PALEOBIOLOGY OF A NEOPROTEROZOIC TIDAL FLAT/LAGOONAL COMPLEX: THE DRAKEN CONGLOMERATE FORMATION, SPITSBERGEN

A. H. KNOLL, K. SWETT, AND J. MARK

Botanical Museum, Harvard University, Cambridge, Massachusetts 02138,
Department of Geology, University of Iowa, Iowa City 52242, and
Department of Organismic and Evolutionary Biology,
Harvard University, Cambridge, Massachusetts 02138

ABSTRACT—Carbonates and rare shales of the ca 700–800 Ma old Draken Conglomerate Formation, northeastern Spitsbergen, preserve a record of environmental variation within a Neoproterozoic tidal flat/lagoon complex. Forty-two microfossil taxa have been recognized in Draken rocks, and of these, 39 can be characterized in terms of their paleoenvironmental distributions along a gradient from the supratidal zone to permanently submerged lagoons. Supratidal to subtidal trends include: increasing microbenthic diversity, increasing abundance and diversity of included allochthonous (presumably planktonic) elements, decreasing sheath thickness of mat-building organisms (with significant taphonomic consequences), and an increasing sediment/fossil ratio in fossiliferous rocks. Five principal and several minor biofacies can be distinguished. The paleoecological resolution obtainable in the Draken Conglomerate Formation rivals that achieved for most Phanerozoic fossil deposits. It documents the complexity and diversity of Proterozoic coastal ecosystems and indicates that both environment and taphonomy need to be taken into explicit consideration in attempts to understand evolutionary trends in the early fossil record. Three species, *Coniunctiophycus majorinum*, *Myxococcoides distola*, and *M. chlorelloidea*, are described as new; *Siphonophycus robustum*, *Siphonophycus septatum*, and *Gorgonisphaeridium maximum* are proposed as new combinations.

INTRODUCTION

IN 1954 Tyler and Barghoorn reported well-preserved microfossils in cherts of the Paleoproterozoic Gunflint Iron Formation. Their discovery promised a paleontological understanding of life's early history, as well as micropaleontological tools for the stratigraphic correlation and paleoenvironmental interpretation of Archean and Proterozoic sedimentary rocks. The more general promise of Precambrian paleontology has been fulfilled. We now have confidence that life appeared early in our planet's development, that aerobic prokaryotes and mitochondria-bearing eukaryotes radiated much later, and that complex multicellularity in protists and animals evolved still later, in Meso- to Neoproterozoic times.

In contrast, the fuller promise of Tyler and Barghoorn's discovery—that Archean and Proterozoic microfossil taxa might be delimited in space and time, facilitating the kinds of contribution that paleontology has made to Phanerozoic stratigraphy and evolution—remains tantalizingly half fulfilled. Beginning with Timofeev (1959), palynologists have used acritarchs in the broad biostratigraphic subdivision of Neoproterozoic successions (e.g., Vidal, 1976; Jankauskas, 1982, 1989; Vidal and Knoll, 1983), while others have shown that certain microbenthic populations illuminate paleoenvironmental analysis (e.g., Golubic and Hofmann, 1976; Green et al., 1987, 1988). The Proterozoic is not the Phanerozoic, just as the Paleozoic is not the Pleistocene; but research completed during the past decade clearly indicates the potential for much finer stratigraphic, paleoenvironmental, and, hence, evolutionary resolution of the Proterozoic fossil record. Realization of this potential requires that microfossil distributions be brought into sharper focus through detailed systematic and paleoecological studies of well-preserved fossil assemblages within carefully measured stratigraphic sections.

The Neoproterozoic Draken Conglomerate Formation, Spitsbergen, provides an opportunity to test the limits of paleoecological resolution in Proterozoic micropaleontology. The preliminary work of Knoll (1982), based on Draken samples collected by the late Colin Wilson of the Cambridge Spitsbergen Expedition, showed that Draken cherts contain exceptionally well-preserved microfossil populations. Field expeditions to northeastern Spitsbergen in 1981, 1982, and 1986 have resulted in the documentation of 42 fossil-bearing horizons in cherts, carbonates, and shales collected from measured sections in three areas spanning a distance of just over 100 km along strike.

GEOLOGICAL SETTING AND AGE

The Neoproterozoic Lomfjorden Supergroup contains some 6,000 m of quartz arenite, shale, and carbonate exposed in nunataks throughout northeastern Spitsbergen (Figure 1; Wilson, 1961; Harland and Wright, 1979). Along with correlative beds in neighboring Nordaustlandet and central East Greenland, it documents deposition in a rapidly subsiding intracratonic basin that extended at least 650 km along strike. The lower two-thirds of this succession, the Veteranen Group, consist predominantly of cross-bedded and rippled quartz arenite with interbedded siltite, shale, and minor carbonate (Wilson, 1958; Knoll and Swett, 1985). In contrast, the overlying Akademikerbreen Group contains mostly carbonate, with only minor siliciclastic intercalations (Wilson, 1961; Knoll and Swett, 1990).

Akademikerbreen limestones and dolomites accumulated on a carbonate ramp. Constituent facies record depositional environments ranging from tidal flats through lagoons, oolitic shoals, and bioherms to offshore sites below fair weather wave base (Knoll and Swett, 1990). Although a marine setting is often difficult to demonstrate for Proterozoic rocks that lack skeletal fossils, several features strongly suggest that Akademikerbreen carbonates precipitated from sea water. The dimensions of the package—650 km long and, especially, 2,000 m thick—are hard to reconcile with known lacustrine deposits. Sedimentary structures and facies relationships are those expected for marine-platform deposition, and there is no evidence of intercalated alluvial deposits. Carbon and strontium isotopic ratios in Akademikerbreen carbonates also suggest marine deposition (Knoll et al., 1986; Derry et al., 1989). Perhaps most important, some of the fossils described from Akademikerbreen rocks and their equivalents in East Greenland have close modern counterparts known only from marine environments (e.g., Green et al., 1987, 1988, 1989; Knoll et al., 1989).
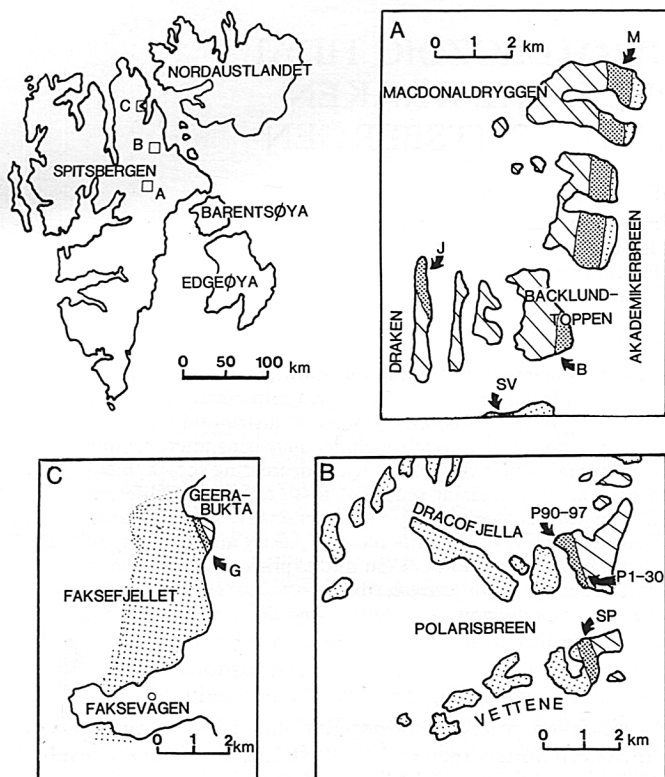
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FIGURE *1*—Map of Spitsbergen and neighboring islands, showing the locations of measured sections and samples (M, B, SV, J, G, SP, and P) of the Draken Conglomerate Formation discussed in this paper. Densely stippled areas indicate Draken outcrop; lightly stippled areas represent pre-Draken successions; and diagonal stripes indicate post-Draken rocks. White areas are ice covered.

The 150–250-m-thick Draken Conglomerate Formation begins just above the mid-point of the Akademikerbreen Group. It consists principally of cm- to dm-scale beds of intraclastic dolarenite to dolorudite, with interbedded dolomicrites (Figure 2). Oolites and oncolites are common, especially in the middle third of the formation. In the upper third, stratiform stromatolites, commonly associated with tepee structures, occur in intimate association with thin intraclastic dolomites and dolomicrites. Columnar stromatolites are rare except for regionally extensive bioherms that mark the base of the formation in southern exposures (Swett and Knoll, 1985; see below).

For the most part, the intraclastic conglomerates and dolomicrites exhibit petrographic evidence for early marine diagenesis. In contrast, horizons containing abundant stratiform microbial laminae commonly contain evidence of subaerial exposure, leaching, oxidation, and vadose as well as artesian cementation (Fairchild et al., in press). As documented more completely elsewhere (Fairchild et al., in press) and discussed below in the context of individual fossil assemblages, the Draken Conglomerate Formation was deposited during one of the lowest sea-level stands represented within the Akademikerbreen Group. Draken dolomicrites record the deposition of carbonate mud, possibly from whitings, in a protected lagoon. Decimeter-scale intraclastic carbonates were deposited in the lagoons during storms, whereas oolites and oncolites originated in shoals that presumably formed the seaward lagoonal barrier. In situ stratiform mats and associated thinly bedded intraclastic units were deposited landward of the lagoons on extensive tidal flats.

Draken carbonates were deposited during the Late Riphean Era, and probably during the latter part of this interval. This conclusion is supported by their stratigraphic position some 700 m below the lowermost Varangian (lower Vendian) tillite in Spitsbergen (Hambrey, 1982) and by the presence in Draken and surrounding formations of acritarchs and vase-shaped microfossils known only from rocks ca 850–650 Ma old. Carbon isotopic ratios in Akademikerbreen carbonates and organic matter approximate those of other 700–800 Ma old rocks, but differ from older Neoproterozoic successions (Knoll et al., 1986). Preliminary correlation of the Akademikerbreen Group with well-dated successions in northwestern Canada by means of acritarch biostratigraphy and carbon and strontium isotopic chemostratigraphy suggests that the Draken carbonates post-date 780 Ma old dikes that intrude correlative beds in the Canadian Cordillera (Knoll et al., unpublished data). If confirmed, this will provide a strong lower boundary for Draken deposition. For now, a broad age assignment of 700–800 Ma seems reasonable.

TAXONOMY AND TAPHONOMY

The principal interpretations in this paper are paleoecological, but such conclusions are necessarily built on a solid foundation of systematic paleontology and taphonomic understanding. In this paper, frequent reference is made to species and diversity, and many populations are given Linnean binomial names. To what extent are we justified in borrowing such concepts and procedures from biology, and what allowance must be made in paleobiological interpretation?

Taphonomy.—Taphonomy has been applied widely in the study of fossil vertebrates, invertebrates, and, increasingly, plants. There is widespread appreciation that some organisms and, indeed, parts of organisms are more likely to be preserved than others, that some environments are more likely to be represented by fossil assemblages than others, and that post-mortem transport has significant but predictable and detectable consequences for fossil accumulations. These generalizations are derived from numerous actualistic studies and specific ancient–modern comparisons (e.g., Behrensmeyer and Kidwell, 1985).

For nearly 20 years, comparable studies have illuminated the Proterozoic microfossil record, with broadly similar results. Within organisms, degradationally resistant walls, sheaths, or envelopes are differentially likely to become incorporated into the fossil record. To the extent that systematic studies of living microorganisms rely on ultrastructural or biochemical features, this indicates a significant loss of information. However, as illustrated by the paradigmatic study of the living cyanobacterium *Entophysalis* and its Paleoproterozoic counterpart *Eoentophysalis* (Golubic and Hofmann, 1976), preserved envelopes may provide morphological information comparable to that obtainable from populations of living organisms. Thus, in favorable circumstances, fossil cell-wall or envelope populations may justifiably be treated as biological entities, even though systematic relationships may not be clear at the phylum or even kingdom level.

Within environments, organisms that produce organic "hard parts" are differentially likely to be preserved. This is illustrated by actualistic studies of Recent microbial mat communities in which some cyanobacterial and flexibacterial sheaths as well as protistan cysts survive early biological decomposition, while more diverse bacterial heterotrophs disappear without a (morphological) trace (e.g., Horodyski and vonder Haar, 1975; Aizenshtat et al., 1984). Among environments, probability of preservation also varies, for two different reasons. The first is that the physico-chemical conditions promoting microfossil preservation (e.g., anoxia) are variably distributed among environments. The second is that organisms likely to produce
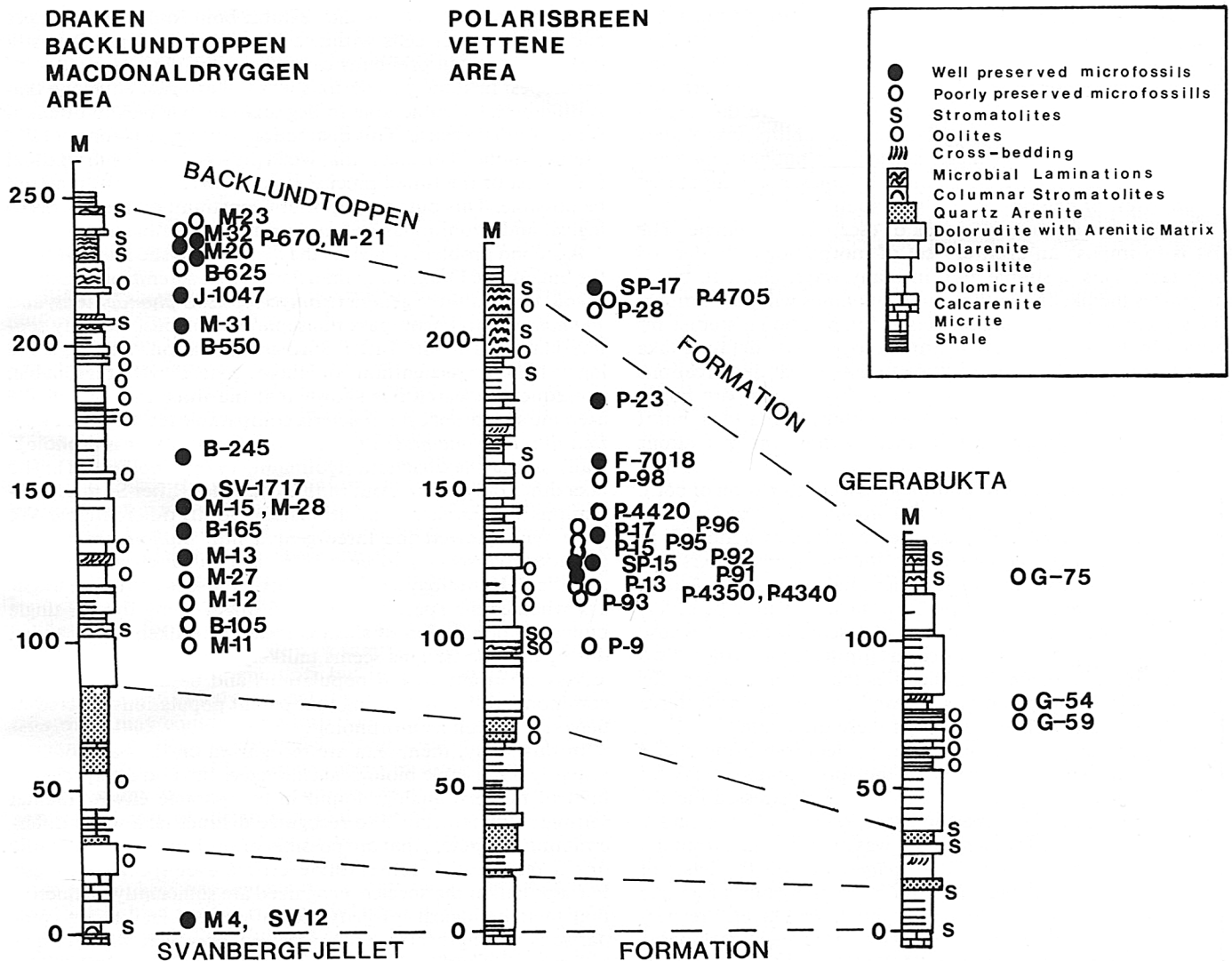
FIGURE 2—Generalized stratigraphic sections of the Draken Conglomerate Formation in northeastern Spitsbergen. The three sections correspond to the three areas labelled A, B, and C in Figure 1.

fossilizable envelopes or walls are also variably distributed. Subtidal cyanobacteria, for example, often produce thin, degradationally vulnerable envelopes, whereas populations inhabiting frequently exposed tidal flats form robust sheaths (Golubic and Barghoorn, 1977).

In the case of the Draken Conglomerate Formation, this means that part of the original biota is missing. Comparison with modern tidal flats suggests broad classes of probable absentees, but more specific discussion is speculative. Ultimately, we must concentrate on what is preserved—on the abundant sheaths (and rare cells) and cyst walls of photoautotrophic Eubacteria and protists, as well as on supplemental information provided by organic geochemistry. These provide a proxy for original communities, but quantitative measures such as species richness may not be directly comparable. The best that taphonomy may allow us is to draw qualitative inferences about environmental or temporal trends in diversity, and even these must be approached with caution.

Most Draken fossils are preserved in early diagenetic chert nodules. This preservation itself introduces some environmental bias, in that diagenetic chert formation is not equally likely or likely to be equally early in all environments (Yin, 1987; Maliva et al., 1989). Fortunately, the peritidal facies that constitute the Draken Formation are among those in which early diagenetic chert emplacement is most likely. Equally fortunate, chert is not necessary for microfossil preservation. Some of the best preserved Neoproterozoic fossils come from siliciclastic mudstone (e.g., German, 1981; Jankauskas, 1982, 1989; Butterfield et al., 1988; Zang and Walter, 1989). In the Draken, well-preserved microfossils occur both in shales and in fine-grained carbonates (where extremely local silica precipitation was sometimes important). Additional microfossil populations occur as carbonate-lined filaments comparable to *Girvanella* and other Phanerozoic fossils. These reinforce the observation that chert, carbonate, and clay can all provide physico-chemical conditions conducive to the preservation of life's early record. In this sense, the Draken biota is a microcosm of the Proterozoic fossil record as a whole. Comparison of populations preserved in different minerals is not always straightforward, and is aided markedly by morphological complexity or, as seen in a few Draken occurrences, by the ability to trace individual assemblages across preservational boundaries.

Taxonomy.—Some of Proterozoic paleontology's most difficult problems stem from its greatest success, the demonstration that Proterozoic rocks are abundantly fossiliferous. Early and influential monographs (e.g., Timofeev, 1959; Barghoorn and Tyler, 1965; Schopf, 1968) were published before the importance of taphonomy and populational variability was widely appreciated. Building on these, subsequent publications have resulted in a minor jungle of taxonomic names, many supported by the barest of description or illustration.

There are two potential means of escaping this jungle. The first is to impose an arbitrary set of morphologically defined form taxa. This is simple and, in many ways, efficient, but it minimizes the likelihood that Linnean names will mean much. The second way is to conduct detailed populational studies informed by taphonomy and sedimentology—only defining taxa when there is sufficient information to make clear demarcations among species. This minimizes our ability to compare populations among (and sometimes, even within) formations, but it maximizes the biological significance of those interpretations that can be made.

In practice, systematic paleontology is a combination of both. Some taxa, such as species of *Eoentophysalis, Trachyhystrichosphaera,* or *Polybessurus,* are circumscribed by a number of characters and surely come close to the meanings understood by neontological taxonomists for microbial species and genera. At the other extreme are simple form taxa that may be differentiable into populations within local assemblages, but whose comparison across time and space has limited significance. Two brief examples illustrate the difficulties that form taxa pose for paleoecological interpretations, as well as the paths we have chosen in our attempts to surmount these difficulties.

Among the most common fossils in Neoproterozoic cherts are spheroidal vesicles referred to the form genus *Myxococcoides.* In his original diagnosis, Schopf (1968) stressed the absence of individual envelopes and the presence of amorphous mucilage in colonies. *Myxococcoides* was distinguished from the genera *Glenobotrydion* and *Caryosphaeroides* on the basis of dense internal organic structures and internal organic structures surrounded by a partially collapsed "inner wall layer," respectively. Subsequent research has shown internal cellular remains to be fickle characters (Hofmann, 1976; Knoll, 1981). Although typically constant within a single Bitter Springs cluster, these internal organic bodies are not invariably so, and there is no other way to differentiate populations consistently. The occasional arrangement of vesicles in uniseriate pseudofilaments (Schopf, 1968) may be significant at the species level. In this paper, we have not considered internal organic blebs to be taxonomically significant.

Having resolved one taxonomic difficulty, another remains. The genus *Gloeodiniopsis* is differentiated from *Myxococcoides* by its multiple envelopes that surround an internal vesicle and by its common retention of 2–8 daughter cells within the external envelope (Schopf, 1968; Knoll and Golubic, 1979). This distinction follows directly from Schopf's diagnosis of *Myxococcoides* and provides a ready means of differentiating populations in the Bitter Springs Formation. Problems arise, however, in the determination of populations that differ in only one of the two characters used to differentiate genera. In the Draken Formation, there occur spheroidal populations that have both internal and external layers, but no record of binary division. Knoll (1982) originally assigned these populations to *Gloeodiniopsis gregaria,* but restudy indicates that these populations form one end member of a morphological continuum running to typical *Myxococcoides cantabrigiensis.* Single clusters may include specimens with a well-defined internal "wall" adjacent to empty vesicles. Therefore, in this study, we reserve the name *Gloeo-*

diniopsis for populations that exhibit both multiple envelopes and 2–8 daughter cells within a common envelope. This still does not solve all problems caused by variable preservation of envelopes; in some populations it is the external envelope that is differentially vulnerable to degradation, whereas in others it is the internal vesicle. This distinction may prove taxonomically useful, but the plain fact is that when preservation is sub-optimal (i.e., most of the time), precise systematic assignment may not be possible. This puts an important constraint on the paleoecological and evolutionary comparisons of assemblages.

A second problem concerns the filamentous sheaths that form the bulk of the Draken and many other mat assemblages. Schopf (1968) erected three genera (*Eomycetopsis, Siphonophycus,* and *Tenuofilum*) to encompass nonseptate or inconspicuously septate filaments in the Bitter Springs Formation. Although the logic behind recognition of three genera was reasonable, subsequent research has shown that the three taxa are all aseptate sheaths of cyanobacteria comparable to *Lyngbya, Phormidium, Plectonema* (LPP-type cyanobacteria), or morphologically similar flexibacteria (Hofmann, 1976; Knoll, 1981). The taxa differ only in size, but in this character Bitter Springs populations (and Draken populations) are cleanly differentiable. We have synonymized the three genera into *Siphonophycus* and consider five species to be present in Draken cherts (see Systematic Paleontology section for further discussion). One might ask whether the species recognized might come from a single biological population of sheaths locally shrunken or expanded during diagenesis. This seems unlikely both because size is relatively invariant within populations and because mat fabrics commonly differ, indicating that parent populations differed in behavior as well as morphology.

In this study, then, taxa are recognized on the basis of consistently observable biological characteristics and interpreted in light of modern analogs found in comparable environmental settings. Our reluctance to recognize distinct taxa when differentiating characters that are possibly or probably of taphonomic origin results in a conservative estimate of species richness. Perhaps half of the species recognized are sufficiently distinctive that their biological integrity seems assured, facilitating comparisons among basins. Other species, however, while clearly differentiable within the Draken biota, remain form taxa whose biological relationships to morphologically similar populations in other basins cannot be assumed. As in classical taxonomic treatments of living cyanobacteria (e.g., Geitler, 1930–1932), fossil genera are differentiated on the basis of qualitative differences among populations; species within genera are differentiated on the basis of quantitative differences.

MICROFOSSIL ASSEMBLAGES

In situ stratiform stromatolites.—Within the Draken Conglomerate Formation, many of the best preserved microfossils occur in redeposited clasts, complicating paleoenvironmental interpretation. In the upper part of the formation, however, silicified, microbially laminated carbonates preserve a record of in situ mat communities that provides a key to the interpretation of intraclasts elsewhere in the succession.

The rocks in questions are stratiform stromatolites up to one meter thick, which are interbedded with dolarenites and thin shaly units (Figure 3.1). Laminae are flat to slightly undulatory and about one mm thick. Isolated low, irregular domes occur in several beds (Figure 3.2), but these appear to be a product of soft-sediment deformation, at least in part. Syndepositional deformation is independently documented by tepees that occur in the same sections. The stromatolites are dolomitic. Patchy silicification occurred early in diagenesis, but chert emplacement post-dates soft-sediment deformation (Figure 3.2). In the Po-

larisbreen area, quartz and carbonate sand grains are important constituents of laminated rocks, and dolarenite interbeds are abundant. To the south, along MacDonaldryggen and Backlundtoppen nunataks, arenitic material is less common. These carbonates exhibit petrographic evidence of subaerial exposure and cementation from vadose and saline artesian groundwaters (Fairchild et al., in press). They apparently accreted under upper intertidal to supratidal conditions on the broad Draken tidal flat.

Reasonably well-preserved fossil assemblages (Table 1) occur at MacDonaldryggen (samples M-20 and M-21; see Figures 1 and 2) and Backlundtoppen (B-165, B-550, B-625, B-670). In fossiliferous samples, stromatolitic microfabric is preserved in uniformly fine-grained silica, with no evidence that quartz or carbonate grains larger than silt were trapped and bound (Figure 3.3). Individual laminae are 0.5–3.0 mm thick and are differentiated largely by relatively strong organic pigmentation at lamina tops. Although many laminations appear unfossiliferous at first glance, closer inspection reveals densely tangled filaments preserved as "ghosts." Irregularly distributed patches of well-preserved fossils (Figure 3.4) confirm that the mats were built by dense populations of filamentous microorganisms whose surviving sheaths are assigned to the form species *Siphonophycus kestron* and *S. inornatum*. These sheaths have unusually thick walls (>1 μm), and their large size suggests that they were formed by cyanobacteria rather than anoxygenic photobacteria. Each of these taxa forms essentially monospecific mats that can be interlaminated within a single rock sample. In general, filaments exhibit no preferred orientation, but in a few laminae populations display a distinctly vertical alignment. *Siphonophycus kestron* mats may contain an admixture of large (cross-sectional diameter >20 μm) *Siphonophycus capitaneum* sheaths, and scattered *Myxococcoides* vesicles occur in some laminae.

Taphonomy undoubtedly contributes to the observed low species richness of the in situ mat assemblage, but there are reasons for believing that these mats had a relatively low original diversity. Even within the highly diverse lower flake conglomerate assemblage (see below), most mats have a single-builder population; high species richness is largely a function of diverse mat dwellers and allochthonous populations. In the lower flake conglomerate assemblage, it can be demonstrated that these dwellers and allochthonous microfossils are preserved differentially well relative to builders (see below). Thus, it is unlikely that the low species richness of the in situ mats is a strong function of preferential decay; it reflects a low original abundance and diversity of mat dwellers and washed-in elements. This is consistent with modern microbial mats, where diversity is often inversely proportional to exposure or other environmental stress (Golubic, 1976; Whitton and Potts, 1982; see also Green et al., 1989). The robust sheaths characteristic of this assemblage also bear comparison with those of mat-builders in Recent upper intertidal to supratidal environments; thick extracellular sheaths and envelopes protect cells from desiccation and potentially harmful solar radiation (Bauld, 1981, 1986).

Upper flake conglomerate assemblage.—Silicified dolarenites and fine-grained flake conglomerates from uppermost Draken beds in MacDonaldryggen and Draken nunataks contain well-preserved microbial mat assemblages that link them genetically (in part) to the aforementioned in situ mats. The fossiliferous units occur within a complex interleaving of thin microbially laminated beds, flake conglomerates, dolarenites, pisolites, and black shale (Wilson, 1961). Chert is common in the clastic carbonates, occurring as nodules to more or less continuous beds up to a meter thick (in reality, very long nodules formed during early diagenesis). The fossiliferous flake conglomerates and dolarenites document the erosion of tidal-flat sediments and their

redeposition in sheets or broad shallow channels within the intertidal zone (Fairchild et al., in press).

Sample J-1047, from Draken nunatak, is particularly informative. As seen in thin section, this sample consists of cm-scale beds that grade from thin flakes (<1 × 1–3 mm) without matrix to arenite (Figure 3.5). Flake horizons are pervasively silicified, displaying chalcedonic, void-filling cement and little intergranular compaction. In contrast, the arenitic zones contain substantial dolomite and are compacted so that there is little minuscement porosity. Most of the flakes are fossiliferous, and almost all are redeposited microbial mat shards; few arenitic grains contain fossils.

The composition of the upper flake assemblage is shown in Table 2. Eighty-seven percent of all fossiliferous flakes contain dense populations of *Siphonophycus inornatum, S. kestron,* or mixed *S. inornatum* and *S. capitaneum* sheaths (Table 3; Figures 3.6, 3.7, 4.1). That is, most of the flakes are clearly derived from supratidal to upper-intertidal mats comparable to those described in the previous section. Three percent contain matbuilders different from those found in the in situ mat assemblage—specifically, *Siphonophycus septatum* and *Polytrichoides lineatus,* a form taxon differentiated by its tendency for sheaths to occur in coiled bundles of 6–12 filaments (Figure 4.3, 4.5). The remaining 10 percent of the fossiliferous clasts contain a diverse assemblage that includes *Myxococcoides* spp., *Polybessurus bipartitus, Sphaerophycus parvum, Eosynechococcus* spp., *Synodophycus euthemos,* and *Gloeodiniopsis mikros* (Figure 4.7). This assemblage resembles the lower flake conglomerate biota originally reported by Knoll (1982) and described in greater detail below.

Additionally, sample J-1047 contains apparently planktonic fossils in the intergranular space. Many of these are *Myxococcoides cantabrigiensis* clusters (Figure 4.2), but moderately well-preserved specimens of large acritarchs, including the morphologically complex *Trachyhystrichosphaera vidalii* (Figure 4.8) and *Cymatiopsphaeroides kullingii* (Figure 4.4, 4.6), occur as well. These distinctive Neoproterozoic microfossils are also found in the subtidal silicified carbonate assemblage and in shallow subtidal facies elsewhere in the Akademikerbreen Group and its equivalents (Knoll and Calder, 1983; Knoll, 1984; Butterfield and Knoll, 1989), substantiating their interpretation as coastalmarine planters that were washed onto tidal flats. This facies association contrasts with Zang and Walter's (1989) suggestion that large complex acritarchs indicate offshore Proterozoic environments (see also Knoll and Butterfield, 1989). The systematic, paleoecological, and evolutionary interpretation of *T. vidalii* is discussed below.

Subtidal carbonates and silicified carbonates.—Among the most remarkable assemblages in the Draken Conglomerate are those preserved in lagoonal dolomicrites and their silicified equivalents. The sediments in question are fine-grained carbonates deposited in thin, slightly irregular to subparallel beds a few to 20mm thick. The beds contain abundant particulate organic matter, often as wispy fragments of mats or, possibly, seaweeds (Figure 5.4). A few continuous mat horizons up to several mm thick are intercalated, as are thin dolosiltites and dolarenites. Dolomicrite beds may be truncated by dolarenites displaying low-angle cross-stratification. Chert occurs as continuous nodules, internal molds of vase-shaped microfossils and filamentous microorganisms, and μm-scale micronodules nucleated on particulate organic matter (Figures 5.5, 6.1, 6.2). Pervasive alteration of carbonates to dolomite followed silicification.

