

## Conclusion

Applications of soils data and survey interpretations have steadily broadened in range and precision in response to economic, environmental, social, and political influences. Today, interpretations are becoming increasingly dynamic with the application of information technology to support decision-making. As soils data are integrated into analytical and expert systems, access to digitized soils data is essential. Advances in digital orthophotography (digital imagery that has been rectified to remove distortions resulting from topography and the camera angle, thus equalizing distances represented on the image), maps and digital data for computer manipulation and retrieval enhance the delivery efficiency of soil-survey information. Detailed resource information on specific land areas can now be provided quickly and interactively to help landowners, communities, and others in land-use decision-making.

## Further Reading

- Bartelli LJ, Klingebiel AA, Baird JV, and Heddleson MR (eds) (1966) *Soil Surveys and Land Use Planning*. Madison, Wisconsin: Soil Science Society of America and American Society of Agronomy.
- Gardner DR (1998) *The National Cooperative Soil Survey of the United States*. Historical Notes Number 7.

- Washington, DC: Natural Resources Conservation Service.
- Helms D, Effland A, and Durana P (eds) (2001) *Profiles in the History of the U.S. Soil Survey*. Ames, IA: Iowa State Press.
- Jenny H (1961) *E. W. Hilgard and The Birth Of Modern Soil Science*. Pisa, Italy: Collana Della Rivista 'Agrochimica.'
- Kellogg CE (1943) *The Soils That Support Us*. New York: Macmillan.
- Klingebiel AA (1991) Development of soil survey interpretations. *Soil Survey Horizons* 32(3): 53–65.
- Olson GW (1981) *Soils and the Environment, A Guide to Soil Surveys and Their Applications*. New York: Chapman & Hall.
- Simonson RW (1987) Historical aspects of soil survey and soil classification. *Soil Survey Horizons*. Madison, Wisconsin: Soil Science Society of America.
- Smith GD (1983) Historical development of soil taxonomy – background. In: Wilding LP, Smeck NE, and Hall GF (eds) *Pedogenesis and Soil Taxonomy*, pp. 23–49. New York: Elsevier.
- US Department of Agriculture, Natural Resources Conservation Service, Soil Survey Staff (1999) *Soil Taxonomy, A Basic System of Soil Classification for Making and Interpreting Soil Surveys*, 2nd edn. Agriculture Handbook No. 436. Washington, DC: US Department of Agriculture.
- US Department of Agriculture, Natural Resources Conservation Service, Soil Survey Division Staff (1993) *Soil Survey Manual*. USDA Handbook No. 18. Washington, DC: US Department of Agriculture.

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# ARCHAEA

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## Introduction

In 1977, Carl Woese and his colleagues announced the discovery of 'a new form of life.' The immediate reaction of biologists was largely skeptical. Prior to this, the existing paradigm was that all organisms, except viruses, could be assigned to one of two primary groups, prokaryotes and eukaryotes. The rRNA work of Woese and others confirmed the existence of the archaeal domain, and currently recognized biotic diversity now consists of three groups, two of which are exclusively microbial (Archaea and Bacteria), while the third (Eukarya) contains both microbial life (as unicellular protists) and multicellular organisms.

Although they are metabolically diverse, a property common to the majority of archaeal organisms identified to date is the ability to exist in extreme habitats, including environments of high salt, high temperature, low pH, and acute anoxia. Three general ecological categories represent the overall patterns of archaeal adaptations to extreme environments: thermophilic (heat-loving), methanogenic (methane-producing), and halophilic (salt-loving). Most Archaea belong to at least one of these categories, and a number belong to two. This does not mean, however, that Archaea are limited to extreme environments. Archaea also thrive in freshwater sediments, temperate soils, and other less extreme conditions, confirming that microbes of this domain are ubiquitous.

The harsh environments in which many Archaea flourish have intrigued scientists interested in strategies of coping with life at the extremes. The recent



sequencing of the entire genomes of several Archaea have provided a wealth of knowledge, including the fact that some archaeal genes, including those encoding major metabolic pathway enzymes, are similar to those of Bacteria, while others, such as those for RNA polymerase subunits, are more similar to eukaryal genes, while still others appear to be Archaea-specific.

