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Recent developments in the thermophilic microbiology of deep-sea hydrothermal vents

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Abstract The diversity of thermophilic prokaryotes inhabiting deep-sea hot vents was actively studied over the last two decades. The ever growing interest is reflected in the exponentially increasing number of novel thermophilic genera described. The goal of this paper is to survey the progress in this field made in the years 2000–2005. In this period, representatives of several new taxa of hyperthermophilic archaea were obtained from deep-sea environments. Two of these isolates had phenotypic features new for this group of organisms: the presence of an outer cell membrane (the genus *Ignicoccus*) and the ability to grow anaerobically with acetate and ferric iron (the genus *Geoglobus*). Also, our knowledge on the diversity of thermophilic bacteria from deep-sea thermal environments extended significantly. The new bacterial isolates represented diverse bacterial divisions: the phylum *Aquificae*, the subclass *Epsilonproteobacteria*, the order *Thermotogales*, the families *Thermodesulfobacteriaceae*, *Deferribacteraceae*, and *Thermaceae*, and a novel bacterial phylum represented by the genus *Caldithrix*. Most of these isolates are obligate or facultative lithotrophs, oxidizing molecular hydrogen in the course of different types of anaerobic respiration or microaerobic growth. The existence and significant ecological role of some of new bacterial thermophilic isolates was initially established by molecular methods.

Keywords Deep-sea hydrothermal vents · Thermophilic prokaryotes · Biodiversity

Introduction

Active investigations of thermophilic microbial communities inhabiting deep-sea hydrothermal environments undertaken in the last decades of the twentieth century significantly extended our knowledge on the diversity of thermophiles. At that time, most of known deep-sea thermophilic prokaryotes were represented by hyperthermophilic archaea (Blöchl et al. 1995; Prieur et al. 1995; Stetter 1996). The thermophilic lithotrophic methanogens were represented by the genus *Methanococcus* (Jones et al. 1983; Zhao et al. 1988; Jeanthon et al. 1999) and the endemic genus *Methanopyrus* (Kurr et al. 1991), characterized by outstandingly high temperature characteristics of growth (optimum at 98°C and maximum at 110°C). Another deep-sea lithoautotrophic archaeal isolate, a hydrogen-oxidizing *Pyrolobus fumarii* (Blöchl et al. 1997), could grow at even higher temperatures (optimum at 106°C and maximum at 113°C) by means of nitrate-, thiosulfate-, or microaerobic respiration. Deep-sea hydrothermal vents were also found to be inhabited by hyperthermophilic sulfate- and thiosulfate-reducing archaea of the genus *Archaeoglobus* (Burggraf et al. 1990; Huber et al. 1997). Organotrophic thermophilic archaea inhabiting deep-sea environments are represented by obligate anaerobes with fermentative metabolism—numerous *Thermococcales* (Zillig and Reysenbach 2001) and by members of the *Crenarchaeota* kingdom belonging to the genera *Pyrodictium* (Pley et al. 1991) and *Staphylothermus* (Fiala et al. 1986). During the first period of exploration of deep-sea microbial communities, thermophilic bacteria attracted much less attention of microbiologists than archaea, being represented solely by *Thermosipho melanesiensis* (Antoine et al. 1997), a member of the genus previously shown in shallow-water habitats (Huber et al. 1989). *Desulfurobacterium thermoautotrophum* (L'Haridon et al. 1998), an obligately anaerobic hydrogen-utilizing sulfur-reducing bacterium was found to represent a deep lineage in Bacteria domain. This finding suggested that the

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diversity of bacteria and, specifically, of moderate and extreme thermophiles in deep-sea hydrothermal habitats might be no less than that of hyperthermophilic archaea. Studies of environmental 16S rRNA gene sequences derived from various deep-sea hydrothermal samples also suggested that the known species represented only a fraction of the entire thermophilic species diversity. Molecular phylogenetic analyses revealed many novel bacterial lineages in deep-sea communities, some of which were likely (and further proved) to be represented by thermophiles (Jeanthon 2000; Reysenbach et al. 2000a, b).

Indeed, significant diversity of thermophilic deep-sea prokaryotes was confirmed by cultivation approach in the next few years. This survey is focused on recent progress (2000 through 2004) made in investigations of the thermophilic diversity in deep-sea environments.

New hyperthermophilic archaeal deep-sea isolates

Despite significant progress of the 1990s in the exploration of archaeal diversity in deep-sea hydrothermal habitats, several metabolically and phylogenetically novel archaea were isolated in the 4 years that followed (Table 1). Lithotrophic sulfur respiration, an energy-yielding process, is widespread in hyperthermophilic archaea of terrestrial or shallow-water origin (Schönheit and Schäfer 1995). Yet until recently, such organisms were not found in deep-sea thermal environments. The first hyperthermophilic representative of this metabolic type found in a deep-sea environment was *Ignicoccus pacificus* (Huber et al. 2000). It was isolated from a habitat in the East Pacific Rise and represented the family *Desulfurococcaceae* of the *Crenarchaeota* kingdom. This organism is an obligately anaerobic lithoautotroph utilizing only molecular hydrogen, elemental sulfur, and carbon dioxide as the energy substrate, the electron acceptor, and the carbon source, respectively.

Its unique feature is the presence of an external cell membrane, until that time never found in any archaeal representatives. The huge periplasmic space in this organism contains small distinct particles with unknown function. Another *Ignicoccus* species, isolated from shallow-water vents, was found to host symbiotic representatives of a novel archaeal kingdom *Nanoarchaeota* (Huber H. et al. 2002). In laboratory cultures, these tiny coccoid organisms were found to be obligately dependent on the presence of *Ignicoccaceae*. By using specific PCR primers, they were detected in many thermal habitats including deep-sea vents (Hohn et al. 2002).

