

MICROPALAEONTOLOGY OF THE LATE PROTEROZOIC VETERANEN GROUP, SPITSBERGEN

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ABSTRACT. Shales and siltstones of the Upper Proterozoic Veteranen Group, Spitsbergen, contain abundant and well-preserved microfossil populations. Plankton assemblages from open coastal deposits include a number of taxa previously known from Upper Riphean sequences in Scandinavia, the Soviet Union, and North America. Microfossils from more restricted coastal environments are dominated by small coccoidal unicells and filamentous sheaths of probable cyanobacteria, with locally abundant rod-shaped fossils of blue-greens or other bacteria. Biostratigraphic considerations indicate that the Veteranen Group, which comprises the earliest unmetamorphosed sedimentary sequence in Spitsbergen, was deposited between 800 and 900 Ma ago; this nearly 4000 m sequence was deposited within a relatively brief interval during the early stages of subsidence in a basin that eventually opened to become Iapetus. The preservation of delicate prokaryotic microfossils in lagoonal black shales contributes to the resolution of systematic problems arising from the development of two distinct research traditions in Precambrian palaeontology.

DURING the past decade, it has become clear that the Late Proterozoic earth supported a taxonomically diverse and ecologically heterogeneous biota of micro-organisms, as well as, in its later stages at least, early representatives of the multicellular (tissue grade) kingdoms. This diversity is well documented in the sedimentary successions of the Svalbard archipelago, where beautifully preserved microfossil assemblages are found at numerous stratigraphic horizons throughout a 7000 m sequence that spans some 400 million years of Late Proterozoic to Early Cambrian time. Both planktic and microbenthic fossils are found in rocks representing a variety of sedimentary environments (Knoll 1982*a, b*, 1984; Knoll and Calder 1983), and this record is augmented by stromatolites and microphytolites which are widely distributed in carbonate portions of the succession (Golovanov 1967; Golovanov and Raaben 1967; Raaben and Zabrodin 1972; Swett and Knoll 1985). During the 1981 and 1982 field seasons we conducted detailed stratigraphic and sedimentological studies of several localities in north-eastern Spitsbergen (text-figs. 1, 2). In this paper we describe the distribution of microfossil assemblages preserved in the lowermost unmetamorphosed units of the Spitsbergen Proterozoic succession, the Veteranen Group.

GEOLOGICAL SETTING

The late Precambrian and Palaeozoic geological history of the North Atlantic region centres on the inception, development, and ultimate destruction of the Iapetus Ocean. The closing of this ocean basin is documented by the igneous intrusions, metamorphism, sedimentary patterns, and structural features associated with the Caledonian orogeny. Its early development is reflected in the late Proterozoic sedimentary sequences of the region. In north-eastern Spitsbergen, some 6600 m of unmetamorphosed sedimentary rocks lie beneath the lowermost Cambrian strata of the island; this succession is in turn underlain by a comparably thick sequence of metasedimentary and metavolcanic rocks (Harland 1959; Harland and Wright 1979). The thickness and almost uniformly shallow marine nature of the unmetamorphosed sequence indicates that it was deposited near the margin of a slowly subsiding trough, genetically linked to, but perhaps antedating, the opening of a substantial ocean basin. Fairchild and Hambrey (1985) interpret palaeocurrent data from glaciogenic rocks near



TEXT-FIG. 1. Map of Svalbard showing the location of the study area in northern Spitsbergen. The shaded study area is enlarged in text-fig. 2.

the top of the Proterozoic section as indicating glacial flow from the south-west, a finding that supports the concept of a late Vendian opening for the ocean basin (Harland, pers. comm. 1984). Except for a few hundred metres of well-laminated graded siltstone and shale couplets that may reflect fault control of local deposition, and two thin lava flows at the same general stratigraphic level (Wilson 1958), there is little to suggest an early rifting stage of basin evolution. Evidence for such an event may lie in the metamorphic rocks at the base of the sequence.

In north-eastern Spitsbergen the unmetamorphosed Proterozoic section comprises three easily contrasted groups: the immediately sub-Cambrian Polarisbreen Group, approximately 800–900 m of

TEXT-FIG. 2. Enlargement of shaded area in text-fig. 1. Stippled areas represent outcrop; white areas indicate glacial ice, except for Lomfjorden and the Hinslopestretet (upper right edge of figure) which are water covered. Detailed examinations of the Veteranen Group were undertaken at Faksevågen (A) and Cavendishryggen (B). The upper part of the group was also studied in the Polarisbreen area (C).

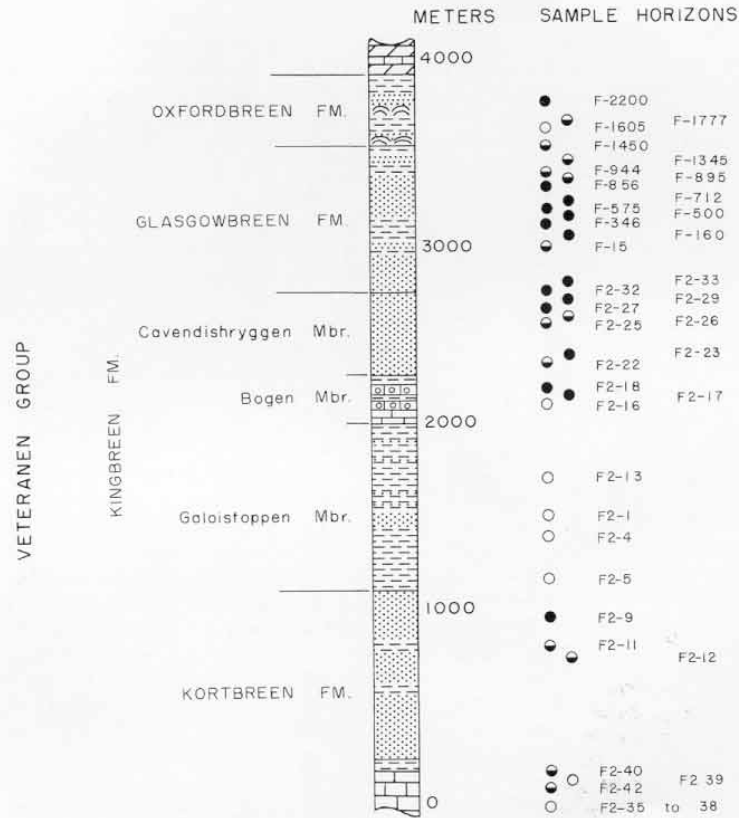


predominantly fine-grained siliciclastic rocks with extensive tillites (Wilson and Harland 1964; Hambrey 1982); the underlying Akademikerbreen Group, up to 2000 m thick and consisting largely of carbonates (Wilson 1961); and, at the base of the succession, the sequence of greatest interest here—the Veteranen Group (Wilson 1958).

The Veteranen Group has been divided into four formations (in ascending stratigraphic order): Kortbreen, Kingbreen, Glasgowbreen, and Oxfordbreen (Harland *et al.* 1966). Basing our field studies on the thorough stratigraphic description of this group by Wilson (1958), we measured sections along the eastern wall of Veteranen Glacier at Cavendishryggen and in the Faksevågen area west of Lomfjorden (text-figs. 2, 3). The oldest Veteranen strata located are thinly laminated and occasionally cross-laminated calcisiltites of the lower Kortbreen Formation, exposed in the core of an anticline at Faksevågen. These limestones are tectonically deformed, but Wilson's (1958) thickness estimate of 300 m agrees well with our observations. Tan-weathering dolomitic units are common in this section, as are thin intercalations of quartzarenite and dark shales. The limestones become increasingly shaly in their uppermost 20 m and are overlain abruptly, but with apparent conformity, by the thick quartzarenites of the upper Kortbreen Formation. These sandstones are well-rounded, fine to medium grained quartzarenites, variously white or tinted pink, buff, maroon, or light green. Ripple marks with wavelengths of a few to 6 cm abound, as do cross-beds with set thicknesses of up to about 15 cm. Mudcracks occur intermittently throughout the unit, and

fossiliferous black shales also occur as thin interbeds. Wilson (1958) characterized these sandstones as 'typically shallow water deposits'. We concur and further suggest that they accumulated in shallow, tidally influenced environments marginal to the exposed continent.

