

# MICROBIOLOGY OF EXTREME ENVIRONMENTS

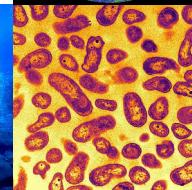
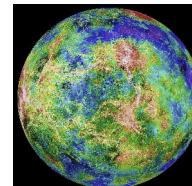
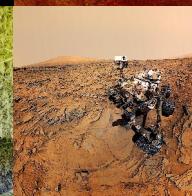
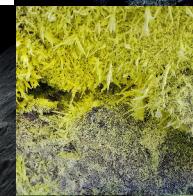
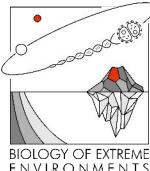
## Extremophiles: Acidic, alkaline and saline environments

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# Acidity and alkalinity

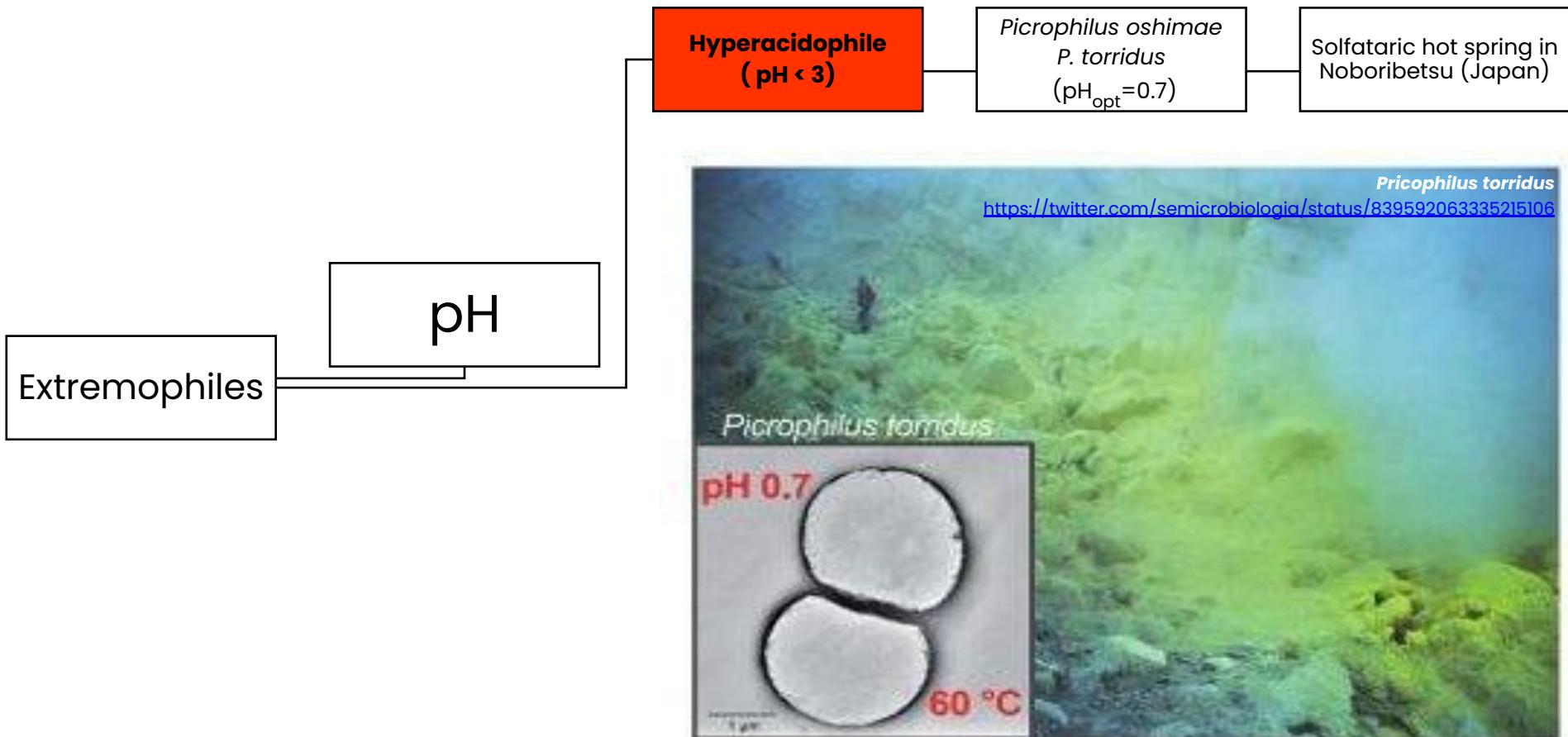
*pH determines which species survives*



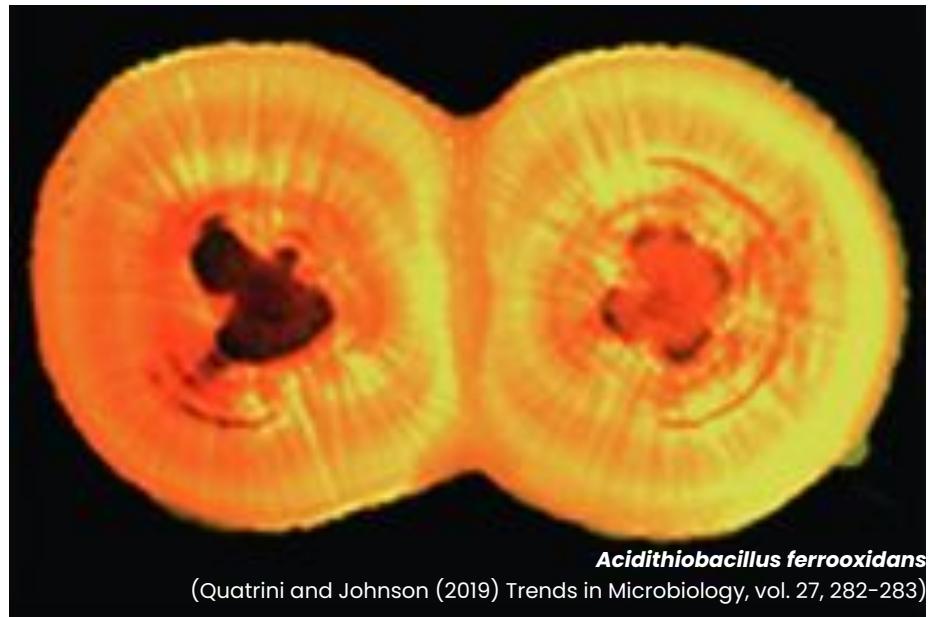
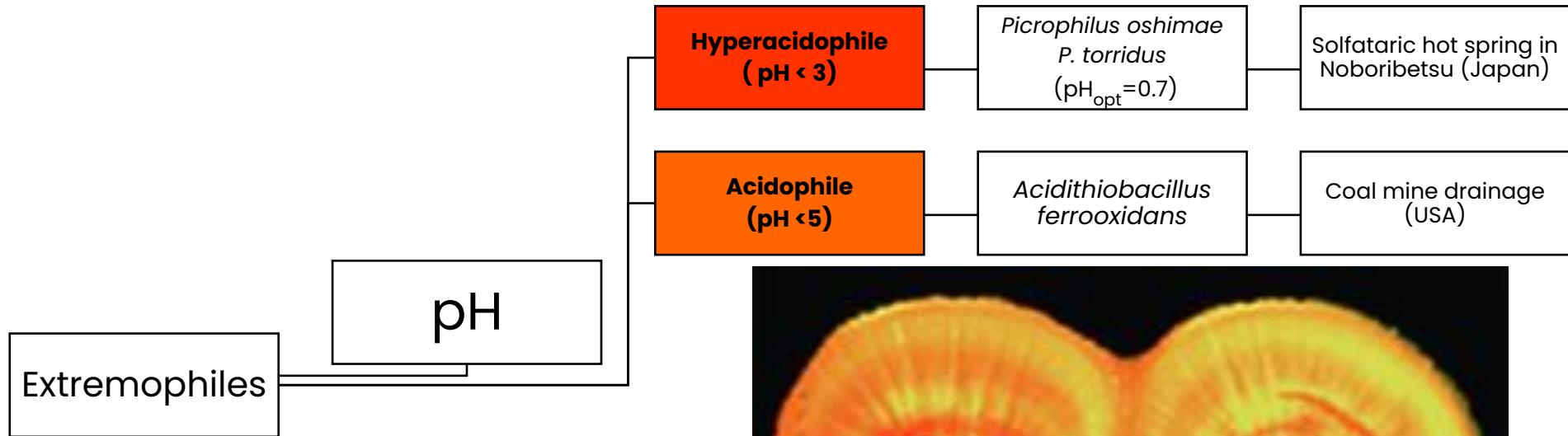
Grand Prismatic Spring, Yellowstone Park (Wyoming)  
<https://www.livescience.com/47263-grand-prismatic-hot-spring-photos.html>

Every microorganism has a pH range, typically about 2–3 pH units, within which growth is possible.