Another archaeal isolate *Geoglobus ahangari*, a novel member of *Euryarchaeota*, was obtained from the Guaymas Basin hydrothermal system (Kashefi et al. 2002). It has motile coccoid cells and is obligately dependent on ferric iron, which it reduces to ferrous iron, the capacity not previously known in hyperthermophilic archaea. The organism can grow lithoautotrophically with molecular hydrogen and can also oxidize completely a wide range of fermentable and nonfermentable organic substrates including acetate. Until the discovery of *G. ahangari*, no anaerobic sink for acetate, a major product of archaeal fermentations (Schönheit and Schäfer 1995), was known within hyperthermophilic microbial communities. Therefore, anaerobic mineralization of acetate by *G. ahangari* through iron reduction closes the anaerobic carbon cycle in deep-sea hyperthermophilic ecosystems.

One more ferric iron-reducing thermophilic archaeon was recently isolated from an active "black smoker" in the Juan de Fuca Ridge and is represented by strain 121, tentatively named "*Geogemma barossii*" (Kashefi and Lovley 2003; Lovley et al. 2004). It is an obligate lithoautotroph that utilizes molecular hydrogen alone. The organism belongs to *Desulfurococcales* and grows at 121°C, the highest growth temperature so far known.

The hunt for new hyperthermophilic methanogens resulted in isolation of new *Methanococcaceae* from

Table 1 Characteristics of new archaeal isolates obtained from the deep-sea hydrothermal sources in 2000–2005 years

| Genus/species | Site of isolation | Growth temperatures (°C) | | | Electron donor(s) | Electron acceptor(s) | References |
|------------------------------------------|------------------------------|--------------------------|---------|-----|----------------------------------------------------------------|--------------------------|-------------------------------------------------|
| | | Min | Opt | Max | | | |
| <i>Ignicoccus pacificus</i> | East Pacific Rise | 70 | 90 | 98 | H ₂ | S ⁰ | Huber et al. (2000) |
| <i>Geoglobus ahangari</i> | Guaymas Basin | 65 | 88 | 90 | H ₂ , volatile fatty acids, organic acids, peptides | Fe(III) | Kashefi et al. (2002) |
| " <i>Geogemma barossii</i> " | Juan-da-Fuca Ridge | – | 105–107 | 121 | H ₂ | Fe(III) | Kashefi and Lovley (2003), Lovley et al. (2004) |
| <i>Palaeococcus ferrophilus</i> | Ogasawara-Bonin Arc, Japan | 60 | 83 | 88 | Peptides | S ⁰ , Fe(III) | Takai et al. (2000) |
| <i>Methanothermococcus okinawanensis</i> | Okinawa Trough, West Pacific | 40 | 60–65 | 75 | H ₂ , formate | CO ₂ | Takai et al. (2002) |
| <i>Methanocaldococcus indicus</i> | Central Indian Ridge | 50 | 85 | 86 | H ₂ | CO ₂ | L'Haridon et al. (2003) |
| <i>Methanoterris formicicus</i> | Central Indian Ridge | 55 | 85 | 83 | H ₂ , formate | CO ₂ | Takai et al. (2004b) |
| <i>Aeropyrum camini</i> | Izu-Bonin Arc, Japan | 70 | 85 | 97 | Organic compounds | O ₂ | Nakagawa et al. (2004) |

hydrothermal vents of the Central Indian Ridge, representing new species of the genera *Methanothermococcus*, *Methanocaldococcus*, and *Methanotorris* (Takai et al. 2002; L'Haridon et al. 2003; Takai et al. 2004b).

The search for organotrophic hyperthermophilic archaea populating a deep-sea hydrothermal chimney, Suiyo Seamount, the Izu-Bonin Arc, Japan led to the isolation of *Aeropyrum camini* (Nakagawa et al. 2004), the first obligately aerobic hyperthermophilic abyssal archaeon found in a deep-sea environment. The new isolate grows by aerobic oxidation of complex proteinaceous substrates at 85°C and neutral pH. An obligately anaerobic organotroph *Palaeococcus ferrophilus*, representing another new genus, the third one in the order *Thermococcales* (Takai et al. 2000), was also isolated from a deep-sea chimney Myojin Knoll near Japan. The physiology of this organism is very close to that of other members of this order including the ability to reduce ferric iron in the course of fermentation, shown previously for some *Thermococcus* isolates (Slobodkin et al. 1999).

The genus *Thermococcus* contains 24 species, more than any other genus of hyperthermophilic archaea, and as many as 14 of its species were isolated from deep-sea habitats. Differing significantly in genomic characteristics, they are surprisingly close metabolically, being obligately organotrophic fermentative anaerobes the growth of which in closed vessels is highly dependent on the presence of an electron acceptor (elemental sulfur). Three recently isolated *Thermococcus* species were found to differ phenotypically in their barophilic (Marteinsson et al. 1999) and radioresistant (Jolivet et al. 2003, 2004) properties. Nutritionally, however, these isolates resembled other *Thermococcales*. The first representative of this genus with novel metabolic characteristics was strain AM-4 isolated from a hot vent in the East Pacific Rise. This organism can grow by oxidizing CO to CO₂ and concurrently forming H₂ from water (Sokolova et al. 2004a). Although enrichment cultures with similar properties were obtained from several environmental samples taken from the East Pacific Rise; none of the 14 previously isolated and/or type strains of *Thermococcales* belonging to nine species were able to carry out this reaction. The ability to grow by “hydrogenogenic CO-trophy” (Svetlichny et al. 2001) was found in numerous thermophilic prokaryotes, including Gram-positive thermophilic bacteria inhabiting deep-sea hydrothermal environments (Sokolova et al. 2001) that will be discussed below.

