

MODERN TERRESTRIAL SEDIMENTARY BIOSTRUCTURES AND THEIR FOSSIL ANALOGS IN MESOPROTEROZOIC SUBAERIAL DEPOSITS

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ABSTRACT: Microbial communities developing on modern clastic sedimentary surfaces of arid lands are dominated by phototrophic microorganisms that form a variety of characteristic “microbially induced sedimentary structures” (MISS) through their interactions with detrital sedimentary grains, aided by secretions of extracellular polymeric substances and other organic materials. In this study, we describe modern MISS from unvegetated arid topsoils and compare them with fossil MISS found within decimeter- to meter-thick sedimentary sequences of Mesoproterozoic siliciclastic outcrops of the Dripping Spring Quartzite formation of the Apache Group in central Arizona, USA. These sequences contain numerous bedding plane exposures with desiccation surfaces including polygonal cracks, curls, and chips. Repetition of these structures within stratigraphic sequences indicates recurring episodes of subaerial exposure. Some of these MISS contain cellular microfossils that exhibit morphological adaptations for surviving desiccation. The strong similarities between modern and ancient MISS in this study provide additional criteria for recognizing morphological biosignatures of terrestrial microbial communities in ancient deposits. Our results provide compelling evidence for the presence of land-based microbial communities by the Mesoproterozoic (~1200 Ma). The association of MISS features further suggests that the primary producers that had colonized Mesoproterozoic land surfaces were likely desiccation-adapted photosynthetic microbes, similar to modern desert soil crust communities.

INTRODUCTION

Evidence for early microbial life on Earth is based primarily on fossils from the sedimentary rock record of aquatic environments (Schopf 1983; Schopf and Klein 1992). However, the discovery of microbial biosignatures in deposits of shallow intertidal, marine, and lacustrine settings has expanded the ancient habitats for Precambrian life to terrestrial environments that were subject to periodic desiccation (Westall et al. 2006; Schieber et al. 2007; Noffke 2010). Despite the fact that examples of terrestrial sedimentary deposits (e.g., alluvial, lacustrine-playa, dune fields, and interdune deposits) have been identified in the Precambrian record (see references in Simpson and Eriksson 1993; Eriksson et al. 1998; Simpson et al. 2002, 2004), evidence for a fossil record of MISS in these environments is rare. This may, in part, reflect unfamiliarity with modern microbial communities of arid settings and the biomediated structures they produce. For this reason, we began the present study by characterizing modern biocrust communities to understand the nature of their interactions with arid sedimentary systems and the biostructures they produce.

In modern terrestrial regions where plant growth is absent or limited (typically in arid areas where water is only available intermittently), sandy sediments support large and complex microbial communities. Examples include biological soil crusts or “biocrusts,” which can cover up to 80% of the surface area of some deserts (Belnap et al. 2001). The global biomass of these systems has been estimated to be as high as 10^{14} g (Garcia-Pichel et al. 2003). Biocrusts can stabilize loose sediment particles, prevent erosion and dust formation (Belnap et al. 2001), sustain intense C and N cycling (Johnson et al. 2005, 2007), and leach metals from surface

sediments (Beraldi-Campesi et al. 2009), all of which are regarded to be biogeochemically important processes. Additionally, biocrusts produce sedimentary biostructures that can be preserved in the fossil record (Noffke 2010; Simpson et al. 2010; Retallack 2011; Sheldon 2012).

Despite their rarity in the sedimentary record, a few well-studied examples from the Meso- and Paleoproterozoic terrestrial sedimentary sequences provide a baseline for recognizing terrestrial MISS (e.g., Eriksson et al. 2000; Prave 2002; Simpson et al. 2010, 2013; Retallack 2011; Sheldon 2012). In addition, microbial biosignatures have also been suggested for even older terrestrial and subaerial deposits, based on the presence of microfossils, organic matter, and geochemical trends (e.g., Fritsch 1907, 1922, 1936; Hallbauer and van Warmelo 1974; Retallack and Mindszenty 1994; Driese et al. 1995, 2011; Rye and Holland 2000; Watanabe et al. 2000; Driese and Gordon-Medaris 2008). Comparative studies of modern microbial mats have played an important role in the interpretation of ancient MISS in aquatic settings (Noffke 2010). However, until now, studies of terrestrial MISS have been limited by a lack of information about their modern counterparts, in spite of the fact that biostructures mediated by microbial phototrophs have been described previously from terrestrial settings (e.g., Fagerstrom 1967; Campbell 1979; Belnap et al. 2001).

To support analog comparisons to the Proterozoic Dripping Springs Quartzite, in this study we describe modern MISS associated with cyanobacteria-dominated microbial communities of plant-poor, arid and semiarid areas of the world, highlighting eight distinctive biostructures commonly observed in modern systems. These comparisons show that remarkably similar ancient counterparts of these terrestrial MISS are

