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REVIEW

A review of microbial-environmental interactions recorded in Proterozoic carbonate-hosted chert

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Abstract

The record of life during the Proterozoic is preserved by several different lithologies, but two in particular are linked both spatially and temporally: chert and carbonate. These lithologies capture a snapshot of dominantly peritidal environments during the Proterozoic. Early diagenetic chert preserves some of the most exceptional Proterozoic biosignatures in the form of microbial body fossils and mat textures. This fossiliferous and kerogenous chert formed in shallow marine environments, where chert nodules, layers, and lenses are often surrounded by and encased within carbonate deposits that themselves often contain kerogen and evidence of former microbial mats. Here, we review the record of biosignatures preserved in peritidal Proterozoic chert and chert-hosting carbonate and discuss this record in the context of experimental and environmental studies that have begun to shed light on the roles that microbes and organic compounds may have played in the formation of these deposits. Insights gained from these studies suggest temporal trends in microbial-environmental interactions and place new constraints on past environmental conditions, such as the concentration of silica in Proterozoic seawater, interactions among organic compounds and cations in seawater, and the influence of microbial physiology and biochemistry on selective preservation by silicification.

KEYWORDS
biosignature, carbonate, chert, fossil, proterozoic

1 | INTRODUCTION

Chert-hosting deposits from the Proterozoic Eon contain both physical and chemical evidence of evolving marine life on early Earth. The morphologies of microbial fossils preserved in these deposits have traditionally been used to relate fossil organisms to modern ones and characterize the diversity, evolution, metabolisms, and lifestyles of fossil communities (e.g., Butterfield, 2015; Demoulin et al., 2019; Schopf & Klein, 1992; Sergeev & Sharma, 2012 and references therein). The general composition and diversity of fossil assemblages have also been correlated with their depositional environments, with some subtidal fossil assemblages containing more diverse biota compared to supratidal fossil assemblages (e.g., Knoll et al., 1991; Knoll et al., 2013). These and other past works have provided transformative insights related to microbial diversity, microbial evolution, and microbial-environmental co-evolution that can now be expanded

through the integration of experimental taphonomy and studies of modern analog environments with studies of the fossil record.

Diagnostic cyanobacterial fossils with distinct morphologies analogous to modern cyanobacteria are preserved alongside simpler morphologies in Proterozoic formations that are formed under diverse chemical and environmental conditions (e.g., Butterfield, 2015; Demoulin et al., 2019; Schopf & Klein, 1992; Sergeev & Sharma, 2012 and references therein). Comparisons of the depositional environments represented in fossiliferous Proterozoic units that sample supratidal to shallow subtidal environments that lie below the mean low tide level (Lasemi et al., 2012) enable the characterization of microbial communities that inhabited these environments and reveal trends in preservation style, environments, and community makeup [(Knoll et al., 2013; Manning-Berg & Kah, 2017; Manning-Berg et al., 2018, 2019) Table 1]. Diagnostic cyanobacterial fossils (e.g., *Eoentophysalis*, *Obruchevella*, *Eohyella*, and *Polybessurus*) and some algal fossils (e.g., *Bangiomorpha*) are especially useful because of their morphological similarities to modern counterparts (Figure 1) enable direct comparisons between modern and ancient organisms. In turn, these comparisons inspire hypotheses about microbial physiology, stress responses, and interactions among organic compounds and silica, magnesium, and calcium in Protozoic marine environments.

Many of the best-preserved Proterozoic microbial fossils and organic-rich textural biosignatures are preserved in facies that contain chert (microcrystalline SiO_2), carbonate (calcite or dolomite), or both (e.g., Butterfield, 2015; Demoulin et al., 2019; Schopf & Klein, 1992; Sergeev & Sharma, 2012 and references therein). The two lithologies and the biosignatures that they preserve differ in some key respects, but they share one important feature: when they preserve kerogen and microbial fossils, the organic matter is associated with amorphous-to-finely-crystalline solid phases that formed very early in the diagenetic history of the marine sediments. The early formation and sometimes microcrystalline (<20 μm) nature of the primary to early diagenetic silica and carbonate minerals are crucial because they enable detailed cellular preservation of microbial fossils and organic-rich textural biosignatures (Table 1). In contrast, late diagenetic dolomite and carbonate-replacing chert commonly overprint or erase microfossils and microbial textures instead of preserving them because of the frequently coarser crystal sizes (>20 μm; Maliva et al., 2005).

Modern analogs and exceptionally preserved Proterozoic textures indicate that microbial communities may have mediated the early precipitation of silica (Moore et al., 2020, 2021) and carbonate minerals (Bischoff et al., 2020; Bontognali et al., 2010; Daye et al., 2019; Gérard et al., 2018; Perri et al., 2018; Petrash et al., 2017). If so, these fossil textures and their compositions may tell us not only about microbial morphology but also how the microbes interacted with the environment and contributed to biogeochemical processes, element cycles, and mineral formation. Although chert rather than carbonate preserves the best examples of microbial body fossils (e.g., Butterfield, 2015; Demoulin et al., 2019; Schopf & Klein, 1992; Sergeev & Sharma, 2012 and references therein), both chert and carbonate preserve organic material and microbial mat structures in peritidal environments, and their formation is spatially and, likely, temporally linked (Kah & Knoll, 1996; Knoll et al., 2013; Manning-Berg & Kah, 2017). The relationship between their formation mechanisms and the microbial communities that they preserve in these environments thus merits consideration. Experimental taphonomy and studies of modern analog environments can now address the influence of environmental factors like UV radiation, subaerial exposure, and water chemistry on the diversity, stress responses, and preservation potential of Proterozoic marine communities (Orange et al., 2013; Phoenix et al., 2000; Wilmeth et al., 2021). Specifically, critical questions remain surrounding the role of Proterozoic microbes in the formation of chert and carbonate minerals and the cycling of silica, calcium, and magnesium during the Proterozoic Eon. These questions particularly apply to cyanobacteria because these photosynthetic primary producers have colonized a wide range of marine benthic environments for more than two billion years (Butterfield, 2015; Demoulin et al., 2019; Fournier et al., 2021; Knoll, 2008; Sánchez-Baracaldo et al., 2022).

In this review, we highlight some advances in experimental taphonomy and studies of mechanisms that drive microbial silicification and carbonate precipitation. We underscore the recent experimental physiological and chemical insights into the relationships between fossilization processes, seawater chemistry, microbial stress responses, and physiology. These relationships and mechanisms can then be used to constrain the chemical and physical environments in which some key Proterozoic fossils were silicified in carbonate-hosted chert and understand how microbes that inhabited these environments lived and responded to the environmental conditions. In this review, we use examples of some canonical Proterozoic deposits that preserve microfossils and attempt to relate large-scale trends in depositional environments and microfossil assemblages to modern microbial communities and environments. By interweaving studies of fossils preserved by silicification, a major Proterozoic taphonomic window, with insights about biological, chemical, and physical mechanisms that preserved microbial biosignatures in Proterozoic deposits, we hope to stimulate new questions about the co-evolution of cyanobacteria, other microbes, and the environment.

2 | MODERN MARINE ENVIRONMENTS AND MICROBIAL ADAPTATIONS

Today, diverse microbial communities thrive in tidal environments around the world. In particular, cyanobacterial mats colonize the supratidal realm, from those in hypersaline Shark Bay, Western Australia [(Allen et al., 2009; Goh et al., 2009) Figure 2] to the sabkhas of Abu Dhabi (DiLoreto et al., 2019; Krumbein et al., 2004). In these environments, mat-forming microbes must cope with environmental stresses including intermittent subaerial exposure and desiccation, high salinity, and high fluxes of UV radiation that are not attenuated by the water column (Garcia-Pichel, 1998; Garcia-Pichel et al., 1992; Garcia-Pichel & Castenholz, 1991; Goh et al., 2009; Skoog et al., 2022; Wong et al., 2015, 2018). In response to these physical and chemical factors, cyanobacteria

TABLE 1 This table details the fossiliferous formations described in this review and contains details related to lithology, depositional environment, and taphonomy of the fossils.

Age	Formation/Group	Locality	Depositional Environment	Lithologies	Fossils	Additional Information	References
1900–2100 Ma	Duck Creek Formation	Australia	Carbonate platform; shallow marine tidal environment; subtidal to lagoonal environment	Chert and dolomite	Filamentous microbes, coccoidal microbes	Fossiliferous chert from two environments (rip-up clasts transported from supratidal and deposited in subtidal, nodules and layers of chert within subtidal carbonate stromatolites)	Knoll et al. (1988); Grey and Thorne (1985); Knoll and Barghorn (1976); Wilson et al. (2010)
2000 Ma	Franceville Group	Gabon	Shallow marine tidal environment (subtidal to supratidal); volcanic activity	Dolomite, chert, siliciclastic (silt and mud), pyrite, iron oxide	Filamentous microbes, coccoidal microbes	Fossils preserved in chert nodules and layers within carbonate stromatolites	Mossman (2001); Mossman et al. (2005); Amard and Bertrand-Sarfati (1997)
2000 Ma	Belcher Island Group	Canada	Shallow marine tidal environment (subtidal to supratidal)	Chert and dolomite	Filamentous microbes, coccoidal microbes, *Eoentophysalis*	Organic-rich microbial lamination in both chert and dolomite. Fossils preserved in chert nodules and lenses within carbonate. Microbial textures range from subtidal stromatolites to supratidal pustular microbial laminae	Hofmann (1974); Hofmann (1975); Hofmann (1976); Golubic and Hofmann (1976)
1650 Ma	Dahongyu Formation	China	Shallow marine tidal environment (subtidal to supratidal)	Dolomite, chert, siliciclastic (silt and mud)	Filamentous microbes, coccoidal microbes, and other rare morphologies	Fossils preserved in chert nodules and lenses within planar laminated and domed stromatolitic carbonates	Shi et al. (2017); Yun (1984)
1500–1600 Ma	Amelia Dolomite	Australia	Shallow marine tidal environment (subtidal to supratidal)	Chert and dolomite	Filamentous microbes, coccoidal microbes	Fossils preserved in chert nodules and layers within carbonate stromatolites (subtidal to supratidal). Sheaths as well as trichomes preserved	Muir (1976); Croxford et al. (1973)
1500–1600 Ma	Balbirini Dolomite	Australia	Supratidal environment	Chert and dolomite	Filamentous microbes, coccoidal microbes, *Eoentophysalis*	Organic-rich microbial lamination in both chert and dolomite. Fossils preserved in chert nodules and lenses within carbonate	Oehler (1978)

(Continues)

TABLE 1 (Continued)

