

Mesoproterozoic silicified microbiotas of Russia and India—Characteristics and Contrasts

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ABSTRACT

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The paper analyses eight silicified Mesoproterozoic microbiotas of peritidal and shallow subtidal settings from Siberia, Ural and India. These microbiotas, subdivided into three main types - Kotuikan, Satka and Kataskin—are characterized by different taxonomic composition of microfossils. Mat-building entophysalidacean algae *Eoentophysalis*, ellipsoidal akinetes of nostocalean cyanobacteria genus *Archaeoellipsoides* and spherical large planktic microfossils *Myxococcoides grandis* of uncertain affinities dominate the Kotuikan-type microbiotas, the short trichomes are a rare but a distinctive element of these assemblages. The Satka type microbiotas are dominated by mat-building hormogonion cyanobacteria of genus *Siphonophycus* and chroococcacean dwellers genera *Gloeodiniopsis*, *Eosynechococcus*, *Sphaerophycus*, whereas entophysalidacean cyanobacteria are conspicuously missing and akinetes of genus *Archaeoellipsoides* occur but never abundant. Besides, microbiotas of Satka type include morphologically simple remains of phytoplanktic eukaryotic microorganisms—sphaeromorphic acritarchs genera *Satka*, *Pterospermopsimorpha*, *Granomarginata?* and *Leiosphaeridia*. The late Mesoproterozoic Kataskin-type microbiotas contain mat-forming entophysalidacean, oscillatoriacean and nostocalean as well as mat-dwelling and planktic chroococcacean cyanobacteria, but the most typical feature of these microfossil assemblages is the presence of a stalked cyanobacterium, *Polybessurus bipartitus*.

Almost all-available data on relevant silicified Mesoproterozoic microbiotas from China, Greenland and North America have been analysed. Further different types of Mesoproterozoic silicified microbiotas have been compared with Palaeo- and Neoproterozoic microbiotas in cherts as well as with the assemblages of organic-walled microfossils throughout the world and explained differences and similarities in their composition. The analysis indicate that the Mesoproterozoic microbiotas have their own specific taxonomic composition and differ from the Palaeo- and Neoproterozoic microfossils occurring in the same and different palaeoenvironmental setting. The presence of newly evolved type of cyanobacteria, red algae and acanthomorphic acritarchs in the Kataskin-type microbiotas and contemporaneous open-shelf facies suggest that the terminal Mesoproterozoic can be separated as an independent biostratigraphical unit.

Key-words—Mesoproterozoic, microfossils, cyanobacteria, India, Southern Urals, Siberia.

रूस एवं भारत के मीसोप्रोटिरोज़ोइक काल के सिलिकीभूत सूक्ष्मजीवजात-अभिलक्षण व विपर्यास

व्लादिमीर एन. सर्गीव, मुकुंद शर्मा एवं योगमाया शुक्ला

सारांश

शोध-पत्र साइबेरिया, उराल एवं भारत से प्राप्त परिज्वारीय एवं उथली उपज्वारीय विन्यास के आठ सिलिकीभूत मीसोप्रोटिरोज़ोइक सूक्ष्मजीवजात का विश्लेषण करता है। ये सूक्ष्मजीवजात तीन मुख्य प्रकारों—कोल्यूकन, सतका एवं कतास्किन सूक्ष्मजीवजातों के विविध वर्गिकीय संघटनों से अभिलक्षित हैं। चटाई सदृश्य संरचना बनाने वाले एन्टोफायसैलिडेसियन शैवाल *इओएन्टोफॉयसेलिस*, नॉस्टोकैलियन साइनोबैक्टीरिया वंश *आर्किओएल्लोइडोइड्स* के दीर्घवृत्तजीय निश्चेष्ट तथा अनिश्चित बंधुताओं के वृत्तीय दीर्घ प्लवकी सूक्ष्मजीवजात *मिक्सोकोक्काइड्स* *ग्रांडिस* कोल्यूकन-प्रकार के सूक्ष्मजीवजात प्रभुत्व है, लघु ट्राइकोम अल्प हैं लेकिन इन समुच्चयों का विशिष्ट तत्व है। सतका-प्रकार सूक्ष्मजीवजात वंश *सायफेनोफॉयकस* व क्रुकोकेसियन वास करने वाले वंश *ग्लोइओडिनियऑप्सिस*, *इओसायनोकोक्कस*,

स्फिरियोफॉइकस के चटाई सदृश्य संरचना बनाने वाले हॉर्मोगोनियन सायनोजीवाणु द्वारा नियंत्रित हैं जबकि एन्टोफायसैलिडेसियन सायनोजीवाणु का पूर्णतयः अभाव है तथा आर्किओएल्लिपसॉइड्स वंश की प्राप्ति होती है लेकिन कभी प्रचुर नहीं हुई। इसके अतिरिक्त, सतका-प्रकार के सूक्ष्मजीवजात पादपत्वकी यूकेरीओटी सूक्ष्मजीवों-स्फैरोसमरूपी एक्रिटार्क वंश सतका, टिरोस्पर्मोप्सीमॉर्फा, ग्रेनोमर्जिनेटा तथा लीओस्फैरिडिय के आकारिकीय रूप से साधारण अवशेष सन्निहित है। अंतिम मीसोप्रोटैरोज़ोइक क्तास्किन-प्ररूप सूक्ष्मजीवजात में चटाई सदृश्य संरचना बनाने वाले एन्टोफायसैलिडेसियन, ऑसिलेटोरिएसियन व नॉस्टोकैलीयन के साथ-साथ चटाई सदृश्य संरचना में रहने वाले एवं प्लवकी क्रुकोकेसीयन सायनोजीवाणु निहित हैं, लेकिन इन सूक्ष्मजीवाश्म समुच्चयों का सबसे जटिल लक्षण सवृंत सायनोबैक्टीरियम पॉलीवेस्सुरस बाइपाटइड्स की मौजूदगी है।

चीन, ग्रीनलैंड एवं उत्तरी अमेरिका से प्राप्त संगत सिलिकीभूत मीसोप्रोटैरोज़ोइक सूक्ष्मजीवजात पर संगत लगभग समूचे उपलब्ध आँकड़ों को विश्लेषित किया गया है। इसके अतिरिक्त मीसोप्रोटैरोज़ोइक सिलिकीभूत सूक्ष्मजीवजात के विविध प्रकारों की तुलना चट्टों में पुरा एवं नियोप्रोटैरोज़ोइक सूक्ष्मजीवजातों के साथ-साथ समूचे संसार में कार्बनिक भित्ति वाले सूक्ष्मजीवाश्मों के समुच्चयों के साथ की गई है तथा उनके संघटन में अंतर एवं सदृशता की व्याख्या की गई है। विश्लेषण इंगित करते हैं कि मीसोप्रोटैरोज़ोइक सूक्ष्मजीवजात का अपना विशिष्ट वर्गिकीय संघटन है तथा उसी व अलग-अलग पुरापर्यावरणीय व्यवस्थापन में उत्पन्न हो रहे पुरा एवं नियोप्रोटैरोज़ोइक सूक्ष्मजीवाश्मों से भिन्न है। क्तास्किन-प्रकार के सूक्ष्मजीवजात एवं समकालीन मुक्त-उपतट संक्षिणियों में सायनोजीवाणु, लाल शैवाल एवं एकैन्थोमॉर्फिक के नवीन रूप से विकसित प्रकार की उपस्थिति सुझाती है कि अंतस्थ मीसोप्रोटैरोज़ोइक को एक स्वतंत्र जैवस्तरिक इकाई के रूप में पृथक किया जा सकता है।

मुख्य शब्द - मीसोप्रोटैरोज़ोइक, सूक्ष्मजीवाश्म, सायनोजीवाणु, भारत, दक्षिणी उराल, साइबेरिया।

INTRODUCTION

THE time span of Mesoproterozoic (aged 1.6–1.0 billion years) with each new discovery holds a great promise in our understanding of the early life. During Mesoproterozoic, cyanobacteria occupied almost all ecological niches ranging from supratidal flats to open shelf marine environments. The eukaryotes were restricted to open shelf facies where from the undoubted remnants of morphologically complex and large protista have been reported at least from the youngest Mesoproterozoic deposits (see below). Probably, some simple spherical unicellular eukaryotic organisms were incorporated in prokaryotic communities preserved in silicified peritidal facies, but those are unrecognisable in the fossil record. During Mesoproterozoic, the nucleated microorganisms evolved significantly that finally resulted in the explosive diversification of morphologically complex eukaryotes and sharp changes in microbiota composition near the end of Mesoproterozoic (Knoll, 1992; Knoll & Sergeev, 1995; Sergeev *et al.*, 1996; Sergeev, 2006a). The Mesoproterozoic silicified microbiotas of peritidal setting demonstrate well known biostratigraphic paradox: despite dominance of evolutionary conservative cyanobacteria, these microbiotas differ from the Neoproterozoic assemblages inhabiting the similar environments (Knoll & Sergeev, 1995; Sergeev *et al.*, 1995; Sergeev, 1997). However, there are lateral variations in the Mesoproterozoic silicified microfossil assemblages related to environmental distribution of microorganisms in ancient basins and probably to palaeoenvironmental zonation.

During last decade, discoveries of numerous exceptionally well preserved silicified and organic-walled microfossil assemblages from peritidal and open marine environments have improved our understanding of taxonomic diversity and ecological complexity of Mesoproterozoic life. It demonstrated the abundant presence of nucleated

microorganisms in the Mesoproterozoic microbial communities of middle to inner and probably of outer shelf settings where they are preserved mainly as organic-walled microfossils in shales (Peat *et al.*, 1978; Veis & Vorob'eva, 1992; Xiao *et al.*, 1997; Javaux *et al.*, 2001, 2003, 2004). The prokaryotic cyanobacterial communities dominated in extremely shallow-water peritidal environments and have been preserved mainly in cherts. However, record of Mesoproterozoic silicified protista are rare and confined mainly to the latest Mesoproterozoic deposits (Butterfield, 2000, 2001; Butterfield *et al.*, 1990; Petrov *et al.*, 1995; Sergeev *et al.*, 1997). Considering this, present investigation on the Mesoproterozoic microbiotas included not only the remains of unicellular eukaryotes preserved in chert lenses and nodules but also fossilised protista preserved as compressions in shales mainly from the inner shelf facies. In view of the presence of the newly evolved eukaryotic and prokaryotic microorganisms in Mesoproterozoic assemblages it was earlier suggested to separate the Mesoproterozoic into two stratigraphical units: the Anabarian (Kotuikan- and Satka-type microbiotas) and Turukhanian (Kataskin-type microbiotas) proterohorizons (Sergeev, 2006b). Based on analyses of about two dozen Mesoproterozoic silicified microbiotas, the authors have established three distinct types of assemblages, namely, Kotuikan, Satka and Kataskin. The paper deals with the characteristic features as well as differences among the three distinct kinds of silicified Mesoproterozoic microfossil assemblages and compare those to the microbiotas of Palaeo- and Neoproterozoic age.

MATERIALS AND METHODS

The paper is based on the study of original materials from the Kotuikan, Yusmastakh, Sukhaya Tunguska, Sveltyi and Debengda formations of Siberia, the Satka and Avzyan

formations of southern Ural Mountains and the Salkhan Limestone Formation of India (Figs 1, 2). Analysis of each assemblage of microfossils is supported with the sufficient data on their geological setting, depositional environments and age constraints. Furthermore, while comparing the assemblage, almost all-available data on relevant silicified Mesoproterozoic microbiotas throughout the world have been included. The characteristics and contrasts are based mainly on the comparison of their composition, and not restricted only to the formal taxonomical comparison, but also, wherever necessary emendations have also been provided. The contemporaneous silicified and some organic-walled microbiotas from China, Greenland and northern America as

well as some Siberian microbiotas from areas where from the authors had not the original material are also included in the present analysis to strengthen resulting conclusions. Comparisons have also been made to the different types of Mesoproterozoic microbiotas in the cherts of Palaeo- and Neoproterozoic assemblages of silicified and organic-walled microfossils and efforts have been made to explain differences and similarities in their composition.

All illustrated micro-organisms in the paper were studied in petrographic thin sections of black cherts. Microfossils were photographed under transmitted light on a REM5 and Leitz microscopes and measured with an eyepiece graticule to the nearest micrometer. For some specimens England Finder

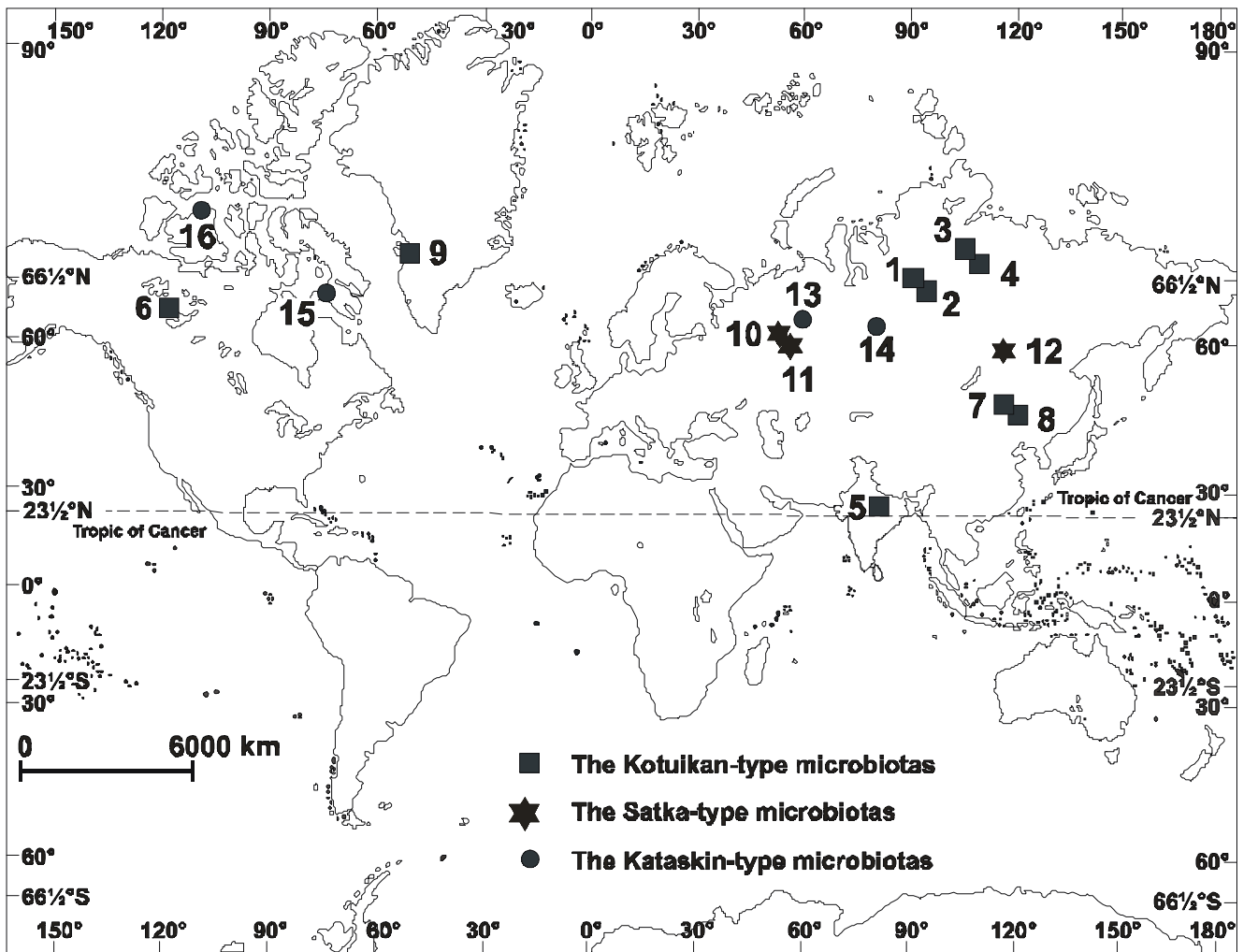


Fig. 1—Geographic distribution of the different kinds of Mesoproterozoic silicified microbiotas. Squares—indicate localities of the Kotuikan type microbiotas, Star – the Satka type microbiotas, circles – the Kataskin type microbiotas. Names of fossiliferous units : 1 - the Kotuikan Formation; 2 - the Yumastakh Formation; 3 - the Debengda Formation; 4 - the Kuytingde Formation; 5 - the Salkhan Limestone Formation; 6 - the Dismal Lakes Group; 7 - the Gaoyuzhuang Formation; 8 - the Wumishan Formation; 9 - the Narssarsuk Formation; 10 - the Satka Formation; 11 - the Revet Member of the Avzyan Formation; 12 - the Svetlaya Formation; 13 - the Kataskin Member of the Avzyan Formation; 14 - the Sukhaya Tunguska Formation; 15 - the Society Cliff and Victor Bay formations; 16 - the Hunting Formation.

coordinates and slide numbers are provided. For other specimens the coordinates cited refer to the numbers of the points on the strips of paper attached at the end of the slides. The strip of paper is glued covering the thin section of rock and the positions of the microorganisms are marked on the paper as numbered points by a sharp pencil. Illustrated specimens are deposited in the Palaeontological Collection of the Geological Institute of the Russian Academy of Sciences (GINPC), bearing numbers # 4684, 4689, 4690 and 4694 and Palaeobotanical Collection of BSIP, Lucknow, India. Besides, some illustrated microfossils from the Kotuikan and Yusmastakh microbiotas of the Anabar Uplift and the Debengda microbiota of the Olenek Uplift which appeared in earlier publications by Sergeev *et al.* 1994 and Sergeev *et al.* 1995 were subsequently deposited in the Palaeontological Collection of the Yakutian Institute of Geological Sciences (PCYIG) of the Russian Academy of Sciences, Yakutsk, Russia and in the Palaeobotanical Collection of the Harvard University Herbaria (HUHPC), Cambridge, USA.

GEOLOGICAL SETTING, AGE CONSTRAINTS AND DEPOSITIONAL ENVIRONMENTS OF DIFFERENT MICROFOSSILIFEROUS MESOPROTEROZOIC FORMATIONS

In this section brief information on geology, palaeoenvironment and age of different formations containing the analysed Mesoproterozoic microbiotas is provided based on published accounts and our experience of field research in these areas. It will facilitate reader to assess the relationship of microfossil assemblage and depositional environment.

Siberia

The Kotuikan and Yusmastakh formations, Anabar Uplift, Siberia

The Billyakh Group is constituted of the Kotuikan, Yusmastakh and Ust'-Il'ya formations. The Kotuikan and Yusmastakh are predominantly carbonate rocks and the underlying Ust'-Il'ya Formation is terrigenous-carbonate in nature. This group contains succession of abundant stromatolites, organic-walled and silicified microfossils, but conclusions on the age of these deposits are contradictory (e.g. Veis & Vorob'eva, 1992 vs. Sergeev *et al.*, 1995). However, considering all biostratigraphic data on stromatolitic and microfossil assemblages, as well as new chemostratigraphic and isotopic-geochronological data, age of the Billyakh Group can be considered between 1500 and 1200 Ma (Bartley *et al.*, 2001; Gorokhov *et al.*, 1991, 1995, 2001). The microfossils are known mainly from the Upper Member of the Kotuikan and the Lower Member of the Yusmastakh formations where they are three dimensionally preserved in early diagenetic cherts.

The Upper Member of the Kotuikan Formation is interpreted to have formed principally in a variety of restricted marine, peritidal and probably supratidal environments. The Yusmastakh Formation represents alternation of restricted marine tidal-flat environments with less restricted environments of shallow marine setting. The beds of its Lower Member contain cherts with abundant microfossils and precipitated textures are considered to have also deposited in peritidal environments with subaerial exposure (Bartley *et al.*, 2000; Sergeev *et al.*, 1995; Sergeev, 2006a).