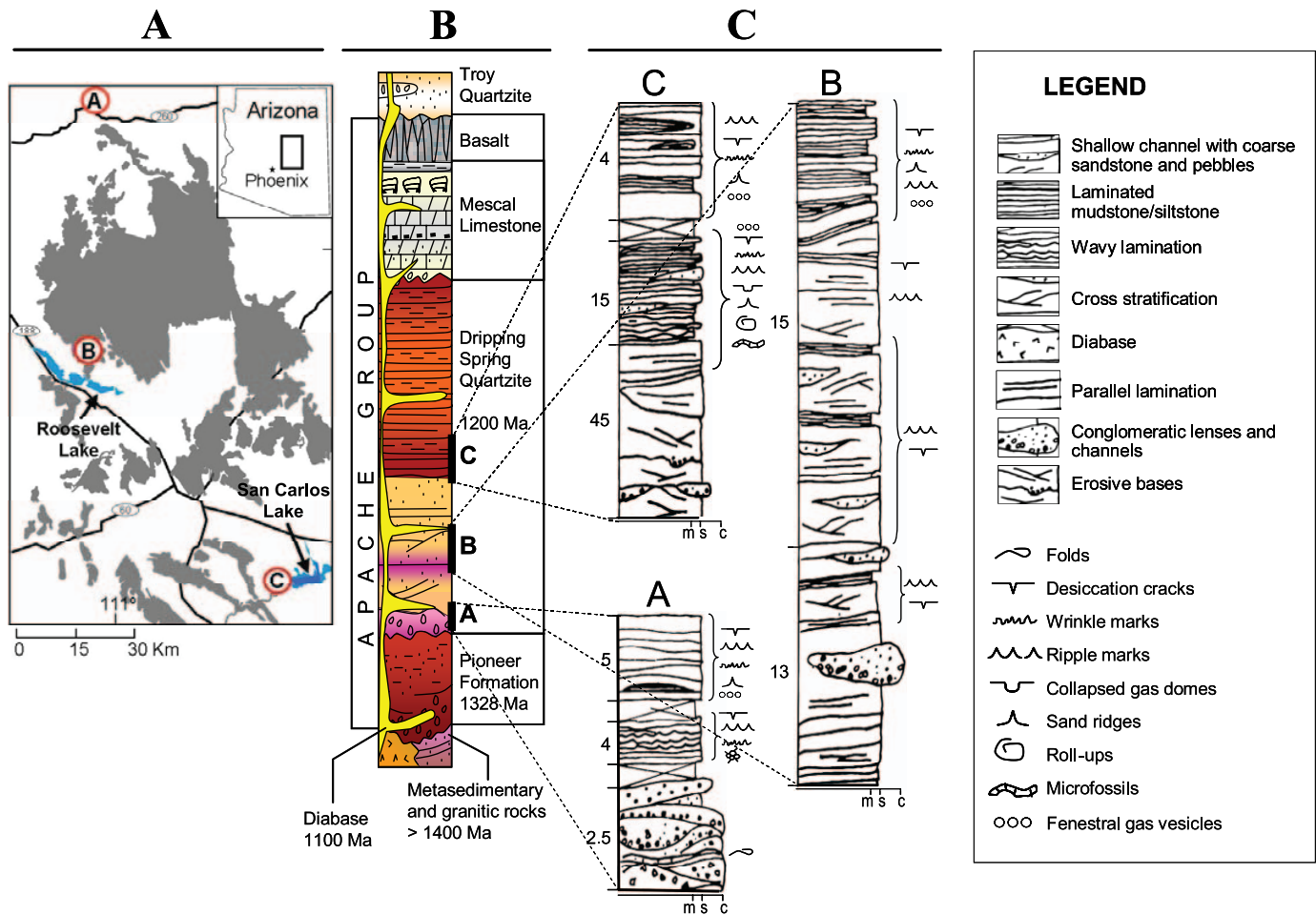


FIG. 1.—Location and stratigraphy potentially biogenic sedimentary structures of the Dripping Spring Quartzite (Dripping Spring Quartzite). **A**) Geographical extent of the Dripping Spring Quartzite (gray area; compiled from Granger and Raup 1964; Shride 1967; Wrucke 1989; Skotnicki and Knauth 2007) and the outcrop localities showing evidence of subaerial exposure (A: Horton Creek; B: Parker Canyon; C: Coolidge Dam), where stratigraphic sections were measured and samples were collected. **B**) General stratigraphy of the Apache Group, indicating the latest known geochronology for the main members and the approximate stratigraphic position within the Dripping Spring Quartzite of the Horton Creek (A; Barnes Conglomerate), Parker Canyon (B; middle member), and Coolidge Dam (C; upper member) sections. **C**) Stratigraphic sections measured at each of the outcrops. Grain size is indicated at the bottom of the sections (m = siltstone–mudstone; s = sandstone, and c = conglomerate). Thickness, in meters, is indicated to the left of each section. Various potentially biogenic sedimentary features are indicated to the right of each column, according to the legend box.

found on exposure surfaces and within associated continental deposits of the Mesoproterozoic Dripping Springs Quartzite, central Arizona (Fig. 1). Evidence for cycles of exposure and desiccation is preserved on extensive mud-cracked bedding plane surfaces. Periods of desiccation are punctuated by evidence for periodic flooding with deposition of thin beds containing redeposited mud curls and rip-up clasts, some with preserved cellular microfossils. Some MISS observed in the Dripping Springs Quartzite share similarities with those documented for intertidal settings, suggesting alternations of terrestrial and nearshore environments, which is common in modern intertidal settings as well, especially those in extensive flat areas.

GEOLOGICAL SETTING

The Dripping Spring Quartzite (Granger and Raup 1964) is the major siliciclastic formation of the well-preserved Apache Group of Arizona (Fig. 1), which was deposited along the southern margin of Laurentia (Whitmeyer and Karlstrom 2007) between ~1300 and ~1100 Ma (Stewart et al. 2001). Today, it crops out over an area ≥ 100 km². The base of the Dripping Springs Quartzite is defined by a basal

conglomerate, which is overlain by an overall fining-upward sequence. This sequence is similar to the underlying Pioneer Formation, which Middleton and Trujillo (1984) interpreted to be braided-stream alluvial deposits. The Dripping Spring Quartzite represents a complex mix of continental, transitional, and shallow marine environments, including alluvial fan deposits (Montgomery and Middleton 2000). Sediments were deposited over a wide, shallow basin, rimmed by restricted marine embayments (Shride 1967; Wrucke 1989; Engel and Elmore 1990), extensive tidal flats (Granger and Raup 1964), and braided alluvial fan deposits (Middleton and Montgomery 2001).