Thus, isolation of new hyperthermophilic archaea from the deep-sea thermal environment increased significantly our knowledge of their phylogenetic and metabolic diversity and unveiled catabolic processes novel for the archaeal domain.

Analysis of archaeal 16S rRNA clone libraries obtained from hydrothermal and subsea-floor abyssal environments revealed wide distribution and likely significant ecological impact of representatives of *Methanococcales*, *Methanopyrales*, *Archaeoglobales*, and

Thermococcales, previously detected by cultivation methods (Jeanthon 2000; Reysenbach et al. 2000a, b; Huber J.A. et al. 2002; Necessian et al. 2003; Takai et al. 2004c). Moreover, deep-sea environments were shown to be inhabited by many novel archaeal lineages, waiting to be isolated. Some cultivated taxa, e.g., *Thermoplasmatales* (Reysenbach et al. 2000a, b; Huber J.A. et al. 2002), were detected only by molecular methods. This family includes obligate acidophiles that could proliferate in inner parts of hydrothermal chimneys, which are filled with acidic hydrothermal fluid at initial pH about 3.5. Yet, attempts to culture thermoacidophilic organisms from deep-sea samples resulted so far only in detection of acidotolerant representatives of *Thermococcales* (Prokofeva et al. 2005).

New thermophilic bacterial deep-sea isolates

While the archaeal diversity in deep-sea environments was very actively studied over the last two decades and the feats of 2000–2004 can be viewed as continuing very efficient previous work, the thermophilic bacteria from deep-sea habitats remained virtually unknown. At the same time, molecular analyses showed that the diversity of bacteria in the environment was no less significant and represented by novel phyla of uncultured organisms. This gave a great impetus to microbiological studies targeted on isolating new thermophilic bacteria from deep-sea sources.

Thermotogales

The order *Thermotogales* represents a deep phylogenetic lineage in the *Bacteria* domain and comprises obligately organotrophic, strictly anaerobic moderately thermophilic to hyperthermophilic microorganisms with rod-shaped cells surrounded by a sheath (Reysenbach 2001a). Representatives of *Thermotogales* were detected previously in a deep-sea environment (Marteinsson et al. 1997). All isolates were identified as novel species of the genus *Thermosipho* (Antoine et al. 1997; Takai and Horikoshi 2000; Urios et al. 2004a, b) and did not differ much phenotypically from representatives of this genus previously isolated from other thermal habitats. Another two deep-sea anaerobic organotrophic rod-shaped isolates were assigned to a novel genus *Marinitoga* (Wery et al. 2001a, b). Representatives of *Marinitoga* were found to date only in deep-sea hydrothermal habitats. Resembling the type species *Marinitoga camini* in its major phenotypic characteristics (fermentative growth at moderate temperatures and neutral pH), the two new species possess important differentiating features. *Marinitoga piezophila* (Alain et al. 2002c) was found to show a higher growth rate and temperature optimum, as the hydrostatic pressure is increased to an optimal value of 40 kPa. This organism is the first and the only known example to date of a thermophilic

piezophilic bacterium. *Marinitoga hydrogenitolerans* (Postec et al. 2005) is the first representative of *Thermotogales*, the growth of which is not inhibited by molecular hydrogen.

Aquificales and related genera

The order *Aquificales* represents a deeply rooted phylogenetic lineage within the *Bacteria* domain and with minor exceptions is comprised of thermophilic or extremely thermophilic lithoautotrophs utilizing H_2 , S° , S^{2-} or $S_2O_3^{2-}$ as energy sources and O_2 , NO_3^- or S° as electron acceptors (Reysenbach 2001b). *Aquificales* were initially isolated only from terrestrial and shallow-water habitats (Kryukov et al. 1983; Kawasumi et al. 1984; Huber et al. 1992, etc.). Their occurrence in deep-sea habitats was later established by phylogenetic analyses of microbial communities of the East Pacific Rise (Reysenbach et al. 2000a), Mid-Atlantic Ridge, and Central Indian Ridge (Reysenbach et al. 2000b, 2002). Some of these organisms were isolated in pure culture and described as species of the new genus *Persephonella* (Table 2), only remotely (on the family level) related to *Aquifex* (Götz et al. 2002; Nakagawa et al. 2003). Recently, *Hydrogenobacter thermolithotrophum*, another member of *Aquificaceae*, was identified by molecular techniques in a deep-sea hydrothermal environment (Hoek et al. 2003).

Although members of the genus *Persephonella* are microaerophiles, growing optimally at oxygen concentrations under 3%, other deep-sea lithoautotrophs phylogenetically related to *Aquificales* are obligate anaerobes. The genera *Desulfurobacterium* (L'Haridon et al. 1998) and *Thermovibrio* (Huber R. et al. 2002) form a distinct phylogenetic lineage within the phylum *Aquificae*, and *Balnearium* represents a novel genus prior to the divergence of the two former ones (Takai et al. 2003b). *Desulfurobacterium* and *Balnearium* were up to now found only in deep-sea environments, and *Thermovibrio ammonificans* (Vetriani et al. 2004) belongs to a

genus previously discovered in terrestrial hot springs (Huber R. et al. 2002). Like representatives of *Persephonella*, all these microorganisms are morphologically close to *Aquificaceae* (Gram-negative rods with flagella), are extreme thermophiles and lithoautotrophs, growing optimally at 70–75°C, but differ in their nutritional features by using diverse sets of electron donors and acceptors (Table 2).