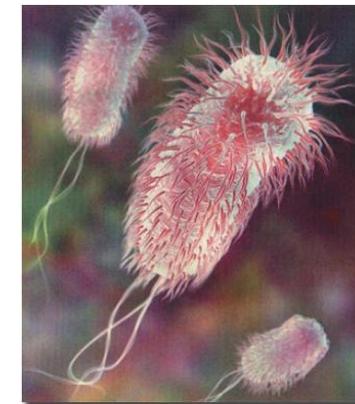
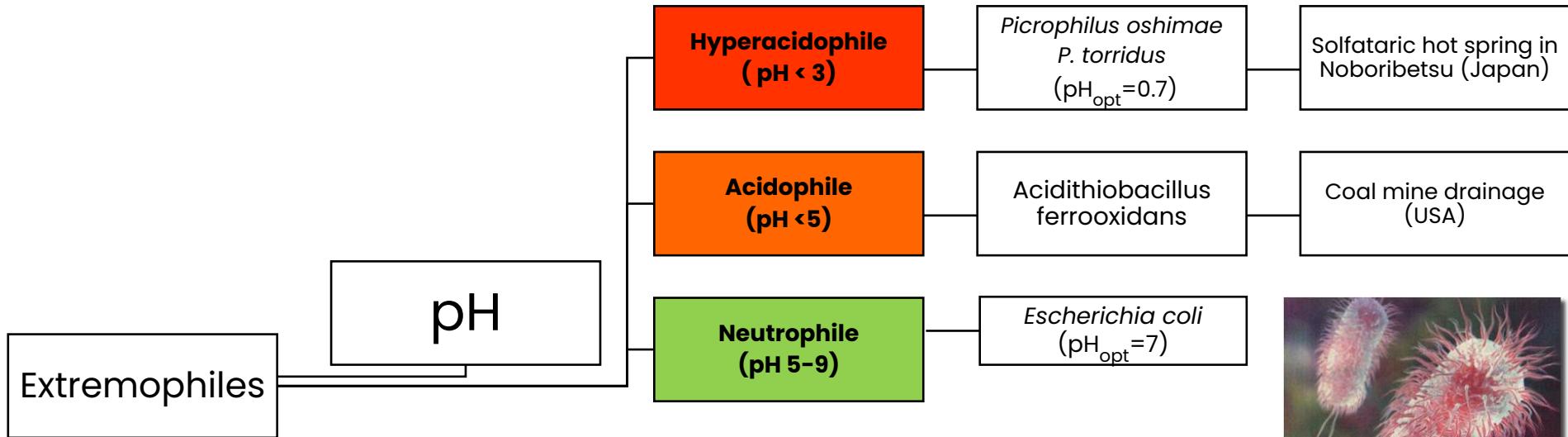
# Acidity and alkalinity dependent extremophiles. Who are they?



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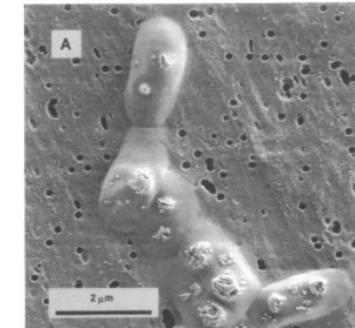
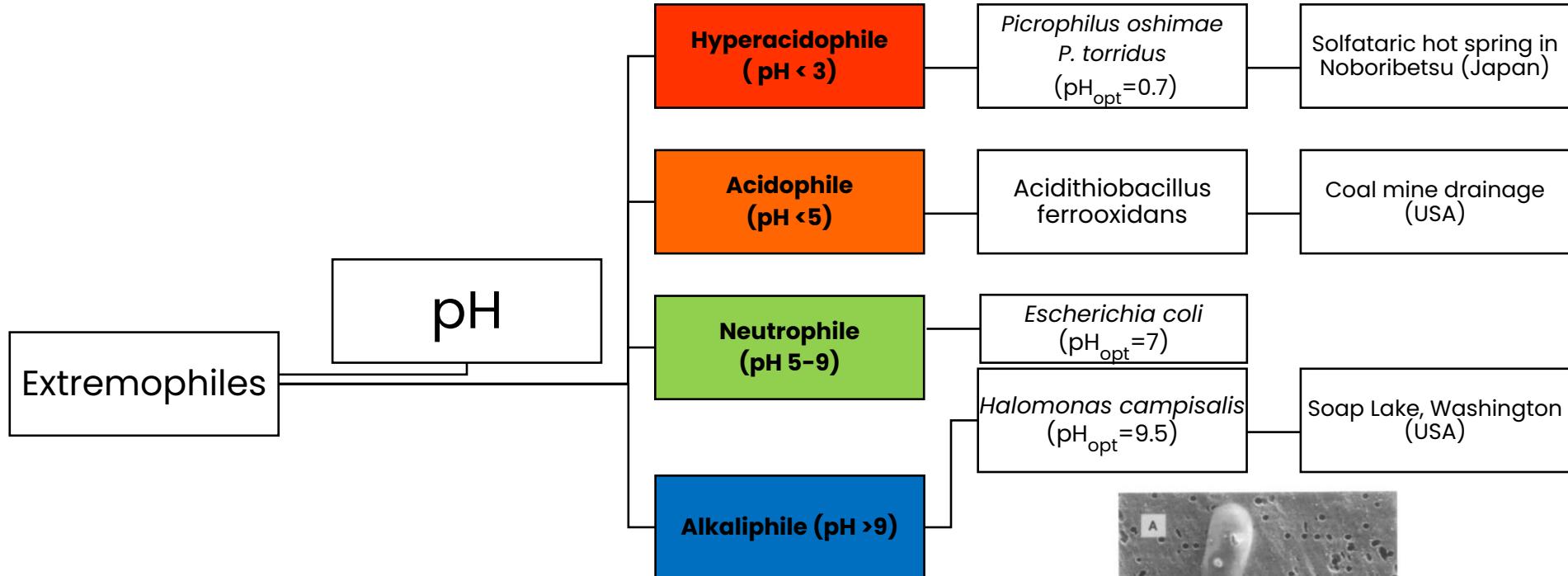
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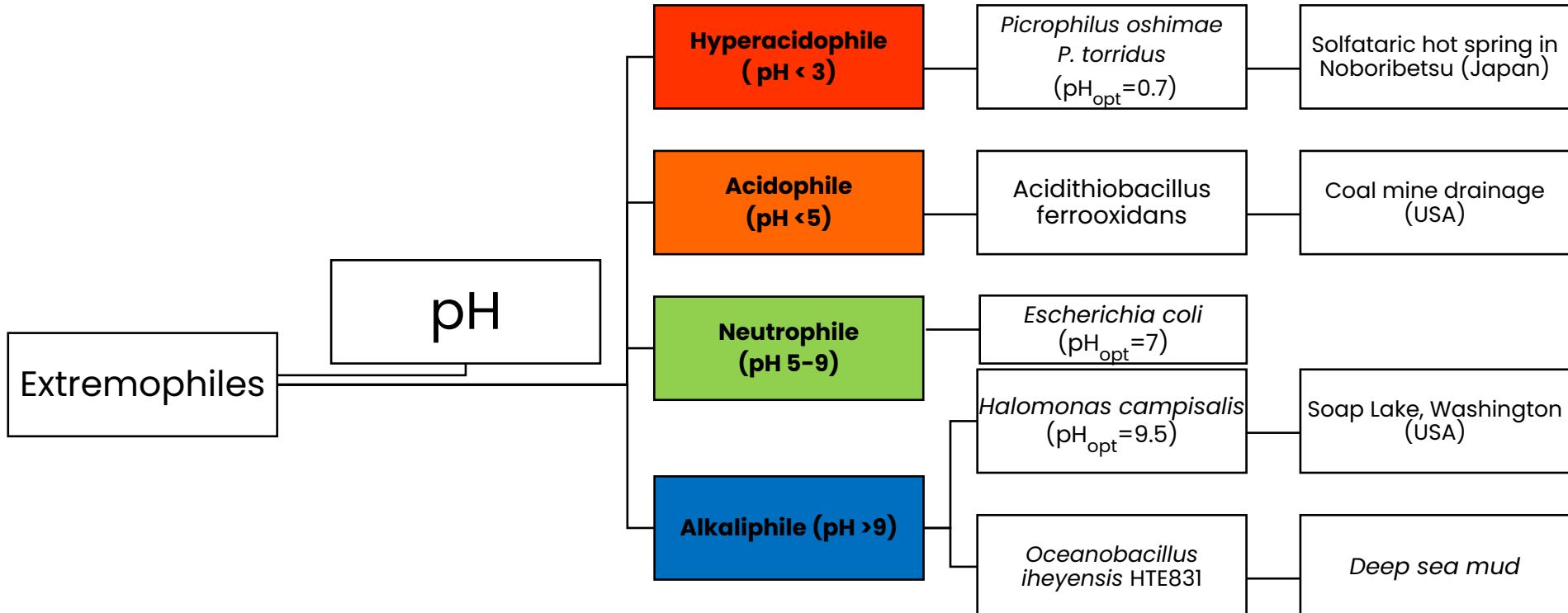
*Escherichia coli*

[U.S. Environmental Protection Agency](http://www.epa.gov)

