Exploring the silicification of microbes and understanding their role in the fossil record

by

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Abstract

Filamentous cyanobacteria that built macroscopic tufted mats in Proterozoic peritidal environments were fossilized by silicification, but the environmental and biological factors that shaped these structures and enabled this type of preservation are not well understood. Recent work has shown that coccoidal cyanobacteria can become fossilized because they can sequester silica from seawater that is undersaturated with respect to silica. Here, we use taphonomy experiments to demonstrate that filamentous cyanobacteria that form tufted and conical mats are also able to mediate the precipitation of silica in seawater that is undersaturated with respect to silica as well. These results show that different marine cyanobacteria and their macroscopic structures have a high potential to be preserved by silicification. We find that the exterior of macroscopic structures such as tufts and pillars are preferentially silicified, and more completely silicifed at silica concentrations below saturation in seawater. The interior of these structures may be preserved by later diagenetic minerals. These results are consistent with microfossil assemblages found in early diagenetic chert deposits throughout the Proterozoic. The data suggest abundant Ca-rich sulfated polysaccharides in the exopolymeric substance (EPS), which are likely the site of silicification. Interactions among similar organisms, seawater chemistry, and silica in evaporative environments may account for the two-billion-year long record of exceptionally silicified filamentous and coccoidal cyanobacteria and their macroscopic aggregates in peritidal environments.

Dedicated to my grandfather, Richard Millman (’62), for always believing in me and challenging me to think about the world in ways I couldn’t have imagined. You gave me the limitless curiosity that has brought me to this point. You made me and everyone around you a better person and you are dearly missed.

Introduction

Fossilized remains of ancient organisms provide a direct glimpse into the history of the evolution of life on Earth. Organisms capable of biomineralization (the formation of shells, bony structures, etc.) are a relatively recent evolutionary invention (<600 Mya, Maloof et al., 2010; Tang, Wan, Yuan, Muscente, & Xiao, 2019), but microbes may have been producing stromatolites and fossilized microbial mats as far back as > 3,500 Mya. Due to difficulties related to assigning simple morphologies to specific modern taxa and the sparseness of well-preserved fossils, this record is somewhat ambiguous (Schopf, 2011).The precipitation of amorphous silica preserved the microbial textures and cells in some Archaean structures (Czaja, Beukes, & Osterhout, 2016; Tice & Lowe, 2004; Walsh & Lowe, 1999; Westall et al., 2001; Wilmeth et al., 2019). Early diagenetic chert also preserved a number of iconic assemblages of Proterozoic microfossils via silicification (Sergeev, Sharma, & Shukla, 2012). Many of these microfossils, including some older Archean fossils, are interpreted as cyanobacteria, the organisms responsible for the oxygenation of the atmosphere and ocean (Sergeev et al., 2012 and citations therein), such as stromatolitic chert containing both coccoidal and filamentous microfossils from the 2,500 Mya Transvaal Supergroup in South Africa (Beukes, 1987). More ambiguous are structures such as pinnacles and tufted microbial mats, whose record extends back to 2,700 Ma (Flannery & Walter, 2012), small conical stromatolites as old as 3,000 Ma (Beukes & Lowe, 1989; T. Bosak, Knoll, & Petroff, 2013; Petroff et al., 2010) and 2,700 Ma bubbly textures surrounded by filamentous organisms (Wilmeth et al., 2019). The formation of these structures requires specific behaviors, metabolisms and microbial morphologies (T. Bosak et al., 2013; T Bosak et al., 2010; Tanja Bosak, Liang, Sim, & Petroff, 2009; Petroff et al., 2010; Sim et al., 2012). Today, the production of tufted microbial structures and pinnacles is largely limited to

vertically aligned bundles of filamentous cyanobacteria in either hypersaline, hydrothermal, or ice-covered environments (Flannery & Walter, 2012; Walter, Bauld, & Brock, 1976), although anoxygenic photosynthetic microbes in laboratory enrichment cultures can give rise to similar structures (T. Bosak et al., 2013). Thus, the nature of the earliest builders of tufted mats and small pinnacles and cones remains unresolved.

The first diagnostic cyanobacterial fossil, *Eoentophysalis*, was found preserved in a silicified pustular microbial mat in a 2,000 Mya chert deposit in the Belcher Islands (Hofmann, 1976). The same chert deposit also contains filamentous fossils that built tufted mats in peritidal environments (Hofmann, 1976), but the simple morphology of these fossils is less diagnostically cyanobacterial. The chert nodules containing these microfossils are found alongside mud cracks, evaporites, and other sedimentary features characteristic of tidal depositional environments (Beukes, 1987; Flannery & Walter, 2012; Hofmann, 1976). These deposits are distinct from later Phanerozoic cherts that are predominantly carbonate-replacing or sinter deposits (Maliva, Knoll, & Simonson, 2005). The difference in these modes of deposition suggest that silica concentrations in the Proterozoic were likely higher than modern values – a result that can in part be understood by the lack of silica-sequestering organisms such as diatoms and radiolarians (Conley et al., 2017; A. R. Manning-Berg & Kah, 2017; Siever, 1992) – but still below concentrations at which, abiotic precipitation of silica is expected (120 ppm; Iler, 1979).

Microbial silicification on the Earth today occurs in silica-rich hot springs where rapid precipitation of silica from the water is able to encase microbial communities (Yee, Phoenix, Konhauser, Benning, & Ferris, 2003), but the ability of these hot springs to explain the silicification in Proterozoic marine environments is questioned (Jones, Konhauser, Renaut, & Wheeler, 2004; Maliva et al., 2005). Instead of large-scale sinter deposits produced by abiotic

precipitation of silica from supersaturated solutions, Proterozoic silicification is primarily reported in isolated nodules and lenses of early diagenetic chert deposited in shallow marine environments (Butterfield, 2015; Sergeev et al., 2012). The temperature, salinity, and silica concentrations in these peritidal settings differ from those found in modern hot springs, and so the mechanism by which this early diagenetic chert was deposited is likely to differ from modern silicification as well (Jones et al., 2004).

One model of silicification that accounts for these differences suggests that the exopolymeric substances (EPS) produced as a stress response by many microorganisms (Rossi & De Philippis, 2015) can play an active role in silicification (Handley, Turner, Campbell, & Mountain, 2008), as opposed to the passive processes observed on the Earth today (Jones et al., 2004). In support of this model, a recent study has shown that photosynthetically active coccoidal cyanobacteria from Shark Bay, Australia, mediate silica precipitation in sea water that is undersaturated with respect to silica (Moore et al., 2020). EPS of these biofilms were found to bind Mg ions and facilitate the formation of a Mg-rich silica precipitate (Moore et al., n.d.). Moore et al. (2020) proposes a plausible mechanism of silicification consistent with the Proterozoic rock record and applicable to the preservation of the oldest diagnostic cyanobacterial fossils. However, it is unknown whether the same model can be applied to filamentous cyanobacteria, including those in tufted and conical microbial mats.