## Archaeal Evolution

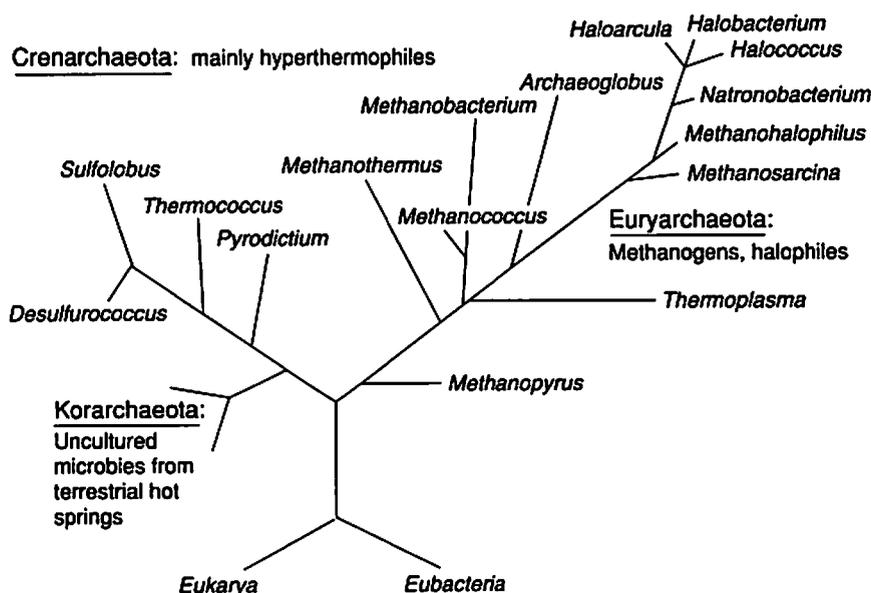
Phylogenetic relationships derived on the basis of 16S and 23S rRNA indicate that the domain Archaea consists of three major kingdoms, the Crenarchaeota, Euryarchaeota, and Korarchaeota (Figure 1). One of the two main branches of this phylogenetic tree contains, in large part, the thermophilic sulfur-dependent Archaea, while the other branch contains the methanogens, the extreme halophiles, and a few thermophilic organisms.

Current phylogenetic evidence deduced from comparison of 16S rRNA sequences suggests that Archaea have evolved more slowly than either Bacteria or the Eukaryotes. This is especially true of hyperthermophilic Archaea. It is not known why Archaea are the slowest-evolving of the three domains, but it may be related to their habitation of extreme environments. For example, organisms living in hyperthermal environments must maintain those genes that specify phenotypic characteristics critical to life at high temperatures, as evolutionary alteration of gene expression could impair organism survival.

Because thermophilic Archaea may have evolved very slowly, it has been proposed that these organisms are likely to have been among the earliest life forms on Earth. The phenotypic properties of thermophiles, including the ability to withstand high temperatures and the use of anaerobic chemoorganotrophic (the use of organic chemicals as electron donors) or chemolithotrophic (the use of inorganic chemicals as electron donors) metabolism, agree well with the phenotype of primitive organisms one would predict, given the geochemical conditions present on the Earth three billion years ago or more. If indeed life first occurred in the form of thermophiles in boiling hot springs deep on the ocean floor, this may explain the mystery surrounding the importance of phosphate in information storage and energy transfer in living cells. In other sea and freshwater environments, phosphate is present in very low concentrations and is often the limiting nutrient for organisms that live there, but water exiting hydrothermal systems often percolates through phosphate-rich minerals, assuring a rich phosphate supply to organisms inhabiting this environment. If thermophiles were present as an early life form, then life on Earth may have evolved in a phosphate-rich environment, thus developing a necessity for this mineral for cellular function.

