

Microbial communities in Messinian evaporite deposits of the Vena del Gesso (northern Apennines, Italy)

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ABSTRACT: The Vena del Gesso (Northern Apennines) is a 230 m-thick succession consisting of up to 16 gypsum-shale cycles belonging to the “Lower Evaporites” formed during the Messinian salinity crisis in the Mediterranean. The study of the microbial communities preserved in the gypsum crystals of one complete cycle (6th cycle at Monte Tondo quarry) showed abundant, regularly arranged filamentous forms that resemble morphologically modern obligate phototrophes, cyanobacteria colonizing modern photic, shallow-water gypsum basins.

At least four different bacterial populations have been recognized:

- filamentous type cyanobacteria with characteristic inserted funnel shaped structure resembling the modern *Scytonematacean*;
- Type 1 organisms consisting of filamentous structures impregnated by clay minerals containing pyrite grains in the outer sheath;
- Type 2 filaments filled by clay minerals with dolomite in the outer sheath;
- Type 3 filamentous organisms with a central hollow tube and an encrusted outer sheath mainly composed of calcium carbonate.

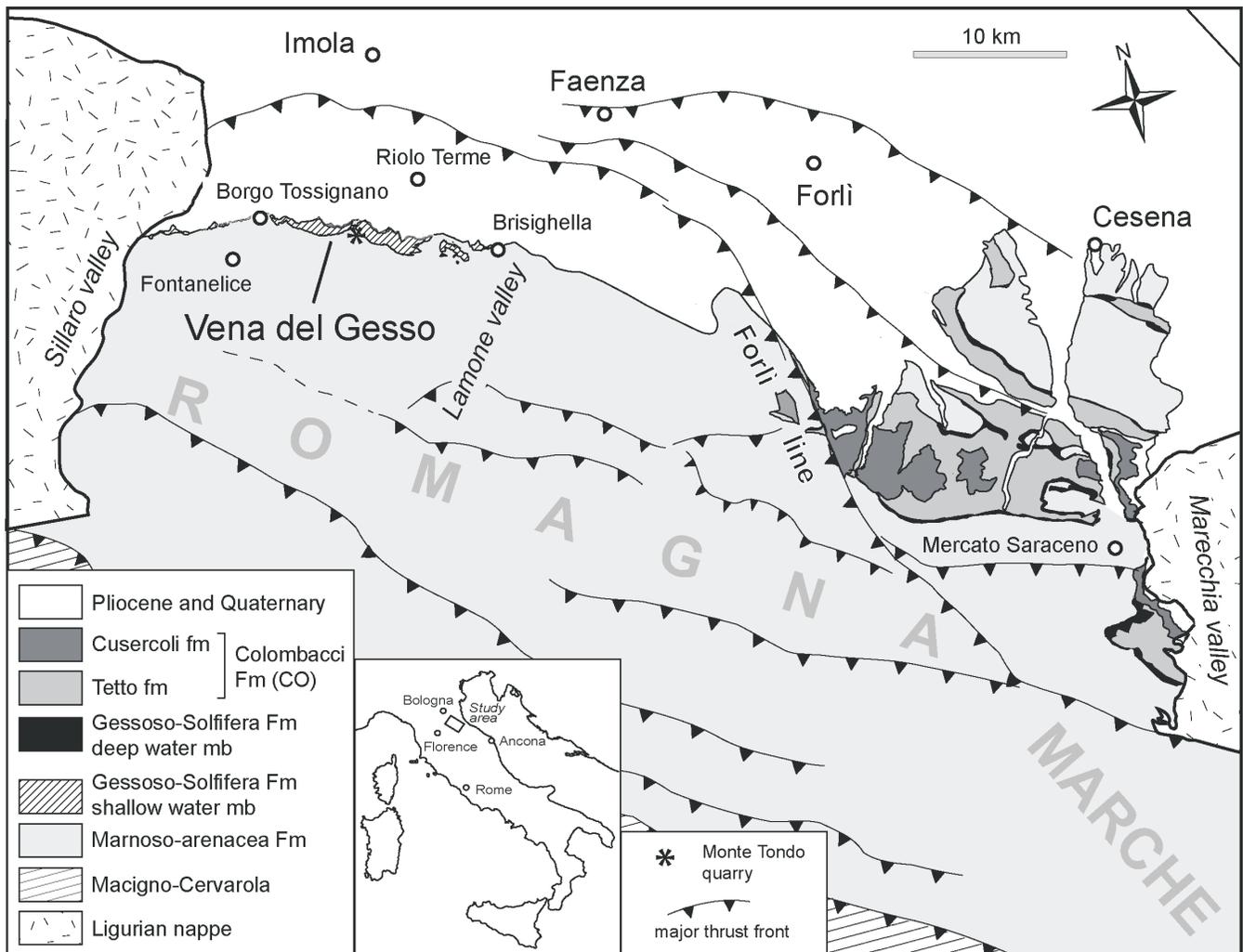
These organisms were probably associated with other heterotrophic bacteria as suggested by the presence of dolomite and pyrite structures. The size and preservation suggest that most of these cyanobacteria were likely conducting oxygenic photosynthesis as presently observed in modern solar salt works. It follows that they were living in shallow water settings or settled down from the water column to the bottom of a relatively deep evaporite basin.