Here, we ask three main questions: 1) to what extent does the mechanism of silicification proposed in Moore et al. (2020) apply to filamentous cyanobacteria as modern analogs of filamentous fossils? 2) what biological traits and environmental factors might contribute to an organism's ability to silicify via this mechanism? and 3) how does this model of silicification relate to micro-scale and macro-scale structures and the contributions of cyanobacteria to the

preservation of tufted microbial mats in the rock record? We address these questions by growing mat-forming filamentous cyanobacteria enriched from Shark Bay microbial mats (Fig. 1) in artificial seawater medium (ASW) that is undersaturated with respect to silica at ~21°C and 1 atm pressure. These experiments model the same Proterozoic shallow marine environments previously shown to be conducive to silicification of pustular mats by Moore et al. (2020) but with different cyanobacterial morphologies, large scale mat structures (pinnacles/pillars), and potential EPS chemistries. Understanding the factors necessary for silicification of filamentous cyanobacteria and their macroscopic aggregates is vital to interpreting the fossil record as well as the environmental conditions of the Proterozoic, and may allow for the reinterpretation of some of the most ancient and most ambiguous fossils, as well as shift our understanding of the preservation of larger silicified structures.

Methods

Enrichment cultures of filamentous cyanobacteria from microbial mats were experimentally fossilized in batch culture experiments. For each experiment, biofilms were incubated in duplicate in sterile plastic culture jars (BioExpress, catalog #C-3122-1, 190 mL, 68 mm x 68 mm) at ~21° C and 1 atm with a 12-hour light/12-hour dark cycle in ASW medium. Concentrations of 70 ppm, 90 ppm, and >110 ppm silica ($Na_2O(SiO_2)x \cdot xH_2O$, Sigma-Aldrich, St. Louis, MO) were tested. Aragonite sand substrate was provided for one trial to replicate the conditions in which microbial mats form in nature. Three trials were run in total. Sterile controls were also conducted in duplicate to experimentally test the amorphous abiotic precipitation of silica under the given conditions. Samples from the batch culture experiments were collected every 3 or 5 days, depending on the duration of the experiment. Additionally, on each sampling day 50 ml of media was replaced, 10 ml of which was collected for chemical analysis.

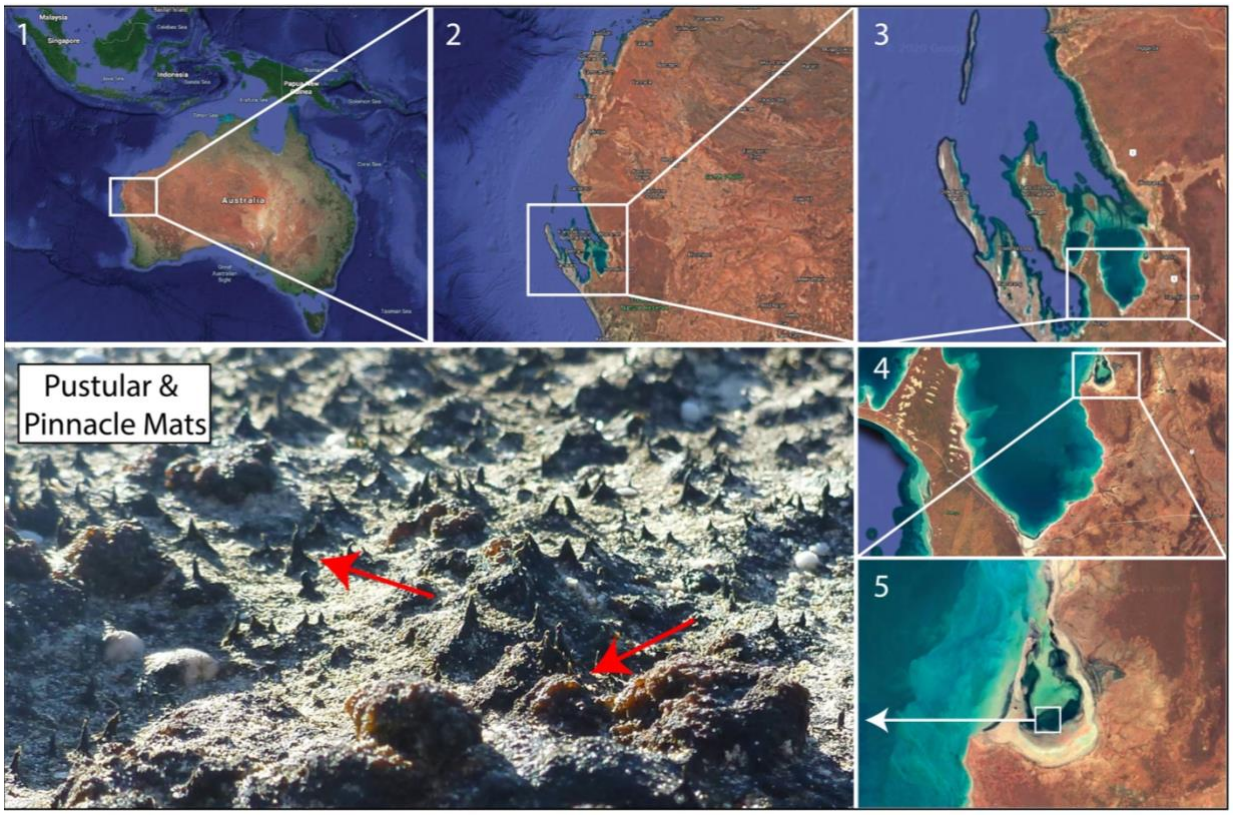


Figure 1: Map of Australia (1), highlighting Shark Bay (2-5). Arrows show rounded pustular and pointed pinnacle mats.