Conformably overlying the Kortbreen quartzarenites is the Kingbreen Formation. This formation is 1200 m thick at Faksevågen and slightly thicker in the wall of Cavendishryggen; it has been divided into three members (Harland *et al.* 1966). At Cavendishryggen the basal Galoistoppen Member contains a thick sequence of millimetre-laminated dark siltstones and shales. As noted above the laminae in this unit comprise distinct graded couplets that are quite similar to beds from the somewhat younger Ocoee Supergroup of Tennessee. Keller (1979) has interpreted the Ocoee couplets as indications of the waning stages of fault influenced sedimentation, prior to the transition from a rift



TEXT-FIG. 3. Stratigraphic column of the Veteranen Group at Faksevågen, based on Wilson (1958) and our own measurements. Palynological sample horizons (with sample numbers) are indicated by circles. Filled circles indicate well-preserved microfossil assemblages; half-filled circles indicate poorly preserved assemblages; samples marked by open circles are barren. In the column, dashed lines indicate shales and siltstones; dotted lines signify sandstones; and rectangles and rhombic patterns indicate limestones and dolostones, respectively. Circles indicate ooids and concave downward arcs signify stromatolitic carbonates.

basin setting to a passive margin continental shelf. Bedding surfaces of the lower Galoistoppen sequence contain textural lineations that indicate unidirectional flow.

In the upper portion of the Galoistoppen Member, quartzose sandstone interbeds become increasingly common, and the dominant character of the sequence shifts to quartzarenites and interbedded black shales, with conspicuous calcareous units that contain low angle cross-beds, shallow channels, and intraformational conglomerates. The section at Cavendishryggen is more conspicuously calcareous than the correlative beds at Faksevågen, where variegated and often mudcracked shales and dolomitic shales are the dominant lithologies.

The overlying Bogen Limestone Member contains frequent oolite and microphytolite-bearing limestones, as well as cross-bedded (including herringbone cross-beds) calcarenites and intercalated siliciclastic units. The uppermost Cavendishryggen Quartzite Member contains massive, cross-bedded quartzarenites with thinner interbedded units of sandy and silty flagstones and shale.

The Kingbreen Formation is conformably overlain by the Glasgowbreen Formation, a 900 m unit that bears many similarities to the underlying Cavendishryggen sequence. This formation contains massive thicknesses of pink, green, and buff quartzarenites. Like those near the base of the Veteranen Group, the Glasgowbreen sandstones are generally compositionally mature, well rounded quartzarenites, marked by conspicuous ripple marks, interference ripples, megaripples, and cross-bedding (including herringbone cross-beds). Interbedded carbonaceous shales are common in some horizons within the formation. Wilson (1958) referred to these carbonaceous units as greywackes, but it is clear that they are discrete shales and sandy shales environmentally related to the tidal sandstones with which they are intercalated. The succeeding Oxfordbreen Formation contains proportionally fewer sandstones and more shales, and is distinguishable by the presence of carbonate interbeds (including oolitic and stromatolitic units). The stromatolites are low profile, laterally linked hemispheres up to 1 m high and 1.7 m across. Maximum synoptic relief developed during deposition was about half this height. Red shales are common in the upper part of the formation; these are generally flat-laminated, but can contain ripples, cross-laminations (in intercalated sandstones), mudcracks, and ripped-up mud flake clasts. These sedimentary features are particularly conspicuous at a locality along the north face of Polarisbreen Glacier (text-fig. 2). The top of the formation is fixed at the base of the massive dolomites and limestones that characterize the Akademikerbreen Group.

It can be seen from the foregoing summary that the rocks of the Veteranen Group document a variety of sedimentary environments, but that variation occurs within fairly strict limits. Almost the entire sequence records shallow marine depositional environments, ranging from below wave base to tidally influenced conditions and quiet lagoons marked by occasional subaerial exposure and storms.

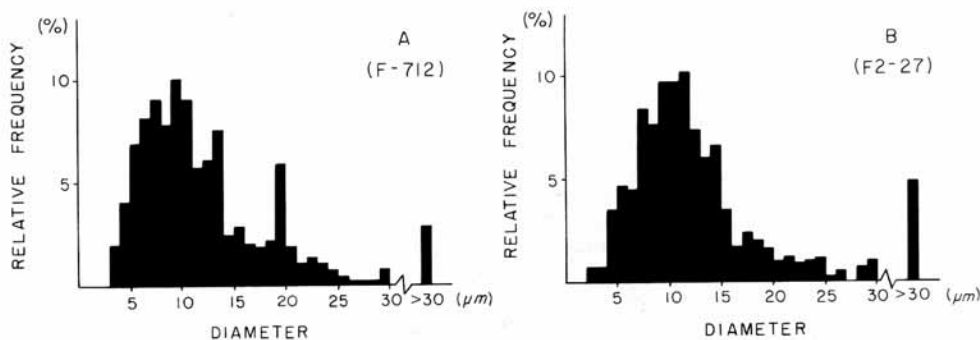
Available radiometric dates from Precambrian rocks of north-eastern Spitsbergen reflect Caledonian overprints of isotopic systems. On the basis of stromatolite and microphytolite distributions, Milstein and Golovanov (1979) have suggested that the Veteranen Group is late Riphean (950–670 Ma) in age. Acritarchs in this group, coupled with those in the correlative Franklinsundet and Celsiusberget groups of Nordaustlandet (Knoll 1982a) and those found in overlying units, indicate that the group as a whole probably exceeds 800 Ma in age, but is unlikely to be much older than 900 Ma (see discussion below).

MICROFOSSIL ASSEMBLAGES

Extensive collections of Veteranen Group samples were made from both the Cavendishryggen and Faksevågen sections. The Cavendishryggen area is characterized by more severe diagenetic alteration, approaching chlorite grade metamorphism. Strata are more highly indurated; they commonly develop a platy aspect, and a weak slaty cleavage is developed in the lower units. As a consequence the organic matter in Cavendishryggen rocks is black and fossil preservation is poor. In contrast, twenty-eight of the thirty-six samples taken from an approximately 3500 m section at Faksevågen contained identifiable fossils. Preservation at this locality is poorest in the youngest formation examined, the Oxfordbreen Formation, despite the abundance of reddish-brown organic matter in dark green to black shales. Preservation is much better in the Glasgowbreen and Kingbreen

formations, where microfossils are often abundant and relatively diverse. The colour of microfossil walls changes systematically as one descends the local stratigraphic column, but identifiable microfossils can still be seen in the dark grey to black organic residues isolated from grey shales within the carbonates at the base of the Kortbreen Formation.

Small ($< 25 \mu\text{m}$) coccoidal unicells are the most abundant fossils in every sample examined (Pl. 51, figs. 8, 11–18). Variation in wall thickness, wall ornamentation, and clustering patterns suggests that these unicell populations are taxonomically heterogeneous, an inference that can also be drawn from the size frequency distributions of sample populations (text-fig. 4A, B). Many taxonomic names have been applied to previously described fossils of similar aspect (e.g. Timofeev 1969) but, because diagnoses have often been based on characters likely to be diagenetic in origin and because published illustrations are often difficult to interpret, it would be hazardous to apply names without first making a careful study of the type materials. In so far as many of the observable differences between these small unicells may be related to intraspecific and/or diagenetically introduced variation, the formal recognition of each discernible morphotype would lead to an overestimate of species diversity. On the other hand the simple morphology of these fossils and the inevitable loss of taxonomically important characters (such as pigment complements) during post-mortem degradation must lead to an underestimate of original species diversity (Knoll and Golubic 1979). We have for these reasons not attempted to quantify the preserved diversity within this size class, preferring instead to treat these fossils as a unit, while acknowledging their probable biological heterogeneity.



TEXT-FIG. 4. Size frequency distribution of small coccoidal unicells from samples F-712, Glasgowbreen Formation (A), and F2-27, Kingbreen Formation (B). For both A and B, $N = 500$.

Among larger spheroidal microfossils, *Leiosphaeridia asperata* (Naumova) Lindgren, 1982 (= *Kildinella hyperboreica* Lindgren, 1982) is easily the most abundant acritarch (Pl. 52, figs. 4–8, 10, 11). It is found in all samples analysed and is common in most. *L. asperata* is morphologically simple, consisting of flexible, smooth-walled vesicles approximately 15–80 μm in diameter (usually 25–45 μm) that apparently dehisced by means of a median split mechanism. It is likely that these fossils are the remains of algal cysts (e.g. Lindgren 1981; Vidal and Knoll 1983) but, as Lindgren (1981, 1982) has pointed out, a variety of taxonomically and functionally different algal remains could be lumped within this form species.

