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1	Microbialite development through the Ediacaran-Cambrian transition in China:
2	Distribution, characteristics, and paleoceanographic implications
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# 20 Abstract

Widespread development of microbialites harbors a series of clues about microbial activity, 21 22 environmental condition, and aquatic chemistry. The Ediacaran-Cambrian transition draws 23 extensive attention on the co-evolution of complex life and Earth's environment but the 24 associated microorganism development has been largely ignored. In this study, we present a high-resolution database with respect to the spatial and temporal distributions of microbialites 25 in China through the terminal Ediacaran to the early Cambrian Period and describe 26 morphological and petrological characteristics of stromatolites and thrombolites in detail to 27 28 shed light on the evolutionary process of microbial carbonates. Microbialite development experienced two thriving intervals during the Ediacaran-Cambrian transition: latest Ediacaran 29 to early Fortunian, and Cambrian Age 3 to middle Age 4. The columnar and domical 30 31 stromatolites show no marked morphological changes in the Ediacaran-Cambrian transition, but stratiform stromatolites exhibit a notable decline in Cambrian time, likely caused by 32 33 increasing bioturbation in the Cambrian shelf environments. Meanwhile, thrombolites evolved 34 to form large and complicated structures in the early Cambrian featured by meter-level mound 35 morphology and columnar-branching microbial forms (fan-like/dendritic structures), likely 36 indicating an improved environmental adaptation (e.g., photosynthesis efficiency and hydrodynamic conditions). Another remarkable change in microbialites is the emergence of 37 38 large numbers of calcified microbial microfossils preserved within the laminated/clotted mesostructures in Cambrian facies, compared with the Ediacaran forms that lack such unique 39 40 structural features. For the main control over the Cambrian microbial calcification event, this study stresses again the essential role of seawater chemistry (Mg/Ca molar ratios and Ca<sup>2+</sup> 41

42	concentrations) in the formation and preservation of calcified microorganisms based on
43	previous insights and elaborate characteristics of their occurrence and microstructures in China.
44	The transition of the Neoproterozoic "aragonite-dolomite sea" to the Cambrian "calcite sea"
45	(likely widely distributed in Age 3) may have promoted to the generation of an original calcite
46	mineralogy in microbial fossils, which has a stronger ability to resist diagenetic dissolution and
47	substitution (e.g., phosphatization and silicification) than that of the aragonite precursor.
48	

Keywords: Stromatolites, thrombolites, microbial carbonates, cyanobacteria, calcified
microbes, calcite sea

# 51 1. Introduction

As one of the oldest sedimentary records related to biological activity on Earth, 52 53 microbialites are a component the evolution of the marine ecological system and seawater chemical composition and thus have been broadly used to restore paleoceanographic and 54 55 paleoenvironmental information about the setting in which they formed (e.g., Burne and Moore, 1987; Grotzinger and Knoll, 1999; Riding, 2000). Microbialites, including stromatolites 56 (laminated structure), thrombolites (clotted structure), and other minor types, largely represent 57 a lithified benthic microbial community with the contribution of authigenic precipitation 58 59 (generally carbonate) during diagenesis, and sometimes with the admixtures of skeletal organisms and terrigenous detritus (Burne and Moore, 1987). In terms of the formation 60 mechanism, both microbially-induced and microbially-influenced processes likely played key 61 62 roles in the mineralization of the microbial community, which contains a series of autotrophic (e.g., cyanobacteria) and heterotrophic (e.g., sulfate reducing bacteria) microorganisms (e.g., 63

64 Visscher and Stolz, 2005; Dupraz et al., 2009; Riding, 2011b).

65 Cyanobacteria are seen as one of the most important producers of carbonate precipitation and organic matter, but their calcified microfossils are not ubiquitously preserved in rocks (Arp 66 et al., 2001; Planavsky et al., 2009). The calcification of cyanobacteria refers to the sheath, 67 68 which is one form of extracellular polymeric substance (EPS) affiliated with (and close to) microorganisms that has been internally crystallized by carbonate minerals, creating calcified 69 microbial microfossils (Riding, 1977, 2011a). Calcified cyanobacteria are rare in modern 70 marine environments, but they are present in several peaks in the geological record, e.g., 71 Cambrian to Ordovician, Devonian to Carboniferous, and Late Triassic (Arp et al., 2001). There 72

is still controversy concerning the development of large-scale cyanobacterial calcification, but
its potential paleoceanographic and paleoenvironmental applications, e.g., seawater saturation
state, atmospheric CO<sub>2</sub> level, and dissolved oxygen state, are attracting increasing amounts of
attention (Knoll et al., 1993; Riding and Liang, 2005; Altermann et al., 2006; Kah and Riding,
2007; Riding et al., 2019).

78 The abundance of calcified cyanobacteria in Precambrian strata is very low when compared to that in Phanerozoic strata (Golubic and Seong-Joo, 1999; Arp et al., 2001; Schopf, 79 80 2006; Schirrmeister et al., 2016). Although numerous studies have reported the presence of 81 microbial microfossils in Ediacaran records, most of the preservation types are post-mortem, e.g., kerogenization, phosphatization, pyritization, and silicification or (partially) replacement 82 83 by Al-silicates during early diagenesis (Zhang et al., 1998; Brasier et al., 2011; Cai et al., 2012; 84 Muscente et al., 2015). The following Cambrian period is regarded to have been an intense "cyanobacterial calcification episode" (Riding, 1992), which is represented by large quantities 85 of calcified microbes in space and time (Riding, 1982; 1992; Rowland and Shapiro, 2002; Lee 86 87 et al., 2015). Most of these sheath/wall calcified microbes are cyanobacteria (e.g., Girvanella 88 and Botomaella groups) and suspected cyanobacteria (Epiphyton and Renalcis groups) (Riding, 89 2001), but they are generalized as calcified microbial microfossils in this study due to their similar preservation characteristics in microstructures and the ambiguous taxonomic 90 assignment in specific types (e.g., Pratt, 1984; Stephens and Sumner, 2002; Ibarra and Sanon, 91 2019). Previous studies have provided a variety of information on the petrological and 92 93 morphological characteristics of these calcified microbes (e.g., Rowland and Gangloff, 1988; Knoll et al., 1993; Shapiro, 2000; Turner et al., 2000; Zhuravlev, 2001; Rowland and Shapiro, 94

2002), but little is known about the evolutionary process of calcified microbes during the
Ediacaran-Cambrian transition and about the similarities and differences of the characteristics
of microbialites formed in the latest Precambrian and earliest Phanerozoic.

High seawater Ca<sup>2+</sup> concentrations or CaCO<sub>3</sub> supersaturation states are interpreted to have 98 driven the cyanobacterial calcification episodes, which provided sufficient Ca<sup>2+</sup> for CaCO<sub>3</sub> 99 nucleation on and within the sheath matrix (Arp et al., 2001; Riding and Liang, 2005). The 100 CO<sub>2</sub>-concentrating mechanisms (CCMs) likely played a role in the specific biologic processes 101 that form an alkaline gradient by transporting bicarbonate into the cell and releasing OH<sup>-</sup> to the 102 103 sheaths during photosynthesis (Kaplan and Reinhold, 1999; Badger and Price, 2003; Riding, 2006). Even so, other potential effects, e.g., the Mg/Ca molar ratio, require systematic 104 assessment in this cyanobacterial calcification episode to understand its possible synergic 105 106 relationship with the seawater chemistry and environmental conditions. Seawater Mg/Ca molar ratio dominates the carbonate mineralogical compositions, and the transition from the 107 aragonite-dolomite sea state in the Neoproterozoic to the calcite sea state in the early Cambrian 108 109 may have favored the preservation of original calcite microfossils due to the thermodynamic 110 differences between the primary carbonate minerals (Morse and Mackenzie, 1990; Brennan et 111 al., 2004; Zhuravlev and Wood, 2008; Hood et al., 2011; Wood et al., 2017). In addition, cyanobacteria are one of the most important sources of atmospheric O<sub>2</sub> in Earth's early history 112 as a result of oxygen-producing photosynthesis, and they possibly played a key role in the 113 Proterozoic oxygenation event (Campbell and Allen, 2008; Lyons et al., 2014). The rise of 114 115 Eukaryotic algae evolved to more efficient phosphorus and organic carbon burial and potentially increased ocean and atmospheric O<sub>2</sub> contents in the Neoproterozoic time (Lenton et 116

al., 2014; Lenton and Daines, 2018), but the roles of prokaryotes (e.g., cyanobacteria) have 117 generally been ignored in the environmental evolution at that time. A case from modern oceans 118 shows that the photosynthetic prokaryote Prochlorococcus, which is one species of 119 cyanobacteria and the most abundant photosynthetic organism on Earth, may contribute about 120 20% O<sub>2</sub> to the atmosphere (Partensky et al., 1999; Munn, 2020); it implies that photosynthetic 121 cyanobacteria are still of crucial value in  $O_2$  production in the younger Earth. For these reasons, 122 photosynthesis-dominated microbial communities with calcified functional microstructures, 123 which were preserved in the laminated and clotted structures of microbialites during the early 124 125 Cambrian, seem to provide vital atmospheric O<sub>2</sub> information about this time period, and this assumption needs to be clarified. 126

The aims of this study are to recover the evolution of microbialites during the transition 127 128 from the Ediacaran to the Cambrian and to understand the paleoceanographic and paleoenvironmental significance of their morphological and functional changes during this 129 crucial period. For this purpose, first we built a database (n = 212) on the development of 130 131 microbialites from the uppermost Ediacaran to Cambrian Series 2 in China. Then, we generalized the exterior (growth forms) and interior (laminated/clotted structures) 132 133 characteristics of the microbialites in different temporal intervals and focused on the occurrence, 134 distribution, and microstructures of the calcified microbes in the early Cambrian. Next, we 135 assessed the potential significance of the microbialite response to environmental changes in the early Cambrian. Finally, we attempted to interpret the startup mechanism of the Cambrian 136 137 cyanobacterial calcification event from a paleoceanographic perspective.

