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PALEOBIOLOGY OF THE NEOPROTEROZOIC (UPPER RIPHEAN) SHORIKHA AND BUROVAYA SILICIFIED MICROBIOTAS, TURUKHANSK UPLIFT, SIBERIA

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ABSTRACT—Diverse assemblages of silicified microfossils have been detected in lenses of black chert within peritidal carbonates of the Neoproterozoic (Upper Riphean) Shorikha and Burovaya formations, Turukhansk Uplift, northeastern Siberia. These microbiotas are represented by 19 species of simple filamentous and coccoidal microfossils, multicellular trichomes, and thick-enveloped sphaeromorphic and acanthomorphic acritarchs. Microfossils include both prokaryotic (possibly cyanobacterial) and eukaryotic (mainly phytoplanktonic) microorganisms. The eukaryotes in these formations are relatively diverse—the result of an explosive radiation near the Meso-Neoproterozoic boundary. The discovery of abundant phytoplanktonic microorganisms in the Shorikha and Burovaya cherts increases the biostratigraphical potential of Proterozoic silicified microbiotas and fills a gap in the paleontological record of the Turukhansk Uplift, a potential candidate for the stratotype of the Meso-Neoproterozoic boundary. The affinities of the formally described taxa are postulated as follows: Oscillatoriaceae: *Eomicrocoleus crassus* Horodyski and Donaldson, 1980; *Oscillatoriopsis obtusa* Schopf and Blacic, 1971; *O. media* Mendelson and Schopf, 1982; Oscillatoriaceae or Nostocaceae: *Siphonophycus robustum* (Schopf, 1968); *S. typicum* (Hermann, 1974); *S. solidum* (Golub, 1979); Nostocaceae or Stigonemataceae: *Archaeoellipsoides minor* (Golovenoc and Belova, 1984); Chroococcaceae: *Gloeodiniopsis lamellosa* Schopf, 1968, *Eosynechococcus grandis* Hofmann, 1976; Incertae sedis: *Scissilisphaera gradata* Green, Knoll and Swett, 1989; *Myxococcoides minor* Schopf, 1968; *M. inornata* Schopf, 1968; *M. stragulescens* Green, Knoll, and Swett, 1989; *Myxococcoides* sp.; *Pterospermopsimorpha?* sp.; *Shorikhosphaeridium knolli* new genus and species; *Leiosphaeridia jacutica* (Timofeev); problematic ellipsoidal forms; and problematic spiny forms.

INTRODUCTION

IN RECENT YEARS the Meso-Neoproterozoic boundary has become a principal focus of research in Precambrian paleobiology because of growing evidence for substantial changes in the organic world during this interval. The primary biological event of the Meso-Neoproterozoic (Middle-Late Riphean) transition was an explosive diversification of eukaryotic microorganisms, including the appearance of morphologically complex microfossils such as acanthomorphic acritarchs, branching filaments of green algae, vase-shaped protists, and thalli of bangiophyte red algae (Yankauskas et al., 1989; Butterfield et al., 1990, 1994; Knoll, 1992a, 1996; Sergeev, 1992; Knoll and Sergeev, 1995). This radiation of eukaryotes, named the “Neoproterozoic revolution” by G. A. Zavarzin (Institute of Microbiology of RAS) (see Sergeev et al., 1996), had important evolutionary and biostratigraphic consequences; the eukaryotes started to replace the morphologically simple and evolutionarily conservative prokaryotes, among other things, providing a reliable tool for biostratigraphy.

The Meso-Neoproterozoic boundary is defined geochronometrically at 1000 Ma (Plumb, 1991), but the application of this definition to a sedimentary succession remains problematic. First, the biological transition was not instantaneous; some latest Mesoproterozoic microbiotas contain remnants of microorganisms that are rather typical for Neoproterozoic deposits, such as red algae in the Hunting Formation of Canada, and spiny acritarchs in the Sukhaya Tunguska Formation, Siberia (Sergeev et al., 1997) and the Ruyang Group of China (Yan and Liu, 1992; Xiao et al., 1997). These finds suggest that the “big bang” of eukaryotes did not occur exactly at 1000 Ma, but possibly closer to 1200 Ma. Second, the composition of Neoproterozoic cyanobacterial assemblages differs from that of earlier assemblages despite evolutionary conservatism of these microorganisms as a group. At least two morphological types of cyanobacteria have been reported only from Neoproterozoic or latest Mesoproterozoic rocks: the cylindrical spirals of *Obruchevella* and the stalked cyanobacterium *Polybessurus*. More generally, the composition of the conservative microbial communities from peritidal environments changes across this interval, possibly due at least in

part to the “hidden” expansion of morphologically simple eukaryotic microorganisms (Sergeev, 1997b). However, such fossilized unicellular eukaryotes at the present level of knowledge are indistinguishable from prokaryotes and, therefore, this suggestion is supported mainly by indirect evidence, e.g., by a decline of entophysalidacean and nostocalean akinete-producing cyanobacteria in Neoproterozoic silicified microbiotas of peritidal settings (Knoll and Sergeev, 1995; Sergeev et al., 1995; Sergeev, 1997a, 1997b).

The successful resolution of these problems requires that Meso-Neoproterozoic boundary successions containing diverse and representative microfossils be investigated in detail. One of the best candidates for this research is the Meso-Neoproterozoic succession of the Turukhansk Uplift, northeastern Siberia. The Turukhansk succession contains diverse and well-preserved assemblages of organic-walled and silicified microfossils (Timofeev et al., 1976; Yankauskas et al., 1989; Hermann, 1990; Veis and Petrov, 1994a, 1994b; Petrov and Veis, 1995; Sergeev et al., 1997; Veis et al., 1998), which document paleontological changes across the Meso-Neoproterozoic boundary and subsequent increases of microfossil diversity. These assemblages, which characterize practically all formations in the Turukhansk sequence, contain the remains of acritarchs, cyanobacteria, and, possibly multicellular algae. Within this succession, the organic-walled Derevnya and Miroedikha microbiotas are among the most diverse Neoproterozoic assemblages of microfossils in the world; the Bezymeny and Sukhaya Tunguska formations also contain diverse and well-preserved microfossils. This paper reports the discovery of abundant microfossils in cherts of the Burovaya and Shorikha formations. These diverse microbiotas, which contain phytoplanktonic eukaryotic unicells as well as multicellular trichomes and coccoidal microorganisms, complete the regional micropaleontological succession and contribute to the reasons for recognizing the Turukhansk Uplift as one of the best-characterized Meso-Neoproterozoic transitions in the world, and possibly even a candidate for a global stratotype for this boundary. These finds also provide an additional opportunity to investigate the influences of evolutionary and ecological trends on the stratigraphic and facies distribution of Proterozoic microfossils. In the following sections, the Shorikha and Burovaya microbiotas are described, the environmental distribution of silicified microfossils is analyzed, and

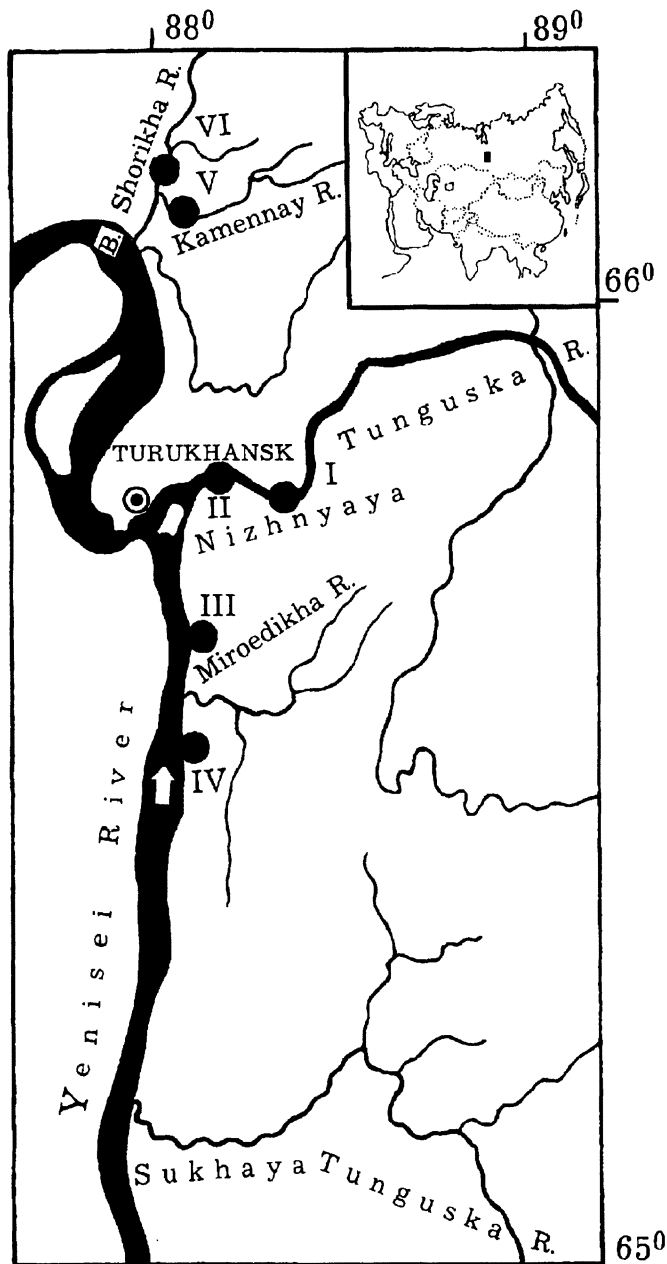


FIGURE 1—Map of the Turukhansk Uplift showing locations of microfossiliferous outcrops of the Burovaya (I) and Shorikha formations (II–VI). Area of main map is shown as the filled box on the insert map of Eurasia. Roman numerals indicate locations of the outcrops: I, II—Nizhnyaya Tunguska River, 18–19 and 12 km upstream from its mouth, respectively; III—Yenisei River, 4–5 km downstream from the Miroedikha River; IV—Yenisei River, 4.5–5 km upstream from the Miroedikha River; V—Kamennay River, 1.5–2.5 km upstream from its mouth; VI—Shorikha River, 1.5–2.0 km upstream from the mouth of the Kamennay River.

relationships between microfossil assemblages and environmental conditions near the Mesoproterozoic–Neoproterozoic boundary and in the early Neoproterozoic Era are evaluated.

PREVIOUS RESEARCH

Microfossils were first reported in the Shorikha cherts by Schopf et al. (1977), who illustrated and briefly described specimens from samples provided by the late B. B. Nazarov (Geological Institute of

the Academy of Sciences, Moscow). However, many microfossils originally assigned to the Shorikha turned out to come from the older Sukhaya Tunguska Formation, leaving only a few simple coccoidal and filamentous forms in the Shorikha microbiota (Mendelson and Schopf, 1982). Subsequently, Sergeev (1984) discovered abundant and diverse filamentous and coccoidal microfossils in silicified stromatolites from the Shorikha Formation, but he overestimated the taxonomic diversity of coccoidal forms. Silicified microfossils in the Burovaya Formation were discovered by Schenfil' (1983), who described empty cyanobacterial sheaths 3.0–4.5 μm in diameter and up to 100 μm long, now identified as *Siphonophycus robustum*. More recently, Golovenok and Belova (1992, 1993) collected samples systematically from all available sections through the Sukhaya Tunguska, Burovaya, and Shorikha formations, and documented 18 taxa in the Sukhaya Tunguska and 9 taxa in the Shorikha cherts. Unfortunately, all taxa reported from the Shorikha Formation were represented by poorly preserved and morphologically simple forms of *Leiosphaeridia*, *Gloeodiniopsis*, *Myxococcoides*, and *Siphonophycus* (*Eomycetopsis*). Golovenok and Belova (1993, p. 280) pointed out that “the microfossils (sic) assemblage from the cherts of the Shorikha Formation is rather poor in its abundance and composition.”

In the following pages, I report the presence of at least 19 distinct taxa from the Burovaya and Shorikha formations, documenting hitherto unrecorded microfossil populations and providing new information on previously known forms. Besides the previously reported morphologically simple filamentous and coccoidal forms, a new and diverse assemblage of morphologically complex multicellular trichomes and phytoplanktonic microorganisms is described. New sedimentological and petrological observations permit an improved understanding of the paleoecology of these microfossil assemblages. This study is based principally on material collected during field work by V. N. Sergeev in 1988 and a joint U.S.–Russian expedition (with A. H. Knoll, Harvard University) in 1995.

GEOLOGICAL SETTING AND AGE OF THE BUROVAYA AND SHORIKHA FORMATIONS

General geology.—The Turukhansk Uplift is located near the northwestern margin of the Siberian Platform (Fig. 1). Proterozoic (Riphean and Vendian) deposits in this region comprise a westward-deepening (15–35 degrees) monocline or asymmetrical syncline 130–150 km long and about 30 km wide disrupted into three main blocks by three major thrusts and a series of minor transverse faults. The most complete Riphean successions occur in the central block, whereas in the eastern block a sub-Vendian unconformity truncates the upper part of the succession. The western block yields only a small fragment of the Riphean succession.

Together with the succession of the Uchuro-Maya uplift (which is a different part of an originally continuous sedimentary succession), the Turukhansk succession is the only succession in Siberia that records the transition from Mesoproterozoic to Neoproterozoic; in fact, it is one of the few successions in the world that documents this transition. All other models for transitional Meso-Neoproterozoic microbiotas are based mainly on microfossil successions reconstructed from different regions. The nearly 4,000 meter thick Mesoproterozoic to Neoproterozoic (late Middle to early Late Riphean) sedimentary package (Fig. 2) begins with the Bezymenny Formation, a thick (up to 1,000 m) succession of carbonaceous shales, sandstones, and subordinate gravelstones that accumulated in mid- to inner shelf environments that deepened to the northwest (Petrov, 1993). The lower boundary of the formation is a fault contact; thus, its true depositional thickness is unknown. Above the Bezymenny Formation follow the carbonate-dominated Linok (180–380 m thick) and Sukhaya Tunguska (560–680 m) formations. An erosional unconformity separates these lower units from the succeeding carbonate-rich Deravnaya (230–300 m), Burovaya, Shorikha, Miroedikha (150–200

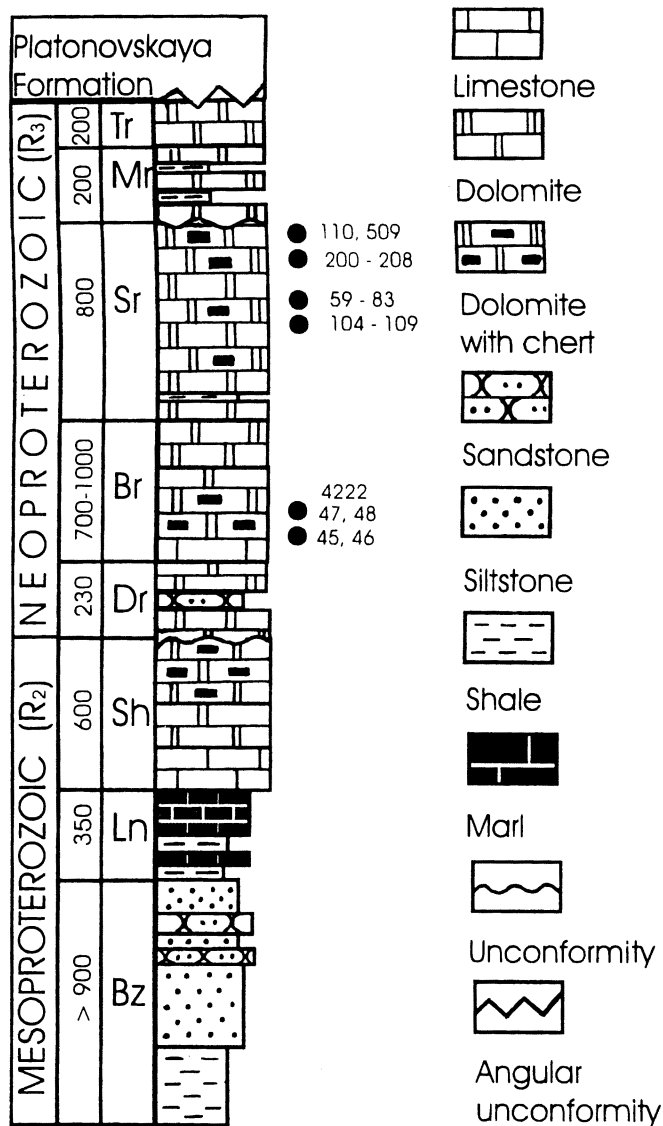


FIGURE 2—Generalized stratigraphic column of the Meso-Neoproterozoic (Riphean) deposits of the Turukhansk Uplift. Formations: Bz—Bezymenyi, Ln—Linok, Sh—Sukhaya Tunguska, Dr—Derevnya, Br—Burovaya, Sr—Shorikha, Mr—Miroedikha, Tr—Turukhansk. Legend is shown in boxes to the right. Thickness of formations in meters. Arabic numbers refer to samples of the fossiliferous cherts from the Burovaya and Shorikha formations; filled circles show approximate stratigraphic levels of the collected samples.

m), and Turukhansk (160–200 m) formations. The entire Turukhansk succession is overlain unconformably (typically no more than 3–5 degrees, but locally up to 80–90 degrees) by terminal Proterozoic (upper Vendian) to Lower Cambrian rocks of the Platonovskaya and Kostinskaya formations (Dragunov, 1963; Petrákov, 1964; Khomentovsky, 1990; Bartley et al., 1998; Petrov and Semikhatov, 1998).

