



Microorganisms from deep-sea hydrothermal vents

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Abstract

With a rich variety of chemical energy sources and steep physical and chemical gradients, hydrothermal vent systems offer a range of habitats to support microbial life. Cultivation-dependent and independent studies have led to an emerging view that diverse microorganisms in deep-sea hydrothermal vents live their chemolithoautotrophic, heterotrophic, or mixotrophic life with versatile metabolic strategies. Biogeochemical processes are mediated by microorganisms, and notably, processes involving or coupling the carbon, sulfur, hydrogen, nitrogen, and metal cycles in these unique ecosystems. Here, we review the taxonomic and physiological diversity of microbial prokaryotic life from cosmopolitan to endemic taxa and emphasize their significant roles in the biogeochemical processes in deep-sea hydrothermal vents. According to the physiology of the targeted taxa and their needs inferred from meta-omics data, the media for selective cultivation can be designed with a wide range of physicochemical conditions such as temperature, pH, hydrostatic pressure, electron donors and acceptors, carbon sources, nitrogen sources, and growth factors. The application of novel cultivation techniques with real-time monitoring of microbial diversity and metabolic substrates and products are also recommended.

Keywords Deep-sea hydrothermal vents · Cultivation · Diversity · Biogeochemical cycle

Introduction

The discovery of deep-sea hydrothermal vents in the late 1970s expanded our knowledge of the extent of life on Earth (Corliss et al. 1979). Hydrothermal-vent environments include positively buoyant and neutrally buoyant (lateral)

hydrothermal plumes (~2 °C), low-temperature hydrothermal fluids (~5–100 °C), high-temperature hydrothermal fluids (~150–400 °C), sulfide rock, basalt, and pelagic and metalliferous sediments. Active deep-sea hydrothermal vents, which are spread along mid-ocean ridges, back-arc basins, and volcanic arcs, occur in different geological contexts, characterized by the presence of different rock types, including basalts, peridotites, and felsic rocks. The associated hydrothermal fluids exhibit substantial chemical variability, depending largely on the compositional differences among the underlying rocks (Amend et al. 2011). Hydrothermal end-member fluids of basalt-hosted systems are usually characterized by greater sulfide than hydrogen concentrations, resulting from magma degassing and high-temperature-leaching of host rocks. In contrast, owing to serpentinization processes, the end-member fluids of ultramafic-hosted vent systems usually exhibit greater hydrogen (normal 10–20 mmol/L, some up to 154 mmol/L) and methane (at mmol/L levels) concentrations than sulfide concentrations (Adam and Perner 2018; Charlou et al. 2002; Perner et al. 2013). Because of the mixing processes with the oxygenated ambient seawater, deep-sea hydrothermal fluids of these ultramafic systems may contain numerous possible electron

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acceptors (primarily oxygen, nitrate, sulfate, elemental sulfur, and iron) (Adam and Perner 2018).

Deep-sea hydrothermal vents are representative areas of high biological productivity on the seafloor, fueled primarily by microbial chemoautotrophy, which is in contrast to most ecosystems fueled by photosynthesis (Reysenbach and Shock 2002). Hydrothermal vent microorganisms, including free-living cells, animal symbionts, and cells in microbial mats, use the energy produced by the oxidation of sulfur, hydrogen, methane, sulfide, and iron to fix carbon. In turn, this organic carbon supports dense animal communities, largely through symbiotic relationships with bacteria, but also via grazing or suspension-feeding and subsequent trophic transfer (Dick 2019).

This article reviews the current knowledge of microorganisms inhabiting deep-sea hydrothermal vents and, in particular, the isolates grown from this unique environment and their involvement in the biogeochemical cycles. In addition, it highlights the understanding of metabolically versatile microbial taxa and future challenges for microbiologists in the field of microbial culture.

Microbial diversity and biogeochemistry

Carbon cycle

The geological activity of hydrothermal vents produces a large number of carbon compounds (Jannasch and Mottl 1985). Hydrothermal vent plumes contain high concentrations of methane and carbon monoxide, with methane concentrations of up to 107 times that of the surrounding ocean water (Jannasch and Mottl 1985). Short-chain fatty acids, such as formate and acetate, have been repeatedly found in hydrothermal fluids. Autotrophic chemosynthetic microorganisms fix inorganic carbon and provide much of the organic carbon that supports heterotrophic life in the hydrothermal ecosystem (Dick 2019).

Carbon fixers

At hydrothermal sources, CO₂ fixation can be carried out by members of the Alphaproteobacteria, Gammaproteobacteria, Deltaproteobacteria, Zetaproteobacteria, Campylobacterota (formerly Epsilonproteobacteria), Thermodesulfobacteria, Aquificae, Deferribacteres and by several members of the

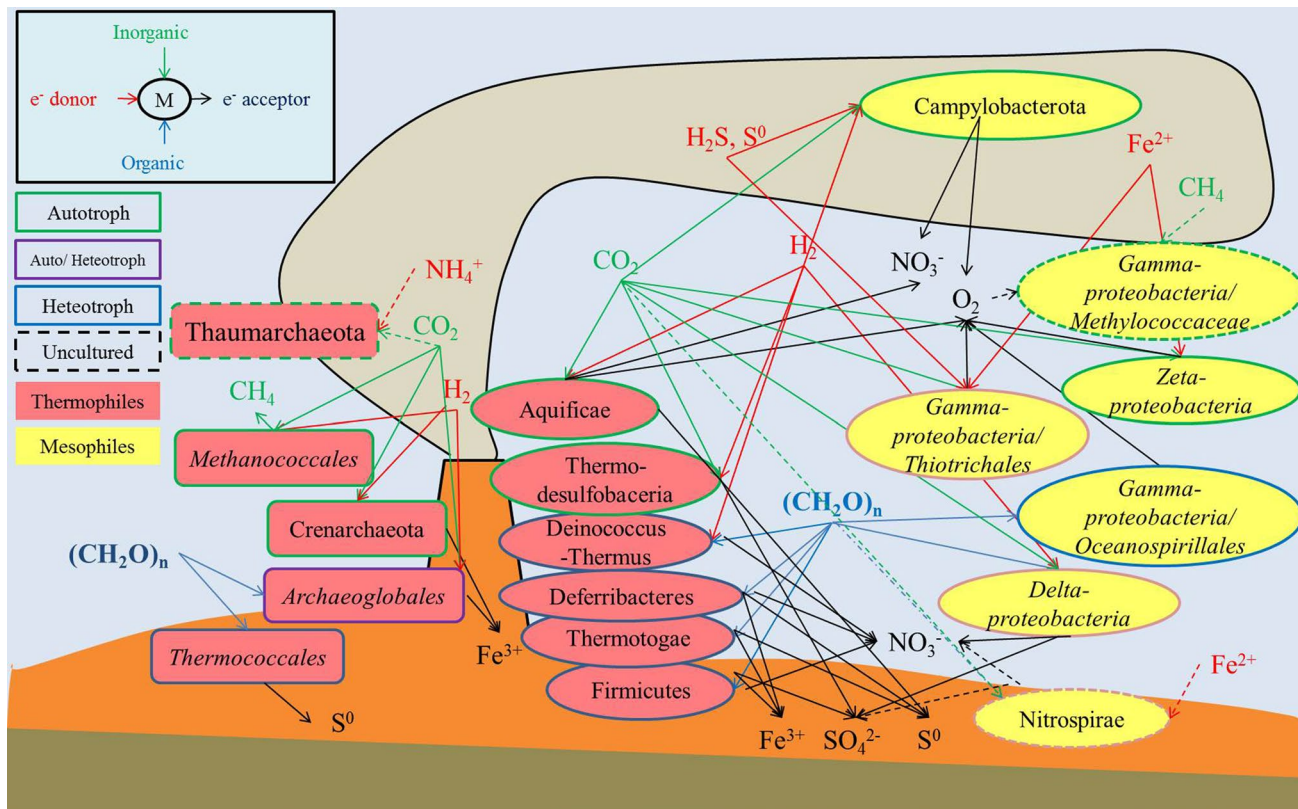


Fig. 1 Schematic illustration of microbial metabolisms in deep-sea hydrothermal fields. Carbon source in green or blue: CO₂, CH₄, (CH₂O)_n; Electron donors in red: H₂, H₂S, S⁰, NH₄⁺, Fe²⁺; Electron acceptors in black: O₂, S⁰, SO₄²⁻, NO₃⁻, Fe³⁺

Table 1 List of cultured genera in the domain of Bacteria and Archaea from the deep-sea hydrothermal vent environments and their metabolisms. Opt T, optimal growth temperature

| Categories | Genus (species number) | Opt T (°C) | Source | Main metabolism |
|------------------|--------------------------------|--------------------------|---------------------------------|--|
| Bacteria | | | | |
| Aquificae | <i>Balnearium</i> (1) | 70–75 | Chimney | Anaerobe, autotroph, sulfur-oxidizer, denitrifier |
| | <i>Desulfurobacterium</i> (5) | 65–75 | Chimney, sulfide, animal | Aerobe or anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer, denitrifier |
| | <i>Hydrogenivirga</i> (1) | 70–75 | Chimney | Aerobe or anaerobe, autotroph, sulfur-oxidizer, denitrifier |
| | <i>Persephonella</i> (1) | 73 | Chimney | Aerobe or anaerobe, autotroph, sulfur-oxidizer, denitrifier |
| | <i>Thermovibrio</i> (2) | 75–80 | Chimney | Anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer, denitrifier |
| | <i>Thermosulfidibacter</i> (1) | 70 | Sediment | Anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer |
| Calditrichaeota | <i>Caldithrix</i> (1) | 60 | Chimney | Anaerobe, autotroph or heterotroph, hydrogen-oxidizer, denitrifier |
| Campylobacterota | <i>Caminibacter</i> (3) | 55–60 | Chimney | Aerobe or anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer, denitrifier |
| | <i>Cetia</i> (1) | 55–60 | Chimney | Anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer, denitrifier |
| | <i>Hydrogenimonas</i> (1) | 55 | Fluid | Aerobe or anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer, denitrifier |
| | <i>Lebetimonas</i> (2) | 50–55 | Fluid, animal | Anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer, denitrifier, selenite-reducer |
| | <i>Nautilia</i> (4) | 40–60 | Chimney, animal | Anaerobe, autotroph or heterotroph, hydrogen-oxidizer, sulfur-reducer, denitrifier, selenite-reducer |
| | <i>Nitratifractor</i> (2) | 37 | Chimney | Aerobe or anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer, denitrifier |
| | <i>Nitratiruptor</i> (1) | 55 | Chimney | Aerobe or anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer, denitrifier |
| | <i>Sulfurovum</i> (4) | 28–35 | Chimney, sediment, rock, animal | Aerobe or anaerobe, autotroph, sulfur-oxidizer, hydrogen-oxidizer, denitrifier |
| | <i>Sulfurimonas</i> (3) | 25–33 | Chimney, sediment, animal | Aerobe or anaerobe, autotroph, sulfur-oxidizer, hydrogen-oxidizer, denitrifier |
| | <i>Thiofractor</i> (1) | 37 | Chimney | Anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer, denitrifier |
| | Deferribacteres | <i>Deferribacter</i> (3) | 60–65 | Chimney, fluid |

