

Extremophiles: from abyssal to terrestrial ecosystems and possibly beyond

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Abstract The anthropocentric term “extremophile” was introduced more than 30 years ago to describe any organism capable of living and growing under extreme conditions—i.e., particularly hostile to human and to the majority of the known microorganisms as far as temperature, pH, and salinity parameters are concerned. With the further development of studies on microbial ecology and taxonomy, more “extreme” environments were found and more extremophiles were described. Today, many different extremophiles have been isolated from habitats characterized by hydrostatic pressure, aridity, radiations, elevated temperatures, extreme pH values, high salt concentrations, and high solvent/metal concentrations, and it is well documented that these microorganisms are capable of thriving under extreme conditions better than any other organism living on Earth. Extremophiles have also been investigated as far as the search for life in other planets is concerned and even to evaluate the hypothesis that life on Earth came originally from space. Extremophiles are interesting for basic and applied sciences. Particularly fascinating are their structural and physiological features allowing them to stand extremely selective environmental conditions. These properties are often due to specific biomolecules (DNA, lipids, enzymes, osmolites, etc.) that

have been studied for years as novel sources for biotechnological applications. In some cases (DNA polymerase, thermostable enzymes), the search was successful and the final application was achieved, but certainly further exploitations are next to come.

Keywords Extremophilic microorganisms · Extreme environments · Taxonomy · Physiology · Application

Introduction

The majority of “higher” organisms live under conventional conditions, that is, they grow and thrive under conditions of moderate temperature, pH, salinity, water availability, oxygen levels, pressure, and carbon and energy availability. These parameters, i.e., what defines moderate, are anthropocentric, clustering around temperature 37 °C, pH 7.4, salinity from 0.9% to 3%, and 1 atm pressure and represent the ideal conditions for growing *Escherichia coli* as well as those conditions which are comfortable for human beings. Formerly, these conditions were referred to as “normal” or “physiologic”, but particularly over the last century, exploration of other environments has shown that a large number of organisms live under, or actually require, more “extreme” conditions, i.e., conditions hostile to humans and most of their microbial commensals (Grant 1988; Aguilar 1996; Aguilar et al. 1998; Antranikian et al. 2005).

MacElroy coined the term “extremophile” in 1974 to describe these organisms, and while containing some protozoal, algal, and fungal species, the majority of extremophiles are prokaryotic (MacElroy 1974). “As conditions become more demanding, extreme environments become exclusively populated by prokaryotes” (Horikoshi 1998). While improved or more avid culture techniques are responsible for

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the isolation of some of these species, the initiative to look into environments formerly considered uninhabitable, and the development of technology necessary for these activities, has allowed isolation of many more. Any environment is likely to contain living organisms—one just has to know how to recognize their presence. One example of this is the Dead Sea, thought to be lifeless, but actually containing quite a variety of exciting prokaryotic (Arahal et al. 2000) and even eukaryotic (Buchalo et al. 1998) life forms.

Aside from intellectual curiosity, interest in studying extremophiles stems from their possible utility in industrial processes, their possible links to the origins of life on this planet, and possible clues as to how and where to look for extraterrestrial life (Stetter 1996; Shock 1997; Litchfield 1998; Wiegel and Adams 1998; Javaux 2006; Lentzen and Schwarz 2006; Villar and Edwards 2006). Some examples of industrial applications of extremophiles are shown in Table 1.

Extremophiles may be divided into two broad categories: true (obligate) extremophiles which require one or more extreme conditions in order to grow and multiply and facultative extremophiles which can tolerate quite well conditions which are toxic and/or lethal to the overwhelming

majority of living organisms, though growing optimally at “normal” conditions. Presently, some orders or genera contain only extremophiles, whereas other orders or genera contain both extremophiles and non-extremophiles; however, with constantly novel organisms identified and the assumptions that we have identified less than 2% of the assumed existing microorganisms, this division may change frequently. In some cases, it is assumed that extremophiles are phylogenetically the older ones (e.g., thermophilic *Clostridia*), whereas in other instances, the extremophiles are assumed to be secondary adaptations (Wiegel and Adams 1998). Extremophiles are best characterized by the minimum, maximum, and optimum parameters of the extreme condition for growth, i.e., the T_{\min} , T_{opt} , and T_{\max} for thermophiles. This review will discuss the various categories of extremophilic prokaryotes and explore their habitats, biochemistry, interesting cellular processes or products, and possible scientific and practical uses. Of course morphological investigations have always been important issues as far as the characterization of extremophiles is concerned (Fig. 1), but they will not be discussed here; the same for the specific description of different extreme environments (examples in Figs. 2 and 3) that will be mentioned but not in detail.

Table 1 Biotechnological applications of major groups of extremophiles

| Extremophilic organisms | Enzymes and organic compounds | Applications and products |
|--|-------------------------------|---|
| Thermophiles and hyperthermophiles (T_{opt} 55–105 °C) | Amylases | Glucose, fructose for sweeteners |
| | Xylanases | Paper bleaching |
| | Proteases | Amino acid production from keratins, food processing, baking, brewing, detergents |
| | DNA polymerases | Genetic engineering |
| Psychrophiles and psychrotolerants ($T_{\text{opt}} < 20$ °C) | Neutral proteases | Cheese maturation, dairy production |
| | Proteases | Polymer-degrading additives in detergents |
| | Amylases | |
| | Lipases | |
| Acidophiles ($\text{pH}_{\text{opt}} < 3$) | Polyunsaturated fatty acids | Pharmaceuticals |
| | Dehydrogenases | Biosensors |
| Alkaliphiles ($\text{pH}_{\text{opt}} > 8.5$) | Sulfur oxidation | Desulfurization of coal, biomining of ores |
| | Cellulases | Polymer-degrading additives in detergents |
| | Proteases | |
| | Amylases | |
| | Lipases | |
| | Cyclodextrines | Stabilization of volatile substances |
| | Antibiotics | Pharmaceuticals |
| Halophiles (growing with 3–20% salt) | Carotene | Food coloring |
| | Glycerol | Pharmaceuticals |
| | Compatible solutes | Pharmaceuticals |
| | Membranes | Surfactants for pharmaceuticals |

References: Wiegel and Ljungdahl (1996), Canganella and Wiegel (1993), Salameh and Wiegel (2007), Canganella et al. (1995), Aguilar et al. (1998), Sellek and Chaudhuri (1999), Lentzen and Schwarz (2006), Antranikian et al. (2005), Rawlings and Johnson (2007), Tiquia and Mormile (2010)

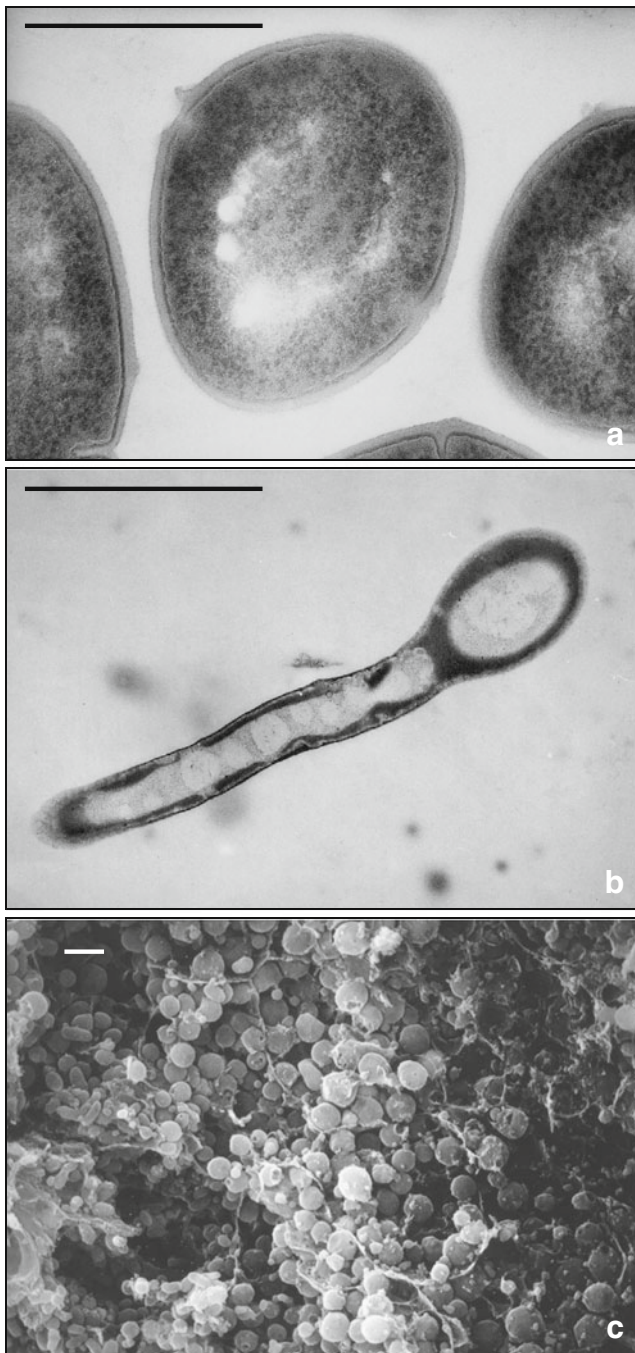


Fig. 1 Electromicroscopic pictures showing different extremophiles that have been studied in environment at elevated temperatures: **a** *Thermococcus guaymasensis*, **b** *Clostridium thermobutyricum*, **c** syntrophic bacteria of *Riftia pachyptilia* (courtesy by CM Cavanaugh). Scale bar 1 μm

Extremes of temperature

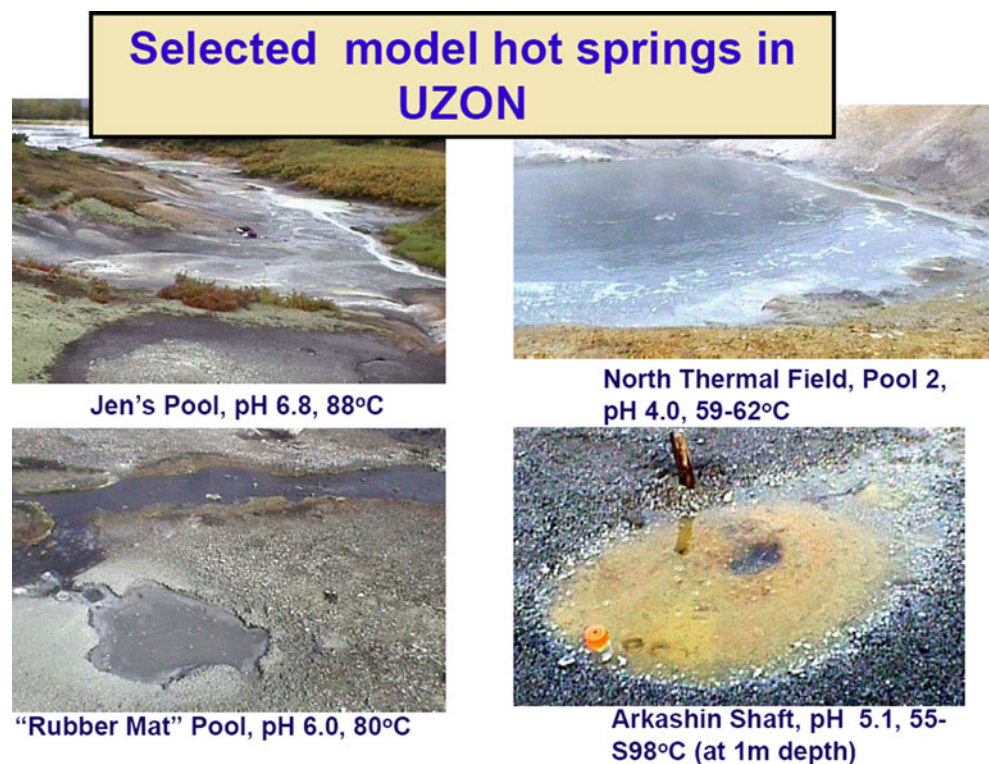
Mesophiles usually thrive in a temperature range of about 7–10 °C to 35–42 °C, with thermophiles and psychrophiles growing optimally in higher and lower temperature ranges, respectively. An organism is classified as “tolerant” to



