MICROBIOTAS OF THE LATE PRECAMBRIAN RYSSÖ FORMATION, NORDAUSTLANDET, SVALBARD

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ABSTRACT. Silicified carbonates of the uppermost Riphean (800–700 Ma) Ryssö Formation, Nordaustlandet, Svalbard, contain abundant, well-preserved microfossils that represent several palaeoenvironmental settings, life habits, and trophic modes. The fossils fall into three distinct assemblages. A stromatolitic microflorule preserved in flat cryptalgal laminated cherts includes seven taxa: three mat building cyanobacteria, two mat-dwelling or probable mat-dwelling blue-greens, one allochthonous element, and one rare species of indeterminate ecological role. An open coastal planktonic assemblage contains fourteen distinguishable taxa, including many acritarch species that have commonly been found in Upper Riphean shales and siltstones. The third assemblage is dominated by organically preserved skeletons and siliceous casts of vase-shaped heterotrophic protists. Collectively, these assemblages provide an unusually broad picture of microbial life in the Late Proterozoic Era. The Ryssö Formation contains twenty-one taxa, of which one, *Scissilisphaera regularis* gen. et sp. nov., is formally described as new.

IT is well known that the record of Precambrian microbial life observable in thin sections of silicified carbonates differs significantly from that found in macerations of ancient siliciclastic rocks. The differences are real and, in large part, ecological in origin, reflecting the predominantly benthic nature and restricted environmental setting of most 'cherty' microbiotas and, in contrast, the planktonic nature and normal marine setting of the large organic-walled microfossils that are common in late Precambrian shales.

The distinctive taxonomic and palaeoecological differences between cherty carbonate and siliciclastic biofacies present an interesting problem for palaeobiological reconstruction of late Proterozoic life. This problem is compounded by occurrences in uppermost Riphean and lower Vendian rocks, both siliciclastic and carbonate, of dense populations of vase-shaped microfossils interpreted as the remains of heterotrophic protists. Where these distinctive fossils are well preserved, other fossils are often poorly fossilized or absent.

All three types of microfossil assemblage are necessary to provide the breadth of evidence required for critical interpretations of late Proterozoic biology. Rarely does a single formation contain all three assemblage types, but one unit that does is the uppermost Riphean (800–700 Ma) Ryssö Formation exposed in Nordaustlandet, Svalbard. In providing a record of both benthic and planktonic life, open coastal to intertidal habitats, and both primary producers and heterotrophs, the Ryssö biota contributes to the construction of an integrated picture of late Precambrian life.

GEOLOGICAL SETTING AND AGE

In the Murchisonfjorden region of western Nordaustlandet and in adjacent north-eastern Spitsbergen, approximately 6000 m of folded but essentially unmetamorphosed Upper Proterozoic sedimentary rocks lie atop an older series of metavolcanics and metasediments (Odell 1927; Harland *et al.* 1966; Harland and Wright 1979). The unmetamorphosed sedimentary deposits of western Nordaustlandet have been placed in the Murchisonfjorden Supergroup and divided into four groups: the Gotia Group (600 m), an uppermost detrital series containing conspicuous tillites; the Roaldtoppen Group (1300 m), a thick series of dolomites and limestones with associated cherts and shales; the Celsiusberget Group (2100 m), composed predominantly of shallow water

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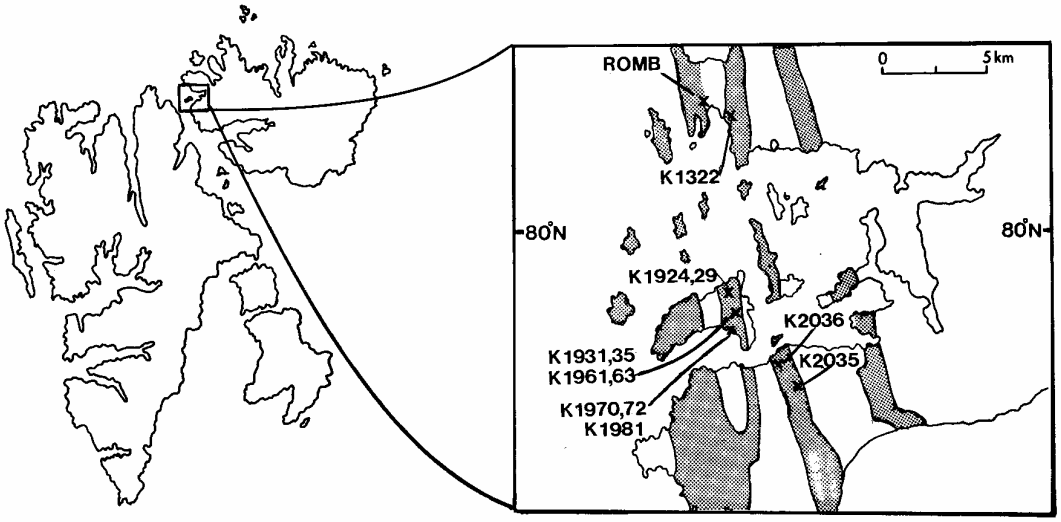
sandstones and siltstones; and the lowermost Franklinsundet Group (1800 m), a succession of limestones, quartzites, and shales (Flood *et al.* 1969; Harland and Wright 1979).

The Ryssö Formation is located stratigraphically within the Roaldtoppen Group. It conformably overlies the fossiliferous, predominantly dark limestone Hunnberg Formation (see Knoll 1983) and is in turn overlain by carbonaceous mudstones of the lower Gotia Group. No unconformity is visible at the Ryssö/Gotia contact, but palynological investigations suggest that a significant time gap separates the depositions of the two units (Knoll 1982*b*). The Ryssö Formation is the dominant geological feature of the Murchisonfjorden area (Kulling 1934;



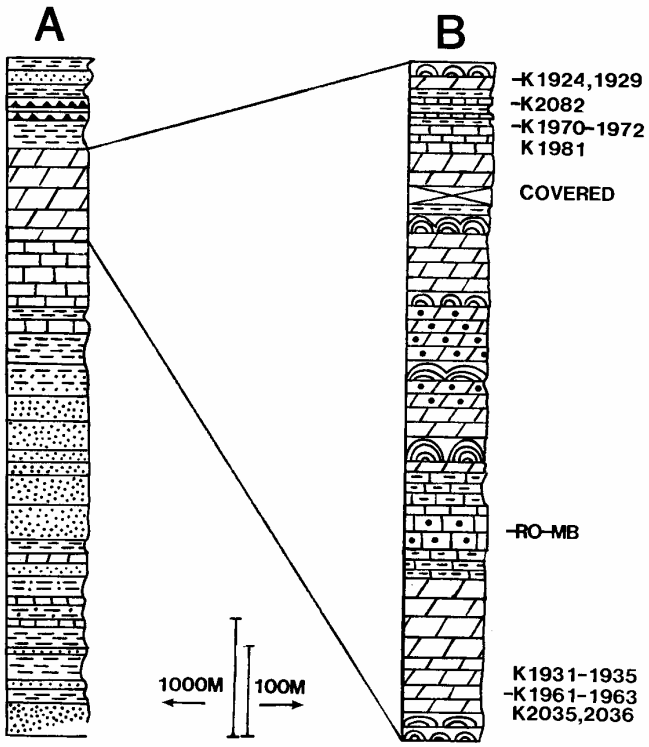
TEXT-FIG. 1. Location map showing the position of the Murchinsonfjorden area (boxed and enlarged region) within Svalbard. Outcrop area of the Ryssö Formation is indicated by stippling. Fossiliferous localities are noted on the map.

text-fig. 1). Text-fig. 2 shows a stratigraphic section of the Ryssö Formation measured by Flood *et al.* (1969) on Söre Russöya, a large island in the middle of Murchisonfjorden. Except for minor intercalations of shale and quartzitic sandstone, the formation consists throughout of dolomite and dark bituminous limestones. Columnar and domal stromatolites are common throughout the formation, as are flat laminated cryptalgal beds. Oolites and pisolites occur in the lower half of the formation along with intraformational edgewise conglomerates, shallow channels, and occasional low angle cross-beds. It is apparent that the entire formation was deposited in coastal carbonate flat environments ranging from intertidal to very shallow subtidal marine.

Silicification is common in microbially laminated dolomites near the base of the formation, as well as in associated carbonate conglomerates. Chert also occurs as replacements of oolites and pisolites, in thin originally carbonate beds within a predominantly black shale unit near the top of the formation, and, rarely, as nodules and lenses in 'algal' dolomites near the top of the section. In all cases, the silica appears to be of early diagenetic origin. Many of the cherts are carbonaceous and it is in these rocks that most Ryssö microfossils are preserved, although scattered specimens have also been obtained by maceration of black shales.

Existing radiometric dates place few constraints on the timing of Ryssö deposition, but two independent lines of biostratigraphic evidence provide a reliable age estimate for the formation. Columnar stromatolites collected by A. A. Krasil'shchikov in 1963 and 1964 have been extensively studied by Soviet palaeontologists. Identified forms include *Gymnosolen murchisonicus* Golovanov, *Inseria blingica* Gol., *I. chunnbergica* Gol., *Jacutophyton spitsbergensis* Gol., *Yungulsia* sp., *Kussiella* (?) sp., and *Conophyton* sp. (Milstein and Golovanov 1979). Raaben and Zabrodin (1969) also report the presence of *Boxonia grumulosa* and *Tungussia russa* in the Ryssö Formation. On the basis of columnar stromatolites, a Late Riphean (approximately 950 to 700 Ma) age is suggested for the formation (Golovanov and Raaben 1967; Raaben and Zabrodin 1969; Milstein and Golovanov 1979).

Soviet workers have also employed microphytolites (oncolites) as biostratigraphic indicators. A Late



TEXT-FIG. 2. Generalized stratigraphic columns for the Upper Proterozoic Murchisonfjorden Supergroup in Nordaustlandet (A) and the Ryssö Formation (B). Black circles within carbonate symbols indicate oolites and pisolites. The stratigraphic positions of fossiliferous localities are indicated in column B. Stratigraphy modified from Flood *et al.* (1969).

Riphean to Vendian age for Ryssö deposition is suggested by Milstein and Golovanov (1979) on the basis of microphytolite distribution.

The reliability of columnar stromatolites in stratigraphic correlation has been widely debated (see Walter 1977, for a fair appraisal of both sides of the argument), and the use of microphytolites as biostratigraphic markers has enjoyed little support outside the Soviet Union; however, an independent and reliable scheme for the subdivision and correlation of late Precambrian sequences is provided by the organic walled remains of eukaryotic plankters which radiated in Late Riphean and early Vendian times (Timofeev 1959, 1969; Vidal 1976, 1981*a*, *b*; Vidal and Knoll 1983). Robust-walled planktonic microfossils, usually referred to as acritarchs (e.g. Downie 1973), are widespread geographically and lithologically in Upper Proterozoic sequences, have limited and delimitable stratigraphic ranges, and are easily identified. Thus, they constitute excellent fossils for biostratigraphic correlation on an international scale.

Table 1 lists the acritarchs recognized in the open coastal planktonic assemblage of the Ryssö Formation. This is a typical Late Riphean assemblage, comparable to previously described microbiotas from Europe and the Soviet Union. A Late Riphean depositional age is supported by the stratigraphic first appearance of vase-shaped microfossils in the upper third of the formation. These distinctive fossils have been found on four continents, and where their biostratigraphic context is well known, they appear near the top of the Riphean sequence and continue into lower Vendian beds (Knoll and Vidal 1980). Their presence in the Ryssö Formation may indicate that this formation accumulated late in the Late Riphean interval. In round figures, one can broadly estimate the age of the formation as 800 to 700 Ma.

TABLE 1. Microfossils present in the Ryssö Formation. Fossils are listed by assemblage along with their size (diameters or, for filaments, cross-sectional diameter) and inferred paleoecological role. For species occurring in more than one assemblage, size data are presented only once.

