SnapShot: Microbial Extremophiles

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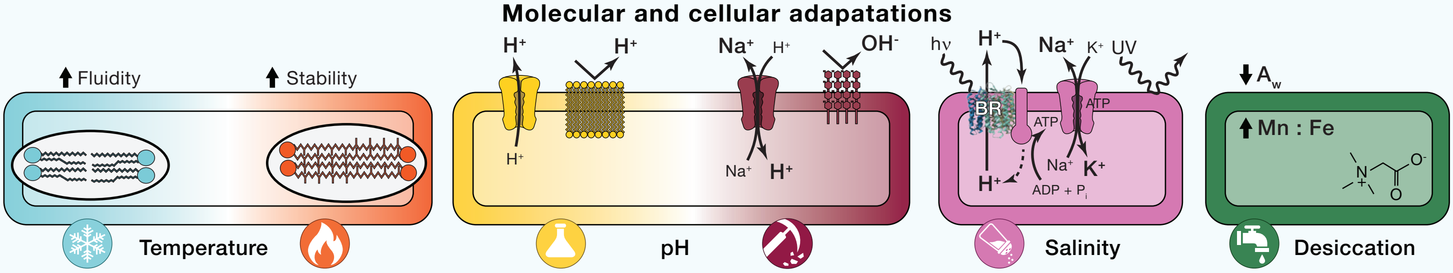
Global distribution of extremophiles

For GPS coordinates and to find out more, explore the interactive Google map online: http://bit.ly/Schmid-extremophiles-map

Molecular and cellular adapatations



Temperature

- Membrane bilayers
- Unsaturated lipids
- Reduced hydrophobic protein core
- Bacteria dominate microbial communities

- Membrane monolayer
- Branched lipids
- Compact proteins
- Reverse gyrase winds DNA helix
- Archaea dominate

pH

- Proton efflux
- Proton impermeability
- Metallotolerance
- Sulfur-oxidizing archaea dominate >65°C

- Proton import
- Acidic polymer cell wall repels OH^-
- Archaea dominate communities

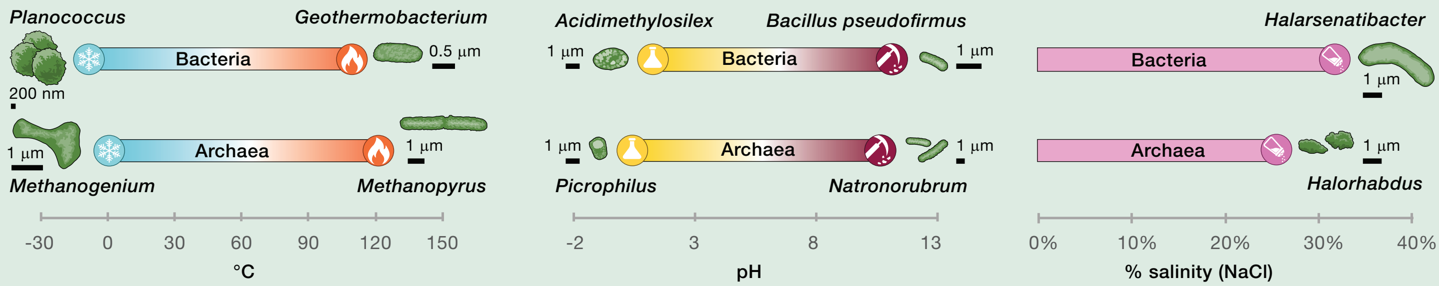
Salinity

- Salt-in: high cytoplasmic K^+; acidic proteome
- Salt-out: accumulation of compatible solutes
- Bacteriorhodopsin-mediated phototrophy (BR)
- Photopigments: UV protection

Desiccation

- Compatible solutes (e.g., betaine) to combat low water activity (a_w)
- Abundant antioxidants
- Radiation resistant: high Mn : Fe ratio

Limits of life and extreme record holders



See online version for legends and references

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Cell

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Extremophiles are overwhelmingly single-celled microbes that teach us about the limits of life, both on this planet and beyond. Life evolved under conditions that were harsher than those today and continues to thrive in environments that humans consider extreme. Earthly environments hosting extremophiles resemble extraterrestrial locations; therefore, characterizing extremophile adaptations and mechanisms of survival is essential to guide our search for life elsewhere. Knowledge of extremophiles and their enzymes has driven industrial and technological advances.

Poly-extremophiles are adapted to more than one extreme condition and are surprisingly common. Adaptation to one harsh condition often facilitates resistance to another condition as a by-product. However, the condition-based categories used to classify extremophiles do not adequately reflect their natural environment or phylogenetic history and, instead, reflect convergent evolution. Nonetheless, these categories are useful for illustrating the cellular and molecular adaptations that have evolved for thriving at the extremes, which we delineate in this SnapShot. See the online interactive map for additional detail on biogeography, record holders, and literature references: http://bit.ly/Schmid-extremophiles-map.