## 139 2. Geologic background

Paleogeographically, there are three major blocks in China: the South China, Tarim, and 140 North China blocks. These blocks were located at low latitudes (approximately between 30°N 141 and 30°S) adjacent to Gondwana during the transition from the Ediacaran to the Cambrian (Fig. 142 1A and B) (Torsvik et al., 2013). The time interval of this study ranges from the latest Ediacaran 143 (informal Age 6) to the end of the early Cambrian (informal Age 4) according to the newly 144 published reference stratigraphic framework in China, which approximatively corresponds to 145 550 to 509 Ma (Fig. 1C) (Zhou et al., 2019; Zhu et al., 2019). The South China and Tarim 146 147 blocks experienced similar shallow-water depositional successions in the upper Ediacaran and lower Cambrian, but the North China Block contains a large unconformity between the upper 148 Tonian (Neoproterozoic) and the Cambrian Terreneuvian (hiatus of 150-300 Ma) (He et al., 149 150 2017). Until Cambrian Epoch 2, the transgressive sediments gradually overlay the large unconformity in the North China Block (Meng et al., 1997). 151

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153 2.1 South China Block

The South China Block consisted of two collided blocks (the Yangtze and Cathaysia blocks) during the Ediacaran-Cambrian transition (Fig. 1A) (Zhang et al., 2013). The Yangtze Block was covered by carbonate-dominated sedimentation in the latest Ediacaran and principally exhibited extensive microbial carbonate factories characterized by massive stromatolites and thrombolites in space and time (Ding et al., 2019; Zhai et al., 2020). The Yangtze shelf was exposed above sea level to varying degrees during the global regression near the Ediacaran– Cambrian boundary (Shahkarami et al., 2020), which led to an extensive hiatus between the upper Ediacaran and lower Cambrian strata. Some areas that were located within intracratonic
rifts (e.g., northern Yunnan) or in a slope setting (e.g., Hunan and eastern Guizhou) on the
Yangtze Block preserve relatively complete successions from the uppermost Ediacaran to
Cambrian Terreneuvian, and they are characterized by phosphorites, phosphorous siltstones,
calcareous-siliceous phosphorites, and a few phosphate stromatolites (Chen and Chen, 1987;
Mu and Wu, 2005; Sun et al., 2020a).

The following transgression from Age 2 to Age 3 flooded most of the Yangtze shelf and 167 developed broad fine-grained, organic-rich siliciclastic deposits that likely extended to the early 168 169 Age 3 (Mei et al., 2007; Mou et al., 2012; Peng et al., 2020). Subsequently, clastic and mixed carbonate-siliciclastic sedimentation was preserved in several of the near-shore environments 170 adjacent to the massifs in the northern and western parts of the Yangtze Block during the middle 171 172 to late parts of Age 3 (Mou et al., 2012; Liu et al., 2015; Zeng et al., 2020). This depositional sequence was episodically intercalated by a carbonate-dominant depositional succession 173 characterized by oolites, microbialites, and microbial-archaeocyathan limestones deposited in 174 175 high-energy shoals and microbial mound/reef environments on the western Yangtze shelf 176 (Hicks and Rowland, 2009; Yang and Yuan, 2012; Zhang et al., 2017b; Tang et al., 2019). With the gradual aggradation/progradation developed in the interior of the Yangtze Block from Age 177 3 to Age 4, the western Yangtze area formed a system of lagoons and restricted platforms (Li 178 and He, 2014). Meanwhile, the middle (the Three Gorges area) and southeastern (Guizhou and 179 Hunan areas) parts of the Yangtze Block gradually developed shallow-water ooid shoals and 180 181 microbial reefs/mounds on the rims of the shelf (Zhang and Yuan, 1994; Li and He, 2014). During the late Age 4, the rimmed margins of the northeastern and southeastern parts of the 182

Yangtze shelf extended to northern Hubei, western Hunan and eastern Guizhou, respectively
(Mou et al., 2012; Zheng, 2016). In addition, the available studies on the eastern Yangtze area
are insufficient, and some studies show the development of stromatolites in the shallow subtidal
settings in Epoch 2 (e.g., Zhang and Sun, 1991).

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188 2.2 Tarim Block

189 The upper Ediacaran and lower Cambrian shallow-water depositional successions are well exposed in northwestern Tarim (Keping area) and are partially present in southwestern Tarim 190 (Tiekelike area). During the latest Ediacaran, the Tarim Block was split into two depositional 191 basins along an east-west massif (Shi et al., 2016). In the Keping area, the Ediacaran 192 microbialites developed mainly in tidal flat and inner ramp settings of the Chigebrak Formation, 193 194 which roughly corresponds to the Dengying Formation in the South China Block based on biostratigraphic and C and Sr isotope chemostratigraphic evidence (Gao, 1990; Zhang et al., 195 2020). The Yurtus Formation that covers the upper part of the Chigebrak Formation is 196 197 characterized by calcareous-siliceous phosphorites, phosphorous siltstones, and thinly bedded siliciclastic rocks (small shelly fossil (SSF) zone, Anabarites-Protoherzina Zone, Fortunian 198 Stage), while its upper part consists of alternating dolomite and siltstone successions and 199 200 nodular dolomite (SSF, Lapworthella-Ninella-Cambroclavus assemblages, lower Stage 3) (Fig. 1C) (Zhou, 2001; Zhu et al., 2019). Stromatolites are not very common in the Yurtus Formation 201 202 (Gao et al., 1987). The depositional sequences of the Xiaoerbrak Formation overlie the Yurtus 203 Formation and likely correspond to Stage 3 in light of the positive C isotope variation that is similar to the MICE (Mingxinsi carbon isotopic excursion) and the Shizhudiscus, Ushbaspis, and 204

Kepingaspis-Tianshanocephalus trilobite zones (Fig. 1C) (Zhou, 2001; Zhang et al., 2020). The 205 Xiaoerbrak Formation consists of thickly bedded microcrystalline dolomites with large-scale 206 207 microbialite mound/reef structures in its upper part. It is overlain by the Wusonger Formation, which is characterized by medium to thinly bedded, finely crystalline dolomite (trilobite 208 209 Paokannia Zone, lower part) (Fig. 1C) (Zhou, 2001; Zhang et al., 2017a). The basal Shayilik Formation overlying the Wusonger Formation exhibits a significant negative C isotope 210 excursion ( $\delta^{13}C_{minimum} = -13\%$ , VPDB) (Zhang et al., 2020), which is consistent with the 211 ROECE (Redlichiid-Olenellid extinction C-isotope excursion) between Series 2 and the 212 213 Miaolingian, evidence that the Wusonger Formation ranges from the uppermost part of Stage 3 to Stage 4 (Zhu et al., 2019). 214

In the Tiekelike area, upper Ediacaran microbialites are developed in members II and IV 215 216 of the Kezisuhumu Formation, which exhibit depositional successions similar to those in the Chigebrak Formation of the Aksu area (Peng and Gao, 1984). In addition, large amounts of 217 glacial diamictites (Hankalchough Formation) developed in eastern Tarim during the late 218 219 Ediacaran (Gao et al., 1980). Although some stromatolite breccias appear near the top of the 220 glacial diamictites in the Hankalchough Formation in northwestern Tarim, the source of the 221 breccias is uncertain and has been inferred from the underlying Shuiquan Formation (Gao et al., 1980). Since the sedimentary age of the Shuiquan Formation remains controversial 222 (possibly middle Ediacaran) (Xiao et al., 2004; Xu et al., 2009; Zhou et al., 2019; Xiao and 223 Narbonne, 2020), the microbialite record in the Hankalchough Formation was not incorporated 224 225 into this study.

