The Biodiversity of Organic-Walled Eukaryotic Microfossils from the Tonian Visingsö Group, Sweden

Biodiversiteten av eukaryotiska mikrofossil med organiska cellväggar från Visingsö-gruppen (tonian), Sverige

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Abstract

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The diversification of unicellular, auto- and heterotrophic protists and the appearance of multicellular microorganisms is recorded in numerous Tonian age successions worldwide, including the Visingsö Group in southern Sweden. The Tonian Period (1000-720 Ma) was a time of changes in the marine environments with increasing oxygenation and a high input of mineral nutrients from the weathering continental margins to shallow shelves, where marine life thrived. This is well documented by the elevated level of biodiversity seen in global microfossil record.

The Visingsö Group contains a taxonomically rich assemblage of cyanobacteria, stromatolites, algal phytoplankton, and vase-shaped microfossils. A new study of organic-walled, phytoplanktic microfossils, which are extracted by palynological method from the Visingsö 1 borehole samples, reveals the presence of morphologically disparate taxa. They are in gross cysts of microalgae (Pterospermopsimorpha, Pterospermella, Cerebrosphaera, Trachysphaeridium, Simia and certain Leiosphaeridia with pylome) and some are of uncertain affinities (acritarchs). Representative taxa of two lineages among green algae, Prasinophyceae and Chlorophyceae, are recognized. Cyanobacterial clusters and filaments are abundant and specimens of multicellular, yet systematically unrecognized taxa are recorded.

Taxonomically, the assemblage is similar to some from other successions distributed along the margins of Baltica, Laurentia and Siberia in the Tonian Period. The ecological habitats of those organisms are inferred by comparing with their potential modern analogues and from the sedimentological setting of the upper formation of the Visingsö Group.

Keywords: Organic-walled microfossils, Tonian, cyst, green algae, eukaryote, Visingsö Group

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Populärvetenskaplig sammanfattning

Biodiversiteten av eukaryotiska mikrofossil med organiska cellväggar från Visingsögruppen (tonian), Sverige

Corentin Loron

Denna studie handlar om biodiversiteten och den biologiska affiniteten av mikrofossil från den neoproterozoiska eran, tonianperioden (1000-720 Ma). De har extraherats från övre formationen av Visingsögruppen i södra Sverige.

Mikrofossilen har organiska cellväggar, är encelliga och har förmodats representera algcystor (resistenta reproduktiva strukturer), cyanobakterier, och andra organismer av okänd tillhörighet. Neoproterozoikum har den högsta graden av biologisk diversitet under prekambrium. Det är därför viktigt att studera diversiteten för att förstå utvecklingen av biosfären under denna period i samband med utvecklingen av miljöer. Den studerade samlingen härrör från ett borrhål på Visingsö i Vättern, och visar på större diversitet än från tidigare studier.

Denna nya studie syftar till att bestämma biodiversiteten i den övre formationen av Visingsögruppen och att känna igen affiniteten av mikrofossilen med organiska väggar och deras ekologi. Vissa av de undersökta mikrofossilen hör sannolikt till grönalgerna. Kluster och fiber av cyanobakterier är rikligt förekommande, och några prover är ej biologiskt igenkännbara. Med hjälp av moderna analyser och sedimentologiska data är ekologin hos dessa mikrofossil utläst.

Nyckelord: Mikrofossil med organiska cellväggar, tonian, cysta, grönalger, eukaryot, Visingsögruppen

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1 Introduction

The Proterozoic Eon is a time interval spanning almost two billions of years from the end of the Archean at 2.5 Ga to the beginning of the Cambrian at 541±1 Ma. It is divided in three chronostratigraphic units according to the IUGS, International Chronostratigraphic Chart, 2015: Paleoproterozoic (2.5–1.6 Ga), Mesoproterozoic (1.6–1.0 Ga) and Neoproterozoic (1000–541±1 Ma). Significant biotic radiations are recorded in the Neoproterozoic and this present study is dedicated to its initial period, the Tonian Period (1000–720 Ma). This period is known for the final assemblage of the supercontinent Rodinia and the subsequent onset of its break-up, resulting in tectonic and environmental changes. In this way the Tonian Period differed from the preceding Mesoproterozoic which was relatively stable in terms of environmental and chemical conditions (Holland, 2006), and from the following Cryogenian Period of drastic climate changes. In the latter period of the so-called “Snowball Earth” conditions (Hoffman and Schrag, 2000), the planet was covered by extended ice caps reaching low latitudes but not necessary the entire globe (Arnaud et al., 2011). The effects of such conditions on life are recorded by decrease of diversity although many species have survived and quickly radiated in the Ediacaran (Grey, 2005; Moczydłowska, 2008a). The question rises what was the pattern of diversity in the Tonian Period? The present study is intended to contribute to this quest.

At the beginning of Tonian the biosphere has been already relatively well developed. The eukaryotic organisms had radiated throughout the Proterozoic Eon (Schopf and Klein, 1992; Porter, 2006; Moczydłowska et al., 2011; Javaux, 2011; Knoll, 2014; Butterfield, 2015) and this is supported by genomic phylogenies (Pace, 1997; House and Fitz-Gibbon, 2002). Sexual reproduction and multicellularity have been recognized since the Mesoproterozoic (Hermann, 1990; Butterfield, 2009; Knoll, 2011; Moczydłowska et al., 2011; Agić et al., 2015), while the ecosystems were becoming more complex. The billion years of evolution had populated the marine realm with minute microorganisms comprised of organic wall. These organic-walled microfossils (OWM) are disparate in morphology, from simple spheres to ornamented vesicle and filamentous trichomes in sheath, and varying in sizes, ranging from a few to hundreds micrometers. They are inferred to represent polyphyletic biota, including cyanobacteria, algae, fungi, heterotrophic protists, and other of unknown affinities (Evitt, 1963; Moczydłowska, 1991, 2005, 2010, 2015; Colbath and Grenfeld, 1995; Sergeev et al., 2002; Playford, 2003; Porter, 2006; Retallack, 2015). The general term “acritarchs” (Evitt, 1963; from the Greek “unknown origin”) is used for grouping of microfossils with uncertain affinities up to the moment their systematic position is recognized.

The earliest known suggested eukaryote is the ribbon-shaped and coiled fossil Grypania, dated from ca. 1.9 Ga (Han and Runnegar, 1992). By the time of 1.8–1.6 Ga microfossils with excystment structure and multilayered wall structure and then lavish ornamentation are thought to be algal in origin (Lamb et al., 2009; Agić et al., 215). The recognition of certain microfossil affinities and the
time of appearance of phylogenetic lineages is still unreconciled between fossil record and molecular clock estimates, or unresolved and just left in general terms as “eukaryotes”. By using key diagnostic features such as the shape of the vesicle, the presence of internal body or bodies, the presence of opening structures on the wall surface or particular sculptures and ultrastructure of the wall, many Proterozoic taxa can be placed in known systematic divisions and classes (Moczydłowska et al., 2010, 2011; Moczydłowska, 2015)

Among the microfossil record of eukaryotes in the Proterozoic, the maximum diversity is observed during the Neoproterozoic times (Cohen and Macdonald, 2015). The diversification of protists, notably primary producers, during this time was significant in changing the complexity of Earth’s biosphere, influencing the environments by steady release of free oxygen, and paving the way for the evolution of metazoans (Moczydłowska, 2002; Erwin and Valentine, 2013). The studied Tonian assemblage may improve the understanding of these biotic and environmental processes.

2 Aims

The purpose of the study is to identify the OWM in a Tonian assemblage preserved in the Visingsö Group, southern Sweden, and to recognize their biological affinities. The Tonian Period is a hinge period of time between the stable Mesoproterozoic and the Cryogenian glaciations. Therefore it is really important to document and understand the diversity of the marine life during the Tonian. In order to reconstruct the evolutional trend of marine microorganism it is also crucial to know more about the affinities of the OWM which constitute the major record of life for that time.

The examination will be performed in three main steps: (1) microfossils will be observed under light microscope and grouped based on their body plan and diagnostic features; (2) their generic and specific taxonomic attribution will be established using comparative morphologic studies of fossil collections and literature, and (3) comparisons of the studied morphotypes with extant lineage of various eukaryotic microorganism and prokaryotic cyanobacteria will be led to infer biological affinities.
3 Geological setting and age

3.1 The Visingsö Group

Figure 1. A, Map of the Fennoscandian shield showing the location of the Vättern Lake; modified from Lundmark and Lamminen, (2016). B, map of the Vättern Lake showing the extension of the Visingsö Group and the site of the Visingsö 1 borehole; modified from Martí Mus and Moczydłowska (2000).

The Visingsö Group is preserved within the lake Vättern Basin and in the surrounding area in southern Sweden and is one among a few Neoproterozoic sedimentary successions in the mainland of the Fennoscandian Shield on the Baltica palaeocontinent (Vidal and Moczydłowska, 1995; Lundmark and Lamminen, 2016; Fig. 1). The depositional basin of the lake Vättern is a fault-bounded tectonic graben extended northeast-southwest within a crystalline basement (Vidal, 1974, 1976a; Martí Mus and Moczydłowska, 2000; Pease et al., 2008). It has been formed through rifting, faulting and then erosion and sediment infilling in the pre-Cryogenian time (Vidal, 1985).
The Visingsö Group represents a thick, exceeding 1400 m succession of mainly terrigenous clastic rocks with subordinate carbonates exposed on the coasts of the lake Vättern and on the Visingsö island (Fig. 1, Fig. 2), and also known from several boreholes in the vicinity of the lake (Brotzen 1941; Collini, 1951; Vidal, 1974, 1976a, 1982, 1985; Martí Mus and Moczydłowska, 2000). The sediments within the group have been divided by Collini (1951) into three informal lithostratigraphic units, which are in the status of formations (Vidal, 1982; Fig. 3).

Figure 2. Photograph of the outcrop of the upper formation of the Visingsö Group. Visingsö island, Vättern lake, southern Sweden. Courtesy of M. Moczydłowska-Vidal.

The lower formation is composed of cross-bedded quartz and feldspatic sandstone with some conglomerates and shales, ca. 400 m in thickness, and it has been deposited in a fluvial-deltaic environment (Vidal, 1982; Larsen and Nørgaard-Pedersen, 1988). The microfossils are very rare within this formation because their presence depends on marine sediments, which are represented only by a few ingression layers, and the preservation is restricted to layers of fine-grained siliciclastic rocks that are non-oxidized. The middle formation is ca. 446 m in thickness and comprises feldspatic conglomerates and sandstones, mudstones and shales deposited in a deltaic shallow marine environment (Vidal, 1976a). Sedimentary structures such as ripple marks, cross-bedding and desiccation cracks in the middle formation are indicators of depositional environments in a tidally influenced shallow marine shelf with mud flats (Vidal, 1976a; 1982).
The upper formation consists of alternating micaceous shale and siltstone with occasional phosphate nodules, succeeded by banded algal stromatolite-rich dolomitic limestone at the top and an interval of coarse-grained sandstone (Vidal, 1972, 1976a, 1985; Martí Mus and Moczydłowska, 2000; Fig. 3). The total thickness is estimated to ca. 580 m (Collini, 1951). The upper formation shows a great abundance of OWM including cosmopolitan species and indicating a free connection between the Lake Vättern Basin and a global open ocean (Vidal, 1985; Martí Mus and Moczydłowska, 2000). In addition to OWM, the presence of stromatolites and vase-shaped microfossils (VSM) clearly indicates shallow marine environments with variable water depths between subtidal and intertidal zones (Vidal, 1972, 1976a, 1982). The shales of the upper formation are organic-rich and record a total organic carbon (TOC) value of 3.56 mg C/g, which is higher than the value of 2.30 mg C/g generally recorded in Proterozoic shales (Strauss and Moore, 1992; Samuelsson and Strauss, 1999). Such value coupled with the presence of the phosphate nodules provides good evidence for nutrient-rich water upwellings in the basin (Knoll and Vidal, 1980). Stromatolites, cyanobacterial mats, and VSM conform to tropical or relatively warm climatic conditions during the deposition of the upper formation (Vidal 1972, 1976; Martí Mus and Moczydłowska, 2000).

3.2 Age of the Visingsö Group

The K–Ar dating of detrital micas have bracketed the maximum depositional age of the Visingsö Group between 1060 and 985 Ma (Magnusson, 1960). The dolerite dykes cutting the surrounding Paleoproterozoic basement have yielded Rb–Sr ages of 1020–870 Ma (Patchett and Bylund, 1977) and this time interval may suggest the beginning of the sediment deposition within the lake Vättern Basin. The Rb–Sr dating of shale and clay fractions from the upper formation yielded the age of 703–663 Ma, which is interpreted as the late diagenesis age of the sediments of the Visingsö Group (Bonhomme and Welin, 1984).

The biostratigraphic relative age based on the occurrence of several OWM species and VSM known from other regions, including some globally distributed, has been estimated to late Riphean approximatively 800–700 Ma (Vidal and Moczydłowska, 1997). This time interval corresponds to the Tonian Period (IUGS, International Chronostratigraphic Chart, 2015; Fig. 4). The upper formation may be estimated to ca. 780–720 Ma considering the stratigraphic range of VSM currently established in the Chuar and Mount Harper groups (Dehler, 2014; Strauss et al., 2014).
**Figure 3.** Composite lithostratigraphic section of the Visingsö Group showing the three formations (lower, middle and upper), the depositional environments and the palaeontological records. Based on Vidal (1972, 1976a, 1985); Martí Mus and Moczydłowska (2000). The red arrow corresponds to the studied interval. OWM= organic-walled microfossils, VSM= vase-shaped microfossils.
4 Material and methods

The microfossils were obtained from rock samples from the Visingsö 1 borehole that is located on the Visingsö island in the lake Vattern in southern Sweden (Fig. 2). The samples derive from the depths of 3.7 m, 9.7 m, 11.5 m, 12.2 m, and 13.2 m of the borehole. To extract the microfossils, the samples were treated following the palynological maceration method described by Vidal (1988). The maceration included hydrofluoric and hydrochloric acids treatment in order to eliminate the minerals, and then ethanol and acetone rinsing for dehydration. The remaining residue composed of acid-resistant organic matter fraction and microfossils was mounted on microscopic slides. For each depth four microscopic slides were examined using an optical, light transmitted microscope. Identified organic-walled microfossils were counted on each slide and relevant specimens were photographed. Some of the images are illustrated on Plates I–XVI and all taxa are listed in Table 1. The microfossils are taxonomically described following the rules of The International Code of Nomenclature for Algae, Fungi and Plants, Melbourne Code (2011). For specimens identified at the species level, a synonymy is compiled. The stratigraphic ranges are summarized from occurrences listed in synonymy. Certain occurrences are cited using Russian regional chronostratigraphic units (stages) and correlation of these units with the international units is presented in Figure 4.

![International chronostratigraphic chart for Meso- and Neoproterozoic (2013, 2015) and correlation with Russian regional chronostratigraphic units Vendian and Riphean (Semikhatov et al., 1991).]
5 Palaeontological descriptions

5.1 Acritarchs


Type species – *Cerebrosphaera buickii* Butterfield, 1994; northeastern Spitsbergen, Polarisbreen, Akademikerbreen Group, Svanbergfjellet Formation, Lower Dolomite Member, Neoproterozoic (Butterfield *et al.*, 1994; p. 29–30, fig. 12D–E).

*Cerebrosphaera* sp.
Plate I, Figures A–B

Material – Abundant fragments at various state of preservation including very well preserved specimens.

