

RESEARCH ARTICLE

Early taphonomic processes in a microbial-based sedimentary system from a temperate salt-pan site (Cervia salterns, Italy)

Roberto Barbieri¹  and Barbara Cavalazzi^{1,2} 

¹Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Alma Mater Studiorum – Università di Bologna, Bologna, Italy

²Department of Geology, University of Johannesburg, Johannesburg, South Africa

Author for correspondence: Roberto Barbieri, E-mail: roberto.barbieri@unibo.it

Received: 07 December 2021; **Revised:** 29 June 2022; **Accepted:** 11 July 2022; **First published online:** 02 August 2022

Keywords: Bio-sediments, textures, Cyanobacteria, diatoms, evaporite environments, taphonomic processes, terrestrial analogues

Abstract

In the only salt evaporation pond retaining its natural setting of the historic *Salina di Cervia* (Italy), the northernmost salterns of the Mediterranean area, a number of potentially preservable textures derive from the interactions between photosynthetic mat producers and the sedimentary substrate. These morphologies occur at the beginning of the taphonomic processes when repeated emerged-submerged conditions take place. In these conditions the cohesive nature of the diatom- and cyanobacterial-derived mucilage favours the stabilization of otherwise ephemeral structures. Surface micromorphologies for which diatoms and cyanobacteria have played some active role when still living in the soft microlayer and down to the sediment-water interface, such as during the gliding motility, can overcome the surface layer of most intense mixing (i.e., the taphonomically active zone) and keep traces of them in the fossil record either as body fossils or as texture contributors. Tiny microbial-derived remnants, such as filaments and biofilm strands of halotolerant microorganisms, while fragile upon their formation, can therefore stabilize as biosignatures when combined with salt precipitation. Halophilic and halotolerant ecosystems are models for life in extreme environments (analogue sites) with similarity to those strongly suspected to occur and/or have occurred on Mars and on other planetary bodies. The study of hypersaline systems such as *Salina di Cervia* which harbour diverse and abundant microbial life, can be relevant for astrobiology since it allows the investigation of potential biosignatures and their preservation, and of further understand the range of conditions and the planetary processes sustaining potentially habitable systems.

Contents

Introduction	309
Saline environments in a temperate climate zone and their function as habitats for microbial mats	309
Cervia salt-pans	311
Environmental context and site description	311
Mucilage biofilm producers in a saline clayey substrate of temperate climate	312
Sampling and analytical methods	313
Optical microscopy analysis	313
From submerged to occasionally or permanently emerged areas	313
Environmental scanning electron microscope analysis	318
Microbe-evaporite surface structures	318
Bio-sedimentary ‘packaging’	322

The Cervia hypersaline environment from an astrobiological perspective	322
Concluding remarks	325

Introduction

Salt from the Cervia salterns has been extracted since pre-Roman times (Guarnieri, 2019). Included in the Po Delta Regional Park, the largest wetland zone in Italy, these salterns represent an excellent example of the coexistence of historical heritage, economical interest and nature. The high naturalistic interest of the area hosting this man-made system of ponds is evidenced by its inclusion in the Ramsar Convention as a wetland of international importance. Therefore, since 1979 the *Salina di Cervia* has been declared a natural repopulation reserve for a number of water bird species that nest here.

The considerable extent of the Cervia salt pans makes the site unique along this area of the northern Adriatic Sea, where systems of coastal dunes represent the main physiographic features (Caruso *et al.*, 2005) partitioning the sea from the wide lowlands of the Po River delta and its neighbouring areas (Gambolati *et al.*, 1998).

With the transition to an industrial production system of saltworks in Cervia, today only one area, the *Salina Camillone* (Fig. 1a), remains as a document of the ancient artisan production system of salt. In this area, which is currently included in the *Salina di Cervia* Nature Reserve, a single salt evaporation pond (Fig. 1b and c) is still preserved in its natural condition and where, therefore, no evaporation and salt collection takes place. This provides an opportunity of analysing the relationships between a physical surface environment and its microbiological component.

The objective of this study is to examine the anatomy of surficial macro- and microscopic structures determined by the interactions between cohesive microbial mats and salt precipitation and clastic sediments in a temperate, saline confined habitat. The ultimate goal is to assess the bio-sedimentary origin of cm- to mm-scale morphologies and their preservation during the first steps of their formation in an intermediate environmental context between emerged and submerged conditions largely controlled by recurrent desiccation processes.

Saline environments in a temperate climate zone and their function as habitats for microbial mats

In temperate coastal regions, aquatic environments typically consist of salt marshes developed in sheltered intertidal areas or lagoons. These saltwater wetlands produce a variety of habitats that sustain a remarkable biodiversity (e.g., Adam, 1990), including phototrophic microorganisms. For example, diatoms such as *Nitzschia* are producers of phototrophic biofilm and efficient early colonizers (Anderson, 2016) of substrates through their abundant secretion of extracellular polymeric substances (EPS). Filamentous cyanobacteria belonging to halotolerant form-genera, such as *Microcoleus* and *Phormidium*, also typify these environments and largely contribute to the formation of microbial slimes (e.g., Tkavc *et al.*, 2010). EPS can constitute up to 90% of biofilm composition (Nielsen *et al.*, 1997), and their ability to store large amounts of water can protect cell colonies against moisture deficiency in temporarily emerged areas that may occur in such environmental settings. Conditions of high salinity and evaporation comparable to those inducing salt crusts precipitation in arid environments, however, are rarely found in temperate areas. Due to the climatic conditions of temperate regions, salt pan environments – and associated interactions between mudflats, saline crusts and microbial communities – exist only in exceptional cases. The Cervia salterns, together with those from Slovenia (Tkavc *et al.*, 2010), are the northernmost salterns of the Mediterranean and can be included within these exceptional areas.

The abundance of microbial mats and specific interactions with their immediate environment enables the formation of microbial-induced sedimentary structures (MISS, Noffke *et al.*, 2001a), a discrete class of sedimentary structures defined as the result of the interaction between sediments and microbial mat-induced products (Davies *et al.*, 2016; Callefo *et al.*, 2021). These surface morphologies

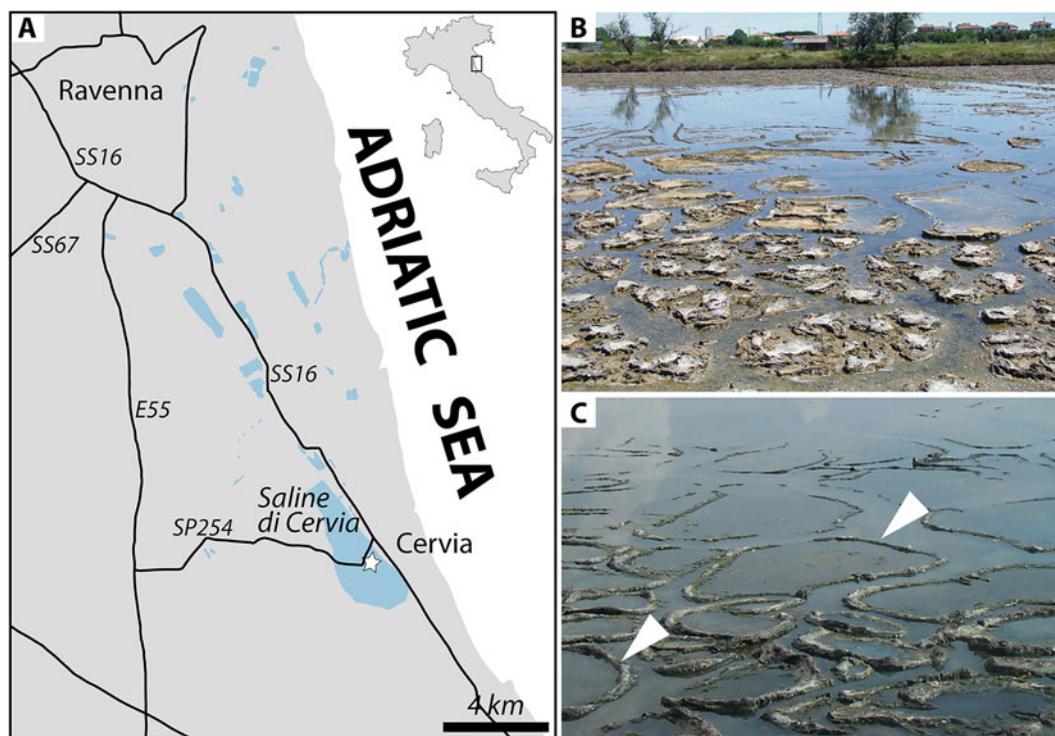


Fig. 1. (a) Location map of the study area, white star locates the Salina Camillone, next to the town of Cervia, approx. 2 km away from the Adriatic Sea. (b) The Salina Camillone pond still preserved in its natural state as it appears in the sampled site. (c) Thickened, subrounded margins (arrows) of the polygonal cracks that make up the surface of the shallow pond. Note water trapped by curb-shaped margins of the polygons.

and textures were described from different climatic conditions, such as the coastal areas of the North Sea (Noffke *et al.*, 1997; Noffke, 1999) and of southern Tunisia (Noffke *et al.*, 2001b), and they have not changed significantly over 3.5 billion years (Noffke *et al.*, 2013b). In undisturbed environments, such as a natural salt-pan pond, the extremely low and fine-grained sedimentary supply enables microbial mat fabrics to grow and bind the fall-out of sedimentary particles through the biofilm they secrete. In this regard, it is noteworthy that most of the EPS secreted by cyanobacteria, including the filamentous genera *Microcoleus* and *Phormidium*, contain uronic acids (Stal, 1994; Moreno *et al.*, 1998; Rashmi *et al.*, 2017), carbohydrates that increase their adhesive, ‘sticky’ capacity towards the materials they enwrap. This has been experimentally documented for the case of loose fine-grained sediments, where enhanced erosion resistance of sedimentary particles, through an increase of boundary shear stress, takes place in the presence of cyanobacterial binders capable of synthesizing uronic acids (Dade *et al.*, 1990; Chen *et al.*, 2019).

Additionally, diatoms have strong adhesive properties due to both intrinsic cell adhesion abilities, as in the case of certain *Nitzschia* species (Laviale *et al.*, 2019), and mucilage strand properties leading to efficient sediment stabilization (e.g., Vos *et al.*, 1988). In the latter case, similarly to bacterial mucilage, high amounts of uronic acids in EPS appear to be the primary factor promoting adhesiveness in diatoms (Sutherland, 2001; de Brouwer *et al.*, 2005; Poulsen *et al.*, 2014). The end result is that some microbial mat and associated morphologies may leave records in sediments and, at last, in the sedimentary record (e.g., Gerdes, 2007).

At Cervia, recurrent desiccation and moisturizing may also offer a means of evaluating microorganisms in terms of their contribution to the formation of distinguishable micromorphologies under such stressful conditions.

