Bonch-Osmolovskaya et al., 2004). If estimation of subterranean microbiota in 10^{30} organisms (Whitman et al., 1998) is correct, than we can assume that life did not develop numerically.

Oxidized iron, remaining from H_2O reduction, might be reduced to magnetite by thermophilic iron reducing bacteria (FeRB) (Slobodkin et al., 1995) or to siderite. Magnetite is formed by thermophiles under high pCO_2 , excess of $Fe(OH)_3$, and absence of organic colloids, while siderite is formed under high pCO_2 , limited iron hydroxide, presence of utilizable organic compounds (Zavarzina, 2004). The iron cycle driven by geochemical reactions at high temperatures seems to be the key process for Archean—Early Proterozoic. Is it possible to regard the period before the accumulation of sulfate in the ocean and sulfate reducers as a period of biospheric ‘iron cycle’? Production of Fe(III) by phototrophs, which is known both for cyanobacteria and anoxygenic non-sulfur bacteria, could serve as an oxidant. BIF’s make an existing evidence for the possibility of such hypothetical cycle. The iron cycle is compatible neither with the sulfur cycle nor with the present type of oxygen cycle. Phototrophic microbial participants for all three possibilities are available. Even patches of appropriate extant communities are found somewhere. To what extent are these possibilities of anoxygenic primary producers consistent with Archean-Paleoproterozoic $^{13}C \approx -25\%$ kerogen accumulation record?

The second type of hydrothermal environment on the Earth surface leads us to the stem of biospheric evolution. Low temperature, approximately less than $65^\circ C$, hydrotherms characterized by a CO_2 stream are inhabited by moderately thermophilic cyano-bacterial communities dominated by mat-forming cyanobacteria like *Mastigocladus laminosus* and *Phormidium laminosum*, the species epithete indicating the structure of the communities. Studied by Brock (1986) in Yellowstone and by our group in Kamchatka and the Kuril Islands (Zavarzin et al., 1989) thermophilic cyano-bacterial communities seem to be trophically complete with closed cycles. In addition to cyanobacterial primary producers they include various thermophilic organotrophs, which comprise trophic chains leading to methanogens and sulfate reducers. In methanogenic trophic chain thermophilic acetogens and acetoclastic methanogens as *Metanosaeta* (formerly *Methanotherix*) *acetophila* are present. However, thermophilic methanotrophs are remarkably absent, biogenic oxidation of methane starts at lower temperature. The sulfur cycle starts with thermophilic sulfate reducing *Thermodesulfobacterium*, which represents a separate phylogenetic lineage, but functionally is equivalent to conventional desulfovibria. Oxidation of H_2S is mediated by

various thionic bacteria with spectacular streamers of *Thermothrix* capable of oxidizing H_2S into S_0 aerobically and to reduce sulfur in anaerobic conditions. Excessive sulfur is oxidized outside the cyano-bacterial community by extremely acidophilic aerobic microbial biocenoses, which are the main producers of sulfuric acid and initiate geochemical events resulting in rock-leaching by sulfuric acid and acid iron-bearing streams ending with limonite deposition. The highly acidophilic microbial community that includes both archaea and/or eubacteria is most characteristic of the thermal fields marked by snow-white clays in place of weathered lava rocks. However, it should be left outside the present discussion since it is oxygen dependent.

The thermophilic cyano-bacterial community that develops in CO_2 dominated mophetes represents an actualistic example of how gaseous exhalations were transformed into a modern type atmosphere. Cyano-bacterial communities taken both in situ or in vitro and exposed under light to volcanic exhalations or their analogs in the laboratory transform gaseous composition into an air like mixture with about 25% O_2 , which is the upper limit. Remarkably, methane behaves as an inert gas—it is not oxidized by the communities (Gerasimenko, Zavarzin, 1982). The question is dynamics of the process: cyano-bacterial communities in hydrotherms on the day-surface represent local sites. Is it possible to extend the application of these results to the ancient Earth surface? Landscapes of what kind and extension are needed?

