




REVIEW ARTICLE

Bacteria *Acidithiobacillus ferrooxidans*, terrestrial analogue of extraterrestrial microorganisms?

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Abstract

In this comprehensive review, *Acidithiobacillus ferrooxidans*, an acidophilic bacterium, has been thoroughly examined as a plausible analogue for microbial life in Venus's lower cloud layer. Given its ability to adapt to extreme conditions, including low pH environments and metal-rich settings, *Acidithiobacillus ferrooxidans* is considered a promising candidate for studying life analogues in Venus's clouds. This article comprehensively analyses the bacterium's distinctive phenotypic and genotypic features, investigating its metabolic pathways, adaptive strategies and potential ecological niche within Venusian cloud ecosystems. After careful consideration of the environmental parameters characterizing Venus, the unidentified UV absorber in its clouds, and the prospects for microbial life, this review underscores the imperative nature of future Venus missions and the pivotal role that *Acidithiobacillus ferrooxidans* may play in exploring the possible habitability of Venus and advancing astrobiological research.

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Introduction

Extremophiles are organisms such as prokaryotic bacteria and archaea and eukaryotic organisms (Salwan and Sharma, 2020) that are able to grow, from an anthropocentric point of view, in extreme and inhospitable environmental conditions (Gallo *et al.*, 2021) such as high or low pH, or very low or high temperature (Rampelotto, 2013). Moreover, various types of extremophiles, such as psychrophiles and thermophiles, in the case of Deception Island volcano in Antarctica, can coexist (Bendia *et al.*, 2018). Extremophiles have adapted to life in extremely harsh conditions, evolving traits that

allows them to survive in given physicochemical conditions (Horikoshi *et al.*, 2010). The extremophiles can be delineated according to a given environmental factor and the limit values for specific terrestrial microorganisms (Table 1).

In this review, after taking into account the environment and physicochemical conditions in the lower layer of Venus clouds located 47.5–50.5 km above its surface, the focus was on a representative of acidophilic extremophiles, the bacterium *Acidithiobacillus ferrooxidans*. Studies on the properties of this bacterium, in particular experimental studies under laboratory-recreated conditions prevailing in the lower layer of Venus clouds, may contribute to distinguishing the types of terrestrial analogues to those potentially existing in the clouds of this microbial planet (Limaye *et al.*, 2018).

A brief description of acidophilic bacteria and their natural environment

Acidophiles are organisms that grow optimally in an environment with a pH significantly lower than 7 (Johnson, 2007). The environment of moderate acidophiles is characterized by a pH in the range of 3–5, while extreme acidophiles develop at a pH less than 3 (Johnson, 2007). The intracellular pH of acidophilic organisms is approximately neutral (Johnson, 2007). The methods developed by acidophiles to maintain this pH are: (a) high impermeability of their cell membranes to hydronium ions (H_3O^+), as well as (b) positive potential within these membranes (Johnson, 2007). Extreme acidophiles are strictly microorganisms and can be both prokaryotes and eukaryotes (Johnson, 2007), with representatives found in each of the three domains in the phylogenetic tree of life (Johnson, 2007). The group of acidophilic, iron- and sulphur-oxidizing organisms includes microorganisms such as (Johnson, 2007): *Leptospirillum* spp. (*Leptospirillum ferrooxidans*, *Leptospirillum thermoferrooxidans*, *Leptospirillum ferriphilum*, *Leptospirillum ferrodiazotrophum*), *Acidithiobacillus* spp. (*Acidithiobacillus ferrooxidans*, *Acidithiobacillus thiooxidans*, *Acidithiobacillus albertensis*, *Acidithiobacillus caldus*), *Hydrogenobaculum acidophilum* (*Hydrogenobaculum acidophilum*,

Table 1. Classification of extremophilic organisms, taking into account their limit values for growth

Species of extremophile	Environmental factor limiting development	Limits of the environmental factor/bacterium
Acidophiles	Low pH	pH = –0.06 <i>Picrophilus torridus</i> (Schleper <i>et al.</i> , 1996)
Alkaliphiles	High pH	pH = 13 <i>Plectonema nostocorum</i> and <i>Hydrogenophaga</i> sp. (Coker, 2019)
Halophiles	Salinity	6 M NaCl <i>Halorubrum sfaxense</i> sp. nov. (Amoozegar <i>et al.</i> , 2017)
Hyperthermophiles	High temperature	$T = 129^\circ\text{C}$ <i>Geogemma barossii</i> (Sunny <i>et al.</i> , 2021)
Piezophiles	Pressure	$p = 100\text{ MPa}$ <i>Shewanella benthica</i> (Zhang <i>et al.</i> , 2019a)
Psychrophiles	Low temperature	$T = -12^\circ\text{C}$ <i>Psychromoa ingrahamii</i> (Sunny <i>et al.</i> , 2021)
Radioresistants	Radiation	$>100\text{ J m}^{-2}$ (UV) $>12\text{ kGy}$ (gamma radiation) <i>Halobacterium</i> sp. <i>NRC-1</i> and <i>Deinococcus radiodurans</i> (Coker, 2019)
Xerophiles	Low water activity (a_w)	$a_w = 0.62$ <i>Xeromyces bisporus</i> (Su-lin <i>et al.</i> , 2011)

Hydrogenobaculum (H55)), and *Thiobacillus* spp. (*Thiobacillus thioparus*, *Thiobacillus prosperus*, *Thiobacillus ferrooxidans*). Acidophilic sulfur-oxidative archaea are represented by: *Sulfolobus acidocaldarius*, *Sulfolobus metallicus*, *Sulfolobus tokodaii*, *Metallosphaera* spp. and *Sulfurococcus yellowstonensis*.

Characteristics of the *Acidithiobacillus ferrooxidans* bacteria

Acidithiobacillus ferrooxidans, a genus of Gammaproteobacteria, are known for their role as sulphur and iron oxidants (Schuler and Tsuchiya, 1975) and are classified as Gram-negative, chemolithoautotrophs (Wang *et al.*, 2024). This means that they can grow on inorganic substances (Lin *et al.*, 2024). This ability to utilize inorganic substrates in extreme conditions, such as very low pH environments, makes them an important model for studying extraterrestrial life. These bacteria, originally isolated from a sour coal mine and described by Colmer and Hinkle (1947), gained recognition for their unique morphological and physiological properties. Before the reclassification in 2000 (Kelly and Wood, 2000), *Acidithiobacillus ferrooxidans* bacteria were known as *Thiobacillus ferrooxidans* (Zhang *et al.*, 2018c). In this study 98 strains of them were listed (Table 2). Moreover, micrographs of *Acidithiobacillus ferrooxidans*, strain DSM 583 are presented (Figs. 1 and 2).