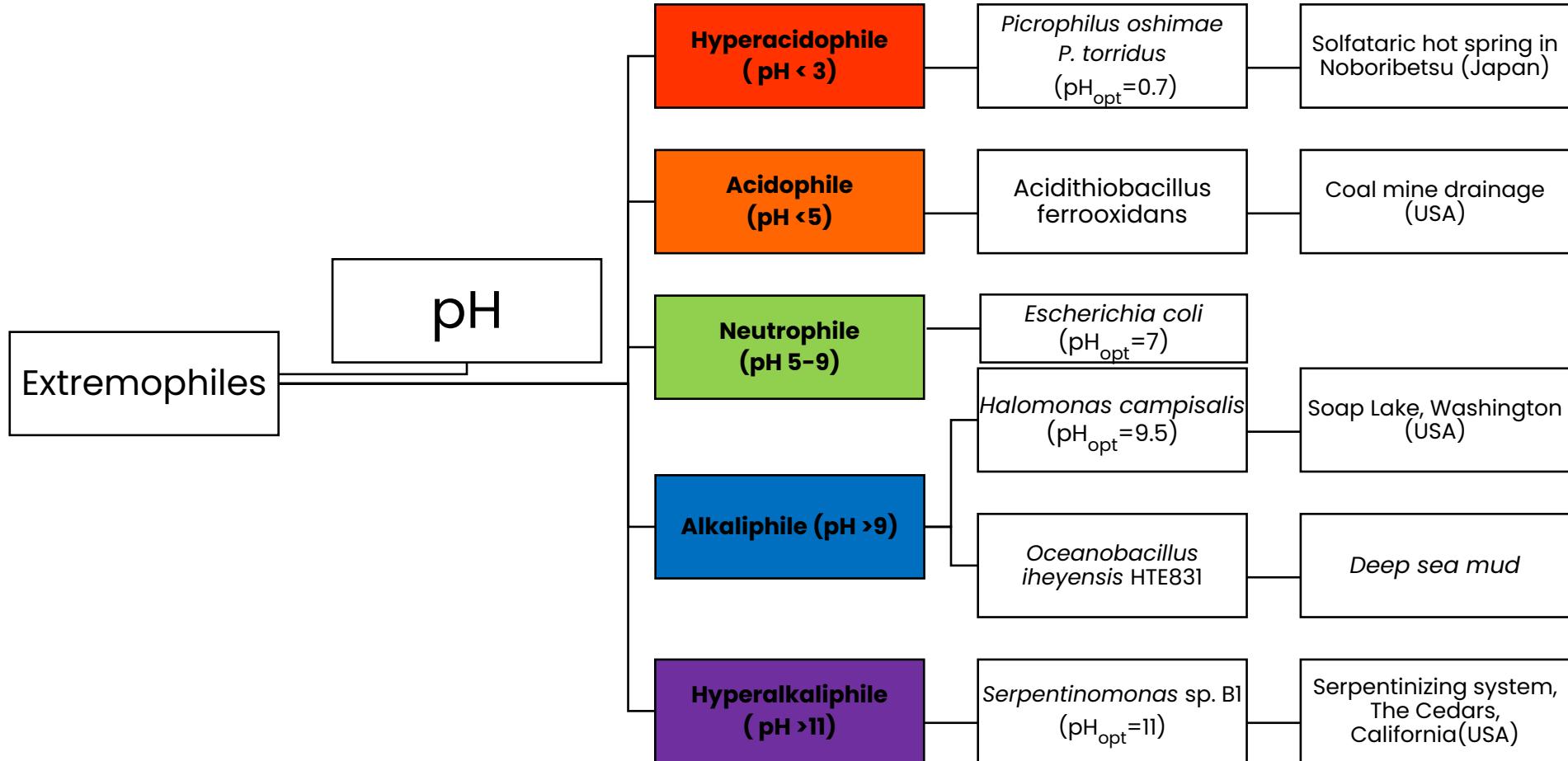
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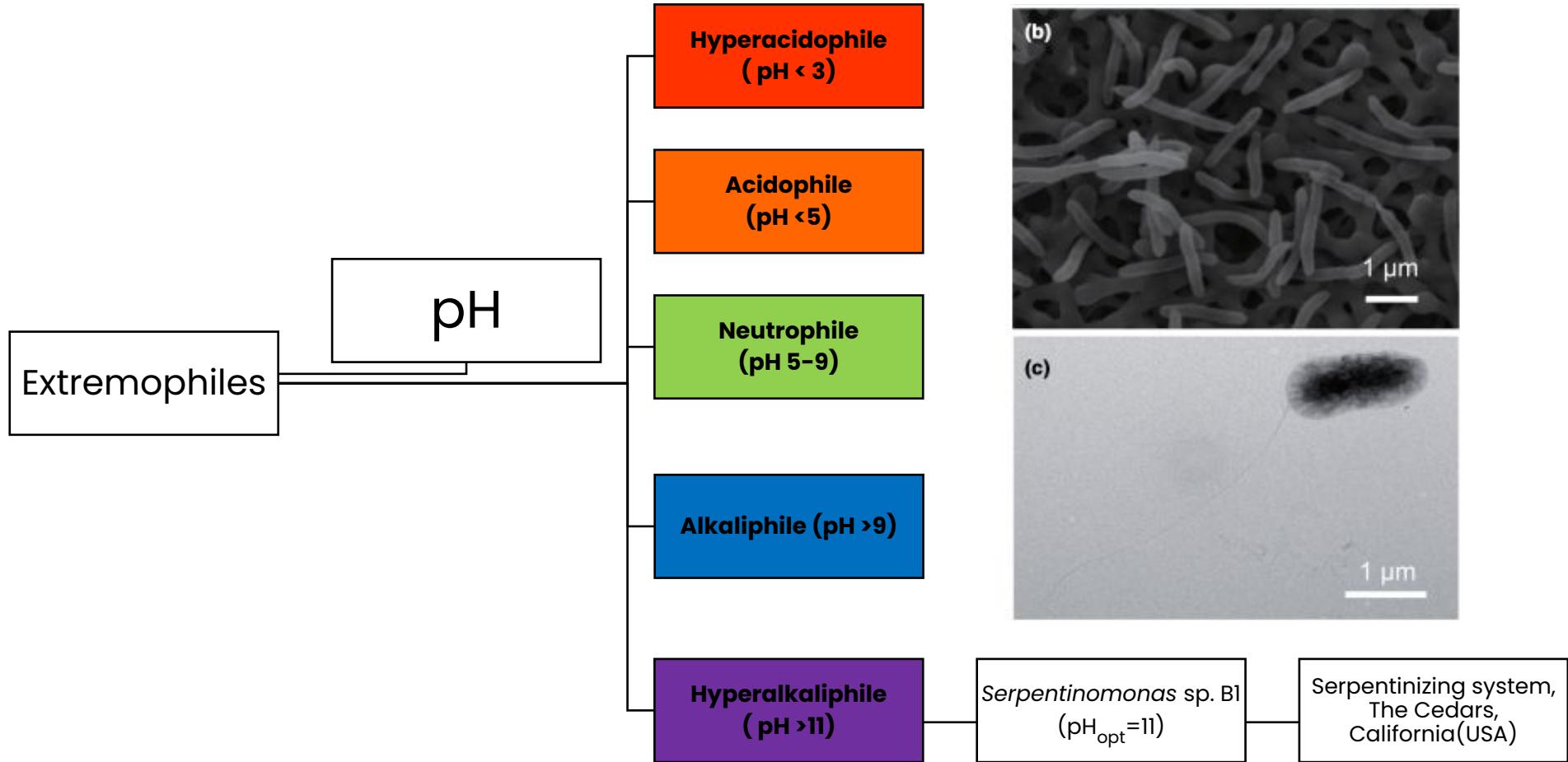
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# Acidity and alkalinity dependent extremophiles. Who are they? The “known” extremes

INTERNATIONAL JOURNAL OF SYSTEMATIC BACTERIOLOGY, July 1996, p. 814–816  
0020-7713/96/\$04.00+0  
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Vol. 46, No. 3

## *Picrophilus oshimae* and *Picrophilus torridus* fam. nov., gen. nov., sp. nov., Two Species of Hyperacidophilic, Thermophilic, Heterotrophic, Aerobic Archaea

CHRISTA SCHLEPER, GABRIELA PÜHLER, HANS-PETER KLENK,  
AND WOLFRAM ZILLIG\*

*Max Plank Institut für Biochemie, D-82152 Martinsried, Germany*

We describe two species of hyperacidophilic, thermophilic, heterotrophic, aerobic archaea that were isolated from solfataric hydrothermal areas in Hokkaido, Japan. These organisms, *Picrophilus oshimae* and *Picrophilus torridus*, represent a novel genus and a novel family, the *Picrophilaceae*, in the kingdom *Euryarchaeota* and the order *Thermoplasmatales*. Both of these bacteria are more acidophilic than the genus *Thermoplasma* since they are able to grow at about pH 0.

# Acidity and alkalinity dependent extremophiles. Who are they? The “known” extremes



## ARTICLE

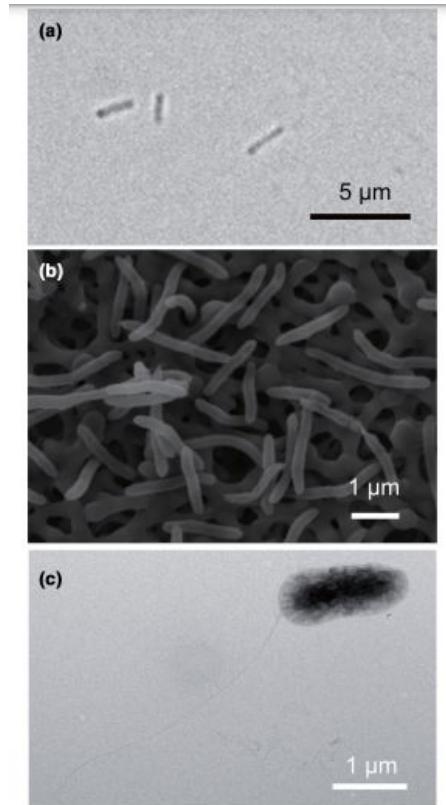
Received 17 Dec 2013 | Accepted 16 Apr 2014 | Published 21 May 2014

DOI: 10.1038/ncomms4900

OPEN

## Physiological and genomic features of highly alkaliphilic hydrogen-utilizing *Betaproteobacteria* from a continental serpentinating site

Shino Suzuki<sup>1</sup>, J. Gijs Kuenen<sup>2,3</sup>, Kira Schipper<sup>1,3</sup>, Suzanne van der Velde<sup>2,3</sup>, Shun'ichi Ishii<sup>1</sup>,  
Angela Wu<sup>1</sup>, Dimitry Y. Sorokin<sup>3,4</sup>, Aaron Tenney<sup>1</sup>, XianYing Meng<sup>5</sup>, Penny L. Morrill<sup>6</sup>, Yoichi Kamagata<sup>5</sup>,  
Gerard Muyzer<sup>3,7</sup> & Kenneth H. Nealson<sup>1,2</sup>



**Fig. 3.** Microscopic observation of strain A1T. (a) Phase contrast microscopy image of strain A1T grown on acetate and oxygen. The three strains are visually indistinguishable. (b) SEM image of strain A1T on carbon filter paper. Morphologies are indistinguishable for the three strains. (c) TEM image of strain A1T grown on acetate with oxygen.

