Unveiling the bioleaching versatility of *Acidithiobacillus ferrooxidans*

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Abstract

Acidithiobacillus ferrooxidans, a Gram-negative bacterium thriving in extreme acidic conditions, has emerged as a key player in biomining and bioleaching technologies thanks to its unique ability to mobilize, directly or indirectly, a wide spectrum of elements, such as Li, P, V, Cr, Fe, Ni, Cu, Zn, Ga, As, Mo, W, Pb, U, and its role in ferrous iron oxidation, *A. ferrooxidans* catalyzes the extraction of metals by generating iron (III) ions in oxic conditions, which are able to react with metal sulfides. This review explores the bacterium's versatility in metal mobilization, with a focus on the mechanisms involved and its encompassing role in the recovery of industrially-relevant metals from complex ores. The application of biomining technologies leveraging the bacterium's natural capabilities not only enhances metal recovery efficiency, but also reduces reliance on conventional, energy-intensive methods, aligning with the global trend towards more sustainable mining practices. However, its use in biometallurgical application poses environmental issues through its effect on the pH levels in bioleaching systems, which produce acid mine drainage that effluents in rivers and lakes adjacent to traditional and abandoned mines. This dual effect underscores its potential to shape the future of responsible mining practices, including potentially in space, and highlights the importance of monitoring acidic releases in the environment.

Keywords: *Acidithiobacillus ferrooxidans*, acidophiles, biomining, bioleaching, metals, trace elements, ISRU

1. Introduction

Extreme acidophilic microorganisms, which thrive in highly acidic conditions with pH below 2.5 (Merino et al., 2019), are of particular importance in the biometallurgy context because they facilitate the mobilization of a diverse array of elements, including transition metals. This is achieved as a result of a spectrum of reactions involving various elements from the periodic table, through a process known as bioleaching (Bosecker, 1997; Ilyas et al., 2007; Navarro et al., 2013; Zhao and Wang, 2019). Extremophiles are optimal microorganisms for developing mining applications on Earth (Niehaus et al., 1999; Watling, Shiers, & Collinson, 2015; Giovanella et al., 2020), as well as in space (Cockell et al., 2020; Santomartino et al., 2022; Tonietti et al., 2023).

The Acidithiobacillaceae family, part of the Gammaproteobacteria class, encompasses acidophilic bacteria adept at surviving in extremely acidic environments (Valdés et al., 2008). These chemolithoautotrophs derive energy through the oxidation of inorganic compounds and fix carbon dioxide as their carbon source, significantly contributing to the biogeochemical cycling of sulfur and iron (Wang et al., 2019). *Acidithiobacillus ferrooxidans* and other members of the Acidithiobacillaceae family are widely acknowledged for their ability to mobilize a variety of elements, including metals and metalloids, amidst extreme conditions (Valdés et al., 2008; Kaksonen and Petersen, 2023). Their metabolism harnesses inorganic energy sources, such as Fe^{2+}, H_2S, S^0, and molecular hydrogen, to sustain their metabolic activities (Ibáñez et al., 2023) (Figure 1A).

Among the Acidithiobacillaceae, *A. ferrooxidans* is notably well-studied. This Gram-negative, rod-shaped gammaproteobacterium is renowned for its ability to oxidize ferrous iron to ferric iron and reduced sulfur compounds to sulfate. *A. ferrooxidans* thrives in highly acidic environments, typically within a pH range of 1.5 to 2.5. Its genome encodes enzymes critical for iron and sulfur oxidation, as well as mechanisms for adapting to acidic conditions (Valdés et al., 2008). Ecologically, Acidithiobacillaceae are predominantly found in environments such as acid mine drainage, sulfuric hot springs, and sulfide mineral deposits (Baker and Banfield, 2003). They are key players in biomining, facilitating the extraction of metals from ores through bioleaching. In acid mine drainage, these bacteria oxidize sulfide minerals, resulting in the release of sulfuric acid and metal ions, which can lead to environmental contamination. *A. ferrooxidans* is frequently associated with mine tailings and acidic drainage waters, contributing significantly to the oxidation of pyrite and other sulfide minerals (Pedersen, 2001). In these environments, *A. ferrooxidans* coexist with other hyperacidophiles, including other *Acidithiobacillus* species and members of the archaeal genera such as *Ferroglobus* and *Thermoplasma* (Hafenbradl et al., 1996). These microorganisms form complex consortia that facilitate the biogeochemical cycling of sulfur and iron, playing a crucial role in the formation and maintenance of acidic conditions.

The metabolic activities of these microorganisms are pivotal in bioleaching and bioremediation processes. *A. ferrooxidans*, along with its consortia partners, leads to the generation of sulfuric acid. This acid production is essential in the leaching of heavy metals from mine tailings, contributing to the environmental impact observed in mining areas (Nguyen and Lee, 2015). The interactions between *A. ferrooxidans* and other hyperacidophiles in these consortia are complex and involve synergistic relationships that enhance the overall efficiency of mineral oxidation and acid production.

1.1 General Bioleaching process

A. ferrooxidans thrives in either aerobic or anaerobic conditions. Under aerobic conditions Fe^{2+} and/or reduced sulfur compounds in the ores undergo oxidation, resulting in the formation of Fe^{3+} and sulfuric acid (H_2SO_4) (BS Maluckov, 2017). In aerobic conditions (Figure 2A), the redox reactions of the *A. ferrooxidans*'s metabolism can be summarized as follows:

$$Fe^{2+} \rightarrow Fe^{3+} \; \mathit{(1)}$$

$$H_2 \rightarrow H^+ \; \mathit{(2)}$$

$$S^{2-} \rightarrow SO_4^{2-} \; \mathit{(3)}$$

$$CO_2 \rightarrow HCOOH \; \mathit{(4)}$$

$$O_2 \rightarrow H_2O \; \mathit{(5)}$$

The resultant oxidation products, Fe^{3+} and H_2SO_4 (Eq. 1, Eq. 2), engage in chemical interactions with metal sulfide minerals within ores, leading to the dissolution of metal cations and the elimination of sulfur (Quatrini et al., 2006; Zhan et al., 2019). The conversion of sulfur/sulfide to sulfuric acid (Eq. 3) culminates in the formation of an intensely acidified medium, due to the production of H_2SO_4 (Liu and Lan, 2004). This process facilitates the abiotic and biotic leaching of sulfides in mines, leading to the acidification of waters and the generation of acid mine drainage (Fortin et al., 1995). Moreover, oxidation and reduction processes can also be found in immobilization processes (Figure 1B).

In the absence of oxygen (Figure 2A), *A. ferrooxidans* undergoes anaerobic growth, performing the reductive dissolution of ferric iron (Fe^{3+}) oxy-hydroxide through the oxidation of elemental sulfur (S^0 to $S_2O_3^{2-}$). This reaction assumes pivotal significance in the "Ferredox" process, exemplified by the extraction of nickel from lateritic ores (Pronk et al., 1992; du Plessis et al., 2011). The major reactions involved in the anaerobic metabolism can be summarized as follows (Quatrini et al., 2006; Valdés et al., 2008):

$$Fe^{3+} \rightarrow Fe^{2+} \; \mathit{(6)}$$

$$S^0 \rightarrow S^{2-} \quad (7)$$

$$H_2 \rightarrow H^+ \quad (8)$$

$$S^0 \rightarrow S_2O_3^{2-} \quad (9)$$

$$CO_2 \rightarrow HCOOH \quad (10)$$

In natural environments, sulfide minerals undergo abiotic oxidation facilitated by the presence of O_2 or chemical oxidants together with water or moist air (Akcil and Koldas, 2006). Microorganisms instead utilize Fe^{2+} and sulfur for metabolic processes, leading to the formation of Fe^{3+} and sulfate ions. This metabolic activity results in a higher concentration of these ions subsequently intensifying the dissolution of sulfide minerals and augmenting the volume of acidic water (González-Paz et al., 2022). A quintessential illustration of this bioleaching phenomenon is the process involving chalcopyrite ($CuFeS_2$) microbial-mediated dissolution (Eq. 11) (Córdoba et al., 2008):

$$CuFeS_2 + 2Fe_2(SO_4)_3 \rightarrow CuSO_4 + 5FeSO_4 + 2S^0 \quad (11)$$

Which is driven by the abiotic reactions (Eq. 12-14):

$$CuFeS_2 + 2H_2O + 3O_2 \rightarrow Cu^{2+} + Fe^{2+} + 2H_2SO_4 \quad (12)$$

$$CuFeS_2 + H_2SO_4 \rightarrow Cu^{2+} + FeSO_4 + 2H^+ + 2S^0 \quad (13)$$

$$CuFeS_2 + 4H^+ + O_2 \rightarrow Cu^{2+} + Fe^{2+} + 2H_2O + 2S^0 \quad (14)$$

In the presence of *A. ferrooxidans*, the $FeSO_4$ produced by the abiotic reaction (Eq. 13) is oxidized at the expenses of oxygen in $Fe_2(SO_4)_3$ by the microbe metabolism (Eq. 15), releasing further acidity that supports the overall reaction.

$$2FeSO_4 + H_2SO_4 \rightarrow Fe_2(SO_4)_3 + 2H^+ \quad (15)$$

The resultant primary sulfur product in the process of metal sulfide dissolution is related to the specific sulfide mineral being subjected to bioleaching, subsequently undergoing chemical or biological transformations into elemental sulfur and sulfate (Vera et al., 2022). Disulfides, such as FeS_2, MoS_2, and WS_2, can undergo degradation through thiosulfate ($S_2O_3^{2-}$) as the principal intermediate of the reaction (Sand et al., 2001). Only Fe^{3+} ions, arising from the microbial oxidation of Fe^{2+}, serve as oxidative agents for solubilization. The degradation of $S_2O_3^{2-}$ leads to the formation of SO_4^{2-}, with elemental S^0 generated as a by-product. This elucidates why exclusively Fe^{2+} oxidizing bacteria possess the capability to oxidize these specific metal sulfides. Two main mechanisms contribute to the enhancement of metal leaching from mineral ores by microbial activity: direct and indirect action (Sand et al., 2001). Direct action can be summarized as follows (M is a bivalent metal):

$$MS + H_2SO_4 + 0.5O_2 \rightarrow MSO_4 + S^0 + H_2O \quad (16)$$

$$S^0 + 1.5O_2 + H_2O \rightarrow H_2SO_4 \quad (17)$$

While the indirect one uses Fe^{3+} as an oxidizing agent, microbes regenerate Fe^{3+} from Fe^{2+} as follows:

$$MS + 2Fe^{3+} \rightarrow M^{2+} + 2Fe^{2+} + S^0 \quad (18)$$

$$2Fe^{2+} + 0.5O_2 + 2H^+ \rightarrow 2Fe^{3+} + H_2O \quad (19)$$

The leaching of mineral sulfides in natural ecosystems is probably a combination of both direct and indirect mechanisms (Figure 2B) (Suzuki, 2001).

