

1 Evidence for cavity-dwelling microbial life in 3.22 Ga-old tidal deposits

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10 **ABSTRACT**

11 Cavities are considered as plausible and favorable habitats for life on early Earth. In such
12 microenvironments, organisms may have found an adequate protection against the intense
13 ultraviolet (UV) radiation that characterized the Archean ozone-free atmosphere. However, while
14 there is clear evidence that benthic life existed in the Paleoproterozoic, the oldest traces of cavity-
15 dwelling microbes (coelobionts) have been found thus far in Neoproterozoic rocks. Here we present
16 the results of a detailed investigation of early-silicified cavities occurring in the oldest well-
17 preserved siliciclastic tidal deposits, the 3.22 Ga-old Moodies Group of the Barberton Greenstone
18 Belt (South Africa). Downward-growing microstromatolitic columns, comprised of kerogenous
19 laminae, are commonly present in planar, bedding-parallel, now silica-filled cavities that formed
20 in sediments of the peritidal zone. *In-situ* $\delta^{13}\text{C}_{\text{PDB}}$ measurements of the kerogen range from -32.3‰
21 to -21.3‰ and are consistent with a biogenic origin. Scanning electron microscopy (SEM) analysis
22 of the silicified cavities show well-preserved chains of cell-sized molds that we interpret as fossil
23 filamentous microorganisms. The geological context, the morphology of the microstromatolites,
24 the $\delta^{13}\text{C}$ composition of the kerogen, and the presence of microfossils all suggest that a microbial

25 community inhabited the cavities. Our results extend the geological record of coelobionts by ~0.5
26 Ga, supporting the view that cavities were among the first ecological niches to have been occupied
27 by early microorganisms.

28

29 **INTRODUCTION**

30 Stromatolites interpreted as fossil microbial mats, permineralized microfossils in chert, and
31 kerogen with characteristic carbon isotopic signatures all suggest that microbial life was
32 widespread in the photic zone of Paleoproterozoic coastal environments (Nisbet and Sleep, 2001;
33 Altermann and Kazmierczak, 2003; Brasier et al., 2006; Schopf, 2011; Bontognali et al., 2012).
34 However, due to the absence of an ozone shield, the high surface UV-flux in that period was
35 presumably harsh to lethal for unprotected microorganisms within minutes to days (Cockell, 2000;
36 Cockell and Raven, 2007). Under such unfavorable conditions, early microbial communities
37 thriving in the photic zone supposedly employed one or several protective mechanisms, e.g., high
38 DNA repair capability, biosynthesis of pigments, radiation screening by mineral incrustation or by
39 matting, the accumulation of surficial dead biomass (Garcia-Pichel and Bebout, 1996; Cockell,
40 1998; Phoenix et al., 2001). Furthermore, organisms can actively migrate to and colonize UV-
41 protected subsurface habitats within the sediment (endobenthic; Noffke, 2010), within solid rocks
42 (endolithic; Walker et al., 2005; Walker and Pace, 2007) or in cavities (coelobiontic; Kobluk and
43 James, 1979; Phoenix et al., 2006). Unambiguous evidence for those strategies, however, is hard
44 to find in the fossil record; currently, the oldest remnants of cavity-dwelling microbial communities
45 have been identified in 2.75 Ga-old fluvio-lacustrine sediments of the Fortescue Group, Australia
46 (Rasmussen et al., 2009). We here present remarkably well-preserved remains of a 3.22 Ga-old
47 microbial community that colonized subsurface cavities beneath microbial mats in tidal sands of
48 the Barberton Greenstone Belt (BGB), South Africa.