The lower units of the Dripping Spring Quartzite comprise an overall fining- and thinning-upward sequence, with lenticular, cross-bedded, pebbly conglomerate and sandstone-filled channels, indicative of deposition under channelized flow. The arkosic and quartzitic composition of these sandstone beds suggests delivery from nearby granitic highlands, as highlighted for similar sequences within this formation (Middleton and Trujillo 1984). The middle member contains laterally extensive, tabular-bedded sandstone beds, interpreted as deposits laid down during shallow marine incursions that reworked sandy alluvial sediments (Granger and

Raup 1964; Engel and Elmore 1990), similar to other North American continental basins (Wrucke 1989). The upper Dripping Spring Quartzite is dominated by siltstone and organic-rich shale (Granger and Raup 1964; Engel and Elmore 1990), with occasional crosscutting channels. These upper units, which provide a primary focus for the present study, show widespread evidence for recurrent subaerial exposure and desiccation in the form of extensive, mud-cracked bedding surfaces, some with raindrop impressions. Overall, these sequences suggest distal alluvial fan to estuarine tidal flat sedimentation, with extensive subaerial habitats subject to cycles of flooding and desiccation. The locations of the study sites discussed here and their stratigraphic relationships are summarized in Figure 1, as well as the supplementary materials.

COMPARISON OF MODERN AND ANCIENT SEDIMENTARY BIOSTRUCTURES

To better understand the potential for MISS in subaerial environments, we studied cyanobacteria-dominated biological soil crust communities from the Sonoran Desert (see supplementary data Fig. S2). Structures from these modern analog environments were compared to similar structures found in the Dripping Spring Quartzite. In both cases, microbial communities impart unusual physical properties to clastic sediments, such as enhanced cohesion, elasticity, strength, shrinking and swelling capacity, and hydraulic resistance (Campbell 1979; Bauld 1981; Schieber 1999; Krumbein et al. 2003; Noffke 2010; Rossi et al. 2012). These properties ultimately affect the local geochemistry and sedimentology of the deposits (Beraldi-Campesi et al. 2009; Beraldi-Campesi and Garcia-Pichel 2011). Common MISS associated with modern biocrusts are described in the following paragraphs, with comparisons to similar sedimentary features observed in the Dripping Spring Quartzite.

Gas-derived Features

Fenestral Gas Vesicles.—Fenestral cavities, 0.5 to 5 mm in diameter, were conspicuous in both modern and ancient MISS assemblages. Vesicles possess smooth internal walls and are usually ovoid in shape (Fig. 2A, B), but with a range of morphologies, including lenticular to tubular, or they are connected to other vesicles through fractures. In modern biocrusts, fenestral fabrics were observed in silty soils as vesicular horizons (see supplementary data Fig. S3). Similar vesicles were recreated in the laboratory by inoculating sandy substrates with filamentous cyanobacteria (see supplementary data Fig. S3). Moreover, similar fenestral fabrics have been previously documented in marine siliciclastic Precambrian rocks (Gerdes 2007; Noffke 2010), where they were attributed to biogenic gas accumulation beneath microbially sealed surfaces. In modern soils, extracellular polymeric substances (EPS) act as sealants, even in sandy substrates, and have well-known pore-clogging effects (Or et al. 2007). In the Dripping Spring Quartzite, vesicular horizons were commonly observed just beneath beds that displayed other microbially mediated surface features (see supplementary data Figs. S3F, S4C), such as wrinkle marks and gas domes (see descriptions below). In fact, this association of distinctive MISS was a conspicuous feature of both modern and ancient examples. In petrographic thin sections, Dripping Spring Quartzite fenestrae showed no evidence of having been formed through clast dissolution. Rounded clasts of comparable size were absent from the matrix, and the smooth margins of fenestrae conformed to surrounding sedimentary laminae formed at the time of deposition (see supplementary data Fig. S3). This indicates that the fenestrae existed in the sediments before lithification. Their size, shape, and distribution in siltstone–sandstone profiles were also similar to vesicular horizons observed in modern biocrusts. Thus, we interpret fenestral fabrics in the Dripping Spring Quartzite to be well-preserved primary structures formed by the accumulation of biogenic gases below sealed surfaces

where sediment permeability had been reduced by the accumulation of microbial biomass and associated exopolymers.

Gas Domes.—These features are distinctive bedding plane structures that were observed to form beneath modern biocrusts where gas accumulation occurred under a sealed surface (see supplementary data Fig. S4). They have also been reported from intertidal environments (Schieber et al. 2007; Bose and Chafetz 2009; Noffke 2010). Gas domes often collapse upon desiccation, to form crater-like convex depressions, often delimited by fractures along their rim (Fig. 2C–D; see supplementary data Fig. S4E).

Collapsed Gas Domes.—These features were observed forming in modern deserts and were also present in paleosurfaces of the Dripping Spring Quartzite, upper member. The latter were centimeter-sized hemispherical depressions, delimited by a perimeter-defining crack (Fig. 2C), sometimes in close association with vesicular horizons. Allochthonous, coarse sediments can accumulate in these depressions after they form, as seen in both modern and ancient examples (see supplementary data Fig. S4D). Collapsed gas domes in the Dripping Spring Quartzite were observed in muddy sediments, where a layer of fine, wet mud could have acted as an abiotic sealant to entrap subsurface gases. However, they were also observed in sandy, porous sediments, where a mud sealing veneer was conspicuously absent. In the latter case, it seems likely that a biological agent, such as EPS, was required for their formation. Again, the common association of gas domes, vesicular horizons, wrinkle marks, and desiccation features, often within sandy sediments, strengthens the case for a biogenic origin of these structures.

Deformation and Desiccation Features

Wrinkle Marks.—The complex interplay of biogenic gas entrapment, soft sediment deformation, surface desiccation, microbial taxis, and weak water currents moving over loose microbial mat debris seems to be the basis for the formation of low-relief wrinkles and pustular surfaces, generally referred as wrinkle marks (Hagadorn et al. 1999; Schieber et al. 2007). Most of these features have been reported from the fossil record of intertidal marine environments (Hagadorn and Bottjer 1997; Hagadorn et al. 1999) and interpreted to be microbially mediated MISS. We have found similar features in both modern deserts and on bedding surfaces in the Dripping Spring Quartzite that we interpret as biogenic (Fig. 2E–H). Both the modern biocrusts and analogous fossil examples in the Dripping Spring Quartzite display a similar range of morphologies, including smooth, ripple-like features and surfaces having an “elephant skin” appearance.

