

Meso–Neoproterozoic bacterial microfossils from the Sukhaya Tunguska Formation of the Turukhansk Uplift, Russia

Soo-yeun Ahn }
Seong-Joo Lee* } Department of Geology, Kyungpook National University, Taegu 702-701, Korea

ABSTRACT: The stratiform stromatolitic cherts from the Meso–Neoproterozoic Sukhaya Tunguska Formation (ca. 1,100–900 Ma) of the Turukhansk Uplift, Russia, preserve an abundant and varied record of ancient microbial life. The assemblages found in the silicified stratiform stromatolites are dominantly composed of empty sheaths of filamentous bacteria and envelopes of coccoid ones, most of which are interpreted as ancient cyanobacterial remains. Three filamentous species (*Siphonophycus kestron*, *S. inornatum*, *S. robustum*) belonging a single genus were identified, while five coccoid species belonging to 3 genera (*Glenobotrydion aenigmatis*, *Gleodiniopsis lamellosa*, *G. sp.*, *Myxococcoides grandis*, *M. minor*, *Eoentophysalis sp.*) were documented.

Key words: chert, coccoid, cyanobacteria, filament, Meso–Neoproterozoic, Russia, stromatolite, Sukhaya Tunguska Formation

1. INTRODUCTION

There have been many researches since the first discovery of silicified Precambrian microfossils by Tyler and Barghoorn in 1954. Such studies have dramatically increased our understanding of early Earth biotas, their evolutionary pathway, and early Earth history (e.g., Schopf, 1968; Schopf and Blacic, 1971; Hofmann, 1976; Horodyski and Donaldson, 1983; Knoll et al., 1991; Seong-Joo et al., 1999). However, studies on ancient bacteria still occupy a minor portion in the whole paleontological realm. In general, that is not only because it is a multi- and interdisciplinary study requiring a lot of knowledge about many fields such as biology, geology, etc, but also because it is quite difficult to find tiny mineralized bacterial remains from Precambrian rocks.

A true understanding of the Precambrian bacterial fossils starts with the fundamental recognition of modern biology of prokaryotic organisms, and is culminated only through filtering the morphological changes caused by taphonomic and/or post-mortem processes (Golubic and Hofmann, 1976; Golubic and Campbell, 1979; Bartley, 1996). Without these perceptions, many form taxa could be created disorderly, which causes some confusion in the systematic classification of fossil bacteria. In fact, early studies conducted before the introduction of taphonomic and post-mortem aspects yielded enormous numbers of form taxa, most of which have now been abandoned or revised (Knoll et al., 1991;

Schopf and Klein, 1992; Seong-Joo and Golubic, 1998).

Precambrian microfossil studies in Korea are wholly lacking. Consequently, the stratigraphic ordering of many Precambrian rocks in Korea is still debatable. In part, this is due to the absence of researchers, but primarily it results from a deficiency of suitable rocks to study. Most Precambrian rocks in Korea are composed mainly of igneous rocks and/or highly metamorphosed sedimentary rocks. Even low grade metamorphosed sedimentary rocks, including shale and carbonate, hardly contain bacterial remains and stromatolites as well. Recently, fragmentary bacterial remnants were first documented from the less metamorphosed Precambrian sedimentary rocks on Socheong Island, Korea (Lee et al., 2003). Such findings encourage further Precambrian fossil studies that could provide clues about early life in Korea, and subsequently provide a guidepost for stratigraphic ordering of Precambrian strata in Korea.

In this paper, we report fossil bacteria found in the Sukhaya Tunguska Formation, Russia. The Sukhaya Tunguska Formation is regarded as a transitional zone between late Mesoproterozoic and early Neoproterozoic, and is very similar to Precambrian successions of Socheong Island, Korea in its age, fossil assemblage, and depositional environments. (Knoll and Sergeev, 1995).

2. GEOLOGICAL SETTINGS

The Turukhansk Uplift is made up of a westward dipping monocline and an asymmetrical syncline, and is located near the northwestern margin of the Siberian Platform, east of the Ural Mountain, Russia (Fig. 1). In this area known as Turukhansk region, the Neoproterozoic to Mesoproterozoic (upper Middle to lower Upper Riphean) sedimentary strata are well exposed, particularly along the valleys of the Sukhaya Tunguska, Miroyedikha and Nizhnyaya Tunguska Rivers. These Precambrian sedimentary successions (often called the Turukhansk succession) are mostly composed of less metamorphosed siliciclastic and carbonate rocks, beginning with the siliciclastic Bezymyanni Formation which has a faulted contact at its lower boundary. This siliciclastic Bezymyanni Formation is conformably succeeded by carbonate-dominated successions including the Linok, Sukhaya Tunguska, Derevnya, Burovaya, Shorikha, Miroyedikha, and

