

1 **Small microbialites from the basal Triassic mudstone (Tieshikou,**
2 **Jiangxi, South China): geobiologic features, biogenicity, and**
3 **paleoenvironmental implications**

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12

13 **Abstract**

14 We report small microbialites from the calcareous mudstone slightly above the
15 Permian–Triassic boundary (PTB) in the Tieshikou section, southern Jiangxi Province,
16 South China. The newly found microbialite is a bowl-like structure, which contrasts
17 with the surrounding calcareous mudstone. The small microbialite is composed of
18 columnar forms and fan-shaped structures. Mini-columnar structures resemble mini
19 stromatolites. In plane view, most branches are patchy or strip-shaped, with clotted
20 structures, resembling that of a thrombolite. Fan-shaped cement precipitates are
21 comprised of multiple crystal fans that have a radiating texture that show distinct
22 growth laminae. The radiating fabrics are represented by rod-shaped filaments under
23 SEM, which are interpreted as calcified trichomes/filaments. Prominent micropores
24 occur within the rods, and they may be the plane views of multiple sheaths of the false
25 branching zone of trichomes. Thus, both the columnar forms and radiating fans are

26 probably microbial in origin. Moreover, three types of nano-sized structures:
27 intraparticle micropores, fibrous biofilms, and filamentous sheaths are also
28 pronounced in both the columnar structures and cement fans of the Tieshikou
29 microbialite, all suggestive of biogenicity. These well-preserved fibrous biofilms
30 probably represent calcified extracellular polymeric substances (EPS), and linear
31 sheaths are interpreted as the traces of bacterial activities during the precipitation of
32 dolomite crystals. The Tieshikou microbialite therefore shares similar biogenetic
33 mechanisms with other PTB microbialites. The combination of the absence of pyrite
34 framboids, slightly negative carbon isotope values, and an association with abundant
35 ammonoids, bivalves, and gastropods indicates oxic conditions during the growth of
36 the Tieshikou microbialite. Moreover, the nodular preservational state resembles
37 widely distributed nodular mudstones or muddy limestones of the Lower Triassic
38 successions worldwide. This implies that nodular mudstone or argillaceous limestones
39 might also be deposited in microbe-rich environments, in which terrigenous supply
40 was also abundant.

41

42 **Key words:** mass extinction; Early Triassic; limestone nodule; carbonate precipitate;
43 clotted structure; filamentous structures; microbial bloom

44

45 **1. Introduction**

46

47 Widespread microbialites (stromatolites, thrombolites, and dendrolites)
48 characterize carbonate facies of Permian–Triassic boundary (PTB) beds in the
49 Paleo-Tethys region ([Kershaw et al., 2012](#)), and often form pronounced microbial
50 build-ups. These PTB microbialites usually overly the end-Permian mass extinction

51 horizon, and thus are related to the biotic extinction and subsequent harsh
52 environments (Kershaw et al., 2012; Lehrmann et al., 2015). Although some studies
53 clarify that the irregular clotted micritic structures and coccoid-like objects are
54 suggestive of the microorganisms that constructed the PTB calcimicrobial buildups
55 (Kershaw et al., 1999, 2002, 2007, 2012; Lehrmann, 1999; Ezaki et al., 2003, 2008;
56 Wang et al., 2005; Yang et al., 2011; Wu et al., 2014, 2016, 2017; Lehrmann et al.,
57 2015; Tang et al., 2017; Fang et al., 2017; Bagherpour et al., 2017; Friesenbichler et
58 al., 2018; Pei et al., 2018), their accretion process and mechanism have long remained
59 enigmatic. Chen and Benton (2012) also hypothesized that the resurgence of
60 microbial buildups immediately after the end-Permian ecologic crisis signals a
61 calcimicrobe bloom in the post-extinction oceans. If so, microbes should be
62 widespread in various habitats, and occur in different forms in other facies (e.g.,
63 mudstone successions).

64 To test the model of Chen and Benton (2012), we examined the existence of
65 microbes in mudstone facies successions deposited immediately after the PTB mass
66 extinction in South China. Recently, we found abundant small microbialites from
67 calcareous mudstones located slightly above the PTB at the Tieshikou section,
68 southern Jiangxi Province, South China (Fig. 1A). The newly found small
69 microbialite offers additional material that reveals geobiologic features of the PTB
70 microbialites, and provides a better understanding of the accretion processes and
71 biogenic mechanisms of calcimicrobes and their proliferation in various
72 paleoenvironmental settings following the PTB biocrisis. Abundant ammonoids,
73 gastropods, ostracodes, and foraminifers are also found in association with the small
74 microbialite, further confirming that the metazoans associated with the microbialite

75 are more diverse than previously thought (Yang et al., 2011, 2015a, b; Forel, 2014;
76 Forel, et al., 2015).

77

78 **2. Geologic and stratigraphic settings**

79

80 The South China block was located near the equator in the eastern Paleo-Tethys
81 during the Permian–Triassic (P–Tr) transition; a massive, shallow carbonate platform,
82 the Yangtze Platform, extended from west to east across the South China block (Feng
83 et al., 1997; Ziegler et al., 1998). The western part of the platform is referred as the
84 Upper Yangtze Platform, while the eastern part is termed the Lower Yangtze Platform
85 (Sun et al., 1989; Fig. 1B). The Tieshikou section was situated at the junction between
86 the southeastern margin of the Lower Yangtze Platform and a shallow siliciclastic sea
87 to the southeast (Fig. 1B). The lower part of the section is made up of massive
88 bioclastic limestone of the uppermost Permian Changxing Formation, and the upper
89 part of the section is comprised of siliciclastics of the the lowermost Triassic
90 Tieshikou Formation (Fig. 2).

91 The Changxing Formation is made up of massive bioclastic limestone and
92 represents a shallow platform depositional environment, in which bioherms and
93 patchy sponge reef buildups are commonly present. This formation contains a diverse
94 assemblage of open marine biotas: foraminifers, dasycladacean algae, crinoids,
95 echinoids, articulate brachiopods, bivalves, gastropods, calcareous sponges, rugose
96 corals, and bryozoans (Ma, 2016). In particular, calcareous sponges include large,
97 complex, chambered sphinctozoan forms and form bioherms that are pronounced in
98 the field (Sun, 1988; Zhu et al., 1994). The *Clarkina yini* conodont Zone and the
99 *Palaeofusulina sinensis* fusulinid Zone, characteristic of late Changhsingian faunas of

100 South China (Sheng et al., 1984; Chen et al., 2015), are established from the
101 uppermost Changxing Formation (Sun, 1988; Ma, 2016). The Tieshikou Formation is
102 dominated by calcareous mudstone interbedded with muddy limestone layers and
103 calcareous nodules, and represents a subtidal habitat (below fair-weather wavebase)
104 within relatively deep siliciclastic shallow sea setting. The conodont *Hindeodus* cf.
105 *parvus* was reported from a thin, muddy limestone layer, 0.5 m above the top of the
106 Changxing Formation (Zhu et al., 1999; Wu et al., 2003). The calcareous mudstone of
107 the basal Tieshikou Formation yields *Claraia* spp. bivalves, and the ammonoids
108 *Hypophiceras* sp., *Lytophiceras* sp., and *Ophiceras* sp. (Sun, 1988; Zhu et al., 1994;
109 Fig. 2). The small microbial buildup is preserved as limestone nodules embedded in
110 three mudstone layers within the basal Tieshikou Formation (Fig. 3A–C). Associated
111 metazoans include micro-gastropods, ostracodes, and the foraminifer *Earlandia* sp.
112 (Fig. 2).

113 The presence of *H. cf. parvus* marks the PTB in Tieshikou (Zhu et al., 1994; Wu
114 et al., 2003). This age assignment is also strengthened by the presence of *Claraia* sp.,
115 *Hypophiceras* sp., *Lytophiceras* sp., and *Ophiceras* sp. from the same horizons. The
116 latter all occur in Beds 26–29 of the GSSP Meishan section, Changxing county,
117 Zhejiang Province, South China (Yin et al., 2001; Chen et al., 2009, 2010, 2015), and
118 are characteristic of the macrofaunas within the interval spanning the *Hindeodus*
119 *changxingensis* to *Isarcicella staeschei* conodont zones in Meishan (Chen et al., 2015).
120 The new calcimicrobial nodules therefore are earliest Griesbachian in age, and
121 contemporaneous with widespread PTB microbialites from South China.

122

123 3. Material and methods

124

125 A total of 54 oriented samples were collected, slabbed, and thin-sectioned using
126 conventional petrologic techniques. All thin sections were observed under the
127 objective lens of a Leica DM2500P Microscope. A SU8010 FESEM equipped with
128 EDS was also employed to observe thin sections and diagnose the mineral
129 composition of the microbialites. Cathodoluminescence (CL) analyses were carried
130 out on polished, uncovered thin sections with a Leica DM2500 Polarization
131 Microscope with a Cambridge Image Technology (CITL) 8,200 Mk5 cold cathode
132 instrument. This equipment is operated at a beam voltage of 12 kV and current of 198
133 uA. All images were produced under sufficient exposure times.

134 Some of suspected microbialite samples were etched with 1 % acetic acid for 5
135 min and submerged in distilled water to clear away residue attached to the surfaces.
136 Samples were prepared for SEM examination by coating with platinum prior to SEM
137 imaging and EDS analysis. All equipments are housed and analyses carried out at the
138 State Key Laboratory of Biogeology and Environmental Geology, China University of
139 Geosciences (Wuhan).

140 A micro drill was employed to obtain samples of microbialites for $\delta^{13}\text{C}_{\text{carb}}$
141 analysis. The sample powder was reacted offline and under vacuum with 100 %
142 H_3PO_4 for 24 h at 25 °C. The carbon isotope composition of the generated CO_2 was
143 measured using a Finnigan MAT 251 mass spectrometer. All isotopic data are reported
144 as per mil (‰) relative to the Vienna Pee Dee belemnite (V-PDB) standard. The
145 laboratory standard used for carbonate carbon and oxygen isotope compositions is
146 TB-1 ($\delta^{13}\text{C} = 1.61$ ‰, $\delta^{18}\text{O} = -11.59$ ‰ relative to VPDB). The analytical precision is
147 better than ± 0.1 ‰ for $\delta^{13}\text{C}$ and ± 0.2 ‰ for $\delta^{18}\text{O}$ based on duplicate analyses.

148

149 **4. Results**

150

151 *4.1. Mega-, macro- and meso-structures*

152

153 The basal Triassic calcareous mudstones with bowl-like nodules overlie Permian
154 limestones. A few bowl-like nodules occur in at least three calcareous mudstone
155 layers, 0.2 m, 0.6 m, and 0.7 m above the PTB, respectively (Fig. 3A). The bowl-like
156 nodules are elliptical on the top and hemispherical in profile (Figs 3–4). The
157 bowl-shaped structure contrasts with the surrounding calcareous mudstone (Fig. 3C);
158 laminations in the muddy host sediments are deflected around the nodules. The largest
159 nodule is up to 17 cm × 24 cm × 12 cm, and the smallest is 10 cm × 8 cm × 5 cm.

160 The bowl-shaped structures are clearly made up of the branching forms (Fig.
161 4A–C), which have a sharp contact with surrounding micritic sediments (Fig. 5B–C).
162 Dark colored columns, 1–5 mm wide and 10–12 cm high, are pronounced in profile;
163 all columnar branches point towards the bedding surface, indicating growth position.
164 The branches resemble mini-stromatolites, and are laminated and embedded within
165 grey micrite (Fig. 4A–C). In plane view, most of the dark colored branches are patchy
166 or strip-shaped, with a clotted structures (Fig. 4D), resembling that of a thrombolite.
167 The long axis of the branches is orientated to be perpendicular to bedding surface, and
168 most branches radiate from the center core towards the top of the bowl-like structure
169 (Fig. 4D). Some discrete spheroids show a structure that consists of
170 concentrically-stacked hemispheroids, 0.5–1.0 cm in diameter (Fig. 4E).