Desiccation Cracks and Polygons.—These features are commonly seen on dry, fine-textured soil surfaces in modern alluvial settings of modern deserts, and they are also common features of the Dripping Spring Quartzite paleosurfaces discussed here (Fig. 3C, D). They owe their origin to the shrinkage of cohesive sediments, driven by cycles of wetting and drying. In fine-grained sediments, expansive clays typically serve as both a cohesive and swelling agent for the abiotic formation of desiccation polygons. However, in coarser sediments, which typically lack clays, cellular and extracellular microbial biomass may impart similar binding properties to sediments (Beraldi-Campesi and Garcia-Pichel 2011). Mud-free sandstone beds with similar desiccation features have been reported previously and interpreted to be biogenic (Porada and Druschel 2010). In the present study, desiccation polygons and cracks were observed in modern, mud-free, coarse sediments, where biocrusts were present (Fig. 3). Reminiscent of “earth cracks” (Picard and High 1973), these biological soil crust features tended to be rather shallow, with

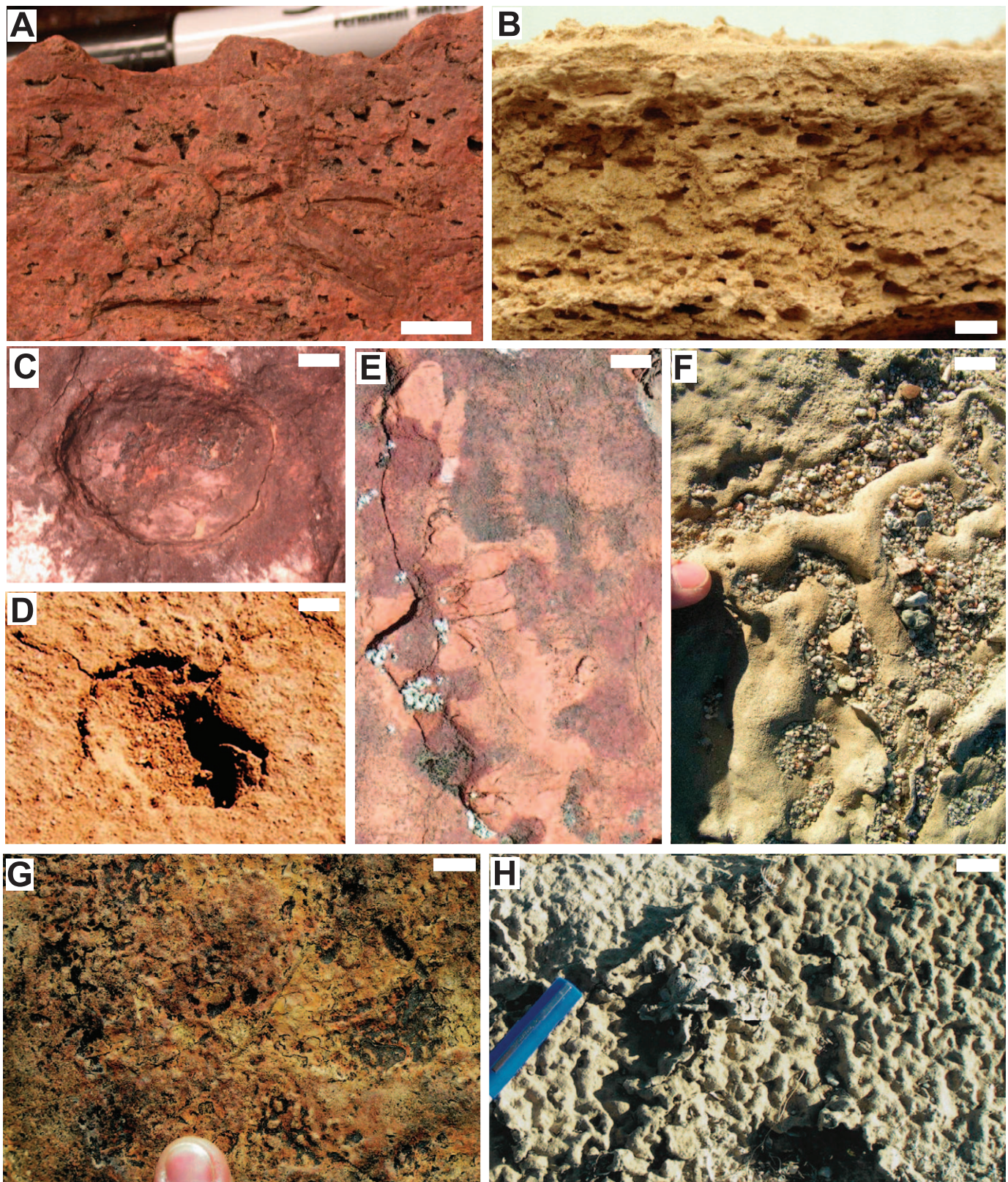


FIG. 2.—Sedimentary structures generated by gas trapping and/or sediment cohesiveness. Ancient examples in paleosurfaces of the Dripping Spring Quartzite are paired with their modern counterparts from biological soil crusts. All scale bars are 1 cm. **A)** Fenestral gas vesicles shown in cross section (surface of the bed is at the top of the image) of a siltstone sample from the Dripping Spring Quartzite. Sawn sections of several samples prove that voids had not been in-filled (see supplementary data Fig. S3). **B)** Modern fenestral gas vesicles are commonly found under biological soil crusts today, as shown here in a cross section. **C)** Dripping Spring Quartzite example of a collapsed gas dome. Note also wrinkles at the surface. **D)** Modern collapsed gas dome displaying a cracked rim and coarse sediment in its interior. **E)** Ancient (Parker

depths equivalent to the thickness of the microbial crusts present. Comparable desiccation cracks, with comparatively shallow depths (<5 mm), were also observed on exposure surfaces in the Dripping Spring Quartzite. These occurred in well-sorted, mud-free sandstone beds, consistent with a biogenic origin.