Bacteria, in bioleaching of sulfide ores, can be momentarily or permanently connected to the mineral substrate, forming a biofilm which often plays a key role in the extraction process (Figure 2B) (Van Gerven et al., 2004; Liu et al., 2021). Extra-polymeric substances (EPS) facilitate the adhesion of bacteria to metal sulfides, offering a survival advantage in adverse environments (Vu et al., 2009). Adsorption affinity of *A. ferrooxidans* can be strengthened by hydrophilic substrates. This indicates that the geobiological affinity of the organism derives from the properties of the different substrates (Tan and Chen, 2012). EPS renders apolar surfaces more polar, facilitating water infiltration through rocks and minerals. The EPS primarily comprises neutral sugars and lipids, releasing H^+ and Fe^{3+} ions (Vu et al., 2009). Layers of Fe^{3+} ions precipitate on the mineral surface creating an oxygen transport barrier and generating a region of elevated redox potential. EPS concentrates Fe^{3+} ions complexed with glucuronic acid at the mineral surface (Maluckov, 2017). Environmental alkali cations and sulfate ions, follow reaction occurs:

$$3Fe^{3+} + 2SO_4^{2-} + 6H_2O + M^+ \rightarrow MFe_3(SO_4)_2(OH)_6 + 6H^+ \quad (20)$$

where M= K^+, Na^+ or NH_4^+

The precipitation of Jarosite $MFe_3(SO_4)_2(OH)_6$ is responsible for the passivation of certain minerals. The formation of a secondary mineral layer on the mineral surface serves as a diffusion barrier for reactant and product fluxes (Nazari et al., 2014). The principal contribution of *A. ferrooxidans* to metal extraction arises from its ability to convert insoluble sulfides into corresponding soluble sulfur-metal compounds (Vera et al., 2022).

A. ferrooxidans has potential applications in bioremediation, e.g. addressing challenges associated with abiotic acid mine drainage (AMD) production at mining sites, remediating heavy metal-contaminated sites, and recovering electrical wastes (Jerez, 2017). Its efficacy in the removal of various metals from contaminated sources has been actively explored at the laboratory scale (Hocheng et al., 2012; Cai et al., 2021). A mercury-resistant strain of *A. ferrooxidans* facilitated the recovery of mercury compounds from sediments and polluted fluids (Takeuchi and Sugio, 2006). *A. ferrooxidans* has been employed in the bioremediation of Cr^{6+} and Cr^{3+} from electroplating waste (Cabrera et al., 2007). The bacterium also plays a crucial role in arsenic bioremediation, leveraging its resistance mechanisms conferred by genes on its chromosome to participate in arsenic precipitation (Camm et al., 2004). Regarding electronic waste (E-waste), the sulfuric acid produced by chemolithotrophic organisms, including *A. ferrooxidans*, serves as a leaching agent (Adetunji et al., 2023) increasing the acidity of the system and causing possible further releases of minerals into solution (Hubau and Bryan, 2023). Due to this ability, the metals can be recovered with a feedback mechanism in which the acidity is increased causing further acidification of the AMDs. This on one hand, increases the risk of environmental damage, but on the other allows the recovery of toxic metals in confined systems.

1.2 Chemical Elements mobilized by *A. ferrooxidans*

Biomining and bioleaching are arising as one of the best tools in the context of In Situ Resource Utilization (ISRU) for space exploration, particularly utilizing extremophiles, e.g. *A. ferrooxidans*, or heterotrophic/chemolithoautotrophic organisms, e.g. *Sphingomonas desiccabilis, Bacillus subtilis* or *Cupriavidus metallidurans*. Bioleaching has been proposed as a technique for extracting valuable resources from regolith on Solar System bodies (Santomartino et al., 2022). Regolith, a crucial *in situ* resource, contains elements such as oxygen, water, and trace metals that can help life-supporting devices and fuel production (Hadler et al., 2020). Bioleaching is a promising approach for extracting metals from regolith with a two-fold advantage for the space missions: 1) minimizing their cost limiting the need of Earth-based resources; 2) mitigating their logistical complexities (Cockell et al., 2020; Santomartino et al., 2022). Bioleaching in ISRU operations can contribute to optimizing the selection of landing sites in the frame of human planetary exploration and infrastructure development in space (Gumulya et al., 2022). Biomining and bioleaching processes coupled with biosensors for space applications and new space technologies will be future methods to perform mineral extraction procedures on planets, comets, asteroids, moons (Cinti et al., 2023).

A. ferrooxidans is capable of mobilizing or affecting the mobilization of many different elements in the periodic table (Table 1) utilizing biochemical strategies depending on the specific element and the mineral/ore involved. The aim of this review is to report a comprehensive and updated list of elements which are mobilized by *A. ferrooxidans*, including its biochemical leaching mechanisms, and highlighting applications and limitations (Table 2).

2. Lithium

The alkali metals (Group 1 of the periodic table) constitute a highly reactive group of elements: lithium (Li), sodium, potassium, rubidium, cesium, and francium. These metals share common characteristics: low melting points, high reactivity with water, tendency to form ionic compounds, ability to readily donate electrons, leading to the formation of alkali metal cations with a +1 charge (Dye, 2015). Regarding bioleaching processes performed by the acidophile *A. ferrooxidans*, only Li can be actively leached.

Being the lightest alkali metal, and due to its distinctive electrochemical reactivity, Li finds extensive applications in metallurgy, aerospace, ceramics, battery technology, and fuel cells (Garcia et al., 2023). The utilization of Li-ion batteries for powering portable devices and electric vehicles, has led to an escalating demand for Li (Wang et al., 2023). Naturally occurring sources of Li include lake brines, pegmatites ore bodies, and sedimentary rocks, with over 80% of the current global production being derived from brines (Ding et al., 2023). Developing technologies capable of extracting Li from solid ores holds significant importance in addressing future Li demand (Vikström et al., 2013).

In comparison to brine extraction, the process of obtaining Li from rocky sources is notably more intricate. This procedure encompasses a series of distinct operations, including roasting rocks in sulfate or carbonate environments to render Li into water-soluble species (Marcinov et al., 2023).

One of the primary industrial minerals for Li extraction, is spodumene ($LiAlSi_2O_6$) a Li-bearing pyroxene found in pegmatites, i.e., coarse-grained igneous rocks rich in Li, with a relatively low occurrence of other metals. Lepidolite ($3Li_2O*2K_2O*5Al_2O_3*10SiO_2*2SiF_4$), a form of pegmatite, member of the mica group, represents the most abundant Li ore, with a distribution far surpassing that of Li-brines (Szlugaj and Radwanek-Bąk, 2022). The Li_2O content in lepidolite ranges from 3.0 % to 7.7 % by weight (1.39–3.58 % Li), comparatively lower than that of spodumene, 6–8 % by weight as shown by Sedlakova-Kadukova et al., 2020. Lepidolite exploitation in industrial processes is constrained by the elevated costs associated with Li recovery from the mineral, necessitating high concentrations of acid in purification procedures (Guo et al., 2019).

The adoption of alternative technology has gained importance due to its potential for cost reduction, heightened efficiency and environmentally sustainable processing (Moazzam et al., 2021). A bio-extraction approach utilizing a consortium of different bacterial strains—namely, *A. ferrooxidans, A. thiooxidans*, as well as the heterotrophic fungus *Aspergillus niger* and yeast *Rhodotorula* *mucilaginosa*—has been investigated (Sedlakova-Kadukova et al., 2020). These microorganisms play integral roles in processes such as bio-weathering of rocks, mobilization of metals from minerals, metal precipitation, and deposition (Biswal and Balasubramanian, 2023). For this reason, they have been extensively employed in biohydrometallurgical practices.

The mechanisms underlying lepidolite bioleaching by bacteria remain undisclosed. Nevertheless, it has been observed that, apart from H^+ ions, no other substance contributes to the dissolution of Li^+ ions. This implies that the dissolution of Li in lepidolite is facilitated by acidic conditions (Xin et al., 2009; Sedlakova-Kadukova et al., 2020). Presumably, the primary reaction involved in the bioleaching of mixed alkali metals can be expressed as follows:

$$M_2O + H_2SO_4 \rightarrow M_2SO_4 + H_2O \quad \textit{(21)}$$

where M presents alkali metals. Metals inside the mineral can be dissolved to form the sulfate counterpart, resulting in lepidolite dissolution (Sedlakova-Kadukova et al., 2020). The reaction of lepidolite bioleaching in sulfuric acid produced by bacteria is the following:

$$3Li_2O*2K_2O*5Al_2O_3*10SiO_2*2SiF_4 + 20H_2SO_4 \rightarrow 3Li_2SO_4 + 2K_2SO_4 + 5Al_2(SO_4)_3 + 11SiO_2 + H_2SiF_6 + 18H_2O + 2HF \quad (22)$$

$$3Li_2O*2K_2O*5Al_2O_3*10SiO_2*4H_2O + 20H_2SO_4 \rightarrow 3Li_2SO_4 + 2K_2SO_4 + 5Al_2(SO_4)_3 + 12SiO_2 + 24\ H_2O \quad (23)$$

In bacterial involvement, the composition of the medium emerged as the predominant factor influencing Li bioleaching. Mishra et al. (2008) report that, within a nutrient-rich medium tailored for acidophilic chemoautotrophic acidithiobacilli, featuring essential energy sources in the form of ferrous ions and elemental sulfur, no Li bioleaching was observed throughout the entire duration of the process. Conversely, in a medium with restricted nutrient content and limited energy sources, comprising solely sulfuric acid and elemental sulfur, the presence of Li^+ ions was discernible within a matter of days. This suggests that bacteria, essential for Li bioleaching from lepidolite, as no Li was detected in abiotic control samples, may have been compelled to directly utilize nutrients vital for their sustenance from the leached material. Li extraction, achieved through bacterial intervention, necessitates at least 22 days to occur (Sedlakova-Kadukova et al., 2020).

