Limits of Life and the Habitability of Mars: The ESA Space Experiment BIOMEX on the ISS

Jean-Pierre de Vera,1 Mashal Alawi,2 Theresa Backhaus,3 Mickael Baqué,1 Daniela Billi,4 Ute Böttger,5 Thomas Berger,6 Maria Bohmier,6 Charles Cockell,7 René Demets,8 Rosa de la Torre Noetzel,9 Howell Edwards,10 Andreas Elsaesser,11 Claudia Fogliarone,4 Annelle Fiedler,12 Bernard Foing,8 Frédéric Foucher,13 Jörg Fritz,14 Franziska Hanke,5 Thomas Herzog,15 Gerda Horneck,6 Heinz-Wilhelm Hübers,8 Björn Hüwe,12 Jasmin Joshi,12,16 Natalia Kozyrovska,17 Martha Kruchten,3 Peter Lasch,10 Natuschka Lee,19 Stefan Leuko,6 Thomas Leya,20 Andreas Lorek,1 Jesús Martínez-Frias,21 Joachim Meessen,3 Sophie Moritz,12 Ralf Moeller,6 Karen Olsson-Francis,22 Silvano Onofri,23 Sieglinde Ott,3 Claudia Pacelli,23 Olga Podolich,17 Elke Rabbow,6 Günther Reitz,6 Petra Retberg,6 Oleg Reva,24 Lynn Rothschild,25 Leo Garcia Sancho,26 Dirk Schulze-Makuch,27 Laura Selbmann,23,28 Frances Westall,13 David Wolter,1 and Laura Zucconi23

1German Aerospace Center (DLR), Institute of Planetary Research, Management and Infrastructure, Research Group Astrobiological Laboratories, Berlin, Germany.
2GFZ, German Research Centre for Geosciences, Helmholtz Centre Potsdam, Section 5.3 Geomicrobiology, Telegrafenberg, Potsdam, Germany.
3Institut für Botanik, Heinrich-Heine-Universität (HHU), Düsseldorf, Germany.
4University of Rome Tor Vergata, Department of Biology, Rome, Italy.
5German Aerospace Center (DLR), Institute for Optical Sensor Systems, Berlin, Germany.
6German Aerospace Center (DLR), Institute of Aerospace Medicine, Radiation Biology Department, Köln, Germany.
7School of Physics and Astronomy, University of Edinburgh, Edinburgh, UK.
8European Space Research and Technology Centre (ESTEC), European Space Agency (ESA), Noordwijk, the Netherlands.
9Departamento de Observación de la Tierra, Instituto Nacional de Técnica Aeroespacial (INTA), Madrid, Spain.
10Raman Spectroscopy Group, University Analytical Centre, Division of Chemical and Forensic Sciences, University of Bradford, West Yorkshire, UK.
11Institut für experimentelle Physik, Experimentelle Molekulare Biophysik, Frei Universität Berlin, Berlin, Germany.
12University of Potsdam, Biodiversity Research/Systematic Botany, Potsdam, Germany.
13CNRS, Centre de Biophysique Moléculaire, UPR 4301, Orléans, France.
14Museum für Naturkunde - Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany.
15TH Wildau (Technical University of Applied Sciences), Wildau, Germany.
16Hochschule für Technik HSR Rapperswil, Institute for Landscape and Open Space, Rapperswil, Switzerland.
17Institute of Molecular Biology & Genetics of NASU, Kyiv, Ukraine.
18Robert Koch Institute, Centre for Biological Threats and Special Pathogens, Berlin, Germany.
19Department of Ecology and Environmental Sciences, Umeå University, Umeå, Sweden.
20Extremophile Research & Biobank CCCryo, Fraunhofer Institute for Cell Therapy and Immunology, Branch Bioanalytics and Bioprocesses (IZI-BB), Potsdam, Germany.
21Instituto de Geociencias, CSIC-Universidad Complutense de Madrid, Madrid, Spain.
22School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, UK.
23Department of Ecological and Biological Sciences, University of Tuscia, Viterbo, Italy.
24Centre for Bioinformatics and Computational Biology, Department of Biochemistry, Genetics and Microbiology, University of Pretoria, Pretoria, South Africa.
25NASA Ames Research Center, Moffett Field, California, USA.
26LCM, Universidad Complutense Madrid, Madrid, Spain.
27Technical University Berlin, ZAA, Berlin, Germany.
28Italian National Antarctic Museum (MNA), Mycological Section, Genoa, Italy.
29AWI, Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Potsdam, Germany.
30TU Berlin, Institute of Environmental Technology, Environmental Microbiology, Berlin, Germany.
31University of Potsdam, Institute of Earth and Environmental Sciences, Potsdam, Germany.

