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Cyanobacteria as drivers of surface micromorphology

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ABSTRACT - Throughout their extensive geological history, cyanobacteria –one of the biosphere's most successful prokaryotic groups– have been a driving force behind pivotal events shaping the planet's biological and physical evolution. Cyanobacteria, particularly those possessing filamentous morphology, have interacted so significantly with the formation of sedimentary deposits that they have become key drivers in the micromorphological evolution of the Earth's surface. Their ability to bind loose sediment has manifested across diverse spatial and temporal scales, establishing biosediment as a critical factor in the formation of surface landforms. In addition to sediment stabilization, cyanobacteria are active agents in rock weathering and soil formation. The impact of cyanobacteria on geobiology and sedimentology is attributed not only to their morphology but also to their bioecology, which involves extracellular polymeric substance (EPS) production for biofilm formation and the capacity to establish symbiotic relationships with other prokaryotic and eukaryotic microorganisms. The most remarkable manifestation of this architectonic capacity is the formation of stromatolites. This paper summarizes how cyanobacteria act as agents that shape surface micromorphologies on Earth.

INTRODUCTION

When did the special relationship between microorganisms and sediment first manifest its effects? Addressing this question leads us to the origins of the earliest sediments and life forms, presenting the perennial "chicken or the egg" dilemma. Although direct evidence of the earliest terrestrial microbial life remains elusive, the Jack Hills zircons in Western Australia –dated to 4.4-4.3 Ga (Wilde et al., 2001)– provide insights from the oldest terrestrial material ever discovered, excluding meteorites. A remarkable aspect of these zircons is their detrital nature; as mineral fragments documenting transport (Nebel et al., 2014), they represent the earliest evidence of sedimentary processes observed on Earth. We can therefore presume that the intrinsic link between life and sediments is as ancient as life itself.

Two factors are decisive in the geomorphological role of microorganisms: the basic morphology of individual cells and the characteristics of microbial community lifestyles. Despite possessing highly diversified morphologies that allow for shape-based classification (e.g., Kysela et al., 2016), the basic cell shapes of bacteria and archaea capable of fossilization can be grouped into a few categories. These include cocci (globose, oval, or spherical) and elongated morphologies, which encompass bacilli (rod-shaped cells and filaments/trichomes), as well as spiral or curved forms. Furthermore, other significant morphologies involve the organization of cocci into clusters or bacilli into long chains. The shape and arrangement of prokaryotic cells across different groups are primary factors in their adaptation to environmental conditions; in other words, form follows function (e.g., Koch, 1995; Young, 2006; Kysela et al., 2016).

A key factor for the lifestyle of prokaryotic communities (including certain unicellular eukaryotes) is their ability to thrive within biofilms. Defined as "matrix-enclosed bacterial populations adherent to each other and/or to surfaces or interfaces" (Costerton et al., 1995, p. 712), biofilms and their hosted microorganisms likely represent the most successful organization of terrestrial life (Flemming & Wingender, 2010). With a matrix primarily composed of polysaccharides, biofilms evolve into microbial mats as they thicken, a process typical of cyanobacteria (Stal, 1995; Davey and O'Toole, 2000; Stolz, 2000; Flemming et al., 2016). These mats can reach significant thicknesses, ranging from millimeters to centimeters, developing into highly efficient, multilayered communities (Costerton et al., 1995; Boomer et al., 2009; Berne, 2023). This lifestyle is ubiquitous; for up to 80% of all prokaryotes, it represents the standard mode of existence (Flemming & Wuertz, 2019).

The evolutionary advantage of biofilm organization is documented by its widespread distribution and early appearance at the dawn of life (Westall et al., 2001; Westall, 2016). This success stems from the biofilm's ability to act as a shield, protecting communities from harsh environmental conditions –such as fluctuations in temperature/pH, dehydration, or intense UV radiation– thereby promoting environmental stability (Shu & Huang, 2022). Stability is also the hallmark of extracellular polymeric substances (EPS), whose cohesive effect enables biofilms to stabilize loose mineral sediments (Neumann et al., 1970; Paterson et al., 2008; Viles, 2012; Zhao et al., 2012). It is primarily through this mechanism that the micromorphological contribute of microorganisms is manifested.

Many microorganisms self-produce biofilms (Bozan et al., 2025). This lifestyle is common among cyanobacteria, both in free-living aquatic forms –where floating biofilm flocs aggregate cells (Mullineaux & Wilde, 2021; Zhong et al., 2024; Bozan et al., 2025)– and in typical biofilm-

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forming filamentous species attached to static surfaces. Because cyanobacteria are exceptionally versatile microorganisms with an extensive geological history, they constitute a unique geomorphic agent. While the first unambiguous fossils date to approximately 1.9 Ga (Demoulin et al., 2019), their origin likely dates back at least a billion years earlier (Fournier et al., 2021). This capability is the subject of the present paper.

BIOSEDIMENT VS. BIOCRUST: A GEOBIOLOGICAL SYNTHESIS

Within the complex and ancient relationship between microbiota and sediment, at least two aspects highlight the primary role of biofilms and microbial mats: the first concerns the stabilizing activity that microbiota, via biofilms, exerts on sediment; the second refers to the role of biofilms in fossil preservation. In both respects, cyanobacteria play a leading role due to their extensive chronological and geographical distribution.

The stabilizing effect of microbial mats on loose, unconsolidated sediment dates back to the earliest morphological records of terrestrial life: the Australian stromatolites from 3.5 Ga (Allwood et al., 2006), the most ancient fossils with conclusive evidence known on Earth. At the time of their formation, sedimentary transport on the Earth's surface was a process already long underway, as evidenced by the extraordinary detrital zircon minerals from Jack Hills.

Perhaps the most striking case of microbial stabilization of fine detrital sediment is that which laid the groundwork for the emergence of terrestrial vegetation (Gibling & Davies, 2012), a pivotal event that impacted the biosphere on a planetary scale. This revolution –occurring much later than the age of the first unambiguous terrestrial microbial fossils discovered in rocks from approximately 3.5 Ga (Noffke et al., 2013; Djokic et al., 2017)– took place during the Cambro-Ordovician period. During this time, the spread of microbial mats on land likely paved the way for bryophytes, the first land plants. This allowed for the progressive modification of detrital sediment composition in alluvial plains, which became increasingly enriched in clay components (Fischer, 2018; McMahon & Davies, 2018). Such an increase in mudrocks continued throughout the Paleozoic through the development of vascular plants and the formation of vast forests. The emergence of these forests subsequently triggered an explosion in insect diversity (Misof et al., 2014), contributing substantially to the structure of Phanerozoic biodiversity.

Due to their desiccation tolerance, cyanobacteria contribute significantly as sedimentary binders (Holzinger & Karsten, 2013). This capability is observable in temporarily emerged areas, which allow for monitoring as hydration levels fluctuate. In these environments, the formation of sediments coated by and mixed with biofilm, commonly defined as biosediment (Fang et al., 2015, 2020), manifests through a variety of forms.

Suitable environments for direct investigation of biosediments include the coastal margins of seas and lakes, as well as areas subject to temporary flooding, such as ephemeral lakes (e.g., desert sabkhas) or salterns. The Cervia salterns in the northern Adriatic Sea, where cyanobacteria play a primary role in biosediment formation (Barbieri & Cavalazzi, 2022), serve as a notable modern example. Within these temperate-climate salterns, certain submerged sectors are not subject to salt extraction; consequently, the local natural systems remain free from anthropogenic modification. However, these areas are periodically exposed to stress induced by emersion phases, during which cyanobacterial mats face dehydration and potential destruction. These settings allow for the observation of how cyanobacteria exhibit desiccation tolerance (Potts, 1999), attributed to both mucilage protection and cell wall thickness, a species-specific factor. At the Cervia site, biosediments composed of dark green-to-brown slimy films and clayey minerals (Fig. 1a) lead to the formation of thickened biocrusts (Fig. 1b-c). These are characterized by a biological component dominated by cyanobacterial trichomes and various diatom species. Owing to their resistance to degradation, biocrusts facilitate the preservation of structures seldom represented in the fossil record, such as the morphological expression of microbial gliding motility (Fig. 2).

