

The Importance of Precambrian Microfossils for Modern Biostratigraphy

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Abstract—A new model of the distribution of Proterozoic microorganisms is developed, based on studies of Riphean and Vendian silicified and organic-walled microfossils from the reference sections of northern Eurasia, and on their comparison with other known microfossil assemblages. Within the interval from 2.0 to 0.535 Ga, seven successive informal global microphytological units (referred to as proterohorizons) are determined: (1) Labradorian proterohorizon occupies the upper part of the Lower Proterozoic (Paleoproterozoic), 2.0–1.65 Ga; (2) Anabarian proterohorizon, Lower Riphean–lower Middle Riphean (lower and middle Mesoproterozoic), 1.65–1.2 Ga; (3) Turukhanian proterohorizon, upper Middle Riphean (upper Mesoproterozoic), 1.2–1.03 Ga; (4) Uchuromayan proterohorizon, lower Upper Riphean (lower Neoproterozoic), 1.03–0.85 Ga; (5) Yuzhnouralian proterohorizon, upper Upper Riphean (upper Neoproterozoic without Ediacaran); (6) Amadeusian proterohorizon, Lower Vendian (Ediacaran), 0.6–0.55 Ga; and (7) Belomoryan proterohorizon, Upper Vendian (Ediacaran), 0.55–0.535 Ga.

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INTRODUCTION

During the past 10–15 years, considerable advances have been made in the study of Proterozoic microorganisms. First, the remains of unicellular eukaryotes that are characterized by morphological complexity and high evolutionary rate (compared to other Precambrian organisms) were discovered in assemblages of both organic-walled and silicified microfossils. Second, a biostratigraphic paradox of cyanobacterial assemblages was revealed: transient taxa form temporarily differentiated assemblages with a relatively limited vertical distribution. As a result, a series of Proterozoic microphytological units was defined on the basis of successive assemblages of microfossils; and these units do not correspond to standard units of either the Russian or International Stratigraphic Scales. This discrepancy led the author to the invention of informal units that might be useful in the current study of microfossils and may serve as the basis for defining formal units of the global stratigraphic scale of the Upper Precambrian. The term *proterohorizon* is proposed, a close Proterozoic analogue of *local zone* (with fauna), which is commonly used in biostratigraphic practice. The established proterohorizons are correlated with the Russian Proterozoic Scale, which is a chronostratigraphic scale (*Resolutions...*, 2001). In addition, a comparison is made with the main units of the International Proterozoic scale (Plumb, 1991), which are also widely used in stratigraphy; this scale is chronometrical (Paleoproterozoic, Mesoproterozoic, Neoproterozoic, and Edi-

acaran). However, the more detailed units of the International scale (now virtually abandoned), such as the Tonian or Cryogenian, are not considered here (for the comparative analysis of both scales see Semikhatov, 1995).

The model of the distribution of different morphotypes that is described below is based on the studies of successive Riphean and Vendian microbiotas in cherts from reference sections of northern Eurasia and the global comparison with other Precambrian assemblages of silicified and organic-walled microfossils. Not only the remains of microorganisms but also the chemostratigraphic and isotopic-geochronological data are compared. As a result, seven proterohorizons have been established for the Proterozoic, which embrace definite time intervals varying from 2.0 to 0.535 Ga: Labradorian, Anabarian, Turukhanian, Uchuromayan, Yuzhnouralian, Amadeusian, and Belomoryan (Fig. 1). The unique microphytological characteristics of each unit reflect both the evolution of the microorganisms themselves (mostly eukaryotes and, possibly, some groups of cyanobacteria) and the directional changes in the physicochemical parameters of the atmosphere, hydrosphere, and lithosphere that caused environmental variations and affected the composition of fossil microbial assemblages. The lower temporal limit of the succession is determined by the moment in the geological history (about 2 Ga ago) when the fossil record becomes representative and enables adequate subdivisions to be defined. Since the more ancient remains of microorgan-

isms from the Lower Proterozoic and Archean are rare, and their biological nature is often debatable, they are inapplicable to biostratigraphy. For formal reasons, the upper limit of this succession is restricted to the Precambrian/Cambrian boundary, although major changes in the composition of microbiota occur slightly later, approximately at the base of the Atdabanian Stage of the Lower Cambrian. According to the rules of the Phanerozoic stratigraphy, the range of subdivisions is determined by the position of the lower boundaries of the equivalent strata. Such boundaries are defined by the appearance of characteristic microfossil assemblages. Each proterohorizon is characterized by the most typical microbiota, and its name is derived from the location of this microbiota.

It should be noted that this subdivision of the Upper Precambrian is based solely on silicified and organic-walled microfossils, even for Vendian deposits. Although problematic remains of multicellular animals were recently found in the Pre-Vendian as well, the Lower Riphean including, they are too rare, and their animal (biogenic) origin is often uncertain; therefore, they currently cannot be used in biostratigraphic reconstructions of the Pre-Redkino deposits. Remains of macroscopic organisms that are preserved mostly on the bedding surfaces remain virtually unused in the analysis, in spite of their common occurrence in the temporal range under consideration, because they are so far insufficiently studied.

THE CHARACTERISTICS OF THE PRECAMBRIAN PROTEROHORIZONS

Labradorian proterohorizon occupies the upper part of the Lower Proterozoic (Paleoproterozoic), 2.0–1.65 Ga. The typical microbiota comes from the Gunflint Formation (North America), approximately 1.9 Ga.