The genus *Desulfurobacterium* currently consists of the type species *D. thermolithotrophum* (L'Haridon et al. 1998), and a recently described *D. crinifex* (Alain et al. 2003). Both are thermophilic hydrogen-oxidizing anaerobes capable of sulfur reduction. *D. thermolithotrophum* can also utilize thiosulfate or sulfite as alternative electron acceptors, and *D. crinifex* is able to reduce nitrate to ammonia. By using the molecular phylogenetic approaches, a wide distribution of phylogenotypes affiliated with the genus *Desulfurobacterium* was shown in deep-sea hydrothermal habitats (Reysenbach et al. 2000a, b; Huber et al. 2003). Bacteria of the genera *Desulfurobacterium* and *Balnearium* could play an important role in deep-sea hydrothermal ecosystems as primary producers of organic matter in anaerobic zones.

Thermodesulfobacteriaceae and related taxa

Thermophilic sulfate-reducing bacteria of the *Thermodesulfobacteriaceae* family represent a deep lineage in the *Bacteria* domain (Henry et al. 1994) and until a few years ago were found only in terrestrial and deep-surface environments (Hatchikian et al. 2001). Lately, however, two representatives of this group were isolated from deep-sea thermal habitats (Jeanthon et al. 2002; Moussard et al. 2004). Both organisms are extreme thermophiles, growing in the temperature range from 55 to 80°C and optimally at 70°C. *Thermodesulfobacterium hydrogeniphilum* (Jeanthon et al. 2002) belongs to a previously known genus but unlike its terrestrial and deep-subsurface species, it is an obligate lithoautotroph, utilizing hydrogen and CO_2 as sources of energy and

Table 2 Characteristics of representatives of *Aquificales* isolated from the deep-sea hydrothermal sources

| Genus/species | Site of isolation | Growth temperatures (°C) | | | Electron donor(s) | Electron acceptor(s) | References |
|-------------------------------------|----------------------|--------------------------|-------|------|-----------------------------------|-------------------------------------------------------|----------------------------|
| | | Min | Opt | Max | | | |
| <i>Persephonella marina</i> | East Pacific Rise | 55 | 73 | 80 | S° , $S_2O_3^{2-}$, H_2 | O_2 (2–3%), NO_3^- (reduced to N_2), S° | Götz et al. (2002) |
| <i>Persephonella guaymasensis</i> | Guaymas | 55 | 70 | 75 | S° , $S_2O_3^{2-}$, H_2 | O_2 (2–3%), NO_3^- (reduced to N_2) | Götz et al. (2002) |
| <i>Persephonella hydrogenophila</i> | Izu-Bonin Arc, Japan | 50 | 70 | 72.5 | H_2 | O_2 (0.8% opt), NO_3^- (reduced to N_2) | Nakagawa et al. (2003) |
| <i>Desulfurobacterium crinifex</i> | Juan de Fuca Ridge | 50 | 60–65 | 70 | H_2 | NO_3^- (reduced to NH^+), S° | Alain et al. (2003) |
| <i>Balnearium lithotrophicum</i> | Izu-Bonin Arc, Japan | 45 | 70–75 | 80 | H_2 | S° | Takai et al. (2003a, b, c) |
| <i>Thermovibrio ammonificans</i> | East Pacific Rise | 60 | 75 | 80 | H_2 | NO_3^- (reduced to NH^+), S° | Vetriani et al. (2004) |

carbon, respectively. Another isolate, *Thermodesulfator indicus* (Moussard et al. 2004), exhibited very similar phenotypic characteristics but was found to be only distantly related to *Thermodesulfobacteriaceae* (<90% 16S rRNA gene sequence similarity).

Deferribacterales

The order *Deferribacterales* is another deep bacterial lineage. Its first representative, isolated from a high temperature oil reservoir, was the first Fe(III)- and Mn(IV)-reducing Gram-negative thermophilic bacterium (Greene et al. 1997). The occurrence of this group in deep-sea hydrothermal environments was first shown by DGGE analyses of Fe(III)-reducing enrichments (Slobodkin et al. 2001); and later *Deferribacter desulfuricans* (Takai et al. 2003a) and *Deferribacter abyssi* (Miroshnichenko et al. 2003a) were isolated. The first organism, obtained from the Suiyo Seamount hydrothermal chimney (Japan), differed from the type strain by an inability to reduce ferric iron but could reduce nitrate (to nitrite), elemental sulfur, and arsenate. The latter organism was found in hot vents of the East Pacific Rise and in hot vents of the Mid-Atlantic Ridge. Cells of *D. abyssi* are vibrios rather than rods. This obligately anaerobic bacterium can utilize a surprisingly diverse range of electron donors and acceptors. Molecular hydrogen supports lithoautotrophic growth with elemental sulfur but growth with ferric iron requires, unexpectedly, the presence of yeast extract. Like the type strain, deep-sea *Deferribacter* species can oxidize diverse organic substrates: peptides, volatile fatty acids, and organic acids.