FORMATION OF LANDSCAPE IN PROKARYOTIC BIOSPHERE

Let us define landscape as an entity of biota and geographic environment, large enough to regard it as uniform. Landscapes are classified hierarchically from large climatic and orographic zones to small elementary habitats. The Earth’s surface was never as uniform as a well-mixed atmosphere, even the ocean might be regarded as more uniform than the terrestrial environment. There were always mosaics of environments during the history of the Earth’s surface. The generalist approach of a homogenic environment on Earth during certain periods of geological time is entirely unacceptable to microbiologists, whose study organisms occur in microhabitats. The reason is that microbes are easily disseminated by wind in aerosols including non-habitable surfaces like the Antarctic—which calls into question the statement that the biosphere is everywhere where life forms are found. Microbes have a short life cycle and that makes adaptive dynamics with the change of species, not adaptation, the main mechanism for formation of microbiogeocenoses. Landscapes, which could have global influence, should have a large enough moist sunlit surface for accommodation of chlorophyll containing photoautotrophic primary producers. Since assimilation of CO_2 is proportional to active chlorophyll and the wet surface was approxi-

mately the same throughout the Earth's history it is realistic to accept present annual production 10^{18} grams C_{org} as approximately constant value, within an order of magnitude, for the biosphere of the modern type.

Oceans, of course, represents the largest wet surface. At present it produces about a half of primary production. For the prokaryotic biosphere, cyanobacterial picoplankton is of primary importance. Quantitatively, it delivers a quarter of present annual global C_{org} production. Was the ocean the cradle of life? There are certain limitations in discussing the role of Archean ocean as a continuous body of water since our understanding of its chemistry is most deceptive. Of course it worked as a sink for deposits, its surface was in dynamic equilibrium with the atmosphere, and most probably its bottom represented the main route for volcanic degazation. However, ocean is too large to be a cradle. Life could not be concentrated there. The distances, except for veils in stagnant zones, limit interactions between organisms. Another drawback for microbial evolution in the ocean is the permanency of physical and chemical conditions: there is no need to change and adaptation facilities are limited by restrictive evolution. Nevertheless the presumed role of ancient cyanobacterial picoplankton as a possible source of oxygen seems to be undisputable. It is a source large enough for the oxidation of iron for Banded Iron Formations and able to produce enough C_{org} to reduce part of it into magnetite by anaerobic DIR (dissimilatory iron reducers). At least two known limitations for cyanobacterial picoplankton of nowadays were absent: limitation by iron and limitation by filtrating zooplankton which keeps the concentration level below 10^5 cells per ml. The presence of this type of cyanobacteria is not yet proved by paleontology. It would be quite difficult to identify minute $0.5\text{--}0.8 \times 0.7\text{--}1.6 \mu\text{m}$ coccoid cells of *Prochlorococcus* morphotype as microfossils of cyanobacteria. In this case the time gap between BIF and the first undisputable trichomic cyanobacteria might be deceptive. Is it possible to consider nannoplankters in the nutrient-poor "blue ocean" as remnants of an ancient community?

Terrestrial plains of humid climatic zones, which are now occupied by forests, seem to be an appropriate environment for cyanobacterial mats. Nowadays there are only patches of mats in ephemeral bodies of water on the ground. These sites are immediately occupied by oscillatorian cyanobacteria. Nostocaceans dominate in drier climate. Production of C_{org} by soil cyanobacteria is highly variable but considerable. This is an indication of the possibility of ancient subaerial terrestrial life, which is not yet supported by paleontologists or geologists. The crucial point for these habitats is the formation of a water proof bottom under the mat either by calcination from allochthonous deposits, or, which is much more promising, by microbially mediated transformation of lithogenic minerals into clays with smectites as the most suitable ground material.

