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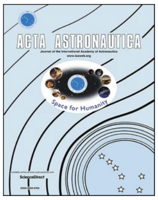

Desert cyanobacteria under non-Earth conditions: Implications for astrobiology and sustainable life support

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ABSTRACT

The astonishing capability of life to adapt to extreme conditions provides a new perspective on what habitable means. Desert cyanobacteria of the genus *Chroococcidiopsis* have been investigated for survival potential under laboratory simulations of space and planetary conditions as well as under real space conditions or Mars conditions simulated in LEO. When exposure conditions did not exceed repair capabilities, insights were gained on constraints that life can withstand. When accumulated damage exceeded repair potential, biomarker detectability contributed to the search of life beyond Earth. Results of the ESA BIOMEX and BOSS space missions performed outside the ISS showed that ultraviolet radiation greatly affects cellular survival and biomarkers stability. On the contrary, ionizing radiation does not significantly impair biomarker detectability in dried cells as revealed by Raman spectroscopy and fluorescence immunoassay. The capability of repairing upon retrieval back to Earth and rehydration, the DNA damage accumulated during 1.5-year exposure in LEO has implications for future cyanobacterial-based technologies. In this context, the effect of microgravity on DNA repair capability will be investigated with the ASI BIORIDER experiment to be performed in the maiden flight of the ESA Space Rider. During the ASI project Life in Space the survival potential of dried *Chroococcidiopsis* under laboratory-planetary simulations was investigated, yielding new insight into endurance under salty-ice conditions simulating icy worlds. The capability of desert strains to harvest near-infrared is under investigation in the context of the ASI ASTERIA project that holds implications for oxygenic photosynthesis on exoplanets. The gathered knowledge will contribute to perform new experimentations and advance the scientific utilization of the space platforms that are under development or in advanced planning stage for experiments beyond LEO. The endurance of desert cyanobacteria under space and Mars-like conditions and their capability to grow using resources available *in situ* on the Moon and Mars have bene investigated in the ASI ReBUS project and on-going results gathered in the Space It Up project will further contribute to fill the gaps in developing cyanobacterial-based life systems to support human settlements on the Moon and Mars.

1. Introduction

The astonishing life's capability to adapt to extreme environments on Earth provides new insights into the question of whether life is unique in our planet or whether there are inhabited worlds in the Solar system or around other stars [1]. Extremophiles colonize inhospitable places like hot and cold deserts or sub-glacial lakes, that provide a proxy for possible past or present habitability of Mars or the icy moons Enceladus and Europa [2]. Moreover, the existence on Earth of cyanobacteria capable of oxygenic photosynthesis under infrared light [3] supports the possibility of exotic photosynthesis in exoplanets orbiting M-dwarf stars, the most common stars in our Galaxy, that are characterized by a strong

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; ASTERIA, Adaptability of Cyanobacteria from Extreme Environments to Stellar UV Radiation; BIOMEX, Biology and Mars Experiment; BOSS, Biofilm Organisms Surfing Space; CyanoTechRider, Enabling Cyanobacteria-based Technologies for Human Space Exploration using the Space Rider; BIOSIGN, Bio-Signatures and Habitable Niches; LDEF, Long Duration Exposure Facility; CCMEE, Culture Collection of Microorganisms from Extreme Environments; EURECA, European Retrievable Carrier; FaRLiP, Far-Red Light Photoacclimation; ISRU, In-Situ Resource Utilization; ISS, International Space Station; LEO, Low Earth Orbit; UVR, Ultraviolet Radiation; SOLID-LDChip, Signs of Life Detector.

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infrared emission [4].