At each sampling interval both biofilm and media samples were collected. Biofilms were collected with sterile tweezers and transferred to 1.5 mL Eppendorf® microtubes (Eppendorf North America, NY, USA, cat#022364111). Biofilms were prepared for scanning electron microscopy (SEM/EDS) by fixation in 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer with 0.1% $CaCl_2$ at pH 7.4 at 4° C overnight. Fixation and buffering steps were carried out in an effort to avoid cellular degradation or sample fracturing. Prior to SEM plating, biofilms were washed using a 0.2 M sodium cacodylate buffer, rinsed with milliQ water and dried using an ethanol dehydration series (50%, 80%, 90% and 100% ethanol in 10-minute steps). Samples were mounted on 12.7 mm diameter SEM stubs (Ted Pella Inc., Product #16111, Redding, CA, USA) with double-coated carbon conductive tape (Ted Pella Inc., Product #16084-7, Redding,

CA, USA), coated with an 80:20 mixture of Pt:Pd on the HAR-052 Carbon Coater equipped with metal coater and imaged using a JEOL 7900F SEM at the Harvard Center for Nanoscale Systems (CNS). SEM images were collected at 3 keV. Electron Dispersive X-ray spectroscopy (EDS) total area spectra were collected at 10 keV and processed using AZtec software (Oxford Instruments, Abingdon, United Kingdom).

Medium was filtered using 10 mL syringes and 0.2 µm Pall Acrodisc® Sterile Syringe Filters with Supor® Membrane (VWR, Radnor, PA, USA, catalog # 28143-350) into sterile 15 mL Falcon® Centrifuge Tubes (VWR, Radnor, PA, USA, catalog # 21008-936) for chemical analysis. Dissolved silica concentrations in media samples were determined using the molybdate blue spectrophotometry method (Strickland & Parsons, 1972). Water samples were diluted tenfold with milliQ water and analyzed together with six standards obtained by the dilution of a silica standard solution (Sigma-Aldrich cat# 16259). The absorption values of samples and standards were measured spectroscopically at a wavelength of 810 nm using a BioTek microplate reader instrument with BioTek Gen5 Data Analysis software. All samples were measured in replicates of 5 with 1% error in absorption values and the absorption values were averaged. Tubing and containers were specifically selected to minimize potential sources of silica contamination, and all samples were stored in the dark at room temperature.

Results

Silicification of Filamentous Cyanobacteria

To investigate whether filamentous cyanobacteria are able to silicify in seawater that is undersaturated with respect to silica, batch culture experiments were conducted with pillar-forming filamentous cyanobacteria (Fig. 2). These experiments were performed in the presence of light at room temperature (~21°C) and pressure (1 atm) in sterile plastic culture jars and ASW

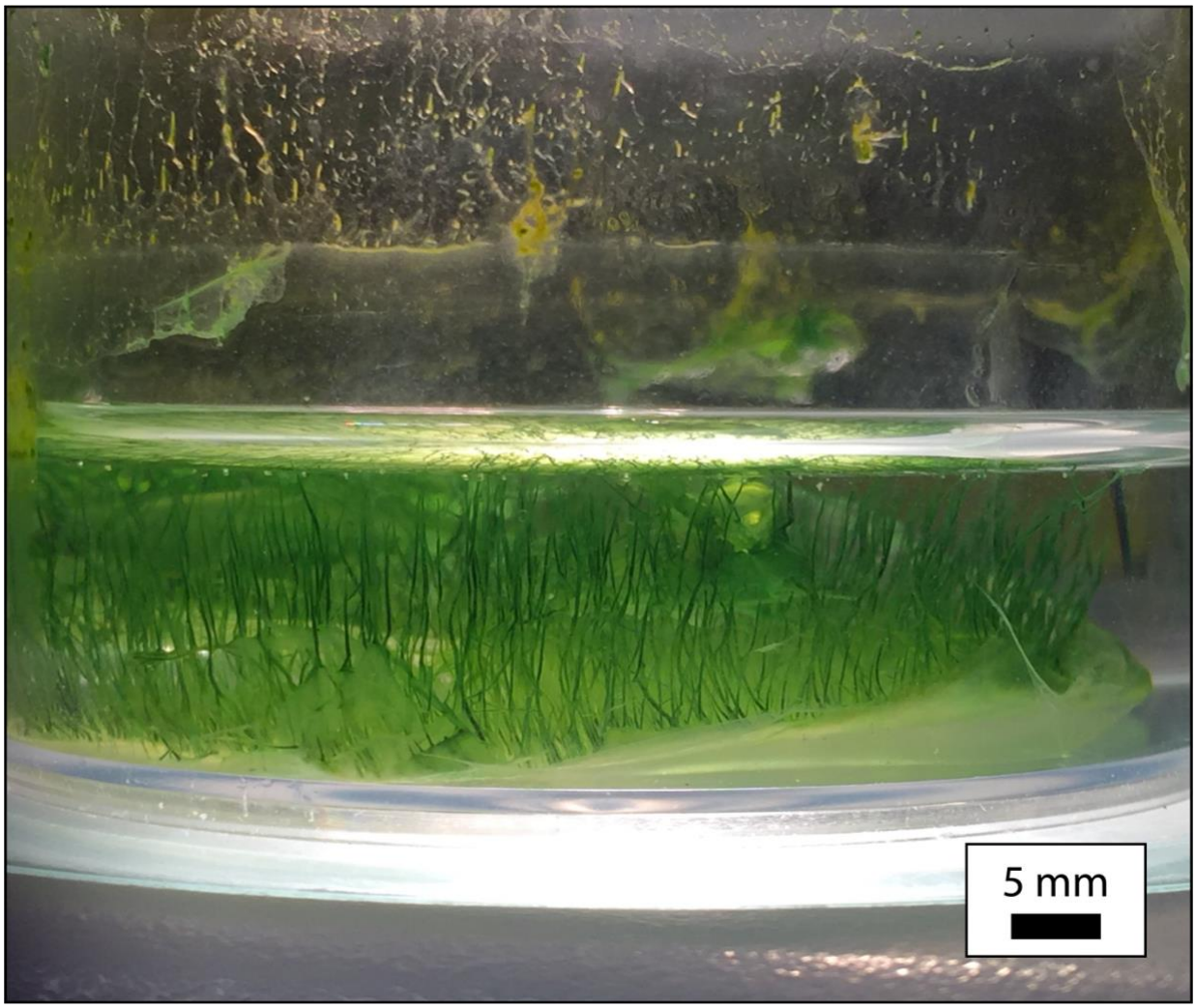


Figure 2: Enriched culture of pillar-forming filamentous cyanobacteria from Shark Bay.

with 90 ppm silica. This concentration has been shown to promote effective silicification in coccoidal cyanobacteria (Moore et al., 2020) and is elevated with respect to previous estimates for typical Proterozoic marine silica concentrations (~60 ppm; Siever, 1992) but is below amorphous silica saturation (120 ppm; Iler, 1979). To determine whether or not silica would precipitate abiotically under these conditions, we incubated two sterile controls with ASW that contained 90 ppm silica in the same manner. Throughout the experiment, no abiotic precipitation was observed in the sterile controls and dissolved silica concentrations remained at 90 ppm