This brings us to the most crucial problem of weathering in the Proterozoic. Since it was stated by Retalack (1990) and confirmed by many other observations, Precambrian soil profiles are regarded as much the same as at present. In Russian usage since the pioneering works of B.B. Polynov term humic soil *sensu stricto* differs from mineral weathered rock while English usage is soil *sensu lato*. Mechanism of weathering includes substitution of metals in initial minerals by protons retaining Si-Al backbone. Acid in question is mainly carbonic acid and the process represents the main sink for CO_2 with carbonates as the synthesized end product and clays in the rest. Weathering was reviewed with emphasis on kinetics at high temperature and it was stated that this process is too slow at mild temperatures (see Schwartzman, 1999). Formation of clays occurs very rapidly on thermal fields not only in the steam but also due to the intervention of acid-forming bacteria (Karpov et al., 1984). Metals are transported in humid zone to the sea by run-off or accumulated in the depositional basins of endorheic arid regions. In this case soda lakes are formed. To my understanding, scavenging of the atmosphere from CO_2 is essentially a subaerial process, while endogenic generation of CO_2 most probably occurs mainly via deep-sea subaquatic degazation. If so, the ocean was a net source of atmospheric CO_2 , while the terrestrial subaerial surface represented a net sink.

There are two main problems for weathering at mild temperatures. The first is the concentration of carbon, which takes place during autotrophic assimilation and is followed by the release of CO_2 locally in the sites of decomposition of dead biomass ("mortmass"). Organic acids might be produced as additional strong leaching agents. Decomposition of organic matter provides the main mechanism of leaching. Another problem is transformation of inert CO_2 into carbonic acid as a leaching agent. The chemical process is drastically enhanced by the enzyme carbonic anhydrase (CA): $\text{CO}_2 + \text{H}_2\text{O} + \text{CA} \longleftrightarrow [\text{CO}_2\text{-CA-H}_2\text{O}] \longleftrightarrow \text{HCO}_3^- + \text{H}^+ + \text{CA}$, which is universally present in living cells to transport CO_2 in and out of the cells. The only report on extracellular CA known to me is its location in glycolyx of the halophilic *Microcoleus* (Kupriyanova et al., 2004).

Amphibial landscapes look most promising as a cradle for microbiota. Exchange between the gaseous, water, and solid phases occurs here most easily. These landscapes with shallow water of marine or lacustrine origin usually represent concentration of life with strong aerobic-anaerobic interaction. They are densely populated by diverse microbiota. This facilitates trophic interaction between microorganisms. Such landscapes are unstable and promote diversification and adaptive changes both for subaquatic and subaerial development.

The illuminated wet surface indicates shallow water bodies as preferable sites for cyanobacterial community. What does shallow mean? Limited by the photic

zone? Being more restricted, let us define as amphibial landscape such area where solid and liquid phases are in an approximate 1 : 5 ratio and easy exchange with the atmosphere is available. Two types of amphibial landscapes immediately come to mind: marine or thalassic and terrestrial or athalassic. As examples of thalassic type lagoons, tidal flats, sabkhas, marshes, German Watte of different kinds with spectacular microbial "Farbstreifbandsandwatt" might be mentioned. For athalassic types ombrotrophic bogs as autonomous, and swamps as subordinate type, lakes and dry lakes as accumulating sites, and takyr on the peniplaine come to mind. All of them are quite diverse. Thalassic amphibial landscapes are particularly important for epicontinental seas that developed in thalassocratic epochs on the passive margin of continents. Epicontinental (epeiric) seas are the beloved sites for both paleontologists and sedimentologists. Geochemically, marine and terrestrial landscapes differ in domination of chlorine in marine environment ("halite-ocean") and bicarbonate in terrestrial waters ("soda continent").