Stratigraphy of the Burovaya and Shorikha Formations.—The Burovaya Formation (700–1,000 m thick) is underlain conformably by the Derevnya Formation and grades up-section into dolomites of the Shorikha Formation. Different authors (Dragunov, 1963; Serebryakov, 1975; Schenfil', 1991; Gorokhov et al., 1995; Knoll et al., 1995; and others) place the boundary between the Burovaya and Derevnya as well as that between the Burovaya

and Shorikha formations in various positions. The Burovaya/Shorikha boundary is especially contentious due to significant lithological variability of Burovaya successions and the often superficial similarity of the two formations. Some geologists divided the formations by color, placing dark carbonates in the Burovaya and light carbonates in the Shorikha Formation. However, the Shorikha Formation is represented by interbedded dark- and light-colored dolomites; therefore, this criterion is not reliable. I accept the positions of the lower and upper boundaries of the Burovaya Formation as suggested by Petrov and Semikhatov (1998). The lower boundary is placed between the dark gray flat- and cross-bedded dolomites (sometimes with stromatolites) of the terminal unit of the Derevnya Formation and dark dolarenites and stromatolitic limestones of the Burovaya Formation. (This boundary marks the beginning of flooding, which concluded in early Burovaya time). The upper unit of the Burovaya Formation is bound by a siliciclastic unit (predominantly argillites with sandstones near the base), which marks the beginning of the Shorikha transgression. This unit is observed only in the northern part of the region; its thickness varies from 3–6 m between the Maly and Bol'shoy Shorikha river basins to 40–50 m in the Nizhnaya Tunguska River basin (Petrov and Semikhatov, 1998).

The Burovaya Formation consists mainly of dark-colored limestones and dolomites, and thin- to medium-bedded grainstones interbedded with flat-pebble conglomerates and oolites. Petrov and Semikhatov (1998) provide a detailed description of this succession. Fine-grained dolomites are fetid and commonly contain syneresis cracks. The Burovaya Formation can be divided into two subformations separated by a sharp erosional boundary (Petrov and Semikhatov, 1998). The lower subformation (100–600 m thick) consists mainly of dark gray limestones and dolomites and, in turn, may be divided into four members (Petrov and Semikhatov, 1998, p. 542, fig. 2). The first member comprises columnar stromatolitic bioherms, built by *Baicalia lacera* Semikhatov and *B. rara* Semikhatov, interbedded with intraformational breccias, along with subordinate cross-bedded grainstones in the northern part of the region and dark dolarenites in its western part. The total thickness of this member varies from 45 to 80 m; its greatest thickness is observed in the central block. The second member is marked by the prevalence of dark gray (pelitomorphic and clastic) dolomites. Complete sections are only encountered in the southern zone along the Sukhaya River, where the thickness is as much as 100 m, and in the northern zone of the Turukhansk region along the Kamennaya River, where the thickness is reduced to 45–50 m.

The parallel and wavy-laminated dolomite association corresponds to the fossiliferous third member (thickness 20–25 m). In the southern block, it is composed of monotonous, light gray dolosparites with a vague, but fine parallel lamination. In the northern zones, the association is split into two parts. The lower part contains subordinate varieties of dolosparites with an irregular wavy lamination that likely includes microbial laminae. These rocks incorporate rare and small stratiform stromatolites, a few nodular buildups, and local erosional traces. They are marked by structures that can be interpreted as a result of the fixation and cementation of migrating ripples by cyanobacterial mats. The upper part of this association in the northern zones is characterized by the prevalence of wavy-laminated dolosparites over parallel-laminated dolosparites and the appearance of polygonal desiccation cracks and dissolution breccia, which are confined to erosion surfaces, particularly in the central and northern zones. In the central Turukhansk block, wavy-laminated dolomites incorporate early diagenetic cherty concretions containing microfossils. The top of the association includes small (1–3 mm) slit-type cavities resulting from the leaching of gypsum crystals. The major unit of this association, represented by dolosparites with a continuous parallel microlamination, was likely formed at the expense of fine-clastic carbonate silts, whereas the wavy-laminated dolomites were

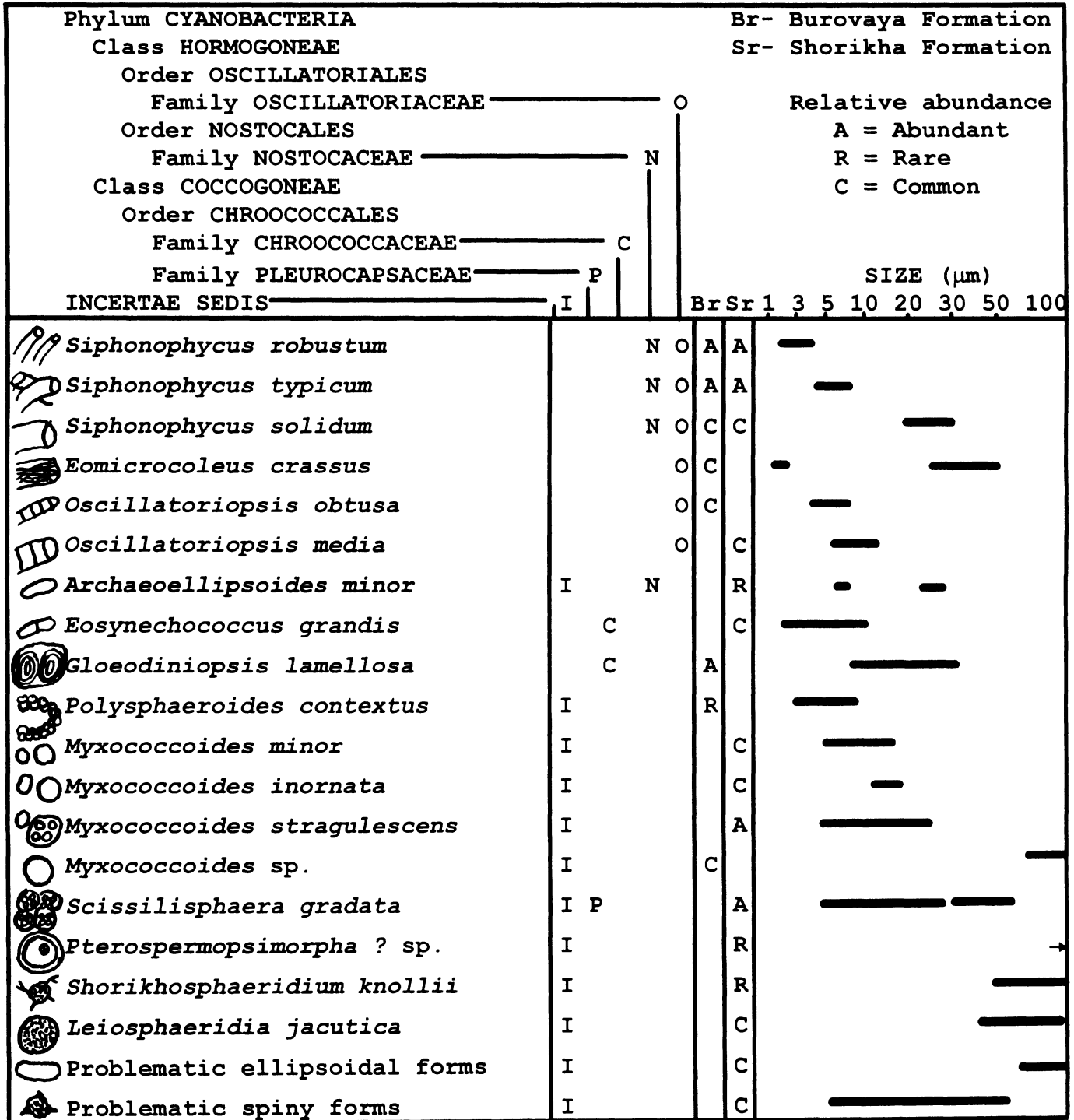


FIGURE 3—Synopsis of microfossil taxa in cherts of the Burovaya and Shorikha formations. Size ranges of microfossils are displayed on a logarithmic scale. Arrows indicate that the maximum diameter of the microfossils is greater than 200 µm.

formed from sediments associated with the microbial activity. This inference follows from both the lamination pattern of these rocks and the abundance of cyanobacterial mat remains in the carbonate-replacing cherts. On the whole, the third association reflects the lateral differentiation of depositional environments and the subsequent shallowing of the basin. In the southern zone, all types of sediments of this association accumulated in still water conditions of the upper subtidal zone. In the northern zones, such conditions were retained

only during the accumulation of the lower units of this association, whereas the upper units represent sediments deposited in intertidal to supratidal environments.

The fourth member consists of clastic, stromatolitic, and fine-grained carbonates in the south (more than 330 m), brecciated to laminated dolomites and limestones in the center (140 m), and a thin (25 m) package of the same dolomites and a thick (250–270 m) sequence of black bituminous dolomites in the north. The total

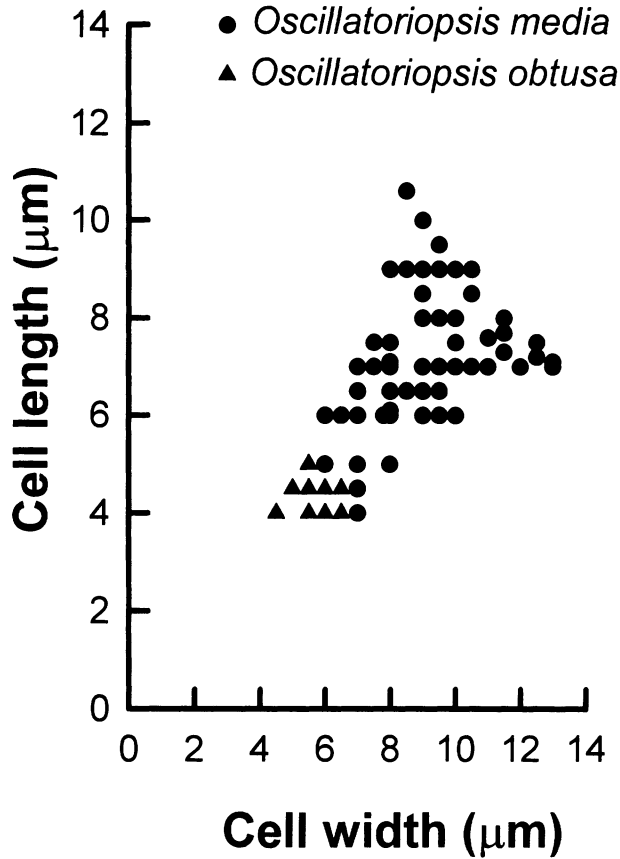


FIGURE 4—Scatter diagram showing the dimensions of medial cells in trichomes from the Burovaya and Shorikha formations.

thickness of the lower subformation is greatest (more than 520 m) in the southern zone and rapidly diminishes to 80–100 m in the central and northern zones. In the central block, the thickness is 250–450 m.

The upper subformation of the Burovaya Formation (380–580 m thick) also consists mainly of dark dolomites with abundant syneresis cracks, but its deposits have survived only in the central and northern parts of the Turukhansk region (the basins of the Miroedikha, Sukhaya Tunguska, and Shorikha Rivers; see Fig. 1). In the basin of the Sukhaya Tunguska River, to the south, the upper subformation was truncated by pre-Vendian (pre-Platonovskaya) erosion. The composition of the upper subformation varies significantly, but its core is represented mainly by stromatolitic dolomites and limestones forming a reef massif. This reef complex is supplemented by fine-grained and brecciated carbonates surrounding in complicated facies relationships the central body (Petrov and Semikhatov, 1998, p. 554, fig. 6).

The overlying 500–800 meter thick Shorikha Formation consists mainly of light-colored, recrystallized, massive to finely laminated dolomites, with abundant nodular chert in its upper part. Complete sections are preserved in the western block only (localities II, III, V and VI, Fig. 1). In the other blocks, the formation has been partly (central block, Nizhnyaya Tunguska River, locality I, Fig. 1) or completely (eastern block, Sukhaya Tunguska River, locality IV, Fig. 1) removed by pre-Vendian erosion. The formation is conventionally divided into lower and upper members (Dragunov, 1963; Serebryakov, 1975), but still has not been studied in detail.