228	Available studies indicate that the development of uppermost Ediacaran strata in the North
229	China Block is rare and no microbialite records have been reported in this interval although the
230	uncertainty remains (Wan et al., 2019; Zhou et al., 2019). The initial transgressive
231	sedimentation was diachronous in the different areas of the North China Block during the early
232	Cambrian, which shows that the earliest sediments were composed of phosphorite, phosphorite
233	breccia, and phosphorous siltstone and carbonate with the emergence of diagnostic fossils in
234	the upper part of Stage 3 to the lower part of Stage 4 in the northeastern (Shuidong Formation,
235	Jilin) (Yue et al., 1990), western (basal Suyukou Formation, Ningxia; trilobite Estaingia
236	(Hsuaspis) Zone) (Regional Stratigraphic Chart Writing Group, 1980), southwestern (lower
237	Xinji Formation, Shaanxi; SSF Stenotheca drepanoida-Pelagiella madianensis Zone; trilobite
238	Estaingia (Hsuaspis) Zone) (Yun et al., 2016), and southeastern (lower Houjiashan Formation;
239	trilobite Estaingia (Hsuaspis) Zone) margins of the North China Block (Fig. 1C) (Zhang and
240	Zhu, 1979; Miao, 2014; Wan et al., 2019). Since the diachronicity generally occurs in the
241	lithostratigraphic units of the lower Cambrian in the North China Block, the initial deposition
242	within the interior of the North China Block was generally younger than in its marginal settings
243	(Meng et al., 1997).

A continuous transgression caused extensive near-shore siliciclastic and mixed siliciclastic-carbonate successions on the North China Block, with numerous shallow-water ooid and microbial deposits in the scattered shoal settings in Age 4 (generally corresponding to the trilobite *Palaeolenus (Megapalaeolenus) fengyangensis, Redlichia chinensis*, and *R. nobilis* zones in ascending order) (Fig. 1C) (Lee et al., 2018). Microbialite records have been reported

in tidal flat and inner ramp successions (lower to middle part of Stage 4), including in the 249 Heigou, Jianchang, Cangping, Zhushadong, Houjiashan (upper member), and Xinji (upper 250 251 member) formations (Hong et al., 1991; Lee and Chough, 2011; Chang et al., 2013; Miao, 2014; Du et al., 2019). The microbialite in the overlying Mantou Formation (member I, upper Stage 252 253 4) exhibits a much wider spatial distribution in the interior of the North China Platform than the older Cambrian successions (e.g., Lee and Chough, 2011; Chang et al., 2013). These 254 microbialites (member I of the Mantou Formation) developed in mixed siliciclastic-carbonate 255 systems, generally in tidal flats, and they are underlain by the widespread transgressive 256 257 sequences (shales and mudstones; trilobite Yaojiayuella Zone) that generally overlies the lower Cambrian strata in the North China Block (Wu et al., 2018). 258

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#### 260 **3. Materials and methods**

### 261 3.1 Microbialite development database

We compiled a microbialite development database (MDD), which systematically catalogs 262 the microbialite development sites and other relative information, including ages, 263 lithostratigraphic units, locations, and morphological characteristics from the latest Ediacaran 264 to Cambrian Age 4 in China (~550 to 509 Ma) (Table S1). The sources of the MDD includes 265 our visited field outcrops, peer-reviewed papers, books, doctoral and master's theses, and 266 regional geological reports (scale 1:200 000 and others), which were mostly written in Chinese. 267 The lithostratigraphic units of all of the sites have been corrected to the latest 268 chronostratigraphic framework for the upper Ediacaran and lower Cambrian in China (Zhou et 269 al., 2019; Zhu et al., 2019). Some of the microbialite sites lack available biostratigraphic and/or 270

chemostratigraphic evidence, and thus, their corresponding development ages mainly rely on
neighboring well-studied sections (Table S1).

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274 3.2 Description of the microbialites

275 For the description of the characteristics of the microbialite in the Ediacaran-Cambrian transition, we follow the terminologies of Shapiro (2000) and Riding and Voronova (1985) for 276 the external morphology and the internal fabric and microbial groups, respectively. The 277 278 macrostructure (meter level) and mesostructure (cm level) characteristics of the microbialites 279 rely on field observation and on polished slabs (n = 42). In addition, microstructure examinations were conducted on thin-sections (n > 400) using a polarizing microscope (Leica 280 DM2700P) at Southwest Petroleum University. One-half of each thin-section was stained with 281 282 Alizarine Red S to distinguish the carbonate mineralogical compositions (calcite vs. dolomite). For purposes of comparison, we counted the width and the longest diameter of the *Epiphyton* 283 in the microscopic photos, which were acquired from the thin-sections of Cambrian Stages 3 284 and 4 (n = 419 and 601, respectively). It should be noted that all the measured values are 285 286 reported as mean $\pm 1\sigma$ , unless otherwise indicated.

287

288 **4. Results** 

4.1 Spatial and temporal distributions of microbialite records in the Ediacaran–Cambriantransition

291 Detailed information on the microbialite development was tabulated in the MDD (Table
292 S1), and corresponding specific sites were plotted on the paleogeographic maps (uppermost

Ediacaran and lower Cambrian) of China using their latitude-longitude coordinates (Figs. 2 and 293 3). Based on the MDD, the development of microbialites in China during the Ediacaran-294 295 Cambrian transition can be subdivided into two intervals: Ediacaran Age 6 to Cambrian Fortunian, and Cambrian Age 3 to middle Age 4 (Table S1). The South China and Tarim blocks 296 experienced two periods of microbialite development, but the North China Block contains only 297 the interval from the lower to middle Stage 4 (Figs. 2 and 3). Both stromatolites and 298 thrombolites developed in the latest Ediacaran and Cambrian Age 3 to 4, but only stromatolites 299 appear in the Cambrian Fortunian based on the available data (Table S1). 300

301 The stromatolites are widely distributed in the Yangtze shelf and occupy a predominant position in the uppermost Ediacaran in the middle and eastern areas. The thrombolites are 302 generally associated with stromatolites in the shallow-water depositional successions of the 303 304 western Yangtze shelf, while they formed composite laminated and clotted framework structures (Fig. 2 and Table S1). The situation of the development of the microbialites in Tarim 305 is similar to that of the western Yangtze shelf. The following flourishing of stromatolites 306 307 appeared in the Aksu area of the Tarim Block and in the southwestern South China Block during 308 the Cambrian Fortunian (Fig. 3). The earliest Cambrian thrombolite dominant microbial bioherms are located in the northwestern South China Block and are preserved within the lower 309 310 to middle Stage 3 strata. Subsequently, the thrombolite and stromatolite records spread to the 311 Aksu area of the Tarim Block and the Guizhou area of the South China Block in upper Stage 3 depositional successions (Fig. 3). The broadest distribution of the microbialite beds in the lower 312 313 Cambrian occurs in the lower and middle parts of Stage 4, which show a gradual eastward expansion on the Yangtze shelf, and a seaward expansion in the Tarim Block (Fig. 3). In the 314

North China Block, the earliest appearance of microbialites in the Cambrian strata was likely in early Age 4, and according to the available MDD, they were mainly distributed in temporal proximity in the northeastern, western, southwestern, and southeastern edges of the block (Table S1). Subsequently, the distribution of the microbialite successions underwent a stepwise expansion from the near-shore settings on the edges of the North China Block to the interior during Age 4 (Fig. 3).

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322 4.2 Macrostructure and mesostructure of microbialites and their sedimentary characteristics 323 Based on the MDD and the examination (field and slab) of the microbialites in the Ediacaran–Cambrian transition (Figs. 4–7), the stromatolites can be divided into three major 324 categories: (1) columnar or domical in shape, a general height of <0.3 m, and close-packed with 325 326 a roughly uniform thickness (Figs. 4A-B, 6A, and 7A); (2) a regular linear structure, alternating dark and light layers, and a thickness generally ranging from tens of centimeters to one meter 327 (Figs. 4C, 5A, 6B, and 7B); and (3) a low- or high-relief laminated fabric coupled with a 328 329 convex-upward characteristic (Figs. 4D and E, and 6C). For the thrombolites, they are present 330 as (1) narrow-laminar or patchy structures (with thickness <0.1 m), generally developed 331 between the stromatolitic layers in the upper Ediacaran (Figs. 4F, 5B-C); (2) a thinly bedded 332 tabular fabric ( $\sim 1$  to 10 cm) with large numbers of tens of millimeter clots, and alternating laminated and clotted structures (Figs. 4G, 5D, and 7C); (3) low- or high-relief mounds (one to 333 tens of meters in width) composed of plentiful clotted textures ranging from millimeters to 334 335 centimeters in size, partially with the participation of the macro-organisms (e.g., archaeocyath) (Figs. 6D–E, and 7D–G); and (4) meter-level frameworks with a variety of columnar branching 336

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structures (e.g., fine and thick branches; Figs. 6F–G, and 7H).

