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ORIGINAL PAPER

Jacek Wierzchos · Carmen Ascaso

Life, decay and fossilisation of endolithic microorganisms from the Ross Desert, Antarctica

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Abstract The adaptation and survival of the endolithic microorganisms that colonise the near-surface layer of porous sandstone rock in the Ross Desert (Antarctica) depend upon a precarious equilibrium of biological, geological and climatic factors. Any unfavourable change in external conditions can result in the death and disappearance of microscopic organisms, and this may be followed by trace microfossil formation. The sequence of events leading to the extinction of life in the Antarctic desert is considered to be a terrestrial analogue of the disappearance of possible life on early Mars. The present paper reviews the current state of knowledge on the endolithic microorganisms of the Ross Desert with particular reference to their decay and fossilisation processes. Ideas for in situ further research on this microbial ecosystem are also proposed, including several new microscopy techniques such as CLSM, LTSEM, SEM-BSE and EDS. Preliminary images are presented and it is proposed that, for the first time, such techniques will permit the in situ study of the ecology of Antarctic lithobiontic microorganisms and the identification and characterisation of fossilised traces of past life.

Introduction

Most of the surface of continental Antarctica is covered with ice. However, in southern Victoria Land there is a region denominated the Ross Desert (76.5–78.5°S, 160–164°E) that includes a large snow and ice-free area. This area, of some 4,800 km^2, is much drier and colder than the remaining regions of Antarctica, and is considered one of the most extreme deserts in the world. The climatic conditions of the Ross Desert are characterised by a mean annual temperature of –20°C and infrequent snowfall. The landscape mainly features mountain ridges formed by sedimentary deposits (sandstone), which overlie metamorphic granitic and doleritic rocks. In the Ross Desert, the life forms on rock surfaces, such as lichen and/or mosses, are scarce. This is a consequence of the extremely dry and cold climatic conditions. However, in the interior of some types of rocks such as Beacon sandstone (orthoquartzite), a narrow biotic band may be observed below the rock surface. Friedmann and Ocampo (1976) were the first to note the predominance of *Gloeocapsa* cyanobacteria within these sandstone rocks. This direct demonstration of the presence of indigenous microflora within the Antarctic desert rock is a landmark in extreme environment microbial ecology.

The aim of the present paper was to review present knowledge on the endolithic microorganisms of the Antarctic cold desert, their survival mechanisms, death processes and telltale signs of past life. Special attention was paid to potential further studies of this peculiar ecosystem, including the application of new in situ microscopy methods. This type of research effort may have important implications for astrobiological research.

The endolithic microorganisms of the Ross Desert

Cyanobacteria (*Gloeocapsa* red, *Hormathonema-Gloeocapsa* and *Chroococcidiopsis*) are the predominant microorganisms of the cryptoendolithic communities found within the sandstone rocks of the Ross Desert (Friedmann and Ocampo 1976; Friedmann et al. 1988). These prokaryotic microorganisms are able to grow in culture, although it is highly probable that other prokaryotic and/or eucariotic microorganisms, unable to grow in laboratory conditions, inhabit the rocks. Indeed, organisms such as cryptoendolithic protolichens containing algae and/or cyanobacteria have also been found

J. Wierzchos (✉)
Servei de Microscopia Electronica, Universitat de Lleida,
c/Rovira Roure, 44, 25198 Lleida, Spain
E-mail: jacekw@suic-me.udl.es