Age	Formation/Group	Locality	Depositional Environment	Lithologies	Fossils	Additional Information	References
1400 Ma	Gaoyuzhuang Formation	China	Peritidal environments (intertidal to subtidal); deeper marine environments near storm wave base (possibly turbidites)	Dolomite, chert, siliciclastic (silt and mud)	Filamentous microbes, coccoidal microbes, *Eoentophysalis*	Fossils preserved in chert nodules and layers within carbonate stromatolites (subtidal to supratidal). Sheaths as well as trichomes preserved	Zhu et al. (2016); Seong-Joo and Golubic (1998); Seong-Joo and Golubic (2000); Seong-Joo and Golubic (1999); Schopf et al. (1984); Seong-Joo et al. (1999); Yun (1981); Shi et al. (2017); Guo et al. (2018)
1300–1500 Ma	Bil'yakh Group	Siberia	Shallow marine tidal environment (subtidal to supratidal)	Chert, dolomite, siliciclastic (mud and silt)	Filamentous microbes, coccoidal microbes, *Eoentophysalis*	Fossils preserved in chert nodules and layers within carbonate stromatolites (subtidal to supratidal). Sheaths as well as trichomes preserved	Sergeev et al. (1995); Bartley et al. (2000); Sergeev et al. (2007)
1300–1400 Ma	Kyutingde Formation	Siberia	Shallow marine tidal environment (subtidal to supratidal)	Chert and dolomite	Coccoidal microbes	Fossils preserved in chert nodules and layers within carbonate	Stanevich et al. (2009); Yakshin (1999)
1300–1400 Ma	Arymas Formation	Siberia	Subtidal marine environment	Dolomite, chert, siliciclastic (silt and mud)	Acritarchs	Organic-rich microbial lamination in both chert and dolomite. Fossils preserved in chert nodules and layers within carbonate	Stanevich et al. (2009)
1300–1400 Ma	Debengda Formation	Siberia	Shallow marine tidal environment (subtidal to supratidal)	Dolomite, chert, siliciclastic (silt and mud)	Filamentous microbes, coccoidal microbes, *Eoentophysalis*, *Obruchevella*	Organic-rich microbial lamination in both chert and dolomite. Fossils preserved in chert lenses and layers within carbonate	Sergeev et al. (1993); Stanevich et al. (2009)
1100–1200 Ma	Sukhaya Tunguska Formation	Siberia	Shallow marine tidal environment (subtidal to supratidal)	Chert and dolomite	Filamentous microbes, coccoidal microbes, *Polybessurus*	Organic-rich microbial lamination in both chert and dolomite. Fossils preserved in chert lenses and layers within carbonate	Sergeev et al. (1997)
1200 Ma	Dismal Lakes Group	Canada	Shallow marine tidal environment (subtidal to supratidal)	Dolomite, chert, siliciclastic (silt and mud)	Filamentous microbes, coccoidal microbes, *Eoentophysalis*	Organic-rich microbial lamination in both chert and dolomite. Fossils preserved in chert lenses and layers within carbonate	Horodyski and Donaldson (1980); Horodyski and Donaldson (1983); Horodyski et al. (1980); Donaldson and Delaney (1975)

TABLE 1 (Continued)

Age	Formation/Group	Locality	Depositional Environment	Lithologies	Fossils	Additional Information	References
1200 Ma	Hunting Formation	Canada	Shallow marine tidal environment (subtidal to supratidal)	Chert and dolomite	Filamentous microbes, coccoidal microbes, *Polybessurus*, *Bangiomorpha*	Organic-rich microbial lamination and microfossils preserved in nodules and lenses of supratidal carbonate. *Polybessurus* and *Bangiomorpha* preserved in subtidal chert bands that lack microbial lamination	Butterfield (2001); Butterfield et al. (1990); Butterfield (2000)
1000 Ma	Angmaat Formation	Canada	Shallow marine tidal environment (subtidal to supratidal)	Chert and dolomite	Filamentous microbes, coccoidal microbes, *Eoentophysalis*, *Polybessurus*, *Bangiomorpha* endoliths	Fossils preserved in chert nodules, lenses, and layers (subtidal to supratidal)	Knoll et al. (2013); Manning-Berg et al. (2018); Manning-Berg et al. (2019); Manning-Berg and Kah (2017)
900 Ma	Bitter Springs Chert	Australia	Hypersaline lake or marine supratidal environment	Chert and dolomite	Filamentous microbes, coccoidal microbes, *Eoentophysalis*	Organic-rich microbial lamination in both chert and dolomite. Fossils preserved in chert nodules and layers within carbonate	Barghoorn and Schopf (1965); Knoll and Golubic (1979); Schopf, 1968; Schopf and Blacic (1971); Oehler (1977); Oehler (1976); Wacey et al. (2019); Williford et al. (2013)
800 Ma	Scotia Group, Prins Karls Forland	Svalbard	Shallow marine environment	Chert and dolomite	Filamentous microbes, *Obruchevella*	Chert rip-up clasts deposited in subtidal carbonates. Fossils preserved within chert clasts	Knoll and Ohta (1988); Knoll et al. (1991)
780–850 Ma	Little Dal Group	Canada	Shallow subtidal marine environment	Limestone, dolomite	Filamentous microbes	"Calcified" fossils preserved in dolomitized microbialites	Turner et al. (1993); Hofmann and Altken (1979); Altken (1988); Aitken and Nabonne (1989)
750–800 Ma	Chichkan Formation	Kazakhstan	Subtidal and deep subtidal marine environment	Chert and dolomite	Filamentous microbes, coccoidal microbes, *Polybessurus*, eukaryotes	Fossils preserved in chert nodules, lenses, and layers within carbonate stromatolites and in beds of chert that lack microbial lamination	Kempe et al. (2002); Schopf and Kudryavtsev (2009); Schopf et al. (2017); Sergeev and Schopf (2010); Schopf and Kudryavtsev (2011); Williford et al. (2013)

(Continues)

TABLE 1 (Continued)

Age	Formation/Group	Locality	Depositional Environment	Lithologies	Fossils	Additional Information	References
700–800 Ma	Draken Conglomerate	Spitsbergen	Marine lagoon; shallow marine tidal environment (subtidal to supratidal)	Chert and dolomite	Filamentous microbes, coccoidal microbes, *Polybessurus*, acritarchs, VSMs	Organic-rich microbial lamination in both chert and dolomite. Fossils preserved in chert nodules and lenses within carbonate stromatolites (supratidal). Chert rip-up clasts deposited in subtidal carbonates contain microbial mats and fossils. Potential planktonic fossils preserved in rip-up clasts and chert nodules and lenses	Knoll et al. (1991); Knoll (1982)
700–800 Ma	Svanbergfjellet Formation	Spitsbergen	Marine lagoon; shallow marine tidal environment (subtidal to supratidal)	Dolomite, chert, siliciclastic (silt and mud), phosphate	Filamentous microbes, coccoidal microbes, *Eoentophysalis*, *Obruchevella*, *Polybessurus*, acritarchs, algae	Fossiliferous chert from two environments (rip-up clasts transported from supratidal and deposited in subtidal, nodules and layers of chert within subtidal carbonate stromatolites)	Butterfield et al. (1994); Butterfield et al. (1988); Butterfield (2004); Anderson et al. (2020)
700–800 Ma	Eleonore Bay Group	Greenland	Carbonate platform; marine lagoon; shallow marine tidal environment (subtidal to supratidal)	Chert and dolomite	Filamentous microbes, coccoidal microbes, *Eoentophysalis*, VSMs	Fossiliferous chert from two environments (rip-up clasts transported from supratidal and deposited in subtidal, nodules and layers of chert within subtidal carbonate stromatolites). Endolithic fossils silicified within carbonate ooids	Knoll et al. (1986); Green et al. (1987); Green et al. (1988); Campbell (1982)

Also included in this table are references to relevant papers describing the formations. (Aitken, 1988; Aitken & Narbonne, 1989; Amard & Bertrand-Sarfati, 1997; Anderson et al., 2020; Barghoorn & Schopf, 1965; Bartley et al., 2000; Butterfield, 2001, 2004; Butterfield et al., 1988, 1990, 1994; Campbell, 1982; Croxford et al., 1973; Donaldson & Delaney, 1975; Golubic & Hofmann, 1976; Green et al., 1987, 1988; Grey & Thorne, 1985; Guo et al., 2018; Hofmann, 1974, 1975, 1976; Hofmann & Aitken, 1979; Horodyski, 1980; Horodyski & Donaldson, 1980; Horodyski & Donaldson, 1983; Kempe et al., 2002; Knoll, 1982; Knoll et al., 1986, 1988, 1991, 2013; Knoll & Barghoorn, 1976; Knoll & Golubic, 1979; Knoll & Ohta, 1988; Manning-Berg et al., 2018, 2019; Manning-Berg & Kah, 2017; Mossman, 2001; Mossman et al., 2005; Muir, 1976; Oehler, 1976, 1977, 1978; Schopf, 1968; Schopf et al., 1984; Schopf & Blacic, 1971; Schopf & Kudryavtsev, 2009, 2011; Seong-Joo & Golubic, 1998; Seong-Joo & Golubic, 1999, 2000; Sergeev et al., 1995, 1997; Sergeev et al., 2007; Sergeev & Schopf, 2010; Shi et al., 2017; Stanevich et al., 2009; Turner et al., 1993; Wacey et al., 2019; Williford et al., 2013; Wilson et al., 2010; Yakshin, 1999; Yun, 1981, 1984; Zhu et al., 2016)

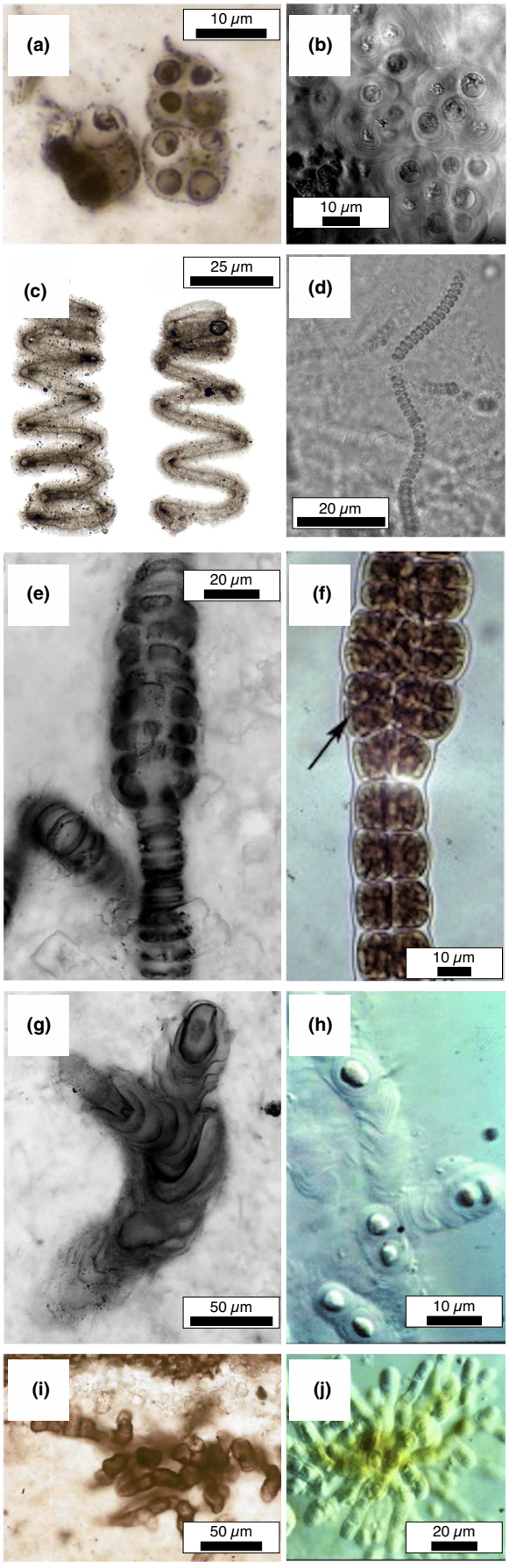

FIGURE 1 Side-by-side comparisons of some of the most diagnostic Proterozoic microbial fossils and their modern analogs. (a) *Eoentophysalis* (Butterfield, 2015), (b) Modern *Entophysalis* (see Moore et al., 2020 for culturing conditions), (c) *Obruchevella* (Butterfield, 2015), (d) Modern *Spirulina* (see Moore et al., 2020 for culturing conditions), (e) *Bangiomorpha* (Butterfield, 2000), (f) Modern red algae (Sheath & Vis, 2015), (g) *Polybessurus* (Butterfield, 2001), (h) modern stalk forming cyanobacteria (Demoulin et al., 2019), (i) *Eohyella* (Butterfield, 2015), (j) modern endolithic cyanobacteria (Demoulin et al., 2019). [Correction added on 26 October 2022, after first online publication: the figure caption related to part figure (f) was corrected in this version.]

produce thick envelopes of exopolymeric substances (EPS; Figure 2 inset) (Dupraz & Visscher, 2005; Moore et al., 2020), sunscreen-shielding pigments such as scytonemin (Gao & Garcia-Pichel, 2011; Garcia-Pichel, 1998; Garcia-Pichel et al., 1992; Garcia-Pichel & Castenholz, 1991 and references therein), osmoprotectants (Goh et al., 2009) and exhibit other adaptations. Some cyanobacteria and marine algae additionally produce sulfated extracellular polysaccharides, compounds that are thought to have protective functions against UV radiation, oxidative stress and free radicals, desiccation, and trace nutrient limitation, among other stresses (Costa et al., 2010; Jiao et al., 2011; Moore et al., 2021; Raguraman et al., 2019; Richert et al., 2005; Skoog et al., 2022).

