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# Stromatolite

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## Introduction

If you visit Shark Bay of Australia, located on the western coast of Australia, you will see several thousands of centimeter- to meter-scale dome-shaped structures (Fig. 1). These are stromatolites, layered sedimentary rocks formed by microbial organisms. Stromatolites are considered to be among the oldest forms of life on Earth. The oldest stromatolites are found in Australia, which are about 3.5 billion years old. Since then, stromatolites are found throughout most of the geological record, but mainly during the Precambrian, before complex life forms flourished on the planet. The Shark Bay stromatolites, now protected as an UNESCO World Heritage Site, are therefore truly “living fossils” that show what the Earth would have been like several billion years ago.

The most important organisms responsible for stromatolite formation could be cyanobacteria, which are prokaryotes lacking the nucleus and other membrane-bound organelles. They are the only photosynthetic prokaryotes that can produce oxygen; in other words, they were the first organism on Earth that invented a method to use sunlight to produce energy and released oxygen as a by-product. Cyanobacteria have many different forms—unicellular, filamentous colonies, sheets, etc. Among them, those forming filamentous colonies are the ones mainly responsible for stromatolite formation. Cyanobacterial filaments trap and bind detrital sediments, or precipitate minerals and form stromatolite layers. Considering the size of cyanobacterial filaments—a few tens of  $\mu\text{m}$  in diameter—stromatolites are huge; each stromatolite column may be a few centimeters to meters wide, and some stacked stromatolite reefs are over



**Fig. 1** Recent stromatolites from Shark Bay, Australia.

tens of meters to hundreds of meters high. The relationship between stromatolites and cyanobacteria therefore can be compared with those of forests and trees.

The term stromatolite was coined by the German geologist Ernst Kalkowsky in 1908, based on Triassic lacustrine stromatolites in Central Germany. However, stromatolites had already been described in 1825, from upper Cambrian successions of New York State, United States (**Fig. 2**). Stromatolite research has therefore lasted for almost 200 years, and it is still ongoing. Google Ngram Viewer (<http://books.google.com/ngrams>) shows a trend that stromatolite research initiated in 1970s, in the middle of the Cold War, and continues to be important to the scientific community (**Fig. 3**).



**Fig. 2** Cryptozoön, the first reported and formally named stromatolite. It occurs along a glaciated surface, showing cabbage-head like structures. Coin (24 mm) for scale. Upper Cambrian Hoyt Limestone, Petrified Gardens, Saratoga Springs, New York State, United States.

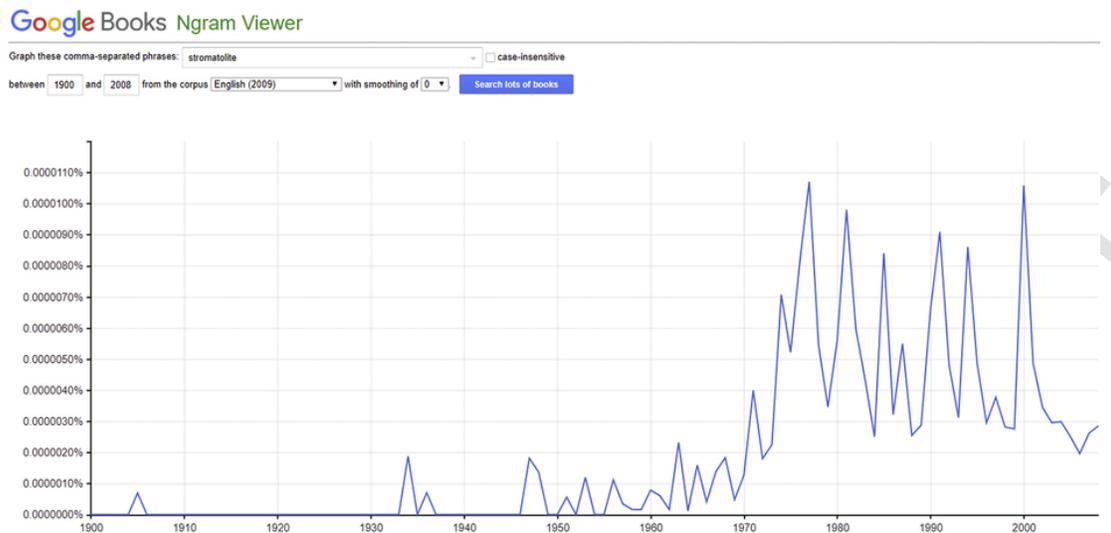


Fig. 3 Google Ngram trend for “stromatolite.” Acquired from <https://books.google.com/ngrams/>.

## Definition

### What Is a Stromatolite?

The term “stromatolite” came from a combination of two Greek words: στρώμα (strōma), meaning “layer” and λίθος (lithos), meaning “rock”. As one can infer from its etymology, a stromatolite is typically a layered, mostly with convex-up layers, sedimentary rock formed by microbial organisms. However, there are many other sedimentary rocks with convex-up layered structures. Some animals (e.g., sponges, stromatoporoids, bryozoans) as well as algae, form thin layers and produce structures similar to that of stromatolite. They may form reefs by themselves or together with microbial layers, thereby confusing the definition of stromatolites. If we go to an earlier part of geologic history, such as the Archean and Proterozoic, it becomes more complicated. In these ancient stromatolites, abiogenic sparry crusts are common components of stromatolites. Some stromatolites are formed by alternation of these sparry crusts and biogenic layers. Thus, what is a stromatolite, and how can we define it?

### Problems With Stromatolite Definition

There is no universally accepted definition of stromatolite. When Kalkowsky first introduced the term stromatolite, he believed that microbial organisms were responsible for the formation of stromatolites. Other early stromatolite workers (although the name “stromatolite” was not used at that time!) thought stromatolites are remains of simple animals, large foraminifers, sponges, or protozoans, or even nonorganic calcareous concretions. Stromatolites in modern oceans—for example, those at Shark Bay—are evidently formed by microbes, so there is no problem to define the Shark Bay stromatolites as “sedimentary deposits formed by microbes.”

