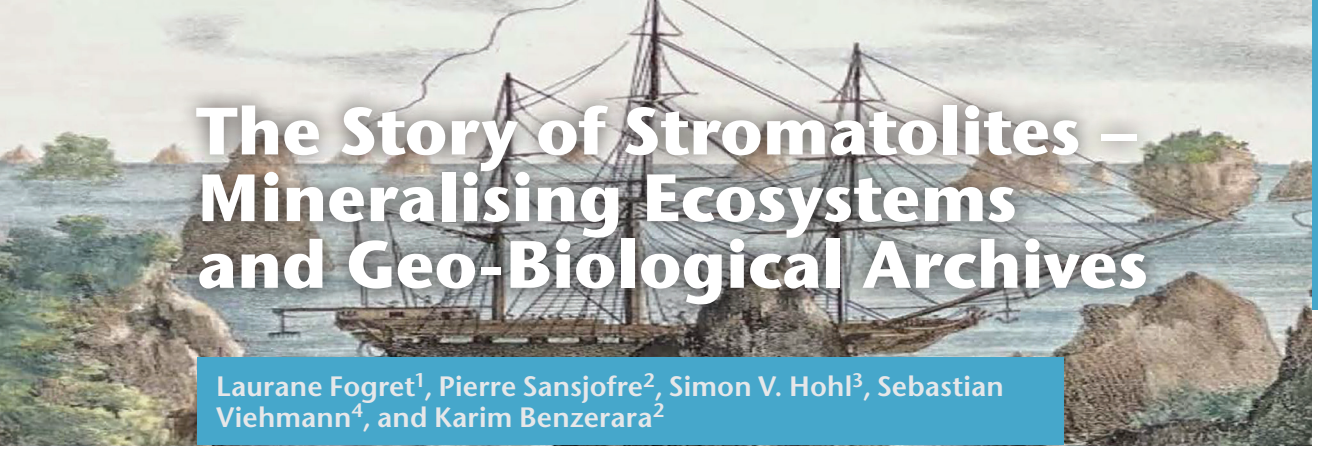

The Story of Stromatolites – Mineralising Ecosystems and Geo-Biological Archives

The French corvette *Uranie* during its scientific expedition around the world.

Laurane Fogret[1], Pierre Sansjofre[2], Simon V. Hohl[3], Sebastian Viehmann[4], and Karim Benzerara[2]

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Stromatolites represent some of the oldest and most persistent records of life on Earth. These organo-sedimentary structures have formed through complex interactions between microorganisms and their environment for nearly 3.5 billion years. Here, we trace the evolving scientific narrative surrounding these structures, from their early 19th-century descriptions to their integration into the broader concept of microbialites. This journey reflects a profound conceptual shift: once classified as distinct fossil species, stromatolites are now understood as mineralising ecosystems and dynamic biogeochemical archives. This modern perspective allows for the reconstruction of early life and its environment while highlighting key scientific challenges, such as disentangling microbial from environmental controls and interpreting biogenicity in ancient terrestrial and extra-terrestrial rocks.

KEYWORDS: stromatolite; microbialite; biogenicity; diversity; history

STROMATOLITES: FROM DISCOVERY TO DEFINITION

Stories Written in Stone, Read Anew

In September 1817, the French corvette *Uranie* set sail on a scientific voyage to the far reaches of the globe. Led by navigator and naturalist Louis de Freycinet, the expedition aimed to chart the world, collect natural specimens, and expand the boundaries of human knowledge. However, no one could have anticipated that, during their stay in Australia, they would map and sample a site now world-renowned for stromatolite research that was designated a UNESCO World Heritage Site in 1991.

