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SMALL-SIZED AKINETES FROM THE MESOPROTEROZOIC SALKHAN LIMESTONE, SEMRI GROUP, BIHAR, INDIA

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ABSTRACT

Early Mesoproterozoic (~1600 Ma old) stromatolitic cherts of the Salkhan Limestone of the Semri Group, Vindhyan Supergroup exposed in Rohtas district, Bihar contain well-preserved, distinctive population of nostocalean akinetes belonging to different species of *Archaeoellipsoides*. These are smaller in size in comparison to other known assemblages of *Archaeoellipsoides* and are comparable to the akinetes of modern bloom forming *Anabaena*. Small-sized akinetes of heterocystous cyanobacteria display rod-shaped, ellipsoidal to spindle-shaped morphologies, with prominent intracellular mass in two species out of three. Their distribution indicates allochthonous, presumably planktic and possibly dormant resting nature. Their presence also helps in understanding the evolution of marked cell differentiation in cyanobacteria. The recognition and record of akinetes are important to trace the antiquity of Nostocales and understanding the concentration of oxygen in the atmosphere in the geological past, corroborating the geochemical evidence of atmospheric oxygen level about 15% PAL for Late Palaeoprterozoic to Early Mesoproterozoic.

Keywords: Akinetes, *Archaeoellipsoides*, Mesoproterozoic, Salkhan Limestone, India

INTRODUCTION

The Mesoproterozoic microbial assemblages are mainly constituted of cyanobacterial remains. Most of these fossilized remains belong to chroococcalean, pleurocapsalean and oscillatorean taxa that can closely be compared with many extant genera and species found in analogous extant environment (Schopf, 1968; Knoll *et al.*, 1975; Golubic and Hofmann, 1976; Golubic and Campbell, 1979; Knoll and Golubic, 1979, 1992; Knoll *et al.*, 1986; Green *et al.*, 1987; McMenamin *et al.*, 1983; Shukla *et al.*, 1986; Kumar and Srivastava, 1992, 1995; Srivastava and Kumar 2003; Sharma, 2006). Although the cyanobacterial records are in plenty, yet heterocyst and akinetes are not well known in Proterozoic rocks. Heterocysts forming cyanobacteria have evolutionary significance, because in the presence of environmental oxygen, these specialized cells provide protective environment for the functioning of nitrogenase, an oxygen-sensitive, energy requiring, dinitrogen-fixing enzyme (Golubic *et al.*, 1995). Palaeoweathering profile studies (Holland and Beukes, 1990; Ohmoto, 1996; Rye and Holland, 1998) suggest that the major environmental shift, in terms of oxygen enrichment, occurred around 2200-1900 Ma ago. Around this time, atmospheric oxygen concentrations first exceeded 1-2% PAL and rose to 15% PAL or more (Holland and Beukes, 1990). Sulphur isotope studies also corroborate the status of oxygen evolution in the atmosphere (Canfield, 1998; Catling *et al.*, 2001; Kasting and Seifert, 2002) to the level of 1% PAL between 2200-2400 Ma to promote heterocyst formation and pushed the datum of oxygen enrichment to 2400 Ma (Kasting, 2001). Therefore, recognition and record of akinetes, formed as a result of oxygen in the atmosphere, are important to trace the antiquity of Nostocales and understanding the concentration of oxygen in atmosphere in the geological past.

GENERAL GEOLOGY AND AGE OF SALKHAN LIMESTONE

The akinete-bearing Salkhan Limestone is a part of the Semri Group of the Vindhyan Supergroup that is well exposed in Central India. The Vindhyan sediments are unmetamorphosed and tectonically little disturbed. This supergroup unconformably overlies the Budelkhand massif and the slightly metamorphosed Bijawar Group (~2500 Ma, Crawford and Compston, 1970; Mondal *et al.*, 2002). The Vindhyan sediments comprise a thick pile of sandstone, porcellanite, shales and limestone. The rocks of the Vindhyan Supergroup are divided into four groups, namely the Semri, the Kaimur, the Rewa and the Bhander, in ascending order. The Semri Group is traditionally designated as the Lower Vindhyan, whereas the Kaimur, the Rewa and the Bhander Groups are referred to as Upper Vindhyans. Each group is further divided into formations and members. Following Auden (1933) and Bhattacharyya (1996), the generalized lithostartigraphic succession of the Vindhyan Supergroup exposed in the Sonbhadra district and Rohtas district is given in Table 1.