The Debengda Formation, Olenek Uplift, Siberia

The Solooliiskaya Group consists of ~1500 m of quartz arenites, shale and carbonates and divided into the Sygynakhtakh, Kyutingde, Arymas, Debengda and Khaipakh formations. The Debengda Formation (ca. 200-250 m thick) is constituted of sandstones, siltstones, and argillites, as well as abundant limestone and dolomite with stromatolites, oolites, pisolites and intraformational conglomerates. The fossiliferous cherts and precipitates occur in its Upper Member (Sergeev *et al.*, 1994). The age of Solooliiskaya Group is poorly constrained by radiometric data and based principally on stromatolite and microfossil biostratigraphy. Stromatolite assemblages permit reliable correlation of the Khaipakh Formation to the Upper Member of the Yusmastakh Formation of the Anabar Uplift and microfossil assemblage are in favour of Mesoproterozoic age for the Kyutingde and Debengda formations (Semikhatov, 1991; Sergeev *et al.*, 1994). The Solooliiskaya and Billyakh groups belong to the same basin and their intrabasinal correlation is beyond doubt. Considering the new data on the Anabar Uplift, the age of the Solooliiskaya Group should be bracketed between 1500 and 1250 Ma as well (Gorokhov *et al.*, 1991, 1995, 2001).

The depositional environment of the Debengda Formation is similar to other Mesoproterozoic formations containing silicified dolomites and precipitates. Data for the palaeoenvironmental interpretation of the Debengda microbiota have been derived both from the lithological evidence as well as from the fossils themselves. These support the interpretation of the fossiliferous deposits as tidal flat facies (Sergeev *et al.*, 1994).

The Svetlyi Formation, Uchur-Maya Region, Siberia

The Svetlyi Formation consists of mixed siliciclastic and carbonate sediments: first and third units are predominantly dolomitic whereas the second and fourth are composed of shales and sandstones. The microfossils occur in cherts of the first and third units (Sergeev & Seong-Joo, 2001; Sergeev, 2006a). The Svetlyi and the underlying Talynskaya formations constitute the Aimchan Group that is separated from the underlying Uchur and the overlying Kerpyl groups by angular unconformity. Latest U/Pb dating yielded 1700 Ma age for the volcano-plutonic deposits underlying the Uchur-Maya

Name of the fossiliferous unit	Geographic locality	Stratigraphic position on International and Russian scales and estimated age, Ma	Isotopic age, Ma (wherever available)	References
The Ust'-Ilya Formation	The Anabar Uplift, northeast Siberia	Lower Mesoproterozoic (Lower Riphean) 1500-1400	1483 ± 5 – Rb-Sr 1459 ± 10 – K-Ar	Gorokhov <i>et al.</i> , 1991; Sergeev <i>et al.</i> , 1995
The Kotuikan Formation	The Anabar Uplift, northeast Siberia	Lower Mesoproterozoic (Lower Riphean) 1500-1300		Bartley <i>et al.</i> , 2001; Gorokhov <i>et al.</i> , 2001
The Yusmastakh Formation	The Anabar Uplift, northeast Siberia	Middle Mesoproterozoic (Lower-Middle Riphean) 1400-1200	1284.8; 1272.8 – Rb-Sr 1270 – K-Ar	Gorokhov <i>et al.</i> , 2001; Precambrian Geochronology..., 1968
The Sukhaya Tunguska Formation	The Turukhansk Uplift, northeast Siberia	Upper Mesoproterozoic (Middle Riphean) 1100-1000	1017±91, 1035 ± 60 – Pb-Pb	Ovchinnikova <i>et al.</i> , 1994, 1995
The Burovaya Formation	The Turukhansk Uplift, northeast Siberia	Neoproterozoic (Upper Riphean) 1000-850		Knoll <i>et al.</i> , 1995; Gorokhov <i>et al.</i> , 1995
The Svetlyi Formation	The Uchur-Maya Region, southeast Siberia (Yakutia)	Lower-Middle Mesoproterozoic (Middle Riphean) 1500-1300		Sergeev, 2006a
The Totta Formation	The Uchur-Maya Region, southeast Siberia (Yakutia)	Middle-Upper Mesoproterozoic (Middle Riphean) 1300-1200	1300±5 – U-Pb	Khudoley <i>et al.</i> , 2001
The Lakhanda Group	The Uchur-Maya Region, southeast Siberia (Yakutia)	Upper Mesoproterozoic (lower Upper Riphean) 1030-1000	1005±4, 974±7 – U-Pb	Rainbird <i>et al.</i> , 1998
The Satka Formation	The southern Ural Mountains	Lower Mesoproterozoic (Lower Riphean) 1500-1400	1635±30 – U-Pb 1354±20 – U-Pb	Krasnobaev, 1986; Kozlov <i>et al.</i> , 1989
The Avzyan Formation	The southern Ural Mountains	Upper Mesoproterozoic (Middle Riphean) 1200-1000	1200 and 1011-1167? – K-Ar	Keller, 1983; Bibikova <i>et al.</i> , 1989; Sergeev, 2006
The Myn'yar Formation	The southern Ural Mountains	Neoproterozoic (Upper Riphean) 800-850	780± 50 – Pb-Pb	Ovchinnikova <i>et al.</i> , 2000
The Kyrpy Group	The Cis-Ural Area	Lower Mesoproterozoic (Lower Riphean) 1500-1300		Veis <i>et al.</i> , 2000; Sergeev, 2006
The Kyutingde Formation	The Olenek Uplift, northern Siberia	Lower Mesoproterozoic (Lower Riphean) 1500-1250		Gorokhov <i>et al.</i> , 1991, 1995, 2001
The Debengda Formation	The Olenek Uplift, northern Siberia	Lower Mesoproterozoic (Lower Riphean) 1500-1250		Gorokhov <i>et al.</i> , 1991, 1995, 2001
The Chichkan Formation	The southern Kazakhstan	Neoproterozoic (Upper Riphean? – Vendian?) 650-550		Sergeev, 2006
The Salkhan Limestone	Central India	Lower Mesoproterozoic (Lower Riphean) ~ 1600 Ma	1601±1 Pb-Pb 1601±5 1599±48 Pb-Pb	Ray <i>et al.</i> , 2002; Sarangi <i>et al.</i> , 2004

Fig. 2—Names and locations of the fossiliferous Meso-Neoproterozoic units from Russia (including adjacent areas) and India.

Proterozoic sedimentary succession (Larin *et al.*, 1997) and 1300 Ma for the basal horizons of the Kerpyl Group (Khudoley *et al.*, 2001). Therefore, the Svetlyi Formation seems to be Mesoproterozoic in age bracket probably between 1500 and 1300 Ma.

The dolomites with fossiliferous cherts possibly were deposited in the peritidal environment on a very broad tidal flat. However, the lithological data on the Svetlyi carbonates are insufficient to prove any reliable interpretation of its depositional environments. Data on the microfossils

themselves are also insufficient due to absence of one of the typical palaeoenvironmental indicators of intertidal setting—the entophysalidacean cyanobacteria. Almost exclusively empty sheaths of *Siphonophycus* represent the Svetlyi microbiota that is a characteristic of very harsh environments (Knoll, 1982; Knoll *et al.*, 1991). The depositional environments during accumulation of the Svetlyi carbonates could range from supratidal to subtidal (Sergeev & Seong-Joo, 2001; Sergeev, 2006a).

The Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia

The 530-670 m thick Sukhaya Tunguska Formation consists mainly of limestones and dolomites, with fossiliferous cherts in its lower and upper parts. Reported Pb/Pb age dates for early diagenetic carbonates within the formation are 1017 ± 91 and 1035 ± 60 Ma (Ovchinnikova *et al.*, 1994, 1995). Biostratigraphic and chemostratigraphic data are broadly consistent with Pb/Pb data suggesting the latest Mesoproterozoic age for the Sukhaya Tunguska Formation. For the most part, the Sukhaya Tunguska cherts preserve fossil populations and precipitates from a limited range of peritidal environments (Petrov *et al.*, 1995; Sergeev *et al.*, 1997). Petrov *et al.* (1995), based on compelling sedimentological evidence, proposed that the entire Upper Member records deposits of peritidal setting, probably of restricted coastal environments within local depressions separated by elevated ridges subject to subaerial exposure, and with its uppermost beds indicating inter to supratidal conditions. For the fossiliferous beds of the Lower Member, deposition is inferred to have taken place below storm wavebase in a relatively deep inner shelf environment.

Southern Ural Mountains

The Satka and Avzyan formations, western slope of southern Ural Mountains


The Meso-Neoproterozoic rocks on the western slope of the southern Urals comprise a type section for establishing the Riphean as a Proterozoic time-stratigraphic subdivision of

high rank and can be divided into four groups (in ascending order)—Burzyan (a Lower Riphean stratotype-early Mesoproterozoic), Yurmata (a Middle Riphean stratotype-late Mesoproterozoic), Karatau (an Upper Riphean stratotype–Neoproterozoic) and Asha (Vendian). The Burzyan and Yurmata groups comprise of thick succession of lithologically varied sedimentary rocks and subordinate volcanics. The Burzyan Group can be divided into terrigenous-volcanic Ai Formation and predominantly carbonate Satka (up to 2000-2400 m thick) and Bakal formations. The lower 80% of the Yurmata Group consists predominantly of turbiditic shales and greywackes, with intercalated acidic volcanics (Mashak, Zigalga and Zigazino-Komarov formations) overlain by 900-1800 m of dolomites, limestones and intercalated siliciclastic sediments (the Avzyan Formation). The Avzyan Formation itself can be divided into six members (in ascending order) - Kataskin, Maloinzer, Ushakov, Kutkur, Revet and Tulmen (Keller, 1983). The first, third and fifth members consist largely of carbonates-limestones, with subordinate dolomites, marly limestones and dolomitic limestones. The second, fourth and sixth members consist predominantly of dark-grey argillites and sandstones. The microbiotas in cherts are known from the Kataskin and Revet members.

The radiometric data on the volcanic rocks from the Ai Formation yielded 1635 ± 30 Ma age (Krasnobaev, 1986) whereas Rb/Sr and U/Pb dating for the basic volcanic dykes and granites (the Berdyaush intrusion) penetrating the Burzyan Group yielded 1348 ± 13 Ma and 1354 ± 20 Ma age, respectively (Krasnobaev, 1986). Whole rock Rb-Sr ages and U-Pb zircon ages determined for Mashak Volcanics at the base of the Yurmata Group, some 5 km below the Avzyan Formation, are consistent and yielded ages of 1346 ± 41 and 1350 ± 30 Ma, respectively (Krasnobayev, 1986; Kozlov *et al.*, 1989). Therefore, the Satka Formation seems to be bracketed between 1650 ± 50 and 1350 ± 50 Ma (Semikhatov *et al.*, 1991).

The isotopic age of the Avzyan Formation is poorly constrained. Mineralogically unstudied glauconite from the upper part of the Avzyan Formation and diabase dykes cutting through the formation were reported to have K-Ar ages equal to 1200 Ma and 1011-1167 Ma (Keller, 1983). However, these

PLATE 1

Microfossils from the Lower-Middle Riphean (Mesoproterozoic) Kotuikan Formation, Anabar Uplift, Siberia. 

1. *Filiconstrictosus* ex gr. *majusculus*, slide 563, O-29-2, p. 4, HUHPC # 62946.
- 2, 3, 6, 11. *Partiofilum yakschinii* Sergeev and Knoll, 2 - slide 565, O-34-3, p. 17, GINPC # 479; 3 - slide 571, L-48-2, p. 18, HUHPC # 62944; 6 - slide 551, N-34-0, p. 15, GINPC # 480; 11 - slide 551, O-37-1, p. 16, GINPC # 481.
4. *Filiconstrictosus magnus* Yakschin, slide 574, P-41-2, p. 17, HUHPC # 62943.
5. *Eosynechococcus moorei* Hofmann, slide 560, A-36-0, p. 2, HUHPC # 62930.
7. *Eoentophysalis belcherensis* Hofmann, slide 461, P-43-3, p. 16, GINPC # 396.
8. *Filiconstrictosus cephalon* Sergeev and Knoll, slide 53-A, G-61-3, HUHPC # 62922.
- 9, 10. *Myxococcoides grandis* Horodyski and Donaldson, 9 - slide 452, M-36-4, p. 12, GINPC # 498; 10 - slide 452, L-41-2, p. 24, HUHPC # 62926.
12. *Oscillatoriopsis majesticum* (Allison) Butterfield, slide 578, M-59-2, p. 12, HUHPC # 62945.

For all figures shown on the palaeontological plates 1-4 and 7-12, thin scale bars equals to 10 μ m and thick – to 50 μ m. For the specimens the slide numbers, England Finder coordinates, the point numbers at the attached strips of paper, as well as the specimen numbers are provided.

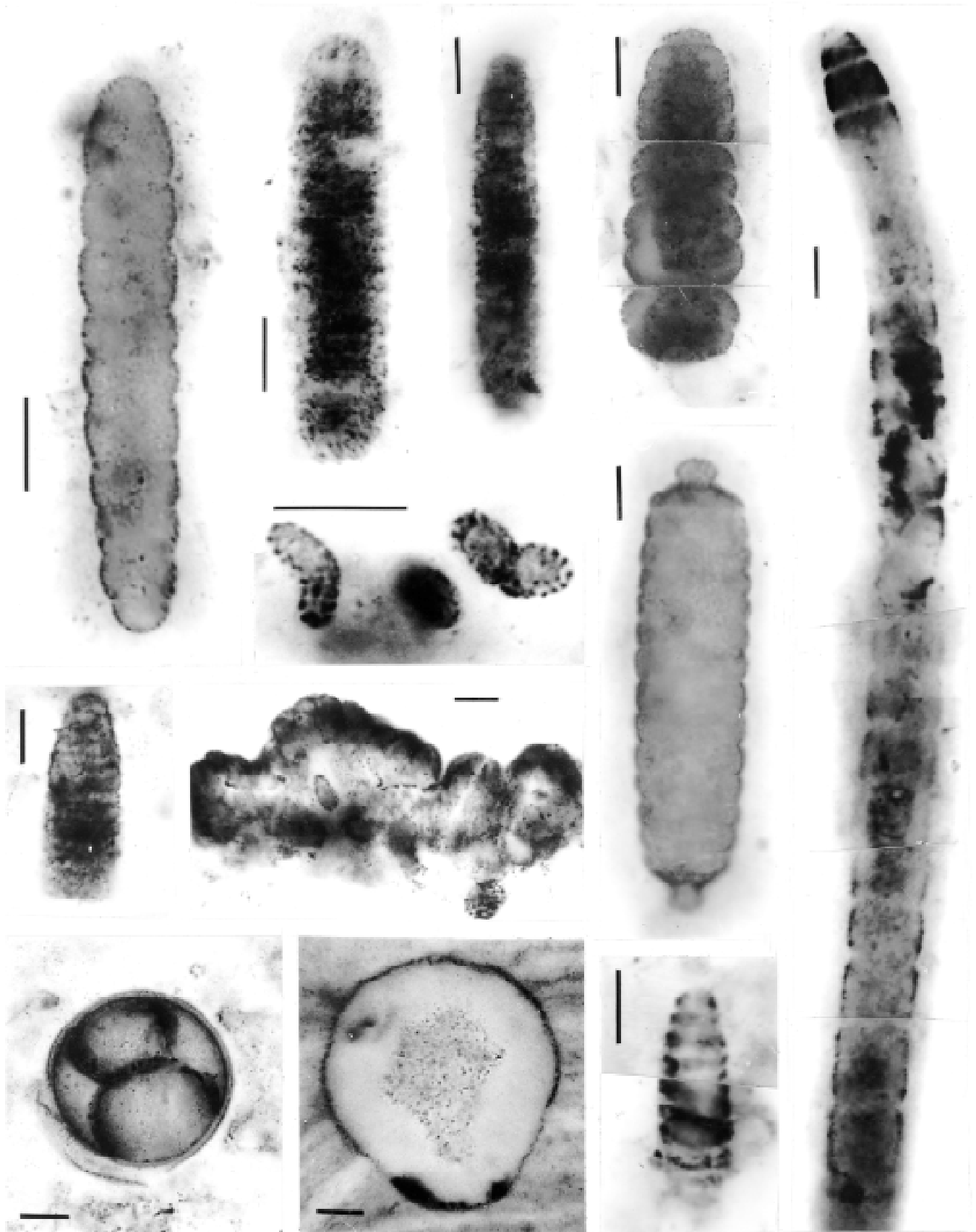


PLATE 1

determinations were obtained in the late 1960's and their reliability may be questioned (Bibikova *et al.*, 1989). The Neoproterozoic Karatau Group, the type section of the Upper Riphean, unconformably overlies the Avzyan Formation. The boundary between Middle and Late Riphean is estimated at 1030 Ma, but reliable radiometric age determination of the basal Karatau Group rocks has proven difficult (Semikhatov *et al.*, 1991). Considering the above data, the depositional age of the Avzyan Formation seems to be bracketed between 1200 and 1000 Ma.

There are no relevant publications analysing the Satka and Avzyan sedimentology. Published accounts dealt with only gross lithologies and stratigraphic successions. For this reason, we rely principally on palaeontological data in drawing inferences about their palaeoecology (Sergeev, 1992, 1994; Sergeev & Seong-Joo, 2004, 2006) although, the interpretation of the particular layers that contain microfossils cannot be extrapolated to the entire formations, which is up to many hundred meters thick. The fossiliferous beds of the Satka Formation are interpreted as deposits of subtidal origin due to lack of entophysalidacean cyanobacteria and abundance of phytoplanktic microorganisms. The abundant silicified edgewise-conglomerate pebbles contain fossilised cyanobacterial communities that suggest the depositional environments in the upper subtidal above storm wavebase in a relatively shallow water shelf environment. This shows the environmental vs taphonomical bias of any assemblage.

In the Kataskin dolomites, the presence of entophysalidacean and stalked cyanobacteria suggest intertidal-peritidal marine or lagoonal (possibly semi-arid) environments with at least locally high sedimentation rates during the accumulation. Possibly, zones of high and lower rates of sediment accumulation occupied contiguous areas along the Kataskin peritidal environmental gradient, as it is typical for modern intertidal environments (Sergeev, 1994).

For the Revet Member, it may be suggested that the microorganisms inhabited a series of nonmarine saline lakes and ponds on a coastal plain. Saline groundwaters 'pickled' the Revet cyanobacterial communities and inhibited their early bacterial degradation. Such an explanation accounts for exceptionally good preservation of microfossils, in which even

the finest layers are preserved (Sergeev, 1994). Earlier the similar interpretation was proposed for the Bitter Springs microbiota by Southgate (1986), who studied the sedimentology of the Bitter Springs Formation in detail.


India

The Salkhan Limestone, Bihar

The Vindhyan Supergroup is unmetamorphosed, tectonically almost undisturbed Proterozoic sedimentary sequence in India that can be divided into Semri, Kaimur, Rewa and Bhandar groups. The Semri Group is best-exposed in Son Valley area of the Sonbhadhra District, Uttar Pradesh, where it is divided into Mirzapur, Kheinjua and Rohtas subgroups. Kheinjua Subgroup in turn is divided into Olive Shale, Koldaha Shale, Salkhan Limestone and Katudandr Glaucanitic Sandstone formations. The Salkhan Limestone Formation consists of light-grey, thick-laminated, wavy-bedded dolosiltites and stromatolitic, oolitic and intraclastic dolomites and limestones interbedded with fine-grained dolarenites, edgewise conglomerates, and fine-grained siliciclastic lithologies up to 30 m thick. The lenses and nodules of black fossiliferous bedded and stromatolitic cherts are common throughout the formation.

Recent SHRIMP U-Pb Zircon geochronological dating of the Semri Group have provided a robust data set for Lower Vindhyan. Rasmussen *et al.* (2002) have shown that the sediments were deposited between $1,628 \pm 8$ Ma and $1,599 \pm 8$ Ma, respectively. Ray *et al.* (2002) have dated the rhyolitic volcanic horizons from the Deonar Formation, between the Kajrahat and Rohtasgarh Limestone that yield U-Pb zircon ages of $1,631 \pm 5$ Ma and $1,631 \pm 1$ Ma. Sarangi *et al.* (2004) have reported a Pb-Pb isochron age of $1,599 \pm 48$ Ma for the Rohtas Formation in central India. These results suggest that the Kajrahat Limestone is of latest Palaeoproterozoic age and the Rohtasgarh Limestone of Rohtas Subgroup is of Early Mesoproterozoic age. The fossil-yielding horizon of Salkhan Limestone is therefore early Mesoproterozoic. Kumar *et al.* (2001) dated glauconites occurring in the Basal Shale of the Mirzapur Subgroup exposed in the Chitrukut area in the central India and suggested $1,600 \pm 50$ Ma minimum age for the onset

PLATE 2

Microfossils from the Lower-Middle Riphean (Mesoproterozoic) Yusmastakh Formation, Anabar Uplift, Siberia. 