Table 1 (continued)

| Categories | Genus (species number) | Opt T (°C) | Source | Main metabolism |
|----------------------------|---------------------------------|------------|---------------------|---|
| Deinococcus-Thermus | <i>Marinithermus</i> (1) | 67.5 | Chimney | Aerobe, heterotroph, hydrogen-oxidizer |
| | <i>Oceanithermus</i> (2) | 60 | Chimney | Aerobe, heterotroph, hydrogen-oxidizer |
| | <i>Rhodothermus</i> (2) | 70–75 | Chimney | Aerobe, heterotroph, sulfur-reducer, denitrifier |
| | <i>Thermus</i> (1) | 75 | Chimney | Aerobe, heterotroph, hydrogen-oxidizer |
| | <i>Vulcanithermus</i> (1) | 70 | Chimney | Aerobe, heterotroph, hydrogen-oxidizer |
| Firmicutes | <i>Anoxybacter</i> (1) | 60 | Sulfide | Anaerobe, heterotroph, iron-reducer |
| | <i>Caloranaerobacter</i> (2) | 55–60 | Chimney, sulfide | Anaerobe, heterotroph, iron-reducer |
| | <i>Caminicella</i> (1) | 55–60 | Animal | Anaerobe, heterotroph |
| | <i>Desulfohalotomaculum</i> (1) | 50 | Sediment | Anaerobe, heterotroph, sulfur-reducer |
| | <i>Vulcanibacillus</i> (1) | 55 | Sediment | Anaerobe, heterotroph, denitrifier |
| | <i>Wukongibacter</i> (1) | 30 | Sulfide | Anaerobe, heterotroph, iron-reducer |
| Proteobacteria | | | | |
| <i>Alphaproteobacteria</i> | <i>Piezobacter</i> (1) | 50 | Chimney | Aerobe or anaerobe, autotroph or heterotroph, hydrogen-oxidizer, sulfur-oxidizer, denitrifier |
| <i>Gammaproteobacteria</i> | <i>Guyparkeria</i> (1) | 35 | Chimney | Aerobe, autotroph or heterotroph, sulfur-oxidizer |
| | <i>Halomonas</i> (4) | 20–35 | Fluid, plume, rock | Aerobe, heterotroph |
| | <i>Hydrogenovibrio</i> (2) | 25–40 | Fluid, animal | Aerobe, autotroph or heterotroph, sulfur-oxidizer, |
| | <i>Salinisphaera</i> (1) | 30–35 | Fluid | Aerobe, autotroph or heterotroph, sulfur-oxidizer |
| | <i>Thiolapillus</i> (1) | 40 | Chimney | Aerobe or anaerobe, autotroph, sulfur-oxidizer, denitrifier |
| | <i>Thiomicrothrix</i> (1) | 28 | Sea water | Aerobe or anaerobe, autotroph, sulfur-oxidizer |
| | <i>Thiopropinquum</i> (2) | 39–40 | Chimney, rock | Aerobe or anaerobe, autotroph, sulfur-oxidizer, denitrifier |
| <i>Vibrio</i> (1) | 40 | Animal | Aerobe, heterotroph | |
| <i>Deltaproteobacteria</i> | <i>Deferrisoma</i> (1) | 50 | Chimney | Anaerobe, heterotroph, sulfur-reducer, iron-reducers |
| | <i>Desulfonauticus</i> (1) | 45 | Animal | Anaerobe, autotroph or heterotroph, hydrogen-oxidizer, sulfur-reducer |
| | <i>Desulfothermus</i> (1) | 50 | Chimney | Anaerobe, heterotroph, sulfur-reducer |
| | <i>Desulfovibrio</i> (1) | 35 | Chimney | Anaerobe, autotroph or heterotroph, hydrogen-oxidizer, sulfur-reducer |
| | <i>Dissulfuribacter</i> (1) | 61 | Chimney | Anaerobe, autotroph, sulfur-disproportionator |
| | <i>Geothermobacter</i> (1) | 55 | Fluid | Anaerobe, heterotroph, denitrifier, iron-reducers |
| | <i>Pseudodesulfovibrio</i> (1) | 30–35 | Rock | Anaerobe, heterotroph, hydrogen-oxidizer, sulfur-reducer |
| <i>Zetaproteobacteria</i> | <i>Ghiorsea</i> (1) | 20 | Iron mat | Aerobe, autotroph, iron-oxidizers |
| | <i>Mariprofundus</i> (2) | 25–30 | Iron mat, sediment | Aerobe, autotroph, iron-oxidizers |

Table 1 (continued)

| Categories | Genus (species number) | Opt T (°C) | Source | Main metabolism | |
|--------------------------|-----------------------------------|------------------------|--|---|---|
| Thermodesulfobacteria | <i>Thermosulfurimonas</i> (1) | 74 | Chimney | anaerobe, autotroph, sulfur-reducer, sulfur-disproportionator | |
| | <i>Thermosulfuriphilus</i> (1) | 65 | Chimney | Anaerobe, autotroph, sulfur-reducer, sulfur-disproportionator | |
| | <i>Thermodesulfatator</i> (3) | 65–70 | Chimney | Anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer | |
| | <i>Thermodesulfobacterium</i> (1) | 75 | Sediment | Anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer | |
| Thermotogae | <i>Marinitoga</i> (4) | 55–65 | Chimney | Anaerobe, heterotroph, sulfur-reducer | |
| | <i>Kosmotoga</i> (1) | 70 | Sediment | Anaerobe, heterotroph, sulfur-reducer | |
| | <i>Thermosipho</i> (4) | 65–72 | Chimney, fluid, animal | Anaerobe, heterotroph, sulfur-reducer | |
| Archaea Euryarchaeota | <i>Aciduliprofundum</i> (1) | 70 | Sulfide | Anaerobe, autotroph or heterotroph, sulfur-reducer, iron-reducer | |
| | <i>Geoglobus</i> (2) | 81–88 | Chimney | Anaerobe, autotroph or heterotroph, hydrogen-oxidizer, iron-reducer | |
| | <i>Methanocaldococcus</i> (6) | 80–85 | Chimney, sediment, fluid | Anaerobe, autotroph, methanogen | |
| | <i>Methanofervidicoccus</i> (1) | 70 | Chimney | Anaerobe, autotroph, methanogen | |
| | <i>Methanopyrus</i> (1) | 98 | Chimney | Anaerobe, autotroph, methanogen | |
| | <i>Methanothermococcus</i> (1) | 60–65 | Chimney | Anaerobe, autotroph, methanogen | |
| | <i>Methanotorris</i> (1) | 75 | Chimney | Anaerobe, autotroph, methanogen | |
| | <i>Palaeococcus</i> (2) | 80 | Chimney, sediment | Anaerobe, heterotroph, sulfur-reducer | |
| | <i>Pyrococcus</i> (5) | 95–105 | Chimney, fluid | Anaerobe, heterotroph, sulfur-reducer | |
| | <i>Thermococcus</i> (18) | 75–90 | Chimney, sediment, rock, fluid, animal | Anaerobe, heterotroph, sulfur-reducer, iron-reducer | |
| | Crenarchaeota | <i>Aeropyrum</i> (1) | 85 | Chimney | Aerobe, heterotroph |
| | | <i>Geogemma</i> (1) | 100 | Chimney | Anaerobe, autotroph, hydrogen-oxidizer, iron-reducer |
| | | <i>Ignicoccus</i> (1) | 90 | Chimney | Anaerobe, autotroph, hydrogen-oxidizer, sulfur-reducer |
| | | <i>Pyrodictium</i> (1) | 90–92 | Chimney | Anaerobe, autotroph, hydrogen-oxidizer, denitrifier, iron-reducer |
| <i>Pyrolobus</i> (1) | | 106 | Chimney | Aerobe or anaerobe, autotroph, sulfur-reducer, denitrifier | |

Archaea (Fig. 1, Table 1). Seven major metabolic pathways for carbon fixation are found in microbial vent communities including the Calvin–Benson–Bassham (CBB) cycle, reductive tricarboxylic acid (rTCA) cycle, 3-hydroxypropionate bicycle (3-HP), 3-hydroxypropionate/4-hydroxybutyrate cycle (3-HP/4-HB), reductive acetyl-coenzyme A (acetyl-CoA) pathway, dicarboxylate/4-hydroxybutyrate cycle, and the recently proposed reversible tricarboxylic acid cycle (“roTCA cycle”) (Minic and Thongbam 2011; Nakagawa and Takai 2008; Nunoura et al. 2018). The CBB cycle is the most common CO₂ fixation pathway found among autotrophs. Ribulose biphosphate carboxylase (RuBisCO), a key CO₂ assimilation enzyme, has been identified in members of the microbial community, such as *Zetaproteobacteria* and *Gammaproteobacteria*, including the genera *Thiomicrospira*

and *Beggiatoa*, and some endosymbionts of tubeworms, bivalves, and gastropods (Cerqueira et al. 2018). The rTCA cycle is preferred by anaerobes that inhabit anoxic zones of the hydrothermal vent system, for example, some members of Desulfobacterales, Aquificales, and Thermoproteales (Nakagawa and Takai 2008) and by many aerobic genera in the phylum Campylobacterota (Li et al. 2018). Most of the organisms using the 3-HP and 3-HP/4-HB cycle pathways are mixotrophs with the ability to utilize organic carbon in addition to carbon fixation, e.g., the deltaproteobacterial sulfate-reducer *Desulfobacterium autotrophicum*, acetogens, and methanogenic archaea (Nakagawa and Takai 2008). *Deferribacter autotrophicus* in the phylum Deferribacteres was found to use both the dicarboxylate/4-hydroxybutyrate cycle and the roTCA cycle (Slobodkin et al. 2019).

In addition, at hydrothermal vents, geothermal light might drive photosynthetic reactions using the photosynthetic pigments found in a few microorganisms. An obligately photosynthetic green sulfur anaerobic bacterium is reported to grow anaerobically using light, H₂S or elemental sulfur, and CO₂, by capturing geothermal radiation with isorenieratene carotenoid pigments and chlorosome BChl e, a photosynthetic antennae complex (Beatty et al. 2005). Additionally, geo-chip surveys of the inside of an active chimney found abundant RubisCO genes of photosynthetic organisms closely related to cyanobacteria and green sulfur bacteria, further suggesting the presence of microorganisms that utilize photoradiation for energy (Wang et al. 2009). Perez et al. (2013) speculated that species that have very high efficiency in the use of infrared photons up to 1300 nm, can achieve good rates of photosynthesis in hydrothermal vents.

Methanogens

Thermophilic and hyperthermophilic methanogens that perform hydrogenotrophic methanogenesis are believed to be the numerically largest and most important group in higher temperature regimes. These methanogens require higher concentrations of hydrogen (e.g., ≥ 17 mmol/L according to the experiments carried out with hyperthermophilic *Methanocaldococcus* species) to support chemolithoautotrophic growth than organisms that use coupled hydrogen oxidation for respiration of alternative electron acceptors, for example, oxygen, nitrate, ferric iron, and sulfate (Ver Eecke et al. 2012). From mesophilic to hyperthermophilic methanogens, MGG (Huber et al. 1982), 141, and MMJ media (Takai et al. 2002) could be used for anaerobic cultivation techniques.

Archaea—Euryarchaeota

Among the archaea, the order *Methanococcales* is one of the most commonly found methanogen autotrophs in hydrothermal environments. They convert H₂ and CO₂ from degassing magma and water–rock reactions into CH₄ and H₂O. Many methanogens have been isolated from hydrothermal vents (Table 1, Supplementary Table S1), including *Methanocaldococcus fervens* (Jeanthon et al. 1999), *M. indicus* (L’Haridon et al. 2003a, b), *M. infernus* (Jeanthon et al. 1998), *M. villosus* (Bellack et al. 2011), *M. vulcanius* (Jeanthon et al. 1999), *M. bathoardescens* (Stewart et al. 2015), *M. jannaschii* (formerly *Methanococcus jannaschii*) (Jones et al. 1983), *Methanopyrus kandleri* (Kurr et al. 1991), *Methanotorris formicicus* (Takai et al. 2004a), *Methanothermococcus*

okinawensis (Takai et al. 2002), and *Methanofervidicus abyssii* (Sakai et al. 2019). These marine organisms collectively have permissive growth temperatures ranging from 45–110 °C with respective optimums between 80 and 98 °C. They grow optimally at circumneutral pH (~6.5). Hydrogen and carbon dioxide can be used by all of these organisms to produce methane. Alternative substrates, such as formate, acetate, methanol, or methylamines, cannot be utilized. Tungsten, selenium, or yeast extract have always been found to significantly stimulate their growth. The methyl coenzyme-A reductase (McrA) gene is a key functional gene for methanogenesis present in all methanogenesis pathways (Luton et al. 2002).