These microorganisms do not produce spore forms (Quatrini and Johnson, 2019) and are widespread in nature (Zhang *et al.*, 2018c), inhabiting various geoclimactic natural environments characterized by low pH (Quatrini and Johnson, 2019). Across the different strains of *Acidithiobacillus ferrooxidans*, there are differences in oxidative ability of the same substrates, resistance to heavy metal ions, and optimal pH and temperature for growth (Ageeva *et al.*, 2001). These bacteria can grow in mineral rich, acid

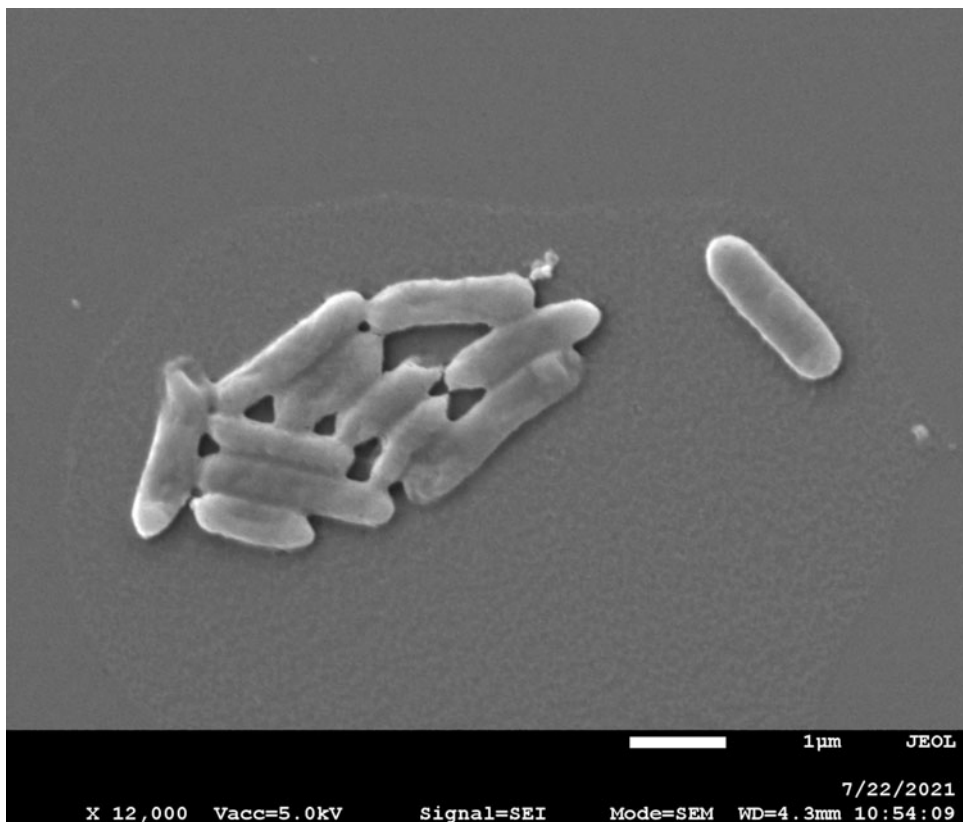


Figure 1. Micrograph of *Acidithiobacillus ferrooxidans* (DSM 583) at 12 000 \times magnification.

Table 2. *Strains of the Acidithiobacillus ferrooxidans bacteria*

2Y	Harneit <i>et al.</i> (2006)
A1	Leduc <i>et al.</i> (1997)
A2	Harneit <i>et al.</i> (2006)
AK1	Braddock <i>et al.</i> (1984)
A-4	Harneit <i>et al.</i> (2006)
AP19-3	Sugio <i>et al.</i> (2003)
ATCC 13661	Baldi <i>et al.</i> (1992), Valkova-Valchanova and Chan (1994)
ATCC 14859	Kaewkannetra <i>et al.</i> (2009)
ATCC 19859	Espejo and Romero (1987), Brahmprakash <i>et al.</i> (1988), Barron and Lueking (1990), Holmes <i>et al.</i> (2001), Brasseur <i>et al.</i> (2004), Harneit <i>et al.</i> (2006), Priya and Hait (2020), Escobar and Godoy (2002)
ATCC 21834	Pronk <i>et al.</i> (1991)
ATCC 23270	Ronk <i>et al.</i> (1991), Sampson and Blake (1999), Giudici-Ortoni <i>et al.</i> (2000), Yarzabal <i>et al.</i> (2002a), Harneit <i>et al.</i> (2006), Valdés <i>et al.</i> (2008), Nieto <i>et al.</i> (2009), Esparza <i>et al.</i> (2010), Thurston <i>et al.</i> (2010), Bustamante <i>et al.</i> (2012), Ponce <i>et al.</i> (2012), Bustamante <i>et al.</i> (2014), Liu <i>et al.</i> (2015), Dekker <i>et al.</i> (2016), Kocaman <i>et al.</i> (2016), Ai <i>et al.</i> (2018), Jung <i>et al.</i> (2022)
ATCC 33020	Oppon <i>et al.</i> (1998), Appia-Ayme <i>et al.</i> (1999), Yarzabal <i>et al.</i> (2002a), Yarzabal <i>et al.</i> (2002b), Yarzabal <i>et al.</i> (2003)
ATCC 53993	Orellana and Jerez (2011), Bustamante <i>et al.</i> (2014), Ramos-Zúñiga <i>et al.</i> (2019)
B-458-Cu	Kondrat'eva <i>et al.</i> (2002)
B-86	Belyi <i>et al.</i> (2006)
BRGM	Giudici-Ortoni <i>et al.</i> (2000)
BKM B-458	Kondrat'eva <i>et al.</i> (2002)
BY-3 (CCTCC-M203071)	Yan <i>et al.</i> (2010), Chen <i>et al.</i> (2011)
BYQ-12	Yan <i>et al.</i> (2017)
C-52	Gehrke <i>et al.</i> (2001), Harneit <i>et al.</i> (2006)
CCM 4253	Ceskova <i>et al.</i> (2002), Pakostova <i>et al.</i> (2013a, 2013b), Kucera <i>et al.</i> (2016)
CCTCC M20405	Yang <i>et al.</i> (2008)
ConTf	Mason and Rice (2002)
CUMT-1	Feng <i>et al.</i> (2012), Feng <i>et al.</i> (2015)
D2	Leduc <i>et al.</i> (1997)
D6	Leduc <i>et al.</i> (1997)
D7	Leduc <i>et al.</i> (1997)
DECp	Harneit <i>et al.</i> (2006)
DLC-5	Xu <i>et al.</i> (2019)
DSM 583	Baillet <i>et al.</i> (1998), Sampson and Blake (1999), Harneit <i>et al.</i> (2006)
DSM 584	Africa <i>et al.</i> (2013)
DSM 14882	Tan and Chen (2012)
DSM 16786	Latorre <i>et al.</i> (2016)
DSMZ 583	Haghshenas <i>et al.</i> (2009)
F1	Leduc <i>et al.</i> (1997)
FC1	Harvey and Crundwell (1997), Fowler and Crundwell (1999)
FY-3	Leng <i>et al.</i> (2009)
GF	Yang <i>et al.</i> (2013)
KCTC 2677	Soo <i>et al.</i> (2002), Ko <i>et al.</i> (2013)
LR	Novo <i>et al.</i> (2000), Bevilaqua <i>et al.</i> (2002)