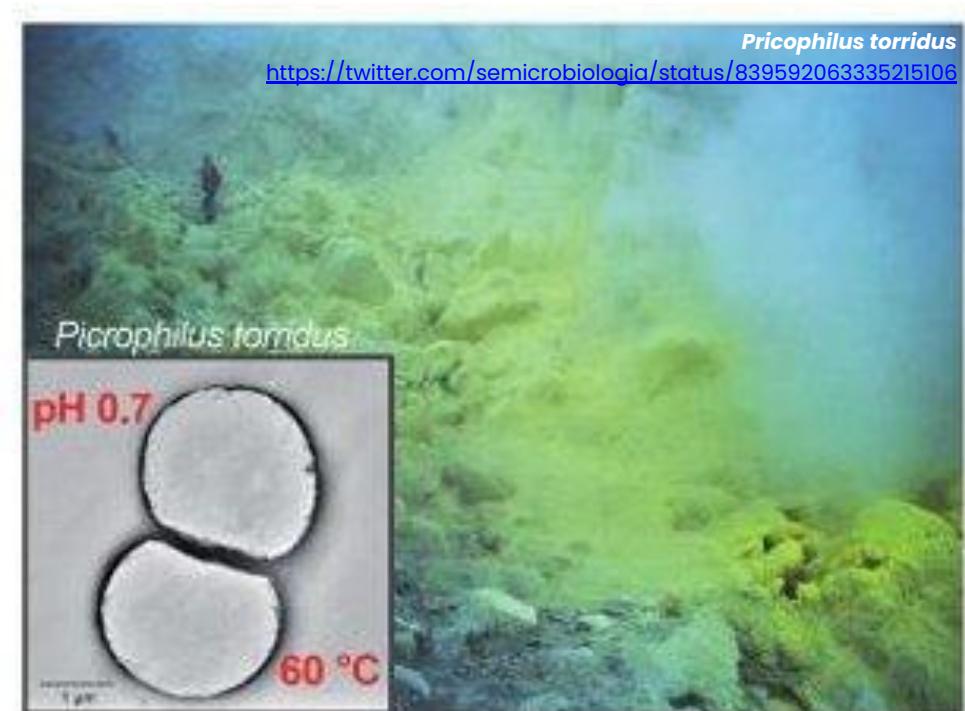
# Acidity and alkalinity dependent extremophiles. Interactions with other parameters

## Acidophiles

### Temperature

✓ High temperatures:

Acido-thermophiles like  
*Picrophilus torridus*



# Acidity and alkalinity dependent extremophiles. Interactions with other parameters

## Acidophiles

### Temperature

- ✓ Low temperatures (<5°C):  
Psychro-tolerant *Acidithiobacillus ferrooxidans* and *Acidophilium*  
(Quatrini and Johnson, 2018)



# Acidity and alkalinity dependent extremophiles. Interactions with other parameters

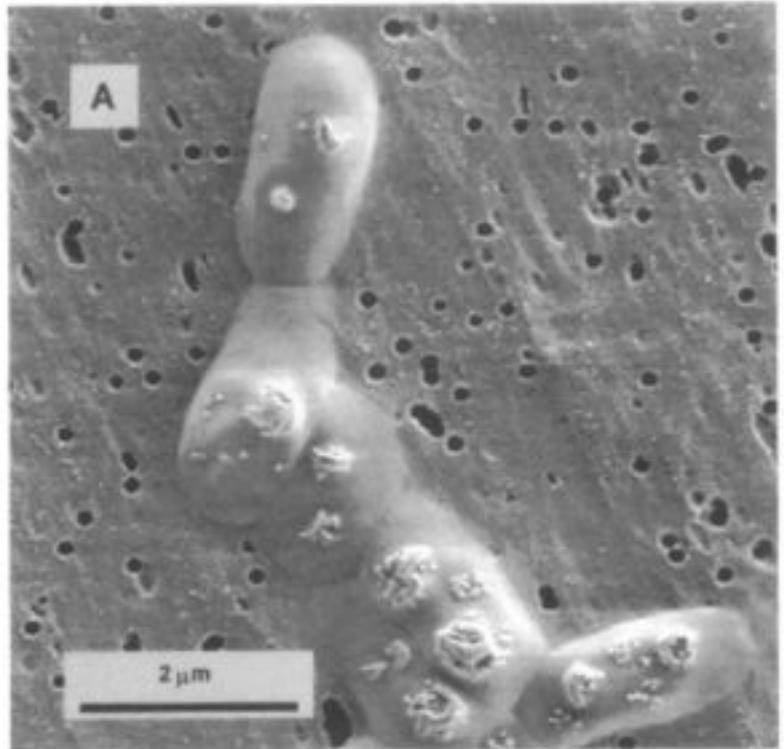
## Alkaliphiles

Salt concentration:

- ✓ Halo-alkaliphiles

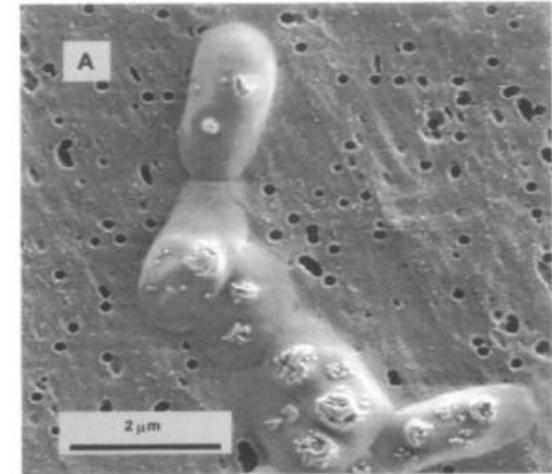
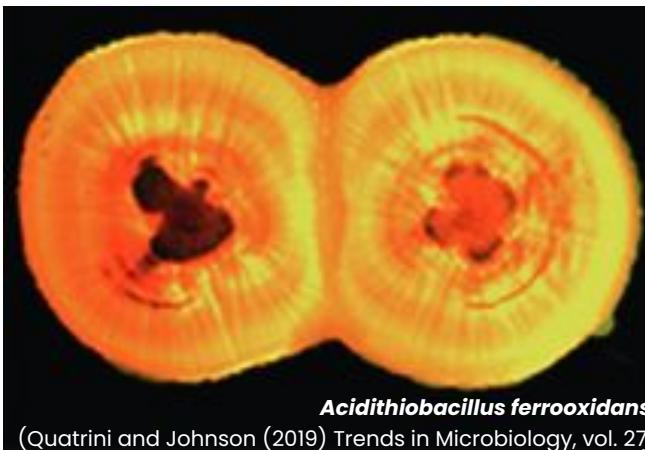
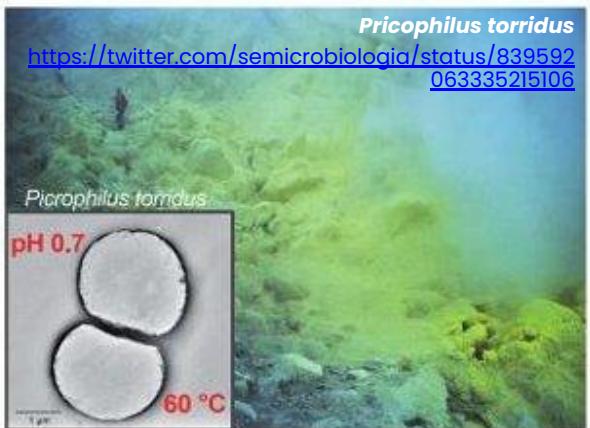
Low water activity:

- ✓ Xero-tolerant alkaliphiles



Scanning electron microphotograph of *Halomonas campisalis* (Mormile et al. 1999)

# Acidity and alkalinity dependent extremophiles. Interactions with other parameters



**Tolerance or preference for more than one parameter can allow the expansion of the extremophile ecological niche.**

# Acidity and alkalinity : Physiology

How can acidophiles thrive at low pH?



**active and passive acid-resistance mechanisms**

# The active and passive acid-resistance mechanisms in acidophiles

H<sup>+</sup> pump:  
*F<sub>1</sub>F<sub>0</sub>-ATPase complex*  
pump protons out of  
the cells through ATP  
hydrolysis