3. Phosphorus

Non-metals encompass a variety of elements critical for chemical reactions and biological processes (Yao et al., 2020). Non-metals, characterized by their lack of metallic luster, malleability and conductivity, such as oxygen, nitrogen, and carbon, are included in compounds essential for life, i.e., water, proteins, and DNA (Jomova et al., 2022). They contribute significantly to the Earth's atmosphere, with oxygen being a crucial component for sustaining aerobic life (Yao et al., 2020). Phosphorus (P) is the only non-metal of industrial interest bioleached by *A. ferrooxidans*, which can actually metabolize other non-metal elements such as carbon, nitrogen, and sulfur.

P, a crucial plant nutrient, has attained increasing importance as a natural resource, given its finite supply (El Wali et al., 2021). The leaching of P into superficial waters poses a significant environmental challenge. Sewage sludge represents a substantial reservoir of P and, considering its substantial quantities generated globally daily, projections indicate a surge production attributable to population growth (Daneshgar et al., 2018). The disposal of such large volumes of sewage sludge raises substantial environmental apprehensions. The application on agricultural land emerges as an attractive option, offering nutrient recycling and augmentation of soil organic content (Mabrouk et al., 2023). However, this approach confronts several constraints, as sludge: (1) harbors numerous pathogens, (2) may contain elevated levels of heavy metals, and (3) its bulkiness and associated transport costs pose logistical challenges (Tytła, 2019).

P recovery from sewage sludge in the form of phosphoric acid is facilitated by the use of sulfuric acid. Nevertheless, the process entails the costly steps of sludge drying and the utilization of significant quantities of commercial acid (Jama-Rodzeńska et al., 2021). The active P extraction from P-sludge, deriving from the metabolic activities of acidophiles, is well-connected with environmental remediation challenges, linking bioleaching and bioremediation. The bioleaching of rock phosphate employing acid-generating microorganisms has been extensively investigated (Priha et al., 2014; Calle-Castañeda et al., 2018). The biochemical approach offers distinct advantages, notably its cost-effectiveness, heightened efficacy, and eco-friendly attributes (Chi et al., 2006). The development of a biochemical process for P recovery from sludge is a highly advantageous endeavor.

A. ferrooxidans and *A. thiooxidans* present viable candidates for the recovery and bioleaching of P-rich sludge (Cortés et al., 2020). These microorganisms possess the capability to generate sulfuric acid through the oxidation of reduced sulfur compounds, allowing for the establishment of an acidic pH level, potentially below 1. This produced sulfuric acid serves to solubilize the P content. *A. thiooxidans* demonstrate the capacity to recover 94% of P from rock phosphate, while *A. ferrooxidans* can be employed to solubilize P from desiccated sewage sludge (Pradhan et al., 2021). The chemical reactions governing the leaching of P from the sludge are delineated as follows:

$$2S^0 + 3O_2 + 2H_2O \rightarrow 2H_2SO_4 \quad (24)$$

$$3H_2SO_4 + Ca_3(PO_4)_2 \rightarrow 2H_3PO_4 + 3CaSO_4 \quad (25)$$

$$3H_2SO_4 + 2FePO_4 \rightarrow 2H_3PO_4 + Fe_2(SO_4)_3 \quad (26)$$

The process takes circa 63 days to recover 92 % of the P from the sludge. The extracted phosphoric acid can be used for different purposes, including the production of ammonium phosphate (Pradhan et al., 2021).

4. Transition metals

Transition metals exhibit distinctive electronic configurations, with partially filled d-orbitals contributing to their characteristic properties. Their ability to form stable coordination complexes makes them essential in fields such as catalysis, where they play a crucial role in accelerating chemical reactions (Durrant, 2019). Transition metals are known to be fundamental to many organisms, in microbes they drive the global biogeochemical cycling of the elements (Giovannelli, 2023; Hay Mele et al., 2023). Today 25% of the total transition metals can be mobilized by *A. ferrooxidans*.

4.1 Vanadium

Vanadium (V) represents a prototypical redox-sensitive transition metal widely employed in industries, including metallurgy, manufacturing, and petroleum refining (White and Levy, 2021). Its incorporation into steel enhances critical attributes such as hardness, tensile strength, and fatigue resistance, thereby elevating overall performance. V serves as a catalytic agent in denitrification processes, acting as a metallic cofactor within enzymes responsible for catalyzing such reactions (Yang et al., 2021). V redox batteries present a further potential application in addressing the escalating global energy demand (Zhang et al., 2018).

A significant proportion of the world's V production stems from slags generated during steelmaking operations employing V-titanium magnetite (Odebiyi et al., 2023). Conventional methods for V extraction are marked by high costs and inefficiencies, accompanied by pronounced environmental challenges, encompassing alkali melting, chloridizing roasting, acid leaching, water leaching, and deposition (He et al., 2007). Bioleaching has been successfully employed for the solubilization of V from solid waste sources, including spent refinery catalysts and oil-fired ash (Rastegar et al., 2015). Its integration with established processes holds considerable promise. Successful bioleaching of V through heterotrophic organisms has been demonstrated in microgravity conditions aboard the International Space Station (ISS) (Cockell et al., 2021).

Minerals conducive to V extraction encompass V-titanium magnetite ($(V, Ti),Fe^{2+}Fe^{3+}{}_2O_4$), maghemite (a specific variant of magnetite characterized by a low Fe^{2+} concentration), bixbyte (containing V along with $(Mn, Fe)_2O_3$)), V oxide, and jacobsite, typically $(Mn, Mg)Fe_2O_4$ (Peng et al., 2023). A prominent participant in the interaction with these mineral types for V extraction is *A. ferrooxidans*, catalyzing the conversion of Fe^{2+} to Fe^{3+} under acidic conditions, as depicted below (Bredberg et al., 2004):

$$4Fe^{2+} + 4H^+ + O_2 \rightarrow 4Fe^{3+} + 2H_2O \quad (27)$$

$$V_2O_3 + 2Fe^{3+} + 2H^+ \rightarrow 2VO^{2+} + 2Fe^{2+} + H_2O \quad (28)$$

$$VO_2 + Fe^{3+} \rightarrow VO_2^+ + Fe^{2+} \quad (29)$$

$$10VO_2 + 10Fe^{3+} + 5H_2O \rightarrow HV_{10}O_{25}^{2-} + 10Fe^{2+} + 9H^+ \quad (30)$$

Presumably, V^{5+} represents the predominant speciation in the leachate. V manifests three principal valence states in natural aqueous solutions, with V^{5+} prevailing as the most prevalent form in oxidizing environments (Shearer et al., 2006). V^{5+} can be readily retrieved from the leachate through NH_4Cl precipitation (Peng, 2019). In summary, *A. ferrooxidans* prove highly effective in the recovery of V from both raw minerals and intermediate materials utilized in V extraction processes. The average recovery efficiency is estimated to be approximately 30 % (Li et al., 2021b).

4.2 Chromium

Chromium (Cr) slags represent a category of hazardous waste characterized by the prevailing toxicity of Cr^{6+}. This hexavalent Cr species possesses a robust oxidizing potential toward living cells and has been associated with gene mutations and carcinogenic effects in animal studies (Sharma et al., 2022). In specific Cr slag compositions, such as $Ca_3Al_2(H_4O_4, CrO_4)_3$ and $Ca_4Al_2(OH)_{12}(CrO_4)_3{*}26H_2O$, approximately 20-25 % of the total mass is constituted by hexavalent Cr (Liu et al., 2013). Cr salts are extensively employed in the leather industry for tanning processes, a treatment that safeguards leather against various environmental stressors, including microbial degradation, and moisture (Zeiner et al., 2011). An estimated 90 % of tanneries employ Cr salts as a principal tanning agent. Cr exhibits limited biodegradability and tends to accumulate within biological organisms, resulting in severe health ailments. Disposal methods for tannery sludge encompass incineration, solidification, landfills and ocean dumping, with the last two facing mounting scrutiny in numerous countries due to environmental considerations (Garg et al., 2012).

The recovery of Cr from sludge can be facilitated through the action of sulfur and iron-oxidizing bacteria. This microbiological approach enables the ready solubilization of metals via the oxidation of metal sulfides into soluble sulfates, or through acid dissolution employing sulfuric acid (Anekwe and Isa, 2023). Subsequently, released Cr can be efficiently removed. Cr is naturally occurring in minerals such as the Cr-bearing phase of goethite $Fe^{3+}O(OH)$, or in limonite deposits (Santos et al., 2022). The liberation of Cr from sludge or rocks is contingent upon redox processes. The activity of *A. ferrooxidans* mediates the oxidation of iron from Fe^{2+} to Fe^{3+}, thereby facilitating the reduction of Cr^{6+} to the less toxic and water-insoluble Cr^{3+} species increasing bioremediation processes (Meruane and Vargas, 2003). In this process, Fe^{2+}, reduced sulfur and organic matter constitute the principal sources of electrons.

$$Cr^{6+} + 3Fe^{2+} \rightarrow Cr^{3+} + 3Fe^{3+} \quad (31)$$

The reduction of Cr under experimental conditions (Bolaños-Benítez et al., 2018) is a process that iron-oxidizing bacteria, such as *A. ferrooxidans*, *A. thiooxidans* and *P. putida*, can mediate.

