Microbiology, Vol. 71, No. 6, 2002, pp. 623–637. Translated from Mikrobiologiya, Vol. 71, No. 6, 2002, pp. 725–740.
Original Russian Text Copyright © 2002 by Sergeev, Gerasimenko, Zavarzin.

REVIEW PAPERS

The Proterozoic History and Present State of Cyanobacteria

V. N. Sergeev*, L. M. Gerasimenko, and G. A. Zavarzin****
**Geological Institute, Russian Academy of Sciences, Pyzhevskii per. 7, Moscow, 109017 Russia*
***Institute of Microbiology, Russian Academy of Sciences, pr. 60-letiya Oktyabrya 7, k. 2, Moscow, 117312 Russia*

Received July 9, 2001

Abstract—The paper delves into the main regularities of the distribution of fossil microorganisms in Precambrian rocks, beginning from the Archean Eon about 3.5 billion years ago and ending in the Cambrian Period about 0.5 billion years ago. The paper analyzes facial peculiarities in the lateral differentiation of microfossils in Proterozoic basins and the main stages of temporal changes in fossil cyanobacterial communities, which are based on the irreversible succession of physicochemical conditions on the Earth and the evolution of eukaryotic microorganisms and their incorporation into prokaryotic ecosystems. To gain insight into Proterozoic fossil record, modern stratified cyanobacterial mats built up from layers of prokaryotes are considered. The analysis of phosphatization, carbonatization, and silification processes in modern algal–bacterial communities suggests that analogous processes took place in Proterozoic microbiotas. A comparison of modern and Precambrian living forms confirms the inference that cyanobacterial communities are very conservative and have changed insignificantly both morphologically and physiologically during the past two billion years.

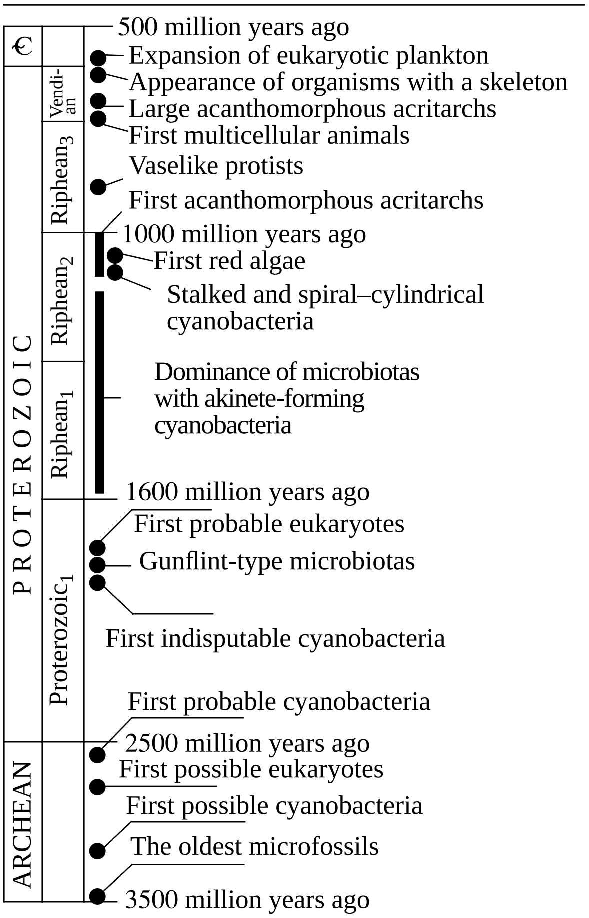
Key words: Precambrian, Archean, Proterozoic, microfossils, cyanobacteria, prokaryotes, eukaryotes.

INTRODUCTION

The development of the living world should be considered as an interaction of the biosphere with the geosphere. Endogenous processes in the geosphere follow certain laws, which are mainly determined by the thermal history of Earth on a time scale of hundreds of millions or billions of years. A general trend in this thermal history is toward a loss of endogenous heat and a decrease in the portion of igneous rocks in the Earth's cover. The primary igneous rock–weathering–sedimentary rock cycle tends to involve an increasing portion of sedimentary and metamorphic source rocks. Surface sedimentary rocks, essential for biotas, are formed in most climatic zones over tens of millenia, which is the typical time of formation of the weathering crust and the first meters of sediment deposits. Therefore, during each geologically significant time period, a biota interacts with the sedimentary cover, interrupted by regions of igneous rocks, which are also colonized by the biota. The biota largely depends on the climate, which in turn depends on the solar luminosity (on a scale of hundreds of millions or billions of years), as well as on various astronomical factors, the position of the Earth in space, its endogenous activity, the gas composition of the Earth's atmosphere, and the interaction of the biosphere with the hydrosphere and the atmosphere. The Earth's climate is also determined by many regional factors, first of all by the distribution of terrestrial and oceanic masses on the Earth. Therefore, the consideration of evolution on the Earth on a scale of Ga, i.e. billions of years (typically it is considered on a scale of 10^2 Ma, i.e. hundreds of millions of years) implies a different approach, in which prokaryotes appear as a primary biotic force most closely related to the geosphere due to their ability to catalyze the geochemically significant reactions of the solid-phase conversion and to affect the composition of the atmosphere and the hydrosphere (the latter depends on chemical weathering). Biospheric reactions give impetus to the carbon cycle, whose initial stage is the formation of organic carbon (C_{org}) in the photoautotrophic assimilation of CO_2. The formation of C_{org} on Earth quantitatively depends on a single type of photosynthesis, oxygenic photosynthesis. Fortunately, it is the group of oxygenic photoautotrophic organisms (cyanobacteria) that have left the most complete fossil record, which will be considered in the next section.

The development of the biosphere–geosphere system involves a powerful feedback relationship between the biotas and geospheric processes of weathering and sedimentogenesis, together with the associated processes of formation of natural waters and the atmosphere. This relationship is due to biotic reactions, the carbon cycle above all. Until now, biologically mediated reactions have received little attention in the literature. On a large time scale, biologically mediated reactions are related to the formation of an oxidative atmosphere and the related subaerial transformations of all the cycles (primarily, the sulfur and iron cycles), which come into thermodynamic equilibrium under altered geochemical conditions with the involvement of microorganisms. Of great significance also is the modification of the cycles of alkaline earth metals and the entire weathering process under the action of biotas. All these

Appearance of various types of organisms in the Precambrian



processes result in the so-called biogeochemical succession [1], which, until the appearance of vegetation cover on the terrestrial surface about 300 million years ago, almost completely depended on the activity of microorganisms.

On a very large time scale, the history of geospheric–biospheric biotas can be divided into the following stages (table):

The Archean Eon is characterized by the presumably important role of hydrogenotrophic microbiota (including microbiota able to utilize endogenous sources) and by locally developed oxygenic photosynthesis (in spite of the fact that Archean cyanobacterial microfossils are scarce). Without recognizing the important role of cyanobacteria in the transformation of the Earth's atmosphere due to the accumulation of unoxidized organic matter in the incomplete C_{org} cycle, it is impossible to understand the so-called oxygen revolution (which occurred about 2 billion years ago, after the end of the iron cycle), the deposition of iron oxides, and the development of the biogenic sulfur cycle with sulfate reduction in the ocean.

The Proterozoic Eon is characterized by the dominance of cyanobacterial communities with a high degree of coupling of various biogeochemical cycles and by the transfer of the main mass of endogenous carbon dioxide from the carbon cycle to sedimentary carbonate rocks, including stromatolites, through weathering processes highly modified by biotas. After this period, since the Phanerozoic Eon, carbonates have been recycled with the involvement of organisms possessing skeleton.

The course of terrestrial subaerial weathering during this period remains largely unknown, while it is a key issue for the proper understanding of the carbonate cycle and the associated processes of clay formation through the conversion of residual weathering products. Geochemists believe that the silicate–carbonate weathering of subaerial continental rocks is the major route of CO_2 removal from the Earth's atmosphere. It is accomplished via two biotic mechanisms: (1) the biologically enhanced weathering of metal–aluminosilicate rocks and (2) the deposition of carbonates at the alkaline geochemical barrier with the involvement of cyanobacterial communities. Silicified microfossils are considered to be related to the incorporation of silicates into carbonates, while organic-walled microfossils are referred to compacted clays. There is no certainty as to whether the finding of a fossilized material can really serve as a universal characteristic of ancient biotas; however, no other direct methods for the evaluation of biopaleontological events are available.

The development of protists during the Neoproterozoic revolution superimposed on the biogeochemical system formed by bacteria. The development of the protistan world was mainly governed by combinatory principles. Of the great number of combinations, only three combinatory variants led to the appearance of the animal, fungal, and plant kingdoms. The biogeochemical consequence of the Neoproterozoic revolution was the incorporation of the concentrating function of organisms having skeleton and thereby capable of forming deposits of inert biogenic materials into the bacteria-driven biogeochemical cycles. The fixation of mobile sediments by cyanobacterial communities and the formation of stromatolite belts with carbonate platforms was then substituted by the development of the reef-producing formations of colonial eukaryotes and parazoan organisms. Both types of formations gave rise to intense biogenic and diagenetic processes of sedimentogenesis in transreef areas, which can be exemplified by the accumulation of phosphate-bearing thick deposits.

To gain better insight into the Preriphean or Neoproterozoic history of the Earth and the functioning of its biogeochemical machinery, let us consider two topics: (1) the paleontology of cyanobacteria and (2) the actuopaleontology of cyanobacterial communities.

PALEONTOLOGY OF CYANOBACTERIA

Cyanobacteria. Cyanobacteria, which are among the most structurally organized and morphologically differentiated prokaryotic organisms, possess a well-documented paleontological history (Figs. 1, 2). This is due to their large size, exceeding that of many other microorganisms, and to the specific taphonomic conditions of the fossilization of cyanobacterial communities, which provided for good conservation of fossilized cyanobacteria.