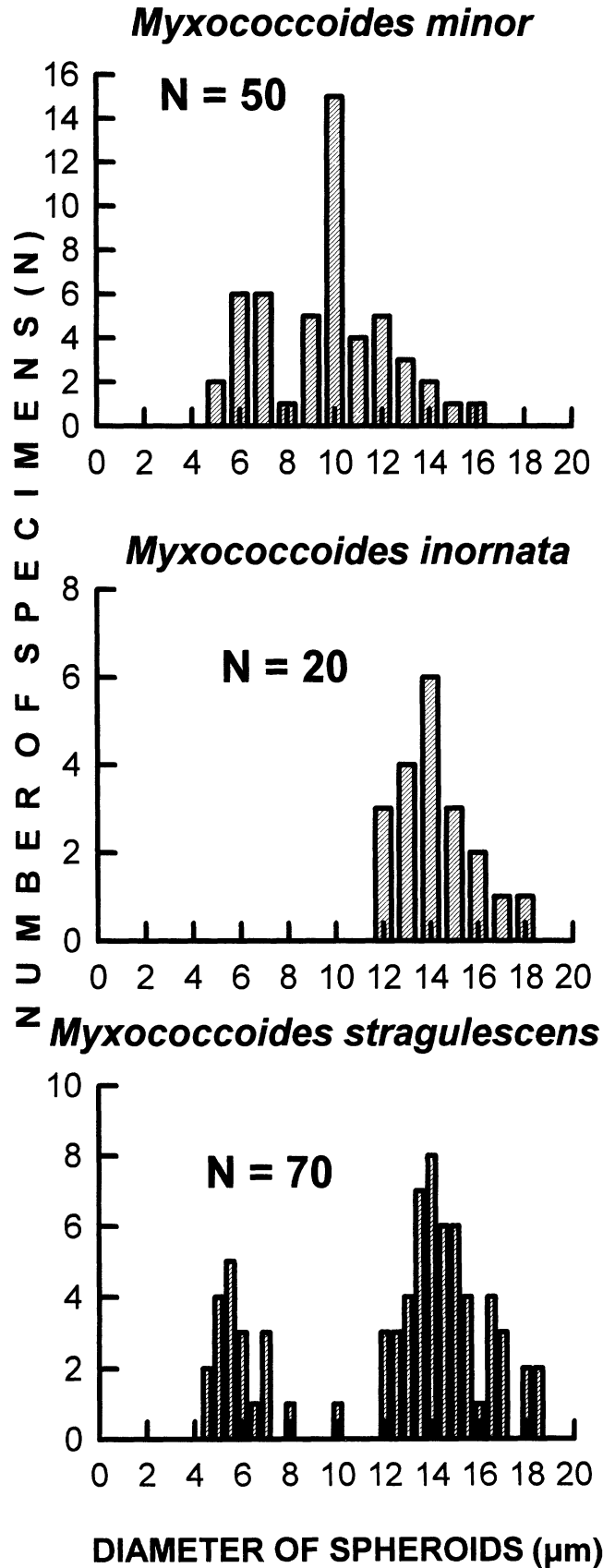


FIGURE 5—Histograms showing size-frequency distribution of the diameter of spheroids of *Myxococcoides minor*, *M. inornata* and *M. stragulescens* from the Shorikha Formation. Diameters in μm .

Scissilisphaera gradata

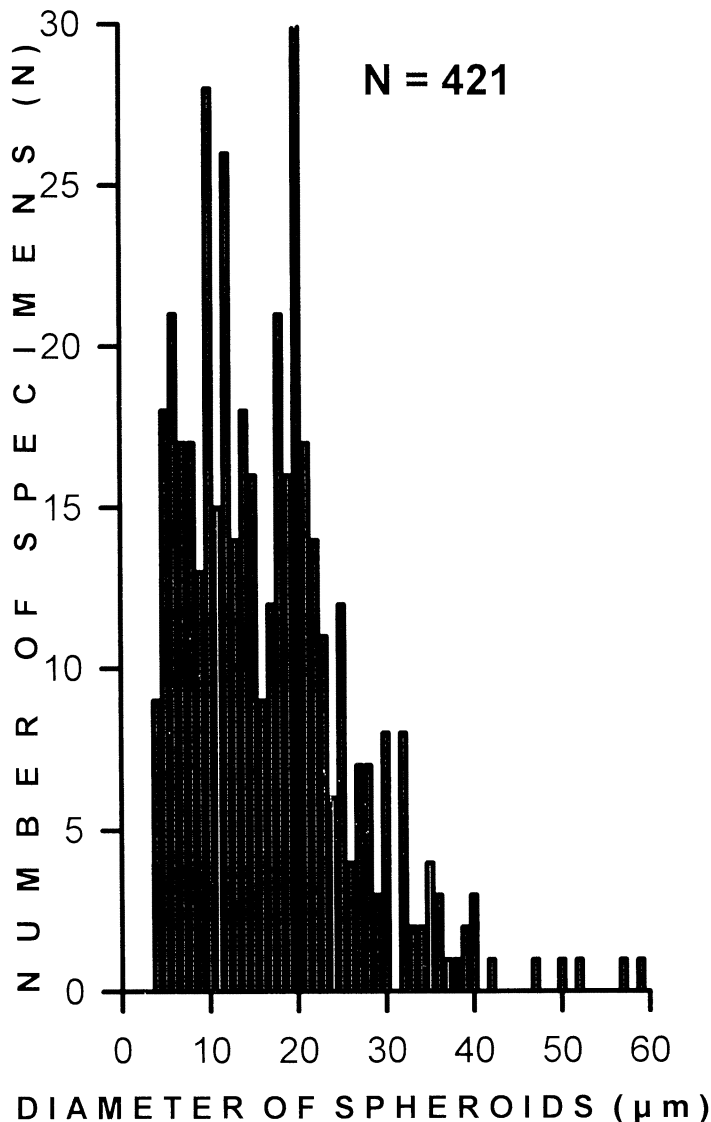


FIGURE 6—Histogram showing size frequency distribution of the diameter of spheroids of *Scissilisphaera gradata* from the Shorikha Formation. Diameters in μm .

In the eastern block the lower member of the Shorikha Formation is about 400–450 m thick and consists of light-gray stromatolitic, dolomitic and intraclastic dolostones. In the western section this member is up to 800–850 m thick and the above lithologies are interbedded with 30 to 80 meter thick units of hummocky cross-laminated carbonaceous dolostones with scattered chert nodules. Deposition of the lower member occurred in subtidal settings, above fair-weather wave base and, in the western sections, periodically near storm wave base. The basal part of the Shorikha Formation is characterized by the columnar stromatolites *Baicalia lacera*, *Tungussia confusa*, and *Inzeria confragosa*; upper strata of the lower member contain the columnar forms *Minjaria uralica*, *Katavia karatavica*, *Jacutophyton* sp., *Conophyton* sp., and *Gymnosolen* sp.

The upper member of the Shorikha Formation (160–320 m) is

a peritidal succession of thick-bedded light gray clastic and subordinate microbially laminated and stromatolitic dolostones containing abundant and richly fossiliferous chert beds and nodules. This member contains mainly indistinctly stratified, stratified columnar, and nodular poorly preserved stromatolites. The uppermost strata of the formation contain the silicified columnar stromatolite *Parmites* sp. with abundant microfossils (Sergeev, 1984). Deposition of the upper member took place in subtidal and probably intertidal settings, especially the uppermost strata of the section.

Age of the Shorikha and Burovaya formations.—Time constraints on the Turukhansk Riphean succession are defined by radiometric as well as paleontological and chemostratigraphic data.

Radiometric dates on the succession proper are limited. A reported 16-point Pb-Pb isochron for middle Sukhaya Tunguska carbonates yields an age of 1035 ± 60 Ma (Ovchinnikova et al., 1995). K-Ar determinations on glauconite from the Bezmeny (830–910 Ma), Derevnya (800–860 Ma), and Burovaya (830–895 Ma) formations are considered to reflect resetting of the K-Ar clock about 850 to 900 Ma ago (see Semikhatov and Serebryakov, 1983; also see Gorokhov et al., 1995, for a review and bibliography). However, counterparts of the Bezmeny and Derevnya formations exposed in the southeastern part of the Yenisei Ridge show K-Ar glauconite ages of 1100 Ma (Pogoryui Formation) and 900–940 Ma (Dzhurskaya Formation), respectively, whereas correlatives of the whole Turukhansk Riphean succession are cut by ca. 830 Ma old granites (see Schenfil', 1991, for review and bibliography). Correlation of the Turukhansk Uplift and Yenisei Ridge successions is based on a striking coincidence in the sequences of lithologically very similar formations and comparable successions of stromatolite assemblages (Semikhatov, 1962, 1991; Semikhatov and Serebryakov, 1983; Schenfil', 1991).

Determination of the minimal age of the pre-Platonovskaya part of the Turukhansk succession is complicated by a new radiometric date obtained on the sills that cut the Lakhanda and Ui Groups of the Uchuro-Maya Uplift. In the sedimentary Proterozoic succession of the Uchuro-Maya Uplift, the Lakhanda Group is considered as the counterpart of the Derevnya, Burovaya, Shorikha, and Miroedikha Formations of the Turukhansk Uplift; the Lakhanda Group is overlain unconformably by the Ui Group (Semikhatov and Serebryakov, 1983). The recent U-Pb analyses on baddelyite from mafic sills that cut the Lakhanda and lower Ui Group yielded ages of 974 ± 7 and 1005 ± 4 Ma (Rainbird et al., 1998), whereas Sm-Nd isochron age of the same sills yielded an age of 948 ± 18 Ma (Pavlov et al., 1992). However, the succession of the Uchuro-Maya Uplift is much thicker and lithologically more complicated than its Turukhansk counterpart. Therefore, these data still cannot prove either an older age for the Burovaya and Shorikha Formations or that the entire Uchuro-Maya pre-Yudoma succession is older than the Turukhansk pre-Platonovskaya unconformity.

Biostratigraphic data are broadly consistent with radiometric constraints. Stromatolites in the Turukhansk succession have been used to support several different stratigraphic interpretations dependent on different stromatolite models. Krylov and other early workers (Krylov, 1975; Semikhatov, 1962) drew the Meso-Neoproterozoic boundary above the disappearance of *Conophyton*, *Jacutophyton*, and *Baicalia*, and below the first appearance of *Minjaria*; using these criteria, the boundary was placed at the base of the Shorikha Formation. Following the discovery of *Conophyton*, *Jacutophyton*, and *Baicalia* in the Upper Riphean stratotype in the Southern Urals, the Meso-Neoproterozoic boundary was repositioned between the Sukhaya Tunguska and Derevnya formations; the latter contains distinctive interregional newcomers known to appear in the lower Neoproterozoic elsewhere—*Baicalia lacera*, *Inzeria tjomusi*, and *Gymnosolen* sp. (see Semikhatov, 1962, 1991;

Schenfil', 1991; and references therein). Stromatolites in the underlying Sukhaya Tunguska Formation are represented by endemic forms of *Baicalia*. However, using stromatolite microstructure, Komar (1990) has argued that the entire Turukhansk succession falls within the Neoproterozoic (Upper Riphean). The latter point of view is shared by some other researchers. Using broad lithostratigraphic and tectonic arguments (Khomentovsky et al., 1985) and microfossil size and complexity as a function of time (Veis, 1988), these authors placed the Meso-Neoproterozoic boundary beneath the Bezymenyy Formation.

The successive silicified and organic-walled assemblages of the Turukhansk Uplift also provide time constraints on Turukhansk deposition. The Derevnaya Formation contains a diverse assemblage of organic-walled microfossils, including large thalli of *Ulophyton*, *Majaphyton*, *Archaeoclada*, various sheaths of *Asperatophyton*, *Rectia*, *Taenitrichoides*, cylindrical spirals of *Obruchevella*, and several other morphotypes widely distributed in Neoproterozoic deposits elsewhere. There are also abundant acanthomorphic acritarchs, *Trachyhystrichosphaera aimika* and *Prolatiforma*, which are considered to indicate a Neoproterozoic age for the Derevnaya Formation (Veis, 1988; Petrov and Veis, 1995). The underlying Sukhaya Tunguska Formation contains long-ranging and stratigraphically uninformative taxa, as well as the stalked cyanobacterium *Polybessurus bipartitus*—a taxon that appears in the latest Mesoproterozoic and is widely known in the Neoproterozoic (Green et al., 1987; Knoll et al., 1991; Hofmann and Jackson, 1991; Sergeev, 1992, 1994; Butterfield et al., 1994). In addition, problematic acanthomorphic acritarchs have been reported from the lower member of the Sukhaya Tunguska Formation (Petrov et al., 1995; Sergeev et al., 1997). However, presence of spines on these specimens is uncertain (Sergeev, 1996). In any event, spiny acritarchs have been reported from late Mesoproterozoic deposits of China (Yan and Liu, 1992; Xiao et al., 1997). Thus, the presence of spiny processes, even if confirmed, does not demonstrate a Neoproterozoic age for the Sukhaya Tunguska Formation.

The oldest fossils in the Turukhansk succession, the Bezymenyy assemblage, besides containing long-ranging and morphologically simple forms, also contain large (up to 1,000–1,500 μm) acritarchs (*Leiosphaeridia jacutica* and *Chuarina circularis*), the colonial coccoidal form *Ostiana microcystis*, filamentous ribbon-like morphotypes (*Asperatofilum experatus* and *Taenitrichoides jaryshevicus*), and broad thalli with longitudinal striations and several other complex morphotypes (Veis and Petrov, 1994a, 1994b, and references therein). Some workers (Veis, 1988) regard this assemblage as early Neoproterozoic (late Riphean) in age; however, this assemblage varies from those described by Knoll and Sergeev (1995) and Sergeev et al. (1995, 1997). This assemblage also contains small problematic spiny forms of *Trachyhystrichosphaera parva*, but a few morphologically complex forms attributed to this Neoproterozoic index-genus appear only in the Derevnaya Formation. This observation argues in favor of a latest Mesoproterozoic age for the Bezymenyy Formation. The overlying Linok Formation contains remnants of poorly preserved silicified and organic-walled morphologically simple coccoidal and filamentous microfossils (Veis, 1988; Golovenok and Belova, 1993; Veis and Petrov, 1994a, 1994b), which do not provide any useful biostratigraphic information.

The microfossils from the Burovaya and Shorikha formations are represented by filamentous and coccoidal forms as well as typical Neoproterozoic (Late Riphean) phytoplanktonic eukaryotic microorganisms (see below). The Miroedikha Formation yields probably the most diverse assemblage of organic-walled microfossils in the entire Turukhansk succession (Hermann, 1974; Veis, 1984; Veis et al., 1998). This microbiota includes all the

above-mentioned taxa and such newcomers as *Cymatiosphaeroides*, *Cerebrophaera*, *Cephalonyx*, *Pellicularia*, and *Pseudotawuia*. However, the distinctive large acritarchs described from many formations of early Vendian (Early "Neoproterozoic-III") age elsewhere, e.g., the Pertatataka Formation of Australia (Zang and Walter, 1992), the Doushantou Formation of China (Zhang et al., 1998), and the Scotia Group of Spitsbergen (Knoll, 1992b), are missing in the Miroedikha assemblage.