The most widely accepted definition of stromatolite is a benthic layered microbial deposit, not only to scientific communities but also to the public, as in high school textbooks. However, how can we say for sure that certain layered structures in sedimentary rocks are made by microbes, if there is no evidence of microbes? In fact, some Precambrian “stromatolites” have later proved to be abiogenic calcite precipitates with convex-up laminae. The earliest reported Precambrian stromatolite-resembling “fossil”, *Eozoön*, described in 1865, later turned out to be a metamorphic alternation of crystalline calcite and serpentine. Some natural structures in modern environments—e.g., limestone stalagmites that formed on cave floors by abiogenic precipitation of calcium carbonate—superficially resemble stromatolites, but do not require microbial activity in their formation. On the other hand, some microbially formed mounds do not contain layers within them, but rather contain a macroscopically “clotted” or massive texture. Are these structures “stromatolites,” or something else?

### Definition of Stromatolite

Until now, three major definitions of stromatolites have been proposed: (1) microbial and laminated, (2) microbial but not necessarily laminated, and (3) laminated but not necessarily microbial. The first definition is perhaps the most widely accepted one. It fits with Kalkowsky’s original proposal—microbially formed benthic structure. But, this definition requires that formative processes must be studied in detail to prove a microbial origin, and it is not an easy question to answer as we go back into the geologic past (see “[How to Identify Stromatolite](#)” section).

The second definition includes everything that is microbial in origin. This is a definition that is not widely used nowadays, because (1) the word “stroma” indicates “layered structure”, and (2) we now have other terms such as “microbialite” to refer to nonlayered microbial structures (see next section).

The third definition—everything that is laminated—separates observation and interpretation, and is easy to apply in the geologic past, when it is not easy to determine the origin of a “stromatolite.” However, we do need terms to encompass origins of sedimentary rocks. For example, sedimentologists use terms such as “tempestite” or “seismitite” to infer rocks formed by storm activities or sedimentary structures produced by earthquakes. Also, we know that some well-laminated skeletal reefs—for example, those formed by the alternation of coralline algae and foraminifers—superficially resemble columnar stromatolites. Do we need to call these algal-foraminiferous reefs “stromatolites”?

In this text, I will use the most widely used definition of stromatolite: “laminated benthic microbial deposits.” However, it is also true that not all benthic microbial deposits formed a laminated structure. How should we refer to these nonlaminated benthic microbial deposits?

### **“Microbialite” to encompass all types of benthic microbial deposits**

The term “microbialite” was introduced in 1987 to include all types of benthic microbial deposits. According to this definition, a stromatolite is a specific kind of microbialite with layered structure. This definition excludes all abiogenic layered structures, and is essentially the same as the second definition of stromatolite—microbial but not necessarily laminated. Readers may refer to the glossary at the end of this article and the section **“Other Types of Microbial Deposits”** for other definitions.

Other terms, for example, microbial carbonate, have been proposed to substitute for the term microbialite. The term microbial carbonate has been used in the geologic community to encompass all kinds of microbially induced carbonate sediments, not only stromatolites but also other nonbenthic structures such as oncoids. This definition, however, cannot include rarely-occurring siliciclastic or phosphatic stromatolites, and cannot be treated as a synonym of microbialite.

### **How to Identify a Stromatolite**

How can you identify a stromatolite? The simple answer is to look at its cross-section. If you look at cross-sections of stromatolites, you will easily recognize convex-upward laminae. It is not easy to generate such structures by physical sedimentological processes, thereby evincing a biological origin of stromatolites. In some cases, however, chemical precipitation of minerals from water can form convex-upward laminae similar to stromatolites. Stalagmites in limestone caves can be a good example. Structurally folded strata may also produce similar, convex-upward structures.

It is thus important to correctly describe stromatolites to identify whether they are true stromatolites formed by microbes or pseudo-stromatolites formed by abiotic processes. There are eight criteria to identify the biogenicity of stromatolites, which are:

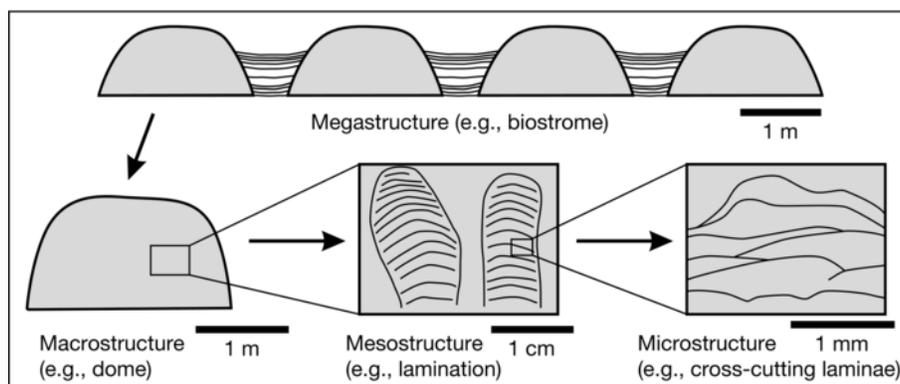
1. The structures must occur in sedimentary (or metasedimentary) rocks.
2. The structures must have formed together with the deposition of surrounding sediments.
3. Convex-upward layers should occur dominantly within the structures.
4. Laminae are thicker over crests and thinner over troughs.
5. Laminae are not flat, but rather wavy or wrinkled.
6. Microfossils may be present within the structures.
7. Microfossil assemblages change together with stromatolite morphologies.
8. Microfossils would show evidence of trapping/binding of detrital sediments or organically induced precipitation.

Unfortunately, only a few stromatolites meet all these criteria. This is partly because of nature of the geologic record; as we go into past, less amount of information is preserved within rocks. In fact, only a few stromatolites preserve microfossils within them, and they are often found in the relatively later part of geologic history (Neoproterozoic to Phanerozoic). In many cases, we need to rely on criteria 1–5 to test the biogenicity of stromatolites, and determining biogenicity is often problematic, especially in metasedimentary rocks and/or Precambrian strata.

### **How to Describe and Classify Stromatolites**

Shapes of stromatolites have a wide variety, including domes, columns, branched columns, cones, and wavy lamination. There is also great size variation. Some stromatolites are huge, forming reefs of several tens of meters to hundreds of meters thick, and some are tiny, and can only be identified under microscope. We often use four scales of description—mega-, macro-, meso-, and microscale structures—to describe stromatolites (**Fig. 4**).