Defined as "the living skin of the earth" (Bowker et al., 2018, p. 1), biocrusts –a specialized form of biosediment with a robust biological component (Belnap et al., 2003; Weber et al., 2022)– hold significant global relevance. They develop across a wide range of habitats, occupying an estimated 12% of the Earth's current land surface (Rodríguez-Caballero et al., 2018). By binding soil (or subaqueous substrate) particles together, biocrusts act as stabilisers, preventing erosion from wind or water.

Thick biocrusts, such as those observed in the Cervia salterns, represent a highly developed example where the backbone consists of cyanobacterial mats; here, slender masses are clearly visible on the surface even to the naked eye, owing to their distinct blue-green hue. The processes of biofilm formation, followed by desiccation and the subsequent development of thick biocrusts, result in polygonal patterns of desiccation cracks (Fig. 1b). Repeated folding around polygon margins leads to the formation of curb-like shapes (Fig. 1c), structures derived from the behavior of microbial mats, which grow during submerged phases and undergo desiccation during emersion (Noffke et al., 2001a; Barbieri & Cavalazzi, 2022; Blattmann et al., 2025). Crucial for soil aggregation (Weber et al., 2022), biocrusts can also persist in submerged environments, largely due to the degradation resistance of cyanobacterial communities that induce the formation of cohesive, yet elastic, surfaces.

An extensive body of literature describing the intimate relationship between microbiota and sandy sediment refers to biostabilization processes (Viles, 2012; Harris et al., 2024, and references therein); these occur where microorganisms, by colonizing a substrate through their biofilms, impart specific shear resistance. Microbial Induced Sedimentary Structures, commonly referred to as MISS (Noffke et al., 2001b), represent a characteristic biostabilization product. MISS constitute a class of structures in which microbial mats, predominantly those produced by cyanobacteria, act as genuine architects of sedimentary frameworks (Noffke et al., 2022). Furthermore, through sediment trapping and binding, they serve as the primary agents mediating erosion and deposition of loose sediment in aquatic environments

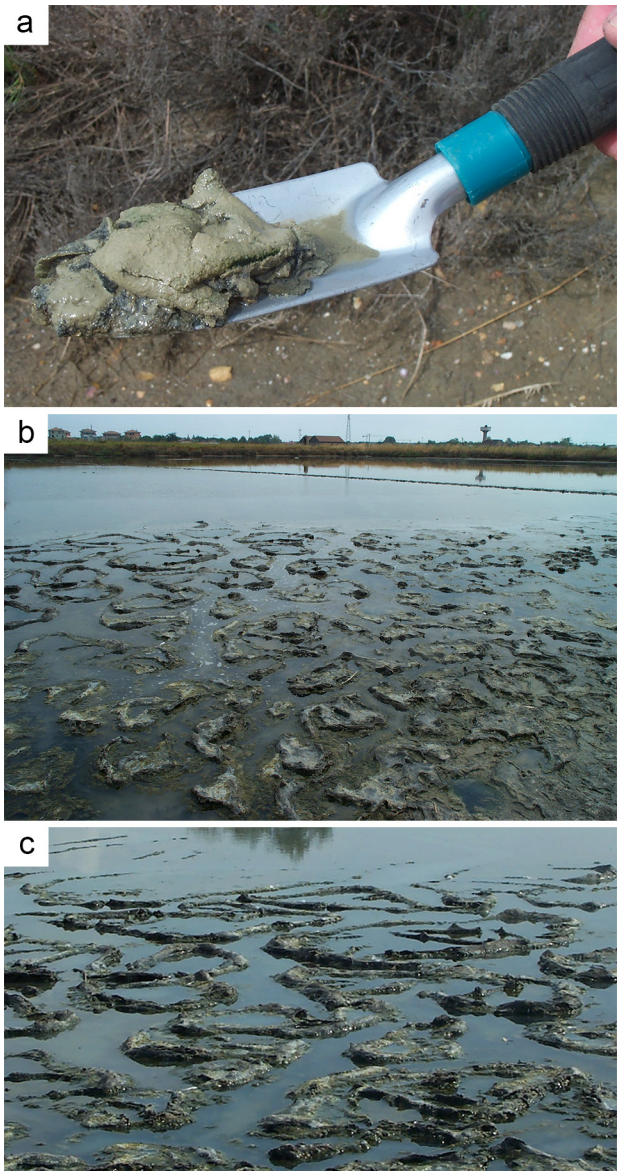

Fig. 1 - Biocrusts at the Cervia salterns, northern Italy. a) Soft, cyanobacteria-dominated biocrust, composed of dark green to brown slimy films and clayey sediment. b) Upon repeated subaerial exposure, the biocrusts develop desiccation polygons that thicken and harden, attaining a leathery appearance. c) Curb-like margins around desiccation polygons result from the formation of microbial mats which, by folding, create thickening.

(Noffke & Paterson, 2008). The result is the formation of remarkably stable biosedimentary structures, capable of being preserved and identified within the fossil record, even from very ancient geological periods.

As mat producers, cyanobacteria can create protective envelopes surrounding biological remains, such as animal or plant debris; this significantly delays degradation, thereby facilitating fossilization. Through this process, their EPS mold surfaces, forming fine negative impressions and positive replicas of the original structures (e.g., Briggs, 2003; Wu et al., 2014; Iniesto et al., 2016). Furthermore, biofilm surfaces can influence mineralization processes, contributing to the overall preservation of fossils.

The case of Ediacaran (and Ediacara-style) fossils, where fossilization frequently occurs within coarse-

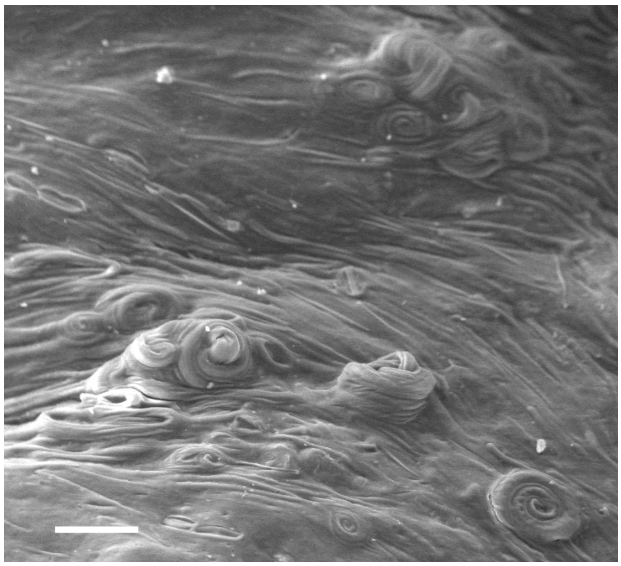

Fig. 2 - Cervia salterns, northern Italy. Environmental scanning electron microscope (ESEM) micrograph of coiled cyanobacterial trichomes plunged in their mucilage secretion. Coiling is a presumable result of gliding motility (after Barbieri & Cavalazzi, 2022). Scale bar: 100 µm.