(Supp. Fig. 1). Additional duplicate cultures were incubated in ASW without silica and compared to the cultures that grew in the medium amended by silica. The cells in all cultures initially had smooth surfaces and lacked silica precipitates (Fig. 3). Cells from cultures incubated without silica remained smooth throughout the experiment (Fig. 4a) and EDS spectra of their biofilms did not contain Si peaks (Fig 4b). After 20 days, cells incubated in ASW with 90 ppm silica developed a grainy surface texture (Fig. 4c) due to the accretion of ~100 nm diameter spheroidal particles, characteristic of colloidal silica (Benning, Phoenix, Yee, & Konhauser, 2004). EDS spectra showed the accumulation of silica in the EPS surrounding the cells starting at day 5, with more notable buildup and precipitation by day 20 (Fig. 4d). These spectra were similar to those of Mg-rich amorphous silica precipitates reported by Moore et al. (2020), but the former contained more prominent Ca peaks. X-ray Diffraction (XRD) and Fourier-Transform Infrared Spectroscopy (FT-IR) analysis would be required to confirm the amorphous or crystalline nature of the silica precipitate. In fact, EDS spectra of all samples at all times contained persistent peaks of calcium and sulfur. Given that the same peaks were present in cultures that had not been exposed to silica, these peaks likely arise from the specific biochemistry of microbial EPS rather than mineral precipitation. Because 50 ml of the sample's total 70 ml of medium was replaced every 5 days, we did not measure a change in dissolved silica concentration in the cultures (Supp. Fig. 1).

Environmental Constraints on Silicification

Silica concentrations in Proterozoic peritidal environments varied due to evaporation and other environmental controls (Maliva et al., 2005; Siever, 1992). The local concentration of silica would have fluctuated as a function of the environment in which they lived. To examine the effect of different concentrations of dissolved silica, additional batch culture experiments were

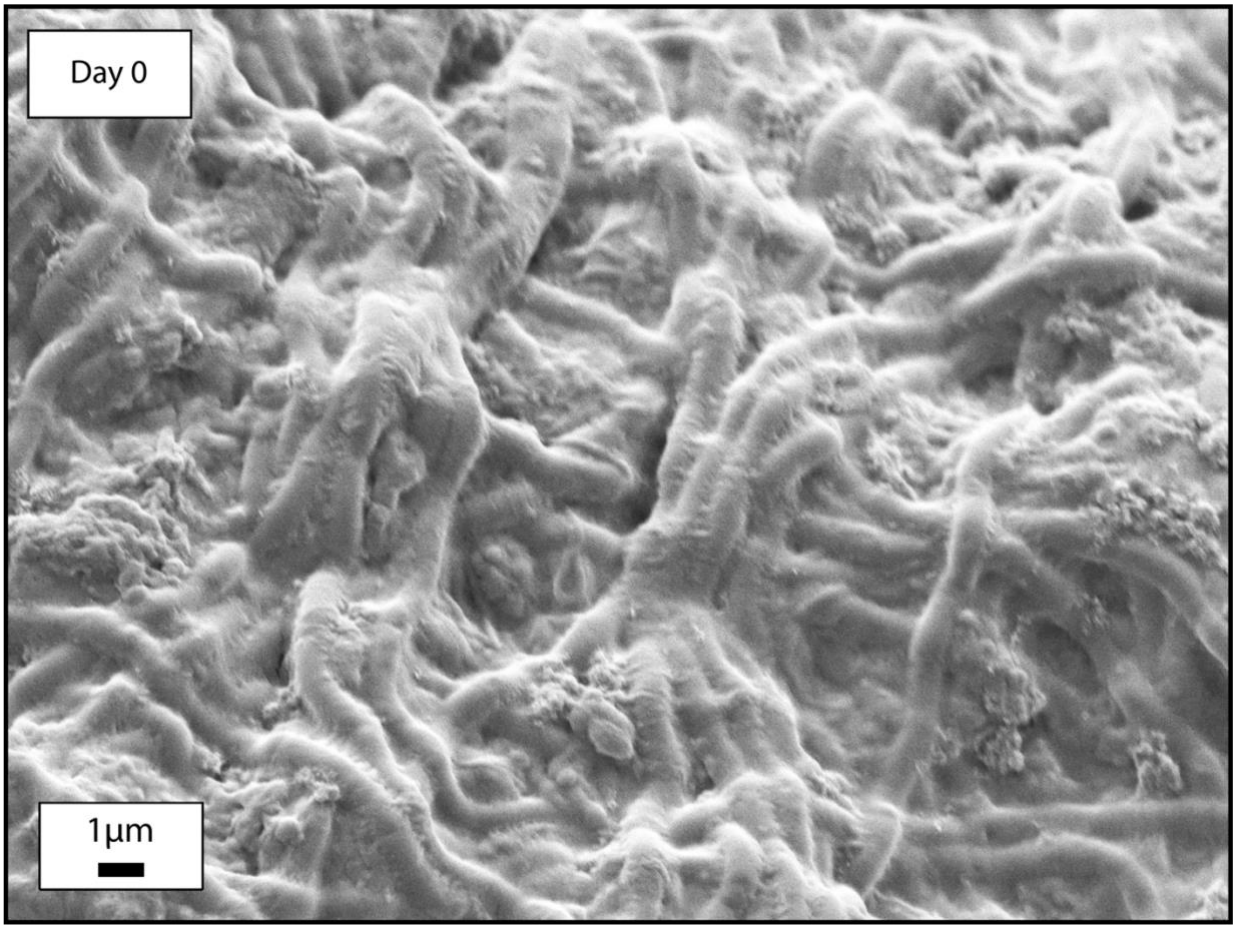


Figure 3: Scanning electron micrograph of cyanobacterial biofilm at Day 0 before silica exposure. The biofilm is a mixed community, with smaller organisms interspersed between the longer interwoven filamentous cyanobacteria.

conducted with ASW that contained 70 ppm, 90 ppm, and ~120 ppm silica. One experiment contained cultures incubated on aragonite sand, others did not contain any substrate. The cells from cultures incubated in ASW with 70 ppm silica developed a grainy surface texture due to the precipitation of colloidal silica particles (Fig. 5a), as observed in previous experiments containing 90 ppm silica. At higher silica concentrations (90 ppm, > 110 ppm), we observed larger silica-covered areas (Fig. 5c, 5e). Because the bacteria were growing and accumulating biomass throughout the experiment, the biofilms did not show uniform precipitation of silica, as newer regions would have had less time to accumulate silica. At or above the threshold

