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Terrestrial iron biosignatures and their potential in solar system exploration for astrobiology

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ABSTRACT

Iron (Fe) is one of the most abundant elements in the solar system. It plays an important role in life by participating in redox reactions for energy generation (e.g., by Fe(II)-oxidizing and Fe(III)-reducing microorganisms) and as a cofactor in multiple assimilatory metabolisms (e.g., DNA replication). Fe-metabolizing microorganisms are ubiquitous on Earth, from soils and sediments to deep-sea hydrothermal vents. They catalyze Fe redox transformations between its most common redox species Fe(II) and Fe(III), and couple this to carbon degradation, CO_2 fixation, nitrate reduction and photosynthesis, thus linking the biogeochemical cycles of Fe with carbon and nitrogen. Biogenic Fe (oxyhydr)oxide minerals (BIOS), i.e. the products of neutrophilic Fe(II)-oxidizing microorganisms, are biosignatures of interest on Earth and potentially on other habitable bodies in our solar system, such as Mars and icy moons. Here, we review the habitats, mechanisms, products and preservation of Fe-metabolizing microorganisms on Earth. We translate this knowledge into a biosignature context for the search of potential Fe-metabolizing microorganisms in the solar system.

Contents

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1. Introduction

Iron (Fe) is abundant in the solar system, especially in the rocky inner planets (Mercury, Venus, Earth and Mars). On Earth, Fe is the fourth most abundant element in the crust and the second most abundant redox-sensitive element, after oxygen. Although the majority of iron was sequestered in the core during accretion (McDonough, 2016), the remaining Fe in the crust, particularly Fe nanoparticles from hydrothermal and meteoritic origin could have acted as catalysts for the formation and complexification of organic compounds from the CO_2-rich early Earth atmosphere (Peters et al., 2023).

Besides being an essential micronutrient in assimilatory metabolisms (with functions in DNA replication and gene expression), microorganisms can harvest energy from redox transformation between Fe(II) and Fe(III) through multiple mechanisms. For instance, at neutral pH conditions, Fe(II)-oxidizing microorganisms (FeOM) can use electrons from Fe(II) to fix CO_2 in photosynthesis (2.1 Photoferrotrophs), reduce O_2 (2.2 Microaerophilic FeOM) or reduce nitrate (2.3 Nitrate-reducing Fe (II)-oxidizing microorganisms (NRFeOM)), while others respire Fe(III) (2.5 Fe(III)-Reducing Microorganisms (FeRM)) (Fig. 1) (Kappler et al., 2021; Knoll et al., 2012; Konhauser et al., 2011), often in competition with abiotic processes. Neutrophilic FeOM produce various biogenic iron (oxyhydr)oxide minerals (BIOS) such as ferrihydrite ($(Fe^{3+})_{4-5}(OH, O)_{12}$), goethite ($\alpha$–$Fe^{3+}O(OH)$), magnetite ($Fe^{2+}Fe^{3+}_2O_4$) and lepidocrocite ($\gamma$-$Fe^{3+}O(OH)$) (Cornell and Schwertmann, 2006). Compared to abiotically formed Fe(III) (oxyhydr)oxides, the minerals within BIOS are usually poorly crystalline with larger surface areas due to their smaller crystal sizes which is primarily due to the presence of organic matter that blocks the surface from further growth (Vollrath et al., 2012; Zegeye et al., 2014). Moreover, they are intimately associated with organic matter such as lipids, polysaccharides and even whole cells. This tight association leads to different properties, which is of interest for the utilization of BIOS as potential biosignatures.

Fe-based biosignatures are useful to understand the biological history of the Earth - ranging from the role of FeOM in the formation of Banded Iron Formations (BIFs) (2.8–2.5 Ga) (Chan et al., 2016; Croal et al., 2009; Klein, 2005; Posth et al., 2014; Posth et al., 2013b), Fe oxide filaments with organic matter in hydrothermal vent deposits from 4280 to 490 Ma (Dodd et al., 2017a; Little et al., 2004) and spheroidal Fe(III) (oxyhydr)oxides in 100 Ka in Jurassic rocks (Potter-McIntyre et al., 2014). Using Earth as a case study, and with the knowledge that other bodies in the solar system are rich in Fe, Fe-based biosignatures can be promising in the search for life in these places.

The possibility for the presence of Fe-metabolizing bacteria has been raised on Mars, in particular regarding NRFeOM and phototropic FeOM (photoferrotrophs) (Price et al., 2018; Tabata et al., 2021). A handful of experiments and models have shown that these microorganisms can grow under Martian-like conditions (Bauermeister et al., 2014; Khuller et al., 2024; Palma et al., 2024; Silva et al., 2024). More recently, the possibility of Fe biogeochemistry on icy worlds has been proposed (Ray et al., 2021; Sahai et al., 2024). The bottom of oceans in icy worlds likely contained reduced FeS and Fe—Ni minerals (Zolotov and Shock, 2004a). Furthermore, the reaction between water and ultramafic rock around possible hydrothermal vents will generate Fe(II) on the seafloor (Běhounková et al., 2021; Glein and Waite, 2020; Hsu et al., 2015). Hence, similar to around Earth's hydrothermal vents, dissolved iron could serve as electron source or precipitate as Fe minerals (e.g., goethite) (Emerson and Moyer, 2002). After formation, Fe minerals can be transformed or even destroyed by certain processes e.g., diagenesis, burial, and reduction by Fe(III)-reducing microorganisms (FeRM), opening questions about the preservation of BIOS under these conditions.

In this review, we briefly describe the different mineral phases of Fe on Earth and their role in dissimilatory Fe-based metabolisms (Table 1). Using this as a guideline, we then review the potential of Fe-based metabolisms beyond Earth, focusing on Mars and icy worlds. We end by highlighting Fe-based biosignatures that may exist in these environments as a guide to search for life in the solar system.

2. Earth

On Earth, Fe can be oxidized and reduced abiotically by various oxidants (O_2, MnO_2, NO_2^-, light) and reductants (sulfide, natural organic matter, light). In addition to these abiotic processes, microbial activities contribute significantly to the redox cycle of Fe due to their ubiquity on Earth and their rapid enzymatic kinetics (Kappler et al., 2021). In modern times, Fe(II), a soluble and bioavailable form for assimilatory metabolisms, is typically found in suboxic and anoxic environments such as wetlands, groundwater and paddy soils (Bhattacharyya et al., 2018; Huang et al., 2021a). Fe(II) occurs as dissolved species in acidic environments where the low pH prevents its rapid oxidation or at circumneutral pH as Fe(II)-ligand complexes, where the associated organic matter alters its redox potential and stabilizes it against oxidation (Daugherty et al., 2017; Kappler et al., 2021). Finally, it also occurs as Fe (II)-containing minerals such as vivianite ($Fe_3(PO_4)_2\ 8H_2O$), siderite ($FeCO_3$), Fe sulfides or clays (Pentráková et al., 2013; Mansor et al., 2025a). In oxic surface environments, Fe occurs predominantly in the form of Fe(III), which is poorly soluble at neutral pH and less bioavailable for assimilatory metabolisms, therefore requiring the production of siderophores to make it available by chelation (Ahmed and Holmström, 2014). Fe(III) is found mainly forming (oxyhydr)oxide minerals such as ferrihydrite (Fh), goethite and hematite (α-Fe_2O_3) (Pentráková et al.,

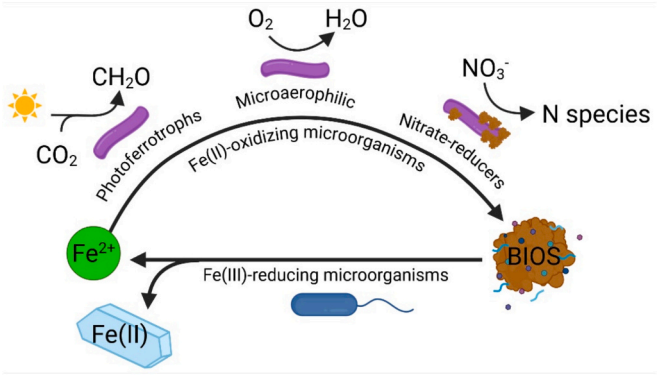

Fig. 1. Overview of various microorganisms using Fe-based dissimilatory metabolisms that can produce, transform or degrade BIOS at neutral pH conditions.

Table 1
Relevant Fe minerals in the context of biosignatures on Earth and Mars.

Mineral (formula)	Occurrence	Relevance
Ferrihydrite ($(Fe^{III})_{4-5}(OH,O)_{12}$)	Earth: major component of soils and sediments (Elias et al., 2021). Mars: one of the main components of the Martian surface (Valantinas et al., 2025).	It is the most bioavailable Fe(III) (oxyhydr)oxide on Earth (Nixon et al., 2012), present in many BIOS (Langley et al., 2009b; Miot et al., 2009b).
Goethite (α–$Fe^{III}O(OH)$)	Earth: common component of soils and sediments (Van Der Zee et al., 2003). Mars: Gale crater (Klingelhöfer et al., 2005).	Earth: one of the biogenic minerals within BIOS. Mars: its occurrence in Gale crater supports the presence of water in early Mars (Klingelhöfer et al., 2005).
Hematite (α-Fe_2O_3)	Earth: BIF deposits (Hagemann et al., 2016). Mars: it occurs as small spherules in the rocks at Meridiani planum (Squyres et al., 2004).	Mars: its formation on Mars can constrain the water budget and therefore add on the habitability of early Mars (Hynek et al., 2002; Squyres et al., 2004).
Magnetite ($Fe^{II}Fe^{III}_2O_4$)	Earth: found in soils, sediments and deposits such as the Atacama-Coquimbo Ferriferous Belt, Northern Chile (Espinoza, 1990) and BIF (Hagemann et al., 2016).	Earth: biogenic magnetite differs from abiogenic magnetite in their size, chemical purity and magnetic properties (Kappler et al., 2023; Pérez-Huerta et al., 2022). It has been used as biosignature for the presence of magnetotactic bacteria (e.g., by comparing the single-domain (SD) magnetic state and the uniaxial anisotropy of the magnetite chains) (Mathon et al., 2024; Petryshyn et al., 2016; Slotznick et al., 2023).
Siderite ($FeCO_3$)	Earth: sediments, hydrothermal environments (Ohmoto et al., 2004) and BIF (Konhauser et al., 2017).	Earth: one of the main byproducts of Fe(III) reduction. It plays a role in Fe and C biogeochemistry and C sequestration (Roh et al., 2003).
Vivianite ($Fe_3(PO_4)_2$ $8H_2O$)	Earth: sediments, waterlogged soils, bogs, hydrothermal deposits and wastewater sludges (Rothe et al., 2016)	Earth: main byproduct of biogenic reduction of BIOS under controlled laboratory conditions (Langley et al., 2009b).
Jarosite ($KFe^{III}_3(SO_4)_2(OH)_6$)	Earth: oxidation of sulfide deposits, clay environments, acidic soils, mine tailings and one of the main components of the Iberian Pyrite Belt (IPB) (Dutrizac and Jambor, 2000). Mars: Meridiani Planum (Morris et al., 2006).	Mars: its presence in Meridiani Planum, Mars is proof of a wet, oxidizing and acidic environment on early Mars (Morris et al., 2006).