Methane oxidizers

Hydrothermal ecosystems emit methane, which can originate from both geological and biological processes (Jannasch and Mottl 1985). Microbially mediated methane oxidation occurs with different electron acceptors, with sulfate being quantitatively the dominant electron acceptor for methane oxidation, because methane production occurs below the sulfate-rich zone in sediments. In hydrothermal vent communities, aerobic oxidation of methane (so-called methanotrophy) is also commonly found in microbial endosymbionts of vent animals (Nakagawa and Takai 2008) and the adjacent seawater (Valentine et al. 2001).

Gammaproteobacteria

The family *Methylococcaceae* in the class *Gammaproteobacteria* also uses methane as both an energy and carbon source and has been reported in deep-sea vents (Cerqueira et al. 2018).

Archaea—Euryarchaeota

Anaerobic oxidation of methane (AOM) is prevalent in methane-rich sediments found around some hydrothermal vents and may be responsible for consuming up to 75% of the methane produced by the vent (Wankel et al. 2012). Species that perform AOM include archaea of the phylum Euryarchaeota, referred to as anaerobic methane-oxidizing lineages (ANME). In the absence of pure cultures, high-throughput sequencing surveys, coupled with functional approaches and analytical monitoring of the metabolism based on $\delta^{13}\text{C}$ signatures of CH₄ and sulfate reduction rates, have demonstrated the ability of different ANME lineages (ANME-1, 2a-c, and 3) to oxidize methane coupled to the reduction of sulfate, and the presence of these archaea has been reported in several hydrothermal vent fields (Biddle et al. 2012; Merkel et al. 2013; Wankel et al. 2012). Efforts to cultivate the hydrothermal microorganisms carrying out AOM deserve to be continued.

Heterotrophs

There is also a rich heterotrophic microbial life at hydrothermal vents. Versatile heterotrophic *Alpha*- and *Gammaproteobacteria* have been found, for example, in different venting areas of the Menez Gwen hydrothermal field; from the diffuse fluid discharge points through the mixing gradients to the plumes and the surrounding seawater (Meier et al. 2016). Generalist species belonging to the genera *Marinobacter*, *Vibrio*, *Pseudoalteromonas*, *Halomonas*, *Pseudomonas*, and *Alcanivorax*, among others, have been repeatedly isolated from hydrothermal vent samples (Kaye et al. 2004; Ragu n s et al. 1997; Teske et al. 2000; Vetriani et al. 2005) and their abundance in vent fluids collected from the Pacific Ocean was estimated to be up to 28% of the total microorganisms (Kaye and Baross 2000). Strains of the phylum Deferribacteres are the heterotrophic taxa commonly found in deep-sea vents that can grow with organic acids and proteinaceous compounds as energy sources, for example, *Caldithrix abyssi* (Miroshnichenko et al. 2003b), *Deferribacter abyssi* (Miroshnichenko et al. 2003a), *D. autotrophicus* (Slobodkina et al. 2009a), *D. desulfuricans* (Takai et al. 2003a, b, c). A high fraction of heterotrophic microbial lineages related to cultivated members within the order *Thermotogales* and Bacteroidetes, and many novel lineages were also enriched using a novel in situ enrichment strategy (Stokke et al. 2020). Isolates in the phylum Deinococcus-Thermus have not only been isolated from hydrothermal vents but have often also been isolated from terrestrial hot springs. They include six genera, *Thermus* (Marteinsson 1999), *Marinithermus* (Sako et al. 2003), *Oceanithermus* (Miroshnichenko et al. 2003c; Mori et al. 2004), *Vulcanithermus* (Miroshnichenko et al. 2003d), *Rhodothermus* (Marteinsson et al. 2010) and *Rhabdothermus* (Steinsbu et al. 2011). Most of them are aerobic thermophilic heterotrophs capable of growing solely on complex organic substrates, while some can grow anaerobically with nitrate and elemental sulfur as electron acceptors.

At hydrothermal vent systems, alkanes are formed over relatively short geological time scales via thermogenic processes (including Fischer–Tropsch reactions and serpentinization) and often exist at high concentrations. Besides, the Guaymas Basin, is characterized by hydrothermal alterations that transform large amounts of organic carbon into methane, polycyclic aromatic hydrocarbons, low-molecular weight alkanes, and organic acids, allowing for diverse microbial communities to thrive (Dombrowski et al. 2017; He et al. 2013; Li et al. 2016a, b; Wang et al. 2019). Recently, the McrABG-like complex (Methyl coenzyme M reductase) involved in the oxidation of short-chain alkanes has been identified in various taxa, including *Candidatus Syntrophoarchaeum* spp., and closely related sequences have been detected in Guaymas Basin hydrothermal sediments (Wang

et al. 2019). Gene coding for enzymes involved in the activation of hydrocarbons for anaerobic degradation was detected in Bacteroidetes, Chloroflexi, Latescibacteria and candidate bacteria KSB1 phyla (Dombrowski et al. 2017). The archaeal genome of GoM-Arc1 is also predicted to encode novel pathways for short-chain hydrocarbon oxidation by alkyl-coenzyme M formation (Dombrowski et al. 2017). Using discrete temperature (25, 55, and 75 °C) anaerobic batch reactor incubations of hydrothermal sediments supplemented with individual alkanes (C1–C4), a novel sulfate-reducing lineage of Deltaproteobacteria, was identified as the likely taxa mediating the oxidation of C2–C4 alkanes (Adams et al. 2013). The hyperthermophilic archaeon *Geoglobus acetivorans* can also degrade aromatic compounds (Mardanov et al. 2015). Recently, after enrichment at low temperatures under high hydrostatic pressure (HP), several chemoautotrophs previously recognized as sulfur oxidizers, such as the SAR324 group, clade SUP05, and representatives of the genus *Sulfurimonas*, were identified as bacteria capable of degrading hydrocarbons (Wang et al. 2020).

Fermentative microorganisms are often associated with methanogens, because methanogenic activity maintains a hydrogen concentration low enough to make the fermentation pathway energetically favorable. Many fermenters have been isolated under anaerobic culture conditions, in the domain Archaea, such as the *Aeropyrum camini* (Nakagawa et al. 2004), Thermococcales (Teske et al. 2009), *Geoglobus* species (Kashefi et al. 2002), *Desulfurococcus* species (Jannasch et al. 1988) and ‘Firmicutes’ such as *Caminiella sporogenes* (Alain et al. 2002b), *Caloranaerobacter azorensis* (Wery et al. 2001b), *Caloranaerobacter ferrireducens* (Zeng et al. 2015a), *Anoxybacter fermentans* (Zeng et al. 2015b), and *Wukongibacter baidiensis* (Li et al. 2016).

The distribution, abundance, and function of microbial eukaryotes in hydrothermal environments are still poorly understood but recent progress has revealed considerable diversity. Fungi can be associated with a wide variety of substrates in deep-sea hydrothermal vent systems, including seawater, sediments, minerals, and animals such as shrimps, mussels, tubeworms, corals, sponges, and gastropods (Luo and Pang 2014). At the Lucky Strike and Rainbow hydrothermal fields along the Mid-Atlantic Ridge, the presence of ciliates related to *Stylonychia pustulata*, fungi, and alveoloid-related metazoans were revealed through 18S rRNA gene surveys (Lopez-Garcia et al. 2003). Black yeast (order Chaetothyriales) was found in mussels (*Bathymodiolus brevior*) at the Mussel Hill hydrothermal vent in the Fiji Basin (Van Dover et al. 2007). Burgaud et al. (2009) focused on the occurrence and diversity of culturable filamentous fungi in deep-sea hydrothermal vents and isolated 62 filamentous Ascomycota fungi. Molecular methods revealed unsuspected species diversity in three of the five fungal phyla and discovered a new branch of Chytridiomycota, forming

an ancient evolutionary lineage and many unknown species in Chytridiomycota, Ascomycota, and Basidiomycota (Calvez et al. 2009). Connell et al. (2009) investigated fungal diversity in actively growing Fe-oxide mats and basalt rock surfaces from deep-sea hydrothermal vents. A diverse fungal community, belonging to the genera *Pichia*, *Cryptococcus*, *Rhodospordium*, *Rhodotorula*, *Dioszegia*, *Clavispora*, *Sporidiobolus*, *Aremonium*, *Geomyces*, *Aspergillus*, and *Fomitopsis*, was recovered. All yeast species obtained can produce siderophores for Fe acquisition and utilization, and one isolate, *Rhodotorula graminis*, could oxidize Mn (II), suggesting that fungi in deep-sea hydrothermal vent ecosystems may play a role in biomineralization processes (Connell et al. 2009). Malassezia-like fungi and members of the order *Malasseziales* are exceedingly widespread and ecologically diverse, having even been found in hydrothermal vents (Amend et al. 2014). The study analyzed the species richness and abundance of fungi from a South Mid-Atlantic Ridge hydrothermal site, and found that the fungal community structures in the chimney samples were distinct from those in three sulfide samples, where the Ascomycota was significantly more abundant (2–3 orders) than the Basidiomycota (Xu et al. 2017). Xu et al. (2018) also found that there was a high fungal diversity, with 723 operational taxonomic units (OTUs) belonging to 79 taxa (Ascomycota and Basidiomycota contributed to 99% of all samples), in the deep-sea hydrothermal sediments of Southwest Indian ridge.

Sulfur cycle

Microbial communities at hydrothermal vents convert reduced sulfur, such as H_2S , produced by geological activity into other more oxidized forms, such as sulfite, sulfate and elemental sulfur for energy production or assimilation into organic molecules (Sievert et al. 2008). Sulfide is abundant in hydrothermal vents, with concentrations ranging from one to several tens of mmol/L, whereas the surrounding ocean water generally has concentrations of only a few nanomolars (Radfordknoery et al. 2001).

Sulfur-oxidizers

Sulfide from hydrothermal vents is available to various sulfur-oxidizing microorganisms using oxygen (or nitrate) from the upper layers of the sea. Many reduced sulfur compounds, such as elemental sulfur (S^0), hydrogen sulfide (H_2S), methanethiol (CH_3SH), dimethylsulfide [$(CH_3)_2S$], pyrrhotite ($Fe_{1-x}S$), pyrite (FeS_2), chalcopyrite (CuS), and sphalerite (ZnS) are used as electron donors by microorganisms (Orcutt et al. 2011). Sulfide and thiosulfate oxidation occur in sulfide-rich basalt-hosted hydrothermal fields, which provide the greatest energy yields of the hydrothermal vent biotopes (McCollom et al. 2007). Meier et al. (2017)

found that representatives of the genus *Sulfurovum* in the phylum Campylobacterota thrive, mainly attached to surfaces exposed to diffuse venting, while the SUP05-clade dominated the bacterioplankton in highly diluted mixtures of vent fluids and seawater (Meier et al. 2017). Campylobacterota and *Gammaproteobacteria* also dominated the microbiota of chemosynthetic metazoans, such as polychaetes, mussels, gastropods, and shrimps (Nakagawa 2008). The sulfur-oxidizing Aquificae, however, generally occupy a narrow thermophilic niche (Reysenbach et al. 2001) of this singular ecosystem, and sulfur-oxidizing archaea (order *Sulfolobales*) are quite rare in the marine environment (Friedrich et al. 2005).

