



developed in extreme environments, including benthic communities of deep, perennially ice-covered Antarctic lakes, where physical and chemical conditions, and/or geographical isolation preclude larger organisms that could otherwise disrupt organised microbial structures (Wharton, 1994; Andersen et al., 2011). Many organised sedimentary structures that emerge in these conditions are laminated and accrete through episodic trapping of sediments or grains and precipitation of minerals within a growing biogenic matrix (e.g. Arp et al., 2001; Reid et al., 2003). In perennially ice-covered lakes, the seasonality of growth imposed by the summer-winter light-dark conditions can induce annual growth laminations (Hawes et al., 2001), reinforced by calcite precipitation during growth and sediment diagenesis (Wharton et al., 1982; Wharton, 1994; Sutherland and Hawes, 2009). Calcite precipitation is not, however, a prerequisite for laminated, stromatolite-like communities (Walter, 1976; Schieber, 1999; Yamamoto et al., 2009).

Precipitation of calcite by expulsion (segregation) is also a common process in the nature related with the freezing of common low ionic strength  $\text{Ca}^{2+}$  -  $\text{HCO}_3^-$  waters. Calcite precipitation related to water freezing was observed and described also from various polar-alpine settings, e.g. from lake bottoms of Dry Valleys in Antarctica (Nakai et al., 1975); as a result of aufeis (icing, naled) formation in Northern Canada (Clark and Lauriol, 1997); as crystalline precipitates that form subglacially on bedrock, reported from numerous locations (Ng and Hallet, 2002); as fine-grained calcite powders in subglacial deposits and in aufeis formations, Svalbard (Wadham et al., 2000); in basal ice and subglacial clastic deposits of continental glaciers of Switzerland (Fairchild et al., 1993); as calcite pendants occurring beneath coarse clasts in well-drained sediments, Svalbard (Courty et al., 1994); as calcite coatings in cavities in cold-climate Pleistocene deposits of Western Transbaikalia, Russia, and in modern surface deposits at Seymour Island, Antarctica (Vogt and Corte, 1996); cryogenic calcite powder from modern cave environment (Clark and Lauriol, 1992).

James Ross Island belongs to a transitory zone between the maritime and continental Antarctic regions (Øvstedal and Lewis Smith, 2001). Air temperature records indicate progressive warming trends from 1.5 to 3.0 °C over the Antarctic Peninsula

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during the past 50 years (Turner et al., 2014). More than 80 % of the island surface is covered with ice (Rabassa et al., 1982). Only the northernmost part of the island, the Ulu Peninsula, is significantly deglaciated and represents one of the largest ice-free areas in the northern part of the Antarctic Peninsula. The origin of the lakes on James Ross Island is related to the last glaciations of the Antarctic Peninsula ice sheet and retreat of the James Ross Island ice cap during the late Pleistocene and the Holocene (Nývlt et al., 2011; Nedbalová et al., 2013). Interactions between volcanic landforms and glacial geomorphology during previous glacial-interglacial cycles, the Holocene paraglacial and periglacial processes and relative sea level change have resulted in the complex present-day landscape of James Ross Island (Davies et al., 2013). All of these processes have influenced the development of the lakes which are found on the Ulu Peninsula at altitudes from <20 m above sea level (a.s.l.) near the coast to 400 m a.s.l. in the mountain areas (Nedbalová et al., 2013).

During two Czech research expeditions (2008 and 2009) to James Ross Island, lake ecosystems of the Ulu Peninsula were studied in respect to their origin, morphometry, physical, chemical and biological characteristics (Nedbalová et al., 2013, together with detailed cyanobacterial and microalgal diversity descriptions (Komárek and Elster, 2008; Komárek et al., 2011; Kopalová et al., 2013; Škaloud et al., 2013; Komárek et al., 2015). As part of this study, we encountered 1 to 5 mm scale calcareous organosedimentary structures on the floor of two endorheic lakes, 1 and 2, which are quite different to any microbially mediated structures yet described from modern environments. These shallow lakes on higher-lying levelled surfaces originated after the deglaciation of volcanic mesas which became ice-free some 6.5–8 ka ago (Johnson et al., 2011) and are considered among one of the oldest in the region. However, a later appearance of these lakes is also possible, as we have no exact dates from their sediments (Nedbalová et al., 2013).

