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Proterozoic Fossil Cyanobacteria

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ABSTRACT

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A monographic account is presented on the fossil Proterozoic cyanobacteria. It chronicles the 60 years of history of investigations on the Precambrian microfossils. The researches on Precambrian microfossils have revealed a new, earlier unknown, world of oldest microorganisms and divulged the steps in life's evolution on the earth. Documented records show that cyanobacteria occupied all available ecological niches of the Precambrian biosphere and filamentous and coccoidal cyanobacteria were the dominant microbial community. Extinct fossilized cyanobacteria in diagenetic cherts of the Precambrian are comparable in morphology and behavior with extant forms. These oxygenic phototrophic microorganisms were masters for at least first 3.0-3.5 billion years of the Earth history and almost did not change for billion years. The unprecedented evolutionary conservatism of the cyanobacteria is established so much so that modern systematics of cyanobacteria can be applied on Proterozoic forms at least, up to the family level. More than half a century of research on Precambrian microfossils demands refinement in taxonomy and allows differentiation between products of taphonomy and primarily biological features of fossilized cyanobacteria as well as those features formed as a result of *post-mortem* degradation and subsequent diagenetic alternations. The paper embodies all cyanobacterial taxa broadly accepted by most of the researchers and provides complete revision of all Precambrian fossil cyanobacterial remains. It presents a comprehensive information on the taxonomy of cyanobacterial and related microorganisms along with emendations with due considerations of possible processes of *post-mortem* alterations. Detailed analysis of fossil cyanobacteria populations has revealed 50 genera and 92 species as truly acceptable forms. Of this, more than 10 genera and 18 species are recognized as problematic cyanobacterial taxa that could be alternatively interpreted as Protista. The present review contains diagnosis and descriptions of genera as well as type and some other very important species. The information on other species (size, type specimen, distribution) is given in the table format along with the described genera. All valid taxa described from the Proterozoic microbiotas are incorporated in this work. Problematic remains of Archaean (?) cyanobacteria are not included because of their uncertain and disputable biogenic origin. The relevant data of molecular biology and other methods applied in systematics of modern cyanobacteria are discussed in the paper. Besides, main taxonomic part and relevant discussion on the morphology of microfossils the palaeobiology, palaeoecology and geological history of cyanobacteria are also provided. The present paper contains following taxa: Family- CHROOCOCCACEAE: *Brachypleganon, Coniunctiophycus, Corymbococcus, Eoaphanocapsa*, *Eogloeocapsa, Eosynechococcus*, *Gloeodiniopsis, Gloeotheceopsis*, *Gyalosphaera, Sphaerophycus, Tetraphycus*; Family- ENTOPHYSALIDACEAE: *Coccostratus*, *Eoentophysalis*; Family- DERMOCARPACEAE: *Polybessurus*; Family- HYELLACEAE: *Eohyella;* Family- PLEUROCAPSACEAE: *Palaeopleurocapsa*, *Scissilisphaera*; Family- XENOCOCCACEAE: *Synodophycus;* Family- OSCILLATORIACEAE: *Calyptothrix, Cephalophytarion*, *Cyanonema*, *Eomicrocoleus*, *Eoschizothrix*, *Filiconstrictosus, Heliconema, Obruchevella, Oscillatoriopsis*, *Palaeolyngbya, Partitiofilum, Siphonophycus*, *Uluksanella*; Family- NOSTOCACEAE: *Eosphaeronostoc*, *Veteronostocale;* Family- SCYTONEMATACEAE: *Circumvaginalis, Ramivaginalis*; Order- NOSTOCALES OR STIGONEMATALES: *Archaeoellipsoides, Orculiphycus,* INSERTAE SEDIS: *Animikiea, Chlorogloeaopsis, Chuaria*, *Clonophycus, Glenobotrydion*, *Gunflintia*, *Huroniospora, Leiosphaeridia*, *Leptoteichos, Myxococcoides, Phanerosphaerops*, *Polysphaeroides, Polytrichoides*.

Key-words—Cyanobacteria, Proterozoic, Precambrian Palaeobiology, Fossil, India, Russia.

प्राग्जीव जीवाश्म सायनोजीवाणु

वी.एन. सर्जीव, मुकुंद शर्मा एवं योगमाया शुक्ला

सारांश

जीवाश्म प्राग्जीव सायनोजीवाणु पर विनिबंध विवरण प्रस्तुत किया गया है। यह कैंब्रियन पूर्व सूक्ष्मजीवाश्मों पर अन्वेषणों के 60 वर्षों के इतिहास को लिपिबद्ध करता है। कैंब्रियनपूर्व सूक्ष्मजीवाश्मों पर अनुसंधानों ने नवीन पहले अज्ञात सूक्ष्मजीवों की प्राचीनतम दुनिया उद्घाटित की है तथा पृथ्वी पर जीवन का उद्भव प्रकट किया है। प्रलेखित अभिलेख दर्शाते हैं कि सायनोजीवाणु ने कैंबियनपूर्व जीवमंडल की समस्त उपलब्ध पारिस्थितिकीय कर्मता घेर ली थी तथा तंतुमय एवं गोलाभीय सायनोजीवाणु प्रबल सूक्ष्मजीवी समुदाय थे। कैंब्रियनपूर्व के प्रसंघाती चर्टों में विलुप्त जीवाश्मीकृत सायनोजीवाणु मौजूदा रुपों से आकृतिविज्ञान व आचरण में तुलनीय हैं। पृथ्वी इतिहास के कम-से-कम पहले 3.0 से 3.5 अरब वर्षों तक ये ऑक्सीजनी प्रकाशपोषित सूक्ष्मजीव प्रमुख थे तथा लगभग अरब वर्षों तक परिवर्तित नहीं हुए। सायनोजीवाणु का अपूर्व उद्भवी रुढ़िवाद बहुत अधिक स्थापित है ताकि सायनोजीवाणु का आधुनिक वर्गीकरणविज्ञान कम-से-कम परिवार स्तर तक प्राग्जीव रुपों पर अनुप्रयुक्त किया जा सके। कैंब्रियनपूर्व पर आधे से ज़्यादा सदी शोध होने पर सूक्ष्मजीवाश्म वर्गीकरणविज्ञान में परिमार्जन की दरकार करते हैं तथा जैवसादिकी के उत्पादों एवं जीवाश्मीकृत सायनोजीवाणु व शव-परीक्षा अवनति और अनुगामी प्रसंघाती रद्दोबदल के फलस्वरुप जो लक्षण बने के प्राथमिक रुप से जैव लक्षणों के बीच विभेदन मानते हैं। शोध-पत्र अधिकांश शोधकर्त्ताओं द्वारा विस्तृत रुप से स्वीकृत समस्त सायनोजीवाणुजन्य टैक्सा साकार करता है और सर्व कैंब्रियनपूर्व जीवाश्म सायनोजीवाणुजन्य अवशेषों को संपूर्ण परिशोधन प्रदान करता है। यह शव-परीक्षा तबदीलों के संभावित प्रक्रमों के उचित महत्व सहित संशोधनों के साथ-साथ सायनोजीवाणुजन्य व संबंधित सूक्ष्मजीवों के वर्गीकरणविज्ञान पर बोधगम्य जानकारी प्रस्तुत करता है। जीवाश्म सायनोजीवाणु के विस्तृत विश्लेषण से वस्तुतः स्वीकार्य रुपों में 50 वंश व 92 जाति उद्घाटित हुई हैं। इसकी संदिग्ध सायनोजीवाणुजन्य टैक्सा के रुप में 10 वंश एवं 18 जाति से ज़्यादा पहचानी गई हैं जो वैकल्पिक रुप से आद्यजीव के रुप में व्याख्यायित की जा सकती हैं। मौजूदा समीक्षा वंश के निदान व विवरण के साथ-साथ प्रकार एवं कुछ अन्य अति महत्वपूर्ण जाति सन्निहित है। अन्य जाति (आकार, प्रतिदर्श प्रकार, वितरण) पर जानकारी वर्णित वंश के साथ-साथ सारिणी के रुप में दी गई है। इस शोध कार्य में प्राग्जीव सूक्ष्मजीवजातों से वर्णित समस्त वैध टैक्सा समाविष्ट हैं। आद्यमहाकल्पी (?) सायनोजीवाणु के संदिग्ध अवशेष उनकी अनिश्चित व विवाद्य जीवजनित उद्गम की वजह से शामिल नहीं किए गए हैं। शोध-पत्र में अणुजीवविज्ञान का प्रासंगिक आंकड़ा तथा आधुनिक सायनोजीवाणु की वर्गीकरणविज्ञान में अनुप्रयुक्त अन्य विधियां विवेच्य हैं। इसके परे, मुख्य आकारवर्गिकीय भाग तथा सूक्ष्मजीवाश्मों की आकृतिविज्ञान, पुराजीवविज्ञान, पुरापरिस्थितिविज्ञान एवं सायनोजीवाणु के भू-वैज्ञानिक इतिहास पर प्रासंगिक विवेचना भी दी गई है। वर्तमान शोध-पत्र में निम्नांकित टैक्सा समाविष्ट हैं :-

परिवार : *क्रूकोक्केसीः ब्रचीप्लेगैनन, कोनिअंक्सीओफायकस, कोरीम्बोकोक्कस, इओएफ्नोकेप्सा, इओग्लोइओकेप्सा, इओसायनेकोकोक्कस, ग्लोइओडिनिऑप्सिस, ग्लोइओथेसीऑप्सिस, ग्यालोस्फैरा, स्फैरोफायकस, टेट्राफायकस;* परिवार- *एंटोफिजेलिडेसीः कोक्कोस्ट्रेटस, इओएंटोफिसेलिस;* परिवार - *डर्मोकार्पेसीः पॉलीबेसुर्रस; परिवार-हायल्लेसीः इओहील्ला;* परिवार- *प्लुरोकेप्सेसीः पैलियोप्लुरोकेप्सा, साइस्सीलिस्फैरा;* परिवार- *ऐक्सेनोकोक्कोसीः सायनोडोफायकस;* परिवार- *ऑसिलेटोरिएसीः कैलीप्टोथ्रिक्स, सेफ्लोफायटेरियन, सायनोनेमा, इओमाइक्रोकोलियस, इओसायज़ोथ्रिक्स, फिलिकंस्ट्रक्टोसस, हेलिकोनेमा, ऑब्रुचवेल्ला, ऑसिलेटोरिऑप्सिस, पैलियोलींग्ब्या, पर्टीटिओफिलम, सिफोनोफायकस, उलक्सनेल्ला;* परिवार- *नॉस्टोकेसीः इओस्फैरोनॉस्टॉक, वेटेरोनोस्टोकेल;* परिवार- *सायटोनेमाटेसीः सर्कमवेजिनेलिस,रमीवेजीनेलिस;* क्रम- *नॉस्टोकेल्स* और *स्टिगोनेमाटेलीज : आर्चिओल्लीप्सॉइड्स, ऑर्कुलीफायकस, इनसर्टेसेडिस : एनिमिकीआ,क्लोरोग्लोइऑप्सिस, चुआरिआ,क्लोनोफायकस, ग्लेनोबाट्रीडिऑ, गनफ्लिंटिआ, हुरोनिओस्पोरा, लीओस्फैरीडिआ, लेप्टोटीकॉस, मायक्सोकीक्कोइड्स, फनेरोस्फैरॉप्स, पॉलीस्फैरॉइडिस, पॉलीट्रिकॉइडिस* ।

संकेत-शब्द—सायनोजीवाणु, प्राग्जीव, कैंब्रियनपूर्व पुराजीवविज्ञान, जीवाश्म, भारत, रुस।

INTRODUCTION

For a long while the Precambrian was considered as "Cryptozoic" or "cryptic life" stage of the Earth's history where any traces of organic remains were not found. The biggest breakthrough in Precambrian palaeontology was made in the second half of twentieth century only. Remnants of earliest microorganisms were found in shales of North Eurasia and cherts of North America as well as macroscopic soft-bodied animal imprints were discovered in Australia. The earliest research on the Precambrian microfossils has revealed that these microbiotas are dominated by, and may be composed exclusively of, filamentous and coccoidal cyanobacteria. It turned out that these oxygenic phototrophic microorganisms were masters for at least first 3.0-3.5 billion years of the Earth history occupying all available ecological niches. The evolutionary paradox is that cyanobacteria almost did not change for billion years and fossilized forms as old as 2 Ga old have modern counterparts on generic and even specific level. Inevitably many errors crept in initial interpretations of ancient microorganic remains. Many secondary morphological features of microorganisms, *viz.* outer texture and inner inclusions, were misinterpreted as having primarily biological origin. These peculiarities of microfossils shape were considered as extremely important for biological interpretation of reported microscopic remains and the enormous significance was attributed to these features in the numerous evolutionary scenarios. As a result, many remains of cyanobacteria were interpreted as heterotrophic bacteria and protists and visa verse. Later investigations on comparative *post-mortem* alteration of modern eukaryotic and prokaryotic cells helped very much in separation of primarily and secondary biological features of fossilized microorganisms. Gradually, the short comings in initial biological interpretation and taxonomy of Precambrian cyanobacteria and protists were rectified and paved way for the refined classification of earliest microorganisms. Many taxa of Proterozoic microfossils were emended and in the following pages mainly those genera and species currently widely used in Precambrian palaeobiology are described. The information related with various Precambrian microbiotas was spread over scores of journals and research publications. As a rule, all revisions embraced taxa of both cyanobacteria and protists from one or a few geological units. There was a sincere need of a special publication collating all cyanobacterial taxa broadly accepted by the most of the researchers in the field. In early attempts, a very few monographs presented complete revision of all Precambrian microfossils, but did not provide the refined taxonomy of cyanobacterial remains. Therefore, the comprehensive publication on Precambrian cyanophyceae including refined cyanobacterial and relative microorganism's taxa described or emended with consideration of all possible processes of *post-mortem* alteration is still desirable.

The purpose of the publication is bringing together most taxa of Proterozoic cyanobacteria currently used in palaeobiological research on ancient microorganisms that have survived numerous taxonomic revisions. The work could be of significant interest not only for researchers working in the field of Precambrian palaeobiology, but also for the microbiologists engaged in the study of modern cyanobacteria and other relict prokaryotic communities as well as palaeontologists and stratigraphers of broader interests keeping a keen eye on the Proterozoic palaeontology. In general, problem with classification of Proterozoic cyanobacteria appears similar to modern cyanophyceae where numerous taxa were described, but later their numbers were reduced significantly due to subsequent revisions. Cyanobacteria demonstrate quite complicated life cycles that should be reconstructed for both modern and fossil forms. For recent microorganisms, life cycle can be reconstructed just observing various stages through a population growth and development, but the same task for fossilized cyanophyceae is much more difficult. A palaeontologist can observe clusters of microfossils only to guess relationship between morphologically similar and different remains. Of course, modern cyanobacteria provide a powerful key for understanding relations among their Precambrian counterparts, otherwise any reconstructions of fossil populations would be little possible or impossible at all. Moreover, fossilized microorganisms suffered significant *post-mortem* alteration often changing their morphology significantly that complicated possible reconstruction of life cycles and grouping together all observed microscopic fossils.

Currently, two taxonomic approaches are applied to fossil cyanobacterial remains. The real biological taxa are reliably established for the well preserved Proterozoic cyanobacteria almost identical to modern counterparts when a proper palaeobiological reconstruction is possible. However, many scarce cyanobacterial remains could not be joined together even in a hypothetical way (e.g., detached spores of nostocaleans or stigonemataleans) or changed so significantly that easily could be derived from various cyanobacteria or protists. For such cyanobacterial or relevant microorganisms, a standard palaeobotanical approach is applied where separated parts of fossilized plants (e.g., roots, leaves, seeds and so on) are described as different taxa. While selecting Proterozoic cyanobacteria genera to be included in this publication (monograph = handbook = treatise), we have limited our efforts to well described and photodocumented genera and species and left uncountable Precambrian microfossils described in numerous publications in obscure ways. Many, almost identical, Precambrian microfossils of very simple filamentous and coccoidal morphology (e.g., empty sheaths, isolated coccoids and so on) could turn out to be

remains of various cyanobacteria or protists making their proper comparison almost impossible. Considering these factors we selected 50 genera of Proterozoic cyanobacteria and relevant microfossils broadly accepted by researchers working in the field of Precambrian micropalaeontology to be included in the publication. Taxa of fossil cyanobacteria are based on morphology only and that is the only way currently applicable to fossilized cyanophyceae. The relevant data of molecular biology and other methods applied to systematic of modern cyanobacteria are discussed in the publication as well.

Like all handbooks (treatise), the present publication contains diagnosis and descriptions of genera as well as type and some other very important species. The information on other species (size, type specimen, distribution, and so on) is given in the table form as an attachment to all described genera. All valid taxa described from the Proterozoic microbiotas are incorporated in this publication and problematic remains of Archaean (?) cyanobacteria are not included because their true biogenic origin is still uncertain and disputable. The illustrated material came mainly from the reference sections of North Eurasia and India with a few additional forms from North America, most fossil microorganisms are three-dimensionally preserved in cherts and cherty parts of carbonate formations; additionally some compressions (preserved organic-walled microfossils mainly in shales as well as other siliciclastic rocks) are also included.

Development of the living world is considered as an interaction of the biosphere with the geosphere. Since early Archaean, the sedimentary rocks were formed in various depositional environments in different ways over tens of millennia during each geologically significant time period. 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. 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 Ma, i.e. hundreds of millions of years) implies a different approach, in which prokaryotes, mainly cyanobacteria 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 formation of oxygen and C_{org} on Earth 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. 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. On a large time scale, biologically mediated reactions are related to the formation of an oxidative atmosphere and the related sub-aerial 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. All these processes result in biogeochemical succession, which, until the appearance of vegetation cover on the terrestrial surface about 400 million years ago, almost completely depended on the activity of microorganisms, primarily cyanobacteria.

On a very large time scale, the history of geospheric–biospheric biotas can be divided into the following stages: The Archaean Eon is characterized by the presumably important role of hydrogenotrophic microbiota (including microbiota able to utilize endogenous sources) and by locally developed oxygenic photosynthesis (despite Archaean cyanobacterial microfossils are problematic and scarce). Without recognizing the important role of cyanobacteria in the transformation of the Earth's atmosphere due to the accumulation of oxygen and un-oxidized organic matter in the incomplete C_{org} cycle, it is impossible to understand formation of the oxygenic atmosphere, the deposition of iron oxides, and the development of the biogenic sulfur cycle with sulfate reduction in the oceans. 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. After this period, since the Phanerozoic Eon, carbonates have been recycled with the involvement of organisms possessing skeleton. The course of terrestrial sub-aerial weathering is largely unknown, while it is a key issue for the proper understanding of the carbonate cycle.

The development of protists, during Neoproterozoic, masked the biogeochemical systems formed by cyanobacteria and heterotrophic 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 the carbonate platforms were then substituted by the development of the reef-producing formations of colonial eukaryotes and parazoan organisms.

Precambrian cyanobacteria survived as silicified microfossils are 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 palaeontological events are available. Therefore, in the publication besides the main taxonomic part and relevant discussion on the morphology of microfossils we have also analyzed palaeobiology, palaeoecology and geological history of cyanobacteria. These sections provide the required information on the described taxa and the systematic and taxonomy acceptable in the publication.

A PRÉCIS OF PRECAMBRIAN CYANOBACTERIA & OTHER MICROORGANISMS

In the early part of the twentieth century, presence of a few Precambrian silicified microfossils, mainly cyanobacterial remains, were documented from the Palaeoproterozoic Gunflint Iron Formation of Lake Superior, Canada (Cayeux, 1911). Later, these microorganisms were photodocumented by Moore (1918) and Grüner (1923). These are now considered to be the earliest record of Precambrian microfossils. However, majority of the contemporary palaeontologists were skeptical of these reports. Most of them even disbelieved their existence and preservation of microorganisms without mineralized skeleton in such ancient rocks. Therefore, for quite sometime further investigations of Precambrian microfossils were not attempted.

Researches on Precambrian silicified (chert-embedded) microorganisms started once again with impetus in the second half of the last century with the discovery of microfossils in the thin sections of the Gunflint Iron Formation, Canada (Tyler & Barghoorn, 1954). In comparison to silicified microfossils, the compression-preserved organic-walled microfossils (OWM) in shales were described, a little earlier, from the Riphean sequences (Meso-Neoproterozoic) of the East European Platform and the southern Ural Mountains (Naumova, 1949, 1950, 1951; Timofeev, 1952, 1955). Almost simultaneously the macroscopic soft-bodied animal imprints were discovered in Australia (Sprigg, 1947; Glaessner, 1958). But the quantum jumps in study of the most ancient life began in the middle of sixties after publication of the paper by Barghoorn and Tyler (1965) with the detailed description of the Gunflint microbiota. In the following decade diverse microorganisms constituted of cyanobacteria and bacteria were recorded from the Gunflint Iron Formation (Cloud, 1965; Cloud & Hagen, 1965; Edhorn, 1973; Schopf *et al*., 1965; Cloud & Licari, 1968; Hofmann,1971; Awramik & Barghoorn, 1977). Considering the fact that to date most of the Precambrian microfossils reports are constituted of cyanobacterial (= blue-green algae= cyanophyceae) remains (especially those preserved in cherts), the history of Archaean and Proterozoic biosphere is by any yard stick 90 percent investigation of the fossil cyanobacteria. Gunflint microfossils discovery was followed by the several publications reporting the silicified microfossils in the Proterozoic and Archaean deposits of Australia, Africa and Northern America (Barghoorn & Schopf, 1965, 1966; Cloud, 1965; Schopf & Barghoorn, 1967, 1969; Licari & Cloud, 1968; Schopf, 1968; Cloud *et al*., 1969; Licari *et al*., 1969; Hofmann & Jackson, 1969; Schopf & Blacic, 1971). Simultaneously the compression-preserved organic-walled microfossils were studied extensively from the Riphean and Palaeoproterozoic of Northern Eurasia (Timofeev, 1966, 1969). Some of these early studies were not without pitfalls. In an attempt to document the existence of a life on the Earth in its earliest stages of history, many microscopic structures were reported as fossil microorganisms from the most ancient Archaean metamorphic rocks. Unfortunately most of these subsequently proved to be either modern contaminants or pseudofossils (Schopf & Walter, 1983).

Remarkable morphological similarity of majority of Precambrian fossil microorganisms with modern cyanobacteria became quite evident after the first find of silicified microfossils (Barghoorn & Tyler, 1965). Morphological similarity in Precambrian microfossils was entirely different phenomenon from fast evolving groups of various organisms of Phanerozoic where gradually advanced forms appeared in succession. Most of the Proterozoic cyanobacterial taxa have modern counterparts at the generic or even specific levels (Barghoorn & Schopf, 1965; Licari & Cloud, 1968; Schopf, 1968; Hofmann, 1976). Therefore, the taxonomical approach suggested by Schopf (1967, 1968) was adopted and followed for fossil cyanobacterial taxonomy in nearly all the subsequent publications. Names of modern counterparts were used as a practice and prefixes such as *Palaeo*-or *Eo*- were added to them or suffixes were changed emphasizing the antiquity of microfossils (for example, *Lyngbya-Palaeolyngbya*, *Synechococcus-Eosynechococcus, Oscillatoria-Oscillatori-opsis*). In early stages of studies various features, *viz.* spatial cellular arrangement, presence of inclusions in the cells and also the size were considered for establishing eukaryotic nature of microfossils. For example, dark inclusions in spherical forms were interpreted as nucleus or pyrenoids and tetrahedral tetrads were considered as the result of meiotic cell fission (Schopf, 1968; Schopf & Blacic, 1971). These characteristic features subsequently proved to be incorrect and most of these microfossils interpreted as eukaryotes turned out to be cyanobacterial remains.

Early microfossil studies did not consider the role of the taphonomy as well as role of sedimentary environmental factors in the preservation of microorganisms. Majority of researchers considered that tender cells were fossilized either

during their lifetime or immediately after the entrapment in adverse conditions (Schopf, 1968; Schopf & Blacic, 1971). Many a times structures found inside the fossilized cells were interpreted as having primary origin that led to erroneous evolutionary conclusions. It was soon realized, that many morphological features used for biological interpretation of the most ancient microorganisms are due to *post-mortem* degradation, taphonomic factors and diagenetic alterations. Therefore, the dark inclusions mentioned inside the cells (Schopf, 1968) proved to be collapsed protoplasm and pyramidal tetrads in colonies or tri-radiate mark on some of the smooth walled vesicles as a sign of meiotic division were in fact compressed or squeezed cells (Awramik *et al*., 1972; Knoll & Barghoorn, 1975; Hofmann, 1976; Golubic & Hofmann, 1976; Golubic & Barghoorn, 1977; Knoll *et al*., 1978). Similarly, sculptured surface of many Precambrian microfossils, especially small spines, were considered as undoubted proof of eukaryotic level of a cell organization, but subsequently demonstrated to be the result of diagenetic deformation of originally smooth surface of microorganisms (Sergeev, 1992a, b, 1994, 2006).

By the close of sixties, a plethora of artifacts were described and taxonomically dealt with erroneous interpretations as compression-preserved organic-walled microfossils. As a result it became a challenge to differentiate between true microfossil with dubio- and pseudofossil records while some useful criteria were proposed to differentiate microscopic remains and overcome this problem (Cloud, 1976; Hofmann, 1971; Schopf & Walter, 1983). In spite of these limitations, the number of publications describing new microfossil assemblages with sedimentological inputs from various stratigraphical units increased manifolds. Usefulness of the microfossils in biostratigraphy was not the objective of any of these publications. So much so that, in 1963, a significant publication on the stratigraphy of the former USSR did not even consider the importance of microfossils in delimiting the stratigraphical units based on micro-organic remains (Keller, 1963). Nevertheless, many new reports of Precambrian microfossil added to our understanding of morphological analogues with modern microorganisms.

Publications of the late seventies show the increasing influence of sedimentological data in understanding the distribution of Precambrian microfossils in any lithological suit. These studies were further strengthened by involving the experts of modern cyanobacteria in Precambrian microfossil investigations. The Bitter Springs microfossils laid the foundation for such detailed studies (Knoll & Golubic, 1979). It demonstrated the possibility to identify and differentiate the basic mat forming communities, coccoidal symbionts and allocthonous planktonic forms in these assemblages (Golubic, 1976 a, b; Golubic & Hofmann, 1976; Francies *et al*., 1978 a, b; Knoll *et al*., 1978). Many studies on Proterozoic silicified microbiotas showed the commonality between the features of *post-mortem* decompositions in fossilized cells and modern cyanobacteria. These analyses suggest that the microfossil assemblages were not just the casual set of heterogeneous entities but were product of well established system of cyanobacterial mat with rigid structurally-trophic interrelations between various groups of fossilized microorganisms.

Initially, the studies of microfossils were restricted to the description of silicified communities thriving near shore-shallow water environments which were mainly constituted of morphologically simple and evolutionary conservative cyanobacteria that have not shown any significant change during the past 2 billion years (Barghoorn & Schopf, 1965; Schopf, 1968; Schopf & Blacic, 1971; Hofmann, 1976; Muir, 1976; Schopf *et al*., 1977; Kumar 1978 a, b; D. Oehler, 1978; Schopf & Prasad 1978; D. Oehler *et al*., 1979; Lo, 1980; Knoll, 1982; Nyberg & Schopf, 1981, 1984; Mendelson & Schopf, 1982; Hofmann & Schopf, 1983; McMenamin *et al*., 1983). Later, it became evident that formation of early diagenetic cherts, which were the source of most of these fossil assemblages, had special facies distribution and majority of cherts were confined to shallow marine environment having characteristic microbial communities (Southgate, 1986; Maliva *et al*., 1989; Knoll *et al*., 1991).

The Proterozoic microfossils found in the cherts were mainly constituted of simple, filamentous and coccoidal cyanobacteria; this situation gave rise to the impression of *'typically Precambrian microbiotas'* and lack of evolutionary features made them unsuitable for biostratigraphic considerations (Hofmann, 1976; Golubic & Hofmann, 1976; Knoll & Golubic, 1979; Mendelson & Schopf, 1982). Later it was proved incorrect. In early phases of the studies, most of the researchers were so convinced about the prokaryotic nature of the Precambrian microbiotas (Schopf, 1968; Knoll & Golubic, 1979) that they inadvertently overlooked the presence of large spiny acritarchs and Vase Shaped Microfossils (VSM) in the Bitter Springs Formation (personal observation of VNS).

In late seventies, the first integrated study of biostratigraphic usefulness correlated with the isotopic age of the lithostratigraphic units containing Precambrian microfossils was attempted (Schopf, 1977). Based on the statistical data and occurrence of complexity in microorganisms, two discernable boundaries in the early biosphere were marked at 1.4 and 1.0 Ga ago. In this exercise, however, lateral distribution of microorganisms in Proterozoic basins and variations in their sizes were not considered. But, sharp morphological changes in the lateral distribution of the compression-preserved organic walled microfossil assemblages were independently established while studying the Riphean and Vendian (Meso- through Neoproterozoic) sequences of the southern Ural Mountains and Siberia (Keller & Yankauskas, 1980; Yankauskas, 1982, 1989; Sergeev, 1992a).

Study of the Palaeoproterozoic microbiotas of the McLeary and Kasegalic Formations of North America shows

their strong similarity not only with the Palaeoproterozoic microbiota of the Gunflint Formation but also with much younger microbiota of the Bitter Springs Formation (Late Riphean-Neoproterozoic) of Australia (Hofmann, 1976). It once again underlines the strong facies dependence in distribution of microfossils and unprecedented conservatism (braditely) of cyanobacteria (Schopf, 1974a, b, 1994). But biostratigraphical importance of Proterozoic microfossils gradually set in such studies. The rise of publications on the Precambrian microfossils helped in the demarcation of the top and bottom horizons of Riphean in eighties and also established the gradational differentiation of microorganisms in Proterozoic basins. In early eighties, lateral differentiations of microorganisms in Proterozoic basins were established (Knoll, 1984). In this model, the most primitive and morphologically simple forms, mainly cyanobacteria, lived near the shore and in the lagoons. Knoll (1984) also suggested the association of fast evolving microorganisms present in the sediments of open marine facies. There was gradual change in the size of micro-organisms in proximal and distal parts of the facies. Similar model was previously established for Palaeozoic and Mesozoic acritarchs distribution (Staplin, 1961; Wall, 1965). Gradually it was established that taxonomically most varied, morphologically complex and evolutionary quickly changing microfossils are present in open marine facies (Knoll & Calder, 1983; Knoll, 1984, 1985). This model explains the conservatism known in the silicified microfossils comprising mainly cyanobacterial remains, as the chert nodules or layers are formed in the near shore-shallow marine carbonate facies whereas other complex communities of organic walled microfossils lived in open sea environment conditions found in siliciclastic sequences and also shows the presence of eukaryotic phytoplankton.

In eighties, the former USSR became the active center of study of the microfossils found in cherts. Earlier it was known for its expertise in the documentation of compressed organic walled microfossils found mainly in terrigenous sequences. The main aim of the Russian (Soviet) scientists was to explore the biostratigraphic potential of microfossils whereas elsewhere researchers were addressing the problems of biological evolution through the studies of the microfossils mainly cyanobacteria. These two distinct approaches of the study of microfossils are popularly known as Soviet and North American palaeomicrophytological schools. In Russia, compression-preserved organic-walled microfossils studies were so prevalent, deeply enrooted and overshadowing that the first silicified microfossils were reported in mid seventies, that too, as a result of teamwork of the Soviet and American researchers (Schopf *et al*., 1977, 1979). It resulted into the report of varied silicified microbiotas found in Riphean, Vendian and Cambrian successions of Ural Mountains, Siberia and Central Asia. In some of the studies, even biostratigraphical potential have been estimated (Schenfil', 1978, 1980, 1983; Yakschin & Luchinina, 1981; Golovenok & Belova, 1983, 1984, 1985, 1986; Kolosov, 1982; Sergeev, 1984, 1988; Ogurtsova, 1985; Sergeev & Krylov, 1986; Krylov *et al*., 1986, 1989; Krylov & Sergeev, 1986; Ogurtsova & Sergeev, 1987; 1989; Sergeev & Ogurtsova, 1989). Similar cooperation in the field of study of organic-walled microfossils in shales has enriched our knowledge of fossil Precambrian microorganisms including cyanobacteria.

Earliest undoubted processed acritarch were reported from the Late Riphean (Timofeev *et al*., 1976). At that time long spiny organic walled forms were known only from the Cambrian and younger sediments and considered as the Palaeozoic marker. Therefore, when the organic-walled microfossils with processes were first recovered from the shales of older strata (Vendian) most of them were seen with skepticism and subsequently rejected (see for details Yankauskas, 1989). Even when similar processed forms, now known as acanthomorphic acritarch, were recorded from the many Vendian sequences of the Siberian platform (Pyatiletov, 1986, 1987; Pyatiletov & Rudavskaya, 1985) they were considered as the proof of the Cambrian age for the strata holding them or considered belonging to Yudoma Group (Moczydtowska & Vidal, 1986; Rudavskaya & Vasil'eva, 1989). For a long time these acritarchs were considered as stratigraphic riddle or inconsistency in acritarchs occurrences (Khomentovskii *et al*., 1987).

Gradually acanthomorphic acritarchs were reported from many other older strata of different regions having the lower Vendian sediments and it was noted that they have global distribution and taxonomically are distinct from Lower Cambrian complex spiny microfossils (Zang & Walter, 1992; Tiwari & Knoll, 1994; Zhang Y. *et al*., 1998; Grey, 2005; Vorob'eva *et al*., 2006, 2007, 2008, 2009 a, b). Acritarchs found in Vendian/ Ediacaran sediments of Australia are conspicuously distinct and are designated as Pertatataka type or Ediacaran Complex Acanthomorphic Palynoflora (ECAP) (Grey, 2005). Spiny acritarchs found in the Ruyan Group of China (Xiao *et al*., 1997; Yin *et al*., 2005) from those found in and the Roper Group of Australia (Javaux *et al*., 2001) are taxonomically different from those found in the Neoproterozoic formations (Timofeev *et al*., 1976; Yankauskas, 1989; Veis *et al*., 1998; Sergeev, 2006, 2009; Sergeev *et al*., 2010). These demonstrate that the level of complexity in the microfossils found in the Meso- to Neoproterozoic is distinct and this difference can be used in biostratigraphic subdivision of the sediments. Besides, in the younger Proterozoic basins cyanobacteria and eukaryotic microorganisms were found in association.

In Russia, the Precambrian compression-preserved organic-walled microfossils recorded during 1970-80s posed a great problem as number of morphotypes proposed by different workers increased manifold (Herman, 1974, 1979; Timofeev & Herman, 1979; Timofeev *et al*., 1976; Yankauskas, 1980, 1982; Veis, 1984; Mikhailova, 1986). Based on these

morphotypes (many a times unrealistic morphotypes) several models of microphytological divisions of the Proterozoic were proposed (see, in particular Yankauskas, 1982; Veis, 1988). A generalization based on both the silicified and organic walled microfossils resulted into the publication of a monograph "Precambrian Microfossils of the USSR" (Yankauskas, 1989). In this monograph not only the data on vertical distribution of Precambrian microorganism assemblages are provided, but also the essential revision of previously described taxa of cyanobacteria as well as eukaryotic microorganisms have also been attempted.

Studies undertaken in nineties incorporated the sedimentological, ecological and facies distribution data of microfossils bearing litho units. It was commonly practiced by the North American school however; it was a new approach for the Russian school pursuing compression-preserved organic-walled microfossil studies. In Russia, this approach was initiated by Veis and Petrov (1994a, b) who combined the detailed lithological inputs on microorganism remains containing strata, their thickness and facies distribution in recording the microfossil assemblages (Petrov & Veis, 1995; Veis *et al*., 1998, 1999). It was shown that the models of Staplin (1961) and Wall (1965) proposed for the distribution of Mesozoic and Palaeozoic phytoplanktons were equally applicable on Precambrian assemblages (Knoll, 1984); although Knoll's model did not consider the distribution of microfossils in deep-water facies yet it was found correct in analysis of microfossil assemblages of shale facies (Veis & Petrov, 1994a, b; Petrov & Veis, 1995; Veis *et al*., 1998, 1999, 2000). Thus, gradually the study of phytoplanktonic microfossil associations and their implications in biostratigraphy became a common practice (Veis *et al*., 1999). Similar but restricted approach was applied in the study of silicified microbiotas of the Sukhaya Tunguska Formation of the Turukhansk Uplift dominated by cyanobacteria. It revealed that the microfossil assemblages are in general prokaryotic (cyanobacterial) but there are also few eukaryotic phytoplanktonic microorganisms present in the open sea facies of sediments (Petrov *et al*., 1995; Sergeev *et al*., 1997). However, in many subsequent studies, the eukaryotic elements have been reported in the assemblage of silicified microbiotas dominated by cyanobacteria without providing detailed sedimentological analysis of encompassing lithologies (Sergeev, 1999, 2001, 2006).

In 1992, Schopf and Klein published a detailed account of the Precambrian organic remains found since beginning of their studies in a book entitled *The Proterozoic Biosphere*. This work mainly summarized the results obtained under a PPRG project (Precambrian Palaeobiological Research Group – a research group on Palaeontology of Precambrian). Most of the results reported by that time were considered, a few were revised and some were treated as stratigraphical models. A specific case may be wherein the idea proposed earlier, regarding an increase in size of cyanobacterial filaments or vesicle (Schopf, 1977) was discarded (Schopf, 1992b). Considering the work on the PPRG project was complete in the middle eighties, the detailed review of the silicified as well as compression-preserved microorganisms of Russia by Yankauskas (1989) missed any reference in "The Proterozoic Biosphere". In Schopf and Klein's monographic study, neither the existing problems in taxonomy of the Precambrian studies were addressed nor were the solutions proposed. Even most frequently consulted publications by Schopf (1968) and Schopf and Blacic (1971), for which good number of revisions and cyanobacterial synonymies existed (Knoll & Barghoorn, 1975; Golubic & Barghoorn, 1977; Knoll & Golubic, 1979) were missing.

Later, many unsolved problems of taxonomy in Precambrian microfossils were addressed by Butterfield *et al*. (1994). In this study many superfluous and irrelevant taxa were merged or synonymised with other taxa but without critical remarks. In a simplified exercise they used certain features for separation or merger of taxa instead of considering the spectrum of morphometric parameters to meet this objective. Further revision of filamentous and coccoidal taxa of cyanobacterial microfossils was undertaken by Sergeev *et al*. (1995, 1997) yet still there is necessity to clarify the status of taxonomy of Precambrian microfossils.

In spite of these limitations the research progressed on the taxonomy of Precambrian microfossils in the last decade of 20th century and newer silicified and compression-preserved organic-walled microfossils were reported. These include morphologically complex eukaryotes with ornamentation and spines and also filamentous forms of varied morphology found in late Middle Riphean (late Mesoproterozoic), Late Riphean and Vendian (Neoproterozoic) (Butterfield *et al*., 1994; Knoll *et al*., 1991; Petrov & Veis, 1995; Petrov, *et al*., 1995; Sergeev *et al*., 1997; Veis *et al*., 1998, 1999, 2000, 2001; Zhang Y. *et al*., 1998; Sergeev, 1999, 2001). Application of acritarchs, which were widely used in biostratigraphy of Palaeozoic, looked promising when they were found in the Lower Riphean (early Mesoproterozoic) sediments (Javaux *et al*., 2001; Xiao *et al*., 1997). During Riphean they evolved fast and manifested in many forms that helped the division and zonation of Riphean and Vendian.

Except for Proterozoic eukaryotic microfossils, which demonstrate morphological changes during Riphean, Proterozoic cyanobacteria show the simple morphology and evolutionary conservatism and often have modern analogues at a specific level. Biostratigraphy based on microfossils is, to an extent, facies controlled. The cyanobacterial assemblages change according to the sampling pattern and also concerned with the global change of physical and chemical conditions on the surface of the Earth. For a long time it was considered that the Palaeoproterozoic Gunflint type microbiotas containing taxa of iron bacteria had global but limited vertical distribution

(genetically connected with BIF) and disappeared in the Mesoproterozoic (Hofmann & Schopf, 1983; Zhang Y., 1984; Cloud, 1976; Knoll *et al*., 1988). Later it was established that lower Middle Riphean (Mesoproterozoic) silicified microbiotas from coastal shallow facies differ from Late Riphean (Neoproterozoic) microbiotas occurring in similar facies. This difference is mainly because of the appearance of unicell eukaryotic microorganisms in the assemblages that started replacing cyanobacteria since Neoproterozoic or earlier (Sergeev *et al*., 1994, 1995; Knoll & Sergeev, 1995; Sergeev, 1997, 1999, 2006).

Although evolutionary conservatism of cyanobacteria is well known yet some morphological changes have been documented at certain levels in Riphean. The distinct changes are like stalked cyanobacterium *Polybessurus* and spirally-cylindrical cyanobacterium *Obruchevella* which were first noted in the youngest horizons of Middle Riphean and youngest horizon of the Late Riphean (Schopf, 1975, 1977; Golovenok & Belova, 1983; Green *et al*., 1987, 1989; Knoll *et al*., 1989; Sergeev, 1989, 1992a, b, 1997, 2006, 2009). However, there are reports of spiral *Obruchevella*-like cyanobacteria in older deposits, antiquity of these forms are still uncertain (Rai & Singh, 2004; Stanevich *et al*., 2009).

In recent times, evolution of Precambrian microorganisms is seen through the window of molecular biology of extant microorganisms. Most widely applied practice is the analysis of nucleiotides sequence of modern organisms in 16S Ribosomal RNA (Giovannoni *et al*., 1988, 1996; Sogin *et al*., 1989; Wilmotte & Golubic, 1991; Knoll, 1992a, 1999; Knoll & Sergeev, 1995; Sergeev *et al*., 1995; Golubic *et al*., 1995; Xiao *et al*., 1997; Zhang Y. *et al*., 1998; Tomitani *et al*., 2006). Application of molecular biology data in the study of Precambrian microfossils, in some cases undoubtedly, is useful; however in palaeontology it should be considered only as an auxiliary tool. For example, early diversification of eukaryotes revealed by 16S RNA is known as "the big explosion" (Sogin *et al*., 1989), whereas the same diversification deduced on the basis of fossil record was named as "Neoproterozoic revolution" (Zavarzin, 2003; see also Sergeev *et al*., 1996), signatures of both the events are found near the Meso-Neoproterozoic boundary (Knoll, 1992a, 1999). It was followed by appearance of morphologically different eukaryotes in the Upper Riphean rocks (Petrov *et al*., 1995; Xiao *et al*., 1997; Veis *et al*., 1998, 2000, 2001; Javaux *et al*., 2001) and this event probably could be correlated to "the big explosion" in the evolution of eukaryotes.

Thus, with the experience of more than 50 years of the existence of the Precambrian palaeobiology we can draw the following conclusions:

First, Precambrian silicified and compression-preserved organic-walled microorganisms are the main components of the Proterozoic fossil record. Mostly constituted of cyanobacteria, these are morphologically simple and show evolutionary conservatism in comparison to complex and rather fast evolving eukaryotic microorganisms.

Second, traces of prokaryotic microorganisms mainly cyanobacteria are known from Palaeoproterozoic strata and have modern analogues on generic or even on specific levels. Before fossilization all microorganisms passed through complex *post-mortem* transformations and many a times changes in their morphology are beyond recognition. Therefore, all biological interpretation of Precambrian prokaryotes should be based on their analysis as components of existing ecology of cyanobacteria and detailed analysis of *post-mortem* transformations of morphology.

Third, compression-preserved and silicified organic-walled microbiotas show strong facies dependence which was caused by lateral differentiation of communities of microorganisms in Proterozoic basins. Thus, most evolutionary conservative cyanobacterial communities lived in shallow near shore-sea and lagoonal conditions, replaced mainly by eukaryotic, complex phytoplanktonic microoganisms that reached a maximum of a variety in the open shelf.

Fourth, the other morphologically complex eukaryotic microorganisms become abundant in the youngest horizons of Middle Riphean, and are the most reliable tool in Precambrian biostratigraphy. These innovations among eukaryotes are accompanied also by occurrence of complex cyanobacterial forms, not found in more ancient rocks. However, communities of prokaryotic microorganisms from near shore-shallow lithologies are characterized by the development of several stages that were irreversible and brought by the change in physical and chemical conditions in an atmosphere and hydrosphere as well as lithosphere.

TECHNIQUES AND APPROACH TO STUDY AND INTERPRET PRECAMBRIAN CYANOBACTERIA

Precambrian cyanobacteria (as well as protists) are preserved mainly as organic-walled envelopes with remains of primarily organic matter comprising cell walls and surrounding sheaths. There are two main types of microfossils preservation. The first type comprises of three-dimensionally preserved silicified or chert-embedded microfossils in cherts and cherty parts of dolomite and limestone formations. These microorganic remains are not extracted from the rocks and studied in thin sections of cherts (standard petrographic slides about 50 microns thick or thicker up to 200 microns). The second type includes compression-preserved usually flattened microfossils preserved in terrigenous rocks, mainly in shales

(also called organic-walled microfossils – OWM). The compression-preserved organic-walled microfossils are extracted from the encompassing rocks by dissolving in hydrofluoric acid and subsequently treated by standard palynological technique or just picked up from residue by a preparation needle/brush and mounted on maceration slides with gelatin, resin or special mounting medium. Besides, there is a third type of fossilized cyanobacteria preserved mainly as three-dimensional organic-walled microorganic remains in carbonate rocks known as calcareous microfossils. This type of cyanobacteria occurs rarely in Proterozoic dolomite and limestone, but became very common in Palaeozoic carbonate rocks. Precambrian calcareous microfossils were continuously deformed during diagenesis by the growth of aragonite, calcite and dolomite crystals. These forms occur mainly in stromatolites which together with microphytolites (oncolites and catagraphs) are products of growth and metabolic activity of cyanobacterial communities.

METHODS OF STUDY

Technique of field sampling

The silicified microfossils have been found preserved in lenses and nodules of early diagenetic cherts which play a role of impervious shell for skeleton-less microorganisms. Unlike Phanerozoic cherts, the majority of Precambrian early diagenetic silica concretions result from sediments of shallow- or even extremely shallow-water setting often part of shallowing-up cycles (Southgate, 1986, 1989). During Palaeozoic and Mesozoic, chert sedimentation areas moved to more deep-water sites of basin that was related to expansion of phyto- and zooplankton with silica skeleton (Maliva *et al*., 1989) turned into the kernels of chert concretion growth (Maliva & Siever, 1989). In absence of the similar skeletal bodies in the Precambrian the formation of silica nodules occurred basically on intertidal regions in playa lakes or temporary pools inhabited mainly by cyanobacterial communities (Southgate, 1986). Sometimes in case of abundant silica input, chert nodules were formed in open shelf environments as well where eukaryotic phytoplankton thrived (Knoll, 1984; Knoll *et al*., 1991; Sergeev, 1992a, 2006; Petrov *et al*., 1995; Sergeev *et al*., 1997).

The technique of silicified cyanobacteria collection and subsequent laboratory study is although simple, yet demands the certain skills. The most appropriate lithology for recovery of microfossils are concretions of early diagenetic cherts, bluish-black in colour, with the glassy shine, forming lenses, thickness varies between several mm up to 10-15 cm and lateral extent from few tens centimeters up to several meters. Black color of concretions is imparted by presence of organic substance and the darkness of colors depends on its concentration. There is a lesser concentration of microfossils in dark grey, grey, and brownish-grey cherts; nevertheless, often remains of interesting microorganisms occur in these types. The size of selected samples of a match box is enough for preparation of several thin sections. However, as a rule after finds of good microfossils, it is required to make a subsequent series of thin sections or even to dissolve a part of sample. Therefore, chert samples up to 1 kg are rather desirable; otherwise, a researcher needs to visit the localities again for additional sampling.

Most Precambrian shales contain compression-preserved organic-walled microfossils. The most prospective shales for microfossils recovery are greenish-grey or dark grey in color with thin lamination. As a rule, the most diverse assemblages are reported from the strata comprising inter-bedded limestone and shale layers. Dark black and bluish-black shales are not very promising considering high decomposition of organic matter due to probably bacterial destruction of cyanobacterial mats and other microorganic remains. Like silica concretions, the intensity of shale colour depends on organic matter concentration; but in cherts, the decomposition was arrested probably by early diagenetic silicification, Precambrian black clays demonstrate complete decay of microbial communities. Shales contain the most diverse protista communities and nicely preserved cyanobacterial remains; other terrigenous rocks, like siltstone or fine-grained sandstones of grey and greenish-grey color, sometimes contain poorly preserved microfossils.

The fossiliferrous cherts and shales are collected from stratigraphic sections (including boreholes) with every sample designated to specific layers. Cherts and shales are usually collected not only from a stratigraphic section to obtain a good synoptic collection, but also from a series of parallely located sedimentary successions. The sampling technique allows tracing of fossil microbial variations across and along the strike and their distribution in significant areas. Additional inputs from sedimentological analysis of fossiliferrous deposits create a reliable framework for understanding of Proterozoic microorganisms, distribution in ancient basins and revealing the most favorable conditions for cyanobacterial communities allocation in different environments.

Technique of laboratory processing

Silicified microfossils are studied in standard thin section under transmitted light. Selected chert samples are cut perpendicular to lamination by a diamond saw in a series of slabs used for preparation of covered or uncovered petrographic slides. Uncovered thin sections preferably allow using any oil immersion lenses and used for study under new techniques like Confocal Laser Scanning Microscopy (CLSM) and Raman Spectroscopy. Release of microfossils from chert matrix by dissolving it in hydrofluoric acid is not reasonable unless not required for special research (application of

electron-microscopic, biochemical and other methods) or morphological peculiarities (if microfossils diameter exceed 100 microns and more they inevitably could be seen in petrographic slides as incomplete ring-like sections). Microorganic remains are freed from chert concretions by dissolution in a weak solution of a hydrofluoric acid (see description of a technique in Schopf, 1970; D. Oehler, 1976, 1977), by only about 10 percents of preserved population can be extracted and cyanobacterial mats structure disintegrate completely (Sergeev, 1992a, 2006). The phenomenon is explained by recrystallization of embedded microfossils silica with grown quartz crystals crossing microorganic remains borders making that is well visible in thin sections in polarized light. Some microfossils are completely replaced by silica (Krylov & Tikhomirova, 1988) making their extraction from chert concretions almost impossible.

Compression-preserved cyanobacteria in shales are usually extracted from encompassing clay particles dissolving in the hydrofluoric acid (after processing of samples in hydrochloric acid) by a standard palynological technique. In contrast to chert embedded microorganisms, remains of compression-preserved organic-walled microfossils are extracted successfully. Released microfossils are mounted on a base glass and imbedded in gelatin, epoxy resin or some other transparent media and subsequently covered by a cover glass. Traditionally the dissolved shales and claystones are centrifuged to separate microorganic remains from clay particles using heavy liquid. However, as a result of centrifuging large microfossils are usually disintegrated and cyanobacterial mats got fragmented and dispersed into insignificant fragments. Picked up by a needle under stereoscopic microscope, large fragments of cyanobacterial mats and big eukaryotic microfossils are recovered as a result of improved maceration method commonly know as low agitation process of microfossils recovery. This low agitation process with some variations was successfully applied for study of cyanobacteria and large, profusely ornamented acritarch found in the Precambrian Pertatataka-type compression-preserved microfossil assemblages (e.g., Burzin, 1987; Hermann, 1990; Veis *et al*., 1998, 1999, 2000; Grey, 1999, 2005). The simple and effective technique avoid centrifuge and heavy liquid treatment keep untouched large, process-bearing acritarch, other high elaborated microfossils and fragments of cyanobacterial mats (well preserved hormogonian cyanobacteria filaments and chroococcacean cyanophyceae vesicles) intact. Besides, compression-preserved organic-walled microfossils are studied in thin sections usually preparing parallel to lamination along the zone especially rich in organic matter (Burmann , 1968; Kalvacheva, 1982; Butterfield *et al*., 1994). Occasionally, morphologically simple microfossils obtained during maceration are misinterpreted as the Proterozoic cyanobacteria remains that turn out to be the fragments of morphologically complex Palaeozoic eukaryotic phytoplanktonic microorganisms (Kalvacheva, 1982).

Silicified cyanobacterial remains are studied almost exclusively in thin sections in transmitted light without using phase or differentiated-interferential contrast. As usual there is no physical difference between microfossils and embedding homogeneous chert matrix and application of other techniques do not demonstrate further improvement in resolution. In contrast, compression-preserved organic-walled cyanobacteria are investigated in transmitted light as well, but application of phase or differentiated-interferential contrast provides good and useful results. Recently, silicified microfossils are studied by newly developed techniques of CLSM and Raman spectroscopy (see Schopf & Kudryavtsev, 2005; Schopf *et al*., 2005, 2010). Microfossils usually are photographed in transmitted light and measured with an eyepiece reticule to the nearest micrometer. Most microphotographs illustrated in the present paper were photographed in transmitted light with a Zeiss microscope REM5 and MBI-15I in Geological Institute of the Russian Academy of Science, and also Leitz and Nikon microscopes at the BSIP with use of a blue optical filter on films MIKRAT-300 and Kodak-100. For some specimen, digital images are taken on digital cameras which are now widely in use for Precambrian microfossil investigations. For many microfossils England Finder (grid subdivisions on standard base glass manufactured by Graticules Ltd., UK) or Stage coordinates are provided. But the most coordinates here cited refer to the numbers of the points at the strips of paper attached at the end of the slides: a strip of paper is glued covering the thin section of rock and the positions of microorganisms are marked onto the paper as numbered points by a sharp pencil. These points provide easy and quick way to find the microfossils: just to bring the point with the relevant number under the microscope's transmitted light and remove the paper. This convenient way to fix the position of the microfossils was suggested by the late palaeobotanist S.V. Meyen (Geological Institute of RAS, Moscow, Russia). Illustrated specimens are deposited in the Palaeontological Collections of the Geological Institute of the Russian Academy of Sciences (GINPC, collections # 3893, 4313, 4681, 4688, 4689, 4694, 4698 and 14700) and in the Birbal Sahni Institute of Palaeobotany.

Methods of Precambrian cyanobacterial assemblages comparison

The Precambrian history of cyanobacteria is reconstructed on the basis of their subsequent assemblages arranged into a generalized succession using various methods of correlation. An empirical database for the model of Precambrian cyanobacteria and other microorganisms in space and time distribution is based on the regional microfossil assemblage successions derived from natural fossiliferrous

rocks exposures and boreholes. A starting point for all late Palaeoproterozic as well as Meso- and Neoproterozoic (Riphean and Vendian) constructions are subsequent microfossil assemblages established within the reference sections and observable vertical changes of their taxonomic composition. The established microfossils assemblages contain remains of both cyanobacteria and protists. They are stratigraphically taxonomically different allowing distinction and correlation of the rocks at least starting from 2.0 Ga. Surprisingly not only eukaryotic organisms, but also cyanobacterial remains proved to be biostratigraphically useful. This approach, as a whole, corresponds, to a principle which was originally applied for division of Phanerozoic, and in Proterozoic was applied for the Riphean phythemes on the basis of stromatolites and microphytolites. However, there are some limitations in the Upper Proterozoic type sections mainly related to non-representative and inadequate palaeontological record of microorganisms as well as a discrete kind of microfossil assemblages distribution. Currently it has been established that many basic Upper Proterozoic sections are not continuous sedimentary successions, but fragments of subsequently accumulated deposits separated by significant hiatuses and disconformities.

Difficulties in Proterozoic strata correlation are supplemented with peculiarities of silicified and compression-preserved organic-walled microfossil assemblages distribution. First, in general, fossiliferrous rocks with microfossils and especially silicified microbiotas occupy total Proterozoic sedimentary successions. Second, majority of three-dimensionally preserved microfossil assemblages in cherts are dominated by remains of evolutionary conservative cyanobacteria demonstrating very few changes during Proterozoic. Third, in many sedimentary successions there are one or a few microfossil assemblages containing interesting forms, including cyanobacteria, which are useful in palaeobiological and biostratigraphical interpretaions. Of course, exception of these microfossils from analysis would impoverish a general evolutionary model of Precambrian organism's vertical distribution. Four, Proterozoic microfossil assemblages demonstrate significant lateral variability due to strong ecological-facial dependence of ancient microorganism communities, and, probably, their palaeoclimatic or palaeogeographic zonal variation.

Investigating the ancient remains of cyanobacteria, a whole set of regional sedimentary successions correlation methods are applied. These are physical methods of isotopic or absolute age determination using unstable isotopes of radioactive elements and their ratio in the igneous and sedimentary rocks like U-Pb, Pb-Pb, Sm-Nd, Rb-Sr, K-Ar and others. All these methods, their advantages and disadvantages are discussed in countless works on Precambrian isotopic geochronology. Besides, there are methods of chemostratigraphic correlation based on light elements isotopic vertical variations through sedimentary successions. The chemostratigraphic records of elements like carbon, oxygen, sulfur and others not only facilitate Precambrian sedimentary successions correlation, but also provide additional data on ancient microorganisms considering these elements are fractionated actively during organism's metabolic activity. Physical methods are especially important for early Palaeoproterozoic older than 2.0 Ga and Archaean rocks where biostratigraphic methods are not applicable. Only isotopic methods of absolute age determinations allow recording different events in the geological past (Precambrian as well as Phanerozoic) and evaluating duration of various organisms existing including cyanobacteria.

Therefore, for reconstruction of the Precambrian cyanobacterial history, the multidisciplinary approach of correlation of sedimentary succession is to be applied. Along with the study of three-dimensionally silicified and compression-preserved organic-walled microfossil assemblages, it requires involvement of well data obtained by others biostratigraphic (basically stromatolite assemblages), and physical methods. These methods mainly include study of fossiliferrous rocks, isotopic (absolute) age, and chemostratigraphic analysis of vertical sedimentary successions.

METHODS OF MICROFOSSILS INTERPRETATION

Method of morphological analysis

For majority of Precambrian microfossils, if separate them from palaeoenvironments, it is possible to find analogues among five or six groups of modern microorganisms. The exception is only the rare remains of morphologically complex microorganisms in Proterozoic microbiotas. However, such microorganisms are eukaryotes often belong to the extinct groups of early organisms and consequently have no modern analogues. It is almost impossible to make direct comparison of fossilized and modern microorganisms on the basis of morphological similarity only. A simplistic approach of ascertaining superficial similarity with modern counterparts of Precambrian microfossils resulted in a series of serious mistakes in their biological interpretation (see Précis). Method of multiple analysis, considering not only Precambrian microfossils morphology, but also their facial-ecological setting, relationship in fossilized community and *post-mortem* changes is the only correct way for interpretation of earliest microorganisms. The crucial point turned out to be evolutionary conservatism of blue-green algae demonstrating identity of recent and Proterozoic taxa on generic and even specific level as well as structural identity of modern and fossil cyanobacterial mats.

As it becomes obvious, the absolute majority of Precambrian silicified microfossils are remnants of

cyanobacteria. The conclusion is supported basically by comparison of Precambrian microbiotas in cherts and modern cyanobacterial communities living within upper subtidal and tidal flats of arid basins like Shark Bay in Australia or Persian/ Arabian Gulf with adjoining sabkhas (Golubic, 1976a, 1983, 1985; Playford & Cockbain, 1976; Kinsman & Park, 1976; Hofmann, 1976; Golubic & Hofmann, 1976; Knoll & Golubic, 1979). Sedimentological analysis of fossiliferrous deposits demonstrated that the majority of Precambrian microbial communities preserved in chert concretions inhabited similar environments. As usual dolomites bear desiccation cracks, tepee structures, ripple marks and crystal pseudo moulds after gypsum and halite (Schopf, 1968; Hofmann, 1976; Golubic & Hofmann, 1976; Knoll & Golubic, 1979; Knoll, 1985; Southgate, 1986, 1989). Structure of modern and fossil cyanobacterial mats is identical as well as composition of mat-builders and mat-dwellers including the same hormogonian and chroococcacean cyanobacteria.

A comprehensive morphological approach to classification, identification and evolutionary conservatism of cyanobacteria make it possible to ascertain exact palaeoenvironmental position of fossil microbial communities. It is applicable to completely fossilized cyanobacterial mats only where mat-building forms and coccoidal symbionts are clearly distinguished. Some cyanobacteria of complex morphology are easily identifiable, even if found separately as an isolated specimen. Many lower eukaryotes also have quite distinguishable morphology and remarkable life cycles making possible morphological comparison. However, there are always chances of misidentification of single specimen with morphologically similar forms among various groups of prokaryotic and eukaryotic organisms, e.g., trichomes of sulfur bacteria like *Beggiatoa* can be misinterpreted as those of hormogonian cyanobacteria, especially if they came from maceration slides where technique of preparation erase all original relations among fossilized microorganisms. The situation is much more complicated for morphologically simple coccoidal microorganisms where laws of bacteriology are rather applicable. As a rule modern cyanobacterial communities are formed by blue-green algae only, but in some cases hormogonian mats nesting inside as symbionts eukaryotic organisms as green, red, diatom algae and even protozoa. Small coccoidal microfossils nested inside fossilized hormogonian mats are widely accepted as chroococcacean cyanobacteria. But in some cases these small microfossils could turn out to be remains of morphologically similar eukaryotes. The situation is especially difficult with interpretation of small (size of a few micrometers) ellipsoidal or coccoidal remains even if post-mortem degradation almost did not take place. These small ellipsoidal forms are probably remains of *Synechococcus*-like cyanophyceae which according to data of molecular biology is a heterogenic group having phylogenetically different roots despite similar morphology. But some of them can be remains of phototrophic or heterotrophic bacteria or even small akinetes.

Thus, a method of morphological analysis has its limitations due to morphological simplicity of ancient microorganisms and external similarity of physiologically various organisms and complicating influence of post-mortem transformations. Nonetheless, the method allows to recognize in fossilized microbial communities the principal taxa of blue-green algae mainly mat-forming species and various groups of ancient eukaryotes. Data of a morphological method now are supplemented with data obtained by molecular biology and palaeobiochemical methods which are considered as an auxiliary tool in interpretation of Precambrian cyanobacteria.

Comparative method of molecular biology

Data of molecular biology about relations of various groups of living microorganisms including cyanobacteria are broadly applied on the analysis of Precambrian microfossils and their possible steps of evolution. However, because of discrepancy in different events in the evolution of organisms as well as taxonomical status ascertained by molecular biology data versus palaeontological data many palaeontologists confront with a molecular phylogeny (see for discussion Knoll, 2003; Teyssedre, 2006). Molecular biology data obtained by various methods are important for general evaluation of cyanobacterial taxonomy and evolution, but many discrepancies in these data interpretation currently make any final evolutionary and systematic conclusions on this group of microorganisms premature and tentative.

The most popular method among the molecular biology is the analysis of the basic nucleotide sequence 16S rRNA in ribosomes. These sequences allow estimate a degree of mutual relationships between organisms as well as steps of evolution and divergence of the basic groups. Popularity of this method in comparison with other methods of molecular biology is explained by its convenience evaluating a wide spectrum of evolutionary relations between various microorganisms, including higher taxa. Although, molecular phylogeny does not always allow establish an exact taxonomy, it helps to avoid gross errors due to homoplasy or morphological convergence.

There are two procedures of study of 16S rRNA in modern cyanobacteria: the reconstruction of real nucleotides sequence in molecules and their subsequent phylogenetic interpretation. For an establishment of partial and full nucleotides sequence a series of standard techniques are applied which are year after year improved, faster and more reliable. Procedure of an establishment of empirical nucleotide sequences should be executed carefully as the correctness of the further evolutionary reconstructions depends on its accuracy. On the basis of the obtained nucleotide sequences the following stage assumes importance for the creation of the evolutionary tree reflecting phylogenetic mutual relations between organisms.

Improvement of methods of phylogenetic interpretation, on the basis of molecular biological data, can lead to change in reconstructed evolutionary relations of various groups of organisms. For Precambrian palaeobiology, the relationship revealed among mitochondria and chloroplast by the molecular biology as well as some group of microorganisms, including morphologically different forms within cyanobacteria are of great significance. But exponentially developing science like molecular phylogeny with introduction of new techniques can radically change organic evolutionary interpretations in a few years. Like molecular phylogeny, new finds of certain fossil microorganisms at lower stratigraphic levels in a new and fast developing field of Precambrian palaeontology sometime change all existing palaeobiological models drastically. Below we discuss in short advantages and disadvantages of 16S rRNA method application to phylogenetic interpretation of fossilized Precambrian cyanobacteria. The properties and limitations of 16S rRNA method are evaluated in numerous works on molecular phylogeny (Woese, 1987; Olsen, 1988; Wilmotte & Golubic, 1991; Gupta, 1998; Teyssedre, 2006; Tomitani *et al*., 2006; Knoll, 2007) and we summarize those in this section with some critical remarks from us as palaeontologists.

Advantages of sequencing nucleotides 16S rRNA

16S ribosomal RNA possesses a series of properties that turn it into a basic tool of analysis of phylogenetic relations between organisms.

1. rRNA have global distribution in cells of all living organisms that assume they evolved very early and changed their functional properties rather insignificant after origin.

2. The functional importance of rRNA in synthesis of proteins provides it with an irreplaceable role in all processes proceeding in cells.

3. Nucleotide sequence and rRNA secondary structures are conserved globally. The basic parts of molecules are identical in all three kingdoms of existing organisms: Archaea, Bacteria and Eukarya. At the same time, some parts of molecules evolved fast, that provides an opportunity of comparison of closely related organisms.

4. rRNA are numerous in cells, especially in areas of intensive growth; they are easily isolated, identified and used in partial 16S rRNA sequences technologies. The 16S rRNA molecules form long circuits that provide high resolution applicable for the analytical methods of their structures deciphering and an opportunity of statistical comparison of the received results.

5. The 16S rRNA is a good «molecular chronometer», i.e. provide exact enough measurement of speed of evolutionary changes from ancestors to descendants.

Problems of application of sequencing nucleotides 16S rRNA

Except for advantages of a method of comparison of sequences nucleotides 16S rRNA, there are number of the problems complicating phylogenetic interpretation of obtained results: the presence of multiple rRNA gene in the cyanophyceae genome, a sequence correct arrangement, multiple mutations, gaps in nucleotide sequences, secondary structures in rRNA, functional restrictions, differences in speed of evolution of various organisms, topology of a tree, and applicability.

1. Multiple of rRNA a genetic code consists that within one strain of microorganism can reveal two or more gene clusters. Existence of similar rRNA multiple genes create a problem at an establishment of sequence nucleotides. Though, divergences between various variants of genes within the limits of one genome are usually insignificant, nevertheless they create some uncertainties at reconstruction of a phylogenetic tree. Moreover, these discrepancies can be complicated by presence of microorganisms of several rRNA types.

2. The correct arrangement of nucleotide sequence alignment is a preliminary step to any analysis of data, the purpose of which is to provide comparison between homologous nucleotides. Though it is never precisely known, which genes and which nucleotides are homologous; in practice, nucleotides sequence construction are made on the basis of similarity: identical sites of chains are usually used as marking horizons for an arrangement of their more differing parts. However, there is a danger that nucleotides sequence parts between the two mutations could be deleted and then compensated.

3. Two homological nucleotides in consecutive sequences at their identity could result from various evolutionary events. On the contrary, different nucleotides can be resulted not from evolutionary changes, but several subsequent mutations.

4. When the gaps are more than in one nucleotide sequence, there is a question, whether nucleotides have been added or erased during one or a series of mutations. Solution of these problems in most cases demands enough experience to arrive at any decisions.

5. 16S rRNA is not a simple linear molecules, but complex, crumpled structure with central stems and loops. It is unclear where the nucleotide sequences in most conservative in stems or loops and where secondary structures are present.

6. The functions of ribosome in cells are diverse, and the deciphered nucleotide sequences can reflect not only real distinctions between organisms, but also various functions of ribosomes at synthesis of protein.

7. All methods of phylogenetic tree construction are not reliable in the respect that not all consecutive branches on a reconstructed trunk reflect equal pace of microorganism's

evolution. If pace of evolution in some organisms was higher, than in others it led to earlier branching on a phylogenetic tree. As a result some sites of a phylogenetic tree can look more primitive than others and can be misinterpreted as result of earlier diversification in time between various groups of organisms. Adjustments are required for correction of similar aberrations in topology of the phylogenetic tree.

8. Interpretation and display of data are especially inconvenient when a divergence of various nucleotide sequences is a result of "the big bang" and the basic part of branching are observed on the basis of a tree. Apparently fast occurring changes are observed in early evolution of cyanobacteria (Giovannoni *et al*., 1988; Wilmotte & Golubic, 1991) as well as eukaryotic organisms (Sogin *et al*., 1989). In this case the available branches are correctly arranged with difficulty on a tree. The risk of error is greatest if branches are long enough, and the intermodal distances between their branches are short. Generally, the longer the branches the more difficult the correct guess their arrangement due to possible multiple mutations and convergences.

9. 16S rRNA method is applied mainly for study of microorganism strains which are capable to grow in culture and easily adaptable for the conditions which are essentially distinct from observable in their natural dwelling environments. Strains easily growing in similar cultivation conditions invite a competition with dominating strains in natural environments, but slowly growing oligotrophic microorganisms which are difficult to grown in laboratory and hitherto insufficiently investigated. That explains why many kinds of cyanobacteria actively grow in natural environments have been dropped out of the16S rRNA analysis (e.g., *Cyanostylion,* modern counterpart of fossil cyanobacterium *Polybessurus*, widespread in modern intertidal setting like Bahama Islands tidal flats).

10. All the evolutionary conclusions made on the basis of 16S rRNA sequences possess one general basic fault. If the group of organisms has completely extinct, there are not any molecular biology methods to restore its history and palaeontology only can make it.

Above mentioned observations make one extremely cautious in using of a molecular biological method for the analysis of a possible phylogenetic interpretation of various fossil microorganism groups. At the same time completely ignoring these data in relation to fossil microorganisms and especially cyanobacterial remains is impossible. As a result of the comparative analysis of modern cyanobacteria 16S rRNA, different morphological groups and morphotypes are set at place and are widely used for interpretation of Precambrian cyanophyceae (Knoll, 1992a, 1999; Sergeev *et al*., 1995, 1997; 2007b; Golubic *et al*., 1995; Semikhatov *et al*., 1999; Tomitani *et al*., 2006; Sergeev, 2006). The comparable molecular biology data on modern cyanobacteria would certainly facilitate the palaeobiologal and evolutionary interpretation of fossil cyanophyceae and confirm applicability of morphological approach in systematic and classification. In the following pages, we provide a concise outlook how molecular biology data are applied in the cyanobacteria systematic.

Palaeobiochemical methods

In the fossil records, there are not only structurally preserved cyanobacterial remains like cells and sheaths, but also non-decomposed fragments of organic matter as well. In the beginning of diagenetic alterations sediments contain colloidal solution, firm particles of organic substance, complete cells and aggregates of cyanobacterial cells. Initially the organic substance is slightly changed, contains a plenty of carbon skeletons of organic matter and informative macromolecules of proteins and amino acids, and therefore the source of its origin is easily recognizable.

Bacterial destruction of blue-green algal remains begins with the onset of the process of burial mainly in underlying layers of cyanobacterial mat. First it occurs in aerobic, and then in anaerobic conditions of lowermost layer where sulfur-reducing and methanobacteria play a leading role in decomposition. Subsequently, molecules of cyanobacterial organic components that survived bacterial destruction during diagenesis and catagenesis suffer significant changes and as a result are fossilized in rocks in different forms. Kerogens - insoluble unstructured, geochemically changed and usually unrecognizable organic substance - are more widespread and occur in most sedimentary rocks. Besides kerogens oil and gas, molecular fragments with preserved primary structure (chemofossils), coal and graphite are found in the rocks.

Palaeobiochemical methods were applied for the first time for the analysis of unstructured fossilized organic substance (kerogens) on silicified microfossils (Schopf *et al*., 1968). Unfortunately, several studies of unstructured organic substance did not provide any valuable information (see Hayes *et al*., 1983). It seems isotopes of carbon and other light elements in sedimentary rocks could provide more information about the nature of cyanobacteria and other Precambrian microorganisms.

The most interesting aspect of the study of biomarkers - characteristic and sturdy against decomposition molecules basically lipids being by derivatives of the certain biochemical components specific for the particular groups of organisms only (Peters & Moldowan, 1993). For example, a characteristic product of metabolic activity of many eukaryotes and prokaryotes are sterols, the integral components of the majority of algal cytoplasmatic membranes, transformed in sedimentary rocks into sterans. Finds of 2-methylhopanes derived from 2-methyl-bacteriohopanepolyols, lipids of cyanobacterial cytoplasmic membranes and synthesized in a plenty only by cyanobacteria are found in the shales underlying the Hamersley Group of Australia about 2.7 Ga (Summons *et al*., 1999; Knoll,

1999). These reports provide independent geological evidence for the antiquities of cyanobacteria and points toward the older antiquity, still earlier origin, although incomplete phylogenetic sampling leaves open the possibility that other bacteria might also produce similar biomarker (Knoll, 2003; Tomitani *et al*., 2006). From the same deposits 14-methyl and C-28 and C-30 steranes derived from various groups of eukaryotic microorganisms were extracted (Brocks *et al*., 1999; Knoll, 1999). A few bacteria incorporate sterols into their membranes, but now prokaryotes are known to form the more elaborated sterols that were precursors of the C-28-C-30 steranes (see also Brocks *et al*., 2005). These finds are another proof of existence of cyanobacteria and earliest eukaryotes about 2.7 Ga in Archaean and provides an opportunity for generation of more data on biomarkers, along with palaeontological data, for the analysis of a variety of microorganisms at least in late Archaean and Proterozoic.

There are limitations of a method of biomarkers application on Precambrian cyanobacteria and other microorganism studies. It is yet to be established that all microorganisms possess any biochemical components that are characteristic only for them. The subjective aspect as well as applicability of methods of molecular biology requires expensive equipment and reagents. It should be noted that though the majority of biomarkers are high-molecular connections and is a part of bitumens with low migratory ability, nevertheless a chance of contaminations into older rocks cannot be excluded completely. The good controlling factor is occurrences of the morphologically specific microorganism biomarkers in the same layers where there are possible producers of these molecules.

Thus, the methods of fossilized microorganisms study create an adequate and representative picture of Precambrian cyanobacteria development and distribution. The technique of microfossils investigation in thin sections excludes any chance of contamination by modern microorganisms and allows investigation of the fossilized microbial communities *in situ,* reconstructing their structure and interconnection of various elements. Together with data extracted from shales (compression-preserved organic-walled cyanobacteria), analysis of light isotopes and palaeobiochemical composition of ancient fossiliferrous rocks, and supplemented with comparative information of molecular biology of modern organisms, provide a basis for reliable biological interpretation of various microorganic remains and creation of models of evolutionary development of cyanobacteria in Precambrian.

MORPHOLOGY, TERMINOLOGY AND SYSTEMATICS OF CYANOBACTERIA

GROSS MORPHOLOGY AND TERMINOLOGY

Precambrian cyanobacteria

All the living organisms, depending on the presence or absence of various organelles *viz*. nucleus, mitochondria, chloroplasts, and Golgi bodies, etc. in a cell surrounded by a cytoplasmic membrane are traditionally subdivided into prokaryotes and eukaryotes. About 25 years ago, on the basis of the study of 16S ribosomal RNA sequence, amino acids and nucleotides, one more kingdom Archaea has been added to living world (Fig. 1). This kingdom, uniting some groups of microorganisms with the most primitive type of metabolism, occupies intermediate position between prokaryotes and eukaryotes (Woese, 1987; Woese *et al*., 1990); but on a number of parameters it is even closer to eukaryotes (Gogarten *et al*., 1989; Iwabe *et al*., 1989; Sogin *et al*., 1989; Rivera & Lake, 1992). Phylogenetic interpretation of molecular biology data can be reconstructed in various different ways and many researchers doubt separating some groups of the most primitive microorganisms in an independent Kingdom Archaea or Archaebacteria (see, for example: Gupta, 1998). There are prokaryotic (Kingdom Bacteria) as well as lowest eukaryotic (Kingdom Eukarya) microorganic remains among Precambrian fossilized microbial communities. Remains of true archaebacteria reported over the time are unknown in the Precambrian fossil record that is apparently connected with low taphonomical potential of their cell walls (Westall *et al*., 1995; Westall, 1997).

For most part of the Precambrian, cyanobacteria dominated on the Earth occupying almost all possible ecological niches. They changed the atmosphere of early Earth so much that beyond doubts without this group of phototrophic prokaryotic microorganisms other organisms on our planet neither would have appeared nor evolved, including mankind. Active research on Precambrian cyanobacterial remains started in the middle of sixties and since then the numerous papers describing cyanobacterial communities were published. A number of new supposedly cyanobacterial taxa were erected describing either poorly preserved microscopic remains or various stages of degradation and *post-mortem* alteration of the same microorganisms. Many revisions reduced the number of inappropriately established species and genera significantly (Hofmann, 1976; Knoll & Golubic, 1979; Knoll, 1982, 1984; Hofmann & Schopf, 1983; Knoll *et al*., 1991; Schopf, 1992c; Sergeev, 1992a, 2006; Butterfield *et al*., 1994), but all described valid taxa of fossil cyanobacteria were neither systematized nor available in one publication as a monograph for palaeobiologists and biostratigraphers. The present publication attempts to put together the different taxa of

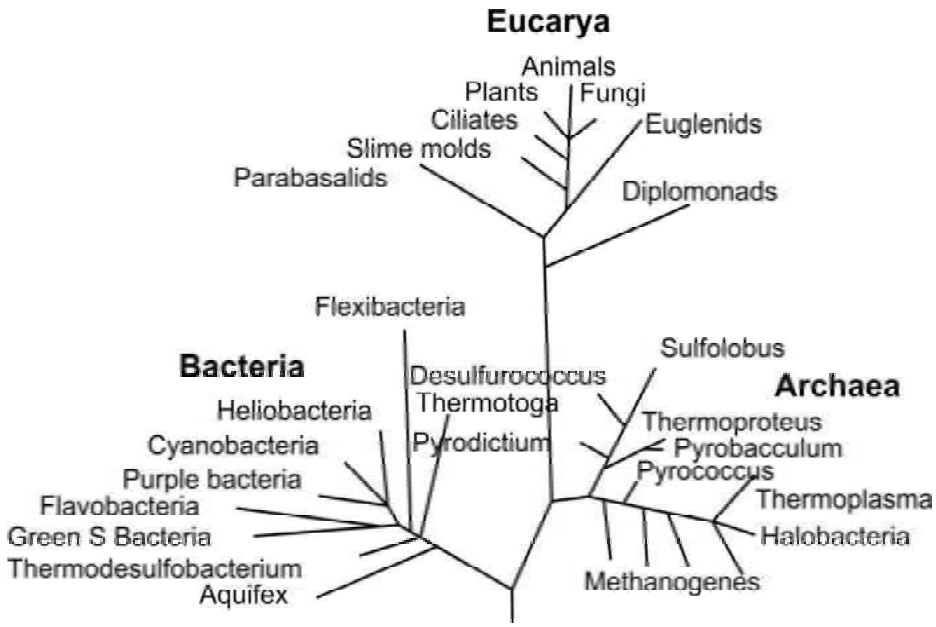


Fig. 1—The phylogenetic tree illustrating evolutionary relationships among various groups of organic world inferred from 16S rRNAs data (after Knoll, 2003, fig. 2.1).

Proterozoic cyanobacteria described over the last fifty years and revise, merge, discard and differentiate the taxa broadly accepted among researchers in the field of Precambrian palaeobiology. Before considering the actual systematics of the fossil cyanobacteria, it would be appropriate to mention the other related topics which would facilitate these microorganisms understanding.

Prokaryotes and cyanobacteria: types of metabolism

All prokaryotic microorganisms utilize biochemical energy in their life processes but draw energy by different mechanisms. Photosynthesis probably became one of the most effective and accessible way realized by ancient microorganisms, i.e. transfer of light energy absorbed by light-harvesting pigments into other kind of the energy using in cell metabolism. Apparently, the transformation of energy through various complex mechanisms such as catabolism and anabolism were developed during billions of year of evolution. Photosynthesizing prokaryotic and eukaryotic microorganisms are known to have a big spectrum of various pigments in their photosynthetic apparatus such as: bacteriochlorophyll a, b, c and d, and chlorophyll a, b and c, keratins, etc.

Simplest mechanism of light energy conversion by a cell is realized in purple and green non-sulfur bacteria of *Chloroflexus* type. Quantum of light move electrons to higher power level, and then they fall to their original levels (Fig. 2a) releasing energy. The energy is reserved basically in molecules of ATP (adenosine triphosphate) by ADP (adenosine diphosphate) reduction; as photosynthesizing pigments are used bacteriochlorophyll a, b, d and keratins. However, inevitable deficiency of electrons – carriers is created, and subsequently sulfur purple and green bacteria developed more complex mechanism where hydrogen sulfide is used as electrons donor; or more precise HS^- ions. By use of additional components (NAD – nicotinamide-adenine dinucleotide- the primary electrons acceptor where energy is accumulated), in sulfur purple and green bacteria is carried out usual cycle ADF-ATF (see Fig. 2b). Bacteriochlorophyll c, d, keratins and other compounds with photo sensitization effects are used as light-harvesting pigments. However sources of sulfur on Earth are limited, that, apparently, has compelled a part of photosynthesizing microorganisms to search alternative electron donors. The most widespread and convenient electrons donor undoubtedly is water. But there is a barrier that in system water-oxygen ($H_2O \rightarrow ½O_2+2H^++2e^-$) standard mid-point redox potential is 800–1000 mV while the potential of chlorophyll a, using the most high energetic photons of dark blue and violet parts of a spectrum, equals to about 400 mV.

Cyanobacteria have solved the problem by creating a mechanism of photosynthesis with two reaction centers I and II or defined as photosystem I and II. Due to 'electrons transfer' from energetically lower center I to higher II, using as a primary electrons acceptor NADP (Nicotinamide adenine dinucleotide

phosphate), they could achieve mid-point redox potential water-oxygen (Gottschalk, 1986; Castenholz *et al*., 1992; Stal, 2000). Having realized this mechanism, cyanobacteria got practically unlimited source of electrons using all waters of World Ocean as a potential donor and releasing free oxygen as a by-product (see Fig. 2c). As photosynthesizing pigments cyanobacteria use chlorophyll a and b, phycocyanin, phycokeratins and keratins which, apparently, play as well a role of protective elements from influence of the strongest oxidizer- oxygen. The choice of water as the electrons donor has allowed using carbonic acid to synthesize organic substances from CO_2 and H_2O almost in unlimited amount even at presence of a minimum level of a solar energy. This model appeared to be so successful that it subsequently has been realized by all plants, and symbiotically a little bit changed cyanobacterial cells including a group prochlorophyta producing organic components from inorganic according to a standard stoichiometric equation $CO_2 + H_2O + h\nu \rightarrow C_6H_{12}O_6 + O_2 + 2H_2O$.

However, like purple or green sulfur bacteria some species of cyanobacteria are capable of anoxygenic photosynthesis. Anoxygenic photosynthesis is defined as photosystem I mediate fixation of CO_2 with sulfide as an electronic donor. Anoxygenic photosynthesis in cyanobactria depends on sulfide as the electron donor whereas when its presence inhibits oxygenic photosynthesis. "Electrons transfer" from lower reaction centers I to higher reaction center II is not required because standard mid-point redox potential is much lower during anoxygenic photosynthesis. Both types of photosynthesis are mutually exclusive in some groups of cyanobacteria and occur concurrently in others. With increasing sulfide concentration especially at low illumination anoxygenic photosynthesis is more important: $6CO_2 + 12H_2S + h\nu = C_6H_{12}O_6 + 12S + 6H_2O$ (See Stal, 2000).

SYSTEMATICS OF CYANOBACTERIA

Approaches to cyanobacteria systematics

There are various approaches to systematics of cyanobacteria. In XIX century, it was mainly based on morphological attributes (Thuret, 1875; Bornet and Flahault, 1886-1888; Gomont, 1892); this practice continued up to the middle of XX century (Geitler, 1925, 1932; Frémy, 1930, 1934; Elenkin, 1936, 1938, 1949; Fritsch, 1945; Desikachary, 1959). With the advancement of modern methods of microbiology, biochemical and physiological studies of communities in cultures and ultrastructural studies, the systematics of cyanobacteria based on gross morphology only gradually became obsolete. However, unlike the majority of others

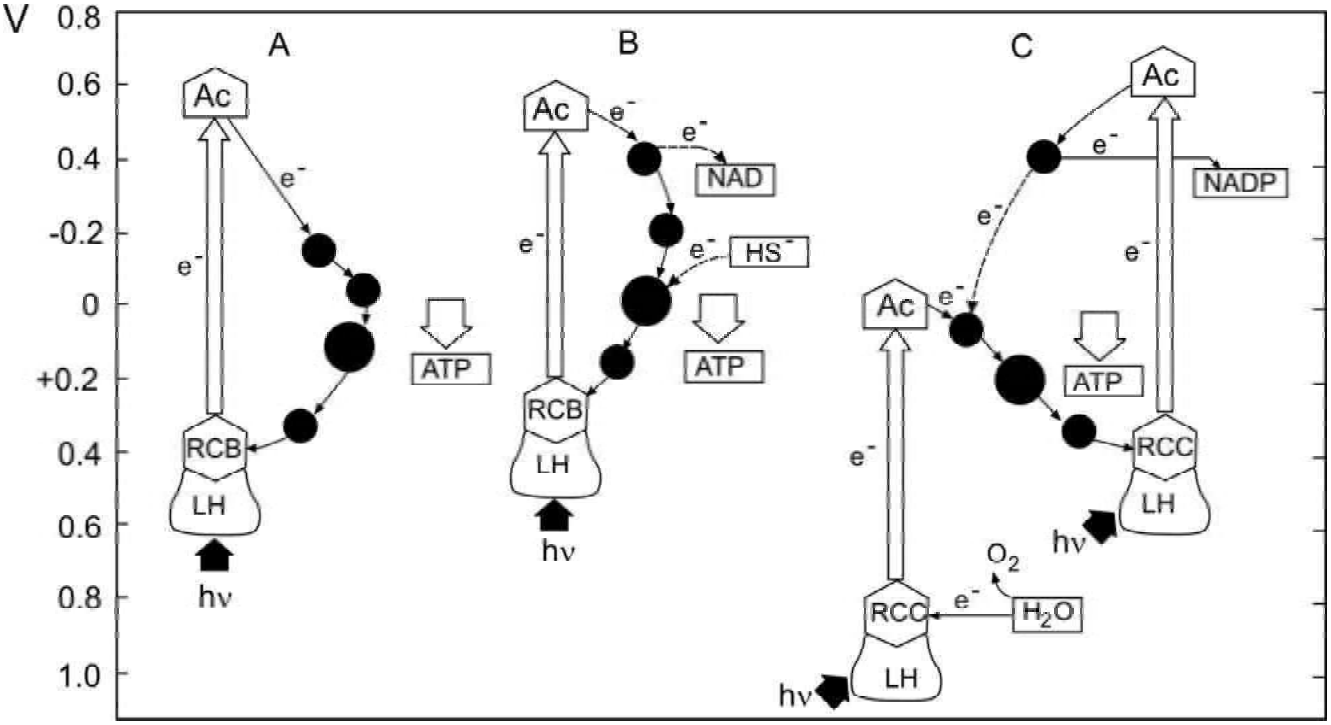


Fig. 2—Schematic drawings of the photosynthetic process in (A) purple and *Chloroflexus* (green non-sulfur bacteria), (B) in green sulfur bacteria, and (C) in cyanobacteria or the chloroplasts of eukaryotic organisms. V = voltage of E_0 (standard mid-point redox potential), LH = light harvesting pigments, Ac = primary electron (e^-) acceptor, RCB = reaction center bacteriochlorophyll, RCC = reaction center chlorophyll a, dark circles = electron carriers, see text for more details (modified after Gottschalk, 1986; Dawes, 1986; from Castenholz *et al*., 1992 in Schopf & Klein, 1992; with permission of Prof. J.W. Schopf).

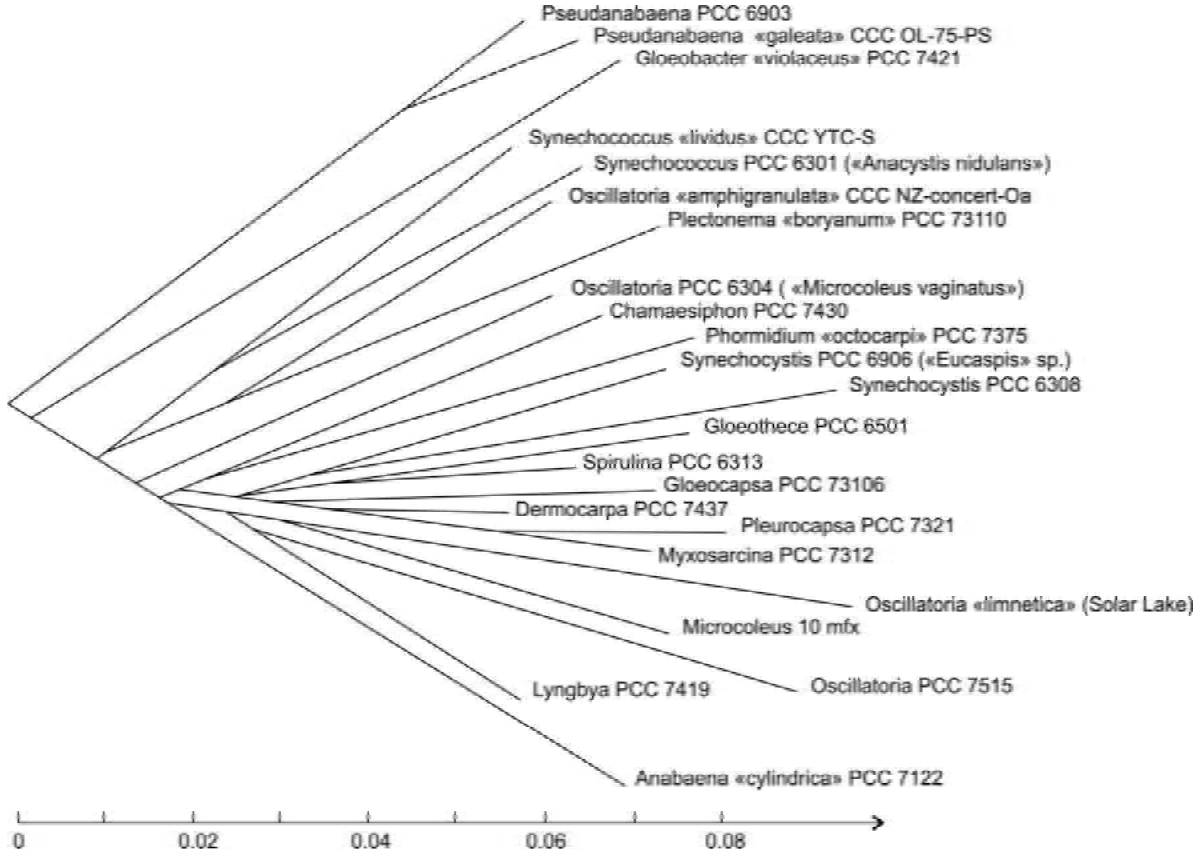


Fig. 3—Rooted-tree topology illustrating evolutionary relationships among 16S rRNAs from cyanobacteria (only one heterocystous cyanobacterium is included in this tree). Evolutionary distances are proportional to horizontal component of segment length. The scale is in units of fixed points mutations per sequence position (from Giovannoni *et al*., 1988, fig. 4).

prokaryotes, cyanobacteria possess enough distinguishable morphological characters that are certainly applicable in their systematics. 16S rRNA molecular analysis has revealed close relationship within groups of morphologically complex forms, i.e., heterocyst-bearing and baeocyte forming cyanobacteria; similar results are obtained for *Lyngbya* and *Oscillatoria* species with highly differentiated trichomes (Fig. 3-5; Giovannoni *et al*., 1988, 1996; Wilmotte & Golubic, 1991; Tomitani *et al*., 2006; Knoll, 2007). But in morphologically poorly differentiated forms of hormogonian and chroococcacean cyanobacteria, the same data have revealed doubtless heterogeneity of their main taxa (e.g., *Synechococcus*, *Synechocystis* and some species of *Lyngbya*, *Oscillatoria*, *Phormidium* and *Plectonema*). In fact, the difference between the lowest filamentous and coccoidal forms is quite tentative and division of cyanobacteria in hormogonian and chroococcacean, broadly in filamentous and coccoidal forms, was convenient enough for researchers at early stages of the study. But in a critical analysis it becomes obvious that morphologically poorly differentiated filamentous forms can develop from coccoidal forms by growth of cells in one direction (see Golubic *et al.*, 1995, fig. 2). The problem of the morphological approach in the study of cyanobacteria is especially important in the case of fossil cyanobacteria. However, morphological analysis is especially important for fossil cyanobacteria because their remnants 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.

Using the traditional classifications, currently for the purposes of molecular phylogeny, morphological distinctions are used to divide cyanobacteria into five subsections (Rippka *et al.*, 1979; Castenholz, 2001). Cyanobacteria of subsection I (order Chroococcales) and II (order Pleurocapsales) are unicellular coccoids divide by binary fission (subsection I), whereas those of subsection II can also undergo multiple fission to produce small, easily dispersed cells (baeocytes). Filamentous cyanobacteria of subsection III (order Oscillatoriales) have only vegetative cells, but in subsections IV (order Nostocales) and V (order Stigonematales), vegetative cells can differentiate into morphologically and ultrastructurally distinct heterocysts and akinetes. The former

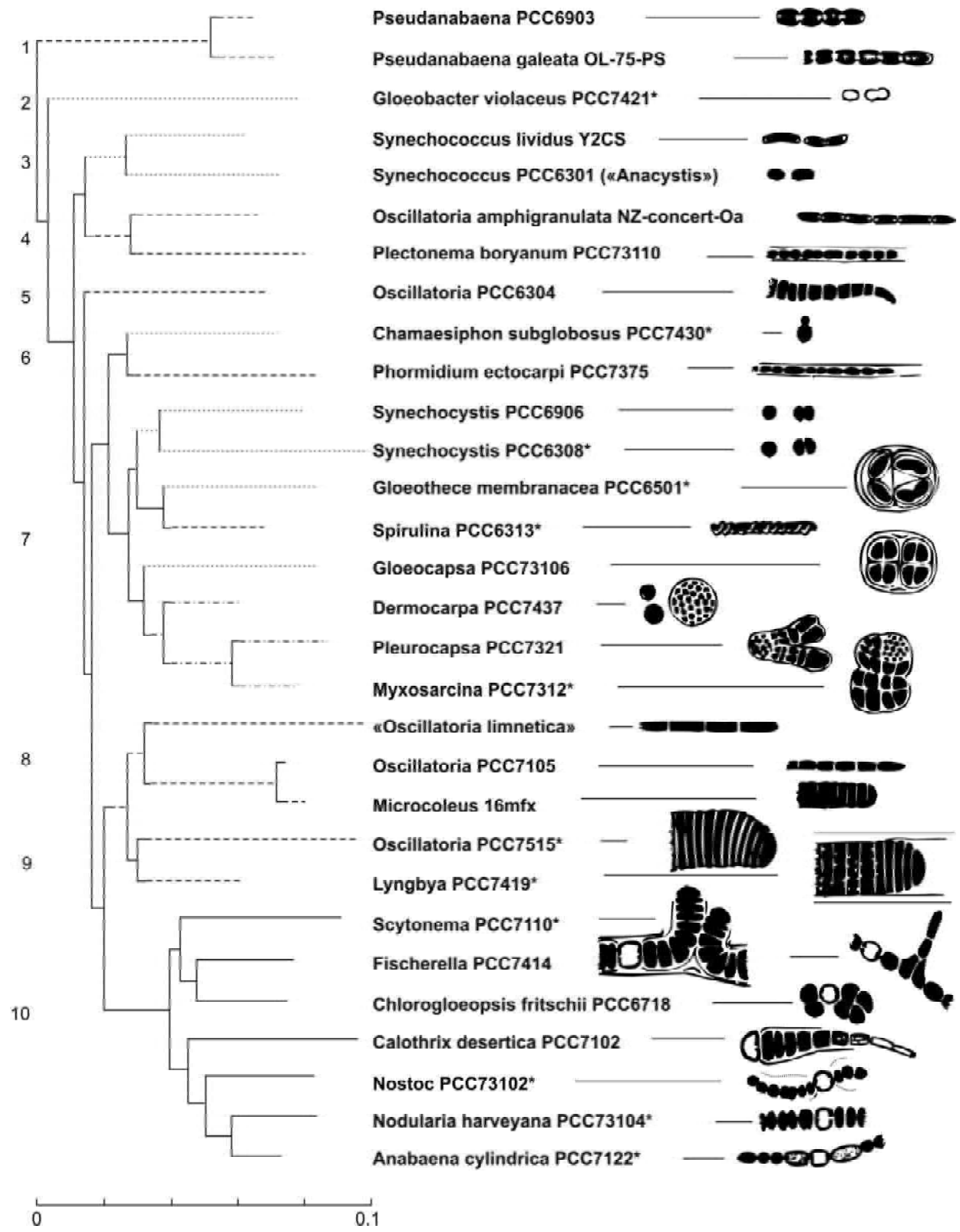


Fig. 4—Dendrogram showing phylogenetic relationships among cyanobacteria different morphological groups inferred from 16S rRNA-sequences data of Giovannoni *et al*., 1988 (from Wilmotte & Golubic, 1991, fig. 3). Dotted lines – simple coccoidal strains, dashed lines – simple filamentous strains, dashed-dotted lines – baeocyte-forming strains, full lines – heterocystous strains. Horizontal axis is in units of fixed points mutations per sequence position, vertical axis identify 10 main branches recognized in the cyanobacterial tree.

