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Review article

Important extremophilic model microorganisms in astrobiology

Simge Emlik*[1], Sevgi Marakli[1]

[1] Yildiz Technical University, Faculty of Arts and Sciences, Department of Molecular Biology and Genetics, 34220, Istanbul, Türkiye

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Abstract

Humankind has been curious about the sky and beyond since its existence. Since the most primitive times, researchers have been trying to find answers to this curiosity. In recent years, a relatively new discipline, astrobiology, has emerged to answers to frequently asked questions. Astrobiology is an interdisciplinary field that tries to explain beyond the sky, and extraterrestrial life, where life origin came from, evolution, and the big bang. Extremophiles draw attention as the only creatures that will enlighten us in understanding extraterrestrial conditions and the mechanisms of creatures living in these conditions. This review examines the recent discoveries and the principal advances concerning both bacteria (*Chroococcidiopsis* sp., *Colwellia psychrerythraea*, *Planococcus halocryophilus*) and archaea (*Halorubrum lacusprofundi* and *Halobacterium salinarum* NRC-1) species which have potentials to examine in astrobiology as model organisms. Obtaining findings from different studies open new perspectives and strategies for several unresolved questions in astrobiology.

Keywords: *Chroococcidiopsis* sp.*; Colwellia psychrerythraea; Extremophiles; Halorubrum lacusprofundi; Halobacterium salinarum NRC-1; Martian environment; Planococcus halocryophilus*

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1. Introduction

Russian astronomer Gavriil Adrianovich Tikhov mentioned “astrobiology” for the first time in 1953 (Tikhov, 1953; Thombre et al., 2020). Later, the space age began and astrobiology studies have been accelerated with the first artificial satellite, Sputnik, in 1957. In 1960, Joshua Lederberg studied Exo-biology and explored any clue about life in the universe (Lederberg, 1960). Lederberg together with Carl Sagan instituted exobiology as a scientific study field in NASA. The discovery of a meteorite coming from Mars increased the interest in the exobiology area in 1996. This meteorite was named AH 84001 (Allan Hills 84001) and it was observed that it had microfossil-like organic compounds (Blumberg, 2003).

Researchers wanted to promote their studies related to astrobiology, hence the NASA Astrobiology Institute (NAI) established (Morrison, 2001). Moreover, ESA (European Space Agency) was also established in 1996 (Brack et al., 1999). Later, the European Astrobiology Network Association (EAA) was founded by the European astrobiology community in 2001. The aim is to collect information about astrobiology studies in European countries and provide collaborations among countries (Horneck et al., 2016). Thus, the term exobiology was replaced by astrobiology. Artemis program is generated by the world’s space agencies (NASA, CSA, ESA, JAXA, etc.). This program declared two main goals: going to the Moon and establishing a sustainable entity there by 2028 (Fernandez et al., 2023; Smith et al., 2020; Tarasashvili et al., 2023).

Model organisms can be easily produced, and observed, providing valuable information about their life cycle and other extinct and extant organisms. Therefore, the utilization of these species is very important to figure out what the life is. Among model organisms, extremophiles are also a fairly new field of study. Extremophiles have species in all domains. Due to their adaptations, species can live in harsh environments such as deserts, acidic mine drainage, volcanoes, glaciers, etc. Extremophiles are divided into categories according to the environments in which adapted. These divisions include

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* Corresponding author.
E-mail address: simge.emlik@std.yildiz.edu.tr (S. Emlik).

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thermophiles (develop above 55°C) (Atalah et al., 2019), psychrophiles (develop below 20°C) (Kirkinci et al., 2021), oligophiles (survive at low nutrient concentration) (Stan-Lotter, 2019), alkaliphiles (develop pH above 9.0) (Merino et al., 2019), acidophiles (grow at pH below 3-4) (Tripathi et al., 2021), halophiles (grow above 15% NaCl) (Stan-Lotter, 2019), barophiles or piesophiles (develop more than 0.1 MPa) (Sharma et al., 2022), etc.