Schieber (1989) recently published a facies classification of Proterozoic shales based on the Middle Proterozoic Belt Supergroup. Textural and bedding characteristics of the Draken
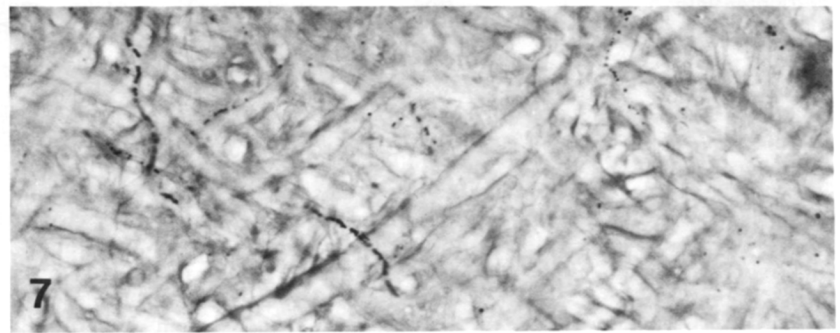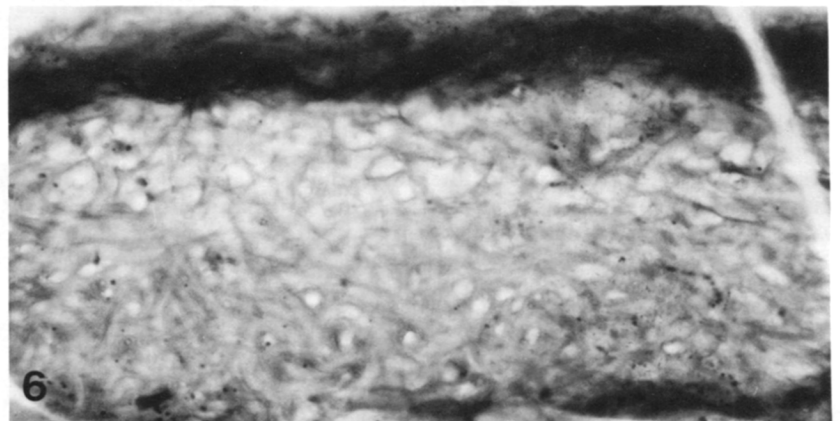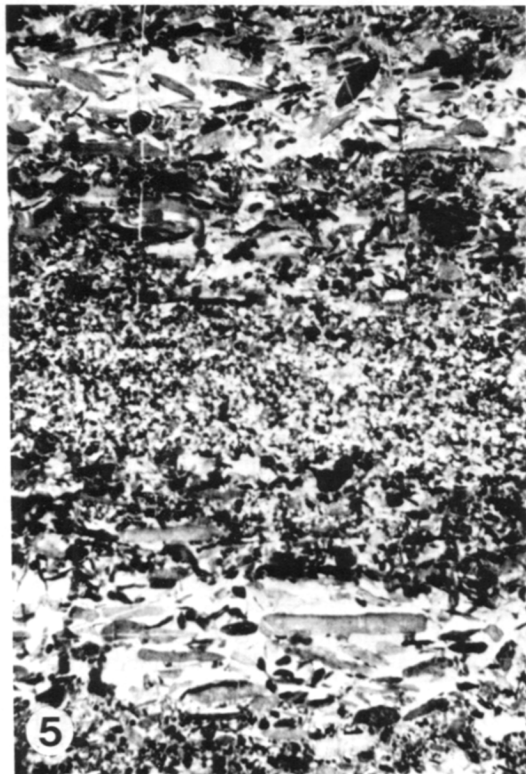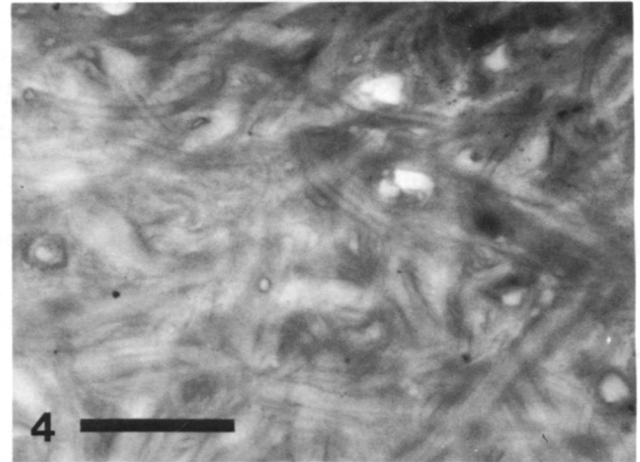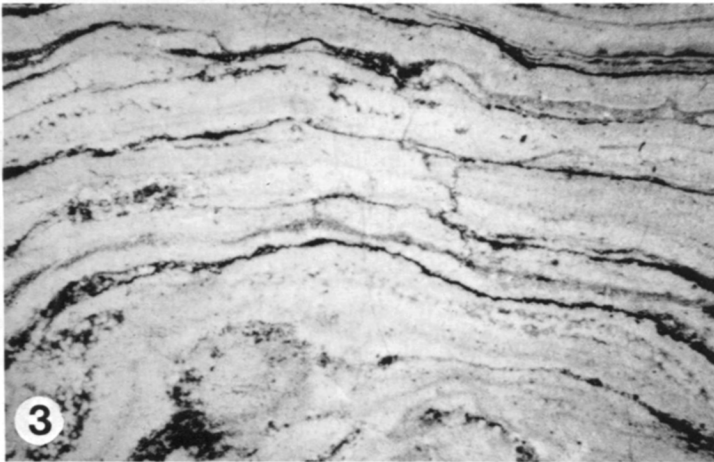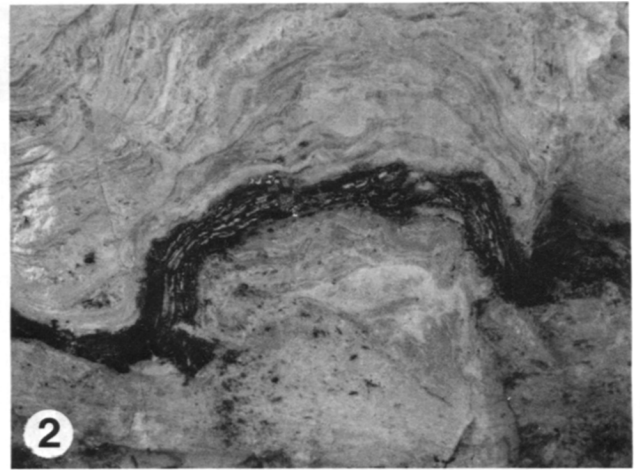
sediments do not conform in their entirety to any one of Schieber's shale types, but they do exhibit features that Schieber associated with his "carbonaceous swirl" and "striped" shales. These facies are interpreted as having been deposited subtidally between fair-weather and weak to average storm wave bases (Schieber, 1989). It is likely, therefore, that the Draken dolomicrites accumulated in a normally low-energy subtidal environment subject to episodic storms. As this environment lay adjacent to tidal flats, it was probably a protected lagoon broadly comparable to those forming today behind reefs or bars, or a wide shallow platform leeward of the tidal flat and land. A subtidal interpretation is corroborated by vase-shaped microfossils and acritarchs known to have broad geographic distribution in shallow subtidal marine sediments of Neoproterozoic age. These fossils are essentially absent from intertidal Draken mats.

Exceptional preservation of filamentous microorganisms as siliceous (or, less conspicuously, dolomitic) internal molds (Figure 5.1–5.3, 5.6) shows that at least some of these subtidal carbonates supported microbenthic populations capable of stabilizing fine-grained sediments. The casts are 13–60 μm in cross-sectional diameter and up to 500 μm long; filaments are oriented approximately perpendicular to bedding and display rare but clear branches (Figure 5.2, 5.3). No traces of carbonaceous walls or sheaths are preserved; nor is there evidence for filament calcification or tufa deposition. The filaments appear to have been buried in carbonate mud, following which early diagenetic silica emplacement insured a fossil record despite oxidation, compaction, neomorphism, and dolomitization.

The systematic interpretation of these fossils is problematic. Their size and branching habit clearly distinguish them from any of the mat-builders found in the intertidal assemblages. The gross morphology of the tubes invites comparison with molds of the cyanobacterial filament *Scytonema* reported from levees and freshwater algal marshes of Andros Island (Monty, 1967; Hardie, 1977). Like the Draken filaments, *Scytonema* species branch; however, several observations discourage too close a comparison. According to Black (1933) and Monty (1967), Andros *Scytonema* populations are inhibited by salinities approaching that of normal sea water, but there is nothing in this Draken facies to suggest fresh or brackish water. Sedimentary features associated with the Andros filaments, such as tufa and fenestrae, are absent from the Draken carbonates in question. Indeed, while reasonable, an assumption of cyanobacterial affinity is not necessarily correct. Riding (1979) has described filamentous molds of the probable green alga *Cladophorites* in lacustrine bioherms from the Miocene of Germany. Once again, the petrological characteristics of the *Cladophorites* carbonates do not match those of the Draken samples, but Riding's work establishes the point that eukaryotic algae can produce casts and molds comparable to those found in the Draken. Subtidal siliciclastic mudstones from the Svanbergfjellet Formation (immediately subjacent to the Draken) contain carpets of possible cladophoralean algae whose general size and branching fre-

TABLE 1—Taxa present in the in situ mat assemblage (samples M-20, M-21, B-550, and B-670).

Taxon	Size (μm)[1]	Comments
Siphonophycus kestron	11.0 (0.9)	Principal mat-builder
Siphonophycus inornatum	5.1 (0.8)	Principal mat-builder
Siphonophycus capitaneum	17.3 (3.9)	Auxiliary mat-builder in *S. inornatum* mats
Myxococcoides spp.	8.0–18.0	Scattered in mats

[1] Mean and standard deviation (in parentheses) or observed range for maximum diameter (cross-sectional diameter for filamentous fossils).

quency approach those of the Draken tubes (Butterfield et al., 1988).

Other microfossils in the subtidal carbonate facies include abundant siliceous internal molds of vase-shaped microfossils (Figure 7.1–7.3), common *Myxococcoides cantabrigiensis* individuals and clusters (Figure 6.1, 6.2), scattered leiosphaerid acritarchs, and, of particular interest, *Trachyhystrichosphaera vidalii* (Figure 7.4–7.8). The *Trachyhystrichosphaera* population is sufficiently large to permit confident determination of its basic morphology and within-population variability.

The genus *Trachyhystrichosphaera* (type species *T. animika*) was established by German (*in* Timofeev et al., 1976) for microfossils from the Upper Riphean Lakhanda Formation of eastern Siberia. Knoll (1984) described a second species, *T. vidalii*, from subtidal cherts of the Upper Riphean Hunnberg Formation, Nordaustlandet, Svalbard. The genus is now known to occur in late Riphean to (?)Vendian rocks from additional localities in Siberia (Pjatiletov, 1988; Jankauskas, 1989), the southern Urals (Jankauskas, 1982), Svalbard (Knoll and Calder, 1983; Butterfield and Knoll, 1989), Alaska (Allison and Awramik, 1989), and Arctic Canada (Butterfield and Knoll, 1989). Seven species have been described, but not all are well differentiated.

Trachyhystrichosphaera acritarchs are large spheroidal vesicles that bear 4–8-μm-wide conical to cylindrical processes of variable length and distribution (German *in* Timofeev et al., 1976). Processes are hollow and open to the vesicle interior. In *T. vidalii,* this process-bearing inner vesicle is enveloped in a thin outer vesicle whose surface may or may not mirror the projections of processes (Figure 7.8). Most previously described populations contain few individuals, and the size ranges reported are 250–700 μm; however, the Draken population indicates that *T. vidalii* individuals could reach the truly macroscopic size of 2,700 μm. (One 4,200-μm vesicle was found among the *T. vidalii* population, but as processes could not be identified with certainty, this specimen has not been included in the censused population.) The size frequency distribution of a sample population is shown in Figure 8. The mean diameter is 913 μm (s_x = 490 μm), and the median is 790 μm. (Note that these measurements were made on specimens observed in thin sections. Insofar as some specimens may be represented by tangential rather than equatorial slices, these diameters must be

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FIGURE 3—Facies and microfossils of the stratiform stromatolite and upper flake conglomerate assemblages. In this and all following figures, slide number, England Finder coordinates, and Harvard University Herbaria Paleobotanical Collection catalog number are given for each microfossil or population illustrated. *1, 2,* outcrop photographs of in situ stratiform stromatolites showing early diagenetic chert (dark areas); doming in *2* is probably due to soft-sediment deformation; *3,* thin-section view of silicified stratiform stromatolite, showing irregular lamination (highlighted here by dark, dolomite-rich layers); light coloration is provided by preserved filamentous microfossils; *4,* dense mat of *Siphonophycus inornatum* and *S. capitaneum* in in situ stratiform stromatolites (P-670-2A, E25/1, HUHPC #62356); *5,* thin-section view of upper flake conglomerate, showing grading between arenitic and small flake (mostly mat fragments) clasts; *6, 7,* clasts of mixed *S. inornatum/S. capitaneum* mats from upper flake conglomerate (*6,* J-1047-1A, N20/4, HUHPC #62357; *7,* J-1047-2, K23-4, HUHPC #62357). Ruler in *1* is 15 mm long; for other photographs, the bar in *4* = 4 cm for *2;* = 4 mm for *3;* = 100 μm for *4* and *7;* = 2 mm for *5;* and = 200 μm for *6.*
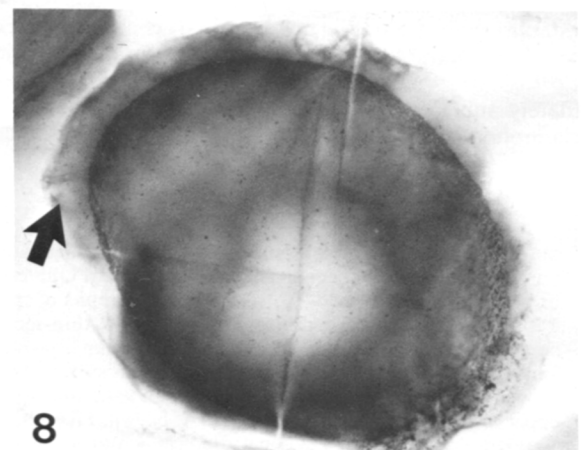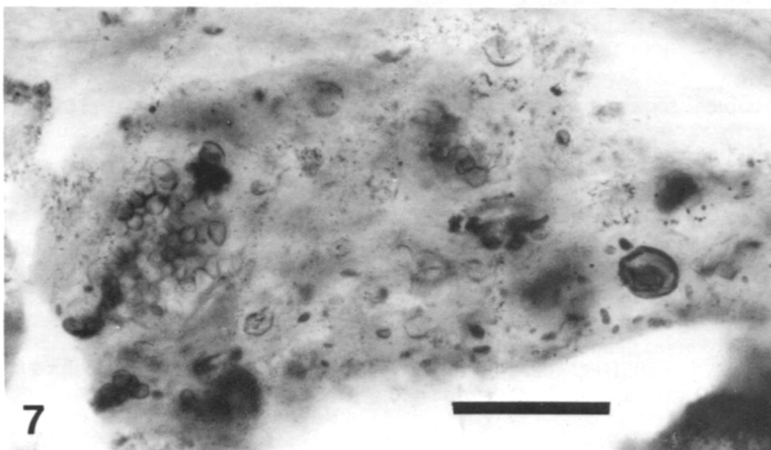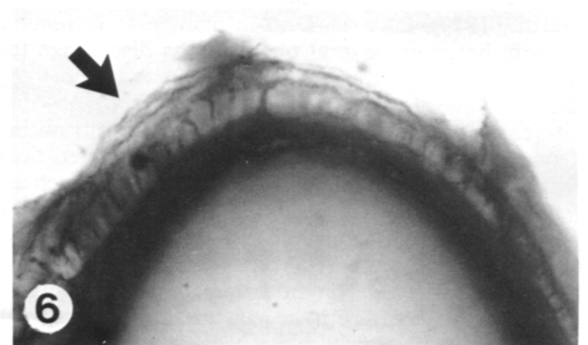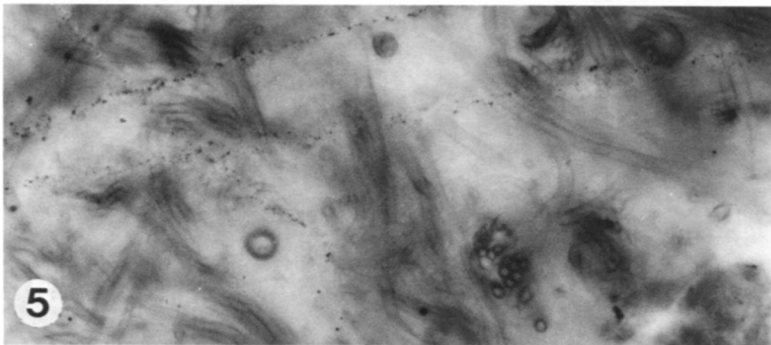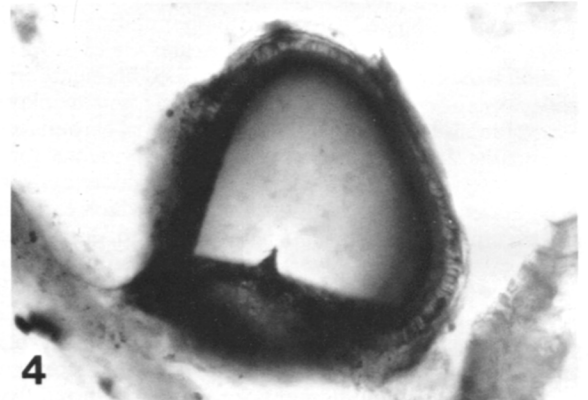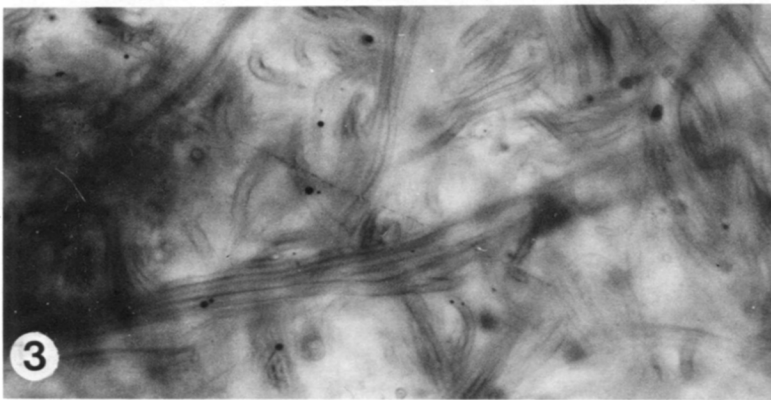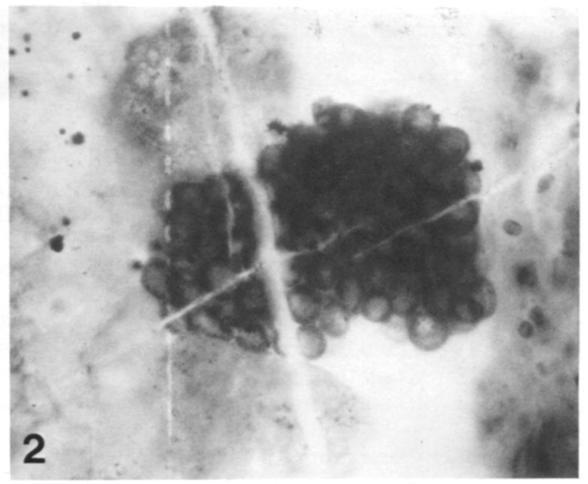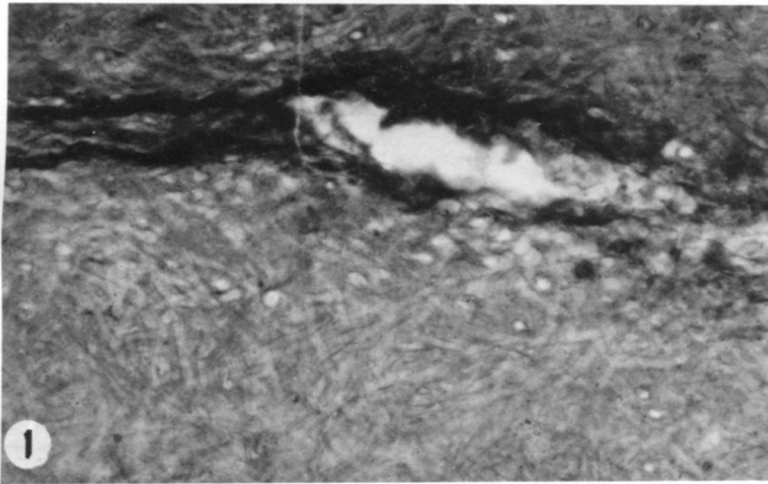
TABLE 2—Taxa present in the upper flake conglomerate assemblage [samples J-1047, B-625, and M-31 (partim)].

Taxon	Size (μm)[1]	Comments
Siphonophycus kestron	11.0 (1.4)	Principal mat-builder
Siphonophycus inornatum	4.7 (0.6)	Principal mat-builder
Siphonophycus capitaneum	17.0 (2.0)	Auxiliary mat-builder in *S. inornatum* mats
Polytrichoides lineatus	3.6 (0.7)	Rare principal mat-builder
Myxococcoides spp.	8.0–25.0	Scattered within mats
Polybessurus bipartitus	35.0–75.0	Restricted to rare high diversity clasts
Gloeodiniopsis mikros	5.5 (0.9)	Restricted to rare high diversity clasts
Synodophycus euthemos	5.0–7.0	Restricted to rare high diversity clasts
Eosynechococcus brevis	2.0–4.0	Restricted to rare high diversity clasts
Eosynechococcus medius	5.0–8.0	Restricted to rare high diversity clasts
Siphonophycus septatum	ca 1.0	Restricted to rare high diversity clasts
Trachyhystrichosphaera vidalii	410–500	Rare in intergranular chert
Cymatiosphaeroides kullingii	140	Rare in intergranular chert
Large leiosphaerid	650	Rare in intergranular chert

[1] Mean and standard deviation (in parentheses) or observed range for maximum diameter (cross-sectional diameter for filamentous fossils).

considered minimum figures.) Small individuals tend to have a relatively high density of processes. Also, processes are of varying length, even within individuals, suggesting that new processes continued to erupt as vesicles increased in size. These observations suggest that the vesicle-producing stage of *T. vidalii* was not dormant, but rather metabolically active and capable of continued growth. Among extant algae, this phenomenon is seen in the prasinophycean green algae (Tappan, 1980). Prasinophyte life cycles alternate between a motile phase and a non-motile phycoma-producing stage. The phycoma is a degradation-resistant wall that expands as the enveloped cell grows. In modern prasinophytes, the cell may increase in volume 5,000 times or more before multiple mitoses produce a new generation of motile cells (Tappan, 1980).

Draken *T. vidalii* specimens commonly display internal organic contents, which demonstrate that these vesicles contained a single large cell (Figure 7.5). As outlined above, it is likely that this encysted cell was metabolically active, altering the morphology of its vesicle as it grew. The size range of Draken specimens indicates a minimum volumetric increase of 500-fold, well within the range exhibited by living prasinophytes. Thus, the features of *T. vidalii* are consistent with its interpretation as the phycomata of (unusually large) Neoproterozoic prasinophytes. That interpretation is provisionally accepted here, although we stress its uncertainties. With even less certainty, many of the leiosphaerid acritarchs found abundantly in Proterozoic rocks have been attributed to the Prasinophyceae (Muir and Sarjeant, 1971; Tappan, 1980; Vidal and Knoll, 1983).

Lower flake conglomerate assemblage.—This facies contains the best preserved and most diverse microfossils in the Draken Formation. Originally described from a single locality in Dracofjella, on the northern side of Polarisbreen (Knoll, 1982), this assemblage has now been found in localities elsewhere in Dracofjella and in Vettene, MacDonaldryggen, and Backlundtoppen nunataks (especially samples P-13, P-91, B-165, M-11, M-12, M-13, and M-28). In all cases, the fossils occur in silicified clasts within dm-scale flake conglomerate beds (Figure 9.1–9.3). The beds commonly exhibit unidirectional cross-lamination with set thicknesses of up to 10 cm. These flake conglomerates are interbedded with, and commonly truncate, lagoonal dolomicrites. This sedimentary association and petrographic evidence indicating that early diagenesis occurred under the influence of marine pore waters, with limited evidence for subaerial exposure or leaching, suggest that these flake conglomerates formed when storms ripped up and redeposited locally derived clasts in subtidal lagoons (Knoll, 1982; Fairchild et al., in press).

Some fossiliferous flakes were clearly derived from the lagoonal micrite facies (Table 3), but others cannot be related to in situ sediments. These include clasts of biologically diverse microbial mats built by *Siphonophycus inornatum* or *S. septatum* (Figures 6.4–6.6, 10–19). The presence in these clasts of populations whose living counterparts are intertidal and the absence of organisms indicative of subtidal deposition (e.g., vase-shaped microfossils or *Trachyhystrichosphaera*) suggest that such clasts originated on the tidal flats. It is possible that the exceptional preservation of microfossils in this facies relates to

TABLE 3—Assemblage compositions of clasts in upper and lower flake conglomerates. Assemblages other than subtidal micrite assemblage named according to dominant mat-building taxa. Abundances recorded as the percentage of clasts characterized by each assemblage.

Assemblage type	Upper flake conglomerate (sample number) J-1047	Lower flake conglomerate (sample numbers)			
		P-91	M-13	W-839	P-13
S. kestron mat	16	0	0	0	2
P. lineatus mat	1	0	0	0	0
Mixed *S. inornatum/S. capitaneum* mat	16	0	0	0	4
S. inornatum mat (thick sheath, low diversity)	55	0	6	3	20
S. inornatum mat (thin sheath, high diversity)	10	13	21	19	30
S. septatum mat	2	47	23	28	22
Subtidal micrite assemblage	0	27	39	16	10
Indeterminate	0	13	11	25	12

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FIGURE 4—Microfossils from the upper flake conglomerate facies. *1*, *Siphonophycus kestron* (lower) and *S. inornatum* (upper) mats in a clast (J-1047-1A, A19/2, HUHPC #62358); *2*, *Myxococcoides cantabrigiensis* in intergranular space (J-1047-1A, T40/4, HUHPC #62359); *3*, *5*, *Polytrichoides lineatus* mat clast (J-1047-1, Y27/4, HUHPC #62360); *4*, *6*, *Cymatiosphaeroides kullingii* in intergranular space (detail showing multiple wall layers and processes at arrow; J-1047-1, Q24/0, HUHPC #62361); *7*, a relatively high diversity clast; *8*, *Trachyhystrichosphaera vidalii* in intergranular space; note process visible at arrow (J-1047-1A, D31/3, HUHPC #62362). Bar in *7* = 200 μm in *1* and *6*; = 80 μm in *2*, *3*, and *5*; = 60 μm in *4*; = 125 μm in *7* and *8*.

the sedimentary juxtaposition of tidal-flat microorganisms (with their degradationally resistant envelopes and walls), rapid burial during storms, and early diagenesis in a coastal-marine setting where the probability of early silicification is relatively high.

At least 32 taxa occur in these flake conglomerates (Table 5), but they do not occur as a homogeneous assemblage. As indicated in Table 3, at least three discrete associations can be differentiated: *Siphonophycus inornatum*-built mats, *S. septatum*-built mats, and subtidal muds containing vertical tubes of the type described in the preceding section. (Knoll, 1982, recognized a fourth mat type dominated by *Siphonophycus* (=*Eomycetopsis*) *robustum*, but that assemblage is here reinterpreted as a *Siphonophycus septatum* mat in which the auxiliary mat-builder *S. robustum* is differentially well preserved; Figure 10.3.) *Siphonophycus inornatum* mats in this facies differ from those characteristic of the in situ stratiform stromatolites and upper flake conglomerates. The sheaths of filamentous mat-builders are much less robust and are, correspondingly, more easily degraded. Also, the thin-sheathed *S. inornatum* mats contain as many as a dozen dweller species and abundant allochthonous microfossils belonging to at least four taxa. The *S. septatum* mats are comparably diverse, preserving two auxiliary builders (which never occur together), up to seven or eight dweller species, and extremely abundant allochthonous elements. Low diversity associations of the types characterizing in situ stratiform stromatolites and the upper flake conglomerate assemblage are rare or absent from this facies (Table 3).

Of the many taxa preserved in this facies, two may be singled out for special consideration. First is *Polybessurus bipartitus*, a morphologically distinctive stalk-forming microorganism (Figure 12). *Polybessurus* has been compared with modern *Cyanostylon*-like cyanobacteria that form crusts (and exclude clastic sediments) in upper intertidal to supratidal environments on Andros Island, Bahamas (Green et al., 1987). The major difference between the Neoproterozoic and living organisms is the significantly larger size of the fossils. In the Draken Conglomerate Formation, *Polybessurus* occurs only among *S. inornatum* mats. In clasts containing diverse taxa, *Polybessurus* occurs as isolated individuals or in small clusters, but in less diverse mats it sometimes forms monospecific crusts at least 3–4 cm in linear dimension. These are seen most clearly in silicified carbonates from correlative beds in the Eleonore Bay Group, central East Greenland (Green et al., 1987), but they can be observed in calcified microfossil assemblages in the Draken Formation (see below).

A second remarkable population occurs in a single thin lens in sample M-21 (Figure 13.1–13.4); the lens certainly originated within the *S. inornatum*/*S. septatum* mat zone, but where in that zone is uncertain. This lens contains what superficially appear to be several taxa: 12–15 μm vesicles, larger vesicles up to 40 μm in diameter, and vesicles containing a partially collapsed inner body. Several observations indicate that these all belong to a single entity. First, a few single clusters of cells include both empty vesicles and individuals containing a differentiated inner body. This demonstrates that within this pop-

ulation, the presence or absence of an inner body is diagenetically determined. Second, single clusters may contain both large and small individuals, usually in distinct subpopulations. The biological basis of this size differential is revealed by one fortuitously preserved subpopulation in which large vesicles (20–30 μm) contain closely packed smaller (10–17 μm) cells that fill vesicle interiors (Figure 13.1–13.3). Of 43 such vesicles observed, 30 are clearly tetrads, 7 are dyads, 3 are octads, 1 is a monad, and 2 are not determinable (Figure 14). It is clear that upon reaching a certain size range and—to judge from the population—at infrequent intervals, cells underwent division to form smaller daughter cells that were then released. The observation that cells in dyads, tetrads, and octads have volumes slightly larger than half of their divisional precursors indicates that slow growth continued during the interval of cell division (Figure 14).

This population superficially resembles *Gloeodiniopsis lamellosa*, originally described from lacustrine cherts of the Bitter Springs Formation (Knoll and Golubic, 1979), but similarities are probably fortuitous. The Draken population shows no evidence of multiple envelopes, a key distinguishing feature of *G. lamellosa*. Further, whereas in *G. lamellosa* most individuals are preserved in some stage of cell division, evidence of division is found only in one small subpopulation of the Draken fossils. The systematic position of this population, described below as *Myxococcoides chlorelloidea*, is uncertain, but candidate modern counterparts occur among chlorococcalean green algae. The common alga *Chlorella* is quite similar morphologically (Francis et al., 1978; Pickett-Heaps, 1975). Like the fossils, *Chlorella* populations can exhibit significant size variation, and this can be exaggerated by a several-fold post-mortem expansion of cell walls (Francis et al., 1978; personal observation). The walls of at least some *Chlorella* species contain sporopollenin (Atkinson et al., 1972), increasing their likelihood of preservation. Vesicle size in the Draken population exceeds that for most living *Chlorella*, but given the common occurrence of post-mortem wall expansion, this does not present a major interpretational problem. Thus, the case for placing this population among the chlorococcalean green algae is reasonable; however, given the simplicity of the fossils, we cannot regard it as compelling and so formally regard this species as incertae sedis.

