Current Progress on the Geological Record of Microbialites and Microbial Carbonates

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Abstract: This paper reviews the current progress and problems in the study of microbialites and microbial carbonates. Microbialites and microbial carbonates, formed during growth of microbes by their calcification and binding of detrital sediment, have recently become one of the most popular geological topics. They occur throughout the entire geological history, and bear important theoretical and economic significances due to their complex structures and formative processes. Microbialites are in place benthic microbial buildups, whereas microbial carbonates can be classified into two categories: stabilized microbial carbonates (i.e., carbonate microbialites, such as stromatolites and thrombolites) and mobilized microbial carbonates (i.e., microbial carbonate grains, such as oncoids and microbial lumps). Various texture, structures, and morphologies of microbialites and microbial carbonates hamper the systematic description and classification. Moreover, complex calcification pathways and diagenetic modifications further obscure the origin of some microbialites and microbial carbonates. Recent findings of abundant sponge spicules in previously identified "microbialites" challenge the traditional views about the origins of these "microbialites" and their implications to reef evolution. Microbialites and microbial carbonates did not always flourish in the aftermath of extinction events, which, together with other evidences, suggests that they are affected not only by metazoans but also by other geological factors. Their growth, development, and demise are also closely related to sea-level changes, due to their dependence on water depth, clarity, nutrient, and sunlight. Detailed studies on microbialites and microbial carbonates throughout geological history would certainly help understand causes and effects of major geological events as well as the co-evolution of life and environment.

Key words: microbialite, microbial carbonate, reef, calcification, calcimicrobe

1 Introduction

Microbialites and microbial carbonates are produced by calcification and sediment-trapping/binding of microbes during their growth and metabolism (Burne and Moore, 1987; Riding, 2000) (Fig. 1). They developed throughout the entire geological periods: the oldest has been dated back to 3.45 billion years ago (Hofmann et al., 1999), whereas the youngest occurs in various modern environments (e.g., Awramik and Vanyo, 1986; Dill et al., 1986; Couradeau et al., 2012). Microbialites and microbial carbonates especially flourished in some critical intervals including the Meso- to Neoproterozoic, Cambrian–Ordovician, Late Devonian–Early Carboniferous, and Early Triassic (e.g., Elicki, 1999; Ezaki et al., 2003;

Sheehan and Harris, 2004; Adams et al., 2005; Wang et al., 2005; Jiang et al., 2008; Woo et al., 2008; Shen et al., 2010; Kershaw et al., 2012). Flourish and decline of microbialites and microbial carbonates are closely related to some major geological events, paleoclimate, and paleoceanographic conditions (Riding, 2006b). Therefore, studies on these microbial-induced sediments are important with respect to revealing paleoceanographic, paleoclimatic, and paleoecological conditions. In addition, microbialites and microbial carbonates can also serve as reservoirs of minerals and hydrocarbon due to their complex structures and biogenic origins, which bear certain economic significances (Dai et al., 1995; Parcell, 2002; Chen et al., 2004; Wang and Tao, 2005; Yang et al., 2007; Shi et al., 2008; Tian et al., 2011).

Microbialites and microbial carbonates have recently

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become a popular topic in the field of sedimentary geology. Studies on microbialites and microbial carbonates are thus often reviewed and summarized at certain stages, which is essential for the development of sciences (e.g., Burne and Moore, 1987; Dai et al., 1996; Riding, 2000, 2011; Han et al., 2009a; Wang et al., 2011; Luo et al., 2013). Many of the previous reviews focused on the classification of microbialites and microbial carbonates, with each type (e.g., stromatolite, thrombolite, dendrolite, leiolite, etc.) described and discussed in details (Fig. 1). This paper will not reiterate these descriptions, but will provide a review and present new views on current progress and problems in the study of microbialites and microbial carbonates, based on literatures and the authors' recent studies. However, this review does not encompass every aspects of microbialites and microbial carbonates, but only focuses on some of the important issues concerning basic conceptions, calcimicrobes, relationship with metazoans, and responses to major extinction events and sea-level changes.

2 Basic Conceptions

2.1 Differentiation of definitions

The terms "microbialite" and "microbial carbonate" are similar in definition, but they differ in common usage. Microbialites are "organosedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding detrital sediment and/or forming the locus of mineral precipitation" (Burne and Moore, 1987), whereas microbial carbonates are "produced by the interaction of microbial growth and metabolism, cell surface properties, and extracellular polymeric substances with mineral precipitation and grain trapping" (Riding, 2011). By definition, both terms can indicate sediments that are produced by microbes (Fig. 1). The difference is that the former is composed of either carbonates (in many cases) or siliciclastics, or sometimes chemically precipitated minerals (e.g., Martin et al., 1993; Lee and Chough, 2011; Johnson et al., 2013) (Fig. 2), whereas the latter is composed merely of carbonates (e.g., Riding, 2000). Recently, Riding (2011) supplemented that microbialites are "in place benthic sediments produced by microbial processes", which commonly project upward from the substrate showing domal or columnar morphology. Thereby, microbialites generally indicate microbial buildups such as stromatolites and thrombolites, and do not include microbial grains such as oncoids.

On the contrary, microbial carbonates are used to indicate all carbonate sediments that are produced by microbes (Riding, 2000). They can be collectively classified into stabilized microbial carbonates (i.e.,

carbonate microbialites or reefal microbial carbonates) and mobilized microbial carbonates (microbial grains and some lime mud) (Fig. 3). Mobilized microbial carbonates such as oncoids, ooids, and microbial lumps are commonly bedded, which also show various sedimentary structures such as ripple, cross-stratification, and grading; they are basically similar to inorganic carbonate sediment or siliciclastic sediment with respect to sedimentary structures. Microbial carbonates and microbialites are not really equal; neither one includes the other. The intersection of the two, namely carbonate microbialites (or reefal microbial carbonates) is the research focus in recent years (Fig. 3).

In addition, a concept of microbially induced sedimentary structures (MISS) was recently introduced to describe non-reefal sedimentary structures which are formed mostly on siliciclastic substrates (Noffke et al., 2001). MISS are formed by binding, baffling, and trapping of detrital grains by cyanobacterial films and mats, which commonly lack calcite precipitation in extracellular polymeric substances (Noffke and Awramik, 2013). Five main categories of MISS have been introduced, containing seventeen individual types that are produced by "epibenthic cyanobacteria interacting with the physical agents of erosion, deposition, transportation, or deformation" (Noffke et al., 2001). Microbial laminites were previously regarded as flat and planar stromatolites, but they are put in the category of MISS (Noffke et al., 2001) (Figs. 1e and 2b). However, in the brief summary, MISS are still being regarded as a specific group of stromatolites (Noffke, 2009) or as the fifth group of microbialites (Noffke and Awramik, 2013).