## The Archaeal Cell

Archaeal cells display a wide variety of morphological types. Some, similar to species of the bacterial domain, are strictly rod-shaped or spherical. Others



**Figure 1** The phylogenetic tree of the Archaea. (Reproduced with permission from Howland JL (2000) *The Surprising Archaea: Discovering Another Domain of Life*. New York: Oxford University Press.

**Table 1** Some cellular features of the Archaea

Feature of cell	Most similar to domain
Morphology	Some unique
Cell wall with pseudopeptidoglycan	Resembles bacteria
Genome consisting of single circular piece of DNA	Bacteria
DNA polymerase, DNA helicase, DNA ligase	Bacteria
Protein trafficking for sugars and inorganic ions	Bacteria
Multisubunit RNA polymerase	Eukarya
Ether-linked lipids	Unique
Promoter site for transcription	Eukarya
Lack of nuclear membrane	Eukarya
Flagellar composition and assembly	Unique
Chaperonin heat-shock proteins	Bacteria

are disks, spirals, or filaments, or exhibit amebal irregularity, with variable protuberances. Still others have a mineral-like geometry, with shapes similar to cubes or triangles. Other irregular cells are bumpy spheres (e.g., *Thermococcus*) or are vaguely rod-shaped, but of highly variable diameter (e.g., *Pyrodictium*).

Archaeal cells possess many characteristics similar to those of the Bacteria and Eukarya, and others that are unique to the archaeal domain (Table 1). With one exception, all Archaea contain a cell wall that, like the cell wall of bacteria, functions to prevent osmotic lysis and to define cell shape. The ability of Archaea to adapt to extreme environments is assisted by the possession of unique cell wall types, which vary from those containing molecules composed of pseudopeptidoglycan, closely resembling bacterial peptidoglycan, to cell walls completely lacking a polysaccharide component. A common wall type is a paracrystalline surface layer (S-layer), consisting of protein or glycoprotein, generally of hexagonal symmetry. Although S-layers are common to all groups of Archaea, the biochemical makeup of S-layers among species is very diverse and, in some cases, this layer is too supple to contribute to the stability of the cell. In these cases, the function of the S-layer is unknown, but it has been proposed that the space between the cytoplasmic membrane and the outer surface of the S-layer may fulfill the role of a periplasmic space reminiscent of Gram-negative bacteria.

Archaeal RNA polymerases are complex, consisting of up to 14 subunits (compared to 4 in the bacterium *Escherichia coli*). Like Bacteria, Archaea possess a single RNA polymerase, but the archaeal RNA polymerase resembles those of eukaryotes in multi-subunit complexity and sequence homology. In addition, archaeal RNA polymerases are unable to initiate transcription *in vitro*, a feature also seen in

eukaryotes where general transcription factors are required for initiation.

## Three Archaeal Groups

### Extreme Halophiles

Extremely halophilic Archaea inhabit environments with salt concentrations high enough to kill most organisms. They occur in hypersaline bodies of water such as the Dead Sea or the Great Salt Lake, saline soils, and have also been isolated from dry deposits where salt is mined commercially. Halobacteria can also be found on salted fish, salted hides, bacon, and sausage, and these microorganisms can often be attributed to the spoilage of these foods.

The formation of saline waters throughout the world can result from the geologic separation of seawater from the open ocean and concentration of salts by evaporation, or may result from the dissolution of salts from rocks into bodies of water. The ionic composition of hypersaline water bodies varies widely, from high  $\text{Na}^+$  ( $\sim 100 \text{ g l}^{-1}$ ) and  $\text{Cl}^-$  ( $\sim 200 \text{ g l}^{-1}$ ) in the Great Salt Lake, to high  $\text{Cl}^-$  ( $>200 \text{ g l}^{-1}$ ) in the Dead Sea, to high  $\text{SO}_4^{2-}$  ( $>200 \text{ g l}^{-1}$ ) in Hot Lake in Washington state, USA. The varied chemical and physical properties of saline habitats result in colonization by a widely diverse group of archaeal prokaryotes, which possess some common features that allow them to thrive in these high-solute environments.

