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Citation for published version:
Mcmahon, S, Bosak, T, Grotzinger, JP, Milliken, RE, Summons, RE, Daye, M, Newman, SA, Fraeman, A, Williford, KH & Briggs, DEG 2018, 'A Field Guide to Finding Fossils on Mars', *Journal of Geophysical Research: Planets*. https://doi.org/10.1029/2017JE005478

Digital Object Identifier (DOI):
10.1029/2017JE005478

Link:
Link to publication record in Edinburgh Research Explorer

Document Version:
Publisher's PDF, also known as Version of record

Published In:
Journal of Geophysical Research: Planets

A Field Guide to Finding Fossils on Mars

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Abstract The Martian surface is cold, dry, exposed to biologically harmful radiation and apparently barren today. Nevertheless, there is clear geological evidence for warmer, wetter intervals in the past that could have supported life at or near the surface. This evidence has motivated National Aeronautics and Space Administration and European Space Agency to prioritize the search for any remains or traces of organisms from early Mars in forthcoming missions. Informed by (1) stratigraphic, mineralogical and geochemical data collected by previous and current missions, (2) Earth's fossil record, and (3) experimental studies of organic decay and preservation, we here consider whether, how, and where fossils and isotopic biosignatures could have been preserved in the depositional environments and mineralizing media thought to have been present in habitable settings on early Mars. We conclude that Noachian-Hesperian Fe-bearing clay-rich fluvio-lacustrine siliciclastic deposits, especially where enriched in silica, currently represent the most promising and best understood astropaleontological targets. Siliceous sinters would also be an excellent target, but their presence on Mars awaits confirmation. More work is needed to improve our understanding of fossil preservation in the context of other environments specific to Mars, particularly within evaporative salts and pore/fracture-filling subsurface minerals.

Plain Language Summary This paper reviews the rocks and minerals on Mars that could potentially host fossils or other signs of ancient life preserved since Mars was warmer and wetter billions of years ago. We apply recent results from the study of Earth's fossil record and fossilization processes, and from the geological exploration of Mars by rovers and orbiters, in order to select the most favoured targets for astrobiological missions to Mars. We conclude that mudstones rich in silica and iron-bearing clays currently offer the best hope of finding fossils on Mars and should be prioritized, but that several other options warrant further research. We also recommend further experimental work on how fossilization processes operate under conditions analogous to early Mars.

1. Introduction

The search for evidence of life on Mars is one of the outstanding scientific challenges of our time. Low temperatures and pressures, intense ionizing radiation, oxidizing soil chemistry, and low levels of thermodynamic water activity greatly reduce the possibility of life at the Martian surface today. However, extensive ancient valley networks and sedimentary rocks laid down in the Noachian and Hesperian Periods of Martian history (respectively, ~4.0–3.6 billion years ago [Ga] and ~3.6–3.0 Ga; Fassett & Head, 2011; Werner & Tanaka, 2011) are suggestive of much more clement global conditions, including widespread liquid water at the surface. The uncertain timing and duration of water availability are still debated and have important implications for the potential viability, complexity, distribution, and preservation potential of any life that arose on early Mars. Nevertheless, Noachian and Hesperian rocks have long been recommended as a target for fossils, that is, the physical or chemical remains of organisms and their activities (e.g., McKay & Stoker, 1989). On Earth, these remains are preserved as casts or molds in sediment, as mineral coatings or replacements, and as surviving biominerals, organic matter, or stable isotopic signatures. Locating samples on Mars that are likely to preserve such signals and studying them with appropriate instrumentation, both in situ and possibly after returning them robotically to Earth, are now strategic priorities for both NASA (National Aeronautics and Space Administration) and ESA (the European Space Agency). One of the primary objectives of NASA's Mars 2020 rover is to cache a variety of drill-core rock samples from astrobiologically promising

paleoenvironments; some of these samples may be returned to Earth by subsequent missions for analysis (Farley & Williford, 2017; Mustard et al., 2013). The ESA-Roscosmos ExoMars 2020 rover will also be equipped to test technologies required for subsequent sample-return missions (Vago et al., 2017). Understanding how, why, and where morphological, molecular, or isotopic biosignatures might have survived on Mars will significantly enhance the success of these missions by informing the selection of landing sites, rover traverse pathways, and sampling strategies.

There is no compelling evidence for life on Mars, now or in the geological past. However, there is now a very strong case that the surface of early Mars was habitable. Orbital data reveal fluvial valley networks draining thousands of square kilometers, exhumed meandering and branched distributary channels, paleolake deposits in topographic depressions, and alluvial fans/deltas entering these lakes, all of which reflect sustained precipitation and subaqueous sediment transport during the Noachian and Hesperian periods (Cabrol & Grin, 1999; Fassett & Head, 2008; Goudge et al., 2016; Grant et al., 2008; Grotzinger, Gupta, et al., 2015; Malin & Edgett, 2003; Metz et al., 2009; Moore & Howard, 2005). Some fan-shaped deposits, possibly deltaic, have been interpreted as aligned along the shoreline of a large ocean (Di Achille & Hynek, 2010; DiBiase et al., 2013) that would have covered the northern lowlands, although this is controversial. At Gale Crater, however, the Mars Science Laboratory mission (Curiosity rover) has explored the sedimentary record of a Late Noachian/Early Hesperian paleolake that persisted for thousands to millions of years, with evidence for mild salinity, moderate pH, and local redox gradients (Grotzinger et al., 2014; Grotzinger, Gupta, et al., 2015; Hurowitz et al., 2017). The presence of liquid water at the surface over this length of time implies a denser atmosphere, which should also have minimized the radiation flux. Tantalizingly, these rocks contain organic molecules (Freissinet et al., 2015) preserved under relatively reducing conditions (Grotzinger et al., 2014). Such Noachian-Hesperian water bodies could have hosted microbial life, which was present on Earth during this time interval (Grotzinger et al., 2014). There is experimental support for the long-standing idea that meteorites could have transported viable microbial cells between the two planets, although the ecological obstacles to continued growth on arrival may be considerable (Fajardo-Cavazos et al., 2005; Foucher et al., 2010; Mileikowsky et al., 2000; Shuster & Weiss, 2005; Weiss et al., 2000).

The Martian surface has been cold and predominantly dry for at least the last three billion years (i.e., the Amazonian Period, immediately following the Hesperian), but the subsurface could have sustained stable reservoirs of geothermally heated liquid water for much of this time, representing a long-lived habitat that could have exchanged living cells with shorter-lived habitats at the surface (Boston et al., 1992; Clifford et al., 2010; Ehlmann et al., 2011; Fisk & Giovannoni, 1999; Thomas et al., 2017; Travis et al., 2003). Transport from the surface would probably have been required to provide the initial inoculum or at least chemical precursors to life (e.g., Patel et al., 2015). Once established, however, a "deep biosphere" would have been protected from the deteriorating conditions at the surface and able to persist far longer given indigenous sources of energy and nutrients (Des Marais, 2010; Westall, Foucher, et al., 2015). Potentially analogous subterranean ecosystems have been studied most intensively in the Witwatersrand Basin of South Africa, where anaerobic microbial populations achieve densities of at least 10^3–10^4 cells/mL at depths of 3–4 km (Lin et al., 2006; Moser et al., 2005). Life in this setting appears to have been isolated from the surface for millions of years (Lin et al., 2006) and relies largely on abiotic carbon sources and electron donors, the latter dominated by molecular hydrogen supplied by water-rock reactions (Lin et al., 2005; Sherwood Lollar et al., 2006). There is clear evidence that such reactions occurred on Mars, including the presence of the mineral serpentine at the Martian surface and in Martian meteorites (Blamey et al., 2015; Changela & Bridges, 2011; Ehlmann et al., 2010). The putative detection of intermittent traces of methane in the Martian atmosphere—which could be a product of water-rock reactions or even of hydrogen-oxidizing microbes themselves—may imply the persistence of a habitable environment into geologically recent time (Krasnopolsky et al., 2004; Mumma et al., 2009; Webster et al., 2015).

It is thus highly likely that various Martian paleoenvironments were habitable, and plausible that they were inhabited, but could they have preserved fossils? On Earth, most organisms fail to fossilize because their remains are physically destroyed, chemically oxidized or dissolved, digested by their own enzymes, or consumed by other organisms. Fossilization only occurs when processes of preservation outpace degradation (Allison, 1988). Fossilization usually begins when organisms are buried in sediment or entombed in minerals, fixing their remains in place, and reducing their exposure to degradative processes including heterotrophic consumption (animal, fungal, or bacterial). Minerals may replicate the morphology of the buried organism,

cement the sediment around it, or fill the remaining void following decay. Microbes commonly self-fossilize by entombing themselves in the mineral byproducts of their own metabolic activity (see section 4). Organic cells and tissues are usually short lived, but they can serve as a template for the nucleation of more permanent minerals or their precursors, which in turn can stabilize the original organic matter, particularly when clay minerals form (Gabbott, 1998; Naimark, Kalinina, Shokurov, Markov, et al., 2016). Organic material can also survive when passively entombed by rapid precipitation, as in Precambrian marine cherts and Phanerozoic hydrothermal sinters (e.g., Campbell et al., 2015; Pancost et al., 2006; Schultze-Lam et al., 1995; Yee et al., 2003). Organic molecules with robust chemical backbones can be indicative of general or specific biological origins (i.e., "biomarkers" or "molecular fossils") and are common in fine-grained sedimentary rocks (Peters et al., 2005; Summons & Lincoln, 2012).

