Microbialite-Associated Microbial Communities, Present and Past

Massive microbialites forming at Atexcac crater lake (Mexico).

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This chapter describes the biological composition of modern microbialites, aiming at identifying the major microbial actors that may contribute to their mineralization and growth. Despite the vast diversity in community composition, environmental conditions, and dominant mineral phases, certain key components emerge as critical drivers of these processes. Additionally, the dominance of specific microbial populations can serve as a proxy for identifying key metabolisms involved in mineralization, such as oxygenic and anoxygenic photosynthesis, sulfate reduction, and methanogenesis. Finally, we discuss how these insights enhance our understanding of ancient microbialites, bridging the gap between modern observations and the geological record.

KEYWORDS: core microbial community; cyanobacteria; metabolism; microbial diversity; photosynthesis

INTRODUCTION

Microbial communities associated with microbialites are remarkably diverse, yet photosynthesis appears as a dominant primary production process. Cyanobacteria and anoxygenic photosynthetic bacteria are invariably present in high relative abundances, often accompanied by sulfate-reducing bacteria (SRB) (Dupraz et al. 2009; López-García et al. 2005) and different heterotrophic populations. The metabolic activity of these bacteria is thought to promote carbonate precipitation by increasing local alkalinity, supplying cations, and providing nucleation centers, thereby contributing to microbialite formation (see Zeyen et al. 2026 this issue).

Studying modern microbialites offers valuable insights into Earth's early ecosystems. Isotopic and morphological signatures preserved in ancient stromatolites suggest that oxygenic photosynthesis and sulfur cycling have played pivotal roles even in the Precambrian (Allwood et al. 2006; Baumgartner et al. 2006; Thomazo et al. 2026 this issue). However, direct comparisons between modern and ancient systems remain challenging due to secular changes in Earth's atmosphere (e.g., changes of atmospheric pCO_2, temperature, and pO_2; see Hofmann et al. 2026 this issue) and the fragmentary preservation of microbial fossils (Bosak et al. 2007).

In this chapter, we briefly review the phylogenetic and functional diversity of microbial communities associated with modern microbialites, with a focus on the metabolic activities that potentially drive mineralization across diverse environments. We also explore the implications for interpreting ancient microbialite formation, aiming to bridge modern microbial ecology with paleobiology. By doing so, we intend to refine proxies for reconstructing Earth's earliest ecosystems.

MICROBIAL DIVERSITY AND CORE COMMUNITIES IN MODERN MICROBIALITES

Environmental Controls on Community Composition

The composition of microbial communities in microbialites is shaped by both biotic and abiotic factors, resulting in substantial shifts across environmental gradients. Understanding the drivers of these variations offers a framework for interpreting paleoenvironments from fossilized structures.

Microbialite-associated communities comprise widely diverse photosynthetic and heterotrophic microbes, but depending on local conditions and notwithstanding local variations, some microbial taxa can dominate over others. FIGURE 1 illustrates microbialites whose diversity has been characterized using 16S rRNA gene metabarcoding, allowing for comparative analysis. (Please note that not all locations containing microbialites are included in this figure). In some lacustrine systems, like Lake Alchichica (Mexico), conditions favor cyanobacterial dominance. There, *Pleurocapsa*, *Leptolyngbya*, or *Phormidium* relatives are prevalent. These organisms produce thick layers of extracellular polymeric substances (EPS) that promote carbonate precipitation. Although the diversity of heterotrophic microbes is important, SRB are scarce. By contrast, in marine microbialites, such as those from Highborne Cay or Little Darby (Bahamas) and Mari Ermi (Sardinia), SRB are more prevalent in otherwise hugely diverse communities. This is likely due to the high sulfate content of seawater, which fuels sulfate reduction. This metabolic activity can be linked to distinct isotopic signatures ($\delta^{34}S$, see Toolkit) that might mirror those in Proterozoic counterparts.

