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Growth patterns of the Cambrian microbialite: Phototropism and speciation of *Epiphyton*

J. Woo^{a,b}, S.K. Chough^{a,*}^a School of Earth and Environmental Sciences, Seoul National University, Seoul 151-747, South Korea^b Division of Polar Earth-System Sciences, Korea Polar Research Institute, Incheon 406-840, South Korea

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ABSTRACT

Microbes started constructing shallow marine stromatolitic bioherms in the Archean, but they transferred their role as a major buildup maker to metazoans in Phanerozoic. Microbial buildups often recovered their predominance in the carbonate platform when reefal metazoan communities collapsed. *Epiphyton*, an extinct taxon of calcified microbe that possessed branching filamentous trichomes, was an important reef builder in the shallow marine carbonate platform during Middle Cambrian, aftermath of an extinction of archaeocyath sponges which were major reef-building sessile organisms in the Early Cambrian. Here we present direct evidence of phototropism of *Epiphyton*, found from fossilized behavior in micro- and macro-structures of meter-scale microbial bioherms of the Zhangxia Formation (Middle Cambrian), North China Platform, Shandong Province, China. The bioherms consist of stacked growth layers with the inner and outer divisions divided by distinct boundary. The inner division of growth layers of the *Epiphyton* bioherm is dominated by dense uniform bush-shaped *Epiphyton* thalli, whereas the curved outer division has layered texture normal to the surface, comprised of elongated and chambered thalli. It suggests that photosynthetic *Epiphyton* reacted actively to the spatial changes in intensity of sunlight, controlled by angle of illumination on the curved growth surface of the bioherm. The inner and the outer divisions comprise different morpho-types of *Epiphyton*. The spatial distributions of different morpho-types in variously illuminated divisions of *Epiphyton* might have caused further speciation of *Epiphyton*.

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1. Introduction

Life can produce distinct morphologies in response to exposure to the external environments. Not only the higher organisms, but simple modular and/or colonial organisms also show wide range of morphological plasticity of colony. Colonies of corals grow in branching or nodular morphology according to the intensity of wave energy, the pattern of disturbance, the degree of turbidity, and the amounts of available light. Among these controlling factors, light intensity significantly modulates the distribution of different species and diverse morphologies of the species with photosynthetic symbiont, zooxanthelles. Considering that some group of microbes can be colony-like and exhibit some characteristics similar to multicellular organisms (Shapiro, 1998; Ben-Jacob and Lebine, 2006), it is unsurprising that the microbial colony, as a whole, also reacts to the external stimuli. The controls of external factors on morphology of microbial colonies are known from culture experiments of microbes such as *Escherichia coli* (Shapiro, 1998), *Paenibacillus dendritiformis* (Ben-Jacob and Lebine, 2006), *Nostoc flagelliforme*

(Liu and Chen, 2003), and *Nostoc sphaeroides* (Gao and Ai, 2004) and from modern cyanobacterial mat of *Schiothrix gebeleinii* (Seong-Joo et al., 2000). These microbes could transform the shape of the colony in order to cope with physical or chemical limiting factors such as the amounts of nutrients, the hardness of substrate, and the concentration of certain ions in solution. In the case of photosynthetic cyanobacteria, similar to the corals, availability of sunlight is the prerequisite of their living (Mullineaux, 2001; Bhaya, 2004) and it controls their distribution and morphology.

Recent fulfillment of complete gene sequencing of a cyanobacterium *Snechocystis* sp. Strain PCC6803 has increased possibility to reveal these mechanisms in gene scale (Kaneko et al., 1996; Bhaya, 2004). Larger-scale behavioral and metabolic reactions to the light include positive (or negative) phototaxis, phototropism, pigmentation, and formation of extracellular polymeric substances (Seong-Joo et al., 2000). In modern microbial environments, especially in cyanobacterial mat some modes of the phototropism and phototaxis are represented by different orientation of filaments in the day and at night (Castenholz et al., 1991), as well as up-and-down movement of cells (Ramsing et al., 2000). Different intensity and quality of light in microbial mat result in the stratification of the mat, in which one species of the microbes occupies its optimum niche at a certain level of the mat (Seong-Joo et al., 2000). Buildups of stacked microbial

* Corresponding author. School of Earth and Environmental Sciences, Seoul National University, Seoul 151-747, South Korea.

E-mail addresses: jusunwoo@kopri.re.kr (J. Woo), sedlab@snu.ac.kr (S.K. Chough).

mats, e.g., stromatolite, may have such stratified structure. On the other hand, non-mat-forming microbes, e.g., *Epiphyton* and related microbes, would show different reaction to the various intensity of the light. The meter-scale *Epiphyton* bioherms in the Middle Cambrian Zhangxia Formation (Changhian Stage, *Crepicephalina*–*Damesella* zone) (Zhang and Jell, 1987; Geyer and Shergold, 2000) preserve pristine micro- and macro-scale morphologies of the microbes and associated sediments and cements. This warrants unusual opportunity to reveal controls of illumination on microbial bioherm growth.