Calcified microbial assemblages.—Columnar stromatolites are not common in the Draken Conglomerate, but a conspicuous horizon of lithoherms (bioherms) marks the base of the formation in southern outcrops (Figure 20.1). The sedimentology and petrology of these stromatolites are described in detail elsewhere (Raaben, 1969; Swett and Knoll, 1985; Fairchild et al., in press). In brief, they can be characterized as tabular lithoherms 20 to more than 50 m long and 4–5 m thick that accumulated in offshore coastal environments. Contacts with underlying cross-bedded microphytolitic dolarenites and enclosing micrites and dolarenites are sharp. Basal portions of the lithostromes consist of highly branched cylindrical columns showing low to moderate inheritance. The columns are 2–8 cm in diameter and lobate in cross-sectional view. Laminae are smooth and steeply convex, developing synoptic relief up to 8 cm. In

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FIGURE 5—Microfossils in the subtidal (lagoonal) carbonate facies. *1*, low power photomicrograph of thin section, showing abundant silicified internal molds of vertical tubes in dolomicrite; upper (light) portion is chert; *2, 6*, higher magnification views of facies illustrated in *1*; in *2* (P-13, G24/0, HUHPC #62363), note branching at arrow; in *6* (P-13-3A, M7/3, HUHPC #62364), the ovoid chert bodies are oblique sections through silicified internal molds of vase-shaped microfossils. *3*, SEM of a silica filament internal mold showing branching and the imprint of dolomite euhedra on its surface; *4, 5*, low power thin-section views of lagoonal facies showing the distribution of *Trachyhystrichosphaera* acritarchs, silica internal molds of vase-shaped microfossils, and organic debris; *4* is a chert nodule; in *5*, a silicification front runs through the section, with dolomite (but with silica-filled VSM's and silica micronodules nucleated on organic debris) to the left and chert to the right. Bar in *5* = 800 μm in *1, 4*, and *5*; = 200 μm in *2* and *6*; and = 50 μm in *3*.
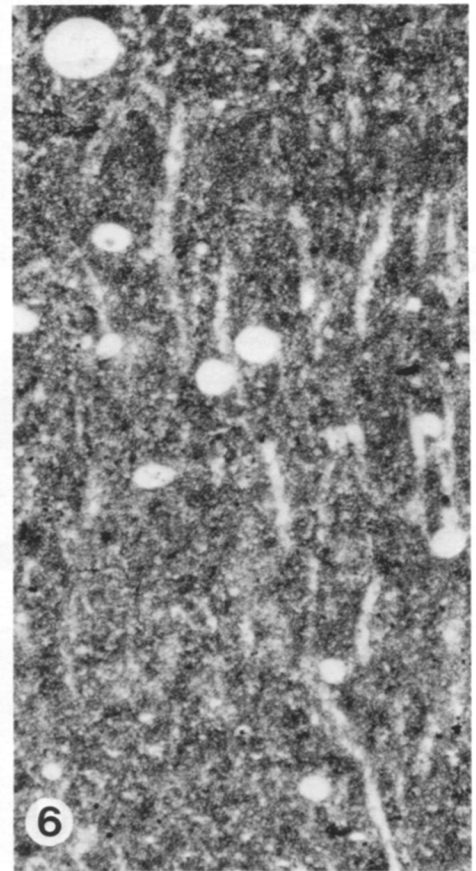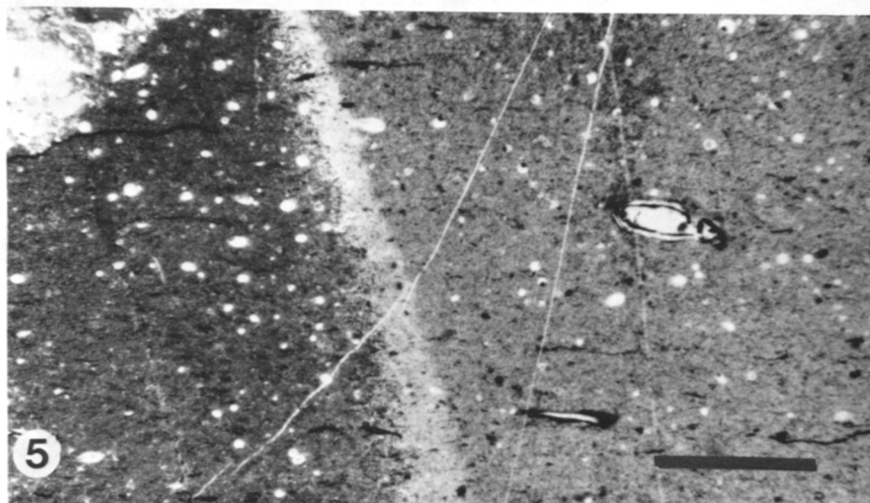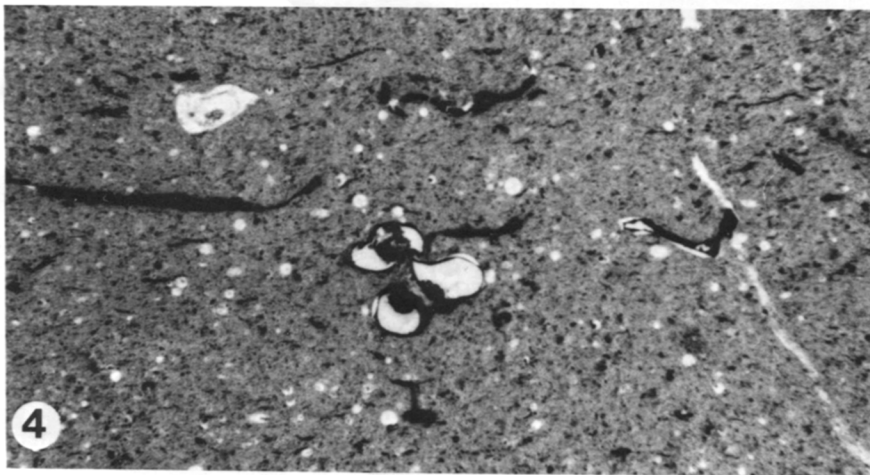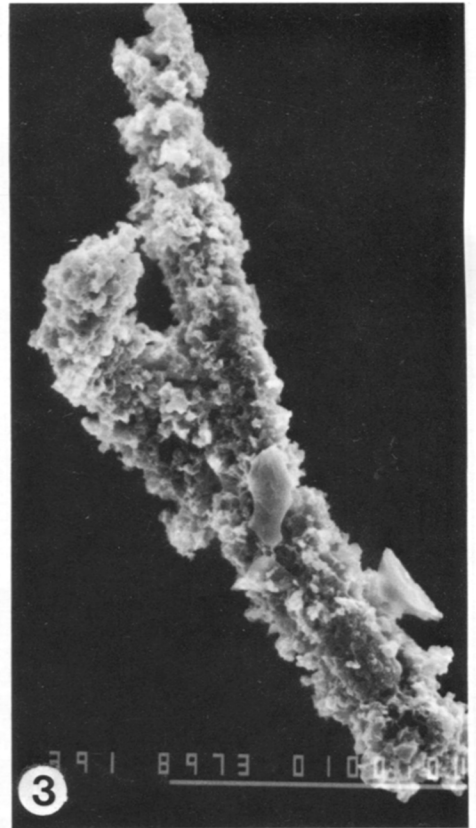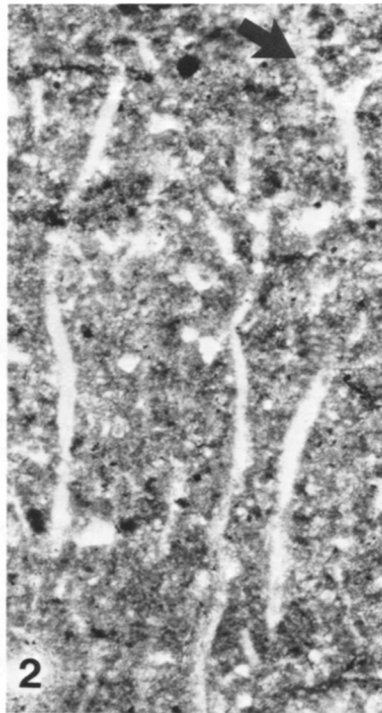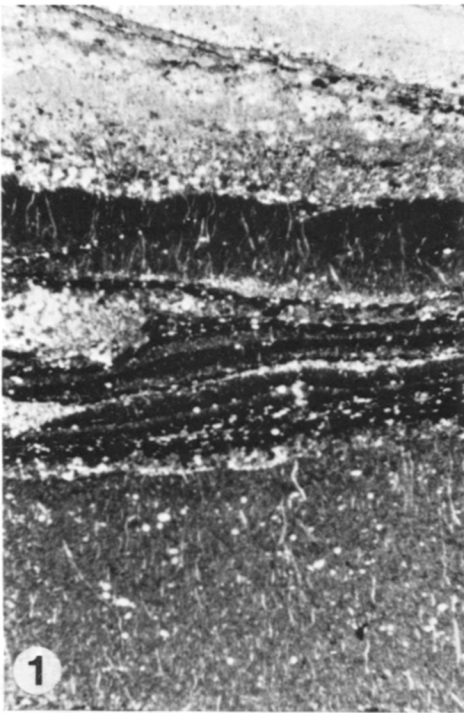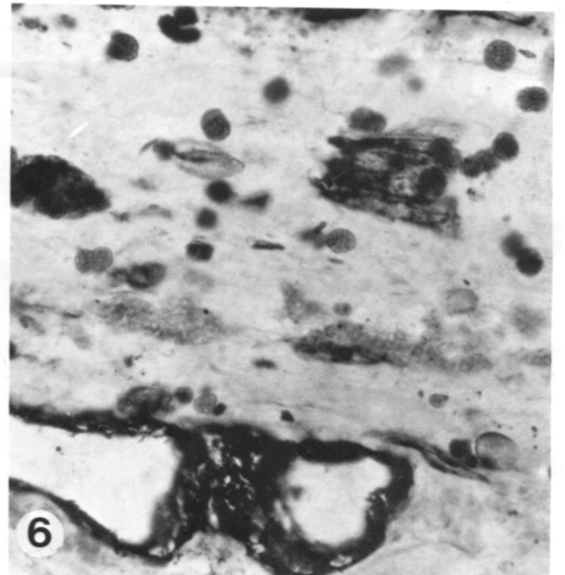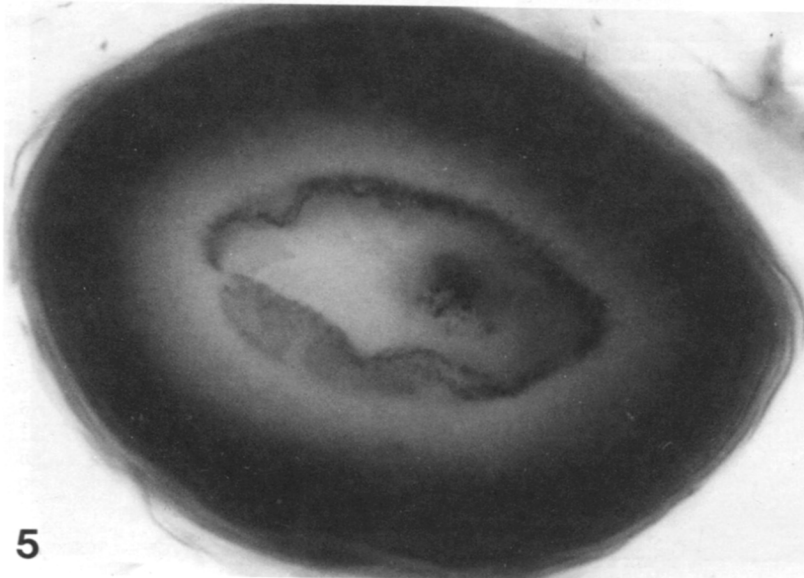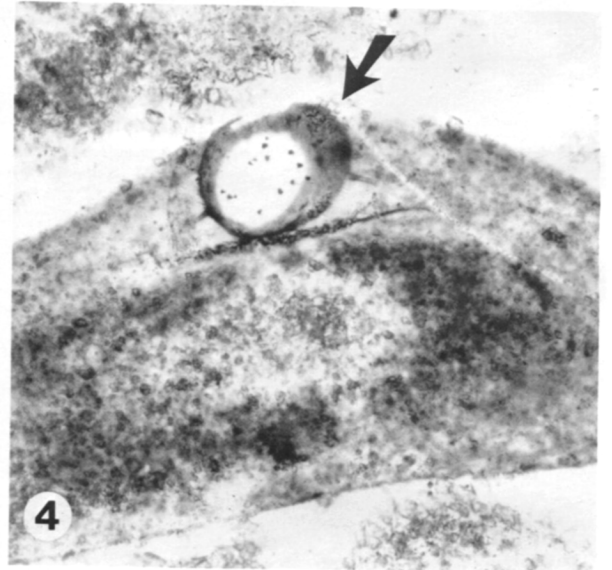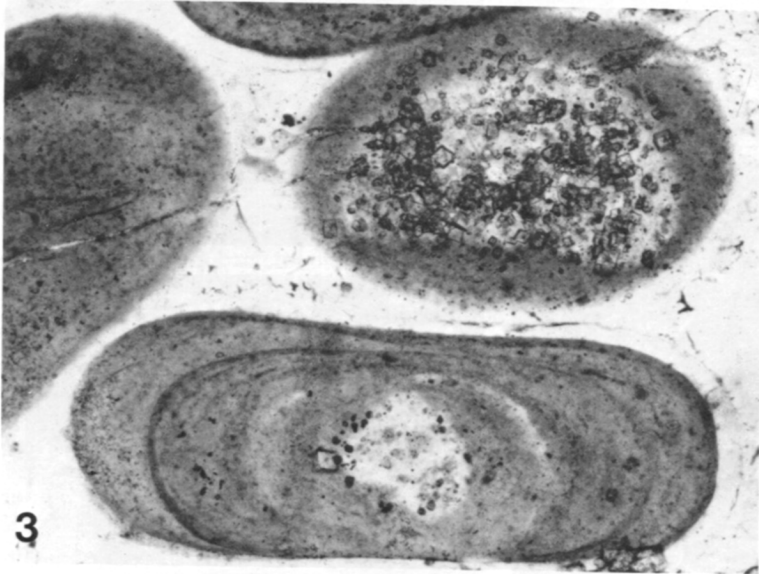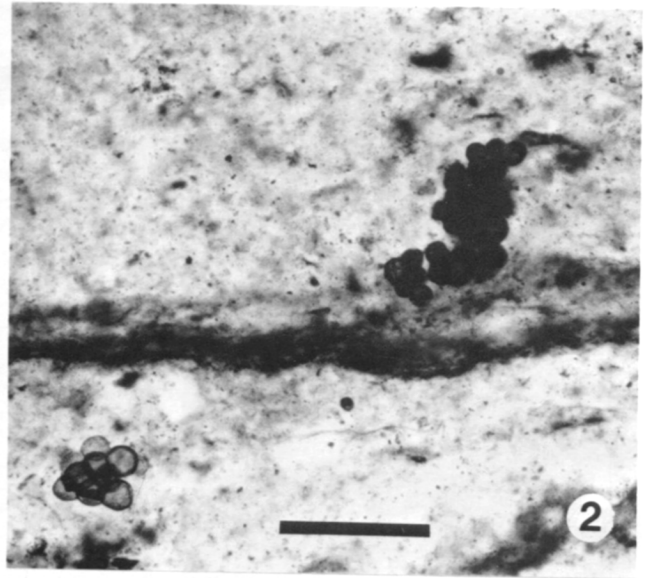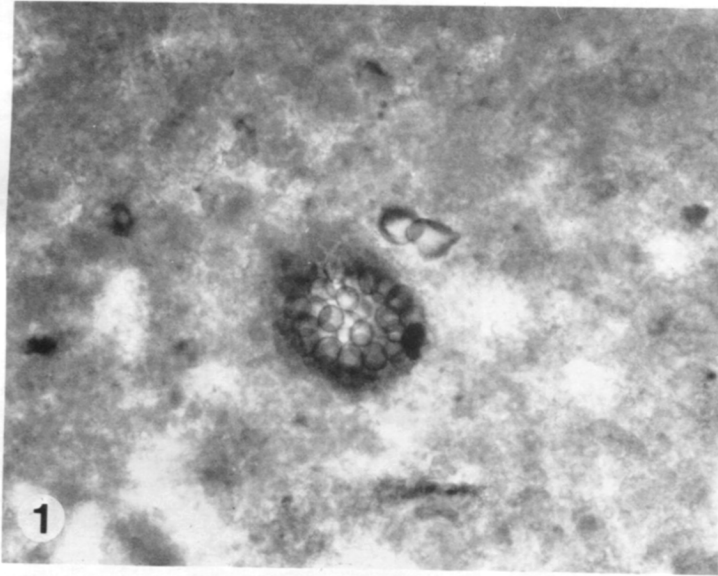
TABLE 4—Taxa present in lagoonal silicified carbonate assemblage [samples P-245, P-13 (partim), P-17, P-92, P-96, P-4350, P-4420, and M-31].

Taxon	Size (μm)[1]	Comments
Vertical tubes	24.2 (7.7)	Siliceous internal molds of problematic organisms
Siphonophycus robustum	2–3	Uncommon among vertical tubes; oriented perpendicular to bedding
Myxococcoides cantabrigiensis	11.5 (2.3)	Probable phytoplankton
Myxococcoides minor	ca 8–12	Probable phytoplankton
Myxococcoides ovata	11.8 (1.8)	Probable phytoplankton
Trachystrichosphaera vidalii	916 (490)	Probable phytoplankton
Leiosphaeridia crassa	25–60	Probable phytoplankton
Leiosphaeridia jacutica	108–400	Probable phytoplankton
Vase-shaped microfossils	64 × 30–230 × 105	Probably planktonic; siliceous internal molds
Siphonophycus spp.	ca 4–20	Fragments; probably allochthonous

[1] Mean and standard deviation (in parentheses), or observed range for maximum diameter (cross-sectional diameter for filamentous fossils).

upper portions of the lithoherms, columns are more regularly cylindrical, parallel, and sparsely branched (Figure 20.2). Inter-columnar sediments include fine-grained carbonates, micro-phytolites, and stromatolitic intraclasts.

In thin section, laminar fabrics are porostromate; they consist of interwoven dolomitic filaments (Figure 20.3–20.5; Pia, 1927). Filaments are 2–6 μm in diameter, unbranched, and oriented roughly parallel to lamination. Because of their small size, it is often difficult to determine whether filaments are hollow or solid, but scattered, clearly hollow specimens have walls defined by a thin rind of tiny dolomite crystals surrounded by radiating acicular dolomite euhedra up to 5 μm long. These acicular crystals give the visual impression of a diffuse boundary. Filaments float in a matrix of interlocking 1–25 μm dolomite euhedra. Irregular porostromate laminae 100–500 (rarely 700) μm thick are separated by subequal thicknesses of filament-free dolomite microspar. Quartz sand grains and the carbonate molds of vase-shaped microfossils are minor components of both porostromate and filament-free laminae.

The Draken filaments are unusual in two respects. Mat-building populations are seldom preserved in Proterozoic columnar stromatolites, and (?)cyanobacterial calcification is uncommon in carbonates older than late Vendian or Cambrian. Microfossils have been reported from silicified columnar stromatolites, and where mat-building populations can be identified, they are often sheath-forming oscillatorian cyanobacteria similar in general morphology to the Draken filaments (e.g., Licari, 1978; Sergeev, 1984). Oscillatorians are also important components of micro-bial communities that build subtidal columnar stromatolites today on the Bahama Banks (Dill et al., 1986). The Draken and other columnar stromatolitic fossils are significant insofar as they show that models of stromatolite growth based predomi-nantly on modern flat-laminated mats and ancient stratiform stromatolites apply to a morphologically broad range of stro-matolite types (Swett and Knoll, 1985); however, taphonomic information loss precludes detailed biological comparisons.

Girvanella and other calcified microorganisms are well known from Phanerozoic carbonates (e.g., Johnson, 1961; Wray, 1977), but as noted above, comparable preservation is uncommon in Proterozoic rocks. Indeed, calcified (?)cyanobacteria are often assumed to be absent from pre-Phanerozoic rocks, and this has been used to infer significant changes in ocean chemistry near the Proterozoic–Cambrian boundary (e.g., Riding, 1982). How-ever, not only do calcified filaments occur in Draken stromat-olites, this occurrence is not unique. Aitken (1989) has described carbonate-lined structures from stromatolites that form pin-nacle reefs in basinal facies of the Neoproterozoic Little Dal Group, Canada, and calcitized filaments also occur in Upper Riphean columnar stromatolites from the Yenisey Ridge, U.S.S.R. (Komar, 1979). The origin of the Draken calcified fossils is uncertain, but their presence indicates that under the right conditions, the calcification of microorganisms was pos-sible long before the dawn of the Cambrian Period.

In fact, the *Girvanella*-like tubes are not the only calcified fossils in the Draken Formation. One sample from the Polar-isbreen region contains thin horizons of closely packed cylin-drical tubes oriented perpendicular to bedding (Figure 12.8). The tubes range from 40 to 170 μm in diameter, and can reach lengths of 2 mm. Most appear unbranched but one convincing dichotomy was observed. Tube walls are defined by a dark rim of minute dolomite crystals. Inter-tube dolomite is also finely crystalline, while intra-tube dolomite forms a coarse mosaic.

Despite differences in preservational mode, these dolomitic fossils can be compared with encrusting populations of *Poly-bessurus bipartitus* described from partly correlative beds in East Greenland (Green et al., 1987; compare their fig. 5) and South Australia (Fairchild, 1975). Similarities include general mor-phology and encrusting habit. Calcified Draken populations do not display the chevron-like stacking of envelopes seen in silic-ified *P. bipartitus,* but this is explained easily as a taphonomic difference; the "stalks" of large *Polybessurus* specimens in the East Greenland crusts are frequently degraded to hollow tubes and may be filled by diagenetic carbonate. The Greenland and Draken crusts are further similar in their common inclusion of *Siphonophycus inornatum* sheaths aligned more or less parallel to *Polybessurus* "stalks." Draken crusts occur in highly fenes-trate grainstones, but clasts appear to have been excluded from crust horizons.

Shale assemblage.—Carbonaceous shale and siltstone occur sporadically throughout the Draken Formation as partings to thin beds (generally less than 25 cm thick). Few of these units are fossiliferous, but sample P-23, collected from a thin shale exposed in the Polarisbreen area, contains abundant and mod-erately well-preserved organic-walled fossils. The shale is one of a population of partings to thin beds intercalated among a complex interleaving of 10–20-cm-thick cross-bedded dolar-

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FIGURE 6—*1, 2, Myxococcoides cantabrigiensis* clusters in lagoonal facies. *1,* the fossils are silicified, but the surrounding sediment is dolomite; *2,* from a chert nodule. *3,* silicified oncoids in the oncolitic facies; *4,* a *Trachyhystrichosphaera* individual incorporated into an oncoid lamina (P-97-1A, U35/0, HUHPC #62367). *5,* unnamed form E from the lower flake conglomerate facies (P-4353-4A, T30/1, HUHPC #62368); *6,* lower power view of lower flake conglomerate mat assemblage containing, among other things, *Synodophycus euthemos* and poorly preserved leiosphaerid acritarchs. Bar in *2* = 60 μm in *1* and *2;* = 200 μm in *3;* = 150 μm in *4* and *6;* and = 20 μm in *5.*
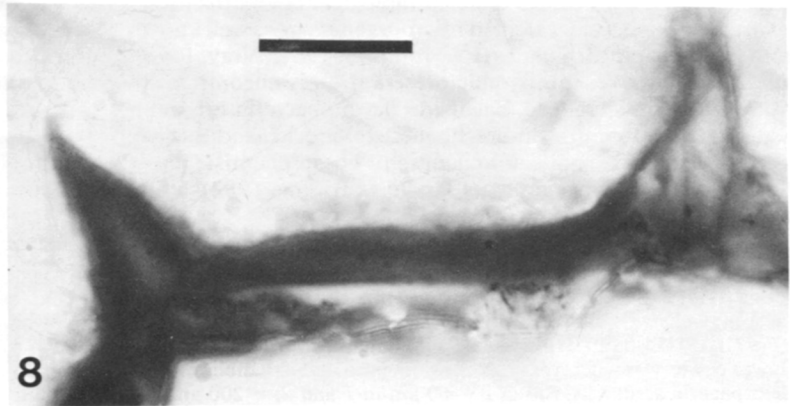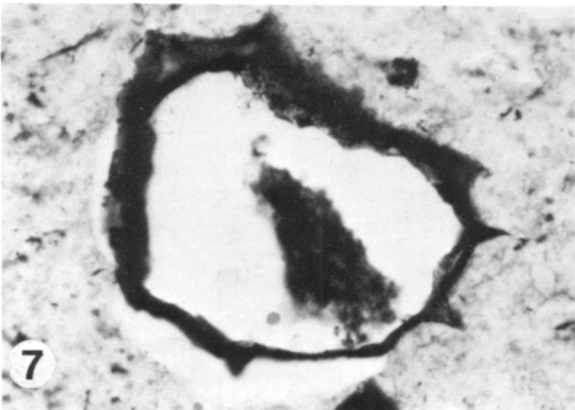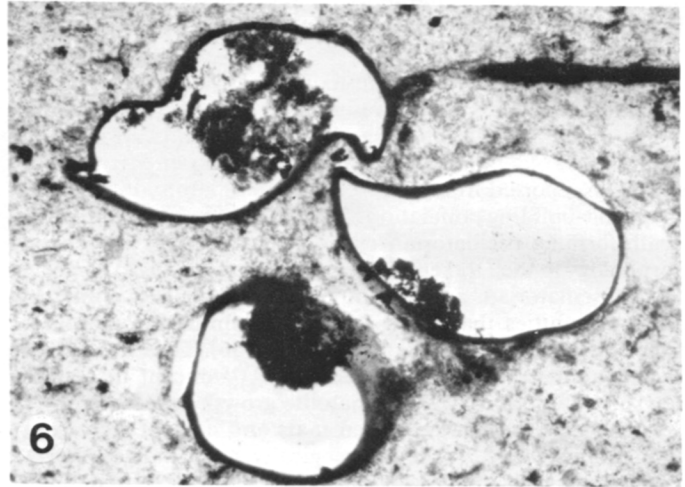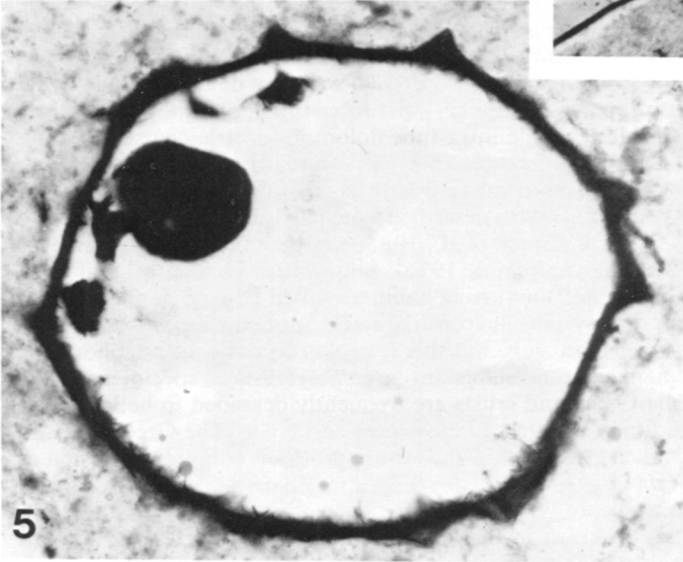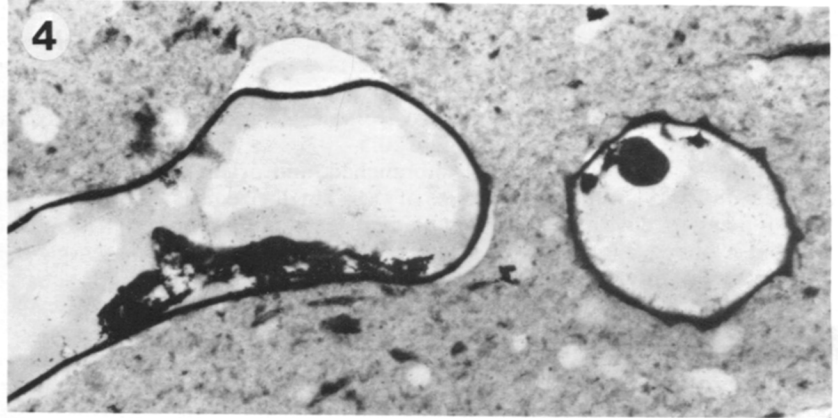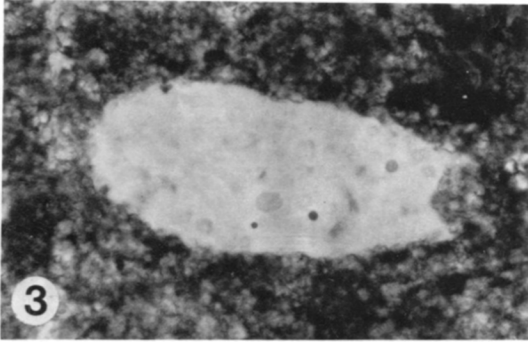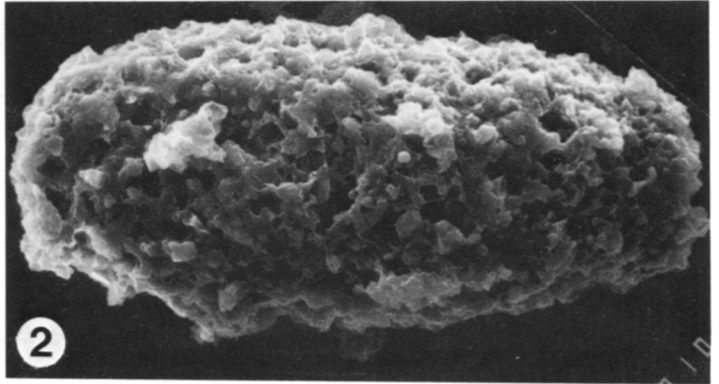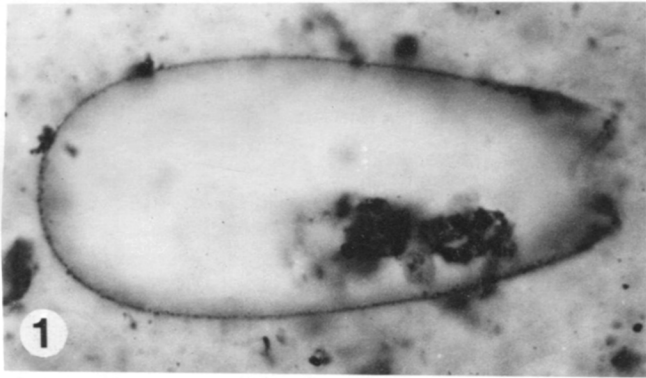
enites, stratiform stromatolites, and subtidal dolomicrites and carbonaceous micrites. The fossiliferous shale is interpreted as a coastal subtidal deposit, an interpretation supported by its fossil content.