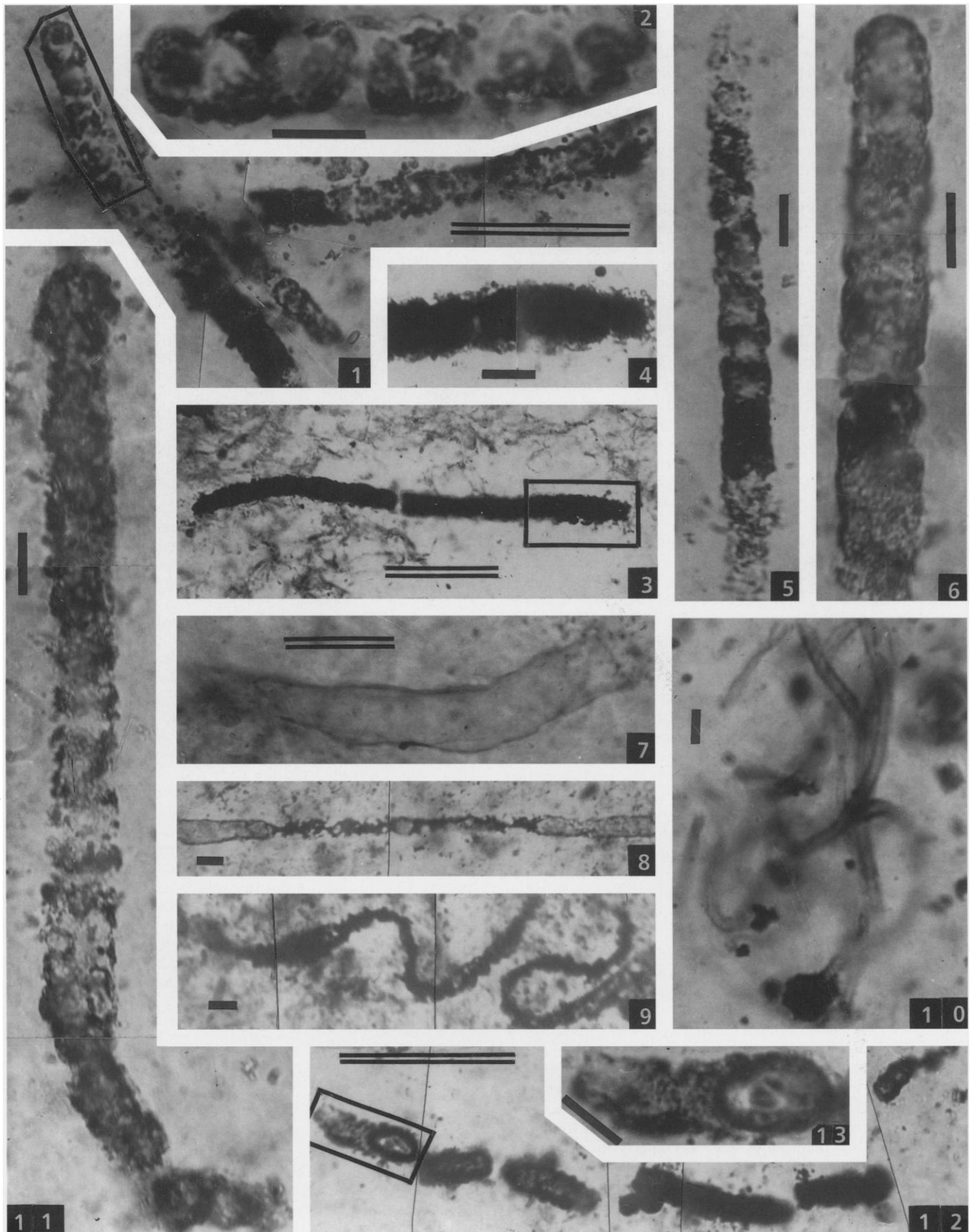
Carbon isotopic profiles for multiple sections through the Turukhansk succession (Knoll et al., 1995) show repeated stratigraphic variations of $\delta^{13}\text{C}$ between ca. -1 and $+3\%$, similar to those of other late Mesoproterozoic to early Neoproterozoic successions (Beanus and Knauth, 1985; Kah et al., 1999; Schidlowski et al., 1975), but distinctly different from either older (e.g., Veizer et al., 1992; Knoll et al., 1995; Buick et al., 1995) or younger (Kaufman and Knoll, 1995) Proterozoic intervals. Carbon isotopic profiles through the Platonovskaya Formation, which unconformably overlies the Turukhansk succession, yield $\delta^{13}\text{C}$ values between ca. -7.5 to $0 \pm 0.4\%$, with a positive spike up to 1.2 – 1.9% typical for many transitional Precambrian-Cambrian successions in the world. The overlying Kostinskaya Formation contains Middle-Cambrian trilobites in its upper part (Dragunov, 1963); these data suggest a late Vendian-Cambrian age for the Platonovskaya Formation (Bartley et al., 1998).

Thus, all the evidence taken together supports a late Middle-early Late Riphean (Meso-Neoproterozoic, earlier than "Neoproterozoic-III") age for the pre-Platonovskaya part of the Turukhansk succession. Available paleontological, radiometric, and chemostratigraphic data suggest that the Meso-Neoproterozoic (Middle-Upper Riphean) boundary is located at the base of the Derevnaya Formation. The All Union Conference on the General Problems of Precambrian Stratigraphy of the USSR, held in Ufa in 1990 (see Semikhatov, 1991), has placed the Meso-Neoproterozoic (Middle-Upper Riphean) boundary in the Turukhansk Region at the unconformity between the Sukhaya Tunguska and Derevnaya formations, and I accept this decision here.

Microfossil localities.—The samples (Figs. 1, 2) from the Burovaya Formation were secured from the third member of the lower subformation (samples 45–48 and 4222) in a section (locality I) along the right bank of the Nizhnyaya Tunguska River, 18–19 km upstream from the river's mouth. The samples from the Shorikha Formation were obtained from its upper member at locality II about 12 km upstream from the mouth of the Nizhnyaya Tunguska River (samples 200–208, 509), along the Bol'shoy Shorikha River 1.5–2.0 km upstream from the mouth of the Kamennay River (locality VI, samples 59–62), along the Kamennay River 1.5–2.5 km upstream from its mouth (locality V, samples 82, 83), along the right bank of the Yenisei River 4.5–5 km upstream (locality III, samples 104–107), and 4–5 km downstream from the mouth of the Miroedikha River (locality IV, samples 108–110). Sample 509 was provided by the late V. A. Komar and sample 4222 by P. Yu. Petrov, Geological Institute of the Russian Academy of Sciences.

COMPOSITION AND PALEOECOLOGICAL SETTING OF THE BUROVAYA AND SHORIKHA MICROBIOTAS

The Burovaya and Shorikha microbiotas share some features and also resemble many other Proterozoic microbiotas in cherts. They are dominated by morphologically simple filamentous and coccoidal microfossils that are predominantly remnants of cyanobacteria. However, there are differences in the composition of both microbiotas, probably reflecting significant differences in the biological nature of the constituent microorganisms despite their morphological simplicity. The Shorikha microbiota also contains remnants of morphologically complex eukaryotic phytoplankton. Therefore, the two microbiotas are analyzed separately and then



compared with each other as well as with other Proterozoic silicified and shale-hosted microbiotas.

The Burovaya microbiota.—The Burovaya Formation is dominated by filamentous and coccoidal microfossils that are mainly remnants of cyanobacteria. The most abundant forms are empty sheaths of hormogonion cyanobacteria assigned to three species of the genus *Siphonophycus*: *S. robustum* (Schopf, 1968) Knoll et al., 1991; *S. typicum* (Hermann, 1974) Butterfield, 1994; and *S. solidum* (Golub, 1979) Butterfield, 1994 (Fig. 7.7–7.10) (characteristics of all species from the Burovaya microbiota are shown in Fig. 3). In addition to these common Proterozoic taxa, the Burovaya microbiota contains rare remnants of multicellular trichomes and some microfossils of ellipsoidal morphology. Among the multicellular trichomes the most abundant are *Oscillatoriopsis obtusa* Schopf, 1968, with cell width 4.5–6.5 μm and cell length 4.0–5.0 μm ; this species, which forms colonies of densely interwoven trichomes, probably represents mat-forming hormogonion cyanobacteria (Fig. 9.4). Other filamentous forms, showing compressed spherical cells, include *Polysphaeroides contextus* Hermann, 1974 (Fig. 9.1–9.3); these fossils may be the remains of either stigonematalean cyanobacteria or green algae. Clusters of shrunken trichomes surrounded by a common sheath, *Eomicrocoleus crassus* Horodyski and Donaldson, 1980 (Fig. 9.5), are interpreted as the remnants of polytrichomatous cyanobacterial filaments comparable to species of the modern genera *Microcoleus*, *Hydrocoleum*, and *Schizothrix* (Seong-Joo and Golubic, 1998). These modern hormogonion cyanobacteria are active mat-forming microorganisms in peritidal environments, but because of taphonomic bias (Horodyski et al., 1977) they are, as a rule, preserved in the fossil record as single filaments.

The coccoidal microfossils of the Burovaya Formation are also diverse and abundant. *Gloeodiniopsis lamellosa* Schopf, 1968 emend. Knoll and Golubic, 1979 (Fig. 9.8, 9.9), one of the most widespread Proterozoic chroococcacean cyanobacteria (Schopf and Blacic, 1971; Knoll and Golubic, 1979; Knoll, 1982; Sergeev, 1992), occurs as independent colonies within mat-like populations of *Siphonophycus* spp. Another interesting ellipsoidal microfossil 30–43 μm wide and up to 150 μm long was identified as problematic (Fig. 9.6, 9.7, 9.11, 9.12). These microfossils do not demonstrate binary fission and probably are resting cysts of prokaryotic or eukaryotic microorganisms. Despite their morphological similarity to preserved cyanobacterial akinetes assigned to the genus *Archaeoellipsoides*, the Burovaya ellipsoids are larger than the akinetes of modern cyanobacteria; the maximum length of the latter is 100–110 μm (Elenkin, 1938). Thus, the large dimension may favor their interpretation as the cysts of eukaryotic microorganisms. It remains possible, however, that the problematical ellipsoidal forms (Fig. 9.6, 9.7, 9.11, 9.12) are anomalously large cysts of hormogonion cyanobacteria.

The simple spheroids of *Myxococcoides* sp. (70–100 μm in diameter) are probably remnants of planktonic microorganisms. The biological affinities of *Myxococcoides* are uncertain but their widespread and essentially random distribution in Burovaya cherts suggests that they are planktonic.

The Shorikha microbiota.—The Shorikha microbiota is dominated by simple spheroids of *Myxococcoides stragulesens* Green,

Knoll, and Swett, 1989 (Figs. 8.12, 10.2, 10.3). Interpretation of these fossils is uncertain; in many features, this taxon is comparable to the modern green alga *Dunaliella* (Green et al., 1989). The nonclumped pattern of distribution of these fossils in the Shorikha cherts clearly indicates their planktonic nature. Another abundant form, *Scissilisphaera gradata* Green, Knoll, and Swett, 1989 (Fig. 10.4–10.7), is comparable to pleurocapsalean cyanobacteria (Green et al., 1989). Other species of *Myxococcoides*—*M. minor* (Fig. 8.11) and *M. inornata* (Fig. 10.1)—are common components of the Shorikha microbiota; their simple morphology precludes systematic interpretation.

The empty sheaths of the hormogonion cyanobacterial genus *Siphonophycus* are represented in the Shorikha cherts by three species: *S. robustum*, *S. typicum*, and *S. solidum* (Fig. 7.7–7.10). The sheaths of *S. robustum* and *S. typicum* are abundant, suggestion that these species were the mat-forming and stromatolite-building microorganisms in the Shorikha microbiota. They occur in non-stromatolitic cherts and in columnar branching stromatolites (*Parmites* sp.) with a column width of 1–2 cm and up to 6 cm long. These stromatolites also contain *Scissilisphaera gradata* and some probable planktonic microfossils such as *Myxococcoides stragulesens*, *Shorikhosphaeridium knollii* n. gen. and sp., *Pterospermopsis* sp., and *Leiosphaeridia jacutica* Timofeev.

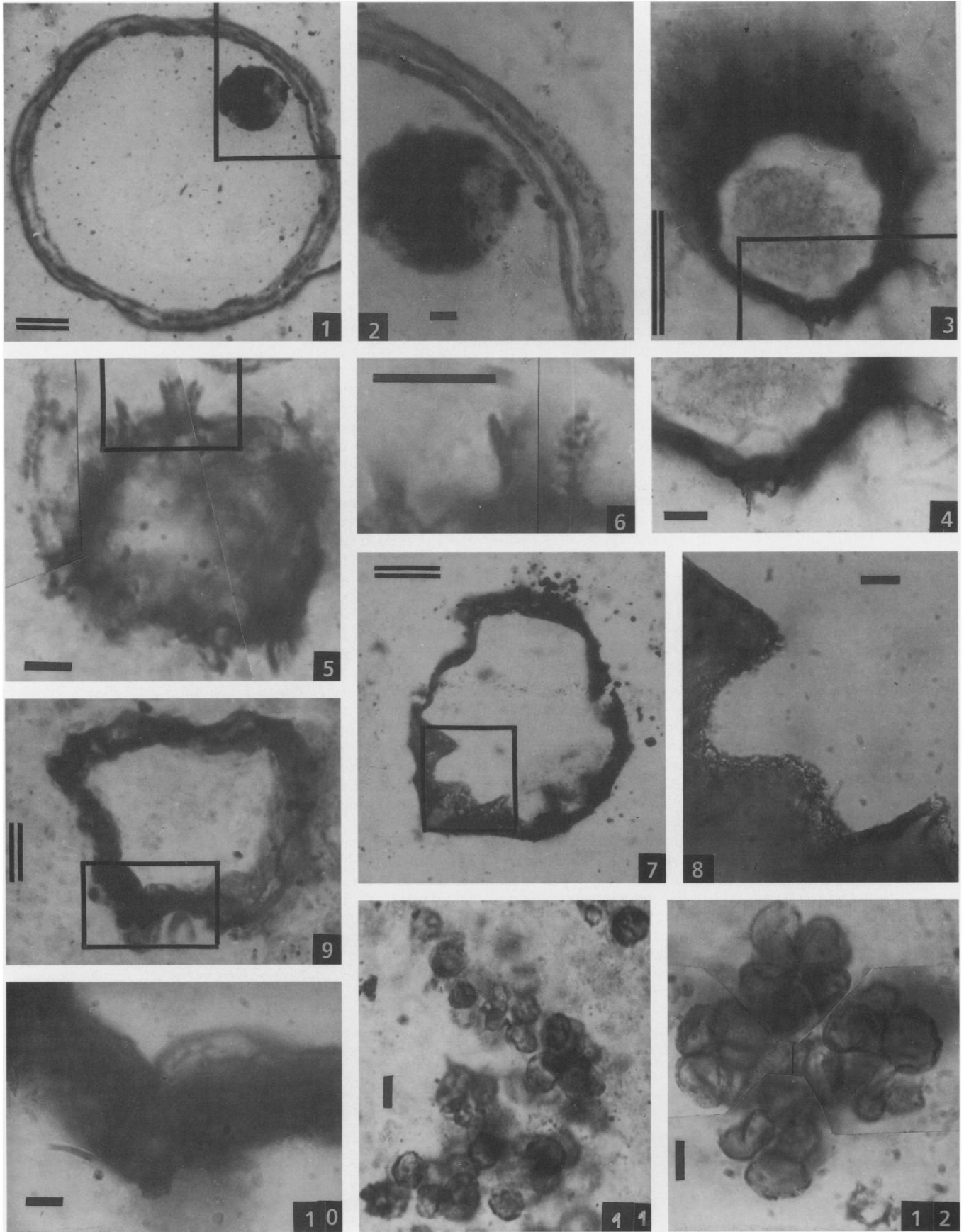
In addition to ubiquitous sheaths of *Siphonophycus*, the Shorikha cherts contain multicellular trichomes of *Oscillatoriopsis media*—remnants of hormogonion (probably oscillatoriacean and nostocalean) cyanobacteria (Fig. 7.1–7.6, 7.11–7.13). However, the mat-forming role of these cyanobacteria in the Shorikha microbiota is unclear. They are either scattered in silicified carbonate mud or occur in mats formed by sheaths of *S. robustum* and *S. typicum*. On the other hand, these scattered trichomes may turn out to be preserved fragments of former mat builders. In general, the relationship herein of *Oscillatoriopsis* and *Siphonophycus* is similar to that of filaments of the modern cyanobacteria *Lyngbya* and *Phormidium* in joint mats.

In contrast to most Proterozoic silicified microbiotas, the *S. robustum* and *S. typicum* mats in the Shorikha Formation contain few remnants of mat-dwelling microorganisms; all coccoidal microfossils occur in small independent colonies or as solitary individuals. Most are remnants of allochthonous planktonic coccoidal microorganisms.