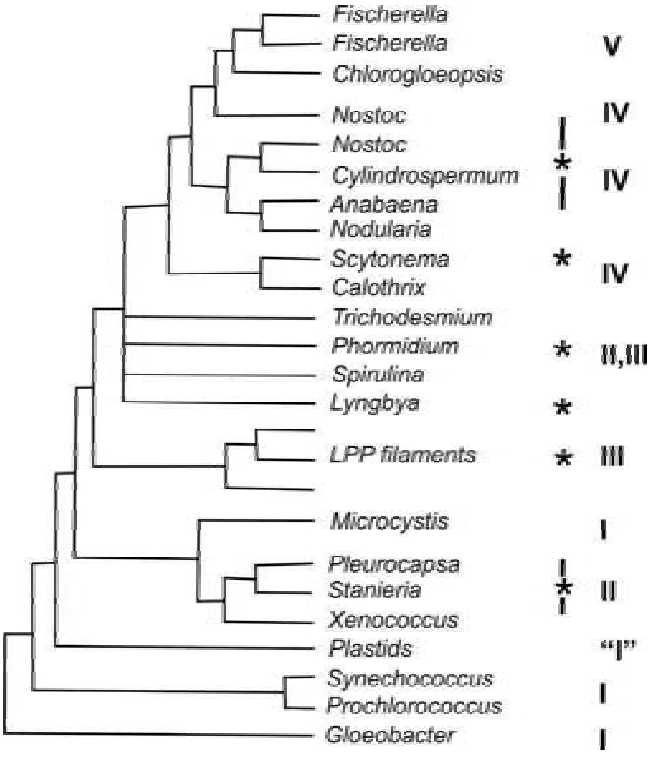


Fig. 5—Phylogenetic relationships within the Cyanobacteria, based on molecular sequences comparisons, particularly those reported by Sánchez-Baracaldo *et al*. (2005) and Tomitani *et al*. (2006). Roman numerals denote members of Groups I-IV, as recognized in morphologically based classification. Asterisks mark morphotypes recorded from 2000-1500 Ma fossil assemblages (from Knoll, 2007, fig. 1.1, with permission of Prof. A.H. Knoll).

are specialized in nitrogen fixation under aerobic conditions (Wolk *et al*., 1994) while the latter survive environmental stresses such as cold and desiccation (Herdman, 1987). In addition, filaments of subsection V have complicated branching patterns. Molecular phylogeny analyses based on 16S rRNA sequences (Giovannoni *et al*., 1988; Turner *et al*., 1999; Wilmotte & Herdman, 2001) indicate that cyanobacteria producing baeocytes (subsection II), heterocysts (subsections IV and V), and true-branching filaments (subsection V) are each phylogenetically coherent. In contrast, phylogenies reconstructed by using *nifH* (Zehr *et al*., 1997) and *nifD* (Henson *et al*., 2004), structural genes for nitrogenase enzyme that catalyses biological nitrogen fixation, do not support monophyly of subsection V (Gugger & Hoffmann, 2004; Tomitani *et al*., 2006); the *nifH* phylogeny also indicates paraphyly of subsection II. Not all cyanobacteria fix nitrogen and, therefore, genes such as *nifH* or *nifD* cannot be used to analyze non-nitrogen-fixing species. In the *rbcL* tree subsectionV (*Chlorogloeopsis* and *Fischerella*) did not form a cluster; instead, the two *Chlorogloeopsis* strains clustered with the nostocalean *Scytonema (*Tomitani *et al.*, 2006*)*. On the other hand, *hetR*, which plays a key role in the early stage of heterocyst differentiation (Wolk *et al.*, 1994) and is unique to filamentous cyanobacteria, should provide better resolution of the relationship between subsections IV and V. Species of subsection V form a monophyletic clad in *hetR* trees, consistent with the 16S rRNA phylogeny (Tomitani *et al*., 2006), but not with analyses of *rbcL*, *nifH* (Zehr *et al*., 1997), and *nifD* (Henson *et al*., 2004) phylogenies. Species able to fix nitrogen (all taxa in subsections IV and V and some among I–III) do not form a monophyletic group, indicating either that the ability to fix nitrogen existed in the common ancestor of cyanobacteria and was subsequently lost independently in multiple descendants or that this capability spread through the group by lateral gene transfer. Phylogenetic analyses of *nifH* and *nifD* from various nitrogen-fixing bacteria and archaea suggest that cyanobacterial genes form a cluster (Zehr *et al*., 1997; Henson *et al*., 2004; Tomitani *et al*., 2006). Although all cyanobacterial nitrogen fixation may have a common origin, it remains unclear whether the present distribution of this trait reflects vertical descent and secondary losses or horizontal gene transfer within the cyanobacteria.

In present work, we follow a morphological system of cyanobacteria widely accepted on fossil blue-green algae/ cyanobacteria. The concise description of this system was provided by Golubic (1976b). The system is intermediate between those of Geitler (1925, 1932) and Desikachary (1959), originally widely accepted in European countries and USA, and the system of Elenkins (1936, 1938, 1949) preferentially used in Russia. The combination of systems accepted in the present paper incorporate from Geitler's book including chamaesiphonaleans and pleurocapsaleans as orders Chamaesiphonales and Pleurocapsales in class Coccogoneae against their allocation in a separate class Chamaesiphonophyceae in Elenkin's treatise.

However, heterocyst-less oscillatoriaceans are separated in an order Oscillatoriales as in Elenkin's system rather contrast merging with heterocyst-bearing cyanobacteria inside order Nostocales as in the Geitler's books. This morphological system is supported by molecular phylogeny that revealed existence of a few coherent morphologically complex groups like baeocyte-forming pleurocapsalean and heterocyst-forming nostocalean and stigonematalean cyanobacteria as well as heterogenic origin of morphologically simple forms. With exception of some simple coccoids and undifferentiated trichomes placement in the relevant classes and orders, the molecular phylogeny tree is broadly congruent with phylogenies based on morphology. Morphologically simple forms like *Synechoccocus* and *Synechocystis* are of heterogenous origin and follows principles of Bacterial World. These coccoidal forms are also very close to morphologically simple filamentous forms that are explainable by cells unidirectional growth.

Before providing characteristics of different classes, orders and families of cyanobacteria, we should define the name of this oxygenic phototrophic prokaryotic microorganisms group. In the present work, terms cyanobacteria/blue-green bacteria/cyanophyceae/blue-green algae are accepted as synonyms. It would be more appropriate using two last names only, because fossils cyanobacteria are separated on morphological criteria only and therefore regulations of the International Code of Botanical Nomenclature to be followed. However, long practice of using term cyanobacteria prevailed in most works on silicified Precambrian microfossils.

Division Cyanobacteria

Division cyanobacteria unites oxygenic phototrophic prokaryotic microorganisms of the various form: monocelled and multicellular (individuals from the several cells connected with each other by cytoplasm connections), single and colonial, coccoidal and filamentous, including morphologically highly differentiated forms. The basic source of energy in all these forms is a photosynthesis using following photosynthetic pigments: chlorophyll a (chlorophyll b is absent), phytobiliproteins (c-phycocyanin, c-phycoerathrin and c-allophycocyanin) and keratins are localized either inside folds of cell's cytoplasmic membrane (thylakoids) or on its surface. Reproduction is basically asexual, predominantly by simple cell fission, and also by exospores (outer cells), baeocyts (internal cells) and akinites (thick-walled spores with a large stock of nutrients inside). Like many other prokaryotes, cyanobacteria are characterized by para-sexual processes, i.e. a partial exchange of a genetic material between cells (Kumar, 1985; Kumar & Uedo, 1984; Wasser, 1989). Diameter of cyanobacterial cells varies from less than 1 micron to 50-60 microns in coccoidal forms, to a maximum 100 microns of diskoidal-cylindrical (pill-like) cells of filamentous forms. There are the two classes of Cyanobacteria: Coccogoneae and Hormogoneae.

Class Coccogoneae (Chroococcophyceae) – coccogonian- This class includes unicellular cyanobacteria of simple spherical and elliptical or sometimes more complex form, naked or surrounded by single- or multilayered sheath, occur individually or in colonies. Reproduction takes place by division of cells in one, two or several directions, chaotic or ordered, by exospores or endospores (baeocyts). In the accepted system there are three orders of class Coccogoneae.

Order Chroococcales – chroococcaceans- It comprises morphologically the most simply colonial and single forms reproducing by binary division or baeocyts- set of naked cells in which protoplast breaks up at high speed. It has been divided into two families:

Family Chroococcaceae- It comprises single- and multicellular cyanobacteria of various morphology, without sheaths or surrounded by single- or multilayered sheaths.

Family Entophysalidaceae- It comprises mainly colonial cyanobacteria and differ from family Chroococcaceae by polarized growth of cells and presence of pallmelloid colonies consisting of motionless cells, embedded in common mucilage.

Order Chamaesiphonales – chamaesiphonaceans- It comprises unicellular and colonial attached forms reproducing by exospores. The order includes one family only — Chamaesiphonaceae.

Order Pleurocapsales – pleurocapsaceans- It comprises coccoid cyanophytes ranging from simple unicells to complex colonial forms with frequent division of cells in a parallel pseudofilamentous arrangement of cells in colonies. These are both epilithic (living to the surface) and endolithic (penetrating predominantly carbonate substrate) pleurocapsacean cyanobacteria. The most distinctive feature of these cyanobacteria is a reproduction by baeocyts or endospores that are formed inside the cells. On the basis of morphology of colonies and features of life cycle this order comprises three families:

Family Dermocarpaceae (often classified inside the order Chamaesiphonales)- It is characterized by the least variations of the sizes and morphology of cells in colonies, but the majority of forms are attached to a substrate, including by means of a special small stalk.

Family Pleurocapsaceae- It is characterized by complexly differentiated colonies of cells, with an arrangement of cells in parallel and usually pseudofilamentous rows with lateral and dichotomous ramification. Ramifications are caused by occasional change in the plane of cell division. Cell division in two or three planes results in packing of pseudoparenchymatous three-dimensional cell aggregates or in formation of crusts.

Family Hyellaceae- It also comprises morphologically differentiated pseudofilamentous colonies, but the distinguishing feature of this family is a presence of endolithic forms getting into a substrate.

Class Hormogoneae (Hormogoniophyceae)- hormogonian- It comprises filamentous forms consisting of trichomes (connected in chain-like structures, cells joined together by cytoplasmic connections) often surrounded by a single- or multilayered sheath; set from a trichome and a surrounding sheath refers to as a filament. Reproduction is mainly by means of hormogonians (fragmented trichome not surrounded by a sheath), hormospores, hormocysts (fragmented trichome surrounded by a thick sheath), gonidians, coccusis and planococcusis (monocellular trichome fragment), and also akinetes (resting spores). Forms are both single, and colonial; the colonial forms are also often surrounded by the common sheath. Classification is based mainly on a degree of cellular differentiation, features of

branching and presence of specialized cells. It is divided into three orders.

Order Oscillatoriales – oscillatorialeans- It comprises homocytic trichomes, consisting of similar types of cells but undifferentiated in form and function. The weak differentiation is observed between intercalary (medial), basal and terminal cells; the terminal cell is frequently transformed into the calyptra. Within sheaths there can be one (monotrichomous filament) or a few (polytrichomous filaments) trichomes; sheath can be absent and trichome is twisted into a cylindrical spiral. Reproduction by means of hormogonians and gonidians. In order Oscillatoriales several families were distinguished, but all varieties can be considered within the limits of one family-Oscillatoriaceae.

Order Nostocales – nostocaleans- It comprises heterocystic trichomes consisting of differentiated cells in form and function. Besides vegetative cells, there are specialized cells: akinetes (resting spores) and heterocysts. Heterocysts are designed especially for molecular nitrogen fixation with two-layered envelope having either intercalary or terminal/ basal positions. Trichomes are singled row (uniseriate), symmetrical or asymmetrical, frequently with meristematic zones of growth; filaments are characterized by false branching: sheaths bifurcate only, but trichomes remain unbranched. False branching is determined by the position of heterocyst location which restricts the growth of trichomes inside sheaths while the growth of trichome between heterocysts cause localized growth pressure. As a result, trichomes rupture and penetrate sheaths forming false branching. In order Nostocales, eight families were established, but only three families clearly demonstrate profound differences:

Family Nostocaceae- It comprises forms with non branching filaments, with or without sheath, single or colonial, sometimes embedded in common mucilage or with a spherical envelope of colonies. Trichomes symmetric, unipolar, heterocysts and akinetes are intercalary or terminal.

Family Scytonemataceae- It unites filaments with sheaths demonstrating false branching, single or forming colonies. Trichomes are rather symmetric, but the terminal parts with apical meristematic zone of growth are a little protruding out of sheaths; heterocysts intercalary.

Family Rivulariaceae-. It comprises branched or non branched filaments, with or without sheaths around trichomes, single or colonial. Trichomes are asymmetrical, heteropolar, narrowed towards the apices, and often terminating by a terminal hair. Heterocysts and akinetes are intercalary or basal.

Order Stigonematales – stigonemataleans- It comprises heterocyst-bearing units-or multiseriate trichomes, demonstrating true branching in trichomes and surrounding sheaths. This order encompasses the most complex differentiated cyanobacteria. Filaments show heteromorphism, i.e. morphology of cells of trichome in central part can noticeably different from morphology of cells in its branches, and akinetes, heterocysts and hormospores are present. The majority of filaments form colonies prostrating on substrate, frequently with rising upwards lateral branches; a number of forms are endolithic. It should be noted that there are no undoubted Proterozoic stigonematalean cyanobacteria, probably due to taphonomical reasons, but some akinetes or group of cells can probably be assigned to this order. In order Stigonematales, some families were established, but three are generally accepted.

Family Mastigocladaceae- It comprises of filaments with V-shaped (loop-like) branching and strong heteromorphism.

Family Nostochopsidaceae- It comprises of filaments with T-shaped branching formed as a result of simple lateral bulging of intercalary cells.

Family Stigonemataceae- It comprises of filaments with normal dichotomizing Y-shaped branching and morphologically most strongly differentiated trichomes.

Structure of cyanobacterial mats

Coexistence of primary producer – cyanobacteria- and primary consumer- destructive bacteria- consuming organic matter formed as a result of metabolic activity of photosynthetic microorganisms has led to formation of stable systems (so-called cyanobacterial mats) traceable through Proterozoic and at least in parts of the late Archaean. These cyanobacterial mats have basically a three-layered or multilayered structure and consist of (1) the upper aerobic cyanobacterial layer comprising mat-forming cyanobacteria, (2) the middle layer inhabited by purple and green phototrophic not the sulfur bacteria, and (3) the bottom layer formed mainly by the strictly anaerobic destructive bacteria (Stolz, 1983a, b; Bauld *et al*., 1992; Stal, 2000; Schopf, 1994, 1999). Thickness of the top layer varies within several millimeters, in a well developed mat making usually 2.0-2.5 mm for an upper layer and 1.0-1.5 mm of a middle layer, whereas bottom anaerobic zone can reach up to several centimeters in which consequently buried cyanobacterial communities are observed. In some cases, there are additional layers, i.e. in lagoons of the Sivash Gulf, Crimea, a layer of flexibacteria about 1 mm thick is localized beneath the cyanobacterial layer, but able to migrate upward at increase of solar radiation has been recorded (Venetskaya & Gerasimenko, 1988). Significant distinction of conditions within the different mat layers, from 100 percents oxygenic environments to completely anaerobic, that resulted into the formation of geochemical gradients on their borders have been noted.

The known steps in the formation of the cyanobacterial mats are as follows: cyanobacterial films, forming upper mat layer starts develop first and only after its accumulation some necrobiosis- destructive bacteria appear in bottom zone creating anaerobic environments there. As a consequence, an

intermediate buffer zone inhabited mainly by facultative anaerobes appears between an upper aerobic and a bottom anaerobic layers. This zone, also an intermediate, where on light exposure, only low-energy quanta of spectrum red part gets to, is basically not used by cyanobacteria. Therefore, purple and not the sulfur bacteria using this part of the spectrum for photosynthesis colonize the ecological niche such as *Chloroflexus aurantiacus* in thermophilic mats, *Thiocapsa* in halophilic mats, and *Ectothiorhodospira* in alkaliphilic mats (see Sergeev *et al*., 2002). 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 (Gerasimenko & Zavarzin, 1993). 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 (Zavarzin, 1983; Gerasimenko *et al*., 1989; Zavarzin & Kolotilova, 2001). Probably the close cooperation of the mat community organisms predetermined the extreme conservatism of both the mat-forming and mat-dwelling microorganisms, which has not changed for at least 2.0-2.5 billion years. It should be noted that fossilized forms were only undegraded cyanobacteria from mat's upper layer, which were either silicified or mummified at the early stages of diagenesis and had no time undergoing considerable *post-mortem* alterations.

The main components of cyanobacterial mats are mat-forming microorganisms composing upper layer. In general, there are three basic types of modern cyanobacterial mats. First type mats are formed by palmelloid colonies of entophysalidacean cyanobacteria *Entophysalis*. Second type is formed by oscillatorialean and nostocalean hormogonian cyanobacteria, mainly belonging to non-heterocyst forms of so-called LPP-type *(Lynbya-Phormidium-Plectonema;* Rippka *et al*., 1979*)* and heterocyst-bearing cyanobacteria like *Nostoc*. Third type of mats are formed by stigonematalean cyanobacteria with highly differentiated multiseriate filaments of *Mastigocladus* and *Stigonema* mainly; such heteromorphic trichomes are unknown from the Proterozoic rocks, but observed in the Devonian Rhynia cherts of Scotland (see Schopf, 1974a).

There are many symbiotic microorganisms in mats of modern oscillatoriacean and nostocalean cyanobacteria, diversity of which as a rule, depend on harshness of environments: the more favorable the environment, the higher is a diversity of occurring microorganisms (Golubic, 1976a). The most typical dwelling symbiotic microorganisms are chroococcacean cyanobacteria; besides there are many eukaryotic microorganisms occurring among the hormogonian cyanobacteria and others like diatoms, green, red and other unicellular algae as well as protozoa (Golubic, 1976a; Margulis *et al*., 1983; Stolz, 1983a, b).

Modern mats are commonly dominated by filamentous oscillatorian cyanobacteria, although there are some exceptions. The high-temperature mats of Yellowstone Park and Kuril Islands are dominated by *Synechococcus elongatus* (*Synechococcus lividus*); the mats of Kamchatka Peninsula, by *Mastigocladus laminosus*; and Australian coastal 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 hormogonian 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, oscillatorian cyanobacteria are motile, which allows cyanobacterial filaments to interweave with each other, forming a dense tissue. The upper layers of mats 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 *Phormidium, Oscillatoria, Lyngbya*, and *Spirulina*.

The stratified mat structure results into microlamination of the majority of Precambrian carbonate rocks, including stromatolites. However finding of a zonal microbial community preserved in ancient rocks is extremely difficult, as their initial structures are deformed under the influence of abiogenic processes of fossilization and sedimentation. To date, there is no report of Precambrian fossilized three-layered cyanobacterial mats comparable in details to modern counterparts. However, there are a few finds of well preserved palmelloid colonies of entophysalidacean and gregarious numerous empty sheaths of hormogonian cyanobacteria in which occur nesting coccoidal dwellers forming together the upper layer of cyanobacterial mats, e.g. the Lower-Middle Riphean (Mesoproterozoic) Yusmastakh Formation of the Anabar Uplift, Siberia (plate X; see also Sergeev *et al*., 1995;

Sergeev, 2006) and the Upper Riphean Min'yar Formation, the southern Ural Mountains (plate IV; see also Sergeev & Krylov, 1986; Sergeev, 1992a, 2006).

MORPHOLOGY AND CLASSIFICATION OF PRECAMBRIAN MICROFOSSILS

The form and variety of Precambrian microfossils

As discussed above, Precambrian cyanobacteria are preserved either as silicified or chert-embedded three-dimensionally preserved microfossils in cherts and cherty parts of dolomite and limestone formations or compression-preserved as usual flattened remains in terrigenous rocks. The ratio of cyanobacteria and protists in any Precambrian microfossil assemblage depends on age and palaeoenvironmental settings of the rocks. Morphology of Precambrian silicified and compression-preserved organic-walled microfossils are shaped significantly by processes of *post-mortem* transformation, diagenetic alteration, selective fossilization of various components of microbial communities, and taphonomic bias imposed by different palaeoenvironments. Remains of morphologically simple filamentous and coccoidal microorganisms, predominantly cyanobacteria, are prevalent in the Precambrian silicified microfossil assemblages. There are also some bizarre microorganic remains, i.e. star-like, dumbbell-like and other complex morphologies, branching thalli and microfossils with spines and processes, but they are very few and found rarely.

Coccoidal microfossils are represented by the cellular remains, but as usual a protoplast and a cell wall after destruction of an organism, shrinking to size of a tiny ball, and surrounded by mucilaginous sheath which keeps original spherical form of a cell (Awramik *et al*., 1972; Knoll & Barghoorn, 1975; Hofmann, 1976; Golubic & Hofmann, 1976; Golubic & Barghoorn, 1977; Knoll *et al*., 1978; Knoll & Golubic, 1979; Sergeev, 1992a). Therefore, in the paper, instead of using the term "cell" for coccoidal microfossils, a more neutral term "vesicle" uniting both a mucilage sheath, as well as cell itself has been used. Vesicles are spherical (Fig. 6.1-6.3, 6.5, 6.6) or ellipsoidal in shape (Fig. 6.4) and can be surrounded by single-layered (Fig. 6.1, 6.2, 6.4-6.6) or multilayered (Fig. 6.3) envelope. Vesicles often occur in pairs (Fig. 6.3), in fours (tetrads) in one plane (flat tetrads, Fig. 6.1) or form a triangular pyramid (tetrahedral tetrads). Vesicles can form colonies in which they are located in a certain order. There are some types of colonies distinguished on the basis of their structure and shape.

Palmelloid colonies are formed by numerous vesicles occurring together randomly, in common amorphous mucilage (Fig. 6.5). Freely occurring vesicles can be surrounded by a common environment and colonies of such type are referred to as *Gloeocapsa*-like (Fig. 6.2) and *Aphanocapsa*-like. Vesicles can be located on the periphery of spherical colonies, leaving central cavity remains free; such colonies are called *Coelosphaerium*-like. Besides there are packages of vesicles in which they are densely adpressed to each other resulting into smooth-triangular, egg-like or trapezoid forms.

There are other colonies characterized by ordered arrangement of vesicles. Colonies with vesicles arranged either as planar tetrads or in mutually perpendicular rows in one plane are called *Merismopedia*-like. Colonies comprising of spheroidal vesicles, arranged in three mutually perpendicular directions in a packages of cubic form are called *Eucapsis*-like; in the latter case colonies get the cubic form as well. Sometimes the vesicles are arranged in parallel pseudofilamentous rows and in packages where they are densely pressed to each other; the resultant colonies are called *Pleurocapsa*-like (Fig. 6.6). Some pleurocapsalean cyanobacteria form stalks composed of regularly spaced, upwardly concave, funnel- shaped layers and terminate with cap-shaped sporangium-like structures containing baeocytes (Fig. 7.11). Besides the colonial forms, vesicles often occur in occasional groupings, but it is sometimes difficult to distinguish a colony from such *post-mortem* cluster of vesicles (this is especially important problem in the study of *Pleurocapsa*-like and palmelloid-like colonies which sometimes are indistinguishable from secondary accumulated vesicle clusters).

Hormogonian cyanobacteria occur basically as hollow single-or multilayered tubular sheaths (Fig. 6.10, 6.11) and trichomes (Fig. 6.7-6.9) as well as mono-or polytrichomous filaments (Fig. 7.1, 7.8, respectively). Trichome cells have discoid, elongated, square-cylindrical, ellipse, as well as cask or spherical shape (Fig. 7.2-7.7). Cells have lateral walls and are divided by cross-walls or septa, and their position can be terminal, medial or intercalary, and basal. The majority of fossilized trichomes are uniseriate, non-tapering (Fig. 6.7, 6.8) or tapering toward apices (Fig. 7.9), but multiseriate forms occur as well. There are sheaths and trichomes twisted into a flat or cylindrical spiral shape, with or without the adjoining forms, flattened ribbon-like sheaths (Fig. 7.10), and three dimensionally preserved tubular helixes (Fig. 6.9). Hormogonian cyanobacteria often occur in layered mat-like colonies (fragments of cyanobacterial mats) where they, as a rule, are strongly bound and intertwined, inside coccoidal microfossils, usually remains of chroococcacean cyanobacteria (Fig. 6.11). Sometimes gregarious sinuously intertwined filaments are surrounded by common single-walled envelope forming *Sphaeronostoc*-like colonies (Fig. 7.13).

Precambrian microfossil assemblages contain not only cyanobacteria but also numerous remains of eukaryotic microorganisms. There are large spherical envelopes up to a few millimeters in diameter (Fig. 7.14), large ribbon-like macroscopic remains several millimeters across and up to a few tens of millimeter long (Fig. 7.12), vase-shaped microfossils of few hundred microns across, branching filaments (thalli),

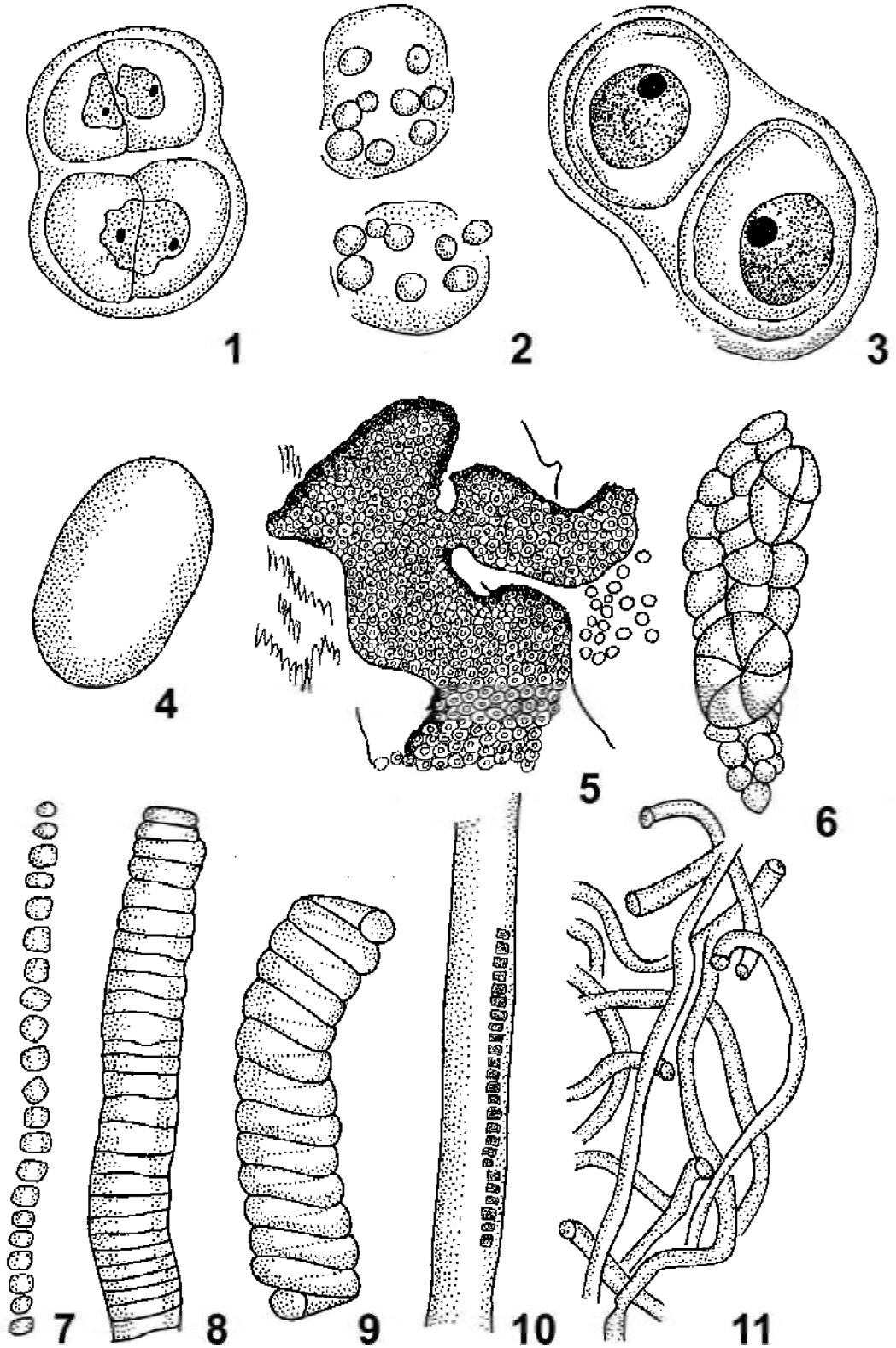


Fig. 6—Morphological types of fossilized cyanobacteria; 1, 3 - spherical vesicles of chroococcaceans, 2 - *Gloeocapsa*-like colonies, 4 – ellipsoidal vesicles (akinetes and *Synechococcus*-like chroococcaceans), 5 - palmelloid colonies are formed by numerous vesicles occurring in common amorphous mucilage, 6 - *Pleurocapsa*-like colonies are formed by vesicles arranging in parallel pseudofilamentous rows, 7, 8 – uniseriate, non-tapering sheath-less trichomes of oscillatoriaceans; 9 – tubular helixes of *Spirulina*-like filaments; 10 – hollow tubular sheath with shrunk cells of trichome inside; 11 – cyanobacterial mat formed by empty sheaths of oscillatoriaceans.

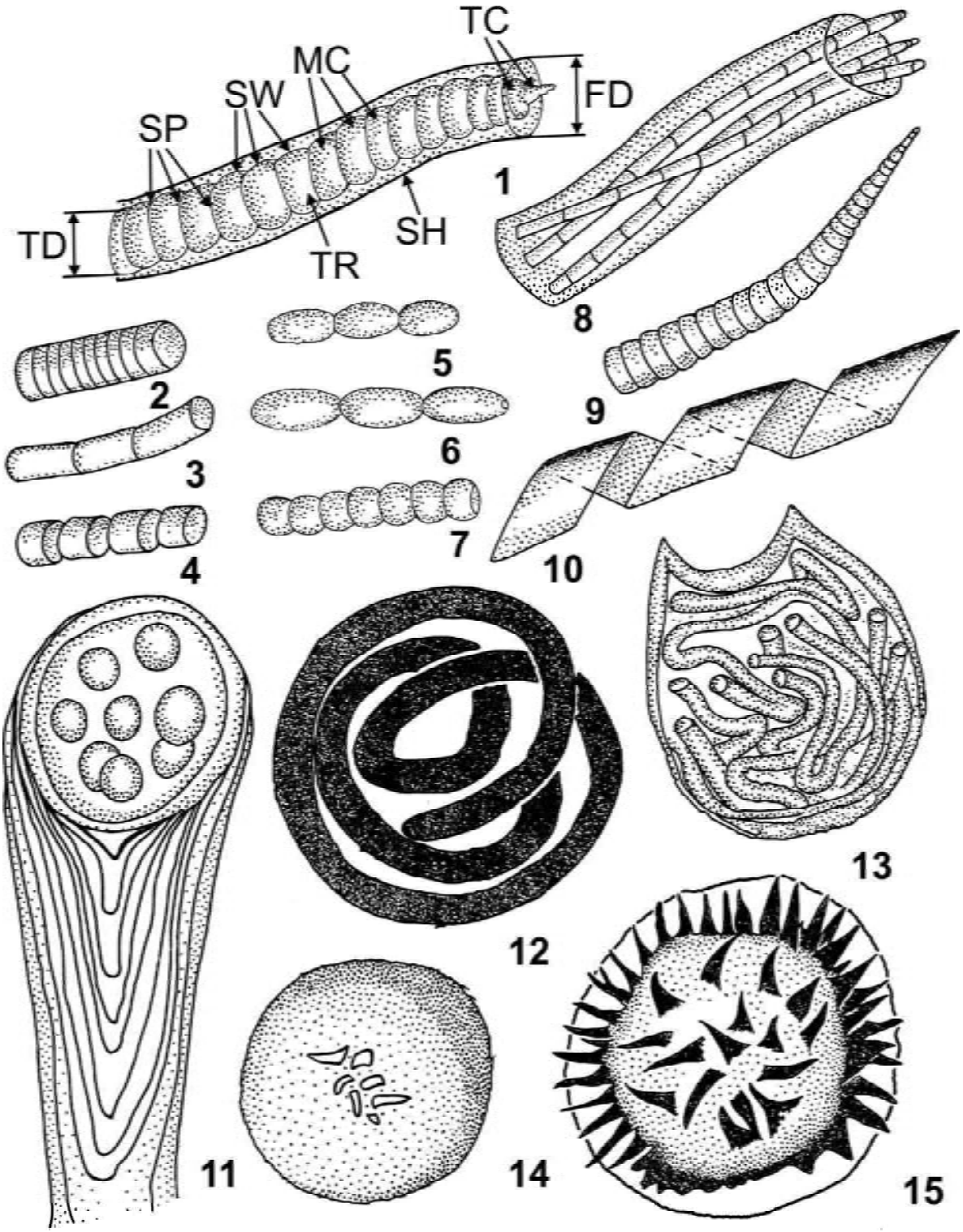


Fig. 7—Morphological types of fossilized cyanobacteria and protista; 1 – monotrichomous filament with single layered sheath and uniseriate, non-tapering trichome, key: FD – filament diameter, TC – terminal cells, TD – trichome diameter, TR – trichome, MC – medial cells, SH – sheath, SP – septa, SW – side walls; 2 – discoid-cylindrical cells; 3 – elongated-cylindrical cells; 4 - square-cylindrical cells; 5 – cask-like cells; 6 – ellipsoidal cells; 7 – spherical cells; 8 – polytrichomous filament; 9 – tapering toward apices trichome; 10 – *Heliconema*-like empty sheath twisted into a flat spiral; 11 – *Polybessurus*-like stalk composed of upwardly concave, funnel shaped layers and terminate with a sporangiumlike structures containing baeocytes; 12 - ribbon-like macroscopic filament several millimeters across; 13 - *Sphaeronostoc*-like colony from gregarious filaments surrounded by a common envelope; 14 - large spherical envelope a few millimeters in diameter; 15 - spherical vesicle bearing processes.

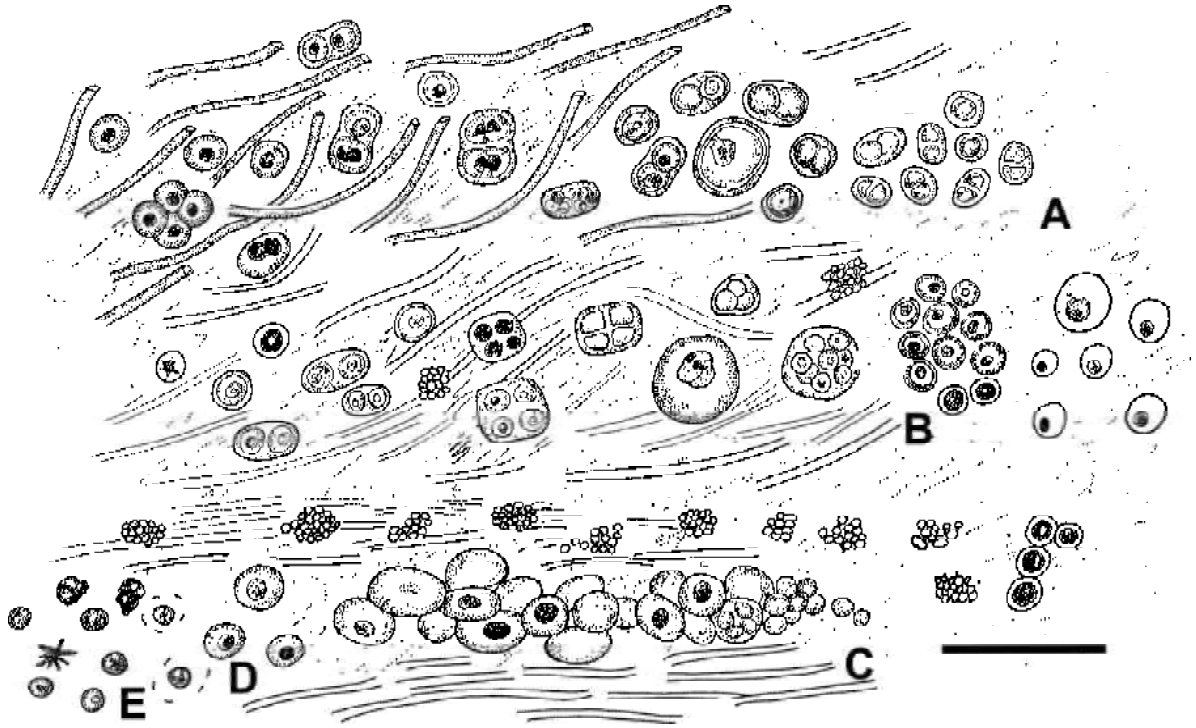


Fig. 8—Gradual degradation stages of *Siphonophycus* spp. and *Gloeodiniopsis lamellosa* cyanobacterial community from the Satka Formation. A – slightly changed fossilized community, B – medium altered microfossils, C-E – high altered community with compressed spheroids forming *Pleurocapsa*-like aggregates and empty sheaths aligning parallel to lamination. Scale bar ~ 100 μm.

spherical vesicles bearing processes and spines (Fig. 7.15). All microfossils are characterized by certain structure of a surface (smooth, granular or granulated), accordingly walls have amorphous, granular or granulated structure. Many of these morphologies have counterparts not only among eukaryotes, but among various groups of prokaryotic microorganisms, including cyanobacteria. It is related with significant morphological similarities of many lowest protista, bacteria and cyanobacteria at significant distinction in their biochemistry and physiology. Difficulty of biological interpretation increases with *post-mortem* processes of alteration sometimes completely changing cell morphology.

Post-mortem alteration and fossilization

Precambrian silicified and compression preserved cyanobacteria as well as other microorganisms passed through significant *post-mortem* changes prior to fossilization changing sometimes their morphology significantly. Originally it was suggested that silicified microorganisms did not suffer significant degradation (Schopf, 1968; Schopf & Blacic, 1971) and were fossilized probably alive like ancient Roman towns Pompeii and Herculaneum covered with volcanic tuff and lava within no time. However, living microorganisms are not capable to be silicified considering presence of osmotic pressure inside cells (turgor). Study of modern cyanobacteria from the hot springs of Kamchatka Peninsula (Geyser Valley) has revealed lack of any possibility living mats to be silicified properly (Krylov & Tikhomirova, 1988). If silica gel nonetheless replaces living mats, there are only empty holes left after cyanobacterial cells in chert matrix (such structures are often observed in Precambrian silicified rocks and cherty parts of carbonate formations). Therefore, all microorganic remains embedded in cherts passed through *post-mortem* degradation during certain time interval after cell termination and prior to fossilization. First a cytoplasm membrane separates from a cell wall, and a protoplast shrinks to a size of a tiny (comparable to cell diameter) ball which sticks to internal part of a cell wall (Awramik *et al*., 1972; Knoll & Barghoorn, 1975; Westall, 1997). Protoplast often is followed by a cell wall and sheath layers collapsing inside vesicle to form multilayered structures with central dark inclusions (Pl. 7.1-5). These inner inclusions are typical for cyanobacterial as well as lower eukaryotic algal remains fossilized in cherts. However, the dark spots inside fossilized vesicles could turn out to be pyrenoids of green algae of other inner cellular inclusions (D. Oehler, 1976, 1977). Frequently, entire cell contents are destroyed and only empty vesicles are preserved in the embedded cherts which could be remains of either cyanobacteria or protists. Nucleus is extremely fragile and delicate structure therefore unable to be preserved in any Proterozoic silicified microfossil assemblage. Mainly, fossilized sheaths are preserved as the most rigid parts of cell and could

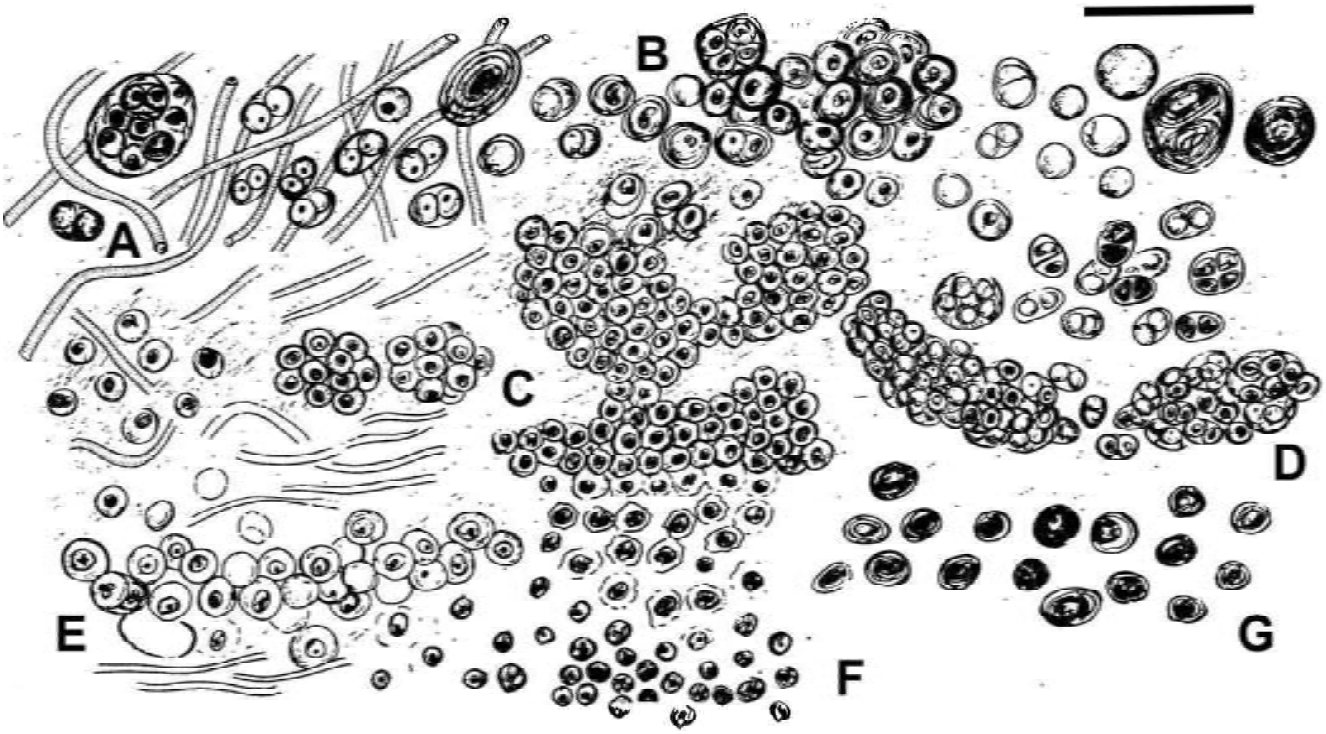


Fig. 9—Gradual degradation stages of *Siphonophycus* spp. and *Gloeodiniopsis lamellosa* cyanobacterial community from the Min'yar Formation. A, B – slightly changed fossilized community initially consisting of sheaths of *Siphonophycus robustum* and *S. typicum* and *G. lamellosa* (A) and *G. lamellosa* vesicles only (B); C - E – medium altered microfossils forming pseudopalmelloid *Eoentophysalis*-like (C) and pseudofilamentous *Palaeopleurocapsa*-like aggregates (D, E); F, G – high altered vesicles where only central degraded parts survived forming *Glenobotrydion*-like (F) and *Globophycus*-like aggregates (G). Scale bar ~ 100 μm.

be compared to shells of Phanerozoic skeletal organisms. But there are fossilized cells embedded in cherts without any surrounding sheaths that are typical for multicellular trichomes and some chroococacean unicells. Evidently processes of decomposition are determined by microenvironments in which cell get into after termination of its biological activity.

Primary morphological features are used for classification of coccoidal microfossils, mainly cyanobacterial remains: such as form and size of vesicles, number of sheath layers, structure of a colony; however internal structures are not given much attention being products of decomposition. Colonies after decomposition can break up into separate cells, and on the contrary, separate cells can stick together forming *post-mortem* accumulations (clusters), in turn, reminding colonies of microorganisms (Fig. 8 and 9; see also Sergeev, 1992a). Coccoidal cyanobacteria suffer significant changes after bacterial destruction and deformation and by crystals growth during the diagenesis (Sergeev, 1988, 1992a, b; Sergeev *et al.*, 1995; 2008). As a result secondary spine-like structures could be formed on the originally smooth external layer of an envelope and remains of chroococcacean cyanobacteria get similarity with acanthomorphic and herkomorphic acritarchs (Pl. 7.8-10, Pl. 27.5).

Hormogonian cyanobacteria also pass through the significant *post-mortem* changes that resulted into destruction of trichomes as well as sheaths. As usual, hollow tubular sheaths are formed as a result of full or partial destruction of trichomes; sometimes remains of trichomes are present inside sheaths as thread-like relicts or chains of shrunk cells (Fig. 6.10). However, hollow sheaths can also be formed as a result of trichomes partition into hormogonia and their subsequent evacuation.

There are fossilized filaments twisted into planar or cylindrical spirals (Fig. 6.9, 7.10). Most of these are of primary biological origin being fossil counterparts of modern *Spirulina*-like cyanobacteria. But in some cases, formation of spiral by filaments is associated with the ecology: under favorable conditions filaments twist into a regular plane spiral (*cf. Contortothrix* Schopf, 1968) and in three dimensional intertwined irregular structures in harsh environments (Gorunova *et al.*, 1969). Often enough cylindrical flat spirals are formed by empty abandoned trichome sheaths subsequently twisting into flat regular coiled cylindrical structures (e.g. *Heliconema australiense* Schopf, 1968; see Elenkin, 1949, Fig. 479; Golubic & Barghoorn, 1977). But origin of some fossilized flat spirals are uncertain and they could turn out to be either secondary twisted sheaths of straight filaments or flattened primarily and subsequently coiled into regular spiral forms (e.g., *Heliconema funiculum* Schopf & Blacic, 1971). Shrinkage of hollow sheaths even can transform

them into thin thread-like structures less than a half micron thick and being superimposed against each other forming false branching filaments (Sergeev, 1992a, pl. XIX, fig. 9, 10), similar to hyphae of actinomycetes (*cf*., *Ramacia* J. Oehler, 1977).

Second way of filaments degradation is complete sheaths destruction while trichomes are survived (only protoplast collapses inside trichome cells). In many cases, trichomes are fossilized practically untouched, but frequent processes of decomposition change their morphology significantly. Oscillatoriacean trichomes are the most resistance to *post-mortem* changes. However, their cell septa can collapse and hollow thread-like tubular structures similar to empty sheaths are formed. There can be a selective swelling or shrinking of trichome cells resulting into formation of enlarged bodies reminding akinetes and heterocysts of nostocaleans or stigonemataleans (Golubic & Barghoorn, 1977; Gerasimenko & Krylov, 1983; Hofmann & Schopf, 1983). Further some cells shrinkage can results into trichome's breaking apart on segments tapering toward ends and reminding trichomes of nostocalean cyanobacteria of family Rivulariaceae. There are many tapering trichome fragments ending in a terminal "hair" (Golubic & Barghoorn, 1977; Sergeev, 1992a, pl. XIX, fig. 8) and originally described as *Caudiculophycus* Schopf, 1968. Trichomes after destruction can break up into separate cells changing their morphology from cylindrical to spherical (Schopf, 1968; Golubic & Barghoorn, 1977; Sergeev, 1992a).

The same processes of *post-mortem* degradation are observed for nostocalen cyanobacteria as well complicated by heterotrichal construction of trichomes. After filament destruction vegetative cells change significantly and often became indistinguishable from heterocysts and akinetes. Heterocysts and akinetes as well become the centers of secondary transformations and trichomes break apart usually near heterocysts. As a rule, after akinetes get matured other trichome cells are destroyed in an explosive way and only spherical to elliptical akinetes can be fossilized in cherts and shales (Kondratyeva, 1975; Sergeev *et al.*, 1995; Sergeev, 2006).

Trichomes of stigonematalean cyanobacteria suffer probably the most significant *post-mortem* changes. Clearly these processes were observed in destroyed filaments of *Mastigocladus laminosus*, demonstrating significant variations in morphology and forming up to 20 forms of fossilized remains (Gerasimenko & Krylov, 1983). Apparently, stigonematalean cyanobacteria have very unstable filaments disintegrating after destruction into separate groups (clusters) of cells and possibly preserved in fossil record by this way (Sergeev, 1992a, 2006). It probably explains why there are no undoubted Precambrian multiseriate filaments of stigonematalean cyanobacteria found in the cherts or shales, though their problematic finds have been reported (e.g. Golovenok & Belova, 1985). It could be suggested that stigonemataleans being widespread in Proterozoic, that proved to be true also by data of molecular biology, but they were preserved either as akinetes or loose cell clusters usually described as chroococcacean cyanobacteria or eukaryotic algal remains.

As mentioned above, cyanobacteria can be fossilized either embedded in chert or compressed between clay sediments layers. There have been several efforts to understand this process. Since 70's, a series of experimental works were conducted on artificial silicification of prokaryotic and eukaryotic microorganisms (J. Oehler & Schopf, 1971; J. Oehler, 1976a, b; Francis *et al*., 1978a, b; D. Oehler, 1977; Westall *et al*., 1995, 2003; Westall, 1997; Gerasimenko & Ushatinskaya, 2002; Ushatinskaya, 2002). These works simulated various parameters of environment which ancient microorganisms could undergo during silicification and subsequent embedding in silica matrix. In many early experiments, the high pressure and heat were used to simulate processes of metamorphism which Archaean and Proterozoic microfossiliferrous rocks probably suffered (J. Oehler & Schopf, 1971; J. Oehler, 1976 a, b). In these experiments silicification was simulated at lower temperatures between 50º and 70º Centigrade (Francis *et al*., 1978a, b; Ferris *et al*., 1986, 1988). On the contrary, Westall *et al*. (1995) simulated artificial silicification of sea bacteria under the conditions corresponding with deep-water oceanic environments at 4º Centigrade temperature and 500 atmospheric pressure.

As a result of these experiments microorganisms finally appeared entombed in silicon matrix, similar to chert concretions, containing Precambrian microfossils. In all experiments a gel of silica was used which finally polymerized and hardened, superseding water and «...eventually siloxane polymers could replace the organics, often retaining the cellular detail as a lithomorph» (Francis *et al*., 1978a). It has also been revealed that different microorganisms are silicified in the different ways and cells of some organisms demonstrated much higher resistance to silicification than of others. It suggests a bias towards preservation of different organisms in Precambrian cherts and the selective palaeontological record of earliest microorganisms.

Inner contents of cell like mitochondria, chloroplasts, nuclei are not found preserved inside the silicified microfossils whether they are cyanobacterial or eukaryotic remains. During silicification, cell wall and sheath act mainly as centers for polymerization of silicon acid gel; and higher the degree of cytoplasm decomposition faster the gel coagulation occurs. Finally, decayed organic material appears completely entombed inside the silica matrix. Further growth of silica crystals can result in total replacement of all organic matter inside the artificial chert concretions.

Gram-positive and gram-negative bacteria are fossilized differently: for example, gram-negative spirochetes could not be silicified even after four months from the moment of their life activity termination while gram-positive bacteria are completely silicified in less than a week (Westall *et al*., 1995,

2003; Westall, 1997). It is likely that this preferential silicification is apparently related with features of an extracellular structure. Cytoplasmic membrane and cell wall of gram-positive bacteria are surrounded by usually thick external layer (a sheath) from several up to first tens micron thickness. Gram-negative bacteria have much more complex external sheath and a cytoplasmic membrane. It is surrounded by a thin peptidoglycan layer which, in turn, is surrounded by the double envelopes: an internal layer consists of phospholipids, and an external one consists of lipopolysaccharides. Therefore, bacterial cells physiology predetermines their selective preservation in palaeontological record, providing undoubted taphonomic advantage for the gram-positive cyanobacteria.

There are also modern silicified microfossils: they have been found in thermal springs of Kamchatka Peninsula Geyser Valley (Krylov *et al*., 1983) and Iceland (Schultze-Lam *et al*., 1995). Krylov and Tikhomirova (1988) demonstrated silicification based on the study of the silicified cyanobacterial mats from the thermal springs of Kamchatka applying a scanning electronic microscopy. In this model, silica replaces microorganisms first and only then fills space between silicified cells. However, this path of organic matter replacement by silica is not acceptable for at least most Precambrian silicified microfossils which can be freed from chert concretions dissolving in hydrofluoric acid (Schopf, 1970; D. Oehler, 1976, 1977; Sergeev, unpublished data). These data are rather in favor of the model suggested by Westall *et al*. (1995), though the mechanism of microorganisms silicification is undoubtedly complicated, multiple and probably requires an individual analysis of every case (Gerasimenko & Ushatinskaya, 2002; Ushatinskaya, 2002).

Thus, *post-mortem* degradation of microorganisms and peculiarities of their silicification should be considered while dealing with biological interpretation of chert-embedded microfossils. The situation is complicated by similarity in morphology and life cycles of cyanobacteria and biologically different eukaryotic microorganisms. The problem to the solution is in analysis of a fossilized microbial community as a whole with reconstruction of possible relations between various microorganisms as well as evaluation of *post-mortem* alteration of every microfossil. To date, ways of *post-mortem* degradation and fossilization are better known and investigated for microorganisms embedded in cherts than for compression-preserved organic-walled microfossils in shales. Definitely, processes of *post-mortem* alteration are supposedly to be the same for both types of microfossils preserved in cherts and shales. But how the compression-preserved organic-walled microfossils in shales stay in place is still undetermined. Evidently clay particles also worked as impervasive for compression-preserved microfossils keeping them untouched for a few billion years like cherts. But it still unclear how microorganism remains in shales could survive before lithification. It was observed for modern entophysalidacean cyanobacteria from the sabkhas of Persian/Arabian Gulf that their remains survived for 6000 years due to high salinity and acidity of coastal pools (Golubic & Hofmann, 1976). Similar ways of fossilization could be suggested for the cyanobacterial remains preserved in shales as flattened envelops.

Biological interpretation of fossil cyanobacteria and relevant microorganisms

The correct biological interpretation of ancient microorganisms is possible for numerous and only well-preserved remains allowing observation of transitions between various forms of preservation and life cycle stages of fossilized microbes. The interpretation based on poorly preserved microfossils is of a little help considering modern different microorganisms undergoing decomposition and subsequent silicification provide surprisingly similar preservational forms. The key to decipher the majority of Precambrian silicified microfossils nature in their comparison with communities of modern cyanobacterial mats. It is possible only due to unprecedented evolutionary conservatism of cyanobacteria (hypobradytelia) when their main taxa practically have not changed for at least ~ 2 billion years. Cyanobacteria occupied almost all ecological niches during Precambrian, but were especially diverse and abundant in shallow-water and lagoonal environments of ancient carbonate platforms preserved in cherts and cherty parts of dolomite and limestone formations.

To date, three main types of cyanobactrial mats have been recongnized among Proterozoic fossilized microbial communities. First, monospecific coccoidal mats formed by palmelloidal colonies of entophysalidacean cyanobacteria *Eoentophysalis* (modern counterpart *Entophysalis*) without any other microorganisms. Second, also monospecific mats composed by stalks of pleurocapsalean cyanobacterium *Polybessurus bipartitus* (modern *Cyanostylon*-like counterpart is still not described, but found thriving in Bahama Islands) forming thick crusts. Third, filamentous mats formed by hormogonian cyanobacteria hollow sheaths *Siphonophycus* (fossil counterparts of LPP-type cyanobacteria) and trichomes *Oscillatoriopsis*, *Palaeolyngbya*, *Cephalophytarion* and others (modern counterparts are *Oscillatoria*, *Lyngbya*, *Phormidium*, and others) with filaments and coccoids inside. The coccoidal microorganisms are mainly remains of chroococcacean cyanobacteria symbiotically incorporated into hormogonian mats, but remains of eukaryotic organisms occur as well including subsequently buried planktonic forms. Significant part of the coccoidal microfossils cannot be unequivocally interpreted as prokaryotic or eukaryotic microorganisms, especially less than 10 microns in diameter and having a single-layered envelope. Mats formed by empty sheaths of *Siphonophycus* are most widespread in Proterozoic and apparently they were the main stromatolite builders.

There are not only remains of cyanobacterial mats in the fossil record, but also inhabitants of temporary ephemeral pools existed on tidal flats (Knoll & Golubic, 1979), playa lakes (Southgate, 1986) as well as planktic organic remains. It is well known that the majority of cyanobacteria cannot be strictly differentiated into benthic and planktic forms. Mat forming filamentous *Lyngbya*- or *Phormidium*-type cyanobacteria can shift to a planktic way of life (Vladimirova, 1968), while some cyanobacteria (for example, *Aphanocapsa*) normally leading the planktic way of life, can coexist in mats of hormogonian cyanobacteria (Awramik, 1978). Planktic microorganisms after death often get entrapped in cyanobacterial mats and fossilized together with benthic organisms thriving there.

Allochthonous and autochthonous fossilized cyanobacteria as usual differ by character of distribution. Both benthic and planktic forms show strong facial dependence, however within the limits of a thin section remnants of planktic forms, as a rule, are distributed in regular intervals and occur irrelevant inside as well as outside cyanobacterial mats (Knoll *et al*., 1978; Awramik & Semikhatov, 1979). The best way to recognize fossilized planktic forms is their morphological features, but the same can be applied to eukaryotic microorganisms mainly.

There are two main criteria for the differentiation of fossilized eukaryotes from prokaryotes, mainly cyanobacteria: size and morphology. Envelopes bearing spines and processes seem to be the most reliable eukaryotic microorganic remains, probably phytoplanktic forms (Tappan, 1980; Knoll, 1994, 1996, 2003; Mendelson & Schopf, 1992; Sergeev, 1992a, 2006). The maximum diameter of modern prokaryotic cells does not exceed 60 microns (Hofmann & Schopf, 1983), but in a fossil record not only remains of separate cells, but also envelopes of microorganism colonies are preserved (Fairchild, 1985; Sun, 1987; Sergeev, 1992a, 1994, 2006; Steiner, 1996). Therefore, the size criterion should be applied very carefully in interpretation of fossilized large spherical microorganisms as eukaryotic remains. An additional attribute help to interpret a large spherical microfossil as eukaryote, is presence of a dense envelope resistant to dissolution in acids (Vidal & Ford, 1985). Fossiliferrous layer bearing biomarkers, typical for particular group of nucleated organisms, is also considered as another independent criterion in favor of eukaryotic microorganisms presence (Summons *et al*., 1999; Knoll, 1999). But poorly preserved imprints on the layers surface, even having the macroscopical size, cannot unequivocally be interpreted as the remains of eukaryotes or prokaryotes (Sharma & Shukla, 2009a, b).

Almost undisputable attribute of a eukaryotic level of organization is presence of true spines and processes on surfaces of fossilized coccoidal forms. But at the same time, it is difficult to decipher exact biological nature of true spiny forms; probably some of them even belong to completely extinct group of early eukaryotes (Knoll, 1984, 1992a). Some acanthomorphic acritarchs are interpreted as phycomatas of green prasinophycean algae (Tappan, 1980; Colbath, 1983), dinoflagellates or diapause egg cysts of invertebrates (Cohen *et al*., 2009). Of course one should keep it in mind that little microfossils with small unclear spines could turn out to be remains of chroococcacean cyanobacteria changed by diagenetic alteration.

Classification of Microfossils

Ambiguity of Precambrian microorganisms, biological interpretation and *post-mortem* degradation of destroyed/ entrapped cells create difficulties in silicified microfossils classification. The system used for modern cyanobacteria could be definitely applied for the majority of microfossils occurring in cherty-dolomitic deposits being remains of benthic cyanobacterial communities (Schopf, 1968; Schopf & Blacic, 1971; Knoll & Golubic, 1979; Hofmann, 1976; Hofmann & Schopf, 1983; Schopf, 1992a, 1999, 2004; Sergeev *et al*., 2002; Sergeev, 1992a, 2006). But Precambrian microfossil taxa are different: in some cases they have been described or emended after study of good material with easy recognizable fossilized microorganisms, morphological variations and a sequence of decomposition stages (for example, *Eoentophysalis*, *Gloeodiniopsis*, *Eosynechococcus*, *Palaeolyngbya*, *Oscillatoriopsis*, and others). These almost exclusively cyanobacterial taxa can be placed up to a level of a class, an order or a family depending on their preservation. In other cases, taxa have been described using either highly altered *post-mortem* decomposed cells or morphologically simple remains (for example, *Myxococcoides*, *Glenobotrydion*, *Globophycus* and so forth). The single or colonial simple vesicles described by this way can be chroococcacean cyanobacteria as well as unicellular eukaryotic algae. Such microfossils are considered as objects of uncertain systematic position and described in this paper under the group *Insertae sedis*.

Recently, Precambrian microfossil taxa are distinguished by some researchers on formal and informal basis. Formal taxa contain genera and species established for microremains of a various degree of preservation without analysis of their life cycle and *post-mortem* stages of degradation (Lee Seong-Joo & Golubic, 1998). The group incorporates, for example, hollow sheaths *Siphonophycus* and coccoidal microfossils *Myxococcoides*, and also polytrichomous filaments *Eomicrocoleus*. Unlike this, palmelloidal colonies of *Eoentophysalis* and polytrichomous filaments *Eoschizothrix* are considered as informal or truly biological, adequately reflecting biological nature of fossilized microorganisms. It demonstrates the situation existing in the field of Precambrian micropalaeontology where many microfossil taxa cannot be unequivocally interpreted as remains of certain biological organisms.

Because of difficulties in biological interpretation a number of authors consider all Precambrian microfossils as objects of uncertain systematic position. Classification on this concept is *a priori* formal and all microfossils are divided into various groups using formal morphological attributes only. The similar approach was applied to silicified microremains (Schopf, 1977; Hofmann & Schopf, 1983), and to a greater degree to compression-preserved organic-walled microfossils (Veis, 1988; Yankauskas, 1989). Following this, Precambrian microfossils are separated into formal groups, e.g. spherical monocellular forms, multicellular filaments, cylindrical sheaths, branching filaments, remains of complex morphology and so forth incorporating cyanobacteria as well as eukaryotic microorganism remains.

It should be noted, that the artificial classification developed by Downie *et al*. (1963) is successfully applied for morphologically complex eukaryotic phytoplanktic microorganisms, mainly from Lower Palaeozoic deposits, since mid 60's. These forms were united in the group Acritarcha subdivided into differing morphological subgroups: Sphaeromorphitae, Oomorphitae, Tasmanititae, Disphaeromorphytae, Acanthomorphitae, Herkomorphitae, Pteromorphitae, Polygonomorphitae, Netromorphitae. Subsequently, Diver and Peat (1979) have tried to develop this classification for all Precambrian microfossils, including remains of undoubted cyanobacteria. Group Cryptarcha (besides Acritarcha) uniting the most simply arranged filamentous (subgroup Nematomorphitae) and coccoidal (Synaplomorphitae) forms has been separated. The last 30 years have seen an inconsistency in the approach: the allocated new formal groups of Precambrian microfossils practically have not been used anywhere. Introduction of similar classification in relation to silicified microfossils, represented mainly by remains of cyanobacteria, would be a retrograde and it would deny all successes achieved in the field of Precambrian palaeobiology.

Therefore, in this paper, the most prevalent approach in the study of Precambrian microfossils has been adopted. Majority of microorganic remains can confidently be compared with modern cyanobacteria and to them the morphological system analyzed above can be applied. Other Precambrian morphologically simple taxa (probably also cyanobacterial remains), where nature is not sufficiently clear, are considered as objects of uncertain systematic position *(Insertae sedis)*, and possible biological interpretation is analyzed in remarks to the descriptions.

Finally, we have discussed a problem of relations among microfossil taxa described from Proterozoic silica-embedded and compression-preserved organic-walled microbiotas. After the discovery of hormogonian cyanobacteria in shales and acanthomorphic acritarchs in cherts it became evident, that in many cases we deal with different forms of the same organisms. However, various morphological types of microorganisms are differently comparable. Taxa of hormogonian cyanobacteria and acanthomorphic acritarchs in shales and in cherts are compared almost without significant difficulties. Empty tubular sheaths are compared easily, but there are difficulties in considering the tubular structures which are often remains of different filamentous microorganisms, and the problem is pointed to formal differentiation of described taxa (see Butterfield *et al*., 1994). The most problematic aspect is a comparison of morphologically simple siliceous and compression-preserved organic-walled microfossils with diameter of vesicles within a hundred microns. These forms almost have an ambiguous biological interpretation and presence of a plenty of similar stages in life cycle and *post-mortem* degradation makes it difficult for comparison with silica-embedded microfossils even with each other and difficult to compare with compression-preserved organic-walled forms. Probably, it is better to keep separate silicified and compression-preserved organic-walled species and genera of simple spherical morphology and use the parallel taxa, described from thin sections and maceration slides.

Precambrian silica-embedded and compression preserved organic-walled microbiotas contain remains of both cyanobacteria and eukaryotic microorganisms. Application of biological interpretation and classification for various microfossils depends both on morphology of microorganisms, and a degree of their diagenetic alteration. Apparently, morphologically simple and highly altered microfossils cannot unequivocally be compared to various groups of organic world while morphologically differentiated and well preserved forms can be compared to various groups of prokaryotic and eukaryotic microorganisms. In the present paper, a system of modern cyanobacteria is used for the majority of easily diagnosed microfossils, and others problematic microbial remains share some common features with cyanophyceae as well as lowest eukaryotes are considered as objects *Insertae sedis*.

THE PALAEONTOLOGICAL RECORD, EVOLUTION (HYPOBRADITILIA), PALAEOECOLOGY AND BIOSTRATIGRAPHICAL SIGNIFICANCE

ACTUOPALAEONTOLOGY OF CYANOBACTERIA

Modern cyanobacterial communities

Considering extreme tolerance of cyanobacteria to various environments, they occupy all possible ecological niches of modern environments. Indeed, they are widely distributed in aquatic and terrestrial environments, although highly organized competitors displaced them from propitious habitats

to extreme econiches, such as hot springs, deserts, hypersaline lagoons, volcanic areas and polar regions. They are even able to sustain in radioactively polluted environments and able to withstand g-radiation as much as 2 million roentgens. They are globally important primary producers today and have been through much of our planet's history. Some diazotrophic cyanobacteria are reported to be important agents in the global nitrogen budget; therefore, the group plays a significant role in the nitrogen cycle as well as in the cycles of oxygen and carbon. Accepting that the chloroplasts of plants and algae are derived from a cyanobacterial ancestor implicate that the blue–green bacteria played a great role in eukaryotic evolution. Undoubtedly cyanobacteria are a key to any understanding of Earth's early biological and environmental history.

Modern cyanobacterial communities or mats are main producers of organic matter and have become the subject of extensive research since 1970s. Best studied are the thermophilic mats of Yellowstone National Park, Geyser Valley of the Kamchatka peninsula and Iceland as well as the halophilic mats of the Sinai, Israel, Mexico, Bermudas, Crimea (Sivash Bay), Bahamas and Australia (Shark Bay) (see Sergeev *et al*., 2002). Studies on alkaliphilic microbial communities are few (Doemel & Brock, 1977; Guerrero *et al*., 1994; Schultze-Lam *et al*., 1996), but interest is increasing due to the possible role of these communities in the origin of continental biota (Zavarzin, 1993; Zavarzin *et al*., 1999). While drawing an analogy between ancient and modern cyanobacterial communities, researchers must take into account the great difference between ancient and modern global geochemical conditions on the Earth. For this reason, experimental data on modern communities growing under natural conditions must be completed with the simulation of those communities development of under a wide range of laboratory conditions (Bil'dushkinov *et al*., 1985).

Gas production 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 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 (Gerasimenko *et al*., 1989). These changes in the gas composition were additionally studied in detail in laboratory experiments. The mat obtained in the laboratory correspond to natural mats in the structure and species composition (Orleanskii & Gerasimenko, 1982) 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 (Orleanskii & Raaben, 1996, 1997). 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) (Cohen *et al*., 1975) and H_2 (Gerasimenko *et al*., 1987) stimulating growth of cyanobacteria. Thus, cyanobacteria transform the gases composition 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 (Bil'dushkinov *et al*., 1985) while H_2 is utilized in the hydrogenase reaction (Gerasimenko *et al*., 1987). When cyanobacterial communities are placed in an atmosphere similar to the gas mixture emanated by thermal springs or in an atmosphere presumable similar to the Early Earth, they change the gas composition so that O_2 increases to slightly above 20% and the content of reduced gases, except for CH_4, decreases to zero (Gerasimenko & Zavarzin, 1993). However, probably oxygen at a concentration of 20% hinders the growth of cyanobacteria. This does not mean that accumulation of O_2 in the ancient atmosphere resulted in decline of cyanobacteria. Indeed, under the conditions of active photosynthesis, O_2 bubbles are retained in mats whereas cyanobacteria and other mat dwellers survive in 100% oxygen saturation environments. 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 ancient stromatolites. This makes it possible the study of mineralization under both field and laboratory conditions in order to gain insight into the activity of cyanobacteria in the geological past. The experiments and observations of Gerasimenko and Krylov (1983) showed that the diversity of the chertified microfossils of Uzon Thermal Spring 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 *post-mortem* alterations in cells and filaments. There is another important problem of cyanobacteria mineralization, namely, phosphatization of cyanobacterial communities, a process directly related to accumulation of phosphate deposits. The abundant cyanobacterial remains found in ancient phosphorites (mainly Ediacaran/Vendian through Cambrian) and similarity of ancient stratified phosphorites structure with modern cyanobacterial mats suggest their crucial role in phosphate deposits formation. Experiments with a

Microcoleus 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 (Gerasimenko *et al*., 1996, 1999). A comparative study of phosphorites from different deposits unambiguously showed that cyanobacterial mats are typical of the biocenoses in which these deposits were formed (Zhegallo *et al*., 2000).

The ability of cyanobacteria to precipitate carbonates has been studied by many researchers (see Riding, 1991; Riding & Awramik, 2000; and references therein). The fundamental property of cyanobacteria is that at a low concentration of CO_2 they are able to utilize ions in the course of oxygenic photosynthesis. Calcium carbonate crystals are deposited either on the cyanobacterial cell walls or on the slimy sheaths surrounding cells. The capacity for calcium precipitation varies among species, and some species exhibit individual shape of the formed crystals (Gleason & Spackman, 1974; Krumbein & Giele, 1979; Gorbushina *et al*., 1999; Merz, 1992). Most often calcium carbonate is deposited on the sheaths, forming tubes, but it may also be deposited between cyanobacterial filaments or cells. 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 (Gerasimenko *et al*., 1989) 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 maximal under the conditions optimal for photosynthesis (Nekrasova *et al*., 1983). 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. It is established in saturated calcium carbonate solutions that carbonate can be deposited not only biogenically but also chemogenically. For this reason, the type of genesis of calcium carbonate is routinely difficult to be established. 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 (Delado & Lapointe, 1994).

As a result of growth and metabolic activity of algal (mostly cyanobacterial) communities and their interaction with the environment organo-sedimentary structures – stromatolites – are formed due to calcite and aragonite deposition in the cyanobacterial mats. This interaction involves binding of carbonate particles by algae and their subsequent cementation into a rock. Stromatolites dominated throughout the development of the biosphere in Precambrian Eon. In Phanerozoic, occurences of stromatolite drastically decreased due to appearance and expansion of organisms possessing skeleton, such as archaeocytha, sponges, bryozoans, corals, and red lithothamnion algae, which competitively displaced cyanobacteria to unfavorable econiches (Krylov, 1963, 1975). However, there are modern and ancient layered sedimentary textures called precipitates or precipitated textures formed without active involvement of cyanobacterial communities (see Sergeev *et al*., 1995, 1997; Sharma & Sergeev, 2004). Precipitates were abundant in Archaean and Palaeo- through Mesoproterozoic almost declining in Neoproterozoic (see Grotzinger, 1993; Knoll & Sergeev, 1995; Grotzinger & Knoll, 1999; Sergeev & Lee Seong-Joo, 2006).

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 (Merz, 1992; Golubic, 1973; Pentecost, 1978). 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 environments with high carbonates concentration where differentiation between biogenic and abiogenic types of carbonate sedimentation is difficult (Merz-Preiß, 2000). Calcareous microfossils were scarce during cyanobacteria dominance in Precambrian (Komar, 1979; Knoll *et al*., 1993; Knoll & Semikhatov, 1998). However, calcareous cyanobacteria and eukaryotic algae became abundant near Precambrian–Cambrian boundary as well as in Palaeozoic and Mesozoic (Riding, 1991). The reasons are unlikely related to cyanobacterial metabolism variation, but rather determined by evolution of the environment and appearance of organisms with skeletons, which radically changed all biogeochemical cycles in the biosphere and hydrosphere (Knoll *et al*., 1993). In the Palaeogene and Neogene, the occurrence of stromatolites and in the Cretaceous Period algae with calcified sheaths in marine (but not lacustrine) lime sediments drastically decreased. This may be due to the appearance of lithothamnion algae in the Cretaceous Period, which almost completely forced cyanobacteria out of shallow-water normal salinity marine environments (Maliva *et al*., 1989).

PRECAMBRIAN HISTORY OF CYANOBACTERIA

Ancient cyanobacterial communities

Cyanobacteria, which are among the most structurally organized and morphologically differentiated prokaryotic organisms, possess a well documented palaeontological history. This is due to their large (for microorganisms) size, exceeding that of many other microorganisms, and to the specific taphonomic conditions of cyanobacterial communities' providing general excellent environments for their fossilization. The remains of Precambrian microorganisms, as mentiond above, are mainly fossilized as chertified pseudomorphs

through their complete or partial silicification in chert–carbonate rocks or as mummified remains in shale deposits. These two forms of remains, which are referred to as silicified-embedded and compression-preserved organic-walled microfossils, represent remains of biologically close but facially different groups of microorganisms. The microorganisms preserved in chert–carbonate rocks represent fossilized cyanobacterial communities mainly inhabited shallow-water, lagoon, and littoral environments, whereas mummified organic-walled microfossils are remains of phytoplanktonic organisms from open-sea shelf zones 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 often formed in shallow water environments. The term facies is used here in its classical sense, i.e. designating geochemically and sedimentologically different zones of a sediment layer or a suite of layers subdividing into within their horizontal distribution limits. Actually, there are several tens of facies definitions, and their analysis and comparison could be the subject of a separate paper. In case of modern environments, the facies definition implies a differentiation (in some parameters) of the lateral zones of non-lithified sediments. Taken together, palaeontological data on silicified and compression-preserved organic-walled microfossils as well as stromatolites give an adequate idea of the evolution of microbial communities and their palaeoecological structure. The most ancient stages of biosphere evolution, especially Archaean, are characterized almost exclusively by silicified microorganism remains, whereas information on organic-walled microfossils from shales is scarce. This can easily be explained by the fact that ancient microorganisms became chertified soon after they had encompassed in a cherty rock (Maliva *et al*., 1989) and, hence, were more protected from unfavorable environmental effects than the mummified organic-wall microfossils formed in siliciclastic rocks.

Cyanobacterial communities in space and time

Precambrian embracing a time span from 542 Ma to more than 4600 Ma is subdivided into Hadean (Informal, more than 4000 Ga), Archaean (4000-2500 Ma) and Proterozoic (2500-542 Ma) Eons. Analyzing Precambrian cyanobacterial communities, we used both International (IUGS) stratigraphic (Plumb, 1991) and Russian time scales (Semikhatov, 1995) as a framework considering most microfossil assemblages came from the reference sections of North Eurasia (Russia and Kazakhstan). The Russian Proterozoic Scale is *de facto* a chronostratigraphic scale (Semikhatov, 1995; Resolutions…, 2001) and the International Proterozoic scale (Plumb, 1991; Gradstein *et al*., 2004; Ogg *et al*., 2008) is chronometric, except for the Ediacaran Period (Knoll *et al*., 2004, 2006a). Despite theoretical differences in the bases of the two scales, they divide Proterozoic time in similar ways. Besides we used a series of Proterozoic microfossil-defined biostratigraphic informal units which have been proposed by Sergeev (2009) based on the successive occurrence of distinctive microfossil assemblages. Although these informal units do not correspond exactly to standard units of either the Russian or the International (IGS) stratigraphic time scales, they represent a promising basis for continuing micropalaeontological research, perhaps helping to identify prospective formal units of the global stratigraphic time scale. The term "unit" is used for these subdivisions as a close Proterozoic analogue of the local or assemblage zone (of a given fauna) commonly used in biostratigraphic practice. The subdivisions of Russian and International (IGS) stratigraphic time scales as well as informal units are shown in Fig. 10.

Large time duration of the Archaean, for the convenience, is further divided: rocks older than 3600 Ma are categorised as Eoarchaean, Palaeoarchaean (3600-3200 Ma), Mesoarchaean (3200-2800 Ma) and Neoarchaean (2800-2500 Ma).

Archaean microfossils

Any record of earliest life is to be found in the oldest surviving sediments on the Earth which are now considered part of Archaean (4000 Ma-2500 Ma) Eon. Although most of the Archaean rocks were subjected to repeated alteration and deformation in the geological past yet, the evidence of early life, if any, were entombed in the sediments of this age. Most of the Archaean sediments occurring on the different cratons of the world are metamorphosed to the level of Garnet-Almandine facies making them rather unsuitable for search of Archaean life. Any remnant of slightly metamorphosed rocks, i.e. Prehnite-Pumpelleyite or low grade Greenschist facies, is the only possible store-house for investigations.

The oldest (4280 Ma old) whole rock of Precambrian Eon has been found in the Nuvvagittuq Greenstone Belt in northern Québec, Canada represented by the rock termed "faux amphibolite" that formed shortly after the Earth formation and may be oldest preserved crustal section on earth (O'Neil *et al*., 2008); the oldest sedimentary rocks are found in the Isua Supracrustal Belt, on the Godthabsfjord region, southwestern Greenland (3.77 ± 0.042 Ga) (McKeegan *et al*., 2007). Attempts to find remnants of the Archaean and Proterozoic life in the early 20th Century (Grüner, 1923, 1924) were seen with skepticism (Hawley, 1926), and subsequently there was a lull in the interest of early life investigations. After the discovery of the Gunflint microfossils (Tyler & Barghoorn, 1954; Barghoorn & Tyler 1965), sediments from these Eras were investigated with vigour by the number of experts. But even today the Archaean fossils record is poorly known and whatever is known is debatable; new techniques are being explored to conclusive prove the antiquity, syngenicity and biogenicity of reported objects. Since this paper deals with

Precambrian microfossils specially the cyanobacteria, it would be prudent to look the Archaean records to see the existence of cyanobacteria or the other bacteria during Archaean.

Before considering the report for cyanobacterial occurrences in the Archaean one need to establish the biogenicity, syngenicity, and antiquity of the reported remains. Between 1960 and 1980, researchers described a great number of chertified microfossils found in Archaean 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. In 1983, Schopf and Walter reviewed 43 categories of putative Archaean microfossils known by that time and they considered that the microfossils reported from Warrawoona, Hamersley and Fortescue Groups, all from Western Australia, were very close to be considered as possible microfossils. Microfossils reported from North Pole Dome, Warrawoona Group, Western Australia were most interesting and drawn maximum attention. Dunlop *et al*. (1978) reported several types of spheroidal carbonaceous microfossils in the chert which, however, later proved to be non-biogenic origin (Schopf & Walter, 1983). From the carbonaceous stromatolitic chert of the same area, Awramik *et al*. (1983) reported 4.0 to about 7.5 µm diameter spheroids. Although these spheroids were like many younger Proterozoic microfossils where filamentous forms are also found yet their fewer number and similarity to known non-biogenic microstructures pressed Schopf and Walter (1983) to regard them as non-compelling evidence of Archaean life. Another set of fossils which were rosette-like aggregate of filaments, also found in the carbonaceous chert, were described by Awramik *et al*. (1983). These were composed of fine unbranched filaments of 0.5 µm to 1.0 µm in diameter and more than 100 µm in length. Counting on several possibilities these were also considered as possible fossils or aggregated microstructures of solely non-biogenic origin. In 2001, Ueno *et al.*, also recorded carbonaceous filaments from chert barite unit of Warrawoona Group in the North Pole area of Western Australia. $\delta^{13}C$ values of carbonaceous filaments range from-42 to-32‰ suggesting biologically fixed organic compound and indicating that autotrophy existed on the Archaean Earth (Figs 11, 12).

Among the various microfossils, cell-like spheroids described by Muir and Grant (1976) from the carbonaceous cherts of the Kromberg Formation of the Onverwacht Group, South Africa were considered close to be biogenic but their origin remained uncertain (Schopf & Walter, 1983). Later, Walsh and Lowe (1985) and Walsh (1992) recorded filamentous microfossils from ~ 3.5 Ga old Onverwacht Group, Barberton Mountain Land, South Africa. From the same region, Westall *et al*. (2001) reported fossil bacteria and biofilms in hydrothermally influenced sediments.

Similarly, LaBerge (1967), and Muir and Grant (1976) reported spheroids of 12-25 µm from Brockman and Marra Mamba Formations, Western Australia (~ 2.5 Ga). Some amount of poorly preserved carbonaceous material was also noted around these spheroids but their biogenicity was not

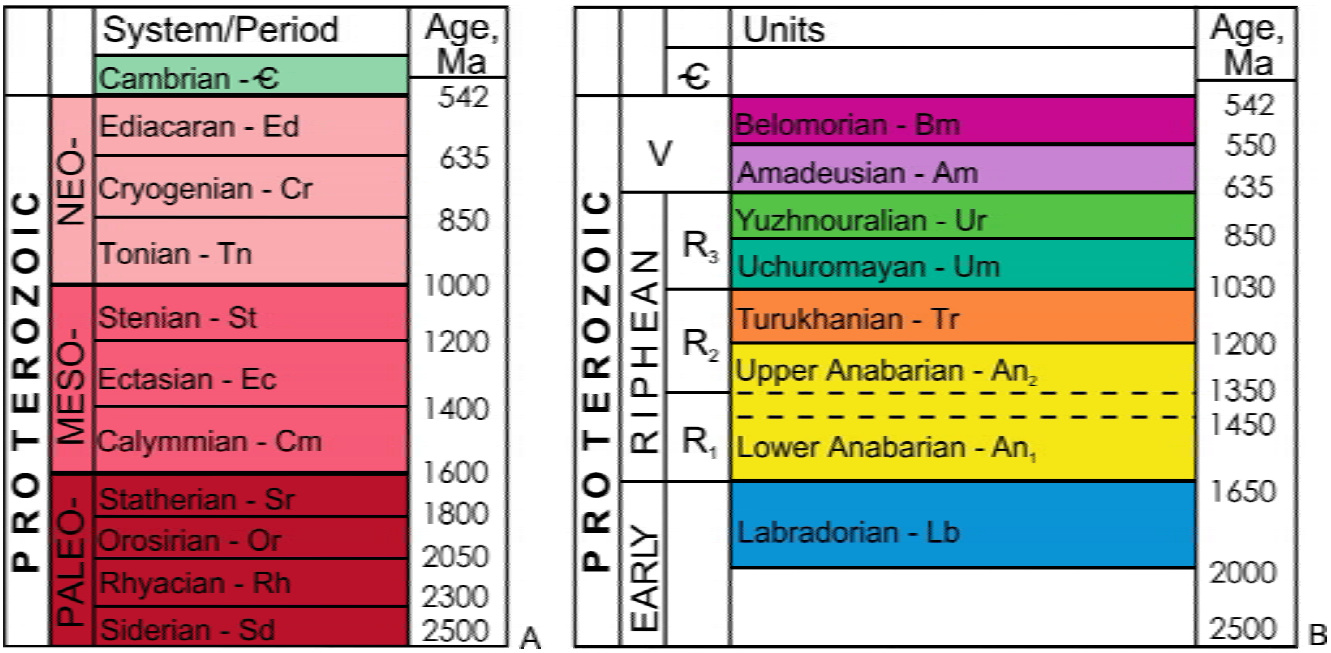


Fig. 10—Geochronological and stratigraphic scales of Proterozoic. A. The International Stratigraphic Scale. B. The Russian Stratigraphic Scale and the micropalaeontological units of the Precambrian (cf. Sergeev, 2009). Key: R_1 – Lower Riphean, R_2 – Middle Riphean, R_3 – Upper Riphean, V – Vendian. The two dashed lines show alternative positions of the boundary between Lower and Upper Anabarian micropalaeontological units.

unquestioned and therefore these spheroids were also considered under the category of possible fossils.

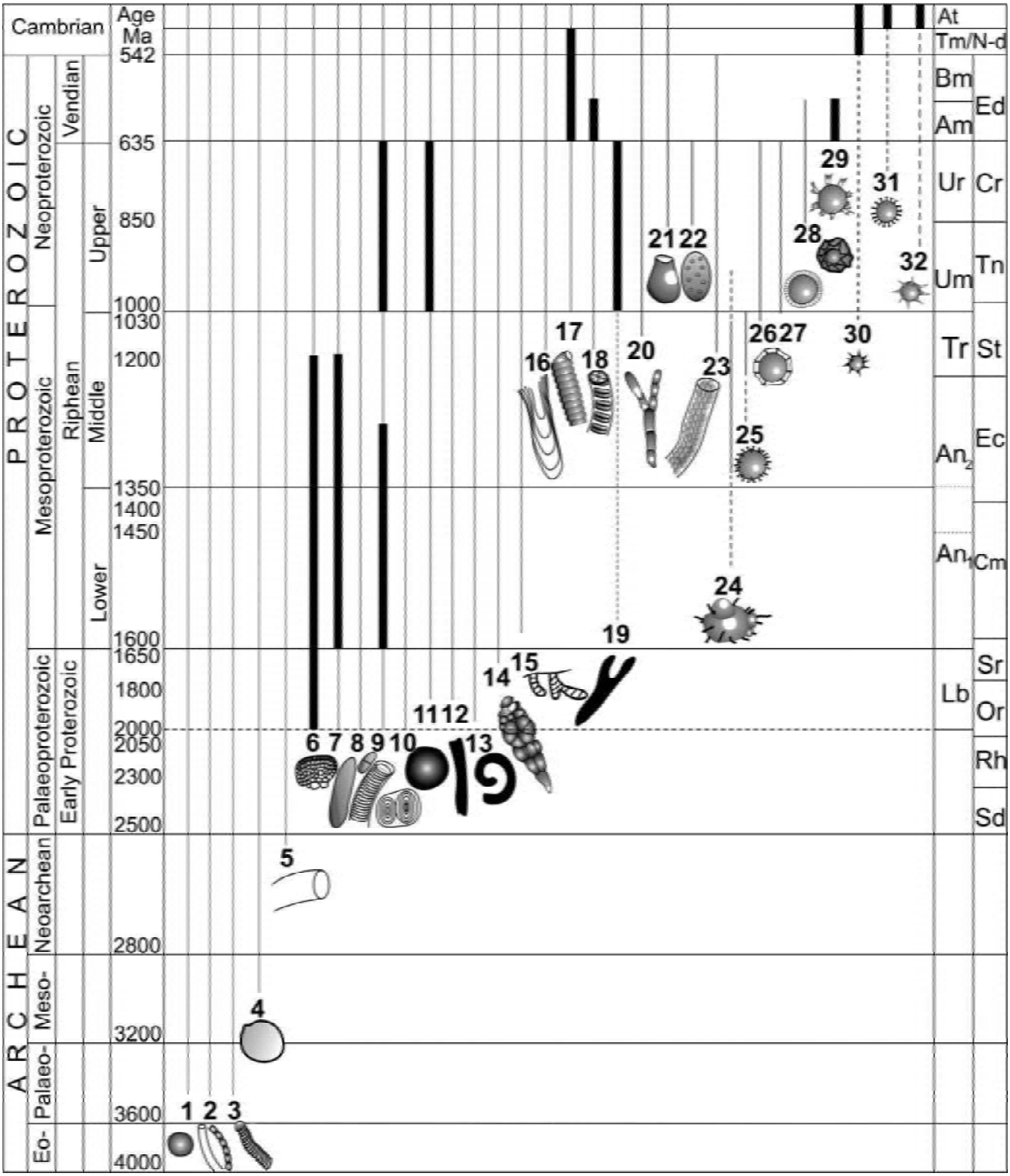
Among the three assemblages discussed above only assemblage of filamentous fossil bacteria from ~ 3.5 Ga old Warrawoona Group (Awramik *et al*., 1983), satisfies all the criteria (*viz.*, age, indigenousness, syngenicity and biogenicity) for establishing the authenticity of Archaean Microfossils. Later, eleven more taxa of fossils were described from this unit and bedded cherts in the Apex Basalt, Western Australia (Schopf & Packer, 1987; Schopf, 1993) with strong arguments in favour of biogenicity through Laser-Raman imagery of these fossils (Schopf *et al*., 2002). But the Warrawoona fossils were repeatedly challenged (Buick, 1984, 1991; Brasier *et al*., 2002, 2004).

With so much of uncertainty about the biogenicity of each reported object of the Archaean age that it is difficult to consider whether these objects represent the cyanobacterial remains or some other bacterial forms in Archaean. Schopf (1993), however, initially considered the forms reported from the Apex Basalt and Tower Formations belong to as trichomic cyanobacterium-like microorganisms and later further categorised them as six of the eleven species probably are cyanobacteria belonging to Oscillatoriaceae, three are members of more primitive bacteria and two could be either cyanobacteria or bacteria (Schopf, 1999, 2006; Schopf *et al*., 2007; Schopf & Kudryavtsev, 2009). It was also suggested that the members of this assemblage were oxygen-producing and oxygen-breathing cyanobacteria. These are, at present, supposedly the oldest fossil record of cyanobacteria. Skepticism still remains there (Knoll, 2003, p. 63); presently, it is believed that microfossils occurring in Palaeoarchaean (3600-3200 Ma) sediments are remains of coccoidal and filamentous bacteria having affinity for chemolithotrophic metabolism (Sergeev *et al.*, 2007a).

Another set of interesting objects were reported from mafic and ultramafic pillow lavas of the Komati, Hooggenoeg and Kromberg Formations of the Onverwacht Group (Furnes *et al*., 2004). In these formations, glassy margins of lavas revealed a network of tubular structures of 1-9 μm in diameter and 200 μm long. The distribution pattern of the tubules in lavas is orthogonal in comparison to fractures that are mineralized with titanite and having fine films of organic matter on their walls. In their shape, size and spatial distribution, tubules are comparable with mineral casts of cavities which appear in volcanic glass of recent oceanic basalts in response to metabolic activity of chemolithotrophic bacteria (Staudigel *et al*., 2004). In both the cases, organic carbon is isotopically lighter in outer margins than in the inner zones of Palaeoarchaean and recent pillow lavas. With this similarity, the Palaeoarchean tubular microstructures likely represent to be formed by microbes and filled with titanite during subsequent metamorphic event. Incidentally, eruption of lava of Komati Formation and metamorphism was almost concurrent ($^{40}Ar/^{39}Ar$ ages determined for metamorphic minerals from tubules and volcanogenic zircons from lavas correspond to 3486 ± 8 and 3482 ± 4 Ma) (Furnes *et al*., 2004). Cyanobacterial filaments have been shown to colonize the lava first (Schwabe, 1972). Therefore, it is most likely that microbial community of the Palaeoarchean colonized oceanic lavas very soon after their eruption ~ 3.48 Ga ago. Iron Ore

Fig. 11—The occurrence of the main types of cyanobacteria and other microfossils in the Archaean and Proterozoic. 1 – small (<10 μm) solitary spherical microfossils; 2 – small (diameter <10 μm) filamentous microfossils; 3 – trichomes and trichome-like fossils having a diameter >10 μm; 4 – coccoidal microfossils containing dense bodies or with lack of inclusions (*Myxococcoides*), possibly remains of chroococcacean cyanobacteria; 5 – large (up to 35 μm in diameter) non-septate filaments, tubular sheaths presumably of oscillatorialean cyanobacteria; 6 – remains of entophysalidacean cyanobacteria (*Eoentophysalis*); 7 – akinetes of cyanobacteria (*Archaeoellipsoides*); 8 – unicellular ellipsoidal chroococcacean *Synechococcus*-type cyanobacteria; 9 – trichomes and filaments of cyanobacteria; 10 – unicellular chroococcacean *Gloeocapsa*-like cyanobacteria (*Gloeodiniopsis*); 11 – large *Chuaria*-like spheroidal microfossils; 12 – large ribbon forms (*Tawuia*); 13 – large spiral macroscopic microfossils (*Grypania*); 14 – pleurocapsalean cyanobacteria (*Palaeopleurocapsa* and other genera); 15 – endolithic cyanobacteria (*Eohyella* and other genera); 16 – stalked cyanobacterium (*Polybessurus*); 17 – spiral-cylindrical cyanobacteria (*Obruchevella*); 18 – red algae (*Bangiomorpha, Wengania, Thallophyca* and other genera); 19 – branching filaments of uncertain affinities (*Ulophyton* and *Majaphyton*), remains possibly of stigonematalean cyanobacteria or of red or green algae; 20 – filaments of a siphonocladalean green alga (*Proterocladus)*; 21 – remains of eukaryotic vase-shaped microorganisms (*Melanocyrillium* and other genera); 22 – scale microfossils comparable to modern siliceous-scale Chrysophyta (*Characodictyon, Paleohexadictyon* and other genera); 23 – trichomes of cyanobacteria or filaments of green algae (*Polysphaeroides*); 24 through 32 – morphologically complex eukaryotic phytoplanktonic microorganisms (acanthomorphic acritarchs); 24 – *Tappania*; 25 – *Shuiyousphaeridium*; 26 – *Trachyhystrichosphaera*; 27 – *Cymatiosphaeroides*; 28 – *Vandalosphaeridium*; 29 – Ediacaran Complex of Acanthomorphic Palynoflora (*Alicesphaeridium, Appendisphaera, Tianzhushania, Cavaspina, Papillomembrana, Tanarium* and other genera*)*; 30 – *Micrhystridium*; 31 – *Skiagia*; 32 – *Baltisphaeridium*.

Units of the International and Russian stratigraphic time scales are indicated on the left and the International Stratigraphic Scale systems and micropalaeontological units are shown, respectively, in the right two columns; the two dashed lines show alternative positions of the boundary between Lower and Upper Anabarian micropalaeontological units. Abbreviations, systems: Sd – Siderian, Rh – Rhyacian, Or – Orosirian, Sr – Statherian, Cm – Calymmian, Ec – Ectasian, St – Stenian, Tn – Tonian, Cr – Cryogenian, Ed – Ediacaran; micropalaeontological units: Lb – Labradorian, An – Anabarian (An_1 – Lower Anabarian, An_2 – Upper Anabarian), Tr – Turukhanian, Um – Uchuromayan, Ur – Yuzhnouralian, Am – Amadeusian; Bm – Belomorian. Other abbreviations: N-d - Nemakit-Daldynian Stage, Tm – Tommotian Stage, At – Atdabanian Stage.