	Size range (and mean diameter) in μm	Paleoecological interpretation
I. Stromatolitic assemblage		
Siphonophycus kestron Schopf	9–18 (14·3)	Common mat builder
Eomycetopsis robusta Schopf emend. Knoll and Golubic	2–4 (2·6)	Common mat builder
Tenuofilum septatum Schopf	0·5–1·5 (1·0)	Rare mat builder
Multilamellated sheath	39	?
Myxococcoides spp.	9–30	Allochthonous (planktonic?)
Coniunctiophycus sp.	2–9 × 2–6 (3·1 × 2·3)	Locally common mat dweller
Scissilisphaera regularis gen. et sp. nov.	11–45 (18·2)	Locally abundant mat dweller (?)
II. Coastal Plankton Assemblage		
Chuaria circularis Walcott	180–800 (282)	Common plankton
Kildinella hyperboreica Timofeev	22–70 (43)	Common plankton
Kildinella sinica Timofeev	23–76 (40)	Common plankton
Trachysphaeridium laufeldi Vidal	72	Rare plankton
Trachysphaeridium levis (Lopukhin) Vidal	56–92 (74)	Rare plankton
Trachysphaeridium sp. A of Knoll (1983)	42–65 (54)	Common plankton
Trachysphaeridium sp. B of Knoll (1983)	220–450 (268)	Rare plankton
Trachyhystrichosphaera vidalii Knoll	210–255 (241)	Rare plankton
Phanerosphaerops capitans Schopf	43–57 (49)	Rare plankton
Pterospermopsimorpha sp.	150–172 (161)	Rare plankton
cf. *Stictosphaeridium* sp. (*sensu* Vidal, 1976)	43–130 (78)	Common plankton
Myxococcoides spp.	—	Abundant plankton
Glenobotrydion aenigmatis Schopf	7–12 (9·2)	Common plankton
Unnamed Form B of Knoll (1983)	75–210 (145)	Common plankton
Eomycetopsis robusta Schopf emend. Knoll and Golubic	—	Rare fragmented specimens; allochthonous
Filament clusters (*Eomycetopsis* sp.)	3–4	Common, allochthonous
Siphonophycus kestron Schopf	—	Rare, fragmented specimens, allochthonous
III. Vase-Shaped Microfossil Assemblage		
Vase-shaped Microfossils	34–257 × 16–119 (106 × 50·5)	Abundant planktonic Heterotrophs
Kildinella hyperboreica Timofeev	—	Rare plankton
Myxococcoides spp.	—	Rare, allochthonous (plankton?)
Eomycetopsis robusta Schopf emend. Knoll and Golubic	—	Some allochthonous, some *in situ* benthos
Siphonophycus kestron Schopf	—	Rare, allochthonous

Late Riphean acritarchs also occur in the underlying Hunnberg Formation (Knoll 1982*a*), and superjacent Gotia mudstones contain scattered Vendian microfossils, thus corroborating the age assignment for the Ryssö Formation. Further corroboration comes from biostratigraphic comparison to the Eleonore Bay and Tillite Groups of East Greenland. The lithological similarities between these rocks and the Precambrian Hecla Hoek sequence of eastern Spitsbergen and Nordaustlandet were early recognized by Koch (1929) and Kulling (1934). Acritarch assemblages described by Vidal (1979) from various horizons throughout the Greenland succession correspond closely to those found in the various formations of the Murchisonfjorden Supergroup (Knoll 1982*b*).

Of particular interest here is Vidal's report of a diverse suite of Late Riphean acritarchs, including vase-shaped microfossils, from the upper Limestone–Dolomite 'Series' of Ella Ø and the adjacent coast. This supports Harland and Gayer's (1972) suggestion that eastern Svalbard and East Greenland were situated along a contiguous eastern North American continental margin in late Precambrian times, and adds strength to the latest Riphean age assignment for the Ryssö Formation.

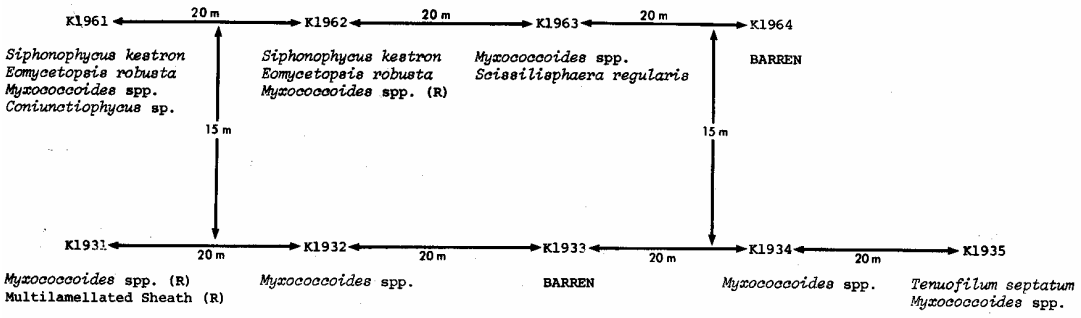
MICROFOSSIL ASSEMBLAGES

Stromatolitic microfossils. In general aspect, the stromatolitic microfossil assemblages of the Ryssö Formation are similar to those described from the Bitter Springs, Draken, and other formations of comparable age and palaeoenvironmental setting. Like the Bitter Springs biota, Ryssö assemblages are found within silicified portions of flat, cryptalgal laminated dolomites. Laminae are wavy and irregular. Commonly, a few millimetres to more than a centimetre thick layer of sand- to angular gravel-sized clastic material separates two mat horizons. The clasts themselves consist of locally derived stromatolitic dolomite or chert. Chert occurs as irregular patches to more or less continuous beds 2 to 15 cm thick. The secondary nature of the silica is indicated by the fact that chert distribution does not conform to bedding; bedding planes commonly cross lithological boundaries. There is no evidence for evaporites, and desiccation cracks are rare. Deposition apparently took place on a very shallow carbonate flat subjected to occasional storms. Early diagenetic silicification insured the long-term preservation of microfossils and amorphous organic matter.

A single horizon of densely matted *Eomycetopsis robusta* filaments is found near the top of the formation (Locality K 1924; text-figs. 1 and 2). All other stromatolitic microfossils are confined to a single thin unit near the formation's base (Localities K 1931–1935, K 1961–1963, K 2035, and K 2036; text-figs. 1 and 2).

The preservational variability and (in part related) apparent biological heterogeneity of closely spaced samples of Ryssö chert is noteworthy. Text-fig. 3 shows schematically the distribution of microfossils within a grid of samples taken at 20 m intervals along two bedding horizons separated by 15 m of intervening section. All nine samples are comparable in petrology and sedimentary structure, yet several are barren while others contain abundant and well-preserved fossils belonging to as many as four distinct species. Species composition changes from sample to sample. Interestingly, microfossils from the same stratigraphic level exposed 5 km south of the sample grid do not differ significantly from those contained in grid cherts. Such local biological and preservational heterogeneity is not surprising in the light of previous studies of microfossil distribution within the Bitter Springs (Knoll 1981) and Draken (Knoll 1982*a*) formations, but it counsels care in the construction of sampling strategies for Proterozoic stromatolitic cherts.

Where the remains of mat building microbes are preserved, the builders are densely interwoven populations of the 8–15 μm diameter tubular sheath *Siphonophycus kestron* Schopf (Pl. 58, figs. 4–6) and/or the somewhat thinner (2–4 μm) sheath *Eomycetopsis robusta* Schopf emend. Knoll and



TEXT-FIG. 3. Diagram showing the sampling grid and microfossil assemblages for a suite of closely spaced chert samples collected from the Ryssö Formation on Söre Russöya.

Golubic (Pl. 57, figs. 1, 4, 5). Both are interpreted as the evacuated extracellular sheaths of oscillatorian cyanobacteria. Some horizons consist exclusively of one species or the other, while at other levels, the two blue-greens occur together. This suggests that the two species had distinct microecological preferences and tolerances, but that their tolerance ranges overlapped. In modern microbial mats, it has sometimes been observed that two or more cyanobacterial species will participate in mat building under normal conditions, but should local environmental conditions change temporarily, growth of one species will increase at the expense of the other (Golubic 1973). This represents one of several ways in which individual horizons within a single stromatolite can be dominated by one or another species, or a bispecific association of the two taxa (Golubic 1973, 1976*b*). *Siphonophycus* and *Eomycetopsis* species have been recognized as primary or auxiliary mat builders in a number of Proterozoic stromatolitic biotas (e.g. Knoll 1981, 1982*a*; Zhang 1981; Mendelson and Schopf 1982). In Ryssö sample RO-MB, *E. robusta* also occurs in oncolites (see also Schopf *et al.* 1973).

Only two other filamentous microfossil species have been found in the Ryssö biota. A densely interwoven population of 1 μm thick tubular sheaths assignable to *Tenuofilum septatum* Schopf was observed in a single lamina in sample K 1935 (Pl. 57, fig. 2), and a single large (39 μm diameter) multilamellar sheath occurs within a rip-up clast in sample K 1931 (Pl. 57, fig. 6).

Mat-dwelling microbes are not widely preserved in Ryssö cherts, but in sample K 1961, irregular colonies of small (average dimension = 3·1 × 2·3 μm; $N = 100$) psilate unicells assigned to *Coniunctiophycus* sp. occur at more or less regular intervals in some bedding planes. Individual cell clusters contain two dozen to several hundred specimens; colonies are spaced 50 to 800 μm apart, with an average intercolony lateral distance of approximately 150 μm. Many of the colonies are relatively simple framboidal aggregations (Pl. 58, fig. 2), but several large colonies contain numerous simple aggregations apparently originally set in copious mucilage (Pl. 58, figs. 1, 3). Zhang's (1981) interpretation of *Coniunctiophycus* colonies as chroococcalean blue-greens is tentatively accepted here, but in truth, a bacterial interpretation for this population cannot be dismissed.

More certain are the taxonomic affinities of another benthic population. In samples K 1963, K 2035, and K 2036, large numbers of ensheathed unicells and fairly regular colonies occur in some laminae (Pl. 59, text-fig. 4). The unicells consist of rounded extracellular envelopes 11 to 45 μm in diameter which usually contain partially collapsed cellular material. Colonies are clearly large unicells that have undergone successive binary fissions (without intervening growth) in three planes to produce a regular spherical colony of 4, 8, 16, 32, or, rarely, 64 cells, all of which are preserved as individual envelopes. Occasionally, larger cuboidal colonies of more than 100 cells are found. In all cases, the retention of extracellular envelopes secreted by daughter cells following *each* successive fission preserves the divisional pattern characteristic of the species. As discussed more fully in the Systematic Palaeontology section, this population, given the name *Scissilisphaera regularis* gen. et sp.

EXPLANATION OF PLATE 57

For each figure, thin section number, stage co-ordinates (where 'x' on slide K2023–1F = 1·9 × 120·2), and Harvard University Paleobotanical Collection number are given. Bar in Fig. 8 = 50 μm for Figs. 1, 2, 6, and 8, and = 20 μm for Figs. 3–5, 7, 9, and 10.

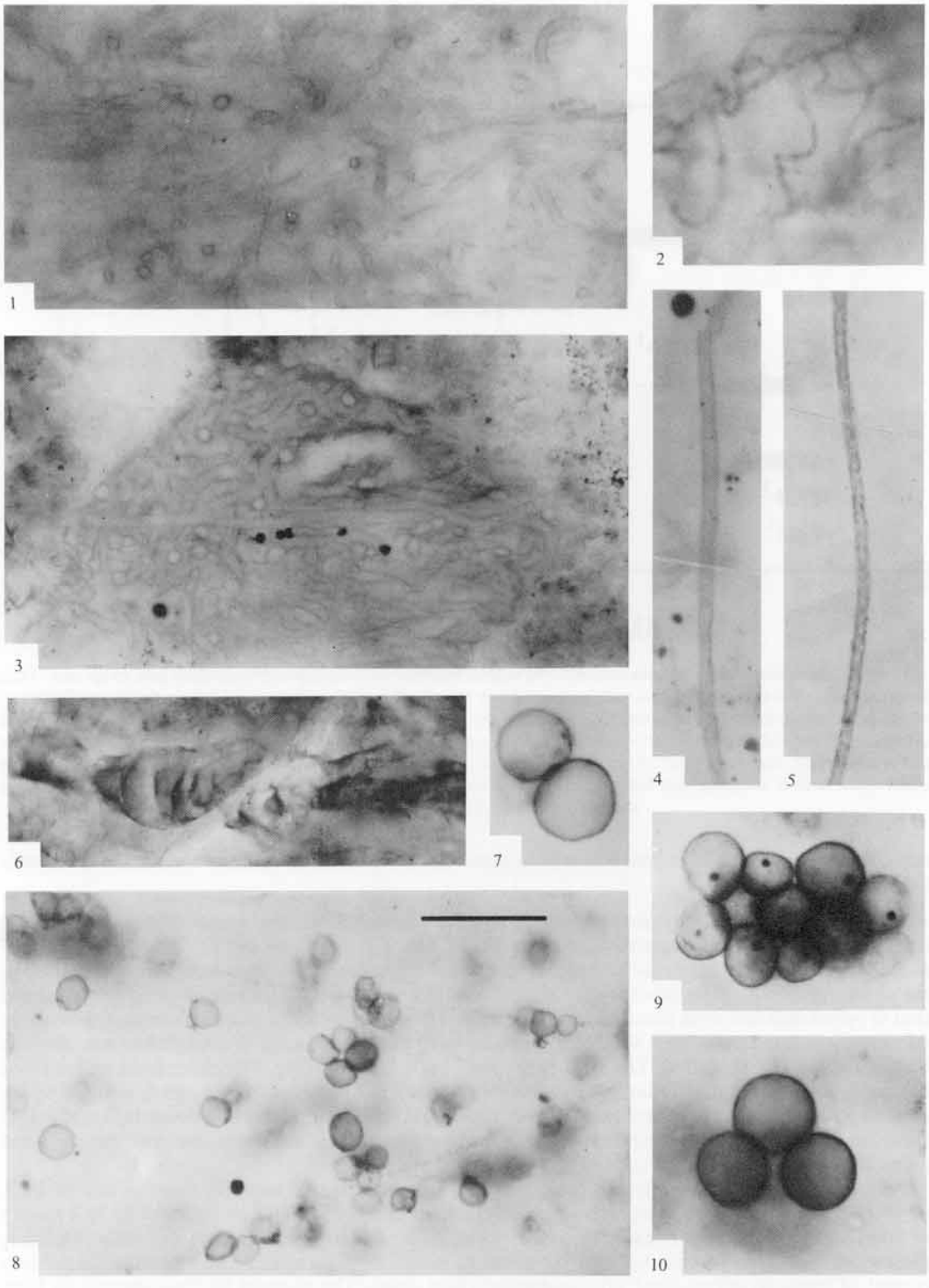
Figs. 1, 3–5. *Eomycetopsis robusta* Schopf emend. Knoll and Golubic. 1, matted population, K2035–3N, 8·6 × 101·5, H.U. No. 60616. 3, filament cluster (note borders of clast), K2035–3I, 17·4 × 125·4, H.U. No. 60617. 4, K1962A–1B, 8·5 × 122·1, H.U. No. 60611. 5, K1962A–1B, 12·6 × 123·1, H.U. No. 60612.

