Review

Interaction between Microbes, Minerals, and Fluids in Deep-Sea Hydrothermal Systems

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Abstract: The discovery of deep-sea hydrothermal vents in the late 1970s widened the limits of life and habitability. The mixing of oxidizing seawater and reduction of hydrothermal fluids create a chemical disequilibrium that is exploited by chemosynthetic bacteria and archaea to harness energy by converting inorganic carbon into organic biomass. Due to the rich variety of chemical sources and steep physico-chemical gradients, a large array of microorganisms thrive in these extreme environments, which includes but are not restricted to chemolithoautotrophs, heterotrophs, and mixotrophs. Past research has revealed the underlying relationship of these microbial communities with the sub-surface geology and hydrothermal geochemistry. Endolithic microbial communities at the ocean floor catalyze a number of redox reactions through various metabolic activities. Hydrothermal chimneys harbor Fe-reducers, sulfur-reducers, sulfide and H_2-oxidizers, methanogens, and heterotrophs that continuously interact with the basaltic, carbonate, or ultramafic basement rocks for energy-yielding reactions. Here, we briefly review the global deep-sea hydrothermal systems, microbial diversity, and microbe–mineral interactions therein to obtain in-depth knowledge of the biogeochemistry in such a unique and geologically critical subseafloor environment.

Keywords: hydrothermal vent; deep sea; microbe–mineral interaction; biomineralization; metabolic processes

1. Introduction

It has become increasingly apparent that microbial communities are not limited to shallow near-seafloor environments but could extend into the deep subsurface. Hydrothermal vents form one such habitat, abundant in microbial communities that harbor energy through processes largely different from the surface photosynthetic biosphere. These structures are formed when superheated, mineral-rich hot water percolate cracks, fissures, and comes into contact with cold seawater. Deep hydrothermal vents are located in areas with high tectonic activity, mid-ocean ridges, and seamounts. With their first discovery in the Galapagos rift [1], it uncovered new potential habitats previously unknown to us and changed our view of life on Earth. In the complete absence of light, chemosynthesis is a process in which chemical energy is used to convert carbon dioxide into sugar, which is the predominant form for organic carbon production in this environment [2].

To date, about 600 active vent sites are known, mostly along ridge boundaries [3]. Hydrothermal vents globally occur at sea-floor spreading zones and along the spreading zones [4,5] (Figure 1), with the discovery of new vent systems being studied in detail. While during eruptions some vents produce black smokers (such as the Mid Atlantic Ridge system (MAR), temperature ~400 °C) with diverse microbial communities on the vent exteriors, others such as the Lost City Hydrothermal Field (temperature of ~90–150 °C), in contrast, are dominated by carbonates and profoundly different than black smokers in terms of their geochemistry and microbial community structures depending on the temperature [6].
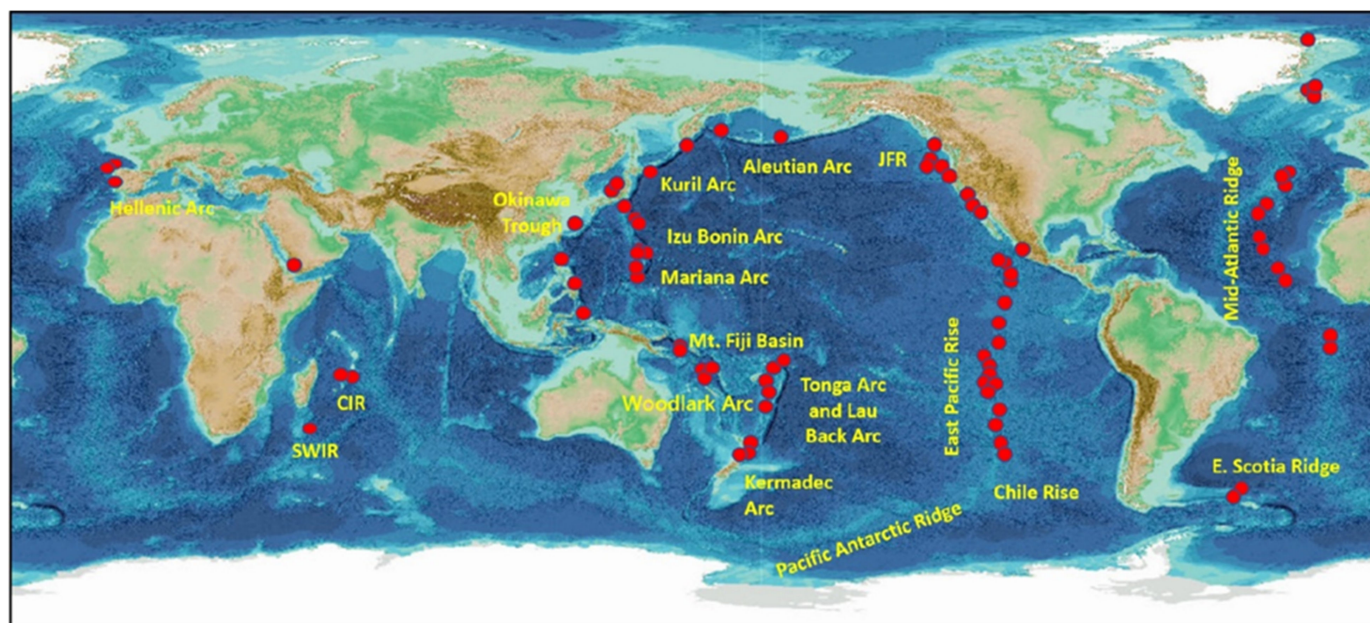
Figure 1. Global distribution of major deep-sea hydrothermal systems. CIR: Central Indian Ridge and SWIR: South West Indian Ridge.