Landscape is a receptacle for both microbiota and the products of microbial activity. The landscape is changed under the influence of microbiota. Visible landscape extends for microbiota by invisible chemical landscape of porous waters and mineral surfaces. Due to SEM studies it is clear now that all surfaces are covered by biofilms (see Fossil and Recent Biofilms, 2004). The problem is, to what extent are biofilms causative agents of particular geochemical transformations. The surface of minerals is covered by organo-mineral cutanae originating from the soil solution. Pedogenic minerals are formed according to the thermodynamic equilibrium with microbially modified soil solution, both by dissolution and by precipitation. Microbes, as DIR for example, at the first step produce disperse amorphous insoluble compounds, ferrihydrite in this case, which is stabilized during early diagenesis into magnetite or siderite with dynamic of crystallization (Zavarzina, 2004). In colloid environments electrostatic interactions dominate. Coagulation of mineral colloids is an important process not only for the purification of potable water in water supply systems but also as a large-scale natural processes.

The texture of deposits is modified due to the colloid matrix formed by microbes and biofilms leading to multilayered laminated structures such as stromatolites. The process might be simulated in the laboratory when cyanobacterial film develops on sediments. When a new portion of sediment covers the surface, part of the cyanobacteria (hormogonia) move to the surface. As an exotic example of such a process, layers of *Phormidium laminosum* in thermal spring with layers of colloid sulfur might be observed. In a large scale, the same process takes place with carbonate precipitates in evaporative environment. For alkaliphilic communities of Central Asia and halophilic communities of marine-dependent Satonda lake, the role of glycocalix in carbonate lamination was argued by Apt (1999).

Formation of landscape on the macrolevel is illustrated by the well known formation of stromatolites. It includes the formation of reefs as bioherms in the hydrodynamically active outer region, formation of lagoons and tidal flats leading to carbonate platforms as described by Grotzinger (1989). The outer line of bioherms protects the shallow zone from hydrodynamic impacts. Cyanobacteria develop here in hard ground, protected from mechanical stresses by a mineral crust. It is important to interpret this total event as an evaporative process: carbonate deposits are formed as evaporites on shallow or dry surface due to degazation of CO₂ from the bicarbonate solution and concentration of dissolved solids to the beginning of carbonates precipitation (higher 10 fold concentration over saturation index). For microbiologists it means that moderately halophilic community should dominate the habitat. This community differs both from marine and freshwater communities. Nowadays *Microcoleus chthonoplastes* dominates most of these haline environments. New biofilm up to 2 mm thick develops on the layers of older and dead cells as a kind of multilayered cyano-bacterial 'peat'.

Stromatolites correlate with dolomite and magnesite formation epochs. Their formation occurred within carbonate provinces, being restricted by the photic zone. It was supposed that decline of stromatolites around 2 Ga on Fennoscandian shield occurred due to the transformation of landscape with numerous shallow-water lakes saturated with Ca and Mg carbonates as terrestrial basins, devoid from sulfates, to a deep-water sea during 'oceanization' of the region (Melezhik et al., 1997, 2001), but now formation of sulfates either local or marine is recognized.

There is an old idea that carbonates are deposited by the photoautotrophic activity due to the rise of pH. In this case there is a ratio $C_{org} : C_{carb} \approx 1 : 1$ as for corals and *Halimeda* lime formation. However, in our experiments with alkaliphilic cyanobacteria *Microcoleus* it was found that living photosynthesizing bacteria do not precipitate carbonates even under chemically favorable conditions. By contrast, mineral deposits rapidly encrust dead bacteria turning the sheaths into microfossils. This observation excludes photosynthesis as the driving force of lithification in the case studied, but makes an emphasis on the role of glycocalix as the site for nucleation. This is in accordance with the observations in situ by Apt (2003). The reason of the difference between glycocalixes of living and dead cyanobacteria might be the presence of CA in the former, since CA serves as bicarbonate ion producing mechanism (Kupriyanova et al., 2004), preventing carbonatization. On the other hand, production of CO₂ from bicarbonate stimulates formation of carbonate-ion needed for precipitation.