The silicified microbiotas known in this temporal range are of two main types: Belcher type and Gunflint type, differing in both the taxonomic composition of fossil microorganisms and in facial-ecological position (Fig. 2).

Gunflint-type microbiotas. The typical microbiota of the Labradorian proterohorizon is described from the Gunflint Iron Formation of the Animikie Supergroup, 1.9 Ga (Barghoorn and Tyler, 1965; Awramik and Barghoorn, 1977; Hofmann and Schopf, 1983; etc.). It includes two groups of microfossils. The first group comprises morphologically simple trichomes and sheaths of the genera *Gunflintia* and *Animikia*, as well as coccoid microfossils of *Huroniospora*, *Leptoteichos*, and *Corumbococcus*, representing remains of cyanobacteria and iron-oxidizing bacteria (Knoll, 1996). The second group embraces remains of more morphologically advanced microorganisms (umbrella-, dumbbell-, star-shaped, etc.) belonging to *Kakabekia*, *Xenothrix*, *Archaeorestis*, *Eoastrion*, *Eosphaera*, *Eomicrhystridium*,

		Proterohorizons		Ma
Proterozoic	Neo-	Є		535
		V	Belomoryan-Bm	550
			Amadeusian-Am	600
	R ₃	Yuzhnouralian-Ur	850	
		Uchurumayan-Um	1030	
		R ₂	Turukhanian-Tr	1200
			Anabarian-An	1350
	Meso-	R ₁		1650
				2000
	Paleo-			2500

Fig. 1. Microphytological proterohorizons of the Precambrian.

and other genera. The latter genera may contain remains of heterotrophic bacteria, including iron bacteria (*Eoastrion*) and, supposedly, unicellular eukaryotes (*Eosphaera* and *Eomicrhystridium*). The sedimentation conditions of the Gunflint-type microfossil assemblages are considered to be relatively deep-water within the proximal or distal part of open shelf. The distinctive features of the microbiotas are predetermined by their close relationship with iron-ore formations, thus resulting in a taxonomic composition consisting of morphologically complex microfossils. Assemblages of the Gunflint type are described in several Upper Paleoproterozoic beds: the Odjick and Sokoman formations of Canada; the Chuanlinggou Formation of China; and the Frere, Barney Creek, and Duck Creek formations of Australia (for reviews see Hofmann and Schopf, 1983; Semikhatov et al., 1999).

Belcher-type microbiotas are dominated by morphologically simple entophysalidacean (*Eoentophysalis*) and chroococcacean (*Eosynechococcus*, *Myxococcoides*, and other genera) cyanobacteria and remains of less numerous filamentous hormogonion cyanobacteria, mostly by hollow sheaths of *Siphonophycus*, a genus that has modern analogues at the generic and even specific levels. Belcher microbiotas, which are considered as a deeper-water analogue of Gunflint biotas, are described from shallow (upper sublittoral–littoral) carbonates, 2.0–1.65 Ga: the MacLiry, Kasegalik, and Rocknest formations of Canada and the Amelia, Balbirini, Bungl Bungl, and Paradise Creek formations of Australia (Hofmann, 1976; Hofmann and Schopf, 1983).

Macroscopic problematic remains of eukaryotes. *Grypania*-, *Chuar*-, and *Tawuia*-like carbonaceous films, which may be remains of macroscopic eukary-

