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Review

Bioleaching of Rare Earth Elements: Perspectives from Mineral Characteristics and Microbial Species

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Abstract: Bioleaching exhibits high potential for the processing of low-grade complex mineral resources. With the development of the economy and an increase in demand, rare earth elements (REEs) in secondary resources, such as phosphogypsum, red mud and coal-related resources, are gaining more and more attention. In this review, the bioleaching performance of diverse microorganisms is summarized and compared for primary (mainly monazite) and secondary REE resources, based on publications from the past decade. The mineral characteristics of these REE resources are different, as they can be found in phosphate, sulfate, or silicate forms. Correspondingly, microbial species suitable for use in bioleaching differ. The most efficient bioleaching microbe for monazite is *Paecilomyces* sp., while *Acidianus manzaensis* is effective in processing red mud. Acidophilic sulfur oxidizers are suitable for processing acidic phosphogypsum. *Acidithiobacillus thiooxidans* could recover a significant amount of REEs from coal fly ash. In particular, monazite has a high REE content but extremely low bioleaching efficiency compared to that of secondary resources, supporting the understanding that bioleaching approaches are more competitive for minerals with low REE contents. Overall, great progress has been made over the last decade, as considerable REE recovery rates have been achieved, and the main metabolites of microbes were identified. However, numerous challenges still exist. Future efforts should focus on improving biorecovery efficiency, reducing the cost of cell-culture media, and exploring the interaction mechanism between cells and minerals, with an emphasis on mineralogical phase transformations and the molecular regulation mechanisms inside cells during the bioleaching process.

Keywords: biorecovery; mineral structure; metabolites; specificity; interaction

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1. Introduction

Rare earth elements (REEs) are national strategic resources widely applied in industries such as petrochemicals, electronics, national defense and new energy [1]. The primary REE resources are monazite, bastnaesite, xenotime and ion-adsorption type rare earth ore [2]. With the rapid development of the economy and the consumption of REE resources, unconventional resources, such as phosphogypsum, coal fly ash, red mud, and NdFeB magnets [3,4], show increasing exploitation value. Despite being considered industrial wastes which cause severe environmental problems and landfill issues, these resources contain a substantial amount of REEs. Therefore, recovering REEs from these secondary resources not only helps to alleviate environmental problems but also turns waste into wealth. Physical and chemical approaches, including flotation; magnetic separation; gravity separation; roasting (with or without additives); and alkaline and acid leaching (e.g., H_2SO_4, HCl and HNO_3) [5–7] are usually used to extract REEs from these resources. The rare earth elements in the leachate are then separated and recovered using chelating extractants, organophosphorus compounds, ionic liquids, etc., [8–11]. In the extraction process, high temperatures are often required to enhance extraction efficiency, which is energy-consuming [12–14].

Bioleaching is a process that solubilizes metals from minerals using microorganisms, and has been applied commercially to extract metals such as Cu, Au, Zn, U, Ni, and Co [15,16]. Because of its mild condition and low cost, bioleaching shows advantages in dealing with complex low-grade ores, waste materials, and rocks compared to traditional methods like pyrometallurgy and hydrometallurgy [17,18]. Recently, various microorganisms, such as bacteria, fungi, and archaea, have been exploited to extract REEs from primary and secondary resources. Most of these are bacteria or fungi, while a few are archaea species. Both autotrophs and heterotrophs have shown promise in the bioleaching of REEs. For example, autotrophic sulfur/iron oxidizing bacteria, e.g., *Acidithiobacillus ferrooxidans* and *Acidithiobacillus thiooxidans* were used to process monazite ores [19], phosphogypsum [20], coal fly ash [21,22], and red mud [23]. REE resources are usually oxidized and non-sulfidic, and these autotrophs do not exhibit many advantages compared to heterotrophs, as an extra electron donor is required and acid mine drainage is produced, which affects the environment. Heterotrophic microbes like *Aspergillus* and *Penicillium* have also been employed for the leaching of monazite ores [24,25] and bauxite residues [23,26]. During the bioleaching process, the microbial cells produce various metabolites, such as inorganic acid, organic acids, proteins, and exopolysaccharides which interact with minerals mainly through acidification, complexation, redox reaction, and biosorption [27–29]. However, bioleaching efficiency needs to be improved, and cell–mineral interactions mechanisms remain to be further explored.

The mineralogical characteristics of REE resources and the function of microbes are key factors affecting leaching efficiency [30,31]. Bioleaching microorganisms are diverse in terms of their nutritional types and metabolites, and the chemical composition and structure of minerals (especially REE occurrence modes) also vary significantly. REE resources include phosphate, silicate, and sulfate minerals (Figure 1), and thus the appropriate microbes to solubilize REEs from different resources should, theoretically, be different. For example, *Penicillium* sp. was employed to process weathered monazite and monazite concentrate separately [25]. As a result, 12.32 mg/L of REEs were released from the weathered monazite after eight days of incubation. In contrast, almost no REEs (<0.06 mg/L) were leached from the monazite concentrate under the same conditions. Although with similar REE contents (~30%), the monazite concentrate was composed of (Ce, La, Nd, Th)PO_4 and zircon $ZrSiO_4$, while monazite and florencite (Cd, La, Nd)$Al^{3+}(PO_4)_2(OH)_6$ were present in the weathered monazite. The findings demonstrate that the leaching performance of microorganisms depends on the chemical composition and structure of the minerals.

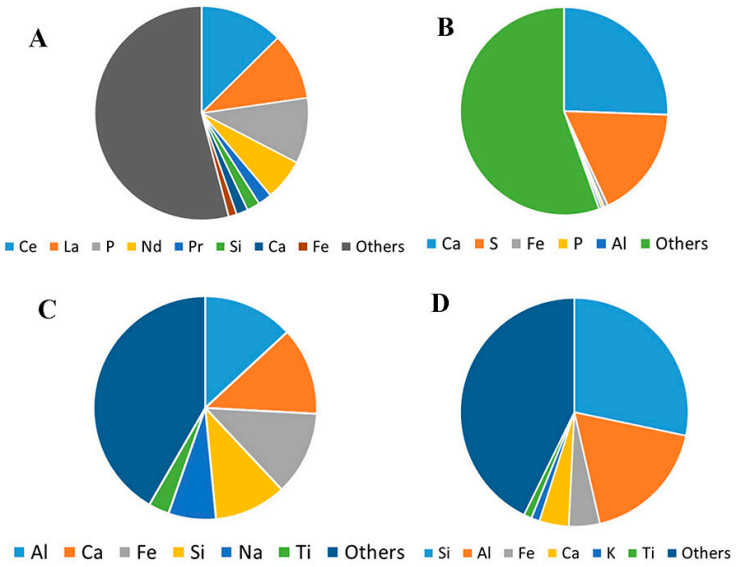


Figure 1. Major chemical composition of: (**A**) monazite [19]; (**B**) phosphogypsum [32]; (**C**) red mud [33]; and (**D**) coal fly ash [21].