*Corresponding author: sjl@knu.ac.kr

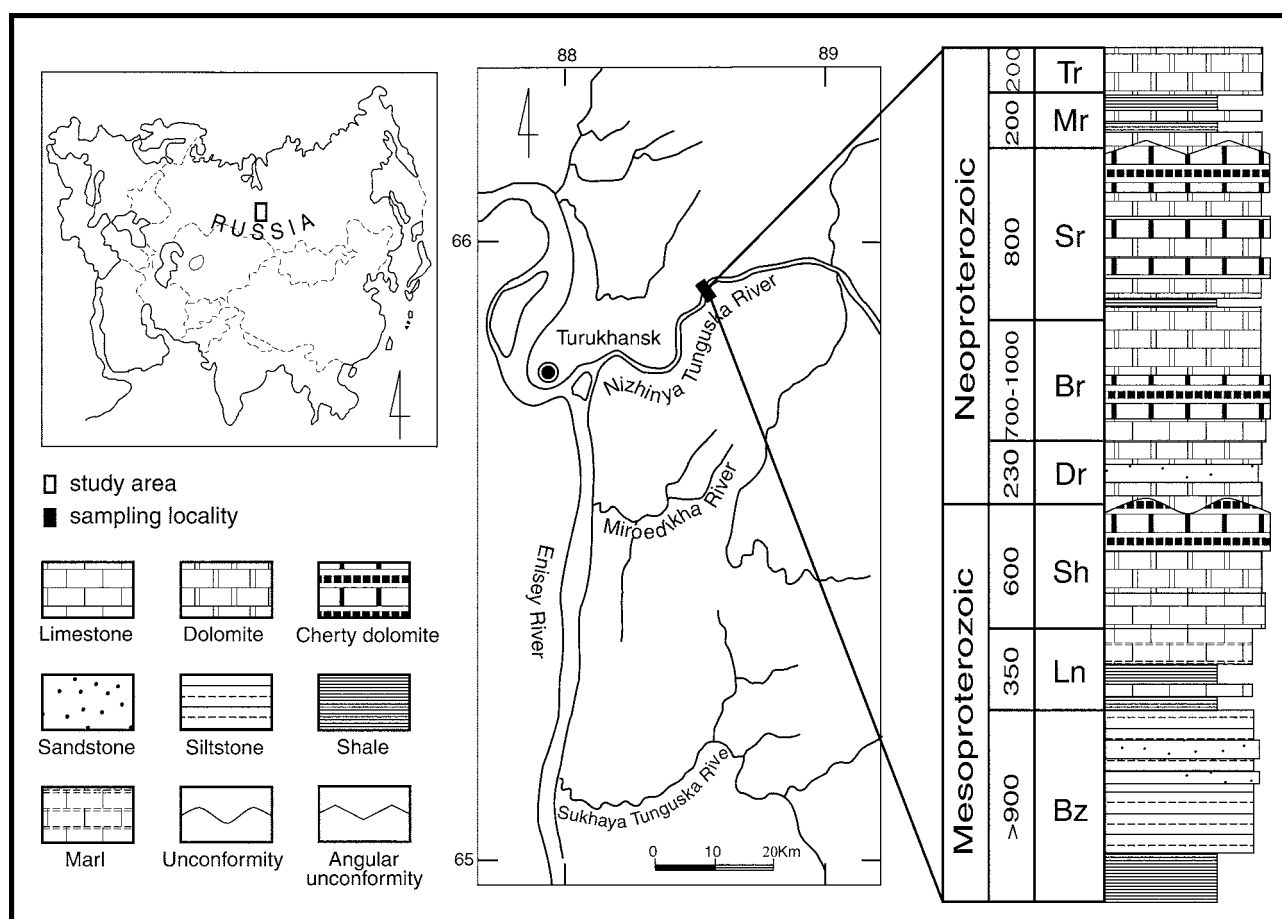


Fig. 1. Locations of the studied area, sampling locality, and simplified stratigraphic column of the Sukhaya Tunguska Formation, Russia. Bz=Bezmyannyi; Ln=Linok; Sh=Sukhaya Tunguska; Dr=Derevnya; Br=Burovaya; Sr=Shorikha; Mr=Miroyedikha; Tr=Turukhansk. Numbers next to the formation name in stratigraphic column represent thickness of the corresponding formation in meters.

Turukhansk formations in ascending order. The entire Turukhansk succession is overlain unconformably by terminal Proterozoic (Vendian) rocks (Fig. 1).

The Sukhaya Tunguska Formation is a thick (about 600 m) package composed predominantly of gray to black limestones and dolostones. It is conformably underlain by the Mesoproterozoic Bezmyannyi Formation and unconformably overlain by the Neoproterozoic Derevnya Formation (Sergeev, 1999). The formation is conventionally divided into the upper member and the lower member (Dragunov, 1963). The lower member of the Sukhaya Tunguska Formation is 240–300 m thick, is chiefly composed of dark gray to black carbonaceous deposits, and various chert nodules are found intercalated within these deposits (Petrov et al., 1995; Sergeev et al., 1997). The upper member of the Sukhaya Tunguska Formation has a thickness of 300–380 m and the principal rock type is light to dark gray dolomite with nodules, interbeds, lenses, and chert concretions.

There have been numerous debates on the age of the Sukhaya Tunguska Formation. About three age dating methods have been reported in the Turukhansk succession which

includes the Sukhaya Tunguska Formation; radiometric, chemostratigraphic, paleontological measurements. An age of 1035 ± 60 Ma was obtained by the Pb–Pb method using Sukhaya Tunguska carbonate (Ovchinnikova et al., 1995). A K–Ar age on glauconite and hydromica occurring throughout the Turukhansk succession is around 800–900 Ma (Mendelson and Schopf, 1982; Gorokhov et al., 1995; Sergeev et al., 1997). C-isotope determinations were also used for chemostratigraphy and indicate an approximate age of 850 Ma (Knoll et al., 1995; Kah and Knoll, 1996; Schidlowski et al., 1975). In addition, biostratigraphic analysis from acritarchs and stromatolites of the Sukhaya Tunguska Formation yielded an age between late Mesoproterozoic and early Neoproterozoic (Petrov and Veis, 1995). Consequently, the age of the Sukhaya Tunguska Formation is confined between late Mesoproterozoic and early Neoproterozoic.

3. MATERIAL AND METHODS

Cherts are predominantly found in the upper member of the Sukhaya Tunguska Formation, where they occur as a

form of nodules, concretions, and interbeds (Schopf et al., 1977; Mendelson and Schopf, 1982; Golovenok and Belova, 1993; Petrov et al., 1995; Sergeev et al., 1997). The cherts are very hard and dense chemical rocks composed predominantly of microquartz, megaquartz, and chalcedony. Fine laminations are clearly visible in thin sections and even in hand specimens. Lateral continuity of the lamination is well developed, and is composed of couplets of thick, light-colored, sediment rich layers and thin, dark-colored, organic rich layers.

Fossiliferous chert samples were collected from three horizons of the Sukhaya Tunguska Formation by Sergeev in 1996; the sampling locality is identical to that of Sergeev et al. (1997). Raw chert materials were left by Dr. Sergeev in the paleontological laboratory of the Kyungpook National University when he visited Kyungpook National University in 2001 as a co-worker. The chert materials were cut perpendicular to the lamination, from which 22 petrographic

thin sections were prepared. Among 22 petrographic thin sections, five thin sections turned out to be fossiliferous, and bacterial microfossils were observed and photographed under a high magnification Nikon-E800 microscope. Coordinates cited here indicate distances from a point at the right corner of the thin section.

4. BACTERIAL FOSSIL ASSEMBLAGES

The Sukhaya Tunguska microfossils are exclusively made up of morphologically simple coccoids and filaments, and both types of fossils are preserved as very thin and brown micritic lines forming vesicle-like coccoids and cylindrical tubes. Internal structures are generally lacking, and thus no distinguishing structures are recognized inside the vesicles and tubes. The general absence of the internal structures is due to mobilization of organic cellular materials during diagenesis (Golubic, 1980; Knoll et al., 1988). The diffused

