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Authors: KNOLL, ANDREW H., WÖRNDLE, SARAH, and KAH, LINDA C.

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COVARIANCE OF MICROFOSSIL ASSEMBLAGES AND MICROBIALITE TEXTURES ACROSS AN UPPER MESOPROTEROZOIC CARBONATE PLATFORM

ANDREW H. KNOLL,^{1*} SARAH WÖRNDLE,² and LINDA C. KAH³

¹Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA, aknoll@oeb.harvard.edu; ²Université Lyon-1 Claude Bernard, Département des Sciences de la Terre, 69622 Villeurbanne Cedex, France, sarah.worndle@hotmail.fr; ³Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, Tennessee 37996-1410, USA, lckah@utk.edu

ABSTRACT

Early diagenetic chert nodules and beds in the upper Mesoproterozoic Angmaat (formerly Society Cliffs) Formation, Baffin and Bylot islands, preserve microfossils and primary petrofabrics that record microbial mat deposition and lithification across a range of peritidal carbonate environments. Five distinct microfossil assemblages document the distribution of mat-building and mat-dwelling populations across a gradient from restricted, frequently exposed flats to more persistently subaqueous environments. Mats built primarily by thin filamentous or coccoidal cyanobacteria give way to a series of more robust forms that show increasing assemblage diversity with decreasing evidence of subaerial exposure. Distinct fabric elements are associated with each microbial assemblage, and aspects of these petrofabrics are recognizably preserved within unsilicified carbonate in the same beds. These include some features that are distinctly geologic in nature (e.g., seafloor cements) and others that reflect microbial growth and decomposition (e.g., tufted microbialites). A particularly distinctive, micronodular fabric is here interpreted as carbonate infilling of primary voids within microbial mat structures. Such structures mark the co-occurrence of cyanobacterial photosynthesis that produced oxygen gas, filamentous mat builders that imparted the coherence necessary to trap gas bubbles, elevated carbonate saturation required to preserve void fabrics via penecontemporaneous cementation, and a relative paucity of detrital sediment that would have inhibited mat growth. Petrofabrics preserved in Angmaat samples are widespread in upper Paleoproterozoic and Mesoproterozoic carbonate successions but are rare thereafter, perhaps recording, at least in part, the declining carbonate saturation state of seawater. Covariation of microfossil assemblages with petrofabrics in both silicified and unsilicified portions of carbonate beds supports hypotheses that link stromatolite microstructure to the composition and diversity of mat communities.

INTRODUCTION

Stromatolites constitute the most conspicuous record of life in Proterozoic sedimentary rocks. Stromatolites vary in morphology and fabric across individual basins and through time, but despite a century of research, there is little consensus on how this variation relates to microbial diversity (Grotzinger and Knoll, 1999). Aspects of stromatolite macrostructure clearly reflect sedimentary environment (Cloud and Semikhatov, 1969; Serebryakov, 1976; Semikhatov et al., 1979; Andres and Reid, 2006), but petrologic fabric may additionally preserve a record of distinct microbial communities and metabolic activities active during stromatolite accretion (Monty, 1976; Walter, 1992; Dupraz et al., 2006, 2009; Bosak et al., 2013). Testing biological hypotheses, however, is complicated by diagenesis, which can result in both the alteration of original petrofabrics and obliteration of the mat-building populations in stromatolites. An exception occurs in the upper

Mesoproterozoic Angmaat Formation, Bylot Supergroup, Nunavut, where early diagenetic chert nodules preserve both microbial mat populations and distinctive mat petrofabrics. Silicified fabrics, in turn, can be compared directly to textures preserved in unsilicified carbonate in the same beds, allowing us to address specifically the question of how microbial community composition relates to mat fabric in selected Proterozoic carbonate successions.

GEOLOGIC SETTING AND AGE

The Bylot Supergroup comprises a >6-km-thick succession of nearly undeformed, upper Mesoproterozoic to lowest Neoproterozoic sedimentary rocks exposed within the fault-bounded Borden Basin of northernmost Baffin and Bylot islands (Fig. 1; Jackson and Ianelli, 1981; Turner, 2009). Timing of sedimentation within the Bylot Supergroup is broadly constrained by U-Pb baddeleyite ages on basalts that both pre- and postdate sediment deposition. Basalts near the base of the Bylot succession have yielded an age of 1270 ± 4 Ga (Le Cheminant and Heaman, 1989), and Franklinian dikes that crosscut the supergroup as a whole record a maximum age of ca. 723 Ma (Heaman et al., 1992; Pehrsson and Buchan, 1999). Consistent with these constraints are a Pb-Pb age for Angmaat carbonate beds of 1199 ± 24 Ma (unpublished data, in Kah et al., 2001) and a U-Th-Pb whole rock age of 1092 ± 59 Ma for black shale of the underlying Arctic Bay Formation (Turner and Kamber, 2012). Carbon isotope stratigraphy independently suggests an age younger than ca. 1250 Ma and older than ca. 850 Ma (Kah et al., 1999, 2012), and microfossils suggest that the depositional age of Angmaat Formation strata lies closer to the lower than to the upper boundary established by regional basalts (Hofmann and Jackson, 1991, 1994). Micropaleontological data on correlative successions in northwestern Greenland (Strother et al., 1983; Samuelsen et al., 1999) and Somerset Island (Butterfield, 2001) further support a late Mesoproterozoic age for Angmaat deposition.

Sedimentary rocks of the Bylot Supergroup crop out extensively within the fault-bounded Borden Basin of northern Baffin and Bylot islands (Fig. 1; Jackson and Ianelli, 1981; Kah et al., 1999; Turner, 2009). Traditionally, deposition of a laterally extensive package of carbonate-dominated strata—originally distinguished as the Society Cliffs Formation—was considered to represent a period of relative tectonic quiescence within the basin, during which sea-level rise promoted an extensive, northwestward-deepening carbonate ramp (Blackadar, 1956; Lemon and Blackadar, 1963; Geldsetzer, 1973). Building on the work of Jackson and Ianelli (1981), who recognized a pronounced diminution of siliciclastic material upward in the Society Cliffs Formation, and Kah (1997, 2000) and Kah et al. (1999, 2001), who recognized a distinct shift to deeper-water facies west of a persistent oolitic shoal in the region of Tremblay Sound, Turner (2009) divided the strata into four formations (Iqqittuq, Angmaat, Nanisivik, and Ikpiarjuk) that better reflect regional lithologic trends. Here we focus on the southeastern successions of the former Society Cliffs Formation, now considered the Angmaat Formation.

* Corresponding author.

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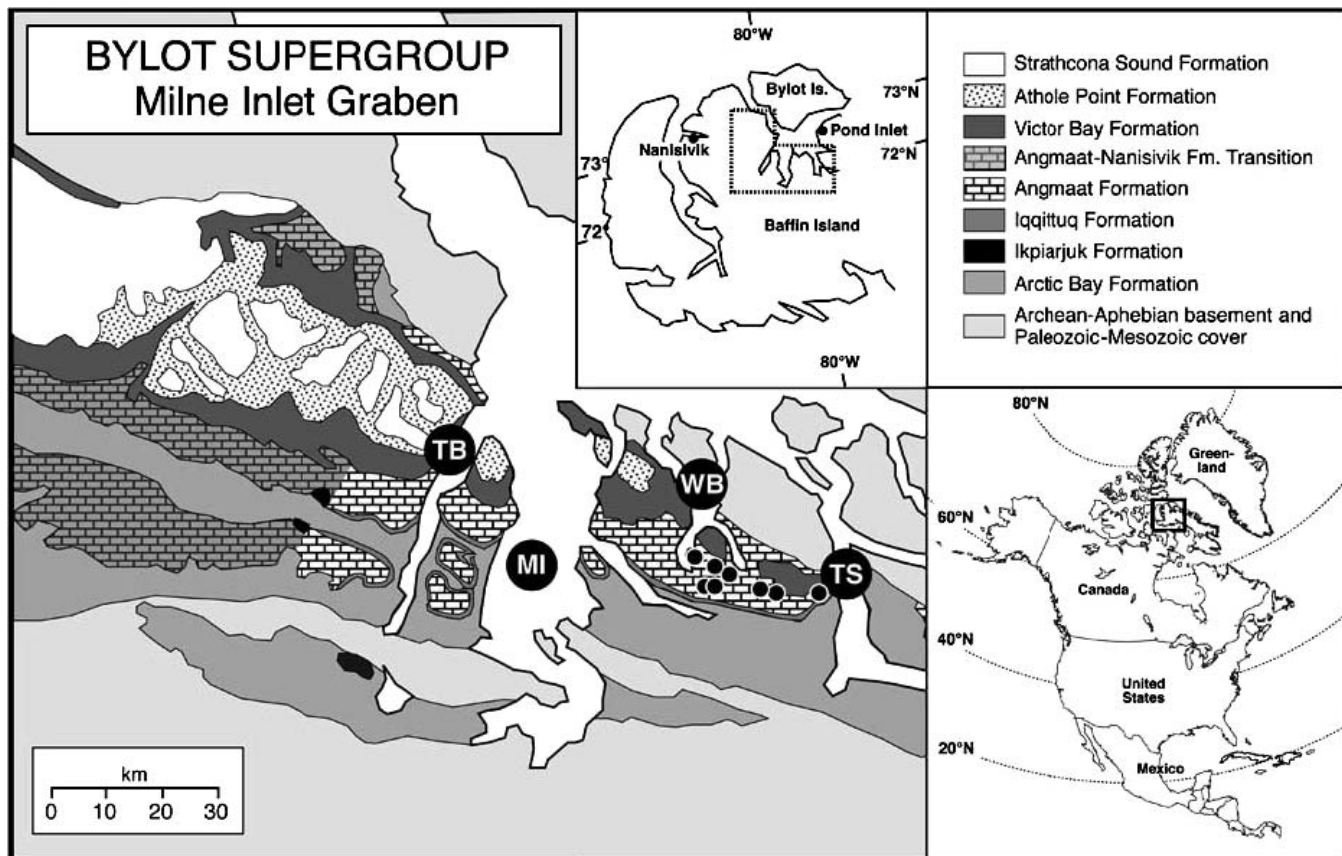


FIGURE 1—Geologic map of the Milne Inlet region, Baffin Island, showing location and distribution of stratigraphic units within the Bylot Supergroup. Samples are tied to measured sections between White Bay (WB) and Tay Sound (TS). Oolitic facies of the Angmaat Formation occur primarily between White Bay (WB) and Tremblay Sound (TB).

The Angmaat Formation records predominantly intertidal to supratidal carbonate deposition, with auxiliary siliciclastic, evaporite, and chert lithologies (Kah and Knoll, 1996; Kah et al., 2001). The majority of the Angmaat Formation represents *in situ* deposition within an evaporative microbial flat that was frequently restricted from open marine waters by subaerial exposure of a mid-ramp oolitic/intraclastic shoal complex (Kah, 1997; Kah, 2000; Kah et al., 2001). Inner ramp carbonate facies are dominated by microbialite facies, with subordinate precipitate facies and rare detrital lithologies.

Microbialites comprise a variety of low-relief stratiform, domal, columnar, and coniform structures. Coniform stromatolites with distinct concave upward laminae form interlinked features up to 20 cm in synoptic relief, and are restricted to deepest-water portions of the Angmaat platform, where they are interbedded with columnar stromatolites and oolitic/intraclastic shoal facies. In the inner ramp, coniform microbialites are restricted to mm- to cm- scale tufted mats (see below) that interfinger laterally with the more abundant smooth and micronodular laminae that comprise the majority of stratiform mat facies. Tufted laminae, however, are more common in restricted portions of the ramp, where they are interlaminated with precipitated carbonate facies, often in the construction of broad, domal features.