Other common microfossils include *Kildinosphaera chagrinata* Vidal in Vidal and Siedlecka, 1983 (= in part *Kildinella sinica*, according to Vidal and Siedlecka 1983), *Synsphaeridium* sp., and cf. *Stictosphaeridium* spp. (*sensu* Vidal 1976). More complex acritarchs are rare; these include *Kildinosphaera granulata* Vidal in Vidal and Siedlecka, 1983, *Tasmanites riphejicus* Jankauskas, 1978, *Satka colonialica* Jankauskas, 1979a, *Bavlinella faveolata* (Schepeleva) Vidal, 1976, *Favoso-*

sphaeridium sp., and fragmentary remains of very large acritarchs, probably *Chuarina circularis* Walcott, 1899 (Pl. 51, figs. 1, 2). Tubular microfossils, the probable extracellular sheaths of filamentous cyanobacteria, occur in many samples (Pl. 51, fig. 19; Pl. 52, figs. 1-3, 12), and small rod-shaped remains are common in sample F-712 (Pl. 51, figs. 5, 6, 9, 10). Within any one sample, morphological diversity is low (text-fig. 5), a characteristic of late Riphean acritarch assemblages previously noted by Vidal and Siedlecka (1983).

TAXON	SAMPLE HORIZON		KO		KI			GL				OX	
	F-2-9	F-2-40	F-2-17	F-2-23	F-2-27	F-2-32	F-3-46	F-5-00	F-5-73	F-7-12	F-8-56	F-1-346	F-2-200
<i>Bavlinella faveolata</i> (Schepeleva) Vidal					R						R		
<i>Eosynechococcus</i> sp.				R	R			R		C			
<i>Tasmanites rifejicus</i> Jankauskas						R		R	R		R		
? <i>Chuarina circularis</i> Walcott	R		R					R	R	R	R		R
<i>Favosphaeridium</i> sp.										R			
<i>Kildinosphaera chagrinata</i> Vidal	R			R		R	C	R	R		C		R
<i>Kildinosphaera granulata</i> Vidal								R	R		C		R
<i>Leiosphaeridia asperata</i> (Naumova) Lindgren	C	C	R	C	R	R	C	C	C	R	C	C	C
<i>Satka colonialica</i> Jankauskas								R	R	R	R		R
cf. <i>Stictosphaeridium</i> sp. (<i>sensu</i> Vidal)						C		C	C	R	C		
<i>Synsphaeridium</i> sp.			R			R	C	R	R	R	R	R	R
Small Unicells	C	C	A	A	A	C	A	A	A	A	A	A	C
Filaments	C	R	A	A	A	C	R	R	R	C	C	R	R
Number of taxa	4	4	4	6	7	5	7	11	11	7	11	4	8

TEXT-FIG. 5. Chart showing the distribution of microfossil taxa within selected samples of the Veteranen Group. Samples are arranged stratigraphically, with the oldest sample on the left. KO, Kortbreen Formation; KI, Kingbreen Formation; GL, Glasgowbreen Formation; OX, Oxfordbreen Formation. R, rare; C, common; A, abundant.

Despite the thickness of the Veteranen Group, there is no evidence for stratigraphically significant changes in assemblage composition within the sequence. This is not to say that all recovered assemblages are identical; certainly, they are not. Gray and Boucot (1975) have noted, however, that variation in assemblage composition can reflect taphonomic and/or palaeoecological, as well as stratigraphic differences. Relatively poor preservation through much of the Oxfordbreen Formation may mask evolutionary changes in the plankton biota: fossils in the overlying Akademikerbreen Group do differ in ways that are most likely a consequence of evolutionary turnover. On the other hand, one well-preserved assemblage from the Oxfordbreen Formation (sample F-2200) is indistinguishable from assemblages found in the lower formations of the group.

Much of the variation evident in the relative abundance of microfossil groups represented is thought to reflect palaeoenvironmental variation within the coastal marine sedimentary deposits. Filamentous sheaths provide a case in point. In several samples (e.g. F-2-27), filaments are conspicuously abundant, comprising some 40% or more of all preserved specimens. The filaments are long (often more than 100 μm in length) and not infrequently intertwined with one another. Large acritarchs (> 30 μm diameter) comprise only 3-5% of the assemblage, and biostratigraphically significant taxa are generally rare or absent. Filament rich assemblages are found in thin, black to greenish shale interbeds within predominantly cross-bedded and rippled quartz sandstones or oolitic and cross-bedded calcarenites. We interpret these assemblages as the remnants of very near-shore

coastal to lagoonal communities. The filaments are thought to represent autochthonous or nearly autochthonous, probably benthic, cyanobacterial populations.

At the other end of the spectrum are assemblages in which filaments occur only as rare, fragmented and probably allochthonous individuals. In these assemblages, large acritarchs are relatively common (10–15% of all individuals in sample populations from sample F-575) and diverse. Such assemblages tend to occur within thicker, green to black siltstone and shale units, with only minor sandstone intercalations. We interpret these biological and sedimentary assemblages as representing the most off-shore or 'normal marine' setting within the Veteranen Group. Most if not all of the spheroidal microfossils found in these assemblages are thought to have been planktic.

DISCUSSION

Biostratigraphy

The Veteranen biota contains several taxa that have long stratigraphic ranges and hence limited biostratigraphic utility. Among these fossils are: *Leiosphaeridia asperata*, cf. *Stictosphaeridium* sp., *Synsphaeridium* sp., and the small unicells, filaments, and rods. More useful are *Kildinosphaera granulata*, *Tasmanites riphejicus*, and *Satka colonialica* which to date are known only from Upper Riphean rocks. Along with co-occurring *L. asperata*, *K. chagrinata*, and probable *Chuar*, these fossils form an assemblage similar to previously described assemblages from Upper but not uppermost (Kudashian, possibly equivalent to Vidal's (1976) Lower Vendian) Riphean rocks elsewhere in the Northern Hemisphere.

Two forms, *Favosphaeridium* sp. and *Bavlinella faveolata*, are morphologically similar to taxa best known from uppermost Riphean to Cambrian rocks. The occurrence of *Bavlinella* is particularly interesting because this distinctive fossil has sometimes been considered an index fossil for Vendian rocks. Its actual range is now known to extend from the latest Riphean to the Cambrian, and this new population confirms earlier reports of its questionable occurrence in Upper Riphean rocks (see discussion in Vidal 1976). *Bavlinella* is often an abundant constituent of Vendian assemblages associated with glaciogenic rocks and has been interpreted as an opportunistic taxon by Knoll *et al.* (1981). Such an interpretation carries with it the prediction that *B. faveolata* should occur as a minor component of earlier and later microfloras, and this seems to be the case.

The apparent stratigraphic homogeneity of the Veteranen assemblages may reflect a slower rate of morphological evolution among early algae, a rapid rate of deposition for the Veteranen Group, or both. Comparable thicknesses of miogeosynclinal sediments are known to have accumulated during the approximately 70 million year long Cambrian Period along the eastern and western margins of North America (Bond *et al.* 1983; Cook and Bally 1975). The relatively rapid subsidence required for such accumulation is thought to be related to the cooling of the lithosphere following rifting (McKenzie 1978; Bond *et al.* 1983; Armin and Mayer 1983). It is also true, however, that our present understanding of late Riphean palaeontology is such that it is only possible to divide the period into a handful of assemblage zones, each the same order of length as the Cambrian (Vidal and Knoll 1983). This may reflect slow rates of morphological (but not necessarily physiological) evolution. Thus, the stratigraphic indivisibility of the Veteranen Group may well be a consequence of both rapid deposition and slow morphological change.

Absolute age estimates for the Veteranen assemblages must be inferred from radiometric dates assigned to comparable microbiotas from other areas. Biotas containing the distinctive elements that characterize the Veteranen Group are found in the Klubbnes and Andersby formations of the Vadsø Group, East Finnmark (Vidal 1981); the lower Båtsfjord Formation of the upper Barents Sea Group, also in East Finnmark (Vidal and Siedlecka 1983); the Chuar Group, Arizona (Vidal and Ford 1985); the Red Pine Shale of the Uinta Mountain Group, Utah (Vidal and Ford 1985); the 'type' Upper Riphean beds of the southern Urals (Jankauskas 1982); and the lower part of the Upper Visingsö Beds, Sweden (Vidal 1976; Vidal and Ford 1985).

With the exception of a K-Ar determination recalculated as approximately 640 Ma for dolerite dykes that cut the Barents Sea Group in northern Norway (Beckinsale *et al.* 1975), available radio-

metric dates on Upper Proterozoic sequences in Scandinavia are largely Rb-Sr whole rock analyses of shales (reviewed in Vidal and Knoll 1983). Klubbnes Formation shales have yielded dates of 807 ± 19 Ma (recalculated by Vidal from Sturt *et al.* 1975), while Visingsö occurrences are overlain by shales dated at 707 ± 37 Ma (Vidal 1981). Western North American assemblages antedate a structural disturbance bracketed at 820–770 Ma (reset K-Ar dates on basalts) and postdate an episode of basaltic extrusion dated at 1070 ± 70 Ma by Rb-Sr whole rock analyses (Elston and McKee 1982). Rb-Sr whole rock determinations of Red Pine Shale specimens yield an age of 950–925 Ma for that formation (Crittenden and Peterman 1975; Chaudhuri and Hanson 1980). K-Ar dates for Upper Riphean sedimentary rocks in the Urals suggest a depositional age of 850–940 Ma (Keller 1982).