Microbialites also thrive in some extreme environments, including:

- Hypersaline lagoons (e.g., Kiritimati Atoll, Central Pacific, Rottnest Island, Australia, or Guerrero Negro, Mexico, not shown in FIG. 1), dominated by halophilic cyanobacteria (e.g., *Halothece*) and SRB (e.g., *Desulfonatronum*). The limitation of grazers in these environments

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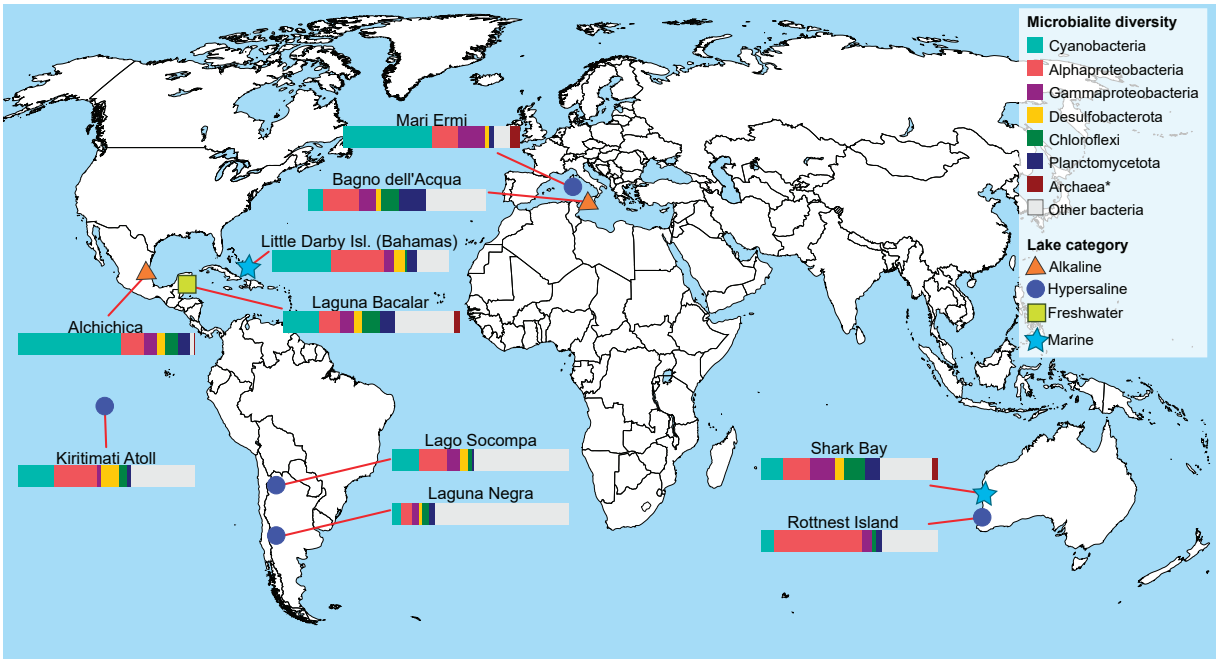


Figure 1 Microbial diversity (phylum level) and location of selected modern microbialites from different marine and lacustrine ecosystems. Only microbialites whose diversity has been characterized using 16S rRNA gene metabarcoding by next-generation sequencing (NGS) are shown, allowing for comparative analysis. Barplots show the relative abundance of the major taxa identified. Even when comparing microbialites from similar environments, such as alkaline or hypersaline lakes, the associated microbial communities exhibit high phylogenetic diversity, especially within the different phyla.

is generally thought to facilitate the development of thick microbial mats that can, depending on the local chemistry, favor mineralization.

- Hydrothermal systems (e.g., Socompa Lake (Argentina), where a stream of hydrothermal water is associated with columnar round-dome stromatolites or Yellowstone's Mushroom Spring (USA), 60–70 °C, not shown in Fig. 1) can host microbialite-like structures bearing thermophilic photosynthetic members (e.g., Synechococcus, *Roseiflexus*, *Phormidium*) as well as organisms typically associated with high temperature environments, such as members of the Deinococcus-Thermus group (Farias et al. 2013). These systems are usually silica-rich, and the biological control of their formation is controversial.

Understanding the environmental fingerprints associated with these modern microbialites (preserved in mineralogy, isotopic ratios, and microfossil textures) can serve as a "Rosetta Stone" for interpreting ancient microbial ecosystems.

Dominant Microbial Groups, their Metabolic Roles, and Biomineralization Potential

Modern microbialites are living laboratories, where the interplay between microbial metabolism and mineral precipitation can be directly observed. These ecosystems are phylogenetically diverse (Fig. 2) but rely on a few functional guilds (e.g., populations sharing similar trophic characteristics and exerting comparable effects on their environment), whose activities have remained remarkably consistent across environments and geological time.

