
REVIEW

Thermophilic Microbial Communities of Deep-Sea Hydrothermal Vents

M. L. Miroshnichenko

Institute of Microbiology, Russian Academy of Sciences, pr. 60-letiya Oktyabrya 7, k. 2, Moscow, 117312 Russia
e-mail: alfamirr@mail.ru

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Abstract—The most recent publications on the phylogenetic and functional diversity of thermophilic prokaryotes inhabiting thermal deep-sea environments are reviewed. Along with a general physicochemical characterization of the biotope studied, certain adaptation mechanisms are discussed that are peculiar to the microorganisms inhabiting it. A separate chapter addresses the phylogenetic analysis of deep-sea hydrothermal microbial communities and uncultivated microorganisms recently discovered therein using molecular biological techniques. Physiological groups of thermophilic microorganisms found in deep-sea hydrothermal vents are considered: methanogens, sulfate-, iron-, and sulfur-reducers, aerobic hydrogen-oxidizing prokaryotes, aerobic and anaerobic organotrophs. In most cases, the isolates represent novel taxons.

Key words: deep-sea hydrothermal vents, barophily, hyperthermophilic archaea, the subvent biosphere hypothesis.

The discovery of deep-sea hydrothermal vents (also known as *black smokers*) in the Galapagos Rift in 1977 had a powerful impact on the development of deep-sea marine biology and microbiology of hydrothermal systems [1, 2]. Among all ecosystems known, the hydrothermal biotopes proved to be unsurpassed in terms of the biomass production rate. In contrast to the majority of biological communities, which have photosynthetic microorganisms as the first link of the trophic chain, it is chemolithotrophs that are the primary producers of organic matter in the deep-sea hydrothermal vents [3–5].

Although quite unique, the physicochemical processes in deep-sea hydrothermal vents have by now been studied in detail [3–6]. In the regions of tectonic activity, seawater interacts with the hot basaltic rocks below the ocean floor. As a result of this interaction, the water changes its chemical composition and gets overheated, but still remains liquid because of the enormous hydrostatic pressure. At the discharging sites, this so-called hydrothermal fluid rises along the cracks in the oceanic crust and mixes with the cold seawater. This leads to sedimentation of calcium sulfate and polymetallic sulfides (“black smoke”) and the subsequent formation of sulfide structures (“black smokers”) from which the hydrothermal fluid discharges at a temperature of about 350°C. The hydrothermal fluid may also mix with cold water before reaching the oceanic floor. In this case, so-called diffuse percolation occurs, characterized by considerably lower temperatures (10–20°C). It is these areas that provide conditions for abundant and diverse communities of invertebrate animals, genuine oases of life that produced a strong impression on the pioneers of deep-sea research.

Because of basaltic rock leaching by hot seawater, the hydrothermal fluid differs substantially from cold oceanic water in terms of its chemical composition. Typically, it has a low pH (about 2) and a high concentration of dissolved gases (H₂, CH₄, H₂S, CO₂) and minerals (silicon, iron, magnesium, and zinc compounds). The chemical composition and temperature of the fluid vary depending on the age and geographical location of the hydrothermal vent. For instance, one of the hydrothermal sites of the Mid-Atlantic Ridge (MAR) is characterized by the following concentrations of elements and gases: H₂S, 3–12 mmol kg⁻¹; CH₄, 25 μmol kg⁻¹; iron, 750–6500 μmol kg⁻¹; manganese, 360–1140 μmol kg⁻¹. For St, Cu, and Zn, the concentrations were determined to be 10–360 nmol kg⁻¹, 10–40 μmol kg⁻¹, and 40–100 μmol kg⁻¹, respectively. Magnesium and sulfate ions were not detectable [7].

To complete this section, it is worth mentioning that the total number of active hydrothermal sites that have so far been discovered in the Atlantic, Pacific, and Indian Oceans is approaching 40.

SPECIFIC FEATURES OF HYDROTHERMAL MICROBIAL COMMUNITIES

The microbial community is the core of the complex ecosystem of a hydrothermal biotope. The habitat is characterized by extreme environmental conditions: high temperature and hydrostatic pressure, elevated concentrations of heavy metals, sharp gradients of all physicochemical parameters and concentrations of substances required for metabolism.

Typically, hydrothermal vents occur at depths of 800 to 3500 m, which corresponds to hydrostatic pressures of 80 to 350 bars (8–35 MPa). Deep-sea thermophilic microorganisms are known to react differently to increasing pressure. According to Deming and Baross, there are four types of such reactions: in barotolerant microorganisms, the growth rate does not depend on the pressure; in barophiles, it increases with increasing pressure; barosensitive microorganisms are suppressed by increasing pressure (in terms of cell yield and doubling time); and, finally, for the growth of obligate barophiles, increased pressure is a necessary condition [8].