Cervia salt-pans

Environmental context and site description

As the largest salt pan habitat along the upper Adriatic coast, the Cervia salterns make up a selective environment inhabited by a wealth of species able to survive high salt concentrations and water depths not exceeding a few centimetres. This wetland ecosystem spans 785 hectares (Ramsar area) less than 2 km away from the sea (Fig. 1a). Coastal deposits accumulating south of the Po River delta are primarily composed of sands and sandy/silty clays; their deposition is strongly dependent on the anti-clockwise circulation regime of the northern Adriatic Sea that distributes fine-grained sediments transported from the Po River mouth to the south (Franco *et al.*, 1982). This type of sedimentary regime also takes place in the Cervia salterns area. As in other hyperhaline areas, the water becomes seasonally reddened by bloom of *Dunaliella salina*, a halotolerant, unicellular green alga able to accumulate carotenoids to as much as 13% of its dry weight (Abd El-Baky *et al.*, 2004). *Dunaliella salina* is in turn the food for *Artemia salina*, a micro-crustacean, which is a favourite food of the flamingos and pink herons whose presence typifies the man-made shallow ponds of the Cervia salterns. For the preservation of habitats and species, as well as salt production, recurrent seawater circulation is necessary; this explains the presence of euryhaline species, such as the benthic foraminifer *Ammonia beccarii*.

After the industrialization of salt extraction, that began at the end of the 1950s, only in a very limited area – the *Salina Camillone* – have traditional salt-production methods been preserved. Next to this area and along the provincial road SP 254, connecting the hinterland to Cervia (Fig. 1a), is the only pond not involved in the extraction activity that, since it lacks a direct human disturbance, has been preserved in a rather natural condition (Fig. 1b). This shallow pond, while maintaining a necessary connection with the circulation of the open seawater, reaches a maximum depth of approximately one metre and an extent of approx. 5000 square metres. Sampling was conducted at its SW margin (coordinates: 44°15'15"N, 12°20'03"E). Most of its clayey surface (mudflat) is permanently covered by seawater, the same water that feeds the salt production system. If surface layers of the mudflat are removed, a distinct smell of hydrogen sulphide can be detected, a by-product of the anaerobic decay of organic matter.

Maximum flooding in the pond occurs in the autumn season (average monthly rainfall: 68 mm), and the average air temperature ranges from 22.7°C in July to 3.1°C in January.

Due to the seasonal variation of the water level within the pond, some parts, especially towards the margins, repeatedly emerge. Because of recurrent subaerial exposure, polygonal oscillation cracks, ranging in size from a couple of metres down to a few centimetres, are formed at the surface of clayey sediments and develop a distinct morphology throughout the surface of the pond (Fig. 1b and c). Even where polygons are completely inundated, wide open cracks persist. This is because on top of the polygonal oscillation cracks crusts made up of multiple microbial mats interbedded with laminae of clayey (prevailing) and sandy mud and saline precipitates are present and produce further shrinkage morphologies (see also McMahon *et al.*, 2017); the final result is the formation of compact and cohesive, although still elastic, surfaces (Fig. 2a), similar to those described from tidal flat and coastal sabkha areas (e.g., Cameron *et al.*, 1985; Noffke *et al.*, 1996; Gerdes, 2007; Porada *et al.*, 2007; Bouougri and Porada, 2011; Chen *et al.*, 2019), with overfolded margins of the desiccation polygons (Fig. 1b and c).

The mode of formation of the overgrowth around the polygons has been previously described in a southern Tunisia lagoon (Noffke *et al.*, 2001a) as a consequence of repeated upturning of microbial layers leading to the development of curb-shaped thickenings that exceptionally emphasize their margins (Fig. 1c). The leathery surface produced by the recurrent subaerial exposure of the polygons has enabled their recovery even in fossilized microbialites of up to Neoproterozoic age (Eriksson *et al.*, 2007; Noffke *et al.*, 2008).

Close (hand lens) observation on the field of the microbial mat (Fig. 2a and b) shows that they exhibit amorphous, bumpy surfaces draping plant remnants and other microbial crust portions produced during previous desiccation phases. The colours of the crusty microbial surfaces include shades of brown and green produced by clayey components and photosynthetic pigments, together with light

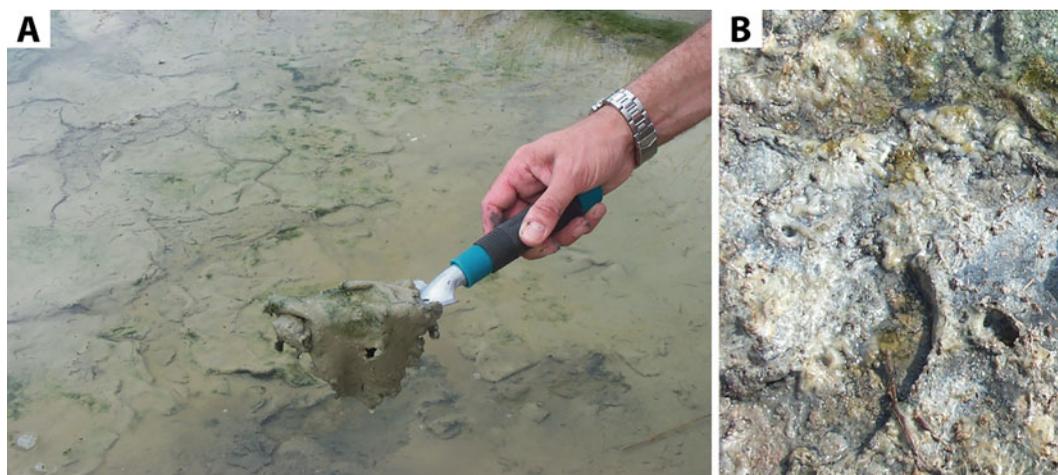


Fig. 2. (a) Effect of a strongly cohesive microbial mat: bio-sedimentary sample collected in a submerged (approx. 10 cm water depth) area where the mucilaginous component (slime) gives a surface stabilization such as to favour the preservation of different superficial micro-morphologies. In the background, slight polygonal cracks document previous phases of emersion. (b) Close-up of a typically irregular bio-sedimentary surface composed of a mix of salt efflorescence (whitish), clayey sediment (grey) and slime-producing microbes, such as diatoms (whitish) and cyanobacteria (brownish). Width of view 7 cm.

spots derived from saline exudation locally mixed with dense concentrations of diatom frustules (Fig. 2b).

Mucilage biofilm producers in a saline clayey substrate of temperate climate

Being ubiquitous in natural hydrated environments, microbial biofilms have a strong influence on sedimentary surfaces, such that sediment particles coated with the biofilm – for which the term bio-sediment has been proposed (Fang *et al.*, 2015) – can determine the properties of sediment and the formation of surface micromorphologies. In the Cervia salterns, the sedimentary substrate on which the microbial communities secrete their mucilage biofilm is composed of clayey minerals associated with evaporitic salts. As in many other areas, these photosynthetically active microbial mats are thin (less than 1 millimetre in thickness), strongly cohesive and placed above fine-grained sediments of low-energy environments in which their black colour and strong hydrogen sulphide smell indicate persistent anoxic conditions (Skyring and Bauld, 1990). Thin biological crusts observed in ephemerally emerged areas of the Cervia pond that still retains its natural state derive from the ability of biofilm producers to trap and bind loose mineral or skeletal particles for stabilizing a sediment surface (Neumann *et al.*, 1970; Paterson *et al.*, 2008). This ability may determine surface micromorphological features derived from the interactions between physical environments and microbes (Viles, 2012), which can be preserved through the deep time (Noffke *et al.*, 2013b).

Although interspecific interactions between different slime-producing microbial components (e.g., between prokaryotes and unicellular eukaryotes) have often been detected, they are still poorly known. Evidence of interactions has been observed in diatoms from different species (Roubeix and Coste, 2017) and between diatoms and bacteria (Amin *et al.*, 2012), and may provide mutual benefits via symbiotic relationships. Regarding the latter case, surface morphologies potentially preservable as fossil biosignatures have been observed as the result of the interactions between diatoms and filamentous cyanobacteria in continental sabkha environments (Barbieri and Cavalazzi, 2018). Even in the present case study, the leading players are filamentous cyanobacteria – which can form dense mats in

saltern ponds (Oren, 2015) and dominate the surface part of the microbial mats of hypersaline (or other harsh) environments (Stal, 2000) – and the benthic diatom *Nitzschia*, a widespread genus living in freshwater and marine habitats all over the world, where it can accumulate in great numbers in undisturbed surface sediments (Kocielek *et al.*, 2015). Communities belonging to this diatom genus have also been described from more challenging conditions, such as geothermal (e.g., Owen *et al.*, 2008; Stavreva-Veselinovska and Todorovska, 2010) and hypersaline environments (e.g., DasSarma and DasSarma, 2017; Balakrishnan *et al.*, 2019) where they behave as extremophiles. *Nitzschia* secretes abundant EPS for locomotion (e.g., de Brouwer and Stal, 2002), which may significantly contribute to the stabilization of loose sediment in low-energy environments (Stal and de Brouwer, 2003). Although some active competition has been observed between filamentous cyanobacteria and *Nitzschia* species in muddy habitats (Watermann *et al.*, 1999), their adhesive mucilages may both contribute to the biostabilisation of a loose substrate.

Sampling and analytical methods

This study is based on samples collected in May 2016 from a lateral margin of the only pond preserved in natural condition at the Cervia salt-pans (Fig. 1b; Fig. 3a). Samplings of the surficial crusts and sediment portions, with a mean thickness of 1 cm, involved three different types of materials collected in contiguous areas: (i) wet (submerged) and then naturally dried samples; (ii) moderately crustose samples (from a recently desiccated part of the pond); and (iii) completely dried and crustose samples (from a permanently dry part of the pond). These materials include a range of still active (living) and desiccated surface and subsurface microbial mats variously associated with clayey sediment and saline precipitates (Fig. 3). Sampling was performed at the beginning of the dry season (end of May). In the samples collected from the submerged part, a 10 to 20 cm thick layer of water covered a still active microbial mat at the water-sediment interface. Samples were then placed in a box to avoid any deformations during transport from the field to the laboratory.

Whereas the samples taken in emerged parts were then investigated under the binocular microscope as they were at the time of sampling, samples collected from submerged parts were first observed with a field microscope immediately after the collection and before removing the surface water, to avoid changes to the surface features, especially to the microbial mat component. Subsequently, they were air-dried at room temperature for further investigation.

The samples of living microbial mats and organo-sedimentary mixed samples were investigated through freshly, randomly broken mat portions, dissected in points chosen ad hoc by using a scalpel, in order to observe both the surface morphology and the millimetre- to micrometre-scale microstratigraphy. A combination of transmitted-light and environmental scanning electron microscopy (ESEM) analyses with both backscattered-electron (BSE) and secondary electrons imaging was used. For the evaluation of the surface microscopic morphologies and of the microenvironmental context with respect to the different components, reflected light observations were performed by using a Wild M8 stereomicroscope and a Zeiss Axioplan binocular optical microscope equipped with a Nikon digital camera Head DS-Fi2. ESEM observations were performed on uncoated samples using an FEI Quanta 200, under low vacuum conditions, with an accelerating voltage of 20–25 kV. The elemental compositions were performed with an OXFORD-SATW light elements X-ray spectroscopy (SEM-EDX).

In the field, water characteristics including electrical conductivity, pH and temperature, were measured by using an XS Instruments pH 70 portable laboratory.