Cyanobacteria, such as the filamentous *Coleofasciculus*, *Leptolyngbya*, or *Phormidium*, the pseudofilamentous *Pleurocapsa* and coccoid forms (e.g., Chroococcales), are the architects of many microbialite systems. They fix CO_2 by oxygenic photosynthesis (see Toolkit), thereby increasing pH, which favors carbonate precipitation. In addition, their thick EPS layers can act as nucleation centers, accumulating cations (notably Ca^{2+}) that also promote carbonate precipitation upon degradation by tightly associated heterotrophic bacteria. In addition, EPS provides a sticky scaffold that traps and binds sediments, thereby contributing to microbialite growth in marine ecosystems (Reid and Browne 1991). However, these processes may differ in lacustrine systems, where biomineralization, rather than sediment trapping, is likely to dominate microbialite formation. In addition to this metabolic implication, filamentous cyanobacteria, also referred to "mat builders," are also fundamental for the stability and coherence of modern microbialites.

Oxygenic photosynthesis favors carbonate precipitation (Table 1). For instance, in shallow marine systems, such as Highborne Cay (Bahamas), different cyanobacterial populations exhibit diurnal cycling of CO_2 uptake, creating pH fluctuations (8.2–9.1) that drive aragonite precipitation within EPS matrices (Dupraz et al. 2009). Furthermore, cyanobacterial trichomes (i.e., colonies of cyanobacteria forming filaments) guide mineral growth directionality. Filament molds in Proterozoic stromatolites suggest this process has operated since the Precambrian (Allwood et al. 2006; Bosak et al. 2013).

Anoxygenic photosynthetic bacteria (APB) (Fig. 2) group a diversity of taxa using H_2S or other electron donors for photosynthesis. In modern microbialites, members of the Alphaproteobacteria, Gammaproteobacteria and Chloroflexi are the most prevalent APB representatives. They are abundant in both lacustrine (e.g., Iniesto et al. 2021) and marine (e.g., Mobberley et al. 2012) microbialites. They are invariably present and often abundant in the suboxic and anoxic layers of microbial mats, which can be located a few hundred micrometers below the microbialite surface. They are also particularly prominent in hot spring microbialites (e.g., Yellowstone's Chocolate Pots, USA) or hypersaline lagoons (e.g., Rottnest Island, Australia), and contribute to primary production under low-oxygen conditions.

Table 1 MINERAL PRECIPITATION/DISSOLUTION CAPABILITIES OF THE MAJOR METABOLIC PROCESSES PRESENT IN MICROBIALITES. The type of mineral phase more likely to be precipitated and the taxonomic groups frequently performing such metabolism are cited.

Metabolism	Role in microbialite structure	Examples of taxa involved
Oxygenic photosynthesizers	Promotes carbonates (calcite, aragonite), Fe/Mn oxides	Cyanobacteria, algae
Anoxygenic photosynthesizers	Promotes carbonates, Fe sulfides, gypsum	Chromatiales, Rhodobacterales, Chlorobi, some Chloroflexi
Sulfate reduction	Promotes carbonates (dolomite, siderite), different sulfides	Desulfobacterales, Desulfovibrionales, etc.
Fermentation	Favors carbonate dissolution	Cyanobacteria (night), Clostridiales, Bacillales, etc.
Methanogenesis	Promotes carbonates (dolomite, high-Mg calcite), magnetite	*Methanosarcina*
Iron reduction	Promotes carbonates (siderite) precipitation, magnetite formation	*Shewanella*, *Geobacter*
Manganese reduction	Favors Mn-oxide dissolution	*Shewanella*, *Geobacter*
Nitrate reduction & denitrification	Favors the development of green rust	*Pseudomonas*, *Paracoccus*
Methanotrophy	Promotes carbonates, pyrite	*Methylomonas*, ANME archaea
Hydrogen oxidation	Promotes serpentine	*Aquifex*, *Ralstonia*

Considering the euxinic conditions sometime in the Precambrian, this metabolic process likely played a key role in the formation and persistence of microbialites before the emergence and dominance of cyanobacteria. In sulfidic environments like Yellowstone's Chocolate Pots hot spring (50 °C, pH 6.2), *Chloroflexus* mats perform sulfide-driven photosynthesis ($2H_2S + CO_2 \rightarrow CH_2O + 2S^0$). This process produces elemental sulfur globules that can serve as nucleation sites for nanocrystalline Fe-sulfides, thereby generating textures similar to those observed in the 2.7 Ga Tumbiana Formation microbialites. These systems exhibit isotopic signatures that might be consistent with microbial sulfur cycling ($\delta^{34}S$ of sulfides: +2‰ to +5‰) and anoxygenic photosynthesis ($\delta^{13}C_{org}$: ~−12‰).