Fig. 2 Some environments where extremophiles can be isolated: **a** a power plant in Iceland, **b** the salt desert of Atacama (Chile), **c** deep-sea hydrothermal vents at Okinawa Trough (Japan)

extreme temperatures if it has its temperature optimum for growth in the mesophilic range but is able to grow and multiply in extreme temperatures as well and considered “-philic” if it requires the elevated or lowered temperature to grow and divide, with the optimal and maximal cardinal temperature parameters outside the mesophilic range. For example, a bacterium which is able to grow at 60 °C, but also able to grow at 30 °C, with an optimum at 37 °C, should be considered thermotolerant, while a bacterium which grows optimally at 60 °C, but not below 45 °C, and

Fig. 3 Examples of model hot springs in Uzon caldera, Kamchatka, Russia



with a maximum temperature approximately 70 °C is a thermophile. For organisms which grow optimally in the thermophilic range, e.g., $T_{\text{opt}}=65^{\circ}\text{C}$, but have extended temperature ranges for growth below 45 °C, e.g., $T_{\text{min}}=3^{\circ}\text{C}$ (i.e., exhibiting a temperature span for growth of 35 °C or more), Wiegel has coined the term “temperature-tolerant thermophile” (Wiegel 1990). Extreme thermophiles are those able to grow above 70 °C and have a T_{opt} above 60 °C, whereas hyperthermophiles have a T_{opt} at and above 80 °C and frequently can grow above 100 °C; the highest temperature maximum so far observed is 121 °C. The terms “obligate psychrophile” or “obligate thermophile” are sometimes used, but are actually redundant.

Biotechnological applications of psychrophiles and psychrotolerant organisms were mainly focused on enzymes, which include detergent additives for cold water washing (more eco-friendly and accessible than hot water washing) and cellulases for fabric processing, such as reducing “pilling” of garments. The cold-adapted enzymes excise protruding cotton fiber ends from garments without decreasing the strength and durability of the garment because they are less resistant to subsequent inactivation than currently used enzymes (Gerday et al. 1997; Evangelista et al. 2009; Matsuo et al. 2010). Cold-adapted enzymes are useful in the food industry for food modifications (Sproessler 1993) and in bioremediation (Margesin and Schinner 1998; Lettinga et al. 1999).

Thermophiles are also interesting from the viewpoint of the trend toward biotechnology—many chemical industrial

processes employ high temperatures, which would have to be lowered in order to use bioprocesses from mesophiles, and this could be avoided using enzymes from thermophiles (Canganella and Wiegel 1993; Huber and Stetter 1998; Bustard et al. 2000; Hong et al. 2009; Kumar et al. 2009; Zhong et al. 2009). Research into thermophilic microorganisms has demonstrated that thermotolerant proteins are generally more stable than other proteins and retain this property when cloned and expressed in mesophilic bacteria (Connaris et al. 1998; Hayakawa et al. 2009).

Psychrophiles

Definitions A psychrophilic prokaryote is defined by a temperature optimum for growth of $<15^{\circ}\text{C}$, with no growth above 20 °C, while those prokaryotes with temperature optima for growth $>20^{\circ}\text{C}$, but able to grow well below 5 °C, are designated as psychrotolerant. Bowman et al. (1997) used the term psychrotroph; however, this wrong term (translating to “eating cold”) is outdated and should not be used anymore despite being used in older literature. Psychrophiles are likely more abundant than one assumed—some are difficult to culture. With no doubt, recent investigation into naturally cold habitats has produced numerous culturable bacterial and archaeal species with temperature optima between 4 °C and 15 °C, as well as evidence for more novel taxa coming from genetic probes and metabolic studies of non-cultured species living under

these conditions. Some microorganisms are reported to grow at temperatures as low as $-20\text{ }^{\circ}\text{C}$. However, little reproduced and confirmed data on pure cultures are available at this time; thus, the question about the lowest growth temperature has no answer yet.

Habitats Over 80% of the total biosphere of the Earth has permanent temperatures of $<5\text{ }^{\circ}\text{C}$ (Cavicchioli and Thomas 2000). Cold environments include permafrost, rocks in very cold regions, Arctic or Antarctic ice, permanently cold sea water of polar regions, abyssal sea or fresh water, permanently cold marine (e.g., $-2\text{ }^{\circ}\text{C}$ in Antarctic waters), or freshwater sediments, deep rock aquifers, and the bodies of coldblooded higher organisms tolerant to low-temperature environments. There are algal and fungal species which live in this habitat as well, and prokaryotes may be seen in assemblages with these, especially diatoms (Staley and Gosink 1999). Of course, there are man-made cold habitats, thanks to refrigeration technology, and the study of psychrophiles improves our ability to rid these habitats of microbial contamination, i.e., refrigerator mold or bacteria in milk-holding tanks. With some exceptions, most psychrophiles live in environments with abundant nutrients, possibly because the affinities of uptake and transport systems diminish with decreasing ambient temperatures.

Organisms Psychrophilic archaea include methanogenic *Methanococcoides burtonii* and *Methanogenium frigidum*, as well as the extreme halophilic *Halorubrum lacusprofundi*; moreover, *Cenarchaeum symbiosum* is an archaeon isolated from a marine sponge. Gram-type negative psychrophiles are more numerous than taxa belonging to the phyla Firmicutes and Actinobacteria (formerly called low and high G + C Gram-type positives) and include species of *Pseudomonas*, *Achromobacter*, *Flavobacterium*, *Alcaligenes*, *Cytophaga*, *Cellulophaga* (including *Cellulophaga baltica* and *Cellulophaga fucicola*), *Aeromonas*, *Vibrio*, *Serratia*, *Escherichia*, *Proteus*, *Psychroflexus*, *Psychromonas*, and *Psychrobacter* (i.e., *Psychrobacter pacificensis*, isolated from the Japan Trench—Maruyama et al. 2000). As an example, *Psychromonas antarctica* is an aerotolerant, halophilic anaerobe which grows optimally at $12\text{ }^{\circ}\text{C}$ with a NaCl concentration of 3% (Mountfort et al. 1998). The psychrophiles belonging to the phyla Firmicutes and Actinobacterium include members of the genera *Bacillus*, *Clostridium*, *Arthrobacter*, and *Micrococcus* and relatively new genera within the actinomycetes, respectively. *Bacillus marinus* contains one strain with a T_{\max} of $4\text{ }^{\circ}\text{C}$ (Ruger et al. 2000), while *Clostridium vincentii* grows optimally at $12\text{ }^{\circ}\text{C}$ with a T_{\min} of $2\text{ }^{\circ}\text{C}$ and a T_{\max} of $20\text{ }^{\circ}\text{C}$ and is unable to survive at temperatures above $25\text{ }^{\circ}\text{C}$ for more than 20 h (Mountfort et al. 1997). The actinomycete

Frigoribacterium faeni has a T_{opt} ranging from $2\text{ }^{\circ}\text{C}$ to $10\text{ }^{\circ}\text{C}$, but it was adapted to growth up to $20\text{ }^{\circ}\text{C}$ (Kampfer et al. 2000), while *Modestobacter multiseptatus* grows from $0\text{ }^{\circ}\text{C}$ to $20\text{ }^{\circ}\text{C}$ (Mevs et al. 2000). Discovered species of psychrophiles also include the Arctic bacteria *Marinobacter psychrophilus*, *Phaeobacter arcticus*, and *Moritella dasa-nensis* (Kim et al. 2008; Zhang et al. 2008a, b); the Antarctic bacteria *Maribacter antarcticus*, *Sporosarcina antarctica*, and *Exiguobacterium soli* (Chaturvedi et al. 2008; Yu et al. 2008; Zhang et al. 2009); and the methanol-utilizing methanogen *Methanolobus psychrophilus* (Zhang et al. 2008c). There are even numerous examples of cold-adapted yeast and fungi (*Candida* and *Torulopsis* species as well as some *Penicillium* and *Aspergillus* species and others), and peculiar isolates were described such as the yeasts *Mrakiella cryoconiti* and *Rhodotorula himalayensis* (Margesin and Fell 2008; Shivaji et al. 2008). Moreover, the most common snow alga is *Chlamydomonas nivalis*, which produces dramatic red spores and can give alpine snow the frequently observed pink/reddish color.

Cold adaptation Much research has focused on the molecular basis for cold adaptation of psychrophilic proteins, enzymes, and lipids (Alimenti et al. 2009; Chiuri et al. 2009; Cotugno et al. 2009; Kundu and Roy 2009; Rossi et al. 2009). Important alterations were already detected a decade ago in membrane lipids, although variations occur but generally an increase of unsaturated bonds in the fatty acid allows continued fluidity at extremely low temperatures. Also observed were structural changes in proteins, e.g., leading to less side chain interactions, which allow enzymes to function in environments with extremely low kinetic energy (Gerday et al. 1997). The relation of the cold-shock response (which is encountered in psychrophiles as well as mesophiles) to cold adaptation has also been studied (Russell 1997; Ray et al. 1998), particularly as far as regulatory molecular processes and configuration of proteins are concerned. As a group, psychrophiles exhibit a diversity of metabolism as shown for a complex cyanobacterial–bacterial community conducting photosynthesis as well as nitrogen fixation in the ice cover of an Antarctic lake (Paerl and Priscu 1998), methanogenic archaea and acetogenic bacteria located in deep rock groundwater (Kotelnikova and Pedersen 1997), and sulfate reducers from cold oligotrophic lakes and other cold habitats (Sass et al. 1998; Knoblauch et al. 1999).

Thermophiles

Definitions Thermophilic prokaryotes were previously categorized as those whose optimum temperature for growth was between $45\text{ }^{\circ}\text{C}$ and $80\text{ }^{\circ}\text{C}$ (reiterated in Cavicchioli and

Thomas 2000). However, with the development of proper techniques of cultivation, prokaryotes growing at up to 113 °C (*Pyrolobus fumarii*)—and above under elevated hydrostatic pressure—have been characterized from black “smoker” chimneys in deep ocean thermal vent environments (Stetter 1996). This author divided the organisms into hyperthermophiles ($T_{\text{opt}} > \text{ or } = 80$ °C), extreme thermophiles (T_{opt} 70 °C to 80 °C), and moderate thermophiles (T_{opt} 45 °C to 70 °C), these being the generally adapted definitions (Mesbah and Wiegel 2008; Wagner and Wiegel 2008). Other classifications have been proposed in the past (e.g., Wiegel and Ljungdahl 1996; Wiegel 1992), but should not be used anymore. One exception is the use of the term “temperature-tolerant (extreme/hyper) thermophiles” for thermophiles growing over an extended growth span of more than 35 °C (Wiegel 1990).

