



## Microbes in mercury-enriched geothermal springs in western North America



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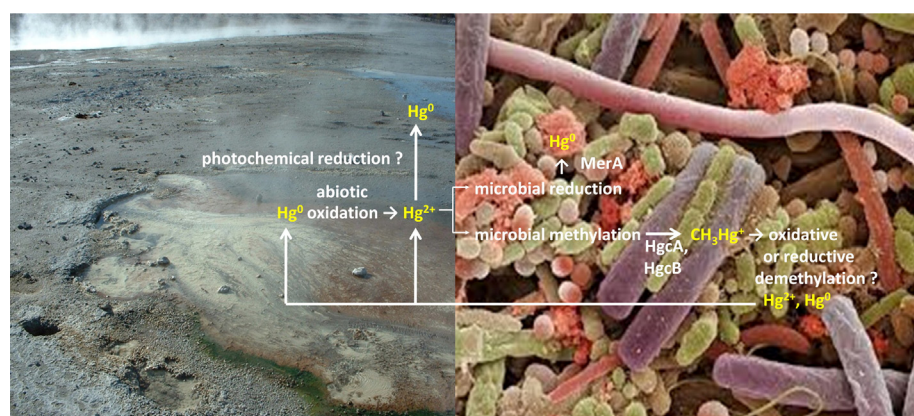
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### HIGHLIGHTS

- Of 245 prokaryotic taxa at 271 geothermal sites, 103 were in 56 sites with Hg.
- 46% of Archaea and 40% of Bacteria taxa were in those reported to contain Hg.
- Richness of Bacteria > Archaea across the Hg-containing sites with pH  $\geq$  4.5
- Homologs of Mer genes for Hg reduction at higher frequency in acidic sites
- MerA homologs in Western U.S. hot springs are most like those in 4 archaeal orders.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Because geothermal environments contain mercury (Hg) from natural sources, microorganisms that evolved in these systems have likely adapted to this element. Knowledge of the interactions between microorganisms and Hg in geothermal systems may assist in understanding the long-term evolution of microbial adaptation to Hg with relevance to other environments where Hg is introduced from anthropogenic sources. A number of microbiological studies with supporting geochemistry have been conducted in geothermal systems across western North America. Approximately 1 in 5 study sites include measurements of Hg. Of all prokaryotic taxa reported across sites with microbiological and accompanying physicochemical data, 42% have been detected at sites in which Hg was measured. Genes specifying Hg reduction and detoxification by microorganisms were detected in a number of hot springs across the region. Archaeal-like sequences, representing two crenarchaeal orders and one order each of the Euryarchaeota and Thaumarchaeota, dominated in metagenomes' MerA (the mercuric reductase protein) inventories, while bacterial homologs were mostly found in one deeply sequenced metagenome. MerA homologs were more frequently found in metagenomes of microbial communities in acidic springs than in circumneutral or high pH geothermal systems, possibly reflecting higher bioavailability of Hg under acidic conditions. MerA homologs were found in hot springs prokaryotic isolates affiliated with Bacteria and Archaea taxa. Acidic sites with high Hg concentrations contain more of Archaea than Bacteria taxa, while the reverse appears to be the case in circumneutral and high pH sites with high Hg concentrations. However,

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MerA was detected in only a small fraction of the Archaea and Bacteria taxa inhabiting sites containing Hg. Nevertheless, the presence of MerA homologs and their distribution patterns in systems, in which Hg has yet to be measured, demonstrates the potential for detoxification by Hg reduction in these geothermal systems, particularly the low pH springs that are dominated by Archaea.

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## 1. Introduction

Western North America (NA) hosts a large number of hot springs, many of which result from the tectonic processes in this part of the world. Accordingly, many are associated with the belts of recent past or present volcanic activity. Thermal springs are also found in other areas where rocks have been faulted and intensely folded in geologically recent time. Approximately 840 geothermal areas have been identified in the western contiguous United States, not counting the >10,000 geothermal features found in Yellowstone National Park, and the additional 79 identified in Alaska (Waring, 1965). Across this geothermal landscape, temperatures range from slightly above ambient to over 100 °C (Berry et al., 1980), pH ranges from 1 to 10 (Ball et al., 2008; Thompson and DeMonge, 1996) and sulfide concentrations range from <0.3 to 5.8 mM (Dodsworth and Hedlund, 2010; Kulp et al., 2008). This wide range of environmental conditions creates niches that support diverse assemblages of prokaryotic life (Spear et al., 2006). Of the environmental parameters examined to date, temperature, pH, and sulfide vs. dissolved oxygen concentrations have been shown to be the key determinants of microbial community composition in a number of these geothermal systems (Inskip et al., 2013; Miller et al., 2009; Purcell et al., 2007; Sharp et al., 2014).