INTRODUCTION

The salinity crisis that affected the Mediterranean during the Messinian is one of the most significant evaporitic episodes of the stratigraphic record (Hsü et al. 1973, 1978, Montadert et al. 1978, Rouchy 1982, Cita and McKenzie 1986). Although numerous data have been produced from studies concerning different disciplines, the abundant microbial content of evaporites has not been studied in detail. The microbial realm can provide very useful information to reconstruct the environmental aspects of evaporite deposition. Molecular investigations have been previously carried out only in marl beds of the evaporitic cycles of the Vena del Gesso (Kenig et al. 1995, Sinninghe Damsté et al. 1995). The only previous reference to filamentous structures preserved in selenite crystals in the Vena del Gesso is that of Vai and Ricci Lucchi (1976, 1977). Their study dealt with micritic algae laminae preserved in lenticular layers (5-30cm thick) where carbonate cemented algal mats were replaced by selenite crystals and described these deposits as stromatolitic selenite. The micritic filamentous coating (0.06-1 mm in diameter and 1cm in length) recognised within the algal laminae, were called “Spaghetti-like” structure. Vai and Ricci Lucchi (1976) may have been the first to discover that the filaments could be cyanobacteria even though they did not mention their origin. Afterwards, Vai and Ricci Lucchi (1977) describing the massive selenite (Facies 3) previously reported as “coarse twinned selenite” by Hardie and Eugster (1971), indicate that those filaments rounded by carbonate, clay and or-

ganic impurities form an open framework of turbid twins interpreted as a first stage of crystal growth. The second stage “enlarged the crystals by adding displacive clear overgrowth which squeezed and concentrated the remaining interstitial material”. Rouchy and Monty (2000) described two distinct microbial laminites in large selenite crystals. One type observed in the Messinian gypsum of Cyprus and Crete consists of calcified filaments alternating with laminae with no filaments. The filaments are composed of aggregates of small crystals of calcite. The second type reported from the Messinian of the Northern Apennines, Sicily, Ionian Islands, Algeria, Crete and Cyprus, are filaments which appear as “ghosts defined by minute grains” disseminated in the gypsum crystals. Some of the filaments which exhibit inserted funnel-shaped units are reminiscent of *Scytonema*. In order to attempt to understand microbial fossil structures Cornée (1982, 1984) started studies on different bacteria from cultures and modern sediment samples collected in Santa Pola (Spain) salt works and Saline-de-Giraud (Southern France) posing the base for interpretation of complex relations between microbial realm and evaporate environments.

The purpose of this paper is to provide a detailed description of the filamentous structures preserved in the selenite crystals in order to decipher these “spaghetti-like” features and contribute to the definition of the paleoenvironmental aspects of Messinian evaporites deposition.



TEXT- FIGURE 1
Schematic geological map of the study area (Lugli et al. 2007).