Habitats The naturally hot environments on Earth range from terrestrial volcanic sites (including solfataras) with temperatures slightly above ambient to submarine hydrothermal systems (sediments, submarine volcanoes, fumaroles, and vents) with temperatures exceeding 300 °C, subterranean sites such as oil reserves, and solar-heated surface soils with temperatures up to 65 °C. There are also human-made hot environments such as compost piles (usually around 60–70 °C but as high as 100 °C), slag heaps, industrial processes, and water heaters (Oshima and Moriya 2008). The deep sea is in general cold, but it is now known that there are areas of superheated water and widespread still-hot volcanic ocean crust beneath the flanks of the mid-ocean ridge and other rock structures, as well as geothermally heated shallower ocean waters. Many environments are temporarily hot, adaptation to which may be the reason that some thermophiles are very fast growing. Among the geothermally heated habitats are the alkaline, mainly carbonate-containing hot springs around neutral pH and acidic areas including some mud holes. Most of the acidic high-temperature habitats contain elemental sulfur and metal sulfides, and most isolates from these areas metabolize sulfur by either anaerobic respiration or fermentation. Ocean depths are under extreme pressures from the weight of the water column, and thus, most isolates from these areas are piezotolerant, some are truly piezophilic, others such as *Pyrococcus* strain ES4 and *Methanococcus kandleri* show extensions of T_{max} under increased pressure (Pledger et al. 1994; Summit et al. 1998, Takai et al. 2008), and all are at least halotolerant (Adams 1999), while those isolated from solfataras are generally acidophilic. While most described species of obligately aerobic thermophilic archaea are acidophilic, the anaerobic thermophilic bacteria are generally unable to grow at acidic pH, but many anaerobic bacteria and some archaea grow at alkaline pH

(Wiegel 1998). The anaerobic alkali thermophilic bacteria thus form an interesting group to study and their relationships between temperature optimum and pH optimum for growth are presented in Fig. 4. This adaptability to high pH environments involves both cellular and biomolecular peculiar traits that are currently under investigation, particularly to exploit their potential applications.

Hyperthermophiles

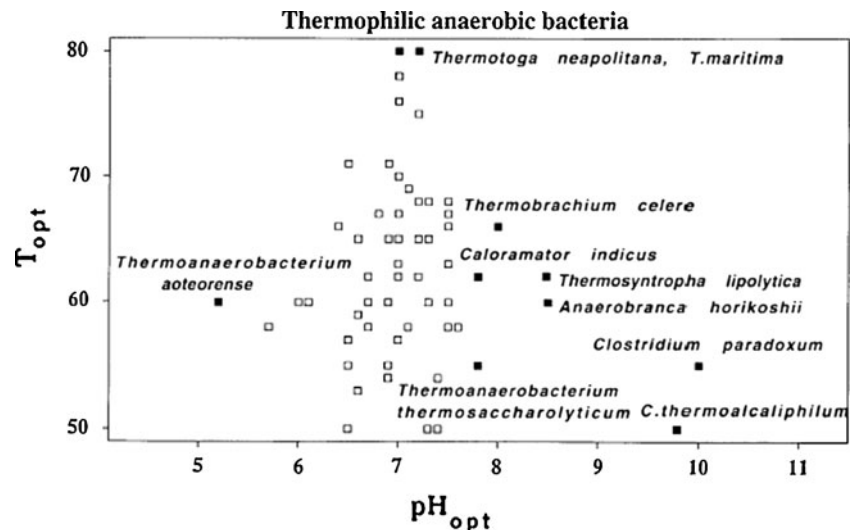
Most of the hyperthermophilic organisms are archaea, and many of these perform common metabolic processes such as methanogenesis; anaerobic respiration via sulfate reduction, sulfur reduction, nitrate reduction, iron reduction, etc.; aerobic respiration; or even fermentation. *P. fumarii* had for a long time the highest T_{max} (113 °C), a T_{opt} of 106 °C, being unable to grow below 90 °C. However, the record is held by *M. kandleri* strain isolated from the deep ocean near Japan with a T_{max} of 122 °C under high atmospheric pressure (Takai et al. 2008). The discovery of deep-sea hydrothermal vents in 1977 opened the way for the first study of an ecosystem based on primary production of chemosynthetic extreme and hyperthermophilic bacteria (Prieur et al. 1995). Representative genera include *Archaeoglobus*, *Thermoplasma*, *Thermoproteus*, *Acidianus*, *Pyrococcus*, *Thermococcus*, and *Desulfurococcus*, which reduce sulfur or sulfate; *Sulfolobus*, which can oxidize H₂S or elemental sulfur; the methanogens *Methanothermobacter*, *Methanococcus*, and *Methanopyrus*; and the nitrate reducers *Pyrobaculum* and *Pyrolobus*. *Sulfolobus* and *Acidianus* isolates can also oxidize ferrous iron and with no doubt such a process plays a major role in the local environment and biogeochemical cycles. Examples of hyperthermophilic bacteria are included in the genera *Thermotoga* and *Aquifex*.

A great novelty was represented by the first description of *Nanoarchaea* (Vainshtein and Kudryashova 2000; Branciamore et al. 2008; Podar et al. 2008; Burghardt et al. 2009) and these microorganisms have drawn the attention of deep-sea hydrothermal vent investigators. A work describing the colonization of nascent, deep-sea hydrothermal vents by novel archaeal and nanoarchaeal assemblages was reported by McCliment et al. (2006).

Extreme and moderate thermophiles

Extreme thermophiles as bacteria include the anaerobic Firmicutes, the cellulolytic *Caldicellulosiruptor saccharolyticus* (Rainey et al. 1994), the ethanol-producing *Thermoanaerobacterium ethanolicus* (Wiegel 1992; Wiegel and Ljungdahl 1996), as well as the acetogenic facultative chemolithoautotrophic *Thermoanaerobacterium kivui*

Fig. 4 Relationship between temperature optima and pH optima for growth of representative anaerobic thermophilic bacteria. Note that the most acidic pH_{opt} is only in the acidotolerant range, while there are several alkaliphiles (from Wiegel 1998)



(Leigh and Wolfe 1983) and *Ammonifex degensii*, the latter being capable of forming ammonium from nitrate via chemolithoautotrophic growth (Huber et al. 1996). Among the aerobic ones are the well-known *Bacillus stearothermophilus* (Firmicutes) and some species within the Gram-type negative genus *Thermus* which can be isolated from hot water boilers. Recently novel thermophilic species were described, interesting for both basic and applied scientific issues: the citrate-fermenting *Sporolituus thermophilus* (Ogg and Patel 2009), the novel bacterial phylum *Caldiseria* (Mori et al. 2009), the deep-sea bacterium *Nautilia abyssi* (Alain et al. 2009), the thermal mud-inhabiting *Anoxibacillus thermarum* (Poli et al. 2009), and the novel microaerophilic, nitrate- and nitrite-reducing thermophilic bacterium *Microaerobacter geothermalis* (Khelifi et al. 2010).

Among the moderate thermophiles and thermotolerant organisms are the cellulolytic *Clostridium thermocellum*, the acetogenic *Moorella thermoacetica/thermoautotrophica*, and *Thermoanaerobacterium* (former *Clostridium*) *thermosaccharolyticum*, capable of growing in vacuum-packed foods and thus known as the “can-swelling” organism (Kristjansson 1992; Wiegel and Canganella 2000; Prevost et al. 2010). The obligate mixotrophic *Thiomonas bhubaneswarensis*, the marine *Lutaonella thermophila*, the cellulolytic bacteria *Clostridium clariflavum* and *Clostridium caenicola*, the facultative microaerophilic *Caldinitratiruptor microaerophilus*, and a novel hydrogen-producing bacterium from buffalo dung were described (Arun et al. 2009; Panda et al. 2009; Shiratori et al. 2009; Fardeau et al. 2010; Romano et al. 2010). The last overview on anaerobic thermophiles and their main properties was published by Wagner and Wiegel (2008).

Evolutionary interest The hyperthermophilic organisms are contained in the deepest, least evolved branches of the

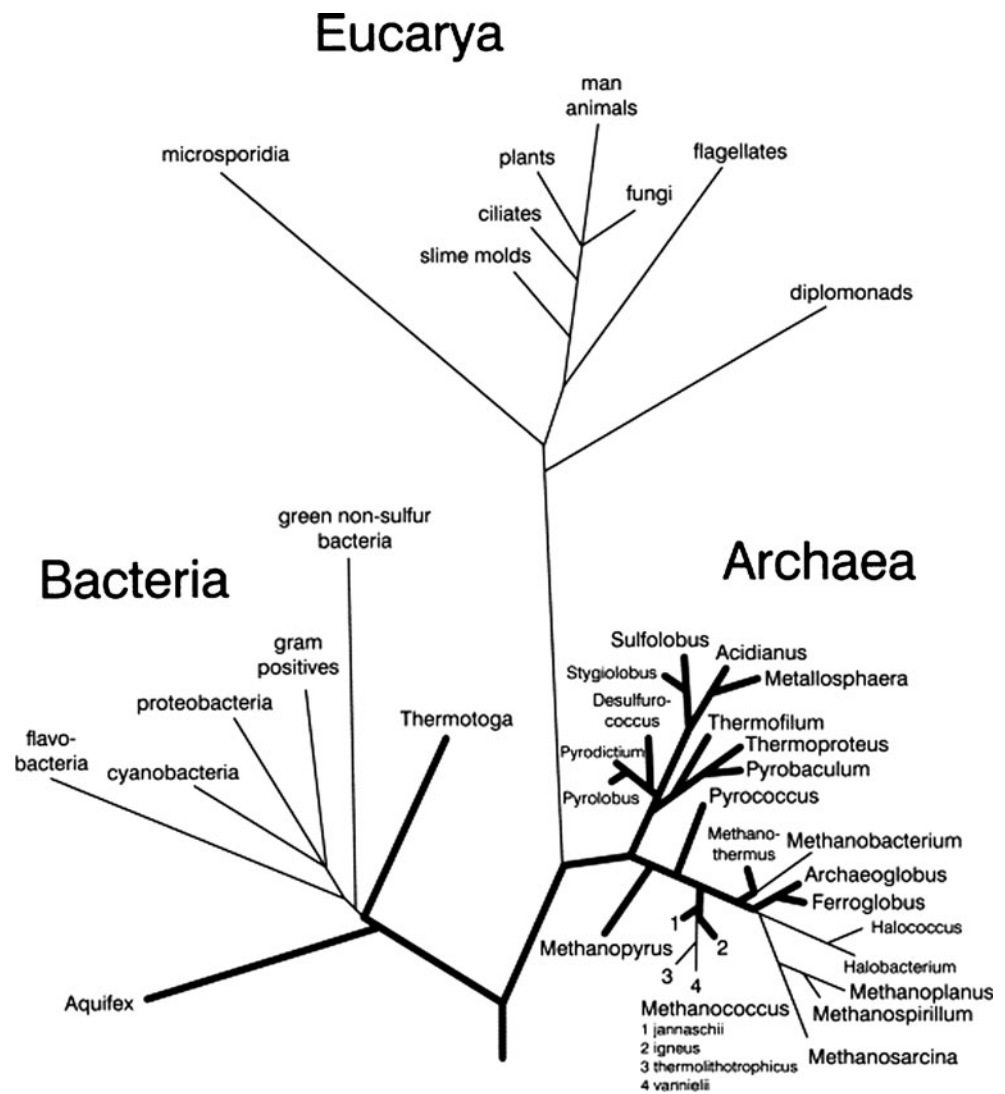
universal phylogenetic tree (Fig. 5), often use substrates which are thought to have been predominant in the primordial terrestrial makeup, and produce substances which predominate in the present geochemistry—indications that they could have been the first life forms on this planet (Wiegel and Adams 1998). This is possible and it is one reason why thermophiles are studied so extensively. The study into how they manage thermostability at the protein and membrane structural level has elucidated many traits of the protein, membrane, and nucleic acid structure; however, there is not yet a full understanding of the principles of thermostability (Daniel 1996; Vieille and Zeikus 2001; Basu and Sen 2009; Kim et al. 2009; Averhoff and Müller 2010). The development of better genetic tools for use with these organisms portends for more practical applications in the future (Bustard et al. 2000).