TROPHIC STRUCTURE OF CYANO-BACTERIAL COMMUNITY

Cyano-bacterial communities are the most persistent components of the modern type biosphere. Persistence is guaranteed by almost closed cycles of biogenic elements. Light provides the ultimate energy source; for early stages lower sun luminosity and different spectral transparency of the atmosphere should be considered. Transport of aerosols is usually forgotten, which it should not be where terrestrial environments are concerned. Volatile compounds such as CO₂ are consumed from the atmosphere. Waste compounds such as O₂ and minerals formed in biotically mediated reactions—the list should be specially considered by geologists since it includes not only typomorphic minerals as Ca and Mg carbonates, iron and manganese oxides but also clays—make the driving force for the geochemical succession in sedimentary record. Autonomous community has approximately closed cycles of productive and destructive branches; the later is sometimes called the “regenerative cycle.”

Trophic structure follows the Winogradsky's (1896) rule: each natural compound has its specific microbial consumer. If chemical compounds are listed in one column, then in other column corresponding consumers should be listed. Producers have constant composition of biomass with atomic ratio close to C_{org} : N_{org} : P_{org} ≈ 100 : 16 : 1 and approximately the same bulk composition of aminoacids, nucleotides, lipids, carbohydrates. The difference is mainly in storage compounds and structural components. Chemical diversity, which makes a ground for chemotaxonomy, deals mainly with minor compounds and is out of scope in our gross scale. Similarity in chemical composition leads to involvement of similar trophic groups, which have their trivial designations accordingly to the substrates consumed and products formed. The system is complete. Philosophical generalization formulated by Winogradsky was that “cycle of Life” represents one “huge organism.”

The trivial functional classification of bacteria, elaborated in its general lines at the end of XIX century by Winogradsky, Beijerinck and their followers, is what is needed for practical use in natural sciences. There are groups like photoautotrophs divided into conventional oxygenic and anoxygenic, proteolytics and saccharolytic, aerobic and fermenters, anaerobic methanogens and sulfidogens. It is the firm knowledge needed to each natural scientist. Detailed elaboration leads to the number of other functional groups, which make the basis of general microbiology. Functional trophic structure is much the same for different microbial communities in spite of diversity. It provides the possibility of predicting organisms from missing vortex in the trophic network. Each of these functional groups contains a lot of representatives adjusted to a special environment. Bacteriologists know more than 2×10^4 molecular sequences (ribotypes) from which less than 6000 species are validated. Diversity of known microorganisms

started to expand extremely fast when molecular methods came into wide use, with description of taxa by the methods of discrete mathematics. Cladistic trees used nowadays do not represent acceptable topology for microbial diversity (Woese, 2004).

The general scheme of trophic network in prokaryotic community includes groups of primary producers, aerobic hydrolytics and dissipotrophs (organisms utilizing low molecular weight compounds dissipating from the places of origin), anaerobic microorganisms starting with particulated organic matter (POC) sinking through oxicline created by depletion of O₂ by aerobes. Anaerobic pathway is started by hydrolytics, which decompose insoluble cell wall constituents, fermentative dissipotrophs like spirochetes, syntrophic associations decomposing non-fermentable fatty acids in conjunction with hydrogen-scavenging lithotrophs, represented by sulfate reducing bacteria (SRB) or methanogens. The cycle is closed by aerobic gas-consuming methanotrophs and sulfide-oxidizing bacteria, which protect their anaerobic benefactress from oxygen. As a variant, the trophic loop is closed by anaerobic anoxygenic phototrophic bacteria, responsible for purple layers on the illuminated surfaces. Their development is most pronounced in mineral-rich waters and even in brine. The trophic network is spatially organized in cyano-bacterial mats with their regular structure. The upper layer up to 2 mm is occupied by cyano-bacteria, followed by white sulfur oxidizers, below are purples, and in the bottom is black mud with sulfidogens. The structure is repetitive due to the type of burial. It was studied in hypersaline lagoons and reviewed many times (*Microbial Mats...*, 1989, 1993; *Biostabilization of Sediments*, 1995; *Fossil and Recent Biofilms...*, 2003). The mats are regarded as the predecessors of stromatolites, which represent geological evidence for domination of these type of cyano-bacterial communities during the Proterozoic.