Research has shown that extreme halophiles not only tolerate salty conditions, but they also require high concentrations of salt. A generally accepted definition of an extreme halophile is that the organism requires at least  $1.5 \text{ mol l}^{-1}$  NaCl for growth, but most species require  $2\text{--}4 \text{ mol l}^{-1}$  for optimal growth. Virtually all extreme halophiles can grow at the limit of saturation for NaCl ( $5.5 \text{ mol l}^{-1}$ ), although some species grow only very slowly at this salinity. The plasma membrane of halophiles does not exclude salts, but can select for certain ions so that internal concentrations of ions can be controlled and cellular functioning can be maintained. Cells of *Halobacterium*, for example, pump large amounts of potassium from the environment into the cell such that the concentration of  $\text{K}^+$  inside the cell is higher than the  $\text{Na}^+$  concentration outside. Thus, the total ionic strength remains the same on both sides of the plasma membrane but potassium, required for many cellular functions, is the prevailing cation on the inside. In this manner, *Halobacterium* employs an inorganic ion as its compatible solute and remains in positive water balance.

The cell wall of *Halobacterium* is stabilized by sodium ions and in low- $\text{Na}^+$  environments the

cell wall breaks down, resulting in cell lysis. The halobacterial cell wall is composed of a glycoprotein with an exceptionally high content of the acidic amino acids aspartate and glutamate, and the sodium ions shield the negative charges contributed by the carboxyl groups of these amino acids. When sodium is diluted, the negatively charged parts of the proteins actively repel each other, leading to cell lysis. Thus, the cellular components of halophiles exposed to the external environment require high sodium for stability, whereas internal components require high potassium. This requirement for specific cations in such high amounts is a feature unique to halophilic bacteria. Another unique quality of Halobacteria are cytoplasmic proteins with very low levels of hydrophobic amino acids, perhaps representing an evolutionary adaptation to the highly ionic cytoplasm of extreme halophiles. In environments of high ionic strength, polar proteins would tend to remain in solution, whereas nonpolar molecules would tend to cluster and perhaps lose activity.

Some extreme halophiles possess a unique light-mediated synthesis of adenosine triphosphate (ATP) that does not involve chlorophyll pigments. When light is available and their ability to obtain energy through respiration is compromised, *Halobacterium salinarum* and certain other extreme halophiles synthesize and insert a protein, bacteriorhodopsin, into their membranes. Conjugated to this is a molecule of retinal, a carotenoid-like molecule that can absorb light and catalyze the transfer of protons across the cytoplasmic membrane. Light-mediated ATP production in *H. salinarum* has been shown to support slow growth of this organism anaerobically in the absence of organic energy sources and under conditions in which other energy-generating reactions do not occur.

## Methanogens

Two features common to all methanogenic Archaea are the inability to tolerate oxygen or reactive oxygen species and the ability to produce methane gas. Methane production in soils characteristically occurs under anaerobic, highly reducing conditions in the absence of nitrate, sulfate, or ferric iron, including the mud of swamps and marshes, the beds of fresh and marine bodies of water, and mud originating from sewage plants and rice paddies. In some instances, methanogens live in small anoxic pockets in soils in an otherwise oxygen-rich area. Such regions are often formed by the action of microorganisms that locally consume all of the available oxygen, and several studies have confirmed that methanogens can be present throughout a macroscopically oxic soil

and that methane-producing activity can respond rapidly to the establishment of appropriate anoxic conditions.

Methanogens also flourish in the digestive systems of ruminants. Production of methane gas worldwide from cattle, goats, sheep, and camels is greater than methane production from paddy fields and swamps. The rumen utilizes a mixed population of microorganisms, including Eubacteria, methanogenic Archaea, and anaerobic protozoa to carry out the digestion of cellulose and other polymeric sugars. Methanogens are responsible for regulating the overall fermentation in the rumen by removing hydrogen gas during methane production. This action keeps the hydrogen concentration in the rumen low, encouraging the activity of hydrogen-producing species and altering their metabolism towards higher-yielding pathways. These pathways result in the synthesis of more microbial cells, increasing the available protein to the ruminant.