Whole rock chronometric analyses of detrital sedimentary rocks have been the subject of much debate, as have many K-Ar determinations of presumably early diagenetic glauconites from Precambrian sediments. None the less, available radiometric data, coupled with corroborative tectonic and palaeomagnetic considerations (Elston, pers. comm. 1984) suggest that assemblages of the type found in the Veteranen Group very likely fall in the 800–900 Ma range. While it is clear that planktic microfossils are of demonstrated value in Proterozoic biostratigraphy (e.g. Vidal and Knoll 1983), it is also apparent that the full stratigraphic potential of early plankton will be realized only when better radiometric, palaeoecological, and biogeographic control is available.

Palaeoecology

The palaeoenvironmental variability of late Proterozoic microfossil assemblages has frequently been discussed in the literature (Vidal 1976, 1981; Knoll 1981, 1982*b*, 1984; Knoll and Calder 1983; Vidal and Knoll 1983). Recognition of palaeoecological patterns of distribution is important for both biological and geological reasons: biological because 'lateral' variation must be taken into account in any evolutionary interpretation of the fossil record (e.g. Strother *et al.* 1983); and geological in that Proterozoic fossils, like their Phanerozoic counterparts, are potentially valuable as indicators of sedimentary environment. In the Veteranen Group, both the diversity and the relative abundance of large ($> 30 \mu\text{m}$) acritarchs increase along a gradient from inshore, often lagoonal deposits to more open coastal siltstones and shales. As noted above, the abundance and preservational quality of filament populations decreases along the same gradient. (Environments are established on the basis of sedimentary structures, textures, and bedding sequences.) Similar distributions have been recognized in other Upper Proterozoic sequences, both carbonate and siliciclastic (reviewed by Vidal and Knoll 1983); the Veteranen observation serves to increase one's faith in the generality of the pattern.

Palaeoecological and biogeographic distributions are also relevant to biostratigraphic determinations. For example, *Trachysphaeridium laminaritum* Timofeev, 1966 is an important constituent of many late Riphean microfloras but has not been found in the Veteranen Group. Vidal and Ford (1985) have observed that in rocks of the Grand Canyon and elsewhere this species and *Kildinosphaera chagrinata* have mutually exclusive distributions. *K. chagrinata* is relatively common in the Veteranen Group, so perhaps some poorly defined environmental parameter excluded *T. laminaritum* from the Veteranen sea. A more problematic example concerns the distinctive microfossil *K. lophostriata* (Jankauskas) Vidal in Vidal and Siedlecka, 1983 which occurs in late Riphean assemblages from the Soviet Union, Scandinavia, and North America, but which has not been recognized in Veteranen assemblages. Does this absence indicate that *K. lophostriata* had not evolved at the time of Veteranen deposition, that it was extinct by the time the Svalbard shelf originated, or that *K. lophostriata* is missing for reasons of ecology, biogeography, or chance? We simply do not know, it being impossible to eliminate any one of these possible explanations on the basis of present evidence. Once again this underscores the need for further investigations of late Proterozoic micro-biotas conducted within a framework of strict stratigraphic and sedimentological control.

Systematics and palaeobiology

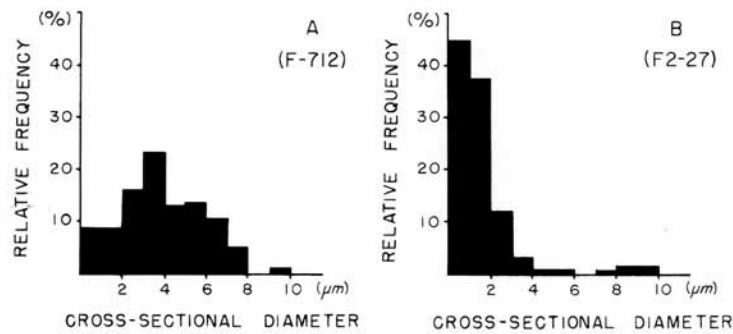
Proterozoic microfossils are generally studied by the petrographic examination of silicified carbonates or by the palynological maceration of siliciclastic rocks. In a critique of the systematic

problems created by this dichotomy of approach, Diver and Peat (1979) have suggested that many of the apparent differences between 'chert' and 'shale' biotas are illusory, the result of separate research schools with independently evolved taxonomic practices. Systematic traditions certainly pose a serious problem for comparative studies of Precambrian microbiotas, as do differences in preservation potential that may separate shales and silicified carbonates. On the other hand, some of the observed differences among assemblages are real and reflect the ecological partitioning of Proterozoic environments. Recognition of this aspect of the problem suggests a path toward the solution of the 'chert-shale' dilemma.

Most of the known biostratigraphically useful, open shelf acritarch assemblages come from carbonaceous siltstones and shales (e.g. Timofeev 1969; Vidal 1976); however, not all open coastal rocks are siliciclastic. Compacted and compressed acritarchs have been isolated from carbonaceous limestones and dolomites of the Upper Visingsö Beds of Sweden (Vidal 1976) and the Båtsfjord Formation of East Finnmark, Norway (Vidal and Siedlecka 1983); and open coastal carbonates from the uppermost Riphean Hunnberg and Ryssö formations of Nordaustlandet, Svalbard, contain microfossils preserved by early diagenetic silicification (Knoll 1984; Knoll and Calder 1983). The assemblages in these cherts are comparable to contemporaneous 'shale' biotas and demonstrate that, if present in silicified carbonates, large acritarchs such as *Trachysphaeridium*, *Kildinosphaera*, *Chuarina*, or *Trachyhystrichosphaera* species can be recognized and identified. Silicified carbonates from lagoonal and intertidal facies of the same formations do not contain abundant large acritarchs.

Several assemblages from lagoonal shales of the Kingbreen (samples F2-27, F2-29) and Glasgowbreen (F-712) formations of the Veteranen Group exemplify the converse distribution. Here, colonies of small spheroidal unicells, filaments, and rods—the stuff of most 'cherty' microbiotas—constitute the fossil populations. This demonstrates that early diagenetic silicification is not a prerequisite for the preservation of delicate prokaryotic remains, and it provides a second opportunity to compare assemblages from similar physical environments preserved in different ways. In the relative abundance and size frequency distribution of unicell and filament populations (text-figs. 4, 6), the Veteranen lagoonal assemblages closely resemble those from lagoonal silicified carbonates of the slightly younger Draken and Ryssö formations of Svalbard, as well as the subtidal associations of the approximately contemporaneous Bitter Springs Formation, Australia (Schopf 1968; Knoll 1981). They do not closely resemble microbiotas from open coastal shales or intertidal to supratidal silicified carbonates.

Similar preservation of delicate 'cherty' microfossils in shales has been reported from the approximately 1300 Ma old Roper Group of northern Australia (Peat *et al.* 1978) and the Upper Riphean of the southern Urals (Jankauskas 1982). Thin-section examination of microbiotas



TEXT-FIG. 6. Size frequency distribution of filamentous sheaths from samples F-712, Glasgowbreen Formation (A) and F2-27, Kingbreen Formation (B). For both A and B, $N = 200$.

preserved in shales has been successful in a few instances (Moorman 1974; Peat *et al.* 1978; Horodyski 1980, *et al.* 1980; Knoll *et al.* 1981; Chauvel and Mansuy 1981) but most siliciclastic microfloras are best observed in maceration residues. A principal disadvantage of this procedure is that it loses the important information of spatial distributions of populations within rock. Such data are valuable in both systematic and palaeoecological studies (Knoll and Golubic 1979; Knoll 1981, 1982*b*). Of particular significance to the present discussion is the fact that when populations can be defined spatially their size frequency distribution, degradational variability, and (sometimes) cell division sequences can be determined. Comparisons of small unicell populations from the Draken, Hunnberg, Ryssö, and Bitter Springs formations with those from the Veteranen Group and other siliciclastic units suggests that, although different names have been applied to permineralized and compressed populations, they are very similar in their morphological modes and ranges of variation. The same is true of filament and rod populations. In these cases, parallel taxonomic schemes hinder biological comparisons, and some systematic revision is necessary. However, drawing a lesson from analogous comparative studies of Carboniferous coal ball and compression floras, any revisions must be undertaken on a case by case basis using all available fossil materials. Simplistic taxonomic solutions will obscure biological differences as surely as the present systems hide similarities.

