Carbonates Evaporites (2016) 31:239–248
DOI 10.1007/s13146-015-0255-4

ORIGINAL ARTICLE

Thermogenic travertine deposits in Thermopylae hot springs (Greece) in association with cyanobacterial microflora

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Accepted: 28 May 2015 / Published online: 2 July 2015

Abstract The present paper deals with the investigation of abiotic and biotic influence on thermogenic travertine formation in Thermopylae hot springs, one of the largest active thermogenic travertine systems in Greece. Geological, mineralogical and microbiological data from three different types of travertines (cascades, terraces and fluvial crusts) revealed different cyanobacterial communities. Microscopic analysis of fresh and cultured material has shown that epilithic and endolithic cyanobacteria are almost the exclusive components of travertines' photosynthetic microflora. Thirty-one (31) taxa of cyanobacteria are presented here, among them the frequently found, in such environments, *Phormidium incrustatum* and *Aphanocapsa thermalis*, as well as the taxonomically interesting diazotrophic morphotype identified as *Chlorogloeopsis* sp. Sampling sites I and II have similar formation conditions characterized by laminated travertines with low porosity and shrub lithotypes, with the cyanobacterium *Leptolyngbya ercegovicii* occupying an endolithic zone, while the upper part is occupied by colonial chroococcalean species. On the contrary, sampling site III is characterized by laminated travertine with fenestrial type porosity and absence of shrub lithotypes resulting in a completely different community of cyanobacteria.

Keywords Travertines · Lithotypes · Cyanobacteria · Hot springs · Thermopylae (Greece)

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Introduction

Travertine is the chemically precipitated continental carbonate deposit formed around springs, along streams, and occasionally in lakes, consisting of calcite and/or aragonite. The first and most significant chemical process of precipitation is the transfer (evasion or invasion) of carbon dioxide (CO_2) from or to a groundwater source leading to calcium carbonate supersaturation, and finally to the nucleation and the formation of crystals (Pentecost et al. 1997; Fouke et al. 2000; Pentecost 2003, 2005; Okumura et al. 2011). The precipitation of calcite and/or aragonite crystals in travertines is basically induced by CO_2 degassing, which elevates the pH and the mineral saturation state (Kitano 1963; Pentecost 1995).

Since the publication of Ferdinand Cohn's pioneering work at Tivoli (Cohn 1864), it has been proven that bacteria and especially cyanobacteria play an important role in certain kinds of travertine formation (Pentecost 2005). Cyanobacteria are the major oxygenic microorganisms representing the most abundant phototrophic prokaryotes on travertines worldwide. Several species of cyanobacteria are widely distributed and often dominate on actively growing travertine surfaces playing a significant role in the biologically induced precipitation of $CaCO_3$. This is presumably because these organisms are among the few which thrive in hot, sulfide-containing waters, while many species tolerate a wide range of light intensities, salinity and high pCO_2 (Castenholz 2002; Banerjee et al. 2009).

The biologically induced mineralization (BIM) occurs through various metabolic processes, such as photosynthetic uptake of CO_2 and/or HCO_3^- by cyanobacteria, as well as ammonification, denitrification and sulfate reduction by other bacteria (Riding 2000; Beltrán-Magos et al. 2013). Especially for cyanobacteria, the following processes are known to contribute to the construction of carbonates: (a) increase of pH due to photosynthesis, (b) trap of $CaCO_3$ grains by entangled filaments, (c) biogenic activity of some cyanobacterial species (e.g., *Rivularia haematites*) to secrete carbonate structures and (d) binding of $CaCO_3$ grains in extracellular polymeric substances (EPS). EPS constitute a protective and adhesive material that anchors cells, colonies and filaments to the substrate, favoring sediment trapping. EPS possess the ability to concentrate Ca^{2+} cations favouring calcium carbonate encrustation by providing an ideal surface for adsorption of ions and mineral nucleation (Braissant et al. 2003; Beltrán-Magos et al. 2013). Furthermore, it is known that minerals originated through BIM nucleate and grow both extracellularly and also intracellularly. For example, calcite is capable of precipitating in *Chlorogloea lithogenes* sheath (Komárek and Montejano 1994).

Nevertheless, cyanobacteria play also a decisive role in the deconstruction of carbonate substrata, by weathering rocks and travertines (Schneider and Le Campion-Alsumard 1999). Lithobiontic cyanobacteria grow as epilithon and/or endolithon contributing to the biogenic and abiogenic deposition of $CaCO_3$ as well as in the deconstruction of carbonate surfaces (Pentecost 2003, 2005; Pentecost and Whitton 2000; Whitton et al. 2012). The biocorrosive mechanism of lithobiontic cyanobacteria and especially of euendoliths is probably through the secretion of acidic substances or complexing agents such as extracellular polymers resulting in the production of little crystals, which are more susceptible to the inorganic process of dissolution (Schneider and Le Campion-Alsumard 1999). As a result, the cyanobacterial contribution to the formation of travertines is an adjunct activity of the two controversial processes: (a) construction and (b) deconstruction.