grained siliciclastic sandstone, such as in the classic Australian site of the Flinders Ranges (Gehling & Droser, 2009; McMahon et al., 2021), is paradigmatic. In this context, the preservation of fine morphological details, in a sediment type that would otherwise be unsuitable (Fig. 3), is significantly enhanced by rapid mineral precipitation. In this way, the so-called "death masks" (Gehling, 1999) are formed: microbial biofilms which, by rapidly cementing the sediment around soft-bodied organisms, have allowed them to be preserved as casts. Cyanobacteria and other biofilm-producing microorganisms were instrumental in

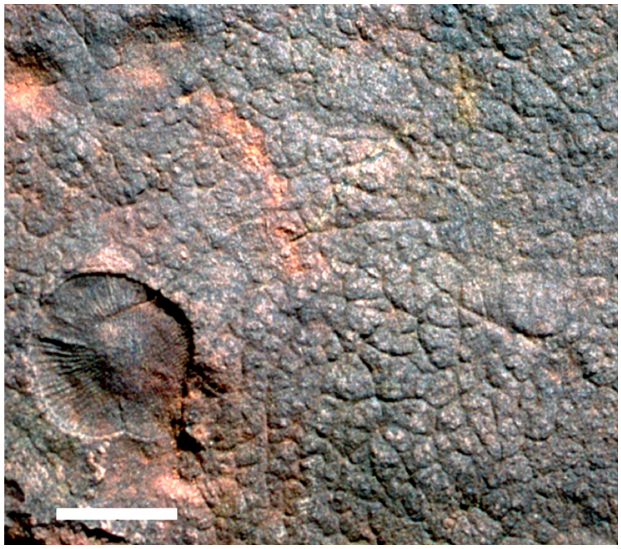

Fig. 3 - Ediacara biota from the Flinders Ranges of South Australia. "Elephant skin" texture, a microbial induced sedimentary structure (MISS), on a medium-grained sandstone overprinted by *Dickinsonia* (bottom left), a typical Ediacaran genus (after Gehling & Droser, 2009). Scale bar: 2 cm.

this process (Newman et al., 2016; Moore et al., 2021; Slagter et al., 2022).

The generally high level of microbially mediated taphonomy observed in Ediacaran fossils (Laflamme et al., 2011, and references therein) is attributable to the predominantly epibenthic lifestyle of this fauna. The widespread establishment of microbial mats at the sediment-water interface likely increased the structural stability of both the sedimentary surface (via biostabilization) and the macroscopic organisms, thereby creating a taphonomic pathway conducive to their preservation.

LIFE BENEATH A ROCK: STRATEGIES FOR SURVIVAL

It is estimated that up to 70% of all microorganisms on Earth live beneath its surface (Li et al., 2020), ranging from the interior of rocks, pores, and fissures near the surface down into the deep biosphere. In these environments, life is centered on a "life in the slow lane" strategy, characterized by minimal resource requirements sufficient to sustain extremely slow growth rates. This world is dominated by highly diverse chemosynthetic communities (e.g., Walker & Pace, 2007; Sajjad et al., 2022), where habitat variety fosters high biological diversity. Closer to the Earth surface, however, shallow endolithic environments are inhabited by photosynthetic microorganisms (Fig. 4). These occupy the thin, outermost layer (up to a few centimeters) of the subsurface, reaching as far as sunlight can provide a viable energy source. This sector of superficial endolithic life plays a significant geomorphic role.

Among photoautotrophs, cyanobacteria hold a key position due to the extensive nature of their endolithic communities. Their long geological history –with presumed cyanobacterial microfossils reported from early Archean strata, though their biological origin remains controversial (Demoulin et al., 2019)– has allowed them to adapt to highly diversified conditions. Indeed, cyanobacteria are widespread in extreme environments characterized by limiting factors such as hyperaridity, high UV radiation, hypersalinity, or hydrothermal activity (e.g., Stal, 2007). In desert regions (Fig. 5), where stressors like low humidity and intense UV radiation coexist, the endolithic lifestyle is particularly advantageous for promoting water retention and UV screening. Regarding desiccation, the coccoid genus *Chroococcidiopsis* (Fig. 5d) is remarkable; this endolithic cyanobacterium has developed a successful strategy (i.e., extreme dehydration) to survive under extreme desiccation stress (Li et al., 2025).

Widespread in desert regions such as Salar Grande (Stivaletta et al., 2012), the most arid sector of the Atacama, the world's driest desert, the presence of *Chroococcidiopsis* can be rapidly diagnosed by the coloration of its pigments within host rocks, such as evaporitic salts (Fig. 5b-c). Endolithic cyanobacteria have also developed a high resistance of their photosynthetic apparatus to fluctuations in sunlight intensity (Murray et al., 2022), significantly enhancing their adaptative capacity.

In high-altitude deserts, the endolithic lifestyle serves a protective purpose, manifested in the vertical zonation of colonies based on their photosynthetic pigments (Wierzchos et al., 2018). In the Atacama salt flats, for instance, one of the regions with the most intense UV radiation on Earth, millimeter-scale green layers rich

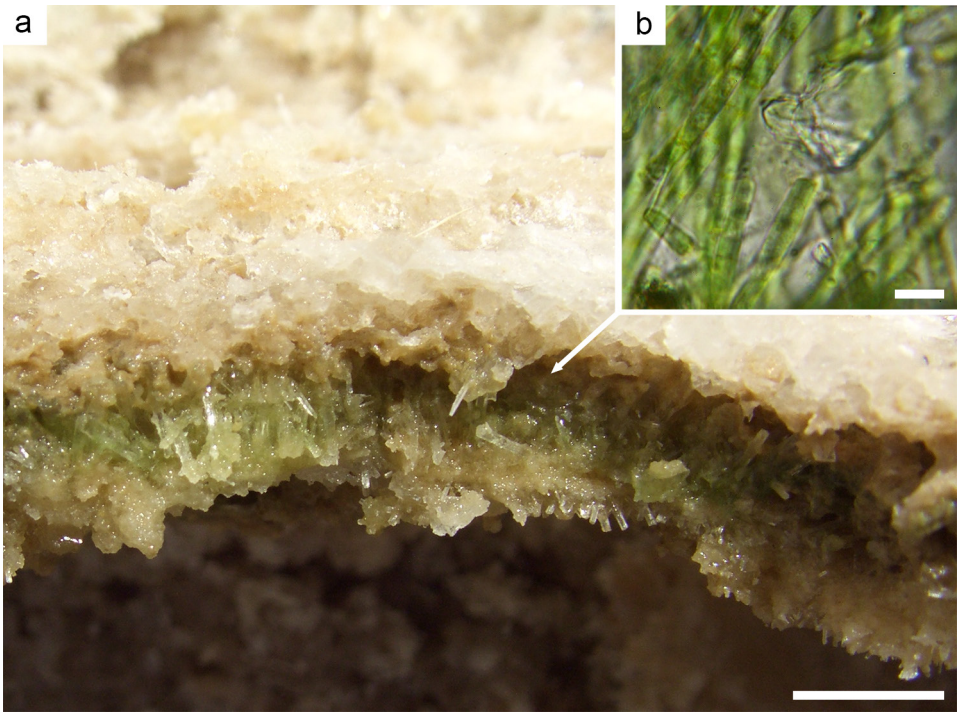

Fig. 4 - Salt lake of the Chott el Jerid, Tunisia. Halite crust where cyanobacterial trichomes (b) find protection. Scale bars: 1 cm (a), 10 µm (b).

in cyanobacterial chlorophyll are situated beneath orange-colored layers of green algae rich in carotenoids (Wierzchos et al., 2015). This suggests that carotenoids exert a shielding effect against UV radiation, acting as a protective factor for the underlying cyanobacteria. Such a vertical arrangement is also driven by light intensity. This is observed with pigments such as bacteriochlorophyll, found in purple bacteria, which require lower light levels than cyanobacteria (e.g., Wang et al., 2025). In the Atacama, purple bacteria are regularly observed positioned below the layers colonized by cyanobacteria (Stivaletta et al., 2011).