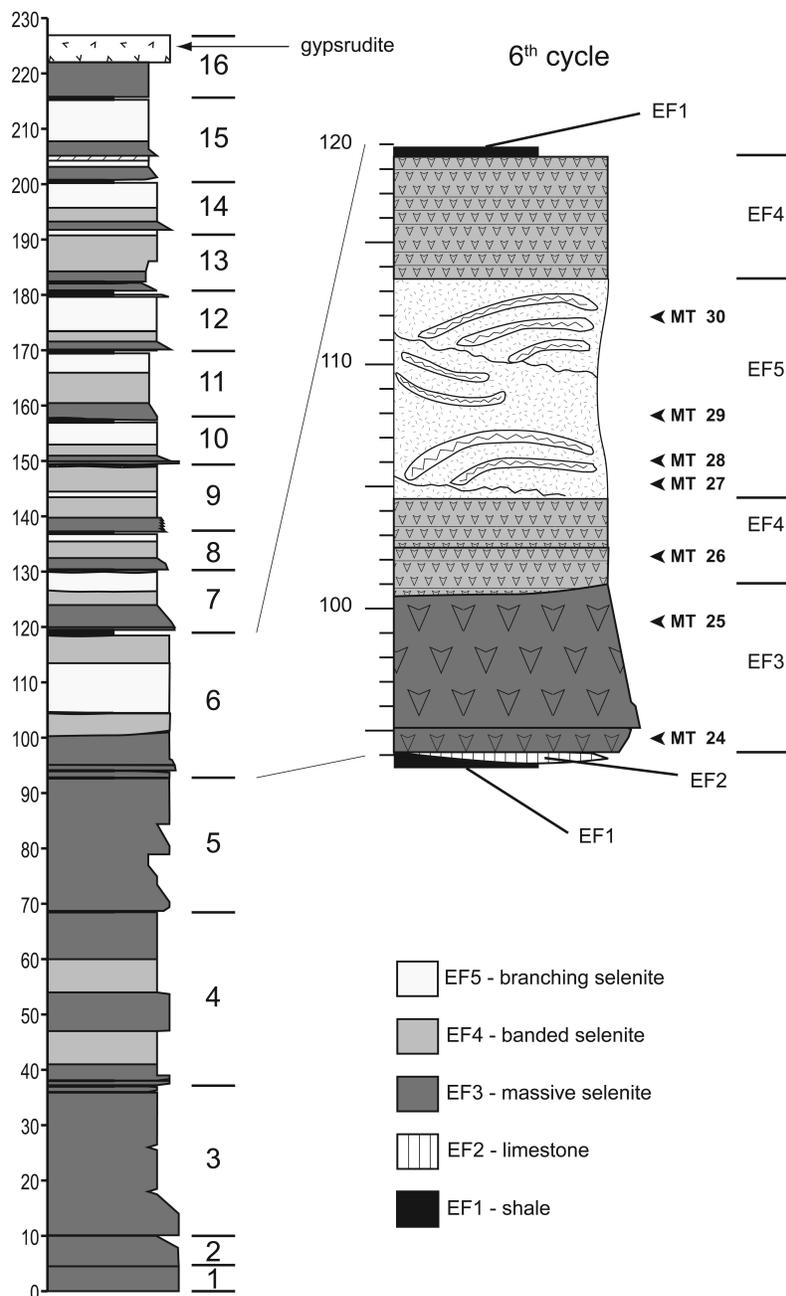
The “Vena del Gesso” evaporites

The “Vena del Gesso” is a NW-SE elongated relief, approximately 15 km in length, located in the northern Apennines between the Sillaro and the Lamone river valleys (text-fig. 1); it is characterized by primary evaporites (selenite), belonging to the Gessoso-Solfifera Formation (GS), that were deposited in one of the small trust-top basins in the northern Apennines. The evaporite succession is up to 230 m thick and consists of 16 lithological cycles produced by the alternation of m- to dm-thick gypsum beds separated by thin shale horizons. According to Krijgsman et al. (1999a, b) the deposition of these cycles was controlled by astronomical precession in a time span ranging from 5.96 to 5.61±0.02 Ma. These deposits were dismantled and redeposited in adjacent structural lows during a post-evaporitic Messinian tectonic phase (Roveri et al. 2003).

The earlier studies on these deposits (Vai and Ricci Lucchi 1977, Marabini and Vai 1985), led to the formulation of the sedimentary model for the cyclical deposition of primary selenite. This model has been recently revisited (Lugli et al. 2006, Roveri et al. 2006) and we refer to the new facies model. Each cycle consists of a facies sequence starting with basal thin or-

ganic-rich shales (facies EF1), overlain by stromatolitic limestone (EF2) and by thicker massive (EF3), banded selenite (EF4). The upper part of the cycle is characterized by large diagenetic flat-lying selenite crystals (EF6). The upper part of the sequence, starting from the 6th cycle, shows on top of the banded selenite an additional facies, the branching selenite (EF5), which represents the growth with selenite branches projecting laterally from a conical nucleation centre. According to the new interpretation proposed by Lugli et al. (2006) these features are not related to sabkha environment as originally proposed by Vai and Ricci Lucchi (1977), but can be rather considered as lateral termination of the super-cones structures described by Dronkert (1985) in the Sorbas basin (Spain) and therefore are considered fully subaqueous growth structures. In this section, clastic deposits are absent, a gypsum bed is present only on top of cycle 16, thus marking the onset of the post-evaporitic phase (Lugli et al. 2006, Roveri et al. 2006).

The crystals reach their maximum length (a few dm) in the basal massive selenite and are up to a few cm long in the banded and branching selenite facies (Vai and Ricci Lucchi 1977). This evolution can be related to a progressively decreasing level of the saturation surface that produced a permanent cover of Ca



TEXT- FIGURE 2
Lithostratigraphic log of the 6th cycle with investigated samples.

sulphate-saturated brine only in the lower part of the cycle (highstand, massive selenite, EF3). Continuous evaporation and drawdown produced an oscillating brine level and variable saturation conditions (lowstand, banded selenite, EF4) followed by a general brine level rise with the formation of large selenite cones showing peripheral branches spreading laterally (transgression, branching selenite, EF5).

The gypsum crystals are of high purity and transparency, contain V-shaped internal lamination composed of dense fossil microbial colonies (text-fig. 3A-D). The crystals did not recrystallize since their formation. Clear overgrowth ("second

stage" of crystal growth reported by Vai and Ricci Lucchi in 1977) enlarges the crystal size (text-fig. 3C). Gypsum and carbonate geochemistry indicates that evaporite deposition occurred during major oceanic influxes in a general setting dominated by solutions strongly modified by continental waters (Lugli et al. 2007).

MATERIALS AND METHODS

The samples (MT24-MT30; text-fig. 2) were collected from freshly exposed quarry cuts at Monte Tondo. The 6th cycle has been chosen for sampling because it is the thickest one (30m-thick) showing the complete facies association.

The mineralogy of samples was determined by X-ray diffractometry (XRD) on a Philips PW 1480, CuK1, X-ray diffractometer.

For the preliminary investigations of microbial structures, standard (5x4 cm) thin sections with different orientation respect the bedding plane (parallel and transversal) obtained from resin-impregnated blocks of gypsum were prepared. This methodology has not to be useful for massive and banded selenite allowing observations of only small portion of the filamentous structures. For this reason, for samples MT24-26 cleavage fragments (0.50-1 mm thickness, 0.5 to 1 cm² portions) of large crystals were sliced using a sterilized scalpel.

Repeated analyses were performed on several thin slices and sections of each sample using reflected-light and fluorescence Zeiss Axioskop 50 microscope equipped with transmitted light, phase contrast, fluorescence and Nomarski interference contrast illumination. The fluorescence was induced at excitation 365 nm, beamsplitter 395nm, emission 420nm, using green filter. For scanning electron microscopy pieces of samples were gold sputtered (Balzers Union, SCD 030) and examined with ZEISS DSM 940 and Hitachi S-450 scanning electron microscope operated at 10 or 20 kV and with working distances of 7 to 9 mm. For analyses of the energy dispersion spectra of the characteristic X-ray radiation (EDX) samples were carbon sputtered and examined on Zeiss DSM 940, EDX Link Analytical QX2000.