To date, a number of reviews on the bioleaching of REEs have been published [27,34,35]. One review proposes that factors affecting the biorecovery of REEs are aeration, pulp density, temperature, pH, redox potential, and metal toxicity [34]. Rasoulnia et al. also highlighted the importance of the culture-medium composition of microbes, the particle size of minerals, and bioleaching methods (e.g., one-step and two-step methods) in influencing REE bioleaching [27]. However, the significance of mineral composition and structure, as well as the correlation between mineral properties and microbial types are seldom discussed. In this review, we will summarize publications on the bioleaching of REEs from the perspectives of mineral characteristics and microbial species, with an emphasis on non-conventional REE resources characterized by large reserves, and low-grade (<1000 ppm) and complex compositions, including phosphogypsum, red mud and coal-related resources. Other secondary REE resources (NdFeB magnets) have high REE contents and are rarely processed using bioleaching approaches [36], so they are not included in this review. We aim to explore the relationship between the characteristics of minerals and the metabolism of microbes, and to identify microbes with high bioleaching potential for each type of REE resource. Finally, gaps in the current research and future perspectives in this field are also explored.

2. Primary REE Resources

2.1. Monazite Ore

Monazite, bastnaesite, xenotime and ion-adsorption rare earth ore (IRE-ore) are primary REE resources. Currently, the application of bioleaching approaches is mainly focused on monazite, while studies on the bioleaching of bastnaesite and IRE-ore are scarce, and there are no relevant studies on xenotime. Of these, monazite ((Ce,La,Nd,Th)PO_4) is a kind of REE phosphate mineral, and an important industrial light REE resource. It is mainly composed of P_2O_5, Ce_2O_3, La_2O_3, Nd_2O_3 and ThO_2 (Figure 1A) [24]. Low-grade monazite ores also contain ilmenite, silicate and zircon with both crystal and amorphous structures [37], making them complex in composition and difficult to dissolve. For example, a monazite-bearing rock contains monazite (51%), florencite (41%), and nontronite (8%) [19]. A sequential extraction procedure in the study showed that the majority (85%) of REEs were present in the residual fraction, and around 12% of REEs were found in the acid-soluble fraction. Conventionally, concentrated sodium hydroxide or sulfuric acid is employed to extract REEs from monazite, resulting in the production of toxic waste [38,39]. Organic acids are able to selectively release REEs from monazite, including oxalic acid, citric acid and ethylene diamine tetra-acetic acid (EDTA), but they have a lower recovery rate than inorganic acids [40,41]. To date, microorganisms that have been utilized to release REEs from monazite involve *Penicillium* sp., *Aspergillus niger*, *Paecilomyces* sp., *Acidithiobacillus ferrooxidans*, *Enterobacter aerogenes*, and so on.

The fungus *A. niger* is a widely used microorganism in bioleaching. It is geoactive and extensively applied in industry, and also exhibits a high tolerance to REEs. With glucose as an energy source, the maximum concentration of Ce extracted from monazite was 0.7 mg/L after 30 days of leaching at 30 °C and a 1% pulp density [24]. The authors also noted that monazite can provide a phosphorus source for cells, and maybe other essential trace metals, illustrating the feasibility of monazite bioleaching. In another study, using a minimal medium, *A. niger* solubilized 1.37 mg/L of REEs at a 1% pulp density, which was significantly higher than that in a rich medium (0.97 mg/L) [29]. The results suggest that obtaining nutrients from monazite favors the bioleaching of REEs. Also, X-ray diffraction (XRD) analyses revealed that aluminum cerium phosphate hydroxide in monazite ore is decomposed by *A. niger*. Furthermore, the direct interaction mechanisms between *A. niger* and monazite were explored by scanning electron microscopy and energy-dispersive X-ray analysis in one research study [42]. The authors proposed that *A. niger* released REEs and phosphate by the tunnelling, splitting, and penetration of mineral particles. Moreover, *A. niger* can produce siderophores and various organic acids, including oxalic acid, acetic acid, and citric acid (Figure 2) [24]. Of these, citric acid plays a role in REE

dissolution through acidolysis and chelation, as the citric acid concentration is positively correlated with the contents of the released REEs. Osman et al. found that siderophores produced by *A. niger* are trihydroxymate in nature, extracting the REEs from phosphorites via chelation [43].

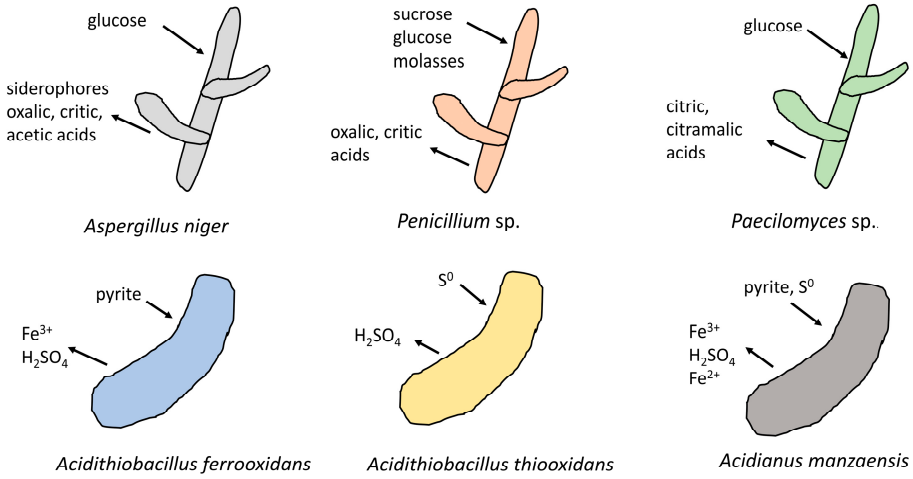


Figure 2. Microorganisms frequently utilized in REEs bioleaching, as well as their main metabolic substrates and products, including *Aspergillus niger*, *Penicillium* sp., *Paecilomyces* sp., *Acidithiobacillus ferrooxidans*, *Acidithiobacillus thiooxidans*, and *Acidianus manzaensis*.