The active vents are characterized by the presence of different rock types, such as basalts, peridotites, and felsic rocks. The vented fluids exhibit large chemical variability depending on the mineralogical differences in the underlying rocks [7]. Hydrothermal fluids may be nearly colorless and have low concentrations of chemical species of dissolved minerals, or may be white or black, characterized by high concentrations of minerals. Sulfides and other sulfur minerals are common in this environment. The vent ecosystems host a lively habitat and complex ecosystem characterized by steep temperatures and geochemical gradients [8]. These deep-sea chemosynthetic ecosystems are fueled by chemical reactions between oxidizing components in seawater (e.g., O_2 and SO_4) and reducing components originating from/beneath the sea-floor (e.g., H_2, CH_4, and H_2S). Permeable mineral structures and the continued mixing of both reduced vent fluids and oxidized seawater provide favorable growth conditions for microbial communities [9]. Additionally, termed as chemolithoautotrophs, these microorganisms synthesize organic matter that form the base of the food chain in these ecosystems. Abiotic redox reactions in the mixing zones also play a potentially vital role in hydrothermal fields. Hydrocarbon formation at the Piccard field was shown to be contributed by biomass pyrolysis, while abiotic sulfate reductions produced large depletions in H_2 [10]. Since chemolithotrophs commonly colonize hydrothermal vents, a combination of biogenic and thermogenic processes is likely to contribute to the production of H_2, CH_4, and other organic compounds, such as in the MAR and in the South West Indian Ocean (SWIR) systems [11,12].

Gaps in the understanding of hydrothermal vent ecosystems [13] have been partially filled in the last ten years of research through the application of both culture-dependent and independent studies. Combined with advanced geochemical analyses, we now have a better perspective of the microbial communities inhabiting such ecosystems e.g., [14–17]. Lipid biomarkers were also used as proxies to reconstruct the community structure of vent systems. Branched fatty acids (iso/anteiso-C15 and C17) were detected in a SWIR sulfide chimney sample, indicating the presence of sulfate-reducing bacteria [18]. Recently, brGDGTs were detected from both active and inactive hydrothermal chimneys from the SWIR (Dasgupta et al. unpublished data) and were considered to be associated with autochthonous thermophilic bacteria [19,20]. Studies have shown that geochemical differences within vent systems are the strongest driving forces in structuring the microbial communities of a particular vent field [21]. The role of geochemistry is particularly critical

when comparing sites with different host rock geology. Sulfur oxidation is the prevalent electron donor in basalt-hosted fast-spreading ridges, while hydrogen and methane are the key electron sources for the microbial metabolism of ultramafic systems, with slow and ultraslow spreading rates [5].

The manifestation of chemical sources for lithotrophs along mid-oceanic ridges (MOR) occurs in three ways. First, when seawater circulates through hot subsurface igneous rocks, the resulting hydrothermal fluid becomes enriched in reduced compounds such as H_2S, H_2, Fe, and CH_4, including other metals. The chemical reactions that follow between the reduced components and oxidized seawater are promoted by microbes to derive energy. Evaluation of the metabolic energy sources during fluid-mixing suggests that oxidation of H_2S and H_2 supply the highest levels of energy at >90%, the rest being derived from methanogenesis, sulfate reduction, and oxidation of Fe, Mn, or other metals [22–24]. The second source of energy is derived when oxidized seawater comes into contact with seafloor rocks. Basaltic rocks exposed at the seafloor are rich in reduced Fe, S, and other elements. Further precipitates from hydrothermal fluids form an extensive accumulation of reduced sulfides and other metals. Lithoautotrophs promote oxidative surface reactions when these reduced compounds are exposed to seawater. Oxidation of Fe and S by these microorganisms is one of the major energy sources for lithoautotrophs that can use mineral substrates in the seafloor environment [22–24]. The third type of energy source has been suggested to occur at high temperature hydrothermal vents [25–27]. In this process, hydrogen acts as the primary energy source, generated by the reaction of seawater with reduced metals in basaltic glass or Fe-rich minerals. This hydrogen can be combined with SO_4^{-2} by sulfate reducers or with CO_2 by methanogens for metabolic energy gain.