Sand Ridges.—Microbially formed polygons can actually expand by the hydration of EPS, through microbial growth, and by thickening of sediment profiles with the accretion of trapped and bound sedimentary grains. Lateral expansion of desiccation polygons during such processes can result in the buckling and uplift of opposing edges to form “sand ridges” (Fig. 3A, B). We know of no reports of sand ridge development around desiccation polygons in subaerial environments without microbial mediation. On Dripping Spring Quartzite bedding surfaces, sand ridges up to 12 cm long and 1.2 cm high were commonly observed along the margins of desiccation polygons. This contrasts with the 2- to 3-cm-high sand ridges seen in modern biocrusts. One should caution that polygon edges can also be upturned following burial, due to the upward escape of fluidized sediments during dewatering of the buried sediment column with compaction. However, cross sections of sand ridges in the Dripping Spring Quartzite showed that the underlying sedimentary layers were undisturbed, eliminating the potential role of postburial dewatering in their genesis.

Sand Folds.—We also observed “sand folds” on both modern biocrust and Dripping Spring Quartzite surfaces (Fig. 3E, F). These features show clear evidence for internal cohesiveness and elasticity atypical of sandy sediments and have been previously interpreted to be biologically mediated (Schieber 1999). In the modern examples reported here, sand folds were formed where water currents folded sheets of sediment over onto themselves during shallow flooding events. Modern examples require the presence of a sediment-binding microbial EPS and associated microbial filaments, to maintain the integrity of the unconsolidated sediments during folding. On this basis, we interpret the sand folds in the Dripping Spring Quartzite as biogenic, with the necessary sediment cohesion and elasticity having been imparted by microbial biomass.

Sedimentary Roll-up Structures.—Sedimentary roll-up structures were also observed in both modern and ancient examples discussed here. These structures form when highly cohesive, leathery surface layers undergo desiccation, shrinking and curling upwards and onto themselves. A recent in-depth study of these structures strongly suggests that terrestrial fossil roll-up structures are biogenic in origin (Beraldi-Campesi and Garcia-Pichel 2011). Fossilized roll-ups were detected in the profile of one Dripping Spring Quartzite siltstone, which consisted of thin, enrolled layers of fine-grained mudstone embedded in a silty sandstone matrix (Fig. 3G, H).

ORGANICALLY PRESERVED MICROFOSSILS

An additional and important line of evidence for microbial community colonization of exposure surfaces in the Dripping Spring Quartzite paleosurfaces is the well-preserved, organic-walled microfossils (Fig. 4). The microfossils were found within a single, fine-grained, iron-oxide-cemented siltstone, containing mudstone rip-up clasts and roll-up structures. There was no evidence for secondary fracturing of the siltstone matrix during diagenesis, but mudstone clasts did show evidence for soft sediment

deformation during compaction. The best-preserved examples are a small population of amber-colored spheroids. The diameter of the microfossils ranged from 35 to 65 μm . The microfossils were bounded by a 2- to 5- μm -thick envelope, containing a matrix of dark, granular kerogenous matter. Some individuals in the population showed evidence for cell division by fission, and layered teguments, typical of some modern desiccation-resistant terrestrial cyanobacteria and algae. Some displayed cellular arrangements in tetrads (Fig. 4B), which may indicate recurrent cell division in a low-energy environment (Tyson 1995). Nearly all of the described examples were found within subspherical voids, which we interpret to have formed by postmortem shrinkage of cells, likely due to desiccation after burial and lithification. Some of these cellular structures, such as the teguments that bound the fossils, were most visible when comparing bright-field and fluorescence microscopy (Fig. 4F, G). The organic composition of these microfossils was confirmed using 532 nm laser Raman spectroscopy (Fig. 4H).

A common process in ephemeral streams of dryland environments is the fragmentation and short-range transport of fine-grained, desiccated surfaces by shallow sheet flow following a rainstorm. The mud chips containing the cellular microfossils appear to have been locally derived in this manner. Indeed, the subangular shape of the mud clasts in the rock and evidence of soft sediment deformation following deposition suggest that the rip-up clasts experienced a relatively short-range transport, following a brief erosional event of limited energy. Sealing of the fossils in a fine-grained, iron-oxide-cemented matrix during early diagenesis was undoubtedly a major contributing factor to their preservation. The heavy tegument, large size, and internal structure of the microfossils may be interpreted as representing eukaryotic forms. Indeed, spherical, thick-walled, sometimes tetrad-forming chlorophytes (Fig. 4J) are common over a broad range of modern environments, including soil habitats. However, the general characteristics of the Dripping Spring Quartzite microfossils are also typical of many modern pluricellular colonies of terrestrial cyanobacteria, including genera like *Gloeocapsa* sp. or *Chroococcidiopsis* sp. (Fig. 4I). Unfortunately, we are presently unable to distinguish between these alternatives. Regardless of their affinity and paleoecology, we interpret these structures to be bona fide microfossils, based on the criteria articulated by Buick (1990) and Schopf (1993), including appropriate provenance, indigenosity, syngenicity, and biogenicity.

IMPLICATIONS FOR EARLY LIFE ON LAND

The recognition of MISS in modern desert environments has provided a set of useful criteria for identifying similar features in the Dripping Spring Quartzite, a middle Proterozoic formation that records episodes of periodic subaerial exposure. The recurring association of different MISS in the Dripping Springs Quartzite suggests that Proterozoic land surfaces had been colonized by microbial communities, similar to those that form MISS in modern subaerial settings on Earth today. This interpretation is consistent with reports of a diverse microbiota in terrestrial, but still aquatic environments in younger strata of the Apache Group (McConnell 1974; Horodyski and Knauth 1994), as well as the broader compilation of evidence that suggests a continuous presence of land-based life since the Paleoproterozoic (Beraldi-Campesi 2013). The presence of a Proterozoic terrestrial biota requires that effective microbial adaptations for resisting long-term desiccation and intense radiation be in place. Pre-adaptations for fully terrestrial life may have developed in intertidal coastal

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Canyon) examples of “ripple-like” wrinkle marks. **F)** Modern, ripple-like wrinkles formed by terrestrial cyanobacterial communities. **G)** Typical wrinkle marks on a bedding surface at the Coolidge Dam outcrop displaying “elephant skin” texture. **H)** Similarly wrinkled, modern soil surface in the Sonoran Desert, containing a well-developed cyanobacterial community.