However, the leaching efficiency of REEs was low (<3%) in these studies, which may be attributed to the adsorption of REEs to cells and precipitation of the REEs induced by oxalic acid (Figure 3A). Adsorption of the REEs onto cells was observed via SEM, and the presence of La and Ce oxalate were detected by XRD after bioleaching [29]. Furthermore, the REE oxalates were identified as $Ce_2(C_2O_4)_3{\cdot}10H_2O$ and $La_2(C_2O_4)_3{\cdot}10H_2O$, with various morphologies such as sheets, needles, and tablets [44]. Considering that the leaching of monazite with microbial culture supernatants generates REE oxalates of high purity, it could serve as a novel method for the biorecovery of REEs.

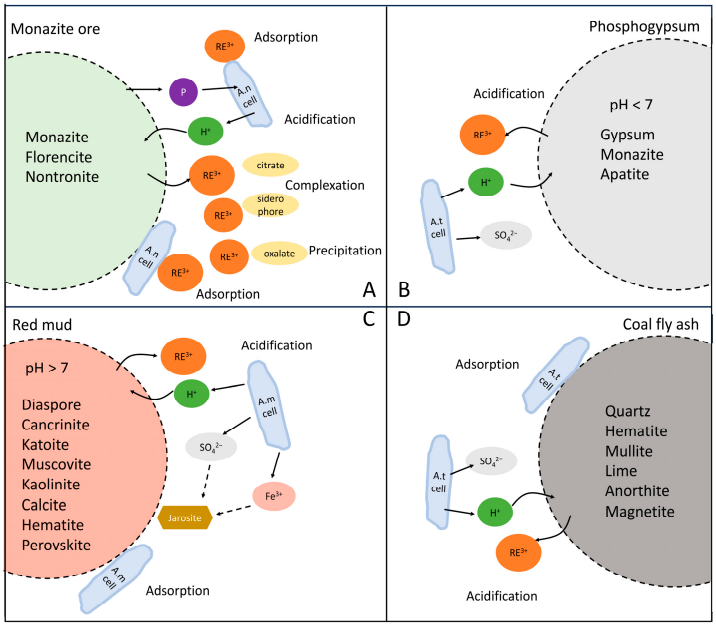


Figure 3. Schematic diagram of bioleaching mechanisms of: (**A**) monazite ore [24,29,44,45]; (**B**) phosphogypsum [20,46]; (**C**) red mud [33]; and (**D**) coal fly ash [22]. A.n, *Aspergillus niger*; A.t, *Acidithiobacillus thiooxidans*; A.m, *Acidianus manzaensis*.

A study on monazite bioleaching using heterotrophic bacteria *Enterobacter aerogenes* showed that microbial contact contributes to the leaching of REEs [45]. *E. aerogenes* secreted malic, acetic and gluconic acid, which decreased the pH and complexed with REE^{3+}. Exopolysaccharides produced by the bacteria facilitated the attachment of cells to minerals. After 18 days of incubation at 30 °C and a 1% pulp density, the biotic-contact bioleaching approach showed a higher REE recovery (3.66 mg/L) than the non-contact approach (0.94 mg/L), indicating that microbial contact contributes to the leaching of REEs. Consistently, the attachment of cells onto a monazite surface was observed by atomic force microscopy (AFM) and confocal Raman microscopy (CRM). The adsorption of cells onto minerals creates a microenvironment where high concentrations of organic acids accumulate, thereby enhancing the solubilization of REEs.

In addition, *Penicillium* sp. released 12.32 mg/L of REEs from weathered monazite [25], which is higher than that observed in *A. niger* and *E. aerogenes*, but lower than that of *Paecilomyces* sp. The fungus *Paecilomyces* sp. was able to leach REEs from monazite using monazite as the sole phosphorous source [47]. The consumption of phosphorous by microbes in the leachate induces further solubilization of monazite. After six days of incubation at room temperature and a 1% pulp density, the maximum REE concentration in the leachate was 112 mg/L, which is 1.7–3.8 times higher than that of HCl leaching (with a comparable pH). It is worth noting that the radioactive element Th remains undissolved in the process, demonstrating the high selectivity of the bioleaching approach. Furthermore, a metabolomic analysis of *Paecilomyces* sp. detected 210 metabolites, in which citric and citramalic acids contributed largely to the monazite bioleaching (Figure 2) [48]. Hence, increasing the production of citric and citramalic acids could potentially enhance the bioleaching efficiency of *Paecilomyces* sp.

A roasting pretreatment was proven to increase the bioleaching efficiency of monazite rock. Maes et al. found that after roasting monazite with Na_2CO_3 and NaCl at 800 °C, the leaching efficiency of La and Nd increased significantly [49]. During the roasting, REE phosphates were transformed into more soluble REE oxides. As a result, 279 mg/L of Nd and 287 mg/L of La were obtained after seven cycles of leaching with the fungal supernatant (*Paeciliomyces* sp.), which were significantly higher than results obtained in the other studies mentioned above. Acetic, succinic, and gluconic acids in the fermentation supernatant were the main factors that solubilized the REEs. It is the first time that roasting was combined with bioleaching to process monazite rock, and it is innovative to adopt a multiple-cycle leaching approach. The results of this study are enlightening for researchers seeking to promote monazite bioleaching efficiency.

Compared to single strain microorganisms, cooperation among different microorganisms often demonstrates higher bioleaching efficiency. In one study, heterotrophic *E. aerogenes* and autotrophic *At. ferrooxidans* were co-cultured to leach REEs from a high-grade monazite ore [19]. *At. ferrooxidans* is able to oxidize inorganic ferrous ions or reduced sulfur compounds (e.g., elemental S, pyrite) to obtain energy, while *E. aerogenes* needs organic carbon and an energy source (glucose) to survive. After 12 days of incubation at 30 °C and a 1% pulp density, REE concentrations reached 40 mg/L in the co-culture bioleaching system, significantly higher than that of the single culture of *E. aerogenes* (5.8 mg/L) or *At. ferrooxidans* (23.6 mg/L). The synergic effect is attributed to the cooperation of organic acids and sulfuric acid. Additionally, *At. ferrooxidans* may help *E. aerogenes* to obtain a phosphorus source. A synergic effect could also occur between indigenous and inoculated microorganisms. The bioleaching of non-sterile monazite using *Penicillum* sp. resulted in a total REE concentration of 23.7 mg/L in eight days, significantly higher than that of sterile monazite (12.32 mg/L) [50]. Further investigations showed that *Firmicutes* accounted for the majority (78%) of the indigenous microbial community and contributed to the increased REE recovery rate. The authors also claimed that the inoculated microorganisms secreted secondary metabolites that simulated the growth of the indigenous microbial community, but experimental evidence was not supplied. The research is meaningful for industrial applications, as the actual bioleaching system operates in open air rather than in a sterile

environment. Therefore, an investigation of the effect of indigenous microorganisms on inoculated microbes is imperative. Overall, the interactions between different microbes could be leveraged to enhance bioleaching, yet the interaction mechanisms remain to be further studied.