Novel insights into what makes a world *hospitable to life,* at least as we know it, might be provided by challenging extremophiles with the exposure to laboratory-simulations of non-Earth conditions and to real space conditions. So far, space technology has provided various facilities to investigate the effects on microorganisms of space radiation beyond the protection provided by Earth's atmosphere and magnetic field [5,6]. Breakthroughs on the extraordinary endurance of simple life forms, like bacteria, have been obtained in the eighties and early nineties using the NASA LDEF and the ESA EURECA satellite, respectively. These experiments demonstrated the survival of bacterial spores after 1 and 6 years of permanence in LEO, respectively [5,6]. Moreover, evidence on bacterial survival after exposure to deep-space conditions was provided during the Apollo 16's return to Earth [5,6]. Starting from the early 2000s the ESA EXPOSE facility installed outside the ISS permitted long-term exposure (about 2 years) of microorganisms to real space conditions and Mars-like conditions. Since the EXPOSE platform allowed the integration only of dried samples, the investigated microorganisms were desiccation tolerant, such as cyanobacteria and fungi from deserts and lichens from high mountain regions [5].

2. Desert cyanobacteria as a model system for astrobiology and life support

Desert strains of the *Chroococcidiopsis* genus are well-known for their capability of withstanding extreme desiccation and high doses of both ionizing and ultraviolet radiation [7]. These features make them a suitable model for experimentations on space platforms not only to unravel the limits of life, but also to develop biotechnologies to support human space exploration [8]. Their relevance for space applications was first suggested in 1995 [9]. Indeed, the story of desert strains of *Chroococcidiopsis* has been linked to space exploration since the very beginning: The discovery of endolithic communities in the Negev Desert occurred at the time of the Sputnik [10], while the existence of endolithic communities in the McMurdo Dry Valleys in Antarctic was reported when in the 1970s the NASA Viking missions failed to find evidence for life on Mars [11]. Since then, E. Imre Fridmann and Roseli Ocampo-Friedmann isolated hundreds of desert strains of *Chroococcidiopsis*, currently maintained as part of the CCMEE at the University of Rome Tor Vergata. These strains provide a unique reservoir of cyanobacteria to investigate the limit of life on Earth and to search for it in the Solar system and beyond [12].

Starting from the early 2000s desert strains of *Chroococcidiopsis*, namely CCMEE 029, 057 and 064, have been used in space experiments first in the context of the interplanetary transfer of photosynthesis inside rocks, as part of the lithopanspermia theory [13] and then to investigate microbial survival and biomarker stability under space and Mars-like conditions [5,7], taking part in various space missions as summarized in Table 1.

Table 1
Space experiments in which desert strains of Chroococcidiopsis have been included

Strain/colonization type/sampling site	Space mission/experiment/year	Relevance
CCMEE 029/cryptoendolithic in sandstone/Negev Desert, Israel	Foton-M3/STONE/2005	Barriers to interplanetary transfer of photosynthesis
	EXPOSE-E/ADAPT/2008–2009	Survival under extraterrestrial UVR
	EXPOSE-R/ROSE-1/ENDO 2009–2011	Survival and biomarker stability (carotenoids) under extraterrestrial UVR
	EXPOSE-R2/BIOMEX/2014–2016	Role of Martian mineral analogues on survival and biomarker stability (chl*a*, carotenoids, genomic DNA) under space and Mars-like conditions
	EXPOSE-R2/BOSS/2014–2016	Biofilm survival compared to planktonic counterparts under space and Mars-like
	Space Rider/CyanoTechRider/TBD	Effect of microgravity on genomic DNA repair
CCMEE 057/chasmoendolithic in granite/Sinai Desert, Egypt	EXPOSE-R2/BOSS/2014–2016	Biofilm survival compared to planktonic counterparts under space and Mars-like conditions
CCMEE 064/hypolithic under stone pavement/Sinai Desert, Egypt	EXPOSE-R2/BOSS/2014–2016	Biofilm survival compared to planktonic counterparts under space and Mars-like
CCMEE 010/chasmoendolithic in granite/Negev Desert, Israel	EXPO/BIOSIGN/TBD	Role of Martian mineral analogues on survival and biomarker detectability (chl*f*/*d*, carotenoids, genomic DNA) under space and Mars-like conditions
CCMEE 130/cryptoendolithic in sandstone/Canyonlands, Utah	EXPO/BIOSIGN/TBD	Role of Martian mineral analogues on survival and biomarker detectability (chl*f*/*d*, carotenoids, genomic DNA) under space and Mars-like conditions

Recently the screening of the CCMEE identified two strains, namely *Chroococcidiopsis* sp. CCMEE 010 and CCMEE 130, as capable of FaRLiP [14,15], a process based on the synthesis of chlorophylls *d* and *f* that absorb beyond the visible light region [3]. These two strains provide a suitable model for ground-based simulations of M-dwarf stars that are of interest for the habitability of rocky planets orbiting M-dwarf stars as they receive lower intensities of visible light and higher intensities of infrared light [4].

