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1 **Unusual microbial mat-related structural diversity 2.1 billion**
2 **years ago and implications for the Francevillian biota**

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15
16 **Abstract**

17 The 2.1-billion-year-old (Ga) Francevillian series in Gabon hosts some of the oldest reported
18 macroscopic fossils of various sizes and shapes, stimulating new debates on the origin,
19 evolution and organization of early complex life. Here we document ten representative types
20 of exceptionally well-preserved mat-related structures, comprising ‘elephant-skin’ textures,
21 putative macro-tufted microbial mats, domal buildups, flat pyritized structures, discoidal
22 microbial colonies, horizontal mat growth patterns, wrinkle structures, ‘kinneyia’ structures,
23 linear patterns and nodule-like structures. A combination of petrographic analyses, scanning
24 electron microscopy, Raman spectroscopy and organic elemental analyses of carbon-rich
25 laminae and microtexture converge on a biological origin for these structures. The observed
26 microtextures encompass oriented grains, floating silt-sized quartz grains, concentrated heavy

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3 27 minerals, randomly oriented clays, wavy-crinkly laminae and pyritized structures. Based on
4
5 28 comparisons with modern analogues, as well as an average $\delta^{13}\text{C}$ organic matter (C_{org})
6
7 29 composition of $-32.94 \pm 1.17\text{‰}$ (1 standard deviation, s.d.) with an outlier of -41.26‰ , we
8
9 30 argue that the mat-related structures contain relicts of multiple carbon pathways including
10
11 31 heterotrophic recycling of photosynthetically derived C_{org} . Moreover, the relatively close
12
13 32 association of the macroscopic fossil assemblages to the microbial mats may imply that
14
15 33 microbial communities acted as potential benthic O_2 oases linked to oxyphototrophic
16
17 34 cyanobacterial mats and grazing grounds. In addition, the mat's presence likely improved the
18
19 35 preservation of the oldest large colonial organisms, as they are known to strongly biostabilize
20
21 36 sediments. Our findings highlight the oldest community assemblage of microscopic and
22
23 37 macroscopic biota in the aftermath of the 'Great Oxidation Event', widening our
24
25 38 understanding of biological organization during Earth's middle age.
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31 **Introduction**

32
33 41 The Paleoproterozoic Era hosted one of the most important geochemical events in Earth's
34
35 42 history, marked by a measurable accumulation of atmospheric oxygen, the so-called 'Great
36
37 43 Oxidation Event' (GOE) between 2.45–2.32 billion years ago (Ga). Evidence for the GOE
38
39 44 comes from the disappearance of detrital pyrite, uraninite and siderite from fluvial and deltaic
40
41 45 deposits, an increase in the retention of iron in paleosols, an enrichment of Cr and U in iron
42
43 46 formations, and perhaps most importantly, the disappearance of sedimentary sulfur isotope
44
45 47 mass-independent (S-MIF) anomalies indicative of atmospheric SO_2 processing in the
46
47 48 absence of appreciable ozone (Holland, 2002; Bekker *et al.*, 2004; Farquhar *et al.*, 2011;
48
49 49 Konhauser *et al.*, 2011; Partin *et al.*, 2013a; Lyons *et al.*, 2014). In the wake of the GOE,
50
51 50 large positive excursions in the $\delta^{13}\text{C}$ of marine inorganic carbon, during the 'Lomagundi
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53 51 Event' *ca.* 2.22–2.1 Ga (Karhu & Holland, 1996), is believed to reflect large-scale burial of
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3 52 organic matter in marine sediments (Berner, 2004; Bekker & Holland, 2012). New evidence
4
5 53 suggests that the ‘Lomagundi Event’ ended with a drastic drop in Earth’s oxygen content (*e.g.*
6
7 54 Partin *et al.*, 2013b), perhaps related to large-scale oxidation of organic carbon (Canfield *et*
8
9 55 *al.*, 2013) and/or changes in ocean biogeochemical processes that may have inhibited primary
10
11 56 productivity (Chi Fru *et al.*, 2015).

13 57 The Francevillian sedimentary rocks *ca.* 2.1 Ga record these biogeochemical
14
15 58 fluctuations in Earth’s oxygen accumulation dynamics through extreme excursions in the
16
17 59 carbon cycle, in addition to hosting the oldest large colonial macroorganisms (El Albani *et al.*,
18
19 60 2010, 2014). Major elements, trace metals, organic carbon and isotope analyses offer
20
21 61 constraints on the basin geochemistry, revealing variations from the base to the top that are
22
23 62 linked to sea level changes (Canfield *et al.*, 2013; Bankole *et al.*, 2016). The Lower
24
25 63 Francevillian fluviatile rocks were deposited in oxygenated waters (Bankole *et al.*, 2016),
26
27 64 whereas the Upper Francevillian marine rocks were deposited in oxic, ferruginous and euxinic
28
29 65 waters (Canfield *et al.*, 2013). The large macrofossils are highly variable in terms of size,
30
31 66 shape and pyritization process being represented by lobate, elongated and rod-shaped as well
32
33 67 as disk-shaped morphotypes. The pyritization process did not fully occur in the circular disks,
34
35 68 indicating that their organic composition differs from that of pyritized specimens (El Albani *et*
36
37 69 *al.*, 2010, 2014). In addition, some carbonaceous spheroidal microstructures have also been
38
39 70 reported as organic-walled acritarchs that might have a planktonic origin.

41
42
43 71 Recently, microbial fossils were found in the Francevillian sequence, including
44
45 72 putative bacteriomorphous structures (Dubois *et al.*, 2015) and a Gunflint-type assemblage of
46
47 73 microfossils in the stromatolitic units (Lekele Baghekema *et al.*, 2017). The presence of
48
49 74 colonial macroorganisms and microfossils makes the Francevillian biota unique, but
50
51 75 interestingly, evidence of microbial mats has never been demonstrated. In this work, we
52
53 76 describe for the first time ever microbial mat-related structures (MRS) from 2.1 Ga
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3 77 siliciclastic sandstones and black shales from the FB2 Member of the Francevillian basin,
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5 78 Gabon. MRS are physical remains of destroyed mats and structures associated with decay,
6
7 79 instead of well-preserved mat growth features (Eriksson *et al.*, 2010). Their sedimentary
8
9 80 features are preserved because microbes secrete extracellular polymeric substances (EPS), an
10
11 81 adhesive mucilage (Decho, 2000), that provide a coherent and protective coating that is
12
13 82 unlikely to arise in sediments without a biological input (Gerdes *et al.*, 1993, 2000; Porada &
14
15 83 Bouougri, 2007; Noffke, 2010).

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17
18 84 Microbial life in the Paleoproterozoic has been poorly described (Davies *et al.*, 2016)
19
20 85 even though existing paleontological and biogeochemical evidence points towards the
21
22 86 existence of significant microbial diversity previously in the Archean. Through a combination
23
24 87 of macroscopic and microtexture analyses, petrographic, geochemical, organic elemental
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26 88 analyses and stable carbon isotope composition of bulk organic matter, we compare modern
27
28 89 and fossil mat-related structures, in order to characterize the marine paleoenvironment in
29
30 90 which the putative microbial mats formed. The data reveal the biogenicity of these structures,
31
32 91 adding new insights into the origins of the Francevillian biota (El Albani *et al.*, 2010; Ossa
33
34 92 Ossa, 2010; Parize *et al.*, 2013; El Albani *et al.*, 2014; Ngombi Pemba, 2014; Reynaud *et al.*,
35
36 93 2017). Importantly, we assessed and described the organisational, ecological and
37
38 94 taphonomical processes that led to the development and preservation of the unique
39
40 95 Francevillian biota.

41 42 43 44 45 46 97 **Geological background**

47
48 98 The Francevillian basin, located in the southeastern part of the Republic of Gabon (Figure 1a),
49
50 99 is a 35,000 km² depression comprising 2.2-2.0 Ga marine sedimentary rocks that
51
52 100 unconformably overly an Archean basement (Weber, 1969). Petrographic and geochemical
53
54 101 analyses indicate that the Francevillian sediments were not affected by metamorphic

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3 102 transformation (maximum temperature 100 °C; Gauthier-Lafaye & Weber, 1989; Ngombi-
4
5 103 Pemba *et al.*, 2014), resulting in the preservation of seawater composition at the time when
6
7 104 deposition took place. Moreover, carbon isotopic and redox sensitive element compositions
8
9 105 suggest that the ‘Lomagundi Event’ was a global event (Canfield *et al.* 2013).

10
11 106 The basin fill, composed of siliciclastic fluvial and marine deposits that are 1000–2500
12
13 107 m thick, is subdivided into four major lithostratigraphic formations, FA to FD (Figure 1b;
14
15 108 Weber, 1969; Gauthier-Lafaye & Weber, 1989; Gauthier-Lafaye, 2006; El Albani *et al.*, 2010,
16
17 109 2014). Fluvial to deltaic conglomeratic sandstones, overlain by marine sandstones
18
19 110 deposited in a tidal environment (i.e., syntectonic filling), make up the FA Formation, with
20
21 111 the overlying sediments hosting diagenetic uranium ore deposits and the natural nuclear
22
23 112 fission reactors of Oklo (Gauthier-Lafaye & Weber, 1989, 2003). The marine-dominated FB
24
25 113 sequence rests unconformably on FA. The former was deposited below storm wave base
26
27 114 during basin deepening, and is subdivided into the FB1 (a, b and c) and FB2 (a and b)
28
29 115 subunits. The FB1a and FB1b subunits are composed of interbedded shales, sandstones and
30
31 116 conglomerate, stacked into fining upwards packages, while the overlying FB1c subunit
32
33 117 mainly consists of black shales with a thin iron formation, likely corresponding to a maximum
34
35 118 flooding surface. This is then overlain by thick Mn-rich carbonates. Massive sandstone beds
36
37 119 of the FB2a subunit, probably deposited in channels near the fair-weather wave base, are
38
39 120 capped by thinly laminated black shales that are 5 m thick, and interbedded with thin siltstone
40
41 121 layers (FB2b), presumably deposited by waning storm surges. Outcrops of the FB2b subunit
42
43 122 are scarce but host the well-known colonial macroorganisms described in El Albani *et al.*
44
45 123 (2010, 2014). The overlying FC Formation consists of dolomite and thickly-banded
46
47 124 stromatolitic cherts that were deposited under shallow-water conditions (Bertrand-Sarfati &
48
49 125 Potin, 1994). The uppermost FD Formation consists mainly of black shales, with pyroclastic
50
51 126 material at the top deposited in a deep marine environment (Gauthier-Lafaye & Weber, 2003).

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2
3 127 The Francevillian basin has been intensively studied because of economic interests in
4
5 128 their uranium and manganese ore content (Gauthier-Lafaye & Weber, 1989, 2003).
6
7 129 Consequently, various ages have been obtained for the Francevillian sediments. For example,
8
9 130 monazites contained in Archean plutonic rocks from the Chaillu massif close to the FA
10
11 131 Formation transition provided U-Pb ages of 2998 ± 25 Ma to 2621 ± 30 Ma (Mouélé *et al.*,
12
13 132 2014). A U-Pb age of 2050 ± 30 Ma reported for uranium mineralization, delineates early
14
15 133 diagenesis at the FA-FB boundary (Gancarz, 1978). Coarse-grained syenites of the N’Goutou
16
17 134 volcanic complex, in the northern part of the Republic of Gabon, that are interlayered with
18
19 135 rocks at the base of the FB1 sequence, yield an Rb-Sr age of 2143 ± 143 Ma (Bonhomme *et*
20
21 136 *al.*, 1982). It is considered that these volcanic rocks were formed simultaneously with the
22
23 137 sedimentary rocks. Diagenetic illites from the top of the FB1b subunit have been dated at
24
25 138 2099 ± 115 Ma by using the Sm-Nd method (Bros *et al.*, 1992). Finally, recent dating of
26
27 139 zircons from welded tuffs near the top of the FD Formation produced a U-Pb age of 2083 ± 6
28
29 140 Ma (Horie *et al.*, 2005).

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33 141 The Paleoproterozoic Francevillian MRS were discovered in the Moulendé quarry, the
34
35 142 same fossiliferous quarry where large colonial organisms have been reported (El Albani *et al.*,
36
37 143 2010, 2014). MRS are heterogeneously distributed in the Upper FB2a subunit, as well as in
38
39 144 the overlying laminated black shale. The latter is 5 m thick and forms the FB2b subunit
40
41 145 (Figure 2), covering a ~20 m thick host interval.
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45

46 147 **Methods**

47 148 **Sampling and sample preparation**

48
49 149 About one hundred samples were collected in order to describe large-scale variability in
50
51 150 morphology, structural organization and diversity from outcrops localized in one locality over
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53 151 several years (Figure 1). All samples were logged to provide information on their spatial and
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3 152 time repartitions of the studied area (Figure 2), and then photographed at the University of
4
5 153 Poitiers using a Nikon Europe D610 digital single-lens reflex camera equipped with a Nikon
6
7 154 AF-S 24-120 mm f/4G ED VR lens. Polished slabs were observed using a ZEISS
8
9 155 Discovery.V8 stereoscope combined with Axio Cam ERc 5s microscope camera. Based on
10
11 156 this pre-screening analysis, representative samples were selected and powdered in an agate
12
13 157 mortar for elemental and carbon isotope systematics.
14
15
16 158

17 18 159 Petrographic and mineralogical analysis

19
20 160 Petrographic and mineralogical examinations were performed by transmitted and reflected
21
22 161 light on eight polished thin sections using a Nikon ECLIPSE E600 POL microscope equipped
23
24 162 with a Nikon Digital Sight DS-U1 camera and NIS-Element D software for scanning
25
26 163 observations. Seven thin sections were carbon coated and examined for textural and
27
28 164 compositional analyses using a FEI Quanta 200 scanning electron microscope (SEM) at the
29
30 165 University of Lille 1. The SEM, coupled to Rontec energy-dispersive spectra (EDS) for semi-
31
32 166 quantitative mineral analysis in backscattered electron mode (BSE), was operated at 15 kV
33
34 167 accelerating volts and a 1 nA beam current at a working distance of 10.5 mm.
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38 168

39 40 169 Carbon analysis

41
42 170 Raman spectroscopy was used to determine the composition of carbon preserved within the
43
44 171 MRS on two representative samples. Analyses were carried out at the University of Poitiers
45
46 172 with a HORIBA JOBIN YVON Labram HR800UV, an integrated Olympus confocal
47
48 173 microscope coupled to a Peltier-cooled CCD detector. All analyses were performed by means
49
50 174 of 514.5 nm Ar⁺ laser of 1 mW, 200 µm confocal hole, 1800 grooves/mm grating. Data
51
52 175 recording and treatment were done with LabSpec 5 software.
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55 176 Ten representative samples, composed of five mat samples and five associated
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3 177 surrounding sediments, were crushed for the determination of the elemental content of
4
5 178 associated organic matter, as well as carbon and sulfur composition, at the University of
6
7 179 Poitiers. Analyses were performed using a CHNS analyser, model FlashEA 1112
8
9 180 (ThermoFisher Scientific) by flash dynamic combustion at 970 °C under a constant flow of
10
11 181 helium. Data were recorded using Eager 300 software. A calibration curve was obtained with
12
13 182 sulfanilamide and BBOT – 2,5-Bis(5-tert-butyl-benzoxazol-2-yl)thiophene – before each
14
15 183 analysis. The results of carbon contents include both inorganic and organic carbon, but
16
17 184 petrographic analyses showed that calcium carbonate and dolomite concentrations were low.