In this article, we review, in brief, the dominant microbial diversity and community structure of deep-sea hydrothermal vents, microbe–mineral interactions, and the biogeochemistry involved in such unique ecosystems.

2. Microbial Diversity in Deep-Sea Hydrothermal Vent Systems

2.1. Sulfur Oxidizers and Sulfate Reducers

Sulfide and thiosulfate oxidation in sulfide-rich basalt-hosted hydrothermal systems provide the greatest source of energy yields [28]. Bacterial sulfur-oxidation pathways include sulfide oxidation to elemental sulfur by sulfide dehydrogenase (FccAB) or sulfide-quinone reductase, which is further oxidized to sulfate. The reverse sulfate reduction is another alternative pathway in which thiosulfate can be oxidized to sulfate.

Campylobacterota is highly abundant in hydrothermal vent fields [14,29–32]; (refer to Table 1 for microbial groups identified in specific hydrothermal fields). Takai et al. [33–35] first reported sulfur-oxidizers from deep-sea hydrothermal vents, such as in the Suiyo Seamount hydrothermal system. Other mesophilic S-oxidizers isolated from these environments include those from genus *Sulfurimonas* [36], *Sulfurovum* [37], and *Lebetimonas* [38]. A majority of strains of the genus *Sulfurovum* grow chemolithoautotrophically using sulfur as an energy source. Similar communities were also found in cool, diffusive flows at the Axial Seamount on the Juan de Fuca Ridge (JFR) [39] and at the chimney walls' biofilms at the Loki's Castle vent field [31]. Ding et al. (2017) [15], in their study, recovered both *Sulfurovum* and *Sulfurimonas* from all active chimneys of SWIR and inactive sulfides in the East Pacific Rise (EPR) [40]. Thus, these groups possibly represent the most widely distributed species at active sulfide vents. The *Sulfurimonas* species have also been isolated from the Kairei and Pelagia active chimneys from the Central Indian Ridge (CIR) system [16]. Several sulfur-oxidizing bacteria (SOB) belonging to the class Gammaproteobacteria have been isolated from deep hydrothermal habitats. In a study at the Edmond vent field, called the CIR system, [41] observed that the bacterial phylotypes in the Edmond microbial mats are primarily affiliated (> 90%) with the epsilon and gamma subclasses of the Proteobacteria. Furthermore, a number of samples from the Rainbow and Lucky Strike hydrothermal fields in the MAR system were dominated by Gammaproteobacteria (Rb-2, -3) that included mesophilic sulfide-oxidizing *Thiomicrospira* and several genera within *Methylococcaceae* [21].

Gammaproteobacteria were also present in all the chimney samples of the SWIR system [24], with the SOBs within the genera of *Thiotrichaceae*, *Ectothiorhodospiraceae*, *Thiohalophilus*, and *Piscirickettsiaceae* [15]. Both subclasses are closely related to sulfur oxidation.

Sulfate reduction is one of the primary processes in hydrothermal vents at a wide temperature range (4–90 °C) in the anoxic areas of the vent. Isolated genera include *Caminibacter*, *Nautilia*, *Lebetimonas*, and *Cetia*. Some deltaproteobacteria, such as *Desulfovibrio*, *Desulfonauticus*, and *Desulfothermas*, were isolated from sites at 13° EPR, SWIR, and Southern Okinawa Trough (SOT) [21,42–44]. Within the aquificales class, sulfur-reducing bacteria (SRB) including *Desulfurobacterium indicum* was isolated from an Indian Ocean hydrothermal vent [43] and from SWIR [24]. Another obligate anaerobic chemolithotroph *Thermosulfidibacter takaii* was isolated from the SOT that could couple hydrogen oxidation to sulfate reduction [45]. Cha et al. (2013) [46] isolated *Desulfotomaculum tongense* sp., a novel moderately thermophilic SRB belonging to phylum Firmicutes, from the Tofua Arc in the Tonga Trench. Firmicutes have also been identified from the Lost City hydrothermal vents [5]. A few reports of SRBs in inactive chimneys indicate that sulfate-reducing Nitrospirae dominate such hydrothermal environments [47]. Furthermore, in the SWIR, the phylotypes of deltaproteobacteria were primarily similar to a sulfate-reducing benzene-mineralizing consortium clone and a mud volcano microbial mat clone [24].