An example of an obligate barophile is *Pyrococcus abyssi*, found at a depth of 2000 m and able to grow at temperatures in excess of 102°C [9]. *Methanococcus jannaschii* is an example of a barophilic microorganism [10]. Its doubling time decreases at a pressure of 40 MPa (the pressure at the sampling site was 26 MPa) [11].

Note that in most of such studies, the isolation of the organisms was carried out at atmospheric pressure. The only exception is *Thermococcus barophilus* isolated at an elevated pressure [12]. At atmospheric pressure, this organism was shown to synthesize the so-called heat shock proteins. At 40 MPa, the maximum growth temperature of *T. barophilus* gets higher, and its growth rate doubles.

Deming and Baross emphasized that for many barophilic microorganisms the optimal growth pressure substantially exceeds the pressure at their habitats. For instance, *Pyrococcus abyssi* was isolated from samples collected at a hydrothermal site characterized by a pressure of 20 MPa, whereas the optimal pressure for the growth of this organism is 40 MPa [8].

Elevated temperature, characteristic for hydrothermal biotopes, is another stress factor affecting the microorganisms. The majority of microorganisms isolated from deep-sea hydrothermal environments up to now are thermophiles or hyperthermophiles (Tables 2, 3). A remarkable representative of this group is the archaeon *Pyrolobus fumarii*, which has one of the highest maximum growth temperatures known [13]. Quite recently, another microorganism, isolated from an active black smoker but still not described fully, has expanded the upper temperature limit of life to 121°C [108].

It seems likely that the thermoadaptation mechanisms of deep-sea thermophiles do not differ much from those of other thermophilic microorganisms. A few most important mechanisms are listed below [14, 15]:

(1) multiple amino acid substitutions stabilizing proteins of thermophiles under conditions of thermal denaturation;

(2) a high G+C content of tRNA and rRNA, which stabilizes their active conformations;

(3) high intracellular concentrations of salts, polyamines, and low-molecular-weight DNA-binding proteins;

(4) DNA stabilization by means of reverse gyrase in the case of the majority of thermophilic archaea and histones in the case of *Euryarchaeota*.

Both thermophilic and hyperthermophilic microorganisms are supposed to have highly efficient mechanisms of DNA repair. The details of these mechanisms are, however, yet unknown.

Mechanisms supporting the ability of hydrothermal microorganisms to adapt to high concentrations of heavy metals are also insufficiently studied. A number of such mechanisms that regulate intracellular concentrations of heavy metals at a sublethal level were reported for mesophilic microorganisms (specific plasmids and/or chromosomal genes that control membrane transport systems or are responsible for enzymatic transformation of more toxic forms of heavy metals into less toxic ones). None of these adaptations, however, have been found in deep-sea hydrothermal thermophiles [16].

The microbial population of deep-sea hydrothermal vents may be tentatively subdivided into the following groups of microorganisms [7]:

1. Mesophilic and moderately thermophilic endo- and exosymbionts associated with hydrothermal fauna. Endosymbiotic bacteria are chemoautotrophs extremely resistant to laboratory cultivation [17, 5]. It is only indirect investigation techniques that proved successful in studying certain physiological aspects of the symbiosis and made it possible to reveal the ways by which the symbionts gain energy and assimilate carbon [104–107, 18–21]. The majority of symbionts are thioautotrophs that use sulfide as the electron donor and oxygen as the electron acceptor, with CO₂ serving as the source of carbon. The second type of symbionts are methanotrophs that use methane as the source of carbon and energy. The taxonomical position of these specialized microorganisms is still uncertain. However, phylogenetic analysis of the 16S rRNA genes showed that the majority of them belong to the gamma-subclass of *Proteobacteria* [22].

Extensive data on episymbiotic microbial populations have been published for the polychaetous annelid *Alvinella pompejana* and the shrimp *Rimicaris exoculata*, endemics of the East Pacific Rise and MAR, respectively [21, 24, 26]. The density of episymbionts on the epidermal surfaces of these invertebrates is very high; their morphology is diverse, and their function in the symbiosis is yet unknown. For a long time, all attempts to cultivate the episymbionts of *A. pompejana* failed and all the data was obtained exclusively by molecular biological techniques. In particular, the analysis of rDNA using specific oligonucleotide probes showed that the dominant phylotypes of microbial episymbionts of both *A. pompejana* and *R. exoculata* belong to *Epsilonproteobacteria* [23–29]. Recently, some bacteria of this population have been isolated as pure cultures, representing new genera [30, 31].