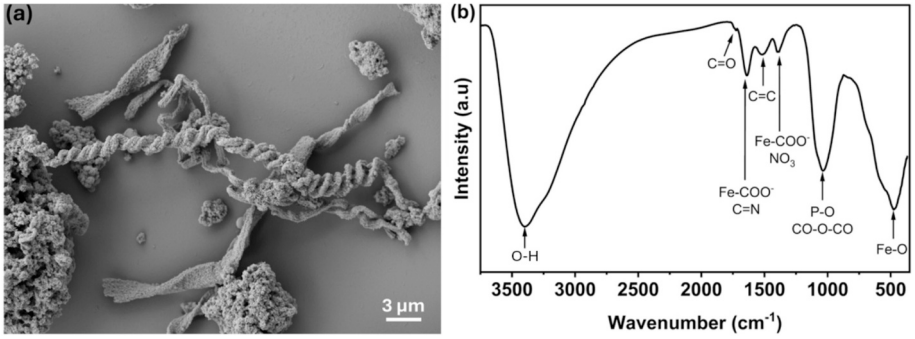

Fig. 2. (a) Scanning electron micrograph of a sample from the iron-rich Segen Gottes mine (Black Forest, Germany). (b) Fourier transform infrared spectrum of BIOS from the nitrate-reducing Fe(II)-oxidizing strain *Acidovorax* sp. BoFeN1 grown in 22 mM bicarbonate-buffered medium and amended with 3 mM $FeCl_2$, 2 mM acetate and 6 mM nitrate, showing the signals from various organic functional groups. BIOS can adopt intriguing morphologies that may be useful as biosignatures. In particular, microaerophilic FeOM (capable of growing with O_2 concentrations as low as 3 µM) can produce twisted stalks or sheaths (Fig. 3) (Chan et al., 2009, 2011; Krepski et al., 2013). These are extracellular organo-mineral structures mainly composed of poorly crystalline Fe(III) (oxyhydr)oxides and polysaccharides. They are produced to prevent cell encrustation and to position the cells at the optimal redox boundary (i.e., where both O_2 and Fe(II) are present, by growing the stalk in the opposite direction of the cell movement) (Chan et al., 2009; Krepski et al., 2013). The organic matter associated with these biominerals alters the properties and reactivity of the Fe(III) minerals, leading to differentiation from abiogenic minerals (see Section 2.6).

2013).

BIOS are metabolic products of neutrophilic FeOM. BIOS are mixtures of Fe minerals, organic matter and cells (Fig. 2 and 3). The mineral portion of BIOS is typically composed of Fh, goethite and amorphous Fe (III) phosphates (Ferris, 2005; Langley et al., 2009b; Miot et al., 2009a). BIOS are highly mixed with organic matter and biopolymers, mainly lipid and polysaccharide moieties (Chan et al., 2009; Sowers et al., 2019; Whitaker et al., 2021). The outermost part of the BIOS is mainly composed of aliphatic groups associated with carboxylic moieties and acidic polysaccharides, while carboxylic and aromatic moieties are incorporated in the structure (Chan et al., 2009; Sowers et al., 2019). The Fe(III) minerals can also cover the cell membrane, leading to full or partial encrustation (Li et al., 2013; Miot et al., 2015). In fact, examples of exceptional preservation of cellular features associated with Fe(III) minerals are well known. Proteins from dinosaurs as old as 195-million years old were found to be preserved in hematite and goethite formed from Fe in Fe chelators (e.g., hemoglobin), which decreased the degradation of organic matter (Lee et al., 2017; Schweitzer et al., 2007). Thylakoid features detailing chloroplasts from phototrophic mats are preserved in modern hydrothermal iron deposits in Yellowstone National Park (Parenteau and Cady, 2010). Hence, Fe-rich BIOS may also preserve exceptional cellular features.

Naturally occurring poorly crystalline Fe(III) (oxyhydr)oxides are highly bioavailable for dissimilatory metabolisms (functioning as electron acceptors in anaerobic respiration), while with increasing crystallinity, their bioavailability decreases (Nixon et al., 2012). Under normal conditions, poorly crystalline Fe(III) (oxyhydr)oxides (e.g., Fh) are more thermodynamically favorable for reduction than more crystalline phases. The relative bioavailability of different Fe(III) minerals can be determined by calculating their reduction potential (E_H), which can then be extended to the Gibbs free energy of reaction (ΔG_r). More negative ΔG_r implies higher bioavailability for reduction, which has been shown repeatedly for ferrihydrite over more crystalline Fe(III) minerals such as goethite and hematite (Kappler et al., 2021; Nixon et al., 2012; Schwerdhelm et al., 2025). However, as ΔG_r varies as a function of pH, temperature, pressure, substrate/reactant concentrations and particle size (Amend and LaRowe, 2019; Kappler et al., 2021; Schwerdhelm et al., 2025), calculations should be performed under the environmental

conditions of interests (e.g., Earth vs Mars vs icy moons) whenever possible.

Geobacter and *Shewanella* are two model FeRM typically used to investigate biogenic Fe(III) reduction on Earth. *Shewanella putrefaciens* CN-32, for instance, is capable of reducing hematite, although the reduction rate varies according to the size and facet. Both hematite and goethite are more bioavailable with smaller particle sizes (Xu et al., 2025a). Hematite {001} is more bioavailable than hematite {100}, due to the different cell-mineral interactions and the higher conductivity of hematite {001} (Hua et al., 2022), highlighting the importance of mineral characterization to understand controls on Fe(III) reduction rate. Fe(III) minerals within phyllosilicates (montmorillonite, nontronite, and illite) are also available for biogenic reduction (Jaisi et al., 2007; Liu et al., 2016; Liu et al., 2023; Vodyanitskii, 2007). Importantly, BIOS are more bioavailable than abiotic Fh, due to their higher surface area that provides more reactive sites per g of biomineral. The associated organic matter content may also act as a carbon source or facilitate electron transfer between the cells and the minerals (Langley et al., 2009a; Li et al., 2016; Roden, 2003; Ye et al., 2022). The origin of BIOS also affects their bioavailability. For example, BIOS from *Gallionella*-like FeOM were found to be less bioavailable for reduction by *Shewanella putrefaciens* CN-32 than those from *Leptothrix*-like FeOM (Langley et al., 2009a).

In the next subsections we expand on the different Fe metabolisms, describing their occurrence in space and time. We highlight the BIOS that they produce, the transformations that they can undergo and their preservation potential.

2.1. Photoferrotrophs

Photoferrotrophs are a type of FeOM that can utilize sunlight energy and electrons from Fe(II) to fix CO_2 (Eq. (1)) (Camacho et al., 2017; Widdel et al., 1993).

$$HCO^-_3 + 4Fe^{2+} + 10H_2O \xrightarrow{h\nu} CH_2O + 4Fe^{III}(OH)_3 + 7H^+ \quad (1)$$

On modern Earth, they have been found in sediments and water bodies, where they prefer anoxic conditions and low light intensity (Hegler et al., 2008). The rock record suggests that the first photoferrotrophs appeared around ~3.5 Gyr ago, before oxygenic phototrophy (Gupta et al., 2021; Lyons et al., 2024a; Xiong, 2006). As a result of Fe(II) oxidation, they form BIOS composed mainly of poorly crystalline minerals (e.g., Fh) and goethite (Jiao et al., 2005). Due to the negative charge of the cells, positively charged iron ions can be sorbed to the cell wall, leading to the precipitation of minerals on the cell membrane. This cell-mineral association can protect cells from dangerous UV radiation (Gauger et al., 2015), although it can also interfere with photosynthesis (Wu et al., 2014). Therefore, some species of photoferrotrophs have developed mechanisms to avoid this, such as by modifying its surface composition to cause an electrostatic repulsion between the cell and the minerals (Stukalov et al., 2008; Thompson et al., 2019). They may also produce negatively charged extracellular polymeric substances (EPS) that complex the Fe(III) produced during oxidation, preventing its attachment to the cell surface (Chan et al., 2011; Wu et al., 2014). In addition, they can acidify the surrounding microenvironment to keep the Fe(III) dissolved and allow Fe(III) diffusion away from the cell (Hegler et al., 2010; Schädler et al., 2009).

The early appearance of photoferrotrophy and the lack of encrustation suggest that these bacteria might have played a role in the formation of BIFs (Kappler et al., 2005). BIFs are extensive deposits of Fe(III) (oxyhydr)oxides (mainly magnetite and hematite) and silica that were enigmatically formed already on early Earth when atmospheric O_2 was low (and later when O_2 was formed by cyanobacteria to a larger extent). The mechanism of deposition of the oldest BIFs (i.e. the identity of the Fe (II) oxidation mechanism that lead to Fe(III) mineral precipitation) is debated. Several mechanisms were proposed including ultraviolet (abiotic) photooxidation, direct enzymatic Fe(II) oxidation by anoxygenic photoferrotrophs, chemical oxidation by traces of O_2 produced by the earliest cyanobacteria, enzymatic oxidation by microaerophilic Fe (II)-oxidizers using the traces of O_2 produced by the earliest cyanobacteria, or a combination of these processes (Dodd et al., 2022; Dreher et al., 2021; Thompson et al., 2019; Konhauser et al., 2007). Photoferrotrophic Fe(II) oxidation likely played a role for the deposition of the oldest BIFs given (a) the suitable conditions for photoferrotrophy in the ancient ocean (high Fe(II) and low O_2 in the photic zone) (Kappler et al., 2005) (b) lack of organic matter in BIFs, explainable by low association between photoferrotrophs and the Fe(III) minerals that they formed (Posth et al., 2010; Thompson et al., 2019), (c) consistency between BIF deposition rate ($1.4\,mol\ m^{-2}\ yr^{-1}$) (Canfield et al., 2006) with those calculated for model photoferrotrophs (Kappler et al., 2005) and measured in modern ferruginous lakes ($3.4\,mol\ C\ m^{-2}\ yr^{-1}$) (Llirós et al., 2015). The roles of abiotic ultraviolet photooxidation and oxidation via O_2 produced by the earliest cyanobacteria cannot be fully ruled out, and ongoing research are discovering how interactions between Fe(II), silica, reactive oxygen species and Fe(III) reducing bacteria can affect Fe(II) oxidation rate and extent and the identity of the precipitated minerals (Dreher et al., 2025; Gauger et al., 2016; Huang et al., 2021b; Schad et al., 2022; Swanner et al., 2015; Yang et al., 2024). After precipitation and sedimentation, diagenesis would transform ferrihydrite (main component of BIOS), that may have been the initial mineral phase, into hematite and magnetite, the main components of BIFs today (Konhauser et al., 2023). Additionally, should organic carbon (OC) precipitate with the Fe(III) minerals, long-term diagenesis and metamorphism would degrade the OC and produce Fe(II)-bearing minerals (Halama et al., 2016; Köhler et al., 2013; Posth et al., 2013a). Hence, preservation of direct biosignatures in BIF deposits is still an open question.