The abiotic and biotic influence on thermogenic travertine formation is an interdisciplinary subject and to study it, we have to investigate how geological and biological phenomena interact simultaneously in nature. For that reason, in the latest studies a combination of geological and biological aspects are combined to investigate the biotic influence on $CaCO_3$ formation (Kandianis et al. 2008; Dupraz et al. 2009; Obst et al. 2009; Fouke 2011; Okumura et al. 2011, 2012; Kamennaya et al. 2012).

Greece offers an ideal place for the investigation of thermogenic travertine deposits, since they are scattered in many areas near hot springs (Gioni-Stavropoulou 1983; Orfanos 1985; Sfetsos 1988). Magmatic processes and active fault systems favor the rise of deep hydrothermal waters that are discharged at the surface as hot springs. The geochemical features of the majority of geothermal springs in Greece have been the focus of several studies (reviewed by Lambrakis and Kallergis 2005), but only recently have the active thermogenic travertine systems in Greece been geologically studied in detail (Kanellopoulos 2011, 2012, 2013; Winkel et al. 2013). Despite the fact that Greece is characterized by a great number of hot spring environments, the microflora of these unique ecosystems remains more or less unknown and the cyanobacteria of geothermal environments have received relatively little attention, as for example by Anagnostidis (1961, 1967) and Anagnostidis and Pantazidou (1988).

In Thermopylae area (lat. 38°47.5′–38°47.9′ and lon. 22°31.4′–23°32.4′, Fig. 1), one of the largest active thermogenic travertine-forming systems of Greece presents a great variety of morphological forms and lithotypes (Kanellopoulos 2012, 2013).

The aim of the present study is to investigate the geological and biological aspects of active travertine deposits of hot springs ($T = 41$ °C) in Thermopylae (Greece) and examine the role that the cyanobacterial microflora played in their formation.

Geological setting

Thermopylae is located in the eastern part of central Greece (Fig. 1) and belongs to the western most geotectonic unit of the Internal Hellenides, the Sub-Pelagonian Unit (Aubouin 1959; Mountrakis 1986; Jolivet et al. 2013). The basement in Thermopylae area consists mainly of carbonate rocks (limestones and dolomites) of Middle Triassic–Middle Jurassic age. An ophiolitic sequence (peridotides, serpentinites, gabbros) is overthrusted on the carbonates. Fluvio-deltaic sediments of Neogene age fill the Sperchios graben and consist of alternations of marls, clays, sandstones and conglomerates (Philip 1974). The whole area is highly faulted due to extensional tectonics in the backarc region of the Hellenic subduction system (McKenzie 1970, 1972; Le Pichon and Angelier 1979; Jolivet et al. 2013).

There are two main sites in Eastern Central Greece with hot spring manifestations, namely Kamena Vourla and Thermopylae. These are the surface expression of an active hydrothermal field beneath the broad area, which also extends in the neighboring part of northern Euboea Island (e.g., Edipsos, Gialtra, Ilia; Fig. 1). The hydrothermal field expands around the volcanic center of Lichades (Kanellopoulos 2011). The volcanic islands of Lichades are