Stratigraphically the most important form is the spine-bearing acanthomorphic acritarch *Shorikhosphaeridium knollii* n. gen. and sp. (Fig. 8.3–8.6). Acanthomorphic acritarchs and remains of other eukaryotic organisms offer the best prospect for a detailed biostratigraphic subdivision of the Neoproterozoic (see Knoll, 1984, 1992a, 1996; Sergeev, 1992; and others). However, we have still not investigated “the full biostratigraphic potential of the Precambrian rocks” (Vidal and Knoll, 1983) and every new find provides additional information about Proterozoic microfloras. Thus, *Shorikhosphaeridium knollii* n. gen. and sp. is probably an important contribution to the database of Neoproterozoic acritarchs.

Another interesting and stratigraphically important microfossil population consists of double-walled and relatively large (up to 280 μm in diameter) envelopes without clear spines between inner and outer layers (Fig. 8.1, 8.2). This fossil has been identified

FIGURE 7—The slide number, locality and sample numbers (in parentheses), and catalog number for the Paleontological Collection of the Geological Institute (GINPC) are given. “p.” number indicates position on slide. Filamentous microfossils from the Shorikha (1–6, 8–13) and Burovaya (7) formations. 1–6, 11–13, *Oscillatoriopsis media*. 1, 2 (hexagon in 1), 726 (IV, 110), p. 15, GINPC 601; 3, 4, (square in 3), 723 (IV, 110), p. 14, GINPC 6055, 726 (IV, 110), p. 15; 5, GINPC 602; 6, 726 (IV, 110), p. 15, GINPC 603; 11, 723 (IV, 110), p. 32, GINPC 604; 12, 13 (pentagon in 12), 726 (IV, 110), p. 16, GINPC 610. 7, *Siphonophycus solidum*. 728 (I, 47), p. 8, GINPC 606. 8, 9, *Siphonophycus robustum*. 8, 672 (III, 104), p. 1, GINPC 607; 9, 678 (III, 104), p. 5, GINPC 608. 10, *Siphonophycus typicum*. 741 (IV, 110), p. 9, GINPC 609. Single scale bars = 10 μm , double bars = 50 μm .



as *Pterospermopsimorpha?* sp. and is similar to microfossils of this type described from other Neoproterozoic formations, e.g., the Russö Formation of Spitsbergen (Knoll and Calder, 1983). Nonetheless, the relationship of this eukaryotic phytoplanktonic microorganism to other acritarchs of the Shorikha microbiota is uncertain. This microfossil may turn out to be a specimen of *Trachyhystrichosphaera aimika* that lost its processes as a result of post-mortem alteration. Butterfield (in Butterfield et al., 1994) suggested that the morphologically similar form *Pterospermopsimorpha pileiformis* from the Backlundtoppen Formation of Spitsbergen may be *Cymatiosphaeroides* specimens lost their spines during diagenesis. The dark spherical envelopes of *Leiosphaeridia jacutica* (70–210 μm in diameter) are also possible remnants of eukaryotic phytoplanktonic microorganisms, possessing the robust, shagrinated wall typical for eukaryotic microfossils (Fig. 8.7–8.10). Such envelopes, however, also can be formed as a result of post-mortem compaction and shrinkage of originally smooth and transparent envelopes of prokaryotic cell colonies (Vidal and Knoll, 1983; Sergeev, 1992). In addition, the Shorikha microbiota contains smaller double-walled microfossils (Fig. 10.10–10.13) with problematic spines (diameters of these fossils vary from 5 to 65 μm). Apparent spines in these fossils may be of secondary origin; similar pseudospines sometimes formed by the deformation of originally smooth surfaces by diagenetically growing crystals of dolomite or magnesite (Sergeev, 1992, 1994; Sergeev et al., 1995; Knoll, 1996).

Differences between the Burovaya and Shorikha microbiotas.—As noted above, the Burovaya microbiota is dominated by empty sheaths of *Siphonophycus* along with abundant and diverse coccoidal microorganisms—mainly remnants of cyanobacteria. In contrast, the Shorikha microbiota is dominated by coccoidal phytoplanktonic microorganisms, *Myxococcoides stragulescens*, which are possible remnants of eukaryotic microorganisms. The sheaths of *Siphonophycus* in Shorikha cherts are abundant but not a dominant element of the microbiota, and these mats practically do not contain dwellers—all coccoidal microfossils in these mats appear to be remnants of phytoplanktonic microorganisms. The common feature for both microbiotas is the presence of multicellular trichomes; but the taxonomic composition of these trichomes is different. The taxa from the Burovaya Formation are rather similar to those in the Derevnya Formation; the Shorikha trichomes are practically identical to those from the overlying Miroedikha Formation, but have poorer preservation. The taxonomic composition of the coccoidal microfossils of the Burovaya Formation share features in common with the microbiota from the underlying Sukhaya Tunguska Formation. The difference in composition of the Burovaya and Shorikha microbiotas is probably due to facies differences. The Burovaya microfossils come from the third member of its lower subformation (Figs. 1, 2); these strata are interpreted as shallow-water deposits (Petrov and Semikhatov, 1998). The microfossils in the Shorikha cherts are found in some localities along the Nizhnyaya Tunguska, Kamenaya, and Sukhaya Tunguska Rivers, but the bulk of the Shorikha microbiota was secured from the upper parts of its upper member along the Yenisei River. These dolomites and stromatolitic dolomites interbedded with shales are interpreted as sediments deposited in open-marine middle-shelf environments. This pattern of

distribution of the Burovaya and Shorikha microorganisms in general supports ideas about the increasing diversity of phytoplanktonic assemblages from near-shore to open-marine environments (Knoll, 1984; Knoll et al., 1991; Sergeev, 1992), as well as the existence of the most diverse assemblages in the middle part of the open shelf (Veis and Petrov, 1994a, 1994b; and others).

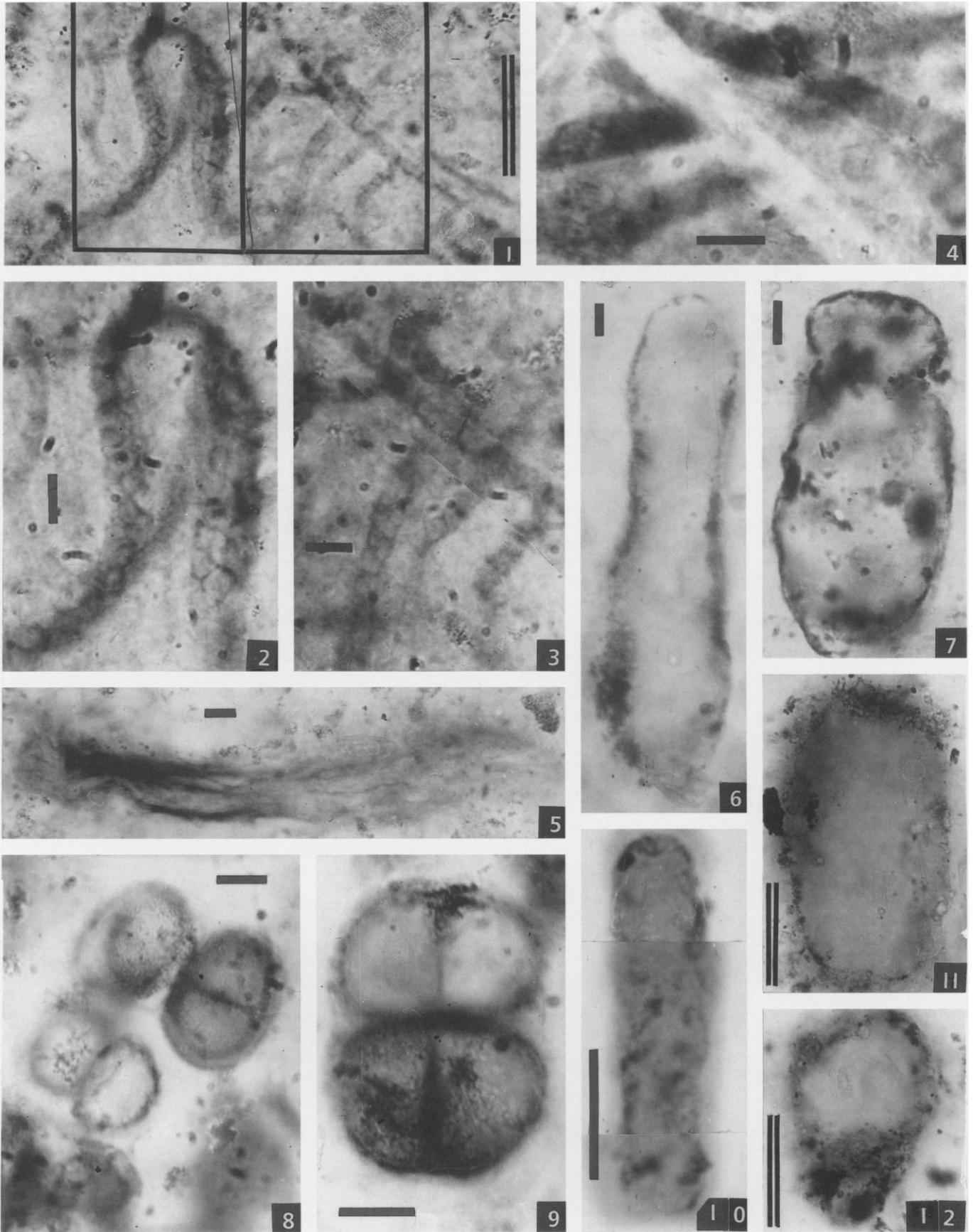
BIOSTRATIGRAPHIC AND EVOLUTIONARY SIGNIFICANCE OF THE BUROVAYA AND SHORIKHA MICROBIOTAS

The most biostratigraphically and evolutionarily significant fossils are the acanthomorphic, pterospermopsimorphic, and sphaeromorphic acritarchs in the Shorikha microbiota. The emergence of acanthomorphic and other morphologically complex acritarchs is one of the main features of eukaryotic diversification about 1,000 Ma and many researchers have suggested that the first appearance of acanthomorphic acritarchs of the genus *Trachyhystrichosphaera* might be used as a basis for establishing the lower boundary of the Neoproterozoic Era (Knoll, 1984, 1992; Sergeev, 1992; Butterfield et al., 1994). The discovery of acanthomorphic acritarchs in the Mesoproterozoic Baicaooping Formation of China (Yan and Liu, 1992; Xiao et al., 1997) means that spiny microfossils in general cannot indicate a Neoproterozoic age. However, the Mesoproterozoic microfossils from China differ morphologically and taxonomically from the typical Neoproterozoic *Trachyhystrichosphaera* and other Neoproterozoic acritarchs; thus, these finds only increase the biostratigraphic potential of the Proterozoic microfossils. The presence in the Shorikha Formation of *Shorikhosphaeridium knollii* n. gen. and sp. is a new addition to the database of acritarchs that might contribute to a detailed subdivision of the Neoproterozoic Era. These phytoplanktonic microorganisms also have paleoecological significance because they are broadly represented in Neoproterozoic open-marine, silicified and organic-walled microbiotas.

Other phytoplanktonic microorganisms from the Shorikha microbiota are consistent with a Neoproterozoic age for this formation. The double-walled envelopes of *Pterospermopsimorpha?* sp. are known mainly from Neoproterozoic organic-walled and silicified microbiotas (Knoll and Calder, 1983; Butterfield et al., 1994). The large, robust envelopes of *Leiosphaeridia jacutica* are also rather typical for Neoproterozoic deposits (Timofeev et al., 1976; Knoll, 1984; Yankauskas et al., 1989), although large spheroidal compressions occur in shales of Mesoproterozoic (Peat et al., 1976; Veis and Vorobyeva, 1992; Hofmann, 1992) and even Paleoproterozoic age (Hofmann and Jinbiao, 1981; Hofmann, 1992; Han and Runnegar, 1992).

Despite the evolutionary conservatism of the benthic prokaryotes that dominate the Burovaya and Shorikha microbiotas, these fossils have, in general, a “Neoproterozoic” appearance. Multicellular trichomes of hormogonion cyanobacteria are known from assemblages ranging in age back to the Paleoproterozoic (Klein et al., 1987; Knoll et al., 1988). Trichome width was proposed as a criterion to subdivide the Proterozoic biostratigraphically (Schopf, 1977; Veis, 1988), but this approach now seems to be useless (Schopf, 1992). On the other hand, trichome length has unexpectedly turned out to be useful in correlation (Knoll and Sergeev, 1995; Sergeev et al., 1995). Of course, this criterion is purely statistical and can be applied only when large populations

←
FIGURE 8—Phytoplanktonic microorganisms from the Shorikha Formation (1–8 from Locality IV; 9–12 from Locality II). 1, 2 (square in 1), *Pterospermopsimorpha?* sp. 754(IV, 110), p. 7, GINPC 611. 3–6, *Shorikhosphaeridium knollii*; n.gen and sp. 3, 4 (square in 3), 754 (IV, 110), p. 8, GINPC 612; 5, 6 (square in 5), holotype, PCGI-RAS 758 (IV, 110), p. 2, GINPC 613. 7–10, *Leiosphaeridia jacutica*. 7, 8 (square in 7), 765 (IV, 110), p. 4, GINPC 614; 9, 10 (square in 9), 849 (509), p. 22, GINPC 615. 11, *Myxococcoides minor*. 695 (II, 207), p. 20', GINPC 616. 12 *Myxococcoides stragulescens*. 695 (II, 207), p. 20, GINPC 617. Single scale bars = 10 μm , double bars = 50 μm .



are available. Nonetheless, temporal variation in trichome length may reflect deep changes in the composition of microbial communities across the Meso-Neoproterozoic boundary. Short trichomes are mainly germinated akinetes of nostocalean cyanobacteria, which were widespread along the tidal-flats of Mesoproterozoic basins and were replaced in the Neoproterozoic by other communities of prokaryotic or eukaryotic microorganisms (Sergeev et al., 1995; Knoll and Sergeev, 1995; Golubic et al., 1995; Sergeev, 1997a, 1997b). Thus, the assemblages of long trichomes from the Burovaya and Shorikha formations are more typical for the Neoproterozoic. Some taxa of filamentous microfossils, for example *Polysphaeroides contextus*, are known only from Neoproterozoic deposits. If those fossils are remnants of hormogonion cyanobacteria, their presence in Neoproterozoic deposits can be explained by taphonomical bias, and one can expect to find this taxon in older deposits. On the other hand, some taxa of cyanobacteria, e.g., *Polybessurus* and *Obruchevella*, are still known only from the late Mesoproterozoic and younger deposits (Golovenok and Belova, 1983; Green et al., 1987; Hofmann and Jackson, 1991; Sergeev, 1992, 1994). If *Polysphaeroides contextus* represents remnants of the green or other eukaryotic algae, then the appearance of this form in Neoproterozoic deposits can be a result of evolutionary diversification near the Meso-Neoproterozoic boundary.