Table 1. Phylogenetic diversity of thermophilic prokaryotes in deep-sea hydrothermal vents

Domain, kingdom	Genus	Species	Place of isolation	Reference
Archaea; Euryarchaeota	<i>Methanothermococcus</i>	<i>M. okinawensis</i>	Mid-Okinawa Trough	[44]
"	<i>Methanocaldococcus</i>	<i>M. jannaschi</i>	Guaymas Basin	[10, 53]
"	"	<i>M. fervens</i>	Guaymas Basin	[51]
"	"	<i>M. infernus</i>	Mid-Atlantic Ridge	[50]
"	"	<i>M. vulcanius</i>	East Pacific Rise	[51]
"	"	<i>M. indicus</i>	Central Indian Ridge	[52]
"	<i>Methanopyrus</i>	<i>M. kandleri</i>	Guaymas Basin	[49]
"	<i>Archaeoglobus</i>	<i>A. profundus</i> <i>A. veneficus</i>	Mid-Atlantic Ridge	[57, 84]
"	<i>Geoglobus</i>	<i>G. ahangari</i>	Guaymas Basin	[68]
"	<i>Thermococcus</i>	<i>T. profundus</i> ; <i>T. siculi</i>	Mid-Okinawa Trough	[101, 99]
"	"	<i>T. guaymaensis</i> , <i>T. aggregans</i>	Guaymas Basin	[91]
"	"	<i>T. peptonophilus</i>	South Mariana Trough	[97]
"	"	<i>T. fumicolans</i>	North Fiji Basin	[94]
"	"	<i>T. chitonophagus</i> ; <i>T. hydrothermalis</i> ; <i>T. barossii</i>	East Pacific Rise	[76], [96], [92]
"	"	<i>T. gammatolerance</i>	Guaymas Basin	[95]
"	"	<i>T. barophilus</i>	Mid-Atlantic Ridge	[12]
"	<i>Pyrococcus</i>	<i>P. abyssi</i>	North Fiji Basin	[9]
"	"	<i>P. glycovorans</i>	East Pacific Rise	[89]
"	<i>Palaeococcus</i>	<i>P. ferrophilus</i>	Ogasawara-Bonin Arc., Japan	[90]
Archaea; Crenarchaeota	<i>Pyrodictium</i>	<i>P. abyssi</i>	Guaymas Basin	[73]
"	<i>Staphylothermus</i>	<i>S. marinus</i>	East Pacific Rise	[72]
"	<i>Pyrolobus</i>	<i>P. fumarii</i>	Mid-Atlantic Ridge	[13]
"	<i>Aeropyrum</i>	<i>A. camini</i>	Izu-Bonin Arc., Japan	[111]
Bacteria	<i>Thermosipho</i>	<i>T. melanensis</i>	Southwestern areas of the Pacific Ocean	[77]
"	<i>Marinotoga</i>	<i>M. piezophila</i>	East Pacific Rise	[79]
"	"	<i>M. camini</i>	Mid-Atlantic Ridge	[78]
"	<i>Tepidibacter</i>	<i>T. tallasicus</i>	East Pacific Rise	[81]
"	<i>Caldithrix</i>	<i>C. abyssi</i>	East Pacific Rise	[42]
"	<i>Caminiella</i>	<i>C. sporogenes</i>	East Pacific Rise	[83]
"	<i>Caloranaerobacter</i>	<i>C. azorensis</i>	Mid-Atlantic Ridge	[82]
"	<i>Marinithermus</i>	<i>M. hydrothermalis</i>	Izu-Bonin Arc., Japan	[87]
"	<i>Oceanothermus</i>	<i>O. profundus</i>	East Pacific Rise	[85]
"	<i>Vulcanithermus</i>	<i>V. mediatlanticus</i>	Mid-Atlantic Ridge	[86]
"	<i>Caldanaerobacter</i>	<i>C. subterraneus</i> ssp. <i>pacificus</i>	Mid-Okinawa Trough	[70]
"	<i>Thermodesulfobacterium</i>	<i>T. hydrogeniphilum</i>	Guaymas Basin	[58]
"	<i>Thermodesulfatator</i>	<i>T. indicus</i>	Central Indian Ridge	[109]
"	<i>Deferribacter</i>	<i>D. abyssi</i>	Mid-Atlantic Ridge	[69]
"	<i>Persephonella</i>	<i>P. marina</i> , <i>P. guaymasensis</i>	Guaymas Basin	[63]
"	"	<i>P. hydrogeniphila</i>	Izu-Bonin Arc., Japan	[64]
"	<i>Nautilia</i>	<i>N. lithotrophica</i>	East Pacific Rise	[30]
"	<i>Caminiibacter</i>	<i>C. hydrogeniphilus</i>	East Pacific Rise	[31]
"	"	<i>C. profundus</i>	Mid-Atlantic Ridge	[43]
"	<i>Thermovibrio</i>	<i>T. ammonificans</i>	East Pacific Rise	[112]
"	<i>Desulfurobacterium</i>	<i>D. hydrogenophilum</i>	Mid-Atlantic Ridge	[61]
"	<i>Balnearium</i>	<i>B. lithotrophicum</i>	Izu-Bonin Arc., Japan	[62]
"	<i>Hydrogenomonas</i>	<i>H. thermophilus</i>	Central Indian Ridge	[41]