The Salkhan Limestone which has yielded the *Archaeoellipsoides* fossils is constituted of stromatolitic dolomite, chert and lime mud. It has been noted in the entire Son Valley with the best exposure in the Salkhan area of Sonbhadra district, Uttar Pradesh and in Nauhatta and Jaradag localities of Rohtas district, Bihar. The fossiliferous chert samples have been collected from Rohtas district, Bihar (Fig. 1). On the basis of sedimentary structures, the depositional environment of Salkhan Limestone have been suggested to be carbonate tidal flat; and the lower part was deposited in the high intertidal zone of low to moderate energy. The middle part is also marked by similar depositional environment with low to moderate energy and the upper part of stromatolite-bearing dolomitic limestone has been suggested to be deposited in supratidal zone of carbonate tidal flat (Kumar, 1978). However, Gupta *et al.* (2003) have suggested protected, lagoonal intertidal to shallow subtidal environmental for the Salkhan Limestone.

Earlier, on the basis of the glauconite mineral dating by the K-Ar method (Vinogradov and Tugarinov, 1964) the Semri Group was suggested to be of Mesoproterozoic age. The

Table 1: Generalized lithostratigraphic succession of the Semri and the Kaimur groups of the Vindhyan Supergroup exposed in Sonbhadra district (modified after Auden, 1933 and Bhattacharyya, 1996).

		After Auden, 1933	After Bhattacharyya, 1996
VINDHYAN SUPERGROUP	KAIMUR GROUP	Dhandraul Quartzite	Dhandraul Sandstone
		Scarp Sandstone and Shale	Mangesar Formation
		Bijaigarh Shale	Bijaigarh Shale
		Upper Quartzite and Sandstone	Ghaghar Sandstone
		Susnai Breccia	Susnai Breccia
		Lower Quartzite and Shale	Sasaram Formation
		---UNCONFORMITY---	
	SEMRI GROUP	Nodular Limestone and Shale	Bhagwar Shale
		Banded Shale and Limestone	
		Nodular Limestone	Rohtasgarh Limestone
		Glauconite Beds	Rampur Formation
		Fawn Limestone	Salkhan Limestone
		Olive Shale	Koldaha Shale
		Porcellanite	Deonar Formation
		Kajrahat Limestone	Kajrahat Limestone
			Arangi Formation
		Basal Conglomerate	Deoland Formation

Basement granite

Majhgawan Kimberlite pipes intruding the Kaimur Group have been dated by Rb/Sr method as 1140 ± 12 Ma (Crawford and Compston, 1970). Recent dating of Lower Vindhyan based on Pb-Pb, U-Pb, Rb/Sr and SHRIMP methods are summarized in Table-2. The Deonar Formation that underlies the Salkhan Limestone has been dated 1628 ± 8 Ma by Rasmussen *et al.* (2002) and 1631 ± 1 Ma, 1631 ± 5 Ma by Ray *et al.* (2002). The overlying Rampur (Shales) Formation has been dated 1599 ± 8 Ma by Rasmussen *et al.* (2002). In a recent review, Ray (2006) has suggested that the sedimentation of the Vindhyan Supergroup in Son Valley started sometime prior to 1721 Ma and continued up to about 1600 Ma without any major break. On the basis of recent data, the age of the akinete-bearing Salkhan Limestone should be very close to ~1600 Ma (Earliest Mesoproterozoic or Latest Palaeoproterozoic).

EXTANT AKIENTES

It is known that many extant heterocystous filamentous cyanobacteria belonging to Nostocales and Stigonematales produce akinetes and these are common in the planktic genera

Table 2: Recent radiometric dates of different horizons of Lower Vindhyan.

Formation	Geographical Position	Method	Age	Reference
Rohtas Limestone	Tikaria, Katni, M.P.	Pb-Pb, isochron	1599 ± 48 Ma	Sarangi *et al.* 2004
Rohtas Limestone	Different localities in Son Valley, M.P. & Rajasthan	Pb-Pb, isochron	1601 ± 130 Ma	Ray *et al.* 2003
Rampur Shale	Sidhi District, M.P.	SHRIMP,U-Pb, Zircon	1599 ± 8 Ma	Rasmussen *et al.* 2002
Rampur Shale (Tuff Bands)	Sidhi District, M.P.	SHRIMP, U-Pb, Zircon	1602 ± 10 Ma 1628 ± 12 Ma	Rasmussen *et al.* 2002
Deonar Formation (Two rhyolitic volcanic horizons)	Sidhi District, M.P.	U-Pb, Zircon, $^{87}Sr/^{86}Sr$ Isotope	1631 ± 1 Ma 1631 ± 5 Ma	Ray *et al.* 2002
Deonar Formation (Porcellanite Formation)	Sidhi District, M.P.	SHRIMP, U-Pb, Zircon	1628 ± 8 Ma	Rasmussen *et al.* 2002
Base of Semri Group	Chitrakoot area, U.P.	Rb-Sr Model ages	1409 ± 14 Ma to 1531 ± 15 Ma	Kumar *et al.* 2001
Basement Rocks	Bundelkhand Granite	Pb-Pb Zircon (SIMS)	2492 ± 10 Ma	Mondal *et al* 2002