171 Clotted macrofabrics are prominent on polished blocks, and are comparable to
172 those of thrombolites (Fig. 5). Laminations are also occasionally visible in
173 macrofabrics in the vertical position. Except for the dark-colored, clotted fabrics, the
174 microbialite block also contains abundant ammonoid shells that are mainly distributed

175 along the outer margins of the microbialite (Fig. 5C) and occasionally scattered within
176 clotted fabrics (Fig. 5B).

177 Most columns are cylindrical (Figs 6, 7A–D) or dendritic in outline (Fig. 7E–F);
178 others are cotton-like (Fig. 7G–H), or cabbage-shaped (Fig. 7K–L). Moreover, some
179 columns are composed of 2–3 smaller columns (Fig. 7A–B). Dissolution boundaries
180 are pronounced between the microbialite and surrounding micritic sediments (Fig. 7H,
181 J).

182

183 4.2. Microstructure

184

185 In petrographic thin section, the dark colored, branching columns are primarily
186 made up of sparry calcite; clay minerals surround the branches. Ammonoids,
187 micro-gastropods, ostracodes, and foraminifers (*Earlandia* sp.) are found within dark
188 colored micrites, which make up the matrix surrounding the microbialites. Of these,
189 ammonoids are commonly present at the top of the bowl-like structures.

190 The microbialite is comprised of columnar forms and fan-shaped structures (Figs
191 7–8). The columnar structures grow on carbonate precipitate fans and *vice versa* (Fig.
192 7A–B). One or more cement fans (~2 mm in width) are commonly found to grow
193 from the outermost area of individual columns (Fig. 7C–F). Radial fibrous structures
194 are distinct in both columns and fans (Fig. 7G–H). Pyrite particles are randomly
195 distributed along the margins of cement fans or scattered on the dark-colored laminae
196 of cement fans (Figs 7G–H, 8A). Pyrite crystals show octahedral or cubic
197 morphologies in SEM images (Fig. 12B). The bases of the columns are circular (1–3
198 mm in diameter) (Fig. 7G–J).

199 Laminae are pronounced in most columns and cement fans, and consist of an

200 alternating ~0.1 mm wide dark colored layer and a ~0.5 mm wide light colored layer
201 (Fig. 7). Most laminae are arched, with arcs directed upwards. Radiating structures are
202 clustered to form features that are interpreted here as trichomes and are aligned
203 perpendicular to concentric laminae within columns and cement fans (Figs 7G–H, 8A,
204 D).

205 EDS element maps of the columns show high amounts of Silicon (Si), along with
206 aluminum (Al), oxygen (O), and magnesium (Mg) in the micrite, and high amounts of
207 calcium (Ca) in the columns (Fig. 9B–C). The dark colored laminae contain high Si
208 and Al contents, indicating a clay source (Fig. 9B). The laminae and fibrous fabrics
209 contain similar amounts of Si and Al in the EDS element maps. These
210 micro-structures are also pronounced in CL images of the columnar structures (Fig.
211 8A, 8D). Except for radiating structures, the columns also possess some bright, bent
212 calcite structures with dark edges that are distinct in CL images (Fig. 8A, 8D).

213

214 *4.3. Ultra-structures*

215 The dark colored lamina contain micrites, which demonstrate clay mineral (Al, O)
216 signatures in EDS analysis (Fig. 10C). The microbialite is surrounded by layers of
217 micrite (Fig. 12A). The micrite is made up of small particles that contain elevated
218 levels of Mg (Figs. 9C, 10C), indicating the presence of dolomite in the micrite
219 coatings. Nano-sized particles within columns (Fig. 10D) are interpreted to represent
220 calcified extracellular polymeric substances (EPS). These nano-sized carbonate
221 crystals irregularly interweave to form networks (Fig. 10D) that contain pronounced
222 rounded intraparticle pores, 1–2 μm in diameter (Fig. 10E). These micro-pores are
223 surrounded by walls made up of a mixture of calcium carbonate and silicates (Fig.
224 10D–E).

225 Rod-shaped filamentous structures, which form fibrous fabrics in CL images, are
226 also commonly present in sparry calcites of columnar structures within the
227 microbialites (Fig. 11A–D). Individual rods are straight to slightly curved in outline,
228 and range from 4–10 μm in diameter. EDS analysis shows that the Ca content is
229 pronounced. Some rods are solid, with smooth surfaces with a concave end in cross
230 section (Fig. 11C–F); others possess corroded surfaces (Fig. 11G–H) and 6–10
231 pronounced micropores in cross section (Fig. 11F, 11J–L). Single micropores are ~
232 0.5–1 μm in diameter (Fig. 11K–L).

233 Dolomite is also present in the microbialite as rhombohedral crystals (Fig. 12D),
234 which are frequently corroded on surfaces and near the margins (Fig. 12F–H). Some
235 are strongly corroded, with only the diamond shape remaining (Fig. 12H–I).
236 Filamentous sheaths (Figs 11I, 12G–I) and fossilized biofilms (Fig. 12E) are present
237 on the corrosion surfaces and probably represent calcified extracellular polymeric
238 substances (EPS). These filamentous sheaths, 0.7–1.0 μm in diameter, are usually
239 curved and randomly distributed on the surfaces of dolomite crystals or extend
240 through the crystals (Fig. 12G, 12I).

241

242 *4.4. Carbon and oxygen isotopes and pyrite framboid analysis*

243

244 Powders of the three components defined here (laminae within the microbialite,
245 fan-shaped structures, and micrite surrounding the microbialites) were collected using
246 a micro-drill and analyzed for carbon and oxygen isotopes using the techniques of
247 McCrea (1950). All analytical results appear in Table 1. Laminae within the
248 microbialite yield $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of $-0.54 - +0.07$ ‰ and $-8.16 - -7.68$ ‰,
249 respectively. Both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the fan-shaped structures are $-0.82 -$

250 +0.02 ‰ and -8.23 – -8.16 ‰, respectively. Micrite surrounding the microbialites
251 has $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of -0.96 – -0.91 ‰ and -8.74 – -7.99 ‰, respectively. The
252 $\delta^{13}\text{C}$ values therefore are not significantly different among the three components, and
253 are also broadly similar to those previously published for lowermost Triassic
254 carbonate-siliciclastic mixed successions (cf. $\sim +1.5$ ‰ from [Magaritz and Holser,](#)
255 [1991](#)). $\delta^{18}\text{O}$ values, which are depleted in ^{18}O relative to unmetamorphosed
256 equivalents, probably reflect the low-grade metamorphism that affected the formation.

257 None of the samples obtained from the six horizons near the PTB (Fig. 2) in the
258 Tieshikou section contain pyrite framboids, which may indicate oxic conditions ([Bond](#)
259 [and Wignall, 2010](#)), but it is important to note that pyrite needs sufficient iron, sulphur
260 and organic matter to form, and the lack of framboids is not an absolute indicator of
261 oxygenated conditions.

262

263 **5. Discussion**

264

265 *5.1. Difference between the small microbialite and red algae*

266

267 The Tieshikou section microbialite bears a remarkable resemblance to calcite
268 crusts described from the Late Neoproterozoic. The latter have been interpreted as the
269 remains of coralline red algae ([Grant et al., 1991](#)); red algae are commonly present in
270 Triassic successions ([Flügel and Senowbari-Daryan, 2001](#)), strengthening the
271 identification of red algae from the Tieshikou section. However, the microbialite
272 differs clearly from red algae based on a lack of outer walls. In contrast, Tieshikou
273 section microbialite possesses pronounced laminae and very faint radial structures.
274 Moreover, the Tieshikou microbialite is also characterized by conspicuous fan-shaped

275 branches (Fig. 7), which are significantly different from red algae branches; in the
276 microbialite, amorphous branches grow above the older branches (Fig. 7). The
277 Permian red alga *Solenopora* described by Wu (1991) from the Longlin area, Guizhou,
278 South China possesses radiating filaments with prominent walls, which resemble
279 radial structures of Tieshikou section microbialite. The latter, however, are very faint
280 and overlapped with distinct laminae, and never form filaments, as observed in red
281 alga *Solenopora* (Wu, 1991). Moreover, pyrite particles are dispersed in the
282 microbialite, similar to those seen in other PTB microbialites (Wang et al., 2005; Liao
283 et al., 2010; Yang et al., 2011), but rarely present in red algae.

284

285 5.2. *Taphonomy and geobiologic process associated with accretion of the microbialite*

286

287 The nodular morphology and occurrence of widespread PTB microbialites in
288 carbonate platform settings in South China suggest that the bowl-like microbialite
289 may have been transported from the adjacent platform and re-deposited in the
290 siliciclastic setting of the Tieshikou section. Although PTB microbialites have been
291 reported from 38 sites across South China, they are rare in the Lower Yangtze
292 platform (Wu et al., 2017). The closest known PTB microbialite site is located in the
293 Xiushui area, ~400 km north of the Tieshikou section (Wu et al., 2017; Fig. 1). In
294 addition, ammonoid fossils are unique to the Tieshikou microbialite, and have never
295 been found in any known PTB microbialites in South China (Yang et al., 2008, 2011;
296 Kershaw et al., 2012; Adachi et al., 2017; Fang et al., 2017). More importantly, all
297 microbialite columnar branches within the bowl-shaped structures point towards the
298 bedding surface, indicating an upright growth position (Fig. 4A–C). This also
299 indicates that the microbialites are in place and have not been transported. Horizontal

300 laminae in surrounding mud sediments are deflected around the nodules (Fig. 3C),
301 indicating syn-deposition of nodule with surrounding sediments. Thus, the bowl-like
302 structures are *in situ* and are not transported.

303 The Tieshikou section microbialite resembles amalgamated structures of
304 stromatolites and crystal fans reported from the Cambrian and Carboniferous to
305 Pleistocene strata (Riding, 2000, 2008, 2011). Of these, Cambrian and Carboniferous
306 fine-grained stromatolitic crusts possess uneven to discontinuous, poorly defined
307 layers (Riding, 2011, figs. 5, 18). Similar characteristics are also observed in the
308 Tieshikou microbialites (Figs. 4–6). The small stromatolites exhibit uneven to
309 discontinuous (Fig. 4), poorly defined layers (Fig. 6). Moreover, microfabrics of
310 fine-grained stromatolitic crusts from Carboniferous and Pleistocene strata show
311 dense, clotted, peloidal, and/or filamentous morphologies (Riding, 2000, figs. 5–7),
312 are dominated by micrite and microspar and may contain fenestrae and allochthonous
313 grains (Riding, 2000, 2011). The Tieshikou radiating cement fans do not show all
314 microfabric morphologies of stromatolitic crusts mentioned above, but do possess
315 dark, laminated layers that contain allochthonous clay minerals (Fig. 9). To sum up,
316 the amalgamation of stromatolitic crusts and crystal fans from the Tieshikou
317 microbialite share many features with Phanerozoic fine-grained stromatolitic crusts:
318 both have microfabric and irregular or poorly-layered macrofabrics that are suggestive
319 of a biogenic origin (Riding, 2011).

320

321 5.2.1. Laminated columns

322 All columns of the Tieshikou microbialite possess laminar structures that exhibit
323 alternating dark and bright layers within columns. The columnar laminae exhibit
324 similar characteristics as those of modern marine stromatolites. The thin micrite layers

325 of modern stromatolites are interpreted to be the result of bacterial activity ([Visscher](#)
326 [et al., 2000](#); [Dupraz et al., 2004, 2009](#); [Dupraz and Visscher, 2005](#)), and also
327 contribute to the formation of the laminated fabric ([Arp et al., 1999a, b, 2001, 2003](#);
328 [Reid et al., 2000](#)). SEM imaging of stromatolites from Shark Bay, Western Australia
329 shows that the dark-colored layers are comprised of polyhedral clay aggregates, which
330 are interpreted to form as the result of a benthic microbial community (BMC)
331 trapping and binding detrital sediment and/or forming the locus of mineral
332 precipitation ([Reid et al., 2000](#)). Similar clay aggregates are also observed within the
333 columnar structures of the Tieshikou microbialite (Fig. 9B–C). The Tieshikou
334 laminated columns are therefore thought to be biogenic.