MAL 4-1	Natarajan <i>et al.</i> (1994), Devasia and Natarajan (2010)
MON-1	Sugio <i>et al.</i> (2003)
NatTf	Mason and Rice (2002)
N1	Leduc <i>et al.</i> (1997)
N2	Leduc <i>et al.</i> (1997)
NCIB 8455	Bacon and Ingledew (1989)
NFP31	Kato <i>et al.</i> (2022)
PD-2	Lei and Xie (2012)
PH	Harneit <i>et al.</i> (2006)
PTCC 1647	Haghshenas <i>et al.</i> (2009)
R1	Leduc <i>et al.</i> (1997), Gehrke <i>et al.</i> (2001), Harneit <i>et al.</i> (2006)
R2	Rojas-Chapana and Tributsch (2001)
R6	Harneit <i>et al.</i> (2006)
R7	Gehrke <i>et al.</i> (2001), Harneit <i>et al.</i> (2006)
R9	Harneit <i>et al.</i> (2006)
R10	Harneit <i>et al.</i> (2006)
S2	Leduc <i>et al.</i> (1997)
SPIII/3	Gehrke <i>et al.</i> (2001), Harneit <i>et al.</i> (2006)
SPIII/7	Harneit <i>et al.</i> (2006)
SUG2-2	Sugio <i>et al.</i> (2003)
T23-3	Kawabe <i>et al.</i> (2003)
TFAs2	Kondrat'eva <i>et al.</i> (2002)
TFBk	Ageeva <i>et al.</i> (2001), Kondrat'eva <i>et al.</i> (2002), Ageeva <i>et al.</i> (2003)
TFBk-Cu	Kondrat'eva <i>et al.</i> (2002)
TFI	Kondrat'eva <i>et al.</i> (2002)
TFI-Fe	Kondrat'eva <i>et al.</i> (2002)
TFN-d	Ageeva <i>et al.</i> (2001), Kondrat'eva <i>et al.</i> (2002), Ageeva <i>et al.</i> (2003)
TFD	Kondrat'eva <i>et al.</i> (2002)
TFG	Kondrat'eva <i>et al.</i> (2002)
TFI-35	Bhatti <i>et al.</i> (1993)
TFO	Ageeva <i>et al.</i> (2001), Kondrat'eva <i>et al.</i> (2002), Ageeva <i>et al.</i> (2003)
TFL-2	Ageeva <i>et al.</i> (2001), Kondrat'eva <i>et al.</i> (2002), Ageeva <i>et al.</i> (2003)
TFNi-3	Kondrat'eva <i>et al.</i> (2002)
TFR1	Kondrat'eva <i>et al.</i> (2002)
TFV-1	Ageeva <i>et al.</i> (2001), Kondrat'eva <i>et al.</i> (2002), Ageeva <i>et al.</i> (2003)
TFV-1-Cu	Kondrat'eva <i>et al.</i> (2002)
TFK _m	Kondrat'eva <i>et al.</i> (2002)
TFN	Kondrat'eva <i>et al.</i> (2002)
TFP	Kondrat'eva <i>et al.</i> (2002)
TFT	Kondrat'eva <i>et al.</i> (2002)
TFU _{ch}	Kondrat'eva <i>et al.</i> (2002)
TFU _d 2	Kondrat'eva <i>et al.</i> (2002)
TFU _d 3	Kondrat'eva <i>et al.</i> (2002)
TfW	Das <i>et al.</i> (1997), Das <i>et al.</i> (1998)
TfCu ₂₀	Das <i>et al.</i> (1998)
TFW _c	Kondrat'eva <i>et al.</i> (2002)
TKY-2	Leng <i>et al.</i> (2009)
TFZ	Kondrat'eva <i>et al.</i> (2002)
TM	Silverman and Lundgren (1959)
VKM-458	Kondratyeva <i>et al.</i> (1995)

VKM458As2	Kondratyeva <i>et al.</i> (1995)
W1	Leduc <i>et al.</i> (1997)
W-18	Lei and Xie (2012)
WR1	Harneit <i>et al.</i> (2006)
WR2	Harneit <i>et al.</i> (2006)
XZ11	Zhang <i>et al.</i> (2015)
Yellow 7	Harneit <i>et al.</i> (2006)
YNTRS-40	Zhang <i>et al.</i> (2019b)

ATCC, American Type Culture Collection; CCM, Czech Collection of Microorganisms; KCTC, Korean Collection of Type Cultures.