Bacterial sulfur-oxidation pathways include: sulfide oxidation to elemental sulfur by sulfide dehydrogenase (FccAB) or sulfide-quinone reductase (Sqr), which is further oxidized to sulfate by the reverse sulfate reduction pathway or by SoeABC in the cytoplasm. Thiosulfate can be oxidized to sulfate by the Sox system (SoxABCDXY) in the periplasm. These systems are classified into two different types: (1) the reverse sulfate reduction and (2) the Sox multienzyme system. Reverse sulfate reduction is a reversal of the sulfate reduction pathway in which sulfide is oxidized to sulfate via sulfite. This pathway uses the same families of enzymes as the sulfate reduction pathway, such as dissimilatory sulfite reductase (Dsr), adenyphosphosulfate reductase (Apr), and sulfate adenylyltransferase (Sat). Sox multienzyme complexes catalyze the oxidation of inorganic sulfur compounds. Four protein components, SoxYZ, SoxXA, SoxB, and SoxCD are required for the complete oxidation of thiosulfate to sulfate (Wasmund et al. 2017; Yamamoto and Takai 2011). However, in some strains, SoxCD was not necessary (Friedrich et al. 2005). The deep-sea Campylobacterota possesses versatile energy metabolisms: (i) they can couple the oxidation of hydrogen to the respiration of sulfur using hydrogenases and polysulfide reductase (Psr); (ii) they can couple the oxidation of sulfur compounds using the Sox multienzyme system, to the respiration of oxygen or nitrate; and (iii) they can also couple the oxidation of hydrogen to the reduction of oxygen or nitrate (Yamamoto and Takai 2011). Most of the chemotrophic sulfur-oxidizing Gammaproteobacteria harbor both incomplete Sox and complete Dsr systems, similar to the phototrophic gammaproteobacterial species of the family *Chromatiaceae* (Nakagawa and Takai 2008). Nevertheless, there are some exceptions, such as the species *Thiomicrospira crunogena* that possesses a complete Sox system but lacks the Dsr system (Scott et al. 2006).

Strains of the phyla Proteobacteria, Campylobacterota, Aquificae, and Thermodesulfobacteria that have so far been isolated from hydrothermal vents are shown in Fig. 1 and listed in Table 1 and Supplementary Table S1. They have been isolated under various conditions using different cultural methods, including thiosulfate-based solid media,

oxygen-sulfide gradient tubes, or liquid media with controlled atmospheres, under lithoautotrophic conditions or heterotrophic conditions (Adair and Gundersen 1969; Ruby et al. 1981; Takai et al. 2003a, b, c; 2009).

Campylobacterota

Campylobacterota (formerly *Epsilonproteobacteria*), which are highly abundant in hydrothermal vents, take advantage of their versatile metabolisms to colonize different niches, where conditions are mesophilic to moderately thermophilic. Takai et al. (2003a, b, c) were the first to report that various kinds of sulfur-oxidizing Campylobacterota inhabit marine hydrothermal vents. Numerous novel mesophilic sulfur-oxidizers of this phylum have been isolated from these environments, including the most abundant genus *Sulfurimonas* (Inagaki et al. 2003), *Sulfurovum* species (Inagaki et al. 2004), and the genus *Lebetimonas* (Takai et al. 2005). Representatives of this genus have been isolated from hydrothermal vent lithological samples and vent animals. These include *Sulfurovum lithotrophicum* (Inagaki et al. 2004), *Sulfurovum aggregans* (Mino et al. 2014), *Sulfurovum riftiae* (Giovannelli et al. 2016), and *Sulfurovum denitrificans* (Mori et al. 2018). Most strains of the genus *Sulfurovum* grow chemolithoautotrophically using sulfur as an energy source, under mesophilic temperatures. The only exception is *S. aggregans*, which is a strictly hydrogen-oxidizing, sulfur-, nitrate-, and thiosulfate-reducing mesophilic bacteria (Mino et al. 2014). The genus *Sulfurimonas* has been reported to be one of the dominant groups in hydrothermal vent fields and may represent 70% and 20% of the bacterial abundance at sites in plume waters and diffuse fluids, respectively, e.g., in the Axial seamount in the Pacific Ocean (Akerman et al. 2013; Perner et al. 2013). The type species of this genus is *Sulfurimonas autotrophica* OK10, isolated from deep-sea hydrothermal vent sediments, can use molecular hydrogen, elemental sulfur, or thiosulfate as the energy source, carbon dioxide as the sole carbon source, ammonium or nitrate as the sole nitrogen source, and elemental sulfur, sulfide, or thiosulfate as the sulfur source (Inagaki et al. 2003). The species *Sulfurimonas parvalvinellae* from polychaete nests and *Sulfurimonas indica* from sulfide chimney were also capable of growth using thiosulfate, sulfide or elemental sulphur as the sole energy source (Takai et al. 2006; Hu et al. 2020).

Proteobacteria

Several sulfur-oxidizing bacteria (SOB), belonging to the class *Gammaproteobacteria*, have also been isolated from hydrothermal habitats (Table 1, Supplementary Table S1). The main sulfur-oxidizing gammaproteobacterial taxa are in the order *Thiotrichales*, including *Hydrogenovibrio crunogenus* (formerly *Thiomicrospira crunogena*) (Jannasch et al. 1985), *Hydrogenovibrio thermophile* strain I78 (formerly

T. thermophile) (Takai et al. 2004d), *H. thermophilus* strain S5 (Jiang et al. 2017), *Thiomicrohabdus indica* (Liu et al. 2020); *Thiomicrohabdus* sp. Kp2 is mentioned in the reclassification of these genera (Boden et al. 2017b). *T. crunogena* uses the energy of reduced sulfur compounds (sulfide, thiosulfate, and elemental sulfur) for carbon fixation and cellular maintenance (Jannasch et al. 1985). Its main carbon source is the CO₂ released from hydrothermal vents. Given its changable environment, *T. crunogena* has a carbon concentrating mechanism that allows it to grow in the presence of low CO₂ concentrations, by increasing cellular affinity for both HCO₃⁻ and CO₂ to generate a high concentration of intracellular dissolved inorganic carbon under low CO₂ conditions, such as seawater, near hydrothermal vents (Dobranski et al. 2005).

Some thermophilic SOB of the order *Chromatiales* (Gammaproteobacteria) have also been isolated from pure cultures, such as *Thioprofundum lithotrophica* (Takai et al. 2009) and *T. hispidum* (Mori et al. 2011). Another example, *Thiolapillus brandeum* was isolated from a chimney fragment and grows on sulfur, thiosulfate, and tetrathionate, using oxygen and nitrate as terminal electron acceptors (Nunoura et al. 2014). *Salinisphaera hydrothermalis* strain EPR70 can grow under aerobic chemolithoautotrophic conditions in the presence of thiosulfate and CO₂, or heterotrophically with acetate or n-alkanes as sole carbon and energy sources, and in complex artificial seawater medium (Crespomedina et al. 2009). *Guy-parkeria hydrothermalis* (formerly *Thiobacillus hydrothermalis*) grows obligatorily under lithoautotrophic conditions using thiosulfate, tetrathionate, sulfide, and sulfur as electron donors (Boden 2017a; Durand et al. 1993). Using pressure cultivation approaches, *Piezobacter thermophilus*, affiliated with the family *Rhodobacteraceae* within the Alphaproteobacteria, was isolated. It is a facultative chemoautotroph, capable of both chemolithoautotrophic growth with H₂ and S oxidations and organotrophic growth with complex organics or organic acids using nitrate and O₂ as electron acceptors. Interestingly, chemolithoautotrophic growth is observed strictly under piezophilic conditions and under organotrophic growth conditions, this strain grows only at atmospheric pressure (0.1 MPa) (Takai et al. 2009).

In addition, giant microbial mats and SOB snowblowers have been identified as the filamentous bacteria *Beggiatoa*, such as *Arcobacter* sp. and as members of the SUP05-clade (Moussard et al. 2006; Nelson et al. 1989).

Aquificae

Species in the order *Aquificales* are thermophilic hydrogen- and/or sulfur-oxidizers. A variety of strains and environmental clones belong to the genera *Aquifex* (Reysenbach et al. 2002), *Hydrogenivirga* -including *Hydrogenivirga okinawensis* (Nunoura et al. 2008a) and *Persephonella* -including *Persephonella marina*, *P. guaymasensis* (Gotz

et al. 2002) and *P. hydrogeniphila* (Nakagawa et al. 2003) have been isolated or detected in deep-sea hydrothermal environments. These can grow with hydrogen, elemental sulfur, or thiosulfate as electron donors and with nitrate or O₂ as terminal electron acceptors.

Thermodesulfobacteria

An extremely thermophilic, anaerobic, chemolithoautotrophic bacterium *Thermosulfuriphilus ammonigenes* can grow anaerobically with inorganic carbon as a carbon source, with elemental sulfur as an electron donor and nitrate as an electron acceptor producing sulfate and ammonium. This strain is also able to grow by disproportionation of elemental sulfur, thiosulfate, and sulfite (Slobodkina et al. 2017).

Sulfur-reducers

Microorganisms that perform sulfur reduction coupled with the oxidation of H₂, methane, small chain fatty acids, or other carbon compounds are one of the main drivers of the hydrothermal carbon cycle. Sulfate reduction is one of the most important processes from low temperature to high temperature (4–90 °C) in highly anoxic areas of the hydrothermal environment, for example, hydrothermal sediments (Frank et al. 2013), hydrothermal fluid, sulfide structures, and *Alvinellid* worm sheaths (Bonchosmolovskaya et al. 2011). Elemental sulfur can also be used to detoxify dihydrogen in fermentation processes carried out by many *Thermococcales* and some representatives of *Desulfurococcales* (Bonchosmolovskaya et al. 1994, 2011; Teske et al. 2009). Molecular inventories of Guaymas hydrothermal sediments, targeting the 16S rRNA and functional genes such as the dissimilatory sulfite reductase (*dsrAB*), revealed the existence of a major clade closely related to the acetate-oxidizing deltaproteobacterial genus *Desulfobacter*, and a few clones affiliated with *Desulfobacterium niacini*, *Desulfobacula toluolica*, and *Desulfotignum balticum* (Dhillon et al. 2003).

Numerous sulfate, thiosulfate, and sulfur reducers, isolated from hydrothermal vents, belong to different taxonomic groups: Archaea, Campylobacterota, Thermodesulfobacterium, Thermotogae, and *Deltaproteobacteria* (Table 1). For anaerobic, heterotrophic sulfur-reducing thermophiles, such as members of *Thermococcales* and *Thermotogales*, MJYPS medium, and *Thermococcales* Rich Medium (TRM) with sulfur as an electron acceptor are often used under an atmosphere of N₂ (Takai et al. 2000; Zeng et al. 2009). For hydrogen-oxidizing, sulfur-reducing autotrophs and mixotrophs such as members of *Desulfurococcales*, *Desulfurobacteriales*, *Nautiliales*, and *Deferribacteres*, KA22 (Alain et al. 2002a), MJAYS-YTF (Nakagawa et al. 2005a, b), and MJAYS media (Takai et al. 2003a, b, c) are frequently used and incubated in

an atmosphere of H₂/CO₂. For anaerobic dissimilatory Fe(III)- and/or sulfate-reducers, such as members of the *Archaeoglobales*, *Deferribacteres*, *Thermodesulfobacteria*, and *Deltaproteobacteria*, MJNS and MMJHFe media are often used (Takai et al. 2003a, b, c, 2008).