Precipitate facies consist of smooth submillimeter laminae that can often be traced across tens to hundreds of meters of outcrop exposure and reflect a continuum of nucleation patterns. Continuous nucleation along the substrate results in laterally extensive isopachous crusts; isolated nucleation sites result in the formation of small (generally <5 mm) cement botryoids on bedding surfaces. Successive lamina growth atop these smooth to bumpy surfaces resulted in formation of a range of precipitate forms from hemispherical domes to microdigitate, or asperiform, structures (cf. Hofmann and Jackson, 1987).

Detrital carbonate facies are rare within the Angmaat Formation, and consist primarily of thin micritic drapes, local arenites, and a variety of intraclastic conglomerate units deposited under higher-energy, less restricted conditions. Evaporite lithologies—predominantly gypsum—are broadly distributed within the Angmaat Formation (Kah et al., 2001), but are relatively rare in the Milne Inlet Trough, where they occur only as cm-scale nodules within stratiform mats and within a few discrete beds (up to 1.45 meters thick; Kah et al., 2001). Within the Milne Inlet trough, bedded gypsum occurs primarily in the southeast, where it is intimately associated with precipitate facies and thin beds of terrigenous red to green shale.

Finally, the Angmaat Formation (and correlative strata in adjacent grabens in northwestern Greenland and on Somerset Island; Kah et al., 1999) contains abundant nodular to bedded chert (Jackson and Ianelli, 1981). Chert nodules and beds display a wide range of colors, from white to gray, yellow to orange, green to purple, and brown to black, and occur in variously shaped bodies that are commonly discordant to bedding (Jackson and Ianelli, 1981; Hofmann and Jackson, 2001). Black chert is most abundant, especially in the region between Milne Inlet and Tay Sound (Fig. 1), forming beds and nodules oriented parallel to bedding and up to 10 cm in thickness. Black chert typically preserves microfossils (Hoffman and Jackson, 2001; Kah and Knoll, 1996; see also Strother et al., 1983, and Butterfield, 2001, for fossiliferous chert from coeval strata in adjacent grabens), although more poorly preserved microfossils have been found in a wide variety of colored chert (Hoffman and Jackson, 2001).

MICROFOSSILS IN ANGMAAT MICROBIALITES

Attempts to evaluate the relationship between microbial community and microbialite petrofabric begin with the elucidation of preserved

microfossil assemblages. Hofmann and Jackson (1991) described silicified microfossils from throughout the (then) Society Cliffs and overlying Arctic Bay formations. Their most diverse fossil localities occur in the Arctic Bay succession and there was no attempt to relate fossils to petrofabric. Nonetheless, most of the taxa found in our Angmaat chert samples were noted by Hofmann and Jackson (1991).

Most mat-building populations in Angmaat microbialites are preserved as hollow filamentous tubes—the preserved extracellular polysaccharide sheaths of *Lyngbya*- or *Phormidium*-type cyanobacteria (Figs. 2–4). By convention, single sheaths are assigned to the genus *Siphonophycus* Schopf (1968) and divided into species based on cross-sectional diameter. Remarkably, most Proterozoic *Siphonophycus* populations fit comfortably within one of these operationally defined species (e.g., Knoll et al., 1991). Hofmann and Jackson (1991) recognized the three species-level *Siphonophycus* taxa noted in our study, although the population here assigned to *S. capitaneum* on the basis of size was placed into the smaller *S. kestron* by these authors. They also named several small and poorly preserved taxa, which we view as degradational variants of the principal mat-building filaments.

Distinctly larger (up to 70 μm in cross-sectional diameter) filamentous sheaths (Fig. 3D) that originally enclosed multiple cellular trichomes (see cross section in Fig. 3E) are assigned to *Eomicrocoleus crassus* Horodyski and Donaldson (1980) and interpreted in terms of the extant mat-building cyanobacterium *Microcoleus chthonoplastes*. Note that when the microscope is ratcheted up and down through *E. crassus* specimens, the internal reflections of trichomes (seen as lineations in Fig. 3D) can be shown to form a ropelike coiling that, in the modern, is a diagnostic feature of *M. chthonoplastes* (Desikachary, 1959).

Microfossils in Angmaat chert also include abundant and diverse coccoidal populations, many, if not most of them, cyanobacterial (Figs. 4–6). Early in the modern era of Proterozoic paleontology, spheroid-rich assemblages were discovered on several continents and assigned to a large number of narrowly diagnosed taxa. Butterfield (2001) summarized the resulting challenges for taxonomy. Whereas some of the complications simply reflect synonymy, others stem from aspects of life cycle and taphonomy (e.g., Knoll and Golubic, 1979), offering a principled path toward resolution. Sorting out all issues of Proterozoic microfossil taxonomy is beyond the scope of this paper, but we do propose distinctions among the main mat-forming populations present in the Angmaat assemblage.

Populations of small, mat-building coccoidal colonies are assigned to *Eoentophysalis belcherensis* Hofmann (1976) and interpreted in terms of the extant mat-building genus *Entophysalis*. Small (2–5 μm) cell-like units are bound into colonies by extracellular envelopes secreted with each new cell division; resulting clusters contain 2–32 cells within up to five nested envelopes. Colonies are palmelloid to cumulate (Fig. 4B), but also include isolated unicells, dyads, and smaller clusters, many of which were described as separate species in early papers (e.g., Muir, 1976). A principal problem with the taxonomic circumscription of *Eoentophysalis* is that new colonies begin with individual cells, so colonizing eoentophysalids may be difficult or impossible to differentiate from similarly small, noncolonial taxa such as *Sphaerophycus parvum* Schopf (1968). *Sphaerophycus* populations are not always eoentophysalid colonists, as many *S. parvum* (Figs. 4D–E; ~2 μm cell-like units) and (slightly larger; 4–5 μm units) *S. medium* Horodyski and Donaldson (1980; Figs. 5C–D) populations occur in facies where eoentophysalid colonies are absent, both in the Angmaat and in other formations. Populations of small coccoids could include heterotrophic bacteria. Erring on the side of caution, we recognize *Sphaerophycus* populations only when isolated unicells, dyads, and tetrads are distributed through mats in the absence of reasonably well-formed *Eoentophysalis* colonies.

Like Hofmann and Jackson (1991), we also recognize two species of the cyanobacterial form genus *Gloeodiniopsis* Schopf (1968) *emend.*

Knoll and Golubic (1979). *Gloeodiniopsis lamellosa* is applied to populations of multilamellate (or single envelope, by differential decay) unicells, dyads, tetrads, and rare octads, distributed as isolated individuals in eoentophysalid and filamentous mats but never found in dense colonies (Figs. 4I–L). The simple life cycle and taphonomic pattern inferred for these populations compares closely with those of the extant cyanobacterium *Chroococcus turgidus* (Knoll and Golubic, 1979). A second *Gloeodiniopsis* species, *G. magna* Nyberg and Schopf (1984), is spatially distinct and much larger, but shares the basic life cycle inferred for *G. lamellosa* (Figs. 4G, 5E).

Eogloeocapsa bella Golovenok and Belova (1984) can be difficult to differentiate, given its high degree of taphonomic variation, but well-preserved populations document a life cycle comparable to that observed in extant species of *Gloeocapsa* (Geitler, 1930–1932). *Eogloeocapsa* thus differs from *Gloeodiniopsis* in three principal ways: internal envelopes formed around a single cell fill a smaller percentage of the volume formed by enclosing envelopes (that is, cell-like internal envelopes are not close-packed but rather appear to float); there is a single external envelope, unlike the multilamellate exterior of *Gloeodiniopsis*; and colonies can be closely packed to form monospecific surfaces in peritidal environments (Figs. 6A–C). As discussed by Sergeev (1994), there is some potential for confusion in terms of another Proterozoic taxon *Clonophycus elegans* Oehler (1977), but the type of *C. elegans* is an outer envelope filled by a large number of closely packed cells, with no evidence of intermediate envelopes. This differs substantially from both the type of *E. bella* and the Angmaat material.

Polybessurus bipartitus Fairchild *ex* Green et al. (1987) is a coccoidal cyanobacterium distinguished by its prominent stalk formed by downwardly elongated envelopes (Figs. 5A–B). In terms of morphology, life cycle, and environmental preference, these fossils find a close counterpart in *Cyanostylon*-like cyanobacteria from peritidal carbonate environments in the present-day Bahamas (Green et al., 1987).

At least two additional populations of simple spheroids occur in filamentous mats, one 8–10 μm (Fig. 5F) and the other 25–30 μm in diameter (Fig. 3F). These populations are readily placed within the form genus *Myxococcoides* Schopf (1968), and might be assigned to *M. minor* Schopf (1968) and *M. grandis* Horodyski and Donaldson (1980) on the basis of size, but the Angmaat populations are sufficiently different from the types of these species to warrant caution. For this reason, we refer to them simply as *Myxococcoides* sp. 1 and sp. 2. Two more unnamed populations consist of poorly preserved, *Hyella*-like endolithic cyanobacteria, interpreted on the basis of overall morphology and orientation, which clearly indicates downward growth into the substrate (Fig. 4A); and clustered unicells ~25 μm in diameter from which 10–12 μm tubes extend outward for up to 50 μm (Fig. 4H). The latter fossils appear to be germinating cysts, like the Neoproterozoic *Germinosphaera* (see Butterfield et al., 1994, for interpretation), but at a much smaller size scale. Multilamellate unicells that appear to open on one end (Fig. 4F; also documented by Butterfield, 2000, from the correlative Hunting Formation on Somerset Island) may be an incipient excystment stage of the same population.

The final constituents of our Angmaat samples are isolated cellular filaments found within *E. robustum* mats. These fossils can be assigned to the early red alga *Bangiomorpha pubescens* Butterfield (2000), described from potentially correlative strata (Kah et al., 1999) on Somerset Island and, possibly, northwestern Greenland (Enzien, 1990). Angmaat specimens (Figs. 6D–E) observed to date do little to augment the paleobiological interpretation of this taxon, adding only that the envelopes surrounding cellular filaments can form septa that separate packets of a dozen or more cells. When preserved in the absence of cells, these would be closely comparable to the unnamed septate tubes described by Butterfield (2000; his fig. 3E) from *Bangiomorpha*-bearing beds on Somerset Island.