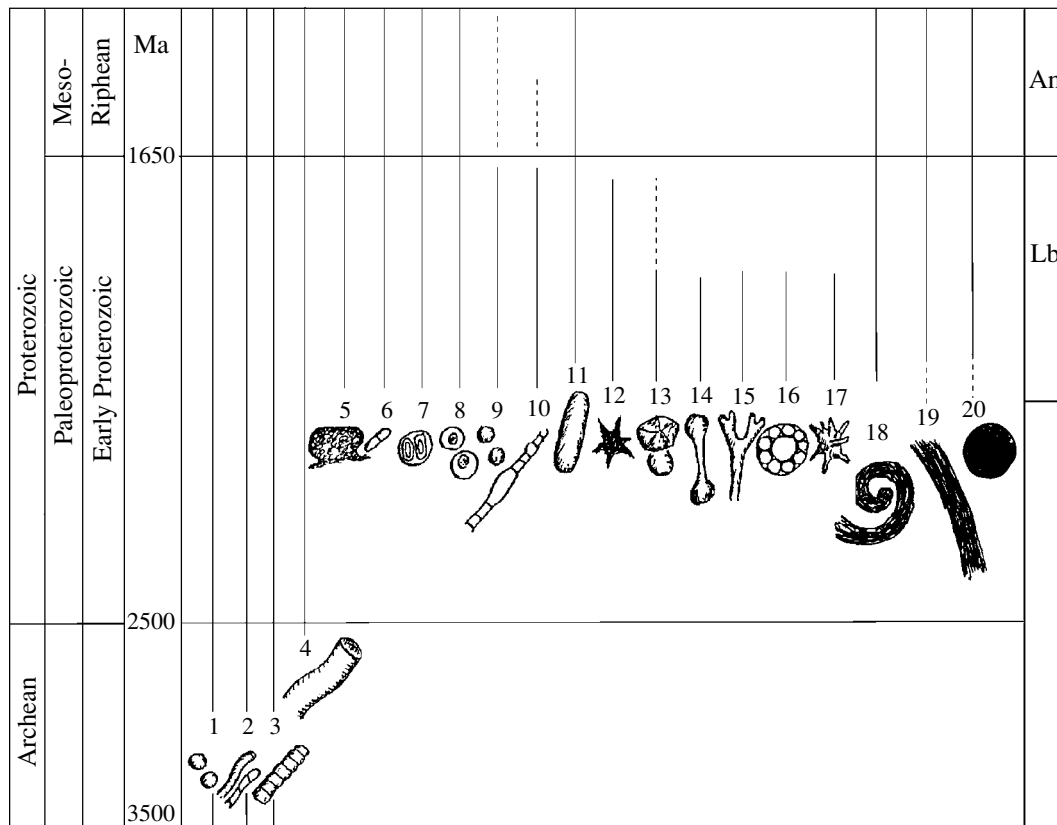


Fig. 2. Distribution of main types of microfossils in the Archean and Early Proterozoic: (1) small (<10 μm) solitary spherical microfossils; (2) small (<10 μm in diameter) filamentous microfossils; (3) trichomes and trichome-like fossils (>10 μm in diameter); (4) large (up to 35 μm in diameter) non-septate filaments, supposed empty sheaths of oscillatoriacean cyanobacteria; (5) remains of entophysalidacean cyanobacteria (*Eoentophysalis*); (6) unicellular ellipsoid chroococcacean *Synechococcus*-like cyanobacteria (genus *Eosynechococcus*); (7) unicellular chroococcacean *Gloeocapsa*-like cyanobacteria (genus *Gloeodiniopsis*); (8) coccoidal microfossils with dense bodies inside; (9) coccoidal microfossils without inclusions (*Myxococcoides*); (10) trichomes with individual enlarged cells (*Gunflintia*); (11) large ellipsoid envelopes, supposed akinetes of cyanobacteria; (12–17) microfossils of complicated morphology from Gunflint-type assemblages; (12) *Eoastrion*; (13) *Kakabekia*; (14) *Xenothrix*; (15) *Archaeorestis*; (16) *Eosphaera*; (17) problematic acanthomorphic acritarchs *Eomicrhystridium*; (18) imprints of large spiral fossils (genus *Grypania*); (19) imprints of large ribbon *Tawuia*-like fossils; (20) remains of large *Chuarita*-like spherical forms. To the left of the scheme of distribution, units of International and Russian stratigraphic charts of the Precambrian are shown; to the right, the introduced proterohorizons; (Lb) Labradorian; (An) Anabar.

otes, were found in the 1.9-Ga-old shaly Negaunee Formation of North America (Han and Runnegar, 1992) and in the Chuanlinggou and Tuanshanzi formations (Hofmann, 1994).

Anabar proterohorizon, Early and early Middle Riphean (Early and Middle Mesoproterozoic), 1.65–1.2 Ga. The type microbiota comes from the Kotuikan Formation of the Billyakh Group of the Anabar Uplift, Lower Riphean of Siberia.

Gunflint microbiotas disappeared at the Early Proterozoic/Riphean boundary (Paleoproterozoic/Mesoproterozoic), suggesting a possible relationship with the extinction of Banded Iron Formations. In the Lower–lower Middle Riphean there were two main types of silicified microbiotas: Anabar and Satka types (Fig. 3).

Anabar-type microbiotas. The main distinctive feature of the Lower–lower Middle Riphean is the pre-

dominance of assemblages of akinete-bearing cyanobacteria in shallow-water deposits of the littoral and upper sublittoral zones. Their remains are mostly represented by fossilized spores of *Archaeoellipsoides* (Golubic et al., 1995; Knoll and Sergeev, 1995; Sergeev et al., 1995; Sergeev, 2006). Similar elliptic microfossils that were described as different species of the genera *Archaeoellipsoides*, *Brevitrichoides*, and *Navifusa* are also known from Pre-Riphean, Upper Riphean, and Vendian deposits (Yankauskas et al., 1989; Sergeev, 1992, 2006); however, the assemblages in which they dominate are restricted to the Lower–Middle Riphean. The second key character of Anabar microbiotas is the common occurrence of short trichomes of the genera *Filiconstrictosus*, *Orculiphycus*, and *Partitiofilum*, which were apparently germinating akinetes of *Archaeoellipsoides*. In addition to these and coccoid microfossils of *Myxococcoides grandis* Horodyski et Donald-