Optical microscopy analysis

From submerged to occasionally or permanently emerged areas

Recurrent field observations have shown that wide areas of the pond are permanently emerged, whereas other areas have periodic (occasional) emersion connected with the water exchanges of the salt pan.

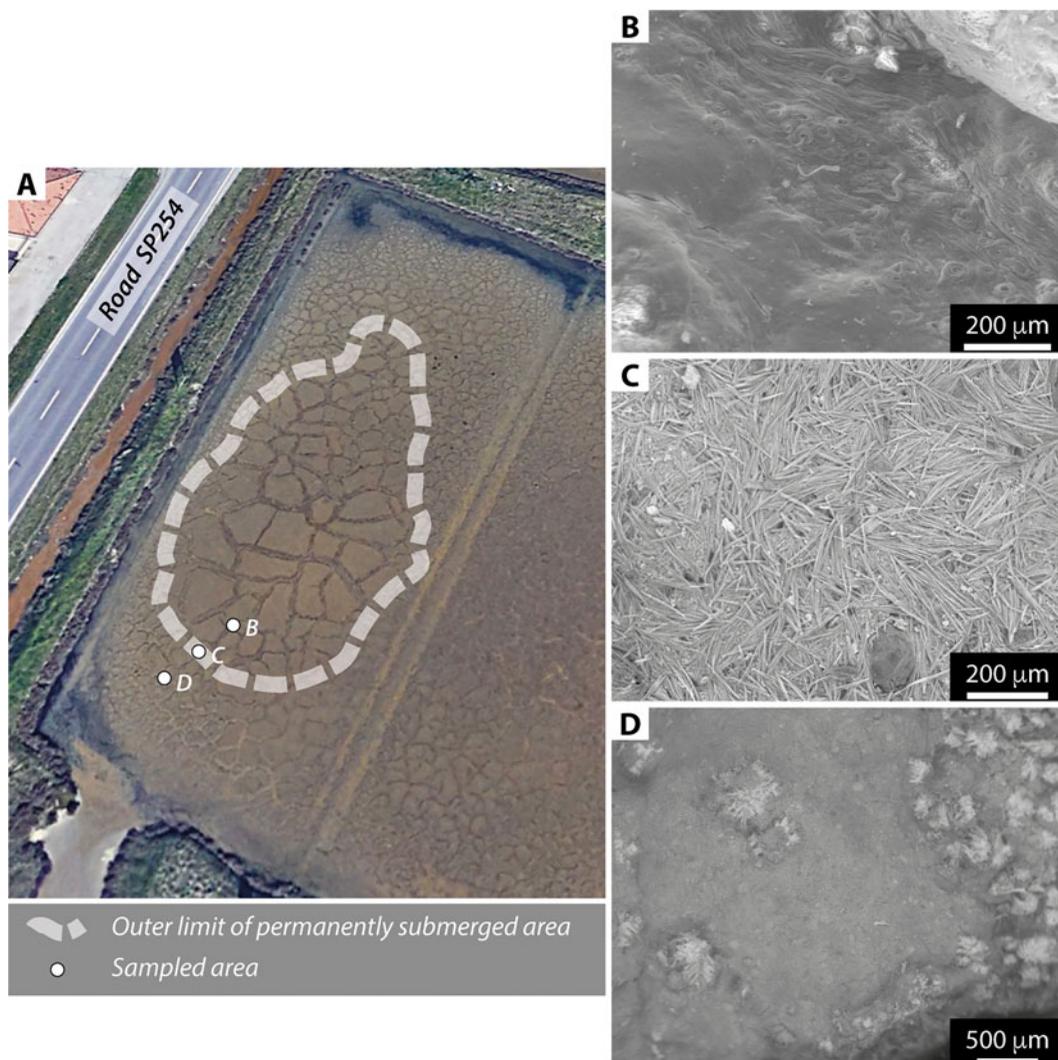


Fig. 3. (a) Google Earth view of the Salina Camillone, the broken line delimits the permanently submerged area. Letters position the sampled sites in submerged – recently emerged (b, c) and permanently emerged (d) areas. (b–d) Examples (ESEM micrographs) of what the sampled sedimentary surface looks like: trichome masses of filamentous cyanobacteria (b, see details in Fig. 8); diatom valves accumulation (c, see details in Fig. 9); clumps of halite ribbons protruding from a diatom-rich surface (d, see details in Figs. 6 and 9).

Optical microscope observations were performed in samples from both permanently submerged and emerged (occasionally or permanently) areas. They enabled an evaluation of the microenvironmental context where the data collected during the ESEM investigations are framed, and to make comparative observations between the active (submerged or still wet at the time of sampling) and (permanently emerged) areas.

On-site observations with a field microscope of samples from submerged parts revealed that at the top of the mucilaginous mat growing over the clayey substrate a grey, soft microlayer (less than one millimetre thick) represents the actual sediment-water interface and consists of clay particles, amorphous fragments of biofilm, diatoms thecae and single strands of cyanobacteria (Fig. 4). At its topmost portion the microlayer consists of a watery suspension where loose cyanobacteria filaments mimic a

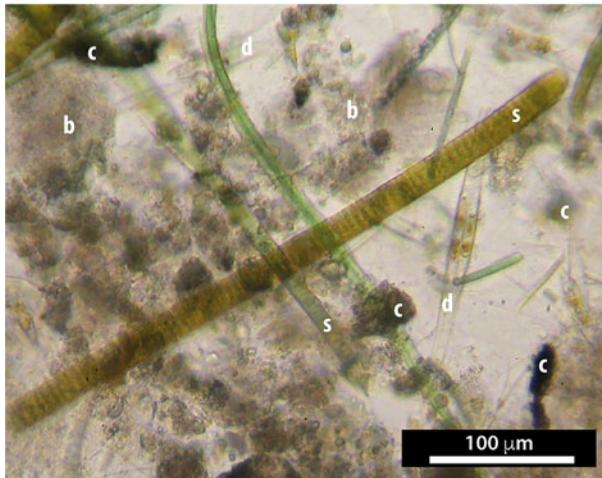


Fig. 4. Transmitted light micrograph from a sample of the soft microlayer at the sediment-water interface from submerged parts of the pond (see text for further details). At its topmost portion, this watery suspension contains clay particles (c), amorphous fragments of biofilm (b), diatoms thecae (d) and single strands of cyanobacteria (s).

phototactic behaviour, and a denser lower portion where tangles of filamentous cyanobacteria are immersed in a water, biofilm- and granules-rich medium that fall-out to the substrate.

Beneath the surficial soft microlayer, microbial communities are organized in thick, planar to undulose bundles of filamentous cyanobacteria densely aligned parallel to the sedimentary surface (Fig. 5a). The bright and dark green-blue colour of this packed surface microlayer remains preserved even after its complete desiccation (Fig. 5b). The thickness of this pigmented horizon can reach one millimetre with dense bundles that lie on surfaces made of silt-clay material, salt precipitates and organic remnants. Filamentous bundles appear overall clean from clay sediment, thereby contrasting with the sediment-microbe interactions that typify certain MISS structures, such as in modern sandy tidal flats. In permanently desiccated areas, the bundles are masked by salt precipitation that barely enables their dark colour to be detected.

Along with the cyanobacterial strands, dense accumulations of the needle-shaped diatom *Nitzschia* cover rather irregular and knobbed surfaces (Fig. 5c and d). The siliceous felt produced by diatom frustules may completely drape some surface portions. When viewed in a microstratigraphic section, just below the thin diatom microlayer are filaments of cyanobacteria organized as dark laminae alternating with light layers composed of a mix of clayey sediments and saline precipitates (Fig. 5c).

In samples collected from permanently or temporary emerged (still wet) areas, a readily observable feature are the whitish, siliceous felts consisting of thin needles associated to microcrystalline aggregates of evaporation salt and the seeming ‘fluid weaving’ of the dark green bundles of filamentous cyanobacteria. Sub-millimetre thick siliceous felty layers produced by the accumulation of *Nitzschia* thecae, associated with cyanobacterial laminae, overlay irregular surfaces produced by bulges and lumps making up a recurrent micromorphological feature in the salt-pan surface of Cervia (Fig. 5d). The combined action of the drying of the clayey sediment and the salts evaporation is the possible agent responsible for these irregular surfaces.

Overall, in the top centimetre, the microstratigraphy exhibits a biolaminite organization developed just beneath the sediment-water interface, with an irregular alternation of millimetre-scale layering of dark laminae of microbial mats, and lighter silty/clayey/evaporite layers (Figs. 5b and c and 6a and b). This microstratigraphic organization has some lateral continuity, and it is observable in both recently and permanently emerged areas. Depending on their location, however, the thickness of laminae differs

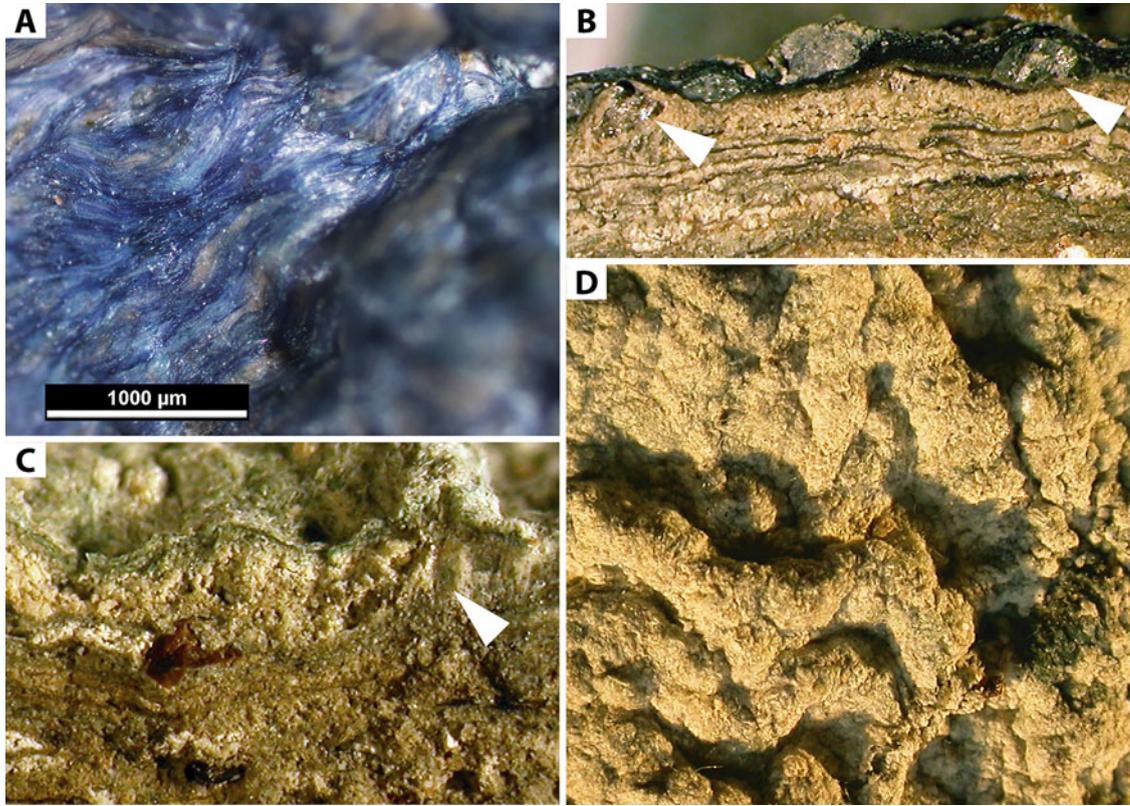


Fig. 5. (a) Dark blue bundles of filamentous cyanobacteria aligned parallel to the surface of a sample from a just emerged (still wet at the time of sampling) area. The typical dark colour was maintained by the cyanobacterial colonies even after drying. (b, c) Vertical cross section with normal stratigraphic orientation of the bio-sedimentary interval (microbial + sediment) in the top 5–10 mm of the muddy substratum. Note the dark laminae (cyanobacteria) alternating with the light layers composed of a mix of clayey sediments and saline precipitates. Whereas in B the top of the section entirely consists of filamentous cyanobacteria that envelope growing salt crystals (arrows), in C a thin siliceous felt made up of diatom frustules partially masks the underlying dark green cyanobacterial layer. Arrow in C shows the upwelling of sediment and the development of evaporitic material leading to the surface micromorphology observable in D. (d) Bulges and lumps produced by ongoing desiccation and evaporitic precipitation on a just emerged (still wet at the time of sampling) surface almost completely covered by diatom frustules. Width of view: B and C: 1 cm; D: 2 cm.

