

Diversity of Thermophilic Anaerobes

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Thermophilic anaerobes are Archaea and Bacteria that grow optimally at temperatures of 50°C or higher and do not require the use of O₂ as a terminal electron acceptor for growth. The prokaryotes with this type of physiology are studied for a variety of reasons, including (a) to understand how life can thrive under extreme conditions, (b) for their biotechnological potential, and (c) because anaerobic thermophiles are thought to share characteristics with the early evolutionary life forms on Earth. Over 300 species of thermophilic anaerobes have been described; most have been isolated from thermal environments, but some are from mesobiotic environments, and others are from environments with temperatures below 0°C. In this overview, the authors outline the phylogenetic and physiological diversity of thermophilic anaerobes as currently known. The purpose of this overview is to convey the incredible diversity and breadth of metabolism within this subset of anaerobic microorganisms.

Key words: thermophile; anaerobe; thermobiotic; diversity of anaerobic thermophiles; Bacteria; Archaea

Introduction

Bacteria and Archaea that grow optimally at elevated temperatures and do not require oxygen for growth are described as thermophilic anaerobes, and the taxa having this physiology are of interest from basic and applied scientific perspectives. Because these prokaryotes grow optimally at elevated temperatures, thermophilic anaerobes are designated *extremophiles* and are studied to understand how life can thrive in environments previously considered inhospitable to life. Such environments include volcanic solfatares and hot springs high in sulfur and toxic metals, as well as abyssal hydrothermal vents with extremely high pressure and temperature.^{1,2} Isolated species of thermophilic anaerobes include astonishing forms of life: for example, the mothercell of the alkalithermophile *Clostridium paradoxum* becomes highly motile when sporulating,³ and *Moorella thermacetica*-like strains have exceptionally heat-resistant spores with D₁₀ times of nearly 2 h at 121°C.⁴ Also, *Pyrolobus fumarii* grows optimally at 106°C,⁵ and a recently isolated *Methanopyrus kandleri*-like strain grows at 122°C under increased pressure.⁶ *Thermobrachium celere* strains have doubling times of about 10 min under optimal conditions,⁷ and the triple extremophile *Natranaerobius thermophilus* grows optimally at high temperature (53°C), high pH (9.5),

and high salt concentration (3.3–3.9 M Na⁺) simultaneously.⁸

The analyses of the biodiversity and patterns of biodiversity within thermal environments is an area of active research that continually expands as technology allows for novel approaches and more detailed analyses. Additionally, their thermostable enzymes, among other characteristics, make thermophilic anaerobes of significant interest for their biotechnological potential.^{9–11}

Thermophilic anaerobes also attract research attention because it is assumed that they have properties similar, in various aspects, to those of the early evolutionary life forms on Earth.⁴ There is little doubt that the first forms of life on Earth occurred at a time when significantly less oxygen was present. Apparent biogenic signatures have been dated to 3.85–3.8 billion years ago (Ga) and complex microfossil communities are dated to 3.5–3.4 Ga, whereas the accumulation of oxygen happened later, approximately 2.1–2.3 Ga.^{12,13} The early forms of life from which everything else then evolved (i.e., the progenotic life forms), were therefore anaerobes.¹⁴ Considering Earth history and these progenotic life forms, the authors believe that present-day life has several roots as proposed by Kandler.¹⁵ In addition to having an anoxic origin, the current mainstream opinion is that life began at elevated temperatures, and was

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⁴Further discussion of thermophiles and the origin of life can be found in the conference proceedings book: Wiegel, J. and M.W.W. Adams. 1998. Thermophiles: the Keys to Molecular Evolution and the Origin of Life? Taylor & Francis Ltd. London.

consequently thermophilic. Although some contest this view of a thermophilic origin of life and postulate that prebiotic chemistry implies the emergence of living systems at a low temperature or a rapid selection for hyperthermophiles during the late bombardment,^{16–18} many believe that evolution from mesophily to hyperthermophily is improbable.¹⁹ Thus, the authors and most others posit that life began around 80°C on clay or iron-sulfur mineral surfaces in shallow pools.²⁰

Although the first forms of life no longer exist, natural thermal environments do still exist and some have properties similar to those environments in which life presumably first began. Many of these environments are characteristically anaerobic or have low levels of oxygen. The anaerobic feature can stem from a number of factors: remoteness of the environment from the atmosphere; low solubility of oxygen in water at elevated temperatures; hypersalinity; inputs of reducing gasses, such as H₂ and H₂S; or the consumption of oxygen by aerobic microorganisms on or near the water surface.^{21,22} Broadly, natural thermobiotic environments are of terrestrial, marine, or subsurface nature. Terrestrial or continental geothermally heated features include hot springs, geysers, solfatares, mud pools (“mud pots”), and some solar-heated environments. One example, Yellowstone National Park, USA, contains the highest concentration of terrestrial geothermal features on Earth.²³ Other locales of notable terrestrial thermal activity include Japan, New Zealand, Iceland, the Hawaiian volcanoes, various South Pacific Islands located at The Ring of Fire, and the Kamchatka Peninsula in the Russian Far East. Thermobiotic marine environments include geothermally heated beaches, shallow hydrothermal vents, and abyssal hydrothermal vents, where water escapes at temperatures over 300°C.²⁴ Two examples of geothermally heated beaches are those on the North Island of New Zealand and on SavuSavu (Fiji Islands); the geothermally heated spots are exposed at low tide and covered with water at high tide. Some shallow thermal marine systems where thermophilic anaerobes have been isolated include Volcano Shore of Sicily and Lucrino Beach near Naples, Italy; Palaeochori Bay of Milos, Greece; the coastal hot springs of Ibuski, Kanagoshima Prefecture, Japan; the marine solfataric fields of Kraternaya Cove, Ushishir Archipelago, Northern Kurils; a hydrothermal field at a depth of about 100 m at the Eyjafjörður Fjord, Northern Iceland; and the Kolbeinsey Ridge located at a depth about 105 m, north of Iceland. First described in the 1970s on the Galapagos Rift,²⁵ deep-sea hydrothermal vent regions have been found and studied in the Pacific and Atlantic Oceans, including: the “Rainbow,” “Snakepit,”

and Logatchev hydrothermal vent regions of the Mid-Atlantic Ridge; the 9°N, 13°N, and 21°N deep-sea hydrothermal vent systems of the East Pacific Rise; the Iheya Ridge and Yonaguni Knoll IV of the Okinawa Trough; the Guaymas Basin, Gulf of California; and recently, hydrothermal vents were discovered as far north as the Mohns Ridge, Norway.²⁶ Oil reservoirs, mines, and geothermal aquifers are examples of subsurface environments thermophiles populate. Species of the genera *Geotoga* and *Petrotoga* (family Thermotogaceae {B34}^b) have thus far only been found in deep subsurface oil reservoirs; on this basis, it has been proposed that these taxa represent typical indigenous *Bacteria* in this particular ecosystem.²⁷ Geothermal aquifers, such as the Great Artesian Basin of Australia, are considered to be markedly different from volcanically related hot springs in that they have low flow rates and long recharge times (around 1000 years) that affect the microbial populations therein.²⁸ Besides natural thermal environments, thermophilic anaerobes are also found within anthropogenically heated environments, including coal refuse piles; compost heaps, which contain not only spore-forming species, but also methanogenic Archaea²⁹; and nuclear power plant effluent channels. Contrary to expectations, thermophilic anaerobes have also been isolated from mesobiotic and even psychobiotic environments: two *Thermosediminibacter* species were isolated from ocean sediments of the Peru Margin at temperatures at or below 12°C,³⁰ uncharacterized *Thermoanaerobacter* species have been isolated from melted snow from Antarctica (J. Wiegel, unpublished results), alkalithermophiles have been isolated from many river sediments and wet meadows,⁷ and *Methanothermobacter thermoautotrophicus* and other thermophilic methanogens can readily be found in lake sediments (e.g., Lake Mendota, Wisconsin, USA) and rivers, streams, and ponds (e.g., in Northern Germany).³¹ Possible reasons for the presence of thermophilic anaerobes in environments where they ought not to grow, considering their physiological properties, include (a) that the microorganisms are present but not growing in these environments, (b) that they dispersed only transiently from other thermal environments, or (c) as the authors propose, that they are surviving by taking advantage of temporary thermal microniches that become available when proteinaceous biomass is degraded.⁷

^bThe designation within the brackets corresponds to the particular thermophilic anaerobe-containing family as shown in FIG. 1., a 16S rRNA gene sequence-based phylogenetic tree, and as listed in TABLE 1, which lists the validly described thermophilic anaerobes.

Undoubtedly, the wide spectrum of properties of the environments thermophilic anaerobes inhabit has been, and continues to be, of significance in the evolution and diversification of these microorganisms. The evolutionary implications are a fascinating topic alone. Nevertheless, the result of this diversification—the diversity of thermophilic anaerobes—is examined in this chapter. The goal herein is to provide an overview of the diversity of thermophilic anaerobes from phylogenetic and physiological perspectives and, where appropriate, to highlight unique and noteworthy taxa.

Measuring the Diversity of Thermophilic Anaerobes

Although biological diversity is usually considered to be a combination of two qualities of a population, species richness (the number of different kinds) and species evenness (the relative numbers of those present),³² the focus herein will primarily be species richness. As such, this overview of the diversity of thermophilic anaerobes will be primarily limited to describing diversity as a function of what is known of these Bacteria and Archaea through studies on axenic cultures. The caveat is that most of the prokaryotes from any environment, including the thermal environments previously discussed, are currently uncultured.³³ Consequently, our understanding of prokaryotic biodiversity and physiological properties is based on very limited knowledge. Although culture-independent studies are not the focus of this chapter, such studies, including analyses of environmental 16S ribosomal RNA gene sequences, metagenomics (i.e., the sequencing of DNA isolated from an environment), and sequences of genes encoding particular functional proteins, help address this major limitation.

Culture-independent studies of terrestrial thermobiotic sites include sites in Yellowstone National Park,^{34–38} hot springs of Japan,³⁹ hot springs of New Zealand,⁴⁰ hot springs of Greenland,⁴¹ subterranean and terrestrial Icelandic hot springs,^{42,43} the thermal subterranean Great Artesian Basin of Australia,⁴⁴ and sun-heated salt lakes (Wadi An Natrun) in Egypt,⁴⁵ to name a few. Examples of deep-sea hydrothermal sites studied by culture-independent means include the Manus Basin near Papua New Guinea,⁴⁶ the Suiyo Sea Mount and Myojin Knoll in the Ogasawara area of Japan, and the hydrothermal fields at the Iheya Basin in the Okinawa area of Japan.⁴⁷ Besides strictly culture-independent techniques, additional methods

have been developed or employed to study the thermophilic anaerobes inhabiting thermobiotic environments. For example, an *in situ* growth chamber deployed at a hydrothermal vent field revealed novel lineages.⁴⁸ 16S rRNA hybridization probes developed for members of the *Thermoanaerobacter*/*Caldanaerobacter* clade detected *Thermoanaerobacter* members from deep-sea hydrothermal regions, an environment not previously known to harbor *Thermoanaerobacter* species.⁴⁹ Similarly, *Desulfotomaculum* 16S rRNA hybridization probes were employed to measure the change in abundance in thermophilic anaerobic digesters among other sites.⁵⁰

Thermophilic anaerobes in pure culture are characterized through the polyphasic approach, in which phenotypic and genotypic/phylogenetic properties are examined.^{51,52} Phenotypic characteristics of particular interest for this discussion include oxygen relationships and metabolic properties, such as energy production and carbon assimilation. Group-defining properties, such as temperature growth range (e.g., T_{\min} , T_{opt} , and T_{\max}) and pH growth range (e.g., pH_{\min} , pH_{opt} , and pH_{\max}), are particularly important. These values should be determined by measuring the doubling times over the range for growth and specifically noting where growth was obtained and where growth was not obtained. (For example, in the authors' laboratory, a shaking gradient incubator with 1°C–3°C intervals is used to determine the temperature growth profile for a strain.) Other properties, such as salt tolerance and response to pressure, are important when considering thermophilic anaerobes from habitats such as hypersaline lakes and deep-sea hydrothermal regions. Although genotypic characteristics such as G+C mol% and DNA–DNA relatedness between strains have been studied since the 1960s, in the past 20 years, analysis of the 16S rRNA gene sequence has become standard, and the analysis of housekeeping genes and whole-genome sequencing of prokaryotes is becoming increasingly common.⁵³ Known thermophilic anaerobes with available sequenced genomes are designated within TABLE 1 with the § symbol, but the continually increasing number can be obtained from the National Center for Biotechnology Information Taxonomy Database: http://www.ncbi.nlm.nih.gov/genomes/MICROBES/microbial_taxtree.html. Analysis of the 16S rRNA gene sequence-based phylogenetic tree (FIG. 1), reveals that, at present (November 2007), thermophilic anaerobes reside in 51 known prokaryotic families (TABLE 1). Still, this will undoubtedly change as novel thermophilic anaerobes are isolated and the subsequent phylogenetic reorganization of taxa proceeds.

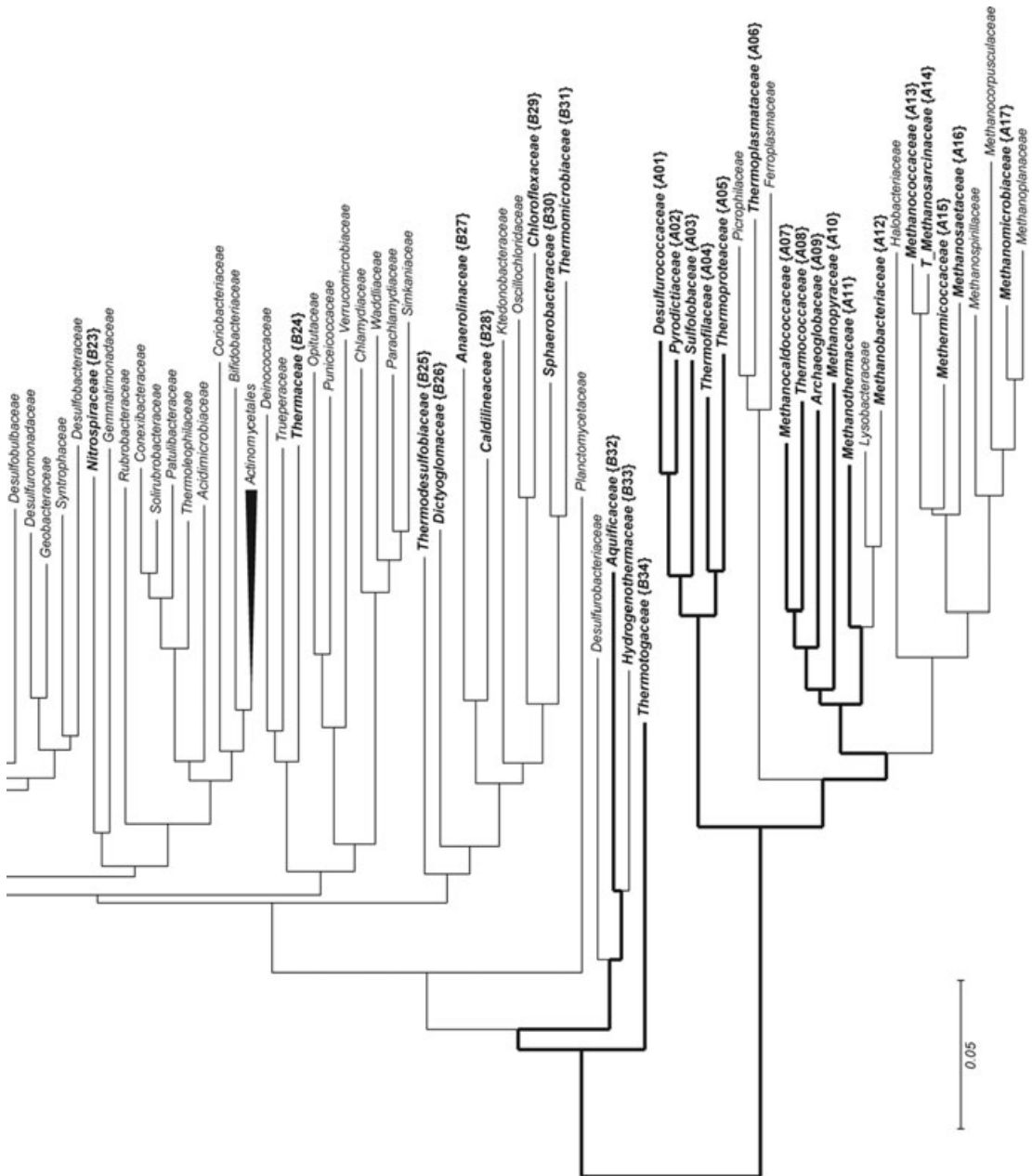


FIGURE 1 (Continued). *Conexibacter woesei* AJ440237; *Coriobacteriaceae*, *Coriobacterium glomerans* X79048; *Cryomorphaceae*, *Cryomorpha ignava* AF170738; *Cystobacteraceae*, *Cystobacter fuscus* M94276; *Cytophagaceae*, *Cytophaga hutchinsonii* CP000383 (region 120118–121499); *Deferribacter thermophilus* U75602; *Deinococcaceae*, *Deinococcus radiodurans* Y11332; *Desulfarculaceae*, *Desulfarculus baarsii* M34403; *Desulfobacteraceae*, *Desulfobacter postgatei* AF418180; *Desulfobulbaceae*, *Desulfobulbus propionicus* AY548789; *Desulfobulbaceae* {B21}, *Desulfobulbium retbaense* U48244; *Desulfomicrobiaceae*, *Desulfomicrobium baculatum* AF030438; *Desulfonatronaceae*, *Desulfonatronum lacustre* Y14594; *Desulfovibrionaceae*, *Desulfovibrio desulfuricans* AF192153; *Desulfurellaceae* {B16}, *Desulfurella acetivorans* X72768; *Desulfurobacteriaceae*, *Desulfurobacterium thermolithotrophum* AJ001049; *Desulfurococcaceae* {A01}, *Desulfurococcus mobilis* M36474; *Desulfuromonadaceae*, *Desulfuromonas acetoxidans* NZ_AAEW02000008 (region 189409–190966); *Dictyoglomaceae* {B26}, *Dictyoglomus thermophilus* X69194; *Entomoplasmataceae*, *Entomoplasma freundii* AF036954; *Erysipelotrichaceae*, *Erysipelothrix rhusiopathiae* M23728; *Ferropasmaceae*, *Ferroplasma acidiphilum* AJ224936; *Flavobacteriaceae*, *Flavobacterium anhuiense* EU046269; *Gemmatimonadaceae*, *Gemmatimonas aurantiaca* AB072735;