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19
20 185 Stable carbon isotope measurements (^{12}C , ^{13}C) of organic matter from 14 mat samples
21
22 186 (from both FB2a and FB2b subunits) were conducted at the Stable Isotopes Laboratory of
23
24 187 UMR Pegase (INRA Rennes, France), using an elemental analyser coupled with an isotope
25
26 188 ratio mass spectrometer (IRMS) (VG Isoprime; UMR PEGASE – INRA Rennes). More than
27
28 189 500 mg of fine-grained powders were analysed and loaded in tin capsules for each sample.
29
30 190 IAEA-C6 (sucrose ANU, $\delta^{13}\text{C} = -10.63\text{‰}$), USGS-24 (graphite, $\delta^{13}\text{C} = -15.98\text{‰}$), USGS-40
31
32 191 (glutamic acid, $\delta^{13}\text{C} = -26.32\text{‰}$) and Urea Isotopic Working Standard ($\delta^{13}\text{C} = -38.3\text{‰}$) were
33
34 192 used as reference standards. Data are expressed as delta values (‰) relative to Vienna Pee
35
36 193 Dee Belemnite (V-PDB). No correction was added to the measured values, and the analytical
37
38 194 uncertainty is estimated to be lower than 0.2‰.

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42 43 196 **Facies analysis of the Moulendé Quarry**

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45 197 The Moulendé quarry has been examined over an area of ~ 5 ha, for a total of nine studied
46
47 198 outcrops (Figure 3a). Among them, the F8 outcrop (Figure 3a-c) was logged in detail because
48
49 199 of its well-exposed strata and sedimentary structures. It is the only outcrop where the FB2a-
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51 200 FB2b transition is observed with accompanying black shale deposits. Lithological
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53 201 composition, vertical facies relationships and sedimentary features allow recognition of two
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3 202 depositional facies from the MRS-bearing strata.
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7 204 Facies 1
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10 205 Thick-bedded, coarse-grained sandstones represent the main facies of the Moulendé quarry.
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12 206 These deposits are commonly referred to the Poubara sandstones (FB2a subunit; Figures 2,
13

14 207 3a-c). This facies is 15 m thick in the quarry, as well as in the closest drill core (GR5; Azziley
15

16 208 Azzibrouck, 1986), but could be up to 100 m thick elsewhere in the basin (Weber, 1969).
17

18 209 Interbedded thin-bedded, coarse-grained sandstones and laminated black shales form
19

20 210 heterolithic beds. The uppermost massive sandstone bed is laterally heterogeneous in
21

22 211 thickness and its bedding surface is undulatory. At the top of several massive sandstone beds,
23

24 212 sedimentary features, including load structures, sandstone clasts and water escape structures,
25

26 213 such as dishes, are present. These beds occasionally contain dm-scale hummocky cross
27

28 214 stratification (HCS), restricted to the upper part of the succession (Figures 2, 3d; Reynaud *et*
29

30 215 *al.*, 2017).
31

32 216
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34
35 217 Facies 2
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37 218 Numerous thin-bedded, parallel-laminated black shales with interbeds of siltstones lie
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39 219 conformably upon Facies 1. They form stacks of variable thickness in the upper part of the
40

41 220 studied succession and are about 5 m thick. Connected to the underlying facies and
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43 221 approximately 0.4 m in height, a sandstone dyke cross-cuts these multilayered black shales
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45 222 (Figures 2, 3e). There is no evidence of fracturing along the dyke, indicating that the
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47 223 sediments were not consolidated prior to injection. The main component of facies 2 is
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49 224 characterized by rhythmic successions of mm-scale light and dark laminae of siltstones and
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51 225 shales. Small-scale cross-laminae are found within mm-thick interbedded siltstones. Load-
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53 226 shaped and flame-shaped structures forming convolute bedding (Figures 2, 3f) are observed in
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3 227 interbedded medium-to-coarse-grained siltstone beds ranging from 2 to 5 cm in thickness.
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5 228 Interference ripples are also observed, indicating paleowaves coming from two directions
6
7 229 (Figures 2, 3g). Lastly, a dm-scale bed containing dark-coloured convex laminae associated
8
9 230 with cm-scale current ripples comprise the thickest interbedded coarse-grained siltstones
10
11 231 (Figures 2, 3h).

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13 232

14 15 16 233 Interpretations

17
18 234 The variation in thickness of the uppermost massive sandstone level (at ~15 m in the
19
20 235 stratigraphy) may be related to detachment folds and troughs later infilled by overlying
21
22 236 sediments (Reynaud *et al.*, 2017). Sudden and rapid deposition of coarse-grained sediments
23
24 237 produce load and dish structures by immediate dewatering (Reineck & Singh, 1980). Rapid
25
26 238 sedimentation also results in sandstone dykes formed by elevated pore pressures leading to
27
28 239 fluidization of the unconsolidated sediment. In addition, conditions that are favourable for the
29
30 240 formation of HCS are commonly found between the fair-weather and storm wave base
31
32 241 (Immenhauser, 2009). Various interpretations have been proposed for the paleoenvironmental
33
34 242 setting of the FB2a subunit. They range from a deltaic paleoenvironment subjected to tidal
35
36 243 influence (El Albani *et al.*, 2010; Ossa Ossa, 2010), to a shoreface paleoenvironmental setting
37
38 244 (Ngombi Pemba, 2014), to a turbidite lobe setting in waters deeper than 200 m (Parize *et al.*,
39
40 245 2013). Reynaud *et al.* (2017) showed that the Poubara sandstones are composed of high-
41
42 246 density sediment gravity flow deposits, emplaced during a forced regressive system tract.
43
44 247 These authors underline that the Francevillian basin was likely isolated because of the absence
45
46 248 of wave deposits. They also noticed the presence of linguoid and interference ripples that is
47
48 249 consistent with shallow water settings.

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52
53 250 Thinly laminated black shales are deposited in a relatively quiet water setting but
54
55 251 interrupted by quickly deposited supplies of millimetre-to-centimetre-scale siltstones. These

1
2
3 252 laminae host many sedimentary structures that indicate a strong current. Reynaud *et al.* (2017)
4
5 253 suggest that these sediments were deposited close to the maximum regressive surface whereas
6
7 254 Parize *et al.* (2013) argue for the deposition of turbidites on an upper slope setting.
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10 255

11 256 **Mat-related structures (MRS) in the FB2 Member**

12
13
14 257 The MRS documented here come from a 20 m thick interval of the FB2 sequence (Figure 2).
15
16 258 Some specimens are entirely or partially pyritized, while others display a few isolated pyrite
17
18 259 grains within the mat layers. Following the classification scheme by Sarkar *et al.* (2008), the
19
20 260 Francevillian MRS are divided into two major categories: (1) mat-layer structures,
21
22 261 representing potential in situ growth of a microbial mat (Figures 4-5, Figure S1) and (2) mat-
23
24 262 protected structures (Figure 6), possibly formed by abiotic processes but requiring the
25
26 263 protection of a microbial mat (Davies *et al.*, 2016).
27
28
29 264

30 31 265 1. Mat-layer structures

32
33 266 This group of MRS represents the “mat-layer itself that may be intact, deformed or rafted”
34
35 267 (Sarkar *et al.*, 2008). In this work, we interpret well-preserved, intact mat growth according to
36
37 268 the following criteria.
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39
40 269

41 42 270 1a. ‘Elephant-skin’ textures

43 44 271 Description

45
46 272 ‘Elephant-skin’ textures (Runnegar & Fedonkin, 1992) encompass quasi-polygonal,
47
48 273 geometrically distinct reticulate patterns, ranging from the millimetre to centimetre scale, and
49
50 274 bearing bulges or ridges (Figure 4a-c). They are both identified at the top of the massive
51
52 275 Poubara sandstones and the interbedded siltstones in the black shales (Figure 2). Individual
53
54 276 polygons are 0.3–1.3 cm in diameter, with a maximum relief of 0.2 cm.
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3 277 Microscopic analyses show reticulate patterns preserved as non-homogenous dark
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5 278 laminae above a light, coarser material 200 to 600 μm thick (Figure 7a, f). The overlying
6
7 279 layer consists of abundant wavy-crinkly laminae entangling 20 to 50 μm quartz grains and
8
9 280 heavy minerals (*e.g.*, titanium oxides, apatites and monazites); the latter suggested by the
10
11 281 relative proportions of the elements found through SEM-EDS analysis (Figure S2), as well as
12
13 282 transmitted and reflected light microscopy. Most of the grains in the wavy-crinkly laminae are
14
15 283 randomly arranged within a clayey matrix, and are dominated by O, Al, Si, Mg, K and Fe
16
17 284 (Figure S2; Table S1). Reticulate patterns are also C-rich (up to 8.52%) compared to the
18
19 285 underlying sandstone bed, as evident from the Raman (Figure 8a-c) and organic elemental
20
21 286 analyses (Table S2). The carbonaceous layer is punctuated by tufted microstructures, either on
22
23 287 bulge rims or within the bulges, with similar striking morphologies to each other and where
24
25 288 clay layers are almost vertically oriented (Figures 7f, 9a-b). Based upon the description by
26
27 289 Noffke *et al.* (2013), the height/base index is 30/100 μm to 120/220 μm long, separated at
28
29 290 regular distances of 150 – 230 μm from each other.
30
31
32

33 291

35 292 Interpretation

37 293 ‘Elephant-skin’ textures are formed by a specific arrangement of tufts, pinnacles, bulges and
38
39 294 smaller-scale bulges arranged into ridges. Tufts, often arising in ridge junctions or at the
40
41 295 intersection of microbial bulges, are proposed as a particular type-feature of cyanobacterial
42
43 296 mat filaments growing vertically towards a light source (phototaxis) (Gerdes *et al.*, 2000;
44
45 297 Porada & Bouougri, 2007; Bose & Chafetz, 2009). These textures are known in modern
46
47 298 supratidal environments (Gerdes *et al.*, 2000; Gerdes, 2007; Bose & Chafetz, 2009; Taj *et al.*,
48
49 299 2014), but have also been recorded and described in some ancient shallow water
50
51 300 environments from the terminal Proterozoic (Runnegar & Fedonkin, 1992; Gehling, 1999),
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53 301 and perhaps even the Archean (Flannery & Walter, 2012). However, Shepard & Sumner
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2
3 302 (2010) debated the role of phototaxis in the formation of reticulate patterns and tufted
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5 303 structures. They investigated whether filamentous cyanobacteria were influenced by light to
6
7 304 form polygonal structures or whether they were related to their own morphotype. Thus,
8
9 305 reticulate patterns may result from an undirected motility of filamentous bacteria without the
10
11 306 influence of light.

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13 307

14 308 1b. *Putative macro-tufted microbial mat structures*

15 309 Description

16 310 The putative macro-tufted microbial mats are preserved as positive epireliefs that display
17 311 patches of vertical bump-like structures protruding 0.05–0.2 cm on the upper surface of
18 312 interbedded, coarse-grained siltstones (Figures 2, 4d).

19 313 Microscopic features seen in longitudinal thin sections reveal that the coarse-grained
20 314 siltstone is draped by a 50–500 μm thin, dark, clay-rich layer with floating quartz grains
21 315 (Figure 7b, g-h). These grains are clearly different in size compared to the coarser grains in
22 316 the underlying sediment. Some clay particles are micaceous and oriented more or less parallel
23 317 to the bedding plane. Furthermore, it can be noted that the thickness of this overlying dark
24 318 layer varies along the longitudinal section. The thinner dark-coloured layer is found at the top
25 319 of the microtopography, whereas the thicker one overlies the troughs.

26 320 SEM imaging reveals that the dark lamina encompasses heterogeneously-sized, 5–40
27 321 μm quartz grains and heavy minerals (Figure 9c), while clay minerals are positioned sub-
28 322 vertically. In addition, EDS analyses suggest that these laminated minerals are mainly made
29 323 of O, Si, Al, K elements, with minor Mg, Fe and Na (Table S1), consistent with the elemental
30 324 composition of mica and illite minerals (*e.g.* Velde & Meunier, 2008).

31 325

32 326 Interpretation

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3 327 A similar macro-tufted microbial mat was recorded from a 2.0 Ga paleodesert environment
4
5 328 where 0.2 cm high mound-like structures are randomly arranged on a fine-grained sandstone
6
7 329 (Simpson *et al.*, 2013). The mechanism behind the development of this feature in the
8
9 330 sedimentary rock record remains unclear. However, by changing the polarity of their
10
11 331 filamentous structure, the growth of a microbial biofilm is able to produce similar bump-like
12
13 332 structures in modern sedimentary environment (Gerdes *et al.*, 2000; Gerdes, 2007; Bose &
14
15 333 Chafetz, 2009; Taj *et al.*, 2014). This pattern may also result from the direct filling of the pre-
16
17 334 existing microtopography by mat-building organisms as they grow and expand (Simpson *et*
18
19 335 *al.*, 2013). The smooth but bumpy morphology is likely enhanced by synsedimentary loading
20
21 336 and post-depositional compaction, and so this bio-sedimentary expression could be viewed as
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23 337 a combined microbial and compaction feature.
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29 339 1c. *Domal buildups*

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31 340 Description

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33 341 Domal buildups are preserved as positive bed-top features on bedding surfaces of black shales
34
35 342 (Figure 2). They are characterized by 0.1–0.4 cm convex, domal structures projecting
36
37 343 upwards from the bedding plane. Distinctive features include a cluster of low mound-shaped
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39 344 structures, 0.4 cm in diameter, nearly equal in all instances and without any central
40
41 345 depressions (Figure 4e-f). Alternatively, they can be isolated structures with a diameter
42
43 346 ranging from 0.7 cm to 1.5 cm that seem to reveal a cauliflower-like texture associated with
44
45 347 extensive positive-relief, wrinkled structures (Figure 4g). Circular disks belonging to the
46
47 348 oldest large colonial organisms (El Albani *et al.*, 2014) seem closely associated with these
48
49 349 specific structures. Both isolated and clustered domal structures have been shown to be
50
51 350 pyritized (Table S2). Bulk sulfur level of up 22.16% within the domal structures is associated
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53 351 with a carbon content <0.53%. There are also flat, pyritized mat-related structures without any
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3 352 particular distinctive features that tend to develop close to the clustered domes (Figure 4f,
4
5 353 Figure S1).

6
7 354 Thin sections reveal a well-defined alternation of clay and silt layers beneath the
8
9 355 domal structures (Figure 7c). Most of the quartz particles from the underlying sediment are
10
11 356 laminated and/or have a length of grain-to-grain contact of mostly 20–80 μm . None of these
12
13 357 grains were found in the topmost dark, clay layer. Furthermore, the domal structures typically
14
15 358 show an indication of internal convex lamination between all pyrite grains (Figure 7i), which
16
17 359 reflects the position of the domes in epirelief.

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20 360
21
22 361 Interpretation

23
24 362 Domal buildups have been reported from fluvial and fluviodeltaic settings in Mid-Proterozoic
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26 363 (Garlick, 1988; Schieber, 1998, 1999; Sheldon, 2012; Wilmeth *et al.*, 2014) to shallow water
27
28 364 settings in Late Cambrian times (Bottjer & Hagadorn, 2007). The latter authors proposed that
29
30 365 they “may represent different life histories, biological affinities, and/or histories of interaction
31
32 366 with the physical environment”. Previous studies have also invoked a distinct mat growth
33
34 367 pattern (Wilmeth *et al.*, 2014) and inferred that domal structures are built by an upward
35
36 368 growth of microbial mats. This might reflect competition for light (Garlick, 1988; Schieber,
37
38 369 1999). The $\delta^{13}\text{C}_{\text{org}}$ isotopic signatures of Mesoproterozoic domal-like structures in Copper
39
40 370 Harbor Conglomerate (Upper Peninsula of Michigan) are attributed to photosynthesis
41
42 371 (Sheldon, 2012).