C. Ascaso
Centro de Ciencias Medioambientales, CSIC, c/Serrano,
115 bis, 28006 Madrid, Spain

in the interior of cold desert rocks (Friedmann et al. 1988). It has been shown that the adaptive mechanism of these cryptoendolithic protolichens is not physiological but rather morphological (Friedmann et al. 1981) and involves changes in growth patterns such that they are able to the penetrate the small pores within the sandstone. In this manner, cryptoendoliths find refuge within this protected microhabitat. These protolichens show a different internal organisation with respect to the usual epilithic thalloid lichens occurring in maritime Antarctica (Friedmann et al. 1988). Their mycobiontic hyphae show lax growth inside the rock pores. A lack of coherent plectenchyma has also been observed. This organisation showing parallel horizontal bands may be functionally compared to the layers observed in common thalloid lichen (Friedmann et al. 1981). Though scarce in quantity, the occasional presence of liquid water in this ecological system is the primary condition for the existence of life in Antarctica (Kennedy 1993). Friedmann (1980) reported that the water content of sandstone colonised by endolithic microorganisms in dry valleys is about 0.1–0.2% of the weight of the rocks. It would appear that this small quantity of water is sufficient to provide a water vapour-saturated atmosphere within the microscopic pore system of the cold desert rocks. This low moisture content of the rocks seems to affect the pH, the formation of primary iron stains and the distribution of the microbial communities.

Life decay mechanisms in the Ross Desert

As in all polar regions, the Ross Desert ecosystem is extremely sensitive to small climatic changes. Further, a slight change in temperature can substantially affect the delicate hydrological balance. The particular landscape topography would also be expected to affect the biodiversity, biological activity and biogeochemical processes of the microorganisms of the present dry valley ecosystems. The cryptoendolithic habitat is a highly unstable system, affected by continuous freezing-thawing and hydration-dehydration processes. In this unstable and harsh environment, the metabolic cost of survival is high. If climatic conditions deteriorate even slightly, the organisms are no longer able to cope and they die (Friedmann and Weed 1987). In some parts of the Ross Desert (Mount Fleming-Horseshoe Mountain), the microbial communities inside the frozen rocks are dead and the presence of mummified cells has been observed. By means of transmission electron microscopy, Friedmann and Koriem (1989) described the damage incurred by some endolithic cells from the Ross Desert leading to their death. If this process continues, it is possible that all organic matter will eventually disappear, leaving behind the remains of cells in the form of mineralised trace fossils. Given the peculiar characteristics of the ecology of Antarctic cryptoendoliths and their possible decay mechanisms, this ecosystem is proposed as a good terrestrial model for the last stages of possible life in the history of Mars, when the surface cooled down, and the atmosphere and water disappeared (McKay et al. 1992; McKay 1993).

Microorganism fossils

Current knowledge on fossils of microorganisms or traces of microbiological activity once present within terrestrial rocks is extremely scarce. Most Precambrian microfossils described are considered ''supposed cyanobacteria'' (Awramik et al. 1983; Schopf and Parcker 1987; Schopf 1993). Very few investigations have focussed on traces of past microbial activity within Antarctic rocks. To date, only two biomarkers of the past activity of cryptoendoliths have been described: one consists of the geophysical bioweathering of rock surfaces forming characteristic exfoliation mosaic patterns (Kappen 1993; Sun and Friedmann 1999), and the other corresponds to geochemical bioweathering patterns resulting from iron leaching, observed in the surface layers of sandstone rocks (Friedmann and Weed 1987). It is clear that much further work in the field of detection of traces of past life is required.

Microscopy techniques available for the study of Antarctic endoliths and their possible microfossils

The study of microorganisms colonising the inside of lithic materials has been confronted with enormous difficulties. These ecological niches first need to be characterised in detail in terms of mineralogical and biological features in order to understand the dynamic relationships occurring between them. According to Brock (1987), the chemical characterisation of the microenvironment surrounding the endoliths is of great relevance and requires the use of electron microscopy techniques. In contrast, several indirect techniques (e.g. molecular biology) have been widely applied to describe the lithobiontic biofilm (Rölleke et al. 1996). One would think that such procedures could be useful for the study of endolithic Antarctic microorganisms. However, along with plate and/or mixed culture techniques, molecular approaches will not serve to explain the morphological and structural characteristics of the biological components of the endolithic microhabitat. Moreover, they could not support any mineralogical and/or geophysicochemical characterisation of the endolith surrounding minerals. For this reason, we believe that the study of the lithobiontic ecosystem generally requires the application of electron microscopy and microanalytical techniques. These techniques should be accompanied by the necessary and complementary isolation and culture techniques. However, it should be noted that it has not been possible to successfully culture most Antarctic endoliths.