In summary, most Proterozoic open coastal and shelf microbiotas are preserved as compressions or compactions in siltstones and shales, while most late Precambrian petrifications come from restricted coastal environments where early diagenetic silicification was most likely. Many algae that were thus precluded from restricted lagoonal and intertidal habitats are found as acritarchs in shales, while some mat building micro-organisms (e.g. *Eoentophysalis* Hofmann, 1976) characteristic of intertidal zones are preserved only or predominantly in silicified carbonates. Because the correspondence of environments and preservational modes is not absolute, silicified shelf biotas and compressed or compacted lagoonal assemblages allow hypotheses of differential preservational effects to be tested. The limited observations available to date suggest that the most serious problems of taxonomic obfuscation concern populations of small unicells and, to a lesser extent, filaments.

A geophysical aside

Although taxa differ in the rates at which their remains change colour with increasing temperature, colour characterization of fossil pollen, spores, and algal cysts is useful in studies of organic thermal maturation (Gutjahr 1966; Staplin 1969; Hunt 1979). Acritarchs in the Hecla Hoek succession of north-eastern Spitsbergen vary systematically from amber in Cambrian shales to an opaque black in the oldest parts of the Veteranen Group. Within the Veteranen succession exposed at Faksevågen, colours range from a slightly reddish Moderate Brown (Kelly and Judd 1976) in sample F-2200 from the upper Oxfordbreen Formation to a dark Brownish Black to Black in the lowermost Kingbreen and Kortbreen formations. In so far as the Faksevågen section comprises the limb of an open folded anticline without apparent intrusions in the immediate vicinity, one can hypothesize that observed colour changes are primarily due to maximum burial depth achieved in the Ordovician Period, just prior to Caledonian deformation. Oxfordbreen sample F-2200 sits beneath some 4300 m of preserved late Precambrian and Cambro-Ordovician strata. Assuming that any additional (now eroded) thickness of Upper Ordovician and Silurian strata was minimal, and assigning a maximum temperature to this rock of 125–150°C based on the organic maturation index (Hunt 1979, p. 324), one can estimate an early Palaeozoic geothermal gradient of about 1°C per 29–35 m. Estimates based on the occurrence of Dark Greyish Brown acritarchs and filaments in the upper Kingbreen Formation (samples F2-17 to 33) and nearly black materials in the Kortbreen Formation (F2-12, and slightly lighter in F2-40) fall in the same range. This falls within the normal range for continental geothermal gradients and suggests that at Faksevågen the temperature history of the Veteranen Group was controlled primarily by burial. At Cavendishryggen and in correlative rocks on Nordaustlandet other factors, probably related to Caledonian tectonism, intensified the thermal regime.

SYSTEMATIC PALAEOBIOLOGY

No new or emended taxa are here proposed and we have limited our systematic discussions to brief remarks designed to complement existing data and interpretations of the taxa found in the Veteranen Group. All samples and prepared slides are housed in the Paleobotanical Collections of the Botanical Museum, Harvard University.

Kingdom MONERA Haeckel, 1866
 Division CYANOPHYTA (Sachs) Pascher, 1931
 Class COCCOGONAE Thuret, 1875
 Order PLEUROCAPSALES Geitler, 1925
 Family UNKNOWN
 Genus BAVLINELLA (Schepeleva) Vidal, 1976

Type species. Bavlinella faveolata (Schepeleva) Vidal, 1976.

Bavlinella faveolata (Schepeleva) Vidal, 1976

Plate 51, figs. 3, 4

Discussion. This distinctive fossil occurs in small numbers in samples F2-27 and F-856. Multisphere size is 5–12 μm , and individual microsphere units are less than 1 μm in diameter. Chauvel and Mansuy (1981) noted that in the Brioverian of Normandy and Brittany, *B. faveolata* specimens with small unit cells characterize older (> 670 Ma) portions of the sequence, while Vendian (640–580 Ma) deposits additionally contain many specimens having a significantly larger unit cell size. (Chauvel and Mansuy used the name *Sphaerocongregus variabilis* Moorman, regarded by Vidal (1976) as a junior synonym of *B. faveolata*.) Veteran specimens are consistent with these unit cell size observations.

B. faveolata reached its acme in the Vendian, when it apparently expanded opportunistically with the climatic restriction and extinction of other previously dominant taxa. Its complete stratigraphic range runs at least from the late Riphean (this paper) to the early Cambrian (Vidal 1981). Moorman (1974) and Knoll *et al.* (1981) compared *B. faveolata* with pleurocapsalean cyanobacteria, noting the close correspondence in size frequency distribution, unit cell or baecocyte size frequency, and multiple fission pattern of reproduction (see Waterbury and Stanier 1978). Mansuy and Vidal (1983) suggested a chroococcalean origin for *B. faveolata*, comparing the fossil populations with species of the colonial chroococcalean genera *Gomphosphaeria*, *Coelosphaerium*, and *Microcystis*. Although most species of these genera differ from *Bavlinella* in colony size and shape, colony architecture, unit cell size frequency distribution, or unit cell shape (see Geitler 1932; Desikachary 1959), some species of *Microcystis* do form tightly packed spheroidal colonies. Ecologically, *Bavlinella* does resemble some modern colonial chroococcaleans in its inferred planktic mode of life and tendency to bloom under eutrophic conditions (Knoll *et al.* 1981; Mansuy and Vidal 1983).

The critical data bearing on the affinities of *B. faveolata* concern patterns of cell division. Pleurocapsalean multispheres and tightly packed chroococcalean colonies may have similar morphologies, but the development of these morphologies occurs quite differently in the two orders.

EXPLANATION OF PLATE 51

For each figure, slide number (which includes a sample number from text-fig. 3), stage co-ordinates (where 'x' on slide F500-14 = 23.7×102.2) and Harvard University Paleobotanical Collection number are given. Bar in fig. 2 = 40 μm for figs. 1, 2, and = 10 μm for all other figures.

Figs. 1, 2. ?*Chuarina circularis* Walcott. Fragmentary remains; note small unicell (comparable in size to fig. 18) in fig. 1. 1, F575-5, 52.2×107.8 , 60754. 2, F575-5, 45.5×95.6 , 60755.

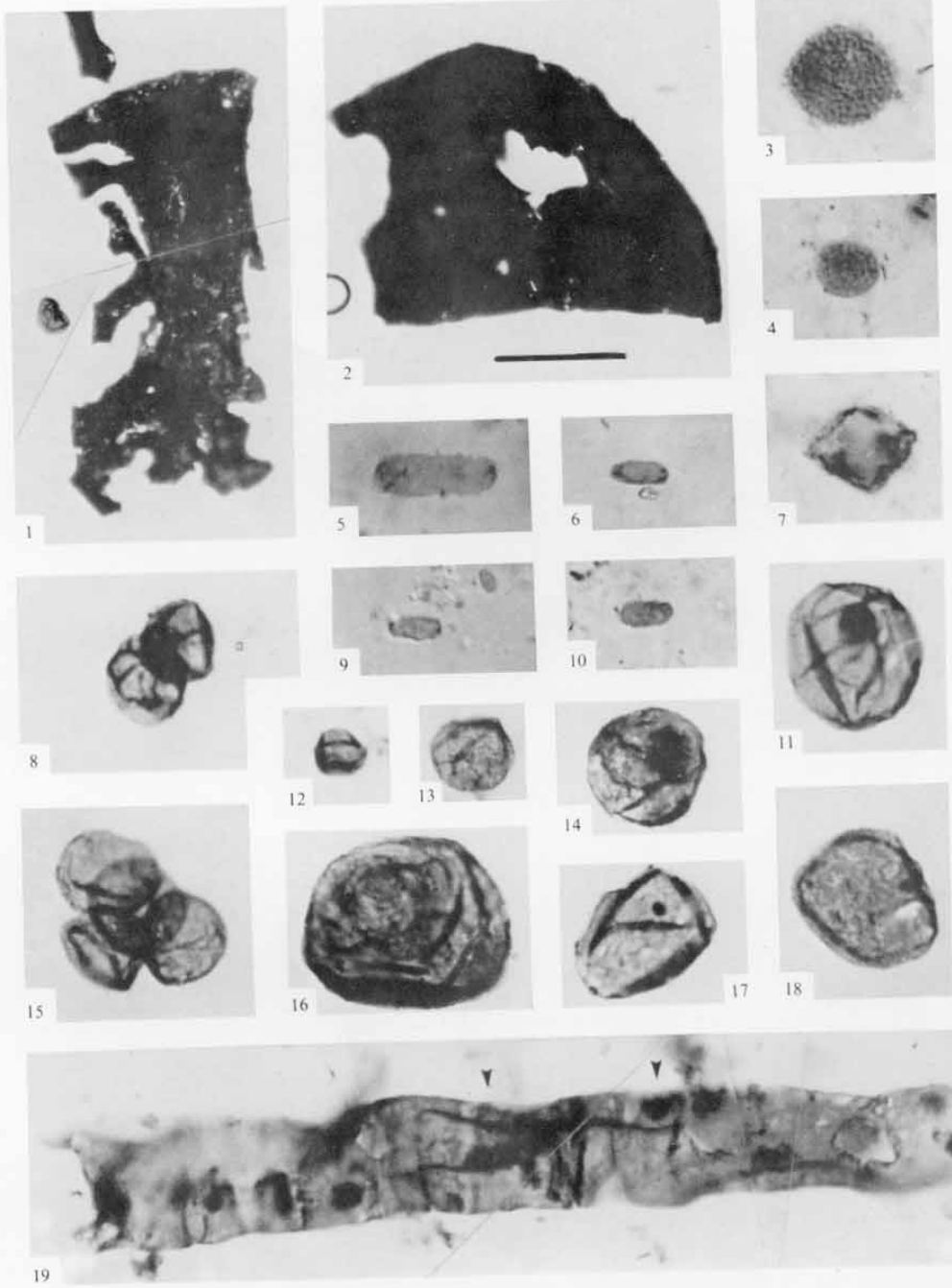
Figs. 3, 4. *Bavlinella faveolata* (Schepeleva) Vidal. 3, F2-29-2, 55×96.5 , 60756. 4, F2-29-2, 33.3×102.3 , 60757.