Description – Fragmented portions of originally spheroidal vesicles with thick, rigid and opaque wall with wall surface covered by evenly distributed, numerous, regularly arranged cerebroid wrinkles forming occasionally sinusoidal wrinkles that are connected by their ends. The wall surface between the wrinkles is psilate.

Dimensions – The observed fragments range in diameter from tens of µm up to hundreds of µm and are within the size range of the genus.

Remarks – The differences between the two species of *Cerebrosphaera*, which are *C. buickii* Butterfield, 1994 (*in* Butterfield *et al.*, 1994) and *C. anaguae* Cotter, 1999, are in the observed width of the cerebroid wrinkles, a feature that may be subjectively recognized. It has been observed among these species from the Cryogenian sediments that their morphology is similar and the size ranges formed a continuum and therefore the two morphotypes likely belong to the same species (Cornet *et al.*, 2015).

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m, 12.2 m and 13.2 m.

Type species – Germinosphaera bispinosa Mikhailova, 1986; Siberian Platform, Krasnoyarsk region, River Uderei, Dashkin Formation, Upper Riphean (Mikhailova, 1986; p. 36, fig. 6).


Plate I, Figures C–D.

Synonymy –
1976 Phycomycetes – Timofeev et al., table VII, fig. 8.
1986 Germinosphaera bispinosa Mikhailova sp. nov. – Mikhailova, p. 36, fig. 6.
1986 Germinosphaera unispinosa Mikhailova sp. nov. – Mikhailova, p. 36, fig. 5.
1991 Germinosphaera sp. – Knoll et al., p. 561, fig. 19.6.
1994 Germinosphaera bispinosa Mikhailova, 1986, emend. – Butterfield et al., p. 38, fig. 16D–E
1999 Germinosphaera unispinosa Jankauskas, 1989 – Yin and Guan, p. 130, fig. 5.2, 5.4, 5.6, 5.9.
2001 Germinosphaera unispinosa Jankauskas, 1989 – Prasad and Asher, p. 121, pl. 13, fig. 11; p. 117, pl. 11, fig. 9.
2007 Germinosphaera unispinosa Mikhailova, 1986 – Yin and Yuan, p. 353, fig. 2.11.

Material – One well-preserved specimen and one broken specimen.

Description – Spheroidal vesicle with a thin psilate wall bearing a single unbranched tubular process gradually extending from the vesicle wall and having slightly conical proximal basis. The distal termination of the process is blank or broken. The process is hollow inside and freely communicates with the vesicle cavity.

Dimensions – N=2. The specimens are 40 µm and 38 µm in width. Their processes are respectively 30 µm and 71 µm in length and 5 µm wide in both specimens.

Remarks – Butterfield (in Butterfield et al., 1994) has emended the species diagnosis to include specimens bearing 1–4 processes arranged equatorially on vesicle with psilate wall. The emended species comprised of two formerly recognized species diagnosed by Mikhailova (1986) as having single or double processes, in G. unispinosa and G. bispinosa respectively. The synonymized species with additionally observed new specimens with up to 4 processes were argued to be otherwise indistinguishable morphologically in a simple vesicle with psilate wall (Butterfield et al., 1994). The vesicle diameter defined in the emended diagnosis was 13–35 µm. The present specimens are larger in their width, 38–40 µm (and presumable even larger in full dimensions) but showing a single robust process that is consistent with feature of G. unispinosa or emended G. bispinosa that conversely may
have 1–4 processes.

Present record – Visingsö upper formation, Visingsö 1 borehole at a depth of 11.5 m.

Occurrences and stratigraphic range – Yakutia, East Siberian Platform, Krasnoyarsk district, River Uderei, Dashka Formation, Upper Riphean, ca. 750 Ma (Mikhailova, 1986; Mendelson and Schopf, 1992) and Turukhansk region, Miroedikha River, Miroedikha Formation, Upper Riphean, ca. 850 Ma (Timofeev et al., 1976; Mendelson and Schopf, 1992); northeastern Spitsbergen, Akademikerbreen Group, Svanbergfjellet Formation, Algal Dolomite Member, Neoproterozoic (Butterfield et al., 1994) and Spitsbergen, Draken Conglomerate Formation, Neoproterozoic, ca. 800 – 700 (Knoll et al., 1991); Australia, Officer Basin, Alinya Formation, early Neoproterozoic (Zang, 1995); India, Ganga Basin, Bahraich Group, Avadh Formation, early Middle Riphean and Ujhani Formation, Latest Vendian – Lower Cambrian (Prasad and Asher, 2001); North China, Henan Province, Lushan County, Jiuyudong Section, Donjia Formation, Neoproterozoic (Yin and Guan, 1999; Yin and Yuan, 2007); Eastern European Platform, Vychegda Formation, upper assemblage, early Ediacaran (Vorobeva et al., 2009). The total stratigraphic range is from Neoproterozoic to Lower Cambrian.


Type species – *Leiosphaeridia baltica* Eisenack, 1958; Estonia, Ashgill, Ordovician (Eisenack, 1958; p. 8, pl. 2, fig. 5).

*Leiosphaeridia* spp.

Plate II and III

Material – Around 3300 specimens in various state of preservation. Paired or clustered specimens are counted separately. Numerous fragments are observed.

Description – Spheroidal or sub-spheroidal, morphologically simple vesicle with psilate surface. The vesicle wall varies in thickness and robustness from thin translucent and delicate in appearance to thick, semi-translucent and firm wall.

Dimensions – N=20. Vesicle 12–154 µm in width. The mean size is ca. 35 µm. Among observed abundant specimens, there is no differentiation into size classes but rather a gradual change in dimensions both in thin- and thick-walled specimens.
Remarks – The genus *Leiosphaeridia* is the most common microfossil morphotype through geological ages both in the abundance and its variability in dimensions and wall thickness. It is understood as polyphyletic in origin (Tappan, 1980; Moczydłowska, 2011). Proterozoic leiosphaerid microfossils have been subdivided into numerous species (Jankauskas *et al.*, 1989; Butterfield *et al.*, 1994) depending on their diameter and the thickness of the wall (based on transparency). Most frequently recognized are four species: thin-walled *L. minutissima* defined by the vesicle diameter less than 70 µm, and *L. tenuissima* 70–200 µm or larger 92–624 µm, and thick-walled *L. crassa* being less than 70 µm in diameter and *L. jacutica* 71–796 µm (Jankauskas *et al.*, 1989, Butterfield *et al.*, 1994). These arbitrary chosen classes (divided by 70 µm size limit) do not reflect any natural division that could be indicated by a distinct size-frequency class distribution (see in Grey, 2005) and specimens display a continuous array of dimensions. It is difficult to measure or estimate the wall thickness with precision and only a limited number of specimens have been measured in TEM thin-sections of the vesicle wall (Arouri *et al.*, 1999, 2000; Talyzina and Moczydłowska, 2000; Javaux *et al.*, 2004; Moczydłowska *et al.*, 2010). There is neither a recognizable stratigraphic sequence of their appearances or defined ranges of these species (Mendelsson and Schopf, 1992) to support their differentiation. The studied specimens could be assigned to all these species but because of the lack of distinctive morphological characters (other than the vesicle size and wall thickness), they are described under *Leiosphaeridia* spp.

In present material there are two groups of leiosphaerids: thin- and thick-walled with psilate wall surface and narrow, delicate compression folds randomly distributed on the entire vesicle (Plate II, Figs. A, B, D) or wider folds (Plate II, Figs. F, G, J, K, L). Specimens smaller in diameter vesicles have fewer compression folds (Plate II, Fig. H) and all these folds are taphonomic features resulting from the collapse of the originally spheroidal vesicle. The microgranular wall sculpture of some specimens (Plate II, Figs. C, E) are not the effect of wall corrosion because the pattern of microgranulation is even over the entire vesicle and of consistent size. They may therefore represent taxa distinct from Leiosphaeridia, and previously recognized as *Kildinosphaera*. The genus *Kildinosphaera* Vidal, 1983 (in Vidal and Siedlecka, 1983) is morphologically close to some specimens of *Leiospheredia*, and the two genera have been synonymized (Jankauskas *et al.*, 1989). *Kildinosphaera* is spheroidal to sub-spheroidal having thin wall with fine granulation on its surface and may preserve a large opening, generally located on the vesicle pole. Some specimens from the present material may be attributed to the genus *Kildinosphaera* (Plate II, Figs C, E) by showing an apparent granulation and a possible opening.

Some specimens exhibit an internal inclusion of condensed organic matter within the vesicle (Plate III, Fig. H). This is a common feature among Proterozoic leiosphaerids (Jankauskas *et al.*, 1989; Hofmann and Jackson 1994; Hofmann, 1990; Grey 2005). This feature has been interpreted as both morphologic and preservational (see discussion below).
Some specimens are split in half along a median axis (Plate III, last Fig.). This is considered as an excystment feature (Le Herrissé, 1984).

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m; 11.5 m; 12.2 m and 13.2 m. Very rare and mature fragments attributed to *Leiospheridia* spp. are found at the depth of 9.7 m.

Plate IV, Figures A – E.

Synonymy –
1966 *Turuchanica ternata* sp. nov. Timofeev – Timofeev, p. 45, pl. 9, fig. 8.
1989 *Leiosphaeridia ternata* (Timofeev, 1966), emend. Mikhailova et Jankauskas, comb. nov. – Jankauskas et al., plate XI, figs. 2–4; plate XII, figs. 4, 5, 8.
1997 *Leiosphaeridia ternata* (Timofeev, 1966), emend. Mikhailova – Cotter, p. 264, fig. 7J.

Material – 105 complete specimens in various state of preservation.

Description – Vesicle circular in outline, originally spheroidal, thick-walled, very dark to opaque with smooth surface and characteristically broken marginally into trapezoid portions.


Remarks – The vesicles often exhibit peripheral splits that are radially arranged and show a few thick, broad wrinkles due to compression of the very thick wall. The narrow size range and the consistent thick wall are morphologically relevant to consider the specimens as a distinct species:
Leiosphaeridia ternata.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m and 12.2 m.

Occurrences and stratigraphic range – Arctic Canada, Baffin Island, Bylot Supergroup, Eqalulik, Uluksan and Nunatsiaq groups, 1270 – 750 Ma (Hofmann and Jackson, 1994); China, Anhui and Jiangsu Provinces, Liulaobei, Shijia, Zhaowei and Jiayuan formations, upper Proterozoic, and Jingshanzhai and Gouhou formations, lower Cambrian (Zang and Walter, 1992a); Australia, Amadeus Basin, Bitter Springs Formation, upper Proterozoic, Pertatataka Formation, Ediacaran, and Tempe Formation, Cambrian (Zang and Walter, 1992b), and Officer Basin, Browne Formation, Neoproterozoic (Cotter, 1997); Russia, Arkhangelsk Region, Ust'-Pinega Formation, Zimnie Gory Beds, upper Vendian (= upper Ediacaran) (Ragozina et al., 2003). The species occurs in 10 localities in Russian Federation, Eastern Europe and Siberian platforms, dated from ca. 1800 Ma to 670 Ma (Jankauskas et al., 1989; listed in Mandelson and Schopf, 1992). The species total stratigraphic range is Paleoproterozoic to Cambrian.

Leiosphaeridia sp. A
Plate IV, Figures F – G.

Material – Four well-preserved specimens.

Description – Vesicle circular in outline, originally spheroidal, having smooth, thick and firm wall. The vesicle possesses a large, slightly polygonal trilobate opening with sharp outline and thicken rim.

Dimensions – N=2. Vesicles are 29x21 µm in diameter and an opening 13x15 µm (rim ca. 2 µm), and 29x29 µm in diameter with an opening 29x29 µm (rim 4–5 µm).

Remarks – The peculiar but consistent shape of the opening can be interpreted as an excystment structure and therefore constitute a taxonomically relevant diagnostic feature (Loeblich and Tappan, 1969; Loeblich, 1970; Le Hérissé, 1985).

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m, 12.2 m, and 13.2 m.

Leiosphaeridia sp. B
Synonymy –
2009 Leiosphaeridia sp. – Nagy et al., p. 416, fig. 1C.

Material – Fifty well-preserved specimens and additional partly broken specimens.

Description – A species of Leiosphaeridia with slightly granular and relatively thick wall. The vesicle is spheroidal to sub-spheroidal in shape and possesses a circular structure on the surface, which is defined by a circular, granular rim surrounding a lighter zone with tightly arranged coarse granulation.

Dimensions – N=8. Vesicle 23–59 µm in diameter. The surface structure is 5–12 µm in width and surrounding rim is ca. 2 µm thick. The granulae are 0.5–1.0 µm in diameter.

Remarks – Vidal and Ford (1985) described a Leiospheridia sp. A, which is very similar in overall morphology to the present specimens but it has psilate surface in contrast to the granular wall sculpture in the present fossils.

The circular structure with granulation greatly resembles the ones preserved in the specimens of Trachysphaeridium laufeldii and Leiospheridia sp. A from Vidal and Ford (1985), which has been interpreted as operculate excystment openings (Vidal, 1976a; Vidal and Ford, 1985). Excystment structure is a diagnostic feature in microfossils (Loeblich and Tappan, 1969; Loeblich, 1970; Le Hérissé, 1984), and in the studied specimens it is defined morphologically, together with the wall sculpture that is also morphologic and not taphonomic feature. Because of the presence of excystment structure, the circular pylome, and the granular surface of the wall, the specimens are attributed to a distinct species Leiospheridia sp. B.

Jankauskas et al. (1989) described the species Leiosphaeridia kulgunica Jankauskas, 1980, with a large, circular pylome that shows an opening similar in size and shape than in L. sp. B, but L. kulgunica is smooth-walled and the opening is without the rim-like feature around or granulation.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m, and 12.2 m.

Occurrences and stratigraphic range – USA, northern Arizona, Chuar Group, Galeros Formation, Jupiter Member and Kwagunt Formation, Awatubi Member, Late Proterozoic (Vidal and Ford, 1985; Nagy et al., 2009); Russian Federation, Southern Urals Mountains, Podinzer Formation (=Sim

*Leiosphaeridia* sp. C  
Plate VI, Figures A–D.

Material – 135 complete, well-preserved specimens, and additional fragmented specimens.

Description – Small to large spheroidal vesicles with thick and firm wall that has fibrous or slightly reticulate texture. The vesicle is regularly circular in outline but has an uneven margin and surface resulting from the wall texture.

Dimensions – N=15. Vesicle diameter is variable, ranging 60–244 µm, with a mean value *ca.* 110 µm (n=11). Smaller forms are rare and range from 20–35 µm (n=3). Some fragments can be larger and one reached 385 µm (n=1).

Remarks – The vesicle wall thickness, robustness and the surface texture differ from smooth-walled specimens of *Leiospheridia* spp. and specimens described here may represent a separate species with morphologically distinct wall texture.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m, 12.2 m and 13.2 m.


Type species – *Macroptycha uniplicata* Timofeev 1976; Russia, Southern Ural Mountains, Turukhansk District, Miroedikha Formation, Upper Riphean (*in* Timofeev *et al.*, 1976; plate XI, fig. 4).

Plate VII, Figures A–H.

Synonymy –
1976 *Macroptycha uniplicata* Tim. – Timofeev *et al.*, pl. XI, figs. 4, 6.  
1976 *Macroptycha biplicata* Tim. sp. n. – Timofeev *et al.*, pl. XI, figs. 8-9, 10.
Material – 40 well-preserved specimens.

Description – Vesicle ellipsoidal to fusiform in shape having shagrinate to slightly granular wall surface and consisting of one or two large fusiform internal chambers (bodies) located centrally and with their apices directed toward the vesicle poles, which may or may not be attached to the vesicle wall.