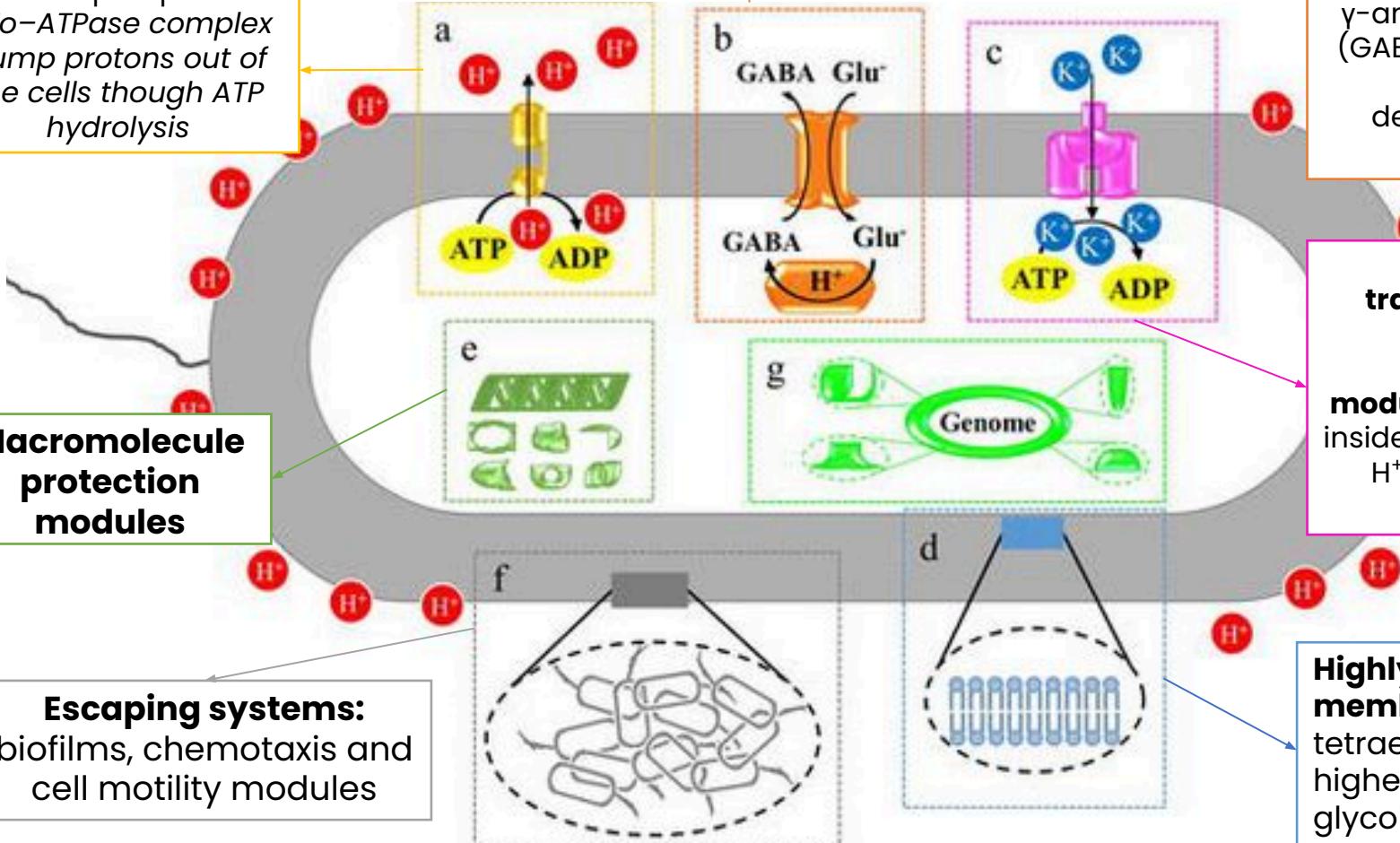
**Macromolecule  
protection  
modules**

**Escaping systems:**  
biofilms, chemotaxis and  
cell motility modules

**H<sup>+</sup> consumption  
Module:** the  
transformation of  
glutamate to  
γ-aminobutyric acid  
(GABA) consumes H<sup>+</sup>  
thanks to  
decarboxylation  
reactions

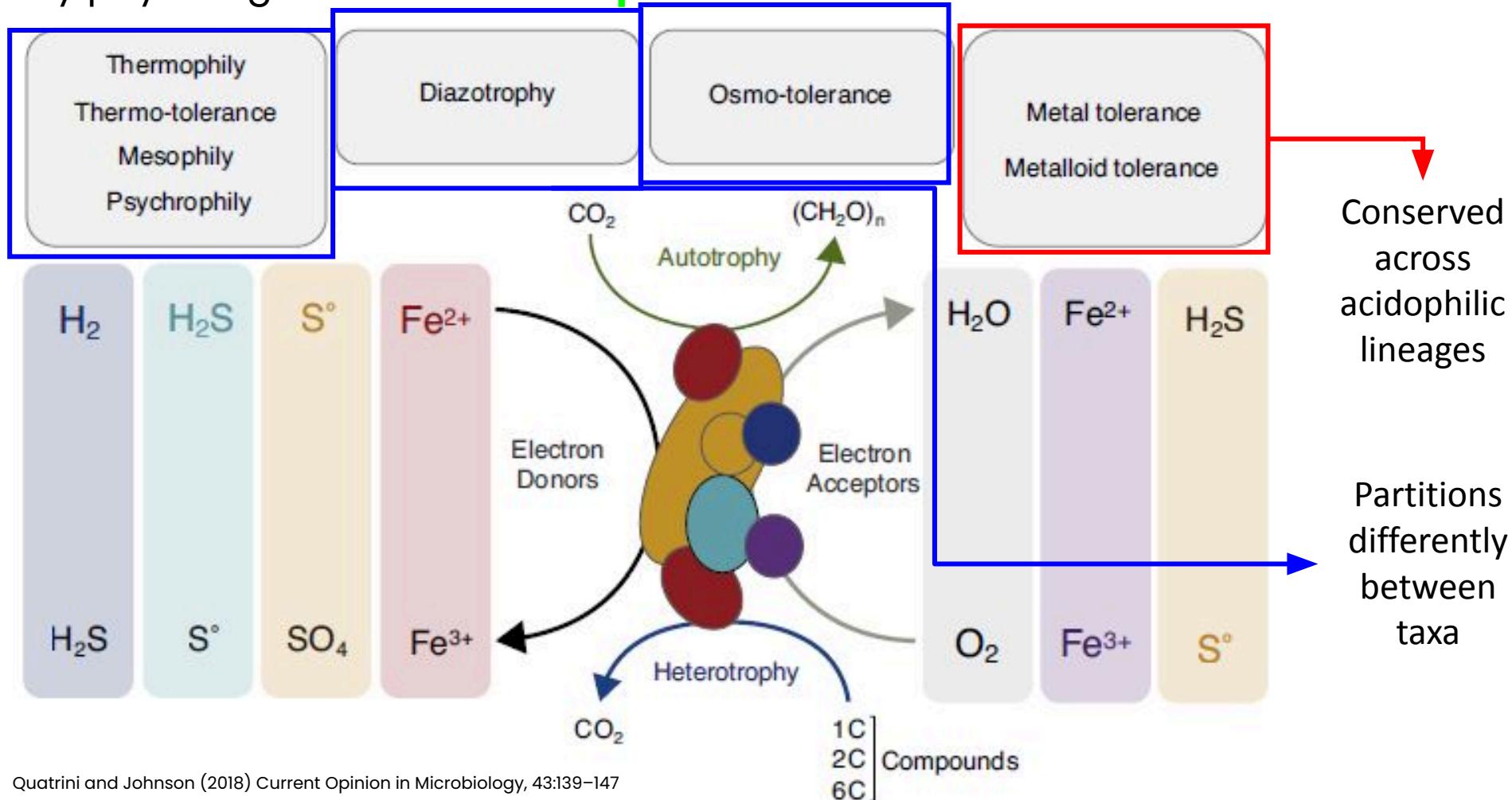
**Reversed  
transmembrane  
electrical  
potential  
modules** (positive  $\Delta\psi$   
inside the cell prevents  
H<sup>+</sup> into the cells)

**Highly impermeable  
membranes system:**  
tetraether lipids,  
higher content of  
glycolipids



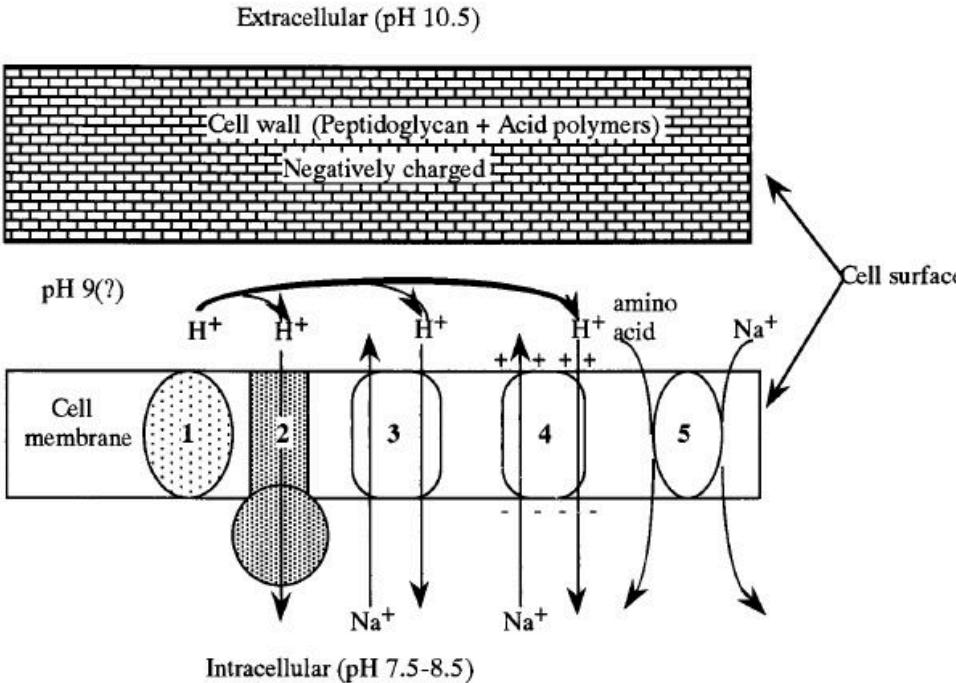
# Acidity and alkalinity : Physiology

Key physiological traits of **acidophilic** communities



# Acidity and alkalinity : Physiology

How alkaliphilic microorganisms can grow in such an extreme environment?



1: Respiratory chain; 2: FoF1-ATPase

3:  $\Delta\text{pH}$  dependent  $\text{Na}^+ / \text{H}^+$  antiporter

4:  $\Delta\psi$  dependent  $\text{Na}^+ / \text{H}^+$  antiporter

5: Amino acids/ $\text{Na}^+$  symporter



# Acidity and alkalinity : Physiology

How alkaliphilic microorganisms can grow in such an extreme environment?