Cambrian
Age
Ma
542
635
850
1000
1030
1200
1350
1400
1450
1600
1650
1800
2000
2050
2300
2500
2800
3200
3600
4000
PROTEROZOIC
ARCHEAN
Neoproterozoic
Mesoproterozoic
Palaeoproterozoic
Neoarchean
Meso-
Palaeo-
Eo-
Vendian
Riphean
Early Proterozoic
Upper
Middle
Lower
At
Tm/N-d
Bm
Am
Ed
Ur
Cr
Um
Tn
Tr
St
An2
Ec
An1
Cm
Lb
Sr
Or
Rh
Sd
1 2 3
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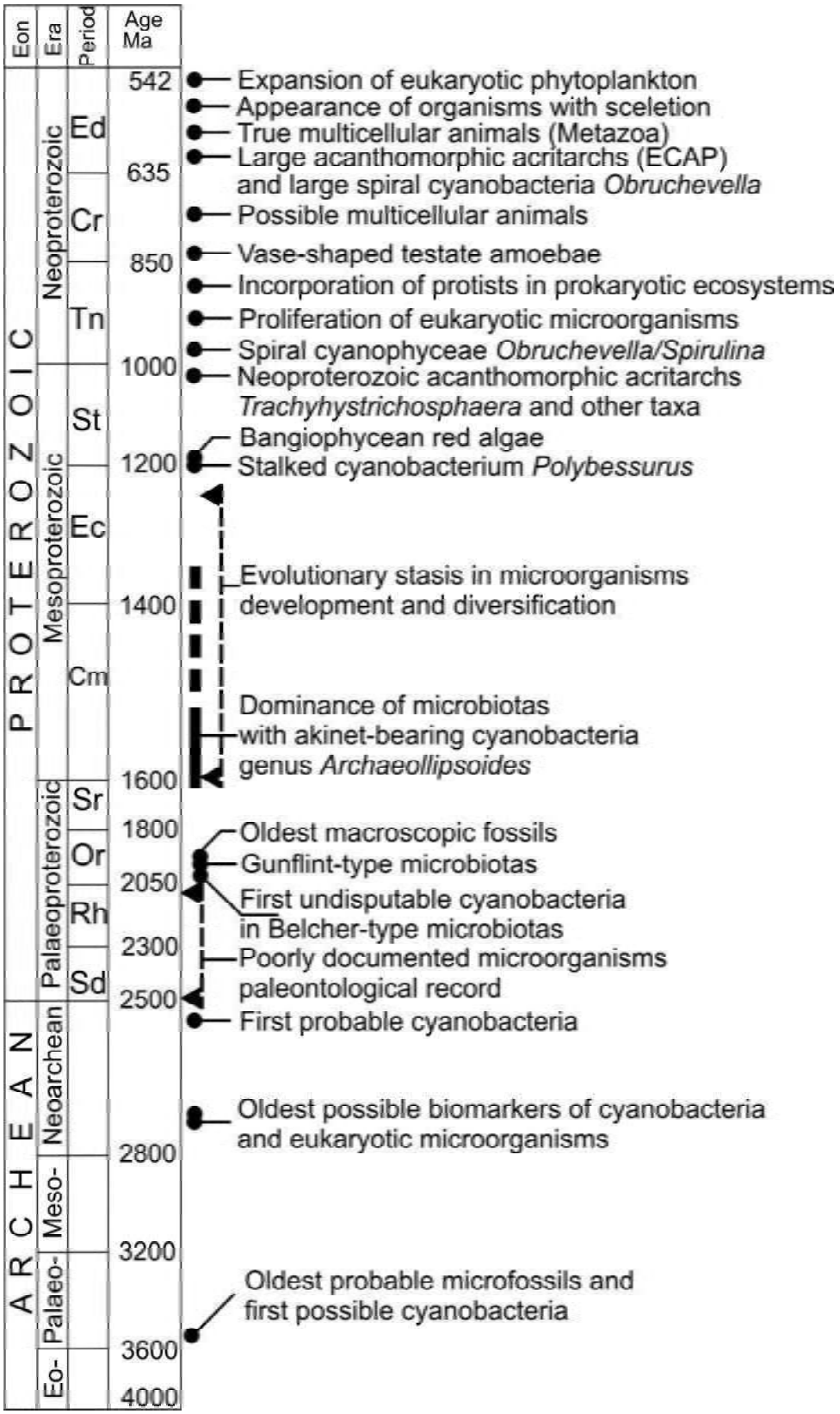


Fig. 12—Succession of the main events observed in Precambrian palaeontological record of cyanobacteria and relevant microorganisms. Abbreviations of the International Stratigraphic Scale systems (periods) are given in Fig. 11.

Supergroup (~ 3.2 Ga) of Orissa also in India yielded spheroids of 5-10 μm diameter (Maithy *et al*., 2000).

Mesoarchaean and Neoarchaean silicified microfossils have been reported from India, South Africa and Western Australia. In India, rod shaped and coccoidal bacteria were reported from 2.9-2.8 Ga old Bababudan Iron Formation (Venkatachala *et al*., 1986) while filamentous microfossils were discovered from the 2.7-2.65 Ga old cherts of the Donimalai Formation of the Sandur Schist Belt (Naqvi *et al*., 1987; Venkatachala *et al*., 1990a). Very well preserved Donimalai microfossils are compared with cyanobacteria which show characteristic features of *Phormidium* and designated as *Phormidella tenue* and *Phormidella sandurense*.

Silicified microfossils constituted of biolith, non-branching sheaths of 35 μm in diameter and coccoidal forms of 1.0–5.0 μm across are recorded from the Gamohaan Formation of the Transvaal Supergroup in South Africa (Klein *et al*., 1987; Altermann & Schopf, 1995; Altermann, 2002). These forms have been considered as obvious empty sheaths of fossil hormogonian and chroococcacean cyanobacteria (Sergeev *et al*., 2007a). Report of rod shaped heterotrophic bacteria from the same formation (Lanier, 1986) is regarded as pseudofossils. Diverse microstructures have been reported by Sugitani *et al.* (2007, 2009) and Grey and Sugitani (2009) from the Mount Goldsworthy-Mount Grant area, Pilbara Craton, Western Australia (> 2.97 Ga). Among these, film-like structures, small spheres associated with films, large spheroids and spindle-like structures are highly probable fossil remains of microorganisms, presumably cyanobacteria.

These reports suggest that in Palaeoarchaean, records of cyanobacteria are tentative where as the Mesoarchaean and Neoarchaean records are most plausible of the existence of cyanobacteria. Besides these body fossils in Archaean we have some indirect evidence of the existence of biosphere of the Archaean. This information is gathered from the analysis of $\delta^{13}C$ values of the carbonates and associated kerogens. In Palaeo- and Mesoarchaean kerogen samples from the Warrawoona, Onverwacht and Fig Tree Groups characterising different environmental facies (normal marine sediments and rocks of hydrothermal origin included), $\delta^{13}C_{org}$ is usually limited by-40 and-30‰. Ueno *et al*. (2006) provided the evidence of methanogens in > 3.4 Ga old sediments of the Dresser Formation at North Pole area in Pilbara Craton, Western Australia with the carbon isotope composition of less than-56‰. In Neoarchaean kerogen samples, this parameter is much more variable, ranging from-60 to-40‰, when host rocks are 2.8-2.6 Ga old, and again from-45 to-30‰ in younger Neoarchean samples (2.6-2.5 Ga). At the same time average values of $\delta^{13}C_{carb}$ in associated Palaeo- to Mesoarchean and Neoarchaean carbonates corresponds to 0 ± 2 and 0 ± 5‰, respectively (Hayes *et al*., 1992; Des Marias, 1997; Brocks *et al*., 2003a, b). Thus, the extent of biogenic carbon isotope fractionation sharply increased at 2.8-2.6 Ga ago, and this event is logically explained by reworking of buried organic matter by obligate anaerobic methanogens and microaerophilic methanotrophic bacteria (Hayes, 1994; Des Marias, 1997; Knoll & Canfield, 1998; Brocks *et al*., 2003a, b), which produce organic matter with $\delta^{13}C_{org}$ up to-42 and-85‰, respectively, i.e. extremely enriched in light carbon isotope (Schidlowski, 2000). On this basis it has been inferred that methane oxidation by bacteria is possible, when oxygen concentration in seawater is slightly above zero at least, and these conditions appeared already in the earliest Neoarchaean. Second, $\delta^{13}C_{org}$ increase in terminal Neoarchean suggests displacement of methanogenic and methanotrophic bacteria communities into anaerobic biotopes (probably deep-water in part) because of progressive biosphere oxygenation under influence of metabolic activity of cyanobacteria. Therefore both fossil and isotopic fractionation records indicate the existence of cyanobacteria by the terminal Neoarchaean. This conclusion is supported by the finds of 2-methylhopanes – biomarkers are typical for cyanobacteria only in the Neoarchean in the shales underlaying the Hammersly Group of Australia ~ 2.7 Ga (Summons *et al*., 1999; Knoll, 1999; Brocks *et al*., 1999, 2003a, b). Another data in favor of earlier history of cyanobacteria are evidence of presence of free oxygen in atmosphere as old as 2.7-2.4 Ga ago (Karhu & Holland, 1996; Bau *et al*., 1999; Watanabe *et al*., 2000, 2004) being approximately about 15% of present atmospheric level (PAL) that could be formed only as a result of cyanobacteria or alike microorganisms metabolic activity.

Early Palaeoproterozoic fossil record

In lower horizons of the Palaeoproterozoic (2.5-2.0 Ga) fossil cyanobacteria or relevant microorganisms are extremely rare, poorly preserved and in many cases are of doubtful organic origin. This situation is paradoxical considering cyanobacterial remains occur in Archaean and especially in late Palaeoproterozoic rocks and the gap in the fossil record embracing time span about a half billion years still has not a reasonable explanation. Silicified microfossils from the lower Palaeoproterozoic are represented by poorly preserved doubtful small coccoidal forms (possible chroococcacean cyanobacteria) from the Kalasyok Group of the Kola Peninsula (2.1-2.06 Ga; Ivanova *et al*., 1988; Melezhik *et al*., 1997) and by coccoidal and filamentous forms (possible sheaths of hormogonian cyanobacteria) from the Aravalli Group of India (Chauhan, 1989; Semikhatov & Raaben, 1994). Remains of cyanobacteria and possibly protists *Leiosphaeridia, Leiominuscula, Myxococcoides*?, *Eosynechococcus* and *Bavlinella*? are known from the Jatulian deposits and the Pechenga Group of the Baltic Schield, the Krivoi Rog Group of Ukraine and the Udokan Supergroup of the Olekma-Vitim Mountain Land (2.5-2.0 Ga; Melezhik *et al*., 1997;

Resolutions…, 2001; Shcherbak *et al*., 1993; Terleev *et al*., 2006).

The cyanobacterial remains are well preserved, diverse and abundant in sediments younger than approximately 2.0 Ga ago. However, the observed sharp change in the fossil record is due to evolution of Earth's crust and environments rather than microorganisms.

The main factor probably was formation of the abundant platformal areas known as Episvecofenian cratons following the extensive transgression about 2.3 Ga ago resulted in emergence of vast shallow-water areas with predominant carbonate sedimentation. The shallow-water carbonate platform favoured lateral expansion of benthic cyanobacterial communities resulted in formation of abundant stromatolitic build-ups. The appearance tectonically stable areas of these ancient platforms facilitated preservation of almost unmetamorphosed sediments in first carbonates with cherts and shales containing practically non-altered cyanobacterial remains. Almost all types of fossil cyanobacteria are observed in 2.0 Ga old microbiotas that have modern counterparts on generic or even specific level with a couple of exceptions demonstrating the evolutionary history of this group. Having analyzed geological background of 2.0 Ga event and presence of sparse problematic remains of cyanobacteria in much older rocks we consider the sharp change in the fossil cyanobacteria record as a consequence of taphonomic factors. Therefore, we belive that cyanobacteria probably have a longer history before and paucity of their fossil record in time span 2.0-3.0 Ga (and possibly down to 3.5 Ga) is mainly because of taphonomy and due to numerous geological factors. However, only since 2.0 Ga cyanobacterial remains are enough well preserved to be analyzed in details and provide reliable data about palaeoecology, evolution (hypobradytellia *sensu* Schopf, 1999) and vertical distribution of this group. Considerable progresses have been achieved in study of fossil cyanophyceae during the past ten to fifteen years that has revealed a biostratigraphic paradox of cyanobacterial assemblages. Some taxa of cyanobacteria which have modern counterparts and do not demonstrate any changes in morphology from early in the Proterozoic to the present (over at least the past 2 Ga), nonetheless occur in fossil assemblages having limited temporal distribution that differ in microbial composition through Precambrian. Together with recently discovered assemblages of organic-walled, both compression-preserved and silicified, microfossil remains of unicellular eukaryotes characterized by high morphological complexity and high (for the Precambrian) rates of evolutionary turnover created a basis for biostratigraphic subdivision of the Proterozoic (Sergeev, 2006, 2009; Sergeev *et al.,* 2010). Biostratigraphic correlation is a major pursuit of palaeontology, and equally applicable for the Proterozoic.

Late Palaeoproterozoic (Orosirian-Statherian) or Labradorian unit (2.0-1.6 or 1.65 Ga)

The microorganisms in cherts provide crucial information about composition and diversity of late Palaeoproterozoic cyanobacterial communities like in the older deposits. Compression-preserved organic-walled microfossils are still poor in composition and in many cases of doubtful organic origin. But microscopic carbonaceous imprints on shales bedding planes provide complimentary information on late Proterozoic microorganisms and probably cyanobacteria. Silicified microbiotas known from this interval are of two main types: Belcher and Gunflint, differing both in the taxonomic composition of microorganism remains and in facial-ecological position (Figs 11, 12).

Gunflint-type microbiotas. The most typical microbiota of the late Palaeoproterozoic Labradorian unit is described from the Gunflint Iron Formation of the Animikie Supergroup, approximately 1.9 Ga (Barghoorn & Tyler, 1965; Awramik & Barghoorn, 1977; Hofmann & Schopf, 1983). It includes two groups of microfossils. The first group comprises morphologically simple trichomes and sheaths of *Gunflintia* and *Animikiea*, as well as coccoidal microfossils of *Huroniospora, Leptoteichos,* and *Corymbococcus*, representing remains of cyanobacteria or iron-oxidizing bacteria (Knoll, 1996). The second group embraces remains of morphologically bizarre umbrella-shaped, dumbbell-shaped, star-like (and other relevant shapes) microorganisms belonging to *Kakabekia, Xenothrix, Archaeorestis, Eoastrion, Eosphaera*, and other genera. Among these genera, supposedly remains of heterotrophic bacteria are present, including iron bacteria (*Eoastrion*) and, putatively, even unicellular eukaryotes (*Eosphaera*). The sedimentation of the Gunflint-type microfossil assemblages is estimated as relatively deep-water within the proximal or distal part of open shelf. The singularity of the microbiotas is predetermined by their close relation with iron-ore formations, canalizing their taxonomic composition of morphologically complex microfossils. Assemblages of the Gunflint-type are described from several upper Palaeoproterozoic localities: the Odjick and Sokoman Formations of Canada, the Chuanlinggou Formation of China, and the Frere, Barney Creek, and Duck Creek Formations of Australia (see review in: Hofmann & Schopf, 1983; Semikhatov *et al*., 1999; Southgate *et al*., 2000; Sergeev *et al*., 2008).

Belcher-type microbiotas are dominated by morphologically simple entophysalidacean (*Eoentophysalis*) and chroococcacean (*Eosynechococcus*, *Myxococcoides*, and other genera) cyanobacteria and less numerous filamentous hormogonian cyanobacteria, mostly the hollow sheaths of *Siphonophycus*. These forms have modern counterparts at the generic and even specific level among living cyanobacteria of shallow-water ecological settings. Belcher microbiotas are

described from shallow coastal (upper subtidal-intertidal) carbonates 2.0-1.65 Ga: the Amelia, Balbirini, Bungle Bungle, and Paradise Creek Formations of Australia (Hofmann, 1976; Hofmann & Schopf, 1983; Southgate *et al*., 2000). The Gunflint-type microbiotas are restricted to the Palaeoproterozoic only and disappear along with iron formations while the Belcher-type microorganisms continue into the Mesoproterozoic thriving together with the akinete-bearing cyanobacteria in the extremely shallow-water environments.

Macroscopic problematic remains of cyanobacterial colonies or eukaryotes. The macroscopic carbonaceous remains preserved in shales as compressions on bedding planes are abundant through all Proterozoic history starting from the upper Palaeoproterozoic Negaunee Formation of North America, 1.9 Ga (Han & Runnegar, 1992; Semikhatov *et al*., 1999). Coiled macroscopic filaments referred to *Grypania* (a few mm wide) besides the Negaunee Formation are widely distributed in the upper Palaeoproterozoic and Mesoproterozoic occuring in the Chuanlinggou and Tuanshanzi Formations of China, the Rohtas Formation of India (Hofmann & Chen, 1981; Walter *et al*., 1990; Hofmann, 1994; Kumar, 1995; Yan & Liu, 1998; Sharma & Shukla, 2009a, b). Besides, *Grypania* the spherical and elongated macrofossils *Chuaria* and *Tawuia* (also a few mm wide) are found in a range of late Palaeo- and early Mesoproterozoic formations demonstrating an early capacity for large body size (Walter *et al*., 1990; Kumar, 1995, 2001; Sharma *et al*., 2009). They could be remains of macroscopic, probably early coenocytic eukaryotes, with transverse markings interpreted as helical fibres responsible for the larger-scale coiling (Han & Runnegar, 1992). However, such large filaments are similar to the colonies of *Sphaeronostoc*-like cyanobacteria as well (Schopf, 1994, 1999; Sharma & Shukla, 2009b). To date, available data are insufficient to distinguish the macroscopic microfossils as eukaryotic or prokaryotic remains.

Early Mesoproterozoic (Calymmian-Ectasian) or early Middle Riphean or Anabarian unit (1.6 or 1.65-1.2 Ga)

Gunflint microbiotas disappeared at the Early Proterozoic/ Riphean boundary (Palaeoproterozoic/Mesoproterozoic), likely related to the disappearance of banded iron formations (BIFs). In the Lower Riphean-lower Middle Riphean there were two main types of silicified microbiotas: Kotuikan and Satka types (Fig 11, 12).

Kotuikan-type microbiotas. The main singularity of Lower Riphean and lower Middle Riphean (Calymmian-Ectasian) is the dominant presence of akinete-bearing nostocalean or stigonematalean cyanobacteria in intertidal to shallow subtidal environments. Their remains are mostly represented by fossilized akinetes of *Archaeoellipsoides* (Sergeev, 1993, 1997, 2006, 2009; Sergeev *et al*., 1995, 2008; Knoll & Sergeev, 1995; Sharma & Sergeev, 2004; Sharma, 2006b). Such ellipsoidal microfossils, described as species of *Archaeoellipsoides*, *Brevitrichoides*, and *Navifusa*, are also known from Palaeoproterozoic and Neoproterozoic deposits (Yankauskas, 1989; Amard & Bertrand-Sarfati, 1997; Sergeev, 2006); however, assemblages in which they are dominant occur only in the early Mesoproterozoic (Lower-Middle Riphean). The second key character of Kotuikan microbiotas is the common occurrence of short trichomes *Filiconstrictosus*, *Orculiphycus*, and *Partitiofilum*, which apparently were germinating akinetes of *Archaeoellipsoides*. In addition, Anabarain assemblages contain abundant coccoid microfossils of *Myxococcoides grandis* which are probably remains of cyanobacteria (akinetes or empty sheaths of *Sphaeronostoc*-type colonies) or protists and other taxa also found in Belcher-type assemblages. The most common are entophysalidacean and chroococcacean *Synechococcus*-like and *Gloeocapsa*-like cyanobacteria (*Eosynechococcus* and *Gloeodiniopsis*) as well as sheaths of hormogonian cyanobacteria. Sheaths of scytonematacean cyanobacterium *Circumvaginalis* consist of elongated funnel-like segments with terminal ring-like thickenings (Sergeev, 1993; Sergeev *et al*., 1995). Anabar microbiotas are common in the Lower and Middle Riphean deposits of 1650-1200 Ma, including the Gaoyuzhuang and Wumishan Formations of China, the Dismal Lakes Group of Canada, the Kyutingde and Debengda Formations of the Olenek Uplift, Siberia, and the Kheinjua Formation of India (see review in Sergeev, 2006, 2009; Sergeev *et al*., 2008; Sharma, 2006a).

The predominance of *Archaeoellipsoides* in the Calymmian-Ectasian deposits is most likely explained not in evolutionary, but in an ecological-facial context with akinete-producing forms regarded as a cyanobacterial terminal group on the basis of 16S rRNA phylogenies (Giovannoni *et al*., 1988; Wilmotte & Golubic, 1991; Golubic *et al*., 1995; Sergeev *et al*., 1995; Tomitani *et al*., 2006; Knoll, 2007). However, in the *nifH*-based tree, two nostocalean sequences do not cluster with other heterocystous-cyanobacterial *nifH* genes (Tomitani *et al*., 2006).

The global evolution of sedimentation and geochemical environments and, in particular, carbonate sedimentation, appears to have played a principal role in the preservation of *Archaeoellipsoides* akinetes. Evidently, the abundant occurrence of *Archaeoellipsoides* in strata of this age is a result of the transformation of nostocalean cyanobacterial filaments into chains of akinetes under conditions of inorganic precipitation of carbonates from oversaturated solutions in shallow-water environments. Thus, the abundance of akinetes in the Early–Middle Riphean basins is apparently related to the existence in this period of extensive tidal flats, that led to the alternation of favorable and unfavorable conditions and mass production of spores of *Anabaena*-like cyanobacteria, which colonized these niches (Sergeev *et al*., 1995, 2008; Knoll & Sergeev, 1995; Bartley *et al*., 2000; Sharma & Sergeev, 2004).

However, modern akinete-producing cyanobacteria are common not only in coastal marine environments (Stal, 2000) but also in other settings as well, so their high abundance in strata of this time might reflect a nitrogen limitation in the mid-Proterozoic oceans (Anbar & Knoll, 2002).

Satka-type microbiotas, which occur more rarely, are dominated by sheaths, trichomes and filaments of hormogonian cyanobacteria *Siphonophycus, Palaeolyngbya* and *Oscillatoriopsis* as well as chroococcacean cyanophyceae *Gloeodiniopsis* and *Eosynechococcus*. Such assemblages were found in the Satka Formation of the stratotypic section of the Lower Riphean, southern Ural Mountains, and in the Svetlyi Formation (Middle Riphean) of the Aimchan Group, Uchur-Maya Region. The Satka microbiota is the only example of this type of microbiota with numerous remains of eukaryotic spherical non-spiny phytoplanktonic remains up to more than 100 μm in diameter, assigned to various species of *Leiosphaeridia*, *Pterospermopsimorpha*, and *Myxococcoides*.

Such Satka-type microbiotas differ from the Belcher-type microfossil assemblages by lacking *Eoentophysalis* and containing dominant *Siphonophycus* mats in which occur nesting coccoidal colonies such as those of *Gloeodiniopsis* and other chroococcacean cyanobacteria (Sergeev, 1992a, 2006, 2009; Sergeev & Lee Seong-Joo, 2001, 2004). Microbiotas of this type are similar to those known from Neoproterozoic cherts occurring in shallow-water carbonates, such as the microbial assemblages of the Min'yar Formation of the southern Ural Mountains (Nyberg & Schopf, 1984; Sergeev, 1992a, 2006) and the Allamore Formation of Texas (Nyberg & Schopf, 1981) and others. *Archaeoellipsoides* akinetes occur in Satka-type microbiotas, but they are relatively minor components.

Compression-preserved organic-walled microbiotas. Microfossil assemblages from the Burzyan Group of the type section of the Lower Riphean, southern Ural Mountains, and the Uchur Group of the Uchur-Maya Region are characterized by the presence of morphologically simple and small remains of coccoidal and filamentous microorganisms predominantly remnants of hormogonian and chroococcacean cyanobacteria. The most diverse assemblages of compression-preserved microfossils of the Lower Riphean come from open-sea facies of the Ust'-Il'ya and Kotuikan Formations of the Anabar Uplift (Veis & Vorob'eva, 1992; Veis *et al*., 2001; Sergeev *et al*., 2007b) and from the Kyrpin Group of Cis-Urals, an analogue of the Burzyan Group (Veis *et al*., 2000). In these microbiotas not only morphologically simple filamentous and coccoidal small microfossils (chroococcaceans?) of *Leiosphaeridia*, *Ostiana* (=*Coniunctiophycus*?), and *Sphaerocongregus*, sheaths of *Siphonophycus* and *Rectia*, akinetes of *Brevitrichoides* (=*Archaeoellipsoides*), wide trichomes of *Botuobia*, and some other forms occur, but also sphaeromorphids of *Chuaria*, branching *Ulophyton*-like filaments (stigonemataleans or eukaryotic algae), and some forms of complex morphology (protists?) are found (Veis & Vorob'eva, 1992; Veis *et al*., 2001). Recent Sm-Nd dating of the basic sills and dykes cutting through the entire Billyakh Group yield isochrones age 1513 ± 51 Ma (Pavlov *et al*., 2007).

Undoubtful protists came from the microbiota of the Roper Group, Australia, U-Pb zircon data indicate the maximal age of 1.5 Ga. Shales of this group contain the most ancient remains of microorganisms with true spines and processes assignable to the genus *Tappania*, some relatively complex forms of *Valeria*, *Dictyosphaera*, and *Satka* (Javaux *et al*., 2001, 2004), and large filaments and spheroids up to 100 and 500 μm in diameter, respectively (Peat *et al*., 1978). A similar assemblage was found in the Baicaoping and Beidajian Formations of the Ruyang Group, China (Xiao *et al*., 1997), the age of which is not reliably dated and may vary from the Early Riphean to the upper part of the Middle Riphean, and the lower part of the Kamov Group attributed to the early Mesoproteroic (upper Lower- Middle Riphean) in the Siberian platform (Nagovitsin, 2009).

Macroscopic carbonaceous fossils of various outlines (spiral *Grypania*, circular *Chuaria*, wide bands with rounded ends of *Tawuia*, and others) are quite common in siliciclastic deposits of the Mesoproterozoic (Lower and Middle Riphean): the Gaoyuzhuang Formation of China, the Rohtas Formation, India (Sharma and Shukla, 2009a, b; Sharma *et al*., 2009), the Belt Supergroup, North America (Walter *et al*., 1990), the Bangemall Group of Australia (Buick & Knoll, 1999).

Late Mesoproterozoic (Stenian) or late Middle Riphean or Turukhanian unit (1.2-1.03 or 1.0 Ga)

The changes in composition of microfossil assemblages near the Mesoproterozoic/Neoproterozoic (Middle/Upper Riphean) boundary are among the most prominent in the Precambrian. The new data prove that these changes started in the second half of the Middle Riphean, about 1200 Ma and led to crucial alternation in the composition of microorganism communities. The main event that took place near the Middle/ Upper Riphean Mesoproterozoic/Neoproterozoic) boundary was the explosive proliferation of eukaryotic microorganisms, which resulted, first, in the appearance of morphologically complex forms and, second, global incorporation of eukaryotes into ecosystems previously dominated by cyanobacteria. However, some changes are observed among cyanobacteria as well.

Silicified microbiotas. First find of the stalked cyanobacterium *Polybessurus bipartitus* is known from late Mesoproterozoic (Schopf, 1975, 1977, 1999; Green *et al.*, 1987), the appearance of which supposedly reflects a new phase of the evolution of prokaryotic microorganisms. These stalked cyanobacteria are abundant in the late Mesoproterozoic microbiotas, other components of the assemblages are sheaths

of *Siphonophycus*, entophysalid cyanobacteria *Eoentophysalis dismallakesensis* and *E. belcherensis*, chroococcacean cyanobacteria *Gloeodiniopsis, Eoaphanocapsa,* and *Eosynechococcus*, and several more forms of simple morphology and broad temporal distribution (Hofmann, 1976; Knoll & Golubic, 1979; Hofmann & Schopf, 1983; Nyberg & Schopf, 1984; Sergeev *et al*., 1994; Sergeev, 1992a, 2006). Remains of akinetes of the genus *Archaeoellipsoides* are lacking or insignificant. Open-sea deposits of these beds contain unambiguous remains of phytoplanktonic eukaryotic microorganisms, often with problematic spines and processes and supposedly being acanthomorphic acritarchs similar to species of *Shuiyousphaeridium* or *Trachyhystrichosphaera*. Such assemblages of microorganisms occur in the Sukhaya Tunguska Formation, which terminates the Middle Riphean section of the Turukhansk Uplift (Sergeev *et al*., 1997; Sergeev, 2006); the Uluksan Group of the Baffin Island, Canada (Hofmann & Jackson, 1991); the Kataskin Member of the Avzyan Formation, Middle Riphean stratotype of the southern Ural Mountains (Sergeev, 1992b, 1994, 2006), and Hunting Formation of the North America, 1.2 Ga (Butterfield, 2001). The latter microbiota contains the remnants of bangiacean red alga *Bangiomorpha pubescens* that is the most ancient morphologically complex and differentiated eukaryotic microorganism having definite biological interpretation (Butterfield, 2000).

Compression-preserved organic-walled microbiotas. The composition of late Middle Riphean organic-walled microbiotas vary significantly both laterally and vertically. The Tulmen Member of the Avzyan Formation of the Ural Mountains contains remains of cyanobacteria and protists *Leiosphaeridia*, *Valeria*, *Sphaerocongregus, Ostiana, Polytrichoides, Asperatofilum*, and *Brevitrichoides*, as well as some other forms that occur in the underlying and overlying deposits (Yankauskas, 1989; Veis *et al*., 1990, 2003). The Kuzha Group of the southern Ural Mountains, which is generally correlated with the Yurmata Group, yields transitional microfossil taxa of large size such as the sphaeromorphic *Chuaria,* broad filaments, and various more complicated morphological types, the analogues of which are present in the Kotuikan Formation and the Kyrpin Group (Veis *et al*., 2000). In the Uchur-Maya and Turukhansk regions of Siberia, rich and diverse microbiotas are known only starting with the Totta and Bezymyannyi Formations of the upper Middle Riphean (Veis & Vorob'eva, 1993). Apart from the morphotypes that are known in the Lower Riphean microbiota of the Omakhta Formation, there are also large (up to 1100 μm) spherical specimens of *Chuaria*, filamentous *Asperatofilum, Taenitrichoides, Rectia, Rugosoopsis,* and *Trachytrichoides*, branching filaments of *Ulophyton* and *Majaphyton*, as well as some other forms that are also known in the Kotuikan microbiota.

Neoproterozoic excluding Ediacaran (Tonian-Cryogenian) or Late Riphean or Uchuromayan and Yuzhnouralian units (1.0 or 1.03-0.635 Ga)

The changes in the composition of the silicified and compression-preserved microbiotas, which started about 1200 Ma and mostly included proliferation of eukaryotic microorganisms, became distinct near the Middle/Upper Riphean (Meso-Neoproterozoic) boundary. The most characteristic taxa that appeared in the Late Riphean are *Trachyhystrichosphaera* and *Prolatoforma,* which bear spines and processes. Some scientists even consider the presence of *Trachyhystrichosphaera* as a crucial characteristic of Upper Riphean (Tonian-Cryogenian) microbiotas that differentiates them from older and younger microfossil assemblages. Besides *Trachyhystrichosphaera*, there are other taxa that appear to be restricted to Neoproterozoic rocks, e.g. *Cymatiosphaeroides*, an envelope bearing thin processes surrounded by an outer envelope (Knoll, 1984, 1994, 1996; Sergeev, 1992a, 2006, 2009; Butterfield *et al*., 1994). In addition to remains with spines, several other eukaryotic microorganisms having complicated morphology are known from Upper Riphean deposits, e.g. true branching filaments of *Aimophyton*, *Palaeosiphonella*, *Palaeovaucheria*, and *Proterocladus*, which are reliably compared with modern green vaucheriacean algae (Timofeev & Hermann, 1979; Yankauskas, 1989; Hermann, 1990; Butterfield *et al*., 1994). In particular, they are known from the type section of the Upper Riphean, southern Ural Mountains, the Lakhanda Group of the Uchur-Maya Region, the Derevnya and Miroedikha Formations of the Turukhansk Region (Petrov & Veis, 1995; Veis *et al*., 1999), the Tindir Group of Alaska (Allison & Awramik, 1989), Ryssö, Hunnberg, and Svanbergfjellet Formations of Spitsbergen (Knoll & Calder, 1983; Knoll, 1984; Butterfield *et al*., 1994), Seryi Kluch Formation of the Yenisei Mountain-Ridge (Nagovitsin, 2000, 2001), and many others.

In spite of evolutionary conservatism of cyanobacteria, spiral-cylindrical filaments of *Obruchevella* are known only from Upper Riphean (Tonian-Cryogenian) and younger deposits. The most ancient *Obruchevella* were reported from the Valyukhta Formation, considered to be lower Upper Riphean (Belova & Golovenok, 1999). However, the primary origin of these spirals has been questioned, and, perhaps more to the point, the Valyukhta Formation itself is now considered to be Vendian (Ediacaran) (Chumakov *et al*., 2007). Indisputable spiral-cylindrical filaments of *Obruchevella* are known in the Seryi Klyuch Formation (Yenisei Ridge), in the Miroedikha Formation of the Turukhansk Uplift (Hermann, 1990), and in slightly younger deposits of the Chichkan Formation in southern Kazakhstan (Sergeev, 1992a).

Changes occurred also in composition of silicified assemblages of morphologically simple microorganisms predominantly cyanobacteria from shallow-water nearshore

palaeoenvironments. Akinetes of nostocalean and possibly stigonematalean cyanobacteria, and entophysalidacean cyanobacteria are relatively rare in Upper Riphean assemblages of silicified microorganisms (Knoll & Golubic, 1979; Sergeev, 1992a, 2006). The Late Riphean (Neoproterozoic) microbiotas are dominated by mats formed by tubular sheaths of *Siphonophycus* with remains of chroococcacean cyanobacteria *Gloeodiniopsis* and *Eoaphanocapsa* that occur among intertwined sheaths. Such microbiotas occur in the Min'yar Formation of the Upper Riphean type section, southern Ural Mountains (Nyberg & Schopf, 1984; Sergeev, 1992a, 2006), in the Burovaya Formation of the Turukhansk Uplift (Sergeev, 1999, 2001). Some Neoproterozoic deposits contain remains of stalked cyanobacteria of *Polybessurus*: they were reported from the Limestone-Dolomite "Series" of Greenland (Green *et al*., 1989), the Skillogalee Formation of Australia (Schopf, 1977, 1992b, 1999), the Draken Conglomerate Formation of Spitsbergen (Knoll *et al*., 1991).

To date, peculiar vase-shaped microfossils are found only in the upper Upper Riphean; these are interpreted, at least in part, as testate amoebae (Schopf, 1992a, p. 592), with some ten genera described: *Melanocyrillium*, *Cycliocyrillium*, *Trigonocyrillium*, and others (Porter *et al*., 2003). They occur in the Chuar Group of North America (Bloeser, 1985; Porter *et al*., 2003), the Ryssö Formation of Spitsbergen (Knoll & Calder, 1983), the Visingsö Formation of Sweden (Vidal, 1976), the Eleonore Bay Group of Greenland (Green *et al*., 1988), in chert beds of the Black River Dolomite, Australia (Saito *et al*., 1988), in the Chichkan Formation of Southern Kazakhstan (Sergeev & Schopf, 2010) and the Bitter Springs Formation of Australia (Sergeev, unpublished data). The latter two microbiotas also contain the most diverse Proterozoic assemblages of cellular trichomes (Schopf, 1968, 1992b, 1999; Sergeev and Schopf, 2010; Schopf *et al.*, 2010). The age of all above-mentioned deposits enclosing *Melanocyrillium* does not exceed 850 Ma (Knoll & Sergeev, 1995; Sergeev *et al*., 2010), or even possibly 750 Ma (Porter *et al*., 2003). This point is crucial for more detailed biostratigraphic subdivision of the Neoproterozoic, but no changes are observed among cyanobacteria during this time span.

Another interesting microorganisms occurring in the Yuzhnouralian unit are scale microfossils (*Characodictyon, Paleohexadictyon* and other genera) comparable to modern scales made by a number of protistan groups, including Chrysophyta (Allison & Hilgert, 1986). Like the testate amoebae mentioned above, these are peculiarly Neoproterozoic microfossils, but they are currently known from two locations only: the Tinder Group of Alaska (Allison & Hilgert, 1986) and the Beck Spring Formation of California (Licari, 1978).

Ediacaran or Vendian (Amadeusian-Belomorian) units (0.635-0.542 Ga)

At the end of the Late Riphean, many morphologically complex eukaryotic microorganisms abruptly became less abundant or disappeared (Vidal & Knoll, 1982, 1983; Sergeev, 2006; Sergeev *et al*., 2010). Most Riphean taxa of phytoplanktonic microorganisms with spines and processes (*Trachyhystrichosphaera*, *Prolatoforma*, *Cymatiosphaeroides*, and others) are unknown in the Vendian. This extinction is apparently related with a series of late Neoproterozoic glaciations (Sturtian-Marinoan-Gaskiers and Baikonurian, Chumakov, 2009) and probably particularly with most significant the Marinoan (Laplandian or Elatina) glaciation. The latter glaciations is believed to be global when ice covered entire Earth including the equatorial areas (the "Snow Ball Earth" hypothesis), the beginning of which defines the base of Vendian (Sokolov, 1997) and its termination, the base of Ediacaran Period (Knoll *et al*., 2006a). Data for the interglacial period is sparse and only about ten Cryogenian species have been recorded from strata immediately younger than the Elatina glaciation and its equivalent (Williams *et al*., 2008).

But in contrast to protista, cyanobacteria survived and passed through these late Neoproterozoic glaciations without any extinction. Remains of chroococcacean and hormogonian cyanobacteria are widespread in the post-glacial deposits (Zhang Z., 1985; Zhang Y. *et al*., 1998; Sergeev, 2006, 2009). Moreover, one of distinctive feature of Ediacaran (Vendian) strata is the presence of spiral-cylindrical microfossils of *Obruchevella* (Knoll, 1992b; Tiwari & Knoll, 1994; Zhang Y. *et al*., 1998), which are larger than their Late Riphean analogues (Golovenok *et al*., 1989). Remains of *Spirulina*-like cyanobacteria are closely associated with floridean red algae, having characteristically complex differentiated thalli, are also abundant in the lower Vendian deposits, belonging to the genera *Wengania, Thallophyca, Gremiphyca*, and *Paratetraphycus* (Zhang Y., 1989; Zhang Y. & Yuan, 1992; Zhang Y. *et al*., 1998).

Of course, the most significant changes on the post-glacial Earth are observed not among the cyanobacteria, but in the eukaryotic organisms. Above the glacial layer, Pertatataka-like assemblages or Ediacaran Complex Acanthomorph Palynoflora (ECAP) (Grey, 2005) became abundant in Ediacaran (Vendian) deposits. These microfossil assemblages are dominated by taxonomically diverse, large (up to 800 microns) acanthomorphic and herkomorphic acritarchs *Alicesphaeridium, Appendisphaera, Bullatosphaera, Cavaspina, Eotylotopalla, Galeasphaeridium, Keltmia, Tanarium, Wiessiella* and others, and distinct from older microfossils. Microbiotas that include large spiny acritarchs are found in terrigenous and siliceous deposits of the Pertatataka Formation and Ungoolya Group, Australia; the Doushantuo Formation of China; the Scotia Group of Spitsbergen; the Infrakrol Formation of the lesser Himalaya, India; the Biskopas Conglomerate, Norway; the Vychegda Formation of Timan Uplift, the East European Platform, and

the Motta, Khamahta, Kursov, Parshin and Ura Formations of the Siberian Platform (in all these microbiotas cyanobacterial remains and spiral filaments of *Obruchevella* are abundant, diverse and well-preserved). (See Knoll, 1992b; Zhang Y. *et al*., 1998; Grey, 2005; Shukla *et al*., 2006; Vorob'eva *et al*., 2006, 2007, 2008, 2009a, b; Sergeev, 2009; Sergeev *et al*., 2010, 2011).

In the upper Ediacaran (Vendian) deposits, microfossil diversity is depleted; Pertatataka-type assemblages or ECAP disappear and acanthomorphic acritarchs are represented chiefly by small-sized species of *Micrhystridium*. Only organic-walled microfossils in shales occur in the Vendian stratotypic region subdivided into several assemblages, restricted to the Laplandian, Redkino, Kotlin, and Rovno horizons or regional stages. Spheroidal or filamentous taxa mainly remains of chroococcacean and hormogonian cyanobacteria such as *Leiosphaeridia, Bavlinella, Trachysphaeridium, Stictosphaeridium, Symplassosphaeridium, Polytrichoides, Oscillatoriopsis,* and *Oscillatorites* prevail. In addition to the helical *Obruchevella*, there are also spiral filaments of the genera *Tortunema*, *Volyniella*, and *Cochleatina*. The acanthomorphic acritarch *Micrhystridium tornatum* and morphologically complex members of *Teophipolia, Ceratophyton*, and other genera appear in the upper horizons (Volkova, 1985; Burzin, 1990, 1994).

Remains of shallow-water assemblages of chert-embedded microfossils of Vendian siliceous carbonates are not numerous; however, there are no significant differences between their composition and that of older microbiotas from analogous facies. The microbiota of the Yudoma Group (Vendian, Siberia) is dominated by morphologically simple chroococcacean (including entophysalid) cyanobacteria together with hormogonian cyanobacteria that are mostly represented by sheaths of the genus *Siphonophycus*, spirals of *Obruchevella* sp., and endolithic cyanobacteria belonging to *Eohyella* (Lo, 1980; Sergeev, 2002).

The most significant event of the Upper Vendian (Ediacaran) is widely believed to be the appearance of soft bodied Metazoa (Sokolov, 1997), analysis of which is beyond the scope of the present paper.

Lower Cambrian

Communities of the fossilized microorganisms suffered drastic changes near the Precambrian/Cambrian boundary like biosphere on entire Earth. However, there is a paradox of both silicified and compression-preserved organic-walled microfossil assemblages from Lower Cambrian pre-trilobite deposits in having a "Precambrian appearance". Organic-walled assemblages in shales are composed predominantly of morphologically simple coccoidal and filamentous forms whereas microbiotas in siliceous shallow-water near shore facies dominated by fossilized cyanobactrial communities *Siphonophycus*, *Gloeodiniopsis, Eoaphanocapsa* and in first by abundant spiral-cylindrical filaments of the genus *Obruchevella* (Sergeev, 1989, 1992a, 2009; Sergeev & Ogurtsova, 1989). These communities occur mainly in chert-phosphorite deposites worldwide and there is not much difference in composition of Edicaran (Vendian) assemblages of the same ecological setting: the Chulaktau Formation of South Kazakhstan, the Yuhucun Formation of China, the Khesen Formation of Mongolia and many others (see Sergeev, 1992a, 2006, and refrence therein). These cyanobacteria-dominated microbiotas are replaced in open-shelf offshore facies by microfossil assemblages dominated by acanthomorphic acritarchs of the genus *Micrhystridium* (= *Asteridium* + *Heliosphaeridium*). They were described from the Tal Formation in the Lesser Himalaya, India (Tiwari, 1999), the Meishucunian cherts and phosphorites of the Yangtze Platform of South China, the Yurtis and Xishanblaq Formations of north-west China (Yin, 1995; Xiao *et al*., 2004; Yao *et al*., 2005) and probably the Koktal Formation of Central Kazakhstan (Sergeev, 1992a, 2009). The high concentration of *Micrhystridium* in these and other strata of similar age suggest that a major change in the composition of microfossil assemblages may have occurred at the beginning of the Nemakit-Daldynian (Meishucunian) Stage.

However, the most sudden changes took place at the beginning of the Atdabanian Stage (marked on the East European Platform by the Lukata horizon) is the abrupt and rapid diversification of acanthomorphic acritarchs such as *Skiagia*, *Baltisphaeridium*, *Micrhystridium*, and others that continued into immediately younger deposits (Volkova *et al*., 1983; Sergeev, 1992a). The acanthomorphic-acritarchs containing assemblages are of open-shelf setting and cyanobacteria occur here as a minor component, but became overwhelming dominant in nearshore environments. In fact, a global turnover occurred at this level: from the morphologically simple and predominantly cyanobacterial prokaryotic phytoplankton of the Precambrian to the eukaryotic morphologically complex forms having a decidedly more Phanerozoic affinity.

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 on the Earth, life was dominanted by 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 palaeobiological 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.

Importantly, throughout the Proterozoic there was profound interaction between the evolving biota and the evolving environment, changes over time in the composition of shallow-water prokaryotic communities, for example, occurring in concert with gradual changes in the environment, despite the extreme evolutionary conservatism (Schopf, 1968; now termed "hypobradytely," Schopf, 1994) of cyanobacteria. The particular paleoenvironmental setting of fossil communities is very important for their biostratigraphic usefulness, primarily because the most rapidly evolving Proterozoic eukaryotic microorganisms inhabited open-marine environments. Such eukaryotic protists provide a basis for more refined stratigraphic resolution than do the prokaryotic communities of lagoonal and near-shore settings, long-considered biostratigraphically useless. Therefore, a biostratigraphic paradox of cyanobacterial assemblages was discovered: some taxa which have modern counterparts at the generic or even specific level and do not demonstrate any changes in morphology from early in the Proterozoic to the present (over at least the past 2 Ga), nonetheless occur in fossil assemblages having limited temporal distribution that differ in microbial composition from those of the present. Cyanobacteria demonstrate only two evolutionary innovations through Proterozoic: appearance about 1200 Ma (late Mesoproterozioc) stalked cyanobacterium *Polybessurus* (modern counterpart a *Cyanostylon*-like cyanobacterium) and about 1000 Ma (Neoproterozoic) spiral filaments *Obruchevella* (modern counterpart *Spirulina*).

Further research of modern and fossil cyanobacterial communities should reveal additional details of the microorganisms group evolution through Precambrian and their significance in chang of ancient atmosphere and hydrosphere to form modern Earth's biosphere. Cyanobacteria have played a key-role in change of ancient environments and developed suitable conditions for further evolution of animals and plants whose existence would have been impossible without these microorganisms.

LIST OF ABBREVIATIONS USED IN THE PAPER UNDER THE HEADING REPOSITORY

BC	University of Alaska Museum at Fairbanks, Fairbanks, USA
BGPZD = BGP	Collection of the Paleontological Section, Department of Geology, Beijing University, Beijing, China
BSIP	Birbal Sahni Institute of Palaeobotany, Lucknow, India
CPC	Commonwealth Palaeontological Collection, BMR, Canberra, Australia
Gb	Biological Science Center, Boston University, USA
GINPC	Geological Institute, Palaeontological Collection, Moscow, Russia
GSC	Geological Survey of Canada, Canada
GTL	Geological Survey of Finland, Helsinki, Finland
HUHPC	Harvard University Herbarium Palaeobotanical Collection, USA
IGG = CSGM	Institute of Geology and Geophysics of the Siberian Branch of Russian Academy of Sciences, Novosibirsk, Russia
IGGP	Institute of Geology and Geochronology of Precambrian, Russian Academy of Sciences, Sanct-Petersburg Russia
IGS NAS	Institute of Geological Sciences of the National Academy of Sciences, Kiev, Ukraine
L	Department of Biology, Nanjing University, China
LitNIGRIPC	Lithuanian Institute of Geological Sciences, Vilnius, Lithuania
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
UCLA	University of California, Los Angeles, USA
UCSB	University of California, Santa Barbara, USA
VSEGEI	All Russian Geological Institute, St. Petersburg, Russia
YFSOANUSSR	Geological Institute Yakutian Filial of the Siberian Branch of Russian Academy of Sciences, Yakutsk, Russia

DESCRIPTION OF THE FOSSIL CYANOBACTERIA TAXA

Kingdom—EUBACTERIA Woese and Fox, 1977

Phylum—CYANOBACTERIA Stanier *et al.*, 1978

Class—COCCOGONEAE Thuret, 1875

Order—CHROOCOCCALES Wettstein, 1924

Family—CHROOCOCCACEAE Nägeli, 1849

Genus—BRACHYPLEGANON Lo, 1980

Brachypleganon Lo, 1980, p. 154-156.

Type species—Brachypleganon khandanum Lo, 1980.

Diagnosis—Rod-shaped, elongated, single-walled vesicles with rounded ends and length to width ratio up to 7. They occur in loose colonies or as isolated individuals and never form chains.

Remarks—Lo (1980) suggested that *Brachypleganon* may be considered as the fossil counterpart of some modern elongated chroococcacean cyanobacteria, e.g. *Rhabdoderma* Schmidle and Lauterborn and *Gloeothece* Nägeli. In comparision to ellipsoidal chroococcacean cyanobacterium *Eosynechococcus*, *Brachypleganon* demonstrates more elongated vesicles. However, Butterfield in Butterfield *et al.* (1994) expressed reservation regarding *Brachypleganon* to be considered as chroococcacean cyanobacterium and placed it under *Incertae sedis*. The main reasons for these conclusions are insufficient information and uncertainity about the physiological behaviour and lack of dividing cells in fossil population of *Brachypleganon*. Therefore, some of the elongated bodies described as *Brachypleganon* may turn out to be the remains of akinetes or morphologically similar bacteria or eukaryotic microorganisms. However, we prefere to keep this form under family chroococcaceae considering that in our material ellipsoides assigned to *Brachypleganon* definitely differ from those assigned to akinetes of *Archaeoellipsoides*.

Contents—Monospecific genus.

Age—Neoproterozoic (and may be much older).

Brachypleganon khandanum Lo, 1980

(Pl. 3.7, 8; Fig.13)

Brachypleganon khandanum Lo, 1980, p. 156, Pl. II, Figs 9-12; Butterfield *et al.*, 1994, p. 72, Figs 22J-22K; Sergeev, 2002, p. 555, Pl. II, Figs 13, 14; Sergeev, 2006, p. 187-188, Pl. XXV, Figs 13,14.

Fig. 13—Line diagram of *Brachypleganon khandanum* (Lo, 1980; Here and downward the references in the relevant articles are given). Scale bar = 10 μm.

Repository—UCSB-C670(2).

Stratum typicum—Ediacaran (Vendian), Yudoma Group, Siberia.

Description—Rod-shaped, elongated, single-walled vesicles with rounded ends. They occur in loose colonies or as isolated individuals and never form chains. The vesicles length is 6.0 to 20.0 μm, width is 0.8 to 2.7 μm; width/length ratio ranges from more than 4 to 7 times. The wall is fine-grained and its thickness is about 0.5 μm.

Age and distribution—Neoproterozoic, Cryogenian?, Svanbergfjellet Formation, Spitsbergen; Ediacaran, Yudoma Group, Siberia.

Genus—CONIUNCTIOPHYCUS Zhang Y., 1981

Coniunctiophycus Zhang Y., 1981, p. 499.

Eomicrocystis Golovenok and Belova, 1984, p. 29.

Type species—Coniunctiophycus gaoyuzhuangense Zhang Y., 1981.

Diagnosis—Spheroidal to ellipsoid vesicles with usually single layered wall. Vesicles arranged in subspheroidal colonies or in packets comprising several to tens individuals that in turn form smooth to lobate larger colonies.

Remarks—Zhang Y. (1981) described the genus *Coniunctiophycus* as complex aggregated colonies of numerous small, spheroidal cells and compared this Precambrian genus to the living planktonic chroococcoid cyanobacteria *Microcystis*, *Coelosphaerium* and

Aphanothece. Subsequently, Golovenok and Belova (1984) described similar fossils from the Kotuikan and Yusmastakh Formations of the Billyakh Group as species of newly established genus *Eomicrocystis*, again comparing the fossils to *Microcystis*. Later on *Eomicrocystis* was considered to be a junior synonym of *Coniunctiophycus* (Sergeev *et al.*, 1995); however, the biological interpretation of the Billyakh populations by Golovenok and Belova (1984) is correct.

Some small coccoidal fossils described under other generic names also can rather belong to genus *Coniunctiophycus,* e.g. Knoll *et al.* (1991) have suggested that *Palaeoanacystis magna* described by Allison and Awramik (1989) from the Neoproterozoic Tindir Group (Formation) of Canada certainly should be transferred to this genus.

Contents—C. gaoyuzhuangense, C. conglobatum, C. majorinum and *C. totticus* (Table-1).

Age—Meso-Neoproterozoic (and may be much older).

Coniunctiophycus conglobatum Zhang Y., 1981

(Pl. 1.1, 3, 4, 6; Fig. 14A)

Coniunctiophycus conglobatum Zhang Y., 1981, p. 499, Pl. 4, Fig. 11, Pl. 5, Figs 1, 2; Sergeev *et al.*, 1995, p. 26-27, Figs 13.15, 13.16; Sergeev *et al.*, 1997, p. 213-214, Figs 13D, 13F; Sergeev, 2006, p. 188-189, Pl. VI, Figs 15, 16, Pl. XV, Figs 9, 10.

Eomicrocystis parvulus Yakschin, 1991, p. 23, Pl. VIII, fig. 9.

Repository—BGP-7804.

Stratum typicum—Early Mesoproterozoic, Gaoyuzhuang Formation, China.

Description—Single-walled spheroidal vesicles occurring in spherical to ellipsoidal colonies of several to several ten of individuals. Spheroid diameters 0.8 to 2.0 μm, colony diameters 10 to 25 μm. Colonies, in turn, gathered into aggregates of several colony units.

Remarks—Yakschin (1991) described the populations from the Billyakh Group of the Anabar Uplift as *Eomicrocystis parvulus*, but his description is nearly identical to that of *Coniunctiophycus conglobatum* Zhang Y. (1981) and later it was considered as its junior synonym (Sergeev *et al.*, 1995). However, *C. conglobatum* from the Billyakh Group has little larger dimensions than its type population from the Gaoyuzhuang Formation; its diameter ranges from 1.0 to 4.0 μm.

Age and distribution—Mesoproterozoic: Gaoyuzhuang Formation, China, and Kotuikan and Yusmastakh Formations, Anabar Uplift, Siberia; Meso-Neoproterozoic: Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia; Neoproterozoic: Draken Conglomerate Formation, Spitsbergen.

Coniunctiophycus gaoyuzhuangense Zhang Y., 1981

(Pl. 1.2; Fig. 14B)

Coniunctiophycus gaoyuzhuangense Zhang Y., 1981, p. 499, Pl. 5, fig. 3; Sergeev *et al.*, 1995, p. 25-26, fig. 12.5; Kumar and Srivastava, 1995, p. 104, Figs 12A,12B; Srivastava and Kumar, 2003, p. 20, Pl. 3, Figs 3, 4; Sergeev and Lee Seong-Joo, 2004, p. 11, Pl. I, Figs 3, 4, 7; Sergeev, 2006, p. 188, Pl. V, fig. 15, Pl. XXIX, Figs 9-11; Sergeev *et al.*, 2008, Pl. 2, fig. 13.

Eomicrocystis irregularis Golovenok and Belova, 1984, p. 29, Pl. II, Figs 16, 17; Yankauskas, 1989, p. 91, Pl. XIX, fig.16; Yakschin, 1991, p. 22, Pl. VIII, fig. 4.

Eomicrocystis elegans Golovenok and Belova, 1984, p. 29-30, Figs 12-15; Yankauskas, 1989, p. 91, Pl. XIX, fig. 9; Yakschin, 1991, p. 22-23, Pl. VIII, fig. 3.

Repository—BGP-7803.

Stratum typicum—Early Mesoproterozoic, Gaoyuzhuang Formation, China.

Description—Single-walled spheroidal vesicles occurring in spheroidal colonies of several ten of individuals. Colonies, in turn, gathered into aggregates of several colony units. Spheroid diameters 2.5 to 6.5 μm; colony diameters 15 to 17 μm; aggregates up to 35 μm.

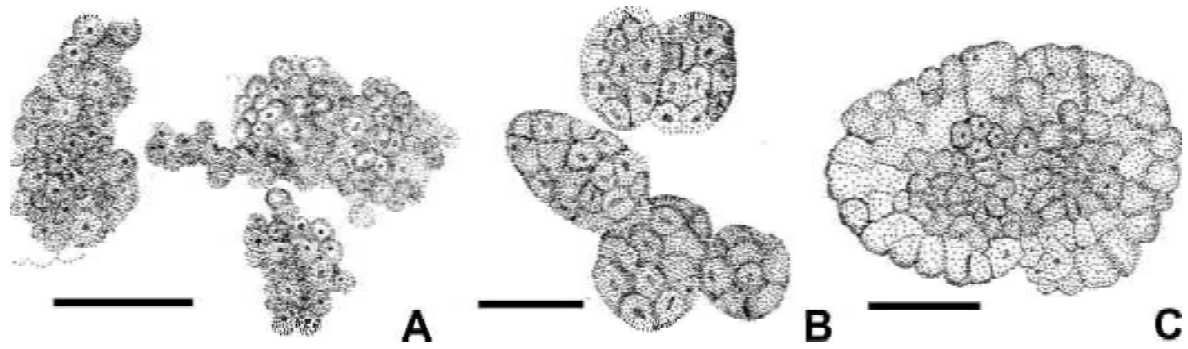


Fig. 14—Line diagrams of species of *Coniunctiophycus*. A- *C. conglobatum* (Zhang Y., 1981); B-*C. gaoyuzhuangensis* (Zhang Y., 1981); C- *C. majorinum* (Knoll *et al*., 1991). Scale bar = A, B = 10 μm, C = 20 μm.

Name of species	Diagnostic features	Size, µm	Palaeoenvironmental setting	Repository, age and type locality	References
C. majorinum Knoll *et al.*, 1991 Fig. 14C	Small vesicles arranged in packets that form smooth to lobate colonies	2-4	Subtidal to intertidal, recorded from cherts in dolomites	HUHPC-62353; Neoproterozoic, Draken Conglomerate Fm., Spitsbergen	Knoll *et al.*, 1991
C. totticus Veis, 1989	Large vesicles arranged in spherical to lobate colonies	15-17	Subtidal recorded from shales	GINPC 4123-62; Neoproterozoic, Totta Fm., Siberia, Russia	Yankauskas, 1989

Table 1—Comparative characteristics of genus *Coniunctiophycus* species (Type Specimens).

Remarks—Earlier, Golovenok and Belova (1984) recognized two species within genus *Eomicrocystis,* currently a junior synonym of genus *Coniunctiophycus* from the Billyakh Group, which differ one from another mainly in the degree of regularity in form of colonies. But the observed intergrading forms in the Billyakh material suggest that the differences noted by Golovenok and Belova reflect population and diagenetic variations within a single species that is morphologically indistinguishable from *C. gaoyuzhuangense* and is considered as its junior synonym (Sergeev *et al.*, 1995).

Age and distribution—Mesoproterozoic: Gaoyuzhuang Formation, China; Kotuikan and Yusmastakh Formations, Anabar Uplift, Siberia; Kheinjua Formation, India; Meso-Neoproterozoic, Deoban Formation, India.

Genus—CORYMBOCOCCUS Awramik and Barghoorn, 1977

Corymbococcus Awramik and Barghoorn, 1977, p. 132.

Type species—*Corymbococcus hodgkissii* Awramik and Barghoorn, 1977.

Diagnosis—Spheroidal to slightly ellipsoidal double-or thick single-walled vesicles occur in loose colonies enveloped in unlamellated sheath.

Remarks—Awramik and Barghoorn (1977) compared this genus to modern cyanobacterium genus *Aphanocapsa*. Subsequently, Nyberg and Schopf (1984) described genus *Eoaphanocapsa* as a fossil counterpart of modern genus *Aphanocapsa* as well. From formal taxonomical point of view, both genera (*Corymbococcus* and *Eoaphanocapsa)* can be synonymous. But on the other hand, some morphological differences are evident, e.g. thickness of vesicle walls and encompassing envelopes, and we prefer to treat both genera separately. Like many other forms from the BIF-associated Gunflint-type microbiotas, these microfossils could turn out to be remains of iron-loving bacteria (Knoll, 2003). However, unlike benthic mat-forming filaments of *Animikiea* and *Gunflintia* (see below), *Corymbococcus* colonies are rather remains of planktonic microorganisms which were suspended in water column and very possibly they are cyanobacteria.

Contents—*C. hodgkissii* and *C. rexii.*

Age—Palaeo-Mesoproterozoic and probably Neoproterozoic.

Corymbococcus hodgkissii Awramik and Barghoorn, 1977

(Pl. 2.8-10)

Corymbococcus hodgkissii Awramik and Barghoorn, 1977, p. 132, 134, Figs 5A, 5B; Sergeev *et al.*, 1998, Pl. II, Figs 1, 2.

Repository—HUHPC-44480.

Stratum typicum—Palaeoproterozoic, Gunflint Formation, Canada.

Description—Spheroiodal to slightly ellipsoidal thick walled vesicles of 5.0 to 18.0 µm in diameter occur in loose colonies enveloped in unlamellated sheath. Individual vesicle walls are granular and ~ 1.5 µm thick and not enclosed by a sheath.

Remarks—Besides *Corymbococcus hodgkissii,* Awramik and Barghoorn (1977) have described another genus and species *Thymos halis* from the Gunflint Iron Formation based on single specimen only. By the elongated shape of colony this form resembles to *Corymbococcus rexii* and probably belongs to genus *Corymbococcus* as well. Some other microfossils described from the Gunflint Chert, *viz*. *Xenothrix inconcreta* and *Exochobrachium triangulum*, are also based on single specimens. They all have similar morphological features and comparable dimensions and possibility of their being the morphological variants of the same population, e.g. *Corymbococcus hodgkissii,* can not be ruled out.

Age and distribution—Palaeoproterozoic, Gunflint Formation, Canada.

Corymbococcus rexii Sergeev and Lee Seong-Joo, 2004

(Pl. 3.9-11; Fig. 15)

Corymbococcus rexii Sergeev and Lee Seong-Joo, 2004, p. 11, Pl. I, Figs 14, 15; Sergeev, 2006, p. 189, Pl. XXVI, Figs 10, 11.

Repository—GINPC-4688, Specimen No. 717.

Stratum typicum—Early Mesoproterozoic (Early Riphean), Satka Formation, southern Ural Mountains.

Description—One-or two-layered wall vesicles, occur in loose colonies of a few to hundred specimens encompassed inside amorphous sheath 20.0 to 75.0 μm wide and 30.0 to 165.0 μm long. The vesicles external diameter range from 4.5 to 7.0 μm and internal diameter-from 2.5 to 5.0 μm; inner vesicle layers are coarse-grained and about 1.0 μm thick, outer vesicle layeres are fine-grained and less than 0.5 μm thick.

Age and distribution—Early Mesoproterozoic, Satka Formation, southern Ural Mountains.

Genus—EOAPHANOCAPSA Nyberg and Schopf, 1984

Eoaphanocapsa Nyberg and Schopf, 1984, p. 759.

Type species—Eoaphanocapsa oparinii Nyberg and Schopf, 1984.

Diagnosis—Single-walled or multilamellated spheroidal and ellipsoidal vesicles in loose clusters of a few to many tens of individuals commonly embedded in diffuse organic matrix or surrounded by outer envelope.

Remarks—The type species of genus *Eoaphanocapsa* from the Neoproterozoic (Late Riphean) Min'yar Formation, southern Ural Mountains, was interpreted as the remnants of chroococcoidal cyanobacteria similar to species of the extant genus *Aphanocapsa* (Nyberg & Schopf, 1984). It is possible, however, that these colonies represent only a stage in life cycle of other chroococcoidal fossils, in particular *Gloeodiniopsis*.

Genus *Eoaphanocapsa* provides a useful form genus for colonies of multilamellate spheroids that lack the division cycle characteristic of *Gloeodiniopsis*. Accepting this, the Bitter Springs population described as *G. gregaria* by Knoll and Golubic (1979) probably should be transferred to *Aphanocapsa* (Sergeev *et al.*, 1997). *G. gregaria* differ from *E. oparinii* only in the smaller size of constituent cells.

Contents—E. oparinii and *E. molle.*

Age—Meso-Neoproterozoic to Lower Cambrian (and probably older).

Eoaphanocapsa molle Sergeev, 1989

(Pl. 4.7)

Eoaphanocapsa molle Sergeev and Ogurtsova 1989, p. 65, Pl. II, fig. 9; Sergeev, 1992a, p. 78-79, Pl. XXVI, fig. 3.

Repository—GINPC-4681, Specimen No. 208.

Stratum typicum—Lower Cambrian, Chulaktau Formation, South Kazakhstan.

Description—Single-layered spheroids occurring in loose colonies of spherical or triangular shape 60 x 60 μm in dimension from a few ten individuals. Envelopes are translucent, walls are fine-grained 0.5-1.0 μm thick. Spot-like inclusion 1-2 μm in diameter can be attached to the innermost side of wall. The outer diameter of spheroids ranges from 8 to 17 μm.

Age and distribution—Lower Cambrian, Chulaktau Formation, South Kazakhstan.

Eoaphanocapsa oparinii Nyberg and Schopf, 1984

(Pl. 4.1-6, 8, 9; Figs 16, 17, 18)

Eoaphanocapsa oparinii Nyberg and Schopf, 1984, p. 759, 761, Figs 13A-13C, 13D?-13F?; Yankauskas, 1989, p. 90, Pl. XXIII, fig. 8; Krylov *et al.*, 1989, Pl. I, Figs 3, 4; Sergeev, 1992a, p. 78, Pl. XII, Figs 1a, 1в, Pl. XIII, Figs 1, 4, 5; Schopf, 1992b, Pl. 47, Figs E_1, E_2, F?, Sergeev *et al.*, 1997, p. 219-221, Figs 10E, 10F; Sergeev, 2006, p. 189-190, Pl. XII, Figs 1-5, Pl. XL, Figs 1, 2, Pl. XLI, Figs 1, 5, 6; Sergeev *et al.*, 2008, Pl. 12, fig. 1.

"Undifferentiated chroococcacean cyanobacteria" (partim): Schopf *et al.*, 1977, Figs 2H, 2I; Schopf *et al.*, 1979, Pl. VIII, Figs з, и; Mendelson and Schopf, 1982, p. 69-72, Pl. 2, Figs 2, 3.

"Larger chroococcacean cyanobacteria" Schopf, 1992c, Pl. 10, fig. J.

Repository—UCLA, R_3mn-st-2K.

Stratum typicum—Neoproterozoic, Min'yar Formation, southern Ural Mountains.

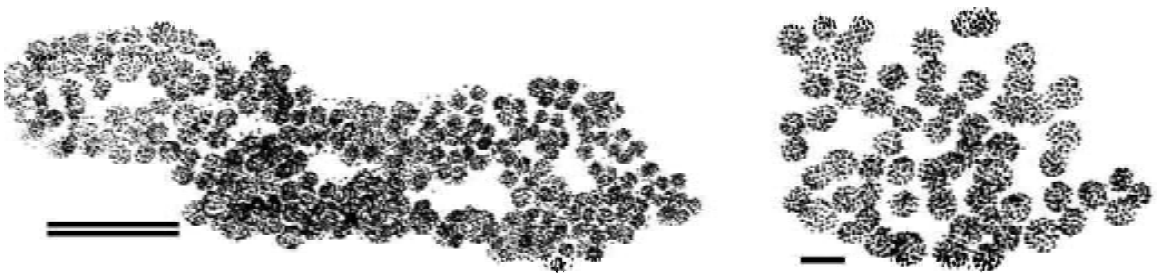


Fig. 15—Line diagram of *Corymbococcus rexii* (Sergeev & Lee Seong-Joo, 2004). Scale bar = double = 50 μm, single bar = 10 μm.

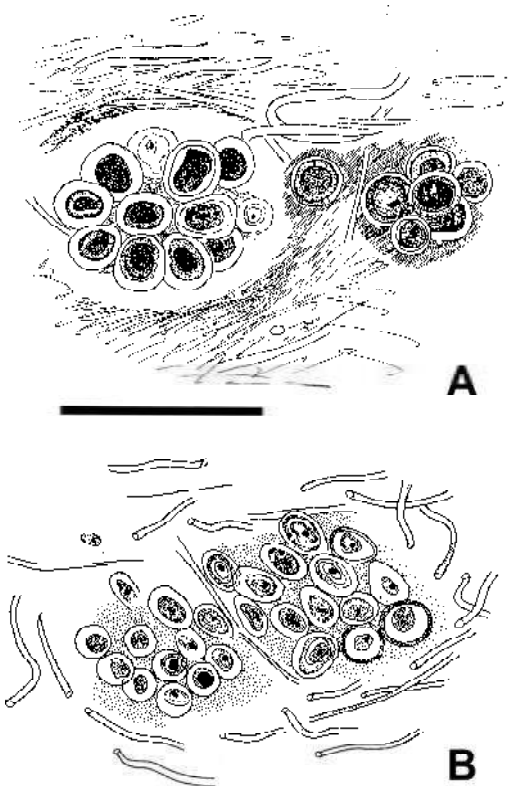


Fig. 16—Colonies of *Eoaphanocapsa oparinii* from the Min'yar Formation. Scale bar= 50 μm.

Description—Single-walled or multilamellated spheroidal and ellipsoidal vesicles. Diameter of inner layers is 11-27 μm, outer layers-13-42 μm; inclusions, commonly attached to the interior of the innermost wall layer, 0.5-3 μm in diameter. Individual vesicle lamellae 0.5 to 1 μm thick; vesicles in loose clusters of a few to many tens of individuals commonly embedded in a diffuse organic matrix or surrounded by an transparent envelope about 1 μm thick.

Remarks—E. oparinii differs from *E. molle* in its size.

Age and distribution—Meso-Neoproterozoic: Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia; Neoproterozoic: Min'yar Formation, southern Ural Mountains.

Genus—EOGLOEOCAPSA Golovenok and Belova, 1984

Eogloeocapsa Golovenok and Belova, 1984, p. 28.

Type species—Eogloeocapsa bella Golovenok and Belova, 1984.

Diagnosis—Isolated colonies of single-or sometimes multilayered spheroidal vesicles surrounded by a common envelope of spherical or elongated shape. The main colonies sometimes contain 2 or 3 generations of daughter colonies.

Contents—E. bella and *E. avzyanica*.

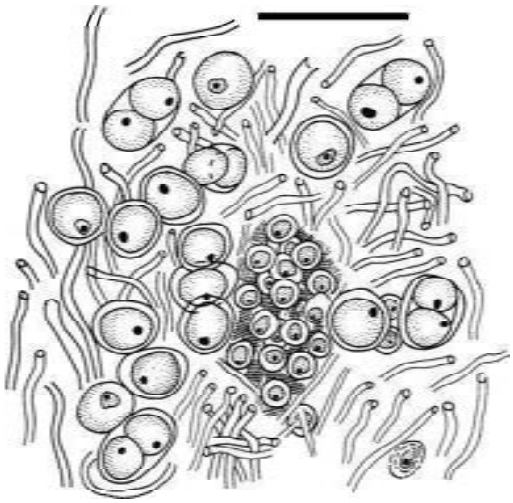


Fig. 17—Cyanobacterial mat formed by empty sheaths of *Siphonophycus robustum* and *S. typicum* nesting inside vesicles of *Gloeodiniopsis lamellosa* and a colony of *Eoaphanocapsa oparinii* (in the center). Scale bar= 50 μm.

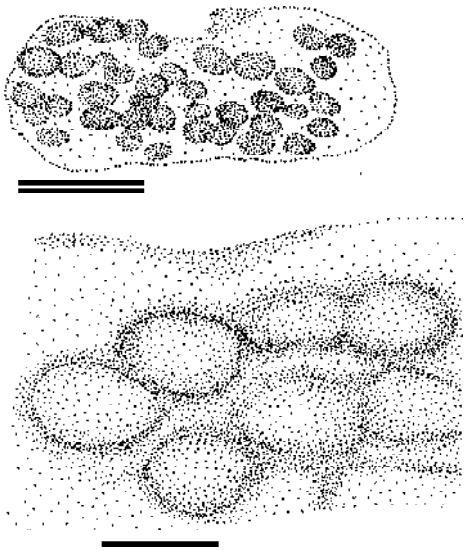


Fig. 18—Line diagram of *Eoaphanocapsa oparinii* (Nyberg & Schopf, 1984). Scale bar = double = 50 μm, single bar = 10 μm.

Remarks—The genus *Eogloeocapsa* Golovenok and Belova is recognized on the basis of the common presence of a few daughter vesicles within the envelope (Golovenok & Belova, 1984). They compared *Eogloeocapsa* with the living chroococcacean cyanobacterium *Gloeocapsa* Kützing demonstrating similar colonies from daughter cells inside common sheath. However, the similar gloeocapsoid colonies are typical in the life cycle of both modern and ancient

entophysalidacean algae as well (Hofmann, 1976; Golubic & Hofmann, 1976). Another difficulty is distinguishing between the genera *Eogloeocapsa* Golovenok & Belova, 1984 and *Gloeodiniopsis* Schopf, 1968. The genus *Gloeodiniopsis* is recognized on the basis of its multiple envelopes and common presence of 2-8 daughter spheroids within the outer vesicle (Knoll & Golubic, 1979). But such colonies of *Gloeodiniopsis* also compare with certain colonies of *Eogloeocapsa*. So it is possible that both taxa are different ecological variants of the same taxon. Moreover, the presence of spheroids within the common envelope is also a characteristic of genus *Clonophycus* J. Oehler, 1977, emend. D. Oehler, 1978 and distinction between these two genera is difficult. Considering these factores genus *Eogloeocapsa* is treated as purely formal taxonomical entity encompasing isolated colonies with vesicles inside that is a common feature for both chroococcacean and entophysalidacean colonies. In spite of these limitations, we believe, that if such colonies are found separately, they deserve formal taxonomic treatment as *Eogloeocapsa*.

Age—Meso-Neoproterozoic (and probably Paleoproterozoic).

Eogloeocapsa avzyanica Sergeev, 1992 (in Sergeev, 1992b) emend.

(Pl. 5.1-4)

Eogloeocapsa avzyanica Sergeev 1992b, p. 109, Pl. IX, Figs 8, 12, Pl. X, Figs 5-7; Sergeev, 1992a, p. 79, Pl. VI, Figs 4, 5, 7, 9, 10, Pl. VIII, Figs 3, 7, 9; Sergeev, 1994, p. 245-246, Figs 5A-5D, 5F-5H, 7F; Kumar and Venkatachala, 1998, p. 60, 62, Figs 6e, 6p; Yakschin, 1999, Pl. I, Figs 8a, 8b; Sergeev *et al.*, 2008, Pl. 8, Figs 2, 4, Pl. 11, fig. 4.

Category 4 microfossils: Sergeev, 1988, p.709, Figs 1e-1и.

Eoentophysalis dismallakesensis Horodyski and Donaldson, 1980 (partim): Sergeev, 2006, Pl. XXXI, Figs 1-5; Sergeev and Lee Seong-Joo, 2006, Pl. I, fig. 4.

Repository—GINPC-4688, Specimen No 42.

Stratum typicum—Late Mesoproterozoic (Middle Riphean), Avzyan Formation, southern Ural Mountains.

Description—Colonies with dispersed, well-defined spheroidal vesicles having diameter 8.0-23.0 μm and walls about 0.5 μm thick, set within a common hyaline envelopes with a thin rounded outline 24-60 μm across. Sometimes one or more common envelopes encircle a few such colonies. Colonies of *E. avzyanica* occur as isolated individuals within *S. robustum* mats or as loose clusters of several dozens or hundreds individuals between those mats.

Remarks—For the first time, Sergeev (1992b) described this taxon from the Kataskin Member of Avzyan Formation as a chrooccocacean cyanobacterium. Later on the typical features of entophysalidacean cyanobacteria, e.g. polarized unidirectional growth and formation of dense mat-like colonies were revealed for some clusters of *E. avzyanica*. Therefore, Sergeev (2006) transferred all these microfossils to *Eoentophysalis dismallakesensis*. However, as a result of our continued reinvestigation of the type material we came to the conclusion that some of these fossils do not demonstrate above mentioned diagnostic features of entophysalidacean cyanobacteria and should rather be retained as *Eogloeocapsa avzyanica* than to be transferred to *Eoentophysalis dismallakesensis*.

Age and distribution—Mesoproterozoic: Avzyan Formation, southern Ural Mountains, Kyutingde Formation, Siberia.

Eogloeocapsa bella Golovenok and Belova, 1984

(Fig. 19)

Eogloeocapsa bella Golovenok and Belova, 1984, p. 28, Pl. II, Figs 6-10; Yankauskas, 1989, p. 90, Pl. XIX, fig. 10; Hofmann and Jackson, 1991, p. 377, Figs 10.17, 10.18.

Repository—VSEGEI-445 m (Golovenok & Belova, 1984, Pl. II, fig. 10).

Stratum typicum—Early Mesoproterozoic (Early Riphean), Kotuikan Formation, Siberia.

Description—Isolated colonies of single-or sometimes multilayered spheroidal vesicles (2-8 up to a few tens in a colony) surrounded by common envelope of spherical shape. Vesicles diameter range from 7.2 to 20.0 μm, colonies diameter range from 16 to 48 μm, vesicles wall are fine-grained about 0.5 μm thick and colonies envelopes are hyaline and less than 0.5 μm thick.

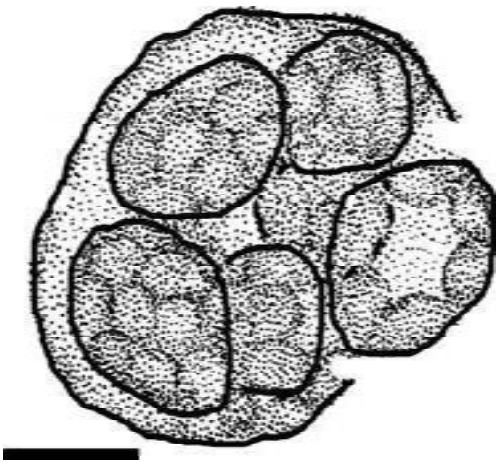


Fig. 19—Line diagram of *Eogloeocapsa bella* (Golovenok & Belova, 1984). Scale bar = 10 μm.

Remarks—When Golovenok and Belova (1984) described *E. bella* from the Kotuikan Formation of the Anabar Uplift, they pointed out that there are no remains of entophysalidacean algae in this formation and isolated gloeocapsoid colonies definitely belong to a separate taxon. However, later on the entophysalidacean colonies were found in the Kotuikan microbiota (Sergeev, 1993; Sergeev *et al.*, 1995) and therefore, problems with taxonomical position of *E. bella* emerged. We can not rule out a possibility that these gloeocapsoidal colonies from the Kotuikan Formation, in fact, are only a stage of life cycle of entophysalidacean cyanobacterium.

The similar explanation holds good for *Eogloeocapsa amplus* described by Yakschin (1999) from the Mesoproterozoic (Lower Riphean) Kyutingde Formation of the Olenek Uplift, Siberia. These gloeocapsoid colonies may belong to *Eoentophysalis* as well, but without restudy of the type material we refrain from making comments on validity of this taxon.

Age and distribution—Mesoproterozoic: Kotuikan Formation, Siberia; Society Cliffs Formation, Canada.

Genus—EOSYNECHOCOCCUS Hofmann, 1976

Eosynechococcus Hofmann, 1976, p. 1057.

Type species—Eosynechococcus moorei Hofmann, 1976.

Diagnosis—Single-walled, rod-like, empty nonseptate ellipsoidal vesicles, solitary or in pairs, occurring in loose clusters or in densely packed colonies of a few to ten or more individuals.

Remarks—In original diagnosis, Hofmann (1976) included all morphologically simple ellipsoidal unicells in the form genus *Eosynechococcus*. Thus, the palaeontological genus *Eosynechococcus* is much broader than its modern counterpart *Synechococcus*, which includes only non-colonial unicellular cyanobacteria of ellipsoidal morphology. Many species assigned to *Eosynechococcus* are colonial, similar to living species of the genus *Gloeobacter* (*Gloeothece)* (Golubic & Campbell, 1979; Knoll & Golubic, 1979; Golovenok & Belova, 1984, 1993). On this basis, Zhang Y. (1988) erected the genus *Gloeotheceopsis* for colony-forming species originally placed in *Eosynechococcus.*

Golovenok and Belova (1984) have described some large ellipsoidal microfossils as various species of genus *Eosynechococcos, viz., E. crassus, E. elongatus, E. giganteus* and *E. major.* However, subsequently it turned out that these large ellipsoidal vesicles are the remains of nostocalean cyanobacteria akinetes and they were transferred to genus *Archaeoellipsoides* (Sergeev *et al.*, 1995). Besides few other ellipsoidal fossils were described as various species of genus *Eosynechococcous*, *viz., E. minutus* (Nautiyal, 1980)*, E. burzjanicus* and *E. karatavicus* (Yankauskas, 1989). However, some of these forms are probably remains of ellipsoidal akinetes of nostocalean cyanobacteria and others are poorly illustrated and their organic origins are in doubts.

Contents—E. amadeus, E. brevis, E. depressus, E. grandis, E. isolatus, E. medius, E. moorei and *E. thuleënsis*. (Table-2)

Age—Proterozoic.

Eosynechococcus brevis Knoll, 1982

(Pl. 6.7-9, Fig. 20B, C)

Name of species	Diagnostic features	Size, µm	Palaeoenvironmental setting	Repository, age and type locality	References
E. amadeus Knoll & Golubic, 1979 Fig. 20A	Small ellipsoidal vesicles clumped into aggregates	1.85-4.53 x 0.96-1.88	Tidal flat, recorded from cherts in dolomites	HUHPC -60203, Neoproterozoic, Bitter Springs Fm., Australia	Knoll & Golubic, 1979
E. depressus Knoll, 1982 Fig. 20D	Occures in loose clusters flattened ellipsoidal vesicles	6.0-10.0 x 2.0-4.0	Intertidal, recorded from cherts in dolomites	HUHPC -60509, Neoproterozoic, Draken Conglomerate Fm., Spitsbergen	Knoll, 1982
E. thuleënsis Strother *et al.*, 1983 Fig. 20G	Medium-sized ellipsoidal vesicles occur in loose clusters	5.0-25.0 x 3.0-4.6	Intertidal, recorded from cherts in dolomites	HUHPC -60470, Mesoproterozoic, Narssârssuk Fm., Spitsbergen	Strother *et al.*, 1983
E. isolatus McMenamin *et al.*, 1983 Fig. 20I	Ellipsoidal vesicles loosely associated into ovoidal groups	1.7-8.5 x 1.7-6.8	Intertidal, recorded from cherts in dolomites	UCSB 029-2, Early Mesoproterozoic, Kheinjua Fm., India	McMenamin *et al.*, 1983

Table 2—Comparative characteristics of genus *Eosynechococcus* species (Type Specimens).

Eosynechococcus brevis Knoll, 1982, p. 780-781, Pl. 1, Figs 5-7; Sergeev, 1993, Pl. III, fig. 9; Sergeev *et al.*, 1995, p. 27, Figs 9.9-9.11; Sergeev, 2006, p. 191-192, Pl. II, Figs 9-11; Sergeev *et al.*, 2008, Pl. 2, fig. 12.

Repository—HUHPC-60476.

Stratum typicum—Neoproterozoic, Draken Conglomerate Formation, Spitsbergen.

Description—Single-layered, rod-like, empty nonseptate ellipsoidal vesicles, solitary or in pairs, occurring in loose clusters of a few tens of individuals. Length is 2.0 to 8.0 µm, width is 1.5 to 4.5 µm; length/width ratio changes from 1.3 to 4. Dark inclusions < 0.5 µm in diameter commonly present within vesicles. Amorphous mucilage-like envelope sometimes present, 2-4 µm thick.

Remarks—This species is distinguished from *E. moorei* by its smaller size and from *E. amadeus* by abundance of nearly spherical individuals and absence of contiguous multicellular aggregates.

Age and distribution—Mesoproterozoic, Kotuikan and Yusmastakh Formations, Anabar Uplift, Siberia; Neoproterozoic, Draken Conglomerate Formation, Spitsbergen.

Eosynechococcus grandis Hofmann, 1976

(Pl. 6.11, 12; Fig. 20E)

Eosynechococcus grandis Hofmann 1976, p. 1058, Pl. 2, Figs 11-14; Hofmann and Schopf, 1983, Photo 14-2-M; Sergeev, 1984, p. 438, Figs 2к-2н ; Sergeev, 2001, p. 441, fig. 10.8, 10.9; Sergeev, 2006, p. 192, Pl. XXI, fig. 8, 9.

Repository—GSC-43588.

Stratum typicum—Palaeoproterozoic, McLeary Formation, Canada.

Description—Single-layered, rod-like, empty ellipsoidal vesicles, occurring as solitary unicells and in pairs in close association with colonies of *Siphonophycus robustum* and *S. typicum*; vesicle length 5-10 µm, width 2-5 µm, length/width = 1-3; walls are translucent, medium-grained and ca. 0.5 µm thick.

Remarks—*Eosynechococcus grandis* is differentiated from other species of *Eosynechococcus* by its bigger size.

Age and distribution—Widely distributed in Proterozoic chert assemblages.

Eosynechococcus medius Hofmann, 1976

(Pl. 6. 10, 13; Fig. 20H)

Eosynechococcus medius Hofmann 1976, p. 1058, Pl. 2, Figs 9, 10; Mendelson and Schopf, 1982, p. 72-74, Pl. 3, Figs 1, 2; Knoll, 1982, p. 780, Pl. 8, Figs 11-13; Hofmann and Schopf, 1983, Photo 14-2-L; Hofmann and Jackson, 1991, p. 371-372, Figs 7.14, 7.15; Schopf, 1992c, Pl. 10, fig. O; Sergeev *et al.*, 1997, p. 221-222, Figs 13B, 13G; Sergeev, 2006, p. 191, Pl. XVI, Figs 6, 9; Sergeev *et al.*, 2008, Pl. 4, fig. 10.

Repository—GSC-43588.

Stratum typicum—Palaeoproterozoic, Kasegalik Formation, Canada.

Description—Single-walled, rod-like, empty ellipsoidal vesicles, occuring in densely packed, irregular colonies in close association with colonies of *Eoentophysalis dismallakesensis*, *Siphonophycus robustum* and *S. typicum*. Vesicle length 5-10 µm, width 2-5 µm, length/width = 1-3; walls are translucent, medium-grained and ca. 0.5 µm thick.

Remarks—*Eosynechococcus medius* is differentiated from other species of *Eosynechococcus* by its size range, which is intermediate among other species.

Age and distribution—Widely distributed in Proterozoic chert assemblages.

Eosynechococcus moorei Hofmann, 1976

(Pl. 6.1-5, Fig. 20F)

Eosynechococcus moorei Hofmann, 1976, p. 1057-1058, Pl. 2, Figs 1-7, 8?; Golubic and Campbell, 1979, Figs 2E-2J, 3C, 3D; Hofmann and Schopf, 1983, p. 347, Photo 14-2-N, 14-6-N; Krylov and Sergeev, 1986, p. 107, Pl. I, Figs 8, 9; Sergeev, 1992a, p. 100-101, Pl. IV, Figs 7-9; Butterfield *et al.*, 1994, p. 54, fig. 23J; Petrov *et al.*, 1995, Pl. I, fig. 12; Sergeev *et al.*, 1995, p. 27, Figs 9.8, 9.12, 9.13; Sergeev *et al.*, 1997, p. 221, fig. 13E; Sergeev, 2002, Pl. II, fig. 10; Sharma, 2006a, p. 79, 81, Figs 7h-7k; Sergeev, 2006, p. 190-191, Pl. II, Figs 8, 12, 13, Pl. XVI, fig. 8, Pl. XXIX, Figs 1-4; Sergeev *et al.*, 2008, Pl. 1, fig. 5, Pl. 5, Figs 5, 7, Pl. 7, fig. 9.

Microphycus curtus Yakschin, 1991, p. 28, Pl. VIII, fig. 7.

Repository—GSC-42770.

Stratum typicum—Palaeoproterozoic, Kasegalik Formation, Canada.

Description—Single-walled, rod-like, empty nonseptate ellipsoidal vesicles 3.0 to 9.0 µm long and 1.2 to 3.5 µm wide, occurring in loose clusters. Dark inclusions < 0.5 µm in diameter occur in some ellipsoidal vesicles.

Remarks—*Eosynechococcus moorei* is distinguished from the most species of *Eosynechococcus* mainly by its small size. Golubic and Campbell (1979) demonstrated the close resemblance of Proterozoic *E. moorei* populations to the modern cyanobacterial species *Gloeobacter* (*Gloeothece*) *violaceus* (*coerula)* (Geitler, 1927) emend. Rippka *et al.*, 1974. Modern *G. violaceus* populations inhabit wet rock exposures in fresh water environments, so if the resemblance is more than superficial, it would indicate a shift in environmental distribution through time.

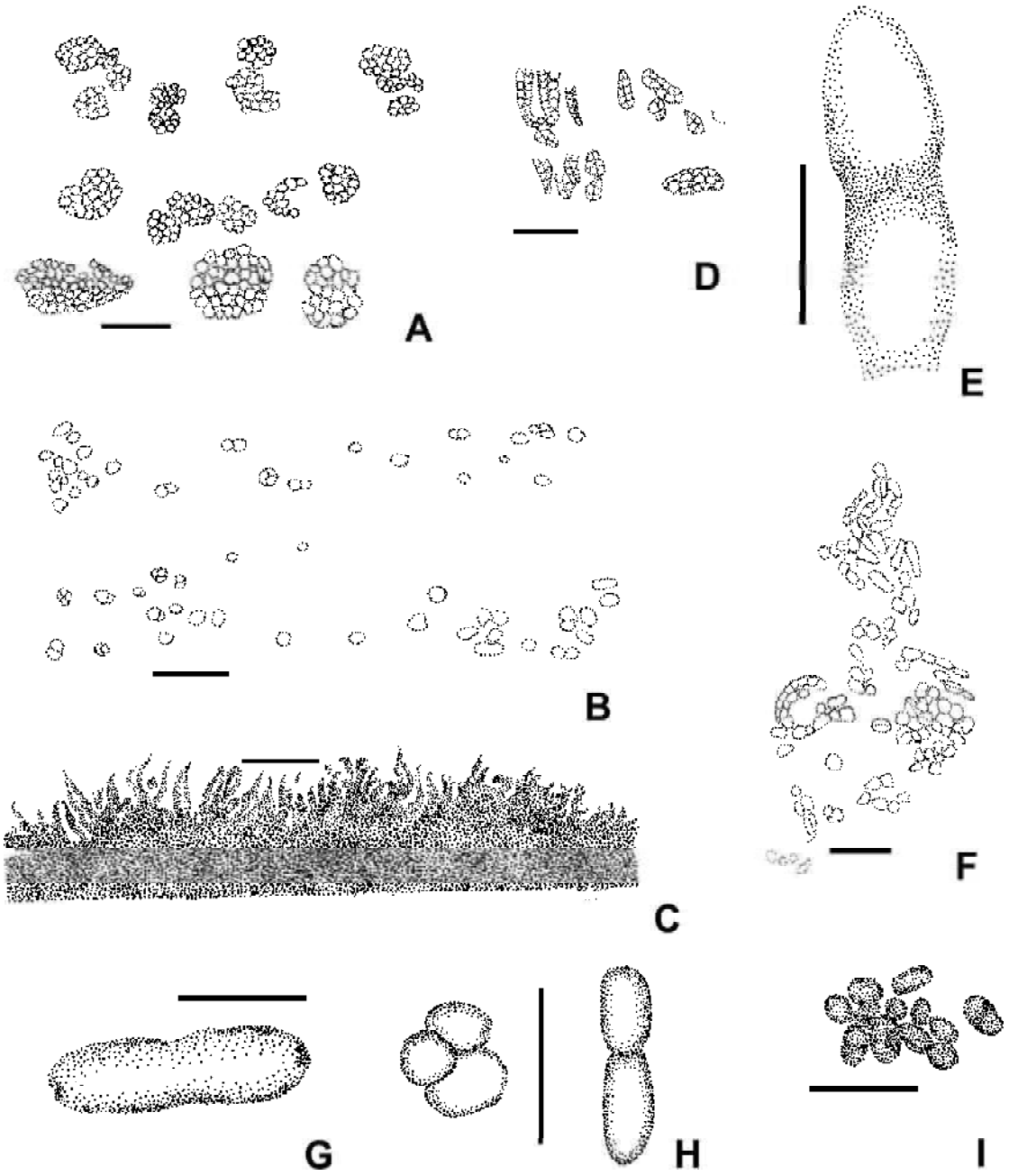


Fig. 20—Line diagrams of species of *Eosynechococcus*. A- *E. amadeus* (Knoll & Golubic, 1979); B, C- *E. brevis* (Knoll, 1982); D- *E. depressus* (Knoll, 1982); E- *E. grandis* (Hofmann, 1976); F- *E. moorei* (Hofmann, 1976); G - *E. thuleënsis* (Strother *et al.*, 1983); H - *E. medius* (Hofmann, 1976); I - *E. isolatus* (McMenamin *et al.*, 1983). Scale bar = 10 μm.

In some Proterozoic formations, the ellipsoids dimensions can be slightly different than in the type population, e.g. in the Kotuikan Formation of Siberia vesicles are 1.5 to 12.5 μm long and 1.0 to 6.0 μm wide.

Age and distribution—Widely distributed in the Proterozoic microfossil assemblages.

Genus—GLOEODINIOPSIS Schopf, 1968, emend. Knoll and Golubic, 1979

Gloeodiniopsis Schopf, 1968, p. 684; Knoll and Golubic, 1979, p. 147.

Bigeminococcus Schopf and Blacic, 1971, p. 952.

Eotetrahedrion Schopf and Blacic, 1971, p. 955.

Eozygion Schopf and Blacic, 1971, p. 953.

EXPLANATION OF PLATES

The illustrated material came from the Palaeoproterozoic Gunflint Formation, North America, the Mesoproterozoic (Early-Middle Riphean) Kotuikan and Yusmastakh Formations of Anabar Uplift, the Svetly Formation of Uchur-Maya Region, the Sukhaya Tunguska Formation of Turukhansk Uplift (all three regions belong to Siberia), the Satka and Avzyan Formations of South Urals as well as Neoproterozoic (Late Riphean-Vendian) the Burovaya and Shorikha Formations of the Turukhansk Uplift, the Fawn Limestone, Semri Group, the Sirbu Shale, Bhander Group, Vindhyan Supergroup, India, the Min'yar Formation of South Urals, the Chichkan Formation of South Kazakhstan, the Vychegda Formation of East Europen Platform and the Yudoma Group of Uchur-Maya Region. Some cyanobacterial remains from the Lower Cambrian (Tommotian Stage) Chulaktau Formation of South Kazakhstan are also incorporated.

Most of the illustrated specimens are reposited in the Palaeontological Collections of the Geological Institute of Russian Academy of Sciences, Moscow (GINPC No. 3893, 4313, 4681, 4688, 4689, 4694, 4698 and 14700), Russia. Repository details of the other illustrated specimens are given as acronym with respective illustrated specimens in beginning of the description of the fossil cyanobacteria. Photo-documented microfossils were recorded in thin sections of the cherts with the exception of those from collection No. 14700 (the Vychegda Formation) and Kumar's collection (Bhander Group, Vindhyan Supergroup) which were compression-preserved microorganism remains in maceration slides or carbonaceous compressions on shales bedding surfaces. Some of the specimens, from the Kotuikan Formation of the Anabar Uplift, Siberia, were illustrated in the joint relevant publications with Prof. A. H. Knoll and co-authors (Sergeev *et al*., 1995; Golubic *et al*., 1995; Knoll & Sergeev, 1995) and deposited in the Harvard University Herbaria Paleobotanical Collection (HUHPC). They are illustrated here with the permission of Prof. A.H. Knoll.

Microfossils were photographed in transmitted light and measured to the nearest one micron by use of a microscope eyepiece reticule, typically using a 40 x objective. At Geological Institute of RAS, transmitted light optical photomicrographs of the illustrated specimens were acquired using RME 5 microscope (Rathenower, Germany) equipped with a Practica film camera, and a Zeiss Axio Imager. A1 microscope (#3517002390) equipped with an AxioCam MRc 5 digital camera (both microscope and camera being products of Carl Zeiss, Germany). At BSIP, photomicrographs were obtained using Leitz Diaplan High Power Microscope equipped with Microscope Camera (Leitz, Wetzlar, Germany).

Each thin section of GINPC collection is provided with a strip of paper glued on it covering the petrographic thin section of rock and the positions of the microorganisms are marked onto the paper as numbered points by a sharp pencil. The coordinates provided for each specimen is denoted by letter 'p' followed by a number. The point and thin section-specific specimen number denoted on an overlay-map attached on one margin of the thin section. These points provide easy and quick way to find the microfossils: just to bring the point with the relevant number under the microscope's transmitted light and remove the paper. This convenient method to fix the position of the microfossils on the slides was devised by the late palaeobotanist S.V. Meyen (Geological Institute of RAS, Moscow, Russia). England Finder Location coordinates (EFL) are also provided for some microfossils. For example, for the specimen of *Filiconstrictosus magnus* shown in Plate XVII, fig. 1, the relevant information —Sample No. 4689-48, Slide No. 576, p. 26, EFL F-38-0, GINPC No. 478 —indicates that the fossil-bearing rock belongs to field collection 4689; that from that collection, the illustrated fossil occurs in petrographic thin section 576 prepared from a rock sample of the Kotuikan Formation 48; that within this thin section, the fossil occurs at location point 26 and within the England Finder slide central circled F38 area; and that the specimen, itself, is catalogued as GINPC 478.

For all the plates, single lines for scale = 10 μm, double lines = 50 μm, double lines with three cross bars = 1 mm.

PLATE 1

Chroococcacean cyanobacteria genera *Coniunctiophycus* Zhang Y., 1981 and *Gyalosphaera* Strother *et al*., 1983.

1, 3, 4, 6. *Coniunctiophycus conglobatum* Zhang Y., 1981: 1 —Sample No 4689-26, Slide No 581, EFL J-42-0, GINPC No 468; 3 —Sample No 4694-38, Slide No 518, p. 8, GINPC No 1105 (in the upper left corner above the gloeocapsoid colony of *Eoentophysalis dismallakesensis* Horodyski and Donaldson, 1980, GINPC No 779); 4 —Sample No 4694-38, Slide No 648, p. 6, GINPC No 626; 6 —Sample No 4689-26, Slide No 581, EFL T-43-1, GINPC No 469.

2. *Coniunctiophycus gaoyuzhuangense* Zhang Y., 1981, Sample No 4689-21g, Slide No 489, EFL X-38-2, GINPC No 458.