Extremes of pH

The cells of humans and of other “higher” life forms exist stably only within a narrow pH range, with a value around 7.4 often referred to as “physiologic”. Marine fish and invertebrates do best with an external pH range of 8.1–8.4, the pH of ocean water.

One might expect that microorganisms would require that the pH of the external medium conforms to an equally narrow or even narrower range of acidity or alkalinity, but this is not generally the case. Microorganisms are able to thrive in a wider range of pH than most human and other eukaryotic cells do, and some even require extremes on either the acidic or alkaline ends of the scale, without the ability to survive exposure to neutral pH. Obviously, many bacteria have been known for years to live in moderately

Fig. 5 Phylogenetic tree highlighting possible evolutionary relatedness of hyperthermophiles. From Huber and Stetter (1998), after Woese et al. (1990)



low pH, such as those which are used in food fermentations and do well at pH as low as 4.5 (Stiles and Holzappel 1997; Caplice and Fitzgerald 1999). However, in the past, it has been assumed that nothing could live at pH 0 or above pH 11, but now many species of bacteria and archaea are known which not only can live at these extremes but also require them (e.g., *Picrophilus* species can grow at pH 0 at 60 °C) as a result of evolutionary processes (Poli et al. 2007; Hou et al. 2008; Zhou et al. 2008; Johnson et al. 2009).

Research and development has been particularly focusing on the potential use of mesophilic and psychrophilic acidophiles for biomining such as tank leaching processes and heap leaching processes. Moreover, the application of moderately thermophilic and extremely thermophilic acidophiles for biomining and in the treatment of both refractory gold-bearing and base–metal mineral sulfide concentrates has also been extensively investigated (Johnson 1995; Das et al. 1999; Castro and

Moore 2000; Johnson 2001; Dopson et al. 2004; Rawlings and Johnson 2007; Johnson and Hallberg 2008; Cardenas et al. 2010; Dopson 2011). Some research activities regarded the problems of arsenic toxicity to certain strains of moderately thermophilic bacteria when oxidizing both refractory gold and base–metal sulfide concentrates. Other potential applications of thermophilic acidophiles are usually related to the mineral industry and in allied disciplines including treatment of metalliferous mine wastes, acid mine waters, and sulfurous gases.

Though earlier reports occurred on the isolation of alkaliphilic organisms from human and animal feces (Vedder 1934), the first systematic study of alkaliphilic prokaryotes was undertaken in the early 1970s, specifically to look for industrially useful enzymes (Horikoshi 1971). Indeed, alkaliphilic bacteria (able to grow above pH 10, with a pH_{opt} around 9, and unable to grow at pH 7 or less—Kumar and Takagi 1999) were used anonymously for centuries in processing dye from indigo plants, though

only cultured and isolated in the last century (Takahara and Tanabe 1960). This group of extremophiles is another example of potential usefulness, with alkaline proteases and cellulases adapted for use in laundry and other detergents (Horikoshi 1996), xylanases for use in the pulp/paper industry (Nakamura et al. 1993), and lipases in bioprocessing of lipids (Bornscheuer et al. 2002; Salameh and Wiegel 2007). Enzymes of alkaliphiles are also used for dehairing of hides in leather tanning, making of food additives, and drug manufacture. One particularly important industrial application has been the production of cyclodextrin for use in foodstuffs, chemicals, and pharmaceuticals, using alkaline cyclomalto-dextrin glucanotransferase (Horikoshi 1996); moreover, other possible applications are being explored for enzymes from these organisms (Asha Poorna and Prema 2007; Singh et al. 2008).

Acidophiles

Definitions It is generally accepted to define acidophilic organisms as those which can grow at pH values lower than 5 and showing pH optima between 2 and 4. The fact that microorganisms growing at pH values close to 0 have been described will certainly expand further the group of the so-called extremely acidophilic organisms.

Most acidophiles have evolved extremely efficient mechanisms to keep the cytoplasm at or near neutral pH, and several processes are associated with pH homeostasis in acidophiles (Johnson 1998; Booth 1985; Dopson et al. 2004; Baker-Austin and Dopson 2007): (1) Acidophiles reverse the reversed membrane potential to partially deflect the inward flow of protons. One potential mechanism of generating a reversed membrane potential is by potassium transport—a predominance of potassium-transporting ATPases is found in acidophile genomes. (2) Many acidophiles have evolved highly impermeable cell membranes to retard the influx of protons into the cell. (3) Δ pH is maintained through active proton export by transporters. (4) The sequencing of several acidophile genome sequences has indicated that there is a higher proportion of secondary transporters than in neutralophiles. Overall, they reduce the energy demands associated with pumping necessary solutes and nutrients into the cell. (5) The presence and availability of enzymes and/or chemicals capable of binding and sequestering protons might help maintain pH homeostasis. (6) Comparative genome analysis suggests that a larger proportion of DNA and protein repair systems might be present in acidophiles compared with neutralophiles and that this could be associated with the cellular demands of life at low pH. (7) Organic acids that function as uncouplers in acidophiles might be degraded by heterotrophic acidophiles.

Studies of proteins adapted to low pH have revealed a few general mechanisms by which, for instance, proteins can

achieve acid stability. In most acid-stable proteins (such as pepsin and the soxF protein from *Sulfolobus acidocaldarius*), there is an overabundance of acidic residues which minimizes low pH destabilization induced by a buildup of positive charge. Other mechanisms include minimization of solvent accessibility of acidic residues or binding of metal cofactors.

As far as life at high temperature is concerned, some microorganisms tend to use a higher proportion of purines in their codons, which are more resistant to heat denaturation than pyrimidines, but unfortunately, at low pH, purines are highly susceptible to acid hydrolysis. Some thermophilic acidophiles have adapted to growth at high temperatures by a general increase in the concentration of purine-containing codons as a heat-stabilizing adaptation, while simultaneously reducing the concentration of purine-containing codons in long open reading frames that are more prone to acid hydrolysis-associated mutations.

Habitats and biochemistry Acidic habitats are abundant and there are a number of natural processes which result in net acidity. Representatives among these may be several types of prokaryotic metabolism, including nitrification, accumulation of organic acids during fermentative or aerobic metabolism, and the oxidation of elemental sulfur, reduced sulfur compounds (RSCs) and ferrous iron (especially in the form of pyrite). Some soils of volcanic origin, such as in solfataras and fumaroles, are generally acidic and rich in elemental sulfur or sulfidic ores, as are many hot springs and areas which surround them. However, the majority of extremely acidic habitats are at least partially anthropogenic, owing their existence to one particular human activity—the mining of metals and coal (Johnson 1998; Bond et al. 2000). These habitats include coal refuse piles; abandoned mine shafts or pits; copper-leaching dumps; and soils, rivers, or lakes contaminated by acidic runoff from these sites. There is a synergy at work, in that many valuable metals (i.e., likely to be mined) occur as sulfide ores, and acidophilic microorganisms are often able to oxidize the sulfides such that net acidity in the form of sulfuric acid results. The dissimilatory oxidation of metal sulfides (where Me represents a cationic metal) can be written as: $\text{Me}^{2+}\text{S}^{2-}$ (insoluble metal complex) $\text{Me}^{2+} + \text{SO}_4^{2-}$. When water is available, sulfuric acid will form and cationic metals and metalloid elements (iron, zinc, copper, aluminum, lead, and arsenic) will be solubilized: the process is referred to as microbial ore leaching (Johnson 2001). The biological activities of ore leaching require air and water in addition to the metal sulfide substrates—a situation available in coal spoils, pit lakes, abandoned mines, and other such sites exposed to air and rainwater. Contamination of lakes, rivers, soils, and groundwater by acid mine drainage and runoff not only acidifies these sites but also brings the solubilized metals to often toxic levels. Much industrial interest has been shown on extreme acidophiles,

with subsequent application having been successful in the area of biomining: the use of acidic bioprocesses to remove valuable metallic minerals from sulfide ores (Das et al. 1999). Other uses are envisioned: acidophilic sulfate reducers may actually contribute net alkalinity to the sites and could be used for acid mine drainage remediation (Johnson 1995; Castro and Moore 2000); the utilization of aliphatic compounds by some acidophiles, in combination with their tolerance of heavy metals, makes them candidates for bioremediation of acidic wastewaters contaminated with toxic organic compounds and heavy metals (Gemmell and Knowles 2000). Most of the prokaryotes useful in these areas are extreme acidophiles, with $\text{pH}_{\text{opt}} < 3$ (Norris and Johnson 1998), and are often subclassified based on their temperature range preferences, or their metabolic processes, i.e., heterotrophic vs. autotrophic and iron oxidizing vs. non-iron oxidizing (see Table 2).

Acidophilic and autotrophic organisms

As most extremely acidic environments contain low concentrations of dissolved organic carbon (<20 mg/l), acidophilic organisms may be metabolically classified as oligotrophic. Primary production in sites which do not receive sunlight is dependent on chemolithoautotrophy, generally by metal ion oxidizer such as ferrous iron oxidizers and/or reduced sulfur compound oxidizers. The most well-studied among these prokaryotes is the iron/sulfur-oxidizing bacterium *Acidithiobacillus ferrooxidans* (Leduc and Ferroni 1994), a mesophilic, facultatively anaerobic member of the γ -proteobacteria. Other mesophiles in this category include *Thiobacillus prosperus* (which is halotolerant), and *Leptospirillum ferrooxidans*, which uses Fe(II) as its sole electron donor. An isolated and previously described archaeon, *Ferroplasma acidiphilum*, was the first ferrous iron oxidizing, cell-wall lacking archaeon and has been classified within a new family in the order *Thermoplasmatales* (within the *Euryarchaeota* branch of the Archaea); it can facultatively grow autotrophically using only ferrous iron as electron donor but it can also use organic carbon (Dopson et al. 2004). Much like *L. ferrooxidans*, this novel archaeon uses ferrous iron as its sole electron donor and fixes inorganic carbon as its sole carbon source—making it obligately autotrophic, unlike its closest relatives, *Picrophilus oshimae* and *Thermoplasma acidophilum*. Its optimal pH for growth is 1.7, with a range of 1.3–2.2, and its temperature range for growth is 15–45 °C (Golyshina et al. 2000). Moderately thermophilic, acidophilic autotrophs which can oxidize iron include the bacterium *Leptospirillum thermoferrooxidans*, while among extremely thermophilic archaea, there are several species of *Acidianus* as well as *Metallosphaera sedula* and *Sulfurococcus yellowstonii*.

