

DISCOVERY OF CALCAREOUS MICROBIALITES IN COASTAL PONDS OF WESTERN SARDINIA (ITALY)

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Abstract. The discovery of microbialites in small coastal ponds of western Sardinia provides new evidence for understanding the microbial-related lithification phenomenon. The distribution of microbialites is specified, as well as their main characteristics. The succession of various layers corresponding to microbial mats with varying compositions also indicates significant environmental variations in ponds that can suffer a complete seasonal desiccation. The diatomaceous assemblage associated with microbialite support interesting data on the involved microorganism's consortium and the micritic mineralization within EPS (Exopolymeric substances) products. The Sardinian microbialites are considered as specific, given their occurrence under very special to extreme environmental conditions and should be integrated into a broader environmental classification of microbialites.

Key words: mediterranean, coastal ponds, microbial consortium, cyanobacteria, diatoms, biomineralization, extreme environments.

1. INTRODUCTION

The microbialites represent the earliest manifestation of the life-mineral interactions and continuously accompanied the vicissitudes of the history of the biosphere and geosphere on Earth. The microbialites, organosedimentary structures that result from the trapping, binding, and lithification of sediments by microbial mat communities (Riding, 2000), are currently present in many environments, from the mainland, to the deep ocean, at the earth surface and in the cryptic ones. Thus, numerous studies are reported on the genesis of these geobiological objects, resulting in very complex bio-physical-chemical processes involving diverse microbial communities whose functioning has the capacity to be recorded in the geological record.

In the coastal realm, modern microbialites develop in a wide spectrum of environments, from open sea to intern coastal water bodies of various forms and dimensions, under marine, freshwater or hypersaline conditions. The microbialite formed in bodies of water located near the sea shore, communicating or not with it, were particularly studied, especial-

ly in regions characterised by a rather warm climate, such as in coastal areas of Australia, Bahamas, Mexico, Venezuela, Brazil, Gulf of California... (Burne and Moore, 1993 ; Reitner *et al.*, 1996 ; Konishi *et al.*, 2001 ; Dupraz *et al.*, 2004 ; Vasconcelos *et al.*, 2006 ; Damazio *et al.*, 2006 ; Siqueiros-Beltrones, 2008 ; Iespa and Damazio Iespa, 2009 ; Smith *et al.*, 2010 ; Spadafora *et al.*, 2010 ; Johnson *et al.*, 2012 ; Petrash *et al.*, 2012 ; Siqueiros-Beltrones, 2012). There are very sensitive environments with quick variations of physico-chemical parameters. These microbialites are often associated with the development of non-lithified extensive microbial mats. However, it should be noticed that water bodies of small scale are poorly documented for their microbialitic content.

In the Mediterranean coastal lagoon systems, although microbial mats are widely represented, especially in temporarily or permanently hypersaline environments, microbialites resulting from direct or indirect mineralization of microbial structures have never been observed until now, to our knowledge. Here, we present the unexpected discovery of calcareous microbialites forming in coastal ponds of western Sardinia. The aims of this work is consequently to determine

the distribution of discovered microbialites, to provide a first description of involved construction processes and discuss their specificity regarding the microbialite formation phenomenon.

Microbial mats are formed by a consortium of microorganisms whose complex interactions are the trigger of this particular ecosystem. Among these microorganisms only diatoms have a mineralized skeleton of silica which, despite the phenomena of rapid dissolution of opal, are likely to be preserved. Several publications have emphasized the importance of diatoms as key player in the microbialite accretion (Winsborough and Golubic, 1987; Winsborough, 2000; Bonny and Jones, 2007; Bowlin *et al.*, 2012), but they were, in fact, not much studied in detail. In this work, we will, therefore, pay particular attention to data issued from the presence of diatoms intimately associated with the discovered microbialites.

2. REGIONAL SETTINGS

2.1. SARDINIAN COASTAL WETLANDS

Given the shape of the Sardinian coast (Fig. 1), the paleogeographic evolution and the historical events, there are numerous ponds, lagoons and marshes. Firstly, Stefani (1855) already divided Sardinian coastal ponds into three categories: the ponds which communicate with the sea, intern ponds and marshes. According to Cataudella *et al.* (2015), "Lagoon" is a term used in Italy only for large lagoons, 5000 to 50 000 ha. Thus, within the typologies *sensu* WFD (Water Framework Directive from UE), ponds and coastal lakes comprise small and large non-tidal basins. With specific regard to the classifying of the Italian coastal water bodies, including, naturally, Sardinia, a characterization based on geological features (Cataudella and Tancioni, 2007) can also be considered according to Valloni *et al.* (2006):

- pond: marine-adjacent basin without natural channels for communication with the sea;
- pond system: pond integrated with wetlands in the shoreline and/or with swamps.

So, brackish coastal areas are highly developed and of great interest, but rather than real lakes it comes to more or less large ponds, often completely during dry summer (Stoch, 2008). Currently, in the Sardinian island there are about 80 ponds and lagoons, which cover an area of nearly 12000 ha, the more extensive being situated in the west, southwest and south.

2.2. SINIS PENINSULA

The Sinis Peninsula, is one of the most important wetland territory in the Mediterranean, the second largest in Italy, only after the Po delta, and is designated by the Ramsar Convention as a site of international importance. The Sinis peninsula is characterised by a complex mosaic of a large dune system, sandy beaches, cliffs, reefs, farmlands, and a myriad of brackish ponds. The landscape is mainly characterised by a complexity of elements belonging to the hydrographic sys-

tems such as coastal lagoons and ponds. The ponds - artificial or natural - vary a lot in size and hydraulic regime: permanent, like the large Cabras lagoon (Fig. 1B), or temporary, with static or flowing water, fresh, brackish or salt water. Many temporary ponds can dry out completely, in summer, leaving behind a thick crust characteristic of salt ponds. Consequently, the salinity fluctuates between brackish and hypersaline, depending on the ratio of precipitation *versus* evaporation, during the dry and wet seasons.

The Sinis peninsula is characterised by a coastal system articulated by alternating small coves and more extensive beaches, headlands and cliffs. The most recent sand deposits are represented by the current and Holocene sands forming along the coast, due to the intense action of the Mistral, an important dune system inherently unstable over time. This dune system bordering the beach landward forms extended ridges separating the sea from several coastal ponds and protecting the areas behind the dunes from the wind action and the effects of marine aerosol.

The main climatic features of the area result from a typically two seasonal regime, with moderately cold winter, sub-humid with moderate water surplus and hot summer with large water deficit.

2.3. THE STUDIED COASTAL PONDS OF SINIS PENINSULA

2.3.1. Mari Ermi ponds

The Mari Ermi area is situated in the central western part of the Sinis coast (Fig. 1D). The Mari Ermi littoral consists of a beach of white fine sand, composed of characteristic granules of quartz glass. The quartzose coast near Mari Ermi is very wide, bordered by impressive dune formations and low vegetation, which separate it from a series of temporary ponds behind the dunes. Behind the Mari Ermi dune systems, there are depressions that give rise to features marshes (Fenu *et al.*, 2006). The Mistral, which, often, blows along the coast, generates waves of larger amplitudes. In this low coast, erosion is expressed with the retreat of the shore line, mainly, along the sandy shores.

The site of the Mari Ermi ponds consist of two water bodies parallel to the shore and separated by a transversal land strip (Fig. 1D), corresponding, in all, to an area of 20 hectares rich in vegetation (Mulas, 1986). The bottom of the ponds is filled with black sapropelic deposits.

Human activities, mainly touristic, occur during short periods of the year, on the emerged beach, dune fields and backwaters, triggering imbalance natural phenomena that induce abnormal redistribution of sediments with emphasis on the erosion phenomenon and nutrients supply.

2.3.2. Su Pallosu area

In the northern part of the Sinis Peninsula, near Su Pallosu, wetlands are represented by temporary ponds with highly saline waters. From either side of the headland of Su Pallosu