Geobacteraceae

The family *Geobacteraceae* includes representatives of *Deltaproteobacteria* capable of dissimilatory ferric iron

reduction (Lovley et al. 2004); and until recently consisted only of mesophilic species. The first thermophilic member of this family—*Geothermobacter ehrlichii* (Kashefi et al. 2003) was isolated from hydrothermal fluid of a Juan de Fuca Ridge deep-sea vent. Cells of *G. ehrlichii* are highly motile short rods. This organism was found to oxidize volatile fatty acids, organic acids, and alcohols and reduce ferric iron to ferrous and nitrate to ammonium.

Thermaceae

Gram-negative thermophilic bacteria of the family *Thermaceae* constitute one of the best-studied group of thermophilic prokaryotes. Most species were isolated from terrestrial and shallow-water thermal habitats and are obligate organotrophs with aerobic respiration, although some are also able to grow anaerobically with nitrate (Williams and Da Costa 1992). The first representative of *Thermaceae* isolated from a deep-sea habitat under aerobic conditions was *Thermus thermophilus*, a strain of a widely occurring terrestrial species (Martinson 1999). Recently, several new members of *Thermaceae* were isolated from different deep-sea hydrothermal habitats, which differed from previously known terrestrial and shallow-water species both phylogenetically and metabolically (Table 3). In their morphology and most of metabolic and chemotaxonomic features (including the temperature and pH growth profiles and respiratory type of metabolism), the new organisms are similar to other *Thermaceae*. However, some of their features are completely new for this group. Unlike previously obtained shallow-water *Thermaceae*, which are halo-tolerant, the growth of all new deep-sea isolates is obligately dependent on marine salinity of the culture medium. *Marinithermus hydrothermalis* is the only obligate aerobe among new isolates. It was obtained from a sample of hydrothermal chimney surface

Table 3 Characteristics of new representatives of *Thermaceae* isolated from the deep-sea hydrothermal sources

| Genus/species | Site of isolation | Growth temperatures (°C) | | | Electron donor(s) | Electron acceptor(s) | References |
|--------------------------------------|----------------------|--------------------------|-------|-----|----------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------|
| | | Min | Opt | Max | | | |
| <i>Marinithermus hydrothermalis</i> | Izu-Bonin Arc, Japan | 40 | 60–65 | 75 | Peptides, amino acids, carbohydrates, acetate, pyruvate | O ₂ | Sako et al. (2003) |
| <i>Oceanithermus profundus</i> | East Pacific Rise | 40 | 60 | 68 | Carbohydrates, peptides (0.1–0.15%), acetate, propionate, pyruvate, alcohols, H ₂ | O ₂ (<6%), NO ₃ ⁻ reduced to NO ₂ ⁻) | Miroshnichenko et al. (2003b) |
| <i>Oceanithermus desulfurans</i> | Izu-Bonin Arc, Japan | 30 | 60 | 65 | Peptides, amino acids, butyrate, propionate, pyruvate, succinate | O ₂ (<5%), NO ₃ ⁻ (reduced to NO ₂ ⁻) NO ₂ ⁻ , S ⁰ | Mori et al. (2004) |
| <i>Vulcanithermus mediatlanticus</i> | Mid-Atlantic Ridge | 37 | 70 | 80 | Peptides, carbohydrates, acetate, butyrate, succinate, fumarate, alcohols, H ₂ | O ₂ (opt 4–8%), NO ₃ ⁻ (reduced to NO ₂ ⁻) | Miroshnichenko et al. (2004) |

material, a likely habitat for aerobic thermophiles because of its contact with aerated water (Sako et al. 2003). This organism is an obligate organotroph and obligate aerobe, unable to grow by nitrate reduction. The three other *Thermaceae* isolated from deep-sea vents turned out to be microaerophiles, the first in this family. Growth of *Oceanithermus profundus* and *Oceanithermus desulfurans* is restricted by oxygen content and does not occur at concentrations exceeding 6 and 5%, respectively (Miroshnichenko et al. 2003b; Mori et al. 2004). *Vulcanithermus mediatlanticus* (Miroshnichenko et al. 2003c) can grow under air in liquid medium but not on plates and shows optimal growth at 8% oxygen. The microaerophily of these species is consistent with the environmental characteristic of their isolation sites, namely, exposure to extremely steep gradients of temperature and oxygen concentration. Another important capacity of *O. profundus* and *V. mediatlanticus*, for the first time found in representatives of *Thermaceae*, is the ability to grow lithoheterotrophically by utilizing molecular hydrogen as an energy source. The ability to use elemental sulfur as an energy source was previously found in terrestrial *Thermus scotoductus* (Skirnisdottir et al. 2001). The distinguishing feature of *O. desulfurans* is its ability to use a wider range of electron acceptors than other *Thermaceae*. In addition to nitrate, it can also grow by reducing elemental sulfur or nitrite. Unfortunately, the original description of *O. desulfurans* failed to name reduced products formed from nitrate and nitrite. Given that all *Thermaceae* reduce nitrate to nitrite, *O. desulfurans* might perform a different process not reported so far for this group of microorganisms.