Many geothermal systems also contain toxic metals, among them mercury (Hg) (Becker, 1888; Cobble, 1987; de Beaumont, 1847; Dreyer, 1940a; Dreyer, 1940b; White, 1955; White, 1957; White et al., 1963). Mercury in these systems exists in gaseous, liquid and solid forms. Subsurface hydrothermal fluids leach Hg from reservoir rock and transport it to the surface in either an aqueous or vapor phase (Fig. 1). The concentration and solubility of Hg in these phases is influenced by the amount of Hg in the rock as well as by fluid temperature and chemistry (Engle et al., 2006). Gaseous Hg typically exists as Hg<sup>0</sup> and HgS. Thermodynamic calculations indicate that aqueous ionic Hg may exist at parts per trillion concentrations, depending on conditions (Cobble, 1987; Varekamp and Buseck, 1984). Since most analyses measure only total Hg (THg) after filtration to remove suspended solids, the concentrations of the different forms of aqueous ionic Hg that exist under the various geothermal conditions are not well documented. However, it is known that sulfide and chloride concentrations and

temperature are important determinants of the forms and concentrations of aqueous ionic Hg species in these systems (Glew and Hames, 1972; Krup, 1988). The concentration of THg can be as high as 2.23 mg/L in unfiltered acidic, sulfidic hot spring water as a result of the penetration of thermal plumes of cinnabar (Simbahan et al., 2005). If Hg is transported in the fluid as Hg-S or Hg-Cl, it can precipitate as cinnabar, metacinnabar or calomel, the former being the more stable under hot springs conditions (Cobble, 1987).

Biota inhabiting geothermal springs has had to adapt to the high concentrations of Hg in many of these systems. Hot springs microorganisms in particular have had to evolve strategies to deal with the toxic effects of high Hg concentrations under the various conditions that exist in these habitats. Molecular and phylogenetic analyses clearly show that the MerA protein, whose homodimer forms the active mercuric reductase enzyme which specifies Hg detoxification among many prokaryotes, first evolved in thermophilic microbes in geothermal environments (Barkay et al., 2010) prior to its spread to broadly distributed mesophilic microbes (Boyd and Barkay, 2012). The Mer detoxification system involves reduction of the inorganic Hg to the elemental volatile form, Hg(0), an activity found in several thermophilic microbes common in geothermal springs (Barkay et al., 2010). Thus, the activities of these microorganisms as well as temperature, pressure, and composition of solution affect the behavior (volatility, redox state, solubility) of Hg which impacts its fate and its influence on other life forms in the system. Here we synthesize information on the microbiology of hot springs of western NA, the relationships between the microbiology and the physicochemical properties, including Hg, and the MerA-mediated mechanism of Hg detoxification maintained by the microorganisms in these environments.

## 2. Microbiology of terrestrial geothermal systems of western North America

Hot springs of western NA have provided much information on the constraints of temperature and pH on microbial diversity. For example, temperature and pH have been shown to exert a strong influence on the diversity and types of microbial inhabitants in these systems (Miller et al., 2009; Purcell et al., 2007; Sharp et al., 2014). Correspondingly, the types of microorganisms inhabiting acidic hot springs differ greatly from those found in circumneutral thermal features (Reysenbach et al., 2005). Neutral-alkaline springs have consistently higher microbial diversity than acid springs, and acid spring communities are distinct from those in neutral and alkaline springs regardless of temperature (Sharp et al., 2014). Alkaline environments support greater algal diversity than acidic habitats, and diversity decreases regardless of pH when heavy metal concentrations are high (Amaral-Zettler, 2013). In general, the more extreme the environmental conditions, the lower the microbial diversity. However, the influence of Hg on the microbial communities in these systems is poorly understood.

### 2.1. Description of sites

Published information on prokaryotic taxa was collected from 271 geothermal sites across western NA with known pH, temperature and sulfide concentration, hereafter referred to as sites with both microbiological and physicochemical data. Of these sites, 44 had a pH > 8.0 (high pH sites), 141 sites had a pH ≥ 4.5 ≤ 8.0, (circumneutral sites) and 86

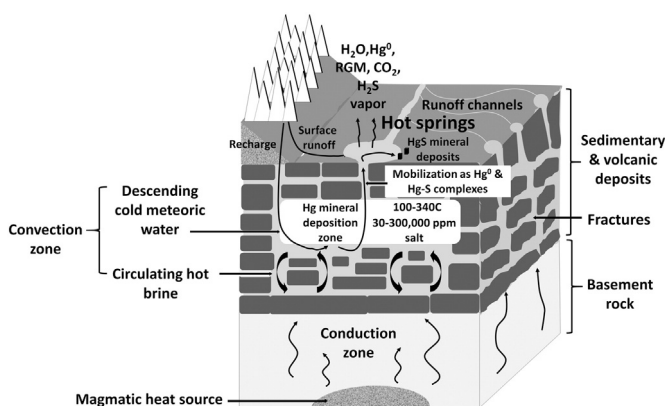


Fig. 1. Overview of mercury pathways and transformations in terrestrial geothermal systems as constructed from Sabadell and Axtmann, 1975; Varekamp and Buseck, 1984; Varekamp and Bruseck, 1986.

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