Fig. 2. *Tenuofilum septatum* Schopf. Densely interwoven population. K1935–1A, 6·5 × 103·3, H.U. No. 60615.

Fig. 6. Multilamellated sheath. K1931–2A, 12·8 × 127·8, H.U. No. 60614.

Figs. 7, 8, and 10. *Myxococcoides* sp. 7, K1963–1A, 19·8 × 118, H.U. No. 60618. 8, lower power photograph of population that includes 7, showing spatial distribution of individuals. 10, K2035–1A, 18·2 × 128, H.U. No. 60622.

Fig. 9. *Glenobotrydion aenigmatis* Schopf. K2035–3A, 13·2 × 125·2, H.U. No. 60623.



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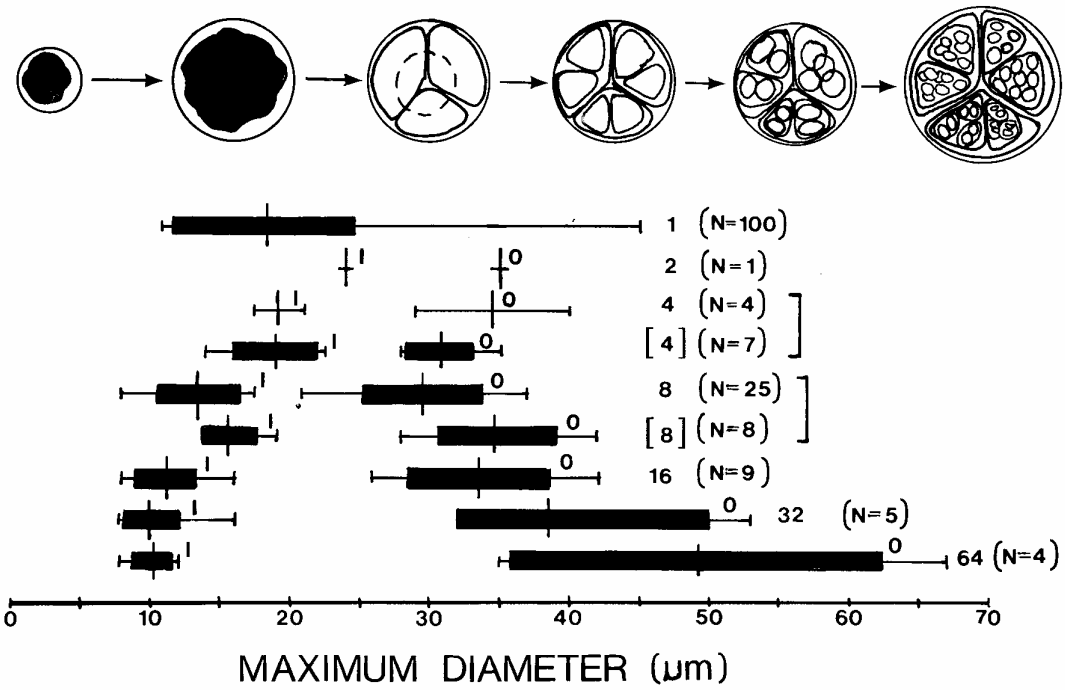


TEXT-FIG. 4. Size distribution of unicells and cells within colonies of *Scissilisphaera regularis* gen. et sp. nov. Thin lines indicate total size range; thick blocks extend one standard deviation above and below the mean diameter, which is indicated by the vertical line. Statistics are provided for individual unicells [1]; overall diameter [0] and diameters of individual cells for two-cell colonies [2], quartets [4], octads [8], sixteen-cell colonies [16], thirty-two cell colonies [32], and sixty-four cell colonies [64]; and for four-cell [(4)] and eight-cell [(8)] divisions that remain observable within colonies that later continued to divide. The growth and divisional cycle of *S. regularis* is diagrammed above the size distributions.

nov., is comparable in all salient features to members of the modern cyanobacterial family Pleurocapsaceae.

Planktonic microfossils. Simple spheroidal unicells assignable to the genus *Myxococcoides* are scattered throughout the stromatolitic cherts (Pl. 57, figs. 7, 8, 10; Pl. 60, fig. 14). Their wide range of size and wall thickness suggests that several species are represented, and their irregular distribution in the cherts further suggests that they are allochthonous elements, perhaps near-shore phytoplankton that dropped into and were preserved with the mats. Large planktonic acritarchs comparable to those commonly isolated from open shelf detrital rocks have been found only in a single horizon near the base of the Ryssö Formation. The locality in question (K 2035, text-fig. 1) consists predominantly of flat microbially laminated dolomites with lenses and irregular patches of black chert, some of which contain stromatolitic microfossil populations. Chert and limestone pebble conglomerates and gravel stones occur within shallow channels in the carbonates, and it is in the conglomerates that the large planktonic microfossils are found.

Petrographically, the fossiliferous rocks consist of moderately well rounded clasts of micrite 1 × 1 to 14 × 4 mm in size, along with carbonaceous chert pebbles up to 40 mm long, both set in a matrix of what was originally an organic rich carbonate. Although still preserved as dolomite in places, the matrix has largely been replaced by silica. Some relatively angular chert pebbles themselves consist of sand- to gravel-sized silica-cemented chert clasts. The channel fill thus appears to have

originated as lime muds and sands, in part organic rich, that were ripped up and redeposited in channels. Between episodes of conglomerate deposition, carbonaceous lime muds draped the accumulated pebbles and gravel. Silicification occurred early in diagenesis and was incomplete; the compound clast-in-clast nature of some pebbles demonstrates that materials were sometimes reworked more than once.

Siliceous clasts in the carbonate are always carbonaceous, while associated limestone pebbles are almost invariably devoid of organic matter. This circumstance prompts the suggestion that chert was preferentially precipitated in carbonaceous sediments. A chemical hypothesis advanced by Leo and Barghoorn (1976) to explain the silicification of wood may also explain the close relationship between chert and organic matter in Proterozoic carbonates. Leo and Barghoorn proposed that functional groups, particularly hydroxyl groups, in partially degraded wood form hydrogen bonds with dissolved monosilicic or polysilicic acid in ambient ground water. As silicic acid molecules build up, they begin to polymerize, with the expulsion of water. In this way, both the exquisite preservation of some petrified woods and the intimate relationship of silica and organic matter in petrifactions are explained. Similar features in the fossiliferous Ryssö cherts (and other stromatolitic microbiotas) may best be explained by invoking analogous geochemical processes in Precambrian microbial mat sediments.

Although the conglomerates under consideration occur within a stromatolitic carbonate succession, clasts containing populations of interwoven mat filaments are rare (Pl. 57, fig. 3). Most clasts are not laminated. Conglomeratic chert pebbles do contain fossil cells, sheaths, mucilage, and indeterminate organic particles which are closely crowded together. Microfossils are more or less randomly distributed within clasts, in silicified areas of the matrix, in clasts-within-clasts, and, occasionally, in the silicified spaces between clasts in compound conglomeratic pebbles. Evidently, some fossils dropped into accumulating organic rich muds and were transported within clasts to the site of deposition, while other specimens were carried directly into the channel by transporting currents.

Twelve distinct types of large, robust-walled microfossils (acritarchs) have been identified in this assemblage (Pl. 58, figs. 7–9; Pl. 60; Table 1). Smaller spheroidal unicells also occur in abundance. Most of these smaller microfossils can be accommodated within the genus *Myxococcoides*, a form genus covering small, morphologically simple single-walled vesicles; however, it is clear that several biological species are present. Based on size-frequency distribution, characteristic clustering patterns, vesicle thickness, and the presence or absence of extracellular mucilage, most populations can be related to the previously described species *M. minor* Schopf, *M. inornata* Schopf, and *M. cantabrigiensis* Knoll. A few populations containing internal organic blebs are assigned to *Glenobotrydion aenigmatis* Schopf, although it is not clear that these differ biologically from certain *Myxococcoides* populations. Rare fragments of *Eomycetopsis robusta* and *Siphonophycus kestron* sheaths occur and are considered to be allochthonous.

Among previously described silicified Precambrian microbiotas, assemblages preserved in the underlying Hunnberg Formation (Knoll 1983) compare most closely with this Ryssö florule. The Hunnberg biota includes three phytoplankton assemblages: a taxonomically depauperate lagoonal association, an open coastal shelf assemblage containing more than two dozen morphologically diverse taxa, and, within intercolumnar spaces in stromatolite bioherms that separate the first two facies, a third assemblage of intermediate character. The intermediate Hunnberg biota, representing very near shore, but none the less approximately normal marine conditions, is most similar to the Ryssö assemblage under consideration. Both assemblages are dominated by *Chuaria circularis* Walcott and Unnamed Form B of Knoll (1983), and several other taxa are found in common. The Ryssö microbiota differs from known Hunnberg assemblages in that it contains the large and distinctive fossil *Pterospermopsimorpha* sp. (Pl. 58, figs. 7, 8) and *Trachysphaeridium laufeldi* (Pl. 60, figs. 1, 2). The presence of these forms in the younger but not the older biota may indicate an evolutionary first appearance, but environmental factors and chance cannot be ruled out as causes of microfloral differences. In general, the Ryssö acritarch florule is more similar to assemblages described from Precambrian siltstones and shales than it is to silicified microbiotas.

Biologically, the affinities of most of these fossils are uncertain. Large, robust-walled acritarchs are generally considered to be the reproductive cysts of eukaryotic phytoplankton (see discussions in Downie 1973 and Vidal and Knoll 1983); however, the algal division or divisions represented are unclear. Much opinion favours a green algal relationship for Precambrian sphaeromorphs, by comparison to the large cysts of the modern green flagellates, the prasinophytes; but at the moment such inferences remain conjectural. The stratigraphic import of these microfossils is more certain. Late Precambrian and Cambrian acritarch assemblages show clear evolutionary trends, and a number of assemblage zones have been recognized and used to correlate strata on an intercontinental basis (Vidal 1981*b*; Vidal and Knoll 1983). The Late Riphean character of the Ryssö biota demonstrates that even the local occurrence of planktonic microfossils can allow accurate biostratigraphic placement of an Upper Proterozoic succession.

Vase-shaped microfossils. In the upper third of the Ryssö Formation, acritarchs and cyanobacterial microbenthos are rare, occurring only as scattered and, in general, poorly preserved individuals. Flask- or vase-shaped microfossils (VSM's), on the other hand, occur in great abundance (Pl. 61).

A few, apparently washed-in, VSM's can be found in silicified patches within platy bedded, krinkly laminated dolomites near the top of the formation (samples K 1929, K 1931). These carbonates record very shallow, near shore marine conditions. Much larger VSM populations occur in a stratigraphically lower sequence dominated by pyritic black shales (samples K 1970–2, K 1981, K 13322). In this succession, bituminous micrite beds a few centimetres to 1·5 m thick occur at several metre intervals within some 30 m of fissile, organic-rich shales. In some horizons, the carbonates have been almost entirely replaced by silica, but more commonly chert occurs as oblong concretions a few centimetres thick within the limestone. This sequence appears to have been deposited in a local basin characterized by restricted bottom circulation. VSM's have been recognized in macerations of bituminous limestone and shale samples, but they are most easily studied in petrographic thin sections of chert.

Petrographically, the fossiliferous cherts consist of a mosaic of extremely small quartz crystals (< 10 μm in diameter). Carbonate replacement tends to be incomplete, with small, etched grains persisting throughout the matrix. Late-stage diagenetic rhombs of dolomite occur sporadically throughout the samples studied, and these truncate both quartz crystallization patterns and, occasionally, microfossils (Pl. 61, figs. 2, 9). The cherts are richly carbonaceous. Amorphous organic debris is distributed in closely spaced, discontinuous organic lamellae, as well as in continuous layers up to 100 μm thick.