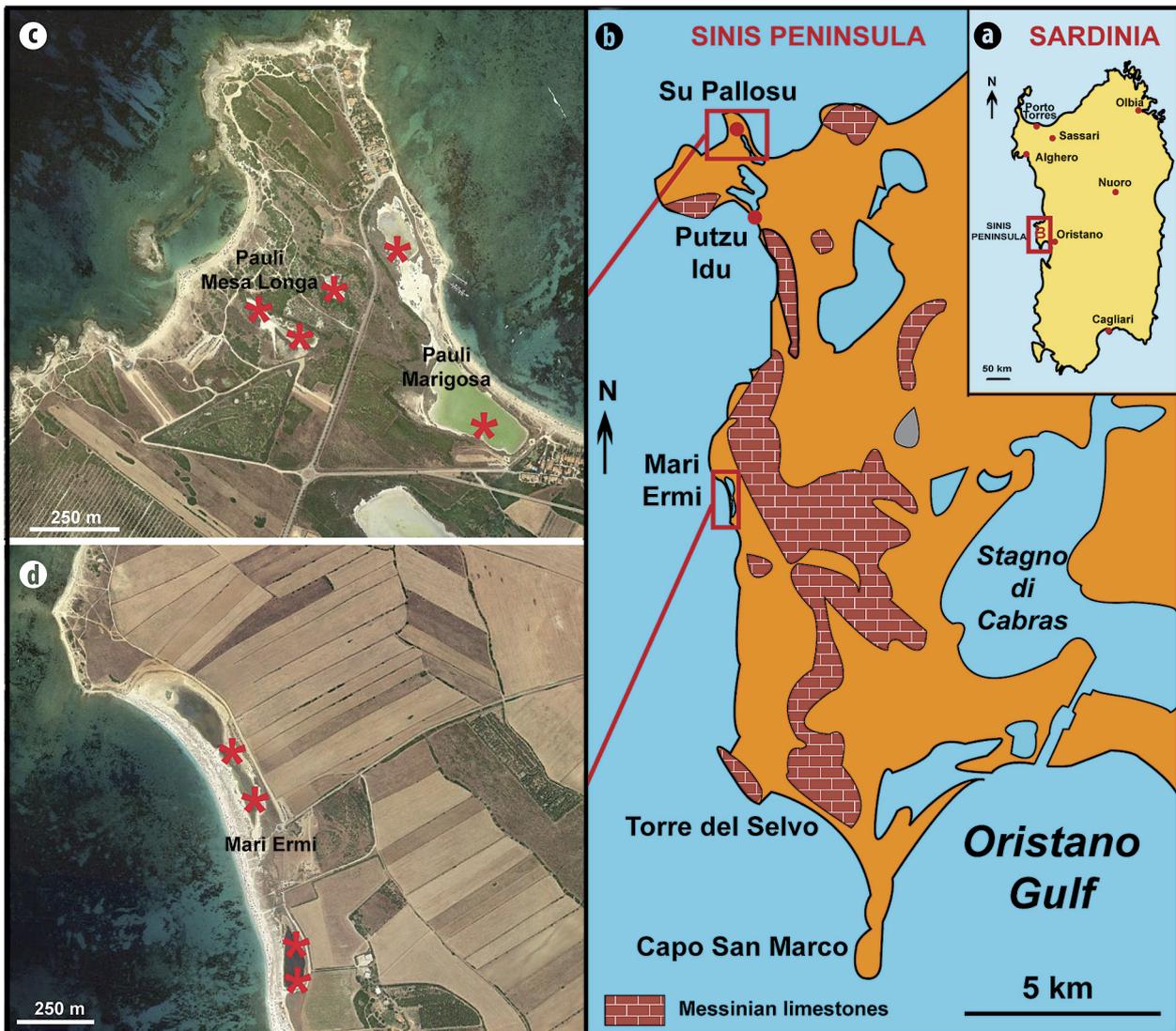


Fig. 1. **A.** Location of the studied area in Sardinia; **B.** Map of the Sinis Peninsula with the calcareous outcrops of the Messinian carbonate sediments; **C.** Aerial view of the Su Pallosu site showing the examined ponds (red stars), *Google Earth source*; **D.** Aerial view of the Mari Ermi site showing the two studied ponds (red stars – main sampling zones) *Google Earth source*.

there are, bordering the beaches, Pauli Mesa Longa, at the east, and Pauli Marigosa, at the west (Fig. 1C).

The Pauli Mesa Longa pond system corresponds to depressions behind the dunes. It includes three main pools, less than 20 cm deep, during the period of temporary flooding that may become hypersaline and, then, almost completely desiccated, in summer.

The Pauli Marigosa pond, extending southeast to Su Pallosu, covers about 25 hectares and has an average depth of 0.40 meters and a maximum of 0.80 meters. It is separated from the sea by a narrow strip of sand and has no tributaries and does not communicate with the sea. The Pauli Marigosa pond only collects rainwater and, in summer, often dries up completely, resulting in high salinity variations. Due to eutrophication and algal-cyanobacterial blooms, the water is generally brown or reddish.

3. MATERIAL AND METHODS

Microbialites and associated biofilms were observed *in situ* and collected during two periods: the dry season (June-July) and wet season (November).

Polished slabs were performed for macroscopic observations. Petrographic thin sections of standard thickness of 30 microns, covered with a cover-slip, were used, both for the optical and confocal microscopy observations.

For optical microscopy, the thin sections were studied under a microscope Zeiss Axioscope (Germany) 40 at x40, x60 and x100 (oil immersion Zeiss) magnifications and photographed with a Canon PowerShot A620 camera. Images taken at several focus levels were processed with specific image processing software (Helicon Focus®).

The use of Confocal Laser Scanning Microscopy (CLSM) naturally allows to confirm the data from optical techniques and also provides other valuable information. The CLSM is a tool used for localization of fluorescent microorganisms or organic matter (Hernández Mariné *et al.*, 2004). The observations were performed on a Leica TCS SP5 microscope at the University Pierre et Marie Curie in order to detect a possible autofluorescent signal which reveals the distribution of organic matter. Samples were studied through 20x0.70 NA and 40x1.25-0.7 NA oil-immersion objectives. Fluorescence images of the microbialite transversal sections were obtained with concomitant excitation at wavelengths of 561 nm, and 633 nm and collection of the emitted fluorescence between 516-556 nm and 647-693 nm, respectively. The images obtained from confocal microscopy allow viewing the autofluorescent objects in false colours.

Fragments of samples used to produce thin sections were first prepared by critical point drying method and, then, coated with gold-palladium and observed by scanning electron microscopy using a Philips XL 30 ESEM (Aix-Marseille University) and a Hitachi SU3500 (Muséum National d'Histoire Naturelle, Paris), both of which provide EDS micro analysis. Images were collected in secondary electron mode.

4. RESULTS

4.1. FIELD OBSERVATIONS

4.1.1. The microbialites from Mari Ermi (Figs. 2-4)

Separated from the open sea by the barrier beach (Fig. 2A), the southern water body of the Mari Ermi area is bordered, especially in their south and east edges, by concentrations of numerous pebbles with black surface color (Figs. 2B-C). During humid season, the pebbles are partly submerged (Figs. 2A, 2F, 3A-B) while during the dry period, the edges of the pond are desiccated and the pond possibly invaded by cyanobacterial mat (Figs. 2D-E, 2G, 3C-E). More detailed observation shows that the pebbles are, in fact, generally made of a rocky nucleus of various lithologies covered by microbialite. The microbialite formations are clearly characterised, in addition to the black color of the surface, by a cerebroid pustular aspect (Figs. 2F-G, 3C-F). Generally, the original rocky nucleus is entirely covered with microbialite which gives the appearance of macro-oncoids scattered on the edge of the pond (Fig. 2D-G). In some cases, the microbialite covers also part of the boulders, forming more large masses (Fig. 3A-B) and patches (Figs. 2E, 3B-C). Finally, the microbialite recovery may be more extensive on rocky outcrops. The thickness of the microbialite is variable and can reach 10 to 15 cm. We can observe that the microbialite does not fully cover the larger rocks, probably because they are limited by the maximum height of the water level reached in the pond (Fig. 3D).

The northern coastal pond of Mari Ermi area shows approximately the same features. The pond is also separated from the open sea by a narrow barrier beach (Fig. 4A). Accumulations of macro-oncoids are located, mainly, at the eastern edge (Fig. 4B-C). Scattered pebbles (Fig. 4C) and patches (Fig. 4D-F) occur exhibiting the characteristic cerebroid pustular appearance (Fig. 4E-F). During the dry season, the patches of macro-oncoids are partially covered by extensive cyanobacterial mat. As in the southern pond, rare large rocky block can be covered by thin regular digitate microbialite (Fig. 4G). Breaks on microbialite reveal that the pustular aspect results in a digitate growth of microbialite (Fig. 4H).

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4.1.2. The microbialites from Su Pallosu area (Fig. 5)

In the Pauli Mesa Longa site, the studied pond system is clearly separated from the sea and consists of three water bodies (Figs. 1C, 5A), while the Pauli Marigosa site corresponds to a pond along the coast separated from the sea by a narrow dune ridge (Figs. 1C, 5B).

At the periphery of the Pauli Mesa Longa pond, pebble accumulations exhibit black microbialitic coating and are partially covered by cyanobacterial mat, during the dry season (Figs. 5C-D) or submerged, during the humid season (Fig. 5F). The microbialite coating showing the characteristic cerebroid aspect of the surface (Fig. 5F-G) reaches a thickness limited to a few centimeters.

The hypersaline Pauli Marigosa pond has no evident accumulations of pebbles with black surfaces as in other sites, but a thin microbialitic pustular crust can occur on rocky substrate (Fig. 5H).

Both Mari Ermi and Su Pallosu sites exhibit microbialites that develop only on hard substrate, such as pebbles and rocks, and never on soft substrate.