Autotrophic prokaryotes which can oxidize reduced sulfur compounds but not iron include the mesophiles *Acidithiobacillus thiooxidans* and *Acidithiobacillus albertensis* and the moderate thermophile *Acidithiobacillus caldus*; on the other hand, the extremely thermophilic archaeon *Sulfolobus metallicus* is capable of oxidizing both ferrous iron and pyrite (Bathe and Norris 2007). There is some debate as to whether *S. acidocaldarius*, previously classified here, can actually grow autotrophically on sulfur. *Stygiolobus azoricus* is a chemolithotroph which is anaerobic and does not oxidize iron or sulfur, but can reduce elemental sulfur (Cavicchioli and Thomas 2000).

Phototrophic and acidophilic organisms

Illuminated extremely acidic environments contain phototrophic microorganisms as primary producers, including the mesophilic eukaryotic algae *Euglena* spp., *Chlorella* spp., *Chlamydomonas acidophila*, *Ulothrix zonata*, and *Klebsorbidium fluitans* (Gyure et al. 1987; Lopez-Archilla et al. 1995), as well as the unicellular rhodophyte *Galdieria sulphuraria* (Brock 1978). The latter is a moderate thermophile which (like *Euglena* species) may also grow in the dark as a heterotroph and has been reported to grow at pH values around 0 (Schleper et al. 1995). The green alga *Dunaliella acidiphilia* is adapted to the narrow pH range from 0 to 3 (Cavicchioli and Thomas 2000), and the thermophilic acidophilic alga *Cyanidium caldarium* has been investigated for its regulation of polyphosphate content (Nagasaka and Yoshimura 2008).

Mixed metabolism Many more acidophiles are mixotrophic or heterotrophic and include the iron oxidizers *Ferrimicrobium acidiphilum* (a mesophilic obligate heterotroph), *Sulfobacillus acidophilus*, *Sulfobacillus thermosulfidooxidans*, and *Acidimicrobium ferrooxidans* (moderately thermophilic bacteria which can grow as autotrophs, mixotrophs, or heterotrophs). Sulfur oxidizers in this category include the mesophiles *Acidiphilium acidophilus*, *Thiomonas cuprina*, and *Sulfobacillus disulfidooxidans*; the extreme thermophiles *Sulfolobus shibitae*, *Sulfolobus solfataricus*, and *Sulfolobus hakonensis*; and *Sulfurococcus mirabilis* and *Metallosphaera prunae*. Obligately organo-heterotrophic acidophiles include the mesophiles *Acidiphilium* spp., *Acidocella* spp., *Acidomonas methanolica* (which is methylotrophic), *Acidobacterium capsulatum*, the moderate thermophiles *Alicyclobacillus* spp., *T. acidiphilum*, *Thermoplasma volcanium*, *P. oshimae*, and *P. torridus*. The two latter species of *Picrophilus* have the lowest recorded pH optima for growth of any microorganisms (around pH 0.7) as reported by Schleper et al. (1995). Some species of *Acidiphilium* and *Alicyclobacillus* can reduce Fe (III).

Table 2 Representative acidophilic prokaryotes grouped by growth temperature optima, with relevant metabolic features noted

| Temperature designation | Metabolic feature | Examples |
|-------------------------|---|--|
| Mesophilic | Autotrophic iron and sulfur oxidation | <i>Acidithiobacillus ferrooxidans</i> <i>Thiobacillus prosperus</i> |
| | Autotrophic, only oxidizes iron | <i>Leptospirillum ferrooxidans</i> |
| | Autotrophic oxidation of RSCs but not iron | <i>Acidithiobacillus thiooxidans</i> <i>Acidithiobacillus albertensis</i> |
| | Heterotrophic Iron oxidation | <i>Ferromicrobium acidophilus</i> |
| | Heterotrophic or mixotrophic sulfur oxidation | <i>Acidithiobacillus acidophilus</i> <i>Thiomonas cuprinus</i> <i>Sulfobacillus disulfidooxidans</i> |
| | Obligately organoheterotrophic | <i>Acidiphilium</i> <i>Acidocella</i> <i>Acidomonas methanolica</i> <i>Acidobacterium capsulatum</i> |
| Moderately thermophilic | Iron oxidation | <i>Leptospirillum thermoferrooxidans</i> |
| | Oxidation of RSCs but not iron | <i>Acidithiobacillus caldus</i> |
| | Heterotrophic or autotrophic iron oxidation | <i>Sulfobacillus acidophilus</i> <i>Sulfobacillus thermosulfidooxidans</i> <i>Acidimicrobium ferrooxidans</i> |
| | Obligately organoheterotrophic | <i>Alicyclobacillus</i> <i>Thermoplasma acidophilus</i> <i>Thermoplasma volcanium</i> <i>Picrophilus oshimae</i> <i>Picrophilus torridus</i> |
| | Iron oxidation | <i>Acidianus</i> (several species) <i>Sulfurococcus yellowstonii</i> <i>Metallosphaera sedula</i> |
| | Oxidation of RSCs and iron | <i>Sulfolobus metallicus</i> |
| Extremely thermophilic | Heterotrophic or mixotrophic sulfur oxidation | <i>Sulfolobus shibatae</i> <i>Sulfolobus solfataricus</i> <i>Sulfolobus hakonensis</i> <i>Sulfurococcus mirabilis</i> <i>Metallosphaera prunae</i> |

Eukaryotic heterotrophs which inhabit extremely acidic sites include species of the yeasts *Rhodotorula*, *Candida*, and *Cryptococcus*. The filamentous fungi *Acontium cylatium*, *Trichosporon cerebriae*, and a *Cephalosporium* sp. can grow around pH 0 (Schleper et al. 1995). Protozoa have also been isolated which are obligately acidophilic, such as *Eutreptiall/Bodo* spp., *Cinetochilium* sp., and *Vahlkampfia* sp., which can grow as low as pH 1.6 and graze mineral-oxidizing and other acidophilic bacteria (Johnson and Rang 1993).

Alkaliphiles

Definitions As with most extremophilic categories, there are many subdivisions to be made, but a simplistic division

implies to define alkalitolerant organisms as those which can grow at a pH of 9 or 10 but which have pH optima near neutrality (Krulwich 1986; Krulwich and Guffanati 1989; Wiegel 1998). On the other hand, the term “alkaliphile” is used for microorganisms that grow optimally or very well at pH values above 9 but cannot grow or grow only slowly at the near neutral pH value of 6.5. Many different taxa are represented among the alkaliphiles, and some of these have been proposed as new taxa. Alkaliphiles can be isolated from normal environments such as garden soil, although viable counts of alkaliphiles are higher in samples from alkaline environments. The cell surface may play a key role in keeping the intracellular pH value in the range between 7 and 8.5, allowing alkaliphiles to thrive in alkaline environments, although adaptation mechanisms have not yet been clarified.

Habitats Naturally extremely alkaline environments occur in “soda lakes”, where high evaporation rates in closed drainage basins occur. The water contains scarce amounts of Mg^{2+} and Ca^{2+} and is near-saturated with sodium salts, especially chloride, carbonate, and bicarbonate, with the pH generally around 10 due to high levels of sodium carbonate (Duckworth et al. 1996). Alkaline environments also are noted in pockets in ordinary soils where transient alkalinity is proposed due to various biological activities (Grant et al. 1990)—indeed, alkaliphilic microorganisms have often been isolated from ordinary soils and other non-alkaline environments (Jones et al. 1998; Wiegel 1998). A few natural habitats are hypersaline and alkaline, harboring a large group of haloalkaliphiles, especially from Lake Magadi, Kenya, the Wadi Natrun Lakes in Egypt (Imhoff et al. 1978, Mesbah et al. 2009), and recently from soda lakes of Kulunda Steppe in Altai, Russia (Sorokin and Muyzer 2010a, b). Many of these organisms are also thermotolerant to various degrees, making these lakes interesting sources of novel microorganisms (Jones et al. 1998; McGenity et al. 2000). Man-made alkaline environments include effluents from tanneries, paper mills, food and textile processing plants, calcium carbonate kilns, detergents, and other industrial processes. They all have in common high levels of sodium [though it may be as low as 5% (w/v)] and concentrations of carbonate and bicarbonate which greatly exceed those of Mg^{2+} and Ca^{2+} . Thus, the Mg^{2+} and Ca^{2+} tend to precipitate as insoluble compounds with carbonate, leaving the excess anion to form sodium salts and counter the buffering effect of CO_2 . In addition, microbial processes such as ammonification and sulfate reduction lead to the establishment of a stable, perpetually alkaline environment (Cavicchioli and Thomas 2000).

Organisms Taxonomic groupings of alkaliphilic prokaryotes include, within the cyanobacteria, some members of the order *Chroococcales* and several species within the genus *Spirulina*. Alkaliphiles within the aerobic Firmicutes are widespread and include members of the order *Actinomycetales*, the families *Micrococcaceae*, the genera *Streptomyces*, and *Nocardia* and related actinomycetes and various genera within the order *Bacillales* (see Bergey’s Manual for new Systematic). Among the anaerobic alkaliphiles are various members of families within the orders *Clostridiales*, *Haloanaerobiales*, and *Natronaerobiales*. The Proteobacteria contain many alkaliphiles, especially the gamma subdivision’s *Ectothiorhodospira*, *Halomonadaceae*, and *Pseudomonas*. Moreover, an alkaliphilic and halophilic member of the *Thermotogales* was isolated, *Thermopallium natronophilum* (Duckworth et al. 1996). The Archaea contain many alkaliphiles, namely within the Euryarchaeota: *Halorubrum vacuolatum*, *Natrialba magadii*, several *Natronobacterium* species, and several *Natro-*

nococcus species. Alkaliphilic Methanomicrobiales include several species of *Methanohalophilus*.

Ecology and physiology Alkaliphiles have important roles in their native ecosystems. High primary productivities are seen in soda lakes in East Africa, as a result of dense populations of cyanobacteria provided with nearly unlimited supplies of CO_2 , high ambient temperatures, and high daily light intensities. This presumably supports the heterotrophic members of the microbial community, and a diversity of microbial metabolism, such as hydrogenotrophic sulfate reduction, acetogenesis, sulfur oxidation, and methane oxidation is also seen (Duckworth et al. 1996). Some alkaliphiles are anaerobic, many are halophilic, and most are halotolerant (Zhilina et al. 1996), and while most grow in the mesophilic temperature range, there are also some interesting (halophilic) alkalithermophiles (Wiegel 1998; Mesbah and Wiegel 2008).