4.3 Iron

Iron (Fe) is a fundamental element in various industrial processes, serving as a critical component in the production of steel, alloys, and numerous other materials essential for modern infrastructure. The demand for iron in industry underscores the significance of efficient extraction methods. Fe is also fundamental in household applications e.g. refrigerators, stoves, washing machines, packaging, etc. (Teixeira et al., 2012).

A. ferrooxidans exhibit the ability to oxidize ferrous iron to ferric iron, a process crucial for the solubilization of Fe minerals in ore deposits. This metabolic proficiency includes Fe oxidases, cytochromes, and electron transport chains within the bacterial cell. The unique redox chemistry of A. ferrooxidans enables it to thrive in highly acidic environments, where conventional mining operations are impractical (Zhan et al., 2019). The oxidation of ferrous Fe by A. ferrooxidans can be represented by the following chemical equation:

$$4Fe^{2+} + O_2 + 4H^+ \rightarrow 4Fe^{3+} + 2H_2O \quad (32)$$

The use of *A. ferrooxidans* in Fe biomining from pyrite and Fe sulfides, such as bornite (Cu_5FeS_5), offers several significant environmental advantages. Unlike traditional mining practices, which often result in extensive environmental degradation and habitat destruction, biomining is a less-impacting process (Zhang et al., 2008). By harnessing the metabolic capabilities of *A. ferrooxidans*, the extraction of Fe from ore deposits can be achieved with minimal disturbance to surrounding ecosystems in a controlled environment. The reduction in chemical reagents and energy consumption associated with biomining contributes to a lower carbon emissions compared to conventional mining techniques (Jerez, 2017).

The application of *A. ferrooxidans* in Fe biomining holds immense potential for the mining industry. With advancements in biotechnology and microbial engineering, there is a growing opportunity to optimize the efficiency and scalability of this process (Watling, 2016). Ongoing research efforts are focused on expanding the repertoire of biomining microorganisms, potentially unlocking new niches for the extraction of valuable metals from diverse mineral resources (Kaksonen and Petersen, 2023).

The unique metabolic capabilities of *A. ferrooxidans* in Fe biomining hold promise for extraterrestrial applications. In space exploration the availability of essential resources such as Fe is of paramount importance for construction, habitat development and various technological endeavors. Leveraging *A. ferrooxidans* in biomining processes could facilitate the sustainable extraction of Fe from planetary bodies, reducing reliance on resource-intensive transportation from Earth (Tonietti et al., 2023).

4.4 Nickel

Nickel (Ni) plays a prominent role in the manufacturing of electronic devices, which are subject to heightened demand driven by planned obsolescence and rapid market penetration. This results in a substantial accumulation of electronic waste (E-waste) that constitutes a vital reservoir of metals relevant for industry and rare elements (Manikandan et al., 2023). Printed circuit boards (PCBs) account for approximately 3% of the total E-waste mass (Qiu et al., 2020). PCBs encompass notable quantities of Cu (10-20 %), Ni (1-3 %), Fe (1-4 %), Pb (1-5 %), as well as precious metals (0.3-0.4 %) including Au, Ag, and Pt, rendering them a valuable secondary metal resource (Priya and Hait, 2018). Metal recovery from E-waste stands as a more sustainable and resource-efficient endeavor in terms of energy utilization, environmental protection, and overall sustainable resource management (Qiu et al., 2020). While hydrometallurgical and pyrometallurgical processes present notable drawbacks, e.g. concentrated acidic effluents, high energy consumption and big volumes of hazardous waste, (Rossini and Bernardes, 2006; Cui and Zhang, 2008), bioleaching contributes to the conservation of non-renewable energy (Rendón-Castrillón et al., 2023).

Ni and its compounds exert detrimental effects on the human heart and liver (Genchi et al., 2020). Coupling Ni hazard with its high demand in the electronics industry, bioleaching emerges as a promising method for its recovery from waste sources. In oxygen-rich environments and under acidic conditions, *A. ferrooxidans* demonstrates the capacity to mobilize this metal, as illustrated by the following reaction (Arshadi and Yaghmaei, 2020):

$$4Fe^{2+} + O_2 + 4H^+ \rightarrow 4Fe^{3+} + 2H_2O \ (32)$$

$$Fe^{3+} + H_2O \rightarrow Fe(OH)^{2+} + H^+ \ (34)$$

$$Fe^{3+} + 2H_2O \rightarrow Fe(OH)_2^{+} + 2H^+ \ (35)$$

$$Fe^{3+} + 3H_2O \rightarrow Fe(OH)_3 + 3H^+ \ (36)$$

$$Fe^{3+}\ 3EPS(\text{extracellular polymeric substance})\text{-}H \rightarrow Fe(EPS)_3 + 3H^+ \ (37)$$

ferric ions produced by *A. ferrooxidans* can also be bonded to sulfate ions:

$$Fe_2(SO_4)_3 + M^0 \rightarrow M^{2+} + SO_4^{2-} + 2FeSO_4M \ (38)$$

in this manner, Ni^0 present in E-waste undergoes oxidation through ferric ions, which are subsequently reduced to ferrous ions:

$$Ni^0 + Fe^{3+} \rightarrow Ni^{2+} + Fe^{2+} \ (39)$$

The ferrous ions are oxidized back to ferric ions through *A. ferrooxidans* activity: a recurrent iron cycle is instituted within the Ni bioleaching process, whose efficiency depends on pH adjustment (88.9 % with pH adjustment vs. 92.1 % without it) (Arshadi and Mousavi, 2015). Arshadi and Yaghmaei (2020) demonstrated the generation of jarosite and goethite, two frequently occurring minerals produced in bioleaching processes:

$$3Fe^{3+} + 2HSO_4^- + 6H_2O + M^+ \rightarrow MFe_3(SO_4)_2(OH)_6 + 8H^+ \ (40)$$

where M= K^+, Na^+, NH_4^+ or H_3O^+.

4.5 Copper

Copper (Cu), a vital element in various industries, including electronics, construction, and transportation, necessitates efficient extraction methods to meet global demands. It is a fundamental material for electrical wiring, power transmission, and electronic components due to its superior conductivity, making it essential for powering homes, industries, and electronic devices (Li et al., 2021a). Cu is also widely employed in plumbing, roofing, and architectural elements. Its corrosion resistance and durability make it a preferred choice for water pipes, roofing materials, and decorative features in buildings. Cu is used in transportation and automotive industry and intensely in industrial machinery and equipment (Seck et al., 2020).

A. ferrooxidans can use its enzymatic machinery within the bacterial cell, including iron and sulfur oxidases, facilitating the conversion of insoluble Cu sulfides into soluble Cu ions. The presence of Fe^{2+} acts as an electron donor in this redox process, enabling the sustenance of *A. ferrooxidans* in highly acidic environments (Rawlings, 2005).

The bioleaching of Cu minerals, e.g. chalcopyrite, can be represented by the following chemical equations (see also Figure 1):

$$4Fe^{2+} + O_2 + 4H^+ \rightarrow 4Fe^{3+} + 2H_2O \ (41)$$

$$CuFeS_2 + 6Fe^{3+} \rightarrow Cu^{2+} + 7Fe^{2+} + 2S^0 \ (42)$$

By harnessing the metabolic capabilities of *A. ferrooxidans*, the extraction of Cu can be achieved with reduced ecological impact. The decreased dependence on harsh chemical reagents and energy-consuming methods results in a smaller environmental footprint relative to traditional mining techniques (Lennox and Blaha, 1991).

Biohydrometallurgy processes, including bioleaching, account for approximately 20-25% of the world's Cu production (Schippers et al., 2014). These processes involve the microbial oxidation of sulfide minerals, converting insoluble metal sulfides into soluble metal sulfates according to Eq. 11. This approach is particularly efficient for low-grade ores, which are economically unfeasible to process using traditional methods. Traditional methods, such as smelting, require high energy input and produce significant environmental pollution. In contrast, bioleaching operates at ambient temperatures and pressures, utilizing natural microbial processes to extract metals with minimal environmental disruption (Villares et al., 2016).

The efficiency of bioleaching in low-grade ore deposits makes it an invaluable tool for mining operations. These deposits, often overlooked due to their low metal content, become viable sources of Cu through bioleaching. *A. ferrooxidans* can thrive in these environments, continuously oxidizing iron and sulfur compounds to release Cu ions. This not only maximizes the utilization of available resources but also minimizes waste and environmental impact, aligning with sustainable mining practices (Yi et al., 2021). Consequently, bioleaching with *A. ferrooxidans* represents a cost-effective, environmentally friendly alternative to conventional methods, contributing significantly to the global supply of Cu.

4.6 Zinc

Zinc (Zn), critical in the galvanizing, cosmetic, die-casting, and manufacturing sectors, Zn global production >$8x10^6$ tons, is primarily extracted utilizing sulfide ores through hydro-metallurgical processes (roasting, leaching, and electro-winning) with the leaching kinetics playing a key role in comprehending the Zn smelting procedure (Hussain et al., 2022). Zn sulfide ores, especially sphalerite (ZnFe)S, are suitable and useful sources for Zn extraction as they are easily separated and concentrated by flotation from waste rocks (Picazo-Rodríguez et al., 2020). Due to the increasing demand for Zn and Zn-compounds, new Zn sources, e.g. low-grade oxide ores, have been considered.