VSM's occur as organically preserved fossils and, more commonly, as casts. Casts are filled by single large crystals of carbonate conforming to the shape of the original organism, by silica, or by some combination of the two minerals. Where carbonate and chert co-occur, the carbonate crystals are often markedly etched, indicating the diagenetic sequence of mineralization. Chert often is in the

EXPLANATION OF PLATE 58

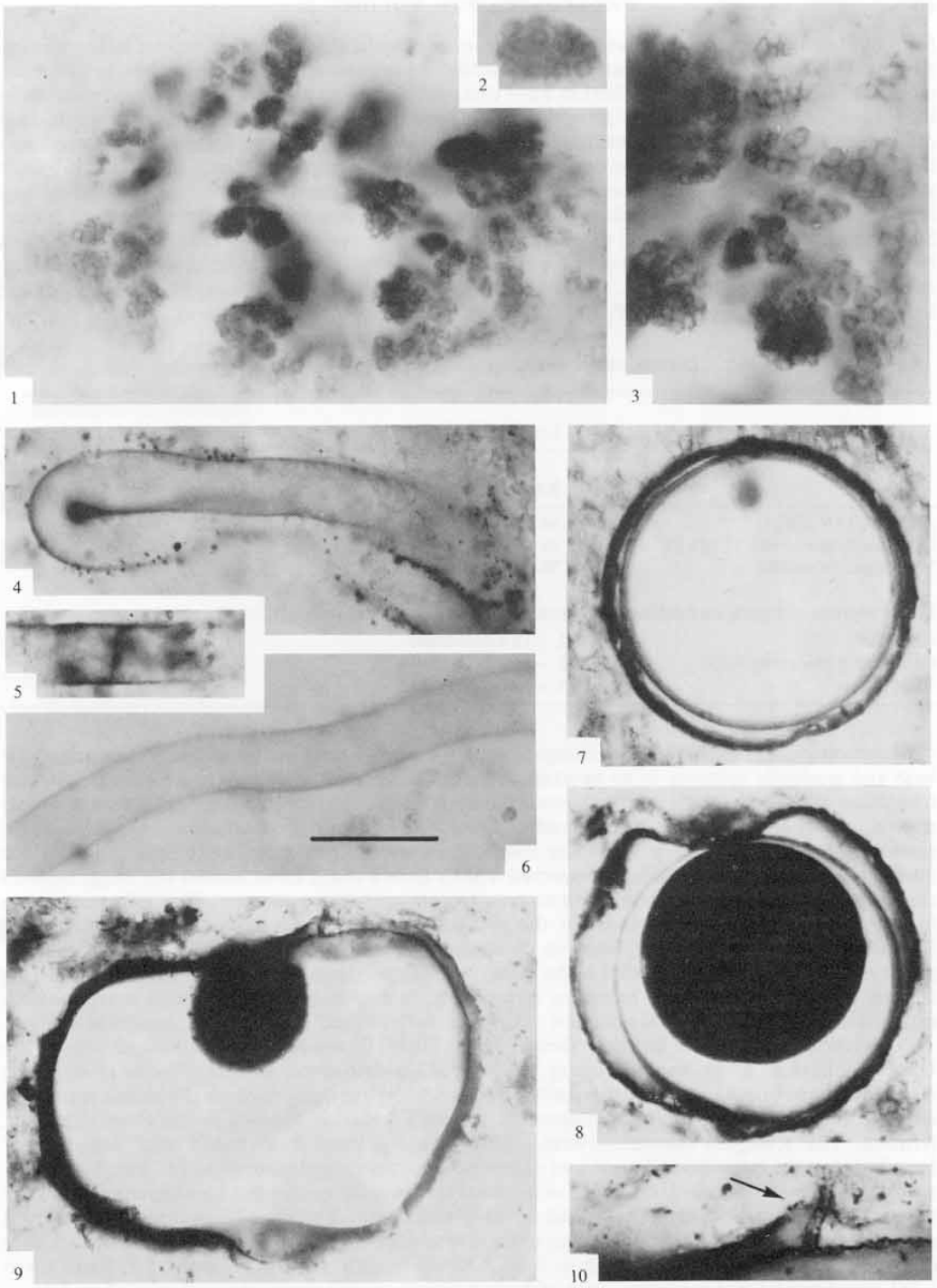
For each figure, thin section number, stage co-ordinates (where 'x' on slide K2023–1F = 1·9 × 120·2), and Harvard University Paleobotanical Collection number are given. Bar in Fig. 6 = 25 μm for Fig. 1; = 20 μm for Figs. 2–6, and 10; = 60 μm for Figs. 7 and 8; and = 70 μm for Fig. 9.

Figs. 1–3. *Coniunctiophycus* sp. 1, large colony, K1963–1A, 23·5 × 102, H.U. No. 60631. 2, small cluster, K1963–10, 18 × 110, H.U. No. 60632. 3, details of colony shown in 1.

Figs. 4–6. *Siphonophycus kestron* Schopf. 4, 1962–1B, 20·2 × 130·6, H.U. No. 60607. 5, K2035–3E, 18·5 × 110·3, H.U. No. 60608. 6, K1962A–1B, 9·1 × 111·6, H.U. No. 60609. Note apparent septation in 5.

Figs. 7 and 8. *Pterospermopsimorpha* sp. 7, K2035–3E, 8·6 × 120·7, H.U. No. 60633. 8, K2035–3E, 12·1 × 111·8, H.U. No. 60634.

Figs. 9 and 10. *Trachyhystrichosphaera vidalii* Knoll. 9, K2035–3M, 8·2 × 118·3, H.U. No. 60635. 10, detail of 9. Arrows point to characteristic columnar processes.



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form of fibrous chalcedony, radiating inward from cast walls. It is likely that at least in some cases, silica was precipitated in a microscopic cavity within the organic structure, rather than as a replacement of pre-existing carbonate. Chert in VSM casts can also occur as more or less equant crystals. In these cases, crystal size is notably larger than in the surrounding matrix and there is always a mineral discontinuity at microfossil boundaries; i.e. chert crystals do not transgress fossil walls whether these be organically preserved or defined by casts. In summary, petrographic evidence suggests that VSM's accumulated in anoxic carbonaceous micrites during Ryssö times. After decomposition of any internal cellular material, many skeletons were filled with carbonate, while others remained empty. Subsequent to the partial or total degradation of the walls themselves, the VSM-bearing sediments became silicified. Internal void spaces were filled and carbonate casts were, for the most part, partially or completely replaced by silica. Casts are often draped in amorphous organic matter, further accentuating their morphology (Pl. 61, figs. 7, 13).

TABLE 2. Dimensions of vase-shaped microfossils in the Ryssö Formation

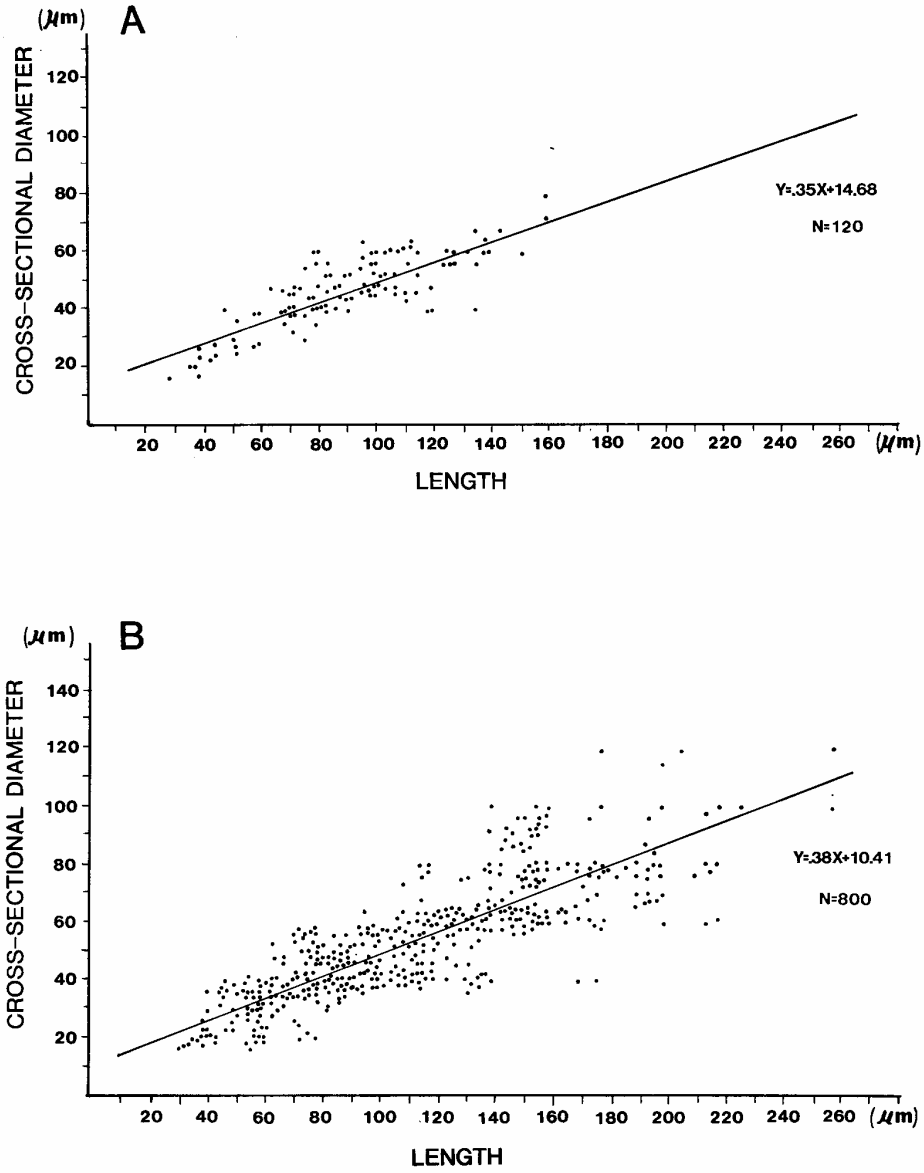
	Length (μm)			Maximum cross-sectional diameter (μm)		
	Range	Mean	Standard deviation	Range	Mean	Standard deviation
All VSM's ($N = 920$)	34–257	106	38	16–119	50·5	16
Organically preserved VSM's ($N = 120$)	34–158	90	27	16–79	46	12
VSM casts ($N = 800$)	78–257	108	39	16–119	51	16

Linear regression equations for length, L, versus diameter, D. (Reduced major axis.)

All VSM's	$D = 0{\cdot}36\,L + 12{\cdot}4$ ($r = 0{\cdot}80$)
Organically preserved VSM's	$D = 0{\cdot}35\,L + 14{\cdot}7$ ($r = 0{\cdot}80$)
VSM casts	$D = 0{\cdot}38\,L + 10{\cdot}4$ ($r = 0{\cdot}82$)

Morphologically, the VSM's are elongate ovoid to pear-shaped bodies, broadly rounded at the base and gradually tapering to an aperturate apex. The aperture may appear as a simple circular truncation of the vesicle or it may be surrounded by a distinct collar region. Dimensions for a sample population are given in Table 2, as are reduced major axis linear regression equations for length *vs.* maximum cross-sectional diameter. Size distribution is displayed graphically in text-fig. 5. It is interesting to note that organically preserved VSM's have a much more limited size range than do casts. Specifically, very large casts have no counterpart among organic tests. This is in spite of the facts that the regression equations for the two subpopulations are nearly identical (slopes not significantly different at the 5% level, as determined by use of the Z statistic) and that the two preservational forms occur together in the same beds, often in the same microhorizons. Whether the organic and cast populations represent one species or two is unclear, although a taphonomic explanation for the preferential retention of organic walls in small specimens is considered likely.

Precambrian VSM's were first described by Ewetz (1933) from silicified phosphate nodules of the Upper Riphean to lower Vendian (*sensu* Vidal 1976) Visingsö Beds, Sweden. Bloeser *et al.* (1977) discovered large populations of organically preserved VSM's in carbonaceous shales and (rarely) in cherty pisolite beds of the Upper Riphean Kwagunt Formation exposed in the Grand Canyon, Arizona. The Kwagunt specimens were initially divided into 'flask-shaped' and 'tear-shaped' morphotypes, the latter being longer and narrower. Lengths ranged from 48 to 145 μm ($\bar{x} = 96$ μm, $s = 20$ μm, $N = 90$). Bloeser (1980) has considered that several species can be differentiated on the basis of collar morphology. The Ryssö VSM population, especially the organically preserved subpopulation, is morphologically similar to the Grand Canyon VSM assemblage. Svalbard tests are on the average more elongate than those from Arizona (length to width ratios are 2·1 : 1 and 1·4 to 1·7 : 1, respectively), but the entire range of flask- and tear-shaped morphologies reported by Bloeser



TEXT-FIG. 5. Bivariate plots of size distribution for vase-shaped microfossils in the Ryssö Formation. A, organically preserved individuals. B, specimens preserved as casts. Lines indicate reduced major axis regression lines relating length and width.

et al. (1977) can be found in the Ryssö Formation. Bloeser *et al.* (1977) and Bloeser (1980) also reported the presence of opercula plugging the apical openings of Kwagunt VSM's. We have not observed any opercula in Ryssö microfossils, although the complete absence of organically tinted sedimentary matrix from VSM interiors might be advanced as an indirect argument for the former

presence of an opercular structure. Because the details of collar morphology are rarely well defined in the Ryssö population, we are unable to subdivide the Svalbard populations by Bloeser's criteria; however, the points of similarity between the two populations are such that we regard them as representing closely related micro-organisms.

In the wake of Bloeser *et al.*'s (1977) initial paper on these distinctive microfossils, VSM's have been discovered in a number of late Precambrian deposits. Fairchild *et al.* (1978) reported VSM's 16 to 120 μm long from limestone cobbles in conglomerates of the Urucum Formation of south-western Brazil. Additional specimens were found in shallow marine dolomites from Jabal Rokham, Saudi Arabia, a sequence that has been correlated with the 638 to 600 Ma Murdama Group (Binda and Bokhari 1980). Knoll and Vidal (1980) described large new populations of VSM casts from phosphate nodules in silty argillites and siltstones of the upper Visingsö Beds, Sweden. Sizes in this population range from 60 to 130 μm × 25 to 62 μm; average dimensions equal 98 × 52 μm for $N = 300$. Finally, VSM's have been reported from several carbonate units thought to be depositionally related to the Ryssö Formation. Abundant specimens occur in the Backlundtoppen and Draken Conglomerate formations of Ny Friesland, Svalbard (Knoll 1981, and unpublished data), and other populations are found in the Limestone–Dolomite 'Series' of the upper Eleonore Bay Group, East Greenland (Vidal 1979).