2.2 Classification and nomenclature

Classification on microbialites and microbial carbonates was made based mainly on their texture (i.e., meso-scale structures) (Riding, 2000). Four major types of microbialites (and microbial carbonates) were classified: stromatolite, thrombolite, dendrolite, and leiolite (Burne and Moore, 1987; Riding, 2000) (Fig. 1). Stromatolite (originally stromatolith) was firstly proposed by Kalkowsky (1908) to indicate laminated deposits formed by biologic processes. Later, stromatolite was re-described as "a laminated benthic microbial deposit" (Riding, 1999). Thrombolites, coined by Aitken (1967) to differentiate from stromatolites, are used to describe non-laminated, "clotted" microbial deposits. Later, Shapiro (2000) discussed about thrombolites and limited "clots" to mm- to cm-scale mesostructures (mesoclots); Aitken's original clots were re-studied and defined as maze-like maceria structures, which are included in a macro-scale structure (Shapiro and Awramik, 2006). Dendrolites are also
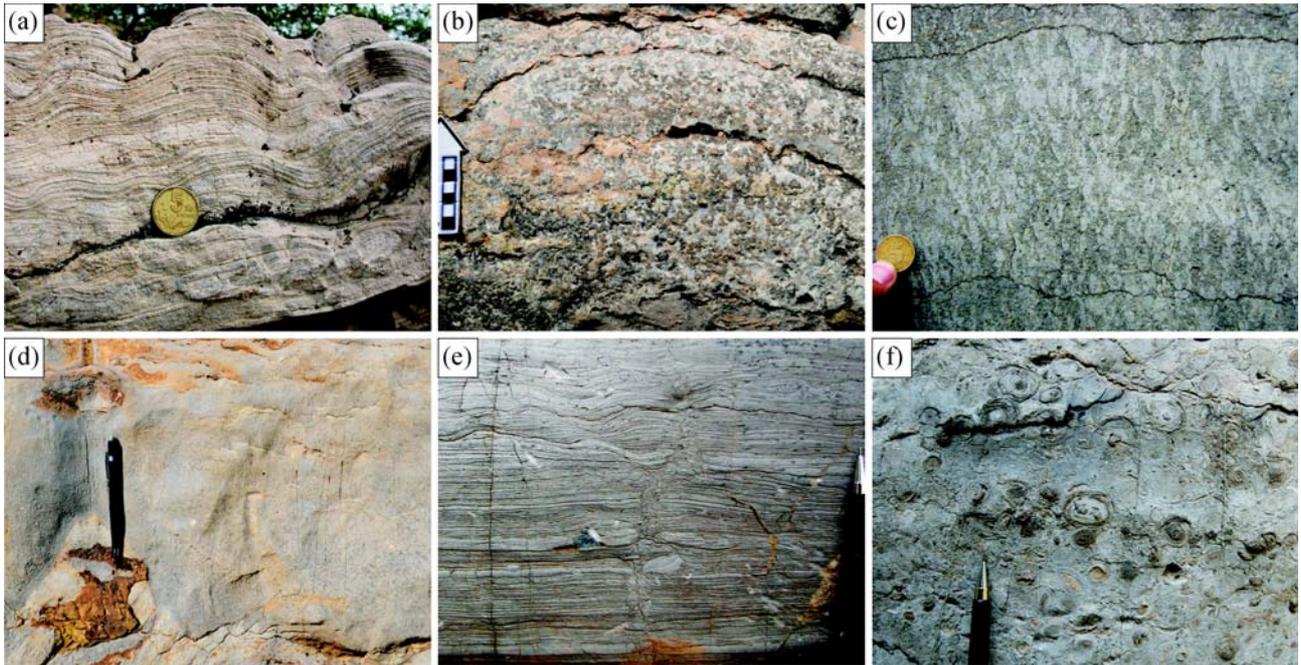
Fig. 1. Representative photographs of various microbialites and microbial carbonates.
(a) Irregular to domal stromatolite, Cambrian Series 2, Laiwu region, Shandong, China. (b) Thrombolite with irregular, dark-gray microbial clots, Cambrian Series 3, Jinan region, Shandong, China. (c) Dendrolite with bush-like structures, Cambrian Series 3, Jining region, Shandong, China. (d) Leiolite with aphanitic texture, Cambrian Series 3, Laiwu region, Shandong, China, which was firstly recognized by Woo (2009). (e) Microbial laminites with desiccation crack, Cambrian Series 3, Linyi region, Shandong, China. (f) Oncoid with spheroidal shapes and crudely-laminated cortex, Cambrian Series 3, Jinan region, Shandong, China.
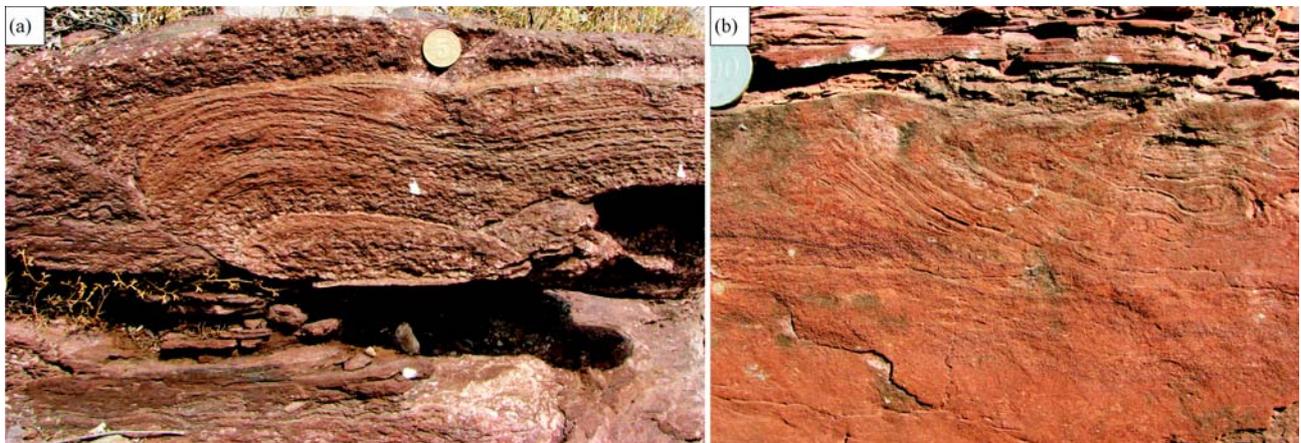

Fig. 2. Siliciclastic stromatolites and laminites.
(a) Laterally linked hemispheroidal stromatolites covered by thrombolitic microbialite, Cambrian Series 3, Linyi region, Shandong, China. (b) Microbial laminites with rolling and convoluting structures, Cambrian Series 3, Jinan region, Shandong, China.
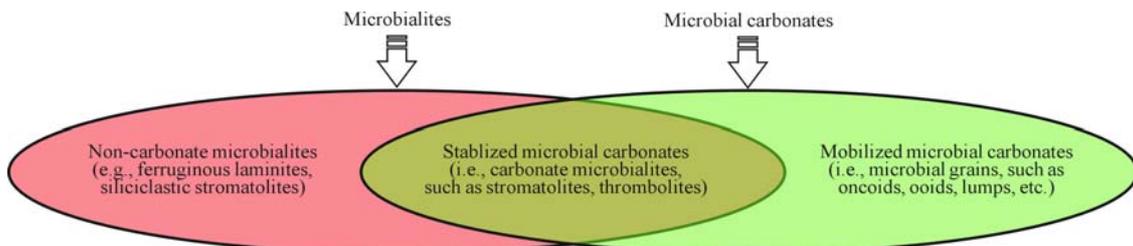

Fig. 3. Relationship between microbialites and microbial carbonates. The intersection of the two, i.e., stabilized microbial carbonates or carbonate microbialites, is the focus of studies.

characterized by dendritic clotted structures that commonly show upward widening shapes, suggesting their biologic origin (Riding, 1991b, 2000; Howell et al., 2011). The transition from irregular clots (thrombolites) to dendritic clots (dendrolites) is gradational and subtle, which might bring confusions as to their naming. Leiolites, term proposed by Braga et al. (1995), are to indicate microbialites with structureless, relatively homogeneous (aphanitic) texture. Leiolites are not common in geological record, but they may be otherwise regarded as small-scale carbonate mud mounds (cf. Riding, 2002).