(Continued)

FIGURE 1 (Continued). *Geobacteraceae*, *Geobacter metallireducens* U07834; *Halanaerobiaceae* {B06}, *Halanaerobium praevalens* AB022034; *Halobacteriaceae*, *Halobacterium salinarum* AJ496185; *Halobacteroidaceae*, *Halobacteroides halobius* U32595; *Helicobacteraceae*, *Helicobacter pylori* Z25741; *Heliobacteriaceae* {B13}, *Heliobacterium sulfidophilum* AF249678; *Hydrogenimonaceae* {B18}, *Hydrogenimonas thermophila* AB105048; *Hydrogenothermaceae* {B33}, *Hydrogenothermus marinus* AJ292525; *Kofferiaceae*, *Kaistella flava* AM421015; *Ktedonobacteraceae*, *Ktedobacter racemifer* AM180156; *Lactobacillaceae*, *Lactobacillus delbrueckii* M58814; *Leptospiraceae*, *Leptospira interrogans* Z12817; *Lysobacteraceae*, *Lysobacter enzymogenes* AY947529; *Methanobacteriaceae* {A12}, *Methanobacterium thermaggregans* AF095264; *Methanocaldococcaceae* {A07}, *Methanocaldococcus jannaschii* NC_000909 (region 157985–159459); *Methanococcaceae* {A13}, *Methanococcus vannielii* NC_009634 (region 155–1619); *Methanocorpusculaceae*, *Methanocorpusculum parvum* AY260435; *Methanomicrobiaceae* {A17}, *Methanomicrobium mobile* AY196679; *Methanoplanaceae*, *Methanoplanus limicola* M59143; *Methanopyraceae* {A10}, *Methanopyrus kandleri* AE010349 (region 6963–8474); *Methanosaetaceae* {A16}, *Methanosaeta thermoacetophila* AB071701; *Methanosarcinaceae* {A14}, *Methanosarcina thermophila* M59140; *Methanospirillaceae*, *Methanospirillum hungatei* AY196683; *Methanothermaceae* {A11}, *Methanothermus fervidus* M32222; *Methermicoccaceae* {A15}, *Methermicoccus shengliensis* EF026570; *Mycoplasmataceae*, *Mycoplasma mycoides* EU040177; *Myxococcaceae*, *Myxococcus fulvus* AB218224; *Nannocystaceae*, *Nannocystis exedens* AB084253; *Natranaerobiaceae* {B08}, *Natranaerobius thermophilus* DQ417202; *Nautiliaceae* {B17}, *Nautilia lithotrophica* AJ404370; *Nitrospinaceae*, *Nitrospina gracilis* L35504; *Nitrospiraceae* {B23}, *Nitrospira moscoviensis* X82558; *Opiritaceae*, *Opiritatus terrae* AJ229235; *Oscillochloridaceae*, *Oscillochloris trichoides* AF093427; *Oscillospiraceae*, *Oscillospira guilliermondii* AB040495; *Parachlamydiaceae*, *Parachlamydia acanthamoebae* YO7556; *Pasteuriaceae*, *Pasteuria hartismerei* AJ878853; *Patulibacteraceae*, *Patulibacter minatonensis* AB193261; *Peptococcaceae* {B11}, *Peptococcus niger* X55797; *Picrophilaceae*, *Picrophilus oshimae* X84901; *Planctomycetaceae*, *Planctomyces brasiliensis* AJ231190; *Planococcaceae*, *Planococcus citreus* X62172; *Polyangiaceae*, *Polyangium vitellinum* AJ233944; *Prochloraceae*, *Prochloron* sp. X63141; *Prochlorotrichaceae*, *Prochlorotrix hollandica* AJ007907; *Puniceicoccaceae*, *Puniceicoccus vermicola* DQ539046; *Pyrodictiaceae* {A02}, *Pyrodicticum occultum* M21087; *Rubrobacteraceae*, *Rubrobacter radiotolerans* X87134; *Simkaniaceae*, *Simkania negevensis* U68460; *Solirubrobacteraceae*, *Solirubrobacter pauli* AY039806; *Sphaerobacteraceae* {B30}, *Sphaerobacter thermophilus* AJ420142; *Sphingobacteriaceae*, *Sphingomonas paucimobilis* U20776; *Spirochaetaceae* {B05}, *Spirochaeta bajacaliforniensis* AJ698859; *Spiroplasmataceae*, *Spiroplasma citri* AM157769; *Spirosomaceae*, *Spirosoma lingual* AM000023; *Streptococcaceae*, *Streptococcus pyogenes* AB002521; *Sulfolobaceae* {A03}, *Sulfolobus acidocaldarius* NC_007181 (region 1107140–1108619); *Syntrophaceae*, *Syntrophus buswellii* X85131; *Syntrophobacteraceae* {B22}, *Syntrophobacter wolinii* X70905; *Syntrophomonadaceae* {B12}, *Syntrophomonas wolfei* NC_008346 (region 43738–45267); *Thermaceae* {B24}, *Thermus aquaticus* L09663; *Thermithiobacillaceae* {B01}, *Thermithiobacillus tepidarius* AJ459801; *Thermoactinomycetaceae*, *Thermoactinomyces vulgaris* AF138739; *Thermoanaerobacteriaceae* {B09}, *Thermoanaerobacter ethanolicus* L09162; *Thermococcaceae* {A08}, *Thermococcus celer* M21529; *Thermodesulfobacteriaceae* {B20}, *Thermodesulfobacterium commune* AF418169; *Thermodesulfobiaceae* {B25}, *Thermodesulfobium narugense* AB077817; *Thermofilaceae* {A04}, *Thermofilum pendens* CP000505 (region 366243–367743); *Thermoleophilaceae*, *Thermoleophilum album* AJ458462; *Thermolithobacteraceae* {B07}, *Thermolithobacter ferrireducens* AF282252; *Thermomicrobiaceae* {B31}, *Thermomicrobium roseum* M34115; *Thermoplasmataceae* {A06}, *Thermoplasma acidophilum* NC_002578 (region 1474300–1475770); *Thermoproteaceae* {A05}, *Thermoproteus tenax* M35966; *Thermotogaceae* {B34}, *Thermotoga maritime* M21774; *Treponemataceae*, *Treponema pallidum* M88726; *Trueperaceae*, *Truepera radiovictrix* DQ022076; *Veillonellaceae*, *Veillonella parvula* X84005; *Verrucomicrobiaceae*, *Verrucomicrobium spinosum* X90515; *Waddliaceae*, *Waddlia chondrophila* AF042496.

Oxygen Relationship

As noted previously, many thermobiotic environments are either anaerobic or low in oxygen. Therefore, one would expect that thermophiles are predominantly anaerobic and, indeed, this is what is seen. Most axenic thermophiles are anaerobes or facultative aerobes.^{21,22} By the authors' definition, anaerobes are unable to use O₂ as the terminal electron acceptor, even if they can grow in the presence of O₂ (i.e., an O₂-tolerant anaerobe). Facultative aerobes are able to use oxygen as a terminal electron acceptor and some obligately anaerobic thermophiles can survive exposure to oxygenic atmospheres, especially if they

are metabolically inactive (e.g., at suboptimal temperatures, or with the absence of metabolizable substrates). In the absence of oxygen, respiring anaerobic or facultative aerobic thermophiles can use, via energy production through electron transport phosphorylation, a variety of compounds as electron acceptors, including: CO₂, CO, NO₃[−], NO₂[−], NO, N₂O, SO₄^{−2}, SO₃^{−2}, S₂O₃^{−2}, S⁰, Fe(III), Mn(IV), and Mo(VI).^{54,128} The energy gleaned from these respiratory pathways is in addition to the energy produced anaerobically through substrate-level phosphorylation.

An examination of families of thermophilic anaerobes reveals that most (38 of 51) are currently composed solely of anaerobic taxa. Although a majority

TABLE 1. Validly described thermophilic anaerobes^c

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Bacteria; Proteobacteria; Gammaproteobacteria; Acidithiobacillales; Thermithiobacillaceae</i> {B01};				
Genus: <i>Thermithiobacillus</i>				
<i>Thermithiobacillus tepidarius</i> ^{151,152}	AN CLA	37–50 [43–45]	5.5–7.7 [6–7.5]	The Roman Bath, Avon, UK
<i>Bacteria; Proteobacteria; Gammaproteobacteria; Chromatiales; Chromatiaceae</i> {B02};				
Genus: <i>Thermochromatium</i>				
<i>Thermochromatium tepidum</i> ^{113,114§}	AN PA/PH	34–57 [48–50]	[7]	Mammoth Hot Spring, Yellowstone National Park, USA
<i>Bacteria; Proteobacteria; Betaproteobacteria; Burkholderiales; Burkholderiaceae</i> {B03};				
Genera: <i>Thermothrix</i> , <i>Thiobacter</i> (unclassified <i>Betaproteobacteria</i>)				
<i>Thermothrix thiopara</i> ¹⁵³	FAE F-CLA	55–85 [70–73]	[7]	Jemez Spring, New Mexico, USA
<i>Thiobacter subterraneus</i> ¹⁵⁴	AN CLA	35–62 [50–55]	5.2–7.7 [6.5–7]	Subsurface geothermal aquifer, Hishikari gold mine, Japan
<i>Bacteria; Bacteroidetes/Chlorobi group; Bacteroidetes; Bacteroidetes; Bacteroidales; Bacteroidaceae</i> {B04};				
Genera: <i>Acetomicrobium</i> , <i>Anaerophaga</i>				
<i>Acetomicrobium flavidum</i> ¹⁵⁵	AN COH	35–65 [58]	6.2–8	60°C biogas sewage fermentor
<i>Acetomicrobium faecale</i> ¹⁵⁶	AN COH	55–74 [70–73]	5.5–9 [6.5–7]	Mesophilically digested sewage sludge
<i>Anaerophaga thermohalophila</i> ¹⁵⁷	AN COH	37–55 [50]	NR	Blackish-oily sedimentary residues of an oil separation tank near Hannover, Germany
<i>Bacteria; Spirochaetes; Spirochaetes; Spirochaetales; Spirochaetaceae</i> {B05};				
Genus: <i>Spirochaeta</i>				
<i>Spirochaeta caldaria</i> ¹⁵⁸	AN COH	[48–52]	5.8–8.5 [7.2]	Cyanobacterial mat samples from Oregon and Utah, USA
<i>Spirochaeta thermophila</i> ¹⁵⁹	AN COH	40–73 [66–68]	5.9–7.7 [7.5]	Marine hot spring on the beach of an island from Kamchatka, Russia; also a hot spring, Raoul Island, New Zealand
<i>Bacteria; Firmicutes; Clostridia; Halanaerobiales; Halanaerobiaceae</i> {B06};				
Genus: <i>Halothermothrix</i>				
<i>Halothermothrix orenii</i> ^{160§}	AN COH	45–68 [60]	5.5–8.2 [6.5–7]	Chott El Guettar hypersaline lake, Tunisia
<i>Bacteria; Firmicutes; Thermolithobacteria; Thermolithobacterales; Thermolithobacteraceae</i> {B07};				
Genus: <i>Thermolithobacter</i>				
<i>Thermolithobacter ferrireducens</i> ⁹⁹	AN F-CLA	50–75 [73]	6.5–8.5 [7.1–7.3]	Calcite Spring, Yellowstone National Park, USA
<i>Thermolithobacter carboxydivorans</i> ⁹⁹	AN CLA	40–78 [70]	6.6–7.6 [6.8–7.0]	Terrestrial hot spring at Raoul Island, Archipelago Kermadec, New Zealand
<i>Bacteria; Firmicutes; Clostridia; Natranaerobiales; Natranaerobiaceae</i> {B08};				
Genus: <i>Natranaerobius</i>				
<i>Natranaerobius thermophilus</i> ^{8§}	AN COH	35–56 [53]	8.5–10.6 [9.5]	Sediment of alkaline, hypersaline lakes of the Wadi An Natrun
<i>Bacteria; Firmicutes; Clostridia; Thermoanaerobacteriales; Thermoanaerobacteriaceae</i> {B09};				
Genera: <i>Coprothermobacter</i> , <i>Gelria</i> , <i>Moorella</i> , <i>Thermacetogenium</i> , <i>Mahella</i> , <i>Thermoanaerobacterium</i> , <i>Thermoanaerobacter</i> , <i>Thermosediminibacter</i> , <i>Caldanaerobacter</i> , <i>Thermovenabulum</i> , <i>Tepidanaerobacter</i> , <i>Ammonifex</i> , <i>Thermanaeromonas</i> , <i>Thermhydrogenium</i>				
<i>Coprothermobacter platensis</i> ¹⁶¹	AN COH	35–65 [55]	4.3–8.3 [7]	Methanogenic mesophilic reactor treating protein-rich wastewater