In the context of using cyanobacteria to develop sustainable ecosystems to support human outposts beyond LEO, *Chroococcidiopsis* sp. CCMEE 029 was cultivated using minerals present in simulants of Moon or Martian regoliths with implications for the development of ISRU-technologies based on cyanobacteria [16–18].

2.1. Astrobiology experiments under laboratory-simulated conditions

Laboratory facilities can simulate only individual parameters present in space, nevertheless they provide relevant information by defining the boundary conditions for life, as least as we know it. In the early 2000s, *Chroococcidiopsis* sp. CCMEE 029 was selected by E. Imre Friedmann for laboratory simulations of Mars-like UV flux. Results revealed that dried monolayers were 10 times more resistant than *Bacillus subtilis* spores [19]. Later, in the context of the STARLIFE project [20] *Chroococcidiopsis* sp. CCMEE 029 and CCMEE 057 were exposed to different types of ionizing radiation (X-rays, γ-rays, heavy ions) representing the major components of the galactic cosmic radiation spectrum [20]. Results revealed that dried cells were more tolerant than hydrated counterparts, for example hydrated cells tolerated up to 11.59 kGy of γ-irradiation, whereas dried cells survived 23.92 kGy [21]. In the laboratory set up a dose rate of 100 Gy/min of gamma radiation was used, whereas a dose rate of 76 mGy/year reaches the Martian surface [22]. Therefore, on Mars a hypothetical microorganism would accumulate such a high dose over extended periods of time. Also, the lifetime of a metabolically active microorganism with a duplication time of a few hours or even days (as in the case of *Chroococcidiopsis*) would be largely inferior to the time needed to accumulate such a lethal dose. Nevertheless, the survival of cells irradiated in the dried state is relevant since dormant microorganisms accumulate damage and activate repair mechanisms upon reactivation. A similar situation might have happened during the Martian history, when clement climate episodes occurring in the post-Noachian. This might have allowed the revival and repair of radiation-accumulated damage in dormant microbial forms, thus resetting their survival clock [22].

During the exposure to increasing doses of ionizing radiations, when conditions did not exceed the repair capabilities, insights were gained on the constraints that life can withstand. Moreover, knowing radiation tolerance of microorganisms capable of oxygenic photosynthesis has implications not only for astrobiology-related topics, but also to develop biological-driven life-support systems. On the contrary, when accumulated damages exceeded repair potential, insights were gained on biomarker persistence. For example, dried cells of *Chroococcidiopsis* sp. CCMEE 029 irradiated with a lethal dose of 113 kGy of γ-rays were investigated for biomarker detectability by using an antibody-based technique, known as the Signs of Life Detector (SOLID)-LDChip system [23]. This system was developed for biomarker detection on Mars and currently it is part of an instrument suite named Complex Molecules Detector proposed as a scientific payload for future planetary explorations [24]. Positive fluorescence immunoassay indicating the presence of molecules with identical or highly similar structures to those used for antibody production, revealed high biomarker detectability in dried cells exposed to 113 kGy of gamma rays [23]. In addition, almost unaltered Raman carotenoid signals occurred in dried cells of *Chroococcidiopsis* sp. CCMEE 029 irradiated with 113 kGy, a result that added a new insight into the preservation potential of carotenoid-like molecules on Mars [25]. Since 113 kGy correspond to the dose accumulated in 13 Myr at 2m below the Martian surface, results support the possibility of detecting life traces at a depth that the ExoMars rover Rosalind Franklin will be sampling [23].