Biostratigraphically more significant, probably, are the problematic ellipsoidal forms. Similar microfossils are present in the slightly younger Neoproterozoic Draken Conglomerate Formation of Spitsbergen (A. H. Knoll, personal observation); appearance of this taxon can also be related to the "Neoproterozoic revolution" (Sergeev et al., 1996). The spherical microfossils *Myxococoides stragulescens* and *Scissilisphaera gradata* from the Shorikha Formation also may be stratigraphically and evolutionarily important forms; despite their morphological simplicity, these fossils may turn out to be remnants of green algae. Enthophysalidacean cyanobacteria, which are common and abundant in most Paleo- and Mesoproterozoic microbiotas (Hofmann, 1976; Oehler, 1978; Zhang, 1981; Sergeev, 1993; Sergeev et al., 1994, 1995, 1997), are missing from the Burovaya and Shorikha formations. Absence of enthophysalidacean cyanobacteria as well as dominance in the Shorikha microbiota by the spheroids of *M. stragulescens* and *S. gradata* also probably have evolutionary and environmental significance, reflecting the "hidden" expansion of eukaryotic microorganisms and the evolution of substrate conditions (Knoll and Sergeev, 1995; Kah and Knoll, 1996; Sergeev, 1997a, 1997b).

Thus, the Burovaya and Shorikha microbiotas comprise many taxa that are now known only from Neoproterozoic deposits, primarily remnants of eukaryotic phytoplanktonic microorganisms. Nonetheless, both microbiotas are dominated by morphologically simple filamentous and coccoidal, and stratigraphically long-ranging, microfossils. Many of these taxa appeared in the Paleoproterozoic, occur in most Meso- and Neoproterozoic microbiotas, and even have modern counterparts. However, these microfossils may have primitive morphological features whose significance is unrecognized but with time may prove to have evolutionary importance (e.g., the microfossils may turn out to be remnants of morphologically simple but biologically differentiated eukaryotic and prokaryotic microorganisms).

SYSTEMATIC PALEONTOLOGY

All specimens illustrated in this paper occur in thin sections of black chert from the Burovaya and Shorikha formations. Microfossils were photographed in transmitted light with a Zeiss microscope REM-5 and measured with an eyepiece reticule to the nearest micrometer. The positions of illustrated specimens on a slide are cited as numbers that correspond to numbered points recorded on a paper overlay affixed to each slide.

Illustrated specimens are deposited in the Paleontological Collection of the Geological Institute of the Russian Academy of Sciences (PCGI-RAS), Collection 4694.

Kingdom EUBACTERIA Woese and Fox, 1977

Phylum CYANOBACTERIA Stanier et al., 1978

Class COCCOGONEAE Thuret, 1875

Order CHROOCOCCALES Wettstein, 1924

Family CHROOCOCCACEAE Nägeli, 1849

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

Type species.—*Gloeodiniopsis lamellosa* Schopf, 1968, emend. Knoll and Golubic, 1979, emend. Sergeev, 1992.

GLOEODINIOPSIS LAMELLOSA Schopf, 1968 emend. Knoll and Golubic, 1979 emend. Sergeev, 1992
Figure 9.8, 9.9

Gloeodiniopsis lamellosa SCHOPF, 1968, p. 684, pl. 84, fig. 2; SCHOPF AND BLACIC, 1971, pl. 110, figs. 1–5; KNOLL AND GOLUBIC, 1979, p. 147, figs. 6, 7; MENDELSON AND SCHOPF, 1982, p. 66, 68, pl. 1, figs. 13, 15; GOLOVENOK AND BELOVA, 1993, p. 282, pl. 2, fig. b; PETROV, SEMIKHATOV, AND SERGEEV, 1995, pl. 1, fig. 10; SERGEEV, KNOLL, AND PETROV, 1997, p. 216–219, figs. 7, 8A–H.

Gloeodiniopsis magna NYBERG AND SCHOPF, 1984, p. 763, 765, fig. 15C–G; HOFMANN AND JACKSON, 1991, p. 377, fig. 13.1–13.7, 13.11–13.14; GOLOVENOK AND BELOVA, 1992, p. 116, 117, fig. 1, 1993, pl. 2, fig. a; SCHOPF, 1992, pl. 45, figs. D, F, G.

Gloeodiniopsis grandis SERGEEV AND KRYLOV, 1986, p. 90, 91, pl. 10, figs. 8, 9; KNOLL, SWETT, AND MARK, 1991, p. 550–553, fig. 19.4; SCHOPF, 1992, pl. 45, fig. B.

Chroococcus-like morphotype MENDELSON AND SCHOPF, 1982, p. 68–69, pl. 2, fig. 5; SCHOPF, 1992, pl. 10, fig. L.

Globophyscus-like morphotype MENDELSON AND SCHOPF, 1982, p. 68–69, pl. 1, fig. 12.

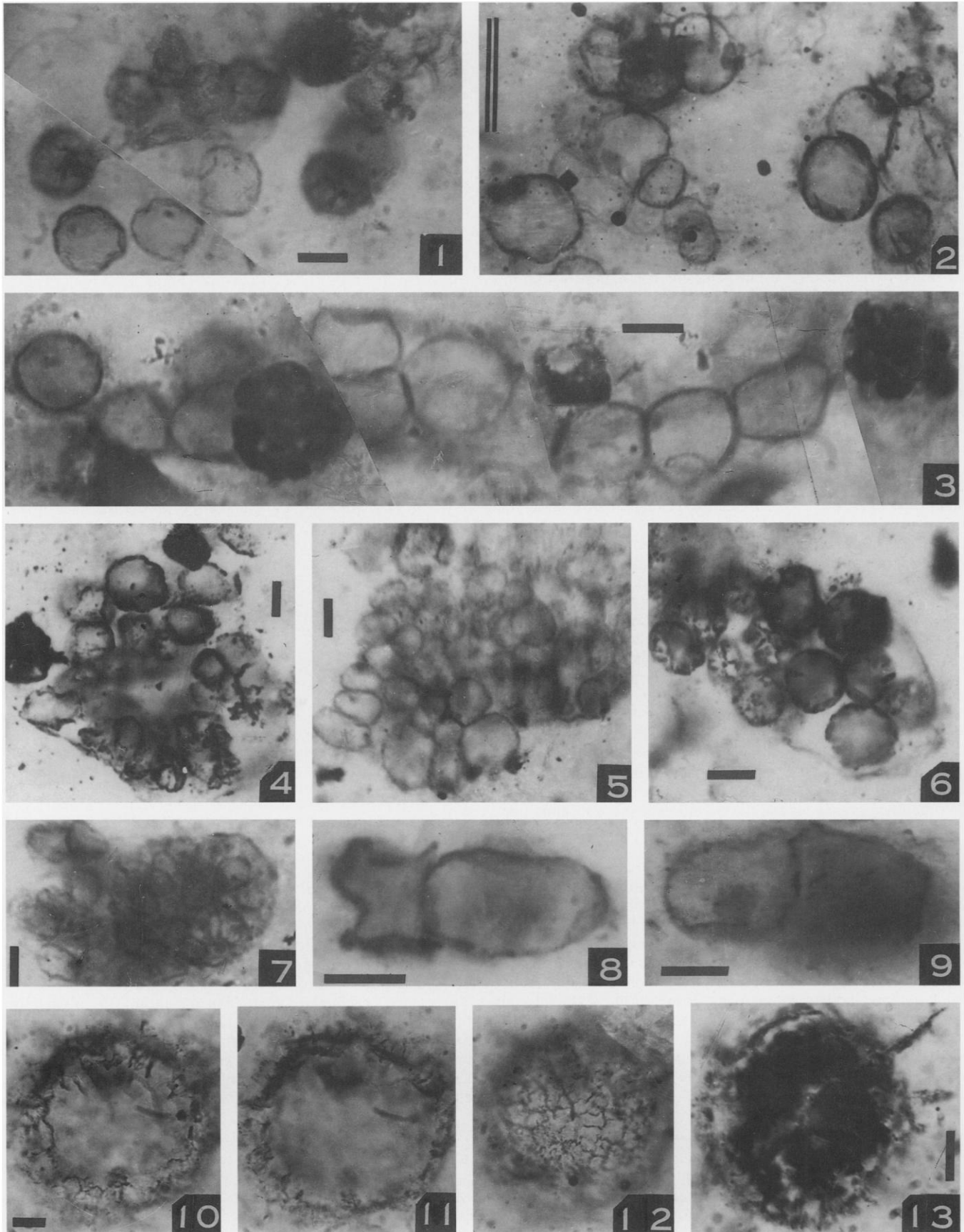
"Undifferentiated Chroococcacean Cyanobacteria" (partim): MENDELSON AND SCHOPF, 1982, p. 68–69, pl. 2, fig. 5.

Tetraphycus giganteus (partim) GOLOVENOK AND BELOVA, 1992, p. 117, figs. 1, 3; 1993, pl. 2, fig. c.

For a complete synonymy, see Sergeev, 1992, 1994.

Description.—Multilamellate spheroidal to ellipsoidal vesicles surrounded by a hyaline zone with one or more thin envelopes of differing density, giving a ringed appearance in cross-sectional view. Lamellae in outer portion with uniform curvature, innermost layers more irregular, in some cases containing a centrally or eccentrically located inclusion of dark matter. Spheroids and ellipsoids occasionally solitary, but commonly in colonies of a few to several hundred individuals. Spheroids arranged in monads, dyads, triads, and tetrads (cross and planar tetrads), sometimes enclosed in thin common envelopes; larger colonies commonly embedded in a diffuse organic matrix. Diameter of inner envelopes 8–26 μm (mean = 17 μm , N = 58); outer envelopes

FIGURE 9—Filamentous and coccoidal microfossils from the Burovaya Formation (1–9 from Locality I, 10 from Locality IV). 1, 2 (left square in 1), 3 (right square in 1), *Polysphaeroides contextus*, 706 (47), p. 11, GINPC 618. 4, *Oscillatoriopsis obtusa*, 706 (47), p. 6, GINPC 619. 5, *Eomicrocoleus crassus*, 736 (46b), p. 3, GINPC 620. 6, 7, 11, 12, Problematic ellipsoidal forms, 6, 747 (47), p. 8, GINPC 621; 7, 728 (47), p. 11, GINPC 617; 11, 747 (47), p. 9, GINPC 626; 12, 747 (47), p. 10, GINPC 627. 8, 9, *Gloeodiniopsis lamellosa*, 8, 704 (47), p. 9, GINPC 623; 9, 704 (47), p. 9, GINPC 624. 10, *Archaeoellipsoides minor*, 723 (110), p. 16, GINPC 625. Single scale bars = 10 μm , double bars = 50 μm .



12–32 μm (mean = 22 μm , $N = 62$); inclusions 1–2 μm , walls 1–1.5 μm thick.

Material examined.—About 60 colonies from cherts of the Burovaya Formation.

Occurrence.—A widespread constituent of microfossil assemblages in Meso-Neoproterozoic (Middle-Late Riphean) cherts, occurring in dozens of formations.

Discussion.—*Gloeodiniopsis lamellosa* was erected by Schopf (1968) for multilamellate spheroids preserved in silicified coastal playa lake carbonates of the Bitter Springs Formation (ca. 800 Ma), Australia. Knoll and Golubic (1979) emended this taxon to include species of *Bigeminococcus*, *Eozygion*, *Eotetrahedron*, and *Caryosphaeroides* (in part), recognizing that previously described differences among these taxa reflect a cell-division cycle and variable post-mortem decay within a single population. In similar fashion, I interpret the range of morphologies found in Burovaya cherts to represent variation within a single species. In contrast to populations of *G. lamellosa* from many late Mesoproterozoic–early Neoproterozoic formations, e.g., the Avzyan and Min'yar formations of the southern Ural Mountains (Sergeev, 1992, 1994), the Sukhaya Tunguska Formation of the Turukhansk Uplift, and the Bitter Springs Formation of Australia (Sergeev et al., 1997), the Burovaya microfossils do not exceed the maximum diameter of this species (about 45 μm).

Genus EOSYNECHOCOCCUS Hofmann, 1976

Type species.—*Eosynechococcus moorei* Hofmann, 1976.

EOSYNECHOCOCCUS GRANDIS Hofmann, 1976
Figure 10.8, 10.9

Eosynechococcus grandis HOFMANN 1976, p. 1058, pl. 2, figs. 11–14; SERGEEV, 1984, p. 438, fig. 2K–2H.

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

Material examined.—Seventeen colonies from the Shorikha cherts.

Occurrence.—Widely distributed in Proterozoic chert assemblages.

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

Class HORMOGONEAE Thuret, 1875

Order OSCILLATORIALES Elenkin, 1949

Family OSCILLATORIACEAE (Gray,) Kirchner, 1900

Genus OSCILLATORIOPSIS Schopf, 1968 emend. Mendelson and Schopf, 1982 emend. Butterfield, 1994

Type species.—*Oscillatoriopsis obtusa* Schopf, 1968.

Discussion.—This genus was described by Schopf (1968) to encompass the sheath-less trichomes of oscillatoriacean cyanobacteria similar to the modern genus *Oscillatoria* Vaucher. Subsequently, this genus was emended by Mendelson and Schopf (1982) as a form-taxa to include all *Oscillatoria*- or *Lyngbya*-like trichomes encompassed by a sheath less than 1 μm thick. Later,

Butterfield (in Butterfield et al., 1994) emended this genus to include unbranched, uniseriate, cellular trichomes with cell length less or equal to cell diameter. However, in my opinion Butterfield included in this genus many morphologically distinguishable species probably should be referred to other genera. For example, the holotype of *Contortothrix vermiformis* combined by Butterfield (in Butterfield et al., 1994) as *Oscillatoriopsis vermiformis* is not a trichome, but the empty sheath of a cyanobacterium with casts of trichome cells; it should be referred to the genus *Siphonophycus* (personal observations, 1996).

OSCILLATORIOPSIS OBTUSA Schopf, 1968 emend. Butterfield, 1994

Figures 4, 9.4

Oscillatoriopsis obtusa SCHOPF, 1968, p. 667, pl. 77, fig. 8; SCHOPF, 1992, pl. 31, fig. G; BUTTERFIELD, KNOLL, AND SWETT, 1994, p. 58, fig. 24A–E, K.

Description.—Solitary or in loose clusters, uniseriate, unbranched trichomes without sheaths. Terminal cells, when preserved, blunt or rounded; medial cells pill-like, translucent or dark, sometimes arranged in pairs, 4.5–6.5 μm wide and 4.0–5.0 μm long; width/length ratio varies from 1.2 to 1.5, maximum length of trichomes up to 110 μm (incomplete specimen). Cross walls are distinct, transparent, or missing; cell walls translucent, fine-grained, 0.5–1.0 μm thick.

Material examined.—About 30–40 specimens from the Burovaya Formation.

Occurrence.—Widely distributed in Proterozoic chert and organic-walled assemblages.

Discussion.—*Oscillatoriopsis obtusa* can be distinguished from other species of *Oscillatoriopsis* by its cell dimensions, and distinct blunt and rounded terminal cells. Schopf (1968) described this form on the basis of a type specimen from the Bitter Springs Formation, Australia; later Butterfield (in Butterfield et al., 1994) emended this species and synonymized it with many other species of *Oscillatoriopsis* as well as with species of *Cephalophytarion*, *Primorivularia*, *Cyanonema* and *Obconicophycus*. I do not consider all species listed by Butterfield as synonymous but am unable to revise this taxon here.

The trichomes of *Oscillatoriopsis obtusa* from the Burovaya Formation clearly demonstrate the cross-walls and cells can be easily measured (see Fig. 4); however, the cross-walls are transparent and difficult to identify on the figure.

OSCILLATORIOPSIS MEDIA Mendelson and Schopf, 1982

Figures 4, 7.1–7.6, 7.11–7.13

Oscillatoriopsis media MENDELSON AND SCHOPF, 1982, p. 64–65, pl. 4, figs. 3, 5, 6; OGURTSOVA AND SERGEEV, pl. 9, figs. 1, 2; SERGEEV, 1992, p. 87–88, pl. 26, fig 4, pl. 27, figs. 1, 2; SCHOPF, 1992, pl. 10, figs. F, H.