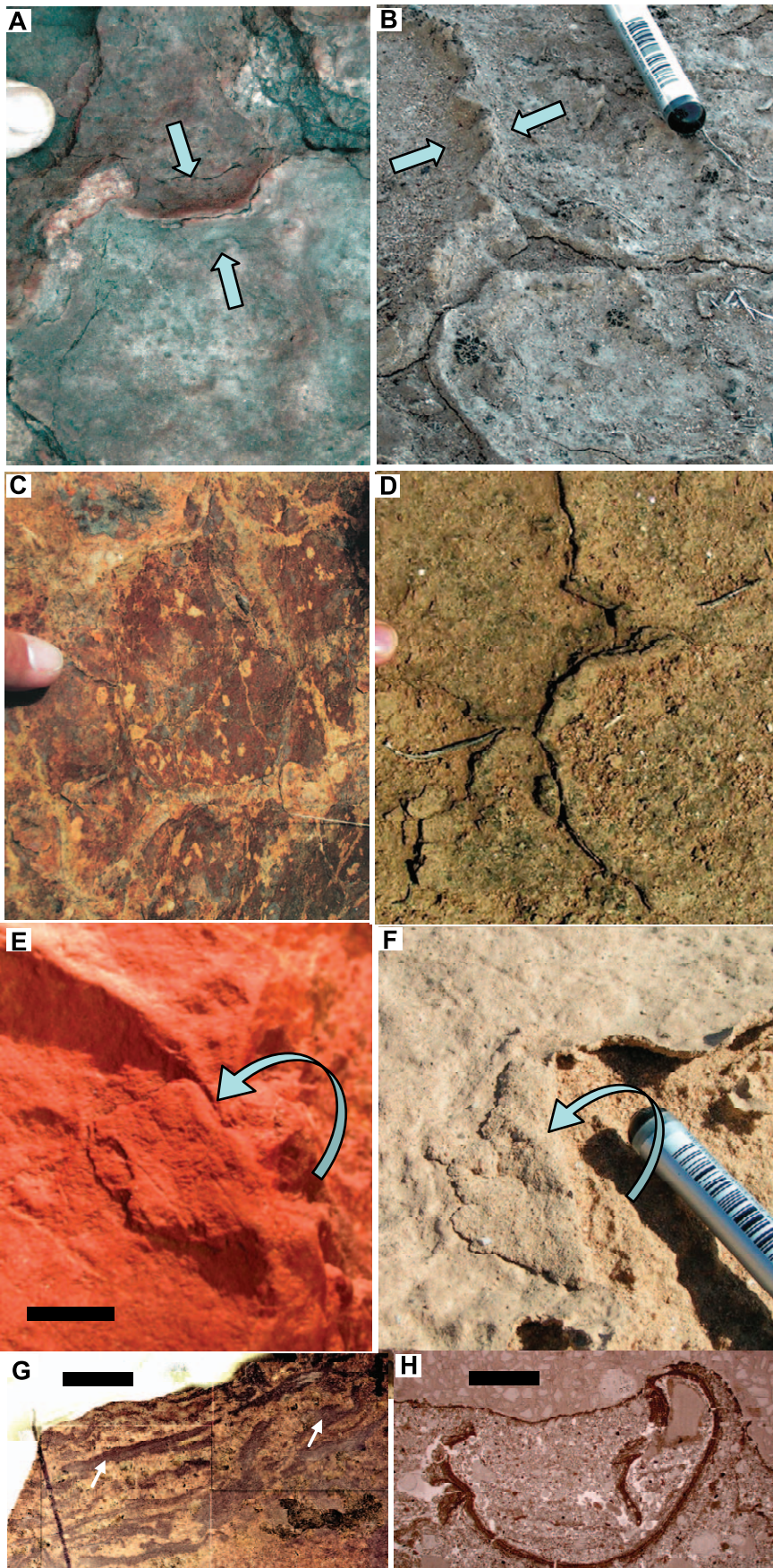


FIG. 3.—Sedimentary structures generated through desiccation and swelling of cohesive sediments. **A)** A siltstone with sand ridges at the margins of desiccation polygons, from the upper member of the Dripping Spring Quartzite. Note the suture along the ridge's summit and its deformation at the convergence (small arrow) with a neighboring, sutureless sand ridge. Big arrows indicate the assumed direction of lateral compression. **B)** Modern example of a sand ridge, originated at the edges of deformed biological soil crust layers. Arrows indicate the direction of lateral compression. **C)** Desiccation cracks and polygons at the surface of a Parker Canyon mud-free sandstone, middle member of the Dripping Spring Quartzite. **D)** Modern cracks and polygons formed by desiccation in sandy, organic-rich biological soil crusts. **E)** Sand fold observed at the surface of an upper bedding plane of layered siltstone, present in fine sediment lenses within the basal, matrix-supported Barnes Conglomerate. Scale bar = 1 cm. **F)** Folded edge of a ripped biocrust in the Sonoran Desert. Arrows indicate direction of folding. **G)** Composite image of a sawn siltstone containing a roll-up structure, from the Coolidge Dam section, upper member of the Dripping Spring Quartzite. The image shows a dark-toned roll-up (arrows) and abundant mud chips embedded in a silty matrix. This sample was the source of the microfossils shown in Figure 4. Scale bar = 1 cm. **H)** Petrographic thin cross section of a modern, buried roll-up. Microbially bound sediment (denser areas) highlights the shape of the roll-up against the more porous and coarser matrix. Scale bar = 5 mm.

environments, where relatively long-term desiccation was common, and may also have influenced the distribution of the biota (Rothrock and Garcia-Pichel 2005). Recent studies suggest that such environments had been colonized by at least ~3500 Ma (Noffke et al. 2013). Collectively, these findings challenge the notion that subaerial continental masses were sterile until the Phanerozoic. Rather, microbial ecosystems appear to have been widespread inhabitants of land surfaces for most of the Precambrian Eon.