Methane is the final product of a complex community of organisms breaking organic materials down into the simple methanogenic substrates and thus, methanogens complete the last step in the anaerobic decomposition of organic matter. Because they are dependent on other organisms for provision of substrate and the establishment of reducing conditions, methanogens can only function as members of microbial communities. Methanogenesis is frequently rate-limited by the activities of the other members of the community, and particularly by how rapidly hydrogen or acetate is made available. At least 10 substrates can be converted to methane by methanogens (Table 2) and three main classes of metabolic reactions can be used to create energy for ATP synthesis. The first class utilizes CO<sub>2</sub>-type substrates (Table 2, lines 1–5), while the second class of reaction involves reduction of the methyl group of methyl-containing compounds to methane (Table 2, lines

**Table 2** Reactions for methanogenesis by methanogenic bacteria

Substrates		Products
4H <sub>2</sub> + CO <sub>2</sub>	→	CH <sub>4</sub> + 2H <sub>2</sub> O
4H <sub>2</sub> + HCO <sub>3</sub> <sup>-</sup> + H <sup>+</sup>	→	CH <sub>4</sub> + 3H <sub>2</sub> O
4 Formate + 4H <sup>+</sup>	→	CH <sub>4</sub> + 3CO <sub>2</sub> + 2H <sub>2</sub> O
4 (2-Propanol) + CO <sub>2</sub>	→	CH <sub>4</sub> + 4 acetone + 2H <sub>2</sub> O
2 Ethanol + CO <sub>2</sub>	→	CH <sub>4</sub> + 2 acetate + 2H <sup>+</sup>
4 Methanol	→	3CH <sub>4</sub> + CO <sub>2</sub> + 2H <sub>2</sub> O
4 Methanol	→	3CH <sub>4</sub> + HCO <sub>3</sub> <sup>-</sup> + H <sup>+</sup> + H <sub>2</sub> O
4 Methylamine + 2H <sub>2</sub> O	→	3CH <sub>4</sub> + CO <sub>2</sub> + 4NH <sub>4</sub> <sup>+</sup>
Methanol + H <sub>2</sub>	→	CH <sub>4</sub> + H <sub>2</sub> O
Acetate + H <sup>+</sup>	→	CH <sub>4</sub> + CO <sub>2</sub>
Acetate + H <sub>2</sub> O	→	CH <sub>4</sub> + HCO <sub>3</sub> <sup>-</sup>

6–9). The third class of methanogenic reactions is acetotrophic, the cleavage of acetate to  $\text{CH}_4$  plus  $\text{CO}_2$  (Table 2, lines 10–11). The conversion of acetate to methane appears to be a very significant ecological process, especially in sewage digesters and in freshwater anoxic environments where competition for acetate between sulfate-reducing bacteria and methanogenic bacteria is not extensive. The reduction of  $\text{CO}_2$  to  $\text{CH}_4$  is generally  $\text{H}_2$ -dependent, but formate, carbon monoxide, and even elemental iron can serve as electron donors for methanogenesis. A few methanogens can utilize simple organic compounds as electron supplies for  $\text{CO}_2$  reduction.

Methanogenesis employs a unique collection of cofactors in its reactions. Methanogens often contain high concentrations of these compounds, whose presence can be used to determine the prevalence of methanogenic Archaea. One cofactor commonly used to identify methanogens is coenzyme 5-deazaflavin F420, an electron carrier involved in several reactions in the methanogenic pathway which also has a role in DNA photorepair. Another cofactor, coenzyme F430, contains nickel, which all methanogens require for growth. A third cofactor unique to methanogenesis, coenzyme M, acts as a methyl-carrying coenzyme in the last step of the methanogenic pathway and is thus involved in the final reduction of a methyl group to form methane.

### Hyperthermophiles

The archaeal kingdom Crenarchaeota consists of a great diversity of organisms. Some form a stable part of the soil microbial community in boreal environments, while others are defined by their extremely thermophilic nature. This latter group, the hyperthermophiles, contains organisms that are the most heat-loving of all known prokaryotes. Several hyperthermophiles are capable of growth at temperatures above the normal boiling point of water, and all have temperature optima above  $80^\circ\text{C}$ .