In the context of laboratory-planetary simulations performed during the ASI Life in Space project [26], *Chroococcidiopsis* sp. CCMEE 029 and CCMEE 171 isolated from a hot and a cold desert respectively, were exposed to salty-ice simulations to investigate their capability to survive under sub-freezing temperatures in samples simulating the environment of icy worlds [27]. While both strains survived the freezing process at 258 K and 233 K and died at 203 K, the strain from the McMurdo Dry Valleys, Antarctica, showed an enhanced survivability at 258 K compared to the strain from the hot desert. Notably, for both strains the survival limit was extended up to 193 K, when exposed to the icy-moon simulation as air-dried cells [27]. This suggested that vitrification might be a survival strategy in habitable niches of icy moons, because by entering a dried, frozen state, a microbial life form could survive the transfer from niches that turned non-habitable to new habitable ones.

Since exoplanets orbiting M-dwarf stars experience powerful stellar flares that may challenge life development [28], in the context of the ASI ASTERIA project, the UVR adaptability of *Chroococcidiopsis* sp. CCMEE 010 and CCMEE 130 capable of far-red photosynthesis is under investigation. Results will have implications not only for the habitability of exoplanets but also of Archean Earth since cyanobacteria were the first to evolve oxygenic photosynthesis in the absence of a protective ozone layer [29]. Implications are foreseen also for the habitability of Noachian Mars, where if life ever occurred, it may have retreated to subsurface environments reached by infrared light, as it occurs on Earth in extremely dry deserts [30]. The survival of hydrated, metabolically active biofilms of strain CCMEE 010 under laboratory simulations of Mars conditions suggested that on the Red Planet during the loss of surface habitability, near-surface, protected niches could have been colonized by phototrophs capable of utilizing low-energy light [31].

2.2. Astrobiology experiments in space

Starting from the early 2000s desert strains of *Chroococcidiopsis* have been used in several space experiments by using the Russian *retrievable* Foton capsule and the ESA EXPOSE facility installed outside the ISS [5] as summarized in Table 1. *Chroococcidiopsis* sp. CCMEE 029 was used for the first time during the ESA STONE 6 experiment that aimed to test the lithopanspermia theory, *i.e.*, the interplanetary transport of microbes inside rocks [13]. Dried biofilms of *Chroococcidiopsis* sp. CCMEE 029 were inoculated into a rock substrate and installed in the heat shield of a Russian Foton satellite, to simulate a meteorite entry into Earth's atmosphere. Results revealed that atmospheric transit acts as a strong biogeographical dispersal filter to the interplanetary transfer of photosynthesis [32]. Later, during the ESA EXPOSE-E space mission [33], dried cells of *Chroococcidiopsis* sp. CCMEE 029 were augmented along with akinetes of *Anabaena cylindrica* and vegetative cells of *Nostoc commune* PCC7524 into a natural community of rock-dwelling phototrophs. Once retrieved back to Earth, *Chroococcidiopsis* sp. CCMEE 029 was the only one surviving the unattenuated UV flux [34].

During the ESA EXPOSE-R space mission [35] it was shown that dried cells of *Chroococcidiopsis* sp. CCMEE 029 inoculated into impact-shocked gneiss survived extraterrestrial UVR. This suggested that endolithic habitats could have allowed surface colonizing of early Earth landmasses that were characterized by the absence of UVC protection [36]. Then during the ESA EXPOSE-R2 space mission [37] *Chroococcidiopsis* strains were exposed with other extremophiles to space and Mars-like conditions in the context of two experiments: i) BOSS investigating the resistance of microbial biofilms compared to planktonic counterparts [38]; and ii) BIOMEX investigating extremophile survival and stability/degradation of their components (pigments, cell wall components, etc.), when mixed with Martian and Lunar regolith simulants [39].