The aim of this paper is to describe in detail the chemical and biological composition of the organosedimentary structures (stromatolites sensu Allwood et al., 2006) together with the limnological characteristics of the two lakes. A hypothesis concerning

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micro fortified mucilaginous lines (Fig. 6c, d). Figure 6a shows the community in early spring whereas Fig. 6b, d originated from later summer when the littoral benthic community was already well developed with a dense coverage of *Hazenia broadyi* green spots. More detailed pictures (Fig. 6e, f) documented the structure of the black leather like biofilm with mucilaginous marble on its surface covered by green spots. When the biofilm gets dry, the net of precipitated micro fortified mucilage mixed with soft mineral particles and crystals of calcium carbonate is visible (Fig. 6g, h).

Scanning electron micrographs document the structure of the biofilm (Fig. 7). Figure 7a shows a lateral view (cross section) of a biofilm with cyanobacterial filaments (*Calothrix elsteri* and *Hassallia andreassenni*). A biofilm upper view (Fig. 7b, d) shows the structure of the cyanobacterial-microalgae community producing the mucilaginous micro fortified net of filaments with spots on its surface.

### 3.4 Inorganic compounds of biofilms

Thin sections, showing both biofilms and rock substrate (Fig. 8), provided information on various inorganic compounds associated with the soft tissue of the cyanobacterial – microalgal community. These inorganic compounds are represented by (1) allochthonous mineral grains that are overgrown and incorporated by biofilms and (2) calcareous spicules of different sizes ranging from 0.5 mm to 1 cm that are precipitated within the cyanobacterial-microalgal community.

The rock substrate of biofilms is formed by subangular to subrounded pebbles to boulders of basaltic rock, which is dark-grey in colour, compact and usually with a microcrystalline porphyric texture. The rock is not homogenous, but contains numerous ball-like empty voids, which are often partly filled with feldspathoids (Fig. 8a). Crystals of plagioclase (feldspar group) and augite (pyroxene group) are easily recognizable in thin sections (Figs. 8a–c).

Biofilms are often partly covered with various mineral grains and rock fragments, but all specimens studied also contain these particles incorporated directly within soft cyanobacterial – microalgal filaments (Fig. 8a–c).

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Mineral grains embedded within biofilms close to the basaltic rock surface are mainly angular to subangular crystal fragments of plagioclase and augite (Figs. 8b, c), i.e. the main mineral components of the basaltic rock substrate described above. In the upper part of biofilms, however, partly or fully incorporated grains of quartz occur, being typically rounded or partly rounded (Figs. 8a, b). One of the thin sections shows a calcareous spicule in situ and mineral grains within the biofilm (Figs. 8c, d).

The structure and morphology of calcareous spicules was studied on SEM (Fig. 9). The spicules (see also Methods) show an intensively worn surface (Fig. 9a), partial or intense recrystallization (Figs. 9a, b) and dissolution (Fig. 9b). Crystal facets on the surface and cleavage (crystallographic structural planes) in the interior of the spicules (Figs. 9a, b) are typical characteristics of calcium carbonate monocystals.

A non-recrystallized superficial layer of microcrystalline calcite (e.g., Fig. 9b) shows the structure of parallel needle-like calcite microcrystals (Figs. 9d–f). Partial corrosion and dissolution of spicules show distinct layering of these needle-like microcrystals (Fig. 9d). The layered structure of even partly recrystallized spicules is confirmed in the ring-like structures with a cyanobacterial filament in the centre (Fig. 10).

The chemical composition of the studied calcareous spicules determined by FDS corresponds to pure  $\text{CaCO}_3$ . Following chemical composition, calcite and aragonite structural models were applied for the EBSD study focused on structural identification of the crystals forming the spicule. Structural identification of the studied specimen especially prepared for the EBSD study confirmed the absolute agreement between the recorded EBSD patterns and modelled patterns for calcite. The presence of aragonite was not confirmed. FSD images acquired for chemical and orientation contrasts (Fig. 10) show a layered structure especially visible in orientation contrast. This feature reflects continual growing processes on layers with very similar crystallographic orientation. Absolute angular differences between individual layers are below  $0.8^\circ$ .