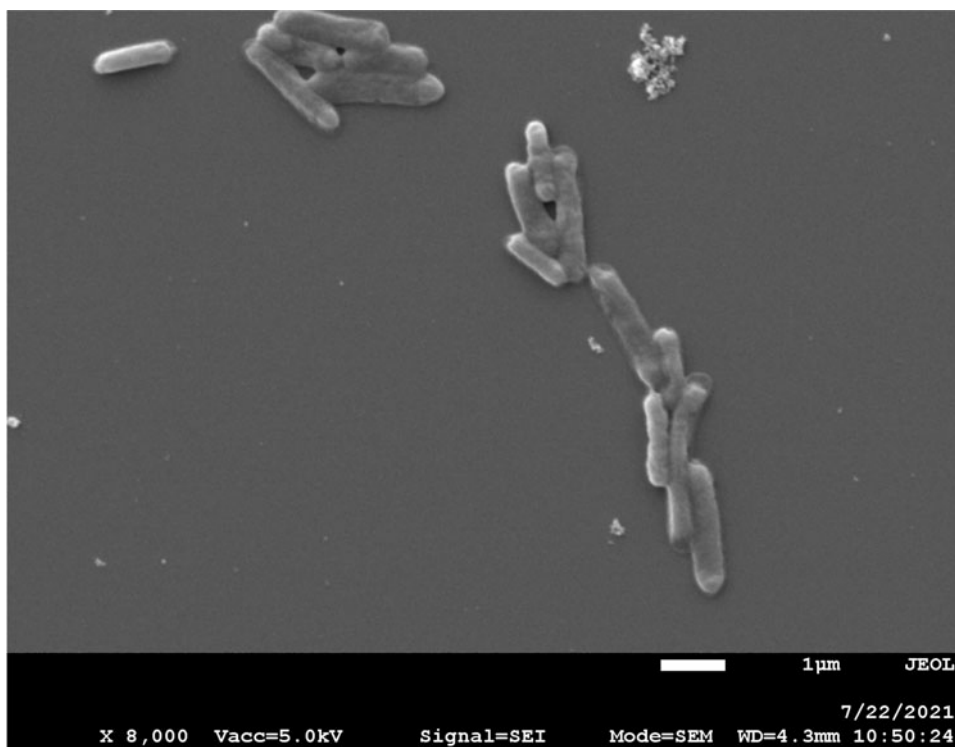


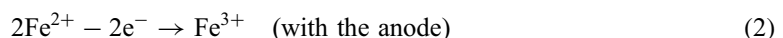
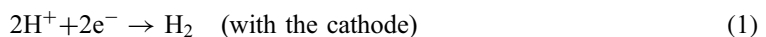
Figure 2. Micrograph of *Acidithiobacillus ferrooxidans* (DSM 583) at 8000× magnification.

environments containing different elements (Table 3). They are found in sulphated soils and rocks as well as in mine waters containing uranium ore (Berthelot *et al.*, 1993), being resistant even to high concentrations of uranium in ore (Dekker *et al.*, 2016). The optimal pH for most strains of *Acidithiobacillus ferrooxidans* is about 2 (Quatrini and Johnson, 2019). The minimum pH required for growth ranges from 1.3 to 1.5, depending on the strain of this bacterium (Johnson, 2007), while the typical extracellular pH values in which they grow are from 1.5 to 3 (Quatrini and Johnson, 2019). The intracellular pH of *Acidithiobacillus ferrooxidans* is about 6.5 (Quatrini and Johnson, 2019). Carbon necessary for the biosynthesis of cellular material is obtained by assimilating carbon dioxide (Campodonico *et al.*, 2016) from the atmosphere in the Calvin–Benson–Bassham cycle (CBB) (Gale and Beck, 1967; Esparza *et al.*, 2010; Quatrini and Johnson, 2019). These bacteria are diazotrophic organisms that can also bind atmospheric nitrogen and assimilate ammonia (Valdés *et al.*, 2008). As an alternative source for phosphorus, *Acidithiobacillus ferrooxidans* can use ethyl and methyl phosphonates for their growth (Vera *et al.*, 2008). They can also proliferate under high

Table 3. Division of *Acidithiobacillus ferrooxidans* bacteria into strains via bacterial activity

Arsenic	Braddock <i>et al.</i> (1984), Collinet and Morin (1990), Kondratyeva <i>et al.</i> (1995), Harvey and Crundwell (1997), Makita <i>et al.</i> (2004), Chen <i>et al.</i> , (2012), Yan <i>et al.</i> (2017), Park <i>et al.</i> (2014)
Chromium	Baillet <i>et al.</i> (1998)
Cadmium	Ramos-Zúñiga <i>et al.</i> (2019)
Cobalt	Gholami <i>et al.</i> (2011)
Cuprum	Torma <i>et al.</i> (1976), BrahmaPrakash <i>et al.</i> (1988), Natarajan <i>et al.</i> (1994), Das <i>et al.</i> (1997), Das <i>et al.</i> (1998), Novo <i>et al.</i> (2000), Bevilaqua <i>et al.</i> (2002), Mason and Rice (2002), Mejía <i>et al.</i> (2009), Yang <i>et al.</i> (2009), Yang <i>et al.</i> (2013), Feng <i>et al.</i> (2015), Liu <i>et al.</i> (2015), Kocaman <i>et al.</i> (2016), Latorre <i>et al.</i> (2016), Zhang <i>et al.</i> (2016), Donati <i>et al.</i> (1996), Duncan <i>et al.</i> (1967), Wang <i>et al.</i> (2009)
Ferrum	Das <i>et al.</i> (1997), Harvey and Crundwell (1997), Bevilaqua <i>et al.</i> (2002), Mason and Rice (2002), Bayat <i>et al.</i> (2009), Liu <i>et al.</i> (2015)
Gold	Nestor <i>et al.</i> (2001)
Lead	Garcia <i>et al.</i> (1995), Nike <i>et al.</i> (2012)
Manganese	Belyi <i>et al.</i> (2006)
Mercury	Novo <i>et al.</i> (2000), Sugio <i>et al.</i> (2003)
Molybdenum	Olson and Clark (2008), Gholami <i>et al.</i> (2011)
Nickel	Novo <i>et al.</i> (2000), Mason and Rice (2002), Yang <i>et al.</i> (2008), Gholami <i>et al.</i> (2011)
Selenium	Bacon and Ingledew (1989)
Tellurium	Lei and Xie (2012), Choi <i>et al.</i> (2018)
Uranium	Abhilash <i>et al.</i> (2009), Rashidi <i>et al.</i> (2012), Dekker <i>et al.</i> (2016)
Zinc	Brahmaprakash <i>et al.</i> (1988), Kondratyeva <i>et al.</i> (1995), Das <i>et al.</i> (1997), Fowler and Crundwell (1999), Novo <i>et al.</i> (2000), Bayat <i>et al.</i> (2009), Haghshenas <i>et al.</i> (2009), Kaewkannetra <i>et al.</i> (2009)