Samples that revealed the presence of organic matter associated with filamentous structures under the fluorescence microscope were analysed using HPLC (High Performance Liquid Chromatography) to identify photosynthetic and photoprotective pigments such as carotenoids, mycosporines and mycosporine like amino acids (MAAs) eventually existing in gypsum samples. Thin slices were then powdered and analysed with HP 1050 pump, an HP 1046 fluorescent detector, and an HP 1050 diode array detector. All sample preparation procedures were performed under aseptic conditions under an extractor hood.

RESULTS

The mineralogical data - X-ray diffraction

The mineralogy of massive and banded selenite (samples MT24-26) is dominated by gypsum with traces of carbonate and clay minerals, whereas the fine-grained portion shows the dominance of dolomite, pyrite with detritic materials (quartz) and gypsum as accessories. The mineralogy of branching selenite (MT27-30) is mainly constituted by gypsum, dolomite and traces of kaolinite and/or smectite. Minor celestine is present in sample MT30.

Light microscopy

Under transmitted light microscopy the gypsum crystals from samples MT24-26 show high purity and transparency and no dissolution features. The crystals although translucent show an internal lamination. The lamination is formed by an alternation of dark-colored translucent layers of *ca* 5 mm in thickness and light-colored opaque laminae (about 1mm to 3mm). Fine-grained carbonate-rich patinas are random and generally light grey in colour. The selenite crystals exhibit a V-shaped internal lamination made up by an alternation of light (translucent) and dark (grey) laminae composed of dense microbial aggregates of fossil filaments. They are mainly constituted by cylindrical structures appearing as whitish tubes, occasionally presenting

internal black grains (text-fig. 3D). Usually they occur as single, unbranched filaments more than 100µm in length, but there are a very few examples of branching forms. The tubes are 20-30µm in diameter and some filaments show a decrease in size close to the tip.

Fluorescence microscopy employed for visualizing placement of chlorophyll in the filaments revealed autofluorescence in some tubes, likely resulting from intracrystalline organic matter (data not shown).

Light microscopy observations of branching selenite (samples MT27-30) showed that the crystals are mostly devoid of filaments. This is probably due to the lateral growth of the crystals, condition which do not favour the entrapment of external material.

Scanning electron microscopy and HPLC

The SEM investigations show morphological proprieties not visible in light microscopy, and EDX analyses provides a qualitative determination of mineral composition of fossil remnants. The SEM images of polished samples MT24-26 that expose the fossil structures in low relief show that at least four different populations are present together:

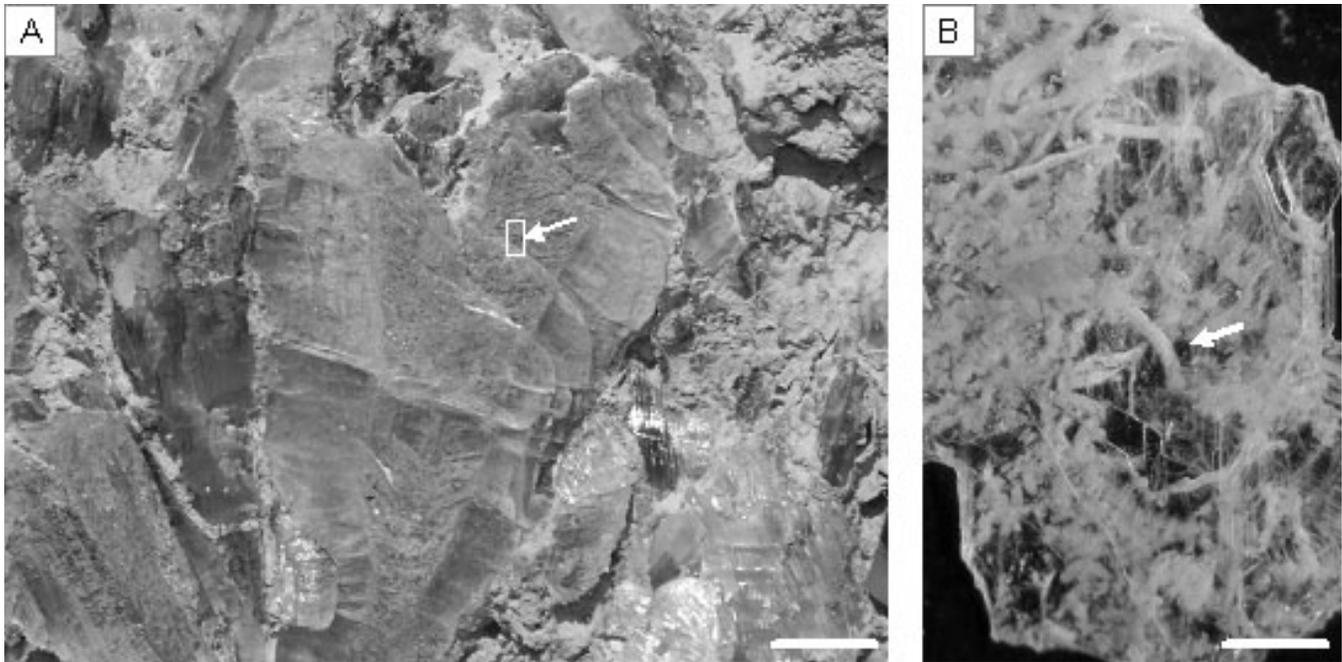
a) structures composed of inserted funnel-shaped units diverging outward (text-fig. 4A-B); the funnel-shaped structures (30-50µm inner diameter, 100µm maximum length observed) are composed of gypsum and are not calcified. The structure is very similar to that reported by Golubić and Barghoorn (1977) and the comparison with cell degradation in modern microbial ecosystems suggests that it may represent *Scytonema*.