Continued

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Coprothermobacter proteolyticus</i> ^{162,163} §	AN	35–70 [63]	5–8.5 [7.5]	Thermophilic digester fermenting tannery wastes and cattle manure
<i>Gelria glutamica</i> ¹⁶⁴	COH			
	AN	37–60 [50–55]	5.5–8 [7]	Thermophilic, syntrophic, propionate-oxidizing enrichment culture
	COH			
<i>Moorella glycerini</i> ¹⁶⁵	AN	43–65 [58]	5.9–7.8 [6.3]	Calcite Spring area hot spring, Yellowstone National Park, USA
	COH			
<i>Moorella thermoautotrophica</i> ^{31,166}	AN	36–70 [55–58]	4.5–7.6 [5.7]	Yellowstone National Park, USA; also Georgia and Hawaii, USA; Zaire, Africa; and Germany
	F-CLA			
<i>Moorella mulderi</i> ¹⁶⁷	AN	40–70 [65]	5.5–8.5 [7]	A methanol-degrading enrichment culture obtained from a thermophilic anaerobic reactor
	F-CLA			
<i>Moorella thermoacetica</i> ^{166,168} §	AN	45–65 [55–60]	NR	Horse manure
	COH			
<i>Thermacetogenium phaeum</i> ¹⁶⁹	AN	40–65 [58]	5.9–8.4 [6.8]	Thermophilic anaerobic methanogenic reactor treating kraft-pulp production plant wastewater, Japan
	F-CLA			
<i>Mahella australiensis</i> ¹⁷⁰	AN	30–60 [50–60]	5.5–8.8 [7.5]	Riverslea oilfield, Bown-Surat Basin, Queensland, Australia
	COH			
<i>Thermoanaerobacterium thermosulfurigenes</i> ¹⁷¹	AN	55–75 [60]	4–7.6 [5.5–6.5]	Octopus Spring, Yellowstone National Park, USA
	COH			
<i>Thermoanaerobacterium saccharolyticum</i> ¹⁷¹	AN	45–70 [60]	5–7.5 [6]	Yellowstone National Park, USA
	COH			
<i>Thermoanaerobacterium xylanolyticum</i> ¹⁷¹	AN	45–70 [60]	5–7.5 [6]	Geothermal areas, Wyoming and Nevada, USA
	COH			
<i>Thermoanaerobacterium aotearoense</i> ⁶⁸	AN	35–66 [60–63]	3.8–6.8 [5.2]	Geothermal hot springs, New Zealand
	COH			
<i>Thermoanaerobacterium polysaccharolyticum</i> ¹⁷²	AN	45–70 [65–68]	5–8 [6.8–7]	Canning factory waste, Illinois, USA
	COH			
<i>Thermoanaerobacterium zeae</i> ¹⁷²	AN	55–72 [65–70]	3.9–7.9	Canning factory waste, Illinois, USA
	COH			
<i>Thermoanaerobacterium aciditolerans</i> ⁶⁹	AN	37–68 [55]	3.2–7.1 [5.7]	Hydrothermal vent in the Orange Field, Uzon Caldera, Kamchatka, Far Eastern Russia
	COH			
<i>Thermoanaerobacterium thermosaccharolyticum</i> ^{166,173}	AN	[55–60]	NR	Soil
	COH			
<i>Thermoanaerobacter brockii</i> subsp. <i>lactiethylicus</i> ¹⁷⁴	AN	37–75 [55–60]	[7.3]	Oilfields of France; and Cameroon, Africa
	COH			
<i>Thermoanaerobacter thermocopriae</i> ^{166,175}	AN	47–74 [60]	6–8 [6.5–7.3]	Compost of cattle feces and grasses, at the University of Tokyo; other strains from camel feces, compost, soil, and a hot spring in Japan
	COH			
<i>Thermoanaerobacter brockii</i> subsp. <i>finni</i> ¹⁷⁴	AN	40–75 [65]	[6.5–6.8]	Sediment sludge, Lake Kivu, Africa
	COH			
<i>Thermoanaerobacter acetoethylicus</i> ^{163,176}	AN	[65]	5.5–8.5	Hot springs, Yellowstone National Park, USA
	COH			
<i>Thermoanaerobacter kivu</i> ^{166,177}	AN	50–72 [66]	5.3–7.3 [6.4]	Lake Kivu sediment, Africa
	F-CLA			
<i>Thermoanaerobacter wiegeleri</i> ¹⁷⁸	AN	38–78 [65–68]	5.5–7.2 [6.8]	Anthropogenically heated freshwater pool, Rotorua, New Zealand
	COH			

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Thermoanaerobacter</i> <i>thermohydrogensulfuricus</i> ¹⁷¹	AN COH	37–78 [67–69]	5.5–9.2 [6.9–7.5]	Extraction juices from beet sugar factories; mud and soil; hot springs in Utah and Wyoming, and a sewage plant in Georgia, USA
<i>Thermohydrogenium kirishiensense</i> ¹⁷⁹	AN COH	45–75 [65]	5–8 [7–7.4]	Industrial yeast biomass at the stages of thermal treatment
<i>Thermoanaerobacter brockii</i> subsp. <i>brockii</i> ¹⁷⁴	AN COH	40–80 [65–70]	5.5–9.5 [7.5]	Washburn thermal spring, Yellowstone National Park, USA
<i>Thermoanaerobacter italicus</i> ¹⁸⁰	AN COH	45–78 [70]	[7]	Thermal spas, water and mud samples, northern Italy
<i>Thermoanaerobacter siderophilus</i> ¹³³	AN F-CLA	39–78 [69–71]	4.8–8.2 [6.3–6.5]	Hydrothermal vents near the Karymsky volcano, Kamchatka, Russia
<i>Thermoanaerobacter mathranii</i> ¹⁸¹	AN COH	50–75 [70–75]	4.7–8.8 [7]	Alkaline hot spring at Hveragerdi-Hengil, Iceland
<i>Thermoanaerobacter ethanolicus</i> ^{84,§}	AN COH	37–78 [69]	4.4–9.9 [5.8–8.5]	Hot springs, Yellowstone National Park, USA
<i>Thermoanaerobacter</i> <i>pseudoethanolicus</i> ^{171, 182, 183,§}	AN COH	[65]	NR	Hot Spring, Yellowstone National Park, USA
<i>Thermoanaerobacter sulfurigignens</i> ¹⁸⁴	AN COH	34–72 [65]	4–8 [5.0–6.5]	Acidic volcanic steam outlet on White Island, New Zealand
<i>Thermoanaerobacter sulfurophilus</i> ¹⁸⁵	AN COH	44–75 [55–60]	4.5–8.0 [6.9–7.2]	Cyanobacterial mat from a hot spring, Uzon Caldera, Kamchatka, Far Eastern Russia
<i>Thermosediminibacter litoriperuensis</i> ³⁰	AN COH	43–76 [64]	5–9.5 [7.9–8.4]	Nonhydrothermal deep sea sediments of Peru Margin
<i>Thermosediminibacter oceanii</i> ³⁰	AN COH	52–76 [68]	6.3–9.3 [7.5]	Nonhydrothermal deep sea sediments of Peru Margin
<i>Caldanaerobacter subterraneus</i> subsp. <i>subterraneus</i> ^{103, 186}	AN COH	45–75 [65]	6–8.5 [7.5]	Oilfield reservoir, southwest France
<i>Caldanaerobacter subterraneus</i> subsp. <i>pacificus</i> ^{103, 187}	AN F-CLA	50–80 [70]	5.8–7.6 [6.8–7.2]	Submarine hot vent in the Okinawa Trough
<i>Caldanaerobacter subterraneus</i> subsp. <i>tengcongensis</i> ^{103, 188, 189,§}	AN COH	50–80 [75]	5.5–9 [7–7.5]	Hot spring, Tengcong, China
<i>Caldanaerobacter subterraneus</i> subsp. <i>yonseiensis</i> ^{103, 190}	AN COH	50–85 [75]	4.5–9 [6.5]	Hot water, mud, and soil from hot streams at Sileri, Java Island
<i>Thermovenabulum ferriorganovororum</i> ¹³⁴	AN COH	45–76 [63–65]	4.8–8.2 [6.7–6.9]	Hydrothermal spring, Uzon Caldera, Kamchatka, Russia
<i>Tepidanaerobacter syntrophicus</i> ¹⁹¹	AN COH	25–60 [45–50]	5.5–8.5 [6–7]	Sludges of thermophilic (55°C) digesters that decomposed either municipal solid wastes or sewage sludge
<i>Ammonifex degensii</i> ^{192,§}	AN F-CLA	57–77 [70]	5–8 [7.5]	Kawah Candradimuka Crater, Dieng Plateau, Java, Indonesia
<i>Thermanaeromonas toyohensis</i> ¹⁹³	AN COH	55–73 [70]	5.5–8.5 [7.5]	Geothermal water at Toyoho Mine, Hokkaido, Japan
<i>Bacteria; Firmicutes; Clostridia; Clostridiales; Acidaminococcaceae {B10};</i>				
Genus: <i>Thermosinus</i>				
<i>Thermosinus carboxydvorans</i> ^{104,§}	AN CLA	40–68 [60]	6.5–7.6 [6.8–7]	Norris Basin hot spring, Yellowstone National Park, USA
<i>Bacteria; Firmicutes; Clostridia; Clostridiales; Peptococcaceae {B11};</i>				
Genera: <i>Desulfotomaculum</i> , <i>Pelotomaculum</i> , <i>Carboxydotherrmus</i> , <i>Thermincola</i>				
<i>Desulfotomaculum thermosapovorans</i> ¹⁹⁴	AN COH	35–60 [50]	[7.2–7.5]	Mixed compost containing rice hulls and peanut shells

Continued

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Desulfotomaculum alkaliphilum</i> ¹⁰⁷	AN CLH	30–58 [50–55]	8–9.15 [8.6–8.7]	Mixed cow/pig manure
<i>Desulfotomaculum solfataricum</i> ¹²⁴	AN COH	48–65 [60]	6.4–7.9 [7.3]	Solfataric mud pools, Krafla, northeast Iceland
<i>Desulfotomaculum thermoacetoxidans</i> ¹⁹⁵	AN COH	45–65 [55–60]	6–7.5 [6.5]	A thermophilic anaerobic digester converting cellulosic waste to methane
<i>Desulfotomaculum thermobenzoicum</i> subsp. <i>thermobenzoicum</i> ¹⁹⁶	AN F-CLA	40–70 [62]	6–8 [7.2]	Thermophilic methane fermentation reactor treating kraft-pulp wastewater
<i>Desulfotomaculum thermobenzoicum</i> subsp. <i>thermosyntrophicum</i> ¹⁹⁶	AN F-CLA	45–62 [55]	6–8 [7]	Thermophilic granular methanogenic sludge
<i>Desulfotomaculum putei</i> ¹⁹⁷	AN COH	22–65 [64]	6–7.8	Deep terrestrial rock, Taylorsville Triassic Basin, Virginia, USA
<i>Desulfotomaculum australicum</i> ¹⁹⁸	AN F-CLA	40–74 [68]	5.5–8.5 [7–7.4]	Bore wells of the nonvolcanically heated waters of the Great Artesian Basin, Australia
<i>Desulfotomaculum geothermicum</i> ¹⁹⁹	AN F-CLA	37–57 [54]	6–8 [7.2–7.3]	Geothermally heated ground water, at a depth of 2500 m, Creil production well, France
<i>Desulfotomaculum luciae</i> ^{197,200}	AN CLA	50–70 [60–65]	6.3–7.8	Hot spring, St. Lucia
<i>Desulfotomaculum thermocisternum</i> ²⁰¹	AN F-CLA	41–75 [62]	6.2–8.9 [6.7]	Brent group formation water originating 2.6 km below the sea floor, Norwegian sector, North Sea
<i>Desulfotomaculum</i> <i>thermosubterraneum</i> ²⁰²	AN F-CLA	50–72 [61–66]	6.4–7.8 [7.2–7.4]	Underground mine in a geothermally active region, Japan.
<i>Desulfotomaculum carboxydivorans</i> ⁹⁷	AN CLH	30–68 [55]	6.8–8 [7.2]	Sludge from an anaerobic bioreactor treating paper mill wastewater
<i>Desulfotomaculum kuznetsovii</i> ^{203,204}	AN F-CLA	50–85 [60–65]	NR	Thermal water sample from a spontaneous effusion from a rift in the Sukhumsk deposit
<i>Desulfotomaculum nigrificans</i> ²⁰⁵	AN COH	[55]	NR	Spoiled food
<i>Pelotomaculum thermopropionicum</i> ^{85§}	AN COH	45–65 [55]	6.7–7.5 [7]	Thermophilic upflow anaerobic sludge blanket reactor
<i>Carboxydotherrnus ferrireducens</i> ^{206,207}	AN COH	50–74 [65]	5.5–7.6 [6–6.2]	Hot springs of Yellowstone National Park, USA; and New Zealand
<i>Carboxydotherrnus</i> <i>hydrogenoformans</i> ^{98,208§}	AN CLA	40–78 [70–72]	6.4–7.7 [6.8–7]	Freshwater hydrothermal springs, Kunashir Island, Kamchatka, Russia
<i>Thermincola carboxydiphila</i> ¹⁰¹	AN CLH	37–68 [55]	6.7–9.5 [8]	Hot spring of the Baikal Lake region, Russia
<i>Thermincola ferriacetica</i> ¹⁰²	AN F-CLA	45–70 [57–60]	5.9–8.0 [7.0–7.2]	Terrestrial hydrothermal spring, Kunashir Island, Kuril Island, Russian Far East
<i>Bacteria; Firmicutes; Clostridia; Clostridiales; Syntrophomonadaceae {B12};</i> Genera: <i>Anaerobaculum</i> , <i>Syntrophothermus</i> , <i>Thermanaerovibrio</i> , <i>Carboxydocella</i> , <i>Anaerobranca</i> , <i>Thermosyntropha</i> , <i>Caldicellulosiruptor</i> , <i>Thermovirga</i>				
<i>Anaerobaculum thermoterrenum</i> ²⁰⁹	AN COH	28–60 [55]	5.5–8.6 [7–7.6]	Redwash oilfield production fluids, Utah, USA
<i>Anaerobaculum mobile</i> ²¹⁰	AN COH	35–65 [55–60]	5.4–8.7 [6.6–7.3]	Anaerobic wool-scouring wastewater treatment lagoon sludge, Trinidad, Uruguay
<i>Syntrophothermus lipocalidus</i> ²¹¹	AN COH	45–60 [55]	5.8–7.5 [6.5–7]	Granular sludge of a thermophilic upflow anaerobic sludge blanket

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Thermanaerovibrio velox</i> ²¹²	AN COH	45–70 [60–65]	4.5–8 [7.3]	Cyanobacterial mat, Uzon Caldera, Kamchatka, Russia
<i>Thermanaerovibrio acidaminovorans</i> ²¹³	AN COH	40–58 [55]	[6.5–8.1]	Granular methanogenic sludge from a sugar refinery, Breda, the Netherlands
<i>Carboxydocella thermautotrophica</i> ¹⁰⁰	AN CLA	40–68 [58]	6.5–7.6 [7]	Hot spring, Gyzer Valley, Kamchatka, Russia
<i>Carboxydocella sporoproducens</i> ²¹⁴	AN F-CLA	50–70 [60]	6.2–8 [6.8]	Hot spring of Karymskoe Lake, Kamchatka Peninsula
<i>Anaerobranca gottschalkii</i> ²¹⁵	AN COH	30–65 [50–55]	6–10 [9.5]	Hot inlet of Lake Bogoria, Kenya
<i>Anaerobranca horikoshii</i> ²¹⁶	AN COH	34–66 [57]	6.9–10.3 [8.5]	Thermal pools, Yellowstone National Park, USA
<i>Anaerobranca californiensis</i> ²¹⁷	AN COH	45–70 [58]	8.6–10.4 [9–9.5]	Paoho Island hot springs Mono Lake, California, USA
<i>Thermosyntropha lipolytica</i> ⁹⁵	AN COH	52–70 [60–66]	7.15–9.5 [8.1–8.9]	Alkaline hot springs, Lake Bogoria, Kenya
<i>Caldicellulosiruptor lactoaceticus</i> ²¹⁸	AN COH	50–78 [68]	5.8–8.2 [7]	Hveragerdi alkaline hot spring, Iceland
<i>Caldicellulosiruptor owensensis</i> ²¹⁹	AN COH	50–80 [75]	5.5–9 [7.5]	Freshwater pond within the dry Owens Lake bed, California, USA
<i>Caldicellulosiruptor kristjanssonii</i> ²²⁰	AN COH	45–82 [78]	5.8–8 [7]	Hot spring, Iceland
<i>Caldicellulosiruptor saccharolyticus</i> ^{221§}	AN COH	45–80 [70]	5.5–8.0 [7.0]	Geothermal spring, Taupo, New Zealand
<i>Caldicellulosiruptor acetigenus</i> ^{222,223}	AN COH	50–78 [65–68]	5.2–8.6 [7.0]	Combined biomat and sediment from a slightly alkaline hot spring, Hveragerdi, Iceland.
<i>Thermovirga lienii</i> ²²⁴	AN COH	37–68 [58]	6.2–8.0 [6.5–7]	Production water obtained from an oil reservoir in the North Sea
<i>Bacteria; Firmicutes; Clostridia; Clostridiales; Heliobacteriaceae {B13};</i>				
Genus: <i>Heliobacterium</i>				
<i>Heliobacterium modesticaldum</i> ^{120§}	AN PH & COH	25–56 [52]	[6–7]	Iceland; and Yellowstone National Park, USA
<i>Bacteria; Firmicutes; Clostridia; Clostridiales; Clostridiaceae {B14};</i>				
Genera: <i>Alkaliphilus</i> , <i>Clostridium</i> , <i>Tepidibacter</i> , <i>Caloramator</i> , <i>Garciella</i> , <i>Caminicella</i> , <i>Caloranaerobacter</i> , <i>Thermobrachium</i> , <i>Thermohalobacter</i> , <i>Tepidimicrobium</i>				
<i>Clostridium isatidis</i> ²²⁵	AN COH	30–55 [50]	5.9–9.9 [7.2]	Fermenting woad vat
<i>Clostridium thermoalcaliphilum</i> ⁸⁰	AN COH	27–57.5 [48–51]	7–11 [9.6–10.1]	Anaerobic digester and aerobic oxidation basin, Municipal Sewage Plant, Atlanta, Georgia, USA
<i>Clostridium straminisolvens</i> ²²⁶	AN COH	46–64 [50–55]	6–8.5 [7.5]	Cellulose-degrading bacterial community
<i>Clostridium thermobutyricum</i> ²²⁷	AN COH	26–61.5 [55]	5.8–9 [6.8–7.1]	Horse manure
<i>Clostridium paradoxum</i> ³	AN COH	30–63 [55–56]	7–11.1 [10.1]	Municipal Sewage Plants, Athens and Atlanta, Georgia, USA
<i>Clostridium thermopaperylyticum</i> ⁹¹	AN COH	45–66 [59]	NR	Sediment from a river bank, Buenos Aires, Argentina
<i>Clostridium cellulosi</i> ²²⁸	AN COH	40–65 [55–60]	6.2–8.5 [7.3–7.5]	Cow manure compost
<i>Clostridium stercorarium</i> subsp. <i>stercorarium</i> ^{229,230}	AN COH	[65]	[7.3]	Compost heap