Desulfovibrio and other SRB thrive in marine and hypersaline environments where sulfate is abundant, such as Shark Bay (Australia). Their metabolism generates bicarbonate and sulfide, increasing local alkalinity and promoting carbonate precipitation, while also contributing to sulfide mineral formation. In oxygen-poor layers of microbial mats, SRB often coexist with anoxygenic photosynthesizers like *Chloroflexus*, which use sulfide for photosynthesis.

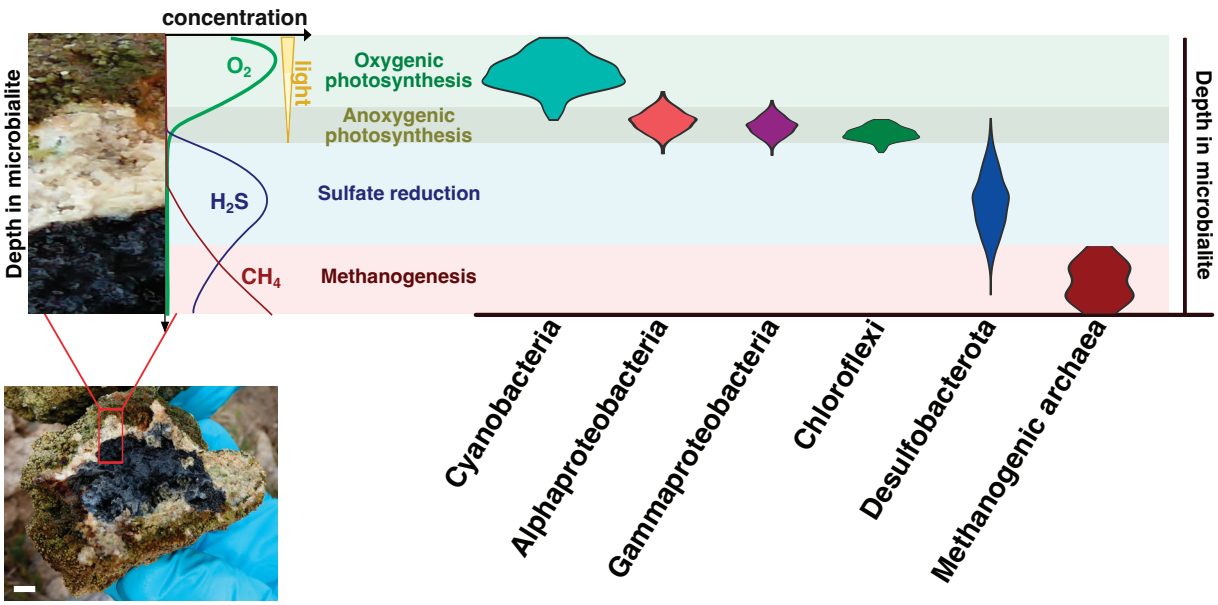


Figure 2 Spatial distribution of the main microbial groups presumably involved in microbialite formation across a microbialite section. The violin plot illustrates the relative abundance of each group at a given depth (indicated by the width of each colored area). The vertical distribution of these groups is primarily determined by physicochemical gradients including oxygen (green line), hydrogen sulfide (blue line), and light penetration (yellow). The line plot shows the depth profiles of these environmental parameters. In the uppermost layers, aerobic organisms, or those tolerant to moderate O_2 concentrations prevail, whereas deeper within the community, populations become increasingly strictly anaerobic. The microbialite shown was collected in Alchichica (Mexico). For photosynthetic taxa, the colors used in the figure represent the actual color observed on the field for the layer dominated by the organisms—green in the upper layers dominated by cyanobacteria, purple/red when anoxygenic photosynthetizers such as Alphaproteobacteria and Gammaproteobacteria are major constituents, or dark green when green sulfur and non-sulfur bacteria (class Chlorobiia and phylum Chloroflexota, respectively) are abundant. Scale bars are 1 cm.

In addition to photosynthetic taxa and sulfate-reducing bacteria, several other microbial groups, like methanogenic archaea or fermenters (Fig. 2), play crucial roles in microbialite ecosystems. These groups contribute to redox cycling, organic matter transformation, and biofilm architecture, highlighting the metabolic versatility and redundancy that sustain microbialite growth across diverse environments. Heterotrophic fermenters (with a widespread distribution across microbialites), such as bacteria from the Bacteroidota and Bacillota (former Firmicutes) phyla, including *Flavobacterium*, *Clostridium*, and *Halanaerobium*, are common in microbialites. They decompose complex EPS, releasing organic acids, CO_2, H_2, and acetate-metabolites that fuel methanogenesis or sulfate reduction. Their activity can shift local redox gradients and pH, influencing mineral nucleation. In hypersaline environments like Guerrero Negro, fermenters are especially important due to limited oxygen availability. Members of the Bacillota group can also impact and favor carbonate precipitation by several mechanisms, such as the hydrolysis of urea, or ammonification, as observed in different *Bacillus* species (White 2020).