b) Type 1 filamentous organism, moderately abundant in the samples, consists of tubes (10-20µm inner diameter; 100µm maximum length observed, text-fig. 4C) filled by clay minerals (elemental composition: Si, Al, Mn and Fe), gypsum, and several pyrite framboids present only on the outer “sheath” (text-fig. 4D).

c) Type 2 filamentous organism (text-fig. 4E) show filaments filled with a more homogeneous material consisting of Ca, Fe and only in the inner part is enriched in Mg and Si. The fossils consist mainly of mineral grains ranging between 2 and 5µm in diameter with sharp euhedral boundaries. SEM observations have also documented that dolomite crystals (3-4µm in diameter) appear mainly on the outer “sheath” as simple or rosette aggregates. Rosettes result from the aggregation of rhombic crystals commonly showing an hollow core (text-fig. 4F).

d) Type 3 filamentous organisms (text-fig. 4G), show two distinct parts: a central hollow tube and an outer sheath. The central hollow tube is up to 50 µm. The observed size can reach 500 µm in length. The central tube has a relatively constant diameter and the sheath is composed entirely by euhedral mineral grains cemented together. EDX analyses indicate the main presence of calcium carbonate. A carbonate-rich patina is located along the gypsum cleavage planes and pyrite framboids are also present (text-fig. 4 H). In some portions “pelletal” structures are abundant showing no traces of wall lining.

Several gypsum fragments parallel to bedding under the microscope show “spaghetti like” structures which are evident without any treatment under light and fluorescence microscopy. They are characterized by filaments showing a weak red



TEXT- FIGURE 3

(A) Macroscopic sample from the lower part of the cycle, described as massive and banded selenite, exhibiting fossil filamentous populations in the inner core. Detail indicated by white arrow showed in (B); Detail indicated by black arrow showed in (C). (B) Photomicrographs illustrating densely-packed filamentous structure appearing as whitish tubes. (C) Inner core with densely-packed filamentous structure and clear overgrowth. (D) Cylindrical structures appearing as whitish tubes, occasionally presenting black grains. Scale bars: (A) 1cm; (B) 1µm; (C) 2mm; (D) 20µm.

autofluorescence due to photosynthetic pigments (chlorophyll *a*).

HPLC analyses revealed a peak at 480nm indicating the presence of polysaccharides, commonly present in most of cyanobacterial sheath.

DISCUSSION

The population of fossil filaments preserved in the Messinian primary evaporites is characterized by the coexistence of different taxonomic group: dominant taxa of cyanobacteria are joined by other subdominant phototrophic and heterotrophic microorganisms. Besides, among cyanobacteria, the different mode of preservations and the different mineralogical composition of the investigated filaments indicate the co-existence of different species. This consortium is confirmed by the co-occurrence of non-calcifying (*Scytonema*), and calcifying (type 1, 2 and 3) groups. Such diverse population has been reported from many systems (Gleason and Spackman 1974, Krumbein and Giele 1979, Défarge et al. 1994).

The different mineralogical composition detected for different groups of cyanobacteria that lived in the same environment is probably due to the differences in the chemical composition and the arrangement of the polysaccharides in their original sheath (Merz 1992). The EPS (extracellular polymeric substance), which consists of a variety of molecules such as polysaccharides and amino acids forming the sheath, might regulate physiological processes and interactions within the microbial community. EPS activity functions as a chelate for cations, because polysaccharides can absorb high amount of divalent ions (Decho 1990), and the template for crystal nucleation. On this

account, structure and composition of the sheath seem to be essential for calcification (Weckesser et al. 1988). The calcification is extracellular and associated with the organic macromolecules of the cell envelope (Pentecost and Riding 1986, Merz and Zankl 1993). Furthermore, the physicochemical characteristics of the environment play an important role in the cyanobacterial calcification. Merz-Preiß (2000) indicates the mineralogy of the precipitated carbonate correspondent to the chemistry of the ambient water.

Identification of fossil structure composed by inserted funnel shaped units is supported by the comparison with modern scytonematacean cyanobacteria; considering that the cell growth is apical, the cell division and the accompanying production of EPS move in acropetal direction and the envelope assumes the asymmetrical shape of inverted cones (Merz 1992), which clearly resembles the structure observed in the Messinian gypsum. This mode is independent of any morphological features of the filament itself. Observed in petrographic thin section or in natural selenite laminae under transmitted light all fossils appear as cylindrical tubes characterized by a white wall with black grains, whereas only the SEM observations show the described peculiar morphological features. Golubic and Barghoorn (1976) suggested that this distinctive feature has a preservation potential and may be recognized in the fossil record.