On September 12, 1818, the *Uranie* anchored in a remote inlet on Australia's western coast. This place was formerly known as "*Baie des Chiens-Marins*" in French, but is now much better known as Shark Bay (FIG. 1). The waters were shallow, salty, and strangely still, but what the crew could not have known was that beneath their skiff, rocky domes were slowly growing, layer by layer, as a result of complex and dynamic bio-sedimentary processes. The hydrographic surveys conducted by the expedition laid the foundation for studying this extraordinary ecosystem, which is acclaimed today for hosting living microbial mats and stromatolites, structures with a geological history spanning over three and a half billion years. Among the *Uranie* expedition's scientific treasures were stromatolite samples, recently rediscovered in the historical collections of the *Muséum National d'Histoire Naturelle* (MNHN) in Paris (FIG. 1). Many other institutions, including the *Natural History Museum* in London and the *Naturalis Biodiversity Center* in the Netherlands, also preserve stromatolite specimens from 19th century scientific expeditions.

Throughout the 19th century, these striking laminated structures fascinated naturalists. Following the taxonomic conventions of the era, early efforts to classify them treated each morphological type as a distinct fossil species (also called morphotaxon) that formed in a unique environment and at a specific time. This approach, inspired by the Linnaean system, viewed stromatolites as discrete, named entities, akin to plants or animals, with defined temporal and stratigraphic boundaries. The genus *Cryptozoön* was first described by Hall (1883) and established stromatolites in the formal lexicon of palaeontology by the late 19th century. Over time, more than 1,500 "species" were described (Awramik and Sprinkle 1999), including *Collenia*, with its finely laminated, bifurcating columns; *Conophyton*, recognised for its large, upward-pointing cones with internal lamination; *Gymnosolen*, with its domed and flattened forms; and *Weedia*, which displays broad, parallel or domal laminae arranged in thick layers (Cloud 1942; Hofmann 1973; Semikhatov and Raaben 2000). These classifications were also documented in publications like the "Stromatolite Newsletter," an informal series that circulated between 1972 and 1993 among researchers.

However, it was not until 1908 that the German geologist Ernst Louis Kalkowsky formally coined the term "*Stromatolith*" (from the Greek for "layered stone") to describe domes and columns of well-layered carbonates embedded in Early Triassic lacustrine oolitic sedimentary rocks near the Harz Mountains in northern Germany. In his paper "*Oolith und Stromatolith im norddeutschen Buntsandstein*" (Kalkowsky 1908), he defined stromatolites for the first time, emphasising their fine, even lamination, which contrasted with the concentric internal lamination

1 Naturalis Biodiversity Center Leiden
2333CR, the Netherlands
E-mail: laurane.fogret@naturalis.nl

2 Muséum national d'Histoire naturelle
Sorbonne Université, UMR CNRS 7590
Institut de Minéralogie, de Physique des Matériaux et de Cosmochimie (IMPMC)
75005 Paris, France
E-mail: pierre.sans-jofre@mnhn.fr
E-mail: karim.benzerara@sorbonne-universite.fr

3 State Key Laboratory of Marine Geology
Tongji University Shanghai
200092, P.R. China
E-mail: sv_hohl@tongji.edu.cn

4 Institute of Earth System Sciences
Leibniz University Hannover
30167 Hannover, Germany
E-mail: s.viehmann@mineralogie.uni-hannover.de

Figure 1 Historical and scientific legacy of the *Uranie* expedition (1817–1820). (**A**, **B**) Pages from historical catalogues of the *Muséum national d'Histoire naturelle* (MNHN, Paris) that describe specimens collected by Louis de Freycinet during the *Uranie* voyage, including microbialite samples from Shark Bay ("*Baie des Chiens-Marins*"). (**C**) A hand-colored engraving depicting *Uranie*'s camp on the Peron Peninsula (Shark Bay), published in *Voyage Autour du Monde* (Freycinet, 1824–1844). (**D**) Drawers from the MNHN geological collections housing these historical specimens from Australia. (**E**) An example of a microbialite sample (A115) that was rediscovered at the MNHN; originally described as a "sandy incrustation," from "*Baie des Chiens-Marins*," and signed by Freycinet.

of oolites. Kalkowsky interpreted both stromatolites and associated ooids as microbial in origin, attributing their formation to "*simply organised plant-like organisms*"—an early and prescient recognition of their biological nature long before modern geobiology. Although earlier names (such as *spongiostromides*; Lee and Riding 2023) had been proposed, Kalkowsky's term rapidly became the standard, initiating a century-long discussion about their nature and definition.