Table 2. Lithotrophic thermophilic prokaryotes from deep-sea hydrothermal vents

Genus	Substrate	Acceptor(s)	Product(s)	Growth, °C (minimum–optimum–maximum)
<i>Methanocaldococcus</i>	H ₂	CO ₂	CH ₄	50–85–91
<i>Methanothermococcus</i>	H ₂ *	CO ₂	CH ₄	40–(60–65)–75
<i>Methanopyrus</i>	H ₂	CO ₂	"	84–98–110
<i>Pyrolobus</i>	H ₂	O ₂	H ₂ O	90–106–113
		S ₂ O ₃ ²⁻	H ₂ S	
		NO ₃ ⁻	NH ₄ ⁺	
<i>Geoglobus</i>	H ₂ *	Fe ³⁺	Fe ²⁺	65–88–90
<i>Archaeoglobus</i>	H ₂ *	SO ₄ ²⁻ S ₂ O ₃ ²⁻	H ₂ S	65–(82–85)–(85–90)
		SO ₃ ²⁻		
<i>Thermodesulfobacterium</i>	H ₂	SO ₄ ²⁻	H ₂ S	50–75–80
<i>Thermodesulfatator</i>	H ₂	SO ₄ ²⁻	H ₂ S	55–70–80
<i>Nautilia</i>	H ₂ *	S ⁰	H ₂ S	37–53–68
<i>Caminiibacter</i>	H ₂ *	S ⁰	H ₂ S	45–(55–60)–(65–70)
		NO ₃ ⁻	NH ₄ ⁺	
<i>Hydrogenomonas</i>	H ₂	O ₂	H ₂ O	35–55–65
		S ⁰	H ₂ S	
		NO ₃ ⁻	NH ₄ ⁺	
<i>Balnearium</i>	H ₂	S ⁰	H ₂ S	45–(70–75)–80
<i>Persephonella</i>	H ₂	O ₂	H ₂ O	55–(70–73)–(75–80)
		S ₂ O ₃ ²⁻	H ₂ S	
<i>Thermovibrio</i>	H ₂	NO ₃ ⁻	NH ₄ ⁺	60–75–80
		S ⁰	H ₂ S	
		S ⁰		
<i>Desulfurobacterium</i>	H ₂	S ⁰	H ₂ S	40–70–75
<i>Deferribacter</i>	H ₂ *	S ⁰	H ₂ S	40–(60–65)–70
		NO ₃ ⁻	NO ₂	
<i>Caldanaerobacter</i>	CO*	H ₂ O	H ₂ CO ₂	50–70–80

* Able to utilize organic substrates as well.

2. Mesophilic nonsymbiotic organisms. The temperature range of 15–45°C is quite typical for areas of hydrothermal activity (diffuse percolation sites). Therefore, one may expect these areas to be habitats of a great diversity of mesophilic microorganisms. Just a few of them have been described so far; however, detailed consideration of the mesophilic members of the hydrothermal microbial communities is beyond the scope of this review.

3. Free-living thermophilic prokaryotes. Over the last decade, extensive studies revealed high phylogenetic

and metabolic diversity of this group [21, 32]. It has been shown that black smokers and the sulfide structures associated with them are habitats of thermophilic and hyperthermophilic microorganisms. Black smokers are distinguished by exceptionally steep gradients of both temperature (which drops from 300 to 2°C over a distance of a few centimeters) and redox potential.

The porous structures of some active smokers form microniches in which oxygenated seawater is heated to 60–70°C, providing a favorable environment for mod-

Table 3. Organotrophic thermophilic prokaryotes from deep-sea hydrothermal vents

Genus	Type of metabolism	Substrates	Growth temperature, °C (minimum–optimum–maximum)
<i>Thermococcus</i>	Fermentation stimulated by elemental sulfur	Peptides, amino acid mixture, maltose, chitin	(50–73)–(80–90)–(90–100)
<i>Staphylothermus</i>	"	Yeast extract	65–92–98
<i>Aeropyrum</i>	Aerobic respiration	Peptides	
<i>Pyrococcus</i>	"	Peptides, amino acid mixture, carbohydrates	(67–80)–(95–98)–(102–104)
<i>Pyrodictium</i>	"	Peptides	80–97–110
<i>Palaeococcus</i>	Fermentation stimulated by elemental sulfur or Fe ³⁺	Peptides	60–83–88
<i>Thermotoga</i>	Fermentation	Mono- and disaccharides, starch, glycogen, yeast extract	55–80–90
<i>Thermosipho</i>	"	Peptides, yeast extract	45–70–80
<i>Marinitoga</i>	"	Peptides, carbohydrates	25–55–65
<i>Caminicella</i>	"	Peptides, carbohydrates	45–(55–60)–65
<i>Caloranaerobacter</i>	"	Peptides, carbohydrates	
<i>Tepidibacter</i>	"	Peptides, starch	33–50–60
<i>Caldithrix</i>	Fermentation or nitrate reduction*	Peptides, acetate	40–60–70
<i>Marinithermus</i>	Aerobic respiration	Peptides, carbohydrates, organic acids	50–67–72
<i>Oceanothermus</i>	Aerobic respiration, nitrate reduction	Peptides, carbohydrates, organic acids, alcohols	40–60–68
<i>Vulcanithermus</i>	Aerobic respiration, nitrate reduction	Peptides, carbohydrates, organic acids, alcohols	37–70–80