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Abstract

BIOMEX (BIOlogy and Mars EXperiment) is an ESA/Roscosmos space exposure experiment housed within the exposure facility EXPOSE-R2 outside the Zvezda module on the International Space Station (ISS). The design of the multiuser facility supports—among others—the BIOMEX investigations into the stability and level of degradation of space-exposed biosignatures such as pigments, secondary metabolites, and cell surfaces in contact with a terrestrial and Mars analog mineral environment. In parallel, analysis on the viability of the investigated organisms has provided relevant data for evaluation of the habitability of Mars, for the limits of life, and for the likelihood of an interplanetary transfer of life (theory of lithopanspermia). In this project, lichens, archaea, bacteria, cyanobacteria, snow/permafrost algae, meristematic black fungi, and bryophytes from alpine and polar habitats were embedded, grown, and cultured on a mixture of martian and lunar regolith analogs or other terrestrial minerals. The organisms and regolith analogs and terrestrial mineral mixtures were then exposed to space and to simulated Mars-like conditions by way of the EXPOSE-R2 facility. In this special issue, we present the first set of data obtained in reference to our investigation into the habitability of Mars and limits of life. This project was initiated and implemented by the BIOMEX group, an international and interdisciplinary consortium of 30 institutes in 12 countries on 3 continents. Preflight tests for sample selection, results from ground-based simulation experiments, and the space experiments themselves are presented and include a complete overview of the scientific processes required for this space experiment and postflight analysis. The presented BIOMEX concept could be scaled up to future exposure experiments on the Moon and will serve as a pretest in low Earth orbit. Key Words: EXPOSE-R2—BIOMEX—Habitability—Limits of life—Extremophiles—Mars. Astrobiology 19, 145–157.