Continued

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Clostridium stercorarium</i> subsp. <i>leptospartum</i> ^{230,231}	AN COH	45–71 [60]	6.7–8.9 [7.5]	Cattle manure compost, Ehime Prefecture, Japan
<i>Clostridium stercorarium</i> subsp. <i>thermolacticum</i> ^{230,232}	AN COH	50–70 [60–65]	6.8–7.4 [7.0]	Sludge from a mesophilic digester fed ground duck weed
<i>Tepidibacter thalassicus</i> ²³³	AN COH	33–60 [50]	4.8–8.5 [6.5–6.8]	Black smoker chimney, hydrothermal vent field, East Pacific Rise
<i>Tepidibacter formicigenes</i> ²³⁴	AN COH	35–55 [45]	5.0–8.5 [6.0]	Menez-Gwen hydrothermal site on the Mid-Atlantic Ridge
<i>Caloramator proteoclasticus</i> ²³⁵	AN COH	30–68 [55]	6–9.5 [7–7.5]	Mesophilic granular methanogenic sludge
<i>Caloramator coolhaasi</i> ²³⁶	AN COH	37–65 [50–55]	6–8.5 [7]	Thermophilic methanogenic granular sludge
<i>Caloramator viterbiensis</i> ²³⁷	AN COH	33–64 [58]	6–7.8 [6.5–7]	Hot spring at the Bagnaccio Spring, Viterbo, Italy
<i>Caloramator indicus</i> ²³⁸	AN COH	[60–65]	6.2–9.2 [8.1]	Natural well of the artesian aquifer, Surat District, Gujarat State, India
<i>Caloramator fervidus</i> ^{166, 239}	AN COH	37–80 [68]	5.5–9 [7–7.5]	Hot spring, New Zealand
<i>Garciella nitrareducens</i> ²⁴⁰	AN COH	25–60 [55]	5.5–9 [7.5]	A water separator collecting fluids, the SAMIII oilfield, Gulf of Mexico
<i>Caminicella sporogenes</i> ²⁴¹	AN COH	45–64 [55–60]	4.5–8 [7.5–8]	Deep-sea vent, East Pacific Rise
<i>Caloranaerobacter azorensis</i> ²⁴²	AN COH	45–65 [65]	5.5–9 [7]	Deep-sea hydrothermal chimney rocks, Mid-Atlantic Ridge
<i>Thermobrachium celere</i> ⁷	AN COH	37–75 [62–65]	5–9.7 [8–8.5]	Geothermally and anthroprogenically heated environments on three continents
<i>Thermohalobacter berrensis</i> ²⁴³	AN COH	45–70 [65]	5.2–8.8 [7]	Solar saltern canal near Berre Lagoon, southern France
<i>Tepidimicrobium ferriphilum</i> ¹⁴⁶	AN COH	26–62 [50]	5.5–9.5 [7.8–8]	Freshwater hot spring at Barguzin Valley, Buryatiya, Russia
<i>Bacteria; Firmicutes; Bacilli; Bacillales; Bacillaceae {B15};</i> <i>Genera: Anoxybacillus, Bacillus, Geobacillus, Vulcanibacillus</i>				
<i>Anoxybacillus pushchinoensis</i> ²⁴⁴	AN COH	37–66 [62]	8–10.5 [9.5–9.7]	Manure from farms near Moscow, Russia
<i>Anoxybacillus ayderensis</i> ²⁴⁷	FAE COH	30–70 [50]	6–11 [7.5–8.5]	Ayder hot spring, Rize province, Turkey
<i>Anoxybacillus voinovskiensis</i> ²⁴⁸	FAE COH	30–64 [54]	7–8	Voinovskie Hot Springs, Kamchatka, Russia
<i>Anoxybacillus kestanbolensis</i> ²⁴⁷	FAE COH	40–70 [50–55]	6–10.5 [7.5–8.5]	Kestanbol hot spring, Canakkale province, Turkey
<i>Anoxybacillus gonensis</i> ²⁴⁹	FAE COH	40–70 [55–60]	6–10 [7.5–8]	Gonen hot spring, Balikesir province, Turkey
<i>Anoxybacillus flavithermus</i> ²⁴⁴	FAE COH	30–72 [60–65]	5.5–9 [7]	A hot spring, New Zealand
<i>Bacillus infernus</i> ²⁴⁵	AN COH	[61]	[7.3–7.8]	Deep terrestrial rock, Taylorsville Triassic Basin, Virginia, USA
<i>Bacillus thermoamylovorans</i> ²⁴⁶	FAE COH	[50]	5.4–8.5 [7]	Palm wine collected in Rafisque, Senegal
<i>Geobacillus thermocatenulatus</i> ^{250,251}	FAE COH	42–69 [55–60]	6.5–8.5	Thermal zone of the Tangan-Tau Mountain, Southern Urals, Russia
<i>Geobacillus thermodenitrificans</i> ^{250,252,253}	FAE COH	45–70	6–8	Sugar beet juice from extraction installations, Austria

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Geobacillus thermoleovorans</i> ^{250,254,255}	FAE COH	35–78 [55–65]	[6.2–6.8]	Soil near hot water effluent, Bethlehem, Pennsylvania, USA
<i>Geobacillus uzenensis</i> ²⁵⁰	FAE COH	45–65	6.2–7.8	The Uzen oilfield, Kazakhstan
<i>Vulcanibacillus modesticaldus</i> ²⁵⁶	AN COH	37–60 [55]	6–8.5 [7]	“Rainbow” deep-sea hydrothermal vent field, Mid-Atlantic Ridge (36° 14' N 33° 54' W)
<i>Bacteria; Proteobacteria; delta/epsilon subdivisions; Deltaproteobacteria; Desulfurellales; Desulfurellaceae</i> {B16};				
Genera: <i>Desulfurella</i> , <i>Hipaea</i>				
<i>Desulfurella kamchatkensis</i> ²⁵⁷	AN F-CLA	40–70 [54]	[6.9–7.2]	The Pauzhetka hot spring, Kamchatka, Far East Russia
<i>Desulfurella propionica</i> ²⁵⁷	AN F- CLA	33–63 [55]	[6.9–7.2]	Cyanobacterial mat from sulfide-rich hot pond, Uzon Caldera, Kamchatka, Russia
<i>Desulfurella acetivorans</i> ²⁵⁸	AN COH	44–70 [52–57]	4.3–7.5 [6.8–7]	Hot water pool, Uzon Caldera, Kamchatka, Russia
<i>Desulfurella multipotens</i> ¹²⁶	AN F-CLA	42–77 [58–60]	6.0–7.2 [6.4–6.8]	Green Lake, Raoul Island, Kermadec Archipelago, New Zealand
<i>Hipaea maritima</i> ²⁵⁹	AN COH	40–65 [52–54]	5.4–6.5 [5.8–6.2]	Shallow water hot vents, Bay of Plenty, New Zealand; and Matupi Harbour, Papua New Guinea
<i>Bacteria; Proteobacteria; delta/epsilon subdivisions; Epsilonproteobacteria; Nautiliales; Nautiliaceae</i> {B17};				
Genera: <i>Nautilia</i> , <i>Lebetimonas</i> , <i>Caminibacter</i>				
<i>Nautilia lithotrophica</i> ²⁶⁰	AN CLA	37–68 [53]	6.4–7.4 [6.8–7]	13°N hydrothermal vent field, East Pacific Rise
<i>Lebetimonas acidiphila</i> ⁷⁰	AN CLA	30–68 [50]	4.2–7 [5.2]	TOTO caldera of the Mariana arc
<i>Caminibacter mediatlanticus</i> ^{261§}	AN CLA	45–70 [55]	4.5–7.5 [5.5]	“Rainbow” deep-sea vent field, Mid-Atlantic Ridge
<i>Caminibacter profundus</i> ²⁶²	AN CLA	45–65 [55]	6.5–7.4 [6.9–7.1]	“Rainbow” deep-sea vent field, Mid-Atlantic Ridge
<i>Caminibacter hydrogeniphilus</i> ²⁶³	AN CLA	50–70 [60]	5–7.5 [5.5–6]	Deep-sea vent region, East Pacific Rise
<i>Bacteria; Proteobacteria; delta/epsilon subdivisions; Epsilonproteobacteria; Campylobacteriales; Hydrogenimonaceae</i> {B18};				
Genus: <i>Hydrogenimonas</i>				
<i>Hydrogenimonas thermophila</i> ²⁶⁴	FAE CLA	35–65 [55]	4.9–7.2 [5.9]	Kairei deep-sea hydrothermal field, Central Indian Ridge
<i>Bacteria; Deferribacteres; Deferribacteres; Deferribacterales; Deferribacteraceae</i> {B19};				
Genera: <i>Deferribacter</i> , <i>Flexistipes</i> , <i>Caldithrix</i> (unclassified <i>Deferribacteres</i>)				
<i>Caldithrix abyssi</i> ¹⁰⁸	AN CLH	40–70 [60]	5.8–7.8 [6.8–7]	Logatchev hydrothermal field, Mid-Atlantic Ridge
<i>Deferribacter thermophilus</i> ¹³⁰	AN COH	50–65 [60]	5–8 [6.5]	Produced formation water collected from a well in the Beatrice oilfield
<i>Deferribacter abyssi</i> ¹³¹	AN CLA	45–65 [60]	6–7.2 [6.5–6.7]	“Rainbow” vent field, Mid-Atlantic Ridge
<i>Deferribacter desulfuricans</i> ²⁶⁵	AN COH	40–70 [60–65]	5.0–7.5 [6.5]	A black smoker vent from the hydrothermal fields at the Suiyo Seamount in the Izu-Bonin Arc, Japan
<i>Flexistipes sinusarabici</i> ²⁶⁶	AN COH	30–53 [45–50]	6–8	Brine water samples of the Atlantis II Deep of the Red Sea, depth of 2000 m

Continued

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Bacteria; Thermodesulfobacteria; Thermodesulfobacteria; Thermodesulfobacteriales; Thermodesulfobacteriaceae</i> {B20};				
Genera: <i>Thermodesulfatator</i> , <i>Thermodesulfobacterium</i>				
<i>Thermodesulfatator indicus</i> ⁸⁶	AN CLA	55–80 [70]	6–6.7 [6.25]	The Kairei deep-sea hydrothermal vent field, Central Indian Ridge
<i>Thermodesulfobacterium hydrogeniphilum</i> ⁸⁷	AN CLA	50–80 [75]	6.3–6.8 [6.5]	Deep-sea hydrothermal vent site, Guaymas Basin
<i>Thermodesulfobacterium commune</i> ²⁶⁷ §	AN COH	50–85 [70]	6.0–8.0	Ink Pot Spring, Yellowstone National Park, USA
<i>Thermodesulfobacterium hveragerdense</i> ²⁶⁸	AN COH	55–74 [70]	NR	Icelandic hot springs
<i>Thermodesulfobacterium thermophilum</i> ²⁶⁹	AN COH	45–85 [65]	NR	Strata water of the oil deposit on the Apsheron Peninsula, Caspian Sea
<i>Bacteria; Proteobacteria; delta/epsilon subdivisions; Deltaproteobacteria; Desulfovibrionales; Desulfobalobiaceae</i> {B21};				
Genus: <i>Desulfothermus</i>				
<i>Desulfothermus naphthae</i> ²⁷⁰	AN COH	50–69 [60–65]	6.1–7.1 [6.5–6.8]	Guaymas Basin, Gulf of California
<i>Desulfothermus okinawensis</i> ²⁷¹	AN COH	35–60 [50]	5.4–7.9 [5.9–6.4]	Black smoker chimney, deep-sea hydrothermal field, Southern Okinawa Trough
<i>Bacteria; Proteobacteria; delta/epsilon subdivisions; Deltaproteobacteria; Syntrophobacteriales; Syntrophobacteriaceae</i> {B22};				
Genera: <i>Desulfacinum</i> , <i>Thermodesulforhabdus</i>				
<i>Desulfacinum infernum</i> ²⁷²	AN F-CLA	40–65 [60]	6.6–8.4 [7.1–7.5]	Oil well of the Beatrice field platform, the North Sea near the coast of Scotland
<i>Desulfacinum hydrothermale</i> ²⁷³	AN F-CLA	37–64 [60]	6–7.5 [7]	Shallow, submarine hydrothermal vent, Palaeochori Bay, Milos in the Aegean Sea
<i>Thermodesulforhabdus norvegica</i> ²⁷⁴	AN COH	44–74 [60]	6.1–7.9 [6.9]	Oilfield water (Norwegian oil platform) from the North Sea
<i>Bacteria; Nitrospirae; Nitrospira; Nitrospirales; Nitrospiraceae</i> {B23};				
Genus: <i>Thermodesulfovibrio</i>				
<i>Thermodesulfovibrio islandicus</i> ²⁶⁸	AN COH	45–70 [65]	NR	Icelandic hot springs
<i>Thermodesulfovibrio yellowstonii</i> ²⁷⁵ §	AN COH	40–70 [65]	[6.8–7]	Thermal vent, Yellowstone National Park, USA
<i>Bacteria; Deinococcus-Thermus; Deinococci; Thermales; Thermaceae</i> {B24};				
Genera: <i>Oceanithermus</i> , <i>Vulcanithermus</i>				
<i>Oceanithermus profundus</i> ¹¹⁰	FAE F-CLH	40–68 [60]	5.5–8.4 [7.5]	13° North hydrothermal vent field, East Pacific Rise, depth of 2600 m
<i>Oceanithermus desulfurans</i> ²⁷⁶	FAE COH	30–65 [60]	6–8 [6.5]	Submarine hydrothermal field at the Suiyo Seamount in Izu-Bonin Arc, Western Pacific
<i>Vulcanithermus mediatlanticus</i> ¹⁰⁹	FAE F-CLH	37–80 [70]	5.5–8.4 [6.7]	Hydrothermal vent, Mid-Atlantic Ridge
<i>Bacteria; Firmicutes; Clostridia; Thermoanaerobacteriales; Thermodesulfobiaceae</i> {B25};				
Genus: <i>Thermodesulfobium</i>				
<i>Thermodesulfobium narugense</i> ²⁷⁷	AN CLA	37–65 [50–55]	4–6.5 [5.5–6]	Nogo hot spring, Miyagi Prefecture, Japan