As revealed by SEM observations the preservation of the other fossil filaments was accomplished in different ways. In the more common mode of preservation, the fossil structures type 1 and type 2 appeared filled by clay minerals. The type 1, which is moderately abundant in samples, have several pyrite grains oc-

curing only on the outer “sheath” whereas EDX analyses of type 2 revealed an enrichment in magnesium and silica only in the inner part and presence of dolomite crystals as simple or rosette-shaped aggregates in the outer part. The presence of pyrite in type 1, especially on the outer portion of the sheath, is likely due to microbial degradation of cyanobacterial material by sulphate reduction. The pyrite may have become calcified *post mortem* in conjunction with bacterial sheath degradation (Arp et al. 1999), or with the possible involvement of sulphate reduction (Visscher et al. 2000, Paerl et al. 2001). Otherwise, cyanobacteria in water may slightly raise the pH on their surface during photosynthesis (Shiraiwa et al. 1993) then may lead to local saturation and iron precipitation within or outside their cells.

The detected enrichment in magnesium in type 2 can be explained considering that cyanobacteria can concentrate, particularly in their sheaths, magnesium up to four times its abundance in seawater (Gebelian and Hoffman 1973). The magnesium concentrated in cyanobacterial sheaths may be liberated during degradation into sulphate-free solutions of high ionic strength and carbonate ion activity, to become available for dolomite formation. Bacterial sulphate reduction has the potential to provide the chemical conditions necessary for dolomite formation wherever benthic microbial communities, including cyanobacteria, dominate a saline aqueous environment (Wright 2000). Besides, high pH in resulting from metabolic activity of specific sulphate reducing bacteria leads to concentration of magnesium and bicarbonate ions then to nucleation of dolomite crystals (Warthmann et al. 2000). The silica in the inner part of the tubes can be explained by the bi-layered sheath of some cyanobacteria (Bertocchi et al. 1990). The inner layer is denser, more structured, and has a clearly defined diameter while the

outer sheath layer is less dense and seems not to be as clearly defined. The different layers could have different pH and if this was the case, then the silica inside the structure can exist at low pH and is dissolved away at higher pH values.