In summary, among the microbial species mentioned above, the fungus *Paecilomyces* sp. leached the highest concentration of REEs from monazite (Table 1), and deserve to be investigated further. Meanwhile, more microbes with the potential to dissolve monazite ores can be employed for bioleaching in the future. One such example is phosphate-solubilizing microorganisms, which can make P soluble and promote plant growth; thus, they are widely applied in agriculture. Phosphate-solubilizing microorganisms involve many microbial taxa which are distantly related [51], such as *Pseudomonas*, *Bacillus*, and *Azotobacter*. Monazite is a kind of phosphate mineral, thus phosphate-solubilizing microorganisms must destroy the structure of monazite in order to release P [52], and may release REE cations in the meantime.

Table 1. A summary of studies on the bioleaching of rare earth elements (REEs) from monazite, bastnaesite and ion-adsorption rare earth ore. The number indicates the weighted mean or a range of listed REEs unless otherwise stated. NA, not provided by the authors.

Publications	REE Resources	Main REEs	REE Content	Microbial Species	Recovery Rate (%)/Concentration (ppm)
[47]	monazite sand	Ce, La, Nd, Pr	NA	*Paecilomyces* sp. *Aspergillus terreus* *Aspergillus niger*	112 ppm 101 ppm 86 ppm
[52]	monazite-bearing ore	Ce, La, Nd, Pr	6.55%	*Acetobacter aceti*	0.13% Ce, 0.11% La
[25]	weathered monazite	Ce, La, Nd, Pr	31%	*Penicillium* sp.	12.32 ppm
	monazite concentrate	Ce, La, Nd	30%	*Penicillium* sp.	<0.06 ppm
[24]	monazite	Ce, La, Nd, Pr, Y	NA	*Aspergillus niger*	0.7 ppm Ce
[49]	monazite	Ce, La, Nd, Pr	NA	*Paecilomyces* sp.	279 ppm Nd, 287 ppm La
[50]	monazite concentrate	Ce, La, Nd, Pr	31%	*Penicillium* sp.	42.3 ppm
[19]	monazite	Ce, La, Nd, Pr, Y	31%	*Acidithiobacillus ferrooxidans*, *Enterobacter aerogenes*	3.1%, 40 ppm
[45]	weathered monazite	Ce, La, Nd, Pr, Y	31%	*Enterobacter aerogenes*	3.66 ppm
[42]	monazite	Ce, La, Nd	NA	*Aspergillus niger*	1.1 ppm
[53]	bastnaesite-bearing rock	Ce, La, Nd, Pr, Sm, Eu, Gd, Tb, Dy, Ho, Er, Tm, Yb, Lu, Y	13.4%	*Streptomyces* sp.	0.08%
[54]	ion-adsorption clay	La, Ce, Dy, Lu	2039.6 ppm	*Aspergillus* sp. *Bacillus* sp.	65% La, Dy, Lu; 15.3% Ce 55% La, Dy, Lu; 14% Ce
[55]	ion-adsorption rare earth ore	La, Nd, Y, Pr, Ce, Sm, Eu, Cd, Tb, Dy, Ho, Er, Tm, Yb	719.2 ppm	*Aspergillus niger* *Yarrowia lipolytica*	48%–60% 40%–55%

However, the biorecovery rate of monazite ores is extremely low (<10%) so far compared to that of chemical leaching [38]. It demonstrates that the bioleaching approach is not competitive for processing monazite with high REE contents. Nevertheless, monazite is a main occurrence phase of REEs, so investigating the bioleaching of monazite will provide theoretical foundations for the bioleaching of other REE resources containing monazite, such as phosphogypsum and red mud.

2.2. Others

Bastnaesite is a kind of fluorocarbonate mineral, and the main light rare earth (Ce and La) resource. Typically, REEs are extracted from bastnaesite via alkaline/acid roasting and leaching at high temperatures [56,57]. Bioleaching approaches are rarely applied. In one study, four actinobacteria were isolated from REE mines and the surrounding soil, and utilized for the bioleaching of bastnaesite-bearing rock, which was mainly composed of quartz, barite, bastnaesite, and aegirine [53]. After incubation at room temperature and a 0.5% pulp density for 20 days, the most efficient strain, *Streptomyces* sp., leached only 0.08% of REEs (548 μg/L) from bastnaesite-bearing rock, showing poor efficiency. Possible reasons for the inefficiency are the precipitation of REE minerals, resorption of REE ions to cells, and an inadequate nutrient supply. High-performance liquid chromatography (HPLC) and a chrome azurol sulfonate (CAS) assay detected organic acids (lactic, oxalic,

and pyruvic acids) and siderophores in the leachate, which contributed to the solubilization of REEs via complexation.

Another type of primary REE resource is ion-adsorption rare earth ore (IRE-ore), which is the main heavy REE reserve around the world. There is quartz, feldspar and kaolinite in IRE-ore, and REEs are mainly adsorbed on the surface of kaolinite. Therefore, REEs are commonly extracted by the ion-exchange method with ammonium sulfate [58]. As for bioleaching, *Aspergillus* sp. and *Bacillus* sp. showed potential for bioleaching ion-adsorption deposits [54] but with lower efficiency (~70%) than that of salt leaching (~80%). Compared to salt leaching, bioleaching was also more time-consuming and released more impurities, such as Si and Fe. These issues need to be addressed to apply the technology in practice. However, bioleaching has a higher heavy-to-light REE ratio compared to salt leaching because the organic acids (gluconic acid, citric acid, oxalic acid) produced by the cells have stronger complexation for HREEs than LREEs. This is advantageous, as HREEs are more valuable. In 2022, Meng et al. reported that both *A. niger* and *Yarrowia lipolytica* could recover REEs from IRE-ore at 30 °C and a 10% pulp density, with a similar leaching rate (~50%) [55]. Citrate is the main metabolite of the two microbial species, thus ammonium citrate $(NH_4)_3Cit$ and citric acid obtained from the fermentation broth were used to leach REEs from IRE-ore to explore the bioleaching mechanism. The authors found that 3.3 mmol/L of $(NH_4)_3Cit$ leached 90% of the REEs from IRE-ore, which was higher than the leaching efficiency achieved by citric acid or $(NH_4)_2SO_4$ at the same concentration. The results suggest that complexation and ion-exchange reactions synergistically lead to the release of REEs. In addition, since REEs are mainly adsorbed on the surface of kaolinite, the leaching process did not alter the mineral phase of IRE-ore. Overall, the study provides a clean and efficient approach to extracting REEs from IRE-ore.