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Bacteria; Dictyoglomi; Dictyoglomi; Dictyoglomales; Dictyoglomaceae</i> {B26};				
Genus: <i>Dictyoglomus</i>				
<i>Dictyoglomus thermophilum</i> ²⁷⁸ §	AN COH	50–80 [73–78]	5.9–8.3 [7]	Hot spring, Kumamoto Prefecture, Japan
<i>Dictyoglomus turgidus</i> ²⁷⁹	AN COH	48–86 [72]	5.2–9.0 [7.0–7.1]	Oranzhevoe pole hot spring, Uzon Caldera, Kamchatka, Far East Russia
<i>Bacteria; Chloroflexi; Anaerolineae; Anaerolineales; Anaerolinaceae</i> {B27};				
Genus: <i>Anaerolinea</i>				
<i>Anaerolinea thermolimos</i> ⁵⁹	AN COH	42–55 [50]	6–7.5 [7]	Sludge from a thermophilic reactor in which wastewater from manufacture of a Japanese distilled alcohol is treated
<i>Anaerolinea thermophila</i> ⁶⁰	AN COH	50–60 [55]	6.0–8.0 [7.0]	Thermophilic upflow anaerobic sludge blanket reactor treating soybean-curd manufacturing wastewater
<i>Bacteria; Chloroflexi; Caldilineae; Caldilineales; Caldilineaceae</i> {B28};				
Genus: <i>Caldilinea</i>				
<i>Caldilinea aerophila</i> ⁶⁰	FAE COH	37–65 [55]	7.0–9.0 [7.5–8.5]	Hot spring sulfur-turf, Japan.
<i>Bacteria; Chloroflexi; Chloroflexi; Chloroflexales; Chloroflexaceae</i> {B29};				
Genera: <i>Roseiflexus</i> , <i>Chloroflexus</i> , <i>Heliothrix</i>				
<i>Roseiflexus castenholzii</i> ¹¹³ §	FAE PH (anaerobic)	45–55 [50]	7–9 [7.5–8]	Hot spring, Nakabusa, Japan
<i>Chloroflexus aggregans</i> ¹¹⁶ §	FAE PH (anaerobic)	[50–60]	7.0–9.0	Hot spring of the Okukinu Meotobuchi hot spring in Tochigi Prefecture, Japan
<i>Chloroflexus aurantiacus</i> ¹¹⁷ §	FAE PH (anaerobic)	[52–60]	[8]	Hot spring in the canyon at Sokokura, Hakone district, Japan
<i>Heliothrix oregonensis</i> ^{118,119} §	FAE PH	[40–55]	NR	Hot spring near Warm Springs River, Oregon, USA
<i>Bacteria; Chloroflexi; Thermomicrobia; Sphaerobacterales; Sphaerobacteraceae</i> {B30};				
Genus: <i>Sphaerobacter</i>				
<i>Sphaerobacter thermophilus</i> ²⁸⁰	AN COH	[55]	[8.5]	A laboratory-scale 60°C fermentor
<i>Bacteria; Chloroflexi; Thermomicrobia; Thermomicrobiales; Thermomicrobiaceae</i> {B31};				
Genus: <i>Thermomicrobium</i>				
<i>Thermomicrobium roseum</i> ²⁸¹ §	AN COH	[70–75]	6–9.4 [8.2–8.5]	Hot spring, Yellowstone National Park, USA
<i>Bacteria; Aquificae; Aquificae; Aquificales; Aquificaceae</i> {B32};				
Genera: <i>Hydrogenivirga</i> , <i>Aquifex</i> , <i>Desulfurobacterium</i> (unclassified <i>Aquificales</i>), <i>Balnearium</i> (unclassified <i>Aquificales</i>), <i>Thermovibrio</i> (unclassified <i>Aquificales</i>)				
<i>Hydrogenivirga caldilitoris</i> ²⁸²	AN CLA	55–77.5 [75]	5.5–8.3 [6.5–7]	Coastal hot spring, Ibuski, Kangoshima Prefecture, Japan
<i>Aquifex pyrophilus</i> ²⁸³	FAE CLA	67–95 [85]	5.4–7.5 [6.8]	Hot marine sediments at the Kolbeinsey Ridge, Iceland, 106 m deep
<i>Desulfurobacterium thermolithotrophum</i> ²⁸⁴	AN CLA	40–75 [70]	4.4–7.5 [6]	“Snake Pit” vent field, Mid-Atlantic ridge

Continued

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Desulfurobacterium crinifex</i> ²⁸⁵	AN CLA	50–70 [60–65]	5.0–7.5 [6.0–6.5]	A Juan de Fuca Ridge hydrothermal vent sample (tubes of the annelid polychaete <i>Paralvinella sulfincola</i> attached to small pieces of hydrothermal chimney), depth of 1581 m
<i>Desulfurobacterium atlanticum</i> ²⁸⁶	AN CLA	50–80 [70–75]	5–7.5 [6.0–6.2]	A deep-sea hydrothermal vent chimney at the Mid-Atlantic Ridge (23°N)
<i>Desulfurobacterium pacificum</i> ²⁸⁶	AN CLA	55–85 [75]	5.5–7.5 [6–6.2]	A deep-sea hydrothermal vent chimney at the East Pacific Rise (13°N)
<i>Balnearium lithotrophicum</i> ²⁸⁷	AN CLA	45–80 [70–75]	5–7 [5.4]	Deep-sea hydrothermal system, Suiyo Seamount
<i>Thermovibrio ruber</i> ²⁸⁸	AN CLA	50–80 [75]	5–6.5 [6]	Submarine hydrothermal vents in the Papua New Guinea region, type strain from sandy sediments taken from the beach off Lihir Island
<i>Thermovibrio ammonificans</i> ²⁸⁹	AN CLA	60–80 [75]	5–7 [5.5]	Deep sea hydrothermal vent area, East Pacific Rise
<i>Thermovibrio guaymasensis</i> ²⁸⁶	AN CLA	50–88 [75–80]	5.5–7.5 [6–6.2]	A deep-sea hydrothermal vent chimney at Guaymas Basin
<i>Bacteria; Aquificae; Aquificae; Aquificales; Hydrogenothermaceae {B33};</i>				
Genera: <i>Hydrogenothermus</i> , <i>Sulfurihydrogenibium</i> , <i>Persephonella</i>				
<i>Hydrogenothermus marinus</i> ²⁹⁰	FAE CLA	45–80 [65]	5–7	Vulcano Beach, Vulcano Island, Italy
<i>Sulfurihydrogenibium subterraneum</i> ^{291,292}	FAE CLA	40–70 [60–65]	6.4–8.8 [7.5]	Subsurface hot aquifer water in the Hishikari Japanese gold mine, Kagoshima Prefecture, Japan
<i>Sulfurihydrogenibium azorense</i> ^{291,293 §}	FAE CLA	50–73 [68]	5.5–7 [6]	Near the Água do Caldeirão, Furnas, on São Miguel Island, Azores
<i>Persephonella hydrogeniphila</i> ²⁹⁴	FAE CLA	50–72.5 [70]	5.5–7.6 [7.2]	The hydrothermal field at the Suiyo Seamount in the Izu-Bonin Arc, Japan
<i>Persephonella guaymasensis</i> ²⁹⁵	FAE CLA	55–75 [70]	4.7–7.5 [6]	Deep-sea hydrothermal vent chimney in Guaymas Basin, Mexico
<i>Persephonella marina</i> ²⁹⁵	FAE CLA	55–80 [73]	4.7–7.5 [6]	9°N deep-sea hydrothermal vent, East Pacific Rise
<i>Bacteria; Thermotogae; Thermotogae; Thermotogales; Thermotogaceae {B34};</i>				
Genera: <i>Geotoga</i> , <i>Marinitoga</i> , <i>Petrotoga</i> , <i>Thermosiphon</i> , <i>Thermotoga</i> , <i>Fervidobacterium</i>				
<i>Geotoga petraea</i> ²⁹⁶	AN COH	30–60 [45]	5.5–9 [6.5]	Oilfield brines, Texas and Oklahoma, USA
<i>Geotoga subterranea</i> ²⁹⁶	AN COH	30–55 [50]	5.5–9 [6.5]	Oilfield brines, Texas and Oklahoma, USA
<i>Marinitoga camini</i> ^{297 §}	AN COH	25–65 [55]	5–9 [7]	Deep sea vent fields, Mid-Atlantic Ridge
<i>Marinitoga piezophila</i> ²⁹⁸	AN COH	45–70 [65]	5–8 [6]	“Grandbonum” deep-sea-vent field site, East-Pacific Rise
<i>Marinitoga hydrogenitolerans</i> ²⁹⁹	FAE COH	35–65 [60]	4.5–8.5 [6]	Deep-sea hydrothermal chimney collected at the Rainbow field on the Mid-Atlantic Ridge
<i>Marinitoga okinawensis</i> ³⁰⁰	AN COH	30–70 [55–60]	5.0–7.4 [5.5–5.8]	Deep-sea hydrothermal field in Yonaguni Knoll IV, Southern Okinawa Trough

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Petrotoga mexicana</i> ³⁰¹	AN COH	25–65 [55]	5.8–8.5 [6.6]	Oil/water mixtures of production well heads in Tabasco, Gulf of Mexico, an offshore reservoir
<i>Petrotoga miotherma</i> ²⁹⁶	AN COH	35–65 [55]	5.5–9 [6.5]	Oilfield brines, Texas and Oklahoma, USA
<i>Petrotoga olearia</i> ⁴¹³	AN COH	37–60 [55]	6.5–8.5 [7.5]	Oil/water mixtures of the Samotlor oilfields, western Siberia, Russia
<i>Petrotoga sibirica</i> ⁴¹³	AN COH	37–55 [55]	6.5–9.4 [8]	Oil/water mixtures of the Samotlor oilfields, western Siberia, Russia
<i>Petrotoga mobilis</i> ^{302§}	AN COH	40–65 [58–60]	5.5–8.5 [6.5–7]	Oil reservoir production water from offshore oil platforms, North Sea
<i>Petrotoga halophila</i> ³⁰³	AN COH	45–65 [55–60]	5.6–7.8 [6.7–7.2]	Oil-producing well of the Tchibouella offshore oilfield in Congo, West Africa
<i>Thermosipho atlanticus</i> ⁴¹⁴	AN COH	45–80 [65]	5–9 [6]	Deep sea hydrothermal vent, Mid-Atlantic ridge
<i>Thermosipho melanesiensis</i> ^{304§}	AN COH	45–80 [70]	3.5–9.5 [6.5–9.5]	Deep sea hydrothermal area, Lau Basin, southwest Pacific Ocean
<i>Thermosipho gelei</i> ³⁰⁵	AN COH	45–75 [70]	6–9.4 [7.5]	Production well-head oil/water mixture of a deep continental petroleum reservoir, western Siberia, Russia
<i>Thermosipho japonicus</i> ³⁰⁶	AN COH	45–80 [72]	5.3–9.3 [7.2]	Hydrothermal field, Iheya Basin of the Okinawa Trough, Japan
<i>Thermosipho africanus</i> ^{307,308}	AN COH	35–77 [75]	6–8 [7.2]	Hydrothermal springs, Gulf of Tadjoura, Republic of Djibouti, Africa
<i>Fervidobacterium gondwanense</i> ³⁰⁹	AN COH	[65–68]	[7]	Great Artesian Basin, Australia
<i>Fervidobacterium islandicum</i> ³¹⁰	AN COH	50–80 [65]	6–8 [7]	Hot spring in Hveragerdi, Iceland
<i>Fervidobacterium nodosum</i> ^{311§}	AN COH	41–79 [70]	6–8 [7]	Hot spring in New Zealand
<i>Fervidobacterium pennavorans</i> ³¹²	AN COH	50–80 [70]	5.5–8.0 [6.5]	Hot springs of São Miguel Island, Azores, Portugal
<i>Fervidobacterium changbaicum</i> ³¹³	AN COH	55–90 [75–80]	6.3–8.5 [7.5]	Hot spring, Changbai Mountains, China
<i>Thermotoga lettingae</i> ^{314§}	AN COH	50–75 [65]	6–8.5 [7]	Thermophilic, sulfate-reducing, slightly saline bioreactor
<i>Thermotoga elfii</i> ³¹⁵	AN COH	50–72 [66]	5.5–8.7 [7.5]	African oil well
<i>Thermotoga hypogea</i> ³¹⁶	AN COH	56–90 [70]	6.1–9.1 [7.3–7.4]	Oil-producing well, Cameroon, central Africa
<i>Thermotoga subterranea</i> ³¹⁷	AN COH	50–75 [70]	6–8.5 [7]	Deep continental oil reservoir, East Paris Basin, France
<i>Thermotoga thermarum</i> ³¹⁸	AN COH	55–84 [70]	5.5–9 [7]	Hot water and mud from the shore of Lac Abbe, Republic of Djibouti, Africa
<i>Thermotoga maritima</i> ^{319,320}	AN COH	55–90 [80]	5.5–9 [6.5]	Geothermally heated sea floors, Italy and the Azores
<i>Thermotoga petrophila</i> ^{321§}	AN COH	47–88 [80]	5.2–9 [7]	Production fluid of the Kubiki oil reservoir in Niigata, Japan

Continued

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Thermotoga naphthophila</i> ³²¹	AN COH	48–86 [80]	5.4–9 [7]	Production fluid of the Kubiki oil reservoir in Niigata, Japan
<i>Thermotoga neapolitana</i> ^{322,§}	AN COH	55–90 [80]	5.5–9 [7]	Shallow submarine hot springs, Lucrino Bay, Naples, Italy
<i>Archaea; Crenarchaeota; Thermoprotei; Desulfurococcales; Desulfurococcaceae</i> {A01};				
Genera: <i>Acidilobus</i> , <i>Staphylothermus</i> , <i>Ignicoccus</i> , <i>Desulfurococcus</i> , <i>Thermosphaera</i> , <i>Sulfophobococcus</i> , <i>Stetteria</i> , <i>Thermodiscus</i> (also <i>Ignishpaera</i> of the <i>Ignishpaera</i> group)				
<i>Thermosphaera aggregans</i> ³²³	AN COH	65–90 [85]	5–7 [6.5]	“Obsidian Pool,” Yellowstone National Park, USA
<i>Acidilobus aceticus</i> ³²⁴	AN COH	60–92 [85]	2–6 [3.8]	A hot spring of the Mountmovski volcano, Kamchatka, Far East Russia
<i>Staphylothermus marinus</i> ^{325,§}	AN COH	65–98 [92]	4.5–8.5 [6.5]	Vulcano Island, Italy; also a deep-sea black smoker of the East Pacific Rise
<i>Staphylothermus hellenicus</i> ³²⁶	AN COH	70–90 [85]	4.5–7 [6]	Palaeochori Bay, Milos, Greece
<i>Ignicoccus islandicus</i> ³²⁷	AN CLA	70–98 [90]	3.8–6.5 [5.8]	Submarine hydrothermal system, Atlantic Ocean, at the Kolbeinsey Ridge north of Iceland
<i>Ignicoccus hospitalis</i> ³²⁸	AN CLA	73–98 [90]	4.5–7.0 [5.5]	Kolbeinsey Ridge, north of Iceland
<i>Ignicoccus pacificus</i> ³²⁷	AN CLA	75–98 [90]	4.5–7 [6]	Submarine hydrothermal system, black smoker samples, 9°N, 104°W, Pacific Ocean
<i>Desulfurococcus fermentans</i> ⁹²	AN COH	63–89 [80–82]	4.8–6.8 [6]	Freshwater hot spring of the Uzon Caldera, Kamchatka, Far East Russia
<i>Desulfurococcus amylolyticus</i> ^{329,330}	AN COH	68–97 [90–92]	5.7–7.5 [6.4]	Thermal springs of Kamchatka and Kunashir Islands, Far East Russia
<i>Desulfurococcus mucosus</i> ³³¹	AN COH	[85]	[6]	Solfataric hot springs, Iceland
<i>Desulfurococcus mobilis</i> ³³¹	AN COH	[85]	[6]	Solfataric hot springs, Iceland
<i>Sulfophobococcus zilligii</i> ³³²	AN COH	70–90 [85]	6.5–8.5 [7.5]	Hot spring near Hveragerdi, Iceland
<i>Stetteria hydrogenophila</i> ¹⁰⁶	AN CLH	68–102 [95]	4.5–7.0 [6]	Marine hydrothermal sediment, Paleohori Bay, Milos, Greece
<i>Thermodiscus maritimus</i> ^{333–335}	AN COH	75–98 [90]	5–7 [5.5]	Submarine solfataric field close to Vulcano, Italy
<i>Ignishpaera aggregans</i> ³³⁶	AN COH	85–98 [92–95]	5.4–7 [6.4]	Geothermal Rotorua, Tokaanu, New Zealand
<i>Archaea; Crenarchaeota; Thermoprotei; Desulfurococcales; Pyrodictiaceae</i> {A02};				
Genera: <i>Pyrodictium</i> , <i>Hyperthermus</i> , <i>Pyrolobus</i>				
<i>Pyrodictium abyssii</i> ⁶²	AN COH	80–110 [97]	4.7–7.1 [5.5]	Deep-sea hydrothermal areas of Guaymas Basin, Gulf of California and Kolbeinsey Ridge, north of Iceland
<i>Pyrodictium brockii</i> ⁶³	AN CLA	[105]	5–7 [5.5]	Shallow submarine solfataric field at Porto di Levante, Vulcano Island, Italy
<i>Pyrodictium occultum</i> ⁶³	AN CLA	[105]	5–7 [5.5]	Shallow submarine solfataric field at Porto di Levante, Vulcano Island, Italy