5, 7-10. *Gyalosphaera golovenokii* Sergeev and Knoll, 1997, Sample No 4694-40, Slide No 613, p. 5: 5 —GINPC No 1106; 7 —GINPC No 504 (left colony) and GINPC No 505 (right colony); 8, 9 —GINPC No 503 (Holotype, shown at two different focal depths); 10 —GINPC No 1107.

Specimens GINPC No 458, 468 and 469 (figs 1, 2 and 6) are from the Kotuikan and Yusmastakh Formations and specimens GINPC No 503 - 505, 626, 779, 1105, 1106 and 1107 (figs 3-5 and 7-10) are from the Sukhaya Tunguska Formation.

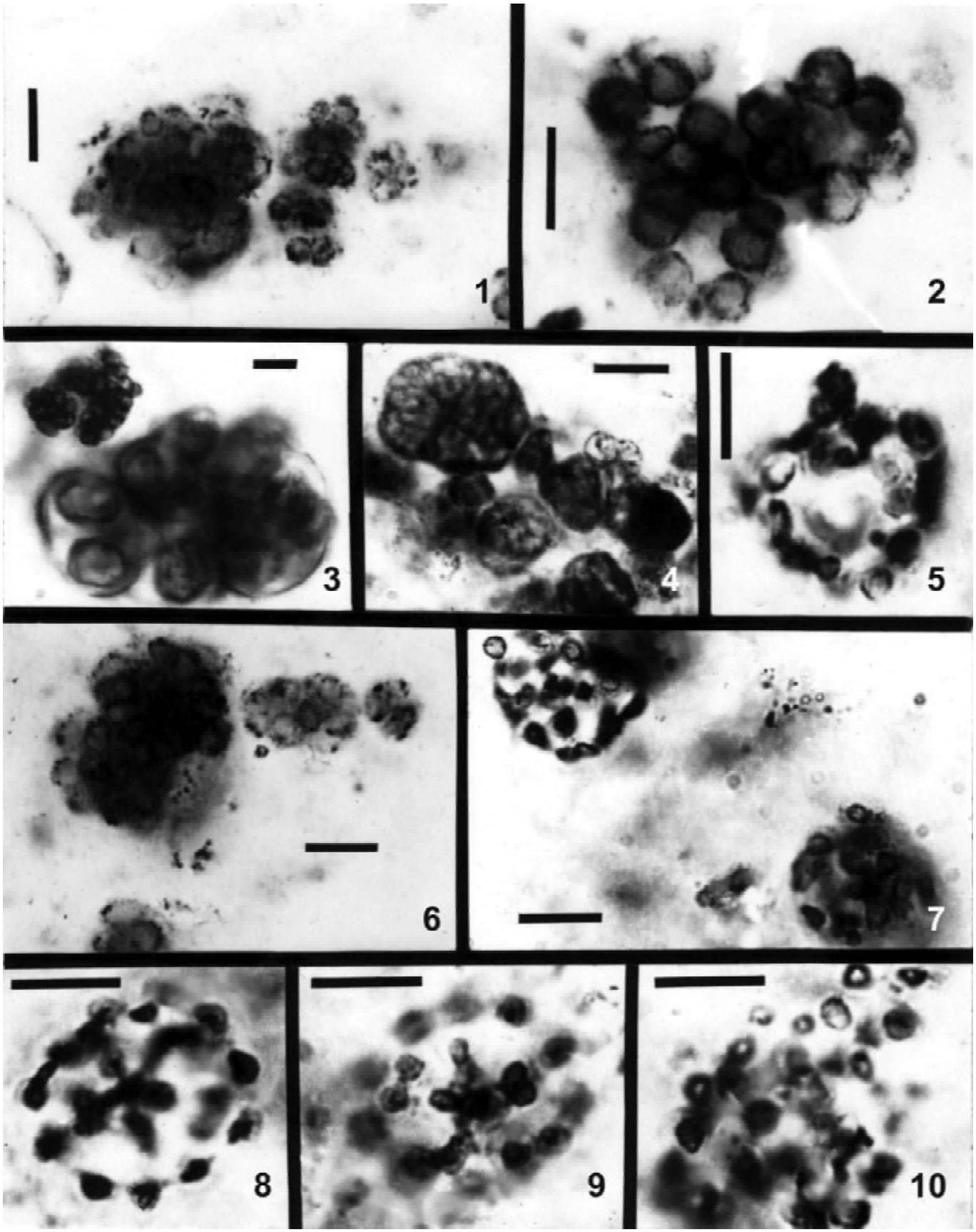


PLATE 1

PLATE 2

Problematic cyanobacterial remains genera *Glenobotrydion* Schopf, 1968, *Huroniospora* Barghoorn, 1965 and *Corymbococcus* Awramik and Barghoorn, 1977.

1, 2, 3 (left square in 1), 4 (right square in 1). *Glenobotrydion majorinum* Schopf and Blacic, 1971: 1, 3, 4 —Sample No 4681-250, Slide No 22, p. 1, EFL F-30-2, GINPC No 163; 2 —Sample No 4681-315, Slide No 73, p. 10, EFL M-33-3, GINPC No 1011.

5-7. *Huroniospora microreticulata* Barghoorn, 1965, Sample No 4313-1043, Slide No 745: 5 —p. 1', GINPC No 1108; 6 —p. 2, GINPC No 1109; 7 —p. 3, GINPC No 1110.

8 (square in 10), 9, 10 (square in 9). *Corymbococcus hodgkissii* Awramik and Barghoorn, 1977, Sample No 4313-1043, Slide No 744, p. 2, GINPC No 1111.

Specimens GINPC No 163 and 1011 (figs 1-4) are from the Chichkan Formation and specimens GINPC No 1108-1111 (figs 5-10) are from the Gunflint Formation.

PLATE 3

Pleurocapsalean cyanobacterium genus *Eohyella* Zhang Y. and Golubic, 1987 and chroococcacean cyanobacteria genera *Brachypleganon* Lo, 1980 and *Corymbococcus* Awramik and Barghoorn, 1977.

1-6. *Eohyella dichotoma* Green *et al*., 1988: 1, 3 (square in 1) —Sample No 4698-49, Slide No 799, p. 2, GINPC No 695; 2, 5 (enlarged fragment of 2) —Sample No 4698-49, Slide No 799, p. 1, GINPC No 660; 4, 6 (hexagon in 4) —Sample No 4694-49, Slide No 797, p. 1, GINPC No 659.

7, 8 *Brachypleganon khandanum* Lo, 1980, Sample No 4698-35, Slide No 826: 13 —p. 20, GINPC No 679; 14 —p. 15, GINPC No 680.

9 (square in 10), 10, 11. *Corymbococcus rexii* Sergeev and Lee Seong-Joo, 2004, Sample No 3893-932, Slide No 2; 9, 10 —p. 6, GINPC No 717 (Holotype); 10 —p. 6', GINPC No 1104.

Specimens GINPC No 695, 659, 660, 679, and 680 (figs 1-8) are from the Yudoma Group and specimens GINPC No 717 and 1104 (figs 9-11) are from the Satka Formation.

PLATE 4

Chroococcacean cyanobacterium genus *Eoaphanocapsa* Nyberg and Schopf, 1984.

1-6, 8, 9. *Eoaphanocapsa oparinii* Nyberg and Schopf, 1984: 1-5 —Sample No 4694-38, Slide No 518: 1, 2 (square in 1), 4 (square in 2, turned 90° clockwise) —p. 33, GINPC No 517; 3, 5 (square in 3) —p. 25', GINPC No 776; 6 (central colony), 8, 9 —Sample No 3893-277, Slide No 151: 6 —p. 10, GINPC No 98; 8 —p. 12, GINPC No 105; 9 —p. 12', GINPC No 106.

7. *Eoaphanocapsa molle* Sergeev, 1989 —Sample No 4681-98, Slide No 368, p. 7, GINPC No 206 (Holotype).

Specimens GINPC No 517 and 776 (figs 1-5) are from the Sukhaya Tunguska Formation, specimens GINPC No 98, 105 and 106 (figs 6, 8, 9) are from the Min'yar Formation, and specimen GINPC No 206 (fig. 7) is from the Chulaktau Formation.

PLATE 5

Chroococcacean cyanobacterium genus *Eogloeocapsa* Golovenok and Belova, 1984 and entophysalidacean cyanobacterium genus *Eoentophysalis* Hofmann, 1976.

1-4. *Eogloeocapsa avzyanica* Sergeev, 1992: 1 —Sample No 4688-26, Slide No 423, p. 19, EFL 0-38-2, GINPC No 40 (holotype); 2 —Sample No 4688-22, Slide No 424, p. 11, GINPC No 41; 3 and 4 —Sample No 4688-22a, Slide No 416, p. 11, GINPC No 46 and 45.

5-11. *Eoentophysalis dismallakesensis* Horodyski and Donaldson, 1980: 5, 6 —Sample No 4688-60, Slide No 894, 5 —p. 20, GINPC No 750, 6 —p. 12, GINPC No 792; 7 —Sample No 4688-22a, Slide No 416, p. 7, GINPC No 58; 8, 9 —Sample No 4688-22a, Slide No 415, 8 —p. 5, GINPC No 60, 9 —p. 1, GINPC No 44; 10, 11 —Sample No 4681-29; 10 —Slide No 265, p. 12, EFL T-24-3, GINPC No 177; 11 —Slide No 276, p. 18, EFL T-29-2, GINPC No 178.

Specimens GINPC No 177 and 178 (figs 10 & 11) are from the Chichkan Formation, other specimens are from the Avzyan Formation.

PLATE 6

Chroococcacean cyanobacterium genus *Eosynechococcus* Hofmann, 1976.

1-5. *Eosynechococcus moorei* Hofmann, 1976: 1, 2, 4 —Sample No 4689-47b, Slide No 560, EFLA-36-0, p. 2, HUHPC No 62930; 3 —Sample No 4689-47e, Slide No 482, EFL M-47-2, p. 2, GINPC No 453 (vesicles of *Eoentophysalis belcherensis* are above); 5 —Sample No 4694-40, Slide No 613, p. 9, GINPC No 533.

6. *Eosynechococcus* sp. —Sample No 4681-K1, Slide No 53K, p. 18, GINPC No 167.

7-9. *Eosynechococcus brevis* Knoll, 1982 —Sample No 4689-23, Slide No 489; 7, 8 —EFL X-37-2, p. 6, GINPC No 420; 9 —EFL W-36-3, GINPC No 475.

10, 13. *Eosynechococcus medius* Hofmann, 1976: 10 —Slide No P-4353-7B, EFL Z-22-3, HUHPC No 62401; 13 —Sample No 4694-40, Slide No 612, p. 13, GINPC No 529.

11, 12. *Eosynechococcus grandis* Hofmann, 1976 —Sample No 4694-509, Slide No 850; 11 —p. 4, GINPC No 636; 5 —p. 3, GINPC No 635.

Specimens GINPC No 453 and HUHPC No 62930 (figs 1-4) are from the Kotuikan Formation, specimens GINPC No 533 and 529 (figs 5 and 13) are from the Sukhaya Tunguska Formation, specimens GINPC No 420 and 475 (figs 7-9) are from the Yusmastakh Formation, specimens GINPC No 167 (fig. 6) is from the Chichkan Formation, specimens GINPC No 635 and 636 (figs 11 and 12) are from the Shorikha Formation, and specimen HUHPC No 62401 (fig. 10) is from the Draken Conglomerate Formation, Spitsbergen.

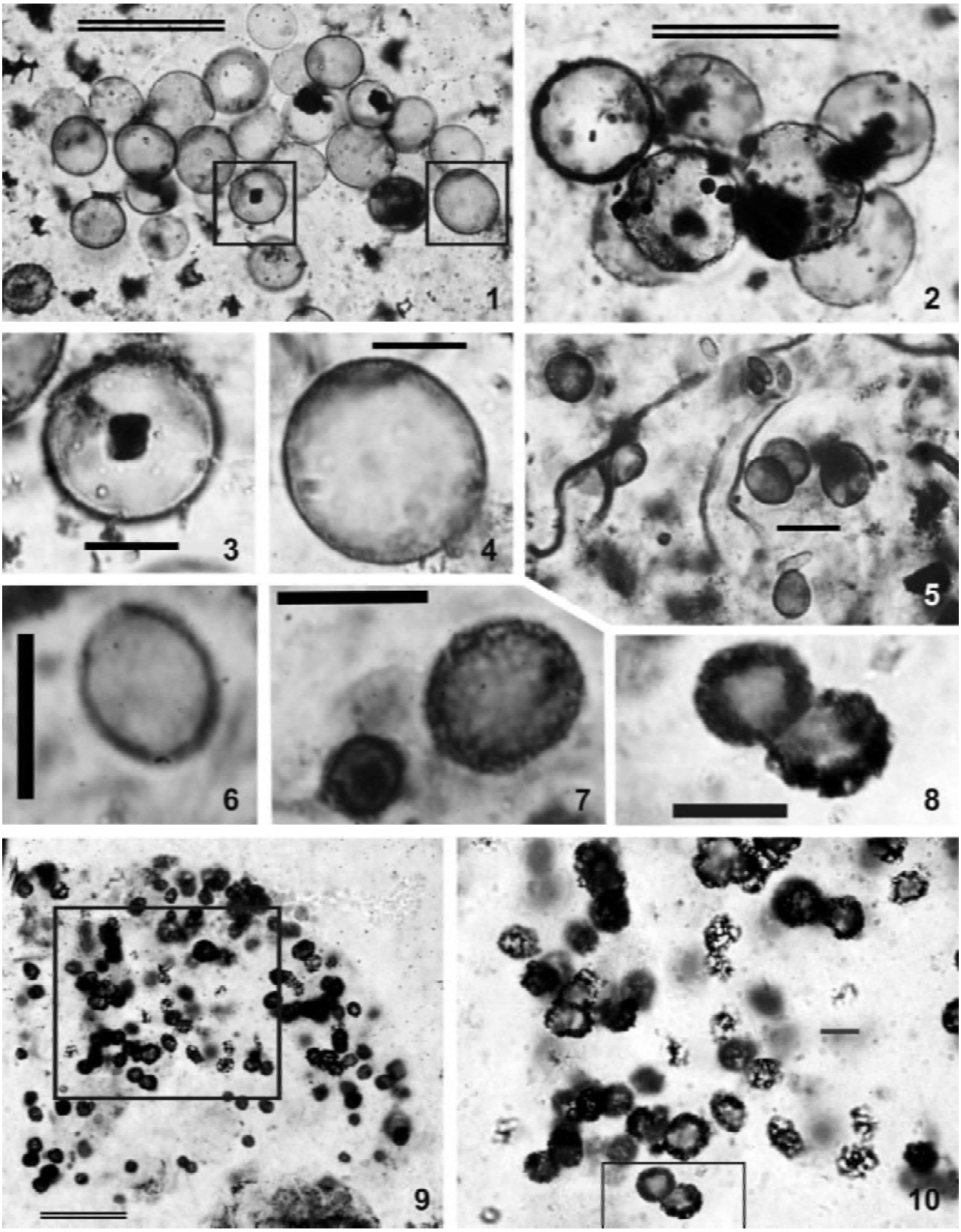


PLATE 2

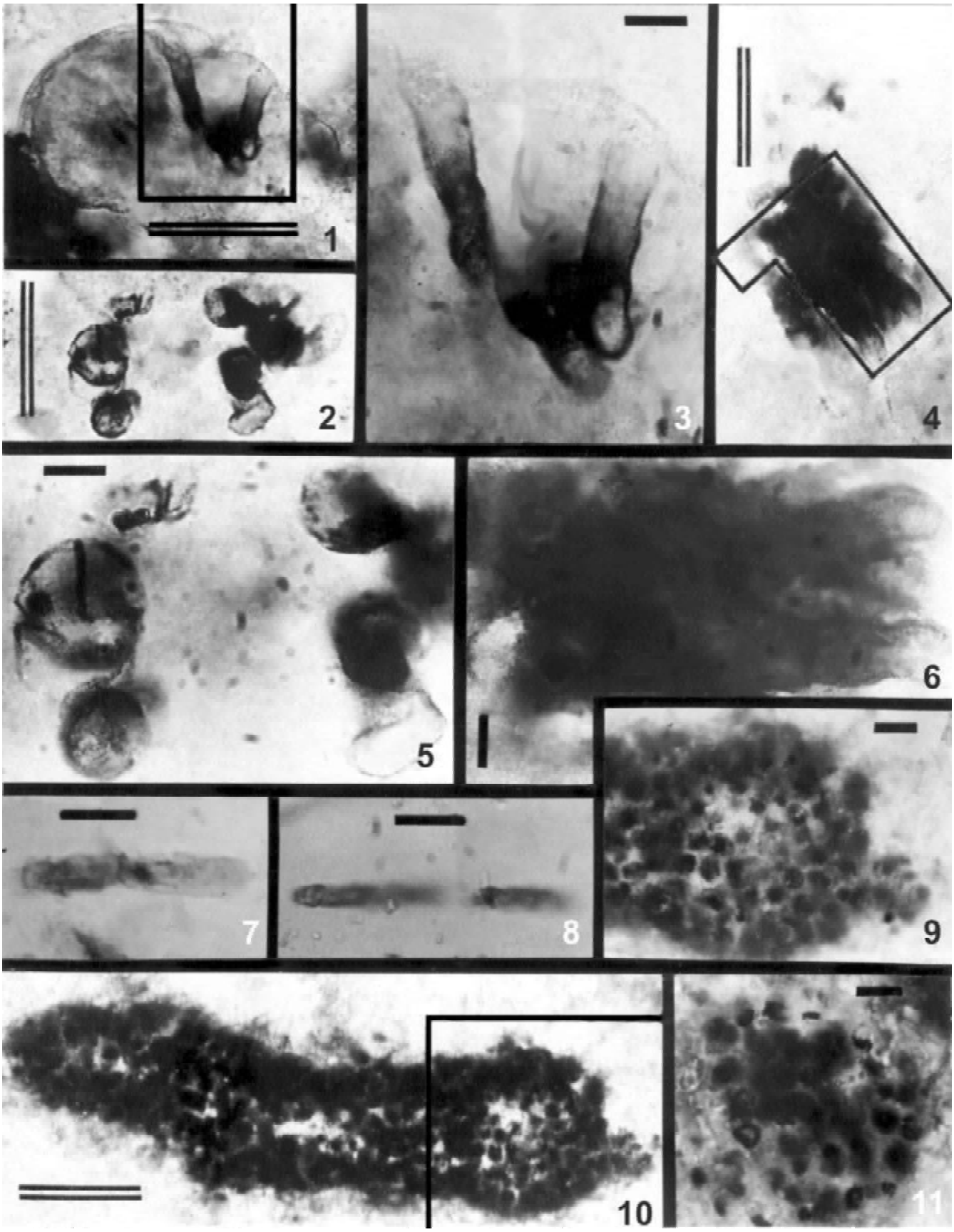


PLATE 3

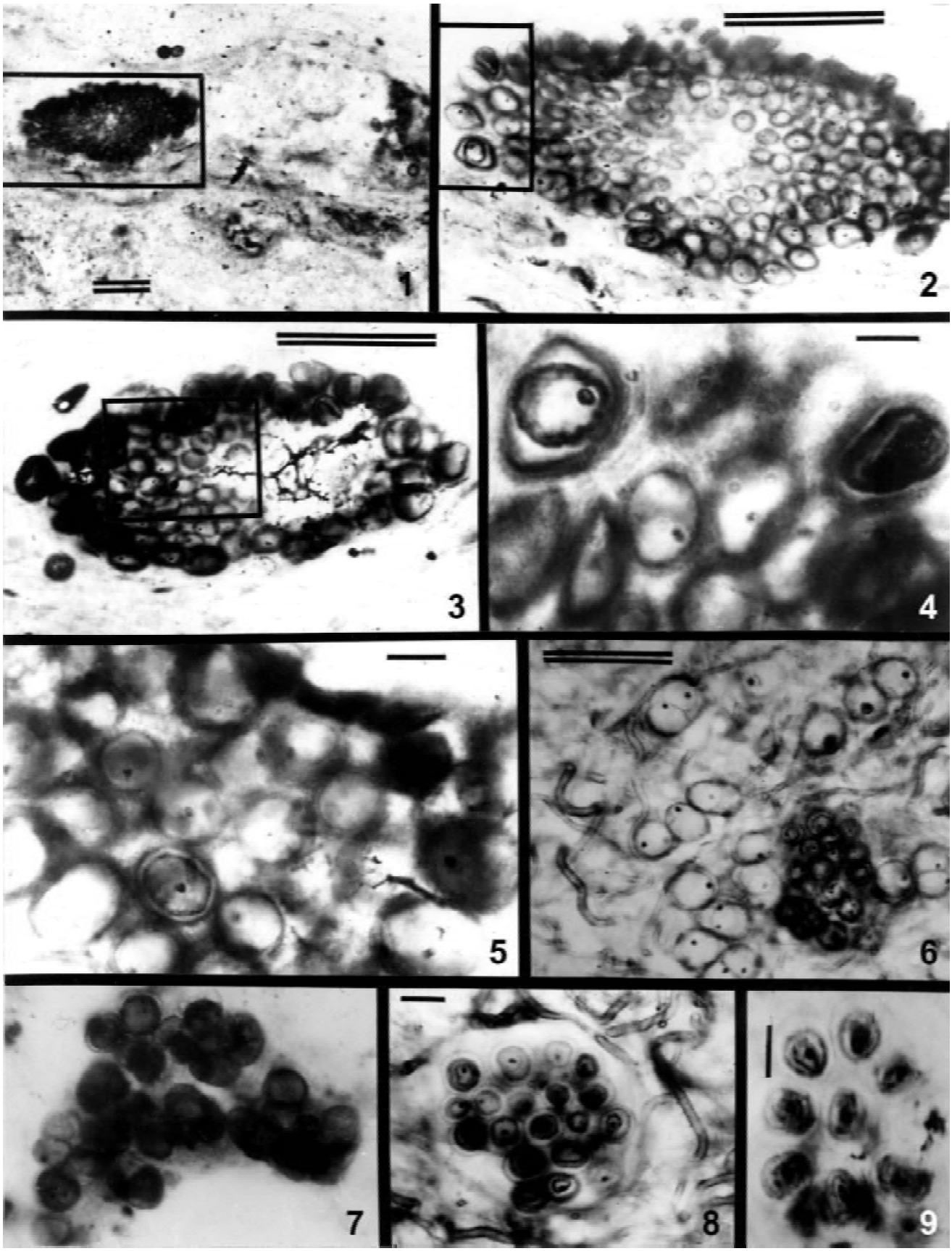


PLATE 4

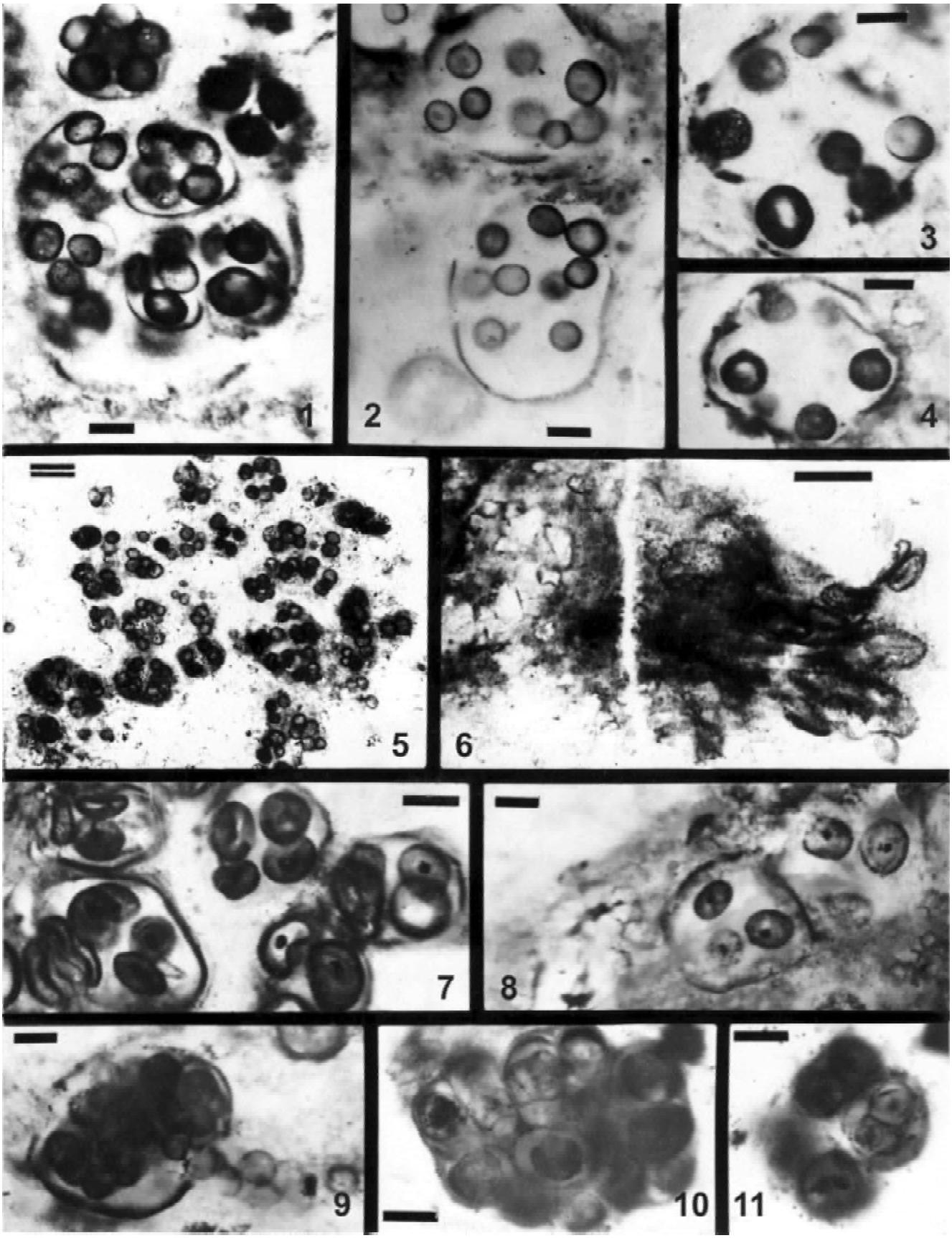


PLATE 5

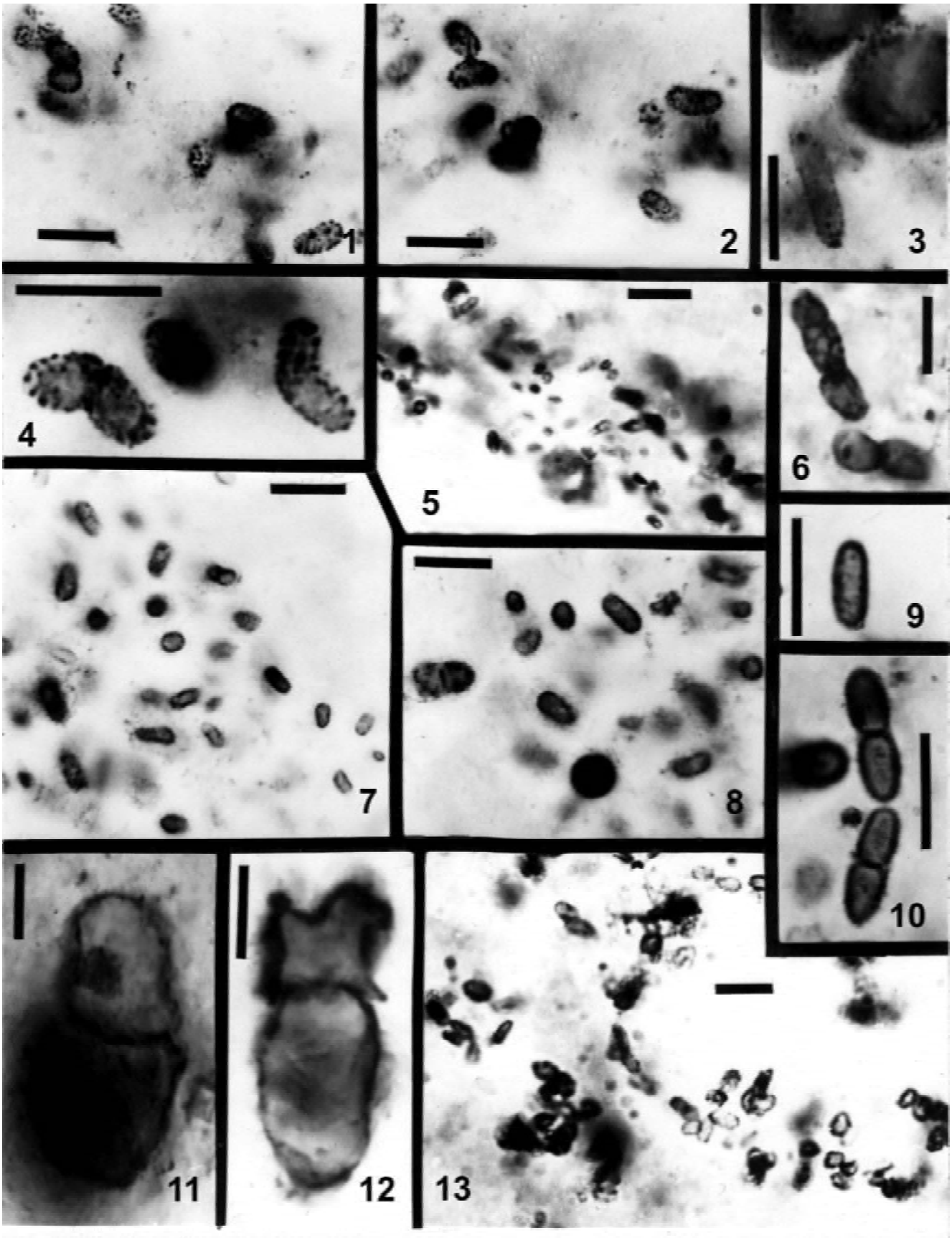


PLATE 6

Caryosphaeroides (partim), Schopf, 1968, p. 677.

Type species—*Gloeodiniopsis lamellosa* Schopf, 1968.

Diagnosis—Spheroidal to ellipsoidal vesicles with usually multilayered envelope. They are occasionally solitary, but commonly in colonies of a few to several hundred individuals. Spheroidal and ellipsoidal vesicles are arranged in monads, dyads, triads, tetrads (cross and planar tetrads) and octets, sometimes enclosed in thin common envelopes; larger colonies commonly embedded in a diffuse organic matrix. The envelope comprises one or more thin layers of differing density. Layers in outer portion with uniform curvature, innermost layers more irregular, occasionally containing a centrally or eccentrically located inclusion of dark matter.

Remarks—As emended by Knoll and Golubic (1979), the genus *Gloeodiniopsis* was interpreted as a fossil counterpart of the modern chroococcoid cyanobacteria *Gloeocapsa* or *Chroococcus* (Schopf & Blacic, 1971; Knoll & Golubic, 1979). Many researchers do not separate *Gloeocapsa* and *Chroococcus* (Elenkin, 1938; Komarek and Anagnostides, 1986) because based on the presence or absence of colored sheaths and sheath thickness, the differences between them are minor (Geitler, 1932; Desikachary, 1959; Golubic, 1976a). Sheath color, at least, cannot be recognized in fossil cyanobacteria.

In the emended diagnosis, Knoll and Golubic included not only single spheroids, but dyads, triads, tetrads and octets within a common envelope (Knoll & Golubic, 1979). Groups of spheroids set within a common vesicle were described as the genus *Clonophycus* (J. Oehler, 1977; D. Oehler, 1978) and as the genus *Eogloeocapsa* (Golovenok & Belova, 1984). Later on it was proposed to use the genus *Gloeodiniopsis* for the isolated fossilized predominantly multilayered morphological analogues of modern *Gloeocapsa-Chroococcus* cyanobacteria and the genera *Clonophycus* and *Gloeocapsa* for the remnants of multiple coccoidal microorganisms predominantly set within a single common envelope (Sergeev *et al.*, 1994, 1997).

About a dozen species of *Gloeodiniopsis* have been described, but most of them are just morphological variants of *G. lamellosa*. It is quite typical for modern cyanobacteria genera *Gloeocapsa* Kütz and *Chroococcus* Nägeli as well as for many others small chroococcacean cyanobacteria that demonstrate high polymorphism of populations and described species meet difficulties to be compared one to another.

Contents– *G. lamellosa, G. pangjapuensis, G. mikros, G. gregaria* and *G. hebeiensis* (Table-3).

Distribution– Meso-Neoproterozoic.

Gloeodiniopsis lamellosa Schopf, 1968, emend. Knoll and Golubic, 1979, emend. Sergeev, 1992 (in Sergeev, 1992a)

(Pl. 7.1-10, Pl. 8.1-13; Figs 8, 9, 17, 21, 22A-A')

Gloeodiniopsis lamellosa Schopf 1968, p. 684, Pl. 84, fig. 2; Schopf and Blacic, 1971, Pl. 110, figs 1-5; Knoll and Golubic, 1979, p. 147, figs 6, 7; Mendelson and Schopf, 1982, p. 66, 68, Pl. 1, figs 13,15; Maithy and Mandal, 1983, p. 133, Pl. 1, figs 5-6, Pl. 2, fig. 30; Nyberg and Schopf, 1984, p. 761, 763, figs 14A-14W, 15A, 15A'; Sergeev and Krylov, 1986, p. 90, Pl. X, figs 10-12; Sergeev, 1988, p. 709, figs. 1к-1л; Yankauskas, 1989, p. 93, Pl. XXIII, fig. 5; Krylov *et al.*, 1989, Pl. I, fig. 4; Allison and Awramik, 1989, p. 269, 271, fig. 8.1; Green *et al.*, 1989, figs 7A, 7B; Sergeev, 1992a, p. 74-76, Pl. IX, figs 4-9, Pl. X, figs 1, 3, 4, Pl. XI, figs 1, 3-8, Pl. XII, figs 1, 2, Pl. XIII, figs 1-3, 7-9, Pl. XIV, figs 1-7, Pl. XV, figs 1-7, Pl. XVII, figs 7a-7г; Sergeev, 1992b, Pl. IX, figs 4, 7, 9, 11; Kumar and Srivastava, 1992, p. 310, fig. 9K;

Name of species	Diagnostic features	Size, μm	Palaeoenvironmental setting	Repository and type locality	References
G. pangjapuensis Zhang Y., 1981 Fig. 22B	Vesicles soilitary or in small colonies or inside encompassing envelops	0.8-3.0	Intertidal, recorded from cherts in dolomites	BGP-7804; Early Mesoproterozoic, Gaoyuzhuang Fm., China	Zhang Y., 1981
G. mikros Knoll, 1982 Fig. 22C	Spherical vesicles contained inside encompassing envelopes	3.0-6.0	Intertidal, recorded from cherts in dolomites	HUHPC-60512-60516; Neoproterozoic, Draken Conglomerate Fm., Spitsbergen	Knoll, 1982
G. hebeiensis Zhang Y., 1981 Fig. 22D	Vesicles arranged in tetrads or triads or crowded within envelopes	1.0-4.5	Intertidal, recorded from cherts in dolomites	BGP-7814; Early Mesoproterozoic, Gaoyuzhuang Fm., China	Zhang Y, 1981
G. gregaria Knoll & Golubic, 1979 Fig. 22E	Spherical vesicles with single or multilamellated envelopes	4.0-8.0	Intertidal, recorded from cherts in dolomites	HUHPC-60301; Neoproterozoic, Bitter Springs Fm., Australia	Knoll & Golubic, 1979

Table 3—Comparative characteristics of genus *Gloeodiniopsis* species (Type Specimens).

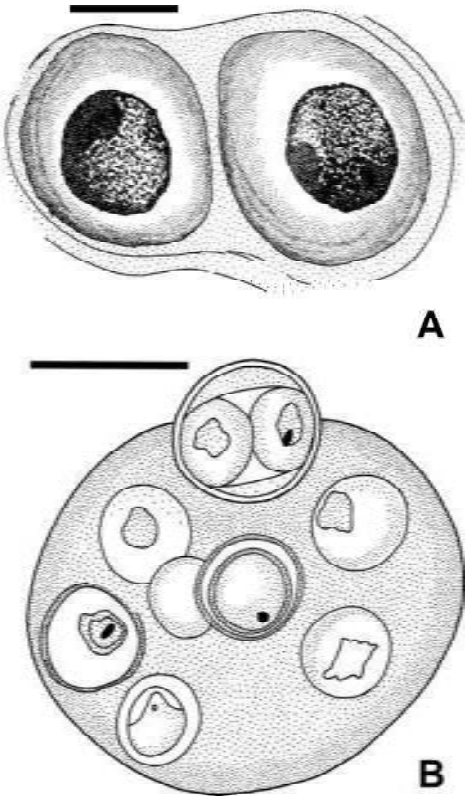


Fig. 21—Vesicles of *Gloeodiniopsis lamellosa* from the Min'yar Formation. Scale bar= 10 μm for A and 50 μm for B.

Schopf, 1992b, Pl. 10, fig. K, P, Pl. 32, fig. J, Pl. 45, fig. E, H, I; Golovenok and Belova, 1993, Pl. II, fig. b; Sergeev, 1994, p. 246-248, figs 6A-6F,7A-7D, 8B, 10B-10H; Butterfield *et al.*, 1994, p. 50, fig. 20H; Petrov *et al.*, 1995, Pl. I, fig. 10; Sergeev *et al.*, 1997, p. 216-219, figs 8A-8H; Kumar and Venkatachala, 1998, p. 60, fig. 6k; Sergeev, 2001, p. 439, 441, figs 9.8, 9.9; Srivastava and Kumar, 2003, p. 21, Pl. 1, figs 8-10,12, Pl. 2, fig. 1, Pl. 3, fig. 9, Pl. 4, fig. 4; Sergeev and Lee Seong-Joo, 2004, p. 11, 13, Pl. I, figs 1, 2; Sergeev, 2006, p. 192-194, Pl. XI, figs 1-9; Pl. XVIII, figs 8, 9; Pl. XXVI, figs 1-9; Pl. XXVII, figs 6, 7, 9-14; Pl. XXIX, figs 15-17; Pl. XXXIII, figs 1-8; Pl. XXXIV, figs 3-7; Pl. XXXIX, figs 2-8; Pl. XL, figs 1, 3-11, 15; Pl. XLI, figs 1-4, 7, 8; Pl. XLII, figs 1-9; Pl. XLIII, figs 1-6, 10; Sergeev *et al.*, 2008, Pl. 8, fig. 3, Pl. 10, figs 1, 3-8, Pl. 11, figs 6, 8, 9, Pl. 12, fig. 8.

Gloeodiniopsis magna Nyberg and Schopf, 1984, p. 763, 765, figs 15C-15G; Hofmann and Jackson, 1991, p. 377, figs 13.1-13.7,13.11-13.14; Golovenok and Belova, 1992, p. 116, 117, figs 1б, 1г; Schopf, 1992c, Pl. 45, figs D, F, G.

Gloeodiniopsis aff. *lamellosa* Schopf, 1968: Sergeev *et al.*, 1994, p. 25-26, Plate I, figs 2, 3, 6, 7.

Gloeodiniopsis grandis Sergeev and Krylov, 1986, p. 90, 91, Pl. X, figs 8, 9; Yankauskas, 1989, p. 93, Pl. XXIII, fig. 7; Knoll *et al.*, 1991, p. 550-553, fig. 19.4; Schopf, 1992b, Pl. 45, fig. B.

Gloeodiniopsis uralicus Krylov and Sergeev, 1986, p. 103, Pl. III, figs 1-7; Yankauskas, 1989, p. 94, Pl. XXII, figs 2, 8, 13; Sergeev, 1992a, p. 77–78, Pl. I, figs 1– 6, Pl. II, figs 1–3, 5–7, Pl. III, figs 1–4, Pl. IV, figs 1–2.

Gloeodiniopsis tchuchonoica Kolosov, 1982, p. 63-64, Pl. I, figs 1а, 1б, 1в; Yankauskas, 1989, p. 94, Pl. XLIV, fig. 1.

Bigeminococcus lamellosus Schopf and Blacic, 1971, p. 952-953, Pl. 111, figs 1a-1c, Schopf, 1992b, Pl. 33, fig. A_1, A_2.

Bigeminococcus mucidus Schopf and Blacic, 1971, p. 953, Pl. 112, figs 3a-3c, 4a-4c.

Eotetrahedrion princeps Schopf and Blacic, 1971, p. 955, 956, Pl. 112, figs 1, 2; Schopf, 1992b, Pl. 33, fig. D_1, D_2.

Eozygion grande Schopf and Blacic, 1971, p. 953, 954, Pl. 111, figs 2a-2c, 6, 7, Pl. 112, figs 5a, 5b; Schopf, 1992b, Pl. 33, fig. C_1, C_3.

Eozygion minutum Schopf and Blacic, 1971, p. 954, Pl. 111, figs 3, 5; Schopf, 1992b, Pl. 33, figs H, J.

Caryosphaeroides pristina Schopf, 1968 (partim): Schopf, 1968, p. 677, Pl. 85, figs 1-3, 4, 5; Schopf, 1992b, Pl. 33, fig. G.

Glenobotrydion majorinum Schopf and Blacic, 1971(partim): Nyberg and Schopf, 1984, p. 766, 769, figs 5A, 16A-16R, 17A-17F, 17H; Schopf, 1992b, Pl. 47, figs A-D, G.

Eoentophysalis yudomatica Lo, 1980 (partim): Sergeev and Krylov, 1986, p. 86-88, Pl. IX, figs 1-4; Yankauskas, 1989, p. 90, Pl. XXIII, figs 2, 4, 6; Krylov *et al.*, 1989, Pl. I, figs 5a, 5b.

Eoentophysalis sp.: Krylov *et al.*, 1989, Pl. I, fig. 6.

Palaeopleurocapsa kamaelgensis Sergeev and Krylov, 1986, p. 91, Pl. X, fig. 6; Yankauskas, 1989, p. 97, Pl. XXIII, fig. 9; Schopf, 1992b, Pl. 45, fig. C.

Chroococcus like morphotype: Mendelson and Schopf, 1982, p. 68-69, Pl. 2, fig. 5; Schopf, 1992b, Pl. 10, fig. L.

Globophycus like morphotype: Mendelson and Schopf, 1982, p. 69, Pl. 1, fig. 12.

"Undifferentiated chroococcacean cyanobacteria" (partim): Mendelson and Schopf, 1982, p. 69-72, Pl. 1, fig. 14, Pl. 2, figs 1, 4.

Tetraphycus giganteus Zhang Z., 1985 (partim): Golovenok and Belova, 1992, p. 117, figs 1ж-1з; Golovenok and Belova, 1993, Pl. II, fig. c.

Repository– HUHPC – 58502.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Multilamellated spheroidal to ellipsoidal vesicles surrounded by a hyaline zone with one or more thin layered envelope of differing density, giving a ringed appearance in cross-sectional view. Lamellae in outer portion with uniform curvature, innermost layers more irregular, occasionally containing a centrally or eccentrically located inclusion of dark matter. Spheroidal and ellipsoidal vesicles occasionally solitary, but commonly in colonies of a few to several hundred individuals. Spheroids arranged in monads, dyads, triads, tetrads (cross and planar tetrads) and octets,

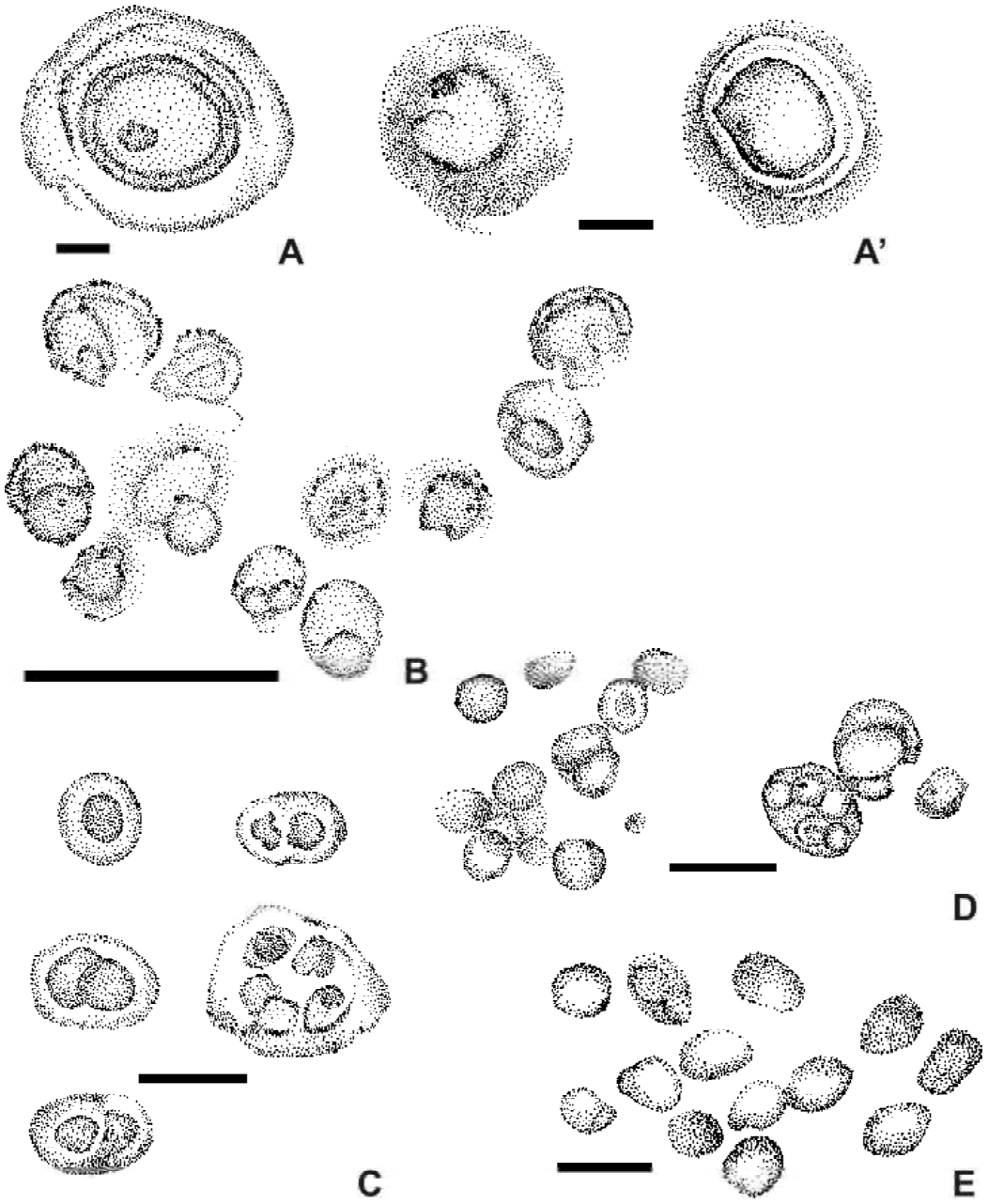


Fig. 22—Line diagrams of species of *Gloeodiniopsis*. A, A' - *G. lamellosa* (Schopf, 1968); B- *G. pangjapuensis* (Zhang Y., 1981); C- *G. mikros* (Knoll, 1982); D- *G. hebeiensis* (Zhang Y., 1981); E- *G. gregaria* (Knoll & Golubic, 1979). Scale bar =A-E = 10 µm.

sometimes enclosed in thin common envelops; larger colonies commonly embedded in a diffuse organic matrix. Diameter of inner layeres 8-36 mm; outer layeres 13-45 mm; inclusions 2-5 µm.

Remarks—1. *Gloeodiniopsis lamellosa* was erected by Schopf (1968) for mutlilamellated spheroids preserved in silicified coastal playa lake carbonates of the ca. 800 Ma Bitter Springs Formation, Australia. Knoll and Golubic (1979) emended this taxon to include species of the genera *Bigeminococcus, Eozygion, Eotetrahedrion* and *Caryosphaeroides* (in part), recognizing that previously described differences among these taxa reflect a cell division cycle and variable *post-mortem* decay within a single population. Many species of *Gloeodiniopsis* have been described, but their reported size ranges overlap. One of the most abundant Proterozoic species, *G. lamellosa* commonly occurs with the larger vesicles described as *G. magna* (Nyberg & Schopf, 1984). In the studies of coccoidal microfossils from

the Avzyan and Min'yar Formations of southern Ural Mountains (Sergeev, 1992a, 1994) and the Debengda and Sukhaya Tunguska Formations respectively, it was concluded that these "species" represent the extremes of intraspecific variation within a single population (Sergeev *et al.*, 1994, 1997). This interpretation is supported by the presence of both large and small individuals in single cell clusters. Evidently, cells grew to a maximum size of 35-45 μm, following which two or three binary divisions occurred with little intervening growth. The result was quartets and octets of vesicles with envelope diameters of 12-20 μm. On the basis of published reports, it appears Siberian and Uralian *G. lamellosa* differ from the Bitter Springs population in displaying a greater size range (Schopf, 1968; Knoll & Golubic, 1979); however, a reinvestigation of the type material indicates that the largest Bitter Springs specimens reach approximately 35 μm in diameter (Sergeev *et al.*, 1997). We suspect that many other described species of *Gloeodiniopsis* are synonymous with *G. lamellosa*. On the other hand, the possibility cannot be ruled out that *G. lamellosa* is a form taxon that encompasses multiple biological species of cyanobacteria and, perhaps, protists.

2. Sometimes spheroids of *G. lamellosa* (Sergeev, 1994) bear prominent solid, unbranched, sharply conical, 1-2 μm long spine-like pseudoprocesses; they are interconnected by septa at their bases, dividing spheroids into irregular polygonal fields. Such specimens of *G. lamellosa* superficially resemble acanthomorphic acritarchs described from Meso-Neoproterozoic (Riphean and Vendian) and Cambrian deposits. But these "spines" are definitely of secondary origin because it is evident that they are formed at the surface of typical *Chroococcus*-like unicells (Plate 7.8-10). Possibly, these pseudospines are casts of crystals of dolomite or magnesite that grew at the surface of cyanobacterial envelopes. Nonetheless, found separately these microfossils might be misinterpreted as remnants of true acanthomorphs.

3. A further complication in the circumscription of *G. lamellosa* is that cross-sections through the stalked cyanobacterium *Polybessurus bipartitus* can be mistaken for large *G. lamellosa* individuals (see Knoll *et al.*, 1991; Sergeev *et al.*, 1997).

Age and distribution—Mesoproterozoic: Satka and Avzyan Formations, southern Ural Mountains; Tshipanda Formation, Uchur-Maya Region; Debengda Formation, Olenek Uplift; Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia; Neoproterozic: Min'yar Formation, southern Ural Mountains; Bitter-Springs Formation, Austarlia; Svanbergfjellet Formation, Spitsbergen; Burovaya Formation, Turukhansk Uplift; Kumakhta and Sen'skaya Formations, Baikalo-Patom Uplift, Siberia; Dhararmkot Limestone Formation, Panna Shale Formation, Deoban Limestone Formation, Vaishnodevi Limestone Formation, India.

Genus—GLOEOTHECEOPSIS Zhang Y., 1988

Gloeotheceopsis Zhang Y., 1988, p. 173.

Type species—Gloeotheceopsis aggregata Zhang Y., 1988.

Diagnosis—Ellipsoidal to rod-shaped vesicles surrounded by diffused sheath and aggregated into colonies.

Contents—G. aggregata and *G. grandis*.

Remarks—Genus *Gloeotheceopsis* is considered to be fossil counterpart of modern cyanobacterium *Gloeothece* Nägeli. It differs from *Eosynechococcus* by its diffuse sheath and irregular colony form (Zhang Y., 1988).

Age—Proterozoic.

Gloeotheceopsis aggregata Zhang Y., 1988

(Fig. 23)

Gloeotheceopsis aggregata Zhang Y., 1988, p. 173-174, Figs 3A-3E.

Repository—BGPZD-9-8212.

Stratum typicum—Palaeoproterozoic, Dahongyu Formation, China.

Description—Ellipsoidal to rod-shaped vesicles, sometimes with dark inclusions at both ends, aggregated into colonies. Vesicles 1.7-4.0 μm long and 0.7-1.5 μm wide (length to width ratio is 4:2) are surrounded by diffused sheaths.

Age and distribution—Palaeo-Mesoproterozoic, Dahongyu and Gaoyuzhuang Formations, China.

Genus—GYALOSPHAERA Strother *et al.*, 1983

Gyalosphaera Strother *et al.*, 1983, p. 17.

Type species—Gyalosphaera fluitans Strother, Knoll and Barghoorn, 1983.

Diagnosis—Spheroidal vesicles arranged into spheroidal to ellipsoidal colonies and located evenly along the periphery of colony, leaving its interior empty. Extra-colonial sheaths are absent, but sometimes coating can be seen on larger colonies.

Fig. 23—Line diagram of *Gloeotheceopsis aggregata* (Zhang Y., 1988). Scale bar = 10 μm.

Remarks—Genus *Gyalosphaera* is considered as a fossil counterpart of modern chrococcacean cyanobacteria genera *Gomphosphaera* Kützing and *Coelosphaeridium* Nägeli (Strother *et al.*, 1983).

Contents—G. fluitans and *G. golovenokii.*

Age—Proterozoic.

Gyalosphaera fluitans Strother *et al.*, 1983

(Fig. 24)

Gyalosphaera fluitans Strother *et al.*, 1983, p. 17-18, Pl. 2, Figs 4-11, Pl. 3, Figs 1, 2.

Repository—HUHPC-60465.

Stratum typicum—Meso-Neoproterozoic, Narssarssuk Formation (Group), Greenland.

Description—Spheroidal colonies 12-100 μm in diameter, composed of few dozen small vesicles arranged evenly along the colony periphery, leaving its interior empty. Bifurcating stalks are observed inside colonies. Spheroidal to ellipsoidal vesicles are 0.5-3.0 μm in diameter consisting of single-walled envelope. Extra-colonial sheaths are absent, but sometimes coating can be seen on larger colonies.

Age and distribution—Meso-Neoproterozoic, Narssarssuk Formation (Group), Greenland.

Gyalosphaera golovenokii Sergeev and Knoll, 1997 (in Sergeev *et al.*, 1997)

(Pl. 1.5, 7-10)

Gyalosphaera golovenokii Sergeev and Knoll, 1997 in Sergeev *et al.*, 1997, p. 214-216, Figs 6E, 6F; Sergeev, 2006, p. 195, Pl. XII, Figs 8, 9а, 9б; Sergeev *et al.*, 2008, Pl. 12, fig. 4.

Gyalosphaera cf. *fluitans* Strother, Knoll and Barghoorn, 1983: Petrov *et al.*, 1995, Pl. I, fig. 13.

Repository—GINPC-4694, Specimen No. 503.

Stratum typicum—Meso-Neoproterozoic, Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia.

Description—Spheroidal to ellipsoidal colonies 10-27 μm in diameter, with 10 to 20 small vesicles arranged evenly along the colony periphery, leaving its interior empty. Vesicles envelope consist of two concentrically arranged envelopes with an outer diameter of 2-6.5 μm; the outer layer is spherical or ellipsoidal (compressed tangential to colony surface), chagrinate, translucent ca. 0.5 μm thick; inner layeres (1-3.5 μm in diameter) are similar in structure, but coarse-grained and 1-1.5 μm thick. An opaque, spheroidal inclusion 1.0-1.5 μm in diameter is sometimes attached to the inner layer of envelope.

Remarks—Gyalosphaera golovenokii from the Sukhaya Tunguska Formation differs from type species *G. fluitans* by the larger size of its constituent vesicles, it lacks bifurcating stalks within colonies, and the smaller size range of its colonies. Despite these differences, the overall structural organization of the Sukhaya Tunguska population compares closely with that found in the type species. Indeed, it cannot completely rule out the possibility that the Turukhansk and Greenland populations represent degradational variants of a single taxon. However, on the basis of available data, the Sukhaya Tunguska population was separated as a second species of the genus *Gyalosphaera* (Sergeev *et al*, 1997).

Age and distribution—Meso-Neoproterozoic, Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia.

Genus—SPHAEROPHYCUS Schopf, 1968

Sphaerophycus parvum Schopf, 1968, p. 672.

Type species—Sphaerophycus parvum Schopf, 1968.

Diagnosis—Small spheroidal vesicles, in dyads, triads or tetrads, surrounded by a common envelope. Vesicles occur in loose stratiform colonies or scattered among filaments of *Siphonophycus*.

Remarks—Genus *Sphaerophycus* includes small spheroidal unicells that occur as isolated individuals or in dyads, tetrads or larger groups of vesicles that reflect successive binary divisions (Schopf, 1968; Horodyski &

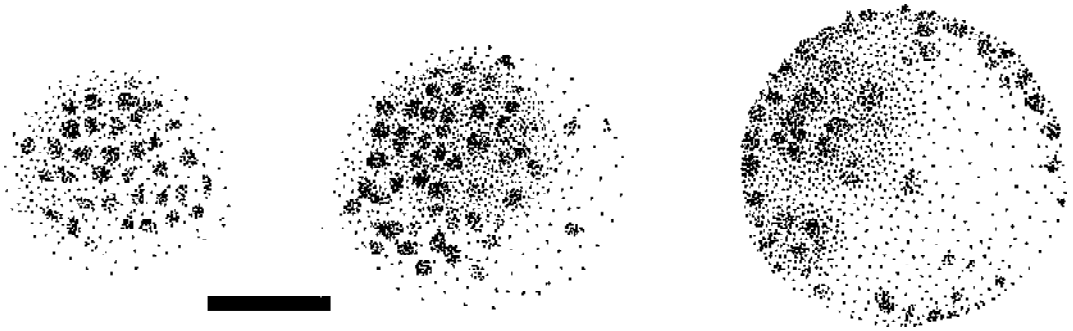


Fig. 24—Line diagram of *Gyalosphaera fluitans* (Strother *et al*., 1983). Scale bar = 10 μm.

Donaldson, 1980; Knoll, 1982; Knoll *et al.*, 1991). Its type species, *S. parvum* (Schopf, 1968), is similar to extant chroococcacean cyanobacteria such as species of *Synechocystis*, as well as, other physiologically dissimilar bacteria. However, some *Sphaerophycus* populations resemble early growth stages of *Eoentophysalis* (e.g. *S. reticulatum* Muir, 1976 and *S. tetragonale* Muir, 1976) and may reflect part of its life cycle.

Many species have been described within *Sphaerophycus*, however some of them of late been transferred to other species as synonymes or considered as dubiofossils, non-fossils, poorly preserved remains of other taxa or even in some cases figures of published specimens do not permit interpretation, *viz., S. gigas* Edhorn, 1975, *S. densus* Maithy, 1975, *S. reticulatum* Muir, 1976, *S. tetragonale* Muir, 1976 and *S. miriabilis* Moorman, 1974.

Contents—*S. medium* and *S. parvum.*

Age—Proterozoic.

Sphaerophycus medium Horodyski and Donaldson, 1980

(Pl. 9. 4-11; Fig. 25A-A')

Sphaerophycus medium Horodyski and Donaldson, 1980, p. 140-141, Figs 5J, 5K?, 5L?, 5M?, 5N?, 5O?, 5P?, 6C, 6D; Horodyski and Donaldson, 1983, Figs 5C, 5D?-5H?; Green *et al.*, 1989, fig. 5J; Knoll *et al.*, 1991, p. 553, fig. 19.3; Schopf, 1992b, Pl. 9, Figs F?-H?; Sergeev *et al.*, 1995, p. 27, Figs 9.6, 9.7; Kumar and Srivastava, 1995, p. 107, Figs 8M, 12F; Tiwari, 1996, pl. 2, fig. 10; Sergeev, 2002, p. 555, Pl. 11, Figs 12-15; Sergeev, 2006, p. 196, Pl. II, Figs 6, 7, Pl. XXIII, Figs 12-15, Pl. XL, Figs 12-14; Sharma, 2006a, p. 85, Figs 5j, 5k, 5m, 5n, 7a-7d.

Sphaerophycus wilsonii Knoll, 1982, p.783-784, Pl. 9, Figs 5-9.

Tetraphycus conjunctum Lo, 1980, p. 150-152, Pl. 3, Figs 1-5.

Gloeodiniopsis aff. *gregaria* Knoll and Golubic, 1979 (partim): Sergeev, 1993, Pl. II, Figs 8, 10.

Repository—GSC-57989.

Stratum typicum—Mesoproterozoic, Dismal Lakes Group, Canada.

Description—Spheroidal vesicles solitary, in dyads, triads or tetrads, surrounded by a common envelope. Vesicles occur in loose stratiform colonies comprising thousands of individuals. Outer diameter of spheroids is 3.0 to 6.5 µm. An opaque, spheroidal inclusion about 0.5 µm in diameter sometimes occurs attached to the innermost layer of envelope.

Remarks—*Sphaerophycus medium* populations resemble early growth stages of *Entophysalis* and may reflect part of the life cycle of *Eoentophysalis belcherensis*; however, in the absence of intermediate forms, such a relationship cannot be demonstrated. Therefore, following Horodyski and Donaldson (1980), we recognize *S. medium* as a distinct taxon.

Age and distribution—Mesoproterozoic: Dismal Lake Group, North America; Kotuikan and Yusmastakh Formations, Anabar Uplift, Siberia; Kheinjua Formation, India; Meso-Neoproterozoic: Sukhaya Tunguska Formation, Turukhansk

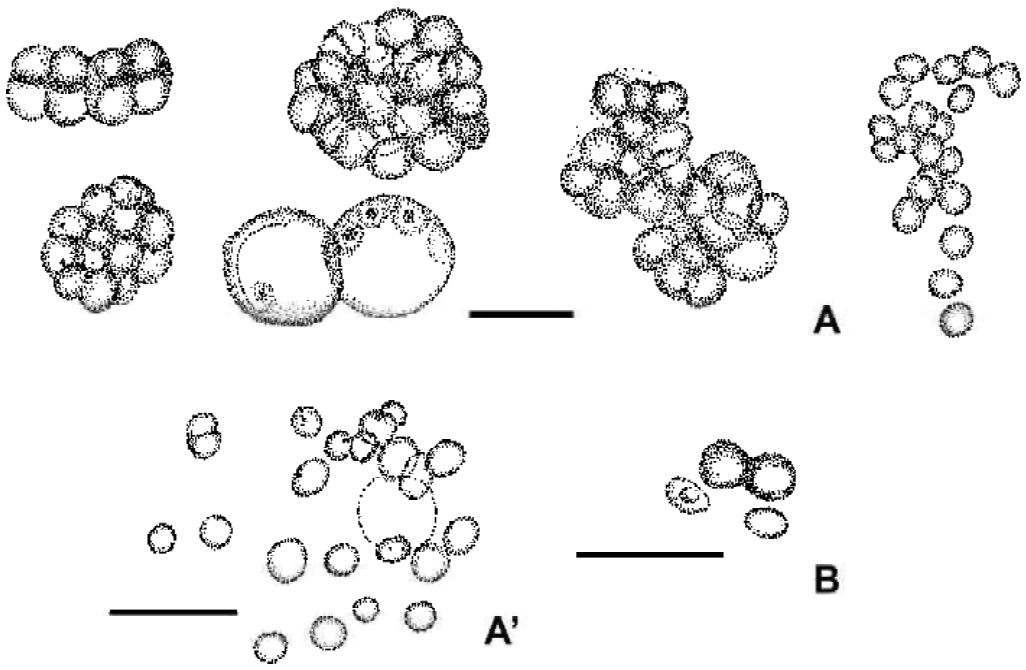


Fig. 25—Line diagrams of species of *Sphaerophycus.* A, A' - *S. medium* (Knoll, 1982); B- *S. parvum* (Schopf, 1968). Scale bar = 10 µm.

Uplift, Siberia; Neoproterozoic, Tonian-Cryogenian: Draken Conglomerate Formation, Spitsbergen, Limestone-Dolomite "Series", East Greenland; Ediacaran: Yudoma Group, Uchur-Maya Region, Siberia; Infrakrol Formation, India.

Sphaerophycus parvum Schopf, 1968

(Pl. 9.1-3; Fig. 25B)

Sphaerophycus parvum Schopf, 1968, p. 672, Pl. 80, Figs 4-10; Hofmann, 1976, p. 1058, 1061, Pl. 2, fig. 8?, Pl. 3, Figs 1-6; J. Oehler, 1977, p. 343, Figs 12H, 12I; 12D; D. Oehler, 1978, p. 293, Figs 10R, 10S; Horodyski and Donaldson, 1980, p. 140, Figs 5A-5E; Knoll, 1982, p. 783, Pl. 6, Figs 3, 4; Hofmann and Schopf, 1983, p. 348, Photo 14-8-P, 14-9-H, 14-9-I; Horodyski and Donaldson, 1983, p. 140, Figs 5A, 5B; Shukla *et al.*, 1986, p. 349, Pl. 2, Figs 11-18; Green *et al.*, 1989, fig. 5K; Tiwari and Azmi, 1990, p. 389, Pl. 1, Figs 16, 17, 20; Hofmann and Jackson, 1991, p. 374, Figs 8.9, 8.10, 8.11?, 10.1-10.3, 11 (partim); Knoll *et al.*, 1991, Figs 15.10-15.12; Kumar and Srivastava, 1992, p. 310, fig. 8D; Schopf, 1992b, Pl. 9, fig. G, Pl. 33, fig. F; Butterfield *et al.*, 1994, p. 54, Figs 20L-20T; Kumar and Srivastava, 1995, p. 107, fig. 8L; Tiwari, 1996, Pl. 2, fig. 8; Sergeev *et al.*, 1997, p. 222, fig. 13A, 13C; Tiwari and Pant, 2004, fig. 3s; Prasad *et al.*, 2005, Pl. 4, fig. 7; Sergeev, 2006, 195-196, Pl. XVI, Figs 5, 7; Sharma, 2006a, p. 83, 85, fig. 5l; Sergeev *et al.*, 2008, Pl. 12, fig. 5.

Undifferentiated chroococcacean cyanobacteria (partim): Mendelson and Schopf, 1982, p. 69-72, Pl. 1, fig. 11.

Repository—HUHPC-58472.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Spheroidal vesicles, commonly including dyads, in loose clusters comprising hundred of individuals or scattered among filaments of *Siphonophycus*. Vesicles are 2.0-4.0 μm in diameter and opaque spheroidal inclusions less than 0.5 μm in diameter occasionally present in their interior.

Age and distribution—Widely distributed in Proterozoic chert assemblages.

Genus—TETRAPHYCUS D. Oehler, 1978

Tetraphycus D. Oehler, 1978, p. 294.

Type species—T. gregalis D. Oehler, 1978.

Diagnosis—Spherical single-walled vesicles occur in plane tetrads although cross tetrads, diads, and octets may be present as well. Tetrads may occur in groups in a single area or as isolated individuals.

Remarks—In shape and size modern counterparts of *Tetraphycus* can be found among various Chroococcacean or Entophysalidacean cyanobacteria as well as some eukaryotic algae, e.g. Chlorococcacean green algae. Plane tetrads are common stage in life cycles of these forms and genus *Tetraphycus* probably encompasses just simlar living stages of various cyanobacteria. In spite of overarching characters of *Tetraphycus* with not enough compelling evidence to ascertain the taxonomical position of this genus, we wish to

Name of species	Diagnostic features	Size, μm	Paleoenvironmental setting	Repository and type locality	References
T. acinulus D.Oehler, 1978 Fig. 26B	Compressed vesicles with psilate walls in planar tetrads	0.4-1.3	Intertidal to supratidal, recorded from cherts in dolomites	CPC-18353; Palaeoproterozoic, Balbirini Dolomite Fm., Australia	D. Oehler, 1978
T. congregatus McMenamin *et al.*, 1983 Fig. 26C	Subspherical to elongated vesicles in tetrads or rectangular colonies	4.6-9.1	Intertidal, recorded from cherts in dolomites	UCSB – 029-2; Mesoproterozoic, Kheinjua Fm., India	McMenamin *et al.*, 1983.
T. diminutivus D.Oehler, 1978 Fig. 26D	Small vesicles in tetrads sometimes closely adpressed	0.7-1.9	Intertidal to supratidal, recorded from cherts in dolomites	CPC - 18353, Palaeoproterozoic, Balbirini Dolomite Fm., Australia	D. Oehler, 1978
T. hebeiensis Liu, 1982	Elongated vesicles in planar solitary and clumped tetrads	3.0x4.0-8.5x10.0	Peritidal, recorded from cherts in dolomites	W 7914 C(1) Mesoproterozoic, Wumishan Fm., China	Liu, 1982
T. major D. Oehler, 1978 Fig. 26E	Vesicles commonly in planar tetrads generally isolated	2.2-5.0	Intertidal to supratidal, recorded from cherts in dolomites	CPC-18351; Palaeoproterozoic, Balbirini Dolomite Fm., Australia	D. Oehler, 1978

Table 4—Comparative characteristics of genus *Tetraphycus* species (Type Specimens).

keep it independent for practical purposes of paleontological descriptions only. We also consider that most small tetrads of vesicles occur in Precambrian microbiotas belong to chroococcacean cyanobacteria.

There is some confusion with description of one of the species of *Tetraphycus*: *T. grandis* Luo *et al.*, in 1983 described a microfossil under this specific name for the first time. However, Yakschin (1999) probably unaware of this publication erected a species under the same specific epithet. Under ICBN regulations Luo *et al.* (1983) have a priority over this a specific epithet.

Contents—*T. acinulus, T. congregatus, T. diminutivus, T. hebeiensis, T. grandis, T. gregalis* and *T. major* (Table-4).

Age—Proterozoic.

Tetraphycus gregalis D. Oehler, 1978

(Fig. 26A)

Tetraphycus gregalis D. Oehler, 1978, p. 294, Figs 9I-K; Hofmann and Schopf, 1983, Photo 14-8-G; Prasad *et al.*, 2005, Pl. 5, fig. 2.

Repository—CPC-18352.

Stratum typicum—Palaeoproterozoic, Balbirini Dolomite Formation, Australia.

Description—Spherical single-walled vesicles of 2.0 to 4.0 μm in diameter occur in plane tetrads but no sheaths observed. Tetrads may occur in closely packed group in common organic matrix.

Age and distribution—Palaeoproterozoic: Balbirini Dolomite Formation, Australia; Kheinjua Formation, Vindhyan Supergroup, India.

Family—ENTOPHYSALIDACEAE Geitler, 1932

Genus—COCCOSTRATUS Lee Seong-Joo and Golubic, 1999

Coccostratus Lee Seong-Joo and Golubic, 1999, p. 204.

Type species—*Coccostratus dispergens* Lee Seong-Joo and Golubic, 1999.

Diagnosis—Stratified single layered spheroidal vesicles without common envelops forming either irregular colonies from a few individuals or laterally fused colonies composed of several thousand individuals. Free vesicles or isolated small colonies are often found above or below mats.

Remarks—Rather than including it into *Eoentophysalis,* Lee Seong-Joo and Golubic (1999) erected *Coccostratus* as an independent taxon, because of the absence of distinct envelope, mode of reproduction and colony formation as well as smaller vesicles size. But in our view, it just can be an ecological variant of *Eoentophysalis* in extremely hostile environmental conditions where even no opportunity existed for either production of mucilage or reproduction and only

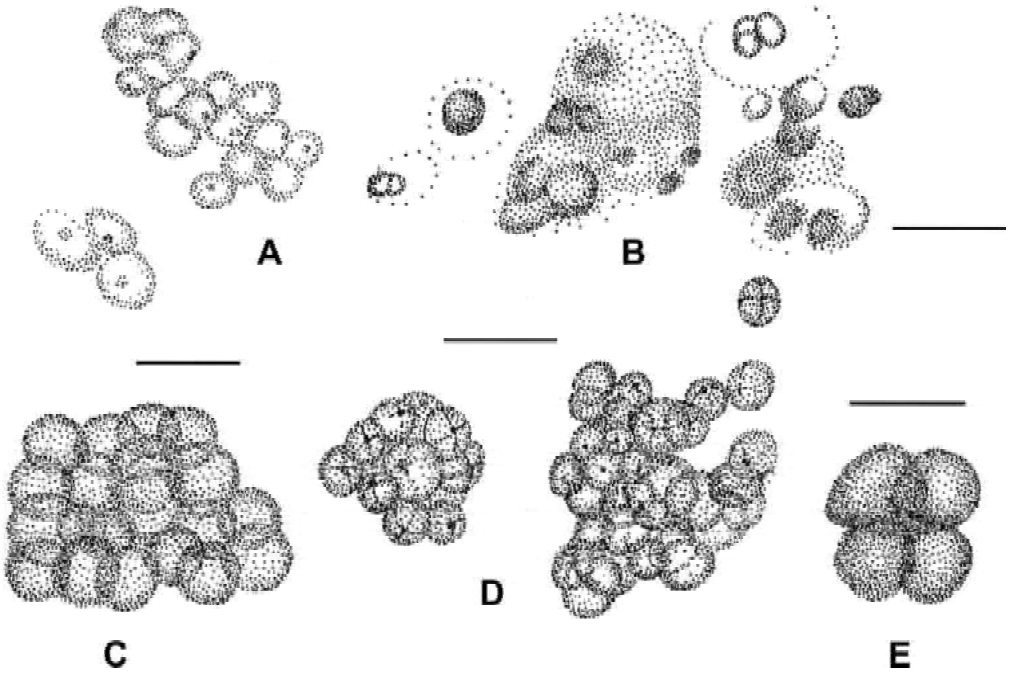


Fig. 26—Line diagrams of species of *Tetraphycus*. A- *T. gregalis* (D. Oehler, 1978); B- *T. acinulus* (D. Oehler, 1978); C- *T. congregatus* (McMenamin et al., 1983); D- *T. diminutivus* (D. Oehler, 1978); E- *T. major* (D. Oehler, 1978). Scale bar = A, B, D, E = 5 μm, C = 10 μm.

solitary cells could survive and fossilized as such. Nonetheless, we support an independent treatment for the genus *Coccostratus* unless we are proven correct.

Content—Monospecific genus.

Age—Proterozoic.

Coccostratus dispergens Lee Seong-Joo and Golubic, 1999

(Fig. 27)

Coccostratus dispergens Lee Seong-Joo and Golubic, 1999, p. 204-206, Figs 7B, 10A-10E; Golubic and Lee Seong-Joo, 1999, fig. 4; Lee Seong-Joo and Golubic, 2000, Figs 3A, 3B, 6A.

Repository—Gb9-31, Biological Science Center, Boston University.

Stratum typicum—Early Mesoproterozoic, Gaoyuzhuang Formation, China.

Description—Conspicuously spheroidal single layered vesicles without any common envelopes forming either irregular colonies from a few individuals or laterally fused colonies composed of several thousand individuals with billowy to mammillate, dark pigmented upper surface. Single vesicles or small clusters of vesicles are detached from main bodies and often occur separately. They occur sometimes in pairs and equatorially constricted cells might be in the phase of division. The vesicles diameter varies from 2.0 to 6.5 μm, the wall thickness is about 0.5 μm

Remarks—Colonies of *Coccostratus dispergens* often are found together with the mat-builders microorganisms *Siphonophycus* spp. and *Eoentophysalis belcherensis*. *Coccostratus dispergens* has similar behavioral ability like *E. belcherensis,* i.e. benthic mat builders, in microstructures and extracellular pigmentation on colony surface. It, however, differes from *E. belcherensis* by absence of distinct envelope encapsulation, mode of reproduction, colony formation, and to escape burial by recolonizing sediment surface. There is every likelihood that further studies may prove that both the taxa are just ecological variants of the same taxon.

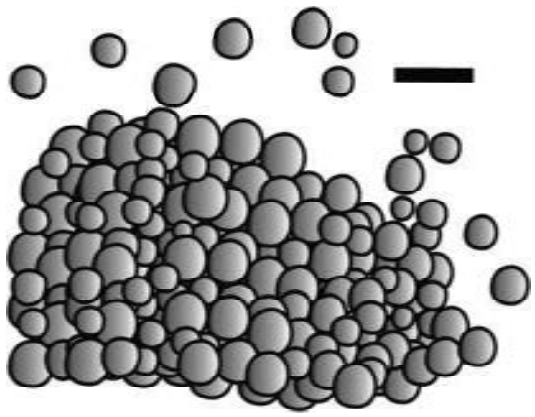


Fig. 27—Line diagram of *Coccostratus dispergens* (Lee Seong-Joo & Golubic, 1999). Scale bar = 10 μm

Age and distribution—Early Mesoproterozoic, Gaoyuzhuang Formation, China.

Genus—EOENTOPHYSALIS Hofmann, 1976 emend. Mendelson and Schopf, 1982

Eoentophysalis Hofmann, 1976, p. 1069-1070; Mendelson and Schopf, 1982, p. 74.

Type species—Eoentophysalis belcherensis Hofmann, 1976.

Diagnosis—Single-walled or multilamellated spheroidal and ellipsoidal vesicles in dyads, tetrads and octets that form colonies of a few to several thousand individuals. Colony morphology varies significantly from loose clusters to palmelloid colonies of spherical, hemispherical, mushroom-like or tooth-like shape. The margins of practically all colonies are marked by a prominent dark-brown pigment. Even numbers of layers nested within envelopes and an opaque inclusion may occur within innermost layer. Individual envelopes are commonly preserved only at colony margins, leaving the central part hollow.

Contents—E. belcherensis, E. dismallakesensis and *E. croxfordii*?

Remarks—The modern counterparts of *Eoentophysalis* are found among different species of genus *Entophysalis* Kützing. The closest counterpart has been revealed for the species *Eoentophysalis belcherensis-Entophysalis major* Ercegovic (Golubic & Hofmann, 1976). Some *Eoentophysalis* colonies are also very similar to the species of genus *Chlorogloea* which differ from *Entophysalis* mainly by structure of mucilage nesting cells inside. However, this diagnostic feature is quite hard to recognize in the fossil cyanobacteria.

Eoentophysalis is one of the most commonly recorded genera in the Palaeo-Mesoproterozoic formations of the world. This genus demonstrates high variations of its morphology due to complex life cycle and complicated *post-mortem* alterations (Hofmann, 1976; Golubic & Hofmann, 1976; Hofmann & Schopf, 1983; Knoll *et al.*, 1991; Sergeev *et al*, 1995; Sergeev, 2006), leading to erection of several distinct genera and species as is evident from the synonymy given below. In the present monograph, we have unified many forms described under other generic and specific names into either of the two species, i.e. *E. belcherensis* or *E. dismallakesensis*. There are some microfossils described as *Eoentophysalis* which do not belong to the genus. *E. gilesis* described from the Neoproterozoic Alinya Formation of Australia (Zang W., 1995) does not demonstrate such diagnostic features as

polarized growth and palmelloid colonies and should be excluded from *Eoentophysalis.*

Age—Widely distributed in Palaeo-and Mesoproterozoic cherts; less abundant in Neoproterozoic assemblages.

Eoentophysalis belcherensis Hofmann, 1976

(Pl. 10. 1-10, Fig. 28A-A')

Eoentophysalis belcherensis Hofmann, 1976, p. 1070,1072, Pl. 4, Figs 1-5, Pl. 5, Figs 3-6, Pl. 6, Figs 1-14; D. Oehler, 1978, p. 285, 288, Figs 2B-2D, 2H-2K, 3A-3H, 7C, 7D-7E, 8E-8F, 8R, 9P-9Q, 10T-10W, 11A-11E, 11H; Zhang Y., 1981, p. 497, Pl. 3, Figs 1-5, Pl. 4, Figs 1, 2; Hofmann and Schopf, 1983, p. 347, Pl. 14-2, Figs G-J, Pl. 14-6, fig. L-M, Pl. 14-8, fig. C, Pl. 14-9, Figs O-Q; McMenamin *et al.*, 1983, p. 261, Figs 10A-10C; Strother *et al.*, 1983, p. 26, Pl. 4, Figs 4-8; Knoll, 1985, fig. 21.3 C, D; Sergeev, 1988, p. 708, Figs 1в-1д; Green *et al.*, 1989, Figs 4E, 4F; Venkatachala *et al.*, 1990b, p. 481, 482, Pl. 1, Figs 5-9; Sergeev, 1992a, p. 81-82, Pl. IX, Figs 1-3; Sergeev, 1992b, Pl. IX, Figs 1-3; Kumar and Srivastava, 1992, p. 306, 307, fig. 9B; Sergeev, 1993, Pl. I, Figs 7, 8; Pl. II, Figs 1-6; Sergeev, 1994, p. 248, Figs 8C-8E; Sergeev *et al.*, 1994, p. 27, Pl. I, Figs 10, 11; Butterfield *et al.*, 1994, p. 50, Figs 20D-20E; Kumar and Srivastava, 1995, p.109, Figs 8A, 8C; Sergeev *et al.*, 1995, p. 27-28, Figs 12.1-12.4, 12.6, 12.12-12.14, 17.1-17.10; Kumar and Venkatachala, 1998, p. 56, 58, Figs 4d-4f, 5a-5e; Lee Seong-Joo and Golubic, 1999, Figs 11A-11F; Golubic and Lee Seong-Joo, 1999, Figs 2, 3; Lee Seong-Joo and Golubic, 2000, Figs 3C-3F; Sharma and Sergeev, 2004, Figs 5A, 5C, 9A, 9B; Prasad *et al.*, 2005, Pl. 5, fig. 6; Sergeev, 2006, p. 196-197, Pl. V, Figs 1-4, 6, 12-14, Pl. VIII, Figs 1-10; Pl. XXXIV, Figs 1, 2, Pl. XLI, Figs 11-15; Sharma, 2006a, p. 90, Figs 8j-8l, 9a-9g; Sergeev *et al.*, 2008, Pl. 1, fig. 7, Pl. 3, Figs 7, 9, Pl. 4, Figs 7, 9, Pl. 5, Figs 3, 6, Pl. 6, fig. 10, Pl. 11, Figs 1-3; Sergeev *et al.*, 2010, Pl. I, fig. 7.

Eoentophysalis cumulus Knoll and Golubic, 1979, p. 148-149, Figs 2E, 3A-3E; Sergeev and Krylov, 1986, p. 88-90, Pl. IX, Figs 5-7; Yankauskas, 1989, p. 90; Sergeev, 1992a, p. 82-83, Pl. XVII, Figs 3-6; Kumar and Srivastava, 1992, p. 308, 309, fig. 9F.

Eoentophysalis magna McMenamin *et al.*, 1983, p. 261, 263, Figs 10D, 10E; Kumar and Srivastava, 1992, p. 307, 308, fig. 9I; Kumar and Srivastava, 1995, p. 109, Figs 8E, 11G.

Myxocococcoides kingii Muir, 1976, p 151-152, fig. 6H.

Sphaerophycus parvum Schopf, 1968 (partim): Schopf and Blacic, 1971, Pl. 113, Figs 4-10.

Corynophycus varius Yakschin, 1990, p. 9-10, Pl. IV, Figs 2, 3, Pl. V, fig. 3.

Corynophycus compositus Yakschin, 1990, p. 10, Pl. V, fig. 5, Pl. VI, fig. 6.

Corynophycus solidus Yakschin, 1990, p. 10, Pl. V, fig. 4.

Corynophycus procerum Yakschin, 1990, p. 11, Pl. VI, fig. 5.

Eoxenococcus guttiformis Yakschin, 1990, p. 12, Pl. VI, Figs 1, 2.

Palaeoanacystis vulgaris Schopf, 1968 (partim): Yakschin, 1991, p. 23-24, Pl. VI, Figs 3, 5, 6, 8, Pl. VII, fig. 6.

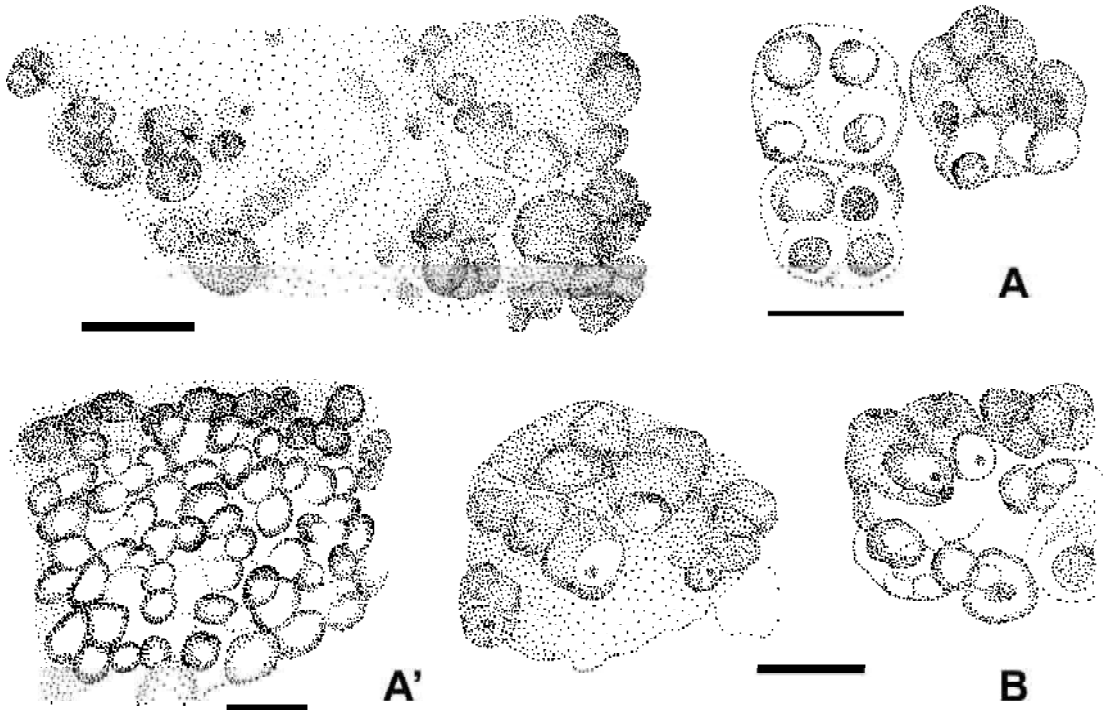


Fig. 28—Line diagrams of species of *Eoentophysalis*. A, A'- *E. belcherensis* (Hofmann, 1976); B- *E. dismallakesensis* (Horodyski & Donaldson, 1980). Scale bar = 10 μm.

Palaeoanacystis parvicellularis Yakschin, 1991, p. 24, Pl. VI, Figs 2, 4, 9.

Palaeoanacystis magnicellularis Yakschin, 1991, p. 24, Pl. VI, Figs 1, 7, Pl. VII, fig. 5.

Tortiliphycus bifilamentosus Yakschin, 1991, p. 38-39, Pl. XV, fig. 3.

Phanerosphaerops tenuichlamis Yakschin, 1991, p. 15-16, Pl. III, Figs 9, 11.

Myxococcoides minor Schopf, 1968 (partim): Yakschin, 1991, p. 21, Pl. IX, Figs 1, 2, 4, 5.

Archaeophycus venustus Wang, Zhang X. and Ruihan, 1983 (partim): Yakschin, 1991, p. 20, Pl. III, fig. 10, Pl. VIII, Figs 1, 6, Pl. IX, fig. 3.

Bulbiphycus sectilis Yakschin, 1991, p. 25, Pl. VIII, fig. 2.

Eoentophysalis cf. *belcherensis*, Hofmann 1976: Sergeev *et al.*, 1997, p. 224-225, Figs 11G, 11H.

Sphaerophycus medium Horodyski and Donaldson, 1980 (partim): Sergeev, 2006, Pl. XXXVI, fig. 9; Sergeev and Lee Seong-Joo, 2006, Pl. I, fig. 5.

Repository—GSC-42770.

Stratum typicum—Palaeoproterozoic, Kasegalik Formation, Canada.

Description—Single-walled or multilamellated spheroidal and ellipsoidal vesicles in dyads, tetrads and octets that form colonies of a few to several thousand individuals. Even numbers of layeres nested within envelopes. Colony morphology varies significantly from loose clusters to palmelloid colonies of spherical, hemispherical, mushroom-like or tooth-like shape and from single-layered sheet-like colonies to multilayered, pustuloses laminae. The number of spheroids per colony varies from a few dozen in loose clusters to several thousand in stratiform laminae. Margins of practically all colonies are marked by a prominent dark-brown pigment. An opaque inclusion < 1.0 μm in diameter may occur within the innermost layer of envelopes. The outer diameter of vesicles ranges from 3.0 to 10.0 μm; the inner diameter ranges from 2.0 to 6.0 μm. Vesicle morphology varies from regular and spherical to subpolyhedral. Multilamellated vesicles are commonly preserved only at colony margins, leaving the central part hollow.

Remarks—E. belcherensis differs from *E. dismallakesensis* by its smaller size [2-10 μm vs 11(4-6)-22 μm] with a slight overlapping due to *post-mortem* compaction and degradation. The morphology of population of *E. belcherensis* from different Proterozoic formations varies significantly and differs from type material described from the Belcher Supergroup (Hofmann, 1976). There are descriptions of the loose colonies of *Eoentophysalis* which do not constitute dominant mat-builders (Zhang Y., 1981; Hofmann & Schopf, 1983; Knoll, 1985; Knoll *et al.*, 1991; Sergeev 1992a, b, 1994). In many formations *E. belcherensis* have only single-layerd envelopes (Zhang Y., 1981, Muir, 1976, D. Oehler, 1978, Hofmann & Schopf, 1983, Sergeev *et al.*, 1994). However, all these variations are believed to be interspecific.

From the Neoproterozoic Bitter Springs Formation of Australia Knoll and Golubic (1979) have described *E. cumulus* which morphologically identical, but differs in age from *E. belcherensis*. N. Butterfield in Butterfield *et al.* (1994) has synonymised these 2 species suggesting *E. cumulus* to be junior synonym of *E. belcherensis*. McMenamin *et al.* (1983) also have described the spherical cells of the same size range as *E. magna* from the Mesoproterozoic Kheinjua Formation of India. However, careful reinvestigation of the paratypes by one of us (MS) revealed that they are no different from *E. belcherensis* and we consider *E. magna* as the morphological variation of this taxon as well.

Age and distribution—Palaeoproterozoic: Kasegalik and McLeary Formations, Canada; Mesoproterozoic: Amelia and Balbirini Formations, Australia; Gaoyuzhuang and Wumishan Formations, China; Kotuikan and Yusmastakh Formations, Anabar Uplift, Avzyan Formation, southern Ural Mountains; Kheinjua Formation, India; Meso-Neoproterozoic, Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia; Neoproterozic: Min'yar Formation, southern Ural Mountains, Svanbergfjellet Formation, Spitsbergen; Bitter Springs Formation, Australia; Deoban Limestone and Jammu Limestone Formations, India.

Eoentophysalis dismallakesensis Horodyski and Donaldson, 1980

(Pl. 5.5-11, Pl. 11.1-8; Fig. 28B)

Eoentophysalis dismallakesensis Horodyski and Donaldson, 1980, p. 146-149, Figs 10A-10D, 11A-11F, 11G?, 12A, 12B; Ogurtsova and Sergeev, 1987, Pl. 10, Figs 11, 12; Sergeev, 1992a, p. 83, Pl. XXII, Figs 7-9; Schopf, 1992b, Pl. 9, fig. E; Sergeev *et al.*, 1994, p. 27, Pl. 2, Figs 1-10; Sergeev and Lee Seong-Joo, 2006, p. 12-13, Pl. I, Figs 1-3, 6; Sergeev, 2006, 198-199, Pl. XIII, Figs 1-10, Pl. XIV, Figs 1-6, Pl. XXIII, Figs 5-11, Pl. XXXI, fig. 6, Pl. XXXII, Figs 1-8, Pl. XXXVI, fig. 2, Pl. XLII, Figs 10, 11, Pl. XLVI, Figs 11a, 11б, 12a, 12б; Sergeev *et al.*, 2008, Pl. 4, fig. 6; Sergeev and Schopf, 2010, p. 390, 391, Figs 11.6, 11.7.

Eoentophysalis yudomatica Lo, 1980, p. 146-150, Pl. 2, Figs 4-8; Sergeev, 2002, p. 555, 557, Pl. I, Figs 5-11.

Eoentophysalis arcata Mendelson and Schopf, 1982, p. 76, 77, Pl. 2, Figs 1a, 1b; Yankauskas, 1989, p. 90, Pl. XIX, Figs 11-12; Schopf, 1992b, Pl. 10, fig. E; Petrov *et al.*, 1995, Pl. I, Figs 11, 14, 16, 17; Sergeev *et al.*, 1997, p. 222-224, Figs 10A-10D, 11A-11F; Sergeev *et al.*, 2008, Pl. 8, fig. 1, Pl. 12, fig. 2.

Four categories of microfossils (partim): Sergeev, 1988, p. 709, fig. 1e.

Eogloeocapsa arcata Golovenok and Belova, 1992, p. 115-116, Figs 1a, 1b, 2, Golovenok and Belova , 1993, Pl. I , Figs a-d.

Eogloeocapsa avzyanica Sergeev, 1992b (partim): Sergeev, 1992b, p. 109, Pl. IX, Figs 6, 8, Pl. X, Figs 8-10; Sergeev, 1992a, p. 79, Pl. VI, Figs 1, 6-10, Pl. VII, Figs 9, 12, Pl. VIII, Figs 1, 2, 4-6, 8; Sergeev, 1994, p. 245, 246, Figs 5E-5H, 6G-6I, 7E, 7G; Sergeev *et al.*, 2008, Pl. 8, fig. 4, Pl. 11, fig. 5.

Eogloeocapsa sp_1 (partim): Sergeev, 1992a, p. 79, 80, Pl. XVII, Figs 1, 2.

Unnamed microfossils: Golovenok and Belova, 1993, Pl. II, fig. 3.

Eoentophysalis belcherensis Hofmann, 1976 (partim): Knoll and Sergeev, 1995, fig. 5.

Not *Eoentophysalis dismallakesensis* Horodyski and Donaldson, 1980. Sergeev, 2006, Pl. XXXI, Figs 1-5; Sergeev and Lee Seong-Joo, 2006, Pl. I, fig. 4.

Repository—GSC-57987.

Stratum typicum—Mesoproterozoic, Dismal Lakes Group, Canada.

Description—Multilamellated spheroidal, ellipsoidal and polyhedral vesicles in dyads, tetrads and octets occur in colonies from a few to several thousand individuals. Colony morphology varies significantly from loose clusters of gloeocapsoid vesicles to large aggregations of regular, cuboidal aspect to palmelloid colonies that form crustose stratiform laminae of spherical or hemispherical shape. Vesicle envelopes elongation common and sometimes pronounced-possibly a result of polarized growth during attempted escape from burial. Margins of many colonies are marked by dark-brown pigments. Commonly, fossils are preserved only at colony margins, leaving the central part hollow. Outer layers of vesicles envelopes are translucent, fine-grained about 0.5 μm thick. Inner layers are medium-to course-grained, about 1.0 μm thick. An opaque inclusion 0.5-3.0 μm in diameter is commonly found within the innermost envelope layer. The outer diameter of vesicles ranges from 6 to 22 μm, the inner diameter (measured at the inner layer of envelope) ranges from 4 to 13 μm; diameter of gloeocapsoid colonies 15-45 μm.

Remarks—The microfossils assigned to *E. dismallakesensis* differ from the type population in having a slightly greater size range (vesicles of *E. dismallakesensis* from the Dismal Lake Group are 4-13 μm long and 3-10 μm wide). However, in the type population of *E. dismallakesensis*, the outer sheaths have become amorphous (Horodyski & Donaldson, 1980, fig. 11) and in fact, the diameters of Dismal Lakes Group vesicles are only the inner diameters.

Mendelson and Schopf (1982) has described coccoidal microfossils from the Sukhaya Tunguska Formation as *E. arcata* despite lack of diagnostic characters of the Entophysalidaceae such as polarized growth and attached palmelloid colonies in the material they illustrated. Therefore, Golovenok and Belova, (1992, 1993) transfered this species to genus *Eogloeocapsa*. However, later on the attached, palmelloid colonies of *E. arcata* showing unidirectional, polarized growth was observed and a complete morphological gradiation from these to conical gloeocapsoidal *E. arcata* (= *E. dismallakesensis*) was demonstrated (Sergeev *et al.*, 1997). Thus, the entophysalidacean affinities of the Sukhaya Tunguska microfossils are established eliminating any need of transfer of these fossils to *Eogloeocapsa*.

After careful reinvestigation of the populations of Entophysalidaceae in the Debengda and Sukhaya Tunguska Formations as well as in the Yudoma Group, it became evident that they are identical in morphology, size ranges and behavior and belong to the species which by priority is *E. dismallakesensis*. This species can be differentiated from *E. belcherensis* by the larger diameter of its constituent vesicles. More difficult is the differentiation of *E. dismallakesensis* from *E. croxfordii* (Muir, 1976) comb. Butterfield, 1994 in Butterfield *et al.*, 1994 (diameter of spheroids 8.0-16.0 μm)-both can be separated as a group of "large" entophysalids, with vesicle diameters of 10-20 μm or more. Continuing study may reveal that *E. croxfordii* is a junior synonym of *E. dismallakesensis* or *E. belcherensis.*

Age and distribution—Mesoproterozoic: Dismal Lakes Group, North America; Debengda Formation, Olenek Uplift; Meso-Neoproterozoic: Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia; Neoproterozoic: Cryogenian, Chichkan Formation, South Kazakhstan; Ediacaran, Yudoma Group, Siberia.