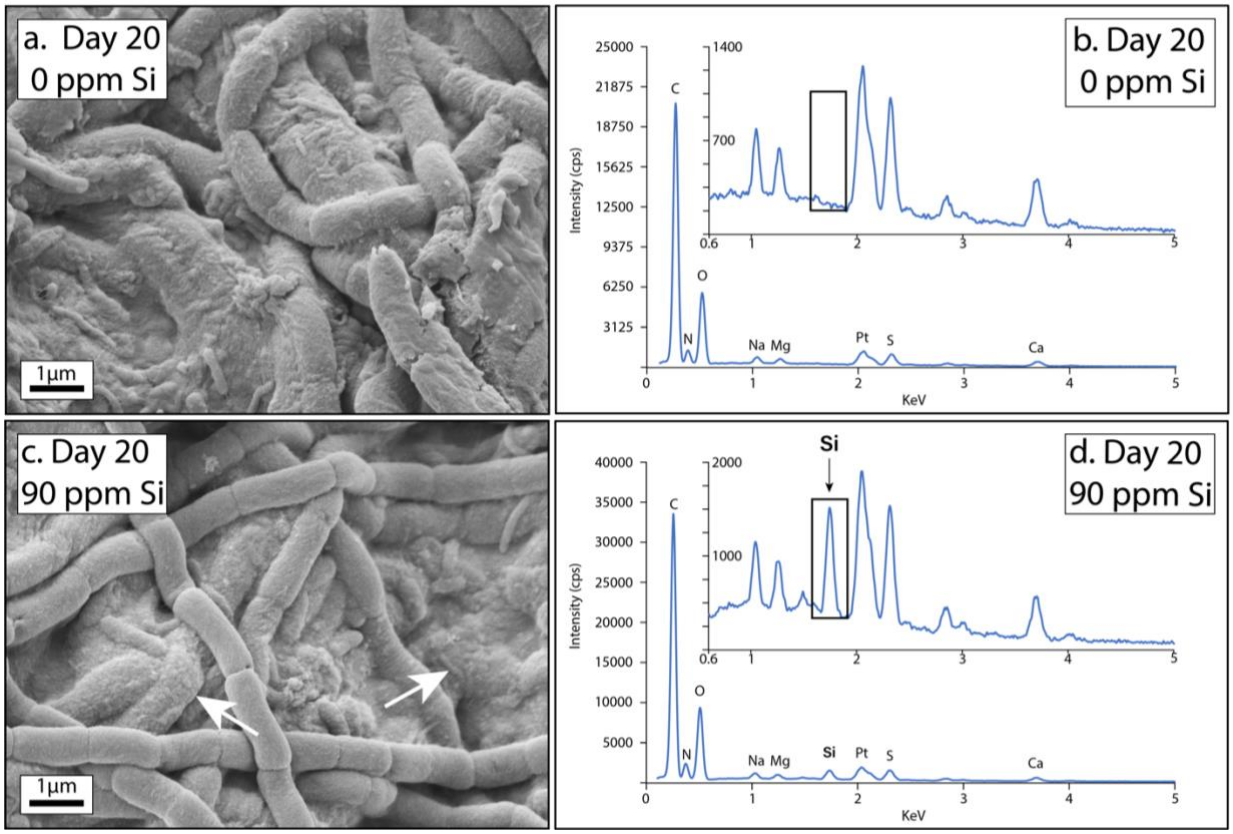


Figure 4: Scanning electron micrograph (SEM) and energy dispersive X-ray spectrograph (EDS) of cyanobacterial biofilms after 20 days. When not exposed to silica the surface of the cells remained smooth (a) and no Si peak is visible in the EDS spectra (b). When exposed to 90 ppm silica, a rough and grainy surface texture developed (c) and a notable buildup of Si in the EDS spectra (d). Arrows point to regions of silica accumulation. Insets with enhanced vertical scale show Mg, Si, and Ca peaks.

concentration required for amorphous precipitation (120 ppm), silica was present in large clusters within the EPS (Fig. 5e inset). This can be attributed to both abiotic precipitation as well as the biologically mediated process. EDS spectra showed that silica was present in all samples after 15 days, and notable buildup had accumulated by day 60 (Fig. 5b, 5d, 5f). Thus, filamentous, tuft- and pillar-forming cyanobacteria were capable of sequestering silica at a wide range of concentrations. Sulfur and calcium peaks were again present in the biofilms at all samples at all intervals. In samples where a calcium carbonate substrate was provided, the Ca peak was especially pronounced due to the entrapment of carbonate grains within the biofilm.