1. **Megastructure:** Bed-scale structures. Biostrome (stromatolites forming bed) or bioherm (separated mounds) are examples of megascale structures.
2. **Macrostructure:** Outline of each stromatolite. Varieties of macrostructures exist, including straight to branching columns, domes (or mounds), and crusts. Macrostructures are usually decimeter to several tens of meters in size.
3. **Mesostructure (or macrofabric):** Hand specimen-scale structures, such as laminations. These are the basic building units of stromatolites. Mesostructures of stromatolites can be regarded as textures or sedimentary structures of sedimentary rocks.
4. **Microstructure (or microfabric):** The structures that are too small to be observed by the naked eye. Microstructures often represent organisms/processes that form stromatolites.



**Fig. 4** Four scales of stromatolite description: mega-, macro-, meso- and microscales.

There are two major ways to classify stromatolites. The first is regarding each stromatolite as a separate fossil, and giving them a binominal Linnaean name, Latinized and italicized, following the International Code of Botanical Nomenclature (ICBN). This method has been used by the scientific community since the first discovery of stromatolites. The earliest formally named stromatolite is *Cryptozoön* Hall, 1883, from New York State, United States, which is also the first reported stromatolite (Fig. 2). Since then, more than 1000 stromatolite “taxa” have been formally described.

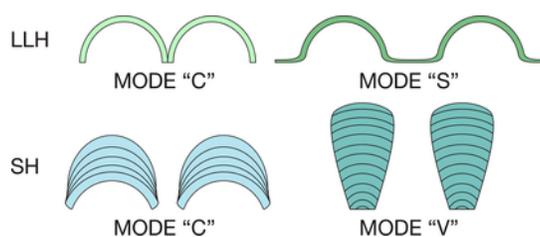
This method regards stromatolites as similar to other fossils, showing temporally restricted occurrences. Scientists even use stromatolites to “biostratigraphically” correlate strata in different localities. It is true that at least some stromatolites show a temporally restricted occurrence, like other biostratigraphically important fossils, but their resolution is not as good as other index fossils. This is because changes in stromatolite morphology are likely caused by several different mechanisms, not only restricted to the evolution of stromatolite-forming organisms but also to environmental conditions that are unique to certain geologic intervals (see “**Are stromatolites “fossils”?**” section below for more detailed discussion).

The second method is to classify them based on their geometric forms (Fig. 5). This method regards stromatolites as sedimentary structures affected by environmental changes, rather than as “fossils.” Three main types of arrangement appear to exist in recent stromatolites. These are laterally linked hemispheroids (LLH), discrete, vertically stacked hemispheroids (SH), and spheroidal structures (SS). Suffixes are added to detail these structures. In LLH-types, hemispheroids are either closely linked or space-linked, abbreviated as LLH-C and LLH-S types respectively. SH-types, the domal/columnar structures, are vertically stacked with a constant (SH-C) or variable (SH-V) basal radius. Type SS refers to oncoids, small mobile substrates coated by microbial mats. Single stromatolites may consist of several different types of structures. For example, SH-V type stromatolites may grow upward, expand laterally and merge together, resulting in a LLH-C type (Fig. 5).

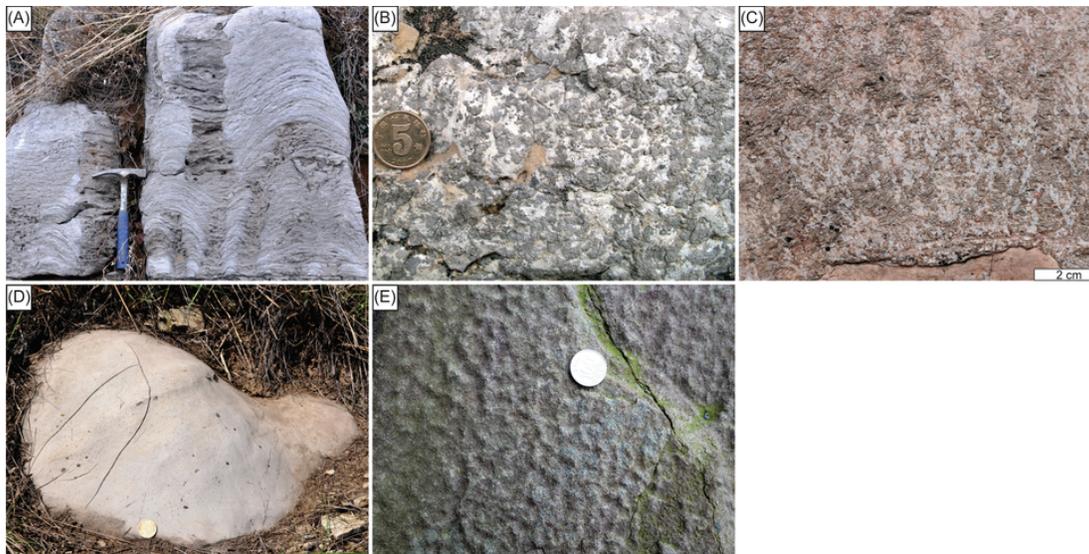
So, how would you classify a stromatolite? You may choose a method that you prefer, giving them a Linnaean name or describe them based on abbreviated types. However, in reality, it is not easy to fit a specific example of a stromatolite into these classification methods. As far as my knowledge goes, not even a single microbialite was newly named with binominal nomenclature system during the last 10 years. Also, many stromatolites show diverse morphologies that cannot be fitted into a geometric form classification. Probably the best way is to describe each stromatolite in detail, according to four different scales of observation.

### Other Types of Microbial Deposits

Although stromatolites are the most common and widely known type of microbial deposits (Fig. 6A), there are other types of microbial deposits as described earlier. This section summarizes other important types of microbial deposits: thrombolite, dendrolite, leiolite, oncoid, and microbially induced sedimentary structures (MISS).



**Fig. 5** Stromatolite classification method based on their geometric forms. Modified after Logan, et al. (1964). *The Journal of Geology* 72, 68–83.



**Fig. 6** (A) Stromatolite, (B) thrombolite, (C) dendrolite, (D) leiolite, and (E) MISS. (A–D) from mid-upper Cambrian (c. 509–490 Ma) of Shandong, China. (E) from Cretaceous (c. 120 Ma) nonmarine Gyeongsang Basin, Korea. Hammer in (A) is 27 cm. Coins for scale in (B) and (D) are 20.5 mm. Coin for scale in (E) is 24 mm.