Subtidal communities do not experience the same periods of extended subaerial exposure and desiccation that supratidal communities do. However, the permanently submerged microbes still must cope with stresses like salinity and UV radiation—though to a lesser extent than in supratidal communities—as well as physical forces such as currents, potentially rapid rates of sedimentation, and wave action [(Gebelein, 1969; Mariotti et al., 2014; Murshid et al., 2021; Neumann, 2004; Wong et al., 2015) Figure 3]. Subtidal microbes—especially cyanobacteria—also produce EPS and sheaths in response to these stresses and as a means of binding to the solid substrates (Wong et al., 2015). Given that sheaths and EPS are selectively preserved by silicification (Butterfield, 2015; Golubic & Seong-Joo, 1999; Sergeev & Sharma, 2012 and references therein), the chemical and physical properties of these polymers may have contributed to the fossilization potential of supratidal through subtidal microbial mats. If so, supra- and subtidal microfossils and organic-rich textural biosignatures in the rock record may contain information about the evolutionary continuity of microbial stress responses and their influences on the production and composition of EPS, interactions with seawater, and fossilization processes.

3 | CHERT AND SILICIFICATION

3.1 | Insights into silicification from modern environments and fossilization experiments

Microbes and microbial mats that inhabit modern supratidal to subtidal environments are analogous to some iconic Proterozoic fossil assemblages, but the modern and the ancient communities differ

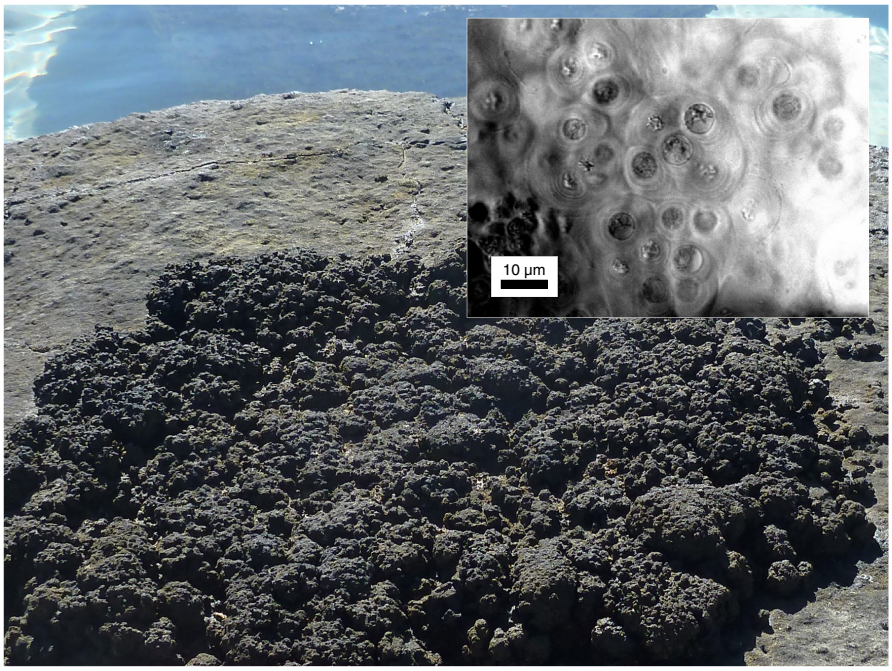

FIGURE 2 Pustular supratidal microbial mats in Shark Bay, Western Australia. A photomicrograph (inset) shows the coccoidal cyanobacteria that form pustular mats and produce concentric envelopes of EPS around cells and cell clusters (see Moore et al., 2020, and Skoog et al., 2022, for culturing conditions).

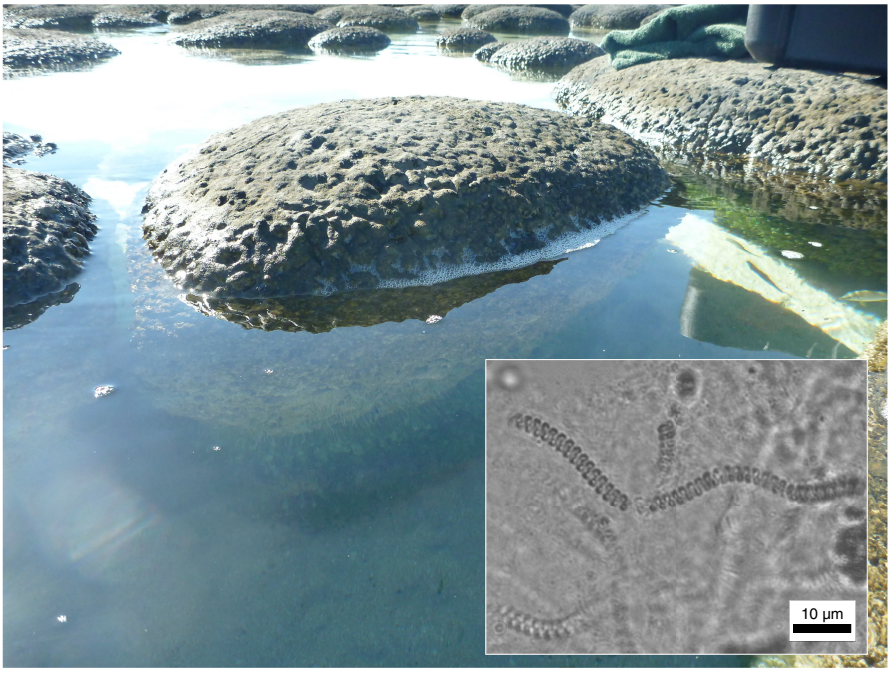

FIGURE 3 Subtidal to intertidal stromatolites in Shark Bay, Western Australia with photomicrograph of *Spirulina* (inset), one of the cyanobacteria enriched from these stromatolites (see Moore et al., 2020 for culturing conditions).

in several key respects. One, of course, is that the organisms, communities, and their genomes have evolved over the intervening billions of years (Fournier et al., 2021). Another is seawater chemistry, which likely influenced the fossilization potentials of modern and ancient marine microbial mats. Silica in modern oceans exists in μM concentrations (Tréguer et al., 1995). In contrast, some estimates of these concentrations during the Proterozoic, before the evolution of silicifying organisms, exceed 1 mM (Conley et al., 2017; Knoll, 2008; Maliva et al., 2005; Siever, 1992), but still are below amorphous silica saturation in the absence of other cations (2 mM; Iler, 1979). This chemical difference likely contributed to the precipitation of chert in Proterozoic tidal environments and the preservation of exquisite body fossils (Manning-Berg & Kah, 2017; e.g., Figure 1), a phenomenon that does not generally occur in modern tidal environments, with rare exceptions (e.g., Kremer et al., 2012). The localized nature of the marine Proterozoic chert (e.g., Anderson et al., 2020; Barghoorn & Schopf, 1965; Butterfield, 2000, 2001; Butterfield, 2004; Butterfield et al., 1988, 1990, 1994; Campbell, 1982; Croxford et al., 1973; Donaldson & Delaney, 1975; Green et al., 1987, 1988; Hofmann, 1976; Horodyski & Donaldson, 1980, 1983; Kempe et al., 2002; Knoll, 1982; Knoll et al., 1986, 1991; Knoll et al., 2013; Knoll & Golubic, 1979; Manning-Berg et al., 2018, 2019; Muir, 1976;

Oehler, 1976, 1977, 1978; Schopf, 1968; Schopf & Kudryavtsev, 2009, 2011; 1995, 1997; Sergeev & Schopf, 2010; Stanevich et al., 2009) and the inability of amorphous silica, the precursor to chert, to precipitate abiotically at concentrations below 2 mM silica (Iler, 1979) suggest that the fossil-preserving chert may not have precipitated due to abiotic processes alone. This, and the lack of modern marine analog environments that are both supratidal and contain high concentrations of silica, suggests that different chemical and biological conditions in Proterozoic supratidal environments favored the preservation of marine organisms by silicification.

Studies of microbial-environmental interactions in modern environments and experimental taphonomy have taken steps toward elucidating how silicification of microbial cells may have occurred. Although microbial silicification is not known to occur in modern tidal environments due to low modern marine silica concentrations, it does occur in the extensively studied hydrothermal systems around the world in Iceland (Konhauser et al., 2001; Konhauser & Ferris, 1996; Konhauser & Urrutia, 1999; Schultze-Lam et al., 1995), New Zealand (Campbell et al., 2002, 2015; Jones et al., 1997, 1998, 2001, 2004, 2005; Jones & Renaut, 1996), Yellowstone National Park (Cady & Farmer, 2007; Ferris et al., 1986; Walter et al., 1972), and Chile (Gong et al., 2020; Wilmeth et al., 2021), to name just a few locations. In these environments, the high temperature of the fluid that emanates at the source of a hot spring allows for elevated concentrations of dissolved silica that exceed 2 mM. Once the fluid reaches the surface, it rapidly cools as it flows away from the source and dissolved silica becomes supersaturated and precipitates quickly out of solution, coating all surfaces. As a result, microbial mats living in and around hydrothermal systems become encased in amorphous silica and are preserved in a manner similar to the preservation of Proterozoic fossils in chert [(Schultze-Lam et al., 1995; Konhauser et al., 2001; Yee et al., 2003) Figure 4a]. The precipitation of silica in hot springs occurs abiotically, but some studies have suggested that the surfaces of the microbes may act as a template upon which the silica binds and precipitates, facilitating the preservation of detailed microbial cell shapes as well as the morphologies and textures of the larger-scale textures (Francis, Barghoorn, & Margulis, 1978; Gong et al., 2020; Handley et al., 2008; Jones et al., 2001; Konhauser et al., 2004; Oehler & Schopf, 1971; Schultze-Lam et al., 1995).