2.2. Microaerophilic FeOM

Increasing O_2 concentration in the atmosphere after the Great Oxidation Event around 2.4 billion years ago led to the expansion of habitats suitable for the proliferation of microaerophilic FeOM. Microaerophilic FeOM use Fe(II) as electron donor to reduce O_2 (Eq. (2)) at circumneutral pH environments (Hedrich et al., 2011).

$$4Fe^{2+} + 10H_2O + O_2 \rightarrow 4Fe^{III}(OH)_3 + 8H^+ \quad (2)$$

These microorganisms are generally found in environments where the concentration of O_2 is between 3 and 50 μM that allows them to outcompete abiotic oxidation (Druschel et al., 2008; Lueder et al., 2022; Maisch et al., 2019). Microaerophilic FeOM (e.g., *Gallionella ferruginea*, *Mariprofundus ferrooxydans*) produce various BIOS typically comprising of poorly crystalline Fh, lepidocrocite, goethite and/or akageneite (Hallbeck and Pedersen, 1990; Krepski et al., 2013; Laufer et al., 2017a). These BIOS can adopt unique morphologies such as twisted stalks, tubular sheaths, granular or dreadlock-like structures (Fig. 3) (Chan et al., 2011; Chan et al., 2016a; Hallberg, 2004). The morphology of these BIOS is highly dependent on the niche and the FeOM species. For instance, BIOS of *Gallionella*, an autotrophic microaerophilic FeOM that preferentially occurs in low-OC environments can be in the form of twisted stalks, while *Leptothrix*, an heterotrophic FeOM that is typically found in high-OC environments can produce sheaths (Tothero et al., 2024). Moreover, the formation of these structures is regulated at the gene level by specific genes such as the xag operon, associated to stalk-formation (Kato et al., 2015). These structures are originally EPS secreted by the microorganisms, which then become a template for Fe (III) mineral nucleation and precipitation. The EPS also differs among species (Chan et al., 2004; Miot et al., 2009b), but the compositions are unknown for most FeOM (Makita, 2018). This strategy allows them to avoid cell wall encrustation by Fe(III) minerals that would hinder their metabolic activities.

Some microaerophilic FeOM are able to live in environments with

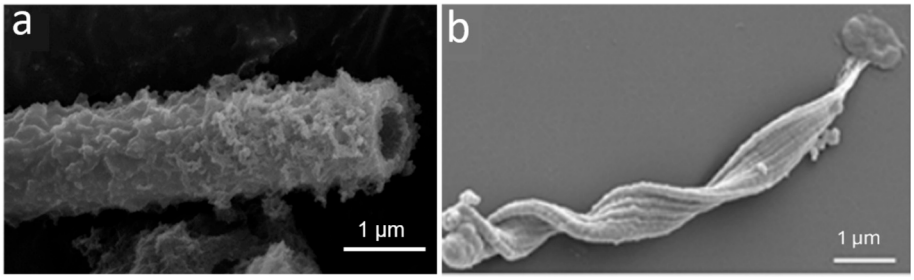

Fig. 3. Different morphologies of BIOS. a. Scanning electron microscopy (SEM) image of *Leptothrix* spp. sheath coated with Fe(III) (oxyhydr)oxides (Suzuki et al., 2015) b. Field emission SEM image of a *M. ferrooxydans* PV-1 stalk (Chan et al., 2016a).

higher concentrations of O_2. For example, Baker et al. (2023) demonstrated that *Ghiorsea bivora* TAG-1 excretes exometabolites that increase the half-life of Fe^{2+} by two orders of magnitude (from 3.3 to 335.5 days) in oxic seawater. The BIOS of *G. bivora* TAG-1 also differed from abiogenic Fe(III) (oxyhydr)oxides. This BIOS consisted of small particles (~100–500 nm) aggregated in a globular shape mainly composed of poorly crystalline phases (Fh-like), while in the abiotic control, the Fe (III) (oxyhydr)oxides were needle-like and bigger (~1 μm in length) composed of more ordered phases (lepidocrocite, akaganeite, goethite, feroxyhyte) (Baker et al., 2023).

These special morphologies of the BIOS formed by microaerophilic FeOM have been used as biosignatures of Fe metabolism in sediments from 1.7 Ga (Slack et al., 2007; Little et al., 2004). They also provide information about the redox state of the atmosphere of the early Earth, given that their formation relies on the presence of O_2 (Chan et al., 2011). Interpreting these structures in the rock record requires caution, as abiotic processes can form Fe(III) minerals with BIOS-like shapes, leading to false positives (Criouet et al., 2021; McMahon, 2019; Cosmidis and Templeton, 2016). This highlights the importance of a profound understanding of BIOS, their formation and transformation under different conditions and their unique morphology and composition (cell-mineral associations) compared to false positives in the investigation of Fe-based biosignatures (see Section 2.6).

2.3. Nitrate-reducing Fe(II)-oxidizing microorganisms (NRFeOM)

NRFeOM harvest electrons from Fe(II) for the reduction of nitrate (NO_3^-) to gain energy (Eq. (3)).

$$10Fe^{2+} + 2NO_3^- + 24H_2O \rightarrow 10Fe^{III}(OH)_3 + N_2 + 18H^+ \quad (3)$$

After the radiation of oxygenic photosynthesis, the high oxygen concentration allowed for the expansion of the nitrogen cycle (Stüeken et al., 2016), paving the way for direct coupling between the nitrogen and iron biogeochemical cycles. NRFeOM can either fix CO_2 (autotrophic) or use a bioavailable carbon source (e.g., acetate) as a co-substrate (mixotrophic) (Dopffel et al., 2022; Huang et al., 2021a; Tominski et al., 2018). NRFeOM produce various nitrogen intermediates that follow a sequential reduction: $NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$ (Jakus et al., 2021). Nitrite and nitric oxide rapidly oxidize Fe(II) abiotically (Klueglein et al., 2014), which may play a crucial role in the oceanic primary production by limiting the sedimentary Fe supply to the surface (Scholz et al., 2016).

NRFeOM have been isolated from modern freshwater sediments, groundwater and soils (Liu et al., 2019; Straub et al., 1996). They cohabitate with phototrophs and microaerophilic FeOM in the sediments and in water columns (Laufer et al., 2016; Otte et al., 2018). However, it has been found that reactive nitrogen species (e.g., NO) byproducts of NRFeOM are toxic to photoferrotrophs (Nikeleit et al., 2024). This raises questions on microbial interactions and competition for Fe as an energy source, particularly on early Earth. Contrary to phototrophic and microaerophilic FeOM, some NRFeOM can become encrusted (especially mixotrophs) and entombed by the residual Fe(III) that precipitates in the cell membrane due to attraction to the negatively charged membrane (Miot et al., 2009a). To some extent, this encrustation could be beneficial, preventing cell dehydration, but it can also prevent the uptake of nutrients leading to cell death (Knoll et al., 2012). This encrustation is of geological importance because it increases the preservation potential of the cells in the rock record, not only of FeOM but also of other microbes in the community (Miot et al., 2015; (Parenteau and Cady, 2010). BIOS preserve protein globules and peptidoglycan such as those in the periplasm of *Acidovorax* sp. strain BoFeN1 (Miot et al., 2011) and can preserve the cell shape completely under diagenetic conditions (up to 20 h at 600 °C or for 100 h at 300 °C) (Li et al., 2013).

2.4. Acidophilic FeOM

Under acidic conditions (pH <4), Fe(II) and oxygen are stable together in solution (Stumm and Morgan, 2013). The redox potential of the ferrous/ferric iron couple (+770 mV at pH 2) makes oxygen the most suitable electron acceptor for acidophilic FeOM (Eq. (4)).

$$4Fe^{2+} + 4H^+ + O_2 \rightarrow 4Fe^{3+} + 2H_2O \quad (4)$$

Hence, the isolates of acidophilic FeOM are obligate aerobes (Barrie Johnson and Hallberg, 2008; Bird et al., 2011; Johnson, 1998). To the best of our knowledge, no acidophilic photoferrotrophs or NRFeOM have been described so far. Acidophilic FeOM differ in their affinity for Fe. Bacteria of the genus *Leptospirillum* are expected where the concentration of Fe(III) is high, while *Acidithiobacillus ferrooxidans* is dominant where Fe(II) is depleted and pH is low (<3) (Johnson, 1998; Jones et al., 2015).

The main product of acidophilic FeOM is dissolved Fe^{3+}. No direct BIOS formation can be attributed to them. Nonetheless, as Fe^{3+} concentration increases, Fe(III) minerals precipitate once supersaturation is reached. Indirect Fe(III) minerals produced include schwertmannite and jarosite, that later transform into goethite in aqueous environments at pH $\geq$ 4 (Acero et al., 2006; Bigham et al., 1996). The formation of schwertmannite or jarosite will depend on the presence of cations (K^+, NH_4^+, Na^+ and H^+) and the pH. Jarosite is favored at high cations concentration and low pH (Sandy Jones et al., 2014). No particular biogenic morphology is attributed to these Fe(III) minerals, although EPS produced by acidophilic FeOM can facilitate their precipitation (Kaksonen et al., 2014). These minerals can help in the preservation of molecular biosignatures that would otherwise degrade in acidic environments (Souza-Egipsy et al., 2010). Goethite is particularly known to aid in lipid preservation by strongly binding to carboxylic and hydroxyl functional groups, preventing exposure of their reactive groups (Filius et al., 2000; Kaiser and Guggenberger, 2007; Tan et al., 2018). Lipids are commonly used as molecular biosignatures because as opposed to other biomolecules, they preserve their hydrocarbon skeleton for thousands of millions of years (Finkel et al., 2023a). Hence, despite the lack of BIOS, the Fe^{3+} produced by acidophiles can help in the preservation of molecular biosignatures.