Campylobacterota

The genera *Caminibacter*, *Nautilia*, *Lebetimonas*, and *Cetia* of the order *Nautiliales* have cultured representatives that include autotrophs and mixotrophs, which couple the oxidation of hydrogen to the reduction of sulfur- or nitrogenous compounds to produce H₂S and NH₃. These moderately thermophilic bacteria have been found in association with invertebrates, chimney edifices, or in situ colonization devices. At present, the genus *Caminibacter* encompasses the species *Caminibacter hydrogeniphilus* (Alain et al. 2002a), *C. mediatlanticus* (Voordeckers et al. 2005), and *C. profundus* (Miroshnichenko et al. 2004). The genus *Nautilia* contains four species of anaerobic, thermophilic chemolithotrophs: *Nautilia lithotrophica* (Miroshnichenko et al. 2002), *N. abyssi* (Alain et al. 2009), *N. profundicola* (Smith et al. 2008), and *N. nitratreducens* (Perezrodriguez et al. 2010). The genus *Lebetimonas* encompasses two species: *Lebetimonas acidiphila* (Takai et al. 2005) and *L. natsushimae* (Nagata et al. 2017). The genus *Cetia* has been more recently cultivated and encompasses only the species *Cetia pacifica*, which branches separately from the three other genera that are close to each other, *Caminibacter*, *Nautilia*, and *Lebetimonas*, within the family *Nautiliaceae* (Grosche et al. 2015).

Hydrogenimonas thermophila, in the order *Campylobacterales*, can use molecular hydrogen as the sole energy source and carbon dioxide as the sole carbon source. Molecular oxygen, nitrate, or elemental sulfur (S⁰) can act as electron acceptors for its growth (Takai et al. 2004b). *Thiofractor thiocaminus* is a strict anaerobic, obligate chemolithoautotroph, which can grow using molecular hydrogen as its sole energy source, carbon dioxide as its sole carbon source, ammonium or nitrate as its sole nitrogen source, and elemental sulfur as a terminal electron acceptor. This isolate is distantly related to the taxa described above (Makita et al. 2012). Recently, Wang et al. (2020) reported that most species of *Sulfurimonas* have their potentials in sulfur reduction, with periplasmic and cytoplasmic polysulfide reductases (PsrA₁B₁CDE and PsrA₂B₂).

Proteobacteria

Some *Deltaproteobacteria*, such as *Pseudodesulfovibrio*, *Desulfovibrio*, *Desulfonauticus*, and *Desulfothermus* species have been isolated from the hydrothermal ecosystem (Table 1, Supplementary Table S1). *Pseudodesulfovibrio indicus* was isolated from a serpentinized peridotite sample collected from a hydrothermal area of the Indian Ocean. This

strain uses organic acid and hydrogen as energy sources and sulfate, thiosulfate, sulfite, fumarate, and nitrate as terminal electron acceptors (Cao et al. 2016). *Desulfovibrio hydrothermalis*, isolated from a chimney sample collected at 13° N on the East-Pacific Rise, can use H₂/CO₂, lactate, formate, ethanol, choline, and glycerol as electron donors. It can respire sulfate, sulfite, and thiosulfate (Alazard et al. 2003). *Pseudodesulfovibrio indicus* and *Desulfovibrio hydrothermalis* have both been reported as piezophilic taxa with an optimal growth pressure of 10 MPa. *Desulfonauticus submarinus*, isolated from a matrix of *Alvinella* and *Riftia* originating from the EPR 13° N, can grow on H₂/CO₂, oxidize formate, and use acetate as a carbon source. Sulfate, sulfite, thiosulfate, and elemental sulfur are used as terminal electron acceptors during hydrogen oxidation (Audiffren et al. 2003). *Desulfothermus okinawensis* is a thermophilic and obligate heterotrophic sulfate-reducing bacterium that was isolated from a deep-sea hydrothermal field at the Yonaguni Knoll IV in the Southern Okinawa Trough (Nunoura et al. 2007a).

Nitrospirae

Frank et al. (2013) proposed that Thermodesulfobacter-like organisms may have a role in sulfate reduction in warmer parts of the hydrothermal ecosystem and that heterotrophic sulfate reduction may be quite common in deep-sea vents. Other studies based on metagenome and metaproteome analyses have shown that sulfate-reducing Nitrospirae dominate most inactive chimney communities (Meier et al. 2019).

Firmicutes

The gram-positive taxon *Desulfohalotomaculum tongense* (formerly *Desulfotomaculum tongense*) in the class *Clostridia*, isolated from hydrothermal sediment collected at the Tofua Arc in the Tonga Trench, was found to use pyruvate and H₂ as electron donors and sulfate, sulfite, and thiosulfate as electron acceptors (Cha et al. 2013).

Aquificae

Aquificales represent a deeply rooted phylogenetic lineage within the bacterial domain and, with few exceptions, it includes thermophilic or hyperthermophilic lithoautotrophs utilizing H₂, elemental sulfur, sulfide, or thiosulfate as energy sources and oxygen, nitrate, or elemental sulfur as electron acceptors. This metabolically versatile group plays a significant role in deep-sea hydrothermal ecosystems as primary producers of organic matter in anaerobic zones (Reysenbach et al. 2001). Members of the family *Desulfurobacteriaceae*, such as the genera *Desulfurobacterium* and *Thermovibrio*, are sulfur-reducing chemolithoautotrophs using hydrogen as the sole electron donor. This family includes the taxa *Desulfurobacterium atlanticum* (L'Haridon et al. 2006a), *Desulfurobacterium pacificum* (L'Haridon et al. 2006a),

Desulfurobacterium thermolithotrophum (L'Haridon et al. 1998), '*Desulfurobacterium crinifex*' (Alain et al. 2003), *Desulfurobacterium indicum* (Cao et al. 2017), and *Therulfurobacterium guaymasensis* (L'Haridon et al. 2006b), all of which have been isolated from deep-sea hydrothermal systems. For example, *Desulfurobacterium indicum*, which was isolated from a sulfide sample from an Indian Ocean hydrothermal vent, is an obligate chemolithoautotroph combining thiosulfate, sulfur, or nitrate respiration to H₂ oxidation (Cao et al. 2017). *Thermosulfidibacter takaii*, which was isolated from a deep-sea hydrothermal field at the Southern Okinawa Trough, is an obligately anaerobic chemolithotroph coupling hydrogen oxidation coupled to sulfur reduction (Nunoura et al. 2008b).

Thermodesulfobacterium

In the *Thermodesulfobacteria* class, *Thermodesulfobacterium hydrogeniphilum* (Jeanthon et al. 2002), *Thermodesulfatator indicus* (Moussard et al. 2004), *Thermodesulfatator atlanticus* (Alain et al. 2010), and *Thermodesulfatator autotrophicus* (Lai et al. 2016) all are autotrophic sulfate-reducing bacteria; the growth of a few of these strains can be stimulated by organic compounds.

Thermotogae

In the Thermotogae phylum, the genera *Thermosipho*, *Kosmotoga*, and *Marinitoga* appear to be environmentally relevant in the deep-sea hydrothermal environment. These microorganisms can ferment a variety of carbohydrates as well as complex organic matter. The addition of yeast extract is often required for their growth. The products of glucose fermentation are acetate, H₂, and CO₂. H₂ inhibits their growth, and these taxa often grow better in the presence of sulfur compounds, such as thiosulfate, elemental sulfur, cysteine, or thiosulfate, which is reduced to hydrogen sulfide, a less toxic compound than dihydrogen. The genus *Marinitoga* includes the species *Marinitoga camini* (Wery et al. 2001a), *M. hydrogenitolerans* (Postec et al. 2005), *M. okinawensis* (Nunoura et al. 2007b), and *M. piezophila* (Alain 2002c). *Thermosipho* spp. are also frequently isolated from deep-sea hydrothermal vents, for example, *Thermosipho melanesiensis* (Antoine et al. 1997), *T. japonicus* (Takai and Horikoshi 2000), *T. atlanticus* (Urios et al. 2004), *T. affectus* (Podosokorskaya et al. 2011), *T. globiformans* (Tomohiko et al. 2011), and *T. activus* (Podosokorskaya et al. 2014). *Kosmotoga pacifica*, in the genus *Kosmotoga*, was isolated from hydrothermal sediments mixed with fragments of inactive sulfide chimneys collected in the South Pacific Ocean (L'Haridon et al. 2013).

Deferribacteres

Some strains in the genus *Deferribacter*, such as *Deferribacter desulfuricans*, *D. abyssis*, and *D. autotrophicus*, can

use elemental sulfur as a terminal electron acceptor (Miroshnichenko et al. 2003a; Takai et al. 2003a, b, c).

Archaea—Euryarchaeota

Deep-sea hydrothermal vent Euryarchaeota 2 (DHVE2) is extremely widespread in marine hydrothermal ecosystems and may account for up to 15% of the archaeal 16S rRNA gene sequences, suggesting that they are important players in deep-sea hydrothermal habitats (Flores et al. 2012). The only representative of this group, *Aciduliprofundum boonei*, is an obligate thermoacidophilic heterotrophic archaeon, which uses electron acceptors, such as elemental sulfur, sulfate, and ferric iron and is capable of growing from pH 3.3–5.8, and between 60 and 75 °C (Reysenbach et al. 2006).

Archaea of the order *Thermococcales*, distributed in three genera (i.e., *Thermococcus*, *Pyrococcus*, and *Palaeococcus*), have versatile physiologies to thrive in active hydrothermal vents, sediments, and even below the surface under hydrothermal vents (Teske et al. 2009; Zeng et al. 2013). Eighteen *Thermococcus* species, five *Pyrococcus* species, and two *Palaeococcus* species have been isolated from hydrothermal vents (Table 1, Supplementary Table S1), for example, *Pyrococcus abyssi* (Erauso et al. 1993), *Pyrococcus horikoshii* (González et al. 1998), *Pyrococcus glycovorans* (Barbier et al. 1999), *Pyrococcus yayanosii* (Birrien et al. 2011; Zeng et al. 2009), *Pyrococcus kulkankii* (Callac et al. 2016), *Palaeococcus ferrophilus* (Takai et al. 2000), and *Palaeococcus pacificus* (Zeng et al. 2013). All *Thermococcales* species can ferment a variety of organic compounds, such as peptides, amino acids, organic acids, and diverse sugars, with S^0 as the electron acceptor. The growth of many of them is better in the presence of sulfur compounds, which are reduced to hydrogen sulfide. Some strains, such as *Pyrococcus kulkankii* or *Palaeococcus ferrophilus*, require sulfur or Fe (II) in the culture medium to grow, and some others can grow via carboxydutrophy. *Thermococcales* strains require high temperatures to grow; some of them also can survive for a long time in cold conditions, such as hydrothermal sediments and then quickly respond to the high temperature and energy supply by complex organic matter or elemental sulfur (Mora et al. 2014; Zeng et al. 2020). Piezophilic features are also widespread in this order (Dalmasso et al. 2016; Zeng et al. 2009) and some strains tolerate high doses of gamma radiation (Jolivet et al. 2004).

Archaea—Crenarchaeota

In the phylum Crenarchaeota, *Pyrolobus fumarii* is an archaeon that has long held records for high-temperature growth, with growth observed between 90 °C and 113 °C (optimum 106 °C) (Blochl et al. 1997). It is a facultatively aerobic obligate chemolithoautotroph, gaining energy by H_2 -oxidation. It can respire NO_3^- , $S_2O_3^{2-}$, and low concentrations of O_2 (up to 0.3% v/v), which are, respectively,

reduced to NH_4^+ , H_2S , and H_2O (Blochl et al. 1997). In addition, another study on the colonization of hydrothermal chimneys of different ages showed that chemolithoautotrophic Crenarchaea of the genus *Ignicoccus* and their symbionts *Nanoarchaeum* dominated the initial colonization of high-temperature chimneys, while heterotrophs related to Thermococcales are more abundant in mature edifices (McCliment et al. 2006). The taxa *Ignicoccus islandicus* and *I. pacificus*, isolated from the Kolbeinsey Ridge in northern Iceland and the Pacific Ocean, gain energy by the reduction of elemental sulfur to hydrogen sulfide using molecular hydrogen as an electron donor (Huber et al. 2000, 2002).