The wide facies distribution of VSM's suggests that they are the remains of planktonic micro-organisms. Morphologically, VSM's are not closely comparable to unicellular algae, but they are quite similar to protozoans of several types. Bloeser *et al.* (1977) originally described the Grand Canyon VSM's as probable chitinozoans, stressing the morphological resemblance between the Precambrian fossils and members of the Ordovician–Silurian chitinozoan genus *Desmochitina*. In a more conservative assessment, Bloeser (1980) later classified them as microfossils *incertae sedis*.

Fairchild *et al.* (1978) suggested protistan affinities for the Brazilian VSM population, specifically citing the ciliate Tintinnida. Other amoeboid and ciliate protists build organic loricas similar in size and shape to VSM's; however, tintinnids make an intriguing comparison for several reasons. Ecologically, tintinnids are marine, pelagic protists that can be among the most important micropredators in coastal ecosystems. They form robust pseudochitinous tests similar to those of VSM's. In VSM's, the basal region is preferentially preserved relative to the collar, a phenomenon also recorded for modern tintinnids. Tappan and Loeblich (1968) noted differences in wall characteristics of base and collar regions of *Codonellopsis*, a modern vase-shaped ciliate protist; the long and very delicate collar region is solely organic and is, hence, less resistant to post-mortem degradation, while the solidly constructed base of the lorica consists of a combination of secreted and agglutinated materials and is therefore much more likely to be preserved.

Reid and John (1981) recently examined reproductive cysts of modern tintinnids. These bodies are vase-shaped, collared, and operculate. The resemblance to some morphologically simple chitinozoans prompted Reid and John to conjecture that certain chitinozoans may be tintinnid cysts. A cyst explanation for the Ryssö VSM populations merits consideration although it cannot be demonstrated to the exclusion of other hypotheses.

It seems, therefore, that at present it is impossible to ascertain unequivocally the exact biological affinities of Precambrian VSM's; however, we reiterate the conclusion of Knoll and Vidal (1980) that the organisms preserved as VSM's were most likely heterotrophic protists, similar in general ecological role to the modern Tintinnida.

DISCUSSION

The record of latest Riphean coastal marine life revealed by the Ryssö biotas is far from complete. Processes of fossilization strongly constrain our views of ancient life, limiting our vision to the microbiotas of selected environments in which post-mortem degradation was arrested at an early stage. Within those biotas, species differentially resistant to decomposition were selectively preserved, and even within individual organisms, those *parts* of the organisms most resistant to post-mortem

degradation were preferentially incorporated into the record. One might think that the record that has survived would seem depressingly impoverished, but that is in fact not the case. On the contrary, preserved Ryssö assemblages suggest that a taxonomically and ecologically diverse microbiota thrived along the Svalbard coast 800 to 700 Ma ago. Stromatolites are widely distributed in the Ryssö Formation, indicating that microbial mats covered much of the shallow Ryssö sea floor. The heterogeneity of the stromatolite morphologies and microstructures implies a concomitant heterogeneity in the microbial communities responsible for mat accretion. Only a single stromatolite type is represented by a preserved microbiota, but this assemblage reveals heterogeneity in both cyanobacterial mat builders (three different builders occurring singly or in combination) and in mat dwelling micro-organisms (0 to 2 preserved dwellers in mats). This is not unexpected in view of the impressive diversity of mat associations present in other flat laminated stromatolites of comparable age (Knoll 1981, 1982*a*).

The shallow and perhaps somewhat restricted seas that periodically inundated the broad Ryssö carbonate flats had a limited plankton biota. The small allochthonous unicells associated with some Ryssö stromatolitic microbiotas are interpreted as inshore phytoplankton or periphyton. The taxonomic affinities of these cells are uncertain, although at least some of them may have been eukaryotic algae. Eukaryotic phytoplankters that produced large, robust, morphologically complex reproductive cysts thrived in more open coastal waters. Again, this 'lateral' distribution of plankton types is not unique to the Ryssö Formation. It appears to be as characteristic of late Precambrian phytoplankton as it is of Phanerozoic algae (Vidal 1976; Knoll 1983; Vidal and Knoll 1983).

Ecological and environmental differences (modified by the effects of disturbance and chance colonization) thus provide a satisfying explanation for the distribution of phytoplankton and stomatolitic microbenthos in the Ryssö Formation, but what of the VSM's? These organisms were probably micropredators and so must have coexisted with phytoplankton populations, yet where VSM's are abundant, other organisms are rare or absent and vice versa. The key to this distributional problem may lie in fossil preservation. To our knowledge, the best preserved organic tests of VSM's are found in organic-poor carbonates and cherts. The chemical composition of these tests is unknown, but it may be such that early diagenetic conditions inimical to the preservation of most algae and cyanobacteria have little effect on VSM's. Conversely, good conditions for algal and blue-green fossilization may promote the dissolution of VSM tests. Therefore, the segregation of VSM populations as a distinct assemblage type may be associated with taphonomy and only indirectly reflect the ecological distribution of the living organisms.

In summary, the biota of the latest Riphean Ryssö coastal seaway included a variety of essentially prokaryotic microbial mat communities distributed across the intertidal to shallow subtidal carbonate flats. Cyanobacteria constitute the best preserved members of these communities, but the mats undoubtedly also contained a host of metabolically diverse aerobic and anaerobic, photosynthetic and heterotrophic bacteria. The benthos may also have included eukaryotic algae and simple seaweeds, although such organisms are not preserved in the Ryssö Formation. A diverse, eukaryote dominated phytoplankton biota lived in the water column above open coastal sediments, but in more restricted inshore waters only a depauperate assemblage of simple unicells thrived. Heterotrophic protists capable of micropredation were an integral part of coastal food webs. The Ryssö Formation thus provides an unusually clear picture of the complexity of microbial life just prior to the initial radiation of metazoans.

SYSTEMATIC PALAEONTOLOGY

All specimens come from exposures of the Upper Riphean Ryssö Formation in the vicinity of Murchisonfjorden, Nordaustlandet, Svalbard. Illustrated material is housed in the Palaeobotanical Collections of Harvard University. Comparative materials are housed in the Palaeontological Museum of Oslo University. In the interests of brevity, full synonymies are not presented for each species. These can be found in the recent monographs of Vidal (1976, 1981*a*) and Mendelson and Schopf (1982).

Kingdom MONERA Haeckel, 1878
Division CYANOPHYTA (Sachs) Pascher, 1931
Class COCCOGONEAE Thuret, 1875
Order CHROOCOCCALES Wettstein, 1924
Family CHROOCOCCACEAE Nägeli, 1849
Genus CONIUNTIOPHYCUS Zhang, 1981

Type species. Coniunctiophycus gaoyuzhuangense Zhang, 1981

Coniunctiophycus sp.

Plate 58, fig. 3

Description. Spheroidal to slightly elongated organic walled vesicles; walls thin, psilate to very finely granular. Individual cells 2–9 μm long ($\bar{x} = 3{\cdot}1$ μm, $s_x = 1{\cdot}0$ μm, $N = 100$) and 2–6 μm wide ($\bar{y} = 2{\cdot}3$ μm; $S_y = 0{\cdot}7$ μm; $N = 100$); see text-fig. 6. Cells arranged in tight, irregularly spheroidal clusters 10 to 20 μm in diameter containing 50–200 cells. Cell clusters commonly occur together in botryoidal aggregates up to 200 μm in maximum diameter. Large aggregates commonly give the appearance of growth inward into a cavity from cell populations lining the cavity walls. No external mucilage is apparent, but the spacing of clusters within the large aggregates suggests that some mucilage was originally present. Cell contents generally absent. Cell division apparently occurred by repeated binary fissions.

Discussion. Zhang (1981) erected the genus *Coniunctiophycus* for small spheroidal unicells clustered into ellipsoidal to spheroidal colonies, which, in turn, were aggregated into larger colonies. From fossil assemblages in the 1500–1400 Ma Gaoyuzhuang Formation, China, he described two species belonging to this genus: *C. gaoyuzhuangense* (average diameter = 4.0 μm) and the distinctly smaller *C. conglobatum* (average diameter = 1·4 μm). The Ryssö populations in question clearly fall within the limits of the genus *Coniunctiophycus*, but fall midway in size between the two described species. For this reason, we have elected to refer to the Svalbard fossils as *Coniunctiophycus* sp.

Among modern cyanobacteria, a number of coccoidal genera can produce colonies resembling *Coniunctiophycus*. A cyanobacterial interpretation for these fossils is accepted here, although it is acknowledged that other bacterial affinities cannot be completely ruled out.

Coniunctiophycus colonies occur in specific laminae at fairly regular intervals of 50 to 800 μm. This distribution within filamentous mats supports their interpretation as mat-dwelling microbenthos.

Order PLEUROCAPSALES Geitler, 1925
Family PLEUROCAPSACEAE Geitler, 1925
Genus SCISSILISHAERA gen. nov.

Type species. Scissilisphaera regularis sp. nov.

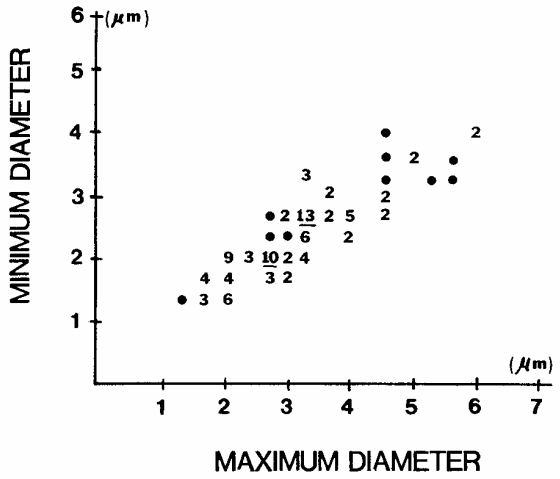
Diagnosis. Spherical to spheroidal vesicles; vesicle wall single, light, thick, and finely granular, or multilamellated. Individual vesicles sometimes containing a single, large, irregular organic body with a well-defined wall. More often, the vesicle is subdivided internally into 2, 4, or 8 smaller vesicles, each having a single wall comparable to that of the external wall. Internal vesicles often contain 2, 4, or 8 still smaller vesicles, resulting in a total of up to 64 spheroidal vesicles packed within the outer wall. Subdivided vesicle geometry reflects division in three planes. Larger aggregates form irregularly cuboidal packages of 100 or more vesicles; in these colonies the outermost vesicle wall is absent.

Etymology. From the Latin *scissilis*, meaning 'that which may be split readily', and *sphaera*, meaning 'sphere'. Thus, an easily divided sphere.

Scissilisphaera regularis sp. nov.

Plate 59

Diagnosis. Qualitatively, as for genus. Undivided vesicles 11 to 45 μm in diameter, averaging 18·2 μm.



TEXT-FIG. 6. Bivariate plot of maximum vs. minimum diameter for a sample population ($N = 102$) of *Coniunctiophycus* sp. Numbers indicate number of specimens having a given pair of dimensions. Single specimens are indicated by dots.

Small undivided vesicles may be closely packed in irregular aggregates; larger individuals are solitary or occur in loose clusters. Subdivided vesicles are generally equal in size to the largest of the undivided vesicles—for dyads, tetrads, octads, and 16-cell colonies, the diameters of the external vesicle wall are 35 μm, 34·5 μm, 29·5 μm, and 34·8 μm, respectively. Internal vesicle diameters are 24 μm, 19·2 μm, 13·5 μm, and 11·2 μm, respectively. Vesicles containing 32 or 64 small, internal vesicles are often larger (up to 70 μm), but still retain a spherical to slightly tuberous shape. Colonies containing more than 64 subdivided units tend to be irregularly cuboidal packets.

Holotype. The specimen illustrated on the left in Pl. 59, fig. 8 has been designated the type of the species. Harvard University Botanical Collections No. 60643.

Etymology. From the Latin *regularis*, meaning 'according to a rule or pattern'. This name reflects the regular geometric pattern of cell division in this species.

Type Locality. Outcrops of Ryssö Formation exposed 2 km south of Roaldtoppen (south shore of Murchisonfjorden) in Nordaustlandet, Svalbard, near small, unnamed lake.

Description. Populations dispersed irregularly along bedding planes. Individuals consist of a spherical to spheroidal, thick, finely granular wall or a multilamellated wall. Diameter of unicells ranges from 11 to 45 μm ($\bar{x} = 18{\cdot}2$ μm, $s_x = 6{\cdot}4$ μm, $N = 100$). Internal contents—raisin-like, folded, and wrinkled organic bodies with well-defined walls—indicate that even the largest undivided vesicles contained only a single cell. Smaller individuals often occur in tightly packed, irregular clusters, although they are sometimes found as loosely aggregated populations or as scattered solitary fossils. Larger individuals (those > 20 μm) usually occur in loosely aggregated groups or as solitary cells. Vesicles larger than 25 μm are often subdivided internally into 2, 4, or 8 tightly packed vesicles, each having a wall thinner than, but comparable in quality to, the outer vesicle wall. These internal vesicles, in turn, may be subdivided internally into 2, 4, or 8 smaller vesicles, resulting in spheroidal colonies of 2, 4, 8, 16, 32, or 64 cells (although the occasional failure of some vesicles to divide produces colonies whose cell number deviates from the geometric series). Size distribution for colonies of various cell numbers are presented in text-fig. 4, as is a diagram of the observed divisional sequence. Colonies of more than 64 cells are irregularly cuboidal, and are not bound by an all-encompassing vesicle wall (Pl. 60, figs. 10, 12).