In general, the fossils preserved within sample P-23 can be compared with those found in previously discussed carbonate lithologies (Table 7). Small (9–25 μm), relatively thick-walled spheroidal vesicles are the most abundant constituent of this assemblage, making up 50 percent of all identifiable remains. These fossils occur as isolated individuals or, rarely, in clusters of up to 10–20; they cannot be differentiated from *Myxococcoides cantabrigiensis* populations preserved in Draken subtidal to lower intertidal cherts. About 10 percent of the assemblage consists of filamentous sheaths ranging from 2 to 20 μm in cross-sectional diameter (Figure 21.7). Essentially all of these remains are fragmental and, hence, most likely allochthonous. The observed size range compares closely with that established for tidal-flat mat-builder populations, and it is thus reasonable to assume that many of these sheaths originated with tidal-flat cyanobacteria. Trichome remains (Figure 21.8–21.10) are nearly as common as sheaths in sample P-23, in line with previous work suggesting that preservation in siliciclastic lithologies can equal or exceed that generally attributed to cherts (e.g., Jankauskas, 1982; Butterfield et al., 1988; Butterfield, 1990). Like the sheaths, trichome remains are generally fragmental and 2–19 μm in cross-sectional diameter. Trichomes, of course, provide morphological data on cell length and morphology as well as width, and Draken shale filaments suggest a species diversity higher than that discernible in silicified tidal-flat populations or shale fragments. A final component possibly derived from adjacent tidal flats consists of rare (1 percent of the assemblage) prokaryotes otherwise found in tidal-flat mats, such as *Gloeodiniopsis mikros* (Figure 21.11).

The remaining third of the shale assemblage consists of acritarchs. Thin-walled spheroidal vesicles comparable to *Stictosphaeridium* spp. (sensu Vidal, 1976) are relatively common, as are more robust spheroids in the 30–70 μm range, assignable to *Leiosphaeridia crassa* (Figure 21.4, 21.5). Individual vesicles display some variation in wall texture, but much if not most of this variation appears to be diagenetic in origin (Figure 21.6). Large leiosphaerids (*Leiosphaeridia jacutica* and *Leiosphaeridia* sp. cf. *L. atava*) commonly occur as fragmental remains, although whole vesicles can be recovered (Figure 21.1–21.3). Morphologically comparable acritarchs are common in coastal marine facies of Neoproterozoic age (e.g., Vidal, 1976; Jankauskas, 1982, 1989; Knoll, 1984). Rare incomplete specimens of *Trachyhystrichosphaera vidalii*, *Gorgonisphaeridium maximum* comb. nov. (Figure 21.12), and *Satka* sp. round out the assemblage.

Oncolitic assemblage.—Thin oncolite beds occur sporadically in the middle and upper thirds of the Draken succession. Sedimentologically and paleontologically, grains in the Draken oncolites are very similar to the minute fossiliferous oncoids described from the overlying Backlundtoppen Formation (Knoll et al., 1989); thus, only brief mention is made here. The oncoids are ellipsoidal structures up to approximately one millimeter long (Figure 6.3). Crescentic laminae generally contain only amorphous organic matter, but in samples P-4665, P-28, and
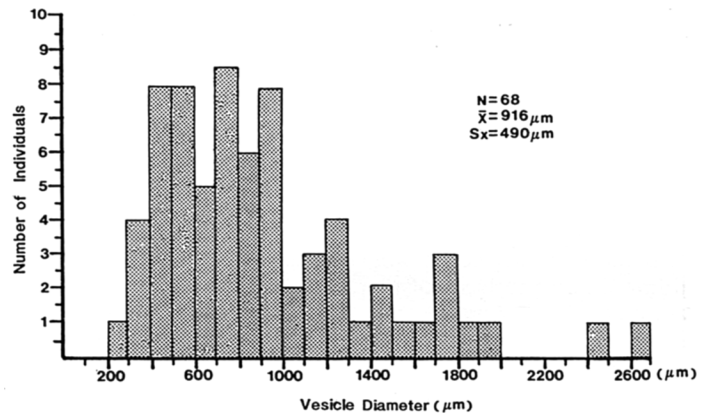

FIGURE 8—Size frequency distribution of a sample population of *Trachyhystrichosphaera vidalii* from the subtidal (lagoonal) carbonate facies.

P-97 a few grains preserve densely interwoven sheaths of *Siphonophycus robustum*, the presumably oscillatorian oncoid- and mat-builder. These oncoids appear to have accreted in shallow water on the flanks of protecting shoals, an interpretation corroborated by the incorporation of *Trachyhystrichosphaera vidalii* into the laminae of one grain (Table 8; Figure 6.4).

PALEOENVIRONMENTAL SYNTHESIS

The paleoenvironmental distribution of Draken microfossils.—Along present-day coast lines, the environmental distributions of bacterial and protistan populations are often sharply delimited (e.g., Round, 1981). Realized habitat ranges are generally narrower than those circumscribed by physiological tolerances, strongly suggesting that organism–organism interactions such as competition and predation play an important role in determining population distributions (e.g., Knoll and Bauld, 1989). One might expect that Proterozoic microorganisms would also be distributed along environmental gradients, and indeed the common paleontological observation is that populations are strongly facies dependent (e.g., Hofmann, 1976; Knoll, 1981; Green et al., 1989). The Draken Conglomerate Formation clearly contains a number of distinct microfossil biofacies. Those in situ rocks—stratiform stromatolites and lagoonal micrites—are easily mapped onto the supratidal–subtidal gradient, but associations confined to redeposited clasts present an interpretational challenge. Fortunately, the ranges of many individual species extend across several associations, so that the simple assumption of range contiguity permits an unambiguous paleoenvironmental ordering of biofacies. The five principal biofacies recognized in Draken rocks are shown in Table 9 and Figure 22, and the distributions of individual species among biofacies are shown in Figure 23. Of the eight taxa of benthic filaments recognized, seven have clearly defined distributions that can be used to define and link assemblages. *Siphonophycus kestron* mats fall at the upper end of the exposure scale, while vertical, branched filaments characterize submerged lagoonal muds. Mats dominated by *Siphonophycus inornatum* (thick and thin walled) and *S. septatum* are intermediate, and are ordered on the basis

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FIGURE 7—Microfossils from the subtidal (lagoonal) carbonate facies. *1–3*, vase-shaped microfossils preserved as organic vesicles in chert (*1*, M-31-1A, L23/0, HUHPC #62369) and as silica-filled internal molds in dolomite (*2*, SEM showing impressions of dolomite euhedra; *3*, P-13, K15/0, HUHPC #62370); *4–8, Trachyhystrichosphaera vidalii* (*4* and *5*, P-245-1B(5), U27/3, HUHPC #62371; *6*, P-245-1B(1), O18/1, HUHPC #62372; *7*, P-245-1B(3), M19/4, HUHPC #62372; *8*, a detail of *7* showing process structure. Bar in *8* = 25 μm in *1* and *2*; = 50 μm in *3*; = 200 μm in *4* and *6*; = 150 μm in *7*; and = 20 μm in *8*.

of the distributions of *S. capitaneum* and *S. robustum*. All other populations can be mapped onto this framework; resulting ranges are continuous and trends in morphology and/or abundance are predictable or at least logical. Thus, of the 42 taxa recognized in Draken rocks, 39 have paleoenvironmental distributions that can be characterized in detail. Those of the three remaining species can be constrained to within a portion of the gradient, but because the fossils are isolated in individual clasts, their precise distributions remain somewhat ambiguous.

While these paleoenvironmental interpretations are derived primarily on the basis of empirical paleontological considerations, they are supported by independent petrological microfacies analysis (Fairchild et al., in press). They also make sense in light of microbial distributions along modern tidal flats. For example, several distinct trends are evident along the Draken supratidal to subtidal gradient (Figure 24). Extracellular sheaths of mat-building cyanobacteria are commonly thick in the most frequently exposed assemblages, thinning markedly toward permanently submerged lagoons. As noted above, a similar trend is seen in modern systems and appears to reflect the important role of sheaths in cyanobacterial tolerance to desiccation and high fluxes of solar radiation. At the same time, the diversity of both mat-dwelling microbenthos and allochthonous fossils increases along the same gradient, much as it does in modern mat communities, where diversity is inversely proportional to environmental stress (Golubic, 1976; Whitton and Potts, 1982). Microbenthic diversity appears to decrease in the lagoons, but this may be misleading in that permanently submerged microorganisms often lack robust sheaths and/or cysts that facilitate preservation (Golubic and Barghoorn, 1977). Plankton/allochthon diversity is clearly highest in lagoonal muds; although plankton-bearing sea water regularly flooded the tidal flats, many populations were able to avoid becoming marooned on mat surfaces.

A final trend evident in thin sections is that the ratio of sediment to fossils in a given volume of rock increases markedly from upper intertidal or supratidal mats across the tidal flat to the lagoons.

Broader paleoecological considerations.—The environmental range of the Akademikerbreen Group exceeds that recorded in the Draken Conglomerate Formation, as does its paleontological diversity. The tidal flat/lagoonal environments of the Draken Formation can be related sedimentologically to oolitic shoals and more open coastal-marine environments represented elsewhere in the group (Knoll and Swett, 1990). Fossil assemblages have been recorded for much of this range. Endolithic, epilithic, and interstitial populations from oolitic shoals are well displayed in the Backlundtoppen Formation and its equivalents in East

Greenland, and oncoid-building and mat-forming cyanobacteria that apparently lived on the flanks of shoals occur as well (Green et al., 1988; Knoll et al., 1989). Both tidal flat and open-coastal assemblages occur in the Svanbergfjellet Formation (Butterfield et al., 1988). The overall pattern is a series of microbial-mat communities deployed along extensive tidal flats; a lagoonal biota characterized by both distinct microbenthos and plankton; oncoids and thin mats built along shoal margins by *Siphonophycus robustum*, an auxiliary builder in some marginal intertidal/subtidal *S. septatum* mats; an oolitic assemblage consisting of 8–10 distinct endolithic cyanobacterial populations, accompanied by several cyanobacterial and protistan epiliths and interstitial space dwellers; and a quiet offshore biota containing diverse prokaryotic microbenthos, seaweeds, and diverse phytoplankton. Microbial mats formed in these offshore environments and locally built up into stromatolitic patch reefs. Within individual biofacies, species diversity may vary from one or two species to 30 or more. As many as 80 morphologically distinguishable taxa occur in the group as a whole, and no one species occurs in all facies. Neither does any one facies represent Akademikerbreen diversity as a whole, although the quiet subtidal mudstones display the greatest variety of forms (Butterfield et al., 1988).

Just as no one facies characterizes overall Akademikerbreen biology, neither do Akademikerbreen fossils exhaust the diversity of the late Riphean fossil record. Extensive data from the Soviet Union corroborate many features of Akademikerbreen paleontology, but the Soviet record contains both environments and taxa not represented in Spitsbergen (summarized in Jankauskas, 1989). Other extensions include *Eoentophysalis* mats and associated assemblages from arid-zone tidal flats (represented in the Neoproterozoic by the Narssârssuk Formation, Greenland; Strother et al., 1983), the ecologically heterogeneous and locally diverse coastal playa-lake biotas of the Bitter Springs Formation, Australia (Schopf, 1968; Schopf and Blacic, 1971; Knoll and Golubic, 1979; Knoll, 1981; Southgate, 1986), and even assemblages of small phytoplankton from deep-water turbidites such as the lower Hedmark Group, Norway (Vidal and Nystuen, 1990).

CONCLUSIONS

Neoproterozoic oceans were diverse and ecologically heterogeneous, but not randomly so. Patterns of diversity and species distribution among environments can be resolved using approaches and gaining insights comparable to those routinely associated with Phanerozoic fossils. Moreover, many of these patterns can be interpreted in light of Recent sedimentological and biological analogs. For the first time, we are coming to

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FIGURE 9—*1, 2*, outcrop views of lower flake conglomerate facies; chert nodules and silicified clasts are black. *3*, thin-section view of lower flake conglomerate, showing compacted dolomite grains (dark) and relatively uncompacted grains in silicified area (light); ghosts of vertical tubes are faintly visible in the large silicified clast at the top of the picture; *4, 5, Siphonophycus inornatum* mats in lower flake conglomerate clasts (*4*, P-4353-7G, G20/0, HUHPC #62373; *5*, P-4353-1A, R21/1, HUHPC #62374); *6, S. inornatum* mat in which filaments are preserved as iron-oxide infillings. Ruler in *1* is 15 mm; bar in *4* = 25 mm for *2*, = 1.5 mm in *3*, and = 100 μm in *4–6*.

FIGURE 10—Lower flake conglomerate assemblage. *1*, low magnification view of *Siphonophycus septatum* mat containing *Myxococcoides; 2, S. septatum* mat population (P-4353-13A, T19/1, HUHPC #62375); *3, 5, S. robustum* differentially well preserved in *S. septatum* mats (*3*, P-91, U22/4, HUHPC #62376; *5*, W(P)-839-B, V31/3, HUHPC #60475); *4, 6, Salome svalbardensis* filaments in *S. septatum* mat clasts, note the absence of diffluent outer sheaths in *6* (see Knoll, 1982) (*4*, W(P)-837-D, K23/2, HUHPC #60483; *6*, W839-D, L26/0, HUHPC #60487); *7*, large *Myxococcoides cantabrigiensis* population in clast (P-4353-12F, F19/3, HUHPC #62377); *8, Myxococcoides minor* (W(P)-837-B, L8/4, HUHPC #60511). Bar in *5* = 50 μm in *1, 2*, and *3*; = 35 μm in *4* and *6*; = 20 μm in *5*; = 200 μm in *7*; and = 15 μm in *8*.

FIGURE 11—*Myxococcoides cantabrigiensis* in the lower flake conglomerate facies. *1, 5*, low magnification views of populations; *2, 4*, details of individual vesicles (P-4353-7G, G21/0, HUHPC #62378); *3*, cluster of vesicles within a split larger vesicle (P-91-1A, R20/4, HUHPC #62379); *6*, cluster showing variable preservation of internal contents (M-13-8A, V22/4, HUHPC #62380). Bar in *4* = 60 μm in *1*; = 12 μm in *2–4* and *6*; and = 200 μm in *5*.
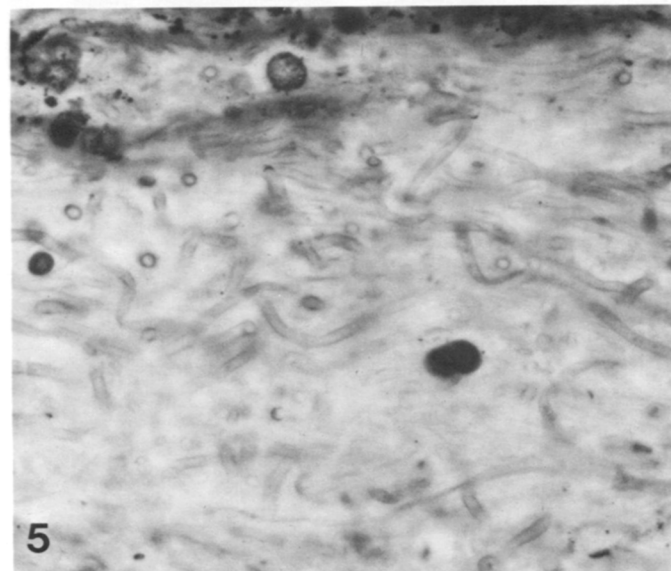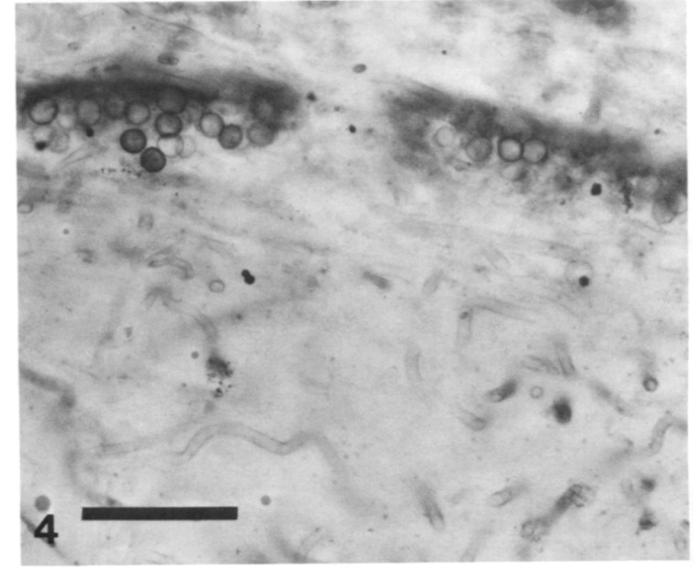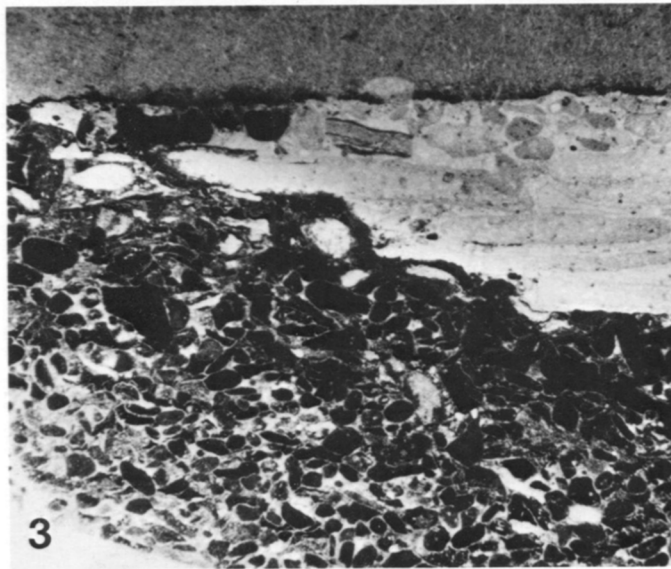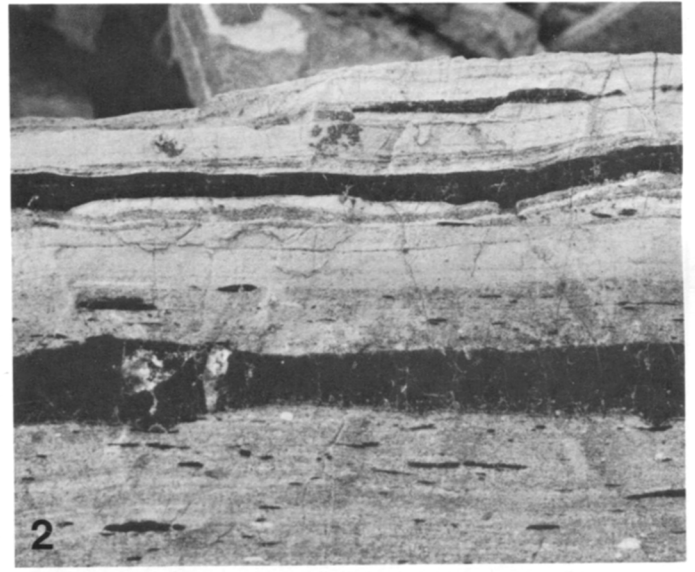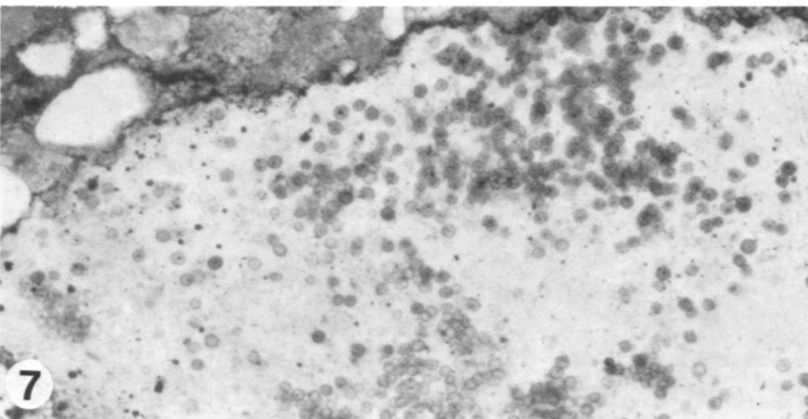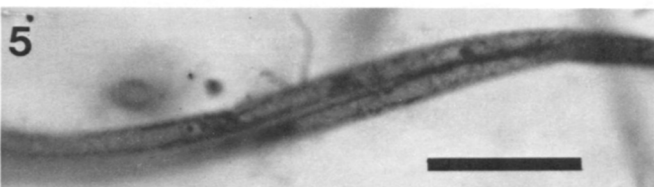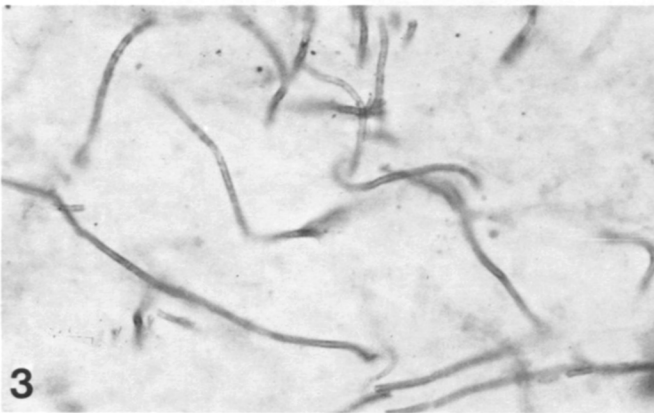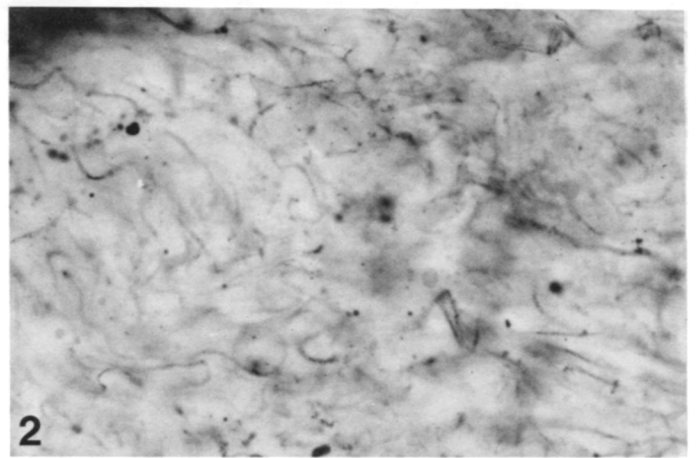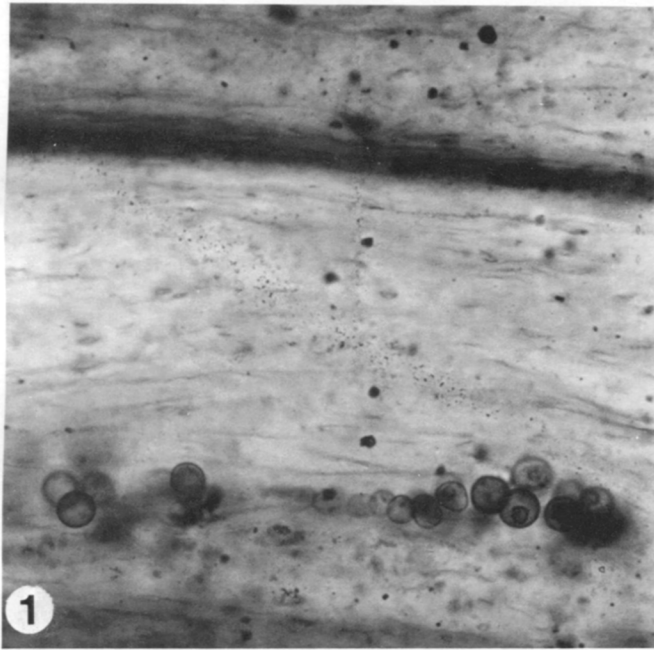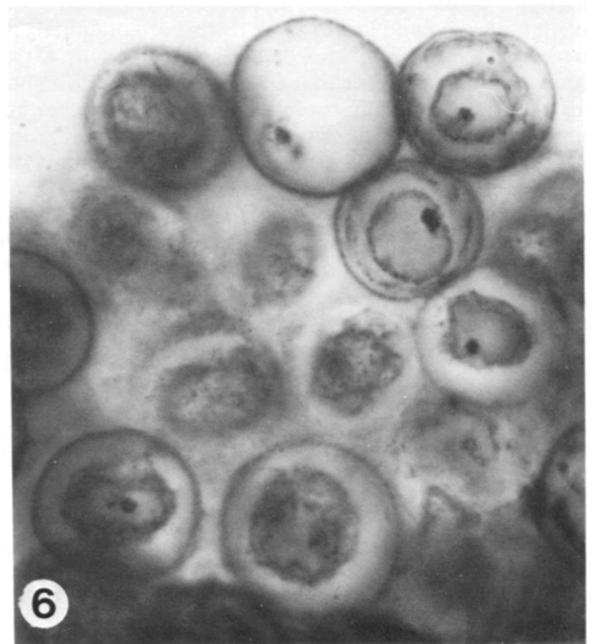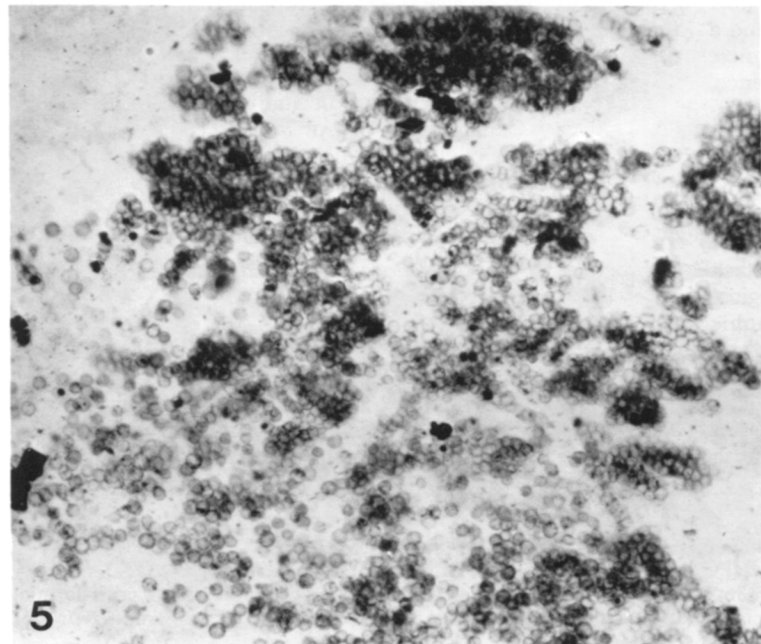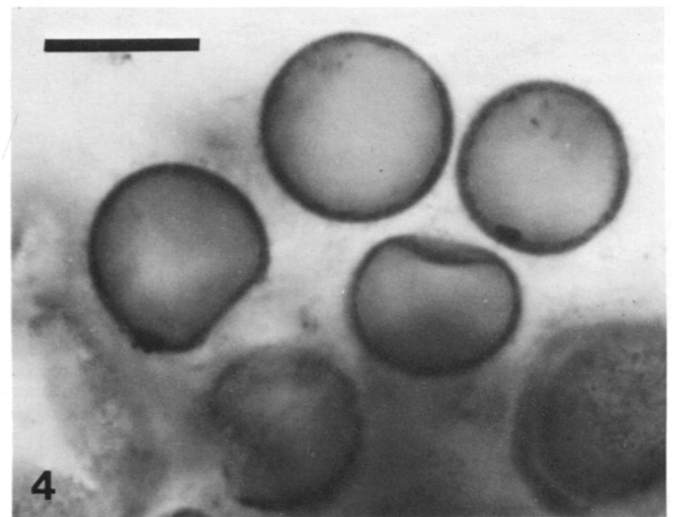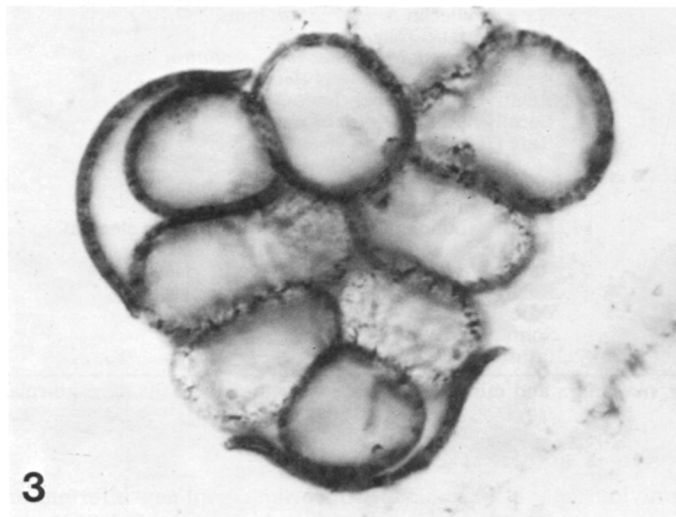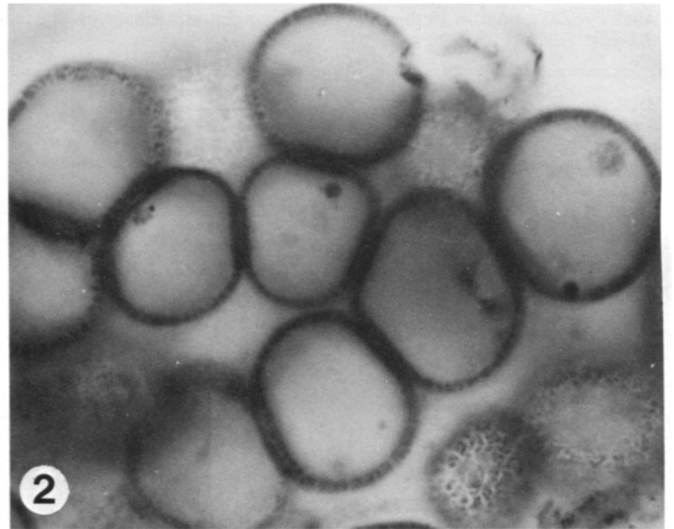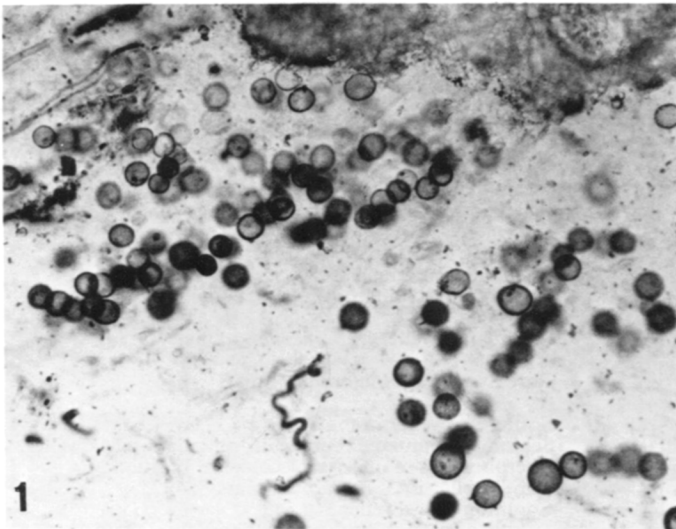
TABLE 5—Taxa present in the lower flake conglomerate assemblage (samples P-13, P-91, P-4340, P-4420, B-165, SP-15, M-11, M-12, M-13, and M-28).