Through the production of colorful pigments and extracellular substances, cyanobacteria play a remarkable, often hidden, geomorphic role. These colors document functional adaptations that drive chemical

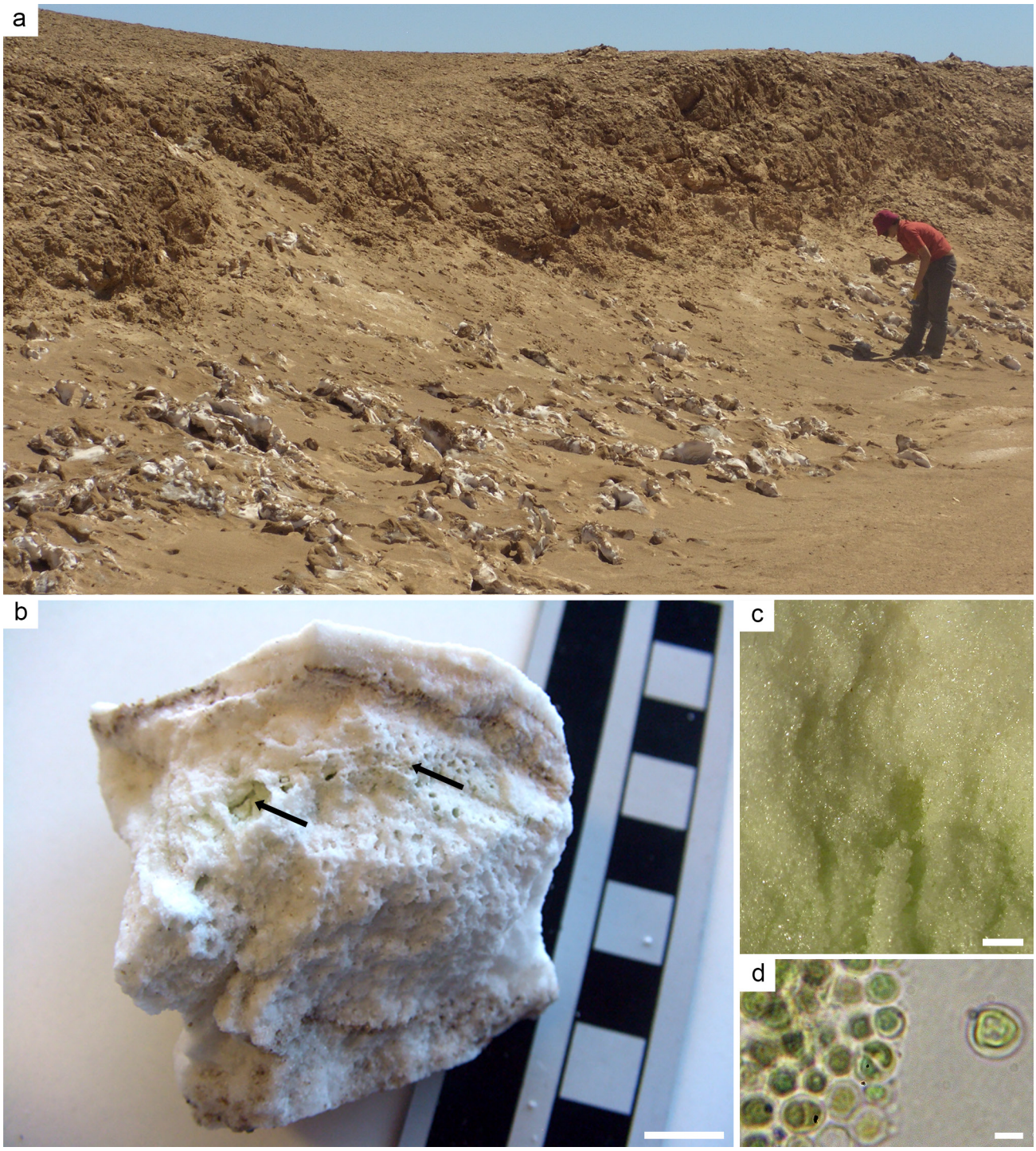

Fig. 5 - a) Fossil salt (halite) extensively outcrops at Salar Grande in the Cordillera de la Costa, the driest sector of the Atacama region, Chile. b) Fragment of finely crystalline halite featuring light green sectors (arrows); normal stratigraphic orientation. c-d) Cross-sectional detail of a light green sector within the crystalline halite; the coloration results from colonization by cells of *Chroococcidiopsis*, a coccoid endolithic cyanobacterium (transmitted light micrograph in d). Scale bars: 1 cm (b and c), 10 µm (d).

weathering, surface stabilization, and erosion (Zhao et al., 2012; Villa et al., 2022; Wild et al., 2022). The role of endolithic cyanobacteria as geomorphic agents is primarily manifested through their activity as euendolithic colonizers. Their ability as mineral-boring organisms is widely observed across space and time; in carbonate substrates, the oldest known case involves cyanobacteria penetrating early Proterozoic stromatolites in China (Zhang & Golubic, 1987; Demoulin et al., 2019). Their high preservation potential and distinctive morphology make their remains easily recognized in the fossil record (Golubic & Seong-Joo, 1999), especially due to their ability to colonize carbonate and dolomitic rocks. During microboring, the resulting damage can be so intense that it produces micrometer-sized debris, leading to the progressive dissolution of the rock (e.g., Schneider & Campion-Alsumard, 1999; Roush & Garcia-Pichel, 2020; Wassenaar et al., 2023). Consequently, endolithic microboring is a major contributor to the morphogenesis of carbonate rocks. This process occurs across vastly different scales: from entire geological formations down to single limestone pebbles (Wetzel et al., 2024) and even sand-sized particles, such as fossil and modern ooids (Knoll et al., 1986; Al-Thukair & Golubic, 1991).

The contribution of cyanobacteria as a destructive force is also evident in carbonates of biological origin (Wyness et al., 2022). The most prominent case is that of reef-building corals and other calcifying organisms, where they participate in the biogenic destruction of calcium carbonate alongside other bacteria, algae, and fungi (Yamazaki et al., 2008; Pernice et al., 2020). This degradation occurs primarily through bioerosion, although the specific extent of damage caused by cyanobacteria compared to other phototrophic endoliths remains to be fully elucidated.

THE MESSINIAN SALINITY CRISIS: A SPECIAL CASE

A compelling case highlighting the role of microbial communities, including endolithic cyanobacteria, is provided by the Messinian Salinity Crisis (Krijgsman et al., 2024). During this massive geological event at the end of the Miocene –which led to the desiccation of most Mediterranean basins and the formation of vast expanses of evaporitic salts (primarily chlorides and sulfates)– cyanobacteria played a primary role as geomorphic and sedimentological agents. Before environmental conditions favored evaporite precipitation and transformed the Mediterranean into a complex of ephemeral lakes similar to modern Saharan sabkhas, microbially-mediated formations were deposited. A key example is the Calcare di Base (Fig. 6), a stromatolitic limestone (Vai & Ricci Lucchi, 1977). These rocks contain fossils of filamentous microbes, including cyanobacteria, sulfur-oxidizing bacteria, and other chemosynthetic taxa that mediated carbonate precipitation (Perri et al., 2017; Vescogni et al., 2025).