Dimensions – N=11. Vesicle 23–35 µm in width and 47–88 µm in length. The internal bodies are 5–25 µm in width and represent 58–72 % of the vesicle width.

Remarks – The large internal “chamber” located inside the vesicle cavity has a consistent shape and mimics the shape of the vesicle has been originally interpreted as an internal body (Timofeev, 1973; Timofeev et al., 1976), and subsequently as a “megalo-fold” (Yin, 1987; Schopf and Klein, 1992). Jankauskas et al. (1989, pl. VIII, fig. 6, 7, 8, 9, 12, 15, 17) attributed several specimens of Timofeev’s Macroptycha species (reproduced holotypes and other specimens) to Leiosphaeridia crassa and to Arctacellularia, although did not formally synonymized them. These authors considered the “internal chambers” to be lensoidal compression folds.

The present observations indicates the presence of internal body or bodies that are occasionally rolled-up (Fig. 7E, F) as at the beginning of the process of splitting into two separate bodies (Fig. 7D). The single body occupying most of the vesicle cavity is often detached from the outer vesicle wall (Fig. 7A, G) and is formed by its own thin and semi-transparent wall (Fig. 7H) or thick and darker wall (Fig. 7A, G). In specimens with two bodies, they are aligned parallel and close to the poles of outer vesicle wall (Fig. 7D, E). Taphonomic compression folds are observed on the outer vesicle wall and they are randomly distributed also perpendicular to the internal body axis (Fig. 7H).
Timofeev (in Timofeev et al., 1976) described four species of *Macroptycha* based on the number of “internal chambers” that are understood as internal bodies. These are: *Macroptycha uniplicata* which has a single body, and *M. duplicata, M. triplicata*, and *M. multiplicata* which have double, triple, and quadruple to multiple bodies respectively. They are treated here provisionally as a single form taxon (being conspecific) because of transitional forms between morphotypes with varying number of internal bodies or showing their transformation stages. It is likely that these morphotypes belong to a single biological species. The studied specimens are assigned to *Macroptycha uniplicata* Timofeev, 1973 as is the type species of the genus, although conversely showing also two internal bodies.

The *Macroptycha* specimens morphologically resemble individual cells of the filamentous species *Arctacelluria ellipsoidea* Hermann, 1976. Timofeev et al. (1976, pl. XI, fig. 7) described laterally conjugating specimens of *Macroptycha*, which were reproduced in Jankauskas et al. (1989, pl. VIII, fig. 17) and alternatively attributed to conjugating *Arctacellularia*.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m and 12.2 m.

Occurrence and stratigraphic range – Yakutia, East Siberian Platform, Krasnoyarsk District, Turukhansk region, Miroedikha River, Miroedikha Formation, Upper Riphean, ca. 850 Ma, and Torgo River, Torgo G-2 borehole, Torgo Formation, Upper Riphean (Kolosov, 2014; the age of the Torgo Formation is Ediacaran, Moczydłowska et al., 1993); Ukraine, Carpathian Mountains, Vendian, 600 Ma (Timofeev et al., 1976; Hermann, 1990; Schopf and Klein, 1992; Mendelson and Schopf, 1992; Kolosov, 2014); China, Jilin Province, Hunjiang district, Qinggou Formation, Upper Riphean (Yin, 1987). The total stratigraphic range is Neoproterozoic.


Type species: *Navifusa navis* Eisenack, 1976; Sweden, Öland Island, Silurian (Eisenack, 1976; p. 192, pl. 3, fig 17, neotype). The holotype by synonymy is *Bion navis* Eisenack, 1938 (Eisenack, 1938; p. 229, pl. 16, fig. 8). Combaz et al. (1967) designated *Leiofusa navis* Eisenack, 1938 as the type species of the genus.

*Navifusa majensis* Pyatiletov, 1980.

Plate VII, Figures I–J.

Synonymy –

1980 *Navifusa majensis* n. sp.; Pyatiletov, p. 144, fig 1.

1997 *Navifusa majensis* Pyatiletov, 1980 – Samuelsson, p. 177, figs 7G, 7J-7K


2001 *Navifusa majensis* Pyatiletov, 1980 – Prasad and Asher, p. 105, pl. 5, figs 1-3.

2011 *Navifusa majensis* Pyatiletov, 1980 – Couëffé and Vecoli, p. 169, fig. 6.7.

2013 *Navifusa majensis* Pyatiletov, 1980 – Tang *et al.*, p. 163, fig. 5H.


Material – Three well-preserved specimens and one well-preserved conjugating specimen.

Description – Naviform elongated vesicle with narrower central part, rounded poles and with thin, smooth wall.

Dimensions – N=4. Vesicle length 59–65 µm and vesicle width 23–29 µm (n=3). One specimen is ca. 105 mm in length and 20–25 µm in width (n=1); the two vesicles attached in this specimen are 45 x 25 µm and 60 x 20 µm.

Remarks – Attached specimens have been observed and interpreted as conjugating cells by Agić (2015). Similar attachment of specimen can be observed in Samuelsson *et al.*, 1999 (fig 5a).

Present records – Visingsö upper formation, Visingsö 1 borehole at the depths of 11.5 m, 12.2 m, and 13.2 m.

Occurrence and stratigraphic range – Siberian Platform, Uchur-Maya region, Khabarovsk District, Maya River, Lakhanda Formation, Upper Riphean, ca. 950 Ma (Pyatiletov, 1980; Mendelson and Schopf, 1992); Canada, Baffin Island, Bylot Supergroup, Eqalulik Group, Arctic Bay Formation; Uluksan Group, Society Cliffs Formation and Nunatsiaq Group, Strathcona Sound Formation, Mesoproterozoic, 1270 – 750 Ma (Hofmann and Jackson, 1994); Northwest Russia, Kola Peninsula, Sredni Peninsula, Kildinskaya Group, Poropelonskaya and Karuyarvinskaya formations; Volokovaya Group, Pumanskaya Formation, and Tiersky Coast, Chapoma Formation, Early Neoproterozoic (Samuelsson, 1997); Northwest Greenland, Thule Supergroup, Dundas Group, Olrik Fjord, Steensby Land and Kap Powell Formations; Baffin Bay Group, Qaanaaq Formation, Proterozoic (Samuelsson *et al.*, 1999); India, Ganga Basin, Bahraich Group, Sarda and Avadh Formations, Mesoproterozoic (Prasad and Asher, 2001); Ghana, southern margin of the Volta Basin, Kwahu Group, Anyabony Formation, lower unit, Meso- to Neoproterozoic (Couëffé and Vecoli, 2011); Northern China, northern Anhui Province, Huainan region, Huainan Group, Liulaobei Formation, early Neoproterozoic (Tang *et al.*, 2013), and Huaibei region, Huaibei Group, Jushan and Jiayuan
Formations, Tonian (Tang et al., 2015). The total stratigraphic range is from Mesoproterozoic to early Neoproterozoic.

Genus *Ostiana* Hermann, 1976 (in Timofeev et al., 1976)

Type species – *Ostiana microcystis* Hermann, 1976 (in Timofeev et al., 1976); Yakutia, East Siberian Platform, Krasnoyarsk District, Turukhansk region, Miroedikha River, Miroedikha Formation, Upper Riphean (Timofeev et al., 1976; p. 43, Table XII, figs. 5, 6). Mendelson and Schopf (1992) estimated the age of the formation at ca. 850 Ma.

*Ostiana microcystis* Hermann, 1976

Plate XII, Figures F–H.

Synonymy –
1976 *Ostiana microcystis* Hermann gen. et sp. n. – Timofeev et al., p. 43, pl. XII, Figs. 5, 6, pl. XVII, fig. 8.
1994 *Ostiana microcystis* Hermann, 1976 – Butterfield et al., p. 19, fig. 5F–I.
2009 *Ostiana microcystis* Hermann, 1976 – Vorob'eva et al., p. 190, fig. 14.11.
2013 *Ostiana microcystis* Hermann, 1976 – Tang et al., p. 163, fig. 5C–G.

Material – 128 well-preserved although fragmented colonies of various size and shape.

Description – Spheroidal small vesicles with psilate wall, which are tightly arranged in planar colonies consisting of tens of individual vesicles (cells). The vesicles within a colony are often overlapping at marginal parts and are embedded in a common matrix or coalesced by mucus.

Dimensions – N=5. Colonies are ca. 20–200 µm in size. Individual cells are 5–12 µm in diameter.

Remarks – The observed specimens, in a similar way as *Synsphaeridium* Eisenack, 1965, comprise of individual vesicles, which if preserved individually would be identified as a smaller leiospherid.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 11.5 m, 12.2 m and 13.2 m

Occurences and stratigraphic range – Yakutia, East Siberian Platform, Krasnoyarsk District, Turukhansk region, Miroedikha River, Miroedikha Formation, Upper Riphean, ca. 850Ma (Timofeev et al., 1976; Mendelson and Schopf, 1992), and Uchur-Maya region, Khabarovsk District, Maya
River, Lakhanda Formation, Upper Riphean, ca. 950 Ma (Hermann 1990; Mendelson and Schopf, 1992); Spitsbergen, Akademikbreen Group, Svanbergfjellet Formation, Early Neoproterozoic (Butterfield et al., 1994); East European Platform, Kel’tminskaya-1 borehole, Lower Assemblage, Neoproterozoic, Cryogenian (Vorobeva et al., 2009); North China, Huainan region, Liulaobei Formation, early Neoproterozoic (Tang et al., 2013). The total stratigraphic range of the species is Neoproterozoic.

**Genus Pterospermella Eisenack, 1972**

Type species – *Pterospermella aureolata* (Cookson & Eisenack) Eisenack, 1972; p. 597, Figs. 1-3 (originally *Pterospermopsis aureolata* Cookson & Eisenack, 1958, p. 49, pl. 9, Figs. 10 – 12 ); Australia, Cretaceous.

*Pterospermella sp.*
Plate IX, Figures D – F.

Material – 24 well-preserved specimens.

Description – Spheroidal vesicle consisting of a dense internal body encapsulated within a very thin envelope, irregular in outline. The internal spheroidal body is darker than the surrounding envelope and exhibits an uneven outline with no supporting elements.


Remarks – The morphology correspond to the genus *Pterospermella* Eisenack, 1972 having an internal body surrounded by a very thin wrinkled envelope developed in the equatorial plan (Eisenack, 1972; Moczydlowska, 2015). This “saturn-shape” morphology can also be observed in the genus *Simia* Mikhailova and Jankauskas, 1989 (*in* Jankauskas et al., 1989). The present specimens don't show radial support for the envelope and therefore are morphologically closer to the species *Pterospermella velata* Moczydlowska, 1988 but the size ratio of internal body to envelope is smaller in studied specimens than in *P. velata*.

*Pterospermella* Eisenack, 1972 is mostly a Phanerozoic taxon ranging from Cambrian to Holocene (Fensome et al., 1990; Moczydlowska, 1991; Guy-Ohlson, 1996) but it has been reported for Mesoproterozoic sediments at ca. 1250 Ma (Samuelsson et al. 1999; Moczydlowska et al. 2011, 2015).
Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m and 11.5 m.


Type species – *Pterospermopsimorpha pileiformis* Timofeev, 1966 emend. Mikhailova, 1989 (in Jankauskas et al., 1989). The holotype is lost and a lectotype has been selected from Siberian Platform, Turukhansk region, Miroedikha River section, Miroedikha Formation, ca. 850 Ma (Jankauskas et al., 1989, pl. III, fig. 7; estimated age of the formation by Mendelson and Schopf, 1992).

Original description – [Translated from Russian] “Spheroidal or ellipsoidal vesicles, diameter from 30–40 µm to 80–90 µm, thick (=thick-walled), robust, large, included within thick-walled vesicles, (which are) smooth or slightly sculptured. Color of the internal vesicle brown, yellow, the outer (=outer vesicle) light yellow. Diameter of internal vesicle not less than 2/3 of the outer wall diameter.” (Timofeev, 1966, p. 33).

Emended diagnosis – [Translated from Russian] “Vesicle spheroidal, inclosing internal body. Internal body–dense, thick (=thick-walled), poorly transparent, more often opaque, smooth, shagrinate, granular; the outline is sharp, even, sometimes slightly wavy; diameter is at least than 2/3 of the vesicle outline. The outer wall is thinner, always translucent, smooth, shagrinate, granular, diameter 10–500 µm.” (Jankauskas et al., 1989, pp. 48–49).

Remarks – The genus morphology corresponds to a “sphere within a sphere” vesicle and has been formerly considered as a double-walled vesicles (Moczydłowska, 2015). Both the vesicle wall (the outer vesicle wall) and the internal body wall are clearly differentiated and firm. Sixteen species have been described in this genus (Fensome et al., 1990; Jachowicz-Zdanowska, 2013), but it is likely that some of them are synonymous.


Plate VIII, Figures A – H.

Synonymy –

1969 *Pterospermopsimorpha insolita* sp. n. – Timofeev, pp. 16-17, pl. III, fig 8.


1999 *Pterospermopsimorpha insolita* Timofeev, 1969 – Cotter, p. 75, fig. 7B.

2001 *Pterospermopsimorpha insolita* (Timofeev 1969) Mykhailova – Prasad and Asher, p. 117, pl. 6, fig. 1, 5, and pl. 11, fig. 7.

2001 *Pterospermopsimorpha binata* Timofeev, 1966 – Prasad and Asher, pl. 6, figs. 6, 8.

2009 *Pterospermopsimorpha insolita* – Nagy et al., p. 416, fig. 7e.

2014 *Pterospermopsimorpha sp.* – Riedman et al., p. 1013, fig. 2N.

Material – 32 well-preserved specimens, including 5 specimens with two internal bodies.

Description – Vesicle circular to oval in outline, originally spheroidal, having thin but firm psilate wall and consisting of one internal body defined by its own psilate, even in outline and thick wall. The internal body wall is thicker than the vesicle wall and is darker and semi-translucent making the internal body clearly differentiated. Occasionally, vesicles may contain two bodies surrounded by a common outer wall.

Dimensions – N=11. Vesicle 23–70 µm in width, internal body 17–67 µm in width and represent 74–96 % of the total vesicle width (n=9). Vesicles with two internal bodies are 42 x 23 µm and 43 x 24 µm in dimensions (n=2).

Remarks – Among described species of *Pterospermopsimorpha*, *P. insolita* and *P. binata* Timofeev, 1966, are considered here synonymous because both were diagnosed as having a smooth vesicle surface (Timofeev, 1966, 1969), compared to other species with microsculpture or texture of the vesicle wall. *P. binata* would have the priority of publication, however, the holotype of *P. binata* has been illustrated only by hand drawing (Timofeev, 1966, 1969), and this may not be the objective documentation. This species was described as having an internal body consisting of two parts, in contrast to a single internal body in *P. insolita*, which the holotype is photographed and clearly shows the smooth vesicle wall (Timofeev, 1969). The species *P. binata* has not been revised or illustrated in the following taxonomic synthesis by Jankauskas et al. (1989) alongside the other species of *Pterospermopsimorpha*, although the genus has been emended. The species *P. insolita* emended by Mikhailova (in Jankauskas et al., 1989, p. 49-50, pl. III, fig. 6) demonstrates the features of original diagnosis by Timofeev (1969), and therefore we rely on the identification of this species and abandon *P. binata*.