For the BOSS experiment *Chroococcidiopsis* sp. CCMEE 029, CCMEE 057 and CCMEE 064 were selected according to different modality of rock colonization (Table 1, Fig. 1A). Post-flight analyses after 1.5-year-exposure in LEO showed that biofilms recovered better than their planktonic counterparts, and that accumulated less damage to genomic DNA and photosynthetic pigments [40]. It was pointed out that biofilm enhanced survival was due to UVR shielding provided by top-cell layers combined with abundant extracellular polymeric substances [40]. *Chroococcidiopsis* sp. CCMEE 029 was selected for the BIOMEX space experiment and post-flight analyses after 1.5-year-exposure in LEO (Table 1, Fig. 1B), showed that regoliths provided efficient UVR shielding and that damage accumulated to genomic DNA and photosynthetic pigments was repaired upon rehydration [41]. In addition, a space-derivate strain, obtained upon rehydration of dried cells of strain CCMEE 029 exposed to LEO, was investigated for the robustness of the repair of DNA damage accumulated while in space. The comparative analysis of the whole-genome sequence of the space-derivate strain showed no increased variant numbers compared to the reference-laboratory strain [42]. This result highlights the repair robustness of DNA lesions and advances the interest in life support technologies based on this cyanobacterium that might maintain genetic stability under non-Earth conditions. Indeed, the capability of repairing DNA damage will be further investigated during the CyanoTechRider experiment as part of the ASI BIORIDER space mission to be performed in the maiden flight of the ESA Space Rider. In this experiment dried cells of *Chroococcidiopsis* sp. CCMEE 029 will be pre-irradiated on Earth, re-activated in orbit to allow DNA repair under microgravity and finally analyzed for genome stability after retrieval to Earth (Table 1, Fig. 1D).

Finally, *Chroococcidiopsis* sp. CCMEE 010 and CCMEE 130 will be part of the future ESA BIOSIGN space mission to be performed outside the ISS (Table 1, Fig. 1C). This experiment will investigate the survival and biomarker stability/degradation of microorganisms and microfossils isolated from planetary analogues of Mars and icy moons [43]. In particular the results on cyanobacterial strains capable of far-red photosynthesis exposed to Mars-like conditions, will further contribute to unravel the past habitability of Mars and biosignature detectability [44].

2.3. Genomic landscape for endurance under space conditions

The first insights into the presence in the genome of *Chroococcidiopsis* sp. CCMEE 029 of crucial genetic components accounting for space-survival date back to the EXPOSE-E space mission, when it resulted more resistant than other cyanobacteria [34]. No doubt bioinformatic pangenome-based comparative analysis of space-sensitive and space-resistant cyanobacteria along with the investigation of the