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45 372 EPS possess chemical properties that protect cells by creating sharp geochemical
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47 373 gradients (Decho, 2000), while the anaerobic decay of the buried mat material facilitates the
48
49 374 precipitation of diagenetic minerals such as pyrite, depending on sulfate and iron
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51 375 bioavailability. If this diagenetic mineralization follows individual layers within the EPS
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53 376 demarcated boundaries, or if it is associated with specific features, the former presence of
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3 377 microbial mats are overprinted and preserved as a mineralized signature (Schieber, 1999).
4
5 378 Thus, sulfate-reducing microorganisms probably used the carbonaceous material from the
6
7 379 domal buildups as their electron donor, thereby releasing hydrogen sulfide to react with
8
9 380 available iron. This mechanism is supported by the recurrent low carbon to high sulfur
10
11 381 contents in the materials. Analyses of the sulfur isotope contained in pyrite from the
12
13 382 Francevillian series measured by Secondary Ion Mass Spectrometry (SIMS) further revealed
14
15 383 negative $\delta^{34}\text{S}$ values associated with widespread microbial decay, linked to the activities of
16
17 384 the sulfate-reducing microorganisms (El Albani *et al.*, 2014).
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22 386 1d. *Discoidal microbial colonies*

23 24 387 Description

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26 388 A discoidal microbial colony (Grazhdankin & Gerdes, 2007) is a term for a mat-layer that
27
28 389 includes disk-shaped, internal, centimetre-scale features (Figure 5a-g). Two major distinct
29
30 390 discoidal microbial colony-like morphologies occur on bedding planes in the black shale unit
31
32 391 (Figure 2). The first is characterized by centimetre to the decimetre scale clusters of outward-
33
34 392 convex, rod-shaped structures with internal pyritized concentric bands, possessing a series of
35
36 393 ~0.4 cm wide light and dark zones (Figure 5a-b). This specific feature does not exhibit any
37
38 394 relief. The second variety is made up of well-marked circular bodies represented by sharp
39
40 395 outlines separating the specimens from the surrounding black shale (Figure 5c-g). The disk-
41
42 396 shaped colonies display slight internal concentric zonations, wrinkle features or a lack of any
43
44 397 specific morphological characteristics. A variety of the specimens have a 1.1–1.7 cm high
45
46 398 disk-shaped relief with concentric rims restricted to the edges, which may present themselves
47
48 399 as cauliflower-like patterns varying between 3.3 and 8.2 cm in diameter (Figure 5c-e). There
49
50 400 are numerous distinct large euhedral pyrite crystals on these structures. Less common are
51
52 401 disk-shaped bodies of 2.3 cm in diameter and represented by a minor relief, internal
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3 402 millimetre-scale wrinkles, and devoid of sharp outlines (Figure 5f). Other observable
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5 403 discoidal structures are relatively small (~ 0.5 cm diameter) that do not have particular
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7 404 features (Figure 5g). However, these are the only structures that are entirely pyritized by tiny
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9 405 pyrite crystals.

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11 406

12 13 407 Interpretation

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15 408 Previous studies have shown that a wide range of variability exists in the morphology and
16
17 409 organization of modern discoidal microbial colonies in natural environments (Gerdes *et al.*,
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19 410 1993; Banerjee *et al.*, 2014; Sarkar *et al.*, 2014) as well as under laboratory conditions
20
21 411 (Matsushita *et al.*, 2004). Concentric zonations with a series of light and dark bands represent
22
23 412 a particular variety of discoidal microbial colony known as ‘fairy rings’. Modern ‘fairy ring’
24
25 413 structures are ubiquitous in salt marshes (Gerdes *et al.*, 1993; Gerdes, 2007) and in shallow
26
27 414 water environments (Banerjee *et al.*, 2014). The concentric ring-shaped structures of the
28
29 415 Francevillian series discoidal structures clearly display the same striking morphologies. All
30
31 416 modern examples indicate that filamentous cyanobacteria and diatoms, which are embedded
32
33 417 in EPS and crowned by micro-pinnacles, form these concentric ring-shaped structures. This
34
35 418 arrangement is likely not random but represents an oriented behaviour that might be triggered
36
37 419 by external environmental factors (Gerdes, 2007). So far, the generally accepted mechanism
38
39 420 of formation involves escaping gas bubbles from the substrate, which may cause concentric
40
41 421 wave propagation (Gerdes *et al.*, 1994). Subsequently, chemotactic responses initiated by
42
43 422 adapted filamentous cyanobacteria may form the concentric organizational patterns. Presently,
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45 423 the oldest discoidal microbial colonies that have been described are from Mesoproterozoic
46
47 424 and Neoproterozoic shallow submarine environments (Grazhdankin & Gerdes, 2007;
48
49 425 Banerjee *et al.*, 2010, 2014; Sarkar *et al.*, 2014), where pyritized filamentous structures are
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51 426 sometimes preserved (Grazhdankin & Gerdes, 2007).
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3 4274
5 428 1e. *Horizontal mat growth pattern*6
7 429 Description8
9 430 A unique, outward-convex, spindle-shaped structure extending over 34 cm is developed on
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11 431 the bedding plane surface of the black shale unit (Figures 2, 5h). The structure appears similar
12
13 432 to the spindle-shaped ‘fairy ring’ structures described above. However, this structure is
14
15 433 represented by tiny, 0.1 cm tall, arched ridges, rising horizontally, following a well-defined
16
17 434 geometric pattern. These sharp-crested ridges of 0.15 cm in width are regularly spaced,
18
19 435 commonly dissected and slightly undulated. It appears that the laminae convexity of the
20
21 436 whole structure is unevenly distributed, ranging from 55 to 86 degrees.
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26 438 Interpretation27
28 439 The horizontal mat growth pattern could be related to ‘fairy ring’ structures with which the
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30 440 pattern shares some similarities (*e.g.* outward-convex, spindle-shaped, sharp-crested ridges).
31
32 441 Nevertheless, there are no alternations of light and dark zones. Processes implicated in the
33
34 442 formation of ‘fairy ring’ structures may be involved here, but topography is added. The
35
36 443 orientation of the wave propagation and subsequent millimetre-sized ripples may be induced
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38 444 by gravity. Then, pinnacle-forming organisms would interact with the nutrient front by
39
40 445 chemotactic responses to colonize the substratum, producing the distinct morphology
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42 446 preserved in the sedimentary record. Alternatively, localized mat failure and strain induced by
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44 447 gravity, waves or currents could also explain the morphology as a mechanical deformation of
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46 448 biogenically stabilized sediment. Although it has not been suggested in other studies,
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48 449 morphological features including a point of origin, persistent “growth” in one vector, and
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50 450 sharp boundaries could also be explained by an underwater seep that is confined by a biomat
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52 451 and promotes mat growth in a downslope direction. In any case, the parallel arrangement of
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3 452 ridges, as well as the regularity of components in the horizontal mat growth pattern, suggests
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5 453 a biotic origin.

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8 9 455 2. Mat-protected structures

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11 456 This category of mat-related structures arises from structures that probably require mats for
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13 457 their preservation, the exception being wrinkle marks.

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17 18 459 2a. *Wrinkle structures*

19 20 460 Description

21
22 461 Based on morphology, three types of wrinkle structures are categorized here: wrinkle marks,
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24 462 parallel wavy wrinkle structures and cross-cutting wrinkle structures. Wrinkle marks are
25
26 463 represented as laterally continuous or discontinuous, slight, outward-convex positive relief on
27
28 464 bedding plane of the black shales (Figures 2, 4h).

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30
31 465 Parallel wavy wrinkle structures are preserved as sinuous, continuous ridges separated
32
33 466 by parallel, narrow valleys extending for less than 10 cm on bedding surfaces of sandstones
34
35 467 and interbedded thin-to-medium-bedded siltstones (Figures 2, 6a-b). The ridges have rounded
36
37 468 tops and steep sides, with an individual ridge elevation of 0.1 cm and a spacing of 0.4 cm.
38
39 469 Organic elemental analysis of one sample from the black shale unit does not reveal significant
40
41 470 differences in carbon content between the parallel wavy wrinkle structures and the
42
43 471 surrounding sediment (Table S2). However, microscopic analysis of thin sections, cut
44
45 472 perpendicularly through the wrinkles, indicates that a dark-coloured layer caps the coarse, silt-
46
47 473 sized rippled structures. Further down, the sediment displays quasi-planar laminations (Figure
48
49 474 7d). For the length of the section, the topmost carbonaceous layer is similar in thickness and
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51 475 does not onlap the rippled bed, but instead reproduces its topography (Figure 7j). Oriented
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53 476 quartz grains trapped within the carbonaceous layer (Figure 7j) appear to have the same grain
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3 477 size as those found in the rippled structure. Tiny floating grains are also embedded in the clay-
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5 478 sized fractions. Sheets of various clay particles entangle several heavy minerals, mainly
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7 479 titanium oxides (Table S1).
8

9 480 Cross-cutting wrinkle structures (Banerjee & Jeevankumar, 2005) are characterized by
10
11 481 bifurcating and frequently interconnected asymmetric ridges with intervening sub-parallel
12
13 482 troughs on the bedding surface of black shales (Figures 2, 6c). The rounded ridges are 0.1 to
14
15 483 0.2 cm high, 0.4 to 0.5 cm wide, and their spacings vary from 0.4 to 1 cm. A few dome-like
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17 484 structures of 0.5 to 0.6 cm are close to these cross-cutting wrinkle structures (Figure 6c).
18

19 485 20 21 22 486 Interpretation

23
24 487 Wrinkle structures are one of the most common sedimentary features related to microbial
25
26 488 mats. They are found over a large paleogeographic range, including the deep-sea (Buatois &
27
28 489 Mángano, 2003; Flood *et al.*, 2014), shallow marine (Hagadorn & Bottjer, 1997; Banerjee &
29
30 490 Jeevankumar, 2005; Sarkar *et al.*, 2006; Porada & Bouougri, 2007; Mata & Bottjer, 2009;
31
32 491 Banerjee *et al.*, 2014; Buatois *et al.*, 2014; Sarkar *et al.*, 2014, 2016; Yang *et al.*, 2017),
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34 492 fluvial and lacustrine (Chu *et al.*, 2015, 2017), and even continental environments (Simpson *et*
35
36 493 *al.*, 2013). Some researchers claimed that relative microbial community growth correlates to
37
38 494 with irregular surface of wrinkle structures (Hagadorn & Bottjer, 1997; Banerjee &
39
40 495 Jeevankumar, 2005; Sarkar *et al.*, 2006, 2014).
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44 496 Loading and dewatering processes have also been proposed for wrinkle generation
45
46 497 (Noffke *et al.*, 2002). A recent study has proposed that abiotic mechanisms are unable to
47
48 498 create millimetre-scale ripples (3–15 mm wavelengths) because waves with small orbital
49
50 499 amplitudes are not strong enough to mobilize sand and silt grains (Mariotti *et al.*, 2014). In
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52 500 wave tank experiments, millimetre-scale ripples were perfectly reproduced by means of
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54 501 microbial aggregates rolling along the substrate and transporting grains. The preservation of
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3 502 such structures requires burial by fine material that may be represented by the biostabilization
4
5 503 of a bacterial community. The dark-coloured layer overlapping the silt-sized rippled structures
6
7 504 (Figure 7d, j) is probably induced by EPS that acts as a trap for particles from the surrounding
8
9 505 environment (Hagadorn & Bottjer, 1997). Oriented grains are result of a growing biofilm that
10
11 506 envelops, lifts, rotates and orientates the grains (Noffke *et al.*, 1997, 2001). By combining
12
13 507 morphological description and petrographic study, it appears that wrinkle structures are
14
15 508 polygenic. Both mat-layer and mat-protected structures are therefore most likely represented
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17 509 in this case.
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21 511 2b. '*Kinneyia*' structures

22 512 Description

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25 513 '*Kinneyia*' structures are characterized by clearly distinct, short, sinuous ridges and troughs of
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27 514 0.2 cm in width and less than 0.1 cm in height on the bedding surface of the black shale unit
28
29 515 (Figures 2, 6d). These structures fit with the definition of '*Kinneyia*' as proposed by (Porada
30
31 516 *et al.*, 2008), *i.e.*, they are “comparatively short, curved, frequently bifurcating, flat-topped
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33 517 crests, 0.5–1 mm high and 1–2 mm wide, which are separated by parallel, round-bottomed
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35 518 depressions. The crests are usually steep sided and may run parallel”.

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40 520 Interpretation

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43 521 The origins of “*Kinneyia*” structures have long been amongst the most problematic to
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45 522 understand. From their initial description as fossil algae (Walcott, 1914) to the present day
46
47 523 where the term is now used to describe MRS, they have been interpreted in various ways
48
49 524 (Hagadorn & Bottjer, 1997; Noffke *et al.*, 2002; Porada & Bouougri, 2007; Porada *et al.*,
50
51 525 2008; Thomas *et al.*, 2013; Mariotti *et al.*, 2014). However, few hypotheses properly explain
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53 526 how the underlying sediment is affected (Davies *et al.*, 2016). Recently, '*Kinneyia*' structures
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3 527 were successfully reproduced in wave tank experiments using microbial aggregates (Mariotti
4
5 528 *et al.*, 2014), although the sharply defined morphology of the depressions preserved might
6
7 529 suggest that gas bubbles formed beneath the biomat could also be a possible mechanism
8
9 530 (Pfluger, 1999). It has also been demonstrated that ‘Kinneyia’ is a polygenetic texture (Davies
10
11 531 *et al.*, 2016), but the Francevillian ‘Kinneyia’ structures do not rule out formation by biotic
12
13 532 mediators.
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17 534 *2c. Linear patterns*

18 535 Description

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22 536 Linear patterns are characterized by 0.1–0.3 cm high, parallel, linear ridges, slightly undulated
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24 537 on the bedding surfaces of massive sandstones and interbedded siltstones (Figures 2, 6e, g).
25
26 538 They are of varying size, ranging from 2 to 8 cm in length and 0.3 to 0.7 cm in width. Around
27
28 539 these linear ridges, the surface morphology is not uniformly flat but bears micrometric spots
29
30 540 that seem to be embedded in the matrix (Figure 6f). Furthermore, Raman spectrometry
31
32 541 indicates this dark-coloured layer is carbon-rich compared to the underlying sediments
33
34 542 (Figure 8d-e).
35

36
37 543 Microscopic observations reveal that the 100 to 300 μm thick, carbon-rich layer lies on
38
39 544 lighter, sand-sized quartz grains and consists of multiple, well-defined sheets of clay minerals
40
41 545 (Figure 7e, k). SEM imaging shows that numerous small quartz grains and heavy minerals,
42
43 546 such as apatite, titanium oxide and zircon, are embedded in the clay matrix (Figure 9d-e). This
44
45 547 matrix is formed by O, Si, Al, Mg, Fe and K elements, *i.e.* chlorite and illite, as expressed by
46
47 548 EDS analyses (Table S1). Furthermore, sand-sized quartz grains are observed inside the
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49 549 ridges as well as the surrounding sediment but are separated by a clayish undulated layer
50
51 550 (Figure 9e). The quartz grains inside the ridges and those from the host rock appear randomly
52
53 551 oriented.
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553 Interpretation

554 According to the identification of linear patterns in modern tidal flats by (Porada & Bouougri,
555 2007) “straight to irregular ridges are developed at distance of 1–2 cm and are locally
556 interrupted or reduced to faint lines on the flat mat surface”. Towards the water line, oriented
557 bacterial filaments dominate these structures. In experimental studies, Shepard & Sumner
558 (2010) observed linear ridges of up to 15 cm long made of cyanobacterial filaments running
559 parallel to the incident light. Moreover, it has been proposed that a faint rippled surface may
560 imply a linear pattern because of the preferential microbial growth following slight ridges
561 (Bouougri & Porada, 2007; Gerdes, 2007; Porada & Bouougri, 2007).

562 The presence of carbonaceous material within the dark-coloured layer is congruent
563 with a biotic origin. Microtextures, such as tiny quartz particles and heavy minerals embedded
564 in the matrix, are caused by the trapping and binding processes related to microbial activity
565 (Gerdes, 2007; Noffke, 2010). Individual grains bound in the organic matrix can be compared
566 to those observed with laboratory-grown cyanobacteria. These are described as oriented
567 grains that are pushed upwards during their growths (Noffke *et al.*, 2001; Noffke, 2010).