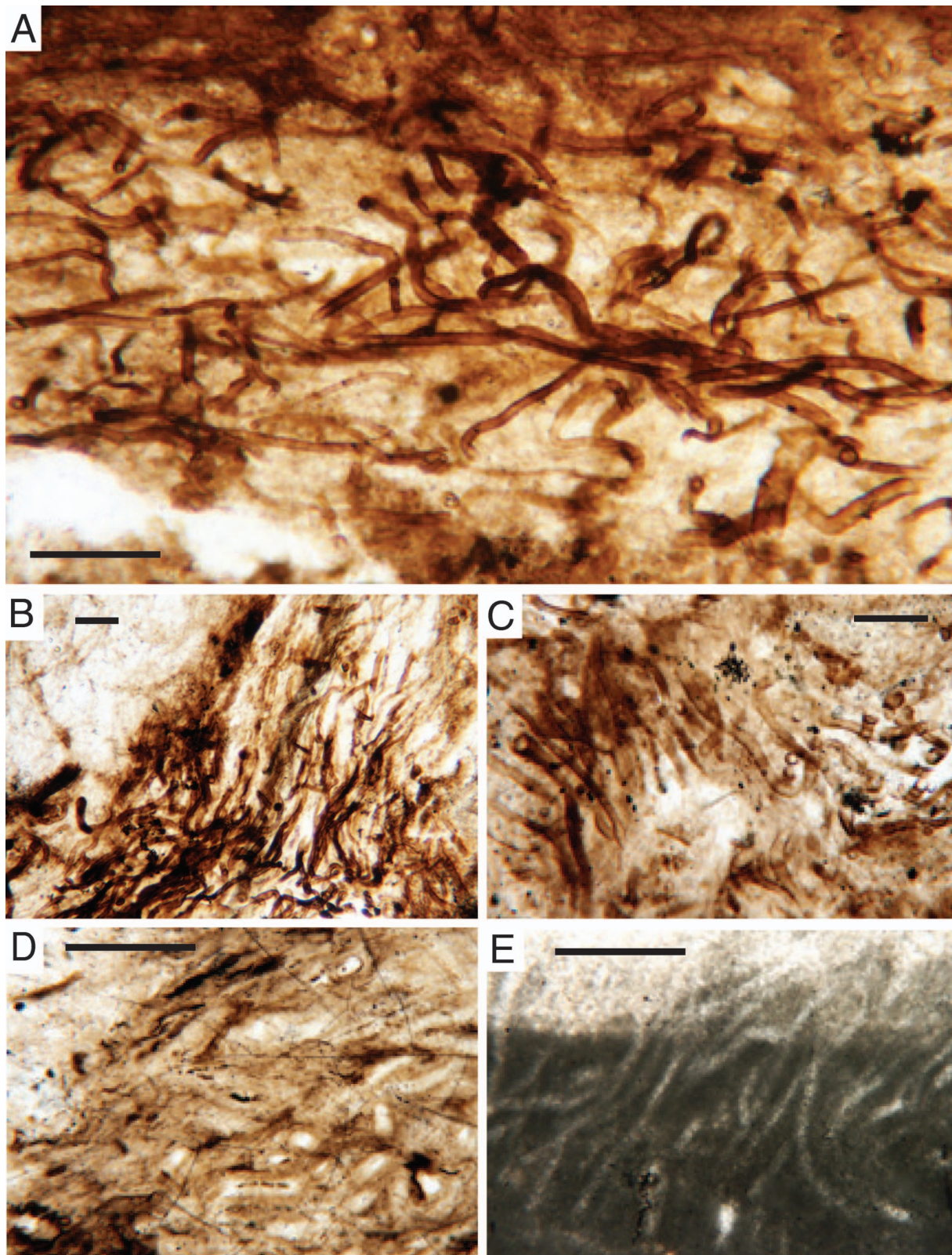


FIGURE 2—Populations of *Siphonophycus inornatum* and *S. capitaneum* in filament-dominated mat facies. A–D) Various oriented silicified populations (A = G4, G53/0; B = G4, J53/0, C = G4, L51/2; D = DAC-10, J38/4). E) Molds of *S. capitaneum* sheaths preserved in carbonate (DAC-10, S62/4). All illustrated specimens are reposit in Harvard University Paleobotanical Collection 64840; England finder coordinates are given in parentheses for thin sections and microfossils. Scale bars = 250 μ m.

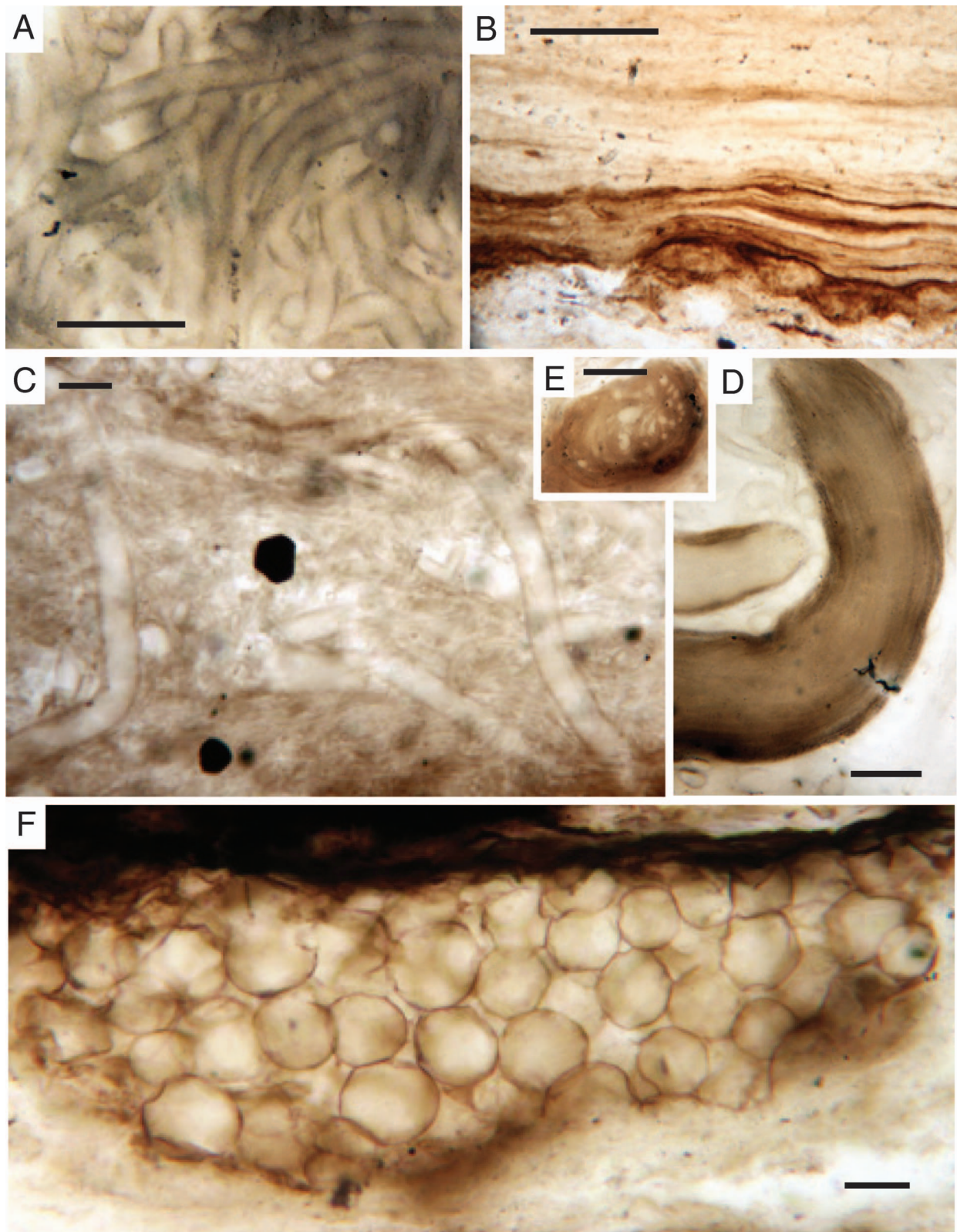


FIGURE 3—Microfossils and fabrics in filament-dominated mat facies. A) *Siphonophycus inornatum* (G23, N49/1). B) Mat fabric of laminated EPS, with no well-preserved microfossils. C) Mat-building assemblage of *S. inornatum* and larger *S. capitaneum* (DAC-5, N70/3). D) *Eomicrocoleus crassus* (G4, B54/3). E) Cross section of *E. crassus*, showing evidence of multiple trichomes (DAC-5, E53/0). F) *Mycoccoides* sp. 2 (DAC-28, M50/0). All illustrated specimens are deposited in Harvard University Paleobotanical Collection 64840; England finder coordinates are given in parentheses for thin sections and microfossils. Scale bar = 30 μ m for all images except B, where it equals 1 mm.

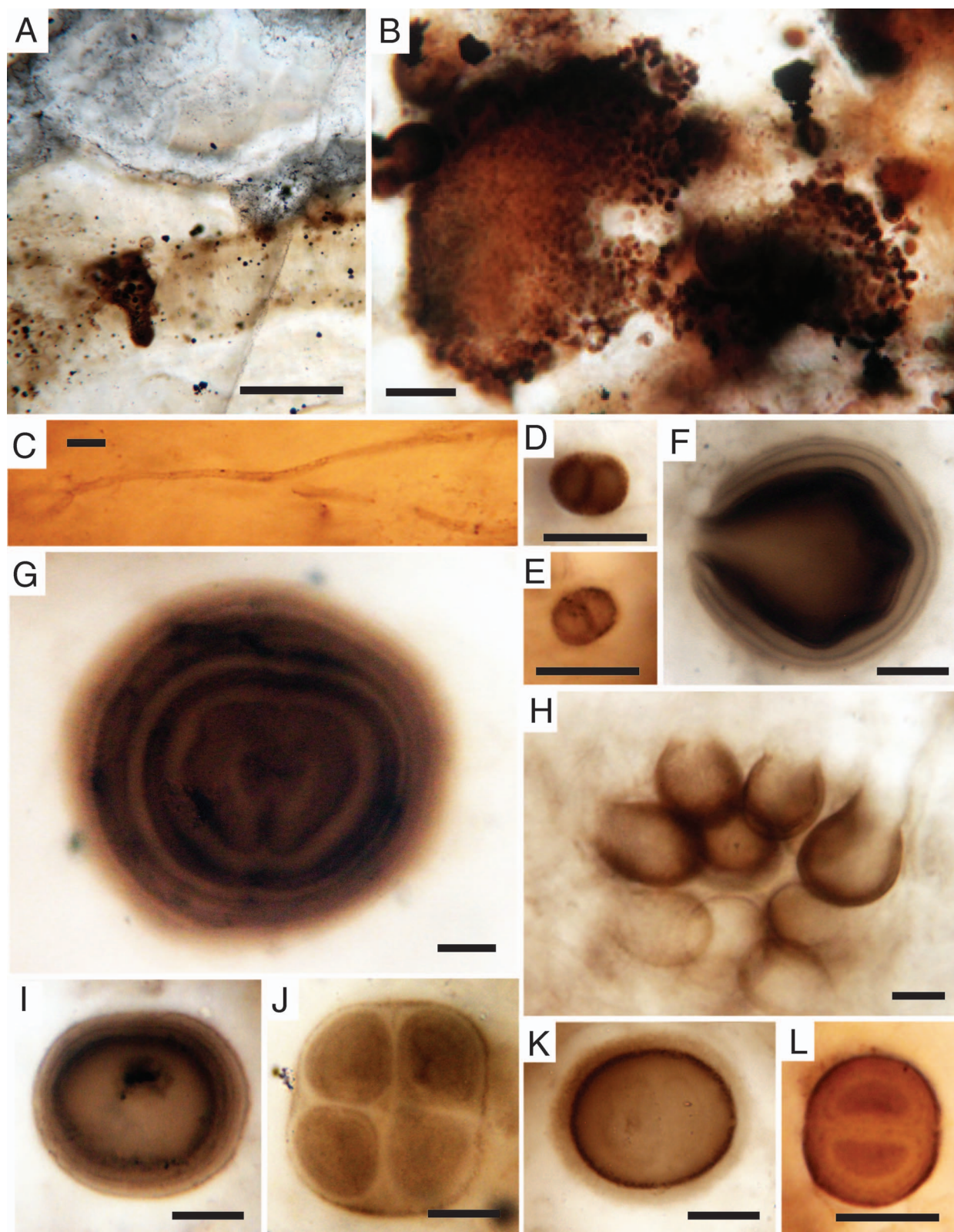


FIGURE 4—Microfossils in Angmaat chert. A) Endolithic cyanobacteria penetrating lamina in laminated precipitate-coccolidal mat facies (34, N48/4). B) *Eoentophysalis belcherensis* colony in coccolidal mat layer (DAS 26, N65/4). C) *Siphonophycus robustum* in thin filament mat (34, F55/2). D–E) *Sphaerophycus parvum* dyads within the filament-dominated mat community (D = G25, M43/1; E = G25, L41/4). F) Unnamed multilamellate spheroid with opening, possibly related to *Polybessurus*, in filament-dominated mat (thin section G4, Efc G57/2). G) *Gloeodiniopsis magna* (thin section 35, Efc V41/2). H) Unnamed spheroids with tubular extensions (G25, Efc). I–L) *Gloeodiniopsis lamellose* (I = G25, M43/4; J = 35, T48/1; K = G4, E59/0, L = DAC-5, H53/0). All illustrated specimens are deposited in Harvard University Paleobotanical Collection 64840; England finder coordinates are given in parentheses for thin sections and microfossils. Scale bars = 100 μm for A and B, and = 10 μm for all other images.