Description.—Solitary or in loose clusters, uniseriate, unbranched trichomes without sheaths. Terminal cells, when preserved, blunt or rounded; medial cells barrel- or pill-like, translucent or dark, sometimes arranged in pairs, 8.0–13.5 μm wide and 6.0–10.5 μm long; width/length ratio varies from 1.5 to 3, maximum length of the trichomes up to 180 μm (incomplete

FIGURE 10—Coccolidal microfossils from the Shorikha Formation (1, 4, 9, from Locality II, 2, 3, 10–13 from Locality IV). 1, *Myxococcoides inornata*, 695 (207), p. 20", GINPC 628. 2, 3, *Myxococcoides stragulescens*, 2, 674 (110), p. 26, GINPC 629; 3, 726 (110), p. 22, GINPC 630. 4–, *Scissilisphaera gradat.*, 4, 245 (509), p. 11', GINPC 631; 5, 241 (509), p. 9, GINPC 632; 6, 245 (509), p. 11, GINPC 633; 7, 241 (509), p. 7, GINPC 634. 8, 9, *Eosynechococcus grandis*, 8, 850 (509), p. 3, GINPC 635; 9, 850 (509), p. 4, GINPC 636. 10–13, Problematic spiny forms, 10–12, 759 (110), p. 15, GINPC 637; 13, 741 (110), p. 16, GINPC 638. Single scale bars = 10 μm , double bars = 50 μm .

specimen). Cross walls distinct or missing, about 1.0 μm thick, fine-grained; 0.5–1.0 μm spaces can separate adjacent cells. Cell walls translucent, medium-grained, up to 1.5 μm thick.

Material examined.—About a hundred specimens from the Shorikha Formation.

Occurrence.—Widely distributed in Proterozoic chert and organic-walled assemblages.

Discussion.—Mendelson and Schopf (1982) described this species from the underlying Meso-Neoproterozoic Sukhaya Tunguska Formation of the Turukhansk Uplift with cell lengths approximately three times shorter than wide (8–11 μm wide and 2–4 μm long). In the material from the Shorikha Formation, cells are longer and may equal the width. However, the width of the cells is a more important classification parameter for the trichomes of modern hormogonian cyanobacteria; the length varies due to cell division (cf. Golubic and Focke, 1978). Moreover, some Shorikha trichomes lost their cross walls during diagenesis and the preserved cells look longer than they originally were. Therefore, I include this form within *O. media*.

In some sections, the trichomes of *O. media* appear to consist of spherical or constricted cask-like cells and resemble representatives of the genera *Veteronostocale* or *Filiconstrictosus* (Fig. 7.1). This similarity is, however, superficial and reflects the oblique orientation of non-constricted trichomes made up of cylindrical cells.

Some trichomes of *O. media* in the Shorikha Formation are short and arranged in a broken line (Fig. 7.12, 7.13). These short trichomes are either hormogonians, representing early life stages of *O. media*, or fragments of diagenetically broken matured filaments.

Genus EOMICROCOLEUS Horodyski and Donaldson, 1980

Type species.—*Eomicrocoleus crassus* Horodyski and Donaldson, 1980.

EOMICROCOLEUS CRASSUS Horodyski and Donaldson, 1980 Figure 9.5

Eomicrocoleus crassus HORODYSKI AND DONALDSON, 1980, p. 154, fig. 15A, 15B.

Description.—Bundles of dark threadlike trichomes closely grouped within a common cylindrical sheath. Trichome diameter 1–2 μm , poorly preserved, consist of organic particles linearly arranged, and evidently have been subject to post-mortem shrinkage; encompassing tube 25–50 μm in cross-sectional diameter, fine- to medium-grained, and ca. 1 μm thick.

Material examined.—A dozen poorly preserved filaments from the Burovaya Formation.

Occurrence.—Widely distributed in Proterozoic chert assemblages.

Discussion.—Despite their poor preservation, the forms described here as *Eomicrocoleus crassus* differ only slightly from the type population discovered in the Mesoproterozoic Dismal Lakes Group, Arctic Canada (Horodyski and Donaldson 1980). In contrast to the type population, trichomes and sheaths of Shorikha specimens have a little larger diameter, but this can be explained by a different degree of shrinkage and contraction (Gerasimenko and Krylov, 1983). These microfossils are interpreted as the remains of polytrichomatous cyanobacterial filaments, comparable to species of the modern genera *Microcoleus*, *Hydrocoleum*, and *Schizothrix* (Seong-Joo and Golubic, 1998).

Order NOSTOCALES? or OSCILLATORIALES?

Genus SIPHONOPHYCUS Schopf, 1968 emend. Knoll and Golubic, 1979 emend. Knoll, Swett, and Mark, 1991

Type species.—*Siphonophycus kestron* Schopf, 1968.

SIPHONOPHYCUS ROBUSTUM (Schopf, 1968) Knoll, Swett, and Mark, 1991 emend. Knoll and Golubic, 1979 Figure 7.8, 7.9

Eomycetopsis robusta SCHOPF, 1968, p. 685, pl. 82, figs. 2, 3, pl. 83, Figs. 1–4; KNOLL AND GOLUBIC, 1979, p. 149, fig. 4A, B; MENDELSON AND SCHOPF, 1982, 59, 60, 62, pl. 1, figs. 9, 10; SERGEEV, 1984, p. 436, fig. 2a–2r; GOLOVENOK AND BELOVA, 1993, pl. 2, fig. e.

Eomycetopsis filiformis SCHOPF, 1968, p. 685, 686, pl. 82, fig. 1, 4, pl. 83, figs. 5–8.

Siphonophycus robustum KNOLL, SWETT, AND MARK, 1991, p. 565, fig. 10.3, 10.5; SERGEEV, KNOLL, AND PETROV, 1997, p. 230, fig. 14A.

Eomycetopsis spp. (partim) MENDELSON AND SCHOPF, 1982, p. 62, pl. 4, fig. 2.

Empty algal tubes SCHENFIL', 1983, p. 471, fig. 1.4, 1.5.

For a full synonymy see Sergeev, 1992, and Butterfield et al., 1994.

Description.—Unbranched nonseptate cylindrical tubes, occasionally solitary, but mostly gregarious in tangled masses. Cross-sectional diameter 2.0–4.5 μm (mean = 3 μm , N = 100); tube walls psilate to finely granular, less than 0.5 μm thick; no septa or cross-walls observed. Dense masses of tubes may be aligned parallel or perpendicular to bedding lamination.

Material examined.—About two thousand individuals in dense mat populations from the Burovaya and Shorikha formations.

Occurrence.—Widely distributed in Proterozoic chert and organic-walled assemblages.

Discussion.—*Siphonophycus robustum* is the predominant mat-building organism in many Proterozoic microbenthic assemblages.

SIPHONOPHYCUS TYPICUM (Hermann, 1974), Butterfield in Butterfield, Knoll, and Swett, 1994 Figure 7.10

Leiotrichoides typicus HERMANN, 1974, p. 7, pl. 6, figs. 1, 2.

Siphonophycus inornatum ZHANG, 1981, p. 491–493, pl. 1, figs. 1, 3–5; PETROV, SEMIKHATOV, AND SERGEEV, 1995, pl. 1, fig. 3.

Eomycetopsis lata GOLOVENOK AND BELOVA, 1985, p. 94–96, pl. 7, fig. 4; GOLOVENOK AND BELOVA, 1993, pl. 2, fig. f.

Siphonophycus typicum BUTTERFIELD in BUTTERFIELD, KNOLL, AND SWETT, 1994, 66–67, figs. 23B–D, 26B, H, I; SERGEEV, KNOLL, AND PETROV, 1997, p. 230–231, fig. 14A, 14B.

For complete synonymy, see Butterfield et al., 1994.

Description.—Unbranched nonseptate tubes, mostly gregarious in tangled masses; cross-sectional diameter 4.5–8 μm ; tube walls psilate to finely granular, ca. 0.5 μm thick. No septa or wall portions observed, but sheaths occasionally broken into rectangular fragments with sharp ends that superficially resemble trichomes.

Material examined.—More than one thousand specimens in the Burovaya and Shorikha cherts.

Occurrence.—Widely distributed in Proterozoic cherts.

Discussion.—Like other *Siphonophycus* species, *S. typicum* is interpreted as the evacuated sheaths of mat-building filamentous cyanobacteria (Knoll et al., 1991). In the Burovaya and Shorikha formations as well as in many other Proterozoic microbiotas, *S. typicum* sheaths are commonly found in close association with those of *S. robustum*, a recurring spatial relationship that resembles the association of *Lyngbya* and *Phormidium* filaments in some modern mats.

SIPHONOPHYCUS SOLIDUM (Golub, 1979) Butterfield in Butterfield, Knoll, and Swett, 1994 Figure 7.7

Omaloophyma solida GOLUB, 1979, p. 151, pl. 31, figs. 1–4, 7.

Siphonophycus solidum BUTTERFIELD in BUTTERFIELD, KNOLL, AND SWETT, 1994, p. 67, figs. 25H, I, 27D; SERGEEV, KNOLL, AND PETROV, 1997, p. 231, fig. 14I, 14K.

Large-diameter "Oscillatoriacean" sheaths: MENDELSON AND SCHOPF, 1982, p. 62–63, pl. 3, figs. 4, 5.

For complete synonymy, see Butterfield et al., 1994.

Description.—Cylindrical to slightly compressed, unbranched, nonseptate tubes, 20–33 μm in cross-sectional diameter, up to 200 μm long (incomplete specimen), tube wall psilate and ca. 1 μm thick.

Material examined.—About 200 specimens from the Burovaya and Shorikha formations.

Occurrence.—Widespread in peritidal mat assemblages of Proterozoic age.

Discussion.—*Siphonophycus solidum* occurs as a subordinate constituent in *S. robustum* and *S. typicum* mats. It is probably the empty sheath of large monotrichomatous *Lyngbya*-like or polytrichomatous *Microcoleus*-like cyanobacteria.

Order NOSTOCALES? or STIGONEMATALES?

Genus ARCHAEOELLIPSOIDES Horodyski and Donaldson, 1980
emend. Sergeev and Knoll, 1995

Type species.—*Archaeoellipsoides grandis* Horodyski and Donaldson, 1980.

ARCHAEOELLIPSOIDES MINOR (Golovenoc and Belova) Sergeev
and Knoll, 1995
Figure 9.10

Archaeoellipsoides minor SERGEEV, KNOLL, AND GROTZINGER, 1995, p. 31, fig. 10.9, 10.10.

For complete synonymy, see Sergeev et al., 1995.

Description.—Solitary, single-layered, nonseptate ellipsoids with rounded ends. Ellipsoids 25–30 μm long and 6 to 7 μm wide; length/width varies from 4 to 5. Vesicle wall translucent, medium-grained, about 0.5 μm thick.

Material examined.—Four specimens from the Shorikha Formation.

Occurrence.—Mesoproterozoic: the Dismal Lakes Group, northern Canada; Wumishan Formation, China; Kotuikan and Yumastakh formations, Anabar Uplift, northern Siberia. Neoproterozoic: the Kirgitey and Lopatinskaya formations, Yenisei Ridge; the Shorikha Formation, Turukhansk Uplift, northeastern Siberia.

Discussion.—These ellipsoidal microfossils from the Shorikha Formation lack evidence for binary cell division and, therefore, are possibly remnants of cyanobacterial cysts. According to formal subdivision of species of *Archaeoellipsoides*, based mainly on size of vesicles, these fossils belong to *A. minor* (Sergeev et al., 1995).

Incertae sedis

Genus POLYSphaeroides Hermann, 1976

Type species.—*Polysphaeroides filiformis* Hermann, 1976.

POLYSphaeroides CONTEXTUS Hermann, 1976
Figure 9.1–9.3

Polysphaeroides contextus TIMOFEEV, HERMANN, AND MIKHAILOVA 1976, p. 42–43, pl. 14, figs. 3, 4; HERMANN, 1990, pl. 7, fig. 8; SCHOPF, 1992, pl. 24, fig. B.

Description.—Solitary, unbranched, unsheathed, nontapering filaments containing spherical compressed cells without any regularity. Sheaths absent; cell walls single-layered, translucent, fine-grained, less than 0.5 μm thick; cell diameters vary from 3.0 to 8.5 μm ($x = 5.75$, $N = 60$), filament diameter about 10 μm , maximum length of filaments up to 250 μm or more (incomplete specimen). Inclusions inside of the cells have not been observed.

Filaments of *Polysphaeroides contextus* occur mainly among trichomes of *Oscillatoriopsis obtusa*.

Material examined.—Two filaments from cherts of the Burovaya Formation.

Occurrence.—Neoproterozoic: the Burovaya and Miroedikha formations, Turukhansk Uplift, northern Siberia.

Discussion.—*Polysphaeroides contextus* differs from *P. filiformis* by its compressed—probably as a result of mutual distortion—and densely packed cells in the filaments and untapering ends; it differs from *P. lineatus* by the irregular arrangement of cells in filaments and from *P. nuclearis* by smaller cells and lack of any intracellular structures.

One specimen of *P. contextus* from the Burovaya cherts demonstrates what may be true branching (Fig. 9.1, 9.2); these tapering branches consist of morphologically dissimilar pill-like cells 3.5–5.5 μm wide and 3.0–5.0 μm long. Alternatively this "branching" may result from the superimposition of originally unbranching filaments of *Polysphaeroides* on trichomes of *Oscillatoriopsis obtusa*. A similar superimposition has been observed for many Precambrian filamentous microfossils, e.g., *Ramacia* or *Circumvaginalis* (see Sergeev, 1992; Sergeev et al., 1995).

In many features, filaments of *Polysphaeroides* are comparable to the modern stigonematalean cyanobacteria; they are composed of a few rows of spheroids and possibly demonstrate true branching. Many modern stigonematalean cyanobacteria have side branches with cells dissimilar to those of the primary filaments. In this case, the trichomes resembling *Oscillatoriopsis obtusa* that co-occur with *P. contextus* may represent early stages in the life cycle of the latter cyanobacteria (see Kondratieva, 1975, p. 123–132). Or, alternatively, *P. contextus* may be remnants of a filamentous eukaryotic alga, e.g., a green alga.

Genus MYXOCOCCOIDES Schopf, 1968

Type species.—*Myxococcoides minor* Schopf, 1968

Discussion.—The genus *Myxococcoides* was described by Schopf (1968) to include simple spheroids without inclusions; originally these fossils were interpreted as chroococcacean cyanobacteria. However, it turned out that such spheroids of simple morphology are comparable to remains of eukaryotes, e.g., green algae (Green et al., 1989; Knoll et al., 1991). Thus, *Myxococcoides* is probably a "wastebasket" taxon that encompasses remnants of eukaryotic and prokaryotic microorganisms of simple spherical morphology and benthic or planktonic ecological setting. Unfortunately, the formal classification of the species of this genus is still unclear due to morphological simplicity and overlapping sizes of most described species. More than 70 species of *Myxococcoides* have been described, but many of them are synonymous. The Burovaya and Shorikha microbiotas include representatives of three species of *Myxococcoides*: *M. minor*, *M. inornata*, and *M. stragulescens*. Their relative sizes are plotted in Figure 5.