4.2. MICROBIALITE FEATURES

4.2.1. Macroscopic and mesoscopic aspects

Polished slabs and thin sections of the microbialitic coating (Fig. 6A-E) show clearly a general digitate growth, inducing, at the surface, the characteristic pustular appearance, around a rocky nucleus of various lithologic natures. These fingering appears composite resulting from several successive distinct layers assigning to the overall microbialite a laminated stromatolitic structure. When the coating by digitate microbialite is complete around the nucleus, the result is a more or less regular and thick oncolite (Fig. 6B, E). In some cases, the digitations are less pronounced and the microbialite, then, consists mostly in a laminated crust of centimetric thickness (Fig. 6F). The contact of the microbialite with the nucleus may be indicated by a red ferruginous line (Fig. 6A,F). The first stage of the microbialite growth can be achieved directly by stromatolitic digitations (Fig. 6A, C, D) or by laminated crust (Figs. 6B,E).

The general thickness of microbialite coating is quite variable, ranging from several millimeters to ten centimeters, at most. The fingering is relatively constant in diameter, typically of the order of 0.5 cm. Many samples show that the surface of the microbialite is covered by a laminated reddish crust, about 1 mm thick (Fig. 6A, B, D).

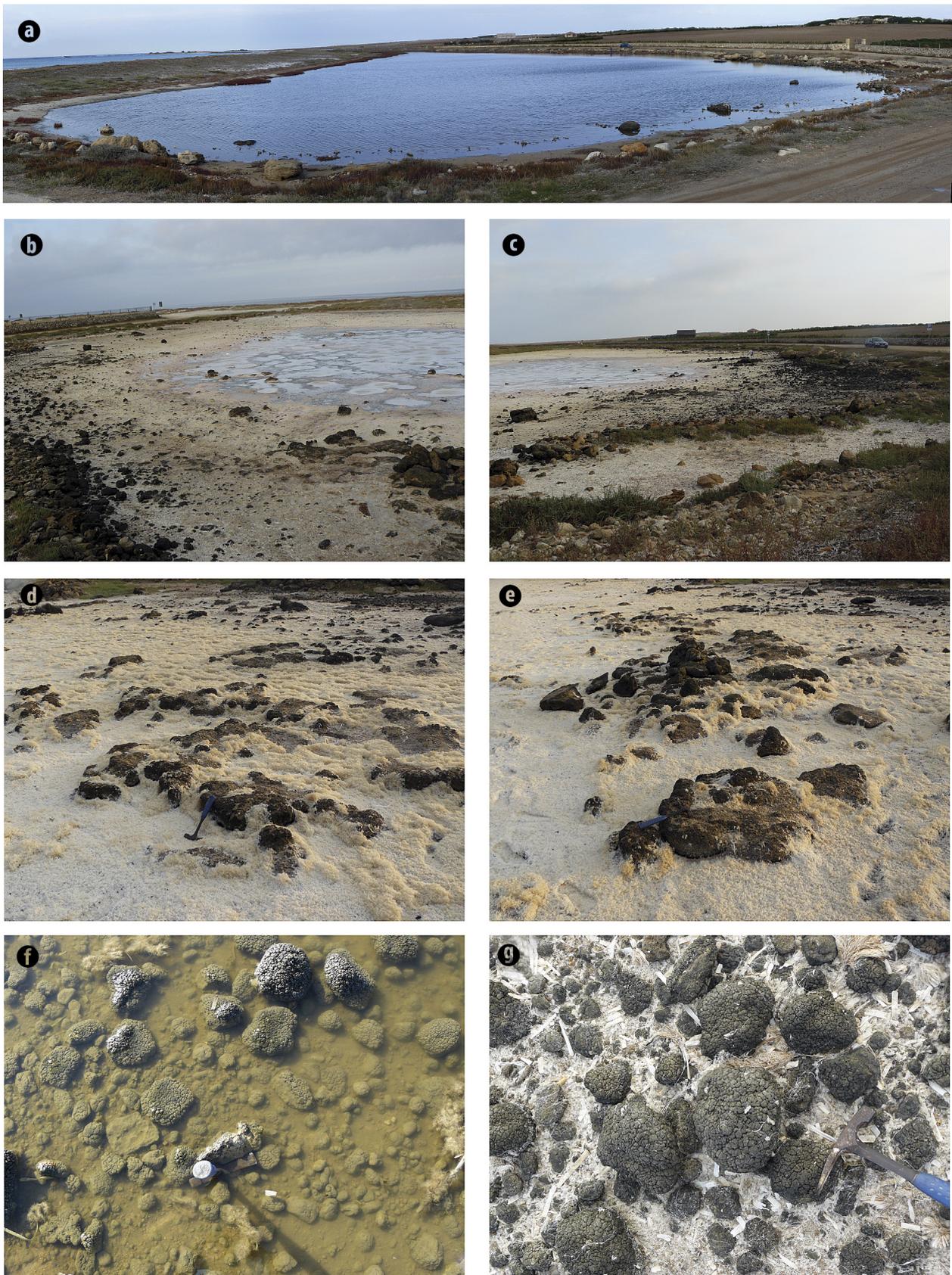


Fig. 2. Southern coastal pond at Mari Ermi. **A.** General view showing the barrier beach separating the pond from the open sea (top left); **B-C.** View of the pond edges with pebble accumulations; **D-E.** Patches of macro-encrusting microbialites partially covered by cyanobacterial mat during the dry season; **F.** Macro-encrusting microbialites during humid season; **G.** Macro-encrusting microbialites during dry season.

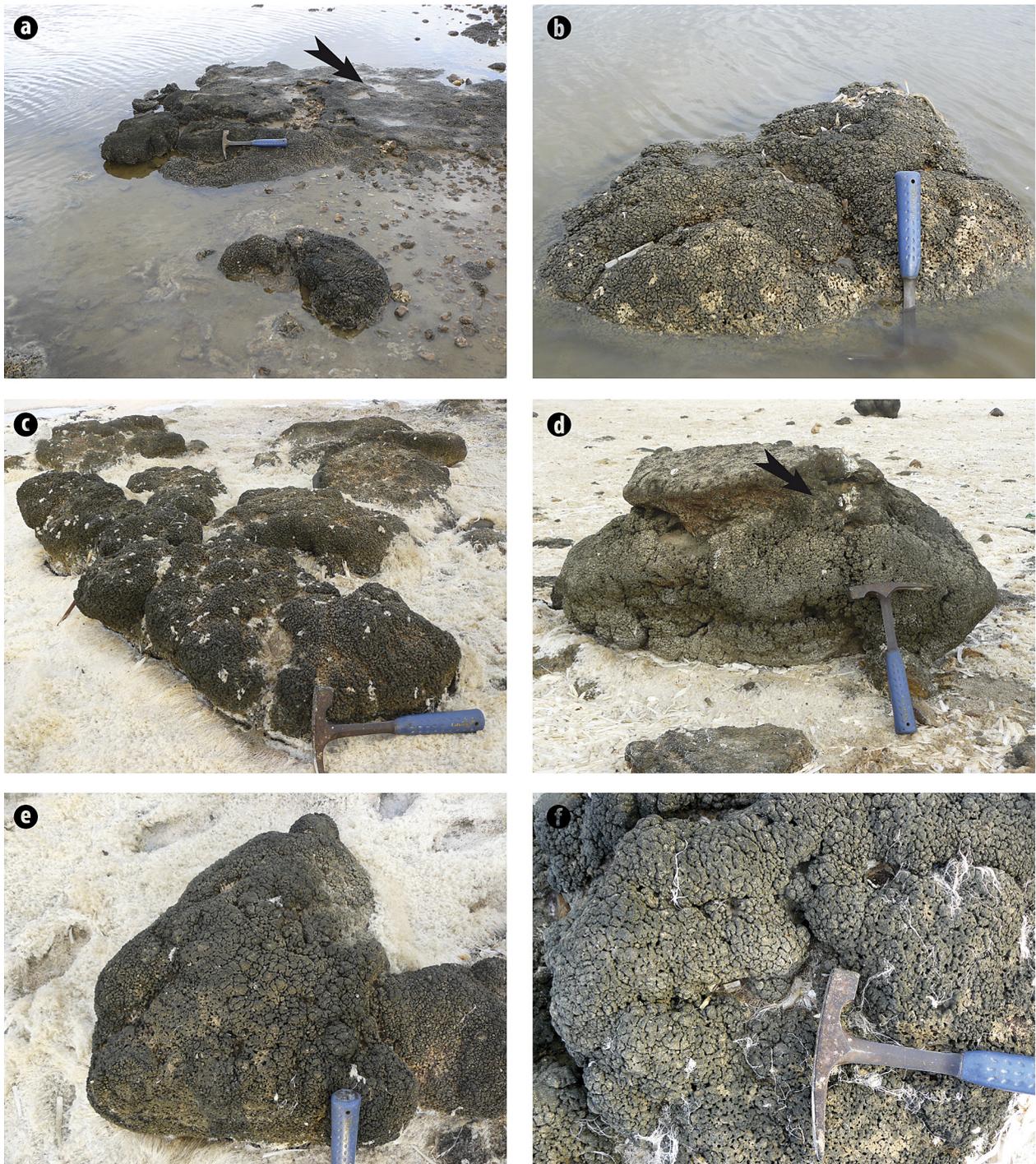


Fig. 3. Microbialites of the southern coastal pond at Mari Ermi. **A.** Microbialites around pebbles or covering the rocky substrate surface (arrow); **B.** Patch of microbialite partially submerged; **C.** Patch of microbialite cleared during dry season; **D.** Rocky substrate covered by microbialite up to the maximum water level (arrow); **E-F.** Detail of microbialite showing the characteristic cerebroid aspect of the surface.