339 4.3 Mineralogical and petrological characteristics of the stromatolites and thrombolites 340 Mineralogical compositions of the microbialites investigated in this study are different. In the uppermost Ediacaran, nearly all the stromatolites and thrombolites have been dolomitized 341 (unstained) but most of their fine structures were retained (Fig. 8). The dark-colored laminae in 342 343 the stromatolites are cryptocrystalline and consist of plentiful very fine dolomite crystals (generally  $< 2 \mu m$ ); and the neighboring light-colored layers are composed of medium- to fine-344 345 grained dolomite grains (4–40  $\mu$ m) and a few dolospar crystals (Fig. 8A). For the Ediacaran thrombolites, the clotted structures are also composed of cryptocrystalline dolomites, and their 346 early-stage cements are generally composed of isopachous, fibrous to acicular dolomite grains 347 348 (Fig. 8B-D). Yet, in the late-stage, the pore-filling cements are either medium- to coarsegrained dolomite (Fig. 8B–G) or coarsely crystalline calcite grains (Fig. 8H). 349 350 Unlike the uniform dolomitization (uppermost Ediacaran; Fig. 8) and phosphatization 351 (Cambrian Terreneuvian) (Fig. 9A), microbialites in Cambrian Stages 3 and 4 exhibit 352 mineralogical and preservation characteristics that differ in the three blocks (Figs. 9B-H and 353 10). The stromatolites and thrombolites generally exhibit well-formed calcified microbial microfossils in Stage 3 and lower Stage 4 (Figs. 9B-G, and 10A and C), but they exhibit poorly-354 355 preserved laminated/clotted structures in upper Stage 4 (Fig. 10D and E), with preservation characteristics resembling those of contemporaneous carbonate ooids (Fig. 10A, B, D, and F). 356 357 In Tarim, the primary microbial fabrics and intergranular spaces in the microbialites have been replaced by fine and medium to coarsely crystalline dolomite grains, respectively (Fig. 9H). 358

#### 360 4.4 Calcified microbes within the stromatolites and thrombolites

361 The parallel and wavy laminae (generally with thickness of <1 mm) of the stromatolites show dark-colored, dense, microcrystalline fabrics in the uppermost Ediacaran; and loose 362 363 peloids, lamination fragments, and aggregate grains are common in the interlaminar layers of the stromatolites (Fig. 8A). The contemporaneous thrombolites exhibit irregular clotted 364 365 structures, which are composed of cryptocrystalline aggregate grains and/or hollow peloidal clusters (Fig. 8B-H). Mineralized globular and botryoidal fabrics are common in the microbial 366 367 carbonates, but no visible calcified microbes were identified under the microscope in the uppermost Ediacaran specimens from a series of sections from the Tarim and South China 368 blocks (Fig. 8). 369

370 In contrast, the stromatolites and thrombolites in Cambrian Stages 3-4 exhibit large numbers of calcified branched, chambered, and tubiform microfossils (Fig. 9B-G). In Stage 3, 371 372 plentiful Epiphyton and Renalcis microbes form the clotted structures of the thrombolites, with 373 minor contributions from Tarthinia, Girvanella, and other groups (Fig. 9B-D). The Epiphyton-374 dominant microbes can also form erect structures that show dendritic (thick) and fan-like (or 375 bushy; thin) branches in the field (Fig. 6F and G). The Girvanella-group is common in the 376 laminated structures of stromatolite in Stage 3, but other calcified groups are rare (Fig. 9B). In Stage 4, tubiform microbes (e.g., Botomaella and Hedstroemia) and Epiphyton became the 377 dominant microfossils in the microbialites (Fig. 9E-G). Among these microbial groups, 378 379 tubiform microbes were identified both in the laminated and clotted structures, and their microstructures are characterized by large numbers of branched and overlapping tubes (Figs. 380

381 6H, 7C, and 9 F). The *Epiphyton* microbes are still the major constructor of the clot structures 382 of the thrombolites and their widths (73±37  $\mu$ m, n = 305) and the lengths (208±118  $\mu$ m, n = 383 296) were uniformly larger in Stage 4 than in Stage 3 (width: 48±11  $\mu$ m, n = 297; length: 384 144±67, n = 122).

385

386 5. Discussion

5.1 Co-evolution of microbialite development and environmental conditions during the
Ediacaran-Cambrian transition

5.1.1 Comparison of the characteristics of microbialites between the uppermost Ediacaran andlower Cambrian

The uppermost Ediacaran and lower Cambrian microbialites have some structural 391 392 similarities. Decimeter-scale, domical and columnar stromatolite types are common in the uppermost Ediacaran, Cambrian Fortunian, and Stage 4 strata, and no substantial changes in 393 morphology and laminated structure occurred during the Ediacaran-Cambrian transition (Figs. 394 395 4A and B, 6A and B, 7A, and 9B; Table S1). These stromatolites may have developed in a 396 shallow subtidal setting resembling that of modern stromatolites in the Hamelin Pool, Australia 397 (Jahnert and Collins, 2011, 2012). These small-scale stromatolites have been regarded as being 398 formed in the intervals of the highstand systems following the transgressive sequences, e.g., the lower Chigebrak Formation (Fig. 4A and B; Ediacaran Stage 6), the basal Yurtus (Fig. 7A) and 399 Meishucun formations (Cambrian Fortunian) (Sun et al., 2020b), and the lower Zhushadong 400 401 Formation (Cambrian Stage 4) (Chang et al., 2012). The shape and size of the thrombolitic clots in the uppermost Ediacaran strata of the Tarim and western Yangtze shelf (Fig. 8B-H) also 402

403 resemble their descendants in Cambrian Stages 3-4 (Fig. 9C, D, and F-H), which exhibit well cemented, millimeter-scale granular aggregates. Especially for some of the thrombolitic clots 404 405 composed of microcrystalline dolomite (Fig. 9H) or cryptocrystalline (Fig. 10E) structures in the Cambrian, their characteristics are very similar to those in the uppermost Ediacaran (Fig. 406 8E-H). In addition, the features of the thrombolitic clots in the uppermost Ediacaran in China 407 are comparable to those in other blocks (Turner et al., 2000; Harwood and Sumner, 2011; 2012; 408 409 Adachi et al., 2019), implying that their morphological compositions were relatively stable in the Neoproterozoic. 410

411 The thickly bedded stratiform stromatolites experienced a marked decline during the Ediacaran-Cambrian transition. It is common to find thickly bedded, meter-scale stratiform 412 stromatolites with nearly parallel millimeter-scale laminae in the Tarim and Yangtze shelf in the 413 414 uppermost Ediacaran strata (Figs. 4C and 5A). Based on their well-preserved, smoothly laminated features, their depositional environment appears to have been situated on the open 415 shelf, generally between the deep subtidal and storm wave base settings (Fig. 11A). However, 416 417 the distribution of the thickly bedded stratiform stromatolites significantly decreased in the 418 lower Cambrian strata in China based on the MDD and our field observations (Table S1). Only a few stratiform stromatolites have been identified in relatively restricted environments in Stage 419 420 4, which is evidenced by extensive dolomitization and the rare appearance of skeletal fossils 421 (Fig. 6B). The stratiform stromatolites were replaced with strongly bioturbated carbonates characterized by micritic, irregularly-distributed burrows and mottled structures (also called 422 423 leopard rock in China) in the shelf environments (Fig. 11B). The latter shows an increasing trend in the early Cambrian in the North and South China blocks (e.g., Zhang et al., 1981; Qi 424

et al., 2014; Yang et al., 2016; Han et al., 2017; Chen et al., 2019). The relationship between
the decline of the stratiform stromatolites and the increase of metazoan activities in terms of
their spatial distributions allows for the assumption that the evolved animals had much
enhanced capabilities to burrow into and out of the microbial mats in Cambrian Epoch 2
compared with the latest Ediacaran (e.g., Xiao et al., 2019), which is consistent with our
understanding of seafloor burrowing activity at that time (Fig. 11B) (Seilacher and Pflüger,
1994; Bottjer et al., 2000).

432 Thrombolites evolved to form complicated structures in the Cambrian. Morphologically, 433 Ediacaran thrombolites generally exhibit patchy and medium to thinly bedded (thickness of a single layer generally <0.5 m) clotted textures (solid and/or hollow), and commonly co-exist 434 with the stromatolites in terms of their depositional successions (Fig. 4F-H). The Cambrian 435 436 thrombolites exhibit mound-like shapes and were much larger than those in the upper Ediacaran (meter-scale), and they developed individual and calcimicrobial-archaeocyath bioherms in the 437 shallow-water settings in China (e.g., Fig. 6D) (Adachi et al., 2013; Tang et al., 2019), which 438 439 is similar to the synthesized ranges of their depositional distribution in other blocks (James and Gravestock, 1990; Zhuravlev and Wood, 1995; Rowland and Shapiro, 2002; Gandin and 440 441 Debrenne, 2010). Structurally, some new erect, columnar-branching forms are present in the 442 lower Cambrian thrombolites, which are characterized by fan-like (thin branches) and dendritic 443 (thick branches) structures (Figs. 6F-G, and 7H). These erect mesostructures show marked differences from the common ellipsoid-like clotted textures in both the terminal Ediacaran and 444 445 the early Cambrian, likely indicating an adaptive response to different hydrodynamic conditions, and to the expanded contact area with seawater for the release of  $O_2$  via photosynthesis (Riding, 446

2006). Another important change in the thrombolites (and stromatolites) was the emergence of
calcified microbial microfossils in their microstructures in the early Cambrian (See Section 5.2).