Archaeal diversity has also been reported in deep-sea hydrothermal vents both from phylum Euryarchaeo-ta and Crenarchaeota. For example, *Pyrococcus yayanosii* [48,49] and *Pyrococcus kukulkanii* [50], both from phylum Euryarchaeota, were isolated from deep-sea vents. *Pyrolobus fumarii*, an archaeon in the phylum Crenarchaeota, was also isolated from high-temperature chimneys [51]

2.2. Methanogens and Methane Oxidizers

Methanogens are one of the most important groups in high-temperature vent areas [52]. While known methanogens (methanococcaceae and methanocaldococcaceae; refer to Table 1 for details) were detected in the Rainbow hydrothermal field, they are strikingly absent at the Lucky Strike of MAR [21]. *Methanococcales* were also detected in Kairei and Pelagia, CIR [16]. Actively venting carbonate chimneys in the Lost City hydrothermal field (LCHF) are dominated by a novel phylotype of anaerobic methanogens from the *Methanosarcinales* order [5,26,53]. Some other species isolated from deep hydrothermal vents include *Methanocaldococcus fervens* [54], *M. infernus* [55], *M. villosus* [56], *M. vulcanius* [54], *M. bathoardescens* [57], *M. jannaschii* [58], *Methanopyrus kandleri* [59], and *Methanothermococcus okinawensis* [60]. Among methane oxidizers, the anaerobic oxidation of methane (AOM) is prevalent around some hydrothermal vents and may consume up to 75% of the methane produced by the vent [61]. Archaea of phylum Euryarchaeota are also found in hydrothermal vents, commonly referred to as anaerobic methane-oxidizing lineages (ANME). Anaerobic methanotrophic clade ANME-1 has been recovered from the LCHF carbonate chimneys [53].

2.3. Hydrogen-Oxidizers

Although different types of microorganisms oxidize hydrogen, only a few are capable of effectively using the energy gain for CO_2 fixation [8]. Such chemoautotrophs have been isolated from various deep-sea hydrothermal fields, including aquificales, delta and gammaproteobacteria, campylobacteria, desulfurococcales, thermodesulfobacteriales, methanococcales, and deferribacterales [62] (refer to Table 1 for details). Hydrogen has also been shown to be an important energy source in vent fluids at the Logatchev and Rainbow fields in the MAR [52]. Deltaproteobacteria contribute to H-oxidation in anoxic vent habitats [63]. *Desulfonauticus*, a genus within Deltaproteobacteria, is a moderately thermophilic hydrogen-oxidizing sulfate reducer and was detected from the Rainbow field, MAR [21]. Two hydrogen-oxidizing *Caminibacter* species isolated from the Rainbow field showed differences in their oxygen tolerance as *C. mediatlanticus* is a strict anaerobe while *C. profundus* grows optimally with 0.5% oxygen [64].

Table 1. Orders and genera of bacteria and archaea reported from deep-sea hydrothermal vents and their energy-yielding processes.

Categories (Bacteria and Archaea)	Main Energy-Yielding Process	Field Locations
Campylobacteria	S-oxidation, S-reduction, H-oxidation, and nitrate-reduction	
Sulfurimonas	S-oxidation, H-oxidation, and nitrate-reduction	JFR; Loki–s Castle, MAR; Suiyo Seamount; SWIR; EPR; and Kairei, Pelagia, CIR
Sulfurovum		
Lebetimonas		
Caminibacter	S-reduction, nitrate-reduction, and H-oxidation	EPR; SWIR; MAR; and JFR
Nautilia		
Lebetimonas		
Cetia		
Gammaproteobacteria	S-oxidation, N-reduction, and H-oxidation	
Thiomicrospira	S-oxidation, N-reduction, and H-oxidation	CIR and MAR
Methylococcaceae	S-oxidation and N-reduction	
Thiotrichaceae	S-oxidation and N-reduction	SWIR
Ectothiorhodospiraceae		
Thiohalophilus		
Piscirickettsiaceae		
Deltaproteobacteria	S-reduction, H-oxidation, and Fe-reduction,	
Desulfovibrio	S-reduction	EPR; SWIR; and SOT
Desulfonauticus		
Desulfothermus		
Desulfonauticus	H-oxidation	Rainbow, MAR
Deferrisoma	Fe-reduction	Eastern Lau Spreading Center
Zetaproteobacteria	Fe-oxidation	
Mariprofundus	Fe-oxidation	Loihi Seamount and Lau Basin
Betaproteobacteria	Ammonium-oxidation	
Nitrospira	Ammonium-oxidation	SWIR
Nitrococcus		
Nitrosomonas		
Aquificae	S-reduction, H-oxidation, and N-reduction	
Desulfobacterium	S-reduction	SWIR
	H-oxidation	Eastern Lau Spreading Center
	N-reduction	JFR
Firmicutes	S-reduction	
Desulfohalotomaculum	S-reduction	Tonga Trench
Euryarchaeota	Methanogenesis, methane-oxidation, and S-reduction	
Methanococcales	Methanogenesis	Kairei, Pelagia, CIR; Rainbow, MAR; and LCHF
Methanocaldococcus		
Methanosarcinales		
Methanopyrus		
Pyrococcus	S-reduction	
ANME-1	Methane-oxidation	LCHF
Crenarchaeota	S-reduction and Fe-reduction	
Pyrolobus	S-reduction	
Archaeoglobacae	Fe-reduction	JFR
Pyrodictiaceae		
Thaumoarchaeota	Ammonium-oxidation	SWIR