335

336 *5.2.2. Fibrous fabrics in cement fans*

337 Carbonate precipitates (also termed seafloor fans, [Woods et al., 1999](#)) comprised
338 of radiating calcite crystals have been frequently reported from Lower Triassic
339 successions worldwide ([Woods et al., 1999, 2007](#); [Baud et al., 2007](#); [Woods and Baud,](#)
340 [2008](#)). Syn-sedimentary cements also occur within some Lower Triassic microbialites
341 ([Baud et al., 2007](#); [Kershaw et al., 2007, 2011](#); [Lehrmann et al., 2015](#)). A lack of
342 similar microbial features in association with seafloor carbonate precipitates from
343 other regions points to an abiotic origin, although it is impossible to exclude the
344 possibility that microbes may have played a role in their formation ([Woods, 2014](#)). In
345 contrast, some biogeochemical signals mirroring various microbial communities
346 associated with benthic microbial mats have been detected from diagenetic carbonate
347 crystal fan deposits of Dienerian-Smithian age ([Heindel et al., 2014](#)). Microbial fossils
348 within cements from Oman provide more robust evidence of a microbial influence
349 during cement growth ([Woods and Baud, 2008](#); [Woods, 2014](#)).

350 When compared with the Tieshikou cement fans, all known synsedimentary
351 cements are slightly different in having radiating calcite crystals (Woods et al., 1999,
352 2007; Woods and Baud, 2008), and lacking concentric laminae and pyrite crystals,
353 which are observed in the Tieshikou precipitate fans (Fig. 7). In contrast, both
354 concentric laminae and radial fibrous fabrics (also trichome-like structures) (Fig. 8A,
355 D) characterize the Tieshikou cement fans, which usually exhibit 3–5 concentric
356 laminae and densely arranged, neatly aligned trichomes. The latter are often
357 perpendicular to the concentric laminae (Fig. 7). Similar micro-structures have also
358 been reported from the Frasnian succession at the Lion quarry of Frasnes, Belgian
359 Ardennes (Monty, 1995). These Devonian micro-structures are interpreted as
360 flagellates and the finely laminated structures are reminiscent of the modern
361 cyanophyte *Rivularia* (Monty, 1995), although the latter is almost always found as a
362 freshwater cyanobacterium (Kershaw and Guo, 2003, 2006; Antonioli et al., 2006;
363 Andrews et al., 2007).

364 Concentric laminae and radial trichomes are also observed in the modern
365 *Rivularia haematites* stromatolite (Caudwell et al., 2001), which are similar to the
366 texture of the Tieshikou cement fan structures. The growth of the *Rivularia*
367 stromatolite is interpreted to reflect a wide range of biological, environmental, and
368 climatic factors (Caudwell et al., 2001). Concentric laminae could be the result of
369 microbial growth, while cement growth is coupled to the growth of the radial
370 trichomes (Caudwell et al., 2001). Accordingly, both biological and sedimentary
371 processes are crucial for the accretion of these unique micro-structures.

372 The rod-like aggregates of the Tieshikou cement fans also share many common
373 characteristics with present-day *Rivularia* structures (Caudwell et al., 2001).
374 Micropores that occur within a single rod, which are prominent in the Tieshikou

375 samples (Fig. 11K–L), are also observed in the trichomes of present-day *Rivularia*
376 *haematites* stromatolites, and are interpreted to represent honeycomb structures found
377 in transverse sections *Rivularia* stromatolite filaments (Caudwell et al., 2001, fig. 8).
378 In addition, the rods of the Tieshikou microbialite share a similar size and
379 interweaving pattern with fossilized cyanobacteria filaments from the literature
380 (Golubic et al., 2000; Seong-Joo et al., 2000) and to modern stromatolites from
381 hypersaline lakes (Każmierczak et al., 2011). Accordingly, the Tieshikou microbialite
382 is highly similar to *R. haematites*, and thus exhibits many features of a
383 cyanobacterium. If so, these putative fossilized bacterial filaments may represent the
384 primary producers that constructed the Tieshikou microbialite.

385

386 5.2.3. Biogenicity recorded in nano-sized structures

387 Three types of nano-sized structures from the Tieshikou microbialite indicate
388 biogenicity, including intraparticle micropores, fibrous biofilms, and filamentous
389 sheaths. The first type structure occurs in the networks woven by nano-sized calcium
390 carbonate crystals within a micritic matrix (Fig. 10D–E). Fibrous biofilms are
391 frequently seen within dolomite crystals (Fig. 12E), and nano-sized filamentous
392 sheaths are abundant on the surfaces of and within dolomite crystals (Fig. 12G–I).

393 Intraparticle micropores often occur within the micritic matrix (Fig. 10D–E) of
394 both the laminated columns and the radiating cement fans of the Tieshikou
395 microbialite, and are distributed throughout the crystals as opposed to being zoned
396 and limited to the crystal edges. The intraparticle micropores share many features
397 with other biogenic micropores observed in modern and ancient stromatolites, except
398 for a slightly smaller size (Bosak et al., 2004), and are thus also interpreted as an
399 indication of a microbial signature.

400 Irregular, but mostly fibrous biofilms frequently are seen in the dolomite crystals
401 when their surfaces are corroded (Fig. 12E). Similar fibrous filaments have also been
402 reported from the dolomite-precipitating environment of a Miocene lacustrine system,
403 and are interpreted to be the residue of extracellular polymeric substances (EPS)
404 (Sanz-Montero et al., 2008). Fibrous biofilms are also commonly present in modern
405 and fossilized stromatolites and microbial mats (Arp et al., 1999a, b, 2001; Noffke et
406 al., 2003; Dupraz et al., 2004, 2009; Dupraz and Visscher, 2005; Shiraishi et al., 2008;
407 Noffke, 2010; Glunk et al., 2011; Luo et al., 2013, 2014; Chen et al., 2014; Neu and
408 Lawrence, 2015; Ionescu et al., 2015; Tu et al., 2016; Xu et al., 2017; Decho and
409 Gutierrez, 2017). Morphologically, the Tieshikou fibrous biofilms are strong evidence
410 of fossilized EPS, however, whether these nano-sized microstructures obtained from
411 geological samples can be compared directly to modern EPS remains to be
412 determined (Arp et al., 2001; Shiraishi et al., 2008; Dupraz et al., 2009; Neu et al.,
413 2010; Glunk et al., 2011; Neu and Lawrence, 2015; Ionescu et al., 2015; Decho and
414 Gutierrez, 2017). This is because few studies have revealed how diagenesis affects the
415 lithification of EPS from living objects to fossilized forms. Thus, the assignment of
416 the Tieshikou nano-sized particles to fossilized EPS is rather tentative, and needs to
417 be confirmed by future work on the effects of diagenesis on nano-sized biogenic
418 structures.

419 Linear sheaths are also frequently found in corroded dolomite crystals within the
420 Tieshikou microbialite (Fig. 12F–G). These linear, hollow tubes resemble
421 microboring traces that can be identified to the ichnospecies level, including
422 *Eurygonum nodosum*, a trace forming a branched meshwork of 6 to 10 μm thick
423 galleries with diagnostic short swollen apophyses, and presumably produced by the
424 filamentous hetroscystous cyanobacterium *Mastigocoleus testarum* (Glaub et al.,

425 2007). However, these tiny tubes are unlikely to be endoliths that are produced by
426 rock-eating bacteria due to their small size (usually 0.5–1 µm in diameter). In contrast,
427 these sheaths are almost identical to the residues of modern bacterial sheaths (in size
428 and shape) that are observed from Lagoa Vermelha (Lith et al., 2003). They also
429 could be the residues of sulphate-reducing bacteria that have been reported from strain
430 LVform6 from modern cultures and are closely related to dolomite dumbbells (Lith et
431 al., 2003). Accordingly, the Tieshikou nano-sized sheaths bear a remarkable
432 resemblance to the moulds of bacteria that form during the precipitation of dolomite
433 crystals. However, several observations of modern microbialites or microbial mats
434 show that similar microbial filaments could have many origins and are not restricted
435 to cyanobacteria (Arp et al., 1999a, b, 2001; Shiraishi et al., 2008; Dupraz et al., 2009;
436 Ionescu et al., 2015; Decho and Gutierrez, 2017). Additional work is needed to clarify
437 the origin of these features.

438

439 5.3. Comparisons with other Early Triassic microbialites

440

441 Although Early Triassic microbialites have been globally reported, detailed
442 geomicrobiologic analysis of these unusual deposits has largely lagged behind the
443 study of their ecologic significance (Chen et al., 2017), although some detailed works
444 have been conducted. The PTB stromatolites from the Bükk Mountains of Hungary
445 yield abundant microstructures such as spheroid clusters, aggregates of micrite clots,
446 and bundles of prostrate micrite threads (Hips and Haas, 2006). These authors
447 interpret the spheroids to be calcified coccoid cyanobacteria. Yang et al. (2011)
448 describe a stromatolite from the Chongyang PTB section of southern Hubei Province,
449 South China. In addition to *Renalcis*-like structures found in stromatolitic laminae

450 (Wang et al., 2005), the Chongyang stromatolite is also dominated by coccoid bacteria
451 (Yang et al., 2011). Other PTB and Early Triassic stromatolites have also been
452 reported from around the world (e.g., Pruss et al., 2006; Baud et al., 2007; Kershaw et
453 al., 2011, 2012). However, their microbial composition remains unclear because no
454 geobiologic studies have been undertaken.

455 Macroscopic features of the Tieshikou microbialites are very similar to those of
456 some PTB thrombolites. However, the Tieshikou microbialites possess laminated
457 structures among coarse grains, whereas other PTB thrombolites have sparitic
458 structures composed of coarse grains. Kershaw et al. (2007) interpreted these sparitic
459 structures within the PTB thrombolites to be altered microbes that have a
460 “*Renalcis*-like” character, but is actually is different from *Renalcis*, so there is no
461 clarity as to the nature of the microbes. Alternatively, Wu et al. (2014, 2016) interpret
462 the same structures as colonies of microbial organisms comparable to the modern
463 cyanobacterium *Microcystis*. However, their identification of *Microcystis* is also
464 questionable because bacterial colonies occur on vertical rock walls of the
465 Laolongdong microbialite, which span a stratal interval of several centimeters in
466 thickness. The compaction and deformation of microbialite sediments after
467 lithification and diagenesis prevent the direct comparison of the imprinted bacterial
468 colonies on microbialites to modern-day planktic *Microcystis* colonies (Luo et al.,
469 2016a; Fang et al., 2017).

470 Filamentous fossils are often found in digitate microbialites and aragonite fans
471 beneath the PTB microbialites in South China (i.e. Lehrmann et al., 2015, fig. 8C–D).
472 Similar microfossils are also reported from other PTBMs in South China (Wang et al.,
473 2005; Yang et al., 2011). The filamentous fossils are thought to be major builders of
474 microbialites (Wang et al., 2005; Yang et al., 2011), although they are absent from the

475 Tieshikou microbialite. Aragonite crystal fans are extensively recrystallized but retain
476 a fine acicular habit and square-tipped crystal terminations, typical of marine
477 aragonite (Lehrmann et al., 2015).

478

479 *5.4. Implications for post-extinction marine conditions in siliciclastic shallow seas*

480

481 Widespread PTB microbialites are usually interpreted as an unusual
482 biosedimentary phenomenon related to the severe PTB mass extinction and its
483 consequences (Kershaw et al., 2012). The microbial composition of several Lower
484 Triassic stromatolites was largely controlled by inhospitable anoxic/sulphidic marine
485 conditions that prevailed in the oceans during that time (Ezaki et al., 2008, 2012;
486 Saito et al., 2014; Luo et al., 2016a). Biogeochemical signals also show that microbes
487 are indeed extremely abundant immediately after the end-Permian extinction, even in
488 microbialite-free carbonate settings such as Meishan, South China (Xie et al., 2005).
489 Thus, microbes existed widely in various niches of carbonate environments after the
490 PTB extinction. However, whether microbes also proliferated in marine siliciclastic
491 habitats immediately after the PTB extinction still remains unclear.