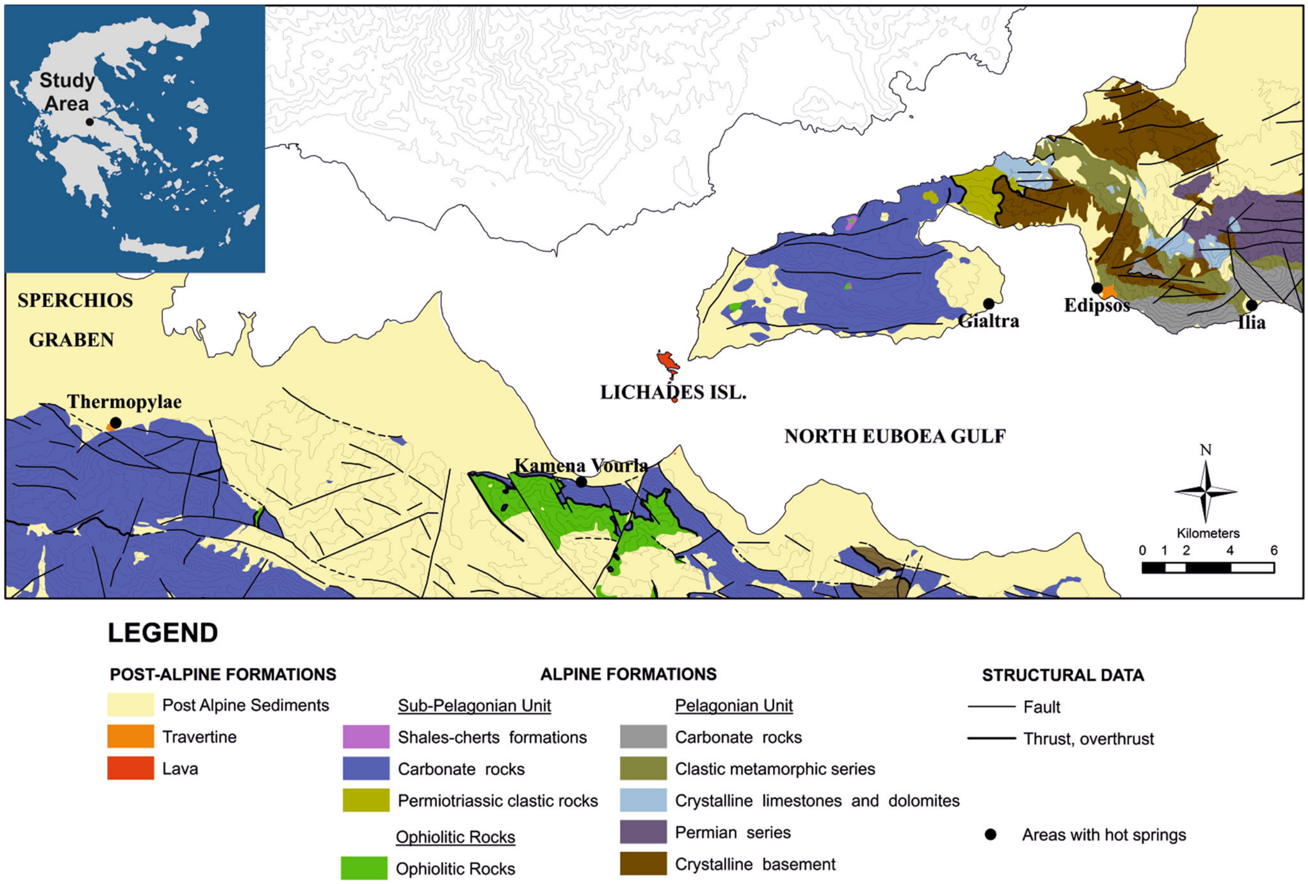


Fig. 1 Geological map showing the study area and the localities sampled (after Kanellopoulos 2013)

located at the center part of North Euboea Gulf (Georgalas 1938) and consist of trachyandesite lava flows, dated at 0.5 Ma (Pe-Piper and Piper 2002). These volcanic rocks are located along a shear zone (Kranis 1999) indicating a tectonic control during their emplacement. Recent studies by Karastathis et al. (2011) prove the existence of a magma chamber at an estimated depth of 7–8 km in the North Evoikos Gulf.

Materials and methods

Hot spring and sampling sites

Hot spring water at Thermopylae has temperatures of 33–40.4 °C, pH of 5.9–6.2 and total dissolved solids (TDS) from 5.5 to 7.5 (g/L) and presents high content in Ca (up to 520 mg/L), S (up to 140 mg/L), Mg (220 mg/L) and Sr (up to 11.9 mg/L) (Kanellopoulos 2011).

Samples were collected from three sites (I–III). The sampling sites were selected at different distances from the hot spring, representing distinct environmental conditions with different cyanobacterial composition. Sites I and II (Fig. 2a, c) are located near the main outflow zone of the hot water. In both cases, the flow velocity is low and the physicochemical parameters of the water are similar (pH = 6.9, temperature = 30 °C, TDS = 8.2 g/L, salinity = 8.5 and EC = 14.7 mS/cm). The site III (Fig. 2f) is located at the main stream of the hot water. The flow velocity is fast and the physicochemical parameters of the water are slightly different (pH = 7.1, temperature = 38.2 °C, TDS = 7.9 g/L, salinity = 8.2 and EC = 14.2 mS/cm).

All samples were collected using sterilized equipment. In all samples the mineralogical composition, the mineral chemistry, the type of lithotypes, as well as the composition of cyanobacterial species were studied.

Mineralogical study

Samples from all studied sites were collected and analyzed at the laboratories of the Department of Geology and Geoenvironment, University of Athens.