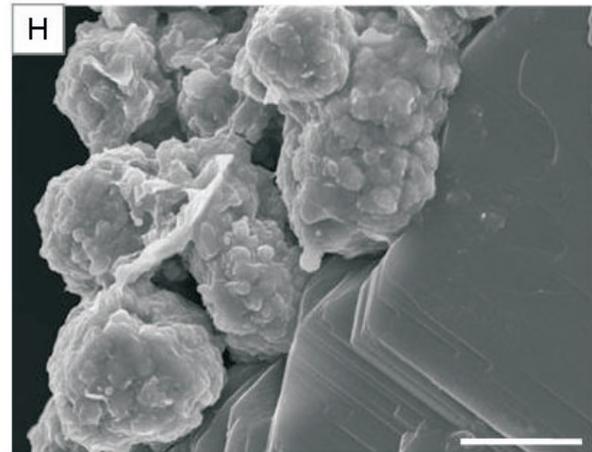
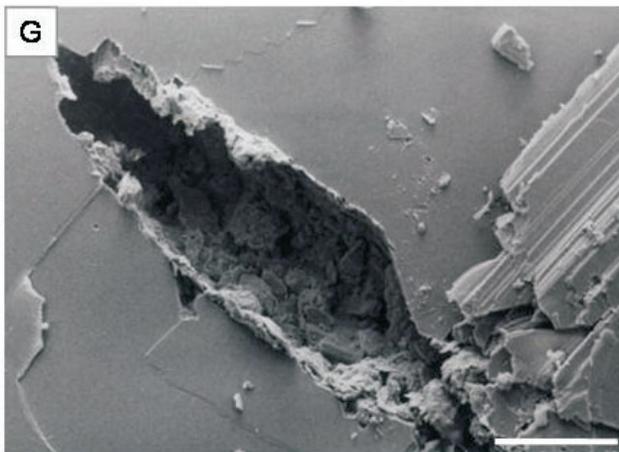
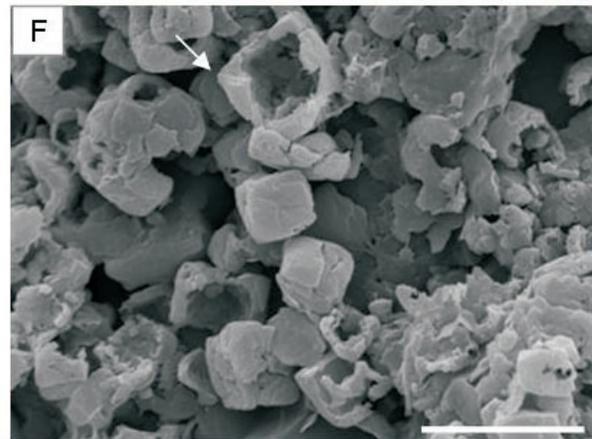
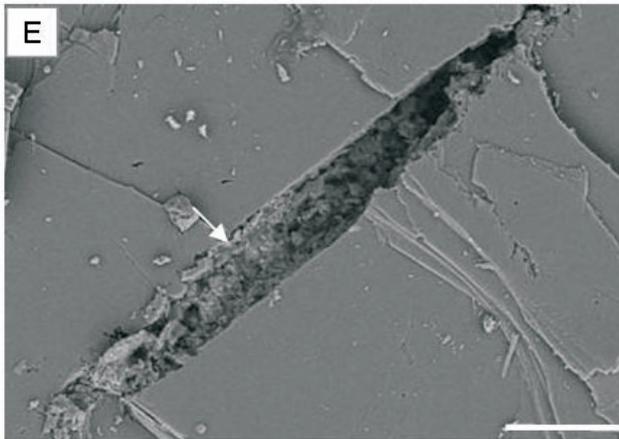
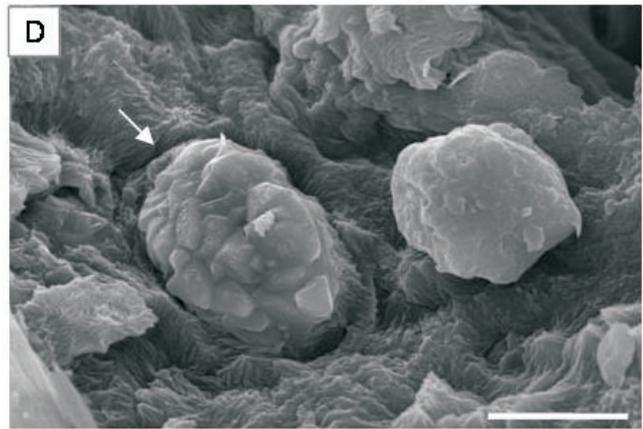
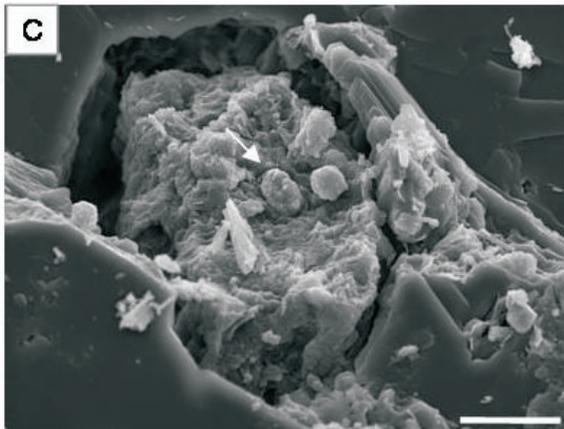
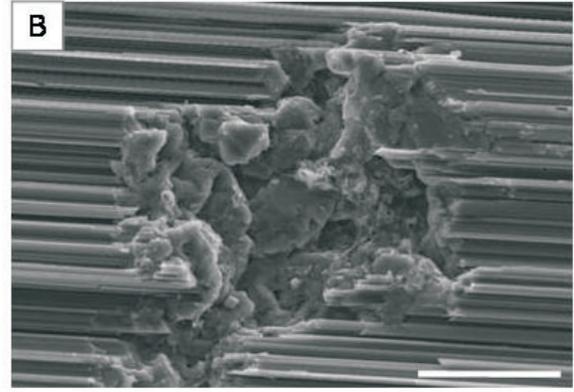
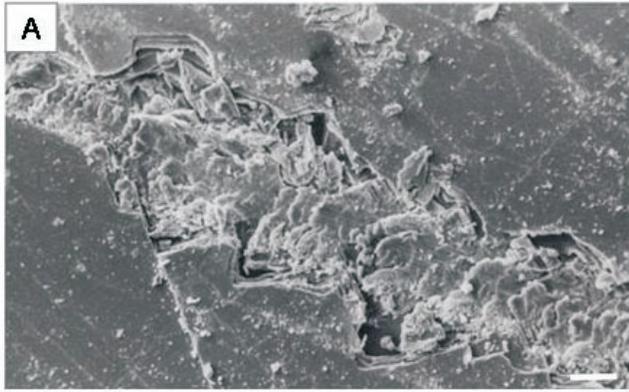
The type 3 filaments, which exhibit a calcified calcium carbonate sheath, present a central hollow tube which represents the area originally occupied by the organism. The encrustation of the sheath was called “encrusted sheath” by Riding (1977) and result as a carbonate tube with an inner diameter reflecting the diameter of the filament. The encrustation indicates inorganic precipitation (Merz 1992) in environment where photosynthetic bicarbonate use occurs. Calcification of filaments also take places in shallow hypersaline settings, which might be exposed to periodic emersion or fresh water influx (Golubic 1983). Also the degradation of dead cyanobacteria can favour calcification (Defarge et al. 1985, Lyons et al. 1984).

The encrustation of the type 1, 2 and 3 filaments was probably initiated and possibly completed while the organisms were alive. This hypothesis, which was previously supposed by Vai and Ricci Lucchi (1977), is supported by different lines of evidence. First, the shape of the filaments are remarkably well preserved, it follows that encrustation started during lifetime. Second, it can be argued that the encrustation of the filaments did not begin the instant the organisms died but would occur following some decay of the filaments. Such decay would probably not affect all parts of the filaments uniformly, because some parts of the filaments would decay more rapidly than others. One result of such differential decay should be a filament of variable diameter, yet, the calcified filaments, in terms of their central, hollow tube and inner sheath are remarkably uniform in size. Third, no evidence of collapsed filament was observed,

TEXT- FIGURE 4

SEM micrographs of natural selenite laminae.