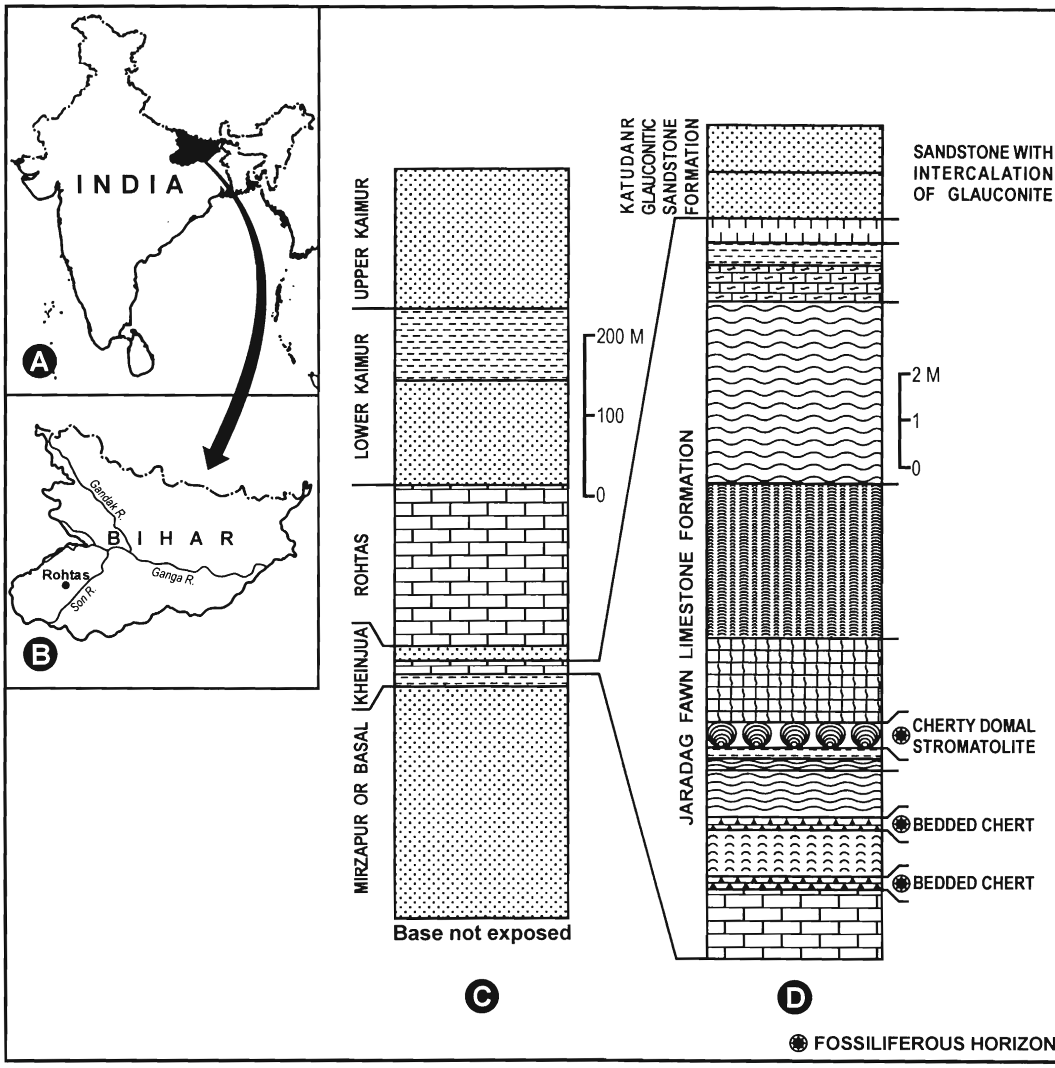

Fig. 1. Geographic and stratigraphic location of fossiliferous cherts from the Salkhan Limestone. (A) Index map of India with position of Bihar State. (B) Outline map of Bihar showing position of Rohtas district where locations of the microfossiliferous outcrops of the Salkhan Limestone occur. (C) Generalized stratigraphic column of the Semri and Kaimur Groups exposed in Rohtas. (D) Detailed litholog of Salkhan Limestone, showing location of fossiliferous horizons (modified after Sharma and Sergeev, 2004).