### **Thrombolite**

Nonlayered microbial deposits, although mega- and macroscopically similar to stromatolites, have been known to the geological community since the mid-20th century. Thrombolite, from the Greek word θρόμβος (thrombus) meaning clot, was first introduced to the geological community in 1960, to refer to “clotted” or nonlaminated microbial deposits. These structures consist of a mesoscopically clotted texture, characterized by centimeter-scale microbial clots within the large domal/columnar macrostructures (Fig. 6B). Absence of any macroscopic reef-builders within thrombolites suggests microbes are the main organisms responsible for the formation of thrombolites. Thrombolites first appeared in the Neoproterozoic (though there is a possible 1.9 Ga old thrombolite) and occurred throughout the Phanerozoic. They are most commonly found in Cambro-Ordovician strata.

### **Dendrolite**

Dendrolite, from the Greek δένδρον (dendron) meaning “tree,” refers to a specific type of thrombolite with bush-like branching clots (Fig. 6C). These bush-like dendritic structures are similar to those of photosynthetic organisms. The delicate dendritic structures are thought to be indicative of evidence of microbial calcification, rather than trapping and binding. Many dendrolites are formed by calcified microbes of the *Epiphyton*, *Renalcis*, and *Angusticellularia* groups, and show temporally restricted occurrences from Cambrian–Early Ordovician and Late Devonian.

### **Leiolite**

Leiolites (from Greek λείος (leios), meaning smooth) have “aphanitic” or structureless mesostructures; they lack clear lamination or clots (Fig. 6D). They may be described as a massive or homogeneous structure, but they clearly have domal or columnar macrostructures that evince their biological origin. Some weakly laminated stromatolites may be classified as leiolites.

### **Oncoid**

These gravel- to cobble-sized rounded structures are mainly formed by microbes that encrust a nucleus, often on shell fragments, and are similar to stromatolites. However, oncoids are technically not “stromatolites,” because they are not autochthonous but mobile. Unlike ooids, laminations surrounding oncoid nuclei are often not continuous and are often irregular. Oncoids are often considered to be indicative of a shallow marine or lacustrine environment. When these grains are larger than 10 mm, they are called macroids. Some other organisms such as calcareous red algae form structures similar to oncoids. In this case, these are referred to as rhodoids.

### **Microbially induced sedimentary structures (MISS)**

Microbially induced sedimentary structures, or MISS, are sedimentary structures produced by symsedimentary deformation of unlithified flexible cohesive sediment-binding mats. Microbial mats bind, biostabilize, baffle, and trap sediments, resulting in characteristic structures that cannot be formed by pure physical/chemical processes (Fig. 6E). MISS do not form relief above the seafloor, which is the most important difference between MISS and stromatolites. Unlike stromatolites, MISS mostly form on siliciclastic substrates and do not involve microbial calcification processes. Readers may refer to the “MISS” chapter in this volume.

## Formative Processes

Microbes form stromatolites via two major processes: trapping and binding of detrital sediments by microbial filaments and mineral precipitation. Both processes are greatly affected by EPS—extracellular polymeric substances—that surround microbial filaments and cells. Various microbes, e.g., bacteria, cyanobacteria, and diatoms, all produce EPS to attach to the substrate, protect themselves, and absorb nutrients, etc. In addition, abiotic precipitation of carbonate minerals is important in stromatolites.

When microbes grow together, they can form submillimetric layers embedded within EPS matrix, forming biofilms. As biofilms grow large and form multilayered sheets, they will form microbial mats a few millimeters to centimeters thick. The upper surfaces of living stromatolites are covered with microbial mats, and it would have been similar in ancient stromatolites, though the composition of microbial mats would have changed throughout Earth history.

### Trapping and Binding

When sedimentary grains settle on a microbial mat, they may be trapped by the adhesive mat and/or by baffling of the rough surface structure. As microbes grow over and bind the trapped grains, grains will be permanently incorporated into microbial mats. Trapped and bound grains within stromatolites therefore reflect the composition of surrounding sediments. The trapping and binding processes result in an agglutinated fabric, either fine or coarse grained.

Coarse-agglutinated stromatolites, similar to some modern Shark Bay and Bahamian stromatolites, trap and bind coarse sediments such as ooids. They are not common in geologic history, and only a few examples are known since the early Mesozoic. It has been postulated that the evolution of diatoms and their incorporation into microbial mats during the past few hundred million years was the main cause of such phenomena, because abundant diatoms could have effectively trapped and bound coarse sediments.

Fine-agglutinated stromatolites mainly occur within surrounding micritic sediments. Four major criteria—(1) low synoptic relief, (2) laminae with cross-cutting relationships and abrupt lateral changes in thickness, (3) branched columns with vertical thickness changes showing lateral migration, and (4) textural similarity between the stromatolite and surrounding matrix—are thought to be indicative of the trapping and binding of fine-grained sediments by stromatolites (Fig. 7). Although not studied in detail, it is possible that many Precambrian fine-grained stromatolites formed by trapping and binding processes (Fig. 8).

### Biotic Mineral Precipitation

Carbonate precipitation in microbial mats mostly occurs within EPS. Recently, intracellular precipitation of the carbonate mineral bensonite ( $\text{Ba}_6\text{Ca}_6\text{Mg}(\text{CO}_3)_{13}$ ) in a unicellular freshwater cyanobacterium was reported, but it is still a rare case. Microbes actively influence carbonate precipitation via biologically-induced (bio-induced) precipitation. Cyanobacteria can actively import bicarbonate ( $\text{HCO}_3^-$ ) into their cells through  $\text{CO}_2$  concentrating mechanisms (CCM), and convert it into  $\text{CO}_2$  for photosynthesis. This active bicarbonate uptake increases pH near the cells and in the EPS. If saturation for  $\text{CaCO}_3$  minerals is high enough, crystals can nucleate on or in the EPS (Fig. 9).

Precipitated stromatolites can show layers of even thickness that are parallel to one another, unlike agglutinated stromatolites (Fig. 7). Some stromatolites formed in hypersaline lakes show such a fabric (Fig. 10). Also, stromatolites with clotted and peloidal microstructures are thought to have originated by microbial precipitation, e.g., by sulfate reduction, that calcifies EPS. Calcified microbial fossils can also form when sheaths of cyanobacteria become calcified, resulting in calcified microbes and thrombolites.