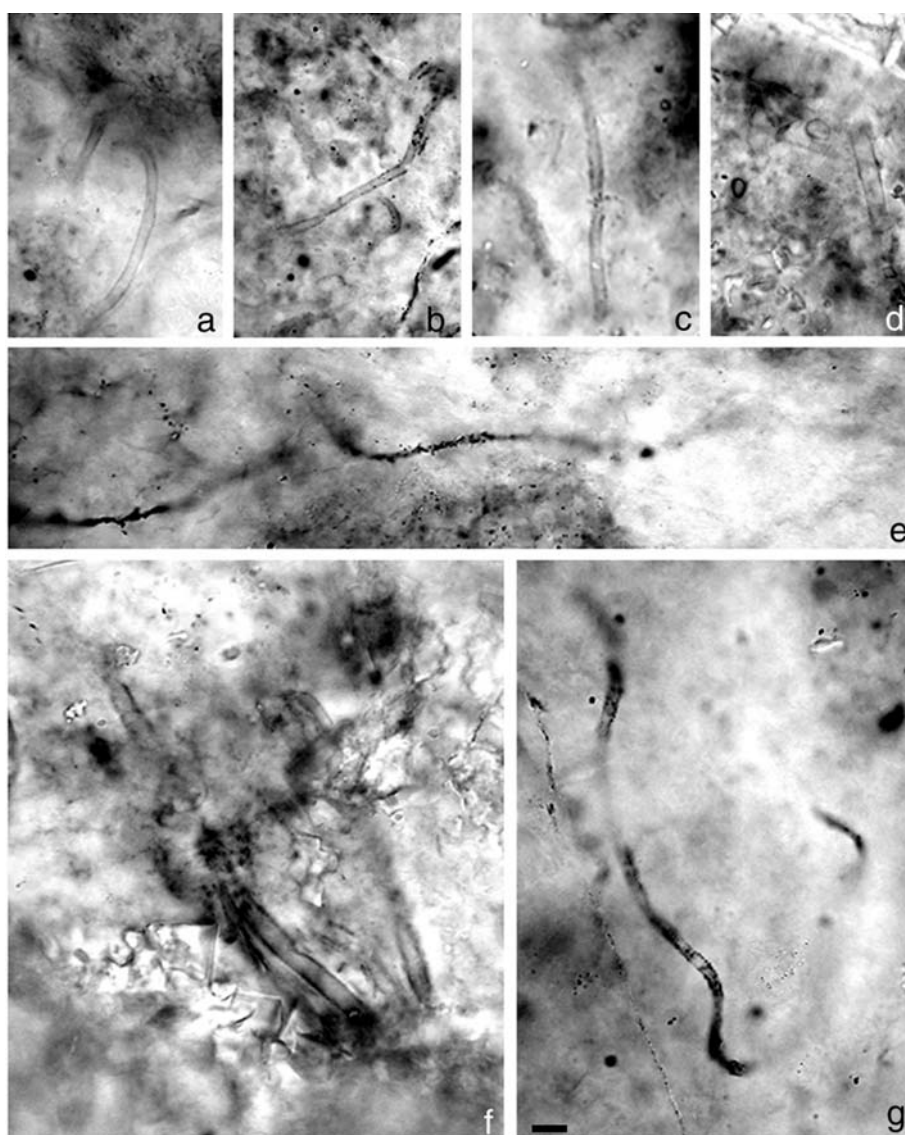


Fig. 2. Filamentous microfossils from the Sukhaya Tunguska cherty stromatolites. For all fossils slide number and coordinate number(y/x) are given. (a–c) *Siphonophycus inornatum* (a: KNULS28-2, 102.3/35.1; b: KNUS28-3, 98.4/29.6; c: KNUS28-5, 98.99/39.5). (d, f) *S. kestron* (d: KNUS28-5, 104.6/34.5; f: KNUS28-5, 99.5/42.0). (e, g) *S. robustum* (e: KNUS28-2, 103.2/33.5; g: KNUS28-2, 101.2/33.5). Scale bar in g is 10 mm for all figures.

remnants of such organic materials are easily detected around the fossils as light brown-colored faint areas (e.g., Fig. 3b). The wall structures that form the abandoned sheath materials of the filaments are also moderately (Fig. 2a–d, f–g) to highly degraded (Fig. 2e). In particular, tiny black speckle-like materials are found along the highly degraded filamentous sheaths. A few coccooid fossils contain spot-like internal remnants that are different in morphology from specimen to specimen (Fig. 3a, j vs. Fig. 4i, j). This is probably a consequence of different stages of degradation (Golubic and Hofmann, 1976).

Most of the Sukhaya Tunguska microfossils are found in organic-rich layers of stromatolitic cherts, but they are also preserved sporadically in sediment-rich layers, particularly in areas between silicified precipitates. In general, preservation is of a higher quality in fossils found in sediment-rich layers than those in organic-rich layers. Even though a few microfossils are found in sediment-rich layers, they exhibit excellent preservation showing their great sphericity and uncompacted original morphology (Fig. 3j–k), mainly because penecontemporaneous carbonate precipitation may

have acted to protect fossils from compaction (Sergeev et al., 1995).

One of the most commonly encountered microfossils from the Sukhaya Tunguska Formation is filamentous forms (Fig. 2). These empty tubular microfossils are straight (Fig. 2c–d, f), sinuous (Fig. 2a, g), thread-like (Fig. 2e), and often broken (Fig. 2b). They are found as solitary, erect or prostrate individuals. The great majority are, however, observed as interwoven filaments (Fig. 2f) preserved in ancient microbial mats as in many Precambrian cherty stromatolites (Schopf et al., 1977; Strother et al., 1983; Mendelson and Schopf, 1982); more than half of the Sukhaya Tunguska interwoven filamentous bacterial mats are unfortunately too degraded to be perceived clearly. Three basic subgroups have been identified throughout the whole Sukhaya Tunguska sheath assemblages, based on size differences (Table 1); the first has a size range of 1.4–4.5 mm in width (*Siphonophycus robustum*, Fig. 2e, g), the second one is 5–6.3 mm (*S. inornatum*, Fig. 2a–c), while the last one is wider than 7 up to 10 mm (*S. kestron*, Fig. 2d, f). The former two species are largely known to occur as main mat building microfossils