Given the high complexity of cold desert ecosystems, and considering that microbial ecology involves the

study of the relationships of microorganisms within their natural environment, Brock (1987) stated that these studies must be performed in situ in the natural lithobiontic microhabitats.

The advent of new microscopy techniques of different characteristics and resolution levels combined with microanalytical facilities should represent a fundamental advance in the study of the relationship between lithobiontic microorganisms and their mineralogical environment.

Materials and methods

Confocal laser scanning microscopy

Confocal laser scanning microscopy (CLSM) offers a novel opportunity for the in situ and in vivo study of the geomicrobiological system (Rautureau et al. 1993). Several researches have successfully analysed the structure of live microbial biofilms (Wolfaardt et al. 1994), live lichen thalli (Ascaso et al. 1998), as well as Antarctic lake-ice microorganisms (Priscu et al. 1998). Here, we present a novel application of CLSM aimed at characterising cryptoendolithic lichens colonising the interior of sandstone rocks from the Tyrol Valley (77.58°S, 160.63°E) (Fig. 1). Our method is based on the phenomenon of glutaraldehyde-induced autofluorescence of plant tissues (Prior et al. 1999). Small fragments of sandstone rock with subsurface layers containing cryptoendolithic protolichens were collected under natural conditions and stored hermetically at –20°C. These specimens were fixed directly in glutaraldehyde (2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer, pH 7.4 for 3 h at 4°C). After washing in buffer, and dehydration in a graded ethanol series, the samples were embedded in LR White resin. Once polymerised (48 h), the blocks were cut transversally using a diamond saw, fine polished and examined under a Zeiss CLSM, model LSM310. Endoliths are visualised through enhanced autofluorescence (chlorophyll, cellulose, chitin, etc.) of the microorganism cells. An argon laser is used to generate an excitation wavelength of 488 nm and the resultant emission is filtered through a long pass filter >515 nm. The translucency of the quartz grain permits the three-dimensional (3D) reconstruction of the endolithic colonies and gives an idea of the protolichen's organisation. To obtain information on the spatial arrangement of the cryptoendolithic microorganisms, stacks of 20–30 single confocal section [vertical (z) resolution about 0.6 μm] images are prepared at 0.5- to 1-μm increments through the sample and digitally stored. The 3D-reconstruction procedure serves to visualise the cryptoendolithic protolichen morphology (Fig. 1a). As reported elsewhere for these lichens, the mycobiont hyphae show lax growth. Associated algae are arranged in clusters of several cells. Figure 1b also shows the 3D-reconstructed structure of a red *Gloeocapsa* community living within the sandstone rock of Battleship Promontory (76.92°S, 160.92°E).

Results and discussion

This brief review of the use of CLSM to visualise endoliths suggests its suitability for in situ microbial ecology studies involving difficult habitats. Community structures may also be examined using "live-dead" microbial stains and fluorescent probes. Moreover, data concerning the spatial distribution of the microorganism cells may also give some idea of the number of microorganisms occupying a particular pore volume.

Low-temperature scanning electron microscopy

The traditionally used method of scanning electron microscopy (SEM) in secondary electron (SE) detection mode gives rise to topographical images of the rock interior but only serves to provide an external morphological description of the endolithic cells. The use of low-temperature scanning electron microscopy (LTSEM) offers several advantages over SEM-SE for the in situ study of endoliths in rock samples from the Ross Desert. Over the past few years, LTSEM has proved valuable for the evaluation of structural changes occurring in epilithic lichen thalli of different water contents (Honegger and Peter 1994; Scheidegger 1994; De los Rios et al. 1999). LTSEM techniques permit the preservation of whole specimens in a close-to-natural state since samples are ultra-rapidly cryofixed, causing the quick and complete immobilisation of cells in their original state. Its application to in situ studies of Antarctic endoliths could centre on the examination of topographical images corresponding to deep-frozen randomly fractured planes, including the microorgan-