The leaching of Zn ores containing oxidized minerals, e.g. carbonates or silicates with sulfuric acid have been investigated (Xu et al., 2010). The Zn general chemical mobilization from ores can be summarized as follows:.

$$ZnS + 0.5O_2 + H_2SO_4 \rightarrow ZnSO_4 + H_2O + S^0 \ (43)$$

$$4Fe^{2+} + O_2 + 4H^+ \rightarrow 4Fe^{3+} + 2H_2O \ (44)$$

$$S^0 + 1.5O_2 + H_2O \rightarrow H_2SO_4 \ (45)$$

Fowler and Crundwell (1998) disentangled experimentally two *A. ferrooxidan* Zn extraction mechanisms: direct and indirect, demonstrating that the indirect mechanism plays a central role in the leaching of Zn sulfide.

4.7 Molybdenum

Molybdenum (Mo) is an important element in sectors such as metallurgy, aerospace, and electronics (Oehlerking et al., 2022). Mo is known for its exceptional heat resistance and high melting point, making it a crucial component in alloys that withstand extreme temperatures. Its ability to facilitate electron transfer makes it indispensable in electronics and electrical applications. Mo finds extensive use in the production of steel and other alloys, contributing to enhanced strength and corrosion resistance (Huang et al., 2022). Given its increasing demand, efforts have been made for the recovery of Mo from waste sources contributing to sustainable resource management (Xu et al., 2023). Bioleaching presents a promising avenue for Mo recovery: *A. ferrooxidans* has shown potential in solubilizing Mo from various sources, offering advantages in terms of safety, environmental sustainability, and energy efficiency (Pistaccio et al., 1994).

Mo is oxidized from its reduced state, Mo^{6+}, to its soluble form, Mo^{4+}, through the activity of *A. ferrooxidans*. The ferrous ions released from this reaction are further oxidized to ferric ions, establishing a recurring iron cycle within the process. The soluble Mo can then be readily extracted, contributing to the efficient recovery of Mo from waste materials (Pistaccio et al., 1994).

$$4MoS_2 + 4Fe^{3+} + 16H_2O \rightarrow 4MoO_4^{2-} + 4Fe^{2+} + 32H^+ + 4S^0 \, (46)$$

This reaction leads to the dissolution of Mo sulfide minerals, releasing Mo ions (MoO_4^{2-}) into the solution (Aracena et al., 2018). *A. ferrooxidans* contribute to the precipitation and immobilization of Mo through biomineralization processes (Pistaccio et al., 1994). Under appropriate conditions, Mo ions in solution can react with other elements to form various Mo-containing minerals. For example, the reaction between Mo ions and calcium ions (Ca^{2+}) can lead to the formation of calcium molybdate $CaMoO_4$ (Wan et al., 2017).

4.8 Tungsten

Among others metal ions (iron, copper, nickel, zinc, molybdenum) tungsten (W) serves as an essential component of various metalloenzymes, playing pivotal roles in biological processes (Hay Mele et al., 2023). Some bacteria have evolved the capability to synthesize metal-binding proteins, facilitating the storage of these crucial metal ions within the cell (Permyakov, 2021). W exhibits multiple oxidation states (e.g., W^{6+}, W^{4+}, W^{2+}, W^0) with limited knowledge regarding its speciation in natural environments. Wolframite - $(Fe,Mn)WO_4$, an iron, manganese and tungstate mineral, alongside scheelite ($CaWO_4$), represents a primary source of tungsten ore (Boury et al., 2023). Wolframite undergoes instability in acidic and oxidizable conditions, leading to the formation of H_2WO_4 as the prevalent secondary tungsten mineral (Han et al., 2023). In acidic and reducing environments, the dominant tungsten species are W^{4+} and metallic W^0. The leaching process of wolframite is a two-step reaction, occurring after the oxidation of sulfides and necessitating interaction with the product of the first-step reaction, H_2SO_4 (Hällström et al., 2020).

$$H_2SO_4 + FeWO_4 \rightarrow FeSO_4 + H_2WO_4 \, (47)$$

$$H_2SO_4 + MnWO_4 \rightarrow MnSO_4 + H_2WO_4 \, (48)$$

The activity of acidophiles can result in the release of natural organic compounds, which have the potential to significantly enhance the mobility of tungsten in the environment (Nguyen et al., 2021). These organic compounds can co-precipitate with ferrihydrite, $Fe(OH)_3$ across a wide pH range (from 4 to 11), potentially interfering with the interaction between soluble tungstate oxyanions (WO_4^{2-}) and ferrihydrite (Zelin et al., 2020). The activity of acidophiles plays a pivotal role in the decomposition of wolframite and the mobilization of W in mining waste environments (Han et al., 2022). During the initial stages of wolframite weathering under acidic conditions, free tungstate ions may bind with various cations, giving rise to a diverse array of secondary tungsten minerals, e.g. gallium-rich tungstate and sanmartinite $(Zn,Fe)WO_4$ (Martins, 2014). This phenomenon could potentially restrict the availability of W in the environment.

The activity of *A. ferrooxidans* and acidophilic organisms holds significant potential for bioleaching W minerals, primarily wolframite. The efficiency of this process is highly contingent on the microbial composition of the environment and the specific speciation of W, which is thermodynamically influenced by the in situ redox state and other environmental variables (Han et al., 2023).

4.9 Gold

Gold (Au) has played a key role in the development of human civilization, as the basis for decorative, ceremonial, and religious artifacts. Due to the physical and chemical properties of gold, such as its ability to non chemisorb oxygen, or the fact that it does not corrode, makes it an excellent catalyst. It is widely used in industrial applications by both homogeneous and heterogeneous Au catalysis (Ciriminna et al., 2016). The recovery of Au from rock mostly relies on the following cyanidation process:

$$4Au^0 + 8NaCN + 2H_2O + O_2 \rightarrow 4NaAu(CN)_2 + 4NaOH \quad (49)$$

The use of cyanide for the dissolution of Au poses harsh environmental risks while bioleaching for Au recovery reveals promising venues for more sustainable practices. Cyanide producing bacteria autonomously convert cyanide to the less toxic form B-cyanoalanine (Alvillo-Rivera et al., 2021). *A. ferrooxidans* in the bioleaching of Au is part of the indirect method towards the elimination of interfering metal sulfides from ores containing precious metals. In Au ores minute Au particles are encapsulated or tightly bound within a sulfide mineral, typically pyrite, arsenopyrite, or a combination of both (El-Midany, 2012). To achieve satisfactory Au recovery, it is important to first oxidize the sulfide minerals prior to subjecting the ore to cyanide treatment for Au dissolution (Medina and Anderson, 2020; Wang et al., 2021a). Coupling both cyanide producing bacteria and *A. ferrooxidans* allowed the recovery of Au from discarded printed circuit boards.

4.10 Mercury

Mercury (Hg), widely used, has been produced globally, with European contribution led by the Spanish mining industry. The Americas and Asia, particularly Kyrgyzstan, Russia, and China, also play significant roles in Hg extraction (Hylander and Meili, 2003). The 20th century saw a spike in global production, driven by industrial use, especially in the chlor-alkali industry, where Hg cells are used for electrolysis (Sznopek and Goonan, 2000; Hylander and Meili, 2005). Beyond industry, Hg has been widely used in dentistry for over a century, with dental amalgam making up a significant portion of its usage in the USA and Sweden (Regeringskansliet, 2003). Despite alternatives and known environmental impacts, international efforts against Hg in dental amalgam, are lacking (Hylander and Meili, 2005).

Cinnabar (HgS) has a long history of use as a natural pigment and in medicine and preservation for thousands of years (Feng, 2005). The dissolution of cinnabar was found to be closely related to iron concentration, particularly influenced by ferric iron generated by *A. ferrooxidans* (Schippers and Sand, 1999). Although natural oxidation of cinnabar is limited (Zhou et al., 2010), ferric iron catalyzes the reaction:

$$HgS + 2Fe^{3+} \rightarrow Hg^{2+} + 2Fe^{2+} + S^0 \, (50)$$

During prolonged reactor operation with immobilized cells it has been observed that a significant number of cells emerge into the liquid medium: this process has been explained by the adhesion of *A. ferrooxidans* on sulfur particles, becoming hydrophilic (Wang et al., 2013). Thermodynamically, the free energy of adhesion is determined by interfacial tensions between bacteria, liquid, and sulfur phases (Devasia and Natarajan, 2010). A hydrophobic secretion by *A. ferrooxidans* reduced, enhancing contact and adhesion (Kinzler et al., 2003). The adhered sulfur particles were further oxidized by *A. ferrooxidans*:

$$2S^0 + 3O_2 + 2H_2O \rightarrow 2H_2SO_4 \, (51)$$

This reaction inhibited ferric iron hydrolyzation (Yujian et al., 2007), maintaining oxidant (ferric iron) concentration (Breed and Hansford, 1999). Substituting this into the cinnabar oxidation equation resulted in:

$$2HgS + 4Fe^{3+} +3O_2 +2H_2O \rightarrow 2Hg^{2+} +4Fe^{2+} + 2H_2SO_4 \, (52)$$

A. ferrooxidans rapidly oxidize ferrous iron. The oxidation process led to a reduction in H^+ concentration, thereby aiding in the dissolution of cinnabar. The detected change in surface area pre- and post- bioleaching suggested a smoother particle surface prior to the reaction, which subsequently became more fragmented. This transformation was attributed to the indirect catalytic effect of ferric iron produced by *A. ferrooxidans* and the direct oxidation function that supplied energy for the growth of the bacteria (Wang et al., 2013). This whole process can be applied in bioremediation to treat environments contaminated with mercury. By utilizing *A. ferrooxidans*, the toxic cinnabar can be broken down, reducing its environmental impact.

5. Post-transition metals

Beyond the classical distinction between metals and nonmetals, a diverse group known as post-transition metals comprise elements found between the transition and metalloid regions. Post-transition metals include aluminum and gallium, showcase a diversity of properties, encompassing malleability, conductivity, and varied oxidation states (Wang et al., 2021b). Their presence in alloys, combined with their unique reactivity patterns, makes them essential in the manufacturing of diverse materials, from lightweight alloys to corrosion-resistant coatings (Tang et al., 2022).