2. Cambrian succession of the North China Platform

The deposition in the North Chian Platform started in the late Early to Middle Cambrian and ensued until Middle to Upper Ordovician, when the entire platform emerged (Meng et al., 1997). It was tectonically quiescent and located in the low latitude tropical region during the Cambrian and Ordovician (Meng et al., 1997; Li and Powell, 2001). The Cambrian succession in Shandong Province, China consists of six formations represented by shallow marine mixed carbonate-

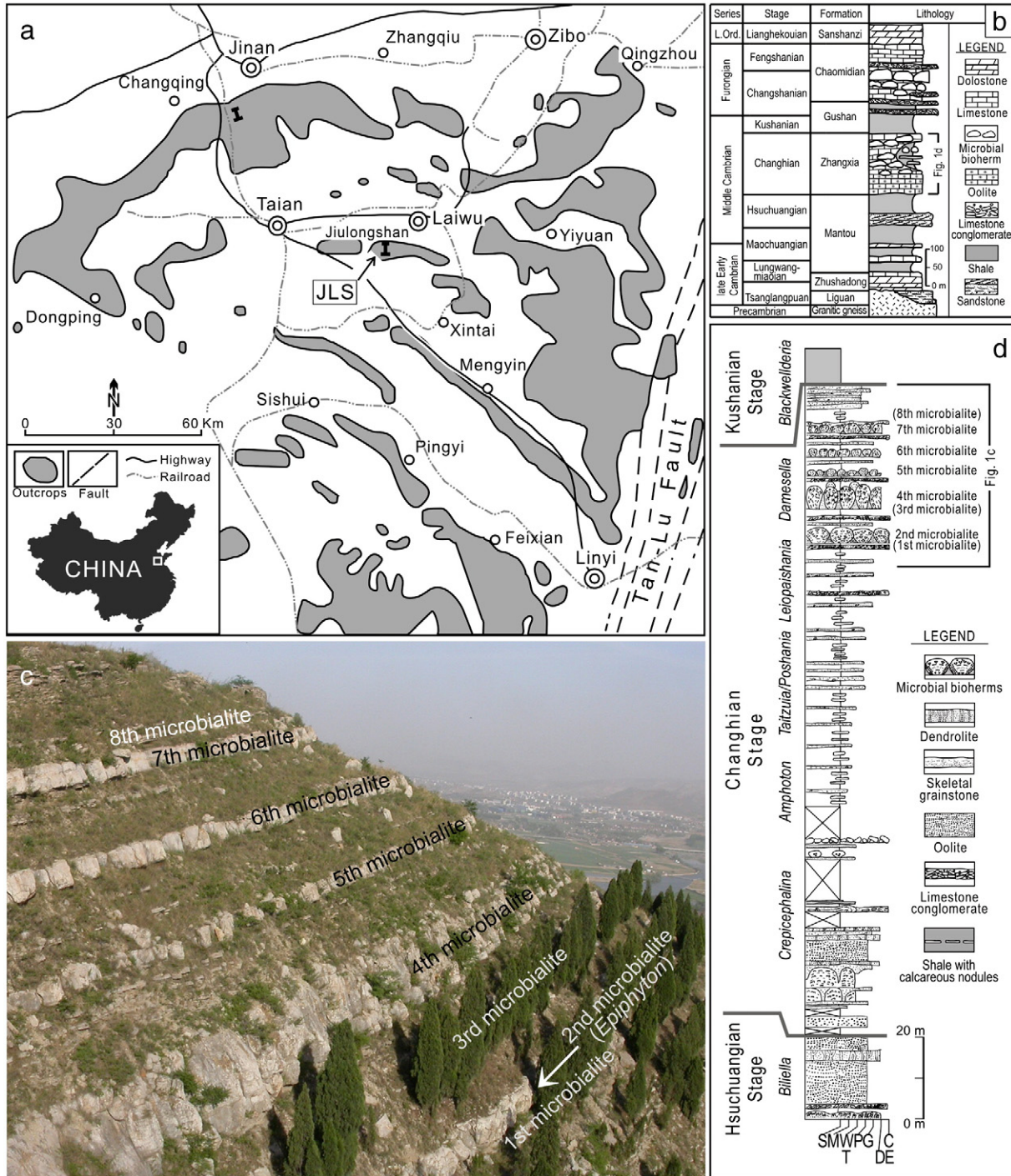


Fig. 1. Geologic settings of the North China Platform in Shandong Province, China. (a) Distribution of Cambrian and Ordovician strata in Shandong Province. JLS: Jiulongshan section. (b) Bio- and lithostratigraphic summary of the Cambrian succession (after Zhang and Jell (1987) and Bureau of Geology and Mineral Resources of Shandong Province (1996)). (c) Outcrop photograph of the Zhangxia Formation in Jiulongshan section, showing the occurrence of eight microbialite bioherm layers. The second layer exclusively comprises *Epiphyton*. (d) Columnar description of the Zhangxia Formation in Jiulongshan section Biozones from Zhang and Jell (1987). S: shale, M: lime mudstone, W: wackestone, P: packstone, G: grainstone, C: limestone conglomerate, T: thrombolite, D: dendrolite, and E: *Epiphyton*.

siliciclastic facies (Fig. 1b). The Ligan Formation is a thin basal quartzose sandstone unit in the eastern part of the Shandong area. The Zhushadong Formation is 15–40 m in thickness and consists of laminated lime mudstone, dolomite and stromatolite, representing shallow marine or supratidal environments. The overlying Mantou Formation is more than 200 m thick and characterized by siliciclastic fine sediments such as purple siltstone and hummocky cross-stratified fine sandstone and laminated dolomitic lime mudstone. The Zhangxia Formation (about 180 m in thickness) comprises oolitic or skeletal grainstone, microbial carbonates (e.g. stromatolite, thrombolite, and *Epiphyton* bioherms) as well as shaley sediments (Fig. 1c) and conformably overlies the Mantou Formation. The overlying Gushan Formation is relatively thin (52–105 m in thickness) and consists of alternating very fine-grained mudstone and limestone layers. The Chaomidian Formation (190–250 m in thickness) consists of various limestone beds ranging from lime mudstone to limestone conglomerate as well as microbial carbonates. The Cambrian succession is conformably overlain by dolomite of the Ordovician Sanshanzi Formation.