MYXOCOCCOIDES MINOR Schopf, 1968
Figures 5, 8.11

Myxococcoides minor SCHOPF, 1968, p. 676, pl. 81, fig. 1, pl. 83, fig. 10.

Description.—Single-walled spheroidal vesicles, 5–16.5 μm in diameter, occurring as solitary unicells or in clusters of a few to many individuals; vesicle wall fine-grained, ca. 1 μm thick. An opaque, spheroidal inclusion about 1.0 μm in diameter sometimes occurs attached to the inner side of the vesicle wall in some species.

Material examined.—About 50 specimens in the Burovaya and Shorikha formations.

Occurrence.—Widely distributed in Proterozoic cherts.

Discussion.—*Myxococcoides minor* differs from other species

of the genus by its size. It is a common component in the Shorikha assemblage.

MYXOCOCCOIDES INORNATA Schopf, 1968
Figures 5, 10.1

Myxococcoides inornata SCHOPF, 1968, p. 676–677, pl. 84, fig. 7.

Description.—Single-layered spheroidal vesicles, occurring as solitary unicells or in clusters of many individuals. The envelope of the spheroids is usually transparent; walls are fine or medium grained, about 1.0 μm thick; spheroid diameters range from 12.0 to 18.0 μm .

Material examined.—Forty-seven specimens from the Shorikha formation.

Occurrence.—Widely distributed in Proterozoic cherts.

Discussion.—In the Shorikha Formation, populations assigned to *M. inornatum* are similar to those referred to *M. minor*, differing principally in size.

MYXOCOCCOIDES STRAGULESCENS Green, Knoll, and Swett,
1989.

Figures 5, 8.12, 10.2, 10.3

Myxococcoides stragulescens GREEN, KNOLL, AND SWETT, 1989, p. 583–584, fig. 10.

Type 7 microfossils (partim) SERGEEV, 1984, p. 438, figs. 2&cyrrj, 2&cyrp;.

Palaeopleurocapsa aff. *wopfnerii* SERGEEV, 1984, p. 437, fig. 2&cyrl;.

Description.—Spheroids with single-layered envelope occurring as solitary unicells, dyads, triads, tetrads (cross and planar), and octads surrounded by a common spherical vesicle, with populations forming monospecific laminae. The spheroid envelope is usually translucent, robust, of spherical shape; walls medium grained about 1.0–2.0 μm thick. An opaque, spheroidal inclusion 2.0–3.0 μm in diameter or dark, irregular blob, or numerous micron-sized dark granules may occur attached to the inner side of the envelope. Many spheroids contain splits in their walls. Spheroid diameters range from 4.5 to 19.0 μm . Vesicles that surround grouped spheroids are spherical or irregular in shape, single- or double-layered, 15–26 μm in diameter, and transparent; vesicle walls medium-grained about 1.0–2.0 μm thick. The diameter of translucent daughter spheroids nested within the common envelope is 4.5–8.0 μm ; spheroid envelopes are 1.0–1.5 μm thick.

Material examined.—More than 2500 specimens from the Shorikha Formation.

Occurrence.—Neoproterozoic: the Limestone-Dolomite Series, central East Greenland; the Shorikha Formation, Turukhansk Uplift, north-eastern Siberia.

Discussion.—*Myxococcoides stragulescens* differs from other species of the genus by having a robust single wall displaying tears, lacking colonial mucilage, and forming dense monospecific layers. Green et al. (1989) have compared *M. stragulescens* to cysts of the green alga *Dunaliella* living today in tidal-flat environments.

Genus LEIOSPHAERIDIA Eisenack, 1958

Type species.—*Leiosphaeridia baltica* Eisenack, 1958.

Discussion.—The formal subdivision of the genus *Leiosphaeridia* proposed by Yankauskas et al. (1989) is followed here. In this classification, all morphologically simple smooth-walled envelopes <1,000 μm fall within the genus *Leiosphaeridia*; this includes taxa described earlier under the names *Trachysphaeridium*, *Kildinella*, *Protoliosphaeridium*, and small specimens of *Chuarina*. The specific subdivision of *Leiosphaeridia* is also purely formal and based on the diameter of envelopes and thickness of the walls (see Yankauskas et al., 1989, p. 24–25).

LEIOSPHAERIDIA JACUTICA (Timofeev) Mikhailova and
Yankauskas in Yankauskas et al., 1989
Figure 8.7–8.10

Leiosphaeridia jacutica (Timofeev) YANKAUSKAS, HERMANN, MIKHAILOVA, SERGEEV, ABDUAZIMOVA, BELOVA, BURZIN, VEIS, VOLKOVA, GOLOVENOK, GRIGORIEVA, KIRYANOV, KOZLOVA, KOLOSOV, KRASKOV, KRYLOV, LUCHININA, MEDVEDEVA, OGURTSOVA, PASCKEVITCHENE, PYATILETOV, RUDAVSKAYA, SIVERTCSHEVA, STANEVICH, TRECHETNICOVA, FAIZULINA, CHEPIKOVA, SCHENFIL', SCHEPELEVA, AND YAKSCHIN 1989, p. 77–78, pl. 12, figs. 3a, 3b, 7, 9; BUTTERFIELD, KNOLL, AND SWETT, 1984, p. 42, fig. 16H.

Description.—Spheroidal, solitary, single-walled vesicles 70–210 μm in diameter (mean = 140, N = 5); walls opaque, dark, shagrinated, or coarse-grained, about 1.5 μm thick.

Material examined.—Fourteen specimens from the Shorikha Formation.

Occurrence.—Widely distributed in Neoproterozoic rocks.

Discussion.—*Leiosphaeridia jacutica* encompasses morphologically simple opaque or translucent envelopes with thick (about 2 μm) walls and 70–800 μm in diameter; the envelopes may bear folds. In certain features (thick, robust, shagrinated wall and large envelope diameter), *L. jacutica* from the Shorikha Formation is similar to *Cerebrophaera buickii* Butterfield (in Butterfield et al., 1994) from the Svanbergfjellet Formation of Spitsbergen, but the latter species demonstrates a regularly and prominently corrugated wall. *Leiosphaeridia jacutica* is a common but not ubiquitous component of the Shorikha assemblage. The biological affinities of the population are uncertain; they may represent empty eukaryotic cells or empty envelopes of colonial cyanobacteria. The distribution of these fossils within the Shorikha formation suggests that they were planktonic.

Genus PTEROSPERMOSIMORPHA Timofeev, 1966 emend.
Mikhailova and Yankauskas in Yankauskas et al., 1989

Type species.—*Pterospermopsimorpha pileiformis* Timofeev, 1966.

PTEROSPERMOSIMORPHA? sp.

Figure 8.1, 8.2

Description.—Spheroidal vesicles consisting of two envelopes separated by empty space; inner envelope translucent, robust, more or less regularly spheroidal in shape, about 2 μm thick; outer envelope translucent, spheroidal, irregular in outline, 14–15 μm thick; envelopes separated by 1–2 μm . Outer diameter of spheroids 280 μm ; inner diameter—250 μm . An eccentrically located, grainy, opaque internal body about 60 μm in diameter is present. No processes were observed to support the outer envelope.

Material examined.—One specimen from the Shorikha Formation.

Discussion.—The identification of this form as *Pterospermopsimorpha* is tentative because this genus as emended (Yankauskas et al., 1989) encompasses spherical vesicles with an internal, dark shagrinated body whose diameter is not less than two-thirds of the outer envelope. The diameter of inner inclusions within spherical microfossils is variable and depends on the stage of degradation (Hofmann, 1976; Knoll and Golubic, 1979). In planktonic microorganisms similar to *Pterospermopsimorpha* sp. from the Neoproterozoic Russö Formation of Spitsbergen, the size of the inner body varies from almost equal to the diameter of the outer envelope to small spot-like inclusions (Knoll and Calder, 1983, pl. 58, figs. 7, 8). Thus, I suggest that the ratio of the inner body diameter to the outer envelope is not a reliable taxonomic character; accordingly, this genus should be emended, but on the basis of better preserved material.

In its general morphology, *Pterospermopsimorpha* resembles populations of characteristically Neoproterozoic phytoplanktonic microorganisms, e.g., the acanthomorphic acritarch *Trachyhystrichosphaera* (the vesicles have regular inner and wavy outer envelopes). The obvious difference between *Trachyhystrichosphaera* and the Shorikha microfossil is that in the former, cylindrical processes arise from the inner vesicle and support the outer envelope. Within *Trachyhystrichosphaera* populations, however, as many as 50 percent of all specimens do not have preserved processes (Knoll et al., 1991; Sergeev, 1992; Butterfield et al., 1994). Therefore, it is possible that the Shorikha specimen originally had processes, but lost them during post-mortem decay. In general morphology, the Shorikha *Pterospermopsimorpha?* sp. resembles microfossils from the underlying Sukhaya Tunguska Formation described as an unnamed planktonic form (Sergeev et al., 1997).

Genus SHORIKHOSPHAERIDIUM new genus

Type species.—*Shorikhosphaeridium knollii* new species by monotypy.

Diagnosis.—Spherical single-walled microfossils less than 100 microns in diameter bearing irregularly located processes of variable morphology. The process morphology varies from conical spine-like to elongated bifurcating; process length/vesicle diameter ratio varies from 1/10 to 1/7.

Description.—Microfossils of spherical morphology bearing numerous processes. The morphology and length of processes varies significantly from short spine-like to those that are long and bifurcated. The vesicles have single-walled envelopes; outer envelopes have not been observed, but many spheroids are surrounded by dark-brown mucilage.

Etymology.—Named for the Shorikha Formation, the source of the type material.

Discussion.—This new genus differs from other genera of Proterozoic acanthomorphic acritarchs mainly by its variable and irregularly located processes; it is distinguished from the genus *Trachyhystrichosphaera* by its size, process heterogeneity, and lack of an outer envelope.

SHORIKHOSPHAERIDIUM KNOLLII new species

Figure 8.3–8.6

Diagnosis.—Spheroidal vesicles 50–100 μm in diameter that bear short, conical, tapering processes and longer bifurcating processes from 5–8 μm up to 14 μm long and 1–2 μm thick.

Description.—Spheroidal single-walled vesicles 50–100 μm in diameter; envelope translucent, robust, more or less regularly spheroidal or elliptical in shape, about 2 μm thick; outer envelope has not been observed, but vesicles may be surrounded by amorphous dark brown mucilage. The vesicle envelope bears conical processes from 5–8 μm up to 14 μm long and 1–2 μm thick near their base; some processes may exhibit terminal branching or funnels.

Etymology.—In honor of Prof. A. H. Knoll, Harvard University, Cambridge, USA.

Material examined.—Eight specimens from the Shorikha Formation.

Type.—Figure 8.5; 758 Neoproterozoic, the Shorikha Formation.

Type locality.—Locality III.

Discussion.—In general morphology and size, these fossils resemble populations of the small Neoproterozoic acanthomorphic acritarch *Trachyhystrichosphaera parva*, in which vesicles have only a single envelope that bears processes. However, Butterfield (in Butterfield et al., 1994) rejected *T. parva* as an invalid taxon and questioned the origin of its processes. For these reasons I

have described the Shorikha population as a new species and genus.

Genus SCISSILISPHAERA Knoll and Calder, 1983

Type species.—*Scissilisphaera regularis* Knoll and Calder, 1983.

SCISSILISPHAERA GRADATA Green, Knoll, and Swett, 1989 Figures 6, 10.4–10.7

Scissilisphaera gradata GREEN, KNOLL, AND SWETT 1989, p. 581–583, figs. 8, 9.

“Type 4 microfossils” SERGEEV, 1984, p. 436–437, fig. 2&cyre;

“Type 7 microfossils” (partim) SERGEEV, 1984, p. 438, fig. 2o, 2p.

Description.—Single- and double-walled spheroidal vesicles solitary, but commonly in colonies of a few to several hundred discrete individuals occurring along a single lamina. The vesicles cluster in discrete groups, from 4 to 60 μm in diameter; a group of small spheroids may be surrounded by a common envelope forming *Gloeocapsa*-like colonies. The diameter of the smaller, apparently daughter, spheroids varies from 4 to 30 μm , and the larger spheroids from 32 to 60 μm with a break in the size distribution (Fig. 6). The inner envelope is translucent, fine-grained, about 1 μm thick; outer envelope, if present, also translucent, fine grained, less than 1 μm thick; the large spheroids sometimes have a robust wall about 1 μm thick.

Material examined.—Two to three thousand spheroids in cherts of the Shorikha Formation.

Occurrence.—Neoproterozoic: the Eleonora Bay Group, central East Greenland; the Shorikha Formation, Turukhansk Uplift, northeastern Siberia.

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

Knoll and Calder (1983) and Green et al. (1989) have compared the species of this genus to modern pleurocapsalean cyanobacteria of the genera *Chroococcidiopsis*, *Stanieria*, and *Xenococcus* because of the presence in their life cycle of packets of smaller vesicles interpreted as baeocytes. Within Cyanobacteria, baeocyte formation is diagnostic for the order Pleurocapsales (Castenholz and Waterbury, 1989); however, the small simple spores are also formed by a diverse assortment of protists, e.g., the green alga *Dunaliella* found today in tidal-flat environments (Green et al., 1989). Therefore, I prefer to treat this species here as *Incertae sedis*.

Problematic ellipsoidal forms

Figure 9.6, 9.7, 9.11, 9.12

Description.—Solitary single-layered ellipsoid with rounded ends. Ellipsoids nonseptate, slightly curved and empty with blebs of amorphous material in vesicle interiors. Ellipsoids 90–160 μm long and 30 to 85 μm wide; length/width varies from 1.75 to 5. Vesicle wall translucent, medium-grained, about 1.5 μm thick.

Material examined.—Five specimens from the Burovaya Formation.

Discussion.—These ellipsoidal fossils differ from species of *Archaeoellipsoides* mainly by their large size. Species of *Archaeoellipsoides* are interpreted as akinetes of *Anabaena*—like nostocalean cyanobacteria (Sergeev et al., 1995; Golubic et al., 1995). The largest akinetes of modern species of *Anabaena*, *A. bornetiana* and *A. lapponica*, are up to 95–110 μm long and 20–12 μm width, respectively (Elenkin, 1938; Golubic et al., 1995). Thus, these microfossils from the Burovaya Formation are probably remnants of physiologically dissimilar, probably eukaryotic organisms and should be described as a new genus and species.

However, the dearth of restricted material (only five specimens were found) precludes formal description.

Problematic spiny forms

Figure 10.10–10.13

Description.—Spherical double-walled vesicles, solitary or in loose clusters from a few to many dozen individuals. The inner envelope is translucent, dark, robust, irregular in outline, about 2 μm thick; outer envelope transparent, more or less regular outline, either fine-grained or with an amorphous, unclear appearance, about 1 μm thick. Outer envelope diameter 12–65 μm ($x = 38.5 \mu\text{m}$, $N = 27$); inner envelope diameter 5–50 μm ($x = 27.5 \mu\text{m}$, $N = 28$); envelopes are separated by 1.5–8.5 μm space. Inner envelope bears thin processes 1–8 μm long, thickening near base.

Material examined.—Sixty specimens from the Shorikha Formation.

Discussion.—These microfossils are probably degradational variants of other coccoidal microfossils originally having smooth envelopes, e.g., *Myxococcoides stragulesens* or *Scissilisphaera gradata*. In some cases, it is possible to find apparent transitional forms between smooth-walled and spine-bearing microfossils. On the other hand, I can not rule out the possibility that these spiny forms are stages in the life cycle of *Myxococcoides*-like eukaryotic algae.

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