of nostocaceae such as *Anabaena*, *Anabaenopsis*, *Nodularia*, *Cylindrospermum*, *Aphanizomenon* and *Aulosira*. These are non-motile resting spores differentiated from vegetative cells and acting as seeds for next generation. At the time of their differentiation normal cell division ceases, cell size and storage products accumulation increases and gas vacuoles, if any, disappear and cellular envelops are thickened. It results into thickening of protoplasts during akinetes differentiation occurring at the end of excessive growth phase and correlated with short supply of nutrients and increase in accumulated metabolic products (Nichols and Adams, 1982; Herdman, 1987). Limitation of energy supply is also one of the important environmental factors triggering the differentiation of akinete formation (Herdman, 1987). Akinetes are formed at different places in different species on the trichomes. They may be single or in chains and it has been noticed that the link between akinetes and vegetative cells is weak and therefore they easily detach themselves from trichomes (Stulp and Stam, 1982). They are able to withstand the adverse environmental conditions viz. low temperature and desiccation, and start growing when environmental conditions are appropriate. Because of their hard outer coat, they remain intact, sink due to their higher density than water, accumulate in the sediments and germinate on getting favorable growth promoting conditions. (Hori *et al.*, 2003). Studies on extant *Anabaena cylindrica* showed that depletion of iron in the surrounding environment induced the differentiation of vegetative cells of *A. cylindrica* into akinetes (Hori *et al.*, 2003).

AKINETES IN FOSSIL RECORDS

As early as 1980, Horodyski and Donaldson reported large ellipsoidal microfossils (up to 100 μm) from Mesoproterozoic strata of the Dismal Lakes Group, Arctic Canada and suggested that these microbial remains could be cyanophycean spores, cyanophycean sporangia, or cyst of eukaryotic algae. Golovenok and Belova (1981, 1984) subsequently reported similar assemblage in cherts of Mesoproterozoic Billyakh Group of Western Anabar region, Northern Siberia. But they assigned the microbial remains to *Synechococcus*-like cells. The ellipsoidal akinetes preserved in shales were released by

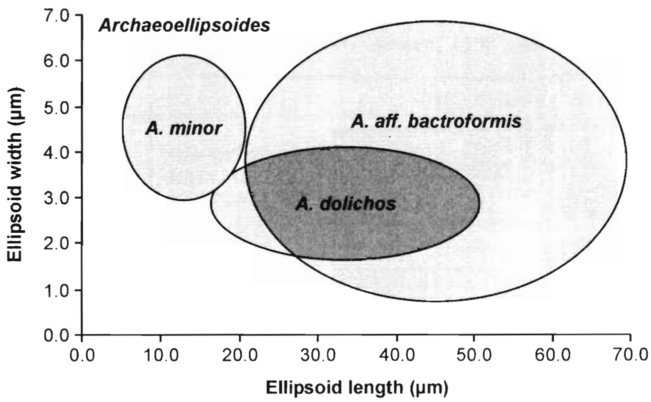

Fig. 2. Positions of ellipsoid size clustures (width vs. length) for different species of *Archaeoellipsoides*.

maceration technique have been described as *Brevitrichoides* species (Jankauskas *et al.*, 1989), whereas those studied in the chert thin sections are referred to the genus *Archaeoellipsoides*. However, some akinetes from the chert were also defined as *Brevitrichoides*, e.g. from the Palaeoproterozoic Epworth Group, Canada (Hofmann and Grotzinger, 1985). Heterocysts and akinetes are reported from Palaeoproterozoic rocks, viz., Franceville Group, Canada (Amrad and Bertrand-Sarfati, 1997); Odjick and Rocknest Formations, Epworth Group, north western Canada (Hofmann and Grotzinger, 1985). Akinete populations have also been reported from many peritidal carbonates of Mesoproterozoic age including Gaoyuzhang and Wumishan Formations, China (Zhang Yun, 1981, 1985; Zhang Penguyan, 1982; Zhang Zhongying and Li, 1985; Cao, 1992; Seong-Joo and Golubic, 1999); the Uluksan Group of Baffin Island, Canada (Hofmann and Jackson, 1991); the Kheinjua Formation, India (McMenamin *et al.*, 1983; Kumar and Srivastava, 1995; Srivastava, 2005); Deoban Limestone Formation, Garhwal Lesser Himalaya, India (Srivastava and Kumar, 2003); the Sukhaya Tunguska Formation, Turukhansk Uplift, Siberia (Sergeev *et al.*, 1997; Sergeev, 1997, 1999); the Kotuikan and Yusmastakh Formations, Anabar Uplift, north-eastern Siberia (Sergeev *et al.*, 1995; Golubic *et al.*, 1995); the Debengda Formation, northern Siberia (Sergeev *et al.*, 1994). The akinete genera *Archaeoellipsoides* declined after the Mesoproterozoic; the two Neoproterozoic occurrences to date come from the Chickhan Formation of southern Kazakhastan (Sergeev, 1989, 1992) and the Shorikha Formation, Turukhansk Uplift, Siberia (Sergeev, 2001). Expanding investigations for the search of microbial remains revealed the presence of large population of akinetes from the Fawn Limestone (=Salkhan Limestone) (Srivastava, 2005) of the Kheinjua Formation of Vindhyan Supergroup in the Newari locality. Further search has revealed the large assemblage of akinetes from the Salkhan Limestone exposed in the Rohtas district of Bihar, which are discussed in the present paper.