## 4 Discussion

### 4.1 Environmental properties

The Ulu Peninsula is a region of high limnological diversity that is related to differences in lake age, bedrock and altitude. The endorheic lakes under study are characterized by a low content of major ions due to their volcanic bedrock and lower marine influence. In comparison with other lakes of this area, the two lakes show no specific lake water chemistry characteristics with moderate SRP and nitrate concentrations frequently below the detection limit (Nedbalová et al., 2013). High pH together with oxygen supersaturation recorded in lake 2 could be associated with high photosynthetic activity of the mats at the time of sampling.

Because water in either liquid or solid form has a large heat storage capacity, it acts as an important buffer to temperature change. Local climatic conditions of shallow freshwater lakes is the principal external factor controlling their ecological functionality. Lake 1 is frozen to the bottom with minimum daily mean temperatures between  $-12$  and  $-10^{\circ}\text{C}$  approximately eight-nine months per year. For most of the year, however, the temperature of the littoral and lake bottom is only from  $-2$  to  $-4^{\circ}\text{C}$ . In such conditions, a thin layer of water probably covers the surface of the littoral benthic community (the community can be metabolically active at temperatures of about  $-4^{\circ}\text{C}$ ) (Davey et al., 1992). The growing season, with liquid water at temperatures between  $2$  to  $4^{\circ}\text{C}$ , covers only two-three months.

In regards to heat balance, the studied shallow lakes are pond (wetlands) environments which freeze solid during the winter. This inevitability is a strong habitat-defining characteristic, which places considerable stress on resident organisms (Hawes et al., 1992; Elster, 2002). In summer, they must withstand drying in large parts of the littoral zone due to a considerable drop in water level. In freezing and desiccation resistance studies of freshwater phytobenthos in shallow Antarctic lakes, several ecological measurements have recorded seasonal, diurnal, and year round temperature fluctuations and changes in water state transitions (e.g., Davey, 1989; Hawes et al., 1992,

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Hawes et al., 1999). In localities with steady moisture and nutrient supplies, the abundance and species diversity of algae is relatively high. However, as the severity and instability of living conditions increases (mainly due to changes in mechanical disturbances, desiccation–rehydration and subsequent changes in salinity), algal abundance and species diversity decreases (Elster and Benson, 2004). The speed at which water state can change between liquid, ice, and complete dryness, is one of the most important ecological and physiological factors of these lakes. Studies based on field or laboratory experiments have shown that some cyanobacteria and algae are able to tolerate prolonged periods of desiccation. It is also obvious that there are strain/species specific differences in the overwintering strategies, and also between strains/species inhabiting different habitats (Davey, 1989; Hawes et al., 1992; Jacob et al., 1992; Šabacká and Elster, 2006; Elster et al., 2008). The ice and snow which cover the endorheic lakes for about eight-nine months per year serve as a natural incubator which moderate potential mechanical disturbances and stabilise the thermal regimes of the lakes.

### 4.2 Biodiversity

Patterns of endemism and alien establishment in Antarctica are very different across taxa and habitat types (terrestrial, freshwater or marine; Barnes et al., 2006). Environmental conditions, as well as dispersal abilities, are important in limiting alien establishment (Barnes et al., 2006). Antarctic microbial (cyanobacteria, algae) diversity is still poorly known, although recent molecular and ecophysiological evidence support a high level of endemism and speciation/taxon distinctness (Taton et al., 2003; Rybalka et al., 2009; de Wever et al., 2009; Komárek et al., 2011; Strunecký et al., 2012; Škaloud et al., 2013).

The floors of the studied lakes are covered with photosynthetic microbial mats composed of previously described species of heterocytous cyanobacteria, mostly *Calothrix elsteri* Komárek 2011 followed by *Hassallia andreassenni* Komárek 2011 and *Hassallia antarctica* Komárek 2011 (Komárek et al., 2011). They are co-dominated by a newly described species of green filamentous and richly branched algae *Hazenia*

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*broadyi* Škaloud et Komárek 2013 (Ulotrichales, Chlorophyceae; Škaloud et al., 2013). All the previously mentioned recently described species have special taxonomic positions together with special ecology and are considered at present as Antarctic endemic species.