Some studied specimens exhibit two internal bodies enclosed in a common outer wall (Plate VIII, 22
Specimen with two internal bodies has been observed in the Society Cliffs Formation, the Bylot Supergroup from Canada (Hofmann and Jackson, 1994; fig 17.11) and described as “divided specimen”. Some specimens from the Siberian Lakhanda Formation show 2–4 internal bodies within one single envelope (Hermann, 1990; pl. IV, Figs 7, 8, 15) similar to the present specimens.

The thickness of the wall is inferred based on the transparency. A more opaque wall will be considered thicker than a transparent one. It is understood that such opacity can also derive from simple superimposition of two layers.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m, 12.2 m, and 13.2 m.

Occurences and stratigraphic range – Yakutia, Siberian Platform, Tunguska River section, Il'yushkana Formation, ca. 1200 Ma, and Veslyana Formation, ca. 750 Ma (Timofeev, 1969; Mendelson and Schopf, 1992), and Krasnoyarsk District, Uchur-Mayra region, Maya River, Lakhanda Formation, Upper Riphean, ca. 950 Ma (Jankauskas et al., 1989; Hermann 1990; Mendelson and Schopf, 1992); Canada, Baffin Island, Bylot Supergroup, Uluksun Group, Society Cliffs Formation, and Eqalulik Group, Arctic Bay Formation, 1270–750 Ma (Hofmann and Jackson, 1994); Western Australia, Officer Basin, Kanpa Formation, Neoproterozoic (Cotter, 1999); India, Ganga Basin, Bahaich Group, Ava and Sarda Formation, Riphean (=Mesoproterozoic) (Prasad and Asher, 2001); USA, Arizona, Chuar Group, Kwagunt Formation, Neoproterozoic (Nagy el al., 2009); Australia and Svalbard, Neoproterozoic, Sturtian (Riedman et al., 2014). The total stratigraphic range is from Paleoproterozoic to Mid-Neoproterozoic.


Plate IX, Figures A – C.

**Synonymy** –

1966 *Pterospermopsimorpha pileiformis* sp. n. – Timofeev, pl. V, fig. 12.
1969 *Pterospermopsimorpha pileiformis* Tim. – Timofeev, pl. III, fig. 7.
1987 *Pterospermopsimorpha* sp. A – Yin, pl. 5, fig 7.
2001 *Pterospermopsimorpha pileiformis* Timofeev, 1966 – Prasad and Asher, p. 107, pl. 6, figs. 2, 3.
Material – Four well-preserved specimens.

Description – Spheroidal vesicle having shagrinate, granular to slightly corrugated surface and consisting of a dense, dark, internal body with its own firm wall also shagrinate. The wall of the internal body is much thicker and darker than the outer vesicle wall.

Dimensions – N=3. Vesicle 36–68 µm in diameter, inner body 18–22 µm in diameter and constitutes 32–50 % of the total vesicle.

Remarks – This species differs from *Pterospermopsimorpha insolita* Timofeev, 1969, by having a corrugated or granular texture of the wall and a very dark internal body. The size of the internal body in ratio to the total vesicle diameter is also much smaller than in *P. insolita*.

The original and emended diagnoses of the genus (Timofeev, 1969; Mikhailova in Jankauskas *et al.*, 1989) state that the internal body represents no less than 2/3 of the total vesicle diameter. The internal body of studied specimens shows a well-defined outline and a robust wall, and together with general morphology of the species and texture of the vesicle wall, the specimens are identified as *P. pileiformis*. The strict limit of the dimensions may not be a diagnostic feature, as it is in case of other taxa (see discussion under *Leiosphaeridia*).

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m and 11.5 m.

Occurences and stratigraphic range – Yakutia, East Siberian Platform, Krasnoyarsk District, Turukhansk region, Miroedikha River, Miroedikha Formation, Upper Riphean, ca. 850 Ma (Timofeev, 1966, 1969; Jankauskas *et al.*, 1989; Mendelson and Schopf, 1992), and Uchur-Maya region, Maya River, Lakhanda Formation, Upper Riphean, ca. 950 Ma (Timofeev, 1966; Mendelson and Schopf, 1992); China, Jilin Province, Hunjiang District, Qinggou Formation, Riphean (Yin, 1987); India, Bahraich Group, Sarda and Avadh formations, Riphean (Prasad and Asher, 2001).

Genus *Schizofusa* Yan, 1982

Type species – *Schizofusa sinica* Yan, 1982; China, Jixian County, Changcheng System, Chuanlinggou Formation (Yan, 1982; pl. I, fig. 1).

*Schizofusa* sp.
Material – Three complete and well preserved specimens and six fragmentarily preserved.

Description – Vesicle fusiform in shape, thin-walled and psilate on the surface with longitudinal slit-like opening bordered by thick folds. The opening extends across the entire vesicle between its poles or across most of it. The marginal folds along the slit opening appear like rolled out vesicle wall.


Remarks – The specimens resemble some of the large specimens of *Macroptycha uniplicata* Timofeev, 1973, however none of the latter exhibit a longitudinal slit. This opening has been interpreted as an excystment feature (Grey, 2005; Peng *et al.*, 2009; Sergeev *et al.*, 2011) because of its specific shape and position on vesicle. Certain fragmented specimens in the present material are rolled up on the sides, which is a commonly observed feature among some species of *Schizofusa* (Grey, 2005; Willman *et al.*, 2006; Peng *et al.*, 2009).

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m and 12.2 m.


Type species – *Simia simica* Jankauskas, 1989; Southern Ural, Podinzersk Formation, Shisheniak River section, Upper Riphean (*in* Jankauskas *et al.*, 1989; pl. VI, fig. 12).


Remarks – The morphology of *Simia* is of a discoidal vesicle with a spheroidal internal body and the outer thin vesicle wall extended in the equatorial plane forming a fringe. The internal body is generally large with a high ratio of the internal body to overall vesicle width. The vesicle outline is more uneven than in the genus *Pterospermopsimorpha* Timofeev, 1966.


Plate X, Figures A – C.
Synonymy –
1969 *Pterospermopsimorpha annulare* sp. n. – Timofeev, p. 17, pl. III, fig. 9.
1993 *Simia annulare* (Timofeev) Mikhailova and Jankauskas – Vidal et al., p. 395, fig. 5A.
1995 *Simia annulare* (Timofeev) Mikhailova – Zang, p. 168, fig. 28E.
1997 *Simia annulare* (Timofeev) Mikhailova, 1989 – Samuelsson, p. 179, figs. 9C-F.
1999 *Simia annulare* (Timofeev) Mikhailova – Samuelsson et al., p. 12, figs. 7a, 7g.
2001 *Simia annulare* Timofeev, 1966, Mikhailova, 1989 – Prasad and Asher, p. 107, pl. 6, fig. 9.
2013 *Simia annulare* (Timofeev) Mikhailova – Grey, p. 18, fig. 3E.
2013 *Simia annulare* (Timofeev) Mikhailova – Tang et al., p. 162, fig. 4G.

Material – Ten well-preserved specimens and a single specimen with three vesicles attached to each other, and relatively well-preserved.

Description – Vesicle circular to oval in outline consisting of a thick-walled spheroidal internal body encapsulated in a thin outer vesicle wall, which extends in the equatorial plane. The surface of the vesicle is smooth. The internal body shows a ring-like fold around its margin and an additional spheroidal, small clumped organic matter with irregular outline in its cavity. This clump of organic matter is located centrally or side of the internal body.


Remarks – One specimen (Plate X, Fig. C) consists of three vesicles that are tightly grouped and it is uncertain if the vesicles are inter-connected or incidentally compressed together. But, looking at the hexagonal pattern of the outline they seem to be biologically arranged.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 11.5 m, and 12.2 m.

Occurrence and stratigraphic range – North Russia, Kildin Island, Kildin Formation, upper Riphean, and more that 20 localities in the Siberian Platform and the Ural Mountains (Timofeev, 1969;
Jankauskas et al., 1989; full list in Schopf and Klein, 1992); Northwest Russia, Kola Peninsula, Sredni Peninsula and Kildin Island, Kildinskaya Group, Iernovskaya, Chernorechenskaya, Pestzovozerskaya, Poropelonskaya and Karuyarvinskaya formations; Volokovaya Group, Pumanskaya Formation, and Tiersky Coast, Chapoma Formation, Neoproterozoic (Samuelsson, 1997); Yakutia, Siberian Platform, Lena-Anabar Depression, Khastakh 930 borehole, Khajpak Formation, upper Riphean (Vidal et al., 1993); Northwest Greenland, Thule Supergroup, Baffin Bay Group, Qaanaaq Formation, Proterozoic (Samuelsson et al., 1999); China, Anhui Provinces, Liulaobei Formation, early Neoproterozoic (Zang and Walter, 1992a; Tang et al., 2013); Australia, Officer Basin, Alinya Formation, early Neoproterozoic, ca. 800 – 750 Ma (Zang, 1995) and Kanpa and Hussar Formations, Neoproterozoic (Cotter, 1999), and Amadeus Basin, Bitter Springs Formation, upper Proterozoic (Zang and Walter, 1992b), Northern Territory, Roper Group, Mesoproterozoic (Grey, 2013); India, Ganga Basin, Bahraich Group, Sarda and Avadh formations, Mesoproterozoic (Prasad and Asher, 2001). The total stratigraphic range is Mesoproterozoic–Neoproterozoic.


Plate X, Figures D–E.

Synonymy –


1999 Simia simica comb. – Yin and Guan, p. 126, figs. 3.4, 3.7.

2009 Simia simica Jank. – Stanevich et al., p. 8, pl. 1, figs. 15 – 16.

Material – Seven well-preserved specimens.

Description – Vesicle circular in outline, originally discoidal and consisting of an internal body surrounded by the extension of the vesicle wall in the equatorial plane forming a narrow fringe with irregular outline. The vesicle wall is shagrinate and translucent, while the internal body is very dark and it gradually merges with the vesicle wall showing an uneven outline.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m, and 12.2 m.

Occurrence and stratigraphic range – Russia, South Ural Mountains, Upper Riphean (Jankauskas, 1980; Jankauskas et al., 1989); China, Anhui Provinces, Liulaobei Formation, upper Proterozoic (Zang and Walter, 1992a); Australia, Amadeus Basin, Bitter Springs Formation, upper Proterozoic and Pertataka Formation, Ediacarian (Zang and Walter, 1992b); North China, Henan Province, Lushan County, Dongjia Formation, Neoproterozoic (Yin and Guan, 1999); Siberia, Udzhinskogo Uplift, Udzhinskoy Formation, Middle Riphean, 1074 Ma (Stanevich et al., 2009). The total stratigraphic range is from late Mesoproterozoic to Ediacaran.

Simia spp.
Plate X, Figures F–I.

Material – Eleven specimens in various state of preservation.

Description – Vesicle circular in outline, originally discoidal, having thin wall with shagrinatae to coarse granular surface and consisting of internal spheroidal body, dense and large, and surrounded by a narrow fringe-like vesicle wall located at the equatorial plane.

Dimensions – N=7. Vesicles 29–42 µm in width, internal body 27–39 µm in width. The internal body represents ca. 93 % of the total vesicle width.

Remarks – The specimens are placed within the genus Simia because of the presence of a large internal body and an equatorial wall extension. They differ from S. annulare due to the lack of a ring-like marginal structure and from S. simica by regular and narrow equatorial fringe.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m, and 12.2 m.

Genus Synsphaeridium Eisenack, 1965

Type species – Synsphaeridium gotlandicum Eisenack, 1965; Sweden, Gotland, Silurian (Eisenack, 1965; pl. 23, fig. 1).

28
\textit{Synsphaeridium} spp.
Plate XII, Figures I – K

Material – 114 well-preserved colonies consisting of tenses of individual cells.

Description – Clusters of simple, spheroidal to ellipsoidal small vesicles (cells) with psilate wall and without an envelope or common matrix surrounding them.

Dimensions – N=5. Colonies 25–100 \(\mu\)m in length, individual cells range from \textit{ca.} 5 \(\mu\)m to \textit{ca.} 20 \(\mu\)m in diameter.

Remarks – The tightly aggregated individual vesicles may have a polygonal outline (Plate XII, Fig. K), and those vesicles preserved outside the cluster are not different morphologically from common leiospherids. The genus \textit{Synsphaeridium} Eisenack, 1965 groups a wide range of clusters formed by vesicles of various sizes. The wide range of vesicle sizes within the same colony may indicate intraspecific or ontogenic variations (Tang \textit{et al.}, 2015).

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m, 12.2 m, and 13.2 m.

Genus \textit{Trachysphaeridium} Timofeev, 1966

Type species – \textit{Trachysphaeridium laminaritum} Timofeev, 1966; Moldava, Vortlyuzhany borehole at a depth of 27.2 m, the \textit{Laminarites} Beds, Vendian (Timofeev, 1966; pl. VII, fig. 3).

Plate XI, Figures A – D.

Synonymy –
1966 \textit{Trachysphaeridium laminaritum} sp. n. – Timofeev, p. 36, pl. VII, fig. 3.
1969 \textit{Trachysphaeridium laminaritum} Tim. – Timofeev, p. 20, pl. 4, fig. 7.
1973 \textit{Trachysphaeridium laminaritum} Tim. – Timofeev, pl. 15, fig. 6, pl. 27, Fig. 6.
1974 \textit{Trachysphaeridium laminaritum} Timofeev, 1966 – Vidal, p. 8, pl. 1, fig. 17.
1997 *Trachysphaeridium laminaritum* Timofeev, 1966 – Samuelsson, p. 180, fig. 10D.

2009 *Trachysphaeridium laminaritum* – Nagy et al., p. 416, fig. 1h.

Material – 67 well-preserved specimens.

Description – Spheroidal to sub-spheroidal vesicle with thick, firm wall and crenulated to alveolar surface and having an opening-like structure, circular in outline. The vesicle is occasionally encapsulated in a very delicate, thin, translucent outer membrane.

Dimensions – N=6. Vesicles 30–70 µm in diameter, the possible opening is ca. 5x8 µm and 5x6 µm in dimension (n=2).

Remarks – The opening of vesicle in some specimens (Plate XI, Figs. B, D), is assumed to be a true structure and not a random breakage of vesicle wall, may represent excystment structure, which is consistent with the presence of surrounding membrane around the vesicle (Vidal, 1976a; Vidal and Ford, 1985).

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m and 12.2 m.

Occurrences and stratigraphic range – China, Qingbaikou Group, Xiamaling Formation, 950 Ma; Moldova, Vendian, 600 Ma; Ukraine, Ukrainian Carpathes, Vendian, 600 Ma; Russia, Blue Clays of the White Sea, 550 Ma and Chapoma Formation, 750 Ma; Siberia, Pestrotsret Formation, 540 Ma (Timofeev, 1966; Mendelson and Schopf, 1992) and Turukhansk region, Miroedikha River, Miroedikha Formation, Upper Riphean, ca. 850 Ma (Timofeev, 1966; Timofeev, 1969; Mendelson and Schopf, 1992); Finland, Muhos Formation, 650 Ma (Tynni and Uutela 1984; Mendelson and Schopf, 1992); USA, Arizona, Chuar Group, K wagunt Formation, Awatubi Member, 863 Ma (Vidal and Ford, 1985; Mendelson and Schopf, 1992; Nagy et al., 2009); Sweden, Visingsö Group, through the entire succession, Upper Riphean to Vendian (Vidal, 1974; Vidal 1976a; Mendelson and Schopf, 1992); Northwest Russia, Kola Peninsula, Sredni Peninsula, Kildinskaya Group, Pestzovozerskaya and Poropelonskaya fms, and Tiersky Coast, Chapoma Fm, Early Neoproterozoic (Samuelsson, 1997). The total stratigraphic range is Neoproterozoic.