2.4. Ammonium-Oxidizers and Nitrate-Reducers

Dissolved inorganic nitrogen in the form of ammonium is common in hydrothermal environments. Ammonia oxidation to nitrite is the first step of nitrification by ammonia-oxidizing bacteria and/or archaea (AOB/AOA), followed by oxidation to nitrate by nitrite-oxidizing bacteria (NOB). *Thaumarchaeota* was assigned as the major AOA in two high-temperature vent systems in the SWIR, apart from other AOB within *Nitrococcus*, *Nitrospira*, and *Nitrosomonas* (Table 1). AOA was also found to be more abundant than AOB in samples from the MAR and South Atlantic Ocean [65]. Affiliates of the group *Nitrosopumilius*, an autotrophic AOA, have been mostly detected in inactive chimneys, although some related sequences were also found in active chimneys [16,66], and accounted for 33% of the archaeal library in chimney samples from the Lau Basin [67]. Furthermore, crenarchaeol, a GDGT specific to ammonia-oxidizing archaea of Marine group I (*Thaumarchaeota*) [68,69] was recently detected in active and inactive chimney samples from the SWIR hydro-thermal field (Dasgupta et al. unpublished data). Fewer studies reported the presence of denitrifying communities in hydrothermal environments. *Sulfurimonas* sp. [36,52], *Caminibacter* sp. [70], and *Sulfurovum* sp. [37,71], all from phylum Campylobacterota, have been isolated as denitrifiers. A number of isolates in the phylum proteobacteria [72] and aquificae [70] have also been reported from the Juan de Fuca Ridge (JFR) and other hydrothermal fields.

2.5. Iron-Oxidizers and Iron-Reducers

Reduced metals such as Fe, Mn, Cu, etc., are potential energy sources for hydrothermal microbial communities. Iron-oxidizing bacteria proliferate at deep-hydrothermal systems, forming microbial mats [73]. Common Fe-oxidizing bacteria (FeOB) include chemolithotrophic Zetaproteobacteria and mixotrophic Gammaproteobacteria. Zetaproteobacteria *Mariprofundus ferrooxydans* [74,75] from the Loihi Seamount and Lau Basin [67], *M. micogutta* ET2 from the Izu-Ogasawara Arc [76], and several Alpha and gammaproteobacteria strains are reported as the chemoautotrophic Fe(II) oxidizers described from deep-sea vents [77] (Table 1). Sequences closely related to FeOBs in low-temperature hydrothermal vents were also detected from the SWIR [78]. Deep-sea hydrothermal fields can be ecological niches for Fe-reducers because they are abundant in oxidized iron [79]. While a few Fe-reducers have been detected in hydrothermal fields, a majority of them are from phylum proteobacteria [80] and deferribacteria [81]. Among archeae, most Fe-reducers belong to the families Archaeoglobacae and Pyrodictiaceae. Few other species were also isolated from the JFR [82] vent chimney on the Endeavor Segment of the North East Pacific Ocean.

3. Biomineralization and Microbe–Mineral Interactions

3.1. Iron-Metabolizers and Biomineralization

Minerals can serve either as electron acceptors or as sources of energy and electrons for microbes. Reduced metals and sulfur precipitate from hydrothermal fluids to form large reserves of metal sulfide minerals at the seafloor and are by far the most abundant source of energy available to microbes that can use mineral substrata in seafloor environments. During the exposure of these reduced compounds to seawater, lithoautotrophs can promote oxidative surface reactions for energy gain. Microbial surfaces can provide a large number of available nucleation sites for Fe-sulfides [83]. Additionally, a variety of biological structures are observed in the cell walls of the outer reactive surfaces of bacterial cell walls that are predominantly negatively charged and lead to the sorption of positive ions from solution as well as to the nucleation of metal sulfides.