5 The black leather like biofilm with mucilaginous marble on its surface is covered by green spots. These macroscopic structures form mats a few mm thick consisting of the above mentioned species packed in mucilage glued together with fine material. The regular leather biofilm structure with distinct cyanobacterial-microalgal composition and incorporated mineral grains is a modern analogue of some of the oldest well-described  
10 Archean stromatolites (sensu Allwood et al., 2006). During the limnological survey of the whole Ulu Peninsula (Nedbalová et al., 2013), this specific biofilm structure was observed only in these two endorheic lakes, although lakes with very similar morphometric and chemical characteristics are found in the area. The mat structure is thus apparently tightly linked to the species composition (Andersen et al., 2011).

15 The low abundance of benthic diatoms in the lakes is unusual, but not unprecedented as there are other areas in Antarctica where diatoms are scarce or absent (Broady, 1996; Wagner et al., 2004). The reason underlying the absence of diatoms is not immediately obvious, because diatoms are quite a common and frequently dominant component of microbial communities in most freshwater habitats of the Ulu Peninsula, James Ross Island (Kopalová et al., 2013). Local geographical separation of lakes  
20 1 and 2 together with founder effect may have precluded successful colonization by the subset of diatoms that are common in the surrounding freshwater habitats. Although it has long been held that diatoms are dispersed widely, some recent reports document very small scale microbial distributions and endemism (Kopalová et al., 2012; Kopalová  
25 et al., 2013).

### 4.3 Inorganic compounds of biofilms

Based on the character of the rock substrate and lake sediments it is suggested, that one of the main prerequisites for existence of this cyanobacterial-microalgal community

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producing unusual biogenic calcite structures is; (1) flat and stable substrate in both lakes and (2) low sedimentation rate.

The substrate for biofilms is composed of boulders and pebbles of the stony littoral zone, petrographically corresponding to compact and massive basaltoids (Smellie et al., 2008; Svojtka et al., 2009). Rounded or sub-rounded quartz grains that are incorporated (“trapped”) within biofilms cannot originate from basaltic volcanic rocks forming  
5 the bottom of both lakes and substrate of the studied biofilms. This is evidenced by the petrographic character of the basaltoids, which do not contain any quartz. The presence of abraded quartz grains in lake 1 and 2 can be easily explained by wind transport (e.g., Shao, 2008).  
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The specific cyanobacterial-microalgal community described above can prosper in the two shallow endorheic lakes, because of low sedimentation rates resulting from minor water input. Low sedimentary input is the main necessary ecological parameter which facilitates the existence of this special microbial community. The community  
15 is, however, well adapted to seasonally elevated sedimentation rates coming from frequent and intense winds. During wind storms, the wind is carrying a relatively large amount of small mineral grains and rock microfragments (intense eolic erosion; e.g., Shao 2008 and references therein). These grains and particles are usually derived from erosion of the rocks either in the very close vicinity of the locality (weathering of  
20 basaltic rocks), but mainly come from remote locations where especially Upper Cretaceous marine sedimentary sequences are outcropping (Smellie et al., 2008; Svojtka et al., 2009). Even elevated amounts of mineral grains transported into the lake by wind do not stop the growth of cyanobacterial-microalgae biofilms, due to their ability of incorporating and “trapping” mineral grains within the living tissue.

25 This study has shown that inorganic substances precipitated by microbial lithogenetic processes are exclusively represented by calcite spicules. Precipitation of carbonate outside of microorganisms during photosynthesis as a mechanism of carbonate construction was described for many filamentous cyanobacterial species (Schneider and Le Campion-Alsumard, 1999). However, the biogenic calcite structures in both lakes