3. Phosphogypsum

REEs often occur as phosphates. Phosphogypsum ($CaSO_4 \cdot 2H_2O$) is generated as acidic waste during phosphoric acid production from apatite with REO (rare earth oxide) contents of 100~2000 ppm [59]. Approximately 4.4–4.5 tons of phosphogypsum are produced per ton of P_2O_5. The primary components of phosphogypsum are Ca, S, as well as Fe, P, and Al (Figure 1B) [32]. Gypsum is the main (70%) REE-bearing phase, while some REEs also occur in monazite and apatite [46]. Inorganic acids release 80%–90% of REEs from phosphogypsum, and organic acids, especially citric acid, can solubilize 60%–80% of REEs [60,61]. The performance of this bioleaching approach is comparable to organic acids and even inorganic acids, involving bacteria *Gluconobacter oxydans*, *At. thiooxidans,* and *Alicyclobacillus tolerans*.

Antonick et al. reported that bio-lixiviant obtained from a *G. oxydans* culture released REEs (Y, Ce, Nd, Sm, Eu and Yb) from synthetic phosphogypsum at 25 °C and a 2% pulp density, with an efficiency (36%–91%) higher than gluconic acid and H_3PO_4, but lower than that of H_2SO_4 [62]. A thermodynamic simulation showed that the solubility of REEs in phosphate was a function of pH, indicating that acidification is the main cause of bioleaching. Additionally, the solubility of REEs in gluconic acid is higher than that of sulfuric acid due to the complexation effect, which is consistent with experimental results. Moreover, other metabolites, except for gluconic acid, also participate in the dissolution of REEs, but remain unknown. The results indicate the high potential of *G. oxydans* for applications in phosphogypsum bioleaching, but the interaction mechanism between the cells and phosphogypsum needs to be investigated further.

Autotrophic sulfur-oxidizing microorganisms have been found to effectively extract REEs from phosphogypsum (Table 2). Totally 60.5% REEs (La, Ce, Nd, Pr) were extracted from phosphogypsum by sulfuric acid producer *At. thiooxidans* at 30 °C and 2% pulp density after 20 days [20]. In particular, the two-step and spent-medium bioleaching approaches yielded higher REE recovery rates than the one-step approach, meaning that only the sulfuric acid produced by bacteria is responsible for REE extraction, and cells or other metabolites play a negligible role in the bioleaching process (Figure 3B). This finding

is very different from that of other studies [22,26]. Probably, the adsorption and absorption of *At. thiooxidans* cells to REEs decreased the content of REE ions in the leaching solution. In addition, the sulfur-oxidizing bacteria *A. tolerans* was reported to extract REEs from phosphorus-containing wastes [63], and performed better than *A. niger* and *Methyloversatilis thermotolerans*, demonstrating the superiority of sulfur-oxidizing bacteria. In another study, a mixed culture of sulfide-oxidizing bacteria (e.g., *Acidithiobacillus*, *Leptospirillum*, *Sulfobacillus*) leached 70% of REEs from phosphogypsum in 14 days [64], and a technological scheme of bioleaching was developed for practical applications.

Table 2. A summary of studies on the bioleaching of rare earth elements (REEs) from secondary resources, including phosphogypsum, red mud, and coal fly ash. The number indicates the wight mean or a range of listed REEs unless otherwise stated. NA, unavailable in publication. * Suspected data.

Publications	REE Resources	Main REEs	REE Content	Microbial Species	Recovery Rate
[62]	synthetic phosphogypsum	Y, Ce Nd, Sm, Eu, Yb	1%	*Gluconobacter oxydans*	36.7%–91.2%
[64]	phosphogypsum	Y	1.3%	*sulfide-oxidizing bacteria*	70% Y
[20]	phosphogypsum	La, Ce, Nd, Pr, Y, Sm, Eu, Gd, Dy, Ho	0.61%	*Acidithiobacillus thiooxidans*	60.5%
[63]	phosphorus-containing wastes	La, Ce, Nd	NA	*Alicyclobacillus tolerans*	NA
[65]	phosphate ore	Y, Ce, Pr, La, Nd, Gd, Er, Dy	826 ppm	*Acidothiobacillus ferrooxidans*	81%
	phosphate ore		826 ppm	*Aspergillus niger*	65%
	phosphate ore tailing		304 ppm	*Acidothiobacillus ferrooxidans*	48%
	phosphate ore tailing		304 ppm	*Aspergillus niger*	38%
[66]	phosphate rock	Y, Ce, La, Nd	7.1%	*Acidothiobacillus ferrooxidans*	27.9%–37.0%
[67]	coal ash	Ce, La, Nd, Y	240 ppm	*sulfur oxidizing microbial communities*	50%–60%
[68]	coal fly ash	Ce, Y, La, Nd, Sc	134 ppm	*Candida bombicola*	27.3%–67.7%
				Phanerochaete chrysosporium	21.8%–50.6%
				Cryptococcus curvatus	19.5%–56.1%
[22]	coal fly ash	Y, La, Ce	642.76 ng/L *	*Acidithiobacillus thiooxidans*	38.3%–87.1%
	pretreatd coal fly ash				70.0%–97.6%
[69]	coal waste	Ce, La, Nd, Y, Sc	200 ppm	*Acidithiobacillus ferrooxidans*	40%–60%
[26]	red mud	Ce, La, Nd, Sc, Y	2689 ppm	*Penicillium tricolor*	30%–80%
[70]	red mud	La, Sc, Eu, Yb	712 ppm	*Aspergillus niger*	30%–60%
[71]	red mud	La, Ce, Nd, Y, Sc	2600 ppm	*Acetobacter* sp.	52%–61%
[72]	red mud	Ce, La, Nd, Sc	409 ppm	*Aspergillus niger*	38% Sc
[33]	red mud	Ce, Gd, Y, Sc	800 ppm	*Acidianus manzaensis*	78.6%–86.8%
[73]	Indian red mud	Ce, La, Nd, Sc, Y	312 ppm	*Gluconobacter oxydans*	70%–80%
	German red mud	Ce, La, Nd, Sc, Y	573 ppm	*Gluconobacter oxydans*	20%–90%
[74]	red mud	Ce, La, Y	NA	*Penicillium chrysogenum*	79% Y, 28% La, 28% Ce
[75]	red mud	Sc	104 ppm	*Acetobacter tropicalis*	42% Sc

In summary, sulfur-oxidizing bacteria are suitable for phosphogypsum bioleaching, probably because they have adapted to the environment of phosphogypsum, which is acidic, oligotrophic, and contains heavy metals. In addition, numerous other microorganisms survive and thrive in this environment. Researchers found that the dominant bacterial genera that inhabited the phosphogypsum pile were *Arthrobacter* (13.25%), *Paracoccus* (12.32%), *Pseudomonas* (6.7%) and *Staphylococcus* (3.63%) [76]. In another study, *Acidiphilium*, *Pseudomonas*, *Leptosprillum*, *Acidithrix*, and *Acidithiobacillus* were detected in leachate released from phosphogypsum stacks [77]. These native microbes possess the ability to tolerate the harsh environments around phosphogypsum, and thus show high potential for extracting REEs from phosphogypsum. For instance, *Bacillus megaterium* isolated from the soil near phosphogypsum exhibited the ability to extract heavy metals from phosphogypsum [78], suggesting its possible application in REE solubilization.