2.5. Fe(III)-reducing microorganisms (FeRM)

To complete the biogeochemical cycle of Fe, we discuss microbial respiration of Fe(III) performed by Fe(III)-reducing bacteria (FeRM). Respiration of Fe(III) is an ancient metabolism (~3.5 Gyr) (Lyons et al., 2024b). FeRM are found in marine and freshwater sediments, where they reduce Fe(III) to Fe(II) coupled to the oxidation of organic carbon, H_2, CH_4 or ammonia (Eqs. (5)–(8)). A recent study also showed that Fe (III) reduction can be coupled to oxidation of sulfur species (Chen et al., 2025).

$$4Fe^{III}OOH + CH_3CHOHCOO^- + 7H^+ \rightarrow 4Fe^{2+} + CH_3COO^- + HCO_3^- + 6H_2O \quad (5)$$

$$2Fe^{III}(OH)_3 + H_2 + 4H^+ \rightarrow 2Fe^{2+} + 6H_2O \quad (6)$$

$$8Fe^{III}(OH)_3 + CH_4 + 15H^+ \rightarrow 8Fe^{2+} + HCO_3^- + 21H_2O \quad (7)$$

$$6Fe^{III}OOH + NH_4^+ + 10H^+ \rightarrow 6Fe^{2+} + NO_2^- + 10H_2O \quad (8)$$

They are capable of oxidizing various organic molecules such as acetate, lactate and even complex aromatic compounds (Wang et al., 2008). To date, both neutrophilic and acidophilic FeRM have been described. Acidophilic FeRM, first described in 1976 (Brock and Gustafson, 1976), can use H_2, sulfur and organic compounds as electron donors and are part of the phyla Crenarchaeota, Euryarchaeota, Acidobacteria, Actinobacteria, Firmicutes, and Proteobacteria (Malik and Hedrich, 2022). FeRM can reduce a variety of Fe(III) minerals (e.g., Fh and hematite) with varying rate and extent depending on the physical properties of the minerals, forming (mixed valent) Fe(II) minerals such as siderite, vivianite, magnetite or green rust ($[Fe(II)_{1-x}Fe(III)_x(OH)_2]^{x+}\cdot[(x/n)A^{n-}, mH_2O]^{x-}$, with A^{n-}: intercalated anions and x: molar fraction of trivalent cations).

Fe(III) is much less soluble than Fe(II). Most organisms depend on the production of siderophores for its assimilation (Ahmed and Holmström, 2014). However, FeRM have developed different reduction strategies to overcome this challenge. They use membrane proteins (c-type cytochrome) in the cell surface to reduce Fe(III) in direct cell-mineral contact (Shi et al., 2009). They can use pili or nanowires to transport electrons to the electron acceptor, increasing the required cell-mineral distance from nm to few μm (Reguera et al., 2006; Smith et al., 2013). Another strategy involves electron shuttles that are reduced enzymatically, with the electrons transferred to the final acceptor abiotically (Bai et al., 2020). Electron shuttles allow the electron transfer to occur in a cm-scale and can be found in the environment (e.g., natural organic matter) or be secreted by microorganisms (e.g., flavins) (Bai et al., 2020).

It is important to clarify that FeRM can use both the mineral and organic components of BIOS as substrates regardless of the different origin and properties (Whitaker et al., 2021). The mineral component of BIOS can be used as electron acceptor. The organic matter associated to BIOS can be used as electron donor. Additionally, the organic component can stabilize poorly crystalline Fe(III) minerals by preventing Fe (II)-catalyzed recrystallization (Kennedy et al., 2004; Warren and Ferris, 1998). This leads to a higher rate and extent of BIOS reduction compared to abiogenic iron (oxyhydr)oxides (Langley et al., 2009a). Hence, the preservation of BIOS as biosignatures also relies on the biogenic processes that affect their fate after initial formation.

2.6. Biosignatures

2.6.1. Morphological biosignatures

Biosignatures are evidence of past and present life. They may include molecules (e.g., lipids), minerals (e.g., BIOS, microfossils) or specific patterns (e.g., isotopic, microbialites) (Des Marais et al., 2008; Eroglu et al., 2023; Javaux and Benzerara, 2009; Runge et al., 2023; Summons et al., 2008). Their correct interpretation is crucial to understand the history of life on Earth and in the search of life elsewhere. BIOS produced by FeOM are prime candidates for Fe-based biosignatures. BIOS are typically poorly crystalline and with an irregular morphology (e.g., minerals associated with twisted stalks and sheaths, Fig. 3) (Chan et al., 2004, 2009, 2011; Cornell and Schwertmann, 2006). They have a higher surface area, mainly due to the small particle size (Eusterhues et al., 2008; Kappler et al., 2005). They also have a higher organic carbon content, mainly from EPS and entire cells entombed by the Fe(III) (oxyhydr)oxides (Chan et al., 2009; Miot et al., 2009b; Miot et al., 2009c). Some BIOS also precipitate on the cells, leading to the preservation of their morphology (i.e., microfossils) (Williams et al., 2015) and associated organic matter. FeOM have unique coenzymes that can be preserved in the rock record (Floyd et al., 2019) and BIOS can also help in the preservation of biomolecules with different origin (e.g., Scytonemin, a cyanobacterial pigment) (Varnali and Edwards, 2013).

The morphological analysis of these structures is performed by microscopic techniques, utilizing a combination of light, scanning and transmission electron microscopy (Fig. 3) (Chan et al., 2011; Suzuki et al., 2012). The organic composition of the BIOS is studied mainly by spectroscopic techniques (e.g., X-ray absorption spectroscopy and FTIR) and secondary ion mass spectrometry for the EPS composition (Chan et al., 2016b; Miot et al., 2009c; Suzuki et al., 2012). Moreover, fluorescence microscopy and sequencing are used to elucidate the distribution and species of the cells (or cell remnants) associated with the minerals (Fleming et al., 2014; Krepski et al., 2013; Suzuki et al., 2012). Confocal fluorescence microscopy is in particular useful to identify the distribution pattern of polysaccharides and cells with respect to the Fe minerals (Krepski et al., 2012, 2013; Laufer et al., 2017b). 3D-based X-ray tomography and focused ion beam-transmission electron microscopy (FIB-TEM) have also been used to investigate putative filaments from a 1.74 Ga jasper deposit (Little et al., 2021).

However, the interpretation of Fe(III) (oxyhydr)oxides minerals for biogenicity is not trivial. Abiotic reactions can form so-called biomorphs, biogenic-like structures that resemble the morphology of microfossils and can lead to misinterpretation. For instance, cell-like structures can be formed by S^0 encapsulated in organic matter that self-assembled in a sulfidic environment (Cosmidis and Templeton, 2016), by diagenesis (200 °C, ~15 bars) of quartz in the presence of RNA (Criouet et al., 2021) and by chemical gardens (biomorphs formed by the reaction of a 'seed' metal salt into an aqueous silicate, phosphate, carbonate, oxalate, or sulfide solution) (McMahon, 2019). In addition, in some conditions abiotic biomorphs can be better preserved than their biogenic counterparts (Nims et al., 2021). Therefore, multiple approaches (e.g., morphologic, isotopic, organic and mineral composition) must be followed to assess the biogenicity of a sample.

2.6.2. Isotopic biosignatures

While Fe isotopes were thought to be initially promising for biosignatures, multiple studies have concluded that the isotopic fractionations associated with biogenic versus abiogenic Fe(II) oxidation and subsequent precipitation showed significant overlaps (Johnson et al., 2020). This is further compounded by Fe isotopic exchange between minerals and aqueous phase during burial and diagenesis (Severmann et al., 2006). In contrast, carbon isotopes seem more promising. Highly negative $\delta^{13}C$ values (<−10 ‰) of C associated to Fe(III) (oxyhydr)oxides are correlated with a biogenic origin (BIOS), while those of an abiotic origin typically have $\delta^{13}C$ values > − 10 ‰ (Ayupova et al., 2016; Kennedy et al., 2010; Weber et al., 2012).

2.6.3. Transformation of BIOS via short term diagenesis

Short term diagenesis of BIOS is carried out by FeRM. The rock record and phylogenetic studies set the appearance of FeRM contemporary to photoferrotrophy (~3.5 Gyr ago) (Lyons et al., 2024a). There are significant differences in the reduction rate, depending on the FeOM that produced the BIOS. For instance, Fe(III) in BIOS from *Gallionella*-like iron(II)-oxidizers were less bioavailable for reduction by *Shewanella*

putrefaciens CN32 than those from *Leptothrix*-like iron(II)-oxidizers (Langley et al., 2009a). In addition, organic matter embedded in the BIOS does not seem to inhibit the Fe(III) reduction, but to promote it, as it can be used as a nutrient source (Langley et al., 2009b). FeRM and fermenters could have been responsible for up to 70 % of Fe(III) reduction in ancient oceans (Konhauser et al., 2005), hence destroying or altering BIOS biosignatures.

Reduction of Fe(III) (oxyhydr)oxides by FeRM produces Fe^{2+} and leads to different mineralogy. The reduction of abiotic minerals forms Fe (II) minerals such as siderite and vivianite (Weber et al., 2006), the mixed-valent Fe(II)-Fe(III) minerals magnetite and green rust (Lovley, 1991; O'Loughlin et al., 2007), and the Fe(III) mineral goethite from dissolution-reprecipitation of poorly crystalline Fh catalyzed by Fe^{2+} (Hansel et al., 2004; Notini et al., 2022). When using BIOS, magnetite (Glodowska et al., 2021), vivianite and other hydrated ferrous phosphates of varying stoichiometries are formed (Langley et al., 2009a). However, little is known about the effect of multiple variables in the reduction products of BIOS, such as the origin of the BIOS, the medium composition, the pH and Fe(III) concentration. One study showed that organic matter can be preserved within biogenic siderite formed by microbial Fe(III) reduction (Han et al., 2024). Hence, FeRM may not completely erase biosignatures, but may preserve them in a different form instead.

Besides FeRM, BIOS can also be reduced abiotically by sulfide, generating a variety of iron sulfide minerals such as mackinawite (FeS), greigite (Fe_3S_4) and pyrite (FeS_2) (Mansor et al., 2025b). The relative contribution of FeRM to other reductants depends on environmental parameters such as pH, sulfate concentration and microbial abundance. In this review, we focus on BIOS transformation under low sulfur conditions, although the impact of sulfur on BIOS preservation should be explored in future studies.