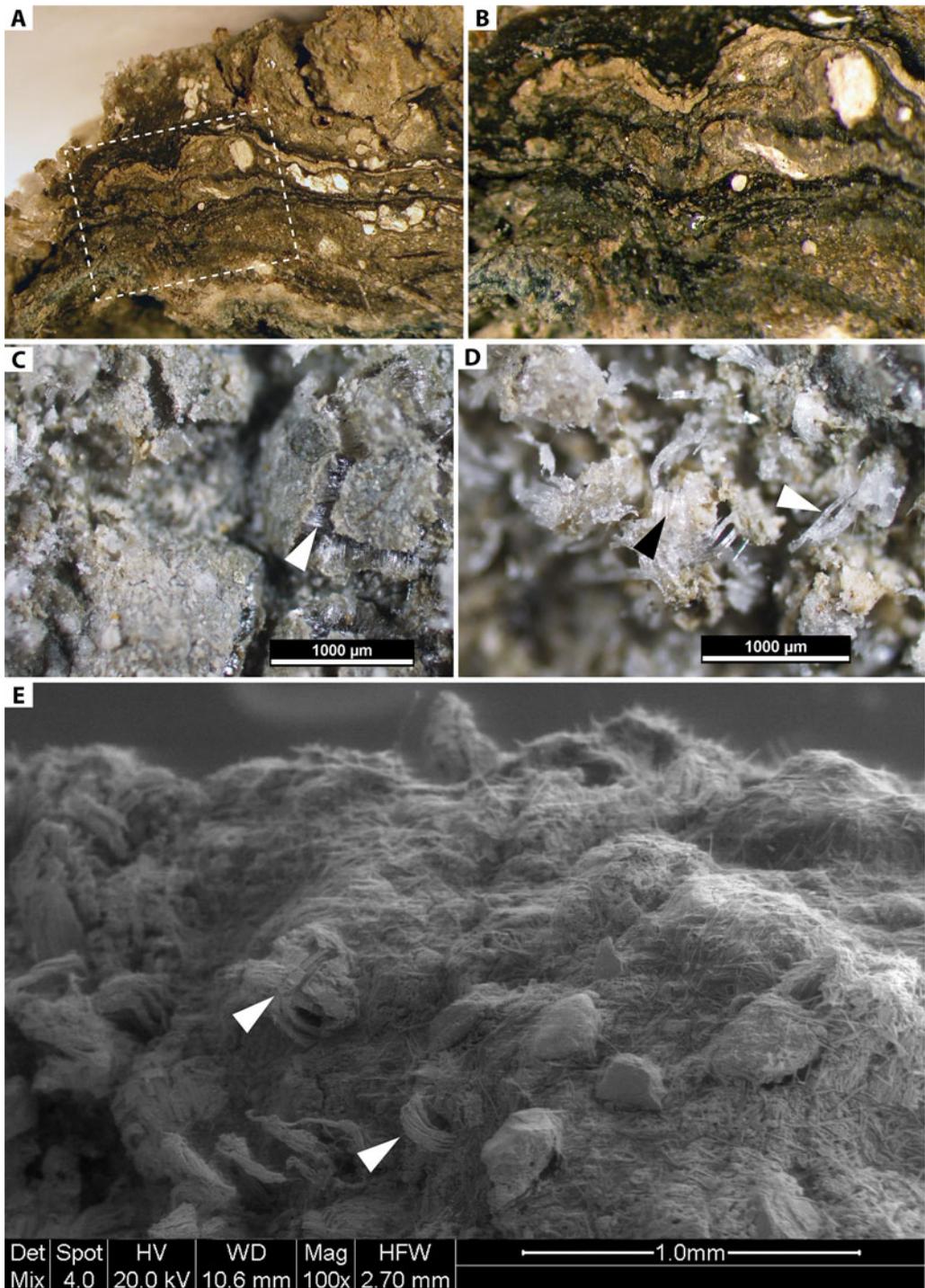


Fig. 6. (a, b) Section across the bio-sedimentary (microbial + sediment) surface crust of a permanently emerged area. The organization and thickness of the thin strata adapt to the surface morphology and local disruptions produced by salt efflorescence. Dark laminae (cyanobacteria) irregularly alternate with sediment and salt (whitish patches). Width of view: A: 1 cm; B: 0.5 cm. (c, d) Bread crust-like surface morphologies in an emerged area from which twisted or curled ribbons of fibrous halite grow (arrows). (E) ESEM micrograph where halite ribbons (arrows) protrude from a recently emerged surface; bulges, lumps and salt crystals are covered by diatom frustules and their biofilm remnants.

considerably for adapting to the ground micromorphology and to some local disruptions by salt efflorescence.

On recently emerged areas, still wet at the time of sampling, surfaces covered with microcrystalline salt precipitates allow to glimpse dark patches that reveal the presence of cyanobacterial bundles. In some portions the salt precipitation has covered filaments and biofilm remnants that previously had contributed to trap loose sedimentary and skeletal grains, such as hydrobiid shells, smooth and thin-shelled ostracod valves and benthic foraminiferal tests (e.g., *Ammonia beccarii*).

Emerged areas are also typified by saline crinkled crusts with long, twisted or curled ribbons of fibrous halite with a characteristic silky appearance (Fig. 6c and d). First described, with several centimetres long ribbons, from the Fayum Depression, in the Western Desert, Egypt (Phillips and Rigby, 1991), at Cervia the salt ribbons are remarkably smaller and attain a maximum size of a few millimetres. They are the likely product of salt efflorescence growth during evaporation. A sort of capillary migration through silty-clayey deposits takes place so that salt ribbons protrude from bread crust-like surface morphologies (Fig. 6c). Similar ribbons were also recovered from samples collected in submerged areas soon after desiccation (Fig. 6e).

Environmental scanning electron microscope analysis

In the surficial sediments covering the Cervia pond the microbiotic components act as inter-particle binders and make up the main framework of the bio-sediment. This is well detectable by ESEM analysis on wet or partially hydrated and unconsolidated bio-sediment samples that, thanks to the flexible structure of the microbial component, still retain their original three-dimensional architecture. Abundant remnants of adhesive mucilage have also been detected in both the samples dried at room temperature after collection and in those collected in naturally dried (permanently emerged) areas. Overall, they contribute to document the transition from a taphonomically active phase – in which surface microbially-controlled features rapidly degrade – to a more stable and potentially preservable bio-sedimentary frame.

Microbe-evaporite surface structures

Both diatom frustules and cyanobacterial filaments concur to the formation of microbial-induced surface morphologies. A common feature is the light-coloured accumulation of *Nitzschia* thecae settled on a clayey and sandy substrate or on pre-existing dark green microbial laminations. These thin diatom-rich surfaces are typified by a strongly iso-oriented organization of frustules (Fig. 7a), which gives the surface a fluid flow-like look. We attribute this organization to gliding motility, a benthic pennate diatom movement performed on the substratum of aquatic environments and based on the secretion of extracellular material through the raphe slit (e.g., Wetherbee *et al.*, 1998; Heintzelman, 2006). Some *Nitzschia* species were also observed to glide in epibenthic (muddy) habitats (e.g., Gupta and Agrawal, 2007). Extremely thin (a few tens of micrometres) layers have also been observed in active (submerged) surfaces, where iso-orientation of diatom thecae may change from layer to layer (Fig. 7b). Since diatom cells require adhesion to a substrate during the horizontal gliding process, they need to maintain direct contact with a physical interface and this could be the factor that determined diatom micro-layers having a very few up to single-cell thickness. Despite the minimal thickness of diatom micro-layers typified by a flow-like look (Fig. 7c), a potential delivery of the effects of gliding to the fossil record can be favoured by the abundance of adhesive mucilage and the stabilizing effect of saline precipitation.

Masses of slender filaments (average diameter: 10 micrometres) commonly aligned and locally coiled, tangled or twisted, make up cyanobacteria colonies (Fig. 8a), which result in long trichome masses (from several hundred micrometres to several millimetres for each single trichome). Similar to diatoms, they display a distinct iso-orientation (Fig. 8b) that gives a fluid flow-like appearance to cyanobacteria masses. Their surface organization in an orientation parallel to the trichome axis takes

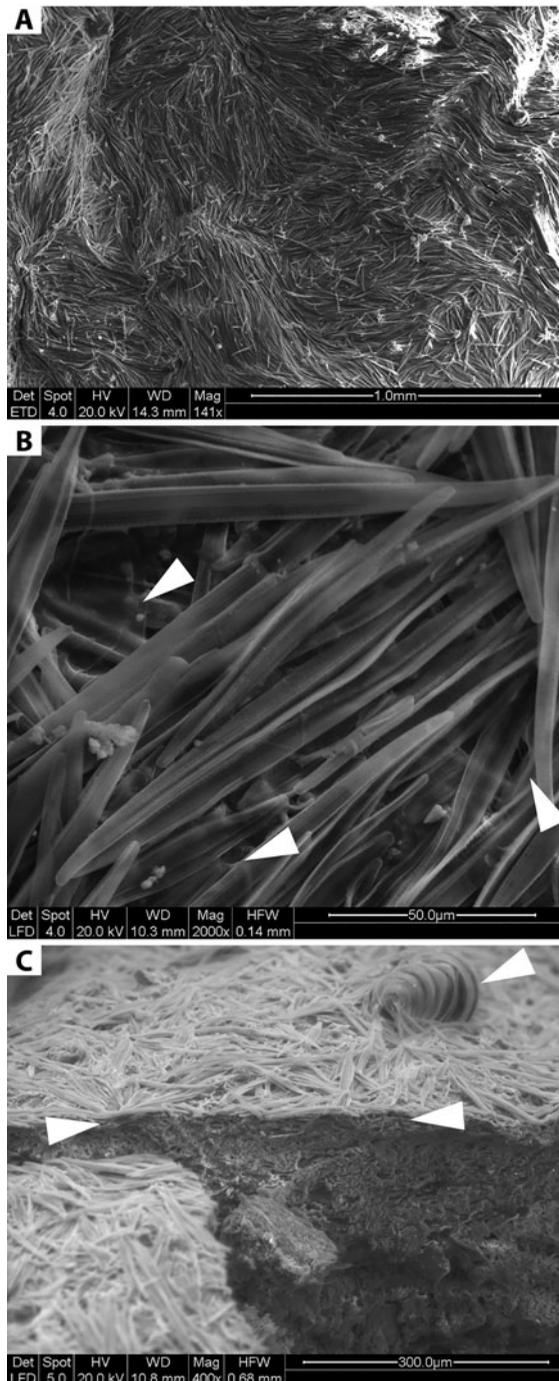


Fig. 7. ESEM micrographs of diatom (*Nitzschia*) frustules of a submerged (approx. 10 cm water depth) area. (a) Fluid flow look produced by the accumulation of iso-oriented frustules. (b) Remnants of mucilage (arrows) secreted by diatoms. (c) Minimal thickness (less than 50 µm) of a surface diatomaceous layer (arrows) from a cross section. At the top right (arrow) a hydrobiid gastropod shell.