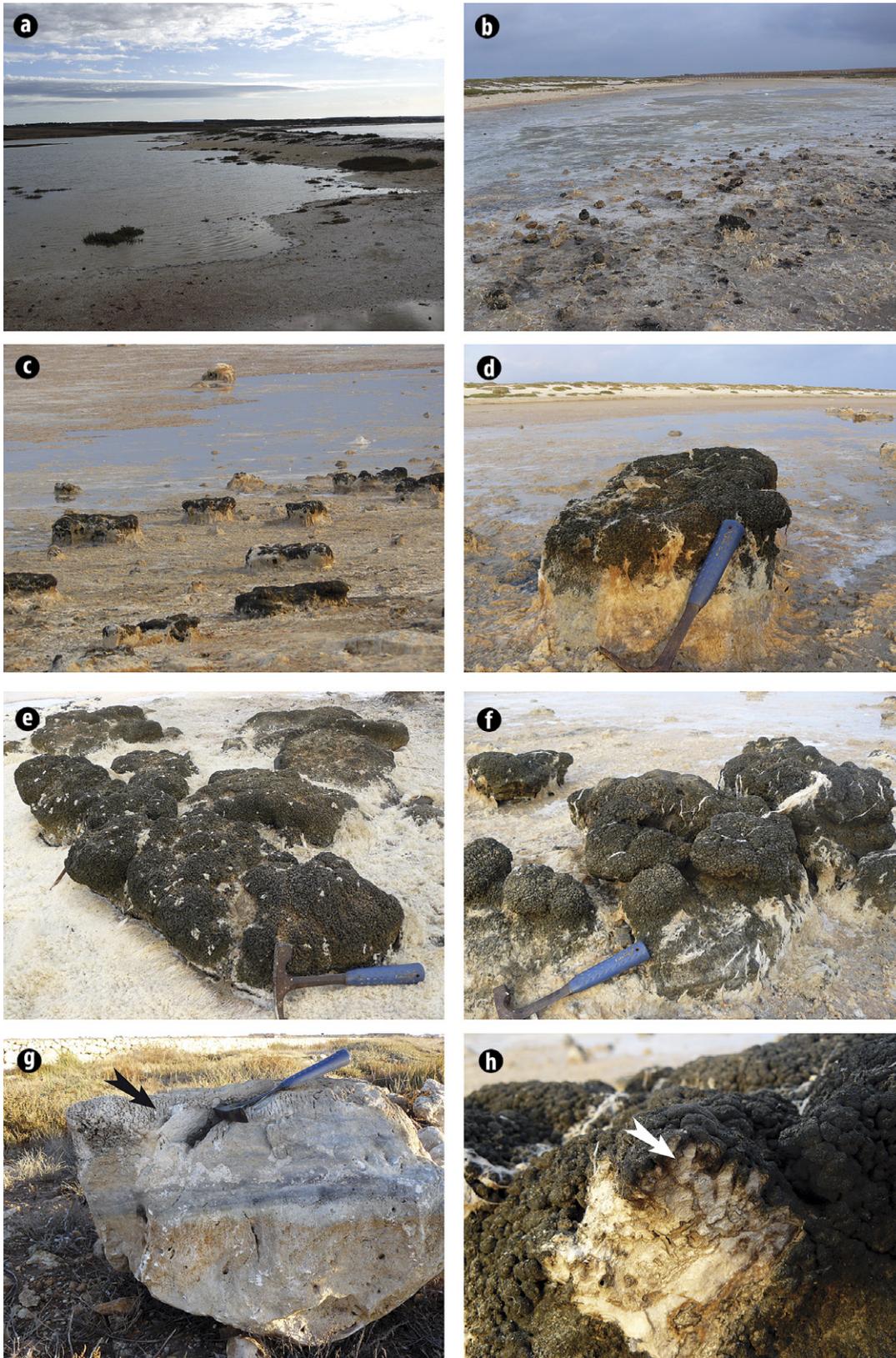


Fig. 4. Northern coastal pond at Mari Ermi. **A.** General view showing the barrier beach separating the pond from the open sea (right); **B-C.** View of the pond edge with macro-encrusting microbialites; **D.** Macro-encrusting microbialite partially covered by cyanobacterial mat during the dry season; **E-F.** Patches of macro-encrusting microbialites partially covered by cyanobacterial mat during the dry season; **G.** Rock covered by regular digitate microbialites (arrow); **H.** Detail of microbialite characterised by a digitate growth.



Fig. 5. Coastal ponds near Su Pallosu. **A.** General view showing the position of the western ponds (arrow) related to the open sea (top left), Pauli Mesa Longa; **B.** View of the eastern pond showing the barrier beach separating the pond from the open sea (arrow), Pauli Marigosa; **C.** View of Pauli Mesa Longa pond periphery with black pebble accumulations; **D.** Pebbles with microbialitic coating partially covered by cyanobacterial mat (arrow) during the dry season; **E.** Pebbles with microbialitic coating partially submerged during humid season; **F-G.** Detail of microbialite showing the characteristic cerebroid aspect of the surface; **H.** Thin microbialitic pustular crust on rocky substrate of Pauli Marigosa pond.

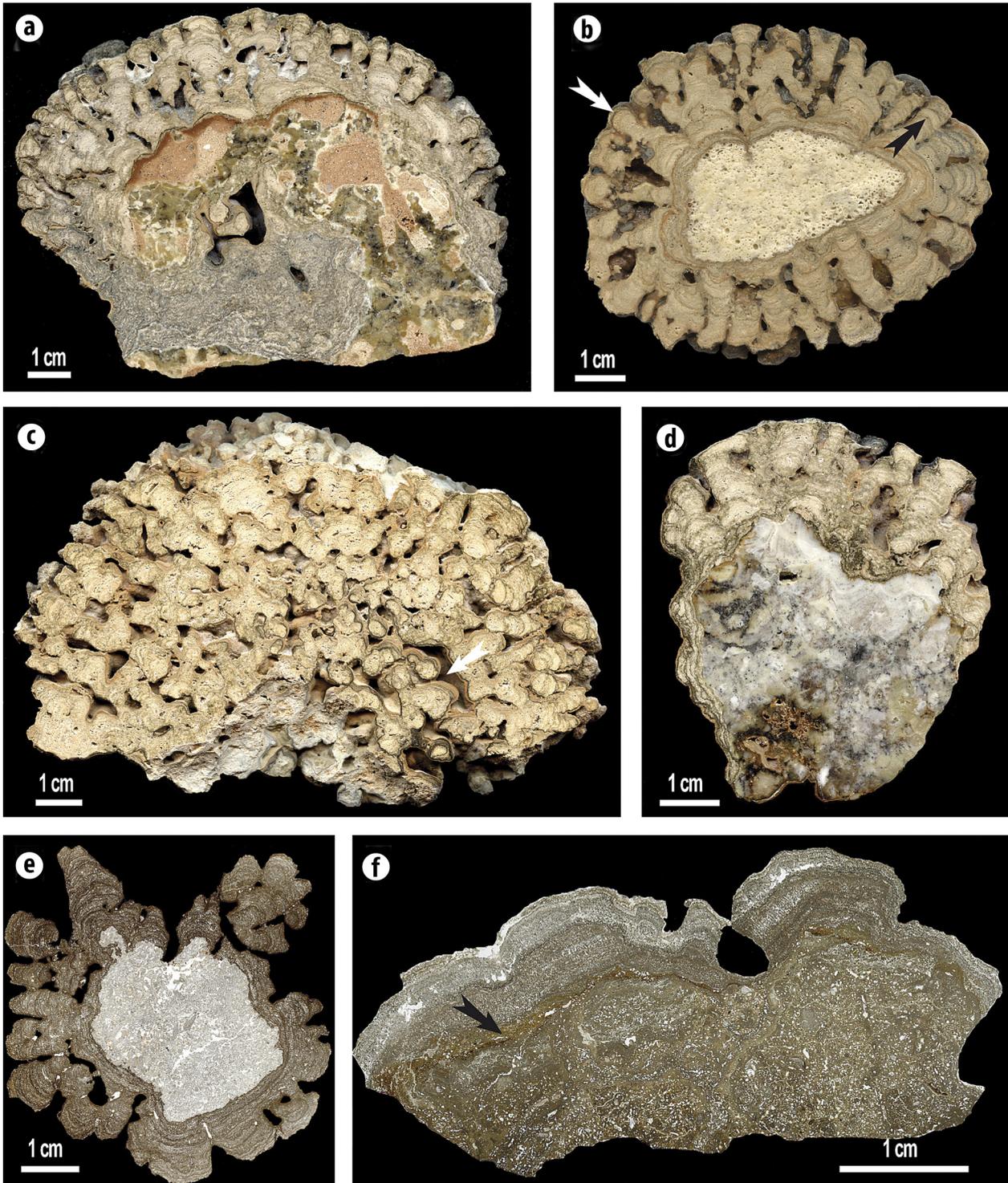


Fig. 6. Microbialite sections. **A-D.** Polished slabs of microbialitic coating from Mari Ermi showing successive laminated crusts and digitations themselves laminated (black arrows). Generally, the construction ends with a millimeter crust (white arrows); **E.** Petrographic thin section from Mari Ermi microbialite showing the discontinuous aspect of the construction; **F.** Petrographic thin section from Su Pallosu microbialite showing the ferruginous contact (arrow) with rocky pebble.