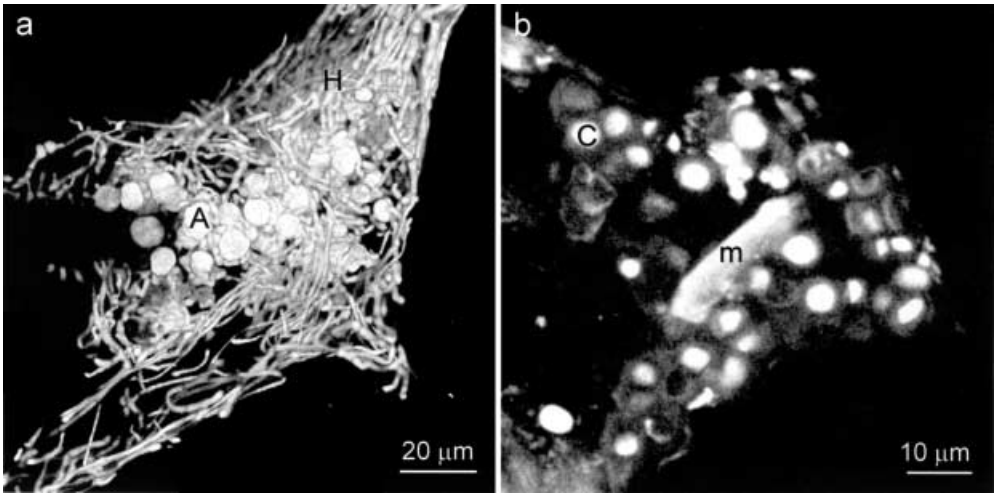

Fig. 1a–b Confocal laser scanning microscopy (CLSM) images of cryptoendoliths colonising Antarctic sandstone rocks. **a** 3D reconstruction of cryptoendolithic protolichen occupying a deep pore space between quartz grains (Tyrol Valley); photobiont cells (*A*), mycobiont cells (*H*). **b** 3D reconstruction of red *Gloeocapsa* cyanobacteria living within sandstone rock (Battleship Promontory); cyanobacteria cells (*c*), mineral particle (*m*)

ism-rock contact zone. Some of the cryofixed endolithic cells may also be randomly cut to reveal ultrastructural elements. Moreover, LTSEM may serve to determine the hydration stage and/or presence of water (ice) in the biological and inorganic components of Antarctic rocks. To our knowledge, no biogeochemical investigation on the use of LTSEM in the study of Antarctic ecosystems has been published to date. In our study, small fragments of sandstone rock were collected and hermetically stored at –20°C. These samples were cryofixed in liquid nitrogen (–196°C) before freeze fracturing and directly observed by LTSEM (De los Rios et al. 1999). Figure 2 is an example of the possible application of an LTSEM in the in situ study of Antarctic endoliths living within sandstone rock from Battleship Promontory. This image shows the freeze fracture line passing through hyphae cells. Note that several mycobiont cells show mitochondria (white arrows) and concentric bodies (black arrow).

The major attraction of the LTSEM technique is the possibility of cytologically identifying the microorganism types in their original microenvironment under low-temperature conditions. The high resolving power of this technique may also permit visualisation of endolithic bacteria (data not shown) and micromorphological changes in the ultrastructural elements of cryptoendoliths in laboratory-simulated conditions (humidity and temperature).