3. *Epiphyton* and *Epiphyton* bioherms in the Zhangxia Formation

The carbonate buildups in shallow marine carbonate platform of the Middle Cambrian were occupied dominantly by microbes during the aftermath of extinction of the Early Cambrian reef-building archaeocyaths (James, 1981; Wood, 1999, pp. 59–63; Pratt et al., 2001; Riding, 2006). Then, *Epiphyton* played a unique role in construction of its own exclusive or composite buildup with other microbes and metazoa. Affinity of this extinct microfossil group is uncertain, although it is regarded as cyanobacteria based on the

comparison with modern cyanobacteria of similar morphology and dimension (Riding and Voronova, 1982, 1985). Red algae similar to *Epiphyton* have more complex body structures; they have thicker main trunk and surrounding branches. On the other hand, *Epiphyton* has uniform branches which have equal rank in structures. This is similar to modern stigonematalean cyanobacteria (Riding, 1991), although their ecological position is quite different from that of *Epiphyton*. Modern freshwater meter-scale microbialites in an alkaline lake preserve micro-structure of branching filaments made by calcification of cyanobacteria which possibly are modern analogues of *Epiphyton* (Laval et al., 2000).

The *Epiphyton* bioherms coalesce laterally to form mega-scale biostrome which is encased by shaley sediments with thin intercalation of oolite and calcarenite. Interbioherm cavities were filled with coarse skeletal packstone to grainstone in the lower part and with dolo-mudstone in the upper part. The individual *Epiphyton* bioherm is about 1.8 m high with variable width (1.5–2.7 m) and is an upside-down, wide cone-shape with gentle convex-upper surface. It essentially consists of thrombolite core and several sets of paired growth layers stacked over the thrombolite. Each growth layer enlarged as they stacked upward, which eventually formed the upward widening bioherm morphology (Fig. 2). The growth layer pairs consist of *Epiphyton* growth layers and dolomitic growth layers (Fig. 2a, b) of which boundary is gradual. *Epiphyton* growth layers are about 20–30 cm in thickness and have laterally uniform thickness throughout the growth layer. The growth layer consists of *Epiphyton* framestone and is characterized by the inner and the outer divisions with relatively straight boundary (Fig. 2a). The division boundary in each growth layer is normal to the surface of the growth layer and steps inward in the overlying layer (Fig. 2a, b, c). The inner division of