1. Results from Previous Spaceflight and Ground-Based Experiments

Previous experiments in spaceflight and ground-based studies, which were performed before the BIOMEX (BIOlogy and Mars EXperiment) proposal submission to ESA, showed that, in particular, microcolonies of bacteria, meristematic black fungi, and symbiotic associations of microorganisms such as lichens are able to survive and be reactivated after simulated and direct space experiments (Tarasenko et al., 1990; Horneck et al., 1994; de Vera et al., 2003, 2004a, 2004b, 2007, 2008, 2010; de la Torre Noetzel et al., 2007; Sancho et al., 2007; Onofri et al., 2008, 2010; Olsson-Francis et al., 2009; de la Torre et al., 2010; de Vera and Ott, 2010). Bacteria strains such as Bacillus subtilis and Deinococcus radiodurans have shown a certain radiation and vacuum tolerance (Horneck, 1993; Horneck et al., 1994, 2001; Retterberg et al., 2002, 2004; Möller et al., 2007a, 2007b, 2007c; Pogoda de la Vega et al., 2007; Wassmann et al., 2012; Panitz et al., 2014). Gram-negative endophytic bacteria and cyanobacteria survived a 14-day shuttle flight (within the shuttle interior) and exhibited enhanced plant colonizing activity in microgravity (Tarasenko et al., 1990). During the BIOPAN 5 and 6 experiments, the lichens Rhizocarpon geographicum and Xanthoria elegans were analyzed after exposure to space conditions of about 11–14 days coupled with parallel tests in ground-based facilities. These results have led to the conclusion that the tested symbiotic eukaryotic associations of alga and fungi in the lichen were not seriously damaged, and nearly 70–100% of the tested lichens survived. The lichens were physiologically active and able to germinate and grow. Furthermore, investigations on the mutation rate of photoproducts on the DNA have shown that the mycobiont (the fungal symbiont) is practically unaffected by UV radiation and that the algal symbiont is more sensitive (de Vera et al., 2003, 2004a, 2004b, 2007, 2008, 2010; de Vera, 2005; de la Torre Noetzel et al., 2007; Sancho et al., 2007; de la Torre et al., 2010; de Vera and Ott, 2010). Cyanobacteria, as has been shown by analysis on akinetes (resting-state cells of cyanobacteria), were also able to survive the low Earth orbit and simulated extraterrestrial conditions (Olsson-Francis et al., 2009), while vegetative cells of Chroococcidiopsis sp. CCME 029 survived prolonged desiccation periods (Billi, 2009; Fagliarone et al., 2017) and a few minutes of exposure to an attenuated Mars-like UV flux (Cockell et al., 2005). Numerous species mentioned in this study were even able to survive simulated catastrophes as induced by asteroid impact simulations (Horneck et al., 2001, 2008; Stöffler et al., 2007; Meyer et al., 2011). Mars simulation tests with methanogenic archaea have also shown a remarkable level of survival and demonstrated physiological activity during exposure to Mars-like environmental conditions (Morozova and Wagner, 2007; Morozova et al., 2007, 2015; Schirmack et al., 2014). The same has been observed for meristematic black fungi during a ground-based experiment in the facilities at the German Aerospace Center (DLR) Cologne named EVT (Experiment Verification Test), which was performed for the Lichens and Fungi Experiment (LIFE) on EXPOSE-E (Onofri et al., 2008) and after the final space experiment (Onofri et al., 2012, 2015). In other ground-based experiments, we were able to show that Paenibacillus sp. caused biocorrosion of anorthosite rock (Lytvyvenko et al., 2006). In total, we can presume that a wide variety of different microorganisms, even from higher evolutionary advanced levels than those of archaea or bacteria, are able to resist and survive space and Mars-like conditions for a period of time (at least for 1.5 years). However, because of the limited capacity of the space exposure facilities, further work with replicates and other samples is still needed to finally answer questions on the degree of Mars’ habitability or the kind of space and Mars-like environmental conditions that are limiting factors in reference to the most important vital functions of life (de Vera et al., 2014; Schulze-Makuch et al., 2015).

The BIOMEX results presented here further advance our knowledge and address pressing questions as mentioned above.
| BIOMEX selected samples for spaceflight |
|----------------------------------------|

**Archaea**  
*Methanosarcina* sp. strain SMA-21 (terrestrial permafrost) (GFZ/AWI Potsdam)

**Bacteria**  
*Deinococcus radiodurans* wild type and crtI or crtB (nonpigmented) (DLR Cologne)

Biofilm containing *Leptothrix, Pedomicrobium, Pseudomonas, Hyphomonas, Tetrasphaera* (TU Berlin)

*Cyanobacterium Nostoc* sp. strain CCCryo 231-06 (Fraunhofer IZI-BB)

*Cyanobacterium Gloeocapsa OU-20* (Astrobiology Center Edinburgh)

*Cyanobacterium Chroococcidiopsis* sp. CCME 029 (Uni Roma)

**Alga**  
Green alga *Sphaerocystis* sp. CCCryo 101-99 (Fraunhofer IZI-BB)

**Lichens**  
*Circinaria gyrosa* (INTA)

*Buellia frigida* (Antarctic lichen) (H-H-Uni Düsseldorf)

**Fungi**  
Cryptoendolithic Antarctic black fungus *Cryomyces antarcticus* CCFEE 515 (Uni Viterbo)

**Bryophytes**  
*Grimmia sessitana* (alpine samples) (Uni Potsdam)

*Marchantia polymorpha* L. (Uni Potsdam)

**Biomolecules**  
Pigment Chlorophyll (H-H-Uni Düsseldorf)

Pigment beta-Carotene (H-H-Uni Düsseldorf)

Pigment Naringenin (H-H-Uni Düsseldorf)

Pigment Quercitin (H-H-Uni Düsseldorf)

Pigment Parietin (H-H-Uni Düsseldorf)

Pigment Melanin (H-H-Uni Düsseldorf)

Cellulose (H-H-Uni Düsseldorf)

Chitin (H-H-Uni Düsseldorf)