Several observations indicate that terrestrial ecosystems in the Dripping Spring Quartzite must have been based on production sustained by oxygen-evolving phototrophs. As a source of energy, sunlight is widespread, but it restricts the occurrence of phototrophs to sunlit surfaces. In contrast, chemotrophy-based ecosystems have been suggested for particular Precambrian continental settings (Rye and Holland 2000; Rasmussen et al. 2009). However, chemotrophy-based surface ecosystems require the presence of widespread reduced environments with geochemically mobile (i.e., non-point-source) electron donors (e.g., Fe^{2+} , Mn^{2+}), to supply vast expanses of subaerially exposed land surfaces. This scenario is highly unlikely for the Dripping Spring Quartzite, which shows clear evidence for early diagenetic Fe-oxide precipitation as sedimentary cements, as well as oxidized red-bed sequences, which dominate the upper Dripping Spring Quartzite. These observations suggest the presence of an oxidizing atmosphere and hydrosphere by the Mesoproterozoic (Anbar et al. 2007). With the exception of water, the same restrictions apply to other potential electron donors that could be used in photosynthesis (e.g., H_2S , S_0 , H_2 , etc.). Thus, we consider the Dripping Spring Quartzite subaerial communities to be not only the morphological analogs of modern biocrusts, but functional analogs as well, in carrying out water-splitting oxygenic photosynthesis. Additionally, some of the traits seen in modern photosynthetic members of biological soil crusts, such as sediment stabilization (Belnap and Gillette 1998), desiccation resistance through development of thick teguments (Potts 1994), and protection from ultraviolet light via interstitial living and specialized protecting pigments (Gao and Garcia-Pichel 2011), were likely early adaptations to life on subaerial habitats. Some of these traits, such as sediment stabilization, the pervasive colonization of surface sediments, and thick teguments in microfossils, are clearly seen in the Dripping Spring Quartzite examples, which reinforces the value of our comparisons to modern biological soil crusts.

In view of the biogeochemical activity displayed by modern biocrusts, their ancient counterparts must have played a fundamental role in land-based weathering and terrestrial biogeochemical cycles. Their widespread presence in the Mesoproterozoic is also consistent with geochemical evidence for the greening of the continents by the late Precambrian (Knauth and Kennedy 2009). Thus, as the early growing continents were progressively colonized by microbes, new biogeochemical processes (e.g., enhanced leaching of nutrients to the oceans, retention of dust–nutrient particles, preventive erosion of siliciclastic environments, incorporation of C, N, P, organic matter, and soil reactants into soils, release of O_2 , mineral corrosion and rock erosion, and new ecological niche development, among others) may have helped to link the land and oceans in ways very different from what would be expected from a sterile Precambrian land surface. Importantly, microbes must have played significant roles in mediating physical and chemical processes on the early land surfaces, helping to pave the way for the onset of younger, plant-dominated ecosystems.

It seems unlikely that the paleobiota we describe here was restricted to the geographical setting of the Dripping Spring Quartzite, since basic requirements for the development of land-based microbial communities (an exposed sedimentary surface, sunlight, and the periodic supply of meteoric water) must have been easily met in other continental settings as well. The evidence for subaerially adapted microbial life in the Dripping Spring Quartzite, primarily as MISS, suggests that microbial ecosystems could have achieved a global continental distribution by the Mesoproterozoic. The plausibility that such terrestrial communities existed before

that time (see references in Beraldi-Campesi 2013) calls for a careful re-examination of the continental rock record for other examples that may have been misinterpreted or overlooked.

CONCLUSIONS

In this study, we compared sedimentary structures that are shared between modern (Sonoran Desert) and ancient (Dripping Spring Quartzite) MISS, developed subaerially. These include (1) gas-generated features, such as fenestral gas vesicles and vesicular horizons occurring underneath modern biocrusts and under thin mudstone veneers, gas domes, collapsed gas domes, and delicate blisters; (2) shear- and deformation-generated features, such as wrinkle marks of several different types; (3) desiccation-generated features, such as desiccation cracks and polygons occurring on sandy and sandstone surfaces; (4) dewatering and laterally expanding features, such as sand ridges; (5) shear- and folding-generated features, such as sand folds and roll-ups (the latter also implying desiccation); and (6) eukaryotic, but also prokaryotic-looking microfossils with thick teguments, likely implying desiccation tolerance. These ancient MISS commonly appear combined in a single sample, which is also commonly observed in modern samples, where environmental and microbial forces are at play simultaneously.