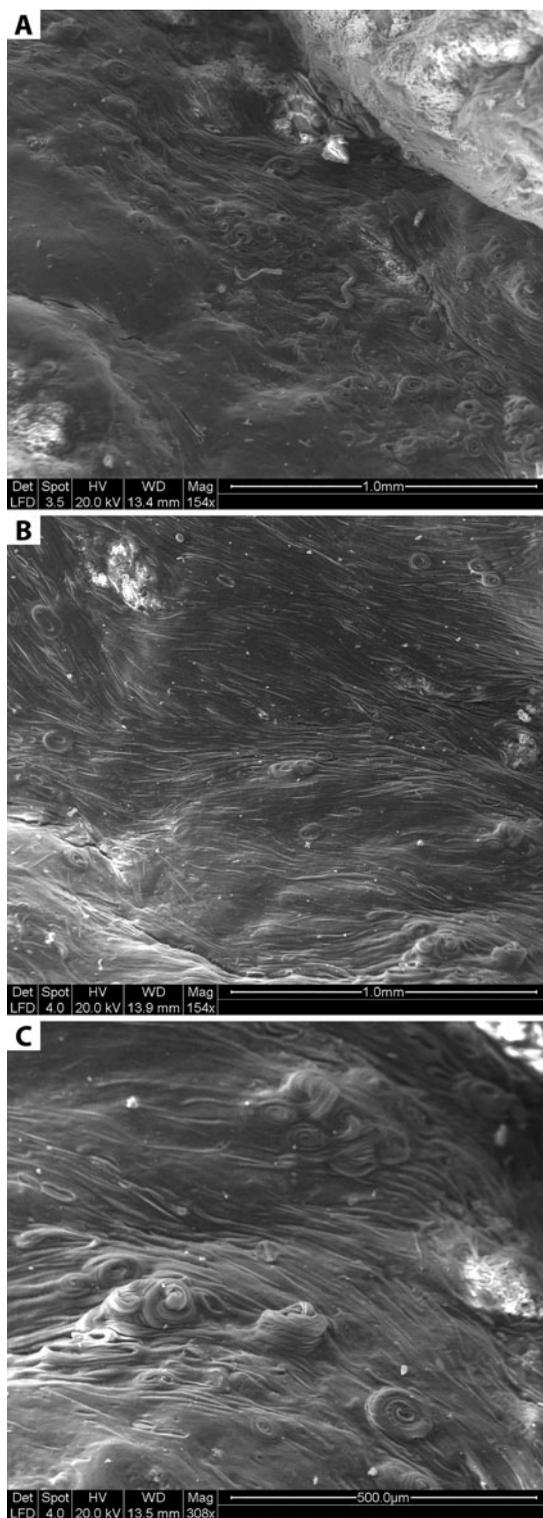


Fig. 8. ESEM micrographs of trichome masses of filamentous cyanobacteria from the surface of a still wet and emerged (at the time of sampling) area. Note the abundant production of mucilage secretion in which the cyanobacteria trichomes (some of them coiled or stretched) are plunged.

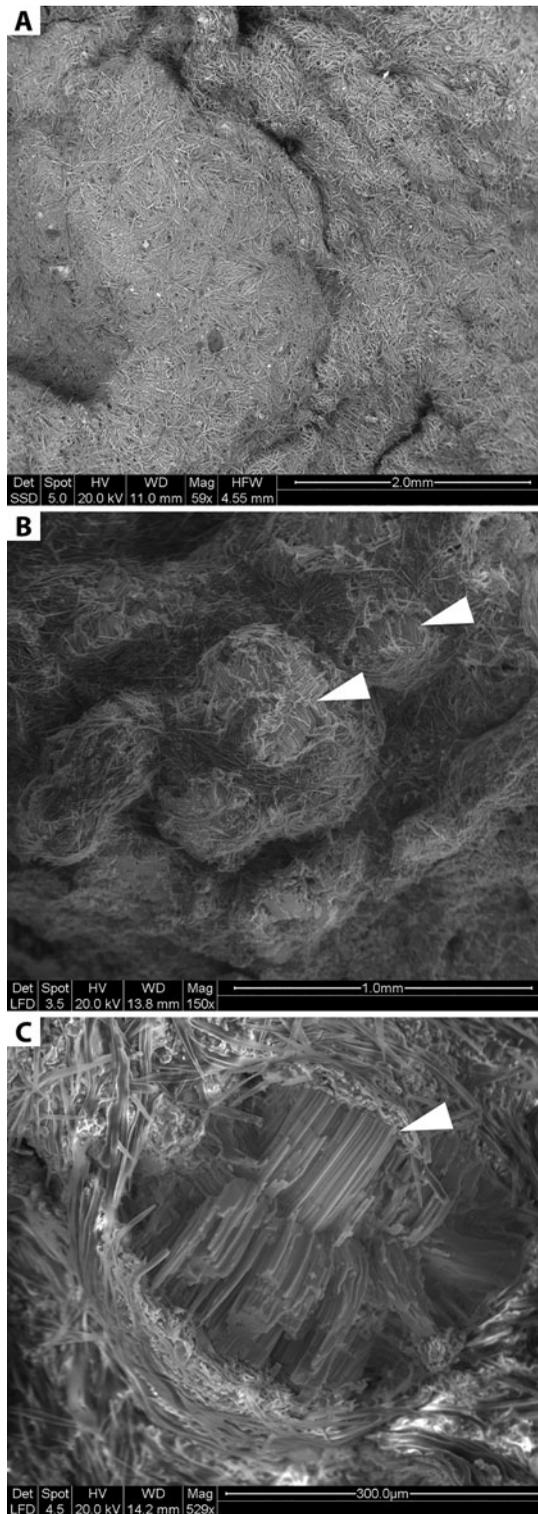


Fig. 9. ESEM micrographs in a submerged (approx. 10 cm water depth) knobbed area (a) covered by diatom (*Nitzschia*) frustules. (b, c) The diatomaceous and sedimentary surface layer has been permanently deformed by the knobs from which salt ribbons have been extruded (arrows).

place in a body of almost still water, keeping direct contact with a muddy substrate. Again similar to diatoms, iso-orientation is interpreted as the product of gliding motility, a trichomes well-known function (Buchard, 1981; Hoiczky, 2000; Ali *et al.*, 2016). In filamentous cyanobacteria that lie on a firm substrate, gliding movements lead to their iso-orientation and is associated to the steady secretion of mucilage (Hoiczky, 2000). Such an abundant production of mucilage sheath leads to the increase the amorphous surfaces in which the cyanobacteria trichomes are often completely plunged. The spiral fashion of the trichomes (Fig. 8c) should be an additional gliding effect (e.g., Tamulonis *et al.*, 2011).

At the microscale, the combined effect of a coarse (sandy grains) component of the sedimentary surface, the salt evaporation, with some early formation of fibrous halite ribbons, and several generations of overlapping microbial slime produced by the symbiotic joint action of filamentous cyanobacteria and diatoms lead to an irregular morphology of the substrate surface. A typical result is the knobbed surface in submerged or just emerged parts where felts of diatom frustules drape the substrate surfaces (Fig. 9a). The thin felt coverage consists of a minimal thickness (less than 50 μm) of a single or very few frustule layers (Fig. 7b and c) where biofilm is only present as membranes remnants. Escaping from the knobs as the efflorescence product of the salt, fibrous ribbons disrupt their surface leaving the sedimentary and diatom top layers permanently deformed (Fig. 9b and c).

Bio-sedimentary ‘packaging’

The firm crusts of the Cervia pond mainly consist of clay mineral clots, some sand-sized grains, and various organic components (Fig. 10a) and primarily derive from the binding action of filamentous living microbiota, organized as dense and compact single to multi-layered systems (Fig. 10b), and its mucilage. Since cyanobacteria have a documented desiccation tolerance (Holzinger and Karsten, 2013 *cum bibl.*), they can efficiently contribute as sedimentary binders (Fig. 10b and c) before their dehydration following water emersion and subsequent destruction. Together with their mucilage protection, also cell wall thickness may have contributed to delay the desiccation of cyanobacteria trichomes at Cervia (Fig. 10d). Especially in temporarily to permanently emerged areas along the pond margins, salt precipitation has also favoured the substrate stabilization. Salt precipitation can be either diffused in the crusts of the emerged areas or associated to a roughly laminated organization capable of enveloping salt crystals during their growth (Fig. 11a and b). Just beneath the substrate (or water-sediment interface in the submerged parts), this laminated bio-sedimentary architecture combines clayey particles, biofilm and trichome remnants and residual porosities (Fig. 11b), whereas at places it consists of an organic alveolar texture (Fig. 11b and c) derived from diatom/cyanobacteria mucilage trapped between laminae during a phase of its biodegradation process. Likewise, the framework of the bio-sediment, that associates trichomes of filamentous cyanobacteria, diatom thecae, sediment and slime remnants, enables the formation of a stable and tight bio-sedimentary ‘packaging’, which appears as an early stage of a bio-sediment fossilization process (Fig. 11d).