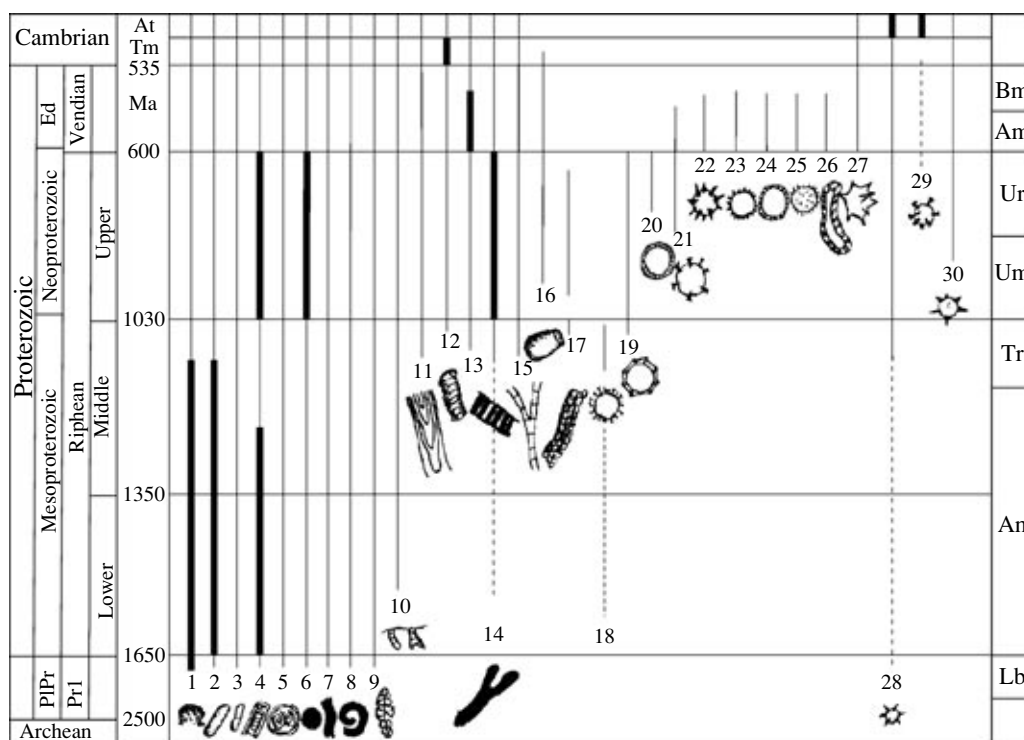


Fig. 3. The occurrence of the main types of microfossils in the Riphean and Vendian: (1) remains of entophysalidacean cyanobacteria (genus *Eoentophysalis*); (2) akinetes of cyanobacteria of the genus *Archaeoellipsoides*; (3) unicellular ellipsoidal *Synechococcus*-like chroococcacean cyanobacteria; (4) trichomes and filaments of cyanobacteria; (5) unicellular chroococcacean *Gloeocapsa*-like cyanobacteria (genus *Gloeodiniopsis*); (6) large *Chuar*-like spherical microfossils; (7) large ribbon forms (*Tawuia*); (8) large spiral macroscopical microfossils (genus *Grypania*); (9) pleurocapsalean cyanobacteria (*Palaeopleurocapsa* and other genera); (10) endolithic cyanobacteria (*Eohyella* and other genera); (11) stalked cyanobacterium (*Polybessurus*); (12) spiral-cylindrical cyanobacteria (genus *Obruchevella*); (13) red algae; (14) branching thalli of unknown origin (*Ulophyton* and *Majaphyton*), remains of stigonematalean cyanobacteria, red or green algae; (15) thalli of siphonocladalean green algae (*Proterocladus*); (16) remains of eukaryotic vase-shaped microorganisms (*Melanocyrrillum* and other genera); (17) trichomes of cyanobacteria or thalli green algae (genus *Polysphaeridium*); (18–30) genera of eukaryotic phytoplankton of complicated morphology; (18) *Tappania* and *Shuiyousphaeridium*; (19) *Skiagia*; (20) *Cymatiosphaeroides*; (21) *Vandalosphaeridium*; (22) *Cavaspina*; (23) *Echinospaeridium*; (24) *Cerionopora*; (25) *Ericiasphaera*; (26) *Papillomembrana*; (27) *Tanarium*; (28) *Micrhystridium* (including *Eomicrhystridium*); (29) *Skiagia*; (30) *Baltisphaeridium*. Units of International and Russian stratigraphic charts are given to the left of the scheme of distribution, and the proterohorizons established are shown to the right of the scheme: (Lb) Labradorian; (An) Anabar; (Tr) Turukhanian; (Um) Uchuromayan; (Ur) Yuzhnouralian; (Am) Amadeusian; (Bm) Belomoryan. Other abbreviations: (Pr¹) Lower Proterozoic; (PIP^r) Paleoproterozoic; (Ed) Ediacaran; (Tm) Tommotian Stage; (At) Atdabanian stage.

son, there are remains of the majority of microorganisms that occur in the Lower Proterozoic Belcher-type assemblages. The most common are entophysalidacean and *Synechococcus*-like cyanobacteria, chroococcacean cyanobacteria of the genus *Gloeodiniopsis*, as well as sheaths of hormogonion cyanobacteria of the genus *Siphonophycus* and peculiar nested elongated funnel-shaped segments with terminal ringlike thickenings of the genus *Circumvaginalis* (Sergeev et al., 1995). Anabar microbiotas are common in the Lower and Middle Riphean deposits of 1600–1200 Ma. They were found in the Gaoyuzhuang and Wimishan formations of China, the Dismal Lakes Group (Canada), Kyutingda and Debengda formations of the Olenek Uplift, and in the Kheinjua Formation of India (for a review see Sergeev, 2006).

The predominance of *Archaeoellipsoides* in the middle Lower Riphean should probably be explained in

an ecological-facies context rather than an evolutionary context. A principal role was played by the global evolution of environmental conditions and geochemical environments and, in particular, carbonate sedimentation. Supposedly, the abundance of *Archaeoellipsoides* is a result of the complete transformation of filaments into chains of akinetes under conditions of chemogenic precipitation of carbonates from oversaturated solutions in shallow-water environments. The abundance of akinetes in the Early–Middle Riphean basins is apparently related to the existence in this period of vast littoral-sublittoral shallow-water regions, resulting in an alternation of favorable and unfavorable conditions and the mass production of spores of the *Anabaena*-like cyanobacteria that colonized these niches (Knoll and Sergeev, 1995; Sergeev et al., 1995; Sharma and Sergeev, 2004; Sergeev, 2006).