It is necessary to clearly distinguish bio-induced and bio-controlled calcification processes when we describe microbial calcification. Many calcifying animals—such as clams or corals—generate carbonate minerals within their body, according to regulated “bio-controlled” calcification processes. These animals can override seawater chemistry, and always form the same minerals. On the other hand, minerals formed by microbial calcification appear to vary according to seawater chemistry, because microbial organisms often do not produce minerals within their body, but rather “induce” precipitation around their cells.

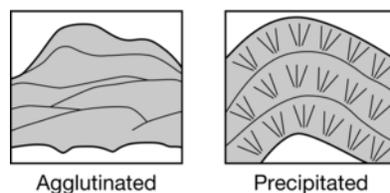
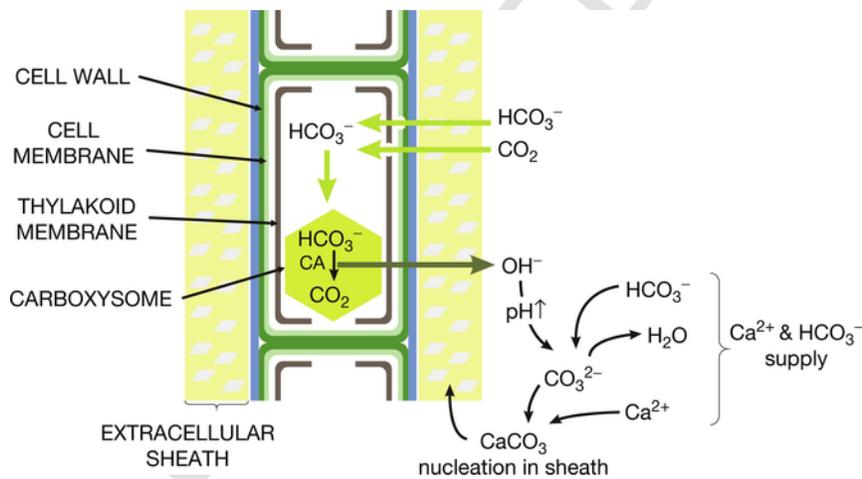


Fig. 7 A schematic model of the microstructures of agglutinated vs. precipitated stromatolites.



**Fig. 8** Fine-grained agglutinated stromatolite. Mesoproterozoic (c. 1420 Ma) Tieling Formation, Jixian, northeastern China.

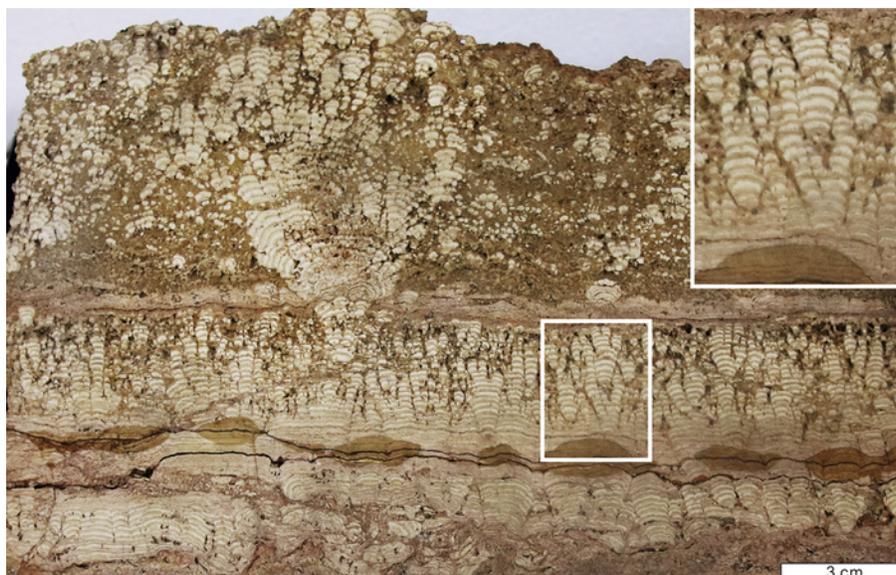


**Fig. 9** Model of extracellular sheath calcification of filamentous cyanobacteria. Modified after Riding (2006). *Geobiology* 4, 299–316.

### Abiotic Precipitation

Fibrous calcite crusts that directly precipitated on the sea floor are common in Archean carbonates, suggesting supersaturation of calcium carbonate in seawater during the Archean, and early in the Proterozoic. Some of these precipitates superficially resemble stromatolites, and have sometimes been described as “stromatolites.” These “abiotic precipitates” include botryoidal/radial fans, microdigitate “stromatolites,” isopachous cements/laminites, herring bone calcites, and dendrites. Some of these partly resemble recent speleothems and hot spring travertines precipitated from calcium carbonate supersaturated water.

Such abiotic crusts would have precipitated not only on the sea floor, but also on stromatolites. In these “hybrid” stromatolites, thin sparry crusts alternate with fine-grained microbial layers. Such hybrid stromatolites are common during the Archean and Proterozoic, but declined during the latter part of the Proterozoic (see “**Geologic History of Stromatolites**” section).

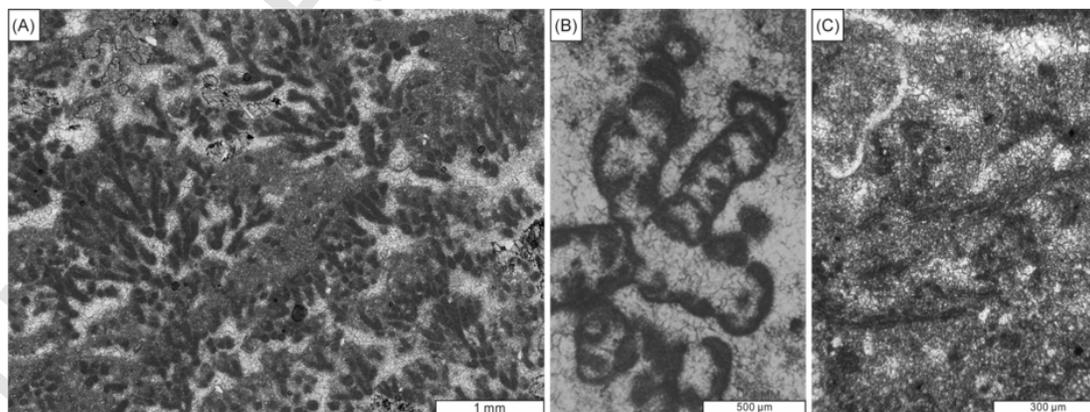


**Fig. 10** Lacustrine stromatolite from late Miocene–Pliocene (~6–4 Ma) Furnace Creek Formation, Death Valley National Park, California, United States. This stromatolite consists of isopachous laminae superficially resembling Proterozoic microdigitate stromatolites, suggesting dominant abiotic precipitation processes. Courtesy of K.S. Woo and J. Hong.