49

50 **GEOLOGICAL AND PALEOENVIRONMENTAL SETTING**

51 The Moodies Group (~3.22 Ga), uppermost unit of the BGB (ca. 3.57-3.22 Ga), comprises mainly
52 fine- to coarse-grained, quartz-rich sandstones and subordinate conglomerates, siltstones, and thin
53 volcanic tuffs deposited in tidal and deltaic settings (Anhaeusser, 1976; Eriksson, 1978; Eriksson,
54 1979; Heubeck and Lowe, 1994; Heubeck and Lowe, 1999; Heubeck et al., 2013). Moodies strata
55 are particularly well preserved on the ~3-km-thick overturned limb of the Saddleback Syncline in
56 the central BGB north of the Inyoka Fault where they have undergone only lower-greenschist-
57 facies metamorphism (Toulkeridis et al., 1998). The lower part of this succession (unit MdQ1 of
58 Anhaeusser, 1976), approx. 1 km thick, contains the world's oldest known record of macroscopic
59 microbial mats in a siliciclastic tidal setting, laterally traceable for about 15 kilometers (Noffke et
60 al., 2006; Heubeck, 2009; Homann et al., 2015). The mats, preserved as kerogen-rich laminae,
61 developed distinct morphological adaptations to coastal floodplain, supra-, and intertidal
62 conditions and were likely formed by phototrophic microbial communities (Homann et al., 2015).
63 They are commonly underlain by chert lenses, which we interpret as former cavities beneath
64 unconsolidated but microbially-bound cohesive sediment (Fig 1A). In the studied unit of the
65 Moodies Group these bedding-parallel chert-filled cavities are restricted to tidal-facies, fine- to
66 coarse-grained sandstones and contain kerogenous microstructures described below.

67

68 **SAMPLES AND METHODS**

69 Outcrop samples were slabbed, polished and thin-sectioned. For scanning electron microscopy
70 (SEM), only fresh chert samples without weathered surfaces or fractures were selected in order to
71 avoid contamination. Samples were mechanically broken, cleaned in an ultrasonic bath and
72 immediately dried and gold-coated. Sample analysis was performed at the Freie Universität Berlin

73 using a ZEISS SUPRA 40 VP SEM operating with 20 kV acceleration voltage. *In situ* carbon
74 isotope analyses of silicified kerogen were performed with a CAMECA IMS 1280 at the Swiss
75 SIMS facility located at the University of Lausanne, Switzerland.

76

77 **RESULTS**

78 **Cavities and associated kerogenous microstructures**

79 The lens-shaped, laterally-tapering cavities are up to 10s of cm in width and less than 0.5 cm in
80 height. They typically occur below a <3 mm thin sandstone layer, which is overlain by a fossil
81 microbial mat (Fig. 1B). Cavity ceilings are commonly coated by dark, kerogenous laminae with
82 downward-facing protrusions and pendant columns that are up to 1.5 mm in length and 0.6 mm
83 wide (Fig. 2A). Well-preserved single or coalescing columns contain multiple, closely spaced, 1-5
84 μm thick, subparallel stromatolitic laminae of kerogenous composition that are oriented convex-
85 down and taper toward the margins of the columns (Figs. 2B and 2C). Occasionally, the columns
86 terminate in a prominent, up to 30 μm -thick lamina (Fig. 2C). Remnants of zoned ferroan dolomite
87 rhombs, 10-100 μm in diameter, occur scattered throughout the cavity-filling chert and are
88 particularly abundant in the tips of some columns (Figs. 2D-F). The dark kerogenous laminae are
89 commonly encrusted by light-colored silicified cements that are 100-400 μm thick and widely
90 discontinuous. In some places, these cement crusts are botryoidal and contain bladed to acicular
91 ghost crystals resembling aragonite (Fig. 2G and 2H; Grotzinger and Reed, 1983). In other places,
92 laminae are disrupted and bent upwards (Fig. 2H) or occur as detached, slightly deformed
93 fragments near the cavity floor (Fig. 2I).

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97 **Filamentous microfossils**

98 SEM images of the cavity-filling chert show a meshwork of interwoven filamentous molds that is
99 completely embedded in the chert (Fig. 3A). These thread-like, non-bifurcating filamentous
100 microstructures are 0.3-0.5 μm in diameter (n=180) and reach several 10s of μm in length. They
101 are commonly bent with abundant changes in orientation; in places, they show a subdivision in
102 regularly-spaced, ~ 2 μm -long, rod-shaped segments (Figs. 3B-D). Individual segments are about
103 five-times longer than wide and have rounded ends. Transverse cross-sections through filamentous
104 structures show that they are cylindrical, hollow and encased by a ~ 100 nm-thick silica layer (Figs.
105 3D-F).