2.6.4. Long term diagenesis

Given enough time, temperature and pressure, the initial BIOS can be further transformed during burial, diagenesis and metamorphism. In aqueous environments, poorly crystalline Fe minerals transform abiotically into lepidocrocite, goethite and hematite, depending on pH, the presence of co-existing substances (e.g., Al, trace metals, organic matter), temperature, pressure and time (Caraballo et al., 2022; Posth et al., 2010). The preservation of Fh is known to up to 80 °C due to its stabilization by organic matter (Kennedy et al., 2004; Toner et al., 2012). At higher temperatures and pressure, Fh transforms to siderite (100 °C, 1–30 MPa) and magnetite (120 °C, 1–50 MPa) in the presence of organic matter (Halama et al., 2016; Kennedy et al., 2004; Köhler et al., 2013; Posth et al., 2013a). Meanwhile, hematite is the most thermodynamically stable Fe oxide and the main diagenetic product over geological timescales under oxidizing conditions (Cornell and Schwertmann, 2006). Transformation of other Fe(III) minerals to hematite is facilitated at high temperatures, pressures and mechanical stress (Cornell and Schwertmann, 2006). Nevertheless, goethite is occasionally found in the geological record, where their transformation to hematite could be suppressed under cool environments with acidic pH (Sephton et al., 2023). Additionally, under reducing and sulfidic conditions, the formation of pyrite is favored (Berner, 1984; Mansor et al., 2025a; Raiswell and Canfield, 1998). Notably, Fe minerals play a key role in the preservation of organic matter in sediments, preserving them on 100,000 years' time scales (Klueglein et al., 2014), with the oldest report being a 3.770 Gy old microfossil of hematite with the morphology of the sheaths produced by FeOM, found in the Nuvvuagittuq Supracrustal Belt, Quebec (Dodd et al., 2017b).

Intriguingly, BIOS can help in the preservation of organic matter. BIOS of NRFeOM (e.g., *Acidovorax* sp. BoFeN1) help to preserve the cell content up to 600 °C (Li et al., 2013). Picard et al. (2015) investigated the effect of diagenetic process (high T and/or P) on twisted stalks and found preservation of their morphology and organic content (up to 250 °C/140 MPa), even though there is transformation into more crystalline minerals (e.g., hematite and magnetite). They concluded that such structures could be preserved in the rock record and be indicators of the presence of FeOM. Moreover, the released Fe^{3+} can precipitate onto other cells beyond the FeOM, thus helping in their fossilization and preservation (Ferris, 2005; Orange et al., 2014) although likely with a reduced efficiency (Beveridge et al., 1983; Picard et al., 2015).

In summary, Fe-metabolizing microorganisms play an important role in the biogeochemical cycle of Fe and other elements on modern and ancient Earth. Various FeOM produce BIOS that give clues to microbial communities and environmental conditions (e.g., O_2 concentration), despite multiple transformation processes after burial in the geological record. Therefore, BIOS are ideal candidates for the search of Fe biosignatures in other Fe-rich environments such as in other rocky planets and icy moons.

3. Mars

Mars, as part of the terrestrial planets, possesses an interior rich in iron and nickel, and a silicate mantle and crust. Despite Fe being slightly less abundant in the bulk Mars (23.7 wt% (Yoshizaki and McDonough, 2020)) compared to Earth (32 wt%, McDonough and Sun, 1995), Fe is preferentially partitioned in the upper Martian crust (11.4 wt% in ~1550 km thick layer; 4th most abundant) (Kim et al., 2023; Knapmeyer-Endrun et al., 2021; Yoshizaki and McDonough, 2020) with a value approximately twice than in Earth's crust (6.3 % in ~2900 km thick layer) (Helffrich and Wood, 2001; McDonough and Sun, 1995), highlighting its availability for microbial metabolisms. Multiple rovers have investigated the planet starting with the Viking landers in 1976. The Mars Exploration Rovers equipped with a Mössbauer spectrometer identified various Fe-bearing minerals and clays including olivine ($(Mg,Fe^{II})_2SiO_4$), pyroxene ($XY(Si,Al)_2O_6$, with X: Ca, Na, Fe(II) or Mg; and Y: Cr, Al, Mg, Co, Mn, Sc, Ti, V, Fe(II) or Fe(III)), ilmenite ($Fe^{II}TiO_3$), magnetite, nanophase ferric oxide (npOx), hematite, goethite, and Fe^{III}-sulfates in Gusev crater (Morris et al., 2006); and hematite, jarosite ($KFe^{III}_3(SO_4)_2(OH)_6$), olivine and magnetite in Meridiani Planum (Christensen et al., 2000; Hoefen et al., 2003; Klingelhöfer et al., 2005; Mustard et al., 2005; Squyres et al., 2006; The Omega Team et al., 2005).

Today there are two operational rovers at the surface: The Curiosity rover from the Mars Science Laboratory mission and the Perseverance rover (Mars 2020). The Alpha Particle X-ray Spectrometer (APXS) onboard Curiosity revealed that the sedimentary rocks are rich in Fe with Fe content (as FeO) from ~20 % to as high as 27.6 %, most of it in the form of magnetite and poorly diffracting (oxyhydr)oxides (Treiman et al., 2016). With the CheMin X-ray diffraction (XRD) and X-ray fluorescence (XRF) instrument (Blake et al., 2012), Treiman et al. (2016) reported iron phases that suggest the presence of Fh which has recently been confirmed by infrared spectra and kinetic calculations (Valantinas et al., 2025). Given that Fh is the most thermodynamically bioavailable of the ferric iron (oxyhydr)oxides (Nixon et al., 2012; Cornell and Schwertmann, 2006), its presence emphasizes the habitability of Mars and the potential for microbial Fe(III) reduction. It opens questions about the possible abundance or even presence of FeOM and FeRM. If Fh is so abundant, was any or all of it produced by FeOM? Is it being reduced or was part of it reduced at a given moment by FeRM?

Despite this ever-present Fe, the Martian surface is not considered habitable today due to the high UV radiation and the high concentration of strong oxidizing agents such as perchlorates and chlorates (Glavin et al., 2013; Hecht et al., 2009; Sutter et al., 2017). On Earth, perchlorates are found at low concentrations, except in arid regions such as in the Atacama Desert, where it can reach 0.1 wt% (Duncan et al., 2005; Srinivasan and Viraraghavan, 2009). On Mars, perchlorate concentration can reach up to 1 wt% (Rzymski et al., 2024). However, the Martian subsurface could be a good habitat for life, given that it is warmer than the surface, it is protected from radiation and the potential presence of water reservoirs (Clark et al., 2021; Longo and Damer, 2020). Conditions conductive to life would have also existed on the surface of early

Mars given the existence of a reducing atmosphere, the presence of water and organics (Amador and Ehlmann, 2020; Westall et al., 2013). Hydrated minerals such as jarosite found at Meridiani Planum, the landing site of the Opportunity rover (Morris et al., 2006), supports the presence of large amounts of water in the past during the Noachian era (~4.1–3.7 Gyr ago) (Marion et al., 2008; Moores et al., 2019). Organic matter would have been supplied by exogeneous sources, potentially exceeding the concentration reached on early Earth (Clark et al., 2021). The presence of an atmosphere and reducing gases would have reduced the toxicity of reactive oxygen species compared to the modern day (He et al., 2023). In this section, we discuss the habitability of early and modern Mars, reviewing studies that test this hypothesis and identifying potential future research on iron-based dissimilatory metabolism and other metabolic processes that the planet could have supported or may still support.

3.1. Life based on Fe on early Mars

Early Mars had a favorable environment where protocells could have been formed (Cary et al., 2024; Clark et al., 2021). In the hypothesis that life originated, the availability of Fe would have been a high selective pressure that shaped the metabolism while catalyzing multiple reactions. Early Mars had a reducing atmosphere rich in N_2/CO_2 ~ 4.3 Gyr ago (Sasselov et al., 2020). Given the reducing conditions and high amounts of Fe (Yoshizaki and McDonough, 2020) and sulfur (S), these elements might have played an important role in the origin and development of life, although we will focus on Fe here. Fe is among the pool of redox-active species present on Mars (besides hydrogen, carbon, sulfur) that can act as both electron donor and acceptor due to its multiple valences.

In addition to an electron donor and acceptor couple, life (as we know it) requires carbon to build biomass and in some cases even uses organic carbon as substrate (i.e., as energy source). In Gale Crater, the discovery of OC raised an interesting question as to its ultimate source. A few studies considered whether the carbon could originate biologically from the activity of NRFeOM. Considering the availability of Fe(II) (Hurowitz et al., 2010), nitrate (Stern et al., 2015), organics (Eigenbrode et al., 2018; Stern et al., 2022), the circumneutral pH and the presence of liquid water in the Gale Crater, Price et al. (2018) proposed a plausible chemolithotrophic metabolism involving NRFeOM. As their metabolism does not require light, they could thrive deeper underground when the surface conditions turned hostile.

Fifer and Wong (2024) went further and estimated the expected concentration of autotrophic NRFeOM that would be needed to explain the amount of organic carbon in Gale Crater, in terms of preserved biomass (biomass per unit volume). Nitrate concentration is known (<1100 ppm) (Stern et al., 2015) and carbon input from other sources (e.g., hydrothermal or atmospheric production) is expected to account for only 61 ppb (20–87 % of the total). Assuming low consumption of nitrate (<10 %), they calculated that ~10^4 cells/mL of NRFeOM could be expected in Gale crater lake in early Mars (Fig. 4). Considering that the global reservoir of nitrate on Mars is 5 × 10^{15} mol (Manning et al., 2009), and that organic carbon is continuously supplied today at a rate of ~2.4 × 10^5 kg $year^{-1}$ endogenously or via meteorites (Yen et al., 2006), NRFeOM could be widespread on Mars. Caution is warranted, however, as nitrate and organic carbon concentrations may vary widely on the Martian surface. Moreover, this model did not include heterotrophs, although their presence cannot be excluded (Raven et al., 2018).

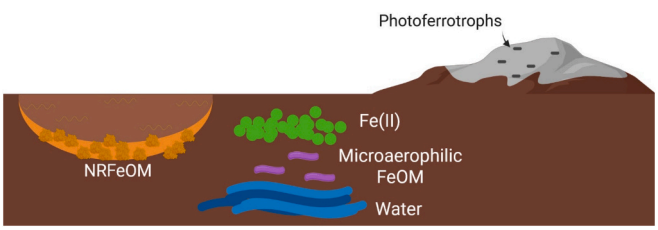

Fig. 4. Potential niches of Fe-metabolizing bacteria on Mars. NRFeOM in craters (left), microaerophilic FeOM in the subsurface (middle) and photoferrotrophs in cryoconites (right).

Early Mars likely had niches suitable for acidophilic microorganisms. The identification of Fe minerals such as hematite and jarosite supports the transport of Fe-rich water (Hynek et al., 2002; Ormö et al., 2004) in an acidic environment on the northern hemisphere on early Mars (Klingelhöfer et al., 2004). *Acidithiobacillus ferrooxidans* has been used as a model organism for Martian life under these conditions. This bacterium was isolated from a coal mine drainage in 1951 (Temple and Colmer, 1951) and is an obligate chemolithotroph, capable of Fe(II), elemental sulfur (S^0), sulfide and hydrogen oxidation, as well as reduction of iron(III) and S^0. Bauermeister et al. (2014) found that it could grow with Martian regolith as the sole nutrient, with a faster growth rate (4–5 days) under oxic than anoxic conditions (8 days) (Quatrini and Johnson, 2018). Biogenic Fe(II) oxidation was shown to be affected by the oxygen concentration and it was lowered when using a Martian O_2 partial pressure (1 Pa). Silva et al. (2024) showed that *A. ferrooxidans* is capable of growing with siderite and vivianite as sole Fe(II) sources coupled to O_2 reduction in oxic conditions and to sulfur oxidation and Fe(III) reduction under anoxic conditions. Moreover, it grew with siderite as sole energy (Fe(II)) and C source under oxic conditions, making this a potential prospering metabolism during the transition to an oxidizing Mars, before migration to the subsurface (Silva et al., 2024).