Besides these akinetes, there are also few reports of heterocystous cyanobacteria from Proterozoic sedimentary rocks. Licari and Cloud (1968), Cloud (1976) and Awramik and Barghoorn (1977) interpreted Gunflint fossil *Gunflintia* as heterocysts or akinetes but Knoll (1986) considered them as diagenetic embolisms or differential shrinkage within filamentous sheaths. Schopf (1968) described heterocystous trichomes from 800 Ma old Bitter Springs Formation of Australia. *Anabaenidium johnsonii* has alternatively been interpreted as an artifact of preservation (Golubic and Barghoorn, 1977; Gerasimenks and Krylov, 1983). Nagy (1978) reported Proterozoic heterocyst-forming cyanobacteria from the Malmani Dolomite Formation which later proved to be modern endoliths that penetrated old rocks (Mendelson and Schopf 1992). Sastry *et al.* (1972) reported heterocyst from the Subsurface Ganga Basin sediments of India.

Unequivocal occurrence of Proterozoic heterocyst, demonstrating their unique functional morphology, is not published (Wilmotte and Golubic, 1991). It is postulated that fossil akinetes detached from vegetative cells must be found in Proterozoic strata. Golubic *et al.* (1995) suggested "that the Proterozoic heterocyst formers existed, lived in terrestrial and coastal marine environments and were preserved, but remained unrecognized". Inspite of these limitations in our understanding of akinetes, based on morphometeric and sedimentary behaviour comparison with the akinetes of modern bloom-forming *Anabaena*, Golubic *et al.* (1995), established that *Archaeoellipsoides* are fossilized akinetes. On the basis of present-day knowledge and records, *Archaeoellipsoides* are considered to represent the detached cyanobacterial spores or akinetes.

SALKHAN MICROBIAL ASSEMBLAGE

Salkhan Limestone facies is exposed over a vast tract in the Son Valley in Central India. Well-preserved microbial assemblage is known from this Formation since long (Kumar, 1978). Later, McMenamin *et al.* (1983) described this assemblage in detail. From the Newari area, another locality where Salkhan Limestone (=Fawn Limestone) is exposed, Kumar and Srivastava (1995) reported an assemblage comprising of 28 species belonging to 18 genera. Further east of these two localities, the Salkhan Limestone is also exposed in the Rohtas district of Bihar. In a preliminary account, Venkatachala *et al.* (1990) reported microfossils from the Nauhatta area. Sharma (1996) reported varied stromatolite assemblage from the same horizon. Sharma and Sergeev (2004) recorded varied precipitate patterns and entrapped *Archaeoellipsoides* from the cherts of the Salkhan Limestone from the Nauhatta area, Rohtas. Recently, Sharma (2006) has described a rich microbial assemblage from Nauhatta locality. The assemblage includes 27 morphoforms belonging to 14 genera and 21 species. Six unnamed forms are also described. The detailed observations and systematic description of the akinetes of the Nauhatta area are presented in the paper.

MATERIAL AND METHODS

Akinetes were studied during the course of study of microbial remains in oriented petrographic thin sections of early diagenetic cherts collected from the outcrops of Mesoproterozoic Salkhan Limestone exposed in the Rohtas district of Bihar in north India. Out of six petrographic slides made from the same sample, one has yielded plenty of akinetes.

SYSTEMATIC PALAEONTOLOGY

All specimens illustrated in this paper are in a chert thin section. For each specimen, slide number and England Finder Co-ordinates are provided. The petrographic slide bearing number BSIP-13175 and the remainder rock specimen are