Although different types of the microbialites and microbial carbonates are often reviewed and described (e.g., Burne and Moore, 1987; Shapiro, 2000; Riding, 2000, 2011; Noffke and Awramik, 2013), many of them are still hardly classified or named due to the chaotic or complex texture and structures. As an example, the microbialites from the Cambrian Series 3 Zhangxia Formation of the North China Platform consist of abundant dendritic calcimicrobes, *Epiphyton* (Zhang et al., 1985; Gao and Zhu, 1998; Mu et al., 2003; Woo et al., 2008). It is, however, hard to classify these microbialites into certain types due to their blur mesostructures. Instead, Woo and Chough (2010) called them "*Epiphyton* framestone" because the main framework of microbialites was built by *Epiphyton*. Similarly, Shen et al. (1997, 2008) also regarded the Devonian microbialites from South China as "*Renalcis* framestone". Another example is the widely developed microbialites (*Favosamaceria cooperi*) in Laurentia, which are classified as thrombolites (Shapiro and Awramik, 2006) (Fig. 4a, b). They are, however, different from the typical thrombolites containing cm-scale clotted texture (Fig. 1b), and show chaotic texture and branching maze-like structures (maceria). Based on these features, Lee et al. (2010) regarded the similar microbialites developed in the coeval succession in the North China Platform as "maceriate microbialite" (Fig. 4c, d), and did not classify them into certain types. Recently,
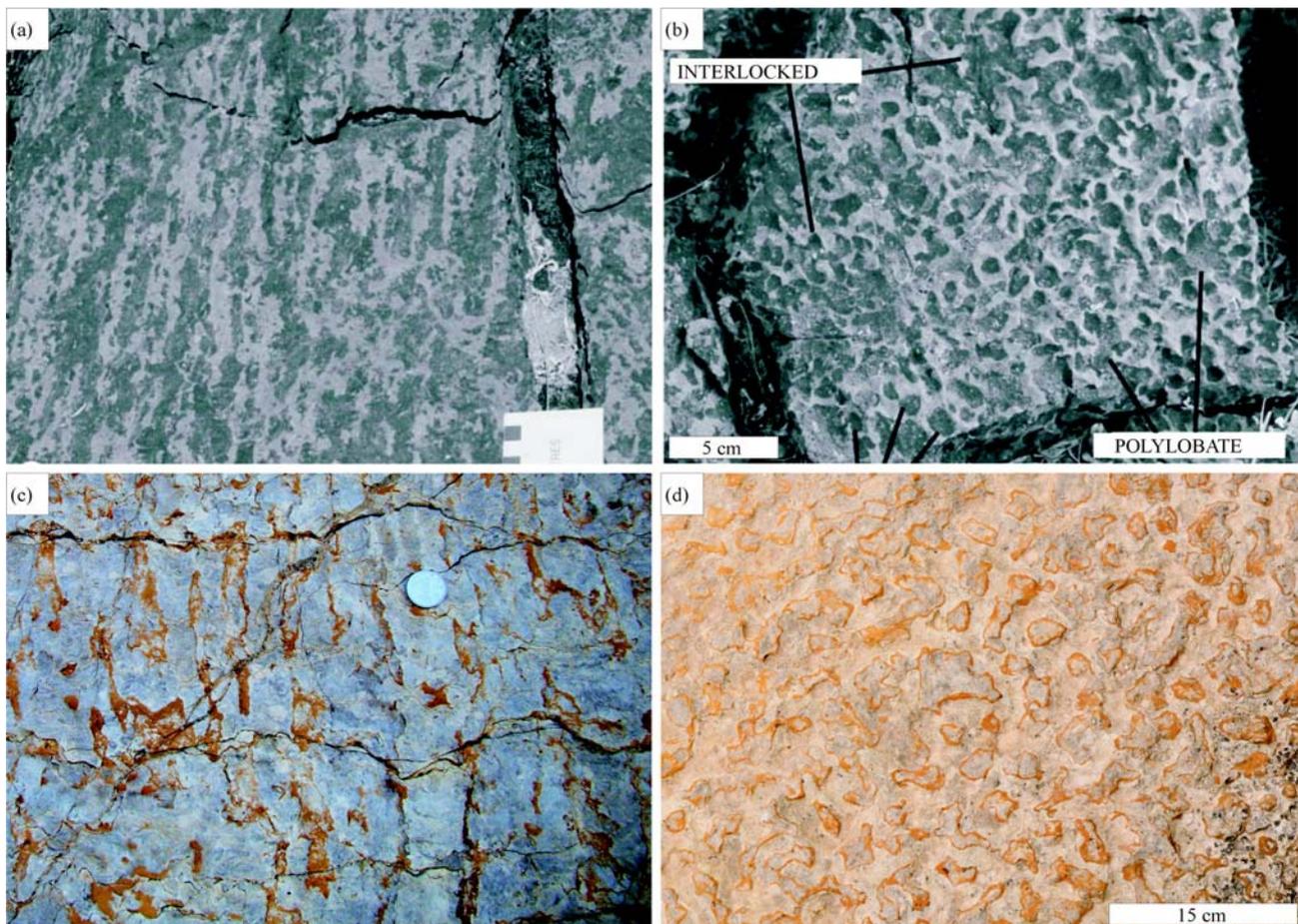

Fig. 4. Maceriate (maze-like) microbialites, flourished during the Furongian and Early Ordovician in Laurentia and North China Platform, are characterized by diverging and converging structures in longitudinal sections, and rambling maze-like structures in horizontal sections.

(a) Longitudinal section of the microbialites in the upper part of the Cambrian in Laurentia (Shapiro and Awramik, 2006). (b) Transverse section of the microbialites in the upper part of the Cambrian in Laurentia (Shapiro and Awramik, 2006). (c) Longitudinal section of the microbialites in the Furongian Chaomidian Formation of the North China Platform (Lee et al., 2010). Coin is 19 mm in diameter. (d) Transverse section of the microbialites in the Furongian Chaomidian Formation of the North China Platform (Lee et al., 2010).

however, Lee et al. (2014) redefined these microbialites as "sponge-microbial reefs" because they discovered abundant sponge spicules that actively constructed the reefs together with calcimicrobes (more details in section 4). Thus, these microbialites, which cannot be classified into the four typical types, need to be described in detail in order to clarify their formative processes.

Microbes also get involved in formation of carbonate grains (mobilized microbial carbonates), such as oncoids, ooids, and microbial lumps (Davaud and Girardclos, 2001; Li et al., 2010; Liu and Zhang, 2012; Mei and Gao, 2012; Barale et al., 2013; Yang et al., 2013). Laboratory experiments show that microbial organisms can form ooids (Brehm et al., 2006). Studies on modern ooids also suggest that microbial organisms are important for the formation of coated grains (i.e., ooids and oncoids) (Davaud and Girardclos, 2001), although other studies suggest that microbial organisms only alter their texture after formation (Duguid et al., 2010). Han et al. (2014) pointed out that ooids could be encrusted by calcimicrobes (e.g., *Girvanella*), forming oncoids, whereas oncoids could also be wrapped by chemically precipitated calcite or aragonite, forming ooids. The alternative wrapping of carbonate grains by organic and inorganic encrustations results in formation of compound grains (e.g., *Girvanella* ooids of Liu and Zhang, 2012).

Furthermore, some carbonate grains from the Cambrian Series 3 in Shandong Province, China show similar external morphology as oncoids, but have no internal lamination and nucleus. These grains were firstly regarded as "thrombolitic oncoids" (Yang et al., 2011) and later "microbial lumps" (Yang et al., 2013). Based on detailed field measurement and observations, Han et al. (2014) found these grains occur in a cross-stratified limestone bed with a sharp erosional base overlying bioturbated wackestone (previously identified as thrombolites by Yang et al., 2013). These grains contain clear calcified microbes inside, and show sharp edges that cut the incorporated sediment and calcified microbe inside, indicating that these grains were most likely derived from microbial buildups nearby, and transported and reworked by currents and waves.