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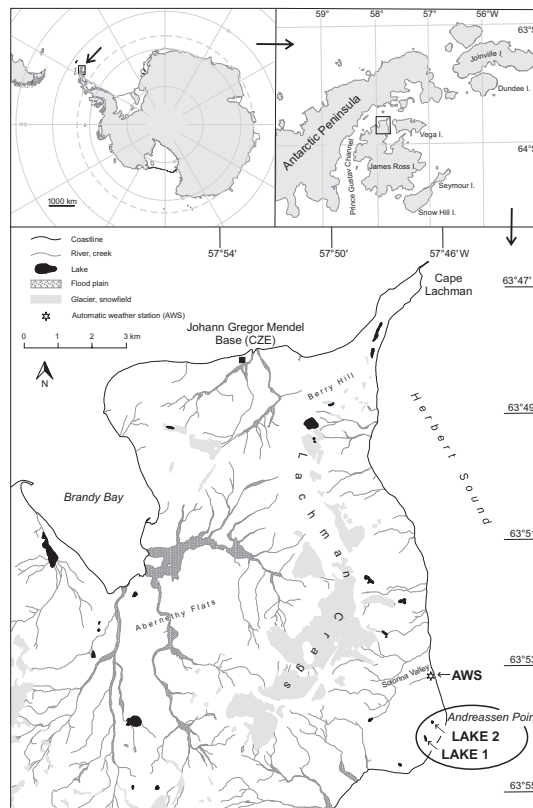
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**Table 1.** Physico-chemical characteristics and chlorophyll *a* concentrations in lake water. Samples were collected from surface of lakes. ND – not determined, ANC – acid neutralization capacity, PN – particulate nitrogen, DP – dissolved phosphorus, PP – particulate phosphorus, SRP – dissolved reactive phosphorus, DOC – dissolved organic carbon, PC – particulate carbon, \* – laboratory values.

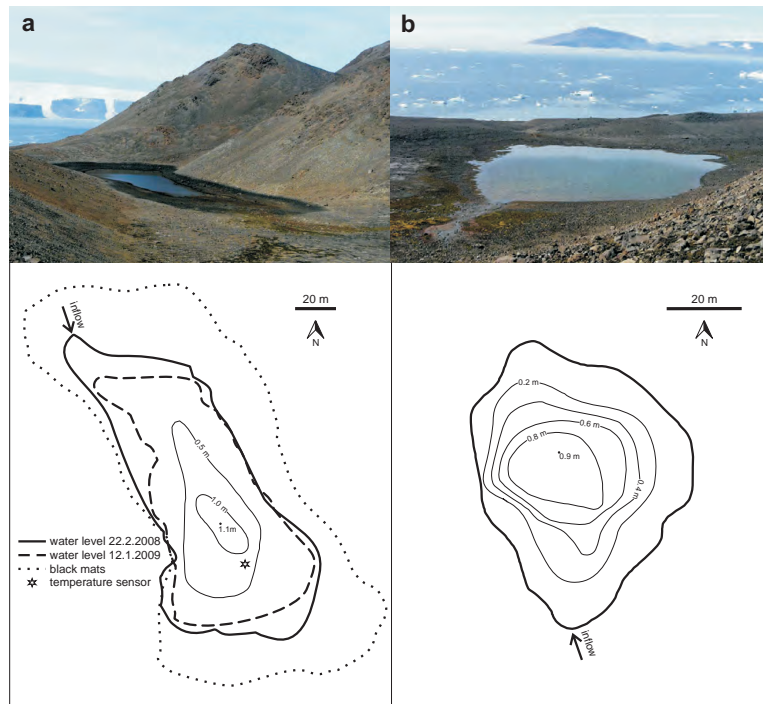
Lake		Green 1	Green 2
Date		22.2.2008	5.1.2009
Temperature	°C	3.5	ND
O <sub>2</sub>	mg L <sup>-1</sup>	13.1	ND
O <sub>2</sub> saturation	%	98.7	ND
pH		7.9	7.4*
Conductivity (25°C)	µS cm <sup>-1</sup>	54	48*
ANC	mmol L <sup>-1</sup>	236	246
Na <sup>+</sup>	mg L <sup>-1</sup>	4.7	5.9
K <sup>+</sup>	mg L <sup>-1</sup>	0.24	0.29
Ca <sup>2+</sup>	mg L <sup>-1</sup>	2.12	1.26
Mg <sup>2+</sup>	mg L <sup>-1</sup>	1.24	0.77
SO <sub>4</sub> <sup>2-</sup>	mg L <sup>-1</sup>	1.74	1.33
Cl <sup>-</sup>	mg L <sup>-1</sup>	5.3	5.1
NO <sub>3</sub> -N	µg L <sup>-1</sup>	<5	11
NO <sub>2</sub> -N	µg L <sup>-1</sup>	0.6	0.2
NH <sub>4</sub> -N	µg L <sup>-1</sup>	6	<5
PN	µg L <sup>-1</sup>	20	50
DP	µg L <sup>-1</sup>	7.8	20.2
PP	µg L <sup>-1</sup>	4.6	5.9
SRP	µg L <sup>-1</sup>	4.0	11.6
DOC	mg L <sup>-1</sup>	1.25	1.13
PC	mg L <sup>-1</sup>	0.13	0.41
Si	mg L <sup>-1</sup>	1.45	0.87
chl <i>a</i>	µg L <sup>-1</sup>	0.9	ND