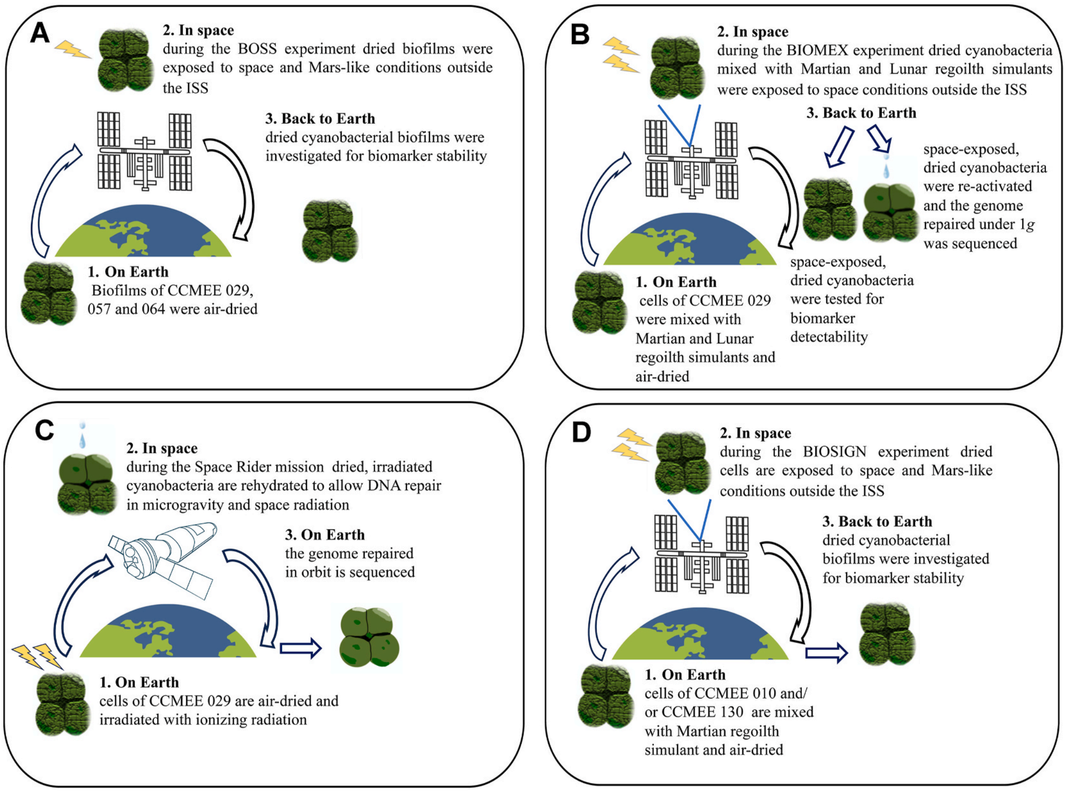

Fig. 1. Workflow of space missions. A. BOSS: Cyanobacterial biofilms were air-dried on the ground and integrated in the EXPOSE-R2 facility. Dried samples were exposed in LEO for 1.5 years. After retrieval to Earth dried cells were tested for viability and biomarker detectability. B. BIOMEX: Cyanobacterial cells were mixed with Martian and Lunar regolith simulants, air-dried on the ground and integrated in the EXPOSE-R2 facility. Dried samples were exposed in LEO for 1.5 years. After retrieval to Earth dried cells were tested for viability and biomarker detectability, while re-hydrated cells were investigated for genome integrity. C. BIOSIGN: Cyanobacterial cells will be mixed with Martian regolith simulant, air-dried on the ground and integrated in the EXPO2 facility. After retrieval to Earth dried cells will be analyzed for viability and biomarker detectability. D. CyanoTechRider: Cyanobacterial cells will be air-dried, exposed to ionizing radiation and integrated into the Space Rider. Dried cells will be re-hydrated in orbit and the genome sequenced after retrieval to Earth.

genomic features of the space-resistant strains CCMEE 057 and CCMEE 064, will contribute to elucidate the genetic features required for space endurance.

Meanwhile the sequencing of the genome of *Chroococcidiopsis* sp. CCMEE 029 [42] allowed an *in-silico* survey that identified genes of the DNA repair pathways. It was shown that genes encoding a photolyase, and proteins of the nucleotide excision repair system were over-expressed during the rehydration of cells exposed to laboratory simulations of a Mars-like UV flux [45]. While genes of the homologous recombination and base excision repair were over-expressed during the rehydration of cells exposed to space vacuum during the EXPOSE-R2 space mission [46]. In addition, the over-expression of genes for the trehalose and sucrose biosynthesis was detected during the air-drying of this cyanobacterium [47] in agreement with the role of these two sugars in preventing membrane phase transition and stabilization of cellular components within vitrified cells [48]. Indeed, this result contributes to unravel the molecular bases of the desiccation-tolerance of *Chroococcidiopsis* sp. CCMEE 029, a feature crucial for exposure in the ESA EXPOSE platforms that allow the integration only of dried cells [5], but also for future space experiments requiring in-orbit reactivation through rehydration [49,50].

2.4. Life support for human space exploration

Cyanobacteria-based technologies are gaining an increasing interest to develop sustainable systems to support human travel in deep space and outposts on the Moon and Mars [51]. The use of lithotrophic cyanobacteria in the so-called ISRU technology takes advance of their capability to produce oxygen and fix carbon, by using local resources like nutrients from Lunar and Martian soil, and carbon dioxide from the Martian atmosphere [52]. In the PowerCell concept, the biomass yielded from cyanobacteria cultivated using Moon and Mars raw materials, is used as feedstock for bacteria employed to produce needed consumables [53]. Indeed, cyanobacterial productivity can be augmented by increasing regolith concentrations, however, the growth with Martian regolith might be harmed by the presence of perchlorates [54] that being chaotropic agents, destabilize macromolecules and trigger oxidative stress [55]. A first investigation showed that *Chroococcidiopsis* sp. CCMEE 029 copes with perchlorates by over-expressing genes involved in the antioxidant defense and DNA damage repair [56]. On-going proteomics and genomics investigation in the context of the Space It Up project, will better elucidate how this cyanobacterium overcomes perchlorate-induced stress and contribute to fill the gaps to develop cyanobacterial-based life support systems.