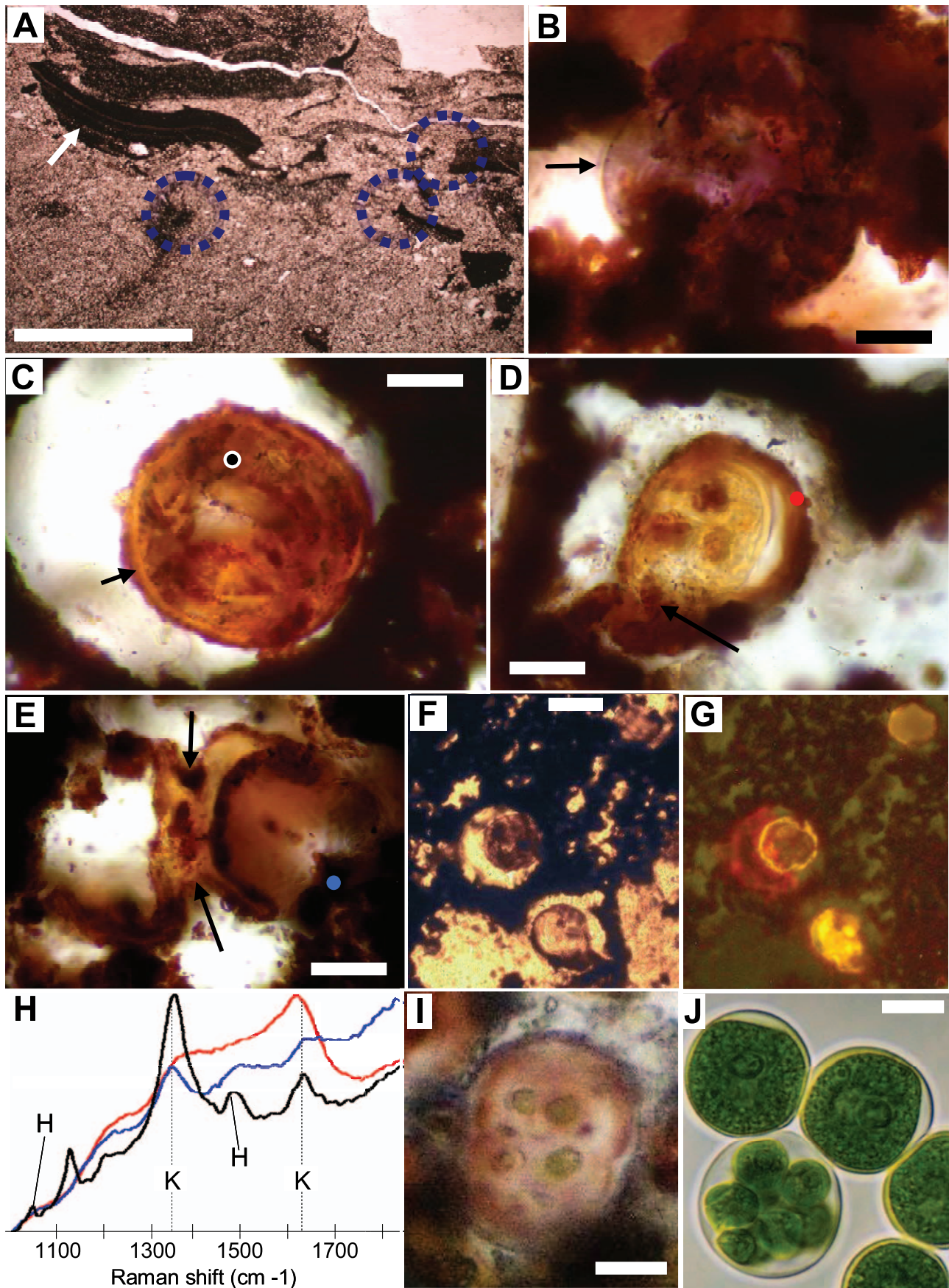
The occurrence of Dripping Spring Quartzite fossils within depositional settings comparable to alluvial floodplains, the occurrence of MISS at paleosurfaces bearing desiccation features, the high abundance and coexistence of fossil MISS, and their strong morphological resemblance to modern biocrust analogs strongly suggest that the Dripping Spring Quartzite surfaces were colonized by biological soil crust-like communities ~1200 million years ago. This clearly implies that communities of microbes were already adapted to live in dry habitats long before the advent of land plants.

ACKNOWLEDGMENTS

We thank anthropologist Adrienne Rankin (Goldwater Air Force Base); Edgardo Ramirez-Reinat, Thomas G. Sharp, David S. Lowry, Kathleen B. Pigg, Scott T. Bates, Emmanuel Soignard, and John C. Benedict (all of Arizona State University); Leticia Alba Aldave and Jaime Diaz Ortega (Universidad Nacional Autónoma de México); Malte Ebach (University of New South Wales); Nathan Wilkens (Shell Oil); Greg Retallack (University of Oregon); Patrick Eriksson (University of Pretoria); John-Paul Zonneveld (University of Alberta); Gonzalo Pardo (University of Zaragoza); and Jörn Peckmann (University of Vienna) for all their comments and technical support. H.B.C. was supported by PAPIIT-DGAPA-UNAM Project IA101212 and CONACyT Project 205981.

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FIG. 4.—Microfossils from the upper member of the Dripping Spring Quartzite, Coolidge Dam section. **A)** Petrographic thin section of a siltstone where laminated mud chips (arrow) and roll-ups are embedded. Blue circles indicate fossiliferous areas. Scale = 1 cm. **B)** Tetrad of spheroids with cell walls in contact. Three spheroids are shown on the focal plane. A fourth spheroid is inferred to be behind the trio. A tegument appears laminated in places (arrow). Scale = 10 μm . **C)** Thick-walled microfossil, with a well-defined 1–2- μm -thick wall and disorganized content. Scale = 10 μm . **D)** Spheroid microfossil showing four internal compartments (arrow), each surrounded by a thick, multilayered tegument. Scale = 10 μm . **E)** Apparent cell division indicated by a constriction (arrows) between two degraded cells. Scale = 10 μm . **F)** Group of microfossils in their respective compartments, under bright-field illumination. **G)** Same group of microfossils under epifluorescence (430 nm) excitation, revealing the presence, shape, and distinct composition an envelope. Scale = 35 μm . **H)** Laser-Raman spectra (543 nm excitation) of the microfossils shown in C, D, and E (colored dots indicate the probed area and the color of the spectra in H). Spectra show characteristic kerogen peaks (52) at ~ 1350 and 1635 cm^{-1} . **I)** *Gloeocapsa* sp. (cyanobacteria) under bright-field microscopy. A common inhabitant of modern biological soil crusts (53), it shows thick, multilayered sheaths, and binary fission, comparable to some microfossils. **J)** *Tetracystis* sp. is an example of green alga with morphological similarities to some microfossils (image by the National Institute for Environmental Studies: <http://mcc.nies.go.jp>). Scales = 10 μm .

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Received 29 August 2013; accepted 14 February 2014.

SUPPLEMENTARY MATERIAL

Supplementary Material is available from the PALAIOS Data Archive: <http://www.sepm.org/Page.aspx?pageID=332>.