106

107 **Carbon isotope data**

108 *In-situ* measured $\delta^{13}\text{C}_{\text{PDB}}$ (Peedee belemnite) values from the kerogenous laminae within the
109 cavities vary between -32.3‰ and -21.3‰ with a mean value of -26.5‰ (n=12; Figs. 4A and 4B),
110 which is consistent with a biotic origin of the kerogen (Schidlowski, 2001). Bulk $\delta^{13}\text{C}_{\text{PDB}}$
111 measurements of extracted kerogenous material from the mats above the cavities show a similar
112 range of values (i.e., between -33.2‰ and -21.9‰) with a slightly more negative mean value of -
113 29.5‰ (n=6). Poorly preserved dolomite crystals within the chert yield mean values of -0.3‰
114 $\delta^{13}\text{C}_{\text{PDB}}$ and -14.9‰ $\delta^{18}\text{O}_{\text{PDB}}$ (n=6) that are common values for dolomitic carbonates of Archean
115 age (Schidlowski et al., 1975; Shields and Veizer, 2002; Grossman, 2012)

116

117 **DISCUSSION**

118 The shape and size of the observed cavities resemble gas-filled, fenestral hollows in modern tidal
119 environments that widely occur near the sediment-water interface a few millimeters to centimeters
120 beneath cohesive, impermeable microbial mats and mat-bound sediments (Gerdes et al., 2000;

121 Schieber et al., 2007). Such cavities form either through accumulation of gases produced by
122 metabolic activity (e.g. O₂, CO₂, CH₄) or simply by tidal-driven hydraulic pumping of the ambient
123 air trapped in pore space.

124 The *in situ* formation of the kerogenous lamina with common columnar microstromatolitic
125 structures at the cavity ceiling is evidenced by their downward accretionary growth habit. This
126 particular geometry is well-known from cavity-dwelling microorganisms attached to the roof of
127 cryptic voids, e.g., in Paleo- and Mesozoic reefal limestones (Kobluk and James, 1979; Olivier et
128 al., 2003; Jakubowicz et al., 2014) and has also been observed in modern sea caves that are
129 encrusted by pendant microbialites (Léveillé et al., 2000). Hence, we conclude that the
130 microstromatolitic structures found in the cavities of the Moodies Group were built by a
131 coelobiontic community distinct from those of the overlying epibenthic microbial mats.

132 The carbonate cement fans alternating with the kerogenous laminae built by coelobionts likely
133 formed through abiogenetic encrustation (Riding, 2008) during periods of partial or complete
134 desiccation, a common feature in tidal environments. Subsequently, early silicification replaced
135 large parts of the carbonates and prevented the destruction of the cavities while promoting the
136 preservation of the biological components (Bartley, 1996).

137 The biogenic origin of the observed filaments is supported by the following attributes: (1) tubular
138 morphology with constant diameter; (2) regular segmentation; (3) hollow interior; (4) colonial
139 occurrence; and (5) curved appearance indicating a former flexibility (Schopf, 2004). The
140 morphology of the filaments with respect to their size, shape, and cell-like segmentation is
141 strikingly similar to that of modern filamentous microorganisms (Boone et al., 2001), such as some
142 chemotrophic (e.g., methanogens) and phototrophic bacteria (e.g., non-sulfur and cyanobacteria),
143 which are known to be well preserved in modern siliceous stromatolites and other settings (Jones
144 et al., 2005). Similar filamentous structures have been identified as former microorganisms in

145 chert-filled cavities from 1.2 Ga-old paleokarst deposits (Horodyski and Knauth, 1994) and in
146 various shallow-marine cherts of Archean age (Schopf, 2006; Westall et al., 2006; Sugitani et al.,
147 2013).