Methanogenic archaea (Fig. 2) are strict anaerobes, highly sensitive to oxygen. They have been identified in microbialites from anoxic lakes, such as Lake Untersee (Antartica) and Lagoa Salgada (Brazil). They perform hydrogenotrophic or acetoclastic methanogenesis, producing CH_4 from $H_2 + CO_2$ or acetate. Their metabolism promotes the precipitation of calcium carbonate minerals, including ikaite and calcite. In addition, methanogens strongly fractionate carbon isotopes, leaving distinct isotopic traces in microbialite carbonates that differ from those produced by photosynthesis (Birgel et al. 2015).

Microbial Eukaryotes Also Contribute to Microbialite Formation

Microbial eukaryotes (or protists) associated with modern microbialites comprise a diverse assemblage of photosynthetic and heterotrophic species that exert a major yet often overlooked control on microbialite structure and function. Eukaryotic photosynthesizers, which include green algae, diatoms, and other microalgae, can also play an active role in the formation of modern microbialites. Harboring cyanobacterial-derived plastids, they carry out oxygenic photosynthesis and could, in principle, promote carbonate precipitation as well (Arp et al. 2001). In many modern microbialite systems, especially in freshwater and alkaline lakes, eukaryotic algae colonize the upper photic layers and significantly contribute to microbialite accretion, often interacting synergistically with prokaryotic consortia to shape layered morphologies. Their presence underscores the importance of eukaryotic metabolism in both the biological and geochemical evolution of benthic microbial systems, which can play a central role in primary production, as highlighted in microbialites from Alchichica (Saghaï et al. 2015). It has also been observed that microbial eukaryotes from some freshwater microbialites, dominated by chlorophyte algae belonging to the group Ulvales and diverse diatoms, differ from those in marine microbialites, with diatoms belonging to Raphid-pennate and Araphid-pennate groups as abundant constituents. The evolution of the first photosynthetic eukaryotes (Archaeplastida algae) and their presence in microbialites coincides with the golden era of these organo-sedimentary structures. Microbialites experienced a period of expansion during the early Proterozoic, as attested by the fossil record (see Hofmann et al. 2026 this issue and Fig. 5 of Fogret et al. 2026 this issue) before they declined about 1–0.7 Gy ago.

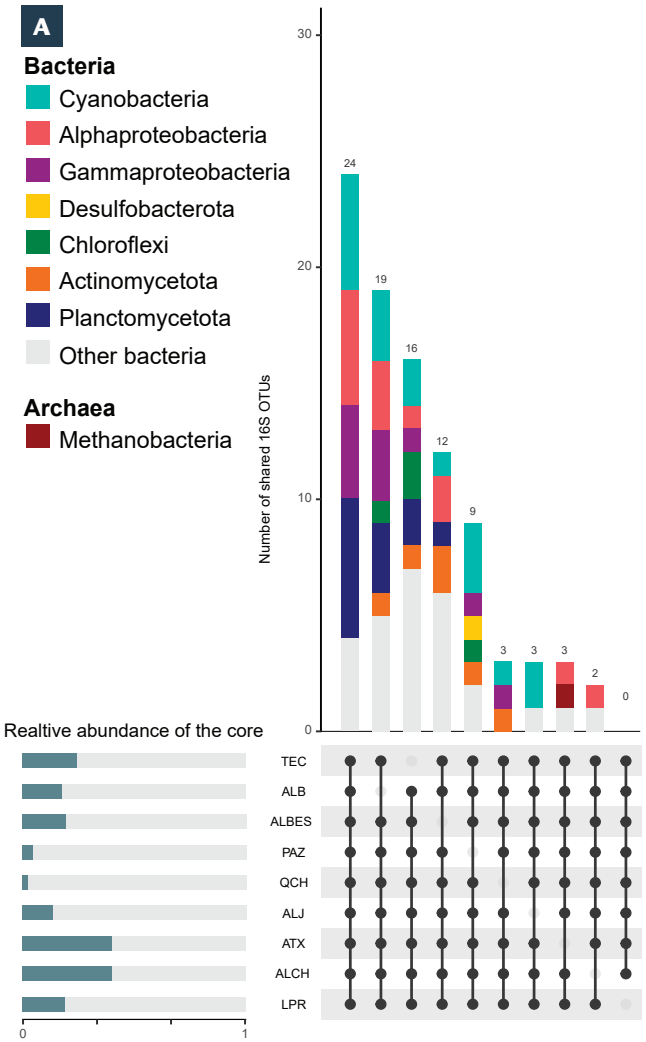
Moreover, diatoms, which can be abundant in some microbialites, may be responsible for the local accumulation of Si. This likely promotes the formation of authigenic Mg-silicates, sometimes enriched in iron and manganese (Zeyen et al. 2015; Muller et al. 2023).