The mineralogical composition was investigated mainly by X-Ray diffraction (XRD). XRD analyses were carried out using a Siemens Model 5005 X-ray Diffractometer, Cu

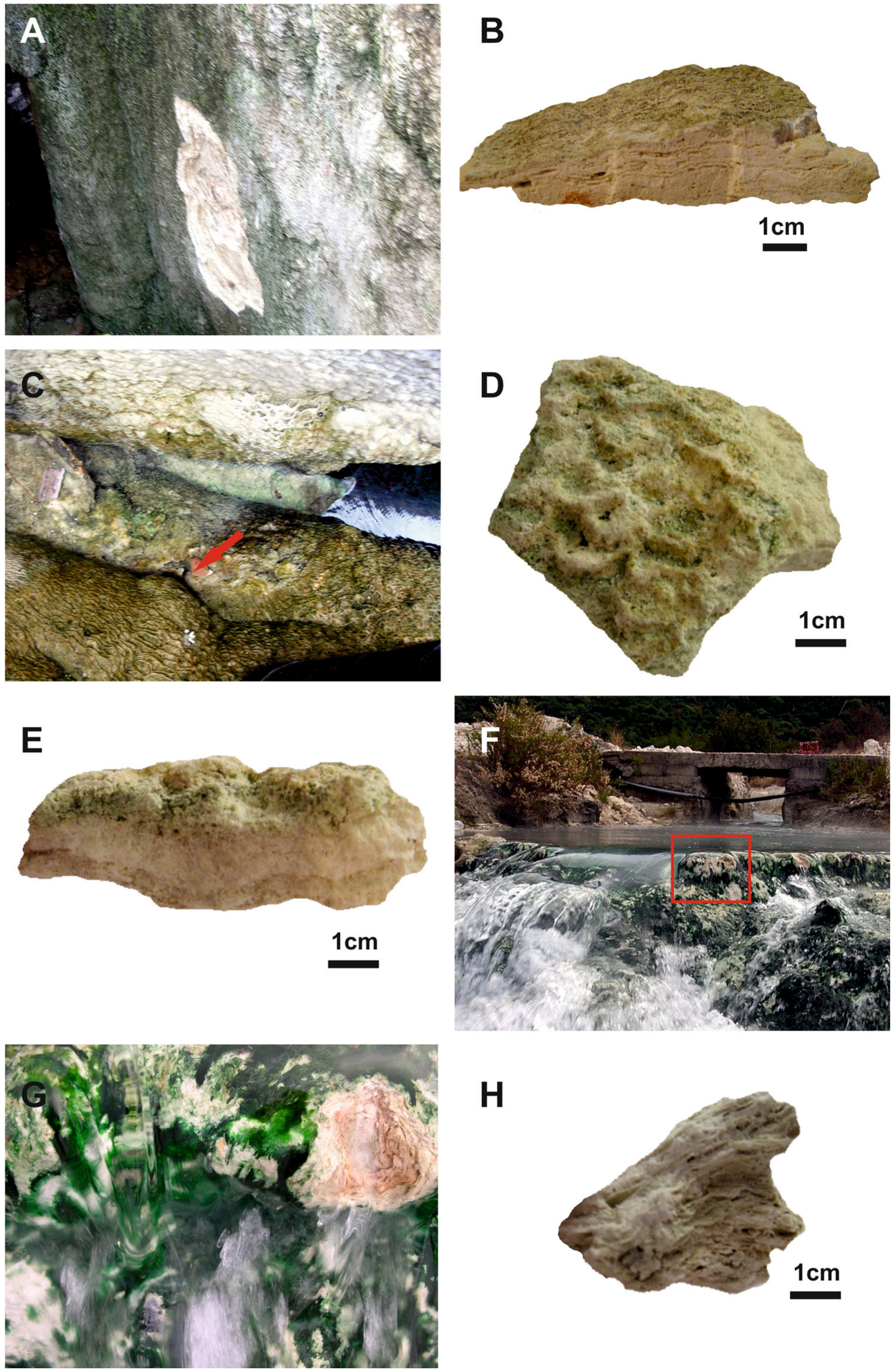


Fig. 2 Morphologies and lithotypes of the studied travertines. **a** Overview image of the external wall of a cistern (site I), where, parallel layers of travertine have been deposited. An early stage cascade. **b** Section of sample from cascade (site I) showing characteristic lamination lithotypes. **c** Overview image of terraces at the Thermopylae (site II). **d** Sample from travertine terraces (site II) with height of dams up to 10 mm. **e** Section of sample from terracettes, where characteristic lamination lithotypes can be seen (site II). **f** Overview image of fluvial crusts in a stream (site III). **g** Details of fluvial crusts (site III). The crusts were formed above the old travertines (bedrock) as fine layers. **h** Section of sample from fluvial crusts (site III) showing lamination lithotypes with an abundance of fenestral-type porosity common throughout the area of Thermopylae

Ka radiation at 40 kV, 40 nA, 0.020° step size and 1.0 s step time. The XRD patterns were evaluated using the EVA v.10.0 program of the Siemens DIFFRACplus and the D5005 software package.