Satka-type microbiotas, which occur much more rarely, are dominated by sheaths of *Siphonophycus*, coccoid microfossils of *Gloeodiniopsis* and *Eosynechococcus*, and trichomes and filaments of *Palaeolynghya* and *Oscillatoria*. Similar assemblages were found in the Satka Formation of the stratotype section of the Lower Riphean, southern Ural Mountains, and in the Svetlyi Formation (Middle Riphean) of the Aimchan Group, Uchur-Maya Region. The Satka microbiota is the only microbiota with numerous remains of eukaryotic spherical, spineless, phytoplanktonic remains more than 100 µm in diameter, belonging to various species of the genera *Leiosphaeridia*, *Pterospermopsis*, and *Myxococcoides* (Sergeev, 1992, 2006; Sergeev and Lee Seong-Joo, 2001, 2004).

Organic-walled microbiotas. Microfossil assemblages from the Burzyan Group of the type section of the Lower Riphean, southern Ural Mountains, and the Uchur Group of the Uchur-Maya Region are characterized by the presence of small, morphologically simple remains of coccoid and filamentous microorganisms. The most diverse assemblages of organic-walled microfossils of the Lower Riphean come from open-sea facies of the Ust'-Il'ya and Kotuikan formations of the Anabar Uplift (Veis and Vorob'eva, 1992; Veis et al., 2001) and from the Kyrpin Group of Cis-Urals, an analogue of the Burzyan Group (Veis et al., 2000). These microbiotas contain not only morphologically simple filamentous and coccoid small microfossils of *Leiosphaeridia*, *Ostiana* (= *Coniunctiophycus*?), and *Sphaerocongregus*, sheaths of *Siphonophycus* and *Rectia*, akinetes of *Brevitrichoides* (= *Archaeoellipsoides*), wide trichomes of *Botuobia*, and some other forms but also spheromorphids of *Chuarina*, branching thalli of the *Ulophyton*-type, and some other forms of complex morphology (Veis and Vorob'eva, 1992; Veis et al., 2001; etc.).

The microbiota of the Roper Group, Australia, is of a specific type. U-Pb zircon data relatively reliably indicate an age of 1.5 Ga. Shales of this group contain the most ancient remains with true spines and processes, assignable to the genus *Tappania*; some relatively complex forms of *Valeria*, *Dictiosphaera*, and *Satka* (Javaux et al., 2001); and large filaments and spheroids up to 100 and 500 µm in diameter, respectively (Peat et al., 1978). A similar assemblage was found in the Baicaoping and Beidajian formations of the Ruyang Group, China (Xiao et al., 1997), the age of which is not as reliably dated and may vary from the Early Riphean to the upper Middle Riphean.

Macroscopic carbonaceous fossils of various outlines (spiral *Grypania*, oval *Chuarina*, wide bands with rounded ends of *Tawuia*, and others) are quite common in siliciclastic deposits of the Lower and Middle Riphean: the Gaoyuzhuang Formation of China, the Rohtas Formation of India, the Belt Group of North America (Walter et al., 1990), and some others.

Turukhanian proterohorizon, late Middle Riphean (Late Mesoproterozoic), 1.2–1.03 Ga. The type microbiota comes from the Sukhaya Tunguska Formation of the Turukhansk Uplift, the Middle Riphean of Siberia.

The changes that occurred in the composition of microfossil assemblages near the Middle/Upper Riphean boundary were among the most prominent in the Precambrian. The new data demonstrate that these changes started in the second half of the Middle Riphean, about 1200 Ma, and led to crucial compositional changes in the communities of microorganisms. The main event that took place near the Middle/Upper Riphean (Mesoproterozoic/Neoproterozoic) boundary was the burst of diversification of eukaryotic microorganisms, which resulted, firstly in the appearance of morphologically complex forms and secondly the total incorporation of eukaryotes into prokaryotic ecosystems.

Silicified microbiotas. The most ancient eukaryotic microorganisms that show a complex differentiation in morphology and have received a biological interpretation are remnants of the bangiophytic red alga *Bangiomorpha pubescens* Butterfield, from the 1.2-Ga-old Hunting Formation of North America (Butterfield, 2001). These algae are in close association with the stalked cyanobacterium *Polybessurus bipartitus*, the appearance of which supposedly reflects a new phase in the evolution of prokaryotic microorganisms. These stalked cyanobacteria are also abundant in other silicified microbiotas of the Turukhansk proterohorizon, which also include sheaths of *Siphonophycus*; entophysalid cyanobacteria *Eoentophysalis dismallakesensis* Horodyski et Donaldson and *E. belcherensis* Hofmann; chroococcacean cyanobacteria of the genera *Gloeodiniopsis*, *Eoaphanocapsa*, and *Eosynechococcus*; and several more forms of simple morphology and broad vertical distribution. Remains of akinetes of the genus *Archaeoellipsoides* are lacking or insignificant. Open-sea deposits of these beds contain unquestionable remains of phytoplanktonic eukaryotic microorganisms, often supplied with problematic spines and processes; these are supposedly acanthomorphic acritarchs similar to members of *Shuiyousphaeridium* or *Trachyhystrichosphaera*. Similar assemblages of microorganisms occur in the Sukhaya Tunguska Formation, which terminates the Middle Riphean section of the Turukhansk Uplift (Sergeev et al., 1997; Sergeev, 2006), in the Uluksan Group of Baffin Island, Canada, 1270–1240 Ma (Hofmann and Jackson, 1991), and in the Kataskin Subformation of the Avzyan Formation, Middle Riphean stratotype of the Ural Mountains (Sergeev, 1992, 1994, 2006).