Laboratory experiments have elucidated the mechanisms that preserve microbial body fossils in hydrothermal and silica-saturated solutions. Some of this work has focused on cellular degradation and morphological alteration during the precipitation of silica from saturated solutions at high (Francis, Barghoorn, & Margulis, 1978; Francis, Margulis, & Barghoorn, 1978) and low (Ferris et al., 1988; Toporski et al., 2002) temperatures. These experiments revealed that the precipitation of amorphous silica around the organisms preserved the shapes of cells in spite of some alteration of cell structure and organic degradation (Ferris et al., 1988; Francis, Barghoorn, & Margulis, 1978; Francis, Margulis, & Barghoorn, 1978; Gong et al., 2020; Toporski et al., 2002). Numerous other studies have sought to address the specific roles of organic surfaces in silicification. Some have suggested that organic compounds act as a template after cell death (Ferris et al., 1988), while others demonstrated that specific types of organic surfaces, such as those that are positively charged (Konhauser et al., 2004; Lalonde et al., 2005; Urrutia & Beveridge, 1993, 1994) or those made by specific organisms (Francis, Barghoorn, & Margulis, 1978; Francis, Margulis, & Barghoorn, 1978; Lalonde et al., 2005; Orange et al., 2009; Phoenix et al., 2000; Urrutia & Beveridge, 1993, 1994; Westall, 1995; Yee et al., 2003), are better or worse templates for the precipitation of silica. The increased production of EPS was also suggested as a major driving force behind silica precipitation (Benning et al., 2004). Many of these experimental and environmental studies highlighted the role of metals such as iron in the silicification process, suggesting that iron acts as a cation bridge that enables silica accumulation and precipitation around microbial cells in freshwater environments (Ferris et al., 1986; Konhauser & Ferris, 1996; Urrutia & Beveridge, 1994). However, Proterozoic cyanobacterial fossils lived in oxygenated marine surface environments that, with the exception of Gunflint biota

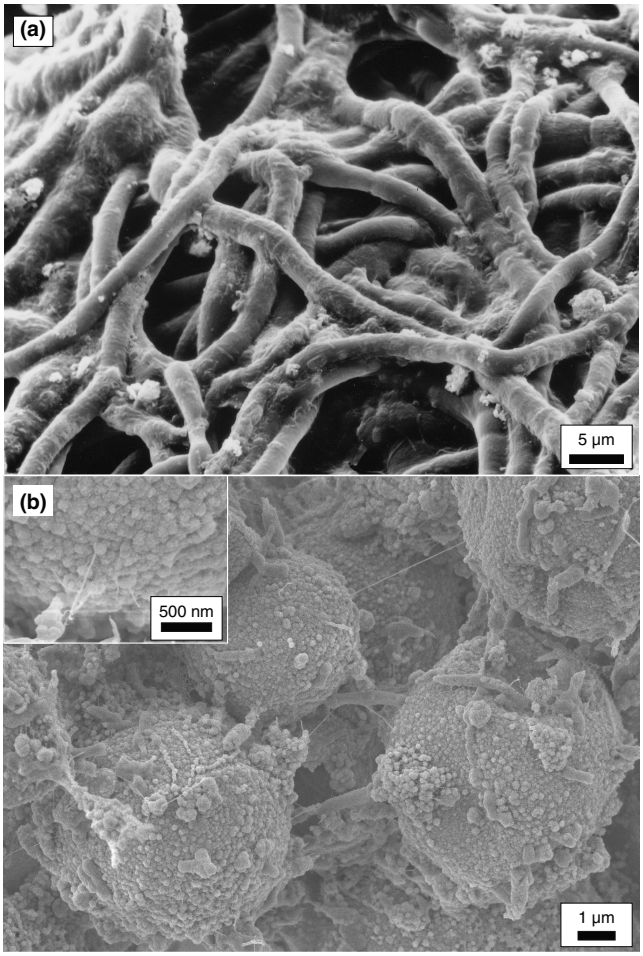

FIGURE 4 SEM images showing modern examples of microbial silicification. (a) Filamentous cyanobacteria coated in silica that were experimentally silicified under supersaturated conditions (see Phoenix et al., 2000, for experimental conditions). (b) Coccoidal cyanobacteria that were experimentally silicified in artificial seawater with 1.5 mM silica (see Moore et al., 2020, for experimental conditions). The inset shows nanoscopic colloidal silica coating cell surfaces.

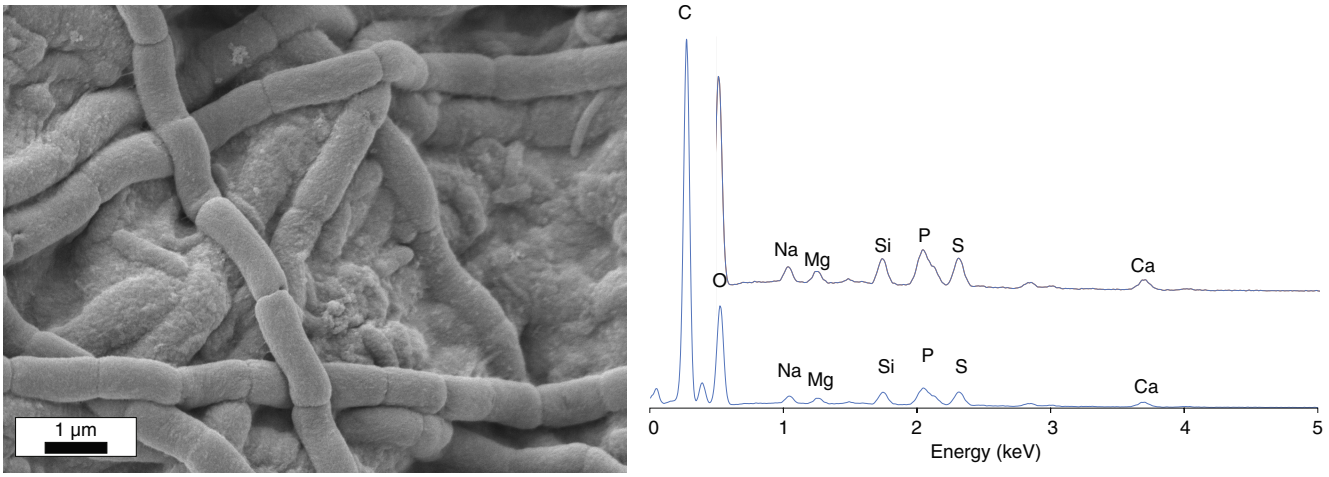

FIGURE 5 Experimentally silicified filamentous cyanobacteria. SEM image shows the silicified microbial mat (left). The corresponding EDS spectra (right) show elevated magnesium, calcium, and silica in these mats (see Moore et al., 2020; Morgenstein, 2020 for experimental conditions).

discussed in Section 3.3, are not noted to contain abundant iron. Thus, the iron cation likely did not have a large role in silicification in most Proterozoic carbonate-hosted chert deposits.

Although these studies demonstrated interactions between organic surfaces and silica, many of the experiments explored concentrations of silica that are higher than what is estimated for Proterozoic tidal environments (e.g., Benning et al., 2004; Ferris et al., 1988; Francis, Barghoorn, & Margulis, 1978; Francis, Margulis, & Barghoorn, 1978; Toporski et al., 2002). Moreover, the environmental studies are situated in very specific, localized, volcanic environments that are relatively uncommon (e.g., Cady & Farmer, 2007; Campbell et al., 2002, 2015; Ferris et al., 1986; Gong et al., 2020; Jones et al., 1997, 1998, 2001, 2004, 2005; Jones & Renaut, 1996; Konhauser et al., 2001; Konhauser & Ferris, 1996; Konhauser & Urrutia, 1999; Schultze-Lam et al., 1995; Walter et al., 1972; Wilmeth et al., 2021). Thus, none are direct analogs for Proterozoic marine carbonate-hosted fossiliferous chert (Jones et al., 2004). The modern large, laterally extensive chert deposits differ in scale, texture, and formation mechanism from the nodules, lenses, and layers of fossiliferous chert that punctuate Proterozoic carbonate deposits from tidal environments (e.g., Anderson et al., 2020; Barghoorn & Schopf, 1965; Butterfield, 2000, 2001; Butterfield, 2004; Butterfield et al., 1988, 1990, 1994; Campbell, 1982; Croxford et al., 1973; Donaldson & Delaney, 1975; Green et al., 1987, 1988; Hofmann, 1976; Horodyski & Donaldson, 1980, 1983; Kempe et al., 2002; Knoll, 1982; Knoll et al., 1986, 1991; Knoll et al., 2013; Knoll & Golubic, 1979; Manning-Berg et al., 2018, 2019; Muir, 1976; Oehler, 1976, 1977, 1978; Schopf, 1968; Schopf & Kudryavtsev, 2009, 2011; 1995, 1997; Sergeev & Schopf, 2010; Stanevich et al., 2009). This underscores the need to explain the more localized precipitation of silica as nodules and lenses in tidal environments, where silica concentrations were likely below 2 mM as evidenced by the lack of large-scale, laterally extensive chert deposits that might be expected from consistently supersaturated waters like those in hydrothermal systems.

Experimental studies that use modern analog organisms provide a means of reconstructing Proterozoic marine conditions to examine the precipitation of chert and fossilization therein. Recent work by Moore et al. (2020) demonstrated that pustular mat-forming cyanobacteria from Shark Bay that are analogous to the oldest diagnostic cyanobacterial fossil, *Eoentophysalis*, can mediate the precipitation of magnesium-rich silica (Figure 4b). These modern organisms grow in environments in which they experience hypersaline waters, periodic desiccation, and high fluxes of UV radiation. In response to these environmental stresses, they produce concentric envelopes of EPS that are very similar to those of their fossil analogs (Golubic & Hofmann, 1976). Experiments in seawater that is undersaturated with respect to silica (<2 mM) at room temperature and pressure (Moore et al., 2020, 2021; Urrutia & Beveridge, 1993, 1994) as well as experiments that used elevated silica concentrations (Benning et al., 2004; Francis, Barghoorn, & Margulis, 1978; Francis, Margulis, & Barghoorn, 1978; Orange et al., 2009; Slagter et al., 2021, 2022; Toporski et al., 2002; Westall, 1995) identified the EPS as the loci of mineral nucleation (Figure 4b). Some studies specifically demonstrated precipitation of amorphous silica through magnesium-dependent cation bridging and noted that silica precipitation required growing and photosynthesizing microbial mats (Moore et al., 2020, 2021). Collectively, these studies suggest that microbes and microbially produced organic compounds can mediate the precipitation of silica even at low silica concentrations and highlight the importance of metabolically induced pH changes, photosynthetic activity, and cations in silicification.

Reports of magnesium-rich colloidal silica precipitates in modern biofilms from Qatar (Bontognali et al., 2010; Gérard et al., 2018; Perri et al., 2018) and in hypersaline or alkaline lakes (Bischoff et al., 2020; Souza-Egipsy et al., 2005) further suggest a potential role of magnesium and other cations in the precipitation of amorphous silica in hypersaline environments. Some cyanobacteria—including *Spirulina* and other filamentous cyanobacteria that form

tufts in Shark Bay—produce EPS that contain calcium and promote the precipitation of amorphous silica rich in both magnesium and calcium in the same solutions where marine coccoidal cyanobacteria bind magnesium and precipitate Mg-rich silica (Figure 5). Other cyanobacteria can promote the precipitation of aluminum-rich silica phases in seawater that contains 0.4–1 mM silica and sedimentary sources of aluminum (Newman et al., 2016) and in active steam vents of Kilauea Volcano, Hawaii (Konhauser et al., 2002). In contrast, the EPS of *Chroococcidiopsis cubana*, a freshwater cyanobacterium, does not strongly promote the binding of cations or silica (Moore et al., 2021). These experimental studies demonstrated that some organisms produce EPS that promote the precipitation of amorphous silica, whereas others do not. This EPS-mediated silicification may rely on the specific chemical makeup of the EPS, the presence of different cations in solution, and other differences in the chemical conditions to which the organisms are exposed. The inability of some organisms to bind cations and silica in their EPS suggests that the chemistry of their EPS may contribute to taphonomic biases that are introduced into the rock record (Moore et al., 2021).