In summary, systematic classification and nomenclature of microbialites and microbial carbonates are still unclear, mainly because of their complex texture and structures, as well as formative processes. It is critical to make a clear description and reasonable classification in order to understand their formative processes and controlling factors.

2.3 Scales of microbialite structures and morphology

In order to systematically observe and describe microbialites, various scales of microbialite structures should be differentiated, which is important for correctly understanding their formative processes and paleoenvironmental implications. Shapiro (2000), after amending Grey (1989), proposed four scales of observation for the study of microbialites, including megastructure (large-scale features of the microbialite bed, such as biostrome or bioherm), macrostructure (gross form of the microbialite bodies such as dome or column), mesostructure (internal textures of macrostructural elements such as lamina and clot), and microstructure (microscopic fabrics such as calcimicrobes, carbonate particles, and cement) (Fig. 5a). These four scales of observation and description can be applied to most of microbialites. All microbialites display certain macro-, meso- and microstructures. Depending on the lateral and vertical development, megastructures may be absent (for example, a cm- to dm-scale, isolated microbialite buildup in bioclastic wackestone may not display a megastructure). On the other hand, macrostructures may be various in scale and grade; they may contain other macrostructures within them (Fig. 5b). For example, meter-scale domal structures may contain decimeter-scale columnar structures that again consist of centimeter-scale branching structures (c.f. Howell et al., 2011) (Fig. 5b). All of the different scales of structures can be described as 'macrostructure', but in different order (e.g., first-, second-, third-, and fourth-order macrostructures) (Fig. 5b).

3 Calcification and Diagenetic Alternation of Microbes

3.1 Occurrence of calcified microbes in geologic history

Precambrian microbialites are mainly represented by stromatolites. Many of these stromatolites are often questioned with respect to their microbial origin due to absence of recognizable microbes, and instead inorganic formative models are put forward (Grotzinger and Rothman, 1996; Pope et al., 2000; Mcloughlin et al., 2008). In some cases, these stromatolites were even thought to be formed by escape of fluids during soft-sediment deformation (Cloud et al., 1974; Hoffman et al., 1998; Kennedy et al., 2001). Recent detailed micro- to nano-scale observations under microscopes reveal that most (if not all) of the Precambrian stromatolites were formed by microbes although calcified microbes are not present in many cases (Corsetti and Grotzinger, 2005; Murphy and Sumner, 2008; Allwood et al., 2009; Tang et al., 2012). Recognizable calcified cyanobacteria were rarely reported from some of the Meso- and Neoproterozoic stromatolites (Swett and Knoll, 1985; Knoll et al., 1993; Turner et al., 1993, 2000; Kah and
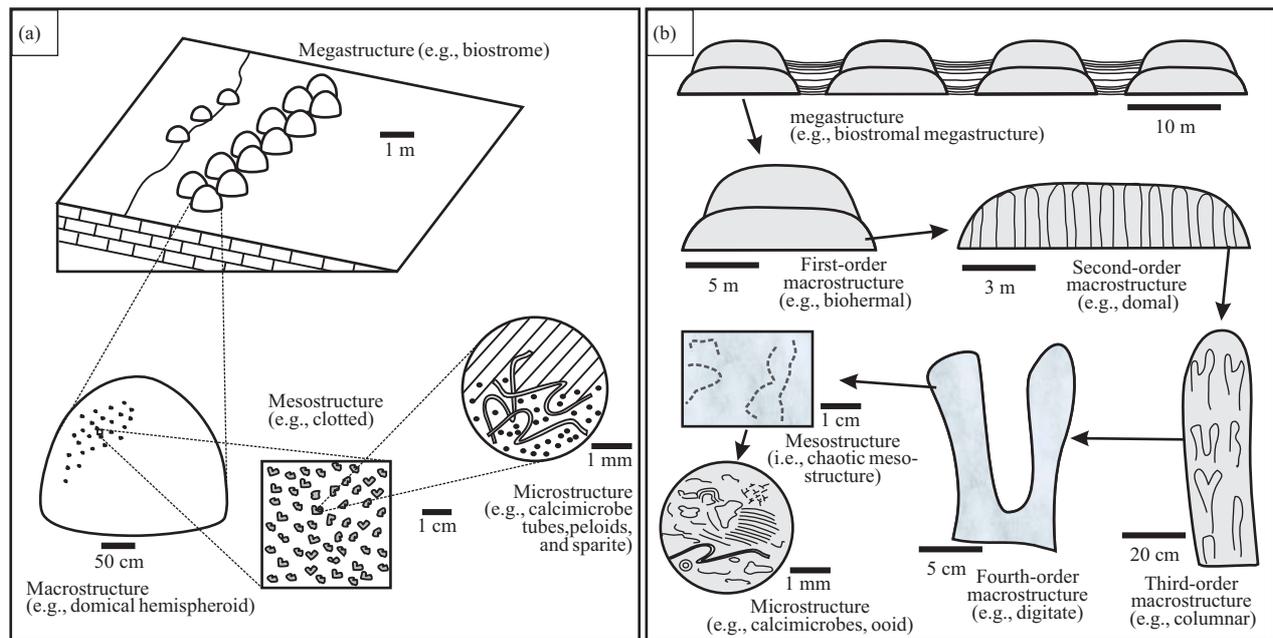
Fig. 5. Different scales of microbialite structures and morphology.
(a) The four investigation scales of microbialites (modified after Shapiro, 2000). (b) Amended investigation scales of microbial structures and morphology.

Riding, 2007).

Together with the Cambrian Explosion, calcified microbes such as *Girvanella, Epiphyton,* and *Renalcis* occur abundantly within the microbial carbonates (Riding, 1991a, 2000; Elicki, 1999; Pratt, 2001; Rowland and Shapiro, 2002; Woo et al., 2008). Since the Cambrian, calcified microbes were found from microbial carbonates of various ages, although some of them (e.g., those from the Early Triassic) are not readily identifiable. One of the most famous examples is from the Late Devonian–Early Carboniferous, where various calcified microbes occur within microbial carbonates (Shen and Webb, 2004a, 2008; Feng et al., 2010). Many of these calcified microbes have their modern analogues of cyanobacteria (e.g., Riding, 1977; Laval et al., 2000).

3.2 Calcification of microbes

Calcification of microbes occurs during their growth (Pratt et al., 2001; Riding, 2006a). Early calcification results in relatively hard surface of microbial carbonates and rapid precipitation rate, which lead to formation of certain synoptic relief, projecting upward from the substrate. Photosynthesis of microbes promotes precipitation of calcium carbonate through absorption of carbon, which results in calcification of microbial sheaths. However, calcification patterns of modern lacustrine microbialites and simulation of photosynthetically induced rise in supersaturation of calcium carbonate indicate that this mechanism applies only in settings with low dissolved inorganic carbon content and high calcium content (Arp et

al., 2001). The discovery of Arp et al. (2001) explains that lack of calcified microbes in Precambrian stromatolites was most likely ascribed to high dissolved inorganic carbon concentration in the Precambrian oceans and occurrence of various calcified microbes in many Phanerozoic microbial carbonates resulted from high Ca^{2+} concentration in Phanerozoic oceans.