The enzymes, metabolites, and biomolecules produced by extremophiles are important to survive in extreme environments and provide the usage of these organisms in biotechnological and industrial applications. In addition, these organisms are also used as model organisms for astrobiology. The aim of this study is to give detailed information and application areas of *Chroococcidiopsis* sp., *Colwellia psychrerythraea, Planococcus halocryophilus, Halorubrum lacusprofundi,* and *Halobacterium salinarum* NRC-1 which are important organisms for astrobiology.

2. Model microorganisms in astrobiology

2.1. Chroococcidiopsis sp.

Chroococcidiopsis sp. is a cyanobacterium and is considered an eoanhydrobiotes, which can survive in cases of extreme desiccation (Billi and Potts, 2002; Li et al., 2022). The member of this genus lives in the dry valleys of Antarctica (Billi, 2020), the Mojave Desert in California (Billi et al., 2013), the hyper-aridity core of the Atacama Desert in Chile (Wierzchos et al., 2006; Stivaletta et al., 2012; Billi et al., 2013) and the Ross Desert in Antarctica. These areas are analogous to Martian conditions, so can be examined to understand the Martian environment and how to live in these conditions. The extraordinary abilities of these microorganisms are to tolerate desiccation, UV radiations, and ionization, making them suitable model organisms (Billi et al., 2013). *Chroococcidiopsis* sp. can be unicellular or can form few-celled packets with a non-motile state.

This extreme genus has several features to combat harsh conditions. *Chroococcidiopsis* sp. has only one nitrogenase for fixation. It protects itself against high UV rays by forming and embedding slime (Baqué et al., 2013; Billi et al., 2019). The pigment formation such as carotenoids and scytonemin provides extra support against UV damage (Vítek et al., 2014; Bothe, 2019). In addition, *Chroococcidiopsis* sp. has an effective antioxidant mechanism that prevents proteins from oxidative damage. This mechanism also protects it from desiccation (Fagliarone et al., 2017). Furthermore, *Chroococcidiopsis* sp. carry out photosynthesis at 51°C (Tracy et al., 2010) and also withstands higher atmospheric pressure (Thomas et al., 2008). At high temperatures, the chances of survival in a desiccated state are higher than in a hydrated state (Cockell et al., 2017). Tolerance against acidic conditions (between pH 3 and 7) are also observed (Del Arco et al., 2018; Bothe, 2019).

Chroococcidiopsis sp. has been used in various experiments in Low Earth Orbit (LEO), simulations based on the ground of space, and Martian conditions to search for clues of life (Rabbow et al., 2009; 2017). Colonization in the interior of evaporites (3-7 mm below the halite crust) is an important research topic in different Martian areas (Stivaletta et al., 2012; Billi et al., 2013). In addition, a terrestrial analog of Martian carbonates has been found in the Mojave Desert (Bishop et al., 2011; Billi et al., 2013). In this desert, *Chroococcidiopsis* sp. found mainly when compared to other microorganisms in red-coated carbonate rocks. It can also be tested for the panspermia theory, as the amount of observable oxygen in the planet's atmosphere increased as cyanobacteria, suggesting that oxygen may act as an indicator for the presence of life (Billi et al., 2013).

In a study, *Chroococcidiopsis* sp. CCMEE 029 was collected from the Negev Desert, and it survived 4 years in polycarbonate filters and Petri dishes, (Billi, 2009; Fagliarone et al., 2017) and 13 years in desiccated agar (Cockell et al., 2017). Moreover, it was showed that dried *Chroococcidiopsis* sp. CCMEE 029 can resist up to 24 kGy of γ-radiation (Verseux et al., 2017; Mosca et al., 2019). The dried monolayers can withstand a UV flux similar to Mars of 15 kJ/m^2. (Cockell et al., 2005). These results are valuable because understanding the mechanisms of desiccation tolerance will also help explain resistance under various stresses including high vacuum and radiation from space.