Sulfur-disproportionators

Disproportionation (dismutation) of inorganic sulfur compounds allows cells to gain energy for growth using a sulfur compound in an intermediate oxidation state as both an electron donor and acceptor, thus minimizing their needs relative to the chemical composition of the biotope (Slobodkin and Slobodkina 2019). It is a type of inorganic fermentation.

Sulfur disproportionators have recently been found in natural thermal ecosystems. Species known so far to carry out sulfur compound dismutation belong to the class Deltaproteobacteria within the phylum Proteobacteria, the class Clostridia within the phylum Firmicutes, and the phylum Thermodesulfobacteria (Slobodkin and Slobodkina 2019).

Thermodesulfobacteria

Thermosulfurimonas dismutans and *Thermosulfuriphilus ammonigenes* thrive in deep-sea hydrothermal vents of the Lau spreading center, in the Pacific (Slobodkin et al. 2012, 2017). Genome analyses revealed that *Thermosulfurimonas dismutans* and *Thermosulfuriphilus ammonigenes* contain a full set of genes for dissimilatory sulfate reduction, including ATP sulfurylase, the AprA and AprB subunits of adenosine-5'-phosphosulfate reductase, and dissimilatory sulfite reductase. While these species cannot grow via sulfate-reduction, these enzymes could be involved in the reductive path of dismutation. These genomes also contain several membrane-linked molybdopterin oxidoreductases that might also be involved in sulfur metabolism as well as subunits of thio-sulfate, polysulfide, or tetrathionate reductases (Mardanov et al. 2016). The routes of dismutation of inorganic sulfur compounds are still unknown and there is likely to be more than one.

Deltaproteobacteria

Dissulfuribacter thermophilus can disproportionate all three types of sulfur compounds (sulfide, thiosulfate, and elemental sulfur) (Slobodkin et al. 2013). Genomic and transcriptomic analyses of epibionts on the hydrothermal vent shrimp *Rimicaris exoculata* have revealed that “Candidatus

Desulfobulbus rimicarensis” an uncultivated deltaproteobacterial epibiont, utilizes the Wood-Ljungdahl pathway for carbon assimilation and harvests energy via sulfur disproportionation (Jiang et al. 2020).

Hydrogen cycle

Hydrogen oxidation and methanotrophy in hydrogen-rich ultramafic-hosted systems are estimated to be the major sources of metabolic energy available in this type of hydrothermal setting (McCollom 2007). There is also evidence of hydrogen conversion capacity in sulfur-oxidizing metazoan symbionts belonging to Campylobacterota and Proteobacteria (Jiang et al. 2020; Miyazaki et al. 2020; Petersen et al. 2011). Terminal electron acceptors commonly used by hydrogen-oxidizing microorganisms are sulfate, iron (III), and nitrate (Vignais et al. 2007) but also elemental sulfur and different metals, such as Mn (III/IV), U (VI), Cr (VI), Co (III), and Tc (VII) (Liu et al. 2002; Nakagawa et al. 2008). Genes encoding hydrogenase have been selectively amplified (group 1 and F420-reducing [NiFe]-hydrogenases) in hydrothermal samples or mined from metagenomes and metatranscriptomes (consisting of the whole genetic information) of vent-derived samples (Adam and Perner 2018). According to the hydrogenase classification of Sondergaard et al. (2016), the [NiFe]-hydrogenases of *Nautilia profundicola*, *Hydrogenovibrio crunogenus*, and *Desulfivibrio vulgaris* belong to group 1b, that of *Aquifex aeolicus* belong to group 1d, and that of *Geoglobus acetivorans* belong to group 1k. The majority of the [NiFe] hydrogenase genes identified in these hydrothermal datasets could be phylogenetically affiliated with members of the Campylobacterota phylum, to other Proteobacteria (Gamma and Delta), and archaeal phyla (Adam and Perner 2018). Hydrogenase is also found in a variety of archaea and bacteria, such as *Thermococcales* and Firmicutes, for catalyzing hydrogen production.

Hydrogen-oxidizing microbes isolated from hydrothermal vents include Campylobacterota, Proteobacteria (*Gamma*- and *Delta*-), Aquificae, Thermodesulfobacteria, and Archaea (Fig. 1, Table 1). The enrichment and purification of hydrogen-oxidizing bacteria could be conducted, for example, in MMJHS medium with low or no oxygen content in the headspace (Takai et al. 2003a, b, c).

Campylobacterota

Campylobacterota plays a major role in hydrogen conversion and hydrogen-based primary production within hydrothermal vents (Adam and Perner 2018). Most isolates in the phylum Campylobacterota are characterized by versatile metabolisms and only a few isolates are strictly hydrogen oxidizers (i.e., they are not capable of using any

other tested organic or inorganic electron donor), such as the mesophilic *Sulfurovum aggregans* (Mino et al. 2014).

Proteobacteria

Through metagenomic analysis of hydrogenases, it was found that H₂-oxidizing Betaproteobacteria belonging to the order Burkholderiales thrive in shallow, aerobic to anoxic transition zones (Brazelton et al. 2012). Gammaproteobacteria has also been demonstrated to be relevant for microbially mediated hydrogen cycling (Adam and Perner 2018). Strains of the genera *Hydrogenovibrio* and *Thiomicrospira* have been shown to use hydrogen (Hansen et al. 2015, 2016). Metagenomic and metatranscriptomic analyses revealed that the numerous deep-sea bacteria in clade SUP05 contain highly expressed genes coding for group 1 [NiFe]-hydrogenase for H₂ oxidation (Anantharaman et al. 2013). Deltaproteobacteria may also contribute to hydrogen consumption in anoxic hydrothermal vent habitats (Adam and Perner 2018). The vent-originating autotrophic, hydrogen-oxidizing *Deltaproteobacteria* are nearly all characterized as thermophiles with optimal temperature between 50 and 61 °C, such as *Desulfacinum hydrothermales* or *Dissulfuribacter thermophilus* (Siefert and Kuever 2000; Slobodkin et al. 2013). One iron-oxidizing Zetaproteobacteria, named *Ghiorsea bivora*, can also use molecular hydrogen (H₂) as the sole electron donor and oxygen as a terminal electron acceptor for energy production (Mori et al. 2017).

Aquificae

Some members of the Aquificales, such as *Thermovibrio ammonificans*, *T. guaymasensis*, *Balnearium lithotrophicum* and members of the genus *Desulfurobacterium*, use hydrogen as the only energy source for autotrophic growth (L’Haridon et al. 2006a; b; Takai et al. 2003a, b, c; Vetriani et al. 2004).

Thermodesulfobacteria

In the phylum Thermodesulfobacteria, the thermophilic sulfate-reducing bacteria *Thermodesulfobacterium hydrogeniphilum*, *Thermodesulfatator atlanticus*, and *Thermodesulfatator indicus* are also known to use H₂ as an electron donor and sulfate as an electron acceptor for autotrophic growth (Alain et al. 2010; Jeanthon et al. 2002; Moussard et al. 2004).

Archaea

Except for thermophilic methanogens of the order *Methanococcales* (mentioned in 2.1.2), other hydrogen-oxidizing hyperthermophilic archaea include *Geoglobus ahangari* (Kashefi et al. 2002), *G. acetivorans* (Slobodkina et al. 2009b), and *Pyrodictium delaneyi* (Lin et al.

2016), which thrive at lower hydrogen concentrations than methanogens.

Nitrogen cycle

Generally, high-temperature fluids (up to 350 °C) contain high levels of NH_4^+ , while low-temperature diffuse fluids (< 50 °C) contain NO_3^- (Butterfield et al. 1997; Lam et al. 2004). These nitrogenous compounds are discharged from hydrothermal vents and serve as potentially important substrates and nitrogen sources for chemolithotrophic bacteria (Bourbonnais et al. 2012; Butterfield et al. 1997; Lam et al. 2004). The deep ocean also contains the largest reservoir of nitrogen available to hydrothermal vents with about 0.59 mmol/L of dissolved nitrogen gas (Bourbonnais et al. 2012).

Ammonium-oxidizers

Ammonium is the dominant species of dissolved inorganic nitrogen and can be produced by mixing water masses below hydrothermal vents and discharged in vent fluids. The quantities of available ammonium vary from one vent to another, from one end-member fluid to another, and with the geological settings/activity. NH_4^+ oxidation is prevalent in hydrothermal plumes, active smokers, animals, and microbial mats. A removal rate of 15 nmol/L NH_4^+ day⁻¹ was observed for incubations carried out at 200 atm with plume samples from the Endeavor Segment of the Juan de Fuca Ridge (Cowen et al. 1998). Xu et al. (2014) found that ammonium oxidizing archaea (AOA) were much more diverse but less abundant than ammonium-oxidizing bacteria (AOB) in samples collected at the Mid-Atlantic Ridge and in the South Atlantic Ocean. By combining 16S rRNA gene sequence analyses, ladderane lipid analyses, and measurements of a ¹⁴N¹⁵N dinitrogen production in isotope-pairing experiments, it was found that active ammonium-oxidizers at deep-sea hydrothermal vents are related to known anammox bacteria (Byrne et al. 2009). No cultures of ammonium-oxidizing archaea (AOA), ammonium-oxidizing bacteria (AOB), or nitrite-oxidizing bacteria (NOB) have been reported from hydrothermal vents.

Archaea—Crenarchaeota

The proportion of the marine group I (MGI) Crenarchaeota, the group that includes the ammonium-oxidizing isolate “*Candidatus Nitrosopumilus maritimus*”, was found to vary from 2–28% of the total prokaryotic community within the first 10 m from the venting source, depending on the vent field and chimney (Takai et al. 2004c). Metagenomic and metatranscriptomic analyses of ammonium-rich hydrothermal plumes from the Guaymas Basin, showed that the most abundant and active lineages were also those of MGI archaea

related to the cultured autotrophic ammonia-oxidizer, “*Candidatus Nitrosopumilus maritimus*”, but with key genomic and physiological differences (Baker et al. 2012).

Betaproteobacteria

AOB found in the plumes of the Endeavor Segment are predominantly *Nitrosomonas* spp., accounting for approximately 7% of the total microbial community (Lam et al. 2004).

Denitrifier

Nitrate and nitrite concentrations are relatively depleted at hydrothermal vents compared to the surrounding seawater. Few studies focusing on denitrifier communities have been conducted in deep-sea hydrothermal vents, but the limited data available suggest that chemolithotrophic denitrification would appear to be an important process given the high concentration of reduced sulfur species (notably H_2S) in these environments (Bowles et al. 2012).

Campylobacterota

The organization of the Nap gene cluster, NapAGHB-FLD, is conserved in numerous vent Campylobacterota, such as *Sulfurimonas autotrophica*, *S. denitrificans*, *Sulfurovum* sp. NBC37, *Nitratiruptor* sp. SB155, and *Nitratiruptor salsuginis*, whereas *Campylobacter jejuni* lacks the napF gene (Vetriani et al. 2014). NirS sequences have been retrieved from these systems, mainly from Campylobacterota (Bourbonnais et al. 2014). Most isolated strains have been characterized as denitrifiers (Table 1), such as *Cetia pacifica* (Grosche et al. 2015), *Caminibacter* spp. (Alain et al. 2002a; Miroshnichenko et al. 2004; Voordeckers et al. 2005), *Sulfurovum* spp. (Giovannelli et al. 2016; Inagaki et al. 2004; Mino et al. 2014; Mori et al. 2018) and *Sulfurimonas* spp. (Inagaki et al. 2003; Takai et al. 2006) and nitrous oxide (N_2O) can be reduced at the final step of the microbial denitrification pathway. Enrichment of the N_2O -reducing microorganisms in the HNN medium revealed that *Hydrogenimonas*, of the phylum Campylobacterota, is the most predominant bacterial group throughout the cultivation period and its relative abundance was greater than 98%, contributing to the consumption of N_2O by the nitrous oxide reductase encoded by the NosZ gene (Mino et al. 2018).