Undivided unicells are the most commonly encountered form in the population. Dyads and quartets occur

infrequently, but octads are very common. Colonies of 16, 32, and 64 cells occur with decreasing frequency. In more highly subdivided colonies, the internal walls formed during the 2- and 4-cell stages are often impossible to differentiate.

Discussion. The vesicle walls described for *Scissilisphaera* are interpreted as originally closely invested extracellular envelopes—the F layer of Waterbury and Stanier (1978). The wrinkled internal bodies found in unicells and some dyads and quartets are interpreted as partially coalesced cellular remains. True cell contents are rarely preserved in subdivided vesicles. From the fossil population, one can reconstruct a divisional sequence for *Scissilisphaera*. The cycle began with relatively small (*c.* 11 μm) individuals surrounded by an extracellular envelope. Cells grew (and envelopes expanded) until they reached a diameter of approximately 30 to 45 μm (mean diameter of subdivided spheres = 32·5 μm; $N = 50$ colonies) and then began to undergo a series of binary divisions in three planes, apparently with little or no growth between fissions. The absence of interdivision growth is attested to by the fact that large unicells, dyads, quartets, octads, and 16-cell colonies all have about the same external diameters. Colonies of 32 and 64 cells tend to be a bit larger; this may indicate resumption of growth or it may simply indicate that larger cells cleave into a greater number of small cells. After each division, a new extracellular envelope was secreted by each daughter cell. Cellular material disappeared during post-mortem degradation, but the envelopes were preserved, and their Matruschka doll arrangement of smaller sheaths inside larger ones makes it easy to reconstruct divisional patterns. At the 8, 16, 32, or 64 cell stage, the outer envelopes ruptured and the small individual cells either dispersed to begin a new cycle or resumed growth and binary fission in three planes without dispersal to produce cuboidal aggregates.

The repeated cleavage of cyanobacterial cells without intervening growth is known as multiple fission, and the small reproductive cells produced by multiple fission have been termed baeocytes (Waterbury and Stanier 1978). Using the terminology of microbiologists, one can interpret *S. regularis* as a cyanobacterium which reproduced by multiple fission to form baeocytes (equivalent to the smallest subdivisions in the spherical colonies). Among extant blue-greens, multiple fission is found only in the order Pleurocapsales, where it is the characteristic mode of reproduction (Waterbury and Stanier 1978).

Another pleurocapsalean trait manifest in *S. regularis* is a distinctive wall structure. Members of the modern Pleurocapsales form cell walls much like other gram negative bacteria; an inner peptidogylcan layer is surrounded by an outer layer that contains lipopolysaccharides. Pleurocapsalean blue-greens, however, characteristically form a third layer (the F layer) similar in ultrastructure to the sheaths and envelopes of other blue-greens, but which closely invests the cell so that it is often difficult or impossible to detect by light microscopy of healthy populations (Waterbury and Stanier 1978). F layers do not participate in binary fission, but a new F layer is secreted by each daughter cell immediately following cleavage. The geometry of the envelopes in *S. regularis* colonies strongly suggests that they are differentially preserved F layers formed after each successive cell division.

Thus, there is little doubt that *S. regularis* belongs to the Pleurocapsales. Genera within this group

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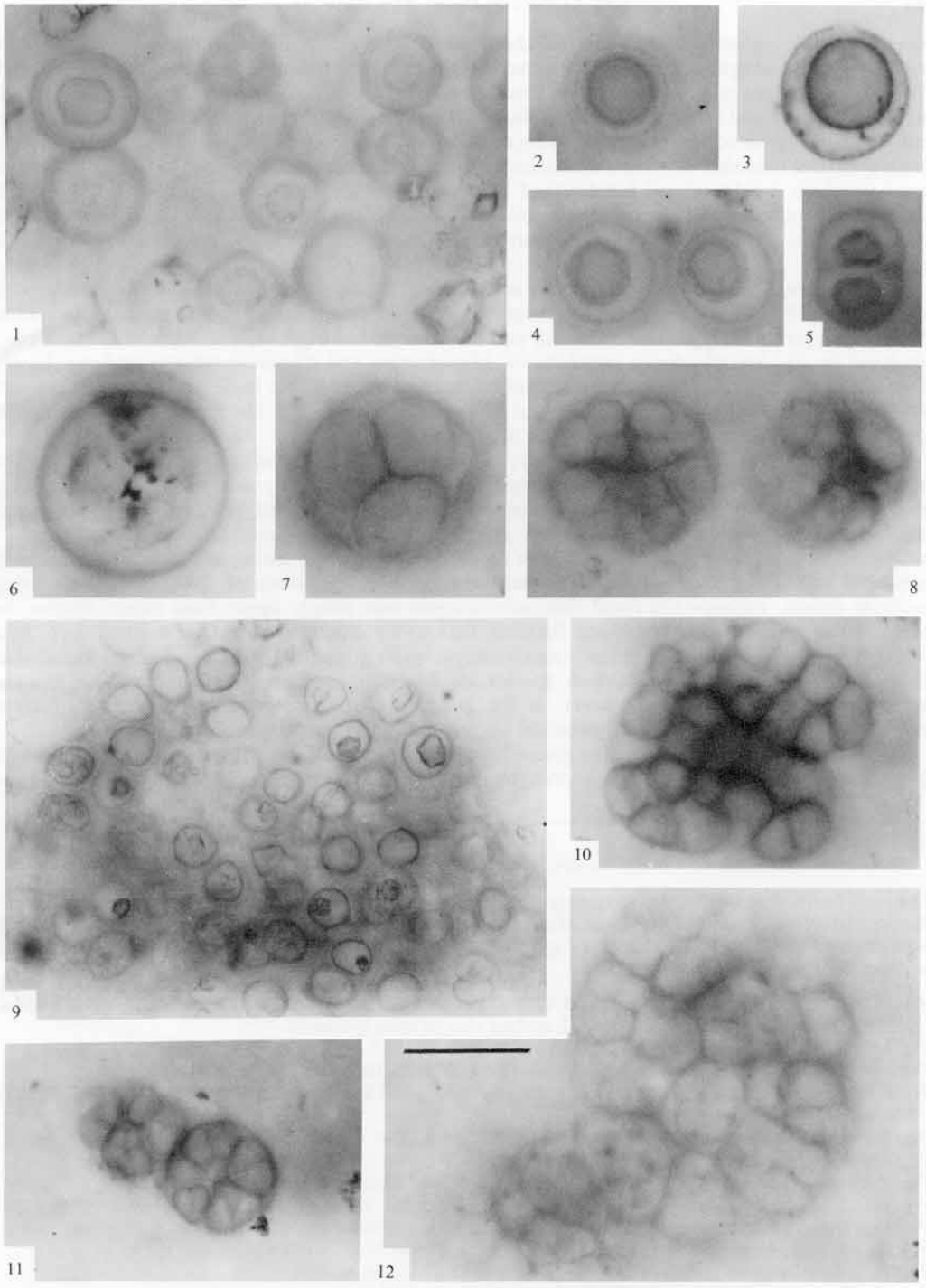
EXPLANATION OF PLATE 59

For each figure, thin section number, stage co-ordinates (where 'x' on slide K2023–1F = 1·9 × 120·2), and Harvard University Paleobotanical Collection number are given. Bar in Fig. 12 = 20 μm for Figs. 1–7; = 25 μm for Figs. 8, 10, and 12; and = 40 μm for Figs. 9 and 11.

Figs. 1–12. *Scissilisphaera regularis* gen. et sp. nov. 1, K2036–6A, 20·3 × 122·7, H.U. No. 60636. 2, K2036–6A, 4·6 × 123, H.U. No. 60637. 3, K2035–2A, 2 × 121·9, H.U. No. 60638. 4, K2036–6A, 4·6 × 123, H.U. No. 60639. 5, K2035–2A, 2·3 × 122·1, H.U. No. 60640. 6, K2035–2A, 3 × 125·6, H.U. No. 60641. 7, K2035–2A, 2·3 × 125, H.U. No. 60642. 8, K2035–2A, 2·8 × 124·6, H.U. No. 60643. 9, K2036–6A, 16·6 × 115·4, H.U. No. 60610. 10, K2035–2A, 2·2 × 123·4, H.U. No. 60647. 11, K2035–2A, 2·5 × 124·9, H.U. No. 60613, two spheroidal colonies showing nature of successive fissions within each individual colony. 12, K2035–2A, 0·9 × 114·8, H.U. No. 60649.



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have been differentiated on the basis of the presence or absence of vegetative binary fissions in addition to the ubiquitous multiple fission, the geometry of colonies, and the motility (or lack thereof) of the baeocytes—apparently a function of whether or not baeocytes are invested by an F layer (Waterbury and Stanier 1978). *Scissilisphaera* is similar to the extant genus *Dermocarpa* in that individual cells grow to a large size (up to 30 μm in *Dermocarpa*) before undergoing multiple fission to form spherical colonies; however, *Dermocarpa* multiple fissions usually result in the formation of large numbers (up to several hundred) of very small baeocytes. *Dermocarpa* baeocytes are not enveloped in individual F layers, and *Dermocarpa* is incapable of forming cuboidal colonies by simple binary fissions. *Xenococcus* has F layer surrounded baeocytes, but again, does not exhibit simple binary fission.

Myxosarcina, *Chroococcidiopsis*, and the several traditionally defined genera placed by Waterbury and Stanier (1978) in the '*Pleurocapsa* group' all divide by binary fission as well as multiple fission. *Pleurocapsa* group blue-greens often form pseudofilamentous outgrowths of colonies, a feature not observed in any *Scissilisphaera* populations. *Myxosarcina* and *Chroococcidiopsis* undergo binary divisions in three planes to produce cuboidal colonies, much as is seen in *Scissilisphaera*. (Compare Waterbury and Stanier 1978, Figs. 24b and 25b with Pl. 59, fig. 12.) The genera are differentiable largely by the presence of motile baeocytes in *Myxosarcina*.

Thus, in its ability to divide by both binary and multiple fission, in the apparently immotile nature of its baeocytes (as evidenced by the presence of envelopes on all cells produced by multiple fission), and in the relatively low number of baeocytes produced per parent cell (4–64), *Scissilisphaera regularis* appears most similar to living blue-greens of the genus *Chroococcidiopsis*. The large size of individual cells is not characteristic of the modern genus, nor is the segregation of vegetatively produced cuboidal packets from the loosely aggregated populations of individuals undergoing multiple fission. Perhaps the fossil chroococcidiopsid was simply larger than extant species, or perhaps the fossil species combined features that today characterize different genera. A third possibility is that more than one pleurocapsalean species is represented in the populations included in *S. regularis*—diverse pleurocapsalean species are found in modern intertidal zones. Militating against this last possibility, however, is the intimate spatial intermingling and the apparent morphological continuity between cuboidal aggregates and spherical colonies.

Several other pleurocapsalean blue-greens have been described from Proterozoic rocks. *Bavlinella faveolata* (Shepeleva) Vidal (= *Sphaerocongregus variabilis* Moorman, according to Vidal 1976) was

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EXPLANATION OF PLATE 60

For each figure, thin section number, stage co-ordinates (where 'x' on slide K2023-1F = 1·9 × 120·2), and Harvard University Paleobotanical Collection number are given. Bar in Fig. 6 = 40 μm for Figs. 1, 2, 7, and 13; = 50 μm for Figs. 3 and 10; = 20 μm for Figs. 4 and 5; = 120 μm for Fig. 6; = 150 μm for Figs. 8 and 9; and = 25 μm for Figs. 11, 12, and 14.

Figs. 1 and 2. *Trachysphaeridium laufeldi* Vidal. 1, cross-section showing small, conical spines at arrow, K2035-3I, 1 × 124·6, H.U. No. 60650. 2, surface view of same specimen.

Fig. 3. *Trachysphaeridium levis* (Lopukhin) Vidal. K2035-3J, 16·5 × 126·6, H.U. No. 60651.

Figs. 4 and 5. *Trachysphaeridium* sp. A of Knoll (1983). K2035-3B, 19 × 112·4, H.U. No. 60652.

Fig. 6. Unnamed Form B of Knoll (1983). Note diagenetic wrinkling of surface K2035-3L, 17·3 × 112·3, H.U. No. 60653.

Fig. 7. *Phanerosphaerops capitans* Schopf. K2035-3C, 6·5 × 103·5, H.U. No. 60673.

Fig. 8. *Trachysphaeridium* sp. B of Knoll, 1983. K2035-3H, 16·5 × 97·3, H.U. No. 60630.

Fig. 9. *Chuaria circularis* Walcott. 2035-3F, 11·5 × 113·5, H.U. No. 60628.