From Stromatolites to the Broader Microbialite Concept

> **Definition 1: Stromatolites** are laminated lithified sedimentary structures, deposited in various aqueous environments. When considered as a subcategory of microbialites, they are characterised by structured lamination, growing from an initiation surface under the combined influence of microbial communities and environmental factors.

The classification of stromatolites has evolved significantly over time. Researchers now recognise that stromatolites are not organisms that can be attributed to a single species, but instead result from the activity of diverse microbial communities, shaped by environmental parameters such as water chemistry, energy regime, and sedimentation rate. For instance, stratiform or domal shapes are typically associated with low sedimentation rates, while columnar and branching morphologies tend to reflect higher or more variable inputs (Walter 1972; Riding 2000). With nearly 3.5 billion years of history, stromatolites exhibit an enduring structural continuity, underscoring the significant influence of environmental factors on their formation (Fig. 2; Hofmann et al. 2026 this issue). As a result, the vast diversity

Figure 2 Photographs of ancient and modern stromatolites from the (**A**) ca. 3.43-billion-year-old Strelley Pool Formation of the Pilbara Craton and (**B**) the hypersaline Shark Bay lagoon in Western Australia.

of factors influencing the external morphology of stromatolites has led to descriptive approaches based on observable physical and chemical features. At least two types of definitions have been proposed for stromatolites. First, a textural definition allows us to describe them on directly observable criteria, such as lamination patterns, without requiring proof of biogenicity, i.e., the proof that microbial life was present in the stromatolite-forming environment (see Life in Stone). Second, a genetic definition considers them as a laminated subcategory of microbialites, i.e., rocks formed by microorganisms. This definition requires evidence of biogenicity for recognition, which is sometimes difficult (see Life in Stone). The persistence of these dual definitions

highlights the conceptual richness of stromatolites, which lie at the intersection of biology, mineralogy, geochemistry, and deep-time paleoenvironmental research. The definition we adopt hereafter in this issue (see Definition 1) seeks to bridge these views.

Definition 2: A **microbialite** is a sedimentary rock formed by microbial life, through processes such as trapping and binding of detrital grains, and/or in situ mineral precipitation.

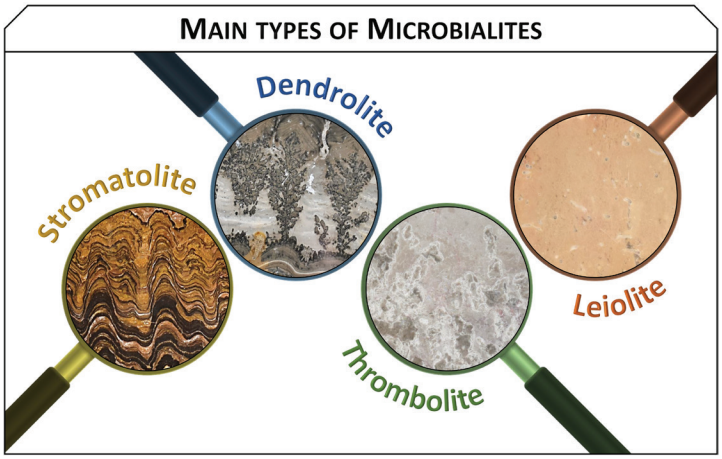

Figure 3 Examples of the four main microbialite types: stromatolite (laminated), dendrolite (branching), thrombolite (clotted), and leiolite (structureless). These terms describe the internal structure (mesostructure) of microbialites; each of these types can occur in various macrostructural forms, such as domes, columns, or cones. They illustrate the key textural diversity of microbial carbonates shaped by microbial activity and sedimentary processes. After Grey and Awramik (2020).