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| 1, 7. <i>Archaeoellipsoides bactroformis</i> Sergeev and Knoll, 1 - slide 496, V-37-1, p. 7, GINPC # 422; 7 - slide KG92-60, M-45-0, HUHPC # 62924. | 9. <i>Phanerosphaerops magnicellularis</i> Yakschin, slide KG92-60, B-49-3, HUHPC # 62927. |
| 2, 5, 6. <i>Archaeoellipsoides major</i> Golovenok and Belova, 2 - slide 496, H-30-1, p. 45, GINPC # 421; 5 - slide 558, W-42-3, p. 8, GINPC # 487; 6 - slide 496, F-36-3, p. 34, GINPC # 486. | 10. <i>Myxococcoides grandis</i> Horodyski and Donaldson, the specimen showing vermiform invaginations, slide 497, S-46-3, p. 2, GINPC # 426. |
| 3, 4. <i>Archaeoellipsoides grandis</i> Horodyski and Donaldson, the specimen showing vermiform invaginations, slide KG92-60, O-49-4, HUHPC # 62938. | 11. <i>Myxococcoides</i> sp., the specimen with secondary pseudospines, slide 487, T-30-4, p. 9, GINPC # 429. |
| 8. <i>Gloeodiniopsis</i> sp., slide 489, X-38-0, GINPC # 476. | 12. <i>Eosynechococcus brevis</i> Knoll, slide 489, X-37-2, p. 6, GINPC # 420. |
| | 13. <i>Coniunctiophycus gaoyuzhuangense</i> Zhang, slide 489, X-38-2, p. 11, GINPC # 458. |

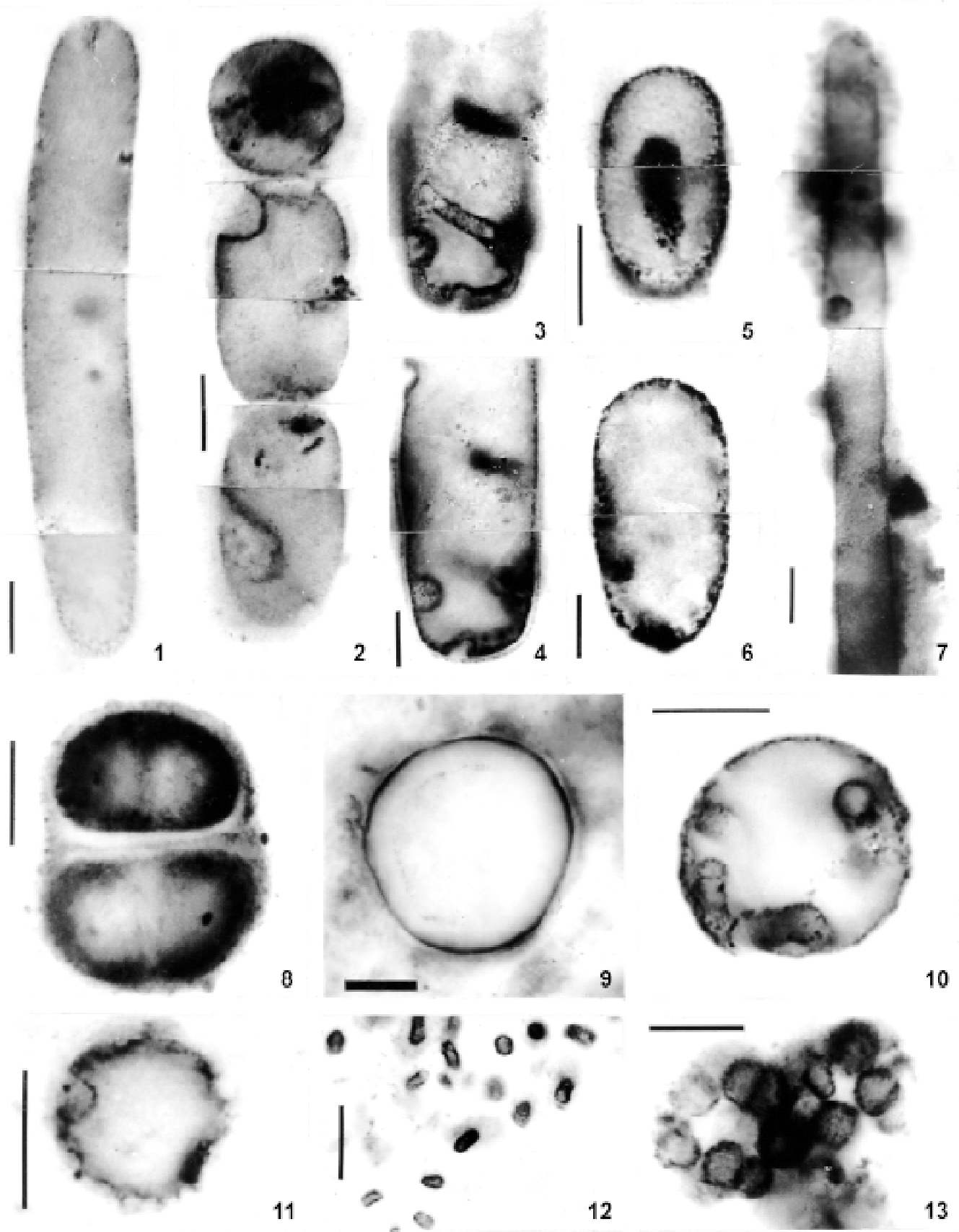


PLATE 2

of earlier Vindhyan sedimentation (for present status of the age of different formations of the Vindhyan Supergroup, see Venkatachala *et al.*, 1996; Sharma, 2006b). Therefore, the fossiliferous strata of the Salkhan Limestone Formation are considered to be older than 1400 Ma and probably about 1600 Ma old.

Data for the palaeoenvironmental interpretation of the Salkhan Limestone like many other Proterozoic fossiliferous formations come both from the lithological evidence and from the fossilised microbial communities themselves. Flaggy fine-grained clastic carbonates, small scale symmetrical ripples, mudcracks and voids as well as presence of entophysalidacean cyanobacteria suggest that the Salkhan Limestone accumulated in arid, intertidal to supratidal, probably sabkha-like environments where some evaporitic minerals could have formed contemporaneously with the cyanobacterial mat formation (Sharma, 2006a).

TYPES OF THE MESOPROTEROZOIC SILICIFIED MICROBIOTAS

On the basis of taxonomic composition, all the studied silicified microbiotas in cherts of Mesoproterozoic age can be divided into 3 main types: Kotuikan, Satka and Kataskin. These names are relevant to the formations containing the most typical, diverse and exceptionally well-preserved microbiotas of each kind. The differences between microbiotas is mainly related to their taxonomic composition and abundance of different kinds of microorganisms. We used the following features of taxonomic composition for the microbiotas classification: (1) presence and abundance of entophysalidacean cyanobacteria; (2) abundance of akinetes of formal genus *Archaeoellipsoides*; (3) presence of assemblages of short trichomes; (4) abundance of the sheaths of mat-forming hormogonian cyanobacteria *Lyngbya-Phormidium-Plectonema* (LPP)-type genus *Siphonophycus*; (5) presence of pleurocapsalean stalked cyanobacterium *Polybessurus bipartitus*; (6) presence or abundance of some other conspicuous microorganism of uncertain affinities, e.g. coccoidal microfossil *Myxococcoides grandis* and (7) presence of morphologically complex eukaryotic microorganisms and acanthomorphic acritarchs.

The Kotuikan type microbiotas

Mat-building entophysalidacean algae, ellipsoidal akinetes of nostocalean cyanobacteria genus *Archaeoellipsoides* and spherical large planktic microfossils *Myxococcoides grandis* of uncertain affinities dominate the microbiotas of Kotuikan type. Populations of mat-forming oscillatoriacean and nostocalean as well as associated chroococcacean cyanobacteria also occur and their abundance varies from one assemblage to another. However, unequivocal remains of morphologically complex protista still have not been reported from numerous biotas of this kind. The microbiotas of Kotuikan type were very widespread in the Mesoproterozoic restricted peritidal environments and can be termed as the 'typical Mesoproterozoic microbiota'.

The Kotuikan microbiota

The characteristic microbiota of the Kotuikan type occurs in the silicified peritidal carbonates of the Kotuikan Formation, Anabar Uplift, Siberia (Pls 1, 3) and contains excellently preserved and abundant remnants of entophysalidacean cyanobacteria (*Eoentophysalis belcherensis*) as well as other chroococcacean cyanobacteria of benthic (genera *Gloeodiniopsis*, *Eosynechococcus*, *Sphaerophycus*) or planktic setting (genus *Coniunctiophycus*), planktic microfossils *Myxococcoides grandis* and *Phanerosphaerops magnicellularis* of almost ideally spherical shape and uncertain affinities, *Anabaena*-like akinetes of nostocalean cyanobacteria (various species of genus *Archaeoellipsoides*), short and long trichomes composed from constricted as well as non-constricted cask-like and pill-like cells (genera *Filiconstrictosus*, *Orculiphycus*, *Partitiofilum*, *Oscillatoriopsis*, *Veteronostocale*), empty sheaths of hormogonian cyanobacteria of LPP type (genus *Siphonophycus*) and unbranched empty cylindrical tube-like structures consisting of elongate funnel-like segments nested one within another are known as *Circumvaginalis elongatus* (Sergeev, 1993, 2006a; Sergeev *et al.*, 1995).

The Kotuikan microbiota is dominated by akinetes of *Archaeoellipsoides*, spherical microfossils of *Myxococcoides grandis*, which at least partly possibly also are akinetes, and conspicuous and abundant entophysalidacean cyanobacteria *Eoentophysalis belcherensis*. The sheaths of *Siphonophycus*

PLATE 3



Microfossils from the Lower-Middle Riphean (Mesoproterozoic) Kotuikan (1-6, 8) and Yusmastakh (7, 9) formations, Anabar Uplift, Siberia and the Lower Cambrian Chulaktau Formation, Lesser Karatau Ridge, Kazakhstan (5).

- | | |
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| <p>1. <i>Filiconstrictosus magnus</i> Yakschin, slide 576, F-38-0, p. 26, GINPC # 478.</p> <p>2, 4. <i>Archaeoellipsoides major</i> Golovenok and Belova, 2 - slide 576, S-29-3, p. 2, GINPC # 494; 4 - slide 482, p. 48, GINPC # 801.</p> <p>3. <i>Archaeoellipsoides costatus</i> Sergeev and Knoll, slide 576, F-39-3, p. 1, GINPC # 465.</p> <p>5. <i>Obruchevella parva</i> Reitlinger, slide 365, p. 2, GINPC # 200.</p> | <p>6. <i>Circumvaginalis elongatus</i> Sergeev, slide 471, L-33-2, p. 14, GINPC # 391.</p> <p>7, 9. <i>Eoentophysalis belcherensis</i> Hofmann, 7 - slide 485, G-42-4, p. 18, GINPC # 415; 9 - slide 485, p. 12, GINPC # 802.</p> <p>8. <i>Myxococcoides grandis</i> Horodyski and Donaldson, slide 482, p. 26, GINPC # 803.</p> |
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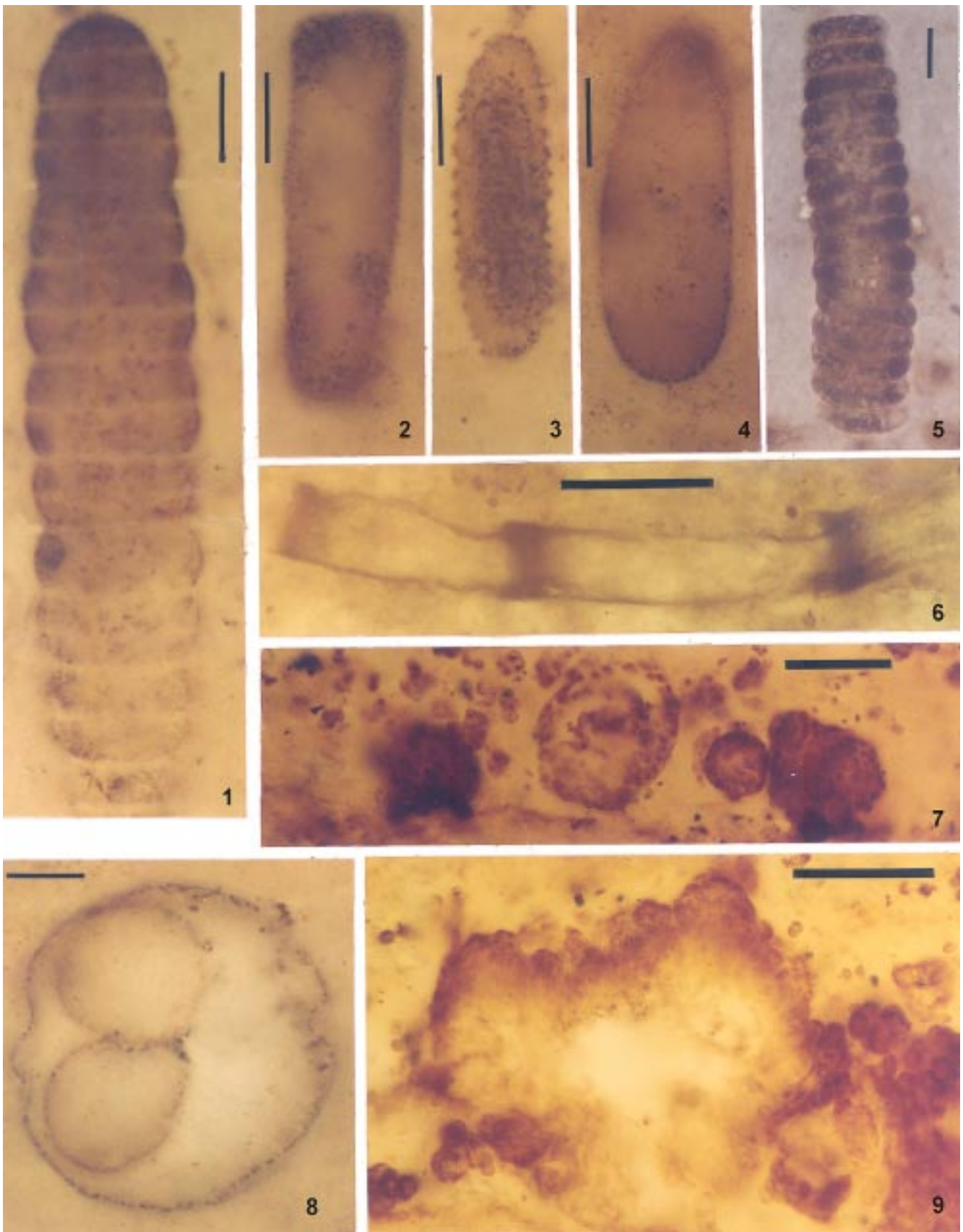


PLATE 3

robustum are common, but this taxon is not the overwhelming element of the microbiota in contrast to many other Proterozoic microfossils assemblages. *Circumvaginalis elongatus* is of particular interest in that it appears to be the empty sheath of a nostocalean *Scytonema*-like cyanobacterium which inhabited periodically emerged environments. All these taxa—*Eoentophysalis belcherensis*, *Siphonophycus robustum* and *Circumvaginalis elongatus*—in the Kotuikan Formation are remains of mat-building microorganisms. Trichomes constitute a rare but distinctive element of the Kotuikan Assemblage and differ from younger examples in that most specimens are quite short. The short length of these trichomes supports their interpretation as possible hormogonia and hormocysts of filamentous cyanobacteria or germinated akinetes. The small coccoidal microfossils genera *Sphaerophycus*, *Eosynechococcus*, *Phanerosphaerops* and *Coniunctiophycus* often occur in the Kotuikan Formation mainly scattered among the precipitates.

These precipitates are the special associated structures superficially resembling stromatolites, but they are of inorganic or mixed biosedimentary origin. At least cyanobacteria did not take active part in the formation of these textures although the remnants of cyanobacterial mats are found inside of precipitates. Bartley *et al.* (2000) have recognised four different textures in the Kotuikan silicified carbonates: radial-fibrous fans, microlaminated stratiform laminae, poorly laminated stratiform laminae and laminated, micritic texture (describing the Kotuikan precipitates, terminology used as by Sharma & Sergeev, 2004). The entophysalidacean mats often colonise the surfaces of radial-fibrous fans and remnants of other microfossils often occur inside of precipitates, especially trichomes where they are very well preserved probably due to early sea floor cementation. It is noticed that the precipitates are abundant almost in all microbiotas of the Kotuikan type and their presence as well as composition of the microbial communities is related to the particular environments of the Mesoproterozoic tidal flats.

The Yusmastakh microbiota


Silicified Kotuikan fossils are strikingly similar in taxonomic composition to many other Mesoproterozoic assemblages from peritidal facies, but differ in significant ways

from Neoproterozoic as well as some Mesoproterozoic microbiotas. The overlying Yusmastakh Formation of the Billyakh Group (Pls 2, 3) contains almost the same microbiota but differs only by absence of assemblage of short trichomes (Sergeev *et al.*, 1995) that are interpreted to be the initial stage of akinetes germination or hormogonia and hormocysts (Knoll & Sergeev, 1995; Sergeev *et al.*, 1995; Sergeev, 1997). The Yusmastakh Formation contains abundant *Archaeoellipsoides* fossils and absence of the short trichomes suggests significant taphonomical bias in favour of the preservation of these fossils. In the Kotuikan Formation as well as in many other formations, the short trichomes were entombed in the precipitates and early cementation helped in their preservation prior to silicification. Otherwise, they would have decomposed as there are no good short trichome assemblages in the silicified dolomites of the Yusmastakh Formation where precipitates are absent.

The Debengda microbiota

Another example of the Kotuikan-type microbiota came from the Debengda Formation of the Olenek Uplift, Siberia (Pl. 4). The taxonomical composition of the Debengda Assemblage is similar to the Kotuikan, Yusmastakh and Salkhan Limestone microbiotas, but with some differences. The Debengda microbiota also is dominated by entophysalidacean cyanobacteria and two distinct species *Eoentophysalis dismallakesensis* and *E. belcherensis* constituting more than 50% of all individuals. But in contrast, the sheaths of *Siphonophycus* are also abundant and mats containing mainly *Siphonophycus typicum* and less common *S. kestron* and *S. robustum* rarely intercalated with *Eoentophysalis* population's laminae. Other, less abundant taxa like *Gloeodiniopsis* aff. *lamellosa*, *G. gregaria*, *Eosynechococcus medius* and *Clonophycus* sp. occur as loose colonies between filaments of *Siphonophycus robustum* or in close association with *Eoentophysalis*. Single individuals represent the trichomes *Palaeolyngbya catenata* and the akinetes *Archaeoellipsoides grandis* whereas the short trichomes are absent in the Debengda assemblage. Most types of precipitated textures known in the Kotuikan and Salkhan Limestone (Jaradag Fawn Limestone) formations are observed in the cherts from the

PLATE 4

Microfossils from the Middle Riphean (Upper Mesoproterozoic) Debengda Formation, Olenek Uplift, Siberia. 