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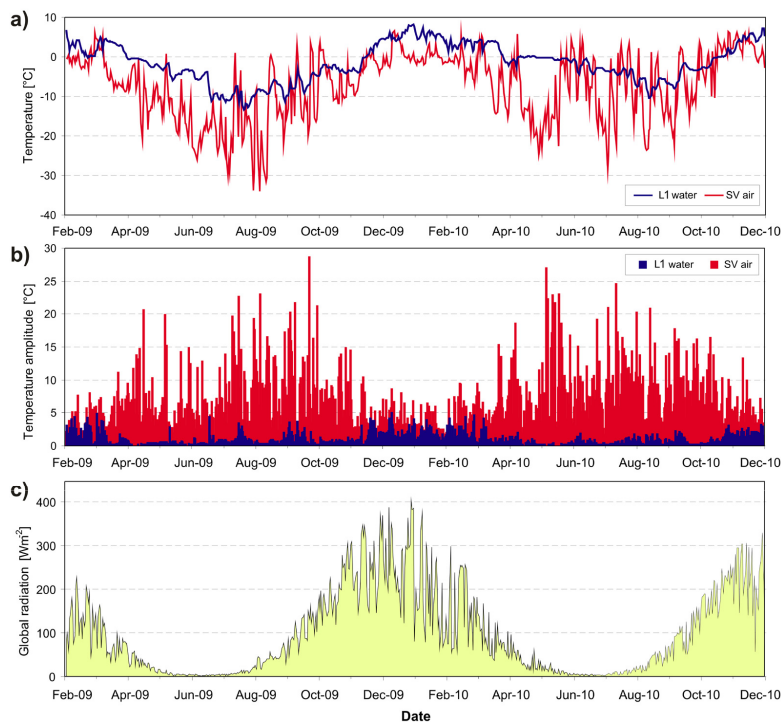
**Figure 1.** Location of lake 1 and 2 and air temperature measurements (ASW) in the Solorina Valley.

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**Figure 2.** Bathymetric parameters of lake 1 (a) and 2 (b) together with marked lines of water level and maximum extent of the photosynthetic microbial mat littoral belt in lake 1.

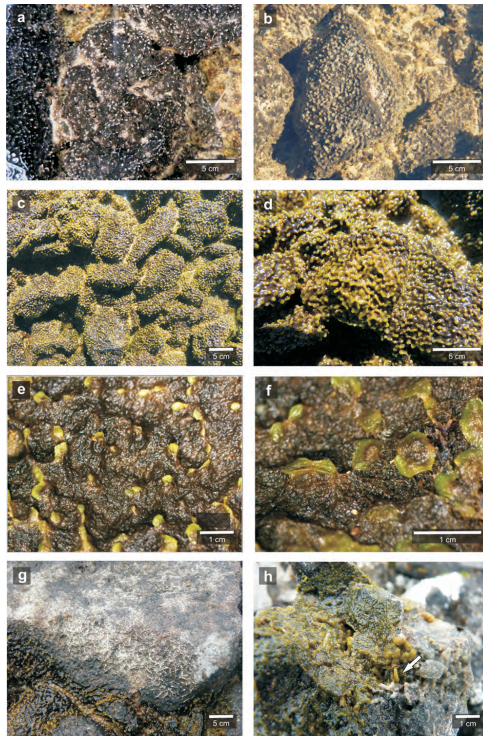
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**Figure 3.** (a) Annual variation of daily mean water temperature in lake 1 (L1water) and annual variation of daily mean air temperature 2 m above ground in the Solorina Valley (SV air), (b) Diurnal temperature amplitudes in lake 1 (L1 water) and diurnal air temperature amplitudes in the Solorina Valley (SV air), respectively. (c) Daily mean global radiation at Mendel Station. All parameters measured from February 2009 to November 2010.