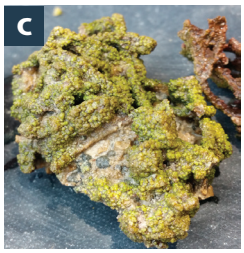
Heterotrophic eukaryotes encompass diverse protists, fungi, and metazoans. These can act as grazers, decomposers, and parasites, and are key agents of biomass recycling, thereby restructuring mat architecture and impacting redox zonation. However, apart from surface-associated activities, only very few heterotrophic eukaryotes are genuinely associated with microbialites, notably some unicellular fungi. Protist grazing activities might contribute to the formation of clotted textures commonly associated with thrombolitic microbialites (Bonacolta et al. 2024). Moreover, potential protist parasites, such as *Chytridium polysiphoniae* and a *Rhyzophidiales* spp., could form a "mycoloop" that channels organic matter from primary producers to higher trophic levels, affecting both carbon cycling and mineralization pathways. Emerging highthroughput sequencing studies have shown that eukaryotic communities, like in the case of prokaryotes, are taxonomically distinct among sites but show functional convergence, suggesting that different eukaryotic consortia can favor processes generating comparable microbialite morphologies under similar environmental conditions.

The Core Community Concept: Functional Stability Amidst Taxonomic Variability

Microbialites worldwide exhibit a remarkable pattern: despite inhabiting vastly different environments, they share a core set of phylogenetic taxa (Fig. 3A) and metabolic functions (Fig. 3B) performed by microbial guilds that persist across space (Louca et al. 2016; Wong et al. 2018). For example, molecular analyses of microbialite diversity in Mexican systems have revealed that, despite a limited number of taxa shared across different sites (only 24 taxa present in all lakes, first vertical histogram in Fig. 3A), these taxa can constitute a substantial proportion of the community. This pattern is particularly evident in lakes hosting well-developed microbialites, such as Alchichica (Fig. 3C) and Atexcac in Mexico (Fig. 3D), where the core group may account for up to 40% of the total community's relative abundance, associated with a metabolic core (Fig. 3B). Moreover, a functional conservation emerges from phylogenetically diverse yet physiologically equivalent organisms that adapt to local conditions while maintaining critical biogeochemical roles.

The cyanobacterial niche demonstrates this principle clearly. In lacustrine systems such as Alchichica, *Pleurocapsa* appears to be actively involved in carbonate precipitation (Gérard et al. 2013). But other cyanobacteria and/or photosynthetic bacteria may take over this function in microbialites from other places or environments. Similarly, sulfate reduction might be a contributing process in several microbialites whether mediated by marine Desulfobacteraceae or alkaline-adapted *Desulfonatronum* (Visscher et al. 2000). Microbial functional redundancy underscores how microbialite formation depends on metabolic networks rather than specific taxa (Iniesto et al. 2021), a mechanism that has been also observed in non-lithifying mats (Gutiérrez-Preciado et al. 2018). Among the core microbiome identified in Mexican microbialites, we detect an overrepresentation of photosynthetic organisms and chemo-organotrophs. These functions can also be found in many other microbialites, but they are associated with distinct phylogenetic compositions (see the section *Dominant Microbial Groups, their Metabolic Roles and Biomineralization Potential* in this chapter).