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Hyperthermus butylicus</i> ^{64§}	AN COH	[95–107]	[7]	Hydrothermally heated flat-sea sediments off the coast of São Miguel Island, Azores
<i>Pyrobobus fumarii</i> ⁵	FAE CLA	90–113 [106]	4.0–6.5 [5.5]	TAG site, Mid-Atlantic Ridge,
<i>Archaea; Crenarchaeota; Thermoprotei; Sulfolobales; Sulfolobaceae</i> {A03};				
Genera: <i>Stygiolobus</i> , <i>Sulfurisphaera</i> , <i>Acidianus</i>				
<i>Stygiolobus azoricus</i> ⁷²	AN CLA	57–89 [80]	1–5.5 [2.5–3]	Solfataric fields of São Miguel Island, Azores
<i>Sulfurisphaera ohwakuensis</i> ³³⁷	FAE COH	63–92 [84]	1–5 [2]	Hot springs of Ohwaku Valley, Hakone, Japan
<i>Acidianus brierleyi</i> ¹³²	FAE CLA	45–75 [70]	1–6 [1.5–2]	Distant acidic geo- and hydrothermal heated areas
<i>Acidianus ambivalens</i> ^{338,339}	FAE CLA	[80]	1–3.5	Leirhnukur fissure, Iceland
<i>Acidianus infernus</i> ¹³²	FAE CLA	65–96 [90]	1–5.5 [2]	Solfatara Crater and Pisciarelli Solfatara, Naples, Italy
<i>Acidianus sulfidivorans</i> ⁷¹	FAE CLA	45–83 [74]	0.35–3.0 [0.8–1.4]	Solfatara on Lihir Island, Papua New Guinea
<i>Archaea; Crenarchaeota; Thermoprotei; Thermoproteales; Thermofilaceae</i> {A04};				
Genus: <i>Thermofilum</i>				
<i>Thermofilum pendens</i> ^{340§}	AN COH	[85–90]	[5]	Icelandic solfataras
<i>Archaea; Crenarchaeota; Thermoprotei; Thermoproteales; Thermoproteaceae</i> {A05};				
Genera: <i>Thermoproteus</i> , <i>Pyrobaculum</i> , <i>Thermocladium</i> , <i>Caldvirga</i>				
<i>Thermoproteus uzoniensis</i> ³⁴¹	AN COH	74–102 [90]	4.6–6.8 [5.6]	Uzon Caldera, Kamchatka, Far East Russia
<i>Thermoproteus tenax</i> ³⁴²	AN F-CLA	[85]	[3.7–4.2]	Icelandic solfataric hot springs
<i>Thermoproteus neutrophilus</i> ^{342,343§}	AN F-CLA	[85]	[6.8]	Hot spring, Iceland
<i>Pyrobaculum oguniense</i> ³⁴⁴	AN COH	70–97 [90–94]	5.4–7.4 [6.3–7]	Terrestrial hot spring at Oguni-cho, Kumamoto Prefecture, Japan
<i>Pyrobaculum arsenaticum</i> ^{345§}	AN F-CLA	68–100 [81]	NR	Hot water pond, Pisciarelli Solfatara, Naples, Italy
<i>Pyrobaculum organotrophum</i> ³⁴⁶	AN COH	74–102 [100]	5–7 [6]	Boiling solfataric waters in Iceland, Italy, and the Azores
<i>Pyrobaculum islandicum</i> ^{346§}	AN F-CLA	74–102 [100]	5–7 [6]	Boiling solfataras and geothermal waters, Iceland
<i>Pyrobaculum calidifontis</i> ^{347§}	FAE COH	75–100 [90–95]	5.5–8.0 [7.0]	Terrestrial hot spring Calamba, Laguna, the Philippines
<i>Pyrobaculum aerophilum</i> ^{348,349§}	FAE F-CLA	75–104 [100]	5.8–9 [7]	Boiling marine water hole, Maronti Beach, Ischia, Italy
<i>Thermocladium modestius</i> ³⁵⁰	FAE COH	45–82 [72]	2.6–5.9 [4]	Sites of volcanic activity, Japan
<i>Vulcanisaeta soumiana</i> ³⁵¹	FAE COH	65–89 [85]	3.5–5.0 [4.5]	Hot spring, Souzan, Kanagawa, Japan
<i>Vulcanisaeta distributa</i> ³⁵¹	FAE COH	70–92 [90]	3.5–5.6 [4.5]	Hot spring, Ohwakudani, Kanagawa, Japan
<i>Caldvirga maquilgensis</i> ^{352§}	FAE COH	62–92 [85]	2.3–6.4 [3.7–4.2]	Acidic hot spring, the Philippines
<i>Archaea; Euryarchaeota; Thermoplasmata; Thermoplasmatales; Thermoplasmataceae</i> {A06};				
Genus: <i>Thermoplasma</i>				
<i>Thermoplasma acidophilum</i> ^{353,354§}	FAE COH	45–63 [59]	0.5–4 [1–2]	Solfatara fields and self-heated coal refuse piles

Continued

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Thermoplasma volcanium</i> ^{353,355 §}	FAE COH	33–67 [60]	1–4 [2]	Submarine and continental solfataras at Vulcano Island, Italy; also from Java, Iceland; and Yellowstone National Park, USA
<i>Archaea; Euryarchaeota; Methanococci; Methanococcales; Methanocaldococcaceae</i> {A07}; Genera: <i>Methanocaldococcus, Methanotorris</i>				
<i>Methanocaldococcus fervens</i> ³⁵⁶	AN CLA	48–92 [85]	5.5–7.6 [6.5]	Deep-sea hydrothermal vent, Guaymas Basin, Gulf of California
<i>Methanocaldococcus indicus</i> ³⁵⁷	AN CLA	50–86 [85]	[6.5–6.6]	Deep-sea hydrothermal vent, Central Indian Ridge
<i>Methanocaldococcus infernus</i> ^{358,359}	AN CLA	55–91 [85]	5.25–7.0 [6.5]	Deep-sea hydrothermal chimney sample collected on the Mid-Atlantic Ridge at a depth of 3000 m
<i>Methanocaldococcus jannaschii</i> ^{358,360,361 §}	AN CLA	50–86 [85]	5.2–7.0 [6.0]	“White smoker” chimney on the 20°N East Pacific Rise
<i>Methanocaldococcus vulcanius</i> ³⁵⁶	AN CLA	49–89 [80]	5.2–7 [6.5]	Deep-sea vent, 13°N thermal field, East Pacific Rise
<i>Methanotorris formicicus</i> ³⁶²	AN CLA	55–83 [75]	6–8.5 [6.7]	Deep-sea vent, Kairei field, Central Indian Ridge
<i>Methanotorris igneus</i> ^{363,364}	AN CLA	45–91 [88]	5.0–7.5 [5.7]	Kolbeinsey Ridge shallow (103 and 106 m) submarine hydrothermal system off Iceland
<i>Archaea; Euryarchaeota; Thermococci; Thermococcales; Thermococcaceae</i> {A08}; Genera: <i>Thermococcus, Pyrococcus, Palaeococcus</i>				
<i>Thermococcus sibiricus</i> ⁴¹⁵	AN COH	40–88 [78]	5.8–9 [7.5]	Samotlor oil reservoir, Western Siberia, Russia
<i>Thermococcus zilligii</i> ³⁶⁵	AN COH	55–85 [75–80]	5.4–9.2 [7.4]	Terrestrial fresh water hot pool, New Zealand
<i>Thermococcus profundus</i> ³⁶⁶	AN COH	50–90 [80]	4.5–8.5 [7.5]	Deep-sea hydrothermal vent system, Middle Okinawa Trough
<i>Thermococcus barossii</i> ³⁶⁷	AN COH	60–94 [82.5]	4–9 [6.5–7.5]	Hydrothermal vent flange formation, East Pacific Rise of the Juan de Fuca Ridge
<i>Thermococcus siculi</i> ³⁶⁸	AN COH	50–93 [85]	5–9 [7]	Deep-sea hydrothermal vent, the Mid-Okinawa Trough
<i>Thermococcus celericrescens</i> ³⁶⁹	AN COH	50–85 [80]	5.6–8.3 [7.0]	Hydrothermal vent at Suiyo Seamount, Izu-Bonin Arc, Western Pacific Ocean
<i>Thermococcus acidaminovorans</i> ⁷⁵	AN COH	56–93 [85]	5–9.5 [9]	Vulcano Island, Italy
<i>Thermococcus aegaeus</i> ³²⁶	AN COH	50–95 [85]	4.5–7.5 [6]	Palaeochori Bay, Milos, Greece
<i>Thermococcus alcaliphilus</i> ⁷⁸	AN COH	56–90 [85]	6.5–10.5 [9]	Vulcano Island, Italy
<i>Thermococcus atlanticus</i> ³⁷⁰	AN COH	70–90 [85]	5–8 [7]	“Snakepit” hydrothermal vent region of the Mid-Atlantic Ridge
<i>Thermococcus barophilus</i> ^{140 §}	AN COH	48–100 [85]	[7]	“Snakepit” hydrothermal vent region of the Mid-Atlantic Ridge
<i>Thermococcus chitonophagus</i> ³⁷¹	AN COH	60–93 [85]	3.5–9 [6.7]	Guaymas Basin hydrothermal vents, Gulf of California
<i>Thermococcus fumicolans</i> ⁷⁶	AN COH	73–103 [85]	4.5–9.5 [8.5]	Deep-sea hydrothermal vent, North Fiji Basin
<i>Thermococcus litoralis</i> ³⁷²	AN COH	50–96 [85]	4–8.5 [6]	Vulcano Island, Italy; also submarine thermal spring, Lucrino Beach, Naples

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Thermococcus thioreducens</i> ³⁷³	AN COH	55–94 [83–85]	5.0–8.5 [7.0]	“Black smoker” chimney material from the “Rainbow” hydrothermal vent site on the Mid-Atlantic Ridge (36.2°N, 33.9°W)
<i>Thermococcus waiotapuensis</i> ³⁷⁴	AN COH	60–90 [85]	5–8 [7]	Terrestrial freshwater hot spring, New Zealand
<i>Thermococcus stetteri</i> ³⁷⁵	AN COH	55–95 [75–88]	5.7–7.2 [6.5]	Marine solfataric fields of Kraternaya Cove, Ushishir Archipelago, Northern Kurils
<i>Thermococcus pacificus</i> ⁴¹²	AN COH	70–95 [80–88]	6–8 [6.5]	Bay of Plenty, New Zealand
<i>Thermococcus aggregans</i> ³⁷⁶	AN COH	60–94 [88]	5.6–7.9 [7]	Guaymas Basin hydrothermal vents, Gulf of California
<i>Thermococcus celer</i> ⁷⁷	AN COH	[88]	[8.5]	Vulcano Island, Italy
<i>Thermococcus gammatolerans</i> ¹⁴³	AN COH	55–95 [88]	[6]	Guaymas Basin, Gulf of California
<i>Thermococcus gorgonarius</i> ⁴¹²	AN COH	68–95 [80–88]	5.8–8.5 [6.5–7.2]	Shore of Whale Island, New Zealand
<i>Thermococcus guaymasensis</i> ³⁷⁶	AN COH	56–90 [88]	5.6–8.1 [7.2]	Guaymas Basin hydrothermal vent site, Gulf of California
<i>Thermococcus hydrothermalis</i> ⁸²	AN COH	55–100 [80–90]	3.5–9.5 [5.5–6.5]	21°N deep-sea hydrothermal vent region, East Pacific Rise
<i>Thermococcus peptonophilus</i> ³⁷⁷	AN COH	60–100 [85–90]	4–8 [6]	Izu-Borin forearc; also from the southern Mariana Trough
<i>Thermococcus kodakarensis</i> ^{378, 379, 380 §}	AN COH	60–100 [85]	5–9 [6.5]	Solfataras on Kodakara Island, Kagoshima, Japan
<i>Thermococcus coalescens</i> ³⁸¹	AN COH	57–90 [87]	5.2–8.7 [6.5]	Hydrothermal fluid obtained from Suiyo Seamount of the Izu-Bonin Arc
<i>Pyrococcus furiosus</i> ^{382, 383 §}	AN COH	70–103 [100]	5–9 [7]	Shallow marine hydrothermal system at Vulcano Island, Italy
<i>Pyrococcus horikoshii</i> ^{383, 384, 385 §}	AN COH	80–102 [98]	5–8 [7]	Hydrothermal fluid samples obtained at the Okinawa Trough vents in the NE Pacific Ocean, at a depth of 1395 m
<i>Pyrococcus glycovorans</i> ⁸³	AN COH	75–104 [95]	2.5–9 [7.5]	Deep-sea hydrothermal vent on the East Pacific Rise
<i>Pyrococcus woesei</i> ^{386, d}	AN COH	[100–103]	[6–6.5]	Marine solfataras at the northern beach of Porto di Levante, Vulcano Island, Italy
<i>Palaeococcus ferrophilus</i> ³⁸⁷	AN COH	60–88 [83]	4–8 [6]	Hydrothermal vent chimney, Myojin Knoll, Ogasawara-Bonin Arc, Japan
<i>Palaeococcus helgesonii</i> ³⁸⁸	FAE COH	45–85 [80]	5–8 [6.5]	Geothermal well on Vulcano Island, Italy
Archaea; Euryarchaeota; Archaeoglobi; Archaeoglobales; Archaeoglobaceae {A09}; Genera: Archeoglobus, Geoglobus, Ferroglobus				
<i>Archaeoglobus veneficus</i> ³⁸⁹	AN F-CLA	65–85 [75–80]	6.5–8 [7]	“Snake Pit” hydrothermal vents of the Mid-Atlantic Ridge
<i>Archaeoglobus profundus</i> ¹⁰⁵	AN CLH	65–90 [82]	4.5–7.5 [6]	The Guaymas hot vent area; cores of hot sediment and active smoker chimneys
<i>Archaeoglobus fulgidus</i> ^{390, 391, 392 §}	AN F- CLA	64–92 [83]	5.5–7.5	Marine hydrothermal systems at Vulcano island and at Stufe di Nerone, Naples, Italy
<i>Geoglobus ahangari</i> ¹²⁹	AN F- CLA	65–90 [88]	5–7.6 [7.0]	Guaymas Basin hydrothermal system, Gulf of California, at a depth of 2000 m
<i>Ferroglobus placidus</i> ³⁹³	AN F-CLA	65–95 [85]	6.0–8.5 [7.0]	Shallow submarine hydrothermal systems at Vulcano Island, Italy