1. Vertically oriented bundles of *Siphonophycus typicum* Hermann, slide 91-11-2A, L-46-3, HUHPC.
2. *Gloeodiniopsis gregaria* Knoll and Golubic, slide 2-91-2, M-45-1, PCYIG.
- 3, 4. *Clonophycus* sp., 3 - slide 546, Q-35-1, GINPC # 563; 4 - slide 2-91-2, G-55-4, PCYIG.
5. Poorly preserved filament of *Palaeolyngbya catenata* Hermann, the arrows indicate the outline of the sheath, slide 2-91, S-55-4, PCYIG.
6. *Eoentophysalis dismallakesensis* Horodyski and Donaldson, slide 2-91-3, M-45-4, PCYIG.
- 7, 9. *Eoentophysalis belcherensis* Hofmann, 7 - slide 2-91-3, N-50-4, PCYIG; 9 - slide 3-91-3, J-55-3, PCYIG.
8. *Siphonophycus kestron* Schopf, slide 549, L-42-2, GINPC # 568.
10. *Eosynechococcus medius* Hofmann, slide 2-91, L-56-1, PCYIG.
11. *Archaeoellipsoides grandis* Horodyski and Donaldson, slide 2-91-3, Q-45-2, PCYIG.

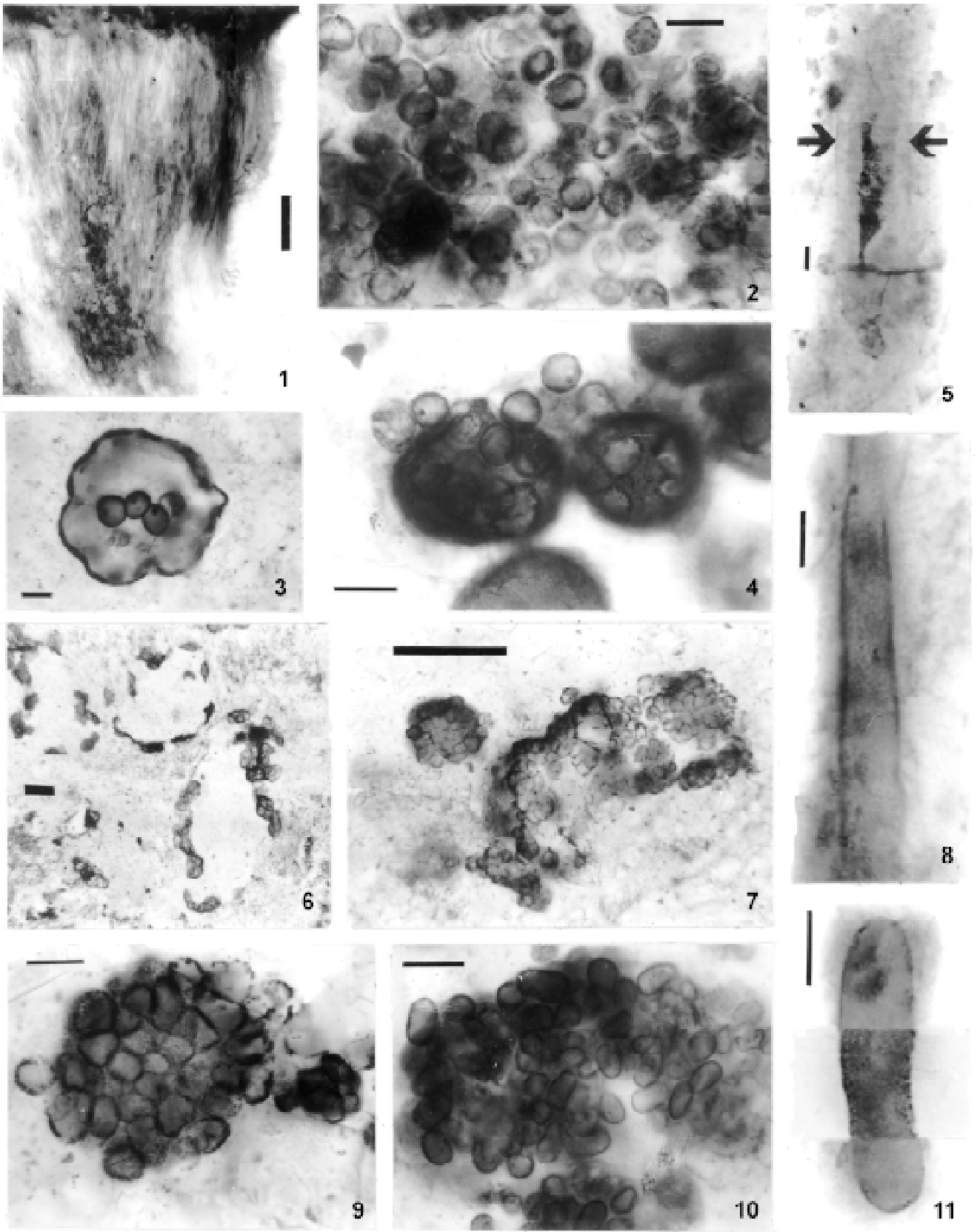


PLATE 4

Debengda Formation and the radial-fibrous fans and microlaminated stratiform laminae are easily recognisable.

The difference of the Debengda microbiota from other microbiotas of Kotuikan type is mainly related to absence of short trichomes and paucity of akinetes of *Archaeoellipsoides*. In this case, the relationship between ellipsoidal akinetes and short trichomes is quite evident because precipitates are well developed in the Debengda Formation and absence of the short trichomes cannot be explained as in a case of the Yumastakh microbiota by the taphonomical bias. Considering the assemblage of the silicified microfossils from the Debengda Formation, as a microbiota of the Kotuikan type, is questionable and all similarity is related mainly to abundance of the entophysalidacean cyanobacteria. However, in the framework of all available Mesoproterozoic silicified assemblages, there is not an alternative opportunity, but to place the Debengda microbiota among other microbiotas of Kotuikan type.

The Salkhan Limestone microbiota

Another very close counterpart of the Kotuikan Assemblage came from the Salkhan Limestone Formation of India (Pls 5, 6) (McMenamin *et al.*, 1983; Kumar & Srivastava, 1995; Srivastava & Kumar, 2003; Sharma, 2006a). At least three distinct mat-building populations are present in the Salkhan Limestone cherts: *Eoentophysalis belcherensis*, *Siphonophycus robustum* and *S. thulenema*. All three taxa are widely distributed in Proterozoic cherts, but like the Kotuikan assemblage, only *E. belcherensis* is the overwhelming element in the Salkhan microbiota whereas *S. robustum* and *S. typicum* are minor components of the assemblage. Other chroococcacean cyanobacteria are also abundant, but some other described taxa—*Coniunctiophycus gaoyuzhuangense*, *Palaeoanacystis vulgaris*, *Sphaerophycus parvum*—may turn out to be developmental or preservational variants of *Eoentophysalis belcherensis*. Chroococcacean cyanobacteria can produce different morphologies and as a rule distinguishing entophysalidacean and associated chroococcacean cyanobacteria is a difficult task. Wherever *Eoentophysalis* has been described, its developmental variants have been distinguished as a distinctive taxa and the Salkhan Limestone Formation is no exception. But remains of other coccoidal microorganisms – *Eosynechococcus medius*, *E.*

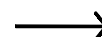
grandis, *Tetraphycus hebeiensis*, *T. major*, *Sphaerophycus medium* and *Diplococcus* sp. – are rather separate taxa of chroococcacean cyanobacteria.

Trichomes are rare but also a distinctive element of the Salkhan Limestone assemblage and several taxa can be distinguished morphologically: *Filiconstrictosus majusculus*, *Oscillatoriopsis longa*, *Oscillatoriopsis* sp. and *Orculiphycus* sp. Most specimens are quite short that support their interpretation as hormogonia and hormocysts or germinated akinetes of nostocalean cyanobacteria. The akinetes-ellipsoidal microfossils *Archaeoellipsoides major* and *A. minor*—occur in the Salkhan Limestone assemblage, but they are not abundant (Sharma, 2006b). The simple spheroidal fossils *Myxococcoides minor*, *Myxococcoides muricata*, *Myxococcoides* sp., *Clonophycus elegans*, *C. ostiolum*, *Conhemisphaera pendulua*, *Leptoteichus golubicii* and *Leiosphaeridia* sp. could be the remains of planktic prokaryotic or eukaryotic microorganisms, e.g., spherical akinetes of nostocalean cyanobacteria.

A variety of precipitates are abundant in the Salkhan Limestone (=Jaradag Fawn Limestone) Formation and they are very similar to the precipitated carbonate textures from the Kotuikan Formation (Sharma & Sergeev, 2004). The radial-fibrous fans and microlaminated stratiform laminae are easily recognisable and almost identical in the Salkhan Limestone and Kotuikan formations, but second texture is not so widespread in former whereas in latter it is quite abundant. However, the Salkhan Limestone Formation containing radial-fibrous fans with mammillated surface have been reported only from Jaradag locality and that makes the Salkhan Limestone precipitates easily recognisable.

Some differences between the Kotuikan and Salkhan Limestone microbiotas nonetheless exist. The ellipsoidal microfossils *Archaeoellipsoides* and coccoidal microfossils *Myxococcoides* are overwhelming in the Kotuikan and Yumastakh microbiotas, but in the Salkhan Limestone, remnants of these microorganisms are not so abundant. The *Circumvaginalis elongatus* filaments do not occur in the Salkhan Limestone microbiota, but this cyanobacterium is conspicuously missing in almost all other Mesoproterozoic microbiotas as well.

PLATE 5



Microbial assemblage recorded from Salkhan Limestone of the Semri Group. In this and Plate 6, slide catalogue number are for the Birbal Sahni Institute of Palaeobotany Museum (BSIP) and stage coordinates for each fossils or population illustrated are given. X and Y slide coordinates given are for Leitz Diaplan Microscope. Scale = Single bar = 10 µm; double bars = 50 µm.

- | | |
|---|---|
| <ol style="list-style-type: none"> 1. <i>Palaeoanacystis vulgaris</i> Schopf, BSIP # 10906, 34.0/99.7. 2. <i>Coniunctiophycus majorinum</i> Knoll <i>et al.</i>, BSIP # 10907, 40.3/100.0. 3, 6. <i>Eoentophysalis belcherensis</i> Hofmann, BSIP #13143, 32.4/105.0; 6 – BSIP # 13142, 39.4/96.5. | <ol style="list-style-type: none"> 4. <i>Tetraphycus major</i> Oehler, BSIP # 10906; 34.3/102.8. 5. <i>Eosynechococcus moorei</i> Hofmann, BSIP # 10906, 31.5/98.7. 7. <i>Eosynechococcus moorei</i> Hofmann, BSIP # 10907, 44.2/97.2. 8. <i>Myxococcoides minor</i> Schopf, BSIP # 13142, 42.4/96.5. 9. <i>Diplococcus</i> sp., BSIP # 10907, 34.4/105.1. |
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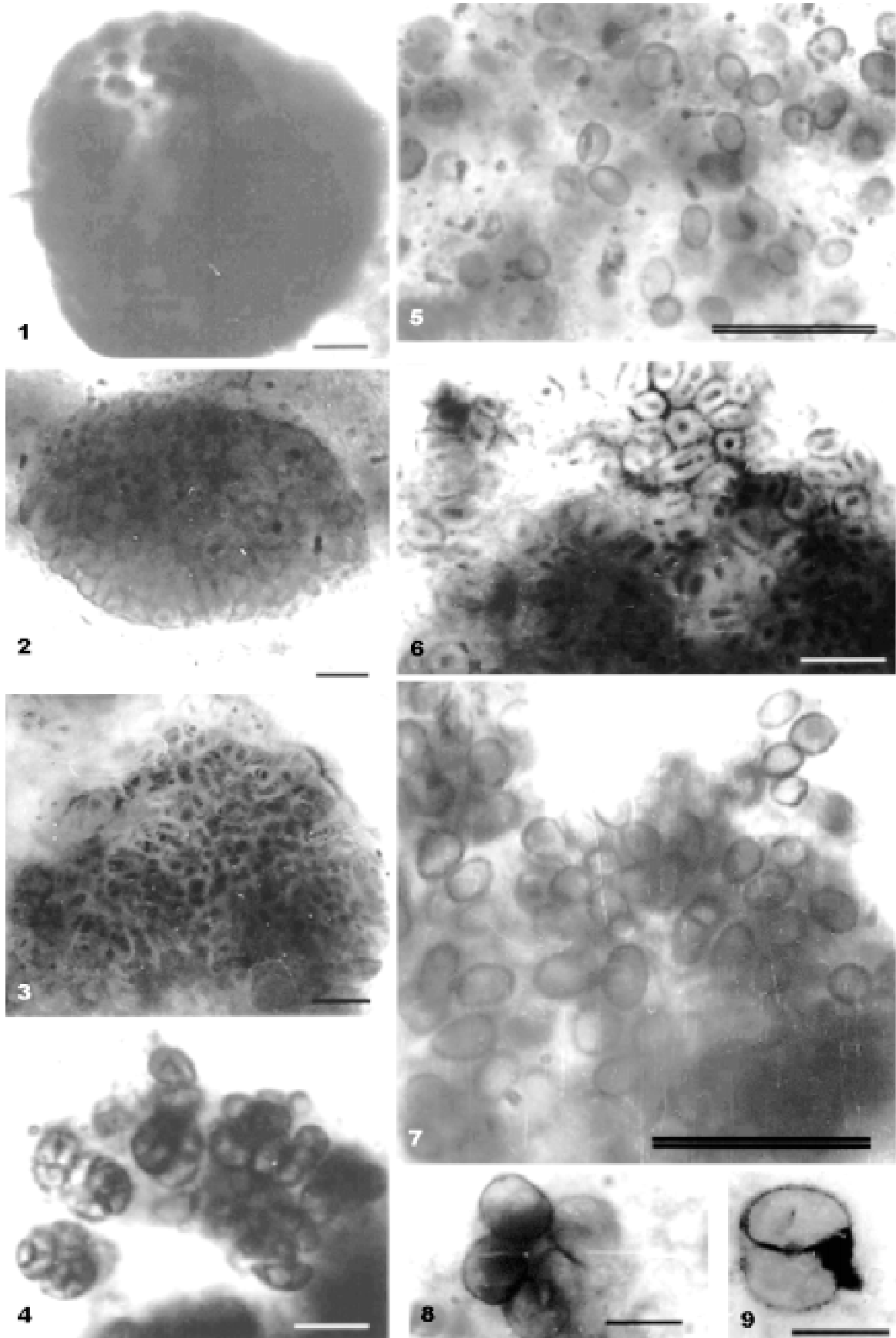


PLATE 5

Other Mesoproterozoic microbiotas of Kotuikan type

Besides our materials from Siberia and India, there are many other Mesoproterozoic Kotuikan-type microbiotas. The similar silicified microfossils assemblage has been described by Yakschin (1990, 1999) from the Kyutingde Formation of the Solooliiskaya Group, Olenek Uplift, Siberia. This assemblage is also clearly dominated by entophysalidacean cyanobacteria (Sergeev *et al.*, 1995). However, from our point of view, Yakschin (1990, 1999) has described many synonymous taxa and the taxonomic composition of the Kyutingde microbiota needs revision as it was done earlier for the Kotuikan microbiota (Sergeev *et al.*, 1995). Without establishing true taxonomic position of the microfossils any comparison of the Kyutingde microbiota with other Mesoproterozoic assemblages would be meaningless.

Probably, one of the best microfossil assemblages of Kotuikan type came from the Gaoyuzhuang and Wumishan formations of China. Radiometric dating of the Gaoyuzhuang Formation, based on Pb-Pb isotopic analysis of galena, yielded an age 1434 ± 50 Ma (Yu & Zhang, 1985). There are not absolute radiometric data on the Wumishan Formation and its age can be approximately estimated as 1200 Ma (Seong-Joo & Golubic, 1999; Zhang, 1985). The Gaoyuzhuang and Wumishan microbiotas are dominated by entophysalidacean (*Eoentophysalis belcherensis* and *Coccostratus dispergens*) and associated chroococcacean cyanobacteria (genera *Coniunctiphycus*, *Eosynechococcus*, *Palaeoanacystis*, *Sphaerophycus*), short and long trichomes (genera *Palaeolyngbya*, *Oscillatorioopsis*, *Partitiofilum*, *Filiconstrictosus*), abundant akinetes of *Archaeoellipsoides* and coccoidal microfossils *Myxococcoides grandis* (Cao Fang, 1992; Seong-Joo & Golubic, 1999, 2000; Zhang P *et al.*, 1989; Zhang Y, 1981, 1985). In contrast to the Salkhan Limestone and Kotuikan formations, the sheaths of *Siphonophycus* are also abundant in the Gaoyuzhuang Formation, but these hormogonian cyanobacteria preferentially colonised soft substrates above the precipitates surfaces. The precipitates from the Gaoyuzhuang Formation are very similar to other Mesoproterozoic, especially from the Salkhan Limestone and Kotuikan formations. Seong-Joo and Golubic (1999, 2000) have described the upward radiating crystal fans (=Radial-Fibrous Fans), flat crustose coating (=Microlaminated stratiform laminae) and spherulites and botryoids from the Gaoyuzhuang Formation which we consider as variations of Radial-Fibrous Fans.

Another diverse assemblage of the Kotuikan type is known from the Dismal Lakes Group of Canada for which 1200 Ma age is suggested (Horodyski & Donaldson, 1980). The Dismal Lakes Group contains microfossil assemblage dominated by entophysalidacean algae *Eoentophysalis dismallakesensis*, akinetes *Archaeoellipsoides*, short trichomes, coccoidal microfossils *Myxococcoides grandis* as well as remains of other cyanobacteria (Horodyski & Donaldson, 1980). The precipitates are also present in the

Dismal Lakes Group (L. Kah, personal comm. 1996 to VNS). The Dismal Lakes microbiota is extremely similar to the microbiotas known from the Kotuikan, Yusmastakh, Salkhan Limestone, Gaoyuzhuang and Wumishan formations and share many elements common with Debengda and Kyutingde.

The Kotuikan type similar microbiota has also been reported from the Narssârssuk Formation/Group, Thule Group/Supergroup (Knoll, 1985; Strother *et al.*, 1983) Greenland which is considered to be around 1200 Ma on the basis of chemostratigraphic correlation (Kah *et al.*, 1999). Although this microbiota is not diverse yet it can be considered as Kotuikan type mainly on the basis of presence of entophysalidacean cyanobacteria. The akinetes of *Archaeoellipsoides* described as *Eosynechococcus thuleënsis* and the short trichomes assigned to *Oscillatorioopsis variabilis* are present, but they are neither dominant nor remarkable elements of the microbiota. The Narssârssuk silicified microfossils assemblage contains some other cyanobacterial remains including empty sheaths of *Siphonophycus robustum* and *Siphonophycus* sp., secondarily coiled cyanobacterial sheaths of *Avictospirulina minuta*, long trichomes *Oscillatorioopsis variabilis* (see Butterfield *et al.*, 1994, for synonymy) and some benthic and planktic chroococcacean cyanobacteria: *Eosynechococcus amadeus*, *Coleogleba auctifica*, *Gyalosphaera fluitans* and possibly *Myxococcoides* sp. To date, the precipitates have not been reported from the Narssârssuk Formation.

The Satka type microbiota

The Satka type microbiotas are dominated by remains of mat-building oscillatoriacean or nostocacean cyanobacterium of genus *Siphonophycus* and chroococcacean cyanobacteria of genera *Gloeodiniopsis*, *Eosynechococcus*, *Sphaerophycus* and some others that dwelled on these mats. The microbiotas of this type differ from the Kotuikan type in following ways. First, entophysalidacean cyanobacteria are conspicuously absent in these microbiotas; second, akinetes of *Archaeoellipsoides* occur, but they never are a dominating element; and, third, short trichomes are almost missing in the Satka type assemblages despite presence of long filaments. In addition the Satka microbiota, from its type locality, include the morphologically simple but large sized acritarchs genera *Satka*, *Pterospermopsimorpha*, *Granomarginata?* and *Leiosphaeridia* – the phytoplanktic micro-organisms of undoubted eukaryotic origin. Microbiotas of Satka type are not widespread and only a few microfossil assemblages of this kind have been reported from the Mesoproterozoic deposits. The best microbiota has been recorded from the Satka Formation of the type section of the Lower Riphean, southern Ural Mountains.