Scanning electron microscopy with back-scattered electron imaging combined with microanalytical procedures

One of the best complementary tools for the in situ characterisation of an organo-mineral interface is indisputably the use of SEM with back-scattered electron (BSE) detection plus an auxiliary X-ray energy dispersive spectroscopy (EDS) microanalytical system. Wierzchos and Ascaso (1994) reported the first successful application of this pioneering method aimed at obtaining sufficient resolution to permit the observation of ultrastructural features of cells of epilithic and endolithic microorganisms without the need to remove them from their natural microhabitat. The SEM-BSE method consists of two steps. The first corresponds to the sample preparation procedure, and combines the glutaraldehyde fixation and osmium tetraoxide and/or uranyl acetate staining techniques with the preparation of finely polished blocks containing resin-embedded rock samples (Wierzchos and Ascaso 1994). In this study, fragments of sandstone rock were collected under natural conditions and hermetically stored at –20°C before chemical fixation. The second step involves visualisation of the carbon-coated biological-mineralogical transverse section using the BSE detector. The BSE signal is strongly dependent on the mean atomic number of the target. Thus, the SEM-BSE technique not only permits the visualisation of samples with different inorganic features but also permits the identification of heavy metal-stained ultrastructure elements in the biological material. This in situ observation method has permitted us to obtain morphological, and most significantly, ultrastructural information on lithobiontic microorganisms (Ascaso and Wierzchos 1994; Ascaso et al. 1995, 1998). The SEM-BSE technique has also been used for the examination of the biophysical action of the lichen thallus (Ascaso and Wierzchos 1994, 1995). It is possible to perform an examination from low to very high magnification (up to ×50,000), thus permitting continuous visualisation of all the levels of the information. The energy dispersive X-ray spectroscopy facility coupled to the SEM-BSE permits the chemical characterisation (elementary qualitative and quantitative, and elemental spatial distribution images) of mineral features (Wierzchos and Ascaso 1996, 1998).

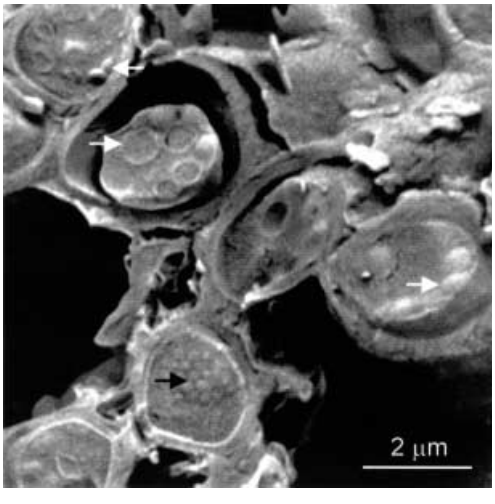

Fig. 2 Low temperature scanning electron microscopy (LTSEM) image of freeze-fractured transverse section of cryptoendolithic hyphae cells living within in sandstone rock from Battleship Promontory; *white arrows* indicate mitochondria and *black arrow* indicates concentric bodies

We present a few examples of the potential use of SEM-BSE and EDS techniques for the in situ study of live Antarctic cryptoendolithic microorganisms and also for the visualisation of real microfossils. The SEM-BSE image in Fig. 3a shows a transverse section of sandstone (Tyrol Valley) with cryptoendolithic Antarctic protolichen cells (algae and fungi) occupying a pore space among grains of quartz. Most of the algal cells appear to be alive and show well-preserved interior structures. Figure 3b shows the ultrastructural elements of one photobiont cell. Note that almost all the cytoplasm organelles in this cell could be identified, including chloroplast tylakoids, lipid globules, vacuoles and pyroglobuli (100 nm diameter), within the central pyrenoid zone indicating that this alga is of the trebuxoid type. Taking into account the high resolving power of the SEM-BSE technique, the visualisation of the endolithic bacteria colonies could also be possible (data not shown). The next SEM-BSE image (Fig. 3c) shows the pore space occupied by remnants of dead microorgan-