148 The radiation-screening effect of epibenthic microbial mats creates UV-protected subsurface
149 habitats a few millimeters beneath the mat. (Garcia-Pichel and Bebout, 1996; Jackson, 2014). The
150 supposedly high Archean UV flux reaching the surface would have made such niches even more
151 favorable for microorganisms (Cockell, 1998). A modern analog environment with increased solar
152 radiation is found in Chilean high-altitude hot-spring sinters where photosynthetic communities
153 thrive in UV-protected voids 1-10 mm below the siliceous sinter surface (Phoenix et al., 2006). If
154 the photosynthetically active radiation penetrating into the cavities described in this study was not
155 sufficient for photosynthesis it can be assumed that the microbial communities were dominated by
156 chemotrophic organisms. Rasmussen et al. (2009) reported geochemical evidence for the presence
157 of chemotrophic coelobionts preserved as columnar microstructures in synsedimentary cavities of
158 the Neoproterozoic Fortescue Group (Australia). They interpreted the negative $\delta^{32}\text{S}$ values (-8.5‰) of
159 pyrites within the columns as evidence for sulfur-respiring microorganism and the extremely
160 depleted $\delta^{13}\text{C}$ values (between -55.4‰ and -43.3‰) of the organic laminae as evidence for
161 methanotrophic metabolism. Although the Moodies Group structures are morphologically similar
162 those described by Rasmussen et al. (2009), Moodies coelobionts lack cavity-associated sulfide
163 minerals and the $\delta^{13}\text{C}$ values of the kerogen (between -32.3‰ and -21.3‰) are not indicative of an
164 ecosystem dominated by methanotrophs. Beyond excluding a methanotrophic metabolism of the
165 coelobionts, the isotopic data and the observed microfossils are consistent with both, a purely
166 chemotrophic or a photosynthetic community (House et al., 2000; Williford et al., 2013); the latter
167 being the dominant metabolism of the surficial mats located a few millimeters above the cavities
168 (Homann et al., 2015). In conclusion, the here reported data not only records the oldest evidence

169 for cavity-dwelling life on Earth, but can also serve as an analog for UV-protected extraterrestrial
170 habitats e.g. on Mars.

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321 *Acta*, v. 104, p. 165–182, doi: 10.1016/j.gca.2012.11.005.