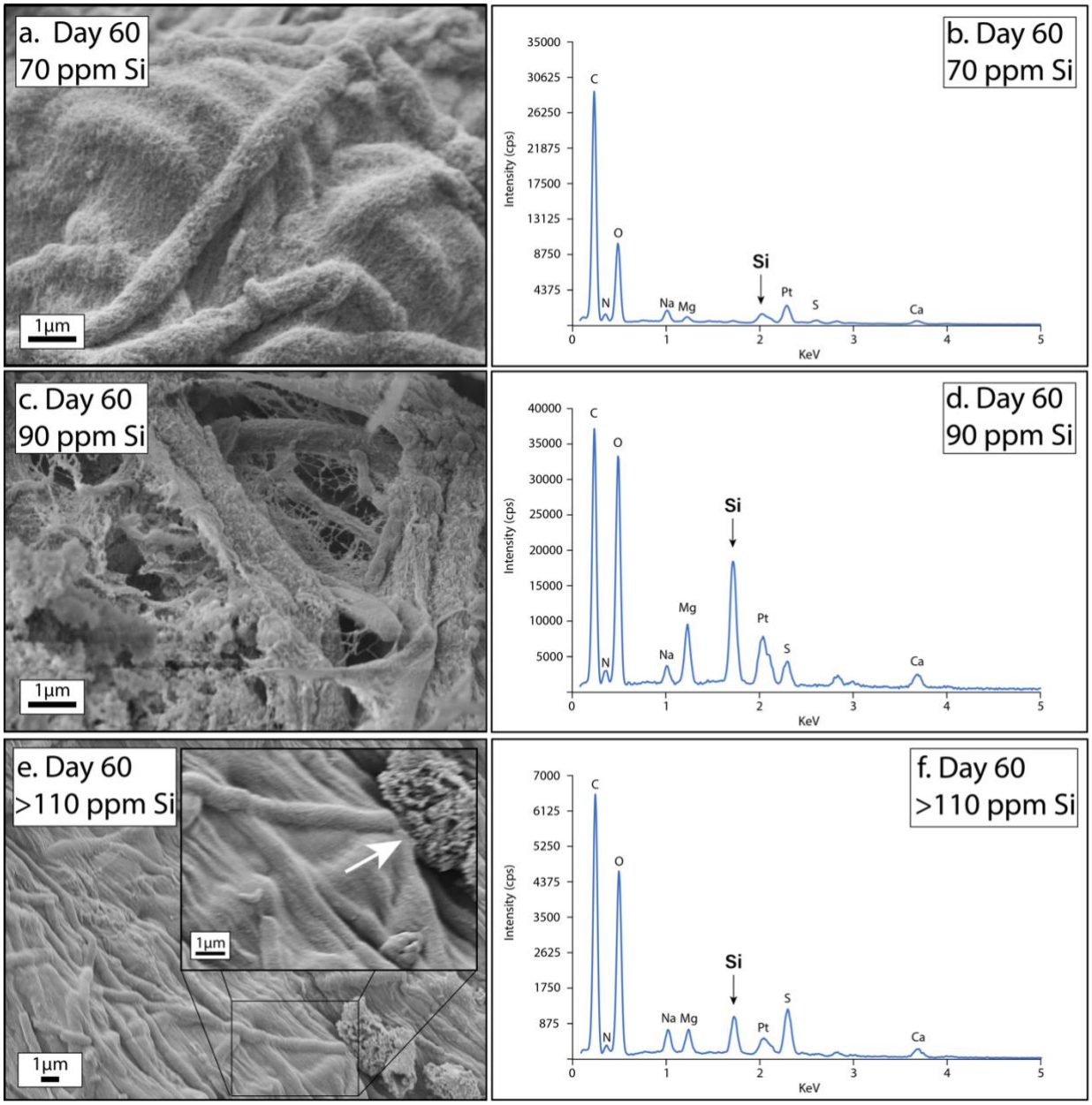


Figure 5: Scanning electron micrograph (SEM) and energy dispersive X-ray spectrograph (EDS) of cyanobacterial biofilms after 60 days. When exposed to 70 ppm silica the surface of the cells developed a grainy surface due to colloidal silica (a) and EDS analysis confirmed a Si peak (b). When exposed to 90 ppm silica, buildup was substantial, coated the surface of the cells (c) and the resulting peak in Si in the EDS spectra was large (d). When exposed to ~120 ppm silica, both abiotic and biologically mediated precipitation of silica occur (e). The abiotic precipitation of silica forms larger isolated clumps (e insert, arrow) compared to the finer grained precipitates at lower Si concentrations. Because this abiotic precipitation only occurs in patches, the resulting Si peak in the EDS spectrum (f) is not as pronounced as the Si peak at 90 ppm.

Preservation of Large Microbial Structures

The filamentous organisms form pinnacle/pillar structures that resemble fossil tufted and pinnacle mats preserved by silicification (Beukes & Lowe, 1989; T. Bosak et al., 2013; Flannery & Walter, 2012; Petroff et al., 2010). To investigate silicification of the macroscopic, ~5 mm tall and ~0.5 mm wide pillars, we imaged and analyzed a cross sectional area of a pillar after 10 days of incubation in 90 ppm silica (Fig. 6a). The external surface of the pillar accumulated silica (Fig. 6c), as revealed by a large Si peak in the EDS spectra (Fig. 6e). Densely packed filaments and no silica precipitates were visible in SEM images of the horizontal cross section of the pillar (Fig. 6b) and only a small Si peak was detected in the EDS spectra (Fig. 6d). Silica appears not to have been able to effectively penetrate the pillar structure, although silica granules coated the entire exterior of the structure. Thus, the exterior of the structure should have a higher preservation potential because it can sequester silica, whereas the interior is more likely to degrade before becoming filled in by minerals such as silica or carbonate during later diagenesis.

Discussion

This study demonstrates that filamentous tuft- and pillar-forming cyanobacteria can mediate their own silicification under conditions that model shallow marine environments at ~21°C and 1 atm pressure in seawater that is undersaturated with respect to silica. Silicified fossils produced by filamentous organisms are well documented in the fossil record (Amard & Bertrand-Sarfati, 1997; Beukes, 1987; Flannery & Walter, 2012; Andrew H. Knoll, Strother, & Rossi, 1988), but neither the taxonomic affiliation nor preservation mechanism of many of these fossils are known. In contrast to modern silicifying environments, the geologic context in which we find these fossils indicates a marine tidal depositional environment (Beukes, 1987; Flannery & Walter, 2012) in which silica likely did not exceed amorphous saturation. Recently, it has been