As with halophiles, discussed in the next section, alkaliphiles require sodium ions for normal growth and metabolism. One would expect a number of unique adaptations to life within an ambient pH of 10 or greater. It was noted early that intracellular enzymes from these organisms had highest rates of catalysis at near neutral pH, while for excreted enzymes, the highest catalytic rates were noted at nearer the optimum growth pH for the organism (Larson and Kallio 1954). This observation led investigators to assume that intracellular pH was somehow kept near neutrality in these organisms. Indeed, this has been confirmed by further observations (Padan et al. 2005), showing aerobic alkaliphiles generally maintain their cytoplasmic pH about 2 units lower than ambient pH, anaerobes around 1 pH unit (Mesbah et al. 2009). Sodium ions are necessary for keeping intracellular H^+ relatively high (despite, at least in aerobes, respiratory activity which extrudes protons—Krulwich et al. 1996; Krulwich and Guffanati 1989), with active extrusion of sodium ions coupled to importation of protons against both gradients by Na^+/H^+ antiporters (Buck and Smith 1995). Many membranes in alkaliphiles are reported to contain sodium-coupled ATPases (similar to those of halophiles) as well as, or rather than, proton-coupled ATPases (Kaieda et al. 1998; Koyama 1999; Ueno et al. 2000); however, other data go against this (Cavicchioli and Thomas 2000). Many of these systems are similar to those of halophiles, even in alkaliphiles which are not strictly halophilic, but are at least halotolerant.

Extremes of salinity

Higher organisms can be divided between those whose cells require relatively low (i.e., 0% to 0.9% for humans

—“normal” or “physiological”) NaCl concentrations and those whose cells require elevated concentrations (i.e., marine fish do best at 3% NaCl—the salinity of ocean water and human tears). However, the very high salt concentrations in hypersaline lakes or soils, salterns, or other man-made environments such as salted foods preclude the growth of most fish, invertebrate animals, plants, and even most prokaryotes—but there are microorganisms which thrive there. Marine microorganisms, like marine fish, mammals, and invertebrates, must at least tolerate ocean water salinity. In contrast to halotolerant organisms, obligate halophiles must require NaCl concentrations higher than 3% (wt/vol) for optimal growth. The requirement for NaCl may be “slight” [most rapid growth at 2% to 5% (0.34 to 0.85 M) NaCl], “moderate” [most rapid growth at 5% to 20% (0.85 to 3.4 M) NaCl], or “extreme” [most rapid growth at 20% to 30% (3.4 to 5.1 M) NaCl] (Larsen 1962). Other definitions have been published including that true halophiles grow optimally at and above 10% NaCl.

Basic research into halophilicity of proteins and membranes, osmoregulation, and genetics of these organisms, especially of archaea, is voluminous. Several practical applications are envisioned from the study of halophiles: better understanding of salted, fermented foods technology; remediation of saline wastewater (Kargi and Dincer 1998; Kargi and Dincer 2000); and bioremediation of toxic compounds such as uranium (Francis et al. 2000), hydrocarbons (Bruns and Berthe-Corti 2000; McGenity 2010), and pollutants (Le Borgne et al. 2008). Furthermore, the production of biopolymer has been described for bacterial and archaeal halophilic microorganisms (Hezayen et al. 2000; Mata et al. 2008; Van-Thuoc et al. 2008; Quillaguamán et al. 2009).

The halophiles

Definitions The most accepted definitions presently used are those from Oren (2006). Many organisms are referred to as halotolerant or slightly halotolerant, which generally mean that the organism grows best with 0–0.5% NaCl concentrations but can tolerate various higher concentrations such as up to 3% NaCl which normally is encountered in marine environments. The salt requirement and tolerance parameters are highly dependent on temperature, pH, and growth medium: a halotolerant organism grown in complex media (such as *Halomonas elongate*—Vreeland et al. 1980) was found to be truly halophilic when grown in minimal media under otherwise identical conditions (Canovas et al. 1996). An interesting phenomenon was found recently—the requirement of chloride ions for (moderate) halophiles (Roeßler and Müller 2002; Bowers and Wiegel, unpublished results).

Habitats The habitats which contain high salt concentrations are diverse. Some authors feel that understanding of the adaptations of terrestrial halophilic archaea may be important in the detection of life on Mars, assuming similar types of salts and a carbon-based life form (Litchfield 1998). Several of the hypersaline “soda lakes” (Lake Magadi in Kenya; the Wadi Natrun lakes in Egypt; and Mono Lake, Big Soda Lake, and Soap Lake in the Western USA) are highly alkaline, with pH values of 9 to 11, while the Great Salt Lake and the Dead Sea have pHs around 7 (Ollivier et al. 1994). Unusual habitats have been found to be populated with halophiles, such as the oil-field water in the North Sea (Lien et al. 1998), preserved salted foods (Kobayashi et al. 2000), and the nasal cavities of desert iguanas (Deutch 1994; Lawson et al. 1996), though the ocean, hypersaline lakes of oceanic (thalassohaline) or non-oceanic (athalassohaline) origin and solar salterns make up the predominant habitats (Antunes et al. 2008). Halotolerant or halophilic microorganisms have also been isolated from polar sea ice (Bowman et al. 1998) and from Antarctic rocks (Smith et al. 2000). Salinities in the various habitats can range from that of brackish waters to saturation, or from about 0.5% to 37% or more. The predominant salts are often Na⁺ and/or Cl⁻, though Mg⁺⁺ or Ca⁺⁺ may be in abundance (except in the soda lakes, see section on “Alkaliphiles”), and all are usually noted in higher concentrations than in more moderate habitats. Sulfate is generally an important electron acceptor in these ecosystems, and salterns generally show precipitation of calcium compounds (CaSO₄ and CaCO₃) as well as NaCl, while soda lakes have carbonate precipitates of magnesium and calcium, with little of these cations in solution.

Physiology Halophilic prokaryotes generally require sodium ions for optimal growth, as they are coupled to active uptake of nutrients, the working of the membrane respiratory chain, and making of ATP (Unemoto 2000). Conversely, and often intimately linked, is the need to control the net diffusion of sodium ions into the cytoplasm from the hypersaline environment to avoid toxic cytoplasmic sodium levels. Many halophilic bacteria maintain elevated levels of sodium ion in their cytoplasm, with their intracellular structures and enzymes adapted to and dependent on those levels; they may employ energy-consuming processes to actively extrude excess sodium (Deppenmeier et al. 1999; Eddy and Jablonski 2000). The gradient of sodium ions thus maintained across cell membranes can be utilized by the organisms. For example, in some methanogens (halophilic or not), a reversible sodium ion pump is utilized, coupling the process of methyl transfer to the transport of Na⁺ across the cytoplasmic membrane. Other ion pumps generate proton motive force by redox-potential-driven proton translocation. Thus, both a sodium ion gradient

and an electrochemical proton gradient are generated by the organisms, with both ion gradients used directly in the synthesis of ATP, in the case of Na^+ by a sodium-dependent ATP synthase (Deppenmeier et al. 1996; Baumer et al. 2000). Several acetogens use a similar process to couple acetogenesis with ATP production (Heise et al. 1992). Marine and other halophilic bacteria have a sodium pump as an integral part of their electron transport chain (the NADH-quinone reductase) which effectively couples ATP production with extrusion of sodium ions from the cell. A similar sodium ion pump is found in many non-halophilic, Gram-type negative pathogenic bacteria, adding new insights into their physiology as well (Unemoto and Hayashi 1993). Many halotolerant or halophilic organisms, including the halotolerant microalga *Dunaliella maritima* (Shumkova et al. 2000), couple the extrusion of sodium ions to the importation of substances such as amino acids, utilizing ATP in the process (Unemoto 2000). Thus, the adaptations of coping with elevated sodium and the requirement for elevated sodium are intricately linked.

Prokaryotes living in hypersaline environments must equalize the osmolarity within and without their cellular envelopes in order to remain intact. Some do this by maintaining high intracellular ionic strength (with KCl or NaCl levels—Galinski and Trüper 1994; Danson and Hough 1997) or by accumulating organic solutes (Roberts 2005; Empadinhas and da Costa 2008 and literature cited therein).

In these organisms, complex intracellular adjustments and unique properties of the cytoplasmic membranes allow existence in the high ionic strength environment. Their enzymatic and structural proteins are also adapted to function in the high-solute load environment; for example, intracellular enzymes from the obligately halophilic archaea are often active and stable at multimolar salt concentrations and denature below 2 to 3 M KCl (Eisenberg 1995). As with the hyperthermophiles, the most halophilic organisms are generally archaea, though a number of halophilic bacteria have also been isolated, even in environments with sodium chloride concentrations close to saturation (Anton et al. 2000; Bowers et al. 2009).

Organisms Halophilic prokaryotes include archaea and bacteria and both anaerobes and aerobes (Kamekura et al. 1997; Kamekura 1998; Oren 2006; Ma et al. 2010).

The anaerobes bacterial halophiles are represented by fermentative, sulfate-reducing, and phototrophic genera and include psychrophiles, mesophiles, and thermophiles (Ollivier et al. 1994). Some of the orders contain only halophiles such as the orders *Natranaerobiales* (type genus *Natranaerobius*; Mesbah et al. 2009) comprising only one family and two genera with halo-alkalithermophilic species

and the order *Haloanaerobiales* containing the two families: *Haloanaerobiaceae* (type genus *Halanaerobium*) and *Halobacteroidaceae* (type genus: *Halobacteroides*) [for an updated list see the website <http://www.bacterio.cict.fr/classifgenerafamilies.htm>]. For example, the species of *Haloanaerobium*, *Haloanaerobacter*, and *Haloicola* live in ranges from 2% to 30% NaCl, with optima from 10% to 18%, and the species of *Halobacteroides* grow in a NaCl range of 5% to 30% with optima from 9% to 18%. Table 3 summarizes some of the characteristics for representative anaerobic and fermentative halophilic bacteria.

The slightly to moderately halophilic sulfate-reducing bacteria (SRBs) are found within various genera: *Desulfovibrio*, *Desulfobacter*, *Desulfotomaculum*, *Desulfococcus*, *Desulfobacterium*, *Desulfonema*, and *Desulfohalobium*. All can be defined as slight halophiles except for *Desulfovibrio halophilus* and *Desulfohalobium retbaense*, which are moderate halophiles. The latter has a salinity range of 3% to 25% NaCl with an optimum of 10% NaCl. The anoxygenic phototrophic halophiles include *Chromatium*, *Chlorobium*, *Rhodospirillum*, *Rhodobacter*, *Thiocapsa*, and *Ectothiorhodospira*, as well as others and span the gamut of NaCl requirements. Two species, *Halorhodospira halophila* and *Halorhodospira halochloris*, are extreme halophiles (Imhoff and Trüper 1977).

Among the halophilic anaerobic archaea are the methanogenic genera *Methanohalophilus*, *Methanosalsum*, and *Methanohalobium*, which contain moderate and extreme halophiles, as well as the halotolerant genus *Methanocaldococcus* (Ollivier et al. 1998), which tolerates salinities of 0–12% with an optimum for growth of 5% NaCl, and the slightly halophilic *Methanogenium*.