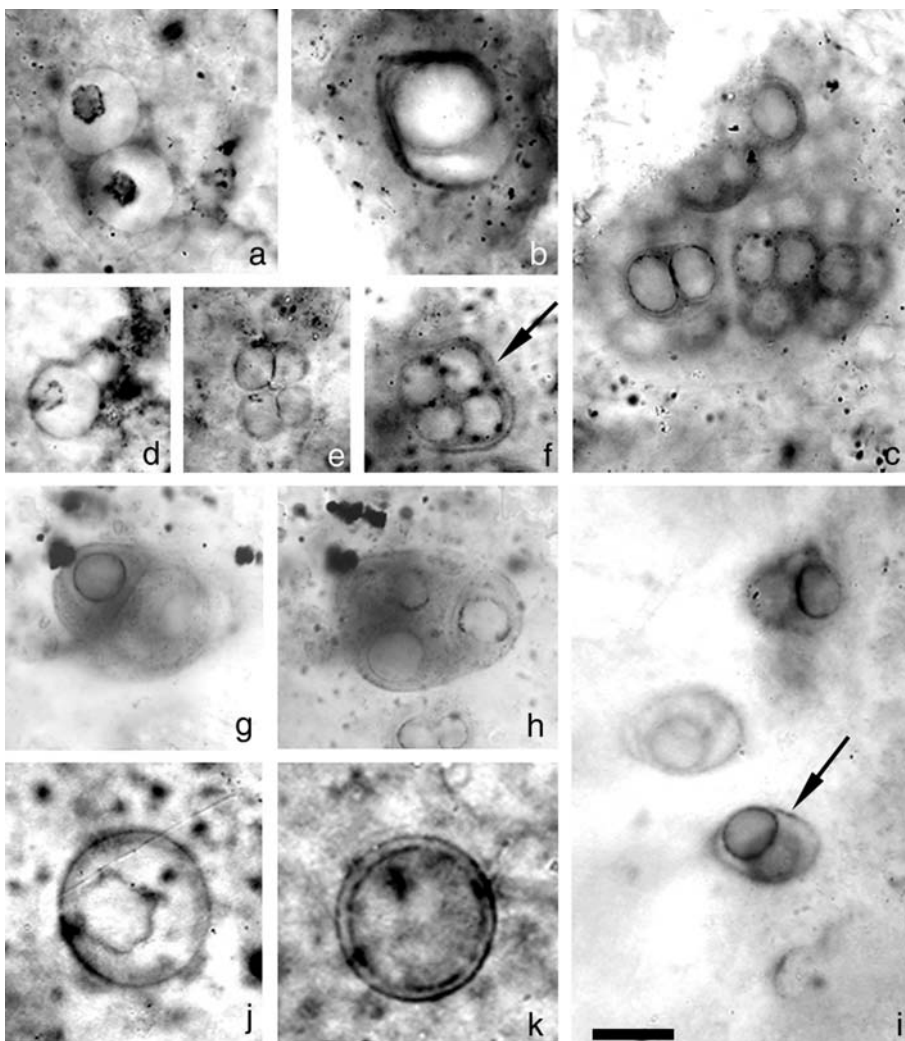


Fig. 3. Coccooid microfossils from the Sukhaya Tunguska cherty stromatolites. For all fossils slide number and coordinate number are given. (a, d) *Glenobotrydion aenigmatis* (a: KNUS28-3, 98.05/34.85; d: KNUS28-3, 99.5/33.1). (g–h, j–k) *Gloeodiniopsis lamellosa* (g–h: KNUS28-5, 104.0/42.3; j: KNUS28-3, 95.5/30.9; k: KNUS28-5, 109.6/40.0). (b–c, e–f, i) *Gloeodiniopsis* sp. (b: KNUS28-5, 102.95/32.6; c: KNUS28-5, 102.3/34.0; e: KNUS28-2, 103.75/38.9; f: KNUS28-5, 102.3/34.0; i: KNUS28-2, 102.9/38.65). Scale bar in i represents 10 mm for a–d, f–k, and 6 μ m for e.

Table 1. List of filamentous microfossils from the Sukhaya Tunguska cherty stromatolites.

Filamentous taxa	Number of cells	Diameter (μm)	Length (μm)	Trichome	Comments
<i>Siphonophycus kestron</i>	15	7–10	>75	absent	non-septate, unbranched sheath
<i>Siphonophycus inornatum</i>	8	5–6.3	>100	absent	non-septate, unbranched sheath
<i>Siphonophycus robustum</i>	104	1.4–4.5	>100	absent	non-septate, unbranched sheath

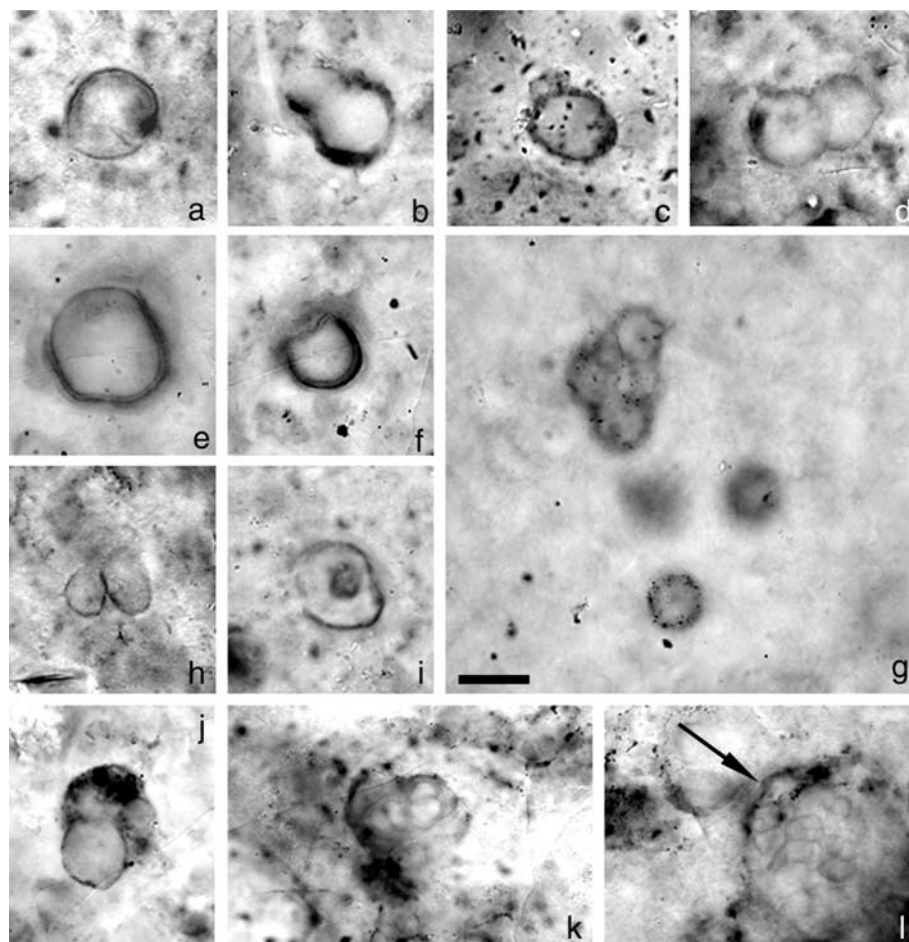


Fig. 4. Other coccoid microfossils. For all fossils slide number and coordinate number are given. (a–f) *Myxococcoides grandis* (a: KNUS28-2, 102.3/45.6; b: KNUS28-3, 100.0/48.0; c: KNUS28-3, 98.75/47.0; d: KNUS28-3, 99.0/48.0; e–f: KNUS28-3, 98.4/38.0). (g–i) *Myxococcoides minor* (g: KNUS28-2, 108.0/37.9; h: KNUS28-5, 101.2/46.0; i: KNUS28-5, 109.0/45.2). (j–l) *Eoentophysalis* sp. (j: KNUS28-3, 98.75/47.0; k: KNUS28-3, 96.1/32.1; l: KNUS28-2, 102.9/38.65). Scale bar in g is 10 μm for a–j, and 30 μm for k–l.

(Knoll and Golubic, 1979). In contrast, large sheaths (> 8 mm, e.g., *S. kestron*) are found scattered randomly or sometimes as locally clumped small aggregates (Knoll et al., 1991). However, such a distribution and paleoecological pattern of the sheath has not been clearly recognized in the Sukhaya Tunguska sheath assemblages.

Coccoid microfossils are also abundant in the Sukhaya Tunguska cherty stromatolites (Table 2). The microfossils are spherical (Fig. 3a–k), or sometimes slightly elongated (Fig. 4c, h). They mostly occur as scattered individuals showing no specific distribution tendency. Sometimes two to four cells are found attached (Fig. 3a–f; Fig. 4b, d), forming small colonies. Cells in those colonies are either enclosed within a large common envelope (Fig. 3f, i arrow) or are simply attached without a common envelope (Fig. 3a, d–e). Such clusters are often found associated with solitary individuals (Fig. 4g). The isolated coccoids are daughter cells released

after forming a mother cluster through binary or multiple fission (e.g., Seong-Joo and Golubic, 1999). Six species of isolated or clustered coccoids are recognized on the basis of the absence or presence of a common envelope, envelope structure, and size (*Glenobotrydion aenigmatis*, *Gleodiniopsis lamellosa*, *G. sp.*, *Myxococcoides grandis*, *M. minor*, *Eoentophysalis* sp.). Some coccoid fossils form huge colonies that are composed of more than 10 individual cells within a huge common envelope (Fig. 4k–l).

5. DISCUSSION

It is more difficult to determine taxonomic position and to understand the biological affinity of the Precambrian bacterial fossils than of most Phanerozoic invertebrate fossils (reviewed by Schopf and Klein, 1992; Knoll, 1996). This is because, on the one hand both Precambrian bacterial fossils

Table 2. List of coccooid microfossils from the Sukhaya Tunguska cherty stromatolites.