Organic-walled microbiotas. The composition of late Middle Riphean organic-walled microbiotas vary significantly both laterally and vertically. The Tulmen Subformation of the Avzyan Formation of the Ural Mountains contains members of the genera *Leiosphaeridia*, *Valeria*, *Sphaerocongregus*, *Ostiana*,

Polytrichoides, *Asperatofilum*, and *Brevitrichoides*, as well as some other forms occurring in the underlying and overlying deposits (Yankauskas et al., 1989; Veis et al., 1990, 2003). The Kuzha Group of the southern Ural Mountains, which is usually correlated with the Yurmata Group, yields transient microfossils and more complicated morphological types, some analogues of which are present in the Kotuikan Formation and in the Kyrpin Group (Veis et al., 2000). In the Uchur-Maya and Turukhansk regions of Siberia, rich and diverse microbiotas are only known starting from the Totta and Bezymyanni formations of the upper Middle Riphean (Veis and Vorob'eva, 1993). In addition to the morphotypes that are known from the Lower Riphean microbiota of the Omakhta Formation, there are also large (up to 1100 μm) spherical specimens of *Chuarina*, filamentous *Asperatofilum*, *Taenitrichoides*, *Rectia*, *Rugosopsis*, and *Trachytrichoides*, branching thalli of *Ulophiton* and *Majaphyton*, as well as some other forms that are also known from the Kotuikan microbiota.

Uchuromayan proterohorizon, early Late Riphean (Early Neoproterozoic), 1.03–0.85 Ga. The type microbiota comes from the Neryuen and Ignikan formations of the Lakhanda Group of the Upper Riphean (Uchur-Maya Region of Siberia).

The changes in the composition of the silicified and organic-walled microbiotas that started about 1200 Ma and mostly included diversification of eukaryotic microorganisms were most distinct near the Middle/Upper Riphean boundary. The most characteristic taxa that appeared in the Late Riphean are members of *Trachyhystrichosphaera* and *Prolatoforma* bearing spines and processes. Some scientists even consider the presence of forms with processes (genus *Trachyhystrichosphaera*) as a crucial characteristic of Upper Riphean microbiotas that differentiates them from older and younger microfossil assemblages (Knoll, 1984; Sergeev, 1992; Butterfield et al., 1994). In particular, they are known from lower horizons of the type section of the Upper Riphean, Lakhanda Group of the Uchur-Maya Region, the Derevnya Formation of the Turukhansk Region and its analogues (Petrov and Veis, 1995), the Tindir Group of Alaska (Allison and Awramik, 1989), Ryssö, Hunnberg, and Svanbergfjellet formations of Svalbard (Knoll and Calder, 1983; Knoll, 1984; Butterfield et al., 1994), and many others.

In addition to remains with spines, several other eukaryotic microorganisms of complicated morphology are known from Upper Riphean deposits; e.g., true branching thalli of *Aimophyton*, *Palaeosiphonella*, *Palaeovaucheria*, and *Proterocladus*, which can be fairly reliably correlated with modern green vaucheriacan algae (Timofeev and Herman, 1979; Yankauskas et al., 1989; Herman, 1990; Butterfield et al., 1994). A form that appeared in the Late Riphean and occurs in the Lakhanda and Derevnya microbiotas is of particular interest: peculiar coccoid microfossils that were described as the genus *Eosaccharomyces* and that are

virtually identical in their morphology to modern cup fungi (Herman, 1990).

In spite of evolutionary conservatism of cyanobacteria, spiral-cylindrical members of *Obruchevella* are restricted to the Upper Riphean and younger deposits. The most ancient *Obruchevella* has been recorded from the Valukhta Formation of the lower Upper Riphean (Belova and Golovenok, 1999). Indisputable spiral-cylindrical filaments of *Obruchevella* are known from the Seryi Klyuch Formation (Yenisei Ridge), in slightly younger deposits of the Miroedikha Formation, Turukhansk Uplift (Herman, 1990), and in the Chichkan Formation, southern Kazakhstan (Sergeev, 1992). Some changes are also observed in the composition of silicified transitional assemblages comprising morphologically simple and conservative microorganisms from the shallow-water parts of basins. Akinetes of nostocalean or stigonematalean cyanobacteria and entophysalidacean cyanobacteria, which dominate Anabar microbiotas of the Lower-lower Middle Riphean, are relatively rare in the Upper Riphean assemblages of silicified microorganisms (Knoll and Golubic, 1979; Sergeev, 1992, 2006). The Late Riphean microbiotas are dominated by mats formed by hollow sheaths of *Siphonophycus* containing remains of the chroococcal cyanobacteria *Gloeodiniopsis* and *Eoaphanocapsa*. Similar microbiotas occur in the Min'yar Formation of the stratotype of the Upper Riphean of the southern Ural Mountains (Sergeev, 1992, 2006), in the Burovaya Formation of the Turukhansk Uplift (Sergeev, 1999, 2001), in the Gillen Member of the Bitter Springs Formation of Australia (Schopf, 1968; Knoll and Golubic, 1979), and in many others. Many Late Riphean deposits contain remains of the stalked cyanobacteria *Polybessurus*: they were reported from the Limestone-Dolomite "Series" of Greenland (Green et al., 1989), the Skillogalee Formation of Australia (Schopf, 1992), and the Svanbergfjellet and Draken Conglomerate formations of Svalbard (Knoll et al., 1991).