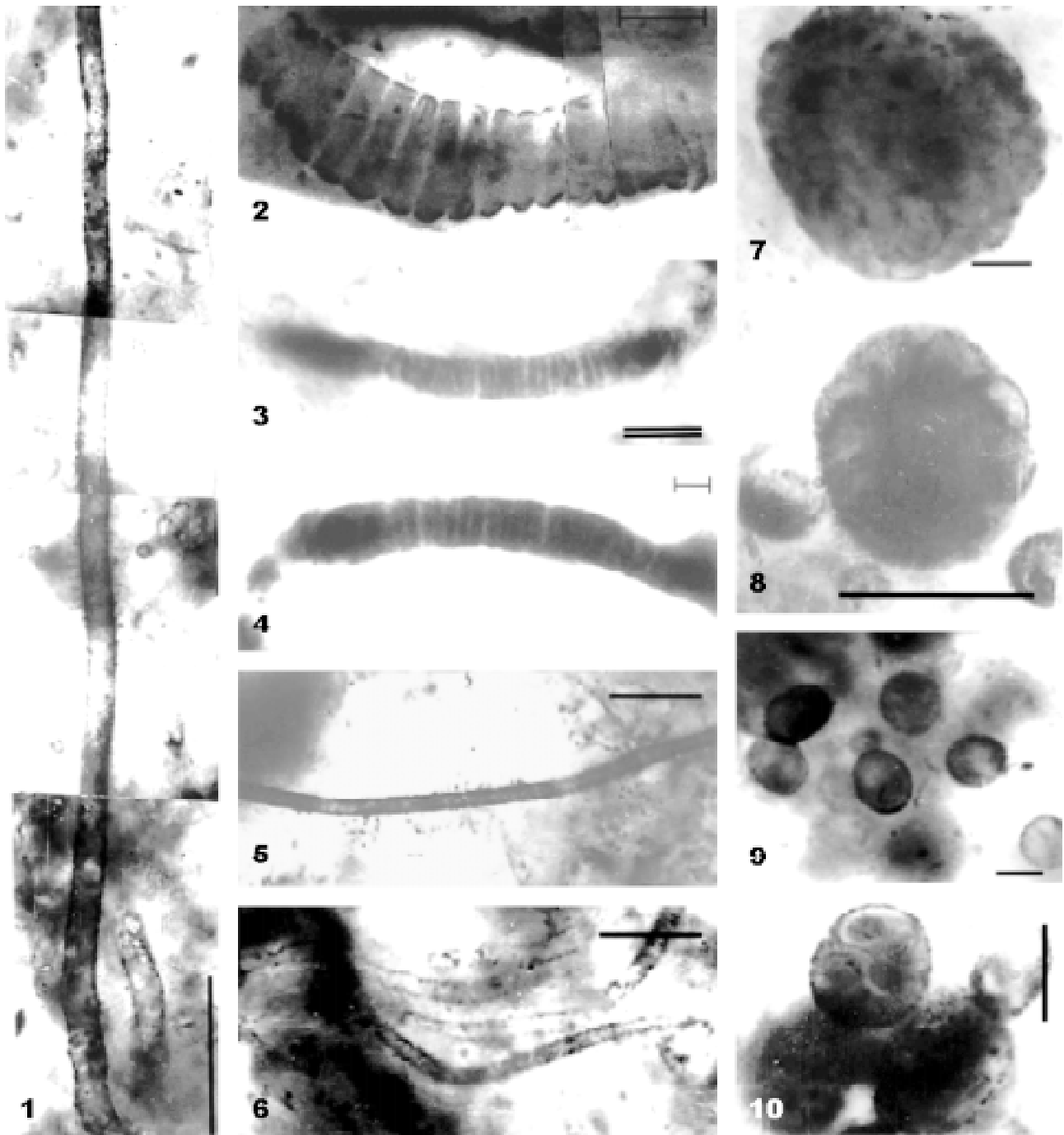


PLATE 6

Microbial assemblage recorded from Salkhan Limestone of the Semri Group.

- | | |
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| 1, 5, 6. <i>Siphonophycus robustum</i> Knoll <i>et al.</i> , 1 - BSIP # 13142, 26.7/100.6; 5 - BSIP # 13142, 26.8/99.0; 6 - BSIP #10907, 40.3/100.0. | 7. <i>Palaeoanacystis vulgaris</i> Schopf, BSIP # 10907, 40.3/100.0. |
| 2, 4. <i>Oscillatoriopsis longa</i> Timofeev and Hermann, 2 - BSIP # 10907, 43.2/98.8; 4 - BSIP # 10906, 36.8/98.2. | 8. <i>Conhemisphaera pendulua</i> Luo and Wang, BSIP # 10907, 26.5/99.9. |
| 3. <i>Oscillatoriopsis media</i> Mendelson and Schopf, BSIP # 10906, 38.1/98.5. | 9. <i>Myxococcoides minor</i> Schopf, BSIP #10906, 38.8/103.2. |
| | 10. <i>Eoentophysalis belcherensis</i> Hofmann, BSIP #10907, 35.0/102.0. |

The Satka microbiota

Empty sheaths of genus *Siphonophycus* forming dense mats dominate the microbiota of Satka Formation (Pls 7, 8). These mats contain abundant remains of chroococcacean cyanobacterium *Gloeodiniopsis lamellosa* which occur either as the laminae or the clusters in the silicified edgewise conglomerates. Other coccoidal microfossils are also nested inside *Siphonophycus* mats and some fossils (e.g. *Eosynechococcus moorei* and *E. amadeus*) demonstrate better preservation among the almost completely decomposed sheaths that can be in favour of their interpretation as the remains of heterotrophic bacteria (Sergeev, 1992, 1994). In addition to these taxa, the Satka microbiota contains rare elements of possibly some other benthic cyanobacteria - polytrichomatous filaments *Eomicrocoleus crassus*, monotrichomatous filaments *Palaeolyngbya catenata*, long trichomes *Oscillatoriopsis vermiformis* and short trichomes *Filiconstrictosus* sp. (Sergeev & Seong-Joo, 2004; Sergeev, 2006a). A few available trichomes of the latter species are replaced by pyrite and their nature can be questioned.

The phytoplanktic forms are abundant and they represent both prokaryotic and eukaryotic microorganisms. The former includes colonies of small spheroids *Coniunctiophycus gaoyuzhuangense* and *Corymbococcus rexii* comparable to modern chroococcacean cyanobacteria genera *Microcystis* and *Aphanocapsa* and some microfossils of ellipsoidal morphology *Archaeoellipsoides major* that are considered as akinetes of nostocalean cyanobacteria (Sergeev & Seong-Joo, 2004). The remnants of eukaryotic microorganisms include relatively large (up to 130.0 µm in diameter) robust-wall or double- and multiple spherical envelope that occur as scattered individuals among the *Siphonophycus* clusters or sometimes they are incorporated in these mats as the allochthonous elements. The eukaryotic nature of these microfossils is proved by their large size, presence of central large cyst-like body inside (*Pterospermopsimorpha pileiformis*) and shagrinated appearance of single- (*Leiosphaeridia atava* and *L. crassa*) or double-walled robust envelopes (*Granomarginata?* sp.). The envelopes of *Satka* sp. are composed of compressed scales and could not be the result of a degradation of the smooth-walled large diameter spherical envelopes of prokaryotic colonies. The simple spheroids of *Myxococcoides inornata* and *Myxococcoides* sp. (30.0-50.0 µm in diameter)


are also probably remnants of planktic micro-organisms due to their pattern of distribution in the cherts of Satka Formation. But the nature of these fossils as well as other species of genus *Myxococcoides* is uncertain. These can either be remnants of chroococcoid cyanobacteria or unicellular eukaryotic microorganisms.

The composition of the Satka microbiota varies from one locality to another as well as in up-sections and in some outcrops it reduces significantly where only the sheaths of *Siphonophycus* and chroococcacean cyanobacteria *Sphaerophycus* and *Eosynechococcus* occur. In these localities, the abundant radial-fibrous fans are present, but they are devoid of any microfossils. The unequivocal entophysalidacean cyanobacteria have not been reported from these facies thus far.

The Svetlyi microbiota

The Svetlyi microbiota is practically monogeneric in its composition and represented almost exclusively by empty sheaths of *Siphonophycus* (Pl. 9). The microbial diversity seems to be one of lowest among the Proterozoic microfossil assemblages despite occasional very good preservation of *Siphonophycus* and a few associated taxa of filamentous microfossils, e.g. *Palaeolyngbya catenata*. Coccoidal forms are represented only by small poorly preserved microfossils *Myxococcoides* sp. about 10.0 µm in diameter. Of course, it is difficult to draw a comparison between the Svetlyi microbiota and other Mesoproterozoic silicified microfossils communities on the basis of its conservative restricted composition. Therefore, merely on basis of absence of entophysalidacean cyanobacteria in the composition of the Svetlyi microbiota, it would not be reasonable to consider it as a Satka type. Such low-diversity of communities of cyanobacteria are represented by remains of mat-forming microorganisms whereas mat dwellers are conspicuously missing, probably owing to very harsh environments of deposition, as according to Golubic's regulation, "...species diversity is inversely proportional to harshness of environmental conditions" (Golubic, 1976, p. 166). Densely woven mats of thick-sheathed *Siphonophycus* with few associated taxa characterise more restricted parts of tidal flats; these are comparable to the sheaths of oscillatorian cyanobacteria found frequently in exposed portions of other ancient (e.g. Knoll *et al.*, 1991; Oehler *et al.*, 1979) and modern

PLATE 7

Microfossils from the Lower Riphean (Lower Mesoproterozoic) Satka Formation, southern Ural Mountains. 

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| <p>1, 2. <i>Pterospermopsimorpha pileiformis</i> Timofeev, 1 - slide 6, p. 25, GINPC # 701; 2 - slide 878, p. 7, GINPC # 703.</p> <p>3. <i>Granomarginata</i> ? sp., slide 867, p. 14, GINPC # 709.</p> <p>4. <i>Leiosphaeridia atava</i> (Naumova), slide 1, p. 19, GINPC # 707.</p> <p>5, 6. <i>Leiosphaeridia crassa</i> (Naumova), 6 - slide 851, p. 12, GINPC # 706; 5 - slide 865, p. 21, GINPC # 705.</p> <p>7. <i>Siphonophycus kestron</i> Schopf, slide 865, p. 21, GINPC # 723.</p> <p>8. <i>Myxococcoides</i> sp., slide 2, p. 20, GINPC # 711.</p> | <p>9. <i>Eosynechococcus moorei</i> Hofmann, slide 125, p. 13, GINPC # 25.</p> <p>10. <i>Archaeoellipsoides major</i> (Golovenoc et Belova), slide 872, p. 17, GINPC # 719.</p> <p>11. <i>Gloeodiniopsis lamellosa</i> Schopf, slide 175, p. 1, GINPC # 15.</p> <p>12. <i>Palaeolyngbya catenata</i> Hermann, slide 337, p. 6, GINPC # 33.</p> |
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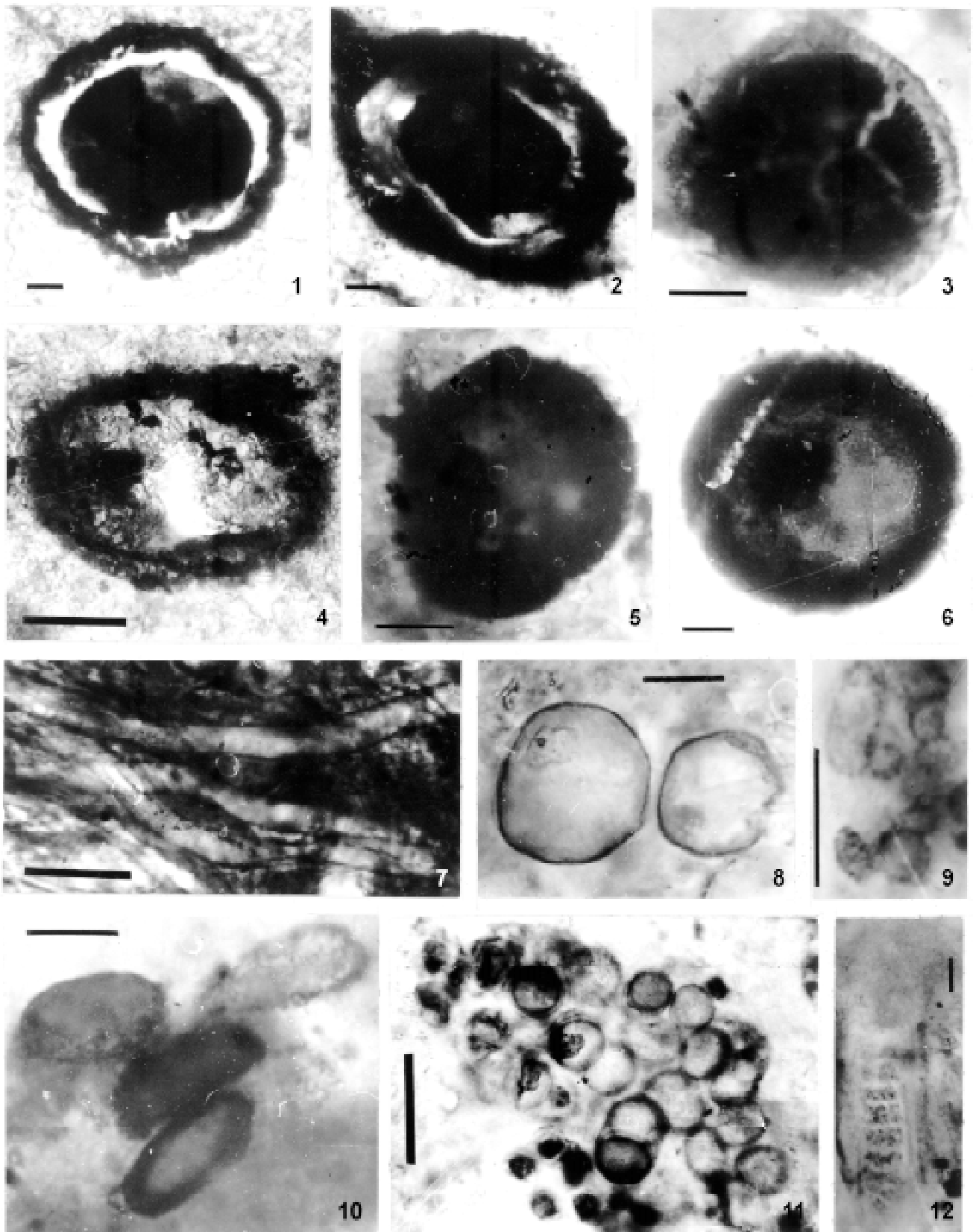


PLATE 7

tidal flats. In general, these communities of cyanobacteria inhabited the tidal flat or upper tidal flat environments where high evaporation could provide reasonable conditions for the growth of precipitate textures.

The precipitates of the Svetlyi Formation are composed of radial-fibrous texture where blades of fibrous crystals are 50.0-100.0 µm across and 800.0-2000.0 µm long. Laminae within these radial-fibrous textures are delineated by layers of (probably) finely dispersed dark organic matter distributed perpendicular to the direction of crystal growth. Laminae are discontinuous and broken by the crystals into separated chord-like segments. The upper surfaces of the fans are wavy- or flat-laminated or sometimes the significant deepening and elevations are observed. The precipitates of the Svetlyi Formation can be considered to be purely inorganic due to lack of any fossils inside or nearby these sedimentary structures.

The Revet microbiota

The Revet microbiota is dominated by *Gloeodiniopsis lamellosa*, which forms loose colonies containing many hundred of individuals (Pl. 10). The empty sheaths of *Siphonophycus robustum* form the low-density populations oriented roughly parallel to lamination whereas *Siphonophycus solidum* occurs as solitary individuals (Sergeev, 1992, 1994).

The Revet microbiota differs from most of the other Proterozoic silicified microbiotas of the shallow-water setting by dominance of *Gloeodiniopsis lamellosa* spheroids. But these forms are not mat-forming organisms as they occur in loose clusters and rather probably inhabited small ponds or puddles in shallow depressions of intertidal environments (Knoll & Golubic, 1979) or a series of nonmarine saline lakes and ponds on a coastal plain (Southgate, 1986). On the other hand, the mat-forming role of *Siphonophycus* spp. in the Revet microbiota is unclear. Whereas *Siphonophycus robustum* probably formed some mats of restricted distribution, the sheaths of *S. solidum* occur as single individuals and could be either remains of mat-forming communities or mat-dwellers.

The Revet microbiota like Svetlyi is characterised by very low diversity; however mat-forming sheaths of *Siphonophycus* is its minor components and non-mat forming chroococcacean cyanobacteria are abundant. Both the Revet and Svetlyi

microorganism communities probably occupied peritidal or non-marine environments of coastal planes. Any assignment of the Revet and Svetlyi microfossil assemblages to the Satka type microbiotas could be questioned because the phytoplanktic eukaryotic microorganisms are absent in these microbiotas. However, on one hand, entophysalidacean algae, short trichomes, akinetes of *Archaeoellipsoides* and some other microfossils typical for the Kotuikan type microfossil assemblages are absent in the Svetlyi Formation and the Revet Member of the Avzyan Formation, and, on the other hand, stalked cyanobacterium *Polybessurus bipartitus* known from the Kataskin type microbiotas is also not present. Therefore, we consider both Revet and Svetlyi microfossil assemblages to be closer to Satka type microbiotas.


The Kataskin type microbiotas

The Kataskin type microbiotas contain many microfossils typical for both Kotuikan and Satka-type microbiotas. Mat-forming entophysalidacean, oscillatoriacean and nostocalean as well as mat-dwelling and planktic chroococcacean cyanobacteria are widespread in the microbiotas of this type whereas abundant akinetes of *Archaeoellipsoides* and associated short trichomes are essentially absent. The remains of morphologically complex protista also occur here as well as in the relevant more deep-water facies. The most typical and characteristic feature of the Kataskin type microbiotas is presence of stalked cyanobacterium *Polybessurus bipartitus* of pleurocapsalean affinities which still has not been reported from the older deposits. Therefore, the taxonomical composition of the Kataskin-type microbiotas as we already said can be considered as the basis for separation of the uppermost part of Mesoproterozoic as an independent stratigraphical unit. However, this type of microbiotas interfingering with Satka-type, occur in the Middle Riphean (late Mesoproterozoic) section of southern Ural Mountains, the Kataskin Member of Avzyan Formation underlying the Revet Member. Distribution of the Kataskin type microbiotas is restricted to the latest Mesoproterozoic and there are a few relevant occurrences of these kinds of silicified microfossil assemblages.

The Kataskin microbiota

The microbiota found in the cherts of the Kataskin Member of the Avzyan Formation, southern Ural Mountains,

PLATE 8

Microfossils from the Middle Riphean (Late Mesoproterozoic) Sukhaya Tunguska Formation (1), Turukhansk Uplift, Siberia and the Lower Riphean (Lower Mesoproterozoic) Satka Formation (3) and the Middle Riphean (Upper Mesoproterozoic) Kataskin member of the Avzyan (2, 4-7) Formation, southern Ural Mountains. 