### Calcified Microbes

Some microbialites preserve calcified microfossils (calcified microbes or calcimicrobes) within them, evincing their biological origin. Some of these calcified microbes resulted from sheath calcification through CCM (see “**Biotic Mineral Precipitation**” section above). Three major morphological groups of calcified microbes are recognized, including tubes (*Girvanella*-type), dendritic shrubs and filaments (*Angusticellularia*- and *Epiphyton*-type), and hollow chambers (*Renalcis*) (**Fig. 11**). These fossils are described in terms of Linnaean binominal nomenclature, because these are considered to be remains of single organisms (or colonies of the same organisms).

However, it is not easy to put these calcified microbes into a tree of life. Some of them are superficially similar to modern calcified cyanobacteria, e.g., hollow filaments (*Girvanella*) resemble calcified sheaths of cyanobacteria (e.g., *Plectonema*), but also red algae or freshwater green algae. On the other hand, some calcified microbes—e.g., dendritic *Epiphyton* and chambered *Renalcis*—are interpreted as different stages of life, based on the occurrence of intermediate forms. Taphonomic/diagenetic influences could also have affected the shapes of these microfossils. It is not even clear whether a single group of organisms is responsible for the formation of a single type of



**Fig. 11** Three major types of calcified microbes. (A) Epiphyton, mid-Cambrian (c. 509 Ma) Zhangxia Formation, Shandong, China. (B) Renalcis, early Cambrian (c. 515 Ma), MacKenzie Mountains, northwestern Canada. (C) Girvanella, late Cambrian (c. 490 Ma) Chaomidian Formation, Shandong, China. (B) Courtesy of A.Y. Zhuravlev.

calcified microbes; they may reflect specific environmental conditions. It is best to classify them as Microproblematica at this moment. Further detailed studies, such as biomarker analysis, may reveal phylogenetic relationships between these enigmatic fossils.

## Geologic History of Stromatolites

### Archean–Proterozoic

The oldest stromatolite reported is from the c. 3.7 Ga old Isua Greenstone Belt of southwestern Greenland, discovered in 2016. However, since this example occurs in “greenstone belt” rocks—comprising metamorphosed volcanics as well as sedimentary rocks—it may be a product of metamorphism. Questions about the biogenicity of very ancient stromatolites have continued throughout the past several decades. Most geologists now agree that organisms would have existed on Earth since at least c. 3.5 Ga, including stromatolites. Stromatolites are the earliest macroscopic evidence of life on Earth.

Stromatolite-forming cyanobacteria produced oxygen in the Archean–Proterozoic ocean. During the Archean, oxygen was often removed from seawater by reaction with dissolved iron or organic matter. Around 2.5 Ga, at the beginning of the Proterozoic, seawater became more oxygenated as all chemically active materials became oxidized and oxygen started to accumulate in the atmosphere. This event is called the “Great Oxidation Event.”

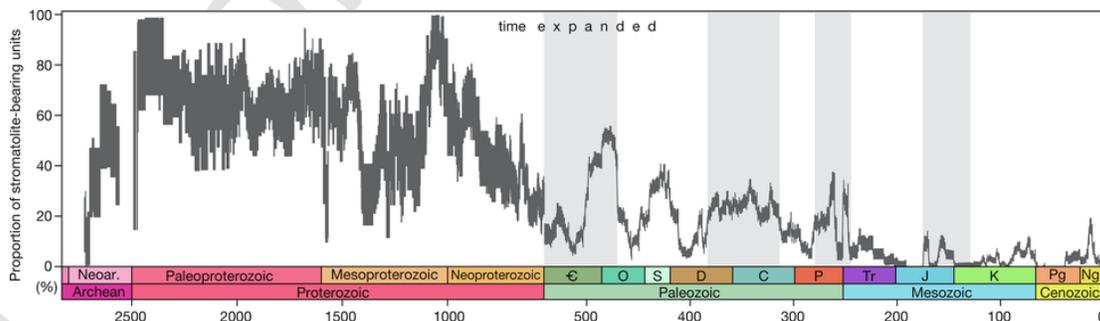
Due to the oxygen release, anaerobic organisms that inhabited the Earth became near-extinct, because oxygen is toxic to them. Only those adapted to oxygen could have survived this “catastrophe,” and anaerobic bacteria only survived in local anoxic environments. In addition, because of the oxygen release into the atmosphere, atmospheric methane combined with the oxygen and formed carbon dioxide and water. Since methane is a greenhouse gas about 30 times stronger than carbon dioxide, the Earth’s surface cooled, resulting in the Huronian glaciation (c. 2.4–2.1 Ga), the oldest and longest ice age on the Earth.

Stromatolites flourished throughout the Pale- and Mesoproterozoic (**Fig. 12**). Archean-Proterozoic stromatolites are often characterized by alternations of biogenic micritic layer and abiogenic sparry crust, forming “hybrid stromatolites.” The formation of Archean and Proterozoic stromatolites was mainly controlled by the seawater carbonate saturation state, because not only abiogenic precipitation, but also the bio-induced calcifying nature of microbes are strongly influenced by seawater chemistry.

### Neoproterozoic Decline of Stromatolites

Stromatolites declined during the Neoproterozoic (c. 1.0 Ga–541 Ma) (**Fig. 12**). This includes not only diversity, but also their abundance (**Fig. 13**). Although the long-term decline in stromatolite abundance could have commenced much earlier, there was a significant change during the Neoproterozoic, which, in contrast to the warmer Mesoproterozoic interval, was a time of several repetitive glaciation events called “Snowball Earth.” The stromatolite decline could have been affected by these global environmental changes. Decrease in temperature and  $p\text{CO}_2$  would have decreased the seawater carbonate saturation state, and reduced cyanobacterial calcification. As atmospheric  $p\text{CO}_2$  declined, cyanobacteria would have developed  $\text{CO}_2$  concentrating mechanisms (CCM), resulting in the appearance of the first calcified microbes around ~1200 Ma.