* Capable of lithoheterotrophic growth with hydrogen.

erately thermophilic aerobic and microaerophilic organisms [33, 34, 5, 21]. Some of these microorganisms, which have been recently isolated as pure cultures, will be discussed below. It is worth noting though that the majority of thermophilic and hyperthermophilic microorganisms isolated from deep-sea hydrothermal vents are anaerobes.

The existence of microniches supporting discrete microbial populations was shown by the example of the archaeal community of a black smoker at MAR, which was investigated using rRNA-specific fluorescently labeled oligonucleotide probes (FISH method) [35] and other methods [36–38].

PHYLOGENETIC DIVERSITY OF THERMOPHILIC PROKARYOTES

Microbial communities of deep-sea hydrothermal vents include microorganisms of both the *Bacteria* and *Archaea* domains. Thermophilic and hyperthermophilic archaea inhabit high-temperature zones of hydrothermal structures and are represented by both *Crenarchaeota* and *Euryarchaeota* (Table 1). In samples of deep-sea hydrothermal structures collected from hydrothermal areas near Japan [36] and obtained using the vent cups technique at Snake Pit (MAR) [28], the

dominant representatives of the domain *Archaea* belonged to the orders *Thermococcales* and *Archaeoglobales*. In both studies, phylogenetic analysis of rDNA clone libraries was used. These works also reported the presence in these biotopes of thermoacidophiles belonging to the order *Thermoplasmatales*, although these microorganisms have not yet been isolated as pure cultures. The molecular biological methods greatly expanded the knowledge on the genetic diversity of archaea in the deep-sea hydrothermal microbial community. In particular, novel archaeal phylotypes were identified that belonged to unknown taxons, possibly those of mesophilic or psychrophilic archaea that have so far escaped laboratory cultivation [28, 36, 37].

The deep-sea hydrothermal vents are also habitat for various representatives of the domain *Bacteria*. Phylogenetically, the members of the subclass *Epsilonproteobacteria* (mentioned above as episymbionts of hydrothermal invertebrates) are of considerable interest. Until now, this subclass comprised just a few mesophilic genera that reduce sulfur compounds under anaerobic or microaerobic conditions. Over the last decade, research based on molecular biological techniques proved that *Epsilonproteobacteria* are dominant in samples associated with the hydrothermal invertebrates *Alvinella* and *Paralvinella*, as well as in the

microbial populations obtained using the vent cups technique [25, 27–29]. Reysenbach *et al.* [28] incubated vent cups for 5 days in the moderate temperature zone of a sulfide structure at the Snake Pit site (MAR). According to phylogenetic analysis of the 16S rDNA extracted from the microbial community obtained, 40% of the bacterial sequences in the clone library belonged to *Epsilonproteobacteria*. The dominant phylotypes were found to be affiliated to the order *Aquificales* (18%) and the genus *Desulfurobacterium* (25%).

Takai *et al.* [40] showed that *Epsilonproteobacteria* found in samples collected at geographically distant sites (Western Pacific and Indian Oceans) were widely diverse phylogenetically. According to the preliminary description of the 30 new strains isolated by the authors, many of them might be new taxons of a genus or family level.

By now, four thermophilic species of *Epsilonproteobacteria*, representing the three new genera (*Nautilia* [30], *Caminiibacter* [31], and *Hydrogenimonas* [41]), have been isolated from deep-sea hydrothermal vents and described.

The representatives of the genera *Nautilia* and *Caminiibacter*, together with the uncultivated *Epsilonproteobacteria*, form a deep phylogenetic branch within the class *Epsilonproteobacteria*. They were classified as a separate order, *Nautiliales*, which so far contains a single family, *Nautiliaceae* [42].

One of the phylogenetically remarkable organisms isolated from a hydrothermal sample collected at MAR is *Caldithrix abyssi* [43]. This anaerobic moderately thermophilic bacterium represents a new phylogenetic phylum. The similarity value of the 16S rRNA gene of *C. abyssi* with other known microorganisms does not exceed 82.3%. Interestingly, the only phylogenetically close relative of *C. abyssi* was detected using the DGGE technique: a fragment of the 16S rRNA gene of this organism was identified in a sample collected from a shallow-water hydrothermal vent located near Milos island [44].