Halophilic aerobic bacteria (Ventosa et al. 1998b) include all genera and species within the Gram-type negative family *Halomonadaceae*, in the phylum of Proteobacteria (Arahal and Ventosa 2006; Arahal et al. 2007). The genus *Glaciecola* was also described within the gamma subdivision of the Proteobacteria, containing two aerobic, psychrophilic, slightly halophilic species (Bowman et al. 1998). The order *Cytophagales*, of the alpha subdivision of Proteobacteria, contains many halotolerant and halophilic genera. There are also several halophilic aerobic methylotrophic bacteria, such as *Methylarcula marina* (Doronina et al. 2000; Sorokin et al. 2007). Aerobic Gram-type positive halophiles belong exclusively to halophilic genera, such as *Halobacillus*, *Marinococcus*, *Salinicoccus*, *Nesterenkonia*, and *Tetragenococcus*. Several species belong to genera within the order Firmicutes *Salimicrobium halophilus*, *Gracilibacillus dipso-sauri* (Lawson et al. 1996), *Bacillus marismortui* (Arahal et al. 1999), and *Salibacillus salexigens* (Garabito et al. 1997). Several halophilic actinomycetes have been isolated which belong to the genera *Haloglycomyces*, *Saccharopolyspora*, *Streptomonospora*, *Actinopolyspora*, *Nocardioopsis*,

Table 3 Comparative features of representative anaerobic and fermentative halophilic bacteria

| | Habitat | pH range | Temperature range (°C) | Doubling time (h) | NaCl range (%) | NaCl opt. (%) |
|--|----------------------|---------------|------------------------|-------------------|----------------|---------------|
| <i>Halobacteriodes halobius</i> | Dead Sea–Lake Sivash | ND | 30–47 | 1–2 | 8–30 | 9–15 |
| <i>Halobacteriodes acetothyliticus</i> | Oil well | 5.4–8 | 15–45 | 7.8–9.5 | 6–20 | 10 |
| <i>Halobacteroides lacunaris</i> | Lake Chokrack | 6–8 | 25–52 | 2.9–4.5 | 5–30 | 15–18 |
| <i>Haloanaerobium praevalens</i> | Great Salt Lake | 6–8 | 15–50 | 4 | 2–30 | 12.5 |
| <i>Haloanaerobium fermentans</i> | Puffer fish ovaries | 6–9 | 15–45 | ND | ND–25 | 10 |
| <i>Haloanaerobacter chitinovorans</i> | Solar saltern | ND | 25–50 | 2.5–2.9 | 3–30 | 12–18 |
| <i>Haloicola saccharolytica</i> | Lake Sivash | 6–8 | 15–47 | 3.9 | 3–30 | 10 |
| <i>Natroniella acetigena</i> | Lake Magadi | 8.1–10.7 | ND–42 | ND | 10–26 | 12–15 |
| <i>Sporohalobacter lortetii</i> | Dead Sea | ND | 25–52 | 8 | 4–15 | 8–9 |
| <i>Sporohalobacter marismortui</i> | Dead Sea | ND | 25–50 | ND | 3–18 | 3–12 |
| <i>Acetohalobium arabaticum</i> | Lake Sivash | 5.6–8.4 | ND–47 | ND | 10–25 | 15–18 |
| <i>Orenia sivashensis</i> | Lake Sivash | (6.3–6.6 opt) | ND–50 | ND | 5–25 | 7–10 |
| <i>Thermohalobacter barrensis</i> | Solar saltern | 7 opt. | ND–70 | ND | ND–15 | 5 |
| <i>Natronoincola histidinovorans</i> | Lake Magadi | 8–10.5 | ND | ND | 4–16 | 8–10 |

and *Zhihengliuella* (Ventosa et al 1998b; Cai et al. 2009; Tang et al. 2009; Guan et al. 2009; Chen et al. 2010). Ventosa et al. (1998a) reviewed excellently the diversity of moderately halophilic Gram-type positive bacteria.

In addition to the anaerobic archaea mentioned above are the aerobic forms. These all lie within the family *Halobacteriaceae* which has been authoritatively summarized by Oren et al. (1997) and include many novel genera all of which are strict halophiles.

Other halophilic extremophiles Unusual halophiles are the *Haloplasma contractile* (Haloplasmataceae) isolates, a wall-less contractile bacterium isolated from the Red Sea, as well as the above mentioned members of the Order *Natranaerobiales*. The later ones are polyextremophilic, i.e., anaerobic halophilic alkalithermophilic bacteria isolated from athalassohaline salt lakes in Egypt and the Kenyan Rift Valley, able to grow under the combined conditions of up to saturation of NaCl in the presence of sodium carbonates, at pH values above 10 and temperatures as high as 70 °C and thus thrive at the present boundaries of live for combined stressors (Bowers et al. 2009).

Extremes of hydrostatic pressure

The piezophiles

Definitions The term obligate, or extreme, piezophile has been used for an organism incapable of growth at atmospheric pressure regardless of temperature, while the term piezotolerant has been applied to an organism which

grows best at atmospheric pressure but which can also grow at elevated pressures. One definition states also that extremely piezophilic bacteria are those unable to grow at pressure <50 MPa, but able to grow well at 100 MPa (Kato et al. 1998).

In 1957, Zobell and Morita isolated some bacteria from environments under extremely high pressure, but were largely unsuccessful (Zobell and Morita 1957). When better technology became available to explore the depths of the oceans and cultivate their microbial inhabitants, new life forms were discovered with unique adaptations to these habitats (Yayanos et al. 1982). While habitats in ocean depths have variable temperatures and pHs, all are under enormous pressure from the weight of the water column (up to 1,100 atm in the deepest part of the Mariana Trench—Abe et al. 1999), and it was obvious that living organisms from those depths were tolerant to such pressures. Some of these microorganisms actually grow better (i.e., faster doubling times) under higher pressures than at atmospheric, and some will not live and grow without pressures of greater than or equal to 2.5 atmospheres (Kato et al. 1996a). These were referred to as barophilic, or now by the more appropriate term piezophilic; however, the majority of them are piezotolerant and only a few are (obligate) piezophiles.

There is a contradiction in the literature as far as definitions about pressure limits for microbial growth are concerned, mainly due to the complicating effects of temperature. The majority of piezophiles (barophiles) are also psychophilic, as the majority of the deep sea is cold (<4 °C). However, many prokaryotes isolated from hydrothermal vent environments are piezophilic (barophilic) as well as (hyper)-thermophilic and mesophilic. To the latter ones belong the symbiotic chemolithotrophic bacteria of the tube-dwelling worm *Riftia pachyptila* that has been taken as a

symbol of deep-sea vent animal communities for many years. These sulfur-oxidizing and carbon-fixing microorganisms are present in enormous numbers inside the animal's body and they are capable of supplying most of the worm's metabolic needs thanks to the fixation and incorporation of CO₂ (Cavanaugh et al. 1981; Robidart et al. 2008).

In most cases, the response to pressure is greatest near the organism's upper temperature limit for growth, or some organisms may experience an elevated T_{\max} at higher pressures (Summit et al. 1998).

Psychrophilic obligate piezophiles generally belong to one of five genera of the gamma-proteobacteria: *Photobacterium*, *Shewanella*, *Colwellia*, *Moritella*, *Psychromonas*, and to a new group containing the strain CNPT3 (DeLong et al. 1997). Among hyperthermophilic piezophiles, the archaeon *Thermococcus barophilus* (Marteinsson et al. 1999) and *Pyrococcus* species have been described (Zeng et al. 2009). The most striking example of elevated pressure effects on a microorganism is the above mentioned *M. kandleri*, which under high pressure is able to grow at 122 °C. How pressure does affect in such a case the upper temperature limit for growth was only partially investigated; it seems that the soluble H₂ concentration in the liquid phase was the most significant parameter to control the ΔG of hydrogenotrophic methanogenesis under different growth conditions and that the correlation may be mainly explained by the kinetic effect of the elevated H₂ concentration.

Much research has focused on the membrane lipid composition in response to elevated pressures, looking at how proper fluidity of the membrane is maintained (Yano et al. 1998; Fang et al. 2000). Genetic research has identified genes in piezophiles and in bacteria adapted to live at atmospheric pressure as well, which are regulated by changes in pressure (Kato et al. 1996b). Responses to temperature and pressure changes are similar in the two groups of organisms—implying that the mechanisms are widely conserved and that in general bacterial growth rates may be stimulated by high pressure near their maximum temperature for growth.

A number of piezophiles have been found to be tolerant to high concentrations of organic solvents, as well as those which are merely tolerant to both conditions. Similar to thermophiles, the cardinal temperatures of psychrophiles can differ when they are grown at various pressures (Patching and Eardly 1997; Bakermans et al. 2009).

Radiation resistance

Electromagnetic radiation of various types continuously bombards the biosphere of the Earth, some being natural

and some owing its origin to human activities. At a shorter wavelength, higher energy radiation such as gamma rays and X-rays, are referred to as ionizing radiation because they can cause atoms to lose electrons or ionize. The bombardment of DNA by X-rays frequently damages the bases or causes breaks in the backbone, inducing mutations or even causing death of the organism. Ultraviolet radiation, next and longer in wavelength to X-rays, primarily does damage to DNA by formation of thymine dimers. Most organisms have mechanisms with which to repair this damage, with varying success. Fortunately, most UV radiation is absorbed by the Earth's atmosphere, including the ozone layer, prior to reaching the surface. Visible light and higher wavelength infrared and radio-waves are less damaging to cellular structures. Areas of the Earth where the atmosphere is thin (some areas near the Poles, especially with the seasonal increase and decrease in the ozone "hole") and those exposed to high amounts of sunlight (near the Equator) receive more radiation than others. Microorganisms can in general resist ionizing and other forms of radiation, or at least cope with their damage and resultant mutations, better than can higher organisms, possibly owing to their single-celled organismal structure. Certain pigments (i.e., carotenoids, melanin) are used by various organisms to absorb or quench the damaging effects of various forms of radiation.

Certain microorganisms have developed highly adapted systems for dealing with radiation. Many Firmicutes are able to form endospores, which in addition to protecting the DNA from damage by placing it in association with small, acid-soluble spore proteins, also have particular DNA reactions to radiation (i.e., spore photoproduct) as well as particular repair mechanisms active at germination (Setlow 1994; Fajardo-Cavazos and Nicholson 2000). The family *Deinococcaceae* containing the genus *Deinococcus* is radioresistant as vegetative cells, even to large doses of ionizing radiation (Zhang et al. 2007; Shashidhar and Bandekar 2009; Yuan et al. 2009). They contain highly active DNA repair systems and several copies of their genomes to use as templates for replacing and repairing radiation-damaged DNA (Battista 1997). Furthermore, it has been demonstrated that specific proteins are extremely important in the gamma radiation resistance of *Deinococcus radiodurans* and related taxa (Hua et al. 2010; Shuryak and Brenner 2010). Many novel *Deinococcus* species were recently isolated from areas such as the Atacama Desert due to the direct correlation and similar mechanisms for dry resistance and gamma radiation resistance. While *Deinococcus* species do not require radiation to live, this extreme resistance qualifies them to be mentioned in this mini-review. *Kineococcus radiodurans* is another highly radiation-resistant bacteria (Phillips et al. 2002). As mentioned in the previous section, the ultramicrobacterium

Sphingomonas is also quite resistant to UV-B radiation. The desiccation-resistant cyanobacterium *Chroococcidiopsis*, which usually lives in deserts and hypersaline environments, is also quite resistant to ionizing radiation (Billi et al. 2000). Other genera or species of prokaryotes have shown to exhibit elevated resistance to gamma and UV radiation such as *Hymenobacter xinjiangensis* (Zhang et al. 2007), but significant resistance (i.e. at the level of *Deinococcus*) has rarely been reported.

Desiccation resistance

The capability to tolerate extreme desiccation conditions has been investigated in the last decades, particularly as far as exobiology is concerned, so further data and references are reported in that specific chapter.