Continued

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Archaea; Euryarchaeota; Methanopyri; Methanopyrales; Methanopyraceae</i> {A10};				
Genus: <i>Methanopyrus</i>				
<i>Methanopyrus kandleri</i> ^{394,395} §	AN CLA	84–110 [98]	5.5–7 [6.5]	Deep-sea sediment from the Guaymas Basin, Gulf of California; and from the shallow marine hydrothermal system of the Kolbeinsey Ridge, Iceland
<i>Archaea; Euryarchaeota; Methanobacteria; Methanobacteriales; Methanothermaceae</i> {A11};				
Genus: <i>Methanothermus</i>				
<i>Methanothermus sociabilis</i> ³⁹⁶	AN CLA	55–97 [88]	5.5–7.5 [6.5]	Hot waters and muds of Icelandic continental geothermal areas
<i>Methanothermus fervidus</i> ³⁹⁷	AN CLA	55–97 [80–85]	NR	Icelandic solfatara fields at Keringarfjoll and Hveragerdi
<i>Archaea; Euryarchaeota; Methanobacteria; Methanobacteriales; Methanobacteriaceae</i> {A12};				
Genera: <i>Methanobacterium, Methanothermobacter</i>				
<i>Methanobacterium thermaggregans</i> ³⁹⁸	AN CLA	40–75 [65]	6.5–9 [7–7.5]	Mud from a cow pasture
<i>Methanothermobacter defluvi</i> ^{73,74}	AN CLA	[60–65]	[6.5–7.0]	Anaerobic sludge obtained from the pilot-scale plant digesting methacrylic wastewater
<i>Methanothermobacter marburgensis</i> ³⁹⁹	AN CLA	45–70 [65]	5.0–8.0 [6.8–7.4]	Mesophilic sewage sludge and hot springs
<i>Methanothermobacter</i> <i>thermautotrophicus</i> ^{399,400} §	AN CLA	40–75 [65–70]	6.0–8.8 [7.2–7.6]	Anaerobic sewage sludge digester
<i>Methanothermobacter thermoflexus</i> ^{73,74}	AN CLA	[55]	[7.9–8.2]	Anaerobic sludge obtained from the pilot-scale plant digesting methacrylic wastewater
<i>Methanothermobacter thermophilus</i> ^{74,401}	AN CLA	45–65 [57]	7.0–8.5 [7.5]	Uzon Caldera, Kamchatka, Far East Russia
<i>Methanothermobacter wolfei</i> ^{399,402}	AN CLA	37–74 [55–65]	6.0–8.2 [7.0–7.5]	Mixture of sewage sludge and river sediment
<i>Archaea; Euryarchaeota; Methanococci; Methanococcales; Methanococcaceae</i> {A13};				
Genus: <i>Methanothermococcus</i>				
<i>Methanothermococcus</i> <i>thermolithotrophicus</i> ^{403,404} §	AN CLA	30–70 [65]	6–8 [7]	Heated sea sediments near Naples, Italy
<i>Methanothermococcus okinawensis</i> ⁴⁰⁵	AN CLA	40–75 [60–65]	4.5–8.5 [6–7]	Deep-sea vent at Iheya Ridge in the Okinawa Trough, Japan
<i>Archaea; Euryarchaeota; Methanomicrobia; Methanosarcinales; Methanosarcinaceae</i> {A14};				
Genera: <i>Methanosarcina, Methanomethylovorans</i>				
<i>Methanosarcina thermophila</i> ⁴⁰⁶ §	AN F-CLA	[50]	[6–7]	55°C anaerobic sludge digester
<i>Methanomethylovorans thermophila</i> ⁴⁰⁷	AN CLA	42–58 [50]	5–7 [6.5]	Methanol-fed thermophilic anaerobic reactor
<i>Archaea; Euryarchaeota; Methanomicrobia; Methanosarcinales; Methermiococcaceae</i> {A15};				
Genus: <i>Methermiococcus</i>				
<i>Methermiococcus shengliensis</i> ⁴⁰⁸	AN CLA	50–70 [65]	5.5–8.0 [6.0–6.5]	Oil-production water of the Shengli oilfield, China
<i>Archaea; Euryarchaeota; Methanomicrobia; Methanosarcinales; Methanosetaeaceae</i> {A16};				
Genus: <i>Methanotherix</i>				
<i>Methanotherix thermophila</i> ⁴⁰⁹ §	AN COH	[55]	6.1–7.5 [6.7]	Mesophilic anaerobic sludge digestors

TABLE 1. Continued

Species	O ₂ relationship and metabolism	Temperature range [optimum]	pH Range [optimum]	Originally isolated from
<i>Archaea; Euryarchaeota; Methanomicrobia; Methanomicrobiales; Methanomicrobiaceae</i> {A17}; Genus: <i>Methanoculleus</i>				
<i>Methanoculleus thermophilus</i> ^{410,411}	AN F-CLA	37–65 [55]	6.18–7.82 [7]	Nuclear power plant effluent channel sediment

^cSymbols and abbreviations: §, sequenced genome; AN, anaerobic; FAE, facultative aerobe; COH, chemoorganoheterotroph; CLA, chemolithoautotroph; F-CLA, facultative chemolithoautotroph; PA, photoautotroph; PH, photoheterotroph; CLH, chemolithoheterotroph; F-CLH, facultative chemolithoheterotroph; NR, not reported.

^dNote that Kanoksilapatham *et al.* suggest reclassifying *Pyrococcus woesei* as *Pyrococcus furiosus* subsp. *woesei*; Kanoksilapatham, W., J.M. Gonzalez, D.L. Maeder, *et al.* 2004. A proposal to rename the hyperthermophile *Pyrococcus woesei* as *Pyrococcus furiosus* subsp. *woesei*. *Archaea*. **1**: 277–283.

of the cultured thermophilic Bacteria and Archaea are anaerobic, it is reasonable to ask whether this observation accurately reflects the ecological situation in thermobiotic environments. This question is largely beyond the scope of the present chapter; however, culture-independent analyses have revealed that members of the Aquificales, (Aquificaceae {B32}), appear to be ubiquitous in the terrestrial hot springs of Yellowstone National Park, as well as in Japan, Iceland, and Kamchatka. It has been postulated that these Aquificales, particularly the obligately aerobic *Thermocrinis ruber*-like microorganisms, are the primary producers (via chemoautotrophic hydrogen oxidation) in these ecosystems.^{34,55}

Temperature Relationship

Etymologically, thermophiles “love” heat, and Bacteria and Archaea with this physiology are further categorized according to their optimal (T_{opt}) and maximal (T_{max}) growth temperatures. The authors classify Bacteria and Archaea with T_{opt} 50°C–64°C as (moderate) thermophiles, those with T_{opt} 65°C–79°C as extreme thermophiles, and prokaryotes with $T_{\text{opt}} \geq 80^\circ\text{C}$ as hyperthermophiles.^{22,56–58} Although not considered true thermophiles, Bacteria and Archaea that grow optimally at mesophilic temperatures but have a $T_{\text{max}} > 50^\circ\text{C}$ are described as thermotolerant.

Thermophilic prokaryotes able to grow over a 35°C–40°C temperature span are considered temperature-tolerant thermophiles.⁵⁷ To the authors’ knowledge, the record widest temperature growth range is 22°C–75°C by a *Methanothermobacter thermautotrophicus*-like strain isolated from river sediment (J. Wiegel, unpublished results). By comparison, some thermophilic anaerobes are reported to have especially narrow temperature growth ranges, such as 42°C–

55°C for *Anaerolinea thermolimosa*⁵⁹ and 50°C–60°C for *Anaerolinea thermophila*⁶⁰—two species from the family Anaerolinaceae {B27}.

Hyperthermophiles with $T_{\text{opt}} \geq 80^\circ\text{C}$ and $T_{\text{max}} > 100^\circ\text{C}$, were first isolated by Stetter from the hot vents at Vulcano Island off the coast of Sicily, Italy, in 1981.²⁴ Isolates growing optimally above 100°C are often found at deep-sea vents,⁶¹ or deep in terrestrial hot spring channels and sediments. This “deep” requirement is ascribed to the increased pressure, which allows water to remain in liquid form at temperatures above 100°C. Within the Bacteria, only the *Thermotogaceae* {B34} and *Aquificaceae* {B32} lineages contain hyperthermophilic members. Within the Archaea, taxonomic families containing hyperthermophilic taxa include: *Methanopyraceae* {A10}, *Methanothermaceae* {A11}, *Methanocaldococcaceae* {A07}, *Thermococcaceae* {A08}, *Archaeoglobaceae* {A09}, *Sulfolobaceae* {A03}, *Desulfurococcaceae* {A01}, *Pyrodictiaceae* {A02}, *Thermofilaceae* {A04}, and *Thermoproteaceae* {A05} (see TABLE 1). Many species with extremely high temperature growth ranges and T_{opt} belong to the *Pyrodictiaceae* {A02}: *Pyrodictium abyssi* with a growth range of 80°C–110°C, T_{opt} 97°C⁶²; *Pyrodictium Brockii* and *Pyrodictium occultum*, both with T_{opt} 105°C⁶³; *Hyperthermus butylicus* with a reported T_{opt} 95°C–107°C⁶⁴; and *P. fumarii* with a growth range of 90°C–113°C and T_{opt} 106°C.⁵ Very recently, Takai provided convincing evidence of a *M. kandleri* strain isolated from a deep-sea hydrothermal region capable of growing under increased pressure at 122°C.⁶

The base of the inferred 16S rRNA gene sequence phylogenetic tree contains hyperthermophilic taxa (FIG. 1). This is one line of evidence for the hypothesis that life evolved at a time of elevated temperature on early Earth. However, thermophilic anaerobes are also found among branches of the phylogenetic tree containing predominantly mesophiles. These taxa

having either evolved after a speciation event, during subsequent phyletic evolution, or they are remnants of the thermophilic origins of the clades. Because of the many specialized properties required for thermophilic life, thermophily is not a trait transferrable via horizontal gene transfer. In cases where thermophilic and mesophilic species exist within a genus, the ability to grow at elevated temperatures occurs via combinations of different properties, including the stabilization of intracellular compounds through binding of cations, such as Ca^{2+} ; the insertion of additional hydrogen bridges in protein structures via the presence of increased acidic amino acids (e.g., by substituting glutamine with glutamic acid); the formation of more globular protein structures with additional hydrophobic regions inside; the stabilization of membrane fluidity by changes in fatty acid lengths and branching⁶⁵; and changes in proton permeability of the cytoplasmic membranes.⁶⁶ In cases where the addition of genes conferred higher growth temperatures, it is assumed that the enzymes encoded by these genes removed the bottleneck of otherwise cryptic thermophiles.^{57,67}

pH Relationship

The pH growth minimum (pH_{\min}), maximum (pH_{\max}), and optimum (pH_{opt}) determine whether a prokaryote is characterized as acidophilic ($\text{pH}_{\text{opt}} < 5.0$), acidotolerant ($\text{pH}_{\min} < 4$, pH_{opt} circumneutral), neutrophilic ($\text{pH}_{\text{opt}} \sim 7.0$), alkalitolerant ($\text{pH}_{\text{opt}} < 8.5$, $\text{pH}_{\max} > 8.5$), or alkaliphilic ($\text{pH}_{\text{opt}} \geq 8.5$). The majority of known thermophilic anaerobes are neutrophilic. None of the known thermophilic anaerobic *Bacteria* grow below pH 3.0.⁵⁸ To the authors' current knowledge, the most acidophilic anaerobic thermophilic *Bacteria* are: *Thermoanaerobacterium aotearoense*, $\text{pH}^{60\text{C}}$ range 3.8–6.8 and $\text{pH}^{60\text{C}}_{\text{opt}}$ 5.2⁶⁸; *Thermoanaerobacterium aciditolerans*, pH range 3.2–7.1, pH_{opt} 5.7⁶⁹; and *Lebetimonas acidiphila*, pH range 4.2–7.0 and pH_{opt} 5.2.⁷⁰ The most acidophilic thermophilic anaerobic *Archaea* belong to the *Thermoplasmataceae* {A06} and *Sulfolobaceae* {A03} families and nearly all are facultative aerobes; the most acidophilic is *Acidianus sulfidivorans*, with pH growth range of 0.35–3.0, and pH_{opt} 0.8–1.4.⁷¹ One exception is the obligately anaerobic *Stygiolobus azoricus* of the *Sulfolobaceae* {A03}, which has a pH growth range of 1–5.5 and pH_{opt} 2.5–3.⁷²

In contrast to the aerobic and truly acidophilic *Archaea*, and to the alkalithermophilic *Bacteria* (TABLE 1), only a few known anaerobic thermophilic *Archaea* grow optimally at high pH. All are obligately

anaerobic and reside within the *Euryarchaeota* clade: species from the *Methanobacteriaceae* {A12}, including *Methanothermobacter thermoflexus*, with pH_{opt} 7.9–8.1^{73,74}; and species from the *Thermococcaceae* {A08}, including *Thermococcus acidaminovorans* with a pH range of 5–9.5 and pH_{opt} 9.0,⁷⁵ *Thermococcus fumicolans*, with a growth range of pH 4.5–9.5 and pH_{opt} 8.5,⁷⁶ *Thermococcus celer*, with pH_{opt} 8.5,⁷⁷ and *Thermococcus alcaliphilus*, with a pH range of 6.5–10.5 and pH_{opt} 9.0.⁷⁸

Alkalithermophilic ($\text{pH}_{\text{opt}}^{55\text{C}} > 8.5$; $T_{\text{opt}} > 55^\circ\text{C}$) anaerobic *Bacteria* are particularly intriguing because of the phylogenetic position of most known taxa and an observed physiological peculiarity. Although anaerobic alkalithermophilic *Bacteria* taxa differ from one another physiologically, almost all belong to the phylum *Firmicutes* (formerly called the Gram-type positive *Bacillus*–*Clostridium* group) phylogenetic subbranch {B07–14}.⁵⁸ The one known Gram-type negative exception is the not validly published and poorly characterized “*Thermopallium natrophilum*.”⁷⁹ Anaerobic alkalithermophilic *Bacteria* include: *C. paradoxum*, the most alkaliphilic thermophile with a $\text{pH}^{60\text{C}}$ growth range of 7–11.1, pH_{opt} 10.1³; *Clostridium thermoalcaliphilum*, $\text{pH}^{60\text{C}}$ range 7–11, pH_{opt} 9.6–10.1⁸⁰; and members of the genus *Anaerobranca* of the family *Syntrophomonadaceae* {B12}. Phylogenetically similar *T. celere*-like strains have been isolated from a variety of niches, including thermobiotic and mesobiotic, and from alkaline and neutrophilic soils and sediments. Isolates from mesobiotic and neutrophilic niches exhibit shorter doubling times (10–15 min) compared with isolates from thermobiotic niches (25–40 min).^{7,81} *N. thermophilus* (*Natranaerobiaceae* {B08}), isolated from an alkaline, hypersaline lake of the Wadi An Natrun, Egypt, classifies within a novel order of the class *Clostridia* in the phylum *Firmicutes*. It is alkalithermophilic (T_{opt} 53°C, $\text{pH}_{\text{opt}}^{55\text{C}}$ 9.5) and additionally halophilic, growing optimally between 3.3 and 3.9 M Na^+ .⁸ It is important to note that the determination of the pH of alkalithermophiles (as well acidothermophiles) has to be done with temperature-equilibrated electrodes and the use of a pH meter standardized with buffers at the elevated temperature range.⁵⁸

As with temperature growth ranges, there are thermophilic anaerobes with wide pH growth ranges spanning six or more pH units; for example, *Thermococcus hydrothermalis* with a pH range of 3.5–9.5⁸² and *Pyrococcus glycovorans* with a pH growth range of 2.5–9.0.⁸³ *Thermoanaerobacter ethanolicus* strain JW200 is another interesting example as it has an unusual pH profile with a broad and flat pH optimum from pH 5.5 to 8.5.⁸⁴ Thermophilic anaerobes have also been discovered with growth ranges of less than one pH unit; for

example, *Pelotomaculum thermopropionicum* with a pH range of 6.7–7.5,⁸⁵ *Thermodesulfatator indicus* with a pH range of 6.0–6.7,⁸⁶ and *Thermodesulfobacterium hydrogeniphilum* with a pH range of 6.3–6.8.⁸⁷

Metabolic Diversity of Thermophilic Anaerobes

A majority of the axenic thermophilic anaerobic Archaea and Bacteria are chemoorganoheterotrophic, using organic compounds for carbon and energy. However, a variety of other metabolic strategies are seen within the set of thermophilic anaerobic prokaryotes, including chemolithoautotrophy, chemolithoheterotrophy, photoheterotrophy, and photoautotrophy. Considering these metabolic strategies and the variation that can be found within each type, an astonishing diversity of metabolism is observed within the thermophilic anaerobes. In this next section, an overview of commonly observed and unique physiologies of thermophilic anaerobes is provided. Amend and Shock have previously described thermophilic and hyperthermophilic energetic reactions in depth, and their work is a key resource for the study of thermophilic metabolisms.⁵⁴