4.2.2. Microbialite features at the microscopic scale

As shown in the “Material and methods” chapter, different techniques (optical microscopy, CLSM investigations, SEM views) were used to characterise, as best as possible, all aspects accessible to observation of the studied microbialites (Figs. 7-9).

In the detail, the discontinuous aspect of the microbialite growth is evident, marked by stages of interruptions or colonization of the microbial communities. Resulting from mineralization processes with only micritic of Mg calcite product identified by EDS micro-analysis, two main types of microbialite features are evidenced: poorly to densely cemented filamentous layers and dark micritic laminated layers. These two types of microbialite can constitute the first crust on the substrate and the last episode visible on the surface, respectively.

The most clearly expressed layers correspond to microbial mats constructed by upward oriented filaments (Figs.7-9) originally corresponding to sheathed unbranched filamentous cyanobacterium. In the upper part of the microbialite, the remains of cyanobacteria sheaths, brown in color by light microscopy (Fig.7F) and with a strong autofluorescence signal by confocal microscopy (Fig. 8A,B) may be often noticed. Although the trichomes are not well preserved in microbialite, the characteristics of filaments, especially with a robust mucilaginous sheath and false branchings, lead to identification of *Scytonema* type cyanobacteria known for being predisposed to calcification (Jones and Peng, 2014). The filament diameter is of about 10 µm (Fig. 9A-F) and the length can reach 1 mm, in some layers (Fig. 7). The outer part of the microbialite displays two features involving the filament pattern near the surface: the erected filaments constituting mineralized mats become prostrate (Fig. 9D) or form tufts with relief of about 100 µm (Fig. 9C). The mineralization of layers is realized by micritic fabric encrusting the cyanobacterial sheaths entirely (Fig. 9D) or, more often, partially (Fig. 9F) and/or in the space between filaments (Figs. 7-9). The filamentous mats suffered variable degrees of lithification, leading to dense layers or layers generally exhibiting elongate voids (Fig. 9H). Under high magnification, the micritic production consists, mainly, of microfibrinous spheroids (Fig. 9E-F). The detail of filamentous crust demonstrates that the biomineralization is not a unique event, but follows several stages independent of the filamentous growth and, sometimes, marked by visible lines (Fig. 8B).

The micritic laminated layers alternating with filamentous layers exhibit two main types of constructions, especially revealed by observation under confocal microscopy. In some cases, the micritic layers, including the last reddish crust (Figs. 7C, 8A), consist of a series of roughly laminae reaching more than 100 µm in total thickness and characterised by very irregular knobby surfaces (Fig. 8C). The so determined wavy microreliefs seem made of the aggregation of micritic spherules with an empty center (Fig. 8E). It is possible that this pat-

tern corresponds to the mineralization fabric around relict coccoid organisms such as cyanobacteria here indeterminable. In other cases, the layers are defined by very fine smooth parallel laminae, probably due to original biofilms (Fig. 8D).

4.2.3. Microbialites and diatom assemblages

It is noteworthy that very few identifiable organisms, other than diatoms, are present within studied microbialites. The diatoms are observable under optical microscopy and electronic microscopy but not by confocal microscopy.

In the studied sites, the diatom assemblage related to microbialites consists of benthic genera, either free living (*Amphora*, *Navicula*, *Mastogloia*, *Tabularia*), or attached (*Cocconeis*, *Cymbella*, *Rhoplaodia*).

The observation in thin sections in optical microscopy and SEM evidenced the presence of preserved diatom frustules, mainly into the upper part of microbialite, locally, very abundant suggesting an original diatom biofilm (Stal, 2012). The genera *Cymbella* seems here frequent with very minute individuals often attached to cyanobacteria (Fig. 10A).

Much more information was obtained by the investigation of broken samples under SEM. Several diatom frustules belonging to *Amphora cf. ovalis* (Kützing) Kützing 1844, *Cocconeis placentula* Ehrenberg 1838, *Navicula cf. cryptocephala* var. *veneta* (Kützing) Rebenhorst 1864, *Nitzschia* sp., *Tabularia fasciculata* (Agardh) D.M. Williams and Round 1986, were identified (Fig. 10B-F). SEM images revealed different stages of diatom preservation. Some frustules are well preserved, exhibiting morphological details (raphe, areolae), such as specimens of *Amphora* (Fig. 10B), *Navicula* (Fig. 10C) and *Tabularia* (Fig. 10D). Other frustules as *Cocconeis* appear to be corroded (Fig. 10G,I) and, partially, embedded in EPS matrix (Fig. 10G-H). We also noticed imprints of frustules preserved in a more calcified material in which morphological details are hardly visible (Fig. 10H-J).

5. DISCUSSION

5.1. IMPORTANCE OF ENVIRONMENTAL FRAMEWORK

Precipitation of micritic crusts is associated with heterotrophic biofilm communities developing under specific conditions. Accordingly, the environmental parameters play an important role in the carbonate mineralization allowing the microbialite formation. In modern marine stromatolites, the extrinsic factors (e.g. light, nutrients, hydrodynamics), together with intrinsic factors (e.g. organic and inorganic compounds production and consumption) are key to explain the lamination features (Reid *et al.*, 2003; Andres and Reid, 2006). The lamination results from iterative growth at the top of the build-ups of different types of microbial mats, which have distinctive mineral fabrics (Reid *et al.*, 2000). The filamentous layers coincide with microbial mat dominated by cyanobacteria of *Scytonema* type. Microbialites with dominant *Scytonema* occur in a wide range of environments from