There are several approaches to the systematics of cyanobacteria. The initial morphological approach, which was developed in the 19th century, dominated until the middle of the 20th century [2–5]. With the development of modern microbiological methods based on the biochemical and physiological study of cultured microorganisms and the investigation of thin sections, morphological criteria largely lost their position in cyanobacterial systematics, although they can be efficiently used to study cyanobacteria with a complex morphology. A good example is the application of sequencing of the 16S rRNA gene to the taxonomic study of cyanobacterial strains [6, 7]. In the case of the taxonomy of cyanobacteria producing heterocysts and baeocytes, morphological and genetic criteria were found to give close results [8]. However, the investigation of morphologically simple chroococcal cyanobacteria and hormogonial cyanobacteria revealed heterogeneity within major taxa at the generic level (for instance, within the genus *Synechococcus*). At the same time, the difference between chroococcal and hormogonial cyanobacteria proved to be insignificant. Closer observations showed that simple hormogonial cyanobacteria can be formed during the monopolar growth of chroococcal forms (see [9], Fig. 2).

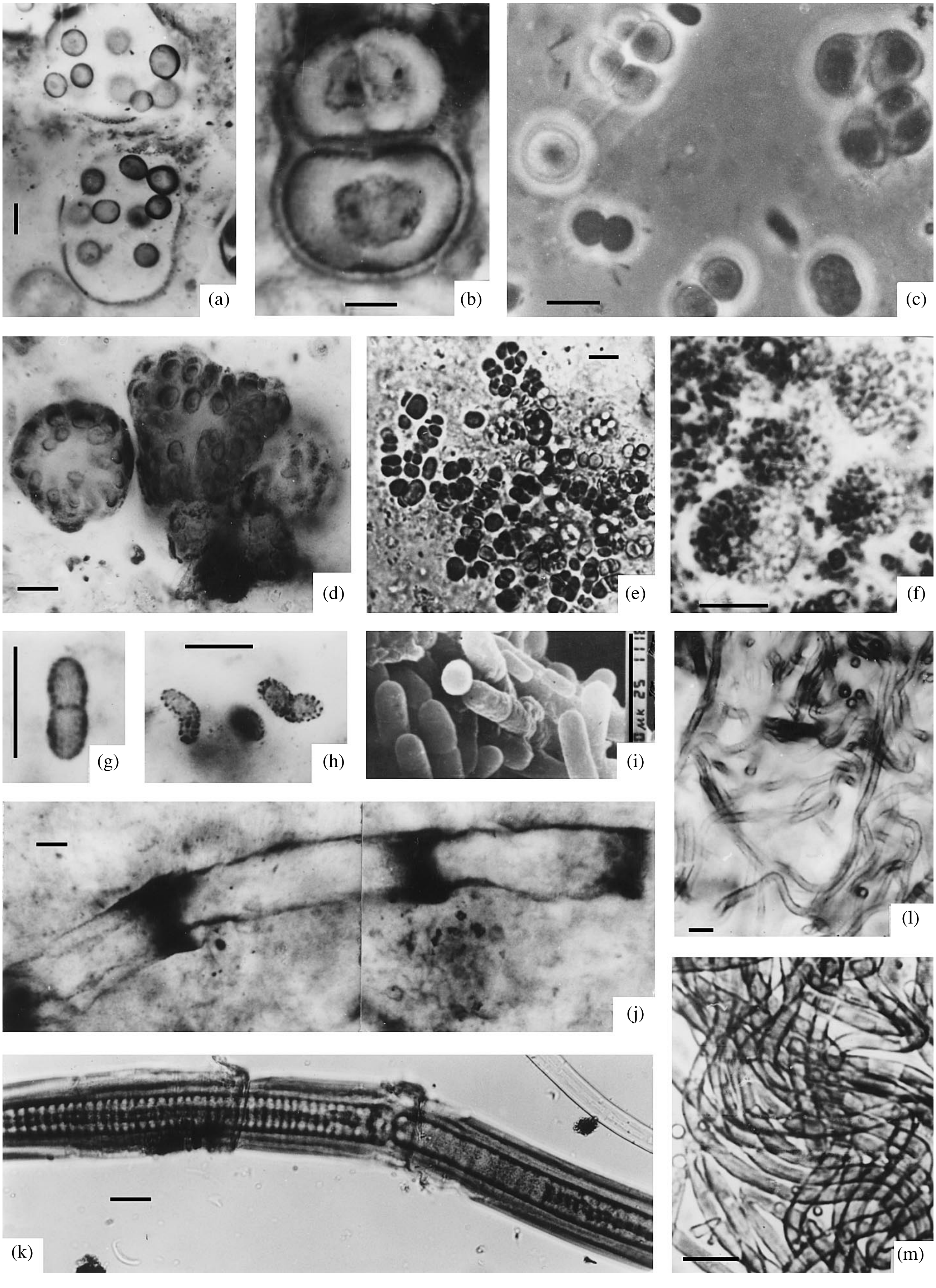
The problem of applicability of the morphological approach to the study of cyanobacteria is especially important in the case of fossil cyanobacteria, which cannot be studied by modern genetic methods. The morphological approach makes it possible to investigate fossil cyanobacteria that existed hundreds of millions of years ago and are preserved in lithified sediments, which conserve well the shape of microorganisms but not their organic composition.

Organic-wall and chertified microfossils. The remains of Precambrian microorganisms were mainly fossilized as chertified pseudomorphoses through their complete or partial chertification in chert–carbonate rocks or as mummified remains in shale deposits. These two forms of remains, which are referred to as chertified and organic-wall microfossils, represent the remains of biologically close but facially different groups of microorganisms. The microorganisms preserved in chert–carbonate rocks represent fossilized cyanobacterial communities that inhabited shallow-water, lagoon, and littoral environments, whereas organic-wall microfossils are the remains of phytoplanktonic organisms that inhabited the open-sea shelf environments of ancient basins. Such a differentiation of microfossils is arbitrary, since chert nodules episodically formed in open-sea facies contain the remains of phytoplanktonic organisms and, conversely, terrigenous deposits were often formed in shallow-water environments. The term facies is used here in the classical sense, i.e., to designate the geochemically and sedimentologically different regions of a sediment layer or of suites of sublayers into which a given layer or suite is divided within the limits of their horizontal distribution. Actually, there are several tens of definitions of facies, whose analysis and comparison could be the subject of a separate paper; however, we will restrict ourselves to the analysis of the difference between facies and landscapes. Facies is a geological term intended for the designation of horizontally adjacent regions of sediment layers. In the case of modern environments, this definition of facies implies a differentiation (in some parameters) of the lateral regions of nonlithified sediments. As for landscape, it is a geographical term intended for the designation of terrestrial and subaqueous regions of the Earth's surface that possess geomorphically similar reliefs and are characterized by identical natural conditions. As is evident from these definitions, one landscape can embrace several geological facies and, vice versa, one facies can embrace several geographical landscapes.

In addition to microfossils, Precambrian rocks contain carbonate stromatolites, i.e., organic sedimentary structures that resulted from the growth and metabolic activity of algal (first of all, cyanobacterial) communities and their interaction with the environment. This interaction involves binding of carbonate particles by algae and their subsequent cementation into a rock. Stromatolites dominated throughout the Precambrian period of the development of the biosphere. In the Phanerozoic Eon, the number of stromatolites drastically decreased due to the appearance and expansion of organisms possessing skeleton, such as archeocytes, sponges, bryozoans, corals, and red lithothamnion algae, which competitively displaced cyanobacteria to unfavorable econiches [10, 11].

Taken together, paleontological data on organic-wall and chertified microfossils give an adequate idea of the evolution of microbial communities and their paleoecological structure [12]. For the most ancient stages of the evolution of the biosphere in the Proterozoic and, especially, in the Archean, a great body of information came from chertified microfossils, whereas pertinent information on organic-wall microfossils is scarce. This can easily be explained by the fact that ancient microorganisms became chertified soon after they had occurred in a cherty rock [13] and, hence, were more protected from unfavorable environmental effects than the mummified organic-wall microfossils formed in silicoclastic rocks.

The Archean and Proterozoic. Between 1960 and 1980, researchers described a great number of cherti-


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)

fied microfossils found in Archean rocks from 2.5 to 3.8 billion years in age, but almost all of them appeared to be pseudofossils of mineral origin or compacted clusters of the amorphous organic substance kerogen [14–16]. Only thin nonseptate filaments found in the Archean Onverwacht and Fig Tree Groups of southern Africa and in the Warrawoon Series of western Australia (from 3.4 to 3.5 billion years in age), as well as small coccoid forms found in the Onverwacht Group, were recognized as actual remains of ancient microorganisms [17, 18].

Most microfossils have been found in Mesoarchean and, especially, Late Archean (Neoarchean) rocks. Of great interest are the Neoarchean microfossils found in the Transvaal Supergroup of southern Africa, from 2520 to 2550 million years in age [19, 20]. These microfossils contain thick (up to 35 μm in diameter) filamentous and small (from 1 to 5 μm in diameter) coccoid forms [16, 21], which are likely the remains of cyanobacteria but may be the remains of heterotrophic bacteria.