5.1 Gallium

The demand for Gallium (Ga) is projected to undergo rapid escalation from 2014 to 2050 (Lu et al., 2017; Ueberschaar et al., 2017) due to development of light-emitting diodes (LEDs) (DenBaars et al., 2013). Bioleaching presents distinct advantages for Ga recovery, characterized by its enhanced safety, environmental friendliness and energy-efficient processes, enabling the leaching of metals even at relatively low concentrations. An adapted strain of *A. ferrooxidans* demonstrated the capacity to leach approximately 60% of the Ga content from powdered LEDs (Pourhossein and Mousavi, 2018). The efficacy of *A. ferrooxidans* for augmenting Ga bioleaching from LED powder establishes a suitable path for Ga recovery from LED waste (Maneesuwannarat et al., 2016). The general bioleaching process can be resumed as follows:

$$Fe_2(SO_4)_3 + M^0 \rightarrow M^{2+} + SO_4^{2-} + 2FeSO_4 \quad M[Cu, Ni, Ga] \ (53)$$

$$2\,M^0 + 2H_2O + O_2 \rightarrow 2M^{2+} + 4OH^- \ (54)$$

5.2 Lead

Lead (Pb) holds a long history of human use dating back many centuries. Its malleability and resistance to corrosion have made it a valuable metal for various applications, including pipes and paints, since the time of the Romans (Ghazi and Millette, 1964). Pb found application e.g. in Pb glazes for pottery and insecticides, despite being recognized for its carcinogenic properties, it is still utilized in the production of car batteries, pigments, ammunition, cable sheathing, radiation shielding, and soldering (Flora et al., 2012). The primary mineral source of Pb is galena (PbS), which is processed through roasting (Cheriton and Gupta, 2005) and among others, Anglesite ($PbSO_4$) (Grant, 2001). Bioleaching using *A. ferrooxidans* and *A. thiooxidans* is a noteworthy alternative to conventional roasting and smelting processes for Pb extraction (Kamoldeen, 2012). The precipitation of Pb^{2+}, released by galena as Pb sulfate, concurs with elemental sulfur and sulfides undergoing oxidation by *A. ferrooxidans*, resulting in SO_4^{2-}(Jiang et al., 2008):

$$PbS + H_2SO_4 + 0.5O_2 \rightarrow PbSO_4 + H_2O + S^0 \, (55)$$

$$2S^0 + 2H_2O + 3O_2 \rightarrow 2SO_4^{2-} + 4H^+ \, (56)$$

$$PbS + 2Fe^{3+} \rightarrow Pb^{2+} + 2Fe^{2+} + S^0 \, (57)$$

$$Pb^{2+} + SO_4^{2+} \rightarrow PbSO_4 \, (58)$$

A. ferrooxidans utilized also hydrogen sulfide dissolves in the solution as an energy source (Eq. 62)

$$PbS + H_2SO_4 \rightarrow PbSO_4 + H_2S \ (59)$$

$$2H_2S + O_2 \rightarrow 2S^0 + 2H_2O \ (60)$$

A.ferrooxidans and microbial consortia can facilitate the bioremediation of lead through various mechanisms such as the one shown in Eq 55-60 and through biosorption, bioaccumulation and biomineralization effectively reducing the toxicity and mobility of Pb in contaminated environments.

6. Arsenic

Arsenic (As) exhibits a pervasive presence, ranking 20th in abundance within the Earth's crust, 14th in seawater, and emerging as the 12th most prevalent element within the human body (Mandal and Suzuki, 2002). Since its initial discovery, As has found diverse applications encompassing medicine, agriculture, metallurgy, and even as a potent toxin for various organisms (Páez-Espino et al., 2009). As is a known toxin, nevertheless: 1) it holds therapeutic potential as a frontline chemotherapeutic agent against specific hematopoietic cancers (Liu and Waalkes, 2008); 2) some prokaryotes thrive and endure elevated As concentrations (Zargar et al., 2010). Among the mineral deposits, the sulfide mineral realgar (alpha-As_4S_4) stands out by notably high As content (Chen et al., 2017).

Among metalloids, As is efficiently mobilized by *A. ferrooxidans*, which exhibits resilience to As concentrations in the gram per liter range—an amount considered toxic for numerous organisms. The catalytic conversion of Fe^{2+} to Fe^{3+} in an acidic solution instigates the generation of cationic As, as illustrated by the ensuing reaction (Chen et al., 2013):

$$4Fe^{2+} + O_2 + 4H^+ \rightarrow 4Fe^{3+} + 2H_2O \ (61)$$

$$As_2S_2 + 6Fe^{3+} \rightarrow 2As^{3+} + 2S^0 + 6Fe^{2+} \ (62)$$

$$H_3AsO_3 + H_2O \rightarrow H_3AsO_4 + 2H^+ + 2e^- \ (63)$$

$$H_3AsO_4 + Fe^{3+} \rightarrow FeAsO_4 + 3H^+ \ (64)$$

In presence of *A. ferrooxidans*:

$$As_2S_2 + 14H_2O \rightarrow 2H_3AsO_3 + 2HSO_4^- + 20H^+ +18e^- \ (65)$$

Bioleaching of As, precipitation, oxidation of arsenite or reduction to arsenate are some valid processes involved in bioremediation activities and in treating contaminated environments such as AMDs, industrial wastewater, and polluted soils.

7. Uranium

Uranium (U) is the only known actinide to be mobilized by *A. ferrooxidans*. The actinides, or actinide series, elements with atomic numbers ranging from 89 to 103, are situated beneath the lanthanide series. From uranium to lawrencium, each actinide brings its own set of intriguing features, making the study of this series crucial for understanding nuclear reactions, reactor design, and the behavior of radioactive materials (Allard et al., 1984).

U finds applications in: nuclear energy generation, production of uranium oxide (U_3O_8), formulation of anti-corrosive alloys and coloring agent for glass and porcelain (Chen et al., 2021). The conventional extraction of U relies on a process that utilizes acids as leaching agents (Costine et al., 2013). Extracting U from low-grade ores through chemical leaching is often economically unfeasible (Vázquez-Campos et al., 2017). In contrast, bioleaching is recognized for its economic viability and environmental compatibility (Kaksonen et al., 2020). *A. ferrooxidans* stands out in bioleaching for U extraction leveraging its indirect oxidation capabilities (Pal et al., 2010):

$$UO_2 + 2Fe^{3+} + SO_4^{2-} \rightarrow UO_2SO_4 + 2Fe^{2+} \quad (66)$$

$$U^{4+} + 2Fe^{3+} \rightarrow U^{6+} + 2Fe^{2+} \quad (67)$$

U exhibits limited solubility in an aqueous medium when it is in the +4 oxidation state. However, within an acidic environment, the ferric ion facilitates the oxidation of U^{4+} to U^{6+}, a form that readily dissolves. In a complementary reaction to the oxidation of U^{4+}, the ferric ion undergoes reduction to become the ferrous ion. Under the influence of *A. ferrooxidans* oxidation function, it is subsequently re-oxidized back to the ferric state. This enables it to once again engage in the oxidation of U (Pal et al., 2010). The oxidation of U leads to the formation of uranyl minerals, which are less mobile and can precipitate out of solution, thereby immobilizing uranium and reducing its environmental impact. In this way extreme acidophilic organisms can be harvested to bioremediate sites contaminated by radiation and by radioactive elements.

8. Conclusions

A. ferrooxidans stands as a cornerstone in trace elements bioleaching and in the biomining and bioremediation industry (Ruiz et al., 2012). Its specialized metabolic pathways, particularly in the oxidation of ferrous iron and sulfur compounds, combined with its ability to thrive and contribute to hyperacidic conditions, empower the efficient solubilization of diverse valuable trace elements from mineral deposits (Valdés et al., 2008). This microorganism has demonstrated remarkable proficiency in boosting metal (including alkali and transition metals, Figure 2) recovery rates, revolutionizing conventional mining methodologies. Its use significantly reduces the environmental footprint of mining operations, representing a critical step towards sustainable and eco-friendly mining practices (Romero-González et al., 2016). This underscores the transformative potential of *A. ferrooxidans* in the journey toward sustainability (Kaksonen and Petersen, 2023), increasing our ability to recover critical metals from low grade ore deposits, recycle E-wastes and bioremediate contaminated sites.

Peering into the future, the application of *A. ferrooxidans* holds exciting prospects in space exploration. Its unique adaptability and capacity to facilitate metal extraction on Earth represents a groundbreaking future opportunity for resource utilization on other planetary bodies. By mitigating the challenges of resource transport from our home planet, the use of *A. ferrooxidans* may support future space missions catalyzing the extraction of key elements for the development of extraterrestrial habitats and advancing technological frontiers (Tonietti et al., 2023).

One major concern with bioleaching and biomining is the production of acid mine drainage, a process that leads to significant environmental challenges (Jerez, 2017). To counteract these negative impacts, it can be useful to employ bioremediation strategies e.g. the usage of either naturally occurring or deliberately introduced microorganisms to consume and break down environmental pollutants, is considered essential (Jerez, 2011). The effectiveness of biomining relies on the intricate interactions among the microbial communities involved. A deep comprehension of these interactions is strictly related to the effective management and optimization of the microbial consortia to enhance biomining efficiency (Johnson, 2010), since the majority of current biomining activities use naturally occurring microbial populations (Brune and Bayer, 2012). It is worth noting that the dangers associated with the discharge of the bioremediating microorganisms into the surrounding environment to counteinteract acid mine drainage production are considered minimal, because these organisms are already present in the ecosystem (Johnson and Hallberg, 2005). As a consequence, while bioleaching and biomining present forward-thinking solutions for extracting metals, it is important to address their environmental repercussions and ensure sustainable resource recovery, aligning with the objectives of a circular economy (Gomes et al., 2020).