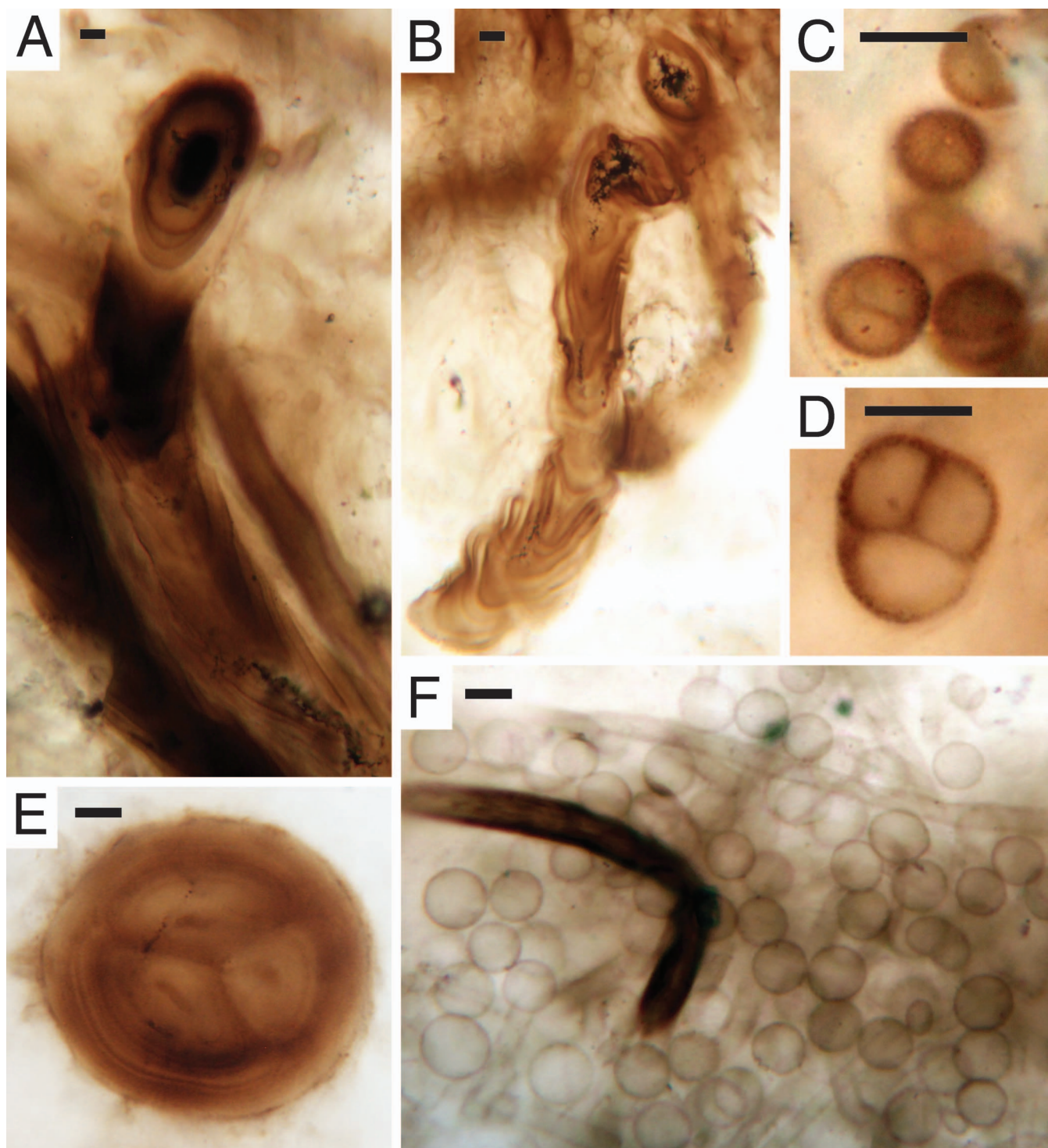


FIGURE 5—Mat-dwelling populations in filament-dominated mats. A–B) *Polybessurus bipartitus* (A = G4, P57/0; B = G4, K61/1). C–D) *Sphaerophycus medium* (C = G25, M43/0; D = G25, M43/2) E) *Gloeocapsa magna* (34, 46/2). F) *Myxococcoides* sp. 1 (G4, O56/0). All illustrated specimens are deposited in Harvard University Paleobotanical Collection 64840; England finder coordinates are given in parentheses for thin sections and microfossils. Scale bars = 10 μ m.

CORRELATING MICROFOSSILS AND PETROFABRIC

Crystal Fan-Dominated Precipitates

Flat-laminated and domal carbonate beds, interpreted as originally aragonitic seafloor precipitates, are conspicuous features of Angmaat outcrops (Kah et al., 2001; Turner, 2009). Where preserved as dolomite, precipitated laminae are mm scale with mm- to cm-scale,

convex-upward microdomal surfaces (Fig. 7A). Laminae consist, for the most part, of interlocking dolomite anhedral up to ~ 80 μ m in maximum dimension capped by thin drapes of dolomitic microspar that commonly preserve ghosts of upward-directed crystal terminations. Even in these relatively coarse-grained dolostones, UV fluorescence highlights organic inclusions that define acicular needles and sprays of crystalline carbonate that grew perpendicular to the substrate. Minute pyrite crystals (or iron oxides formed by diagenetic

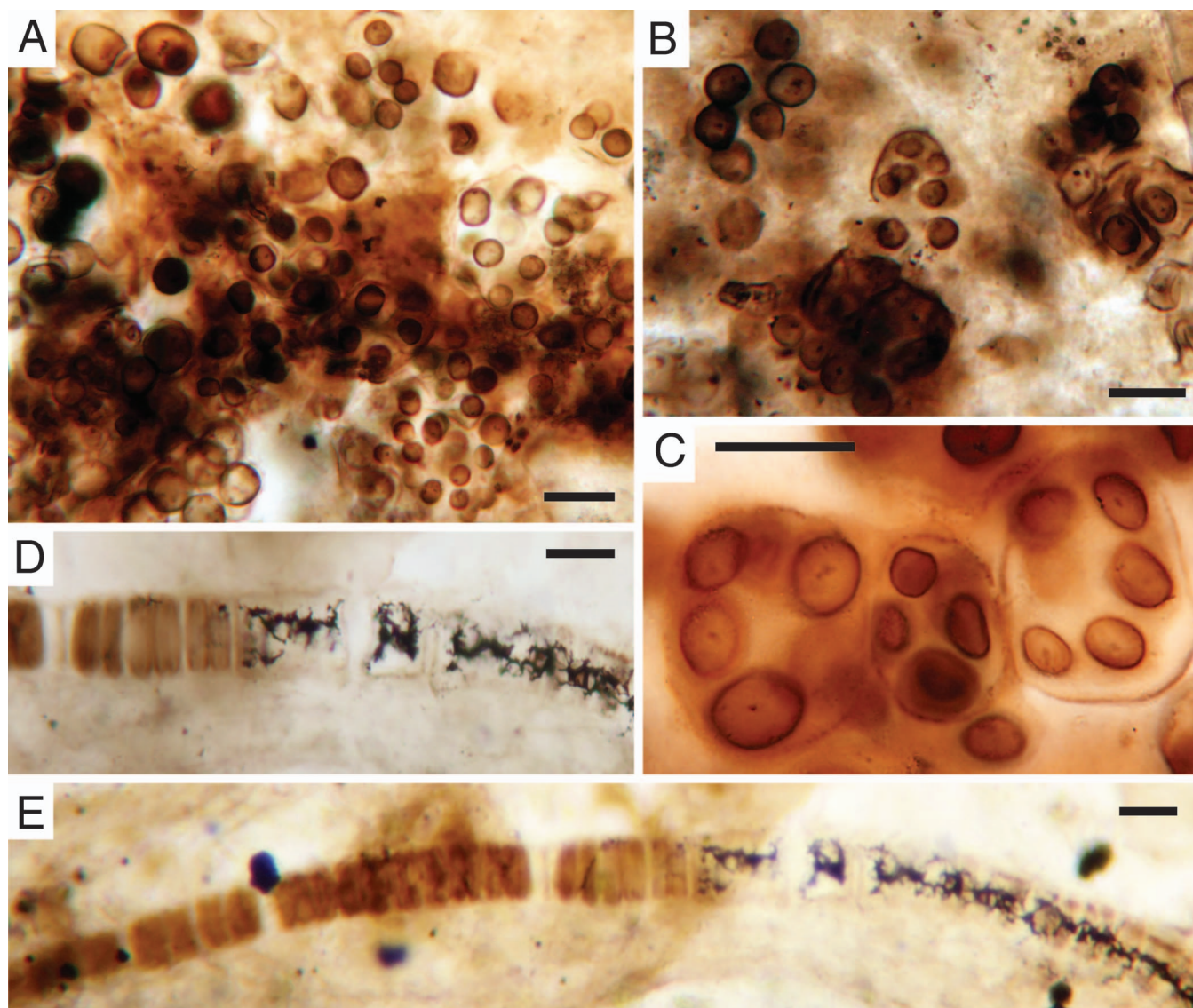


FIGURE 6—Additional Angmaat fossils. A–C) *Eogloeocapsa bella* (A = DAC-5, O67/3; B = DAC-5, V68/0; C = DAC-5, W63/2). D–E) *Bangiomorpha pubescens* (35, F54/3). All illustrated specimens are reposit in Harvard University Paleobotanical Collection 64840; England finder coordinates are given in parentheses for thin sections and microfossils. Scale bars = 25 μ m.

pyrite oxidation) are common within microspar laminae (black minerals in Figs. 7B–C, F). Dolospar laminae also have irregular clear patches that impart a clotted microtexture to the carbonate.

Early diagenetic chert further clarifies the origin of textures observed in encompassing carbonate. The principal fabric elements are mm-scale crystal fans, originally deposited as seafloor carbonate precipitates. The majority of precipitate textures consist of acicular crystals up to 2 mm long but no more than a few μ m thick (Figs. 7B–C). In some places, however, thicker (\sim 30 μ m) crystals show square terminations indicative of original aragonite (Fig. 7E). Discontinuous mm-scale lamination, visible to the naked eye, is resolved in thin section as zoned precipitates, pigmented more or less strongly by included organic matter (Figs. 7A, F). Similar precipitates form today in local environments of extreme oversaturation, for example, calcitic precipitates formed in leachate pipe systems in Florida (Maliva et al., 2000). More continuous surfaces show a granular texture, with relatively abundant 1–5 μ m pyrite crystals; these are interpreted as exposure surfaces that underwent micritization prior to silica emplacement. Light patches in the chert are largely irregular dissolution features, now filled by silica and dolomite euhedra, and often surfaced by tiny pyrite crystals (Figs. 7B–C).

Fabric elements preserved in chert map fairly straightforwardly onto textures apparent in unsilicified carbonate of this facies. The mm-scale laminae so prominent in unsilicified carbonate correspond to the micritized exposure surfaces observed in the chert (Fig. 7A). Crystal fans, well-preserved in chert, have been recrystallized completely to dolospar in carbonate phases, with dissolution features preserved as clear irregular patches within dolospar layers. Microfossils are rare in this facies—the only possible candidate fossils are isolated, hollow organic filamentous structures oriented parallel to the long axes of crystals that could be the remains of endolithic cyanobacteria (Fig. 7D).