Of special interest is the same structure of mats in soda lakes, which represent extreme cases for terrestrial athalassic environment (Apt, 2003; Gerasimenko, Orleanski, 2004). This biocenosis only came to attention recently and representatives of many functional groups were isolated and described during the last decade. Most of the isolated alkaliphilic bacteria belong to new genera (Zavarzin et al., 1999; Zavarzin and Zhilina, 2000). Since soda lakes are the end basins they might be regarded as some kind of natural lysimeters for watershed and weathering thereof in a continental environment. Architecture of cyano-bacterial mats follows the principle of construction of phototrophic community on solid surface which could be traced up to the moss cover as in *Sphagnum*-bog with 5 cm of green layer, 5–10 cm of decomposing “white moss,” and peat below. Offspring grow on the dead bodies of their parents. This style of architecture ceases with vascular plant cover, which commence evapotranspiration and fundamentally change the atmospheric hydrological cycle on terrestrial surfaces.

More important is the fact that the cyano-bacterial community is autonomous and that leads to its persistence on the Earth. It is the most persistent biocenosis on the Earth's surface. Chemical cycles of essential elements are closed within the community. Cyano-bacterial community is sufficient to catalyze all biogeochemical cycles (Zavarzin, 2003). One exception should be taken into account: the cyanobacterial community works as the sink for phosphorus being responsible for the formation of phosphorite deposits. Anaerobic remobilization of phosphates seems to be insufficient to close the phosphorus cycle (Keasling et al., 2000). Cyano-bacterial community is sustainable as complete system.

The role of biotically mediated reactions in the prokaryotic biosphere is still unclear. There are only examples of microbial participation in diagenetic processes, guesses about weathering but no full scale picture, which needs more geological and geochemical knowledge. The pendulum of interpretation of stromatolites as organo-sedimentary structures based on cyano-bacterial activity swing up to the interpretation of formation of laminae based mainly on inorganic evaporative precipitation and followed by rapid colonization of the surface by biofilms. Formation of dolostones and magnesite correlates with high ^{13}C -content are ascribed to an evaporative environment with high bioproductivity (Melezhik et al., 2001). The most important fact is the pronounced negative correlation between C_{org} -poor carbonates depositions with Fe(III) as indicator of oxidative status and rich C_{org} deposits of fine sediments in anaerobic highly productive non-marine basins (Melezhik et al., 1988). Let us keep in mind: spatially separated anaerobic processes, which became to be responsible for the net oxidative state of entire geochemical system, favor misbalance of $\text{O}_2/\text{C}_{\text{org}}$. Paradoxically anaerobes created the oxidative state.

What was the role of microbially mediated processes? Beginning from the appearance of Protists, skeleton-forming ability came into function. With the appearance of radiolarians, diatoms, spongy Si became involved in the biological cycle and came to be a limiting element in the ocean; Sr is used by acantharians. But the main change is in Ca recycle, which came totally under biotic control in skeleton forming CaCO_3 ability and biotically mediated dissolution during weathering.

As the result of completeness of biogeochemical cycles in prokaryotic biosphere all subsequent evolution of biota is submerged into the essential trophic structure created by prokaryotes. Sustainable development retains what had been created before. Everything new can survive if it fits to the old, already existing. The evolution of the biota is additive rather than substitutive at least in the functional aspect. That gives a general explanation why primitive, or I prefer to use word 'pioneer', organisms remain and proliferate in spite of the growing biodiversity of seemingly fitter, more complex

organisms. The line of partial substitution of primary producers from cyanobacteria by protists, by multicellular algae, by mosses, and by vascular plants makes the backbone for the evolution of the biota and to a lesser extent to the biosphere. As feedbacks give new possibilities to microbes, mainly in regenerative cycles. The message is that: "we all originated from the cyanobacterial community."

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