Proteobacteria

Gammaproteobacteria also contain NirS (Bourbonnais et al. 2014). Some isolates in the phylum Proteobacteria, such as *Pseudodesulfobivibrio indicus*, can also reduce nitrate (Cao et al. 2016). It has also been shown that sulfide-oxidizing bacteria can use nitrate as an electron acceptor for the oxidation of hydrogen sulfide in hydrothermal vent systems, for example, *Beggiatoa* spp. (McHatton 1996).

Aquificae

Most isolated strains from hydrothermal vents in the phylum Aquificae, have been characterized as denitrifiers (Table 1), e.g., *Desulfurobacterium* spp. (Alain et al. 2003; Cao et al. 2017; L'Haridon et al. 1998, 2006a, b), *Thermovibrio* spp. (L'Haridon et al. 2006a, b; Vetriani et al. 2004), *H. okinawensis* (Nunoura et al. 2008a) and *Persephonella* spp. (Gotz et al. 2002; Nakagawa 2003). In the *Desulfurobacterium crinifex* isolate, nitrate reduction supported higher growth rates than sulfur reduction.

Deferribacteres

Caldithrix abyssi, in the phylum Deferribacteres, grows chemoorganoheterotrophically or chemolithoheterotrophically utilizing molecular hydrogen as an electron donor and nitrate as an electron acceptor (Miroshnichenko et al. 2003b).

Nitrogen fixation

Mehta et al. (2003) provided the first evidence of the presence of NifH genes in deep-sea hydrothermal vents and found that methanogenic archaea are the dominant diazotrophs. Since then, proteobacterial diazotrophs have also been found to be abundant in deep-sea hydrothermal vents (Cao et al. 2015; Wu et al. 2014).

Iron cycle

In inactive chimney deposits, the dominant microbial processes involve metals (Orcutt et al. 2011). In iron- and manganese-oxide mats that form around diffuse flow venting, metal-cycling types of metabolism dominate, especially around high metal concentration seamounts (Kato et al. 2009; Emerson and Moyer 2002). Iron-oxidizing communities from deep-sea hydrothermal vents include chemolithotrophic Zetaproteobacteria and mixotrophic Gammaproteobacteria, which are generally isolated and characterized using the gradient tube method or in liquid media with low concentrations of Fe (II) and O₂ (Emerson and Moyer 2002). At deep-sea hydrothermal vents, the iron-respiring species belong to the Proteobacteria, Deferribacteres, Archaea, and fermentative types of Firmicutes (Fig. 1, Table 1).

Iron-oxidizers

Chemosynthetic Fe-oxidizing communities are common in diffuse-flow hydrothermal vents throughout the world's oceans (Makita et al. 2018).

Zetaproteobacteria

Zetaproteobacteria is primarily associated with ecosystems fed by ferrous iron, Fe (II) (Emerson et al. 2007).

These strains produce iron oxide products with an aspect distinct from the usual stalks (xag operon), with filamentous and dread-like structures (Makita et al. 2018). Studies on ferro-oxidant taxa carried out on samples from the Southern Mariana Arc, the Hawaiian hot spot and the area of the Vai'lulu/Tonga Arc/East Lau Spreading Center/Kermadec Arc have shown that members of the Zetaproteobacteria fall into different 16S rRNA phylotypes of Zetaproteobacteria and include the microaerobic and chemolithotrophic iron-oxidizer *Mariprofundus ferrooxydans* (Singer et al. 2013). *Mariprofundus ferrooxydans* strains were isolated from the Loihi seamount vent field (strains PV-1 T and JV-1) in the first instance (Emerson and Moyer 2002; Emerson et al. 2007). *M. micogutta* ET2 was isolated from a deep-sea hydrothermal field at the Bayonnaise Knoll of the Izu-Ogasawara Arc (Makita et al. 2016). *Ghiorsea bivora* strains (TAG-1 and SV-108) were isolated from the Mid-Atlantic Ridge (TAG-1) and the Mariana back-arc (SV-108), which are unique in that they can utilize either Fe(II) or H₂ as the sole electron donor and oxygen as the terminal electron acceptor for growth (Mori et al. 2017). Genome analysis of *Mariprofundus ferrooxydans* strain PV1 revealed a complete TCA cycle, the ability to fix CO₂ with two sets of RuBisCo genes, and three carbonic anhydrase-encoding genes predicted to function in the rapid conversion of CO₂ to bicarbonate, carbon-storage proteins, and a sugar phosphotransferase system (PTS). This genome is also found to contain a cytochrome cbb3 oxidase regulon (ccoNOP), two distinct cytochrome bd quinol oxidases and molybdopterin oxidoreductase for electron transport. Heme-containing cytochromes with peroxidase activity are likely to play a significant role in the oxidation of Fe(II) (Singer et al. 2011). Metagenomic analyses have also shown that nitrite reductases, sulfide: quinone oxidases, and RuBisCo are present in Zetaproteobacteria MAGs (Singer et al. 2013). In addition, genome and metatranscriptome analyses focusing on Zetaproteobacteria have shown that a homolog of the Fe oxidase Cyc2 of *Acidithiobacillus ferrooxidans* is highly expressed in incubation in vitro and in situ (McAllister et al. 2020).

Gammaproteobacteria

Some marine aerobic heterotrophic bacteria, such as members of the genus *Marinobacter*, have also been suggested to have physiological traits including nitrate-dependent Fe(II)-oxidation, Mn(II) oxidation, and arsenate and fumarate redox cycling properties (Handley and Lloyd 2013). A gammaproteobacterial strain (strain NP-6) of the genus *Marinobacter* was also isolated from aphyric, cryptocrystalline basalt over 300 m below the seafloor in the North Pond site of the Mid-Atlantic Ridge and found to have neutrophilic iron-oxidizing capabilities (Zhang et al.

2016). Sudek et al. (2009) reported that heterotrophs taxa (e.g., *Pseudoalteromonas* sp. and *Pseudomonas* sp.) isolated from a volcanic seamount, can also catalyze ferrous iron oxidation under micro-aerobic conditions. In addition, *Alphaproteobacteria* (e.g., *Hyphomonas* sp.) taxa from hydrothermal fields of the Juan de Fuca Ridge have been shown to oxidize Fe(II) (Edwards et al. 2003).

Finally, iron-oxidizing capacities have been reported for some sulfur-oxidizing *Gammaproteobacteria*, such as *Thiomicrospira* sp. (Barco et al. 2017) and *Hydrogenovibrio* sp. (Neely et al. 2018).

Iron-reducers

Dissimilatory iron-reducing microorganisms (DIRMs) can use extracellular Fe(III) as an electron acceptor and reduce Fe(III) to Fe(II) (Lovley et al. 1991). Deep-sea hydrothermal fields can be an ecological niche for DIRMs (Melton et al. 2014; Slobodkin et al. 2001), because they are rich in iron, and 60–70% of it is oxidized [Fe(III)] (Toner et al. 2012). So far, only a few DIRMs have been isolated from hydrothermal environments. Most of them belong to the phyla Proteobacteria and Deferribacteres, and are described as “respiratory-type.” Fermentative DIRMs have been reported in the Firmicutes and Euryarchaeota. In mesophilic bacteria, iron reduction by *Geobacter* and *Shewanella* species depends on polyheme c-type cytochrome proteins for electron transfer through the cell wall (Weber et al. 2006). Some hyperthermophilic archaea, such as *Geoglobus ahangari* and *Pyrodictium delaneyi* (strain Hulk), also require direct contact between the cell and the iron mineral to transfer respiratory electrons by c-type cytochromes to the outer surface of the cell (Demey et al. 2017; Manzella et al. 2013). Some DIRMs, such as *Anoxybacter fermentans* from hydrothermal sulfides, *Desulfotomaculum reducens* MI-1 from marine sediments, and *Orenia metallireducens* Z6 from deep underground, lack c-type cytochromes involved in extracellular electron transfer (EET) and these organisms could, therefore, have different iron reduction mechanisms (Dalla et al. 2013; Dong et al. 2016; Li et al. 2020).

To date, studies on the reduction of manganese, arsenic, and other heavy metals (copper, cadmium, and lead) and the resistance of microorganisms to these compounds in hydrothermal vents remain very limited, despite their important role in some areas (Hu et al. 2020; Mandernack and Tebo 1993).

Proteobacteria

Shewanella sp. PV-4, isolated from an iron-rich microbial mat in an active deep-sea hydrothermal vent, performs iron reduction using lactate, fumarate, and H₂ as electron donors, leading to magnetite formation (Roh et al. 2006).

Deferribacteres

Other respiratory-type DIRMs isolated from hydrothermal vents include *Deferribacter abyssii* (Miroshnichenko et al. 2003a), *D. autotrophicus* (Slobodkina et al. 2009a), *Geothermobacter ehrlichii* (Kashefi et al. 2003), and *Deferisoma camini* (Slobodkina et al. 2012).

Firmicutes

A few fermentative DIRMs have been reported in the Firmicutes phylum; they are *Thermoanaerobacter siderophilus* (Slobodkin et al. 1999), *Thermovenabulum ferriorganovororum* (Zavarzina et al. 2002), *C. ferrireducens* strain DY22619 (Zeng et al. 2015a), *Anoxybacter fermentans* strain DY22613 (Zeng et al. 2015b) and *Wukongibacter baidiensis* strain DY30321 (Li et al. 2016a, b). In *Anoxybacter fermentans* strain DY22613, growth is promoted by iron reduction. The mode of action of exogenous and endogenous redox molecules to co-mediate indirect EET was considered important in the process of iron reduction in this strain (Li et al. 2019, 2020). The dissimilatory iron reduction is also catalyzed by hyperthermophilic archaea in hydrothermal vents.

Archaea—Euryarchaeota

These hyperthermophilic iron-reducers belong mainly to the families *Archaeoglobaceae* and *Pyrodictiaceae*. *Geoglobus ahangari*, which was isolated from the Guaymas Basin (MOSC site), is capable of using H₂ as the sole electron donor and reducing Fe(III) without the need for an organic carbon source and can also couple the oxidation of organic carbon, such as fatty acids and complex organic materials, to the reduction of Fe(III) at hyperthermophilic temperatures (Kashefi et al. 2002). *Geoglobus acetivorans* is also an obligate Fe(III) reducer of hydrothermal origin with an optimal growth temperature of 81 °C (Slobodkina et al. 2009b). *Geogemma barossii* strain 121, an obligate lithoautotroph archaeon isolated from an active “black smoker” from the Juan de Fuca Ridge, can utilize molecular hydrogen to reduce ferric iron and grow at 121 °C, the highest growth temperature known so far (Kashefi and Lovley 2003). The hyperthermophilic, autotrophic iron and nitrate reducer, *Pyrodictium delaneyi* strain Su06T isolated from an active deep-sea hydrothermal vent chimney on the Endeavor Segment in the north-eastern Pacific Ocean, is an obligate anaerobic, hydrogenotroph reducing Fe(III) oxide to magnetite and NO₃⁻ to N₂. The heterotroph *Hyperthermus hephaesta* Ro04 isolated from the same area is also able to reduce Fe(III) (Lin et al. 2014, 2016). *Thermococcus indicus* strain IOH1, *T. celericrescens* DSM 17994, and *T. siculi* DSM 12349 have also been reported to reduce soluble Fe(III)-citrate present in their growth medium, which improves their growth (Lim et al. 2020).