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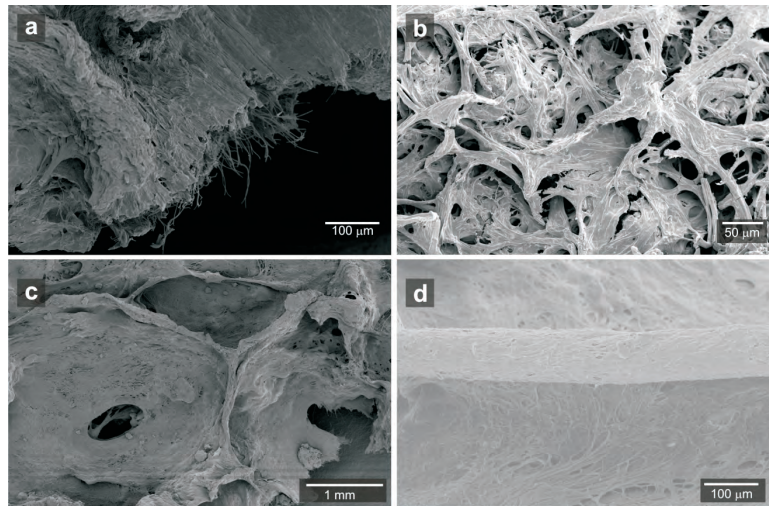




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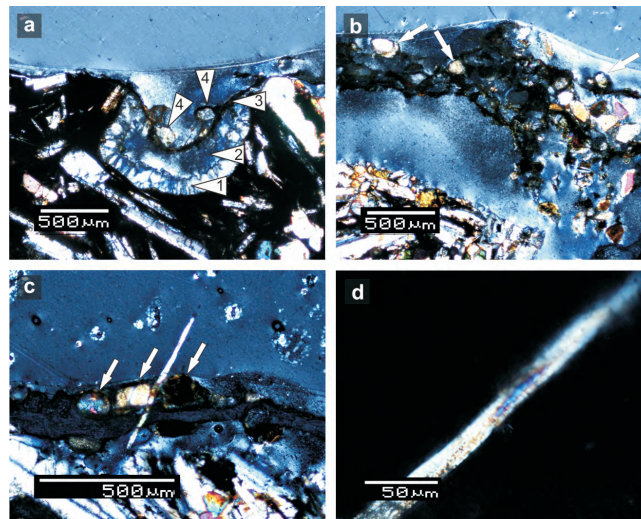
**Figure 6.** Photoautotrophic mats in lakes 1 and 2. **(a)** Rapid development of the mat in January 2009 (lake 1). The two photos show the mat at a one week interval, note the growth of gelatinous clusters of densely agglomerated filaments of the green alga *Hazenia broadyi*, **(c, d)** fully developed mats with mosaic-like structures on the surfaces of stones in the littoral zone of lake 2, **(e, f)** detail, **(g)** drying of the mat in the littoral zone leaves a characteristic structure on the surface of stones, **(h)** calcium carbonate spicule in situ (arrowed).

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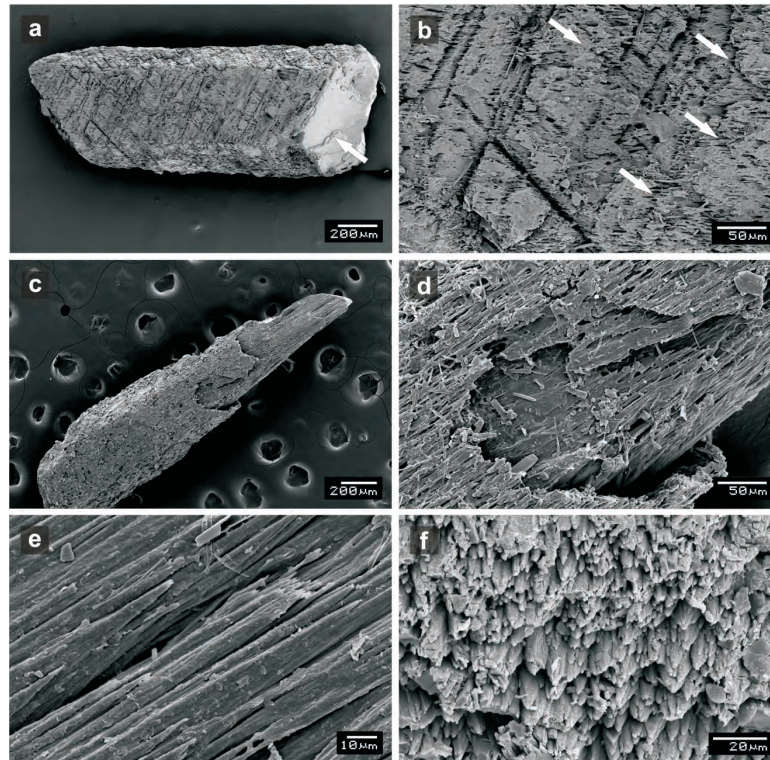
**Figure 7.** SEM macrographs showing the structure of the dried mat in the lakes. **(a)** Transversal section of the mat with visible cyanobacterial filaments, **(b)** surface structure of the mat, **(c)** general view of the surface structure of the mat with the net formed by mucilage (compare with Fig. 7d), **(d)** detail of the same mucilaginous structure.