Many hyperthermophilic Archaea have been isolated from geothermally heated soils or waters containing elemental sulfur and sulfides, and most hyperthermophilic species metabolize sulfur in some way. In fact, the first hyperthermophile discovered, *Sulfolobus*, grows in sulfur-rich hot acid springs. Sulfur-rich environments are found throughout the world, and extensive studies of hyperthermophilic Archaea have been made in Yellowstone National Park (USA), where the highest concentration of sulfur-rich thermal features in the world has been attracting researchers since the first scientific study of the region in the late nineteenth century.

Hyperthermophilic Archaea have also been found in artificial thermal habitats such as the boiling

outflow of geothermal power plants. In addition, a phylogenetically distinct set of hyperthermophilic Archaea has been isolated from submarine volcanic habitats, where the pressure of even a few meters of seawater can raise the boiling point of water sufficiently to select for organisms capable of growth above  $100^\circ\text{C}$ . *Pyrolobus fumarii*, a submarine organism, has a growth optimum at  $106^\circ\text{C}$  but can grow at  $113^\circ\text{C}$ , and can even survive autoclaving at  $121^\circ\text{C}$  for 1 h.

Depending on the surrounding geology, geothermally heated environments may be either slightly alkaline to mildly acidic (pH 5–8) or extremely acidic, with pH values below 1 not uncommon. Such extreme acidity does not deter the hyperthermophiles: *Picrophilus oshimae* has a pH optimum for growth of 0.7 and can grow significantly at pH values approaching zero; however, the majority of thermophilic Archaea inhabit neutral or mildly acidic habitats.

With a few exceptions, hyperthermophiles are obligate anaerobes. Their sulfur requirement is based on the need for an electron acceptor to carry out anaerobic respiration or an electron donor for chemolithotrophic metabolism. Organisms of the genera *Thermococcus* and *Thermoproteus* oxidize a variety of organic compounds (e.g., small peptides, glucose, starch) anaerobically in the presence of  $\text{S}^0$  as an electron acceptor. *Sulfolobus* is an obligate aerobe capable of oxidizing organic compounds,  $\text{H}_2\text{S}$ , or  $\text{S}^0$  to  $\text{H}_2\text{SO}_4$  and fixing  $\text{CO}_2$  as a carbon source. Many hyperthermophilic Archaea can grow chemolithotrophically with  $\text{H}_2$  as an energy source. *Acidianus*, a facultative aerobe resembling *Sulfolobus*, grows anaerobically using  $\text{S}^0$  as an electron acceptor and  $\text{H}_2$  as an electron donor, forming  $\text{H}_2\text{S}$  as the reduced product, and *Pyrodictium* can be cultured under strict anaerobic conditions in a mineral-salts medium supplemented with  $\text{H}_2$  and  $\text{S}^0$  at temperatures up to  $110^\circ\text{C}$ .

A unique property shared by many hyperthermophiles such as *Sulfolobus* and *Acidianus* is an unusually low guanine-cytosine (GC) base ratio. The DNA of *Sulfolobus* is  $\sim 38\%$  GC, whereas that of *Acidianus* is  $\sim 31\%$ . These low GC base ratios are intriguing; in a test tube, DNA of 30–40% GC content would melt almost instantly at  $90^\circ\text{C}$ . Research into how DNA of these organisms is prevented from melting is ongoing; however, it is hypothesized that the DNA may be protected, in part, by high cytoplasmic solute concentrations (the melting temperature of DNA increases as the solute concentration increases). Cytoplasmic concentrations of solutes such as cyclic 2,3-diphosphoglycerate in cells of *Methanopyrus fervidus* and other thermophilic methanogens are