During the subsequent deposition of calcium sulfates at the height of the Messinian Salinity Crisis, sulfur-oxidizing bacteria and cyanobacteria (both filamentous and non-filamentous) became significant microbiological components. Similar to observations in modern evaporitic sulfates (Dong et al., 2007; Stivaletta & Barbieri, 2009), cyanobacteria in Messinian gypsum found both a suitable substrate and effective protection from UV radiation and excessive solar exposure (Rouchy & Monty, 2000; Jehlička et al., 2024 cum bibl.). The "spaghetti-like" structures (Vai & Ricci Lucchi, 1977) described in the Messinian selenitic gypsum of the northern Apennines represent a spectacular case of direct field observation, visible with a standard hand lens, of filamentous microbial communities (Fig. 7). Within large gypsum crystals, microbial filaments are densely packed, reaching a thickness of 100 μm; these were originally attributed to extensive cyanobacterial communities (review in Panieri et al., 2008). Subsequent genetic and molecular analyses aimed at understanding the origin of these filaments have confirmed the presence of both cyanobacterial communities (Panieri et al., 2010) and sulfur-oxidizing bacteria (Natalicchio et al., 2021); both of which are thought to have promoted the growth of the gypsum crystals.

The role of endolithic cyanobacteria as geomorphic agents, which operated on a large scale in the Mediterranean region during the late Messinian, can be observed today in natural laboratories such as modern hypersaline arid regions. In these settings, cyanobacteria contribute to the growth and stabilization of evaporitic gypsum crystals by generating specific microenvironments induced by their biofilms and metabolic products (Thompson & Grant Ferris, 1990; Canfora et al., 2016; del Buey et al., 2021; Orellana et al., 2025). Furthermore, the protective function of gypsum crusts, which filter UV radiation, fosters a mutually beneficial, self-reinforcing cycle between minerals and biota. This phenomenon is clearly observable, for example, in the evaporitic gypsum crusts atop artesian spring mounds in southern Tunisia (Fig. 8). Standing up to ten meters high, these mounds result from sand accumulation cemented by gypsum precipitation, where the endolithic communities within the gypsum crusts are dominated by cyanobacteria associated with other halophilic microorganisms (Stivaletta & Barbieri, 2009; Stivaletta et al., 2009).

STROMATOLITES AND CYANOBACTERIA: AN INTIMATE RELATIONSHIP

The relationship between microbialites, defined as organosedimentary structures built by microbial communities, and cyanobacteria dates back to the Archean and remains highly significant today (e.g., Burns et al., 2009; Grey & Awramik, 2020; Landing & Johnson, 2024; Noffke & Awramik, 2026). Within this context, stromatolites represent the type of microbialite with the most pronounced geomorphic potential, constituting the primary geological record of cyanobacterial activity. During the Precambrian Eon, cyanobacteria played a leading role as builders of sedimentary carbonate platoforms through stromatolite development (Grotzinger & Knoll, 1999; Westall & Xiao, 2024). Although far less widespread than during the Precambrian –a period characterized by huge morphological diversification (Awramik & Sprinkle, 1999)– active cyanobacterially-driven stromatolites persist in several modern marine

Fig. 6 - Romagna Apennines, northern Italy. Stromatolitic limestone deposited by the activity of filamentous microbes; they acted as a precursor to the Messinian evaporitic deposition. Hammer for scale.

and continental environments, including lacustrine and fluvial systems. Similar structures also occur in thermal and calcareous springs (e.g., Makk et al., 2025), environments frequently associated with the formation of carbonate deposits (travertine or tufa) through chemical precipitation. In contrast to temperate settings, certain extreme environments offer a specific advantage to microbial life by excluding most grazers, such as snails, fish, and certain crustaceans (Garrett, 1970; Feazel et al., 2008), that would otherwise consume cyanobacterial mats, thereby precluding the chance of accretion for stromatolitic structures (Fig. 9).

In all settings, stromatolites (especially domal and columnar varieties) are generated by microbial biofilms that trap sedimentary particles or induce mineral precipitation (Riding, 2011). Their characteristic millimetric lamination may reflect changes in sedimentation rates (Seong-Joo & Golubic, 1998) or in calcium carbonate precipitation. The shape of a stromatolite is not random: it is the physical manifestation of the interplay between biofilm growth and environmental energy (Petroff et al., 2010; Noffke & Awramik, 2026). The world's most extensive living stromatolite system thrives in the hypersaline waters of Hamelin Pool at Shark Bay, Western Australia (Bauld, 1984). As in other parts of the world, cyanobacteria – comprising both coccoid and filamentous morphologies– form the structural framework of the Hamelin Pool stromatolites (Goh et al., 2009; Suosaari et al., 2016; Suosaari et al., 2018). Similar to other classic localities, such as the Bahamian stromatolites (Reid et al., 2000; Foster et al., 2009), filamentous cyanobacteria act as the primary agents that bind and trap sediment grains, thereby constituting the supporting structure of the stromatolite body. It is not exclusively filamentous cyanobacteria that, due to evident morphological factors, determine the laminated structure of stromatolites. A direct relationship has been observed between coccoid cyanobacteria, the extent of lamination, and calcification capacity within microbial mats (Suosaari et al., 2016).

In modern sabkhas, which are arid environments characterized by extreme salinity, high temperatures, and intense UV radiation, the formation of stromatolites can be effectively observed (e.g., Duane & Al-Zamel, 1999). Under the extreme conditions typical of these settings, the absence of animal grazing enables the development of complex, stratified microbial biofilms. These communities produce the thick mats that underpin stromatolite construction.

Due to their abundant production of EPS, cyanobacteria often act as pioneer organisms even in hypersaline environments, establishing the initial biofilm upon which the rest of the microbial community is later organized (Oren, 2010). Certain cyanobacterial species are so well-adapted that they can survive even as sodium chloride concentrations approach saturation (Oren, 2015). They behave as extremophiles inhabiting extreme conditions; a classic case is that of *Chroococcidiopsis*. Detected in modern stromatolites, this genus shows a widespread and constant presence in both modern and fossil evaporitic environments (Jehlička et al., 2024).

CASE-STUDY: CYANOBACTERIAL CONTRIBUTION TO STROMATOLITE DEVELOPMENT

Modern examples of active stromatolite formation are essential for understanding the origins of their vast Precambrian expansion and the nature of laminated, accretionary structures that typify stromatolite morphologies: the living testimonies of Earth's earliest ecosystems. A case of considerable interest is found in certain sectors of the Oum Dba sabkha, a wide, salt-encrusted depression located approximately 40 km

north of El Aaiún in Western Sahara (Morocco). Here, a variety of geomorphic features related to microbial biomineralization develop within water- and salt-dominated environments (Barbieri & Cavalazzi, 2018). Along the southernmost margin of the sabkha, where moderately saline groundwater constantly flows to the surface, dome-shaped stromatolites are currently forming through the action of mat-forming microorganisms (Fig. 10a). In these developing morphologies, cyanobacterial trichomes act as pillars, representing the primary scaffolding of the entire system (Fig. 10b-d). Other microorganisms, such as several diatom species detected on the soft surface of the stromatolite domes, also secrete biofilms and are capable of influencing local pH levels.