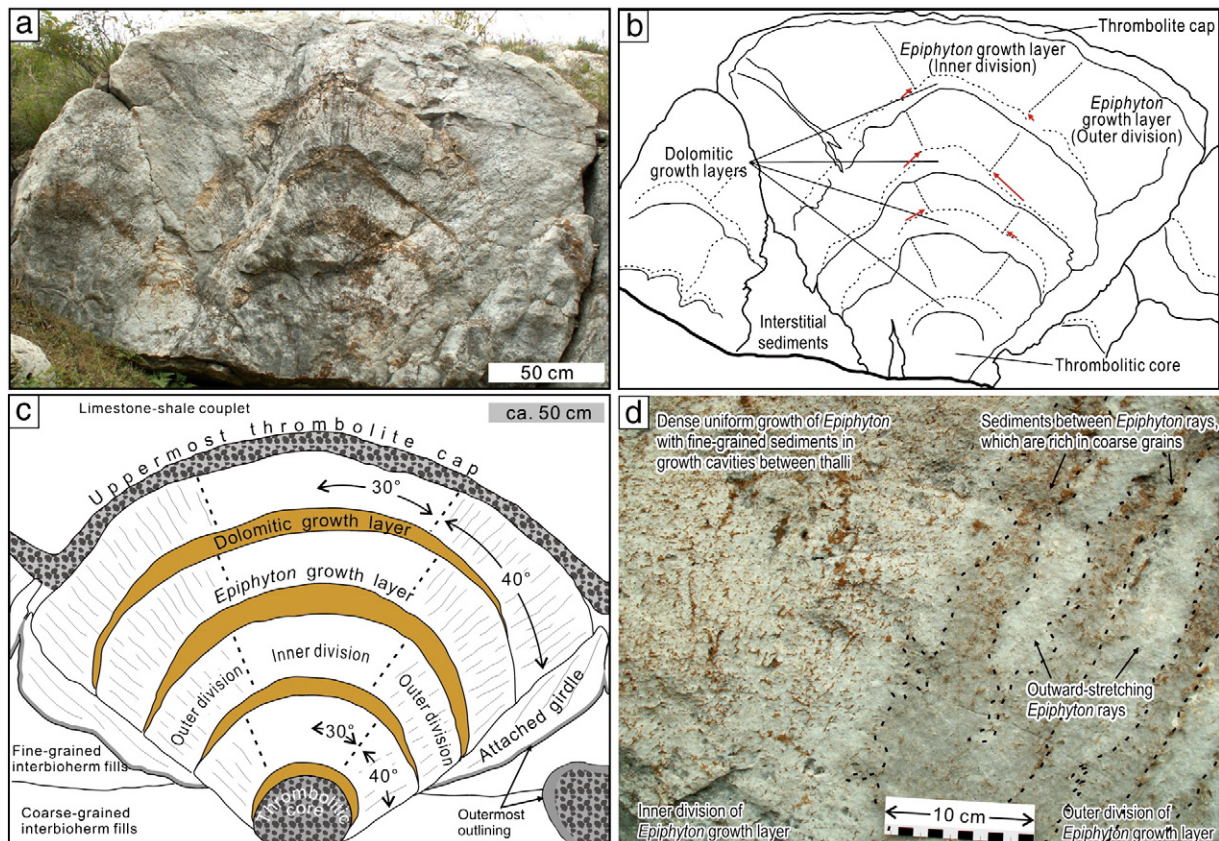


Fig. 2. *Epiphyton* bioherms in the studied section. (a) Outcrop photograph of *Epiphyton* bioherm of Jiulongshan section. Note well-developed *Epiphyton* growth layers and alternating dolomitic mudstone-rich layers. (b) Line drawing of a showing distinct growth layers and their divisions into the inner and outer divisions. Note upward, inward-stepping pattern of the boundary between the inner and outer divisions of the growth layer (red arrows). Hammer for scale is 27 cm long. (c) Schematic drawing summarizing structures of the *Epiphyton* bioherms. (d) Close-up of *Epiphyton* growth layer. Note clear difference in texture of the inner and the outer divisions with sharp boundary.

the *Epiphyton* growth layer is represented by dense uniform *Epiphyton* framestone with small-scale irregular cavities filled with dolomitic fine-grained sediments and calcite cements (Fig. 3a). The outer division of the *Epiphyton* growth layer shows layered texture with elongated and radiating *Epiphyton* framestone (Fig. 3b). The cavity between the *Epiphyton* rays is up to a few centimeters wide and filled with lime mud to skeletal wackestone. The extent of the inner division of the growth layer is about 30° from the vertex of the hemisphere and that of the outer division stretches about 40° from the boundary between the inner and outer divisions (Fig. 2a, b, c). The dolomitic growth layer is less than 10 cm in thickness and pinches out at the margin (Fig. 2). This layer consists of *Epiphyton* colonies, dolomudstone matrix, and coarse-crystalline dolomite. *Epiphyton* colonies are erect and sparsely distributed. Attached girdles are wedge-shaped or irregular bodies of sediment–microbe mixture on the lower side of the bioherm. It is characterized by diverse *Epiphyton* community and large amounts of skeletal grains. The girdle laterally covers several growth layers. The outermost margin of the bioherm is characterized by a thin encrusting layer of laminated micrites. The topmost surface of the bioherm is mantled by a thin thrombolite bed (Fig. 2a, b, c).

Four different types of *Epiphyton* (Woo et al., 2008) occur in the *Epiphyton* bioherm of the Zhangxia Formation (Fig. 4). Type-1 *Epiphyton* has erected dichotomous branches with Y-shaped or forked branching pattern (Fig. 4a). The filaments are uniform in thickness (about 75 μm) throughout the branch or slightly thick in the middle part of the branch. Type-2 *Epiphyton* has transverse segments in the branch (Fig. 4b). The *Epiphyton* with thin branches (40–50 μm) is classified as type-3 (Fig. 4c). Type-4 *Epiphyton* has tube-shaped branches (Fig. 4d). These *Epiphyton* morpho-types form various morphology of thalli: bush-shaped (upward branching and fanning), chambered, and elongated. A semi-quantitative analysis on the

distribution of major components of the bioherm (microbes, sediments, and cements) and the morphologic types (bush-shaped, elongated, and chambered) of *Epiphyton* thalli displays a systematic trend in the growth layer (Fig. 5b). Dense uniform bush-shaped thalli of type-1 *Epiphyton* are predominant in the inner division of the growth layer (Fig. 5b, c) whereas the elongated and chambered thalli are common in the outer division (Fig. 5b, d). Chambered and elongated thalli of type-2, -3, and -4 *Epiphyton* occur mostly in the outer division (Fig. 5d) with large colonies of elongated type-1 and -3 *Epiphyton* thalli (Fig. 5d). The amounts of calcite cement and coarse-grained sediments increase in the outer division of the growth layer (Fig. 5b).

4. Growth model

The growth layers are incremental units of the bioherm, of which morphology and texture deliver environmental conditions. The *Epiphyton* growth layer represents the period that *Epiphyton* flourished in clear and well-illuminated water. *Epiphyton* on the surface of the previous growth layer not only aggraded but also expanded radially as long as the intensity of sunlight was sufficient. According to an estimation of sunlight insolation on a hemispheric growth surface, the inner division of the growth layer received sunlight about 1.5 times stronger than that in the outer division (Fig. 6a). Enough sunlight on top of the growth layer helped *Epiphyton* grow densely with upward-growing bush-shaped gregarious thalli. In dimly lit outer division of the growth layer, in contrast, *Epiphyton* growth was limited by insufficient amounts of sunlight and the thalli preferentially elongated toward the sunlight, forming a layered radial structure (Fig. 5d).