Riding (2006a) suggested that calcification of microbial sheaths is promoted by CO_2 concentrating mechanisms (CCMs) that "actively transport HCO_3^- into cells for carbon fixation". During photosynthesis, microbes consume CO_2 and release OH^- by the CCMs, which results in high extracellular pH and CO_3^{2-} concentration. This process promotes the precipitation of $CaCO_3$, with adequate supply of Ca^{2+}, in the sheaths of microbes, and eventually leads to calcification of sheaths (Riding, 2006a). CCMs are closely related to decrease of atmospheric CO_2 concentration and increase of O_2 concentration during the geological history. Based on the study of modern cyanobacteria, CCMs are induced "when the atmospheric partial pressure of CO_2 (pCO_2) falls below ~0.4% (10 times present atmospheric level)" (Riding, 2006a), which promotes calcification of microbial sheaths. Crossing of the threshold of the pCO_2 is indicated by the occurrence of *Girvanella* 750–700 Ma (Swett and Knoll, 1985, Riding, 2006a). Moreover, the inference that pCO_2 fell below ~0.4% at 750–700 Ma is "consistent with empirical and modeled paleo-atmosphere estimates" (Riding, 2006a). Later, Kah and Riding (2007) found filamentous and shrub-like calcified microbes in stromatolites of ca. 1200 Ma, and

further proposed that these calcified cyanobacteria imply pCO$_2$ levels of <0.36% at ca. 1200 Ma.

Photosynthesis of microbes (especially cyanobacteria) and CCMs are critical to calcification of microbes, but the calcification usually takes place in extracellular sheaths (Riding, 1991a, 2006a; Planavsky et al., 2009) (Fig. 6a). Couradeau et al. (2012) studied modern microbialites from Alchichica Lake, Mexico, and found that these microbialites were mainly constructed by cyanobacteria (*Candidatus* Gloeomargarita lithophora gen. et sp. nov.) that contain 16~26 particles (~270 nm in diameter) of benstonite (Mg-Ca-Sr-Br carbonate) within their cells (Fig. 6b). This discovery proves that calcification of microbes also occurs inside cells, which may help to understand the geologic record of cyanobacteria (Riding, 2012). It may be, however, difficult to find out the evidence of intracellular calcification in ancient microbial carbonates.

3.3 Diagenetic alternation of calcified microbes

Early diagenetic processes (e.g., cementation) can easily alter calcified microbes, forming various characteristics, which may obscure the original features (Pratt, 1984; Turner et al., 2000; Woo et al., 2008). Pratt (1984) studied commonly associated calcified microbes, *Epiphyton* and *Renalcis*, from the Paleozoic succession and proposed that the calcified microbes with various forms and sizes were not formed by genetically distinct microbes, but resulted from calcification of coccoid cyanobacteria, controlled by size variation of microbial colonies, frequency of calcification, and intensity of cementation. It is for this reason that *Epiphyton* and *Renalcis* were regarded as "diagenetic taxa" (Pratt, 1984).

Based on the study of the Cambrian *Epiphyton* in the North China Platform, Woo et al. (2008) revealed that some of the *Epiphyton* show chambered colonies (Fig. 7a). Chambered *Epiphyton* resemble *Renalcis* (Fig. 7b), but they are still characterized by dendritic structures typical of *Epiphyton*, whereas *Renalcis* are usually composed of homogeneous micrite (Zhang et al., 1985; Shen et al., 1997; Woo et al., 2008; Han et al., 2009b). However, delicate dendritic structures of the chambered *Epiphyton*
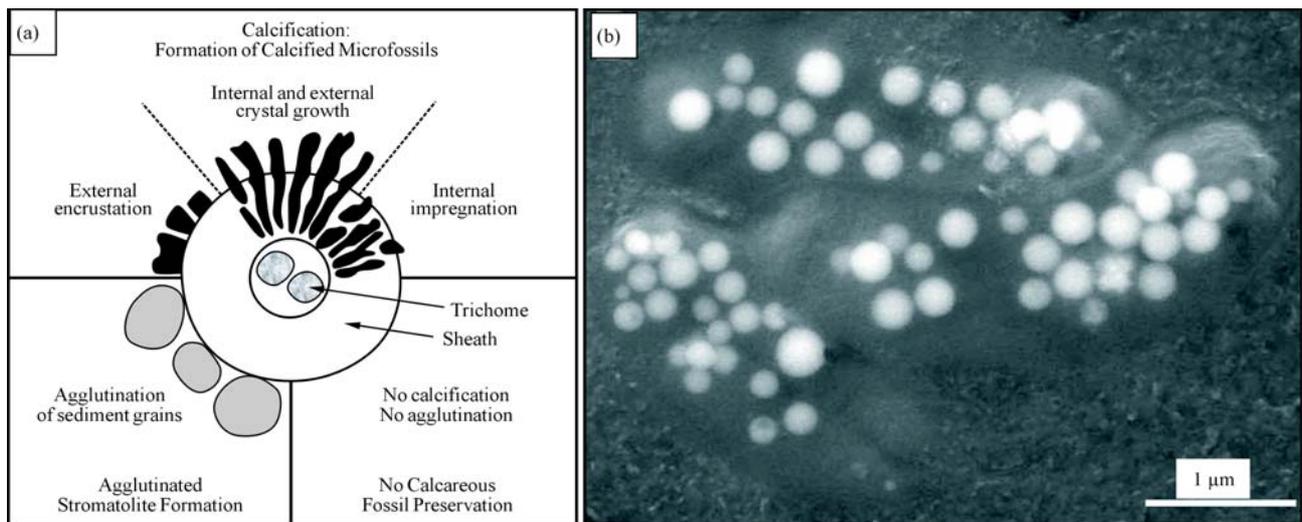

Fig. 6. Extracellular and intracellular calcification of microbes.
(a) Extracellular calcification pathways and agglutination of microbes (Riding, 1991a). (b) SEM image showing three cyanobacteria cells that contain spheroidal benstonite from modern microbialites in Lake Alchichica, Mexico (Couradeau et al., 2012).
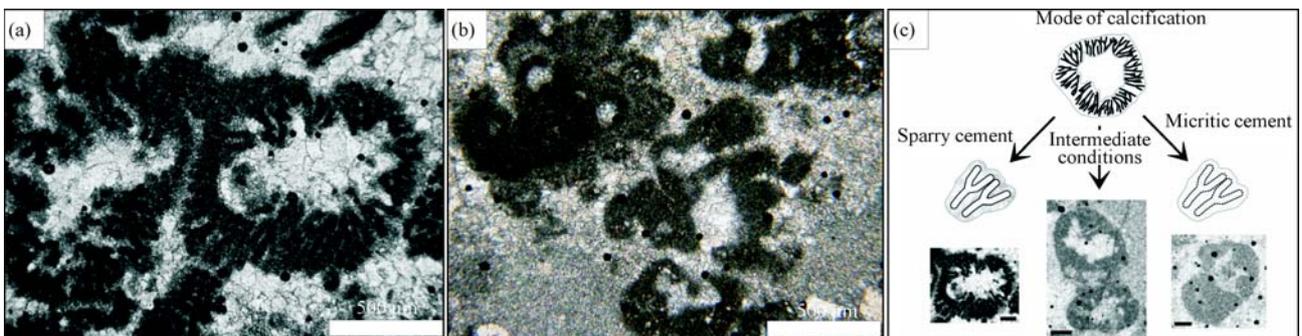

Fig. 7. Chambered *Epiphyton* and *Renalcis* from the Cambrian of the North China Platform.
(a) Chambered *Epiphyton* with internal dendritic structures (Woo et al., 2008). (b) Chambered *Renalcis* with homogeneous micritic texture (Han et al., 2009b).
(c) Different diagenetic pathways and their resultant calcified microbes of chambered *Epiphyton* (Woo et al., 2008).

can be obscured by micritic or microsparitic cementation during early diagenesis (Woo et al., 2008), in which case, it would be difficult to differentiate chambered *Epiphyton* from *Renalcis* (Fig. 7c). Chambered *Epiphyton* also occur in the Cambrian Series 2 of South China, suggesting that they can be a common phenomenon (Adachi et al., 2014).