Taxon	Size (μm)[1]		Comments
Siphonophycus kestron		9.0–13.0	Rare principal mat-builder
Siphonophycus inornatum		5.2 (0.8)	Common principal mat-builder
Siphonophycus septatum		1.0 (0.2)	Common principal mat-builder
Siphonophycus capitaneum		14.0–25.0	Rare auxiliary builder in *S. inornatum* mats
Salome svalbardensis	Outer:	36.0 (8.8)	Auxiliary builder in some *S. septatum* mats
	Inner:	11.4 (2.4)	
Siphonophycus robustum		2.4 (0.5)	Auxiliary builder in some *T. septatum* mats
Vertical tubes		15–50	In subtidal micrite clasts
Polybessurus bipartitus		41.7 (17.3)	Scattered individuals in *S. inornatum* mats; rare crust formers
Gloeodiniopsis mikros	Outer:	9.0 × 11.7 (2.0 × 2.7)	Abundant dweller in *S. inornatum* mats
	Inner:	4.0 (0.8)	
Gloeodiniopsis grandis	Outer:	32.0	Rare dweller in *S. inornatum* mats
	Inner:	23.0 × 10.0–12.0	
Eosynechococcus medius		6.5 × 3.0 (1.7 × 1.0)	Scattered dweller in mats
Eosynechococcus brevis		2.8 × 2.0 (1 × 0.5)	Seldom encountered, but locally abundant mat-dweller
Eosynechococcus depressus		7.2 × 3 × 1 (1.2 × 0.6)	Microbenthos of uncertain ecological position
Eosynechococcus sp.		7.0–12.0 × 1	Rare dweller in *S. inornatum* mats
Sphaerophycus parvum		2.0–3.0	Common mat-dweller
Sphaerophycus medium		3.3 (0.8)	Locally abundant dweller in *S. inornatum* mats
Synodophycus euthemos		5.4 (0.8)	Common dweller in *S. inornatum* mats
Eoentophysalis belcherensis		11.6 (3.6)	Rare dweller in *S. inornatum* mats
Tetraphycus diminutivus		ca 1.0	Rare (?)mat-dweller
Coniunctiophycus majorinum		3.3 (0.5)	Locally abundant dweller in *S. septatum* mats
Myxococcoides cantabrigiensis		12.5 (2.7)	Abundant allochthonous element
Myxococcoides minor		10.5 (0.9)	Relatively rare allochthonous element
Myxococcoides stragulescens		6–16	Locally abundant surface coverer
Myxococcoides chlorelloidea	Outer:	18.0–26.0[2]	Rare (?)mat-dweller
	Inner:	10.0–17.0	
Myxococcoides distola		9.5 (1.7)	Locally abundant (?)microbenthos in mats
Myxococcoides ovata		11.8 (1.8)	Rare in micrite clasts
Myxococcoides sp. B of Knoll (1982)		21.1 (2.7)	Locally abundant dweller or allochthonous element
Myxococcoides sp. D		44.1 (4.7)	Rare, large vesicles in mats
Leiosphaeridia crassa		25–60	Rare individuals in mat and micrite clasts
Leiosphaeridia jacutica		>100–600	Rare individuals in mat and micrite clasts
Germinosphaera sp.		40.3 (6.2)	Rare dweller in *S. septatum* mats
Unnamed Form B of Knoll (1982)		74 × 30	Solitary individual in *S. septatum* mats
Vased-shaped microfossils		80–150	In micrite clasts

[1] Mean and standard deviation (in parentheses) for maximum diameter, maximum and minimum dimensions, three mutually perpendicular dimensions, or, for filamentous fossils, cross-sectional diameter.
[2] See Figure 14 for additional data.

understand how organisms were distributed in Proterozoic oceans, and this has significant implications for studies of both stratigraphy and evolution. Proterozoic microfossils are now available as tools to aid in paleoenvironmental analysis, and a firmer paleoecological knowledge will permit us to recognize those temporal patterns that truly reflect evolution and, hence, are biostratigraphically useful. There can be no confidence in biostratigraphic zonations or evolutionary interpretations without a knowledge of how different paleoenvironments were populated (and sampled) at different time intervals. In Proterozoic paleontology, the primary task of the 1960's was to demonstrate that a pre-Cambrian fossil record existed. In the 1970's and 1980's, it was to demonstrate that the record was rich. The task for the 1990's is to document the Proterozoic paleontological record in sufficient systematic, paleoecological, and stratigraphic detail to fulfill the promise of Tyler and Barghoorn's discovery.

SYSTEMATIC PALEONTOLOGY

Systematic descriptions for many Draken species can be found in Knoll (1982). In this paper, discussion is limited to those

previously described taxa for which significant new information is available and to species not discussed in Knoll (1982). All type and illustrated specimens are reposited in the Paleobotanical Collections of the Harvard University Herbaria.

Kingdom EUBACTERIA Woese and Fox, 1977
Phylum CYANOBACTERIA Stanier et al., 1978
Class COCCOGONEAE Thuret, 1875
Order CHROOCOCCALES Wettstein, 1924
Family CHROOCOCCACEAE Nägeli, 1849
Genus GLOEODINIOPSIS Schopf, 1968,
emend. Knoll and Golubic, 1979

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

GLOEODINIOPSIS GRANDIS Sergeev and Krylov, 1986
Figure 19.4

Discussion.—The genus *Gloeodiniopsis* is recognized on the basis of its multiple envelopes and common presence of 2–4 daughter cells within the multilamellate vesicle. Rare individ-

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FIGURE 12—*Polybessurus bipartitus* silicified in the lower flake conglomerate (*1–7*), and calcified (*8*). *1*, P-4353-7B, Z22/4, HUHPC #62381; *2*, W(P)-839-B, Q30/0, HUHPC #62382), *3*, P-91-3A, F36/1, HUHPC #62383; *4*, P-4353-7A, F15/0, HUHPC #62384; *5*, P-4353-1A, O25/4, HUHPC #62385; *6*, a cluster, M-13D-8A, V23/0, HUHPC #62386; *7*, *B. bipartitus* (large vesicle) among diverse microfossils; *8*, crust-forming *Polybessurus* population preserved by dolomitic coatings in leached and fenestrate dolomite (slide P(F)-7019). Bar in *5* = 20 μm in *1–5*; = 60 μm in *6* and *7*; and = 1,000 μm in *8*.
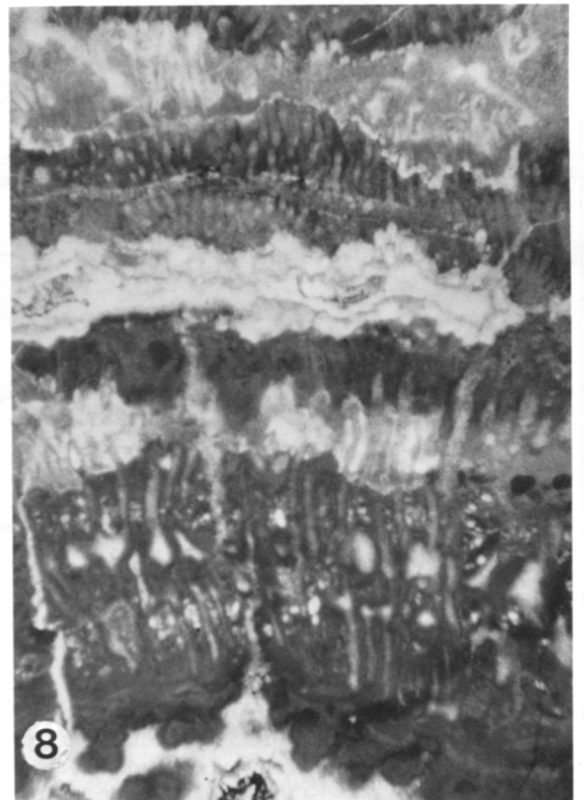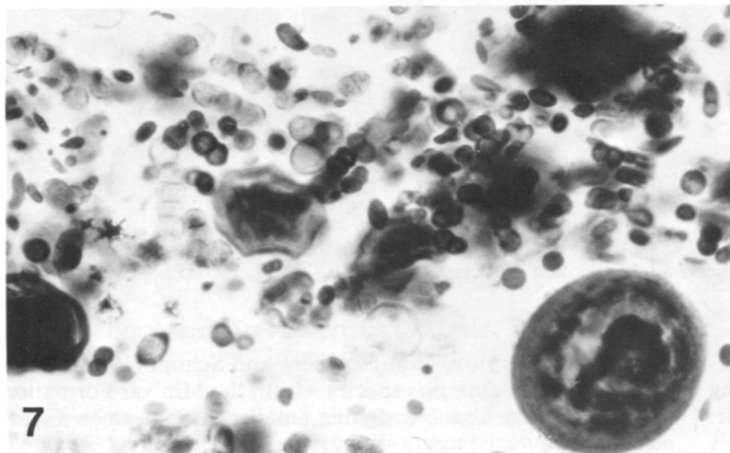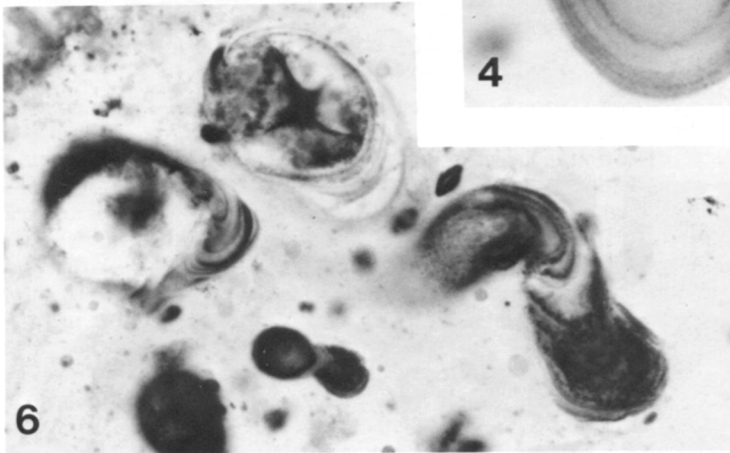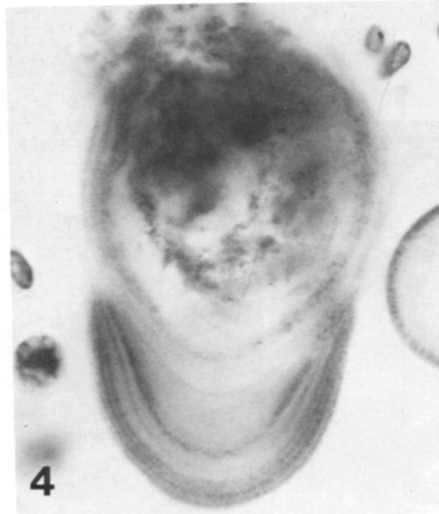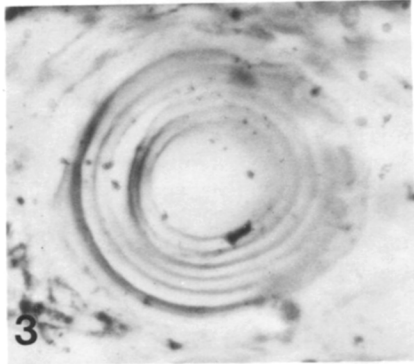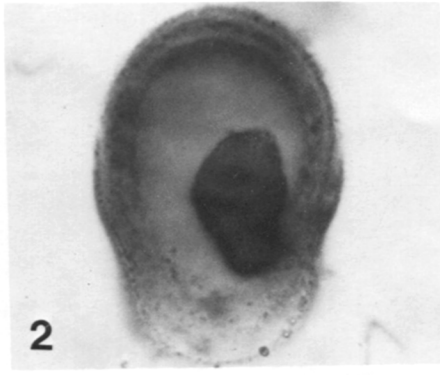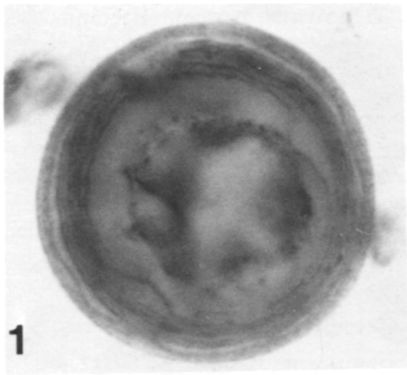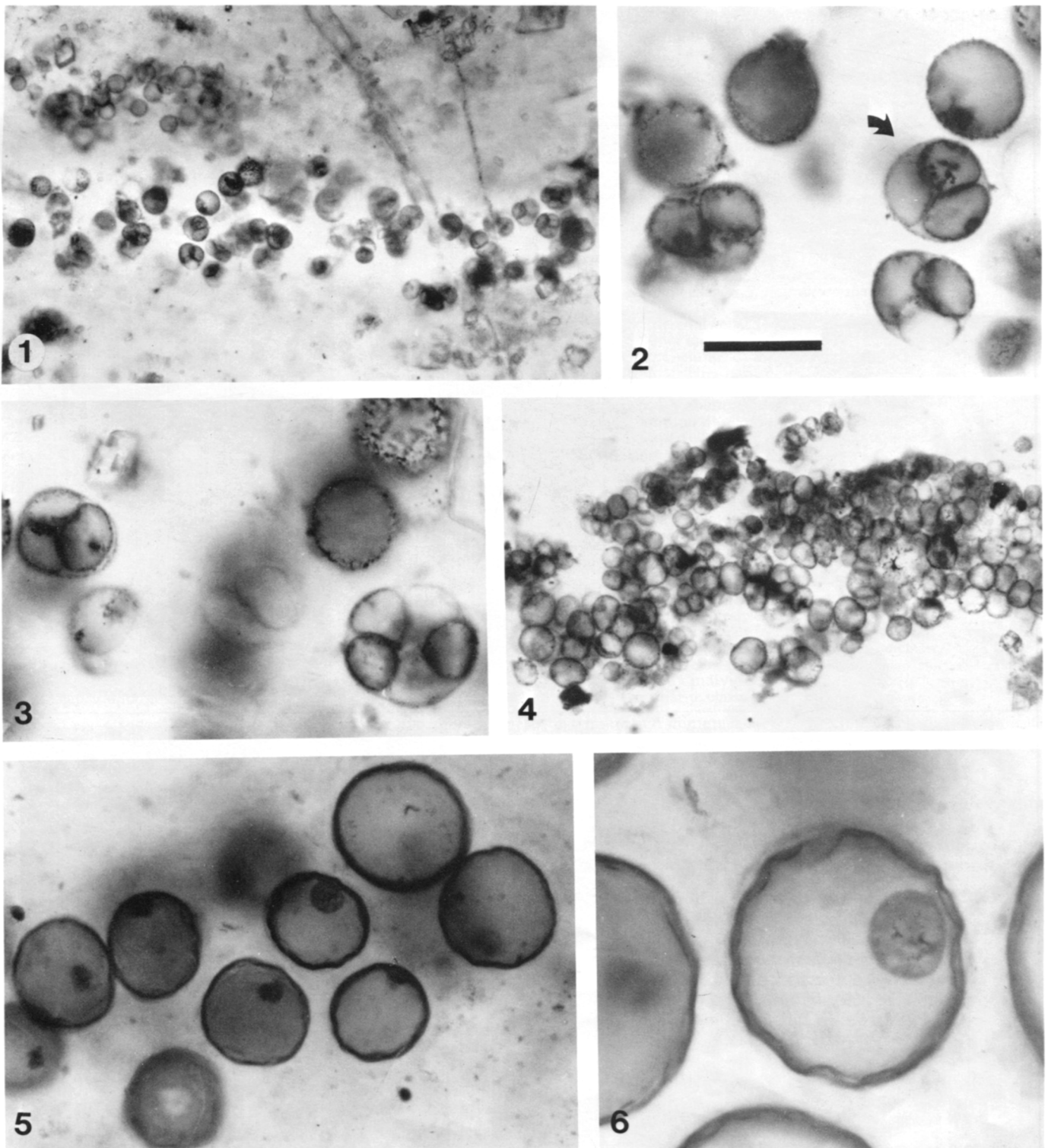
FIGURE *13—1–4, Myxococcoides chlorelloidea* (M-21-1A, S24/2, HUHPC #62354); *2,* specimen marked by the arrow is designated as the type of the species. *5, 6* (detail), *?Leiosphaeridia crassa* population preserved in a silicified mat clast (P-4353-7G, V-17, HUHPC #62387). Bar in *2* = 50 μm in *1, 4,* and *5;* and = 20 μm in *2, 3,* and *6.*

uals within the thin-walled *S. inornatum* biofacies fit this description. Their large size (up to 32 μm in diameter, containing four ellipsoidal inner vesicles) invites comparison with *G. grandis* described from Upper Riphean cherts of the southern Urals

(Sergeev and Krylov, 1986). Nyberg and Schopf (1984) recognized two *Gloeodiniopsis* species within the Min'yar Formation of the southern Urals, assigning smaller specimens to *G. lamellosa* and very large individuals (31–51 μm) to *G. magna.*

Gloeodiniopsis magna differs from *G. grandis* in that dyads and tetrads are not apparent.

It is known that *Polybessurus bipartitus* occurs in Min'yar cherts (V. Sergeev, personal commun.) and that *Polybessurus* individuals without stalks resemble large chroococcoid cells (see Figure 12.1). Therefore, in the absence of evidence for a *Gloeodiniopsis*-like divisional cycle, the proper interpretation of *G. magna* remains in doubt. For these reasons, we have chosen to include the Draken fossils within *G. grandis*. In its morphological features, this fossil compares with living species of *Chroococcus* (Knoll and Golubic, 1979; Sergeev and Krylov, 1986).

Genus SPHAEROPHYCUS Schopf, 1968

Type species.—*Sphaerophycus parvum* Schopf, 1968.

SPHAEROPHYCUS MEDIUM Horodyski and Donaldson, 1980
Figure 19.3

Sphaerophycus medium HORODYSKI AND DONALDSON, 1980, p. 140–141, figs. 5J, 6A, 6B.
Sphaerophycus wilsonii KNOLL, 1982, p. 783–784, Pl. 9, figs. 5–9.

Discussion.—Hofmann (personal commun.) has suggested that Draken populations assigned by Knoll (1982) to *S. wilsonii* have a size frequency distribution and cell-division pattern comparable to those of *S. medium*. Having reexamined described specimens and additional material, we concur and thus place *S. wilsonii* in synonymy with *S. medium*.

Family ENTOPHYSALIDACEAE
Genus EOENTOPHYSALIS Hofmann, 1976,
emend. Mendelson and Schopf, 1982

Type species.—*Eoentophysalis belcherensis* Hofmann, 1976.

EOENTOPHYSALIS BELCHERENSIS Hofmann, 1976
Figure 16.5, 16.6

Description.—Irregularly spheroidal colony composed of ovoid vesicles 8–15 μm long ($\bar{x}$ = 11.6 μm; s_x = 3.6 μm; N = 52) with multiple (1–3) thick lamellae. Individual vesicles contain 1–16 smaller, thin-walled vesicles, often with a small internal bleb of dense organic matter. "Unit" vesicles in groups of 8–16 (rarely 32), these groups forming a loose spheroidal colony.

Discussion.—This population is indistinguishable from *E. belcherensis*, originally described from the Paleoproterozoic Belcher Supergroup, Canada (Hofmann, 1976). Unlike the type and many subsequently described populations, the Draken fossils do not constitute dominant mat-builders. Perhaps this is because the Draken tidal flat did not form along a semiarid coastline. Today, *Entophysalis major* is a minor component of mat communities on mesic Bahamian tidal flats (S. Golubic, personal commun.). Within the Draken Conglomerate Formation, *E. belcherensis* is rare, occurring only as an isolated population in a lower flake conglomerate mat clast. Comparable populations are rare elements in *S. inornatum* mat assemblages from correlative beds in East Greenland (Green et al., 1989).

Order PLEUROCAPSALES Geitler, 1925
Family DERMOCARPACEAE Geitler, 1925
Genus POLYBESSURUS Fairchild, 1975,
ex Green et al., 1987

Type species.—*Polybessurus bipartitus* Fairchild, 1975, ex Green et al., 1987.

POLYBESSURUS BIPARTITUS Fairchild, 1975,
ex Green et al., 1987
Figure 12

Description.—Thick-walled, multilamellate vesicles 30–70 μm in diameter. May be spheroidal or ellipsoidal with lamellae
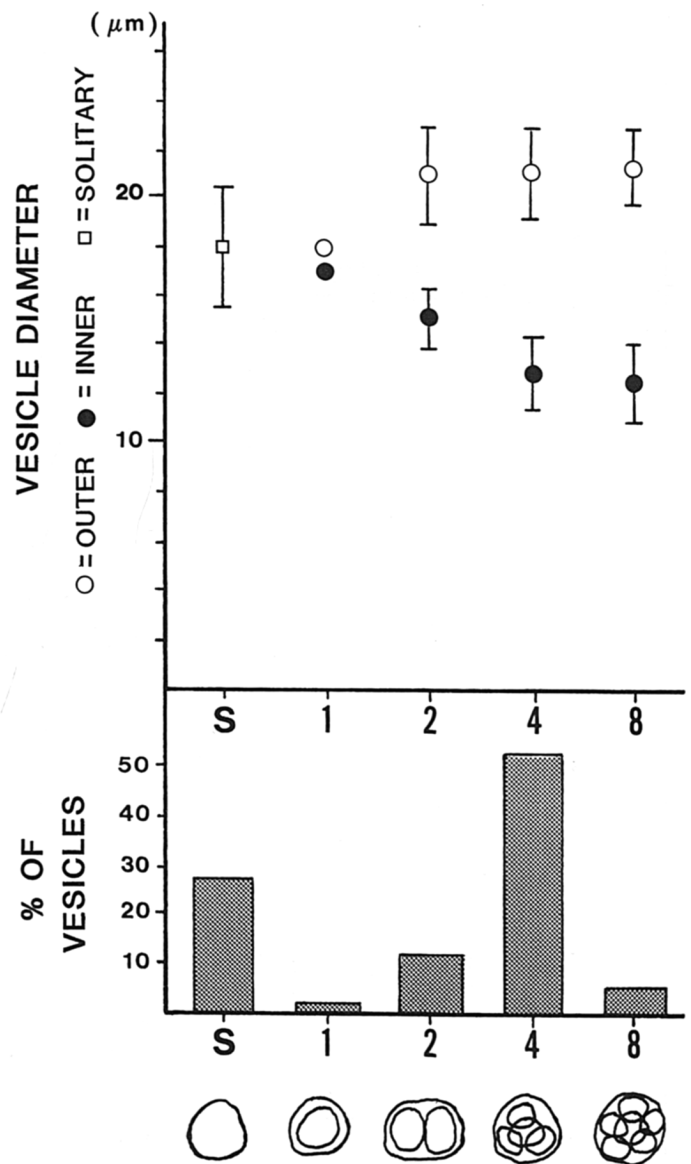
FIGURE 14—Size distribution of *Myxococcoides chlorelloidea* inner and outer (or solitary) vesicles, ordered by number of inner vesicles per outer vesicle.

elongated to form a short or long (up to 400 μm) stalk. Reproduction inferred to be by multiple fission.

Discussion.—In Draken cherts, *P. bipartitus* specimens occur principally as isolated individuals or loose clusters of several individuals within diverse *S. inornatum* mats. In correlative beds in East Greenland, *P. bipartitus* populations form local monospecific crusts among low-diversity *S. inornatum* mats. *Polybessurus* crusts in the Draken Formation are preserved by dolomitic rinds. Draken *Polybessurus* were not recognized by Knoll (1982), but restudy of his material indicates that a specimen illustrated as *Salome svalbardensis* (not the type) should be reassigned to *P. bipartitus* (Knoll, 1982, Pl. 2, fig. 2).

Family XENOCOCCACEAE Ercegovic, 1932
Genus SYNODOPHYCUS Knoll, 1982, emend.

Type species.—*Synodophycus euthemos* Knoll, 1982.
Emended diagnosis.—Pluricellular aggregates of small (<12

μm), approximately equidimensional hyaline unit vesicles closely packed together in an irregularly ellipsoidal colony of 16–64 (rarely more) unit vesicles; colonies may be enclosed within a thin envelope, but internal membrane-enclosed vesicle packets are rare or absent; binary division in three planes; within colonies, one or a small number of individual vesicles may be enlarged and contain two or more small cell-like vesicles.

SYNODOPHYCUS EUTHEMOS Knoll, 1982, emend.
Figure 15.1–15.9

Emended diagnosis. — Qualitatively, as for genus. Unit vesicles 4–7 μm; colonies irregularly ellipsoidal to slightly lobed, 20–40 μm long and 15–30 μm wide, containing 16–64 unit vesicles (rarely more). Uncommonly, individual vesicles in colony enlarged to 11–15 μm and containing 4–8 small (1–2 μm) vesicles.

Discussion. — *Synodophycus euthemos* was described by Knoll (1982) from a single distinctive colony in Draken chert. The defining features of the taxon were considered to be the presence of inner and outer vesicles in colony units and the distinctive close-packing of vesicles into a spheroidal colony. Inner and outer vesicles were interpreted as shrunken cell remains and envelopes, respectively, while the colony was seen as the product of repeated binary divisions in three directions. More recently collected material contains abundant colonies of *S. euthemos* that permit a clearer understanding of its biology and systematic position. Inner vesicles do indeed appear to be shrunken cell remnants within (originally) tightly adhering F-layers; however, inner vesicles are irregular features of colonies. Thus, they have been excluded from the generic and specific diagnoses. More significantly, several colonies exhibit enlarged unit vesicles that contain 4–8 small inner vesicles. These are interpreted as baeocytes formed by cell enlargement followed by multiple fission. This adds greatly to the morphological distinctness of the population and allows it to be placed systematically within the cyanobacterial family Xenococcaceae (Ercegovic, 1932; Komarek and Anagnostidis, 1986). *Synodophycus* populations appear to be particularly similar to species of the extant genera *Myxosarcina* and *Chroococcidiopsis,* both of which form sarcinoid cell packets by repeated binary divisions in three planes and facultatively form baeocytes from individual spherically enlarged cells within colonies (Waterbury and Stanier, 1978; Komarek and Anagnostidis, 1986).

Draken *Synodophycus* populations are widely distributed and locally abundant dwellers within *Siphonophycus inornatum* mats (*contra* Knoll, 1982). Among Proterozoic microfossils described from other formations, they most closely resemble *Phacelogeminus lineatus* from the Neoproterozoic Tindir Formation, northwestern Canada (Allison and Awramik, 1989). Indeed, the two taxa may be synonymous, but in the absence of information on baeocyte formation in the Canadian fossils, formal synonymy is premature.

Incertae sedis
Genus CONIUNCTIOPHYCUS Zhang, 1981

Type species. — *Coniunctiophycus gaoyuzhuangense* Zhang, 1981.

CONIUNCTIOPHYCUS MAJORINUM sp. nov.
Figure 16.1–16.4

Diagnosis. — A species of *Coniunctiophycus* characterized by small spheroidal to ellipsoidal unit vesicles (2–4 μm) arranged in packets that form large (50–100 μm long and 30–75 μm wide) smooth to lobate ellipsoidal colonies.

Description. — Pluricellular aggregates (colonies) consisting of small spheroidal to ellipsoidal unit vesicles that commonly contain a single dense organic bleb less than a micron in diameter. Unit vesicles 2–4 μm in diameter ($x = 3.3$ μm; $s_x = 0.5$ μm; N = 275) and tightly appressed in packets of 2–8 individuals (range = 5–12 μm; $x = 6.1$ μm; $s_x = 1.0$ μm; N = 125). Packets in colony interiors approximately equidimensional, but surficial packets commonly elongated perpendicular to colony surface; length : width ratios in surficial packets commonly 2:1. Packets not clearly enclosed in a common envelope, but within packets interior vesicle walls commonly poorly defined, giving impression of larger units. Packets commonly arranged in larger packets 15–20 μm long. These larger packets may form distinct lobes, or may be cryptic; commonly accentuated during post-mortem degradation. Unit vesicles, small packets, and larger packets comprise smooth to lobate ellipsoidal colonies 55–110 μm long ($x = 70$ μm; $s_x = 17$ μm; N = 32) and 30–75 μm wide ($y = 46$ μm; $s_y = 12$ μm; N = 32). Colony elongation parallel to bedding. No evidence of cell differentiation within colonies.

Etymology. — With reference to the fact that colonies in this species are larger than those of other described species within the genus.

Type specimen. — The specimen illustrated in Figure 16.4 has been chosen as the type and is in the Paleobotanical Collections of the Harvard University Herbaria under catalog number 62353.

Type locality. — South face of Dracofjella nunatak along Polarisbreen glacier, Ny Friesland, Spitsbergen.

Discussion. — *Coniunctiophycus majorinum* colonies occur abundantly within a single shard of *Siphonophycus septatum* mat in the lower flake conglomerate beds. Their sarcinoid colony form compares closely to that expressed by certain pleurocapsalean cyanobacteria, especially species of *Myxosarcina* and *Chroococcidiopsis* (Waterbury and Stanier, 1978). On the other hand, other cyanobacteria (e.g., *Entophysalis* spp.) can form comparable morphologies as can other Eubacteria and certain protists (e.g., *Chlorosarcina*); thus, in the absence of baeocytes, no firm systematic attribution can be made.