Biotic reactions responsible for the formation of biogenic Fe-oxides include the microbial oxidation of Fe(II) to Fe(III) by a wide range of microorganisms under both acidic and neutral pH, as well as under oxic and anoxic conditions [84,85]. Characteristic ultrastructures, such as tubular sheaths, helical or twisted stalks, and irregular filaments, are generally considered as reliable indicators of biomineralization involving the FeOBs [74,86]. Such ultrastructures have been observed in the Lau Basin hydrothermal vent in the West-

ern Pacific Ocean, where dominant mineralogy contained amorphous or poor crystalline minerals from the two-line ferrihydrite to opal-A [67,87]. Dense Fe-rich ultrastructures in the form of twisted stalks, branched stalks, rod-like sheaths, and contorted filaments detected in the Lau Basin are considered the most authentic biosignatures of FeOB species such as *Mariprofundus* sp., *Gallionella* sp., and *Leptothrix* sp. [88,89]. Alternatively, biogenic encrustation of Fe-sulfides around microbes is also feasible. Sulfate-reducing bacteria that supply reactive sulfide ions could be the key to the formation of sulfide minerals [90]. These microbes can further oxidize organic compounds or methane using O_2 under aerobic conditions and SO_4^{2-} in anoxic environments as terminal electron acceptors. More processes of FeOB–mineral interactions suggested that organic matter provides nucleation sites for the reaction of FeS to FeS_2 [91]. The fact that many microbes were encrusted with pyrite and marcasite from the SWIR [24] supports this possible theory of nucleation. Biomineralization was observed in the microbial mats attached to the inner surface of a sulfide chimney (Figure 2) in the Edmond vent field of the CIR [41]. However, no Fe-oxidizing microorganisms were detected in their samples from molecular phylogenetic analysis. Nevertheless, a large number of species detected in the Edmond mat samples were sulfur-metabolizers, a few of which could also survive as Fe-oxidizers [92], that induce the extracellular nucleation of Fe-minerals.
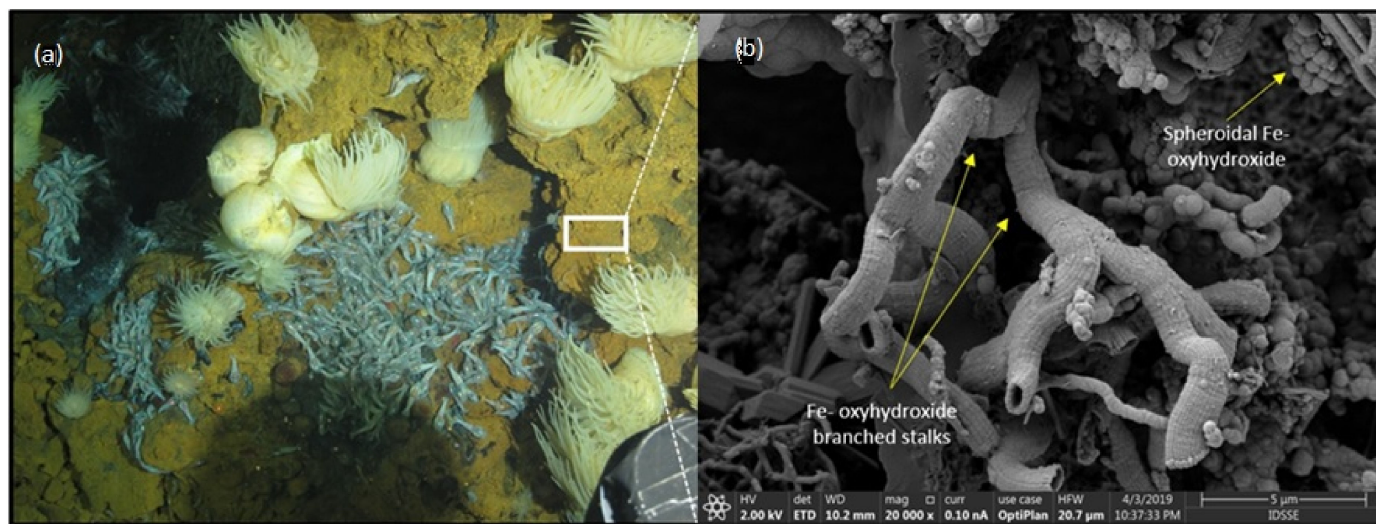

Figure 2. Biomineralization in the chimney at the Edmond field, Central Indian Ridge hydrothermal system. (**a**) Yellow sulfide layers at the chimney exterior; (**b**) SEM image of biomineralized Fe stalks and spheroidal particles within the deposits.

Another possible onset of intracellular mineralization is the viability of cells. It is known that microbes can produce a variety of organic and inorganic intracellular polymers [93,94], and intracellular magnetic iron minerals (magnetite and greigite) can occur in magnetotactic bacteria [95–97]. Fe-reducing bacteria have also been shown to produce intracellular iron oxides. Although Peng et al. (2010) [41] identified magnetotactic bacteria and Fe-reducing archaea that can produce intracellular iron oxides in the Edmond field, the exact mechanisms for the high concentrations of iron (10.5–13.9 mmol/kg) remain arguable. Iron assimilatory reactions [98–101], by which many microbes could undergo intracellular mineralization in high iron solutions, is thought to be a possible mechanism. Iron dissimilatory reactions, where the metal ion is used as an electron donor or acceptor during respiration and is typically not incorporated into the cell, could be another potential mechanism [102,103] for the intracellular mineralization in Edmond microbial mats.