*Trachysphaeridium laufeldii* Vidal, 1976

Plate XI, Figures E–I.

Synonymy –

1976 *Trachysphaeridium laufeldi* n. sp. – Vidal, 1976a, p. 37, fig. 21A–N
1976 *Trachysphaeridium laufeldi* Vidal – Vidal, 1976b, fig. 2A.

1985 *Trachysphaeridium laufeldi* Vidal, 1976 – Vidal and Ford, p. 372, fig. 7A, B, D, F.

1997 *Lophosphaeridium laufeldii* Vidal, 1976 comb. nov. – Samuelsson, p. 177, figs. 7F, H, I.

1999 *Trachysphaeridium cf. laufeldi* (Vidal, 1976) – Yin and Guan, p. 130, fig. 5.1, 5.8, 5.10.


2009 *Lophosphaeridium laufeldi* – Nagy et al., p. 416, fig. 1j.

2011 *Trachysphaeridium cf. laufeldi* Vidal, 1976 – Couëffé and Vecoli, p. 169, Fig. 6.9.

Material – 28 well-preserved specimens.

Description – Spheroidal to sub-spheroidal vesicle with thick wall and surface covered by small tightly arranged conical elements (spikes).Remains of a very delicate, thin outer membrane, are occasionally preserved. In some specimens a clear opening with an uneven outline is observed.

Dimensions – N=7. Vesicles 29–53 µm in diameter. When present, the opening is ca. 7x9 µm in diameter (n=2).

Remarks – The species name should be spelled *T. laufeldii*, following the rules of nomenclature applied to organic-walled microfossils (The International Code of Nomenclature for Algae, Fungi and Plants, Melbourne Code, 2011).

The opening observed here is a small hole with no rim and the margin of opening is folded out and it differs from the structures observed in the species by Vidal (1976a). In the latter case, the opening structures are surrounded by a thick rim resembling a “spinous protuberance” in a side view and is similar to the circular pylome recorded in *Leiospheridia* sp. B (see above) and interpreted as operculate excystment opening (Vidal, 1976a; Vidal and Ford, 1985). The presence of an excystment structure together with a surrounding envelope around the vesicle is consistent with cyst stage of microorganism. In most studied specimens the operculum structure is absent and the vesicle may represent an abandoned cyst. Because of the similarity between the two species, *Leiospheridia* sp. B and *Trachysphaeridium laufeldii* may be conspecific, representing different stages of a life cycle or growth, although their wall structures are different (granular in *L.* sp. B. and with conical spikes in *T. laufeldii*).

Some authors suggested that *Trachysphaeridium laufeldii* Vidal, 1976 is a species of the genus *Lophosphaeridium* Timofeev, 1959 (Samuelsson, 1997; Nagy et al., 2009) because of the conspicuous wall sculpture. However, the morphological features of *T. laufeldii* are in gross morphology similar to those *Trachysphaeridium*, having a thick-walled vesicle with excystment opening encapsulated in a very thin outer membrane. Such features are not observed in *Lophosphaeridium*. 
Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m, 12.2 m and 13.2 m.

Occurrence and stratigraphic range – Greenland, Eleonore Bay Group, 750 (Vidal, 1976b; Mendelson and Schopf, 1992); Sweden, Visingsö Group, middle and upper units, Upper Riphean to Vendian (Vidal 1976a; Mendelson and Schopf, 1992); USA, Utah, Uinta Mountain Group, Mount Watson Formation and Red Pine Shale, 950 Ma, and Arizona, Chuar Group, Kwagunt Formation, Awatubi Member, 863 Ma (Vidal and Ford, 1985; Mendelson and Schopf, 1992; Nagy et al., 2009); Svalbard, Ryssö Formation, 750 Ma (Knoll and Calder, 1983; Mendelson and Schopf, 1992); Northwest Russia, Kola Peninsula, Sredni Peninsula, Kildinskaya Group, Karuyarvinskaya Formation, Early Neoproterozoic (Samuelsson, 1997); China, Henan Province, Lushan County, Dongjia Formation and Hunan Province, Huayuan region, Datangpo Formation, Neoproterozoic (Yin and Guan, 1999; Yin and Yuan, 2007); Ghana, southern margin of the Volta Basin, Kwahu Group, Anyabony Formation, lower unit, Meso- to Neoproterozoic (Couëffé and Vecoli, 2011). The total stratigraphic range is Neoproterozoic.

Unnamed species A
Plate XII, Figures C–E

Material – 18 well-preserved specimens.

Description – Spheroidal aggregate of small sub-spheroidal and overlapping cell-like structures with transparent psilate wall. The aggregate is dense and it is uncertain if individual cell-like structures visible on the specimen outline are attached to the vesicle wall underneath or are true mass-aggregation of small cells.

Dimensions – N = 3. The aggregate ranges from 24–42 µm, individual cell-like structures are 1–2 µm wide and 2–4 µm long.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m, and 12.2 m.

Unnamed species B
Plate XIII, Figure A

Material – A single fragmentarily preserved specimen.
Description – Vesicle rounded, probably originally spheroidal or ovoidal. The vesicle wall is a network of small, circular to polygonal fields formed by solid, rod-like thickenings on wall surface, and it may appear that this rigid mesh has been a surface structure and a part of the vesicle wall.

Dimensions – N=1. The specimen is ca. 55x60 µm in diameter; the polygonal fields are ca. 2–4 µm in diameter.

Present record – Visingsö upper formation, Visingsö 1 borehole at a depth of 11.5 m.

Unnamed species C
Plates XIII, Figure B

Material – A single fragmentarily preserved specimen.

Description – A fragment of rounded vesicle, originally spheroidal, having vesicle wall formed by a network of short filament-like, solid elements giving a “ball of wool” appearance to the specimen.

Dimensions – N=1. Vesicle is ca. 25x42 µm in diameter.

Present record – Visingsö upper formation, Visingsö 1 borehole at a depth of 11.5 m.

Dividing cells
Plate XIII, Figures C – D

Material – Three specimens in various state of preservation.

Description – Two or three subspheroidal vesicles attached by a common wall, not fully separated. The vesicles are simple, smooth-walled or slightly granular. Each vesicle displays 1–2 dark and dense small internal inclusions.


Remarks – The specimens show cells fission in various stage with incomplete separation of the walls
Dividing cells from Proterozoic successions of various ages have been reported (Hofmann, 1990, pl. IV, figs 1–6, and pl. V, figs 8 – 10; Moczydłowska, 2008b, fig. 7B; Wacey et al., 2014, fig. 1B).

Present record – Visingsö upper formation, Visingsö 1 borehole at a depth of 12.2 m.

5.2 Coccoidal and filamentous cyanobacteria

Genus *Eoschizothrix* Seong-Joo and Golubic, 1998


*Eoschizothrix composita* Seong-Joo and Golubic, 1998

Plate XVI, figure D

Synonymy –
1988 *Siphonophycus* sp. – Zang, pl. XLI, fig. K.
1991 Tubular cyanobacterial sheaths – Moczydłowska, pl. 14J.
1992 Tubular sheath with internal trichome – Schopf and Klein, p. 1071, pl. 10D.
1998 *Eoschizothrix composita* n. sp. – Seong-Joo and Golubic, pp. 181–182, figs 2, 3, 5, 6, 10.

Material – Four fragmentarily preserved specimens very well preserved.

Description – Cylindrical unbranched, nonseptate filament enclosed within a tubular non-septate sheath (“tube within tube” morphology). The wall surface of both filaments is smooth. The inner tube is darker than the outer sheath.

Dimensions – N=3. Outer filament 6–20 µm in width, inner filament 3–6 µm in width. The length of
the specimens are 35 to 76 µm.

Remarks – The darker colour of the inner filament may reflect a thicker wall and may not be due to optical appearance of the superimposed two walls of filaments (Moczydłowska, 2008b).

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths 3.7 m, 11.5 m, and 13.2 m.

Occurrences and stratigraphic range – China, Hubei Province, Yichang City, Yangtze Gorges, Huangshandong section, Shipai Formation, Lower Cambrian (Zang, 1988); Yakutia, Siberian Platform, Turukhansk region, Sukhaya Tunguska Formation, locality cf. PPRG 2725, 1000 Ma (Schopf and Klein, 1992), and Uchur-Maya area, Aldan River and Belaya River sections, Yudoma Group, Vendian (Sergeev, 2006); North China, Hebei Province, Pangjiapu Iron Mine area, Gaoyuzhuang Formation, Mesoproterozoic, ca. 1.4 – 1.5 Ga (Seong-Joo and Golubic, 1998; Seong-Joo et al., 1999); Poland, Lublin Slope of the East European Platform, Terebin IG-5 borehole at 3672.0 m, Lublin Formation, Ediacaran (Moczydłowska, 1991) and Lopiennik IG-1 borehole at 5376.7 m, 5382.2 m, and 5385.6 m, Wlodawa Formation, upper Ediacaran (Moczydłowska, 2008b). The total stratigraphic range is Mesoproterozoic to Lower Cambrian.

Genus *Eosynechococcus* Hofmann, 1976

Type species – *Eosynechococcus moorei* Hofmann, 1976; Canada, Belcher Islands, Belcher Supergroup, Kasegalik Formation, Precambrian, ca. 1900 Ma (Hofmann, 1976; pp. 1056, plate II, fig. 4).

*Eosynechococcus moorei* Hofmann, 1976

Plate XII, Figures A–B.

Synonymy –

1976 *Eosynechococcus moorei* n. sp. – Hofmann, p. 1056, pl. 2, figs. 1–7, 8(?).
1979 *Eosynochococcus moorei* Hofmann – Golubic and Campbell, p. 206, 208, figs 2E–J; 3C–D.
1994 *Eosynochococcus moorei* Hofmann, 1976 – Butterfield et al., p. 54, fig. 23J.
1995 *Eosynechococcus moorei* Knoll – Sergeev et al., p. 27, fig. 9.8, 9.12, 9.13.

Material – Five well-preserved large colonies of various shapes and sizes, comprising tens to over
hundred individual cells.

Description – Ellipsoidal cells with smooth walls and tightly aggregated in clusters with sub-spheroidal shape. No organic matrix or outer envelope is present around the cell aggregates.

Dimensions – N=3. The colonies are 23, 50 and 80 µm in length and 10 – 20 µm in width. The individual cells are ca. 2 µm in width and ca. 4 µm in length.

Present record – Visingsö upper formation, Visingsö 1 borehole at a depth of 12.2 m.

Occurrences and stratigraphic range – Canada, Belcher Island, Belcher Supergroup, Kasegalik Formation, Precambrian, ca. 1900 Ma (Hofmann, 1976; Golubic and Campbell, 1979); Spitsbergen, Akademikerbreen Group, Svanbergfjellet Formation, Early Neoproterozoic (Butterfield et al., 1994); northern Siberia, Billyakh Group, Mesoproterozoic (Sergeev et al., 1995); Northern China, Huaibei region, Gouhou Formation, Tonian (Tang et al., 2015).


Type species – Oscillatoriopsis obtusa Schopf, 1968; Australia, Northern Territory, Amadeus Basin, Ross River area near Alice Springs, Bitter Springs Formation, late Precambrian, ca. 1 Ga (Schopf, 1968; p. 667, pl. 77, fig. 8).

Oscillatoriopsis spp.
Plate XVI, Figures F–H

Material – Three well preserved specimens and several slightly altered specimens (with one showing the apical cell).

Description – Multicellular unbranched smooth-walled trichome of uniseriate cells without surrounding sheath. The cells are roughly equal in width but can be compressed and un-equal in length. When present, the apical cells are rounded (Pl. XVI, Fig F).

Dimensions – N=2. The length of trichomes 59–82 µm, the length of cells 3–8 µm and the width 7–12 µm.

Remarks – The genus Oscillatoriopsis Schopf, 1968, emend. Butterfield et al., 1994, has been
subdivided into four species by the size classes of the trichome width by Butterfield et al. (1994). These are: *O. vermiformis*, 1–3 µm in width; *O. obtusa*, 3–8 µm in width; *O. amadeus*, 8–4 µm in width; and *O. longa*, 14–25 µm in width. The subdivision is difficult to objectively apply and lacks taxonomic meaning because the size classes are arbitrarily chosen and overlapping, and thus they do not demonstrate modal size-frequency distribution for recognizing the species. Some of these species may be conspecific and represent various stages of growth and/or intraspecific variants.

Observed herein specimens could fit the diagnosis of *O. obtusa* and *O. amadeus* but, because of the lack of distinctive morphological character (other than size), they are referred to *Oscillatoriopsis* spp.

Present record – Visingsö upper formation, Visingsö 1 borehole at a depth of 3.7 m and 12.2 m.


Type species – *Palaeolyngbya barghoorniana* Schopf, 1968; Australia, Northern Territory, Amadeus Basin, Ross River area near Alice Springs, Bitter Springs Formation, late Precambrian, ca. 1 Ga (Schopf, 1968, pp. 665 – 666, pl. 77, Fig 1). The holotype is re-photographed in Schopf and Klein, 1992, p. 1093, pl. 32C. The age of the formation is re-evaluated as Neoproterozoic, ca. 850 Ma (Mendelson and Schopf, 1992).

*Palaeolyngbya catenata* Hermann, 1974

Plate XVI, Figure E

Material – Two relatively well preserved specimens.

Description – Trichome of uniseriate rectangular cells surrounded by a tubular smooth outer sheath.

Dimensions – N=2. The width of outer sheath is 6–9 µm. The dimensions of cells inside the trichome are 5.0–7.5 µm in width and ca. 2 µm in length. The trichome length is about 120 µm (n=1).

Remarks – The present specimens are superimposed and compressed due to post-depositional deformation and do not represent a branching of filaments.

Present record – Visingsö upper formation, Visingsö 1 borehole at a depth of 12.2 m.

Type species – *Polythrichoides lineatus* Hermann, 1974, emend. Hermann, 1976; Yakutia, East Siberian Platform, Krasnoyarsk District, Turukhansk region, Miroedikha River section, Miroedikha Formation, Upper Riphean (Hermann, 1974; Hermann *in* Timofeev et al., 1976). The age of the formation has been estimated to ca. 850 Ma (Mendelson and Schopf, 1990).


Plate XIV, Figures A – C

Synonymy –

1974 *Polythrichoides lineatus* gen. et sp. n. – Hermann, pp. 7–8, pl. 6, figs. 3, 4.
1976 *Polythrichoides lineatus* Hermann, 1974 – Timofeev et al., p. 37, pl. XIV, fig. 7.
1982 *Polythrichoides lineatus* Hermann, 1974, emend. Hofmann, 1976 – Jankauskas, p. 113, pl. XLV, fig. 6; pl. XLVIII, fig. 16.
1985 *Polythrichoides lineatus* Hermann – Xing et al., p. 64, pl. 12, fig. 10.
1985 *Polythrichoides lineatus* Herm. – Jankauskas, p. 146, pl. 61, Fig. 3.
1990 *Polytrichoides lineatus* Hermann, 1974 emend. 1976 – Hermann, p. 28, pl. IX, figs. 8, 8a (=9) (Misspelled generic name).
1990 *Polytrichoides lineatus* Herm. – Jankauskas, p. 172, pl. 61, fig. 3.
1991 *Polytrichoides lineatus* Hofmann, 1976 – Yin, p. 263, pl. 4, fig. 11.
1991 *Polytrichoides lineatus* Germann, 1974 emend. – Knoll et al., p. 563, figs. 4.3, 4.5 (Misspelled generic name).
1994 *Polytrichoides lineatus* Hermann, emend. Hofmann, 1976 – Yin and Sun, p. 102, figs. 4b, 5m (=5b, 6m).
2015 *Polythrichoides lineatus* Hermann, 1974 – Tang et al., p. 314, fig. 19E, 19F.