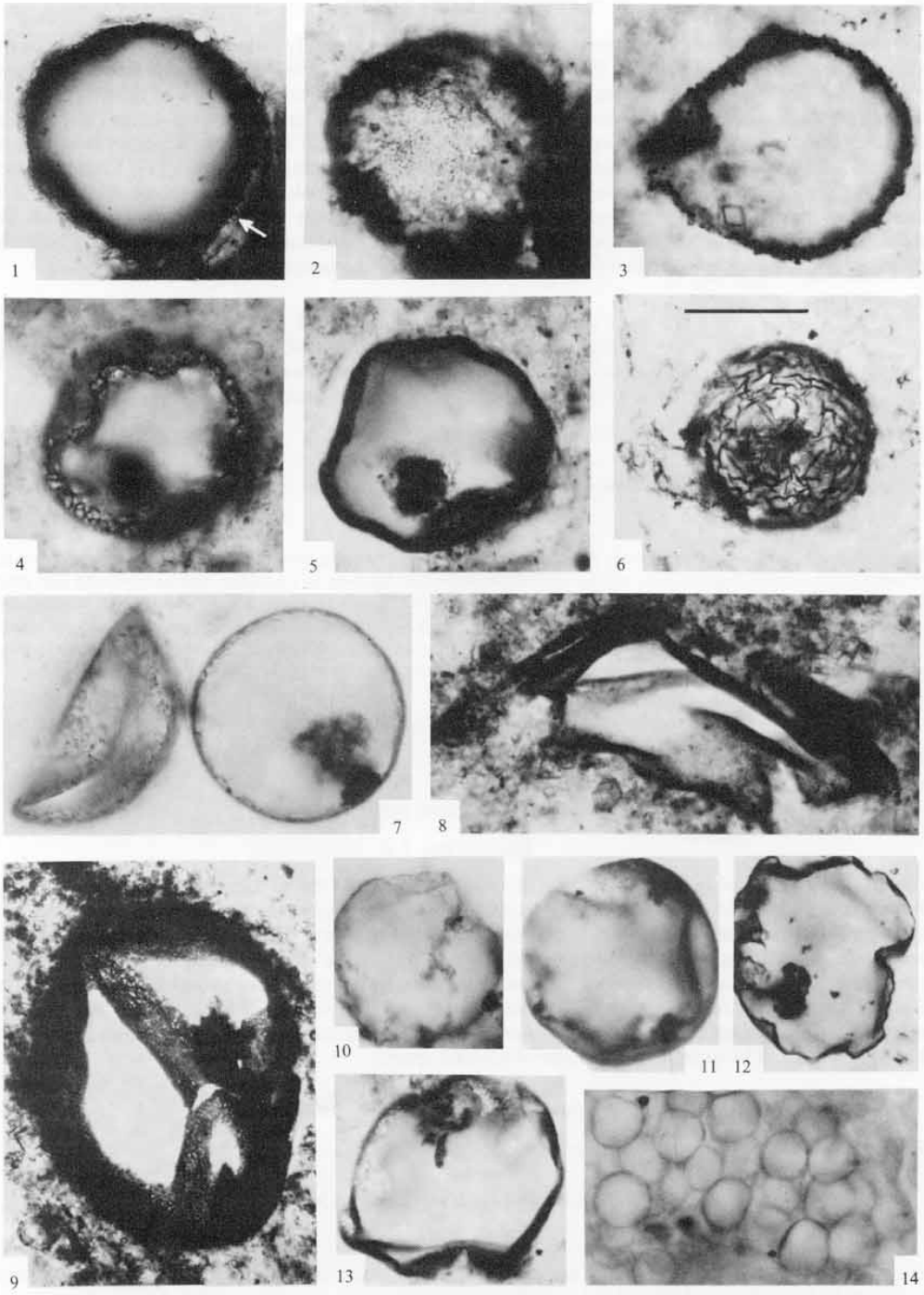
Fig. 10. Cf. *Stictosphaeridium* sp. *sensu* Vidal (1976). K2035-3D, 17·2 × 122·1, H.U. No. 60656.

Fig. 11. ?*Trachysphaeridium* sp. K1961-3A, 8 × 124·9, H.U. No. 60661.

Fig. 12. *Kildinella hyperboreica* Timofeev. K2035-3F, 3·5 × 114, H.U. No. 60654.

Fig. 13. *Kildinella sinica* Timofeev. K2035-3K, 5·3 × 113, H.U. No. 60658.

Fig. 14. *Myxococcoides* sp. K2035-3I, 21 × 106·4, H.U. No. 60625.



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a *Dermocarpa*-like baeocyte producer that was common in glacially influenced environments of the Late Proterozoic era (Moorman 1974; Vidal 1976; Knoll *et al.* 1981). *Palaeopleurocapsa wopfnerii* Knoll *et al.* (1975), described from the Upper Riphean Skillogalee Formation of South Australia, formed filament-like cell arrangements comparable to those found in the modern genus *Pleurocapsa*. Possible *Myxosarcina*-like colonies were illustrated from cherts of the Upper Riphean Boorthanna beds of South Australia by Schopf and Fairchild (1973). Finally, Hofmann (1976) has reported a doubtfully pleurocapsalean colony from the 1900 Ma old Belcher Supergroup, Canada. It is interesting that the three formally described pleurocapsalean microfossil genera—*Bavinella*, *Palaeopleurocapsa*, and *Scissilisphaera*—all compare closely with modern taxa, illustrating both the diversity and the modern nature of the late Precambrian Pleurocapsales.

Class HORMOGONEAE Thuret, 1875
Order OSCILLATORIALES Elenkin, 1949
Family OSCILLATORIACEAE (S. F. Gray) Dumortier ex Kirchner, 1898
Genus EOMYCETOPSIS (Schopf) Knoll and Golubic, 1979

Type species. Eomycetopsis robusta (Schopf) Knoll and Golubic, 1979.

Eomycetopsis robusta (Schopf) Knoll and Golubic

Plate 57, figs. 1–4, 8

Description. In the Ryssö Formation, *Eomycetopsis robusta* occurs as a principal mat builder in flat laminated stromatolites, as an associate mat builder with *Siphonophycus kestron*, in oncolites, and as scattered and often fragmented individuals in non-stromatolitic cherts. All Ryssö *E. robusta* sheaths are similar morphologically (cross-sectional diameter range = 2·0–4·0 μm; $\bar{x} = 2{\cdot}6$ μm; $N = 120$), but it is not clear that all specimens belong to a single cyanobacterial species. As has been discussed previously (e.g. Knoll 1982*a*), a number of modern blue-green species belonging to several genera produce sheaths comparable to *Eomycetopsis*.

Genus SIPHONOPHYCUS Schopf, 1968

Type species. Siphonophycus kestron Schopf, 1968.

Siphonophycus kestron Schopf, 1968

Plate 58, figs. 4–6

Discussion. Siphonophycus kestron was first described from the Upper Riphean Bitter Springs Formation, Australia (Schopf 1968), where populations occur as auxiliary mat builders in association with *Tenuofilum septatum*. *Siphonophycus* sheaths have subsequently been reported from numerous other Proterozoic formations and divided into several species based on size. Members of the Ryssö mat-building *Siphonophycus* populations are slightly larger than those of the original Bitter Springs population (cross-sectional diameter range = 9–18 μm; $\bar{x} = 14{\cdot}3$ μm; $N = 30$), but are referred to the type species *S. kestron*. *S. kestron*, like *E. robusta*, is a sheath form species that may have been formed by more than one cyanobacterial species.

Genus TENUOFILUM Schopf, 1968

Type species. Tenuofilum septatum, Schopf, 1968.

Tenuofilum septatum Schopf, 1968

Plate 57, fig. 2

Discussion. Specimens of *Tenuofilum septatum* from the Ryssö Formation are indistinguishable from those of the Bitter Springs type population (cross-sectional diameter range = 0·5–1·5 μm; $\bar{x} = 1{\cdot}0$ μm;

$N = 50$) and like their Australian counterparts, they are interpreted as the sheaths of mat-building cyanobacteria. *Tenuofilum* occurrences in the Bitter Springs and Draken formations are discussed in detail by Knoll (1981, 1982*a*).

Class HORMOGONEAE Thuret, 1875
ORDER UNKNOWN
Multilamellated Sheath

Plate 57, fig. 6

Description. Filamentous micro-organism, 250 μm long and 39 μm in cross-sectional diameter. Multilaminate construction, with each layer resembling a funnel in which a narrow internal cylinder (20 μm diameter) expands outward to form the filament exterior, the whole resembling a series of stacked funnels.

Discussion. Among previously described microfossils, *Salome svalbardensis* Knoll (1982*a*), a multi-sheathed oscillatorian blue-green from the Upper Riphean Draken Conglomerate of Ny Friesland, Spitsbergen, most closely resembles this Ryssö fossil. The Ryssö individual falls within the size range of *S. svalbardensis*, but its lack of a well-defined inner sheath and a preserved cellular trichome precludes more than informal comparison with the Ny Friesland remains. In its general organization, the Ryssö sheath is also comparable to lamellated cylindrical structures from the Skillogalee Formation of Australia illustrated by Schopf (1977). The Skillogalee fossils, informally termed 'Polybessurus' by Schopf, resemble the Ryssö sheath in their 'funnel in funnel' structure, but differ in their much larger diameter (100 μm) and their arrangement as closely packed, vertical tubes in the Skillogalee cherts.

A number of modern filamentous cyanobacteria form divergent multiple sheaths, including members of the genera *Scytonema*, *Petalonema*, *Tolypothrix*, and *Lyngbya* (Golubic 1976*a*, *b*; Golubic and Marčenko 1965). Three of these genera belong to the Scytonemataceae, but *Lyngbya* is a member of the Oscillatoriaceae. Thus, while it is likely that the Ryssö multilamellate sheath represents a filamentous blue-green, it is not possible to draw further taxonomic conclusions.

Kingdom PROTISTA
PHYLUM UNKNOWN
Vase-Shaped Microfossils

Plate 61

1977 Chitinozoans, Bloeser *et al.*, pp. 676–679, fig. 2.
1978 Possibly protozoan microfossils, Fairchild *et al.*, pp. 75–78, pl. 1, figs. 7–9.
1979 'Chitinozoan-like' microfossils, Vidal, pp. 24–25, pl. 6.
1980 Chitinozoan-like microfossils, Binda and Bokhari, pp. 70–71, fig. 1.
1980 Vase-shaped microfossils, Knoll and Vidal, pp. 207–211, fig. 1.
1981 Vase-shaped microfossils, Knoll, pp. 46–47, fig. 2.32.

Description. Flask- or vase-shaped vesicles, expanding apically from a rounded base and then tapering gradually toward the apex. Vesicle open at apex; apical opening may appear as a simple truncation of the body or may be bordered by a distinct collar region of varying length. Length = 34–206 μm ($\bar{x} = 106$ μm, $s_x = 38$ μm, $N = 920$); maximum cross-sectional diameter = 16–119 μm ($\bar{y} = 50{\cdot}5$ μm, $s_y = 16$ μm, $N = 920$); see Table 2. Vesicle walls organic, thick, brittle, psilate when well preserved to pitted when corroded, and rarely collapsed during sediment compaction. Specimens commonly preserved as casts.

Discussion. This taxon is discussed in detail in the body of this paper.

MICRO-ORGANISMS INCERTAE SEDIS
Genus GLENOBOTRYDION, Schopf, 1968

Type species. Glenobotrydion aenigmatis, Schopf, 1968.

Glenobotrydion aenigmatis, Schopf, 1968

Plate 57, fig. 9

Description. Spheroidal vesicles, 7 to 12 μm diameter ($\bar{x} = 9{\cdot}2$ μm, $s_x = 1{\cdot}1$ μm, $N = 70$); walls smooth to finely granular; cells generally contain a small internal body of organic matter. Cells occasionally occur as solitary individuals, but more often occur in irregular aggregates of a few to more than 100 cells. In aggregates, walls often distorted by mutual appression of adjacent cells.

Discussion. The characteristic feature of *Glenobotrydion* cells is the presence of a small, dense, organic granule within the vesicle walls. No matter how one interprets this 'spot'—as coalesced cytoplasm, starch grains, or a partially decomposed organelle—the question of its taxonomic usefulness is open to debate. In the Bitter Springs Formation, *G. aenigmatis* populations are indistinguishable from many of those assigned to *Myxococcoides minor* (small spheroids *without* internal 'spots') in terms of size frequency distribution, wall structure, patterns of aggregation, or paleoecological distribution (Knoll 1981).

This strongly suggests that many of the specimens segregated as *G. aenigmatis* and *M. minor* belonged to a single biological entity (Hofmann 1976) and that the presence or absence of an internal 'spot' is at least in part a matter of post-mortem cellular degradation. *G. aenigmatis* is here listed as a distinct form species, but it should be borne in mind both that these populations may be closely related to some of the populations assigned to *Myxococcoides* and that *several* morphologically simple algal species may have converged taphonomically on the *Glenobotrydion* form.

Genus MYXOCOCCOIDES Schopf, 1968

Type species. Myxococcoides minor Schopf, 1968.

Myxococcoides spp.