Scanning electron microscopy (SEM) and energy dispersive spectroscopy (EDS) analysis were carried out using a Jeol JSM 5600 SEM instrument, equipped with an Oxford ISIS 300 OXFORD, with the following operating conditions: accelerating voltage 20 kV, beam current 0.5 nA, time of measurement 50 s and beam diameter 1–2 μm. The spectra were processed using the ZAF program (3 interaction). The microprobe analyses were conducted on polished sections of the samples after carbon coating. SEM images of the crystal structures were taken after gold coating of fragments.

Cultures and microscopy

Samples from all studied sites were collected and analyzed at the laboratories of the Department of Biology, University of Athens.

A portion of the sample was fixed with formaldehyde solution at a final concentration of 2.5 %, while another portion was used for culturing. Enriched cultures were obtained in flasks and Petri dishes with BG11 and BG 11_0 culture media (Stanier et al. 1971). Cultures were maintained in an incubator (SANYO, GALLENKAMP) under stable conditions and under natural diurnal cycle (north-facing window) at room temperature.

Both natural and cultured material was studied under a stereo-microscope (Stemi 2000C Zeiss, Germany) and under a high-resolution light microscope (Photomicroscope III, Zeiss, Germany). The observed cyanobacteria were identified using the classical literature such as (Geitler 1932, Desikachary 1959 and Komárek and Anagnostidis 1998, 2005) and many up to date papers. For SEM, fragments of the specimens were dehydrated in an alcohol series (30–100 %), critical point dried, gold coated and were observed at the above-mentioned scanning electron microscopy (SEM Jeol JSM 5600, Department of Geology and Geoenvironment).

Results

Mineralogical study

The main mineral phase identified by XRD analysis in all samples is calcite. It is usually present as rhombohedral crystals. Electron microprobe analyses indicate that in addition to Ca, the analyzed calcite contains up to 2.4 wt% Mg (Table 1), as has been also described by Kanellopoulos (2011, 2012).

Table 1 Representative microanalysis of calcite by SEM/EDS ($CaCO_3$, in compound %)

Mineral	Calcite					
MgO	2.4	1.3	1.7	2.1	1.4	0.7
CaO	49	48.7	50.2	47.8	49.5	50.4
Total	51.4	50	51.9	49.9	50.9	51.1

Morphological types and lithotypes

The thermogenic travertines at Thermopylae are characterized by many morphological types and lithotypes (Kanellopoulos 2012, 2013). In all studied sites, the travertine are white to gray colored and present three different morphological types: cascade (site I), terraces (site II) and smooth fluvial crusts (site III).

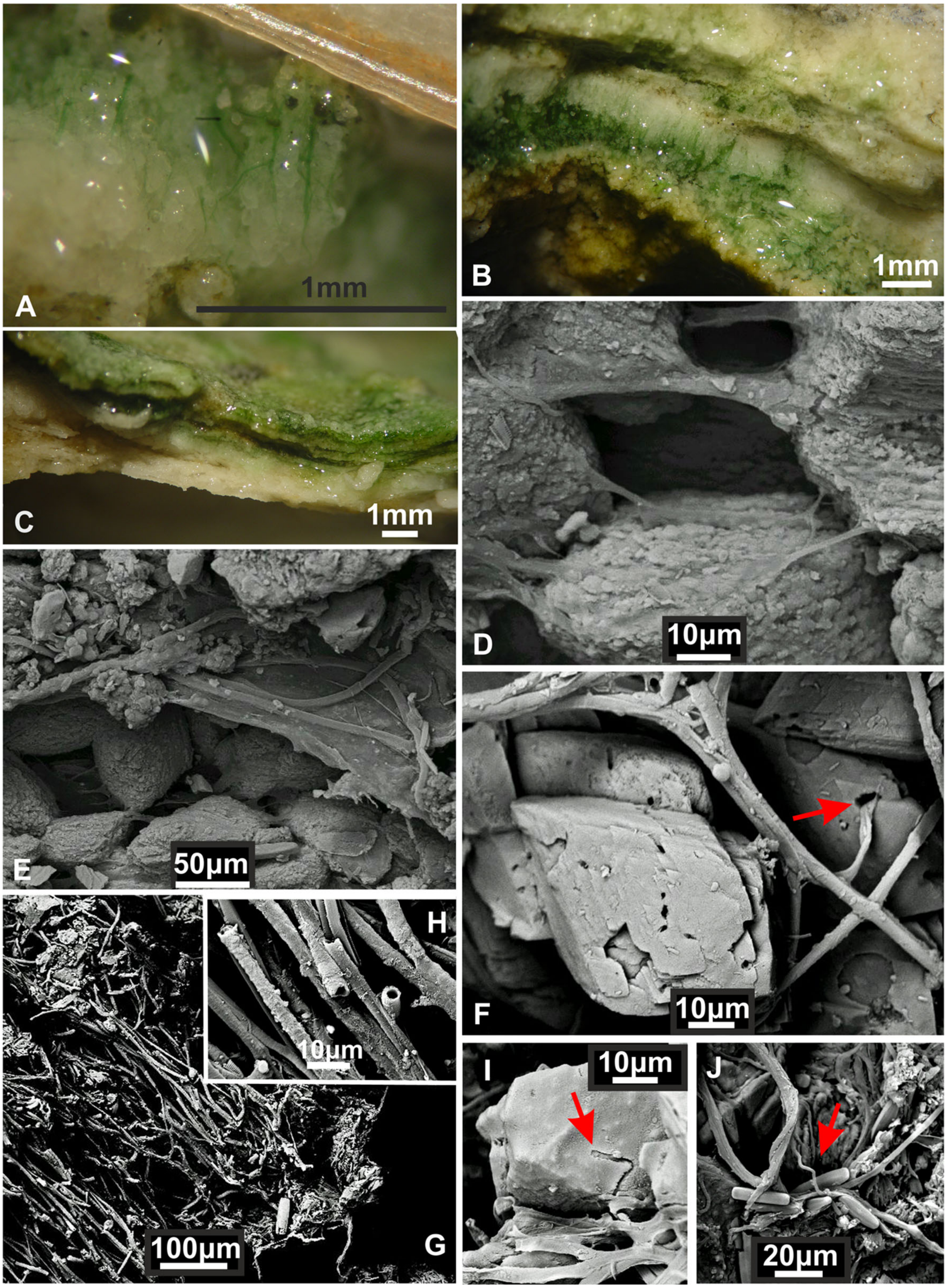
Cisterns were constructed near the main stream to collect and store the hot water. When the main stream overflows or the cisterns overflow, hot water overtops the external walls of cisterns and seeps down with low flow velocity. In that site, approximately parallel layers in section were created, indicating a probably early-stage cascade (site I, Fig. 2a, b).