The same organisms that produce thick envelopes of EPS—filamentous and coccoidal mat-forming cyanobacteria from Shark Bay, *Spirulina*, and marine algae—are the modern morphological and ecological analogs of various filamentous cyanobacteria, *Eoentophysalis*, *Obruchevella*, and *Bangiomorpha*, respectively, in the rock record (Figure 1). It is worth noting that similar environmental stresses in the Proterozoic supra- and subtidal environments where these fossils are found may also have also contributed to the production of abundant EPS by their fossil analogs. As a potentially important nucleation site for silica precipitation, these and other similar compounds may be vital to our understanding of past microbial adaptations and the role of microbial stress responses in mineral precipitation and fossil preservation. In the coming sections, we explore the fossil record of these organisms and the potential influences of environmental stresses and microbial physiology on the selective preservation of cyanobacterial fossils and textures.

3.2 | Supratidal chert in Proterozoic deposits

Proterozoic examples of organic-rich remnants of microbial mats and body fossils provide evidence for microbial colonization of supratidal environments as early as 2 Ga (Hofmann, 1976). The formations that host these supratidal biosignatures are incredibly complex, but are generally dominated by dolomite and calcite (Table 1). Desiccation cracks, teepee structures, evaporites or pseudomorphs of evaporitic minerals, or any combination of these features in these deposits indicate frequent and extended subaerial exposure and high salinity (Hofmann, 1976; Horodyski, 1980; Horodyski & Donaldson, 1983; Oehler, 1978; Seong-Joo & Golubic, 2000). Fossil tufted and pustular mats from supratidal environments differ in size and sometimes morphology from fossil mats and microbial textures in deeper facies, but are similar to the morphologies of tufted and pustular microbial mats found in modern supratidal environments like Shark Bay, Australia (Hofmann, 1976; Goh et al., 2009; Jahnert & Collins, 2012; Knoll et al., 2013; Figure 6).

In Proterozoic supratidal environments, microbial body fossils were preserved almost exclusively in chert, with some rare fossils preserved in carbonate. This chert occurs in the form of isolated patches to semi-continuous layers, but is rarely, if ever, as extensive as the surrounding carbonate [(Golubic & Seong-Joo, 1999; Hofmann, 1974, 1976; Horodyski & Donaldson, 1983; Oehler, 1978; Sergeev et al., 1995) Figure 7]. Microcrystalline silica surrounded and filled in the cells and preserved the organic cell walls or surfaces in fine detail (e.g., Oehler, 1976; Wacey et al., 2012). The remnants preserved in chert are mostly interpreted as former cellular sheaths or envelopes of the organisms [(e.g., Butterfield, 2015; Golubic & Seong-Joo, 1999; Sergeev & Sharma, 2012 and references therein) Figure 1]. The chains of the cells (trichomes) are only occasionally visible within these envelopes [e.g., Amelia Dolomite (Croxford et al., 1973; Muir, 1976), Gaoyuzhuang Formation (Yun, 1981; Schopf et al., 1984; Seong-Joo & Golubic, 1998; Seong-Joo & Golubic, 1999, 2000; Shi et al., 2017), Bil'yakh Group (Sergeev et al., 1995)]. The morphological simplicity of many of these fossils precludes a definitive interpretation of their taxonomic affinity. However, some rare exceptions have unique and distinct characteristics that are identical to those of some modern cyanobacteria.

Among fossils of organisms that occupied Proterozoic supratidal environments, some of the most diagnostic fossils belong to the colonial coccoidal cells of the pustular mat-forming *Eoentophysalis*. These fossils first appear in the rock record in the ~2 Ga Belcher Island Group [(Hofmann, 1974, 1975, 1976) Figures 1 and 6] and are reported in many younger Proterozoic deposits (Table 1). These fossils of pustular mat-forming organisms are always preserved in chert nodules and lenses within supratidal carbonate

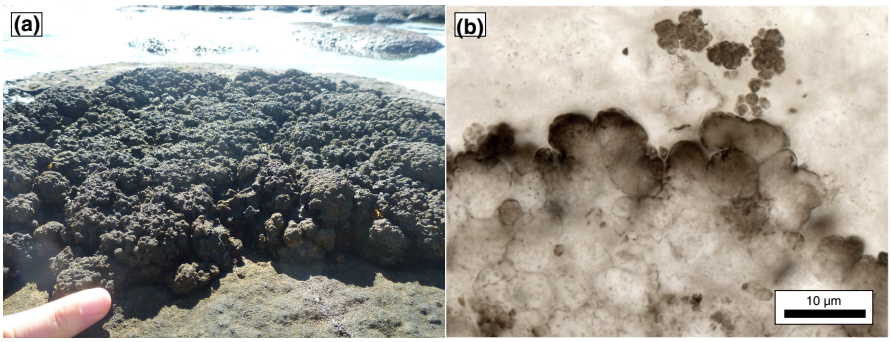

FIGURE 6 Pustular microbial mats built by coccoidal cyanobacteria in supratidal environments. (a) Modern, Shark Bay, Australia. (b) Proterozoic, Belcher Island Group, Canada (Butterfield, 2015).

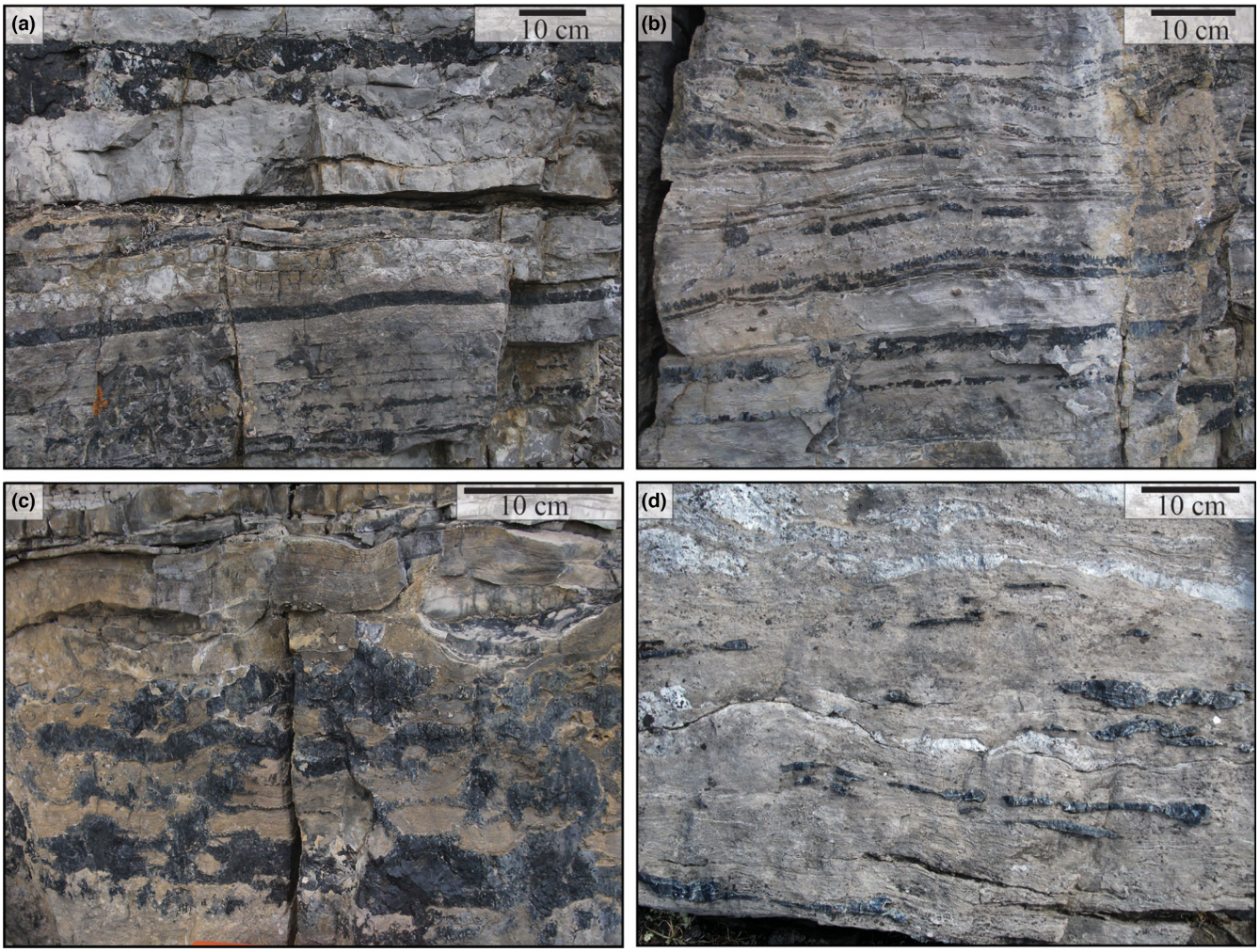

FIGURE 7 Examples of black, fossiliferous chert nodules, lenses, and layers within carbonate strata from the Proterozoic Angmaat Formation (Manning-Berg et al., 2018).

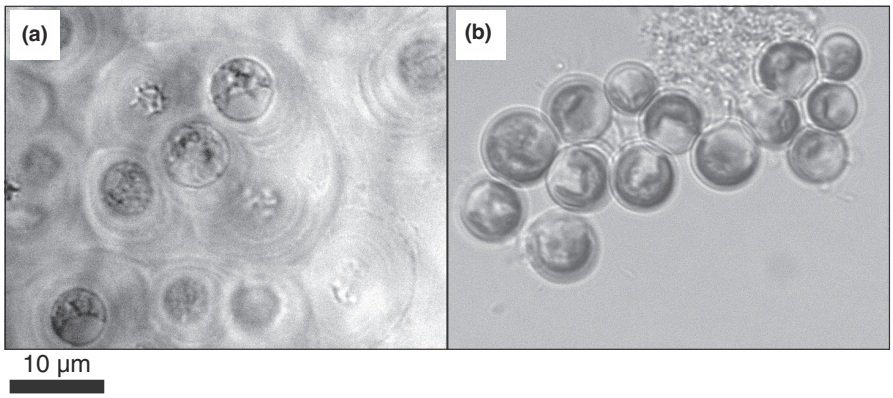

FIGURE 8 Photomicrographs of coccoidal cyanobacteria from Shark Bay, Western Australia grown at different conditions. (a) Cyanobacteria grown under the exposure to LED UV lights (400–420 nm wavelength) and a fluorescent light. (b). Cyanobacteria grown in liquid cultures under a fluorescent light. The same cyanobacteria produce thicker EPS envelopes in response to UV radiation stress (see Moore et al., 2020 for culturing conditions).

deposits (Hofmann, 1974, 1976; Horodyski & Donaldson, 1983; Knoll et al., 2013; Knoll & Golubic, 1979; Manning-Berg et al., 2018, 2019; Manning-Berg & Kah, 2017; Oehler, 1978; Seong-Joo & Golubic, 1999; Sergeev et al., 1995, 1997; Stanevich et al., 2009) or in rip-up clasts and other grains that were transported and deposited in subtidal deposits [e.g., Svanbergfjellet Formation (Butterfield et al., 1994; Eleonore Bay Group; Green et al., 1988)]. In contrast to simpler coccoidal fossils, *Eoentophysalis* mats exhibit a distinct macroscopic pustular texture that arises from the division of the cells along multiple planes and the thick, multilayered envelopes interpreted as EPS that surround cells and clusters of cells (Figure 6). Both the microscopic and macroscopic features of *Eoentophysalis* mats are

strikingly similar to those of coccoidal cyanobacteria that build the pustular microbial mats in Shark Bay, Western Australia, especially those that experience UV radiation (Figure 1).