568 On a macroscopic level, the Francevillian MRS strongly resemble the linear structures
569 described above, commonly equivalent in shape but slightly smaller in size. However, no
570 microscopic features were described until now. Taking microtextures into account, it seems
571 unlikely that bacterial orientation is capable of mobilizing large amount of sediments to form
572 ridges. Microbial shrinkage caused by a period of subaerial exposition, is also a possibility
573 (e.g. Chu *et al.*, 2017; Kovalchuk *et al.*, 2017), although the surface morphologies and
574 microtextures are not consistent with this process. Also, dilational strain on a mildly dipping
575 sediment surface could explain these features, but their orientations are irregular and their
576 distributions are sporadic. Liquefaction underneath the microbial mat, due to a rise in pressure

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2
3 577 (*e.g.* Porada *et al.*, 2007), could have been the cause of these particular ridges but neither
4
5 578 sediment rising nor upward-facing microbial laminae beneath the ridges have been observed.
6
7 579 Finally, linear patterns may result from two growth periods interrupted by small and rippled
8
9 580 sedimentary structures (Figure 9e). This condition might be the best explanation for microbial
10
11 581 laminae throughout the linear ridges, and the second mat growth period may have followed
12
13 582 the ridge orientation as previously thought (Bouougri & Porada, 2007; Gerdes, 2007; Porada
14
15 583 & Bouougri, 2007). Indirectly, linear patterns are considered to be mat-protected structures.
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20 585 2d. *Nodule-like structures*

22 586 Description

24 587 Nodule-like structures are characterized by an elongated shape approximately 10 cm long and
25
26 588 an irregular surface topography on the bedding surfaces of black shales (Figures 2, 6h). The
27
28 589 surfaces of nodule-like structures comprise several millimetre-scale, tiny, crinkled ridges that
29
30 590 are randomly distributed. Composed of silt-sized grains and capped by a dark-coloured
31
32 591 wrinkle layer, the nodule-like structure was observed in a polished slab.
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35 592

37 593 Interpretation

39 594 Similar nodular to biscuit-like surface structures have been observed in laboratory-cultured
40
41 595 bacteria and in modern supratidal settings (Gerdes, 2007). This atypical morphology is
42
43 596 thought to be produced by a relative abundance of coccoid cyanobacteria. However, the
44
45 597 Francevillian nodular structures possibly reflect mat-protected structures instead of mat
46
47 598 growth structures since the internal part of the nodules is not composed of organic matter but
48
49 599 rather of quartz particles.
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52 600

55 601 3. Isotopic analyses

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3 602 The $\delta^{13}\text{C}$ values (V-PDB) of the organic fraction, measured on different mat morphologies in
4
5 603 both sandstone and black shale facies range from -30.67‰ to -41.26‰ (Table 1). These
6
7 604 values are similar to previous determinations on the bulk $\delta^{13}\text{C}$ of the organic matter within the
8
9 605 FB2 sequence, varying between *ca.* -35‰ to -30‰ (Gauthier-Lafaye & Weber, 2003;
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11 606 Canfield *et al.*, 2013).

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14 15 16 608 **Discussion**

17 18 609 **Biogenicity**

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21 610 The biogenicity criteria reviewed in Noffke (2009) and Wacey (2009) establishes the
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23 611 investigated mat-like structures to be of a microbial mat origin, having formed on the shallow
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25 612 marginal self-environment of the 2.1 Ga Francevillian basin (Reynaud *et al.*, 2017). The
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27 613 sedimentary facies on which the structures are identified must not have undergone
28
29 614 metamorphism beyond greenschist grade (Noffke, 2009). This is in agreement with the
30
31 615 absence of metamorphic overprint in the Francevillian facies (maximum temperature 100 °C;
32
33 616 Gauthier-Lafaye & Weber, 1989; Ngombi-Pemba *et al.*, 2014). In terms of shape and size, the
34
35 617 Francevillian MRS are a perfect match to those described in the Precambrian and the
36
37 618 Phanerozoic (Figures S3-S4) in accordance with the size distribution between modern and
38
39 619 ancient MRS, which should be comparable (Noffke, 2009). Typically, the taphonomic
40
41 620 preservation window of MRS in the sedimentary record is valid, but not restricted by
42
43 621 ecological setting (Davies *et al.*, 2016). Noffke (2009) suggested that most MRS are related to
44
45 622 photoautotrophic mats formed in well-lit shallow marine environments, preferentially on fine
46
47 623 sand deposits, even though recent studies argued that such features can also arise on deep
48
49 624 marine sediments that do not receive light (Davies *et al.*, 2016). Regardless, our samples
50
51 625 originated from a shallow marine setting associated with rapid sand flow deposits within a
52
53 626 well-lit portion of the 2.1 Ga Francevillian continental shelf (Reynaud *et al.*, 2017).

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3 627 Microtextural composition of the analysed fabric further support the biological
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5 628 trapping, binding (or 'flypaper' effect) and orientation of grains induced by the growth and
6
7 629 development of microbial mats and their hydrologically-controlled interaction with sediments.
8
9 630 The Francevillian MRS express this biological process by containing clay particles, floating
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11 631 grains of silt-sized quartz and concentrated heavy minerals, as well as by wavy-crinkly
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13 632 laminae (Figures 7f-k, 9, Figure S2; Table S1). These form well-defined organo-sedimentary
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15 633 structures caused by microbial baffling and trapping. The randomly oriented clay minerals in
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17 634 mat laminae suggest that they were trapped on the mat surface whereas laminated clay
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19 635 particles suggest a probable alignment by compaction (Schieber, 1998). Oriented grains
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21 636 reflect a particular microtexture (Figures 6f, 7j), while grain size matches that of the
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23 637 underlying substratum. It is commonly thought that these particles were dragged upwards by
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25 638 cyanobacterial mat growth (Noffke *et al.*, 1997, 2001).

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28 639 In addition, geochemical evidence suggests bacterially induced biological processes
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30 640 characterized by carbonaceous material enriched in light carbon (Figure 8; Table 1) and
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32 641 pyritized structures (Figures 4e-g, 5a-e, g, 7c, i) that are depleted in heavy sulfur. The latter
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34 642 points to diagenetic mat destruction through burial decay (Noffke, 2009; Noffke *et al.*, 2013)
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36 643 and anaerobic respiration of that organic carbon by sulfate-reducing microorganisms (El
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38 644 Albani *et al.*, 2014; Hill *et al.*, 2016).

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42 43 646 **Paleoenvironmental interpretations and implications**

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45 647 Modern mat-related structures are mostly described in carbonate and siliciclastic
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47 648 environments but few have been described from shale deposits. The presence of black shales
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49 649 with large amounts of organic matter deposited in the photic zone may arise in restricted to
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51 650 isolated basins (Schwark & Frimmel, 2004). Some anoxygenic photosynthetic bacteria even
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53 651 prospered in these paleoecological conditions and their high productivity may be related to the
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3 652 availability of essential nutrients. For any MRS-bearing rocks, the hydraulic pattern must be
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5 653 moderated with a low sedimentation rate to promote the development of microbial
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7 654 communities on a substrate (Schieber, 1999; Gerdes *et al.*, 2000; Gerdes, 2007; Noffke, 2009,
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9 655 2010). As an indicator of paleo-hydrological conditions, clay minerals and silt-sized grains
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11 656 within mat layers, are taken to represent currents strong enough to move thin particles but
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13 657 insufficient to transport sand-sized grains (Schieber, 1998; Noffke, 2009). Silt-sized
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15 658 sedimentary particles and heavy minerals can also be baffled and trapped by cyanobacterial
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17 659 filaments moving vertically upwards in order to escape being buried by the small-sized
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19 660 particles, as well as their need to reach optimal light conditions for growth (Noffke, 2009,
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21 661 2010).

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24 662 In this study, some of the mat-like structures, including the ‘elephant-skin’
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26 663 morphotypes, the tufted structures, and the linear patterns, tend to be associated with silty
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28 664 lenses (Figure 2), suggesting that the baffling and grain trapping processes were operating in
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30 665 potential microbial mat-dominated environments at 2.1 Ga. Further, the comparable
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32 666 association of several MRS to the distribution of modern and fossil analogues have been used
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34 667 to improve the reliability of paleoenvironmental marine interpretations, including physical
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36 668 processes such as desiccation and erosion and biological activity (Bose & Chafetz, 2009;
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38 669 Noffke *et al.*, 2013; Banerjee *et al.*, 2014; Sarkar *et al.*, 2014). Importantly, the absence of
39
40 670 desiccation and erosion-induced MRS in the Francevillian rocks suggest a quiet underwater
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42 671 environment from the time of deposition to when the sediments were lithified and buried.
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46 672 The Paleoproterozoic Francevillian MRS possess a wide spectrum of morphologies
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48 673 that can be related to photoautotrophic microbial assemblages. Indeed, discoidal microbial
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50 674 colonies in the modern environments and domal buildups in ancient settings are results of
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52 675 cyanobacterial chemotaxis or phototaxis behaviours (Gerdes, 2007). The biological
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54 676 mechanisms leading to oriented grains has been reproduced with cultures of cyanobacteria
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3 677 (Noffke *et al.*, 2001). Reticulate patterns and tufted microbial mats have striking
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5 678 morphologies with modern analogues built by filamentous cyanobacteria (Figure S3a; Gerdes
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7 679 *et al.*, 2000; Gerdes, 2007; Bose & Chafetz, 2009; Taj *et al.*, 2014). It is thought that their
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9 680 formation implies a phototactic behaviour (Gerdes *et al.*, 2000; Reyes *et al.*, 2013), whereas
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11 681 laboratory-cultured filamentous cyanobacteria show a dependency on oxygen concentration
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13 682 (Sim *et al.*, 2012). It has also been proposed that the undirected gliding motility of
14
15 683 filamentous bacteria species may form these structures (Shepard & Sumner, 2010).
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17 684 Consequently, all bacteria with highly motile filaments are believed to be able to display these
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19 685 morphologies. Filamentous sulfur-oxidizing bacteria may also have the ability to produce
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21 686 ‘elephant-skin’-like and tuft-like structures (Flood *et al.*, 2014). However, research by
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23 687 genomic comparisons reveals that these phenotypic traits were most likely inherited by
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25 688 horizontal gene transfers from the cyanobacteria (Flood *et al.*, 2014). In other words, those
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27 689 aerobic chemolithoautotrophs may not have been in existence at 2.1 Ga. In addition, recent
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29 690 studies in a perennially ice-covered Antarctic lake have shown the specific assemblage of a
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31 691 photosynthetic microbial ecosystem (Sumner *et al.*, 2015; Jungblut *et al.*, 2016), with
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33 692 cyanobacteria forming tuft-related structures exclusively found in the oxic zone where
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35 693 irradiance is at its highest, whereas flat bacterial mats of anoxygenic photoautotrophs are
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37 694 restricted to the deeper euxinic zone experiencing lower irradiance. Thus, ‘elephant-skin’ and
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39 695 tufted structures may possibly have a link with oxygenic photoautotrophic microorganisms.
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41 696 Importantly, Flannery & Walter (2012) and Homann *et al.* (2015) thought that cyanobacteria
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43 697 are the only microorganisms capable of producing vertical structures or tufts.
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50 699 Geomicrobiological implications

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53 700 It is well established that carbon fixation by autotrophic organisms preferentially incorporates
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55 701 light ^{12}C over heavy ^{13}C isotopes in biomass (Schidlowski, 1988, 2001). In this regard, the
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3 702 $\delta^{13}\text{C}_{\text{org}}$ values ranging from -30.67 to -41.26‰ (average $-32.94 \pm 1.17\%$) reported here are
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5 703 within the expected range for autotrophic carbon fixation (Schidlowski, 1988, 2001; Berg *et*
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7 704 *al.*, 2010). The typical $\delta^{13}\text{C}_{\text{org}}$ values generated by the widespread activity of ribulose 1,5-
8
9 705 bisphosphate carboxylase/oxygenase (RuBisCo), common in oxyphototrophic cyanobacteria
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11 706 have average values from -20 to -30‰. These values are less negatively fractionated than
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13 707 anoxygenic phototrophs (Quandt *et al.*, 1977; McNevin *et al.*, 2007; Berg *et al.*, 2010), while
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15 708 more negative values $<-30\%$ are related to autotrophic carbon fixation in the reductive acetyl
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17 709 CoA pathway (*i.e.*, methanogenesis). In the case of the latter, acetoclastic methanogenesis
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19 710 diagenetically supplies isotopically light ^{12}C methane to anaerobic oxidation of methane
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21 711 (AOM), the latter often comprising a consortia of sulfate reducers and methanotrophs (Conrad
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23 712 *et al.*, 2010). Consequently, autotrophic carbon fixation via acetyl CoA pathway, combined
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25 713 with anaerobic oxidation of fixed C_{org} , would effectively lead to deposition of residual C_{org}
26
27 714 enriched in light ^{12}C in the range found in this study. Such fixation of CO_2 coupled with
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29 715 diagenetic recycling of phototrophically derived C_{org} would have inevitably resulted in the
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31 716 sequential overprinting of light $\delta^{13}\text{C}$ in buried biomats. The bulk $\delta^{13}\text{C}_{\text{org}}$ signatures $<-30\%$
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33 717 are, therefore, most parsimoniously interpreted to represent a mixed isotopic signal resulting
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35 718 from the activities of various primary producers and heterotrophs.

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39 719 The FB2b subunit hosts the first known multicellular organisms closely associated
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41 720 with biomats (Figures 2, 10). Burrows, trails and resting traces of metazoans are often closely
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43 721 associated with biomats in the past, being interpreted as sophisticated feeding behaviours (*e.g.*
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45 722 Buatois & Mángano, 2012; Pecoits *et al.*, 2012; Buatois *et al.*, 2014; Meyer *et al.*, 2014; Chu
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47 723 *et al.*, 2015). In modern environments, photosynthetic bacterial mats create thin O_2 -rich
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49 724 layers, thus providing benthic O_2 oases for macroorganisms that may mine mat layers for
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51 725 unexploited nutrients and O_2 (Gingras *et al.*, 2011). It is perhaps not a coincidence then that
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53 726 the biomats and macroorganisms belong to the same strata. Moreover, the generation of
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3 727 microenvironments due to the chemical properties of EPS (Decho, 2000) may permit soft-
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5 728 tissue mineralization, providing further protection against degradation (Sagemann *et al.*,
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7 729 1999). Thus, the biomats may have stabilized the depositional surfaces and sheltered the
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9 730 macroorganisms, allowing them to become imprinted into the rock record. Interestingly, the
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11 731 large colonial organisms associated with bacterial communities are only known from the
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13 732 FB2b rocks. Although other black shale facies are recorded in the Francevillian basin (*e.g.*,
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15 733 the ~ 2.08 Ga FD black shale formation; Figure 1b), they were deposited in deeper
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17 734 environments beyond the euphotic zone (Canfield *et al.*, 2013).
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22 736 **Conclusion**

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24 737 Mat-related structures of the 2.1 Ga Francevillian series exhibit ten types of surface
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26 738 morphologies, providing a new window into the highly diversified Paleoproterozoic microbial
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28 739 life at that time. Mats are preserved in excellent conservation conditions from a 20 m thick
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30 740 interval of sandstone and black shale facies.
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33 741 Microtexture analyses provide strong evidence in favour of mat-colonized sediment. Oriented
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35 742 grains, floating grains, heavy mineral concentrations, randomly oriented clays, pyritized
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37 743 structures and wavy-crinkly laminae all reflect the growth of microbial communities.
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39 744 Comparisons with ancient and modern analogues, as well as stable carbon isotope analyses,
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41 745 suggest growth within a palaeoenvironmental settings corresponding to the euphotic zone,
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43 746 likely less than 100m deep. Associations between Paleoproterozoic, large colonial organisms
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45 747 and mats may be similar to interactions of Ediacaran early metazoans and microbial carpets
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47 748 where O₂-producing cyanobacterial mats may explain this specific pattern. In addition,
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49 749 microbial mats may have played a major role in sediment biostabilization, fostering the
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51 750 preservation of complex macroorganisms that represent the first ecosystem comprising
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53 751 microbial biofilms and large colonial life forms.
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1082 **Figure captions**

1083 **FIGURE 1 Geological map and lithostratigraphic column.** (a) Geological map of the Francevillian basin. The
1084 studied quarry is Moulendé (green star). Geological map adopted from (Bouton *et al.*, 2009). (b) Synthetic
1085 lithostratigraphy of the Francevillian series. Four sedimentary units rest unconformably on Archean rocks. The
1086 red star indicates the detailed lithostratigraphic column observed in the Moulendé quarry (Figure 2).