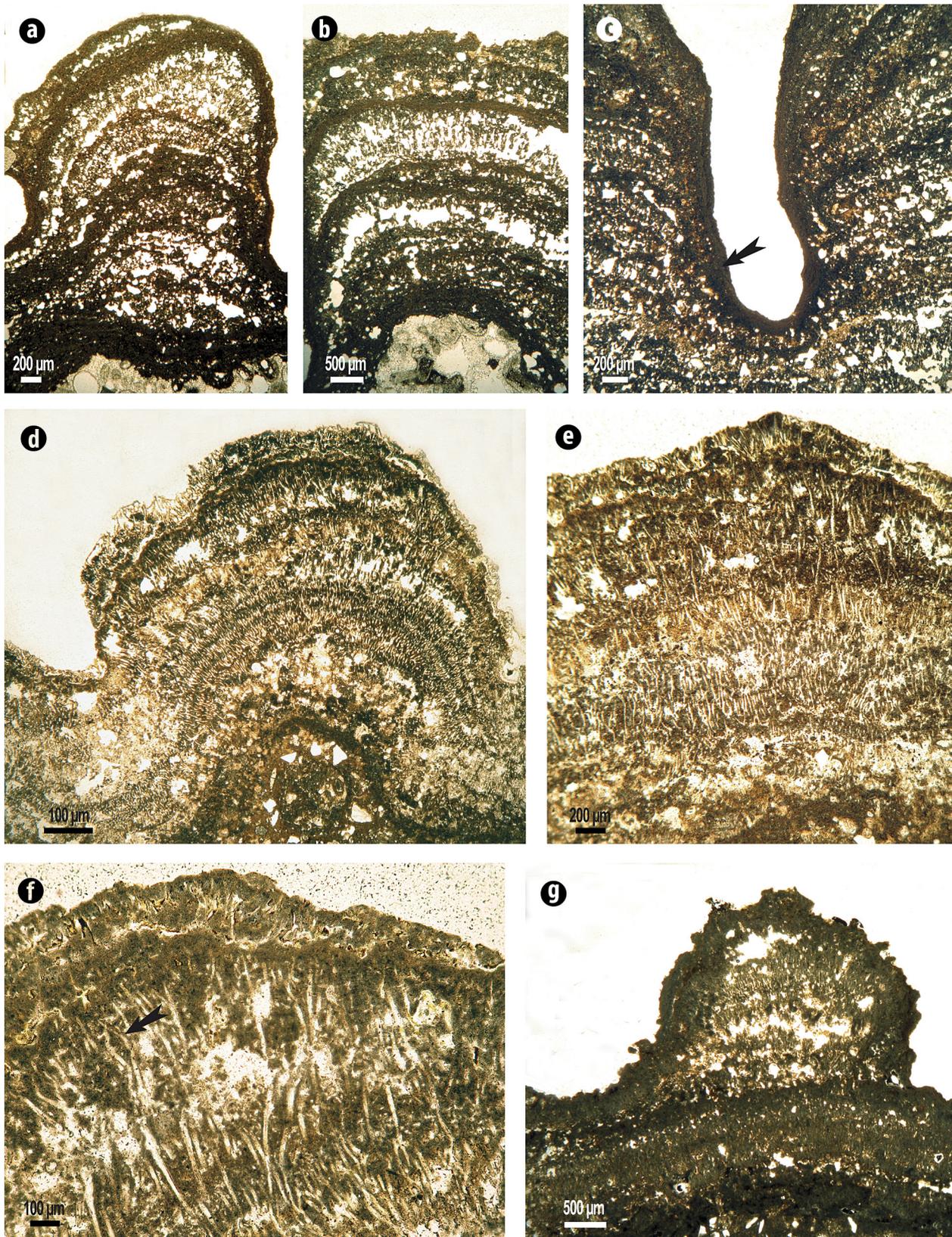


Fig. 7. Microbialite petrographic thin sections. **A-B.** Stromatolite digitations on pebbles showing the variation in the construction characterised by, first, a laminated crust and, then, a succession of filamentous and laminated ones, Mari Ermi; **C.** Interval between two microbialitic digitations showing the conspicuous final laminated crust (arrow), Mari Ermi; **D-E.** Digitations on pebbles with similar characteristics that the A-C views, Pauli Mesa Longa; **F.** Detail of successive filamentous layers, the last exhibiting preserved cyanobacterial sheath (arrow); **H.** Pustular crust corresponding to the succession of filamentous episodes, Pauli Marigosa.

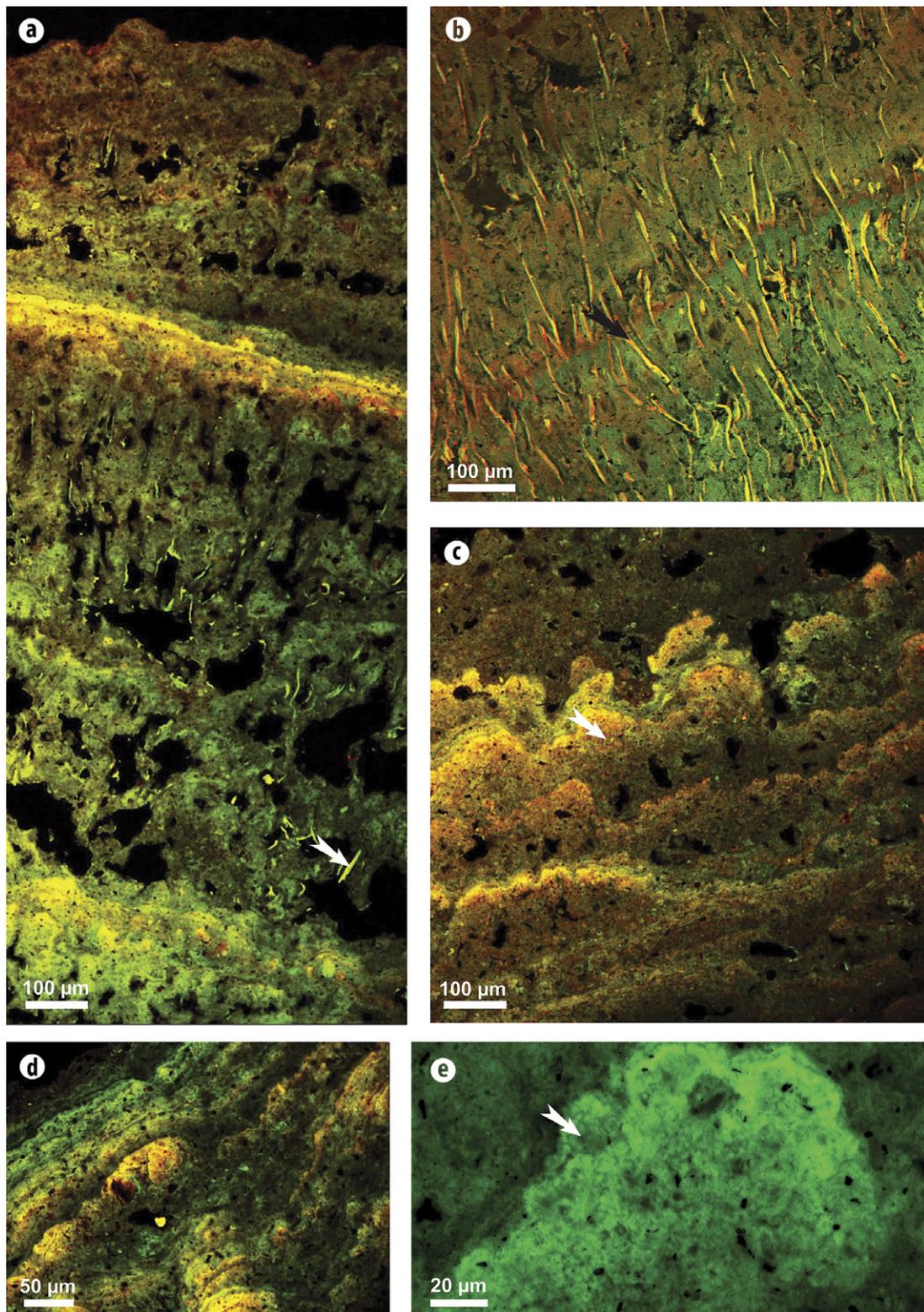


Fig. 8. Petrographic thin sections studied under CLSM (Confocal Laser Scanning Microscopy) technique restituting the autofluorescence signal inside the microbialite. **A.** Transect along a digitation displaying the alternation of laminated and filamentous mineralized crusts with partially preserved cyanobacterial sheath (arrow), Mari Ermi; **B.** The detail of filamentous crust demonstrates that the biomineralization is independent of the cyanobacterial growth and marked by several stages here underlined by red lines, Pauli Mesa Longa; **C.** Detail of crusts constituted by small irregular micritic masses (arrow) covered by very thin lamines, Mari Ermi; **D.** Finely laminated crust, Mari Ermi; **E.** Detail of a micritic masse constituted by the agglomeration of minute spherules (arrow), Pauli Mesa Longa.