A peculiarity of this sabkha, which distinguishes it from others in the El Aaiún region, is the calcium carbonate precipitation induced by the metabolic activities of phototrophic microbial communities, specifically cyanobacteria and diatoms. In continental sabkhas, evaporitic minerals such as calcium sulfates and, predominantly, chlorides typically form; the occurrence of calcium carbonate is far rarer, as it requires specific groundwater geochemistry and ecosystems capable of inducing its precipitation (Dupraz et al., 2009). In a sabkha environment, under appropriate pH conditions and dissolved inorganic carbon concentrations –and provided there are available calcium ions and nucleation sites– calcium carbonate can form through a microbially mediated process governed by the metal-binding properties of EPS and bacterial cell surfaces (Castanier

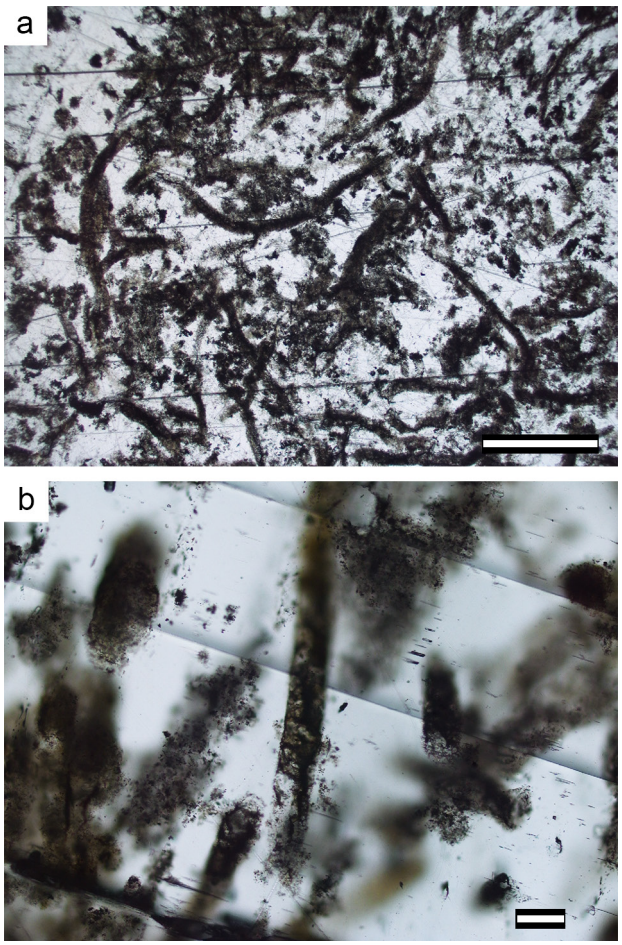

Fig. 7 - Romagna Apennines, northern Italy. Transmitted light micrographs of filamentous microbial communities ("spaghetti-like" structures) hosted within gypsum crystals of the Messinian Salinity Crisis (micrographs courtesy B. Cavalazzi). Scale bars: 1 mm (a), 100 µm (b).

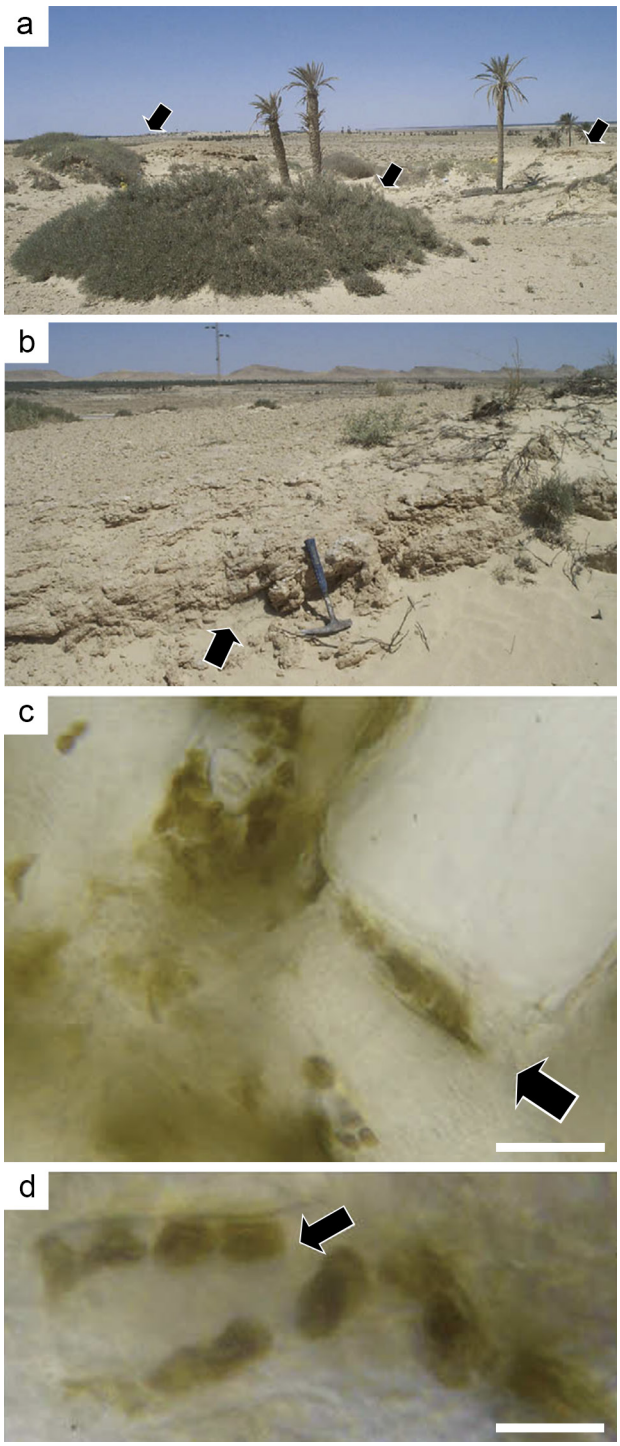

Fig. 8 - Evaporites (gypsum) and eolian sediments constitute spring mounds (arrows in a) in southern Tunisia. These mounds are topped by thick evaporite crusts (arrow in b) where cyanobacteria and other endoliths (transmitted light micrographs in c and d) thrive within the crystal framework (in c) forming chain arrangements (in d) (after Stivaletta & Barbieri, 2009). Scale bars: 10 µm (c), 5 µm (d).

et al., 1999; Braissant et al., 2007; Dupraz et al., 2009; Bontognali et al., 2010). This specific set of conditions coexists in the Oum Dba sabkha, where active travertines (Barbieri & Cavalazzi, 2018) and dome-shaped carbonate stromatolites are readily observable.

A cross-section of one of these stromatolites reveals a progression from the surface layer of living microbial mats to the underlying mineralized portion composed of calcium carbonate laminae. The soft, sticky surface mucilage, rich in photosynthetic pigments, hosts the organisms responsible for its formation: pennate diatoms and filamentous cyanobacteria, both of which are prolific EPS producers. The underlying mineralized framework consists of laminae built by symbiotic colonies of cyanobacteria organized into vertically arranged bundles of filaments (trichomes) (Figs 10c-d, 11). Close observation of the gelatinous surface of the forming stromatolite (Fig. 10a) reveals a distinct microterracette topography. This small-scale feature is also present on the surface of other sabkha sectors characterized by Mg-calcite precipitation, where it results from the interaction between physical factors (i.e., water flow, mineral precipitation, and morphological gradients) and the activity of biofilm-producing microorganisms (Barbieri & Cavalazzi, 2018). Notably, cyanobacteria and diatoms –specifically representatives of the genera *Mastogloia* and *Berkeleya*– contribute significantly through the production of EPS, the primary component of biofilms. The documented symbiotic relationships between *Mastogloia* and cyanobacteria (Snoeijs & Murasi, 2004; Adams et al., 2012) likely further promoted the development of this micromorphology. Recent research highlights that the interaction between prokaryotes (primarily cyanobacteria) and eukaryotes (especially benthic diatoms) is a key synergistic factor in the formation of microbialite textures and fabrics in continental hypersaline settings (Gomez et al., 2018; Lencina et al., 2021; Cubillos et al., 2024).