1087 **FIGURE 2 Detailed lithostratigraphic column.** Composite columnar section of the Moulendé quarry in the
1088 FB2 unit showing the vertical distribution of ten representative types of mat-related structures (MRS) and
1089 sedimentary structures (SS).

1090 **FIGURE 3 Plane view and outcrop pictures of sedimentary facies in the Moulendé quarry.** (a)
1091 Representation of the quarry from plane view. Red box indicates the main studied outcrop in B (F8). F =
1092 outcrops. (b) Details of the bedding geometry at the transition between massive sandstone beds and thinly
1093 laminated black shales. (c) Closer view of B. (d) Cross-section view of decimetre-scale hummocky-cross
1094 stratifications (HCS), FB2a subunit. (e) Sandstone dyke, FB2a - FB2b transition. Coin diameter: ~ 2 cm. (f)
1095 Cross-section view of convolute structures, FB2b subunit. (g) Bedding plane view of interference ripples, FB2b
1096 subunit. (h) Longitudinal view of dark-coloured convex laminae associated with cm-scale foreset beds, FB2b
1097 subunit.

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3 1098 **FIGURE 4 Microbial mat structures in the Francevillian B Formation (FB2): Mat-layer structures.** (a-c)
4 1099 ‘Elephant-skin’ textures. (d) Putative macro-tufted microbial mat. (e-f) Clustered domal buildups and flat
5 1100 pyritized microbial structure (red arrow). Macrofossil specimens (white arrows). (g) Isolated domal buildups. (h)
6 1101 Wrinkle marks.

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9 1102 **FIGURE 5 Microbial mat structures in the Francevillian B Formation (FB2): Mat-layer structures.** (a-b)
10 1103 Discoidal mats likely representing ‘fairy ring’ structures. (c-e) Disc-shaped mats that display a cauliflower-like
11 1104 pattern. (f) Disc-shaped mat with internal wrinkle structures. (g) Small pyritized circular bodies. (h) Horizontal
12 1105 mat growth pattern.

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15 1106 **FIGURE 6 Mat-related structures in the Francevillian B Formation (FB2): Mat-protected structures.** (a-b)
16 1107 Parallel wavy wrinkle structures. (c) Cross-cutting wrinkle structures. (d) ‘Kinneyia’ structure. (e) Linear pattern.
17 1108 Dashed red box indicates the position of the magnification in f. Red arrow shows the location where the
18 1109 spectrometry Raman was performed. The Raman spectra is visible in Figure 8d. (f) Micrometric spots
19 1110 interpreting as oriented grains. (g) Linear patterns with several parallel ridges. (h) Nodular-like structure.

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22 1111 **FIGURE 7 Optical photomicrographs of mat-related structures.** (a) Transmitted thin section of ‘elephant-
23 1112 skin’ texture. Dashed red box denoting area magnified in f. (b) Transmitted thin section of putative macro-tufted
24 1113 microbial mat. Dashed red boxes denoting areas magnified in g and h. (c) Transmitted thin section of an isolated
25 1114 domal buildup. Dashed red box denoting area magnified in i. (d) Transmitted thin section of parallel wavy
26 1115 wrinkle structures. Dashed red box denoting area magnified in j. (e) Transmitted thin section of a linear pattern.
27 1116 Dashed red boxes denoting areas magnified in k and Figure 9e. (f) Tufted microstructures and wavy-crinkly
28 1117 laminae. Dashed red box denoting area magnified in Figure 9a. (g-h) Thickness variation across the mat layer
29 1118 with floating grains embedded by clays (red arrows). Mica (white arrows). Dashed red box denoting area
30 1119 magnified in Figure 9c. (i) Reflected magnified thin section of an entirely pyritized dome. An internal convex
31 1120 lamination is indicated by dashed red lines. (j) Clay laminae do not onlap the rippled siltstone bed but rather well
32 1121 follow its topography. Oriented grains (arrows). (k) High amount of quartz particles (arrows as example) within
33 1122 dark-coloured laminae. Dashed red box denoting area magnified in Figure 9d.

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39 1123 **FIGURE 8 Polished slab of ‘elephant-skin’ texture and Raman spectra of both ‘elephant-skin’ texture and**
40 1124 **linear pattern.** (a) Polished slab in cross-section perpendicular to bedding plane. Non-homogenous dark layer
41 1125 preserved above a pronounced boundary. Red arrow and white arrow indicate Raman spectra in b and c,
42 1126 respectively. (b) Representative Raman spectra of the microbial mat within bulges. It shows the presence of two
43 1127 Carbon peaks (“C”) at 1336 cm^{-1} (the “D1” disordered peak) and 1603 cm^{-1} (the “G” graphite peak). (c) Typical
44 1128 Raman spectra of sandstone with quartz (“Q”) peaks. (d) Representative Raman spectra of mat layers of linear
45 1129 pattern indicated in Figure 6e. It shows the presence of three carbon peaks (“C”) at $\sim 1170\text{ cm}^{-1}$ (“D4” disordered
46 1130 peak), 1344 cm^{-1} (the “D1” disordered peak) and 1603 cm^{-1} (the “G” graphite peak). (e) Typical Raman spectra
47 1131 of host sediment of linear pattern, with quartz (Q) peaks and very small intensities of “C” peaks.

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52 1132 **FIGURE 9 SEM imaging of mat-related structures.** (a) Magnified view of box area in Figure 7f. Upward clay
53 1133 laminae within tufted microstructures and wavy-crinkly layers. (b). Tufted microstructures and heavy minerals
54 1134 constitute bulges of the ‘elephant-skin’ texture. (c) Magnified view of box area in Figure 7h. Quartz grains,
55 1135 heavy minerals and randomly oriented clays constitute the dark-coloured mat layer. (d) Magnified view of box

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3 1136 area in Figure 7k. Detrital particles wrapped by sheet clays. (e) Magnified view of box area in Figure 7e. Clay
4 1137 minerals above and throughout the ridge (arrow). No significant clue of liquefaction nor microbial shrinkage.

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6 1138 **FIGURE 10 Examples of fossil macroorganisms associated with microbial mats.** (a) Pyritized lobate form
7 1139 just beneath ‘fairy ring’ structures. (b) Disk with radially striated core (arrow) lies on domal buildups. (c-d) Disk
8 1140 or lobate form and flat pyritized microbial structures on the same strata are closely associated. (e) Circular disks
9 1141 (arrows) rest on wrinkle marks. (f) Disk and lobate form are close to wrinkle marks on the same level or not.

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33 1153 **Captions for the supplementary information**

35 1154 **FIGURE S1 Additional flat pyritized microbial mats.**

37 1155 **FIGURE S2 EDS elemental maps of bulges of reticulate patterns in cross-section perpendicular to**
38 1156 **bedding plane.** BSE and composite elemental maps. Note the wavy-crinkly laminae with a large amount of
39 1157 embedded heavy minerals.

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42 1158 **FIGURE S3 Photographs of mat-layer structures found in literature.** (a) Analogous ‘elephant-skin’ texture
43 1159 from modern lower supratidal, Bahar Alouane, southern Tunisia. Modified after photo published in Gerdes
44 1160 (2007). (b) Fossil reticulate pattern on bedding plane of siliciclastic beds from the Archean Tumbiana
45 1161 Formation, Australia. Modified after photo published in Flannery & Walter (2012). (c) A 2.0 billion-years-old
46 1162 tufted microbial mat from Makgabeng Formation, South Africa. Modified after photo published in Simpson *et*
47 1163 *al.* (2013). (d) Analogue clustered low mound-like structures with *Protichnites* trackways on bedding surface of
48 1164 quartz arenites from the Late Cambrian, Elk Mound Group, USA. Modified after photo published in Bottjer &
49 1165 Hagadorn (2007). (e) Modern analogous ‘fairy rings’ on soft muddy sediments from Bretagne salterns, France.
50 1166 Modified after photo published in Grazhdankin & Gerdes (2007). (f) Ancient example of outward-convex,
51 1167 spindle-shaped discoidal structures with concentric rings from the Mesoproterozoic, Sonia Sandstone, India.
52 1168 Modified after photo published in Sarkar *et al.* (2014). (g) Modern discoidal microbial colony on tidal flat from

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3 1169 the Gulf of Cambay, India. Modified after photo published in Banerjee *et al.* (2014). Lens cap diameter: 6 cm.
4 1170 (h) Analogue discoidal microbial colony on bedding plane of sandstones from the Precambrian Vindhyan
5 1171 Supergroup, India. Modified after photo published in Banerjee *et al.* (2014).
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7 1172 **FIGURE S4 Photographs of mat-related structures found in literature.** (a) Modern example of submerged
8 1173 wrinkle marks from Redfish Bay, Texas. Modified after photo published in Hagadorn & Bottjer (1997). (b)
9 1174 Patches of wrinkle marks on bedding surface of fine-grained sandstones from the Early Cambrian, Chapel Island
10 1175 Formation, Canada. Modified after photo published in Buatois *et al.* (2014). (c) Parallel wavy wrinkle structures
11 1176 reproduced in wave tank experiments using microbial aggregates. Modified after photo published in Mariotti *et*
12 1177 *al.* (2014). (d) Analogous parallel wavy wrinkle structures on bedding plane of mudstones from the Early
13 1178 Cambrian, Northwest Argentina. Modified after photo published in Buatois & Mángano (2003). (e) Minute
14 1179 “Kinneyia” structures formed with microbial aggregates in wave tank experiments. Modified after photo
15 1180 published in Mariotti *et al.* (2014). (f) Ancient analogue “Kinneyia” structures on bedding surface of siltstones
16 1181 from the Cambrian, Oeland, Sweden. Modified after photo published in Porada & Bouougri (2007). (g) Linear
17 1182 features from modern tidal flats of Bhar Alouane, southern Tunisia. Modified after photo published in Porada &
18 1183 Bouougri (2007). (h) Putative linear patterns on bedding surface of fine-grained quartzites from the
19 1184 Neoproterozoic Katanga Supergroup, Zambia. Modified after photo published in Porada & Bouougri (2007).
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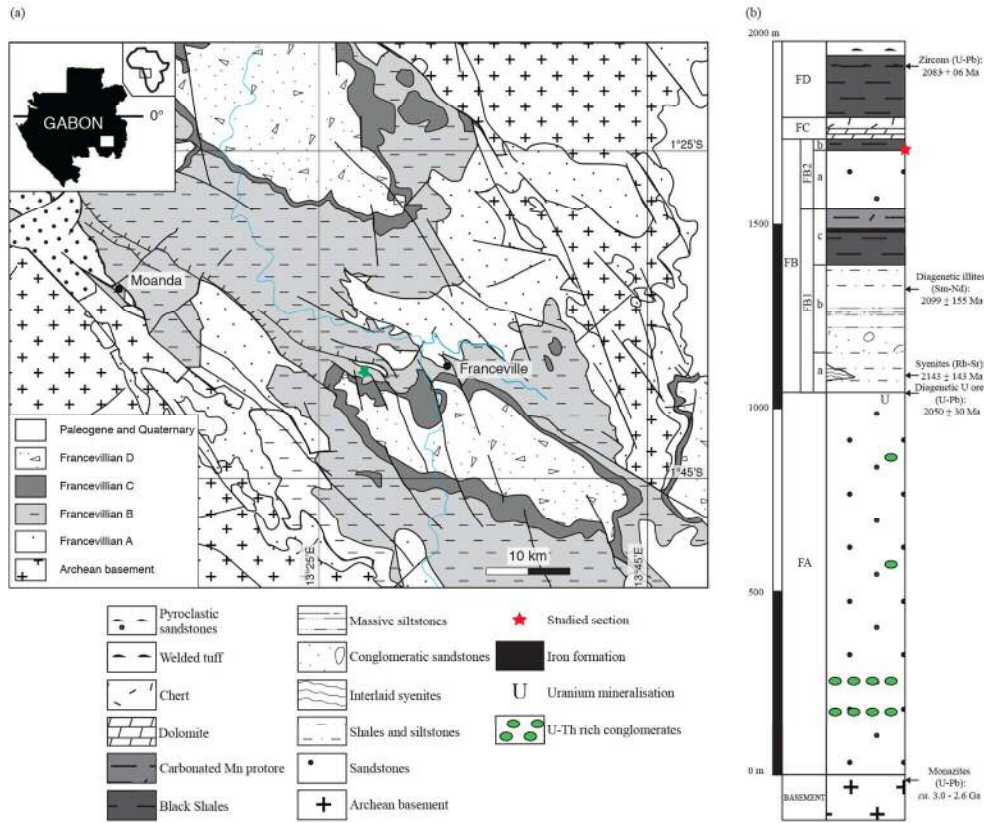


Figure 1

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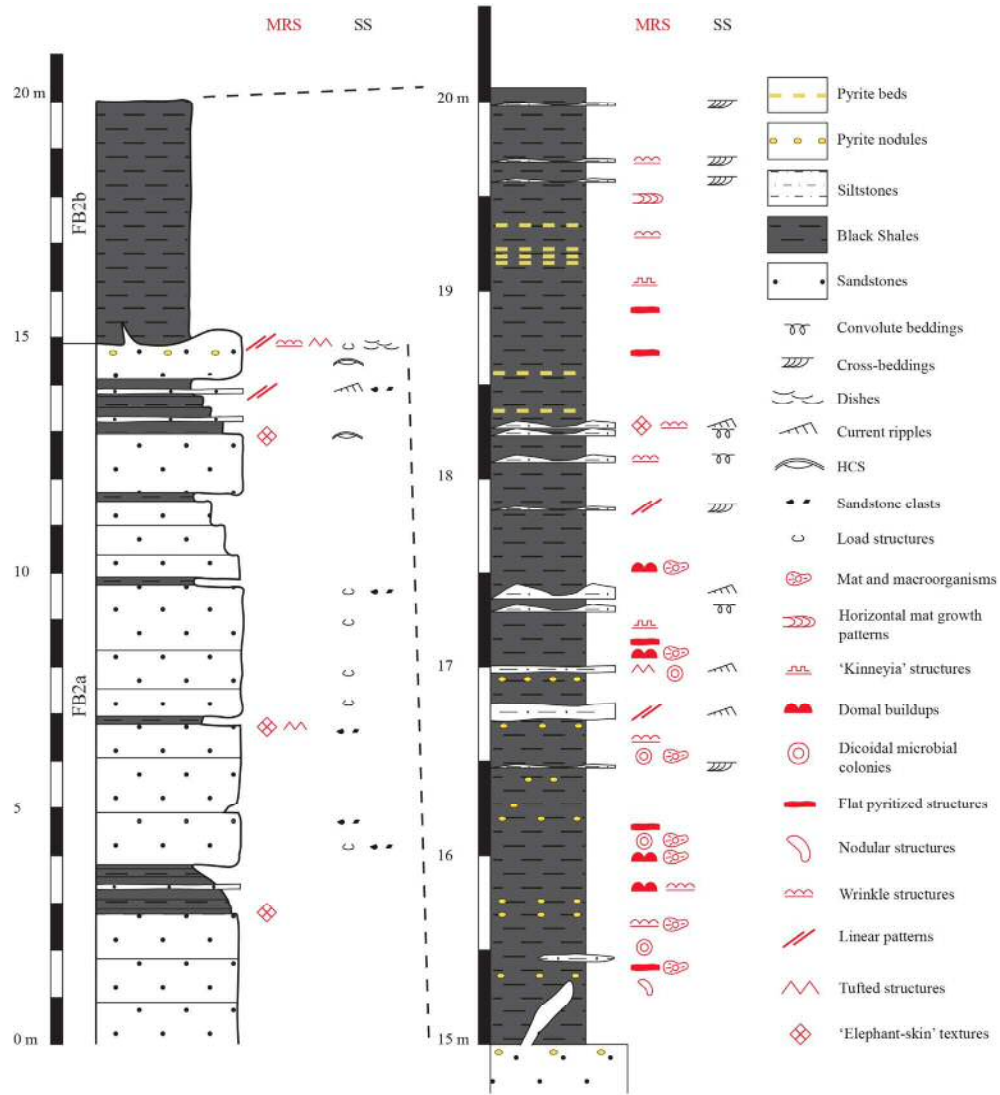


