Microbial communities, processes and functions in acid mine drainage ecosystems

Lin-xing Chen[1], Li-nan Huang[1], Celia Méndez-García[2], Jia-liang Kuang[1], Zheng-shuang Hua[1], Jun Liu[1] and Wen-sheng Shu[1]

CrossMark

Acid mine drainage (AMD) is generated from the oxidative dissolution of metal sulfides when water and oxygen are available largely due to human mining activities. This process can be accelerated by indigenous microorganisms. In the last several decades, culture-dependent researches have uncovered and validated the roles of AMD microorganisms in metal sulfides oxidation and acid generation processes, and culture-independent studies have largely revealed the diversity and metabolic potentials and activities of AMD communities, leading towards a full understanding of the microbial diversity, functions and interactions in AMD ecosystems. This review describes the diversity of microorganisms and their functions in AMD ecosystems, and discusses their biotechnological applications in biomining and AMD bioremediation according to their capabilities.

Addresses
[1] State Key Laboratory of Biocontrol, Guangdong Key Laboratory of Plant Resources, College of Ecology and Evolution, Sun Yat-Sen University, Guangzhou 510275, PR China
[2] Carl R. Woese Institute for Genomic Biology, University of Illinois at Urbana-Champaign, Urbana, USA

Corresponding author: Shu, Wen-sheng (shuws@mail.sysu.edu.cn)

Introduction

Acid mine drainage (AMD) is characterized by low pH and high concentrations of metals and sulfate, representing an extreme environment to life [1] as well as a major environmental challenge worldwide [2**]. AMD ecosystems include distinct environments of AMD solutions, sediments, and biofilms [3**], providing multiple niches for AMD microorganisms. The microorganisms thriving in AMD environments have evolved with distinct mechanisms to the extreme conditions [4**,5], by which they can dramatically accelerate the acid generation process and therefore play significant roles in material and energy flows of the whole ecosystem [3**,6]. Due to the dominance by a few taxa more than a lack of complexity [7*,8] and its remarkably simple geochemical features [9**], AMD environments have been established as model systems for quantitative analyses of microbial ecology and community function [3**,4**], and as ideal targets for biogeochemical studies of iron and sulfur cycles [10–12]. Moreover, microorganisms from AMD environments are the major contributors in biomining of low-grade ores [13], and have significant potentials in AMD bioremediation [2**]. This review summarizes the taxonomic diversity and metabolic functions of AMD microorganisms and their biotechnological applications in biomining and AMD bioremediation.

The diversity of AMD microorganisms

During the last several decades, isolation and cultivation methods [4**,9**], and 16S rRNA gene and meta-omics based molecular analyses [3**,7*,14*], have drastically enlarged our knowledge of microbial diversity in AMD ecosystems (Figures 1 and 2).

Proteobacteria, *Nitrospira*, *Actinobacteria*, *Firmicutes*, *Acidobacteria*, *Aquificae* and Candidate division TM7 represent the primary bacterial lineages detected (Figure 1). The most extensively studied taxa are iron- and/or sulfur-oxidizing *Acidithiobacillus* spp. (*Acidithiobacillia*) [15–17], and iron-oxidizing *Leptospirillum* spp. (*Nitrospira*) [18–20]. The lesser known '*Ferrovum*' spp. (*Betaproteobacteria*), which have been widely detected as dominant members and suggested as major iron-oxidizing populations in less-restrictive pH conditions [7*,21,22,23**], have recently been obtained in pure culture [24]. The majority members in these three genera are validated as autotrophs (Figure 2), fixing carbon from open environments. Multiple heterotrophic acidophiles co-occurring with these carbon-fixers may drive the carbon cycling by consuming organic carbons, including members from *Alphaproteobacteria* (*Acidiphilium*, *Acidocella*, *Acidicaldus*, *Acidomonas*, *Acidisphaera*) [25–27], *Gammaproteobacteria* (*Acidibacter ferrireducens* and *Metallibacterium scheffleri*) [28,29], *Actinobacteria* (*Acidithrix ferrooxidans*, *Ferrimicrobium acidiphilum* and *Acidimicrobium ferrooxidans*) [6,30], and *Acidobacteria* [31,32]. Additionally, *Sulfobacillus* spp. (*Firmicutes*) were detected as mixotrophs [33–35], while *Alicyclobacillus* spp.