Order—PLEUROCAPSALES Geitler, 1925

Family—DERMOCARPACEAE Geitler, 1925

Genus—POLYBESSURUS Fairchild ex Green *et al.*, 1987

Polybessurus Green *et al.*, 1987, p. 938.

Type species—Polybessurus bipartitus Fairchild ex Green *et al.*, 1987.

Diagnosis—Multilamellated cylindrical stalks, composed of regularly spaced, downwardly concave, funnel-shaped layers whose side walls constitute the outer wall of the stalk. Stalks either open at the top or terminate with preserved cells, cap-shaped envelopes or sporangium-like structures containing baeocytes. *Polybessurus* filaments form monospecific colonies from parallel arranged and densely packed stalks or occur as isolated individuals.

Contents—P. bipartitus and *P. crassus* (Table-5).

Remarks—The modern counterpart of *Polybessurus* has been noticed among pleurocapsalean cyanobacteria inhabited within peritidal environments of the Bahama banks more than 30 years ago (Golubic, 1976a; Green *et al.*, 1987). This still

PLATE 7

Chroococcacean cyanobacterium genus *Gloeodiniopsis* Schopf, 1968 - *G. lamellosa* Schopf, 1968.

1-3, 6, 7. Sample No 3893-256; 1-3 —Slide No 130, p. 108, EFL N-23-0, 2 (left square in 1) —GINPC No 3, 3 (right square in 1) —GINPC No 5; 6 —Slide No 185, p. 16, GINPC No 7; 7 — Slide No 144, p. 2, GINPC No 787 (right colony) and 14 (left colony).

4, 5. Sample No 3893-932, Slide No 10; 4 —p. 1, EFL K-9-0, GINPC No 1; 5 —p. 1', GINPC No 2.

8-10. Sample No 4688-22, Slide No 421, p. 20; 8, 9 (square in 10, shown at two different focal depths) —GINPC No 794, 10 (upper left pair of vesicles) —GINPC No 80.

Specimens GINPC No 1-3, 5, 7, 14 and 787 (fig. 1-7) are from the Satka Formation and specimens GINPC No 80 and 794 (fig. 8-10) are from the Avzyan Formation.

PLATE 8

Chroococcacean cyanobacterium genus *Gloeodiniopsis* Schopf, 1968 - *G. lamellosa* Schopf, 1968.

1. Sample No 4688-47, Slide No 441, p. 6, GINPC No 92.

2-6, 13 Sample No 3893-205; 2 —Slide No 62, p. 1, GINPC No 108; 3-6 —Slide No 238, p. 7; 5 (left square in 1), 6 (right square in 1), GINPC No 97; 13 —Slide No 61, p. 1, GINPC No 101.

7. Sample No 3893-277, Slide No 151, p. 5, GINPC No 100.

10, 11. Sample No 3893-206, Slide No 71, EFL K-28-1, p. 1; 10 — GINPC No 119; 11 —GINPC No 118.

8, 12. Sample No 4694-38; 8 —Slide No 513, p. 16, GINPC No 507; 12 —Slide No 635, p. 49, GINPC No 511.

9. Sample No 4694-85, Slide No 615, p. 12, GINPC No 509.

Specimen GINPC No 92 (fig. 1) is from the Avzyan Formation, specimens GINPC No 97, 100, 101, 108, 118 and 119 (figs 2-7, 10, 11 and 13) are from the Min'yar Formation, and specimens GINPC No 507, 509 and 511 (figs 8, 9 and 12) are from the Sukhaya Tunguska Formation.

PLATE 9

Chroococcacean cyanobacterium genus *Sphaerophycus* Schopf, 1968.

1-3. *Sphaerophycus parvum* Schopf, 1968, Sample No 4694-38, Slide No 518, p. 25, GINPC No 525 (A number is given for the colony as a whole).

4-11. *Sphaerophycus medium* Horodyski and Donaldson, 1980: 4 — Sample No 4689-23, Slide No 489, p. 34, GINPC No 419; 5 — Sample KG-92-45, Slide 1A, EFL G-43-1, GINPC No 473; 6, 7 —Sample No 4689-23, Slide No 484, EFL H-42-4, p. 8, GINPC No 472; 8, 9 —Sample No 4698-35, Slide No 782, p. 1, GINPC No 666 and GINPC No 667; 10, 11 —Sample No 4698-35, Slide No 780, p. 7, GINPC No 668 and GINPC No 669.

Specimen GINPC No 525 (figs 1-3) is from the Sukhaya Tunguska Formation, specimens GINPC No 419, 472 and 473 (figs 4-7) are from the Yusmastakh Formation, and specimens GINPC No 666-669 (figs 8-11) are from the Yudoma Group.

PLATE 10

Entophysalidacean cyanobacterium genus *Eoentophysalis* Hofmann, 1976 - *E. belcherensis* Hofmann, 1976.

1-5, 8, 9. Sample No 4689-16, Slide No 485: 1, 2 (left square in 1) — EFL H-38-2, p. 14, GINPC No 413; 3 (enlarged fragment of 4), 4 (right square in 1) —EFL H-39-3, p. 14, GINPC No 414; 5 —EFL K-44-1, GINPC No 477; 8, 9 —EFL G-42-4, p. 18, GINPC No 415.

6, 7. Sample No 4688-22: 6 —Slide No 421, p. 36, GINPC No 70; 7 —Slide No 424, p. 7, GINPC No 71.

10. Sample No 4689-7e, Slide No 461, EFL P-43-3, GINPC No 396.

Specimens GINPC No 413-415 and 477 (figs 1-5 and 8, 9) are from the Yusmastakh Formation, specimens GINPC No 70 and 71 (figs 6 and 7) are from the Avzyan Formation, and specimen GINPC No 396 (fig. 10) is from the Kotuikan Formation.

PLATE 11

Entophysalidacean cyanobacterium genus *Eoentophysalis* Hofmann, 1976 - *E. dismallakesensis* Horodyski and Donaldson, 1980.

1, 4, 5, 6, 8. Sample No 4694-74, Slide No 640; 1 —p. 36, GINPC No 516; 4 (square in 5), 5 —p. 1, GINPC No 521; 6 —p. 23, GINPC No 515; 8 —p. 44, GINPC No 519.

2. Sample No 4694-38, Slide No 518, p. 3, GINPC No 518.

3. Sample No 4694-73, Slide No 664, p. 12, GINPC No 523.

7. Sample No 4694-28, Slide No 602, p. 34, GINPC No 781.

All specimens are from the Sukhaya Tunguska Formation.

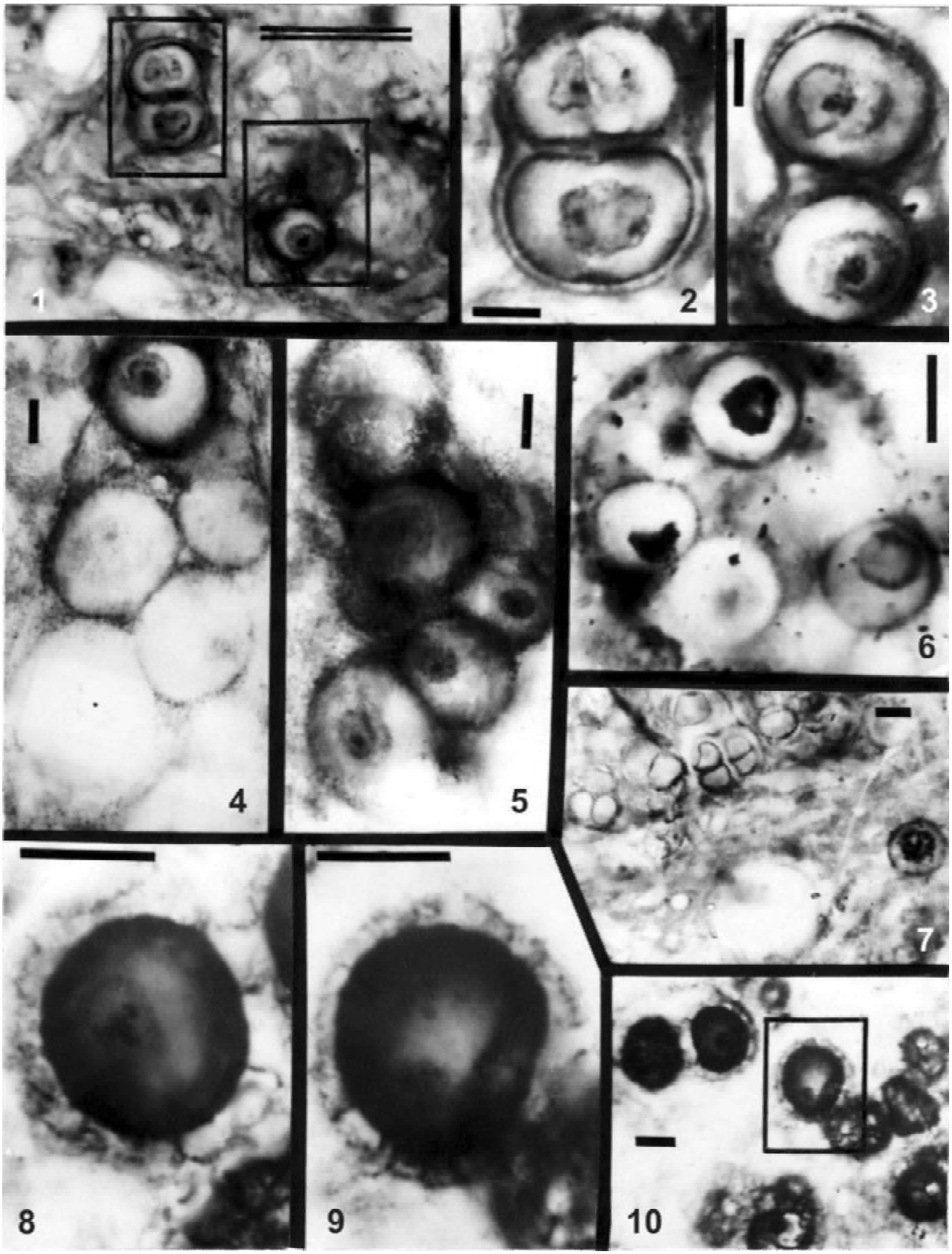


PLATE 7

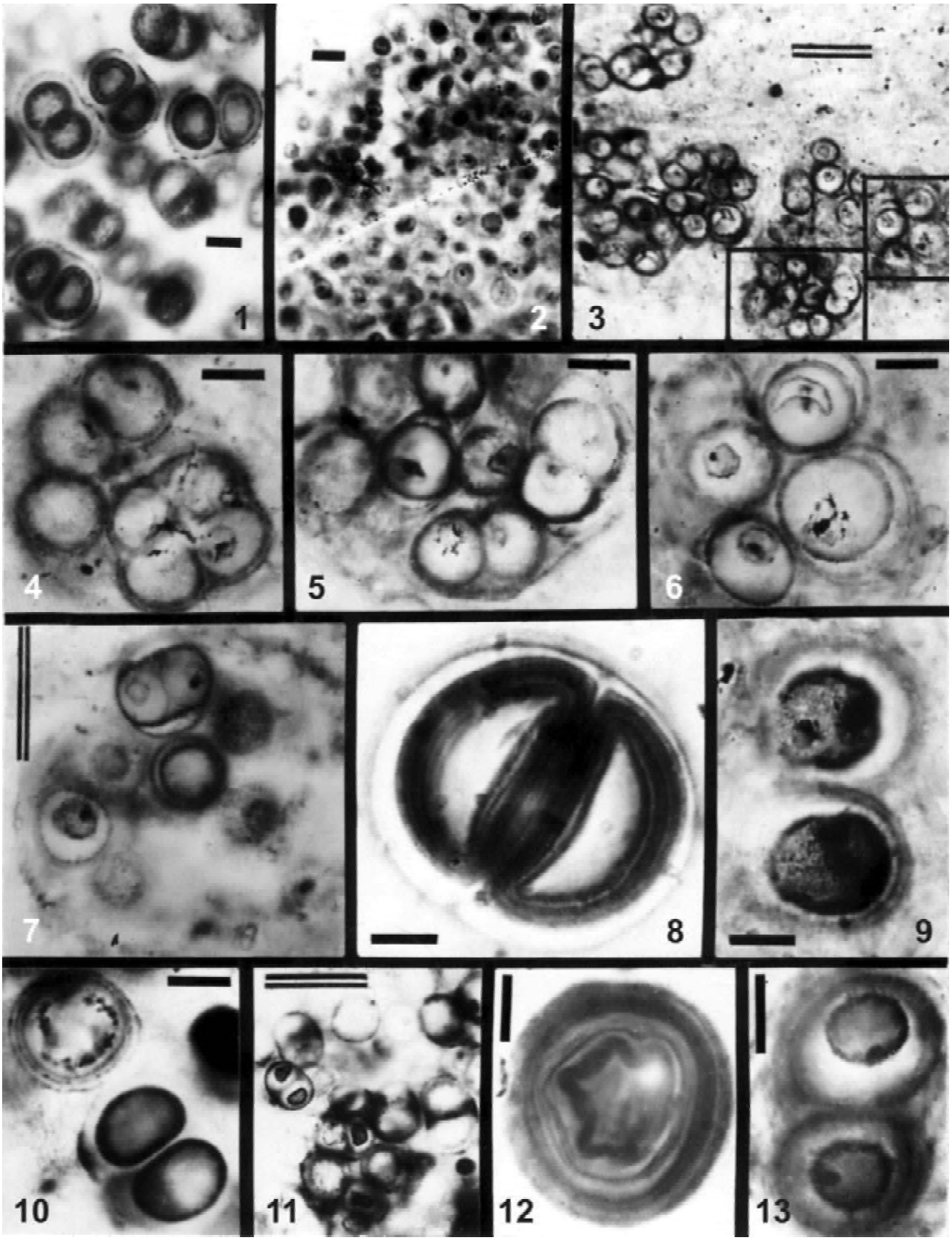


PLATE 8

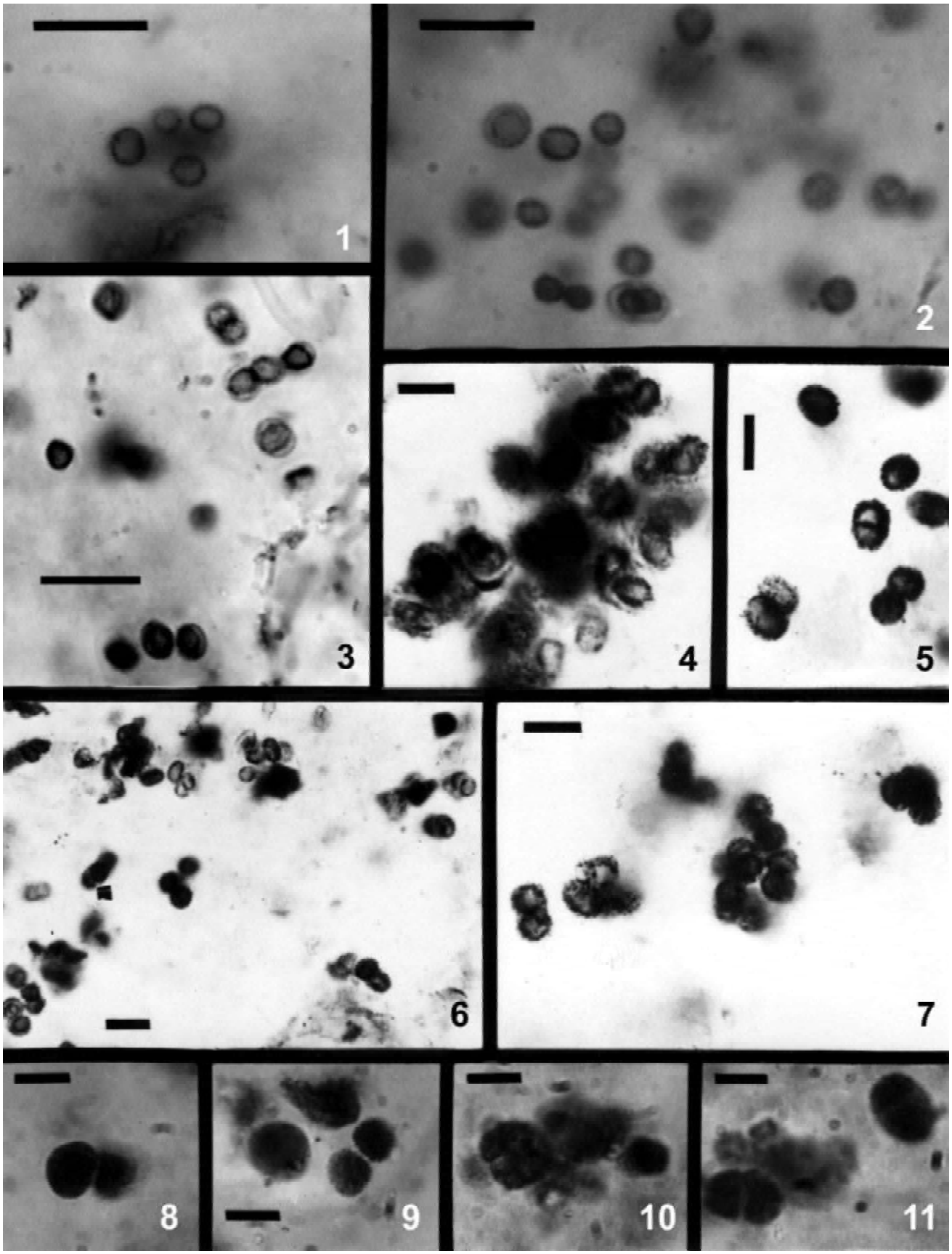


PLATE 9

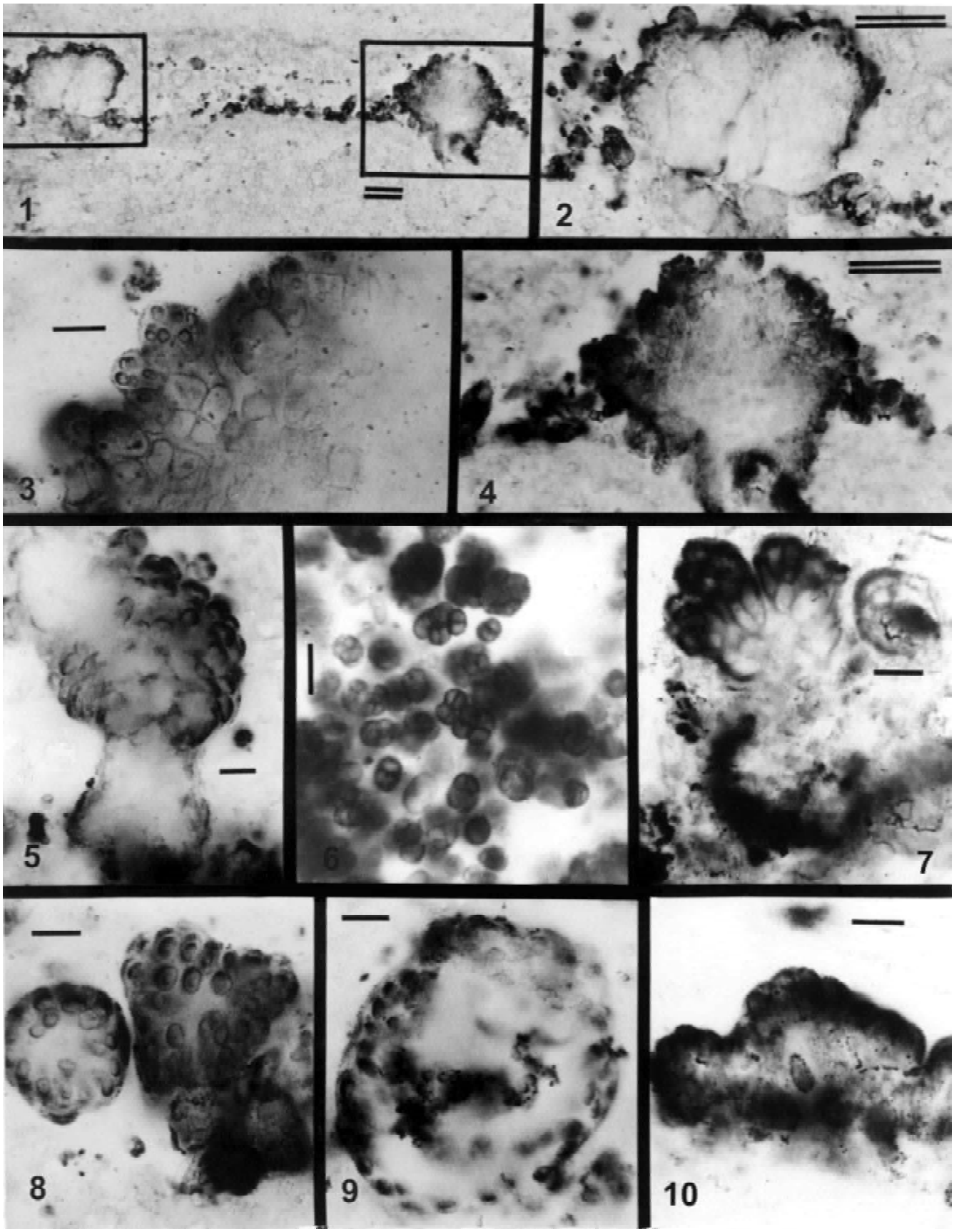


PLATE 10

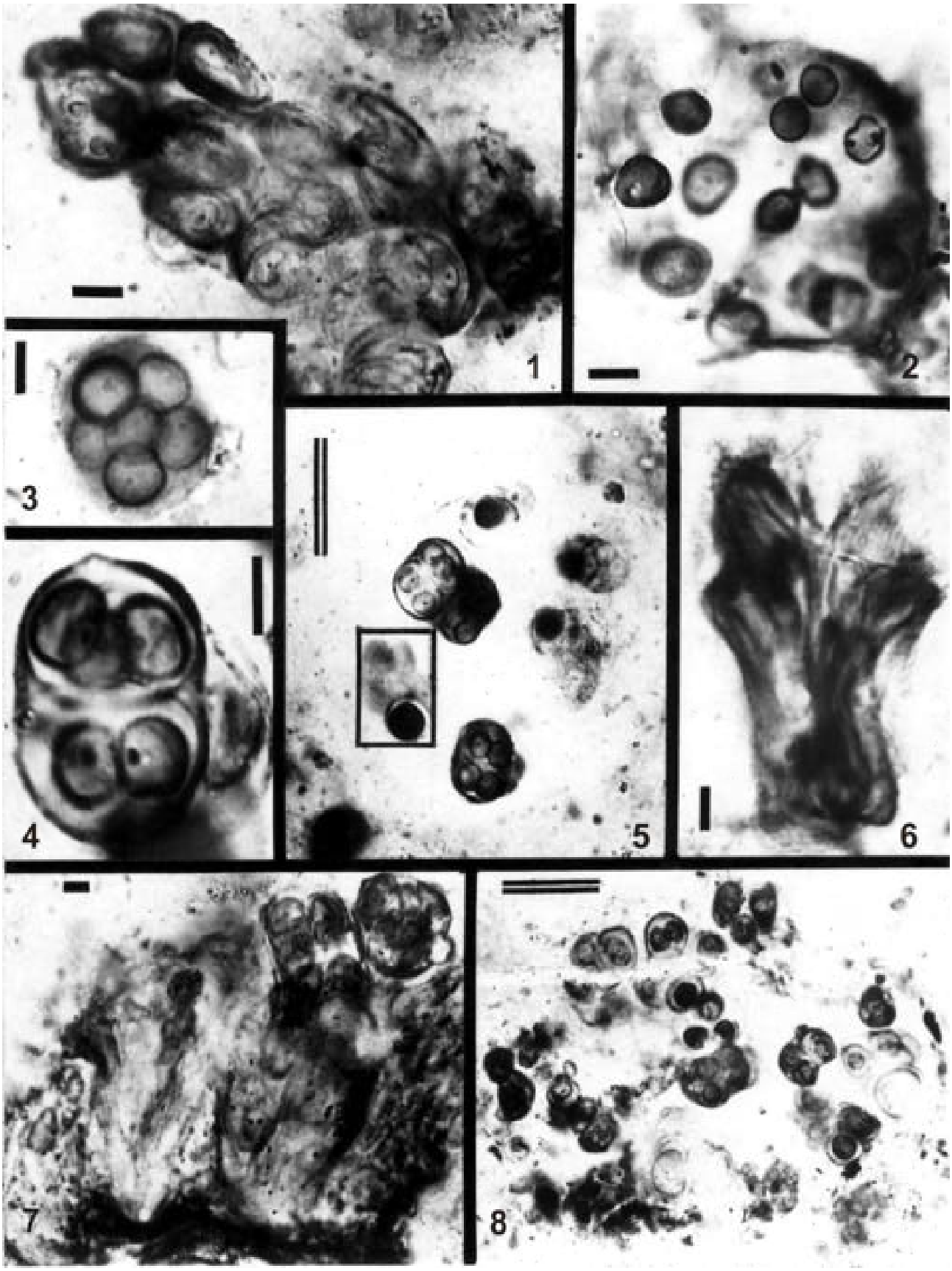


PLATE 11

Name of species	Diagnostic features	Size, μm	Paleoenvironmental setting	Repository and type locality	References
P. crassus Sergeev & Schopf, 2010	Multilamellated cylindrical tubes that contains stalked, downward concave, funnel-shaped thick laminae.	20.0-60.0	Inetrtidal and subtidal setting, recorded in cherts	GINPC – 1005, Neoproterozoic, Chichkan Fm, South Kazakhstan	Sergeev & Schopf, 2010

Table 5—Comparative characteristics of genus *Polybessurus* species (Type Specimens).

undescribed *Cyanostylon*-like cyanobacterium consists of unicells that jet upward to produce stacked-cup type stalks.

Age—Late Mesoproterozoic-Neoproterozoic.

Polybessurus bipartitus Fairchild ex Green *et al.*, 1987

(Pl. 12.1-7; Fig. 29)

Polybessurus bipartitus Green *et al.*, 1987, p. 938-939, Figs 5-12, 15-20; Green *et al.*, 1989, Figs 4G, 4H, 5A; Knoll *et al.*, 1989, Figs 6b, 6c; Knoll *et al.*, 1991, p. 553, Figs 12.1-12.8; Hofmann and Jackson, 1991, p. 378, fig. 7.8; Sergeev, 1992a, p. 85-86, Pl. VII, Figs 3, 4, 7, 8, Pl. IX, fig. 10; Sergeev, 1992b, p. 109-110, Pl. X, Figs 1-4; Schopf, 1992b, Pl. 36, 37, 38; Golovenok and Belova, 1992, p. 117-118, Figs 1д, 1е; Golovenok and Belova, 1993, Pl. II, fig. g; Butterfield *et al.*, 1994, p. 52, Figs 21C, 21F-21G; Sergeev, 1994, p. 248-249, Figs 9A-9G; Petrov *et al.*, 1995, Pl. I, fig. 5; Sergeev *et al.*, 1997, p. 225, 228, Figs 18H, 18I; Sergeev and Lee Seong-Joo, 2006, Pl. III, Figs 1-4; Sergeev, 2006, p. 199-200, Pl. XVI, Figs 1-4, Pl. XXXVII, Figs 1-7; Sergeev *et al.*, 2008, Pl. 8, Figs 6, 7, Pl. 11, Fig. 10, Pl. 12, fig. 9; Sergeev *et al.*, 2010, Pl. I, fig. 10.

"Mini-stromatolite-like" structure: Schopf, 1975, fig. 2J.

"*Polybessurus*": Schopf, 1977, Figs 13H-13J, 13K.

Gloeodiniopsis lamellosa Schopf, 1968 (partim): Petrov *et al.*, 1995, Pl. I, fig. 2.

Fig. 29—Line diagram of *Polybessurus bipartitus* (Green *et al*., 1987). Scale bar = 80 μm.

Repository—HUHPC-62022-A.

Stratum typicum—Neoproterozoic, Bed 18 of the Limestone-Dolomite "Series", Greenland.

Description—Multilamellated unbranched cylindrical stalks, composed of regularly spaced, upwardly concave, funnel-shaped layers whose side walls constitute the outer wall of the envelope. Stalks rarely terminate at the top with the preserved spheroids (baeocytes) entirely encircled by one or more layers composed of the same materials as funnels. More frequently, the envelopes are open at the top and funnel-shaped layers are most elements of the stalk. The layeres comprising the envelope are usually transparent, psilate, but sometimes granular or disappear and the stalk turn into the empty tubular structure as a result of *post-mortem* decay or diagenesis. Stalks and tubular structures sometimes forms monospecific colonies from parallel arranged and densely packed individuals, but more frequent occur principally as isolated individuals within *S. robustum* mats. Stalks width ranges from 15 to 150 μm and length from 20 to 600 μm, the distance between layers varies 10 to 60 μm, their thickness varies between 0.5 to 1.5 μm. The terminal vesicle or vesicles (baeocytes), when present, is/are spheroidal to ellipsoidal shape, 20 to 60 μm wide and 25 to 85 μm long, its wall is usually translucent, psilate or granular 1.0 to 2.0 μm thick.

Remarks—Green *et al.* (1987) explained the formation of stalks by unicells in part because such organisms take better advantage of nutrients in the surrounding water than do attached unicells. But the upward movement of unicells could be explained by necessity to keep up with the accumulation of sediments (Sergeev, 1994). It should be noted that the modern counterpart of *Polybessurus* lives within peritidal

environments of the Bahama Banks (Green *et al.*,1987) where cyanobacterial mats demonstrate high speed of growth (Monty, 1967) to compensate for the rapid accumulation of sediments.

In many occurrences of this taxon, *Polybessurus* stalks never terminate at the top with preserved cells encircled entirely by one or more envelopes (baeocytes), as in the type locality of eastern Greenland (Green *et al.*, 1987). The rarity of preserved cell walls or baeocytes appears to be a taphonomic bias affecting pleurocapsalean cyanobacteria in general (Sergeev *et al.*, 1997) or reflects their loss during preparation of the fossil-bearing thin sections (Sergeev & Schopf, 2010).

Age and distribution—Late Mesoproterozoic, Avzyan Formation, southern Ural Mountains; Society Cliff and Hunting Formations, North America; Meso-Neoproterozoic, Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia; Neoproterozoic: Seryi Cluch Formation, Enisey Ridge, Siberia; Svanbergfjellet Formation, Spitsbergen; Skillogalee Formation, Australia; Limestone-Dolomite "Series", Greenland.

Family—HYELLACEAE Borzi, 1914

Genus—EOHYELLA Zhang Y. and Golubic, 1987, emend. Green *et al.*, 1988

Eohyella Zhang Y. and Golubic, 1987, p. 10-11; Green *et al.*, 1988, p. 844.

Type species—Eohyella campbelliae Zhang Y. and Golubic, 1987.

Diagnosis—Polyhedral coccoidal or isodiametrically elongated vesicles in endolithic thalli forming pseudofilaments penetrating substrate. These pseudofilamentous colonies are uniseriate, biseriate or multiseriate; branching is dichotomous, rare to frequent. Endolithic thalli peneterate substrate in different fashion: either they start from one point and radiate inside or spread out from the globular colonies of vesicles. Vesicles in pseudofilamentous colonies are about the same dimension, but end vesicles occasionally larger; inside oolites the endolithic thalli sometimes disintegrate into groups of non-orieneted vesicles.

Remarks—Most researches consider these microfossils as counterpart of modern boring cyanobacterium *Hyella* Bornet and Flauhault (Zhang Y. & Golubic, 1987; Green *et al.*, 1988; Knoll *et al.*, 1989; Schopf, 1994; Lee Seong-Joo & Golubic, 1999; Sergeev, 2006).

Contents—E. campbelliae, E. dichotoma, E. elongata, E. endoatracta and *E. rectoclada* (Table-6).

Age—Meso-Neoproterozoic (Palaeoproterozoic?).

Eohyella campbelliae Zhang Y. and Golubic, 1987

Eohyella campbelliae Zhang Y. and Golubic, 1987, p. 11, Pl. I, Figs 1-8, Pl. II, Figs 1-6, Pl. III, Figs 1-6; Shukla *et al.*, 2004, fig. 2v.

Repository—BGPZD-9B-8201.

Stratum typicum—Early Mesoproterozoic, Dahongyu Formation, China.

Description—Dense clusters of vesicles forming pseudoparenchyamatous thalli from which uniseriate or multiseriate pseudofilaments project opposite to the growth of accretion of sediment/stromatolite laminae. Vesicles located at apical position of colonies are droplet-shaped, 22.0-6.7 x 11.2-3.9 μm in dimensions. Vesicles at the base of colonies are smaller, spherical, polyhedral, crescent and ellipsoidal, 18.2-4.0 x 2.6-1.9 μm in dimension.

Name of species	Diagnostic features	Size, μm	Paleoenvironmental setting	Repository and type locality	References
E. elongata Knoll *et al.*, 1989 Fig. 30B	Consist of small oriented parallel to substrate pseudofilaments and longer branched perpendicular to substrate	8.0-10.0 x up to 50.0	Inetrtidal, recorded in silicified oolites.	HUHPC -62302; Neoproterozoic, Backlundtoppen Fm., Spitsbergen.	Knoll *et al.*, 1989
E. endoatracta Green *et al.*, 1988 Fig. 30C	Uniseriate pseudofilaments radiating downwards from point of entry, lateral branching frequent.	4.0-19.0 x 7.5 - 42.0	Inetrtidal and subtidal oolitic shoals, recorded in silicified oolites.	HUHPC -62292; Neoproterozoic, Eleonore Bay Group, Bed 18, Greenland.	Green *et al.*, 1988
E. rectoclada Green *et al.*, 1988 Fig. 30D-D'	Uniseriate pseudofilaments, frequent branching by intercalary cell slippage	6.5-21.0 x 8.5 - 21.0	Inetrtidal and subtidal oolitic shoals, recorded in silicified oolites	HUHPC -62286; Neoproterozoic, Eleonore Bay Group, Bed 18, Greenland.	Green *et al.*, 1988

Table 6—Comparative characteristics of genus *Eohyella* species (Type Specimens).

Age and distribution—Mesoproterozoic, Dahongyu Formation, China; Neoproterozoic, the Deo Ka Tibba Formation, India.

Eohyella dichotoma Green, Knoll and Swett, 1988

(Pl. 3.1-6; Figs 30A-A')

Eohyella dichotoma Green *et al.*, 1988, p. 846, 848, Figs 8.5-8.10; Sergeev, 2002, p. 557, 559, Pl. I, Figs 1-4; Sergeev, 2006, p. 200-201, Pl. XXIII, Figs 1-4.

Repository—HUHPC-62281.

Stratum typicum—Neoproterozoic, Bed 18 of the Limestone-Dolomite "Series", Greenland.

Description—Isodiametrically elongated spheroidal, ellipsoidal and polyhedral single-walled vesicles forming pseudofilaments penetrating inside substrate, mainly oolites, leaving behind empty tubular holes. These pseudofilamentous colonies are uniseriate, dichotomous branching and frequent desintegarting into groups of vesicles inside oolites. Vesicles width are 8.0-15.0 μm (= diameter of empty tubular holes), length are 9.0-29.0 μm, pseudofilaments are up to 100-150 μm long. An opaque inclusion 1.0-3.0 μm in diameter may occur within vesicles. Vesicle wall is tranclucent, medium-grained, 0.5-1.0 μm thick.

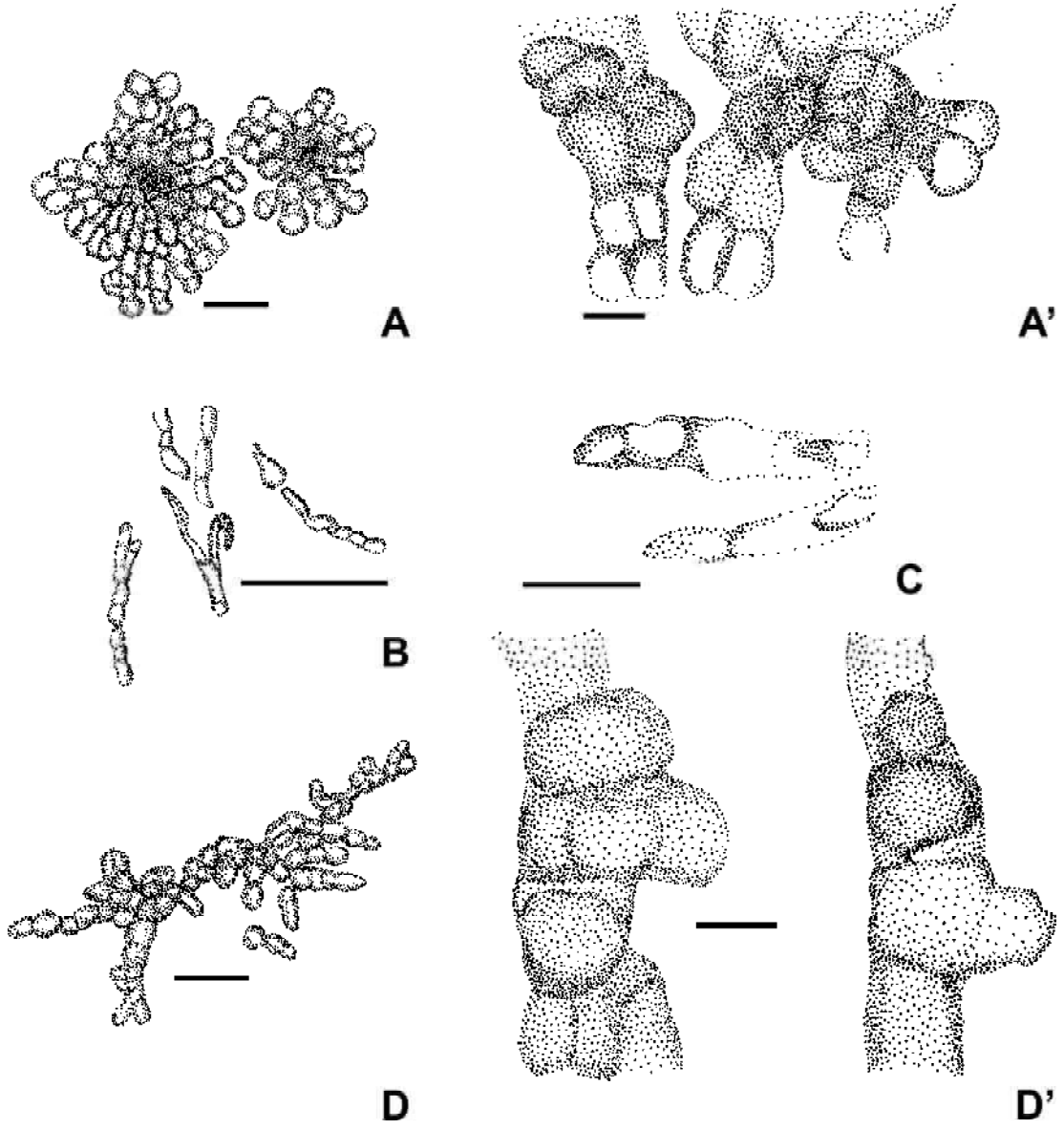


Fig. 30—Line diagrams of species of *Eohyella*. A, A'- *E. dichotoma* (Green *et al*., 1988); B- *E. elongata* (Knoll *et al*., 1989); C- *E. endoatracta* (Green *et al*., 1988); D, D'- *E. rectoclada* (Green *et al*., 1988). Scale bar A = 40 μm, A' = 10 μm, B = 100 μm, C = 20 μm, D = 60 μm, D' = 10 μm.

Age and distribution—Neoproterozoic, Tonian-Cryogenian: Limestone-Dolomite "Series", Greenland; Ediacaran: Yudoma Group, Siberia.

Family—PLEUROCAPSACEAE Geitler, 1925

Genus—PALAEOPLEUROCAPSA Knoll *et al.*, 1975

Palaeopleurocapsa Knoll *et al.*, 1975, p. 2489, 2491.

Type species—Palaeopleurocapsa wopfneri Knoll, Barghoorn and Golubic, 1975.

Diagnosis—Spherical, ellipsoidal and polyhedral vesicles arranged into parallel rows and form pseudofilamentous colonies. Groups of tightly packed spheroids, often ensheathed by common envelopes, either occur inside pseudofilamentous colonies or aggregated into pseudoparenchymatous, crustose thalli. Parallel rows of vesicles are often dichotomously branched, originating from longitudinal cleavage of vesicles and branches remain parallel until turned inward toward the common pseudofilament axis from their ends.

Remarks—Genus *Palaeopleurocapsa* was established as the fossil counterpart of modern cyanobacteria genus *Pleurocapsa* (Knoll *et al.*, 1975). A comparison of the type species *Palaeopleurocapsa wopfneri* with extant genus *Pleurocapsa* shows that many of the characteristics, i.e. filament-like arrangement of spheroidal vesicles resulting from cell division in one plane, pseudoparenchymatous packing, multiple sheaths and co-existence of subpopulation, are common among them though they occur over a period of 1.6 billion years. Because of their large size both *Palaeopleurocapsa wopfneri* and modern *Pleurocapsa* are visible to naked eyes.

Earlier 2 more species of *Palaeopleurocapsa* were described based on pseudofilamentous shape of their colonies and vesicles arrangement into rows or packs surrounded by common envelopes: *P. Kelleri* and *P. kamaelgensis* (Sergeev & Krylov, 1986; Krylov & Sergeev, 1986). However, after careful reinvestigation it turned out that these pseudofilamentous aggregates are purely diagenetic features and probably have been formed as a result of *post-mortem* pressure by sediment on the originally loose colonies of *Gloeodiniopsis lamellosa*- see Figs 8 and 9 (Sergeev, 1992a, 2006).

Contents—*P. wopfneri, P. Knollii , P. oncobyrsoides, P. fusiforma* and *P. reniforma* (Table-7).

Age—Meso-Neoproterozoic (and possibly Palaeoproterozoic as well).

Palaeopleurocapsa fusiforma Ogurtsova and Sergeev, 1987

(Pl. 13.1, 2)

Palaeopleurocapsa fusiforma Ogurtsova and Sergeev, 1987, p. 113-114, Pl. X, Figs 1a, 1б; Yankauskas, 1989, p. 97, Pl. XXIV, fig. 5; Krylov *et al.*, 1989, Pl. I, Figs 10a, 10б; Sergeev, 1989, pl. I, fig. 5; Sergeev, 1992a, p. 83-84, Pl. XXI, Figs 1a, 1б; Schopf, 1992b, Pl. 50, Figs B_1, B_2; Sergeev, 2006, Pl. XLVII, Figs 1a, 1б; Sergeev and Schopf, 2010, p. 391, Figs 10.1, 10.1a.

Repository—GINPC-4681, Specimen No. 164.

Stratum typicum—Neoproterozoic, Chichkan Formation, South Kazakhstan.

Description—Spheroidal, ellipsoidal or polyhedral envelope-enclosed vesicles tightly packed in two more or less parallel rows, the cell packets of which are typically enclosed within spheroidal envelopes, forming spindle-shaped pseudofilamentous colonies. The diameter of vesicles, defined by fine-to medium-grained single-layered walls 0.5 to 1.0 μm thick, ranges from 8.0 to 16.0 mm; envelope-enclosed vesicle packets are 35 to 40 μm in diameter whereas the colonies range up to 50 μm broad and 130 μm long. Individual vesicles commonly contain an opaque inclusion 1.0 to 1.5 μm in diameter.

Remarks—Palaeopleurocapsa fusiforma is distinguished from the other *Palaeopleurocapsa* species by its spindle-shaped colonies and the characteristic sizes of its vesicles and vesicle packets.

Age and distribution—Neoproterozoic, Chichkan Formation, South Kazakhstan.

Name of species	Diagnostic features	Size, μm	Palaeoenvironmental setting	Repository and type locality	References
P. Knollii Golovenok & Belova, 1990	Spherical, ellipsoidal and polyhedral vesicles arranged into parallel rows and form crustose thalli.	7.0-23.0	Intertidal and subtidal setting, recorded in cherts.	VSEGEI – 415-a-2-1; Neoproterozoic, Nalagar Fm., Kharaulakh Uplift, Siberia	Golovenok & Belova, 1990
P. oncobyrsoides Golovenok & Belova, 1990	Spherical and ellipsoidal vesicles forming spindle-like colonies from dichotomously branching pseudofilaments	5.0-17.0	Intertidal and subtidal setting, recorded in cherts.	VSEGEI – 357-B-1; Neoproterozoic, Chernaya Rechka Fm, Igarskoe Uplift, Siberia.	Golovenok & Belova, 1990

Table 7—Comparative characteristics of genus *Palaeopleurocapsa* species (Type Specimens).

Palaeopleurocapsa reniforma Ogurtsova and Sergeev, 1987

(Pl. 13.3, 4)

Palaeopleurocapsa reniforma Ogurtsova and Sergeev, 1987, p. 114, Pl. X, fig. 3; Yankauskas, 1989, p. 98, Pl. XXIV, fig. 8; Sergeev, 1992a, p. 84-85, Pl. XXI, Figs 2a, 2б; Schopf, 1992b, Pl. 50, Figs C_1, C_2; Sergeev, 2006, Pl. XLVII, Figs 2a, 2б; Sergeev and Schopf, 2010, p. 391, fig. 10.2.

Repository—GINPC-4681, Specimen No. 165.

Stratum typicum—Neoproterozoic, Chichkan Formation, South Kazakhstan.

Description—Spheroidal or ellipsoidal vesicles tightly packed in subparallel rows that comprise spheroidal, ellipsoidal, or most commonly kidney-shaped colonies. In smaller colonies, vesicles having significantly different diameters are commonly enclosed within a single spheroidal envelope. The diameter of vesicles, defined by fine-to medium-grained walls 0.5 to 1.0 µm thick, ranges from 8.0 to 21.0 µm; envelope-enclosed vesicle packets are 30 to 40 µm in diameter whereas the kidney-shaped colonies range up to 70 µm broad and 95 µm long. Some individual vesicles contain an opaque inclusion 1.0 to 1.5 µm in diameter.

Remarks—Palaeopleurocapsa reniforma is distinguished by its kidney-shaped colonies and the characteristic sizes of its cells and cell packets.

Age and distribution—Neoproterozoic, Chichkan Formation, South Kazakhstan.

Palaeopleurocapsa wopfneri Knoll, Barghoorn and Golubic, 1975.

(Fig. 31)

Palaeopleurocapsa wopfneri Knoll *et al.*, 1975, p. 2491, Figs 1a, 2a-2f; Nautiyal, 1983, p. 177, 178, Pl. 1, Figs 28-31; Nautiyal, 1984, p. 33, Pl. 1, Figs 33-35; Kumar and Venkatachala, 1998, p. 56, Figs 4a-4c; Buick and Knoll, 1999, p. 756, 760, Figs 8.1-8.4.

Repository—HUHPC-60218.

Stratum typicum—Mesoproterozoic, Skillogalee Dolomite Formation, Australia.

Description—Spherical, ellipsoidal and polyhedral vesicles arranged into parallel rows and form pseudofilamentous colonies often originating from longitudinal cleavage of vesicles and branches remain parallel until turned inwards. Groups of tightly packed spheroids, often ensheathed by common envelopes, either occur inside pseudofilamentous colonies or aggregated into pseudoparenchymatous, crustose thalli. The diameters of vesicles range from 4-26 µm, with an average of 15 µm. Filamentous sheaths are 72 µm long and 26 µm wide.

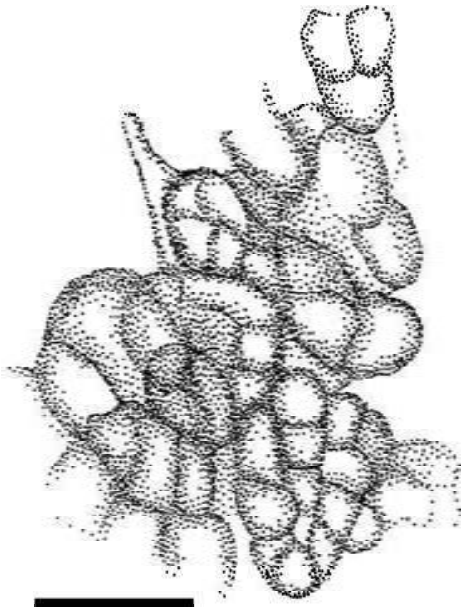


Fig. 31—Line diagram of *Palaeopleurocapsa wopfneri* (Knoll *et al.*, 1975). Scale bar = 50 µm.

Age and distribution—Mesoproterozoic: Skillogalee Dolomite Formation and Bangemall Group, Australia; Kajrahat and Vaishanodevi Limestone Formations, India.

Genus—SCISSILISPHAERA Knoll and Calder, 1983

Scissilisphaera Knoll and Calder, 1983, p. 482.

Type species—Scissilisphaera regularis Knoll and Calder, 1983.

Diagnosis—Single-or multilamellated spheroidal vesicles commonly in colonies of several hundred discrete individuals. Groups of small vesicles numbering 2, 4, 8 and up to 64 often are surrounded by a common envelope.

Remarks—Knoll and Calder (1983) and Green *et al.* (1989) have compared this genus to modern pleurocapcalean cyanobacteria genera *Chroococcidiopsis*, *Stanieria* and *Xenococcus*. This analogy is based on the presence of packets of smaller vesicles interpreted as baeocytes resulting from miltiple fission of larger solitary unicells in life cycle of the living forms. Within the cyanobacteria, baeocyte formation is diagnostic for the order Pleurocapsales (Castenholz & Waterbury, 1989); however, small simple cysts are formed by a diverse assortment of protists, e.g. green alga *Dunaliella* found today in tidal flat environments (Green *et al.*, 1989).

Contents—S. bistratosa, *S. gradata* and *S. regularis.*

Age—Neoproterozoic.

Scissilisphaera bistratosa (Ogurtsova and Sergeev, 1987) comb. Sergeev, 1992 (in Sergeev, 1992a)

(Pl. 13.5-7)

Scissilisphaera bistratosa (Ogurtsova and Sergeev, 1987), Sergeev, 1992a, p. 85, Pl. XXI, Figs 6, 7а, 7б, Pl. XXII, Figs 6а, 6б; Sergeev, 2006, Pl. XLVII, Figs 4, 5, 7а, 7б, 9а, 9б; Sergeev and Schopf, 2010, p. 391, 392, Figs 10.3, 10.4a, 10.4b; Schopf *et al.*, 2010, Figs 4.14-4.18, 5.10-5.13.

Tetraphycus bistratosus Ogurtsova and Sergeev, 1987, p. 114-115, Pl. X, Figs 2а, 2б; Yankauskas, 1989, p. 98-99, Pl. XXIV, fig. 10; Schopf, 1992b, Pl. 50, Figs A_1, A_2.

Repository—GINPC-4681, Specimen No. 170.

Stratum typicum—Neoproterozoic, Chichkan Formation, South Kazakhstan.

Description—Colonies composed of four to several single-to double-layered spheroidal to cuboidal envelope-enclosed vesicle packets, all situated on a single plane or stacked in two parallel planes, with each packet enclosing 2, 4, 8 or 16 tightly adpressed cells. Vesicle diameters range from 11.0 to 20.0 μm, their envelope-enclosed packets ranging up to 70 μm across. Colonies are spherical, subspherical or cuboidal, ranging from 50 x 60 μm to 80 x 90 μm in size. Vesicle walls are translucent, fine-grained, ~ 0.5 μm thick; enclosing envelopes, not discernible in all specimens, are translucent and fine grained, ~1 μm thick.

Age and distribution—Neoproterozoic, Chichkan Formation, South Kazakhstan.

Scissilisphaera gradata Green *et al.*, 1989

(Pl. 13.8-10)

Scissilisphaera gradata Green *et al.*, 1989, p. 581-583, Figs 8A-8F, 9; Sergeev, 2001, p. 445, Figs 10.4-10.7; Sergeev, 2006, p. 231-232, Pl. XXI, Figs 4-7.

"Type 4 microfossils": Sergeev, 1984, p. 436-437, fig. 2з.

"Type 7 microfossils" (partim): Sergeev, 1984, p. 438, Figs 2о, 2р.

Repository—HUHPC-61878-1.

Stratum typicum—Neoproterozoic, Limestone-Dolomite 'Series', central East Greenland.

Diagnosis—Single and double-walled spheroidal vesicles occasionally solitary, but commonly in colonies of a few to several hundred discrete individuals occur along a single laminae. The diameter of vesicle clusters in discrete groups varies from 4 to 60 μm, sometimes a group of small spheroids is surrounded by a common envelope forming *Gloeocapsa*-like colonies. The diameter of smaller, apparently daughter vesicles varies from 4 to 30 μm, larger vesicles are 32-60 μm with apparent break in the size distribution. Inner envelope is transparent, fine-grained, about 1 μm thick; outer envelope, if present, also transparent, fine grained, less than 1 μm thick; large vesicles sometimes have robust walls about 1 μm.

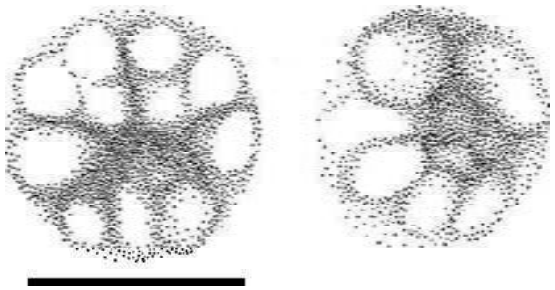


Fig. 32—Line diagram of *Scissilisphaera regularis* (Knoll & Calder, 1983). Scale bar = 25 μm.

Remarks—*S. gradata* differs from *S. regularis* Knoll and Calder, 1983 by its three distinctive morphological forms and by occurrence along a single lamina as separated spheroids rather than in cubical colonies.

Age and distribution—Neoproterozoic: Eleonora Bay Group, central East Greenland; Shorikha Formation, Turukhansk Uplift, Siberia.

Scissilisphaera regularis Knoll and Calder, 1983.

(Fig. 32)

Scissilisphaera regularis Knoll and Calder, 1983, p. 482-484, 486, 488, Pl. 59, Figs 1-12.

Repository—HUHPC-60643.

Stratum typicum—Neoproterozoic, Ryssö Formation, Spitsbergen.

Description—Single to multilamillated spheroidal vesicles occasionally solitary, but commonly in colonies of a few to several hundred discrete individuals sometimes occuring along a single laminae. Vesicles larger than 25 μm are often subdivided into 2, 4 or 8 tightly packed vesicles. Diameter of smaller inner vesicles varies from 11.0 to 45.0 μm, of larger surrounding vesicles up to 70 μm. Groups of small vesicles numbering 2, 4, and 8 and up to 64 occasionally are surrounded by a common envelope forming *Gloeocapsa*-like colonies. Colonies containg more than 64 vesicles, tend to be irregularly cuboidal packets. Inner vesicle wall layers are transparent, fine-grained, about 0.5 μm thick; outer layers, if present, also transparent, fine grained, less than 1 μm thick; larger vesicles sometimes have robust wall about 1 μm thick.

Age and distribution—Neoproterozoic, Ryssö Formation, Spitsbergen.

Family—XENOCOCCACEAE Ercegovic, 1932

Genus—SYNODOPHYCUS Knoll, 1982, emend. Knoll *et al.*, 1991

Synodophycus Knoll, 1982, p. 786; Knoll *et al.*, 1991, p. 553-554.

Type species—*Synodophycus euthemos* Knoll, 1982.

Diagnosis—Almost equidimensional vesicles packed together in irregular ellipsoidal colony formed of 16 to 64 individual vesicles. Colonies may be enclosed within a thin envelope, but internal membrane-enclosed vesicle packets are rare or absent. Within colonies, one or a small number of individual vesicles may be enlarged and contain two or more smaller vesicles.

Remarks—This genus, after emended description, is considered as a member of pleurocapsalean cyanobacteria, family Xenococcaceae (Knoll *et al.*, 1991). Although, it is not a widely reported genus, however, upon restudy many forms described under various generic names may turn out to be colonies of genus *Synodophycus.*

Contents—Monospecific genus.

Age—Neoproterozoic.

Synodophycus euthemos Knoll, 1982, emend. Knoll *et al.*, 1991

(Fig. 33)

Synodophycus euthemos Knoll, 1982, p. 786-787, Pl. 4, Figs 8-10; Knoll *et al.*, 1991, p. 554, Figs 15.1-15.9.

Repository—HUHPC-60493.

Stratum typicum—Neoproterozoic, Draken Conglomerate Formation, Spitsbergen.

Description—Aggregates of equidimensional vesicles 4.0-7.0 μm in diameter packed together in irregular ellipsoidal colony 20-40 μm long and 15-30 μm wide formed of 16 to 64 individual vesicles. Colonies may be enclosed within a thin envelope. Within colonies, one or a small number of individual vesicles may be enlarged and contain two or more smaller vesicles. Sometime individual vesicles in colony are enlarged to 11.0-15.0 μm and containing 4-8 small (1-2 μm) vesicles.

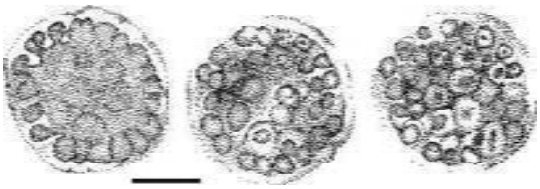


Fig. 33—Line diagram of *Synodophycus euthemos* (Knoll, 1982). Scale bar = 10 μm.

Age and distribution—Neoproterozoic, Draken Conglomerate Formation, Spitsbergen.

Class—HORMOGONEAE Thuret, 1875

Order—OSCILLATORIALES Elenkin, 1949

Family—OSCILLATORIACEAE (S.F. Gray) Kirchner, 1900

Genus—CALYPTOTHRIX Schopf, 1968

Calyptothrix Schopf, 1968, p. 667, 669.

Type species—*Calyptothrix annulata* Schopf, 1968.

Diagnosis—Unbranched filamentous empty single-layered sheaths with the prominent transverse annular ribs.

Remarks—1. Genus *Calyptothrix* was established (Schopf, 1968) for the markedly annulated trichomes with prominent ring-like ridges and sharply truncated apices. However, re-examination of the *C. annulata* type specimens by one of us (VNS) indicates that these are empty sheaths with annulated transverse casts rather than trichomes as originally interpreted. Therefore, we consider that this genus can be retained for the empty, probably cyanobacterial sheaths with ring-like casts of trichome cells on their surface, in contrast to smooth-walled *Siphonophycus*.

2. Subsequently, some other empty sheaths probably of cyanobacterial origin with annulated ribbons were described from many Proterozoic organic-walled microbiotas, e.g. *Tortunema* Hermann, 1976 (in Timofeev *et al.*, 1976), *Rugosoopsis* Timofeev and Hermann, 1979, *Plicatidium* Yankauskas, 1980, etc. Genus *Tortunema* probably should be considered as a junior synonym of genus *Calyptothrix*, but other genera are rather remains of eukaryotic microorganisms.

Contents—*C. alternata, C. annulata, C. geminata*, *C. perfecta* and *C. obsoletus* (Table-8).

Age—Neoproterozoic.

Calyptothrix annulata Schopf, 1968

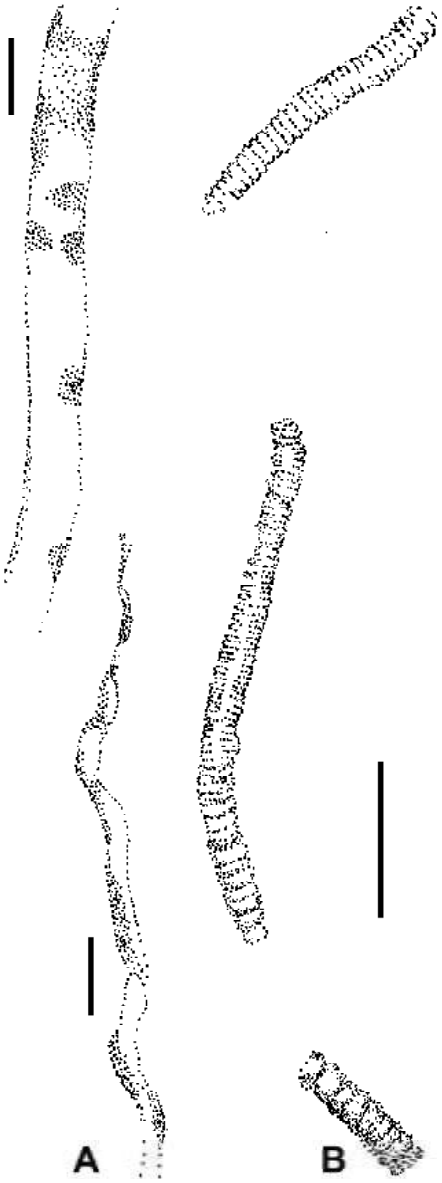
(Pl. 15. 7, 8; Fig. 34B)

Calyptothrix annulata Schopf, 1968, p. 669, Pl. 78, fig. 5-8.

Calyptothrix sp.: Petrov *et al.*, 1995, Pl. I, fig. 8; Sergeev *et al.*, 1997, p. 228, fig. 18J; Sergeev, 2006, p. 208, Pl. XVII, fig. 5.

Repository—HUHPC-58454.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.



Description—Unbranched filamentous empty single-layered sheaths with the prominent transverse annular ribs. Surface texture is coarse-grained, walls are medium-grained, distinct, about 0.5 μm thick. Width of the sheaths is 2.0-2.5 μm, distance between the adjacent ribs varies from 1.0 to 3.5 μm.

Remarks—Four species of genus *Calyptothrix* were described from organic-walled microfossils of Siberia in shales: *C. alternata* Yankauskas, 1980 and *C. geminata* Yankauskas, 1980, *C. perfecta* Veis, 1984 and *C. obsoletus* Mikhailova, 1986 (see Yankauskas, 1989) (Table-8). All these species were described as trichomes, but they all look like the empty sheaths with the prominent ring-like ridges.

Age and distribution—Meso-Neoproterozoic, Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia; Neoproterozoic, Bitter Springs Formation, Australia.

Genus—CEPHALOPHYTARION Schopf, 1968

Cephalophytarion Schopf, 1968, p. 669.

Type species—Cephalophytarion grande Schopf, 1968.

Diagnosis—Trichomes multicellular sheathless composed of cylindrical or discoidal cells slightly constricted at septa gradually tapering toward apices and terminating by enlarged cells.

Remarks—This genus was established by Schopf (1968) and includes trichomes tapering toward apices and often terminating by calyptra-like cells. Later, it turned out the tapering feature toward apices may be not the original, but resulted from *post-mortem* shrinkage of dead filaments (Golubic & Barghoorn, 1977; Gerasimenko & Krylov, 1983; Sergeev, 1992a; Knoll & Golubic, 1992, and others). Selective shrinkage in some of the trichome cells may lead to appear the adjacent

Fig. 34—Line diagram of *Animikiea septata* (Barhoorn & Tyler, 1965), A; and *Calyptothrix annulata* (Schopf, 1968), B. Scale bar = 10 μm.

Name of species	Diagnostic features	Sheaths width, μm	Palaeoenvironmental setting	Repository and type locality	References
C. alternata Yankauskas, 1980	Sheaths with prominent ring-like structures arranged in pairs.	5.0–7.0	Subtidal, middle part of open shelf, recorded from shales.	LitNIGRIPC – 16-4-3526/18; Neoproterozoic, Zilmerdack Fm., South Ural, Russia.	Yankauskas, 1980
C. geminata Yankauskas, 1980	Sheaths with ring-like structures tending to be arranged in pairs.	13.0–15.0	Subtidal, middle part of open shelf, recorded from shales.	LitNIGRIPC – 16-4-3526/6; Neoproterozoic, Zilmerdack Fm., South Ural, Russia.	Yankauskas, 1980
C. perfecta Veis, 1984	Sheaths with prominent ring-like structures.	6.0–7.5	Subtidal, middle part of open shelf, recorded from shales	GINPC – 2678/422; Neoproterozoic, Miroedikha Fm., Siberia, Russia.	Veis, 1984
C. obsoletus Mikhailova, 1986	Sheaths with prominent ring-like structures.	4.0–5.5	Subtidal, recorded from shales	IGGP – 882/2; Neoproterozoic, Dashka Fm., Siberia, Russia.	Mikhailova, 1986

Table 8—Comparative characteristics of genus *Calyptothrix* species (Type Specimens).

cells relatively enlarged. Moreover, some species of modern genus *Oscillatoria* have tapering feature towards apices in trichomes that provoke to include some *Cephalophytarion* species into *Oscillatoriopsis* (Butterfield *et al.*, 1994; Sergeev *et al.*, 1995). However, considering that this taxon has been widely used and tapering observed in some of trichomes are definitely of primarily a biological feature, we prefer to keep this genus as an independent. It should be noticed that fossil cyanobacteria genera are not exactly correspond to living forms; and genus *Cephalophytarion* as presently understood includes some species that might be counterparts of genus *Oscillatoria* species. But in some cases tapering feature in trichomes are definitely a secondary phenomenon, especially when terminal hair-like structures are observed (Pl. 16.5-8).

Phenomenon of *post-mortem* shrinkage of terminal parts of trichome stands true as well for another genus *Caudiculophycus* Schopf, 1968 and its type species *C. rivularioides* Schopf, 1968 demonstrat hair-like terminal feature. We, in general, consider that at least type species of this genus encompasses primarily tapering trichomes of oscillatoriacen, not the rivulariacean cyanobacteria and for this reason probably genus *Caudiculophycus* should be merged to genus *Cephalophytarion.* In contrast, Nagovitsin (2000) has described another species *Caudiculophycus tipicus* Nagovitsin, 2000 from the Neoproterozoic Seryi Klyuch Formation which has some trichomes tapering toward apices, a character primarily of rivulariacean affinities. The problem of taxonomic relationship of genera *Caudiculophycus* and *Cephalophytarion* seems to be complicated and should wait until formal revision of the Bitter Springs microbiota.

Contents—*C. constrictum, C. delicatulum, C. grande, C. laticellulosum, C. majesticum, C. minutum,* and *C. variabile* (Table-9).

Age—Meso-Neoproterozic (possibly as well as Palaeoproterozoic).

Cephalophytarion grande Schopf, 1968

(Fig. 35A)

Cephalophytarion grande Schopf, 1968, p. 669, Pl. 78, Figs 1-4; Schopf, 1972, fig. 2.12; Schopf, 1992b, Pl. 32, Figs A, B.

Repository—HUHPC-58450.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Unbranched sheathless trichomes composed of approximately isodiametrical cells slightly constricted at septa and gradually tapering toward apices. The medial cell width is 2.2-4.0 μm, medial cell length is 1.8-2.8 μm, width/length about 1.5; terminal cells width 1.3-2.2 μm, maximum length of the trichomes up to 90 μm (incomplete specimen preserved).

Name of species	Diagnostic features	Cells width and length, μm	Palaeoenvironmental setting	Repository and type locality	References
C. constrictum Schopf & Blacic, 1971 Fig. 35B	Trichomes composed of cylindrical to barrel shaped medial cells.	4.7-5.3 x 2.0-4.0	Peritidal flat and pluvial lakes, recorded from cherts in dolomites.	HUHPC – 58560; Neoproterozoic, Bitter Springs Fm., Australia.	Schopf & Blacic, 1971
C. delicatulum Schopf & Blacic, 1971 Fig. 35C	Trichomes composed of cylindrical medial cells and dilated terminal cells.	2.7-3.2 x 1.6-2.7	Peritidal flat and pluvial lakes, recorded from cherts in dolomites.	HUHPC – 58594; Neoproterozoic, Bitter Springs Fm., Australia.	Schopf & Blacic, 1971
C. laticellulosum Schopf & Blacic, 1971 Fig. 35D	Trichomes composed of cylindrical medial cells and globose terminal cells.	4.7-6.3 x 2.2-4.3	Peritidal flat and pluvial lakes, recorded from cherts in dolomites.	HUHPC – 58571; Neoproterozoic, Bitter Springs Fm., Australia.	Schopf & Blacic, 1971
C. minutum Schopf, 1968 Fig. 35E	Trichomes composed of cylindrical, quadrate to elongated medial cells.	0.9-1.4 x 1.3-2.1	Peritidal flat and pluvial lakes, recorded from cherts in dolomites.	HUHPC – 58457, Neoproterozoic, Bitter Springs Fm., Australia.	Schopf, 1968
C. variabile Schopf & Blacic, 1971 Fig. 35F	Trichomes composed of cylindrical to cask-shaped medial cells.	2.7-4.7 x 2.0-3.0	Peritidal flat and pluvial lakes, recorded from cherts in dolomites.	HUHPC – 58583, Neoproterozoic, Bitter Springs Fm., Australia.	Schopf & Blacic, 1971
C. turukhanicum Veis, 1984	Trichomes (sheaths?) composed of cylindrical to ellipsoidal medial cells.	10.0-12.0 x 1.6-2.4	Open shelf environments, recorded from shales.	GINPC – 2678/421, Neoproterozoic, Miroedikha Fm., Siberia.	Veis, 1984

Table 9—Comparative characteristics of genus *Cephalophytarion* species (Type Specimens).

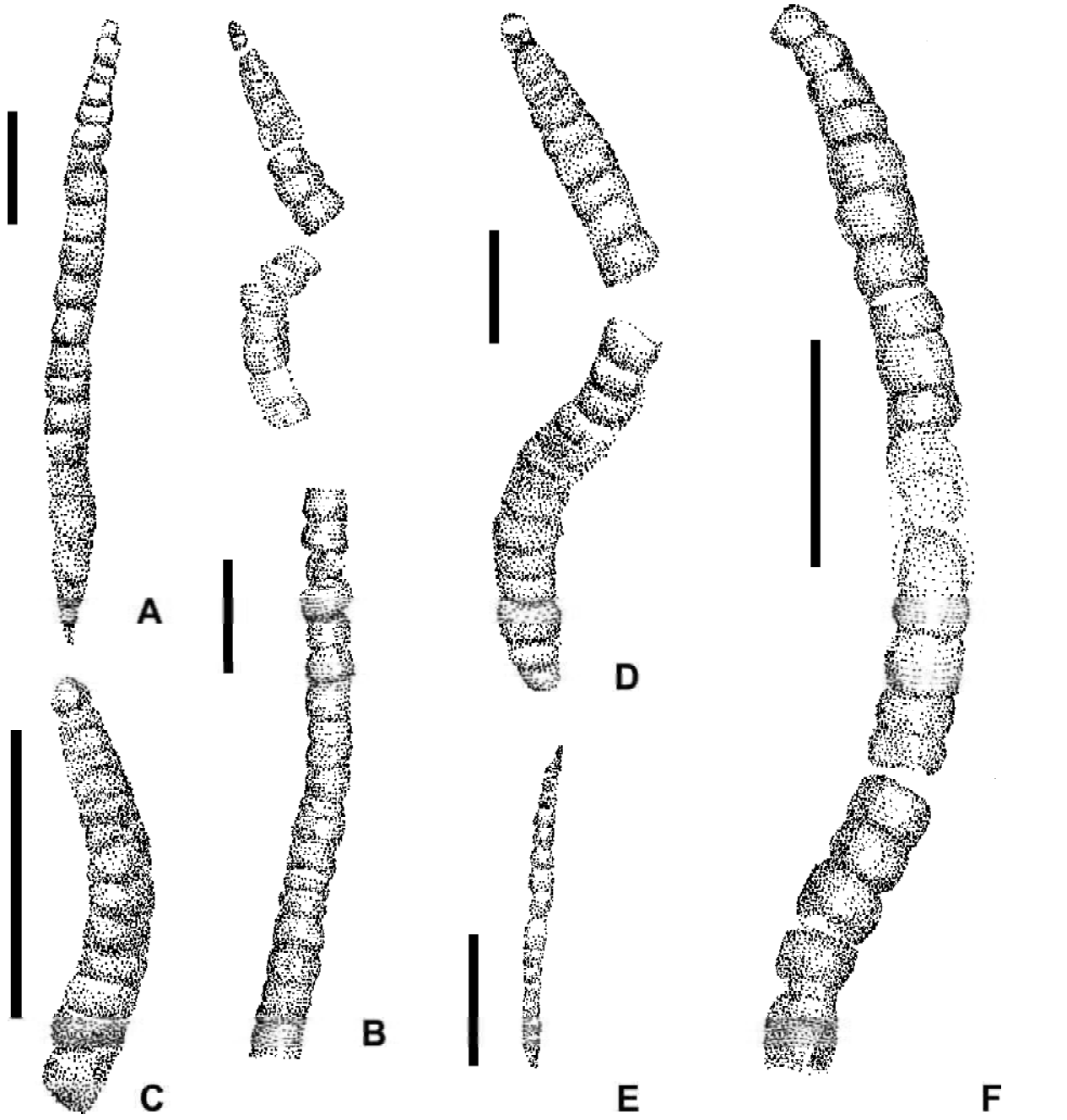


Fig. 35—Line diagrams of species of *Cephalophytarion*. A- *C. grande* (Schopf, 1968); B- *C. constrictum* (Schopf & Blacic, 1971); C- *C. delicatulum* (Schopf & Blacic, 1971); D- *C. laticellulosum* (Schopf & Blacic, 1971); E- *C. minutum* (Schopf, 1968); F- *C. variabile* (Schopf & Blacic, 1971). Scale bar = 10 μm.

Remarks—N. Butterfield in Butterfield *et al.* (1994), has included *C. grande* into *Oscillatoriopsis obtusa* on the basis of identical diameter. But we prefer to keep this species separately considering tapering as its original feature. However, the "neck" and "calyptra"-like cells at the end in the *C. grande* type specimen are rather *post-mortem* degradational features.

Some other species were described under generic name *Cephalophytarion*, e.g. *C. piliformis* Mikhailova, 1986 and *C. turukhanicum* Veis, 1984. Butterfield in Butterfield *et al.* (1994) has included these species into *Oscillatoriopsis obtusa*, but at least *C. turukhanicum* possibly is not a trichome and just a sheath with cast of trichome cells and rather to be transferred to genus *Calyptothrix*. On the other hand, *C. piliformis* looks like the *Oscillatoriopsis* trichome with the secondary formed terminal hair. We prefere not to follow Butterfiled's revision to include other described species of genus *Cephalophytarion*

PLATE 12

Pleurocapsalean stalked cyanobacterium genus *Polybessurus* Fairchild ex Green, *et al*., 1987 - *P. bipartitus* Fairchild ex Green, *et al*., 1987.

1-5. Sample No 4688-22: 1 —Slide No 421, p. 24, EFL J-50-4, GINPC No 766; 2 —Slide No 421, p. 11, GINPC No 767; 3 —Slide No 899, p. 4, GINPC No 768; 4 —Slide No 433, p. 9, GINPC No 78, 5 —Slide No 421-85, p. 36, GINPC No 798.
6, 7. Sample No 4694-38: 6 —Slide No 531, p. 1, GINPC No 554; 7 —Slide No 518, p. 48, GINPC No 1101.

Specimens GINPC No 78, 766, 767, 798 and 899 (figs 1-5) are from the Avzyan Formation, and specimens GINPC No 554 and 1101 (figs 6 and 7) are from the Sukhaya Tunguska Formation.

PLATE 13

Pleurocapsalean cyanobacteria genera *Palaeopleurocapsa* Knoll *et al*., 1975 and *Scissilisphaera* Knoll and Calder, 1983.

1, 2 (square in 1, the part of the specimen situated at a lower depth). *Palaeopleurocapsa fusiforma* Ogurtsova and Sergeev, 1987, Sample No 4681-64, Slide No 315, p. 3, EFL E-38-0, GINPC No 164 (Holotype).
3, 4 (two fragments of the same colony, arrow in 4 points to the specimen shown in 3). *Palaeopleurocapsa reniforma* Ogurtsova and Sergeev, 1987, Sample No 4681-64, Slide No 294, p. 1, EFL E-33-3, GINPC No 165 (Holotype).
5-7. *Scissilisphaera bistratosa* (Ogurtsova and Sergeev, 1987), comb. Sergeev, 1992, Sample No 4681-54: 5 —Slide No 975, EFL T-30-1, p. 44, GINPC No 1001; 6, 7 —Slide No 288, p. 8, GINPC No 170 (holotype, shown at two different focal depths).
8-10. *Scissilisphaera gradata* Green *et al*., 1989, Sample No 4694-509: 8, 9 —Slide No 245; 8 —p. 11', GINPC No 631; 9 —p. 11, GINPC No 633; 10 —Slide No 241, p. 9, GINPC No 632.

Specimens GINPC No 164, 165, 170 and 1001 (figs 1-7) are from the Chichkan Formation and specimens GINPC No 631 - 633 (figs 8-10) are from the Shorikha Formation.

PLATE 14

Problematic cyanobacteria genera *Gunflintia* Barghoorn, 1965, *Animikiea* Barghoorn, 1965 and *Chlorogloeaopsis* Maithy, 1975.

1. General view of *Gunflintia minuta* Barghoorn, 1965 mat with *Huroniospora* spheroids nesting between the filaments, Sample No 4313-1043, Slide No 745, p. 1, GINPC No 1112.
2. *Gunflintia minuta* Barghoorn, 1965, Sample 4313-1043, Slide No 745, p. 2, GINPC No 1114.
3. *Gunflintia grandis* Barghoorn, 1965, Sample 4313-1043, Slide No 745, p. 3, GINPC No 1115.
4-6. *Animikiea septata* Barghoorn, 1965, emend. Awramik and Barghoorn, 1977, Sample 4313-1043, Slide No 745: 4 —p. 4, GINPC No 1116; 5 —p. 5, GINPC No 1117; 6 —p. 6, GINPC No 1118.
7 (right square in 8), 8, 9 (left square in 8). *Chlorogloeaopsis contexta* (Hermann, 1976), Sample No 4694-47, Slide No 706, p. 11, GINPC No 618.

Specimens GINPC No 1112, 1114-1118 (figs 1-6) are from the Gunflint Formation and specimen GINPC No 618 (figs. 6-8) is from the Burovaya Formation.

PLATE 15

Filaments of hormogonian cyanobacteria genera *Eoschizothrix* Lee Seong-Joo and Golubic, 1998, *Eomicrocoleus* Horodyski and Donaldson, 1980, *Calyptothrix* Schopf, 1968 and *Uluksanella* Hofmann and Jackson, 1991.

1 (square in 3), 2 (square in 1), 3. *Eoschizothrix composita* Lee Seong-Joo and Golubic, 1998 in the mat formed by the sheaths of *Siphonophycus typicum* (Hermann, 1974), emend. Butterfield, 1994, Sample No 4698-41, Slide No 773, p. 3, GINPC No 671.
4-6, 9. *Eomicrocoleus crassus* Horodyski and Donaldson, 1980; 4 —Sample No 4688-403, Slide No 855, p. 6, GINPC No 724; 5 —Sample No 4688-22, Slide No 851, p. 21, GINPC No 754; 6 —Sample No 4694-38, Slide No 513, p. 1, GINPC No 785; 9 —Sample No 4694-38, Slide No 513, p. 47, GINPC No 545.
7, 8 (square in 7). *Calyptothrix annulata* Schopf, 1968, Sample No 4694-38, Slide No 518, p. 46, GINPC No 555.
10-12. *Uluksanella baffinensis* Hofmann and Jackson, 1991, Sample No 4694-38, Slide No 518, p. 45; 10 —GINPC No 777; 11 —GINPC No 778; 12 —GINPC No 1123.

Specimen GINPC No 671 (figs 1-3) is from the Yudoma Group, specimen GINPC No 724 (fig. 4) is from the Satka Formation, specimen GINPC No 754 (fig. 5) is from the Avzyan Formation, and specimens GINPC No 545, 555, 777, 778, 785 and 1123 (figs 6-12) are from the Sukhaya Tunguska Formation.

PLATE 16

Hormogonian cyanobacterial genera *Cyanonema* Schopf, 1968, *Oscillatoriopsis* Schopf, 1968 and *Veteronostocale* Schopf and Blacic 1971.

1, 2. *Cyanonema disjuncta* Ogurtsova and Sergeev, 1987, Sample No 4681-70, Slide No 323; 1 —p. 8', EFL J-26-4, GINPC No 1021; 2 —p. 8, J-26-0, GINPC No 156 (Holotype).
3. *Oscillatoriopsis media* Mendelson and Schopf, 1982, Sample No 4681-59, Slide No 291, p. 1, GINPC No 140.
4. *Oscillatoriopsis breviconvexa* Schopf and Blacic, 1971, Sample No 4681-20, Slide No 260, p. 36, EFL Q-23-3, GINPC No 1022.
5, 6, (lower square in 5 turned 60º anticlockwise), 7 (upper square in 5 turned 130º clockwise), 8 (lower square in 5 turned 145º anticlockwise). *Oscillatoriopsis obtusa* Schopf, 1968, Sample No 4681-20, Slide No 246, p. 34, EFL N-31-3, GINPC No 1024.
9, 10 (square in 9). *Veteronostocale copiosus* Ogurtsova and Sergeev, 1987, Sample No 4681-52, Slide No 325, p. 5, EFL K-37-2, GINPC No 157 (Holotype).

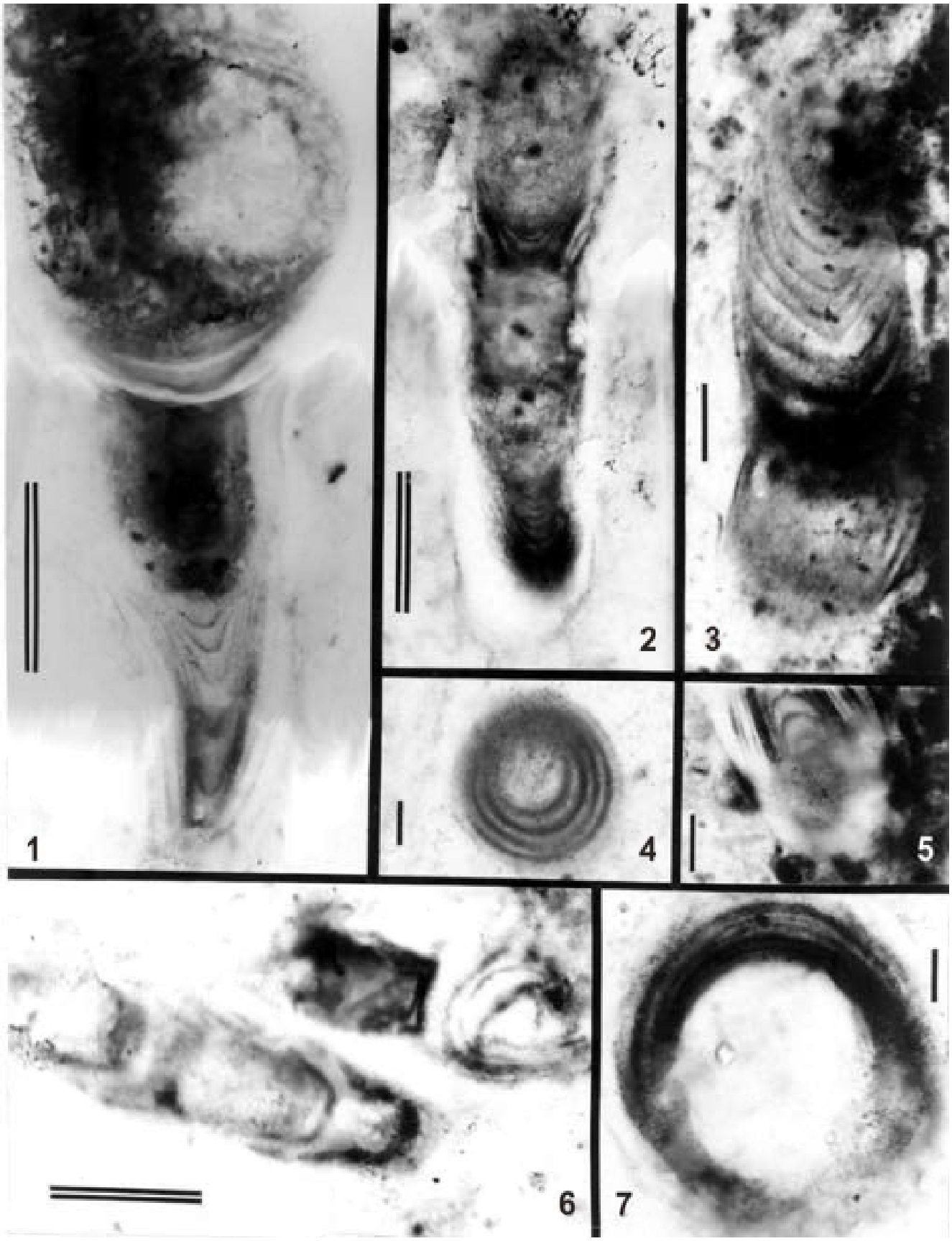


PLATE 12

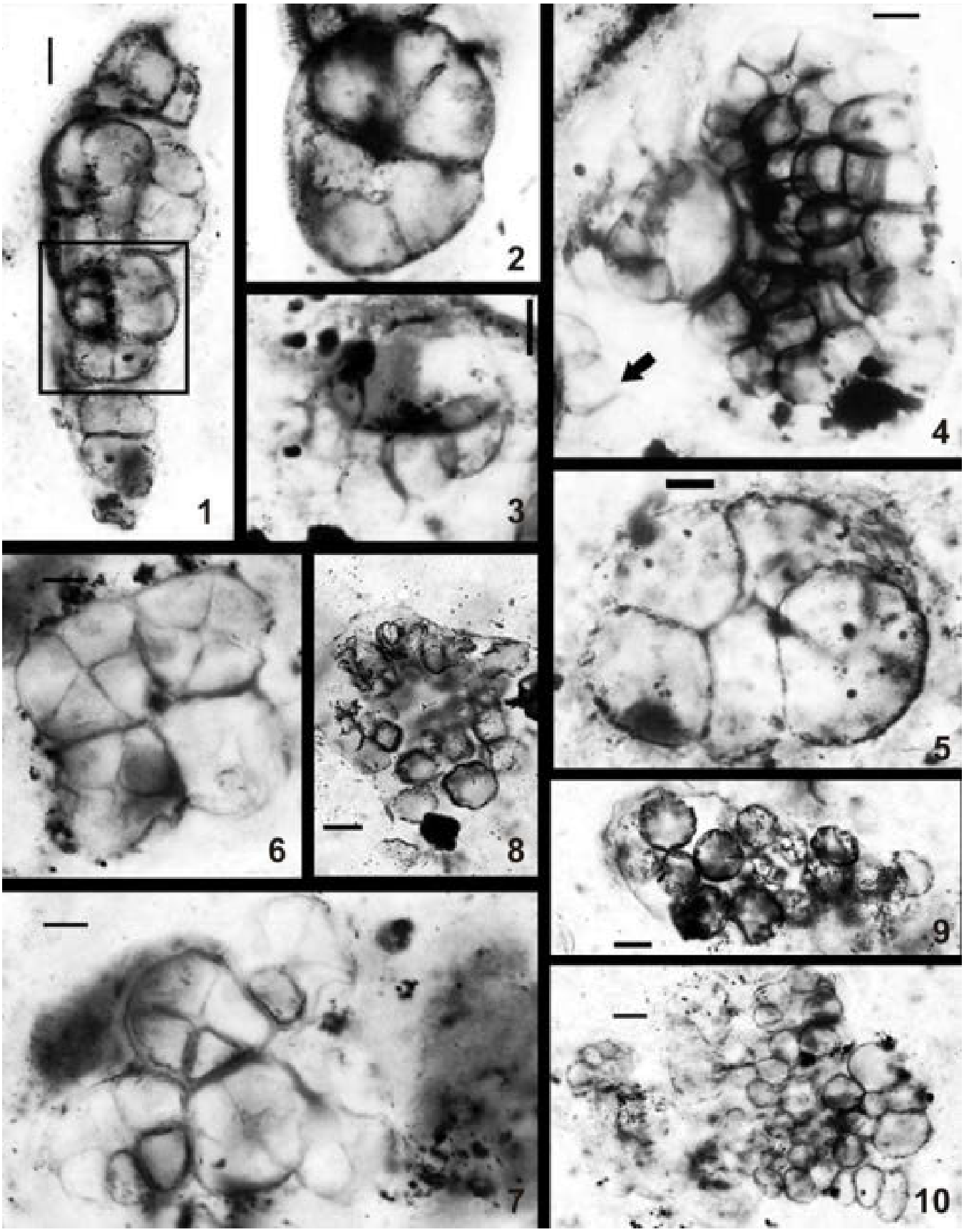


PLATE 13

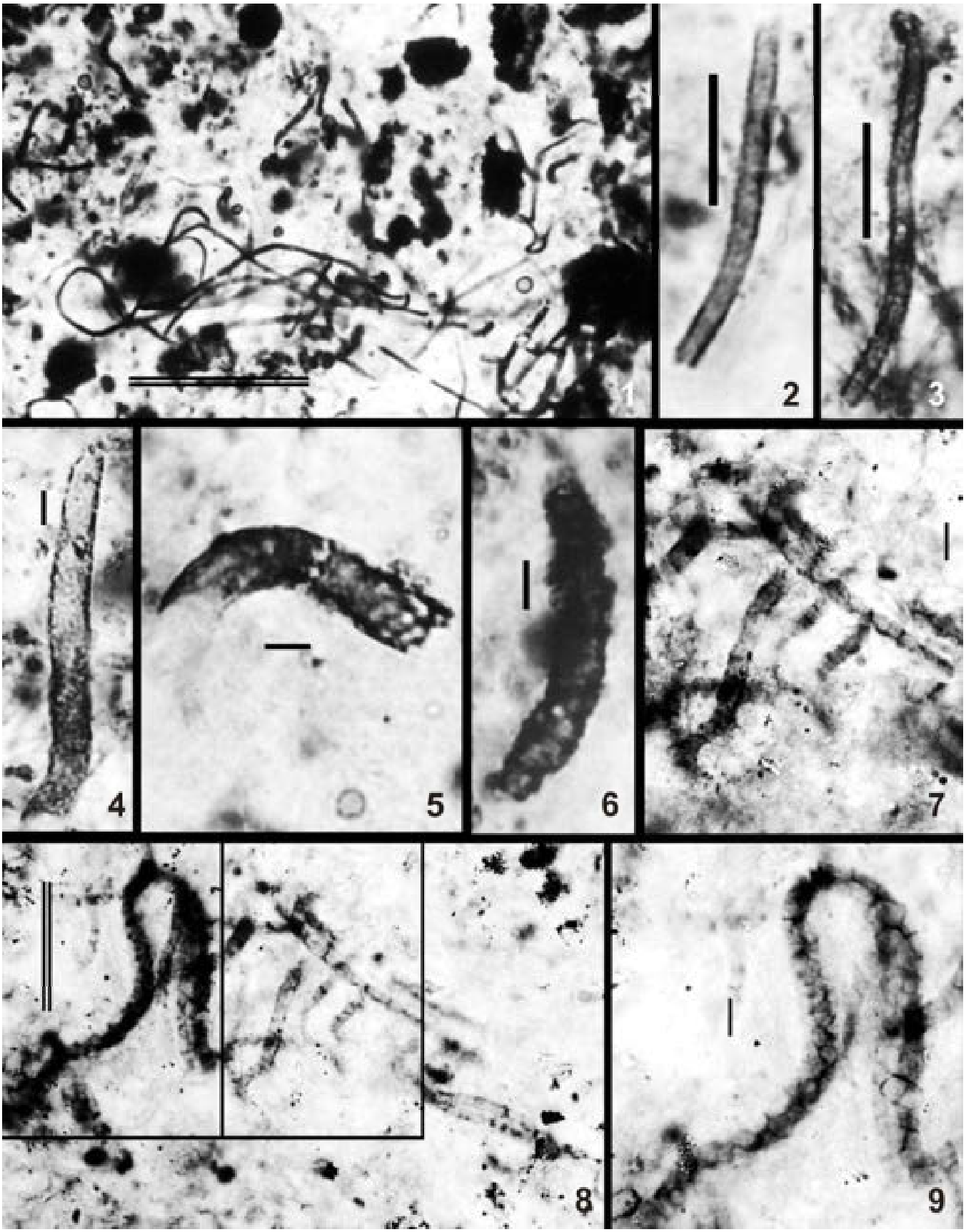


PLATE 14

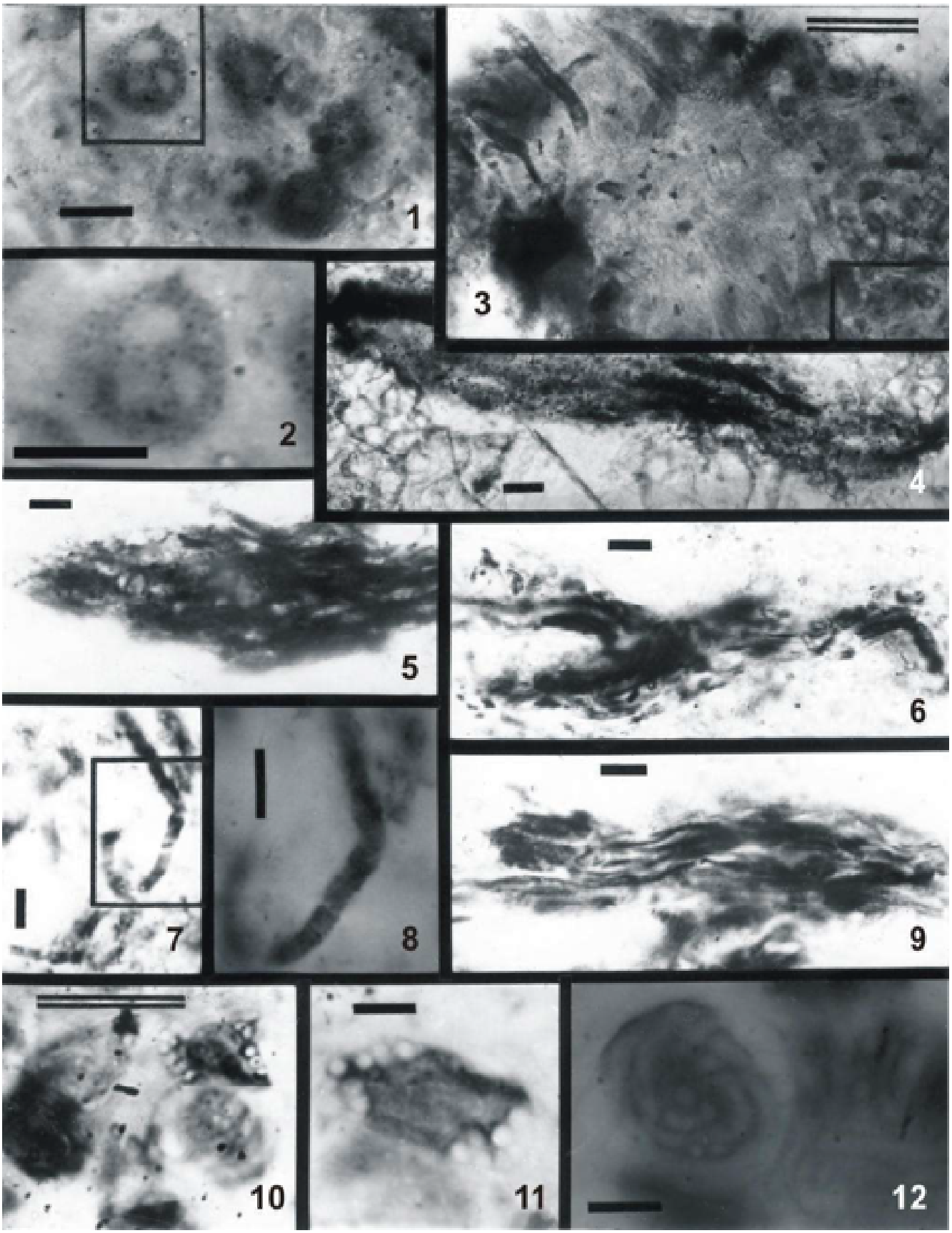


PLATE 15

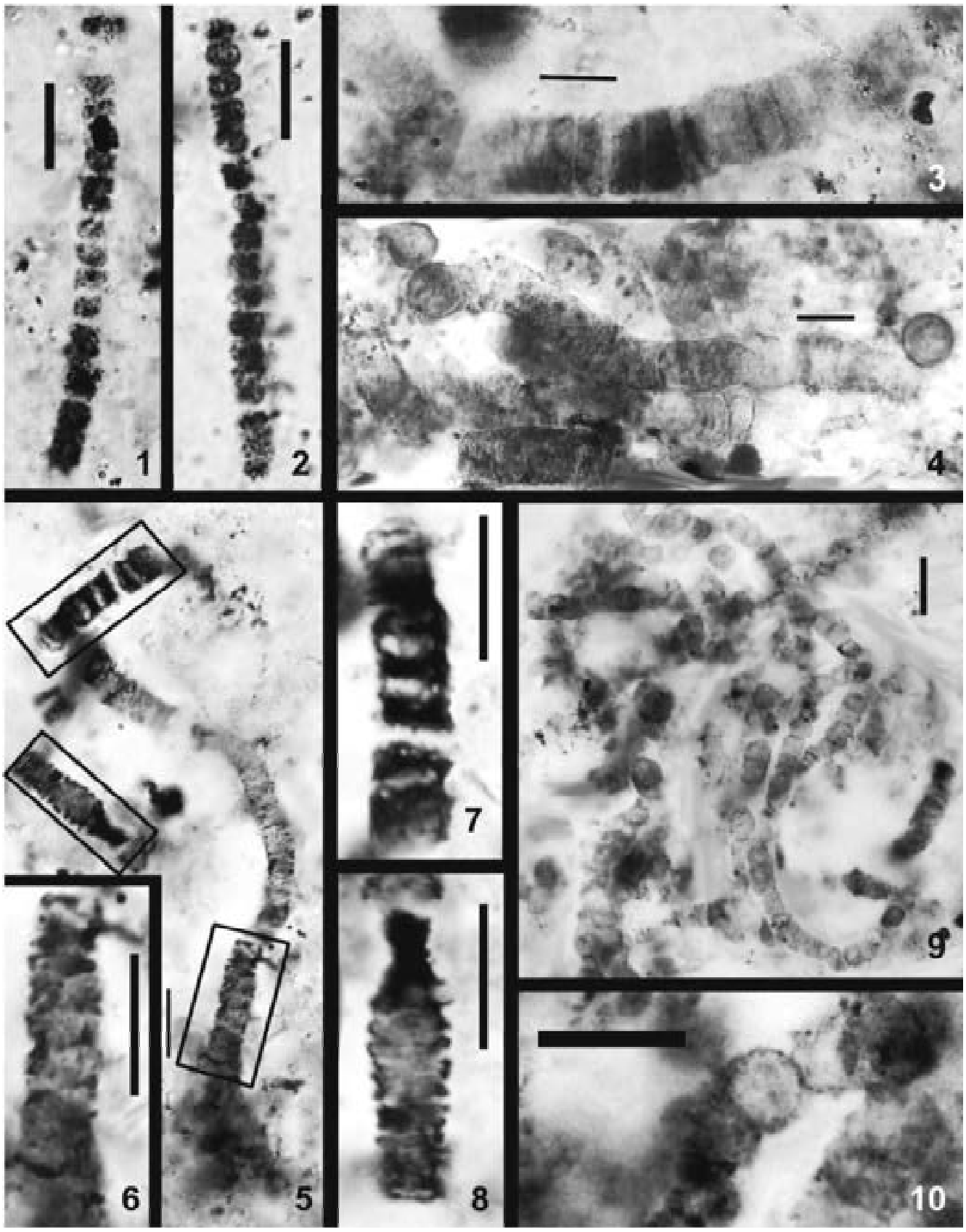


PLATE 16

into *Oscillatoriopsis*. The special case is *Obconicophycus amadeus* emended by Butterfield as *Oscillatoriopsis amadeus.* We do not accept this combination either, but propose this species to be transferred to genus *Cephalophytarion* as *C. amadeus* including *Cephalophytarion majesticum* as its junior synonym described by Allison in Allison and Awramik, 1989 from the Tindir Group of Alaska. Similarily, Sergeev *et al.*, 1995 proposed a new species of *Oscillatoriopsis majesticum* combining *Oscillatoriopsis amadeus* and *Cephalophytarion majesticum.* We do not see reasons enough to validate this combination. We, therefore, are of the view that the group of trichomes currently combined under name *Oscillatoriopsis amadeus* comb. Butterfield should be named *Oscillatoriopsis media*.