Figure 2

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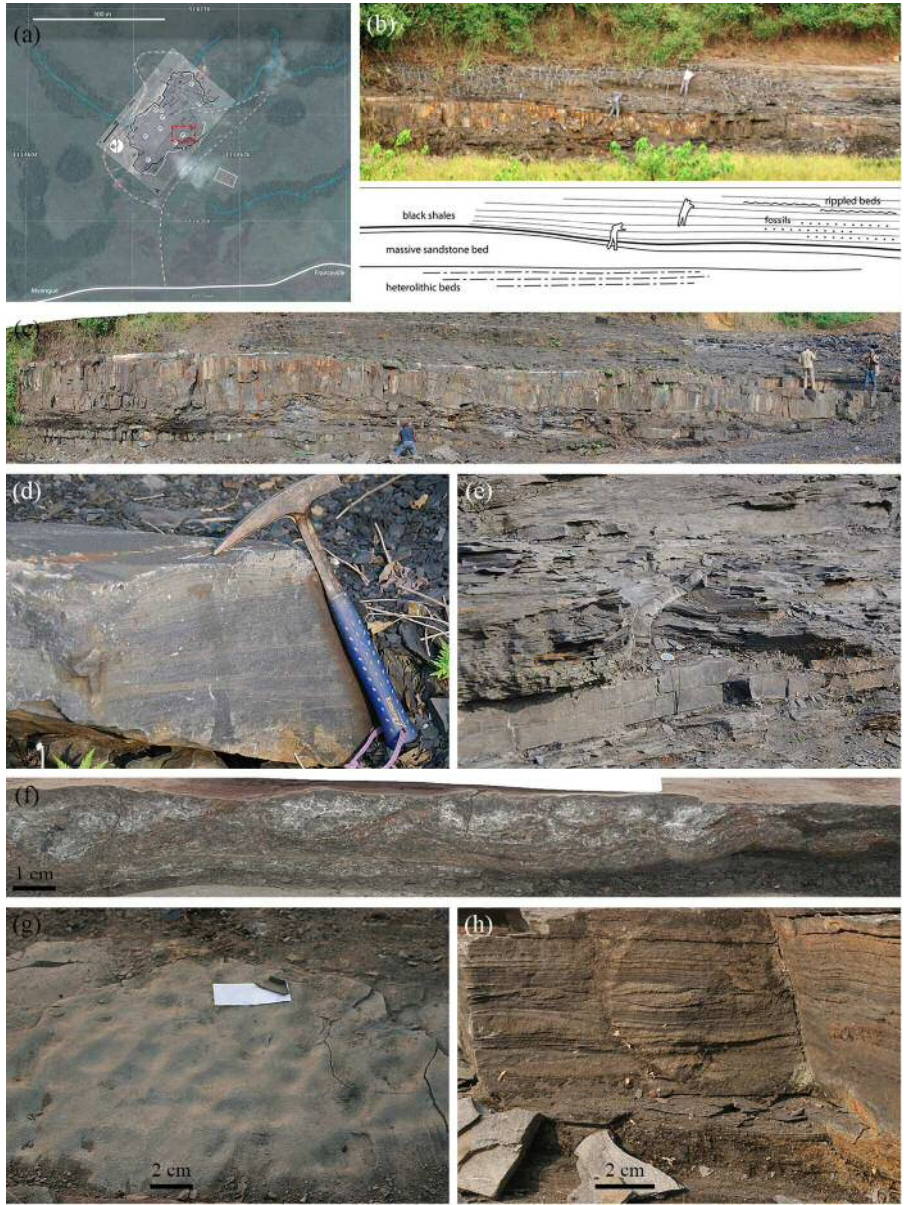


Figure 3

127x170mm (300 x 300 DPI)

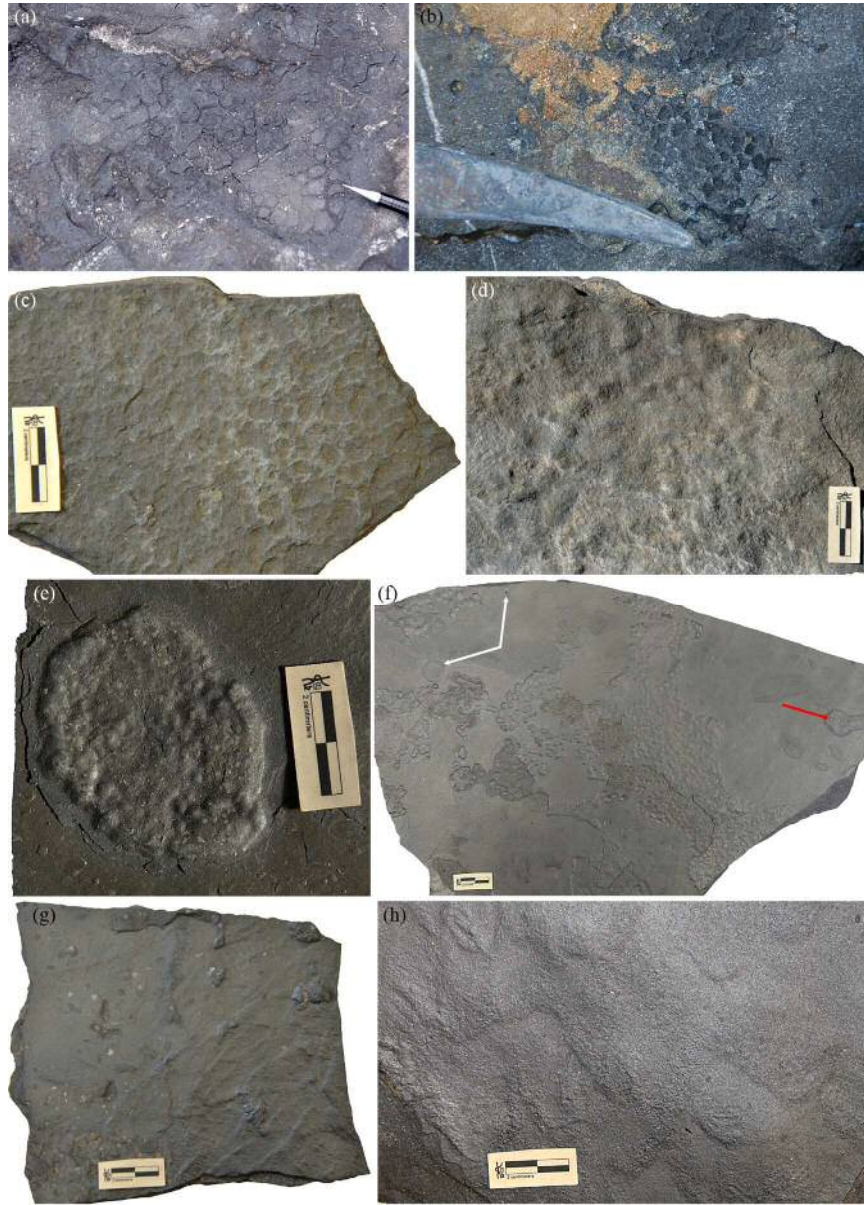


Figure 4

151x211mm (300 x 300 DPI)

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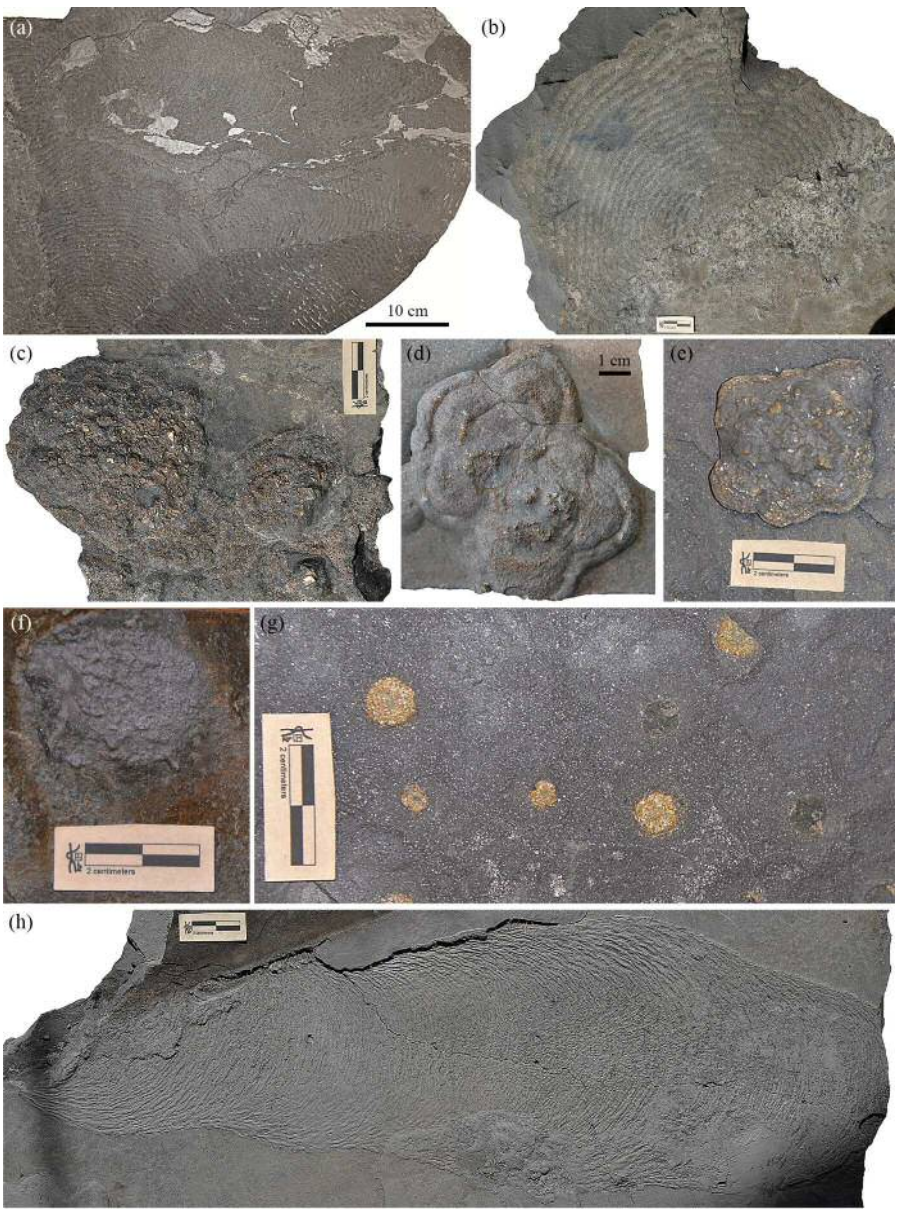


Figure 5

149x201mm (300 x 300 DPI)



Figure 6

142x185mm (300 x 300 DPI)

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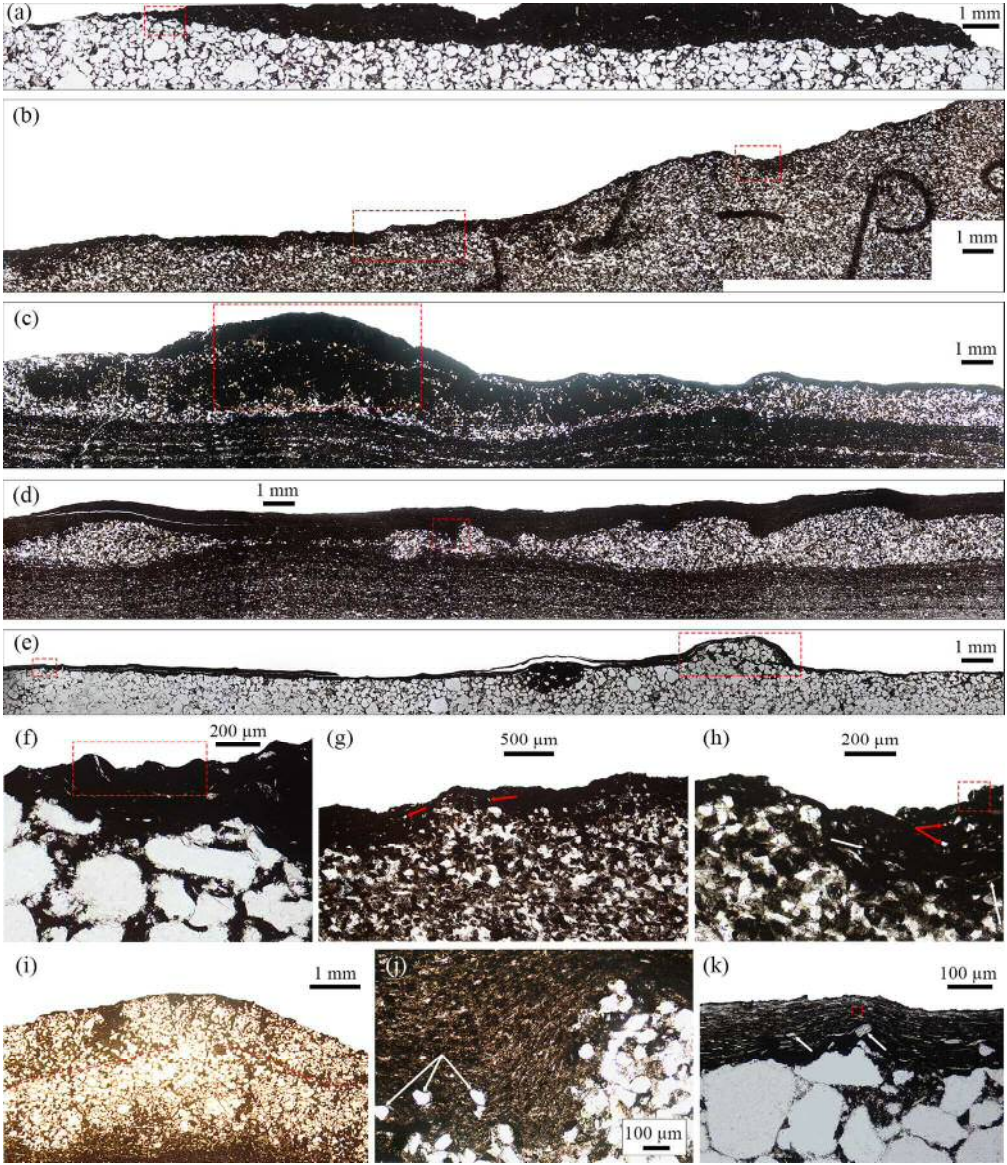


Figure 7

152x176mm (300 x 300 DPI)

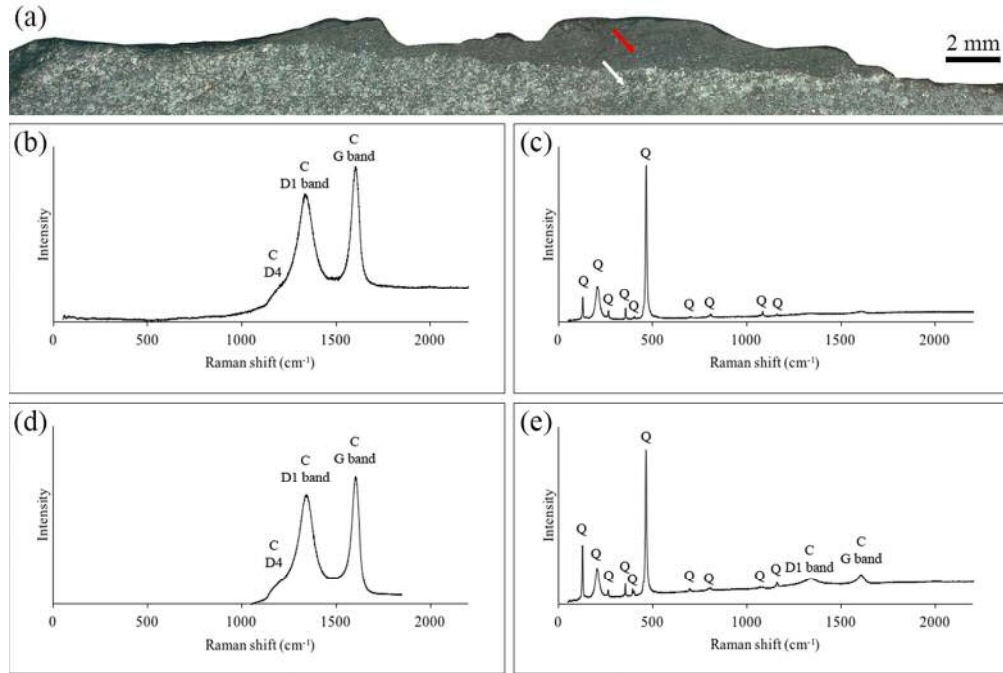


Figure 8

121x81mm (300 x 300 DPI)