Yuzhnouralian proterohorizon, late Late Riphean (Late Neoproterozoic without the Ediacaran = Neoproterozoic-III), 0.85–0.6 Ga. The type microbiota comes from the Inzer Formation of the stratotype of the Upper Riphean in the southern Ural Mountains.

To date, records of peculiar vase-shaped microfossils that have been interpreted with reasonable confidence as testate amoebae are restricted to the upper Upper Riphean. They include ten genera: *Melanocyrrillium*, *Cyclocyrrillium*, *Trigonocyrrillium*, and others (Porter et al., 2003). They occur in the Chuar Group of North America (Bloeser, 1985; Porter et al., 2003), the Ryssö Formation of Svalbard (Knoll and Calder, 1983), the Visingsö Formation of Sweden (Vidal, 1976), the Eleonore Bay Group of Greenland (Green et al., 1988), and some others. The age of all above-mentioned deposits containing *Melanocyrrillium* does not exceed 850 Ma (Knoll and Sergeev, 1995), or even possibly 750 Ma (Porter et al., 2003); i.e., is crucial for more

detailed biostratigraphic subdivision of the Late Riphean on a microphytological basis.

In terms of detailed subdivision, acanthomorphic and other types of acritarchs appear to have the most potential for both the Late Riphean and the Paleozoic. In addition to *Trachyhystrichosphaera*, remains with spines and processes include other phytoplanktonic microorganisms, typical of the upper horizons of the Upper Riphean (Knoll, 1994; Butterfield and Rainbird, 1998). They are assigned to *Cymatiosphaeroides*, a genus with coats bearing thin processes and enveloped in a common outer coat. These fossils were found in the Late Riphean Miroedikha Formation of the Turukhansk Uplift (Veis et al., 1999), Seryi Kluch Formation of the Yenisei Ridge (Nagovitsin, 2000, 2001), Hunnberg and Svanbergfjellet formations of Svalbard (Knoll, 1984; Butterfield et al., 1994), the Tinder Group and the Wynniatt Formation of North America (Allison and Awramik, 1989; Butterfield and Rainbird, 1998), and a number of others. In addition, two genera are characteristic of the Upper Riphean: *Comasphaeridium* (coats covered with thin hairlike processes) and *Germinosphaera* (coats with a single or several stalklike processes), which are present in the Dashkino and the Seryi Klyuch formations in the Yenisei Ridge in Siberia and in the Svanbergfjellet Formation of Svalbard (Yankauskas et al., 1989; Butterfield et al., 1994; Nagovitsin, 2000, 2001). Records of the genus *Sphaeranasillos* (coats with closely spaced short bristlelike processes) are restricted to the lower Tinder Group of North America (Allison and Awramik, 1989), which is also assigned to the upper Upper Riphean (Knoll, 1996). The Svanbergfjellet Formation (upper Upper Riphean, Svalbard) contains microfossils of *Valkyria*, elongate bodies up to 1 mm long and with several elongate processes, which are remains of green (chaetophorean or dasycladacean) or red algae (Butterfield et al., 1994).

One recently discovered Late Riphean microbiota is among the most peculiar; the organic-walled microfossil assemblage of the Wynniatt Formation, Arctic Canada. The distinctive feature of this microbiota is diverse and variously ornamented acritarchs, unknown in other Precambrian microfossil assemblages (Butterfield and Rainbird, 1998). These acritarchs are characterized by the presence of extremely thin processes of complicated morphology and various pores in the envelope interpreted as pylomes. Such morphological features are characteristic of phytoplanktonic dinoflagellates, which appeared as late as the Late Silurian.

Recently, remains of multicellular animals were discovered in upper Upper Riphean deposits, in the Huanan Formation of China and *Parmia-bearing* beds of the Timan Region (Gnilovskaya et al., 2000).

Amadeusian proterohorizon, the Early Vendian (Early Ediacaran), 0.6–0.55 Ga. The type microbiota comes from the Pertatataka Formation of the Amadeus Basin, Lower Vendian, Australia.

At the end of the Late Riphean morphologically complex eukaryotic microorganisms became abruptly less abundant or disappeared (Vidal and Knoll, 1983; Moczydlowska et al., 1993; Moczydlowska, 2005; etc.). Thus, most of the Riphean taxa of phytoplanktonic microorganisms with spines and processes (*Trachyhystrichosphaera*, *Cymatiosphaeroides*, and others) are unknown in the Vendian. This extinction is apparently related to the Laplandian glaciation, which marks the base of the Vendian (Sokolov, 1997).