Considering the phylogenetic uniqueness of the microorganisms inhabiting deep-sea hydrothermal vents, one may note that, presently, only one family was described that consists exclusively of endemics of this biotope. This is the family *Nautiliaceae*, which represents a new order, *Nautiliales* [42].

At the genus level, the endemicity is considerably more pronounced: archaea are represented by four genera that have been found nowhere but in deep-sea hydrothermal vents (the genera *Methanopyrus*, *Geoglobus*, *Palaeococcus*, and *Pyrolobus*), and 14 endemic genera were described for bacteria (Table 1).

Along with the endemics, there are a number of cosmopolitan species of both archaea and bacteria that inhabit deep-sea hydrothermal vents and have also been isolated from other thermal habitats, such as shallow-water, subsurface, and continental hydrothermal vents. For example, a representative of the genus *Thermococ-*

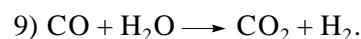
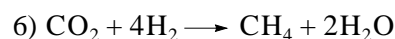
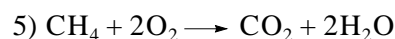
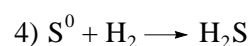
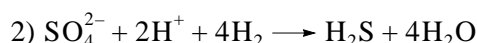
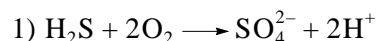
cus, *T. sibiricus*, was isolated from high-temperature formation water of the Samotlor oil field in Western Siberia [45], as well as members of the genus *Petrotoxa*, *P. sibirica*, and *P. olearia* [46].

Yet another example of an organism inhabiting various thermal environments is *Thermus thermophilus*, isolated recently from a deep-sea hydrothermal vent [47].

METABOLIC DIVERSITY OF THERMOPHILIC PROKARYOTES INHABITING DEEP-SEA HYDROTHERMAL VENTS

Chemolithotrophic thermophilic prokaryotes.

Currently, the list of known chemolithotrophic reactions used by microorganisms inhabiting deep-sea hydrothermal vents is as follows [48]:



Most of these reactions are based on utilization of molecular hydrogen, the main component of magmatic gases (Tables 1, 2). Methanogenesis is the main metabolic process for the members of the genera *Methanopyrus* [49], *Methanocaldococcus* [50–53], and *Methanothermococcus* [54]. These archaea are obligately anaerobic hyperthermophiles (their optimal growth temperature is in the range of 85 to 90°C) that use autotrophically hydrogen and CO₂ as the sole sources of energy and carbon, respectively. It is worth noting that the studies of deep-sea hydrothermal vents revealed only lithotrophic methanogenesis. Nevertheless, there are data of radioisotopic measurements for deep-sea hydrothermal vents of the East Pacific Rise that provide evidence for the occurrence of aceticlastic methanogenesis in this environment. The formation of ¹⁴CH₄ from CH₃COONa was detected at 80°C, which is a unique example of high temperature aceticlastic methanogenesis [55].

Sulfate reduction in deep-sea hydrothermal vents of Guaymas basin was also detected by radioisotopic methods [56]. However, the sulfate-reducing microorganisms described are scarce. These are archaea of the genus *Archaeoglobus* (*A. profundus* [57]), chem-

olithoautotrophic bacteria belonging to the new genus *Thermodesulfatator* (*T. indicus* [109]), and a recently isolated representative of the genus *Thermodesulfobacterium* (*T. hydrogeniphilum* [58]).

Elemental sulfur plays an important role in the lithotrophic metabolism of deep-sea hydrothermal microorganisms. It may occur in the hydrothermal plumes or may be formed as a result of either partial oxidation of H₂S or partial reduction of SO₄²⁻ [59].

The reactions describing autotrophic oxidation and reduction of elemental sulfur (equations (3) and (4), respectively) have certain thermodynamic limitations. Thus, thermodynamic calculations showed that sulfur oxidation is energetically advantageous at temperatures below 37°C, whereas sulfur reduction can serve as a source of energy at higher temperatures [48].

Lithotrophic sulfur reduction by oxidation of molecular hydrogen is believed to be one of the most ancient types of catabolism [60] and is widespread in the deep-sea hydrothermal vents. For instance, this process is the only one used by anaerobic bacteria of the genera *Desulfurobacterium* [61] and *Balnearium* [62]. The same metabolic reaction provides energy for the above mentioned thermophilic *Epsilonproteobacteria*. These microorganisms are less specialized: *Nautilia lithotrophica* [30] oxidizes not only hydrogen but also formate, whereas *Caminibacter hydrogeniphilus* [31] can use as an electron acceptor not only sulfur but also nitrate.