Epsilonproteobacteria

Assessment of bacterial diversity of deep-sea hydrothermal environments by means of culture-independent

molecular phylogenetic techniques revealed that *Epsilonproteobacteria* represented an extremely abundant and diverse group in bacterial clone libraries obtained from a wide variety of hydrothermal samples. They were found to dominate in microbial hydrothermal mats (Moyer et al. 1995; Longenecker and Reysenbach 2001), colonization devices (Reysenbach et al. 2000a, b; Corre et al. 2001; Lopez-Garcia et al. 2003; Takai et al. 2003c), in the epibiotic microflora of deep-sea vent metazoans (Habbad et al. 1995; Campbell et al. 2001; Alain et al. 2002a; Lopez-Garcia et al. 2002), and diffuse flow hydrothermal fluids (Huber et al. 2003). The majority of *Epsilonproteobacterial* phylotypes were identified as clades and that at that time, they had no representatives in laboratory cultures. However, some sequences affiliated with previously described members of the Epsilon-subclass of *Proteobacteria* in particular *Thiomicrospira denitrificans* (Teske et al. 2002; Huber et al. 2003), *Archaeobacter* (Lopez-Garcia et al. 2002; Huber et al. 2003), *Thiovolum* (Moyer et al. 1995), and *Sulfospirillum* (Campbell et al. 2001; Hoek et al. 2003).

In 2001, Corre and coworkers classified uncultured *Epsilonproteobacteria* inhabiting deep-sea hot vents into six phylogenetic groups (A–F) and predicted some phenotypic features of these microorganisms on the basis of their phylogenetic position. For a certain time, the *Epsilonproteobacteria* harboring these environmental sequences remained uncultured. Then several isolates were obtained from samples associated with the hydrothermal vent polychaete *Alvinella pompejana* (Campbell et al. 2001). And before long, the first representatives of *Epsilonproteobacteria* from deep-sea hydrothermal vents, *Nautilia lithotrophica* (Miroshnichenko et al. 2002) and *Caminibacter hydrogenophilus* (Alain et al. 2002b) were fully characterized (Table 4). Both microorganisms represented new genera and were described as moderately thermophilic anaerobes able to oxidize hydrogen in the presence of elemental sulfur. *N. litho-*

Table 4 Characteristics of thermophilic *Epsilonproteobacteria* isolated from the deep-sea hydrothermal sources

| Genus/species | Site of isolation | Growth temperatures (°C) | | | Electron donor(s) | Electron acceptor(s) | References |
|-------------------------------------|---------------------------|--------------------------|-----|-----|---------------------------------------------|----------------------------------------------------------------|------------------------------|
| | | Min | Opt | Max | | | |
| <i>Nautilia lithotrophica</i> | East Pacific Rise | 37 | 53 | 68 | H ₂ , formate | S ⁰ , SO ₃ ²⁻ | Miroshnichenko et al. (2002) |
| <i>Caminibacter hydrogenophilus</i> | East Pacific Rise | 50 | 60 | 70 | H ₂ , complex organic substrates | S ⁰ , NO ₃ ⁻ | Alain et al. (2002b) |
| <i>Caminibacter profundus</i> | Mid-Atlantic Ridge | 45 | 55 | 65 | H ₂ | S ⁰ , NO ₃ ⁻ , O ₂ | Miroshnichenko et al. (2004) |
| <i>Caminibacter mediatlanticus</i> | Mid-Atlantic Ridge | 45 | 55 | 70 | H ₂ | S ⁰ , NO ₃ ⁻ | Voordeckers et al. (2005) |
| <i>Hydrogenimonas thermophila</i> | Central Indian Ridge | 35 | 55 | 65 | H ₂ | S ⁰ , O ₂ , NO ₃ ⁻ | Takai et al. (2005) |
| <i>Nitratiruptor tergaricus</i> | Mid-Okinawa Trough, Japan | 40 | 55 | 57 | H ₂ | NO ₃ ⁻ , O ₂ , S ⁰ | Nakagawa et al. (2005) |
| <i>Lebetimonas acidiphila</i> | Mariana Arc | 30 | 50 | 68 | H ₂ | S ⁰ | Takai et al. (2005) |

trophica utilized formate as an alternative electron donor while *C. hydrogenophilus* could use both elemental sulfur and nitrate as electron acceptors. *N. lithotrophica* and *C. hydrogenophilus* represented the first cultivated deep-sea hydrothermal *Epsilonproteobacteria* belonging to the phylogroup D in terms of Corre's phylogenetic classification. These organisms, as well as the isolates obtained by Campbell, originated from samples associated with the tube-dwelling polychaete *Alvinella* spp., an endemic metazoan inhabiting the deep-sea hydrothermal system of the East Pacific Rise. *Caminibacter profundus* (Miroshnichenko et al. 2004) was isolated from a sample of biomass collected using an in situ growth chamber deployed in the deep-sea hydrothermal system on the Mid-Atlantic Ridge. It differed from the type species by its strict lithoautotrophy and ability to grow under microaerophilic conditions. *C. mediatlanticus* (Voordeckers et al. 2005) was the last on the list of characterized *Caminibacter* species. Recently, phylotypes closely related to *N. lithotrophica* were identified in a clone library constructed from a sample of sulfide spire from the Edmont deep-sea hydrothermal vent field in the Central Indian Ridge (Hoek et al. 2003). In the latter study, phylotypes belonging to *Epsilonproteobacteria* accounted for more than 90% of the bacterial clone library and sequences closely related to *N. lithotrophica* were found to constitute the largest fraction (>40%) of all *Epsilonproteobacterial* phylotypes. All these data prove the cosmopolitan distribution of *Epsilonproteobacteria* and suggest their significant role in deep-sea hydrothermal ecosystems.