**Biofilm**  
Kombucha biofilm containing: Yeasts; *Saccharomyces ludwigii, Schizosaccharomyces pombe, Zygosaccharomyces rouxii, Zygosaccharomyces bailii, Brettanomyces bruxellensis; Bacteria; Paenibacillus* sp. IMBG221, *Acetobacter nitrogenifigens, Gluconacetobacter kombuchae* sp. nov., *Gluconacetobacter xylinum* (NAS Ukraine)

**Substrates/Minerals**  
Agar (as a substitute for Murein) (H-H-Uni Düsseldorf)

Minerals lunar analog mixture (MfN Berlin)

Minerals P-MRS: Early acidic Mars analog (Mixture of Fe2O3, montmorillonite, chamosite, kaolinite, siderite, hydromagnesite, quartz, gabbro, and dunite) (MfN Berlin)

Minerals S-MRS: Late basic Mars analog (Mixture of hematite, goethite, gypsum, quartz, gabbro, dunite) (MfN Berlin)

Silica discs (glass) (Astrobiology Center Edinburgh)

Gray shaded cells indicate the samples for which results are available and included in this special collection.
to an extended degree in comparison to previously executed space experiments, which, for the most part, were more restricted and focused on investigating the likelihood of an interplanetary transfer of life as is formulated in the lithopanspermia hypothesis (Richter, 1865; Thomson, 1894; Arrhenius, 1903; see also Lee et al., 2017). Accordingly, these new BIOMEX experiments in space were intended to address new questions in planetary research and improve future space exploration goals. Nevertheless, it is clear that the results obtained by BIOMEX could also be used to evaluate previously performed space experiments in reference to lithopanspermia.

### Table 2. Mars and Lunar Analog Mineral Mixtures

| Component | P-MRS (wt %) | S-MRS (wt %) | LRA (wt %) |
|-----------|--------------|--------------|------------|
| Gabbro (Groß-Bieberau, Germany) | 3 | 32 | - |
| Dunite—Olivine F096 (Aheim, Norway) | 2 | 15 | 5.7 |
| CPx—Diopside (Kragerø, Norway) | - | - | 8.9 |
| OPx—Hyperstenh (Egersund, Norway) | - | - | 5.7 |
| Anorthosite—Plagioclase (Larvik, Norway) | - | - | 66.8 |
| Quarzite (Bayerischen Wald, Germany) | 10 | 3 | - |
| Apatite (Minas Gerais, Brasil) | - | - | 1.1 |
| Hematite (Cerro Bolivar, Venezuela) | 5 | 13 | - |
| Ilmenite (Flekkefjord, Norway) | - | - | 1.1 |
| Iron (Fe) | - | - | 1.3 |
| Montmorillonite (Hallertau, Germany) | 45 | - | - |
| Chamosite (Nucic, Czech Republic) | 20 | - | - |
| Kaolinite (Hirschau, Germany) | 5 | - | - |
| Siderite (Hüttenberg, Austria) | 5 | - | - |
| Hydromagnesite (Albaner Berge, Italy) | 5 | - | - |
| Goethite (Salchendorf, Germany) | - | 7 | - |
| Gypsum (Nütttermoor, Germany) | - | 30 | - |
| Volcanic slag (Aeolian islands, Italy) | - | - | 9.4 |

P-MRS: phyllosilicatic martian regolith = early acidic. S-MRS: sulfatic martian regolith = late basic. LRA: lunar regolith analog.

2. Sample Selection

As a consequence of results obtained in previous space experiments that engendered a significant number of still-open questions, a proposal named BIOMEX (ILSRA-2009-0834) was submitted in 2009. This was in response to the ESA international research announcement for research in space life sciences at the International Space Station (ISS)—ILSRA-2009—and BIOMEX was successfully selected. The proposal included replicate exposure of known species used in previous space experiments such as the reassessed Antarctic

![FIG. 1. Mars analog pellets integrated in the EXPOSE-R2 hardware.](image-url)
fungus *Cryomyces antarcticus*, the cyanobacterium *Chroococcidiopsis* sp., the lichen *Circinaria gyrosa* (formerly known as *Aspicilia fruticulosa* before reclassification; Sohrabi *et al.*, 2013), and a set of new, preselected organisms for further preflight experiments (see Table 1). After survival of these organisms was shown, the samples were incorporated into the BIOMEX experiment, integrated into the final EXPOSE-R2 hardware, and sent to space on the ISS.