- | | |
|---|---|
| <p>1. <i>Eoentophysalis arcata</i> Mendelson and Schopf, slide 637, p. 39, GINPC # 516.</p> <p>2, 4. <i>Eogloeocapsa avzyanica</i> Sergeev, 2 - slide 425, O-38-2, p. 19, GINPC # 40; 4 - slide 425, p. 7, GINPC # 64.</p> <p>3. <i>Gloeodiniopsis lamellosa</i> Schopf, slide 130, p. 10, GINPC # 3.</p> | <p>5. <i>Eosphaeronostoc kataskinicum</i> Sergeev, slide 421, K-49-2C, p. 24, GINPC # 47.</p> <p>6, 7. <i>Polybessurus bipartitus</i> Fairchild ex Green and al., slide 421, 6 - J-50-4, p. 24", GINPC # 804; 7 - p. 11, GINPC # 805.</p> |
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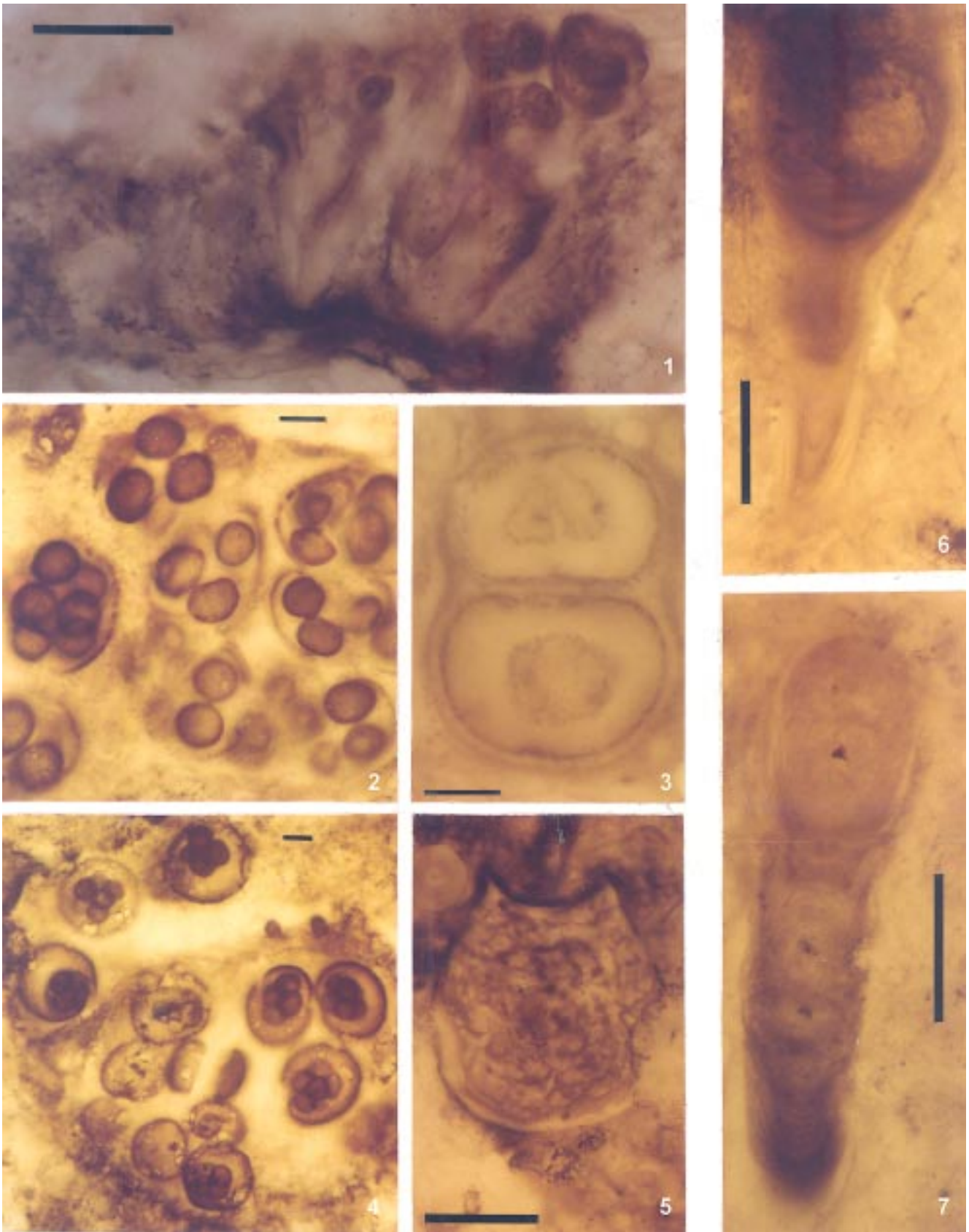


PLATE 8

is considered as one of its kind of Mesoproterozoic microfossil assemblages (Pls 8, 11). The Kataskin microbiota is dominated by *Eoentophysalis dismallakesensis* where spheroids form monospecific palmelloidal crusts in rare cases only and occur mainly in gloeocapsoidal colonies. The Kataskin cherts are dominated also by spheroidal unicellular microfossils *Eogloeocapsa avzyanica* - small colonies with dispersed spheroids set within a common envelope found as loose populations (envelope diameters range from 24.0 to 60.0 µm, spheroids - from 8.0 to 23.0 µm). *Siphonophycus robustum* sheaths, commonly gregarious and sinuously intertwined, are quite conspicuous in the Kataskin microbiota, but it is not so abundant as *E. dismallakesensis* and *E. avzyanica*. *S. robustum* mats contain chroococcacean unicells *Gloeodiniopsis lamellosa*, *Eosynechococcus amadeus*. Abundance of non-mat-forming cyanobacterium *Eogloeocapsa avzyanica* and gloeocapsoidal colonies of *Eoentophysalis dismallakesensis* in the Kataskin microbiota can be explained by at least locally high instantaneous rate of the sediment accumulation along the Kataskin peritidal environmental gradient (Sergeev, 1992, 1994; Sergeev & Seong-Joo, 2006; Sergeev, 2006a). Some colonies of *E. avzyanica* are very similar to those of *Eoentophysalis dismallakesensis* and one of us (Sergeev, 2006a) considered them as synonymous. However, some differences between above mentioned forms in morphology, size and distribution patterns are evident and therefore we rather prefer to differentiate these species.

The second species of genus *Eoentophysalis* - *E. belcherensis* - forms monospecific palmelloid colonies and their upper margins are marked by dark-brown pigments, leaving the central part light. Unlike the type and many other described Precambrian populations, the Kataskin fossils do not constitute dominant mat builders, but occur only as an isolated population in close association with *S. robustum*. The most typical microfossil in the Kataskin assemblage is *Polybessurus bipartitus* - a distinctive cylindrical fossil usually found as successively stacked, concave-upward envelopes 15.0-60.0 µm in diameter. *Polybessurus bipartitus* occurs as solitary individual and only in one lamina that contains practically all other taxa of the Kataskin microbiota.

The prokaryotic planktic forms in the Kataskin microbiota are represented by rare spherical envelopes *Eosphaeronostoc kataskinicum* (50-200 µm in diameter) containing tangled masses of empty sheath-like structures (3.0-5.0 µm in diameter)

and similar to colonies of modern nostocalean cyanobacterium *Sphaeronostoc*. Other planktic micro-organisms of genus *Leiosphaeridia* (*L. crassa*, *L. atava* and *L. jacutica*) - solitary, spherical structure from 30.0 to more than 200.0 µm in diameter - can turn out to be either empty envelopes of prokaryotic colonies or unicellular eukaryotic micro-organisms (cells). Some envelopes of *L. crassa* bear the problematic spine-like processes, but considering presence of pseudospines on the originally smooth surface of *Gloeodiniopsis lamellosa*, these forms were assigned to genus *Leiosphaeridia*.


The sedimentary precipitates also have been reported from the silicified microfossil-bearing strata (Sergeev & Seong-Joo, 2004; Sergeev, 2006a). These are microlaminated stratiform laminae comprising 2.0-5.0 µm thick and totally up to a few cm long layers and often are colonised by *Eoentophysalis dismallakesensis* filling up small depressions on their surface (chasmoendoliths sensu Golubic *et al.*, 1981).

The Sukhaya Tunguska microbiota

The Sukhaya Tunguska microbiota is quite close in its composition to the Kataskin one, but more diverse. The choice in favour of the Kataskin Formation as a name-bearer is mainly related to its localisation in the Riphean stratotype section, but the Sukhaya Tunguska microbiota was named typically for the Turukhansk Proterohorizon (Sergeev, 2006b). The Sukhaya Tunguska microbiota is dominated by entophysalidacean cyanobacteria *Eoentophysalis dismallakesensis* and mat-forming sheaths of *Siphonophycus robustum*, *S. typicum* and *S. solidum* (Pls 8, 12). Despite abundance *E. dismallakesensis* in the Sukhaya Tunguska, as in the Kataskin microbiota, it almost lacks attached palmelloid colonies. Such colonies occur only locally, but they show unidirectional, polarised growth and, therefore, the entophysalidacean affinities of this population can be demonstrated. Another species of genus *Eoentophysalis* - cf. *E. belcherensis* - is a rare component of the Sukhaya Tunguska microbiota occurring in loose clusters to densely packed, irregular, broadly globular colonies.

Polybessurus bipartitus is the most typical microfossil in the Sukhaya Tunguska as well as in the Kataskin assemblage. Sukhaya Tunguska specimens occur principally as isolated individuals within *S. robustum* mats; unlike *Polybessurus*

PLATE 9

Microfossils from the Middle Riphean (Upper Mesoproterozoic) Svetlyi Formation, Uchur-Maya region of Siberia. 

- 1, 2, 7. Sheaths of *Siphonophycus solidum* in colonies formed by sheaths of *S. robustum*, *S. typicum* and *S. kestron*, 1, 3 (indicated by an arrow in 1) - slide 837, p. 8, GINPC # 650; 7 - slide # 846, p. 4, GINPC # 651.
- 2, 5, 6. Sheaths of *Siphonophycus robustum* and *S. typicum*, slide 788, 2 - p. 9', GINPC # 654; 5 - p. 9, GINPC # 653; 6 - p. 9'', GINPC # 655.
4. *Palaeolyngbya catenata* Hermann, slide 788, p. 10, GINPC # 652.
- 8, 9. *Myxococcoides* sp., slide 803, 8 - p. 8, GINPC # 657; 9 - p. 5, GINPC # 656.

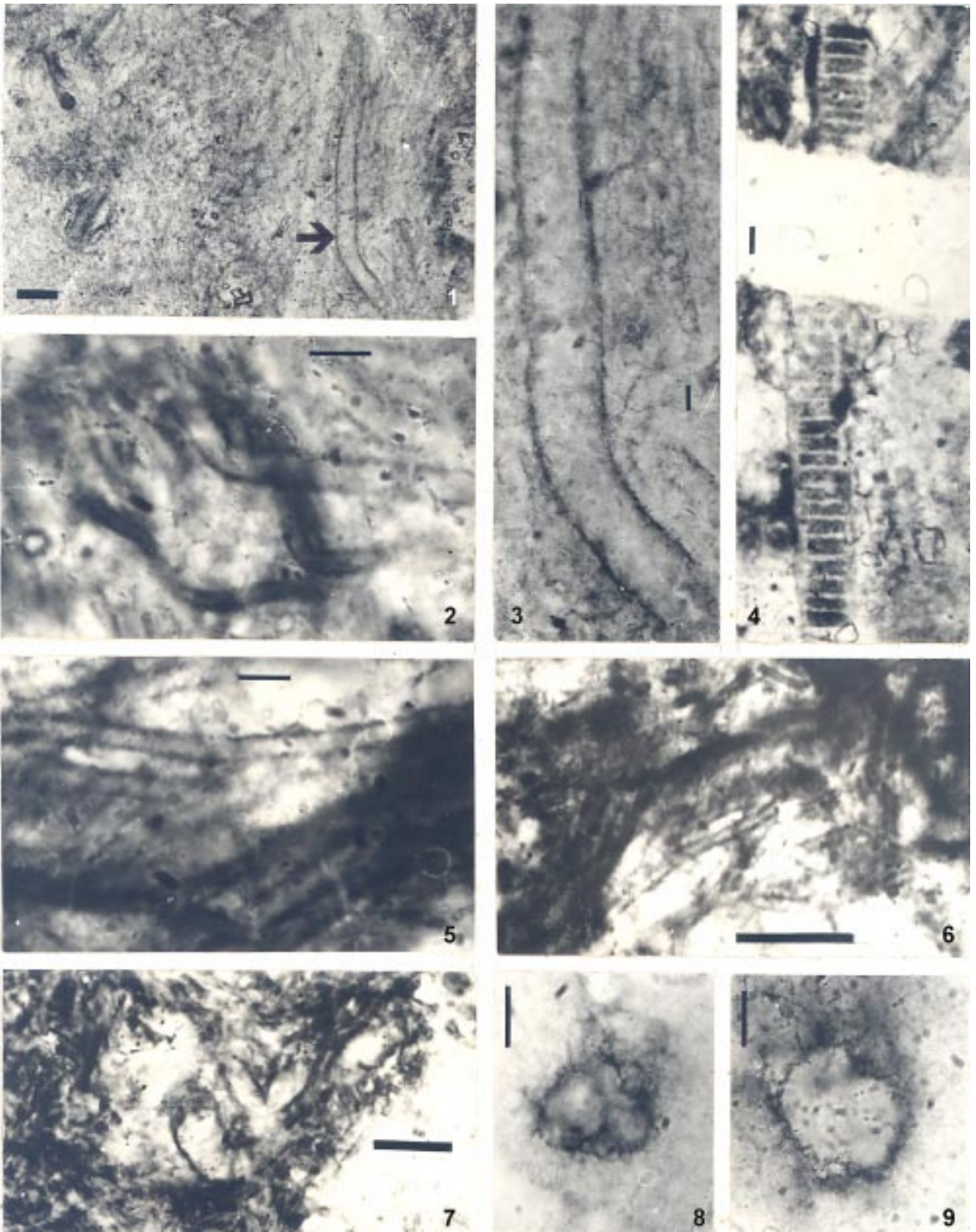


PLATE 9

populations in other assemblages, these have not been found as monospecific crusts.

Other chroococcacean cyanobacteria *Eoaphanocapsa oparinii*, *Gloeodiniopsis lamellosa*, *Eosynechococcus moorei*, *E. medius*, *Sphaerophycus medium* and *S. parvum* occur as loose colonies between filaments of *Siphonophycus robustum* or in close association with *Eoentophysalis*. Sheaths and trichomes of other hormogonian cyanobacteria (*Calyptothrix* sp., *Eomicrocoleus* sp., *Uluksanella* sp., *Oscillatoriaopsis media*, *Palaeolyngbya* sp.) constitute less than 1-2% of all individuals. *Circumvaginalis* sp. is confined to a single sample from a proximal peritidal setting (Petrov *et al.*, 1995). The planktic forms are represented by eukaryotic or prokaryotic (*Myxococcoides minor*, *M. inornatum*, *M. grandis*, *Myxococcoides* sp., and *Leiosphaeridia* sp.) as well as cyanobacterial remains (*Gyalosphaera golovenokii* and *Archaeoellipsoides dolichum*).

Gyalosphaera golovenokii is comparable to some genera of modern planktic chroococcacean cyanobacteria, in particular *Gomphosphaeridium* and *Coelosphaera*. *A. dolichum* is interpreted as the preserved akinete of nostocalean cyanobacteria, but this is a minor component of the Sukhaya Tunguska microbiota. *Myxococcoides minor*, *M. inornatum*, *M. grandis*, *Myxococcoides* sp., and *Leiosphaeridia* sp. are all simple spheroidal fossils that could be the preserved cells of protista, cyanobacterial cell walls, or the extracellular envelopes of coccoidal cyanobacteria.

A different association of microfossils occurs in the relevant open-shelf facies of the Lower Member of the Sukhaya Tunguska Formation where large (up to 320 µm in diameter) acritarchs cf. *Trachyhystrichosphaera* with poorly preserved processes are securely placed among the protista. Despite this, assemblage is of low-diversity composition, the presence of these problematic spiny acritarchs provides a reliable glimpse of eukaryotic phytoplankton in contemporaneous open shelf Mesoproterozoic environments and allows separating the Kataskin-type microbiotas from the older ones.

The Sukhaya Tunguska precipitates are represented by microlaminated stratiform laminae, consisting of individual laminae 2.0-3.0 to 5.0-7.0 µm thick. Individual laminae are of uniform thickness and traceable throughout their lengths; they are defined by concentration of organic matter, producing an alternating pattern of thin dark and thicker light laminae. Microfossils are not preserved in this texture, but the colonies of *Eoentophysalis dismallakesensis* are closely associated and sometimes demonstrate the unidirectional, polarised growth that could be an attempt to escape burial by growing

precipitates. Like all other described precipitates, *Eoentophysalis* did not build these laminates and does not occur within the stratiform laminae. It should also be noted, that the precipitates are not very common in the Sukhaya Tunguska Formation.

Other Mesoproterozoic microbiotas of the Kataskin type

The silicified microfossil assemblage, extremely similar to the Kataskin and Sukhaya Tunguska microbiotas, has been described from the Society Cliff and Victor Bay formations, Uluksan Group, Bylot Supergroup, Baffin Islands, Canada (Hofmann & Jackson, 1991; Kah & Knoll, 1996). Multiple lines of evidence including palaeomagnetic, radiometric, chemostratigraphic and biostratigraphic constrains suggest late Mesoproterozoic age of the Society Cliff sediments about 1200 Ma (Kah & Knoll, 1996; Kah, 2000; Kah *et al.*, 2001). The Uluksan Group microbiota is dominated by mat-forming entophysalidacean cyanobacteria *Eoentophysalis belcherensis*, sheaths of oscillatoriacean or nostocalean cyanobacteria of genus *Siphonophycus*—*S. septatum*, *S. robustum*, *S. typicum* and *S. kestron* (*Siphonophycus* species classification is given according to revision by Butterfield *et al.*, 1994) as well as polytrichomatous filaments of oscillatoriacean cyanobacteria *Eomicrocoleus crassus* (Butterfield, 2001) considering *E. crassus* as well as *S. kestron* described from the Uluksan Group by Hofmann and Jackson (1991) as the junior synonym of *Salome nunavutensis*—[see below] and *Uluksanella baffinensis*. The mats of these hormogonian cyanobacteria are associated with chroococcacean cyanobacteria of probably benthic setting—*Gloeodiniopsis lamellosa* (according to revision by Sergeev *et al.*, 1997), *G. micros*, *Eosynechococcus medius*, *E. grandis*, *Brachypleganon* sp., *Sphaerophycus parvum*, *S. medium*, *Palaeoanacystis* sp. and some others. Plausible planktic forms include rare akinetes of *Archaeoellipsoides major* (= *A. obesus*, see Sergeev *et al.*, 1995), two species of *Myxococcoides*—*M. minor* and *M. grandis*—and *Phanerosphaerops capitaneus* that could be either preserved cells or extracellular envelopes of protista or cyanobacteria. The remnants of problematic eukaryotic organisms include coccoidal and filamentous microfossils *Cymatiosphaera?* sp., *Eupoikilofusa?* sp. and a couple of unnamed forms.

Stalked cyanobacterium *Polybessurus bipartitus*—the diagnostic feature of all late Mesoproterozoic microbiotas of Kataskin type—is conspicuous in the cherts of the Uluksan Group. Hofmann and Jackson (1991) have described only one

PLATE 10

Microfossils from the Middle Riphean (Upper Mesoproterozoic) Revet Member of the Avzyan Formation, southern Ural Mountains. 

1, 3-8. *Gloeodiniopsis lamellosa* Schopf, 1 - slide 440, p. 4, GINPC # 237; 3 - slide 440, p. 4, GINPC # 238; 4 - slide 441, p. 6, GINPC # 89, 5 - slide 441, p. 7, GINPC # 91; 6 - slide 441, p.

6, GINPC # 90; 7 - slide 442, p. 1, GINPC # 89; 8 - slide 428, p. 7, GINPC # 87.
2. *Siphonophycus* sp., slide 442, p. 3, GINPC # 88.