closely correlated with the temperature at which the organisms are grown in laboratory incubations. In addition, it is thought that specific DNA binding proteins of hyperthermophiles somehow prevent DNA from melting, perhaps by folding the DNA into a conformation consistent with thermal stability. *Pyrodictium* cells grown at 110°C produce 80% of their protein biomass as a single protein that functions as a molecular chaperonin, stabilizing other cellular proteins by refolding them as they begin to denature near the upper temperature limits of growth. At 100°C (near the optimum for growth of *Pyrodictium*), very little of this chaperonin protein is made, suggesting that only at very extreme temperatures do the otherwise thermally stable proteins of this organism begin to denature. Additional protein adaptations of hyperthermophiles that allow these organisms to withstand extreme temperatures include sequence modifications, addition of salt bridges, increased hydrophobic interactions, additional ion pairing and hydrogen bonding, improved core packing, and shortening of loops. These strategies, used to differing extents by different thermophilic proteins, not only confer higher thermal stability but also enhance rigidity and resistance to chemical denaturation.

Within the last several years, molecular techniques have uncovered a unique lineage of the kingdom Crenarchaeota that is phylogenetically distinct from the hyperthermophiles. Nonthermophilic Crenarchaeota, which have been identified in marine picoplankton, freshwater sediments, soils, and in continental shelf anoxic sediments, have been shown to account for as much as 2% of microbial rRNA in soils analyzed. Phylogenetic analyses suggest that the nonthermophilic Crenarchaeota may have a common ancestor with the hyperthermophiles, but as yet the ecological significance of the nonthermophiles remains unknown.

### Psychrophiles

Archaea have also been detected in ecosystems with characteristics in direct contrast to hyperthermophilic environments. Psychrophilic (cold-loving) Archaea account for over a third of the prokaryotic biomass in coastal Antarctic surface waters, and the hypersaline lakes of the Vestfold Hills lake system in Eastern Antarctica have been the subjects of a number of studies on microbial distribution. One of these lakes is Deep Lake, with a salinity of 320 g l<sup>-1</sup> and temperatures between -14 and -18°C. The biodiversity of Deep Lake is low, and is dominated by Archaea of the family Halobacteriaceae. To date, only three psychrophilic archaeal strains, all free-living

and members of the subdomain Eukaryarchaeota, are available in pure culture. *Methanococcoides burtonii* ( $T_{\min}$  -2.5°C) and *Methanogenium frigidum* ( $T_{\min}$  -10°C) were originally isolated from the bottom of Ace Lake, Antarctica, where the methane-saturated waters remain between 1 and 2°C.

### Thermoplasma

*Thermoplasma acidophilum* is a prokaryote that does not possess a cell wall and in this respect resembles the mycoplasma. Phylogenetically, however, *Thermoplasma* is a member of the Archaea. *Thermoplasma* is an acidophilic, aerobic, thermophilic chemoorganotroph, and with one exception, all strains of *Thermoplasma* have been obtained from self-heating coal refuse piles, which contain coal fragments, pyrite, and other organic materials extracted from coal. When this refuse is dumped into piles in coal-mining operations, it tends to self-heat by spontaneous combustion and creates conditions conducive to growth of *Thermoplasma*, which apparently metabolizes leached organic compounds. A chemically unique cell membrane allows *Thermoplasma* to survive the osmotic stresses of life without a cell wall and to withstand the dual environmental extremes of low pH and high temperature. This membrane contains a unique lipopolysaccharide that, together with other molecules, renders the *Thermoplasma* stable to hot acidic conditions.

### Biotechnological Use of Extremoenzymes

Biotechnologically useful enzymes represent the main focus of industrial interest in the Archaea, as a result of the abilities of these microbes to function at the temperature, salinity, and pH limits of life. Heat-tolerant enzymes are currently the most investigated of all extremoenzymes because performing biotechnologically related processes at higher temperatures is often advantageous for many reasons. In chemical reactions involving organic solvents, decreased viscosity and increased diffusion at elevated temperatures result in higher reaction rates. In addition, performing reactions at higher temperatures reduces the possibility of complications resulting from contamination. One thermophilic compound of particular interest is DNA polymerase, an enzyme that is responsible for the elongation of the primer strand of a growing DNA molecule and is thus central to the polymerase chain reaction for DNA amplification. DNA polymerases from various hyperthermoarchaea (including *Pwo* from *Pyrococcus woesei* and *Pfu* from *P. furiosus*) are showing biotechnological promise, based on

their stringent proofreading abilities and suitability for the amplification of longer DNA fragments. These hyperthermophilic DNA polymerases possess error rates that are five- to 10-fold lower than that of the widely used thermobacterial *Taq* polymerase from *Thermus aquaticus*.

