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High resolution characterization of stromatolitic iron oxidizing microbial mats from a subterranean deep biosphere

Barbara Zippel (1), Christine Heim (2), Danny Ionescu (3), Thomas R. Neu (1), Dirk de Beer (3), Joachim Reitner (2), and Volker Thiel (2)

(1) Helmholtz Centre for Environmental Research - UFZ, Department of River Ecology, Magdeburg, Germany (barbara.zippel@ufz.de, +49 341 235 459 452), (2) University of Göttingen, Geoscience Centre, Göttingen, Germany , (3) Max Planck Institute for Marine Microbiology, Bremen, Germany

Stromatolitic iron oxidizing microbial mats form on many rock surfaces in the Äspö Hard Rock Laboratory (Southern Sweden). Most intense growth of these mineralizing mats is observed at depths more than 150m below the surface, wherever groundwater drops from the tunnel ceiling. The microbial consortia harbour highly diverse chemolithotrophic microbial communities consisting mainly of iron oxidizing bacteria (*Mariprofundus sp.*, *Gallionella ferruginea)*, ammonia and nitrite oxidizing bacteria (*Candidatus Nitrotoga*, *Nitrosomonas europaea*, *Nitrospira moscoviensis)*, magnetotactic bacteria (*Magnetospirillum magneticum),* and crenarchaeota. Cross-sections of mineralized microbial mats showed a distinctive stromatolitic character, consisting of laminae with internal dendritic structures. These textures strikingly resemble the enigmatic *Frutexites* structures reported from particular Paleozoic carbonate rocks. The mineralized portions of these mats consist of iron hydroxides, iron oxides, and, less abundant, manganese oxides. Small amounts of siderite, calcite, and siliceous material occur along with iron and manganese oxides.

A key role in the biomineralization process of chemolithotrophic microorganisms is assigned to negatively charged organic surfaces like cell surfaces and extracellular polymeric substances (EPS). These reactive interfaces act as "mineralizing templates" via cation binding, complex formation and thus mineral nucleation (Konhauser, 2007; Westall, 2008).

Structural characterization and localization of microbial cells and associated EPS structures within the mineralized mats were achieved by reflected light microscopy and confocal Laser Scanning Microscopy (LSM). LSM provides simultaneous information about the 3-dimensional structure of living, fully hydrated and complex environmental communities. Distribution of microorganisms in the mats was examined using nucleic acid specific fluorochromes (Syto64; Sybr Green) and protein-specific fluorochromes (Sypro-Red, Sypro-Orange). In addition, fluorescence lectin-binding analysis was employed for the characterization of EPS glycoconjugates. To study the vertical distribution of cellular and polymeric constituents within the mats, fresh samples were embedded in special cryomedium (SCEM) and cryosectioned using cryofilm (Finetec). Subsequently, microbial mat sections where stained with nucleic acid and protein-specific fluorochromes as well as selected lectins.

A variety of morphologically distinct bacterial structures was localized within the mats, including cocci-, rod-shaped and filamentous bacteria. In cases, especially single cells were surrounded by a layer stained by protein-specific fluorochromes. Fluorescence lectin-binding analysis resulted in binding of 13 out of 35 lectins tested. They preferentially bound to (i) diffuse ("cloud-like") and (ii) cell-associated EPS glycoconjugates. Diffuse EPS glycoconjugates were visualized by amino sugar – specific lectins only (TL, UDA, PSA, and WFA). They showed a rather homogeneous distribution within the upper 500 μm of the mineralized mats. Cell-associated EPS glycoconjugates were visualized by amino sugar – specific lectins and also reacted with lectins specific for fucose, lactose and galactose residues. This second type of EPS glycoconjugates was found preferentially in deeper parts of the mats and frequently formed large aggregates with bacterial cells inside.

Noticeably, a mineralized thin layer characterized by very dense reflection signals was localized approximately 20 μm below the crust surface. In some cases, a "street"-like colonization by microbes was observed within this thin subsurface layer, whose origin and function is as yet unclear.

The combination of laser scanning microscopy with differential fluorescence staining and lectin-binding using adequate preparation protocols represents a useful tool providing deeper insight into the internal architecture of mineralizing biofilms and their component organic matrices and mineralization templates. Such knowledge will be essential for the interpretation of related morphological and chemical signatures of microbial life in ancient sedimentary rocks. This project is part of the Research Unit 571 "Geobiology of Organo- and Biofilms", funded by the German Research Foundation (DFG-FOR 571; publication #54).