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Mexican core microbialite

Cyanobacteria	
1 Oscillatoriales	Ox.Photos., filamentous
3 Leptolyngbyaceae	Ox.Photos., filamentous
1 Pleurocapsales	Ox.Photos., $CaCO_3$ formation
Alphaproteobacteria	
1 Erythrobacteraceae	Chemo-organotrophic
2 Rhodobacteraceae	PNSB
1 Hyphomicrobiaceae	PNSB; N fixation
1 Hyphomonadaceae	Nitrate reduction
Gammaproteobacteria	
1 Xanthamonadales	EPS production
3 Comamonadaceae	Chemo-organotrophic
Planctomycetota	
5 Planctomycetaceae	anammox, anaerob. resp.
1 *Rhodopirellula sp*	Chemo-organotrophic
Bacteroidota	
1 Saprospiraceae	hydrolysis complex C mol.
1 Flavobacteriaceae	Chemo-organotrophic
Actinomycetota	
1 Microbacteriaceae	Chemo-organotrophic
1 Microtrichaceae	Sponge associated

Figure 3 Microbial core community components in microbialites from nine crater alkaline lakes in central Mexico. (**A**) Taxonomic identification of shared taxa across Mexican microbialites. Horizontal barplots show the relative abundance of the core community (dark grey) with respect to the whole community (light grey). Vertical bars show the taxonomic diversity of the taxa present in all of the lakes (leftmost vertical bar) or all but one of the lakes (remaining bars; dots below the plot show lakes included in the analysis). ALB: Alberca de Michoacán; ALBES: Alberca de los Espinos; ALCH: Alchichica; ALJ: Aljojuca; ATX: Atexcac; LPR: La Preciosa; PAZ: Patzcuaro; QCH: Quechulac; TEC: Tecuitlapa. (**B**) Image of a microbialite from Alchichica. (**C**) Microbialite from Atexcac. (**D**) Detail of the organisms identified as members of the strict Mexican core (first column) and information about their potential involvement in the formation of microbialites (second column). The number represents the number of taxa belonging to the different groups present in the Mexican core microbialite. Anaerob. resp.: anaerobic respiration; C mol.: carbon molecules; Ox.Photos.: oxygenic photosynthesis; PNSB: purple non-sulfur bacteria (anoxygenic photosynthesizers).

The occurrence of a similar metabolic core may have existed in ancient microbialites. The presence of microbial lineages carrying these metabolic activities and/or traces of the activities themselves may in principle be stored in the fossil record despite some uncertainties and confounding factors (Javaux 2019). For example, lipid biomarkers and organic carbon isotopic signatures ($\delta^{13}C$ values < −20‰) are consistent with C fixation in fossil stromatolites, suggesting the presence of cyanobacterial photosynthesis. For instance, mid-chain branched monomethylalkanes recovered from a variety of environments (freshwater microbial mats of calcifying cyanobacteria, microbial carbonates, or carbonate samples from the Late Jurassic) might represent biomarkers for ancient cyanobacteria (Hefter et al. 1993; Thiel et al. 1997; Arp et al. 2001; Lepot 2020). Likewise, sulfur isotope fractionation patterns ($\Delta^{33}S$) in Archean microbialites might record sulfate reduction pathways that may still persist in modern systems (Baumgartner et al. 2006). Finally, microfossil assemblages show filamentous microbes with sheath structures resembling modern mat-formers (Allwood et al. 2006). Extreme environments also provide analogues for some early Earth conditions. For instance, the ice-covered Lake Untersee (Antarctica) hosts microbialites built by *Leptolyngbya* alongside psychrophilic SRB, illustrating how microbial communities could have persisted during Earth's glaciations (Andersen et al. 2011).

The functional redundancy observed across billions of years and different environmental conditions highlights the role of modern microbialites as reliable proxies for reconstructing Earth's earliest ecosystems. The core metabolic networks driving mineral precipitation have most likely remained effective over time, despite dramatic planetary changes.

MICROBIAL DIVERSITY IN MICROBIALITES THROUGH TIME: BRIDGING MODERN AND ANCIENT SYSTEMS

Challenges in Deep-time Interpretation

Because DNA-based characterization is impossible in fossil microbialites (at least for the most ancient ones), microbial diversity must be inferred from indirect evidence preserved in the rock record. These proxies include microfabrics, growth textures, organic biomarkers, carbon/sulfur isotopic compositions, and rare microfossils, which can collectively reveal evolutionary shifts in microbialiteforming consortia from prokaryote-dominated mats to increasingly complex, eukaryote-influenced assemblages (see Hofmann et al. 2026 this issue). In this context, researchers must carefully remember how different Earth's early environments were. The Archean world presented microbial communities with an atmosphere containing less than 0.1 % of modern oxygen levels, and carbon dioxide concentrations were nearly 1,000 times higher, with an obvious impact on the functioning of microbial populations. Furthermore, diagenetic alteration poses significant challenges (see Zeyen et al. 2026 this issue). For instance, Raman spectroscopic studies of Proterozoic examples show how recrystallization can reset $\delta^{18}O$ values, while aragonite-to-calcite replacement obscures original biosignatures. The taphonomic filter is equally daunting: only exceptional preservation, as seen in the silica-encased 1.9 Ga Gunflint Formation microbialites, captures cellular details with nanometer fidelity. Moreover, modern multi-technique approaches, such as time-of-flight secondary ion mass spectrometry (ToF-SIMS), enable detection of signals associated with known biological groups. This is exemplified by several Archean samples in which 2α-methylhopanes (C_{30}–C_{35}) were identified and found to be structurally analogous to compounds present in modern Pleurocapsa cyanobacteria (Naafs et al. 2022). Together, these methods combined form an integrated framework for reconstructing early microbial ecosystems.