The growing interest in the complex interplay between microbial activity, sedimentary, and mineralising processes has shifted the focus from individual and local morphologies to broader biogenic principles. Thus, Burne and Moore (1987) introduced the umbrella term "microbialite" into the literature to describe "organo-sedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding of detrital sediment and/or forming the locus of mineral precipitation." Within this framework, stromatolites represent the specific sub-category characterised by a laminated internal structure. While this issue focuses primarily on stromatolites as the most persistent macroscopic record of life, the microbialite family includes other distinct textural subcategories that are also explored in the following chapters, including branched dendrolites, clotted thrombolites, and structureless leiolites, among others (see Definition 2; Grey and Awramik 2020; Fig. 3).

The growth of microbialites involves two main microbially mediated mechanisms: (i) bio-sedimentation, where microbial mats trap and bind detrital grains from the environment essentially due to the presence of "sticky" extracellular polymeric substances (EPS); (ii) bio-mineralisation, where microorganisms induce or control mineral precipitation via processes such as pH changes or EPS degradation (see Zeyen et al. 2026 this issue and Toolkit). Although carbonate precipitation is the most common example, many other authigenic minerals, such as pyrite, gypsum, and barite, may also form through microbial activity, including in early Earth environments (e.g., Baumgartner et al. 2020).

Stromatolites have been central to naturalist classifications since the 19th century and were celebrated in the 1980s as the oldest macroscopic evidence of life on Earth (e.g., Schopf 1983). However, they have gradually been reframed within the broader, unified concept of microbialites (Fig. 4). This wider vision developed in the 21st century, alongside the rise of astrobiology and the search for candidate biosignatures (Summons et al. 2008)—indicators of life's presence or activity on early Earth and in extra-terrestrial contexts (Joseph et al. 2020; Hickman-Lewis et al. 2022; see Perspective). Microbialites may preserve physical, mineralogical, and chemical traces of microbial life and environmental parameters from their habitats; therefore, they are valuable archives in the geological record. This conceptual turning point means that microbialites now serve not only as windows into Earth's deep past but also as key targets in the search for life beyond our planet.

EMBRACING DIVERSITY IN MICROBIALITES

From Morphological to Microstructural Variability

Microbialites are considered complex organo-sedimentary structures whose unique morphologies develop from the dynamic interplay of physico-chemical, environmental, and ecological conditions. Their morphological, microstructural, and geochemical diversity is critically important because it provides insight into past environmental conditions that shaped microbial habitats throughout Earth's history. Microbialites vary enormously in size from micro-microbialites, which are less than a millimetre thick, to giga-microbialite domes, exceeding 100 metres in diameter (Hofmann 2000). Their size reflects the cumulative effects of microbial-induced growth, local sedimentation, and hydrodynamics. Moreover, the internal structure of a microbialite is often more significant for understanding nested effects across multiple levels, including its fractal texture and structure (Dupraz et al. 2006). This hierarchical classification encompasses morphological characteristics that describe these structures, ranging from large-scale (mega-structures) to smaller-scale (macro-structures and meso-structures) and microscale (micro-structures; see Grey and Awramik 2020 for more details).

The major types of microbialites are most clearly differentiated at the meso-structural level. In addition to studying the well-known stromatolites, dendrolites, thrombolites, and leiolites (Fig. 3), some researchers are considering microbially induced sedimentary structures (Noffke 2009), which are sedimentary structures of microbial origin in siliciclastic sediments. Furthermore, the potential forma-

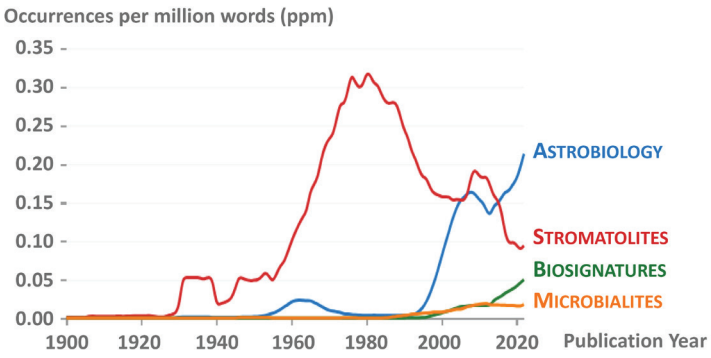

Figure 4 Relative usage frequency of the terms *stromatolites*, *microbialites*, *biosignatures*, and *astrobiology* in English-language books, between 1900 and 2022, based on Google Books Ngram Viewer data. The trajectory of "stromatolites" reflects its early importance in paleontological studies, peaking around the 1980s. The increase in the usage of "microbialites," "biosignatures," and especially "astrobiology" since the late 1990s indicates a shift in focus toward planetary-scale questions and the search for life beyond Earth.