The same high-radiation and oxidizing conditions that limit the habitability of the Martian surface today would also destroy exposed organic remains. The average galactic cosmic ray dose rate measured in Gale Crater was ~0.2 mGy/day (Hassler et al., 2014); energetic particles associated with solar flares and coronal mass ejections can occasionally produce dose rates orders of magnitude higher, and the UV flux combined with strong oxidants also destroys organic matter (e.g., ten Kate et al., 2005; Wadsworth & Cockell, 2017). Although the exact nature of the early Martian climate is still uncertain, the Noachian-Early Hesperian radiation flux was attenuated by a thicker atmosphere that supported stable liquid water at the surface (Grotzinger et al., 2014; Mahaffy et al., 2015), and potentially also by an Earth-like magnetic field, although this may have been lost by the early Noachian (e.g., Lillis et al., 2013). The strong oxidants presently in Martian soil may have been less concentrated or absent in the wetter conditions and milder radiation environment, although chlorine isotope measurements by the Curiosity rover in Gale Crater suggest perchlorate production during the Hesperian (Carrier & Kounaves, 2015; Farley et al., 2016). Any organisms dwelling on early Mars would therefore presumably have been degraded primarily as a result of biological heterotrophy and enzymatic autolysis, as on Earth. Although low temperatures and a lack of burrowing or grazing animals would have inhibited decay and favored preservation, any fossil record on Mars would be biased toward robust, decay-resistant biological materials, such as biominerals/organominerals (Perry et al., 2007) or thick microbial sheaths, and toward environments that promoted preservation. Favorable circumstances for preservation would have included rapid burial, a high accumulation rate of organic remains, the presence of mineralizing fluids, and the inhibition of decay. Research on the nature, distribution, and quality of fossils representing both microsoft- and macrosoft-bodied organisms on Earth, supported by decay experiments on cells and tissues and the environmental conditions required to preserve them ("experimental taphonomy"; Briggs & McMahon, 2016), provides essential guidelines to the minerals, lithologies, and facies most likely to host microbial fossils on Mars (Table 1).

2. Potentially Fossiliferous Rocks and Minerals on Mars

2.1. Secondary Minerals in Basalt

The likelihood that the surface of Mars has been dry for the last several billion years has directed attention to the habitability of fractures and pores in deep basaltic rocks and sediments, where liquid water may have been sustained by geothermal heat (e.g., Cockell, 2014a, 2014b; Hays et al., 2017; Michalski et al., 2013). However, the potential for preserving fossils within the secondary minerals that form in such rock-hosted habitats remains unclear. Microscopic textures in basalt, ranging from simple filled or unfilled pits to elaborate helical "tunnels," are widely reported as "bio-alteration" features or microbial "trace fossils" (e.g., McLoughlin et al., 2009; Staudigel et al., 2008; Thorseth, 2011), but in most cases an abiotic origin cannot be excluded (Fisk et al., 2013). More compelling are reports of filamentous and rod-shaped structures mineralized in basalt void space on Earth by low-temperature submarine or subterranean hydrothermal activity (e.g., Cavalazzi et al., 2011; Hofmann & Farmer, 2000; Ivarsson et al., 2016; McKinley et al., 2000; Peckmann et al., 2008; Schumann et al., 2004). Such structures range from micrometer to millimeter in scale and are typically preserved three-dimensionally in clay, iron oxides, and other minerals within open- or mineral-filled vesicles and fractures. Some appear to have been mineralized in anoxic conditions (e.g., Bengtson et al., 2017; Ivarsson et al., 2016; Schumann et al., 2004). Unfortunately, it has not been demonstrated that any of these structures represent Mars-relevant chemoautotrophs. Indeed, subsurface productivity on Earth is strongly dependent on the heterotrophic remineralization of carbon originally fixed at the surface by photosynthesis (Kallmeyer et al., 2012; McMahon & Parnell, 2014). As such, the bulk of Earth's massive deep biosphere, and

Table 1
Lithofacies and Depositional Environments on Mars and Their Potential to Preserve Biosignatures

Lithofacies			Potential to preserve biosignatures				
Rock type	Paleoenvironment of deposition	Reported occurrence of this facies in Noachian and/or Hesperian terrains on Mars	Organic cells	Mineralized cells	Organic carbon	Molecular fossils	MISS
Siliciclastic sandstone/siltstone	Fluvial systems	Abundant	—	++	—	—	—
Detrital claystone		Inferred; some candidate instances (Milliken & Bish, 2010; Ehlmann et al., 2009, 2013)	+	+	++	++	—
Evaporative sulfates and chlorides	Shoreface or ephemeral lakes	Some probable instances, for example, "bathtub ring" in Terra Sirenum crater (Wray et al., 2011); Meridiani Planum sulfates are interpreted as ex situ playa salts (Grotzinger et al., 2005)	+++ (<)	—	+++ (<)	—	—
Siliciclastic sandstone/siltstone	Distal deltaic, lacustrine and marine	Abundant	—	+++	+	+	+++
Claystone of detrital origin		Abundant	++	++	+++	+++	+++
Chert or fine-grained rock with high amorphous silica content		Globally distributed silica of indeterminate origin; amorphous silica present in "silicilyte"-like rock at Gale Crater (Morris et al., 2016)	+++	+++	+++	+++	+++
Bedded or authigenic carbonates		Scarce possible instances (Ehlmann, Mustard, Murchie, et al., 2008; Michalski & Niles, 2010)	—	+	—	—	+++
Authigenic phosphate		Possible component of amorphous phase at Gale Crater (Forni et al., 2015)	+++	+++	+++	+ (<)	+ (<)
Carbonate/travertine	Calcareous springs	One disputable instance (Morris et al., 2010)	— (<)	++ (<)	— (<)	— (<)	++ (<)
Siliceous sinter	Siliceous springs	Globally distributed occurrences of silica of indeterminate origin; Gusev Crater deposit may be sinter-like (Ruff & Farmer, 2016) but it may alternatively be a fumarolic acid-leachate less favorable to habitability or preservation.	+++	+++	++	+++	+++
Sulfate veins	Groundwater 10^0–10^3 m below surface	Abundant and frequently encountered by rovers	— (X)	— (X)	— (X)	— (X)	— (X)
Authigenic clays		May be globally widespread depending on interpretation of observed phyllosilicates (Ehlmann et al., 2011, 2013)	—	—	—	—	—
Other pore- and vein-filling secondary minerals of low-temperature origin (e.g., calcite, zeolite, goethite, chalcedony, and chlorite)		No unequivocal reports but predicted by Ehlmann et al. (2011) and Michalski et al. (2013); difficult to resolve at spatial resolution of orbital data	++ (<)	++	++ (<)	+ (<)	—

Note. Potential to preserve biosignatures given the former presence of organisms is rated: — low (though not zero); + moderate; ++ high; +++ very high. Caveats are enclosed in parentheses: total absence of any reported examples of preservation from Earth's rock record is indicated by "X," absence of any reported examples older than 1 Ga is indicated by "<." MISS = microbially induced sedimentary structures.

presumably also its fossil record, is a poor analog for any ancient or modern Martian equivalent which, in the absence of a productive surface biosphere, would be much smaller and dominated by chemoautotrophs, not heterotrophs.

Lithoautotrophic communities in deep groundwaters in South Africa and the Canadian Shield are more relevant to scenarios for life on Mars (e.g., Moser et al., 2005; Onstott et al., 2009). However, these stagnant aquifers have chemically equilibrated with their mineralogical environment following long isolation from the surface (Lippmann et al., 2003; Holland et al., 2013) and are therefore unlikely to mineralize actively except during rare tectonic events (McNutt et al., 1990; Sherwood Lollar et al., 2007). To our knowledge, there are no reports of mineralized cells found at these sites nor any definitive fossil record from elsewhere of ancient microbial ecosystems analogous to these. Mineralized fractures and void spaces are difficult to resolve and interpret at the spatial scale of orbital data from Mars, and even on Earth probably do not usually yield robust indigenous biosignatures. A better understanding of the distribution, degradation, and preservation of Mars-relevant microbes in Mars-relevant subsurface environments is therefore needed before landing sites can be selected to search for a fossil deep biosphere on Mars.

2.2. Evaporite Salts

Evaporite salts, including Ca/Mg/Fe/Al-sulfates and chlorides, are widespread in basins on Mars, commonly occurring in Noachian and Hesperian-aged terrains (Ehlmann et al., 2016; Gendrin et al., 2005; Glotch et al., 2010; Murchie et al., 2009; Osterloo et al., 2008; Wray et al., 2011). In some cases, these salts are associated with paleoenvironments inferred to be playa like or lacustrine with strong potential for habitability (Ehlmann & Edwards, 2014; Grotzinger et al., 2005), although salinities may have been so high in Mg-sulfate brines as to render them uninhabitable (Knoll & Grotzinger, 2006; Tosca et al., 2008). Such evaporite minerals have the potential to trap organisms and preserve them as organic fossils which, like those in chert (see below), are readily visible in transmitted light. Gypsum-permineralized carbonaceous microfossils interpreted as algae and bacteria, the latter comparable to anaerobic nitrate-reducing sulfide oxidizers, have recently been found in Permian, Miocene, and recent evaporites (Pierre et al., 2015; Schopf et al., 2012). Calcified organic-rich microbial filaments have also been found in Miocene gypsiferous stromatolites (Allwood et al., 2013; see section 2.3 below for discussion of stromatolites). It has been suggested that fluid inclusions in halite may preserve viable microbial cells over ~100 Myr, although this is controversial because of well-founded doubts that such cells could repair DNA damage induced by natural radiation over these timescales (Fish et al., 2002; Jaakkola et al., 2016; Satterfield et al., 2005; Vreeland et al., 2000). More research needs to be done on potential controls on the presence and long-term persistence of morphological and molecular fossils in evaporites before prioritizing these minerals in landing-site selection. However, vertical and lateral patterns in sulfates and other salts in lacustrine environments can record important information about paleoenvironmental and physiochemical conditions (Bristow & Milliken, 2011). Thus, lacustrine evaporites would be a target for sampling if encountered in the course of a rover traverse, especially if associated with other evidence for habitable water chemistry.

Both Curiosity and Opportunity have also encountered sulfate veins in postburial fractures (Caswell & Milliken, 2017; Vaniman et al., 2014), representing diagenetic precipitates from briny groundwater rather than bottom-nucleated growth at the sediment-water interface, the common style of evaporitic deposition on Earth. The potential for such vein sulfates to yield biosignatures is not well understood.