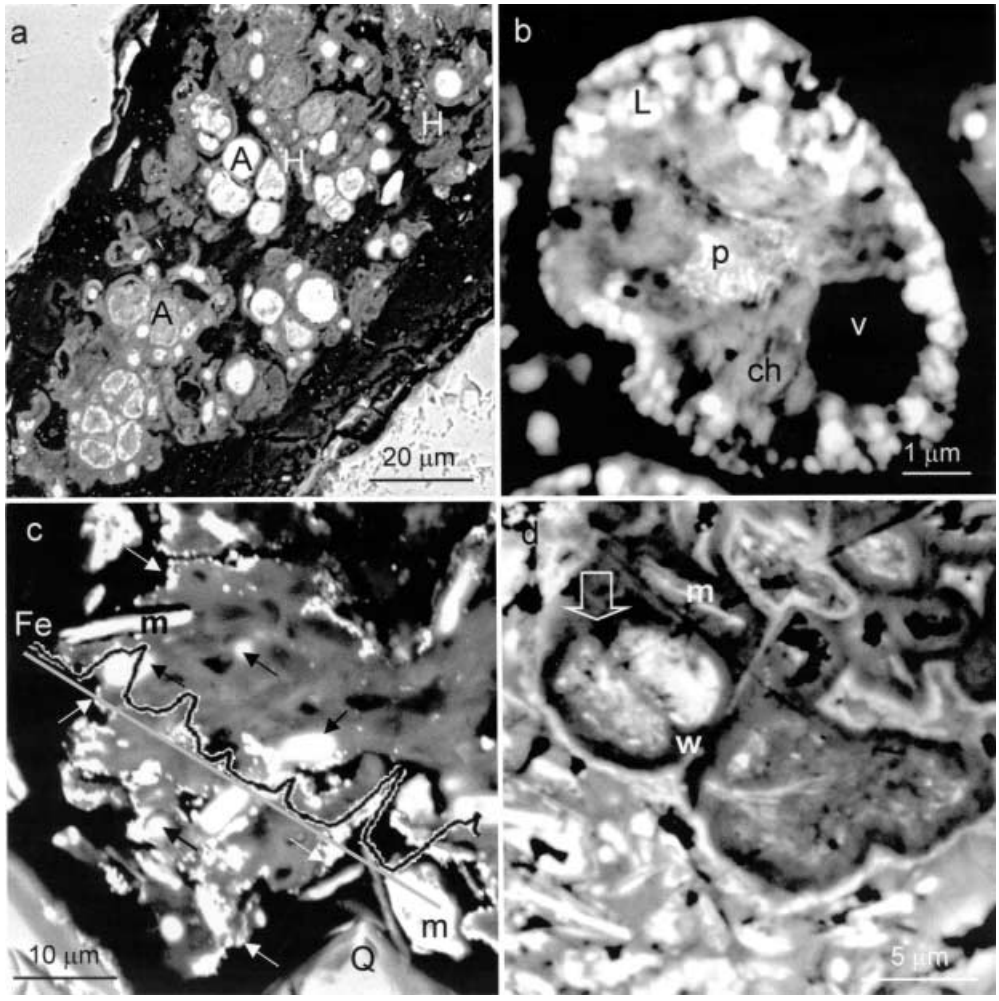

Fig. 3a–d Scanning electron microscopy-backscattered electron (SEM-BSE) images of Antarctic sandstone pore contents. **a** Photobiont (*A*) and mycobiont (*H*) cells forming cryptoendolithic lichen occupying a pore space within sandstone from the Tyrol Valley. **b** High-resolution SEM-BSE micrograph of a cryptoendolithic photobiont (Trebuxoid type) cell from Tyrol Valley sandstone; chloroplast tylakoids (*ch*), lipid bodies (*L*), pyrenoid (*p*), vacuole (*v*). **c** SEM-BSE image of a pore space (Linnaeus Terrace sandstone) occupied by the remnants of dead microorganisms (*black arrows*); quartz grain (*Q*), micaceous mineral (*m*), *white arrows* indicate Fe-rich deposits. The EDS scan-line profile (*black line over grey line*) shows relative iron concentration changes. **d** SEM-BSE micrograph of fossilised microorganism cells (Mt. Fleming sandstone); *white arrow* indicates the cell division process, cell walls (*w*), micaceous mineral (*m*)