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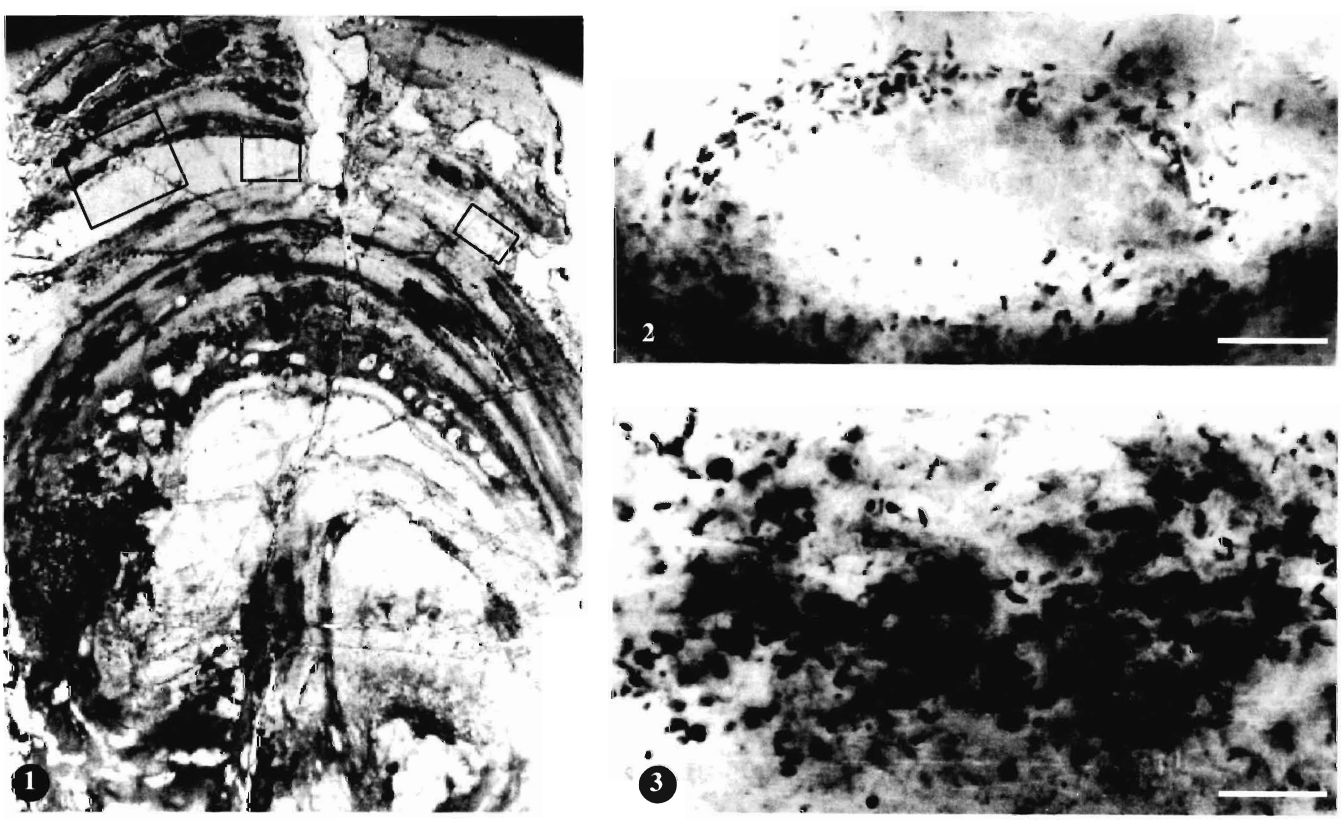
Plate I



SHARMA

EXPLANATION OF PLATE I

1. General view of the stromatolitic chert having zones of akinetes concentration. Boxes show the portions where akinetes are found in clusters. (Slide No. BSIP-13175, Scale bar = 2 mm).
2. A cluster of ***Archaeoellipsoides*** at low magnification (Slide No. BSIP-13175, Scale bar = 100 μm).
3. Another cluster of ***Archaeoellipsoides*** showing random distribution at low magnification (Slide No. BSIP-13175, Scale bar = 100 μm).

deposited in the repository of the Birbal Sahni Institute of Palaeobotany (BSIP), Lucknow.

Kingdom **Eubacteria** Woese and Fox, 1977
Phylum **Cyanobacteria** Stainer *et al.* 1978
Class **Coccogoneae** Thuret, 1875
Order **Nostocales** Geitler, 1925
Family **Nostocaceae** Kützing, 1843
Genus ***Archaeoellipsoides*** Horodyski and Donaldson, 1980 emend. Sergeev *et al.* 1995

Archaeoellipsoides dolichos emend. Sergeev *et al.*, 1995
(Pl. II, figs. 1, 10, 11 and Fig. 2)

Basionym: *Bactrophycus dolichos* Zhang, 1985, p. 298-299, fig. 7Q-U.

Type Specimen: The specimen figured by Zhang, 1985 (Fig-7S).

Synonymy: *Bactrophycus dolichos* Zhang, 1985, p. 298-299, fig. 7Q-U.—Cao, 1992, pl. II, figs. 11-13.

Filamentous microfossils, Horodyski and Donaldson, 1983, fig. 5Z.

Eomycetopsis robusta (partim) Yakschin, 1991, p. 35-36, pl. XII, fig. 3.

Description: Generally solitary, sometime in chain, single layered, straight or gently curved rod-like bodies with rounded ends sometimes pointed. Rods are empty or containing sparse blebs of amorphous organic matter. Rods 18-50 µm long but only 2.4-3.6 µm wide; L/W=5.0-20.0.

Remarks: *Archaeoellipsoides dolichos* differs form other species of the genus by its small cross-sectional diameter and high L/W.