The physiological and morphological responses of modern analogs to UV radiation and desiccation provide clues as to how *Eoentophysalis* may have lived in, adapted to, and interacted with the Proterozoic supratidal environments. In laboratory growth experiments, modern pustular mat-forming cyanobacteria produce more EPS when grown under UV stress compared to those that grow under normal ambient light conditions (Figure 8). Moreover, experimental taphonomy of these cyanobacteria reveals some of these stress responses—especially the production of EPS—as critical to early silicification (see Section 3.1; Moore et al., 2020, 2021). Given that the UV radiation, desiccation, and high salinity impacted organisms such as *Eoentophysalis* that lived in peritidal environments during the Proterozoic eon (Butterfield, 2015), the production of abundant EPS in response to these environmental stresses likely contributed to the early silicification of Proterozoic cyanobacteria in these environments.

3.3 | Subtidal silicification and a shift in organism makeup

Differences in water depth and environmental conditions can select for different cyanobacteria and microbial communities, with consequences for lithification and the preservation of biosignatures. Thus, Proterozoic subtidal biosignatures, preservation modes, and lithologies differ in some key respects from those of supratidal deposits, sometimes even within a given formation or sequence of formations (Table 1). Some stromatolitic subtidal carbonates contain nodules and lenses of fossiliferous chert similar to supratidal deposits [e.g., Franceville Group (Mossman, 2001; Mossman et al., 2005; Amard & Bertrand-Sarfati, 1997)], but more laterally extensive layers of chert within stromatolites are also present in subtidal deposits and tend to contain different fossils compared to supratidal cherts (Table 1). Some Proterozoic chert deposits are additionally unique: chert is associated with iron formations. The Gunflint Formation, for example, preserves a famous and extensively studied assemblage of diverse microfossils—the Gunflint biota (Alleon et al., 2016; Barghoorn & Tyler, 1965; Cloud & Hagen, 1965; Knoll et al., 1978; Lanier, 1989; Lepot et al., 2017; Moreau & Sharp, 2004; Tyler & Barghoorn, 1954; Wacey et al., 2012, 2013; Williford et al., 2013). However, these and other cherts associated with iron formations were deposited in iron-rich environments, and the mechanisms that underpin their formation likely differed from the typical subtidal carbonate-hosted fossiliferous cherts (e.g., Shapiro & Konhauser, 2015).

Deposits like the Duck Creek Formation (Grey & Thorne, 1985; Knoll et al., 1988; Knoll & Barghoorn, 1976; Wilson et al., 2010) demonstrate complexity in the source, type, and extent of chert. In this formation, partially silicified, fossiliferous carbonate grains are thought to have been transported from shallower environments (possibly supratidal; Knoll et al., 1988). The Scotia Group (Knoll et al., 1991; Knoll & Ohta, 1988), Draken Conglomerate (Knoll, 1982; Knoll et al., 1991), Svanbergfjellet Formation (Anderson et al., 2020; Butterfield, 2004; Butterfield et al., 1988; Butterfield et al., 1994), and Eleonore Bay Group (Campbell, 1982; Green et al., 1987; Green et al., 1988; Knoll et al., 1986) also contain chert nodules interpreted as rip-up clasts or transported grains initially formed in the supratidal zone and later transported to the subtidal realm (Butterfield et al., 1994; Green et al., 1988; Knoll, 1982; Knoll et al., 1991; Knoll & Ohta, 1988). In the Duck Creek and Svanbergfjellet formations, transported grains are surrounded by nodules and lenses of a later generation of primary or early diagenetic chert that subsequently formed and preserved a "second generation" of fossils that were preserved in place (Butterfield et al., 1994; Knoll et al., 1988). Alongside these clast-containing carbonate facies, the Duck Creek Formation, Draken Conglomerate, and Eleonore Bay Group contain stromatolitic or flat-bedded carbonates with laterally discontinuous chert layers (Butterfield et al., 1994; Green et al., 1987, 1988; Knoll et al., 1986, 1988). Chert in other subtidal carbonates may occur as bands and layers within otherwise dolomitic stromatolites or even as laterally continuous, unlaminated chert beds (Table 1). The environmental or biological reasons for this diversity in type and extent of chert development currently lack explanation. Nonetheless, one thing is consistent across these deposits: whether in nodules or laterally continuous layers, primary or early diagenetic chert rather than carbonate generally preserves the best body fossils. This difference in preservation potential of delicate microbial cells between chert and carbonate may be the results of timing of mineral formation relative to degradation (Manning-Berg et al., 2018, 2019; Manning-Berg & Kah, 2017), crystal size of the precipitates grains, mechanism of mineral precipitation, or some combination of these and other factors.

The fossils preserved in subtidal chert nodules and lenses may contain important information about the microbes that inhabited these environments and their physiological differences from microbes in supratidal communities. Many of the simple mat-forming fossil morphologies, such as filaments and cocci, can be found in both supratidal cherts and chert layers within deeper water stromatolites (Table 1). However, some studies have noted that subtidal microbial mats are dominated by filamentous fossils, whereas coccoidal organisms are more abundant in supratidal pustular and stratiform microbial mats (Knoll et al., 2013; Manning-Berg et al., 2019). This may reflect colonization of the different environments by organisms best equipped to cope with the various stresses. For example, coccoidal microbes with thick EPS envelopes are found predominantly in supratidal environments (Kah & Knoll, 1996) because they are better equipped to cope with desiccation and salinty stresses in these environments while filamentous microbes can create woven mats that are better able to withstand physical stresses caused by wave action.

Some modern environments and Proterozoic formations do not perfectly follow these trends. For example, pustular mats formed by coccoidal cyanobacteria colonize both the subtidal and the peritidal

areas in Shark Bay, Western Australia (Jahnert & Collins, 2012). The Proterozoic Sukhaya Tunguska Formation similarly contains pustular mat-forming cyanobacteria in both supratidal and subtidal deposits. The subtidal mats there contain less evidence for former pigmentation compared to those preserved in the supratidal chert based on the lighter coloration of the upper portions of the mats compared to those preserved in supratidal deposits (Sergeev et al., 1997). This may be the result of a diminished need for biologically produced UV radiation shielding by microbial pigments due to the protection afforded by the overlying water in the subtidal realm (Golubic & Hofmann, 1976). The precursors to the kerogenous material that darkens the top layers of microbial mats remain unknown, precluding a definitive interpretation for this difference in color distribution from the peritidal to the supratidal mats. This difference may reflect a difference in the amount of UV-shielding pigment produced by the microbes in supratidal and subtidal environments, but it is also possible that the organisms in subtidal environments produced less EPS or that the overall organic preservation was poorer in the subtidal mats. Experimental studies could reveal which biological compounds are produced and can be preserved under a range of conditions and whether the preservation of associations of pigments and EPS can be expected in the Proterozoic mats.

Transported grains in subtidal carbonates from the Eleonore Bay Group contain the silicified fossil *Eohyella* [(Campbell, 1982; Green et al., 1988; Knoll et al., 1986) Figure 1]. The morphology and boring patterns of these fossils are identical to modern euendolithic cyanobacteria that colonize ooids in The Bahamas (Green et al., 1988; Reid & Macintyre, 2000) and other euendolithic cyanobacteria—both filamentous and coccoidal—that colonize other marine carbonate substrates (Chacón et al., 2006; Couradeau et al., 2017; Garcia-Pichel, 2006; Roush & Garcia-Pichel, 2020; Storme et al., 2015). Like other marine cyanobacteria, many of these euendoliths produce thick EPS envelopes and EPS-filled trails (Chacón et al., 2006; Couradeau et al., 2017; Garcia-Pichel, 2006; Roush & Garcia-Pichel, 2020; Storme et al., 2015), similar to the adaptations observed in supratidal cyanobacteria which produce abundant EPS in the face of desiccation and UV radiation. Some even produce UV shielding pigments like scytonemin and gleocapsin (Storme et al., 2015). The fossils of Proterozoic endolithic cyanobacteria are preserved by silicification inside of ooids, peloids, and other carbonate grains into which the cells bored, leaving behind previously empty trails that were infilled by silica with the individual coccoidal cells preserved at the terminal end of the trails (Campbell, 1982; Green et al., 1988; Knoll et al., 1986). The silicification of these trails and the preservation of the body fossils suggest early silicification. The production of EPS in response to the common stresses of desiccation and UV radiation, similar to what is observed in supratidal pustular microbial mats, suggests that this stress response may have similarly facilitated the precipitation of early diagenetic chert and, ultimately, the preservation of these fossils.

Obruchevella, a filamentous cyanobacterial fossil, first appears in the rock record in chert concretions from the subtidal facies of the Gaoyuzhuang Formation (Shi et al., 2017). These fossils are preserved by a variety of modes in a range of lithologies, including as organic compressions in shales [e.g., the Svanbergfjellet Formation (Butterfield & Rainbird, 1998)] and by pyrite in limestones [e.g., Ikiakpuk Formation (Moore et al., 2017)]. The most exceptionally preserved specimens are often found in Proterozoic subtidal cherts including those from the Gaoyuzhuang Formation and the Scotia Group [Table 1 (Knoll & Ohta, 1988; Shi et al., 2017)]. *Obruchevella* is often preserved alongside other filamentous fossils, but is distinguished from other filaments by a helically coiled morphology analogous to modern *Spirulina* (Margheri et al., 2003). Although some other modern organisms like marine algae and other bacteria can have a generally spiraled morphology, only modern spiraled cyanobacteria like *Arthrospira* and *Spirulina* are directly analogous to *Obruchevella* (Fournier et al., 2021; Moore et al., 2017, 2019). As a cyanobacterium living in shallow marine environments, *Obruchevella* likely experienced similar UV- and salinity-related stresses to those faced by other cyanobacteria. Modern *Spirulina* are known to produce calcium spirulan (Hayashi et al., 1996; Lee et al., 1998, 2001)—a sulfated polysaccharide—in response to environmental stresses (Mendhulkar et al., 2020). The fossil counterpart—*Obruchevella*—may have also produced EPS that enabled exceptional silicification. It is also possible that these compounds acted as organic templates for microbial sulfate reduction that led to the preservation of sheaths by pyrite as observed in the Ikiakpuk Formation (Moore et al., 2017).

The subtidal deposits of the Hunting Formation contain the earliest examples of an additional ecological shift from supratidal to subtidal cherts. Alongside the carbonate and chert stromatolites that characterize subtidal facies, unlaminated chert beds in this formation preserve *Bangiomorpha pubescens*, the oldest diagnostic eukaryotic alga, and *Polybessurus*, a stalk-forming cyanobacterium (Butterfield, 2000; Butterfield, 2001; Butterfield et al., 1990). These organisms, preserved in other shallow subtidal bedded cherts in the Angmaat Formation (Knoll et al., 2013; Manning-Berg et al., 2019; Manning-Berg & Kah, 2017), the Chichkan Formation (Schopf et al., 2010; Sergeev & Schopf, 2010), the Svanbergfjellet Formation (Butterfield et al., 1994), and the Eleonore Bay Group (Green et al., 1987), shared similar life modes. Both *Polybessurus* and *Bangiomorpha* were photosynthetic organisms that anchored themselves to the carbonate substratum, grew upward to form stalk-like structures, and contained early-silicified EPS envelopes (Butterfield, 2000; Butterfield, 2001; Butterfield et al., 1990).