isms colonising the sandstone of Linnaeus Terrace (77.60°S, 161.08°E). The fixing and staining compounds are not well absorbed, indicating only mummified remains of microorganisms (black arrows). The bright rim that surrounds the cell debris indicates a high iron concentration, confirmed by EDS scan-line analysis. This is indicated in the figure as a relative iron concentration diagram corresponding to the area outlined in grey. This biomobilised precipitation of iron compounds may be interpreted as trace fossils which preserve the characteristic iron leaching pattern caused by microbial activity. In some zones of the Antarctic desert, the climatic conditions have become too severe for the survival of cryptoendoliths. If extensive biomobilisation of elements occurs during or after the microorganism decay process, the possibility of microorganism fossil formation elsewhere may not be excluded. This is the case of the sandstone rock of Mt. Fleming (77.55°S, 160.10°E). The image in Fig. 3d shows fossilised microorganism cells. Structures resembling bars and/or dots may be observed in some of the cells. Micaceous microdivided minerals provide a source of potassium for the cell mineralisation process leading to fossilisation. The cells appear to accumulate minerals, which serve to maintain their exterior and interior cellular structure even when the organic compounds have disappeared. Note that in Fig. 3d, a cell division process (arrow) was observed. A fossilised cell seems to be embedded within the matrix of a calcium-rich material as determined by EDS. In images of microorganism fossils presented, cell walls appear to be much better preserved than the internal structures. It has been reported that most Precambrian fossilised cell constituents are unstable and that structures such as walls and sheaths are the most stable (Bartley 1996). We consider that the Antarctic cryptoendoliths fossilisation process is a clear example of the extensive biomobilisation of several elements and their subsequent precipitation inside and out of the microorganism cell. In some cases, these deposits occur within the cells and may reflect the particular cell ultrastructure permitting their classification as a microorganism fossil. Using these SEM-BSE and EDS techniques, Ascaso (2000) was able to demonstrate the presence of fossilised endolithic algae cells in Antarctic sandstone. These cells partially maintain their cytological organisation, with characteristic relicts of tylakoids and lipid bodies.

There is an obvious need for extensive further work on cryptoendoliths' fossilisation processes and the for-

mation of inorganic structures or the remains of live microorganism cells. In our opinion, the in situ examination of the interior of Antarctic rocks using SEM-BSE combined with microanalytical EDS techniques might represent the best option to improve present knowledge on these traces of past life. It is foreseen that this type of work may have implications for future astrobiological investigations performed on geological material obtained from Mars.

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References

Ascaso C (2000) Lichens on rock substrates: observation of the biomineralization processes. In: Schroeter B, Schlensog M, Green TGA (eds) New aspects in cryptogamic research. Contribution in Honour of Ludger Kappen. J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, pp 127–135

Ascaso C, Wierzchos J (1994) Structural aspects of the lichen-rock interface using back-scattered electron imaging. Bot Acta 107:251–256

Ascaso C, Wierzchos J (1995) Study of the biodeterioration zone between the lichen thallus and the substrate. Crypt Bot 5:270–281

Ascaso C, Wierzchos J, De los Rios A (1995) Cytological investigations of lithobiontic microorganisms in granitic rocks. Bot Acta 108:474–481

Ascaso C, Wierzchos J, De los Rios A (1998) In situ investigations of lichens invading rock at cellular and enzymatic level. Symbiosis 24:221–234

Awramik SM, Schopf JW, Walter MR (1983) Filamentous fossil bacteria from the Archean of Western Australia. Precambrian Res 20:357–374

Bartley JK (1996) Actualistic taphonomy of cyanobacteria: implications for the Precambrian fossil. Rec Palaios 11:571–586

Brock TD (1987) The study of the microorganisms *in situ*: progress and problems. In: Fletcher M, Gray TRG, Jones JG (eds) Ecology of microbial communities. Society for General Microbiology, Cambridge, pp 1–17

De los Rios A, Ascaso C, Wierzchos J (1999) Study of lichens with different state of hydration by the combination of low temperature scanning electron and confocal laser scanning microscopies. Int Microbiol 2:251–257

Friedmann EI (1980) Endolithic microbial life in hot and cold deserts. Origins Life Evol B 10:223–235