This new sample set was chosen systematically and comprised a selection from archaea, bacteria, and eukaryotes, which represent the three main domains of the tree of life. Most of these organisms were collected from Mars analog habitats distributed on different continents, which include the Alps (climatic and geomorphologic Mars analogy: gullies, polygons, temperatures below 0°C, dryness, and elevated UV irradiation), the steppe highlands of Central Spain (characterized by extreme insolation, high temperature contrasts, and arid summers Crespo and Barreno, 1978), and regions in the Arctic and Antarctica. The aim of selecting a wide variety of species was to identify which are able to demonstrate the limits of life with regard to the applied space and Mars-like conditions in low Earth orbit, as well as further our understanding of the kind of species for which Mars could be habitable.

### 2.1. Biological samples

A set of organisms was tested, which were embedded in, or grown on, Mars (optionally lunar) analogs and other terrestrial minerals. Bacteria, biofilms of bacteria and yeast species, cyanobacteria, archaea, lichens, snow/permafrost algae, meristematic black fungi, and bryophytes of mostly alpine and polar habitats of desiccation- and radiation-resistant strains were chosen because some of these organisms are thought to be among the oldest on Earth (Wang *et al.*, 1999; Schidlowski, 2001; Campbell *et al.*, 2003; Yuan *et al.*, 2005) and, over time, have evolutionarily adapted to different environmental conditions. Some of these organisms could even be Mars-relevant because they use Mars-atmosphere resources such as CO2 to form methane, a trace gas found remotely in the martian atmosphere (Formisano *et al.*, 2004; Mumma *et al.*, 2009) and in situ at Gale Crater by way of the rover Curiosity (Webster *et al.*, 2015). The processes that lead to extreme variations in the methane concentration of the martian atmosphere, in particular the potential for abiogenic origin (Lefèvre and Forget, 2009), have recently been reviewed (Yung *et al.*, 2018). In previous studies, some of the organisms studied in the BIOMEX experiments have also exhibited a high resistance under simulated and real space conditions or simulated martian conditions. Others, like the newly selected bryophytes, provide insights on the resistance capabilities of an evolutionarily younger life-form. Details on the selected species are listed in Table 1.

### 2.2. Mars and lunar analog mineral mixtures

With the BIOMEX experiment, our goal was to analyze the effects of a space environment that approaches as closely as possible Mars-like environmental conditions and includes the use of Mars analog mixtures that could serve as a substrate or an embedding matrix for biological samples (see Table 2 and Figs. 1 and 2). These Mars analog mineral mixtures mimic the regolith cover from early and late evolutionary stages of Mars (Böttger *et al.*, 2012). The components of the mixtures were developed in the Museum für Naturkunde (MfN) Berlin (Germany) in the context of the Helmholtz-Alliance “Planetary Evolution and Life” proposal and based on several observational studies (Bibring *et al.*, 2005, 2006; Poulet *et al.*, 2005; Chevrier and Mathé, 2007). It is important to test the effects of space and the martian environment on minerals in parallel biological investigations. A welcome consequence of this space experiment would be that the investigated samples would also be tested for viability and space-resistance capacity and provide valuable data if used in a replicate space experiment with regard to the probability of lithopanspermia in the Earth-Mars system. The lithopanspermia hypothesis has also been investigated in previous space experiments on FOTON/BIOPAN some years ago and on the EXPOSE-E mission on the ISS. However, replicates are still needed. Besides the Mars analog mineral mixtures, the MfN also provided a lunar regolith analog (see Table 2 and Figs. 1 and 3) for investigation into the influence of the lunar surface material on organisms, which could be relevant for life-support systems such as the selected and tested cyanobacteria (not part of this special collection of articles).
### Table 3. Experiment Verification Tests (EVTs)