- ✓ pH inside the cell is maintained around 8;
- ✓ Cell wall of many alkaliphiles composed of acidic polymers: The negative charges on the acidic non-peptidoglycan components may give the cell surface its ability to adsorb  $\text{Na}^+$  and  $\text{H}^+$  ions and repulse  $\text{OH}^-$  ions;
- ✓ Efflux of  $\text{Na}^+$  generates a  $\text{Na}^+$  motive force that helps with solute transportation inside the cell and with the removal of toxins;
- ✓ Plasma membranes may also maintain pH homeostasis by using the  $\text{Na}^+/\text{H}^+$  antiporter system ( $\Delta\text{pH}$  and  $\Delta\psi$  dependent), the  $\text{K}^+/\text{H}^+$  antiporter, and ATPase-driven  $\text{H}^+$  expulsion.



# **ACIDOPHILIC AND EXTREMELY ACIDOPHILIC MICROBIAL DIVERSITY**

# Acidity and alkalinity: Ecology – Microbial diversity

Extremely acidophilic organisms are exclusively microbial and include both Bacteria and Archaea, like:

## Acidithiobacilia

## γ-proteobacteria

## β-proteobacteria

## α-proteobacteria

## Firmicutes

## Actinobacteria

## Nitrospirae

## Acquificae

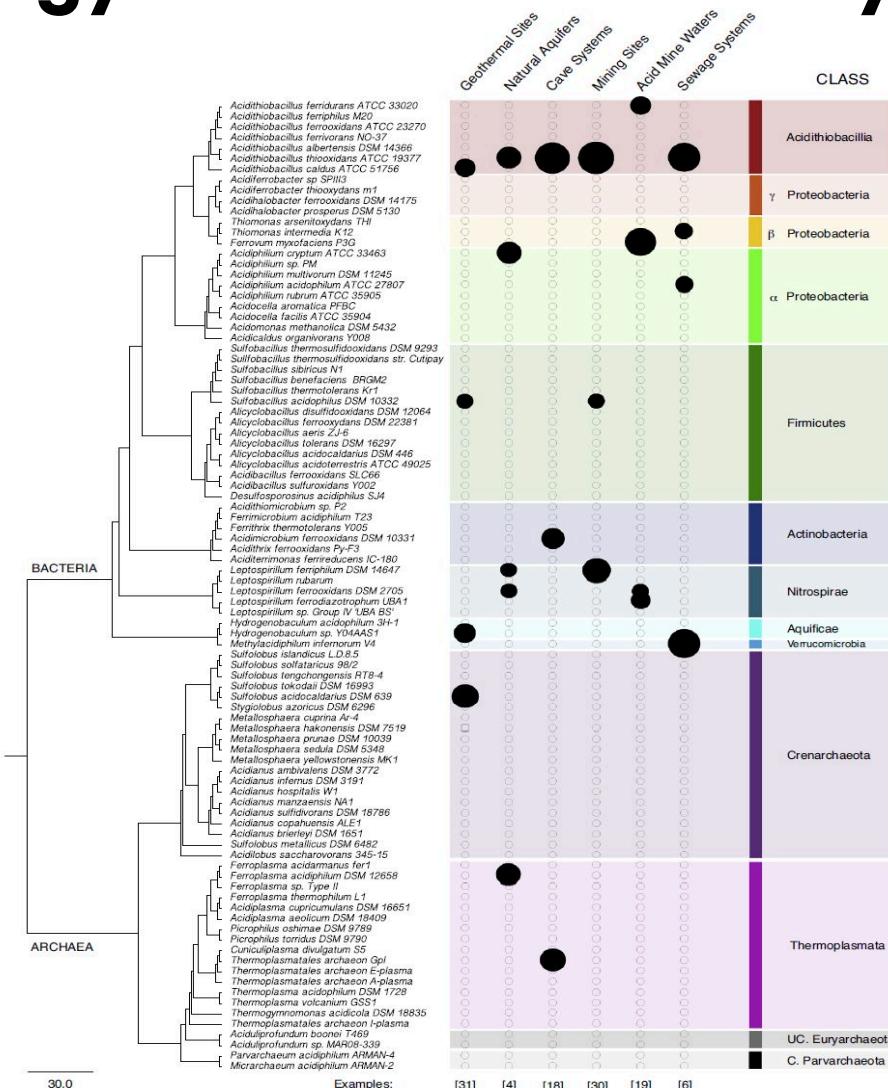
## Verrucomicrobia

## Chrenarchaeota

## Thermoplasmata

## Euryarchaeota

## Paryarchaeota



# Acidity and alkalinity: Ecology – Microbial diversity

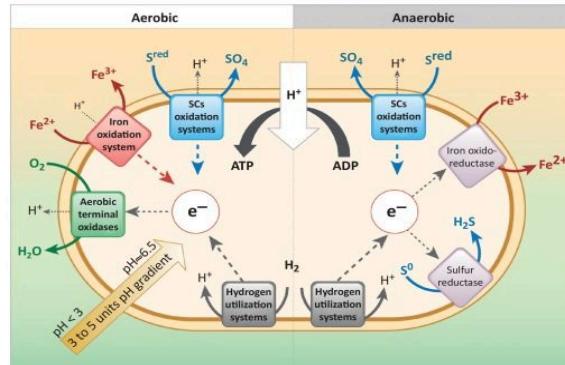
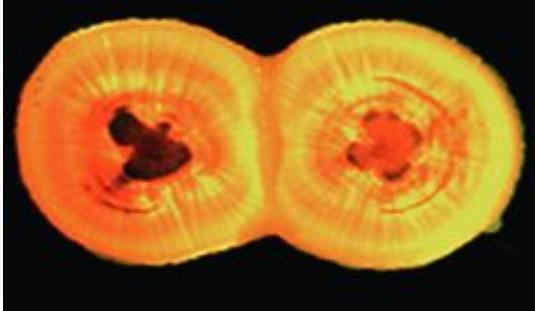
## Chemolithoautotrophy

MICROORGANISMS CONCERNED IN THE OXIDATION OF SULFUR IN THE SOIL

II. THIOBACILLUS THIOOXIDANS, A NEW SULFUR-OXIDIZING ORGANISM ISOLATED FROM THE SOIL<sup>a</sup>

SELMAN A. WAKSMAN AND J. S. JOFFE

Received for publication June 16, 1921



*Acidothiobacillus (At.) thiooxidans*: First and most well studied hyper-acidophilic microorganism

Isolated and characterized in 1921 by Wakman and Joffe.

**Chemolithotroph:** uses inorganic e<sup>-</sup> donors (e.g. Fe<sup>2+</sup> or S<sup>2-</sup> or both);

**Facultative anaerobe:** uses molecular oxygen, ferric iron, or sulfur as electron acceptor;

**Obligate autotroph:** fixes CO<sub>2</sub> via the Calvin–Benson– Bassham cycle in carboxysomes;

**Facultative diazotroph**

# Acidity and alkalinity: Ecology – Microbial diversity

**Photoautotrophy:** Most important mechanism of primary production in acidic ecosystems, mainly for eukaryotic microalgae.



Green algae *Chlamydomonas* spp. isolated from Rio Tinto (Spain)

Aguilera (2013) Life 3,363–374

# Acidity and alkalinity: Ecology – Microbial diversity

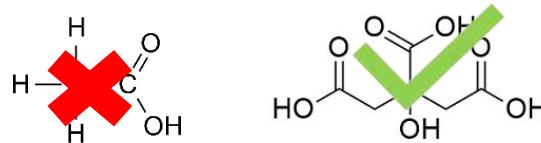
**Facultative autotrophs:** some organisms are able to switch to C assimilation when this becomes available and if there's enough solar energy (e.g. *Galdieria sulphuraria*)



# Acidity and alkalinity: Ecology – Microbial diversity

## HETEROTROPHIC ACIDOPHILES

Large number of acidophilic bacteria and archaea known to use organic compounds (i.e. citric acid, glutamic acid) as energy sources.