Proterozoic Microbialites: Prokaryote-dominated Foundations

The fine lamination, "tufted" structures, and fused filaments observed in most of the recovered microbialites suggest a tight coupling between photosynthesis (anoxygenic photosynthesis in the oldest samples), EPS production, and early diagenesis under anoxia, potentially under higher UV conditions in the early Earth atmosphere. By the Proterozoic, columnar, conical, and domal microbialite morphologies became dominant in the fossil record. Eukaryotes appeared ~2 Gy ago, and rapidly radiated (Javaux and Lepot 2018; Knoll 2014). With rising oxygen levels, and the development of new trophic interactions, including protist grazing post~1.8 Ga, nutrient fluxes changed. Fossil microbialites experienced a sharp decline in the latest Proterozoic and early Cambrian (see Fig. 5 of Fogret et al. 2026 this issue). Lipid biomarkers such as steranes, and cyst-like microfossils (~1.7 Ga) signal the emergence of early eukaryotes within these microbial mats, potentially driving a shift toward more irregular fabrics (Bonacolta et al. 2024). This transition may mark the start of a reorganization of microbial mats in response to eukaryotic grazing pressures. Some authors argue that grazing exerted selective pressure, forcing microbialites to persist in refugia such as hypersaline lagoons and steep ramps, where they evolved into thrombolites (clotted textures) and leiolites (lacking distinct internal structure). These new structures have been interpreted as products of more diverse, three-dimensional mats incorporating algae, fungi, and early protists. Throughout Earth's history, microbialites must have faced diverse environmental conditions and sharp bottlenecks, such as some catastrophic events (e.g., snowball Earth stages). Following such disturbances, microbialites re-formed in multiple locations, frequently dominating carbonate platforms after the collapse of reef-building organisms. It has been suggested that these "disaster" microbialites have served as ecological refugia, facilitating rapid recolonization and buffering biogeochemical cycles during recovery phases.

CONCLUSION

Throughout Earth's history, microbialites, as products of complex microbial benthic communities forming in specific hydrochemical contexts, have witnessed the continuity and phylogenetic diversification of microbial life. Despite this diversification, the core metabolic functions of these communities, organized along redox gradients, have remained remarkably stable.

Microbialites first emerged in anoxic Archean environments, where anoxygenic phototrophs and anaerobic metabolisms dominated. With the expansion of oxygenic photosynthesis by cyanobacteria, more efficient CO_2 fixation pathways, a concomitant increase in pH, and enhanced EPS production became the dominant processes. Cyanobacteria emerged as new key architects of microbialites. These conditions drove conspicuous carbonate precipitation and the development of more complex laminated stromatolitic fabrics, with columnar and domal morphologies.

After eukaryotes evolved, the recruitment of eukaryotic algae, fungi, and/or protists introduced new trophic actors, some of which imposed new grazing pressures, potentially driving the transition towards more clotted, thrombolytic, and irregular textures. Despite diversification and evolution of diverse microbial taxa over time, the metabolic core functions may have been preserved. As a result, modern microbialites seem to consistently harbor a metabolic backbone centered on oxygenic and anoxygenic photosynthesis, sulfate-reduction, methanogenesis, fermentation, and EPS-mediated organo-mineralization.

Today, cyanobacteria, anoxygenic photosynthetic bacteria, sulfate-reducing bacteria, fermenters, and sometimes methanogenic archaea interact within steep redox and chemical gradients to sustain tightly coupled carbon and sulfur cycles within microbialites. Eukaryotes, notably green algae and diatoms, but also heterotrophic grazers and parasites, as well as viruses infecting members of all three domains of life, further enhance carbon cycling in these ecosystems. The persistence of most of this metabolic network across diverse environmental regimes and over billions of years underscores the resilience and adaptability of microbialite-forming consortia.

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