5.1.2 The relationship between large-scale microbialite development and atmospheric  $O_2$  level 450 451 Distributions and characteristics of the microbialites may provide a new perspective on the development of prokaryotes during the Ediacaran-Cambrian transition. The atmospheric and 452 oceanic O<sub>2</sub> contents in the Neoproterozoic and early Paleozoic had a significant impact on the 453 early evolution of eukaryotes, and thus, have received a great deal of attention (e.g., Holland, 454 455 2006; Planavsky et al., 2021). The atmospheric O<sub>2</sub> content experienced a marked increase (from roughly 1% to 100% of the present atmospheric O<sub>2</sub> level) in the late Neoproterozoic (Lenton et 456 al., 2014; Lyons et al., 2014; Reinhard and Planavsky, 2020); and the surface oceans are 457 458 interpreted to have been in an oxic state, which may have facilitated the evolution of life forms despite the fact that the deep oceans remained anoxic (Wood et al., 2019). During this period, 459 the rise of complex eukaryotes might facilitate the burial of more organic carbon and 460 461 phosphorus and indirectly elevate the oceanic O<sub>2</sub> level (Lenton et al., 2014; Lenton and Daines, 462 2018). Direct assessment of the contemporaneous prokaryotic development is quite difficult; 463 the microbialite, as a major sedimentary carrier of prokaryotic communities and activities, may 464 provide a window to understand their evolutionary processes in the Ediacaran-Cambrian 465 transition.

466 The large-scale microbialite development may have been related to oxygenated periods in 467 the surface oceans. Although the principal source of  $O_2$  in early Earth history remains 468 controversial (volcanic degassing versus oxygenic photosynthesis) (Kopp et al., 2005; Kump

469	and Barley, 2007; Campbell and Allen, 2008; Gaillard et al., 2011; Ward et al., 2016), the O <sub>2</sub>
470	produced by oxygenic photosynthesis in shallow marine environments can be seen as an
471	essential O <sub>2</sub> source for sustaining the oxic surface oceans and buffering the anoxic waters of
472	the deeper oceans (Fig. 11). As the major source of atmospheric O <sub>2</sub> in modern oceans (Partensky
473	et al., 1999; Munn, 2020), photosynthetic cyanobacteria may also play an essential role in
474	regulating the O <sub>2</sub> production in the Ediacaran-Cambrian transition due to their vast quantities
475	of biomass. The microbialite development shows two thriving intervals during the Ediacaran-
476	Cambrian transition, i.e., in the latest Ediacaran to early Fortunian (stratiform stromatolite
477	dominant; ca. 550 to 538 Ma), and in Cambrian Age 3 to middle Age 4 (branching thrombolite
478	dominant; ca. 518 to 512 Ma), which is roughly consistent with the higher rates of net
479	atmospheric O <sub>2</sub> production and primary production in the global oceans at that time (Fig. 12)
480	(Wei et al., 2021). Thrombolites and stromatolites appeared in considerable quantities in
481	settings from shallow-water shelf to onshore environments in China (this study) and other
482	continents (Riding and Voronova, 1984; Bechstädt et al., 1988; Rowland and Gangloff, 1988;
483	James and Gravestock, 1990; Wood et al., 1993; Zhuravlev, 1996; Feldmann and McKenzie,
484	1998; Rowland and Shapiro, 2002; Javier Alvaro et al., 2006; Creveling et al., 2013; Cordie et
485	al., 2019), and they could produce adequate $O_2$ and facilitate the oxygenation of the surface
486	oceans during the Ediacaran-Cambrian transition.

488 5.2 The start of the Cambrian cyanobacterial calcification event in China

489 5.2.1 Spatial and temporal distributions of calcified microfossils in the lower Cambrian490 microbialites

491	The Cambrian cyanobacterial calcification event began in early Age 3 in China. Available
492	data show that the earliest appearance of credible calcified microbes was in the early Age 3
493	(Yang, 2005; Hicks and Rowland, 2009; Zhang et al., 2017b; Tang et al., 2019), which
494	corresponds to the strata of the lower Xiannüdong Formation in the northwestern part of the
495	South China Block (northern Sichuan and southern Shaanxi) based on biostratigraphic
496	(archaeocyathan zonations of Dailycyathus xiuqiensis and Dictyocyathus shaanxiensis) and
497	carbon isotope chemostratigraphic (initial stage of the MICE) evidence (Fig. 1) (Yang et al.,
498	2016; Zhu et al., 2019). Microbialites bearing calcified microfossils generally developed in the
499	near-shore settings around the Hannan-Micangshan massif at that time (Zeng et al., 2020); and
500	the major microbial groups included Epiphyton, Renalcis, Tarthinia, and Girvanella (Fig. 9B-
501	D). All of these calcified microorganisms can contribute to the formation of the clotted
502	structures of thrombolites (Fig. 7D-G), but only the Girvanella-group was visible in the
503	laminated fabrics of the stromatolites observed in this study (Fig. 9B).
504	The following interval from late Age 3 to middle Age 4 shows a peak of extensive
505	occurrence of calcified microbes. In the South China Block, a lot of calcified microbe-bearing
506	microbialites develop in Guizhou in the strata of upper Stage 3 based on the biostratigraphic
507	data (archaeocyathan zonation of Sibirecyathus meitanensis; Fig. 1 and Table S1) (Mei et al.,
508	2007; Yang et al., 2016). Moreover, the Epiphyton group (Song et al., 2014) and possibly
509	Tarthinia (Fig. 9H) were present within the thrombolites in the Aksu area of Tarim based on the
510	diagnostic C isotope curve (MICE) and the trilobite zone (Kepingaspis-Tianshanocephalus)
511	(Fig. 1) (Zhou, 2001; Zhang et al., 2020). The association of calcified microbial microfossils

and minor archaeocyaths widely reappeared in the South China Block after the Archaeocyathid

513	Extinction Carbon isotope Excursion (AECE; archaeocyathan Archaeocyathus yanjiaoensis
514	beds/ trilobite Palaeolenus fengyangensis Zone) (Figs. 1 and 3) (Zhang and Yuan, 1994; Yang,
515	2005; Mei et al., 2007; Adachi et al., 2013; Yang et al., 2016). After the archaeocyathan
516	extinction, individual microbial reefs/mounds developed on the rims of the eastern Yangtze
517	shelf in the middle of Age 4 (Hoffetella-R. murakamii and R. guizhouensis trilobite zones) (Fig.
518	3), which consists of plentiful microfossils formed by Epiphyton, Botomaella and other
519	tubiform microbes (Figs. 7C and H, and 9E–G). The microbialites in the North China Block
520	also recorded the emergence of the Girvanella group (Zhang et al., 1981; Mei et al., 2019) and
521	Epiphyton and tubiform microbes (Lee et al., 2014), which is roughly consistent with the timing
522	of those in the South China Block during Age 4 (corresponding to Palaeolenus fengyangensis,
523	R. chinensis, and R. nobilis trilobite zones) (Figs. 1 and 3, and Table S1) (Zhang and Liu, 1996;
524	Bureau of Geology and Mineral Resources of Jilin Province, 1997).