The nearly ubiquitous preservation of microbial sheaths or envelopes in either supratidal or subtidal cherts indicates that EPS may have aided in the nucleation and precipitation of silica. Following the initial nucleation, the more extensive chert development that is apparent in some subtidal deposits compared to the isolated nodules found in supratidal deposits suggests that amorphous silica nucleated more readily in the subtidal environments. Local stratification, increased duration of exposure to silica-rich seawater in deeper settings allowing more time for silica to polymerize and chert to precipitate, or even different surface chemistries of the microbial communities and their affinities for different cations are just some

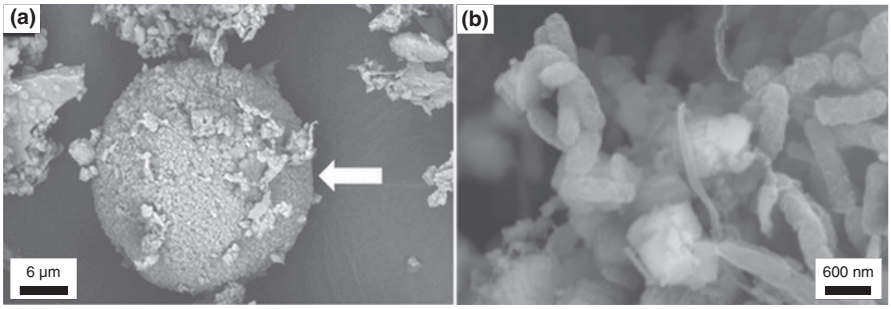

FIGURE 9 Examples of microbial-associated dolomite. (a) An environmental sample from the sabkhas of Abu Dhabi (Bontognali et al., 2010). (b) Experimentally fossilized cells encased in dolomite that nucleated on the surfaces of cells (see Daye et al., 2019 for experimental conditions).

of the factors that may have facilitated the formation of the more extensive chert.

4 | BIOSIGNATURES IN CHERT-HOSTING CARBONATE

4.1 | Carbonate precipitation in modern microbial systems

Carbonate surrounds many of the fossiliferous chert formations from Proterozoic tidal environments. Although it does not preserve cellular shapes and structures with the same detail as chert, early diagenetic microcrystalline or micritic carbonate (calcite, aragonite, or dolomite) and even carbonate precursors that have been replaced by dolomite do preserve kerogen and microbial lamination [e.g., Balbirini Dolomite (Oehler, 1978); Table 1]. As such, the spatial and temporal connections between chert and carbonate and the microbial-environmental interactions that contributed to the early diagenetic mineral precipitation deserve attention.

The precipitation of calcium carbonate in modern microbial mats has well-documented connections to microbial activity and organic compounds (Cutts et al., 2022; Dupraz et al., 2009 and references therein). Experimental studies have highlighted the contribution of metabolic activity to the alkalinity engine and carbonate precipitation (Cutts et al., 2022; Dupraz et al., 2009 and references therein). Both oxygenic photosynthesis (reaction 1; Arp et al., 2001; Dupraz & Visscher, 2005; Kranz et al., 2010; Schneider & Campion-Alsumard, 1999; Zaitseva et al., 2006) and sulfate reduction (reaction 2; Arp et al., 2003; Dupraz & Visscher, 2005; Kempe & Kazmierczak, 1994; Lith et al., 2003; Lyons et al., 1984; Visscher et al., 1998, 2000; Visscher & Stolz, 2005; Walter et al., 1993; Zavarzin, 2002) have been linked to carbonate precipitation through their influence on local alkalinity.

$$2HCO_3^- + Ca^{2+} \rightarrow CH_2O + CaCO_3 + O_2 \quad (1)$$

$$2(CH_2O) + SO_4^{2-} + Ca^{2+} \rightarrow CaCO_3 + H_2S + CO_2 + H_2O \quad (2)$$

Other studies have additionally demonstrated that EPS may play a key role in carbonate precipitation (e.g., Bosak & Newman, 2005; Braissant et al., 2003; Chekroun et al., 2004; Dupraz et al., 2004; Ercole et al., 2007; Hardikar & Matijević, 2001; Rodriguez-Navarro et al., 2007; Sprachta et al., 2001). This is in large part due to the ability of EPS to bind Ca^{2+} from solution (Arp, Reimer, & Reitner, 1999; Arp, Thiel, et al., 1999; Braissant et al., 2007, 2009; Douglas & Beveridge, 1998; Dupraz et al., 2004; Perri et al., 2018) and dictate the morphology of carbonate minerals that nucleate in EPS (Bosak & Newman, 2005). It has also been suggested that carbonate nucleates readily in the EPS in the lower portions of microbial mats where cyanobacterial cells are mostly degraded (Arp et al., 2012; Bosak & Newman, 2003; Dupraz et al., 2004; Dupraz & Visscher, 2005; Skoog et al., 2022; Sprachta et al., 2001; Suarez-Gonzalez & Reitner, 2021). Together, these studies point to a preference for calcite or aragonite precipitation in deeper layers of the modern marine microbial mats. The same may have been true in Proterozoic environments.

There is more uncertainty regarding the formation of early diagenetic dolomite that preserved biosignatures in some Proterozoic carbonate deposits because early diagenetic dolomite does not readily precipitate in modern marine environments. Studies of modern environments and experiments in which dolomite forms at low temperatures have demonstrated a clear biological contribution to this process (Bontognali et al., 2010, 2012; Daye et al., 2019; Lith et al., 2003; Vasconcelos & McKenzie, 1997) (Figure 9). In some modern hypersaline environments, such as Lagoa Vermelha and the sabkhas of Abu Dhabi, dolomite forms in microbial mats below the photosynthetic layer, primarily in the zone of extensive degradation and sulfate reduction (Bontognali et al., 2010, 2012; Lith et al., 2003; Vasconcelos et al., 1995; Vasconcelos & McKenzie, 1997) (Figure 9a). In these mat layers, cells are attached to, or surrounded by, amorphous to microcrystalline carbonate and the nucleation of dolomite is strongly dependent on the presence of organic surfaces as well as sulfate reduction (Bontognali et al., 2010, 2014). Other studies investigating the role of sulfate-reducing bacteria (Krause et al., 2012), halophilic bacteria (Sánchez-Román et al., 2008), and methanogens (Kenward et al., 2009) in dolomite formation also suggested a specific role of cell surfaces and EPS in dolomite nucleation (Kenward et al., 2013; Petrash et al., 2017; Roberts et al., 2013). Recent experimental work additionally revealed that the presence and activity of anoxygenic photosynthetic bacteria and the presence of reduced cations such as Mn^{2+} (Daye et al., 2019; DiLoreto et al., 2019) can lead to the precipitation of dolomite, which in some cases can be fine-crystalline and fabric retentive (Daye et al., 2019) (Figure 9b). More recent analyses also noted the large Mg-binding capacity of the EPS produced by pustule-forming cyanobacteria (Moore et al., 2020, 2021), inviting questions about the release of this cation and its

incorporation into incipient carbonate minerals following the initial degradation of EPS (Cutts et al., 2022; Skoog et al., 2022).

These modern experimental and environmental studies all highlight the ability of carbonate to preserve organic matter and microbial mat textures. This suggests that a common thread may relate microbial activity to early mineral formation and biosignature preservation by both carbonate minerals and silica. Both phases nucleate on organic surfaces and can preserve textural biosignatures. The nucleation of silica may require metabolically-driven pH changes and fresh cyanobacterial EPS (Moore et al., 2020, 2021), whereas anoxic conditions, degradation of EPS, and anaerobic microbial communities may favor the precipitation of dolomite and calcite. If so, the distributions of early diagenetic dolomite, calcite, and chert in time and space may reflect the compositional variations of microbial communities, surfaces, and redox conditions within a mat (Cutts et al., 2022), as well as the temporal trends in seawater Ca:Mg ratios and silica concentrations. In the following section, we review the distributions and spatial correlations of microbially laminated dolomite with fossiliferous chert in light of the potential microbial contributions to the precipitation of both minerals.

4.2 | Biosignatures in supratidal and subtidal carbonate

Whether early diagenetic dolomite, high Mg-calcite, or calcite replaced by dolomite, Proterozoic chert-hosting carbonate frequently preserved evidence of microbial colonization in the form of stratiform, pustular, and sometimes tufted microbial mats with organic-rich laminae (Table 1). In many supratidal formations, these carbonate-hosted laminae extend into the fossil-bearing cherts, where body fossils are also preserved. For example, in the Belcher Island Group and Balbirini Dolomite and some other formations (Table 1), pustular microbial lamination contains densely packed organic matter in the carbonate regions and occurs within millimeters to centimeters of the chert nodules and lenses (Figure 10) (Hofmann, 1975; Oehler, 1978). Many other formations similarly contain organic-rich, microbially laminated regions in the dolomite and other carbonates (Table 1). In the Bitter Springs Formation, several types of dense organic-rich laminations have been described. Most are hosted within chert, but dense organic lamination that exhibits a billowy texture is preserved within both fine crystalline chert and dolomite (Knoll & Golubic, 1979). Fossils are generally absent from dolomite in supratidal deposits, but some formations do contain rare and poorly preserved fossils in the dolomite alongside the chert (Oehler, 1978).

Subtidal deposits can contain a mixture of limestone and dolomite, and it has been suggested that this difference in mineralogy was related to a difference in water depth, with limestone forming in deeper water and dolomite in shallower water settings (Butterfield et al., 1994; Kah, 2000). A few subtidal and platform carbonates, such as those of the Draken Conglomerate, Bil'yakh Group, and Little Dal Formation, among others, also contain rare body fossils preserved in dolomite, dolomitized limestone, or calcite that was later replaced by chert (Aitken, 1988; Aitken & Narbonne, 1989; Bartley et al., 2000; Hofmann & Aitken, 1979; Kah & Riding, 2007; Knoll, 1982; Knoll et al., 1991; Turner et al., 1993). These fossils demonstrate the ability of primary or early diagenetic, fine-crystalline carbonate to replicate the morphology of cells and preserve organic matter, but only in rare circumstances. In most Proterozoic chert-hosting carbonate deposits, however, the only biosignatures preserved by the microcrystalline or micritic carbonate are microbial textures and kerogen. In Proterozoic tidal sequences, stromatolitic carbonates or carbonates with other microbial mat textures are typically associated with chert nodules and layers (e.g., Svanbergfjellet Formation, Balbirini Dolomite, Debengda Formation, Bil'yakh Group), and larger chert beds bounded by carbonate facies (e.g., Angmaat Formation, Hunting Formation). These subtidal carbonates can preserve the crinkly and