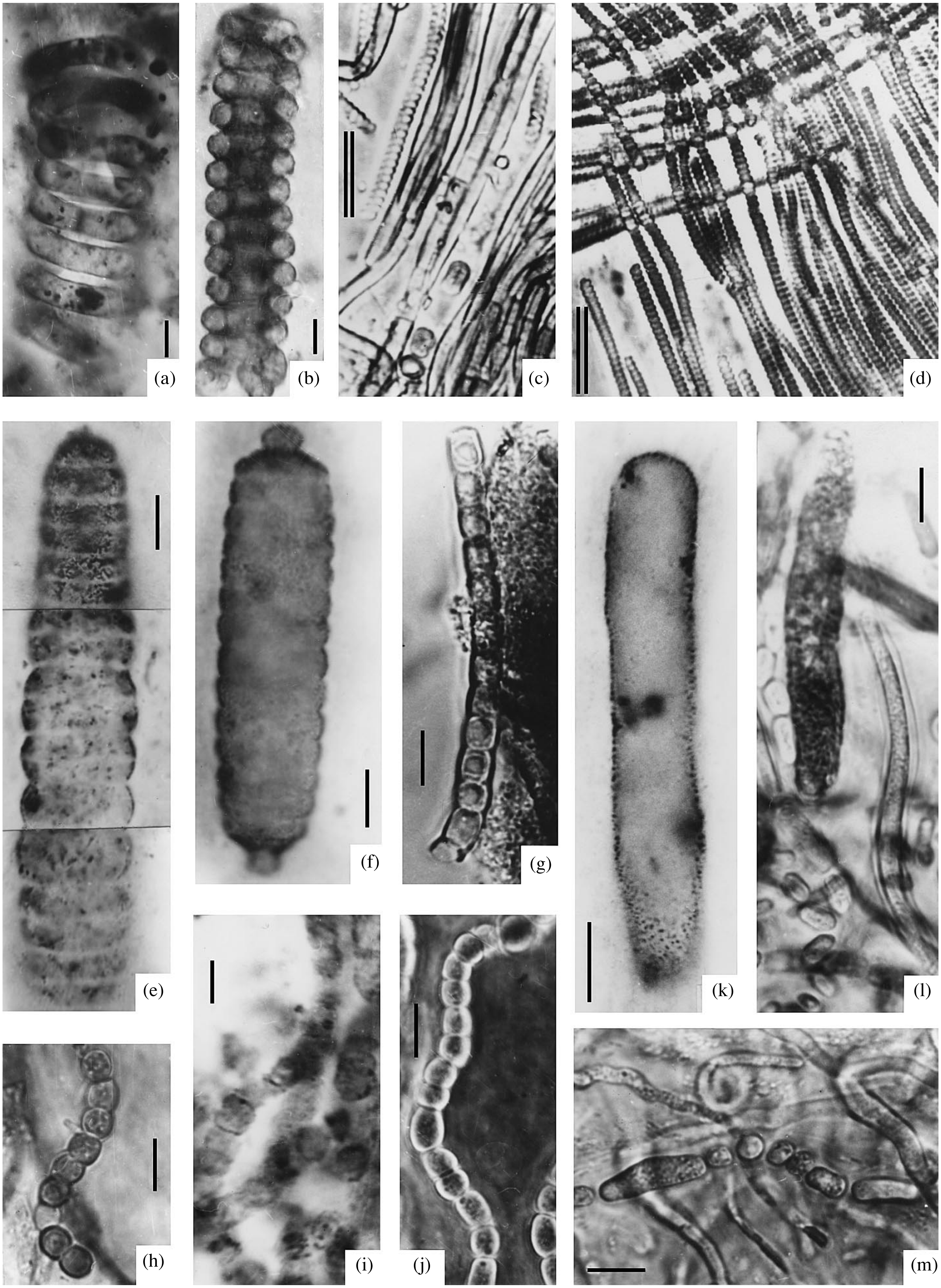
In the Proterozoic deposits (from 2.5 to 1.6 billion years in age), the number and the diversity of chertified microbiotas drastically increases, beginning with the 1.9- to 2.0-billion-year-old sediment layers. This change in the paleontological fossil record is preceded by one of the greatest positive isotopic carbon anomalies in the earth's history, which reached a value of δC^{13} = +15‰ [22]. It is in these layers that the most ancient indisputable fossil cyanobacteria were found. We mean first of all the colonial coccoid microfossils *Eoentophysalis belcherensis* Hofmann from the shallow-water (upper sublittoral–littoral) carbonate formations of the Belcher Supergroup of Canada [15, 23], which are from 1960 to 2000 million years old [24]. In its morphology and developmental stages, this fossil cyanobacterium does not differ from the modern cyanobacterium *Entophysalis major* Ercegovic [25]. In addition, these formations were found to contain small ellipsoidal, spherical, and filamentous microfossils, which may also represent cyanobacteria. Similar chertified microbiotas were found in somewhat younger rocks of Canada [15, 16, 25, 26] and Australia [15, 27, 28].

The deeper-water rocks of the Late Proterozoic contain taxonomically differing associations of microfossils, known as the Gunflint-type microbiota. The two most typical microfossil varieties were found in the 2-billion-year-old Gunflint and Bivabik formations, the Animikie Series, and in some other rocks in North America and Australia [15, 16, 26]. One of these varieties is composed of morphologically simple filamentous and coccoid microfossils (*Gunflintia*, *Animikia*, *Huroniospora*, and others) of hormogonial and chroococcal cyanobacteria [15, 29] and, likely, iron-oxidizing bacteria [19]. The other variety is composed of morphologically more complex fossil forms: *Kakabekia*, *Xenothrix*, *Archaeorstis*, and others, including probable remains of iron bacteria (*Eoastrion*) [19, 30] and, possibly, of lower unicellular eukaryotes (*Eosphaera* and *Eomicrohystridium*).

Additional information on Proterozoic microbiotas has come from the study of organic-wall microfossils, which have been purposefully studied mainly in Russia and China. The most ancient organic-wall microfossils, which represent the remains of simple spherical microorganisms of the genera *Leiominuscula* and *Myxococcoides*, have been found in the 2.8- to 2.9-billion-year-old Neoarchean series of Karelia [31]. Microfossils of the same genera, as well as of the genus *Leiosphaeridia*, were found in the Proterozoic Baltic Shield (2.06–2.3 billion years old) [22], the Besovets Suite (1.9–2.06 billion years old), and in the Pechenga Series of the Kola Peninsula. The very simple morphology of these fossils makes it difficult to unequivocally determine whether or not their nature is biotic. For this reason, they are classified into a conventional group of acritarchs.

The 1.8- to 1.9-billion-year-old Chanchen system of China contains replicas of large (up to several centimeters in diameter) spheroidal microfossils, which were assigned to the genus *Chuaria* [32, 33]. Those fossils are believed to be the remains of either primitive eukaryotes or of empty envelopes of macrocolonies of nostoc cyanobacteria [19, 26, 33–35, 37, 38]. The most ancient known remains of probable eukaryotes were found in the 1.9-billion-year-old Negaunee Iron Formation of North America; these are carbonaceous flat spiral strips, from 0.7 to 1.5 mm in width. The specific morphology and the relatively large size of these fossils suggest that they are the remains of ancient lower eukaryotic algae, which have no modern analogues [33, 39]. Alternatively, they may be the remains of ancient bacteria. It should be noted that the discovery of mats of giant bacteria (up to 1 mm in diameter), such as *Thioploca* and *Thiomarginate*, depreciates the value of cell size as a criterion of eukaryotic affinity.

Fig. 1. Fossil (a, b, d, g, h, j, l) and modern (c, e, f, i, k, m) chroococcal and hormogonial cyanobacteria: (a) *Eogloeocapsa avzyanica* Sergeev, Middle Riphean, Avzyan Suite, southern Urals, ~1200 million years old; (b) *Gloeodiniopsis uralicus* Krylov et Sergeev, Early Riphean, Satkin Suite, southern Urals, ~1400 million years old; (c) modern *Gloeocapsa*; (d) *Eoentophysalis belcherensis* Hofmann, Early–Middle Riphean boundary, Yusmastakh Suite, Anabar Uplift, Siberia, ~1200 million years old; (e) modern *Entophysalis major* Ercegovic, Shark Bay, Australia; (f) modern *Entophysalis*; (g) *Eosynechococcus brevis* Knoll, Early–Middle Riphean boundary, Yusmastakh Suite, Anabar Uplift, Siberia, ~1200 million years old; (h) *Eosynechococcus moorei* Hofmann, Early Riphean, Kotuikan Suite, Anabar Uplift, Siberia, ~1400 million years old; (i) modern *Synechococcus*; (j) *Circumvaginalis elongatus* Sergeev, Early Riphean, Kotuikan Suite, Anabar Uplift, Siberia, ~1400 million years old; (k) modern *Scytonema myochrous* (Dyllwyn) Agardh, Bahamas; (l) *Siphonophycus robustum* (Schopf) empty sheaths, Late Riphean, Minyar Suite, southern Urals, ~800 million years old; (m) modern empty sheaths. Scale bar represents 10 μm.


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(k)
(l)
(h)
(i)
(j)
(m)

Thus, there are grounds to believe that basins in the Late Archean contained diverse prokaryotes and, in the Late Proterozoic, also probable eukaryotes. Since an indisputable demonstration of the biotic origin of the most ancient microfossils is impossible, of great interest is the application of molecular biological approaches to the interpretation of the Early Precambrian fossil record. For instance, the fossil *Gunflintia* trichomes contain bulges, which were first identified as akinetes or heterocysts [29]. Recently, however, such bulges have been interpreted as postmortem alterations of the primarily homogeneous filaments of oscillatorian algae [8, 40]. However, the younger Epworth Group rocks of Canada (about 1.9 billion years in age) contain ellipsoidal fossils classified as *Brevitrichoides* (*Archaeoellipsoides*) [26] and referred with confidence to akinetes of nostoc and anabaena cyanobacteria [9, 41]. The 16S rRNA sequence analysis of modern cyanobacteria suggests that the akinete-forming nostoc and stigonema cyanobacteria are terminal groups on the cyanobacterial phylogenetic tree [6, 8]. If this is the case, the age of the Epworth Group (1.9 billion years) is the minimal age of the main morphological groups of cyanobacteria, whose radiation, according to molecular biological data, occurred very rapidly.