Coccooid taxa	Number of cells	Diameter (μm)	Organic inclusion	Common envelop	Comments
<i>Glenobotrydion aenigmatis</i>	14	6–15.2	present	present	colonies of a few cells
<i>Gloeodiniopsis lamellosa</i>	17	10–23	absent	present	thick lamellated sheath
<i>Gloeodiniopsis</i> sp.	75	6–20	present(s)	present	sometimes solitary
<i>Myxococoides minor</i>	11	6–18	present(r)	absent	colonies of several cells
<i>Myxococoides grandis</i>	43	11–55	present(r)	absent	commonly solitary
<i>Eoentophysalis</i> sp.	7	10–20	absent	distinct	large common envelope

*Present(s): sometime present, present(r): rarely present

and present-day prokaryotic microorganisms are morphologically simple and on the other hand because they are vulnerable to morphological changes, i.e. post-mortem degradation. The Sukhaya Tunguska microfossils are no exception, and the cylindrical tube fossils are one of the best examples of this.

Cylindrical tubes are one of the most dominant microfossils in the Sukhaya Tunguska cherts, much as they are in many Proterozoic assemblages (reviewed by Schopf, 1996). There are only a few diagnostic morphological characteristics such as width and wall structure, and thus, just three genera have been erected for the Precambrian tube fossils. These three widely known form genera (*Tenuofilum*, *Eomycetopsis*, and *Siphonophycus*, in Schopf, 1968) have been recently united into a single form genus *Siphonophycus* with five species on the basis of size alone (Knoll et al. 1991); *S. septatum* (1–2 μm), *S. robustum* (2–4 μm), *S. inornatum* (4–6 μm), *S. kestron* (9–13 μm) and *S. capitaneum* (14–25 μm). There is, of course, some minor discrepancy on the range of size classes among authors (compare Knoll et al., 1991; Zang and Walter, 1992 with Butterfield et al., 1994). For example, the boundaries between species are not always correlated among authors. However, it is noteworthy that in any case, the size distribution frequency of whole sheath populations shows a broad recurring modality as Knoll (1982) documented which suggests some underlying natural distinctions and provides a useful classification scheme.

The entire Sukhaya Tunguska population of sheath microfossils also displays similar size frequency distributions (Fig. 5). A broad bimodality of size frequency distribution is recognizable within the whole sheath assemblage; 1–4.5 μm , 5–6.5, and wider than 7 μm in diameter, classified here as *Siphonophycus robustum*, *S. inornatum* and *S. kestron*, respectively. Two species, *S. robustum* and *S. inornatum*, are easily identifiable by their well-defined bimodality, while the large tube, *S. kestron*, is less distinguishable statistically, characterized by a broad size range. As a result, *S. kestron* in the Sukhaya Tunguska Formation is not clearly defined in this study. This is not only case for the Sukhaya Tunguska Formation. Many authors, in fact, noted that large-sized sheaths tend to show no clearly differentiated modality (e.g., Nyberg and Schopf, 1984), and this phe-

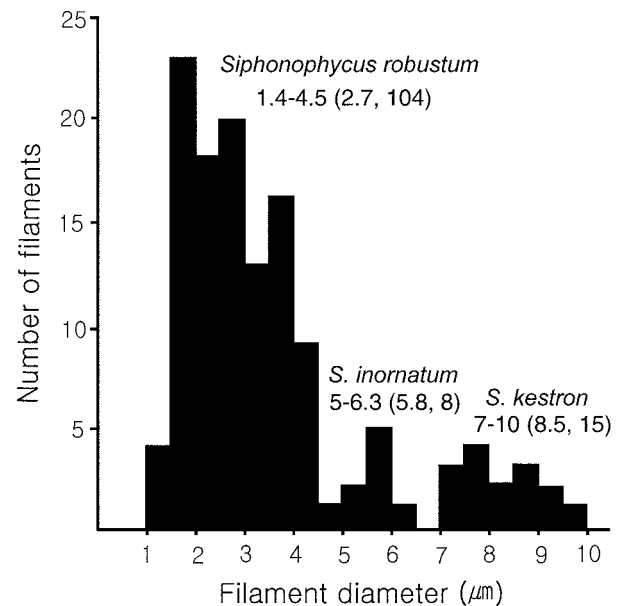


Fig. 5. Size frequency distribution plot of filamentous microfossils showing distinct modality for three species, *Siphonophycus kestron*, *S. inornatum*, and *S. robustum*. Numbers for each species is [maximum size-minimum size (mean, cells measured)].

nomenon may be closely related to its paleoecological position as an auxiliary mat builder.

The biological affinity of the Precambrian empty tube fossils is still in debate. The first genus erected for Precambrian tubular microfossils, *Eomycetopsis* Schopf, 1968 was originally interpreted as a fungal hypha on the basis of its morphological similarity to modern fungi. Since Knoll and Golubic (1979) reinterpreted the fossils as evacuated sheaths of oscillatoriacean cyanobacteria, most of sheath microfossils found in Precambrian silicified stromatolites have conventionally, or sometimes reasonably, been considered as cyanobacterial remains, an interpretation which is accepted in this study. An interpretation as cyanobacterial sheaths, is not, however, unambiguous because alternative interpretations (e.g., as other mat forming, sheathed, *Chloroflexus* type bacteria) are equally possible (see Knoll et al., 1991). In general, their putative modern counterparts could be best identified at the family level as sheathed oscillatoriacean cyanobacteria.

It may also be possible, in some tubular species, to find a modern counterpart at generic level. In particular, among the three species of *Siphonophycus*, *S. kestron* could be considered as ancient remnants of evacuated sheaths of a modern cyanobacterial genus *Lyngbya*, based on the fact that most specimens in the Sukhaya Tunguska *S. kestron* are, in fact, statistically indistinguishable from the well defined outer sheaths of modern *Lyngbya* (Schopf, 1996). Therefore, all tubular sheaths of Sukhaya Tunguska microfossils are formally classified as the genus *Siphonophycus* under the family Oscillatoriaceae of the phylum Cyanobacteria.

6. SYSTEMATIC PALEONTOLOGY

All fossil specimens illustrated in this paper are in petrographic thin sections of Sukhaya Tunguska cherts. Sample coordinates are provided for the described bacterial fossils. The coordinates (x, y) refers to the distances (in mm) from a reference corner marked on the lower right of a thin section, and thin section numbers are cited in figure captions. Thin sections are deposited in Kyungpook National University.

Domain Eucarya Woese, Kandler and Wheelis, 1990
 Phylum Cyanobacteria Stanier, 1977
 Class Hormogoneae Thuret, 1875
 Order Oscillatoriales Copeland, 1936
 Family Oscillatoriaceae (Gray) Kirchner, 1898
 Genus *Siphonophycus* Schopf, 1968, emend. Knoll, Swett and Mark, 1991

Type species: *Siphonophycus kestron* Schopf, 1968

Siphonophycus kestron Schopf, 1968
 Fig. 2d, f

Description: Cylindrical, nonseptate, and unbranched filamentous microfossils. Walls are smooth, straight, and often curved, ranging from 7 to 10 μm in width (15 sheaths measured). The thickness of the sheath wall is up to 1.7 μm .