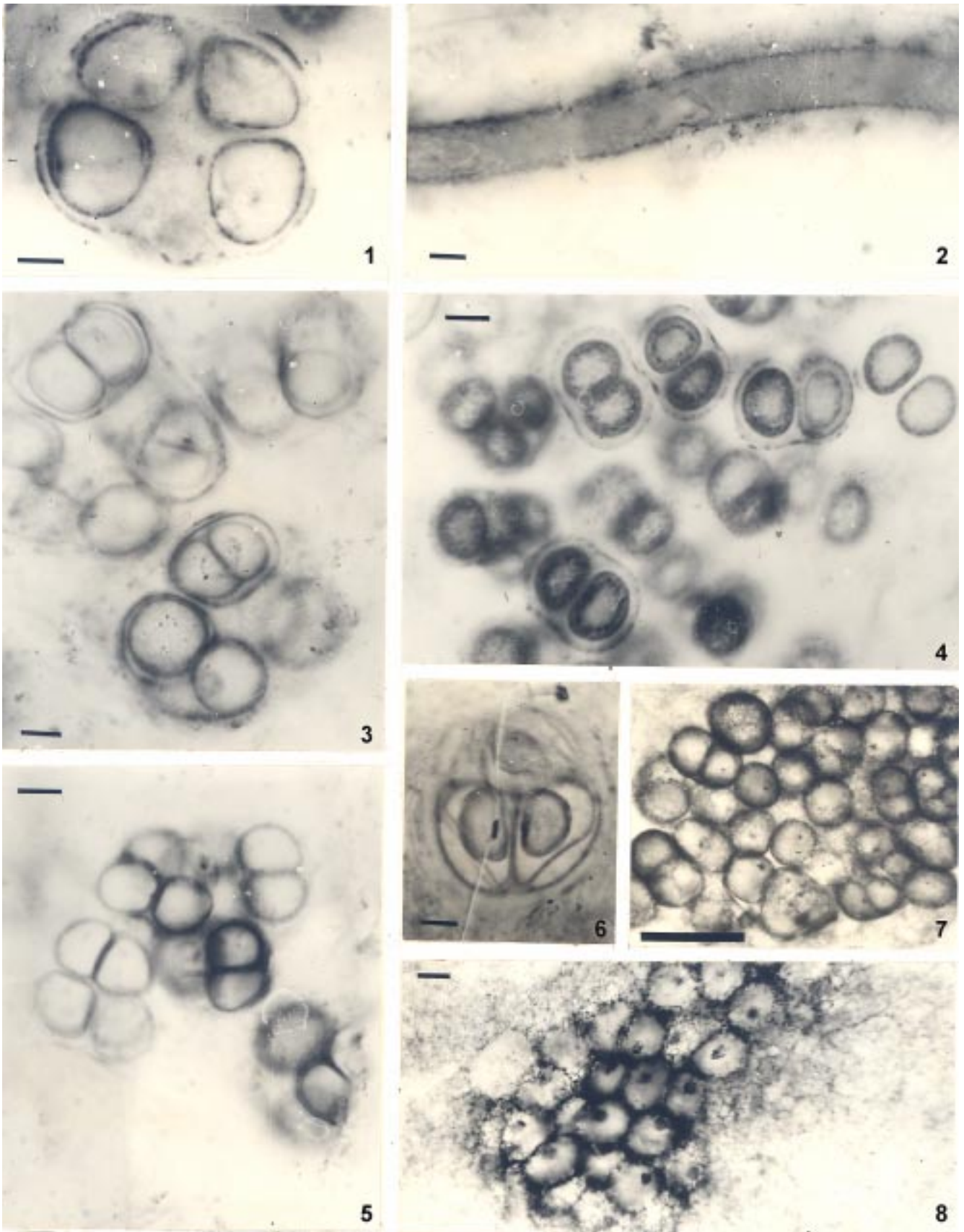


PLATE 10

good preserved specimen of this alga, but subsequently Kah and Knoll (1996) pointed out that *Polybessurus* is quite abundant in the *Siphonophycus-Eomicrocoleus* associations of the Society Cliff Formation

The precipitates are conspicuous among the Society Cliff Formation carbonates as well as other evaporitic lithologies (Kah *et al.*, 2001). The radial-fibrous fans are easily recognisable in cherts where they were named as laminated tufa microfacies (Kah, 2000; Kah & Knoll, 1996). Mats of *Eoentophysalis* colonised upper lithified surface of these radial-fibrous fans, whereas the *Polybessurus*-dominated communities are characteristic of micritic deposits on soft substrates. The major fossiliferous carbonate microfacies of the Society Cliff Formation (cement-and micrite-dominated) occur within a high intertidal to supratidal flats, but locally microfacies are distributed as interfingering mosaic, reflecting relatively small differences in seawater level (Kah & Knoll, 1996).

The silicified microfossil assemblage of the Hunting Formation, Arctic Canada, 1200 Ma years old also can be considered as the Kataskin-type microbiota. However, the similarity is based mainly on the presence of abundant stalked cyanobacterium *Polybessurus bipartitus* in the Hunting microbiota (Butterfield, 2001), whereas the entophysalidacean cyanobacteria are conspicuously absent in this formation. The Hunting cherts include diverse and abundant assemblage of chroococcacean cyanobacteria *Gloeodiniopsis lamellosa* (the following taxa described by N. J. Butterfield: *Gloeodiniopsis magna*? *Myxococcoides distola*, probably ? *Pterospermopsisimorpha* sp. and ? *Eoentophysalis* sp. are considered as the junior synonymies of this species), some spherical-*Bicamera stigmata*, *Gloeodiniopsis micros*, *Myxococcoides* cf. *grandis*, *M.* cf. *stragulens*, ?*Coniunctiophycus* sp., ?*Clonophycus* sp.-and filamentous microfossils-*Rugosoopsis tenuis* and *Salome nunavutensis*-are of problematic eukaryotic or prokaryotic affinities. The empty sheaths of *Siphonophycus robustum* and *S. typicum* form the mat-like colonies, but they are not the overwhelming elements of the microbiota. In many samples, *Siphonophycus* is entirely absent, and the assemblage instead is dominated by the stalk-forming cyanobacterium *Polybessurus bipartitus* and by abundant, vertically oriented filaments of the red alga *Bangiomorpha pubescens*.

Presence of the bangiophytic red alga *Bangiomorpha pubescens* is the most remarkable feature of the Hunting

microfossils assemblage (Butterfield, 2000). This filamentous microfossil has the undoubted affinity of eukaryotic bangiophytic red algae and its presence differentiate the Hunting microbiota from the older Mesoproterozoic and contemporaneous Kataskin-type microbiotas as well.


DISCUSSION

A careful analysis of a number of well-documented Mesoproterozoic assemblages studied by the authors from various regions as well as described elsewhere has been done. About fifteen years ago the Neoproterozoic fossil record contained more Lagerstätten than any other era. However, knowledge of Precambrian life is expanding rapidly and now the Mesoproterozoic fossil record documented so far is almost as good as that of the Neoproterozoic. New discoveries of various eukaryotic remains in the open-shelf environments revealed high diversity and complexity of nucleated organisms in the Mesoproterozoic ecosystems and questioned the time of 'big bang' of nucleated organisms diversification and 'Neoproterozoic revolution' (see Knoll, 1992, 1996; Sergeev *et al.*, 1996; Sergeev, 2006a). In the paper, the authors first concentrated on the remains of essentially prokaryotic communities from the peritidal environments and analysed why these communities differ from the older and younger microbiotas of the same and different facial setting. Besides, discussed the nature and stratigraphic distribution of various eukaryotic remains from both silicified and organic-walled microbiotas and tried to evaluate biostratigraphic and evolutionary importance of recently found Mesoproterozoic microfossils of complex morphology.

Biostratigraphic and evolutionary paradox of the Kotuikan type microfossil assemblages

The Kotuikan type assemblages document a geographically widespread biota dominated by cyanobacteria. No unequivocally recognisable eukaryotes have been demonstrated in these assemblages, but some morphological simple spherical fossils can be either remains of cyanobacteria or protista. Anyhow, morphologically complex acritarchs reported from the open-shelf facies are missing in the peritidal assemblages of Kotuikan type. Nonetheless, almost for fifteen years, the microbiotas of the Kotuikan type demonstrated well known evolutionary and biostratigraphic paradox (Sergeev *et*

PLATE 11

Microfossils from the Middle Riphean (Upper Mesoproterozoic) Kataskin Member of the Avzyan Formation, southern Ural Mountains. 

- | | |
|---|--|
| <p>1-3. <i>Eoentophysalis belcherensis</i> Hofmann, 1 - slide 424, p. 7, GINPC # 71; 2 - slide 421, p. 36, GINPC # 69; 3 - slide 432, p. 20, GINPC # 70.</p> <p>4, 5. <i>Eogloeocapsa avzyanica</i> Sergeev, slide 432, p. 22, GINPC # 67; slide 415, p. 4, GINPC # 60.</p> <p>6. <i>Gloeodiniopsis lamellosa</i> Schopf, slide 416, p. 10, GINPC # 72.</p> | <p>7. <i>Siphonophycus kestron</i> Schopf, slide 431, p. 8, GINPC # 54.</p> <p>8, 9. <i>Gloeodiniopsis lamellosa</i> Schopf with pseudospines, slide 421, p. 20, 8 - GINPC # 83; 9 - GINPC # 82.</p> <p>10. Cross-section of the stalked cyanobacterium <i>Polybessurus bipartitus</i> Fairchild ex. Green and al., slide 433, p. 7, GINPC # 78.</p> |
|---|--|

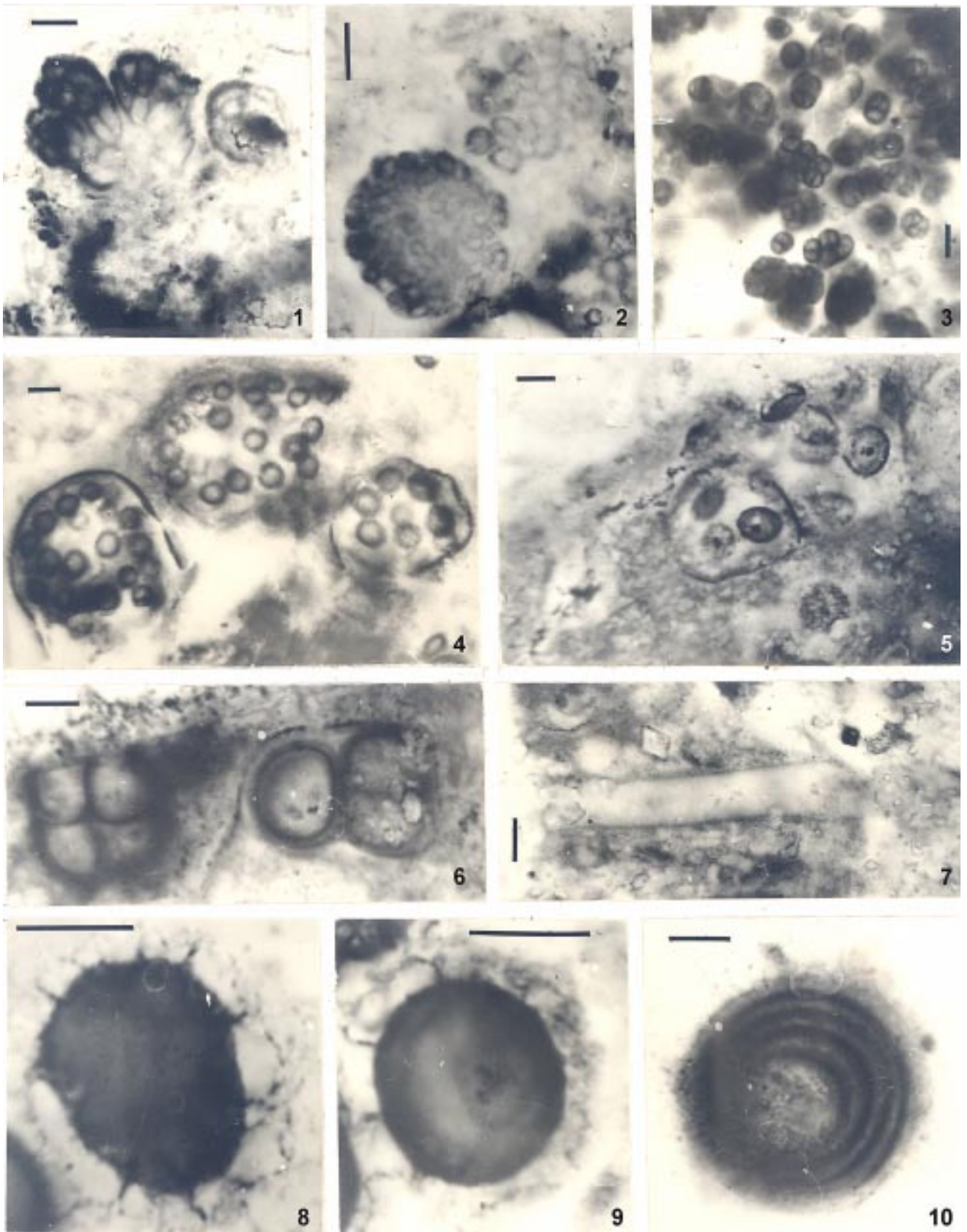


PLATE 11

al., 1994, 1995; Knoll & Sergeev, 1995; Sergeev, 1997, 2006a). These microbiotas are similar to each other, but differ in significant ways from Neoproterozoic as well as Palaeoproterozoic biotas. This difference can be related to either changes in the environments through the Proterozoic Era or evolution and expansion of eukaryotic microorganisms. Mesoproterozoic peritidal assemblages contain abundant and morphologically distinctive microfossils that find close counterparts in living cyanobacteria, but many of these forms are rare or absent in cherts from Neoproterozoic tidal flats. In part, Mesoproterozoic/Neoproterozoic differences in permineralized prokaryotes may be a further reflection of evolving eukaryotes as well as the changing substrates.

The dominance of the entophysalidacean cyanobacteria in the pre-Neoproterozoic microbiotas is clearly correlated to precipitate abundance in the same facies. Entophysalidacean cyanobacteria are widespread mat builders in recent intertidal environments (Golubic & Hofmann, 1976), but they have not been reported from the Neoproterozoic marine rocks, where *Eoentophysalis* occur as scattered colonies in assemblages dominated by other organisms (Knoll *et al.*, 1991; Sergeev, 1992, 2006a). Earlier it has been suggested (Knoll & Sergeev, 1995; Sergeev *et al.*, 1995, 1997; Kah & Knoll, 1996) that the distinctive nature of Palaeo- and Mesoproterozoic peritidal environments, with their widespread deposition of seafloor precipitates, may explain the near absence of *Eoentophysalis*-dominated assemblages in the Neoproterozoic successions. *Eoentophysalis* preferentially colonised the hard substrates and, therefore, clearly thrived in environments where the precipitates formed. When such precipitates ceased to form near the close of the Mesoproterozoic Era, *Eoentophysalis*-dominated assemblages disappeared along with them.

The abundance of akinetes of nostocalean cyanobacteria genus *Archaeoellipsoides* and associated assemblages of short trichomes is also correlated to widespread precipitates in the Mesoproterozoic rocks. Today eukaryotic algae dominate the freshened peritidal pools inferred to be the habitat of *Archaeoellipsoides*-producing cyanobacteria and it is reasonable to hypothesise that radiating Neoproterozoic eukaryotes displaced previously dominant nostocalean cyanobacteria. Of course, *Archaeoellipsoides* does occur locally in Neoproterozoic cherts such as Chichkan Formation of southern Kazakhstan (Sergeev, 1989, 1992, 2006a) or in some

Neoproterozoic shales, where the organic-walled ellipsoid forms were described as genus *Brevitrichoides* (Yankauskas *et al.*, 1989). Probably, high level of CaCO₃ supersaturation evident from the abundant precipitate structures triggered the full transformation of *Anabaena*-like filaments into chains of akinetes that additionally explain the abundance of the *Archaeoellipsoides* akinetes in the rocks of the Mesoproterozoic age (Sergeev *et al.* 1995, Fig. 14.1-14.3, and 14.16; Zhang 1985, Fig. 8.B; Horodyski & Donaldson 1980, Figs. 13.B, 13.E, 13.F). The dominance of *Myxococcoides grandis* in the Mesoproterozoic Kotuikan-type microbiotas also can be related to the precipitates abundance, especially considering their possible interpretation (at least, in part) as the spherical akinetes of nostocalean cyanobacteria.

Mesoproterozoic peritidal silicified microbiotas are clearly distinguishable from those in different facial Palaeoproterozoic setting. There are two kinds of the Palaeoproterozoic silicified microfossils assemblages – the Gunflint and Belcher types 2000-1600 Ma old (Hofmann & Schopf, 1983; Knoll, 1996; Sergeev, 1992). The Gunflint microbiota is dominated by remains of non-photosynthetic prokaryotic microorganisms of complex morphology (genera *Kakabekia*, *Eoastrion*, *Xenothrix*, *Archaeorestis* and *Eoastrion*) as well as filamentous (genera *Gunflintia* and *Animikia*) and coccoidal (genera *Huroniospora*, *Galaxiopsis*, *Leptoteichos* and *Corumbococcus*), morphologically simple microfossils of cyanobacterial, bacterial or even eukaryotic (genera *Eosphaera* and *Eomicrhystridium*) affinities and of benthic or planktic habit (Barghoorn & Tyler, 1965; Awramik & Barghoorn, 1977; Lanier, 1989). Silicified microfossil assemblages very similar to the Gunflint microbiota are known from 5-6 iron formations and subtidal carbonates of Palaeoproterozoic age from northern America, Asia and Australia (Hofmann & Schopf, 1983; Knoll *et al.*, 1988; Knoll, 1996).

The microbiota in silicified tidal-flat carbonates of the contemporaneous McLeary and Kasegalik formations of the Belcher Supergroup, Canada, differs entirely from the Gunflint-type microbiotas. The Belcher microbiota is dominated by entophysalidacean alga *Eoentophysalis belcherensis* and associated chroococcacean cyanobacteria genera *Gloeodiniopsis*, *Sphaerophycus*, *Tetraphycus* and some

PLATE 12

Microfossils from the Middle Riphean (Upper Mesoproterozoic) Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia. →

- | | |
|---|---|
| 1. <i>Eoaphanocapsa oparinii</i> Nyberg and Schopf, slide 518, p. 33, GINPC # 517. | 5. <i>Sphaerophycus parvum</i> Schopf, slide 518, p.25, GINPC # 525. |
| 2. <i>Eoentophysalis arcata</i> Mendelson and Schopf, slide 648, p. 3, GINPC # 518. | 6. <i>Coniunctiophycus conglobatum</i> Zhang, slide 648, p.6, GINPC # 532. |
| 3. <i>Siphonophycus typicum</i> (Hermann), slide 541, p. 7, GINPC # 536. | 7. <i>Circumvaginalis</i> sp., slide 617, p. 7, GINPC # 537. |
| 4. <i>Gyalosphaera golovenokii</i> Sergeev and Knoll, slide 613, p.5, GINPC # 503. | 8. <i>Gloeodiniopsis lamellosa</i> Schopf, slide 635, p. 47, GINPC # 506. |
| | 9. <i>Polybessurus bipartitus</i> Fairchild ex. Green and al., slide # 531, p.1, GINPC # 554. |