In general, the most ancient microfossils are dated as follows: (a) the indisputable remains of cyanobacteria found in the Belcher Supergroup are about 2.0 billion years old; (b) the possible microfossils of early eukaryotes found in the Negaunee Iron Formation are slightly older than 1.9 billion years; (c) the very probable remains of cyanobacteria found in the Transvaal Supergroup are 2.52–2.55 billion years old; (d) possible remains of cyanobacteria and heterotrophic bacteria are 2.69–2.76 billion years old (the Fortescue Series) or even 3.4–3.5 billion years old (the Onverwacht, Fig Tree, and Warrawoon Series). The chronology of these microfossils reflects not only evolutionary but also taphonomic factors.

The Early–Middle Riphean boundary. Further changes in the associations of chertified and organic-wall microfossils were detected at the Proterozoic–Mesoproterozoic boundary. First, the Gunflint-type microfossils do not occur in the rocks of this geological time, probably due to the fact that iron jaspilite deposits were no longer formed. Second, the fossilized remains of cyanobacteria of this time found in the shallow-water deposits of the littoral and upper littoral zones are dominated by akinete-forming cyanobacteria (mainly their fossilized spores were preserved) [9, 42, 43]. One of the peculiar forms widespread at that time is the genus *Circumvaginalis* Sergeev, representing hollow sheaths composed of funnel-like segments with terminal dark bulges, enclosed into each other (Fig. 1j) [42, 43]. These are most likely hollow sheaths of blue-green algae similar to the modern nostocacean cyanobacteria of the genus *Scytonema* (Fig. 1k).

The prevailing Early–Middle Riphean associations are dominated by ellipsoidal microfossils of the genus *Archaeoellipsoides* (Figs. 1g, 1h); in spite of their similarity to unicellular chroococcal cyanobacteria of the genus *Synechococcus* (Fig. 1i), these are the remains of the akinetes of nostoc or stigonema cyanobacteria [42, 43]. Such microfossils were found in the Anabar Shield in Siberia, Russia [42]; in the Doushantou Formation, southern China [44]; and in the Dismal Lake Group, Arctic Canada [45]. In addition, all these rocks contain short trichomes, described as akinetes of the genus *Archaeoellipsoides* (Fig. 2k); many of them are analogues of the akinetes of the modern cyanobacteria, such as *Entophysalis* (Figs. 2l, 2m). It should be noted that anabaena cyanobacteria and their spores are widespread in modern bodies of fresh water and in desalinated shallow marine basins [46]. Consequently, the abundance of the *Archaeoellipsoides* akinetes in the Early–Middle Riphean deposits is due to geochemical rather than evolutionary factors, e.g., to the conditions of carbonate accumulation. This abundance may result from the complete transformation of cyanobacterial filaments into akinetes, a process that is frequently observed in modern cyanobacteria under certain conditions, particularly at a high concentration of calcium glutamate in the medium [47].

Third, organic-wall microfossils became numerous and diverse in the Early Riphean rocks. The most diverse organic-wall microfossils were found in the Ust-Ilim and Kotuikan Suites of the Anabar Shield [48] and in the Roper Group of Australia [49], which contain not only filamentous and coccoid microfossils, but also the remains of thallomes and large spherical envelopes of eukaryotic algae, as well as some other relatively large and complex fossil forms.

The Neoproterozoic revolution. The Middle–Late Riphean boundary is one of the most significant biostratigraphic boundaries of the Precambrian, which is clearly distinguished upon the analysis of both organic-wall and chertified microfossils. The major event of this time, which was very important for the development of the biosphere and was called the Neoproterozoic revolution, was the diversification of protists. As a result, the Late Riphean deposits contain fossil forms much more complex morphologically. This

Fig. 2. Fossil (a, b, e, f, i, k) and modern (c, d, g, h, j, l, m) cyanobacteria: (a, b) *Obruchevella parva* Reitlinger, Early Cambrian, Chulaktaus Suite, Karatau, southern Kazakhstan, ~520 million years old; (c, d) modern *Spirulina*; (e) *Filiconstrictosus magnus* Yakschin; (f) *F. cephalon* Sergeev et Knoll, Early Riphean, Kotuikan Suite, Anabar Uplift, Siberia, ~1400 million years old; (g, h, j) modern *Nostoc*; (i) *Veteronostocale copiosus* Ogurtsova et Sergeev, Late Riphean–Vendian boundary, Chichkan Suite, Karatau, southern Kazakhstan, ~650 million years old; (k) akinetes of *Archaeoellipsoides bactroformis* Sergeev et Knoll, Early Riphean, Kotuikan Suite, Anabar Uplift, Siberia, ~1400 million years old; (l, m) modern *Entophysalis* akinetes. Single-line and double-line scale bars represent 10 and 50 μm, respectively.

outbreak of biodiversity is confirmed by molecular biological data, which indicate the existence of a great outburst in the evolution of eukaryotes [50] about one billion years ago [36]. Beginning from the Middle–Late Riphean boundary, deposits contain fossil forms with spikes, such as those of the genus *Trachyhystrichosphaera* Timofeev et Hermann [35, 51–54]. Spiked microorganisms were found as fossils in the lower horizons of the Late Riphean deposits of the Lakhandin Series (the Uchuro-Maiskii region), the Derevnin Suite (the Turukhan region), their analogues [55], and many other deposits. Some researchers consider the spiked forms of the genus *Trachyhystrichosphaera* to be a distinguishing feature of the Late Riphean microbiotas [56]. Spiked microfossils are beyond doubt the remains of protists, although their exact biological identification is as yet the subject of debate. The majority of researchers identify such microfossils as remains of *Prasinophyceae* [55, 56]. Furthermore, Late Riphean sediments often contain some other complex fossil forms, such as the branching thallomes of the ancient genera *Ulophyton* Timofeev et Hermann and *Proterocladus* Butterfield, which are analogous to certain modern green algae [56], as well as fossil bangiophyta red algae [57] and numerous fossil remains of unicellular phytoplankton algae [35, 53]. The upper layers of the Late Riphean sediments, not older than 850 million years, were found to contain spiked vaselike microfossils of the genus *Melanocyrillium* Bloeser [43].

Fossil cyanobacteria also exhibited some new morphological varieties at that time. For instance, Middle–Late Riphean sediments sometimes contain the remains of the stalked cyanobacterium *Polybessurus* Fairchild ex Green et al. and the spiral–cylindrical microfossils of the genus *Obruchevella* Reitlinger (Figs. 2a, 2b), which became more abundant in the Vendian and Early Cambrian [35]. As was already mentioned, the evolution of cyanobacteria can be considered to have been completed in the Early Proterozoic. However, Wilmotte and Golubic believe that the modern *Spirulina* cyanobacterium (Figs. 2c, 2d) (the modern analogue of the genus *Obruchevella*) differs from other hormogonial cyanobacteria in nucleotide sequence and morphological characteristics [8]. The differences can be explained by the later appearance of this taxon, although there are alternative interpretations of this phenomenon.

Chertified microfossils of associations of conservative cyanobacteria from shallow-water coastal deposits also exhibited some changes in their composition at that time. For instance, the akinetes of *Nostoc–Stigonema*–like cyanophyta and *Entophysalis* cyanobacteria, which dominate in the Early Proterozoic and Early–Middle Riphean sediments, are relatively rare in the Late Riphean chertified biotas [35, 58]. This fact may be due to the expansion of eukaryotic organisms into prokaryotic ecosystems [43, 59, 60]. Taking into account that unicellular lower eukaryotic microorganisms are morphologically almost indistinguishable from prokaryotic organisms, many microfossils found in Late Riphean sediments and commonly identified as chroococcal cyanobacteria may appear to be lower eukaryotic algae [54], which began to drive out cyanobacteria from favorable econiches in the Late Riphean [42, 43, 58].

By the end of the Late Riphean, many morphologically complex eukaryotic microorganisms became minor or extinct [36, 61–63], so that most Riphean phytoplankton microorganisms with spikes and pins (the genus *Trachyhystrichosphaera* and others) have never been found in the Vendian. Prokaryotic organisms virtually did not change, but some of them (e.g., the genus *Obruchevella*) became larger in size [64]. The Early Vendian period after the Lapland glaciation is marked by the appearance of multicellular organisms without a skeleton and the wide distribution of the so-called Pertatatak-type associations, dominated by large spiked microfossils. Such associations, composed of large spiked acritarchs, were found in the Pertatatak Formation of southern Australia, the Prince Karl Forland Series of Spitsbergen, and in some other rocks, being most abundant in the phosphate–chert sediments of the Doushantou Formation of China [65]. These peculiar and morphologically rather complex microfossils, which are formally united into the groups of acanthomorphous, hercomorphous, and other acritarchs, probably represent a heterogeneous group that includes green algae, dinoflagellates, and other protists. It should be noted that spiked forms, which appeared in the Late Riphean and increased their population in the Early Vendian, became dominant only in the Cambrian, when the first organisms producing a skeleton came into being. The expansion of spiked forms began in the Atdabanian time, when they became dominant among both organic-wall and chertified microbiotas. The outbreak of spiked forms reflects a transition from the Precambrian biosphere, dominated by morphologically simple and mostly prokaryotic microorganisms, to the Proterozoic biosphere, dominated by eukaryotic organisms.

ACTUOPALEONTOLOGY OF CYANOBACTERIAL COMMUNITIES

Modern cyanobacterial communities, or mats, in which cyanobacteria are the main producers of organic matter, are analogues of ancient stromatolites. Thus, microbial communities with close metabolic relations between their members turned out to be very stable throughout the Earth's history, although more organized competitors displaced them from propitious habitats to extreme econiches, such as hypersaline lagoons and volcanic environments.

Since the 1970s, cyanobacterial mats have become the subject of extensive research. Best studied are the thermophilic mats of Yellowstone National Park and Iceland and the halophilic mats of the Sinai, Israel, Mexico, and Australia [66–70]. There are data on the mats of the Bermudas and the Bahamas, as well as of Japan [71]. The results of the investigation of the thermophilic mats of Kamchatka Peninsula and Kunashir Island and the halophilic mats of the Sivash are summarized in publications [72–75]. Studies of alkaliphilic microbial communities, few until recently [76–78], are of increasing interest due to the possible role of these communities in the origin of continental biota [79, 80].