2.3. Phosphate and Carbonate

Laminated and nodular phosphates, and to a lesser extent carbonates, are important sources of well-preserved fossil microbes and organic matter on Earth (e.g., Figure 1a; Knoll et al., 1993; Morais et al., 2017; Xiao et al., 2014). Unfortunately, similar deposits have not yet been identified on Mars. Small amounts of phosphorus have been detected at Gale Crater, both as igneous-sourced detrital crystalline apatite in sandstone and as a component of an amorphous/poorly crystalline phase in mudstone, which may be secondary (Forni et al., 2015; Rampe et al., 2017). Magmatic and metasomatic phosphate also occur in Martian meteorites, as do trace amounts of carbonate. Carbonate in the soil at the Phoenix landing site is considered to have formed in situ recently from CO_2 dissolved in thin water films (Boynton et al., 2009); it is absent or below detection limits at Gale Crater (Bristow et al., 2017). Climate models indicate that temperatures would have been too low under the "faint young Sun" to sustain large volumes of water on early Mars without
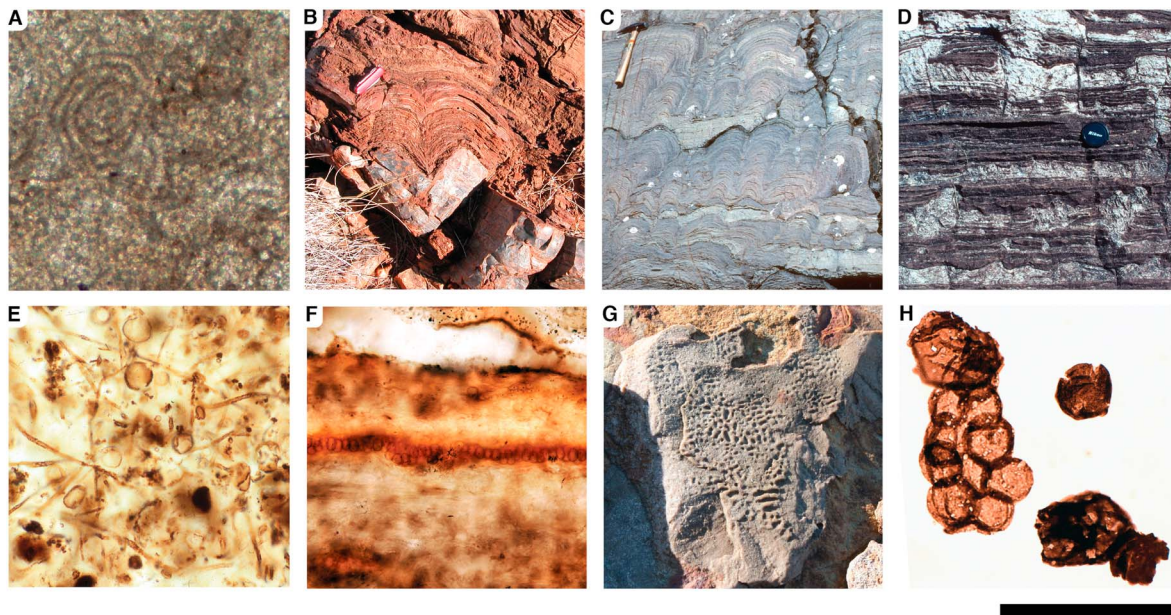
Figure 1. Terrestrial fossils that inform the search for life on Mars: (a) Calcified cyanobacterial sheaths (*Girvanella*) in limestone, upper Cambrian Campbell's Member, western Newfoundland. Image courtesy of S. Pruss, Smith College. (b) Stromatolites in chert, Archean Strelley Pool Formation, Western Australia. (c) Stromatolites in limestone, Paleoproterozoic Rocknest Formation, Wopmay Orogen, northwest Canada. (d) Stromatolites in sandstone, Neoproterozoic Witvlei Group, Namibia. (e) Filamentous and coccoidal microfossils in chert, Paleoproterozoic Gunflint Formation, Ontario, Canada. Image courtesy of A. H. Knoll, Harvard University. (f) Mat-forming colonial coccoidal cyanobacteria in chert, Neoproterozoic Min'yar Formation. (g) Wrinkle structures in siltstone draped over conglomerate, middle Cambrian March Point Formation, western Newfoundland. Image courtesy of S. Pruss, Smith College. (h) Organically preserved cyanobacteria (*Symplassosphaeridium* sp.) macerated from shale, upper Mesoproterozoic Iqqittuq Formation, Arctic Canada. Image courtesy of H. Agić, University of California, Santa Barbara. Scale bar: (a) 200 μm, (e) 75 μm, (f) 625 μm, (g) 60 mm, and (h) 120 μm. The scale of Figures 1c and 1d is indicated by a Swiss army knife, hammer, and lens cap, respectively.

abundant atmospheric CO_2, conditions that would have promoted widespread carbonate mineralization, particularly as basalt would have buffered pH (Niles et al., 2013; Wordsworth, 2016). Thus, the lack of bedded carbonate on the Martian surface is difficult to reconcile with the abundant evidence for wet conditions in the Noachian-Hesperian. The early Martian atmosphere may have been warmed by other greenhouse gases with minimal contribution from CO_2 and hence insignificant carbonate formation (e.g., Bristow et al., 2017). Alternatively, large carbonate deposits may be concealed beneath alteration assemblages, lava flows, or soil (Clark, 1999) and have yet to be discovered; indeed, isolated carbonates formerly buried to several kilometers have been detected in craters (Michalski & Niles, 2010; Wray et al., 2016). However, the origin of these carbonates is not clear, and impact metamorphism might have damaged biosignatures in such exposures.

Despite the apparent lack of bedded carbonate on Mars, carbonates formed at low temperatures (~18°C) are present in the ~4.1 Ga Martian meteorite ALH84001 (Halevy et al., 2011). In addition, carbonates of possible hydrothermal origin offer an alternative target for biosignature detection. The Mars Reconnaissance Orbiter identified magnesium carbonate associated with olivine and clays in the Nili Fossae region (Ehlmann, Mustard, Murchie, et al., 2008), and Spirit discovered carbonate-rich (16–34 wt %) outcrops (named the Comanche outcrops) of similar composition in Gusev Crater (Morris et al., 2010). These carbonates probably formed through the aqueous alteration of mafic precursors by hydrothermal activity. The evidence for hydrothermal activity in Gusev Crater may indicate a genetic similarity between the carbonates there and volcanism-related, nonmarine, Mg-rich travertines on Earth. Some young travertines yield organic biomarkers (e.g., Jorge-Villar et al., 2007) and microbial microfabrics (Riding, 1991). Submarine carbonate vent chimneys can likewise preserve molecular fossils as well as isotopic biosignatures (e.g., Brazelton et al., 2006; Lincoln et al., 2013; Méhay et al., 2013;).

Molecular, microfossil, and isotopic biosignatures in carbonates are vulnerable to damage by fluid through-flow, chemical alteration, and recrystallization over geological time. Young hydrothermal carbonates contain

cellular and molecular fossils (e.g., Zhang et al., 2004), and cellular preservation by iron and carbonate minerals has been reported from Jurassic travertines where Ostwald ripening of calcite seems to have inhibited diagenetic alteration (Potter-McIntyre et al., 2017). Precambrian travertines lack such biosignatures, which may reflect sustained alteration processes on Earth that would be less severe on Mars (Brasier et al., 2013; see section 5 below). However, these rocks do commonly contain stromatolites, that is, layered conical, domal, columnar, or branching macroscopic growth structures attached to a surface and formed by carbonate precipitation and/or the trapping and binding of sediment (Figures 1b–1d; Bosak et al., 2013; Grotzinger & Knoll, 1999; Riding, 1999). Microbes are commonly implicated in these processes, but it has long been clear that not all stromatolite-like features are necessarily biological, especially those formed by precipitation (rather than trapping and binding). This complicates the interpretation of Precambrian precipitated stromatolites and those that have undergone substantial diagenesis (Allwood et al., 2009; Grotzinger & Knoll, 1999; Grotzinger & Rothman, 1996). Triangular structures exposed perpendicular to bedding on a weathered, heavily metamorphosed carbonate in the Isua Supracrustal Belt in Greenland, for example, which were interpreted by Nutman et al. (2016) as Earth's earliest stromatolites, are morphologically ambiguous (their 3-D structure is unreported) and lack organic carbon or other evidence to confirm biogenicity.

Although microfossils are rare in carbonate stromatolites, studies of Precambrian examples and modern analogs have identified structures and morphologies with a high potential to record biological activity (e.g., Allwood et al., 2006; Beukes & Lowe, 1989; Bosak et al., 2009, 2010; Dupraz et al., 2004; Grey, 1994; Hoffman, 1976; Jones et al., 1997, 1998; Komar et al., 1965; Reid et al., 2000; Sim et al., 2012; Sumner, 1997). Only recently, however, through a combination of theory, experiment, and field observations, have we begun to understand the processes that produce robust morphological biosignatures in macroscopic stromatolite-like structures as old as three billion years (Batchelor et al., 2000; Batchelor et al., 2004; Batchelor et al., 2005; Bosak et al., 2013; Cuerno et al., 2012; Dupraz et al., 2006; Mariotti, Perron, et al., 2014, Mariotti, Pruss, et al., 2014; Petroff et al., 2010, 2013; Sim et al., 2012; Walter et al., 1976) or in microscopic textures (Bosak et al., 2009; Bosak et al., 2010; Bosak et al., 2013; Mata et al., 2012). Although most stromatolites are too small to be identified remotely, they would be readily observable by a rover on Mars and would be a prime target for astrobiological sampling. More generally, however, further research is needed to clarify the potential for biosignature preservation in carbonates similar to those so far encountered on Mars.

2.4. Hydrothermal Silica

Hydrothermal systems, both at and below the paleosurface, have long been recognized as likely habitable sites with the potential to preserve fossils (e.g., Farmer & Des Marais, 1999; McKinley et al., 2000; Walter & Des Marais, 1993). Some Noachian terrains are inferred to record mineral alteration by hydrothermal fluids that passed through the Martian upper crust prior to excavation by impact cratering (Ehlmann et al., 2009, 2011; Michalski et al., 2013). The thermal afterglow of impacts themselves can drive hydrothermal circulation in the vicinity of craters (Osinski et al., 2013), which may produce postimpact silica and sulfate veins, as well as Al-rich clays (e.g., as revealed in Endeavour Crater by the Opportunity rover; Arvidson et al., 2014). A recent global survey of crater central peaks using Mars Reconnaissance Orbiter data has shown that ~22% of those with hydrated minerals show spectral evidence for hydrated (opaline) silica associated with uplifted materials, possible impact melt deposits, and various unconsolidated materials (Sun & Milliken, 2015).