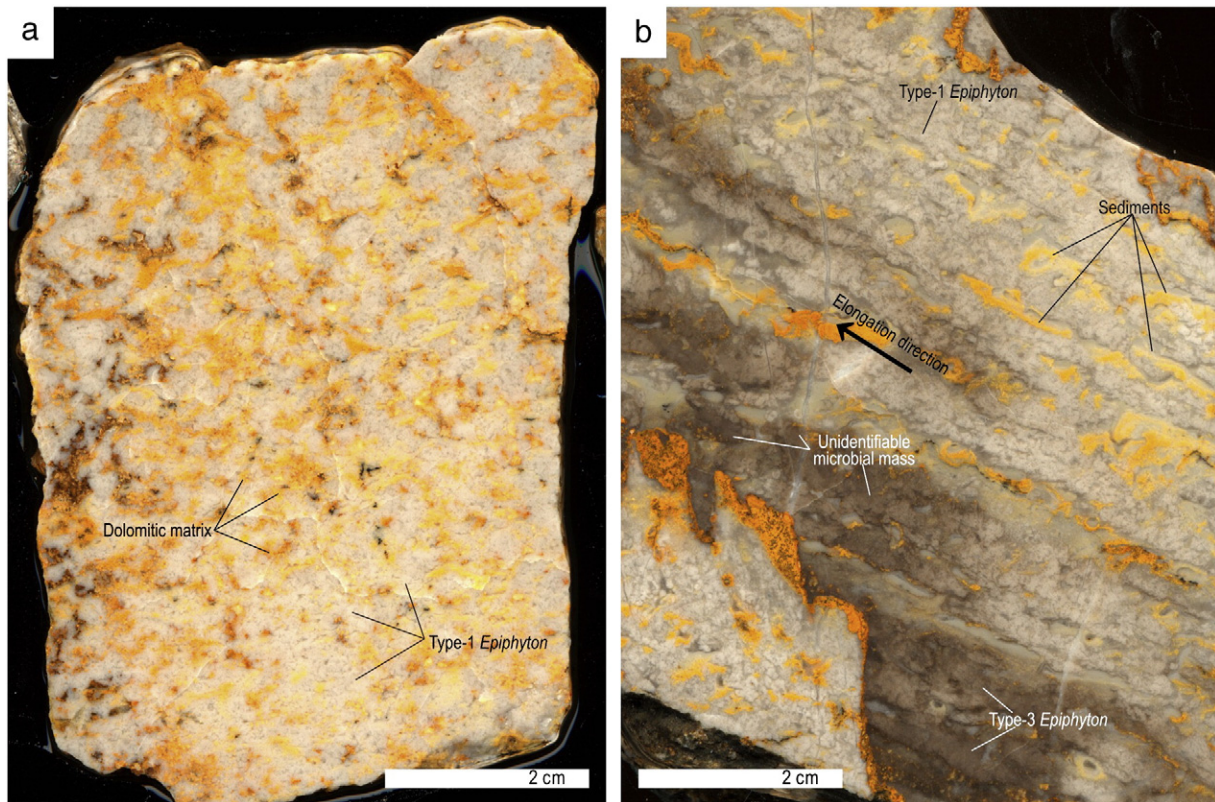


Fig. 3. Polished slabs of *Epiphyton* bioherm. (a) Inner division showing dense uniform growth texture. It is predominated by type-1 *Epiphyton*. (b) Outer division showing elongation toward upper left direction. The upper right half is dominated by type-1 *Epiphyton*, whereas the lower left half consists of association of type-1, type-3, and unidentifiable microbial carbonates. Note a jagged stylolitic boundary with a lot of brown dolomitic insoluble residue.