Numerous cyanobacterial species live organized into trichomes, which can comprise hundreds or even thousands of cells arranged end-to-end. This organization is specifically adapted to optimize solar exposure (Tamulonis et al., 2011; Biddanda et al., 2015; Varuni et al., 2017) in response to light stimuli (phototaxis), a behavior long recognized in both prokaryotes and plants (Haupt, 1966). Consequently, phototaxis plays a fundamental role in determining the motility of filamentous cyanobacteria by imposing a common orientation at the colony scale (Pentecost & Franke, 2010; Menon et al., 2021). In the Oum Dba stromatolites, the stabilization of these trichomes, and thus of the laminae, occurs through mineralization. This process involves the calcification of both the closely spaced trichome tubules in their phototactic arrangement and the surrounding mucilaginous sheath; during organic degradation, this sheath may take on the appearance of fine fibers (Fig. 11a). Calcification occurs concurrently with the life of the microbial communities, representing a form of "real-time" fossilization (Hoffmann et al., 2021 cum bibl.).

A distinct gradient in calcification occurs within the laminae: the lower portion of each lamina consists of compact micrite, whereas the upper sector is only partially mineralized in the spaces between the trichomes, often retaining a significant organic component. This variation

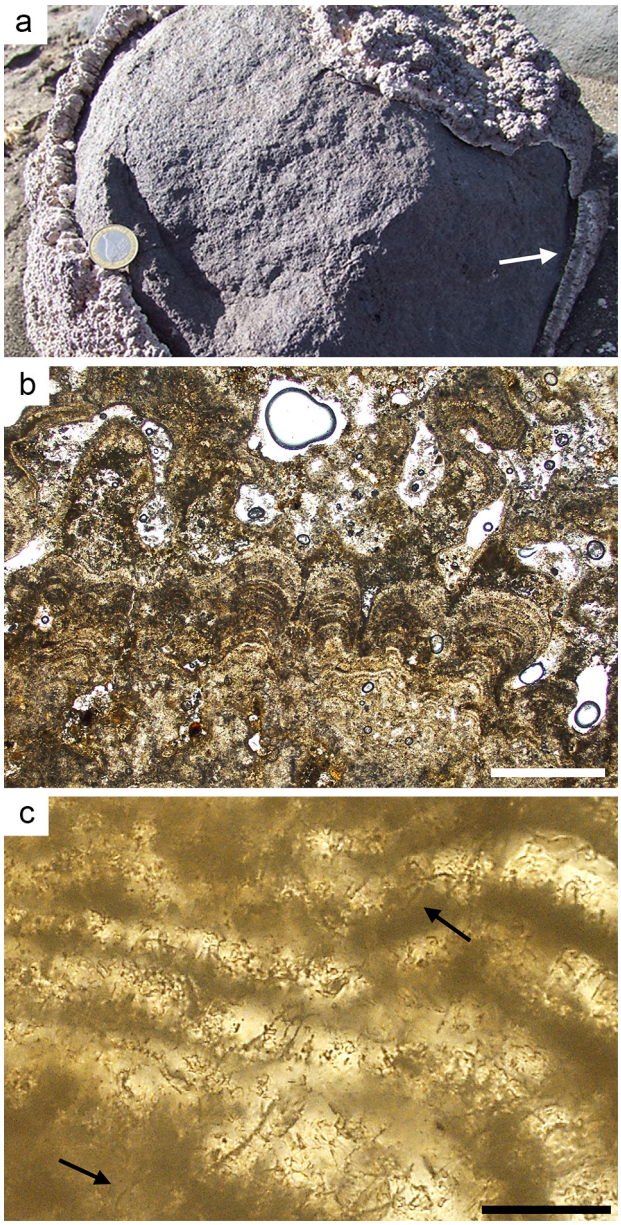

Fig. 9 - a) Centimeter-scale, microstromatolitic crust accreted on a basalt substrate from Lake Abhe, a hyperalkaline and hypersaline environment in the Afar Rift, Djibouti. Coin (3 cm) for scale. b) Optical microscope view of the carbonate microstromatolitic crust, exhibiting a laterally linked microcolumnar fabric and internal laminations. Scale bar: 1 mm. c) Optical microscope view of filamentous structures (interpreted as cyanobacterial sheaths) within the laminae making up the microstromatolite (after Dorneles et al., 2024). Scale bar: 50 µm.

in the degree of calcification (Fig. 11c) may be explained by the impact of mineral precipitation and subsequent burial on the cyanobacteria. It is suggested that upon burial, the microbial mat is no longer able to induce the pH modifications necessary for micrite precipitation (Kromkamp et al., 2007). Processes that cause burial, such as the formation of a micritic layer, which has been observed in this sabkha and elsewhere (e.g., Reid et al., 2000), trigger heterotrophic conditions that contribute to the deactivation of the microbial mat, leading to the cessation of carbonate precipitation. This highlights the