3.2. Life based on Fe on modern Mars

As Martian atmosphere oxidized abiotically (e.g., by O_2) due to the solar wind and radiation about 3.5–3.0 Gyr ago (Cary et al., 2024; Kite et al., 2022; Lanza et al., 2016), it led to a cold dehydrated planet with dangerous UV radiation and a highly oxidizing surface with high concentrations of chlorates and toxic reactive oxygen species (Jakosky et al., 2017). This led to the consideration that under today's environmental conditions, the Martian surface is not habitable. However, oxidizing conditions on Earth have not prevented the proliferation of life.

Antioxidant enzymes – those enzymes used to protect the cells from oxidative stress by neutralizing harmful reactive oxygen species - appeared early in life's history on Earth. Cyanobacteria ancestor ~3.3 to 3.6 billion years ago (Imlay, 2003; Jabłońska and Tawfik, 2021) and archaea ancestors possessed oxidases (Castresana et al., 1994). The environment where life arose on Earth might have had microoxic conditions (Jabłońska and Tawfik, 2021) and oxidases did not appear as a result of the atmospheric oxygenation but might be a casual event potentially triggered by reactive oxygen species and O_2 product of mineral-water interactions (He et al., 2023). Moreover, bacteria have developed mechanisms to avoid or repair damages in the membrane, proteins and/or DNA caused by reactive oxygen species (Addorisio et al., 2022). *Leptospirillum ferrooxidans*, an abundant FeOM in the Río Tinto (Spain), induces genes involved in DNA repair and synthesis of carotenoids and cobalamin to respond to oxidative damage (Ferrer et al., 2016). *Leptospirillum ferriphilum* DSM14647 uses the thioredoxin system (composed by thioredoxins Trx and thioredoxin reductase TR) to maintain redox status of proteins under extreme pH conditions (Norambuena et al., 2012). In the case of *Acidithiobacillus ferrooxidans*, another acidophilic FeOM, the damage by reactive oxygen species is avoided by the synthesis of glutathione and manganese superoxide dismutase (Farías et al., 2021). Therefore, oxidizing conditions on the surface might limit the diversity of microorganisms but do not prevent the development of life.

UV radiation is another threat for the development of life in modern Mars. Despite intense UV radiation (Jakosky et al., 2017), photoferrotrophs could still be present in habitable zones within centimeters to meters depth in the ice caps (Fig. 4). Dusty water ice could

simultaneously provide water and allow enough photosynthetically active radiation to pass through, while attenuating dangerous UV radiation due to the shielding effect of Fe oxide nanophases (Bishop et al., 2006; Khuller et al., 2024). Mars-like conditions have been tested in the laboratory for growing multiple cyanobacteria. *Synechocystis* sp. PCC 6803 grew with Martian regolith simulant amended with nitrate (as sodium nitrate) (Sakon and Burnap, 2006). Antarctic cyanobacteria were also tested and were capable of growing with a Martian regolith simulant. Similar tests employing even stricter Mars-like conditions (e.g. with an analog atmosphere (e.g., Sakon and Burnap, 2006) are encouraged to investigate the potential metabolisms (e.g., photoferrotrophy) that could thrive under those conditions (Fig. 1).

A few centimeters below the surface, where UV radiation is lower and Fe(II) is available, microaerophilic FeOM could thrive on Mars (Fig. 4). The Martian subsurface could be rich in Fe(II) (50–90 % of the total) that is available as an electron donor. The origin of the Fe(II) minerals is mainly basaltic soils (Morris et al., 2006). On Earth, microaerophilic FeOM thrive in environments with low O_2 and high Fe(II) concentrations, such as in a water column or at the sediment-water interface (Chan et al., 2016b; Emerson et al., 2010). This might be a constraint for their growth on modern Mars where subsurface water is likely limited (Hays et al., 2017). Future work is needed to test the growth of microaerophilic FeOM under Mars-like subsurface conditions.

Fe(III) (oxyhydr)oxides are highly abundant on Mars and thus available as electron acceptors for FeRM. The surface may contain <30 wt% of Fe(III) (Blake et al., 2013; Ramkissoon et al., 2019; Valantinas et al., 2025). The majority is in the form of Fe(III) (oxyhydr)oxides such as Fh, hematite, goethite and magnetite that could be formed by photooxidation (Hurowitz et al., 2017; Nie et al., 2017), weathering (Paul and Mormile, 2020), diagenesis of authigenic Fe(III) (oxyhydr) oxides (e.g., Fh) (Peretyazhko et al., 2018; Rampe et al., 2020), or microbial activity (Hurowitz et al., 2017; Tabata et al., 2021). Furthermore, jarosite, present in the Meridiani Planum (Morris et al., 2006) (and evidence of the presence of water on early Mars) has been proven to be bioavailable for reduction by *Shewanella putrefaciens* (Bingjie et al., 2014; Castro et al., 2013) and by *A. ferrooxidans* (Yang et al., 2020). The latter is also able to catalyze the oxidation of elemental sulfur coupled to Fe(III) reduction under anoxic conditions (Silva et al., 2024).

The recent confirmation of Fh being the most abundant Fe(III) mineral in martian dust (Valantinas et al., 2025) raises a question: why has it not been reduced by FeRM? One possible reason is the limited availability of electron donors, even though the Curiosity rover detected a wide range of organic molecules (Millan et al., 2022). *Geobacter* is capable of using an extensive list of electron donors including alcohols (e.g., propanol and butanol), carboxylates (e.g., acetate, propionate) and H_2 (Nixon et al., 2012) and is a plausible microbial taxon on Mars. However, the available carbon sources on Mars (e.g., amino acids from meteoritic origin) are complex and not bioavailable for oxidation by FeRM enriched from Mars analogs, limiting the feasibility of this microorganisms on Mars, unless simple organics are detected. Moreover, none of the organics found on Mars by these rovers is considered a biosignature and greater efforts are needed in their search and identification (Millan et al., 2021). Another challenge for FeRM are reactive oxygen species. FeRM are more sensitive to these compounds than FeOM (Chen et al., 2022). In fact, FeOM contribute to the production of reactive oxygen species, hence indirectly affecting the activity of FeRM (Chen et al., 2022). Thus, the activity of FeRM on the Martian surface could be limited by a number of factors.

3.3. Martian BIOS

Given the possibility of Fe-metabolizing microorganisms on Mars, BIOS could have been formed on the early and modern Mars. This offers an opportunity for the search of morphological and molecular Fe-based biosignatures on Mars (Chan et al., 2016a), being preserved in the rock record as microfossils, as long as they remain under geochemical conditions that are suitable for preservation (e.g., limited metamorphism) (Hays et al., 2017; Williams et al., 2015). They could also contribute to the extensive Fe(III) (oxyhydr)oxides found on the Mars' surface. For example, mineral-encrusted cells of NRFeOM could be present in Gale Crater. Twisted stalks and sheaths consistent with microaerophilic FeOM could be present a few centimeters below the Martian surface (see Section 3.2). Carbon isotope signatures consistent with phototrophic CO_2 fixation could be associated with Fe(III) minerals within cryoconites (Fig. 4). Over time, BIOS could undergo transformation either by FeRM or by diagenetic processes. Hence, our work brings together the repertoire of possible Fe-based biosignatures on Mars.

4. Icy moons

Icy moons refer to satellites orbiting giant planets that are constituted of a water ocean capped by an icy outer layer. Their oceans are main targets for astrobiologists due to their potential habitability. Space missions such as Cassini-Huygens (to Saturn) and Juno (to Jupiter) have provided great insights on the habitability of icy moons. Cassini-Huygens was the first mission to Titan (Saturn's moon) (Lebreton and Matson, 2002; Matson et al., 2002; Sotin et al., 2021), collecting data on its atmosphere and surface. In 2030, the mission Europa Clipper is expected to arrive to Europa and determine whether the subsurface of the moon could harbor life (Becker et al., 2024; Daubar et al., 2024; Pappalardo et al., 2024; Phillips and Pappalardo, 2014; Roberts et al., 2023). In 2031, JUICE mission is planned to explore three of Jupiter's icy moons (Ganymede, Calisto and Europa) (Fletcher et al., 2023; Grasset et al., 2013).

Europa and Enceladus are the most attractive icy moons in terms of habitability. Their ocean is in direct contact with their core, which allows for material exchange and enrichment of the water chemistry (Glein et al., 2015; Porco et al., 2006; Vance et al., 2018). This is not the case for all icy moons, where some are made of an ice layer between the nucleus and the ocean, preventing this exchange to happen. Furthermore, Europa and Enceladus present cracks in the outer layer that allow exchanges between the ocean and the surface (Porco et al., 2006). Enceladus stripes are particularly big (extending up to 130 km) with plumes that typically reach hundreds to thousands of kilometers (Hansen et al., 2006; Spahn et al., 2006; Villanueva et al., 2023; Waite et al., 2006). The plumes, sampled via Cassini's spectrometers, contain H_2, CH_4, CO_2, NH_3, organic molecules (>200 amu), and phosphate salts (Glein and Waite, 2020; Porco et al., 2006; Postberg et al., 2018, 2023; Waite et al., 2017). Although the presence of these molecules builds on the habitability of Enceladus, up to date no biomarkers (e.g., in the form of lipids) have been identified.

The presence of methane (and the bioessential elements, CHONPS) has led to speculation about the possibility of methanogens and sulfate-reducers in the oceans of Enceladus and other icy moons (Higgins et al., 2024; McCollom, 1999; Taubner et al., 2018; Tenelanda-Osorio et al.,

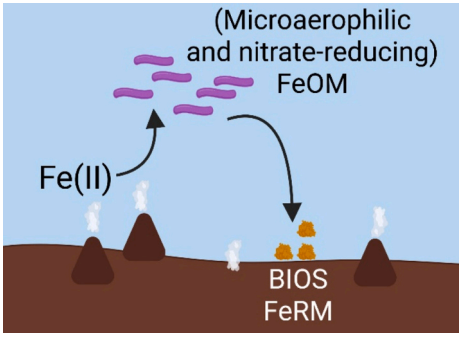

Fig. 5. Potential hydrothermal Fe(II) source on the seafloor of Enceladus and associated Fe microorganisms.