Immediately above the glacial level, Pertatataka-like assemblages become abundant in Vendian deposits. They are dominated by taxonomically diverse and morphometrically large acanthomorphic and herkomorphic acritarchs that vary from tens to a few hundred micrometers in size and differ taxonomically from more ancient assemblages of microfossils. Microbiotas including large spiny acritarchs are found in the Lower Vendian terrigenous deposits of the Pertatataka Formation in South Australia (Grey, 2005), siliceous phosphorites of the Doushantou Formation of China (Zhang et al., 1998), the Scotia Group of Svalbard (Knoll, 1996), the Infrakrol Formation of the Lesser Himalayas of India (Tiwari and Knoll, 1994), the Vychegod Formation of the Timan Region (Veis et al., 2006), the Motta, Kursov, and Parshin formations, and other Vendian deposits of the Siberian Platform (Kolossova, 1991; Moczydlowska et al., 1993; Moczydlowska, 2005; etc.). The taxonomic position of the majority of these remains is somewhat questionable: currently, *Tanarium*, *Cavaspina*, *Appendisphaera*, *Briareus*, *Echinosphaeridium*, and some other genera have been described from Pertatataka-type assemblages (Grey, 2005; Moczydlowska, 2005).

Remains of bangiophytic red algae with complexly differentiated thalli that belong to the genera *Wengania*, *Thallophyca*, *Gremiphyca*, and *Paratetraphycus* are abundant in Lower Vendian deposits. Remains of chroococcacean and hormogonian cyanobacteria are also abundant (Zhang et al., 1998; etc.). It is possible to consider the larger size of the Vendian spiral-cylindrical microfossils of *Obruchevella* as compared with their Late Riphean counterparts to be a distinctive feature of the Vendian as a whole (Golovenok and Belova, 1989).

The Belomoryan proterohorizon, Middle and Late Riphean (Late Ediacaran), 0.55–0.535 Ga. The type microbiota of the Belomoryan proterohorizon comes from the Redkino and Kotlin formations of the East European Platform.

In the Upper Vendian, the taxonomic composition of microfossils was depleted, Pertatataka-type assemblages disappeared, and most acanthomorphic acritarchs were represented by small-sized members of *Micrhystridium*. The absence of Pertatataka-type assemblages in the type section of the Vendian is mostly caused by “a stratigraphic gap,” the presence of which is hypothesized because of the upland position of the East European Platform in the Early Vendian and

the accumulation of marine sediments mostly in aulacogens, where the Vychegod microbiota was discovered (Veis et al., 2006). Only organic-walled microfossils occur in the stratotypic region. They are subdivided into several assemblages, restricted to the Laplandian, Redkino, Kotlin, and Rovno horizons. Filamentous and coccoid members of *Leiosphaeridia*, *Bavlinella*, *Trachysphaeridium*, *Stictosphaeridium*, *Symplastosphaeridium*, *Polytrichoides*, *Oscillatoriopsis*, *Oscillatorites*, and other genera prevail. In addition to cylindrical spirals of *Obruchevella*, there are also spiral filaments of *Tortunema*, *Volyniella*, and *Cohleatina*. Acanthomorphic acritarchs *Micrhystridium tornatum* and morphologically complex members of *Teophypolia*, *Ceratophyton*, and other genera appeared in the upper horizons (Volkova, 1985; Burzin, 1990).

Remains of shallow-water assemblages of silicified microfossils from Vendian siliceous carbonates are not numerous; however, there are no significant differences between their composition and that of more ancient microbiotas from analogous facies. The microbiota of the Yudoma Group of the Vendian of Siberia is dominated by remains of both morphologically simple chroococcacean (including entophysalidacean) and hormogonian cyanobacteria, the remains of which are mostly represented by sheaths belonging to the genus *Siphonophycus*, spirals of *Obruchevella* sp., and endolithic cyanobacteria *Eohyella* (Lo, 1980; Sergeev, 2002). Eukaryotic phytoplankton is represented by small acanthomorphic acritarchs *Micrhystridium* sp. (Lo, 1980) and larger phytoplankton microorganisms with supposed spines (Sergeev, 2002).

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

Lower Cambrian. Although the formal units under consideration belong to the Precambrian, a few words should be said about changes in the composition of microbiotas near the Precambrian/Cambrian boundary. Assemblages of both silicified and organic-walled microfossils that occur in Tommotian deposits mostly comprise morphologically simple filamentous and coccoidal remains of “the Precambrian appearance,” including abundant spiral-cylindrical filaments of *Obruchevella* in siliceous facies (Sergeev, 1992). The most sudden changes took place at the base of the Atdabanian Stage or Lukatiskian Horizon of the East European Platform. They were related to the broadest expansion of acanthomorphic acritarchs of the genera *Skiagia*, *Baltisphaeridium*, *Micrhystridium*, and others that spread further in overlying deposits (Volkova et al., 1979; Sergeev, 1992). In fact, a global turnover occurred at this level: the morphologically simple and predominantly prokaryotic phytoplankton of the Precambrian was replaced by the eukaryotic phytoplankton of more complicated morphology of the Phanerozoic.

CONCLUSIONS

Seven consecutive stages in the development of the Precambrian organic world have been revealed within the late Early Proterozoic, Riphean, and Vendian (Late Paleoproterozoic and Meso-Neoproterozoic, 2.0–0.535 Ga). The stages reflect both the evolution of the organisms and directional irreversible ecological changes, mostly in the composition of the atmosphere and hydrosphere. Vertical stratigraphic units that are established on this basis are termed proterohorizons. Currently, these units are applicable as transient tools for the subdivision and correlation of Upper Proterozoic deposits on a microphytological basis. In future, they should become standard units of the global stratigraphic chart of the Upper Precambrian, which is being constructed on a biostratigraphic basis. The biostratigraphic subdivision of the Upper Proterozoic is based on successive assemblages of organic-walled and siliceous microfossils, which include prokaryotes (mostly cyanobacteria) and eukaryotic unicellular plants and animals.

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