Until the discovery of a wide diversity of *Epsilonproteobacteria* in deep-sea hydrothermal environments, this subclass was represented by a taxonomically heterogeneous assortment of Gram-negative mesophilic bacteria, predominantly pathogenic. It consisted of a single order *Campylobacterales* comprising two families *Campylobacteraceae* and "*Helicobacteraceae*" (Vandamme and De Ley 1991). Recently, on the basis of distinct phylogenetic position and the thermophily of the cultivated *Epsilonproteobacteria* from deep-sea hydrothermal environments, a new order *Nautiliales* of the subclass *Epsilonproteobacteria* with a single family *Nautiliaceae* was proposed (Miroshnichenko et al. 2004). Today, the family *Nautiliaceae* includes three genera: *Nautilia*, *Caminibacter*, and *Lebetimonas*. The latter genus, represented by a single species *Lebetimonas acidiphila* (Takai et al. 2005), shared major phenotypic features with other members of the family *Nautiliaceae* but differed by a slightly acidic pH range for growth.

Over the last 3 years, impressive progress was made in cultivation of other previously uncultivated *Epsilonproteobacteria* representing phylogroups A, B, F, and G according to Corre's classification. Takai and coworkers isolated a variety of new, metabolically and phylogenetically diverse, free-living *Epsilonproteobacteria* from the Mid-Okinawa Trough and the Central Indian Ridge hydrothermal vent systems (Takai et al. 2003c). Some of

these new isolates were already characterized; the descriptions of others are underway.

A novel thermophilic microaerobic to anaerobic lithoautotroph *Hydrogenimonas thermophilus* was the first cultivated representative of the subgroup A (Takai et al. 2004a). Despite its phylogenetic affiliation, the phenotypic features of *H. thermophilus* are almost identical to those of *C. profundus* and similar to other cultivated members of the phylogroup D (Table 4). A novel genus and species *Nitratiruptor tergarcus* (Nakagawa et al. 2005) is another cultivated member of the phylogroup A. Unlike nitrate-ammonifying *H. thermophilus*, *N. tergarcus* is capable of complete nitrate reduction, forming N_2 as a reduced product.

The successful cultivation and characterization of a number of novel *Epsilonproteobacteria* strongly support the view that these microorganisms play a significant ecological role in deep-sea hydrothermal ecosystems. Being chemolithoautotrophs (in some cases, facultative), deep-sea hydrothermal *Epsilonproteobacteria* can utilize diverse electron acceptors and most of these organisms participate in the sulfur cycle by reducing or oxidizing elemental sulfur and sulfur compounds. They can be considered as primary producers of organic matter in anaerobic zones or under aerobic/anaerobic conditions, typical for the mixing interfaces in deep-sea hydrothermal environments. The diversity of metabolic pathways together with a wide variety of temperature characteristics within this taxonomic group give *Epsilonproteobacteria* significant advantages in colonizing diverse newly formed surfaces available for microbial life, both natural (sediment particles or animal teguments) and artificial (colonization devices) (Lopez-Garcia et al. 2003; Alain et al. 2004).

Genus *Caldithrix*

The isolation of *Caldithrix abyssi* from samples collected in the Mid-Atlantic Ridge hydrothermal area (Miroshnichenko et al. 2003a) was further evidence that deep-sea microbial communities were rich in phylogenetically singular microorganisms. Cells of *C. abyssi* are long filaments with Gram-negative envelopes, often accompanied by round bodies. It is a moderate thermophile and an obligate anaerobe, growing either by fermentation of peptides or by nitrate respiration, oxidizing molecular hydrogen or acetate, and reducing nitrate to ammonium. Although this combination of phenotypic capacities is fairly unusual, anyone of them can be found among other thermophilic taxa. However, the analysis of the 16S rRNA gene sequence of *C. abyssi* revealed that it had no close relatives among the cultured microorganisms. The only closely related sequence was that of clone ML-5 (Sievert et al. 2000) obtained from shallow-water hydrothermal vents of the Aegean Sea. The organisms represented by clone ML-5 were dominating in the layer of anaerobic hot sediments 8 cm under the seafloor. It is not clear at present if the eco-

logical function of the shallow-water organisms isolated from the Aegean can be surmised on the basis of our knowledge of metabolism of *C. abyssi*.

Firmicutes

All representatives of *Firmicutes* isolated until now from deep-sea habitats were moderate thermophiles, obligate anaerobes, and (with one exception) obligate organotrophs. The *Thermoanaerobacter* organisms identified in deep-sea habitats were shown to belong to previously known species (Jeanthon 2000; Prokofeva et al. 2005). The characteristics of new *Firmicutes* from deep-sea sources are given in Table 5. Four of them are rather similar phenotypically and represent the new genera *Caloranaerobacter* (Wery et al. 2002), *Caminiella* (Alain et al. 2002c), and *Tepidibacter* (Slobodkin et al. 2003; Urios et al. 2004a, b). These three genera fall into clusters XI (*Caminiella* and *Tepidibacter*) and XII (*Caloranaerobacter*) of the *Clostridium* subphylum and are characterized by an unusually low G + C content of the DNA equal to 24–29 mol%.