492 Kershaw et al. (2007) and Woods et al. (2007) also emphasized that elevated
493 carbonate supersaturation caused by the upwelling of CaCO₃-rich anoxic waters,
494 mixed with aerated surface waters, may be the key driver for the precipitation of the
495 PTB microbialites. Nevertheless, Kershaw et al. (2012) point out that the poor
496 representation of seafloor cements in post-extinction facies in South China reduces
497 the likelihood of supersaturation as a major control on microbialite formation. The
498 saturation issue is a complex one, not least because of the highly saturated carbonate
499 conditions expected in the post-extinction oceans (Grotzinger and Knoll, 1995; Woods

500 et al., 1999; Riding and Liang, 2005; Pruss et al., 2006; Riding, 2006; Baud et al.,
501 2007) due to the loss of skeletal taxa increasing the availability of bicarbonate,
502 combined with factors unfavorable to most normal skeletal organisms. Recent
503 elemental and pyrite framboid analyses reveal that some PTB microbialites may also
504 have been deposited under dysoxic conditions (Liao et al., 2010), yet Loope et al.
505 (2013) present evidence for an oxygenated environment. Similarly, abundant and
506 diverse ostracod, microconchid, and benthic faunas derived from PTB microbialites
507 also indicate that the associated environments of PTB microbialites were neither
508 anoxic nor inhospitable to shelly organisms (Forel et al., 2012; Forel, 2013; Yang et
509 al., 2015a, b; Wu et al., 2017).

510 The Tieshikou fibrous carbonate precipitates share similar accretion process to
511 PTB microbialites, and formed under a similar seawater chemistry to the PTB
512 microbialites. Syn-sedimentary precipitation of calcium carbonate fans was mediated
513 through rapid shifts in the chemistry of ambient waters. The microenvironment (e.g.
514 Eh and pH) was changed due to microbial activity, and such an ambient environment
515 may have stimulated the deposition of more microbial sediments (Heindel et al.,
516 2014). Then, some laminated columns or micro-stromatolites grew along the
517 carbonate precipitate fans (Fig. 13).

518 The Tieshikou microbialites are preserved in the form of nodules within
519 mudstone. The PTB succession in Tieshikou represents an offshore environment (Zhu
520 et al., 1994). The slightly negative carbon isotope values are derived from cement fans,
521 microspars, and micrites of the Tieshikou microbialite (Table 1). All horizons
522 examined here contain no pyrite framboids. Moreover, the micrite surrounding the
523 microbialites yields ammonoids, microgastropods, ostracodes, and foraminifers. All
524 lines of evidence suggest that the Tieshikou microbialite grew in an oxic marine

525 environment immediately after the end-Permian crisis. Surprisingly, contemporaneous
526 siliciclastic or carbonate shallow seas were usually dyoxic to anoxic in South China
527 (Chen et al., 2015; Li et al., 2016; Huang et al., 2017). Accordingly, the growth of the
528 PTB microbialites appears to not be restricted by oxygen levels; instead PTB
529 microbialites were affected by other seawater chemical conditions. Further work is
530 necessary to test such an inference for oceanographic conditions during growth of the
531 PTB microbialites.

532

533 *5.5. Implication for the genesis of calcareous nodules in mudstone or nodular*
534 *limestone of the Lower Triassic*

535

536 Comparable compositions and geobiologic features to those of the PTB
537 microbialites indicate that the Tieshikou microbialite could share similar biogenetic
538 mechanisms to other microbialites. Abundant microbes and a highly saturated water
539 mass could provide a hospitable environment for the growth of microbialites during
540 the P–Tr transition.

541 Besides, the nodular preservational state resembles that of calcareous nodular
542 mudstone or nodular argillaceous limestone, implying that these deposits may share
543 similar biogenetic mechanism to that of Tieshikou microbialites. Nodular mudstone or
544 argillaceous limestone is one of most widely distributed rocks within Lower Triassic
545 successions in South China (Chen et al., 2011; Luo et al., 2016b; Fig. 2B). This
546 implies that nodular mudstone or muddy limestone might also be deposited in a
547 microbe-rich, highly saturated environment, although elevated terrigenous supply
548 immediately after the end-Permian crisis (Algeo and Twitchett, 2010; Zhao et al.,
549 2013) may have modulated sedimentation in siliciclastic settings during that time. If

550 so, the nodular mudstone or muddy limestone is also likely of microbial origin, and
551 they and represent an alternative forms of microbial preservation in Lower Triassic
552 strata. However, further work is necessary to test biogenesis of Lower Triassic
553 nodular mudstone and argillaceous limestone.

554 The Chen-Benton fossilized trophic pyramid model proposes that most primary
555 consumers and higher trophic functioning structures collapsed as a result of the PTB
556 mass extinction (Chen and Benton, 2012). As a consequence, a primary
557 producer-dominated community (i.e., microbes) prevailed in the post-extinction
558 oceans. However, such a microbial proliferation can only be identified from a few
559 types of Lower Triassic sedimentary records, such as microbialites and
560 microbially-induced sedimentary structures (MISSs) (i.e., Xu et al., 2017).
561 Furthermore, microbialites only peaked during several short intervals (i.e. PTB,
562 Griesbachian-Dienerian transition, early Smithian, late Smithian, and late Spathian;
563 Baud et al., 2007; Chen et al., 2014; Luo et al., 2016a), and no sedimentary record
564 shows microbialites across the duration of the Early Triassic.

565 The occurrence of microbialites in Lower Triassic mudstones implies that
566 microbes were still abundant in post-extinction marine habitats, although they may be
567 preserved in the form of nodules embedded within mudstone or argillaceous
568 limestone, at least in South China (Luo et al., 2016b; Fig. 2B), supporting the scenario
569 of a microbial proliferation in post-extinction oceans (Chen and Benton, 2012).

570

571 **6. Conclusions**

572

573 A new type of microbialite is described from the nodular mudstones just above
574 the P–Tr boundary at the Tieshikou section, southern Jiangxi Province, South China.

575 The microbialite occurs as a bowl-like structure that displays densely laminated
576 stromatolitic columns in profile and clotted thrombolite textures in plane view.
577 Radiating cement fans contain concentric laminae and pronounced fibrous fabrics,
578 resembling seafloor carbonate precipitates. Under SEM, the radiating fans are
579 represented by rod-shaped filaments, which are interpreted as calcified
580 trichomes/filaments. Prominent micropores within rods represent the multiple sheaths
581 of false branching zones of trichomes. Thus, both the columns and radiating fans are
582 probably microbial in origin. Moreover, three types of nano-sized structures:
583 intraparticle micropores, fibrous biofilms, and filamentous sheaths are also recognized
584 from the Tieshikou microbialite, and all strongly indicate biogenicity. In particular,
585 the well-preserved fibrous biofilms could represent fossilized EPS, and worm-like
586 sheaths are interpreted as the residues of bacteria that formed during the precipitation
587 of dolomite crystals. These two nano-sized structures are associated with dolomite
588 crystals, suggesting that dolomite in the Tieshikou microbialite is microbial in origin.
589 The geobiologic features of the Tieshikou microbialite resemble those of the
590 widespread microbialites that occur near the P–Tr boundary, suggesting both share
591 similar accretion mechanisms and depositional environments. The combination of an
592 absence of pyrite framboids, slightly negative carbon isotope values, and an
593 association with fairly abundant ammonoids, bivalves, and gastropods indicates oxic
594 conditions during growth of the Tieshikou microbialite. Accordingly, the Tieshikou
595 microbialite is indicative of a microbial bloom that not only occurred in shallow
596 carbonate habitats, but also extended to relatively deep siliciclastic offshore settings
597 after the end-Permian mass extinction. Moreover, the comparable diagenetic state of
598 the microbialite with that of the widespread nodular mudstone or muddy limestone of
599 the Lower Triassic successions implies that abundant microbes may have also existed

600 in the Early Triassic oceans even if microbialites are not found.

601

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611

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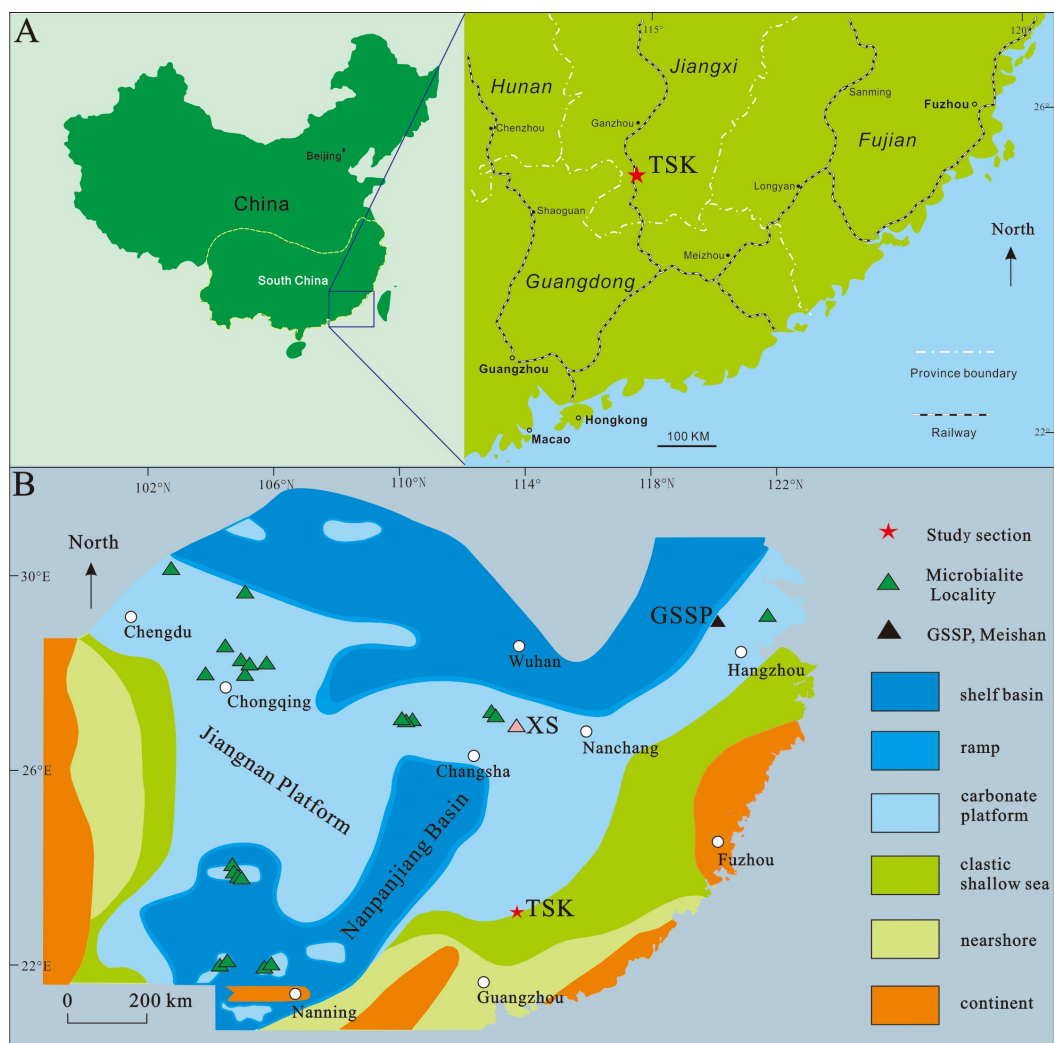
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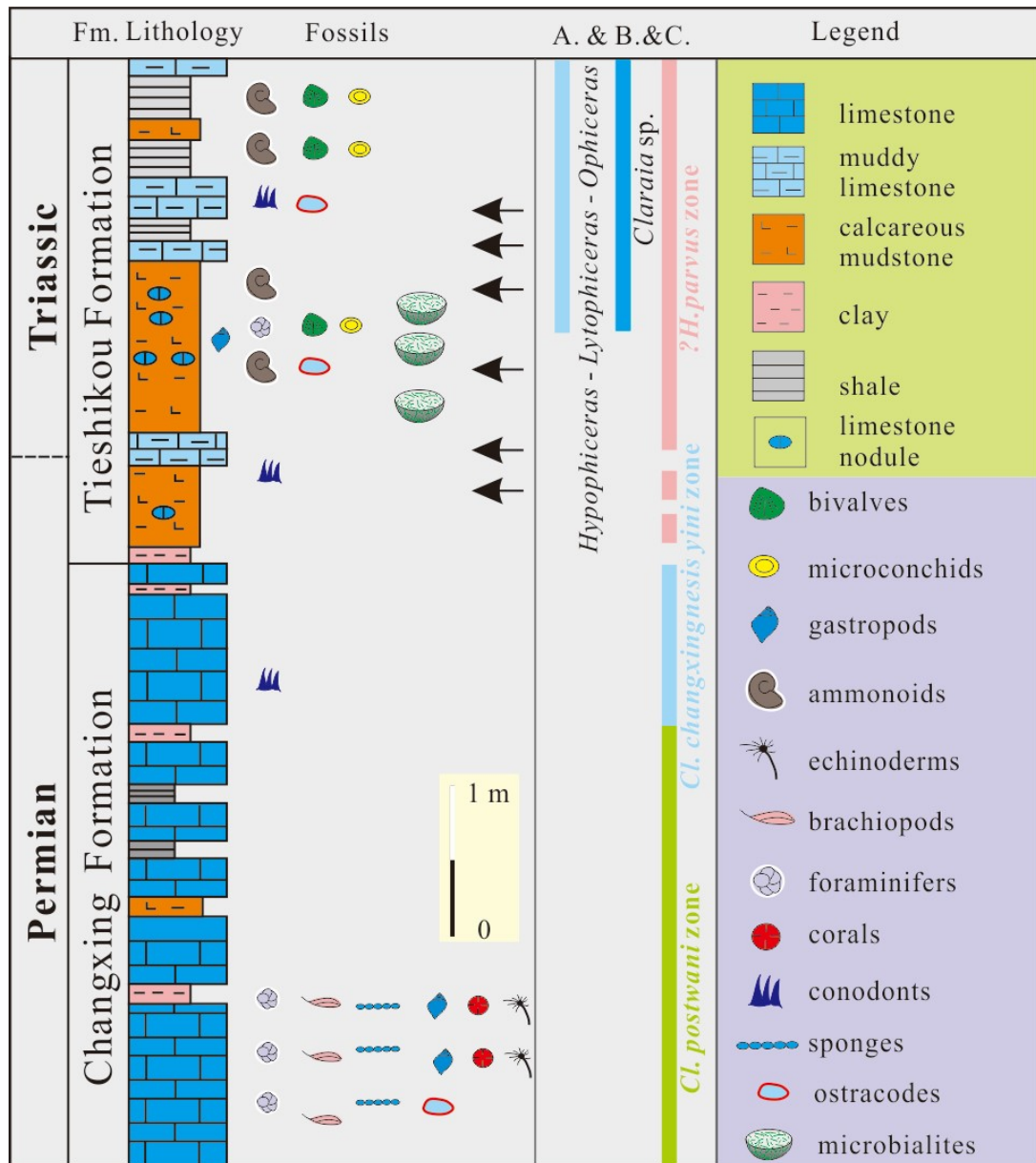
961 **Figure and table captions**