The Draken population conforms in all salient features to Zhang's (1981) generic diagnosis for *Coniunctiophycus* and, indeed, has unit vesicles comparable in size to those of the type species *C. gaoyuzhuangense* (Zhang, 1981); however, its characteristic colony size and shape differ substantially from the type and other described species of *Coniunctiophycus,* justifying the recognition of a new species. Gaoyuzhuang *Coniunctiophycus* species bear an uncertain relationship to *Eoentophysalis* colonies in the same formation, but no close relationship appears likely between Draken *Coniunctiophycus* and *Eoentophysalis.*

This Draken population bears some resemblance to sarcinoid colonies of *Scissilosphaera regularis* from the Ryssö Formation of neighboring Nordaustlandet (Knoll and Calder, 1983), but

→

FIGURE *15—1–9, Synodophycus euthemos. 1–3,* P-4353-7G, E21/0, HUHPC #62388; *4,* type specimen, W(P)-837-B, Q22/4, HUHPC #60493; *5,* specimen containing small cells interpreted as baeocytes (P-91-2A), W24/4, HUHPC #62389; *6, 8,* vesicles with probable baeocytes, note *Eosynechococcus medius* in *8,* P-4353-7B, Z21/0, HUHPC #62390; *7,* showing effects of variable degradation, P-4353-12F, N29/2, HUHPC #62397; *9,* cluster of vesicles containing probable baeocytes, P-4353-7G, H17/3, HUHPC #62391; *10–12, Sphaerophycus parvum; 10,* M-13-1B, K28/1, HUHPC #62392; *11,* P-13-13A, W20/4, HUHPC #62393; *12,* W(P)-839-A, L36/4, HUHPC #62394. Bar in *6* = 20 μm in *1;* = 15 μm in *2–8;* = 30 μm in *9;* and = 10 μm in *10–12.*
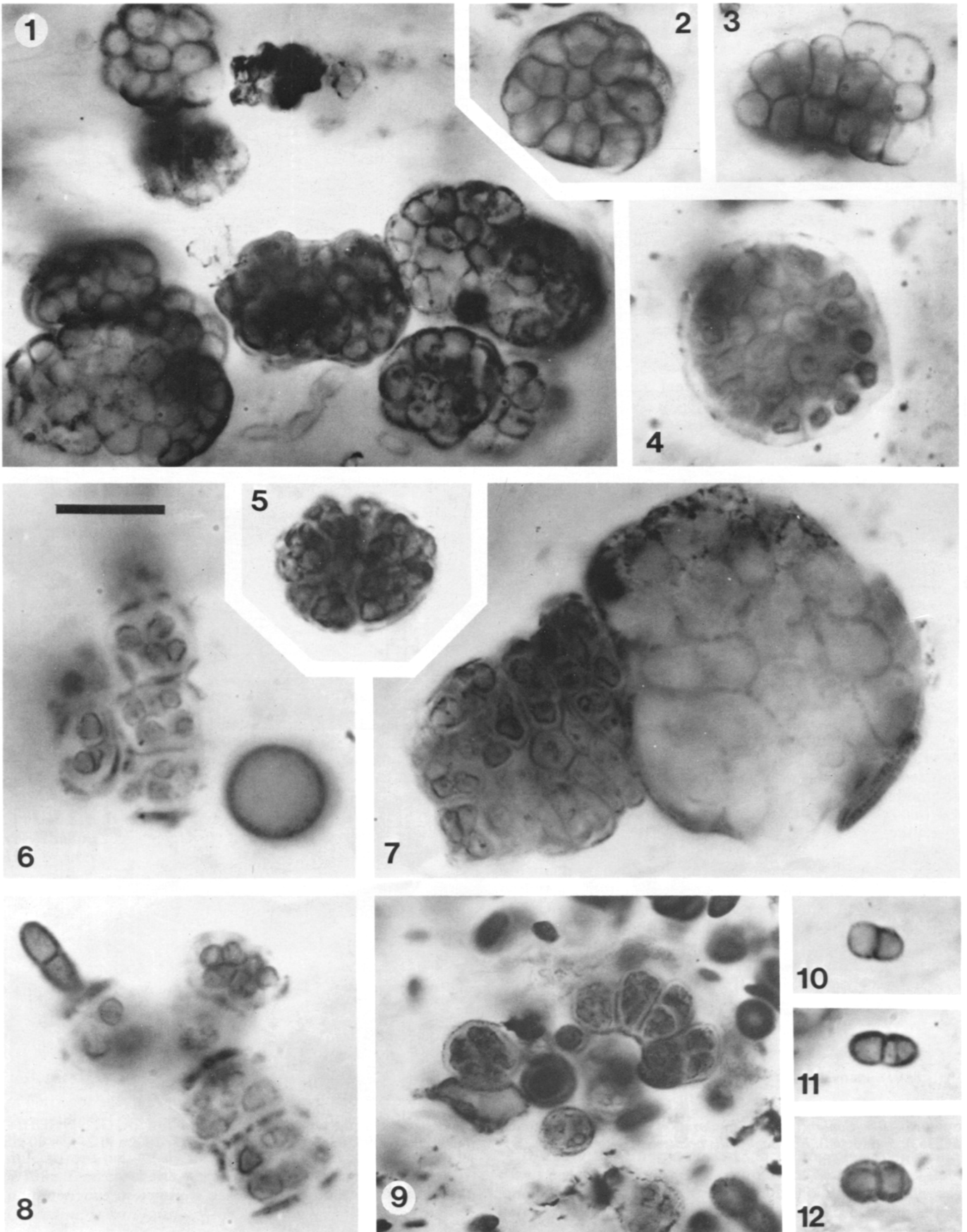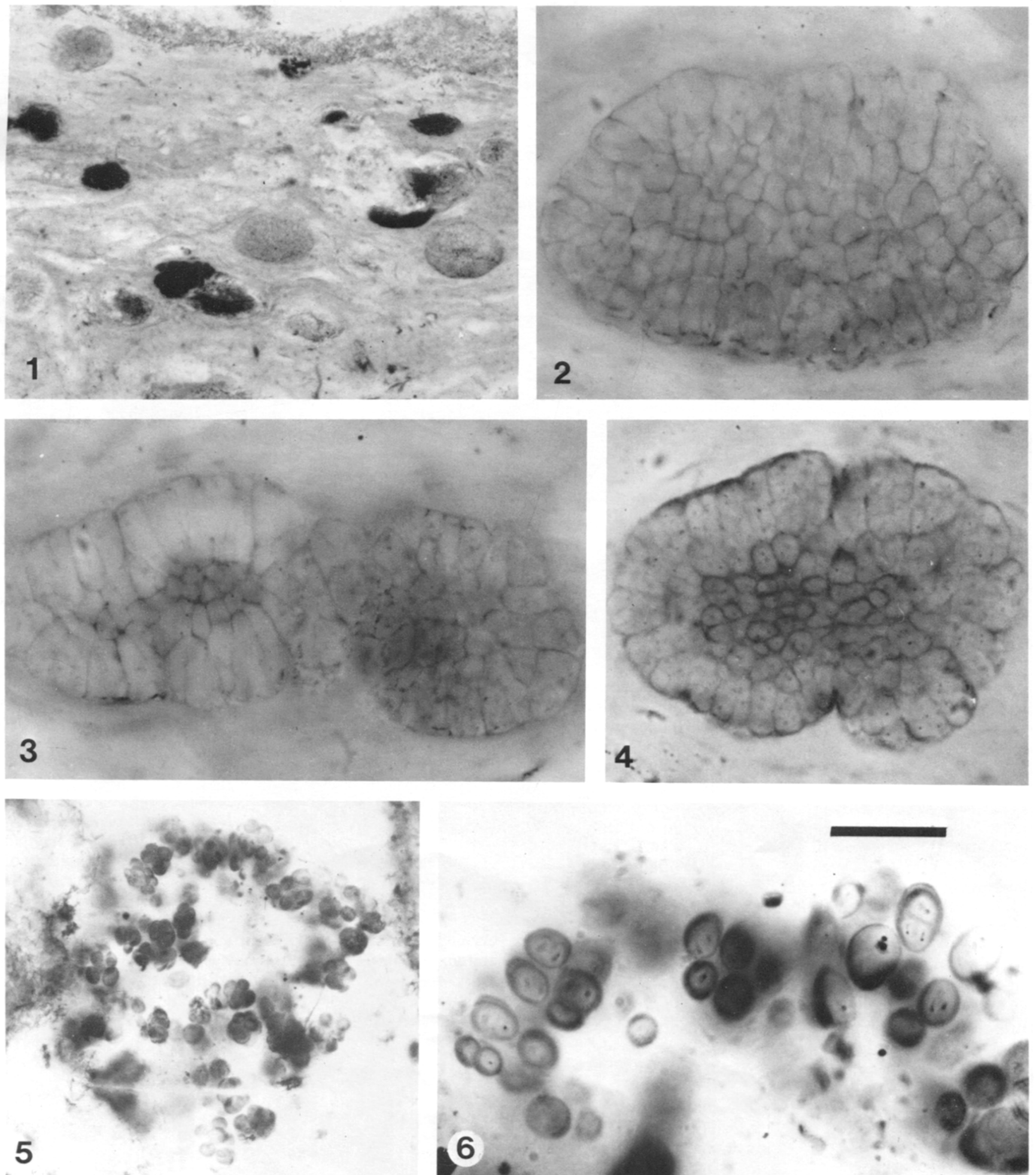
FIGURE 16—1–4, *Coniunctiophycus majorinum* sp. nov. (the specimen in *4* is designated as the type of the species; M-13B-2A, G11/1, HUHPC #62353). *5, 6* (detail), *Eoentophysalis belcherensis*, P-4353-13A, Q17/1, HUHPC #62395. Bar in *6* = 120 μm in *1*; = 20 μm in *2–4*; = 80 μm in *5*; and = 25 μm in *6*.

lacks the clear multiple fission pattern evident in that taxon. It also resembles colonies described as *Palaeoanacystis magna* from the Tindir Formation, Canada (Allison and Awramik, 1989). The Tindir material should certainly be transferred to the genus *Coniunctiophycus*, but its apparently larger unit vesicle size and lack of elongated surface packets suggest that it should be regarded as distinct from the Draken material at the species level. Finally, one can ask whether this population might be related to Draken *Synodophycus euthemos*. Both form sarcinoid colonies, but *S. euthemos* has baeocytes, unequivocally larger unit cells, and distinctly different colony form and size.

Genus CYMATIOSPHAEROIDES Knoll, 1984, emend.

Type species.—*Cymatiosphaeroides kullingii* Knoll, 1984.
Discussion.—A single specimen of *C. kullingii* was observed in interstitial space within the upper flake conglomerate. The specimen has a robust inner vesicle with a diameter of 125 μm connected by numerous slender (ca 1 μm) solid processes 5–6 μm long to a thin outer vesicle 141 μm in diameter. The outer vesicle is, in turn, surrounded by four extremely thin external envelopes.

This specimen and numerous individuals in the subjacent Svanbergfjellet Formation (Butterfield, personal commun.) contain features not described from the Hunnberg Formation holotype (Knoll, 1984), although reexamination shows them to be present. Therefore, emended generic and specific diagnoses are warranted.
Emended diagnosis.—Spheroidal to ellipsoidal vesicle; inner wall robust, bearing numerous thin (ca 1 μm) solid cylindrical processes that connect to a thin single or multilamellate outer wall; processes thicken at both ends and are regularly distributed over the vesicle; no interconnecting septa and no division of vesicle into polygonal fields by septa or membranes; outer wall has a relatively thick inner layer and up to six thin outer membranes; outer membranes may not be evident in partially degraded specimens.

CYMATIOSPHAEROIDES KULLINGII Knoll, 1984, emend.
Figure 4.4, 4.6

Emended diagnosis.—Qualitatively, as for genus; inner wall diameter 70–300 μm; outer wall multilamellate, 80–320 μm in diameter; processes 4–7 μm long.
Discussion.—*Cymatiosphaeroides kullingii* specimens in the Draken, Svanbergfjellet, and Hunnberg Formations all occur in very shallow, coastal-marine facies. Their systematic affinities are obscure.

Genus EOSYNECHOCOCCUS Hofmann, 1976

Type species.—*Eosynechococcus moorei* Hofmann, 1976.

EOSYNECHOCOCCUS sp.
Figure 17.16–17.22

Description.—Small elongate rods, 7–12 μm long and ca 1 μm wide. Rods occur as solitary individuals or as paired vesicles joined end to end.
Discussion.—Four species of *Eosynechococcus* occur in Draken cherts. (*Eosynechococcus* sp. of Knoll (1982) is here considered to be a variant of *E. medius*.) All could be the remains of chroococcalean cyanobacteria, but all could alternatively be the remains of physiologically dissimilar Eubacteria. Therefore, the fossils are treated as incertae sedis. *Eosynechococcus* sp. differs from previously described species in its narrow width. Within Draken cherts, these fossils occur sporadically in *Siphonophycus inornatum* assemblages containing abundant *Gloeodiniopsis mikros*.

Genus GERMINOSPHAERA Mikhailova, 1986

Type species.—*Germinosphaera unispinosa* Mikhailova, 1986.

GERMINOSPHAERA sp.
Figure 19.6

Discussion.—Knoll (1982) noted the presence in *Siphonophycus septatum* mats of spheroidal vesicles from which a single tube extends. Similar fossils have been described from the Soviet Union under the name *Germinosphaera*. Mikhailova (1986) recognized two species based on the presence of one or two tubular projections. Insofar as Draken individuals may contain either one or two projections, we suspect that Mikhailova's two species may come from a single population. Pending restudy of type materials, we refer to the Draken specimens as *Germinosphaera* sp. The systematic affinities of this population are obscure, although Butterfield et al. (1988) noted that comparable morphologies are exhibited by germinating zoospores of the xanthophyte alga *Vaucheria*.

Genus GORGONISPHAERIDIUM
Staplin, Jansonius, and Pocock, 1965

Type species.—*Gorgonisphaeridium winslowii* Staplin, Jansonius, and Pocock, 1965.

GORGONISPHAERIDIUM MAXIMUM (Yin) comb. nov.
Figure 21.13

Basionym.—*Baltisphaeridium maximum* YIN, 1987, p. 439–440, Pl. 14, figs. 14, 15.

Holotype.—The specimen figured by Yin (1987, Pl. 14, figs. 14, 15).
Description.—A single incomplete specimen of this large, echinate acritarch was observed in the Draken shale assemblage. Specimen is 112 μm long (by extrapolation, complete vesicle would have been roughly 200 μm in diameter) and bears numerous closely packed processes. Processes solid, unbranched, bluntly conical, and approximately 4 μm long.
Discussion.—The Draken fossil appears to be conspecific with acritarchs from the Doushantuo Formation, China, that have been described as *Baltisphaeridium maximum* Yin, 1987. True *Baltisphaeridium* species differ from *B. maximum* in having relatively long and flexible, hollow processes that are constricted at their bases. Thus, *Baltisphaeridium* is not the appropriate genus for these fossils. Spheroidal acritarchs bearing solid, echinate processes are placed in the genus *Gorgonisphaeridium*. Numerous Paleozoic species have been described, and although all are much smaller than the specimen described here, they share with it a common process architecture. Therefore, the Draken and Doushantuo fossils are placed in the new combination, *Gorgonisphaeridium maximum*. Zang (1989) assigned three forms from the uppermost Proterozoic Pertatataka Formation, Australia, to *Gorgonisphaeridium*, but claimed that his specimens have hollow processes. If correct, these fossils must be assigned to another genus.

Genus LEIOSPHAERIDIA Eisenack, 1958,
emend. Downie and Sarjeant, 1963

Type species.—*Leiosphaeridia baltica* Eisenack, 1958.

LEIOSPHAERIDIA CRASSA (Naumova) Jankauskas, 1989
Figures 13.5, 13.6, 21.4, 21.5

Discussion.—Unornamented sphaeromorph acritarchs in the size range of 30–70 μm are common in Draken shales and lagoonal carbonates and occur sporadically as allochthonous elements in *Siphonophycus septatum* mats. These simple forms

are assigned to *Leiosphaeridia crassa* (=*L. asperata* = *Kildinella hyperboreica*; see synonymy in Jankauskas, 1989, p. 75).

LEIOSPHAERIDIA JACUTICA (Timofeev)
Mikhailova and Jankauskas,
in Jankauskas, 1989
Figures 19.5, 21.1

Discussion.—In a recent comprehensive revision of Proterozoic leiosphaerid acritarchs, Jankauskas (1989) and colleagues grouped thin-walled leiosphaerids in the size range 70–800 μm as *L. jacutica*. Draken shales contain leiosphaerids up to 265 μm in diameter, and a single thin-walled specimen 600 μm in diameter was found in a clast of *Siphonophycus septatum* mat.

LEIOSPHAERIDIA sp. cf. L. ATAVA (Naumova)
Jankauskas, 1989
Figure 21.2, 21.3

Discussion.—Draken shales contain abundant fragments and less common entire specimens of large (up to 210 μm) leiosphaerid acritarchs bearing distinctively patterned wrinkles on relatively robust walls (Figure 21.3). The wrinkles are probably diagenetic; nonetheless, they appear to indicate a distinctive wall structure or chemistry. Among described forms, they are most similar to *L. atava*.

Genus MYXOCOCCOIDES Schopf, 1968

Type species.—*Myxococcoides minor* Schopf, 1968.

MYXOCOCCOIDES CANTABRIGIENSIS Knoll, 1982
Figure 11

Myxococcoides cantabrigiensis KNOLL, 1982, p. 784–785, Pl. 10, fig. 5, text-fig. 5.
Myxococcoides sp. A KNOLL, 1982, p. 785–786, Pl. 9, figs. 1, 2.
Myxococcoides sp. C KNOLL, 1982, p. 786, Pl. 6, figs. 1–3.

Discussion.—These abundant unicells are often found in association with solitary, relatively large vesicles described by Knoll (1982) as *Myxococcoides* sp. C. Figure 11.3 makes it clear that these two morphotypes are part of a single population; thus, large individuals are here included in *M. cantabrigiensis*. Thin-walled forms originally segregated as *Myxococcoides* sp. A (Knoll, 1982) are likewise placed in synonymy with *M. cantabrigiensis* and are interpreted as degradational variants of this form.

Allison and Awramik (1989) considered *M. cantabrigiensis* and other *Myxococcoides* species to be cyanobacteria, stating (p. 272) that "there is no compelling evidence to indicate otherwise." We consider this statement to be only half correct. There is no definitive evidence linking most *Myxococcoides* species to any protistan group; however, there is equally no

evidence indicating that these fossils are prokaryotic. Thus, we persist in considering these fossils as incertae sedis. The abundant presence of protists in Neoproterozoic rocks demonstrates that one cannot consider Neoproterozoic fossils as cyanobacteria until proven otherwise.

MYXOCOCCOIDES CHLORELLOIDEA sp. nov.
Figure 13.1–13.4

Diagnosis.—A species of *Myxococcoides* characterized by single-walled vesicles 17–26 μm in diameter, some of which contain internal 10–17 μm vesicles in dyads, tetrads, and octads. Internal vesicles well rounded to hemispherical and commonly preserved better than external vesicles. Presence and organization of internal vesicles differentiate this species from other *Myxococcoides* species; lack of multiple lamellae and relatively greater proportion of vesicles that occur in tetrads distinguish this species from *Gloeodiniopsis* species.

Description.—Spheroidal to ellipsoidal vesicles arranged in loose aggregations or solitary. Vesicles with a single wall 17–26 μm in diameter (see Figure 14), ca 0.5 μm thick, and hyaline to granular in surface texture; or vesicles of this description containing 1–8 (commonly four) spheroidal vesicles 10–17 μm in diameter (see Figure 14) that fill outer vesicle. Inner vesicles well rounded or, in dyads, hemispherical; inner vesicles often darker and better defined than encompassing outer vesicles. Inner or solitary vesicles may contain an internal, wrinkled organic body.

Etymology.—With reference to the close resemblance of this population to living green algae of the genus *Chlorella*.

Type specimen.—This species can only be recognized on the basis of features revealed by a population; however, the botanical code of nomenclature requires that a single specimen be chosen as type. Therefore, the specimen in Figure 13.2 that is marked by an arrow has been chosen as the type and is reposited in the Paleobotanical Collections of the Harvard University Herbaria under catalog number 62354.

*Type locality.*—Atop MacDonaldryggen nunatak along the southern edge of Draken Conglomerate Formation exposure.

*Discussion.*—Species of *Myxococcoides* share the property of systematic intractability. *Myxococcoides chlorelloidea* shares this feature to a degree, but its distinctive divisional cycle involving one to three binary divisions with some but not much growth between successive splits (Figures 13, 14) permits comparison to living green algae of the genus *Chlorella*. Populations of *Chlorella pyredinosa* exhibit a closely comparable range of morphologies and division patterns. Unfortunately, this simple life cycle is not unique to *Chlorella*; thus, *M. chlorelloidea* remains problematic.

→

FIGURE *17*—*1, Tetraphycus diminutivus* (P-837-B, L8/4, HUHPC #60517). *2–11, Gloeodiniopsis mikros. 2,* M-13C-2a, 120/0, HUHPC #62396; *3–5, 9,* P-4353-12A, L27/0, HUHPC #62398; *6–8,* P4353-13A, H17/4, HUHPC #62399; *10,* P-4353-13A-1A, Q39/0, HUHPC #62400; *11,* W(P)-839-A, B16/3, HUHPC #60515. *12, Eosynechococcus depressus,* W(P)P-839-B, S32/0, HUHPC #60509. *13–15, Eosynechococcus medius, 13,* SP-15-#A, H14/0, HUHPC #62403; *14,* M13B-1A, S22/3, HUHPC #62402; *15,* P-4353-7B, Z22/3, HUHPC #62401. *16, Eosynechococcus* sp. (arrow) dwarfed by *Myxococcoides,* P-4353-12B, C29/0, HUHPC #62403. *17–22, Eosynechococcus* sp., R-4353-&B, Z21/0, HUHPC #62404. Bar in *12* = 10 μm in *1, 3–16*; = 20 μm in *2*; and = 15 μm in *17–22.*

FIGURE *18*—*1–5, Myxococcoides* sp. B. *1, 5,* W(P)-839-C, G27/0, HUHPC #60508; *2–4,* M-13B-2A, X25/0, HUHPC #62405. *6–10, Myxococcoides distola,* sp. nov. *6–9,* specimen marked by arrow in *9* is designated as the type of the species, M-13-4A, J21/0, HUHPC #62406; *10,* W(P)-839-C, O36/2, HUHPC #60506. Bar in *1* = 60 μm in *1* and *2*; = 15 μm in *3–5, 7, 8,* and *10*; = 80 μm in *6*; and = 20 μm in *9.*

FIGURE *19*—*1, ?Leiosphaeridia* sp., B-165A, M19/3, HUHPC #62411. *2,* unnamed form B, W(P)-8337, K30/3, HUHPC #60529. *3, Sphaerophycus medium,* W(P)-839-B, L10/3, HUHPC #60527. *4, Gloeodiniopsis grandis,* P-4353-13A, K38/2, HUHPC #62407. *5, Leiosphaeridia jacutica,* P-4353-7E, J13/2, HUHPC #62408. *6, Germinosphaera* sp., P-4353-13A, V54/4, HUHPC #62409. *7–9, Myxococcoides* sp. E, P-4353-7G, L17/2, HUHPC #62410. Bar in *8* = 20 μm in *1–4, 7,* and *9*; = 300 μm in *5*; = 40 μm in *6*; and = 80 μm in *8.*
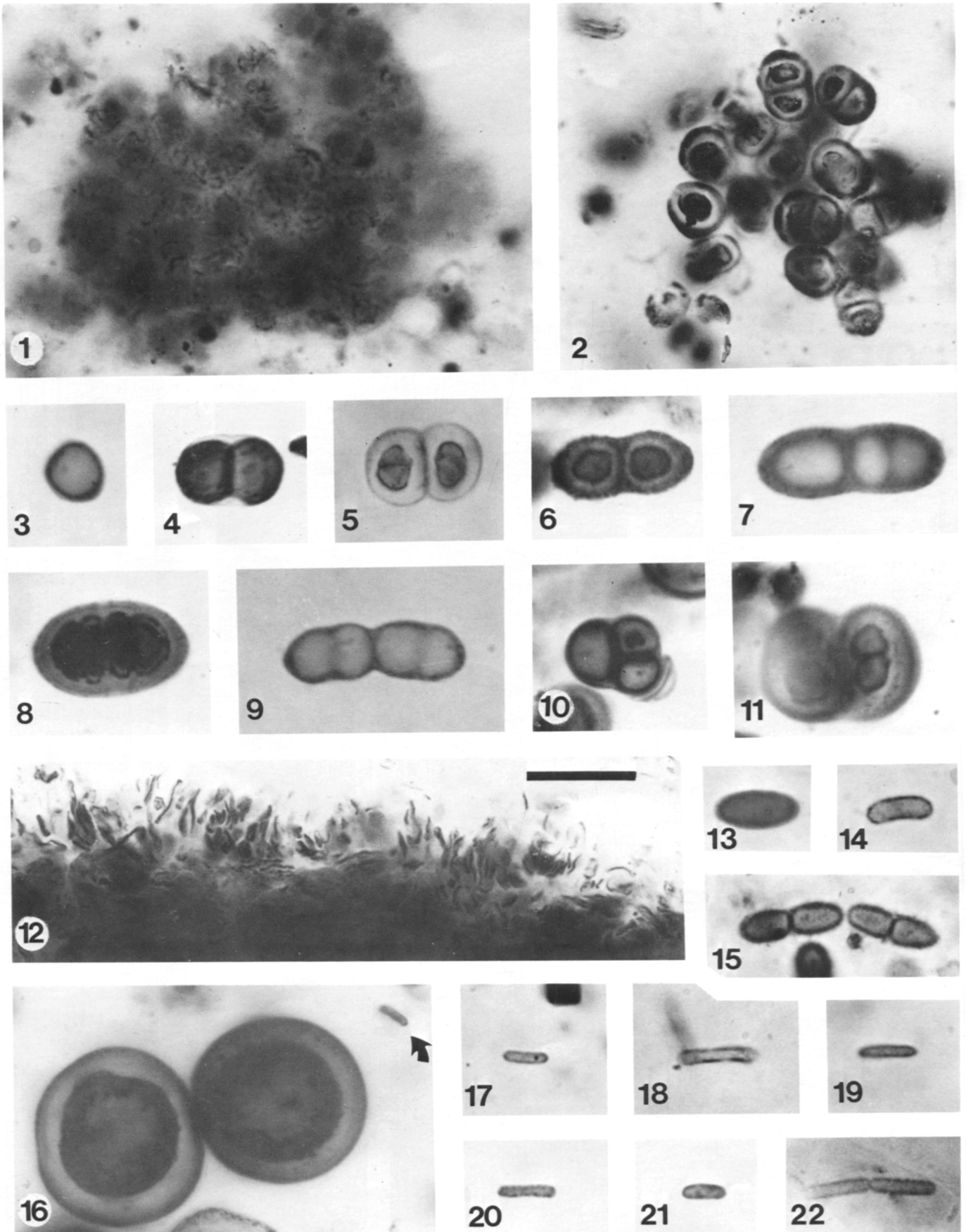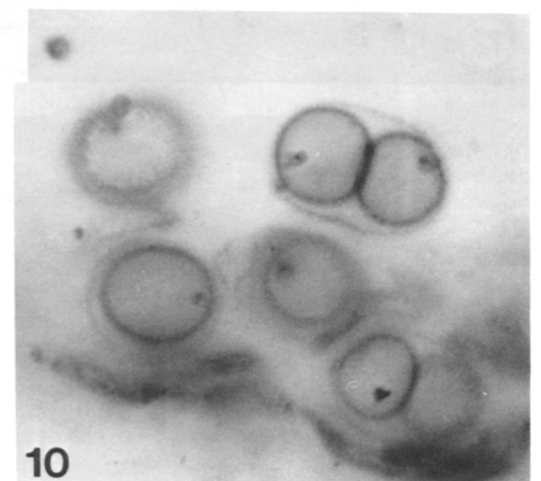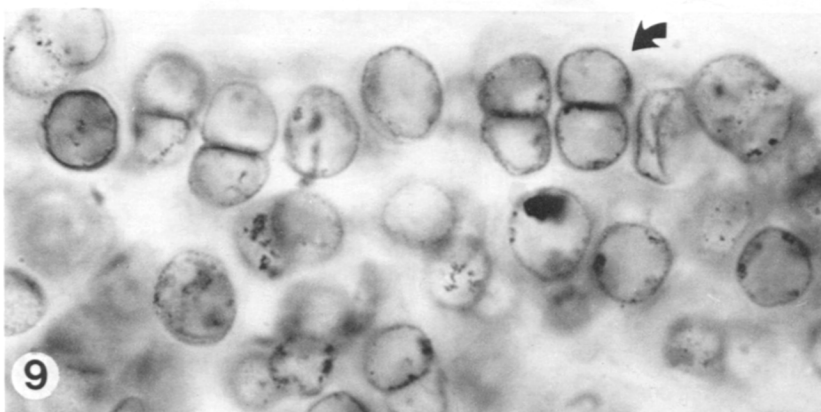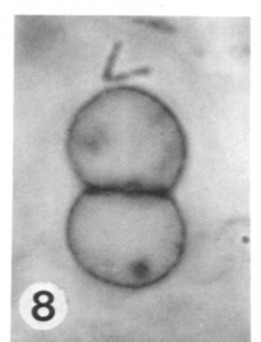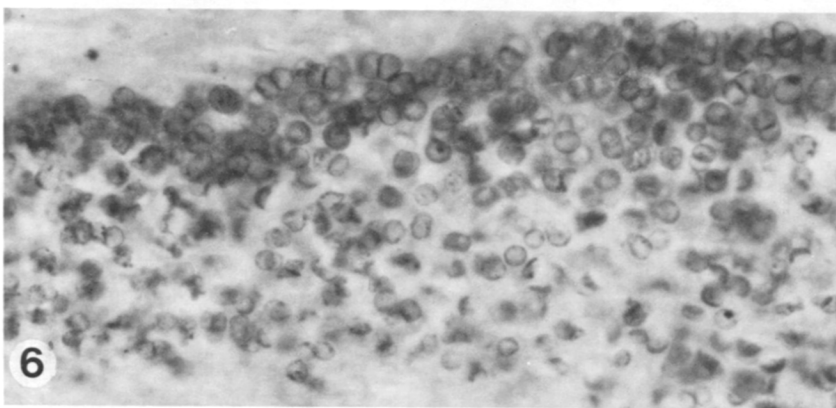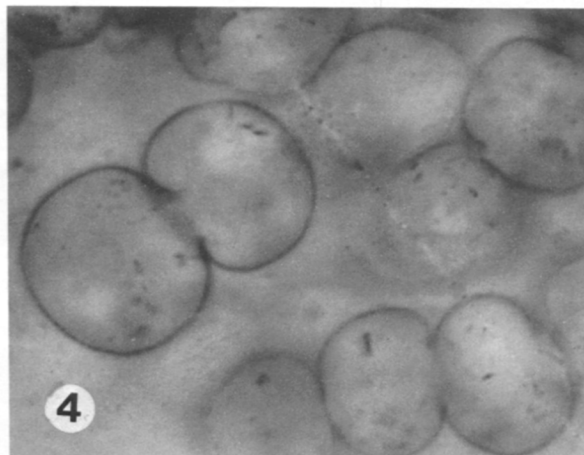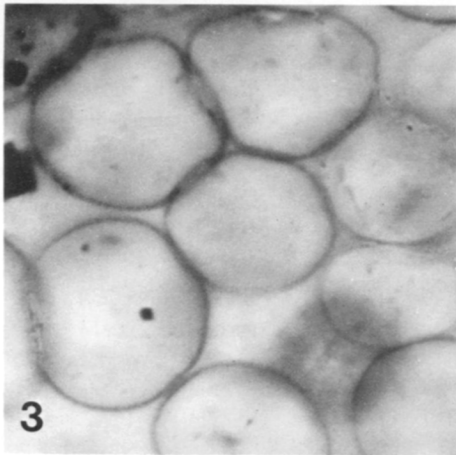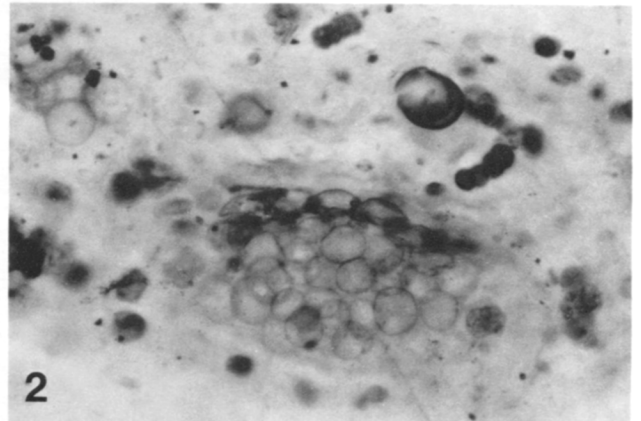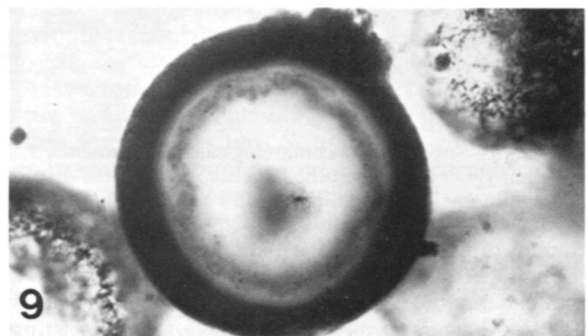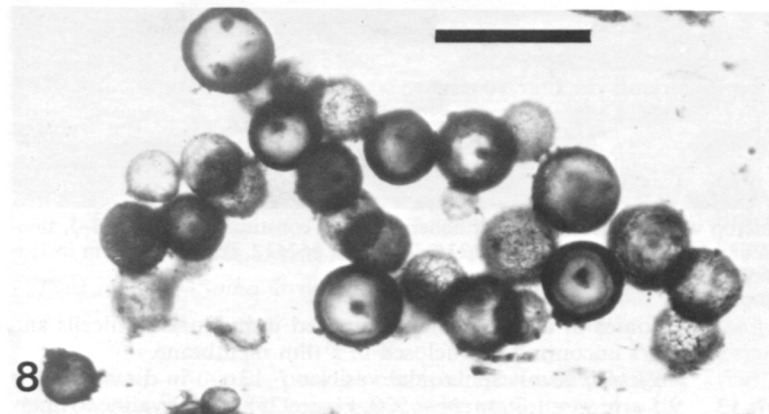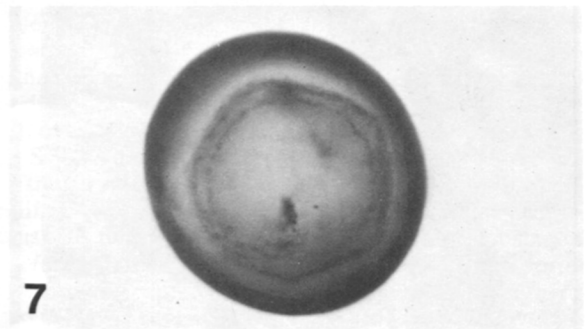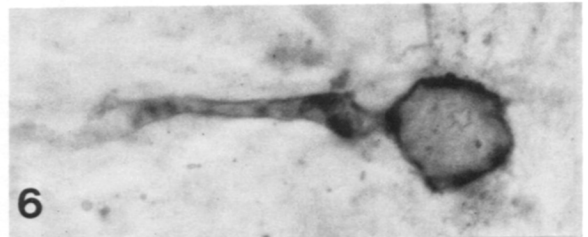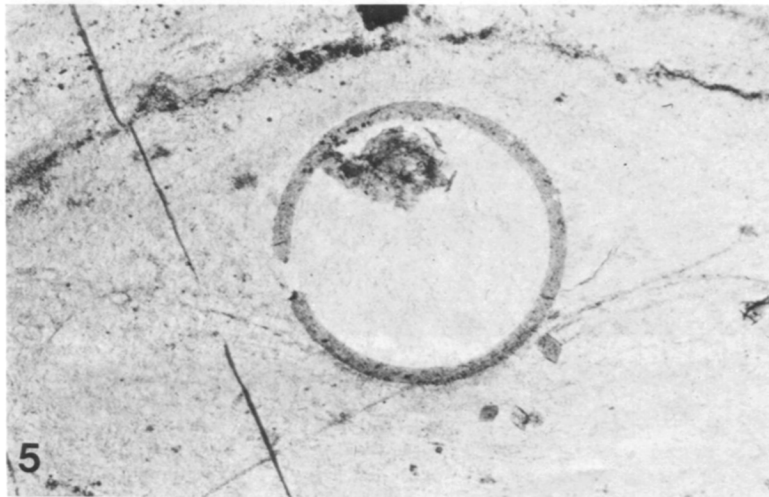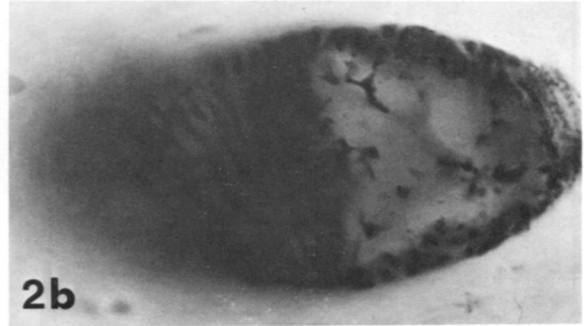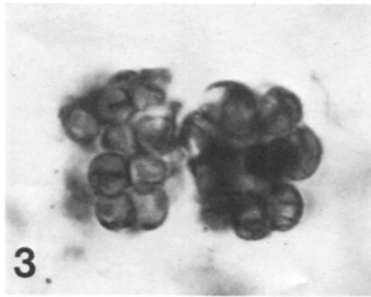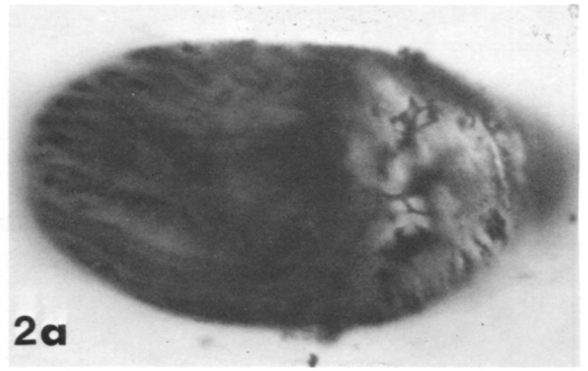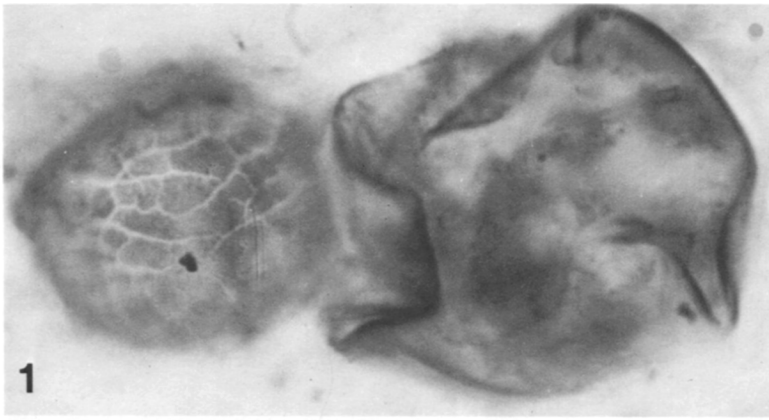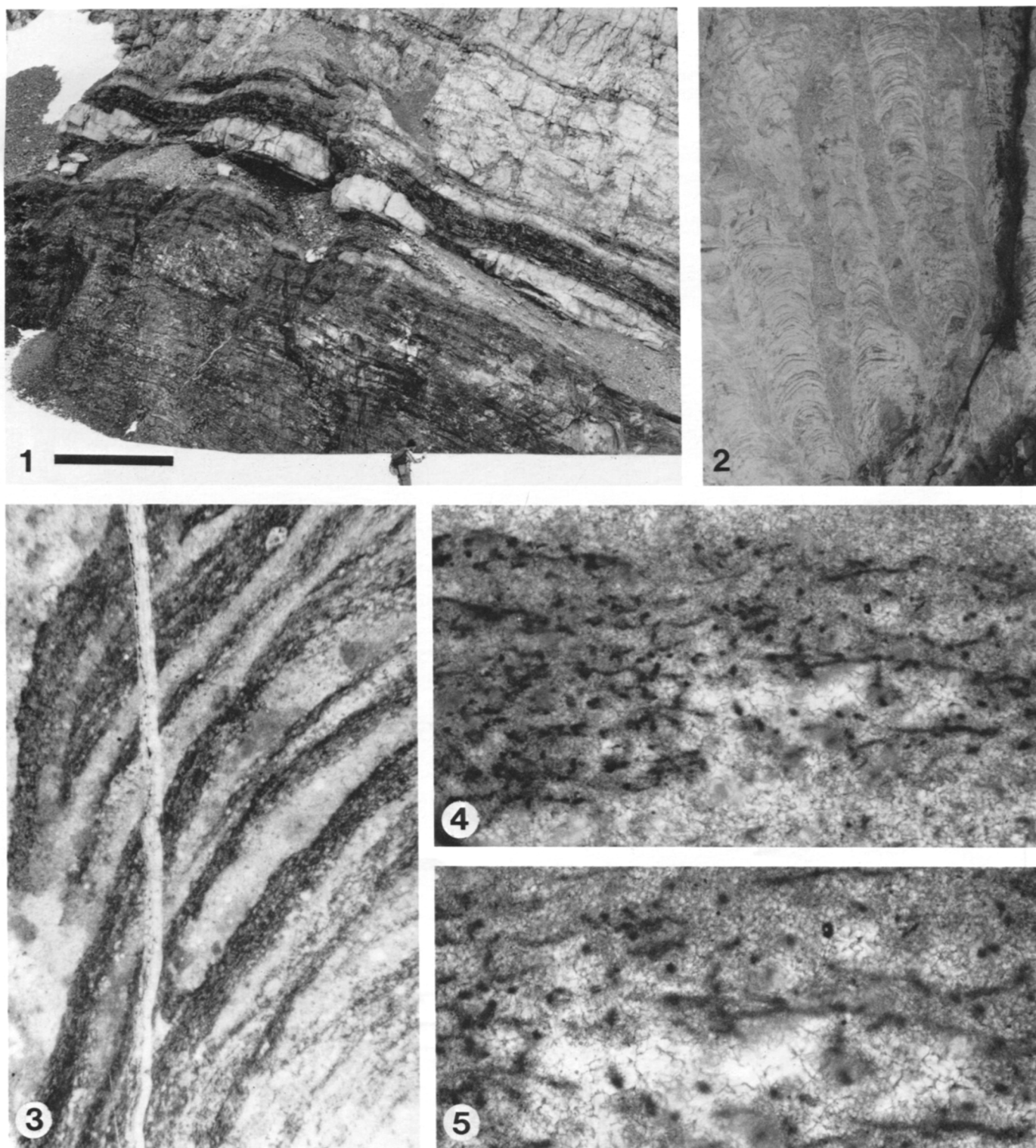
FIGURE *20*—Stromatolites containing calcified filaments. *1, 2,* outcrop views of stromatolitic lithoherm and its constituent columns; *3–5,* thin-section views of stromatolite lamellae, showing the distribution of calcified filaments, M-4, R23/0, HUHPC #62412. Bar in *1* = 20 m in *1;* = 20 cm in *2;* = 1,000 μm in *3;* = 150 μm in *4;* and = 80 μm in *5.*