pressure (Zhang *et al.*, 2018a). *Acidithiobacillus ferrooxidans* bacteria play an important ecological role in the bioremediation process due to their ability to decontaminate soil and industrial wastewater from heavy metals (Appia-Ayme *et al.*, 1999). As electro-trophs, this bacterium can grow powered by electrons from cathodes and anodes, according to the following reactions (Yamanaka, 2008):

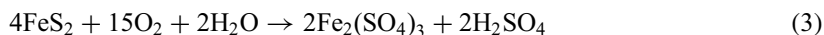


Acidithiobacillus ferrooxidans can also grow anaerobically (Pronk *et al.*, 1992; Valdés *et al.*, 2008). Anaerobic respiration of *Acidithiobacillus ferrooxidans* bacteria is not only based on Fe^{3+} iron, as they can also use other electron donors derived from elemental sulphur and hydrogen (Ohmura *et al.*, 2002).

Metabolic processes of the *Acidithiobacillus ferrooxidans* bacteria

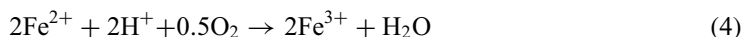
The metabolic processes of *Acidithiobacillus ferrooxidans*, a resilient bacterium with potential implications beyond Earth, have long been a subject of interest and curiosity among researchers. In addition, exploring the metabolic pathways of this organism could offer valuable insights into how microorganisms adapt metabolically to extraterrestrial environments, thereby positioning *Acidithiobacillus ferrooxidans* as a model organism for such studies (Janiczek *et al.*, 1998; Nemati *et al.*, 1998). These acidophilic extremophiles have gained attention for their metabolic prowess, particularly in the context

of industrial biomining and biohydrometallurgical processes (Torma, 1977; Osorio *et al.*, 2003; Yamanaka, 2008; Ai *et al.*, 2018). Due to their abilities *Acidithiobacillus ferrooxidans* can be used to desulphurize coal by oxidizing the pyrite contained in the carbonic substance. This process, with the use of bacteria, can be presented as follows (3) (Janiczek *et al.*, 1998; Nemati *et al.*, 1998):



The process of oxidation (biooxidation) of ferrous ions and pyrite by the ultimate recipients of the energy released is represented by chemical reactions (4) (Bevilaqua *et al.* 2010; Jafari *et al.* 2016) and (5) (Yamanaka, 2008; Colmer *et al.* 1950):

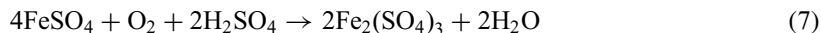
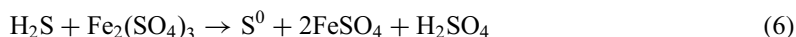
(a) (bio)oxidation of ferrous ion:



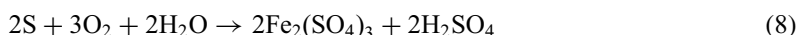
(b) (bio)oxidation of pyrite:



Acidithiobacillus ferrooxidans can also remove hydrogen sulphide (H_2S) from the environment in a two-step process (Halfmeier *et al.*, 1993, Part 1) presented by reactions (6) and (7) (Barsoukov 2018; Bevilaqua *et al.* 2009):



These bacteria can grow on numerous electron donor and acceptor substrates (Yarzabal *et al.*, 2002a), such as elemental sulphur lumps (Espejo and Romero, 1987). The elemental oxidation of sulphur (S) by *Acidithiobacillus ferrooxidans* is illustrated by the following chemical reactions (8) (Janiczek *et al.*, 1998):



The growth kinetics of *Acidithiobacillus ferrooxidans* on sulphur was examined in theoretical and experimental terms and used to determine vital microbiological and stoichiometric values. The data obtained for sulphur was then compared with analogous values obtained for metal sulphides (Konishi *et al.*, 1994). Individual strains of the bacterium show similar behaviour during their action on various sulphide minerals (Harnett *et al.*, 2006).

The metabolic activity of *Acidithiobacillus ferrooxidans* growing on reduced sulphur compounds can be studied by capillary isotachopheresis (Janiczek *et al.*, 1998). The biogeochemical activity of these bacteria can also be monitored via analysis of their cellular ATP (Pakostova *et al.*, 2013a).

Various, simple organic compounds (e.g. formic acid – *Acidithiobacillus ferrooxidans* can grow in formic acid (Pronk *et al.*, 1991), acetic acid, urea and cysteine) on the inhibition of the growth of *Acidithiobacillus ferrooxidans* during the sulphur and iron oxidation processes was also observed (Tuttle and Dugan, 1976). Synergistic cooperation of *Acidithiobacillus ferrooxidans* with other types of bacteria was observed for instance in the process of copper bioleaching (Zheng and Li, 2016). A cooperative interaction during sulphur oxidation between *Acidithiobacillus ferrooxidans* and planktonic cells (which can be characterized as free-floating microorganisms, that inhabit aquatic environments) was also noticed as a result of monitoring which bio-available substrates were delivered to planktonic cells (Pakostova *et al.*, 2013b). A cooperative interaction during sulphur oxidation between

Acidithiobacillus ferrooxidans and planktonic cells was also noticed as a result of monitoring which bio-available substrates were delivered to planktonic cells (Pakostova *et al.*, 2013b).