When drawing an analogy between ancient stromatolites and modern cyanobacterial communities, researchers must take into account the great difference between ancient and modern geochemical conditions on the Earth. For this reason, experimental data on modern communities growing under natural conditions must be completed with the simulation of the development of these communities under laboratory conditions [81]. As natural models, we chose the communities of the relatively low-temperature thermal springs of the Uzon caldera on Kamchatka, the Golovnin caldera on Kunashir, the halophilic mats of the Sivash in the Crimea, and the alkaliphilic mats of Buryatia and Tuva.

The structure of cyanobacterial mats. Cyanobacterial mats have a multilayered structure and consist of three main zones: (1) the upper aerobic zone of cyanobacterial growth; (2) the middle zone of the development of purple or green phototrophic bacteria; and (3) the bottom zone, distinguished by the growth of strict anaerobes.

Modern mats are commonly dominated by filamentous oscillatorian cyanobacteria, although there are some exceptions. Thus, the high-temperature mats of Yellowstone and the Kurils are dominated by *Synechococcus elongatus* (*Synechococcus lividus*); the mats of Kamchatka, by *Mastigocladus laminosus*; and Australian mats, by *Entophysalis* sp. Stratified mats composed of many layers are only formed by filamentous cyanobacteria (communities with the involvement of unicellular cyanobacteria are structurally unstable). There are several reasons why cyanobacteria can ensure structural stability of mats. First, unlike eukaryotic algae, cyanobacteria are capable of oxygenic photosynthesis under extreme conditions. Second, they are able to fix nitrogen. Third, oscillatoria cyanobacteria are motile, which allows cyanobacterial filaments to interweave with each other, forming a dense tissue.

The upper layers of mats, from 0.5 to 1 mm in thickness (in the case of halophilic mats, up to 2 mm thick), contain actively photosynthesizing cyanobacteria: *Phormidium laminosum* and *Oscillatoria terebriformis* in relatively low-temperature thermophilic mats; *Microcoleus chthonoplastes* in halophilic mats (this cyanobacterium forms thick bundles to survive hypersaline conditions); and *Microcoleus chthonoplastes* and *Phormidium molle* in alkaliphilic mats. Apart from these dominant cyanobacteria, the upper layers of mats often contain other species of the genera *Phormidium, Oscillatoria, Lyngbya,* and *Spirulina.*

The middle part of mats is the zone of development of phototrophic bacteria, such as *Chloroflexus aurantiacus* in thermophilic mats, *Thiocapsa* in halophilic mats, and *Ectothiorhodospira* in alkaliphilic mats. These phototrophic bacteria mainly grow organotrophically by oxidizing cyanobacterial metabolites, although they are also able to oxidize hydrogen sulfide and thus to participate in the sulfur cycle.

The bottom, anaerobic, part of mats is the zone where methanogens and sulfidogens develop.

The development of different groups of organisms in mats is accompanied by the formation of a geochemical barrier with abrupt gradients of redox potential (300–600 mV) and pH (2–4 units in magnitude). The oxygen-producing capacity of mats can be estimated from their content of chlorophyll, which reaches 1 g/m^2 and exceeds that of the green parts of higher plants [75].

The similar architectonics of mats from different econiches is likely determined by the similar functions of component organisms and the same organization of trophic chains in the mats. Oxygenic photosynthesis occurs in the upper 1- to 2-mm-thick layer of mats, which almost completely absorbs the incident sunlight. An important role in the degradative part of mats is played by the sulfur cycle.

The degree to which the component organisms of mats can exist individually is unknown, although presumably they are strongly dependent on each other, forming an integral system [73]. It is the close cooperation of the organisms of mats that predetermined the extreme conservatism of both the mats and the component organisms, which has not changed for at least 2–2.5 billion years. It should be noted that fossilized were only undegraded cyanobacteria from the upper layer of mats, which were either silicified or mummified at the early stages of diagenesis and had no time to undergo considerable postmortem alterations.

Gas transformations by cyanobacterial communities. In natural habitats, mats often produce gas bubbles, which occur either beneath the mats or between their layers and may be as large as 50 cm in diameter. In the case of mats occurring in relatively low-temperature thermal springs, the gas composition of the bubbles produced by the mats is considerably different from that of the atmosphere and the gas of the springs. The latter usually contains 70–90% of CO_2 and virtually no O_2, whereas the gas produced by the mats contains less CO_2 and H_2 and more O_2 and CH_4 [73]. These changes in the gas composition were additionally studied in detail in laboratory experiments.

The mat obtained in the laboratory corresponded to natural mats in the structure and species composition [82] and represented an integral community that included cyanobacteria and other microorganisms. It had a stratified structure, in which cyanobacterial layers alternated with mineral streaks. Therefore, the multilayered structure of mats is an inherent property and is not related to the conditions of their diurnal illumination [83, 84].

Both the mat and its component cyanobacteria isolated in pure cultures were able not only to take up CO_2 and evolve O_2, but also to consume H_2S (with the formation of sulfur) [85] and H_2 [86]. Both H_2S and H_2 cause manifold stimulation of the growth of cyanobacteria. Thus, cyanobacteria transform the composition of the gases emerging with the hot spring water. Oxygen exerts a detrimental effect on the growth of cyanobacteria, but it is easily discharged into the atmosphere from the hot water. CH_4 slightly stimulates the growth of cyanobacteria [81]. H_2 is utilized in the hydrogenase reaction [86]. When placed in an atmosphere similar to the gas mixture emanated by thermal springs or in an atmosphere similar to the presumable primary atmosphere of the Earth, cyanobacteria change the gas composition so that the content of O_2 increases to a value slightly above 20% and the content of reduced gases, except for CH_4, decreases to zero [75]. Most probably, oxygen at a concentration of 20% hinders the growth of cyanobacteria. This does not, however, imply that it is the accumulation of O_2 in the ancient atmosphere that was responsible for the termination of the supremacy of cyanobacteria. Indeed, under the conditions of active photosynthesis, O_2 bubbles are retained in mats, and cyanobacteria and their satellites reside under 100% oxygen saturation.

Thus, laboratory and field studies show that cyanobacterial mats transform the gas composition and, hence, they could decrease the concentration of CO_2 and provide the ancient Earth's atmosphere with oxygen.

Mineralization of cyanobacterial communities. Thermal springs often contain mineral structures with travertine or siliceous deposits resembling stromatolites. This makes it possible to study mineralization under both field and laboratory conditions in order to gain insight into the activity of cyanobacteria in the geological past.

By comparing the fossilized remains of microorganisms found in the aforementioned structures, Krylov *et al.* [87] succeeded in conceiving the process of chertification of microbial cells. Silica present in a solution first penetrates into the cell and precipitates in the form of globules on the cell walls and septa. Separate siliceous globules merge into a continuous shell surrounding the cell. The outer surface of the shell is smooth and has the shape of the cell, whereas the inner surface is globular. Then, opal particles fill the empty space between filaments and inside them until complete chertification has occurred and a solid chertified rock has been formed. Laboratory experiments showed that silica penetrates the walls and septa of only such cyanobacterial filaments that are at certain stages of postmortem degradation. Therefore, only dead cells can be chertified. Living cells have thick slimy sheaths, which protect them from high silicon concentrations. Furthermore, silicon can penetrate into a cell only after its death, when the barrier function of the cell membrane is impaired.

The finding of modern fossilized microorganisms in chertified and limed cyanobacterial mats morphologically similar to ancient microfossils gave impetus to the study of postmortem changes in cyanobacteria occurring in different parts of colonies and mats. The experiments of Gerasimenko and Krylov showed that the diversity of the chertified microfossils of Uzon is determined by not only the species diversity of cyanobacteria, but also the morphological diversity of cells (e.g., within the species *Mastigocladus laminosus*) and by the different degree of postmortem alterations in cells and filaments [40].

When considering the problem of mineralization of cyanobacteria, one cannot escape the consideration of the problem of phosphatization of cyanobacteria, a process that is directly related to the accumulation of phosphate deposits. The indisputable similarity of the organic remains found in ancient phosphorites to modern remains of microorganisms (first of all, cyanobacterial) and the similar structure of ancient stratified phosphorites and modern cyanobacterial mats suggest the crucial role of cyanobacteria in the formation of phosphate deposits. Experiments with an *M. chthonoplastes* culture showed that, at a certain concentration of phosphorus in the medium, the culture gives rise to microfossils similar to those found in ancient phosphorites [88, 89].

Phosphorus penetrates into the cell via active transport across the cell membrane [90], which can occur against the phosphorus concentration gradient, and is accumulated in the cell at concentrations higher than in the surrounding medium. This phenomenon is of great biological significance: phosphorus reserves in cells allow them to survive for a long time without external phosphorus sources. In *M. chthonoplastes*, active transport of phosphorus occurs at a maximum rate over the first 3 min, decreasing by two orders of magnitude over the next 3 days. Experiments showed that not all the phosphorus consumed from the medium penetrates into the cell: part of it (which is the greater the higher the concentration of phosphorus in the medium) is adsorbed on the cell surface.

The phosphorus adsorbed on the cell surface as calcium phosphate forms mineral tubes around cyanobacterial filaments. Phosphate mineralizes only the slimy sheath, leaving trichomes unchanged. During such mineralization, the trichomes remain viable and may even leave the mineralized sheath, which in this case looks like a hollow tube. Sufficiently high concentrations of phosphorus in the medium cause the death of cyanobacteria, followed by mineralization of the trichomes themselves.

X-ray studies of the mineralized sheaths formed around cyanobacterial filaments showed that they are composed of slightly crystalline phosphate minerals of the apatite type, with the major diffraction maximum close to that of francolite [89]. In the presence of NaF in the medium, mineralized sheaths consist of microtubes made up of micron-size particles of fluorocarbonate–apatite [91].