MYXOCOCCOIDES DISTOLA sp. nov.
Figure 18.6–18.10

Diagnosis.—A species of *Myxococcoides* consisting of 7–13 μm vesicles characteristically occurring in pairs. Vesicles in loose colonies of a few to many hundred individuals. Unicells and pairs uncommonly enclosed in a thin membrane.

Description.—Spheroidal vesicles 7–13 μm in diameter (x = 9.5 μm; s_x = 1.7 μm; N = 500; Figure 25), walls hyaline to finely granular, ca 0.5 μm thick. Vesicles occur in loose colonies of up

to several hundred individuals. Approximately 50 percent of vesicles in colonies occur as dyads. A thin, light membrane sometimes surrounds solitary vesicles and dyads, but no more encompassing envelope or mucilage is apparent.

Etymology.—With reference to the common occurrence of dyads in this species.

Type specimen.—Under the rules of botanical nomenclature, a single specimen must serve as type, rather than a population. Thus, the specimen noted by the arrow in Figure 18.9 is designated as the type of the species. It is reposited in the Paleobotanical Collections of the Harvard University Herbaria under catalog number 62355.

Type locality.—South face of Dracofjella nunatak along Polarisbreen glacier, Ny Friesland, Spitsbergen.

Discussion.—The characteristic presence of dyads in these fossils distinguishes them from previously described species of *Myxococcoides*. "Diplococcus" populations from the Neoproterozoic Yudoma Formation, Siberia, are similar if not identical (Lo, 1980). Some (but not all) of the paired spheroids illustrated by Sergeev (1988, his fig. 1L, M) from Neoproterozoic cherts in the Southern Urals also resemble *M. distola*.

MYXOCOCCOIDES STRAGULESCENS Green et al., 1989

Discussion.—This species, distinguished by its median splits and tendency to form layers in mats, is common in East Greenland, but rare within Draken *Siphonophycus inornatum* mats.

MYXOCOCCOIDES sp. D
Figure 19.7–19.9

Description.—Spheroidal vesicles 30–50 μm in diameter, with thick dark walls (up to 4 μm thick).

Discussion.—These thick vesicles are problematic and rare. The single cluster observed is placed in open nomenclature as a species of *Myxococcoides*, although the generic assignment remains in some doubt. The population is referred to as *Myxococcoides* sp. D to distinguish it from the three Draken *Myxococcoides* forms (spp. A–C) treated in open nomenclature by Knoll (1982).

Genus POLYTRICHOIDES LINEATUS German, 1974, emend.
Figure 4.3, 4.5

Discussion.—These nonseptate tubular filaments are distinguished from *Siphonophycus* by their occurrence in tightly wound groups. The Draken population consists of 3–5 μm wide tubes wound in rope-like groups of up to 12 individuals that formed mats within the upper intertidal to supratidal zone. Morphologically, but perhaps not environmentally, these populations compare closely with *P. lineatus*, originally described from shales of the Upper Riphean Mireodikha Suite, Siberia (German, 1974).

The filaments are probably the sheaths of oscillatorian cyanobacteria, although this cannot be proven beyond any doubt. Individual sheaths in the Draken populations resemble *Siphonophycus inornatum* and may represent a behavioral variant of this species; however, no intermediate or mixed populations were observed.

Genus SATKA Jankauskas, 1979

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

SATKA sp.

Discussion.—A single, poorly preserved specimen belonging to this widely distributed Proterozoic genus was observed in the Draken shale assemblage.

TABLE 6—Calcified microfossils (samples M-4, P-22, and P(F)-7018).

Taxon	Size (μm)[1]	Comments
cf. *Siphonophycus inornatum*	4.0 (0.9)	Principal builder in columnar stromatolites
cf. *Polybessurus bipartitus*	100 (40)	Crust former on tidal flat

[1] Mean and standard deviation (in parentheses) for cross-sectional diameters of fossils.

Genus SIPHONOPHYCUS Schopf, 1968, emend.

Siphonophycus SCHOPF, 1968, p. 671.
Eomycetopsis SCHOPF, 1968, p. 684.
Tenuofilum SCHOPF, 1968, p. 679.
Leiotrichoides GERMAN, 1974, p. 8–9, fig. 1, table VI.

Type species.—*Siphonophycus kestron* Schopf, 1968.

Diagnosis (emended).—Tubular, filamentous microfossils, nonséptate and unbranched, with little or no tapering toward filament termini; tubes truncated and open at ends or with closed, more or less hemispherical terminations; walls typically preserved as chagrenate to finely reticulate organic matter, but may be preserved as carbonate rinds.

Discussion.—In his seminal monograph on the Bitter Springs microbiota, Schopf (1968) diagnosed the genus *Siphonophycus* as aseptate tubes 8.3–15 μm in cross-sectional diameter. Schopf recognized the occasional preservation of transverse thickenings along filaments and interpreted these fossils as the preserved extracellular sheaths of LPP-type (Rippka et al., 1979) cyanobacteria. A single species, *S. kestron*, whose diagnosis matched that of the genus, was described. *Eomycetopsis* was erected for tubular filaments that differed from *Siphonophycus* in being smaller (2–4.5 μm in cross-sectional diameter) and rarely interrupted by septa. Two species were described and interpreted as possible fungal hyphae. *Tenuofilum*, in turn, was described as a monotypic genus of small (ca 1 μm), uniseriate trichomes with often inconspicuous septa and no sheaths.

Subsequent research showed that the type specimens and associated populations of *Siphonophycus kestron, Eomycetopsis robusta*, and *Tenuofilum septatum* are all aseptate filamentous tubes that differ principally in size (Hofmann, 1976; Knoll, 1981). (As noted by Knoll (1982), *Tenuofilum septatum* specimens figured in Schopf and Blacic (1971) are clearly trichomes and should be transferred to the genus *Cephalophytarion*.) The populations differ quantitatively (i.e., in size) rather than qualitatively; thus, we follow convention in classical cyanobacterial taxonomy (e.g., Geitler, 1930–1932) and view the three forms as distinct species within a single (form) genus. We have therefore placed the three genera in synonymy as *Siphonophycus* and recognize three species of this genus—*S. kestron, S. robustum,* and *S. septatum*—in the Bitter Springs Formation. Pjatiletov (1988) previously synonymized *Leiotrichoides* German (1974) with *Eomycetopsis*; we include these fossils in *Siphonophycus* as well. Draken rocks contain five distinct size classes of *Siphonophycus*, and these populations are assigned to the three Bitter Springs form species plus *S. inornatum* and *S. capitaneum*. The larger populations are presumably cyanobacterial, but *S. septatum* and *S. robustum* could alternatively be flexibacterial in origin (e.g., Aizenshtat et al., 1984). For this reason, the genus is classified as incertae sedis rather than cyanobacterial. It is important to remember that the species of *Siphonophycus* are form species, and that interbasinal comparisons may be suspect; many living cyanobacterial species have morphologies that would converge taphonomically on these fossils.
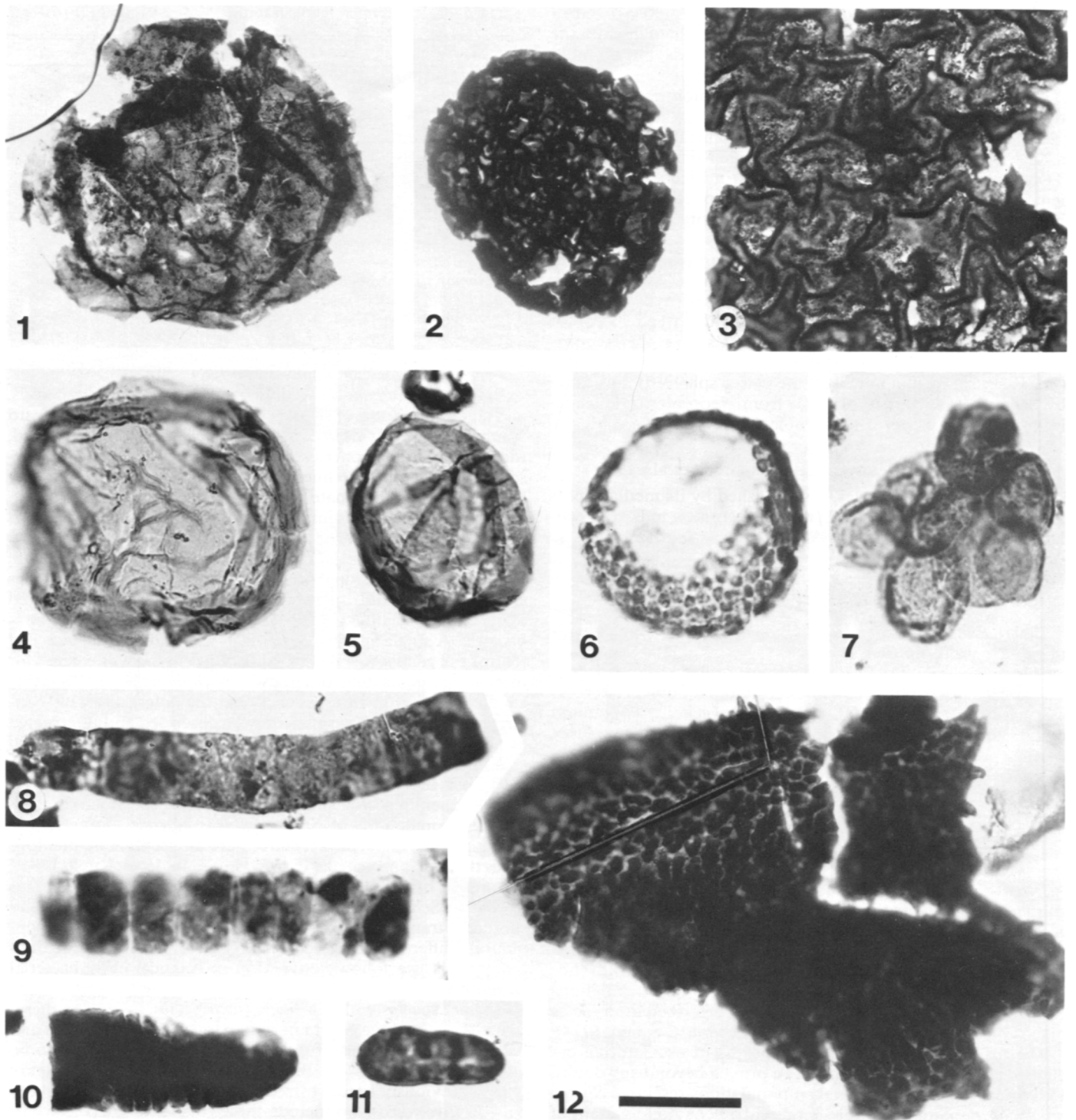
FIGURE *21*—Shale facies microfossils. *1, Leiosphaeridia jacutica*, P-23-10, N42/0, HUHPC #62413; *2, Leiosphaeridia* sp. cf. *L. atava*, P-23-10, M37-3, HUHPC #62414; *3,* detail of *L.* sp. cf. *L. atava* fragment showing characteristic wrinkling pattern, P-23-1, F31/1, HUHPC #62415; *4, 5, Leiosphaeridia crassa*; *4,* P-23-9, V53/2, HUHPC #62416; *5,* P-23-7, K22/8, HUHPC #62417; *6, Leiosphaeridia* sp., P-23-5, H45/0, HUHPC #62418; *7, Myxococcoides* sp., P-23-9, M34/3, HUHPC #62419; *8,* filamentous sheath, P-23-1, E33/0, HUHPC #62420; *9, 10,* trichome fragments; *9,* P-23-11, J33/1, HUHPC #62421; *10,* P-23-5, R59/2, HUHPC #62422; *11, Gloeodiniopsis mikros*, P-23-6, M54/3, HUHPC #62423; *12, Gorgonisphaeridium maximum*, P-23-6, J35/3, HUHPC #62424. Bar in *12* = 85 μm in *1–3*; = 20 μm in *4–7, 9, 10,* and *12*; and = 10 μm in *8* and *11*.

TABLE 7—Taxa present in subtidal shale assemblage (sample P-23).

Taxon	Size (μm)[1]	Comments
Myxococcoides cantabrigiensis	9.0–19.0	Probable phytoplankton
Leiosphaeridia crassa	25.0–80.0	Probable phytoplankton
Trachyhystricho-sphaera vidalii	(2)	Fragments; probable phytoplankton
Leiosphaeridia jacutica	150–300	Probable phytoplankton
Leiosphaeridia sp. cf. *L. atava*	200–260	Probable phytoplankton
Stictosphaerdium sp.	15.0–30.0	Probable phytoplankton
Gorgonisphaeridium maximum	>150	Single specimen; possible phytoplankton
Satka sp.	(2)	Rare in assemblage
cf. *Gloeodiniopsis mikros*	6.0–8.0	Rare; possibly allochthonous, originating on tidal flat
Siphonophycus spp.	2.0–25.0	Fragments; probably allochthonous
Trichome fragments[3]	2.9–19.0	Fragments; probably allochthonous

[1] Observed range for maximum diameter (cross-sectional diameter of filamentous fossils).
[2] Specimens generally incomplete.
[3] Possibly includes several species.

SIPHONOPHYCUS CAPITANEUM Nyberg and Schopf, 1984
Figure 3.4

Discussion.—These large (up to 25 μm in cross-sectional diameter) tubes occur as auxiliary builders in some upper intertidal to supratidal mats.

SIPHONOPHYCUS ROBUSTUM comb. nov.
Figure 10.3, 10.5

Eomycetopsis robusta SCHOPF, 1968, p. 685, Pl. 82, figs. 2, 3, Pl. 83, figs. 1–4; KNOLL AND GOLUBIC, 1979, p. 149, fig. 4A, B.
Eomycetopsis filiformis SCHOPF, 1968, p. 685, Pl. 82, figs. 1, 4, Pl. 83, figs. 5–8.

Discussion.—Consistent with the genus-level synonymy presented above, this species is transferred to *Siphonophycus,* and the specific epithet is accordingly changed to *robustum.*

Draken populations occur as auxiliary builders in *S. septatum* mats, as occasional microbenths in vertical tube-dominated lagoonal carbonates, and as oncoid and thin mat-builders on the inner flanks of oolitic shoals.

TABLE 8—Taxa present in the oncolitic assemblage (samples P-28, P-97, P-4665).

Taxon	Size (μm)[1]	Comments
Siphonophycus robustum	2–4	Oncoid builder
Trachyhystrichosphaera vidalii	155	Allochthonous

[1] Footnote here????

SIPHONOPHYCUS SEPTATUM comb. nov.
Figure 10.2

Tenuofilum septatum SCHOPF, 1968, p. 679, Pl. 86, figs. 10–12.
not *Tenuofilum septatum* Schopf. SCHOPF AND BLACIC, 1971, Pl. 108, figs. 11, 13.

Discussion.—The generic synonymy of *Tenuofilum* with *Siphonophycus* necessitates this new combination.

Draken populations occur mainly as principal mat-builders in lower intertidal to transitional intertidal/subtidal mats.

Genus STICTOSPHAERIDIUM Timofeev, 1966,
emend. Mikhailova and Jankauskas
in Jankauskas, 1989

Type species.—*Stictosphaeridium sinapticuliferum* Timofeev, 1966, emend. Mikhailova and Jankauskas *in* Jankauskas, 1989.

STICTOSPHAERIDIUM sp.

Discussion.—Small (ca 20 μm), very thin-walled, chagrenate vesicles occur as a minor constituent of the Draken shale assemblage. These vesicles are similar to *Stictosphaeridium* populations described widely from Neoproterozoic shales (Timofeev, 1966; Vidal, 1976; Jankauskas, 1989).

Vertical tubes
Figure 5.1–5.3, 5.6

Description.—Vertically oriented, sparsely branched filaments 13–59 μm in cross-sectional diameter ($\bar{x}$ = 24 μm; s_x = 8 μm; N = 125). Filaments preserved as siliceous or dolomitic internal molds, and no organic walls observed; thus, no information available on possible organization of cells or sheaths within individuals.

Discussion.—Vertical tubes occur within fine-grained lagoonal carbonates. As noted in the text, their taxonomic relationships are unknown; possible affinities include, but are not limited to, scytonematacean cyanobacteria and cladophoralean green algae.

FIGURE 22—Diagram illustrating the distribution of the principal biofacies in the Draken tidal flat/lagoonal complex.

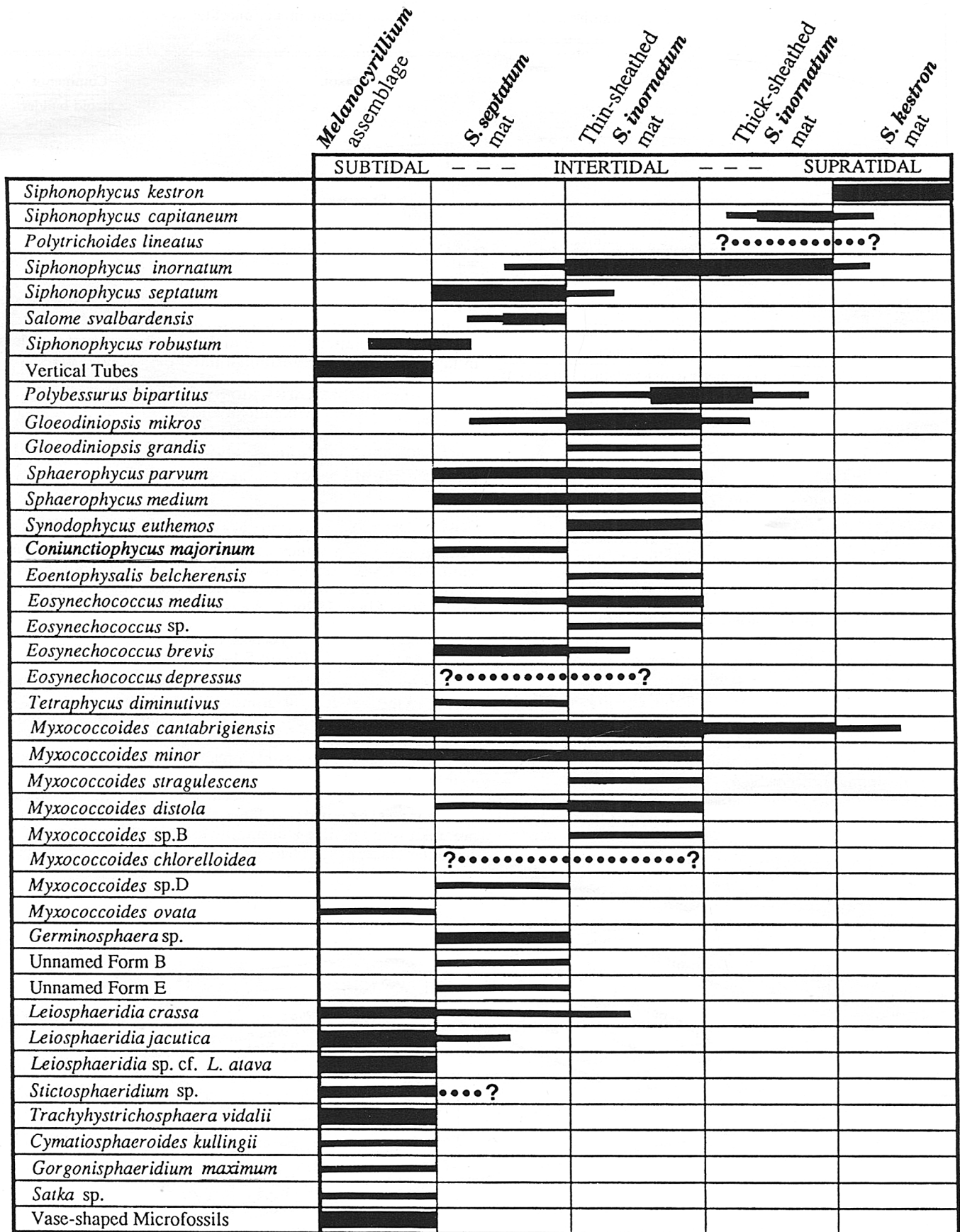|	*Melanocyrillium* assemblage	*S. septatum* mat	Thin-sheathed *S. inornatum* mat	Thick-sheathed *S. inornatum* mat	*S. kestron* mat
	SUBTIDAL – – – INTERTIDAL – – – SUPRATIDAL				
Siphonophycus kestron					▬▬
Siphonophycus capitaneum				▬▬▬	
Polytrichoides lineatus				?•••••••••••••?	
Siphonophycus inornatum			▬▬▬▬▬▬▬▬▬		
Siphonophycus septatum		▬▬▬▬			
Salome svalbardensis		▬▬			
Siphonophycus robustum	▬▬▬				
Vertical Tubes	▬▬				
Polybessurus bipartitus				▬▬▬	
Gloeodiniopsis mikros		▬▬▬▬▬			
Gloeodiniopsis grandis			▬▬▬		
Sphaerophycus parvum		▬▬▬▬▬▬▬			
Sphaerophycus medium		▬▬▬▬▬▬▬			
Synodophycus euthemos		▬▬▬▬▬			
Coniunctiophycus majorinum		▬▬▬			
Eoentophysalis belcherensis		▬▬▬▬▬			
Eosynechococcus medius		▬▬▬▬▬			
Eosynechococcus sp.		▬▬▬			
Eosynechococcus brevis		▬▬▬			
Eosynechococcus depressus		?•••••••••••••?			
Tetraphycus diminutivus		▬▬			
Myxococcoides cantabrigiensis	▬▬▬▬▬▬▬▬▬▬▬▬▬				
Myxococcoides minor	▬▬▬				
Myxococcoides stragulescens			▬▬▬		
Myxococcoides distola		▬▬▬▬▬			
Myxococcoides sp. B			▬▬▬		
Myxococcoides chlorelloidea		?•••••••••••••••••?			
Myxococcoides sp. D			▬▬▬		
Myxococcoides ovata	▬				
Germinosphaera sp.		▬▬▬			
Unnamed Form B		▬▬▬			
Unnamed Form E		▬▬▬			
Leiosphaeridia crassa	▬▬▬▬▬▬				
Leiosphaeridia jacutica	▬▬▬▬				
Leiosphaeridia sp. cf. *L. atava*	▬▬				
Stictosphaeridium sp.	▬▬ ••••?				
Trachyhystrichosphaera vidalii	▬▬				
Cymatiosphaeroides kullingii	▬				
Gorgonisphaeridium maximum	▬				
Satka sp.	▬				
Vase-shaped Microfossils	▬				

FIGURE *23*—Distribution of species among biofacies in the Draken tidal flat/lagoonal complex.