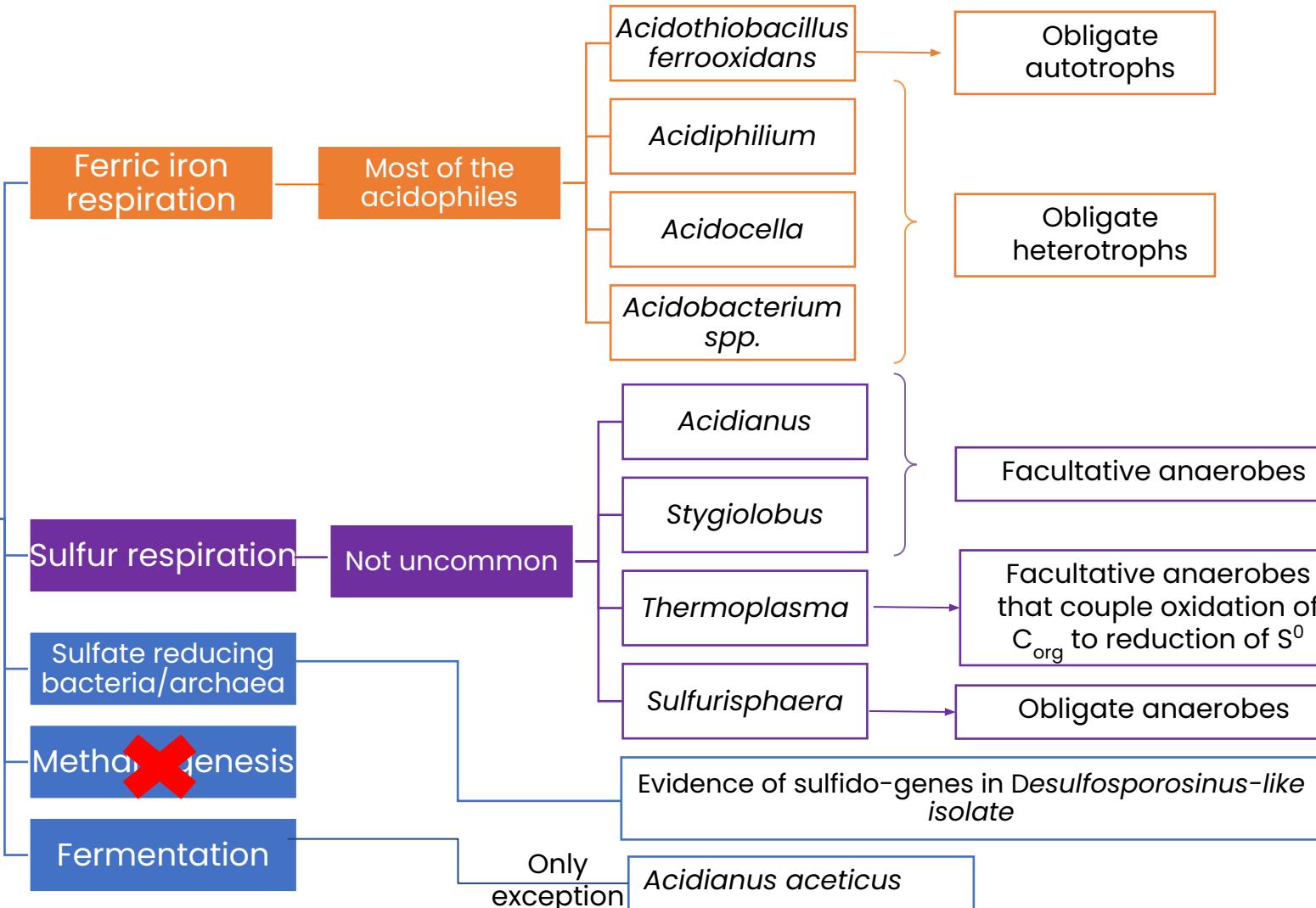


Some are also able to supplement energy budgets by oxidizing inorganic substrates ( $\text{Fe}^{2+}$  or  $\text{S}^{2-}$ ) like ***Ferromicrobium (Fm.) acidiphilum***.

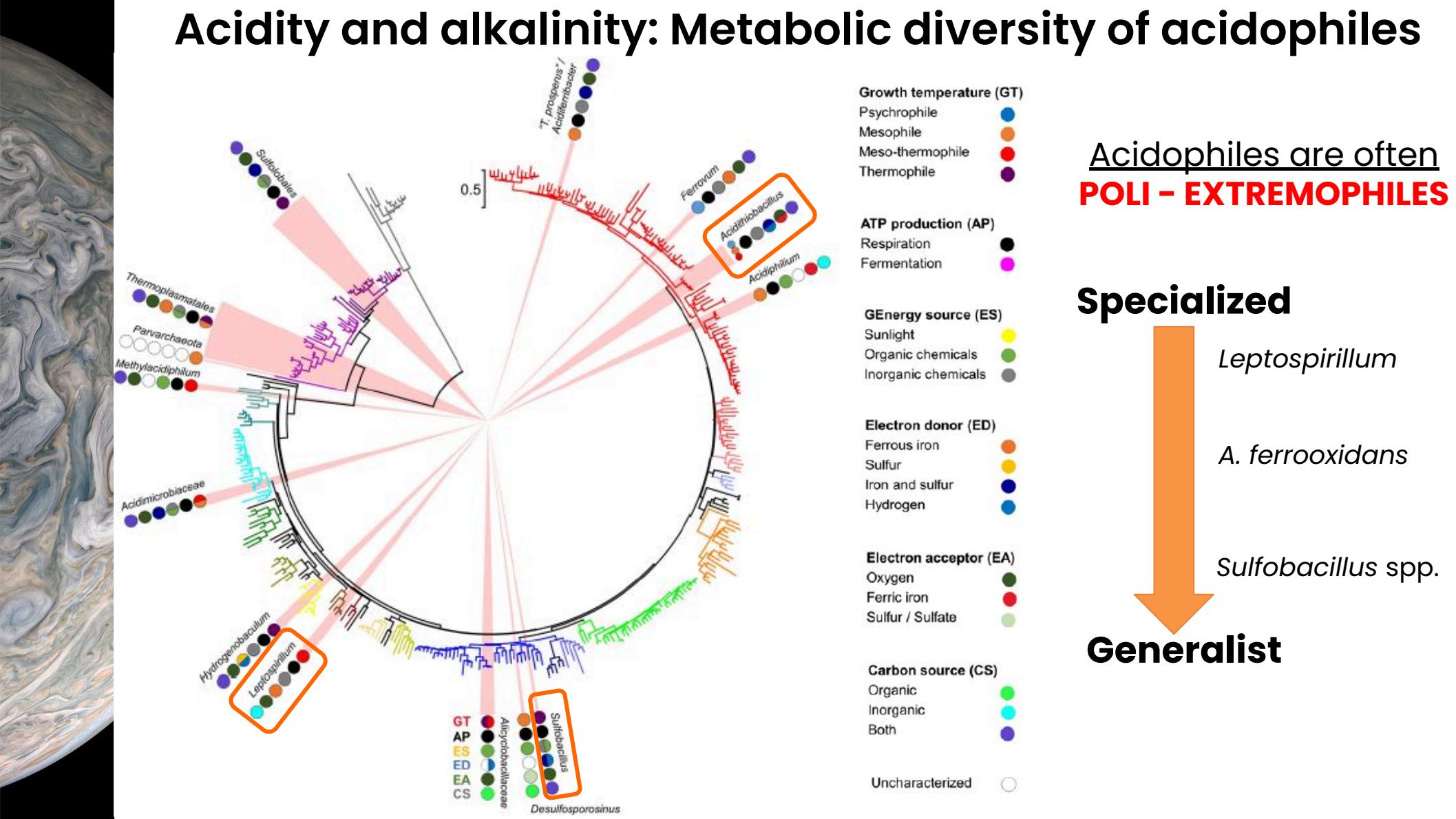
***Acidilobus aceticus***, grows anaerobically on starch to form acetate as the main metabolic product.