The Cervia hypersaline environment from an astrobiological perspective

The exploration of the extreme environments on Earth has long revealed an unexpected diversity and opened new frontiers on the existence and adaptation of life (e.g., Horikoshi and Grant, 1998; Rothschild and Mancinelli, 2001; Hallsworth *et al.*, 2021). Although particularly stressful and challenging for biotic communities, some of the environments where evaporitic salts accumulate, such as coastal lagoons, salt pans and playas, may harbour diverse, salt-tolerant microbial communities (Oren, 2002, 2015; Ley *et al.*, 2006), and in ancient evaporite deposits microbial cells and DNA have been successfully extracted (Vreeland *et al.*, 2000, 2007; Panieri *et al.*, 2010; Stivaletta *et al.*, 2012). With due caution required by both the harsh environment of Mars, unfavourable to a biological context, and the still absence of unambiguous traces of life, the case of terrestrial evaporitic sulphates is particularly illustrative of the role played by environments with chemical precipitation even in searching for life on Mars (e.g., Rothschild, 1990; Barbieri, 2013). It is in fact starting the discovery of

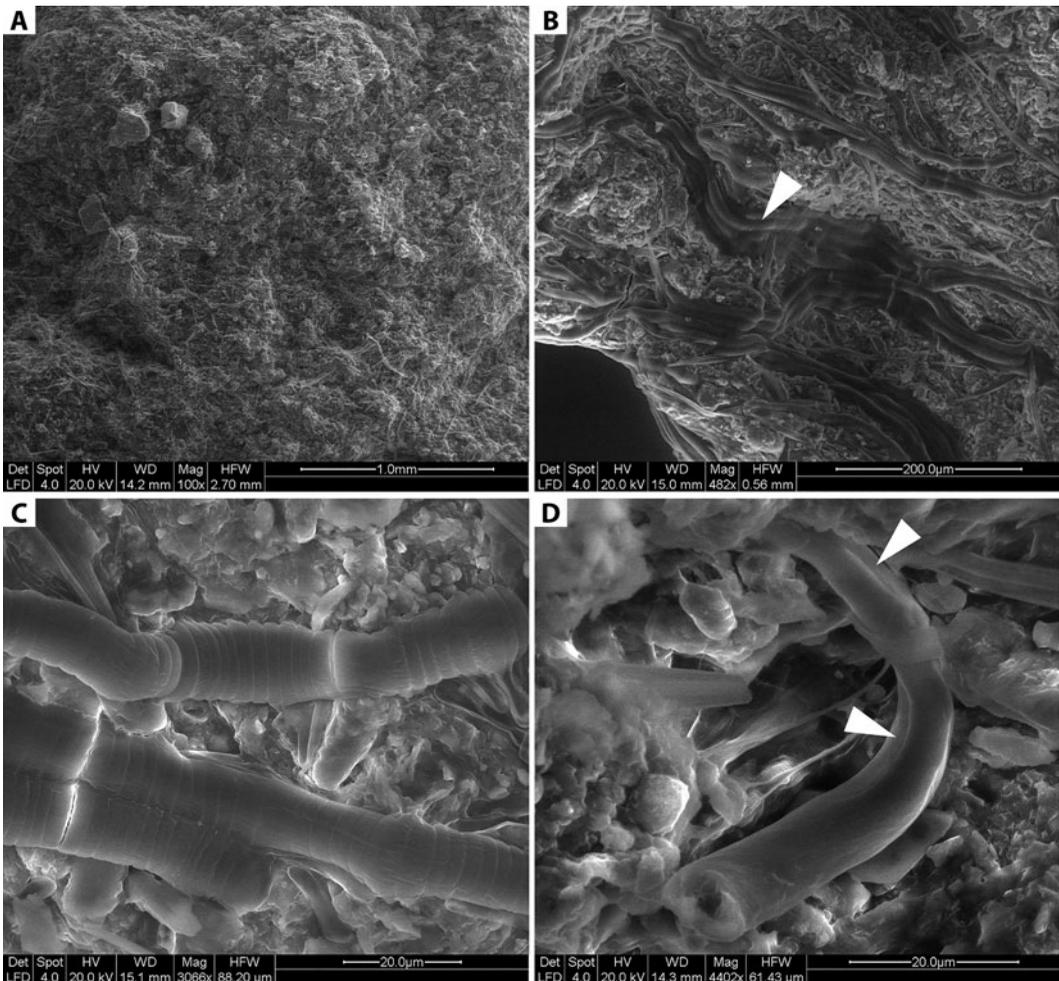


Fig. 10. ESEM micrographs of bio-sedimentary surface crusts from recently and permanently emerged areas. (a) Firm surface crust mainly consisting of sand grains and clayey sediments held together by microbial mucilage produced by diatoms and cyanobacteria filaments as they appear during the early fossilization ('packaging') phase. (b, c) Cyanobacteria trichomes as sedimentary binders from a recently emerged area. Note the cell division pattern. (d) Locally collapsed (arrows) cyanobacteria trichome from a permanently emerged area, with cell division pattern no longer visible.

extensive sulphate (gypsum) deposits on Mars – some of them interpreted as of evaporitic origin (e.g., Bibring *et al.*, 2005; McLennan *et al.*, 2005; Tosca and McLennan, 2006) – that a primary astrobiological relevance has been attributed to evaporitic sulphates as well as to their palaeontological potential, which was previously largely ignored. From evaporitic sulphates permineralized microfossils and other types of preserved microbial signatures were detected (Barbieri *et al.*, 2006; Schopf *et al.*, 2012; Allwood *et al.*, 2013) confirming their excellent ability to preserve biosignatures.

Their being primary target for astrobiological missions also relies on the habitability potential (past and present) of evaporitic salts, which is based on the salts capacity to retain water and generate liquid water brines. In addition to the morphologic biosignatures rapidly incorporated in evaporitic minerals or deposits, the rapid precipitation in salt flats facilitates primary fluid inclusions, a potential tool, not yet developed, for Martian life detection (Benison, 2019). The primary relevance of evaporitic environments as a potential target for the forthcoming astrobiological programs has also benefited from the

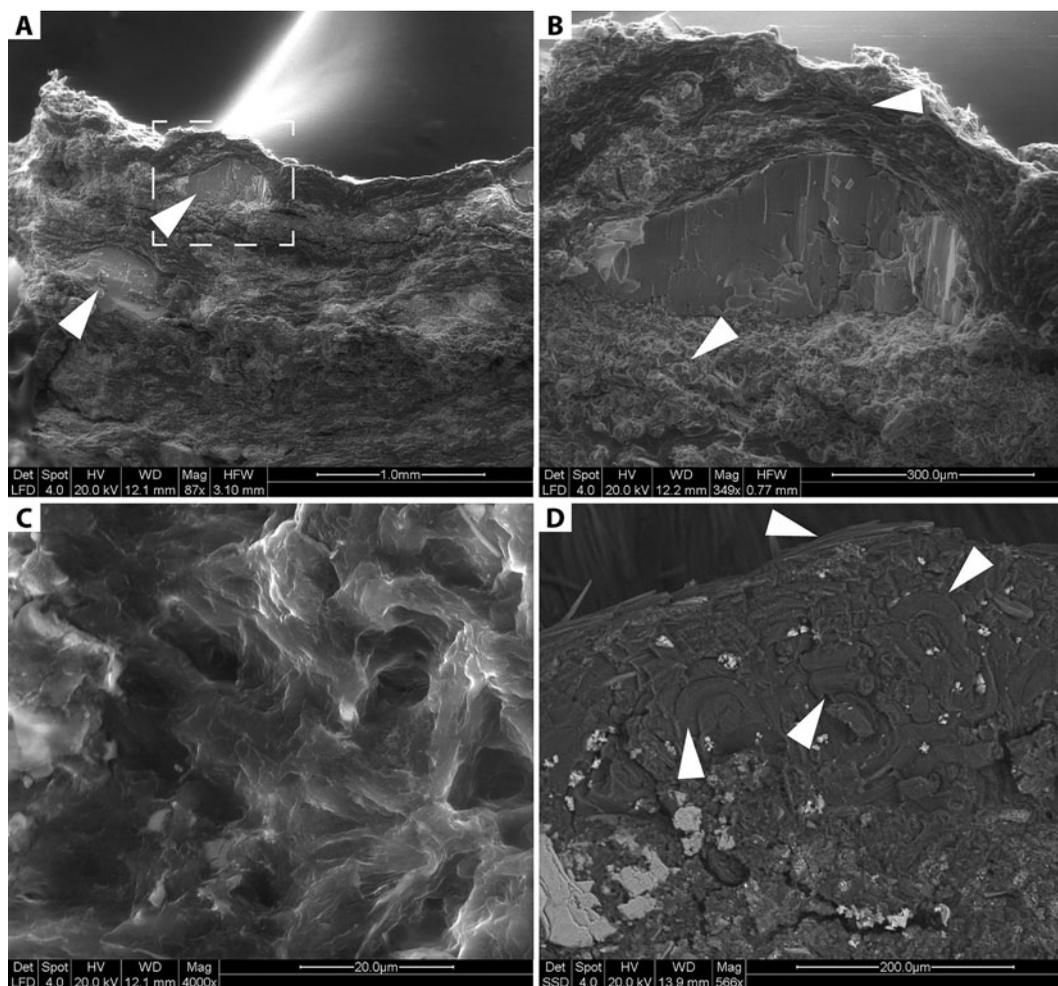


Fig. 11. ESEM micrographs of bio-sedimentary surface sections from a permanently emerged area as they appear during the early fossilization ('packaging') phase. Section across a bio-sedimentary surface crust where salt crystals (arrows in A) appear enveloped by the bio-laminated (arrow at the top in B) consisting of sediment particles, biofilm and trichome remnants, residual porosities and organic alveolar texture of the crust (arrow at the bottom in B, magnified in C) during a phase of their biodegradation process. (d) Bio-sedimentary 'packaging' topped with a thin diatom level (arrow at the top) and where trichomes of filamentous cyanobacteria (other arrows) make up the framework. Samples with normal stratigraphic orientation.

proven ability of halophilic archaea and halotolerant bacteria to survive when exposed to surface Mars conditions (Leuko *et al.*, 2014; Oren, 2014) or to those that hypothetically existed on the early Mars (Bryanskaya *et al.*, 2019). Also the recognized thermochemical stability in Martian conditions of evaporitic minerals (Benison, 2019) has further increased their potential of storing biosignatures, if any.

In this context, the easily accessible Cervia site enables the investigation of a range of MISS produced by the interactions between physical and chemical (siliciclastic and evaporitic) sediments and the products of epibenthic microbial activity during the early taphonomic phases. Similar to the Earth of the early Achaean, when certain MISS already existed (Noffke *et al.*, 2013a), Late Noachian and Hesperian Mars had aquatic palaeoenvironments where structures and textures potentially having the same origin may have formed (Noffke, 2021). At Cervia these morphologies derive

from sediment and microbe accumulations with finely laminated near surface textures, where, despite the sedimentary ‘packaging’, microbial morphologies are still recognizable. Also in desiccation morphologies, such as polygons and their curb-shaped margins, the microbiotic component is recognizable. Morphologies at the scale of those described here will likely be investigated by the analytical technologies of future Martian missions.

Concluding remarks

The Cervia pond enabled the evaluation of features developed on clastic sediment surfaces where biofilms found suitable conditions (i.e., sufficient time span of non-burial) for growing up to microbial mats and develop their strongly cohesive nature by binding and trapping the sedimentary grains. These mats have gone through successive stages in a sedimentary context where repeated subaerial exposures have left their traces during the sediment-microbe interplay, which allowed the formation of irregular leathery crusts up to their bio-sedimentary ‘packaging’. Comparable environmental combinations have been observed in MISS features from different climatic conditions, such as the coastal areas of the North Sea and southern Tunisia. The Cervia pond also shares some geomicrobiological features with other confined habitats of warmer and arid conditions – such as the inland sabkhas from Western Sahara, where diatom and cyanobacteria-dominated mats interact each other (Barbieri and Cavalazzi, 2018) – suggesting a relative independence from temperature as long as the availability of saline water and a relatively dry season, albeit temporary, is ensured.