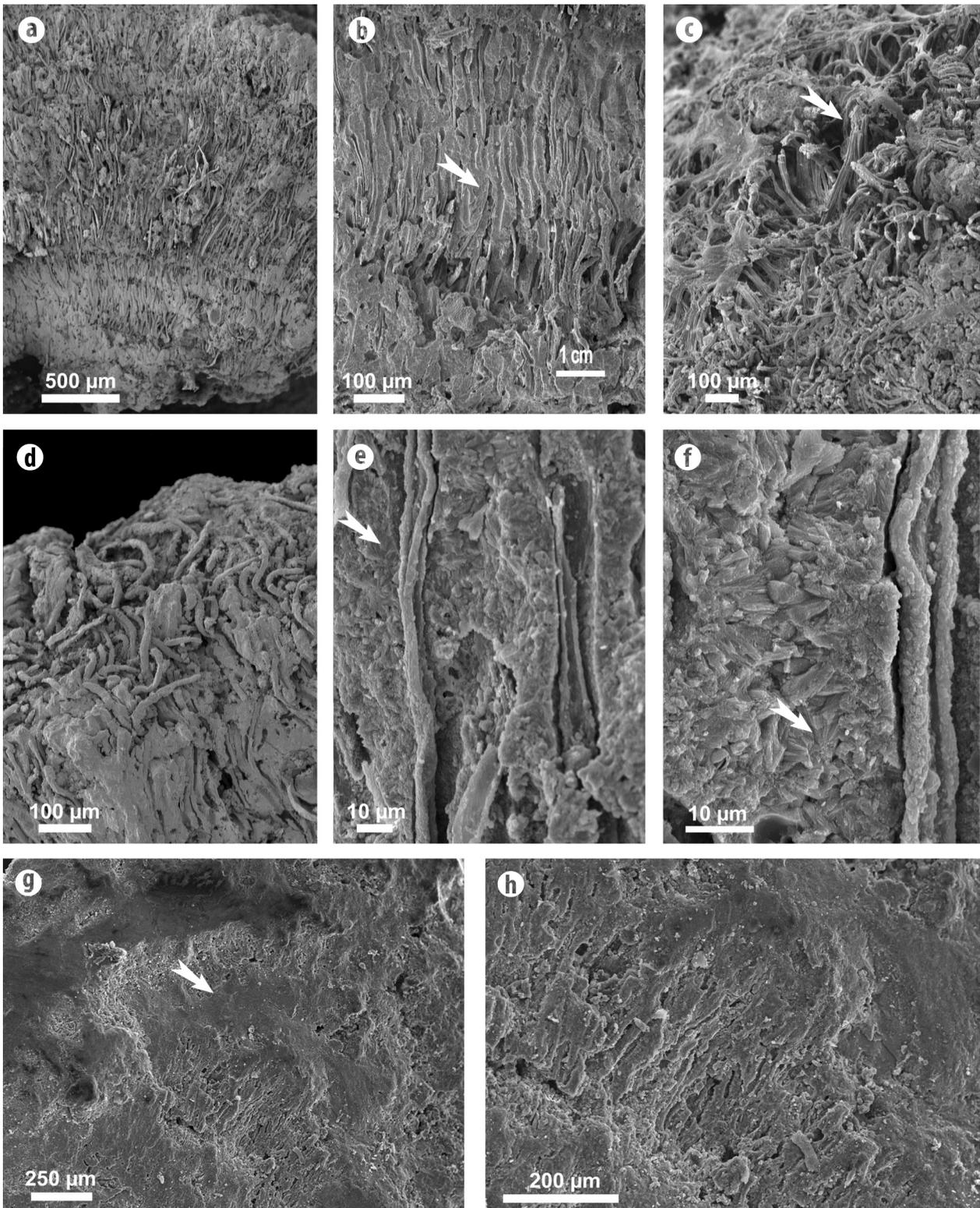


Fig. 9. SEM views of the microbialite. **A.** General view of relatively poorly mineralized microbialite constituted by dense erected filaments, Pauli Mesa Longa; **B.** Detail of filamentous microbialite with micrite cement (arrow) between the filaments, Pauli Mesa Longa; **C.** Microbialite surface showing the formation of tufts of filaments (arrow), Pauli Mesa Longa; **D.** Detail of cerebroid microbialite showing the encrustated cyanobacterial erected filaments becoming prostrate near the surface, Pauli Mesa Longa; **E-F.** Mineralization characterised by spheroid fibrous carbonate (arrow) between cyanobacterial filaments with partially preserved sheath, Pauli Mesa Longa; **G.** Strongly mineralized microbialite with succession of filamentous and dense micritic (arrow) episodes, Mari Ermi; **H.** Filamentous crust (detail of **G**) with elongate void indicating the original presence of cyanobacterial filaments, Mari Ermi.

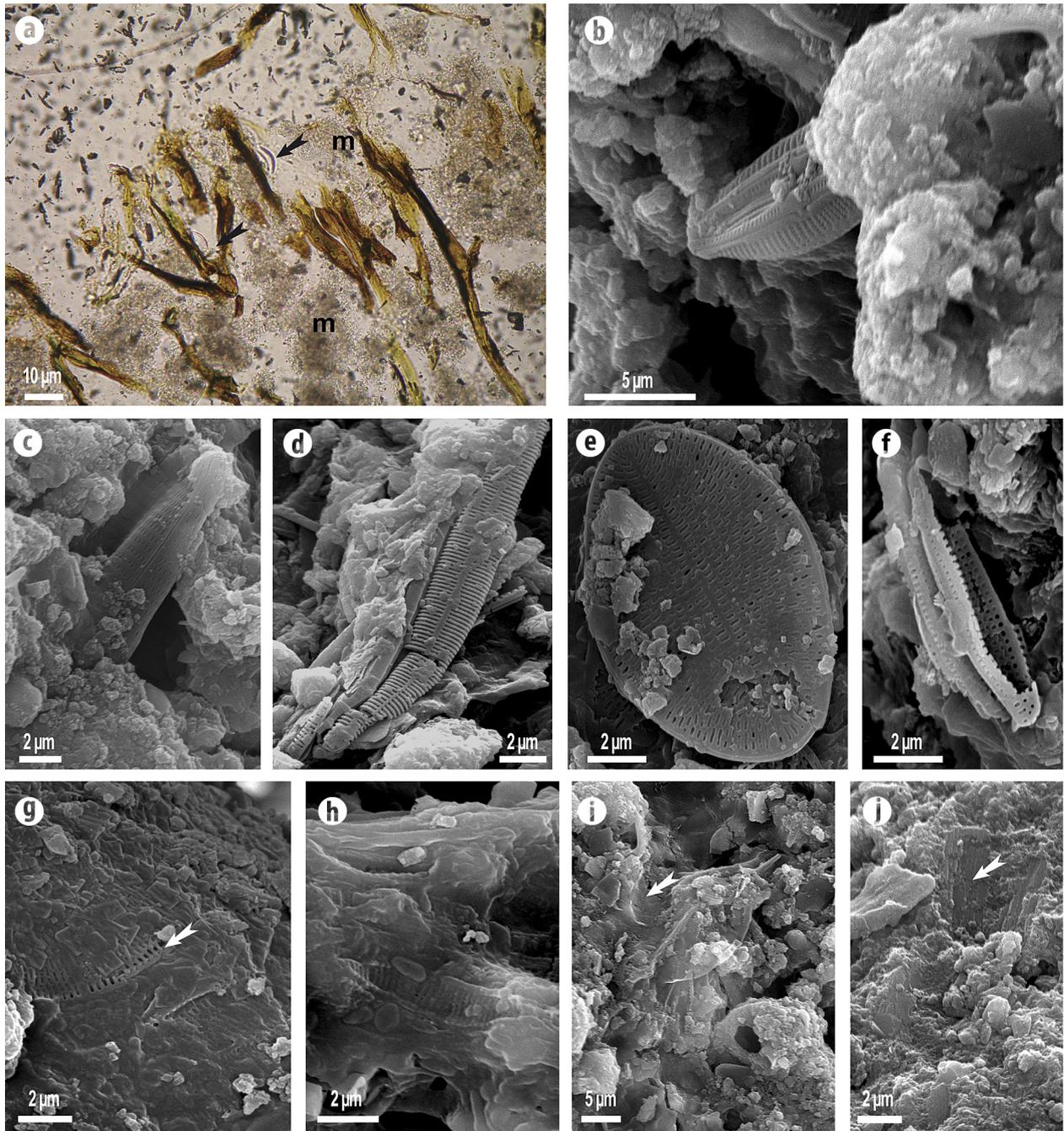


Fig. 10. Diatoms associated with the microbialites. **A.** Thin section showing the cyanobacterial sheath encrusted with spaced micrite (m) and colonized by *Cymbella* sp., an epiphytic diatom (arrows). **B.** Frustule of *Amphora* cf. *ovalis* partially embedded in micrite. **C.** Frustule of *Navicula* cf. *cryptocephala* var. *veneta*; **D.** Frustule of *Tabularia fasciculata*; **E.** Frustule of *Cocconeis placentula* (raphless valve); **F.** Frustule of *Nitschia* sp.; **G.** Partially dissolved frustules of *Cocconeis* sp. entrapped in degraded EPS (Extrapolymers substances); **H.** Partially dissolved frustules of *Navicula* sp. entrapped in degraded EPS; **I.** Diatom biofilm showing advanced frustule degradation and their imprints (arrow); **J.** Internal cast of diatom frustule (arrow) in micritic cement.

freshwater to hypersaline conditions (Pentecost, 1989; Mann and Nelson, 1989; Merz, 1992; Merz and Zankl, 1993; Moore and Burne, 1994; Reitner *et al.*, 1996; Srivastava, 1999; John *et al.*, 2009; Dupraz *et al.*, 2013; Burne *et al.*, 2014). Moreover, *Scytonema* communities can support severe temporary desiccation or live in terrestrial settings due to their capacity to display rapid physicochemical responses to desiccation and rewetting (Couté and Bury, 1988; Gottlieb *et al.*, 2005; Sanders *et al.*, 2010; Jones and Peng, 2014). The black color of the microbialite surfaces is a good indication for the special adverse condition of aerial exposure. Cyanobacteria, such as *Scytonema*, indeed develop a survival strategy consisting in the production of scytonemin, a small pigment biomolecule, located in the cellular polysaccharide sheath, to combat the effects of UV during summer when irradiance is too pronounced (Potts and Whitton 1980; Proteau *et al.*, 1993; Potts, 1994; Rascher *et al.*, 2003; Rastogi *et al.*, 2014). So, the dark color noticed in the studied samples is possible when related to the presence of scytonemin. For ponds of Sardinia, the irradiance has been heightened by the intense reflection of the surrounding white sand dunes. Dupraz *et al.* (2013) provided an interesting hypothesis to explain the succession of erected and prostrate layers in *Scytonema* dominant stromatolites that may be applied in our case: the erected growth of *Scytonema*-like mats would occur during summer-fall period, under high light intensity and temperature, in order to reduce the direct sunlight exposure; the prostrate filamentous layers, almost visible actually at the microbialite surface (Fig. 9D) would in contrary occur during the winter-spring period, such growth mode allowing to collect the maximum amount of light.

It is generally assumed that microbialite morphology is influenced by environmental events. For instance, the observed complete desiccation of Mari Ermi and Su Pallosu ponds during summer accompanied by mud cracks is similar to the summer event described by Glunk *et al.* (2010) when depicting environmental events responsible for mat surface morphologies. The pustular shape of microbialite corresponds to biogenically-controlled morphologies induced by *Scytonema* filaments organized in an erected fan-like framework, as described in hypersaline lakes (Dupraz *et al.*, 2006, 2011, 2013).