The metabolism of microorganisms potentially present in the lower layer of Venus' clouds may be analogous to that of terrestrial microorganisms. The metabolic processes of *Acidithiobacillus ferrooxidans* indicate that the bacteria could potentially serve as an example of such analogue (Limaye *et al.*, 2018). As one of the possible sources of substrates for metabolism of *Acidithiobacillus ferrooxidans*, they could be particles of volcanic ash, which under earth conditions, depending on their size, can stay in the air for weeks and even travel thousands of kilometers from the eruption site (Corradini *et al.*, 2016). The atmospheric dynamics of Venus cause ash particles to be suspended in its lower cloud layer, which could serve as a potential habitat for microorganisms. It is also conceivable that sand and dust particles may play a similar role (Lorenz, 2016). These particulate surfaces, which include volcanic ash, provide a conducive environment for the emergence and evolution of protocells. As templates, they facilitate the assembly of essential biomolecules such as lipids, amino acids and nucleotides, thereby promoting gradual protocell formation and development. Furthermore, their porous nature creates a protective and enclosed environment that encourages the progression towards more complex protocell structures (Ferris, 2006).

The genome of the bacterium *Acidithiobacillus ferrooxidans*

Genomes of selected strains of the *Acidithiobacillus ferrooxidans* bacteria was completely sequenced (Valdés *et al.*, 2008; Zhang *et al.*, 2019b; Kato *et al.*, 2022) in the same manner as the genomes of other acidophilic microorganisms, such as the archaea *Thermoplasma acidophilum*, *Picrophilus torridus*, *Sulfolobus tokodaii* and *Ferroplasma acidarmanus* (Johnson, 2007). Knowledge of the genome sequence of *Acidithiobacillus ferrooxidans* can provide information on the physiology and metabolism of these bacteria (Chen *et al.*, 2015). The genome of *Acidithiobacillus ferrooxidans* bacteria ranges from 2.89 to 4.18 Mb depending on the genomovar in which it exist (Zhang *et al.*, 2018c) four genomovars have been identified based on the strains of *Acidithiobacillus ferrooxidans* collected in different parts of the world, some of which were not attached to any of them (Zhang *et al.*, 2018c). So, for example, the ATCC 23270 strain of *Acidithiobacillus ferrooxidans* is characterized by a genome in the form of a single, circular chromosome containing almost 3 million base pairs (~3 Mb) with almost 60% guanine and cytosine content (Valdés *et al.*, 2008). *Acidithiobacillus ferrooxidans* from the DLC-5 strain have a similar genome size (~3 Mb), with a circular chromosome and a similar percentage of guanine and cytosine in the genome (Chen *et al.*, 2015). The number of proteins in the *Acidithiobacillus ferrooxidans* (ATCC 23270) genome encoding genes is over three thousand (Valdés *et al.*, 2008). The functional categories of the genome of *Acidithiobacillus ferrooxidans* (ATCC 23270) are associated with the cell envelope, transport and binding proteins and the energy of metabolism (Valdés *et al.*, 2008). In the mobile part of the genome, the presence of integrative conjugation elements (ICE), important in the process of horizontal gene transfer (Bustamante *et al.*, 2012), was seen. Phenotypically, many strains of *Acidithiobacillus ferrooxidans* are similar to each other, but differentiated by the 16S rRNA gene sequence and the overall composition of DNA (Zhang *et al.*, 2018b). The transcriptomic studies, based on DNA microarray techniques, have identified a reference set of genes in the genome of *Acidithiobacillus ferrooxidans*: map, rpoC, alaS and era. This has allowed for better interpretation of gene-expression profiles contained in this genome (Nieto *et al.*, 2009). Individual strains of *Acidithiobacillus ferrooxidans* contain plasmids (Rawlings, 2005; Chen *et al.*, 2015), though their presence in the genome of the bacterium was not found at all (Valdés *et al.*, 2008). Plasmids may presumably regulate the intensity of the oxidation process performed by *Acidithiobacillus ferrooxidans* (Ageeva *et al.*, 2003). Studies carried out on 27 strains of *Acidithiobacillus ferrooxidans* showed polymorphism occurring in their plasmid profiles (Kondrat'eva *et al.*, 2002). The *Acidithiobacillus ferrooxidans* genome has genes encoding various forms of the RubisCO enzyme (Dekker *et al.*, 2016). This protein mediates the absorption of atmospheric carbon dioxide (CO₂) (Bracher *et al.*, 2017), but it can also contribute to the resistance of