Evaporation in the Cervia pond led to the formation of curled ribbons of fibrous halite, a distinctive mineral morphology, however ephemeral, which implies emersion and/or arid conditions. Aside from extremely arid areas, in fact, these morphologies lack a real preservation potential. Instead, a different matter regarding preservation are the deformation structures (knobs) associated with ribbons and produced on the substrate during their extrusion. Since they involve a biological component (thin layers of diatom frustules deformed in the knobs from which the salt ribbons are extruded) having a fossilization potential, some preservation in the stratigraphic record might be hypothesized.

The top-most cm in partially stabilized siliciclastic sediments provides an example of biolaminite, where a sub-millimetre-scale accretion is governed by mat-producing communities growing on sediment surfaces. Some biostabilization of the sediment surface allows persistence of the accretion process and the consequent formation of a microstratigraphic record.

In this type of deposit, where some sediment starvation makes easier the growth of microbial slime, phases of desiccation take place. Based on seasonal variations of the water levels in the pond, polygonal oscillation cracks have widened, shrivelled and eventually thickened their margins by differential development of microbial mats at the edges of the polygons as a consequence of repeated desiccation and moistening phases. Exceptionally developed in the Cervia pond, these thickened curb-shaped morphologies, known since the Neoproterozoic, can represent palaeoclimatic indicators capable of suggesting subtle changes in water levels and, therefore, seasonality.

In the Cervia pond, with an extremely low hydrodynamic regime, dark green laminae originating from monolayered microbial mats are set on clayey substrates that may result from minimal clay deposition derived from seawater input or wind action. This energy regime may have allowed the iso-oriented organization and a fluid flow-like appearance of the needle-shaped diatom frustules and cyanobacteria, both attributed to gliding motility, with the potential of leaving traces of a biological function in the geological record.

Acknowledgements. Thanks are due to the *Salina di Cervia* Nature Reserve for repeated permission to visit the site, Veronica Menna (Arpa Emilia-Romagna) for diatoms identification, Massimo Tonelli (University of Modena and Reggio Emilia) for ESEM assistance and the former students Antonio D’Alonzo and Jacopo Vujovic for their assistance during field samplings. The careful work of two anonymous reviewers was much appreciated. This study was funded by the University of Bologna (RFO 2017-2018).

References

- Abd El-Baky HH, El Baz FK and El-Baroty GS (2004) Production of antioxidant by the green alga *Dunaliella salina*. *International Journal of Agriculture and Biology* **6**, 49–57.
- Adam P (1990) *Saltmarsh Ecology*. New York: Cambridge University Press.
- Ali N, Asghar Z, Anwar Bég O and Sajid M (2016) Bacterial gliding fluid dynamics on a layer of non-Newtonian slime: perturbation and numerical study. *Journal of Theoretical Biology* **397**, 22–32.
- Allwood AC, Burch IW, Rouchy JM and Coleman M (2013) Morphological biosignatures in gypsum: diverse formation processes of Messinian (~6.0 Ma) gypsum stromatolites. *Astrobiology* **13**, 870–886.
- Amin SA, Parker MP and Armbrust EV (2012) Interactions between diatoms and bacteria. *Microbiology and Molecular Biology Reviews* **76**, 667–684.
- Anderson OR (2016) Marine and estuarine natural microbial biofilms: ecological and biogeochemical dimensions. *AIMS Microbiology* **2**, 304–331.
- Balakrishnan S, Santhanam P, Jeyanthi S, Divya M and Srinivasan M (2019) Preliminary screening of halophilic microalgae collected from different salt pans of Tuticorin, southeast coast of India. *Proceedings of the Zoological Society* **72**, 90–96.
- Barbieri R (2013) The role of terrestrial analogs in the exploration of the habitability of Martian evaporitic environments. In De Vera J-P and Seckbach J (eds), *Habitability of Other Planets and Satellites*. Dordrecht: Springer, pp. 165–180.
- Barbieri R and Cavalazzi B (2018) Microterraces in sabkha Oum Dba (Western Sahara, Morocco): physical and biological interactions in the formation of a surface micromorphology. *Astrobiology* **18**, 1351–1367.
- Barbieri R, Stivaletta N, Marinangeli L and Ori GG (2006) Microbial signatures in sabkha evaporite deposits of Chott el Gharsa (Tunisia) and their astrobiological implications. *Planetary and Space Science* **54**, 726–736.
- Benison KC (2019) How to search for life in Martian chemical sediments and their fluid and solid inclusions using petrographic and spectroscopic methods. *Frontiers in Environmental Science* **7**, 1–15.
- Bibring J-P, Langevin Y, Gendrin A, Gondet B, Poulet F, Berthé M, Soufflot A, Arvidson R, Mangold N, Mustard J and Drossart P and Omega team (2005) Mars surface diversity as revealed by the OMEGA/Mars express observations. *Science* **307**, 1576–1581.
- Bouougri EH and Porada H (2011) Biolaminated siliciclastic deposits. In Reitner J, Quéric N-V and Arp G (eds), *Advances in Stromatolite Geobiology*. Heidelberg: Springer, pp. 507–523.
- Bryanskaya AV, Berezhnov AA, Rozanov AA, Serdyukov DS, Malup TK and Peltek SE (2019) Survival of halophiles of Altai lakes under extreme environmental conditions: implications for the search for Martian life. *International Journal of Astrobiology* **19**, 1–15.
- Buchard RP (1981) Gliding motility of prokaryotes: ultrastructure, physiology, and genetics. *Annual Review of Microbiology* **35**, 497–529.
- Callefo F, Ricardi-Branco F, Amaral Cataldo R and Noffke N (2021) Microbially induced sedimentary structures (MISS). In Alderton D and Elias SA (eds), *Encyclopedia of Geology*, 2nd Edn. Amsterdam: Elsevier, pp. 545–554.
- Cameron B, Cameron D and Richard J (1985) Modern algal mats in intertidal and supratidal quartz sands, northeastern Massachusetts, U.S.A. In Curran HA (ed), *Biogenic Structures: Their Use in Interpreting Depositional Environments*. Tulsa: SEPM Special Publication 35, pp. 211–223.
- Caruso L, Giambastiani B, Gabbianelli G and Diani L (2005) Geomorphology and evolution of Ravenna's dune system (Italy). In Herrier J-L, Mees J, Salman A, Seys J, Van Nieuwenhuysse H and Dobbelaere I (eds), *Proceedings 'Dunes and Estuaries 2005'* – International Conference on Nature Restoration Practices in European Coastal Habitats, Koksijde, Belgium, 19–23 September 2005 VLIZ Special Publication 19, pp. 591–593.
- Chen X, Zhang C, Paterson DM, Townend IH, Jin C, Zhou Z, Gong Z and Feng Q (2019) The effect of cyclic variation of shear stress on non-cohesive sediment stabilization by microbial biofilms: the role of 'biofilm precursors'. *Earth Surface Processes and Landforms* **44**, 1471–1481.
- Dade WB, Davis JD, Nichols PD, Nowell ARM, Thistle D, Trexler MB and White DC (1990) Effects of bacterial Exopolymer Adhesion on the entrainment of sand. *Geomicrobiology Journal* **8**, 1–16.
- DasSarma S and DasSarma P (2017) Halophiles. eLS, Wiley Online Library. doi: 10.1002/9780470015902.a0000394.pub4
- Davies NS, Liu AG, Gibling MR and Miller RF (2016) Resolving MISS conceptions and misconceptions: a geological approach to sedimentary surface textures generated by microbial and abiotic processes. *Earth-Science Reviews* **154**, 210–246.
- de Brouwer JFC and Stal LJ (2002) Daily fluctuations of exopolymers in cultures of the benthic diatoms *Cylindrotheca closterium* and *Nitzschia* sp. (Bacillariophyceae). *Journal of Phycology* **38**, 464–472.
- de Brouwer JFC, Wolfstein K, Ruddy GK, Jones TER and Stal LJ (2005) Biogenic stabilization of intertidal sediments: the importance of extracellular polymeric substances produced by benthic diatoms. *Microbial Ecology* **49**, 501–512.
- Eriksson PG, Porada H, Banerjee S, Bouougri E, Sarkar S and Bumby AJ (2007) Mat-destruction features. In Schieber J, Bose PK, Eriksson PG, Banerjee S, Sarkar S, Altermann W and Catuneau O (eds), *Atlas of Microbial Mat Features Preserved Within the Coastal Rock Record*. Amsterdam: Elsevier, pp. 76–105.
- Fang H, Fazeli M, Cheng W, Huang L and Hu H (2015) Biostabilization and transport of cohesive sediment deposits in the three gorges reservoir. *PLoS ONE* **10**, e0142673.
- Franco P, Jeftić L, Malanotte Rizzoli P, Michelato A and Orlić M (1982) Descriptive model of the Northehrn Adriatic. *Oceanologica Acta* **5**, 379–389.