The application of bioleaching to E-waste holds significant potential for enhancing social development and bolstering the economies of developing nations. The utilization of thermophilic bacteria, particularly *A. ferrooxidans*, represents a substantial stride towards advancing base metal recovery both on Earth and potentially in extraterrestrial environments e.g. planets (Mars), moons (Moon, Enceladus, etc.), and asteroids (Lutetia, Kleopatra, etc.). As we delve deeper into the intricacies of microbial-driven biomining processes, it is imperative to acknowledge the multifaceted contributions of *A. ferrooxidans*. From bolstering metal recovery rates on Earth to potentially revolutionizing resource extraction in space, this remarkable bacterium exemplifies the transformative potential of biotechnology in mining and beyond. With ongoing research and technological advancements, we are poised to further harness the capabilities of *A. ferrooxidans*, propelling us toward a future marked by sustainability, innovation, and abundant resources.

Author Contributions

LT, AR and DG conceived the review. All the authors contributed equally to the article and approved the submitted version.

Fundings

This work has been conducted thanks to the following funding: the PhD program PON "Ricerca e Innovazione" 2014-2020, DM n.1061 (10/08/2021) and n. 1233 (30/07/2020) by the Ministero dell'Università e della Ricerca (MUR); the ASI-INAF agreements I/024/12/0 and 2020-4-HH.0, by the Italian Space Agency (ASI). This work was supported by funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (Grant Agreement No. 948972—COEVOLVE—ERC-2020-STG).

Acknowledgments

We thank MUR (Ministero dell'Università e della Ricerca) for the PhD program PON "Ricerca e Innovazione" 2014-2020, DM n.1061 (10/08/2021) and n. 1233 (30/07/2020).

Conflict of interest

The authors declare that the review was conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest.

Figure

Figure 1. General mechanisms for acidophile tolerances and immobilization of metals from the environment. A. In the upper left, osmotolerance with proteins and transporters. In the upper right, acid tolerance highlighting membrane transport proteins and the principal mechanisms involving proton transport. In the lower left, thermotolerance is displayed, and in the lower right, tolerance to heavy metals such as Pb, Zn, Hg, etc., is illustrated. Main processes of metal immobilization found in acidophilic organisms such as *A. ferrooxidans*. B. Clockwise from the top, bioaccumulation involves the internalization of heavy metals into the cell as aquo-ions, followed by bioprecipitation where hydrated metals are precipitated into respective hydrogen phosphate, sulfide, and carbonate forms. Bioreduction entails the precipitation of soluble metals as solid metals through redox processes. Finally, biosorption processes involve the absorption of soluble metals by the cell in the form of solids, such as phosphates, or in compatible molecules e.g., amines, organic acids, or hydroxides.

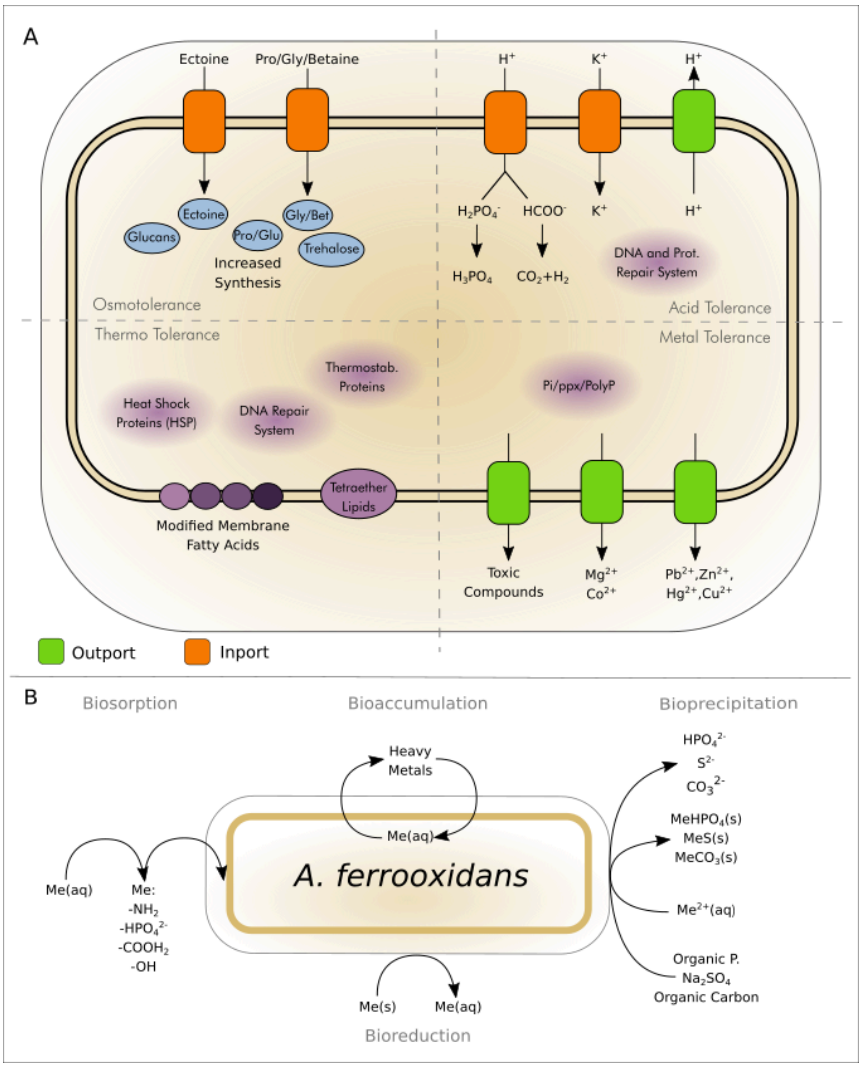
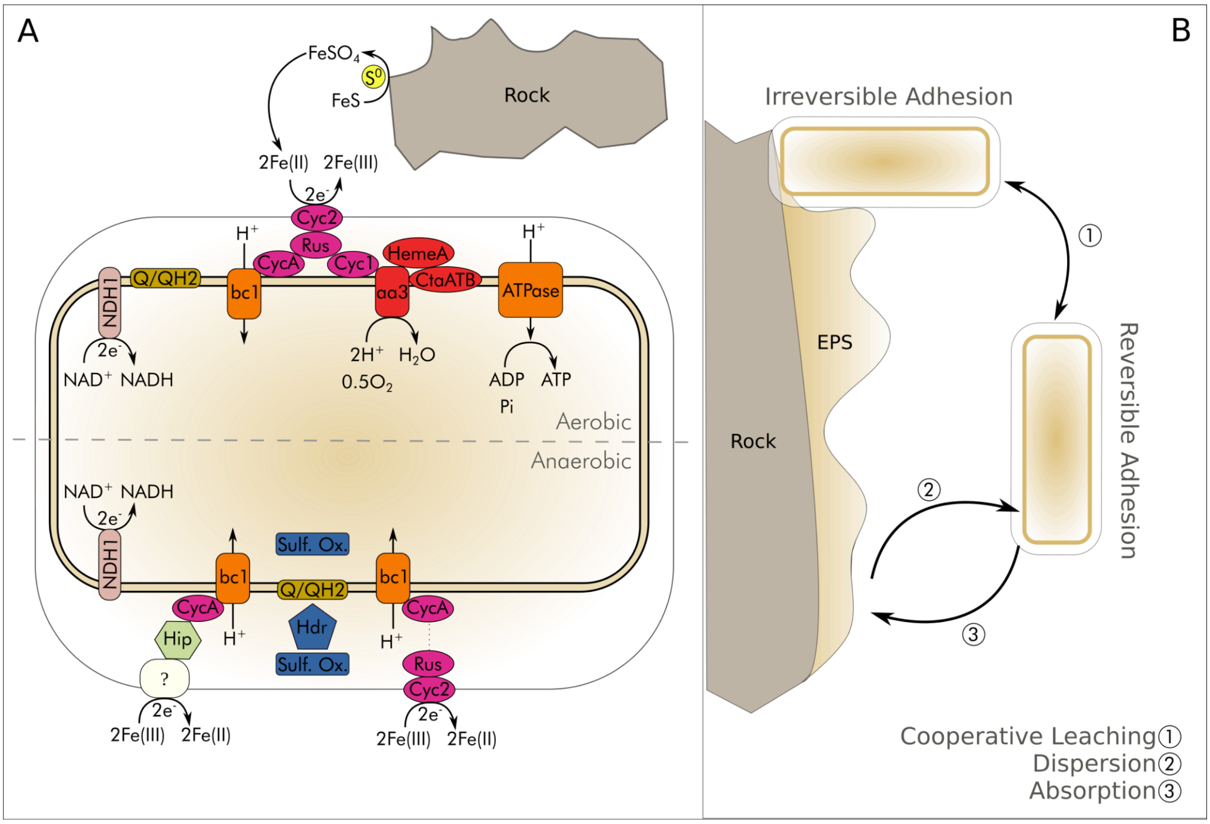


Figure 2. Mobilization mechanisms for *A. ferrooxidans*. A. Aerobic and anaerobic proteins pathway for iron oxidation and reduction. Under aerobic conditions the transition from Fe(II) to Fe(III) occurs through water oxidation, NAD+ reduction, ATP production, and sulfur reduction. In anaerobic conditions, the electron transport chain is mostly understood, except for an unidentified protein (?) responsible for the transformation of Fe(III) to Fe(II). B. Planktonic and sessile cells permanently or non-permanently attached to the substrate. In the case of planktonic or floating cells, leaching occurs in the space between the rock and the organism via a series of redox reactions, while in the case of sessile cells, adherence to the substrate occurs due to extracellular polymeric substance (EPS) production, and leaching is termed direct or contact leaching. Rocks are generally sulfides, but not exclusively. Bioleaching can also be cooperative, wherein sessile and planktonic cells collaborate in metal mobilization between the acidic medium, substrate, and cells. Cell attachment to the substrate can be irreversible if EPS has already been produced, or reversible if not yet produced, and the process by which cells can adhere or detach from the substrate is termed absorption or dispersion.