Discussion: The genus *Eomycetopsis* was originally erected for non-septate filamentous microfossils that are 2.8–4.2 mm in width, and were classified as fossil fungi (Schopf, 1968). After several taxonomic revisions through succeeding studies (Zhang, 1981; Knoll et al., 1991; Zang and Walter, 1992; Butterfield et al., 1994), all the filamentous taxa (e.g., *Tenuofilum*, *Eomycetopsis*, *Siphonophycus*) characterized by non-septate and unbranched tubes that resemble sheaths of oscillatorian cyanobacteria were combined into a single form genus *Siphonophycus* (reviewed by Butterfield et al., 1994). Even though *Siphonophycus* is probably an artificial form taxon, some species, particularly *S. kestron* and *S. inornatum* appear to be the fossilized remains of modern oscillatorian cyanobacterial sheaths (Seong-Joo and

Golubic, 1999). Species are only distinguished by their cross-sectional diameter. The original width range of *Siphonophycus kestron* is between 8–16 μm , and filaments wider than 10 μm are rarely observed in the studied materials.

Siphonophycus inornatum Zhang, 1981
 Fig. 2a–c, g

Description: As for the genus; sheaths are 5–6.3 μm wide (8 specimens measured). They often occur in bundles.

Discussion: This species was originally erected as having a width range of 3.1–9.4 mm, intermediate in size between *S. robustum* and *S. kestron*. *S. inornatum* is generally known to be a main mat builder, showing alternating patterns of prostrate and erect filaments within stromatolites, and thus must have played an active role in the formation of stratiform stromatolites. Similar patterns, however, are not clearly identified in the Sukhaya Tunguska filaments. As a result, the paleoecological role of this species is not applied from the Sukhaya Tunguska *Siphonophycus inornatum*.

Siphonophycus robustum (Schopf, 1968), Knoll, Swett and Mark, 1991
 Fig. 2e

Description: As for the genus; tubular, often sinuous, non-septate filaments with a width range of 1.4–4.5 μm (104 sheaths measured). The wall surface is very smooth, and finely granulated in degraded part. Filaments mainly occur as microbial mats and when they appear as solitary filaments they are generally fragmented.

Discussion: This species is one of the most predominantly encountered filamentous taxa. It is found commonly within the microbial mats of the Sukhaya Tunguska cherty stromatolites, and is thus considered as primary mat-building microorganisms like those in many Proterozoic silicified microbenthic communities (Muir, 1976; Nyberg and Schopf, 1984; Knoll et al., 1989).

Class Coccogoneae Thuret, 1875
 Order Chroococcales Fritsch, 1935
 Genus *Glenobotrydion* Schopf, 1968

Type species: *Glenobotrydion aenigmatis* Schopf, 1968

Glenobotrydion aenigmatis Schopf, 1968
 Fig. 3a, d

Description: Cells are spherical and are 6 to 15 μm in diameter (14 cells measured). Spherical cells are often distorted, giving a polyhedral appearance (when closely compacted). No common envelopes are recognized. They occur

commonly as paired individuals of two spherical cells, which is a characteristic feature of binary division. They are found as solitary individuals, scattered within former microbial mats. Spot-like condensed organic structures are detected in the inner part of cells (Fig. 3a).

Discussion: The overall morphology, cell dimension and distributional pattern of Sukhaya Tunguska microfossils are closely congruent with the original diagnosis of Schopf (1968). Schopf (1968) deduced that the internal organic structures are comparable to pyrenoids found in contemporary chlorophyta, and thus he concluded that *Glenobotrydion* has an affinity to the chlorophyta. Oehler (1977), on the other hand, interpreted the internal spot-like structure in the cells of *Glenobotrydion* as mineral inclusions, as collapsed cell walls or degraded cellular components, or as discrete organelles. However, many post-mortem and taphonomic studies of algal cells including cyanobacteria and green algae have revealed that no specific morphological variations of internal cellular materials can be recognized among different biological groups (Golubic and Hofmann, 1976; Golubic, 1980; Bartley, 1996). Consequently, spot-like internal remnants are not considered valid taxonomic criteria, an interpretation which is also accepted here.

Genus *Gloeodiniopsis* Schopf, 1968, emend. Knoll and Golubic, 1979

Type species: *Gloeodiniopsis lamellosa* Schopf, 1968, emend. Knoll and Golubic, 1979

Gloeodiniopsis lamellosa Schopf, 1968, emend. Knoll and Golubic, 1979

Fig. 3g–h, j–k

Description: Cells are spheroidal, occasionally occurring as solitary spheres, but more commonly in small clusters. Cells range from 10 to 23 μm in diameter (17 cells measured). The outer envelope is lamellated, from which the specific epithet has been coined. Two or more cells are enclosed in thin and lamellated (up to three layers) common envelopes. The thickness of the envelope is up to 1 μm , and the diameter of the outer common envelope is between 38–42 μm . Dark inclusions are sporadically found inside the individual cells.

Discussion- The genus *Gloeodiniopsis* was originally erected by Schopf (1968) for solitary, spheroidal to ellipsoidal coccids that are encompassed by a thick, lamellated common envelope. In the Sukhaya Tunguska Formation, they are commonly found in clusters. Structures denoting reproduction (e.g., binary fission) were not documented by Schopf. However, attached or paired cells are often found from the Sukhaya Tunguska samples, probably suggesting that they were arrested by mineralization soon after binary division.

Gloeodiniopsis sp.

Fig. 3b–c, e–f, i

Description: Individual cells range from 6 to 20 μm in diameter (75 cells measured). A common envelope is clearly visible, within which two to four cells are enclosed. Dimensions of enclosing common envelopes are up to 40 μm . Cells showing division patterns are often observed in thin sections.

Discussion: Knoll and Golubic (1979) emended the genus *Gloeodiniopsis* including various morphotypes, which reflect cell division and several post-mortem degradations within a single population. The general morphology and presence of lamellated envelopes are analogous to those described for the genus in the Sukhaya Tunguska Formation, but *Gloeodiniopsis* sp. differs from previously reported species by its size and reproductive cycle. As a result, some specimens observed in Sukhaya Tunguska cherts are placed in open nomenclature as a species of *Gloeodiniopsis*.

Family Entophysalidaceae Geitler, 1932

Genus *Eoentophysalis* Hofmann, 1976

Type species: *Eoentophysalis belcherensis* Hofmann, 1976

Eoentophysalis sp.

Fig. 4j–l

Description: Several small cells (10–20 μm) are enclosed in a closely packed large envelope. The diameter of the enclosing common envelope is up to 117 μm . More than 20 cells are compacted within the common envelope, forming a large, mushroom-like colony (Fig. 4k–l). Generally in most Sukhaya Tunguska *Eoentophysalis*, the internal daughter cells are less clearly preserved than other microfossils in the assemblage, whereas an outer common envelope is clearly visible. Subunits of *Eoentophysalis* colonies are also detected along the colonies, including detached or released globular shape colonies (Fig. 4j).