Thin-Filament Tufted Mat

In outcrop, vertically striped black and white chert is commonly associated with cm-scale tufted microbialites (Fig. 8), and interbedded with precipitate textures. Tufts are interpreted to reflect symsedimentary cementation that conferred structural rigidity onto vertical tufts of cyanobacterial filaments; and chert similarly reflects interaction of microbial behavior elements and symsedimentary cement. In thin

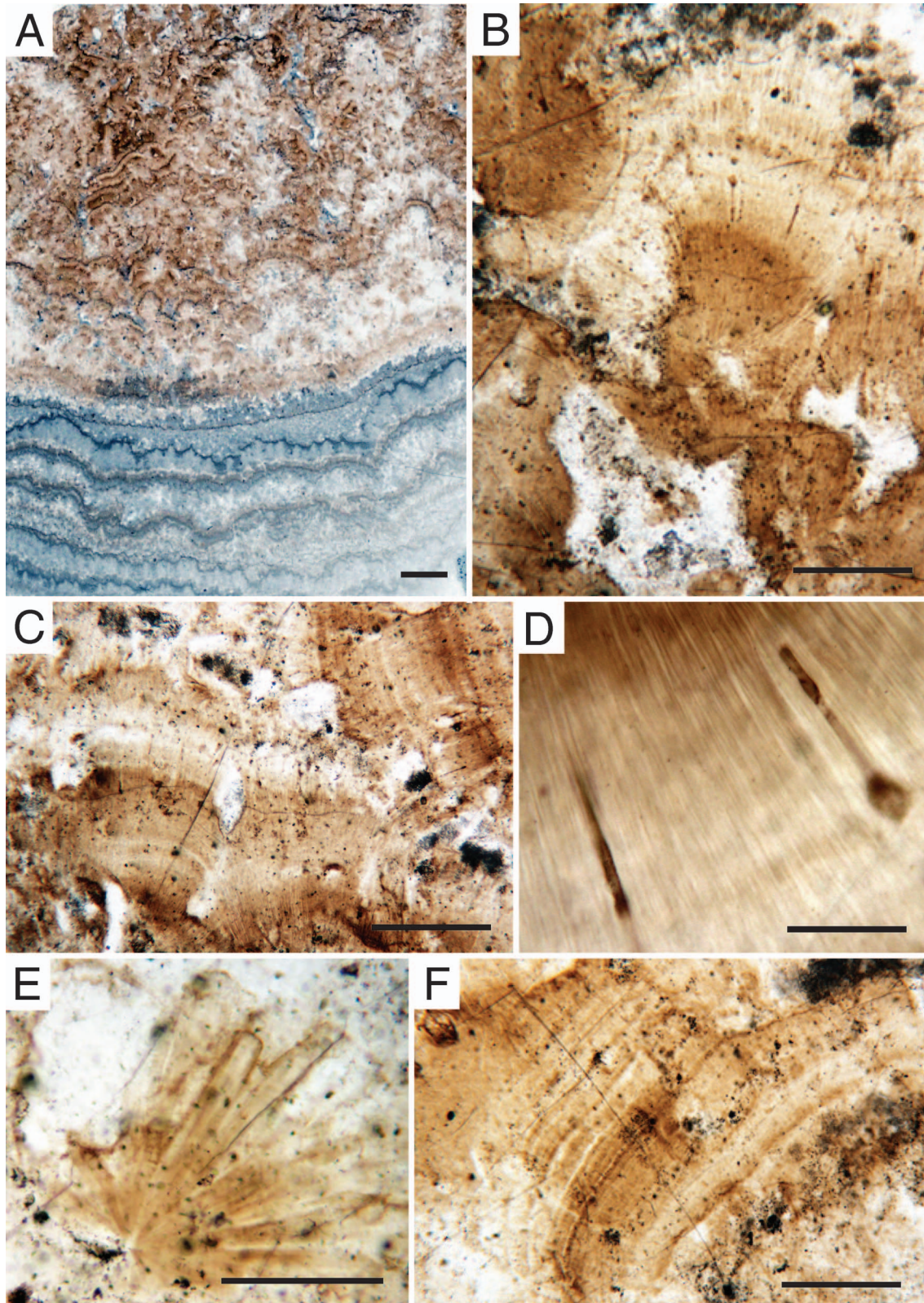


FIGURE 7—Crystal fan-dominated precipitate facies. A) Overview showing silicified region (brown) above diagenetically altered carbonate. B–C, F) Fine acicular microfabrics reflecting original carbonate precipitates, preserved by early diagenetic silicification; note dissolution voids in B and zonation in B–C and F, reflecting variations in the incorporation of organic matter during crystal growth. D) Possible microfossils (endolithic cyanobacteria?) oriented parallel to crystal growth axes. E) Originally aragonitic crystals, with square terminations. All illustrated specimens are deposited in Harvard University Paleobotanical Collection 64840; England finder coordinates are given in parentheses for thin sections and microfossils. Scale bars = 250 μm for all images except D, where the bar = 2 μm .

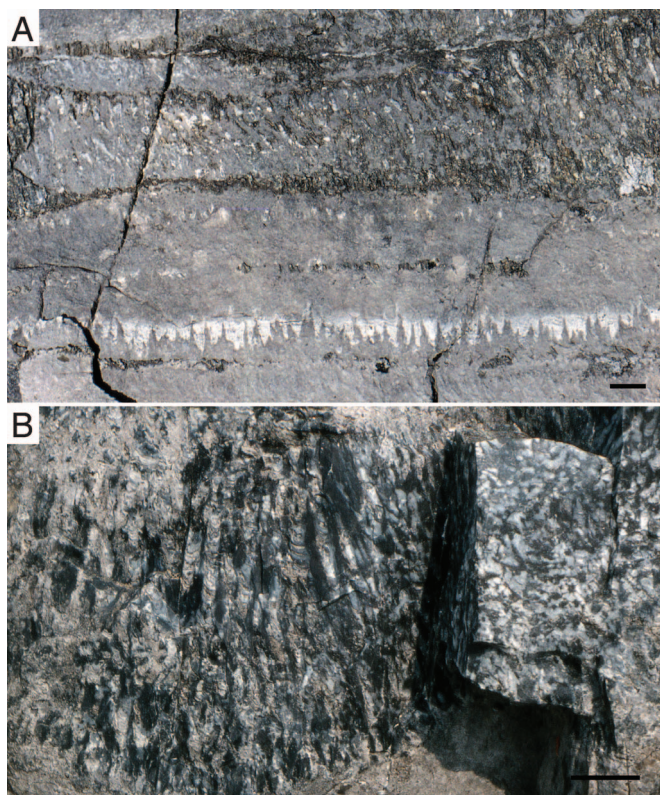


FIGURE 8—Field views of thin filament-tufted mat facies. A) Tufted mats draped by white micrite in lower part and partially silicified tufts in upper part of image. B) Silicified tufts—black chert marks organic-rich tufts of filaments, whereas white chert is predominantly original void space preserved by early mineralization. Scale bars = 2 cm.

section, the black regions of variegated chert nodules are resolved as dense populations of thin filaments and associated biofilm; the white regions are cement-filled voids (Fig. 9).

Microfossils in this facies comprise a single population of thin cylindrical filaments (Figs. 9B–C). Most filaments show evidence of partial decay and collapse, yielding micron-thick, commonly fragmented individuals. In well-preserved regions, filaments are preserved as 2–3 μm hollow, filamentous tubes ascribed to *Siphonophycus robustum* (Schopf) Knoll et al. (1991) and interpreted as the extracellular sheaths of *Phormidium*-like cyanobacteria. The spatial orientation of *S. robustum* populations is distinctive: vertical bundles of filaments form tent-pole structures from which sheets of filaments extend outward and attach to adjacent vertical elements, forming convex downward laminae that isolate primary void space (Figs. 9B–C). Voids are generally subrounded and commonly contain silicified splays of acicular carbonate that formed prior to silicification (arrow in Fig. 9C). The voids closely resemble gas bubbles trapped in modern mats (Bosak et al., 2010; Mata et al., 2012). Some samples also contain mm- to cm-scale voids that crosscut mat fabrics and are interpreted as dissolution features. Void structures within tufted thin-filament mats were filled during diagenesis by an isopachous lining of chalcedony and, in their centers, by large twinned dolomite crystals. Within Angmaat chert, gas bubbles and dissolution features are readily distinguished, but in associated carbonate, differentiation of these structures is more difficult.

The fabric of the thin-filament tufted mats resembles that described by Sumner (1997) from cusped stromatolites in the 2.52 Ga Gamohaam and Frisco formations, South Africa. Microfossils are not preserved in the Archean examples, but preserved petrofabrics suggest that filamentous microorganisms formed vertical supports that were cemented penecontemporaneously with mat growth. Perhaps slightly

flocculent mats draped across the vertical supports, forming highly porous constructions filled by synsedimentary cement. The spatial scale of the Archean structures is much larger—cm- to m-scale cusps as opposed to the mm-scale features observed in Angmaat chert—although similar but larger coniform structures are preserved in deeper-water facies of the Angmaat Formation. Archean coniform structures similarly formed at depth during the drowning of an extensive carbonate platform—a setting far different from the peritidal environments discussed here. Nonetheless, the two examples appear to reflect common processes of population growth and penecontemporaneous cementation.

The thin section illustrated in Figure 9A shows that where these mats were not silicified, compaction commonly resulted in an irregular fabric whose origin would be difficult to interpret in the absence of chert preservation: the fabric is dominated by dark stringers interpreted as compacted mats and lighter clots interpreted as void-filling precipitates. A thin layer at the base of the thin section composed of uniform, isopachous cements indicates that seafloor precipitates and thin filament tufted mats formed in close environmental proximity.

Laminated Precipitates and Coccoid-Rich Mats

Stratiform laminites occur in carbonate successions through the Proterozoic record and are usually interpreted as flat mats that trapped and bound or precipitated carbonate sediments. Consistent with this larger record, stratiform laminites are common in the Angmaat succession, consisting of subtly undulating mm-scale microspar laminae, with finer-grained, and hence darker, microspar-defining lamina surfaces (Fig. 10A). Silicified samples present a more nuanced picture of this facies, with mat layers (Fig. 10B) interlaminated with a combination of finely laminated precipitate structures (Fig. 10C) and fine intraclastic microbreccia beds. The mat layers commonly contain undulating to billowy organic matter; with denser organic accumulations corresponding to the dark microspar surfaces observed in unsilicified portions of the unit. Early diagenetic pyrite is common, especially in organic-rich laminae, but microfossil preservation is typically poor. Precipitate layers up to about 300 μm thick consist of 5–10 μm layers defined by slight organic pigmentation along their surfaces. In carbonate, it is impossible to tell which laminae formed as mats and which originated as precipitate horizons. Intraclastic microbreccia beds are locally common in this facies, and are associated with cement-filled voids formed by dissolution. These features are recorded in nonsilicified facies as detrital layers and sparry patches, both visible in thin section (Fig. 10A).

Where microfossils are preserved, microbial populations are almost exclusively coccoidal, with *Eoentophysalis belcherensis* Hofmann (1976) as the dominant builder (Fig. 4B) and *Gloeodiniopsis* species locally abundant as mat dwellers (Figs. 4I–L). The association between laminated precipitates and entophysalid cyanobacteria has been noted previously, both in the Angmaat Formation and elsewhere (Knoll and Sergeev, 1995; Sergeev et al., 1995; Kah and Knoll, 1996). Either coccoid populations were favored on the substrate provided by seafloor precipitates, or filamentous populations were inhibited. Locally, this facies also contains rare isolated individuals of the stalked cyanobacterium *Polybessurus* (Figs. 5A–B) and endolithic cyanobacteria (Fig. 4A). Within a single thin section, stratiform precipitates and coccoid mats can be interbedded with mats formed by fine filamentous cyanobacteria that trapped gas bubbles preserved as cement-filled primary void space (Fig. 11). Thus, these two biofacies/microfabrics must have been contiguous on the Angmaat platform.