TABLE 9—Principal biofacies in the Draken Conglomerate Formation.

1. *Melanocyrillium* Biofacies	a. Characterized by vase-shaped microfossils (*Melanocyrillium* spp.) and vertically oriented filaments, preserved as molds; large, process-bearing acritarchs; leiosphaerid acritarchs; and *Myxococcoides* spp.
	b. Subtidal, lagoonal
2. *Siphonophycus septatum* Biofacies	a. Principal mat-builder, *S. septatum*; auxiliary mat-builder, *Salome svalbardensis*; diverse dweller taxa; common allochthonous fossils, including some *Myxococcoides* spp.
	b. Lower intertidal or transitional lagoonal margin/lower intertidal zone
3. Thin-walled *Siphonophycus inornatum* Biofacies	a. Principal mat-builder, *S. inornatum* characterized by thin sheaths; diverse dweller taxa; common allochthonous *Myxococcoides* spp.
	b. Lower intertidal zone
4. Thick-walled *Siphonophycus inornatum* Biofacies	a. Principal mat-builder, *S. inornatum* with thick sheaths; auxiliary mat-builder in more exposed areas, *Siphonophycus capitaneum*; dwellers rare; allochthonous elements uncommon
	b. Upper intertidal zone
5. *Siphonophycus kestron* Biofacies	a. Mat-builder, *S. kestron*; mat-dweller and allochthonous elements rare or absent
	b. Upper intertidal to supratidal zone

Although the five biofacies tabulated above collectively account for more than 90 percent of all Draken microfossils, other assemblages occur in the formation:
1. *Siphonophycus robustum* and rare other fossils preserved in the crescentic laminae of oncoids formed in subtidal environments subject to episodic wave or current action.
2. Calcified *Lyngbya/Phormidium*-type filaments in subtidal columnar stromatolites.
3. Leiosphaerid and large, process-bearing acritarchs; *Myxococcoides* spp.; and fragments trichomes and sheaths in siliciclastic siltstone. This assemblage compares closely with that of the carbonate-associated *Melanocyrillium* biofacies.
4. Calcified *Polybessurus bipartitus* populations that form crusts locally in the upper intertidal to supratidal zone. Correlative beds from central East Greenland contain silicified *Polybessurus* crusts that are clearly nestled within *Siphonophycus inornatum* mats.

Unnamed form E
Figure 6.5

Description.—A single fusiform specimen 120 μm long and 75 μm wide. Thin, multilamellate outer walls; thick, dense, somewhat diffluent interior "wall"; granular internal layer approximately 1 μm thick, 70 μm in maximum diameter, and 37 μm across; and granular internal body 15 μm in diameter.

Discussion.—This is a solitary form observed once within a shard of *Siphonophycus septatum* mat. It is illustrative of the rare problematica that increase the species richness of Draken cherts. The designation "unnamed form E" distinguishes this fossil from Draken specimens described informally by Knoll (1982).
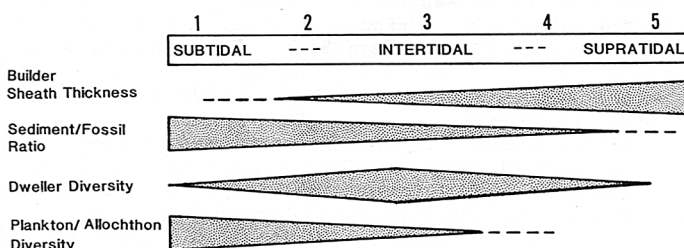
FIGURE 24—Paleoecological trends among biofacies in the Draken tidal flat/lagoonal complex. Biofacies numbers 1–5 correspond to the *Melanocyrillium, Siphonophycus septatum,* thin-sheathed *S. inornatum,* thick-sheathed *S. inornatum,* and *S. kestron* biofacies, respectively.
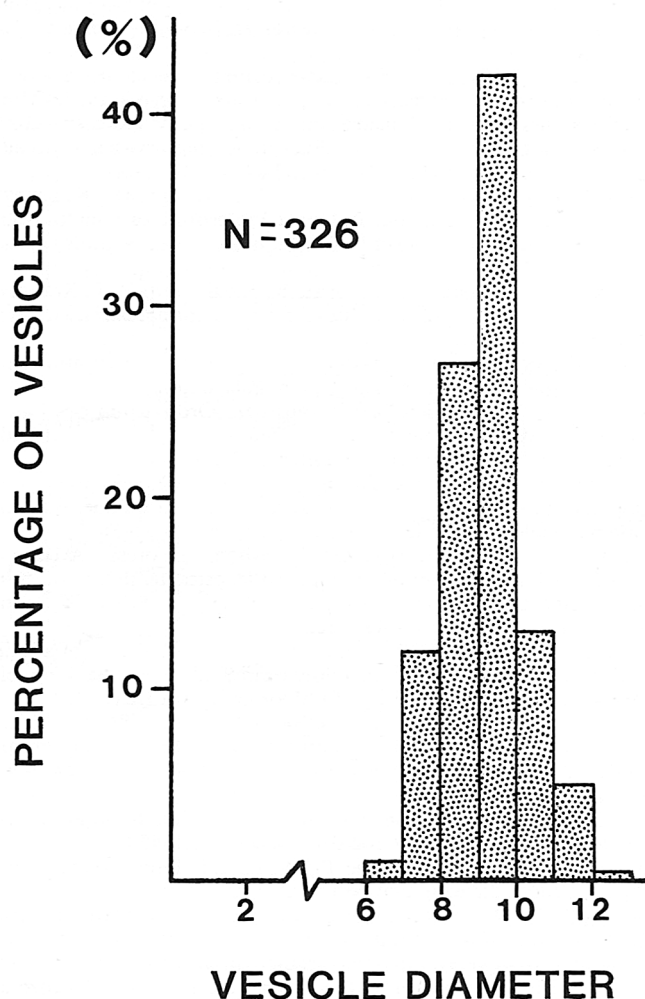

FIGURE 25—Size frequency distribution for a sample population of *Myxococcoides distola.*

REFERENCES

AITKEN, J. D. 1989. Giant "algal" reefs, Middle/Upper Proterozoic Little Dal Group (>770, <1200 Ma), Mackenzie Mountains, N.W.T., Canada, p. 13–23. *In* H. H. J. Geldsetzer, N. P. James, and G. E. Tebbutt (eds.), Reefs: Canada and Adjacent Areas. Canadian Society of Petroleum Geologists Memoir 13.

AIZENSHTAT, Z., G. LIPINER, AND Y. COHEN. 1984. Biogeochemistry of carbon and sulfur in the microbial mats of the Solar Lake (Sinai), p. 281–312. *In* Y. Cohen, R. W. Castenholz, and H. O. Halvorson (eds.), Microbial Mats: Stromatolites. Alan R. Liss, New York.

ALLISON, C. W., AND S. M. AWRAMIK. 1989. Organic-walled microfossils from earliest Cambrian or latest Proterozoic Tindir Group rocks, northwest Canada. Precambrian Research, 43:253–294.

ATKINSON, A. W., B. E. S. GUNNING, AND P. C. L. JOHN. 1972. Sporopollenin in the cell wall of *Chlorella* and other algae: ultrastructure, chemistry, and incorporation of ^{14}C-acetate. Planta, 107:1–32.

BARGHOORN, E. S., AND S. A. TYLER. 1965. Microorganisms from the Gunflint chert. Science, 147:563–577.

BAULD, J. 1981. Geobiological role of cyanobacterial mats in sedimentary environments: production and preservation of organic matter. BMR Journal of Australian Geology and Geophysics, 6:307–317.

——. 1986. Benthic microbial communities of Australian saline lakes, p. 95–111. *In* P. de Deckker and W. D. Williams (eds.), Limnology in Australia. Dr. J. Junk, The Hague.

BEHRENSMEYER, A. K., AND S. M. KIDWELL. 1985. Taphonomy's contributions to paleobiology. Paleobiology, 11:105–119.

BLACK, M. 1933. The algal sediments of Andros Island, Bahamas. Philosophical Transactions, Royal Society, London, B222:165–192.

BUTTERFIELD, N. J. 1990. Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. Paleobiology, 16:272–286.

——, AND A. H. KNOLL. 1989. Large, complex acritarchs in Upper Proterozoic rocks. Abstracts, Geological Association of Canada–Mineralogical Association of Canada, Annual Meeting, Montreal, p. A100.

——, AND K. SWETT. 1988. Exceptional preservation of fossils in Upper Proterozoic shale. Nature, 334:424–427.

DERRY, L. A., L. S. KETO, S. B. JACOBSEN, A. H. KNOLL, AND K. SWETT. 1989. Sr isotopic variations in Upper Proterozoic carbonates from Svalbard and East Greenland. Geochimica et Cosmochimica Acta, 53:2331–2339.

DILL, R. F., E. A. SHINN, A. T. JONES, K. KELLY, AND R. P. STEINEN. 1986. Giant subtidal stromatolites forming in normal salinity waters. Nature, 324:55–58.

DOWNIE, C., AND W. A. S. SARJEANT. 1963. On the interpretation and status of some Hystrichosphere genera. Palaeontology, 6:83–96.

EISENACK, A. 1958. Microfossilien aus dem Ordovizium des Baltikums. 1. Markasitschicht, Dictyonema-Schiefer, Glaukonitsand, Glaukonitkalk. Senckenbergiana Lethaea, 39:389–404.

ERCEGOVIC, A. 1932. Etudes écologiques et sociologiques des Cyanophycées lithophytes de la côte Yougoslave de l'Adriatique. Bulletin Internationale, Academie Yougoslave Sciences, 26:33–56.

FAIRCHILD, I. J., A. H. KNOLL, AND K. SWETT. In press. A coastal lithofacies-biofacies continuum with syndepositional dolomitization and silicification (Draken Conglomerate Formation, Upper Riphean, Spitsbergen). Precambrian Research.

FAIRCHILD, T. 1975. The geologic setting and paleobiology of a Late Precambrian stromatolitic microflora from South Australia. Unpubl. Ph.D. dissertation, University of California, Los Angeles, 272 p.

FRANCIS, S., L. MARGULIS, AND E. S. BARGHOORN. 1978. On the experimental silicification of microorganisms. II. On the time of appearance of eukaryotic organisms in the fossil record. Precambrian Research, 6:65–100.

GEITLER, L. 1925. Cyanophyceae. A. Pascher's Die Süsswasserflora Deutschlands, Osterreichs, und der Schweiz, 12:1–450.

——. 1930–1932. Cyanophyceae. Band 14, Dr. L. Rabenhorst's Kryptogamen-Flora. Leipzig, 1197 p.

GERMAN, T. 1974. Nakhodi massevikh skoplyennii trikhomov v Rifeyi. Microphytofossilii Proterozoya i Rannyogo Paleozoya SSSR, p. 6–10. [The discovery of massive accumulations of trichomes in the Riphean. Microphytofossils of the Proterozoic and Lower Paleozoic, USSR, p. 6–10.]

——. 1981. Nitchatye mikroorganizmy lakhandinskoj svity reki Mai [Filamentous microorganisms from the Lakhanda Suite along the River Maya]. Paleontologicheskiy Zhurnal, 1981:126–131.

GOLUBIC, S. 1976. Organisms that build stromatolites, p. 113–126. *In* M. R. Walter (ed.), Stromatolites. Elsevier, Amsterdam.

——, AND E. S. BARGHOORN. 1977. Interpretation of microfossils with special reference to the Precambrian, p. 1–14. *In* E. Flügel (ed.), Fossil Algae. Springer Verlag, Heidelberg.

——, AND H. J. HOFMANN. 1976. Comparison of Holocene and mid-Precambrian Entophysalidaceae (Cyanophyta) in stromatolitic algal mats: cells division and degradation. Journal of Paleontology, 50:1074–1082.

GREEN, J. W., A. H. KNOLL, S. GOLUBIC, AND K. SWETT. 1987. Paleobiology of distinctive benthic microfossils from the Upper Proterozoic Limestone–Dolomite 'Series', central East Greenland. American Journal of Botany, 62:835–852.

——, ——, AND K. SWETT. 1988. Microfossils in oolites and pisolites from the Upper Proterozoic Eleonore Bay Group, central East Greenland. Journal of Paleontology, 62:835–852.

——, ——, AND ——. 1989. Microfossils from silicified stromatolitic carbonates of the Upper Proterozoic Limestone–Dolomite 'Series', central East Greenland. Geological Magazine, 126:567–585.

HAMBREY, M. J. 1982. Late Precambrian diamictites of northeastern Svalbard. Geological Magazine, 119:527–551.

HARDIE, L. A. (ed.). 1977. Sedimentation on the Modern Carbonate Tidal Flats of Northwest Andros Island, Bahamas. The Johns Hopkins University Studies in Geology 22, 202 p.

HARLAND, W. B., AND N. J. R. WRIGHT. 1979. Alternative hypothesis for the pre-Carboniferous evolution of Svalbard. Norsk Polar Institutt Skrifter, 167:89–117.

HOFMANN, H. J. 1976. Precambrian microflora, Belcher Islands, Canada: significance and systematics. Journal of Paleontology, 50:1040–1073.

HORODYSKI, R. J., AND J. A. DONALDSON. 1980. Microfossils from the Middle Proterozoic Dismal Lakes Group, arctic Canada. Precambrian Research, 11:125–159.

——, AND S. VONDER HAAR. 1975. Recent calcareous stromatolites from Laguna Mormona (Baja California) Mexico. Journal of Sedimentary Petrology, 45:894–906.

JANKAUSKAS, T. V. 1979. Nizhnyerifeyiskii mikrobioti Yzhnogo Urala [Lower Riphean microfossils of the Southern Urals]. Doklady, Akademii Nauk SSSR, 247:1465–1467.

——. 1982. Mikrofossilii Rifeya Yzhnogo Urala [Riphean microfossils from the Southern Urals], p. 84–120. *In* B. M. Keller (ed.), Stratotyp Rifeya: Paleontologiya ee Paleomagnetizm [Stratotype of the Riphean: Paleontology and Paleomagnetics]. Trudy Geologicheskii Institut, SSSR Akademyii Nauk, Moscow.

—— (ed.). 1989. Mikrofossilii Dokembriya SSSR [Precambrian Microfossils of the USSR]. Trudy Institut Geologii ee Geokhronologii SSSR Akademii Nauk, Leningrad, 188 p.

JOHNSON, J. L. 1961. Limestone-building Algae and Algal Limestones. Colorado School of Mines, Golden, 297 p.

KNOLL, A. H. 1981. Paleoecology of late Precambrian microbial assemblages, p. 17–54. *In* N. J. Niklas (ed.), Paleobotany, Paleoecology, and Evolution, Volume 1. New York, Praeger.

——. 1982. Microorganisms from the late Precambrian Draken Conglomerate Formation, Ny Friesland, Spitsbergen. Journal of Paleontology, 56:755–790.

——. 1984. Microbiotas of the late Precambrian Hunnberg Formation, Nordaustlandet, Svalbard. Journal of Paleontology, 58:131–162.

——, AND J. BAULD. 1989. The evolution of ecological tolerance in prokaryotes. Transactions, Royal Society of Edinburgh, Earth Sciences, 80:209–223.

——, AND N. J. BUTTERFIELD. 1989. New window on Proterozoic life. Nature, 337:602–603.

——, AND S. CALDER. 1983. Microbiotas of the late Proterozoic Ryssö Formation, Nordaustlandet, Svalbard. Palaeontology, 26:467–496.

——, AND S. GOLUBIC. 1979. Anatomy and taphonomy of a Precambrian algal stromatolite. Precambrian Research, 10:110–151.

——, J. M. HAYES, J. KAUFMAN, K. SWETT, AND I. LAMBERT. 1986. Secular variation in carbon isotope ratios from Upper Proterozoic successions of Svalbard and East Greenland. Nature, 321:832–838.

——, AND K. SWETT. 1985. Micropaleontology of the Late Proterozoic Veteranen Group, Spitsbergen. Palaeontology, 28:451–473.

——, AND ——. 1990. Carbonate deposition during the Late Protero-zoic Era: an example from Spitsbergen. American Journal of Science, 290A:104–132.

——, ——, AND E. BURKHARDT. 1989. Paleoenvironmental distribu-tion of microfossils and stromatolites in the Upper Proterozoic Back-lundtoppen Formation, Spitsbergen. Journal of Paleontology, 63:129–145.

KOMAR, V. 1979. Klassifikatsia stromatolitov po mikrostrukturam [The classification of stromatolites by microstructure], p. 42–45. In B. V. Sokolov (ed.), Paleontologia Dokembriya i Rannyevo Kembriya [Paleontology of the Precambrian and Lower Cambrian]. Trudy, In-stitut Geologii i Geokhronologii Dokembriya, Akademii Nauk SSSR, Leningrad.

KOMAREK, J., AND K. ANAGNOSTIDIS. 1986. Modern approach to the classification system of cyanophytes. Archiv für Hydrobiologie, Sup-plement to 73(2):157–226.

LICARI, G. R. 1978. Biogeology of the late pre-Phanerozoic Beck Spring Dolomite of eastern California. Journal of Paleontology, 52:767–792.

LO, S.-C. C. 1980. Microbial fossils from the lower Yudoma Suite, earliest Phanerozoic, eastern Siberia. Precambrian Research, 13:109–166.

MALIVA, R. G., A. H. KNOLL, AND R. SIEVER. 1989. Secular change in chert distribution: a reflection of evolving biological participation in the silica cycle. Palaios, 4:519–532.

MENDELSON, C. V., AND J. W. SCHOPF. 1982. Proterozoic microfossils from the Sukhaya Tunguska, Shorikha,and Yudoma Formations of the Siberian Platform, USSR. Journal of Paleontology, 56:42–83.

MIKHAILOVA, N. S. 1986. Noviye nakhodki mikryhtofossilii iz otlozhyenii vekhogo rifeya Krasnoyarskogo kraya [New discoveries of microphytofossils from Upper Riphean sediments, Krasnoyarskog region]. Aktualniye voprosi sovryemennoi paleoalgologii [Topical Problems in Contemporary Paleoalgology], Kiev, p. 31–37.

MONTY, C. L. V. 1967. Distribution and structure of Recent stro-matolitic algal mats, eastern Andros Island, Bahamas. Annales de la Société Géologique de Belgique, 90:55–100.

MUIR, M. D., AND W. A. S. SARJEANT. 1971. Bibliographie commentée des Tasmanacées et de formes vivantes apparentés (Algues: Prasi-nophyceae), p. 51–117. In S. Jardine (ed.), Microfossiles organiques du Paleozoique, 3, les Acritarches. Editions du CNRS, Paris.

NÄGELI, C. 1849. Gattungen einzellinger Algen, physiologisch und systematisch bearbeitet. Neue Denkschriften der Allgemeinen schweizerischen Gesellschaft für die gesamten Naturwissenschaften, 8:44–60.

NYBERG, A. V., AND J. W. SCHOPF. 1984. Microfossils in stromatolitic cherts from the Upper Proterozoic Min'yar Formation, southern Ural Mountains, USSR. Journal of Paleontology, 58:738–772.

PIA, J. 1927. Thallophyta, p. 31–136. In M. Hirmer (ed.), Handbuch der Paläobotanik. Oldenbourg, Munich.

PICKETT-HEAPS, J. D. 1975. Green Algae: Structure, Reproduction, and Evolution in Selected Genera. Sinauer, Sunderland, Massachu-setts, 606 p.

PJATILETOV, V. G. 1988. Mikrophytofossilii pozdnyeto dokembriya Uchuro-Maiskogo raiona [Later Precambrian microphytofossils from the Uchuro-Maya Uplift], p. 47–104. In V. V. Khomentovsky (ed.), Pozdnii dokembrii i rannii paleozoi Sibiri [Later Precambrian and Early Paleozoic of Siberia: Riphean and Vendian]. Trudy, Sibirskoye Otdelyeniye Institut Geologii i Geofysiki, Akademii Nauk SSSR, No-vosibirsk.

RAABEN, M. YE. 1969. Stromatoliti verkhego rifeya (Gymnosolenidi) [Upper Riphean Stromatolites (Gymnosolęnida)]. Trudy, Institut Geologii, Akademii Nauk SSSR, Moscow, 100 p.

RIDING, R. 1979. Origin and diagenesis of lacustrine algal bioherms at the margin of the Ries crater, Upper Miocene, southern Germany. Sedimentology, 26:645–680.

——. 1982. Cyanophyte calcification and changes in ocean chemistry. Nature, 299:814–815.

RIPPKA, R., J. DEUELLES, J. B. WATERBURY, M. HERDMAN, AND R. Y. STANIER. 1979. Generic assignments, strain histories, and properties of pure cultures of cyanobacteria. Journal of General Microbiology, 111:1–61.

ROUND, F. E. 1981. The Ecology of Algae. Cambridge University Press, Cambridge, 653 p.

SCHIEBER, J. 1989. Facies and origin of shales from the mid-Protero-zoic Newland Formation, Belt Supergroup, Montana, USA. Sedi-mentology, 36:203–219.

SCHOPF, J. W. 1968. Microflora of the Bitter Springs Formation, Late Precambrian, Central Australia. Journal of Paleontology, 42:651–688.

——, AND J. M. BLACIC. 1971. New microorganisms from the Bitter Springs Formation (Late Precambrian) of the north-central Amadeus Basin, central Australia. Journal of Paleontology, 45:925–960.

SERGEEV, V. N. 1984. Mikrofossilii v okryemnistikh stolochatikh stro-matolitakh verkhego rifeya Turukhanskogo raiona [Microfossils in Upper Riphean silicified columnar stromatolites from the Turu-khansk area]. Doklady Akademii Nauk SSSR, 278:436–439.

——. 1988. Okryemnenniye mikrofossilii v stratotipe sryednego rifeya na yuzhom Urale [Silicified microfossils from the stratotype of the Middle Riphean, southern Urals]. Doklady Akademii Nauk SSSR, 303:708–710.

——, AND I. N. KRYLOV. 1986. Mikrofossilii minyarskoi sviti Urala [Microfossils of the Min'yar Suite, Urals]. Paleontologichesky Zhur-nal, 1986:84–95.

SOUTHGATE, P. N. 1986. Depositional environment and mechanism of preservation of microfossils, upper Proterozoic Bitter Springs For-mation, Australia. Geology, 14:683–686.

STANIER, R. Y., W. R. SISTROM, T. A. HANSEN, B. A. WHITTON, R. W. CASTENHOLZ, N. PFENNIG, V. N. GORLENKO, E. N. KONDRATIEVA, K. E. EIMHJELLEN, R. WHITTENBURY, R. L. GHERNA, AND H. G. TRÜPER. 1978. Proposal to place nomenclature of the Cyanobacteria (blue-green algae) under the rules of the International Code of Nomenclature of Bacteria. International Journal of Systematic Bacteriology, 28:335–336.

STAPLIN, F. L., J. JANSONIUS, AND S. A. POCOCK. 1965. Evaluation of some acritarchous hystrichosphere genera. Neues Jahrbuch für Geo-logie und Paläontologie, Abhandlung 123:167–201.

STROTHER, P. K., A. H. KNOLL, AND E. S. BARGHOORN. 1983. Micro-organisms from the late Precambrian Narssârssuk Formation, north-western Greenland. Palaeontology, 26:1–32.

SWETT, K., AND A. H. KNOLL. 1985. Stromatolitic bioherms and mi-crophytolites from the Late Proterozoic Draken Conglomerate For-mation, Spitsbergen. Precambrian Research, 28:327–347.

TAPPAN, H. 1980. Paleobiology of Plant Protists. Wiley, San Francisco, 1028 p.

THURET, G. 1875. Essai de classification des Nostochinées. Annales Sciences Naturelle (Botanie), 6:372–382.

TIMOFEEV, B. V. 1959. Drevejshava flora Pribaltiki i ee stratigrafi-cheskoe znachenie [Ancient flora of the Baltic area and its stratigraphic significance]. Trudy, Vsesoyuznogo Neftyanogo Nauchno-Issledo-vatel'skogo Geologorazvedochnogo Instituta, Leningrad, 129:1–320.

——. 1966. Mikropaleofitologichneskoe issledovanie drevnikh svit [Microphytological Investigations of Ancient Formations]. Nauka, Moscow, 145 p.

——, T. N. GERMAN, AND N. S. MIKHAILOVA. 1976. Mikrofitofossilii dokembiya, kembriya, i ordovika [Microfossils from the Precambri-an, Cambrian, and Ordovician]. Trudy, Institut Geologii i Geochro-nologii Dokembri, Leningrad, 106 p.

TYLER, S. A., AND E. S. BARGHOORN. 1954. Occurrence of structurally preserved plants in Precambrian rocks of the Canadian Shield. Sci-ence, 119:606–608.

VIDAL, G. 1976. Late Precambrian microfossils from the Visingsö beds in southern Sweden. Fossils and Strata, 9:1–57.

——, AND A. H. KNOLL. 1983. Proterozoic plankton. Geological So-ciety of America, Memoir 161:265–277.

——, AND J. P. NYSTUEN. 1990. Stratigraphy and micropaleontology of the late Precambrian Hedmark Group, Norway. American Journal of Science, 290A:170–211.

WATERBURY, J. B., AND R. Y. STANIER. 1978. Patterns of growth and development in pleurocapsalean cyanobacteria. Microbiological Re-views, 42:2–44.

WETTSTEIN, R. 1924. Handbuch der Systematischen Botanik, Band 1. Franz Deuticke, Leipzig, 1017 p.

WHITTON, B. A., AND M. POTTS. 1982. Marine littoral, p. 515–542. In N. G. Carr and B. A. Whitton (eds.), The Biology of Cyanobacteria. Blackwell, Oxford.

WILSON, C. B. 1958. The Lower Middle Hecla Hoek rocks of Ny Friesland, Spitsbergen. Geological Magazine, 94:305–327.

——. 1961. The Upper Middle Hecla Hoek rocks of Ny Friesland, Spitsbergen. Geological Magazine, 98:89–116.

WOESE, C., AND G. FOX. 1977. Phylogenetic structure of the prokaryotic domain. Proceedings, National Academy of Science, U.S.A., 74:5088–5090.

WRAY, J. L. 1977. Calcareous Algae. Elsevier, Amsterdam, 185 p.

YIN, L. 1987. Microbiotas of latest Precambrian sequences in China. Stratigraphy and Paleontology of Systemic Boundaries in China, Precambrian–Cambrian Boundary, 1:415–494.

ZANG, W. 1989. Late Proterozoic–Early Cambrian microfossils and biostratigraphy in China and Australia. Unpubl. Ph.D. thesis, Australian National University, Canberra, Australia, 432 p.

——, AND M. R. WALTER. 1989. Latest Proterozoic plankton from the Amadeus Basin in central Australia. Nature, 337:642–645.

ZHANG, Y. 1981. Proterozoic stromatolite microfloras of the Gaoyuzhuang Formation (Early Sinian: Riphean), Hebei, China. Journal of Paleontology, 55:485–506.

UPPER PRECAMBRIAN THROUGH LOWER CAMBRIAN OF CAPE BRETON ISLAND: FAUNAS, PALEOENVIRONMENTS, AND STRATIGRAPHIC REVISION

ED LANDING
New York State Geological Survey,
The State Education Department, Albany 12230

ABSTRACT—Latest Precambrian through Early Cambrian tectonic history and stratigraphy are comparable in southeastern Cape Breton Island and the western Placentia–Bonavista axis, southeastern Newfoundland. The lithostratigraphic nomenclature of southeastern Newfoundland is used for this interval in Cape Breton Island. Upper Precambrian volcanic rocks of the Forchu Group (= "Giant Lake Complex," designation abandoned) are unconformably overlain by uppermost Precambrian through lowest Cambrian strata termed the "Morrison River Formation" (designation abandoned). This depositional sequence consists of three formations: 1) red beds through tidalites of the Rencontre Formation (to 279+ m; ="Kelvin Lake Formation," designation abandoned); 2) prodeltaic clastics of the Chapel Island Formation (to 260 m); and 3) macrotidal quartzites of the Random Formation (to 71+ m). Post-Random block faulting and 300 m of local erosion took place prior to onlap of the "MacCodrum Formation" (abandoned). Siliciclastic mudstones of the lower "MacCodrum" are re-assigned to the middle Lower Cambrian Bonavista Group. Sub-trilobitic faunas from the Bonavista Group include "Ladatheca" cylindrica from the West Centre Cove Formation(?) and higher diversity faunas (23 species) in the Camenella baltica Zone of the Cuslett and Fosters Point Formations. Trilobite-bearing, upper Lower Cambrian (Branchian Series) strata (Brigus Formation, =upper "MacCodrum" and overlying "Canoe Brook" Formations) unconformably overlie the Placentian Series in Cape Breton Island, southeastern Newfoundland, Shropshire, and, probably, eastern Massachusetts. Correlations based on small shelly fossils indicate an earlier appearance of trilobites in Avalon than on the South China Platform. Twenty-six species are illustrated. Halkieria fordi n. sp., the conodont(?) "Rushtonites" asiatica n. sp., and the zhijinitid(?) Samsanoffoclavus matthewi n. gen. and sp. are described. Ischyrinia? sp. may be the oldest ischyrinoid rostroconch.

INTRODUCTION

THE AVALON ZONE of the coastal northeastern Appalachians and southern Britain (see Rast et al., 1976; Williams and Hatcher, 1982) has considerable significance in understanding the evolutionary radiations, immigration events, and geological context of latest Precambrian and earliest Cambrian metazoans (see Landing et al., 1989). Early descriptions of the larger faunal elements (hyoliths, mollusks, and brachiopods) from the sub-trilobitic and trilobite-bearing Lower Cambrian of Avalon (Holl, 1865; Shaler and Foerste, 1888; Matthew, 1889, 1899a, 1899b, 1899c; Groom, 1902; Cobbold, 1919, 1921; Cobbold and Pocock, 1934) have been complemented by the recognition of associated, diverse agglutinated, calcareous, and phosphatic small shelly fossils (Landing et al., 1980, 1989; Bengtson and Fletcher, 1983; Landing, 1984, 1988b, 1989; Brasier, 1984, 1986; Hinz, 1987). These reports and the recognition that many species of dubious validity are described from coeval Asian sequences (Landing, 1988a, 1988b; Conway Morris, 1988; Qian and Bengtson, 1989) suggest a re-interpretation of earliest Cambrian diversity patterns. Skeletalized faunas from the siliciclastic-dominated, cooler water environments of Avalon (Landing, 1989) seem to have been only somewhat less diverse than those from warm-water, carbonate platforms of Soviet Asia and China (see Rozanov et al., 1969; Luo et al., 1982, 1984; Xing et al., 1983). In addition, uppermost Precambrian through lowest Cambrian trace fossils are more diverse in the Avalonian terrane of southeastern Newfoundland (see Crimes and Anderson, 1985; Crimes, 1987; Narbonne and Myrow, 1988) than in Asian sequences. However, trace and body fossils and their paleoenvironmental and stratigraphic distribution remain undescribed from important areas of the uppermost Precambrian and Lower Cambrian of Avalon.

This study was prompted by descriptions of the geology of southeastern Cape Breton Island (Fletcher, 1877, 1879; Matthew, 1903; Weeks, 1947, 1954; Hutchinson, 1952) that indicated the Lower Cambrian of the Mira River valley is similar to the more completely documented sequence in southeastern Newfoundland (Figure 1.1). Weeks (1954) compared the sili-