In addition, bioleaching approach has been employed to process phosphate ores (besides monazite) containing REEs. It is reported that *At. ferrooxidans* and *A. niger* could recover REEs from both phosphate ore concentrate and phosphate ore tailings [65]. After three days of incubation, *At. ferrooxidans* showed a higher leaching rate than *A. niger*, probably due to the lower pH induced by *At. ferrooxidans*. Results also showed that the bioleaching efficiency of REEs from phosphate ore tailings is lower than that from the concentrate, illustrating that REEs in phosphate concentrate (mainly fluorapatite) can be bioleached more easily and that the tailings contain components (clays) that are resistant to bioerosion. In another study, *At. ferrooxidans* extracted 28.46% of REEs from phosphate rock at a 1% pulp density after six days, which is significantly higher than chemical acid leaching (pH 2) [66]. Furthermore, the bioleaching mechanism was explored by XRD, SEM and FT-IR analyses, and results indicated that bacterial contact, Fe^{2+} oxidation, and extracellular polymeric substances contributed to the bioleaching process. The phosphate rock primarily consists of apatite and dolomite, in which REEs exist in an isomorphic form. After bioleaching, the content of apatite and dolomite decreased, and jarosite was formed in the residue which hinder the further dissolution of phosphate rock. Overall, *At. ferrooxidans* can be applied for the bioleaching of phosphate ores, but the efficiency depends on the composition and structure of the phosphate ores.

4. Red Mud

Red mud, or bauxite residue, is an alkaline saline byproduct of Al production from bauxite. Approximately 1–1.8 tons of red mud are generated per ton of aluminum oxide produced, which pollutes land and groundwater, and thus endangers both ecosystems and human health [79]. REEs are enriched in residue during the Al extraction process, reaching up to 1000 ppm in content [80]. Red mud has a small particle size, high pH, and complex composition, mainly containing Fe_2O_3, Al_2O_3, SiO_2, TiO_2, CaO, and Na_2O (Figure 1C) [75,81], depending on the composition of the parent bauxite ore. For example, cancrinite, diaspore, katoite, muscovire, kaolinite, and hematite were detected by XRD (X-ray diffraction) in a red mud sample [33], while gibbsite and calcite were detected in another red mud sample [80]. In red mud, REEs mainly exist in the form of monazite, xenotime, and synchysite. Conventionally, techniques such as physical beneficiation, alkali roasting, sulfation, and acid leaching (sulfuric, nitric, and hydrochloric acid) are adopted for REE extraction from red mud [82]. For example, HCl leached out 70%–80% of REEs from red mud at room temperature [80], and citric acid showed a comparable leaching rate at 90 °C, but with higher selectivity.

Various microorganisms have been shown to effectively solubilize REEs from red mud to date [83], including *Acetobacter tropicalis*, *Penicillium tricolor*, *Gluconobacter oxydans* and *Acidianus manzaensis*. Leaching efficiency varies greatly among different microbes. Of these, heterotrophic *A. tropicalis* leached 42% of Sc from bauxite residue [75] with glucose as an energy source at 35 °C after 20 days. Acetic, oxalic, and citric acids played a role in the process. The main mineralogical phase, hematite, remained unchanged after bioleaching. In another case, *Acetobacter* sp. extracted Lu, Y, and Sc from red mud with a recovery

rate of 52%~61% at 30 °C after 20 days [71]. The organic acids (e.g., acetic, malic, and oxalic acid) excreted by the bacteria determined the bioleaching efficiency to a large extent. Oxaloacetase is believed to be the key enzyme responsible for the production of organic acids, but it requires experimental validation. The bacteria can tolerate high pulp density (10%) and even produce more organic acids with an increase in pulp density. This may be explained by the fact that bacteria need to excrete organic acids to keep the surrounding pH constant in order to survive, as alkaline red mud increases the pH of the leaching system. During bioleaching, calcite, hematite, and gibbsite were easily dissolved, while perovskite was not. Weddellite appeared in the red mud after bioleaching.

Fungus *Penicillium tricolor* RM-10 can leach REEs from red mud, with oxalic and citric acids as the main lixiviants [26]. The total REE content in red mud is over 0.26%, and is enriched in La, Ce, Sc, Y and Nd. The leaching rate of REEs ranged from 30% to 80% at 30 °C and a 2% pulp density. The researchers also compared three different leaching modes, i.e., one-step, two-step, and spent-medium bioleaching. They found that one-step bioleaching exhibited the highest leaching rate, supporting the critical role of cell contact during bioleaching. Interestingly, heavy REEs demonstrated a higher recovery rate than light REEs, which is another advantage of bioleaching. In another study, *Penicillium chrysogenum* leached Y (79%), La (28%), and Ce (28%) from red mud at 30 °C and a 3% pulp density in 14 days, with glucose as a substrate [74]. When the substrate is cheap molasses and saw dust, the REEs leaching rates are lower, showing that these substrates are difficult for the cells to utilize, and thus limit microbial bioleaching performance. Mixed organic acids leaching achieved a considerable REE recovery rate, but this was lower than spent-medium leaching, suggesting that organic acids are the main factors responsible for REE solubilization; however, there are other unknown factors. The authors also noted that higher leaching efficiency was achieved under the one-step bioleaching mode than the two-step and spent-medium bioleaching modes. The result is consistent with other studies, demonstrating the significance of cell contact in the bioleaching process [26].