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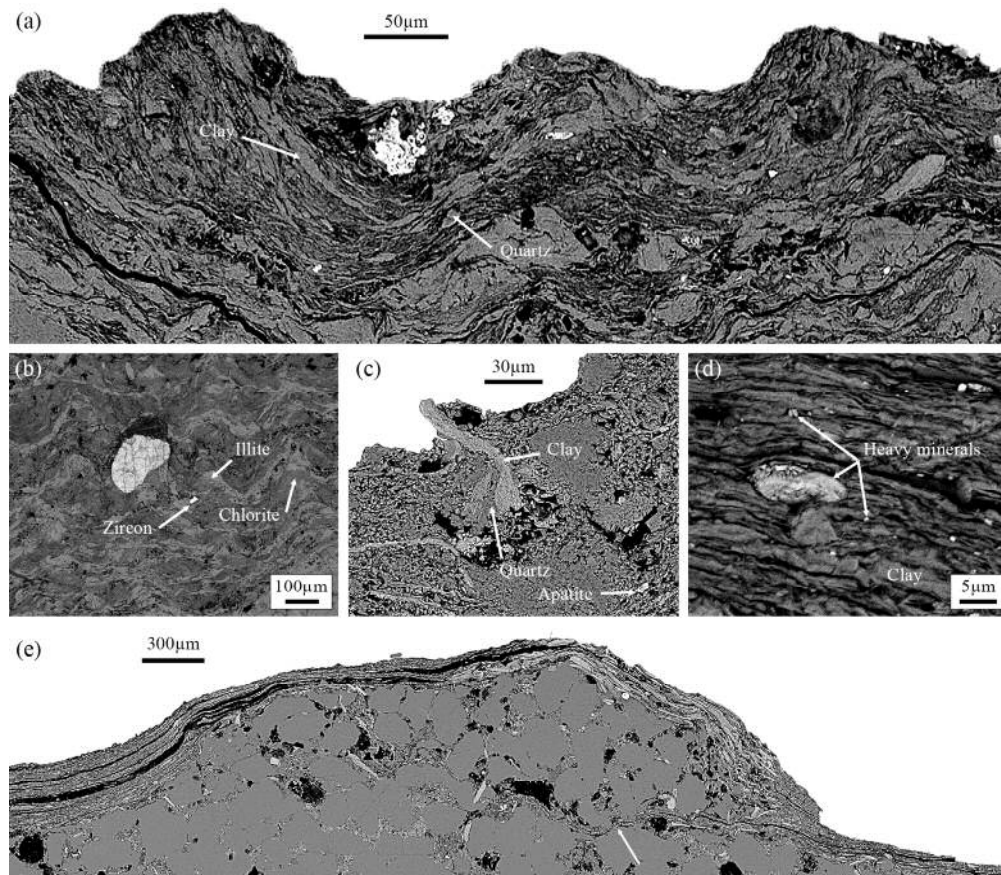


Figure 9

151x132mm (300 x 300 DPI)



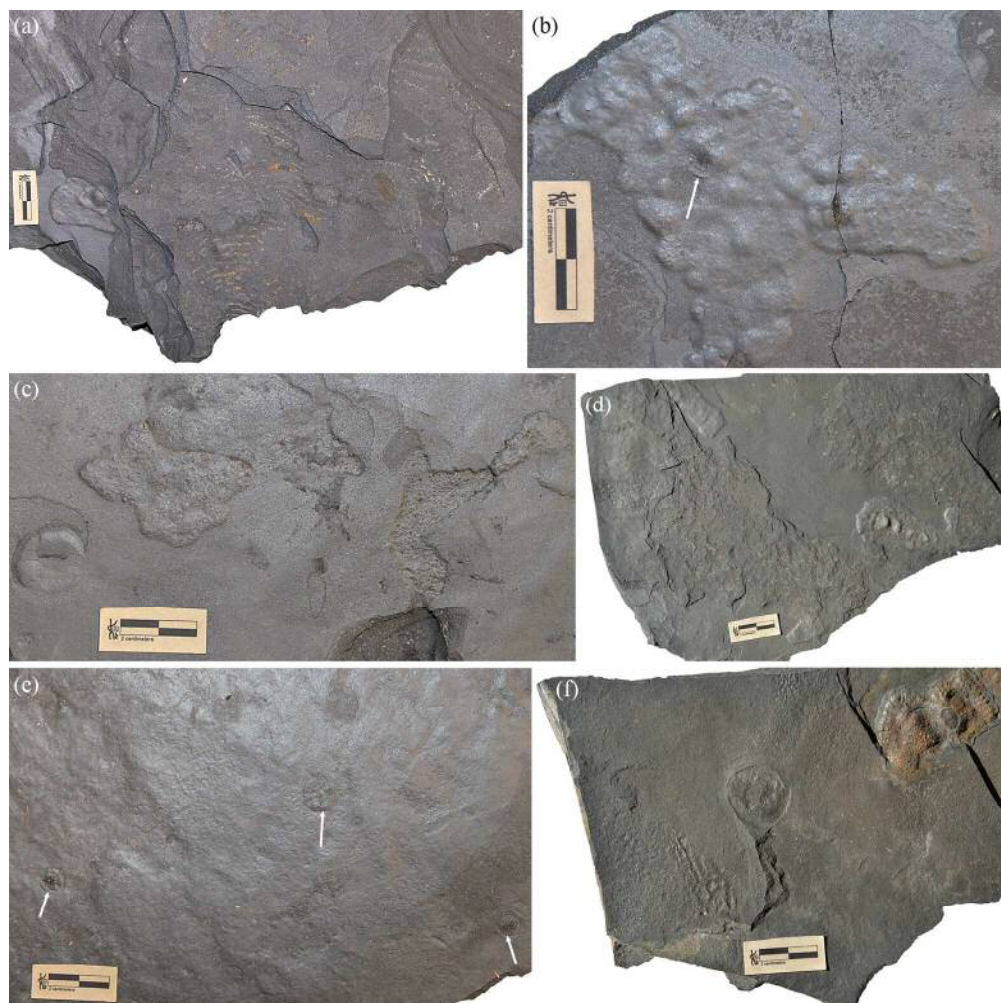


Figure 10

152x151mm (300 x 300 DPI)

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TABLE 1 $\delta^{13}\text{C}$ values of organic matter in mat-related structures (MRS).

Subunits	Samples	$\delta^{13}\text{C}_{\text{org}}$ (‰)
FB2b Black shale	MRS_1	-34.92
	MRS_2	-34.41
	MRS_3	-32.45
	MRS_4	-41.26
FB2a Sandstone	MRS_5	-31.68
	MRS_6-1	-32.72
	MRS_6-2	-33.32
	MRS_7	-33.95
	MRS_8	-33.55
	MRS_9	-33.66
	MRS_10	-33.61
	MRS_11	-32.28
	MRS_12	-30.67
	MRS_13	-31.95
MRS_14	-32.03	

For Review Only

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7 **3 FIGURE S1**
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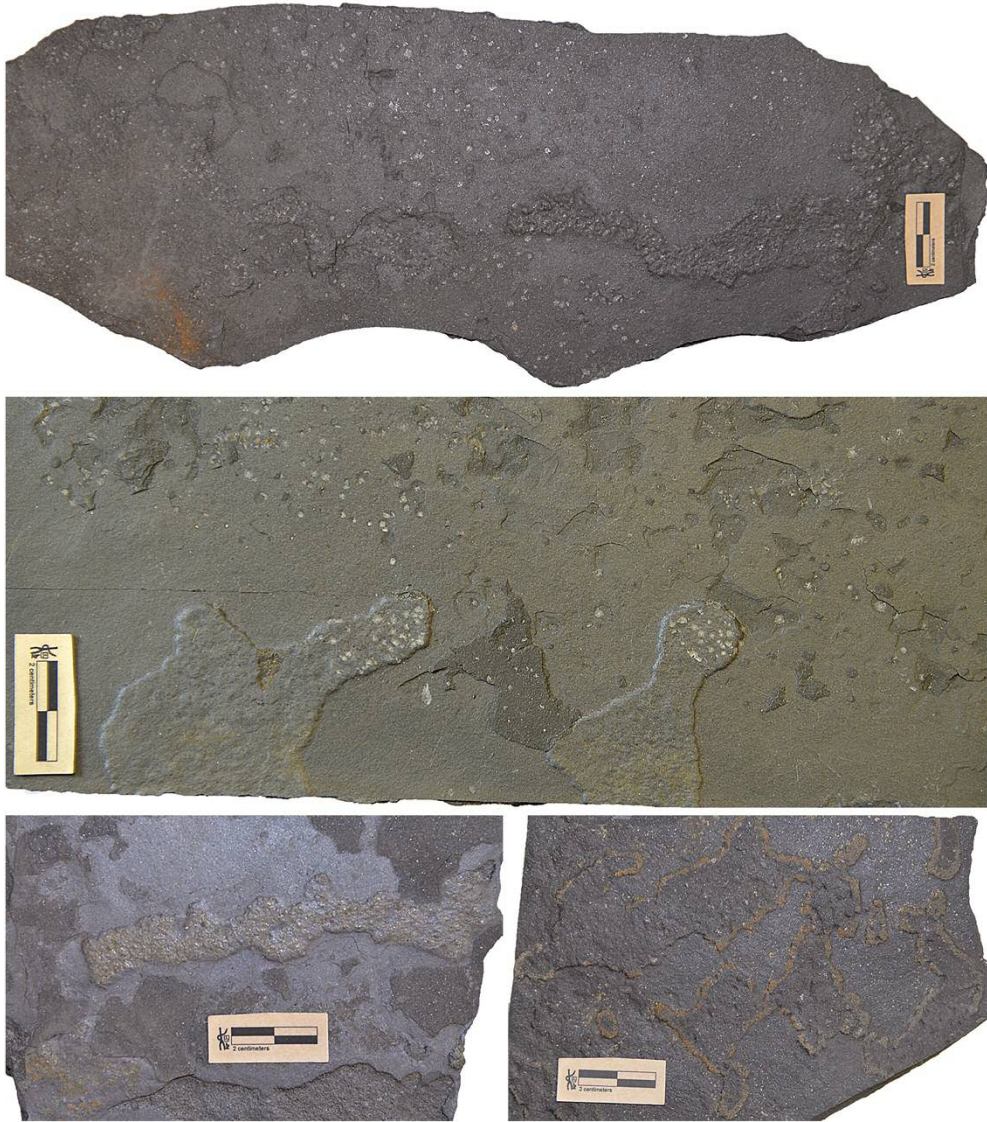
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30 **FIGURE S1 Additional flat pyritized microbial mats.**
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FIGURE S2

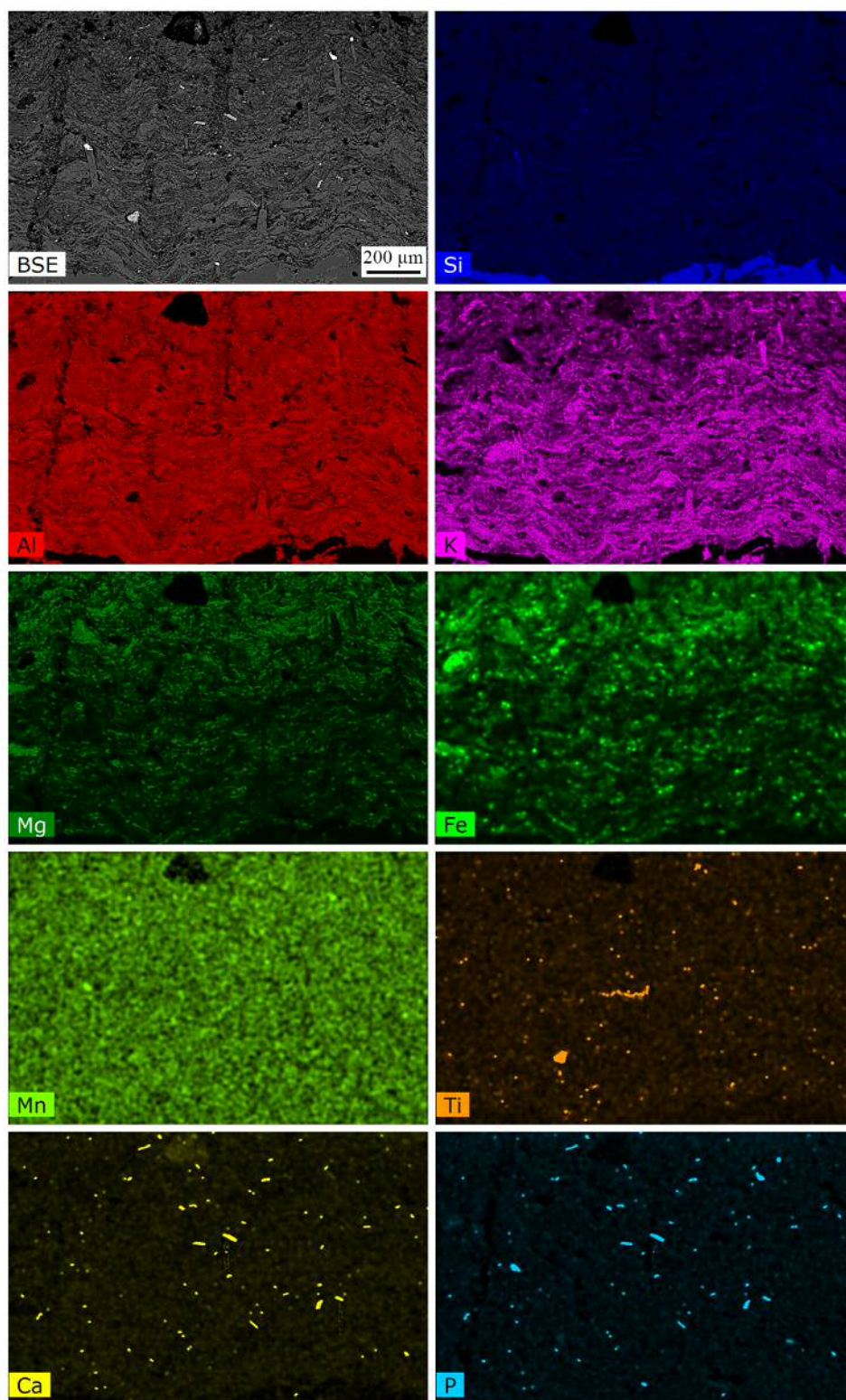
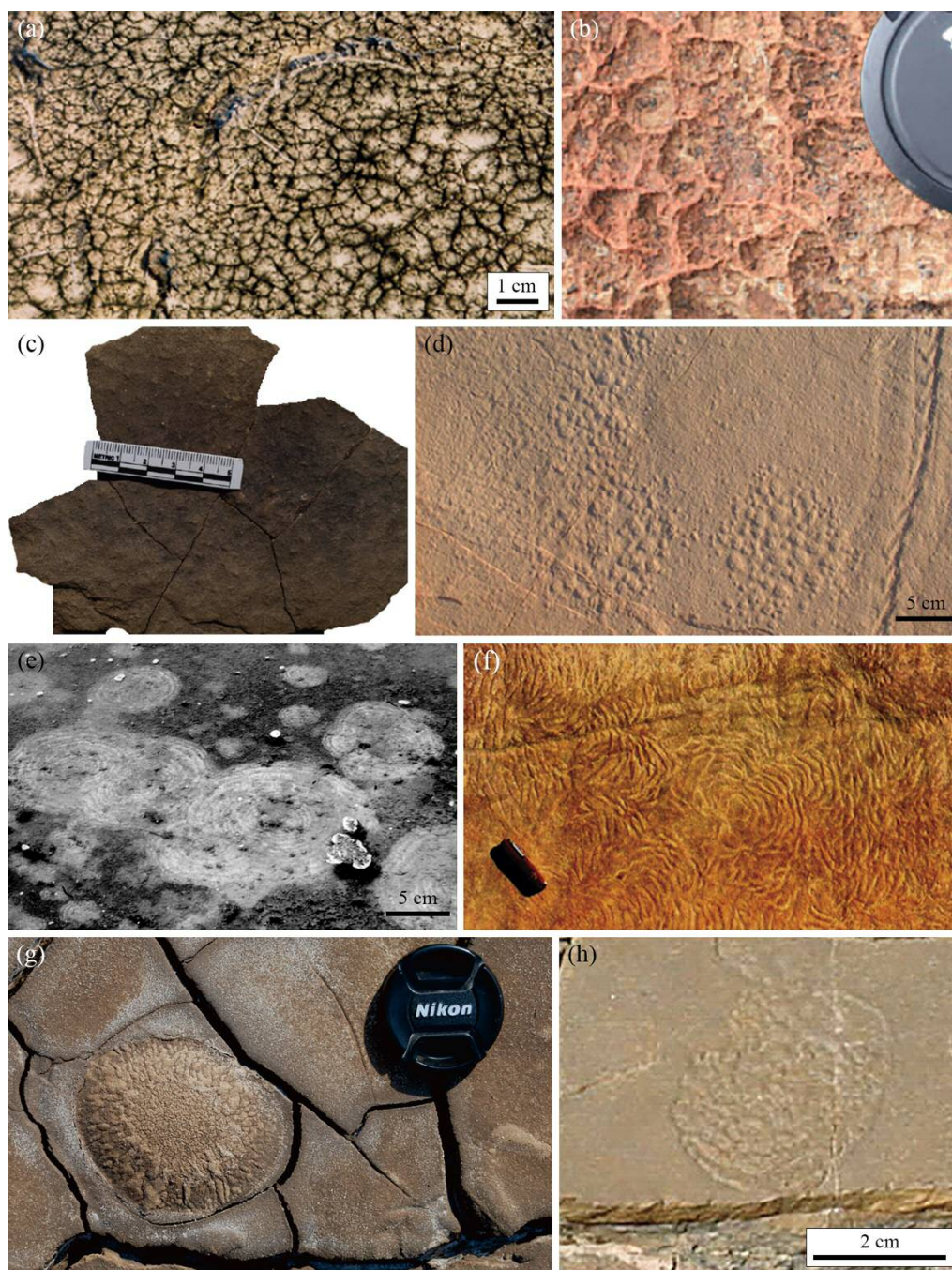