Silica dissolved and mobilized at depth stays in solution at high temperatures, but the expression of hydrothermal systems at the cool sediment-water or sediment-atmosphere interface induces rapid, massive surface precipitation. The resulting sinter deposits typically preserve microbial filaments as silicified casts, molds, and coatings, often in such density and abundance that they constitute a large fraction of the rock and determine its macroscopic texture (e.g., Cady & Farmer, 1996; Munoz-Saez et al., 2016; Trewin et al., 2003). Young examples yield a wide range of lipid biomarkers representative of hot spring organisms (e.g., Gibson et al., 2008; Kaur et al., 2008; Pancost et al., 2006). Other biosignatures can include fenestrae representing silicified bubbles of microbially generated gases (Bosak et al., 2009, 2010; Mata et al., 2012) and millimeter-scale laminated fabrics arising from the interplay of biofilms and silicifying fluids (e.g., Konhauser et al., 2004). Opaline siliceous sinter transforms to solid microcrystalline or cryptocrystalline forms (cristobalite, tridymite, and quartz, i.e., chert) during burial, which may preserve the organic remains of eukaryotes and prokaryotes at submicron resolution. The best-known example is the Devonian (~410 Ma) Rhynie Chert in Scotland, which preserves plants, animals, fungi, and bacteria entombed and permineralized with

silica (Trewin, 1993, 1996) and yields well-preserved organic biomarkers (e.g., Preston & Genge, 2010; Qu et al., 2015). Finely laminated Archean cherts containing hydrothermally silicified biofilms also preserve some organic matter, but the high metamorphic grades of these rocks (Westall, Campbell, et al., 2015) ensure that any molecular biosignatures have been erased. Curie point pyrolysis of an Archean chert from the Warrawoona Formation of the Pilbara Craton in Western Australia yielded alkane/alkene doublets with a slight odd/even preference (Derenne et al., 2008), an indisputable biosignature. However, given the metamorphic grade of rocks from the locality (Flannery et al., 2018) and the possibility of contamination from contemporary surface-dwelling microbes, results such as this should be viewed with caution. Nevertheless, cherts formed on early Mars would not have been subjected to such intense metamorphism and may retain biosignatures in contrast to similar rocks on Earth (see section 5).

Silicification of organic remains involves the bonding of silicic acid to organic cell walls or envelopes, ensuring long-term stability (e.g., Knoll, 1985). Experiments have confirmed that diverse archaeal and bacterial extremophiles and even viruses silicify readily in silica saturated solutions, with minimal dependence on cell/substrate type, pH, or salinity (Orange et al., 2009, 2013, 2014; Westall et al., 1995; Westall, 1997). Such results suggest that silicification could outpace cell lysis and degradative processes in brines on early Mars (e.g., Harrison et al., 2016; Toporski et al., 2002; Yee et al., 2003).

Besides occurring in hydrothermal settings, amorphous silica is expected to be present on Mars as a result of low-temperature chemical weathering of basalt (McLennan, 2003; Tosca et al., 2004), and orbital and in situ observations have shown it to be widespread (Milliken et al., 2008; Squyres et al., 2008; Sun & Milliken, 2015). It may be challenging to differentiate hydrothermal silica from silica enrichment by in situ weathering processes (potentially including "acid fog"; Tosca et al., 2004); such weathered rocks may be aggressively altered and are not expected to preserve biosignatures. Silica-rich deposits near the remotely observed Nili Patera caldera have been suggested to represent ancient hydrothermal systems, although not necessarily formed at the surface, based on their setting and distribution (Skok et al., 2010). Siliceous material examined by the Spirit rover in Gusev Crater has also been interpreted as a hydrothermal deposit, although other explanations of its chemical composition are possible (Squyres et al., 2008). Stratiform, "rubbly" nodules of opaline silica in Gusev Crater have been considered morphologically comparable to digitate, biologically influenced sinter nodules produced in shallow water at the El Tatio volcanic spring in Chile, which are rich in preserved microbial filaments (Ruff & Farmer, 2016). However, the simple digitate appearance of these nodules could arise from abiotic processes (aggregation, concretionary growth, sedimentation, and/or weathering) and is not in itself a biosignature or even definitive evidence of hot spring deposition (Anderson, 1930; Grotzinger & Knoll, 1999; McLoughlin et al., 2008). Nevertheless, true hot spring sinters on Mars would represent an excellent search target for silicified microfossils and organic matter from a paleoenvironment likely to have been habitable. Perhaps, the most promising location for preservation in silica identified to date on Mars occurs at Gale Crater, where a 5–10-m-thick interval of lacustrine strata in the Murray Formation is enriched in silica (see below).

2.5. Chert and Silicified Sediments

Bedded and nodular marine cherts on Earth, which are a diagenetic product of amorphous silica precipitated at or just below the seafloor, represent a major source of well-preserved microfossils, particularly of Precambrian age (e.g., Barghoorn & Tyler, 1965; Schopf, 1968; Schopf et al., 2008) when pore waters became silica saturated in the absence of silica-secreting organisms (Maliva et al., 2005; Siever, 1992). This led to rapid, early (perhaps syndepositional) silica precipitation that formed a rigid, impermeable solid material, resistant to later fluid alteration (Bartley et al., 2000; Ramseyer et al., 2013; Stolper et al., 2017). Such silica-rich rocks on Earth, especially where amorphous content is high, can result in good or even spectacular preservation of cells and colonies (Figures 1e and 1f); dozens of examples are known from the Proterozoic (Schopf & Klein, 1992), including the iconic, densely packed assemblages of filamentous and coccoidal bacteria in the Gunflint Formation (Ontario, Canada, ~1.9 Ga) and the Bitter Springs Formation (Central Australia, ~850 Ma). The Archean record is more haphazardly preserved, probably because of ubiquitous hydrothermal and metamorphic overprinting and recrystallization. Chert (including early replacive chert after carbonate) is the dominant preserving medium of most purported microfossils older than 2.5 Ga (Schopf, 2006, and references therein), although most of these are controversial (Brasier et al., 2006). Historically, however, there has been a lack of attention to siliciclastic lithologies, which have recently begun to prove fruitful (Javaux et al., 2010; Wacey et al., 2011).
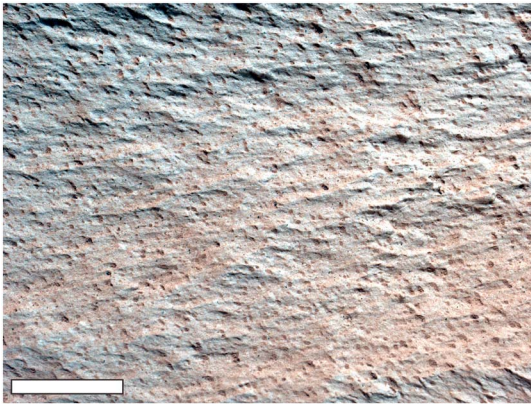
Figure 2. Photograph taken by the Curiosity rover of "Lamoose" target, a float block from the Murray Formation, Gale Crater, Mars. It is minimally dust covered (reddish tone) and sculpted by wind to reveal very fine lamination (here oriented upper left to lower right) and fine grain size. Wind-induced surface striations trend obliquely to the primary depositional lamination. Scale bar: 1 cm.

On Mars, the aqueous alteration of basaltic crust is thought to have supplied abundant silica to rivers and lakes (McLennan, 2003; McLennan & Grotzinger, 2008). As on Earth, this silica could have solidified very early, providing an ideal medium for the preservation of any microorganisms living in the water column, on the lake floor, or in shallow subsurface sediment. Opaline silica has been observed from orbit in laterally continuous, well-stratified deposits adjacent to the Valles Marineris canyon system, and in some cases these deposits occur as inverted channel systems (Milliken et al., 2008; Weitz, Milliken, et al., 2008; Weitz et al., 2010). Silica has also been observed in strata associated with potential sublacustrine fans within Melas Chasma (Metz et al., 2009) and in closed basins in the Noctis Labyrinthus region (Thollot et al., 2012).

More recently, the Curiosity rover recovered evidence for sedimentary silicification in silica-rich mudstones in the Marias Pass area of Gale Crater where the lower Murray Formation forms a thick sequence of lacustrine mudstones that interfingers and overlies fluvial-deltaic sandstones and conglomerates (Grotzinger, Gupta, et al., 2015; Morris et al., 2016; Hurowitz et al., 2017; Rampe et al., 2017). The grain size is below the limit of resolution (<60–70 μm) of the Mars Hand Lens Imager, and parallel stratification with a mean lamina thickness of about $\sim$0.5 mm extends laterally for at least several tens of centimeters (Figure 2). Quiescent subaqueous deposition is further evidenced by the absence of cross stratification, mudcracks, or any evidence for transport, erosion, or reworking. The "Buckskin" rock drilled by the Curiosity rover is characterized by $\sim$40 wt % crystalline and $\sim$60 wt % X-ray diffraction amorphous material, and a bulk composition of $\sim$74 wt % SiO_2. The crystalline silica comprises trydimite and cristobalite with a bulk rhyolite-like composition, suggesting a felsic volcanic provenance for the sediment (Morris et al., 2016). The amorphous material is silica rich, $\sim$39 wt % opal-A and/or silica glass and opal-CT, and most likely represents an authigenic lacustrine precipitate or diagenetic alteration product (Hurowitz et al., 2017; Morris et al., 2016).

Such a facies of finely laminated, fine-grained silica-rich mudstone, with substantial amorphous silica, may represent a favorable context for microfossil preservation. Early lithification would have sealed the rock (and any contained fossils) from later fluids that oxidized other parts of the Murray Formation (Hurowitz et al., 2017; Rampe et al., 2017). The presence of magnetite of probable authigenic origin in one drill hole (rather than hematite as in 14 others spread over $\sim$150 m of section) signifies a lower degree of oxidation in either the primary or diagenetic environment, or both (Grotzinger, Crisp, et al., 2015; Hurowitz et al., 2017; Morris et al., 2016; Rampe et al., 2017; Vaniman et al., 2014). Indeed, magnetite as well as some of the hematite in Gale Crater could have formed by redox-related primary precipitation, a process conducive to the preservation of cellular fossils (Fraeman et al., 2016; Hurowitz et al., 2017). Iron oxides can also adsorb silica and enhance silica precipitation, further strengthening the potential for preservation (Meister et al., 2014). The occurrence of a silica-magnetite mudstone facies in part of the Murray formation demonstrates the potential for finding similar types of sedimentary rocks in lacustrine settings elsewhere on Mars, providing a strong candidate for sample return.