A comparative study of phosphorites from different deposits unambiguously showed that cyanobacterial mats are typical of the biocenoses in which these deposits were formed [92]. These mats are carbonatized, including the component cyanobacteria; the carbonate minerals are represented by aragonite and calcite.

A strong correlation between the concentrations of calcium carbonate and cyanobacterial chlorophyll in mats [73] suggests that one of the causes of mat carbonatization is alkalinization of the medium due to active photosynthesis in cyanobacteria. Experiments showed that the precipitation of calcium carbonate is maximum under the conditions optimal for photosynthesis [93]. Increased concentrations of calcium carbonate in the medium led to morphological changes in cyanobacteria, namely, the formation of a slimy sheath and the precipitation of carbonate particles on it. Then, the entire trichome became mineralized.

The ability of cyanobacteria to precipitate carbonate has been studied by many researchers [94, 95]. The fundamental property of cyanobacteria responsible for this ability is that at a low concentration of CO_2 they are able to utilize HCO_3^- ions in the course of oxygenic photosynthesis. In cells, HCO_3^- ions transform into CO_2. Calcium carbonate crystals are deposited either on the cyanobacterial cell walls or on the slimy sheaths surrounding the cells. The capacity for calcium precipitation varies among species, and some species exhibit individual shape of the crystals formed [96–99]. Most often, calcium carbonate is deposited on the sheaths, forming tubes, but it may also be deposited between cyanobacterial filaments or cells. It should be noted that, in saturated calcium carbonate solutions, carbonate can be deposited not only biogenically but also chemogenically. For this reason, the type of genesis of calcium carbonate is difficult to establish. The presence of other compounds in the medium affects the metabolism of cyanobacterial communities. For instance, increased concentrations of phosphorus compounds in the medium inhibit the deposition of carbonates [100].

Carbonatization of cyanobacterial communities is of great geological significance. Modern stromatolites and algae with calcified sheaths are scarce. Presently, carbonates are deposited by cyanobacteria primarily in freshwater environments, including thermal springs, where carbonate muds and travertines are formed [99, 101, 102]. In marine basins with a normal salinity of waters, the deposition of carbonates by cyanobacteria is insignificant. Calcified algal–bacterial communities and stromatolites mainly occur in hypersaline bodies of water with an increased content of carbonates, in which it is difficult to distinguish the biogenic and abiogenic types of carbonate sedimentation [103].

In the Precambrian, the time of the supremacy of cyanobacteria, calcareous cyanobacteria were scarce [104–106]. Calcareous cyanobacteria and eukaryotic algae became abundant at the Precambrian–Cambrian boundary, in the Paleozoic, and in the Mesozoic [94]. The reasons for this are unlikely to be related to the metabolism of cyanobacteria themselves, but rather are determined by the evolution of the environment and the appearance of organisms with skeletons, which radically changed all biogeochemical cycles in the biosphere and hydrosphere [105]. In the Paleogene and Neogene, the occurrence of stromatolites and algae with calcified sheaths in marine (but not lacustrine) lime sediments drastically decreased. This may be due to the appearance in the Cretaceous Period of lithothamnion algae, which almost completely forced cyanobacteria out of shallow-water marine environments with normal-salinity waters [13].

CONCLUSION

Thus, the available fossil records of Precambrian organisms are sufficiently representative and give an idea of the evolution of life at its early stages. The very term “Cryptozoic” (“cryptic life”) now makes no sense because there is already a more or less adequate knowledge of ancient organisms and their evolution. During the first nearly three billion years of life on the Earth, dominant were prokaryotic, including cyanobacterial, communities and lower eukaryotic organisms. Cyanobacteria, which are well preserved in ancient deposits and have virtually not changed evolutionarily over the last two billion years owing to their remarkable conservatism, provide a unique opportunity to understand the paleobiological features of the ancient biosphere and to retrieve the geochemical and biogeochemical processes that occurred in the Precambrian. This can be done by studying a wide range of modern cyanobacterial communities dwelling in diverse environments and allowing us to gain insight into the processes that occurred on the Earth in the distant past and that have left their traces in ancient deposits.

ACKNOWLEDGMENTS

This work was supported by grant no. 00-05-64603 from the Russian Foundation for Basic Research and by INTAS grant no. 97-30776.

REFERENCES

1. Zavarzin, G.A., The Non-Darwinian Domain of Evolution, *Vestn. Ross. Akad. Nauk*, 2000, vol. 70, no. 5, pp. 405–425.
2. Geitler, L., Cyanophyceae, *A. Pascher’s die Süsswasserflora Deutschlands, Ostrerreichs und der Schweiz*, Jena: Gustav Fisher, 1925, Bans 12.
3. Geitler, L., Cyanophyceae, *Rabenhorst’s Kryptogamen-Flora*, Leipzig: Akademie Verlagsgellschaft, 1932, Bans 14.

4. Elenkin, A.A., *Sinezelenye vodorosli SSSR* (The Blue–Green Algae of USSR), Moscow: Akad. Nauk SSSR, 1938, no. 1.
5. Elenkin, A.A., *Sinezelenye vodorosli SSSR* (The Blue–Green Algae of USSR), Moscow: Akad. Nauk SSSR, 1949, no. 2.
6. Giovannoni, S.J., Turner, S., Olsen, G.J., *et al.*, Evolutionary Relationships among Cyanobacteria and Green Chloroplasts, *J. Bacteriol.*, 1988, vol. 170, pp. 3584–3592.
7. Giovannoni, S.J., Rappé, M.S., Gordon, D., Urbach, V., Suzuki, M., and Field, K.G., Ribosomal RNA and the Evolution of Bacterial Diversity, *Evolution of Microbial Life: 54th Symposium of the Society for General Microbiology,* Roberts Mc., L. *et al.*, Eds., University of Warwick, 1996, pp. 63–85.
8. Wilmotte, A. and Golubic, S., Morphological and Genetic Criteria in the Taxonomy of Cyanophyta, Algol. Studies, 1991, vol. 64, no. 1, pp. 1–24.
9. Golubic, S., Sergeev, V.N., and Knoll, A.H., Mesoproterozoic Archaeoellipsoides: Akinetes of Heterocystous Cyanobacteria, *Lethaia*, 1995, vol. 28, no. 2, pp. 285–298.
10. Krylov, I.N., *Stolbchatye vetvyashchiesya stromatolity rifeya Yuzhnogo Urala i ikh znachenie dlya stratigrafii verkhnego dokembriya* (The Riphean Columnar Branched Stromatolites of Southern Ural and Their Significance for the Stratigraphy of the Late Precambrian), Moscow: Nauka, 1963.
11. Krylov, I.N., *Stromatolity rifeya i fanerozoya SSSR* (The Riphean and Phanerozoic Stromatolites of USSR), Moscow: Nauka, 1975.
12. Vidal, G. and Knoll, A.H., Radiations and Extinction of Plankton in the Late Proterozoic and Early Cambrian, *Nature* (London), 1982, vol. 297, no. 5861, pp. 57–60.
13. Maliva, R.G., Knoll, A.H., and Siever, R., Secular Change in Chert Distribution: A Reflection of Evolving Biological Participation in the Silica Cycle, *Palaios*, 1989, vol. 4, no. 5, pp. 519–532.
14. Schopf, J.W. and Walter, M.R., Archean Microfossils, New Evidence of Ancient Microbes, *Earth's Earliest Biosphaere: Its Origin and Evolution*, Schopf, J.W., Ed., Princeton: Princeton Univ. Press, 1983, pp. 241–299.
15. Hofmann, H.J. and Schopf, J.W., Early Proterozoic Microfossils, *Earth's Earliest Biosphaere: Its Origin and Evolution*, Schopf, J.W., Ed., Princeton: Princeton Univ. Press, 1983, pp. 321–360.
16. *The Proterozoic Biosphaere: A Multidisciplinary Study*, Schopf, J.W. and Klein, C., Eds., Cambridge: Cambridge Univ. Press, 1992.
17. Buick, R., Microfossil Recognition in Archean Rocks: An Appraisal of Spheroids and Filaments from a 3500 M.Y. Old Chert–Barite Unit at North Pole, Western Australia, *Palaios*, 1991, vol. 5, no. 4, pp. 441–459.
18. Walsh, M.M., Microfossils and Possible Microfossils from the Early Archean Onverwacht Group, Barberton Mountain Land, South Africa, *Precambrian Res.*, 1992, vol. 54, no. 2, pp. 271–293.
19. Knoll, A.H., Archean and Proterozoic Paleontology, *Palynology: Principles and Applications, Jansonius, J. and McGregor, D.C., Eds., Am. Assoc. Stratigraphic Palynologists Foundation*, 1996, vol. 1, pp. 51–80.
20. Altermann, W., Discussion on "Zircon–Pb Evaporation Age Determination of the Oax Tree Formation, Chuniesport Group, Transvaal Sequence: Implication the Transvaal–Griqualand West Basin Correlations," *S. Afr. J. Geol.*, 1996, vol. 99, no. 3, pp. 337–338.
21. Klein, C., Beukes, N.J., and Schopf, J.W., Filamentous Microfossils in the Early Proterozoic Transvaal Supergroup: Their Morphology, Significance, and Paleoenvironmental Setting, *Precambrian Res.*, 1987, vol. 36, no. 1, pp. 81–94.
22. Melezhik, V.A., Fallick, A.E., and Clark, T., Two Billion Year Old Isotopically Heavy Carbon: Evidence from the Labrador Trough, Canada, *Can. J. Earth Sci.*, 1997, vol. 34, no. 3, pp. 217–285.
23. Hofmann, H.J., Precambrian Microflora, Belcher Island, Canada: Significance and Systematics, *J. Paleontol.*, 1976, vol. 50, no. 10, pp. 1040–1073.
24. Chandler, F.W. and Parrish, R.R., Age of the Richmond Gulf Group and Implications for Rifting in the Trans-Hudsonian Orogen, Canada, *Precambrian Res.*, 1989, vol. 44, no. 2, pp. 277–288.
25. Golubic, S. and Hofmann, H.J., Comparison of Holocene and Mid-Precambrian *Entophysaliceae* (*Cyanophyta*) in Stromatolitic Algal Mats: Cell Division and Degradation, *J. Paleontol.*, 1976, vol. 50, no. 6, pp. 1074–1082.
26. Hofmann, H.J. and Grotzinger, J.P., Shelf-Facies Microbiota from the Odjick and Rocknest Formations (Epworth Group, 1.89 Ga), NW Canada, *Can. J. Earth Sci.*, 1985, vol. 22, no. 12, pp. 1781–1792.
27. Muir, M.D., Proterozoic Microfossils from the Amelia Dolomite, McArthur Basin, Northern Territory, *Alcheringa*, 1976, vol. 1, no. 1, pp. 143–158.
28. Oehler, D.Z., Microflora of the Middle Proterozoic Balbirini Dolomite (McArthur Group) of Australia, *Alcheringa*, 1978, vol. 2, pp. 269–309.
29. Cloud, P.E., Beginning of Biospheric Evolution and Their Biogeochemical Consequences, *Paleobiology,* 1976, vol. 2, no. 3, pp. 351–387.
30. Zavarzin, G.A., The Biology of Iron Bacteria, *Dokl. Akad. Nauk SSSR*, 1967, vol. 172, no. 3, pp. 764–767.
31. Bibikova, E.V., Lobach-Zhuchenko, S.V., Semikhatov, M.A., *et al.*, The Geochronological Scale of the Precambrian Western European Platform and Its Tectonic Framework, *Izv. Akad. Nauk SSSR, Ser. Geol.*, 1989, no. 4, pp. 3–21.
32. Hofmann, H.J. and Chen, J., Carbonaceous Megafossils from the Precambrian (1800 Ma) Near Jixian, Northern China, *Can. J. Earth Sci.*, 1981, vol. 18, no. 4, pp. 443–447.
33. Hofmann, H.J., Proterozoic Carbonaceous Compression ("Metaphytes" and "Worms"), *Early Life on Earth, Nobel Symp. no. 84*, New York: Columbia Univ. Press, 1994, pp. 342–357.