- A Fossil structure composed by inserted “conical funnel shaped” unit comparable to that of modern scytonematacean cyanobacteria (sample MT24). Scale bar: 10µm.
- B Transversal view of inserted “conical funnel shaped” unit comparable to that of modern scytonematacean cyanobacteria (sample MT24). Scale bar: 40µm.
- C Type 1 filamentous tube, transversals view; the inner part is filled mainly by clay minerals and several pyrite grains occurring only on the outer “sheath” (sample MT24). Scale bar: 20µm.
- D Pyrite crystals occurring on the outer portion of Type 1 filamentous organism. The pyrite occurs as framboids constructed of numerous smaller cubic crystal pyrite and spheroid. The pyrite spheroids are composed by non-crystalline pyrite (sample MT24). Scale bar: 5µm.
- E Type 2 filamentous organisms. The filament appears to be filled (sample MT25). Scale bar: 100µm.
- F Dolomite crystals with hollow core occurring in the filling material of Type 2 filamentous organisms (sample MT25). Scale bar: 7µm.
- G Type 3 filamentous organism. The filament consists of a central hollow tube with relatively constant diameter, and an outer sheath expressed entirely by mineral grain with sharp euhedral boundaries (sample MT25). Scale bar: 50µm.
- H Pyrite occurring as bacterial aggregated spheroids constructed of numerous smaller cubic crystal pyrite in carbonate-rich patina between gypsum laminae (sample MT24). Scale bar: 10µm.



collapse would probably occur following the death of the cyanobacteria, rather than during their biological activity.

The remarkable strong auto-fluorescence emitted by some filaments preserved in banded selenite indicates presence of photosynthetic pigments (chlorophyll *a*). This indicates that pigments remained preserved in a significant proportion of trichomes. It gives the evidence that the microorganisms inside gypsum were able to photosynthesis, and therefore belonged to cyanobacteria or microalgae.

The presence of carbonate minerals randomly dispersed in gypsum samples can be due to microbial conversion of organic matter by heterotrophic bacteria even though it cannot be excluded that the precipitation of carbonate could be a direct by-product of cyanobacteria photosynthesis. The removal of photosynthetic carbon from the water column by cyanobacteria raises pH and triggers the precipitation of calcium carbonate in carbonate-saturated waters. Precipitation of carbonate through the photosynthetic activity of cyanobacteria has been well documented (Schröder and Schneider 1983, Merz 1992, Merz-Preiss 2000). The nucleation occurs, for example, at or within the sheath (Pentecost and Riding 1986) and certain species even exhibit species-specific crystal shape (Gleason and Spackman 1974; Krumbein and Giele 1979, Merz 1992). Moreover, the presence in the Vena del Gesso of dolomite in the carbonate rich-patina between gypsum laminae and in the filamentous structures is likely mediated by bacterial activity. Bacterially induced dolomite precipitation occurs in hypersaline lagoons (van Lith et al. 2003b) and has been reproduced at low temperature in laboratory experiments (Vasconcelos et al. 1995, van Lith et al. 2003a). In modern environments the dolomite precipitation is often associated with sulfate reducing bacteria that remove sulfate, produce alkalinity, and presumably drive dolomite formation (Vasconcelos and McKenzie 1997, Wright 1999). In the Vena del Gesso, the activity of sulphate-reducing bacteria and cyanobacteria appears to be responsible for the dolomite formation. However, the detailed mechanisms of these processes remain, in general, poorly understood.

The presence of pyrite framboids are also developed by microbial processes. The formation of pyrite requires on one side availability of iron and sulphates and on the other side a high percentage of organic carbon to sustain a prolonged activity of sulphate-reducing bacteria (Berner 1970). The organic carbon in this environment is represented by the vast amount of organic matter produced by cyanobacteria. Sulphate-reducing bacteria oxidize organic substrates through reduction of the dissolved sulphate of the interstitial waters. H₂S is produced then it reacts with the bivalent iron giving origin to Fe-monosulphides which later transform into pyrite.

The lack of modern analogues for the ancient large evaporite basins makes the estimation of the possible type of organisms occurring during the Messinian selenite deposition controversial. However, this study indicates that the filamentous fossil structures preserved in the massive and banded selenite of the Vena del Gesso are mainly cyanobacteria communities. The complex communities described in present-day settings and the presence of dolomite and pyrite structures associated to photoautotrophic cyanobacteria suggest that other heterotrophic bacteria with distinct metabolic activities were also present.

CONCLUSIONS

This study shows that the evaporite settings of the Vena del Gesso were characterized by the coexistence of different taxonomic groups of bacteria. From the size and type of preservations many of these are likely photosynthetic oxygenic cyanobacteria as presently observed in modern solar salt works. The different mode of preservations and the different mineralogical composition of the filaments indicate that the microbial population appears to contain a consortium of microorganisms. Besides, the presence of other heterotrophic bacteria with distinct metabolic activities is confirmed by the occurrence of minerals as dolomite and pyrite. The lack of modern analogues for large-scale ancient evaporite deposition makes estimation of the possible depth for selenite deposition difficult. However, the recognition that the fossil microbial communities preserved in the evaporite of the Vena del Gesso resembling morphologically modern obligate phototrophs cyanobacteria which occur in modern photic zone, shallow-water gypsum (formed at or below the pycnocline of the formative hypersaline water body) indicates a habitat characterized by solar light penetration. These conditions could be satisfied either by shallow water settings or by settling of microbial filaments down to the bottom of a relatively deep evaporite basin.

It should also be pointed out that there is a lack of any features that could indicate the occurrence of subaerial exposure in the studied cycle 6, thus implying a fully subaqueous origin for these deposits and consequently also for the ones including filaments.

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