Distribution: Palaeoproterozoic: Franceville Group, Gabon; Mesoproterozoic : Wumishan Formation, China; Kotuikan and Yusmastakh Formation, Anabar uplift, northern Siberia; Dismal Lakes Group, northern Canada; Kheinjua Formation, Deoban Limestone Formation, Garhwal Lesser Himalaya, India.

Material: About hundred specimens from the Salkhan Limestone, Rohtas, Bihar, India.

Archaeoellipsodies minor Sergeev *et al.*, 1995
(Pl. II, figs. 6, 7, 12 and Fig. 2)

Basionym: *Eosynechococcus grandis* Golovenok and Belova, 1984, p. 24, pl. II, fig. 1.

Type specimen: The specimen figured by Golovenok and Belova (1984, pl. II, fig. 1).

Synonymy: *Eosynechococcus grandis* (partim) Golovenok and Belova, 1984, p. 24, pl. II, fig. 1.—Golovenok and Belova, 1985, pl. VI, figs. 5, 6.

Archaeoellipsoides grandis (partim) Horodyski and Donaldson, 1980, p. 154-157, fig. 16G, H.—Cao, 1992, pl. 1, figs. 8, 9, pl. II, figs. 8, 9.

Archaeoellipsoides obesus (partim) Zhang, 1985, p. 295-297 (not illustrated).

Archaeoellipsoides minor Sergeev *et al.*, 1995, p. 31, figs. 10.9, 10.10.—Srivastava and Kumar, 2003, p. 24, pl. 1.6.

Description: Gregarious and solitary, single layered ellipsoids with rounded ends. Ellipsoids generally empty, sometimes may contain amorphous organic matter. Ellipsoids 7.2-18.0 µm long and 3.6-6.0 µm wide; L/W=1.8-5.0. Vesicle wall medium to coarse grained.

Remarks: Sergeev **et al.** (1995) reassigned the ellipsoids described by Golovenok and Belova (1984) as *Eosynechococcus grandis* to *Archaeoellipsoides minor* and also the specimens described by Horodyski and Donaldson (1980) as plausible chain of *A. minor*. They compared the specimens to akinetes of living *Anabaena flos-aquae* that commonly occurs into clumps. The Salkhan population of *A. minor* is smaller in size.

Distribution: Mesoproterozoic: the Dismal Lakes Group, northern Canada; Wumishan Formation, China; Kotuikan and Yusmastakh Formations, Anabar Uplift, northern Siberia; Deoban Limestone Formation, Garhwal Lesser Himalaya; Jaradag Fawn limestone Formation (Salkhan Limestone) Rohtas, Bihar, India; Neoproterozoic : the Kirgitey and Lopatinskaya Formations, Yensei Ridge, eastern Siberia; the Sharikha and Burovaya Formations, Turukhansk Uplift, northeastern Siberia.

Materials: About hundred specimens.

Archaeoellipsoides bactroformis Sergeev *et al.*, 1995
Archaeoellipsoides aff. bactroformis
(Pl. II, figs. 2-5, 8, 9 and Fig. 2)

Description: Solitary or gregarious single layered ellipsoids with rounded ends. Ellipsoides empty or containing amorphous organic matter, elongated dark bodies. Ellipsoides 24-66 µm long and 2.4-6.0 µm wide. L/W= 4.8-27.5. Vesicle wall medium to coarse grained.

Remarks: The Salkhan ellipsoidal microfossils are small in cross section size like the Billyakh and Shorikha microfossils. There are no evidence of binary cell divisions.Because of the close similarity in L/W ratio of these specimens with *A. bactroformis* but the length has wide variation and therefore these are considered *A. aff. bactroformis*.

Distribution: Mesoproterozoic: Yusmastakh Formations, Anabar Uplifts, northern Siberia and Salkhan Limestone, Bihar, India; Deoban Limestone, Garhwal Lesser Himalaya, India.

EXPLANATION OF PLATE II

(In all figs. Bar represents 10 µm)

(Details in parentheses include slide number, stage readings on Leitz Diaplan Microscope and England Finder co-ordinates. All reading are taken keeping the slide label on Left hand side).

1. ***Archaeoellipsoides dolichos*** (BSIP-13175, 28.1: 103.4; N28).
2. ***Archaeoellipsoides major*** (BSIP-13175, 29.0: 108.0; H29).
3. ***Archaeoellipsoides major*** (BSIP-13175, 28.0: 102.6; N28/3).
4. ***Archaeoellipsoides major*** (BSIP-13175, 28.1: 103.4; N28/1).
5. ***Archaeoellipsoides major*** (BSIP-13175, 29.0: 98.0; S29).
6. ***Archaeoellipsoides minor*** (BSIP-13175, 29.9: 96.7; U29).
7. ***Archaeoellipsoides minor*** (BSIP-13175, 27.7: 104.6; L27/4).
8. ***Archaeoellipsoides major*** (BSIP-13175, 28.0: 102.6; N28/3).
9. ***Archaeoellipsoides major*** (BSIP-13175, 28.1: 102.9; N28).
10. ***Archaeoellipsoides dolichos*** (BSIP-13175, 28.1: 103; N28).
11. ***Archaeoellipsoides dolichos*** (BSIP-13175, 29.9: 96.7; T30/3).
12. ***Archaeoellipsoides minor*** (BSIP-13175, 27.7: 104.6; N28/3).