Acidithiobacillus ferrooxidans to uranium (Dekker *et al.*, 2016). The oxygen reduction pathway associated with the multicentre iron respiratory chain in the bacterium *Acidithiobacillus ferrooxidans* (Li *et al.*, 2015) creates a protein supercomplex (Castelle *et al.*, 2008). The proteins that create it lie inside and outside the cell membrane as well as in the periplasm, where oxygen reduction also occurs (Kai *et al.*, 1989; Castelle *et al.*, 2008). In *Acidithiobacillus ferrooxidans*, in the process of iron oxidation, the main electron acceptor is cytochrome *c*, which then transfers it to another protein called rusticyanin (RCy) (Hazra, 1992). This protein plays an important role during electron transfer in the iron respiration process of *Acidithiobacillus ferrooxidans* (Blake and Shute, 1987; Ronk *et al.*, 1991; Djebli *et al.*, 1992; Hazra, 1992; Yarzabal *et al.*, 2003). Rusticyanin is characterized by a very high oxidation–reduction (redox) potential (Barrett *et al.*, 2006). Its amino acid sequence was determined by micro-sequencing and mass spectrometry techniques based on the structural characteristics of tryptic peptides and Asp-N endoproteinase (Ronk *et al.*, 1991). The operon which encodes the specific types of cytochromes *c*, which are proteins involved in energetic metabolism in bacteria, in the process of electron transfer (Appia-Ayme *et al.*, 1999) during Fe²⁺ oxidation (Valkova-Valchanova and Chan, 1994) was also characterized. Computer analysis of the genomes of selected strains of *Acidithiobacillus ferrooxidans* showed that the synthesis of cytochrome *c* in these cells is dependent on the type of electron donor, which is associated with the type of medium (iron or sulphur) on which the mentioned strains grew. *Acidithiobacillus ferrooxidans* bacterial cells growing on iron (Fe²⁺) were characterized by a higher number of cytochrome *c* than those growing on sulphur (S⁰) (Yarzabal *et al.*, 2002a). Identification and characterization of these cytochromes found them to be localized specifically to the outer cell membrane (Yarzabal *et al.*, 2002b). The studies on the molecular mechanisms of iron oxidation (Fe²⁺ to Fe³⁺), from which *Acidithiobacillus ferrooxidans* draws energy to survive, have identified the *tce* gene cluster responsible for coding cytochrome *c* and cytochrome *c*₅₅₂ (type cytochrome *c*₄) (Ai *et al.*, 2018). To investigate the reaction kinetics of electron transport between rusticyanine and cytochrome *c*₄ (CYC₄₁) present in *Acidithiobacillus ferrooxidans*, the stopped-flow spectrophotometric method and the electron paramagnetic resonance (EPR) technique were used. To determine the crystalline structure of cytochrome *c*₄, the multiwavelength anomalous diffraction (MAD) method, a type of X-ray crystallography, can be used (Abergel *et al.*, 2003). The energetics of metabolism of *Acidithiobacillus ferrooxidans* was also analysed in the context of genes encoding electron transfer proteins based on biochemical and genetic data (Appia-Ayme *et al.*, 1999). An analysis of the physicochemical properties of cytochrome *c*₄ was performed, obtaining EPR spectra and absorption spectra of amino acid composition, both in the context of the strains of *Acidithiobacillus ferrooxidans* from which they were obtained (Giudici-Ortoni *et al.*, 2000). The cytochrome *c*₄ of this bacterium in the absorption spectrum is characterized by a Soret peak at wavelength $\lambda = 411$ nm in the oxidized state and $\lambda = 417$ nm, $\lambda = 523$ nm and $\lambda = 552$ nm in the reduced state (Cavazza *et al.*, 1996). Toxin–antitoxin (TA) systems, which work by inhibiting the activity of toxic substances, are also found within the genetic material of *Acidithiobacillus ferrooxidans* (Bustamante *et al.*, 2014). There are three types of TA systems (I, II and III) and they occur in the genomes of almost all bacteria, playing an important role in their survival under stress conditions (Yamaguchi *et al.*, 2011). TA systems whose *Acidithiobacillus ferrooxidans* bacteria may have a high content (28–29), e.g. type II, consist of pairs of genes responsible for toxin (stable) and antitoxin (unstable) coding (Bustamante *et al.*, 2014). Studies (Bustamante *et al.*, 2014) have shown that some of the chromosomally coded TA systems are part of the mobile genome of *Acidithiobacillus ferrooxidans*. The ‘genomic islands’ present in the genome of *Acidithiobacillus ferrooxidans*, which increase their resistance to copper, may also contribute to the possible competitive advantage of these microorganisms (Orellana and Jerez, 2011). *Acidithiobacillus ferrooxidans* have two glutamyl-tRNA synthetases that can indirectly regulate haem (Valdés *et al.*, 2008). Oxidative functions in the genome of *Acidithiobacillus ferrooxidans* are controlled by the *petI* and *rus* operons (Valdés *et al.*, 2008). In two different strains of *Acidithiobacillus ferrooxidans*, ATCC 33020 and ATCC 23270, *rus* operons are organized in a similar manner (Quatrini *et al.*, 2009).

Due to their genetic properties, *Acidithiobacillus ferrooxidans* bacteria can be an important component of the ecosystem formed in terrestrial volcanic sediments, as are *Acidithiobacillus ferrooxidans* bacteria representing the NFP31 strain (Kato *et al.*, 2022). The presence of genes in the genome of *Acidithiobacillus ferrooxidans* bacteria, as in the case of one of its strains YNTRS-40, is involved in the oxidation of both sulphur and iron and related to the process of adaptation to the environment, and also determines the good growth of these bacteria in an environment containing heavy metals and with a very low pH. These genes also allow bacteria to bio-extract metals and remove sulphur from gases (Zhang *et al.*, 2019b). Genetic modification, through genetic engineering, of the bacterium *Acidithiobacillus ferrooxidans* can contribute to the enhancement of the bioleaching process in order to recover more metals (Jung *et al.*, 2022). Perhaps genome-altering processes in microorganisms potentially existing in Venus clouds, which may be possible analogues of the Earth's *Acidithiobacillus ferrooxidans*, with similar effects to genetically engineered ones, would allow said organisms to adapt to the extreme conditions in the lower layers of Venus' clouds and to possibly survive there to this day.

***Acidithiobacillus ferrooxidans* as possible analogues to microorganisms that potentially live in the lower part of the clouds of Venus**

Conditions on Venus

Venus is one of the more geologically rugged planets of the solar system that has a very similar radius and mass to Earth (Taylor *et al.*, 2018). The atmosphere of this planet consists mainly of carbon dioxide (CO₂) – 96% and nitrogen (N₂) – 3.5%. It also contains carbon monoxide (CO) – 0.004%, noble gases: argon – 0.007% and neon – 0.0005%, sulphur dioxide (SO₂) – 150 ppm, water vapour – 30 ppm, carbonyl sulphide (carbon oxysulphide) – 4 ppm and some traces of hydrogen chloride – 0.5 ppm, hydrogen fluoride – 0.005 ppm, hydroxyl and atomic oxygen and hydrogen (Taylor *et al.*, 2018). In the lower part of the clouds on Venus, around 47.5–50.5 km from the surface, very different conditions are observed. The pressure is approximately 1 atm (~1 bar), and the average temperature is around 60°C (Limaye *et al.*, 2018). In Venusian clouds there is also aerosolized hydrated sulphuric acid with a concentration in the range of 75–98%, increasing with the height of the clouds from a level of 48–65 km above the surface of Venus. The particles of this aerosol are characterized by different diameters in the range of three compartments (modes): 0.4–0.6 µm (mode 1), 2–2.8 µm (modes 2 and 2'), and 7.3–8 µm (mode 3). A small number of relatively large particles with a diameter of about 35 µm are also observed (Limaye *et al.*, 2018). In the sulphuric acid aerosol in the lower part of the Venusian clouds, there are about 50 particles cm⁻³ with an approximate diameter in the range of 2–8 µm and about 600 particles cm⁻³ with an approximate diameter of 0.4 µm. Taking into account the environmental conditions of the planet Venus, in particular the presence of sulphuric acid in the aerosol and the associated acidity in the lower cloud layer, and the fact that *Acidithiobacillus ferrooxidans* are characterized by tolerance to the extremely acidic conditions prevailing on Earth, it can be assumed that the atmosphere of Venus is relatively adaptable to these organisms. Additionally, the fact that *Acidithiobacillus ferrooxidans* thrives at pH as low as 1.3 suggests that it could potentially survive and even metabolize inorganic sulphur compounds found in Venus' clouds (Quatrini and Johnson, 2019). Moreover, the average temperature in these cloud layers of around 60°C coincides well with the upper limits of the temperature range that some strains of this bacterium can withstand (Limaye *et al.*, 2018), further supporting the hypothesis that such extremophiles could possibly adapt to the harsh environments (Table 4).