Figs. 5, 6, 9, 10. *Eosynechococcus* sp. 5, F500-13, 54.9×106.2 , 60758. 6, F712-4, 42.4×110.4 , 60759. 9, F712-4, 13×109.6 , 60760; note second, small specimen at the upper right corner of the figure. 10, F712-6, 33.4×107 , 60761.

Fig. 7. A coccoidal unicell distorted by diagenetic crystal growth. Similar morphologies have been described as *Octoedryxium* spp., but genuine *O. truncatum* specimens (e.g. Vidal 1976) do not resemble this specimen.

Figs. 8, 11–18. Small coccoidal unicells. Note small blebs of internal organic matter in 11, 17, and 18. 8, F2-27-2, 29.4×113.7 , 60762. 11, F2-23-1, 30.6×101.7 , 60763. 12, F856-1, 38.9×108.5 , 60764. 13, F500-13, 49.8×108.8 , 60765. 14, F575-5, 38.2×114.9 , 60796. 15, F712-6, 52.8×105.5 , 60766. 16, F575-6, 39×107.6 , 60767. 17, F575-5, 50.5×114.3 , 60768. 18, F575-7, 44×106.1 , 60769.

Fig. 19. Filamentous sheath containing degraded remnants of cells (arrows). F500-14, 45.2×96 , 60770.



KNOLL and SWETT, Late Proterozoic microfossils

In modern pleurocapsalean cyanobacteria, baeocyte clusters are formed by repeated binary fissions of a large initial cell, without intervening cell growth (Waterbury and Stanier 1978). In *Microcystis* and related genera, colonies arise by cell divisions interspersed with growth, so that at no point in the life cycle are any individual cells significantly larger than the cells that are found in the multicellular colony. Thus, if *B. faveolata* has pleurocapsalean affinities, its multispheres should co-occur with unicells, dyads, and tetrads having the same approximate total volume. If *Bavlinella* is a chroococcalean blue-green, no large cells should occur in the population and colony size might be expected to be somewhat variable. In samples processed by maceration, it is risky to infer that unicells are part of the life cycle of multispheres in the same assemblage, especially when the multispheres themselves are as rare as they are in the Veteranen Group. *Bavlinella*-rich assemblages from the Hector Formation, Alberta (Moorman 1974), the Mineral Fork Formation, Utah (Knoll *et al.* 1981), and the Brioverian of France (Chauvel and Schopf 1978; Chauvel and Mansuy 1981; Mansuy 1983) have been studied in thin-section; in at least two of these assemblages (Hector and Mineral Fork), *Bavlinella* multispheres occur in intimate spatial association with unicells and rare spheroidal dyads and tetrads whose maximum diameters are about the same size as the *B. faveolata* multispheres. It can be argued correctly that close spatial association of planktonic populations need not imply taxonomic identity. On the other hand the cell morphologies predicted by the 'pleurocapsalean hypothesis' do occur, while micron-sized unicells and variable colony sizes that might represent a chroococcalean growth series have not been observed. Therefore, pending further morphological data, we prefer to keep this fossil among the Pleurocapsales.

Order CHROOCOCCALES Wettstein, 1924
 Family CHROOCOCCACEAE Nägeli, 1849
 Genus EOSYNECHOCOCCUS Hofmann, 1976

Type species. Eosynechococcus moorei Hofmann, 1976.

Eosynechococcus sp.

Plate 51, figs. 5, 6, 9, 10

Description. Isolated rod-shaped vesicles; 2–9 μm long and 1–3 μm wide (mean dimensions = $3.6 \times 1.8 \mu\text{m}$, $s_x = 1 \mu\text{m}$, $s_y = 0.5 \mu\text{m}$, $N = 50$).

Discussion. *Eosynechococcus* is a form genus for small rod-shaped microfossils, most of which are probably, but not demonstrably, cyanobacteria (see Knoll 1982a). Although many previously described *Eosynechococcus* populations occur as dense aggregations in stromatolitic laminae, occurrences of non-clustered solitary rods and dyads have been described (Hofmann 1976; Knoll 1982a; Jankauskas 1982; Strother *et al.* 1983), and some of these are known to occur in non-stromatolitic muds. The generic diagnosis of *Eosynechococcus* Hofmann, 1976 specifically states that individuals may be solitary or clustered, so there is no question that this generic name is appropriate for the Veteranen fossils. In its size frequency distribution, the Veteranen population resembles *E. moorei* Hofmann, 1976 and *E. brevis* Knoll, 1982b, but maceration has destroyed the evidence of spatial distribution and division patterns that would allow these two species to be distinguished. Thus, we have elected to use the designation *Eosynechococcus* sp. That these are fossils and not modern contaminants can be demonstrated by the colour of their walls, which indicates thermal alteration under conditions of deep burial.

Class HORMOGONAE Thuret, 1875
 Order OSCILLATORIALES Copeland, 1936 or NOSTOCALES Geitler, 1925

Filamentous microfossils

Plate 51, fig. 19; Plate 52, figs. 1–3, 12

Discussion. Filamentous microfossils are abundant constituents of several Veteranen samples,

particularly those from the Bogen Member of Kingbreen Formation. Specimens are uniformly non-septate and are interpreted as extracellular sheaths; however, internal patterns of thickening and attenuation often faithfully record the dimensions of trichome cells that originally occupied sheath interiors (Pl. 52, fig. 2). These 'ghosts' suggest that the micro-organisms had a single trichome composed of undifferentiated cells, much like modern *Lynghya*. In rare instances, partially degraded trichome fragments are preserved inside the sheaths (Pl. 51, fig. 19). Size frequency distributions (text-fig. 6) indicate that several taxa are represented. Like silicified microbiotas from the Bitter Springs (Schopf 1968; Knoll 1981), Draken (Knoll 1982*b*), and Sukhaya Tunguska (Mendelson and Schopf 1982) formations, the Veteranen populations fall into several size classes having modes in the 1, 2-4, 4-8, and 10-12 μm diameter ranges. The widest sheath observed is 16 μm in diameter.

In terms of permineralization taxonomic practice, these populations can be described as species of *Tenuofilum*, *Eomycetopsis*, and *Siphonophycus*, with the generic distinctions based largely on size. Macerated filaments have been assigned to these genera (e.g. Jankauskas 1982) or to the form genus *Taeniatum*. Biologically, most filamentous sheath populations were probably produced by oscillatorial or nostocalean cyanobacteria. The absence of well-preserved trichomes precludes further comparison, although 'ghosts' of cells impressed on sheath interiors do indicate an oscillatorial affinity for many specimens.

Kingdom PROTOCTISTA Copeland, 1956 emend. Margulis, 1971
 Division PRASINOPHYTA Round, 1971
 Order PTEROSPERMATALES Schiller, 1925
 Family TASMANITACEAE Sommer, 1956 ex. Tappan, 1980
 Genus TASMANITES Newton, 1875

Type species. Tasmanites punctatus Newton, 1875.