In the context of the ASI ReBUS project, focusing on the study of a Bioregenerative Life Support System with the integration of different organisms (higher plants, fungi, bacteria, cyanobacteria, insects), a desert *Chroococcidiopsis* strain was shown to grow on Moon and Mars regolith simulants as well as to use water-released minerals, both supplemented with urea as a nitrogen source [16]. In addition, the yielded biomass was used as feedstock to grow bacteria of relevance for biotechnological processes. Such a feature is notable when developing cyanobacteria-based life systems especially if combined with the capability of this cyanobacterium to survive space conditions in the air-dried state, a feature that makes its transfer beyond Earth feasible (Fig. 2). Moreover, *Chroococcidiopsis* versatility to grow either in the planktonic state or as biofilm, along with its capability of using regoliths or water-released elements, might meet different technological requirements of

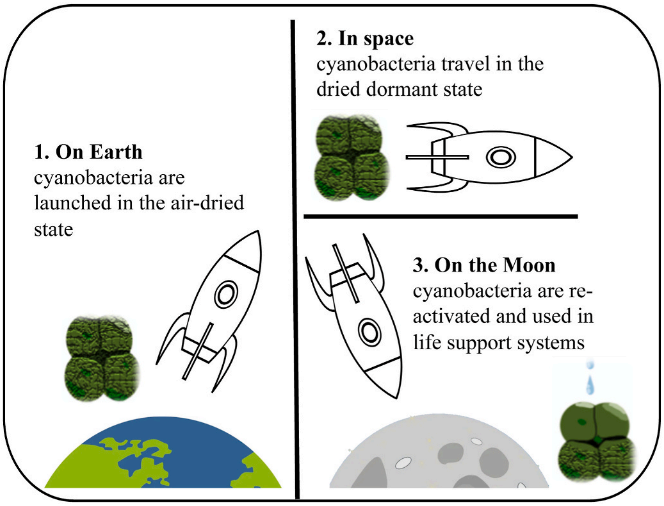

Fig. 2. Workflow of cyanobacterial-based technologies beyond Earth. Cyanobacteria are launched in the air-dried and travel through space in the dormant state and rehydrated once on the Moon (or Mars).

cultivation hardware designed for future space experimentations.

The challenge to develop cyanobacteria-based technologies consists in using cyanobacteria as PowerCell not only to convert *in situ* resources into organic compounds to feed bacteria for downstream production of consumables, but also to utilize cyanobacteria themselves to produce the needed supplies. No doubt this process will be accelerated by synthetic biology due to its approach based on genetic engineering and computational modelling [57]. Therefore, the realization of a tool kit to transform *Chroococcidiopsis* into a suitable chassis for space synthetic biology is foreseen to meet the request of novel solutions for consumable production and waste recycling for human settlements on the Moon or Mars.

3. Conclusions

The exposure of the desiccation-, radiation-tolerant desert strains of *Chroococcidiopsis* to challenging conditions beyond LEO will provide novel insights into what makes a world *hospitable to life and how to* support *human outposts beyond Earth.* Such a possibility is currently offered by the design and implementation of novel space platforms, such as satellites like CubeSats, the ESA/NASA Lunar Orbital Gateway as well as the ESA Large Logistics Lander, named Argonaut [38,39]. Since these platforms do not guarantee samples retrieval to Earth, technologies and payloads are needed to monitor active cellular metabolism and survival while in space.

No doubt future experiments using deserts *Chroococcidiopsis* strains will allow a deeper understanding of the boundaries where life can persist. Unravelling their response to the space environment will also support the development of sustainable bioprocesses for human deep-space travel and long-term presence on the Moon and Mars.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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