In a different study, *Chroococcidiopsis* sp. was isolated from solar panels and was transformable using SEVA vectors. (Baldanta et al., 2023). These vectors contain the Cpf1 nuclease, a typical CRISPR enzyme. It is suggested that this cyanobacterium with its genetically modified and strengthened features as well as its own characteristics will become a useful tool in many fields. In addition, *Chroococcidiopsis* sp. can grow in the presence of sugars such as sucrose, maltose, glucose, and fructose but cannot grow in sugary environments such as lactose, mannose, galactose, arabinose, and glycerol. The fact that *Chroococcidiopsis* sp. can also use urea as a nitrogen source in an environment such as Mars. A similar study was performed by Fernandez et al. (2023). According to their findings, *Chroococcidiopsis* sp. CCMEE 029 can serve as both a PowerCell and a nitrogen source for human synthetic urine. *Chroococcidiopsis* sp. is also important due to the use of wastewater for recycling (Baldanta et al., 2023).

Li et al. (2022) studied the change in physiological and transcriptional properties of *Chroococcidiopsis* sp. ASB-02 when it was exposed to near space in the HH-21-5 mission. It was shown a decrease in photosystem II (PSII) activity and an increase in ROS (reactive oxygen species) levels but the number of living cells remained high. Expression of extracellular polysaccharides and regulation of carotenoid and scytonemin biosynthesis genes reduced the amount of radiation reaching the cells after exposure to UV radiation. Genes involved in protein synthesis were also activated in response to cold conditions in addition to radiation. It was also noted that genes in several DNA and PSII repair pathways were elevated after rehydration. This proved that cells' DNA and PSII proteins had been damaged, highlighting the necessity of repair mechanisms for the cyanobacterium's recovery.

2.2. Colwellia psychrerythraea

Colwellia psychrerythraea belonging to the Colwelliaceae family is a marine heterotrophic bacterium (Liu et al., 2020). This bacterium has become important for studying adaptive strategies against cold and salinity habitats and may be for extraterrestrial conditions (Mudge et al., 2021; Casillo et al., 2022). This species can grow at -12°C to 22°C, and 15 to 70 ppt in salinity (Wells and Deming, 2006). Due to its genome and many eccentric biochemical characteristics, it has become a model microorganism for carbon cycling in cold sea sediments. It can also be utilized for observing growth and survival under simulated Martian conditions (Hallsworth et al., 2021).

It is a polyextremophilic bacterium species isolated from sub-zero marine sediments. *C. psychrerythraea* strain 34H (*Cp*34H) is a Gram-negative psychrophile isolated from Arctic marine sediments at -1°C (Huston, 2003; Methé et al., 2005). To endure fluctuations in salinity in sea ice brines, this strain can transport suitable solutes (small molecular weight organic molecules (Firth et al., 2016). *Cp*34H can live in the cold dark ocean without proteorhodopsins which are photoactive proteins utilized by many bacteria in the ocean to produce additional energy (Béja, 2001).

Enzymes involved in adaptation to cold stress show great economic and ecological benefits in terms of their structures and functions (Kavitha, 2016). It has been shown that *Cp*34H can produce functional extracellular enzymes even in the harshest conditions (-8°C, 35 ppt). Compared to warmer temperatures, enzyme activity rates increased at less extreme temperatures (-1°C) (Huston et al., 2000). On the other hand, *Cp*34H can still survive for a short time when exposed to a warmer and stressful room temperature (Showalter and Deming, 2018). It was also reported that catabolic pathways and flagella-related genes were significantly downregulated as a result of transcriptomic analyses (Czajka et al., 2018; Showalter and Deming, 2018).