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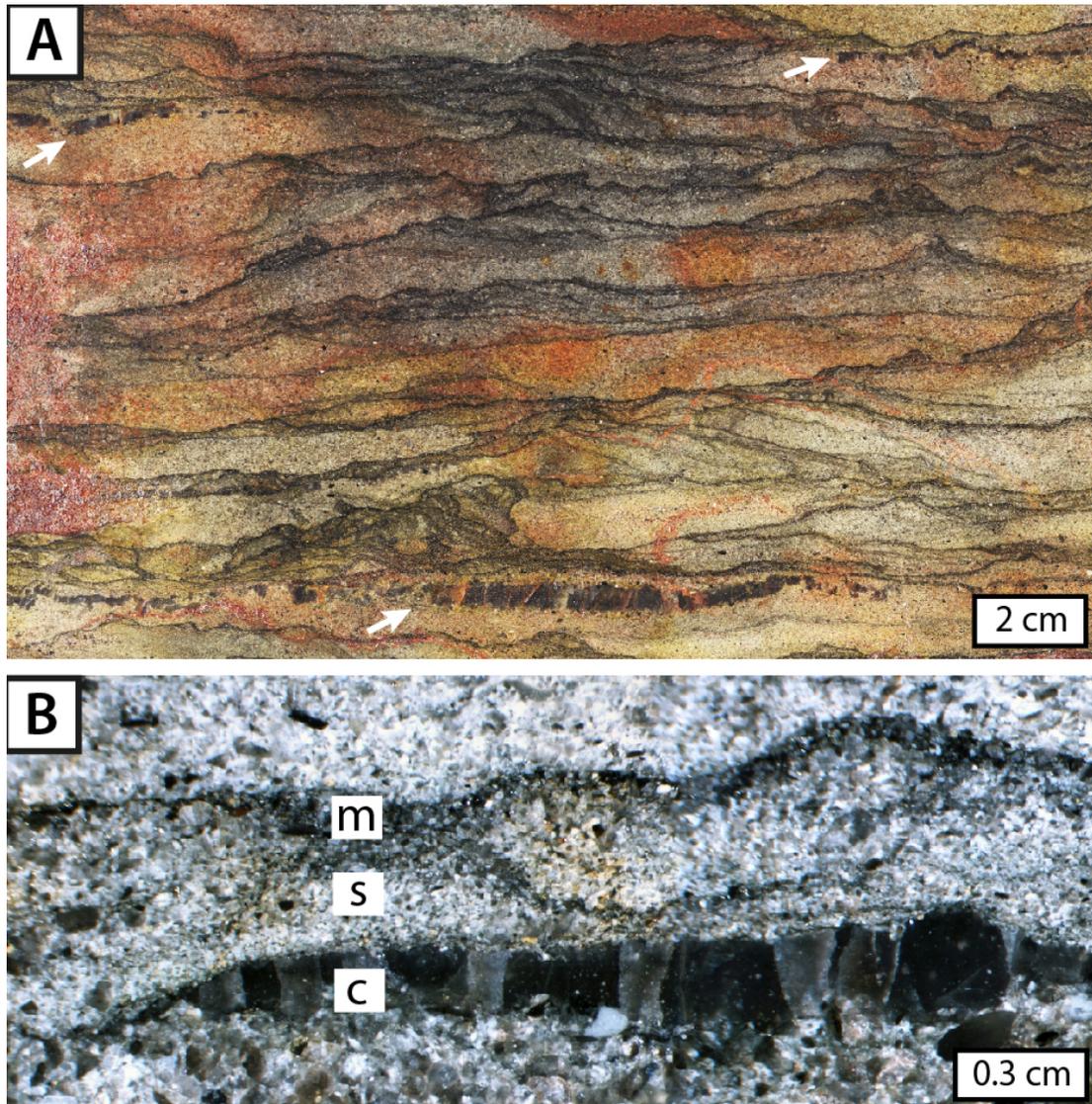
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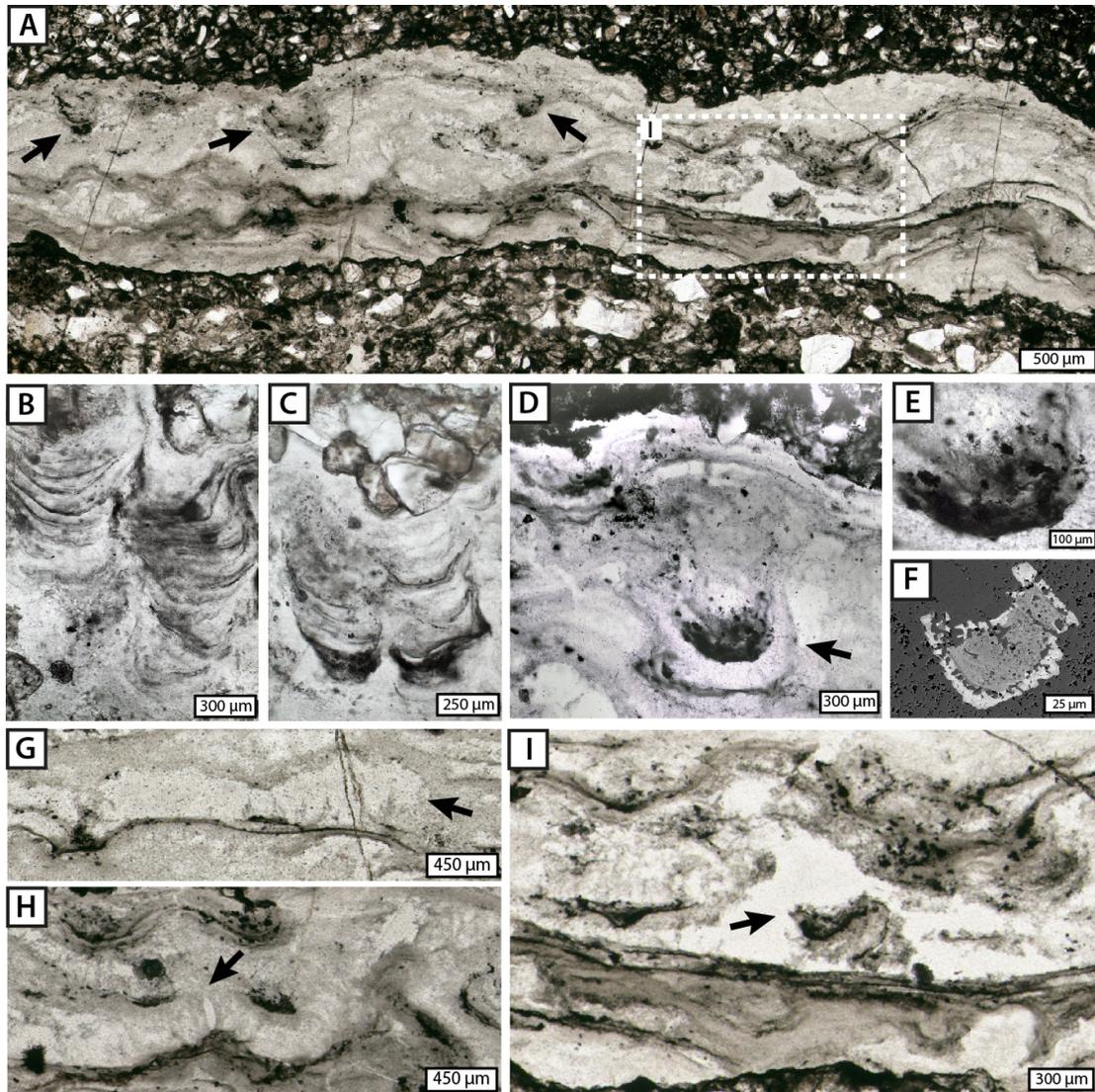
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335 Figure 1. Polished slab photographs of microbial mats (dark laminae) of the Moodies Group
336 associated with chert-filled cavities. A: Lens-shaped, bedding-parallel cavities beneath the mats
337 (arrows). B: Detail view of lateral tapering cavity (c), which contains abundant kerogenous
338 microstructures and occurs below a thin layer of microbially-bound sediment (s) that is overlain by
339 a fossil mat (m).