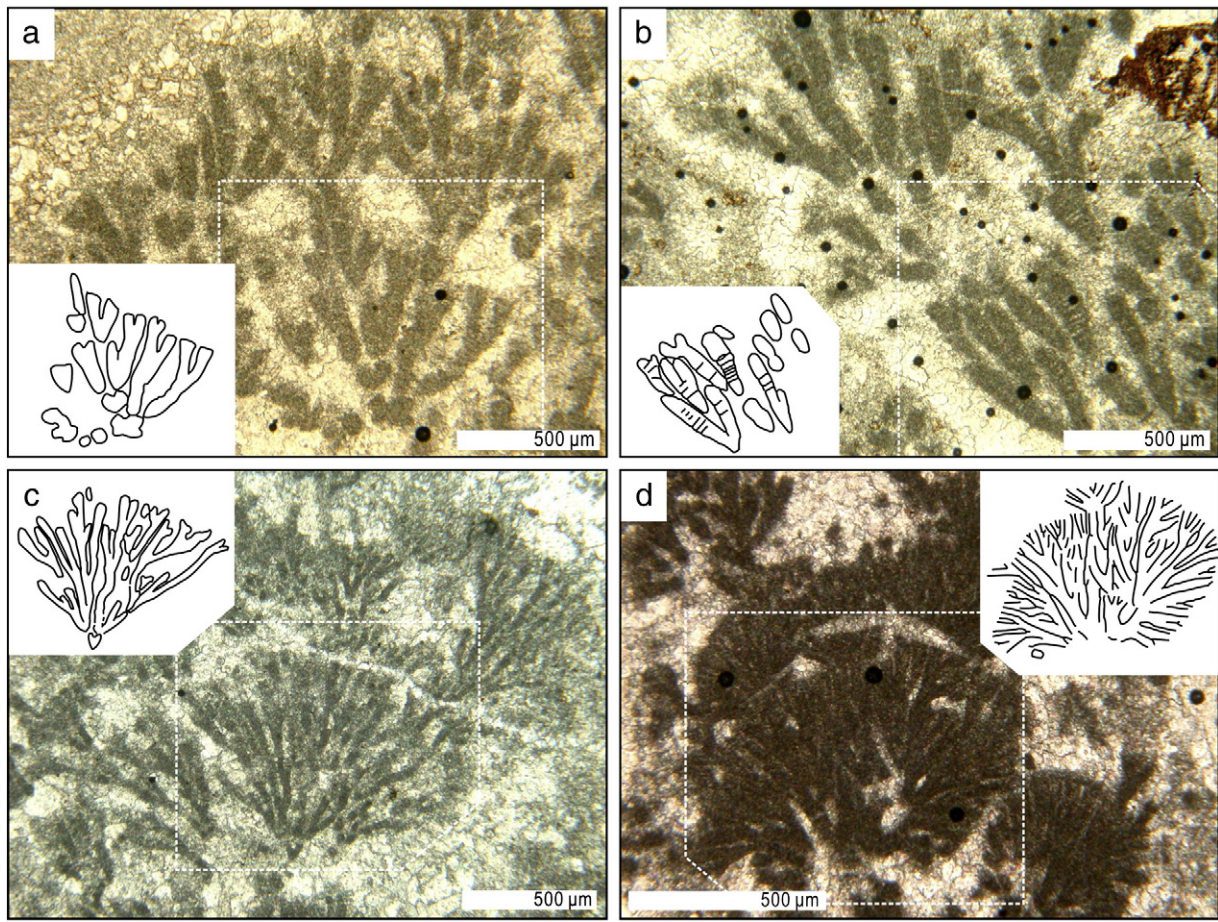


Fig. 4. Photomicrographs and line drawings of *Epiphyton* in the Zhangxia Formation. (a) Type-1 *Epiphyton* of bifurcating *Epiphyton* branches (diameter, 75–80 μm). (b) Type-2 *Epiphyton* showing transverse segments in branches (diameter, 75–80 μm). (c) Type-3 *Epiphyton* characterized by small branches (diameter, 40–50 μm) and large length-diameter ratio. (d) Type-4 *Epiphyton* of bush-shaped thalli with sharp outer margin. Note laterally arrayed hollow branches.

The different texture between the *Epiphyton* growth layers and dolomitic growth layers was controlled by temporal change in amount of sunlight, whereas the textural difference within a growth layer is due to spatial heterogeneity of illumination. The dolomudstone in the dolomitic growth layers represents deposition of calcareous mudstone during the period of high turbidity. Loose *Epiphyton* framework and tapering morphology of this growth layer are suggestive of meager growth of the *Epiphyton*, which was caused by turbid water and consequent decrease in light intensity. The intensity of light probably was too small and refractive to give rise to any meaningful difference in amounts of illumination on the growth surface, which would result in a clear distinction between the inner and outer divisions of the growth layer. The vertical aggradation, due to settling of sediment and growth of *Epiphyton* toward the direction of average insolation, was dominant in these growth layers. The vertical aggradation of the hemispheric growth surface resulted in the growth layer with tapering morphology (Fig. 6b).

The steep outermost part of the bioherm received meager amounts of sunlight, which resulted in absence of *Epiphyton*. The suppressed growth of the bioherm in the outermost and lowermost parts of the growth layer formed a fan-shaped outline of the bioherm (Fig. 6b). The lower surface of the fan-shaped bioherm, which sometimes form completely closed growth cavities, probably was inhabited by different microbes than *Epiphyton*. The different microbial communities and more frequently accreted sediment grains supplied by saltation from the seafloor resulted in attached girdles similar to those in modern Bahamian stromatolites (Dill, 1991). Abrupt sea-level rise resulted in the capping of the thrombolite over the *Epiphyton*

bioherm and, in turn, the bioherm was overlain by limestone and shale alternation.

5. Phototropism and speciation of calcified microbe

The distribution and morphology of photosynthetic calcified microbe, *Epiphyton*, might have been controlled by the variations of sunlight when other conditions were favorable. On the inclined sides of the bioherm, small amounts of sunlight led to phototropic elongation or phototaxis of *Epiphyton* thalli toward better illuminated outer part. This resulted in a radial layered growth pattern of the bioherm in the outer division. The narrow hollow space between layered colonies acted as a skylight parallel to the *Epiphyton* colony, which enabled each layer to get more sunlight than the dense uniform growth form would allow. An increase of surface area and an enhancement of water flowage between colonies, as byproducts, might have helped chemotrophic metabolism to compensate for an ineffective photosynthesis (Eiler, 2006; Yu et al., 2009). Morphological variation responding to sunlight intensity can be found from corals, but they display rather opposite relationship. Corals are known to have branching morphology in well-illuminated condition but domal morphology in poorly-illuminated condition (Porter, 1976; Chappell, 1980). This different reaction of corals to the amount of light is ascribed to the coexistence of two well-established energy producing processes. In poorly-illuminated condition, corals don't have to cope with inefficient photosynthesis, but heterotrophic energy production by uptake of zooplankton overwhelms their metabolism (Crabbe and Smith, 2006). In the case of *Epiphyton*, the