| EXPOSE-R2 EVT part 1 | BIOMEX Experiment |
|----------------------|--------------------|
| **Test parameter**   | **performed**      |
| Vacuum 10⁻³ Pa       | 7 d, pressure: 3.5×10⁻² |
| Mars atmosphere      | 7 d, pressure: 6.5×10² |
| (CO₂ gas composition)| ± 0.12 Pa           |
| 103 Pa               |                    |
| Temperature          | 48 cycles          |
| –10°C to +45°C       |                    |
| Temperature max and min | –25°C ± 0.5°C, 1 h |
| –25°C and +60°C      | +60°C ± 0.5°C, 1 h |
| Irradiation          | 0 s → 0 J/m²        |
| 254 nm               | 18 s → 10.1 J/m²    |
| Hg low-pressure lamp | 2 min 59 s → 100.2 J/m² |
| @ 56 μW/cm²          | 29 min 46 s → 1000.2 J/m² |
|                      | 4 h 57 min 37 s → 9999.9 J/m² |
| **EXPOSE-R2 EVT part 2** (run 1+2) | **BIOMEX Experiment** |
| **Run 1**            |                    |
| Irradiation          | 0 s → dark         |
| 200–400 nm           | 18 min → 1.4×10³ J/m² |
| SOL2000 @ 1,271.2 W/m² | 3 h → 1.4×10⁴ J/m² |
| (200–400 nm)         | 99 h → 4.5×10⁵ J/m² |
|                      | 148 h → 6.8×10⁵ J/m² |
| **Run 2**            |                    |
| Irradiation          | 0 s → dark         |
| 200–400 nm           | 432 s → 5.5×10² J/m² |
| (0.1% ND filter)     | (1.0% ND filter)   |
| SOL2000 @ 1,271.2 W/m² | 1 h 12 min → 5.5×10³ J/m² |
| (as for a 12-month mission duration) | 30 h → 1.4×10⁵ J/m² |
|                      | 60 h → 2.7×10⁶ J/m² |
|                      | 120 h → 5.5×10⁷ J/m² |
| Gluing test          | >24 h vulcanization, glue: Wacker-silicone |

ND: neutral density.

### Table 4. Scientific Verification Tests (SVTs)

| SVT | Duration | Pressure | Atmosphere | Temperature (T) | T extremes | Irradiation |
|-----|----------|----------|------------|-----------------|------------|-------------|
| Tray 1 | December 2013–January 2014, 38 d | vacuum pressure at 4.1×10⁻³ Pa | Mars atmosphere (95.55% CO₂, 2.7% N₂, 1.6% Ar, 0.15% O₂, and ~ 370 ppm H₂O at 1 kPa) | T cycles between –25°C (16 h in the dark) and +10°C (8 h during irradiation) | –23°C | The upper layers of each tray: UVR<sub>200–400 nm</sub> with 1271 Wm<sup>–2</sup> (5.7×10³ J m<sup>–2</sup>) for 5924 min |
| Tray 2 | Mars atmosphere | – – | – | – | – | The lower layers of the trays were kept in the dark |
FIG. 4. Visual table of the sample distribution within the EXPOSE-R2 hardware.

FIG. 5. The distribution of neutral density filters and the values of transmission depending on the used material.
### Table 5. Results Listed According to the Topics “Limits of Life” and Habitability of Life

| Sample category / domain | species                                                                 | Results on limits of life | Results on Habitability of Mars |
|-------------------------|-------------------------------------------------------------------------|---------------------------|---------------------------------|
|                         |                                                                         | selection tests | EVT/SVT | space | selection tests | EVT/SVT | space |
| Archaea                 | Methanosarcina sp.strain SMA-21 (terrestrial permafrost) (GFZ/AWI Potsdam) | −             | +       |       |                 |         |       |
| Bacteria                | Cyanobacterium Chroococcidiopsis sp. CCME 009 (Uni Roma)                | +             | +       |       |                 |         |       |
| Fungi                   | Cryptoendolithic Antarctic black fungus Cryptomyces antarcticus CCFEE 515 (Uni Viterbo) | +             | ±       | +     | ±             |         |       |
| Lichens                 | Circinaria gyrosa (INTA)                                                | ±             | ±       |       | ±             |         |       |
|                         | Buellia frigida (Antarctic lichen) (H-H-Uni Düsseldorf)                 | +             | ±       | ±     | ±             |         |       |
| Bryophytes              | Grimmia sessitana (alpine samples) (Uni Potsdam)                        | −             | +       |       | +             |         |       |
|                         | KOMBUCHA/ Biofilm containing: Yeasts: Saccharomyces ludwigi, Schizosaccharomyces pombe, Zygosaccharomyces rouxi, Zygosaccharomyces bailii, Brettanomyces bruxellensis; Bacteria: Paenibacillus sp. IMBG221, Acetobacter nitrogenifigens, Gluconacetobacter kumbuchae sp. nov., Gluconacetobacter xylinum (NAS Ukraine) | ±             | ±       |       | ±             |         |       |