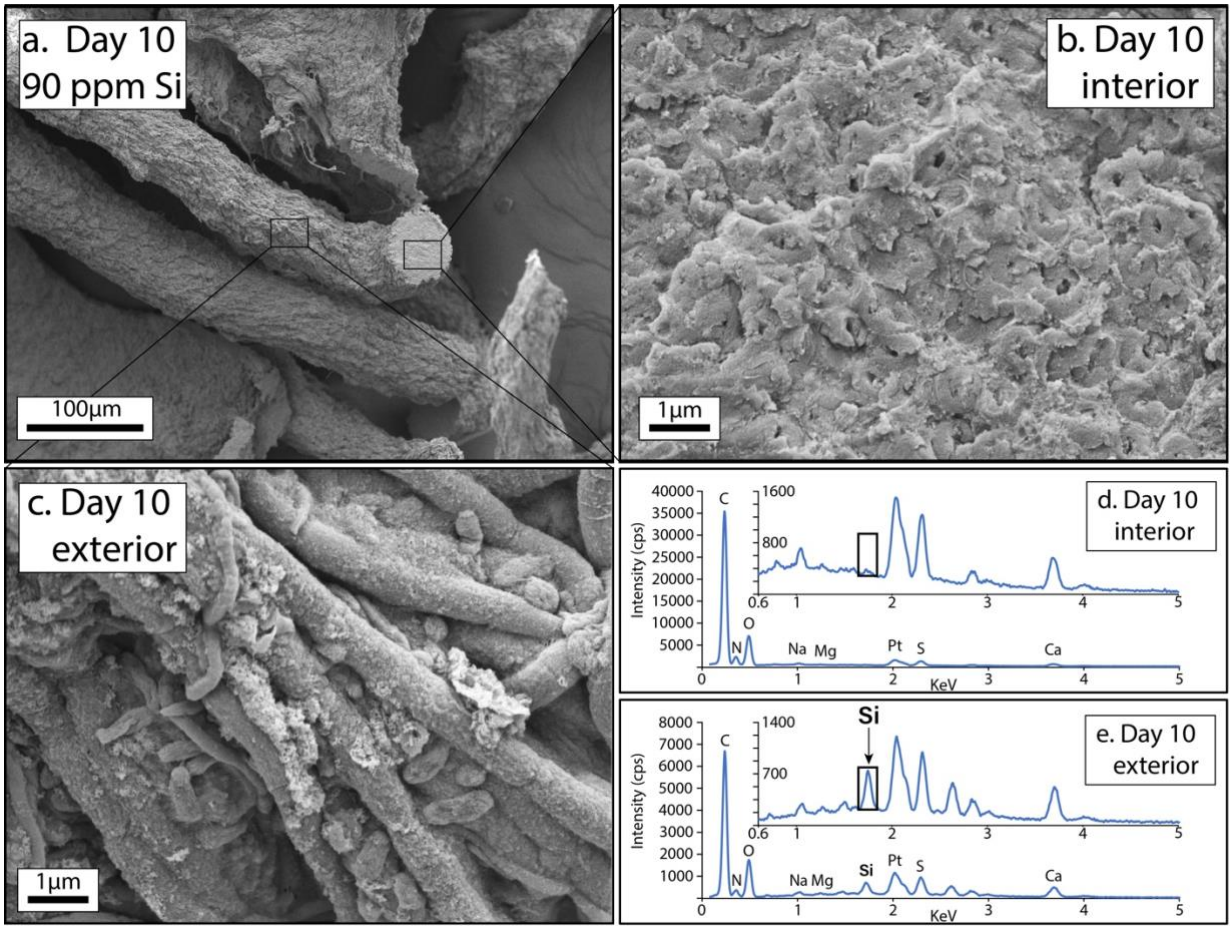


Figure 6: Scanning electron micrograph (SEM) and energy dispersive X-ray spectrograph (EDS) of a cross section of a cyanobacterial pillar (a) after 10 days. The interior of the cross section (b) showed tightly packed filaments and no precipitation of silica, while the exterior (c) showed accumulation of silica along the surface of the filaments. As such, only a minimal peak in Si was detected in the EDS spectra of the interior (d) while the peak in Si on the exterior of the pillar was large.

found that coccoidal cyanobacteria are able to mediate the precipitation of amorphous silica in seawater that is undersaturated with respect to silica through magnesium-cation bridging between silica and negatively charged surface groups in the EPS to promote silica precipitation below amorphous saturation levels (Moore et al., 2020). The extent to which this model applied to other organisms living in similar environments was previously unknown. Our results show that filamentous cyanobacteria are also able to sequester silica in their EPS under conditions that

model Proterozoic shallow marine environments. Thus, we have shown that the model of silicification presented in Moore et al. (2020) may extend to filamentous cyanobacteria as well.

Cyanobacteria are known to produce EPS to protect themselves against environmental conditions such as desiccation, UV radiation, and salinity (Rossi & De Philippis, 2015). EDS analysis of all samples showed a peak in Ca and S in the EPS of the cells. These elements may be indicative of a specific compound found in the EPS of some modern cyanobacteria: calcium spirulan. This sulfated polysaccharide has been studied extensively and shown to have both antioxidant and antiviral properties in some cyanobacteria (K. Hayashi, Hayashi, & Kojima, 1996)(T. Hayashi, Hayashi, Maeda, & Kojima, 1996). Moore et al. (2020) showed that photosynthetic activity may promote silica precipitation by raising the pH of the water. Sulfur containing functional groups are known to have high pKa (Braissant, Decho, Dupraz, Glunk, & Visscher, 2007). When the local pKa is higher than the local pH, functional groups within the EPS lose a proton to solution, leaving negatively charged surface groups free to interact with ions in solution. Cations from solution bind to the negatively charged surface groups, forming sites for silica nucleation. Magnesium appears to be the ion binding to the negatively charged surface groups in both the filamentous cyanobacteria presented here and the coccoidal cyanobacteria presented in Moore et al. (2020), but other divalent cations such as calcium may also be able to facilitate silicification in this way. The pustule-forming coccoidal cyanobacteria reported in Moore et al. (2020) do not contain the Ca signal reported here, highlighting potential underlying physiological and biochemical differences between these coccoidal and filamentous cyanobacteria, even though they were sampled from the same environment. Iron has been reported to play this role for some freshwater microbes in silica-rich hot springs (Konhauser, Jones, Phoenix, Ferris, & Renaut, 2004; Phoenix, Konhauser, & Ferris, 2003; Urrutia &

Beveridge, 1994). Calcium spirulan and other sulfated polysaccharides containing these compounds may therefore require the local pH to be higher in order to achieve conditions favorable to silica nucleation. If these sulfated polysaccharides are present in the EPS, then it is possible that photosynthetic activity – which is known to raise the pH of solution – is promoting silicification within these filamentous cyanobacteria, but further data are needed to characterize the source of the Ca and S signals in the EDS spectra. Given the relationship between the production of EPS as an environmental stress response, photosynthetic activity, and silicification, it is possible that silicification could provide cyanobacteria with a variety of potential evolutionary advantages as well.

Below amorphous saturation level, filamentous cyanobacteria are able to mediate the precipitation of silica in their EPS. These nanoscale particles of silica are able to capture fine details of microbial communities and may result in exceptional preservation of both organism morphologies and macroscopic structure (Hofmann, 1976; A. H. Knoll, Worndle, & Kah, 2013; Ashley R. Manning-Berg, Seth Wood, Williford, Czaja, & Kah, 2019). However, when silica concentrations rise to saturation, this mechanism of silicification is superseded by abiotic precipitation via Ostwald ripening (Iler, 1979). This is observed in the accumulation of large clumps of silica, which appear to nucleate and grow by stripping silica from regions of the EPS where it may have precipitated via the biologically mediated mechanism described above. The large clumps of silica precipitated by this abiotic mechanism of silicification are not able to capture fine details of microbial structures. While cells silicified in this way may still be preserved, the record they produce would be imprecise.