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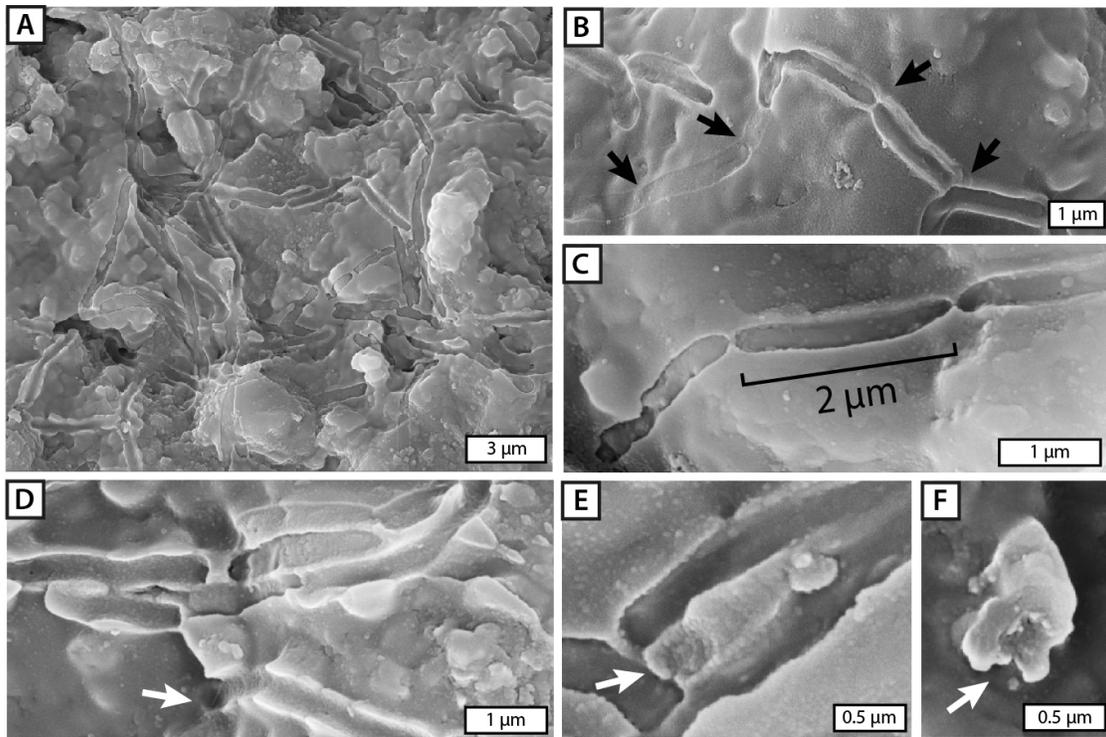
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 343 Figure 2. Transmitted light photomicrographs of downward accretionary kerogenous laminae
 344 occurring within silicified cavities. A: Laminae with pendant protrusions (arrows) coating the
 345 cavity ceiling. B, C: Downward-facing columnar microstromatolites attached to the cavity ceilings
 346 with preserved kerogenous laminae. D: Pendant column with abundant dolomite remnants at the
 347 tip encased by a cement crust (arrow). E: Close-up of the column tip in D showing dispersed
 348 dolomite remnants. F: Backscatter electron photomicrograph of rhombic dolomite. G: Silicified
 349 cement crust of botryoidal shape (arrow). H: Alternation of laminae and cement crusts containing
 350 acicular crystal ghosts (arrow). Note that the lower lamina is disrupted and bent upwards. I: Close-
 351 up of inset in A showing a detached and slightly deformed lamina fragment (arrow).