Some of the research activities were focused on the taxonomy and metabolism of psychrophilic bacteria and yeasts, but desiccation tolerance properties have especially been described in lichens. More specific insights into the physiology and molecular traits of microorganisms capable to withstand extreme desiccation conditions were obtained looking at exopolysaccharide composition and production in phototrophic isolates (Knowles and Castenholz 2008; Ozturk and Aslim 2009), cell structure and metabolism in lichens (Aubert et al. 2007; Jonsson et al. 2008; Heber et al. 2009), survival and stress response (Stevens 1997; Khmelenina et al. 1999; Beblo et al. 2009; Gorbushina and Broughton 2009; Ozturk and Aslim 2009; Smith et al. 2009), and genetic transfer (Billi et al. 2001). Other researches focused on the microorganisms living inside 1–3 in. of translucent rocks including the ones in the rocks of the Dry Valley of Antarctica and the Atacama Dessert (Friedmann 1982; Warren-Rhodes et al. 2006). The other research focus is on those living in the Atacama Desert, the driest place on Earth, demonstrating that the organisms indeed lived there and not just were blown in from the air (Wettergreen et al. 2005; Drees et al. 2006).

Solvent resistance

Most microorganisms are killed by even small concentrations (0.01%) of organic solvents such as toluene or chloroform, likely due to their lipid-destructive properties (Hirayama et al. 1998). In 1989, the first organic solvent-tolerant microorganism was isolated, a *Pseudomonas* thriving in high concentrations of toluene (Inoue and Horikoshi 1989). Many organisms now have been found to tolerate 10% or even 50% toluene or other solvents, such as kerosene, benzene, or various alcohols, though none have been found to require them for life (Sardessai and Bhosle 2002; 2004), including extremophilic yeasts with

potential applications in biotechnology (Kaszycki et al. 2006). There are several mechanisms which probably contribute to this phenomenon: decreased influx via removal of solvent from cell membranes and/or physical impermeability (Heipieper et al. 1992; Pinkart et al. 1996), biochemical degradation or detoxification of the solvent (Ramos et al. 1997), active efflux of the solvent (Kieboom et al. 1998; Ramos et al. 1998), and overexpression of genes (Nakajima et al. 1995). It has been often noted that a correlation between organic solvent tolerance and multiple antibiotic resistance exists, and perhaps the efflux systems, or at least their regulation, are similarly induced (Oethinger et al. 1998; Li and Poole 1999). The so-called multi-drug efflux systems of the Gram-negative pathogens have been fairly well studied (Nikaido 1996; Paulsen et al. 1996), and it is noted that there is increased expression of these or similar operons in organic solvent-tolerant bacteria.

There has been much genetic investigation of organic solvent-tolerant organisms, with certain genes believed to contribute to or confer this property, depending on the mechanisms employed. As would be expected, there does not appear to be a single, universal mechanism, but rather a combination of efflux systems, physical barriers to influx, and adaptation to the presence of the solvents. *Bacillus* and *Pseudomonas* species have been found to possess this characteristic, though several solvent-tolerant *E. coli* strains have been noted also, either naturally, via mutagenesis, under selective pressure, or via transformation with candidate genes from tolerant species. Degrees of cell surface hydrophobicity and/or membrane fluidity seem to correlate with this tolerance and are seen to change with adaptation in the presence of solvents, likely affecting influx of the chemical (Aono and Kobayashi 1997; Tsubata et al. 1997). Some of the changes seen in adaptation to organic solvents are noted to be a general stress response in bacteria.

Organic solvent-degrading bacteria are interesting for their potential use in bioremediation, and obviously, those using active efflux systems identical or similar to those used by pathogens may have usefulness in the understanding of antibiotic resistance. The study of these bacteria has yielded much information on the toxicity of solvents to membrane systems in general. Worrysome is the possibility for selection of multiple antibiotic resistance in pathogens by exposure to unrelated compounds such as pollutants and the fact that the resistance profiles of these organisms are then unrelated to drug type or site of action.

Resistance to low substrate concentration

In the open ocean, as well as in deep lakes, the first 100 to 200 m of water are often illuminated, but contains scarce nutrients. Other habitats also exist which contain less than

20 mg/l organic carbon—“oligotrophic environments”. It is in these habitats that “oligotrophic”—true members are defined by their inability to propagate at elevated nutrient concentrations (Conrad and Seiler 1982; Semenov 1991; Wainwright et al. 1991, 1993; Schut et al. 1997; Lauro et al. 2009)—organisms live and thrive. They grow under such conditions by having highly effective systems for the uptake of inorganic and organic nutrients at nano- and picomolar concentrations and by their efficient utilization systems characterized by unique metabolic regulation. Oligotrophs can be isolated from different natural sources, both with low and high concentrations of organic substances, and those inhabiting soil and aquatic habitats are particularly able to utilize geochemically important, low molecular organic and inorganic substances, which are rapidly processed but occur in very low concentrations.

Sphingomonas is an ultramicrobacterium which is adapted to oligotrophic habitats. Some strains have shown an enhanced ability to recover from UV-B radiation, perhaps adding to their ability to live and thrive in the upper water column where UV radiation exposure is maximal (Joux et al. 1999). This organism also seems to have a distinct response in transcriptional regulation in times of starvation, which could point to further adaptation to depleted nutrients (Fegatella and Cavicchioli 2000). Recently, important insights were elucidated about cell structure and metabolism in microorganisms belonging to the *Roseobacter* and *Collimonas* genera which exhibit oligotrophic behavior (Leveau et al. 2009; Tang et al. 2009).

Exobiology

In the search for extraterrestrial life, our closest neighbor planets are often considered as candidate habitats. The lack of surface water and extremely high surface temperature on Venus make it less likely than Mars as a source for life, but the hygroscopic sulfuric acid clouds in the lower and middle cloud layers surrounding that planet, where the temperatures are considerably lower, could be a favorable environment for acidophilic, sulfate-reducing, chemoautotrophs growing as aerosols (Cockell 1999). Short of making the trip to look, further work on terran acidophiles may help to clarify this possibility.

Understanding the biology of extremophiles and their ecosystems permits developing hypotheses regarding the conditions required for the origination and early diversification of life on a planet including Earth, the possibility of panspermia, and the potential habitats of past or present life beyond Earth in the solar system (on the planet Mars and the Jovian moon Europa; some authors also suggest possible habitats on other icy satellites, in Venus clouds,

and on the Saturnian moon Titan), or even in exoplanetary systems. Recently, the introduction of novel techniques such as Raman spectroscopy into the search of life signs in extremophilic environments (Villar and Edwards 2006; Edwards et al. 2007; Alajtal et al. 2009) has open further chances and issues that might be very useful in exobiology, particularly for the development of unmanned remotely operated vehicles.

Among early microorganisms, cyanobacteria played a major role, inventing oxygenic photosynthesis and causing the most profound alteration of our planet. Cyanobacterial cell walls are commonly covered by S-layers or by carbohydrate structures forming slime or sheaths. They are composed of complex polysaccharides and pigments like scytonemin (Hoiczky and Hansel 2000). These extracellular fibrillar carbohydrates provide a protective coat for the cells against UV radiation and desiccation as they maintain the cells in a highly hydrated gel-like matrix, permitting these organisms to adapt to extreme temperatures and desiccation, as in today's Antarctica, but probably also in early Earth environments (Olsson-Francis et al. 2010). After that, the presence of water on Mars and perhaps on some other planets and their moons has been proven, and extra terrestrial life has become much more possible than before, but the final judgment will be obtained when microorganisms are going to be isolated from aseptic collected samples (Zolensky 2005; McSween 2006).

In Antarctica, Lake Vostok is buried under almost 4,000 m of ice and could serve as a model for the hypothetical ocean under the ice of Europa (Cavicchioli and Thomas 2000; Marion et al. 2003). Technologies are being developed to sample the lake ice and water without introducing surface microbes and could be used in the future on Europa ice or Mars polar caps with respect to planetary protection issues. Studying cold environments such as ice, rocks of the Antarctic Dry Valleys, and permafrost is also interesting for detecting new types of psychrophiles, as well as for studying preservation of microbes. Microorganisms (prokaryotic and eukaryotic) can live in rocks (endoliths) or in sediments of Antarctica and Arctic (Friedman et al. 1988; Sun and Friedmann 1999; Skidmore et al. 2000; Wynn-Williams and Edwards 2000; Siebert et al. 1996), in porosity of impact-shocked rocks (Cockell et al. 2002), and on bare rocks of hot desert (desert varnish) (Gorbushina 2003; Edwards 2004). Besides bacteria, cryptoendolithic merismatic microfungi live in the porosity of rocks of the Antarctic Dry Valleys. These fungi tolerate hard desiccation, high UV exposure, extremely low temperatures, and wide thermal fluctuations (Onofri et al. 2004).

The elevated resistance of microorganisms to extreme conditions, including most of that characterizing space

environments, led in the last two decades to several investigations based on either manned or unmanned space vehicles and modules, particularly the MIR station, the International Space Station, PHOTON, and BION capsules (Horneck et al. 2001; Rettberg et al. 2004; Sancho et al. 2007; van Benthem et al. 2009). This was possible due to developments of spatial technologies allowing the study of adaptations and survival of terrestrial organisms to vacuum, microgravity, and cosmic radiations; moreover, this expansion of human activities to space raised new issues related to microbiology, such as the development of life-support systems for future planetary stations, the control of biocontamination in confined habitats, as well as planetary protection and development of strategies to prevent, detect, and label terrestrial contaminants of extraterrestrial environments.

The deep subsurface biosphere includes chemolithotrophic microbes in anoxic reducing environments under oceans and continents, in deep subsurface sediments, in hydrocarbon and water reservoirs, and in subsurface caves as nicely reviewed by Teske (2005). Analogue habitats in which life is protected from harsh surface conditions are probably common in other planets with some geothermal activity, such as Mars.

Studying the biology and ecology of extremophiles is essential for defining the limits of life as we know it—the envelope of life—as well as for studying the preservation of biosignatures in extreme environments analogous to that of early Earth and/or to potential extraterrestrial habitats and for testing technologies to detect them (Fendrihan et al. 2009; Orange et al. 2009). One caveat might be that on Earth extreme environments are fed by nutrients from “normal” environments brought by winds, rains, etc. Therefore, the question arises as to whether or not a planet with only extreme conditions might sustain life. Nevertheless, not all extremophilic adaptations are derived conditions, and at least some of the anaerobic metabolisms are ancestral.

Conclusions

Environments with extreme physicochemical parameters were thought of as being hostile to life until microbiologists discovered that they are actually inhabited by a wide diversity of microorganisms. Organisms that survive and thrive under conditions that are detrimental to the majority of the currently described species have become a focus of increasing scientific attention over the last few years, with some groundbreaking discoveries of stress-tolerating mechanisms. Extremophiles are certainly promising models to expand our understanding of the functional evolution of stress adaptation and maybe they will lead us to explore a biodiversity so far unrevealed.

We have described an updated overview over the most representative microorganisms living in environments hostile to most of eukaryotic forms of life. Understanding the evolution of microorganisms in extreme environments will increase our basic knowledge of evolutionary processes and allow a better evaluation of the potential ecological consequences of environmental changes.

If, as we believe, extreme environments are important for evolutionary processes, human activities may influence biodiversity even more than previously thought and, after millennia of microbial evolution, the stability of these fragile environments are in danger.

Future research directions, including the refinement of culture media, strategies based on cell–cell communication, high-throughput innovations, and a combination of these approaches, will lead to novel insights into the world that once was thought not to harbor any form of life.

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