Figure 1
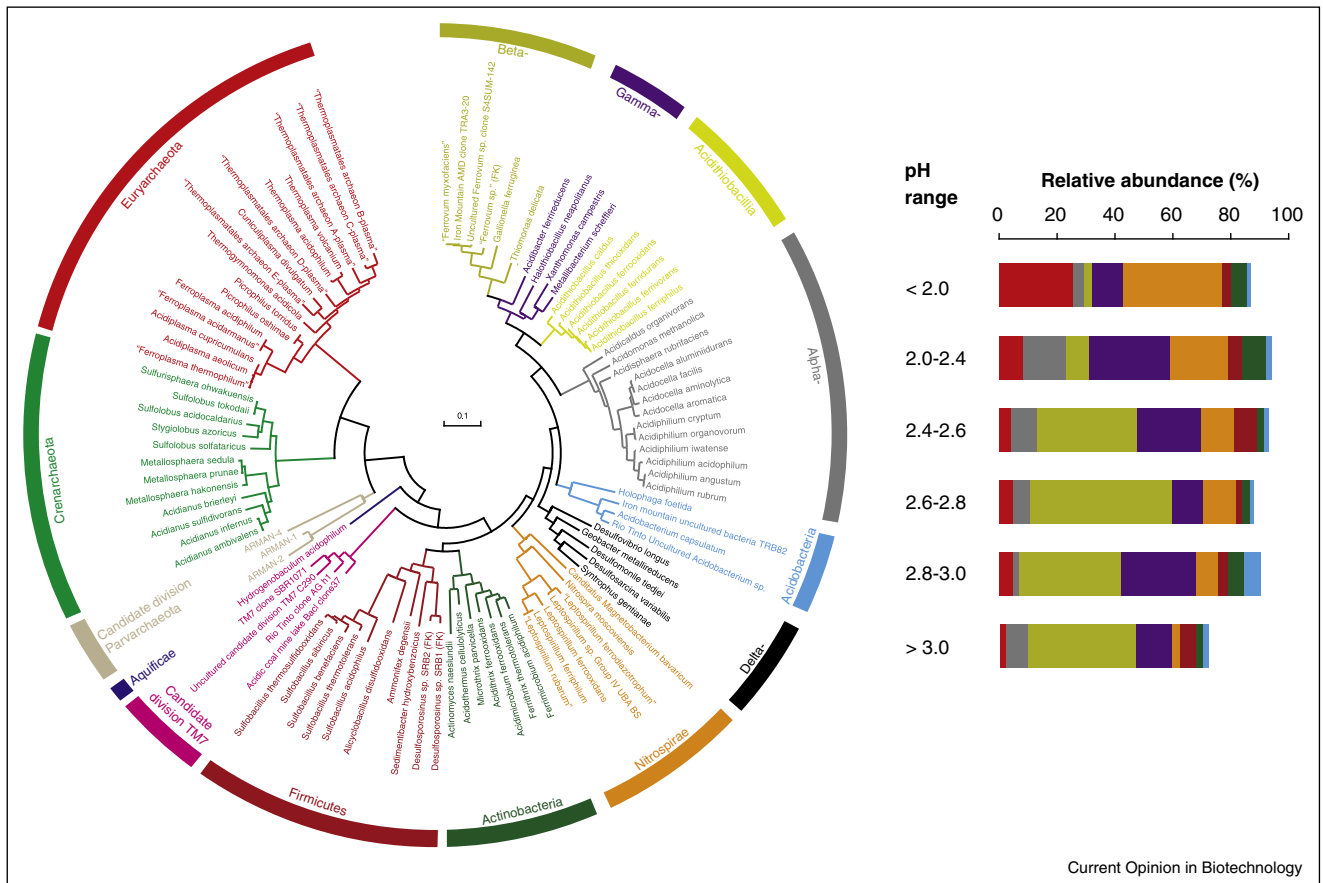
The taxonomic and phylogenetic diversity of frequently detected prokaryotic microorganisms in AMD ecosystems including environments of acid solutions, biofilms and sediments (left panel), and their distribution in AMD solutions of different pH ranges (right panel) (data from [7•]; a total of 125 AMD samples).

(*Firmicutes*) were documented as heterotrophs or chemolithoautotrophs in mine environments or AMD treatment plants [2••,36]. Some representatives of sulfate-reducing bacteria (SRB) within *Gammaproteobacteria*, *Deltaproteobacteria* and *Firmicutes* have also been detected, including members from the genera of *Thermodesulfobium*, *Syntrophobacter*, *Desulfurella*, *Desulfomonile*, *Desulfovibrio* and *Desulfosporosinus* [37]. Other less frequently detected bacterial taxa include *Gallionella ferruginea* and the putative heterotrophic growers *Thiomonas* spp. [38–41].

Archaea, including the phyla of *Euryarchaeota*, *Crenarchaeota* and Candidate division Parvarchaeota, typically constitute a minor fraction of AMD communities [3••,4••,9••,14•], but have been found dominant in specific mining environments [42–44]. In the *Euryarchaeota*, members from the iron-oxidizing and cell wall-lacking genus *Ferroplasma* are the most widely detected [42–45,46••,47–50]. Importantly, *Ferroplasma* spp. have been found to dominate the later stages of the acidification processes of mine wastes [43,44], indicating their critical

roles in AMD generation. Another cell wall-lacking genus *Acidiplasma* was also isolated and detected with iron-oxidation and reduction activities [51]. Besides, multiple *Thermoplasmatales* archaeon genomes (alphabet plasmas) have been reconstructed from metagenomic datasets, and one of those (G-plasma) was cultured as *Cuniculiplasma divulgatum* to represent a new family *Cuniculiplasmataceae* [52]. Within the *Crenarchaeota*, the iron and/or sulfur oxidizers from genera *Acidianus*, *Metallosphaera*, *Stygiolobus*, *Sulfolobus* and *Sulfurisphaera* have been mostly identified as extreme thermophiles inhabiting AMD ecosystems [9••]. The poorly studied archaeal group ARMAN (Archaeal Richmond Mine Acidophilic Nanoorganisms) in Candidate division Parvarchaeota was firstly discovered in the acidophilic biofilms from the Richmond Mine at Iron Mountain, California [53,54]. Closely related gene sequences have been recovered in other AMD environments [42,55], however their ecological roles have not been clearly revealed, due to their relatively low activities [23••,42,54]. The filterable ARMAN spp. were initially speculated to be aerobic based on proteomic data