526 5.2.2 Comparison of the start of the Cambrian cyanobacterial calcification event on a global527 scale

The initiation of the Cambrian cyanobacterial calcification event likely occurred in the Fortunian. After examining the occurrence of calcified microfossils in the lower Cambrian strata in different blocks, it was determined that the Siberia platform has one of the earliest records of calcified microbes (*Renalcis* and *Korilophyton* microbes dominate) with widelydistributed stromatolitic structures (limestones) in the upper Nemakit-Daldynian Stage (*Purella antiqua* Zone) (Khomentovsky and Karlova, 1993; Luchinina et al., 1997; Luchinina et al., 2013), which can be assigned to the upper Fortunian based on the latest international

535	chronostratigraphic framework (Peng et al., 2020). Similar calcified microbial microfossils are
536	also preserved in contemporaneous Mongolia (Kruse et al., 1996). Adachi et al. (2021) recorded
537	a much earlier occurrence of calcified microbial microfossils than that of the previous study in
538	Mongolia, which is $\sim$ 50 m higher than the Ediacaran-Cambrian boundary (according to the
539	Basal Cambrian Carbon isotope Excursion) in height. The distribution of calcified microbes
540	shows a wider range in Age 2, including in Australia (Betts et al., 2016), Mongolia (Riding and
541	Voronova, 1985), Siberia (Riding and Voronova, 1985; Riding and Zhuravlev, 1995; Luchinina
542	and Terleev, 2008), and Morocco (Latham and Riding, 1990); and they began to be associated
543	with archaeocyaths (Riding and Zhuravlev, 1995). Both the major groups of microbial
544	microfossils and the structures of the microbial mounds/reefs in Stages 3-4 exhibit high
545	similarities in China (Figs. 6, 7, and 9) and other contemporaneous regions (Wood et al., 1993;
546	Zhuravlev, 1996; Riding, 2001; Rowland and Shapiro, 2002). A questionable earliest
547	appearance of calcified microbes (Girvanella-rich layer; thickness of ~10 cm) (Zhang and Sun,
548	1991) has been classified in the strata of the Fortunian Stage in the eastern Yangtze shelf based
549	on C isotope chemostratigraphic data (Li et al., 2017), but currently, the biostratigraphic
550	evidence is insufficient and controversial (Zhang and Sun, 1991; Qian, 1999; Xue and Zhou,
551	2006). If the chemostratigraphic correlation in this region is correct, the first occurrence of
552	calcified microbes in the South China Block may be consistent with those in Siberia and
553	Mongolia (Fig. 12). Since the three major blocks in China had latitudinal ranges similar to those
554	of the abovementioned blocks from the Fortunian to Age 2, the lack of coeval calcified microbes
555	(based on microscopically petrological evidence) may be related to the limited shallow-water
556	carbonate records and further investigations may fill in this distribution gap.

558

5.2.3 The eve of the Cambrian cyanobacterial calcification event: a prelude or nothing?

559 The exceptional preservation of non-calcified cyanobacteria from the Ediacaran to the earliest Cambrian cannot be seen as the beginning of the cyanobacterial calcification event. A 560 561 series of sites containing cyanobacterial groups have been identified in the lower Fortunian in 562 the South China and Tarim blocks; however, nearly all of these microfossils are preserved 563 within the phosphorites/cherts and their well-formed microstructures are generally permineralized by apatite and/or quartz (Qian et al., 2007; Cui et al., 2020). These two main 564 565 mineralization processes are generally regarded as very early phosphate/silicate replacements that occurred before the dead microorganisms decayed in a shallow burial environment, and 566 such mechanisms are also documented in the fossil preservation in the Ediacaran (Zhang et al., 567 568 1998; Muscente et al., 2015; Anderson et al., 2017). Evidence from scanning electron microscope photomicrographs also supports the presence of apatite- or quartz-replaced 569 microstructures on the walls of the microbial microfossils (Cui et al., 2020) based on the criteria 570 571 for judging the primary and secondary microstructures (Brasier, 1990).

572 Characteristics of the microbialites indicate a low possibility that the cyanobacterial 573 calcification event began in the Ediacaran. Large numbers of stromatolite and thrombolite 574 records are developed in the uppermost Ediacaran strata in the South China and Tarim blocks, 575 but nearly no reliable calcified cyanobacteria could be identified in this study and previous 576 studies have rarely mentioned their occurrence. Instead, the lithification of microbial mats is 577 common in the uppermost Ediacaran microbialites in China, which occur as numerous dense, 578 mineralized laminated and clotted fabrics (Fig. 8). Most of the microbial mineralization fabrics

579	in the South China and Tarim blocks is regarded as evidence that post-mortem mineralization
580	of degraded microbial communities during early diagenesis (Dupraz et al., 2009). Similar
581	mineralization characteristics of laminated and clotted structures also developed in early to late
582	Neoproterozoic microbialites (e.g., Turner et al., 2000; Harwood and Sumner, 2011; 2012;
583	Adachi et al., 2019). It is not clear which type(s) of microorganisms played the key role in the
584	mat lithification due to the currently limited evidence, but the lack of <i>in vivo</i> cyanobacterial
585	calcification appears to indicate that in the latest Ediacaran the cyanobacteria had a limited
586	mineralization ability, which may have affected their efficiency at fixing carbon and producing
587	$O_2$ during diurnal cycles (Dupraz et al., 2009). One possible reason for this is that the long-term
588	low atmospheric CO <sub>2</sub> concentrations in the Neoproterozoic slowed down the development of
589	CCMs (Riding, 2011a). Since the sheath-calcified cyanobacteria have a longer history than the
590	Neoproterozoic (since the Mesoproterozoic) (Kah and Riding, 2007), the deficiency of the
591	broad occurrence of calcified cyanobacteria preserved in the upper Ediacaran is evidence that
592	the start of the cyanobacterial calcification event was no earlier than the earliest Cambrian.
593	
594	5.3 Paleoceanographic conditions for initiation of the Cambrian cyanobacterial calcification
595	event
596	5.3.1 The primary mineralogical composition of calcified microbes in Cambrian Age 3
597	The well-formed, calcified microbial microfossils in Cambrian Stage 3 indicate a primary
598	calcite mineralogy. There are three major original mineralogical types, i.e., aragonite, low-Mg
599	calcite, and high-Mg (>4 mol% MgCO <sub>3</sub> ) calcite, for the compositions of skeletal and non-
600	skeletal carbonates. Calcified cyanobacteria have these three mineralogies in nature (Plée et al.,

601	2008; Planavsky et al., 2009; Pace et al., 2018), but the preservation of the original aragonite
602	mineralogy in ancient sediments is rather difficult because aragonite has a weak thermodynamic
603	stability and is easily recrystallized and transformed into stable low-Mg calcite (Morse et al.,
604	2007). The high-Mg calcite crystals with $<8.5 \text{ mol}\% \text{ MgCO}_3$ are more stable than aragonite
605	(Berner, 1975); they can preserve a weakly altered morphology in relatively-closed systems
606	when compared to aragonite (James and Kobluk, 1978; Sandberg, 1983; Wilkinson and Owen,
607	1985; Richter et al., 2011). There are three commonly-used criteria for judging original
608	carbonate mineralogies, including (1) the degree of preservation of the primary microstructure,
609	(2) the crystallographic features and secondary inclusions (e.g., microdolomite), and (3) the
610	major element composition (e.g., Sr contents indicating aragonite or calcite; Mg contents
611	indicating high or low Mg calcite) (James and Kobluk, 1978; Sandberg, 1983; Wilkinson and
612	Owen, 1985). The microbial microfossils in Stage 3 generally exhibit well-formed
613	cryptocrystalline microstructures and have very low concentrations of Mg and Sr in their walls
614	(2.4 mol% MgCO <sub>3</sub> and ~350 ppm Sr) (Gong et al., 2021). The associated ooid grains exhibit
615	subtle concentric-radial cortical fabrics and have also low Mg and Sr contents (3 mol% $MgCO_3$
616	and ~385 ppm Sr) (Gong et al., 2021), which indicate a primary low-Mg calcite mineralogy
617	(Fig. 10A and B, arrowed). In addition, very few calcified microfossils show the occurrence of
618	microdolomite inclusions although their petrological features are similar to normal forms (Fig.
619	10C), possibly implying a high-Mg primary mineralogical composition. Microbial microfossils
620	in the lower part of Stage 4 have similar petrological and major element compositions (0.7 mol%
621	MgCO <sub>3</sub> and 245 ppm Sr, unpublished data), which are significantly different from the
622	petrological features of the oolites and microbialites in the upper part of Stage 4 (Fig. 10D-F).