962

963 **Fig. 1.** (A) Location of the Tieshikou section in Xinfeng County, southern Jiangxi
 964 Province, South China. (B) Paleogeographic configuration of the South China Block
 965 during the P–Tr transition (Modified from Feng et al., 1997) showing location of the
 966 study section and 38 other PTB microbialite sites across South China (Wu et al.,
 967 2017). TSK: Tieshikou section; XS: Xiushui section; GSSP Meishan: Global
 968 Stratotype of Section and Point of the Meishan section.

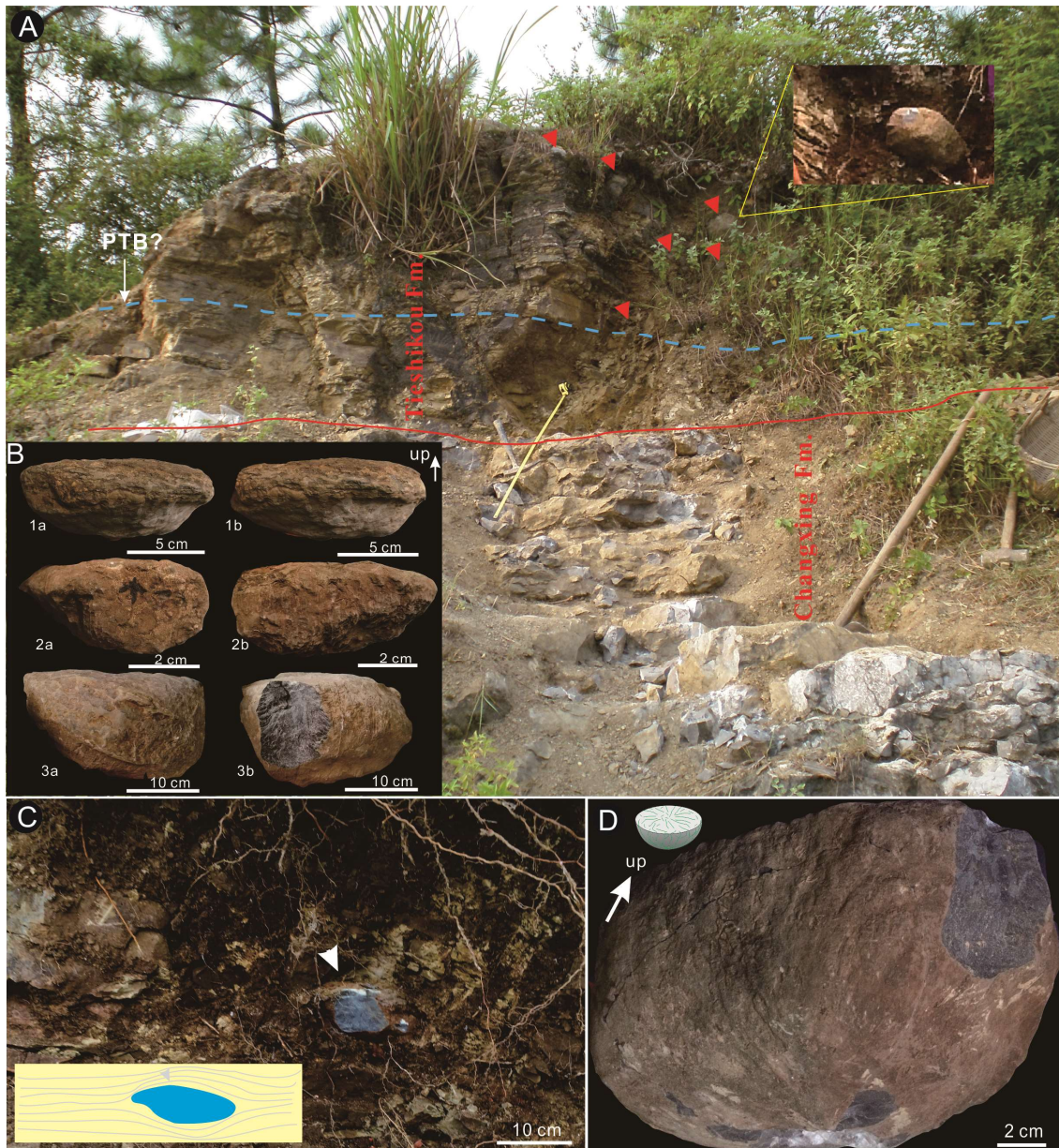
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971 **Fig. 2.** The Permian–Triassic succession exposed at the Tieshikou section, showing
 972 the stratigraphic distribution of various fossils, biozones, as well as the microbialite
 973 horizon. Black arrows indicate sampling horizons for pyrite framboid analysis.
 974 Conodont zones follow Zhu et al. (1999) and Wu et al. (2003), and bivalve and
 975 ammonoid assemblages follow Sun (1988) and Zhu et al. (1994). A. = ammonoids, B.
 976 = bivalves, C. = conodonts, Fm = Formation.

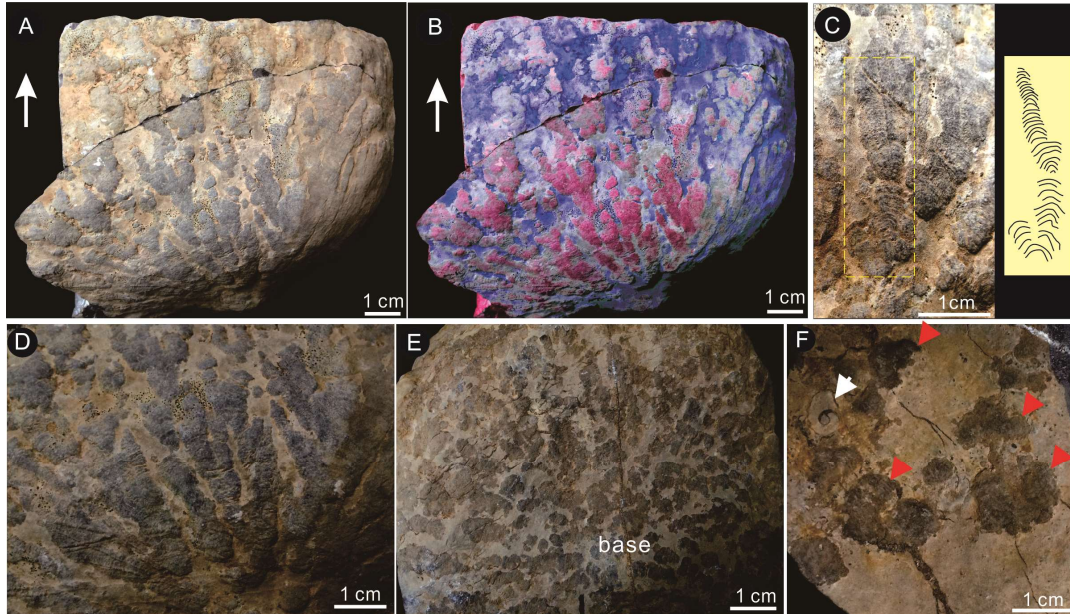
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979 **Fig. 3.** (A) Field photo showing the Permian–Triassic boundary (PTB) succession at
 980 the Tieshikou section. Note the blue line indicates the probable location of the PTB,
 981 and the inserted photo at upper right corner shows a small microbialite embedded in a
 982 mudstone layer (red arrows), 0.7 m above the PTB. (B) Three isolated bowl-like
 983 nodules (B₁–B₃). Note that photos labeled a and b represent anterior and posterior
 984 views, respectively. (C) Close-up of another small microbialite (white arrow)
 985 embedded in a mudstone bed, 1.1 m above the PTB. Cartoon diagram in lower left
 986 corner shows that horizontal laminae are deflected around the small microbialite. (D)