Filament-Dominated Mats

Two distinct filamentous mat assemblages can be differentiated within Angmaat chert units. The first, interlaminated with the

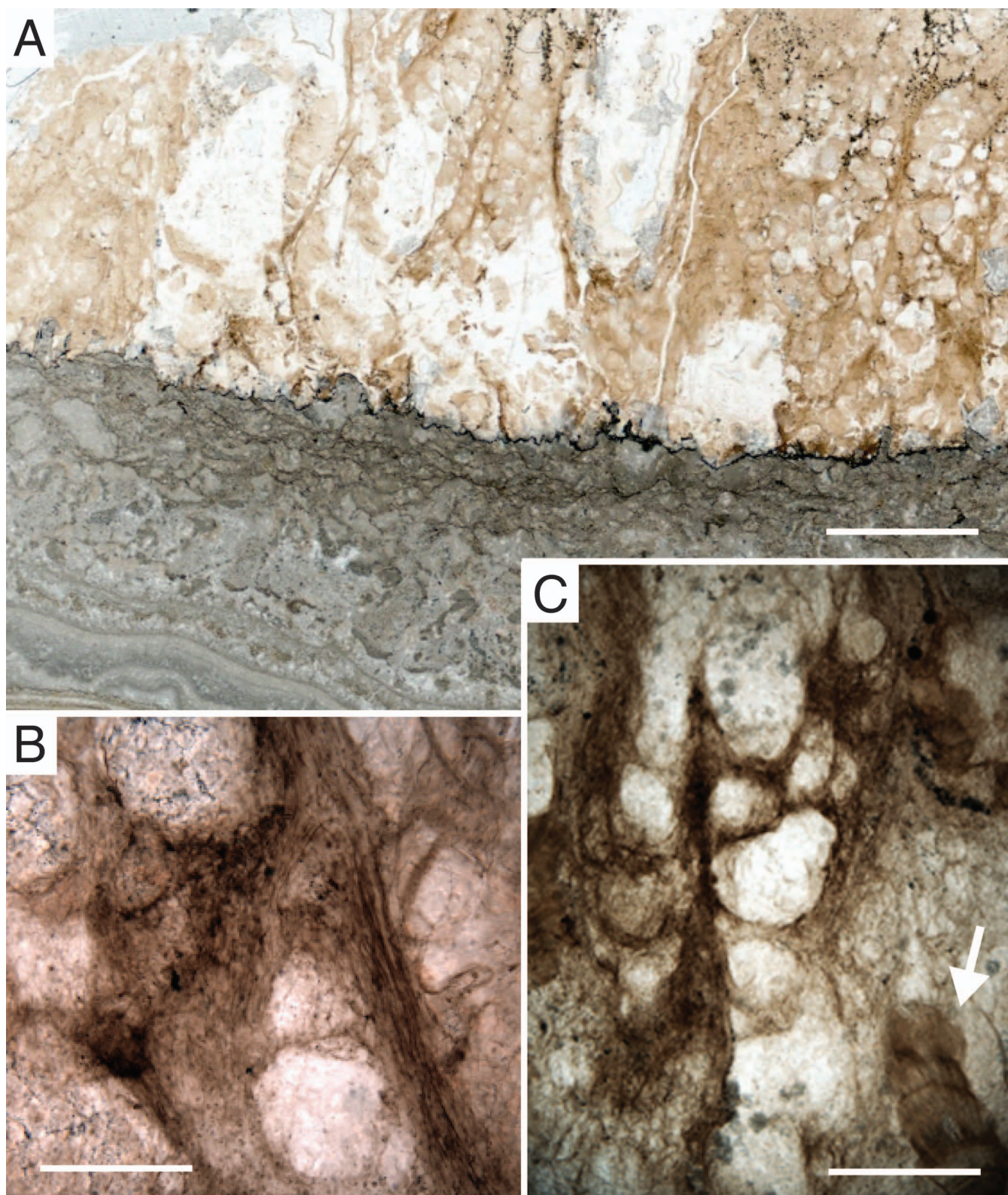


FIGURE 9—Thin filament-tufted mats in thin section (G11). A) Silicified (above) and unsilicified fabrics. B–C) Higher-resolution views of silicified mat fabric, showing oriented thin filamentous microfossils and primary void spaces, some originally filled with fans of precipitated carbonate (arrow in C). Scale bar in A = 4.5 mm; scale bars in B and C = 400 μm .

stratiform precipitates and *Eoentophysalis* mats described in the previous section (Fig. 11A), consists of thin (2–3 μm cross-sectional diameter) filamentous sheaths assigned to *Siphonophycus robustum* (Fig. 4C). The filaments are commonly oriented vertically and are

associated with abundant extracellular polymeric substances, or EPS; coccoidal cyanobacteria occur among filaments in the mat assemblage as do the stalk-forming cyanobacterium *Polybessurus* and the filamentous red alga *Bangiomorpha* Butterfield (2000). Filaments

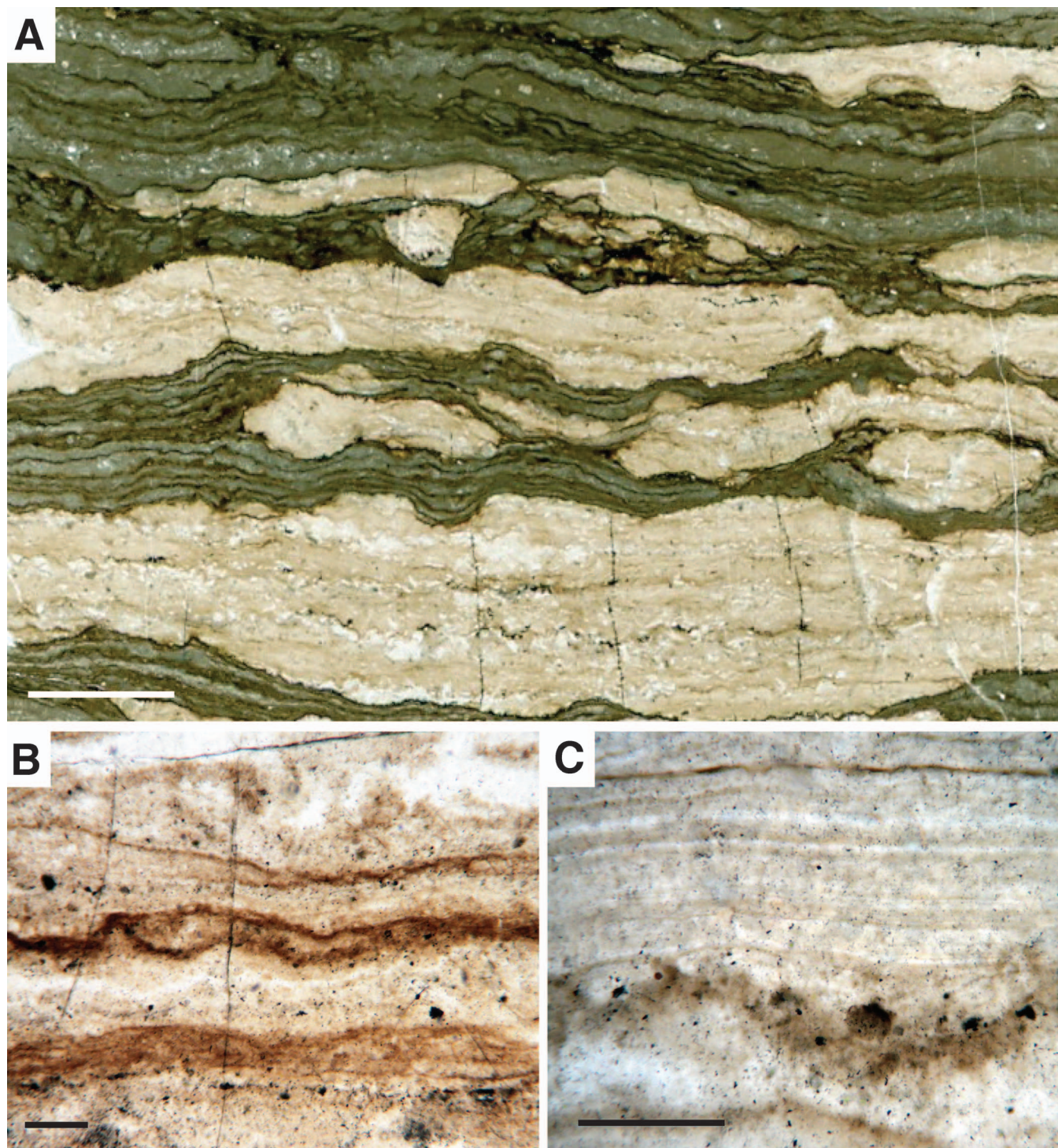


FIGURE 10—Laminated precipitates and coccooid-rich mat facies (G13). A) Interspersed silicified and unsilicified lithologies, showing characteristic fabric development. B) Higher-resolution image showing stacked, organic-rich mat layers preserved in chert. C) Higher-resolution image showing layered precipitates preserved in chert. Scale bar in A = 5 mm; scale bars in B and C = 175 μ m.

commonly line primary, mm-scale globular voids filled by early diagenetic cement. Most of the voids appear to have formed as gas bubbles preserved by penecontemporaneous calcification of entrapping filaments. In some cases, voids remain wholly or partially filled by early microspar cement (Fig. 11A). Evidently these cements occluded porosity, limiting the subsequent incursion of silicifying fluids. Microspar fill is also conspicuous in surrounding carbonate, forming irregular clots lined by highly compacted, commonly organic-darkened mat dolomiticrite (lower part of Fig. 11A).

A much different filament assemblage occurs in thicker (mm-scale lamination) undulating (and less frequently tufted) mats that only occasionally preserve primary void spaces (Fig. 12). The primary mat builder in these mats is *Siphonophycus inornatum* Zhang (1981), $\sim 6 \mu$ m filaments that form densely interwoven populations (Fig. 3A). A subset of these mats also contains thicker (up to 25 μ m cross-sectional diameter) and more deeply pigmented sheaths assigned to *Siphonophycus capitaneum* Nyberg and Schopf (1984) (Figs. 2, 3C), and a smaller subset also contains much larger sheaths that contained multiple

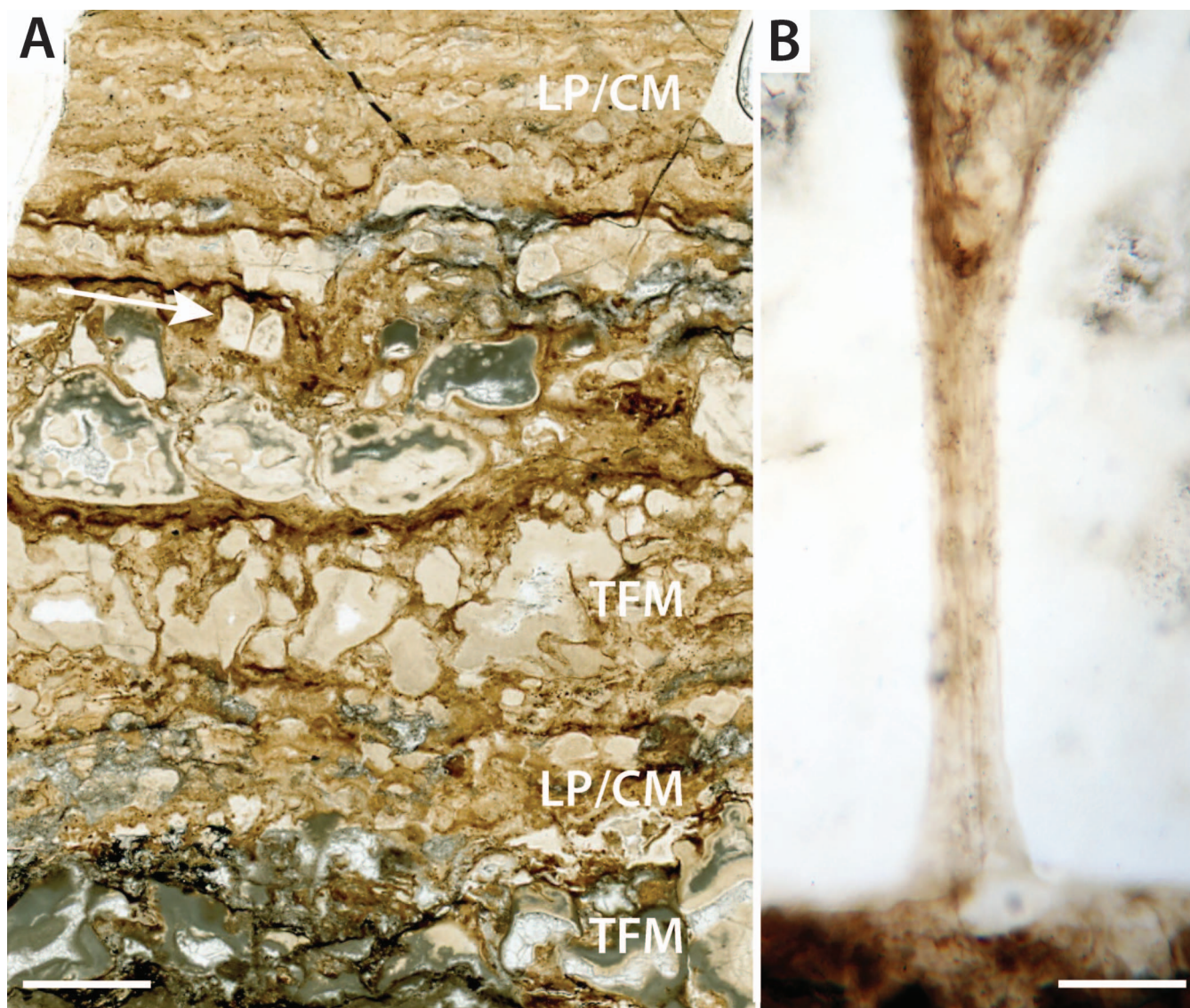


FIGURE 11—A) Interlaminated thin filament mats (TFM) with abundant primary void space and laminated precipitate/coccolidal mats (LP/CM) that display few if any primary voids. Carbonate microspar preserved within many voids in black chert (34). B) Vertical tuft of filamentous microfossils, outlining void space (noted by arrow in A = 34, K53/2). Scale bar in A = 3.5 mm; scale bar in B = 15 μ m.