624	5.3.2 A paleoceanographic model of the start of the Cambrian cyanobacterial calcification event
625	Although the markedly elevated Ca concentrations of the seawater and the enhanced
626	CCMs may have facilitated the extensive calcification in the early Cambrian (Arp et al., 2001;
627	Riding, 2006), whether these microfossils can be readily preserved in rocks depends mainly on
628	their primary carbonate mineralogies. Here, we propose an updated model of the rapid and
629	extensive emergence and preservation of calcified microbes in early Cambrian (Fig. 12). The
630	secular evolution of the Mg/Ca molar ratio of seawater played a key role during the early
631	Cambrian, but this has not been unanimously accepted (Sandberg, 1983; Hardie, 1996). Some
632	recent insights suggest that the turnover from an aragonite-dolomite sea to a calcite sea in terms
633	of seawater compositions began in Age 3 based on halite fluid inclusions and non-skeletal
634	carbonate mineralogies (ooids and cements) (Lowenstein et al., 2001; Brennan et al., 2004;
635	Petrychenko et al., 2005; Porter, 2007; Zhuravlev and Wood, 2008). It is assumed that the
636	capability of cyanobacteria to mediate the mineralogical composition of their calcified sheaths
637	is much weaker than that of the skeletal organisms (Ries et al., 2008; Ries, 2010). The
638	microbially induced mineralization appears not to change the aqueous Mg/Ca molar ratios of
639	microdominants, which means that the Mg/Ca molar ratio of seawater was probably the major
640	factor controlling their mineralogical compositions (Ries et al., 2008; Ries, 2010).
641	The primary low-Mg calcite mineralogy of calcified microfossils generally has the optimal
642	microstructures; and microbial microfossils with a high-Mg calcite precursor (>4 mol% and
643	<8.5 mol% MgCO <sub>3</sub> ) are likely to exhibit medium to good preservation. Calcified microfossils

644 with original aragonite mineralogy are easily dissolved and recrystallized during diagenesis,

making their primary characteristics (e.g., walls and tubes) hard to identify. The low- and high-645 Mg calcite mineralogies of microbial microfossils are beneficial to the preservation of their 646 647 primary morphologies in spite of the fact that the latter may suffer stronger diagenetic alteration than the former. Since the high- and low-Mg non-skeletal carbonates develop under >1 and <1648 Mg/Ca molar ratio conditions (or 2–5.3 and <2 Mg/Ca molar ratio conditions), respectively 649 (Hardie, 1996; Stanley, 2008), the significant decline in the Mg/Ca ratio of the seawater from 650 the late Ediacaran to the early Cambrian seems to be responsible for the extensive preservation 651 652 of calcimicrobes (Fig. 12). It is concluded that the combination of elevated Ca concentrations 653 and enhanced CCMs (for the occurrence of calcified microbes), as well as the calcite sea condition (for their preservation) facilitated the start of the calcification event in the early 654 Cambrian. 655

656

# 657 6. Conclusions

Based on our high-resolution database and systematic petrological examination of microbialites in the three major blocks in China from the terminal Ediacaran to the early Cambrian, we drew the following conclusions:

(1) The Ediacaran-Cambrian transition was marked by the widespread distribution of
microbialites in China, and two thriving intervals in the latest Ediacaran to early Fortunian
and the Cambrian Age 3 to middle Age 4. The development of columnar and domical
stromatolites (inferred from shallow subtidal settings) does not appear to have been affected
during the transition, but the presence of stratiform stromatolites composed of nearly
parallel laminae (inferred from open shelf) significantly decreased in the Cambrian, which

was associated with increasingly bioturbated structures in the seafloor sediments.
Thrombolites evolved to form large and complicated structures in the Cambrian when
compared to those in the Ediacaran, including mound-like shapes and branching forms (fanlike/dendritic textures).

(2) There were no visible changes in the shape of the laminae/clots within the microbialites 671 during the Ediacaran-Cambrian transition. Calcified microbial microfossils are common 672 673 within the stromatolites and thrombolites of Cambrian Series 2, but they are not seen in the mineralized laminated/clotted microstructures in the upper Ediacaran. The types and 674 675 characteristics of the calcified microbial microfossils conform well to those of other blocks during the Cambrian cyanobacterial calcification event. This calcification event likely 676 began in the Fortunian, and the petrological and sedimentological evidence from the 677 678 microbialite microstructures formed in the Precambrian-Cambrian transition do not support an earlier beginning in the Ediacaran. 679

(3) Except for the active CO<sub>2</sub>-concentrating mechanisms and the increase in the Ca<sup>2+</sup>content of
the seawater (for the occurrence of calcified microbes), the primary calcite mineralogical
composition of the microbial microstructures is one potential reason for the preservation of
microfossils in the microbialites during early Cambrian time. Our model predicts that the
transition from the Neoproterozoic aragonite-dolomite sea to the Cambrian calcite sea
promoted formation of an original calcite mineralogy in microbial fossils, which has a
stronger ability to resist diagenetic alteration than that of the aragonite precursor.

687

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Fig. 1 (A) Outline map of China showing the three major blocks (i.e., North and South China, 1165 and Tarim). (B) Global paleogeography in the Ediacaran-Cambrian transition (ca. 540 Ma), 1166 with the location of the North China (NCB), South China, and Tarim blocks. Base map after 1167 Torsvik et al. (2013). (C) The timescale and the regional biostratigraphic correlation in three 1168 blocks from the uppermost Ediacaran to the lower Cambrian. Chronostratigraphic data from 1169 1170 Zhou et al. (2019) and Zhu et al. (2019); biostratigraphic zones from Zhu et al. (2019) and Peng et al. (2020); carbon-isotope chemostratigraphic markers from Zhu et al. (2019), and Xiao and 1171 Narbonne (2020). Note that three types of biozones are in black (trilobite), blue (small shelly 1172 1173 fossil), and pink (archaeocyath) colors, respectively. Abbreviations: A. = Archaeocyathus; AECE = Archaeocyathid Extinction Carbon isotope Excursion; BACE = Basal Cambrian 1174 Carbon isotope Excursion; CARE = Cambrian Arthropod Radiation isotope Excursion; MICE 1175 = Mingxinsi Carbon isotope Excursion; P. = Palaeolenus; ROECE = Redlichiid-Olenellid 1176 Extinction Carbon isotope Excursion; U. = Uppermost. 1177

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1184	Fig. 3 Early Cambrian paleogeography of China (ca. 540-509 Ma), with the distribution of
1185	microbialites. Base map adapted from Zheng and Hu (2010). Site information of microbialite
1186	development is shown in Table S1. Study sections in the text: C1 = Xigou; C2 = Daheba; C3 =
1187	Fucheng; C4 = Shatan; C5 = Tangjiahe; C6 = Limei; C7 = Dilong; C8 = Dingtai; and C9 =
1188	Yankong.

Fig. 4 Field photographs of the uppermost Ediacaran microbialites. (A) Columnar (lower) and 1190 domical (upper) stromatolites. Lower Chigebrak Formation, Xigou section. (B) Plan view of 1191 1192 the yellow dashed box in (A), showing the top-surface of numerous domical stromatolites. (C) Massive stratiform stromatolites with nearly parallel millimeter-level laminated structures. 1193 Dengying Formation, Daheba section. (D) Thick-bedded stratiform stromatolites composed of 1194 rippled and wavy laminae (arrowed), and some cement-filled cavities along the laminar 1195 direction. Dengying Formation, Xiaotan section. (E) Reworked stratiform stromatolites with 1196 irregularly laminated structures. Dengying Formation, Changyangou Section. (F) A 1197 1198 stromatolitic microbialite with some narrow-laminar and patchy structures (clotted microstructures). Xiaoerbrak Formation, Xigou Section. (G) Alternating laminated and clotted 1199 1200 structures in a composite microbialite with a complex cavity system. Dengying Formation, Micangshan Section. (H) Enlarged clotted structures of the sample place (G) showing the 1201 1202 microclots (yellow arrows) and the complex cavity network (pink arrows).

Fig. 5 Polished slabs of the uppermost Ediacaran microbialites (vertical sections). (A) Regularly 1204 1205 laminated structures in a stromatolite. Dengying Formation, Xiaotan section. (B-C) 1206 Intermingled laminated and clotted structures in a thinly bedded microbialite with two large cavities (arrowed). Dengying Formation, Changyangou section. (D) Alternating laminated and 1207 1208 clotted structures in a composite microbialite with abundant cavities. The cavities generally consist of coarse-crystalline cements and micritic rims. Dengying Formation, Micangshan 1209 section. (E) A clotted framework in a thrombolite with large numbers of cavities. Upper 1210 Chigebrak Formation, Xigou section. (F) Composite laminated and clotted structures in a 1211 1212 microbialite with a complex cavity system (arrowed). Upper Chigebrak Formation, Shiairik section. (G) A clotted framework in a thrombolite with irregularly grown cavities filled with 1213 coarse spar (arrowed). The clots are composed of large numbers of solid and hollow peloidal 1214 1215 clusters (see Fig. 8C and D). Upper Chigebrak Formation, Xigou section. (H) A clotted framework in a thrombolite. The clotted structures consist of large quantalities of dense 1216 microclots with diameter of 0.1-0.2 mm (arrowed; for the microstructure, see Fig. 8E). 1217 1218 Dengying Formation, Xiaotan section.

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Fig. 6 Field photographs of the Cambrian microbialites. (A) Small columnar stromatolites. Basal Yurtus Formation (Fortunian). Sugetbrak section. (B) Stratiform and small domical stromatolites. Longwangmiao Formation (Stage 4), Yankong section. (C) Alternating oolitic (thickness of 1-2 cm) and stromatolitic (thickness of 0.5-1 cm) beds. Qingxudong Formation (Stage 4), Dilong section. (D) A calcimicrobial–archaeocyath bioherm developed in a mixed siliciclastic-carbonate depositional system. The inset box in the upper right shows the

characteristics of archaeocyaths (arrowed) and detrital fractions. Xiannüdong Formation (lower 1226 part of Stage 3), Daheba section. (E) Clotted structures in a thrombolite, with some detrital silt 1227 1228 fractions. (F) Fan-like (thin branches; bushy) clots in a thrombolite. (E) and (F) from the Xiannüdong Formation of the Shatan section. (G) Dendritic structures preserved in a massive 1229 1230 thrombolite. Xiannüdong Formation, Tangjiahe section. (H) Dendritic structures (0.5-1 cm in 1231 width) preserved in a thrombolite and composed of filamentous cyanobacteria microfossils. Growth orientation of the branched dendritic structures is marked by arrows. Qingxudong 1232 1233 Formation (Stage 4), Limei section.