Age and distribution—Neoproterozoic, Bitter Springs Formation, Australia.

Genus—CYANONEMA Schopf, 1968, emend. Butterfield, 1994 (in Butterfield *et al.*, 1994)

Cyanonema Schopf, 1968, p. 670; Butterfield *et al.*, 1994, p. 56.

Type species—Cyanonema attenuatum Schopf, 1968.

Diagnosis—Uniseriate unbranched sheathless trichomes with cell width less than length not at all to moderately constricted at septa.

Remarks—Butterfield in Butterfield *et al.* (1994) on the basis of trichome cells width/length ratio separated genus *Cyanonema* from genus *Oscillatoriopsis*. As it was suggested if the ratio is less than one, then the form belongs to genus *Cyanonema*, otherwise to genus *Oscillatoriopsis.* However, this criterion is purely formal and during subsequent divisions cells of trichome can vary from long cylindrical to short pill-like shapes (see Golubic & Focke, 1978). Commonly, the narrower trichome, the longer these cells. Therefore, distinction species of *Cyanonema* from *Oscillatoriopsis* entirely based on this criterion, can meet some difficulties.

Contents—C. attenuatum, C. disjuncta, C. inflatum, C. ligamen and *C. minor* (Table-10).

Age—Proterozoic.

Cyanonema attenuatum Schopf, 1968

(Fig. 36A)

Cyanonema attenuatum Schopf, 1968, p. 670, Pl. 79, Figs 1, 2.

Repository—HUHPC-58461.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Uniseriate unbranched sheathless trichomes strongly attenuated towards apices. Medial cells of trichomes are cylindrical 1.3 to 2.4 μm wide and 1.9 to 4.8 μm long, width/length ratio is 0.25 to 0.75; terminal cells are quadrate to elongate, commonly less than 1 μm wide.

Remarks—The species was described as *C. attenuata* (Schopf, 1968, p. 670), but later was corrected to *C. attenuatum* (Schopf and Blacic, 1971, p. 956).

Age and distribution—Neoproterozoic, Bitter Springs Formation, Australia.

Cyanonema disjuncta Ogurtsova and Sergeev, 1987

(Pl. 16.1, 2)

Cyanonema disjuncta Ogurtsova and Sergeev, 1987, p. 111-112, Pl. IX, Figs 3, 4; Yankauskas,1989, p. 105, Pl. XXIV, fig. 2; Krylov *et al.*, 1989, Pl. I, fig. 9; Sergeev, 1992a, p. 97, Pl. XIX, Figs 3, 4; Schopf, 1992b, Pl. 49, Figs F, G_1, G_2; Sergeev, 2006, Pl. XLV, Figs 12, 13; Sergeev and Schopf, 2010, p. 381, Figs 6.1, 6.2.

Repository—GINPC-4681, Specimen No. 156.

Name of species	Diagnostic features	Cells width and length, μm	Paleoenvironmental setting	Repository and type locality	References
C. inflatum J. Oehler, 1977 Fig. 36B	Trichomes formed of elongated to quadrate medial cells with slightly inflated appearance.	2.1-3.6 x 2.1-5.4	Subtidal, open shelf, observed in cherts from shales.	CPC – 16930; Early Mesoproterozoic, Barney Creek Fm., Australia.	J. Oehler, 1977
C. ligamen Zhang Y., 1981 Fig. 36C	Trichomes formed of elongated medial cells.	1.2-2.2 x 2.5-4.5	Peritidal flat recorded from cherts in dolomites.	BGP – 7812; Early Mesoproterozoic, Gaoyuzhuang Fm., China.	Zhang Y., 1981
C. minor J. Oehler, 1977 Fig. 36D	Trichomes formed of elongated to cylindrical small medial cells.	1.1-1.5 x 1.4-2.9	Subtidal, open shelf, observed in cherts from shales.	CPC – 16924; Early Mesoproterozoic, Barney Creek Fm., Australia.	J. Oehler, 1977

Table 10—Comparative characteristics of genus *Cyanonema* species (Type Specimens).

Fig. 36—Line diagrams of species of *Cyanonema*. A- *C. attenuatum* (Schopf, 1968); B- *C. inflatum* (J. Oehler, 1977); C- *C. ligamen* (Zhang Y., 1981); D- *C. minor* (J. Oehler, 1977). Scale bar = 10 μm.

Stratum typicum—Neoproterozoic, Chichkan Formation, South Kazakhstan.

Description—Uniseriate unbranched sheath-lacking cellular trichomes not attenuated toward apices. Medial cells are cylindrical or barrel-shaped; terminal cells are quadrate to blunt-rounded; cell width ranges from 2.5 to 4.5 μm and cell length, from 2.0 to 4.5 μm; cell width to length ratio varies from 1 to 1.25. Lateral cell walls and transverse walls are muricate to medium-grained, ~1 μm thick. Trichomes occur commonly in groups oriented parallel, subparallel (or less commonly) perpendicular to the bedding plane and have a maximal length of ~ 200 μm.

Remarks—We do not adhere to the suggestion of Butterfield in Butterfield *et al.*, 1994 to transfer *C. disjuncta* to the genus *Oscillatoriopsis* (as a junior synonym of *O. obtusa*). Fossils assigned here to these two genera are morphologically distinct as evident from comparison of specimens of *C. disjuncta* with those of *Oscillatoriopsis* spp.

Age and distribution—Neoproterozoic, Chichkan Formation, South Kazakhstan.

Genus—EOMICROCOLEUS Horodyski and Donaldson, 1980

Eomicrocoleus Horodyski and Donaldson, 1980, p. 154.

Type species—Eomicrocoleus crassus Horodyski and Donaldson, 1980.

Diagnosis—Unbranched trichomes or sheaths in bundles surrounded by a common single layered, multilayered or amorphous sheath.

Remarks—Horodyski and Donaldson (1980) originally described this genus from the Dismal Lakes Group of Canada as the fossil counterpart of polytrichomous cyanobacterial filaments, comparable to species of the modern genera *Microcoleus, Hydrocoleum* and *Schizothrix*. However, subsequently Lee Seong-Joo and Golubic (1998) pointed out that this genus is a form taxon incorporating remains of polytrichomous filaments and fortuitous *post-mortem* accumulation of originally monotrichomous entities. There are several other incidents of description of similar fossils in the literature which can be assigned to *E. crassus viz*., earlier reported by D. Oehler (1978, Figs 12D-12F), Schopf and Prasad (1978, Figs 6a-6c) who interpreted them as large cyanobacterial sheaths. Longitudinal striations have been noted by Butterfield in Butterfield *et al.*, (1994) in *Pseudodendron* with the exception of branching. Earlier, Awramik and Barghoorn (1977, fig. 4D) illustrated a specimen with two inner tubules inside wide sheath from Gunflint Formation that could be earliest record of multitrichomous microfossils. The paucity of multitrichomous filaments in the fossil record could be explained by taphonomical bias of modern *Microcoleus* cyanobacterium where after microorganism's death the filaments disintegrate into isolated sheaths and trichomes that got preserved into fossil record (Horodyski *et al.*, 1977).

Contents—Monospecific genus.

Age—Proterozoic.

Eomicrocoleus crassus Horodyski and Donaldson, 1980

(Pl. 15.4-6, 9; Fig. 37)

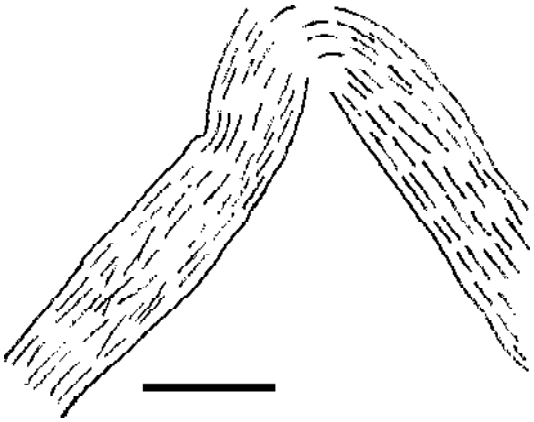


Fig. 37—Line diagram of *Eomicrocoleus crassus* (Horodyski & Donaldson, 1980). Scale bar = 50 μm.

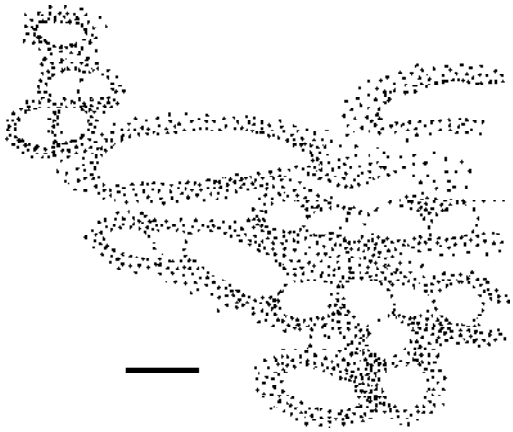


Fig. 38—Line diagram of *Eoschizothrix composita* (Lee Seong-Joo & Golubic, 1988). Scale bar = 10 μm.

Eomicrocoleus crassus Horodyski and Donaldson, 1980, p. 154, Figs 15A, 15B; Sergeev, 2001, p. 442, fig. 9.5; Sergeev, 2002, p. 559, Pl. II, fig. 6; Sergeev, 2006, p. 208, Pl. XVIII, fig. 5, Pl. XXV, fig. 6; Sharma, 2006a, p. 91-92, fig. 10d.

Repository—GSC-57900.

Stratum typicum—Mesoproterozoic, Dismal Lakes Group, Canada.

Description—Bundles of dark thread-like trichomes or sheaths closely grouped within a common cylindrical sheath. Diameter of trichomes (sheaths) 1.0-2.0 μm, they consist of organic particles linearly arranged, and evidently often have been subject to *post-mortem* shrinkage; encompassing common sheaths of 18-50 μm in cross-sectional diameter, and usually fine-to medium-grained, and ~ 1 μm thick.

Remarks—Trichomes and sheaths described from the Sukhaya Tunguska and Burovaya Formations are little larger in diameter in comparision to the type population and sometimes septa inside trichomes are also missing; but this can be explained as different degree of shrinkage and contraction (Gerasimenko & Krylov, 1983, Sergeev *et al.*, 1997).

Age and distribution—Mesoproterozoic, Dismal Lakes Group, Canada; Meso-Neoproterozoic, Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia; Neoproterozoic, Burovaya Formation, Turukhansk Uplift, Siberia.

Genus—EOSCHIZOTHRIX Lee Seong-Joo and Golubic, 1998

Eoschizothrix Lee Seong-Joo and Golubic, 1998, p. 181.

Type species—Eoschizothrix composita Lee Seong-Joo and Golubic, 1998.

Diagnosis—One to several loosely to tightly packed unbranched sheaths or trichomes surrounded by a common outer cylindrical sheath.

Remarks—Lee Seong-Joo and Golubic (1998) proposed that this taxon to be the fossil counterpart of a modern multitrichomous cyanobacterium *Schizothrix*. They also considered this genus as a true biological taxon of Precambrian microfossils meaning thereby that its living cycle and degradational forms can be easily matched with studying fossil populations.

Content—Monospecific genus.

Age—Meso-Neoproterozoic (and probably Palaeoproterozoic).

Eoschizothrix composita Lee Seong-Joo and Golubic, 1998

(Pl. 15.1-3; Fig. 38)

Eoschizothrix composita Lee Seong-Joo and Golubic, 1998, p. 181-182, Figs 2, 3, 5, 6, 10; Sergeev, 2002, p. 559, Pl. II, Figs 2, 4, 5; Sergeev, 2006, p. 209, Pl. XXV, Figs 2, 4, 5.

Repository—Gb94-2, Biological Science Center, Boston University.

Stratum typicum—Mesoproterozoic, Gaoyuzhuang Formation, China.

Description—One to several tightly packed sheaths or trichomes surrounded by a common outer cylindrical sheath; width of the filament (outer sheath) increases with number of trichomes or sheaths inside. The diameter of external sheath with one internal sheath inside 5.0-10.5 μm, and with double or multiple internal sheaths 6.5 to 14.5 μm and that of interior sheaths are 2.5 to 7.5 μm.

Remarks—Eoschizothrix composita sheaths always co-occur with *Siphonophycus* spp. and latter in some cases can turn out to be just degradational versions of the former (see Lee Seong-Joo & Golubic, 1998, fig. 11). Further careful reinvestigation can reveal that plenty of *Eoschizothrix* filaments were earlier described as *Siphonophycus*.

Name of species	Diagnostic features	Cells width and length, μm	Palaeoenvironmental setting	Repository and type locality	References
F. diminutus Schopf & Blacic, 1971 Text-fig. 39C	Trichomes formed of biconvex cells very strictly constricted at septa.	2.9-4.7 x 1.8-2.8	Peritidal flat and pluvial lakes, recorded from cherts in dolomites.	HUHPC – 58575; Neoproterozoic, Bitter Springs Fm., Australia.	Schopf & Blacic, 1971
F. eniseicum Veis, 1984	Trichomes formed of spherical to ellipsoidal cells constricted at septa.	7.0-9.0 x 5.0-10.0	Subtidal middle shelf, recorded from shales.	GINPC – 2678/426; Neoproterozoic, Miroedikha Fm., Siberia.	Veis, 1984

Table 11—Comparative characteristics of genus *Filiconstrictosus* species (Type Specimens).

Age and distribution—Mesoproterozoic, Gaoyuzhuang Formation, China; Ediacaran, Yudoma Group, Siberia.

Genus—FILICONSTRICTOSUS Schopf and Blacic, 1971, emend. Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

Filiconstrictosus Schopf and Blacic, 1971, p. 947; Sergeev *et al.*, 1995, p. 28.

Type species—Filiconstrictosus majusculus Schopf and Blacic, 1971.

Diagnosis—Solitary, uniseriate, short, sheathless, unbranched trichomes composed of barrel-like cells, very strongly constricted at septa and sometimes terminated by rounded cells.

Remarks—In the Bitter-Springs microbiota, Schopf and Blacic (1971) correctly diagnosed the genus *Filiconstrictosus* as trichomes strongly constricted at septa. But they misinterpreted the short trichomes of *F. majusculus* and *F. diminutus* as the incomplete specimens. The reinvestigated type population has revealed that all these trichomes are complete, but short specimens of primarily maximum length up to 67 μm long (Sergeev *et al.*, 1995).

Butterfield in Butterfield *et al.* (1994) has incorporated genus *Filiconstrictosus* within genus *Veteronostocale* based mainly on the similarity in shape of cells of the both genera (spheroidal to subspheroidal). However, length of the trichomes of both genera is different: the former genus incorporates short trichomes whereas the latter encompasses normal long filaments. This feature is of profound significance and allows to interprete *Veteronostocale* trichomes as matured filaments, whereas those of *Filiconstrictosus* are rather germinating trichomes or hormogonia. Considering the barrel-like to subspherical shape of genus *Filiconstrictosus* cells, most of its species should be germinated from akinetes germlings of nostocalean or stigonematalean cyanobacteria rather than oscillatoriacean trichomes. This genus, therefore, should be transferred to family nostocaceae than be retained as oscillatoriacean cyanobacteria as it was earlier considered (Schopf & Blacic, 1971; Sergeev *et al.*, 1995; Sergeev, 2006). At the same time, we do not agree to the revision of Butterfield in Butterfield *et al.* (1994) who incorporated *Filiconstrictosus* into *Veteronostocale* and keep the former as an independent genus. It is for records that Butterfield's taxonomic revision could not be considered while emending *Filiconstrictosus* diagnosis (Sergeev *et al.*, 1995) as both manuscripts were submitted to press almost simultaneously and independently although the monograph by Butterfield *et al.* (1994) formally appeared earlier than that by Sergeev *et al.* (1995).

Contents—F. cephalon, F. diminutus, F. eniseicum, F. magnus and *F. majusculus* (Table-11).

Age—Meso-Neoproterozoic.

Filiconstrictosus cephalon Sergeev and Knoll, 1995 (in Sergeev *et al*., 1995)

(Pl. 17.4; Fig. 39A)

Filiconstrictosus cephalon Sergeev and Knoll in Sergeev *et al.*, 1995, p. 28-29, fig. 15.4; Sergeev, 2006, p. 202, 203, Pl. VII, fig. 4; Sergeev *et al.*, 2008, Pl. 1, fig. 8.

Repository—HUHPC-92922.

Stratum typicum—Mesoproterozoic (Lower Riphean), Kotuikan Formation, Anabar Uplift, Siberia.

Description—Solitary uniseriate, unbranched, short, symmetrical trichome, constricted at septa and consisting of 15 medial and 2 terminal cells. Terminal cells that cap both ends of the trichome are morphologically distinct from medial cells; they are nearly spherical and 5.0 μm in diameter. Medial cells are pill-like or (closer to trichome ends) subconical, 10.5-20.5 μm wide and 1.5-5.0 μm long; width/length ratio 3.5 to 4.5. Trichome length 83 μm; cross walls absent; ca. 0.5 μm spaces separate adjacent cells.

Remarks—Filiconstrictosus cephalon differs from other species of *Filiconstrictosus* by the large size of its medial

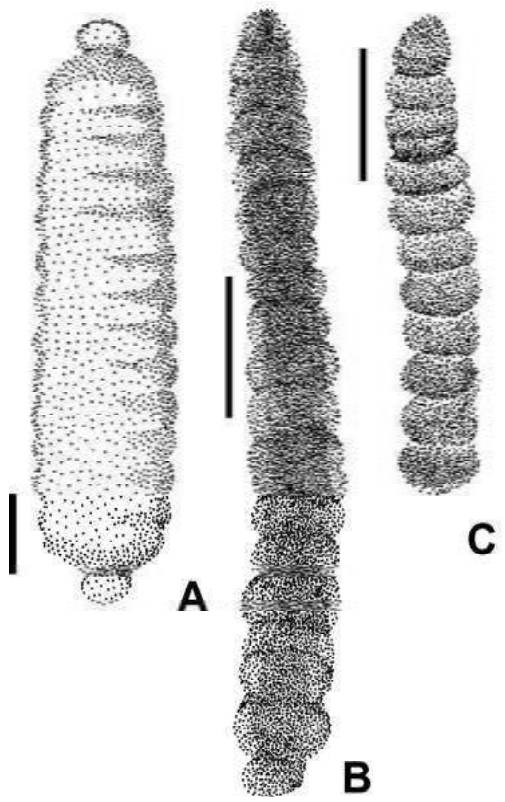


Fig. 39—Line diagrams of species of *Filiconstrictosus* . A- *F. cephalon* (Sergeev et al., 1995); B- *F. majusculus* (Schopf & Blacic, 1971); C- *F. diminutus* (Schopf & Blacic, 1971). Scale bar = 10 μm.

cells and (from *F. magnus*) by its distinctive terminal cells of uncertain origin. Similar bodies have been observed at the ends of desiccating *Lyngbya aestuarii* trichomes at Laguna Mormona, Baja, California (Horodyski, 1977), but the nearly precise bilateral symmetry of the Anabar trichome suggests that its morphology is of biological and not diagenetic origin. Spherical terminal cells sometimes occur at the ends of hormogonia in some species of *Lyngbya*, and in *Anabaena*, spheroidal vegetative may remain attached to germinating akinetes (S. Golubic, pers. comm., 1993).

Age and distribution—Mesoproterozoic, Kotuikan Formation, Anabar Uplift, Siberia.

Filiconstrictosus magnus Yakschin, 1991

(Pl. 17.1, 9)

Filiconstrictosus magnus Yakschin, 1991, p. 32-33, Pl. XI, fig. 2; Sergeev *et al.*, 1995, p. 28, Figs 15.1, 15.2; Knoll and Sergeev, 1995, fig. 1; Sergeev, 2006, p. 201, 202, Pl. VII, Figs 1a, 1б, 2; Sergeev *et al.*, 2008, Pl. 1, fig. 4, Pl. 3, fig. 1; Sergeev *et al.*, 2010, Pl. I, fig. 6.

Orculiphycus magnus Yakschin, 1991, p. 31-32, Pl. XI, fig. 3.

Repository—CSGM-390-AYa-28-4e.

Stratum typicum—Mesoproterozoic (Lower Riphean), Kotuikan Formation, Anabar Uplift, Siberia.

Description—Solitary, uniseriate, unbranched, short trichomes without extra-cellular sheaths. Terminal cells hemispherical in shape, 10.5 and 12.0 μm wide, 3.0 and 4.5 μm long, width/length 3.5 and 2.2 (2 cells measured). Medial cells pill-like, 10.5-21.5 μm wide, 3.5-7.0 μm long, width/length 3.5 to 5.0. Medial cells arranged in pairs, with cross walls commonly missing and 0.5-1.0 μm spaces separating adjacent cells; trichomes constricted where cell pairs meet. Maximum preserved length of trichomes 100 μm.

Remarks—F. magnus is distinguished from other species of *Filiconstrictosus* by its larger cell diameter and more prominent constriction between medial cell pairs. This species is similar to trichomes described as *Oscillatoriopsis robusta* from the Wumishan Formation, but the Chinese fossils do not show constriction between cells (Zhang P. *et al.*, 1989, p. 24, Pl. 1, Figs 2, 6).

Age and distribution—Mesoproterozoic, Kotuikan Formation, Anabar Uplift, Siberia.

Filiconstrictosus majusculus Schopf and Blacic, 1971

(Pl. 17. 2, 3, Fig. 39B)

Filiconstrictosus majusculus Schopf and Blacic, 1971, p. 947-948, Pl. 105, fig. 8; Schopf, 1972, fig. 3; Schopf, 1992b, Pl. 30, fig. R.

Filiconstrictosus ex gr. *majusculus* Schopf and Blacic, 1971: Yakschin, 1991, p. 32, Pl. XI, fig. 1; Sergeev *et al.*, 1995, p. 28, fig. 15.3; Golubic *et al.*, 1995, fig. 8A; Sergeev, 2006, p. 202, Pl. VII, Figs 3a, 3б; Sergeev *et al.*, 2008, Pl. 1, fig. 1.

Orculiphycus agnastus Yakschin, 1991, p. 31, Pl. XI, fig. 6.

Repository—HUHPC-58567.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Solitary, uniseriate, unbranched short trichomes without extra-cellular sheaths composed of barrel-like and subspherical cells. Medial cells are barrel-like, 5.3-7.3 μm wide by 2.5-4.0 μm long; width/length 1.5 to 2.5. Medial cells have distinct cross-walls, with adjacent cells separated by ca. 1.0 μm spaces. Hemispherical terminal cells are 3.3-4.5 μm wide. Trichomes constricted where adjacent cells connect and up to 67 μm long.

Age and distribution—Mesoproterozoic, Kotuikan Formation, Anabar Uplift, Siberia; Neoproterozoic, Bitter Springs Formation, Australia.

Genus—HELICONEMA Schopf, 1968

Heliconema Schopf, 1968, p. 671-672.

Type species—Heliconema australiense Schopf, 1968

Diagnosis—Unbranched, nonseptate, flattened ribbon-like filaments coiled into more or less regular elongated loose spiral.

Remarks—This genus was erected for flattened small ribbon-like structures coiled into elongated loose spiral forms from the Bitter Springs Formation of Australia (Schopf, 1968). These fossils probably formed as a result of *post-mortem* twisting of abandoned sheaths of oscillatoriacean cyanobacteria like *Lyngbya* (Golubic & Barghoorn, 1977; see also Elenkin, 1949, fig. 479, p. 1620). Therefore, we consider genus *Heliconema* as a form taxon embracing empty flattened sheaths of oscillatoriacean LPP-type cyanobacteria coiled into spiral-like structure as a result of *post-mortem* twisting. Some fossil species were described within genus *Heliconema,* but they turned out to be primarily coiled filaments of *Spirulina*-like cyanobacteria and were subsequently transferred to genus *Obruchevella* (see remarks to this genus).

Contents—H. australiense and *H. funiculum*.

Age—Proterozoic.

Heliconema australiense Schopf, 1968

(Fig. 40A)

Heliconema australiense Schopf, 1968, p. 672, Pl. 81, Figs 2, 3.

Repository—HUHPC-58481.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Unbranched, nonseptate, flattened ribbon-like filaments coiled into more or less regular elongated loose spiral at an angel of approximately 45 degree. Ribbons width is 2.5-2.8 μm, spirals diameter is 2.7-3.4 μm; ribbons are fine-grained about 0.5 μm thick.

Remarks—The species was described as *H. australiensis* (Schopf, 1968, p. 672), but later was corrected to *H. australiense* (Schopf & Blacic, 1971, p. 956).

There is another species *Heliconema funiculum* also described from the Bitter Springs Formation of Australia (Fig. 40b). This species differs from *H. australiense* by its larger dimensions: ribbon width is 4.0-4.7 μm and spiral diameter is 4.3-6.0 μm.

Age and distribution—Neoproterozoic, Bitter Springs Formation, Australia.

Genus—OBRUCHEVELLA Reitlinger, 1948, emend. Yakschin and Luchinina, 1981, emend. Kolosov, 1984, emend. Yankauskas, 1989, emend. Burzin, 1995, emend. Nagovitsin, 2000

Obruchevella Reitlinger 1948, p. 78; Reitlinger, 1959, p. 21; Luchinina, 1975, p. 29; Kolosov, 1977, p. 73; Yakschin and Luchinina, 1981, p. 29; Kolosov, 1984, p. 57-58; Song, 1984, p. 181, 183; Yankauskas, 1989, p. 112-113; Burzin, 1995, p. 7-9; Nagovitsin, 2000, p. 14.

Volyniella (Schepeleva ex msc.) Aseeyeva, 1974, p. 95-96; Pashkevichene, 1980, p. 48; Kolosov, 1984, p. 53.

Type species—Obruchevella delicata Reitlinger, 1948.

Diagnosis—Empty tubes, sometimes with rare septa coiled into regular cylindrical spiral, sometime taper or expanding toward ends. In these spirals tubes, walls usually

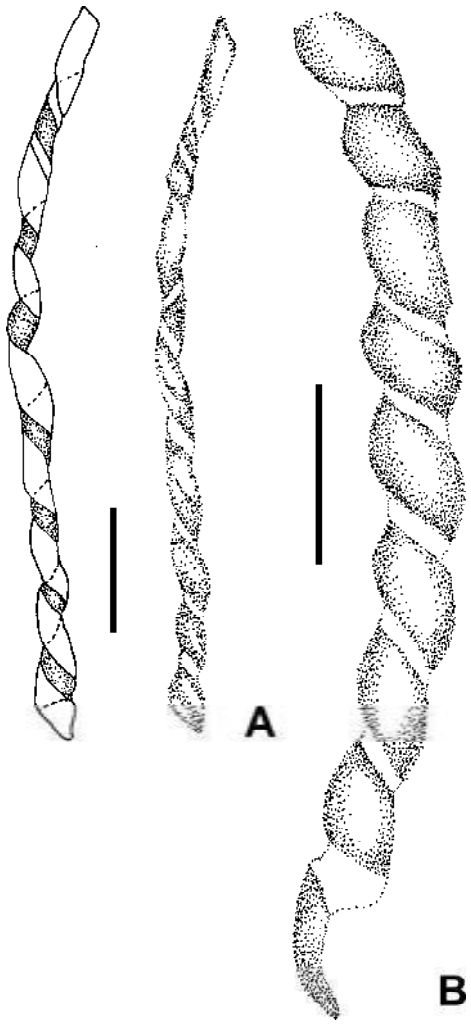


Fig. 40—Line diagrams of species of *Heliconema*. A- *H. australiense* (Schopf, 1968); B- *H. funiculum* (Schopf & Blacic, 1971). Scale bar = 10 μm.

are tightly joined one to another or in rare cases they can be loose.

Remarks—Microfossil genus *Obruchevella* has been recorded mainly as permineralized remains in cherts or silicified phosphorites as well as in the dolomites and as macerates residue from shales. One of the exceptional preservation of *O.* cf. *gigantea* was reported by Golovenok *et al.* (1990) from the Parsha Formation of Yakutia as compressions on shales surfaces like *Chuaria* and some other carbonaceous remains are found in Meso-Neoproterozoic successions.

Spirals of *Obruchevella* originally were described as foraminifera from the Vendian (Ediacaran) Tinna and Lower Cambrian Sinna Formations of Siberia (Reitlinger, 1948, 1959). Later on these fossils were reinterpreted as remains of oscillatoriacean cyanobacteria similar to modern cyanobacterium genus *Spirulina* (Luchinina, 1975; Yakschin & Luchinina, 1981; Yankauskas, 1989). Similar spiraly-coiled trichomes are also observed among other modern oscillatoriacean cyanobacteria genera *Phormidium*, *Lyngbya* and *Romeria* (see Knoll, 1992b). Since the establishment of genus *Obruchevella* it has been emended at least ten times (not always formally) and with every emendation some additional characters were appended as well as other genera were merged with it. But this exercise seems to have been done without objectivity and therefore, calls for indepth reassement of the characters of this genus. For example, the last emendation by Nagovitsin (2000) has included another spiral microfossil genus *Heliconema* Schopf within *Obruchevella.* However, these two spiral forms are entirely different in nature. Regular cylindrical spirals of *Obruchevella* is a primarily biological feature like those of modern cyanobacterium *Spirulina* whereas loose irregular spirales of *Heliconema* were formed as a result of *post-mortem* twisting of abandoned sheaths of oscillatoriacean cyanobacteria like *Lyngbya* (see Golubic & Barghoorn, 1977; Elenkin, 1949, fig. 479, p. 1620). Considering this, we prefere to keep both genera separately and do not follow Nagovitsin's emendation. However, some spiral forms described as *Heliconema* species are rather remains of primarily coiled spiral filaments, e.g. *O. turukhanica* (Hermann, 1981) and *O. uralense* (Yankauskas, 1980); see also Knoll, 1992b. On the other hand, some spiral microfossils described under generic name *Obruchevella* in fact are rather secondary twisted empty sheaths of *Lyngbya*-like cyanobacteria, e.g. *Obruchevella pusilla* Golovenok and Belova, 1983, and should be transferred to genus *Heliconema*.

Nagovitsin (2000) described genus *Palaeogomontiella* as a fossil counterpart of modern cyanobacterium *Gomontiella* Teodoresco demonstrating open pseudospiral colony from circular cells with medial gap. Nagovitsin suggested *P. irregularis* to be a spiral-like tubular structure with medial gap formed by 'C' shaped cells. However, one of us (VNS) had opportunity to investigate this material and consider these microfossils as normal spirals of *Obruchevella* with medial folds, probably formed as a result of *post-mortem* alteration.

The spiral forms from shales were described independently as genus *Volyniella* (Aseeyeva, 1974) and subsequently merged with genus *Obruchevella* (Yankauskas, 1989). However, later on Burzin (1995) has argued against this synonymy and suggested to keep *Volyniella* as an independent genus. But considering all variations inside *Obruchevella* species including *post-mortem* alterations, we do not agree to Burzin and follow by earlier revision proposed by Yankauskas, 1989.

Besides above mentioned taxa many more genera of spiral microorganisms were described during a half-century study of Proterozoic microfossils, e.g. *Avictuspirulina, Glomovertella, Glomerula, Spirellis, Spirillopsis, Boruokia, Jiangispirellus* and others. However, almost all these taxa can be considered as the degradational or ecological variants of genus *Obruchevella*.

Contents—*O. blandita, O. condensata, O. crassa, O. cylindrica, O. delicata, O. ditissimus, O. exilis, O. gigantea, O. inviolata, O. magna, O. meishucunensis, O. minor, O. minuta ?, O. parva, O. parvissima, O. pusilla ?, O. sibirica, O. tungusica, O. turukhanica, O. uralense* and *O. valdaica* (Table-12).

Age—Neoproterozoic.

Obruchevella delicata Reitlinger, 1948

(Pl. 19.8, 9)

Obruchevella delicata Reitlinger, 1948, p. 78, 80, Pl. I, Figs 1, 2; Reitlinger, 1959, p. 21, Pl. VII, Figs 1-3; Luchinina, 1975, p. 29, Pl. XXVII, Figs 2-5; Yakschin and Luchinina, 1981, p. 29-30, Pl. IX, Figs 1-5; Pyatiletov *et al.*, 1981, Figs 1.7; Song, 1984, fig. 3.13; Sergeev, 1989, Pl. 2, fig. 4; Sergeev and Ogurtsova, 1989, Pl. I, fig. 4; Golovenok and Belova, 1989, p. 193-194, Figs 1e-1з; Sergeev, 1992a, p. 89-90, Pl. XXV, Figs 7a, 7б; Mankiewicz, 1992, Figs 6.1-6.5, 8.1-8.7; Prasad *et al.*, 2005, p. 54, Pl. 10, Figs 7, 11, Pl. 11, fig. 11; Prasad, 2007, Pl. 1, Figs 4, 7, 8, 14, 18.

Repository—GINPC-3263, Specimen No. 1.

Stratum typicum—Lower Cambrian, Sinna Formation, Patom Uplift, Russia.

Diagnosis—Empty tubes, sometimes with rare septa coiled into regular cylindrical spiral do not taper toward ends. In these spiral tube walls usually tightly jointed one another or can be loose. Some of the spirals may twist in other direction than main spiral direction, a feature which may be a result of *post-mortem* uncoiling. The tubes diameter ranges from 10 to

Table 12—Comparative characteristics of genus *Obruchevella* species (Type Specimens). →

Name of species	Diagnostic features	Tubes width and spiral outer diameter, μm	Palaeoenvironmental setting	Repository and type locality	References
O. blandita Schenfil', 1980	Tubes tightly coiled into regular spirals.	2.1-2.2; 18.0-20.0	Open shelf recorded from cherts in dolomites.	Schenfil', 1980, fig. 3a-e; Neoroterozoic, Seryi Klyuch Fm., Enisei Ridge, Russia	Schenfil', 1980
O. condensata Liu, 1984	Tubes tightly coiled into regular spirals.	3.0-7.0; 10.0-22.0	Tidal flat, recorded from cherts in dolomites.	L16-2-181e; Jiudingshan Fm., Suining County, Jiangsu Province, China.	Liu *et al.*, 1984
O. crassa Kolosov, 1984	Tubes tightly coiled into regular spirals.	40.0-41.6; 135.0-175.0	Open shelf recorded from shales	YFSOANUSSR – 87-103; Ediacaran, Kursov Fm., Yakutia, Russia.	Kolosov, 1984
O. cylindrica Tynni & Donner, 1980	Tubes tightly coiled into regular spirals.	4.0-5.0; 50.0-70.0	Open shelf recorded from shales.	GTL200:1; Hailuoto Fm, Borehole No. 2, 52.60 m; Ediacaran, Hailuoto Fm., Finland.	Tynni & Donner, 1980, 1982
O. ditissima Schipitzyn & Yakschin, 1981	Tubes tightly coiled into regular spirals.	18.0-25.0; 110.0-115.0	Open shelf and tidal flats, recorded from cherts in dolomites.	IGG – 309-2219-M/3; Neoproterozoic, Martukhin Fm., Kuznetskii Alatau, Russia.	Yakschin & Luchinina, 1981
O. gigantea Golovenok & Belova, 1989	Tubes tighly and loosely coiled into regular spirals.	45.0-55.0; 275.0-360.0	Intertidal and subtidal setting, recorded in silicified phosphorites.	VSEGEI – 671-3-2; Ediacaran, Buton Fm., Middle Ural, Russia.	Golovenok *et al.*, 1989
O. inviolata Kolosov, 1984	Tubes loosely coiled into regular spirals.	27.0-47.0; 200.0-230.0	Open shelf, recorded from shales.	YFSOANUSSR – 87-99; Ediacaran, Kursov Fm., Yakutia, Russia.	Kolosov, 1984
O. magna Golovenok & Belova, 1989	Tubes loosely coiled into regular spirals.	28.0-37.0; 135-175	Intertidal and subtidal setting, recorded in silicified phosphorites.	VSEGEI – 671-2; Ediacaran, Buton Fm., Middle Ural, Russia.	Golovenok *et al.*, 1989
O. meishucunensis Song, 1984 Pl. 19.7 Fig. 41B	Tubes loosely coiled into large regular spirals.	20.0-22.0; 100.0-120.0	Intertidal to supratidal facies, recorded in silicified phosphorites.	Song, 1984, fig. 3.7, M4-38-32; Lower Cambrian, Yuhucun Fm., China.	Song, 1984
O. minor Zhang Z., 1984 Fig. 41C	Tubes coiled into regular spirals.	3.5-5.5.; 10.0-19.5	Intertidal to supratidal facies, recorded in silicified phosphorites.	Ediacaran, the Doushantuo Fm., China.	Zhang Z., 1984
O. minuta ? Allison, 1989	Tubes tightly coiled into small regular spirals.	~ 0.8; 7.0-8.0	Intertidal to supratidal facies, recorded in cherts from dolomites.	BC75 44-9; Neoproterozoic, Tinder Group, Alaska, USA.	Allison & Awramik, 1989
O. pusilla ? Golovenok & Belova, 1983	Tubes loosely coiled into regular spirals.	1.0-1.65; 4.0-4.5	Intertidal to peritidal recorded in cherts.	VSEGEI – 62-e; Ediacaran, Valyukhta Fm., Patom Uplift, Russia.	Golovenok & Belova, 1983
O. sibirica Reitlinger, 1959	Tubes tightly coiled into big regular spirals.	14.0-17.0; 57.0-58.0	Intertidal to supratidal facies, recorded in dolomites.	GINPC – 3434/38; Upper Cambrian, Siberia, Russia.	Reitlinger, 1959
O. tungusica Pyatiletov, 1986	Flattened ribbon-like filaments, loosely coiled.	14.0-16.0; 18.0-20.0	Intertidal recorded from shales.	IGG – not provided; Ediacaran, Vanavara Fm., Katanga Saddle, Russia.	Pyatiletov, 1986
O. turukhanica Hermann, 1981	Tubes (trichomes) coiled into loose spirals.	4.0; 8.0-10.0	Subtidal middle shelf, recorded from shales.	IGGP – 49a/3, Neoproterozoic, Miroedikha Fm., Turukhansk Uplift, Russia.	Hermann, 1981
O. uralense Yankauskas, 1980	Tubes very loosely coiled into regular spirals.	3.5-4.5; 7.0-9.0	Intertidal, recorded in cherts from dolomites.	LitNIGRI – 16-25-9/1; Neoproterozoic, Inzer Fm., South Ural, Russia.	Yankauskas, 1980
O. valdaica Schepeleva ex msc., Asseyeva, 1974	Flattened tubes very loosely coiled into spirals.	11.8-19.0; 46.0-170.0	Intertidal, recorded from shales.	IGS NAS – 242/1; Ediacaran, Yaryshev Fm., Podolia, Ukraine.	Asseyeva, 1974

13 μm, spiral outer diameter is 36-50 μm, spiral length is up to 145 μm. Tube walls are fine-grained about 0.5 μm thick.

Remarks—Tubes of *Obruchevella* can be either sheaths or trichomes transformed into empty structures as a result of diagenetic alteration. Rarely septa could survive *post-mortem* degradation and rarely observed in case of some *Obruchevella* specimens.

Age and distribution—Ediacaran (Vendian): Tinna Formation, Patom Uplift, Siberia; Nagod Limestone Formation, India; Lower Cambrian: Sinna Formation, Patom Uplift, Siberia; Chulaktau Formation, South Kazakhstan; Yuhucun Formation, China; Burgess Shales, Canada.

Obruchevella exilis Sergeev, 1992 (in Sergeev, 1992a)

(Pl. 19.11, 12)

Obruchevella exilis Sergeev, 1992a, p. 91, Pl. XIX, Figs 2а, 2б; Sergeev, 2006, Pl. XLVI, Figs 6а, 6б; Sergeev and Schopf, 2010, p. 383, Figs 8.4a, 8.4b; Schopf *et al.*, 2010, Figs 1.4-1.7; Sergeev *et al.*, 2010, Pl. II, fig. 1.

Obruchevella sp., Krylov., 1989, Pl. I, Figs 7а, 7б; Sergeev, 1989, Pl. I, fig. 3.

Repository—GINPC-4681, Specimen No. 154.

Stratum typicum—Neoproterozoic, Chichkan Formation, South Kazakhstan.

Description—Thin-walled empty cylindrical tubes tightly coiled into a regular spiral that in some specimens decreases in breadth toward one end. Walls of adjacent spirally coiled tubes typically are closely adpressed but the tubes can be more loosely packed, evidently as a result of *post-mortem* uncoiling. Tube diameters range from 2.0 to 3.0 μm; the outer diameter of spiral coils ranges from 11 to 16 μm whereas the inner boundary of coils ranges from 4 to 9 μm; the total length of coiled spirals is up to 45 μm. Tube walls are fine-grained, translucent, and less than 0.5 μm thick.

Age and distribution—Neoproterozoic, Chichkan Formation, South Kazakhstan

Obruchevella parva Reitlinger, 1959, emend. Golovenok and Belova, 1989, emend. Burzin, 1995

(Pl. 19.1-6, 14)

Obruchevella parva Reitlinger, 1959, p. 21, Pl. VI, Figs 1, 2; Kolosov, 1977, p. 73,74, Pl. VI, fig. 1; 1982, Pl. XVI, Figs 1а, 1б; Cloud *et al.*, 1979, p. 87-89, Figs 5J-5K; Yakschin and Luchinina, 1981, p. 30, Pl. X, Figs 1-3; Pyatiletov *et al.*, 1981, Figs 1.11; Golovenok and Belova, 1983, p. 1464, Figs 1в-1д; Song, 1984, p. 183, Figs 3.1-3.3, 3.8, 3.9; Sergeev, 1989, Pl. 2, Figs 1-3, 5, 6, 8; Sergeev and Ogurtsova, 1989, Pl. I, Figs 1-3, 5-9, 12; Golovenok and Belova, 1989, p. 193, Figs 1б-1д; Sergeev, 1992a, p. 89, Pl. XXIV, Figs 5, 6, 11, Pl. XXV, Figs 1а, 1б, 2, 3, 5, 6а, 6б; Burzin, 1995, p. 10-11, 13, Pl. I, Figs 1-3, 4A, Pl. III, fig. 1; Prasad *et al.*, 2005, p. 54, Pl. 10, Figs 4, 12, Pl. 11, fig. 9; Prasad, 2007, Pl. 1, Figs 3, 6, 15 (for additional synonymy, see Burzin, 1995 and Golovenok & Belova, 1989).

Repository—GINPC-3434, Specimen No. 32.

Stratum typicum—Ediacaran (Vendian), Tinna Formation, Patom Uplift, Russia.

Diagnosis—Empty tubes, sometimes with rare septa coiled into regular cylindrical spiral do not taper toward ends. The tubes diameter ranges from 7 to 10 μm, spiral outer diameter is 26-33 μm, spiral length is up to 155 μm. Tube walls are fine-grained about 0.5 μm thick.

Remarks—Numerous emendations of *Obruchevella* species, especially of *O. parva* and *O. delicata*, in our opinion, only complicated the situation of the fossil cyanobacterium genus. Therefore, we try follow the original descriptions by Reitlinger (1948, 1959) with measure corrections done by Golovenok and Belova (1989) on the type material deposited in GINPC.

Age and distribution—Widely distributed in Ediacaran (Vendian) and Lower Cambrian silicified and organic-walled assemblages.

Obruchevella parvissima Song, 1984

(Pl. 19.10; Fig. 41A)

Obruchevella parvissima Song, 1984, p. 183, Figs 3.14-3.16; Sergeev and Ogurtsova, 1989, Pl. I, fig. 11; Sergeev, 1992a, p. 90, Pl. XXV , fig. 4; Prasad *et al.*, 2005, p. 54, Pl. 11, fig. 10; Prasad, 2007, Pl. 1, fig. 16.

Repository—Song, 1984, fig. 3.7, M4-38-32.

Stratum typicum—Lower Cambrian, Yuhucun Formation, China.

Description—Thin-walled empty cylindrical tubes, coiled into a loose regular spiral with walls of adjacent tubes not touching one another. Tube diameters range from 3.0 to 4.0 μm; the outer diameter of spiral coils ranges from 20 to 24 μm whereas the inner boundary of coils ranges from 12 to 14 μm. Tube walls are medium-grained, opaque, and probably less than 1.0 μm thick.

Age and distribution—Lower Cambrian: Yuhucun Formation, China; Chulaktau Formation, South Kazakhstan.

Genus—OSCILLATORIOPSIS Schopf, 1968, emend. Mendelson and Schopf, 1982, emend. Butterfield, 1994 (in Butterfield *et al.*, 1994)

Oscillatoriopsis Schopf, 1968, p. 666; Mendelson and Schopf, 1982, p. 63-64; Butterfield *et al.*, 1994, p. 56-57.

Halythrix Schopf, 1968, p. 678.

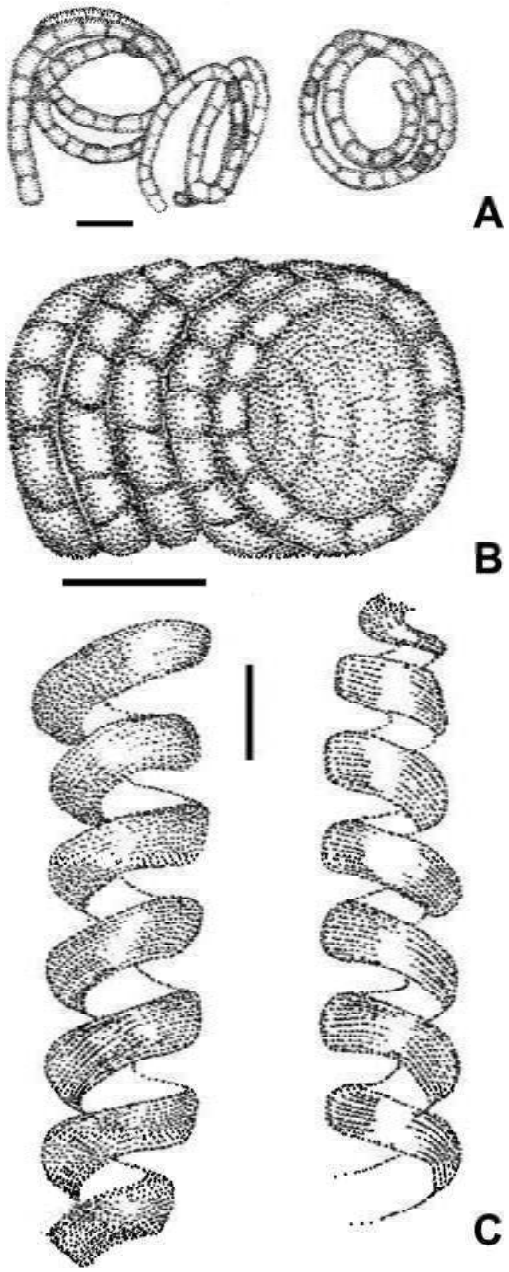


Fig. 41—Line diagrams of species of *Obruchevella*. A- *O. parvissima* (Song, 1984); B- *O. meischucunensis* (Song, 1984); C- *O. minor* (Zhang Z., 1984). Scale bar =A= 10 μm, B = 30 μm, C= 10 μm.

Type species—Oscillatoriopsis obtusa Schopf, 1968.

Diagnosis—Trichomes uniseriate, unbranched, without sheath, tapering or not tapering toward apices, formed of disk or cylindrical medial cells with cell length less or equal to cell diameter. Trichomes solitary or form mat-like colonies from many individuals.

Remarks—This genus was described by Schopf (1968) to encompass sheath-less trichome of oscillatoriacean cyanobacteria similar to modern genus *Oscillatoria* Vaucher. Subsequently, this genus was emended by Mendelson and Schopf (1982) as purely formal to include all *Oscillatoria*-like or *Lyngbya*-like trichomes encompassed by indistinct sheath less then 1 μm thick. Later on, Butterfield in Butterfield *et al.* (1994) has emended this genus again to include unbranched, uniseriate cellular trichomes with cell length less or equal to cell diameter. However, in our opinion, Butterfield oversimplified this problem and included in this genus many morphologically distinguishable species which probably should be referred to other genera. We disagree to synonymies the genus *Oscillatoriopsis* many morphologically different trichomes of genera *Anabaenidium*, *Cephalophytarion*, *Obconicophycus* and others because many of them are definitely remnants of other taxa. Butterfield in Butterfield *et al.*, 1994 merged more than 75 (54 accepetd by him as beloning to this genus) different species of *Oscillatoriopsis* and other genera known by then into 4 species based on diameter of trichome cells only. It definitely complicated the problem of *Oscillatoriopsis* and other taxonomical treatment of Precambrian filamentous microfossils because ranges of these species overlapped and morphological features provide additional base for recognition of species of genus *Oscillatoriopis*. Therefore, in general, we do not accept either formal synonymy of genus *Oscillatoriopsis* or formal separation into four main species. However, we do not either provide the new comprehensive revision of genus *Oscillatoriopsis* or other relevant genera as it is beyond the scope of the present paper. A list of some broadly recognized species of this genus is given below. It should be noted that there are 91 species of the genus *Oscillatoria* presented in the monograph by Elenkin (1949). There are bound to be overlapping of size ranges but distinct medial and terminal cells warranting their independent status as species.

Contents—O. breviconvexa, O. cuboides, O. longa, O. majuscula, O. media, O. obtusa, O. psilata, O. schopfii and *O. vermiformis* (Table-13).

Age—Proterozoic.

Oscillatoriopsis breviconvexa Schopf and Blacic, 1971

(Pl. 16. 4; Fig. 42A)

Oscillatoriopsis breviconvexa Schopf and Blacic, 1971, p. 943, Pl. 105, fig. 5; Ogurtsova and Sergeev, 1987, Pl. IX, Figs 7а, 7б; Yankauskas, 1989, Pl. XXIV, fig. 11; Schopf, 1992b, pl. 31, fig. C; Sergeev, 1992a, p. 86-87, Pl. XVIII, Figs 6а-6в; Srivastava and Kumar, 2003, p. 28, Pl. 7, Figs 4, 10; Sergeev, 2006, Pl. XLV, Figs 5, 8, 9; Sergeev and Schopf, 2010, p. 383, fig. 6.3.

Name of species	Diagnostic features	Cells width and length μm	Palaeoenvironmental setting	Repository and type locality	References
O. cuboides Knoll *et al.*, 1988 Fig. 42D	Trichomes are formed of isodiametric cells.	11.0-3.0 x 10.0-12.0	Shallow water marine environment, recorded from cherts in dolomites.	CPC-27316; Palaeoproterozoic, Duck Creek Dolomite Fm., Australia.	Knoll *et al.*, 1988
O. majuscula Knoll, 1988 Fig. 42E	Trichomes are formed of very broad and short pill like cells.	63.0 x 6.0-11.0	Shallow water marine environment, recorded from cherts in dolomites.	CPC-27317; Palaeoproterozoic, Duck Creek Fm., Australia.	Knoll *et al.*, 1988
O. longa Timofeev & Hermann, 1979	Trichomes formed by wide pill-like cells.	25.0 x 5.0-6.0	Shallow subtidal middle shelf environment, recorded from shales.	IGGP-19/6-76/6, Neoproterozoic, Nuryen Fm., Siberia.	Timofeev & Hermann, 1979
O. psilata Maithy & Shukla, 1977	Cells of trichomes are discoidal.	6-8 x 4	Lacustrine deposit, recoded from shales.	BSIP-4929; Mesoproterozoic, Suket Shale Fm., India	Maithy & Shukla, 1977
O. Schopfii J. Oehler, 1977 Fig. 42F	Medial cells of the trichomes cylindrical to alternately biconcave and biconvex cells.	3.9-5.5 x 1.8-2.9	Subtidal, recorded from cherts in shales.	CPC-16921; Mesoproterozoic, Barney Creek Fm., Australia	J. Oehler, 1977
O. vermiformis Schopf, 1968	Trichome formed of cylindrical cells.	1.0-3.0	Peritidal flat and pluvial lakes, recorded from cherts in dolomites.	HUHPC-58467; Neoproterozoic, Bitter Springs Fm., Australia.	Schopf, 1968

Table 13—Comparative characteristics of genus *Oscillatoriopsis* species (Type Specimens).

Repository—HUHPC-58564.

Stratum tipicum-Neoproterozoic, Bitter Springs Formation, Australia.

Description—Uniseriate, straight to gently curved, unbranched and evidently unsheathed trichomes occurring commonly in loosely interwoven clusters of a few to several specimens. Terminal cells are rounded to hemispheroidal; medial cells are disc-shaped to cuboidal, translucent, 5.5 to 9.0 μm wide and 1.0 to 9.0 μm long and have a width to length ratio ranging from 1 to 5; trichome length ranges up to 100 μm. Lateral and transverse cell walls are distinct, translucent, fine-grained, and ~ 0.5 μm thick.

Remarks—Oscillatoriopsis breviconvexa is distinguished from other species of *Oscillatoriopsis* by its characteristic cell dimensions.

Age and distribution—Neoproterozoic: Bitter Springs Formation, Australia; Chichkan Formation, South Kazakhstan.

Oscillatoriopsis media Mendelson and Schopf, 1982

(Pl. 16. 3; Fig. 42B)

Oscillatoriopsis media Mendelson and Schopf, 1982, p. 64-65, Pl. 4, Figs 3, 5, 6; Sergeev and Krylov, 1986, p. 93-94, Pl. X, fig. 7; Ogurtsova and Sergeev, 1987, Pl. IX, Figs 1, 2; Yankauskas, 1989, p. 116, Pl. XXIV, fig. 1, Pl. XXXII, fig. 6; Krylov *et al.*, 1989, Pl. I, fig. 8; Schopf, 1992b, Pl. 10, Figs F, H; Sergeev, 1992a, p. 87-88, Pl. XVI, fig. 4, Pl. XVIII, Figs 1, 2; Sergeev, 2001, p. 441-442, Figs 7.1-7.6, 7.11-7.13; Sergeev, 2006, p. 205-206, Pl. XIX, Figs 1-6, 11-13, Pl. XLIV, fig. 10, Pl. XLV, Figs 1, 2; Sharma, 2006a, p. 90-91, fig. 12c; Sergeev *et al.*, 2008, Pl. 6, fig. 3; Sergeev and Schopf, 2010, p. 383, 385, Figs 7.1-7.5; Schopf *et al.*, 2010, Figs 3.3-3.11.

Repository—UCLA-59035.

Stratum tipicum-Meso-Neoproterozoic, Sukhaya Tunguska Formations, Turukhansk Uplift, Siberia.

Description—Uniseriate unbranched trichomes without sheaths, occurring singly or in loosely intertwined small clusters. Terminal cells are blunt-rounded; medial cells are disc-shaped, translucent, 8.0 to 14.0 μm wide and 1.5 to 5.0 μm long having a width to length ratio ranging from 3 to 5 and sometimes occurring in distinct pairs; trichomes range up to 200 μm long. Lateral and transverse cell walls are distinct, translucent, fine-grained, 0.5 to 1.0 μm thick.

Remarks—Oscillatoriopsis media is distinguished from other species of *Oscillatoriopsis* by its characteristic cell dimensions.

Age and distribution—Meso-Neoproterozoic: Sukhaya Tunguska and Burovaya Formations, Turukhansk Uplift, Siberia; Neoproterozoic: Bitter Springs Formation, Australia; Min'yar Formation, southern Ural Mountains, Russia; Chichkan Formation, South Kazakhstan and Tian Shan Mountains.

Oscillatoriopsis obtusa Schopf, 1968, emend. Butterfield, 1994 (in Butterfield *et al.*, 1994)

(Pl. 16.5-8; Fig. 42C)

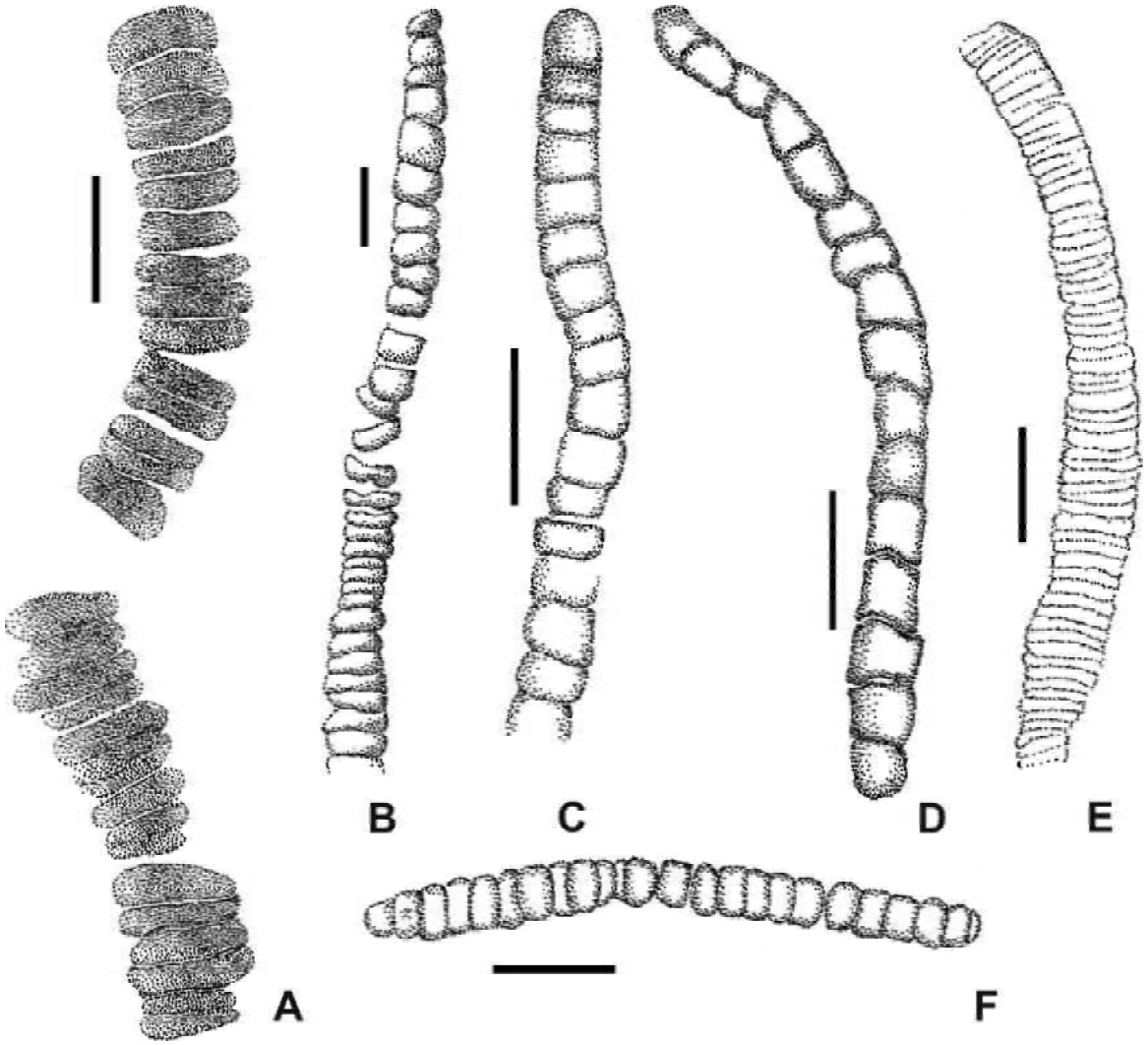


Fig. 42—Line diagrams of species of *Oscillatoriopsis*. A- *O. breviconvexa* (Schopf & Blacic, 1971); B- *O. media* (Mendelson & Schopf, 1982); C- *O. obtusa* (Schopf, 1968); D- *O. cuboides* (Knoll *et al*., 1988); E- *O. majuscula* (Knoll *et al*., 1988); F- *O. Schopfii* (J. Oehler, 1977). Scale bar =A-C= 10 µm, D = 25 µm, E= 100 µm, F= 10 µm.

Oscillatoriopsis obtusa Schopf 1968, p. 667, Pl. 77, fig. 8; Schopf, 1992b, Pl. 31, fig. G; Butterfield *et al.*, 1994, p. 58, Figs 24A-24E, 24K; Sergeev, 2001, p. 441, fig. 9.4; Srivastava and Kumar 2003, p. 28, Pl. 9, fig. 4; Tiwari and Pant, 2004, Figs 3h, 3j; Sergeev, 2006, p. 204, 205, Pl. XVIII, fig. 4; Sergeev and Schopf, 2010, p. 385, Figs 6.5, 6.5a, 6.5b, 6.5c.

Repository—HUHPC-58448.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Solitary or in loose clusters, uniseriate, unbranched trichomes without sheaths. Terminal cells when preserved are blunt or rounded; medial cells pill-like, translucent or dark, sometimes arranged in pairs, 3.5-6.5 µm wide and 3.0-5.0 µm long; width/length ratio varies from 1.2 to 1.5, maximum length of the trichomes up to 110 µm. Cross walls distinct or missing; cell walls are translucent, fine-grained, 0.5-1.0 µm thick.

Remarks—Oscillatoriopsis obtusa can be distinguished from other species of *Oscillatoriopsis* by its cell dimensions and distinct blunt and rounded terminal cells. Schopf (1968) described this form as type specimen from the Bitter Springs Formation of Australia; later on Butterfield in Butterfield *et al.* (1994) emended this species, restricting to only those specimens of 3-8 µm width specimens, and synonymized with it many other species of genus *Oscillatoriopsis* and other genera *viz*., *Cephalophytarion*, *Primorivularia*, *Cyanonema* and *Obconicophycus*. As mentioned above we do not consider all such species listed in the Butterfield *et al*. (1994) as synonymies.

Age and distribution—Widely distributed in Proterozoic chert and organic-walled assemblages.

Genus—PALAEOLYNGBYA Schopf, 1968, emend. Butterfield, 1994 (in Butterfield *et al.*, 1994)

Palaeolyngbya Schopf, 1968, p. 665; Butterfield in Butterfield *et al.*, 1994, p. 60-61.

Type species—Palaeolyngbya Barghoorniana Schopf, 1968.

Diagnosis—Unbranched uniseriate trichomes composed of discoidal to cylindrical cells without any constrictions at septa and surrounded by prominent uni-or multilayered smooth sheaths. Uncollapsed sheath diameter is the principal criterion for determining various species of *Palaeolyngbya*.

Remarks—Genus *Palaeolyngbya* is considered as fossil counterpart of modern cyanobacterium *Lyngbya* Agardh. Butterfield in Butterfield *et al.* (1994) suggested that the name *Palaeolyngbya* be restricted for the smooth-walled filamentous sheaths containing regular uniseriate array of prominently preserved cells. Like genus *Oscillatoriopsis*, many species were described under genus *Palaeolyngbya*, but their number was reduced drastically after the Butterfield's revision. He formally categorized all filaments surrounded by sheath into three or four species using diameter as a criterion: *P. Barghoorniana, P. catenata, P. hebeiensis* and *P. giganteus*. As in the case with *Oscillatoriopsis*, this revision probably oversimplified the situation significantly because some species in the real distinctive populations have overlapping size ranges. If one considers the diversity of modern genus *Lyngbya*, it can be found out that Elenkin (1949) listed 62 species under this genus with overlapping size ranges, but distinguishable morphological variability. Therefore, accepting in part the revision of genus *Palaeolyngbya* suggested by Butterfield in Butterfield *et al.* (1994), we retain some other previously described species as well.

Contents—P. Barghoorniana, P. catenata, P. hebeiensis, P. giganteus and *P. helva* (Table-14).

Age—Proterozoic.

Palaeolyngbya Barghoorniana Schopf, 1968

(Fig. 43A)

Palaeolyngbya Barghoorniana Schopf, 1968, p. 665-666, Pl. 77, Figs 1-5; Schopf, 1972, fig. 8, 11; Venkatachala *et al.*, 1990a, p. 32, Pl. 1, fig. 4; Nautiyal, 1990, Pl. II, fig. 15; Schopf, 1992b, Pl. 32, fig. C;

Repository—HUHPC-58441.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Unbranched uniseriate trichomes composed of discoidal medial cells and rounded terminal cells without any constrictions at septa and surrounded by prominent unilayerd smooth sheaths. Diameter of medial cells 8.3-10.9 μm width and 2.6-3.1 μm length. Cross walls distinct or missing; cell walls are translucent, fine-grained, less than 0.5 μm thick. Sheath hyaline, nonlamellated and pronounced, adjacent to terminal cells where it is 1 μm.

Age and distribution—Neoproterozoic: Bitter Springs Formation, Australia; Infra-Krol and the Gangolihat Dolomite Formations, India.

Palaeolyngbya catenata Hermann, 1974

(Pl. 18.1-5, 8; Fig. 43B)

Palaeolyngbya catenata Hermann, 1974, p. 8-9, Pl. 6, fig. 5; Butterfield *et al.*, 1994, p. 61, Figs 25F-25G; Sergeev and Lee Seong-Joo, 2001, p. 6, Pl. I, Figs 4-6; Sergeev and Lee Seong-Joo, 2004, p. 13, 15, Pl. II, Figs 1-3; Srivastava and Kumar, 2003, p. 30, 32, Pl. 9, Figs 5, 7; Sergeev, 2006, p. 207, Pl. XXII, Figs 4-6, Pl. XXVII, Figs 1-3; Sergeev *et al.*, 2008, Pl. 4, fig. 5, Pl. 7, fig. 12, Pl. 9, fig. 4.

Palaeolyngbya maxima Zhang Y., 1981, p. 495, Pl. 2, Figs 4, 6, 7; Sergeev *et al.*, 1994, p. 30, Pl. III, fig. 8.

Oscillatoriopsis robusta Horodyski and Donaldson, 1980, p. 149-152, fig. 13 H.

Name of species	Diagnostic features	Sheath diameter, μm	Palaeoenvironmental setting	Repository and type locality	References
P. hebeiensis Zhang Y. & Yan, 1984	Trichomes composed of large discoidal cells surrounded by single layered sheath.	30.0-60.0	Restricted tidal flat, recorded from cherts in dolomites.	TIGMR-82029-1 Mesoproterozoic, Gaoyuzhuang Fm., China.	Zhang Y. & Yan, 1984
P. giganteus Yakschin, 1991	Trichomes composed of huge discoidal cells surrounded by hyaline thin sheath.	42.0-85.0	Peritidal flat recorded from cherts in dolomites.	CSGM – 309; Mesoproterozoic, Kotuikan Fm., Siberia.	Yakschin, 1991
P. helva Hermann, 1981	Trichomes composed of discoidal cells tightly encrusted by hyaline thin sheath.	11.0-14.0	Open shelf environments, recorded from shales.	IGGP – 27/6; Neoproterozoic, Miroedikha Fm., Siberia.	Hermann, 1981

Table 14—Comparative characteristics of genus *Palaeolyngbya* species (Type Specimens).

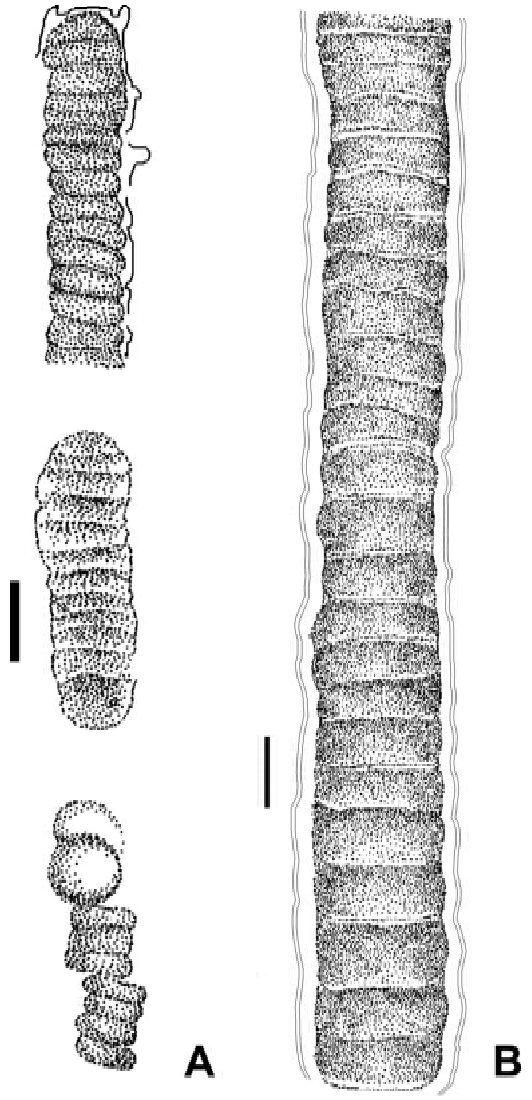


Fig. 43—Line diagrams of species of *Palaeolyngbya*. A- *P. Barghoorniana* (Schopf, 1968); B- *P. catenata* (Zhang Y., 1981). Scale bar = 10 μm.

Scalariphycus tianzimiaoensis Song, 1982, p. 218, Pl. 32, Figs 9-11.

Oscillatoriopsis sp.: Krylov and Sergeev, 1986, p. 100, Pl. I, Figs 3, 4; Yankauskas, 1989, Pl. XXII, fig. 3; Sergeev, 1992a, p. 88, Pl. V, fig. 6.

Repository—IGGP-49/2T.

Stratum typicum—Neoproterozoic, Miroedikha Formation, Turukhansk Uplift, Siberia.

Description—Unbranched uniseriate trichomes composed of discoidal medial cells and rounded terminal cells without any constrictions at septa and surrounded by prominent unilayered or multilayered smooth sheaths. Medial cells are 14.0-33.0 μm wide and 2.0-8.0 μm long, length/width ratio varies from 3 to 7. Cross walls distinct; cell walls are translucent, fine-grained, 0.5-1.0 μm thick. Sheath transparent, prominent, lamellated or non-lamellated, 19.0-40.0 μm wide, 0.5-2.5 μm thick and up to 200 μm long.

Age and distribution—Widely distributed in Proterozoic chert and organic-walled assemblages.

Genus—PARTITIOFILUM Schopf and Blacic, 1971, emend. Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

Partitiofilum Schopf and Blacic, 1971, p. 947; Sergeev *et al.*, 1995, p. 29.

Type species—Partitiofilum gongyloides Schopf and Blacic, 1971

Diagnosis—Solitary, uniseriate, short, sheathless unbranched trichomes composed of pill-like medial and hemispherical terminal cells, not constricted at septa.

Remarks—Partitiofilum was described by Schopf and Blacic (1971) as monospecific genus from the Bitter Springs Formation of Australia and the type species *Partitiofilum gongyloides* incorporates short non-constricted incomplete trichomes. Butterfield in Butterfield *et al.* (1994) has transferred the species of genus *Partitiofilum* to genus *Oscillatoriopsis* considering the short trichomes of the former species as the ecological or reproductive variants (hormogonia) of the latter. Subsequently, but independently, this taxon was emended by Sergeev *et al.* (1995) to incorporate short complete trichomes formed of pill-like cells, non-constricted at septa which are probably hormogonia of various species of hormogonian cyanobacteria. Therefore, we prefere to keep this taxon separately as a formal taxon (cf. Lee Seong-Joo & Golubic, 1998) and in the present usage, the principal distinction between *Oscillatoriopsis* and *Partitiofilum* lies in trichome's length and between *Filiconstrictosus* and *Partitiofilum* on septal constriction (Sergeev *et al.*, 1995). However, *P. yakschinii* from the Kotuikan Formation of the Anabar Uplift, Siberia, could be either hormogonia or germinated akinetes.

Contents—P. gongyloides and *P. yakschinii.*

Age—Meso-Neoproterozoic (possibly Palaeoproterozoic as well).

Partitiofilum gongyloides Schopf and Blacic , 1971

(Fig. 44A)

Partitiofilum gongyloides Schopf and Blacic, 1971, p. 947, Pl. 105, fig. 3, Pl. 106, fig. 6; Schopf, 1992b, Pl. 30, fig. P.

Repository—HUHPC-58562.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

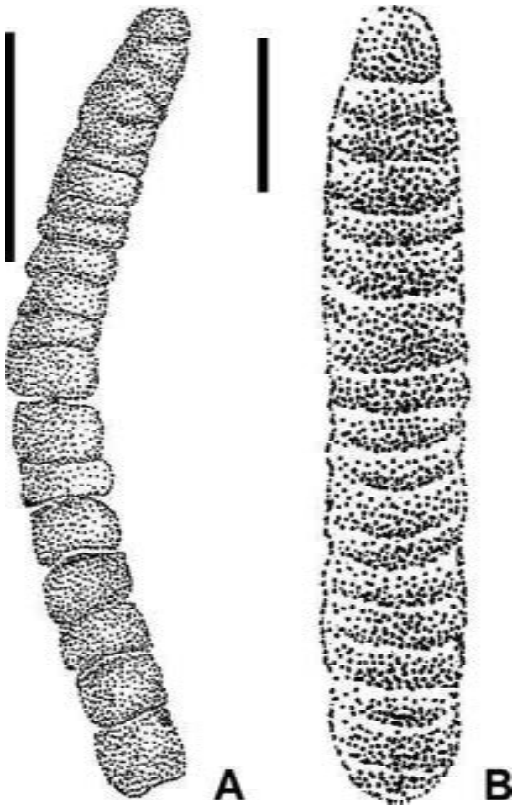


Fig. 44—Line diagrams of species of *Partitiofilum*. A- *P. gongyloides* (Schopf & Blacic, 1971); B- *P. yakschinii* (Sergeev *et al*., 1995). Scale bar = 10 μm.

Description—Solitary, uniseriate, unbranched, short trichomes without extra-cellular sheaths. Medial cells are cylindrical, more or less isodiametrical, 3.7-4.7 μm wide and 1.7-2.7 μm long, width/length 1.5 to 2; maximum trichome length is 55 μm. Terminal cells are rounded, hemispherical, 2.0-3.5 μm wide, cross walls indistinct, non-granulated. The trichomes are usually arranged in a broken line.

Remarks—The short trichomes of *P. gongyloides* from the Bitter Springs Formation arranged in a line are definitely hormogonians which was unclear in the original palaeontological plates of Schopf and Blacic (1971).

Age and distribution—Neoproterozoic, Bitter Springs Formation, Australia.

Partitiofilum yakschinii Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

(Pl. 17.5-8; Fig. 44B)

Partitiofilum yakschinii Sergeev and Knoll in Sergeev *et al.*, 1995, p. 29, Figs 15.5-15.8; Sergeev, 2006, p. 203-204, Pl. VII, Figs 5-8; Sergeev *et al.*, 2008, Pl. 1, Figs 2, 3, 6, 11.

Repository—HUHPC-62923.

Stratum typicum—Mesoproterozoic (Lower Riphean), Kotuikan Formation, Anabar Uplift, Siberia.

Description—Solitary, uniseriate, unbranched, short trichomes sometimes enclosed by faint extra-cellular sheaths. Terminal cells more or less hemispherical, 5.5-9.0 μm wide and 2.5-4.5 μm long; width/length 2 to 3 (7 cells measured). Medial cells pill-like, 6.0-14.0 μm wide and 1.5-5.0 μm long; width/length 2 to 7. Maximum trichome length 65 μm. Cross walls distinct; thin spaces may separate adjacent cells. Sheath nearly transparent, non-laminated, hyaline, < 0.5 μm thick.

Remarks—Partitiofilum yakschinii is distinguished from *P. gongyloides* by its larger cells. Mikhailova (in Yankauskas, 1989) has described a third species, *P. tungusum*, from shales of the lower Neoproterozoic Derevnya Formation, Turukhansk Uplift, Northern Siberia; cells in this species are larger than those of *P. yakschinii*; we concur with Butterfield in Butterfield *et al*. (1994) who transfered the Derevnya form to *Oscillatoriopsis*. The short trichomes of *Partitiofilum yakschinii* from the Kotuikan Formation can be either hormogonians or germinated akinetes.

Age and distribution—Mesoproterozoic, Kotuikan Formation, Anabar Uplift, Siberia.

Genus—SIPHONOPHYCUS Schopf, 1968, emend. Knoll and Golubic, 1979, emend. Knoll *et al.*, 1991

Siphonophycus Schopf, 1968, p. 671; Knoll *et al.*, 1991, p. 563; Butterfield *et al.*, 1994, p. 62, 64.

Eomycetopsis Schopf, 1968, p. 684, 685; Knoll and Golubic, 1979, p. 149.

Leiotrichoides Hermann, 1974, p. 7.

Tenuofilum Schopf, 1968, p. 679.

Euryaulidion Lo, 1980, p. 144-146.

Type species—Siphonophycus kestron Schopf, 1968.

Diagnosis—Unbranched non-septate cylindrical tubes, or somitemes with rare septa, occasionally solitary, but mostly gregarious in tangled masses. Dense masses of tubes sometimes aligned parallel or perpendicular to bedding lamination. Frequently inconspicous casts of trichome septa can be preserved on tube walls.

Remarks—Siphonophycus tubes are regarded as empty sheaths of LPP-type oscillatorian or nostocalean cyanobacteria and is a predominant mat-building organism in many Proterozoic microbenthic assemblages (Knoll & Golubic, 1979; Mendelson & Schopf, 1982; Knoll *et al.*, 1991; Sergeev, 1992a, 2006). Dense masses of *Siphonophycus* tubes, observed in fossil records, are interpreted as remains of cyanobacterial mats. Coccoidal microfossils often nested these mat fragments are either remains of chroococcacean dwellers or planktonic microorganisms buried onto these mats. In general *Siphonophycus* is a form genus embracing remains of various

Name of the species	Diagnostic features	Tube width μm	Palaeoenvironmental setting	Repository and type locality	References
S. punctatum Maithy, 1975	Tubes with open ends.	32.0-64.0	Subtidal recorded from shales.	MRAC-32453/2; Neoproterozoic, Bushimay Group, Zaire.	Maithy, 1975; Buick & Knoll, 1999
S. thulenema Butterfield, 1994 Fig. 45c	Thread-like filaments.	0.5-1.0	Subtidal recorded from shales.	HUHPC-62718; Neoproterozoic, Svanbergfjellet Fm., Spitsbergen.	Butterfield *et al.*, 1994

Table 15—Comparative characteristics of genus *Siphonophycus* species (Type Specimens).

hormogonian cyanobacteria and sometimes probably morphologically similar pro-or eukaryotic microorganisms as well. But most Precambrian fossilized tubes are certainly empty sheaths of oscillatoriacean cyanobacteria. This genus is conveniently separated into species on the basis of tube diameters (Butterfield *et al.*, 1994).

It should be noted that type specimens of *S. solidum* and *S. typicum* probably belong to eukaryotic algae, not cyanobacteria. Both *Leiotrichoides typicus* Hermann, 1974 and *Omalophyma solida* Golub, 1979 have robust translucent to opaque sheaths with prominent ornamentation and sometime fringe margines. Other species that are remains of true cyanobacteria rather to be selected, e.g. *S. inornata* Zhang Y., 1981 instead of *S. typicum*. However, considering that during last 15 years the classification was broadly used we do not like complicate situation with these very morphological simple remains of filamentous microorganisms.

Contents—*S. kestron, S. punctatum, S. robustum, S. septatum, S. solidum, S. thulenema* and *S. typicum* (Table-15).

Age—Proterozoic.

Siphonophycus kestron Schopf, 1968

(Pl. 20. 1, 2, 7; Fig. 45A-A')

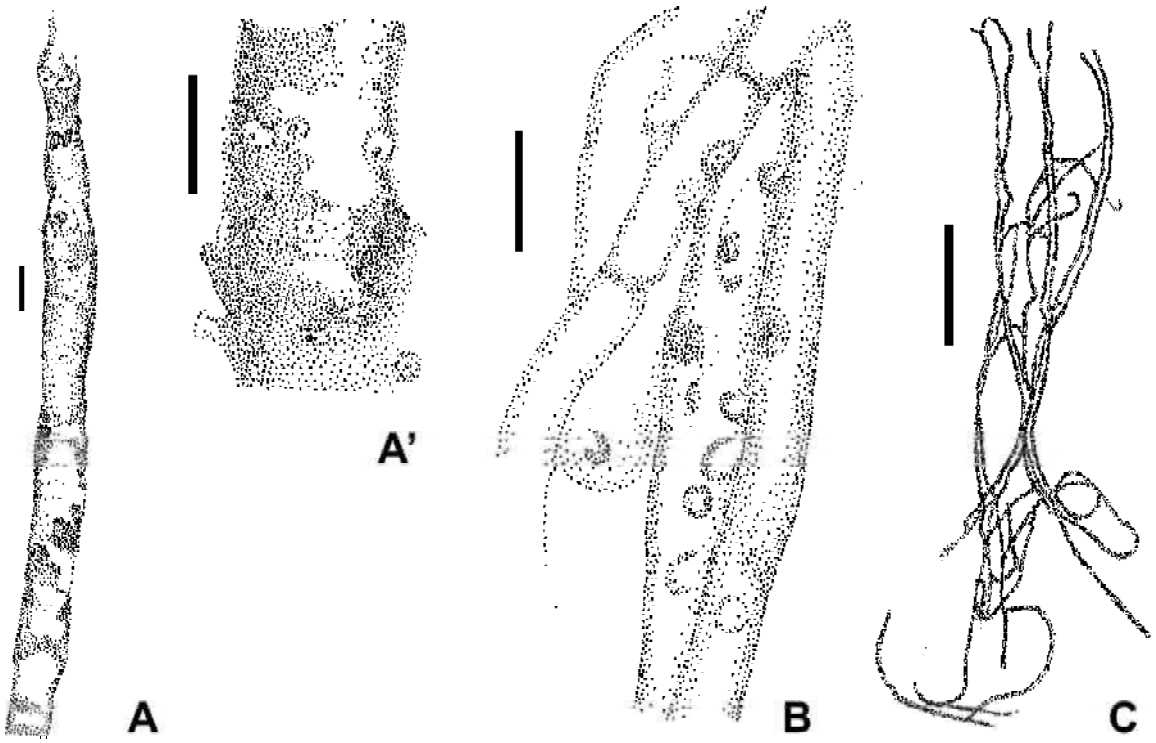


Fig. 45—Line diagrams of species of *Siphonophycus*. A, A'- *S. kestron* (Schopf, 1968); B- *S. typicum* (Zhang Y., 1981); C- *S. thulenema* (Butterfield *et al*., 1994). Scale bar = 10 μm.

PLATE 17

Hormogonian cyanobacteria genera *Filiconstrictosus* Schopf and Blacic, 1971 and *Partitiofilum* Schopf and Blacic, 1971.

1, 9. *Filiconstrictosus magnus* Yakschin, 1991, Sample No 4689-48, Slide No 576, p. 26, EFL F-38-0, GINPC No 478; 9 —Sample No 4689-47a, Slide No 574, EFL P-41-2, HUHPC No 62943 .

2, 3. *Filiconstrictosus majusculus* Schopf and Blacic, 1971 (a single specimen shown at two focal depths), Sample No 4689-47b, Slide No 563, p. 4, EFL O-29-2, HUHPC No 62946.

4. *Filiconstrictosus cephalon* Sergeev and Knoll, 1995, Sample No 4689-53, Slide No 53A, EFL G-61-3, HUHPC No 62922 (Holotype).

5-8. *Partitiofilum yakschinii* Sergeev and Knoll, 1995; 5 —Sample No 4689-53, Slide No 578, p. 32, GINPC No 1120; 6 —Sample No 4689-48, Slide No 565, p. 17, EFL O-34-3, GINPC No 479; 7 —Sample No 4689-47a, Slide No 571, p. 18, EFL L-48-2, HUHPC No 62944 (Holotype); 8 —Sample No 4689-50, Slide No 551, p. 16, EFL O-37-1, GINPC No 481.

All specimens are from the Kotuikan Formation.

PLATE 18

Hormogonian cyanobacteria genera *Palaeolyngbya* Schopf, 1968 and *Siphonophycus* Schopf, 1968.

1, 2 (upper square in 1), 3 (lower square in 1), 4, 5, 8. *Palaeolyngbya catenata* Hermann, 1974: 1-3 —Sample No 4698-18, Slide No 788, p. 10, GINPC No 652; 4 —Sample No 3893-303, Slide No 327, p. 8, GINPC No 34; 5 —Sample No 3893-303, Slide No 337, p. 6, GINPC No 33; 8 —Sample No 3893-256, Slide No 130, p. 3, GINPC No 35.

6, 7. *Palaeolyngbya* sp.: 6 —Sample No 3893-999, Slide No 21, p. 2, GINPC No 129; 7 —Sample No 3893-205, Slide No 62, p. 12, GINPC No 128.

9-11. *Siphonophycus solidum* (Golub, 1979) (empty sheaths with shrunken trichomes inside): 9 —Sample No 4681-26, Slide No 329, p. 1, GINPC No 143; 10 —Sample No 4681-53, Slide No 317, p. 1, EFL U-33-1, GINPC No 144; 11 —Sample No 3893-256, Slide No 129, p. 11, GINPC No 36.

Specimen GINPC No 652 (figs 1-3) is from the Svetly Formation, specimens GINPC No 33- 36 (figs 4, 5, 8 and 11) are from the Satka Formation, specimens GINPC No 128 and 129 (figs 6 and 7) are from the Minyar Formation, and specimens GINPC No 143 and 144 (figs 9 and 10) are from the Chichkan Formation.

PLATE 19

Oscillatoriacean cyanobacterium genus *Obruchevella* Reitlinger, 1948.

1-6, 14. *Obruchevella parva* Reitlinger, 1959: 1, 3, 4, 5 —Sample No 4681-102; 1 —Slide No 365, p. 2, GINPC No 200; 3 —Slide No 391, p. 11, GINPC No 202; 4, 5 (a single specimen shown at two focal depths) —Slide No 369, p. 10, GINPC No 204; 2 —Sample No 4681-18, Slide No 366, p. 7, GINPC No 201; 6, 14 —Sample No 4681-115, Slide No 375; 6 —p. 13, GINPC No 193; 14 —p. 9, GINPC No 194.

7. *Obruchevella* cf. *meishucunensis* Song, 1984, Sample No 4681-102, Slide No 391, p. 17, GINPC No 197.

8, 9. *Obruchevella delicata* Reitlinger, 1948 (a single specimen shown at two focal depths), Sample No 4681-102, Slide No 391, p. 17', GINPC No 206.

10. *Obruchevella parvissima* Song, 1984, Sample No 4681-20, Slide No 370, p. 2, GINPC No 205.

11, 12. *Obruchevella exilis* Sergeev, 1992 (a single specimen shown at two focal depths), Sample No 4681-26, Slide No 255, p. 13, EFL P-23-2, GINPC No 154 (Holotype).

13, 15, 16. *Obruchevella* sp.: 13 —(a single spiral encapsulated inside a secondary phosphate envelope), Sample No 4681-102, Slide No 391, p. 6, GINPC No 207; 15 —Sample No 4681-98, Slide No 394, p. 1, GINPC No 1119; 16 —Sample No 4698-48, Slide No 819, p. 9, GINPC No 674.

Specimens GINPC No 193, 194, 197, 200-202, 204-207 and 1119 (figs 1-10, 13-15) are from the Chulaktau Formation, specimen GINPC No 154 (figs 11and 12) is from the Chichkan Formation and specimen GINPC No 674 (fig. 16) is from the Yudoma Group.

PLATE 20

Empty sheaths of hormogonian cyanobacteria genera *Siphonophycus* Schopf, 1968, and *Circumvaginalis* Sergeev, 1993.

1, 2, 7. *Siphonophycus kestron* Schopf, 1968: 1 —Sample No 3893-130, Slide No 34, EFL D-36-4, GINPC No 130; 2 —Sample No 4681-30, Slide No 266, p. 13, EFL S-25-0, GINPC No 142; 7 —Sample No 4688-412, Slide No 865, p. 21, GINPC No 723.

3. *Circumvaginalis* sp., Sample No 4694-85, Slide No 617, p. 7, GINPC No 537 (in fact, the sheath of *Siphonophycus kestron* Schopf, 1968 pigmented with the transverse rings).

4, 5 (enlarged fragment of 4). *Siphonophycus solidum* (Golub, 1979) in mat formed by filaments of *Siphonophycus robustum* Schopf, 1968, *S. typicum* (Hermann, 1974) and *S. kestron* Schopf, 1968, Sample No 4698-18, Slide No 837, p. 8, GINPC No 650.

6, 8. *Siphonophycus solidum* (Golub, 1979): 6 —Sample No 4688-34, Slide No 442, p. 3, GINPC No 88; 8 —Sample No 4688-412, Slide No 866, p. 10, GINPC No 721.

Specimen GINPC No 130 (fig. 1) is from the Minyar Formation, specimen GINPC No 142 (fig. 2) is from the Chichkan Formation, specimen GINPC No 537 (fig. 3) is from the Sukhaya Tunguska Formation, specimen GINPC No 650 (figs 4 and 5) is from the Svetly Formation, specimen GINPC No 88 (fig. 6) is from the Avzyan Formation, and specimens GINPC No 721 and 723 (figs 7 and 8) are from the Satka Formation.