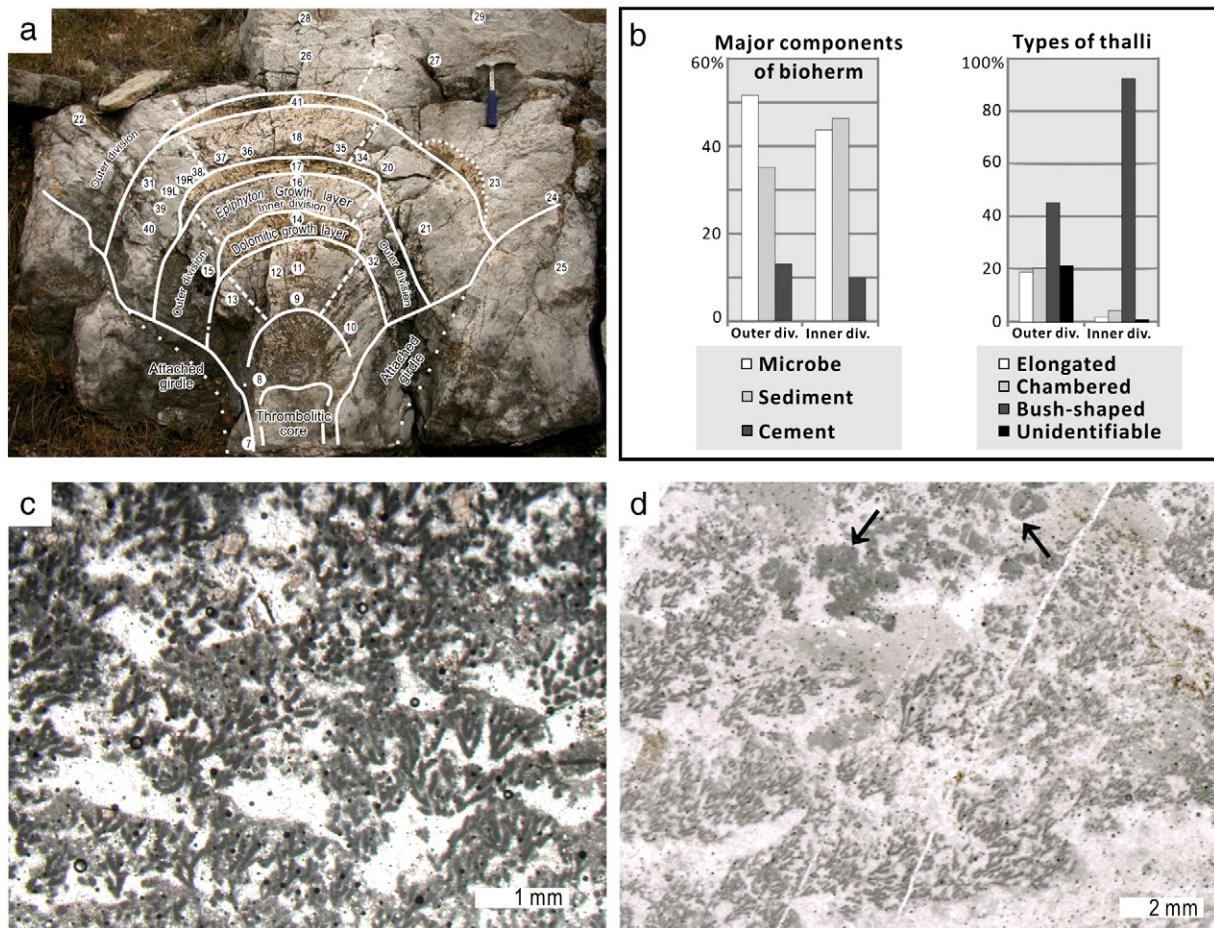


Fig. 5. (a) An *Epiphyton* bioherm with line drawing of its structures. The numbers denote location of samples for analyses of the microbialite components and thalli types. (b) Analyzed data based on macroscopic observation of slabs and microscopic observation of thin sections. (c) Photomicrograph of the inner division of the *Epiphyton* growth layer showing dense uniform colony of bush-shaped thalli. (d) Propagating colony of *Epiphyton* in the outer division of the *Epiphyton* growth layer. Note minor amounts of type-3 and -4 *Epiphyton* (arrows).

compensating roles of possible chemotrophy to phototrophy might be supplementary and *Epiphyton* colony still tried to have better morphology for photosynthesis in poorly-illuminated conditions.

This mixotrophy of *Epiphyton* may explain cryptic and pendant life mode of *Epiphyton* in platform margin settings (James, 1981; Read and Pfeil, 1983; James and Gravestock, 1990; Srinivasan and Walker, 1993; Pratt, 1995). They were attached to crust formed by *Girvanella* and grew downward to form tufts (James, 1981) or attached to wall or underside of the bioherm (Read and Pfeil, 1983). They were even found in deep cavities among *Girvanella* framework (James, 1981). Light conditions of these habitats probably were not favorable for photosynthesis. The absence of any phototropic growth pattern may suggest their reliance on non-photosynthetic energy producing mechanisms, e.g. chemotrophy as shown in modern microbial communities (Eiler, 2006; Yu et al., 2009).

The occurrence of type-2, -3, and -4 *Epiphyton* in the outer division of the growth layer is suggestive of adaptive ability of *Epiphyton*. The differential illumination on a growth surface might have caused different reaction of *Epiphyton*. Growth rate of branches, branching frequency, thickness of sheath, and so on could vary. Occurrence of type-2, -3, and -4 *Epiphyton* in the outer division may suggest these reactions, combined with differential preservational modes. Furthermore long lasting difference of illuminating condition might have led to origination of new species (speciation) of *Epiphyton* with different light preference. Such speciation of cyanobacteria is known in various extreme environments (e.g., hypersaline lakes, hot springs or hydrothermal vents) (Cohan, 2001; Ferris et al., 2003). The speciation

by isolation in ecologically favorable conditions is also reported in tropical normal marine lagoonal environment (Abed et al., 2003) which is similar to the depositional settings of the *Epiphyton* bioherm of the Zhangxia Formation.