Chemoorganoheterotrophic metabolisms are further categorized, and include glycolytic, cellulolytic, lipolytic, and peptidolytic metabolisms. The Emden-Meyerhof and Entner-Doudoroff pathways are employed by glycolytic thermophilic anaerobes, but a variety of modifications have been discovered, particularly within the Archaea.⁸⁸ Principal fermentation products formed by glycolytic thermophilic anaerobes include acetate, lactate, ethanol, CO₂, and H₂. The production of ethanol by glycolytic and cellulolytic taxa has previously been studied.⁸⁹ Cellulose is the most abundant renewable natural plant fiber, and its degradation, coupled with the production of “biofuels,” such as ethanol, by thermophilic anaerobes is an intensely studied and timely research area. This metabolism, involving many unusual enzymes, has been studied with axenic cultures as well as in co-culture. An example of the latter is the cellulolytic *Clostridium thermocellum* in culture with the glycolytic *T. ethanolicus*.⁹⁰ Besides *C. thermocellum*, other thermophilic species within the genus *Clostridium* are cellulolytic, these are: *C. sterocorium*, *C. thermolacticum*, *C. thermocopriae*, and *C. thermopapyrolyticum*.⁹¹ Relatively recently, the first hyperthermophilic cellulosic materia degrading archaeon, *Desulfurococcus fermentans*, was isolated.⁹² As with cellulose-degrading thermophilic anaerobes, xylanolytic thermophilic anaerobes generate interest

because the conversion of xylan—a component of plant hemicellulose and the second-most abundant renewable polysaccharide in biomass—to useful products might be coupled to increasing the efficiency of processing lignocellulose and to the production of energy from renewable resources.⁹³ Xylan is widely used among thermophilic anaerobic Bacteria, especially among members of the Firmicutes. Lipolytic chemoorganotrophic thermophilic anaerobes include *Thermosyntropha lipolytica* which, in co-culture, syntrophically grows on saturated and unsaturated fatty acids with 4 to 18 carbon atoms,⁹⁵ and *Desulfurothermus naphthae*, which can use long-chain fatty acids with 6 to 18 carbon atoms as well as alkanes having 6 to 14 carbon atoms.⁹⁴ Although chemoorganoheterotrophic metabolisms appear to be common metabolic strategies for the axenic thermophilic anaerobes studied in the lab, the natural substrates for these microorganisms are largely unknown⁵⁴; furthermore, culture-independent analyses indicate that lithotrophic prokaryotes are the primary producers in certain thermobiotic environments, such as hot springs.³⁵

Among chemolithotrophic pathways, the methanogenic reaction, $4\text{H}_2 + \text{CO}_2 \rightarrow \text{CH}_4 + 2\text{H}_2\text{O}$, is well characterized and used by thermophilic taxa within the *Methanobacteriaceae* {A12}, *Methanothermaceae* {A11}, *Methanocaldococcaceae* {A07}, and *Methanococcaceae* {A13}.⁵⁴ Another interesting chemolithotrophic metabolism of anaerobic thermophiles described relatively recently makes use of CO, which occurs as a normal component of escaping volcanic gas of terrestrial and deep-sea hydrothermal origin.⁹⁶ Several thermophilic anaerobes have indeed been isolated that grow lithotrophically on CO, performing the metabolic reaction $\text{CO} + \text{H}_2\text{O} \rightarrow \text{CO}_2 + \text{H}_2$. Thermophilic anaerobes known to employ this strategy include: *Desulfotomaculum carboxydivorans*,⁹⁷ *Carboxydotherrmus hydrogeniformans*,⁹⁸ *Thermolithobacter carboxydivorans*,⁹⁹ *Carboxydocella thermautotrophica*,¹⁰⁰ *Thermincola carboxydiphila*,¹⁰¹ *Thermincola ferriacetica*,¹⁰² *Caldanaerobacter subterraneus* subsp. *pacificus*,¹⁰³ and *Thermosinus carboxydivorans*.¹⁰⁴ This same CO-using reaction has also been observed within the Archaea in an isolate belonging to the genus *Thermococcus* (family *Thermococcaceae* {A08}).⁹⁶ Another interesting chemolithotrophic strategy is employed by the acetogens using the Wood-Ljungdahl pathway (from the reaction: $3\text{H}_2 + \text{CO}_2 \rightarrow \text{acetate}$). Both mesophilic and thermophilic taxa (e.g., *Moorella* species) are known to perform this reaction (for additional discussion, see the corresponding chapter within this book).

Chemolithoheterotrophs generate energy chemolithotrophically and assimilate carbon heterotrophically. Thermophilic anaerobes with this metabolism include Archaea, *Archaeoglobus profundus*,¹⁰⁵ and *Stetteria hydrogenophila*,¹⁰⁶ and Bacteria, *Desulfotomaculum alkalicophilum*,¹⁰⁷ *Desulfotomaculum carboxydvorans*,⁹⁷ *T. carboxydiphila*,¹⁰¹ *T. ferriacetica* (which can also grow chemolithoautotrophically),¹⁰² *Caldithrix abyssi*,¹⁰⁸ *Vulcanithermus mediatlanticus*,¹⁰⁹ and *Oceanithermus profundus*.¹¹⁰

Two mechanisms for collecting light energy and converting it into chemical energy are known—one depends on photochemical reaction centers containing (bacterio)-chlorophyll and the other employs rhodopsins.^{111,112} However, to the authors' knowledge, there are no rhodopsin-using thermophilic anaerobes. The question of whether there is a biological explanation for this (e.g., that rhodopsin proteins do not function well at high temperature) or whether it is the result of insufficient searching for this particular physiology, appears unanswered at this time. However, there are phototrophic moderately thermophilic anaerobes (TABLE 1). Presumably because of the temperature sensitivity of the photosystem, there are no known hyperthermophilic phototrophs.⁵⁴ Bacteria with (bacterio)-chlorophyll containing photochemical reaction centers have been found within the Cyanobacteria, Chlorobi, Proteobacteria, Chloroflexi and Firmicutes;¹¹¹ the few currently known thermophilic anaerobic phototrophs are found within the latter three of the above phyla. *Thermochromatium tepidum*, of the γ -Proteobacteria clade (Chromatiaceae {B02}), is an anaerobe with T_{\max} 57°C and T_{opt} 48°C–50°C and is one of the very few thermophiles capable of anaerobic photoautotrophic growth.^{113,114} *T. tepidum* is also capable of assimilating compounds such as pyruvate and is, therefore, also a photoheterotroph.^{113,114} Four filamentous, gliding, moderately photoheterotrophic thermophilic facultative aerobes, *Roseiflexus castenholzii*,¹¹⁵ *Chloroflexus aggregans*,¹¹⁶ *Chloroflexus aurantiacus*,¹¹⁷ and *Heliobacterium oregonensis*,^{118,119} are found within the Chloroflexaceae {B29}. *R. castenholzii*, *C. aggregans*, and *C. aurantiacus* have a unique metabolic strategy as they grow photoheterotrophically under anaerobic conditions with available light, but also grow chemoorganotrophically under aerobic light or dark conditions.^{115–117} Within the phylum Firmicutes (family Heliobacteriaceae {B13}), *Heliobacterium modesticaldum* is an obligately anaerobic photoheterotroph that is also capable of growing chemoorganoheterotrophically.¹²⁰ *H. modesticaldum* is among the most recently discovered taxa containing (bacterio)-chlorophyll photochemical reaction centers; however, at present, it is poorly characterized.¹¹¹

Although thermophilic anaerobes are most often studied as axenic cultures—as this is a requirement for the valid publication of any prokaryotic taxon—some intriguing relationships have been observed for microorganisms with this physiology growing in co-culture. For example, in pure culture, the previously mentioned taxon *T. lipolytica* cannot use triacylglycerols or short- and long-chain fatty acids; but when grown in syntrophic co-culture with *Methanobacterium* strain JW/VS-M29, *T. lipolytica* grows on triacylglycerols and linear saturated and unsaturated fatty acids with 4 to 18 carbon atoms.⁹⁵ Many Archaea were initially described as being obligately dependent on S^0 reduction for the production of energy.⁶¹ However, Bonch-Osmolovskaya and Stetter showed that some so-called “sulfur-dependent” Archaea grow well in co-culture with hydrogen-using thermophilic methanogens in the absence of sulfur. This is possible through interspecies hydrogen transfer, whereby growth-inhibiting hydrogen (from H^+ used as an electron acceptor) is removed without sulfur serving as the electron acceptor.¹²¹ The *Ignicoccus*–“*Nanoarchaeum*” system has been described as a symbiotic relationship. It was discovered that small cocci were attached to the larger cells of a strain of *Ignicoccus* isolated from the Kolbeinsey Ridge, north of Iceland. These tiny cocci could be isolated from the larger cells and subsequently studied, but grew only when attached to their host.¹²² The genome sequence analysis of “*Nanoarchaeum*” showed that it is missing most of the enzymes required for nonparasitic growth.¹²³

The importance of sulfur in the metabolism of thermophilic anaerobes becomes evident when one considers that a majority of thermophiles (chemolithotrophs, as well as chemoheterotrophs) take advantage of the sulfur redox system. Amend and Shock posit that the most common energy-yielding reaction may be the reduction of elemental sulfur: $H_2 + S^0 \rightarrow H_2S$.⁵⁴ Indeed, the diversity of known thermophilic anaerobic taxa that use this strategy is notable: the sulfur-reducing reaction has been reported within the Pyrodictiaceae {A02}, Sulfolobaceae {A03}, Thermoanaerobacteriaceae {B09}, Thermoproteaceae {A05}, Aquificaceae {B032}, Desulfurellaceae {B16}, Desulfurococcaceae {A01}, Thermococcaceae {A08}, Thermoplasmataceae {A06}, Thermofilaceae {A04}, and Thermotogaceae {B34}. Thermophilic, sulfate-reducing Bacteria have been isolated from a wide range of environments and many of these thermophiles belong to a phylogenetically coherent cluster of Gram-type positive, spore-forming *Desulfotomaculum* species of the Firmicutes (Peptococcaceae {B11}).^{124,125} Thus, the role of sulfur in the metabolisms of thermophilic anaerobes can vary for different groups:

it can be reduced, it can serve as an electron sink during fermentation, and it can function as a terminal electron acceptor to allow sulfur respiration.¹²⁶

Thermophilic anaerobic Fe(III)-reducing Bacteria and Archaea are found within nearly all thermobiotic environments and are usually respirationally diverse, capable of growing chemoorganotrophically with fermentable substrates or chemolithoautotrophically with molecular hydrogen.^{102,127,128} Although only relatively recently described, a diverse set of thermophilic anaerobes are known to reduce Fe(III). Families of the Bacteria with taxa known to reduce Fe(III) include the *Bacillaceae* {B15}, *Peptococcaceae* {B11}, *Thermoanaerobacteriaceae* {B09}, *Acidaminococcaceae* {B10}, *Syntrophomonadaceae* {B12}, *Deferribacteraceae* {B19}, *Hydrogenothermaceae* {B33}, *Thermotogaceae* {B34}, and the *Thermodesulfobacteriaceae* {B20}. Families of the Archaea with taxa known to reduce Fe(III) include the *Thermoproteaceae* {A05}, *Archaeoglobaceae* {A09}, and the *Thermococcaceae* {A08}.¹²⁸ *Geoglobus ahangari*, of the *Archaeoglobaceae* {A09} was reported as the first dissimilatory Fe(III)-reducing prokaryote obligately growing autotrophically on hydrogen.¹²⁹ In some genera, such as *Thermoanaerobacter*, *Thermotoga*, and *Anaerobranca*, many of the species tested have been found to be capable of dissimilatory reduction of Fe(III), but overall it appears as though the ability to reduce Fe(III) does not correlate to an affiliation at the genus, or sometimes even at the species, level.¹²⁸ For example, although *Deferribacter abyssi* and *Deferribacter thermophilus* are closely related, having 98.1% 16S rRNA gene sequence similarity, *D. abyssi* is unable to reduce Fe(III) whereas it is a primary electron acceptor for *D. thermophilus*.^{130,131} Also, *Thermolithobacter ferrireducens* and *Thermolithobacter carboxydvorans* have 99% 16S rRNA gene sequence similarity to each other; however, *T. ferrireducens* is able to reduce Fe(III) but cannot assimilate CO, whereas *T. carboxydvorans* is able to assimilate CO but cannot reduce Fe(III).⁹⁹

Besides Fe(III), the reduction of other metals coupled to the generation of energy by thermophilic anaerobes includes Mn(IV)—which is known to be used by *Acidianus infernus*,¹³² *Thermoanaerobacter siderophilus*,¹³³ *Thermovibrio parvulus*,¹³⁴ and *D. thermophilus*¹³⁰—as well as Mo(VI), which is used by *Acidianus brierleyi*.¹³⁵ *Pyrobaculum arsenaticum* has the ability to grow chemolithoautotrophically by arsenate reduction, and both *P. arsenaticum* and *Pyrobaculum aerophilum* can use selenate, selenite, or arsenate chemolithoorganotrophically.¹³⁷ Thermophilic anaerobes are also known to reduce a number of other metals, possibly as a detoxification mechanism; for example, *Thermoanaerobacter* strains isolated from Piceance Basin in Colorado were

able to reduce Co(III), Cr(VI), and U(VI), in addition to Mn(IV) and Fe(III).¹³⁶

Unique Physiological Adaptations

In addition to these described characteristics—O₂-relationship, temperature and pH profiles, and metabolic strategies—a number of additional physiological properties of thermophilic anaerobes should be examined and should, thereby, add to what is known about the diversity of thermophilic anaerobes. Nakagawa and Takai recently gave a detailed overview of the metabolic types isolated from deep-sea hydrothermal vents; therefore, these metabolic types are not further discussed here.¹³⁸ The NaCl optimum and tolerance of a prokaryote is often assessed. Thermophilic anaerobes of marine origin, for example, would be expected to grow best at marine salinity—around 3.5% (wt/vol) NaCl. Prokaryotes that grow optimally with high salinity are referred to as halophiles, and halophilic thermophilic anaerobes are known, as are halophilic alkalithermophiles, which are further discussed in the chapter by Mesbah and Wiegel within this volume.

Thermophilic anaerobes living at deep-sea hydrothermal vent sites must cope with the additional pressure exerted by the water column and are, therefore, piezotolerant or perhaps even piezophilic. Both *Methanocaldococcus* (basonym *Methanococcus*) *jannaschii*, isolated from the 21°N East Pacific Rise deep-sea hydrothermal vent site, and *Thermococcus barophilus*, obtained from the Snakepit region of the Mid-Atlantic Ridge, grow faster under increased hydrostatic pressure.^{139,140} At its optimal growth temperature, the growth rate of *T. barophilus* was more than doubled at elevated hydrostatic pressure (40 MPa) compared with the growth rate at low pressure (0.3 MPa).¹⁴⁰ Furthermore, *T. barophilus*, as well as “*Pyrococcus abyssi*” and *Pyrococcus* strain ES4, isolated from deep-sea hydrothermal vent sites, show an extension of their T_{\max} with elevated hydrostatic pressure.^{140–142} Takai reported at the Thermophiles 2007 Meeting that under hydrostatic conditions, an H₂/CO₂-utilizing, methanogenic, *Methanopyrus kandleri*-like isolate was able to grow at 122°C, thus representing the new maximum temperature for sustaining life (i.e., for growing and multiplying).⁶

Some of the isolated thermophilic anaerobes also possess ionizing radiation resistance; for example, this characteristic is found in *Tepidimicrobium ferriphilum* (family *Clostridiaceae* {B14}), which was isolated from a freshwater hot spring within the Barguzin Valley,

Buryatiya, Russia.¹⁴⁶ The level of natural radioactivity at hydrothermal vents can be 100 times greater than that at Earth's surface because of the increased occurrence of elements, such as ²¹⁰Pb, ²¹⁰Po, and ²²²Rn.^{143,144} Indeed, Archaea of the family Thermococcaceae {A08}, *Thermococcus gammatolerans* and “*Thermococcus radiotolerans*” isolated from the Guaymas Basin, of the Gulf of California, and “*Thermococcus marinus*,” isolated from the Snakepit hydrothermal site of the Mid-Atlantic Ridge have γ -irradiation resistance.^{143,145}

Concluding Remarks

More than 300 species of thermophilic anaerobes have been described (TABLE 1). Many of the prokaryotes with this physiology were isolated from natural thermobiotic environments, such as terrestrial hot springs, deep-sea hydrothermal vents, and subsurface environments. Thermophilic anaerobes have also been isolated from anthropogenically heated environments, as well as from mesobiotic environments, such as rivers and lake sediments, and even psychrobiotic environments. The thermophilic anaerobes are metabolically diverse; a majority of isolated taxa are chemoorganoheterotrophic, although it is doubtful that this reflects the ecological situation in most thermobiotic environments. The examples of the phylogenetic and physiological diversity of thermophilic anaerobes given herein are certainly not exhaustive. Besides the diversity found so far, there are physiological types among mesophiles and potentially as-yet unknown or only superficially described physiologies for which no thermophiles have been isolated, probably because of a lack of serious isolation attempts. Thus, the authors believe that additional novel thermophilic anaerobes with unique and exciting properties will undoubtedly be isolated, especially considering the small percentage of assumed existing prokaryotes on Earth that have been described.⁴¹⁶

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Conflict of Interest

The authors declare no conflicts of interest.

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