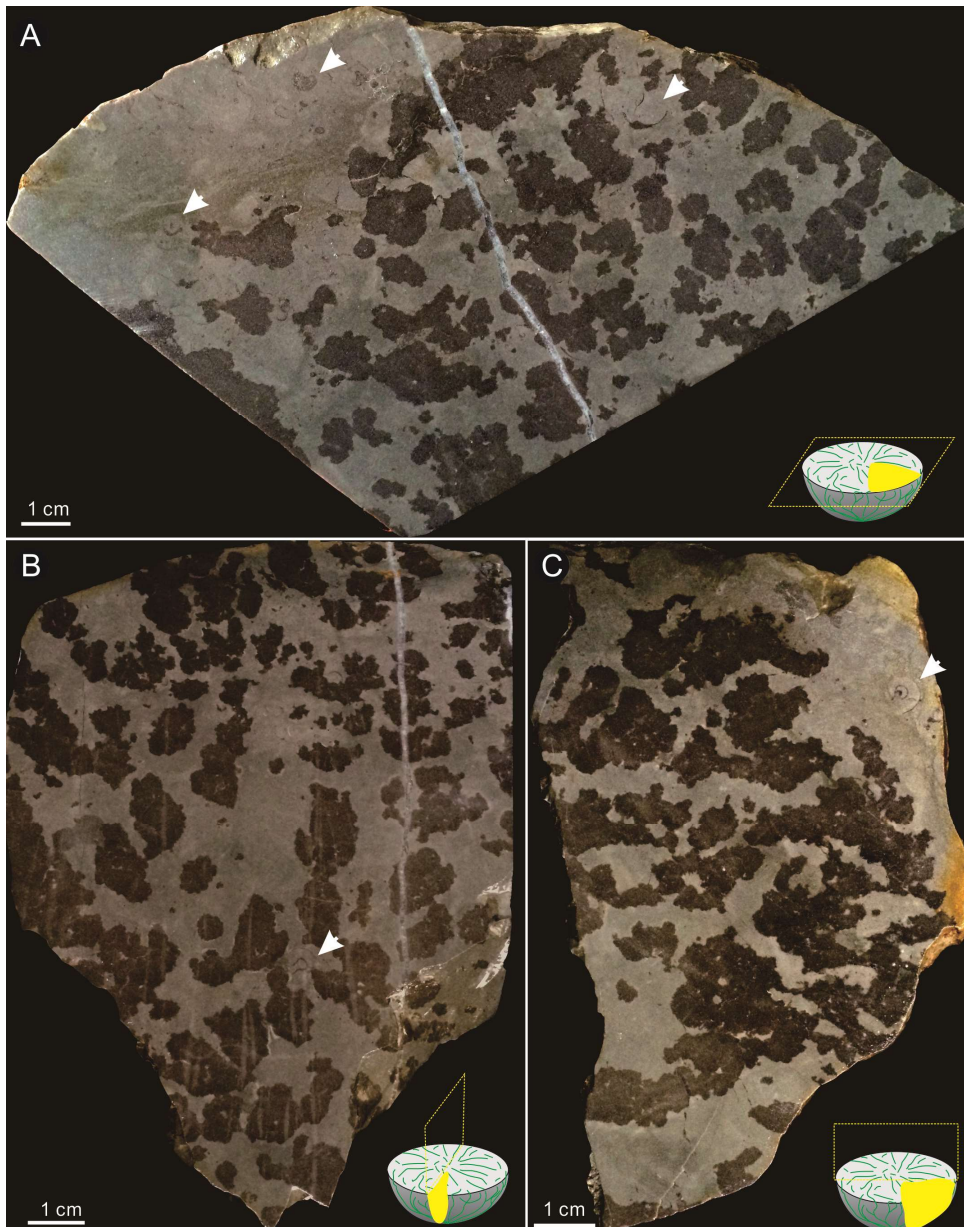
987 Close-up of the small microbialite in A, showing the bowl-like morphology (see also
988 cartoon diagram at upper left corner). Note that the arrow indicates upward direction.
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991 **Fig. 4.** Columnar stromatolites make up the bowl-like microbialites. (A) Side view of
992 a small microbialite, showing dark colored columnar structures that frequently branch
993 upward, demonstrating life position. (B) A false-color image of A (after Photoshop
994 color enhancement) showing pronounced laminated and branching microbialite
995 columns. (C) Close-up of a microbialite column, showing that the column is densely
996 laminated and branches once. (D) Close-up of microbialite columns, showing that
997 columns are densely laminated and branch frequently. (E) Base view of a bowl-like
998 microbialite, showing microbial clots surrounding the core. (F) Close-up of the top of
999 the bowl-like microbialite, showing cloud-like masses (red arrows) and an ammonoid
1000 shell (white arrow).

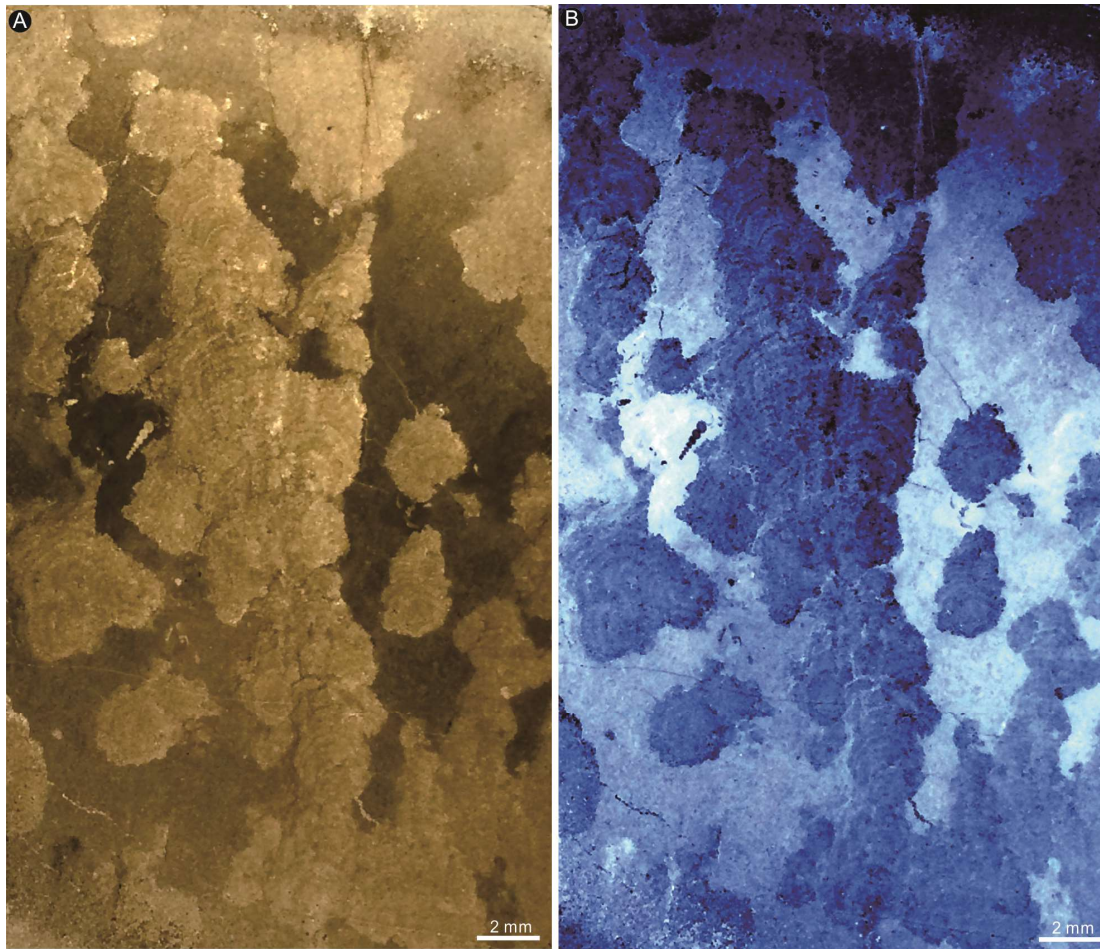
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1004 **Fig. 5.** Polished slabs of one bowl-like structure viewed from various angles. Note
 1005 that cartoon diagrams in the lower right corner of the photographs show the sectioning
 1006 directions of the slab. Ammonoid shells (white arrows) occur along the margins of the
 1007 bowl-like structure or within the clotted texture. (A) Slab view of the microbialite cut
 1008 parallel to bedding, showing microbial clots (dark colored areas) and surrounding
 1009 micrite (gray areas). (B–C) Slab views of the microbialite cut perpendicular to
 1010 bedding, showing clotted texture characterized by microbial clots (dark colored areas)
 1011 and micrite (gray areas).



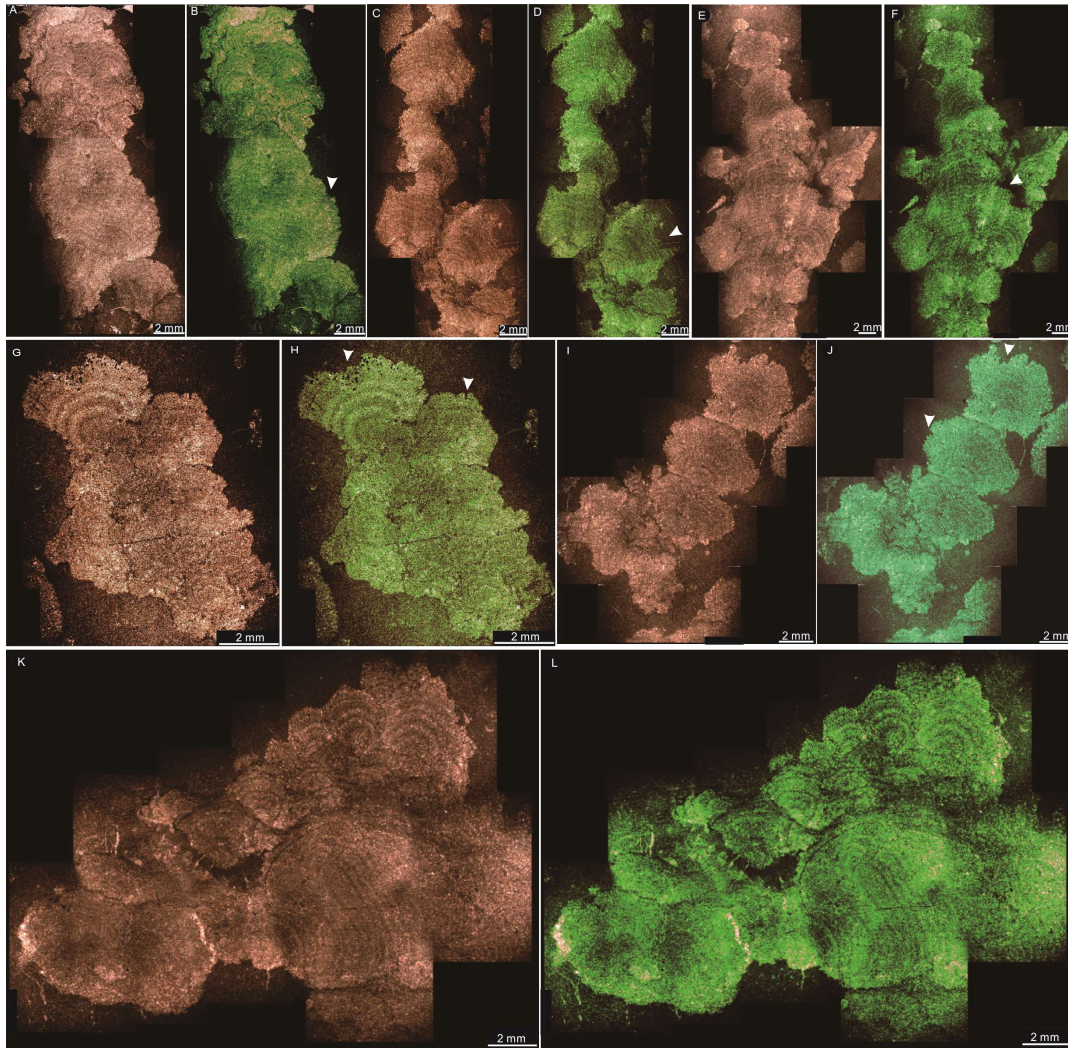
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1013 **Fig. 6.** Photomicrographs of bowl-like microbialite under plane polarized light (A)
1014 and a false-color image (after Photoshop color enhancement) (B) showing the densely
1015 laminated and frequently branching microbial columns (light colored in A and dark
1016 blue in B) and surrounding micrites (dark colored in A, and bright to light blue in B).
1017 Note that the false color helps to bring out some of the details of the thin section.