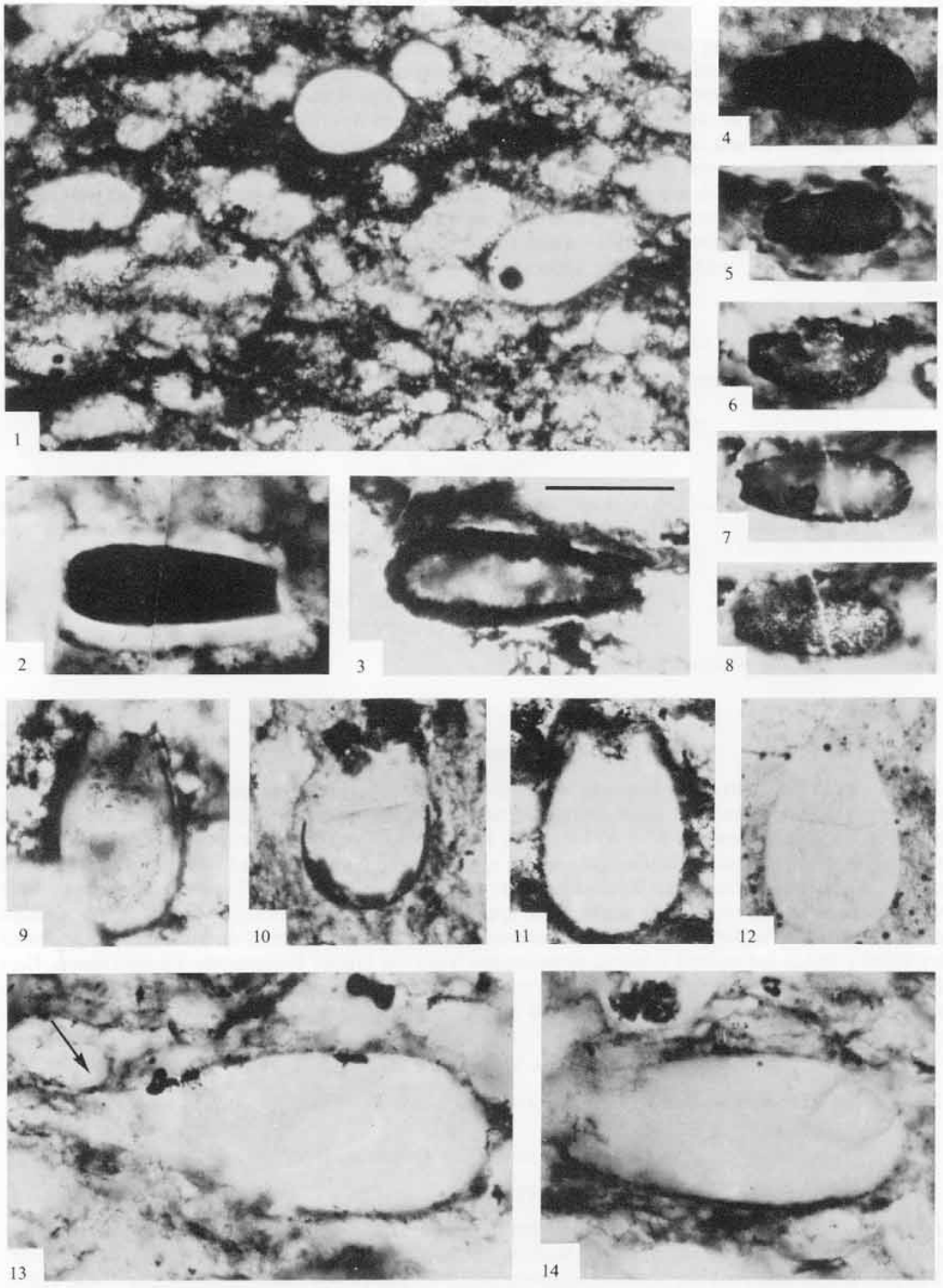
Plate 57, figs. 7, 8, 10; Plate 60, fig. 14

Discussion. Schopf (1968) proposed the genus *Myxococcoides* for the description of certain small spheroidal unicells commonly found in stromatolitic cherts of the Bitter Springs Formation, Australia. The Bitter Springs populations often occurred in colonial aggregates embedded in an amorphous mucilaginous matrix. Species were differentiated on the basis of size frequency distribution, wall characters, and the nature of cell clusters. Over the past decade, the concept of *Myxococcoides* has been enlarged to include a wide variety of small to intermediate size spheroidal vesicles found as solitary individuals or in dense aggregations, and embedded in amorphous organic matter or without extracellular mucilage (Horodyski and Donaldson 1980).

EXPLANATION OF PLATE 61

For each figure, thin section number, stage co-ordinates (where 'x' on slide K2023-1F = 1·9 × 120·2), and Harvard University Paleobotanical Collection number are given. Bar in Fig. 3 = 100 μm for Fig. 1, and = 70 μm for Figs. 2–14.

Figs. 1–14. Vase-shaped microfossils. 1, low magnification view showing numerous casts in organic rich carbonate, K1929–1A, 23 × 99·1. 2, siliceous casts with opaque inner body, K2082–1A, 16·8 × 116·1, H.U. No. 60662. 3–8, organic walled specimens. 3, K1924–3A, 5·3 × 125·8, H.U. No. 60663. 4, K2082–2A, 6·6 × 100·2, H.U. No. 60664. 5, K1929–1A, 9·4 × 115·5, H.U. No. 60665. 6, K1929–1A, 18·5 × 112·1, H.U. No. 60666. 7, K1929–1A, 17·6 × 117·9. 8, same specimen as Fig. 7 in a different focal plane. 9–14, casts in bituminous chert. 9, K2082–1A, 7·5 × 98·3, H.U. No. 60667. 10, note partial preservation of organic wall, K1929–1A, 19 × 104, H.U. No. 60668. 11, K1929–1A, 22 × 107·4, H.U. No. 60660. 12, K2082–2A, 7·5 × 96, H.U. No. 60670. 13, arrow points to extended apical collar on cast, K1929–1A, 18·9 × 99·3, H.U. No. 60671. 14, K1929–1A, 20·3 × 101, H.U. No. 60672.



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Microfossils belonging to the genus *Myxococcoides* are common in both the stromatolitic and planktonic assemblages of the Ryssö Formation. Individual colonies fit the diagnoses for a number of previously described species, including *M. minor* Schopf (for Ryssö populations, range = 6–14 μm, $\bar{x} = 9{\cdot}7$ μm, $N = 140$), *M. inornata* Schopf (range = 15–18 μm, $\bar{x} = 17$ μm, $N = 11$), *M. cantabrigiensis* Knoll (range = 9–18 μm, $\bar{x} = 14{\cdot}3$ μm, $N = 185$), and *Myxococcoides* sp. C of Knoll, 1983 (scattered individuals in the size range 20–30 μm). Also occurring in these assemblages, however, are numerous solitary individuals which are difficult to place into any single species with certainty, as well as cell clusters and colonies that combine features of several previously described species or 'fall into the cracks' between two species. For this reason, Ryssö myxococcoids are lumped under the designation *Myxococcoides* spp., with the clear understanding that the populations are biologically heterogeneous.

Genus PHANEROSHAEROPS Schopf and Blacic, 1971

Type species. Phaneroshaerops capitans Schopf and Blacic, 1971.

Phaneroshaerops capitans Schopf and Blacic, 1971

Plate 60, fig. 7

Description. Large (30–90 μm), spheroidal vesicle; wall psilate to finely granular, thin, but brittle. Cells occur singly, not in colonies. No apparent extracellular mucilage. Three specimens in the Ryssö Formation have diameters of 43, 46, and 57 μm.

Group ACRITARCHA Evitt, 1963
Genus CHUARIA Walcott, 1899

Type species. Chuaria circularis Walcott, 1899.

Chuaria circularis Walcott, 1899

Plate 60, fig. 9

Discussion. Chuaria circularis was originally described from compressed specimens on rock surfaces, and compressions remain the most commonly reported form of preservation for this organism (Ford and Breed 1973; Hofmann 1977). Vidal (1976, 1981*a*) has extensively discussed macerated *Chuaria* specimens, and his criteria for recognition are applicable to permineralized specimens as well. Like other *Chuaria* populations, the Ryssö fossils are large ($\bar{x} = 282$ μm, $N = 27$) spheroidal vesicles with very thick, psilate to chagrinate walls. Most specimens fall in the size range 180–350 μm, although rare specimens up to 800 μm have been observed. A similar size frequency distribution was reported by Vidal (1981*a*) for several *Chuaria* populations from the Upper Proterozoic Vadsø Group, East Finnmark. The phylogenetic relationships of *C. circularis* are not known; however, its eukaryotic status is indisputable and its relationship to the algae (green algae?) is probable.

Genus KILDINELLA Shepeleva and Timofeev, 1963

Type species. Kildinella hyperboreica Timofeev, 1966.

Kildinella hyperboreica Timofeev, 1966

Plate 60, fig. 12

Discussion. Kildinella hyperboreica is a common element in most Late Riphean acritarch assemblages. It is characterized by its robust, psilate walls which are invariably folded in a characteristic fashion. The size range observed for Ryssö specimens is 22–70 μm ($\bar{x} = 43$ μm; $N = 10$). See Vidal (1976, 1981*a*) for a complete list of *K. hyperboreica* occurrences.

Kildinella sinica Timofeev, 1966

Plate 60, fig. 13

Discussion. Kildinella sinica is distinguished from *K. hyperboreica* by its often somewhat granular vesicle surface. Eighteen Ryssö specimens range in diameter from 23 μm to 76 μm ($\bar{x} = 40$ μm). The two *Kildinella* species occur together in the open coastal Ryssö rocks, as they do in many Upper Riphean formations.

Genus PTEROSPERMOPSIMORPHA Timofeev (1962) 1963

Type species. Pterospermopsimorpha pileiformis Timofeev, 1963.

Pterospermopsimorpha sp.

Plate 58, figs. 7, 8

Description. Spheroidal vesicle with two distinct and unconnected walls. Outer wall thick, amber-coloured, well-defined, psilate with numerous fine cracks and wrinkles, 150 to 172 μm in diameter. Inner wall thinner, psilate, 133 to 140 μm in diameter. Large (up to 118 μm), grainy, opaque internal body may be present.

Discussion. Species of *Pterospermopsimorpha* are distinguished by their distinct inner and outer vesicles. Among previously described species, *P. mogilevica* Timofeev (see Vidal 1981*a*) comes closest in general morphology, although the Ryssö specimens are much larger and contain an additional wall layer. The outer wall of the Ryssö species is virtually identical with acritarchs described herein as Unnamed Form B of Knoll (1983), and it may be that the two fossils are morphological or preservational variants of a single biological species. Unnamed Form B is common in the Ryssö assemblage that contains *Pterospermopsimorpha* sp. Set against this is the fact that in the underlying Hunnberg Formation (Knoll 1983), Unnamed Form B is quite common but *Pterospermopsimorpha* sp. has not been observed.

Genus STICTOSPHAERIDIUM Timofeev (1962) 1963
cf. *Stictosphaeridium* sp. (*sensu* Vidal 1976)

Plate 60, fig. 10

Description. Single walled, spheroidal vesicle 43 to 130 μm in diameter ($\bar{x} = 78$ μm, $s_x = 28$ μm, $N = 10$); walls light and very thin, ornamented by a fine irregular meshwork.

Discussion. Specimens assignable to cf. *Stictosphaeridium* sp. occur commonly in upper Proterozoic clastic rocks. As Vidal (1976) has noted, many of these fossils may be extracellular envelopes that once encased other algae and/or cyanobacterial colonies.

Genus TRACHYHYSTRICHOSPHAERA Timofeev and Hermann, 1976

Type species. Trachyhystrichosphaera aimika Hermann, 1976.

Trachyhystrichosphaera vidalii Knoll, 1983

Plate 58, figs. 9, 10

Description. Spheroidal vesicle, double walled; inner wall, robust, finely granular, folded when vesicle is collapsed, 155 to 535 μm in maximum diameter (four Ryssö specimens have diameters of 210 μm, 250 μm, 250 μm, and 255 μm); inner wall bears numerous hollow processes that regularly, but not densely, extend outward from inner wall; processes cylindrical, untapered or tapering gradually toward apex, without internal septations or constrictions, 3 to 8 μm wide and up to 22 μm long; processes support a thinner, psilate to finely granular outer wall or membrane. See Knoll (1983) for a discussion of this distinctive microfossil.

Genus TRACHYSPHAERIDIUM Timofeev (1966) 1969

Type species. Trachysphaeridium attenuatum Timofeev, 1959.

Trachysphaeridium laufeldi Vidal, 1976

Plate 60, figs. 1, 2

Description. Single walled, spheroidal vesicle, 40–72 μm in diameter (42–50 μm reported by Vidal 1976). A single specimen from the Ryssö Formation is 72 μm in diameter; vesicle surface densely covered by short, conical spines.

Trachysphaeridium levis (Lopukhin) Vidal, 1974

Plate 60, fig. 3

Description. Vidal (1974) described *Trachysphaeridium levis* as a single walled, spherical vesical, 10–100 μm in diameter (polymodal size frequency distribution, with modes in the intervals 30–70 and 80–100 μm); the vesicle was described as 'spongy, having a densely granulate ornamentation'. Two Ryssö specimens having diameters of 56 μm and 92 μm fit this description.

Trachysphaeridium sp. A of Knoll, 1983

Plate 60, figs. 4, 5

Description. Single walled, spheroidal vesicle, 42–65 μm in diameter ($\bar{x} = 54$ μm, $N = 6$, compare $\bar{x} = 59$ μm, $N = 16$ for a population in the Hunnberg Formation, Svalbard). Vesicle wall robust and well defined, finely granular; wall may retain spheroidal outline or be slightly tuberose. Specimens occur as solitary individuals.

Trachysphaeridium sp. B of Knoll, 1983

Plate 61, fig. 6

Description. Single walled spheroidal vesicle, 75–210 μm in diameter ($\bar{x} = 145$ μm, $s_x = 63$ μm, $N = 26$; compare to 80–200 μm, $\bar{x} = 156$ μm, $N = 18$ for the Hunnberg Formation), with a robust, amber-coloured wall. Wall characteristically psilate, brittle, and finely wrinkled and cracked. Vesicles occur as solitary individuals; no evidence of external mucilage, excytment structures, or cell division.

Discussion. This common Ryssö fossil is also abundant in the underlying Hunnberg Formation. Its possible taxonomic relationships are discussed by Knoll (1983).

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