Compared to microbes secreting organic acids, the inorganic acid producer *Acidianus manzaensis* is capable of extracting rare earths from red mud more efficiently [33]. Archaea *Acidianus manzaensis* is an Fe/S oxidizer which oxidizes pyrite to generate Fe^{3+} and H_2SO_4 (Figure 2). It can also reduce Fe^{3+} to Fe^{2+} under anaerobic conditions with S^0 as an electron donor. The red mud used in the study was composed of cancrinite, katoite, diaspore, muscovite, kaolinite, and hematite (Figure 3C). In aerobic bioleaching, more than 80% of REEs (Ce, Gd, Y and Sc) were extracted from red mud with pyrite as an energy source at 65 °C and a 0.6% pulp density. Subsequently, the leaching residue, mainly consisting of jarosite, hematite, and diaspore, was subjected to anaerobic bioleaching with the addition of elemental sulfur. As a result, most (74.9%–93.7%) of the residual REEs were released by *Acidianus manzaensis*. The final residue only contained hematite and diaspore. Anaerobic bioleaching is scarcely applied in REE extraction processes, but the study shows its high efficiency; thus, it deserves wide application and in-depth research.

The mineralogical characteristics of red mud also significantly affect bioleaching efficiency. According to a report, *G. oxydans* leached ~70% REEs from Indian red mud and only 40% REEs from German red mud at 37 °C and a 10% pulp density after 20 days [73]. The variation in the leaching rate is related to the chemical composition and structure of red mud. The Indian red mud had a higher iron content than German red mud. Gibbsite is the major phase and the main REE occurrences form in Indian red mud, while boehmite, gibbsite, hematite, and anatase are the dominant phases and the REEs were locked in boehmite in the German red mud. Gibbsite is probably more easily decomposed by *G. oxydans* than boehmite. Notably, the adapted *G. oxydans* achieved a higher REE recovery rate compared to the non-adapted culture, showing that red mud causes stress in the cells and that pre-adaptation is beneficial for REE extraction. The acidification resulting from the gluconic acid secreted by cells is a mechanism for bioleaching. A decrease in redox potential was also observed, but its relationship with REEs solubilization is unknown.

Despite the diverse composition and structure of red mud, *Acidianus manzaensis* appears to be the most efficient microbe for REEs bioleaching, based on the studies above (Table 2). However, the archaea are acidophiles while red mud is alkaline, so the pH of red mud must be adjusted to be appropriate pH (pH 1.8) for cell growth before bioleaching, which increases the cost. Microorganisms suitable for the processing of red mud should survive under challenging conditions such as high-pH, high-salinity, and high-metal-content conditions, as well as in conditions where there is a shortage of nutrients. Diverse microorganisms inhabit red mud after long-time storage, including Firmicutes, Actinobacteria, Chloroflexi, and Proteobacteria [84]. These indigenous alkaliphiles, especially the early colonizers, serve as promising microbial resources for bioleaching [85,86]. For example, *P. tricolor* [26] and *Acetobacter* sp. [71] were isolated from red mud and are able to leach REEs from red mud. Although their bioleaching performance is not yet satisfactory, this demonstrates the feasibility of using indigenous microbes to process red mud, and more indigenous microbes deserve to be exploited in the future.

5. Coal-Related Resources

Coal-related materials, such as coal gangue and coal fly ash (CFA), are byproducts of coal production. They are also promising REE resources, with REE contents ranging from 100 ppm to 1000 ppm [61,87]. Coal fly ash usually contains higher concentrations of REEs than coal gangue, because REEs are enriched during the calcination of coal. An economic analysis showed that the value of REEs in one ton of coal ash is around $250 [88]. The chemical composition of CFA (Figure 1D) mainly contains Si, Al, Fe and Ca, and silicate and aluminosilicate forms are the main occurrence modes of REEs in coal fly ash [89]. In other words, the REEs are wrapped in an Si–O–Al framework resistant to acid corrosion, which causes difficulties in REE extraction processes. Therefore, direct acid leaching usually exhibits a low leaching rate. To date, alkaline pretreatment or thermal treatment combined with acid leaching has been found to be an efficient approach (70%~80%) for REE extraction [7,90]. In addition, physical methods are utilized to enrich REEs, as REEs are enriched in fine-particle-sized, middle-density, and non-magnetic fractions [6].

Organic acids leach REEs from coal ash by complexation and chelation. For example, 5% tartaric acid leached the most (62%) REEs from coal ash, followed by lactic acid, citric acid, malonic acid, and succinic acid [91]. In contrast, only 5% Al, 2% Si, and 6% Fe were leached by tartaric acid, showing its high selectivity towards REEs; the different complexation ability of metals with tartaric acids may be a reason for this. Similarly, organosulphonic acids leached 70% of REEs but only 10% of other metals from coal ash [60]. These findings provide clues for the screening of microorganisms capable of bioleaching, as microbes capable of producing these target organic acids are likely to be effective in REE extraction.

Compared to physical and chemical extraction methods, bioleaching is still in its primary stage. There have been limited studies on REE bioleaching from CFA, in which the involved microorganisms are *Candida bombicola*, *At. ferrooxidans* and *At. thiooxidans*. As early as 2015, Muravyov et al. reported that sulfur-oxidizing microbial communities released 50%–60% of REEs (Sc, Y, La) from coal ash at 45 °C after 10 days of leaching [67], which was higher than that released at 28 °C or 40 °C. Sulfuric acid produced by microbes are the main reason for REE solubilization, and high temperatures enhance the chemical reaction. High temperatures also affect the composition of microbial community, making thermophilic *A. caldus* and some *Sulfobacillus* species more abundant. The study demonstrates the potential of sulfur-oxidizing microbes for the processing of coal ash. Later in 2019, *C. bombicola*, *Phanerochaete chrysosporium* and *Cryptococcus curvatus* were tested to leach REEs from coal fly ash. Among them, the heterotrophic fungus *C. bombicola* performed the best, leaching 27.3%~67.7% of REEs (e.g., Yb, Er, Sc, Y) from coal fly ash at 28 °C in 6 h [68]. It is quite unusual that one-step and spent-medium approaches were combined in this study, as the microbes were first cultured with CFA for three days and then a fermentation broth was used to leach the fresh CFA. The pH decreased during the REE leaching process, so the

authors deduced that sophorolipids and organic acids play important roles in the process; however, experimental verification is lacking. The chemical structure of the CFA was not provided, and the bioleaching mechanism needs to be further explored.