In site II, small pools with small depth and low flow velocity (terraces) exist. The slow passage of water through lakes means that CO_2 evasion is reduced, while photosynthesis and evaporation become increasingly important as progenitors of carbonate precipitation. Over the rim and on the steep outside wall of the terrace (dam), water flows in a thin sheet resulting in the increase of the flow velocity. Morphological classification schemes for travertine terrace have been proposed by several authors (Bargar 1978; Bates and Jackson 1987; Pentecost and Viles 1994; Fouke et al. 2000). Using the classification suggested by Bargar (1978) and Fouke et al. (2000) in Thermopylae "microterracettes" of a few square centimeters or less, with maxima height of dams up to 10 mm, were identified (Fig. 2c, d). However, in the present paper the term "terrace" is used as a general term regardless of size, as suggested by Hammer et al. (2010).

In site III a range of superficial deposits formed inside the main stream of running hot water (Fig. 2f). They develop on a variety of structures, which are either smooth, or nodular and coralloid creating fluvial crusts. This morphological type is common in Thermopylae. Usually laminated smooth surfaces were developed above previous layers of travertine or around bedrock (Fig. 2g).

Concerning the lithotypes in sites I and II, the travertines show lamination with low porosity (Fig. 2b, e) and formation of shrubs, while in site III the travertines are laminated, without shrub formation and with an abundance of fenestral-type porosity (Fig. 2h).

Lamination (sites I, II and III) (Fig. 2b, e, h) was the common lithotype in our samples. The laminaes can usually be distinguished through eye observation consisting of gray- and white-colored layers with sometimes a last-top green color layer (Figs. 2e, g, 3c). Laminaes can reach a maximum of 1 mm thickness. Their magnified view shows fine-scale laminae of a few tens of micrometers (Fig. 2b). Shrub layers can be distinguished through eye observation


A
1mm
B
1mm
C
1mm
D
10μm
E
50μm
F
10μm
G
100μm
H
10μm
I
10μm
J
20μm

◀ **Fig. 3** Travertine formations and their cyanobacterial microflora under stereoscope (**a–c**) and SEM (**d–i**). **a**, **b** Laminated travertines (site I and II) with shrub lithotypes. **a** Details of the endolithic filaments of *Leptolyngbya ercegovicii* favoring travertine deconstruction. *Scale bars* 1 mm. **c** Fluvial crust with characteristic lamination (site III). *Scale bar* 1 mm. **d**, **e** Extracellular polymeric substances (EPS) favoring the crystal trapping. *Scale bars* 10 and 50 μm, respectively. **f** Rhombohedral crystals of calcite with distinct holes, some of them occupied by filamentous cyanobacteria (site II). *Scale bar* 10 μm. **g** Details of the calcified cyanobacterial sheaths in sites I and II. *Scale bar* 100 μm. **h** Heavily calcified tube formed by the cyanobacterium *Phormidium incrustatum. Scale bar* 10 μm. **i** Cyanobacterial filaments favoring crystal trapping. The *arrow* indicates a trace of lithobiontic cyanobacterium. **j** Diatom frustules embedded in EPS, some of them trapped by filamentous cyanobacteria

between micritic-sized calcite laminaes in many cases (Fig. 2b, e, h).