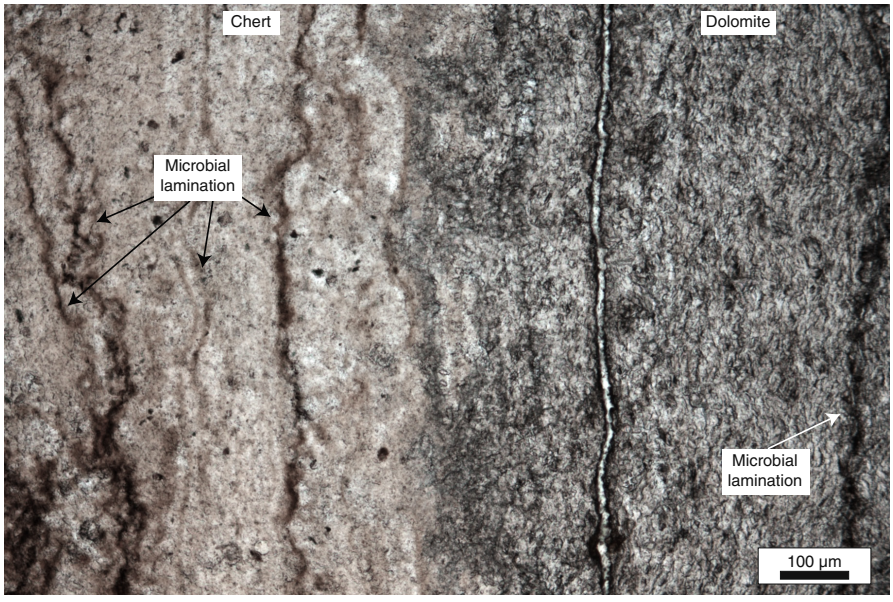

FIGURE 10 Kerogen-rich microbial lamination in dolomite-hosted chert in the Balbirini Dolomite. The chert preserves microbial body fossils, but dolomite does not.

wavy microbial lamination rich in carbonaceous inclusions, though it has been noted that the microbial lamination and organic matter in carbonates appear compressed compared to those preserved in cherts (e.g., the Balbirini Dolomite), indicating that carbonate precipitation was accompanied by more extensive organic degradation relative to chert. All of these observations are consistent with the preservation of microbial lamination rich in carbonaceous inclusions by fabric-retentive carbonate minerals, and the preservation of cyanobacterial and other diagnostic body fossils by chert.

5 | MICROBIAL MEDIATION OF DOLOMITE AND CHERT FORMATION

The close spatial association between chert- and carbonate-hosted biosignatures in Proterozoic formations suggests that microbial activity and/or organic compounds may have played key roles in the formation of both lithologies. This was likely true even in deposits that show evidence of later diagenetic alteration and remineralization. If a biosignature is preserved, the precursor lithology must have formed early enough to preserve the organic matter and body fossils and may have been influenced by the microbes themselves. It is evident from experimental and environmental studies that organic surfaces can facilitate the nucleation of dolomite, calcite, and chert. This key observation is consistent with the interpretations of microbial fossils, where EPS and sheaths are interpreted as the precursor of the carbonaceous material that was coated by silica. An abundance of evidence points to EPS as both a modern and ancient physiological adaptation to a multitude of environmental stresses (see Sections 2 and 3.1). Based on studies of modern microbe-mineral interactions and microbial fossils (Figures 4 and 5), it appears likely that the production, composition, and degradation of EPS in response to environmental stresses may also determine the preservation potential of microbial cells and mats through the interactions of certain types of EPS (Francis, Barghoorn, & Margulis, 1978; Francis, Margulis, & Barghoorn, 1978; Konhauser et al., 2004; Lalonde et al., 2005; Moore et al., 2020, 2021; Orange et al., 2009; Phoenix et al., 2000; Urrutia & Beveridge, 1993, 1994; Westall, 1995) with specific seawater cations (Moore et al., 2020, 2021), silica, and carbonate.

There are several possible explanations for the spatial and temporal relationships between chert and carbonate and the biosignatures that they contain, and it is likely that no one model explains all environments. One explanation is that chert and carbonate precipitated in different layers of microbial mats. Given that chert preserves abundant cyanobacterial fossils, this phase seems to have formed preferentially within the surficial, oxygenated layers of mats where photosynthesis occurred. This is consistent with experiments in which Mg-rich silica precipitates around living cyanobacteria that facilitate a pH increase and produce fresh, Mg-binding EPS (Moore et al., 2021). At the same time, the degradation and modification of EPS in the deeper, subtoxic to anoxic portions of microbial mats may have preferentially promoted carbonate precipitation. This would suggest that chert and carbonate precipitated more or less contemporaneous, but spatially separated by the different redox, pH, and ecological zones of the mats (Figure 11a). Alternatively, or in conjunction with these gradients, seasonal changes in water level and subsequent concentration or dilution of certain ions, changes in pH, and combinations of these factors may have driven the periodic shifts from carbonate precipitation to silica precipitation (Figure 11b).

6 | OUTLOOK

The microbial ability to mediate mineral formation in modern environments and experimental settings suggests a continuity of biosignature-preserving microbial-environmental interactions in marine environments since at least the Proterozoic Eon. Previous investigations of Proterozoic tidal carbonate deposits have focused largely on characterizing biosignatures and environmental conditions in which fossils were preserved. We demonstrate that new insights can be gained by combining in-depth analyses of microfossil assemblages, minerals that preserve them, and kerogen-associated metal cations with experimental taphonomy and studies of modern analog environments. In particular, combining these studies highlights the influence of microbial stress responses, physiology, and biochemical properties on mineral formation, element cycles, and biosignature preservation.

Numerous studies have identified EPS as a key component of mineral formation. Benthic marine environments host microbes that have many different metabolisms, respond to environmental stresses differently, and produce a range of extracellular compounds depending on chemical and physical conditions (see Section 3.1). Experiments and observations from modern environments indicate that the production of diverse surfaces, often in response to environmental stresses in benthic systems, may have enabled microbes to influence their environments by binding silica and cations. A combination of these processes and microbially mediated changes to the local pH and alkalinity may have driven elemental cycles, nucleation of chert and dolomite, and preservation of biosignatures in chert and surrounding carbonate minerals. Thus, the very stresses that led to the production of abundant EPS may have contributed to specific taphonomic windows, the selective preservation of cyanobacteria in Proterozoic peritidal-to-subtidal environments (Butterfield, 2015), and the fossil record as we know it. The combined insights from experiments and the fossil record motivate continuing studies of how diversity of microbial chemistries, lifestyles, and stress responses, as well as interactions among specific organisms and the environment can help account for the range of preservation modes and lithologies that we observe in the rock record.

Insights from experimental taphonomy and environmental studies (Bischoff et al., 2020; Bontognali et al., 2010; Gérard et al., 2018; Moore et al., 2021; Perri et al., 2018; Souza-Egipsy et al., 2005) can be combined with analyses of fossil materials to identify specific mechanisms of fossilization and microbial-environmental interactions that characterized past environments. For example, a recent

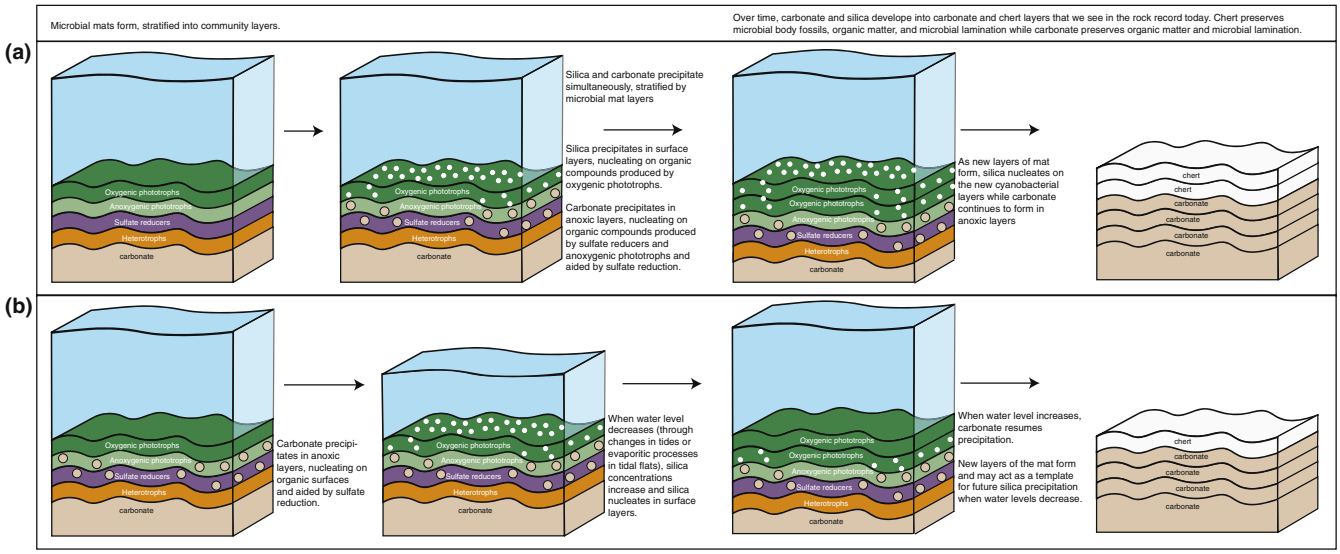

FIGURE 11 Schematics of possible formation mechanisms for biosignature-preserving chert and dolomite. Scenario shown in the top panel shows contemporaneous precipitation of silica and dolomite within a microbial mat. Dolomite forms in anoxic portions of the mat, whereas silica precipitates in surface portions of the mat around actively photosynthesizing cyanobacteria. Bottom panel depicts an alternate scenario in which dolomite precipitates in deeper portions of the mat where heterotrophic processes continuously degrade cyanobacterial cells and surface organic matter. The evaporation during the dry season concentrates silica, magnesium, and other cations and promotes the precipitation of silica in surface portions of the mats dominated by actively photosynthesizing cyanobacteria.

study of Proterozoic fossil assemblages tested the predictions of EPS- and cation-mediated silicification (Moore et al., 2021) by mapping the distribution of cations associated with organic matter in Proterozoic cherts (Moore et al., 2022). These analyses revealed that kerogen preserved in the chert is consistently enriched in Ca and Mg and embedded with cation-rich nanophases (Moore et al., 2022). Based on the findings of taphonomy experiments, these enrichments can be attributed to binding of cations in microbial EPS and the cation bridging process that mediates silica precipitation around organic matter (Bischoff et al., 2020; Bontognali et al., 2010; Gérard et al., 2018; Moore et al., 2021; Perri et al., 2018; Souza-Egipsy et al., 2005).

The combination of experimental fossilization and spatially resolved elemental and molecular analyses of ancient organic matter provides both a mechanistic understanding of organic preservation and a means of recognizing processes that enabled organic preservation in past environments. This approach provides a path toward constraining chemical conditions such as salinity, dissolved ion concentrations, and pH in Proterozoic environments from the combined records of silica and carbonate minerals. These approaches can also be combined with comparative genomic, ecological, and physiological studies that explore the evolution of different microbial surfaces, metabolisms, and stress responses through time and determine if and how these stress responses contributed to mineral forming processes, geochemical cycles, and fossilization. Through these combined approaches, we may also better understand taphonomic biases—why some organisms tend to be preserved in certain environments while others do not—and address the gaps in our knowledge of past biospheres that arise from taphonomic biases. Once we uncover the relationships between microbes and their environments, the processes that lead to mineral formation, and the mechanisms that enable preservation, we can begin to paint a more complete picture of life that colonized and shaped Proterozoic shallow marine environments, how that life influenced biogeochemical cycles of metals, silica, and carbon in benthic ecosystems, and the coevolution of these ecosystems and environments through time.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable; no new data are generated. All data are available in the publications cited throughout the manuscript as well as those cited in the figure and table captions.

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