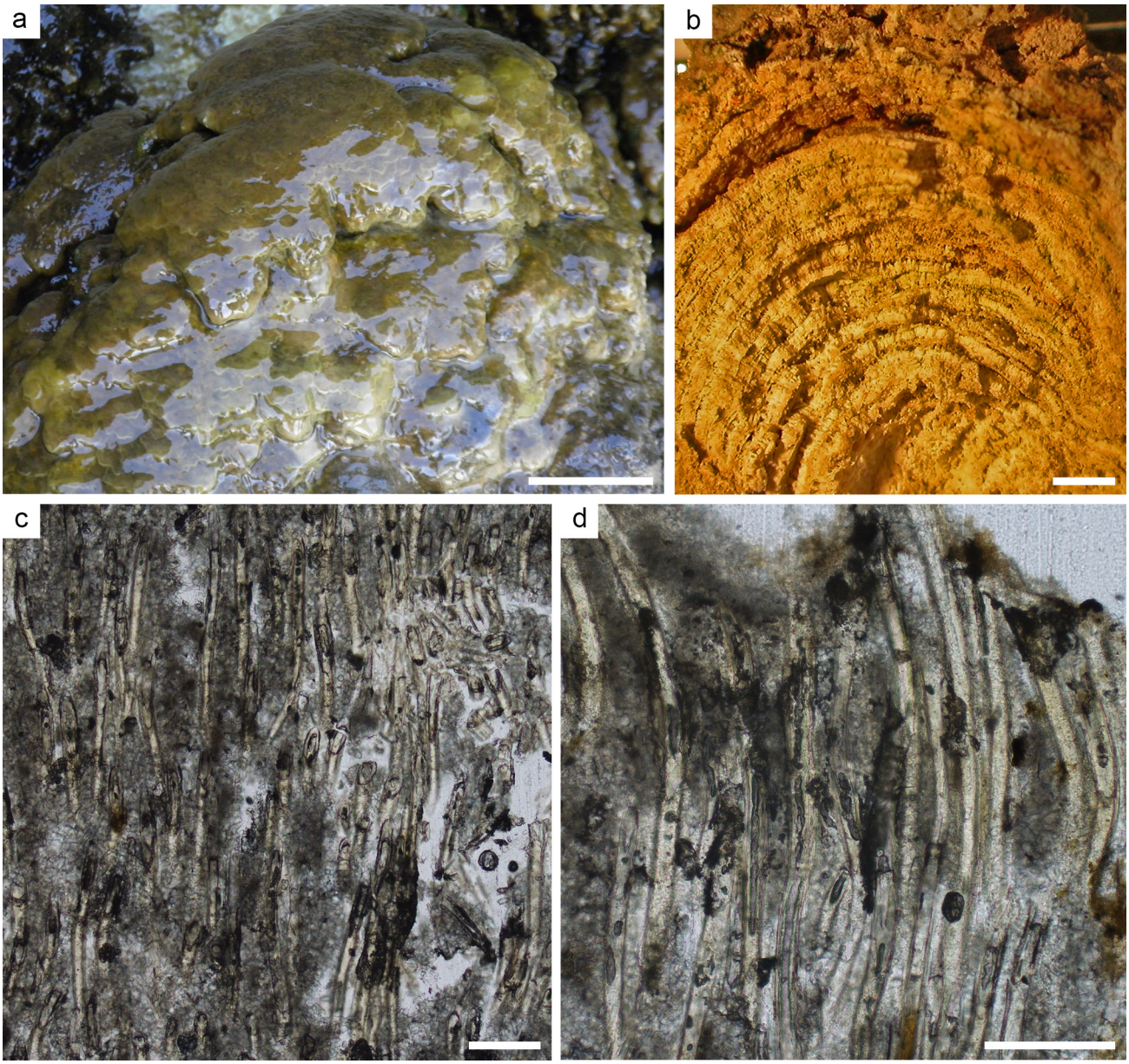

Fig. 10 - a) Actively forming, dome-shaped stromatolite at Oum Dba sabkha, Western Sahara, Morocco; note the gelatinous surface comprising living cyanobacterial mats. Scale bar: 10 cm. b) Optical microscope view of a mineralized section of the stromatolite, displaying calcium carbonate laminae of consistent thickness. Scale bar: 1 mm. c-d) Within a stromatolite lamina: closely spaced trichome tubules in a phototactic arrangement surrounded by mucilaginous sheaths; note the only partial mineralization of the trichome walls and the surrounding mucilage. Scale bars: 100 µm.

direct cause-and-effect relationship between biological activity and mineral morphogenesis.

CONCLUDING SUMMARY

Cyanobacteria and their microbial mats play a unique role in shaping the sedimentary architecture of the Earth's surface, influencing both ancient and modern ecosystems by merging biological activity with geological transformation.

As global-scale geomorphic agents, they have consolidated loose sediments for billions of years, creating a "living skin" that resists erosion and desiccation. This is exemplified by the changes in the sedimentary composition of Cambro-Ordovician alluvial plains, a process that paved the way for the emergence of land plants and the subsequent diversification of terrestrial life. By adopting an endolithic lifestyle, cyanobacteria dwell within rocks to survive UV radiation and hyper-aridity. While seeking protection, they simultaneously act as significant geomorphic agents through microboring (bioerosion) and the mediation of mineral growth (such as evaporites during the Messinian Salinity Crisis), they have actively modified geological formations and influenced the morphogenesis of carbonate rocks.

Cyanobacteria induce mineral precipitation and facilitate "real-time" fossilization, a process highly dependent on active microbial metabolism. As taphonomic mediators, they enable the high-fidelity preservation

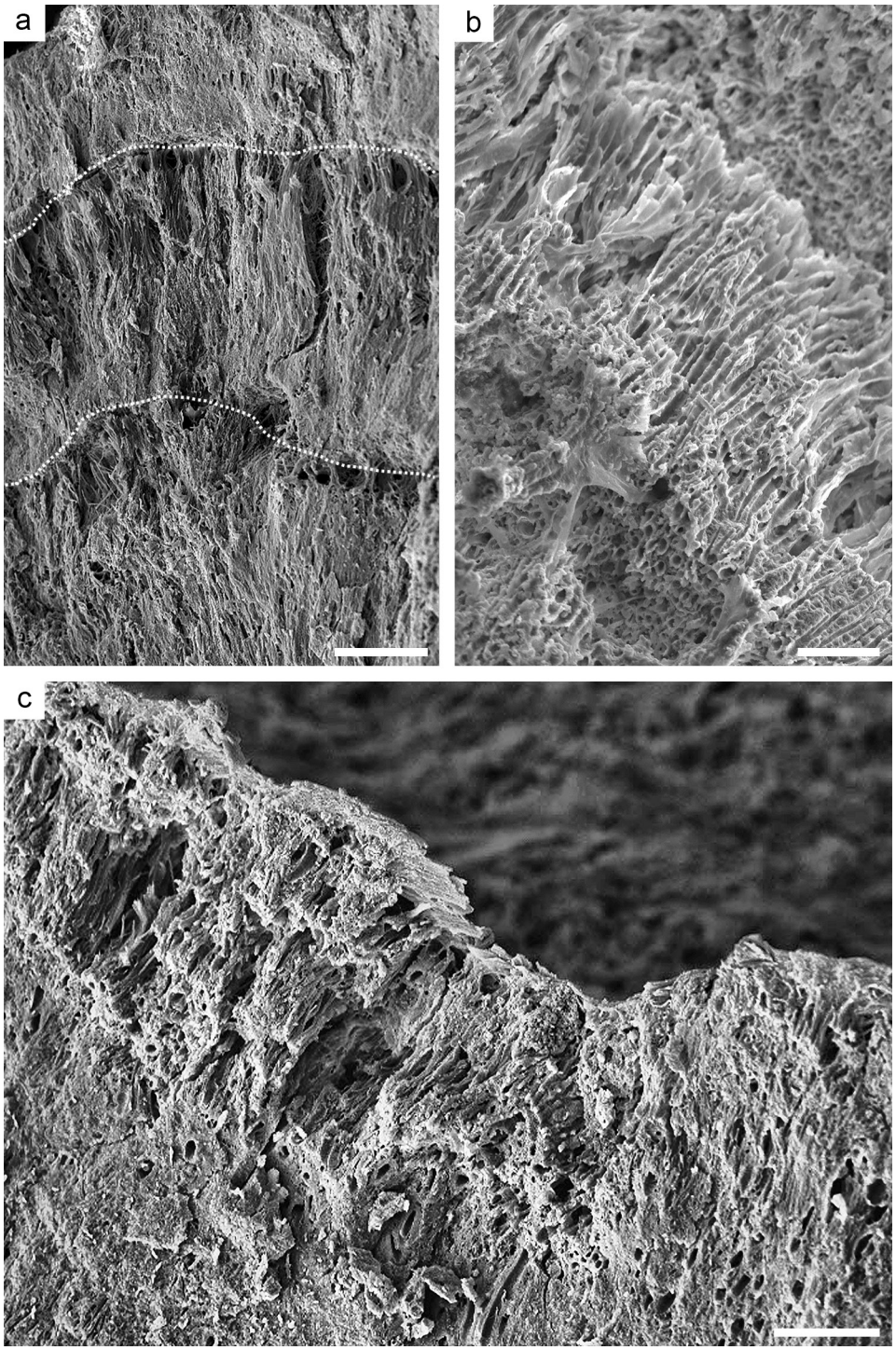

Fig. 11 - Oum Dba sabkha, Western Sahara, Morocco, scanning electron micrographs of a mineralized section of the stromatolite. a) Laminae (delimited by dotted lines) composed of vertically arranged trichomes and fine fibers derived from the degradation of the mucilaginous sheath prior to mineralization. Scale bar: 200 µm. b) Densely packed arrangement (bundles) of trichomes in a side view of a single lamina. Scale bar: 50 µm. c) A whole section of a single lamina; note the incomplete carbonate precipitation in its upper portion. Scale bar: 100 µm.

of the fossil record. By rapidly cementing sediments and forming protective envelopes or "death masks" (as seen in Ediacaran fossils), they ensure the high-fidelity preservation of organic remains. These processes allow for the fossilization of soft-bodied organisms and delicate microbial behaviors, such as gliding, which would otherwise have been lost from the geological record.

Stromatolites represent the pinnacle of cyanobacterial engineering, where biological life and geological record converge. Understanding the interplay between microbially influenced paleoenvironments and stromatolite construction through time depends largely on the investigation of their modern counterparts, ideally under controlled environmental conditions.

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