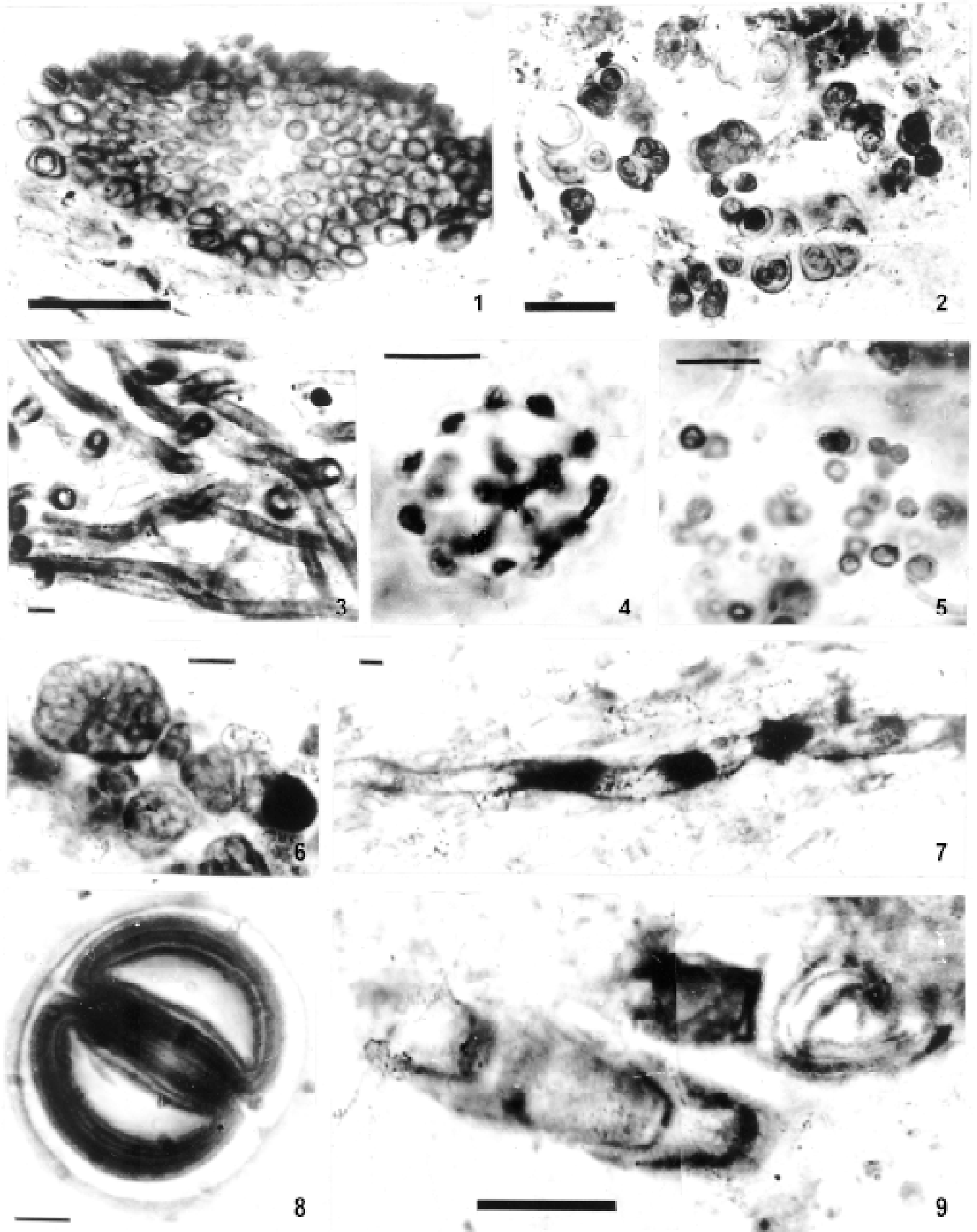


PLATE 12

others (The authors provide composition of this microfossil assemblage according to modern approach to the classification of fossil cyanobacteria) whereas the sheaths of *Siphonophycus robustum* is a subordinate element of the assemblage (Hofmann, 1976). The Belcher-type microbiotas are known from numerous Palaeoproterozoic formations of northern America (Hofmann & Grotzinger, 1985) and Australia (Muir, 1976; Oehler, 1978; Hofmann & Schopf, 1983) and in general similar to the Mesoproterozoic assemblages of Kotuikan type. The precipitates are widespread and abundant in the Palaeoproterozoic carbonate formations (Grotzinger, 1986, 1989, 1993; Grotzinger & Reed, 1983; Grotzinger & Kasting, 1993) that easily explain the abundance of entophysalidacean cyanobacteria in the same rocks. However, the most striking difference between the Palaeo- and Mesoproterozoic peritidal microbiotas is the absence of *Archaeoellipsoides*-dominated assemblages and associated short trichomes, where as only a few ellipsoidal akinetes were described from the Epworth Group (as genus *Brevitrichoides*) of northern Canada (Hofmann & Grotzinger, 1985) and from the Franceville Group of Gabon (Amrad & Bertrand-Sarfati, 1997).

All main types of cyanobacteria are already known from the assemblages of Belcher type (Knoll, 1996; Schopf, 1992). In molecular phylogeny, based on the sequence comparison of 16S rRNA's, the Nostocales and Stigonematales form the shallowest branch of the cyanobacterial tree (Giovannoni *et al.*, 1988; Wilmotte & Golubic, 1991). Therefore, it is possible, that the relatively late appearance of the group in the fossil record reflects the timing of its evolutionary origin. However, considering the presence of a few akinetes in the Palaeoproterozoic rocks, we are rather inclined to explain the virtual absence of the *Archaeoellipsoides*-dominated microfossils assemblages in the Palaeoproterozoic deposits by much worse sampling. At present the Palaeoproterozoic microbiotas are less studied than their Meso- and Neoproterozoic counterparts (exception the Gunflint Iron Formation) and one can expect the *Archaeoellipsoides*-dominated communities to be found in silicified peritidal carbonates older than 1.6 Ga. It should also be noted that not all peritidal Mesoproterozoic silicified assemblages of the Kotuikan type are dominated by akinetes of *Archaeoellipsoides*.

Grouping in the Satka type microbiotas

The Satka type microbiotas in fact contain 2 different groups of microfossils: first, the remains of widespread cyanobacteria; and, second, the phytoplanktic eukaryotic micro-organisms known only from the type locality, southern Ural Mountains, and the contemporaneous organic-walled microfossil assemblages.

Acritarchs from the Satka type microbiotas

The Satka microbiota in its type locality contains the phytoplanktic organisms-undoubtedly remains of eukaryotic microorganisms that are similar to the organic-walled microfossils known in coeval shelf shales. Indeed, the acritarchs currently found in the Satka cherts (Sergeev & Seong-Joo, 2004) are very similar to those previously described from the shales of the Satka and Baikal formations of the southern Ural Mountains (Veis *et al.*, 1990; Yankauskas, 1982). All these microfossil assemblages contain morphologically simple and not so very large envelopes (the biggest *Leiosphaeridia atava* from the cherts of Satka Formation is 130 µm in diameter) with robust wall and sometimes with large cyst-like bodies inside (genus *Pterospermopsis*). But the robust-wall *Chuarina*-like acritarchs larger than 500 µm in diameter and morphologically complex acanthomorphic acritarchs are conspicuously absent in this kind of microbiotas. From the shales of the Satka Formation Yankauskas (1982) has described small (less than 20 µm in diameter) spherical acritarchs with tiny spines as *Micrhystridium* sp. However, considering the relevant finds of *Gloeodiniopsis*-like microfossils with secondary spines on their originally smooth walls in the cherts of the Avzyan Formation (Sergeev, 1992, 1994, 2006a), the small spine-like structures on the surface of Satka fossils are considered to be of secondary origin.

The organic-walled microbiotas of another kind are known from the open-shelf facies of the Ust'-Il'ya and the Lower Member of the Kotuikan formations of the Anabar Uplift and from the Kaltasa Group of Cis-Ural (Petrov & Veis, 1995; Veis & Vorobyeva, 1992; Veis *et al.*, 1998; 2000). These biotas, besides the simple and relatively small filamentous and coccoidal microfossil *Leiosphaeridia*, *Ostiana*, *Sphaerocongregus*, *Siphonophycus*, *Rectia* and akinetes *Brevitrichoides* (= *Archaeoellipsoides*), contain large, up to 1 millimeter in diameter *Chuarina*, branching *Ulophyton*-like filaments and some other forms. However, remains of acanthomorphic and other morphologically complex acritarchs with spines and processes are absent in these microfossil assemblages. The similar kind of organic-walled microbiotas are known from the late Mesoproterozoic deposits worldwide: the Totta Formation of the Uchur-Maya Region (Veis, 1988); the Tulmen Member of the Avzyan Formation, southern Ural Mountains (Veis *et al.*, 1990); the Adams, Arctic Bay, Society Cliff, Victor Bay and some other formations of the Bylot Supergroup, Arctic Canada (Hofmann & Jackson, 1994); the Dundas and Narssârssuk formations/groups of the Thule Group/Supergroup, Greenland (Samuelsson *et al.*, 1999); and the Agu Bay Formation of the Fury and Hecla Høek Group, Greenland (Butterfield & Chandler, 1992). Considering the latest dating on the Uchur-Maya Region (Khudoley *et al.*, 2001), the difference in age between the Totta and Ust'-Il'ya-Kotuikan microbiotas are not so significant as it was supposed about 10 years ago.

A very special kind of the organic-walled microbiotas has been recently reported from the Mesoproterozoic open-shelf deposits of the Ruyang Group of China (Xiao *et al.*, 1997) and the Roper Group of Australia (Javaux *et al.*, 2001, 2003, 2004). Besides the large filaments, *Chuar*-like spheroids up to 500 µm in diameter (Peat *et al.*, 1978) and acritarchs genera *Valeria*, *Dictiosphaera* and *Satka* (Javaux *et al.*, 2001, 2003, 2004), these microfossils assemblages contain morphologically complex acritarchs with true spines and processes of genera *Shuiyousphaeridium*, *Tappania* and some others (Javaux *et al.*, 2001; Xiao *et al.* 1997; Yan & Zhu 1992). The Roper Group has a reliably U-Pb age almost exactly 1500 Ma (Jackson *et al.*, 1999) while the Ruyang Group was dated long ago and is roughly estimated to be older than 1000 Ma (Xiao *et al.*, 1997). Report of acanthomorphic acritarchs in the Mesoproterozoic rocks are sharply contradictory to the existing dogmatic statements about the absence of spiny microfossils in pre-Neoproterozoic deposits for more than 20 years (Butterfield *et al.*, 1994; Knoll, 1984, 1992, 1996; Schopf, 1977, 1992; Sergeev, 1992, Sergeev *et al.*, 1996). Of course, these Mesoproterozoic acanthomorphic acritarchs are taxonomically different from those known from the Neoproterozoic rocks where spinate forms of the genus *Trachyhystrichosphaera* are dominant (Butterfield *et al.*, 1994; Knoll, 1994, 1996; Sergeev, 1992, 1999, 2001). Nonetheless, any spiny pre-Neoproterozoic microfossils have not been reported from the most complete and well-studied organic-walled microfossil successions of southern Ural Mountains and Siberia. To explain this apparent paradox, Javaux *et al.* (2001) have suggested that the Uralian and Siberian organic-walled microfossils assemblages, even of the open marine setting, came from the inner shelf whereas the Roper Group phytoplanktic community inhabited the far distance outer shelf environments. However, the current studies of acritarch from the deep-water facies of Kotuikan and Ust'-Il'ya formations did not yield any remains of morphologically complex eukaryotic micro-organisms, and only *Chuar*- and *Leiosphaeridia*-like smooth-wall envelopes occur (Sergeev *et al.*, 2007). Additional detailed investigations are apparently necessary to clarify the precise level of the spiny microfossils appearance in the fossil record.

Cyanobacteria from the Satka-type microfossil assemblages and the Neoproterozoic microbiotas

Finally, returning to the Satka type microbiotas, let's analyse the distribution and varieties among the group of morphologically simple filamentous and coccoidal microfossils, supposedly cyanobacterial remains. Besides the type locality, the remains of mat building filamentous and nested inside coccoid forms occur in the Svetlyi Formation and the Revet Member of the Avzyan Formation. But taxonomic diversity of the Svetlyi microbiota reduced to the sheaths of *Siphonophycus*, whereas in the Revet Member only the

chroococcacean cyanobacteria are dominated. Co-occurrence of benthic cyanobacterial mats and eukaryotic phytoplanktic forms in the type locality of the Satka microbiota possibly is explained by its shallow-water upper subtidal setting or by frequently changing of upper subtidal and lower intertidal environments.

The dark-brown colour of some *Siphonophycus* sheaths from the Satka Formation, comparable to the scytonemin pigment, produced by modern cyanobacteria in response to direct sun radiation, can indicate to the subaerial exposure. The sharp reduction in diversity of cyanobacterial communities and lack of planktic forms in the Svetlyi and Revet microbiotas suggest their occurrence in very harsh environments, probably on the broad tidal flats.

However, the cyanobacterial components of Satka-type microbiotas are very similar to the Neoproterozoic silicified microfossil assemblages of the peritidal setting. Almost identical to the Satka microbiota, assemblages of filamentous and coccoidal forms have been reported from the Neoproterozoic Min'yar Formation of the Upper Riphean type section, southern Ural Mountains (Nyberg & Schopf, 1984; Sergeev & Krylov, 1986; Sergeev, 1992, 2006a), from the Allamoore Formation of Texas (Nyberg & Schopf, 1981), from the Burovaya Formation of the Turukhansk Uplift (Sergeev, 1999, 2001), from the Gillen Member of the Bitter Springs Formation, Australia (Knoll & Golubic, 1979; Schopf, 1968), from the Draken Conglomerate Formation, Spitsbergen (Knoll, 1982; Knoll *et al.*, 1991), and from many others. Some Neoproterozoic formations, e.g. the Draken Conglomerate Formation, besides remains of cyanobacterial communities, contain phytoplanktic morphologically complex forms that in general resemble the relationship of the benthic and planktic micro-organisms in the Satka microbiota. Of course, the silicified acritarchs reported from the Neoproterozoic microbiotas are taxonomically different from the phytoplanktic micro-organisms of the Satka Formation.

The Kataskin type microbiotas and stalked cyanobacterium problem

The microfossil assemblages of Kataskin type contain a mixture of taxa and their composition is intermediate between the Meso- and Neoproterozoic microbiotas of peritidal setting as well as between different kinds of Mesoproterozoic assemblages. On one hand, such 'typically' pre-Neoproterozoic fossils as entophysalidacean algae dominate almost all Kataskin type microbiotas. But, on the other hand, mat-forming oscillatoriacean or nostocacean cyanobacteria genus *Siphonophycus* are also abundant and contain remains of chroococcacean algae genera *Eoaphanocapsa*, *Gloeodiniopsis*, *Eosynechococcus* and *Sphaerophycus*. The dominance of the hormogonion cyanobacterial mats nesting inside coccoidal dwellers is rather typical for the microbiotas of Satka type and their Neoproterozoic counterparts. The

akinetes of nostocalean cyanobacteria is a minor component and short trichomes are conspicuously absent in the Kataskin type microbiotas. The planktic forms are represented by eukaryotic or prokaryotic genera *Myxococcoides*, *Leiosphaeridia* and *Gyalosphaera* of simple spherical morphology. The silicified microfossil assemblage from the lower part of the Sukhaya Tunguska Formation contains the phytoplanktic eukaryotic forms with evident, but not very well preserved spines, and these eukaryotic microorganisms from the open shelf environments essentially differentiate the Kataskin-type microbiotas from the older microfossil assemblages.

Another diagnostic feature of all these Kataskin-type microbiotas is a presence of the pleurocapsalean stalked cyanobacterium *Polybessurus bipartitus*. This fossil apparently was absent in the assemblages older than 1200 Ma possibly due to evolutionary innovations or secular changes in taphonomic or ecological conditions. Kah and Knoll (1996) have suggested that distribution of entophysalidacean and stalked cyanobacteria in the Proterozoic silicified microbiotas was related to the Neoproterozoic precipitates decline and, therefore, environmental evolution in Precambrian. While the entophysalidacean cyanobacteria preferentially colonise the hard substrates, the stalked cyanobacteria prefer soft substrates. Therefore, after almost complete extinction of precipitates in the Neoproterozoic fossil record, entophysalidacean cyanobacteria abundant in pre-Neoproterozoic microbiotas apparently declined, but *Polybessurus* became widespread, colonising preferentially the soft ground. However, if *Polybessurus* distribution is purely controlled by substrate, one could expect the presence of stalked cyanobacteria in early Mesoproterozoic and Palaeoproterozoic rocks. Pending the discovery of relevant finds Kah and Knoll (1996) hypothesis can not be unequivocally accepted.

Alternatively, Sergeev (1997) has explained this phenomenon by cyanobacterial evolution and 'hidden' expansion of morphologically simple unicellular eukaryotes in cyanobacterial communities. Possibly, drastic changes in dominating substrates near the Meso-Neoproterozoic boundary triggered the evolution of some forms of cyanobacteria, e.g. stalked cyanobacteria. Despite evolutionary conservatism of cyanobacteria, some evolutionary changes could be observed during their Proterozoic palaeontological record. The oldest finds of the spiral cyanobacterium genus *Obruchevella* (fossil counterpart of modern alga *Spirulina*, Pl. 3.5) are reported only from the basal Neoproterozoic deposits (Belova & Golovenok, 1999; Sergeev, 1992; Schenfil, 1983), demonstrating then significantly increasing in size during late Neoproterozoic (Golovenok & Belova, 1994; Sergeev, 1992). Recently, *Obruchevella parva* has been reported from the Salkhan Limestone Formation of the Son Valley Area, India (Rai & Singh, 2004), which is

considered to be early Mesoproterozoic about 1600 Ma old. However, before accepting it to be unambiguous record, the only find of *Obruchevella* should be tested carefully and until replicated by others from the same horizons. Appearance of the spiral cyanobacteria in the Neoproterozoic can be explained from the data of molecular biology, because genus *Spirulina* is one of the two morphologically complex cyanobacterial taxa, whose systematic position based on morphology does not coincide with sequences of the 16S ribosomal RNA (Wilmutte & Golubic, 1991). Unfortunately, the modern counterparts of the *Polybessurus* have not been studied by modern method of 16S rRNA's comparison, probably due to problems to grow this alga in laboratory environments.

Another explanation of the late appearance of *Polybessurus bipartitus* in fossil record may be related to its nature. Broadly accepted interpretation of this microfossil as a stalked cyanobacterium is based mainly on the paper by Green *et al.* (1987). In this publication, the authors brilliantly showed the morphological similarity between the Greenland *Polybessurus bipartitus* fossil population and modern still undescribed *Cyanostylylion*-like cyanobacterium from the Bahama Islands. However, they did not show differences in gross morphology between *Cyanostylylion*-like cyanobacterium and other stalked forming eukaryotic algae, e.g. red alga *Rufusiella*. Therefore, we still cannot completely rule out an opportunity that this late Mesoproterozoic–Neoproterozoic stalked-forming microorganism is not a cyanobacterium, but a eukaryotic alga. At least, in the Hunting Formation the stalks of *Polybessurus* are closely associated by filaments of red alga *Bangiomorpha pubescens* (Butterfield, 2000, 2001) that can be considered as indirect evidence in favour of its interpretation as eukaryotic alga. Whatever may be the solution of the problem, the presence of this stalked microfossil in the microbiotas of Kataskin type marks one of the most easily recognisable benchmarks in the Proterozoic microfossil record. Nonetheless, we should not forget that this fossil distribution is restricted vertically as well as laterally and in the type section of the southern Ural Mountains the Kataskin Member is overlain by the Revet Member containing the microbiota of the Satka type, where *Polybessurus bipartitus* as well as acanthomorphic acritarchs are missing.

CONCLUSIONS

1. There are at least three different kinds of the Mesoproterozoic microbiotas – Kotuikan, Satka, and Kataskin that differ from each other as well as from most Palaeo- and Neoproterozoic microbiotas of various facies.

2. The Mesoproterozoic microbiotas of peritidal setting are dominated by and may be composed exclusively of prokaryotic microorganisms. Morphologically complex undoubted remains of eukaryotic microorganisms are absent in these microbiotas.

3. Nonetheless, the Mesoproterozoic prokaryote-dominated microbiotas of Kotuikan type demonstrate evident biostratigraphic and evolutionary paradox. Most taxa from these microbiotas have counterparts among different groups of modern cyanobacteria, however, as a whole, these silicified microfossil assemblages differ from those of same facies in the Palaeo- and Neoproterozoic. This phenomenon can be related to the environmental evolution and probably the 'hidden' expansion of the lowest morphologically simple eukaryotes in prokaryotic ecosystems.

4. The assemblages of morphologically simple filamentous and coccoidal microorganisms known from the Mesoproterozoic microbiotas of Satka type in many features are indistinguishable from the silicified Neoproterozoic assemblages which inhabited extremely shallow-water environments.

5. The eukaryotic organisms known in the Mesoproterozoic microbiotas of Satka type from subtidal cherts are similar to most contemporaneous organic-walled microfossil assemblages of the same facies. However, these microbiotas do not contain any morphologically complex acanthomorphic acritarchs.

6. The late Mesoproterozoic microbiotas of Kataskin type demonstrate broad variety of different microfossils and evolutionary changes among prokaryotic and eukaryotic microorganisms, emergence of stalked cyanobacteria, and presence of morphologically complex eukaryotic microorganisms in contemporaneous open-shelf facies. These new evolved eukaryotic and prokaryotic microorganisms differentiate the Kataskin-type microbiotas from the older microfossil assemblages and allow separation of terminal part of Mesoproterozoic as an independent stratigraphic unit.

7. In general, the analysed microbiotas have made significant improvement in our knowledge of Proterozoic fossil record and revealed complexity and variety of Mesoproterozoic life comparable to Neoproterozoic microorganism's diversity.

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