Psychrophiles | *Temperature <15°C*

Psychrophiles are found in low-temperature environments, such as polar oceans, lakes, and permafrost (DeMaere et al., 2013). Altered properties of psychrophilic cells include compatible solutes and chaperones, increased membrane fluidity due to shorter side chains and decreased lipid saturation, and exopolysaccharides with cryoprotective roles (Siliakus et al., 2017). To maintain flexibility and activity, psychrophilic proteins are enriched for small amino acids such as glycine; they also have fewer prolines, a reduced hydrophobic core, and a protein surface with fewer charged residues (Reed et al., 2013). These adaptations ensure a lower energy barrier between the various conformations of psychrophilic proteins.

Thermophiles | *Temperature >60°C (>80°C for hyperthermophiles)*

Thermophiles are found in volcanic hot springs and oceanic hydrothermal vents. Their proteins maintain activity at high temperatures via prominent hydrophobic cores, increased electrostatic interactions, and enrichment in salt and disulfide bridges (Reed et al., 2013). The thermophile-specific enzyme reverse gyrase introduces positive supercoils into DNA to maintain the double-stranded helical structure at high temperatures (Ogawa et al., 2015). The membranes of thermophiles feature lipids that often form monolayers, comprising tetra-ester (bacteria) or tetra-ether (archaea) lipids enriched for branched, saturated hydrocarbon chains (Siliakus et al., 2017). These adaptations ensure thermal stability, thereby maintaining nutrient transport and a chemiosmotic gradient.

Acidophiles | *Acidic pH <3*

Acidophiles are found in volcanic hot springs and acidic mine drainage. Most acidophiles keep their cytoplasm close to neutral pH using powerful proton efflux pumps and proton-deflecting membranes with reduced permeability (branched ether monolayers resembling those of thermophiles [Siliakus et al., 2017]). Some species have an acidified cytoplasm and use chaperones to maintain correct protein folding under acidic conditions; their proteins have an overabundance of acidic residues on the surface, which minimizes low pH destabilization. Many acidophiles are also resistant to high concentrations of metal ions.

Alkaliphiles | *Alkaline pH >9*

Alkaliphiles are found in mineral-rich soda lakes and hydrothermal alkaline vents (Banciu and Muntyan, 2015). They maintain an intracellular neutral pH by cytosolic acidification, an active mechanism that uses Na+/H+ antiporters to accumulate intracellular protons (Padan et al., 2005). A passive mechanism found in some alkaliphilic bacteria is an acidic polymer cell wall matrix. This matrix protects the membrane by preventing the entry of hydroxide ions.

Halophiles | *NaCl >0.5 M (or very high sugar for osmophiles)*

Halophiles are found in salt lakes and marine salterns and use either "salt-out" or "salt-in" adaptations. The former strategy is found in bacteria and eukaryotes, which accumulate high intracellular concentrations of compatible osmolytes (e.g., glycerol, betaine) to maintain osmotic homeostasis. The latter strategy is found mainly in archaea that accumulate high levels of KCl in their cytoplasm using a K+/Na+ antiporter (Gunde-Cimerman et al., 2018). This requires protein adaptions, including an increased negative surface charge due to a high acidic amino acid content (Reed et al., 2013). In high light and low oxygen, many halophiles use bacteriorhodopsin (BR), a light-driven proton pump, to generate ATP to drive the antiporter and maintain osmobalance (Gunde-Cimerman et al., 2018). Photoprotective membrane-associated pigments (e.g., carotenoids) protect against frequent UV damage in hypersaline environments. Many hypersaline-adapted archaea are also polyextremophiles adapted to low temperatures and high pH (Banciu and Muntyan, 2015; DeMaere et al., 2013).

Xerophiles | *Desiccation, water activity (a_w) <0.8*

Xerophiles are found in dry environments such as hot and cold deserts, including the Dry Valleys of Antarctica. Xerophiles use similar adaptations to salt-out halophiles, accumulating high intracellular concentrations of compatible osmolytes (glycine, betaine, trehalose or glycerol) to cope with low a_w (Lebre et al., 2017). Xerophiles are often radioresistant because the mechanisms for dealing with desiccation render them resistant to ionizing radiation and oxidative stress (Hallsworth, 2018). Xerophiles have elevated levels of antioxidants to protect against desiccation and radiation-induced damage to proteins. For example, *Deinococcus radiodurans* uses manganese complexes as antioxidants (Daly, 2009).

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