Travertine shrubs are observed in sites I and II. They are short, stubby, dense crystalline masses of calcium carbonate that expand upward by irregular branching. Shrub-like types could present considerably different morphologies. Chafetz and Guidry (1999) distinguished travertine shrubs into those whose outline is typical of the common garden-variety woody shrub or bush (bacterial shrubs, Chafetz and Folk 1984), to those that have regular geometric patterns (crystal shrubs) and to crystalline calcite fans (ray-crystal crusts, see also Folk et al. 1985). In the studied samples, shrubs usually had garden-variety woody shrub or bush patterns (bacterial shrubs, Fig. 3a). They also present irregular morphology without any specific crystallographic influence on their shape. Detailed study of the samples using SEM–EDS revealed that the shrubs were related with calcite tubes encrusting filaments (Fig. 3g, h).

Distribution of cyanobacteria based on morphology

Cyanobacteria were found to prevail at the hot spring and the outflows (downstreams). The predominance of the cyanobacteria is due to the reduced presence of eukaryotic algae such as diatoms. Microscopic analysis of fresh and cultured material from the three sampling sites revealed a total number of thirty-one (31) cyanobacteria (Table 2). The majority of the species identified are non-heterocytous filamentous cyanobacteria thriving at the mats' surface and/or endolithic filaments distributed in the lower part of the travertines (see also Pentecost 2003). Heterocytous filaments with or without true branching have little representation with the exception of the genus *Calothrix* (site II), a commonly reported thermophilic genus (see also Pentecost 2003, 2005; Whitton et al. 2012).

At sites I and II, filaments of *Leptolyngbya ercegovicii* occupy an endolithic zone of 3–5 mm, while the upper part is occupied by colonial chroococcalean species such as

Table 2 Cyanobacterial microflora identified from the three sampling sites (I–III) in Thermopylae hot springs

Sampling Site I	Sampling Site II	Sampling Site III
Asterocapsa jilinica H.X. Xiao 2000	*Aphanocapsa thermalis* Brügger 1863	*Geitlerinema lemmermannii* (Woloszynska) Anagnostidis 1989
Calothrix sp.1	*Aphanothece castagnei* (Brébisson) Rabenhorst 1865	*Jaaginema geminatum* (Meneghini ex Gomont) Anagnostidis & Komárek 1988
Calothrix sp.2	*Aphanothece* sp.	*Oscillatoria ornata* Kützing ex Gomont 1892
Chlorogloeopsis sp.	*Calothrix callida* Richter 1898	*Phormidium terebriforme* (Agardh ex Gomont) Anagnostidis & Komárek 1988
Chlorogloea novacekii Komárek & Montejano 1994	*Chroococcus minor* (Kützing) Nägeli 1849	*Spirulina subsalsa* Oersted ex Gomont 1892
Gloeocapsa cf. *violascea* (Corda) Rabenhorst 1865	*Chroococcus thermalis* (Meneghini) Nägeli 1849	
Gloeocapsa sp.	*Gloeocapsa* cf. *aeruginosa* Kützing 1843	
Gloeocapsopsis crepidinum (Thuret) Geitler ex Komárek 1993	*Gloeocapsa* cf. *compacta* Kützing 1845	
Gloeocapsopsis dvorakii (Nováček) Komárek & Anagnostidis 1986	*Leptolyngbya ercegovicii* (Čado) Anagnostidis & Komárek 1988	
Leptolyngbya ercegovicii (Čado) Anagnostidis & Komárek 1988	*Leptolyngbya tenuis* (Gomont) Anagnostidis & Komárek 1988	
Trichocoleus sociatus (West & G.S.West) Anagnostidis 2001	*Phormidium aerugineo-caeruleum* (Gomont) Anagnostidis & Komárek 1988	
Schizothrix cf. *friesii* Gomont 1892	*Phormidium inundatum* Kützing ex Gomont 1892	
Symplocastrum penicillatum (Kützing ex Gomont) Anagnostidis 2001	*Phormidium incrustatum* Gomont ex Gomont 1892	
	Spirulina major Kützing ex Gomont 1892	

Aphanocapsa thermalis, *Ap. castagnei*, *Chroococcus minor,Ch. thermalis*, *Gloeocapsopsis crepidinum* and *Gl. dvorakii*, *Phormidium incrustatum* is the most common carbonate-incrusted cyanobacterium found at sampling site II. It is noted that trichomes of *Ph. incrustatum* are surrounded by firm sheath of EPS, constituting the locus of intensive calcification (Fig. 3h). The diagenesis of micrite deposit of that particular species is similar to those observed by Golubic et al. (2008). Diatoms frustules or/and calcite crystals are usually observed embedded in EPS in both sites I and II (Fig. 3d, e, g, j).