trichomes, assigned to *Eomicrocoleus crassus* Horodyski and Donaldson (1980) (Figs. 3D–E). On the scale of individual thin sections, assemblage composition (1, 2, or 3 filamentous taxa) appears to be consistent within individual laminae, but varies vertically from one layer to the next. Filament orientation also varies from one lamina to another; populations can be oriented horizontally or vertically, and commonly alternate repeatedly within a single thin section. Vertically oriented filaments occasionally result in cm-scale tufts with substantial void space (Fig. 12B). Thick silicified mats without trapped bubbles or dissolution features invariably contain predominantly horizontally oriented laminae of these three mat-building filaments.

Co-occurring, but numerically subordinate coccolidal populations include *Gloeodiniopsis*, *Polybessurus*, *Sphaerophycus medium* Horodyski and Donaldson (1981), the simple spheroids assigned to two species of *Myxococoides*, and unnamed coccolidal microfossils from which elongate tubes emerge (Figs. 3F, 4H, 5F). Less commonly, *S. inornatum* mats also contain isolated clusters of *Eogloeocapsa*. Fossil preservation is variable through these mats; laminated EPS with few or no discrete microfossils intergrade with expanded mats containing exceptionally well-preserved microfossils. In all cases, the dark *S.*

capitaneum sheaths preserve differentially well. This differential preservation can be observed, as well, in associated unsilicified carbonate, where mat fabrics comprised of vertically oriented filaments of *S. capitaneum* are occasionally preserved via *in situ* mineralization of filament sheaths (Fig. 2E; see also Kah and Riding, 2007).

Modern microbial mats at Laguna Mormona, in Baja California (Horodyski et al., 1975), provide a useful framework for interpreting filamentous microbialites in the Angmaat succession. Microbial mats within peritidal environments at Laguna Mormona have undulating 1–3 mm laminae similar to those in Angmaat chert (fig. 5 in Horodyski et al., 1975) built by a community of filamentous cyanobacteria that includes large *Microcoleus chthonoplastes*, *Lyngbya aestuarii* (with 20–25 μ m sheaths), and smaller filamentous populations. Similar to the Angmaat assemblage, the sheaths of *L. aestuarii* preserve differentially well at Laguna Mormona and become the most apparent taxon at depth within the mats, regardless of their proportional abundance in surface communities. And, as in the Angmaat Formation, filamentous mats at Laguna Mormona occur in close spatial proximity to *Entophysalis* mats that (1) are associated with local seafloor aragonite

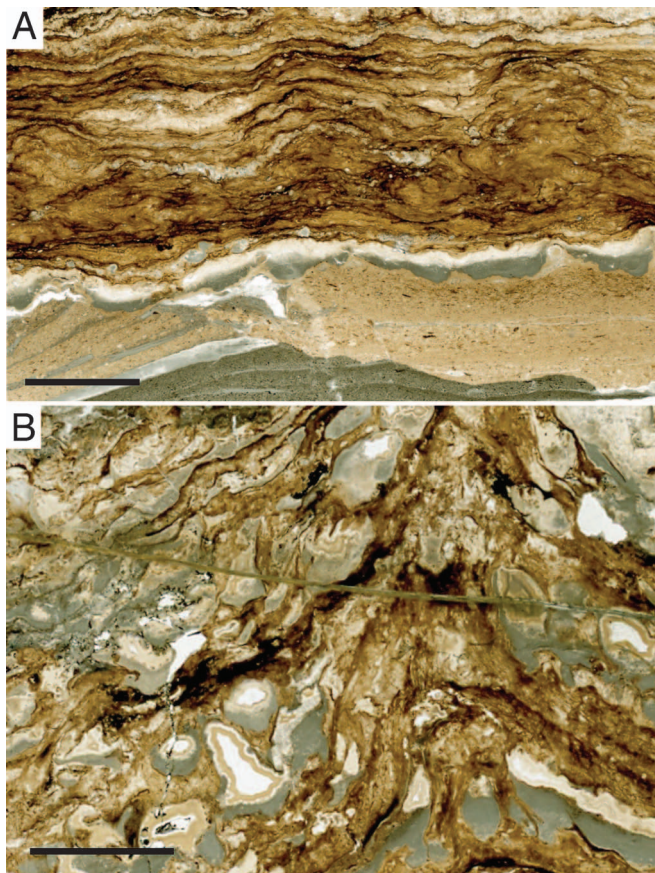


FIGURE 12—A–B) Filament-dominated mat facies (A = DAC-10 and B = G4). Note arenitic carbonate beneath mat accumulation in A. Scale bars = 5 mm.

precipitation and (2) have a relatively low preservation potential (Horodyski and von der Haar, 1975).

Eogloeoecapsa-Rich Laminae

Within thin sections of flat-laminated filamentous mats, a few laminae are texturally and paleobiologically distinct. These layers commonly contain poorly preserved *Eoentophysalis* populations, but they are dominated by large colonial coccoids assigned to *Eogloeoecapsa bella* Golovenok and Belova (1984) (Figs. 6A–C, 13) and interpreted in terms of the extant cyanobacterial genus *Gloeoecapsa*. *Eogloeoecapsa*-rich laminae differ from filamentous mat layers in the same thin section by their cumulate texture and an absence of internal lamination (Fig. 13). Although clearly distinguished in chert nodules, filamentous and *Eogloeoecapsa*-rich layers are difficult to tell apart in unsilicified carbonate beds.

DISCUSSION

Microbes and Microbialites along the Angmaat Platform

Petrographic variations suggest that the principal petrofabrics identified in Angmaat chert can be ordered along a gradient of decreasing environmental restriction and subaerial exposure, identified on the basis of variations in seafloor carbonate precipitates and evidence for post-depositional dissolution (Fig. 14). This ordering may be simplistic, as petrofabric generation might easily vary along axes other than water depth, but it finds support in the distribution of microfossil populations within the formation. Restricted facies with abundant evidence for subaerial exposure also have the lowest diversity of microfossils, whereas petrofabrics interpreted as less frequently exposed (or more persistently wet) harbor a larger number of taxa. Many taxa occur in more than one

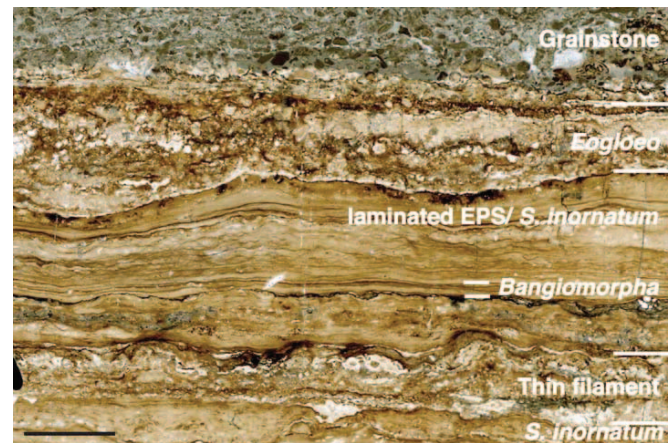


FIGURE 13—Thin section DAC-5, showing interlayering of filamentous mats built by *Siphonophycus inornatum*, thin filament-mats, an *Eogloeoecapsa* accumulation, and a thin grainstone; note position of *Bangiomorpha* within the *S. inornatum* mat interval. Bar = 5 mm.

petrofabric, and when placed in the spatial order suggested by petrofabric, all but one show contiguous distributions (Fig. 14). Kah and Knoll (1996) also noted that the number of chert samples represented by the main fabric types varied spatially within the basin, again indicating a broad-scale covariance between microfossil assemblages and depositional texture preserved in Angmaat chert. To a first approximation, then, microfossil assemblages map one-to-one onto preserved depositional

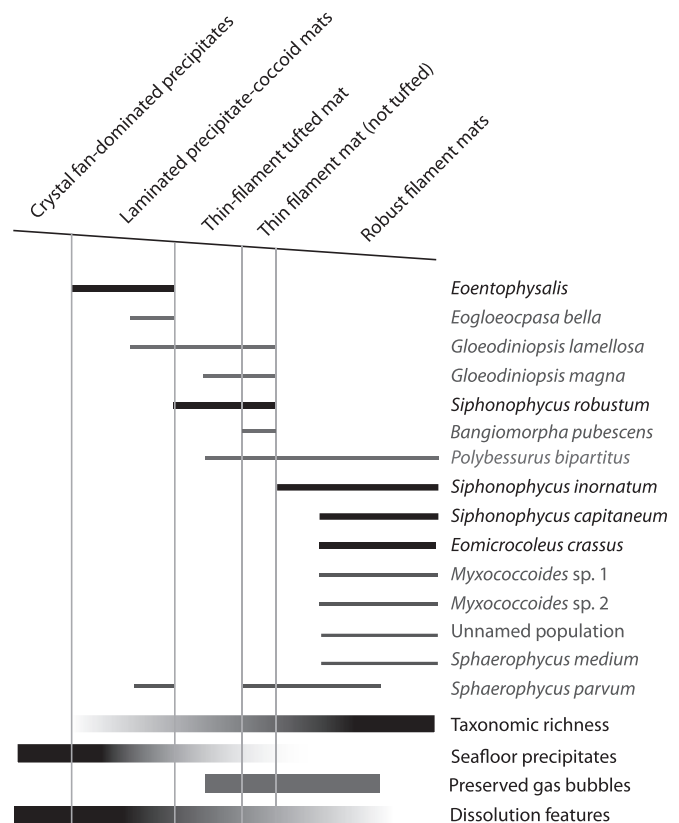


FIGURE 14—Diagram showing the distribution of microfossil taxa, seafloor precipitates, preserved gas bubbles, and dissolution features among the five microfacies recognized in Angmaat samples. Thicker lines indicate principal mat builders, as inferred from the density and orientation of microfossils within these populations. Thinner lines indicate populations that lived in mats but did not play a major role in their construction.