FIGURE S2 EDS elemental maps of bulges of reticulate patterns in cross-section perpendicular to bedding plane. BSE and composite elemental maps. Note the wavy-crinkly laminae with a large amount of embedded heavy minerals.

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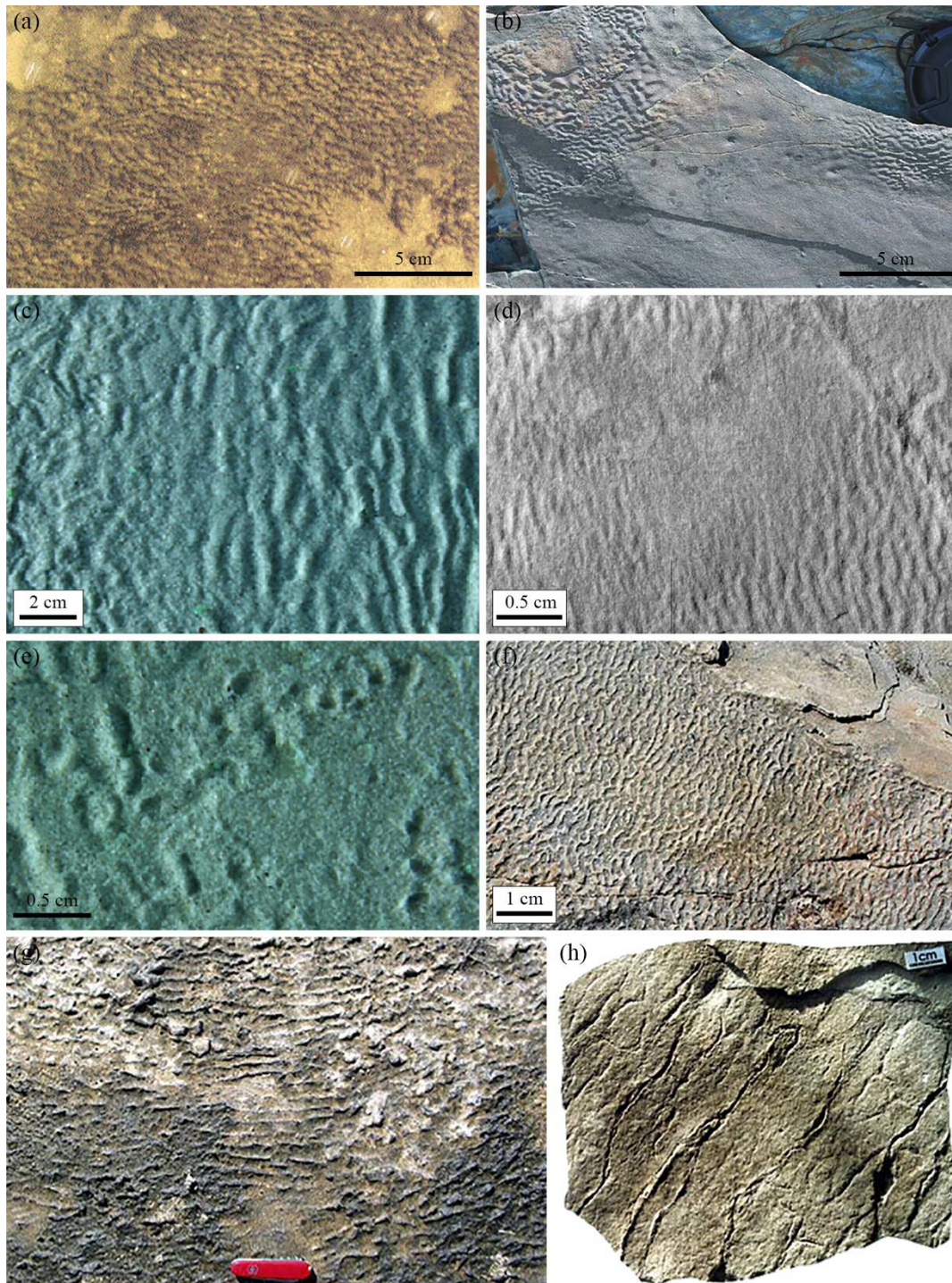
105 **FIGURE S3 Photographs of mat-layer structures found in literature.** (a) Analogous
106 'elephant-skin' texture from modern lower supratidal, Bahar Alouane, southern Tunisia.
107 Modified after photo published in Gerdes (2007). (b) Fossil reticulate pattern on bedding plane
108 of siliciclastic beds from the Archean Tumbiana Formation, Australia. Modified after photo
109 published in Flannery & Walter (2012). (c) A 2.0 billion-years-old tufted microbial mat from
110 Makgabeng Formation, South Africa. Modified after photo published in Simpson *et al.* (2013).

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3 111 (d) Analogue clustered low mound-like structures with *Protichnites* trackways on bedding
4 112 surface of quartz arenites from the Late Cambrian, Elk Mound Group, USA. Modified after
5 113 photo published in Bottjer & Hagadorn (2007). (e) Modern analogous 'fairy rings' on soft
6 114 muddy sediments from Bretagne salterns, France. Modified after photo published in
7 115 Grazhdankin & Gerdes (2007). (f) Ancient example of outward-convex, spindle-shaped
8 116 discoidal structures with concentric rings from the Mesoproterozoic, Sonia Sandstone, India.
9 117 Modified after photo published in Sarkar *et al.* (2014). (g) Modern discoidal microbial colony
10 118 on tidal flat from the Gulf of Cambay, India. Modified after photo published in Banerjee *et al.*
11 119 (2014). Lens cap diameter: 6 cm. (h) Analogue discoidal microbial colony on bedding plane of
12 120 sandstones from the Precambrian Vindhyan Supergroup, India. Modified after photo published
13 121 in Banerjee *et al.* (2014).
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123 **FIGURE S4**

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157 **FIGURE S4 Photographs of mat-related structures found in literature.** (a) Modern

158 example of submerged wrinkle marks from Redfish Bay, Texas. Modified after photo published

159 in Hagadorn & Bottjer (1997). (b) Patches of wrinkle marks on bedding surface of fine-grained

160 sandstones from the Early Cambrian, Chapel Island Formation, Canada. Modified after photo

161 published in Buatois *et al.* (2014). (c) Parallel wavy wrinkle structures reproduced in wave tank

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3 162 experiments using microbial aggregates. Modified after photo published in Mariotti *et al.*
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5 163 (2014). (d) Analogous parallel wavy wrinkle structures on bedding plane of mudstones from
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7 164 the Early Cambrian, Northwest Argentina. Modified after photo published in Buatois &
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9 165 Mángano (2003). (e) Minute “Kinneyia” structures formed with microbial aggregates in wave
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11 166 tank experiments. Modified after photo published in Mariotti *et al.* (2014). (f) Ancient analogue
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13 167 “Kinneyia” structures on bedding surface of siltstones from the Cambrian, Oeland, Sweden.
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15 168 Modified after photo published in Porada & Bouougri (2007). (g) Linear features from modern
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17 169 tidal flats of Bhar Alouane, southern Tunisia. Modified after photo published in Porada &
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19 170 Bouougri (2007). (h) Putative linear patterns on bedding surface of fine-grained quartzites from
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21 171 the Neoproterozoic Katanga Supergroup, Zambia. Modified after photo published in Porada &
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23 172 Bouougri (2007).

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175 **TABLE S1**

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Samples	Si	Al ^{IV}	Al ^{VI}	Al _{Tot}	Mg	Fe	Ti	Mn	K	Na	Ca	Σ Oct	Int
EST	2.78	1.22	1.58	2.8	0.73	0.11	0	0	0.33	0.13	0	2.42	0.47
	3.13	0.87	1.69	2.56	0.15	0.12	0.02	0	0.71	0.15	0	1.98	0.86
	2.89	1.11	1.47	2.58	0.33	0.05	0	0	0.47	0.18	0	1.84	0.65
	3.13	0.87	1.91	2.78	0.11	0	0	0	0.74	0.1	0	2.02	0.84
	2.88	1.12	1.6	2.72	0.52	0.17	0	0	0.52	0.11	0	2.29	0.63
	3.11	0.89	1.94	2.83	0.09	0	0	0	0.79	0.1	0	2.03	0.89
	2.63	1.37	1.17	2.54	0.72	0	0.26	0	0.26	0.17	0	2.15	0.43
PTMM	3.54	0.46	1.79	2.25	0.06	0.04	0	0	0.65	0.06	0	1.89	0.71
	3.41	0.59	1.88	2.47	0.1	0	0	0	0.69	0.07	0	1.98	0.76
	3.34	0.66	1.76	2.41	0.15	0.04	0	0	0.71	0.09	0.03	1.95	0.87
	3.46	0.54	1.69	2.23	0.28	0.06	0	0	0.55	0.09	0	2.02	0.64
	3.61	0.39	1.8	2.19	0.14	0	0	0	0.47	0.17	0	1.94	0.64
	3.35	0.65	1.6	2.25	0.3	0.09	0.01	0.02	0.58	0.12	0.03	2.02	0.73
	3.16	0.84	1.77	2.61	0.14	0.04	0.02	0.02	0.48	0.29	0.04	1.98	0.8
	3.06	0.94	1.56	2.5	0.16	0.25	0.02	0.01	0.86	0.07	0.01	2	0.94
	2.98	1.02	1.83	2.85	0.08	0.04	0.01	0.01	0.89	0.03	0.04	1.98	0.95
	3.03	0.97	1.79	2.76	0.12	0.04	0.01	0.02	0.75	0.11	0.04	1.98	0.9
3.1	0.9	1.83	2.72	0.1	0.04	0.02	0.02	0.39	0.35	0.03	2	0.77	
PWWS	3.17	0.83	1.39	2.22	0.46	0.4	0	0	0.41	0.12	0	2.25	0.53
	3.44	0.56	1.66	2.21	0.3	0.13	0	0	0.45	0.14	0	2.09	0.59
	3.56	0.44	1.67	2.11	0.24	0.1	0	0	0.53	0.09	0	2.02	0.62
	3.38	0.62	1.27	1.89	0.53	0.4	0.03	0	0.34	0.09	0	2.23	0.43
	3.17	0.83	1.91	2.75	0.12	0	0	0	0.75	0.1	0	2.03	0.85
	3.82	0.18	1.77	1.94	0.15	0	0	0	0.5	0.08	0	1.92	0.57
	3.1	0.9	1.76	2.66	0.18	0.07	0.01	0.02	0.62	0.14	0.02	2.03	0.78
	3.04	0.96	1.5	2.46	0.17	0.23	0.07	0.02	0.79	0.09	0.02	1.99	0.89
	3.18	0.82	1.62	2.44	0.32	0.15	0.01	0.02	0.47	0.18	0.02	2.12	0.68
	3.07	0.93	1.39	2.32	0.48	0.3	0.02	0.03	0.55	0.08	0.01	2.22	0.65
2.97	1.03	1.39	2.42	0.47	0.31	0.04	0.03	0.53	0.13	0.02	2.24	0.67	
LP	3.19	0.81	1.85	2.66	2.38	1.64	0.12	0	0.1	0.18	0	5.99	0.28
	3.31	0.69	2.12	2.81	2.48	1.98	0	0	0.02	0.06	0	6.57	0.08
	3.41	0.59	2.25	2.83	2.37	1.64	0.12	0	0.15	0.07	0	6.37	0.22
	3.06	0.94	2.48	3.42	1.98	2.07	0	0	0.2	0.08	0	6.53	0.28
	2.95	1.05	1.5	2.56	0.41	0.29	0.03	0	0.65	0.09	0	2.23	0.74
	3.08	0.92	1.88	2.8	0.08	0.06	0	0	0.77	0.18	0	2.02	0.95
	3.19	0.81	1.82	2.62	0.1	0.06	0	0	0.86	0.05	0	1.98	0.91
	3.11	0.89	0.99	1.88	0.43	0.54	0.09	0.05	0.44	0.05	0.06	2.1	0.55
3.72	0.28	1.44	1.72	0.12	0.1	0.11	0.03	0.48	0.12	0.03	1.8	0.63	

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3 178 **TABLE S1 Representative structural formulae of clays from microbial mats studied with**
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5 179 **EDS.** EST, 'elephant-skin' texture; PTMM, putative tufted microbial mat; WS, wrinkle
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7 180 structure; LP, linear pattern.

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13 184 **TABLE S2**

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Samples	Mass (mg)	%C	%S
EST_mat	10.63	8.62	0.25
EST_host rock	16.62	0.58	0.05
DB_mat	15.32	0.53	22.16
DB_host rock	13.24	4.59	0.22
PWWS_mat	10.37	1.69	0.00
PWWS_host rock	14.17	2.2	0.00
sample4_mat	16.08	1.86	0.06
sample4_host rock	17.53	1.77	0.09
sample5_mat	12.58	1.25	0.54
sample5_host rock	13.18	2.11	0.11

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35 187 **TABLE S2 Organic elemental analyses (carbon and sulfur) on five microbial mats and**
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37 **their host sediments from the FB2 Formation.** EST, 'elephant-skin' texture; DB, domal
38 188 buildup; PWWS, parallel wavy wrinkle structure.
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