2021; Weber et al., 2023). More recently, Fe-metabolizing bacteria have also gained attention, and Fe has been added to the list of potential active redox elements (Roche et al., 2023; Sahai et al., 2024; Weber et al., 2023; Xu et al., 2025b; Zolotov and Shock, 2004b). Here we present some attempts of how to study the habitability of icy moons based on Fe biogeochemistry.

4.1. Enceladus

The saturnian moon, Enceladus, is a small icy moon with a diameter of 500 km. It is the only moon whose interior has been studied in-situ. Its plume is the main source of material of Saturn's E ring, where silica nanoparticles were found. These nanoparticles can be formed only under hydrothermal conditions (>90 °C), thus suggesting hydrothermalism inside the moon (Waite et al., 2017).

The water-rock interactions in the core offer a habitable place, like it does near Earth's ocean hydrothermal vents (Fig. 5). The core of Enceladus is estimated to have a chondritic composition and Fe-bearing hydrated minerals with a porosity 20–30 % (Choblet et al., 2017). Models of Enceladus interior suggest that Fe-bearing minerals include hematite, magnetite, siderite, olivine and pyrite (Hamp, 2022; Sekine et al., 2015). As shown above, hematite is an available electron acceptor for FeRM (e.g., *Shewanella* species), while siderite can function as electron and carbon source for FeOM (e.g., *A. ferrooxidans*) (Silva et al., 2024). Olivine can also be used as an energy source for FeOM (*Pseudomonas* sp. HerB) at temperatures as low as 5 °C (Popa et al., 2012). Electron acceptors (NO_3^- and O_2) are estimated to be available along with reactive oxygen species that could be formed at the surface due to the radiation and supplied downward to the ocean through the stripes (Ray et al., 2021). Therefore, Fe(II) oxidation and Fe(III) reduction are both plausible metabolisms on Enceladus.

One of the arguments against microbial Fe redox metabolisms is the high pH (9–11) of the ocean. The pH limits the biogeochemical reactions that can take place in a given environment based on thermodynamic constraints (Bethke et al., 2011; Jin and Kirk, 2018) that influence the microbial diversity towards metabolisms favored under those conditions (Frankenberger and Johanson, 1982; Lauber et al., 2009; Leprince and Quiquampoix, 1996). In the case of FeOM, higher pH leads to more rapid abiotic Fe(II) oxidation, such that FeOM can no longer kinetically compete for Fe(II) oxidation. In the case of FeRM, although their optimal pH depends on the mineral reduced (Postma and Jakobsen, 1996), it is typically around 7 (Straub et al., 1998). With Fh, the most thermodynamically favored, the pH upper limit is 8.3 (Jin and Kirk, 2018). At higher pH values (9–12), the energy available for Fe(III) reduction decreases to its lowest point. Then, other metabolisms would be more favorable, such as elemental sulfur and sulfate reduction (Bethke et al., 2011; Flynn et al., 2014).

However, a high pH promotes the abiotic degradation of organics, leading to the formation of aromatic compounds that could potentially serve as electron shuttles (Bai et al., 2020). Electron shuttles are organic compounds that participate in the electron transfer in the Fe(III) reduction. Thus, while Enceladus' high pH seems harmful in principle, it could also promote Fe(III) reduction. Notably, the reduction rate at high pH values is expected to be up to 50 % slower than at optimal pH (pH = 7) (Fernández-Calviño and Bååth, 2010; O'Flaherty et al., 1998).

Geobacter sulfurreducens, a well-known FeRM has been tested under an Enceladan ocean-like conditions and showed growth after 7 days at pH 9 (Roche et al., 2023), even though it is not typically considered as an extremophile. Enceladan polyextreme conditions besides pH (nutrients availability, salinity) could be tested with alkaliphilic FeRM (e.g., *Alkaliphilus metalliredigens* (QYMF) (Roh et al., 2007) (see also Zavarzina et al., 2024). This metabolism would also be favored by the constant supply of H_2, an available electron donor for Fe(III) reduction. Through the plumes, H_2 is expelled at a rate of 1–5 × 10^9 mol per year (Waite et al., 2017). This result further supports the need to test other FeRM isolated from alkaline environments (Valencia-Cantero et al., 2007; Williamson et al., 2013).

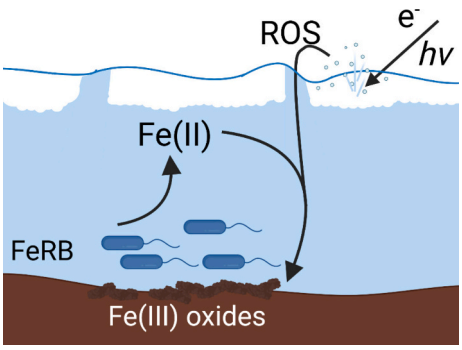

Fig. 6. Hypothetic seafloor in Europa. FeRM would reduce the available Fe(III) (oxyhydr)oxides in the seafloor, producing Fe(II) that stays in solution. Fe(II) would be eventually oxidized by the reactive oxygen species produced at the surface and then fall back to the seafloor in the form of abiotic Fe(III) (oxyhydr)oxides.

As a result of the reduction, biogenic minerals are formed, including magnetite, siderite and vivianite (Hansel et al., 2005; Kappler et al., 2021). Considering the capacity for FeRM to thrive in the ocean of Enceladus and taking advantage of the access to the material from the ocean (via plumes), future work should aim to determine the unique properties (e.g., morphology, composition) of the biominerals formed under enceladan conditions that differ from abiotic (e.g., hydrothermal origin) and the detection capabilities of these minerals.

4.2. Europa

Orbiting Jupiter, Europa is one of the most important astrobiological bodies in the solar system. Europa's surface is in constant interaction with Jupiter and to a lesser extent, with Io. Io supplies sulfur species to Europa's surface (through volcanic eruptions and impacts), while Jupiter's magnetosphere bombards Europa with highly energetic protons and electrons. This bombardment triggers photolysis and radiolysis in the surface creating oxidants (e.g., reactive oxygen species, H_2O_2, O_2) that can be transported to the ocean underneath the icy surface. Like Enceladus, Europa possesses a water ocean below the surface and water vapor plumes have been detected, albeit being about one order of magnitude (~50–200 km) (Roth et al., 2025) smaller than those of Enceladus (~100–9600 km) (Villanueva et al., 2023). These findings have paved the way for the Europa Clipper mission, which is on its way to the moon while this paper is being written.

The possibility of Fe(III) reduction in Europa has been evaluated. With the supply of Fe(II) from the core and the oxidants from the surface, Sahai et al. (2024) proposed an "iron snow" model for the ocean (Fig. 6). They propose that the O_2 from the surface would sink (by surface cycling, melting or diffusion (Greenberg, 2010; Pasek and Greenberg, 2012; Vance et al., 2016)) and oxidize the Fe(II) coming from the vents, forming Fe(III) (oxyhydr)oxides that then precipitated to the seafloor (as "iron snow", taking inspiration from the "marine snow" phenomena depicting the sinking of organic matter-mineral aggregates in Earth's oceans). An estimated production rate of 2.5 × 10^{26} cells yr^{-1} of free-living FeRM in the ocean could be expected (Sahai et al., 2024).

Contrary to Enceladus, Europa's ocean is thought to be acidic and its core is thought to be ultramafic. Hydrothermal processes are expected on the seafloor, powered by tidal flexing, leading to interactions between the rocky silicate seafloor and the bottom of the ocean (Hand and Carlson, 2015; Vance et al., 2007). Nonetheless, direct confirmation is required to constraint the hydrothermal processes, which are hypothesized to depend on the depth of the mantle (Green et al., 2025). In the plausible scenario of hydrothermal fluxes, the Fe(II) supply from the core and the potential presence of nitrate (from the abiotic oxidation of ammonia) (Weber et al., 2023) can cover the energy requirements of

NRFeOM. Moreover, contrary to iron(III) reduction, iron(II) oxidation has higher yields at lower pH values (Peiffer et al., 2024) making Fe(II) oxidation a more suitable metabolism for the seafloor.

4.3. BIOS and biosignatures in icy moons

FeOM offer multiple potential biosignatures that can be targeted on Europa. With a microaerophilic environment (thanks to the O_2 delivered to the ocean from the surface), morphology is one of the best biosignatures one could expect, considering twisted stalks and sheaths that could be produced by microaerophilic FeOM (see Section 2.2). However, its detection will be challenging due to the need of sampling and the required techniques. BIOS would be difficult to be found near the surface as they would most likely sink to the seafloor. Up to date microscopy has been limited to the microscope on board the Phoenix lander on Mars (Hecht et al., 2008) and the microscopic imager on the Mars Exploration Rovers (Herkenhoff et al., 2003). The plumes on Europa might not offer enough material, if the materials from the core would ever reach the surface. Then, the mission requires diving in the ocean, which is being proposed (e.g., Konstantinidis et al., 2015; Neveu et al., 2020), but might take a few years to implement due to planetary protection measures, ensuring the safety of both Earth and other planetary bodies for potential cross contamination (National Academies of Sciences, Engineering, and Medicine (U.S.), 2018). Instead, the detection of other lighter molecules could be more promising. For instance, the membrane of the members of *Ferroplasma*, a genus of acidophilic FeOM, contains caldarchaetidylglycerol tetraether lipids as a response to the low pH in the environments where they are found. Knowing that cell material can be identified with analog mass spectrometers onboard Europa Clipper (Klenner et al., 2024) this specific lipid could be a targeted molecule to search in Europa's ocean (e.g., via mass spectrometry) (Golyshina and Timmis, 2005).

On Enceladus, FeRM would be more favorable than FeOM given the high pH. The discovery of alkaliphilic FeRM (Switzer Blum et al., 1998) offers an opportunity to test the habitability of the moon and potential biosignatures. Alkaliphilic FeRM withstand pH values of 9.0 to 10.4 (Gorlenko et al., 2004; Ye et al., 2004) and a representative species of *Bacillus* (strain SFB) pushes the limit to 11.0 (Pollock et al., 2007). At this pH values, Fe(III) reduction is challenging and more thermodynamically favored in the presence of electron shuttles (Wang et al., 2018). Siderite, magnetite and vivianite are the main Fe(II)-bearing minerals that result from microbial Fe(III) reduction. The identity of the reduction products highly depends on the mineralogy of the initial Fe(III) (oxyhydr)oxides and the presence of phosphate and volatiles as well as OC identity and concentration (Fredrickson et al., 1998; O'Loughlin et al., 2019, 2021; Roh et al., 2003). With increasing concentrations of phosphate, the reduction rate becomes slower but yields higher reduction extents and favors the production of vivianite and green rust while magnetite is formed at lower concentrations (O'Loughlin et al., 2021). The presence of N_2 also promotes magnetite while CO_2 promotes siderite formation (Roh et al., 2007). On Enceladus, the recent discovery of phosphate (Postberg et al., 2023), the presence of H_2 (Waite et al., 2017) and the carbonate-rich ocean (Glein and Waite, 2020) set constraints on the Fe (II)-bearing mineral products of possible microbial Fe(III) reduction, most likely in the form of siderite. In the presence of OC, siderite forms in spindle-, rod-, peanut-, and dumbbell-like structures, which is not the case in the OC-free abiotic formation (Han et al., 2024). Considering the predicted presence of siderite in the Enceladus core (Hamp, 2022), once again microscopic techniques should once again be considered for determining the biogenicity of these Fe biominerals.