Aerobic oxidation of molecular hydrogen (according to reaction (8)) is a key energetic reaction for the members of the genus *Persephonella* [63, 64]. This genus, endemic in deep-sea hydrothermal vents, belongs to the order *Aquificales*, all representatives of which are obligate or facultative chemolithotrophs that can oxidize both hydrogen and reduced sulfur compounds. All members of the genus *Persephonella* are also microaerophiles capable of using nitrate as an electron acceptor alternative to oxygen. The microaerophily of these organisms could be an adaptive feature for living in an epoch when little oxygen, formed abiotically (photolysis of water) and/or by oxygenic photosynthesis, was available for microorganisms [66]. This hypothesis is supported by the fact that bacteria of the order *Aquificales* form one of the ancient branches of the phylogenetic tree [65]. It should be noted that the origin of hydrothermal activity on Earth is believed to date back to at least the early Archaean epoch, and this phenomenon was probably linked to the origin of life on the planet [5].

Autotrophic oxidation of hydrogen under microaerobic conditions is inherent in both *Hydrogenimonas thermophilus*, the only representative of the recently described genus *Hydrogenimonas* [41], and *Caminibacter profundus*, a species of the genus *Caminibacter* [42].

Less characteristic is this type of catabolism for the members of the domain *Archaea* that inhabit the deep-

sea hydrothermal vents. It has been found only in *Pyrolobus fumarii* [13], which is a facultative anaerobe capable of oxidizing molecular hydrogen both aerobically and anaerobically. In the latter case, nitrate or thiosulfate are reduced to ammonium or hydrogen sulfide, respectively (Table 2).

For certain inhabitants of the deep-sea hydrothermal vents, the key metabolic process is iron reduction according to reaction (7). The presence of thermophilic Fe³⁺-reducing microorganisms in the deep-sea hydrothermal microbial community was first shown by Slobodkin *et al.* in enrichment cultures [67]. By now, there are two microorganisms carrying out dissimilatory Fe³⁺ reduction that have been isolated from this biotope. The archaeon *Geoglobus ahangarii*, the only species of the genus *Geoglobus*, reduces Fe³⁺ autotrophically [68]. In contrast to it, *Deferribacter abyssi*, representative of iron-reducing bacteria isolated from deep-sea hydrothermal vents, requires yeast extract for growth [69]. Both of these organisms are also capable of anaerobic oxidation of acetate and some other organic acids.

Anaerobic CO reduction (reaction (9)) has been shown to be the source of energy for the facultative lithotroph *Carboxydobrachium pacificum* [70] reclassified recently into a new subspecies of the new species and genus: *Caldanaerobacter subterraneus* subsp. *pacificus* [110]. So far, it is the only known thermophilic bacterium found in deep-sea hydrothermal vents that is capable of carboxydutrophy. In addition to autotrophic CO reduction, *C. subterraneus* can also ferment some organic substrates, which distinguishes it from other carboxydutrophs. The capacity for anaerobic growth in the presence of yeast extract and CO has recently been shown for archaea of the genus *Thermococcus* [103].

Organotrophic thermophilic prokaryotes. Organotrophic metabolism is common for the majority of anaerobic archaea isolated from deep-sea hydrothermal vents. All species of the genera *Thermococcus*, *Pyrococcus*, and *Palaeococcus*, as well as those of the genera *Staphylothermus* [72] and *Pyrodictium* [73], are organotrophs. The former three genera compose the family *Thermococcaceae* of the order *Thermococcales* [71] and belong to the kingdom *Euryarchaeota*. The genera *Staphylothermus* and *Pyrodictium* represent the kingdom *Crenarchaeota*. The substrates for growth of all these microorganisms are typically peptides or, less frequently, amino acids or proteins.

Fermentation of all these substrates results in the formation of acetate, propionate, isobutyrate, isovalerate, CO₂, and H₂ [74]. Elemental sulfur was shown to considerably stimulate growth, although there are certain strains that do not necessarily need it [75]. A few thermophilic archaea can also use other substrates, such as chitin [76].

The extremely thermophilic organotrophic bacteria inhabiting deep-sea hydrothermal vents are represented by anaerobic species of the genera *Thermosipho* [77]

and *Marinitoga* [78]. By molecular biological methods, these bacteria have been detected at almost every site of hydrothermal activity [35, 80]. Some of them were isolated as pure cultures. The temperature characteristics of the bacteria belonging to the family *Thermotogales* are 10 to 15°C lower than those of the deep-sea archaea. They also differ by preferable growth substrates, which are sugars and polysaccharides. These differences suggest that anaerobic archaea and bacteria do not compete with each other and occupy different microniches.

The bacteria of the genera *Tepidibacter* [81], *Caloranaerobacter* [82] and *Caminiella* [83] are another group of anaerobic moderately thermophilic organotrophs of deep-sea hydrothermal vents that utilize proteinaceous substrates. They are distinguished by a low G+C content in their genomes (24, 27, and 24.2 mol %, respectively).