The only Gram-positive deep-sea thermophilic isolate capable of lithotrophic growth is *Carboxydobrachium pacificum* (Sokolova et al. 2001), recently reclassified as *Caldanaerobacter subterraneus* subsp. *pacificum* (Fardeau et al. 2004). This organism, isolated from the Okinawa Trough, is able to grow by anaerobic oxidation of CO to CO₂ with concomitant formation of molecular hydrogen from water. Comparison of the 16S rRNA gene sequences revealed that it forms a single cluster with several species of the genus *Thermoanaerobacter* described and published concurrently, and this group could be distinguished from other species by a group-specific molecular probe (Subbotina et al. 2003). Fardeau and coworkers showed that this group represented a novel genus *Caldanaerobacter* with a very high level of DNA–DNA homology between all its members. Thereby, all these organisms are subspecies of the only

species of this genus *C. subterraneus*. Like other members of this group, *C. subterraneus* subsp. *pacificum* can grow organotrophically by fermenting multiple organic substrates. Its ability to utilize CO as an energy source might be an advantage in deep-sea hydrothermal communities given that CO is a common component of volcanic exhalations (Symonds et al. 1994). “Hydrogenogenic CO-trophy” (Svetlichny et al. 2001) is a common feature of several Gram-positive thermophilic bacteria isolated from terrestrial habitats that do not form a single phylogenetic group (Svetlichny et al. 1991; Sokolova et al. 2002, 2004b). This evidence and the isolation of the first hyperthermophilic archaeon capable of the same catabolic process call for a detailed genetic investigation of the underlying mechanisms. Apart from the ability to grow with CO, *C. subterraneus* subsp. *pacificum* resembles other deep-sea Gram-positive isolates in being an obligately anaerobic fermentative organotroph not dependent on any electron acceptor. Not belonging to the *Clostridium* group, it also constitutes a Gram-positive bacterium with a low G + C content of the DNA.

Another Gram-positive thermophilic bacterium was recently isolated from the hydrothermal area of the Mid-Atlantic Ridge that differs from all previous Gram-positive isolates. “*Vulcanibacillus modestocaldus*” (L’Haridon et al., manuscript in preparation) is a sporeforming, obligately anaerobic, moderately thermophilic bacterium oxidizing a wide range of organic substrates, including nonfermentable ones and obligately requiring the presence of nitrate, which is reduced to nitrite. It is also able to grow lithoheterotrophically with molecular hydrogen. Phylogenetically, it was assigned to the *Bacillus* group as a novel genus.

Conclusion

The findings of recent years revealed significant metabolic and phylogenetic diversity of cultivated thermo-

Table 5 Characteristics of new Gram-positive thermophilic bacteria isolated from the deep-sea hydrothermal sources

| Genus/species | Site of isolation | Growth temperatures (°C) | | | Electron donor(s) | Electron acceptor(s) | References |
|--------------------------------------------------------------|--------------------|--------------------------|-------|-----|----------------------------------------------|-------------------------------------------------------------------------|-----------------------------------------------|
| | | Min | Opt | Max | | | |
| <i>Caloranaerobacter azorensis</i> | Mid-Atlantic Ridge | 45 | 55 | 65 | Peptides, sugars, polysaccharides | – | Wery et al. (2001a, b) |
| <i>Caminiella sporogenes</i> | East Pacific Rise | 45 | 55–60 | 65 | Peptides, amino acids, sugars | – | Alain et al. (2002a, b, c, d) |
| <i>Tepidibacter thalassicus</i> | East Pacific Rise | 33 | 50 | 60 | Proteins, peptides, amino acids, starch | – | Slobodkin et al. (2003) |
| <i>Tepidibacter formicigenes</i> | Mid-Atlantic Ridge | 35 | 45 | 55 | Peptides, sugars | – | Urios et al. (2004a, b) |
| <i>Caldanaerobacter subterraneus</i> subsp. <i>pacificum</i> | Okinawa Trough | 50 | 70 | 80 | Peptides, sugars, pyruvate; CO | Water (in case of CO) | Sokolova et al. (2001), Fardeau et al. (2004) |
| “ <i>Vulcanibacillus modestocaldus</i> ” | Mid-Atlantic Ridge | 37 | 55 | 60 | Peptides, sugars, acetate, ethanol, pyruvate | NO ₃ [–] (reduced to NO ₂ [–]) | L’Haridon et al., manuscript in preparation |

philic microorganisms inhabiting deep-sea thermal environments. In part, it parallels the phylogenetic diversity of hydrothermal microbial communities discovered by molecular methods, since some of the isolates turned out to be closely related to organisms represented by environmental clones obtained from these habitats. The isolation and characterization of pure cultures allowed the observed metabolic features to be attributed to representatives of novel phylogenetic groups that were found to dominate some of the deep-sea habitats, *Epsilonproteobacteria* being the best example.

A comparatively large number of the new isolates warrant several generalizations. The majority of the new deep-sea thermophilic isolates are lithotrophs, obligately or facultatively dependent on inorganic energy sources. The ability to use H₂ or CO as energy substrates was found even in representatives of taxa previously known to include only organotrophic species (*Thermaceae*, *Thermococcus*, and *Caldanaerobacter*). Most of the new isolates are obligate or facultative anaerobes, in the latter case, microaerophiles. This is in good agreement with the environmental conditions given that the hydrothermal fluid, even suitably cooled by mixing with oceanic water, still remains reduced because of high content of hydrogen sulfide. The new archaeal and bacterial deep-sea isolates obtain their energy for growth via different types of anaerobic respiration by reducing diverse inorganic electron acceptors such as CO₂, elemental sulfur, sulfate, thiosulfate, ferric iron, and nitrate. While CO₂ is a common component of volcanic gases and sulfate is supplied with oceanic water, all other electron acceptors arise most probably from chemical or biological oxidation of reduced components of the hydrothermal fluid. This does not necessarily apply to nitrate, the origin of which in deep-sea hydrothermal ecosystems remains unknown. At the same time, the number and diversity of nitrate-reducing thermophilic prokaryotes forming different products of nitrate reduction (N₂, NO₂⁻, and NH₄⁺) make the origin of nitrate in hydrothermal systems an intriguing and topical problem.

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