Friedmann EI, Koriem AM (1989) Life on Mars: how it disappeared (if it was ever there). Adv Space Res 9:167–172

Friedmann EI, Ocampo R (1976) Endolithic blue-green algae in the Dry Valleys: primary producers in the Antarctic desert ecosystem. Science 193:1247–1249

Friedmann EI, Weed R (1987) Microbial trace-fossil formation, biogenous and abiotic weathering in the Antarctic cold desert. Science 236:645–752

Friedmann EI, Friedmann RO, McKay Ch P (1981) Adaptations of cryptoendolithic lichens in the Antarctic desert. Colloque sur les Écosystèms Subantarctiques. Paimpont, no. 51. CNFRA, Paris, pp 65–70

Friedmann EI, Hua M, Ocampo-Friedmann R (1988) Cryptoendolithic lichen and cyanobacterial communities of the Ross Desert Antarctica. Polarforschung 58:251–259

Honegger R, Peter M (1994) Routes of solute translocation and the location of water in heteromerous lichens visualised with cryotechniques in light and electron microscopy. Symbiosis 16:167–186

Kappen L (1993) Lichens in the Antarctic region. In: Friedmann EI (ed) Antarctic microbiology. Wiley, New York, pp 433–490

Kennedy AD (1993) Water as limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis. Arct Alp Res 25:308–315

McKay CP (1993) Relevance of Antarctic microbial ecosystems to exobiology. In: Friedmann EI (ed) Antarctic microbiology. Wiley, New York, pp 593–601

McKay CP, Friedman EI, Warton RA, Davies WL (1992) History of water on Mars: a biological perspective. Adv Space Res 12:231–238

Prior DA, Oparka KJ, Roberts IM (1999) En block optical sectioning of resin-embedded specimens using a confocal laser scanning microscope. J Microsc Oxford 193:20–27

Priscu JC, Fritsem CH, Adams EE, Glovannoni SJ, Paerl HW, McKay Ch P, Doran PT, Gordon DA, Lanoil BD, Pinckney JL (1998) Perennial Antarctic lake ice: an oasis for life in polar desert. Science 280:2095–2098

Rautureau M, Cooke RU, Boyde A (1993) The application of confocal microscopy to the study of stone weathering. Earth Surface Proc Landforms 18:769–775

Rölleke S, Muyzer G, Wawer C, Wanner G, Lubitz W (1996) Identification of bacteria in a biodegraded wall painting by denaturing gradient gel electrophoresis of PCR-amplified gene fragments coding for 16S rRNA. Appl Environ Microbiol 62:2059–2065

Scheidegger C (1994) Low-temperature scanning electron microscopy: the localisation of free and perturbed water and its role in the morphology of the lichen symbionts. Crypt Bot 4:290–299

Schopf JW (1993) Microfossils of the early Archean Apex chert: new evidence of the antiquity of life. Science 260:640–646

Schopf JW, Parcker BM (1987) Early Archean microfossils (2.2 billion to 3.5 billion-year-old) from Warrawoona Group, Australia. Science 237:70–73

Sun HJ, Friedmann EI (1999) Growth on geological time scales in the Antarctic cryptoendolithic microbial community. Geomicrobiol J 16:193–202

Wierzchos J, Ascaso C (1994) Application of back-scattered electron imaging to the study of the lichen-rock interface. J Microsc Oxford 175:54–59

Wierzchos J, Ascaso C (1996) Morphological and chemical features of bioweathered granitic biotite induced by lichen activity. Clays and Clay Miner 44:652–657

Wierzchos J, Ascaso C (1998) Mineralogical transformation of bioweathered granitic biotite, studied by HRTEM: evidence for a new pathway in lichen activity. Clays and Clay Miner 46:446–452

Wolfaardt GM, Lawrence JR, Robarts RD, Caldwell SJ, Caldwell DE (1994) Multicellular organisation in a degradative biofilm community. Appl Environ Microbiol 60:434–446