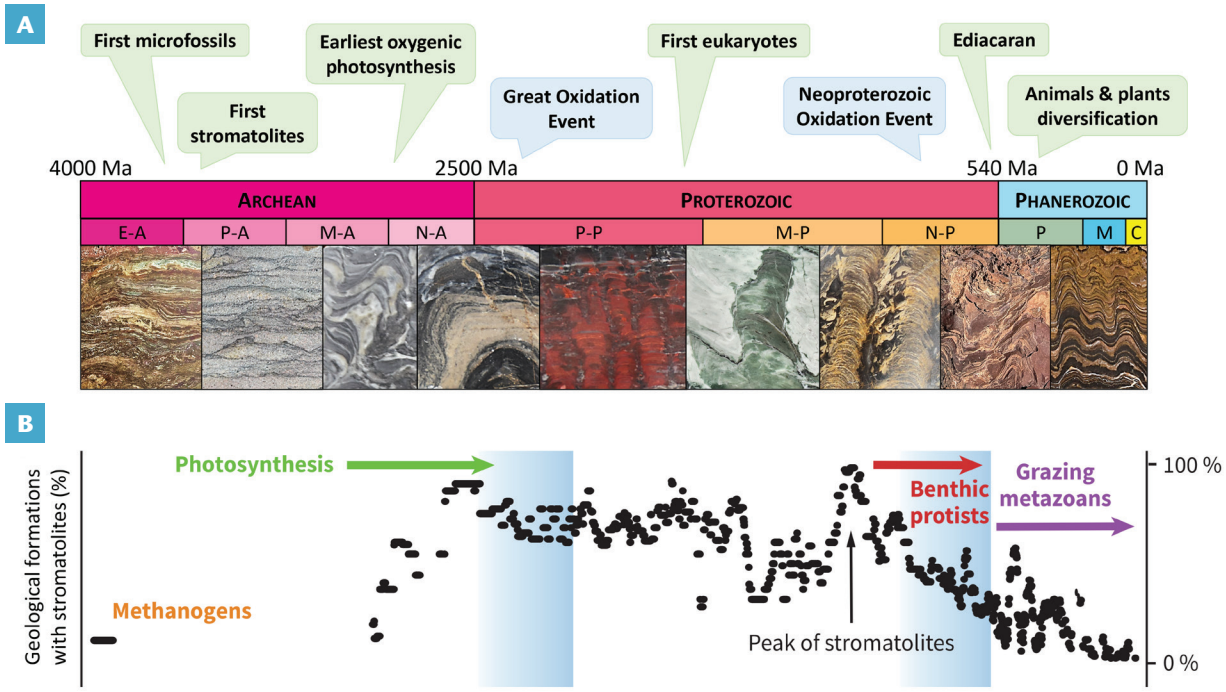

Figure 5 Temporal distribution of stromatolites and major biological and geological milestones throughout geological time. (**A**) Photographs of microbialites from the collection of the MNHN in Paris. Sampling location from LEFT to RIGHT: Dresser Formation (Australia; ca. 3.48 Ga), Moodies Group (South Africa; ca. 3.2 Ga), Pongola Supergroup (South Africa; ca. 2.9 Ga), Campbellrand-Malmani carbonate platform (South Africa; ca. 2.5 Ga), Biwabik Iron Formation (USA; ca. 1.9 Ga), stromatolitic site at Maroonah Station (Australia; ca. 1.5 Ga), Atar Group (Mauritania; ca. 1 Ga), Ouarzazate Group (Morocco; ca. 545 Ma), and Potosí Formation (Bolivia; ca. 70 Ma). (**B**) Relative abundance of stromatolites in the North American marine sedimentary rock record. REPRODUCED FROM PETERS ET AL. (2017). Note: This curve should not be interpreted as a direct global record. The quantification is based on the proportion of North American marine sedimentary formations containing stromatolites, relative to the total number of units. Sampling biases, including uneven preservation and exposure of shallow marine environments (stromatolite-bearing), limit interpretations of stromatolite abundance throughout geological time. While informative, this dataset should be considered a leading indicator of stromatolite trends, pending more globally integrated records.

tion of tufas, sinters, and travertines (de Wet and Davis 2010) under microbial influence is being considered, as well as the formation of calcretes, biocrusts, hydrothermal vents, and speleothems. This broader view of microbialites encompasses all biogenically influenced sedimentary structures, including laminations, branching fabrics, and subtle overprints.

Formation in Diverse Environments

To understand how microbialites form, it is necessary to look beyond their shapes and explore the environmental conditions, ecological dynamics, and microbial metabolisms that control their formation. The complex interplay between external environmental drivers, including light, temperature, salinity, hydrodynamic energy, substrate composition, pH, and nutrient availability, and the internal biological activity of microbial mats is fundamental to the development and preservation of microbialites (e.g., Dupraz and Visscher 2005).

Modern microbialites demonstrate remarkable adaptability, thriving in a wide range of marine, lacustrine, cave, and hot spring environments. This widespread distribution is made possible by the extraordinary diversity of life—a highly complex microbial community spanning all three domains of life (bacteria, archaea, eucaryotes; Mobberley et al. 2015)—that drives microbialite formation. The immense environmental and metabolic versatility of microbialites reflects their ability to