2.6. Siliciclastic Sediments

Orbiter-obtained geomorphological evidence for siliciclastic facies on Mars indicates alluvial fan, fluvio-deltaic, sublacustrine fan, and aeolian deposits (e.g., Dromart et al., 2007; Malin & Edgett, 2003; Metz et al., 2009; Milliken et al., 2014; Moore & Howard, 2005). Rover observations confirmed the presence of proximal to distal fluvial, deltaic, lacustrine, and aeolian facies (Grotzinger et al., 2005; Grotzinger et al., 2014; Lewis et al., 2008; Williams et al., 2013). The organization of fluvial systems at Gale Crater shows facies transitions analogous to terrestrial "source-to-sink" networks leading to accumulation of lacustrine mudstones hundreds of meters thick (Grotzinger, Gupta, et al., 2015; Szabó et al., 2015; Fedo et al., 2017). Fluvial channel sediments represent high-energy depositional environments where the chances of preserving fossils are poor, although allochthonous biosignatures may result from reworking, transport, and sometimes concentration, for example, in fossiliferous clasts, by fluvial processes. Distal deltaic, lacustrine, shoreline and subtidal deposits, on the

other hand, could preserve a wide range of sedimentary microbialites (Figures 1d and 1g), morphological fossils (Figure 1h), and/or organic biosignatures (e.g., Ehlmann, Mustard, Fassett, et al., 2008; Summons et al., 2011; Grotzinger et al., 2014).

Siliciclastic sediments are texturally and chemically diverse and preserve fossils in a variety of modes. Fine-grained and clay-rich siliciclastic lithologies are associated with some of the best preservation of microbes and soft-bodied eukaryotes on Earth (e.g., Butterfield, 1990, 1995; Callow & Brasier, 2009; Farmer & Des Marais, 1999; Javaux & Knoll, 2017; Yuan et al., 2011), including those of Archean age (Javaux et al., 2010). The low permeability of fine-grained sediments limits diffusion away from decaying remains once they are buried and favors the precipitation of authigenic minerals such as carbonate, pyrite, and phosphate. These minerals can replicate cells and tissues and/or cement the grains around them into concretions or high-resolution molds, a process that has been studied experimentally (e.g., McCoy et al., 2015). The charged surface area of sedimentary clay minerals adsorbs and retains organic matter; the organic carbon content of marine mud and ancient shales correlates strongly with the total surface area of clay minerals within these lithologies (e.g., Hedges & Keil, 1995; Kennedy et al., 2002), particularly in sediments rich in smectite (Ransom et al., 1998). Cyanobacteria become coated with clay minerals in less than a week in experiments with sand, silt, dissolved silica, and suspended clays (Newman et al., 2016, 2017), ultimately resembling Precambrian-Cambrian fossil filaments composed of aluminosilicates (e.g., Callow & Brasier, 2009). However, the relative importance of trapping suspended clays versus clay precipitation in natural environments remains unknown, and trapping is thought to dominate (Konhauser et al., 1998; Konhauser & Urrutia, 1999; Newman et al., 2016, 2017).

The late Precambrian and early Paleozoic fossil record includes a large number of clay-hosted Konservat-Lagerstätten that preserve soft tissues as carbonaceous compressions, commonly with a secondary coating of authigenic clays that appears to track the original organic matter (Briggs, 2003). The role of preexisting clay in retarding decay appears to be more important for this style of preservation than the precipitation of early authigenic minerals (Gaines et al., 2008). Al^{3+} and Fe^{2+} ions, for example, may stabilize organic matter by promoting the crosslinking ("tanning") of proteins or inhibiting the activity of autolytic enzymes (Butterfield, 1995; Petrovich, 2001; Wilson & Butterfield, 2014). Experiments have shown that polychaetes and crustaceans buried in the aluminum-rich clay kaolinite for months-to-years are better preserved than those buried in other minerals (Wilson & Butterfield, 2014; Naimark, Kalinina, Shokurov, Boeva, et al., 2016). Clays rich in Al^{3+} and Fe^{2+} have likewise been shown to suppress the growth of various heterotrophic bacteria, including representatives of the microbial community typically involved in tissue decay, providing the first clear evidence of how clays might inhibit decay (McMahon et al., 2016; Morrison et al., 2016). Such interactions may explain why particular clay mineralogies correlate with the presence or absence of fossils in some stratigraphic sections (e.g., Anderson et al., 2014, 2018).

More generally, taphonomic factors identified as favorable for preservation in siliciclastics include reduced microbial activity in sediments, the presence of iron, the type of clay, the activity of microbes in photosynthetic mats, elevated concentrations of silica, redox gradients, and the activity of sulfate reducing microbes that ultimately produce pyrite (Darroch et al., 2012; Gehling, 1999; Laflamme et al., 2011; Naimark, Kalinina, Shokurov, Boeva, et al., 2016; Tarhan et al., 2016; Wilson & Butterfield, 2014). The effects of most of these factors need to be investigated further before we can infer their likely impact on Mars. However, our current understanding suggests that Fe/Mg-rich detrital smectites in fluvio-deltaic and lacustrine deposits in ancient lake basins on Mars provide a promising context for fossil and organic preservation, especially where Fe-rich end-members can be identified (e.g., Ehlmann, Mustard, Fassett, et al., 2008; Hurowitz et al., 2017; Milliken & Bish, 2010; Rampe et al., 2017; Vaniman et al., 2014).

Textural evidence of microbial activity occurs in siliciclastic lithologies from mudstone to sandstone and ranges from patterned textures on bedding planes ("microbially induced sedimentary structures" or "MISS"; Noffke et al., 2001) to three-dimensional stromatolites (Schieber et al., 2007). In the absence of direct evidence of biogenicity, some MISS are difficult to distinguish visually from structures formed by sediment loading, shrinkage or shearing, or by the interaction of sediment with currents, escaping pore water, or early cements (Davies et al., 2016; Schieber et al., 2007). Others can probably only form via the growth of microbial mats on sandy surfaces, which may wrinkle (Figure 1g) or crack subaqueously at scales that indicate microbial aggregation or biostabilization (Gehling & Droser, 2009; Mariotti, Perron, et al., 2014; McMahon et al., 2017).

Interactions between microbial surfaces, clay minerals, and microbial sulfide or silica at the surface of some MISS can preserve organic matter and replicate ~100-μm-scale filamentous microfossils in clay minerals or pyrite, even in relatively coarse lithologies (Callow & Brasier, 2009). MISS could be recognizable at distances of several meters and would warrant investigation if detected. However, the hypothesis that such structures may be visible in Curiosity images from the Gillespie Lake sandstone member within Gale Crater (Noffke, 2015) is not compelling. In common with Davies et al. (2018), we interpret the photographed features as erosional/fracture surfaces, not bedding planes; where dust-free bedding planes are exposed on nearby outcrops, they show no textural features attributable to microbial mats. Indeed, MISS may be difficult to recognize on Mars because exposed bedding planes tend to be effaced by aeolian weathering.

2.7. Sedimentary and Diagenetic Iron Oxides

Iron oxide minerals are widespread on Mars. Remote sensing data have shown that hematite occurs in sedimentary outcrops at Meridiani Planum, chaos terrains around Valles Marineris, and various locations associated with interior layered deposits within Valles Marineris (Bibring et al., 2007; Christensen et al., 2000, 2001; Glotch & Christensen, 2005; Glotch & Rogers, 2007; Weitz, Lane, et al., 2008; Weitz et al., 2012). Detailed orbital geologic mapping and in situ measurements at Meridiani Planum by the Opportunity rover led to a consensus view that hematite in these locations formed through secondary diagenetic processes, likely associated with regional groundwater upwelling (Chojnacki & Hynek, 2008; Le Deit et al., 2008; Lichtenberg et al., 2010; Mangold et al., 2008; Massé et al., 2008; Murchie et al., 2009; Noe Dobrea et al., 2008; Poulet et al., 2008; Roach et al., 2010; Squyres et al., 2004; Sowe et al., 2012; Wendt et al., 2011). Hematite was recently identified within the sedimentary rocks on Mount Sharp in Gale Crater by both orbital (Fraeman et al., 2013; Milliken et al., 2010) and in situ Curiosity data (Rampe et al., 2017). In contrast to other hematite-bearing localities on Mars, hematite appears to be intimately associated with primary sedimentary structures here, suggesting that it reflects pervasive secondary oxidation or authigenesis of hematite (or a ferric precursor phase) in an oxidizing lacustrine environment (Hurowitz et al., 2017). Detailed measurements by Curiosity are currently being used to test these end-member hypotheses.

Environments where hematite and other ferric iron minerals are precipitated have been considered thermodynamically inimical to organic matter preservation because of a variety of complex mechanisms known as Fenton reactions (Fenton, 1894). Fenton chemistry involves the reaction of peroxides with ferrous or ferric iron to form free radicals, which rapidly oxidize organic molecules (Pignatello et al., 2006). On this basis hematite-bearing rocks explored by the Mars Exploration Rover Opportunity in Meridiani Planum have been considered to have poor organic preservation potential (Sumner, 2004). If peroxides (Encrenaz et al., 2012) and perchlorates (Hecht et al., 2009) observed on the modern surface of Mars were similarly abundant early in the planet's history, then Fenton chemistry may have strongly limited organic preservation (and habitability) in iron-rich environments. "Photo-Fenton" chemistry resulting from strong fluxes of UV radiation in combination with peroxide, perchlorate, and hematite has been shown to be lethal to microorganisms (Wadsworth & Cockell, 2017). However, molecular and morphological microbial biosignatures preserved in association with iron minerals on Earth imply that the taphonomic influence of iron is not straightforward. Hematite can aid the preservation of sedimentary organic matter under certain circumstances (Adhikari & Yang, 2014). Evaporatively concentrated iron oxides in the acidic Rio Tinto fluvial system in Spain entomb diverse microbes at the present day and have done so for millions of years, preserving cells, molecular fossils, and microbial laminations in ferruginous siliciclastic sediments (Fernández-Remolar & Knoll, 2008; Preston et al., 2011). Modern lipid biomarkers and permineralized microbial body fossils are also preserved by iron minerals at Yellowstone hot springs (Parenteau et al., 2014; Parenteau & Cady, 2010).