Material – 68 well preserved specimens, mostly fragmented.

Description – Bundles of unseptate and unbranched filaments enclosed in a close cylindrical position within a common sheath or without it. The surface of both the filaments and the outer sheath is smooth. All filaments are equal in width within the same bundle. When the outer sheath is broken, the filaments may extend outside of it and be spread separately from each other (Pl. XIV, Fig C).

Dimensions – N=5. Trichomes range from about 60–240 μm in length and 6–30 μm in width; individual filaments within the trichome 2–6 μm in width. Trichomes consist of 4 to 14 individual filaments.

Remarks – The absence of a common outer sheath in some specimens of *Polythrichoides lineatus* could be the result of taphonomic loss (Tang et al., 2013), as it appears to be thin and translucent, thus prone to destruction.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m and 12.2 m.

Occurrences and stratigraphic range – Yakutia, East Siberian Platform, Krasnoyarsk District, Turukhansk region, Miroedikha River, Miroedikha Formation, Upper Riphean, ca. 850 Ma (Hermann, 1974; Timofeev et al., 1976; Hermann, 1990; Mendelson and Schopf, 1992) and Uchur-Maya region, Maya River, Lakhanda Formation, Upper Riphean, ca. 950 Ma (Jankauskas et al., 1989; Hermann 1990; Mendelson and Schopf, 1992); Southern Ural Mountains, Zilmerdak Formation, ca. 1000 Ma, Podinzer Formation (=Sim Formation), ca. 925 Ma; Zilim River, Uk Formation (=Kudash Formation), ca. 675 Ma, and Bashkiria, Zigan River, Zigan Formation, Kabakovo 62 borehole at a depth of 3636.0–3678.0 m (Jankauskas, 1982; Mendelson and Schopf, 1992), and Sergeevsk- 800 borehole, 2942.5–2946.4 m, Baikibashev Formation, Vendian (Jankauskas, 1985, 1990); Russia, Zimny Coast of the White Sea, Archangelsk area, Zinnie Gory beds, Vendian, Redkino regional stage (Ragozina and Sivertseva, 1990). Arctic Canada, Baffin Island, Bylot Supergroup, Eqalulik Group, Arctic Bay Formation, 1270 Ma; Nunatsiaq Group, Elwin Formation, 750 Ma (Hofmann and Jackson, 1994). NE Spitsbergen, Draken Conglomerate Formation, Neoproterozoic, 800 – 700 Ma (Knoll et al., 1991); China, Jiao-Liao-Xu-Huai Province, Qiaotou and Changlingzi formations, Lower Sinian (Xing et al., 1985); western Shandong, Tongjiazhuang Formation, Upper Proterozoic ca. 800 – 700 Ma (Yin, 1991); northern Anhui, Huainan Group, Liulaobei Formation, Upper Sinian (Zang and Walter, 1992a), and Huainan region, Liulaobei Formation, early Neoproterozoic (Tang et al., 2013); North
China, Huaibei region, Gouhou Formation, Tonian (Tang et al., 2015). Poland, Lopiennik IG-1 borehole at 5385.6 m, Wlodawa Formation, upper Ediacaran (Moczydłowska, 2008b). The total stratigraphic range is Mesoproterozoic to Upper Ediacaran.


Types species – *Siphonophycus kestron* Schopf, 1968; Australia, Northern Territory, Amadeus Basin, Ross River area near Alice Spring, Bitter Spring Formation, ca. 1 Ga (Schopf, 1968; p. 671, pl. 80, figs 1–3), and currently referred to ca. 850 Ma (Mendelson and Schopf, 1992).

*Siphonophycus* spp.
Plate XV; Plate XVI, Figs A–C

Material – More than 1700 specimens in various states of preservation. The specimens preserved in bacterial mat are treated as one specimen due to the difficulties in counting the number of filaments included.

Description – Cylindrical, nonseptate, unbranched, smooth-walled filaments of various sizes with broken apices. Specimens associated together in microbial mats (Plate XVI, Fig A–C) show different width (Plate 16, Fig C).

Dimensions – N=15. Observed specimens range from ca. 0.5 µm to 17 µm in width and from 30 to 180 µm in length.

Remarks – The genus *Siphonophycus* has been divided into several species depending of their width by Butterfield et al. (1994). These are: *S. thulenema*, 0.5 µm in width; *S. septatum*, 1–2 µm; *S. robustum*, 2–4 µm; *S. typicum*, 4–8 µm; *S. kestron*, 8–16 µm; *S. solidum*, 16–32 µm; and *S. punctatum*, 32–64 µm in width. Tang et al. (2013) described another species, *S. gigas* ranging 64–128 µm in width. The subdivision is arbitrary with overlapping size classes between species and it is subjective for taxonomic grouping. It may not reflect biological entities or may comprise conspecific variants.

Studied specimens could be assigned to many of these species — with the exception of *S. punctatum* and *S. gigas* — but, because of the lack of distinctive morphological character and overlapping sizes, they are attributed to *Siphonophycus* spp.

Present record – Visingsö upper formation, Visingsö 1 borehole at the depths of 3.7 m, 11.5 m, 12.2 m; and 13.2 m.
6 Discussion

6.1 Morphologic disparity and diversity of organic-walled microfossils from the Visingsö upper formation.

6.1.1 Previous and present records

Table 1. Distribution and abundance of organic-walled microfossils from the studied assemblage of the upper formation (Visingsö I borehole, depths 3.7–13.2 m).

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Abundance (specimens)</th>
<th>Distribution depths (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1–3</td>
<td>31–100</td>
</tr>
<tr>
<td>Cerebrosphaera sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germinosphaera bispinosa (Mikh., 1986) But., 1994</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leiosphaeridia spp.</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>L. ternata (Tim., 1966) Mikh. and Jan., 1989</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>L. sp. A</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>L. sp. B</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>L. sp. C</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>Macroplycha uniplicata Tim., 1976</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>Navifusa majensis Pyatletov, 1980</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>Ostiana microcystis Hermann, 1976</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>Pterospermella sp.</td>
<td></td>
<td>★</td>
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<tr>
<td>Schizofusa sp.</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>Simia annulata Tim., 1969</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>S. simica (Jan., 1980) Jan., 1969</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>S. spp.</td>
<td>★</td>
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<tr>
<td>Synsphaeridium spp</td>
<td>★</td>
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<tr>
<td>Trachysphaeridium laminaritum Tim., 1966</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>T. laufeldii Vidal, 1976</td>
<td>★</td>
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</tr>
<tr>
<td>Unnamed sp. A</td>
<td>★</td>
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<td>Unnamed sp. B</td>
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<td>Unnamed sp. C</td>
<td>★</td>
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</tr>
<tr>
<td>Dividing cells</td>
<td>★</td>
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</tr>
<tr>
<td>Coccolial and filamentous cyanobacteria:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eoschizothrix composita Seong-J. and Gol., 1998</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>Eosynchococcus moorei Hoffman, 1976</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>Oscillatoriopsis spp.</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>Palasolyngbya caténata Hermann, 1974</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>Polythnicoides lineatus (Herm., 1974) Hoff., 1976</td>
<td>★</td>
<td>★</td>
</tr>
<tr>
<td>Siphonophycus spp.</td>
<td>★</td>
<td>★</td>
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</tbody>
</table>
The studied new assemblage is of a greater diversity than previously recorded and twenty-four species belonging to eighteen genera are identified. Additionally, three unknown morphotypes are recognized (Table 1). The taxonomic diversity is relatively high in the Neoproterozoic and it has been revealed in the previous studies of the Visingsö Group (Vidal, 1974, 1976a). In the entire group, twenty-five species assigned to twelve genera were recognized, and in the upper formation, twenty-four of them were present. Among those, species *Kildinella hyperboreica*, *K*. cf. *sinica*, *K*. cf. *vesljanica*, *Protosphaeridium laccatum*, *P*. cf. *papyreceum*, *P*. cf. *scabridium* and *P*. cf. *tuberculiferum* have been later considered conspecific with *Leiospheridia* spp. (Lindgren, 1981, 1982; Jankauskas et al., 1989).

The studied assemblage is dominated by acritarchs attributed to the genus *Leiosphaeridia*, similar to those occurring in other Proterozoic successions. Specimens of *Leiosphaeria* spp. are recorded in all fossiliferous samples and their fragments are the only organic remains found at a depth of 9.7 m. The spheroidal vesicles in the present material represent a wide range of sizes and vesicle wall thickness. Such variety is common in the genus and many transitional morphotypes exist, making identification of species by their size and wall thickness difficult and subjective (see Taxonomy above). Some specimens are attributed to the species *Leiospheridia ternata* because the vesicles small size, conspicuous thickness of the wall and tendency to be specific wrinkled pattern differentiate them from *Leiospheridia* spp. Additionally, three original morphotypes are assigned to *Leiospheridia* sp. A (smooth vesicles with wide polygonal encystment opening), *L*. sp. B (vesicles with granular, circular pylome on the surface) and *L*. sp. C (big, non-translucent, vesicles with uneven surface and the irregular outline).

The most distinctive species with a spheroidal vesicle is large and diagnostically wrinkled *Cerebrosphaera* sp., which is however preserved only in fragments but present in all sample (except at a depth of 9.7 m). The vesicle wrinkle-like surface ornamentation is a consistent pattern on the wall surface and not a taphonomic alteration (Butterfield et al., 1994).

The specimens assigned to *Schizofusa* sp. are fusiform vesicles with a median longitudinal split. They are often folded or rolled-up. Four specimens recognized as *Navifusa majensis* have been found in the lowest three depths (11.5, 12.2 and 13.2 m). The specimens are solitary and one is conjugated, consisting of two chained vesicles. Chained vesicles are not a rare occurrence among Proterozoic OWM and similar constructions are known from various genera such as *Pololeptus* Yin, 1994 (in Yin and Sun, 1994) or *Arctacellularia* German, 1976 (in Timofeev et al., 1976).

Specimens with internal bodies surrounded by an outer vesicle wall are very common in the Visingsö upper formation. They represent species *Pterospermopsimopha insolita*, *P*. *pileiformis*, *Pterospermella* sp., *Simia annulare*, *S.* *simica* and S. spp. Fusiform vesicles assigned to *Macroptycha uniplicata* are interpreted as having an internal body (see Taxonomy). Specimens showing two distinct features are however morphologically close to some solitary specimen of *Arctacellularia*. Therefore, following previous interpretations, it is possible that the species *Macroptycha uniplicata* comprises several different taxa. The specimens assigned to *Trachysphaeridium laminaritum* and *T.*
laupeldii differ by the presence of a thin envelope wrapping the vesicle — which is not an internal body — and by the presence of openings, interpreted as excystment pylomes (Vidal, 1976a; Vidal and Ford, 1985). In addition to all those morphotypes, *Germinosphaera bispinosa*, a process-bearing taxon, is recognized.

Several taxa within the assemblages are aggregated minute spheroidal vesicles and are understood to be colonies, occasionally enclosed within an outer membrane or mucilage. The colonial forms are attributed to *Ostiana microcystis* comprising of vesicles within a common mucilage, and to *Synsphaeridium* spp., without mucilage. Aggregates composed of numerous small ellipsoidal vesicles are assigned to *Eosynechococcus moorei* and Unnamed sp. A. Specimens of Unnamed sp. A are differentiated by the constant spheroidal shape of the colonies and tightly overlapping vesicles within the cluster.

Thousands of filamentous cyanobacterial microfossils are found within the succession. Among them, the nonseptate tubular filamentous species *Siphonophycus* spp. is the most common and also occurs in dense microbial mats. Bundles of nonseptate filament wrapped or not within a common sheath are assigned to *Polythrichoides lineatus*. Some individual septate filaments are also found. These are recognised as *Palaeolyngbya catenata* and *Oscillatoriopsis* spp. Specimens of *Eoschizothrix composita* and *Palaeolyngbya catenata*, consist of tubular filaments of broadly rectangular uniseriate cells — or trichomes — enclosed within another wider nonseptate filament (“tube within tube” morphology).

**Possible vegetative division**

Vesicles preserved at the stage of ongoing vegetative division are among the most intriguing observations within the present material. Several spheroidal cells possibly preserved at various stages of cellular cytokinesis have been recorded in Proterozoic assemblages (Schopf, 1968; Jankauskas *et al.*., 1989; Hermann, 1990; Moczydłowska 1991, 2008b). The lack of morphological diagnostic structures makes the affiliation with any specific taxon impossible, although some of them can be recognized as *Leiosphaeridia* (Jankauskas *et al*., 1989; pl. VIII, figs. 13, 14, 16, and pl. XVII, figs. 1–3, 5, 7; Moczydłowska, 1991, pl. 13, figs. E–G). Within the observed vesicles (Plate XIII, Figs. C–D), the cell size, wall thickness, tight connection between them, partially constricted cleavage between some cells, and equally distributed resilient cellular material (dark spot) refute a possible prokaryotic fission and support the eukaryotic division (Schopf, 1968; Moczydowska, 2008b). Some specimens may represent anaphase stages (when two daughter cell are not fully divided) as well as early and late stages (prophase/telophase; when the cells possess a complete wall, before or after division) of the cytokinesis (Figure 5).
Figure 5. Specimens in vegetative division (a, b) and their schematic reconstruction (1, 2). Specimen (b) may represent anaphase stage of the cytokinesis, with partially constricted cleavages between the two cells (2); specimen (a) may represent prophase or telophase of the cytokinesis, before or after the division.

6.1.2 Diagnostic features

A certain number of recognizable features such as body plan (presence of internal body/bodies), wall ornamentations, chemistry and ultrastructure, excystment structures may indicate affinities to certain phyla or classes of protists (Loeblich and Tappan, 1969; Loeblich, 1970; Tappan, 1980; Le Herissé, 1984; Vavrdova, 1992; Arouri et al., 1999, 2000; Talyzina and Moczydłowska, 2000; Moczydłowska and Willman, 2009; Willman, 2009; Moczydłowska et al., 2010, 2011; Moczydłowska 2010, 2015).

**Internal bodies**

Vesicles with large internal body within the vesicle outer wall, or an external envelope, are known in cysts and developmental stages of modern microorganisms with complex reproductive life cycle. Consistently it could be inferred that a similar vesicle organization in studied specimens (*Macroptycha, Pterospermella, Pterospermopsimorpha, Simia* and *Trachysphaeridium*) may represent similar stages in reproductive cycle among microfossils (Moczydłowska, 2015). The internal body or bodies in reproductive stages (endocyst or spores) have their own walls and therefore are distinct from a randomly preserved shriveled organic matter in vesicles. Microfossils preserving small, dense organic matter structures occur among Proterozoic assemblages (Schopf, 1968; Jankauskas et al., 1989; Hermann, 1990; Hofmann and Jackson, 1994; Grey, 2005), as well as in the present material (Plate III, Fig. H; Plate XIII, Figs. C–E). Schopf (1968) and Jankauskas et al. (1989) interpreted such structures as nucleus residue. Nucleus exhibits a clearly differentiated double
membrane discernible under light microscopy in living cells but it is not easily preservable and organic inclusions in microfossils are more likely to be remains of cytoplasm (Knoll and Barghoorn, 1977; Moczydłowska, 2015), for example after a pre-encystment contraction (Pang et al., 2013). However, components of nuclei walls are easily dissolved and/or degraded after deposition, notably by bacterial actions (Campbell, 1995; Raff et al.; 2008). The preservation of nucleus in geologic record could only be result of exceptional burial conditions (Moczydłowska, 2015).