34. Sun, W.G., Paleontology and Biostratigraphy of Late Precambrian Macroscopic Colonial Algae *Chuaria* Walcott and *Tawuia* Hofmann, *Palaeontographica B*, 1987, vol. 203, no. 1, pp. 109–134.
35. Sergeev, V.N., *Okremnennye mikrofossilii dokembriya i kembriya Urala i Srednei Azii* (The Precambrian and Cambrian Chertified Microfossils of Ural and Central Asia), Moscow: Nedra, 1992.
36. Knoll, A.H., The Early Evolution of Eukaryotes: A Global Perspective, *Science*, 1992, vol. 256, pp. 622–627.
37. Sergeev, V.N., Microfossils in Cherts from the Middle Riphean (Mesoproterozoic) Avzyan Formation, Southern Ural Mountains, Russian Federation, *Precambrian Res.*, 1994, vol. 1, no. 2, pp. 231–254.
38. Steiner, M., *Chuaria circularis* Walcott 1899: Megaspheromorphic Acritarch or Prokaryotic Colony?, *Acta Univ. Carolinae, Geologia*, 1996, vol. 4, no. 3/4, pp. 234–244.
39. Han, T.-M. and Runnegar, B., Megascopic Eucaryotic Algae from the 2.1-Billion-Year-Old Negaunee Iron Formation, Michigan, *Science*, 1992, vol. 257, pp. 232–235.
40. Gerasimenko, L.M. and Krylov, I.N., Post-Mortem Changes in Cyanobacteria from the Algal-Bacterial Mats of Thermal Springs, *Dokl. Akad. Nauk SSSR*, 1967, vol. 172, no. 1, pp. 201–203.
41. Sergeev, V.N., Knoll, A.H., and Grotzinger, G.P., Paleobiology of the Mesoproterozoic Billyach Group, Anabar Uplift, Northern Siberia, *Paleontol. Soc. Mem. 39*, 1995.
42. Knoll, A.H. and Sergeev, V.N., Taphonomic and Evolutionary Changes across the Mesoproterozoic–Neoproterozoic Transition, *N. Jb. Geol. Palaontol. Abh.*, 1995, vol. 195, nos. 1–3, pp. 289–302.
43. Sergeev, V.N., The Riphean Chertified Microfossils of Anabar Uplift, *Stratigraf. Geol. Korrelyatsiya,* 1993, vol. 1, no. 3, pp. 35–50.
44. Zhang Yun, Coccoid Microfossils from the Doushantou Formation (Late Sinian) of Southern China, *Precambrian Res.*, 1985, vol. 28, pp. 163–173.
45. Horodyski, R.J. and Donaldson, J.A., Microfossils from the Middle Proterozoic Dismal Lakes Group, Arctic Canada, *Precambrian Res.,* 1980, vol. 11, pp. 125–159.
46. Gibson, C.E. and Smith, R.V., Freshwater Plankton, *The Biology of Cyanobacteria*, Carr, N.G. and Whitton, B.A., Eds., Berkeley: Univ. California Press, 1982, pp. 387–412.
47. Nichols, J.M. and Adams, D.G., Akinetes, *The Biology of Cyanobacteria,* Carr, N.G. and Whitton, B.A., Eds., Berkeley: Univ. California Press, 1982, pp. 87–112.
48. Veis, A.F. and Vorob'eva, N.G., The Riphean and Vendian Microfossils of Anabar Uplift, *Izv. Akad. Nauk SSSR, Ser Geol.*, 1992, no. 1, pp. 114–130.
49. Peat, C.J., Muir, M.D., Plumb, K.A., McKirdy, D.M., and Norvick, M.S., Proterozoic Microfossils from the Roper Group, Northern Territory, Australia, *BMR J. Australian Geol. Geophys.,* 1978, vol. 3, pp. 1–17.
50. Sogin, M.L., Gunderson, J.H., Elwood, H.J., *et al.*, Phylogenetic Meaning of the Kingdom Concept: An Unusual Ribosomal RNA from *Giardia lamblia, Science,* 1989, vol. 243, pp. 75–77.
51. Timofeev, B.V., German, T.N., and Mikhailova, N.S., *Mikrofossilii dokembriya, kembriya i ordovika* (Precambrian, Cambrian, and Ordovician Microfossils), Leningrad: Nauka, 1976.
52. Yankauskas, T.V., Mikhailova, N.S., German, T.N., Sergeev, V.N., *et al.*, *Mikrofossilii dokembriya SSSR* (Precambrian Microfossils in USSR), Moscow: Nedra, 1989.
53. Knoll, A.H., Microorganisms of the Late Precambrian Hunnberg Formation, Nordaustlanded, Svalbard, *J. Paleontol.*, 1984, vol. 58, pp. 131–162.
54. Knoll, A.H., Sweet, K., and Mark, J., Paleobiology of a Neoproterozoic Tidal Flat Lagoonae, the Dracen Conglomerate Formation, Spitsbergen, *J. Paleontol.*, 1991, vol. 65, no. 4, pp. 531–570.
55. Petrov, P.Yu. and Veis, A.F., The Facial–Ecological Structure of the Late Riphean Derevnin Microbiota, Turukhan Uplift, Siberia, *Stratigr. Geol. Korrelyatsiya*, 1995, vol. 3, no. 5, pp. 18–51.
56. Butterfield, N.J., Knoll, A.H., and Swett, K., Paleobiology of the Neoproterozoic Svanbergfiellet Formation, Spitsbergen, *Fossils & Strata*, 1994, no. 34.
57. Butterfield, N.J., Knoll, A.H., and Swett, K., A Bangiophyta Red Alga from the Proterozoic of Arctic Canada, *Science*, 1990, vol. 250, pp. 104–107.
58. Sergeev, V.N., Knoll, A.H., Kolosova, S.P., and Kolosov, P.N., Microfossils in Cherts from the Mesoproterozoic (Middle Riphean) Debengdin Suite, Olenek Uplift, Northeastern Siberia, *Stratigr. Geol. Korrelyatsiya*, 1994, vol. 2, no. 1, pp. 23–38.
59. Sergeev, V.N., Mesoproterozoic Microbiotas of the Northern Hemisphere and the Meso–Neoproterozoic Transition, *Proc. 30th Int. Geol. Congress,* Beijing, 1997, vol. 1, pp. 177–185.
60. Sergeev, V.N., Microfossils in Phanerozoic Stratigraphy, *Rifei Severnoi Evrazii. Geologiya. Obshchie problemy stratigrafii* (Riphean in Northern Eurasia: General Stratigraphic Problems in Geology), Yekaterinburg: Ural. Otd. Ross. Akad. Nauk, 1997, pp. 21–28.
61. Vidal, G. and Knoll, A.H., Proterozoic Plankton, *Memoir of Geological Society of America*, 1983, no. 161, pp. 265–277.
62. Burzin, M.B., Organic-Wall Microfossils and Events in Late Vendian, Eastern European Platform, *Stratigrafiya verkhnego proterozoya SSSR: Rifei i vend* (The Stratigraphy of Late Proterozoic in USSR: Riphean and Vendian), Ufa: Bashkirgeologiya, 1990, pp. 37–39.
63. Burzin, M.B., Major Trends in the Historical Development of Phytoplankton in Late Precambrian and Early Cambrian, *Ekosistemnye perestroiki i evolyutsiya biosfery* (Ecological Transitions and the Evolution of the Biosphere), Moscow: Nedra, 1994, pp. 51–62.
64. Golovenok, V.K. and Belova, M.Yu., Precambrian Microfossils in the Billyach Group Cherts, Anabar Uplift, *Paleontol. Zh.*, 1984, no. 4, pp. 20–30.
65. Zhang Yun, Yin Leiming, Xiao Shuhai, and Knoll, A.H., Permineralized Fossils from the Terminal Proterozoic

Doushantou Formation, South China, *J. Paleontol.*, 1998, vol. 72, Memoir 50.