Applied uses exist or have been proposed for a variety of other archaeally derived materials. The extremely stable lipids of archaeal membranes may represent a novel drug delivery system because of their enhanced stability under temperature extremes. Archaeal components such as the S-layer glycoprotein have drawn interest for their use as possible vaccine carriers and other nanotechnological potentials, and it has been shown that much higher immune responses in mice are shown to protein antigens encapsulated in archaeosomes than in conventional liposomes. A thermostable ligase for the ligase chain reaction (an amplification method that involves the ligation of two sets of adjacent oligonucleotides) would be of obvious benefit because the ligation must be carried out near the melting temperature of the DNA, and the ligase enzymes must be stable during the dissociation step that follows. Currently, a ligase from *T. aquaticus* is used, but a more stable equivalent may be available from hyperthermophilic Archaea. Haloarchaeal polymers have been considered as a raw material for biodegradable plastics. Hydrolases from hyperthermophiles could be used in the food-processing industry to hydrolyze fats at high temperatures, reducing bacterial contamination problems. Addition of polymer-hydrolyzing extremoenzymes such as beta-glycanases from psychrophiles to detergents would allow for efficient washing in cold water. The food industry could exploit pectinases that act at lower temperatures in the processing of fruit juices or cheeses.

Often, the mere presence of archaeal communities carries considerable potential economic value. Methanogenic Archaea have proven to be quite valuable in their capacity as clean and inexpensive energy sources, and acidophilic Archaea have been identified at several acid mine drainage sites where their mineral-sulfide oxidizing abilities play an important role in the geochemical sulfur cycle.

The days of Archaea being considered as just 'odd bacteria' adapted to living in extreme environments appear to be over. In the past few years, information on the isolation, characterization, description, and applications of Archaea has mushroomed. Researchers will continue to study the adaptations that allow Archaea to grow at the extremes and to search for new species that will extend the boundaries that limit life of Earth. There is no doubt that many novel features remain to be discovered about these microorganisms, and their continued study will have a major impact on science in the decades to come.

*See also: Bacteria: Soil*

### Further Reading

- Bernander R (1998) Archaea and the cell cycle. *Molecular Microbiology* 29: 955–961.
- Eichler J (2001) Biotechnological uses of archaeal extremozymes. *Biotechnology Advances* 19: 261–278.
- Howland JL (2000) *The Surprising Archaea: Discovering Another Domain of Life*. New York: Oxford University Press.
- Jarrell KF, Bayley DP, Correia JD, and Thomas NA (1999) Recent excitement about the Archaea (Archaeobacteria). *BioScience* 49: 530–542.
- Kates M, Kushner DJ, and Matheson AT (eds) (1993) *The Biochemistry of Archaea (Archaeobacteria)*. New Comprehensive Biochemistry Series, vol. 26. Amsterdam, Netherlands: Elsevier Science.
- Madigan MM, Martinko J, and Parker J (2000) *Brock Biology of Microorganisms*. Upper Saddle River, NJ: Prentice-Hall.
- Oren A (2002) Molecular ecology of extremely halophilic Archaea and Bacteria. *FEMS Microbiology Ecology* 39: 1–7.
- Reysenbach A-L, Voytek M, and Mancinelli R (eds) (2001) *Thermophiles: Biodiversity, Ecology, and Evolution*. New York: Kluwer Academic Plenum.
- Vreeland RH and Hochstein LI (eds) (1993) *The Biology of Halophilic Bacteria*. Boca Raton, FL: CRC Press.
- Woese CR and Wolfe RS (eds) (1985) *The Bacteria: A Treatise on Structure and Function*, vol. VIII. *Archaeobacteria*. Orlando, FL: Academic Press.