Iron formations (sedimentary rocks with >15% Fe content) are abundant in Earth's rock record from ~2.5 to 4 Ga (e.g., Trendall, 2002). Although the mechanisms that formed these lithologies are debated (including the role of bacterial iron oxidation), it is widely thought that iron formations were deposited under a reducing terrestrial atmosphere that permitted the dissolution, transport, and dissemination of ferrous iron across sedimentary basins. The majority of Martian sedimentary outcrops known to yield ferric oxide do not resemble terrestrial iron formations, but several studies have theorized their presence on Mars (Bridges et al., 2008; Burns, 1993; Fallacaro & Calvin, 2006; Schaefer, 1996). The total organic carbon content of banded-iron formations on Earth is typically low compared to that of adjacent shales or carbonates (e.g., Klein & Beukes, 1989), although carbonaceous material is associated with iron minerals in well preserved banded-iron formations as

old as 3.2 Ga (Bontognali et al., 2013). Hematite coatings have been observed intimately associated with organic-walled microfossils in the ~1.9 Gunflint and Biwabik Iron Formations and attributed to postdepositional precipitation from oxidizing fluids (Alleon et al., 2016; Shapiro & Konhauser, 2015), and iron minerals have also been observed within Gunflint microfossil cell lumina (Lepot et al., 2017), demonstrating that iron mineralization does not preclude cellular preservation in kerogen on billion year timescales.

3. Preservation of Molecular Fossils and Other Organics on Mars

Organic molecules were recently detected at the parts per billion level on the Martian surface, consistent with the expectation that trace amounts (Flynn & McKay, 1990) should be present in the soil as a result of meteorite falls throughout Martian history. Nevertheless, the Martian surface is a harsh environment for the survival of organic compounds. Ionizing particles penetrate the surface and cause cascades of secondary particles (Dartnell et al., 2007; Kminek & Bada, 2006). Curiosity's Radiation Assessment Detector instrument revealed that present-day radiation flux, penetrating rock and soil, is sufficient to destroy 99.9% of 100-atomic mass unit biomolecules in the uppermost 4–5 cm within 650 million years (Hassler et al., 2014). The dose of radiation received probably does not vary greatly with lithology (Kim et al., 1998), but molecules stabilized by diagenetic processes and mineral interactions may survive for longer (as does organic matter in carbonaceous chondrite meteorites, which are irradiated in space for millions of years; Hassler et al., 2014). Measurement of cosmogenic nuclides by Mars rovers reveals the exposure age of rocks, enabling the search for organic biomarkers to be focused on the most recently uncovered materials (e.g., Farley et al., 2014). An alternative approach is to extract samples from beneath the irradiated zone; the ESA/Roscosmos ExoMars rover will carry a 2-m drill for this purpose (Vago et al., 2017). Drilling to much greater depths (~1,000 m) would be necessary to allow access to ancient permafrost water-ice unaffected by past warming events, which might contain cryopreserved biomolecules or even cells. Such an enterprise is not currently planned and would face significant engineering and planetary protection challenges (McKay et al., 2013; Smith & McKay, 2005).

UV-promoted chemical oxidation, as well as ionizing radiation, removes organic matter from Martian regolith. In an attempt to rationalize the Viking experimental findings, Benner et al. (2000) hypothesized that the chemical environment on Mars was not conducive to the preservation of organic compounds. In particular, peroxides and hydroxyl radicals were likely continuously produced on Mars via Fenton chemistry that, today, is widely used to clean up waste water. Further, these authors hypothesized that these strong oxidants would progressively attack any organic matter on the Martian surface leaving only a residue of organic acid salts including acetate, oxalate, and benzene carboxylates. Such salts would not be sufficiently volatile to be detected by the thermal desorption/pyrolysis experiments conducted by Viking and Curiosity.

The Sample Analysis at Mars instrument suite on Curiosity detected limited organic compounds via pyrolysis-gas chromatography-mass spectrometry and identified small aliphatic and aromatic organic fragments in pyrolysis-evolved gas analysis experiments (Freissinet et al., 2015; Glavin et al., 2013; Ming et al., 2014), results consistent with the survival of some macromolecular organic matter in Martian sediments, possibly residues of ancient carbonaceous meteoritic infall (Flynn & McKay, 1990). The detection of chlorinated compounds in these sediments may be a result of the reaction during pyrolysis of organic compounds indigenous to mudstone with highly oxidizing oxychlorine compounds also present in the environment (Freissinet et al., 2015; Glavin et al., 2013; Ming et al., 2014). Measurements of cosmogenic nuclides revealed that the host mudstone was exposed only 78 ± 30 million years ago (by scarp retreat) even though crater counting indicates that the sediment was deposited 4.1–3.5 Ga (Farley et al., 2014). Thus, recent exposure may account for the survival of the organics.

4. Preservation Potential of Plausible Mars Analog Microbes

The paleontological term "preservation potential" conventionally refers to the likelihood that a particular taxon, tissue type, or molecule will enter the fossil record given suitable environmental conditions; thus, the primary influence on preservation potential in this sense is the nature of the organism. Earth's macroscopic fossil record is dominated by high-preservation-potential biomineralized animal skeletons, which originated in the Neoproterozoic and rapidly diversified during the Cambrian and Ordovician Periods (Porter, 2007). However, the window of opportunity for such complex life to arise on Mars apparently closed early, and the required innovations seem improbable given that eukaryotes appear to have arisen only once on

Earth (Summons et al., 2011; Westall, Foucher, et al., 2015). Crater count-based ages for valley networks on Mars and the paucity of valleys in younger terrains suggest that the availability of surface water had diminished by middle-to-late Hesperian time (Fassett & Head, 2011), although results from the Curiosity rover show that local-scale in situ observations are necessary to ground truth such global inferences (Grotzinger et al., 2014, Grotzinger, Gupta, et al., 2015; Hurowitz et al., 2017). The period of peak water availability at the Martian surface may thus have been 1–2 billion years before the origin of eukaryotes on Earth (Dacks et al., 2016), and habitable environments on the Martian surface may have been more restricted than on Earth since that time (Ehlmann & Edwards, 2014; Grotzinger & Milliken, 2012). Moreover, the low abundance of free oxygen in the Martian atmosphere at any time in its history probably precluded the evolution of large, multicellular organisms with differentiated tissues (e.g., Erwin, 2015). For these reasons, scenarios for potential life on Mars tend to involve anaerobic microbial models (e.g., Rothschild, 1990; King, 2015; Westall, Foucher, et al., 2015). Anaerobic microbes thought to be capable of living in the conditions of early Mars include methanogens, sulfate and sulfur reducers, photosynthesizers, fermenters, iron reducers, and phototrophic or denitrifying iron oxidizers (Cockell, 2014b; Nealson & Conrad, 1999; Nixon et al., 2013). Favorable conditions for these kinds of organisms have been demonstrated for mudstones deposited in the lacustrine environment of Gale Crater (Grotzinger et al., 2014).

The intrinsic preservation potential of microbial groups depends first on their resistance to physicochemical decay, including degradation by heterotrophic microbes, autolytic enzymes, osmotic stress, heat, and irradiation, and second on their tendency to serve as templates for the nucleation of minerals from the environment or resulting from their own cellular metabolism. Research into the preservation potential of microbial groups that could have lived on early Mars is at an early stage.

4.1. Methanogens and Sulfate-/Sulfur-Reducing Bacteria

Microbial methanogenesis and sulfate/sulfur reduction are inferred to be among the oldest metabolic strategies on Earth (e.g., Bontognali et al., 2012; Shen et al., 2009; Ueno et al., 2006), but microbes that carry out these metabolisms do not produce diagnostic morphological fossils because their cells are simple in shape and lack robust sheaths. However, these metabolisms can generate strong isotopic fractionations in minerals, organic matter, and fluids (Bontognali et al., 2012; Ueno et al., 2006; Williford et al., 2016). Microbial methane is strongly depleted in carbon-13 relative to carbon-12. This signature has been reported in Archean sedimentary organic matter (e.g., Eigenbrode & Freeman, 2006; Hayes, 1994; see Slotznick & Fischer, 2016 for a discussion of other metabolisms that could have produced this signal), in Archean basalt fluid inclusions (~3.5 Ga; Ueno et al., 2006), and in Phanerozoic carbonate generated by methane oxidation (Bristow & Grotzinger, 2013; Campbell, 2006; Peckmann & Thiel, 2004). Sulfate and sulfur reduction can also result in the formation of iron sulfide minerals that coat or replicate cells; when sulfate does not limit the rates of sulfate reduction, the resulting pyrite may be depleted in sulfur-34 relative to sulfur-32. Syntrophic consortia of sulfate-reducing bacteria and anaerobic methane oxidizing archaea have also been found to mediate the encrustation of cells with clay minerals in marine sediments (Chen et al., 2014).