Ornamentation, wall sculpture and wall ultrastructure

OWM are extracted from the rock matrix by using a combination of acids, including especially abrasive hydrofluoric acid in chemical processing (see Material and methods). The reason why the microfossils are not badly affected by such treatment lies in the acetolysis resistant wall chemistry and its resultant structure.

Wall ultrastructure in OWM has been increasingly studied with the development of new observation techniques (Arouri et al., 1999, 2000; Talyzina and Moczydłowska 2000; Javaux et al., 2004; Kemple et al., 2005; Javaux and Marshal 2006; Willman and Moczydłowska 2007; Willman, 2009; Moczydłowska et al., 2010; Cornet et al., 2015). It has been shown that the wall of OWM can be single or multi-layered with various wall structures and be characteristic of certain organismal groups yet individual features alone may not support accurately biological affinities (Willman, 2009). Microfossils exhibiting different wall structures may also belong to the same species at various life stages or to different lineages, but certain pattern, the trilaminar sheath structure of algaenan, is diagnostic of chlorophyte algae (Talyzina and Moczydłowska, 2000; Moczydłowska et al., 2010).

The wall sculpture and micro-ornamentation may also be characteristic of major phylogenetic groups. Most microfossils in the studied assemblage are smooth-walled but some have original sculpture pattern on the wall surface (Cerebrosphaera s p ., Leiosphaeridia s p . C , Pterospermospimorpha pileiformis, Simia sp., Trachysphaeridium laminaritum, T. laufeldii, Unnamed sp. B and Unnamed sp. C). Micro-ornamentation is a common feature among eukaryotic protists. Although prokaryotes may exhibit various organization of their glycoproteins in the surface layer and some kind of process types (pili, fibril, fimbriae), their fine ornamentation occur in a much smaller size range (nanometer scale) and is easily removed by chemical processing and therefore will not be preserved (Javaux et al., 2003). The presence of the resistant, structurally complex and textured or sculptured wall, together with general size range over tens to hundred micrometers of vesicles with excystment structure or internal body is without doubt characteristic of eukaryotic origin of these OWM.
Excystment opening and reproductive cyst

In modern algal lineages, excystment opening is formed within the vesicle wall during the excystment process, for the release of the daughter cells from the mature mother cell (Vavrdova, 1992). Several types of excystment structures in microfossils are recognized and are considered to be important diagnostic features for their classification and inferring relationship with extant organisms (Loeblich and Tappan, 1969; Loeblich, 1970; Le Herissé, 1984). The opening structures can be divided in two main categories, linear raptures and morphologically determined, circular in shape, openings. The lateral or longitudinal raptures are observed in many spheroidal morphotypes, including *Leiospherididida* spp. and in *Schizofusa* sp. in the present material. The rapture lines can be ornamented and located in a constant position on the vesicle or along the medial axis, splitting the vesicle into two equal halves by the so-called median split. The second category of opening is the pylome structure. Pylomes are circular or sub-circular, occasionally with a conspicuous neck or a rim-like thickening around the outline and closed by an operculum (Vidal, 1976; Le Herissé, 1984; Vidal and Ford, 1985; Playford, 2003). The operculum is partly or completely detached after the excystment and can easily be lost (Playford, 2003). Pylome structures in studied specimens are simple round shapes with rim (*Leiosphaeridia* sp. A., *L*. sp. B), without the rim (*Trachysphaeridium laminaritum*; *T. laufeldii*), or sometimes with particular ornamentation (the granulae on *Leiospheridia* sp. B).

Cysts represent reproductive/resistant stages in the life cycle of microorganisms allowing them to survive unfavorable environmental conditions and protecting the offspring cells in either sexual or asexual generations. Internal bodies can be interpreted as endocysts containing a zygote (sexual), a sack of swarmers or multiple spores (asexual) (Moczydłowska 2010, 2015; Moczydłowska et al., 2011; Agić, 2015). Hypothetical life cycles of cyst-forming microorganisms in sexual or asexual conditions are shown in Figure 6.

Based on the overall body plan, the presence of internal body/bodies, wall chemistry and ultrastructure and the presence of excystment opening, a lot of OWM can be recognized as reproductive cysts of eukaryotes (Tappan, 1980; Colbath and Grenfeld, 1995; Moczydłowska et al., 2011; Moczydłowska, 2011, 2015; Agić, 2015). Thus, in the studied material, specimens with well-defined internal bodies in the genera *Macroptycha, Pterospermopsimorpha, Pterospermella* and *Simia* can be recognized as cysts. As mentioned in the taxonomic descriptions, *Leiospheridia* sp. B and *Trachysphaeridium* are likely cysts because they are surrounded by an external envelope. The evident pylome and thick vesicle wall are typical cyst features. Moreover, because of their thick ornamented walls, specimens of *Cerebrosphaera* are likely to represent cysts. Bacteria are also known to produce cysts (akinetes, heterocysts) but their morphologic and structural simplicity and non-resistant biopolymers in their walls are very different than those observed in studied microfossils.
6.2 Affinities of organic-walled microfossils from the Visingsö upper formation

6.2.1 Algal affinities

As stated above, a resistant cell wall is indicative of reproductive stages of micro-organisms, e.g. sexual or asexual cysts. Modern green algae (Chlorophyta), both marine and fresh water, are well known for producing acetolysis-resistant zygotic cysts (sexual) or phycomata (asexual). Chlorophyte cysts exhibit a great variety of morphologies either with complex surface sculptures and processes or relatively simple. The size and the overall body plan also depend of the developmental stage. Many of the present microfossils can be, or have been, recognized as extinct analogues of algal cysts on the basis on their morphology.

The Prasinophyceae, a phylogenetically basal and polyphyletic class of chlorophytes, are exclusively marine and form asexual reproductive cysts known as phycomata (Lee, 2008). The phycoma is spheroidal in shape and consists of a thin and delicate velum developing in the equatorial plan or around the internal body which may be supported by radial wings (alae) or rod-like elements (Margulis et al., 1989). This body plan is observed in the extant species *Pterosperma* and is similar to the body plan of *Pterospermopsimorpha, Pterospermella* and *Simia* in the present material (Fig. 7). These taxa have been recognised as belonging to the class Prasinophyceae (Tappan, 1980; Inouye et al., 1990; Guy-Ohlsson, 1996; Samuelsson et al., 1999; Playford, 2003; Moczydłowska 2008a, 2011,
The genus *Pterospermopsimorpha* is known from sediments *ca.* 1.4 Ga (Sergeev, 2006; Moczydłowska 2008a) and can therefore represent the oldest prasinophyte (Moczydłowska *et al*., 2011; Moczydłowska, 2015). It should be noted that any known species of prasinophytes has a double endocyst as it is observed in some specimens of *Pterospermopsimorpha insolita* (Plate VIII, Figs G–H). Additionally, based on the body-plan with a large, well defined, internal body, studied specimens of *Macroptycha* may be recognized as Prasynophyceae.

![Figure 7. Extant phycomata (asexual cysts of Prasinophyceae) of Pterosperma: Pterosperma vanhoeffenni (1, 3); P. moebii (2); P. moebii with mature cyst (5) and P. type A (4). 1, 5, form the North Sea, photographed by Dr. P. Škaloud (Prague); 3, from the Chukchi Sea (Arctic), photographed by J. Dolan; 4, from the coast of Western Canada, photographed by Dr V. Pospelova (Victoria).](image)

It has been shown that the multi-layered wall with trilaminar sheath structure (TLS) in some *Leiospheridia* spp. of the Mesoproterozoic (Javaux *et al*., 2004), Neoproterozoic (Arouri *et al*., 1999; Willman, 2009; Moczydłowska *et al*., 2010) and Cambrian ages (Talyzina and Moczydłowska, 2000) is similar to the wall present in numerous cyst-forming species of green algae suggesting their affinities (Moczydłowska and Willman, 2009; Moczydłowska, 2015). Green algae form TLS made of algaenan, an aliphatic, insoluble acid- and bacterially resistant biopolymer (Derenne *et al*., 1992a, b;
Gelin et al., 1999; Hagen et al., 2002), which is likely to be preserved through time (DeLeeuw et al., 2006).

*Leiosphedia* has been compared with prasinophycean algae (Wall, 1962; Tappan, 1980; Colbath, 1983; Le Hérissé, 1984, 1989; Guy-Ohlson, 1996). For vesicles showing a medial split, an affinity with some species of *Chorella* (Trebouxiophyceae) has been suggested (Atkinson et al., 1972). It is understood that the polyphyletic spheroidal microfossils described under the form-genus *Leiosphaeridia* comprise various microorganisms and those include Prasinophyceae, Chlorophyceae and other of yet unrecognized affinities (Moczydłowska et al., 2010).

![Figure 8](image)

**Figure 8.** Extant specimens of Chlorophyceae (1–3) and Charophyceae (4). 1, cysts of *Haematococcus pluvialis*, photographed by Franck Fox; 2, vegetative cells of *Tetracystis dissociata*, from Schweiz National Park, Switzerland, source University of Texas, Austin; 3, coenobia of *Coelastrum astroideum*, from Sayama National park, Japan, photographed by Y. Tsukii; 4, zygospores of *Spirogyra* sp., photographed by Biophoto associate.

Other species from the present material can be related to chlorophycean algae. Cysts of such algae (Fig. 8.1) may exhibit various surface sculpture and processes on the wall of the endocyst probably occur during its maturation (Moczyd owska, 2015). Species like *Cerebrosphaera* sp. are recognized as possible green algal cysts because an identical morphotype is known to be an endocyst of *Polygonium* Vavrdová (1966), a Cambrian taxon, recognized as Chlorophycean alga (Moczydłowska, 2015). The complex cerebroid ornamentation and thick, resistant, multi-layered wall is seen in *Cerebrosphaera*. The presence of the pylome, which is not found in Prasinophyceae phycomata, and the thick wall with microsculpture in *Leiosphaeridia* sp. B, *Trachysphearium laminaritum*, and *T. laufeldii* are also indicative of possible chlorophycean affinities (Moczydłowska et al., 2011).
Additionally, some of the dividing cells (Plate XIII, Figs. F–G) resemble specimens of modern Chlorophyceae Tetracystis dissociata (Fig. 8.2).

Comparisons can be made between specimens of Schizofusa sp. with a longitudinal slit and the zygospore of the filamentous Charophyte algae Spirogyra (Fig. 8.4) but the latter is strictly restricted to fresh waters. The peculiar morphology of a species bearing a single process, Germinosphaera bispinosa, may suggest a vegetative stage beginning the reproduction. The vesicles show morphological analogy with the germinating zoospore of Vaucheria, a xanthophyte alga (brown alga), which grows filamentous thalli on its surface (Butterfield et al., 1994). Vesicles of Germinosphaera have then been regarded as possible fungi (Butterfield, 2005; Retallack, 2015; see below). Moczydlowska (2011) inferred a possible analogy between some clusters of small leiospherid vesicles, as Synsphaeridium sp., and the coenobia (vegetative colonies) of some species of Chlorophyceae (Fig. 8.3).

6.2.2 Cyanobacterial affinities

Alongside OWM that are undoubtedly recognized as eukaryotes, many small spheroidal and filamentous microfossils have been assigned as prokaryotes, specifically cyanobacteria (e.g. Tappan, 1980; Schopf and Klein, 1992). Prokaryotes dominate the fossil record and show stratigraphic ranges from the Archean to recent times. Fossils recognized as bacterial cells and cyanobacterial filaments in the Apex Chert of the 3.465 Ga Warrowoona Group (Australia) were inferred to be the oldest morphological traces of life on Earth (Schopf, 1992) and are now debated to be abiotic structures (Brasier et al., 2002). However, bacteria in stromatolites are known from rocks of this age (Allwood et al., 2006). Coccoid and filamentous microfossils resembling cyanobacteria have been described from sediments of ca. 1.9 Ga Gunflint chert, North America (Schopf and Klein, 1992).

Modern cyanobacteria have various shapes, from simple spheroidal (coccoid) to filamentous, and are solitary or colonial, often forming mats. The cell wall may be single- to four-layered, and is mainly composed of peptidoglycan and may be surrounded by a mucilaginous sheath made of fibrous polysaccharides. The cells are also known to form chains enclosed within the sheath and form trichomes, which may or may not be attached to the substrate (Tappan, 1980; Lee, 2008). The reproduction is vegetative (asexual) and occurs mostly by binary fission. In filamentous morphotypes, the reproduction involves formation of akinetes, thick-walled resting cysts that are produced during environmental stress conditions. Due to their thickness and biochemical resilience, cyanobacterial sheaths and akinetes are more resistant to degradation and are likely to be preserved through time (Tappan, 1980; Butterfield et al., 1994; Bartley, 1996; Moczydlowska 2008b).

Present filamentous specimens of the genera Eoschizothrix, Oscillatoriopsis, Palaeolyngbya, Polythrichoides and Siphonophycus have been recognized as members of the order Nostocales, family
Oscillariotoriaceae (Shopf, 1968; Hofmann, 1976; Tappan, 1980; Golubic and Hofmann, 1976; Jankauskas et al., 1989; Schopf and Klein, 1992; Butterfield et al., 1994; Seong-Joo and Golubic, 1998) and are comparable with modern stromatolites builders and microbial mat constructors cyanobacteria (Butterfield and Chandler, 1992). Palaeolyngbia catenata is an analoguous of extant species Lyngbya (Schopf and Sovietov, 1976; Schopf and Klein, 1992; Fig. 9.2), and Oscillatoriopsis spp. of modern specimens of Oscillatoria (Schopf and Klein, 1992; Fig. 9.3). Bundles of filaments are a common feature among cyanobacteria and specimens of Polithrychoides lineatus lacking a common sheath around the trichome can be compared to extant specimens of Aphanizomenon (Fig 9.1) and Trichodesmium (Seong-Joo and Golubic, 1998), whereas specimens with common sheath resemble species as Schizothrix, Microcoleus or Hydrocoleum (Herman, 1974; Timofeev et al., 1976; Schopf and Klein, 1992; Seong-Joo and Golubic, 1998).

Spheroidal specimens of Eosynechococcus moorei are inferred to belong to the order Chroococcales, family Chroococcaceae (Tappan, 1980; Schopf and Klein, 1992; Butterfield et al., 1994) and are morphologically close to species of modern cyanobacteria Aphanothece (Schopf and Klein, 1992; Fig. 9.4). Similarities in size range and shape between cells of Eosynechococcus moorei and Unnamed sp. A suggest a probable common affinity to the Chrococcaceae.

Affinities of other aggregated species are uncertain. The relative small size of the individual cells...
and the surrounding matrix of *Ostiana microcystis* may indicate cyanobacterial affinity (Ragozina *et al.*, 2003). For specimens of *Synsphaeridium* sp. it is more difficult to decipher if the aggregates are representative of true colonial habit or a random clustering of simple leiospherid vesicles. Because of a common appearance of aggregates, some specimens within the genus may represent cyanobacterial colonies.

### 6.2.3 Fungi and heterotrophic affinities

According to molecular clock estimates the origins of fungi are placed back in the Proterozoic (Taylor *et al.*, 2015) and several microfossils known from this time have been claimed to be of fungal affinity (Schopf, 1968; Schopf and Barghoorn, 1969; Timofeev, 1969b; Timofeev *et al.*, 1976; Allison and Awramik, 1989; Butterfield, 2005; Yuan *et al.*, 2005; Retallack, 2015). Despite numerous studies, potential Proterozoic fungi remain controversial (Taylor *et al.*, 2015; Moczydłowska, 2015) and any unquestionable fossil fungi are recognized prior to the record from the Lower Devonian Rhynie Chert (Krings *et al.*, 2012).