(±) Survival / metabolically active / growth capacity, (−) partly survival, more damaged
were additionally applied to the samples of the methanogen archaeon Methanosarcina soligelidi SMA 21. In this case, these filters were used because of the specific nature of this organism’s original habitat, which is situated within permafrost-affected soils and protected by soil particles with different grain sizes. Deinococcus radiodurans was covered by neutral density filters with a transmission of 0.01%. The measured and calculated data with regard to the final doses the samples experienced, which included UVA, UVB, UVC, PAR (photosynthetically active radiation), and Lyman alpha, are represented in Fig. 6 and were kindly provided by ESA via computations completed by the company RedShift Design and Engineering BVBA.

Significant variation was observed in the dose of UV among samples that were placed within sample sites not protected by filters. The observed variations could be explained by the dependence of the sample position in the hardware, which would have been exposed to a variety of shadowing effects during the orbit of the ISS. When filters were not used in the BIOMEX experiments, the final doses varied between $4.5 \times 10^6$ and $8.4 \times 10^5$ kJ/m². Specific organisms exposed without any neutral density filters include the epilithic lichens Cinclaria gyrosa and Buellia frigida, the epilithically living bryophytes Grimmia sp., and Marchantia polymorpha, the iron bacteria biofilm, and the kombucha biofilm. Biomolecules exposed on the surface and embedded in the Mars analog mineral pellets also endured the same direct space conditions without any neutral density filters.

3. Overview of Results within This Special Collection

The results presented in this special collection are arranged to provide an overview of each step of the processes involved in the BIOMEX experiment, that is, from selecting sample categories.

| Table 6. Detailed Result List Explaining the Classification Shown in Table 5 |
| --- |
| **Sample category / domain** |
| **species** |
| **Results on limits of life** |
| **Results on Habilitability of Mars** |

**Archaia**

| Methanosarcina sp strain SMA-21 (terrestrial permissoil) (GFZ/AN Potdam) |
| Decrease of CH₄ production rate on the used Mars-analog high concentration of perchlorates (not applied in BIOMEX space exposure) |
| Methanotrophic bacterial biofilm biomass (P-MRS not exposed to perchlorates) | Survival and recovery on Mars analog minerals, lower DNA-damage particularly in the more protected unialgal/algae biomass. |

**Bacteria**

| Cyanobacterium Gloeocapsa rubogina sp. CCME 029 (Uni Roma) |
| Survival and recovery on Mars analog minerals, lower DNA-damage in the more protected unialgal/algae biomass. |
| On irradiated S-MRS 40% still growing, on irradiated P-MRS 75% growing. In Martian atmosphere without irradiation on S-MRS about 55% growth and on P-MRS about less than 25% growth. In all cases within both MRS significant membrane damage. On LRA no significant changes in growth and loss damaged membranes |

**Fungi**

| Grimmia recurvata (algic lichen) (Uni Potsdam) |
| Quick moderate-high recovery of the PSI activity in the space dark control (vacuum and Mars atmosphere), where also morphology and DNA stability was observed. But irradiated samples under the same conditions were significantly affected. |
| Quick moderate-high recovery of the PSI activity in the more protected dark control areas |

**Lichens**

| Mucoromela porphyria sp. (INTA) |
| Quick moderate-high recovery of the PSI activity in the space dark control (vacuum and Mars atmosphere), where also morphology and DNA stability was observed. But irradiated samples under the same conditions were significantly affected. |
| Quick moderate-high recovery of the PSI activity in the more protected dark control areas |

**Bryophytes**

| Grimmia recurvata (algic lichen) (Uni Potsdam) |
| The mosses were still in their state during the EXPOSE-R2 mission on the ISS. This earliest eustein mosses of land plants is highly resistant to extreme dynamic conditions. |
| The mosses were still vital after other type of radiation expected during the EXPOSE-R2 mission on the ISS. This earliest eustein mosses of land plants is highly resistant to extreme dynamic conditions. |