Furthermore, recrystallization and dolomitization during diagenesis can obscure or eliminate calcified microbes and form clotted fabric instead (e.g., Kershaw et al., 1999; Shapiro and Awramik, 2006). Selective dolomitization and recrystallization could also result in certain microbialite structures (e.g., branch-like dendroid and speckled patches) (Howell et al., 2011; Jiang and Wu, 2013). Detailed microfacies and cathodoluminescence analysis may help to reveal the diagenetic history of calcified microbes and better understand the formative processes of the microbialite structures.

4 Association with Metazoan Reef-builders

Although calcified microbes are able to construct reefs by themselves, they build reefs together with metazoan reef builders in many cases during the Phanerozoic (e.g., sponges, corals, stromatoporoids, and bryozoans) (e.g., Reitner et al., 1995; Kruse and Zhuravlev, 2008; Adachi et al., 2013; Lee et al., 2014). On the other hand, some of the metazoan-constructed reefs contain microbial carbonates: metazoans build the main framework of reefs, baffling sediment particles, whereas microbes may help encrust and stabilize the framework of reefs (e.g., Hong et al., 2012; Wang et al., 2012).

The earliest metazoan-microbial reef that formed during the Neoproterozoic was mainly constructed by microbial carbonates with a few metazoans (Adams et al., 2005; Grotzinger et al., 2005). Followed by the Precambrian example, the early Cambrian (Terreneuvian and Cambrian Series 2) archaeocyaths required microbial carbonates to encrust and stabilize frameworks (Rowland and Shapiro, 2002). Similar trends occur during the Early and Middle Ordovician, when siliceous sponges, corals, bryozoans, and crinoids built reefs together with encrusting and binding calcimicrobes (Great Ordovician Biodiversification Event) (Webby, 2002; Adachi et al., 2011). The microbial carbonates were gradually substituted by metazoan-dominated reefs during the Middle–Late Ordovician as metazoan encrustors (e.g., cnidarian, bryozoan, stromatoporoid, etc.) began to occur (Webby, 2002; Riding, 2006b; Adachi et al., 2011).

During the later period of the Phanerozoic, microbial carbonates still persisted within the metazoan-dominated reefs, although they sometimes resurged and formed pure microbial-dominated reefs (e.g., Late Devonian–Early

Carboniferous, Earliest Triassic, and Jurassic) (Kershaw et al., 1999; Lehrmann, 1999; Parcell, 2002; Shen and Webb, 2004b) or metazoan-microbial reefs (e.g., Carboniferous, Early–Middle Triassic, Jurassic, and Cretaceous) (Reitner et al., 1995; Dupraz and Strasser, 2002; Olivier et al., 2004; Shen and Webb, 2005). Indeed, microbial carbonates occupy significant portion in the Phanerozoic reefs (including modern coral reefs), suggesting that they played an important role in construction of the Phanerozoic reefs (Reitner, 1993; Camoin et al., 1999, 2006; Shen and Wang, 2008; Martindale et al., 2010).

Recent studies reveal that some microbialites contain reef-building metazoans that are invisible by outcrop or hand specimen observations (e.g., Hong et al., 2012; Kwon et al., 2012; Lee et al., 2014). For example, the Furongian (late Cambrian) to Early Ordovician microbialites are often characterized by maze-like cm- to dm-scale structures (maceria), which lack apparent occurrence of metazoan reef builders in the outcrops or hand specimens (Shapiro and Awramik, 2006; Lee et al., 2010). Based on detailed microfacies analysis on relatively well-persevered maze-like (maceriate) microbialites in the North China Platform, however, Lee et al. (2014) found abundant sponge spicule networks in the microbialites, and revealed that the maceria structures were constructed by siliceous sponges, together with some microstromatolites and calcified microbes (Fig. 8). The discovery of the sponge spicules in the Furongian maze-like "microbialites" raised a question as to whether metazoan reef-builders (i.e., sponges) already flourished in the late Cambrian reefal ecosystem prior to their diversification during the Great Ordovician Biodiversification Event (Webby, 2002; Adachi et al., 2011).

5 Relationship with Mass Extinction Events

The abundancy of microbial carbonates fluctuates in the geological history, and started to decline from the Neoproterozoic when metazoans began to occur (Fig. 9a). It is generally accepted that feeding, disturbance, and competition for the living niches were ascribed to the decline of microbial carbonates (Awramik, 1971). Furthermore, modern microbial-dominated reefs mainly developed in stressful conditions where diversity of metazoans is low, such as high-energy conditions (e.g., Bahama stromatolites) or high-salinity conditions (Shark Bay stromatolites). It was suggested that the stressful conditions limited flourish of metazoans and promoted the growth of microbes (Garrett, 1970; Sheehan and Harris, 2004; Riding, 2006b).

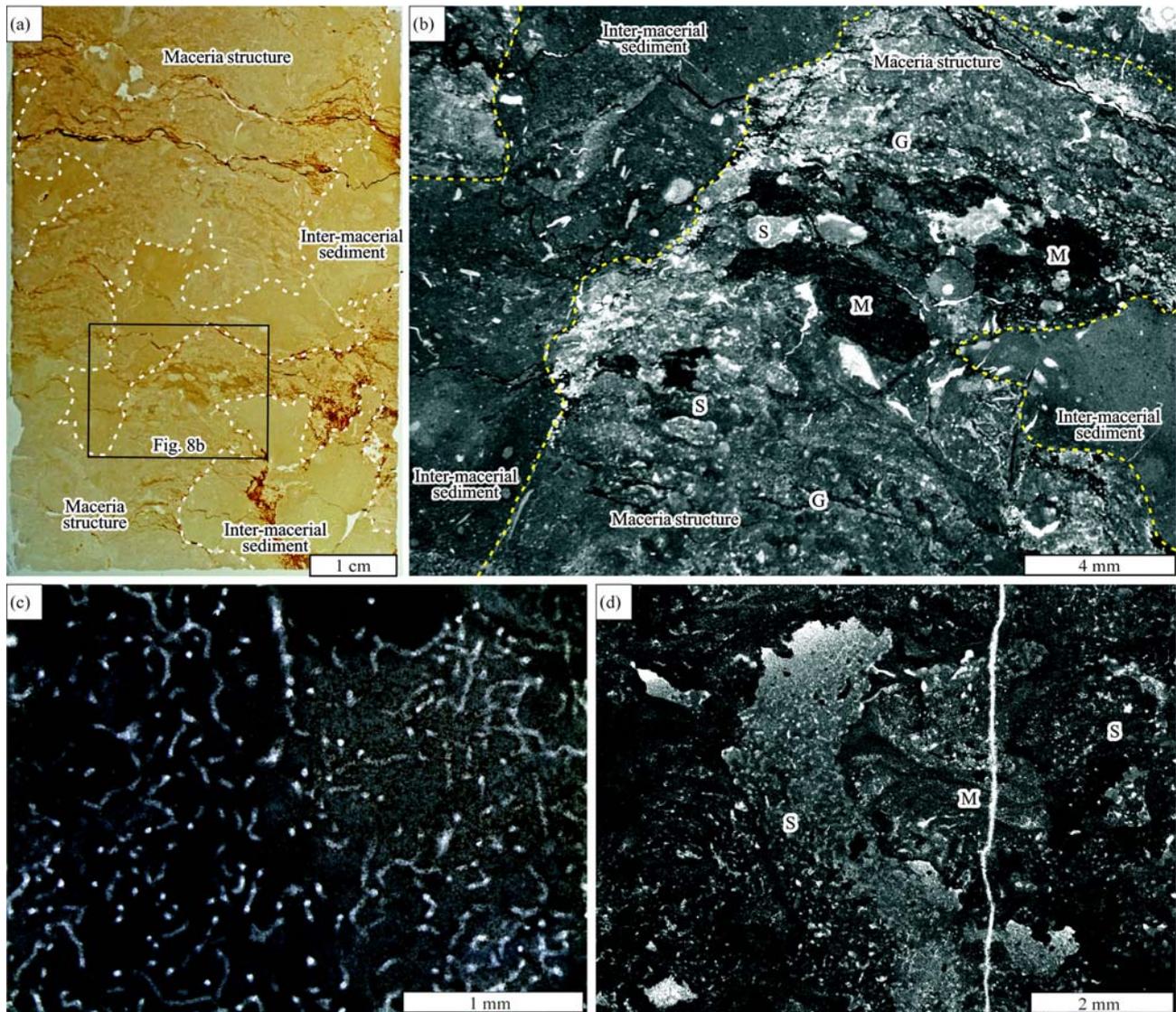In Phanerozoic, microbial carbonates mainly flourished