66. *Microbial Mats: Stromatolites*, Cohen, Y. *et al.*, Eds., New York: Allan R. Liss, 1984.
67. *Microbial Mats: Stromatolites*, Cohen, Y. and Rosenberg, E., Eds., Washington: Am. Soc. Microbiol., 1989.
68. *Microbial Mats: Structure, Development, and Environmental Significance, NATO ASI Series*, Stal, L.J. and Caumette, P., Eds., Heidelberg: Springer-Verlag, 1994, vol. G35.
69. Krumbein, W., Cohen, Y., and Shilo, M., Solar Lake (Sinai): 4. Stromatolitic Cyanobacterial Mats, *Limnol. Oceanol.*, 1977, vol. 22, pp. 635–856.
70. Stal, L., Cyanobacterial Mats and Stromatolites, *The Ecology of Cyanobacteria*, Whitton, B. and Potts, M., Eds., Netherlands: Kluwer Academic, 2000, pp. 61–120.
71. *Microbial Mats in Japan: Microbial Biomineralization*, Tazakik, K., Ed., Kanazava: Kanazava Univ. Press, 1997.
72. *Kal'dernye mikroorganizmy* (Calderic Microorganisms), Zavarzin, G.A., Ed., Moscow: Nauka, 1989.
73. Gerasimenko, L.M., Nekrasova, V.K., Orleanskii, V.K., *et al.*, Primary Production in Halophilic Cyanobacterial Communities, *Mikrobiologiya*, 1989, vol. 58, no. 3, pp. 507–514.
74. Zavarzin, G.A., Gerasimenko, L.M., and Zhilina, T.N., Cyanobacterial Communities in the Hypersaline Lagoons of Sivash, *Mikrobiologiya*, 1993, vol. 62, no. 6, pp. 1144–1158.
75. Gerasimenko, L.M. and Zavarzin, G.A., Relict Cyanobacterial Communities, *Problemy evolyutsii vedushchikh komponentov biosfery* (Some Problems of the Evolution of the Primary Components of the Biosphere), Moscow: Nauka, 1993, pp. 221–252.
76. Doemel, W. and Brock, T., Structure, Growth, and Decomposition of Algal–Bacterial Mats in Alkaline Hot Springs, *Appl. Environ. Microbiol.*, 1977, vol. 34, pp. 433–442.
77. Guerrero, M., Tadeo, A., and de Wit, R., Environmental Factors Controlling the Development of Microbial Mats in Inland Saline Lakes: The Granulometric Composition of the Sediment, *Microbial Mats, NATO ASI Ser. V. G35*, Stal, L. and Caumette, P., Eds., Berlin: Springer-Verlag, 1994, pp. 85–90.
78. Schultze-Lam, S., Ferris, F., Sherwood-Lollar, B., and Gerits, J., Ultrastructure and Seasonal Growth Patterns of Microbial Mats in Temperate Climate Saline–Alkaline Lakes: Goodenouch Lake, British Columbia, Canada, *Can. J. Microbiol.*, 1996, vol. 42, pp. 147–161.
79. Zavarzin, G.A., Epicontinental Soda Lakes as the Possible Relict Biotopes of Terrestrial Biota Formation, *Mikrobiologiya*, 1993, vol. 62, pp. 789–800.
80. Zavarzin, G.A., Zhilina, T.N., and Kevbrin, V.V., The Alkaliphilic Microbial Community and Its Functional Diversity, *Mikrobiologiya*, 1999, vol. 68, no. 15, pp. 579–599.
81. Bil'dushkinov, S.S., Nekrasova, V.K., and Gerasimenko, L.M., The Role of Photosynthesizing Microorganisms in the Gas Metabolism of Cyanobacterial Communities, *Mikrobiologiya*, 1985, vol. 54, no. 4, pp. 517–522.
82. Orleanskii, V.K. and Gerasimenko, L.M., The Laboratory Simulation of a Thermophilic Cyanobacterial Community, *Mikrobiologiya*, 1982, vol. 51, no. 4, pp. 538–542.
83. Orleanskii, V.K. and Raaben, M.E., A Laboratory Model of a Nodular Stromatolite, *Algologiya*, 1996, vol. 6, no. 1, pp. 57–61.
84. Orleanskii, V.K. and Raaben, M.E., A Laboratory Model of Branched Columnar Stromatolites, *Algologiya*, 1997, vol. 7, no. 12, pp. 185–188.
85. Cohen, Y., Jorgensen, B., Padan, E., and Shilo, M., Sulfide-Dependent Anoxygenic Photosynthesis in the Cyanobacterium *Oscillatoria limnetica*, *Nature* (London), vol. 257, pp. 489–492.
86. Gerasimenko, L.M., Miller, Yu.M., Kapustin, O.A., and Zavarzin, G.A., The Uptake of Hydrogen by the Thermophilic Cyanobacterium *Microcoleus chthonoplastes, Mikrobiologiya*, 1987, vol. 56, no. 4, pp. 553–558.
87. Krylov, I.N., Orleanskii, V.K., and Tikhomirova, N.S., Chertification: Secular Preparations, *Priroda*, 1989, no. 4, pp. 73–78.
88. Gerasimenko, L.M., Goncharova, I.V., Zhegallo, E.A., *et al.*, The Mineralization (Phosphatization) of Filamentous Cyanobacteria, *Litologiya Polezn. Iskop.*, 1966, no. 2, pp. 208–214.
89. Gerasimenko, L.M., Zavarzin, G.A., Rozanov, A.Yu., and Ushatinskaya, G.T., The Role of Cyanobacteria in the Formation of Phosphorite Deposits, *Zh. Obshch. Biol.*, 1999, vol. 64, no. 4, pp. 415–430.
90. Kulaev, I.S., *Biokhimiya vysokomolekulyarnykh polifosfatov* (The Biochemistry of High-Molecular-Weight Polyphosphates), Moscow: Mosk. Gos. Univ., 1975.
91. Goncharova, I.V., Gerasimenko, L.M., Zavarzin, G.A., and Ushatinskaya, G.T., Current Formation of Mineral Phosphate Microtubes in the Presence of the Halophilic Cyanobacterium *Microcoleus chthonoplastes, Curr. Microbiol.*, 1983, vol. 27, pp. 187–190.
92. Zhegallo, E.A., Rozanov, A.Yu., Ushatinskaya, G.T., *et al.*, *The Atlas of Microorganisms from the Ancient Khubsugul Phosphorites*, *Mongolia*, Huntsville: NASA.
93. Nekrasova, V.K., Gerasimenko, L.M., and Romanova, A.K., Some Characteristics of Photosynthesis in the Thermophilic Cyanobacterium *Mastigocladus laminosus*, *Mikrobiologiya*, 1983, vol. 52, no. 4, pp. 548–554.
94. Riding, R.J., Calcified Cyanobacteria, *Calcareous Algae and Stromatolites*, Riding, R.J., Ed., Berlin: Springer-Verlag, 1991, pp. 50–56.
95. *Microbial Sediments*, Riding, R.J. and Awramik, S.M., Eds., Berlin: Springer-Verlag, 2000.
96. Gleason, P.J. and Spackman, W., Jr., Calcareous Periphyton and Water Chemistry in the Everglades, *Environments in South Florida: Present and Past*, Gleason, P.J., Ed., Miami Geological Soc., 1974, pp. 146–181.

97. Krumbein, W.E. and Giele, C., Calcification in a Coccoidal Cyanobacterium Associated with the Formation of Desert Stromatolites, *Sedimentology*, 1979, vol. 26, pp. 593–604.
98. Gorbushina, A., Krumbein, W., and Palinska, K., Poikilotrophic Growth Patterns in Rock-Inhabiting Cyanobacteria, *The Phototrophic Prokaryotes*, Pechek *et al.*, Eds., New York: Kluwer Academic, 1999, pp. 657–664.
99. Merz, M.U.E., The Biology of Carbonate Precipitation, *Facies*, 1992, vol. 26, pp. 81–102.
100. Delado, O. and Lapointe, B.E., Nutrient-Limited Productivity of Calcareous versus Fleshy Microalgae in a Eutrophic, Carbonate-Rich Tropical Marine Environments, *Coral Reefs*, 1994, vol. 13, pp. 151–159.
101. Golubic, S., The Relationship between Blue–Green Algae and Carbonate Deposits, *The Biology of Blue–Green Algae*, Carr, N.G. and Whitton, B.A., Eds., Oxford, 1973, pp. 434–472.
102. Pentecost, A., Blue–Green Algae and Freshwater Carbonate Deposits, *Proc. R. Soc. London*, 1978, vol. 200, pp. 43–61.
103. Merz-Preiß, M.U.E., Calcification in Cyanobacteria, *Microbial Sediments*, Riding, R.E. and Awramik, S.M., Eds., Berlin: Springer-Verlag, 2000, pp. 50–56.
104. Komar, V.A., *Klassifikatsiya stromatolitov po mikrostrukturam: Paleontologiya dokembriya i rannego kembriya* (The Classification of Stromatolites by Microstructure: The Paleontology of the Precambrian and Early Cambrian), Leningrad: Nauka, 1979, pp. 42–45.
105. Knoll, A.H., Fairchild, I.J., and Swett, K., Calcified Microbes in Neoproterozoic Carbonates: Implication for Our Understanding of the Proterozoic/Cambrian Transition, *Palaios*, 1993, vol. 8, pp. 512–525.
106. Knoll, A.H. and Semikhatov, M.A., The Genesis and Time Distribution of Two Distinctive Proterozoic Stromatolite Microstructures, *Palaios*, 1998, vol. 13, pp. 408–422.