5. Lessons from model habitats on Earth

5.1. Mars

Modern model habitats on Earth are great field sites for understanding life and their signatures under similar conditions on Mars. One model habitat is the Río Tinto (Spain) as an early Mars analog. Located in the Iberian Pyrite Belt, Río Tinto is a river with high concentration of metals, pH 2.3 and high concentration of Fe(III) (Amils et al., 2014) comparable to the Noachian era (4.1 to 3.7) of Mars. Its similarity to Meridiani Planum is striking given the abundance of Fe(III) (oxyhydr)oxide (goethite) and sulfate (jarosite) minerals that are formed at a highly acidic pH (Finkel et al., 2023b). These minerals are formed in close association with microorganisms in Río Tinto today, leaving behind visible deposits such as iron terraces and microbialites. Proving that these deposits can only be formed in the presence of life is a huge endeavor that is being continued today. Fe(III) minerals also favor the preservation of organic biosignatures, especially in the form of lipids (Fernández-Remolar et al., 2021; Lalonde et al., 2012). While the Río Tinto is an excellent model habitat that reproduces biogeochemical Fe cycling in an acidic environment, it has one huge discrepancy compared to Mars in terms of temperature. Temperature on Mars is often below zero, which means that psychrophiles (organisms capable of living with temperatures below 20 °C) are the best model organisms instead of mesophiles (whose optimal growing temperature is within 20–45 °C).

Hence, other model Martian habitats are focused on subglacial terrestrial environments such as the Atacama Desert, Antarctica and ice caps (Fisher and Schulze-Makuch, 2013). The Atacama Desert is a well-known Mars analog for the study of the Amazonian period (2.9 Gyr ago to present). It has the highest UV radiation levels on Earth and oxidizing soils due to the presence of perchlorates, with similar concentrations to Martian surface (Azua-Bustos et al., 2020; Hecht et al., 2009). Within the desert, two sites are recognized as the most Martian-like ecosystems: the coastal range and the hyperarid core (Azua-Bustos et al., 2022; Navarro-González et al., 2003). Despite the apparent hostile conditions of the desert, microorganisms have been identified, challenging the general view of oxidizing Mars as inhabitable and giving clues of which biosignatures to look for (Azua-Bustos et al., 2023; Bartholomäus et al., 2024).

The ice caps are also analogs of modern Mars, particularly, the cryoconites. Cryoconites are holes in the ice caps, formed by the condensation of dust particles that fall in the surface and favor melting of their surroundings. They host complex communities that include microorganisms and even small invertebrates (e.g., tardigrade), dominated by cyanobacteria (Cameron et al., 2016; Mueller et al., 2001). Photosynthetic microorganisms could thrive in Martian cryoconites that could occur in its ice caps (Clow, 1987) as demonstrated by Khuller et al. (2024). Although non-photosynthetic Fe-utilizers have been enriched from similar cold environments (Nixon et al., 2017), no other study has yet truly focused on analyzing biosignatures under those conditions based on an Fe-based perspective.

5.2. Icy moons

Analog studies for icy moons are more recent, compared with the number of studies and analog sites of Mars. Research has been focused on laboratory ice analogs to study the effect of radiation on the surface of the moons and constraining the ability of detection of the organic material coming out of the plumes (Khawaja et al., 2024; Klenner et al., 2020, 2024; Robinson et al., 2023). Recently, several sites in the Arctic and Antarctica have gained attention for the search of extremophiles and for testing life-detection instruments. Subsurface lakes in the Arctic and Antarctica resemble subsurface oceans in icy worlds (Cassaro et al., 2021). Despite being 4 km beneath the ice sheet (Siegert et al., 2001), Lake Vostok in Antarctica host a community of microbes and enough dissolved OC (~0.5 mg/l) to sustain heterotrophic organisms (Priscu et al., 1999). In Ellesmere Island in the Canadian High Arctic, the supraglacial spring system of Borup Fiord Pass is an analog of the Europan surface. There, the ice contains sulfur minerals with ongoing sulfur chemistry that mimic those thought to be happening on the surface of Europa (Grasby et al., 2003). Also in the Arctic, on the West

Svalbard continental slope, the gases trapped in the ice cap have been used as analog of the ice sheet and plume composition of Enceladus, in an attempt to investigate a potential methane cycle (Franchi et al., 2025).

With respect to the seafloor, hydrothermal systems are analogs to the expected water-rock interactions in the interiors of icy moons. One example of a hydrothermal system on land can be found at Deception Island, Antarctica. The microorganisms there survive across extreme temperature gradients, from the hot fumaroles (100 °C) to the subzero temperatures in the glacier (Bendia et al., 2018; Lezcano et al., 2019; Uribe-Redlich et al., 2024). Oceanic hydrothermal vents are also good analogs of the icy moons' seafloor, characterized by high pressures and temperature gradients. Lost City in the mid-Atlantic ocean is widely studied due to its rich diversity of organisms despite the extreme conditions of high pressure, temperature and limited nutrients. Its ultramafic nature, the high concentration of H_2 and abiotic production of organics make this and other hydrothermal vents (e.g., Mid-Cayman Rise) the best seafloor hydrothermal vent analogs (Kelley et al., 2005; McDermott et al., 2015).

6. Future perspectives

Fe is ubiquitous in life and on multiple bodies in the solar system. Here, we have highlighted several examples of Fe-metabolizing microorganisms on Earth and the biosignatures that they may leave behind. Our review provides new perspectives on the search for Fe-based biosignatures on Mars and the icy moons.

First, the preservation of BIOS should be investigated in more detail under Martian subsurface or icy moon-like conditions. This area can build upon existing studies that investigated BIOS and/or Fe(III) (oxyhydr)oxide preservation under Earth-like diagenetic conditions (up to 250 °C/140 MPa) (Orange et al., 2014; Picard et al., 2015; Westall et al., 2015) or in Mars analog sites (Iron Mountain, CA; Yilgarn Craton, Western Australia; Gunnuhver, Iceland; Hveravellir, Iceland; the Río Tinto and Atacama Desert) (Azua-Bustos et al., 2022; Fernández-Remolar et al., 2021; Williams et al., 2021).

Second, new techniques are needed onboard rovers to better target strategic biosignatures. For example, microscopic techniques (ideally with resolution to the nanoscale) are needed to be able to identify BIOS-like morphology (e.g., sheaths, stalks). The inclusion of scanning electron microscopy, capable of resolving cell-like structures and to correlate morphology with mineralogy and organic content, will be particularly helpful. Furthermore, future work should also include isotopic analysis of organic matter associated with Fe minerals, as C and N could have distinct biological isotopic fractionation (Fifer and Wong, 2024). However, the implementation of these techniques still requires extensive research on miniaturization. This supports the need of sample return missions to incorporate techniques that are still too challenging to include on board space missions (Kminek et al., 2022; McCubbin et al., 2025; Muirhead et al., 2020; Tait et al., 2022).

Finally, detection of Fe-based biosignatures should also take into account capabilities of ongoing and upcoming mission to Mars and icy moons. The Perseverance rover on Mars – equipped with Raman and X-ray spectrometers - (Von Ehrenfried, 2022), have continued to identify Fe minerals (vivianite, iron oxides enriched in Cr and Ti, greigite) that support inferences for habitability (Hurowitz et al., 2025; Kizovski et al., 2025; Mansbach et al., 2024). Upcoming missions such as Rosalin Franklin rover, Europa Clipper and JUICE will provide intriguing clues on the habitability of Mars and Europa. The Rosalind Franklin rover has a Raman spectrometer (RLS, 532 nm) onboard that will continue the characterization of the mineralogy and the possibility of detecting organic compounds (Lopez-Reyes et al., 2014; Rull et al., 2017; Veneranda et al., 2020). For studying Europa, Europa Clipper carries the mapping imaging spectrometer for Europa (MISE) that includes an infrared spectrometer capable of detecting absorption features of iron-bearing minerals (oxides, hydroxides, sulfates) (Blaney et al., 2024). It also carries the surface dust analyzer (SUDA), a mass spectrometer that can capture iron containing particles (Kempf et al., 2025), and a magnetometer that could detect magnetic anomalies caused by iron minerals (Kivelson et al., 2023). Hence, the development of proxies (i.e., indirect measurements) that can be applied remotely is essential in the search of these biosignatures in remote places (e.g., icy moons) where in situ measurements are not possible.

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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Data availability

All data are available in the article

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Glossary

Assimilatory metabolism: Microbial process where inorganic compounds are used to generate biomass.
Banded iron formations (BIF): Sedimentary rocks composed of alternating layers of iron minerals and silica.
Dissimilatory metabolisms: Microbial process where inorganic compounds are used to generate energy.
Electron acceptor: Molecule, atom or ion that receives the electrons during cellular respiration.
Electron donor: Molecule, atom or ion that provides the electrons during cellular respiration.
Extracellular polymeric substances (EPS): Mixture of high-molecular-weight biopolymers (e.g., polysaccharides, proteins, nucleic acids), secreted by microorganisms for stability (mechanical or chemical) and protection.
Fe(II)-oxidizing microorganism (FeOM): Organisms that oxidize Fe(II) to Fe(III) to obtain energy for growth.
Fe(III)-reducing microorganism (FeRM): Organisms that respire Fe(III) as the final electron acceptor, reducing it to Fe(II).
Mesophile: Organisms whose optimal temperature for growth and reproduction is typically between 20 and 45 °C.
Niche: Environmental conditions that a species requires to grow and reproduce.
Nitrate-reducing Fe(II)-oxidizing microorganisms (NRFeOM): Fe(II)-oxidizing microorganisms that couple Fe(II) oxidation to nitrate reduction to gain energy.
Photoferrotroph: Organisms that oxidize Fe(II) using light energy to fix carbon dioxide.
Psychrophile: Organisms whose optimal temperature for growth and reproduction is typically between 20 and 45 °C.
Reactive oxygen species (ROS): Highly reactive molecules derived from molecular oxygen (O_2) including free radicals and non-radical oxygen-containing compounds (e.g., ·OH, O_2^{-}·, H_2O_2).