Fig. 8. Sponge spicules and microbial carbonates in the Furongian maceriate (maze-like) reefs, Shandong, China.
(a) Photograph of a thin section, showing chaotic biogenic maceria structures and micritic inter-macerial sediments. (b) Photomicrograph showing that maceria structures are composed of sponge spicules (S), microstromatolites (M), and *Girvanella* (G), whereas inter-macerial sediments consist of micrite with a few fossil fragments. (c) Evenly distributed sponge spicules in micrite; (d) Lateral occurrence of microstromatolites (M) and networks of sponge spicules (S).

in the aftermath of mass extinction events (e.g., Early Silurian, Late Devonian–Early Carboniferous, and Early Triassic) (Sheehan and Harris, 2004; Wang et al., 2005; Kershaw et al., 2012; Mei and Gao, 2012) (Fig. 9b). These microbial carbonates are therefore regarded as "disaster forms" (Schubert and Bottjer, 1992) or "anachronistic facies" (indicating sedimentary deposits such as microbial carbonates in the aftermath of mass extinction) (Sepkoski et al., 1991; Wignall and Twitchett, 1999). All these phenomena lead to a consensus that flourish and decline of microbial carbonates are closely related to mass extinction and resurgence of metazoans, respectively.

However, some fundamental questions were raised with respect to the relationship between flourish of microbial carbonates and major geological events. Did flourish of

microbial carbonates in the aftermath of mass extinction result directly from the mass extinction or from the crisis-associated paleoenvironmental conditions (e.g., high temperature and supersaturation of $CaCO_3$) (Riding, 2000)? Did calcified microbes increase in absolute abundance in the aftermath of metazoan extinctions, or conspicuously survive due to decline of some other groups (Feng et al., 2010)? Whether microbial carbonates begin to flourish in the aftermath of metazoan extinction or already become major component in the metazoan-microbial reefs prior to the extinction (e.g., Shen et al., 2010)?

Indeed, flourish of microbial carbonates during the Cambrian Explosion, abundant occurrence of calcified microbes in the Frasnian (prior to the Famennian mass extinction), and absence of widely distributed microbial
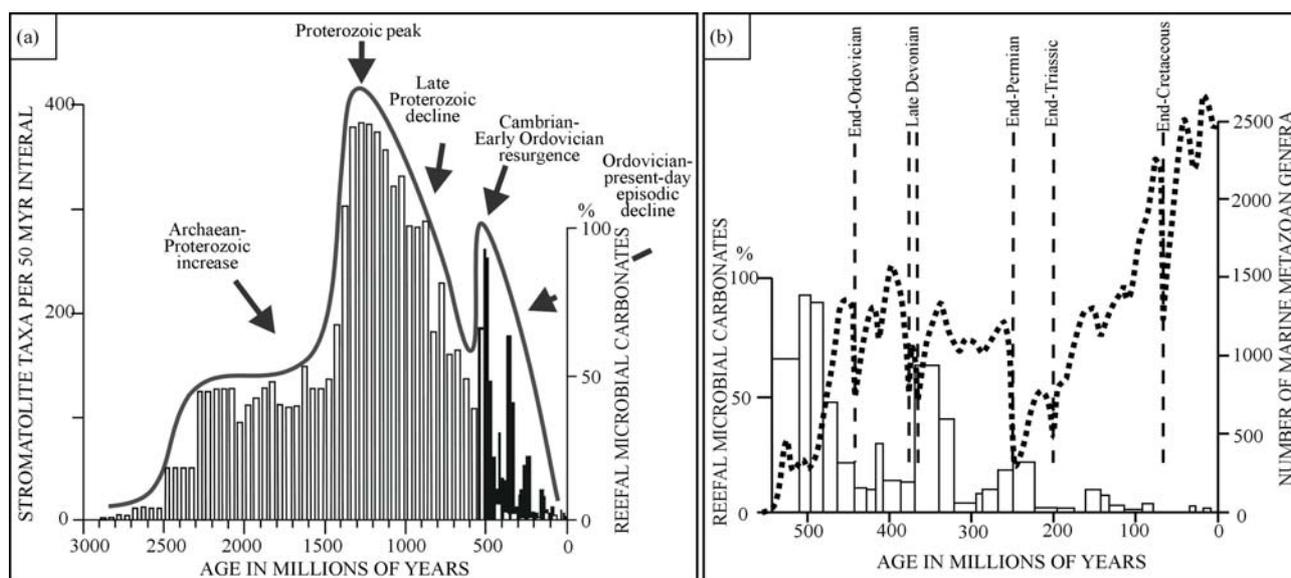
Fig. 9. Occurrence and abundance of microbialites and microbial carbonates in Earth history (after Riding, 2006b).
(a) Stromatolite diversity (white columns) and reefal microbial carbonate (i.e., carbonate microbialites) abundance (black columns). The smooth gray curve shows the overall trend of microbialites. Arrows indicate major elements of the overall trend. (b) Relationship between relative abundance of reefal microbial carbonates (by white columns) and major extinction events (vertical dash lines). The smooth dot line indicates the overall trend of the changes in number of marine metazoan genera.

carbonates in the aftermath of End-Triassic and End-Cretaceous mass extinctions collectively suggest that the abundancy of microbial carbonates in the geological history is not only related with metazoan competition, but also affected by other geological factors such as ocean water pH conditions, Ca^{2+} concentration, and atmospheric CO_2 proportion (Webb, 2001; Riding, 2006a). It is for these reasons that the two interpretive terms "anachronistic facies" and "disaster forms" should be avoided when describing the nature of the deposits (Kershaw et al., 2009).

6 Sequence-stratigraphic and Paleoenvironmental Implications

Most of the microbes that account for the formation of microbialites and microbial carbonates rely on photosynthesis, which is mainly dependent on sunlight (controlled by water depth and clarity) and nutrient (riverine influx and oceanographic perturbation). Microbialites and microbial carbonates are also greatly affected by drowning of carbonate factory, submarine erosion, siliciclastic input, and subaerial exposure; all of these factors are closely related to relative sea-level changes (Tucker, 1977; Grotzinger, 1989; Sami and James, 1994; Kershaw et al., 1999; Whalen et al., 2002; Adams et al., 2005; Grotzinger et al., 2005; Chen et al., 2012; Lee et al., 2012).