The unknown electromagnetic radiation absorber in the UV range existing in the clouds of Venus

The electromagnetic radiation spectrum of Venus has revealed the discovery of an enigmatic ultraviolet (UV) absorber within the 330–400 nm wavelength range. This absorber presents a puzzling characteristic that thus far eludes comprehension. Of particular interest is the fact that this range aligns with the absorbance bandwidths of chlorophyll a and b, suggesting a possible correlation between this

Table 4. Characteristics of the *Acidithiobacillus ferrooxidans* bacteria and comparative analysis with Venus's lower cloud layer conditions

Characteristic	<i>Acidithiobacillus ferrooxidans</i>	Venus's lower cloud layer
Optimal pH	About 2, with growth ranging from pH 1.3 to 1.5. (Quatrini and Johnson, 2019)	Highly acidic conditions due to sulphuric acid aerosols.
Temperature tolerance	Can tolerate high temperatures, optimally growing around 30–45°C, some strains up to 50°C (Johnson, 2007)	Average temperature around 60°C. (Limaye <i>et al.</i> , 2018)
Environment	Inhabits geoclimatic environments characterized by low pH and high metal concentrations (Quatrini and Johnson, 2019)	Acidic aerosols, sulphuric acid predominates, metal-laden particles.
Metabolic substrates	Utilizes inorganic substrates including sulphur and iron; capable of chemolithoautotrophy. (Schuler and Tsuchiya, 1975)	Potential inorganic substrates from volcanic ash and metal particles.
Biochemical adaptability	Does not produce spores but has high resistance to uranium and other heavy metals, adapts to extreme geochemical settings. (Dekker <i>et al.</i> , 2016)	Harsh chemical environment with potential for metal processing.
Potential for extraterrestrial life	Resilience in extreme conditions makes it a model for studying life on other planets, particularly in environments similar to Venus.	Similar harsh conditions might support extremophiles analogous to <i>Acidithiobacillus ferrooxidans</i> .

unidentified absorber and photosynthetic pigments. The presence of the UV absorber has been further confirmed through the emergence of obscure stripes that undergo contortion and morphing in a brief period of time (12 min), as observed in the UV-filtered Venus image (Limaye *et al.*, 2018). *Acidithiobacillus ferrooxidans* are characterized by a similar UV spectrum to that recorded for Venus. The mentioned similarity of UV spectra suggests that the unknown absorber existing in Venus clouds may be of microbial origin, and its earth analogues may be *Acidithiobacillus ferrooxidans*. It is highly probable that due to their metabolism and physicochemical properties, these bacteria would be able to survive in the conditions of the lower part of Venusian clouds. The latest research confirms the existence of extremophilic bacteria which were found on Earth at an altitude of 41 km, which corresponds to the altitude of the lower part of Venusian clouds (Limaye *et al.*, 2018).

Conclusions and future studies

The hypothesis of microbiological life in the clouds of Venus is further strengthened by numerical models describing the evolution of the climate of the second planet from the Sun (Way *et al.*, 2016; Way and Del Genio, 2020), which could have been characterized by a climate that was inhabited in the past for over 700 million years (Way *et al.*, 2016). On the young Venus, it is probable that there was an ocean with warm waters (Grinspoon and Bullock, 2007), in which primordial ocean life could potentially have arisen. The climate changes that have occurred on Venus could have caused its ocean to evaporate, and the microorganisms potentially present there, with various transport mechanisms, could have penetrated and inhabited the clouds of Venus (Limaye *et al.*, 2018). However, according to some researchers, Venusian clouds may have a limited potential for life, which is conditioned by the availability of one of the microelements, molybdenum, which plays a

vital role in various biological processes, including nitrogen fixation and electron transfer reactions (Lingam and Loeb, 2018). The protein that participates in the transport of this element is molybdopterin (Dekker *et al.*, 2016). It has been shown that *Acidithiobacillus ferrooxidans* are able to generate energy in the process of chemolithoautotrophic metabolism using iron contained in a meteorite (González-Toril *et al.*, 2005). In this regard, it can be assumed that these bacteria could have the potential to act as carriers of life, traversing the universe within iron meteoroids, fuelled by the energy provided by the iron contained in meteorites, which facilitates their engagement in chemolithoautotrophic metabolism. This confirms that *Acidithiobacillus ferrooxidans* an important model organism in the context of the development of astrobiological research (Quatrini and Johnson, 2019), and as a pioneering species it can contribute to the exploration of the habitability of Venus. Therefore, it is important to laboratory test the strains of *Acidithiobacillus ferrooxidans* mentioned in this paper in order to find such a strain or to produce it through genetic engineering or artificial selection, so that the bacteria representing it would have such features that would allow them to survive in the environmental conditions of the lower layer of Venus clouds. This applies to the search for the closest possible analogue of terrestrial microorganisms potentially living in the clouds of Venus. Finding ways to effectively research the habitability of Venus, perhaps with the active participation of terrestrial bacteria (genetically modified or specially selected for this purpose) such as *Acidithiobacillus ferrooxidans*, is inextricably linked with stopping and then reversing the Venus greenhouse effect, which is a phenomenon wherein the high concentration of carbon dioxide in the atmosphere traps heat, causing a runaway greenhouse effect and resulting in surface temperatures that can exceed 450°C. Among other things, in this context, Venus can act as a kind of laboratory (Kane *et al.*, 2019) to understand the mechanisms by which the planet, most likely having had water on its surface in the past for a very long time (around 2 billion years) (Way *et al.*, 2016), transformed to the state we are seeing today.

The answers to many questions about Venus' atmosphere can be provided by future research missions on Venus, which are already approved for implementation (O'Callaghan, 2021), and which – among other valuable scientific results – may also find the first extraterrestrial life.

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