*Cp*34H has a proteome with 4910 predicted proteins (Methé et al., 2005) and 2362 of them were identified (Mudge et al., 2021). Proteins play roles in diverse cellular motility consisting of flagellar, pilus, and chemotaxis. This situation supports the results of previous investigations of *Cp*34H in response to sub-zero temperatures, offering biomarkers for motility for life as requested by NASA's Ladder of Life Detection (Nunn et al., 2015; Showalter and Deming, 2018; Neveu et al., 2018). Future astrobiology missions must be able to find biomarkers because the majority of the solar system's planets have high salinities, little water activity, and temperatures below the freezing point of water (Carr et al., 1998; Khurana et al., 1998; Hand et al., 2009; Parro et al., 2018; Hendrix et al., 2019). Findings of small (3–4 amino acid) peptides on ice worlds that are analogous to those found on Earth are crucial for the discovery of observable biomarkers for life in the future (Mudge et al., 2021). Four physiological states were observed in *Cp*34H after 1 month of incubation period: growing and culturable cells (high activity and culturability at -5°C, artificial seawater), active cells (low activity and acceptable culturability at -5°C in brine), viable but not culturable (acceptable activity and very low or no culturability at -10°C, artificial seawater without nutrient) and surviving cells (very low to no activity and not culturable at -10°C in brine) (Mudge et al., 2021).

2.3. *Planococcus halocryophilus*

Planococcus consists of Gram-positive and aerobic cocci. Like other species mentioned above, *Planococcus* can grow at moderate/low temperatures and in salt environments (Arctic, Antarctic, marine) (Mykytczuk et al., 2012). Moreover, some *Planococcus* species are resistant to heavy metals, and some can detoxify pollutants (Li et al., 2006; Hupert-Kocurek et al., 2014; Jung et al., 2018). It is very important to examine this bacterium in non-NaCl salty and sub-zero temperature habitats, and this topic has gained interest in astrobiology (Heinz et al., 2018). In this sense, *P. halocryophilus* is an ideal model organism for Martian environments (Heinz et al., 2018).

P. halocryophilus lives in an active permafrost soil layer in the Canadian High Arctic. It is a psychrotolerant bacterium adapted to cold stress due to the expression of several osmolyte transporters, cold-adapted proteins, and carbohydrate storage as energy (Mykytczuk et al., 2013, 2016). While it can grow at a concentration of 19% NaCl (w/v) and -15°C, some studies reported that it has metabolic activity at -25°C (Mykytczuk et al., 2013; Raymond-Bouchard et al., 2017).

According to laboratory investigations, the survival of cryotolerant and halotolerant bacterial species in concentrated brine depends on the salt concentration, anion parameters, and water activity. The potential habitability of Martian cryobrines was therefore discovered to depend on factors such as anion brine composition, salt content, and water activity (Waajen et al., 2020). It is known that several chlorides (Cl^-) and perchlorate (ClO_4^-) salts are found in Martian soils (Hecht et al., 2009; Kounaves et al., 2010). How well and how long *P. halocryophilus* can survive multiple freeze/thaw cycles, subzero Cl^- and ClO_4^- brines have been explored since these extreme conditions on Mars may exist momentarily and/or continue cyclically (Martínez and Renno, 2013). Heinz et al. (2018) reported that the survival rate of this bacterium in samples containing Cl^- was higher than in ClO_4^- samples at all temperatures. Furthermore, it was also revealed that lifespan enhanced systematically with decreasing temperatures in Cl^- and ClO_4^- samples.

2.4. *Halorubrum lacusprofundi*

In addition to bacteria, the archaea species have been widely examined in extreme conditions and astrobiology. *Halorubrum lacusprofundi* is one of them. It is a halophilic species with vivid pigmentation that forms biofilms in the hypersaline Deep Lake in Antarctica (Anderson et al., 2016). *H. lacusprofundi* can live anaerobically by using perchlorate as a terminal electron acceptor, providing a metabolism for the probability of survival on the Red Planet (DasSarma et al., 2020).