Virus

The limited abundance data available tend to indicate that deep-sea hydrothermal vents also host a large number of viruses, indicating high viral production (Ortmann and Curtis 2005). Samples from the Endeavor hydrothermal vents, located off the coast of southwest British Columbia, showed that active venting black smokers at these sites had viral abundances ranging from $(1.45 \times 10^5 - 9.90 \times 10^7/\text{ml})$ with a drop-off in abundance found in the hydrothermal-vent plume $(3.5 \times 10^6/\text{ml})$ and outside the venting system $(2.94 \times 10^6/\text{ml})$

(Ortmann et al. 2005). The metabolic compensation of hosts by viruses could be a very important aspect of virus-host interactions (He et al. 2017). The characterization of viruses from hydrothermal vents is limited so far with only eight viruses (two archaeal and eight bacterial viruses) described in detail, originating from archaeal and bacterial cultivated hosts (Lossouarn et al. 2015). Among them, one can cite, for example, the PAV1 from *Pyrococcus abyssi* (Geslin et al. 2003), the TPV1 from *Thermococcus prieurii* (Gorlas et al. 2012), and the viruses MPV1, MC1, and MC2 from *Marinitoga piezophila* and *M. camini* (Mercier et al. 2018). The

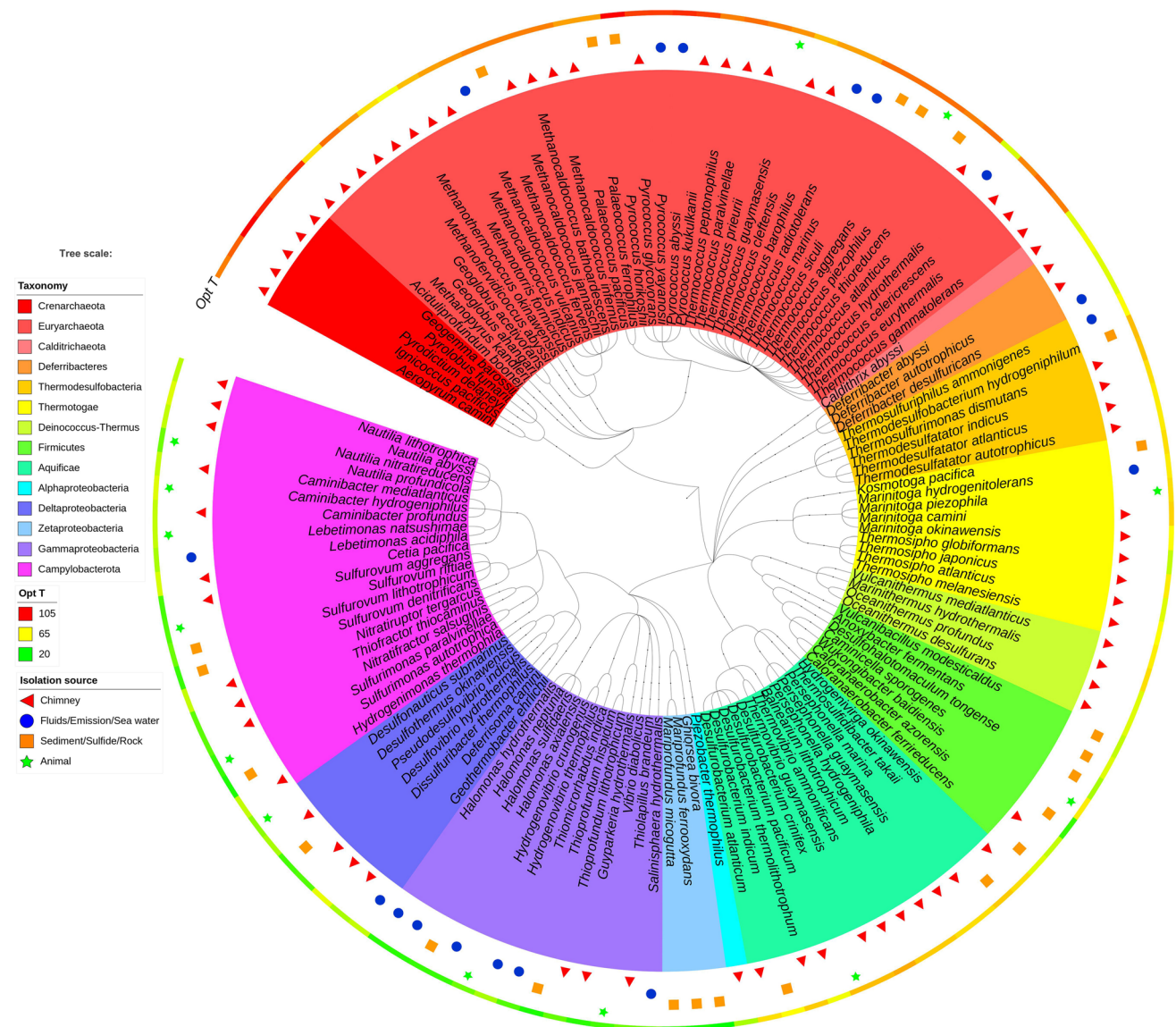


Fig. 2 Phylogenetic tree of 129 representative microbial isolates obtained from the deep-sea hydrothermal sources. The phylogenetic tree, based on 16S rRNA genes of isolates deposited in the NCBI taxonomy database, is constructed by phyloT and visualized by iTOL. The inner color-coded circle indicates the phylum to which the iso-

late belongs; symbols outside the inner ring indicate the matrix from which the isolate was obtained; the outer circle indicates the optimal growth temperature of the isolates. Opt T, optimal growth temperature

high number of viruses and thus viral production (relative to the surrounding deep-sea waters) raises the question of whether viruses are an important source of microbial mortality at the vents and would have, in that case, a crucial ecological role in deep-sea vents, similar to other ecosystems. In our current state of knowledge (which is limited), the majority of viruses described from hydrothermal habitats are temperate and, therefore, do not lyse the host they infect. If they do not have a main role in population turnover, which remains to be clarified, these viruses probably have a very important role in the evolution of hydrothermal communities, as observed in other ecosystems, through gene transfers.

Perspectives

The potential impact of the environment on microbial communities within hydrothermal vent systems could be much more intense than in other habitats due to the dynamic and steep chemical and thermal gradients that prevail there. The characterization of isolates helps us to understand the microbial metabolism and their adaptation mechanisms. Many Campylobacterota genera grow chemolithoautotrophically using a variety of electron donors and acceptors. Some sulfur-oxidizing lithoautotrophic *Gammaproteobacteria*, such as *Thiomicrospira* sp. and *Hydrogenovibrio* sp. are also iron-oxidizers. *Gammaproteobacteria*, such as *Salinisphaera hydrothermalis*, and the archaeon *Pyrobaculum islandicum* can live as autotrophs or heterotrophs. The chemolithoautotrophic growth of *Piezobacter thermophilus* is observed strictly under piezophilic conditions. This adaptation capability is important for effective competition within the hydrothermal ecosystem (Segerer et al. 1993). Furthermore, genomic comparisons of more isolates and metagenome-assembled genomes will also support the elucidation of microbial evolution strategies in hydrothermal vents. For example, Zhang et al. (2014) found that the pan-genome of mesophilic *Epsilonproteobacteria* includes niche-specific and lineage-specific genes and it is a complex process of gene acquisition, conservation, and removal, contributing to their metabolic diversity and versatility. The culturing studies to date have been biased towards hyperthermophiles, thermophiles, and mesophilic sulfur- and metal-metabolizing chemoautotrophs (Fig. 1, Fig. 2, Supplementary Table S1). They include: (1) thermophilic or hyperthermophilic archaeon with an optimal growth temperature upto 106 °C; (2) members of the phyla of Thermodesulfobacteria, Thermotogae, Deferribacteres, Calditrarchaeota, Aquificae, Deinococcus-Thermus, which are thermophiles, mainly from chimney and sediments; (3) Campylobacterota and Proteobacteria are diverse with psychrophiles, mesophiles, and thermophiles, which are found in fluids, plumes, chimneys, sediment, rock, and animals.

Recent discoveries in culture-independent metagenomic, metatranscriptomic, and metaproteomic approaches have led to a better understanding of microbial metabolic pathways and the identification of new microorganisms that have not been isolated (Baker et al. 2012; Cerqueira et al. 2018; Meier et al. 2019). For example, phylogenomic analysis of Juan de Fuca Ridge flank subsurface fluids revealed 53 bacterial and 45 archaeal genomes from metagenomes, of which nearly all are distantly related to known cultured isolates, including Chloroflexi, Nitrospirae, Acetothermia (OP1), EM3, Aminicenantes (OP8), Bathyarchaeota (formerly MCG), and Candidatus “Hydrothermarchaeota” (formerly Marine Benthic Group E, MBGE) (Jungbluth et al. 2017).

According to these results, new culture media and enrichment techniques could be developed to target detected uncultured taxa. We could design the medium, (i) mimicking, as closely as possible, the actual physical–chemical conditions in which these taxa are detected such as temperature, pH, and hydrostatic pressure (ii) multiplying the electron donor and acceptor pairs used, with a range of carbon sources, with different concentrations of oxygen, by high-throughput culturomic; or (iii) directing culturing based on available metagenomic data on target taxa (including metabolic pathways present and auxotrophy). Many studies have recently focused on cultivation. Using low-temperature and high-hydrostatic pressure incubations in the presence of hydrocarbons have been proven to be efficient for enrichment and isolation of certain groups of the yet-uncultivated SAR324 group and the SUP05 clade (Wang et al. 2020). The biopolymer lignin significantly stimulates the growth of the Bathyarchaeota subgroup Bathy-8 (Yu et al. 2018). By deploying in situ enrichment carriers in hot marine hydrothermal sediments, some thermophilic heterotrophic microorganisms that have not yet been cultured have been identified (Stokke et al. 2020). Enrichment cultures of electrogenic communities are obtained on electrodes and show a specific enrichment of Archaea belonging to the Thermococcales and Archaeoglobales orders in microbial electrolysis cells (specially designed bio-electrochemical system) under hyperthermophilic conditions (80 °C) (Pillot et al. 2018). In an environmental context other than hydrothermal sources, high-potential cathodic experiments were also conducted to enrich microorganisms in North Pond crustal samples capable of extracellular electron transport (EET) (Jones et al. 2020). Subsequent analyses of these incubations, using meta-omic analysis, fluorescence in situ hybridization coupled to secondary ion mass spectrometry (FISH-SIMS), isotope labeling experiments, and chemical analysis were necessary to understand the microbial community and metabolic pathways. These innovative culture techniques and highly targeted enrichment culture methods or mimicking in situ conditions will make it possible to obtain new microbes from hydrothermal vents and to

elucidate the keys to their physiological versatility and adaptations to the conditions of their habitat.

Extremophilic microorganisms produce novel organic compounds and stable biocatalysts that function under extreme conditions comparable to those prevailing in various industrial processes. Products from hydrothermal microorganisms that have undergone biotechnological development are quite limited considering the huge reservoir of diversity and molecules contained in hydrothermal sources. Among the best known are the Deep Vent[®] DNA polymerase (New England Biolabs) from *Pyrococcus* strain GB-D and the Vent[®] DNA polymerase (New England Biolabs) from *Thermococcus litoralis* used in molecular biology, the alpha-amylase Fuelzyme[®] (Verenium) from a deep hydrothermal sample used for starch liquefaction in the process of bioethanol production, or the Pyrolase[®] (Verenium) used for example in green chemistry to control viscosity in oil wells. In the future, more microbial products from hydrothermal microorganisms are expected to lead to other industrial applications. This potential for innovation deserves further exploration.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Animal and human rights statement This article does not contain any studies with human participants or animals performed by the authors.

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