Physicochemical pretreatment is combined with bioleaching to improve REE recovery. For example, coal fly ash was roasted with Na_2CO_3 at 850 °C and then subjected to bioleaching. As a result, 63.4% Ce was extracted by *At. ferrooxidans* [21]. Fe^{3+} and H_2SO_4 generated from pyrite oxidation play a role in the bioleaching of coal fly ash. The Coal fly ash was mainly composed of $Al_5Si_2O_{13}$ and Al_2SiO_5, which transformed into $NaAlSiO_4$ and Na_2SiO_3 after roasting. During bioleaching, the $NaAlSiO_4$ converted into pyrophyllite ($Al_2[Si_4O_{10}](OH)_2$) and SiO_2 gel, releasing REEs and other metals. It is noteworthy that alkaline roasting enhances the dissolution of REEs significantly, because it can break Si–O–Al and Si–O–Si bonds. Similarly, a hydrothermal alkali treatment process and *At. thiooxidans* bioleaching were integrated to extract metals from coal fly ash [22]. As a result, 70.0~97.6% of REEs were extracted. Notably, the Ce biorecovery rate from pure coal fly ash was 87.1%, which was lower than that of the pretreated coal fly ash, but higher than that observed in other studies [21,68]. One-step leaching had a slightly higher REE recovery rate than two-step bioleaching, showing that the sulfuric acid produced by *At. thiooxidans* from elemental sulfur S^0 oxidation played a major role in the bioleaching process, and that cell contact contributed little to REE solubilization (Figure 3D). Researchers also found that the hydrothermal alkali treatment decreased the particle size of coal fly ash, and thus increased its specific surface area. Meanwhile, the adsorption of CFA to cells was also enhanced by the hydrothermal alkali treatment, which is conducive to bioleaching.

In summary, *At. thiooxidans* is the most efficient microbial species for the processing of coal fly ash among the studies mentioned above, and physicochemical pretreatment can enhance the bioleaching of REEs (Table 2). In fact, it is difficult to compare among studies, because the CFA used in each study may be different, which greatly affects the leachability of REEs. For instance, the CFA generated from a circulating fluidized bed contains more organic/sulfide and acid-soluble fractions and a lower aluminosilicate fraction than that from a pulverized coal furnace [92]. Hence, the REEs in CFA from circulating fluidized beds may be recovered more easily by acid leaching. Overall, the mineralogical characteristics of CFA are crucial for making meaningful comparisons among studies and are also critical for understanding the bioleaching mechanism; however, these are often overlooked in current studies.

Coal gangue's main components are silica oxide and aluminum oxide, followed by S and Fe. Usually, Si and Al occur in the form of kaolinite, quartz, and boehmite in coal gangue [13,93]. The contents of REEs in coal gangue are around 200 ppm. Sequential chemical extraction tests revealed that REEs are present mainly in insoluble forms (80%), and a small amount of REEs occurred in organic matter-bound and metal oxide-bound forms [94]. Between 70%–80% of REEs can be extracted via calcination pretreatment and acid leaching [13]. However, there has only been one report on the bioleaching of REEs from coal gangue to date. Autotrophic *At. ferrooxidans* extracted 13%~14% of REEs from coal waste (gangue) with the addition of pyrite at 35 °C [69]. Four months of column leaching resulted in a higher REEs leaching rate of 40%–60%. Finally, REEs in a leaching solution were recovered through oxalic acid precipitation. The results demonstrate the feasibility of biologically recovering REEs from coal gangue for the first time, but the bioleaching mechanisms remain to be investigated.

Overall, autotrophic ion- and sulfur-oxidizing microorganisms are suitable for the processing of coal-related resources. Pyrite is discarded during the coal purification process, which may pollute the environment. Using pyrite as a substrate, bioleaching not only recovered REEs, but also recycled waste and eliminated the generation of acid mine drainage [95,96], which is hazardous to the environment. In addition, given that the main components in coal-related resources are aluminosilicate and silicate, which are also the main occurrence forms of REEs, silicate bacteria are likely to be able to release REEs from coal-related resources. Silicate bacteria can break the structure of silicate min-

erals via organic acids and extracellular polymers, and thus release Si. For example, *Bacillus amyloliquefaciens* was able to remove Si from coal fly ash, as 306.26 mg/L of Si in a leaching solution was obtained [97]. Furthermore, the broken silicate structure is beneficial to metal enrichment and dissolution. In one case, *Bacillus barbaricus* concentrated Al by dissolving silica in coal fly ash [98], indicating that REEs could be enriched in a similar manner. Therefore, silicate bacteria show high potential for REE recovery from coal-related resources.

6. Conclusions and Future Perspectives

Bioleaching has emerged as a promising approach to extract REEs from various resources, thus promoting a circular economy. Publications on the bioleaching of REEs from monazite ores, phosphogypsum, red mud, and coal fly ash were reviewed here. These REE resources have different compositions and structures, and suitable bioleaching microbes for their recovery are also different. First, *Paecilomyces* sp. leached the most REEs from monazite, but the recovery rate was very low compared to secondary resources, supporting the understanding that bioleaching approaches are more competitive for the processing of secondary resources with low amounts of REEs. Second, acidophilic sulfur oxidizers are suitable for the processing of acidic phosphogypsum. Third, acidophilic *Acidianus manzaensis* is the most efficient microbe for red mud bioleaching to date, although its tolerance to alkaline red mud is a problem. Lastly, *At. thiooxidans* could be used to recover a considerable amount of REEs from coal fly ash. However, tremendous challenges still exist for the application of bioleaching technology on a large scale (Table 3). The low efficiency of bioleaching and the high cost of cell cultures are problems that need to be solved. Most importantly, the interaction mechanism between microbial cells and REE minerals is still unclear.

Table 3. Current problems that limit the large-scale application of bioleaching technology, and tentative solutions.

Problems	Solutions
Interaction mechanism	Reveal mineral composition and structure, especially occurrence mode of rare earth elements
	Microbial genetic regulation mechanism
	Pure minerals and pure metabolites experiments
Low efficiency	Combination with physicochemical approaches
	Mutagenesis and genetic engineering
	Mixed culture
Toxicity of pulp and metals	Acclimated strain
	Screen strains with high resistance
High cost of energy source for cell growth	Industrial and agriculture wastes
	Autotrophic microbes

The composition and structure of phosphogypsum, red mud, and coal fly ash are complex and even sample-dependent. The cellular component and metabolism regulation of microbes are also complicated. The bioleaching of REEs from these secondary resources requires interactions between two complex systems. Therefore, it is challenging to clarify the underlying molecular mechanism. To address this issue, on the one hand, more efforts for mineralogical characterization using advanced techniques are required [99], especially to elucidate the occurrence modes of REEs, and the chemical bonds formed between REEs and other elements, which are the key factors determining the leachability of REEs. Mineralogical phase transformation during bioleaching also needs to be investigated. On the other hand, the microbial genetic regulation mechanisms during bioleaching need to be better understood, as the metabolism of cells is regulated by genes. Advanced technologies, such as transcriptomic sequencing and genetic engineering, can be utilized. In addition, pure minerals and single metabolites of cells should be used to conduct

experiments in order to identify the key metabolites of cells and their functions. By implementing these approaches, a better understanding of complex bioleaching systems can be achieved, ultimately leading to the development of more efficient and effective strategies for REE extraction.

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