Table

Table 1. List of elements, minerals, chemical composition and chemical reactions involved in bioleaching processes through *A. ferrooxidans*.

Element	Mineral	Chemical Formula	Reactions
Li	Lepidolite	$K\mathbf{Li}_2Al(Si_4O_{10})(F,OH)_2$	$3Li_2O*2K_2O*5Al_2O_3*10SiO_2*2SiF_4 + 20H_2SO_4 \rightarrow 3Li_2SO_4 + 2K_2SO_4 + 5Al_2(SO_4)_3 + 11SiO_2 + H_2SiF_6 + 18H_2O + 2HF$ $3Li_2O*2K_2O*5Al_2O_3*10SiO_2*4H_2O + 20H_2SO_4 \rightarrow 3Li_2SO_4 + 2K_2SO_4 + 5Al_2(SO_4)_3 + 12SiO_2 + 24\ H_2O$
P	P-Sludge	$Ca_3(\mathbf{P}O)_4$	$2S^0 + 3O_2 + 2H_2O \rightarrow 2H_2SO_4$ $3H_2SO_4 + Ca_3(PO_4)_2 \rightarrow 2H_3PO_4 + 3CaSO_4$ $3H_2SO_4 + 2FePO_4 \rightarrow 2H_3PO_4 + Fe_2(SO_4)_3$
V	V-Ti-Magnetite and vanadates	$(\mathbf{V},Ti),Fe^{2+}Fe^{3+}{}_2O_4$ and V_2O_3	$4Fe^{2+} + 4H^+ + O_2 \rightarrow 4Fe^{3+} + 2H_2O$ $V_2O_3 + 2Fe^{3+} + 2H^+ \rightarrow 2VO^{2+} + 2Fe^{2+} + H_2O$ $VO_2 + Fe^{3+} \rightarrow VO_2^+ + Fe^{2+}$ $10VO_2 + 10Fe^{3+} + 5H_2O \rightarrow HV_{10}O_{25}^{2-} + 10Fe^{2+} + 9H^+$
Cr	Cr-Slug	$Ca_3Al_2(H_4O_4, \mathbf{Cr}O_4)_3$	$Cr^{6+} + 3Fe^{2+} \rightarrow Cr^{3+} + 3Fe^{3+}$
Fe	Pyrite	$\mathbf{Fe}S_2$	$4Fe^{2+} + O_2 + 4H^+ \rightarrow 4Fe^{3+} + 2H_2O$
Ni	Ni-sludge	$\mathbf{Ni}^0$	$Ni^0 + Fe^{3+} \rightarrow Ni^{2+} + Fe^{2+}$
Cu	Chalcopyrite	$\mathbf{Cu}FeS_2$	$CuFeS_2 + 2Fe_2(SO_4)_3 \rightarrow CuSO_4 + 5FeSO_4 + 2S^0$
Zn	Zn-Ores	$\mathbf{Zn}S_2$	$ZnS + 0.5O^2 + H_2SO_4 \rightarrow ZnSO_4 + H_2O + S^0$ $4Fe^{2+} + O_2 + 4H^+ \rightarrow 4Fe^{3+} + 2H_2O$ $S^0 + 1.5O_2 + H_2O \rightarrow H_2SO_4$
Ga	Ga-sludge	$\mathbf{Ga}^0$	$Fe_2(SO_4)_3 + M^0 \leftrightarrow M^{2+} + SO_4^{2-} + 2FeSO_4 \quad M[Cu, Ni, Ga]$ $2\ M^0 + 2H_2O + O_2 \leftrightarrow 2M^{2+} + 4OH^-$
As	Realgar	$\mathbf{As}_2S_2$ or alpha $\mathbf{As}_4S_4$	$4Fe^{2+} + O_2 + 4H^+ \rightarrow 4Fe^{3+} + 2H_2O$ $As_2S_2 + 6Fe^{3+} \rightarrow 2As^{3+} + 2S^0 + 6Fe^{2+}$ $H_3AsO_3 + H_2O \rightarrow H_3AsO_4 + 2H^+ + 2e^-$ $H_3AsO_4 + Fe^{3+} \rightarrow FeAsO_4 + 3H^+$
Mo	Mo Sulfide	$\mathbf{Mo}S_2$	$4MoS_2 + 4Fe^{3+} + 16H_2O \rightarrow 4MoO_4^{2-} + 4Fe^{2+} + 32H^+ + 4S^0$
W	Tungstate Salts	$\mathbf{W}O_4^{2-}$	$H_2SO_4 + FeWO_4 \rightarrow FeSO_4 + H_2WO_4$ $H_2SO_4 + MnWO_4 \rightarrow MnSO_4 + H_2WO_4$
Au	Au Ores	$\mathbf{Au}$	$4Au0 + 8NaCN + 2H_2O + O_2 \rightarrow 4NaAu(CN)_2 + 4NaOH$
Pb	Galena	$\mathbf{Pb}S$	$PbS + H_2SO_4 + 0.5O_2 \rightarrow PbSO_4 + H_2O + S^0$ $2S + 2H_2O + 3O_2 \rightarrow 2SO_4^{2-} + 4H^+$ $PbS + 2Fe^{3+} \rightarrow Pb^{2+} + 2Fe^{2+} + S^0$ $Pb^{2+} + SO_4^{2+} \rightarrow PbSO_4$ $PbS + H_2SO_4 \rightarrow PbSO_4 + H_2S$ $2H_2S + O_2 \rightarrow 2S^0 + 2H_2O$
Hg	Cinnabar	$\mathbf{Hg}S$	$2HgS + 4Fe^{3+} + 3O_2 + 2H_2O \rightarrow 2Hg^{2+} + 4Fe^{2+} + 2H_2SO_4$
U	U Oxide	$\mathbf{U}O_2$	$UO_2 + 2Fe^{3+} + SO_4^{2-} \rightarrow UO_2SO_4 + 2Fe^{2+}$ $U^{4+} + 2Fe^{3+} \rightarrow U^{6+} + 2Fe^{2+}$

Table 2. Selected bioleached elements by *A. ferrooxidans* . A = *Acidithiobacillus ferrooxidans*, B = other organisms, C = consortia. 1. According to the literature, the estimated copper extraction through biohydrometallurgy is about 30% worldwide. For the other metals, there is no clear data in literature. * all the biomining experiments made in space are referred to microgravity conditions on the ISS or in simulated environments. d - Estimates according to British Geological Survey

Element	**Main Alloys**	**Application Fields**	**Metal Printing**	**Electronics**	**Extraction Yield (ktons/year)[d]**	**Biomining on Earth**	**Biomining in Space***	**Bioremediation**	**References**
Ti	Alpha/Beta Ti alloys	Aerospace, Construction, Automobile	Yes	Major (hardware)	6,300	Yes (A)	No	Yes (A,B,C)	(Peng et al., 2023)
V	Ferrovanadium	Structural, Fusion Reactor	No	Minor (semiconductors)	81	Yes (A)	Yes (B)	Yes (A,B,C)	(Hao et al., 2018; Cockell et al., 2020; Shi et al., 2020; Santomartino et al., 2022; Tambat et al., 2023; Zhang et al., 2023)
Cr	FeCr, Stainless steel	Automobile, High Temperature	Yes	Minor (anticorrosive coating)	38,600	Yes (A)	No	Yes (A,B,C)	(Cabrera et al., 2007; Garg et al., 2012; Liu et al., 2013; Sharma et al., 2022)
Fe	Steel, Inox	Construction, Automobile, Aerospace,	Yes	Major (solder)	3,040,000	Yes (A,B,C)	Yes (B)	Yes (A,B,C)	(Zhan et al., 2019; Cockell et al., 2020; Santomartino et al., 2022)
Ni	NiCrFe	Medical, Aerospace, Energy, Isolators, Automotive, Cables	Yes	Minor (plating agent)	2,700	Yes (A)	Yes (B)	Yes (A,B,C)	(Arshadi and Yaghmaei, 2020; Cockell et al., 2020; Santomartino et al., 2022)
Cu	Brass, Bronze	Construction, Marine, Automotive, Medical, Aerospace	Yes	Major (cables)	20,700	Yes (A,B,C)[1]	Yes (B)	Yes (A,B,C)	(Cockell et al., 2020; Li et al., 2021a; Santomartino et al., 2022)
Ga	GaAlZn alloys	Semiconductors, Diodes, Circuits	No	Major (diodes)	0,380	Yes (A)	No	No	(DenBaars et al., 2013; Lu et al., 2017)
As	As Bronze	Automobile, Ammunition	No	Minor (batteries)	NA	Yes (A,B,C)	No	Yes (A,B,C)	(Mandal and Suzuki, 2002; Camm et al., 2004)
W	W,Ni,Cu and W,Ni,Fe alloys	Aerospace, Medical, Automobile	Yes	Minor (light bulbs)	91,5	Yes (A)	No	Yes (A,B,C)	(Hällström et al., 2020; Boury et al., 2023; Han et al., 2023)
Au	AuPt alloys	Increasing Corrosion Resistance	No	Major (connector)	3.3	Yes (A)	No	No	(El-Midany, 2012; Sen, 2015; Işıldar et al., 2016; Medina and Anderson, 2020)
Pb	PbCu, alloys	Automobile, Ammunition, Batteries	No	Major (solder)	4,700	Yes (A,C)	No	Yes (A,B,C)	(Flora et al., 2012; Kamoldeen, 2012)
U	Mulberry	Increasing Corrosion Resistance	No	None	53	Yes (A)	No	Yes (A,B,C)	(Pal et al., 2010; Costine et al., 2013; Chen et al., 2021)

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