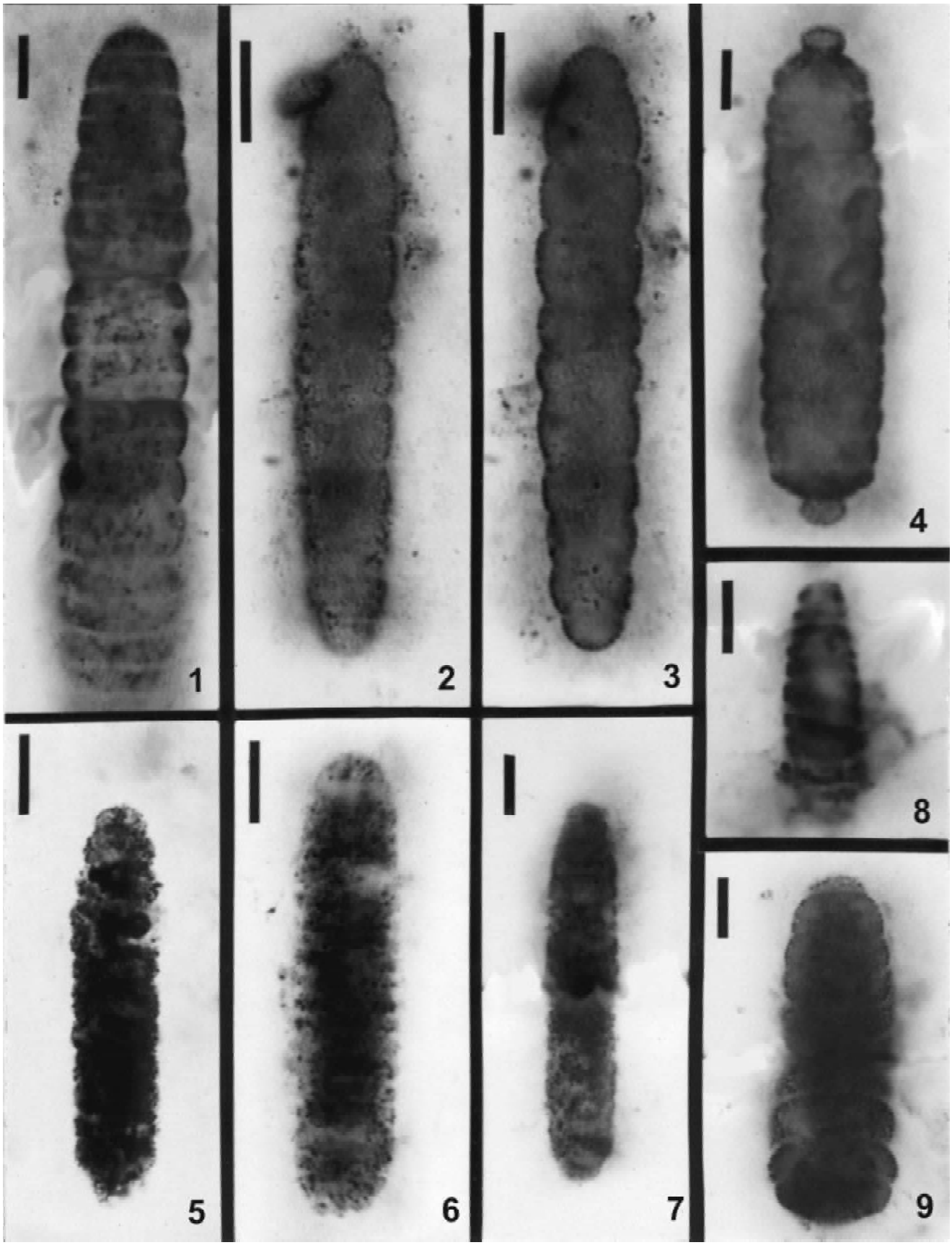


PLATE 17

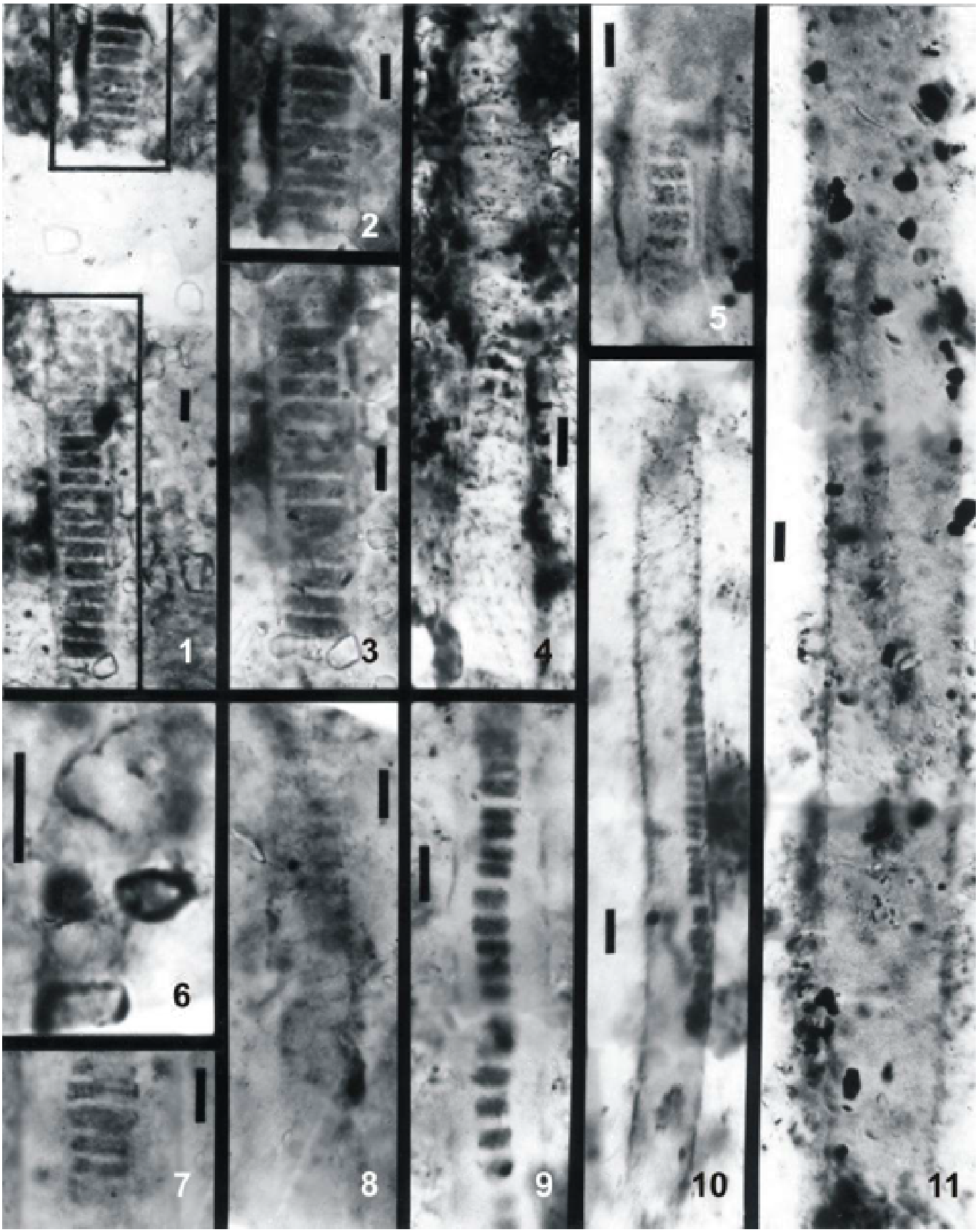


PLATE 18

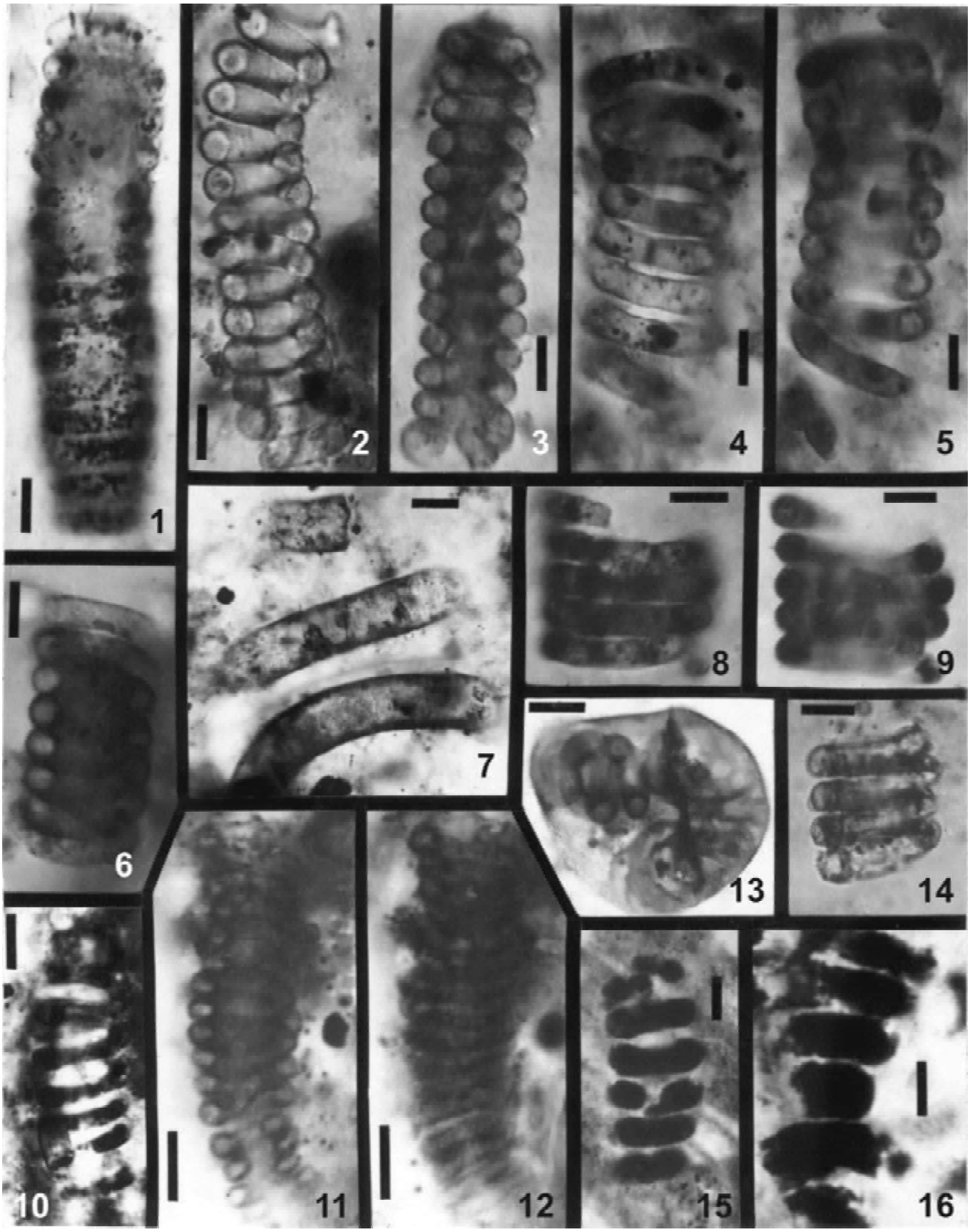


PLATE 19

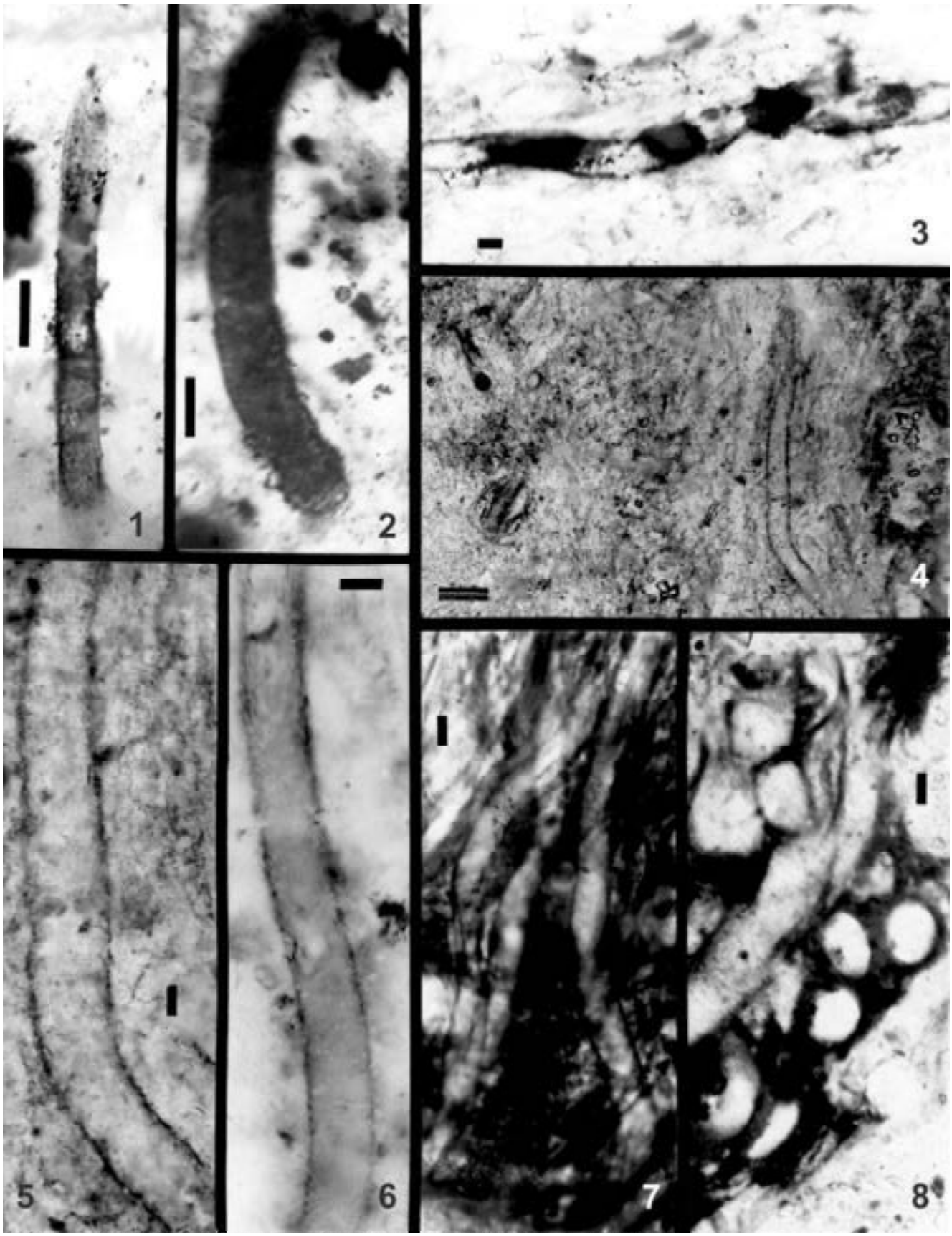


PLATE 20

Siphonophycus kestron Schopf, 1968, p. 671, Pl. 80, Figs 1-3; Schopf and Blacic, 1971, Pl. 109, Figs 3, 4; Shukla *et al.*, 1986, p. 349; Pl. 1, Figs 8, 14; Knoll *et al.*, 1989, fig. 8, 9; Green *et al.*, 1989, fig. 4c; Venkatachala *et al.*, 1990a, p. 32, 34, Pl. 1, fig. 3; Venkatachala *et al.*, 1990b, p. 478, Pl. 1, fig. 1; Tiwari and Azmi, 1992, p. 389, Pl. 1, fig. 8; Kumar and Srivastava, 1992, p. 316, Fig. 10-H; Sergeev, 1992a, p. 95, Pl. XVI, Figs 8, 9; Schopf, 1992c, Pl. 31, fig. J; Butterfield *et al.*, 1994, p. 67, fig. 21D; Kumar and Srivastava, 1995, p. 114, Figs 13D, 14G, 14H; Tiwari, 1996, Pl. 1, fig. 12; Kumar and Venkatachala, 1998, p. 63, fig. 5h; Prasad and Asher, 2001, p. 112, Pl. 9, Figs 8, 12; Sergeev and Lee Seong-Joo, 2001, p. 8, Pl. I, Figs 1-3; Sergeev and Lee Seong-Joo, 2004, Pl. II, fig. 11; Sergeev and Lee Seong-Joo, 2006, Pl. I, fig. 10; Tiwari and Pant, 2004, Figs 3a-3c, 3k, 3o; Prasad *et al.*, 2005, pl. 1, fig. 10; Shukla *et al.*, 2005, p. 1223, fig. 2.18; Sergeev, 2006, p. 214-215, Pl. XXII, Figs 1, 2, Pl. XXVIII, fig. 3, Pl. XXXVI, fig. 3, Pl. XLIV, fig. 11, Pl. XLV, Figs 3, 6; Sergeev *et al.*, 2008, Pl. 4, fig. 8, Pl. 7, fig. 7, Pl. 9, Figs 1, 2, 7, Pl. 11, fig. 7; Sergeev and Schopf, 2010, p. 385, 387, fig. 8.5; Schopf *et al.*, 2010, Figs 2.1-2.4.

Leiothrichoides typicus Hermann, 1974 (partim) in Timofeev and Hermann, 1979, p. 138-139, Pl. XXIX, Figs 1, 2.

Omalophyma angusta Golub, 1979, p. 151-152, Pl. XXX, Figs 13-18.

Isiophyma stricta Golub, 1979, p. 154, Pl. XXXII, Figs 11-12.

Siphonophycus indicus Nautiyal, 1980, p. 3, fig. 1A.

Siphonophycus beltensis Horodyski, 1980, p. 654-656, Pl. 1, fig. 4.

Euryaulidion cylindratum Lo, 1980, p. 146, Pl. II, Figs 1-3.

Judomophyton unifarium Kolosov, 1982, p. 78, Pl. XI, fig. 5, Pl. XII, fig. 4.

Uraphyton distinctum Kolosov, 1982, p. 81-82, Pl. XIV, Figs 2а-2б.

Uraphyton evolutum Kolosov, 1982, p. 82-83, Pl. XIV, fig. 3, Pl. 15, fig. 1.

Gunflintia bruecknerii Nautiyal, 1982, p. 175-176, Figs 1H-1I.

Siphonophycus laishuiensis Zhang Y. and Yan, 1984, p. 198, 203, Pl. 1, Fig. 3.

Eomycetopsis contorta Zhu, 1984 in Zhu and Wane, 1984, p. 173-174, 183, Pl. 3, Figs 1-3, 6.

Eomycetopsis lata Golovenok and Belova, 1985, p. 99, Pl. VII, fig. 4; Yankauskas, 1989, p. 106-107, Pl. XX, fig. 4; Golovenok and Belova, 1993, Pl. II, fig. f.

Siphonophycus ganjingziensis Bu, 1985, p. 210, Pl. 1, Figs 1-5.

Taeniatum punctosum Du, 1985, p. 162, Pl. 2, Figs 22-23.

Siphonophycus sinensis Zhang Z., 1986, p. 32, 36, Pl. 1, fig. 1, 3, Pl. 2, fig. 4.

Siphonophycus sp_3 (partim): Sergeev, 1992a, p. 96, 97, Pl. XVIII, Figs 3, 7.

Repository—HUHPC-58469.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Tubes cylindrical to slightly compressed, unbranched, nonseptate or sometimes with rare septa, 8.0-16.0 μm in cross-sectional diameter; tube wall psilate or fine-granulated and up to 1 μm thick.

Remarks—Schopf (1968) pointed out that tube of type specimen *S. kestron* are somewhat tapered toward apices with broadly conical, bluntly pointed terminus. However, reinvestigation of type material has revealed that tubes are not taperng toward termini. Earlier reported cone-like structutes observed at ends of some *S. kestron* tubes (Schopf, 1968, Pl. 80, fig. 1) are of secondary origin and have been formed as a result of filaments folding.

Age and distribution—Widely distributed in Proterozoic silicified and organic-walled microbiotas.

Siphonophycus robustum (Schopf, 1968), emend. Knoll and Golubic, 1979, comb. Knoll, Swett and Mark, 1991

(Pl. 21.2, 4, 8-10; Figs 8, 9, 16, 17)

Siphonophycus robustum Knoll *et al.*, 1991, p. 565, Figs 10.3, 10.5; Butterfield *et al.*, 1994, p. 64, 66, Figs 26A, 26G; Sergeev *et al.*, 1994, Pl. 3, fig. 6; Kumar and Venkatachala, 1998, p. 6c; Sergeev *et al.*, 1997, p. 230, fig. 14A; Sergeev and Mudrenko, 1997, fig. 2и; Sergeev and Lee Seong-Joo, 2001, p. 6, Pl. 1, Figs 1, 2, 7, 11, 12; Sergeev, 2001, p. 442, Figs 7.8, 7.9; Sergeev, 2002, Pl. II, Figs 1, 3; Sergeev and Lee Seong-Joo, 2004, Pl. II, fig. 4; Prasad *et al.*, 2005, Pl. 1, fig. 7; Sergeev, 2006, p. 213-214, Pl. VI, Figs 9, 10, Pl. XVII, fig. 1, Pl. XIX, Figs 8, 9, Pl. XXII, Figs 1, 2, 7, 8, 11, 12, Pl. XXV, Figs 1, 3, Pl. XXVII, Figs 4, 5, Pl. XXVIII, fig. 2, Pl. XXXVI, fig. 1, 2, Pl. XLIV, Figs 1-7, 13, Pl. XLVI, Figs 7-10, Pl. XLVIII, fig. 4; Sharma, 2006a, p. 92, Figs 10c, 12a, 12d, 12 f; Sergeev *et al.*, 2008, Pl. 6, Figs 1, 5, 6, Pl. 9, Figs 1-3, 5-7; Sergeev and Schopf, 2010, p. 387, fig. 6.4.

Eomycetopsis robusta Schopf, 1968, p. 685, Pl. 82, Figs. 2, 3, Pl. 83, Figs 1-4; Knoll and Golubic, 1979, p. 149, Figs 4A, 4B; Mendelson and Schopf, 1982, p. 59, 60, 62, Pl. 1, Figs 9, 10; Sergeev, 1984, p. 436, Figs 2а-2г; Ogurtsova, 1985, p. 97-98, Pl. III, Figs 4, 6, Pl. X, Figs 1-6, Pl. XI, Figs 2, 3, 5, 6, Pl. XII, Figs 1, 3, 5, 7; Golovenok and Belova, 1989, Figs 1e-1k; Sergeev, 1992a, p. 93-94, Pl. VII, Figs 9, 10, Pl. XVI, Figs 3, 6, 7, 10, Pl. XIX, Figs 1, 5, 6, 7-10, Pl. XXIV, fig. 7; Golovenok and Belova, 1993, Pl. 2, fig. e.

Eomycetopsis filiformis Schopf, 1968, p. 685-686, Pl. 82, Figs 1, 4, Pl. 83, Figs 5-8 (for additional synonymy, see Butterfield *et al.*, 1994 and Sergeev, 1992a, 2006).

Repository—HUHPC-58491.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Unbranched nonseptate tubes, cylindrical to slightly compressed and 2.0 to 4.0 μm broad, rarely contain degraded trichome-like fragments; tube walls range from psilate to finely granulate and are up to 0.5 μm thick. Specimens are rarely solitary, typically occurring entangled in masses of many individuals aligned parallel, subparallel or, less commonly, perpendicular to the bedding lamination.

Age and distribution—Widely distributed both in chert-permineralized and compression-preserved Proterozoic assemblages.

Siphonophycus septatum (Schopf, 1968), comb. Knoll *et al.*, 1991

(Pl. 21.1)

Siphonophycus septatum Knoll *et al.*, 1991, p. 565, fig. 10.2; Butterfield *et al.*, 1994, p. 64, Figs 10H, 22G-22H; Sergeev, 2002, Pl. II, fig. 7; Sergeev and Lee Seong-Joo, 2004, Pl. II, fig. 10; Prasad *et al.*, 2005, Pl. 2, fig. 13; Sergeev, 2006, p. 213, Pl. XXV, fig. 7, Pl. XXVIII, fig. 1; Sharma, 2006a, p. 92-93, Figs 12b, 12h.

Tenuofilum septatum Schopf, 1968, p. 679, Pl. 86, Figs 10, 12.

Archaeotrichion contortum Schopf, 1968, p. 686, Pl. 86, Figs 1, 2.

Eomycetopsis? *campylomitus* Lo 1980, p. 143-144, Pl. I, Figs 9-11.

Judomophyton microscopicum Kolosov, 1982, p. 75, Pl. XI, fig. 1 (for additional synonymy, see Butterfield *et al.*, 1994 and Sergeev, 1992a, 2006).

Repository—HUHPC-58527.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Unbranched nonseptate cylindrical tubes 1.0 to 2.0 μm broad; tube walls range from psilate to finely granulate and less than 0.5 μm thick. Specimens are rarely solitary, typically occurring entangled in masses of many individuals aligned parallel, subparallel or, less commonly, perpendicular to the bedding lamination.

Age and distribution—Widely distributed both in chert-permineralized and compression-preserved Proterozoic assemblages.

Siphonophycus solidum (Golub, 1979), comb. Butterfield, 1994 (in Butterfield *et al.*, 1994)

(Pl. 18.9-11, Pl. 20. 4-6, 8)

Siphonophycus solidum Butterfield in Butterfield *et al.*, 1994, p. 67, Figs 25H, 25I, 27D; Sergeev *et al.*, 1997, p. 231, Figs 14I, 14K; Sergeev and Lee Seong-Joo, 2001, p. 8, pl. I, Figs 1-3; Sergeev, 2001, p. 442-443, fig. 7.7; Sergeev, 2002, Pl. II, fig. 15; Sergeev and Lee Seong-Joo, 2004, Pl. II, fig. 8; Sergeev and Lee Seong-Joo, 2006, pl. I, Figs 11, 12; Sergeev, 2006, p. 215, Pl. XVII, Figs 9, 10, Pl. XIX, fig. 7, Pl. XXII, Figs 1-3, Pl. XXV, fig. 15, Pl. XXVIII, Figs 4, 5, Pl. XXXVI, fig. 4, Pl. XXXIX, fig. 1, Pl. XLV, Figs 4, 7; Sergeev *et al.*, 2008, Pl. 9, Figs 1-3, 7; Sergeev and Schopf, 2010, p. 387, Figs 7.6.-7.8, 8.1, 8.2; Schopf *et al.*, 2010, Figs 2.5-2.15.

Broad tubular sheaths, Schopf and Sovietov, 1976a, Figs 1I, 1J; Schopf and Sovietov, 1976b, Figs 1I, 1J; Schopf *et al.*, 1977, Figs 1A, 1E, 1F; Schopf, 1977, fig. 6K; Schopf *et al.*, 1979, pl. VII, Figs А, Д, Е; Schopf, 1992c, pl. 49, Figs A_1, A_2, A_3, A_4, E.

Large-diameter «Oscillatoriacean» sheaths, Mendelson and Schopf, 1982, p. 62-63, Pl. 3, Figs 4, 5.

Siphonophycus sp., Ogurtsova and Sergeev, 1987, pl. IX, fig. 8; Yankauskas, 1989, pl. XXIV, fig. 7.

Omalophyma solida Golub, 1979, p. 151, Pl. XXXI, Figs 1-4, 7 (for additional synonymy, see Butterfield *et al.*, 1994 and Sergeev, 2006).

Repository—VSEGEI-R-163/3.

Stratum typicum—Ediacaran (Vendian), Smolenskaya Formation, East-European Platform, Russia.

Description—Unbranched solitary nonseptate tubes, cylindrical to slightly compressed and 16.0 to 32.0 μm broad, that rarely contain degraded trichomic fragments composed of disc-shaped cells; tube walls range from smooth to fine-or medium-grained, are 1 to 2 μm thick, and in some specimens exhibit diagenetically produced polygonal ramparts ~0.5 μm high and 0.5 to 1.0 μm wide.

Age and distribution—Widely distributed both in chert-permineralized and compression-preserved Proterozoic assemblages.

Siphonophycus typicum (Hermann, 1974), comb. Butterfield, 1994 (in Butterfield *et al.*, 1994)

(Pl. 15.3, Pl. 21.3, 5-7; Fig. 9, 17, 45B)

Siphonophycus typicum Butterfield *et al.*, 1994, p. 66-67, Figs 23B-23D, 26B, 26H, 26I; Sergeev *et al.*, 1997, p. 230-231, Figs 14A, 14B; Sergeev and Lee Seong-Joo, 2001, p. 6, 8, Pl. 1, Figs 1, 2, 7, 11, 12; Sergeev, 2001, p. 442, fig. 7.10; Sergeev, 2002, Pl. II, fig. 9; Sergeev and Lee Seong-Joo, 2004, Pl. II, fig. 4; Sergeev, 2006, p. 214, Pl. XVII, Figs. 1, 2, Pl. XIX, fig. 10, Pl. XXII, Figs 1, 2, 7, 8, 11, 12, Pl. XXV, fig. 9, Pl. XXVIII, fig. 2, Pl. XLIII, Figs 7-9, Pl. XLIV, Figs 8, 12; Sergeev *et al.*, 2008, Pl. 4, fig. 1, Pl. 9, Figs 1-3, 5-7, Pl. 12, fig. 3; Sergeev and Schopf, 2010, p. 387, 389, fig. 6.4.

Leiothrichoides typicus Hermann, 1974, p. 7, pl. VI, Figs 1-2; Timofeev and Hermann, 1979, p. 138-139, Pl. XXIX, Figs 1, 2; Yankauskas, 1989, p. 111-112, Pl. XXX, Figs 1-3, Schopf, 1992b, Pl. 27, Figs B_1-B_4.

Siphonophycus inornatum Zhang Y., 1981, p. 491, 493, Pl. 1, Figs 1, 3-5; Sergeev, 1992a, p. 95-96, Pl. XVI, Figs 1, 2; Sergeev *et al.*, 1994, Pl. 3, Figs 1-3, 6, 7; Petrov *et al.*, 1995, Pl. I, fig. 3 (for additional synonymy, see Butterfield *et al.*, 1994 and Sergeev, 2006).

Repository—IGGP-49/2T.

Stratum typicum—Neoproterozoic, Miroedikha Formation, Turukhansk Uplift, Siberia.

Description—Unbranched solitary nonseptate tubes, cylindrical to slightly compressed and 4.0 to 8.0 μm broad; tube walls range from psilate to finely granulate and are <0.5 μm thick. Some specimens occur as isolated individuals, but most are entangled in dense masses aligned subparallel or, more rarely, perpendicular to the bedding lamination.

Age and distribution—Widely distributed both in chert-permineralized and compression-preserved Proterozoic assemblages.

Genus—ULUKSANELLA Hofmann and Jackson, 1991

Uluksanella Hofmann and Jackson, 1991, p. 371.

Type species—Uluksanella baffinensis Hofmann and Jackson, 1991.

Diagnosis—Nonbranched strongly curved sheaths generally tightly twisted into rounded and isolated clumps.

Remarks—Hofmann and Jackson (1991) described *Uluksanella* from the late Mesoproterozoic to early Neoproterozoic Bylot Supergroup of Baffin Island, Arctic Canada, pointing out that its filaments are more tightly packed than those of *Siphonophycus*, *Brachypleganon* or *Gunflintia*. Hofmann and Jackson (1991) also suggested that these tightly coiled clumps of sheaths from the Uluksan Group of Canada could be the ancestral form of Palaeozoic or latest Proterozoic taxon *Girvanella*. Comparable fascicles of filamentous cyanobacteria occur in the modern polytrichomous taxa *Microcoleus* and *Hydrocoleum*; however, other hormogonian cyanobacteria form similar clumps when grown under unfavorable conditions. Therefore, in our opinion *Uluksanella* is either a form taxon (*sensu* Knoll *et al.*, 1991) or ecological variants of some filamentous cyanobacteria, e.g. *Siphonophycus*.

Contents—Monospecific genus.

Age—Proterozoic.

Uluksanella baffinensis Hofmann and Jackson, 1991

(Pl. 15.10-12)

Uluksanella baffinensis Hofmann and Jackson, 1991, p. 371, Figs 7.20-7.22;

Uluksanella sp.: Sergeev *et al.*, 1997, p. 229, fig. 14L; Sergeev, 2006, p. 209, Pl. XII, Figs 6, 7.

Repository—GSC-98888.

Stratum typicum—Mesoproterozoic, Uluksan Group, Canada.

Description—Knots of empty unbranched cylindrical sheaths 1.5-4.0 μm in diameter; sheaths walls are usually fine-grained, less than 0.5 μm thick; sheaths tightly packed in round to oblong, generally isolated clumps 20-30 μm in maximum dimension.

Remarks—Originally *Uluksanella baffinensis* was described only from the Uluksan Group of Canada. Later, the same species has been described as *Uluksanella* sp. from the Meso-Neoproterozoic Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia which we place into *Uluksanella baffinensis*.

Age and distribution—Late Meso-Neoproterozoic: Uluksan Group, Canada; Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia.

Order—NOSTOCALES Geitler, 1925

Family—NOSTOCACEAE Kützing, 1843

Genus—EOSPHAERONOSTOC Sergeev, 1992 (in Sergeev, 1992b)

Eosphaeronostoc Sergeev, 1992b, p. 110.

Type species—Eosphaeronostoc kataskinicum Sergeev, 1992.

Diagnosis—Gregarious unbranched tubes, sinuously intertwined and surrounded by a common single-walled envelope of spheroidal shape.

Remarks—This genus was erected by Sergeev (1992b) as a fossil counterpart of modern nostocacean cyanobacterium genus *Sphaeronostoc* Elenkin. However, later on Nagovitsin (2001) considered genus *Eosphaeronostoc* Sergeev, 1992, as synonym of the genus *Glomophycus* Yakschin, 1991 (Yakschin, 1991), because they both represent fossil analogues of sphaeronostocalean cyanobacteria belonging to the genus *Sphaeronostoc*. But the type species *G. tortilis* from the Kotuikan Formation is a form of fossilization of spheroids *Myxococcoides grandis* and *Myxococcoides* sp. apparently having no relations with nostocalean cyanobacteria (Sergeev *et al.,* 1995). The problem is even more complicated, because Nagovitsin (2001) revised the genus *Glomophycus* and distinguished two new species in its composition: *G. bistratosus* Primatchok and Nagovitsin, 2001(in Nagovitsin, 2001) and *G. amplus* Primatchok and Nagovitsin, 2001(in Nagovitsin, 2001) which actually represent spherical colonies of filamentous microfossils, but are of specific structure owing to surficial localization of filaments. Possibly, these forms

deserve to be separated into a new genus. The problem of relations between genera *Eosphaeronostoc* and *Glomophycus* remains open therefore and their synonymy suggested by Nagovitsin is not accepted in the present paper.

Contents—Monospecific genus.

Age—Meso-Neoproterozoic.

Eosphaeronostoc kataskinicum Sergeev, 1992 (in Sergeev, 1992b)

(Pl. 22.1-2)

Eosphaeronostoc kataskinicum Sergeev, 1992b, p. 110-111, Pl. IX, fig. 10; Sergeev, 1992a, p. 92, Pl. VII, Figs 1, 2; Sergeev, 1994, p. 249-250, fig. 8A; Sergeev, 2006, p. 211-212, Pl. XXXV, Figs 1-3; Sergeev and Lee Seong-Joo, 2006, Pl. II, fig. 10; Sergeev *et al.*, 2008, Pl. 8, fig. 5.

Leiosphaeridia sp.: Sergeev, 1992b, Pl. IX, fig. 11 (the upper microfossil).

Repository—GINPC-4688, Specimen No. 48.

Stratum typicum—Late Mesoproterozoic (Middle Riphean), Avzyan Formation, southern Ural Mountains.

Description—Gregarious unbranched tubes sinuously intertwined. Tubes are surrounded by a common single-walled envelope of spheroidal shape. Tubes and surrounding envelopes are generally psilate, their surfaces are smooth, but occasionally they are finely granular. Tube width 3.0-5.0 μm, tube walls 0.5 μm thick; envelope diameters range from 50 to 200 μm.

Remarks—In its type locality, in the cherts of the Kataskin Member *E. kataskinicum* occurs as isolated individuals within diverse *S. robustum* mats. In one envelope there is a concave depression on the relatively robust wall and it resembles a stage in the life cycle of modern *Sphaeronostoc* cyanobacteria in which the outer sheath of mature colonies breaks and trichomes are released (Kondratieva, 1975). However, in case of *E. kataskinicum*, it can not be excluded that the concave depression was formed by a chance.

Age and distribution—Late Mesoproterozoic, Avzyan Formation, southern Ural Mountains.

Genus—VETERONOSTOCALE Schopf and Blacic, 1971

Veteronostocale Schopf and Blacic, 1971, p. 950.

Type species—Veteronostocale amoenum Schopf and Blacic, 1971.

Diagnosis—Unbranched, uniseriate, sheathless trichomes strongly constricted at septa.

Trichomes composed of isometrical spherical to barrel-like medial and terminal cells.

Remarks—This genus is considered to be the fossil counterpart of modern nostocacean cyanobacteria like *Nostoc* (Schopf & Blacic, 1971; Sergeev, 1992a; Schopf, 1994; Sergeev *et al.*, 1995). Some enlarged cells resembling heterocysts were observed among trichomes of *Veteronostocale copiosus* from the Chichkan Formation of South Kazakhstan (Ogurtsova & Sergeev, 1987; Sergeev, 1992 a, 2006), but these structures could be formed as a result of *post-mortem* trichome degradation (Gerasimenko & Krylov, 1983). Therefore, interpretation of genus *Veteronostocale* as nostocacean cyanobacterium is based mainly on spherical shape of its cells in trichomes. However, cells of such shape are characteristic of oscillatoriacean cyanobacterium genus *Pseudoanabaena* as well, but general morphology of this taxon is different (see Castenholz & Waterbury, 1989).

Contents—V. amoenum, V. copiosus and *V. medium* (Table-16).

Age—Meso-Neoproterozoic (and probably older).

Veteronostocale amoenum Schopf and Blacic, 1971

(Fig. 46A)

Veteronostocale amoenum Schopf and Blacic, 1971, p. 950-951, Pl. 107, fig. 4, Pl. 108, Figs 1, 2; Schopf, 1972, fig. 15; Schopf, 1992b, Pl. 30, fig. L.

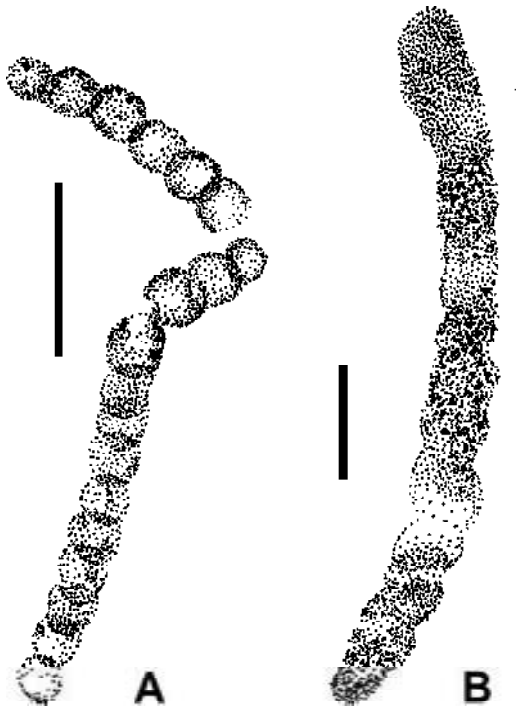


Fig. 46—Line diagrams of species of *Veteronostocale* . A- *V. amoenum* (Schopf & Blacic, 1971); B- *V. medium* (Sergeev *et al.*, 1995). Scale bar = 10 μm.

Name of the species	Diagnostic features	Cells width and length μm	Palaeoenvironmental setting	Repository and type locality	References
V. medium Sergeev & Knoll, 1995 Fig. 46B	Solitary trichomes formed of spherical cells.	5.0-6.5 x 4.5-7.0	Tidal flat, recorded from cherts in dolomites.	HUHPC – 62925; Kotuikan Fm., Anabar Uplift, Russia.	Sergeev *et al.*, 1995

Table 16—Comparative characteristics of genus *Veteronostocale* species (Type Specimens).

Repository—HUHPC-58588.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Terminal and medial cells are not differentiated; all cells are isometrical, subspherical or barrel-shaped. Width of the cells varies from 2.0 to 3.5 μm, length-from 1.8 to 2.6 μm, width/length ratio is 5/4 varies from 0.9 to 1.3. Cross and side walls are distinct; fine-grained, less than 0.5 μm thick.

Age and distribution—Neoproterozoic, Bitter Springs Formation, Australia.

Veteronostocale copiosus Ogurtsova and Sergeev, 1987

(Pl. 16. 9, 10)

Veteronostocale copiosus Ogurtsova and Sergeev, 1987, p. 112, pl. IX, Figs 9a, 9б; Yankauskas, 1989, p. 124-125, Pl. XXIV, fig. 3; Sergeev, 1992a, p. 91-92, Pl. XX, Figs 1a-1в, 3; Sergeev, 2006, Pl. XLVI, Figs 1-3, 5; Sergeev and Schopf, 2010, p. 389, Figs 6.6; 6.6a; Schopf *et al.*, 2010, Figs 1.1-1.3.

Repository—GINPC-4681, Specimen No. 52.

Stratum typicum—Neoproterozoic, Chichkan Formation, South Kazakhstan.

Description—Unbranched, uniseriate, sheath-lacing trichomes strongly constricted at septa, composed of isodiametric spheroidal to barrel-shaped cells, the size of which varies from 5.0 to 8.5 μm in diameter and 3.5 to 9.0 μm in length with their width to length ratio ranging from 0.9 to 1.5; trichomes range up to 180 μm in length. Lateral and transverse walls are distinct, translucent and fine-grained, <0.5 μm thick. Most commonly the trichomes occur entangled in clusters of 10 to 15 individuals.

Age and distribution—Neoproterozoic, Chichkan Formation, South Kazakhstan.

Family—SCYTONEMATACEAE Rabenhorst, 1865

Genus—CIRCUMVAGINALIS Sergeev, emend. Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

Circumvaginalis Sergeev, 1993, p. 276-277; Sergeev *et al.*, 1995, p. 29-30.

Type species—Circumvaginalis elongatus Sergeev, 1993.

Diagnosis—Unbranched, cylindrical single-layered tubular structures consisting of elongated funnel-like segments inserted one in another. Each funnel-like segment is straight or gently curved and terminates in a prominent dark ring.

Remarks—In its morphology, inferred development and ecology, *Circumvaginalis* closely resembles species of the modern nostocalean genus *Scytonema*. *Circumvaginalis* differs from other fossil genera erected for filamentous sheaths (*Siphonophycus*, *Palaeosiphonella* and *Ramivaginalis*) by its nodular construction of funnel-like segments and its absence of branching. *Proaulopora* Vologdin also consists of funnel-like segments, but this Vendian or Cambrian fossil is much larger than *Circumvaginalis*, have thicker walls, and clearly exhibit branching of the filaments. Contrary to it, there is no firm evidence for branching in *Circumvaginalis*. The stacked sheaths of *Polybessurus* (Green *et al.*, 1987) superficially resemble *Circumvaginalis*, but the pseudo-filamentous stalks of *Polybessurus* were secreted by unicellular microorganisms.

Contents—Monospecific genus.

Age—Mesoproterozoic-Neoproterozoic (and probably older).

Circumvaginalis elongatus Sergeev, 1993 emend. Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

(Pl. 23.1-8)

Circumvaginalis elongatus Sergeev, 1993, p. 277, Pl. I, Figs 1-4, Pl. III, fig. 9; Sergeev *et al.*, 1995, p. 30, Figs 18.1-18.11; Kumar and Venkatachala, 1998, p. 63, 64, Figs 5f, 5g; Sharma and Sergeev, 2004, fig. 9G(F); Sergeev, 2006, p. 210-211, Pl. IX, Figs 1-11; Sergeev *et al.*, 2008, Pl. 3, fig. 6; Sergeev *et al.*, 2010, Pl. I, fig. 9.

Siphonophycus ex gr. *kestron* Schopf, 1968: Yakschin, 1991, p. 34, Pl. XII, fig. 4.

Palaeolyngbya giganteus Yakschin, 1991 (partim): Yakschin, 1991, Pl. XII, fig. 2.

Repository—GINPC-4689, Specimen No. 391.

Stratum typicum—Mesoproterozoic (Lower Riphean), Kotuikan Formation, Anabar Uplift, Siberia.

Description—Unbranched empty cylindrical tubular structures consisting of elongate funnel-like segments nested within one another. Structures may be solitary or loosely interwoven along bedding surfaces. Segments straight or gently bent; their surfaces smooth or wrinkled. Each segment terminates in a prominent dark ring with a coarse-grained surface texture; rings sometimes chapped. Segment diameter 18 to 55 μm; diameter of dark-brown rings that terminate segments 27 to 58 μm. Segment length (distance between adjacent rings) 30 to 150 μm.

Remarks—This taxon was described by Sergeev (1993) as tubular microfossils consisting of funnel-like segments with rare lateral branching. Upon restudy, it became clear that observed "branches" are a fortuitous consequence of diagenetic dolomite crystal growth (Sergeev *et al.*, 1995).

Distribution-Mesoproterozoic, Kotuikan and Yusmastakh Formations, Anabar Uplift, Siberia.

Genus—RAMIVAGINALIS Nyberg and Schopf, 1984

Ramivaginalis Nyberg and Schopf, 1984, p. 756.

Type species—Ramivaginalis uralensis Nyberg and Schopf, 1984 .

Diagnosis—Dichotomically branching nonseptate single or double-layered tubular structures, solitary and gregarious.

Contents—Monospecific genus.

Remarks—The genus was erected for empty tubular structures with branch; probably sheaths of nostocalean or stigonematalean cyanobacteria. Filaments of both taxa demonstrate either false or true branching. Exclusive presence of sheaths without trichomes in the Proterozoic deposits, makes it difficult to conclude about true or false nature of filaments branching.

Age—Neoproterozoic (and probably even older).

Ramivaginalis uralensis Nyberg and Schopf, 1984

(Fig. 47)

Ramivaginalis uralensis Nyberg and Schopf, 1984, p. 757, fig. 11D; Schopf, 1992b, Pl. 46E.

Repository—UCLA, PTC-R_3mn-st-1B.

Stratum typicum—Neoproterozoic, Min'yar Formation, southern Ural Mountains.

Description—Dichotomically branching nonseptate single or double-layered tubular structures, solitary and gregarious. Tubes width are 4.0 to 9.0 μm, wall psilate to finely granular about 0.5 μm thick.

Remarks—This species is an extremely rare component of Proterozoic microbiotas. Only known from the Min'yar Formation one specimen was found by Nyberg and Schopf (1984). Paucity of these fossils in Proterozoic deposits can be attributed to either taphonomical or preservational factors where branching filament can not be differentiated among entwined sheath of fossilizied cyanobacterial mats. On the other hand, many branched tubular structures observed in Proterozic microbiotas can be result of overlapping primarely nonbranched filaments.

Age and distribution—Neoproterozoic, Min'yar Formation, southern Ural Mountains, Russia.

Order—NOSTOCALES OR STIGONEMATALES

Genus—ARCHAEOELLIPSOIDES Horodyski and Donaldson, 1980, emend. Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

Archaeoellipsoides Horodyski and Donaldson, 1980, p. 154, Sergeev *et al.*, 1995, p. 30.

Bactrophycus Zhang Y., 1985, p. 298.

Eosynechococcus (partim): Golovenok and Belova, 1984, p. 25-26; Yakschin, 1991, p. 25-26.

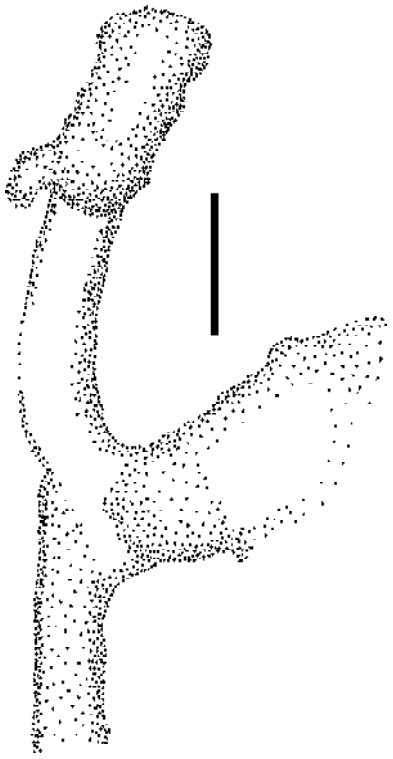


Fig. 47—Line diagram of *Ramivaginalis uralensis* (Nyberg & Schopf, 1984). Scale bar = 10 μm.

Type species—*Archaeoellipsoides grandis* Horodyski and Donaldson, 1980.

Diagnosis—Single or double-layered ellipsoidal vesicles with rounded, flat or slightly depressed ends; solitary, aggregated in clusters, or in short chains connected end to end; no evidence of binary fission. Vesicles empty or containing blebs and thread-like bodies of amorphous dark material or shrunken trichome remnants. Ellipsoid surfaces are smooth or ribbed.

Remarks—1. Width of the ellipsoids of different species of genus *Archaeoellipsoides* varies from 2 to 36 μm, length-from less than 20 to more than 150 μm. Most of species of genus *Archaeoellipsoides* are compared to akinetes of nostocalean *Anabaena*-like cyanobacteria (Sergeev, 1989, 1992a; Sergeev *et al.*, 1995; Golubic *et al.*, 1995; Knoll & Sergeev, 1995). The total range of morphological variation observed among Proterozoic *Archaeoellipsoides* exceeds that characterizing the akinetes of cyanobacteria; however, spatially distinct subpopulations have a range of variation that compares closely with individual nostocalean species.

2. Zhang Y. (1985) separated large ellipsoids in the Wumishan Formation into two genera, *Archaeoellipsoides* and *Bactrophycus*, based on differences in dimensions. Zhang Y. (1985, p. 284, fig. 4) interpreted his plot of specimens in a two dimensional morphological field (length/width vs. width) to indicate two quite different trajectories (demarcated as *Archaeoellipsoides* and *Bactrophycus*) that meet at the extremes of the two point clouds. Given that a plot of one dimension *vs*. its reciprocal will likely yield a hyperbole, later on Zhang's plot was reinterpreted (Sergeev *et al.*, 1995) as a continuous distribution of points along a biologically meaningful axis that is curved (hyperbolic). Therefore, all these forms were placed into the single genus *Archaeoellipsoides*.

3. Horodyski and Donaldson (1980) described the single, broad species *A. grandis*. Subsequently, additional species have been recognized (Golovenok & Belova, 1984; Zhang Y., 1985) and Sergeev and Knoll (Sergeev *et al.*, 1995) used the size ranges of individual subpopulations as a basis for differentiating species. Some species additionally were established on the basis of surface ornamentation (*A. costatus*) or the formation of chains (*A. conjunctivus*). The resulting taxonomy is purely formal; quite possibly larger number of biological species were involved in producing the range of variation observed within the group (Sergeev *et al.*, 1995).

4. Nagovitsin (2001) has described trichomes consisting of elongated ellipsoidal spores connected by vegetative cells as genus *Palaeoanabaena* Nagovitsin, 2001. One of us (VNS) examined the material described by Nagovitsisn (2001) and in our opinion forms are *Archaeoellipsoides*-like bodies connected by degraded sheaths. For the reason of analogus shape and size we would like to merge this genus with *Archaeoellipsoides* but refrain doing so pending new finds of morphologically similar fossil microorganisms.

5. One more species has been described from the Kotuikan Formation by Golovenok and Belova, 1984 as *Archaeoellipsoides (Eosynechococcus) crassus (*Fig. 49I). Vesicles of this species are 32.0-36.0 μm wide and 96.0 μm long and solitary specimen has been found by Golovenok and Belova, 1984, but such large specimens were not detected in subsequent research.

6. Along with *Archaeoellipsoides* the genus *Brevitrichoides* was proposed for large ellipsoidal compression-preserved organic-walled microfossils in Neoproterozoic shales. However, given persistent uncertainties we followed the practice of last 30 years and keep both taxa separately (cf. Sergeev *et al.*, 1995).

Content—*A. bactroformis, A. conjunctivus, A. costatus, A. crassus, A. dolichos, A. elongatus, A. grandis, A. major* and *A. minor.*

Age—Proterozoic.

Archaeoellipsoides bactroformis Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

(Pl. 24.3, Fig. 48A)

Archaeoellipsoides bactroformis Sergeev and Knoll, 1995 in Sergeev *et al.*, 1995, p. 32, Figs 10.1, 10.3, 10.16, 11.9, 11.10; Golubic *et al.*, 1995, Figs 3A, 3D; Sergeev, 2006, p. 221, 222, Pl. III, Figs 1, 3, 16, Pl. IV, Figs 9, 10; Sergeev *et al.*, 2008, Pl. 2, Figs 1, 7.

Repository—HUHPC-69234.

Stratum typicum—Mesoproterozoic (Lower Riphean), Kotuikan Formation, Anabar Uplift, Siberia.

Description—Solitary or gregarious single-and double-layered large rod-like often curved empty vesicles with rounded ends. The length of vesicles varies from 50 to more than 150 μm and width-from 5 to 14.5 μm, length/width changes from 3 to 25. Vesicle envelope is translucent, inner wall is medium or course-grained and its thickness varies from less then 0.5 μm to more then 1.0 μm. Outer envelope (when present) is transparent, fine-grained and less than 0.5 μm thick.

Remarks—This new species differs from other species of genus *Archaeoellipsoides* by their length and high length/width ratio. Some specimens of *A. bactroformis* are as long as 150 and probably up to 200 μm; nonetheless, the akinetes of modern alga *Anabaena* are of comparable size.

Age and distribution—Mesoproterozoic: Kotuikan and Yusmastakh Formations, Anabar Uplift, Siberia.

Archaeoellipsoides conjunctivus Zhang Y., 1985

(Pl. 24.1, 2; Fig. 48B)

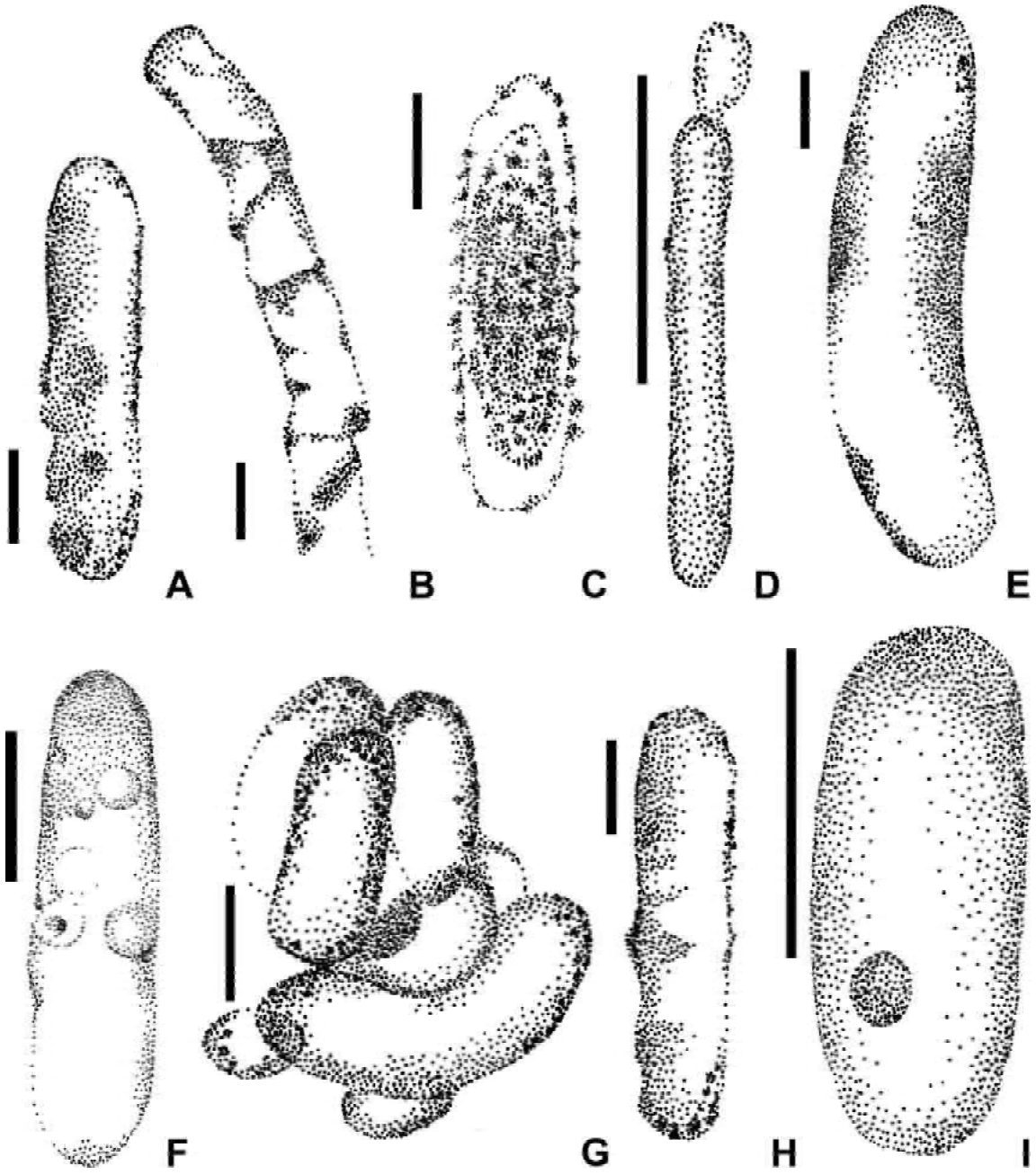


Fig. 48—Line diagrams of species of *Archaeoellipsoides*. A- *A. bactroformis* (Sergeev *et al*., 1995); B- *A. conjuctivus* (Zhang Y., 1985); C- *A. costatus* (Sergeev *et al*., 1995); D- *A. elongatus* (Golovenok & Belova, 1984); E- *A. grandis* (Horodyski & Donaldson, 1980); F - *A. major* (Golovenok & Belova, 1984); G, H- *A. minor* (Sergeev *et al*., 1995); I- *A. crassus* (Golovenok *and* Belova, 1984). Scale bar =A-C, E-H= 10 μm, D, I= 50 μm.

Archaeoellipsoides conjunctivus Zhang Y., 1985, p. 297-298, fig. 8B; Sergeev *et al.*, 1995, p. 31, Figs 11.1-11.3, 11.16; Sergeev, 2006, p. 219-220, Pl. IV, Figs 1-3, 12.

Oscillatoriopsis sp.: Horodyski and Donaldson, 1980, p. 152, fig. 13J.

Curviphycus disarticulans Yakschin, 1991, p. 39, Pl. XV, Figs 2a, 2б.

Eomycetopsis (?) sp_2: Yakschin, 1991, p. 36-37, Pl. XIII, fig. 5.

Repository—BGP-BCWB-04.

Stratum typicum—Mesoproterozoic, Wumishan Formation, China.

Description—Single-layered straight or slightly curved ellipsoidal vesicles with flattened ends, connected end to end

in chains. Chains sheathless or surrounded by single-layered tight envelopes. Vesicles nonseptate and generally empty, but may contain blebs of amorphous organic matter. Ellipsoidal vesicles 45 to > 100 μm long and 12 to 25 μm wide; length/width ratio is 4 to 2; chain length varies from 200 to 800 μm.

Remarks—Zhang Y. (1985) diagnosed *A. conjunctivus* as chains of ellipsoidal bodies. That distinction is retained here, but it is purely formal; most Kotuikan and Yusmastakh akinetes were probably originally arranged in chains. On the other hand, the modern cyanobacterial species *Aulosira* forms chains of akinetes surrounded by a common sheath (Elenkin, 1938, p. 872) similar to *A. conjunctivus*.

Age and distribution—Mesoproterozoic: Wumishan Formation, China; Kotuikan and Yusmastakh Formations, Anabar Uplift, Siberia; Dismal Lakes Group, Canada.

Archaeoellipsoides costatus Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

(Pl. 24.8; Fig. 48C)

Archaeoellipsoides costatus Sergeev and Knoll, 1995 in Sergeev *et al.*, 1995, p. 30-31, fig. 13.11; Sergeev, 2006, p. 218, Pl. VI, fig. 11; Sergeev *et al.*, 2008, Pl. 3, fig. 3.

Oscillatoriopsis (?) sp. Yakschin, 1991, p. 38, Pl. XV, fig. 1.

Repository—GINPC-4689, Specimen No. 465.

Stratum typicum—Mesoproterozoic (Lower Riphean), Kotuikan Formation, Anabar Uplift, Siberia.

Description—Solitary, single-layered ellipsoidal vesicles bearing coarse, regularly spaced ribs perpendicular to the long axis. Vesicles are empty or contain a single elongate dark body. Ellipsoidal vesicle length 37 μm, the width 12 μm, length/width ratio is 3. Ribs dark, rigid, hemispherical in cross-sectional view, ca. 1.5 μm high and 1.0 μm long; the distance between adjacent ribs is about 2.0 μm. Inner body 29 μm long and 7 μm wide, with a coarse-grained, homogeneous wall.

Remarks—This form resembles the short trichomes of *Partitiofilum yakschinii* in its general morphology and might be interpreted as a trichome cast; however, the homogeneous nature of the single elongate body in the vesicle interior precludes such an interpretation. Some living cyanobacteria produce akinetes with rib-like or spine-like surficial structures, prompting inclusion of this fossil within the genus *Archaeoellipsoides*.

Age and distribution—Mesoproterozoic: Kotuikan Formation, Anabar Uplift, Siberia.

Archaeoellipsoides dolichos (Zhang Y., 1985), comb. Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

(Pl. 24.4)

Archaeoellipsoides dolichos Sergeev and Knoll, 1995 in Sergeev *et al.*, 1995, p. 32, fig. 12.7; Sergeev *et al.*, 1997, p. 229-230, Figs 14E-14H; Sergeev 2006, p. 221, Pl. V, fig. 7, Pl. XVII, Figs 6-8; Sharma, 2006b, p. 114, Pl. II, Figs 1, 10, 11.

Bactrophycus dolichum Zhang Y., 1985, p. 298, 299, Figs 7Q-7U; Cao, 1992, Pl. II, Figs 11-13.

Filamentous microfossil: Horodyski and Donaldson, 1983, fig. 5Z.

Eomycetopsis robusta (partim): Yakschin, 1991, p. 35-36, Pl. XII, fig. 3.

Repository—BGP-BCWB-05.

Stratum typicum—Mesoproterozoic, Wumishan Formation, China.

Description—Solitary, single-layered, straight or gently curved rod-like vesicles with rounded ends. Vesicles essentially empty or containing sparse blebs of amorphous organic matter. Rod-like vesicles 10 to 55 μm long, but only 2 to 4.5 μm wide; length/width ratio 20 to 3.

Remarks—A. dolichum differs from other species of *Archaeoellipsoides* by its small cross-sectional diameter and high length/width ratio.

Age and distribution—Mesoproterozoic: Wumishan Formation, China; Kotuikan and Yusmastakh Formations, Anabar Uplift, Siberia; Dismal Lakes Group, Canada.

Archaeoellipsoides elongatus (Golovenok and Belova, 1984), comb. Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

(Pl. 24.5, 6, 9; Fig. 48D)

Archaeoellipsoides elongatus Sergeev and Knoll, 1995, in Sergeev *et al.*, 1995, p. 31-32, Figs. 12.8-12.11; Sergeev, 2002, Pl. II, Figs 11, 12; Sergeev, 2006, p. 220-221, Pl. V, Figs 8-11, Pl. 25, Figs 11, 12.

Eosynechococcus elongatus Golovenok and Belova, 1984, p. 27-28, Pl. II, fig. 5; Yankauskas, 1989, Pl. XIX, fig. 2.

Bactrophycus oblongum Zhang Y., 1985, p. 298, fig. 7L-7P, 8C.

Archaeoellipsoides elongatus Cao, 1992, p. 387, Pl. I, fig. 10.

Repository—VSEGEI-445-m.

Stratum typicum—Mesoproterozoic (Lower Riphean), Kotuikan Formation, Anabar Uplift, Siberia.

Description—Elongated single-layered sausage—like vesicles with rounded ends occurring as solitary vesicles, in pairs, or in loose clusters of many tens to more than one hundred individuals scattered in event beds and precipitates. Vesicles generally empty, but may contain sparse blebs of amorphous organic matter. Ellipsoidal vesicles 15 to 60 μm long and 5.5 to 9 μm wide; length/width ratio is 8 to 2.5.

Remarks—These elongated ellipsoidal microfossils were described by Golovenok and Belova (1984) as a distinct species of *Eosynechococcus*. Subsequently, Zhang Y., (1985) described very similar fossils as *Bactrophycus oblongum* (oblongus = elongated) from the Wumishan Formation.

Some elongated bodies from the Dismal Lakes Group referred by Horodyski and Donaldson to *Oscillatoriopsis curta* are probably remnants of akinetes comparable to *Archaeoellipsoides elongatus* (Horodyski & Donaldson 1980, Figs 13A, 13B, 13G and Horodyski & Donaldson 1983, fig. 5AA).

Age and distribution—Mesoproterozoic: Wumishan Formation, China; Kotuikan and Yusmastakh Formations, Anabar Uplift, Siberia; Dismal Lakes Group, Canada.

Archaeoellipsoides grandis Horodyski and Donaldson, 1980, emend. Golovenok and Belova, 1984, emend. Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

(Pl. 25.1-4; Fig. 48E)

Archaeoellipsoides grandis Horodyski and Donaldson, 1980, p. 154-156, Figs 16A-16C; Zhang P. and Gu, 1986, p. 17, Pl. I, Figs 4, 5, 11; Zhang P. *et al.*, 1989, p. 327, Pl. 2, Figs 7-10; Schopf, 1992b, Pl. 9, Figs I, K, L; Cao, 1992, Pl. I, Figs 11,12; Sergeev *et al.*, 1995, p. 30, Figs 10.2, 10.4, 10.5, 10.11; Knoll and Sergeev, 1995, fig. 2; Golubic *et al.*, 1995, Figs 3B, 3C, 3G; Sergeev, 2006, p. 217-218, Pl. III, Figs 2, 4, 5, Pl. IV, Figs 11a, 11б; Sergeev *et al.*, 2008, Pl. 2, Figs 3, 4, Pl. 4, fig. 11; Sergeev and Schopf, 2010, p. 389, Figs 9.4, 9.5; Schopf *et al.*, 2010, Figs 1.8-1.10; Sergeev *et al.*, 2010, Pl. I, fig. 5.

Archaeoellipsoides obesus Zhang Y. (partim): Zhang Y., 1985, p. 295, 297, Figs 7H-7K.

Archaeoellipsoides longus Sergeev, 1992a, p. 98-99, Pl. XX, Figs 2, 4; Sergeev, 2006, Pl. XLV, fig. 10, Pl. XLVI, fig. 4.

Archaeoellipsoides sp_1: Sergeev, 1989, Pl. 1, fig. 7.

Eosynechococcus giganteus Golovenok and Belova, 1984, p. 27, Pl. II, fig. 3; Yankauskas, 1989, p. 92, Pl. XIX, fig. 4; Yakschin, 1989, Pl. 3, Figs 1, 2; Yakschin, 1991, p. 26, Pl. IX, fig. 9, Pl. X, Figs 1-3, 5, 6, 10.

Repository—GSC-57988.

Stratum typicum—Mesoproterozoic, Dismal Lakes Group, Canada.

Description—Solitary or gregarious, single-and double-layered ellipsoidal vesicles with rounded ends. Vesicles nonseptate, commonly slightly curved, and generally empty, although blebs of amorphous material may occur in vesicle interiors. Ellipsoidal vesicles 50 to > 100 µm long and 15 to 25 µm wide; length/width ratio varies from 2.5 to 5.5.

Remarks—Sergeev (1992a) described ellipsoidal bodies as *A. longus* from the Chichkan Formation of South Kazakhstan which according to formal classification of genus *Archaeoellipsoides* species (Sergeev *et al.*, 1995) should be transferred to *A. grandis*.

Age and distribution—Mesoproterozoic: Dismal Lakes Group, North America; Gaoyuzhuang and Wumishan formations, China; Kotuikan and Usmastakh Formations, Anabar Uplift; Debengda Formation, Olenek Uplift, Siberia; Neoproterozoic, Chichkan Formation, South Kazakhstan.

Archaeoellipsoides major (Golovenok and Belova, 1984), comb. Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

(Pl. 22.7, Pl. 25.5-11; Fig. 48F)

Archaeoellipsoides major Sergeev and Knoll, 1995 in Sergeev *et al.*, 1995, p. 31, Figs 10.6-10.8, 10.12-10.15, 11.4-11.8, 13.8; Golubic *et al.*, 1995, Figs 3E, 3F, 3H, 4A-4D, 8E; Kumar and Venkatachala, 1998, p. 64, fig. 6g; Sergeev and Lee Seong-Joo, 2004, p. 17, Pl. 2, Figs 7, 9; Sergeev, 2006, p. 218, 219, Pl. III, Figs 6-8, 11-15, Pl. IV, Figs 4-8, Pl. VI, fig. 8, Pl. XXVII, fig. 8, Pl. XXVIII, fig. 7; Sharma, 2006b, Pl. II, Figs 2-5, 8, 9; Sergeev *et al.*, 2008, Pl. 2, Figs 2, 5, 6, Pl. 3, Figs 2, 4; Sergeev and Schopf, 2010, p. 390, Figs 9.6, 9.6a.

Archaeoellipsoides grandis Horodyski and Donaldson, 1980 (partim): Horodyski and Donaldson, 1980, p. 154-156, Figs 16D-16F; Horodyski and Donaldson, 1983, Figs 5W, 5X; Zhang P. *et al.*, 1989, p. 327, Pl. 2, fig. 6; Schopf, 1992b, Pl. 9, fig. I; Cao, 1992, Pl. I, Figs 13, 14, Pl. II, fig. 7.

Eosynechococcus major Golovenok and Belova, 1984, p. 27, Pl. II, fig. 2; Yankauskas, 1989, Pl. XIX, fig. 5; Yakschin, 1989, Pl. 3, Figs 3, 8; Yakschin, 1991, p. 26, Pl. IX, Figs 6-8, Pl. 10, Figs 4, 7-9; Sergeev, 1993, Pl. III, Figs 1, 2, 10.

Archaeoellipsoides obesus Zhang Y., 1985 (partim): Zhang Y., 1985, p. 295, 297, Figs 7E-7G; Hofmann and Jackson, 1991, p. 372, 374, Figs 7.17.

Repository—VSEGEI-463F.

Stratum typicum—Mesoproterozoic (Lower Riphean), Kotuikan Formation, Anabar Uplift, Siberia.

Description—Solitary, empty, double-layered round-ended ellipsoidal vesicles, 18 to 60 µm long and 9 to 20 µm wide and having a length to width ratio ranging from 1.5 to 4.5, defined by translucent medium-grained walls 1.0 to 1.5 µm thick. Vesicles tend to be aggregated in loose clusters or in short unconnected chain-like groups.

Remarks—Like the other species of *Archaeoellipsoides*, *A. major* is distinguished by its characteristic range of diameters.

Age and distribution—Widely distributed in Meso-and Neoproterozoic microfossil assemblages.

Archaeoellipsoides minor nom. Sergeev and Knoll, 1995 (in Sergeev *et al.*, 1995)

(Pl. 24.7, 10, 11; Fig. 48G, H)

Archaeoellipsoides minor Sergeev and Knoll, 1995 in Sergeev *et al.*, 1995, p. 31, Figs 10.9, 10.10; Golubic *et al.*, 1995, fig. 8F; Kumar and Venkatachala, 1998, p. 64, fig. 6o; Sergeev, 2001, p. 443, fig. 9.10; Sergeev, 2006, p. 219, Pl. III, Figs 9, 10, Pl. XVIII, fig. 10; Sharma, 2006b, Pl. II, Figs 6, 7, 12; Sergeev and Schopf, 2010, p. 390, Figs 9.7, 9.8.

Eosynechococcus grandis Hofmann, 1976 (partim): Golovenok and Belova, 1984, p. 24, Pl. II, fig. 1; Golovenok and Belova, 1985, Pl. VI, Figs 5, 6.

Archaeoellipsoides grandis Horodyski and Donaldson, 1980 (partim): Horodyski and Donaldson, 1980, p. 154-157, Figs 16G, 16H; Cao, 1992, Pl. I, Figs 8, 9, Pl. II, Figs 8, 9.

Archaeoellipsoides obesus Zhang Y., 1985 (partim): Zhang Y., 1985, p. 295, 297 (not-illustrated).

Repository—VSEGEI-445-m.

Stratum typicum—Mesoproterozoic (Lower Riphean), Kotuikan Formation, Anabar Uplift, Siberia.

Description—Gregarious (in clumps) and solitary single- and double-layered ellipsoidal vesicles with rounded ends. Vesicles generally empty, but may contain amorphous organic matter. Ellipsoidal vesicles 16 to 24 μm long and 5 to 8 μm wide; length/width ratio is 3.5 to 1.5. Vesicle wall translucent, medium or coarse-grained; outer envelope (when present) transparent, fine-grained and < 1.0 μm thick.

Remarks—Golovenok and Belova (1984) designated the smallest unpaired elliposids in the Billyakh Group as *Eosynechococcus grandis*. These fossils differ from the type *Eosynechococcus grandis* of the Belcher Supergroup, Canada (Hofmann, 1976) and, indeed, cannot be remnants of *Synechococcus*-like cyanobacteria because they lack evidence for binary cell division. Therefore, this population was reassigned to the genus *Archaeoellipsoides*. The name *Archaeoellipsoides grandis* was already engaged; therefore, Sergeev and Knoll in Sergeev *et al.*, 1995 proposed the name *A. minor* to denote the small size of this population relative to other *Archaeoellipsoides* species.

Specimens are commonly are aggregated into clumps (Pl. 24.11) similar to those formed by akinetes of living *Anabaena flos-aquae* (Elenkin, 1938, p. 729, fig. 215). A specimen described by Horodyski and Donaldson (1980, fig. 13F) as *Oscillatoriopsis curta* is plausibly a chain of *A. minor* akinetes.

Age and distribution—Mesoproterozoic: Dismal Lakes Group, Canada; Wumishan Formation, China; Kotuikan and Yusmastakh Formations, Anabar Uplift, Siberia; Salkhan Limestone, India; Neoproterozoic: Kirgitey and Lopatinskaya Formations, Yenisey Ridge; Shorikha Formation, Turukhansk Uplift, Siberia.

Genus—ORCULIPHYCUS Yakschin, 1991

Orculiphycus Yakschin, 1991, p. 30.

Type species—*Orculiphycus latus* Yakschin, 1991.

Diagnosis—Trichomes of elongated or ellipsoidal shape surrounded by a sheath. Trichomes are either symmetrical or asymmetrical and consist of pill-like medial and hemispherical basal or terminal cells.

Remarks—Short filaments of genus *Orculiphycus* are completely surrounded by encircling sheath, so it may be hormocysts or germinated akinetes of either nostocalean or stigonematalean cyanobacteria (Sergeev *et al.*, 1995). Yakschin (1991) has described three species of genus *Orculiphycus* (*O. latus, O. magnus* and *O. angastus*), but closer scrutiny suggests that two of them are rather sections of the matured trichomes of *Filiconstrictosus* ex. gr. *majusculus* and *F. magnus* (Sergeev *et al.*, 1995), leaving only *O. latus* as a valid species.

Contents—Monospecific genus.

Age—Mesoproterozoic.

Orculiphycus latus Yakschin, 1991

(Pl. 22.5, 6, 8)

Obculiphycus latus Yakschin, 1991, p. 31, Pl. XI, Figs 4a-4г, 5а-5в, 7; Sergeev *et al.*, 1995, p. 32-33, Figs 13.1,13.3,13.4; Golubic *et al.*, 1995, Figs 8B, 8C; Sergeev, 2006, p. 215-216, Pl. VI, Figs 1, 3, 4.

Palaeolyngbya sp.: Yakschin, 1991, p. 33, Pl. XIV, fig. 1.

Repository—CSGM-309-AYa-28-4c.

Stratum typicum—Mesoproterozoic (Early Riphean), Kotuikan Formation, Anabar Uplift, Siberia.

Description—Short asymmetrical trichomes of ellipsoidal shape consisting of cone-like terminal, hemispherical basal and pill-like medial cells, completely surrounded by sheath. Sheath usually has wavy outlines, transparent, fine-or medium grained 0.5-1.0 μm thick. Cells of trichomes are translusent or opaque, cross-walls unclear or missing, side walls medium-grained 0.5-1.0 μm thick. Terminal cells are 6.0-12.0 μm wide and 2.5-5.5 μm long, width/length ratio 2.5-2. Width of medial cells ranges from 12.0 to 17.0 μm, length-from 2.5 to 6.0 μm, width/length ratio varies from 3 to 4. Basal cells are 17.0-20.0 μm wide and about 5.0 μm long; the maximal length of trichomes up to 50 μm. Width of the sheath ranges from 15.0 to 20.0 μm, length-from 30.0 to 55.0 μm, width/length ratio varies from 2 to 3. Sometimes sheath surrounding trichomes can be missing or trichomes inside sheaths can shrunk significantly.

Remarks—Zhang P. and Gu S. (1986) have described short trichomes from the Wumishan Formation as *Saccolyngbya pinguis* which in many features is similar to *O. latus*.

Age and distribution—Early Mesoproterozoic, Kotuikan Formation, Anabar Uplift, Russia.

PLATE 21

Empty sheaths of hormogonian cyanobacterium genus *Siphonophycus* Schopf, 1968.

1. *Siphonophycus septatum* (Schopf, 1968), Sample No 4688-412, Slide No 861, p. 19, GINPC No 722.
2, 4, 8-10. *Siphonophycus robustum* (Schopf, 1968): 2 —Sample No 3893-276, Slide No 137, p. 10, GINPC No 124; 4 —Sample No 4681-20, Slide No 260, p. 15, GINPC No 147; 8 —Sample No 4681-60, Slide No 302, p. 4, GINPC No 152; 9 —Sample No 4681-24, Slide No 261, p. 7, GINPC No 150; 10 —Sample No 4681-K1, Slide No 51K, p. 15, GINPC No 151.
3, 5-7. *Siphonophycus typicum* (Hermann, 1974): 3 —Sample No 4694-94, Slide No 541, p. 7, GINPC No 536; 5 —Sample No 4694-110, Slide No 741, p. 9, GINPC No 609; 6, 7 —Sample No 3893-276, Slide No 137; 6 —p. 11', GINPC No 123, 7 — p. 7, GINPC No 126.

Specimen GINPC No 722 (fig. 1) is from the Satka Formation, specimens GINPC No 124, 123 and 126 (figs 2, 6 and 7) are from the Minyar Formation, specimens GINPC No 147, 150, 151 and 152 (figs 4, 8-10) are from the Chichkan Formation, specimen GINPC No 536 (fig. 3) is from the Sukhaya Tunguska Formation, and specimen GINPC No 609 (fig. 5) is from the Shorikha Formation.

PLATE 22

Hormogonian cyanobacteria genera *Eosphaeronostoc* Sergeev, 1992, *Orculiphycus* Yakschin, 1991 and *Archaeoellipsoides* Horodyski and Donaldson, 1980.

1, 2. *Eosphaeronostoc kataskinicum* Sergeev, 1992, Sample No 4688-22: 1 —Slide No 421, p. 24, EFL K-49-2, GINPC No 48 (Holotype); 2 —Slide No 913, p. 6, GINPC No 765.
3, 4. *Orculiphycus* spp.: 3 —Sample No 4689-48, Slide No 577, p. 4, EFL H-40-2, p. 5, GINPC No 462; 4 —Sample No 4689-53, Slide No 580, EFL L-50-4, p. 10, GINPC No 461.
5, 6, 8. *Orculiphycus latus* Yakschin, 1991: 5 —Sample No 4689-53, Slide No 580, EFL P-26-2, p. 12, GINPC No 459; 6 —Sample No 4689-7e, Slide No 478, EFL P-39-4, p. 12, GINPC No 446; 8 —Sample No 4689-47b, Slide No 572, EFL T-37-2, p. 15, GINPC No 460.
7. *Archaeoellipsoides major* (Golovenok and Belova, 1984), Sample No 4689-51, Slide No 566, p. 5, EFL M-48-0, GINPC No 444.

Specimens GINPC No 48 and 765 (figs 1 and 2) are from the Avzyan Formation; all other specimens are from the Kotuikan Formation.

PLATE 23

Hormogonian cyanobacterium genus *Circumvaginalis* Sergeev, 1993 - *C. elongatus* Sergeev, 1993.

1-6, 8. Sample No 4689-7g: 1 —Slide No 459, EFL M-32-3, p. 18, GINPC No 392; 2 —Slide No 454, EFL C-30-1, p. 18, HUHPC No 62928; 3, 4 (square in 3) —Slide No 471, EFL L-33-2, p. 14, GINPC No 391 (Holotype); 5 —Slide No 471, EFL N-37-2, p. 12, GINPC No 394; 6 —Slide No 453, EFL P-34-1, p. 9, HUHPC No 62950; 8 —Slide No 453, EFL G-50-3, p. 15, HUHPC No 62949.
7. Sample No 4689-23, Slide No 487, EFL R-33-2, p. 17, GINPC No 431.

Specimen GINPC No 431 (fig. 7) is from the Yusmastakh Formation; other specimens are from the Kotuikan Formation.

PLATE 24

Akinetes of nostocalean or stigonematalean cyanobacterium genus *Archaeoellipsoides* Horodyski and Donaldson, 1980.

1, 2 (square in 1). *Archaeoellipsoides conjunctivus* Zhang Y., 1985 — Sample No KG 92-43, Slide No 2A, EFL M-39-0, GINPC No 491.
3. *Archaeoellipsoides bactroformis* Sergeev and Knoll, 1995 — Sample No KG 92-60, Slide No 1A, EFL M-45-0, HUHPC No 62924 (Holotype).
4. *Archaeoellipsoides dolichos* (Zhang Y., 1985), Sample No 4689-47a, Slide No 571, EFL R-38-2, GINPC No 454.
5, 6, 9. *Archaeoellipsoides elongatus* (Golovenok and Belova, 1984): 5 —Sample No 4689-47b, Slide No 573, EFL N-27-0, GINPC No 456; 6 —Sample No 4689-21g, Slide No 492, EFL W-53-0, GINPC No 457; 9 —Sample No 4698-41, Slide No 818, p. 1, GINPC No 677.
7, 10, 11. *Archaeoellipsoides minor* nom. Sergeev and Knoll, 1995: 7 —Sample No 4694-110, Slide No 723, p. 16, GINPC No 625; 10 —Sample No 4689-47a, Slide No 575, EFL N-35-3, p. 15, HUHPC No 62934; 11 —Sample No 4689-7e, Slide No 461, EFL J-31-3, p. 30, GINPC No 490.
8. *Archaeoellipsoides costatus* Sergeev and Knoll, 1995 —Sample No 4689-48, Slide No 576, EFL F-39-3, p. 1, GINPC No 465 (Holotype).

Specimens GINPC No 454, 456, 465, 490, 491 and HUHPC No 62924 and 62934 (figs 1-5, 8 and 10, 11) are from the Kotuikan Formation, specimen GINPC No 457 (fig. 6) is from the Yusmastakh Formation, specimens GINPC No 625 (fig. 7) is from the Shorikha Formation, and specimen GINPC No 677 (fig. 9) is from the Yudoma Group.

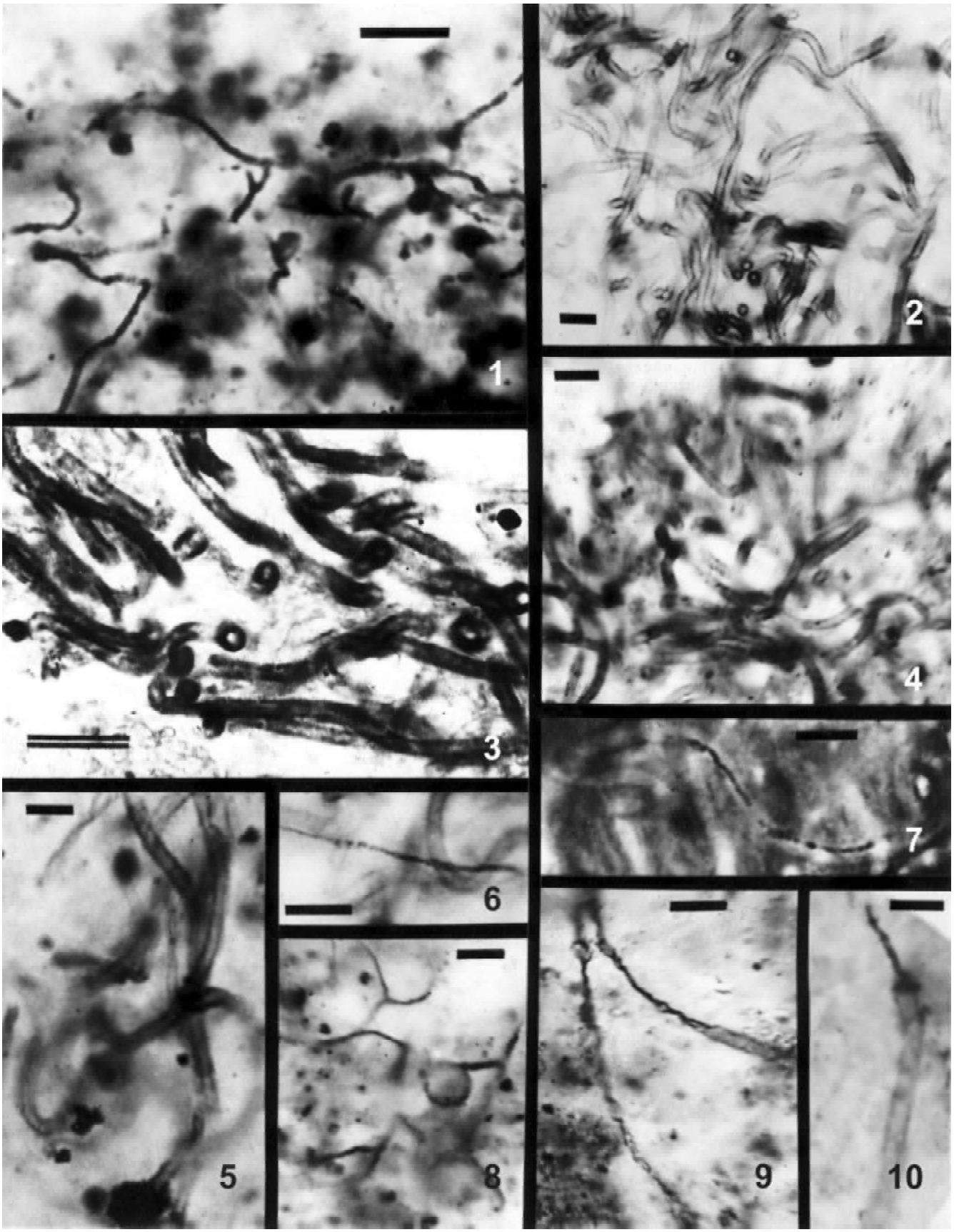


PLATE 21

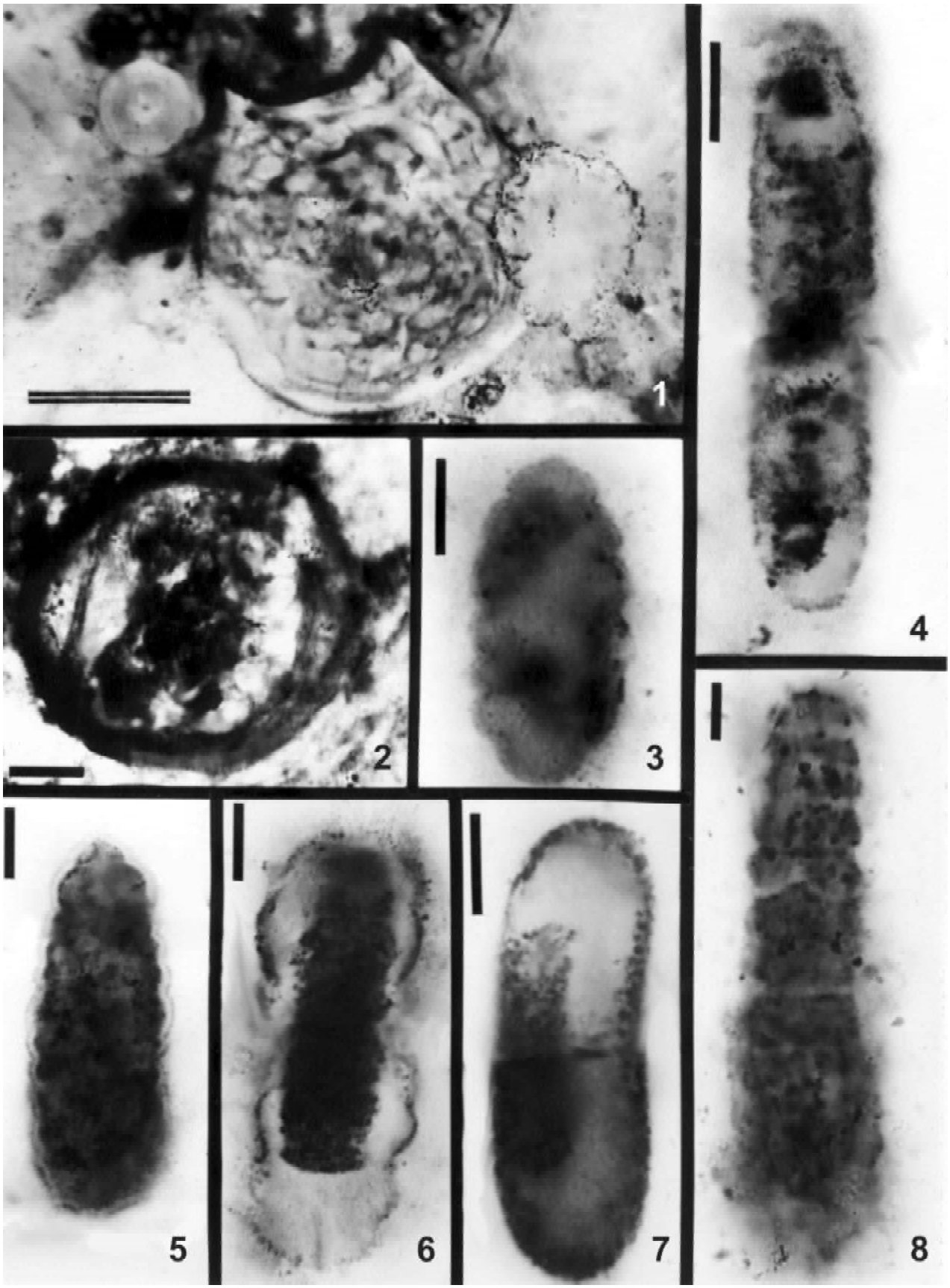


PLATE 22

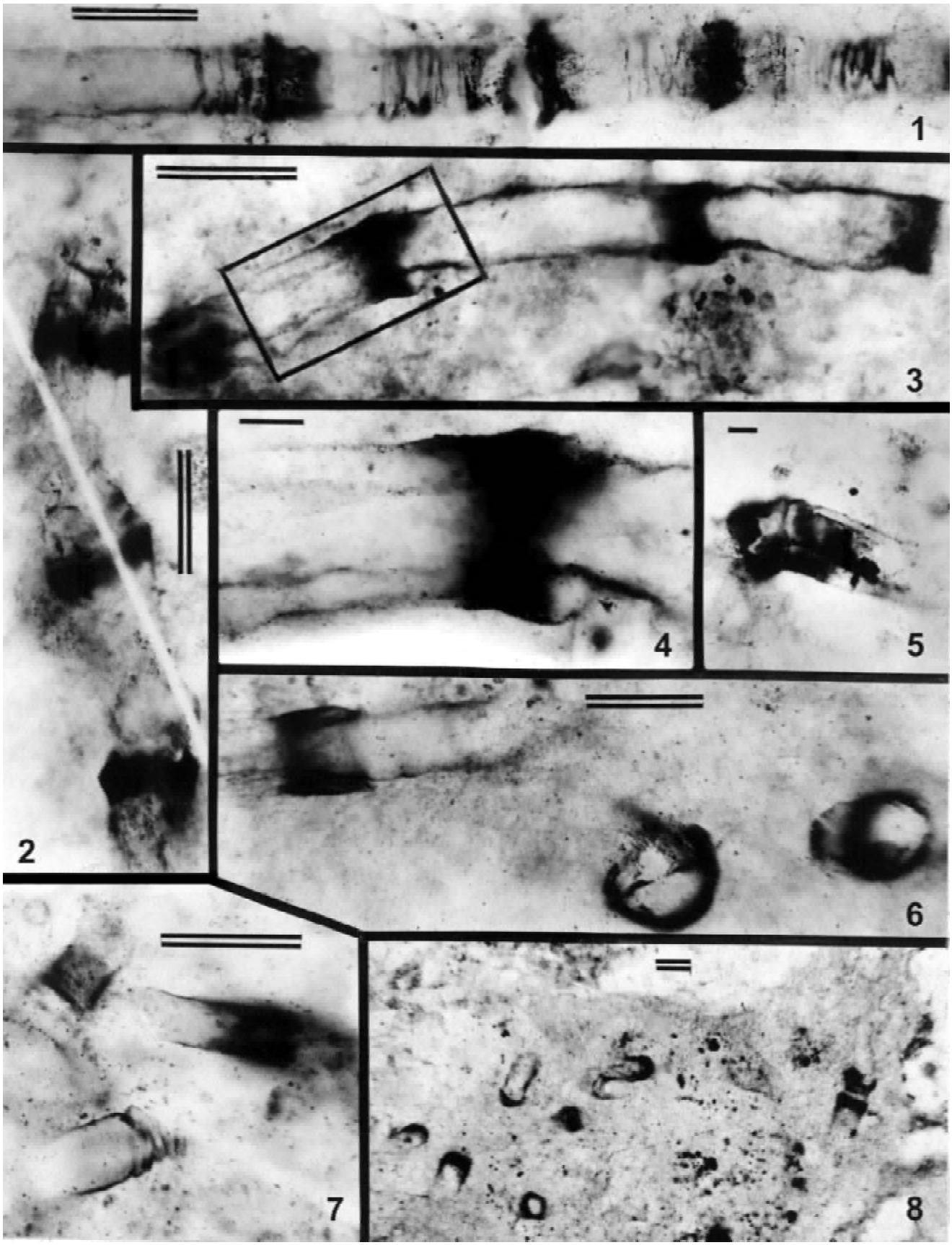


PLATE 23

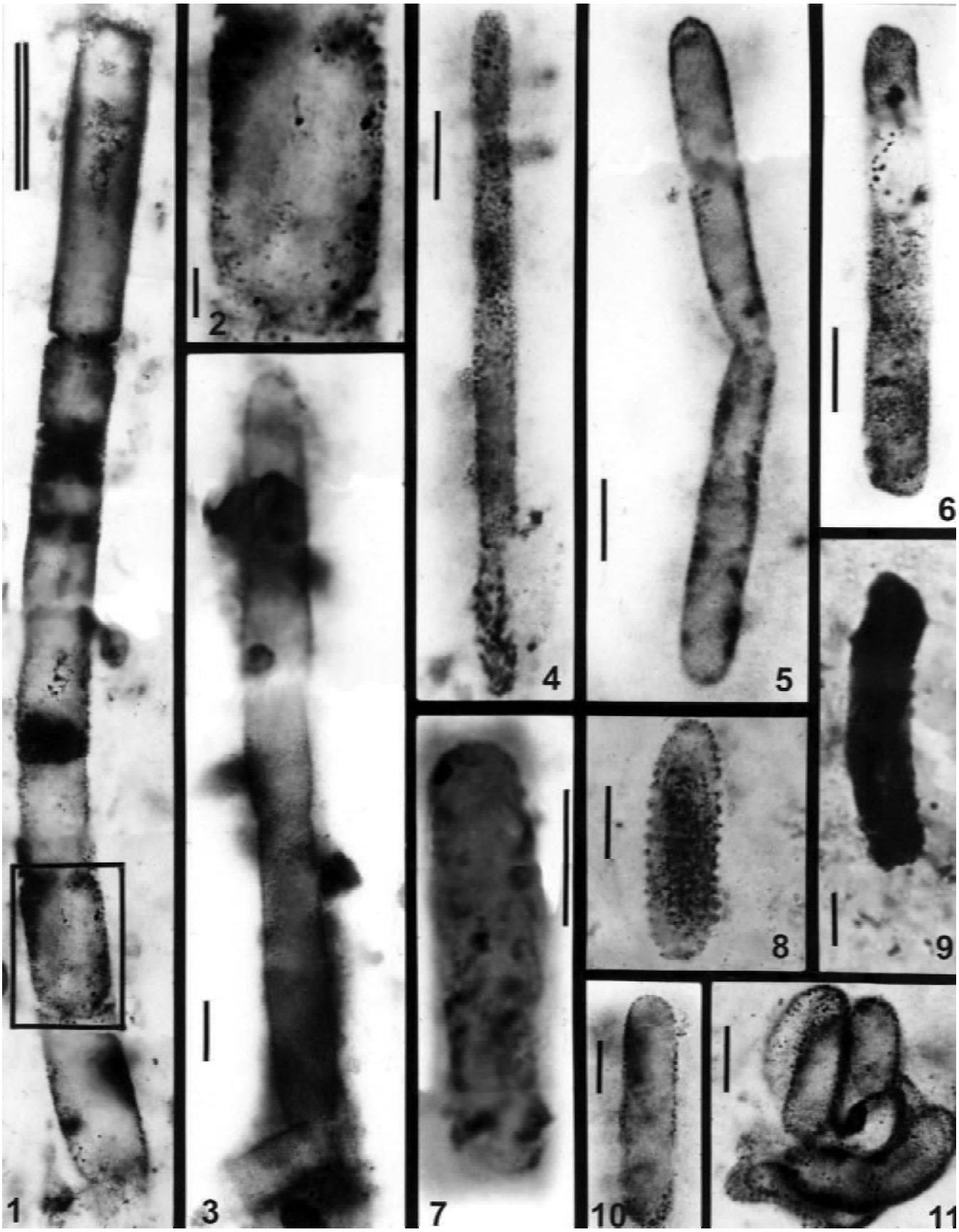


PLATE 24

INSERTAE SEDIS

Genus—ANIMIKIEA Barghoorn, 1965 (in Barghoorn and Tyler, 1965)

Animikiea Barghoorn, 1965 in Barghoorn and Tyler, 1965, p. 576.

Type species—*Animikiea septata* Barghoorn, 1965.

Diagnosis—Unbranched single-layered thick-walled empty tubes with fine ribs giving appearance of rugose surface.

Remarks—These microfossils are considered either as remains of empty sheaths of cyanobacteria order Oscillatoriales or Nostocales (Awramik & Barghoorn, 1977; Hofmann & Schopf, 1983) or iron-loving bacteria (Knoll, 2003).

Contents—Monospecific genus.

Age—Palaeoproterozoic.

Animikiea septata Barghoorn, 1965 (in Barghoorn and Tyler, 1965), emend. Awramik and Barghoorn, 1977

(Pl. 14.4-6; Fig. 34A)

Animikiea septata Barghoorn, 1965 in Barghoorn and Tyler, 1965, p. 576, Figs 3.1-3.3; Awramik and Barghoorn, 1977, p. 139, fig. 7A; Walter and Hofmann, 1983, Figs 9-2E-2F; Hofmann and Schopf, 1983, Photo 14-1-A; Schopf, 1992b, Pl. 2, Figs L, M; Sergeev *et al.*, 2010, Pl. I, fig. 2.

Repository—HUHPC-58253.

Stratum typicum—Palaeoproterozoic, Gunflint Formation, Canada.

Description—Unbranched single-layered empty tubes with coarse-grained thick walls and fine ribs at surface. Tube width is 7.0-11.0 μm and its length can be greater than 100 μm.

Remarks—Such thick sheaths with fine ribs could be a part of any Proterozoic microfossils assemblage. The true affinity of these sheaths is not absolutely decipherable and may be after cyanobacteria even may be after bacteria or some eukaryotic microorganisms. This taxon is currently applicable only for the rugose tubes (sheaths) from the Palaeoproterozoic iron formations.

Age and distribution—Palaeoproterozoic, Gunflint-Biwabik and Sokoman Formations, Canada.

Genus—CHLOROGLOEAOPSIS Maithy, 1975, emend. Hofmann and Jackson, 1994

Chlorogloeaopsis Maithy, 1975, p. 139; Hofmann and Jackson, 1994, p. 18-19.

Polysphaeroides Hermann, 1976 (partim): Timofeev *et al.*, 1976, p. 41-42.

Type species—Chlorogloeaopsis zairensis Maithy, 1975.

Diagnosis—Solitary unbranching sheathless trichomes formed of parallel rows of spherical cells or compressed cells without any regularity.

Remarks—Trichomes composed of spherical cells were described by Maithy (1975) as *Chlorogloeaopsis* from the Bushimay Group of Zaire, Africa. Hermann in Timofeev *et al.* (1976) has described almost identical filaments from the Neoproterozoic Miroedikha Formation of Siberia and erected genus *Polysphaeroides* probably unaware of the previous publication by Maithy. Subsequently, Hofmann and Jackson (1994) have merged *Polysphaeroides* to *Chlorogloeaopsis*, but did not provide either formal synonymy of emended genus or genus composition or status of *Polysphaeroides filiformis* (type species of genus *Polysphaeroides*). To us, it appears that after the long discussion by the Hofmann and Jackson (1994) the genus *Polysphaeroides* stands non-existent and simultaneously all the species there of. Even after this newer work, Sun & Zhu (1998) have mentioned this genus and erected a new species-*P. formosus*. In fact we notice that the status concerning both *Chlorogloeaopsis* and *Polysphaeroides* is still unclear and needs a thorough revision in separate publication. The multicellular filaments of *Chlorogloeaopsis* are considered either as remains of *Stigonema*-like stigonematalean cyanobacteria or eukaryotic algae, e. g. green or red. In some latest publications *Chlorogloeaopsis* has been interpreted as green algae, and similar trichomes (still described as *Polysphaeroides*) are reported from the Palaeoproterozoic rocks (Sun & Zhu, 1998) and are also considered as a proof of early appearance of these eukaryotic microorganisms in the fossil record (Teyssedre, 2006). Therefore, we prefere to keep this taxon as Incertae Sedis.