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355 Figure 3. Secondary electron photomicrographs of filamentous microstructures permineralized by
356 chert. A: Meshwork of filament molds embedded in chert. B, C: Filamentous molds subdivided in
357 regularly-spaced, rod-shaped segments (arrows) of similar length. D, E, F: Cell-molds in transverse
358 cross-section showing a tubular morphology encased by silica (arrows).

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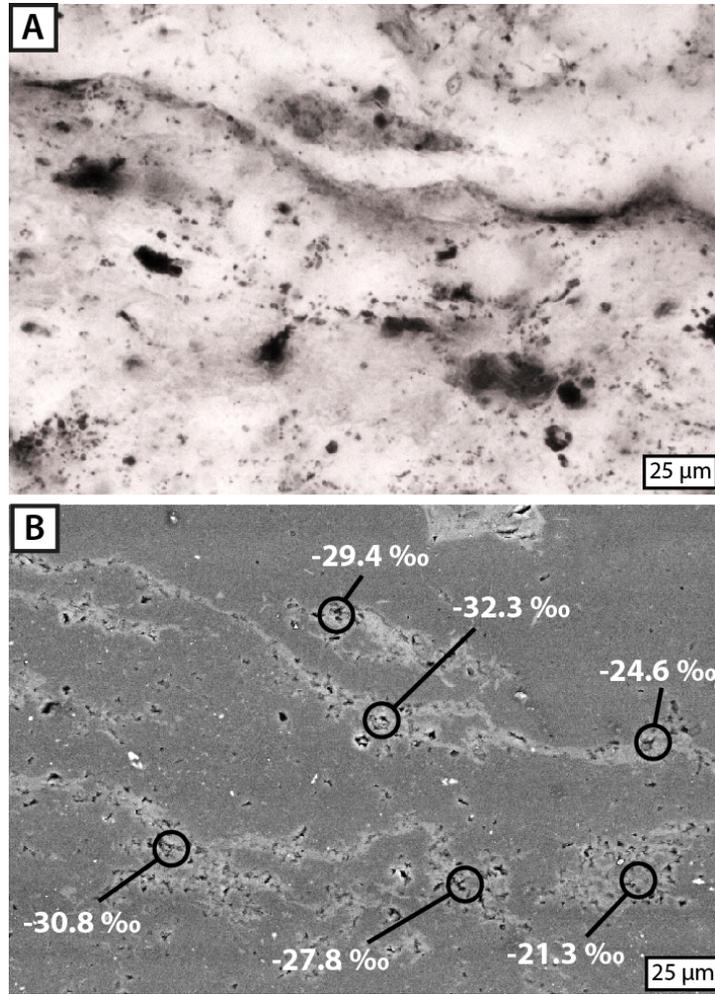
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366 Figure. 4 A: Thin section photomicrograph displaying kerogenous lamina. B: Backscatter electron
367 photomicrograph of A with SIMS analytical areas and corresponding $\delta^{13}\text{C}_{\text{PDB}}$ values.

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387 ¹GSA Data Repository item 2015xxx, Figures DR1-DR4 (sample locality, Raman spectroscopy,
388 filament size distribution) and Table DR1 (SIMS isotope data), is available online at
389 www.geosociety.org/pubs/xxx.htm, or on request from editing@geosociety.org or Documents
390 Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.