As temperature rose after the Neoproterozoic glaciation events, the seawater carbonate saturation state would have been increased. It caused a “resurgence” of microbialites during the Cambrian and Early Ordovician greenhouse intervals. The first definite thrombolites/dendrolites and calcimicrobes appeared during the Neoproterozoic (although there are some possible older examples), and became widespread during the Cambro-Ordovician.



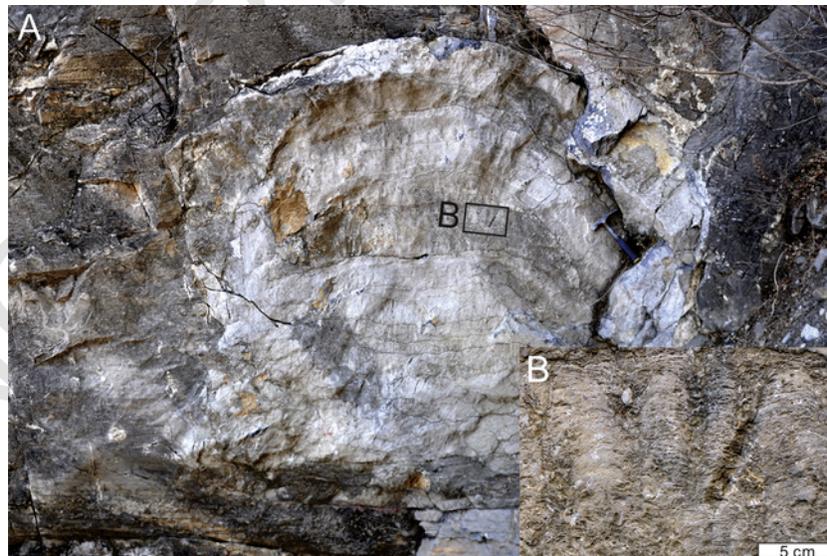
**Fig. 12** Occurrence of stromatolites in North America and Caribbean region. Proportion of stromatolite-bearing units are normalized by marine sedimentary rock units. 100% indicates all rock strata deposited at that time contain stromatolites. *Gray bars* indicate intervals of microbial carbonate abundance during the Phanerozoic. Modified after Peters, S.E., Husson, J.M. and Wilcots, J. (2017). The rise and fall of stromatolites in shallow marine environments. *Geology* **45**, 487–490; Riding, R., Liang, L., Lee, J.-H. and Virgone, A. (2019). Influence of dissolved oxygen on secular patterns of marine microbial carbonate abundance during the past 490 Myr. *Paleogeography, Palaeoclimatology, Palaeoecology* **514**, 135–143.



**Fig. 13** Upper Proterozoic (c. 900 Ma) Jacutophyton from Mauritania. Lens cap for scale is 7.2 cm. Specimen from American Museum of Natural History, New York.

### Phanerozoic

The Phanerozoic record of stromatolites is generally much poorer than that of the Precambrian (**Fig. 14**). It has been suggested that the rise of multicellular animals and plants could have limited stromatolite formation, but the precise mechanisms are still being debated. Extensive occurrences of stromatolites after mass extinction events, e.g., the late-Devonian and end-Permian mass extinctions, suggest



**Fig. 14** (A) Approximately 2-m-high domal stromatolite in the middle Cambrian (c. 500 Ma) Gushan Formation, Beijing, China. The stromatolite is embedded within oolitic grainstone. Hammer for scale is 27 cm. (B) Details of (A), showing small convex-upward laminated columns.

that stromatolite abundance has an inverse relationship with that of multicellular organisms. However, stromatolites thrived during several other periods, e.g., Cambrian–Ordovician, Carboniferous, and Jurassic–Cretaceous (**Fig. 12**).

The most widely held belief (the one written in the textbooks) is that grazing animals could have eaten up microbial mats, preventing their formation. According to this idea, stromatolites can only form extensively in environments where animals are scarce, such as in seasonally hypersaline lagoons like Shark Bay, or during time intervals when the majority of animals became extinct. However, evidence of bioturbation is scarce in many Phanerozoic stromatolites, and there are present-day occurrences of stromatolites in normal marine seawater, such as Bahamian tidal channels.

Nonetheless, competition with other benthic organisms could be an important mechanism to control stromatolite occurrence. It is not easy to estimate the growth rate of stromatolites, especially those in the rock record. However, it is evident that Shark Bay stromatolites—often several tens of centimeters high—took many hundreds of years to form. In contrast, benthic animal reef-builders, such as scleractinian corals, can grow 10 cm per year. Stromatolites could have been outcompeted by these animals and also plants.

Sea-water chemistry, such as calcite saturation state, affects calcification of cyanobacteria and therefore could be important for Phanerozoic stromatolite occurrences. According to this idea, stromatolites were scarce when there was not enough bicarbonate dissolved within seawater, thereby prohibiting calcification. Other chemical factors, such as temperature, dissolved oxygen, and atmospheric CO<sub>2</sub>, could also have affected microbialite abundance.

The most probable idea is that there is no single factor that affected Phanerozoic stromatolite occurrences. All of the ideas mentioned above, together with other yet unknown mechanisms, could have controlled stromatolite occurrences throughout the Phanerozoic through complex mechanisms.

### Modern Stromatolites

Stromatolites are rare in recent environments. Most modern stromatolites are found in hypersaline lakes or lagoons, where animals cannot prosper due to high salinity levels. The most famous example of such hypersaline stromatolites are those of Shark Bay, Australia (**Fig. 1**). Other hypersaline lakes in Western Australia, for example, Lake Thetis, also hold stromatolites. Freshwater stromatolites are also found. Pavilion Lake in British Columbia, Canada, holds large microbialite towers with calcified microbes resembling *Epiphyton*. They are also found from cold environments such as Lake Joyce, Antarctica.

The only modern stromatolite that grows in an open marine environment is known from the Exuma Cays, Bahamas. The Exuma stromatolites are found in tidal channels, sandy embayments, and intertidal settings. Although it is not certain why the Exuma Cays is the only place in the world with open marine stromatolites, it has been suggested that factors such as high sedimentation rate, prohibiting growth of competing algae metazoans, and precipitation-inducing environmental conditions would have been responsible for stromatolite formation.