Along with anaerobes, there are also aerobic organotrophic bacteria that have been found in deep-sea hydrothermal vents and classified as members of the genera *Bacillus* and *Thermus* [33, 34]. The only strictly aerobic archaeon *Aeropyrum camini* is a hyperthermophilic heterotrophic microorganism [111].

There are a number of thermophilic bacteria, recently isolated from deep-sea hydrothermal vents, that are characterized by a mixotrophic type of metabolism. An example of these is the above-mentioned *Caldithrix abyssi*, which can ferment proteinaceous substrates and oxidize both hydrogen and acetate using nitrate as the electron acceptor [43].

The capacity for both chemolithoheterotrophic and organotrophic growth was also found in members of the new genera *Oceanithermus* [85] and *Vulcanithermus* [86]. Currently, there are four representatives of the family *Thermaceae* that have been isolated as pure cultures from deep-sea vents. Among those, *Thermus thermophilus* [47] is not endemic to deep-sea hydrothermal vents. *Marinithermus hydrothermalis* [87] was shown to be an obligate aerobe, whereas the last two, *Oceanithermus profundus* and *Vulcanithermus mediatlanticus*, differ from other members of the family *Thermaceae* by microaerophilily and the ability to oxidize molecular hydrogen lithoheterotrophically. Notably, *O. profundus* cannot grow in the presence of air, whereas *V. mediatlanticus*, although being able to grow aerobically, grows optimally under microaerobic conditions. Other basic morphological, physiological, and genomic features of the deep-sea hydrothermal members of the family *Thermaceae* are similar to those of *Thermaceae* from continental habitats.

Thus, the population of microorganisms in deep-sea hydrothermal vents includes both highly specialized chemolithoautotrophic species and organisms with organotrophic and mixotrophic types of metabolism. The potential ability of microorganisms to use alternative metabolic pathways (litho- and organotrophy) can probably be considered an adaptation to rapidly chang-

ing concentrations of carbon and energy sources in deep-sea hydrothermal vents.

It has been shown that many of the lithotrophic microorganisms from deep-sea hydrothermal vents are capable of nitrate reduction. Nitrate is reduced to either nitrite (genera *Oceanithermus* and *Vulcanithermus*) or ammonium (*Caldithrix*, *Caminiella*, *Hydrogenimonas*, *Thermovibrio*). The only truly denitrifying microorganisms that form molecular nitrogen are members of the genus *Persephonella*. The origin of nitrates in deep-sea hydrothermal vents is not completely understood. Their probable source could be organic matter of biogenic origin.

DEEP-SEA HYDROTHERMAL VENTS AND THE "SUBVENT BIOSPHERE"

In 1993, certain geochemical and microbiological data lead Baross and Deming to put forward the hypothesis of the so-called subvent biosphere located beneath the oceanic crust. This was thought to be an ecosystem that connects the areas of oceanic rifts under the crust and is inhabited by thermophilic microorganisms [8].

The hypothesis states that the black smokers are in fact windows to the subvent biosphere. The idea of the subvent biosphere is supported by the following facts:

(1) The discovery of certain thermophilic archaea in both deep-sea and continental subsurface habitats [88, 45].

(2) A surprisingly high content of DNA in the hydrothermal fluid [8, 36].

(3) The phenomenon of the so-called snow storms, which are powerful sporadic eruptions of organic matter of bacterial origin sometimes observed in some of the areas of hydrothermal activity [5].

(4) The high optimal pressures of growth of barophilic thermophiles that considerably exceed the pressures at their habitats. According to the theory of Baross and Deming, this difference may be explained by the lithostatic pressure that affects the inhabitants of the "subvent biosphere" in addition to the hydrostatic pressure.

Obviously, direct proof of the above hypothesis could be obtained by studying samples from the subvent environment. However, deep submarine drilling at the sites of hydrothermal activity is hardly practical because of high cost and technical difficulties.

CONCLUSION

Over the last two decades, numerous new thermophilic microorganisms have been isolated from deep-sea hydrothermal vents. Their metabolic strategies vary widely and reflect the high variability of the physicochemical parameters of their habitats and the multiplicity of sources of geochemical energy available in this unique biotope. Anaerobic, microaerophilic, and aero-

bic organisms have been found in the deep-sea hydrothermal environments.

Among them, one can further find heterotrophic microorganisms, highly specialized chemolithotrophic microorganisms, and microorganisms capable of both litho- and organotrophy.

In addition to classical cultivation techniques, the phylogenetic diversity of the microbial deep-sea hydrothermal communities has been studied by cultivation-independent molecular biological methods. The latter methods helped discover novel dominant phylotypes of a high taxonomic level that belong to organisms that have not so far been cultivated. One may expect that new approaches that combine classical microbiological and advanced molecular biological techniques will extend our knowledge of the microbial communities of deep-sea hydrothermal vents and of their role in the geochemical processes related to hydrothermal activity.

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