4.2. Photosynthetic Bacteria

Other microbes—most importantly cyanobacteria, which use water as an electron donor—produce extracellular sheaths that are robust against degradation and also provide a favorable locus for mineral nucleation (e.g., Bartley, 1996). Although cyanobacteria-lacking sheaths also have a long fossil record, those that possess them can promote their own preservation by precipitating and trapping clay minerals (Newman et al., 2016, 2017). In environments where iron(II) is abundant, the sheaths can become coated by iron oxides when iron(II) is oxidized by photosynthetic oxygen (e.g., Parenteau & Cady, 2010). Cyanobacteria also trap and bind carbonate grains that are cemented into characteristic coarse laminae; they are the primary builders of modern stromatolites (e.g., Reid et al., 2000). The degradation of exopolymeric material in the zones of sulfate reduction also promotes the precipitation of finer, micritic laminae and cements these structures (Dupraz et al., 2009; Vasconcelos et al., 2006; Visscher et al., 2000). However, textural differences between modern stromatolites and most Archean and Proterozoic examples (Grotzinger & Knoll, 1999), differences in the seawater chemistry now and in the past (Bosak & Newman, 2003), and the late inferred timing of the evolution of cyanobacteria (e.g., Magnabosco et al., 2018) make modern marine stromatolites and microbialites imperfect analogs for structures from the early Earth or Noachian-Hesperian Mars.
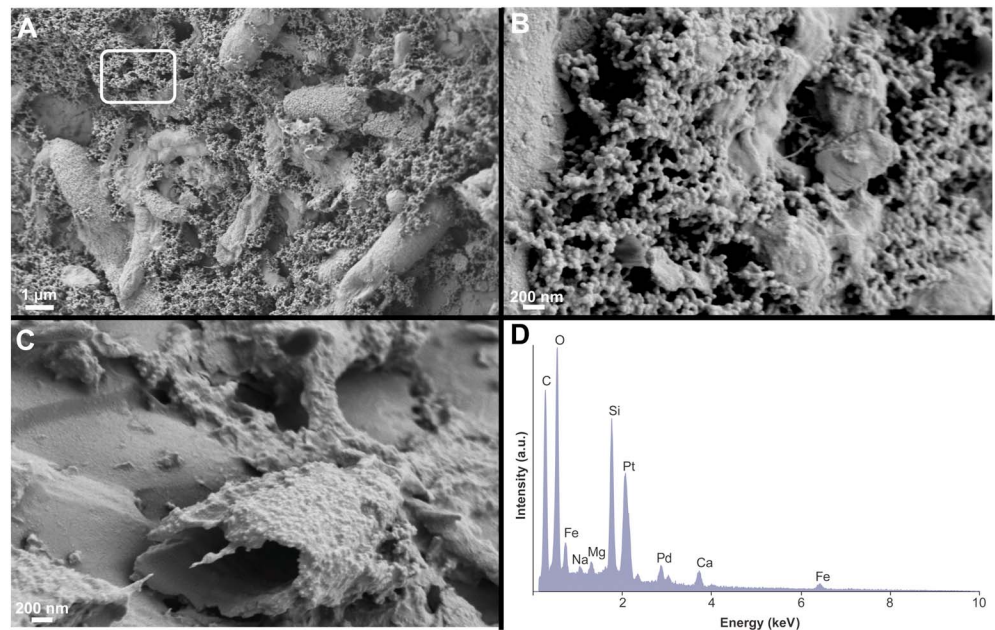
Figure 3. Scanning electron micrographs of cells and precipitates in cultures of anoxygenic photosynthetic microbes enriched from the anoxic mud of Fayetteville Green Lake, NY. The cultures were enriched in a photosynthetic minimal medium with the concentrations of major ions that matched those in Fayetteville Green Lake. The biofilms grew on quartz sand in the presence of 1 mM Fe(II) under an atmosphere of 20% CO_2 and 80% N_2 at pH 7 on a 12-h day:12-h night cycle. Green sulfur bacteria (*Chlorobium* sp.) are the main photosynthetic organisms in these cultures; other strictly anaerobic microbes such as *Geobacter*, *Acholeplasma*, and *Desulfomicrobium* sp. are also present. (a) Cells heavily encrusted by microcrystalline minerals. (b) Close-up of the nanometer-scale minerals covering surfaces of cells. (c) Remnants of a rod-shaped cell encased in minerals. (d) Energy dispersive X-ray spectrum of precipitates marked by the white rectangle in Figure 3a shows the presence of Fe, Si, Ca, and O. The dissolved silica was not added to the culture medium: the silica in the precipitates around cells was derived from the quartz sand.

Earlier photosynthesizers on Earth are thought to have used reduced sulfur, hydrogen, iron(II), hydrogen peroxide, or organic acids as electron donors (Blankenship & Hartman, 1998; Konhauser et al., 2005). Microbial communities enriched on these electron donors have been found to promote mineralization in experiments. Like cyanobacteria, anaerobic iron(II) oxidizing phototrophs can become encrusted with iron minerals (Posth et al., 2013; our Figures 3a–3c). These minerals include iron carbonate, silica, and microcrystalline iron minerals (Figure 3d), illustrating a fossilization mechanism that could occur in an anoxic environment rich in iron and silica, potentially characteristic of early Mars. Similar experimental cultures enriched on hydrogen or methane develop micrometer-thick mineral layers comprising 10-nanometer-sized particles after 1–4 months (Figures 4a–4c). These precipitates include calcite, dolomite, and minor amounts of clay minerals (Figure 4d).

More generally, although anoxygenic photosynthetic microbes lack thick cyanobacterial-like sheaths, they can form cohesive, sturdy microbial mats replete with extracellular polymeric substances that trap sediment grains and stabilize sediments (Bosak et al., 2013). The interaction of anoxygenic photosynthetic communities with sediments and flowing water can therefore be expected to produce different morphological signals at the sediment-water interface. The precipitation of authigenic clays and iron minerals within anoxygenic photosynthetic communities requires more investigation in experiments and also hints at favorable conditions for fossilization.

4.3. Other Iron Oxidizers

Other iron oxidizers can thrive in diverse settings where Fe^{2+} is brought into contact with electron acceptors (including O_2, NO_3^-, ClO_3^-, and ClO_4^-). This metabolism fuels chemosynthesis by bacteria that form distinctive, mineralized tubular sheaths and twisted or branching stalks of iron oxyhydroxides within centimeter-thick mats (Chan et al., 2009, 2011; Edwards et al., 2004, 2011; Emerson et al., 2010). This bacterial iron
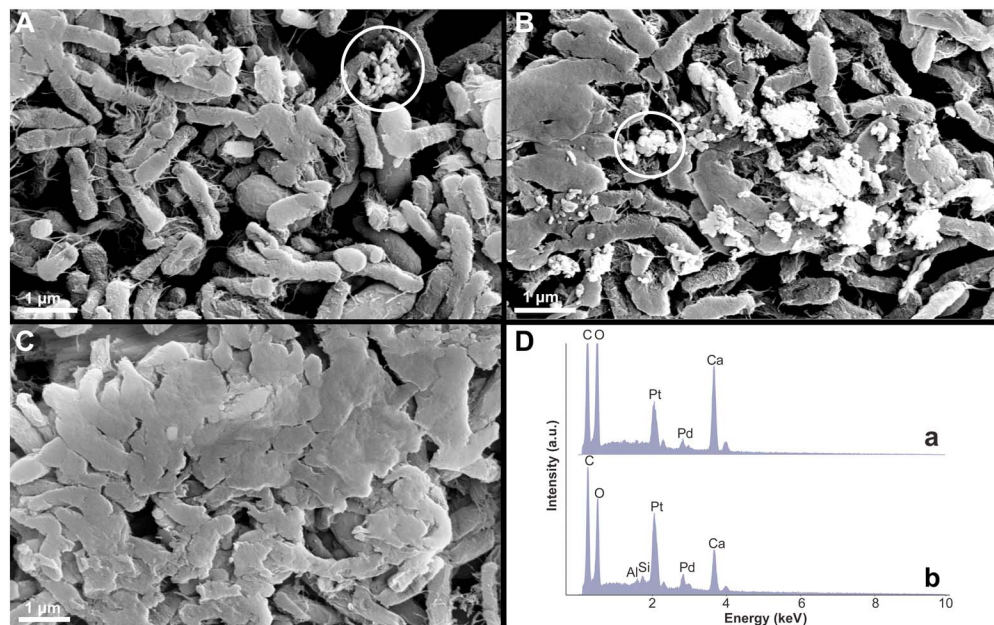
Figure 4. Scanning electron micrographs of photosynthetic cultures enriched from the anoxic mud of Fayetteville Green Lake, NY in the presence of methane (CH_4) and hydrogen (H_2). The cultures were enriched and grown on aragonite sand in a photosynthetic minimal medium with concentrations of major ions that matched those in Fayetteville Green Lake. The medium was reduced by 50-mM Na_2S. All cultures were grown at pH 7, on a 12-h day:12-h night cycle. Cultures enriched in the presence of H_2 were grown under an atmosphere of 5% H_2, 15% CO_2, and 80% N_2, those enriched on CH_4 were grown under an atmosphere of 5% CH_4, 15% CO_2, and 80% N_2. The cultures contain anoxygenic photosynthetic microbes; cultures enriched on hydrogen also produce methane. (a) One-month old culture enriched on CH_4. (b) One-month old culture enriched on H_2. (c) Four-month-old H_2 culture. (d) Energy Dispersive X-ray Spectroscopy spectrum (a) of the precipitates marked by the circle in Figure 4a. The cultures were grown in the absence of added clay minerals, but the Energy Dispersive X-ray Spectroscopy spectrum (b) of the area marked by the circle in Figure 4b and X-ray diffraction analyses suggests that clay minerals form in these cultures.

oxyhydroxide transforms into hematite during diagenesis, and well-preserved examples have been described from hydrothermal jaspers ranging in age from Ordovician to Cretaceous (Little et al., 1999; Little et al., 2004; Little & Thorseth, 2002). Probable iron oxidizing organisms are represented by hematite microfossils in rocks at least as old as 1.74 Ga (Little & Thorseth, 2002; Slack et al., 2007). The bacteria-like microfossils of the ~1.9 Ga Gunflint Iron Formation are preserved on a compositional spectrum from organic carbon to hematite, but it is debated whether the iron oxide represents an original metabolic product or later diagenetic replacement (Planavsky et al., 2009; Shapiro & Konhauser, 2015; Lepot et al., 2017). Hematite microstructures in the Archean Nuvvagittuq Supracrustal Belt in Canada, constrained to 4.3–3.8 Ga, have been interpreted as autofossilized iron oxidizers and thus as the oldest known microfossils (Dodd et al., 2017). Their simple tubular morphology and parallel arrangement, however, are compatible with abiotic alternatives (e.g., Garcia-Ruiz et al., 2003, 2009; Wacey et al., 2018), and a lack of information about field relationships undermines the reported age and biogenicity. Furthermore, the carbon isotopic data provided by Dodd et al. (2017) in support of claims for biogenicity are not distinguishable from abiotic alternatives (Bottinga, 1969; van Zuilen et al., 2002).