Discussion: Distinct colonial forms of *Eoentophysalis* are missing in the Sukhaya Tunguska assemblage. They occur in thick organic-rich layers, within which only small, isolated, mostly globular subunits that are locally preserved. As repeatedly noted by several authors (e.g., Oehler, 1977; Zhang, 1981; Nyberg and Schopf, 1984; Sergeev et al., 1995), such small globular colonies are very similar to several colonial coccoid fossils. Consequently, the exact species cannot be placed in the Sukhaya Tunguska *Eoentophysalis*. However, general shape of the colony, the presence of a common envelope, and the internal organization of daughter cells strongly justify a generic assignment to *Eoentophysalis* (Golubic and Hofmann, 1976; Hofmann, 1976), but species-level determination was not possible.

Incertae Sedis

Genus *Myxococcoides* Schopf, 1968Type species: *Myxococcoides minor* Schopf, 1968*Myxococcoides minor* Schopf, 1968

Fig. 4g

Description- Spheroidal microfossils, 6–18 μm in diameter (11 cells measured). On occasion, they are present as isolated unicells detached from the original colonies, but they are normally found in clumps of somewhat deformed cells formed by mutual depression and enclosed in a sheath which is up to 1 μm in thickness.

Discussion- The genus *Myxococcoides* was erected by Schopf (1968) for microfossils representing simple, spheroidal forms. However, ensuing investigations demonstrated the existence of copious assemblages in many Proterozoic cherts, and the taxon was redefined as consisting of simple circular microfossils of heterogeneous origin (Green et al., 1989; Knoll et al., 1991; Butterfield et al., 1994; Sergeev et al., 1995).

Myxococcoides grandis Horodyski and Donaldson, 1980
Fig. 4a–f

Description- *Myxococcoides grandis* is found chiefly as scattered, spherical individuals in thin event laminae (Sergeev et al., 1995). The size distribution is 11–55 μm in diameter (32 cells measured). Cells generally contain two layers and the thickness of the layer is 1–2 μm , and occasionally small dark, opaque inclusions can be seen inside the vesicles.

Discussion- Sergeev et al. (1995) noticed that *Myxococcoides grandis* is different from other species of the genus *Myxococcoides* mainly in its wide size range. Variations in size and morphology in the population are basically attributable to life cycle and diagenetic processes (Sergeev et al., 1995).

ACKNOWLEDGMENTS: We are very grateful to Dr. V.N. Sergeev in Russian Academy of Science for supplying the Sukhaya Tunguska chert samples and many helpful discussions. Many thanks are also extended to Dr. Golubic for critical pre-review of the manuscript. This work was supported by Korea Research Foundation Grant (KRF-2002-070-C00087).

REFERENCES

- Bartley, J.K., 1996, Actualistic taphonomy of cyanobacteria: implications for the Precambrian fossil record. *Palaios*, 11, 571–586.
- Butterfield, N.J., Knoll, A.H. and Swett, K., 1994, Paleobiology of the Neoproterozoic Svanbergfjellet Formation, Spitsbergen. *Fossils and Strata*, 34, 3–75.
- Copeland, J.J., 1936, Yellowstone thermal myxophyceae. *Annals of the New York Academy of Science*, 36, 1–232.
- Dragunov, V.I., 1963, Turukhanskii I Igar'skii raiony [Turukhansk and Igarka regions]. In: Keller, B.M. (ed.), *Stratigraphiya SSSR. Verchnii Dokembrii* [Stratigraphy of the USSR. Upper Precambrian]. Gosgeoltekhizdat, Moscow, p. 318–331.
- Fritsch, F.E., 1935, The structure and reproduction of the algae, Volume 1. Macmillan, New York, p. 791.
- Geitler, L., 1932, Cyanophyceae. Rabenhorsts Kryptogamen-Flora. Akademie Verlagsgesellschaft. Leipzig, Band 14, p. 1,196.
- Golovenok, V.K. and Belova, M.Yu., 1993, The microfossils in the cherts from the Riphean Deposits in the Turukhansk Uplift. *Stratigraphy and Geological Correlation*, 1, 51–61.
- Golubic, S., 1980, Early photosynthetic microorganisms and paleoenvironmental evolution. In: Holmquist, R. (ed.), *Life Science and Space Research, Cospar 18*, Pergamon Press, Oxford, p. 101–107.
- Golubic, S. and Hofmann, H.J., 1976, Comparison of Holocene and mid-Precambrian Entophysalidaceae (Cyanophyta) in stromatolitic algal mats: cell division and degradation. *Journal of Paleontology*, 50, 1074–1082.
- Golubic, S. and Campbell, S.E., 1979, Analogous microbial forms in Recent subaerial habitats and in Precambrian cherts: *Gloeothoece coerulea* Geitler and *Eosynechococcus moorei* Hofmann. *Precambrian Research*, 8, 201–217.
- Gorokhov, I.M., Semikhatov, M.A., Baskakov, A.B., Kut'yavin, E.P., Melnikov, N.N., sochava, A.V. and Turchenko, T.L., 1995, Sr isotope composition in Riphean, Vendian, and Lower Cambrian carbonates from Siberia. *Stratigraphy and Geological Correlation*, 3, 1–28.
- Green, J.W., Knoll, A.H. and Swett, K., 1988, Microfossils from oolites and pisolites of the Upper Proterozoic Eleonora Bay Group, Central East Greenland. *Journal of Paleontology*, 62, 835–852.
- Green, J.W., Knoll, A.H. and Swett, K., 1989, Microfossils from silicified stromatolitic carbonates of the Upper Proterozoic limestone-dolomite series, central East Greenland. *Geological Magazine*, 126, 567–585.
- Hofmann, H.J., 1976, Precambrian microflora, Belcher Island, Canada: significance and systematics. *Journal of Paleontology*, 50, 1040–1073.
- Horodyski, R.J. and Donaldson, J.A., 1980, Microfossils from the Middle Proterozoic Dismal Lakes Group, Arctic Canada. *Precambrian Research*, 11, 125–159.
- Horodyski, R.J. and Donaldson, J.A., 1983, Distribution and significance of microfossils in cherts of the Middle Proterozoic Dismal Lakes Group, District of Mackenzie, Northwest Territories, Canada. *Journal of Paleontology*, 57, 271–288.
- Kah, L.C. and Knoll, A.H., 1996, Microbenthic distribution of Proterozoic tidal flats: environmental and taphonomic consideration. *Geology*, 24, 78–82.
- Kirchner, O., 1898, Schizophyceae. In: Engler, A. and Prantl, K. (eds.), *Die Natürlichen Pflanzenfamilien*, 1a, 4–92.
- Knoll, A.H., 1982, Microfossils from the Late Precambrian Draken Conglomerate, Ny Friesland, Svalbard. *Journal of Paleontology*, 56, 755–790.
- Knoll, A.H., 1996, Archean and Proterozoic paleontology. In: Jansonius, J. and McGregor, D.C. (eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, Tulsa, p. 51–80.
- Knoll, A.H. and Golubic, S., 1979, Anatomy and taphonomy of a Precambrian algal stromatolite. *Precambrian Research*, 10, 115–151.
- Knoll, A.H. and Sergeev, V.N., 1995, Taphonomic and evolutionary changes across the Mesoproterozoic-Neoproterozoic transition.