**Biofilm**

| KOMBUCHA Biofilm containing Yeasts: Saccharomyces ludwigii, Schizosaccharomyces pombe, Zygospaoroma renulai, Zygospaoroma halii, Brettanomyces broacculae; bacteria: Faebusbacillus sp. IABG/221, Acetobacter meiotigmoglates; Gluconacetobacter kombucha sp. nov., Gluconacetobacter sulfinus (NAS Ukraine) |
| After returning to Earth, the space-floved bacterial-yeast community recovered in two months. Within the UV-irradiated samples, a degradation of DNA, changes in the cellular membranes, and an inhibition of cellulose synthesis were observed. After a series of culture experiments, the revived communities restored partially their composition and the associated activities. |
| After returning to Earth, the space-floved bacterial-yeast community recovered in two months. Within the UV-irradiated samples, a degradation of DNA, changes in the cellular membranes, and an inhibition of cellulose synthesis were observed. After a series of culture experiments, the revived communities restored partially their composition and the associated activities. |

S-MRS: sulfatic martian regolith. P-MRS: phyllosilicatic martian regolith. LRA: lunar regolith analog.
samples for simulation experiments to the final exposure experiments in space. Results from pretests on the chosen methanogenic archaeon of the genus *Methanosarcina* at the preselection level are reported in Serrano et al. (2019). This archaeon was chosen because of its relevance with regard to its potential for being metabolically active on Mars. Therefore, the first tests were designed to use different substrates that contained magnesium perchlorate to establish a Mars-relevant perchlorate environment and mineral mixture before attempting the next selection step of applying atmospheric and radiation-related environmental conditions within the preflight experiments EVTs and SVTs. With regard to the EVTs and SVTs, we present the results obtained by analysis of the fungus *Cryomyces antarcticus* (Pacelli et al., 2019) and the moss *Grimmia* sp. (Huwe et al., 2019). Results obtained after space exposure are shown from a series of analyses on the biofilm kombucha (Podolich et al., 2019), the cyanobacterium *Chroococcidiopsis* (Billi et al., 2019), the cryptoendolithic Antarctic fungus *Cryomyces antarcticus* (Onofri et al., 2019), and the lichens *Buellia frigida* (Backhaus et al., this issue) and *Circinaria glyrosa* (de la Torre et al., not part of this issue). A rough summary of the different studies is given in Table 5, and more details are shown in Table 6. Survival, physiological activity, and growth capacity were detected in all organisms tested. However, life’s vital functions decreased from slight to significant, and the reader is directed to specific articles in this collection for detailed discussion of these findings. Several of the selected archaea, bacteria, and heterogeneous multilayered biofilms formed by a multitude of species were found to be the most resistant to simulated or direct space and Mars-like conditions. Less resistance and a significant decrease in cell numbers and vitality with regard to the Mars-like environment were shown for multicellular life-forms such as the tested fungus *Cryomyces antarcticus* (Onofri et al., 2019) and the lichens *Buellia frigida* (Backhaus et al., 2019) and *Circinaria glyrosa* (de la Torre Noetzel et al., 2019). The bryophyte *Grimmia* sp. was an exception (Huwe et al., 2019), but further analysis after space exposure might show whether this specific moss is also resistant to the conditions in space. Actual results in reference to the bryophytes were shown only for the preflight selection mode of EVT and SVT. Our results so far indicate that present Mars seems to be habitable for archaea and bacteria over longer timescales. However, a clearer understanding of the limits of life would be achievable with the implementation of extended space exposure experiments on the Moon, for example, with similar space exposure facilities as those used in the present study (see de Vera et al., 2012).

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Address correspondence to:
Jean-Pierre de Vera
German Aerospace Center (DLR)
Institute of Planetary Research, Management and Infrastructure
Research Group Astrobiological Laboratories
Rutherfordstr. 2
12489 Berlin
Germany

E-mail: jean-pierre.devera@dlr.de

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**Abbreviations Used**
BIOMEX = BIOlogy and Mars EXperiment
DLR = German Aerospace Center
EVTs = Experiment Verification Tests
ISS = International Space Station
MfN = Museum für Naturkunde
PAR = photosynthetically active radiation
SVTs = Scientific Verification Tests
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