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**Figure 8.** Perpendicular thin sections of rock substrate overgrown by biofilms. Note that biofilms are partly detached from the surface of the rock due to complete drying of the sample. **(a)** Conspicuous U-shaped empty void (arrowed "2") near the surface of basaltic rock partly infilled with crystals of feldspathoids (tectosilicate minerals, arrowed "1"); empty void is bridged by biofilm (arrowed "3") with partly incorporated mineral clasts, represented by semi-rounded quartz grains (arrowed "4"), **(b)** rather thick biofilm with numerous incorporated mineral grains. Note that close to the rock substrate the angular grains of plagioclase (feldspar group) and augite (pyroxene group) dominate, being derived from basaltoids, whereas close to the surface rounded grains of quartz occur (arrowed), **(c)** in situ calcium carbonate spicule penetrating biofilm and surrounded by incorporated grains of feldspars (two arrows on the left) and pyroxene (arrow on the right), **(d)** close up of the same calcium carbonate spicule with a cyanobacterial filament in its centre.

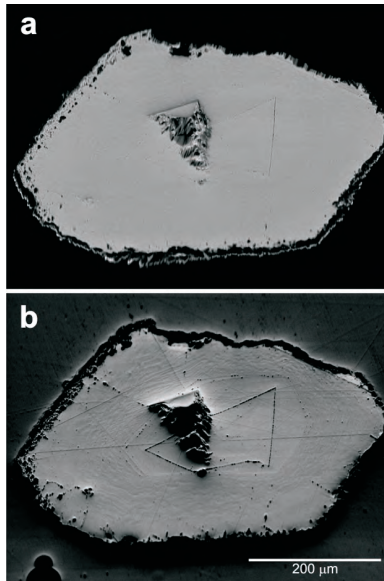
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**Figure 9.** SEM macrographs showing the morphology of partly recrystallized calcium carbonate spicules. Spicules were washed away from the living tissue and collected directly from the surface of biofilms, although residence time on the bottom cannot be determined. **(a)** Calcareous spicule showing intensively worn surface and complete recrystallization of the spicule interior. The spicule shows crystal facets on the surface and cleavage (crystallographic structural planes) in the interior (arrowed) – i.e. typical characteristics of calcium carbonate monocrystal, **(b)** detail of previous image; two parallel systems of deep furrows on the surface are crystallographic structural planes of calcite monocrystal; remnants of a superficial layer of microcrystalline calcite are, however, preserved in places on the surface of the crystal (arrowed), **(c–f)** poorly recrystallized spicule, formed mainly by microcrystalline calcite, **(c)** lateral view of the spicule, **(d)** detail of the surface showing corrosion of needle-like calcite microcrystals with distinct layering, **(e)** parallel needle-like calcite microcrystals on the surface of the central part of the spicule, **(f)** tops of parallel needle-like calcite microcrystals on the surface of the terminal part of the spicule; the view is perpendicular with respect to the previous macrograph.

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**Figure 10.** FSD image of a transversely sectioned, partly recrystallized calcite spicule acquired in **(a)** chemical contrast, **(b)** orientation contrast.