Name of species	Diagnostic features	Cells diameter and filaments width, μm	Paleoenvironmental setting	Repository and type locality	References
C. kanshiensis Maithy, 1975 Fig. 49C	Multicellular sheathless trichomes composed from spherical cells 2-3 in a row	10-15; 18-30	Subtidal recorded from shales.	MRAC - 32400/3; Neoproterozoic, Bushimay Group, Zaire, Africa.	Maithy, 1975; Hofmann & Jackson, 1994

Table 17—Comparative characteristics of genus *Chlorogloeaopsis* species (Type Specimens).

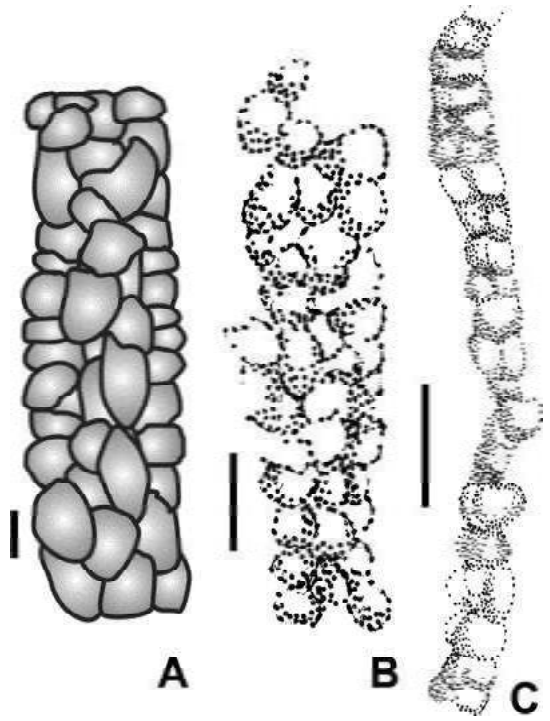


Fig. 49—Line diagrams of species of *Chlorogloeaopsis*. A- *C. zairensis* (Maithy, 1975); B- *C. contexta* (Timofeev *et al*., 1976); C- *C. kanshiensis* (Maithy, 1975). Scale bar = A, B = 10 µm, C= 50 µm.

Content—C. contexta, C. kanshiensis and *C. zairensis* (Table-17).

Age—Neoproterozoic.

Chlorogloeaopsis zairensis Maithy, 1975

(Fig. 49A)

Chlorogloeaopsis zairensis Maithy, 1975, p. 139, Pl. 3, Figs 21-23; Butterfield *et al.*, 1994, p. 73, fig. 20I.

Polysphaeroides biseritus Liu, 1985 in Xing *et al.*, 1985, p. 65, Pl. 7, Figs 14-15.

Repository—MRAC-32440/3.

Stratum typicum—Neoproterozoic, Bushimay Group, Zaire, Africa.

Description—Solitary, nonbranching, sheathless nontapering toward ends trichomes, formed of spherical cells in parallel rows (2-4 in a row) assuming a filament shape. Cell diameters vary from 7 to 13 µm, diameter of filaments vary from 15 to 20 (up to 35) µm. Cell walls are single-layered, translucent, fine-grained, less then 0.5 µm thick.

Age and distribution—Neoproterozoic: Bushimay Group, Zaire; Svangbergfjellet Formation, Spitsbergen.

Chlorogloeaopsis contexta (Hermann, 1976) (in Timofeev *et al.*, 1976), comb. Hofmann and Jackson, 1994

(Pl. 14.7-9; Fig. 49B)

Chlorogloeaopsis contexta Hofmann and Jackson, 1994, p. 19, Figs 12.13-12.15; Prasad *et al.*, 2005, Pl. 7, fig. 9, Pl. 11, fig. 14.

Polysphaeroides contextus Hermann, 1976 in Timofeev *et al.*, 1976, p. 42-43, Pl. 14, Figs 3, 4; Yankauskas, 1989, p. 119, Pl. XXVII, Figs 10a, 10б; Hermann, 1990, Pl. VII, fig. 8; Schopf, 1992b, Pl. 24, Figs B_1, B_2; Sergeev, 2001, p. 443, Figs 9.1-9.3; Sergeev, 2006, p. 230-231, Pl. XVIII, Figs 1-3; see Hofmann and Jackson, 1994, p. 19 for additional synonymy.

Repository—IGGP-49a/3.

Stratum typicum—Neoproterozoic, Miroedikha Formation, Turukhansk Uplift, Russia.

Description—Solitary, nonbranched, sheathless, nontapering filaments consisting from spherical compressed cells situated in the filaments without any regularity. The sheath surrounding filament is missing. Cell walls are single-layered, translucent, fine-grained, less then 0.5 µm thick. Cell diameters vary from 1.5 to 8.5 µm, filament diameter 7.5-27 µm, maximum length of filaments up to 250 µm or more.

Age and distribution—Mesoproterozoic: Bylot Supergroup, Baffin Island, Canada; Neoproterozoic: Burovaya and Miroedikha Formations, Turukhansk Uplift; Nelkan, Kumakhtinskaya, Kandykskaya and Ust'-Kirba Formations, Uchur-Maya Region; Daskinskaya Formation, Yenisey Ridge, Siberia.

Remarks—P. contexta from the Burovaya cherts (Pl. 14.7-9; see also Sergeev, 2001, 2006) demonstrates what may be true branching, tapering toward ends, branches consist of morphologically dissimilar pill-like cells, 3.5-5.5 µm wide and 3.0-5.0 µm long. However, this «branching» may alternatively result from the superimposition of originally nonbranching filaments of *Chlorogloeaopsis contexta* on trichomes of *Oscillatoriopsis obtusa*. In this case, the trichomes resembling *Oscillatoriopsis obtusa* that co-occur with *C. contexta* may represent early stages in the life cycle of the latter cyanobacterium (see Kondratieva, 1975, p. 123-132). Or, alternatively, *C. contexta* may be remnants of a filamentous eukaryotic alga, e. g. a green alga.

Genus—CHUARIA Walcott, 1899

Chuaria Walcott, 1899, p. 234, 235; Vidal and Ford, 1985, p. 357; Yankauskas, 1989, p. 67-68; Butterfield *et al.*, 1994, p. 30, 32. See Vidal and Ford, 1985, p. 357 and Butterfield *et al.*, 1994, p. 30 for additional synonymy.

Type species—Chuaria circularis Walcott, 1899.

Diagnosis—Single-layered large spheroidal vesicles more than 1000 μm in diameter (up to 5000 μm) occur as isolated individuals or sometimes in loose clusters. Walls are robust translucent or opaque more than 2 μm thick.

Remarks—*Chuaria* has been widely discussed and variously interpreted; major recent reviews being offered by Vidal and Ford (1985), Yankauskas (1989), Butterfield in Butterfield *et al.* (1994), Steiner (1996) and Sharma *et al.* (2009). *Chuaria* is a form taxon belongs to group of sphaeromorphic acritarchs and includes large robust-walled vesicles more than 400 or 1000 μm in diameter. Most vesicles are definitely remains of eukaryotic unicellular phytoplanktonic microorganisms (Vidal & Ford, 1985; Yankauskas, 1989; Butterfield *et al.*, 1994). But some vesicles could turn out to be empty envelopes surrounding colonies of *Sphaeronostoc*-like cyanobacteria (Sun, 1987; Sergeev, 1992a, 2006; Steiner, 1996).

Contents—Monospecific genus.

Chuaria circularis Walcott, 1899, emend. Vidal and Ford, 1985, emend. Yankauskas, 1989

(Plate 26.1-3)

Chuaria circularis Walcott, 1899, p. 234, 235, Pl. XXVII, Figs 12, 13; Vidal and Ford, 1985, p. 357-359, fig. 3A; Yankauskas, 1989, p. 67, 68, Pl. XII, Figs 1, 2; Butterfield *et al.*, 1994, p. 32, 34, Figs 8G, 8H, 13G-13I; Rai *et al.*, 1997, Figs 3c-3f, 3h-3j, 3l-3n, 3p-3r, 3t-v, 3x-3z; Sharma and Shukla, 1999, Figs 4c-4f; Gnilovskaya *et al.*, 2000, Pl. I, Figs 3, 6; Srivastava, 2002, p. 101, Figs 5B-5D, 5H-5J; Srivastava, 2004, Figs 2a-2c, 2e, 2o, 2p, 2q; Veis *et al.*, 2004, Pl. IV, fig. 8; Vorob'eva *et al.*, 2009a, p. 185, fig. 14.6; Sharma *et al.*, 2009, Figs 6a-6o, 7n-7q, 10. For additional synonymy see Vidal and Ford, 1985, Steiner, 1994, and Butterfield *et al.*, 1994.

Repository—Vidal and Ford, 1985, fig. 3A (Lectotype).

Stratum typicum—Neoproterozoic, Chuar Group, North America.

Description—Spheroidal, solitary, vesicles 1000 (400, in Butterfield *et al.*, 1994)-5000 μm in diameter. Walls opaque, quite thick; surface texture chagrinate.

Remarks—Besides *Chuaria circularis* some other taxa of similar size and morphology, but differ in some features have been described, e.g. genus *Cerebrosphaera* Butterfield, 1994 encompassing spheroidal solitary vesicles 100 to 1000 μm in diameter, having chagrinate surface texture that exhibits prominent, characteristic, regularly anatomizing (interfingering) wrinkles. The surface texture for some silicified specimen could be of secondary origin (Pl. 26.4).

Age and distributio.-Widely distributed in Proterozoic rocks.

Genus—CLONOPHYCUS J. Oehler, emend. D. Oehler, 1978

Clonophycus J. Oehler, 1977, p. 346; D. Oehler, 1978, p. 303.

Type species—Clonophycus elegans J. Oehler, 1977.

Diagnosis—Groups of single-walled spheroidal vesicles contained within a common vesicle of spheroidal or irregular shape. Sometimes wall of vesicles are broken and inner spheroids lie outside outer wall.

Remarks—Genus *Clonophycus* was described by J. Oehler (1977) and emended by D. Oehler as "cells contained within a psilate to finely granular, spherical sac-like structure..." (D. Oehler, 1978, p. 303). Later, Golovenok and Belova (1984) described genus *Eogloeocapsa* in the following terms: "cells usually form isolated colonies of two to eight cells, sometimes many more, surrounded by a common sheath" (Golovenok &

Name of species	Diagnostic features	Diameters of inner and outer vesicles, μm	Palaeoenvironmental setting	Repository and type locality	References
C. biattina D. Oehler, 1978 Fig. 50B	Vesicles packed inside of larger vesicles.	3.3-13.0 (diameter of outer vesicles not provided)	Tidal flat, recorded from cherts in dolomites.	CPC – 18348; Mesoproterozoic, Balbirini Fm., Australia.	D. Oehler, 1978
C. ostiolum D. Oehler, 1978 Fig. 50C	—	2.0-3.0; 7.0-18.0	Tidal flat, recorded from cherts in dolomites.	CPC – 18350; Mesoproterozoic, Balbirini Fm., Australia.	D. Oehler, 1978
C. refringens D. Oehler, 1978 Fig. 50D	—	12.0–30.0 (diameter of inner vesicles not provided)	Tidal flat, recorded from cherts in dolomites.	CPC – 18349; Mesoproterozoic, Balbirini Fm., Australia.	D. Oehler, 1978
C. vulgaris D. Oehler, 1978 Fig. 50E	—	2.7–13.3; 10.0–25.0	Tidal flat, recorded from cherts in dolomites.	CPC – 18349*; Mesoproterozoic, Balbirini Fm., Australia.	D. Oehler, 1978

* The same number of the type specimens for *C. refringens* and *C. vulgaris* is refered to the thin section containing the microfossils.

Table 18—Comparative characteristics of genus *Clonophycus* species (Type Specimens).

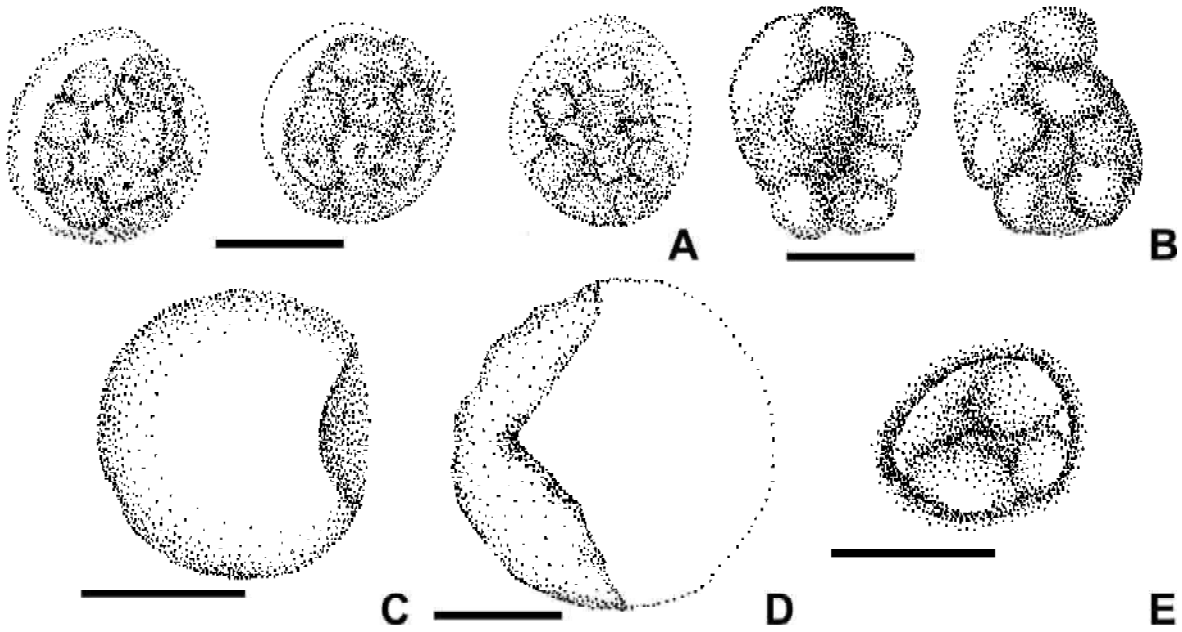


Fig. 50—Line diagrams of species of *Clonophycus* . A- *C. elegans* (J. Oehler, 1977); B- *C. biattina* (D. Oehler, 1978); C- *C. ostiolum* (D. Oehler, 1978); D- *C. refringens* (D. Oehler, 1978); E- *C. vulgaris* (D. Oehler, 1978). Scale bar = A-E = 10 μm.

Belova, 1984, p. 28, English version). It is evident that both taxa cover a single type of microfossil organization, like *Gloeocapsa* or gloeocapsoid colonies of entophysalidacean cyanobacteria.

J. Oehler and D. Oehler did not suggest any certain biological affinities for *Clonophycus* species and only pointed out that they could be the remains of either prokaryotic or eukaryotic organisms. We consider *Clonophycus* as a form taxon embracing gloeocapsoid colonies of cyanobacteria or probably of some eukaryotic algae, e.g. green alga *Chlorella.*

Contents—C. biattina, C. elegans, C. ostiolum, C. refringens and *C. vulgaris* (Table-18).

Age—Proterozoic.

Clonophycus elegans J. Oehler, 1977

(Fig. 50A)

Clonophycus elegans J. Oehler, 1977, p. 346-347, Figs 11A-11D, 11J-11K; Hofmann and Schopf, 1983, Photo 14-7-T; Sharma, 2006a, p. 93, 94, fig. 11e.

Repository—CPC-16929.

Stratum typicum—Early Mesoproterozoic, Barney Creek Formation, Australia.

Description—Groups of single-walled spheroidal vesicles contained within a common vesicle of spheroidal or irregular shape. Sometimes the walls of the vesicles are broken and the inner spheroids lie outside the outer wall. Vesicles may or may not contain internal spot-like inclusion 0.5-0.9 μm diameter. Vesicles longer dimension ranges from 3.6 to 6.8 μm, diameter of outer vesicles ranges from 15 to 20 μm.

Age and distribution—Mesoproterozoic, Barney Creek Formation, Australia.

Genus—GLENOBOTRYDION Schopf, 1968, emend. Nyberg and Schopf, 1984

Glenobotrydion Schopf, 1968, p. 681; Nyberg and Schopf, 1984, p. 765-766.

Type species—Glenobotrydion aenigmatis Schopf, 1968.

Diagnosis—Spherical vesicles with dark inclusions inside occur in loose clusters or forming pseudofilamentous aggregates.

Remarks—Glenobotrydion was described by Schopf (1968) as possible green algae with nuclei or pyrenoides inside. Later, it turned out that such microfossils with inclusions are degraded stages of various coccoidal both pro-and eukaryotic microorganisms (Golubic & Hofmann, 1976; Hofmann, 1976; Knoll & Golubic, 1979; Nyberg & Schopf, 1984; Sergeev, 1992a). Presence of non-lamellated sheath around the pseudofilaments is a characteristic of this genus. But some species have been described without such non-lamellate sheaths, e.g. *G. kanshiensis* (Maithy, 1975) and subsequently synonymized with *Chlorogloeaopsis* as *Chlorogloeaopsis*

Name the species	Diagnostic features	Diameters of vesicles and inclusions μm	Palaeoenvironmental setting	Repository and type locality	References
G. compressus Golovenok and Belova, 1985	Spherical vesicles in elongated colonies.	12.0 - 20.0; 1.0-2.0 to 5.0 – 6.0	Subtidal to intertidal recorded from cherts in dolomites.	VSEGEI – 414-e, Neoproterozic, Kirgita Fm., Enisei Ridge, Russia.	Golovenok & Belova, 1985
G. granulosum Zhang Y., 1988 Fig. 51C	Spherical vesicles with multiple inclusions.	3.3-8.2; 0.7–2.0	Subtidal to intertidal recorded from cherts in dolomites.	BGPZD – 5 - 8401B, Mesoproterozoic, Dahongyu Fm., China.	Zhang Y., 1988
G. varioforme Zhang Y., 1981 Fig. 51D	Vesicles with aster-like, dot-like vesicle-like or irregular inclusions.	2.0-11.5 (diameter of inclusions is not provided).	Tidal flat, recorded from cherts in dolomites.	BGP – 7816, Mesoproterozoic, Gaoyuzhuang Fm., China.	Zhang Y., 1981

Table 19—Comparative characteristics of genus *Glenobotrydion* species (Type Specimens).

kanshiensis comb. Hofmann and Jackson, 1994 (Hofmann & Jackson, 1994, p. 20). Currently, genus *Glenobotrydion* is considered as a form taxon incorporating remains of eukaryotic algae and chroococcaceans as well as probably cells from disintegrated trichomes of nostocalean or stigonematalean cyanobacteria (Sergeev, 2006). One of the important diagnostic features of this genus is formation of pseudofilamentous colonies by many hundred of spheroids. However, such colonies can be formed as a result of pressure of sediments on cyanobacterial mats (Sergeev, 1992a).

Golovenok and Belova (1985) have described genus *Cyanothrixoides* consisting of spherical vesicles and forming pseudofilamentous aggregates. They considered this taxon as chroococcacean cyanobacteria of family cyanothrichaceae, but such pseudofilamentous colonies are described as *Glenobotrydion* and it would be advisable to consider *Cyanothrixoides* as its junior synonym.

Contents—*G. aenigmatis, G. compressus, G. granulosum, G. majorinum, G. tetragonale* and *G. varioforme* (Table-19).

Age—Proterozoic.

Glenobotrydion aenigmatis Schopf, 1968

(Fig. 51A)

Glenobotrydion aenigmatis Schopf, 1968, p. 681, 683, Pl. 81, fig. 5, Pl. 83, fig. 9, Pl. 84, Figs 4, 5; Schopf and Blacic, 1971, Pl. 110, fig. 7; McMenamin *et al.*, 1983, p. 260, 261, Figs 5D, 5F; Knoll, 1984, p. 146, Figs 4G, 4H, 4J, 5I; Shukla *et al.*, 1986, p. 349, 350, Pl. 2, Figs 1, 19, 20; Schopf, 1992b, Pl. 32, fig. E; Kumar and Srivastava, 1992, p. 302-304, fig. 9G; Kumar and Srivastava, 1995, p. 110, Figs 8G, 8K; Shukla *et al.*, 2006, p. 60, Pl. I, fig. 15.

Repository—HUHPC-58505.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Single lamillated spherical vesicles occur in loose clusters or forming pseudofilamentous aggregates. Vesicles contain dark semicircular or spherical inclusions attached to inner sides of their fine-grained walls. Vesicles diameter range from 7.0 to 12.0 μm, inner inclusions diameter varies from 1.5 to 2.5 μm.

Remarks—Schopf (1968) mentioned presence of prominent sheath surrounding pseudofilamentous colonies of *G. aenigmatis*. However, sheath-like structures can be formed as a result of excessive secretion of mucilage or its compaction or fortuitous redistribution of organic matter around the colony of vesicles.

Age and distribution—Mesoproterozoic: Kheinjua Formation, India; Neoproterozoic: Bitter Springs Formation, Australia; Hunnberg Formation, Spitsbergen; Deoban Limestone and Buxa Limestone Formations, India.

Glenobotrydion majorinum Schopf and Blacic, 1971, emend. Nyberg and Schopf, 1984

(Pl. 2.1-4, Fig. 51B)

Glenobotrydion majorinum Schopf and Blacic, 1971, p. 954-955, Pl. 110, Figs 6, 9, 10, Pl. 113, fig. 2; Sergeev, 1992a, p. 101, Pl. XX, Figs 6-8; Sergeev, 2006, Pl. XLVII, Figs 3, 6, 8; Sergeev and Schopf, 2010, p. 392, 393, Figs 11.1, 11.1a, 11.1b, 11.2.

Not *Glenobotrydion majorinum* Schopf and Blacic, 1971. Nyberg and Schopf, 1984, p. 766, 769, Figs 5A, 16A-16R, 17A-17F, 17H; Schopf, 1992b, Pl. 47, Figs A-D, G.

Repository—HUHPC-58617.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Single-walled spheroidal vesicles, defined by fine-grained 1.0-to 1.5-μm-thick walls, that commonly contain a prominent dark spheroidal inclusion and occur in loose colonial clusters or pseudofilamentous aggregates. Vesicles diameter ranges from 10.0 to 23.0 μm with that of the inclusions varying from 1.5 to 3.5 μm.

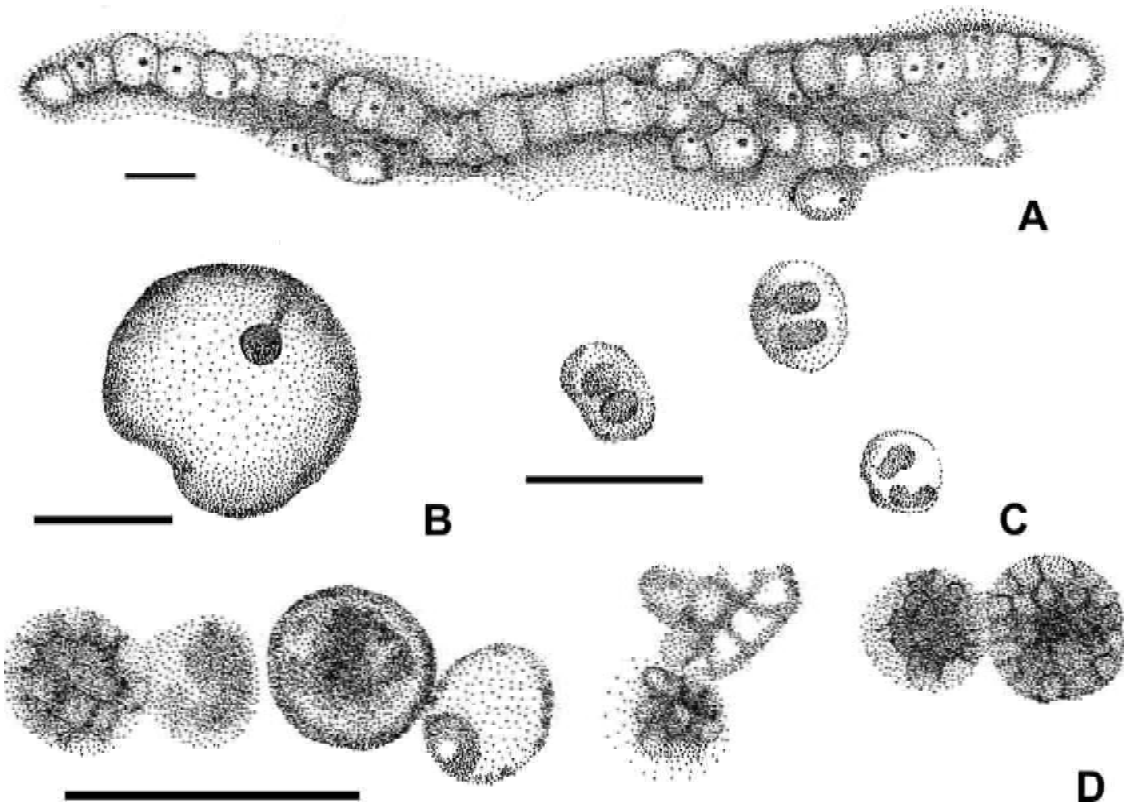


Fig. 51—Line diagrams of species of *Glenobotrydion*. A- *G. aenigmatis* (Schopf, 1968); B- *G. majorinum* (Schopf, 1968); C- *G. granulosum* (Zhang, 1988); D- *G. varioforme* (Zhang Y., 1981). Scale bar = A-D = 10 µm.

Age and distribution—Neoproterozoic: Chichkan Formation, South Kazakhstan; Bitter Springs Formation, Australia.

Genus—GUNFLINTIA Barghoorn, 1965 (in Barghoorn and Tyler, 1965), emend. Awramik and Barghoorn, 1977

Gunflintia Barghoorn, 1965 in Barghoorn and Tyler, 1965, p. 576; Awramik and Barghoorn, 1977, p. 140.

Type species—*Gunflintia minuta* Barghoorn, 1965.

Diagnosis—Unbranched sheathless trichomes formed of isodiametric cylindrical and cask-like cells with weak constriction at septa.

Remarks—These trichomes are considered either as remains of cyanobacteria order Oscillatoriales or Nostocales (Barghoorn & Tyler, 1965; Licari & Cloud, 1968; Awramik and Barghoorn, 1977; Hofmann and Schopf, 1983) or *Leptothrix*-like iron-loving bacteria (Knoll, 2003).

Contents—*G. minuta* and *G. grandis.*

Age—Paleoproterozoic.

Gunflintia minuta Barghoorn, 1965 (in Barghoorn and Tyler, 1965), emend. Awramik and Barghoorn, 1977

(Pl. 14.1, 2; Fig. 52A)

Gunflintia minuta Barghoorn, 1965 in Barghoorn and Tyler, 1965, p. 576, Figs 4.6, 4.8, 6.1; Licari and Cloud, 1968, Figs 1-4, 7-9; Walter *et al.*, 1976, Figs 3a-3c; Awramik and Barghoorn, 1977, Figs 4A, 4D; Walter and Hofmann, 1983, Figs 9-2C-2D; Hofmann and Schopf, 1983, Photo 14-1-B; Knoll *et al.*, 1988, Figs 6a, 6c-6f; Lanier, 1989, Figs 3A-3I, 5C, 6B, 14A-14C; Schopf, 1992b, Pl. 2, Figs J, K; Sergeev *et al.*, 1998, Pl. I, Figs 1-10; Sergeev *et al.*, 2010, Pl. I, fig. 1.

Description—Unbranched sheathless trichomes formed of isodiametric cylindrical and cask-like cells 1.0-2.0 µm width with weak constriction at septa.

Remarks—There are two species of genus *Gunflintia: G. grandis* (Pl. 14.3; Fig. 40b) differs from *G. minuta* in having the bigger cells width from 2.5 to 5.0 µm and by prominent constrictions at septa (Awramik & Barghoorn, 1977). Trichomes of both species sometimes demonstrated enlarged cells which were interpreted either as heterocysts or akinetes of nostocacean cyanobacteria (Licari & Cloud, 1968; Cloud, 1976) or vegetative cells alterated by *post-mortem* processes of selective shrinkage and buldging (Golubic & Barghoorn, 1977; Gerasimenko & Krylov, 1983).

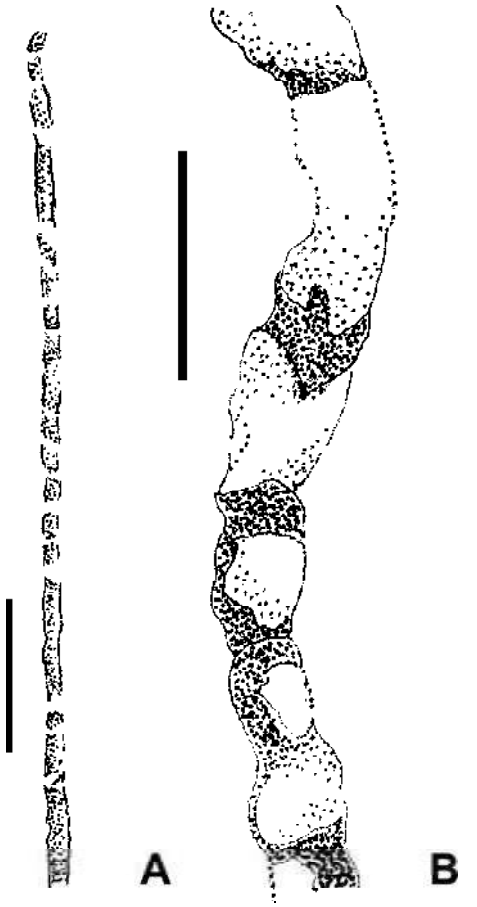


Fig. 52—Line diagrams of species of *Gunflintia*. A- *G. minuta* (Barghoorn & Tyler, 1965); B- *G. grandis* (Barghoorn & Tyler, 1965). Scale bar = 10 μm.

Age and distribution—Palaeoproterozic: Gunflint-Biwabik and Sokoman Formations, Canada; Duck Creek and Frere Formations, Australia.

Genus—HURONIOSPORA Barghoorn, 1965 (in Barghoorn and Tyler, 1965), emend. Awramik and Barghoorn, 1977

Huroniospora Barghoorn, 1965 in Barghoorn and Tyler, 1965, p. 576; Awramik and Barghoorn, 1977, p. 140.

Type species—Huroniospora microreticulata Barghoorn, 1965.

Diagnosis—Spherical to ellispodal vesicles without dark inclusions inside with psilate to murate wall sculpture pattern occur in loose clusters.

Remarks—Huroniospora has been described by Barghoorn (Barghoorn & Tyler, 1965) who compared them to chroococcacean unicellular *Chroococcus*-type cyanobacteria, endospores of hormogonian blue-green algae or iron bacteria, fungus spores or dinoflagellates. The simple morphology of *Huroniospora* allows many interpreatation applied to these microorganism remains. Later on the unicells were compared to the budding bacteria (Hirsch, 1974; see Awramik & Barghoorn, 1977 for discussion) or even to red algae order Porphyridiales (Tappan, 1976). However, most researches consider *Huroniospora* as cyanobacterium consistent with their stromatolitic association and lack in non-stromatolitic facies of the Gunflint Formation (Awramik & Barghoorn, 1977; Knoll *et al.*, 1978; Hofmann & Schopf, 1983). Nonetheless, the simple *Huroniospora* morphology is possibly in favor of its heterogenic composition: most spheroids are probably true cyanobacteria, other can be either cells or spores of iron bacteria and some elongated forms could turn out to be akinetes of nostocalean or stigonematalean cyanophyceae (Cloud, 1976).

Contents—H. microreticulata, H. macroreticulata and *H. psilata* (Table-20).

Age—Palaeoproterozoic.

Huroniospora microreticulata Barghoorn, 1965 (in Barghoorn and Tyler, 1965)

(Pl. 2.5-7, Pl. 14.1; Fig. 53A)

Huroniospora microreticulata Barghoorn, 1965 in Barghoorn and Tyler, 1965, p. 576, fig. 5.1; Hofmann, 1971, Pl. 15, fig. 10; Hofmann and Schopf, 1983, Photo 14-1-L, M; Schopf, 1992b, Pl. 2, fig. E; Sergeev *et al.*, 2010, Pl. I, fig. 1.

Huroniospora sp. Sergeev *et al.*, 1998, Pl. I, Figs 5-10.

Repository—HUHPC-58264.

Name of species	Diagnostic features	Diameters and long axis of vesicles, μm	Palaeoenvironmental setting	Repository and type locality	References
H. macroreticulata Barghoorn, 1965 Fig. 53B	Spherical to ellipsoidal vesicles, wall thick with regularly murate pattern.	1 - 16	Subtidal recorded from cherts of iron formations.	HUHPC – 58266; Palaeoproterozoic, Gunflint Fm., Canada.	Barghoorn & Tyler, 1965
H. psilata Barghoorn, 1965 Fig. 53C	Spherical to ellipsoidal vesicles, wall thin and unornamentd.	1 - 16	Subtidal recorded from cherts of iron formations.	HUHPC – 58267; Palaeoproterozoic, Gunflint Fm., Canada.	Barghoorn & Tyler, 1965

Table 20—Comparative characteristics of genus *Huroniopsora* species (Type Specimens).

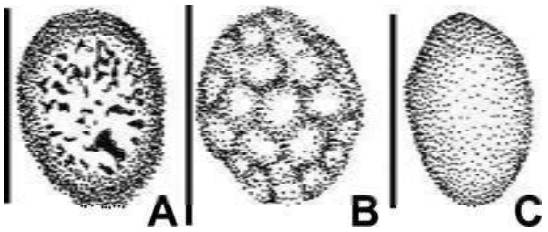


Fig. 53—Line diagrams of species of *Huroniospora*. A- *H. microreticulata* (Barghoorn & Tyler, 1965); B- *H. macroreticulata* (Barghoorn & Tyler, 1965); C- *H. psilata* (Barghoorn & Tyler, 1965). Scale bar = A = 10 μm, B, C = 5 μm.

Stratum typicum—Palaeoproterozoic, Gunflint Formation, Canada.

Description—Solitary, spherical to ellipsoidal vesicles; single-layered wall is thick, with sculpture pattern regularly reticulates. Vesicles sometimes with protrusions, occuring in loose clusters among filaments of *Gunflintia*. Vesicles diameter or range of long axes varies from 1 to 16.0 μm.

Remarks—Originally Barghoorn and Tyler (1965) described 3 species of *Huroniospora* of the same size, but differentiated on the basis of wall sculpture. Later, Awramik and Barghoorn (1977) considered the wall sculpture not a primary biological attribute, but as a result of diagenetic alteration and merged all the three species. However, they did not describe or formally emend species, but joined these forms as *Huroniospora* spp. Even after revision of *Huroniospora* by Awramik and Barghoorn (1977), the three species were remained in usage (Hofmann & Schopf, 1983; Schopf, 1992b). Therefore, we provide in present paper the formal characteristics of all three species originally described by Barghoorn and Tyler (1965) despite we accept diagenetic origin of wall sculpture. But we do not consider the simple spheroids described later from the Meso-and Neoproterozoic deposits as *Huroniospora* (e.g. Muir, 1976; Golovenok & Belova, 1985).

Age and distribution—Palaeoproterozoic, Gunflint Formation, Canada.

Genus—LEIOSPHAERIDIA Eisenack, 1958, emend. Downie and Sarjeant, 1963, emend. Turner, 1984, emend. Yankauskas, 1989

Leiosphaeridia Eisenack, 1958, p. 2-3; Downie and Sarjeant, 1963, p. 88, 94; Turner, 1984, p. 116; Yankauskas, 1989, p. 69-74. See Yankauskas, 1989, p. 69 for complete synonymy.

Type species—Leiosphaeridia baltica Eisenack, 1958.

Diagnosis—Single-layered large spheroidal vesicles less than 400 or 1000 μm in diameter occur as isolated individuals or sometimes in loose clusters. Walls are thin transparent, translucent or opaque 0.5-2 μm thick or sometime more.

Remarks—Formal designation of species within the genus *Leiosphaeridia* by Yankauskas (1989) is followed here. In this classification, morphologically simple smooth-walled envelopes are assigned to the genus *Leiosphaeridia*, including morphologically simple acritarch taxa described earlier as *Trachysphaeridium*, *Kildinella*, *Protoleiosphaeridium*, *Chuaria* (partim) and others. Species of *Leiosphaeridia* are recognized following a purely formal scheme based on envelope diameter and wall thickness (see Yankauskas, 1989, p. 24-25). Like *Chuaria*, most vesicles of *Leiosphaeridia* are definitely remains of eukaryotic unicellular phytoplanktonic microorganisms, but some of them probably are empty envelopes surrounding *Sphaeronostoc*-like or *Gloeocapsa*-like cyanobacterial colonies

Contents—L. atava, L. baltica, L. crassa, L. exculpta, L. jacutica, L. holtedahlii, L. kulgunica, L. laminarita, L. minutissima, L. obsuleta, L. tenuissima and *L. ternata*.

Age and distribution—Widely distributed in Proterozoic rocks.

Leiosphaeridia jacutica (Timofeev, 1969), emend. Mikhailova and Yankauskas, 1989 (in Yankauskas, 1989)

(Pl. 26.8, 10)

Leiosphaeridia jacutica (Timofeev, 1966), emend. Mikhailova and Yankauskas, 1989 in Yankauskas, 1989, p. 77-78, Pl. XII , Figs 3, 7, 9; Butterfield *et al.*, 1994, p. 42, fig. 16H; Gnilovskaya *et al.*, 2000, Pl. 1, fig. 8; Veis *et al.*, 2004, Pl. 4, Figs 5, 7, 9; Grey, 2005, p. 183,184, fig. 63G; Vorob'eva *et al.*, 2009a, p. 185, fig. 14.3. For complete synonymy see Yankauskas, 1989.

Repository—IGGD RAN, No. 1821-1 (Lectotype).

Stratum typicum—Neoproterozoic, Derevnya Formation, Turukhansk Uplift, Russia.

Description—Spheroidal, solitary, single-walled vesicles 70-800 μm in diameter. Walls translucent, chagrinate or coarse-grained, about 2 μm thick, with folds; surface texture smooth.

Remarks—Considering the type species *L. baltica* came from the Palaeozoic deposits, we prefer providing descriptions of a few typically Proterozoic forms: *L. jacutica* and *L. minutissima* (*L. atava, L. crassa* and *L. tenuissima* are also provided in Plate 26.11, 12-5, 6-9, respectively).

Age and distribution—Widely distributed in Proterozoic rocks.

Leiosphaeridia minutissima (Naumova, 1949), emend. Yankauskas, 1989 (in Yankauskas, 1989)

(Pl. 26. 7)

Leiosphaeridia minutissima Yankauskas *in* Yankauskas, 1989, p. 79-80, Pl. IX , Figs 1-4, 11; Grey, 2005, p. 185, fig. 68D; Vorob'eva *et al.*, 2009a, p. 185, fig. 14.9.

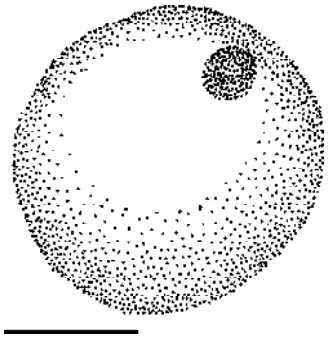


Fig. 54—Line diagram of *Leptoteichos golubicii* (Knoll *et al*., 1978). Scale bar = 10 μm.

Leiotriletes minutissimus Naumova, 1949, pl. 3, fig. 4. For complete synonymy see Yankauskas, 1989.

Repository—LitNIGRI, No. 16-800-2942/9, Specimen No. 1 (Lectotype).

Stratum typicum—Ediacaran (Vendian), Baikibashiev Formation, Cis-Urals, Russia.

Description—Spheroidal, solitary, single-walled vesicles 10-70 μm in diameter. Walls translucent, hyaline to fine-grained, less then 1 μm thick, with folds; surface smooth.

Age and distribution—Widely distributed in Proterozoic rocks.

Genus—LEPTOTEICHOS Knoll *et al.*, 1978

Leptoteichos Knoll *et al.*, 1978, p. 989.

Type species—Leptoteichos golubicii Knoll *et al.*, 1978.

Diagnosis—Spherical vesicles occur solitary or in irregular clumps of a few to more than a hundred individuals held together by an outer layer.

Remarks—Leptoteichos was described by Knoll *et al.* (1978) from the Gunflint Iron Formation as an uncertain planktonic microorganism of prokaryotic origin. These fossils can be remains of chroococcacean cyanobacteria despite other biological interpretations are possible.

Contents—Monospecific genus.

Age—Palaeoproterozoic.

Leptoteichos golubicii Knoll *et al.*, 1978

(Fig. 54)

Leptoteichos golubicii Knoll *et al.*, 1978, p. 989-990, Pl. 1, Figs 1-13, Pl. 2, Figs 6-8; Hofmann and Schopf, 1983, Photo 14-2-R; Lanier, 1989, Figs 7A?-7B?

Repository—HUHPC-60274.

Stratum typicum—Palaeoproterozoic, Gunflint Formation, Canada.

Description—Spherical vesicles occur solitary or in irregular clumps of a few to more than a hundred individuals usually with inner inclusions surrounded by a common outer layer. Diameter of vesicles varies from 5 to 31 μm, wall thickness from 0.5 to 1.0 μm.

Age and distribution—Palaeoproterozoic, Gunflint and McLeary Formations, Canada.

Genus—MYXOCOCCOIDES Schopf, 1968

Myxococcoides Schopf, 1968, p. 676.

Type species—Myxococcoides minor Schopf, 1968.

Diagnosis—Spherical vesicles solitary or in clusters loosely or tightly packed. Vesicles may or may not contain any inclusions or inner bodies.

Remarks—The genus *Myxococcoides* was established by Schopf (1968) for colonial simple spherical microfossils without organic inclusions. Schopf (1968) interpreted his Bitter Springs populations as chroococcacean cyanobacteria. With the subsequent discoveries of abundant populations in many Proterozoic cherts, *Myxococcoides* is considered to be a form genus encompassing microfossils of heterogeneous origin (Green *et al.*, 1989; Knoll *et al.*, 1991; Butterfield *et al.*, 1994; Sergeev *et al.*, 1995). Some species of *Myxococcoides* may belong to the cyanobacterial family Chroococcaceae, although this is by no means clear for the type population of *M. minor* (Knoll, 1982). Others closely resemble chlorococcalean green algae (Green *et al.*, 1989; Knoll *et al.*, 1991), while still others, including *Myxococcoides grandis*, may be akinetes produced by nostocalean cyanobacteria (Sergeev *et al.*, 1995) or the empty envelopes of colonial microorganisms (Fairchild, 1985; Sergeev, 1992 a, b, 1994).

Contents—More than 30 species of *Myxococcoides* are recorded, many of them have been described only superficially.

Age—Proterozoic.

Myxococcoides minor Schopf, 1968

(Pl. 27.1, 2, 3; Fig. 55A)

Myxococcoides minor Schopf, 1968, p. 676, Pl. 81, fig. 1, Pl. 83, fig. 10; Sergeev *et al.*, 1997, p. 234, Figs 18C, 18D; Sergeev, 2001, p. 443-444, fig. 8.11; Sergeev, 2006, p. 225-226, Pl. XV, Figs 2, 5, Pl. XX, fig. 11, Pl. XLVIII, fig. 5; Sharma, 2006a, p. 81, Figs 6g, 6i, 6k, 6m, 7m; Sergeev *et al.*, 2008, Pl. 5, fig. 8, Pl. 6, fig. 9; Sergeev and Schopf, 2010, p. 393, Figs 12.3, 12.4; Schopf *et al.*, 2010, Figs 5.5, 5.6.

Repository—HUHPC-58479.

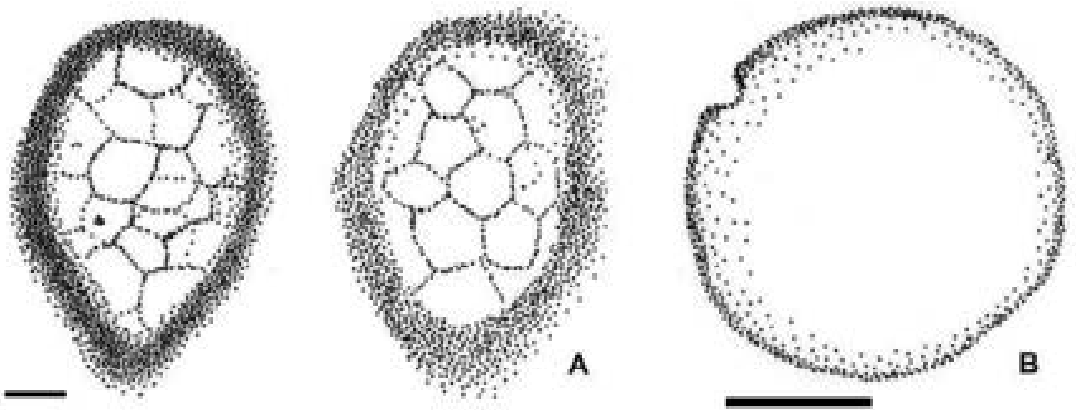


Fig. 55—Line diagrams of species of *Myxococcoides*. A- *M. minor* (Schopf, 1968); B- *M. grandis* (Horodyski & Donladson, 1980). Scale bar = 10 μm.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Single-walled spheroidal vesicles 8.8-10.5 μm in diameter, occurring as solitary unicells or in clusters of a few to many individuals; vesicle wall fine-grained, about 1 μm thick. An opaque, spheroidal inclusions about 1.0 μm in diameter sometimes occur attached to inner side of envelopes.

Remarks—Myxococcoides minor differs from other species by its size.

Age and distribution—Widely distributed in Proterozoic cherts.

Myxococcoides grandis Horodyski and Donaldson, 1980

(Pl. 27. 4, Pl. 28.1-8; Fig. 55B)

Myxococcoides grandis Horodyski and Donaldson, 1980, p. 142, Figs 7A-7N, 8; Horodyski and Donaldson, 1983, Figs 5J-5P, Zhang P. *et al.*, 1989, p. 325, Pl. 1, Figs 10-13; Hofmann and Jackson, 1991, p. 374-375, Figs 8.6-8.8, 10.8, 10.14?, 10.16?, 12.1-12.5, 12.6?, 12.7?, 12.8; Cao, 1992, Pl. II, Figs 1-6; Sergeev *et al.*, 1995, p. 33, Figs 7.1-7.9, 7.13, 9.1-9.5; Knoll and Sergeev, 1995, fig. 4; Kumar and Srivastava, 1995, p. 106, Figs 11B, 12K; Sergeev *et al.*, 1997, p. 232, 234, fig. 18.A; Kumar and Venkatachala, 1998, p. 58, 60, Figs 6a, 6b, 6i; Sergeev, 2006, p. 224-225, Pl. I, Figs 1-9a, 9б, 13, Pl. II, Figs 1a, 1б-5a, 5б, Pl. XV, Figs 1, 3, 4; Sergeev *et al.*, 2008, Pl. 1, Figs 9, 10, Pl. 2, fig. 10, Pl. 3, fig. 8.

Myxococcoides cf. *grandis* Horodyski and Donaldson, 1980: Zhang Y., 1985, p. 289, Figs 5E, 5F, 5G, 5I, 5J, 5K.

Globophycus rugosum Schopf, 1968 (partim): Zhang P. *et al.*, 1989, p. 324, Pl. 2, fig. 2, 5; Yakschin, 1991, p. 13-14, Pl. I, Figs 3, 7, Pl. II, fig. 11, Pl. IV, Figs 4, 8.

Phanerosphaerops polymorphus Yakschin, 1991, p. 15, Pl. I, Figs 6, 8, 11.

Phanerosphaerops capitaneus Schopf and Blacic, 1971 (partim): Yakschin, 1991, p. 15, Pl. I, fig. 4, Pl. II, Figs 1, 8, 13.

Phanerosphaerops granulatus Yakschin, 1991, p. 16, Pl. II, Figs 2, 3, 4.

Caryosphaeroides amplus Yakschin, 1991, p. 17-18, Pl. II, Figs 5, 6.

Bisphaera plana Yakschin, 1991, p. 18, Pl. I, Figs 5, 10.

Tuberiphycus uniparietinus Yakschin, 1991, p. 19, Pl. III, Figs 7, 8, Pl. IV, Figs 5, 7.

Tuberiphycus biparietinus Yakschin, 1991, p. 19, 20, Pl. III, Figs 6, 13

Zosterosphaera tripunctata (?) Schopf, 1968 (partim): Yakschin, 1991, p. 20, Pl. III, fig. 12.

Quaternatiphycus segmentatus Yakschin, 1991, p. 29, Pl. V, fig. 4.

Quaternatiphycus sectorialis Yakschin, 1991, p. 29, Pl. V, Figs 3a, 3б.

Eogloeocapsa composita Yakschin, 1991, p. 22, Pl. VIII, Figs 5, 10.

Tetraphycus amplus Golovenok and Belova 1984, p. 28-29, Pl. II, fig. 11; Yankauskas, 1989, p. 98, Pl. XIX, fig. 13.

Glomophycus tortilis Yakschin, 1991, p. 30, Pl. V, Figs 1, 2, 5a-5в; Sergeev, 1993, Pl. III, Figs 5-7.

Spherical colony with interior spindle-shaped algae: Yakschin, 1989, Pl. 1, fig. 5.

Repository—GSC-57988.

Stratum typicum—Mesoproterozoic, Dismal Lakes Group, Canada.

Description—Single-or double-walled spheroidal vesicles occurring as solitary unicells, dyads, triads, tetrads (cross and planar) and octets surrounded by a common spherical vesicle. Outer layer of envelopes is usually transparent and often of perfectly spherical shape; walls are fine-or medium grained about 1.0-2.0 μm thick. Inner layer of

spheroids when present is translucent and spherical or irregular shape; walls are medium-or course-grained 1.0-3.0 μm thick. An opaque, spheroidal inclusion 2.0-3.0 μm in diameter or dark bleb of irregular shape or numerous micron-sized dark granules sometimes occur attached to inner-or outer layer of envelope. Outer diameter of spheroids ranges from 5.0 to 55.0 μm. Envelopes that surround the grouped vesicles are of spherical or irregular shape, single-or double-layered, up to 55 μm in diameter, transparent; walls are medium-grained about 1.0-2.0 μm thick.

Remarks—1. The morphology of the vesicles of *Myxococcoides grandis* due to life cycle and *post-mortem* alterations is frequently changeable. Many variations in morphology of the spheroids of *Myxococcoides grandis* were described by Golovenok and Belova (1984) and by Yakschin (1991) as different taxa (see synonymy) from the Kotuikan and Yusmastakh Formations of the Anabar Uplift.

2. Golovenok and Belova (1984) described from the Kotuikan Formation as *Eogloeocapsa bella* the groups of spherical vesicles 7.2-20.0 μm in diameter surrounded by a common envelope of spherical shape 16-48 μm across and interpretated them as the remnants of chroococcoidal unicellular cyanobacteria similar to species of modern alga *Gloeocapsa*. Subsequently, Sergeev *et al.* (1995) have found the same type of colonies, but all these groups of spheroids are a stage in life cycle of *Myxococcoides grandis*.

3. Yakschin (1991) described spherical microfossils with filaments inside as *Glomophycus tortilus* from the Kotuikan Formation and compared this form with the representatives of modern nostocalean alga *Nostoc*. But such "filaments" and "spots" are not only inside but also on the surface of spherical (Pl. 28.1, 3-5) as well as ellipsoidal microfosils. It is evident that these structures are of secondary origin and microfossils described as *Glomophycus tortilus* are only altered specimens of *Myxococcoides grandis*. These structures are of diagenetic origin or have probably been formed as a result of bacterial destruction of dead cyanobacteria before fossilization (Sergeev *et al.*, 1995).

Age and distribution—Mesoproterozoic: Dismal Lakes Group, Canada; Kotuikan and Yusmastakh Formations, Anabar Uplift, Siberia; Wumishan Formation, China; Kheinjua Formation, India; Meso-Neoproterozoic, Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia; Vaishnodevi Limestone Formation, India.

Genus—PHANEROSPHAEROPS Schopf and Blacic, 1971

Phanerosphaerops Schopf and Blacic, 1971, p. 951.

Type species—Phanerosphaerops capitaneus Schopf and Blacic, 1971.

Diagnosis—Single-layered large spheroidal or ellipsoidal vesicles occur as isolated individuals or sometimes in loose clusters.

Remarks—Difference of this genus from some other large cocoidal genera like *Leiosphaeridia, Kheinjuasphaera* or *Myxococcoides* is unclear. Considering probably polymorphic origin of all these taxa we prefere to keep it separately. Large spheroids of genus *Phanerosphaerops* could turn out to be either eukaryotic unicells or empty envelopes surrounding colonies of cyanobacteria, e.g. *Eosphaeronostoc* Sergeev, 1992.

Content—P. capitaneus and *P. magnicellularis*.

Age—Meso-Neoproterozoic.

Phanerosphaerops capitaneus Schopf and Blacic, 1971

(Fig. 56)

Phanerosphaerops capitaneus Schopf and Blacic, 1971, p. 951-952, Pl. 110, Figs 11, 14a-14d; Knoll and Calder, 1983, p. 492, Pl. 60, fig. 7; Knoll, 1984, p. 149, Figs 6C, 6E, 6F, 6G?; Hofmann and Jackson, 1991, p. 375, fig. 12.9.

Repository—HUHPC-58621.

Stratum typicum—Neoproterozoic, Bitter Springs Formation, Australia.

Description—Single-lamellated spheroidal vesicles occurring as solitary unicells. Diameter of vesicles ranges from 43.3 to 46.3 μm. Wall is translucent, fine-grained less then 1.0 μm thick; surface is finely granular to psilate.

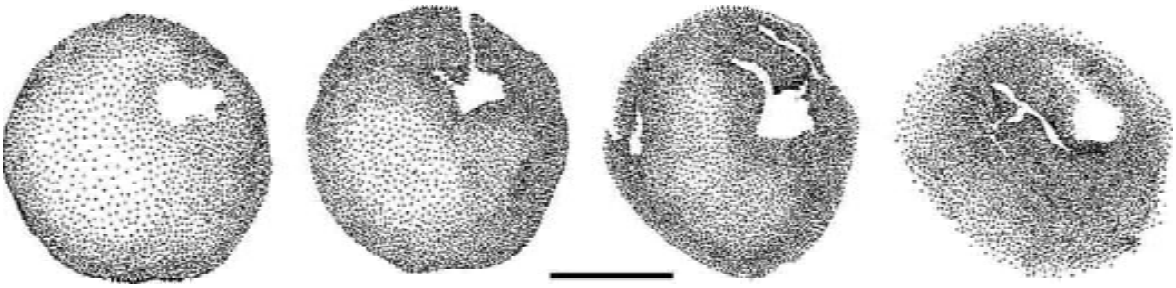


Fig. 56—Line diagram of *Phanerosphaerops capitaneus* (Schopf & Blacic, 1971). Scale bar = 10 μm.

PLATE 25

Akinetes of nostocalean or stigonematalean cyanobacterium genus *Archaeoellipsoides* Horodyski and Donaldson, 1980.

1-4. *Archaeoellipsoides grandis* Horodyski and Donaldson, 1980: 1 —Sample No 4689-48, Slide No 577, EFL K-38-0, p. 8, GINPC No 484; 2 —Sample No 4689-7e, Slide No 452, p. 9, GINPC No 1102; 3 —Sample No 4681-52, Slide No 325, p. 5, EFL N-42-1, GINPC No 158: 4 —Sample No 4681-20, Slide No 260, p. 20, EFL L-16-0, GINPC No 180.

5-11. *Archaeoellipsoides major* (Golovenok and Belova, 1984): 5 —Sample No 4689-47b, Slide No 555, EFL U-34-4, p. 22, GINPC No 429; 6 —Sample No 4689-48, Slide No 576, EFL S-29-3, p. 2, GINPC No 494; 7 —Sample No 4689-48, Slide No 576, EFL Q-31-O, p. 12, GINPC No 495; 8 —Sample No 4689-48, Slide No 577, EFL J-52-3, p. 10, GINPC No 493; 9 —Sample No 4689-53, Slide No 53-A, EFL G-61-3, HUHPC No 63936; 10 —Sample No 4689-47b, Slide No 558, EFL W-42-3, p. 8, GINPC No 487; 11 —Sample No 3893-932, Slide No 5, p. 9, GINPC No 720.

Specimens GINPC No 429, 484, 487, 493, 494, 495, 1102 and HUHPC No 63936 (figs 1, 2 and 5-10) are from the Kotuikan Formation, specimens GINPC No 158 and 180 (figs 3 and 4) are from the Chichkan Formation, and specimen GINPC No 720 (fig. 11) is from the Satka Formation.

PLATE 26

Problematic cyanobacterial remains genera *Chuaria* Walcott, 1899 and *Leiosphaeridia* Eisenack, 1958.

1-3. *Chuaria circularis* Walcott, 1899: 1 —Sample No 14700-62N2, Slide No 30, p. 3, GINPC No 14700-117; 2 —BSIP (Kumar's collection), Ram-10; 3 —BSIP (Kumar's collection), Ram-11.

4. *Cerebrosphaera? (Chuaria?) globosa* (Ogurtsova and Sergeev, 1989), Sample No 4681-20, Slide No 269, p. 22, EFL R-34-1, GINPC No 184.

5, 6. *Leiosphaeridia crassa* (Naumova, 1949), Sample No 4681-73, Slide No 315: 5 - p. 20, EFL M-33-4, GINPC No 1039; 6 —p. 21, EFL M-34-0, GINPC No 1040.

7. *Leiosphaeridia minutissima* (Naumova, 1949), Sample No 14700- 62N2, Slide No 61, p. 6, GINPC No 14700-291.

8, 10. *Leiosphaeridia jacutica* (Timofeev, 1966) : 8 —Sample No 14700-69V, Slide No 9, p. 6, GINPC No 14700-635; 10 —Sample No 14700-62N2, Slide No 37, p. 6, GINPC No 14700-163.

9. *Leiosphaeridia tenuissima* Eisenak, 1958, Sample No 14700-69V, Slide No 11, p. 5, GINPC No 14700-654.

11, 12. *Leiosphaeridia atava* (Naumova, 1960): 11 —Sample No 14700-63S, Slide No 1, p. 1, GINPC No 14700-514; 12 —Sample No 14700-62N2, Slide No 39, p. 4, GINPC No 14700-171.

Specimens GINPC No 14700-117, 14700-163, 14700-171, 14700-291, 14700-514, 14700-635 and 14700-654 (figs 1, 7-12) are from the Vychegda Formation (in maceration Slides), specimens GINPC No 184, 1039 and 1040 (figs 4-6) are from the Chichkan Formation, and specimens Ram-10, Ram-11 (figs 2, 3) are from the Bhander Group, Vindhyan Supergroup (carbonaceous compressions on bedding surfaces).

PLATE 27

Problematic cyanobacteria-related forms genus *Myxococcoides* Schopf, 1968.

1, 2, 3 (square in 1). *Myxococcoides minor* Schopf, 1968: 1, 3 —Sample No 4694-38, Slide No 518, p. 47, GINPC No 549; 2 —Sample No 4694-207, Slide No 695, p. 20', GINPC No 616.

4. *Myxococcoides grandis* Horodyski and Donaldson, 1980 —Sample No 4694-38, Slide No 518, p. 47', GINPC No 1103.

5. *Myxococcoides* sp. —Sample No 4689-23, Slide No 487, EFL T-30-4, p. 9, GINPC No 437.

6, 7. *Myxococcoides inornata* Schopf, 1968: 6 —Sample No 4694-38, Slide No 626, p. 15, GINPC No 548; 7 —Sample No 4694-110, Slide No 741, p. 20", GINPC No 628.

8, 9. *Myxococcoides stragulescens* Green, Knoll and Swett, 1989: 8 —Sample No 4694-110, Slide No 741, p. 26, GINPC No 629; 9 —Sample No 4694-207, Slide No 695, p. 20, GINPC No 617.

Specimens GINPC No 549, 626 and 1103 (figs 1, 3, 4 and 6) are from the Sukhaya Tunguska Formation, specimens GINPC No 616, 628, 629 and 617 (figs 2, 7, 8 and 9) are from the Shorikha Formation, and specimen GINPC No 437 (fig. 5) is from the Yusmastakh Formation.

PLATE 28

Problematic cyanobacteria-related forms genera *Myxococcoides* Schopf, 1968 and *Phanerosphaerops* Schopf, 1968.

1-8. *Myxococcoides grandis* Horodyski and Donaldson, 1980: 1 —Sample No 4689-48, Slide No 576, EFL K-29-4, p. 16, GINPC No 470; 2 —Sample No 4689-7e, Slide No 452, p. X, GINPC No 1126; 3 —Sample No 4689-21, Slide No 497, EFL M-30-0, p. 5, GINPC No 471; 4 —Sample No 4689-21, Slide No 497, EFL S-46-3, p. 2, GINPC No 426; 5 —Sample No 4689-21, Slide No 498, EFL N-43-2, p. 7^, GINPC No 428; 6 —Sample No 4689-7e, Slide No 455, EFL R-38-4, p. 6'", GINPC No 503; 7 —Sample No 4689-7e, Slide No 455, EFL M-36-4, p. 12, GINPC No 498; 8 —Sample No 4689-48, Slide No 568, EFL S-39-2, p. 38, GINPC No 504.

9. *Myxococcoides* sp. —Sample No 4689-48, Slide No 568, EFL S-34-3, p. 37, GINPC No 502.

10, 11. *Phanerosphaerops magnicellularis* Yakschin, 1991: 10 —Sample No 4689-7e, Slide No 452, EFL U-43-1, p. 6^, HUHPC No 62928; 11 —Sample No KG 92-60, Slide No 3A, EFL B-49-3, HUHPC No 62927.

Specimens GINPC No 470, 498, 502-504, 1126 and HUHPC No 62928 (figs 1, 2 and 6-10) are from the Kotuikan Formation, specimens GINPC No 426, 428, 471 and HUHPC No 62927 (figs 3-5 and 11) are from the Yusmastakh Formation.

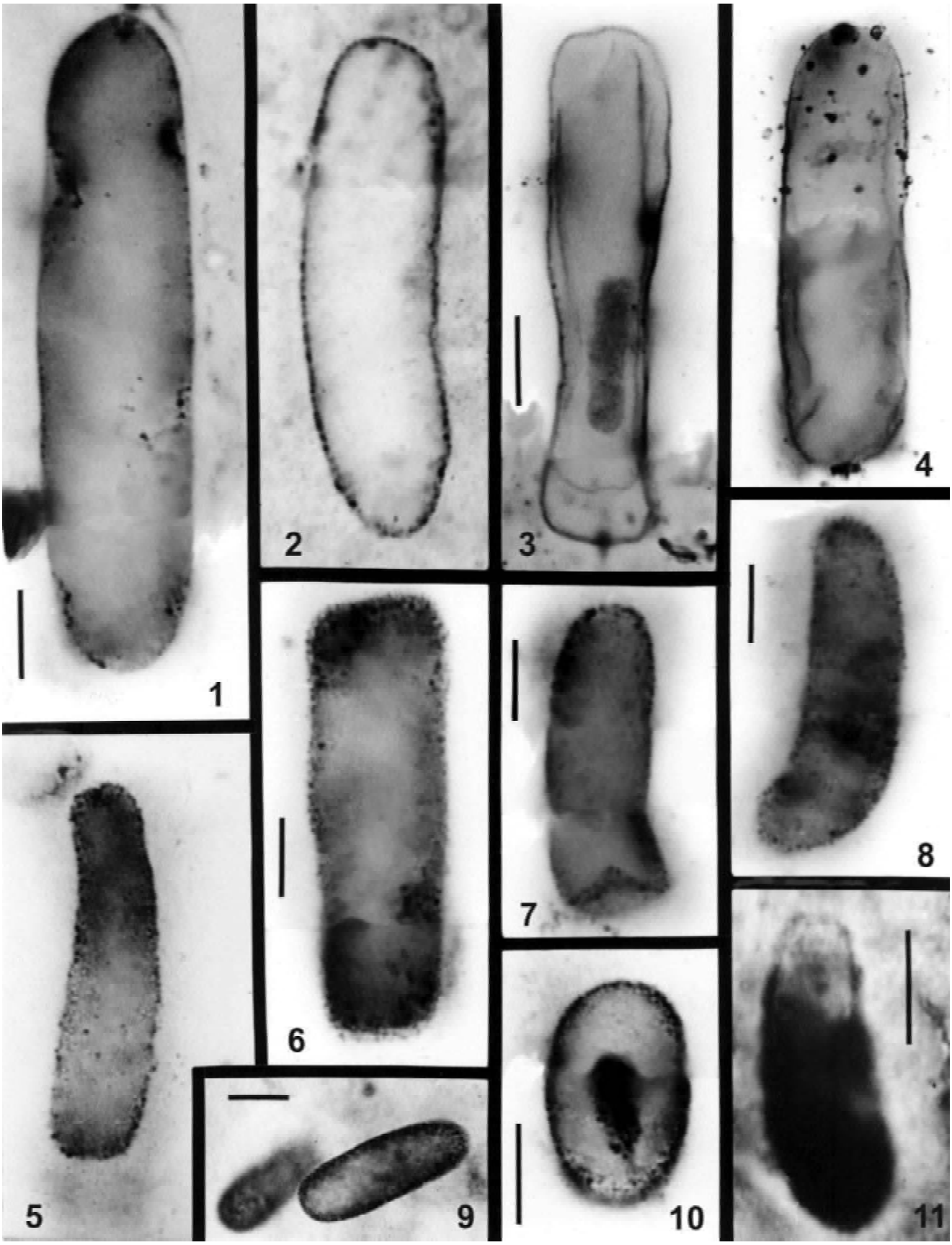


PLATE 25

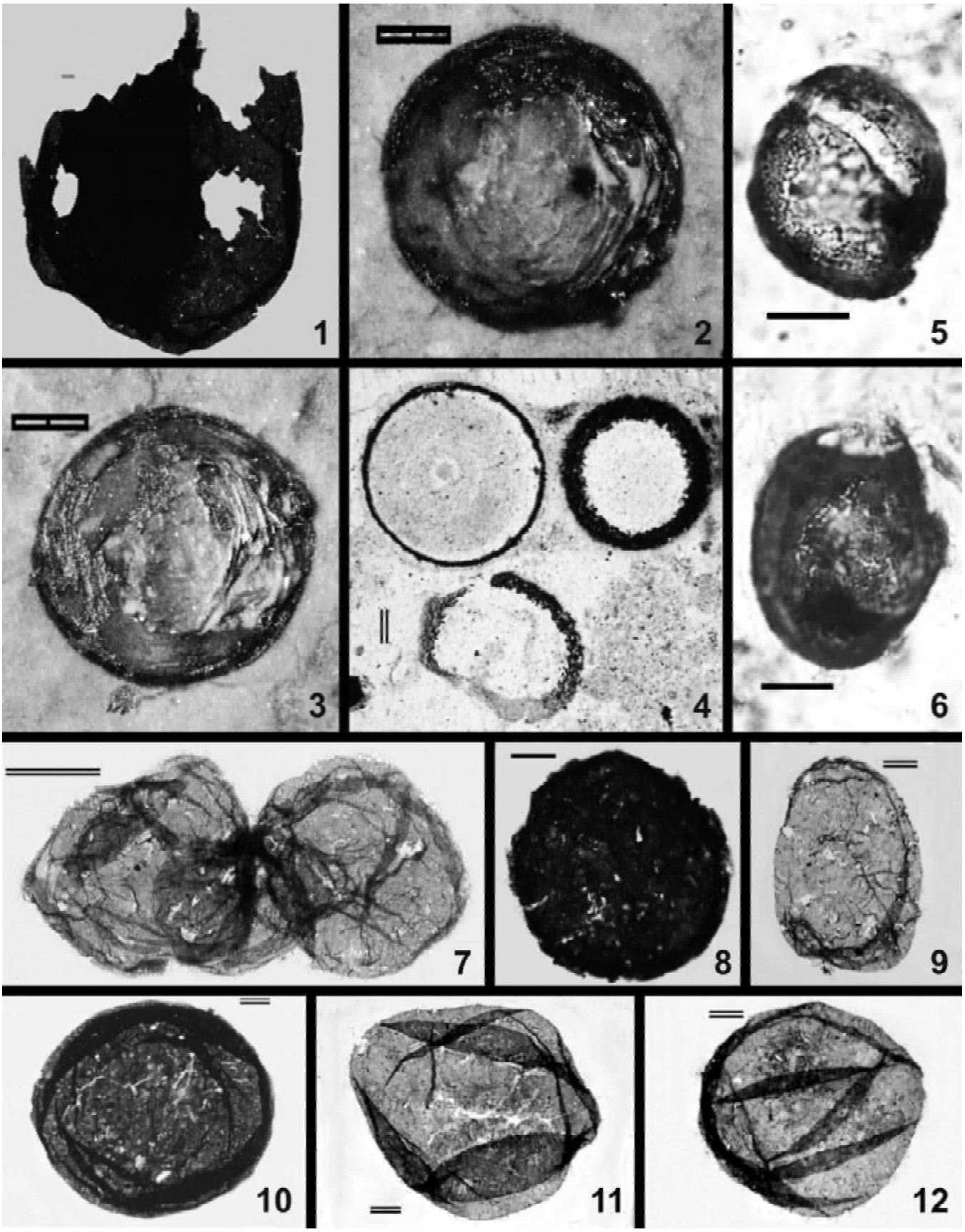


PLATE 26

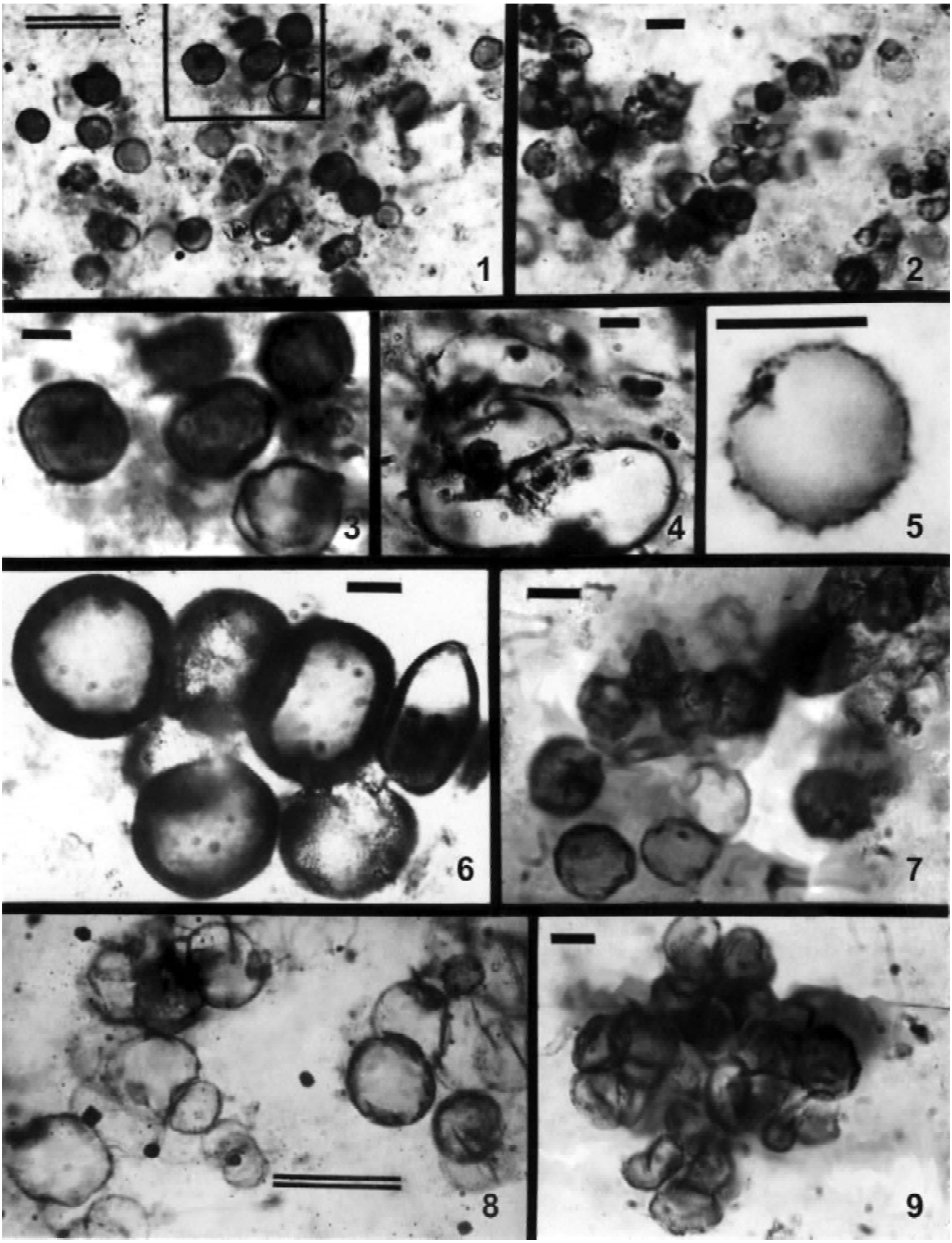


PLATE 27

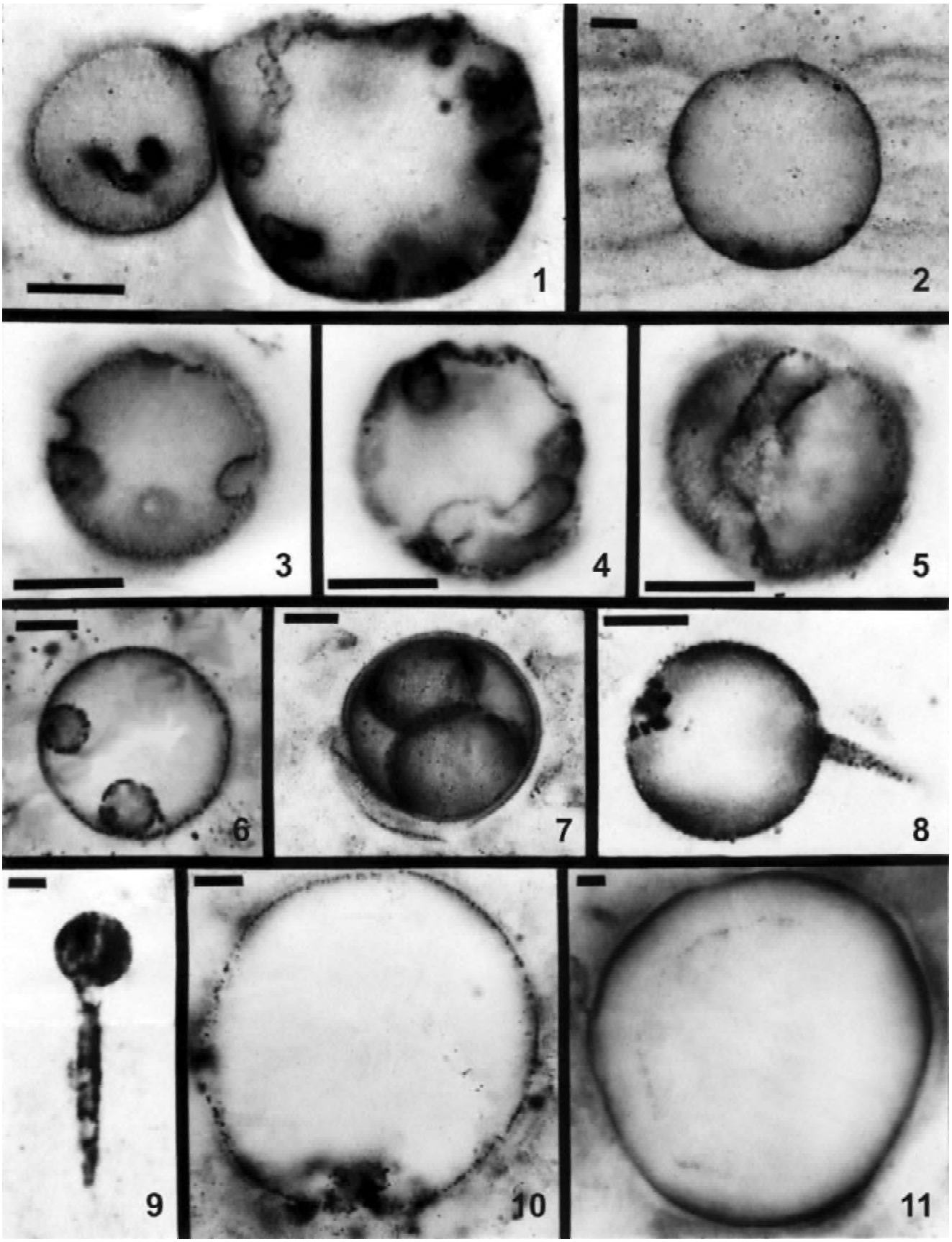


PLATE 28

Remarks—*P. capitaneus* differs from *P. magnicellularis* in having smaller size range. However, *P. capitaneus* reported from some other geological units demonstrate bigger size range than its type polulation from the Bitter Springs Formation, e.g. *P. capitaneus* vesicles from the Hunnberg Formation have diameter ranging from 37 to 93 μm (Knoll, 1984).

Age and distribution—Mesoproterozoic: Uluksan Group, Canada; Neoproterozoic: Bitter Springs Formation, Australia; Hunnberg and Ryssö Formations, Spitsbergen.

Phanerosphaerops magnicellularis Yakschin, 1991

(Pl. 28.10, 11)

Phanerosphaerops magnicellularis Yakschin, 1991, p. 16, Pl. VII, Figs 1, 2; Sergeev *et al.*, 1995, p. 34, Figs 7.11, 7.15; Sergeev, 2006, p. 230, Pl. I, Figs 11, 15.

Phanerosphaerops sp.: Yakschin, 1991, p. 16-17, Pl. I, fig. 9, Pl. II, fig. 12, Pl. IV, Figs 1, 2, Pl. VII, Figs 3, 4.

Repository—CSGM-309-AYa-28-4a.

Stratum typicum—Mesoproterozoic (Early Riphean), Kotuikan Formation, Anabar Uplift, Siberia.

Diagnosis—Single-walled relatively large spheroidal vesicles occurring as solitary unicells. Diameter of spheroids ranges from 55 to 300 μm. Walls are translucent, medium-grained, about 2.0 μm thick.

Remarks—Yakschin (1991) has described three additional species of genus *Phanerosphaerops,* but they were subsequently merged with species of genera *Myxococcoides* or *Eoentophysalis* (Sergeev *et al.*, 1995).

Age and distribution—Mesoproterozoic: Kotuikan Formation, Anabar Uplift, Siberia.

Genus—POLYSPHAEROIDES Hermann, 1976 (in Timofeev *et al.*, 1976)

Polysphaeroides Hermann, 1976 in Timofeev *et al.*, 1976, p. 41-42.

Type species—Polysphaeroides filiformis Hermann, 1976.

Diagnosis—Spheroidal vesicles arranged into loose filamentous aggregates surrounded by a common sheath closed at both ends. Spheroids in these aggregates either dispersed or arranged into pairs, tetrads, octets and spheroidal colonies.

Remarks—Filaments of *Polysphaeroides* usually are compared to modern stigonematalean cyanobacteria, but we cannot rule out eukaryotic algae of similar morphology (Hermann, 1990; Vorob'eva *et al.*, 2009a).

Hofmann and Jackson (1994) have emended *Chlorogloeaopsis* including in this genus almost all species formerly belonging to *Polysphaeroides*. But they did not transfer *Polysphaeroides filiformis* into genus *Chlorogloeaopsis* that really looks different from other species. Accepting transfer of almost all species to *Chlorogloeaopsis* we still consider *P. filiformis* being a distinctive species of genus *Polysphaeroides* (see above).

Contents—Monospecific genus?

Age and distribution—Latest Mesoproterozoic and Neoproterozoic.

Polysphaeroides filiformis Hermann, 1976 (in Timofeev *et al.*, 1976)

(Pl. 29.1-3)

Polysphaeroides filiformis Hermann, 1976 *in* Timofeev *et al.*, 1976, p. 42, Pl. XIII, fig. 12, Pl. XIV, Figs 1, 2; Yankauskas, 1989, Pl. XXVII, Figs 8, 9; Schopf, 1992b, Pl. 23, Figs A_1, A_2; Vorob'eva *et al.*, 2009a, p. 188, Figs 15.8, 15.9, 15.16; Vorob'eva *et al.*, 2009b, fig. 4n.

Leiotrichoides gracilis Pyatiletov, 1980 (partim): Veis *et al.*, 2006, pl. IV, Figs 30, 31.

Stigonema-like branching filaments: Gnilovskaya *et al.*, 2000, Pl. II , Figs 5, 10.

Polysphaeroides sp.: Gnilovskaya *et al.*, 2000, Pl. I , fig. 11.

Repository—IGGP-504/6.

Stratum typicum—Neoproterozoic, Miroedikha Formation, Turukhansk Uplift, Siberia.

Description—Spheroidal vesicles arranged into loose filamentous aggregates surrounded by a common sheath closed at both ends. Spheroids in these aggregates either dispersed or arranged into pairs, tetrads, octets and spheroidal colonies of up to 10-20 individuals. Spheroidal colonies may also be arranged in pairs, forming pseudobranched structures. Vesicle diameter 5-30 μm; filament-like aggregate diameter ca. 15-60 μm; maximum length of filaments up to 500 μm. Vesicle walls single-layered, translucent, fine-grained, 1.0-2.0 μm thick; inclusions inside the vesicles have not been observed. Sheaths surrounding filamentous aggregates are translucent, about 1.0-2.0 μm thick, with compression folds. Sheath diameter 40-70 μm; maximum length of sheaths up to 700-800 μm.

Age and distribution—Latest Mesoproterozoic and Neoproterozoic (Tonian-Ediacaran): Nureyen Formation, Uchuro-Maya Uplift, Burovaya and Miroedikha Formations, Turukhansk Uplift, Siberia; Vychegda Formation, Timan Uplift, East European Platform.

Genus—POLYTRICHOIDES Hermann, 1974, emend. Hermann, 1976 (in Timofeev *et al.*, 1976)

Polytrichoides Hermann, 1974, p. 8; Timofeev *et al.*, 1976, p. 37.

Type species—*Polytrichoides lineatus* Hermann, 1974

Diagnosis—Bundles of 5-6 thread-like trichomes closely grouped within a common cylindrical sheath.

Remarks—Polytrichomous filaments of *Polytrichoides* are compared to modern stigonematalean cyanobacteria (Timofeev *et al.*, 1976). From formal position genus *Polytrichoides* should be a junior synonym of genera *Eomicrocoleus* and *Eoschizothrix*. However, we still consider the synonymy as premature because many forms described inside these genera probably belong to various species of cyanobacteria and eukaryotic algae.

Contents—Monospecific genus?

Age and distribution—Proterozoic.

Polytrichoides lineatus Hermann, 1974, emend. Hermann, 1976 (in Timofeev *et al.*, 1976)

(Plate 29. 6-8)

Polytrichoides lineatus Hermann, 1974, p. 8, Pl. VI, Figs 3, 4; Timofeev *et al.*, 1976, p. 37, Pl. XIV, fig. 7; Yankauskas, 1989, p.119-120, Pl. XXX, Figs 5a, 5б, 6, 7; Hermann, 1990, Pl. IX, Figs 8, 8a(9); Schopf, 1992b, Pl. 27, Figs A_1, A_2; Gnilovskaya *et al.*, 2000, pl. I, Figs 16, 17; Prasad *et al.*, 2005, Pl. 1, fig. 13; Vorob'eva *et al.*, 2006, fig. 2e; Vorob'eva *et al.*, 2009a, p. 188, Figs 15.13, 15.14.

Repository—IGGP-49/29 (Paratype).

Stratum typicum—Neoproterozoic, Miroedikha Formation, Turukhansk Uplift, Russia.

Description—Trichomes consist of elongated cylindrical cells 2.5-6 μm wide and 5-15 μm long; side and cross-walls are dark or translucent, hyaline or fine-grained, less than 0.5 μm thick. Sheath encompassing 5-6 trichomes is cylindrical, commonly tapering toward both ends, 20-50 μm wide and up to 1000 μm long. Sheath walls translucent, hyaline or fine grained, 1-2 μm thick. Filaments sometimes form circular structures (and/or exhibit branching patterns that generate triangular spaces among bundles (Pl. 29.8).

Age and distribution—Widely distributed in Proterozoic rocks.

CONCLUSIONS

Cyanobacteria has been traced deep in the history starting at least 2.0 Ga, possibly 2.5 Ga and probably 3.0–3.5 Ga ago or even older. Among oldest (3.49-3.34 Ga) filamentous and coccoidal microfossils, fine non-septate filaments from the Onverwacht and Warrawoona Groups are probably the oldest organic remains. On the morphological criteria, they could either be heterotrophic bacteria or cyanobacteria, and the last interpretation is supported by analysis of dC^{13} values. Diverse microstructures have been reported from the Mount Goldsworthy-Mount Grant area, Pilbara Craton, Western Australia (> 2.97 Ga). Among these, films-like structures, small spheres associated with films, large spheroids and spindle-like structures are highly probable fossil remain of cyanobacteria. Thus, data of palaeontology, sedimentology, palaeobiochemistry and isotopic geochemistry imply that euphotic zones in oceans of the terminal Archaean were populated not only by cyanobacteria and aerobic heterotrophic bacteria, but also probably by eukaryotic organisms of unclear taxonomic affinity. Transition zone between anoxic and aerated pelagic zones was colonized by microaerophilic heterotrophic prokaryotes, inclusive presumably methanotrophic bacteria as well. Relaible data on Archaean remains of anaerobic prokaryotes are unknown yet, although there are grounds to suspect their active part in global biogeochemical cycles.

Archaean stromatolite formations spread to diverse marine and fresh-water facies zones, and proportion of certainly biogenic buildups was growing among them. Rock-forming stromatolite morphotypes of the terminal Neoarchaean are identical in morphology, microstructure and facies confinement to Palaeoproterozoic stromatolites, the indisputable products of life activity of benthic, primarily cyanobacterial communities. Consequently, the history of stromatolites depicts progressive rock-forming significance of microbial communities, increasing proportion of buildups in carbonate successions, and transformation of cyanobacterial mats into main factor of

PLATE 29

Problematic cyanobacteria genera *Polysphaeroides* Hermann, 1976, *Polytrichoides* Hermann, 1974 and *Clonophycus* J. Oehler, 1977.

1-3. *Polysphaeroides filiformis* Hermann, 1976, Sample No 14700-62N2; 1 —Slide No 79, p. 10, GINPC No 14700-419; 2 —Slide No 66, p. 1, GINPC No 14700-317; 3 —Sample No 14700-62N2, Slide No 60, p. 4, GINPC No 14700-283.

4, 5. *Clonophycus* sp., Sample No 4689-1732; 4 —Slide No 546, EFL Q-35-1, p. 30, GINPC No 1124; 5 —Slide No 547, EFL W-28-3, p. 28, GINPC No 1125.

6-8. *Polytrichoides lineatus* Hermann, 1974, Sample No 14700-62N2; 6 —Slide No 81, p. 13, GINPC No 14700-446; 7 —Slide No 84, p. 10, GINPC No 14700-463; 8 —Slide No 45, p. 3, GINPC No 191.

Specimens GINPC No 14700-191, 14700-283, 14700-317, 14700-419, 14700-446 and 14700-463 (figs 1-3 and 6-8) are from the Vychegda Formation (in maceration Slides), and specimens GINPC No 1124 and 1125 (figs 4 and 5) are from the Debengda Formation.

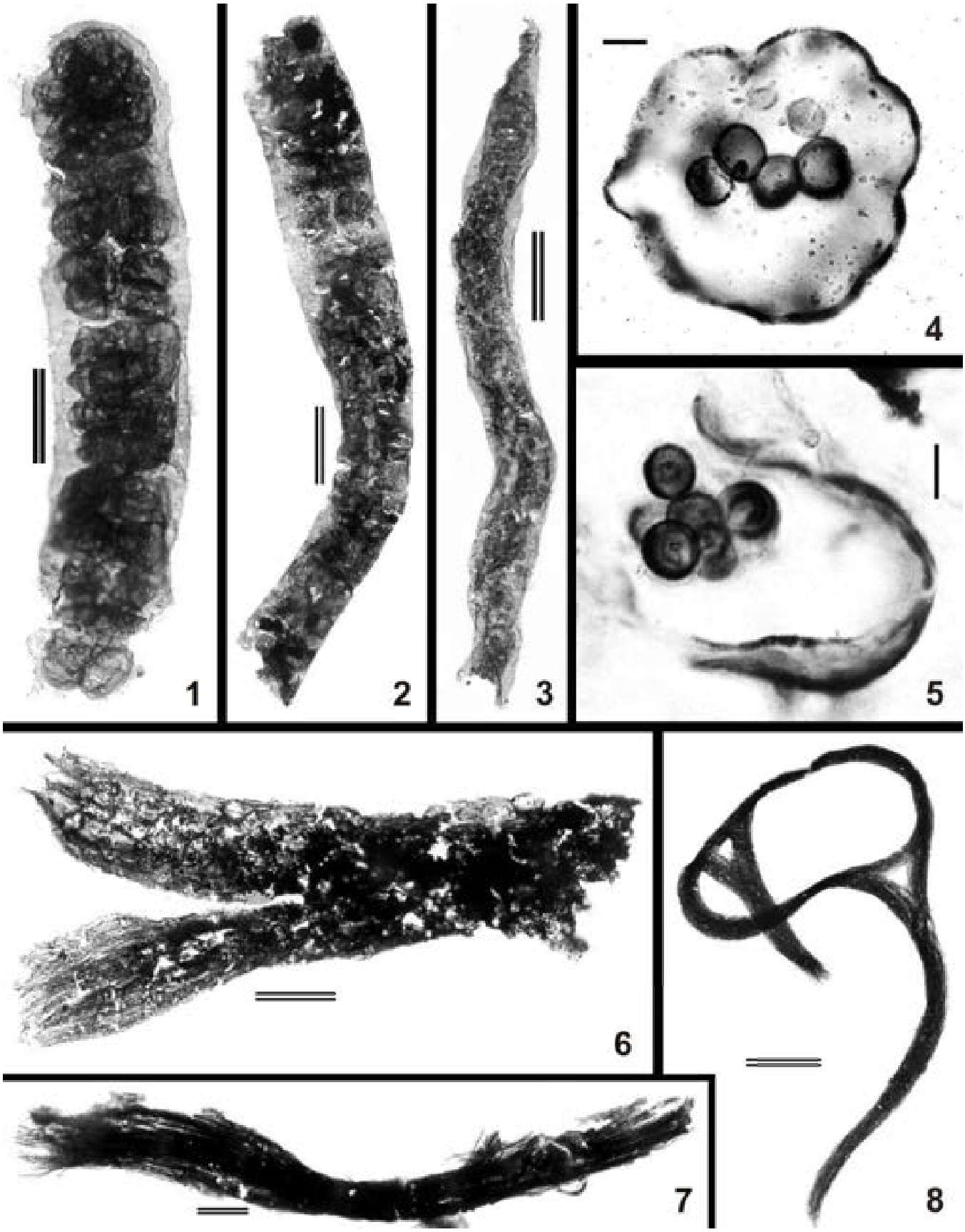


PLATE 29

carbonate accumulation in Precambrian. These trends were controlled to a great extent by emergence and subsequent expansion of stable carbonate platforms, the favorite biotopes of benthic cyanobacteria.

Recent data of biogeochemistry show that oldest biomarkers of cyanobacteria correspond in age to 2.69-2.63 Ga. Data on morphology, fine peculiarities of microstructure, and size ranges of well-preserved microfossils imply that cyanobacteria played an essential part in biosphere already by 2.76-2.63 Ga ago (Fortescue Group), and then, 2.52-2.50 Ga ago (Gamohaan Formation); hormogonian and chroococcacean cyanophyceae were of prime importance in benthic communities. Later, after a drop in microbial assemblages succession that lasted from 2.5 to 2.0 Ga has no explanation yet, cyanobacteria were represented by all principal morphotypes. In addition to available palaeontological records, the last inference is substantiated by occurrence of akinetes of nostocalean and *Anabaena*-like cyanobacteria in the Franceville and Epworth groups. Representatives of the latter likely correspond to the terminal group of cyanobacterial phylogenetic tree, as one can see from 16-S rRNA chain of present-day cyanobacteria.

Starting approximately 2.0 Ga ago, the cyanobacterial remains are well preserved, diverse and abundant. However, the observed sharp change in the fossil record due to rather non evolution of microorganisms, but evolution of Earth's crust and environments, in first formation of the abundant platforms favored lateral expansion of benthic cyanobacterial communities. Almost all types of fossil cyanobacteria are observed in microbiotas 2.0 Ga old in the sediments to younger and have modern counterparts on generic or even specific level. The main singularity of early Mesoproterozoic (Lower and Middle Riphean, 1.6-1.0 Ga ago) is the dominant presence of akinete-bearing nostocaleans or stigonemataleans associated by entophysalidaceans in intertidal to shallow subtidal environments that is apparently related to the existence of extensive tidal flats, colonized by *Anabaena*-like cyanobacteria. This time span, in general, could be characterized as an evolutionary stasis in the evolution of Proterozoic organisms and environments. But the changes in composition of microfossil assemblages near the Mesoproterozoic/Neoproterozoic (Middle/Upper Riphean) boundary are among the most prominent in the Precambrian. The new data prove that these changes started about 1200 Ma and led to crucial alternation in the composition of microorganism communities. The main event was the explosive proliferation of eukaryotic microorganisms, but some changes are observed among cyanobacteria as well. Only since late Mesoproterozoic are known first finds of the stalked cyanobacteria (about 1.2 Ga) and spiral-cylindrical *Spirulina*-like (*Obruchevella)* filaments (about 1.0 Ga ago) that supposedly reflects a new phase of the evolution of these prokaryotic microorganisms. Akinetes of nostocaleans and possibly stigonemataleans, and entophysalidaceans are relatively rare in Neoproterozoic (Late Riphean) assemblages of both silicified and compression-preserved microorganisms and microbiotas of this age are dominated by mats formed by hormogonian and chroococcacean cyanobacteria.

Cyanobacteria survived late Neoproterozoic glaciations without extinction and are widespreaded in the post-glacial deposits. The distinctive feature of Ediacaran (Vendian) microbiotas is the dominant presence of the spiral-cylindrical microfossils *Obruchevella* which are larger than their pre-Ediacaran (pre-Vendian) analogues. These *Spirulina*-like cyanobacteria are abundant in Lower Cambrian shallow-water environments as well and not much differ from the latest Proterozoic counterparts. At least by the end of Proterozoic all types of cyanobacteria were in place and no more changes seem possible.

The research on Precambrian microfossils for more than 50 years has discovered a new earlier unknown world of oldest microorganisms and resulted into numerous models of Precambrian microorganisms development and life evolution on early stages of the Earth's history. To date, all available data on the Precambrian microfossils demonstrate that fossilized cyanobacteria are numerous, well preserved, diverse and do not differ from recent analogs. The unprecedented evolutionary conservatism of blue-green algae that did not evolve for at least last 2 Ga when Precambrian forms have almost identical modern counterparts allow applying of existing cyanobacteria systematics for both living and Proterozoic forms at least on family level. Half a century of research on Precambrian microfossils has refined taxonomy and taphonomy of fossilized cyanobacteria and relevant microorganisms separating primarily biological features from those formed as a result of *post-mortem* degradation and subsequent diagenetic alteration. Detail analysis of fossil cyanobacteria populations reconstructing found microfossils living cycles and deciphering original taxonomically applicable morphological features has revealed more than 50 genera and 150 species accepted in the paper. All these genera bear different names from modern analogs as it was practicing since first steps in the field of Precambrian palaeobiology, but physiologically recent and fossil microorganisms probably are the same. Besides more than 10 genera and 20 species are recognized as problematic cyanobacterial taxa that could be alternatively interpreted as protista remains.

Initially most Proterozoic cyanobacteria and the relevant microorganism genera were established on three-dimensionally preserved silicified microfossils and then recognized among compression-preserved flattened forms. Silica-embedded mirofossils in cherts and cherty parts of the carbonate formations are much more informative about ancient cyanobacteria considering these are preserved *in situ* without changing of original cyanobacterial communities structure. Therefore, fossilized cyanobacterial mats and constituting mat

microorganisms are deciphered in thin sections of fossiliferrous cherts. As a result mat-forming and mat-dwelling hormogonian and chrooccoccacean cyanobacteria are easily recognizable as well as remain of planktonic microorganisms buried and preserved in fossilized algal-bacterial communities. These silicified mats turned out to be primarily important for interpretation of Precambrian cyanobacteria and relevant microorganisms as well as for the establishment of their taxonomy and classification. Totally 50 genera and 92 species of cyanobacteria and relevant forms are described in the paper and data on 77 more species are given in the table form.

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