Understanding the microbe-mineral interactions that lead to the preservation of microbial mats and stromatolites is crucial for the interpretation and reconstruction of ancient

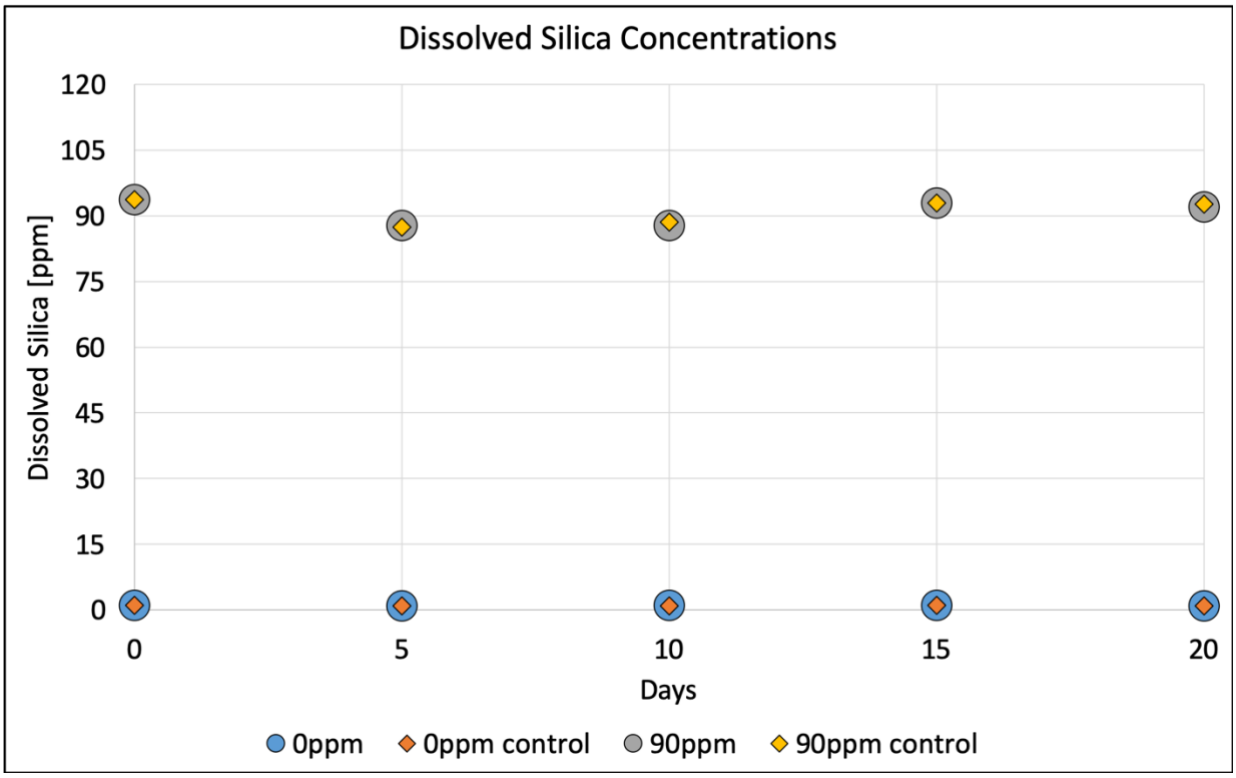
environmental conditions and the ways in which ancient organisms responded to and interacted with the environment on the early Earth. Because their cell morphologies and the structures that they form are morphologically analogous to Proterozoic and Archean fossils and stromatolites, silicified filamentous microfossils allow for the reconstruction of environmental conditions, depositional environments, nutrient cycling, and the state of the Proterozoic biosphere. We show that the preservation of large-scale microbial structures is dominated by surface conditions, and that the interior of these larger structures is unlikely to be fully silicified. This differential silicification is caused by the inability for silica to penetrate tightly bound microbial structures. Instead, incomplete silicification allows for later diagenetic processes to fill in the pore space left by this differential process. It has been suggested that ancient fossils like those of the Angmaat Formation are not uniformly silicified (A. H. Knoll et al., 2013; Ashley R. Manning-Berg et al., 2019). Instead, there is a clear differentiation between microfossils and mat structures preserved in early diagenetic chert and void space filled by carbonate deposits. We present a plausible model of cyanobacterial colony preservation that is consistent with observed Proterozoic microfossils. Moreover, this model may not be unique to cyanobacteria. Because the precipitation of silica is mediated by processes occurring in the EPS, other organisms that produce EPS with similar biochemistries may also be able to mediate their own silicification. Further studies are needed to confirm how prevalent this process may be. Most significantly, we show that filamentous cyanobacteria in marine tidal environments play a role in the local cycling of silica. Understanding the local cycling of nutrients and the depositional environments in which we find preservation of past microbial communities is vital to understanding the evolution of life throughout the Proterozoic. Additionally, understanding the role microbes play in their own preservation may inform the interpretation of extraterrestrial hydrated silica deposits and the

search for evidence of past life on other planets, such as Mars (Beaty et al., 2019). The geologic context in which we find these deposits may be diagnostic of specific environmental and potentially biologic processes, but further study of extraterrestrial depositional environments is needed for this claim to be conclusive.

Conclusions

Microbial mats formed by filamentous cyanobacteria accumulate and precipitate silica at room temperature and pressure in seawater that is undersaturated with respect to silica. This process occurs in the exopolymeric substances (EPS) produced by photosynthetically active cells as a stress response when dissolved silica concentrations are above 70 ppm, but may occur at lower concentrations as well. These silica concentrations are representative of plausible environmental conditions during the Proterozoic. Silica accumulation is restricted to the exterior of the pillars produced by these filamentous cyanobacteria. The interior of these structures may be preserved by later diagenetic materials like carbonates. This observation is consistent with the incomplete silicification observed in many Proterozoic microfossils. Locally elevated silica concentrations may have enabled filamentous cyanobacteria to play a significant role in local silica cycling in marine tidal environments. Microbe-mineral interactions between similar organisms and silica may account for the exceptional silicification and preservation of filamentous and coccoidal cyanobacteria and their macroscopic aggregates in peritidal environments throughout the Proterozoic.

Supplemental Materials



Supplemental Figure 1: Dissolved silica concentrations did not vary throughout the experiment. Because 50 ml of the total 70 ml ASW medium per culture jar was replaced every 5 days, the observed dissolved silica concentration was almost identical to the dissolved silica concentration of the stock solution. Samples were taken every 5 days before the medium was replenished with stock solution. Had the medium not been replaced throughout the experiment, we would expect to see a decrease in the dissolved silica concentration over time of the culture that was initially inoculated with 90 ppm silica because the microbial mat would sequester silica, therefore causing a drawdown and lowering the dissolved concentration.

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