The capacity of hydrothermal Fe-Si systems to preserve organic matter in association with inorganic elemental, mineral and morphological biosignatures is poorly understood. Also unclear is whether the organic carbon associated with these systems preserves diagnostic isotopic biosignatures. One study suggests that autotrophic iron oxidation yields organic matter that is >15‰ lower in $\delta^{13}C$ than organic compounds preserved in association with abiotic iron oxides precipitated in submarine hydrothermal settings (Kennedy et al., 2010). This signature could be preserved in organic matter associated with iron oxides and has been reported from iron-rich Jurassic concretions from a nonhydrothermal setting, which yielded $\delta^{13}C_{org}$ values of −20.55‰ (Weber et al., 2012).

Microbial oxidation of iron could have occurred on early Mars, given the abundance of reduced iron. Electron acceptors may have been limiting; plausible candidates include nitrate (Stern et al., 2015) and perchlorate (Glavin et al., 2013; Hecht et al., 2009), although the latter has not been shown convincingly to support the growth of iron oxidizers (Nixon et al., 2012). If Martian iron oxidizing microbes were preserved in a similar fashion to those on Earth, such structures might even be observable in situ by rover-mounted instruments. Unlike silica-hosted carbonaceous microfossils that commonly occur as filaments and spheroids <10 μm in diameter, microfossils preserved in iron oxide on Earth commonly exhibit textures with dimensions closer to tens to hundreds of micrometers, which is the observational scale of Mars rover-based instrumentation (Williams et al., 2015).

4.4. Iron Reducers

Microbial iron reduction has been implicated in the precipitation of authigenic clays in silica-rich deltaic sediments (Michalopoulos & Aller, 1995, 2004). Enhanced by the trapping of suspended clays, this process may also have contributed to the preservation of some unicellular Neoproterozoic eukaryotes in Fe-rich berthierine (Mus & Moczydłowska, 2000). Some iron reducers actively dissolve ferric clay minerals, liberating both iron and silica, which can generate aggregates of authigenic clay and quartz around the metabolizing cells (Metcalfe et al., 2013; Vorhies & Gaines, 2009). Future work may elucidate whether such processes could have preserved fossils on Mars.

5. Long-Term Preservation on Mars

Entry into the fossil record is no guarantee of long-term preservation; fossils can be destroyed by weathering, diagenetic alteration, and metamorphism in the deep subsurface. Heat and pressure result in the recrystallization of mineral grains and the transformation of organic compounds into kerogen and ultimately graphite. Almost all rocks on Earth of equivalent age to Noachian terrains on Mars have been recycled by Earth processes including subduction. The isolated vestiges that remain have undergone severe, and sometimes multiple, metamorphism but could contain metasedimentary graphite, highly disordered kerogens (e.g., Ohtomo et al., 2014; van Zuilen et al., 2003), or even graphitic inclusions in zircon (Bell et al., 2015). Although the C-isotopic signature of these Eoarchean carbonaceous remains is similar to some imparted by biological processes, abiotic interpretations are also consistent with the data (Bottinga, 1969; van Zuilen et al., 2003).

Mars, however, currently lacks global plate tectonics and may always have done so. A crust tens of kilometers thick and very sporadic volcanism ensure that crustal materials are recycled very slowly; sedimentary rocks older than any on Earth survive as evidence of this lack of recycling (Grotzinger & Milliken, 2012). Older Martian crust has been pervasively fractured by impacts, baked by volcanism, and/or altered by groundwater-rock reactions. The lack of tectonic subsidence, however, results in lower rates of burial, and the temperature gradient with depth is lower than that on Earth, such that metamorphism is generally less severe. The abundance of Fe-Mg smectites in Gale Crater mudstones (Rampe et al., 2017; Vaniman et al., 2014) indicates burial temperatures of less than 100°C, above which these minerals would have been diagenetically transformed. Low geothermal gradients in Martian sedimentary basins are also reflected in the long-term persistence of opaline silica (Frydenvang et al., 2017; Yen et al., 2017), which recrystallizes on Earth in a few million years in the presence of water (Tosca & Knoll, 2009). Likewise, aqueous alteration assemblages, although widespread, are chemically juvenile, indicating that interaction with aqueous fluids was limited (Tosca & Knoll, 2009), probably because of the long-term persistence of cold and dry conditions (Shuster & Weiss, 2005). Nevertheless, this process could have dissolved and reprecipitated evaporites, potentially destroying any fossils within them, and the inferred acidic composition of these fluids may have resulted in the loss of some carbonate and phosphate minerals.

Physical weathering proceeds very slowly on Mars compared to rates on Earth, as evidenced by the survival of Noachian craters, channels, and other topographic features that have been exposed since their formation. Aeolian and freeze-thaw weathering, as well as water-related dissolution and leaching of mobile elements, are prevalent but result only in surficial damage (Grotzinger et al., 2013; McLennan & Grotzinger, 2008). In general, fossiliferous lithologies from early Mars would have a good chance of surviving to the present.

6. Finding and Verifying Fossils

The search for microbial biosignatures in rocks more than a billion years old on Earth typically follows a three-step protocol. First, promising outcrops are explored at macroscopic scales to establish a stratigraphic context and identify sedimentary structures indicative of interactions between biological processes, sediment transport, and mineral precipitation. Second, these are sampled for further analysis, usually beginning with the study of petrographic thin sections (i.e., microscope slides), which may reveal candidate microbial fabrics or even preserved cells and tissues. Third, microscale and nanoscale chemical and isotopic information is acquired from candidate biosignatures in order to confirm and reconstruct the biological processes that contributed to their formation.

An important goal of such work is to exclude the possibility that putative biosignatures are either recent contaminants or abiotic phenomena that merely resemble fossils. Most prokaryotes are morphologically simple spheroids and filaments, and the interplay of abiotic mineral growth, geochemical reactions, and sediment dynamics can generate convincing pseudofossils (e.g., Grotzinger & Rothman, 1996; Garcia-Ruiz et al., 2003, 2009; Hofmann, 2004). Abiotic processes can also fractionate carbon and sulfur isotopes, and the behavior of these isotope systems in Martian environments is not yet fully understood. Robust detection of morphological, isotopic, or any other biosignatures on Mars would therefore require evidence of a paleoenvironmental context and alteration history consistent with biology and incompatible with nonbiological processes alone (Summons et al., 2011). Several authors have attempted to establish criteria for evaluating the syngenicity, antiquity, and biogenicity of putative microbial biosignatures from Mars or Archean Earth, emphasizing that similar protocols apply on both planets (e.g., Brasier & Wacey, 2012). As noted elsewhere in this review, these protocols raise critical questions about purported 3.7-Gyr-old stromatolites and 3.8-Gyr-old filamentous microfossils on Earth (Dodd et al., 2017; Nutman et al., 2016), and about recently hypothesized MISS in Mars surface imagery (Noffke, 2015).

7. Recommendations for Future Experimental Work

Future taphonomic investigations should incorporate our current knowledge of Martian (paleo)environments to better constrain Mars-specific conditions that can preserve or destroy biosignatures and organic matter. There is a particular need for laboratory studies to investigate the impact of likely conditions in habitable environments on early Mars upon the taphonomy of microbial groups that could have been present, such as those represented in Earth's Archean record. Relevant environmental conditions include anoxic CO_2-rich atmospheres, sulfur- and iron-based redox gradients, high-salinity fluids, sulfates and other evaporites, basaltic soil, Fe/Mg-rich detrital clays, oxychlorine compounds, and temperatures and pressures close to the edge of the liquid water stability field. Experiments are necessary to explore microbially mediated clay authigenesis, carbonate precipitation, and other drivers of fossil preservation under such conditions, and to reveal which water-rock interactions in Martian subsurface environments are likely to be conducive to fossil preservation. Postdepositional processes on Mars must also be considered, that is, the long-term preservation of organic molecules in organo-mineral associations in the presence of abundant chlorine, perchlorate, and peroxide (Benner et al., 2000; Glavin et al., 2013; Navarro-Gonzalez et al., 2010). Although the degradation of microbial cells and lipid biomarkers on the Martian surface has been investigated in simulated atmospheres and radiation environments (e.g., de la Vega et al., 2007; Johnson et al., 2011; Kminek & Bada, 2006), such experiments have little relevance to biosignatures entombed within rocks and buried under a radiation shielding but oxidizing soil layer for most of Martian history.

A new program of Mars-centric taphonomic experiments would reduce our reliance on imperfect analogies between paleoenvironments on Mars and Earth. Experimental and theoretical considerations of processes that operate in the absence of biology would also help us to avoid false positives by exploring the potential of water-rock interactions to form abiotic pseudofossils under Mars-relevant conditions, including life-like morphologies, mineral alteration textures, and porous-layered textures within silica sinters.

8. Conclusions

Previous studies highlighted numerous preservational processes, minerals, lithologies, and microbial groups as targets in the search for life on Mars (e.g., Hays et al., 2017; Summons et al., 2011; Westall, Foucher, et al.,

2015). However, planning for forthcoming rover missions requires that this search be optimized. Here we have considered current understanding of (1) the occurrence and distribution of lithologies and minerals on Mars; (2) the habitability of the environments they represent; and (3) the potential of these environments to preserve the remains of organisms most likely to have lived in them, as revealed by studies of fossils on Earth and experiments in the laboratory. On this basis, we recommend that iron-rich lacustrine mudstones, especially those rich in silica, should be prioritized for biosignature exploration. These rocks are present on Mars, represent aqueous environments with a range of redox states suitable for anaerobic metabolisms, and offer the possibility of preservation by silicification, clay authigenesis, clay-organic adsorption, and iron mineralization. Hot spring sinters are also an attractive target based on likely habitability and rapid mineral precipitation, but their presence on Mars remains to be confirmed (Squyres et al., 2008; Skok et al., 2010; Ruff & Farmer, 2016). Pores and fractures mineralized in the subsurface could represent a geologically younger target, but more research is needed to determine whether they can be confidently identified on Mars and whether appropriate Mars-analog organisms in such settings preserve reliable biosignatures, even on Earth. Likewise, it has yet to be determined whether evaporites can rival lacustrine mudstones in their potential to retain biosignatures for billions of years under Martian conditions.

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