- Gambolati G, Giunta G, Putti M, Teatini P, Tomasi L, Betti I, Morelli M, Berlamont J, De Backer K, Decouttere C, Monbaliu J, Yu CS, Brøker I, Christensen ED, Elfrink B, Dante A and Gonella M (1998) Coastal evolution of the upper Adriatic Sea due to sea level rise and natural and anthropic land subsidence. In Gambolati G (ed), *CENAS. Coastline Evolution of the Upper Adriatic Sea due to Sea Level Rise and Natural and Anthropogenic Land Subsidence*. Dordrecht: Springer, pp. 1–34.
- Gerdes G (2007) Structures left by modern microbial mats in their host sediment. In Schieber J, Bose P, Eriksson PG, Banerjee S, Sarkar S, Altermann W and Catuneanu O (eds), *Atlas of Microbial Mat Features Preserved Within the Clastic Rock Record*. Amsterdam: Elsevier, pp. 5–38.
- Guarnieri C (ed.) (2019) *La salina romana e il territorio di Cervia. Aspetti ambientali e infrastrutture storiche*. Ante Quem, pp. 1–304.
- Gupta S and Agrawal SC (2007) Survival and motility of diatoms *Navicula grimmei* and *Nitzschia palea* affected by some physical and chemical factors. *Folia Microbiologica* **52**, 127–134.
- Hallsworth JE, Mancinelli RL, Conley CA, Dallas TD, Rinaldi T, Davila AF, Benison KC, Rapoport A, Cavalazzi B, Selbmann L, Changela H, Westall F and Yakimov MM (2021) Astrobiology of life on Earth. *Environmental Microbiology* **23**, 3335–3344.
- Heintzelman MB (2006) Cellular and molecular mechanics of gliding locomotion in eukaryotes. *International Review of Cytology* **251**, 79–129.
- Hoiczuk E (2000) Gliding motility in cyanobacteria: observations and possible explanations. *Archives of Microbiology* **174**, 11–17.
- Holzinger A and Karsten U (2013) Desiccation stress and tolerance in green algae: consequences for ultrastructure physiological, and molecular mechanisms. *Frontiers in Plant Science* **4**, 327.
- Horikoshi K and Grant WD (1998) *Extremophiles. Microbial Life in Extreme Environments*. New York: Wiley-Liss.
- Kociolek JP, Spaulding SA and Lowe RL (2015) Bacillariophyceae: the raphid diatoms. In Wehr JD, Sheath RG and Kociolek JP (eds), *Freshwater Algae of North America*. San Diego: Academic Press, pp. 709–772.
- Laviale M, Beaussart A, Allen J, Quilès F and El-Kirat-Chatel S (2019) Probing the adhesion of the common freshwater diatom *Nitzschia palea* at nanoscale. *ACS Applied Materials & Interfaces* **11**, 48574–48582.
- Leuko S, Rettberg P, Pontifex AL and Burns BP (2014) On the response of halophilic archaea to space conditions. *Life* **4**, 66–76.
- Ley RE, Harris JK, Wilcox J, Spear JR, Miller SR, Bebout BM, Maresca JA, Bryant DA, Sogin ML and Pace NR (2006) Unexpected diversity and complexity of the Guerrero Negro Hypersaline Microbial Mat. *Applied and Environmental Microbiology* **72**, 3685–3695.
- McLennan SM, Bell JF, Calvin WM, Christensen PR, Clark BC, de Souza PA, Farmer J, Farrand WH, Fike DA, Gellert R, Ghosh A, Glotch TD, Grotzinger JP, Hahn B, Herkenhoff KE, Hurowitz JA, Johnson JR, Johnson SS, Jolliff B, Klingelhofer G, Knoll AH, Learner Z, Malin MC, McSween HY, Pockock J, Ruff SW, Soderblom LA, Squyres SW, Tosca NJ, Watters WA, Wyatt MB and Yen A (2005) Provenance and diagenesis of the evaporite-bearing Burns formation, Meridiani Planum, Mars. *Earth and Planetary Science Letters* **240**, 95–121.
- McMahon S, Van Smeerdijk Hood A and McLlroy D (2017) The origin and occurrence of subaqueous sedimentary cracks. In Brasier AT, McLlroy D and McLoughlin N (eds), *Earth System Evolution and Early Life: A Celebration of the Work of Martin Brasier*, *Geological Society*. London: Special Publication 448, pp. 285–309.
- Moreno J, Vargas MA, Olivares H, Rivas J and Guerrero MG (1998) Exopolysaccharide production by the cyanobacterium *Anabaena* sp. ATCC 33047 in batch and continuous culture. *Journal of Biotechnology* **60**, 175–182.
- Neumann AC, Gebelein CD and Scoffin TP (1970) The composition, structure and erodability of subtidal mats, Abaco, Bahamas. *Journal of Sedimentary Research* **40**, 274–297.
- Nielsen PH, Jahn A and Palmgren R (1997) Conceptual model for production and composition of exopolymers in biofilms. *Water Science & Technology* **36**, 11–19.
- Noffke N (1999) Erosional remnants and pockets evolving from biotic–physical interactions in a recent lower supratidal environment. *Sedimentary Geology* **123**, 175–181.
- Noffke N (2021) Microbially induced sedimentary structures in clastic deposits: implication for the prospection for fossil life on Mars. *Astrobiology* **21**, 866–892.
- Noffke N, Gerdes G, Klenke T and Krumbein WE (1996) Microbially induced sedimentary structures — examples from modern sediments of siliciclastic tidal flats. *Zentralblatt für Geologie und Paläontologie* **1**, 307–316.
- Noffke N, Gerdes G, Klenke T and Krumbein WE (1997) The impact of sediment-stabilizing biofilms on the architecture of sedimentary structures (Mellum Island, southern North Sea). *Courier Forschungsanstalt Senckenberg* **201**, 297–305.
- Noffke N, Gerdes G, Klenke T and Krumbein WE (2001a) Microbially induced sedimentary structures—a new category within the classification of primary sedimentary structures. *Journal of Sedimentary Research* **71**, 649–656.
- Noffke N, Gerdes G, Klenke T and Krumbein WE (2001b) Microbially induced sedimentary structures indicating climatological, hydrological and depositional conditions with recent and Pleistocene coastal facies zones (southern Tunisia). *Facies* **44**, 23–30.
- Noffke N, Beukes N, Bower D, Hazen RM and Swift DJP (2008) An actualistic perspective into Archean worlds – (cyano-)bacterially induced sedimentary structures in the siliciclastic Nhlazatse Section, 2.9 Ga Pongola Supergroup, South Africa. *Geobiology* **6**, 5–20.
- Noffke N, Christian D, Wacey D and Hazen R (2013a) Microbially induced sedimentary structures recording an ancient ecosystem in the ca. 3.48 billion-year-old dresser formation, Pilbara, Western Australia. *Astrobiology* **13**, 1103–1124.
- Noffke N, Decho AW and Stoodley P (2013b) Slime through time: the fossil record of prokaryote evolution. *Palaios* **28**, 1–5.
- Oren A (2002) Diversity of halophilic microorganisms: environments, phylogeny, physiology, and applications. *Journal of Industrial Microbiology & Biotechnology* **28**, 56–63.

- Oren A (2014) Halophilic archaea on Earth and in space: growth and survival under extreme conditions. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **372**, 20140194.
- Oren A (2015) Cyanobacteria in hypersaline environments: biodiversity and physiological properties. *Biodiversity and Conservation* **24**, 781–798.
- Owen R, Renaut RW and Jones B (2008) Geothermal diatoms: a comparative study of floras in hot spring systems of Iceland, New Zealand, and Kenya. *Hydrobiologia* **610**, 175–192.
- Panieri G, Lugli S, Manzi V, Roveri M, Schreiber BC and Palinska KA (2010) Ribosomal RNA gene fragments from fossilized cyanobacteria identified in primary gypsum from the late Miocene, Italy. *Geobiology* **8**, 101–111.
- Paterson DM, Aspden RJ, Visscher PT, Consalvey M, Andres MS, Decho AW, Stolz J and Reid RP (2008) Light-dependant biostabilisation of sediments by stromatolite assemblages. *PLoS ONE* **3**, e3176.
- Phillips WR and Rigby JK (1991) Halite tomb fillings and a distinctive halite-cemented sandstone in the Middle Eocene Gehannam formation, Egypt. *Journal of Sedimentary Petrology* **61**, 419–427.
- Porada H, Bouougri EH and Ghergut J (2007) Hydraulic conditions and mat-related structures in tidal flats and coastal sabkhas. In Schieber J, Bose PK, Eriksson PG, Banerjee S, Sarkar S, Altermann W and Catuneanu O (eds), *Atlas of Microbial Mat Features Preserved Within the Clastic Rock Record*. Amsterdam: Elsevier, pp. 285–265.
- Poulsen N, Kröger N, Harrington MJ, Brunner E, Paasch S and Buhmann MT (2014) Isolation and biochemical characterization of underwater adhesives from diatoms. *Biofouling* **30**, 513–523.
- Rashmi V, Shylajanaciyar M, Prabakaran D and Uma L (2017) Uranium sequestration by marine cyanobacteria and its metabolites: an insight into metabolism-dependent and metabolism-independent interactions. In Das S and Dash HR (eds), *Handbook of Metal-Microbe Interactions and Bioremediation*. Boca Raton: CRC Press, pp. 731–746.
- Rothschild LJ (1990) Earth analogs for Martian life. Microbes in evaporites, a new model system for life on Mars. *Icarus* **88**, 246–260.
- Rothschild LJ and Mancinelli RL (2001) Life in extreme environments. *Nature* **409**, 1092–1101.
- Roubex V and Coste M (2017) A case of close interspecific interactions between diatoms: selective attachment on a benthic motile species. *Aquatic Microbial Ecology* **80**, 55–59.
- Schopf JW, Farmer JD, Foster IS, Kudryavtsev AB, Gallardo VA and Espinosa C (2012) Gypsum-permineralized microfossils and their relevance to the search for life on Mars. *Astrobiology* **12**, 619–633.
- Skyring GW and Bauld J (1990) Microbial mats in Australian coastal environments. In Marshall KC (ed), *Advances in Microbial Ecology*, 11. New York: Plenum Press, pp. 461–498.
- Stal LJ (1994) Microbial mats: ecophysiological interactions related to biogenic sediment stabilization. In Krumbein WE, Paterson DM and Stal LJ (eds), *Biostabilization of Sediments*. University of Oldenburg, Oldenburg: BIS Publishers, pp. 41–53.
- Stal LJ (2000) Cyanobacterial mats and stromatolites. In Whitton BA and Potts M (eds), *The Ecology of Cyanobacteria: Their Diversity in Space and Time*. Dordrecht: Kluwer Academic Publishers, pp. 61–120.
- Stal LJ and de Brouwer JFC (2003) Biofilm formation by benthic diatoms and their influence on the stabilization of intertidal mudflats. In Rullkötter J (ed), *BioGeoChemistry of Tidal Flats, Proceedings of a Workshop at the Hanse Institute of Advanced Study*. Delmenhorst, Germany. Wilhelmshaven: Forschungszentrum Terramare, pp. 109–111.
- Stavreva-Veselinovska S and Todorovska A (2010) Ecology of the diatomic flora in thermo-mineral springs of Katlanovska Banja in the republic of Macedonia. *Ecologia Balkanica* **2**, 1–6.
- Stivaletta N, Barbieri R and Billi D (2012) Microbial colonization of the salt deposits in the driest place of the Atacama Desert (Chile). *Origins of Life and Evolution of Biospheres* **42**, 187–200.
- Sutherland IW (2001) Biofilm exopolysaccharides: a strong and sticky framework. *Microbiology* **147**, 3–9.
- Tamulonis C, Postma M and Kaandorp J (2011) Modeling filamentous cyanobacteria reveals the advantages of long and fast trichomes for optimizing light exposure. *PLoS ONE* **6**, e22084.
- Tkavc R, Gostinčar C, Turk M, Visscher PT, Oren A and Gunde-Cimerman N (2010) Bacterial communities in the ‘petola’ microbial mat from the Sečovlje salterns (Slovenia). *FEMS Microbiology Ecology* **75**, 48–62.
- Tosca NJ and McLennan SM (2006) Chemical divides and evaporite assemblages on Mars. *Earth and Planetary Science Letters* **241**, 21–31.
- Viles HA (2012) Microbial geomorphology: a neglected link between life and landscape. *Geomorphology* **157/158**, 6–16.
- Vos PC, Misdorp R and De Boer PL (1988) Sediment stabilization by benthic diatoms in intertidal sandy shoals; qualitative and quantitative observations. In de Boer PL, van Gelder A and Nio SD (eds), *Tide-influenced Sedimentary Environments and Facies*. D. Dordrecht: Riedel Publishing Company, pp. 511–526.
- Vreeland RH, Rosenzweig WD and Powers DW (2000) Isolation of a 250 million-year-old halotolerant bacterium from a primary salt crystal. *Nature* **407**, 897–900.
- Vreeland RH, Jones J, Monson A, Rosenzweig WD, Lowenstein TK, Timofeeff M, Satterfield C, Cho BC, Park JS, Wallace A and Grant WD (2007) Isolation of live cretaceous (121–112 million years old) halophilic Archaea from primary salt crystals. *Geomicrobiology Journal* **24**, 275–282.
- Watermann F, Hillebrand H, Gerdes G, Krumbein WE and Sommer U (1999) Competition between benthic cyanobacteria and diatoms as influenced by different grain sizes and temperature. *Marine Ecology Progress Series* **187**, 77–87.
- Wetherbee R, Lind JL and Burke J (1998) The first kiss: establishment and control of initial adhesion by raphid diatoms. *Journal of Phycology* **34**, 9–15.