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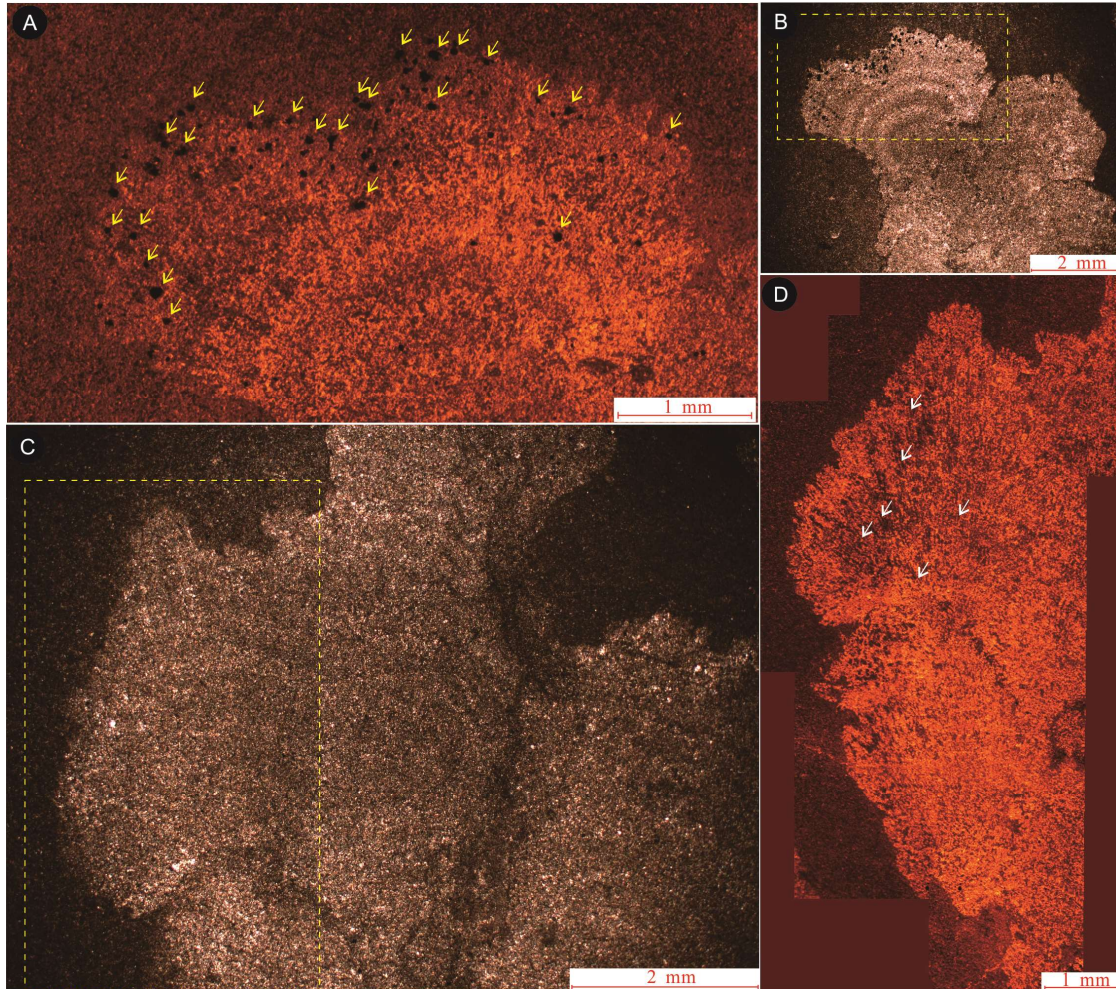
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1022 **Fig. 7.** Photomicrographs of the columnar stromatolites, showing various
 1023 morphologies of the columns. Note that the brown-colored columns are photographed
 1024 under plane polarized light, while the green-colored columns are Photoshop-enhanced.
 1025 White triangles in B, D, F, H, and J indicate dissolution along the margins of fan
 1026 structures or columns. (A–B) Single cylindrical in the lower part are massive to
 1027 clotted, while three small columns cluster in the upper part cluster of the larger,
 1028 cylindrical columns. (C–D) Two overlapping columns. (E–F) Dendritic columns that
 1029 branch and generate smaller columns. (G–H) Microbialite columns with a
 1030 mammillary texture; they are comprised of multiple crystal fans that have a radiating
 1031 texture and show distinct growth laminae. Note that the radiating fans occur
 1032 throughout these structures. (I–J) Three cement fans that stack on top of each other.

1033 (K–L) Cabbage-shaped structures that cluster together, with distinct concentric
1034 laminar laminae within each fan.
1035

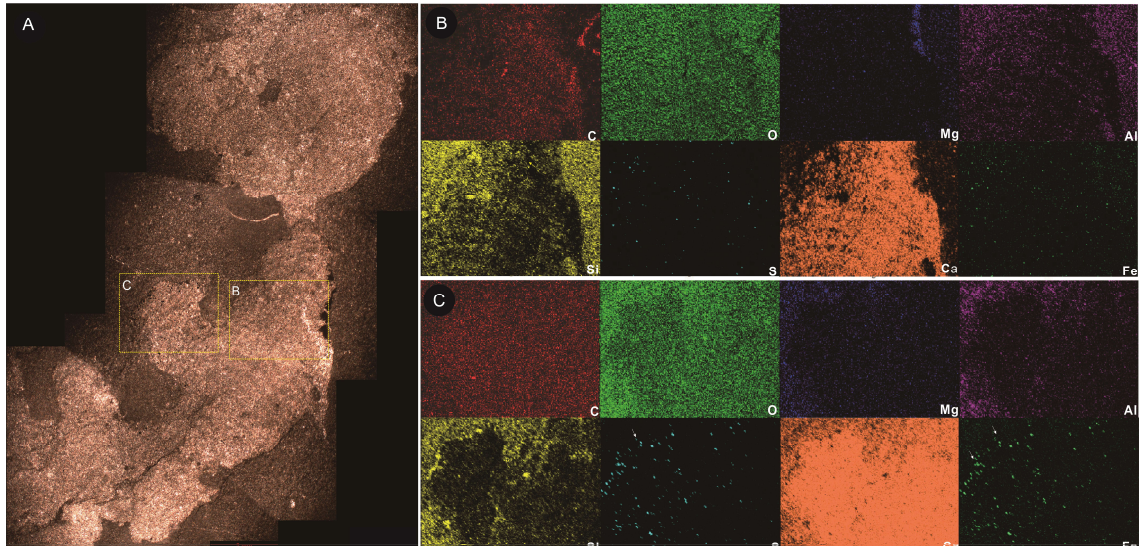


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1037 **Fig. 8.** Photomicrographs of microbialites in transmitted light and
1038 Cathodoluminescence (CL). (A) CL image showing close-up of the boxed area in B,
1039 illustrating concentric laminar and radiating structures within the cement fan, as well
1040 as pyrite grains (yellow arrows) that occur scattered in laminae or along margins of
1041 the cement fans. (B–C) Two fans at different orientations to each other, showing
1042 distinct concentric laminar structures and radiating lines. Note that dashed yellow
1043 squares in C show the areas illustrated in A and D, respectively. (D) CL image
1044 showing close-up of the boxed area in C, showing radiating rod-shaped structures on

1045 the cement fan.

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1048 **Fig. 9.** Photomicrograph and EDS element mapping images of cement fan structures.

1049 (A) Photomicrograph of microbialite columns. Note the yellow squares B and C show

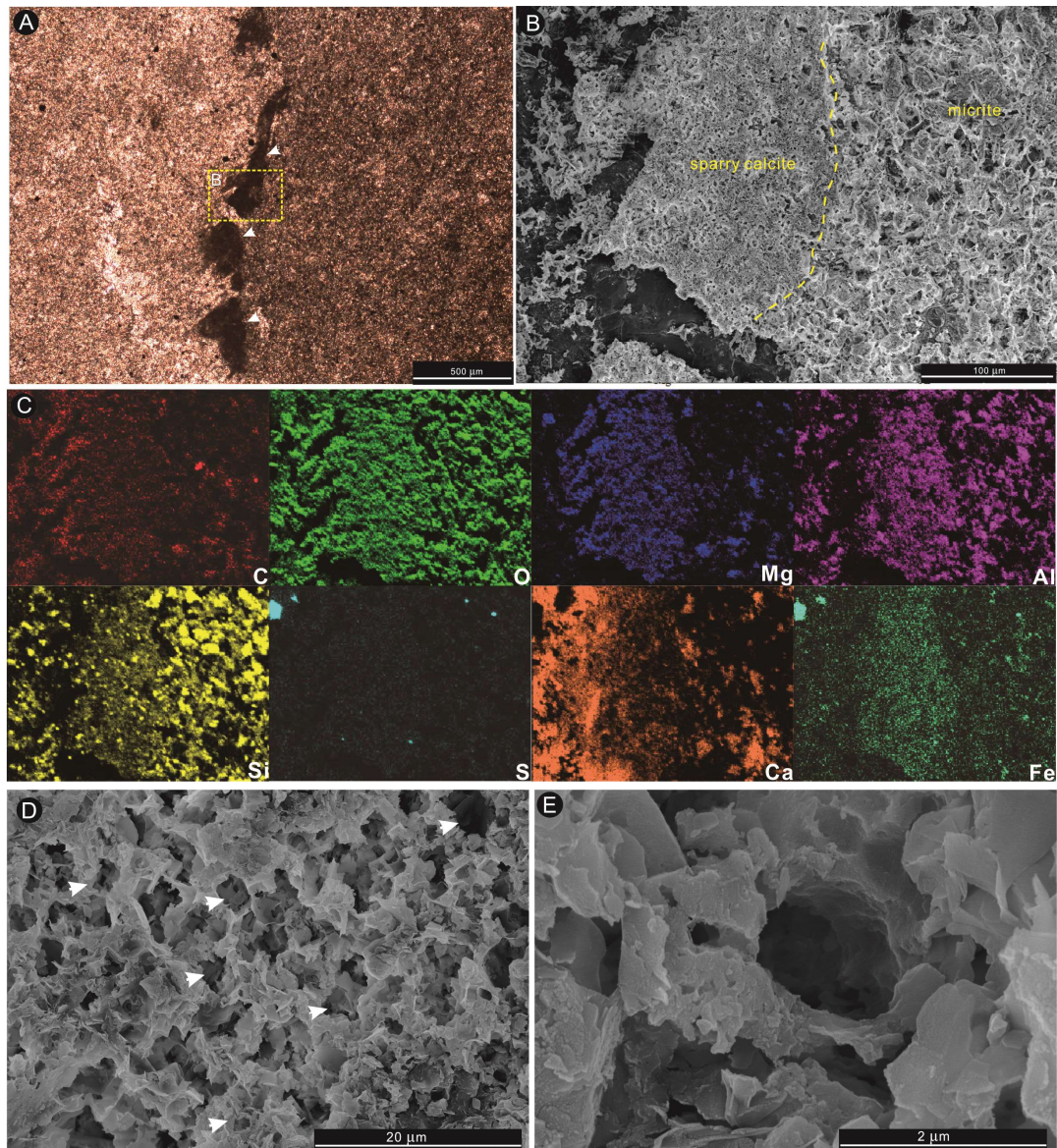
1050 the EDS element mapping areas. (B) EDS element map images of the boxed area (B)

1051 in A, showing the concentrations of C, O, Mg, Al, Si, S, Ca, and Fe. (C) EDS element

1052 map images of the boxed area (C) in A, showing concentrations of C, O, Mg, Al, Si, S,