A certain number of diagnostic features can be used for comparing studied specimens to possible Glomeromycotan fungi. Fungi produce internal bodies within oogonia (female gametangia) and spores (Krings *et al.*, 2012; Taylor *et al.*, 2015) having simple spheroidal shape and a recalcitrant chitin wall (Kalgutkar and Jansonius, 2000; Taylor *et al.*, 2015). Their sizes are between 40 and 800 µm in diameter (Taylor *et al.*, 2015). Vesicles for this size range with internal bodies and resistant walls are common in the present material (see above). Spores of fungi are also known for producing tubular structures, usually open-ended (Butterfield, 2005), attached on the vesicles, freely open to the interior and susceptible of fusion (Retallack, 2015). Such features are observed in studied specimens of *Germinosphaera bispinosa* which are comparable morphologically to modern spores of Glomeromycota (Fig. 10.1). Although no complex excystment structure, such as pylome, are observed in fungal spores (Butterfield, 2005), the spores of Glomeromycota show breaking of their wall in a comparable way to some OWM (Fig. 10.2). Such a breaking pattern is observed in *Leiospheredia* spp. and *Schizofusa* sp. Retallack (2015) considered sharp slits in vesicles as evidence for a solid chitin-composed wall in comparison with the more flexible cellulose or algaenan-composed wall of algae. Additionally, multilayered walls of some species of OWM (see above) are shown comparable with spore walls of Glomeromycota and cysts of Mesomycetozoa (Retallack, 2015).

A group of OWM occurring in Proterozoic sediments are considered to belong to the Amoebozoa and to represent encystment stages of testate or walled amoebae (Schopf, 1992, 1999; Porter and Knoll, 2000). These are the commonly called vase-shaped microfossils (VSM). Those fossils display a characteristic shape of vesicle, open at the oral pole and rounded at the aboral pole with a smooth wall (Martí Mus and Moczydłowska, 2000). VSM are well known in the Visingsö Group and are preserved in phosphate nodules in the shales of the upper formation (Ewetz, 1933; Knoll and Vidal, 2000).
They have been described from various localities worldwide (Martí Mus and Moczydłowska, 2000). Such microfossils have not been observed in the studied assemblage, although a few specimens of *Leiospheridia* sp. A with ovoid shape and a large pylome-like opening (Plate IV, Figs. F–G) may resemble modern testate amoeba of the species *Centropyxis aerophila* (Fig. 10.3). The size range is much greater in the latter species.

Figure 10. Extant specimens of glomeromycotan fungal spores (1–2), testate amoeba (3) and dinoflagellate cyst (4). 1, 2, spores of *Glomus* sp., from Canada, photographed by Dr. Y. Dalpé; 3, *Centropyxis aerophila*, from Koigakubo marsh, Japan, photographed by Y. Tsukii; 4, Cyst of *Islandinium brevispinosum*, from New England, USA, photographed by V. Pospelova (Victoria).

Proterozoic OWM inferred to represent heterotrophic lineages of Chromalveolata are rare, and most microfossils belonging to this group are recorded among Phanerozoic mineralized Rhizaria (Foraminifera, Radiolaria). Some specimens have however been tentatively assigned to cysts of Dinoflagellates (Moldowan et al., 1996; Moldowan and Talyzina, 1998; Arouri et al., 2000; Meng et al., 2005) but subsequently revised and dismissed (Butterfield, 2015; Moczydłowska, 2015). Dinoflagellates are a major constituent of modern marine trophic webs. Although almost half of them are autotrophic, they are considered to be originally heterotrophic (Dodge and Lee, 2000; Hackett et al., 2004). As with some studied OWM, dinocysts can exhibit sculptured walls and excystment openings (Fig 10.4) but it has to be noted that, in the absence of tabulations, this comparison cannot clearly determine an affinity. Tabulations are the main preservable diagnostic features for fossils
dinocysts (Moczydłowska, 2015). Moreover, the first undisputed fossils from this group are known in the early Triassic strata (Fensome et al., 1999) and they evolved during Mesozoic (Fensome et al., 1996; Delwiche, 2007; Moczydłowska, 2015).

6.3 Ecology of organic-walled microfossils from the Visingsö upper formation

The upper formation of the Visingsö group has been deposited in a shallow marine environment, on a shelf with subtidal and intertidal zones (Vidal, 1976a, 1982; Larsen and Nøgaard-Pedersen, 1988), located at low palaeolatitudes, in relatively warm and nutrient-rich waters during the deposition and having free contact with a global ocean (Martí Mus and Moczydłowska, 2000). The sediments consist of a diverse assemblage of fossils including OWM, VSM, and stromatolites, and are kerogen-rich recording high values of the total organic carbon (TOC) content, an indicator of a high productivity (Vidal, 1972, 1976a; Knoll and Vidal, 1980; Martí Mus and Moczydłowska, 2000; Samuelsson and Strauss, 1999). Based on the morphological comparisons, some studied OWM can be interpreted as remains of eukaryotic phytoplankton and a few possible fungi. The ecology of microfossils can be inferred from the modern analogous organism adaptations.

Extant chlorophyte algae are predominantly fresh-water (Lee, 2008) but the origin of early lineages is linked to marine environments and the basal lineage of Prasinophyceae is still thriving in the marine realm, with a few taxa occupying brackish or fresh water habitats (Reynolds, 2006). The genus Pterosperma, and its probable extinct analogue Pterospermella, have been recorded mostly from marine, nearshore environments or brackish waters (Kustatscher et al., 2014 and references therein). On this basis it may be suggested that other species assigned to Pterosperma analogues (Pterospermopsismorpha, Simia) or simply to Prasinophyceae (some Leiospheridia spp. and Macroptycha) are likely to display the same ecological adaptations. Some of the present species have been recognized as possible Chlorophyceae (Leiospheridia spp., Cerebrosphaera, Trachysphaeridium, Synsphaeridium sp.). Based on modern representatives of this class, those species would require well oxygenated open water environments (aerobic conditions and easy access to the photic zone for photosynthesis) as well as a periodic access to the substrate for cyst deposition (Margulis et al., 1989; Moczydłowska, 2008 a, b).

Glomeromycotan fungi are known for inhabiting both marine and terrestrial environments and are decomposers (Taylor et al., 2015). Proterozoic specimens representing probable fungi analogues, as Germinosphaera, would have likely exhibited identical life behavior.

Filamentous cyanobacteria are known for occurring abundantly in littoral marine zones where they form biofilms and microbial mats. Coccolidal cyanobacteria are more characteristic of open waters, living freely in the water column (Lee, 2008). As photosynthesizing organisms, they need an easy
access to light and can accommodate a various range of nutrient supplies (Lee, 2008). Cyanobacteria also show high survival rate in extreme temperature ranges, oxic stresses, acidity, UV exposure and desiccation (Schopf, 1999). Extant specimens of *Siphonophycus, Eoschizothrix, Palaeolyngbya* and *Polythrichoides* are inferred to be similar to extant mats and stromatolites builder cyanobacteria (Butterfield and Chandler, 1992; see above). Those organisms needing well-oxygenated water in the photic zone for metabolism (Golubic and Hofmann 1976; Schopf and Walter, 1982; Golubic, 1999a, b) fit consistently with shallow marine conditions observed in the upper formation of the Visingsö Group depositional basin.

6.4 Limitations

Most of the microfossils from the present material exhibit smooth-walled vesicles (for example specimens of *Leiosphaeridia* spp.). Because of this lack of particular ornamentation it is difficult to infer relationships among them and/or to link them to extant lineages. On the other hand, when the ornamentations seem evident because they are consistently present in all specimens and through all the studied depths, like in specimens of *Trachysphaeridium*, one have to be careful that those wall structures are not the result of taphonomic processes, erosion or pressure by mineral crystals. Numerous specimens of OWM within the assemblages show degradation by mineral grain pressure (likely pyrite crystals), easily recognized by a characteristic polygonal shape and the craters they form on the vesicle wall. Those specimens have not been used to infer taxonomic ranking or affinities. In addition to that, microfossils have likely been subject to transportation during or after deposition. They have passed though the maceration processes and filtrations. These are likely to affect the vesicle structure and the fossils appearance. The uneven outline observed on some vesicles of *Leiosphaeridia* sp. C for example, could be a result of such phenomena, and may not be a biological feature.

In addition, the observations conducted under light microscope could have led to misinterpretations. For instance, the thickness of a wall being inferred by its degree of transparency. New observations under scanning electron microscope could be used in order to minimize the possible biases. Internal bodies, which constitute one of the main morphological feature in the studied material, cannot be shown under SEM, because of the electron-dense nature of the organic wall of the fossils. It is therefore a good way to know if such feature can be recognize as a true internal body or just a taphonomic fold on the vesicle surface.
7 Conclusion

The assemblage of organically preserved microfossils extracted by palynological method from the upper formation of the Visingsö Group, southern Sweden, was studied using light microscope. The taxonomic identification of microfossils by morphological observations and recognition of diagnostic features resulted in describing twenty four species belonging to eighteen genera. Among them, species are described under open nomenclature and they may represent new species or may need taxonomic revision of existing taxa to be accommodated. The assemblage shows substantial biodiversity and several taxa are related biologically to extant phylogenetic lineages.

Several form-genera are known from many Proterozoic succession worldwide such as *Leiosphaeridia*, *Pterospermella*, *Pterospermopsimorpha*, *Synsphaeridium*, *Siphonophycus*, *Polythrichoides*, and they have long stratigraphic ranges. Some taxa are recorded for the first time in the Visingsö sediments including *Cerebrosphaera*, *Leiosphaeridia ternata*, *Macroptycha*, *Ostiana*, *Simia* and other distinct morphotypes attributed to *Leiosphaeridia* sp. A, L. sp. B, L. sp. C. Unnamed sp. A, B, C are left unidentified.

Species of *Pterospermopsimorpha* and *Pterospermella*, known in their stratigraphic occurrences from the Mesoproterozoic to Cambrian times, prove that they survived the Cryogenian ice-ages and severe glaciations. *Cerebrosphaera* is restricted in range to Neoproterozoic and is a potential biostratigraphic index fossil. The diversity recorded in the upper formation of the Visingsö Group, documents the global trend of the evolution of eukaryotic protists during the Tonian Period.

The presence of diagnostic morphological features observed in certain species, including excystment openings, surface sculpture and internal body or bodies are indicative for inferring a cyst stage and affinities of microfossils. The acid resistant nature of the biopolymers constituting the vesicle wall, as well as the multilayered ultrastructure, further support recognition of certain taxa as representative of chlorophyte lineages, both of the Prasinophyceae and Chlorophyceae classes. Similar features observed in modern spore of fungi may infer a fungi affinity for some taxa. In the present material only *Germinosphaera unispinosa* is a potential candidate for such affinity. Filamentous species and small coccoid forms are undoubtedly recognized as cyanobacteria.

Based on modern analogues and sedimentological setting, ecological habitats can be inferred. The microfossils in the studied succession are recognized as photosynthesizing organisms. They needed a substantial light availability, aerobic conditions as well as the access to the substrate for benthic filamentous cyanobacteria and for cyst deposition in planktonic algae lineages. Those criteria are fitting consistently with the shallow marine conditions, well-oxygenated water and connection with an open ocean, during deposition of the upper formation of the Visingsö Group.
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10 Plates

Note: caption refers to the plate on the opposite page.

Note: England Finder coordinates are given with label on the bottom left corner.
PLATE I

A, B = *Cerebrosphaera sp.*

C, D = *Germinosphaera unispinosa.*
(C) Depth 11.5, slide 4, England Finder C38; (D) Depth 11.5, slide 3, England Finder X39.
PLATE II

A–L = *Leiosphaeridia* spp.

PLATE III

A–I = Leiosphaeridia spp.
A–E = *Leiosphaeridia ternata.*
(A) Depth 12.2, slide 4, England Finder P46; (B) Depth 12.2, slide 4, England Finder X57;
(C) Depth 13.2, slide 4, England Finder Q49-4; (D) Depth 3.7, slide 4, England Finder Q35-4;
(E) Depth 11.5, slide 4, England Finder G36.

F, G = *Leiosphaeridia sp. A.*
A–H = *Leiosphaeridia sp. B.*

PLATE VI

A–D = Leiosphaeridia sp. C.
(A) Depth 11.5, slide 5, England Finder P314; (B) Depth 3.7, slide 5, England Finder H55; (C) Depth 3.7, slide 6, England Finder R24; (D) Depth 3.7, slide 6, England Finder R33.
PLATE VII

**A–H = Macroptycha uniplicata.**
(A) Depth 3.7, slide 3, England Finder D54-4; (B) Depth 3.7, slide 3, England Finder Q27-4; 
(C) Depth 3.7, slide 5, England Finder L36-4; (D) Depth 3.7, slide 5, England Finder G35-3; 
(E) Depth 3.7, slide 3, England Finder Q53-3; (F) Depth 3.7, slide 4, England Finder G52; 
(G) Depth 3.7, slide 6, England Finder V50; (H) Depth 3.7, slide 5, England Finder P47.

**I–J = Navifusa majensis.**
PLATE VIII

A–H = *Pterospermopsimarpha insolita*.

PLATE IX

A–C = *Pterospermopsimorpha pileiformis.*
(A) Depth 12.2, slide 3, England Finder V55; (B) Depth 11.5, slide 4, England Finder D27-1; 
(C) Depth 3.7, slide 6, England Finder S52.

D–F = *Pterospermella sp.*
(D) Depth 3.7, slide 6, England Finder K42; (E) Depth 3.7, slide 3, England Finder J38-1; (F) 
Depth 11.5, slide 3, England Finder R34-3.

G = *Schizofusa sp.*
(G) Depth 3.7, slide 5, England Finder U39.
A–C = *Simia annulare.*
(A) Depth 11.5, slide 4, England Finder E38; (B) Depth 11.5, slide 3, England Finder C47;
(C) Depth 11.5, slide 5, England Finder H29-3.

D, E = *Simia simica.*

F–I = *Simia spp.*
(F) Depth 12.2, slide 3, England Finder V29; (G) Depth 11.5, slide 5, England Finder Z38-3;
PLATE XI

A–D = *Trachysphaeridium laminaritum.*

E–I = *Trachysphaeridium laufeldii.*
A–B = *Eosynechococcus moorei*.
(A) Depth 12.2, slide 3, England Finder K56-1; (B) Depth 11.5, slide 4, England Finder E42-3.

C–E = Unnamed sp. A.

F–H = *Ostiana microcystis*.
(F) Depth 11.5, slide 4, England Finder T54-1; (G) Depth 11.5, slide 4, England Finder E56-1; (H) Depth 11.5, slide 5, England Finder G46.

I–K = *Synsphaeridium* spp.
PLATE XIII

A = Unnamed sp. B.
(A) Depth 11.5, slide 5, England Finder X47.

B = Unnamed sp. C.
(B) Depth 11.5, slide 4, England Finder J55.

C–D = dividing cells.
PLATE XIV

A–C = Polythrichoides lineatus.
(A) Depth 3.7, slide 6, England Finder X37; (B) Depth 11.5, slide 5, England Finder T29-2;
PLATE XV

A–I = *Siphonophycus* spp.

PLATE XVI

A–C = *Siphonophycus* spp.

D = *Eoschizothryx composita*.
(D) Depth 11.5, slide 4, England Finder P29.

E = *Palaeolyngbya catenata*.

F–H = *Oscillatoriopsis* spp.