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Fig. 7 Polished slabs of the Cambrian microbialites (vertical sections). (A) Columnar 1235 stromatolite. Basal Yurtus Formation (Fortunian). Sugetbrak section. (B) Stratiform 1236 stromatolite with nearly-parallel laminated structures. Longwangmiao Formation (Stage 4). 1237 Yankong section. (C) Alternating laminated and clotted structures showing the preservation of 1238 tubiform microfossils (arrowed). Lower Qingxudong Formation (Stage 4), Limei section. (D-1239 1240 G) Different types of clotted structures in the calcimicrobial-archaeocyath bioherms of the Xiannüdong Formation (lower Stage 3). The white dotted lines in (D), (E), and (G) indicate the 1241 1242 boundaries between the calcimicrobial-archaeocyath structures and terrigenous fine-grained particles. Arch. = archaeocyath. (D) and (G) from the Shatan section; (E) from the Daheba 1243 section; and (F) from the Fucheng section. (H) Clotted structures showing erected dendritic 1244 characteristics, with large quantalities of calcified microbial microfossils (see Fig. 9G). Lower 1245 1246 Qingxudong Formation, Limei section.

Fig. 8 Thin-section photomicrographs of the uppermost Ediacaran microbialites. (A) 1248 1249 Irregularly-arranged laminated structures in a stromatolite. The dark-colored layers are cryptocrystalline and consist of mimetic dolomite crystals (generally <2 µm); the light-colored 1250 layers are generally composed of medium- to fine-grained dolomite grains (4-40 µm). 1251 Dengying Formation, Changyangou section. (B) Well-cemented clotted microstructures in a 1252 thrombolite. The clots are shown as dark-colored, cryptocrystalline aggregate grains with no 1253 visible microfossils. The early-stage cements are composed of fibrous to acicular, isopachous 1254 1255 dolomite crystals; the late-stage cements consist of pore-filling, subhedral to anhedral, coarse 1256 dolomite crystals (generally 100-500 µm). Some clots show the occurrence of dolomite inclusions. Dengying Formation, Micangshan section. (C) Closely-packed clotted structures in 1257 1258 a thrombolite. The clots are composed of large quantities of hollow peloidal clusters, with isopachous crusts and coarse cavity-filling cements. Upper Chigebrak Formation, Xigou 1259 section. (D) Enlargement of the box in (C) showing the micritic (organic-rich) walls and 1260 1261 recrystallized chambers of the peloidal microstructures. (E) Clotted structures showing 1262 numerous dark-colored microclots connected with each other through micritic networks. 1263 Dengying Formation, Xiaotan section. (F) Enlarged microclots of the same thin-section (E) showing the occurrence of tens of micrometer granular aggregates with no visible microbial 1264 microfossils. (G) Clotted structures in a strongly diagenetically altered thrombolite. The clotted 1265 structures consist of the fibrous and microcrystalline dolomite crystals, and the chambered 1266 1267 relics. Chigebrak Formation, Xigou section. (H) Clotted structures in a weakly diagenetically altered thrombolite when compared to (G). The clots contain plentiful granular aggregates and 1268

are filled by medium to finely grained dolomite crystals (red arrows), and medium to coarselygrained calcite crystals (yellow arrows). Chigebrak Formation, Xigou section.

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Fig. 9 Thin-section photomicrographs of the Cambrian microbialites. (A) Stromatolitic 1272 structures preserved in the siliceous phosphorite. Basal Yurtus Formation (Fortunian), Shiairik 1273 section. (B) Microdigitate-columnar stromatolite exhibiting a convex-upward laminated 1274 structure. Enlargement of the arrowed position showing the distribution of filamentous 1275 Girvanella microfossils. Xiannüdong Formation (Stage 3), Fucheng section. (C) Clotted 1276 structures composed of plentiful Epiphyton microfossils within a thrombolitic mound. 1277 Xiannüdong Formation, Tangjiahe section. (D) Renalcis-dominant microfossils developed in 1278 the clotted structures of a thrombolitic mound. Some Tarthinia microbes (arrowed) are 1279 associated with the Renalcis group. Xiannüdong Formation, Tangjiahe section. (E) A branched 1280 1281 microfossil (lower left box) with radiating fans composed of separated tubes, possibly a Hedstroemia group. Lower Qingxudong Formation (Stage 4), Dingtai section. (F) Well-formed, 1282 tubiform microfossils (clotted forms) with a series of irregular tangled tubes (lower right box), 1283 possibly a Botomaella group. Lower Qingxudong Formation (Stage 4), Limei section. (G) Well-1284 cemented clotted structures composed of large numbers of Epiphyton microfossils. Lower 1285 Qingxudong Formation, Limei section. Note that their widths and lengths are much larger than 1286 1287 those in Stage 3 (see Results section). (H) Clotted structures preserved in a thrombolitic mound in the upper Xiaoerbrak Formation (upper part of Stage 3) with some possible microbial 1288 microfossils (arrowed). This type of fossil is presumably a Tarthinia group. Xigou section. 1289

Fig. 10 Mineralogical characteristics of the ooids and calcified microbes in Cambrian Stages 1291 1292 3-4. (A-B) Association of ooids and calcified microbes in the lower part of Stage 3. Ooids are characterized by well preserved (stained), radial-concentric fabrics (arrowed); Renalcis group 1293 shows well-formed cryptocrystalline botryoidal structure. The microstructures and Mg-Sr data 1294 (see Section 5.3.1) indicate a primary calcite mineralogy. (A) from the Xiannüdong Formation 1295 1296 (lower part of Stage 3), Tangjiahe section; (B) from the Xiannüdong Formation, Daheba section. (C) Rare *Epiphyton* microfossils showing the appearance of dolomite inclusions within their 1297 1298 calcified structures. Lower Xiannüdong Formation, Tangjiahe section. (D) Association of ooids and the stromatolitic structure in the upper part of Stage 4. Strongly altered ooids (arrowed) and 1299 microbial laminated structures; their primary fabrics were recrystallized during diagenesis. 1300 Upper Qingxudong Formation (upper part of Stage 4), Dingtai Section. (E) Photomicrograph 1301 of clotted structures in a thrombolite specimen, with no visible calcified microfossils. Upper 1302 Qingxudong Formation, Dilong section. (F) Poorly preserved ooid grains with weakly-radial 1303 1304 and completely-recrystallized cortical fabrics. Upper Qingxudong Formation, Dingtai Section

Fig. 11 Cartoon diagram showing the depositional environments for the thrombolites and stromatolites in the latest Ediacaran (A) and the early Cambrian (B). Note: the development of columnar and domical stromatolites does not appear to have been affected in the transition; the presence of stratiform stromatolites in the open shelf environment markedly decreased in the Cambrian likely caused by increasing bioturbation in the seafloor sediments. The thrombolites

evolved to form mound-like shapes and branching forms (fan-like/dendritic textures), possibly
adapted to increasing bioturbation, hydrodynamic condition, and O<sub>2</sub> production rate. Not to
scale.

1314

1315 Fig. 12 (A) Number of occurrences of the microbialites (stromatolites and thrombolites) and calcified microbial microfossils (within microbialites) from the uppermost Ediacaran to 1316 Cambrian Series 2 in China. Original data are synthesized in Table S1. (B) Total genera of the 1317 calcified microfossils (including cyanobacteria and suspected cyanobacteria) in the lower 1318 Cambrian. Data from Riding (2001). (C) Net atmospheric  $O_2$  production, and net marine 1319 primary productivity. Date from Wei et al. (2021). The development of microbialites and 1320 diversity of calcified microbes are roughly consistent with the higher rates of atmospheric O<sub>2</sub> 1321 production and marine primary productivity during the Ediacaran-Cambrian transition. (D) The 1322 evolution of seawater Mg/Ca molar ratio in the Ediacaran-Cambrian transition. Curve redrawn 1323 using the data of fluid inclusions (squared) in marine halite (Brennan et al., 2004; Petrychenko 1324 et al., 2005). The intervals of aragonite-dolomite sea, aragonite sea, and calcite sea in the 1325 Ediacaran-Cambrian transition are from Wood et al. (2017) and references therein. The 1326 1327 empirical estimates of the primary non-skeletal mineralogical compositions are from Stanley (2008). The primary mineralogies of ooids in this study conform to the seawater Mg/Ca 1328 compositions. 1329

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