The studied coastal ponds of Sardinia are subject of particular environmental conditions concerning an extremely variable hydrological regime, from wet season to dry season, versus evaporation and salt precipitation under high temperature during summer. This evolution implies, for instance, a large fan of water salinity, from fresh to hypersaline. Diatoms can provide interesting information on these environmental aspects. Indeed, diatoms found in studied microbialites are frequent taxa of the marine littoral community (including fluctuating systems, like estuaries and shallow coastal environments) and most of them may support variations in salinity. For instance, the epiphyte *Rhopalodia gibberula* var. *musculus* (Kützing) Ceve-Euler 1952 was reported from brackish to saline environments (estuaries, saline lakes) (Germain, 1981, Vos and Wolf, 1993). *Cocconeis placentula* Ehrenberg 1838 is

a very euryhaline species being recorded from fresh water to marine brackish up to saline environments (e.g. Germain, 1981, Vos and Wolf, 1993; Campeau *et al.*, 1999; Sylvestre *et al.*, 2001). Moreover, this species is considered as opportunistic, since it can proliferate in a wide range of environmental stress induced by maximum confinement conditions, absence of resource competitors (Hickman, 1982), grazing pressure (Kesler, 1981) or herbicide exposure (Goldsborough and Robinson 1986). The occurrence of euryhaline species is relevant of the particular variable conditions of these coastal ponds that may be regarded even as extreme environments. Moreover the frequent degradation of frustules appears to be a common phenomenon in some saline environments (Noël, 1982; Ehrlich, 1978). It is interesting to note that the majority of diatom species associated with studied microbialites are small forms belonging to genera known as showing considerable morphological variability as *Amphora*, *Navicula*, *Nitzschia* and *Mastogloia*. These taxa are among the most ubiquitous and common components of the benthic diatom community in variable environments, such as, for instance, the salt marshes (Sullivan and Currin, 2000). The occurrence of diatoms with robust valves and small sizes, like *Rhopalodia* and some *Nitzschia* is consistent with the hypothesis of Vilbaste *et al.* (2000) that these two characteristics promote a better survival in particular habitats.

Although the ponds were not in direct communication with the sea, it is possible that exchanges occur per subsurface percolation through the beach ridges as in some Brazilian lagoons (Delfino *et al.*, 2012). This influence also may need to be considered for the Sardinian ponds.

Considering the above, we assume that microbialites from Sardinia developed, mainly, during the dry season, before the beginning of the wet period (rainfall season), which is characterised by very shallow water via desiccation, low turbidity and high salinity. The temporal variations induced a seasonal development of microbial mats linked to extreme hydrologic conditions as reported from Brazilian lagoons (Delfino *et al.*, 2012). The balance between evaporation, rainfall and sea water input provide more constant geochemical conditions for microbial mat and potentially microbialite formation (Glunk *et al.*, 2010). The observed succession of layers corresponding to each mineralised microbial mats with interruptions or transitional fabrics suggests that community cycling and resulting lamination is linked, according to Bowlin *et al.* (2012), with predictable seasonal environmental variation and stochastic events. These events related to the particular position of Sardinian ponds may consist, for instance, on storms, direct human action by touristic pressure, nutrient supplies due to agricultural activity, and exceptional duration of drying...

The conservation potential of microbial mats, able or unable to be mineralized, was often linked to the weak action of grazing organisms (Garrett, 1970), although this idea was recently controversial (Tarhan, 2013). Anyway, it seems obvious that extreme environmental conditions may suppress the ac-

tivity of grazing organisms (Fenchel, 1998; Kühl *et al.*, 2003; Bühring *et al.*, 2009). Notably, in the investigated ponds, the fauna is absent or almost absent, probably, due to changing to extreme conditions prevailing there, perhaps due also to the presence of sapropelic deposits making poorly oxygenated and inhospitable residual waters. These particular conditions are so unfavorable for potential microbial mats grazers, but would explain the presence, in the Sardinian ponds, of certain arthropod species, such as *Branchinella spinosa* thriving in waters rich in chlorides and sulfates (Mura, 2001).

The calcareous microbialites discovered in Sardinia provide a new example to be listed in the classification of modern microbialites. According to Dupraz and Vissler (2005) and Dupraz *et al.* (2009) these microbialites can be distributed in several environmental categories: open-marine stromatolites, hypersaline microbialites, freshwater travertine and carbonate deposition in tropical soils. The Sardinian microbialites seem to correspond to another type of mixed environments with strong environmental fluctuations that must be added to the list.

5.2. MICROBIALITES AND EPS MATRIX ROLE

Many studies have pointed out the major role of EPS (Extrapolymeric substances) organic matrix in the processes of organomineralisation responsible for the formation of carbonate microbialites in freshwater, open marine and hypersaline environments (see review of Dupraz *et al.*, 2009). EPS are produced by a plethora of microorganisms, such as bacteria, cyanobacteria, diatoms and other algae (Decho, 1990) and constitute the location of mineral nucleation (Decho *et al.*, 2005; Gallagher *et al.*, 2010). The role of EPS is particularly to prevent desiccation, to retain essential nutrients and to protect against UV radiation (Stal, 2001; Dupraz and Vissler, 2005). The physicochemical properties act for the long-term preservation of the EPS producing communities by facilitating mineral precipitation (Trichet and Défarge, 1995; Braissant *et al.*, 2009).

In our study, the SEM investigations revealed the presence of EPS matrix (Fig. 10G-I). The recorded autofluorescence signal probably comes from preserved organic molecules generally present in EPS, such as polysaccharides, proteins and glycolipids (Stal, 2001; Decho, 2010). From our observations, two types of organisms may be the contributors to the EPS production: cyanobacteria and diatoms.

In the successive layers of the Sardinian microbialites, filamentous cyanobacterial mats are especially conspicuous and the cyanobacteria of *Scytonema* type suspected to originate these layers. Moreover, it is not excluded that coccoid cyanobacteria are also involved in the formation of the dense micritic layers. These different types of cyanobacteria may produce a significant amount of EPS in dominant *Scytonema* microbialites (Dupraz *et al.*, 2013). Cyanobacteria are generally recognized as the most important EPS producers and their cellular and mucilage networks especially from the filamen-

tous taxa constitute an efficient cohesive feature to the sediment surface (Dupraz *et al.*, 2009; Stal, 2012). It was proved that EPS secretions produced by cyanobacteria represent potential structuring agents in the formation of marine stromatolites serving to physically stabilize the uppermost layers and providing a chemically protective microenvironment for cellular and extracellular activities (Kawaguchi and Decho, 2000; Decho *et al.*, 2005).

One of the most significant features of diatoms in biofilms is the production of EPS (Decho, 2000). In studied microbialites, only benthic diatoms occurred and the mucilage they produced is of particular interest. Some benthic diatoms are motile and their movement relative to substrate is coupled with mucilage secretion along the raphe, leaving a trail behind diatom (Round *et al.*, 1990). In our samples, we registered some motile diatom genera: *Navicula*, *Nitzschia*. The nonmotile benthic diatoms are attached to a substrate (sediments or plants) and produced different types of mucilage (apical pads, stalks, film, etc) that allow the adhesion to the substrate (Round *et al.*, 1990). In our samples, we found the representatives for two categories of attachment: a) the adnate closely appressed to the substrate, like *Cocconeis*, *Rhopalodia*, and b) the cells are attached to substrata by pads, like in some *Cymbella* species. The case of *Cymbella* is particularly interesting since our microscopical investigations showed large numbers of attached *Cymbella* frustules on cyanobacteria (Fig. 10A). This observation reveals one of the steps in the development of a microbialite that is similar with the development of microbial mats when, as observed by Allison and Gilberg (1992), the biofilm formed by diatoms is preceded by primary colonization by bacteria helped by the production of EPS. Since there is evidence for the role of diatoms EPS in the trapping and binding sediment in microbial carbonates (for review see Winsborough, 2000), we can assume that benthic diatoms associated to studied microbialites were also involved in these complex processes.

6. CONCLUSION AND PERSPECTIVES

Our discovery of microbialite in small coastal ponds from western Sardinia, without known equivalent in the Mediterranean area, prompts reflections addressed to the comprehension of the processes involved in microbial fossilization. Mineralization in the discovered microbialites froze the succession of events in complex microbial life worlds reflecting the fluctuating conditions of these particular settings that are coastal ponds not in direct communication with the sea.

Microbialites from Sardinian coastal ponds have obvious specificity taking into account not only the building characteristics, but also many other parameters related to the environmental conditions: 1) the construction is carried out only on hard substrates, such as mobile pebbles and rocks; 2) the microbial mat lithification results only in micritic fabric without evident trapping and binding processes; 3) microbialite growth appears to be related to drastic variations in environ-

mental conditions from brackish to hypersaline and drying; 3) several types of microbial mats with a variable composition alternate, the filamentous erected mats being the most common; 3) the involved ponds are submitted to important pressure due to both touristic and agriculture activities.

Further detailed work must now be carried out in order to decrypt the implemented biomineralization processes, to follow the steps of forming the microbialite layers in relation to environmental conditions (physical and chemical water parameters) through targeted monitoring, and prospect, other coastal ponds with identical parameters in the Mediterranean area to measure the extent of the phenomenon.

Finally, such a model of microbialite formation in fluctuating to extreme environment requires an attentive preservation, especially from risks of human coastal development.

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