H. lacusprofundi grows optimally at 31-37°C (Franzmann et al., 1988) but can also live in Antarctica (-18°C to 11,5°C and 21-28%, w/v salt content). Moreover, it develops approximately 3.5 M NaCl concentration (DasSarma et al., 2013; DasSarma and DasSarma, 2018; Laye and Dassarma, 2018). It is crucial to determine the limits of adaptation to hypersaline and low-temperature conditions to predict the presence of life in the icy shells (Trumbo et al., 2019) and oceans of Europa and Enceladus (Lobo et al., 2021), the permafrost on Mars (Morozova et al., 2007), subterranean lakes (Lauro et al., 2021) by using *H. lacusprofundi*. It can also grow anaerobically at low ClO_4^- concentrations. Moreover, reports have shown that magnesium perchlorate ($MgClO_4^-$) is inhibited the growth with greater sensitivity than sodium perchlorate ($NaClO_4^-$) at significantly higher concentrations (50% inhibition at 0.3 M for sodium perchlorate, 0.1 M for magnesium perchlorate) (Laye and Dassarma, 2018). As a result of spectroscopic analysis, Martian soil was found to contain poisonous $NaClO_4^-$ and $MgClO_4^-$ (Mattie et al., 2006; Wadsworth and Cockell, 2017). The levels of growth inhibition and enzyme activity demonstrated that extreme halophiles like *H. lacusprofundi* will not be adversely affected by the anticipated levels of ClO_4^- salts on Mars (Laye and Dassarma, 2018).

2.5. *Halobacterium salinarum NRC-1*

Halobacterium is a halophilic archaea that can develop in hypersaline aquatic environments (DasSarma et al., 2018). *Halobacterium* can be visible as red, pink, or purple due to carotenoids found in their membranes. *Halobacterium* can live in multiple extreme conditions and therefore, are also called polyextremophiles. Similar to other organisms mentioned in this review, these organisms can use as model organisms for astrobiology, thus also given the name “exophiles” (DasSarma, 2006; DasSarma and DasSarma, 2017; DasSarma and DasSarma, 2018). Halophilic archaea show different ways of production of energy and even anaerobic development (Sundarasami et al., 2019). These organisms use trimethylamine N-oxide $[(CH_3)_3NO]$, dimethyl sulfoxide (DMSO), fumarate $(C_4H_4O_4)$, ClO_4^-, and chlorate (ClO_3^-) instead of oxygen as electron acceptors, making them good alternatives for investigations (Müller and DasSarma, 2005; Oren, 2014).

H. salinarum is a rod-shaped, motile, and highly halophilic archaea. The most extensively researched haloarchaeal genome is the 2.57 Mbp genome of *H. salinarum* NRC-1 which was the first genome to be fully sequenced. It has high genetic diversity due to the high GC content of the parent chromosome (~68%) compared to its plasmid (57-60% G+C) (Ng et al., 2000; Pfeiffer et al., 2008). This extremophile model of archaea has been taken into consideration and thoroughly explored, leading to various discoveries and knowledge about the biology of archaea and the adaptations needed to survive in saturated salt concentrations (Soppa, 2006; Beer et al., 2014).

Furthermore, the processes of resistance to high and low osmolarity, high and low temperatures, UV and ionizing radiation have been studied in investigations on *H. salinarum* NRC-1 (DasSarma, 2006). It is believed that because of its effective light and dark healing mechanisms, it can withstand UVC rays up to 100 J/m^2. In one study, *Halococcus dombrowskii*, *H. salinarum* NRC-1 and *Haloarcula japonica* were grown halite after that exposed to UV radiation (200-400 nm) to simulate flux similar to the Martian surface. As a result of the study, it was reported that the cells did not show any loss of viability after exposure to 21 kJ/m^2 radiation. Then the cells continued to grow after 12 days in the liquid medium following the exposure to total radiation of 148 kJ/m^2 (Fendrihan et al., 2009).

3. Conclusion

Organisms living in extreme conditions provide detailed information about not only life on Earth but also space which is the area of astrobiology. This topic has gained interest in the last decades; therefore, studies in multidisciplinary areas are carried out by simulating environmental conditions that are comparable to the conditions in space. In this respect, extremophiles draw attention due to their characteristics including living in low/high temperatures, radiation, salt environments, etc. On the other hand, it is worth pointing out that it is the beginning stage to examine microorganisms to have the potential for usage of astrobiology. As a result, significant advancements in astrobiology could result from fascinating discoveries in the microbial world during the next years, providing a profound effect on how is seen the nature of life.

Conflict of interest: The authors declare that they have no conflict of interests.

Informed consent: The authors declare that this manuscript did not involve human or animal participants and informed consent was not collected.

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