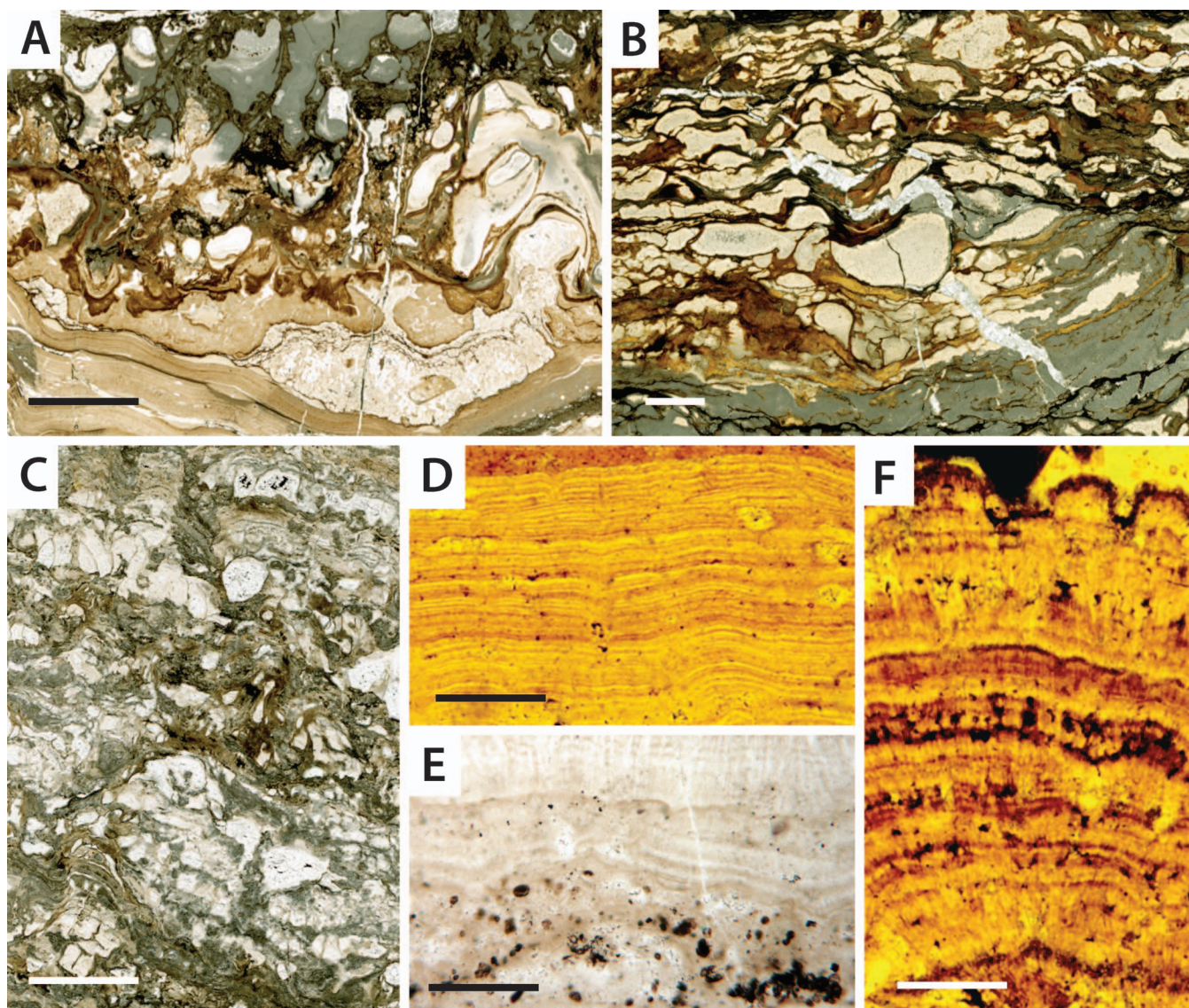


FIGURE 15—Distinctive mat petrofabrics comparable to those of the Angmaat Formation preserved in chert within mid-Proterozoic carbonate accumulations from A) northwestern Greenland; B, D, F) Siberia; C) China; and E) Australia. Scale bars in A–C = 5 mm; scale bars in D–F = 100 μ m.

textures, supporting the hypothesis that microbialite petrofabric reflects, at least in part, microbial community composition.

Microbial populations influence petrofabric development in a number of ways. Mat-building populations can trap and bind fine particulate carbonate, leading to stromatolite accretion when accompanied by cementation. Microbially induced precipitation can also govern carbonate accumulation in the absence of trapping and binding, and this appears to be the case in our Angmaat samples (Kah and Knoll, 1996). More specific features of microbial populations can also influence petrofabric: did the organisms produce extracellular sheaths or envelopes that resist decay and act as nucleation sites for carbonate precipitation? Were filament populations oriented vertically or horizontally (a reflection of microbial behavior that influences the spatial pattern of precipitation)? Did mats have sufficient cohesion to trap gas bubbles and retain them until precipitation occurred?

Of course, physical setting will also influence petrofabric by governing the degree of carbonate oversaturation, imposing shear stress on mat communities, and introducing traction- or suspension-load sediment particles. In most stromatolites, observed petrofabric will reflect both biological and physical processes, as well as later diagenesis. The Angmaat microbialites are exceptional in that early

diagenetic chert allows us to distinguish primary fabrics formed by interacting biological and physical processes from the more common petrofabrics that additionally reflect carbonate diagenesis.

The principal fabric elements in the Angmaat samples include tabular to acicular seafloor precipitates, fine-grained precipitated carbonate that preserves filament orientation, cement-filled primary void space generated by gas bubbles, and cement-filled secondary void space produced by dissolution. Clastic microbreccia beds occur in association with precipitate-rich laminae, and thin sandstones occur locally beneath some of the most diverse mats (Fig. 12A); detrital carbonate, however, appears to have played little role in Angmaat microbialite accretion.

The Stratigraphic Distribution of Angmaat Petrofabrics

Primary voids preserved in Angmaat samples are particularly interesting because comparable petrofabrics are relatively abundant in Mesoproterozoic carbonate rocks (Figs. 15A–C). The formation and preservation of these voids require a source of biogenic gas (Bosak et al., 2010), a mat sufficiently cohesive to trap gas bubbles (Mata et al., 2012), carbonate precipitation on a time scale sufficiently rapid to frame the voids before elimination by compaction or diffusion, and an

absence of traction- or suspended-load sedimentation that would compromise mat development, bubble formation and retention, and rapid cementation.

As pointed out by Bosak et al. (2010), oxygenic photosynthesis is the only form of photoautotrophy that produces gas (O_2) as a by-product. The presence of at least moderately oxidizing surface environments in the Mesoproterozoic era (Kah and Bartley, 2011) makes it likely that cyanobacteria dominated primary production in Angmaat mat communities, and beautifully preserved cyanobacterial fossils corroborate the view that gas bubbles likely originated via oxygenic photosynthesis. Within the Angmaat setting, only filament-dominated mats (and mixed filamentous-cocoid mats) contain primary void fabrics, suggesting that mat communities lacking filamentous populations may not have had the structural coherence required to trap and retain gas bubbles.

Microbial mats dominated by filamentous cyanobacteria occur commonly in Neoproterozoic successions that lack preserved bubble textures (e.g., Knoll et al., 1991; Cao and Yin, 2011). Thus, the additional key to primary void preservation lies in penecontemporaneous mineral precipitation. As found in other Paleo- and Mesoproterozoic carbonate successions (Knoll and Semikhatov, 1988; Bartley et al., 2000; Grotzinger and James, 2000; Kah et al., 2012), (originally) aragonitic crystal fans indicate that the Angmaat basin was at least episodically restricted to the point at which carbonate readily nucleated in or on the shallow seafloor.

Preservation of primary void textures requires that thin mats buoyed by oxygen bubbles also acted as nucleation sites for carbonate precipitation. Local carbonate nucleation could reflect high abundances of Ca^{2+} absorbed onto cyanobacterial sheaths and biofilm polymers (e.g., Pentecost and Riding, 1986; Dupraz et al., 2009). OH^- generated by carbon dioxide-concentrating mechanisms in cyanobacteria might also have facilitated carbonate precipitation, as it does in some modern freshwater environments (Merz, 1992; Kah and Riding, 2007). Microbial sulfate reduction has also been linked empirically to carbonate precipitation within mats; whether dissimilatory sulfate reduction increases or decreases the probability of carbonate precipitation depends on the substrate being metabolized (Gallagher et al., 2012) and the fate of H_2S generated by this process (Canfield and Farquhar, 2009). Under favorable circumstances, the net result is an increase in pH, facilitating carbonate precipitation (Aloisi, 2008). Microbial iron reduction provides another heterotrophic metabolism that would increase carbonate oversaturation within mats (Fischer and Knoll, 2009). Thus, within Proterozoic mat communities, a variety of microbial processes could have contributed to penecontemporaneous carbonate cementation (Aloisi, 2008).

That seafloor carbonate precipitates and preserved gas bubble textures are widespread in peritidal microbialites of late Paleoproterozoic and Mesoproterozoic age (Fig. 15), but are uncommon in younger Neoproterozoic successions (e.g., Knoll and Swett, 1990) prompts the question of what was different in younger coastal environments. Filamentous cyanobacteria and anaerobic bacterial metabolisms didn't go away, suggesting that the most likely shift was in the carbonate saturation state of seawater. This has previously been proposed as a principal driver of secular change in Proterozoic stromatolite morphology (Grotzinger and Knoll, 1999) and changes in the distribution of abiotic carbonate fabrics, such as seafloor precipitates (Kah and Knoll, 1996) and molar-tooth microspar (Pollock et al., 2006), and it has also been used to explain fundamental shifts in the marine C-isotope record (Bartley and Kah, 2004). What governed such changes, however, has proven elusive. Declining CO_3^{2-} is consistent with a Neoproterozoic expansion in gypsum and anhydrite deposition (Kah et al., 2001), and might reflect a general decrease in DIC associated with high rates of organic carbon burial, inferred from carbonate C isotopic abundances (Knoll et al., 1986; Bartley and Kah, 2004; Halverson et al., 2005). Whatever the causation, the sedimentary record indicates that carbonate fabrics like those in the Angmaat

succession, which record precipitation mostly on and within benthic mats and the shallow substrate, were replaced in part by carbonate fabrics that reflect a greater abundance of material precipitated as whittings from the water column (Kah and Knoll, 1996), largely restricting the petrofabrics described here to older successions.

Microbialite Fabric Preservation in Angmaat Carbonate

As described earlier in this paper, microbialite fabrics in Angmaat carbonate can be interpreted in light of biological and physical processes inferred from early diagenetic chert. With the exception of filament cast and molds, direct fossil evidence of mat-building communities is not preserved in unsilicified Angmaat carbonate units. Nonetheless, digenesis has not obliterated fabrics associated with seafloor precipitates, tufts formed by locally vertical filament growth, trapping of gas bubbles by filamentous mat populations, and undulating mats built by filamentous cyanobacteria. That is, diagenesis has operated on a template provided by depositional fabrics, and so microbialite textures preserved in carbonate facies do reflect microbial mat composition, at least in part. As noted above, biological inferences drawn from Angmaat petrology owe much to the physical circumstances of their formation, namely, penecontemporaneous carbonate precipitation from highly oversaturated waters. More generally, however, under favorable circumstances, petrographic textures imparted by trapping and binding, coccoidal versus filamentous mat construction, filament orientation, and mat-builder diversity may all leave a petrographic signature in Proterozoic stromatolites (see also Walter et al., 1988; Knoll and Semikhatov, 1998; and references therein).

CONCLUSION

Silicified carbonate beds in the upper Mesoproterozoic Angmaat Formation preserve depositional fabrics that are widespread in Paleoproterozoic and Mesoproterozoic carbonate rocks but uncommon in Neoproterozoic successions. Abundant microfossil populations preserved in these same chert beds and nodules indicate that the biological composition of mat communities covaried in space with the preserved petrofabrics. Later diagenesis in unsilicified carbonate rocks altered but did not erase mat-specific petrofabrics. Thus, despite the obfuscating influence of carbonate diagenesis, the Angmaat samples support the hypothesis that microstructural fabrics in Proterozoic stromatolites can provide a tractable record of community diversity in ancient mat ecosystems.

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