adapt to extreme and fluctuating conditions as well as "normal" conditions. Modern molecular biology techniques have allowed identification of the communities involved in modern mineralising microbial mats, and metagenomic studies reveal complex interactions between taxa, highlighting the presence of functionally distinct microbial guilds (see Iniesto et al. 2026 this issue). These communities rely on a broad range of metabolic pathways that significantly impact the redox conditions and pH of the local environment and the microbial mat itself (Dupraz et al. 2011).

Persistent through Geological Time

Beyond their environmental ubiquity, microbialites, especially stromatolites, offer one of the most continuous and informative records of life on Earth, spanning nearly 3.5 billion years (FIG. 5). They are the only fossils that have persisted throughout geological time as their abundance, morphology, and environmental distribution have coevolved with major environmental shifts and biological developments. Large-scale stratigraphic reconstructions (Awramik and Sprinkle 1999; Riding 2006; Peters et al. 2017) reveal three main trends (FIG. 5): (i) a progressive rise in the abundance and complexity of microbialites from the Early Archean to the Early Paleoproterozoic (ca. 3.5 to 2.25 billion years ago); (ii) a period of proliferation and morphological diversification—including the peak abundance of stromatolites—through the mid-Paleoproterozoic to the end of the Mesoproterozoic (2.25 to 1 billion years ago); (iii) a gradual decline from the Neoproterozoic to today, with brief resurgences, particularly in the Cambrian–Early Ordovician, Late Devonian, and Triassic, generally attributed to the aftermaths of mass extinctions.

This temporal evolution reflects environmental constraints and biotic interactions. Indeed, the Early Archean record reveals an anoxic Earth with barely emerged continental landmasses. Ocean chemistry was shaped by hydrothermal

activity and a greenhouse-dominated atmosphere. The enhanced stability of continents and extensive development of shallow marine settings enabled the preservation of Late Archean stromatolites. The oldest confirmed microbialites date back ca. 3.5 billion years and are preserved in the Dresser Formation of the Pilbara Craton (Australia) and the Hooggenoeg Formation of the Kaapvaal Craton (South Africa). Despite diagenesis and metamorphism, these ancient microbialites continue to provide critical insights into biogeochemical cycling, early life, and Earth's habitability (Hofmann et al. 2026 this issue). They also continue to stimulate scientific debate, particularly in relation to older, more controversial structures such as the 3.7 Ga putative stromatolites from the Isua Supracrustal Belt in Greenland (e.g., Van Kranendonk et al. 2025).