On the other hand, stromatolites are relatively common within modern reefal cavities (**Fig. 15**). These stromatolites differ from the stromatolites mentioned above, in a sense that they do not form mounds by themselves. They occupy a huge volume within reefs, locally up to 80%, thereby supporting the general reefal framework. These reefal microbialites are mainly formed by sulfate-reducing bacteria in reef cavities with poorly illuminated, anoxic conditions where the decay of organic matter increases alkalinity and enhances microbial calcification.

### Scientific Questions Related to Stromatolites

#### Are Stromatolites Good Environmental Indicators?

A long held belief was that stromatolites can be good environmental indicators. It was primarily because recent stromatolites can be common in inter- to subtidal environments of Shark Bay and the subtidal setting of the Bahamas. However, stromatolites are not really as good of environmental indicators as was thought before; they can occur in deep water, too. Russian geologists used stromatolites for biostratigraphic correlation of otherwise unfossiliferous Precambrian strata, suggesting that temporal (or evolutionary) control on stromatolite morphology is important. Therefore, it may not be relevant to directly compare stromatolites of different ages. However, there are some helpful points to note. It has been generally suggested that the macroscale structures (shape) of stromatolites are more influenced by environmental conditions, whereas microstructures reflect the type of organisms that forms stromatolites. For example:

1. Thin, irregular microbial mats or “LLH-type” stromatolites, which can be compared with those in the modern Persian Gulf are usually attributed to inter- to supratidal environments (**Fig. 16**). They are often associated with sedimentological features, indicating subaerial exposures, such as mineral pseudomorphs and desiccation cracks.
2. Most mound- and column-shaped stromatolites as well as thrombolites formed in inter- to subtidal environments (**Fig. 14**). However, we must be careful when interpreting depositional environment of stromatolites because “subtidal” indicates a very wide range of environments. Sedimentary facies cooccurring with stromatolites may give better indications of depositional environment than the stromatolite itself.

Another point to discuss is whether stromatolites are indicator of light. Modern stromatolites from Shark Bay display evidence of heliotropism—meaning that their growth direction is influenced by sunlight. However, it is not easy to find evidence of heliotropism in ancient stromatolites, because we do not know the position of the sun when these ancient stromatolites formed. Although cyanobacteria—photosynthetic microbes—are thought to be the dominant organisms that formed ancient stromatolites, some stromatolites were definitely formed in the deep ocean or in caves where sunlight cannot penetrate. This suggests that at least some stromatolites are formed by nonphotosynthetic microbes, such as chemotrophic bacteria.



**Fig. 15** Stromatolites in modern coralgal reef cavities. The crust overlies coral and bioclasts. Late Pleistocene–early Holocene, SW Tahiti, IODP 310, Hole M0015B, interval 310-M0015B-21R-01, 85–105 cm. From doi: <https://doi.org/10.1594/PANGAEA.499787>.



**Fig. 16** Thin, irregular microbial-mat induced laminite from the Middle Ordovician (c. 470 Ma) Makgol Formation, Korea.

### Are Stromatolites Formed by Cyanobacteria Only?

Probably not. In the case of modern Shark Bay stromatolites, more than 20 different divisions (same level as phylum in animal kingdom) of prokaryotes in addition to several different eukaryotes (including diatoms and foraminifera) form the large domal structure, although the most common organisms trapping the sediment are diatoms and cyanobacteria. Although it is not possible to conduct the same analysis on ancient stromatolites, it is possible to infer that several different microbial communities would have contributed to the formation of stromatolites. Occurrence of stromatolites in dark environments, which would definitely have been formed by

nonphotosynthetic microbes (probably sulfate-reducing bacteria) other than photosynthetic cyanobacteria, supports this idea. These include stromatolites within recent reef cavities (Fig. 15).

### Are Stromatolites “Fossils”?

To most people, fossils are the remains of ancient organisms preserved in rock. In this sense, stromatolites are fossils. However, the answer to this question depends on how we define a fossil. Stromatolites are not “body fossils,” because each stromatolite represents a complex ecosystem of microorganisms, and they often do not preserve fossils of the microorganism themselves. However, calcified microbes preserved within stromatolites can be classified as body fossils. Each stromatolite is therefore more like a “forest” than a “tree.” In a broad sense, stromatolites can be classified as a kind of ichnofossil—preserved traces of organisms—but ichnologists usually do not consider stromatolites to be their territory. Other ichnofossils are mostly produced by individual organisms, unlike stromatolites.

### How Fast Do Stromatolites Grow?

Modern coral reefs grow fast. Some corals grow up to 10 cm per year, and can form reefs within less than several tens of thousands of years, which is like a moment in the geologic timescale. Precambrian reefs are made by stromatolites, and they occupied ecological niches similar to that of modern coral reefs. How fast do stromatolites grow, and how long will it take them to form a stromatolite barrier reef?

This is not an easy question to answer, because it is very difficult to accurately estimate such short timespans in geologic time. Several tens of thousands of years are much less than the error range in rocks that are several hundred million years old. Also, ancient stromatolites could have been different from modern stromatolites, and their growth rates may not be the same. The only reference we can directly measure is the growth rate of modern stromatolites.

Shark Bay stromatolites, the most famous modern stromatolites, grow at a maximum of 0.3 mm per year. This is slower than the typical sedimentation rate of modern carbonates (c. 1 mm per year), but faster than the net sedimentation rate calculated from ancient carbonate platforms (c. 0.05 mm per year), which involves periods of erosion and nondeposition.

### Are There Extra-Terrestrial Stromatolites?

Probably one of the most intriguing questions for scientists would be whether we can find evidence of life from extra-terrestrial planets. Although there may not be life on other planets nowadays, especially those in our solar system, organisms may have existed in the past. Recent scientific surveys in Mars may help answer this question. Based on observations of photos sent by the Curiosity rover mission, some scientists argue that sedimentary structures found from < 3.7 Ga old sedimentary rocks on Mars resemble MISS from Earth, thereby suggesting that microbes could have existed in ancient Mars. However, this needs to be critically tested. If any human being can land on Mars, they will definitely look for stromatolites to check for evidence of extra-terrestrial life.

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Biography



**Jeong-Hyun Lee** obtained his B.S., M.S., and Ph.D. in Seoul National University, South Korea. He is now an assistant professor at the Chungnam National University, South Korea. His main interest is early Paleozoic metazoan-microbial reefs, focusing on the transition from microbial-dominant Precambrian reefs to metazoan-dominant Phanerozoic reefs.

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