Some thermophilic H-oxidizers in hydrothermal fluids can also interact with the minerals through energy conservation mechanisms [104]. For example, hyperthermophilic Fe-reducers from sulfide chimneys oxidize H_2 and transform ferrihydrite to magnetite, as well as other forms of Fe-minerals [105].

To examine whether mineral compositions have a direct relationship with bacterial and archaeal diversities in the SWIR [16], the proportions of chalcopyrite, pyrite, and sphalerite relative to the microbial community compositions were analyzed. No significant correlation with mineral species and with the abundance of microbial communities could be established. However, based on the nature of the inferred metabolism in the type of microbe detected, the availability of specific sulfide species could be relevant. For example, in the SWIR, while species such as *Sulfurimonas* use reduced sulfur compounds as electron donors, *Desulfobulbus* are sulfate-reducers. Thus, the presence of specific microbial species could indicate an abundance of related mineral groups in the hydrothermal systems.

3.2. Role of Microbes in the Precipitation of Mn-Oxides and Si in SWIR Hydrothermal Deposits

Precipitates of Mn-oxides in the hydrothermal deposits in the SWIR field are commonly attributed to Mn-oxidizing bacteria [24,78,106]. Mineralized ultrastructures of Fe-oxides, such as sheaths, twisted stalks, etc., in the hydrothermal fields are well reported [16,24,75], whereas reports of biogenic Mn-oxides are less frequent. These occur as fibrillar-like aggregates with a porous structure or reticulated filaments [107,108]. Li et al. (2013) [78] detected birnessite (a layered Mn-oxide) in two low-temperature deposits of the SWIR and speculated at least a partial biogenic origin of such a compound based on two observations: several putative Mn-oxidizing bacteria were present in their study and Mn-oxides with a fibrillar-like structure resembling a crumpled tissue are typical of the morphology of biogenic Mn-oxides [107].

Greenish clay mineral nontronite deposits are reported from deep hydrothermal vents, such as in the SE slope of the Eolo Seamount, Tyrrhenian Sea [109], and Okinawa Trough [110]. The tube-like filamentous structure of nontronites indicate the bacteria-assisted precipitation of these deposits. At the Galapagos Rift and Mariana Trough, correlation clay minerals and biological conditions at the hydrothermal chimneys suggested that Fe-oxidizing, sheath-forming bacteria play a decisive role in the nontronite formation at these sites [111]. Mineralized structures composed of silica were also observed in the SWIR deposits. Li et al. (2013) [78] suspects that these structures are abiogenic in origin, controlled by processes such as silica supersaturation and polymerization [112,113]. However, microorganisms present in the vent site could act as substrates and provide nucleation sites for Si-precipitation. Now, additional cooling in hydrothermal sites is essential to precipitate amorphous Si. Large accumulation of FeOB-induced ultrastructures, which locally separate hydrothermal fluid from ambient seawater and largely restrict their mixing, could lead to conductive heat removal of hydrothermal fluid rather than sole cooling through full mixing with seawater [114,115]. This would result in local Si supersaturation and more precipitation as grains of mineral spherules. Thus, there could be multiple indirect ways in which microbe–mineral interactions could facilitate the formation of Si-precipitates in deep hydrothermal deposits.

4. Conclusions

Since the discovery of hydrothermal vents more than four decades ago, it has been established that deep hydrothermal vents are characterized by unique habitats that support their growth by deriving energy from the reduced chemicals available in the hydrothermal fluids or altered bedrock. The steep chemical and thermal gradients prevailing in such environments flourish a rich diversity of microorganisms, with a range of metabolic activities and adaptation mechanisms. A general model of a deep-sea hydrothermal system has been given in Figure 3, depicting the biogeochemical diversity of such vent systems. In terms of converting inorganic carbon to organic biomass, the contribution of hydrothermal vent communities to the global sink is considered negligible. However, endolithic microbial communities in the sub-seafloor environment could have a major impact on chemosynthetic biomass production [6]. The common proposition that mineral particles form abiotically in such systems has been replaced by growing evidence that suggests that microorganisms are also actively moderating the formation of mineral particles within