At sampling site III, the upper part of the travertine formation is colonized by blue-green thin mats of *Geitlerinema lemmermannii* and *Oscillatoria ornata*, while thin vertical sections revealed calcite crystals attached to the filaments of *Phormidium terebriforme* and *Spirulina subsalsa.*

Discussion

Up to the present, it is well known that for about 3.5 billion years the global carbonate cycle has been regulated by photoautotrophic processes, with cyanobacteria being the dominant group with a decisive role in the construction and the deconstruction of carbonates (Schneider and Le Campion-Alsumard 1999).

This study examined the geological characteristics of thermogenic travertines in association with cyanobacterial communities at Thermopylae hot springs, Greece. A large thermogenic travertine deposit in this locality includes highly variable travertine textures and cyanobacteria species. Based on the associations among them, the findings could be useful to understand older formation processes for the different types of travertine. Such processes can be applied to laminated carbonates of the geological past, in which biogenicity remains controversial (Semikhatov et al. 1979; Buick et al. 1981; Lowe 1994; Grotzinger and Rothman 1996).

The thermogenic travertines of Thermopylae hot springs are formed dominantly by in situ precipitation. Travertines in sites I and II have similar formation conditions, i.e., low speed flow and low depth, resulting in the formation of laminated travertine with low porosity and shrubs lithotypes (Fig. 2a–e). The development of laminated lithotype may be due to inorganic processes, where the release of CO_2 caused supersaturation of the solution and precipitation of $CaCO_3$ (Jones et al. 2005) to biogenic processes (Chafetz and Folk 1984), or to the combination of multiple abiotic and biotic factors. Also, the shrub lithotypes identified in the studied samples have garden-variety woody shrub or bush patterns, which are characterized as bacterial shrubs as suggested by Chafetz and Folk (1984). Additionally, chroococcoid cyanobacteria such as *Aphanocapsa thermalis*, *Gloeocapsa* cf. *violacea*, *Gloeocapsopsis crepidinum* and *Gl. dvorakii* have been observed to thrive to the top layer of the shrubs, indicating the relation between the specific lithotype and cyanobacteria.

Detailed study of the samples using SEM–EDS indicated the presence of similar characteristic structures suggesting bio-mineralization processes by *Microcoleus sociatus*, *Schizothrix* cf. *friesii* at the upper part favoring sediment trapping by many ways and endolithic band consisting of *Leptolyngbya ercegovicii* at the inner part of the travertine (Fig. 3a, b) favoring the travertine deconstruction. Typical structures in both sites (I and II) are calcite tubes encrusting the filaments in different stages: during the early stage, calcite crystals, usually as micritic mud, precipitate within the outer sheath layer (Fig. 3d, e) due to photosynthetic bicarbonate uptake; while at a later stage solid calcite tubes are protruding vertically in direction to the surface. These structures were associated with the shrub lithotypes (Fig. 3g, h). After the decomposition of the organic material a solid tube remains, and the usually broken tube tip exposes the coalescing calcite crystals.

Travertine in site III is characterized by different formation conditions (e.g., fast speed flow, greater depth) compared to travertine from sites I and II. In site III, the laminated travertine displays a fenestrial type of porosity and no shrub lithotypes, as a result of a completely different cyanobacterial community. Detailed study of the site III samples using SEM–EDS suggests that no one of the abovementioned phenomena of biomineralization at sites I and II took place here. In site III, characteristic structures attributed to bio-mineralization processes are holes in rhombohedral calcite crystals (Fig. 3f). In this sampling site with the highest temperature, cyanobacterial species that adapted to the extreme and specialized environment of hot springs (belonging to the order Oscillatoriales) were determined.

In conclusion, the formation of thermogenic travertine at Thermopylae shows a variation in morphological types, lithotypes and cyanobacterial species composition. The data presented show correlation between specific lithotypes, suggesting bio-mineralization processes and specific cyanobacteria species. The combination of the geological and biological data seems to suggest that the deposition of thermogenic travertine at Thermopylae (one of the larger active travertine-forming systems in Greece) is due to a combination of multiple abiotic and biotic factors. The open question that remains to be answered by future studies is to quantify the contribution of each factor in the deposition process. The combination of all this information will offer significant help to attain an in-depth understanding of carbonate formation in the geological past. To achieve that, it is necessary to investigate how geological and biological phenomena interact simultaneously in nature.

Acknowledgments The authors would like to thank Assoc. Prof. Pantazidou Adriani of University of Athens, Faculty of Biology, Department of Ecology and Systematics, who provided insight and expertise that greatly assisted the research concerning cyanobacteria.

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