- Neues Jahrbuch Für Geologie und Paläontologie, Abhandlungen, 195, 289–302.
- Knoll, A.H., Kaufman, A.J. and Semikhatov, M.A., 1995, The carbon isotopic composition of Proterozoic carbonates: Riphean successions from north-eastern Siberia (Anabar Massif, Turukhansk Uplift). *American Journal of Science*, 295, 823–850.
- Knoll, A.H., Strother, P.K. and Rossi, S., 1988, Distribution and diagenesis of microfossils from the Lower Proterozoic Duck Creek Dolomite, Western Australia. *Precambrian Research*, 38, 257–279.
- Knoll, A.H., Swett, K. and Burkhardt, E., 1989, Paleoenvironmental distribution of microfossils and stromatolites in the Upper Proterozoic Backlundtoppen Formation, Spitsbergen. *Journal of Paleontology*, 63, 129–45.
- Knoll, A.H., Swett, K. and Mark, J., 1991, Paleobiology of a Neoproterozoic tidal flat/lagoonal complex: the Draken Conglomerate Formation, Spitsbergen. *Journal of Paleontology*, 65, 531–570.
- Lee, S.-J., Kim, J.-Y. and Lee, K.C., 2003, Bacterial microfossils from Precambrian sedimentary rocks, Socheong Island, Korea. *Journal of the Geological Society of Korea*, 39, 171–182.
- Mendelson, C.V. and Schopf, J.W., 1982, Proterozoic microfossils from the Sukhaya Tunguska, Shorikha, and Yudoma Formations of the Siberian Platform, U.S.S.R. *Journal of Paleontology*, 56, 42–83.
- Muir, M.D., 1976, Proterozoic microfossils from the Amelia Dolomite, McArthur Basin, Northern Territory. *Alcheringa*, 1, 143–158.
- Nyberg, A.V. and Schopf, J.W., 1984, Microfossils in stromatolitic cherts from the upper Proterozoic Mynar Formation, Southern Ural Mountains, USSR. *Journal of Paleontology*, 58, 738–772.
- Oehler, D.Z., 1977, Pyrenoid-like structures in Late Precambrian algae from the Bitter Springs Formation of Australia. *Journal of Paleontology*, 51, 885–901.
- Ovchinnikova, G.V., Semikhatov, M.A., Gorokhov, I.M., Belyatskii, B.V., Basileva, I.M. and Levskii, L.K., 1995, U–Pb systematics of Pre-Cambrian carbonates: the Riphean Sukhaya Tunguska Formation in the Turukhansk Uplift, Siberia. *Lithology and Mineral Resources*, 30, 477–487.
- Petrov, P.Yu., Semikhatov, M.A. and Sergeev, V.N., 1995, Development of the Riphean carbonate platform and distribution of silicified microfossils: the Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia. *Stratigraphy and Geological Correlation*, 3, 79–99.
- Petrov, P.Yu. and Veis, A.F., 1995, Facial-ecological structure of the Derevnaya Formation microbiota: Upper Riphean of the Turukhansk Uplift, Siberia. *Stratigraphy and Geological Correlation*, 3, 435–460.
- Schidlowski, M., Eichman, R. and Junge, C.E., 1975, Precambrian sedimentary carbonates: carbon and oxygen isotope geochemistry and implications for the terrestrial oxygen budget. *Precambrian Research*, 2, 1–69.
- Schopf, J.W., 1968, Microflora of the Bitter Springs Formation, Late Precambrian, Central Australia. *Journal of Paleontology*, 42, 651–688.
- Schopf, J.W., 1996, Cyanobacteria: Pioneers of the early Earth. In: Prasad, A.K.S.K., Neinow, J.A. and Rao, V.N.R. (eds.), *Contributions in Phycology*. J. Gramer, Berlin, p. 13–31.
- Schopf, J.W. and Blacic, J.M., 1971, New microorganisms from the Bitter Springs Formation (Late Cambrian) of the north-central Amadeus Basin, Australia. *Journal of Paleontology*, 45, 925–960.
- Schopf, J.W. and Klein, C., 1992, *The Proterozoic Biosphere: A Multidisciplinary Study*. Cambridge University Press, Cambridge, 1,348 p.
- Schopf, J.W., Mendelson, C.V., Nyberg, A.V., Dolink, T.A., Krylov, I.N., Nazarov, B.B., Sovietov, Yu.K. and Yakschin, M.S., 1977, Six new stromatolitic microbiotas from the Proterozoic of the Soviet Union. *Precambrian Research*, 4, 269–285.
- Seong-Joo, L. and Golubic, S. 1998, Multi-trichomous cyanobacterial microfossils from the Mesoproterozoic Gaoyuzhuang Formation, China: Palaeoecological and taxonomic implication. *Lethaia*, 31, 169–184.
- Seong-Joo, L. and Golubic, S., 1999, Microfossil populations in the context of synsedimentary micrite deposition and acicular carbonate precipitation: Mesoproterozoic Gaoyuzhuang Formation, China. *Precambrian Research*, 96, 183–208.
- Seong-Joo, L., Golubic, S. and Verrecchia, E.P., 1999, Epibiotic relationships in Mesoproterozoic fossil record: Gaoyuzhuang Formation, China. *Geology*, 27, 1059–1062.
- Sergeev, V.N., 1999, Silicified microfossils from transitional Mesoproterozoic deposits of the Turukhansk Uplift, Siberia. *Bollettino della Societa Paleontologica Italiana*, 38, 287–295.
- Sergeev, V.N., Knoll, A.H. and Grotzinger, J.P., 1995, Paleobiology of the Neoproterozoic Bilyakh Group, Anabar Uplift, northeastern Siberia. *Paleontology Society Memoirs*, 39, 1–37.
- Sergeev, V.N., Knoll, A.H. and Petrov, P.Yu., 1997, Paleobiology of the Mesoproterozoic- Neoproterozoic transition: the Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia. *Precambrian Research*, 85, 201–239.
- Staneir, R.Y., 1977, The position of cyanobacteria in the world of phototrophs. *Calsberg Research Communications*, 42, 77–98.
- Strother, P.K., Knoll, A.H. and Barghoom, E.S., 1983, Microorganisms from the late Precambrian Narssârssuk Formation, north-western Greenland. *Paleontology*, 26, 1–32.
- Thuret, G., 1875, *Essai de classification des nostochinées*. *Annales des Sciences Naturelles (Botanique)*, 6, 372–382.
- Tyler, S.A. and Barghoom, E.S., 1954, Occurrence of structurally preserved plants in pre-Cambrian rocks of the Canadian shield. *Science*, 119, 606–608.
- Woese, C.R., Kandler, O. and Wheelis, G., 1990, Towards a natural system of organisms: Proposal for the domains Archaea, Bacteria, and Eukarya. *Proceedings of the National Academy of Sciences USA*, 87, 4576–4579.
- Zang, W. and Walter, M.R., 1992, Late Proterozoic and Early Cambrian microfossils and biostratigraphy, Amadeus Basin, central Australia. *Paleontology Society Memoirs*, 12, 1–132.
- Zhang, Y., 1981, Proterozoic stromatolite microfloras of the Gaoyuzhuang Formation (early Sinian: Riphean), Hebei, China. *Journal of Paleontology*, 55, 485–506.

Manuscript received June 18, 2003

Manuscript accepted August 4, 2003