1053 Ca, and Fe. Note that thin sections were etched with acetic acid.

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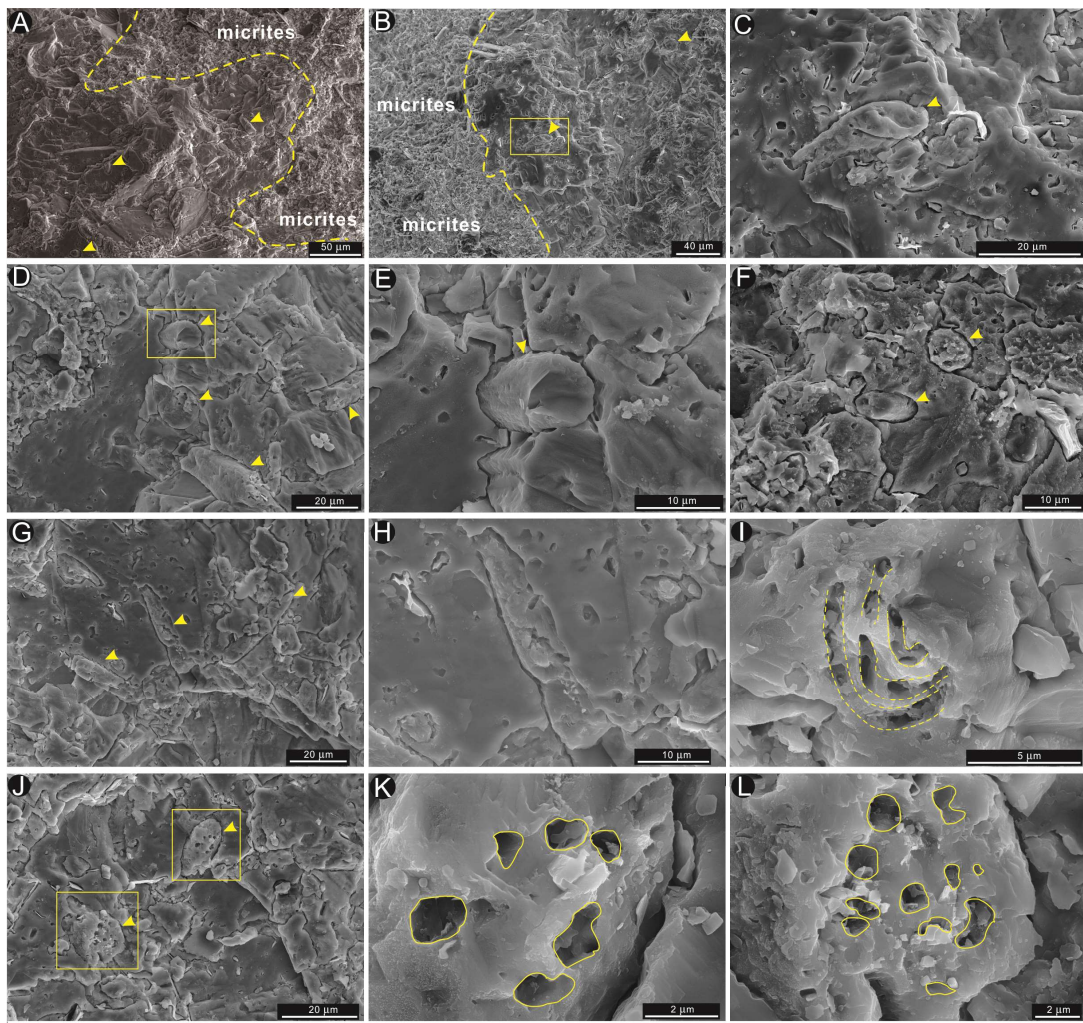


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1056 **Fig. 10.** Photomicrograph and SEM images of the junction between sparry calcites
 1057 and micrites within a microbial column. (A) Photomicrograph showing the contact
 1058 (white arrows) between sparry cement calcites and micrites. (B) SEM image of boxed
 1059 area in A, showing the boundary (dashed yellow lines) between micrite and sparry
 1060 calcite. (C) EDS element maps of C, O, Mg, Al, Si, S, Ca, Fe, and it shows contents of
 1061 Ca, Mg, O, Al, and Si within sparry calcite cement. (D) SEM image showing
 1062 nano-sized particles, representing calcified extracellular polymeric substances (EPS),
 1063 and they interweave to form pore structures that are surrounded by walls made up of a
 1064 mixture of calcium carbonate and silicates. White arrows indicate micro-pore

1065 structures. (E) Close-up of a pore structure.

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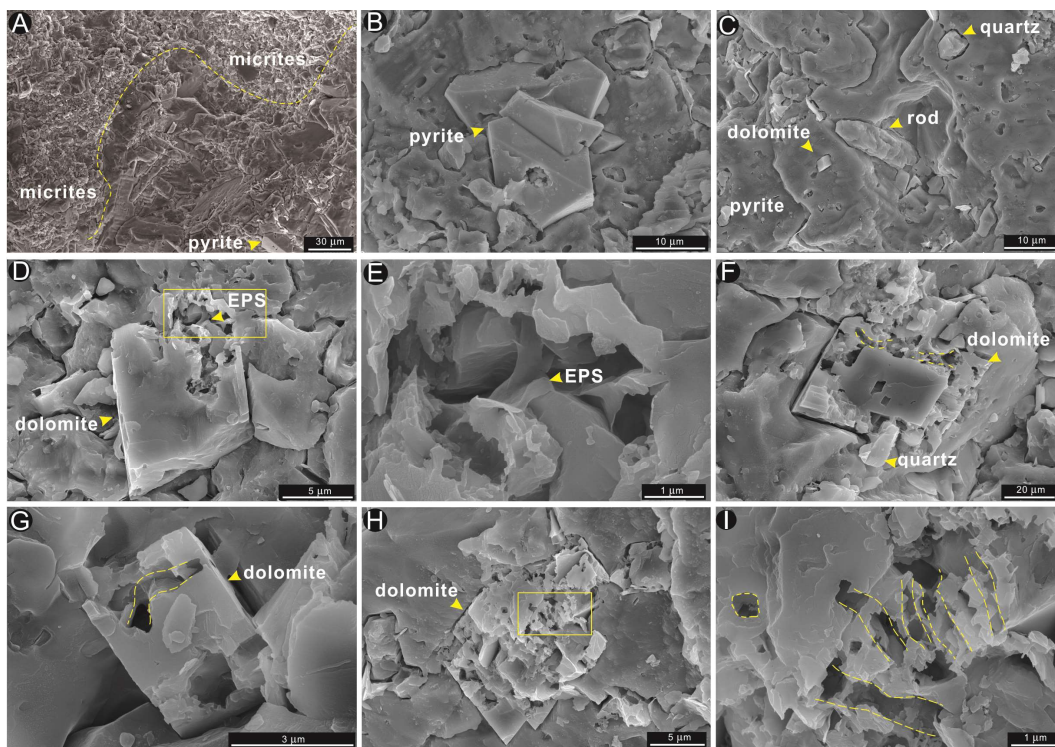


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1068 **Fig. 11.** SEM images of rod-shaped objects and filament sheaths preserved in the
1069 microbialite. (A–B) Close-up of clotted textures in microbialite, showing the contact
1070 between micrite and sparite (dashed yellow line) and rod-shaped objects (yellow
1071 arrows) on sparry calcite. (C) Close-up of boxed area in B showing a rod-shaped
1072 object that has a smooth surface and a depression in cross section. (D) Another
1073 rod-shaped object within sparry calcite. E) Close-up of boxed area in D, showing a
1074 rod-shaped object that has a smooth surface and a depression in cross section. F) Two
1075 rod-shaped objects in vertical profile view. Note that the object on the left has a
1076 smooth surface and depressed end, while the object on the right has multiple

1077 micropores in cross section. (G) Three rod-shaped objects in horizontal plane view. (H)
 1078 Close-up of the middle rod in G showing irregular corrosion traces on its surfaces. (I)
 1079 Worm-like filament sheaths on sparry calcite. (J) Two rods in vertical profile view
 1080 showing multiple micropores in cross section of the rod. (K–L) Close-ups of boxed
 1081 areas in J, showing prominent micropores, 0.5–1.0 μm in diameter, in cross section of
 1082 a rod.

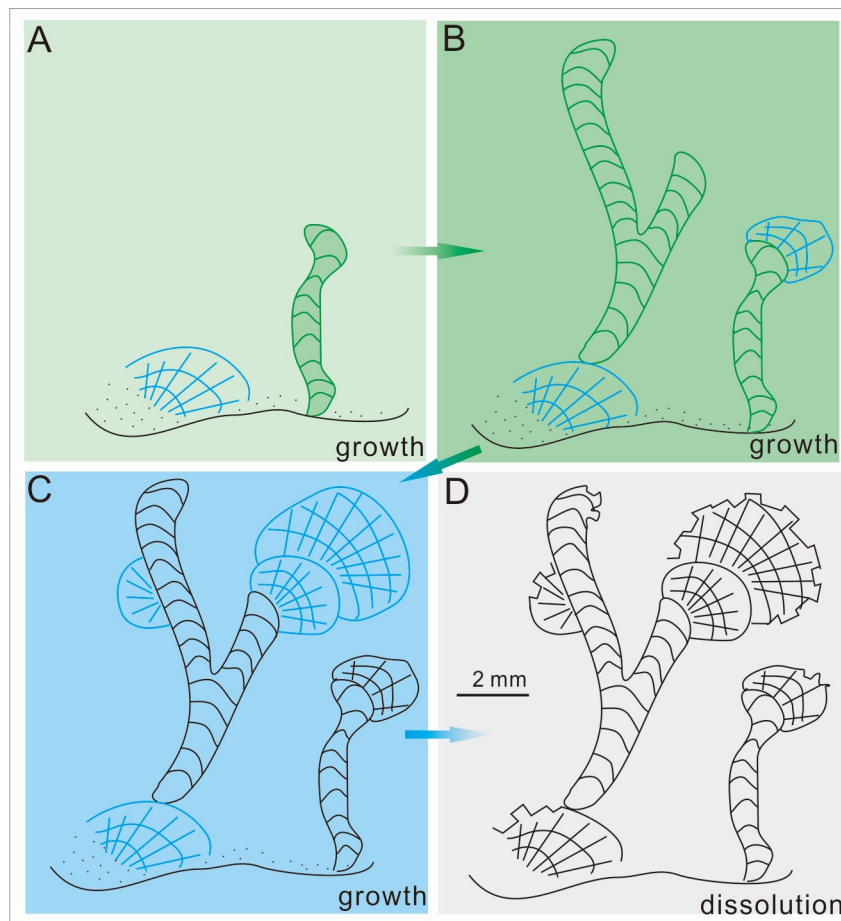
1083



1084

1085 **Fig. 12.** SEM images nano-sized particles on surfaces of pyrite crystals and dolomite
 1086 crystals embedded in microbialite. (A) SEM image showing the contact between
 1087 micrites and sparry calcite. Note that some pyrite crystals occur in the sparry calcites.
 1088 (B) Pyrite crystals with corroded surfaces. (C) Dolomite, quartz, and rod-shaped
 1089 objects on sparry calcites within the microbialite. (D) Dolomite crystal with a broken
 1090 corner from which abundant biofilms, probably representing extracellular polymeric
 1091 substances (EPS), are exposed. (E) Close-up of boxed area in D, showing details of

1092 EPS. (F) One dolomite crystal with a dense, dark colored core and corroded margins,
 1093 with linear filament sheaths (outlined by dash lines). Note one small quartz grain
 1094 (arrow) inserted in the margin of dolomite crystal. (G) Filament sheaths (yellow
 1095 dashed lines) cross the surface of the dolomite crystal and penetrate into the dolomite.
 1096 (H) Strongly corroded dolomite crystal with filament sheaths running through the
 1097 grain. (I) Close-up of boxed area in H, showing nano-sized, linear filament sheaths on
 1098 the surface and running through the crystal.
 1099



1100

1101 **Fig. 13.** Cartoon diagram showing the growth and dissolution of laminated columns
 1102 and cement fans. (A) An isolated cement fan and laminated column grow on a
 1103 siliciclastic sea-floor. (B) A new laminated column grows on the edge of a cement fan
 1104 (left) and branches. Meanwhile, the laminated column gives rise to a new cement fan

1105 (right). (C) The laminated column on the left also gives rise to a cement fan that
 1106 continues to grow and forms a second generation cement fan, while the right
 1107 laminated column structure ceases its growth. (D) Corrosion of edges of laminated
 1108 columns and cement fans due to a submarine dissolution event.

1109

1110 **Table 1.** Carbon and oxygen isotopic compositions of laminated columns, cement
 1111 fans, and micrites.

	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)
	+0.05	-8.11
Laminae	-0.23	-7.92
microbialites	-0.54	-8.16
	-0.17	-7.68
Fans	-0.82	-8.19
	+0.02	-8.23
	-0.96	-7.99
micrites	-0.91	-8.47
	-0.92	-8.05

1112