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Plate II

SHARMA

Material: More than hundred specimens in the Salkhan Limestone, Rohtas, Bihar, India.

DISCUSSION

Akinete is a resting stage in the life cycle of heterocystous cyanobacteria to withstand the conditions unfavourable for growth. Accumulation of storage products and formation of thickened protective covering provide great chances of preservation and fossilization. In living *Anabaena cylindrica*, akinetes are coated with excreted exopolysaccharide, which may protect the cells from physical or chemical trauma (Hori *et al.*, 2003). Such conditions are normally found in peritidal carbonate deposits wherein favourable and unfavourable conditions quite frequently interchange. During Mesoproterozoic, distinct carbonate precipitates were formed; these aragonitic fans document precipitation on and within the shallow sea floor (Sharma and Sergeev, 2004). In these fans and laminites, are preserved *Archaeoellipsoides*-like akinetes.

Archaeoellipsoides specimens of the Salkhan Limestone are rod shaped and ellipsoidal to cylindrical in shape (Pl. II, fig. 6), sometimes slightly curved (Pl. II, figs. 5, 7, 12) with rounded ends. None of the specimens of the Salkhan population show constriction equatorially negating the possibility of binary fission characteristic of chroococcoidal cyanobacteria and therefore cannot be considered remains of large *Eosynechococcus*-like cyanobacterial unicells.

The population of *Archaeoellipsoides* is randomly oriented and their relationship to the surrounding sediments and patchy distribution along the laminae suggest that they are allochthonous elements that have been derived from the water column. Of different species of *Archaeoellipsoides,* most of the individuals occur solitary, rarely in pairs or short chains of unequal length. Abundance varies from cluster to cluster and from lamina to lamina.

Although heterocysts and akinetes have been reported from Palaeo-Meso-and Neo-proterozoic sediments but all reported forms can be interpreted equally well or better as diagenetic features of undifferentiated trichomes and sheaths (Sergeev *et al.*, 1995).

Morphometric measurements of the population (Fig. 2) within the stromatolitic laminae of the Salkhan Limestone suggests that the clusters are made up of three different species and/or species associations. Sergeev *et al.* (1995) also noted the similar type of distribution pattern in the Yusmastakh or Kuitukan Formation population. The other populations of *Archaeoellipsoides* described from the Mesoproterozic cherts (Horodyski and Donaldson, 1980; Zhang Yun, 1985; Srivastava, 2005) show identical morphometric patterns. These attributes suggest that the interpretation of *Archaeoellipsoides* as akinetes produced by planktic heterocystous cyanobacteria is most plausible. However, *Archaeoellipsoides* were first considered to be of uncertain biological affinities (Horodyski and Donaldson, 1980), subsequently interpreted as remnents of giant *Synechococcus* cyanobacteria (Golovenok and Belova, 1984); these fossils are considered as akinetes produced by *Anabaena*-like nostocalean cyanobacteria (Yakschin, 1991; Sergeev *et al.*, 1995).

CONCLUSIONS

The main characteristic of the Salkhan microbial assemblage is their occurrence. Microfossils are reported from bedded chert and stromatolitic chert. *Archaeoellipsoides* occur in between the laminae of the stromatolitic chert. It is a second occurrence of microbiota in the stromatolitic chert after the Franceville Group, Gabon (Amrad and Bertrand-Sarfati, 1997). Franceville population is distinct because it represents the occurrence of larger coccoids or coccoidal colonies including *Archaeoellipsoides* from the Palaeoproterozoic rocks whereas all other known occurrence are from Mesoproterozoic and Neoproterozoic rocks.

The occurrence and abundance of fossil *Archaeoellipsoides* in the silicified peritidal carbonates of Mesoproterozoic Salkhan Limestone represent the akinetes of coastal, planktic, heterocystous cyanobacteria comparable to *Anabaena* species. The independent geochemical data suggest that oxygen-rich environment provided the selection pressure for heterocyst evolution by 2100 Ma (Holland and Beukes, 1990) and molecular phylogenies based on sequence comparison of 16r RNA's suggest that the Nostocales and Stigonematales form the coherent monophyletic clusters (Giovannoni *et al.*, 1988). The presence of *Archaeoellipsoides* in Mesoproterozoic Salkhan Limestone corroborates the geochemical data and constrains the timing of the nostocalean radiation by Early Mesoproterozoic.

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