Microbialites and microbial carbonates can form various texture and structures in response to sea-level changes (e.g., Parcel, 2002). During relative sea-level fall,

development of microbial carbonates stops due to inadequate accommodation space; instead, karstification may develop as a result of subaerial exposure (Myrow et al., 2003). During initial transgression, exposed carbonate platform is submerged again. Relatively small microbial buildups may develop on the flooded topographic highs (Turner et al., 1997; Kershaw et al., 1999; Chen et al., 2011) (Fig. 10a). With subsequent transgression, rate of relative sea-level rise becomes greater than the growth rate of microbial carbonates, resulting in water depth deepening, which may drown the microbial carbonates. When the growth rate of microbial carbonates keeps up with the sea-level rise, thick microbial carbonates form instead (e.g., marginal reef) (Turner et al., 1993). During sea-level highstand, microbial carbonates keep up with sea-level rise and expand laterally, forming relatively extensive microbial flat or reefs, e.g., biostromal microbialites (Lee et al., 2012) (Fig. 10b). In some cases, microbialites may catch up rapid sea-level rise, forming domal megastructures (Lee et al., 2012; Mercedes-Martin et al., 2013) (Fig. 10b). Growth, flourish, and termination of microbial carbonates can, therefore, indicate relative sea-level changes in many cases.

Texture and morphologies of microbialites and microbial carbonates are largely dependent on the water depth and associated environmental conditions (Southgate, 1989; Turner et al., 1997; Parcel, 2002; Jahnert and Collins, 2011; Tang et al., 2013). In fact, same types of microbial carbonates (e.g., stromatolites or thrombolites) with various texture and structures may indicate various
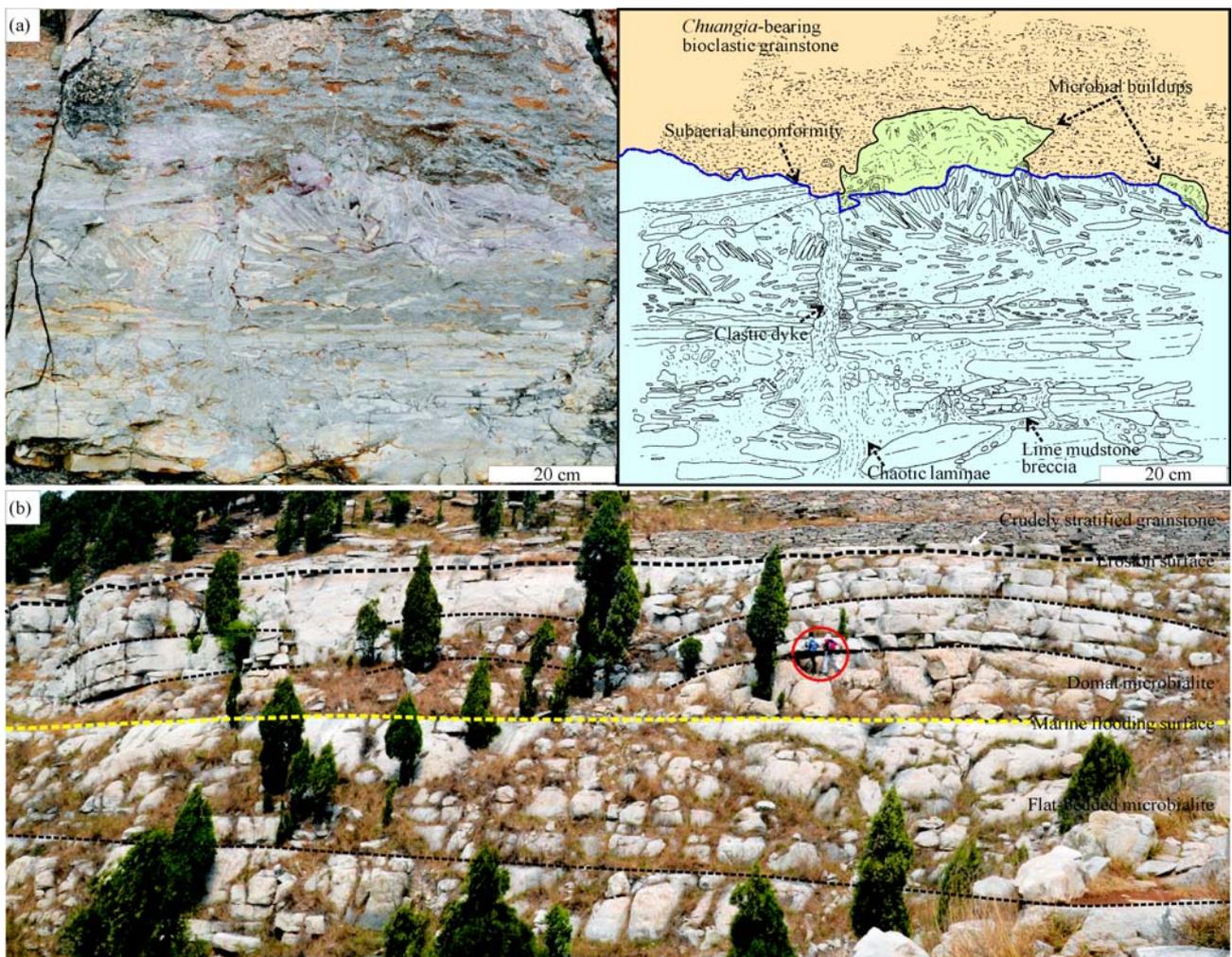
Fig. 10. Microbialites in response to relative sea-level changes.
(a) Photograph and line drawing of small thrombolitic microbial buildups (early Furongian) developing on a submerged subaerial unconformity during initial transgression, Jinan region, Shandong, China (Chen et al., 2011). (b) Thick (~15 m) and laterally extensive (tens of km in distance) flat-bedded and domal microbialites (middle Furongian) developed during sea-level highstand and subsequence sea-level rise, respectively (Jinan region, Shandong, China) (Chen et al., 2012).

water depth and hydraulic conditions (e.g., Mei, 2007; Tang et al., 2013). For example, microbial laminites can form in either deep-water settings (Mei, 2007) or shallow-water settings (inter- to supratidal flat) (Lee and Chough, 2011). These microbial laminites, however, have different features: deep-water laminites have relatively flat and continuous laminae, whereas shallow-water ones commonly contain desiccation cracks and tepee structures. As another example, based on detailed meso- to macro-scale observations on Mesoproterozoic thrombolites in the North China Platform, Tang et al. (2013) revealed that the domal structures formed in lower subtidal zone, whereas tabular structures developed in upper subtidal zone. Therefore, we can only interpret the depositional settings and hydraulic conditions of microbialites and microbial carbonates based on detailed facies analysis (texture, sedimentary structures, geometry, etc.) and stratigraphic correlation.

7 Conclusions

Microbialites and microbial carbonates are organosedimentary deposits that result from a complex interaction among physical, chemical, and biological processes. They are characterized by simple chemical composition (mostly $CaCO_3$) and various complex texture and structures, and thus bear important geological implications. Recent years, microbialites and microbial carbonates have become the focus of carbonate sedimentology and many progresses have been achieved with respect to classification and nomenclature, formative processes, and relationship with metazoan reef-builders and major geological events. There are, however, still many questions left unsolved. In order to promote the advance of studies on microbialites and microbial carbonates, it is highly necessary to carry out integrated studies including detailed sedimentary facies and

microfacies analysis, paleontology and paleoecology, integrative stratigraphy, and geochemistry.

Acknowledgements

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