6. Conclusion

The *Epiphyton* bioherms of the Zhangxia Formation were formed by progressive accretion of the *Epiphyton* and dolomitic growth layers. The *Epiphyton* growth layers are characterized by distinct inner and outer divisions which are characterized by dense uniform and layered texture, respectively. Calculation of the amounts of sunlight illumination on the curved growth surface suggests that the outer division with steeper surface receives about two third of sunlight relative to the inner division. The scant sunlight in the outer division evoked phototropic behavior of photosynthetic *Epiphyton*, represented by elongated morphology of colony. Sufficient amount of light in the inner division of the growth layer led to the vigorous growth of *Epiphyton* and the formation of dense and well-connected uniform texture. Insufficient amount of light led the outermost division of the bioherm to an unfavorable place for microbial growth. Alternation of vertical growth and radial expansion of growth layers with divisions resulted in upward widening bioherms with characteristic internal structures suggesting influences of different illumination. The unique growth patterns and communities of *Epiphyton* in different positions of the bioherm show direct control of sunlight on the distribution and

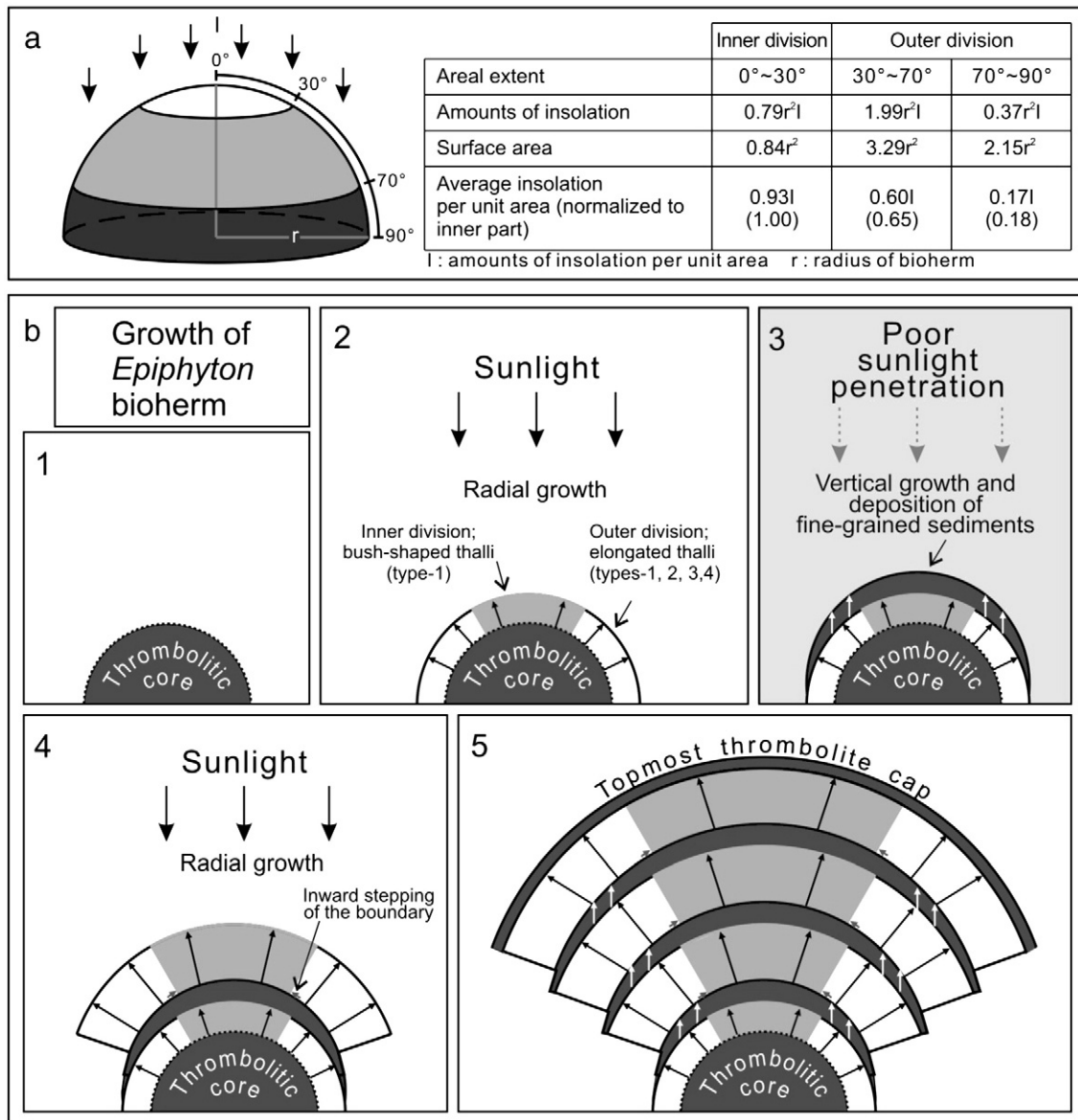


Fig. 6. Model for controls of illumination angle on *Epiphyton* bioherm growth. (a) A schematic diagram for an estimation of average insolation per unit area. (b) A growth model of *Epiphyton* bioherm in the Zhangxia Formation. (1) Formation of the thrombolytic core on the seafloor. (2) The first *Epiphyton* growth layer forms radially on the thrombolytic core in clear water. Type-1 (bush-shaped thalli) in the inner division. Propagating type-2, -3 and -4 in the outer division. (3) Vertical growth in turbid water and deposition of fine-grained sediments (dolomitic growth layer). (4) Radial expansion in clear water forming the second *Epiphyton* growth layer. (5) The resultant bioherm comprises 4 *Epiphyton* growth layers interlayered with 3 dolomitic growth layers. The bioherm is capped by a thrombolite layer.

morphology of the probable photosynthetic microbial colonies and suggest further speciation of simple-formed calcified microbes.

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