Tasmanites rifejicus Jankauskas, 1978

Plate 53, fig. 11

Discussion. Specimens of *T. rifejicus* are rare in the Veteranen Group, but they are easily distinguished by the numerous pores that perforate the vesicle. One Veteranen specimen (112 μm) falls in the size range for the species observed by Jankauskas (1978, 1982) and Vidal and Ford (1985), but others range from 43 to 52 μm . Despite their smaller size, these specimens have been placed in *T. rifejicus* by virtue of their wall structure.

Group ACRTARCHA Evitt, 1963
 Genus ?CHUARIA Walcott, 1899

Type species. Chuaria circularis Walcott, 1899.

?*Chuaria circularis* Walcott, 1899

Plate 51, figs. 1, 2

Discussion. No complete specimens of *C. circularis* have been observed in Veteranen material, but large fragments of robust, and often differentially coalified, spheroidal vesicles are common in some samples. Individual fragments range up to 140 μm in maximum dimension, and the curvature of these broken specimens indicates that the original vesicles were often in excess of 300 μm diameter. Several species of *Trachysphaeridium* and *Kildinosphaera* exceed 200 μm in diameter but, given the robust nature of the walls and the commonness of the fragments, we suggest that the large shards belong to *C. circularis*. *Chuaria* is known to occur in correlative beds in Nordaustlandet, Svalbard (Knoll 1982*a*), and East Greenland (Vidal 1979), and indeed is common in Upper Riphean rocks from many localities throughout the world (Ford and Breed 1973; Hofmann 1977).

Genus FAVOSOPHAERIDIUM Timofeev, 1959, ex Timofeev, 1966

Type species. Favosphaeridium scandicum Timofeev, 1966.

Favosphaeridium sp.

Plate 53, figs. 7, 10

Discussion. A single specimen 95 μm in diameter was observed in sample F-575. The size and irregularly reticulate surface ornamentation of this specimen (Pl. 53, fig. 10) are comparable to those characterizing the specimens of Timofeev described by Vidal (1976) from the Visingsö Beds, Sweden. Poor preservation makes specific comparison impossible.

Genus KILDINOSPHAERA Vidal, 1983

Type species. Kildinosphaera chagrinata Vidal, 1983.

Kildinosphaera chagrinata Vidal, 1983

Plate 53, figs. 1-3

Discussion. Vidal (*in* Vidal and Siedlecka 1983) cut a Gordian knot in Proterozoic acritarch taxonomy by creating the new genus *Kildinosphaera* and describing as its type species *K. chagrinata*. The new genus was necessitated by Lindgren's (1982) transfer of *Kildinella hyperboreica* (the type species of *Kildinella*) to *Leiosphaeridia* Eisenack, and the species was described to impart rigor to a troubled system of morphologically overlapping form species, most prominently *K. sinica* Timofeev, 1966. The Veteranen specimens have flexible, easily foldable walls with a subdued chagrinata surface. Size range is 26-78 μm (\bar{x} = 40 μm , s_x = 10.6 μm , N = 50).

Kildinosphaera granulata Vidal, 1983

Plate 53, figs. 9, 12-14

Discussion. Veteranen specimens of *K. granulata* have flexible walls with a conspicuous, finely granulate surface texture. Size range is 30-85 μm (\bar{x} = 52.2 μm , s_x = 15.2 μm , N = 20). This species is common only in the most diverse, open coastal assemblage, sample F-856 and, less so, F-575.

Genus LEIOSPHAERIDIA Eisenack, 1958

Type species. Leiosphaeridia baltica Eisenack, 1958.

Leiosphaeridia asperata (Naumova) Lindgren, 1982

Plate 52, figs. 4-8, 10, 11

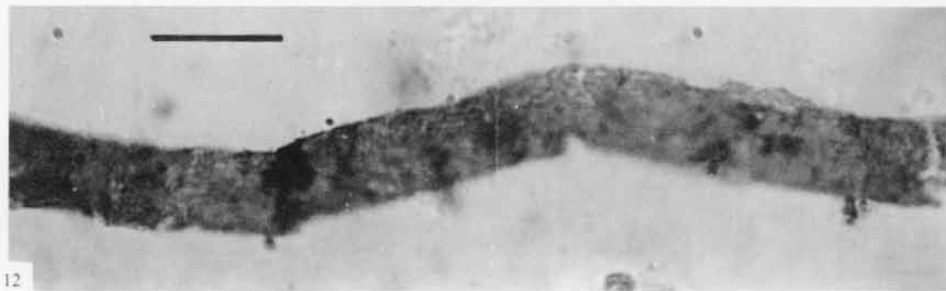
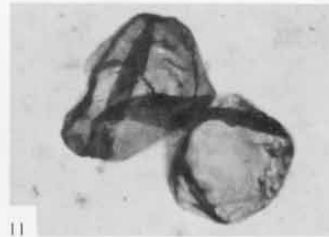
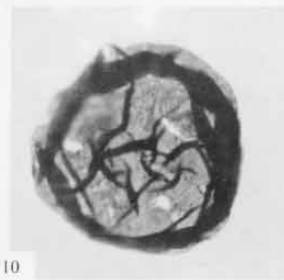
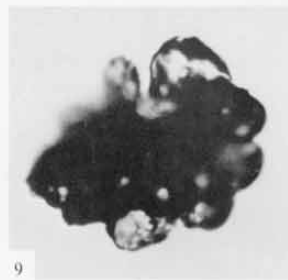
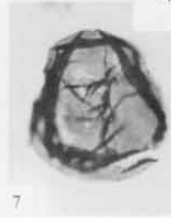
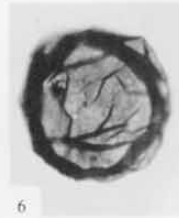
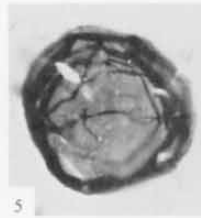
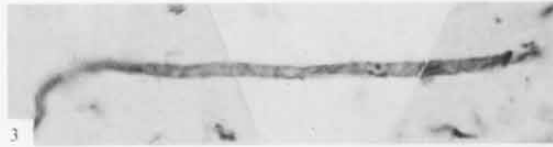
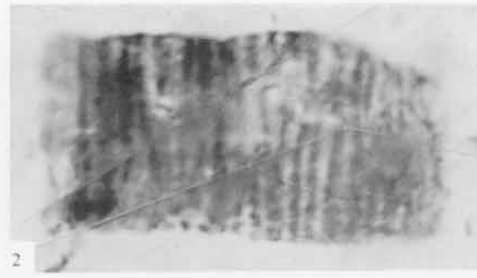
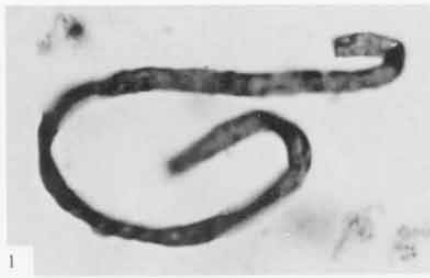
EXPLANATION OF PLATE 52

For each figure, slide number (which includes a sample number from text-fig. 3), stage co-ordinates (where 'x' on slide F500-14 = 23.7 \times 102.2) and Harvard University Paleobotanical Collection number are given. Bar in fig. 12 = 10 μm for figs. 1-3, 12, and = 20 μm for all other figures.

Figs. 1-3, 12. Filamentous microfossils. 1, F500-12, 43.1 \times 103.4, 60771. 2, F2-17-2, 48.5 \times 116.5, 60772. 3, F2-29-2, 40.2 \times 104.3, 60773. 12, F712-2, 42 \times 112.4, 60774.

Figs. 4-8, 10, 11. *Leiosphaeridia asperata* (Naumova) Lindgren. 4, F712-6, 21 \times 107.2, 60775. 5, F500-12, 49 \times 95.5, 60776. 6, F500-6, 50.5 \times 95.7, 60777. 7, F500-12, 48 \times 90.1, 60779. 8, a cluster of vesicles, F2200-1, 47.7 \times 105.3, 60780. 10, F500-10, 31.4 \times 109.1, 60781. 11, F712-6, 34 \times 100.3, 60795.

Fig. 9. *Synsphaeridium* sp. F575-5, 58.4 \times 110.6, 60782.



KNOLL and SWETT, Late Proterozoic microfossils

Discussion. Lindgren (1982) synonymized the well-known Proterozoic acritarch species *Kildinella hyperboreica* Timofeev, 1966 with *L. asperata*. Veteranen *L. asperata* specimens have smooth, flexible walls 20–52 μm in diameter ($\bar{x} = 32.9 \mu\text{m}$, $s_x = 7.7 \mu\text{m}$, $N = 52$).