the vent and plumes. Nevertheless, caution must be exercised since mineral precipitates often resemble microbial morphologies. The interaction of microbes and minerals in deep hydrothermal fields can result in the accumulation of deposits and ultrastructures.
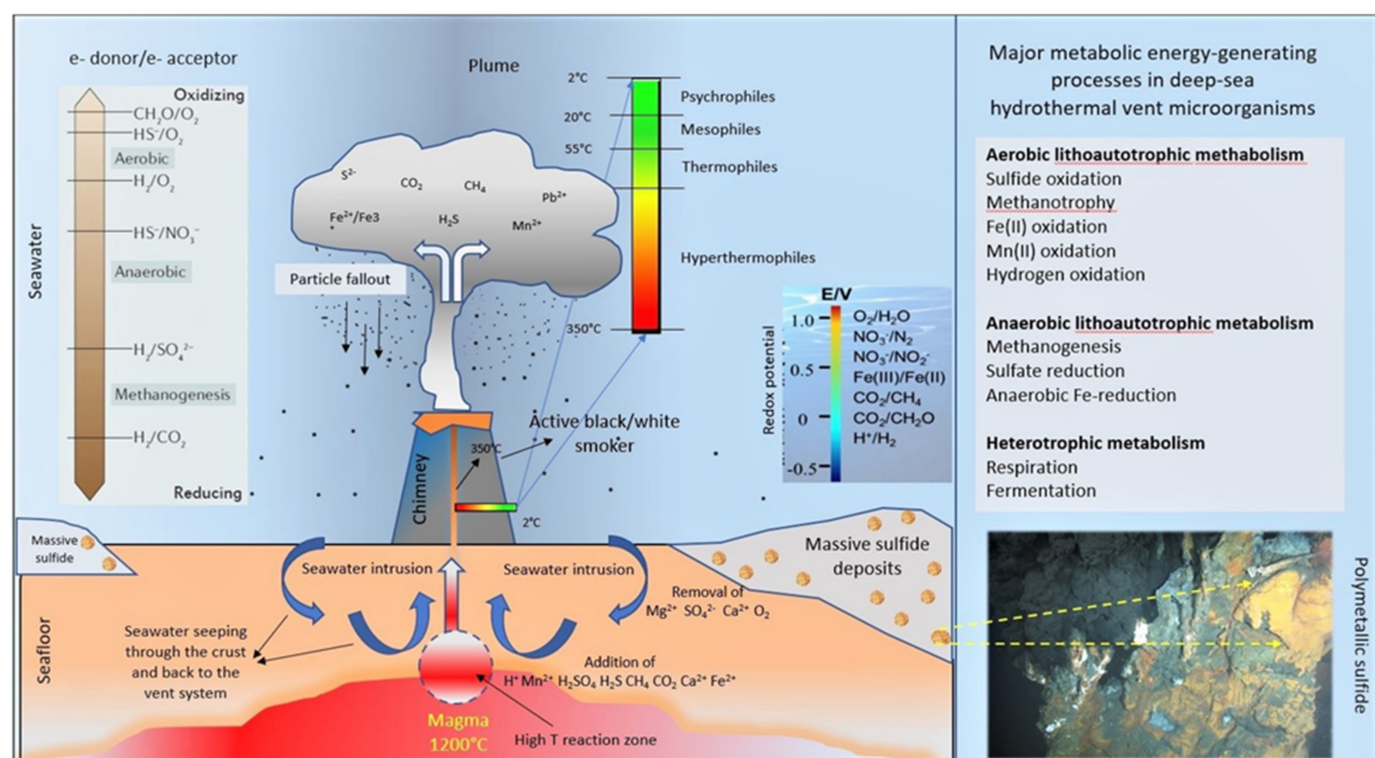

Figure 3. Simplified representation of vent morphology and characteristics in terms of microbial communities with respect to temperature and redox potentials, and a list of the major energy-yielding processes used by microbes. The model is a generalized representation of hydrothermal vent systems and does not depict any particular location [6,17].

Interestingly, modern hydrothermal systems have long been considered as similar, to some extent, to early Earth's conditions and hence can be considered as a place of interest for the search of the origin of life. Microenvironments, such as mineral surfaces, favor adsorption, the concentration of organics, and chemical reactions, and the hydrothermal niche provides physicochemical gradients and non-equilibrium conditions typical for the emergence of living organism [116]. The serpentinization process is also considered as a likely energy source essential for life to have emerged on the primitive Earth [117,118]. Furthermore, alkaline hydrothermal systems, such as the Lost City hydrothermal field, are thought to be more relevant to Archean hydrothermal vents, which can provide insights into the past mantle geochemistry and present a better understanding of the chemical constraints that existed during the onset of life [12]. Few other studies have also proposed a possible relation between low temperature shallow hydrothermal conditions [119], subsurface filamentous fabrics (SFF) [120], and the quest for Martian life.

In terms of technological advancements, a series of advanced analytical technologies or methods are used to study biomineralization. For instance, Fe isotopic compositions, together with nano SIMS (secondary ion mass spectroscopy) and FISH (fluorescence in situ hybridization), have been applied to study the formation mechanisms and preservation of hydrothermal mineralized microbial mats at the Loihi Seamount [121,122]. However, understanding the real depth of the adaptation mechanisms of vent microorganisms, how these microbes interact with minerals biochemically, the thermodynamic constraints, and how deep hydrothermal vents shape the global carbon cycle are some of the future challenges that need to be addressed.

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