Stromatolites, in combination with other geological archives, record the rise of oxygenic photosynthesis since at least the Late Archean (Patry et al. 2025; see Bruggmann et al. 2026 this issue), resulting in the subsequent Great Oxidation Event (2.4–2.2 billion years ago; Lyons et al. 2014). This event marked a significant turning point, as shallow marine microbialites evolved in increasingly oxic settings. Moreover, Neoproterozoic glaciations and the Neoproterozoic Oxygenation Event (800–550 million years ago; Och and Shields-Zhou 2012) further influenced microbialite evolution, thereby enabling the emergence of new microbialite subcategories such as thrombolites and dendrolites. Finally, the decline of stromatolites during the Neoproterozoic and Phanerozoic is commonly attributed to increasing metazoan activity, including grazing, bioturbation, and competition for space. Whilst this biotic pressure may not fully explain the decline of microbialites, given that some modern stromatolites co-exist with metazoans, it is suggested that both biological interactions and changing ocean chemistry shaped the microbialite evolutionary trajectory throughout the Phanerozoic, constraining them to specific ecological niches.

IN THIS ISSUE

Overall, microbialites are both ancient and modern storytellers of Earth's environmental evolution. Preserved and meticulously catalogued in museums and research institutes, microbialites are timeless archives of life's earliest chapters. As science turns toward the frontiers of planetary evolution and astrobiology, these structures invite us to confront the grand questions that will shape tomorrow's discoveries. This issue of *Elements* explores their unparalleled role as dynamic interfaces between biology, chemistry, and geology, archiving our planet's environmental shifts for over 3.5 billion years.

Zeyen et al. (2026 this issue) set the stage by describing the intricate interplay among microbial communities, mineral precipitation, and environmental factors in modern microbialites. They underscore the urgency of preserving these fragile ecosystems in a rapidly changing world, which also offers a direct analogue to early Earth environments and provides critical context for assessing the biogenicity of ancient structures.

Building on this foundation, Iniesto et al. (2026 this issue) describe the microbial communities associated with microbialites and identify the key microbial players involved in biomineralisation. By linking specific biological metabolisms, such as photosynthesis, sulfate reduction, and methanogenesis, to dominant members of these communities, their overview provides valuable insights into the evolution of microbial metabolisms on Earth.

Hofmann et al. (2026 this issue) examine stromatolite occurrences throughout the geological record, linking their morphology, texture, and geochemistry to past depositional environments. Their synthesis demonstrates how these layered structures provide a continuous record of evolving depositional settings and microbial adaptation across Earth's deep history.

Following, Thomazo et al. (2026 this issue) bridge biogeochemistry and ecology by examining the carbon, nitrogen, and sulfur cycles that underpin microbial mat functioning. These elemental cycles not only govern biomineralisation but also mirror shifts in global climate and ocean chemistry, offering a window into how microbial metabolisms have been shaped through Earth's history.

Bruggmann et al. (2026 this issue) investigate the signatures of bio-essential and redox-sensitive trace elements, and their isotopes, in stromatolites. These geochemical proxies are used to reconstruct microbial environmental geochemistry during Earth's history, with a particular focus on oxygenation events. Their insights highlight microbialites as recorders of evolving oxygen oases and examine how trace metals cycled through microbial communities, leading to nutrient accumulation in metabolically diverse microenvironments and shaping deep-time metallome evolution.

Together, these contributions trace a continuum, from modern microbial mats to ancient lithified records, illustrating how life, minerals, and planetary chemistry have co-evolved. As we face accelerating environmental change, understanding these biogeochemical archives not only refines our interpretation of Earth's geologic record but also holds information on how to protect modern microbial habitats and aids in the search for signs of extra-terrestrial microbial life.

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