Genus SATKA Jankauskas, 1979a

Type species. *Satka favosa* Jankauskas, 1979a.

Satka colonialica Jankauskas, 1979b

Plate 53, figs. 4–6, 8

Discussion. Vidal and Ford (1985) have interpreted *S. colonialica* as a thin, chagrinata to finely granular envelope whose outline reflects the dimensions of the numerous, smaller ellipsoidal cells about which it was compressed. Veteranen specimens support this interpretation; both in the Spitsbergen population and in previously described colonies, the ellipsoidal internal bodies are generally absent. Individual *S. colonialica* specimens reach 100 μm in length, but most fall in the 40–50 μm range. Ellipsoidal internal bodies are 7–14 μm long.

Genus STICTOSPHAERIDIUM Timofeev, 1962

Type species. *Stictosphaeridium podolense* Timofeev, 1962.

cf. *Stictosphaeridium* sp. *sensu* Vidal, 1976

Discussion. Very thin-walled, spheroidal vesicles with diameters of 25–63 μm are common in several Veteranen samples.

Genus SYNSPHAERIDIUM Eisenack, 1965

Type species. *Synsphaeridium gotlandicum* Eisenack, 1965.

Synsphaeridium sp.

Plate 52, fig. 9

Discussion. Microfossils assigned to *Synsphaeridium* differ from other small unicells of the Veteranen Group in their possession of a thick (but not brittle) psilate wall that compresses to yield rounded folds rather than the sharp, pleated folds seen in many other taxa. Specimens have diameters of 13–17 μm and commonly occur in clusters.

EXPLANATION OF PLATE 53

For each figure, slide number (which includes a sample number from text-fig. 3), stage co-ordinates (where 'x' on slide F500-14 = 23.7×102.2) and Harvard University Paleobotanical Collection number are given. Bar in fig. 14 = 20 μm for figs. 1–6, 8–14, and = 60 μm in fig. 7.

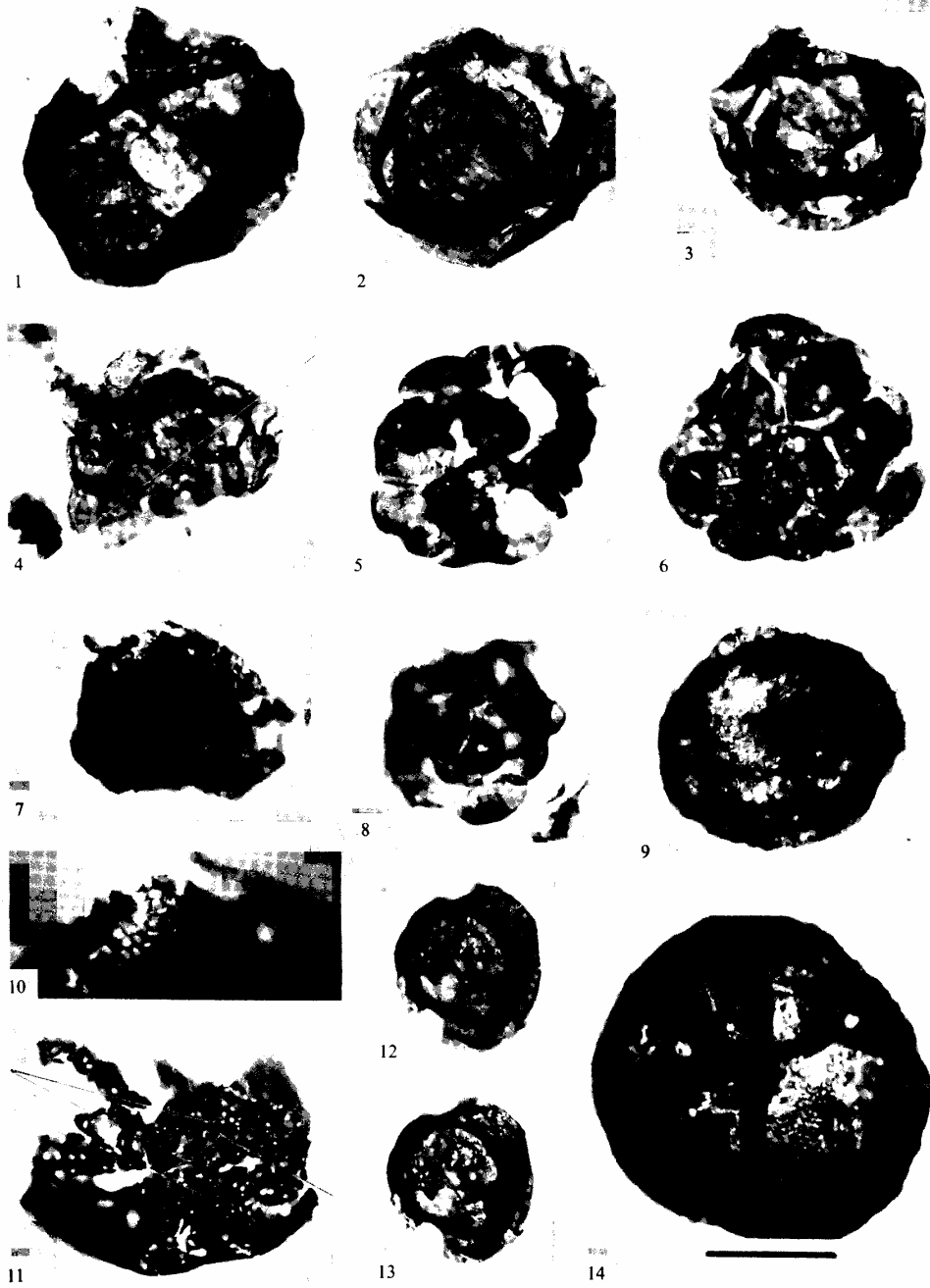
Figs. 1–3. *Kildinosphaera chagrinata* Vidal. 1, F575-7, 34×95.8 , 60783. 2, F500-10, 57×95.2 , 60784. 3, F575-5, 44.2×114.9 , 60785.

Figs. 4–6, 8. *Satka colonialica* Jankauskas. 4, F500-12, 42.3×104 , 60786. 5, F500-10, 57×95.2 , 60787. 6, F575-5, 44.2×114.9 , 60788. 8, F500-12, 45.5×102 , 60789.

Figs. 7, 10. *Favosphaeridium* sp. 7, F575-1, 42.4×109.7 , 60790. Fig. 10 is an enlargement of a portion of fig. 7 showing the structure of the vesicle wall.

Figs. 9, 12–14. *Kildinosphaera granulata* Vidal. 9, F500-10, 51×110.4 , 60791. 12, F2200-1, 39.5×113.1 , 60792. 13, same specimen as fig. 12, photographed using interference contrast. 14, F500-10, 58.2×97.4 , 60793.

Fig. 11. *Tasmanites rifejicus* Jankauskas. F575-7, 34.3×110.1 , 60794.



KNOLL and SWETT, Late Proterozoic microfossils

MICRO-ORGANISMS INCERTAE SEDIS

Small coccoidal unicells

Plate 51, figs. 8, 11-18

Discussion. Numerous taxonomic names have been proposed for the classification of the small (3-25 μm), psilate to granular, spheroidal vesicles that occur as common constituents of late Proterozoic microbiotas (Timofeev 1966, 1969). If found as permineralizations, most of these populations would be assigned to the genus *Myxococcoides* Schopf, especially *M. minor* Schopf, 1968 or *M. cantabrigiensis* Knoll, 1982a. Because maceration destroys original spatial relationships and often scatters individuals from loose clusters, some of the characters that are important in the recognition of *Myxococcoides* species are lost in the acid-resistant residues herein under consideration. Jankauskas (1982) treated comparable materials from the Upper Riphean of the southern Urals as species of the genera *Synsphaeridium*, *Leiosphaeridia*, *Margominiscula*, *Arctacellularia*, *Leiominuscula*, and unnamed spheroids. Pending the opportunity to examine type specimens in the Soviet Union, we prefer to treat these populations informally. Size frequency distributions of two sample populations are shown in text-fig. 4.

Acknowledgements. We thank the Norsk Polarinstitut and the Cambridge Spitsbergen Expedition for logistical and intellectual co-operation, E. Burkhardt and S. Goldberg for assistance in preparing the plates and text-figures, and G. Vidal and W. B. Harland for helpful criticisms of our manuscript. This research was supported in part by NSF Grants DPP 80-19998 and DPP 83-01226.

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Typescript received 15 May 1984

Revised typescript received 14 January 1985