# Acidity and alkalinity: Ecology – Microbial diversity

## Acidophiles



# Acidity and alkalinity: Metabolic diversity of acidophiles

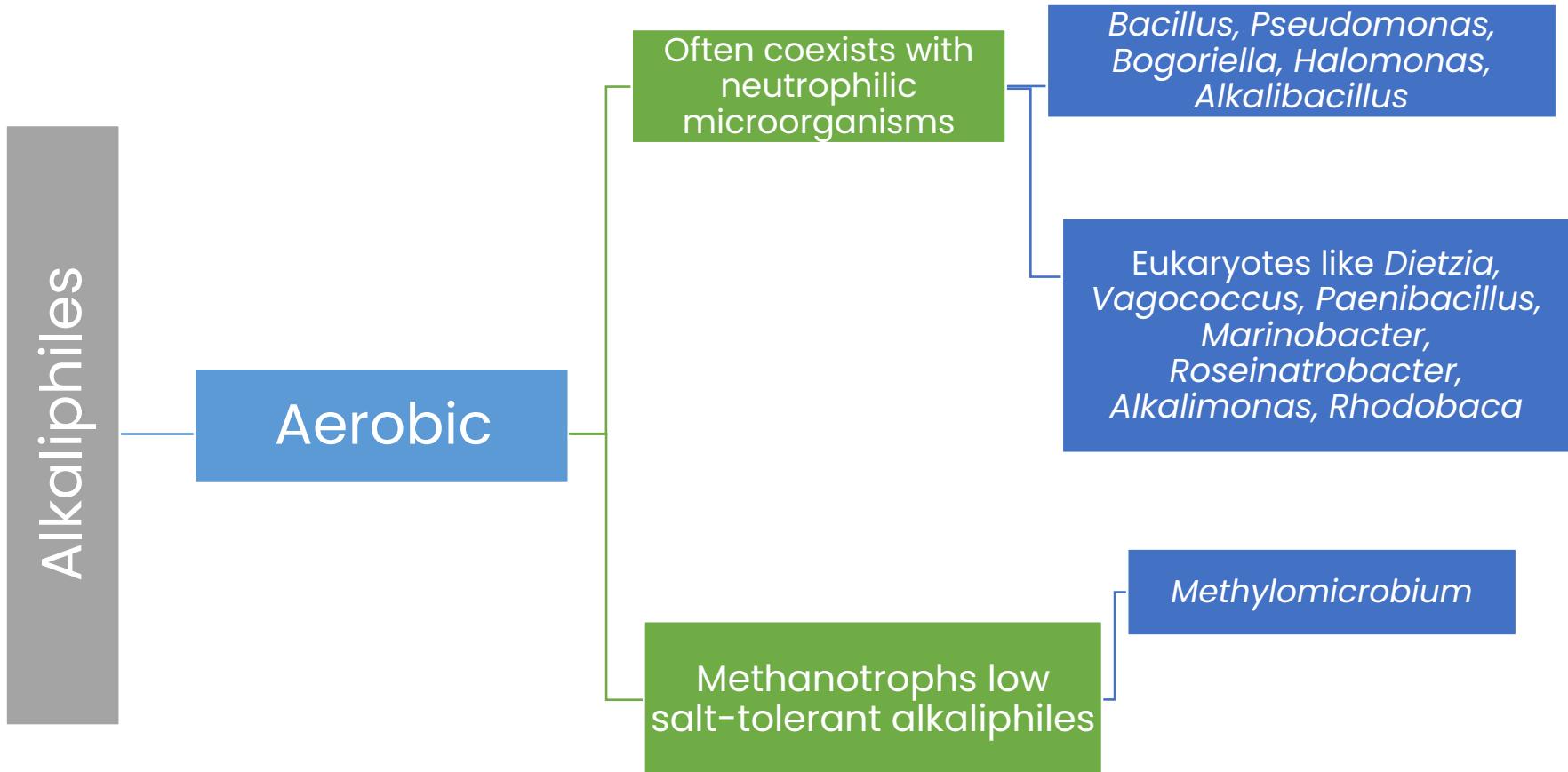


Acidophiles are often  
**POLI - EXTREMOPHILES**

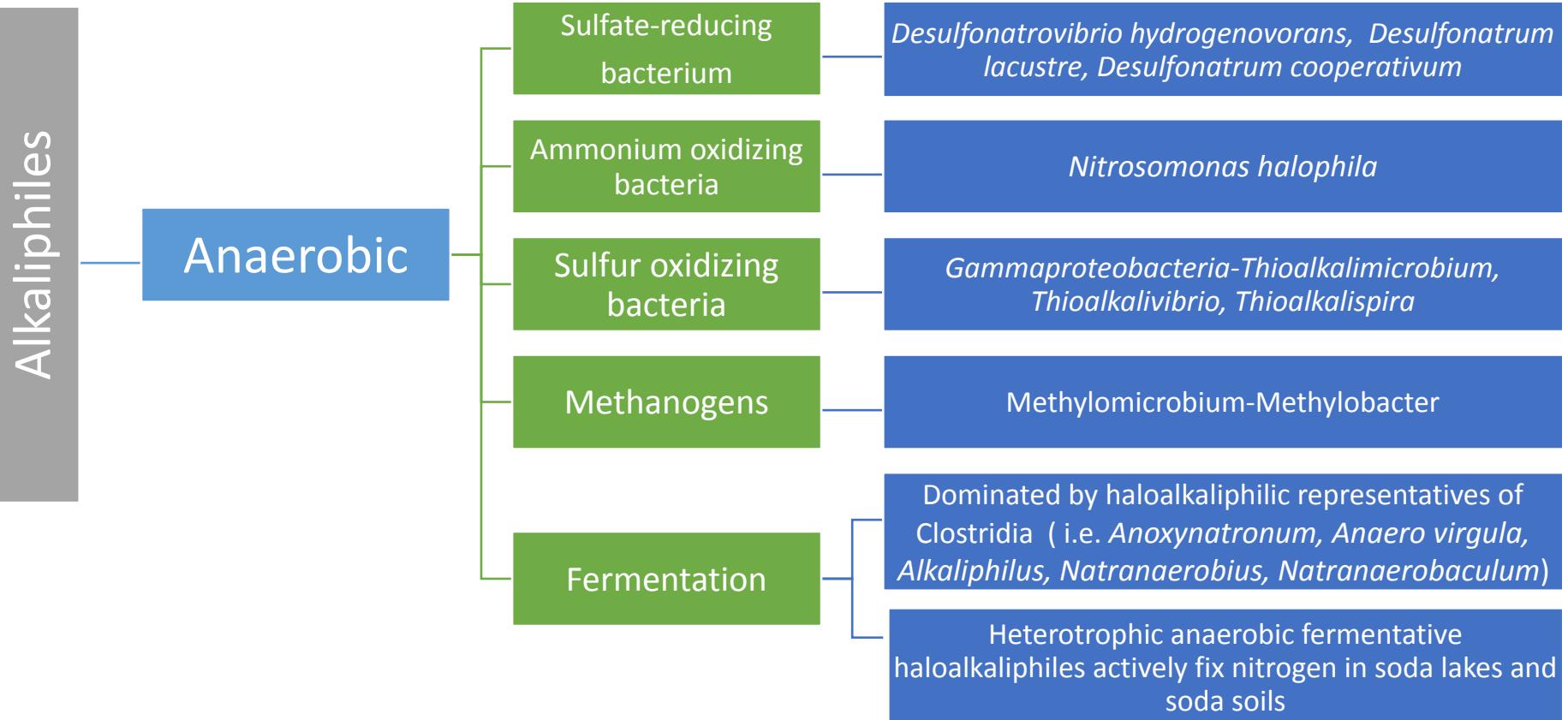


# **ALKALIPHILES MICROBIAL DIVERSITY**

# Acidity and alkalinity: Ecology – Microbial diversity



# Acidity and alkalinity: Ecology – Microbial diversity

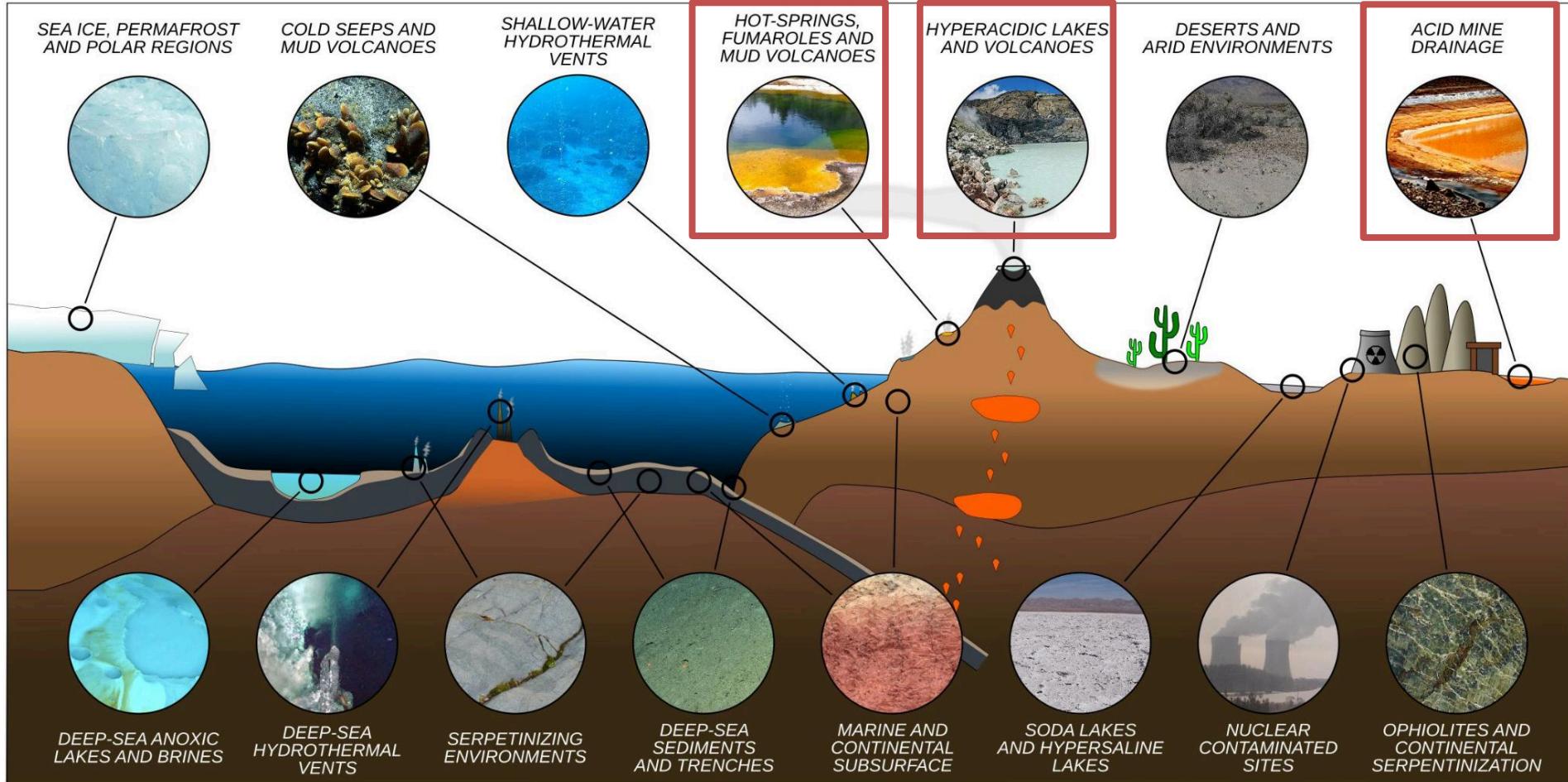


# **Acidity and alkalinity: Ecology – Environments**

**WHERE CAN WE FIND ACIDOPHILES,  
HYPER-ACIDOPHILES AND ALKALIPHILES?**

# Acidity and alkalinity: Ecology – Environments

## ACID AND HYPERACID ENVIRONMENTS



# Acidity and alkalinity: Ecology – Environments



Acidic habitats have two major origins:

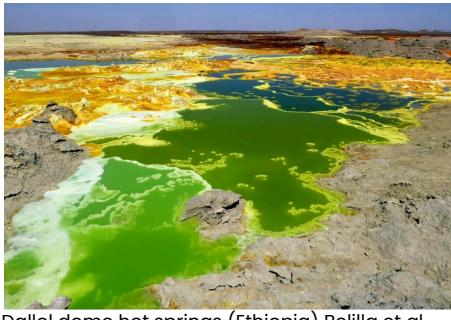
- ✓ Natural: volcanic and magmatic activities (hydrothermal vents, hyperacidic lakes, fumaroles/solfataras, mud volcanoes)
- ✓ Anthropogenic: metal and coal mining

- (A) Geothermal area in Reykjanes Peninsula (SW, Iceland)
- (B) Acidic mining drainage area in Rio Tinto (SW, Spain)
- (C) Acidic rock drainage area in Huascaran National Park (Peru),
- (D) Acidic rock drainage area in Almirantazgo Bay (Shetland Islands, Antarctica)
- (E) Acidic rock drainage area in Pachacoto river (Huascaran National Park, Peru)
- (F) Rio Tinto at Nerva area (Spain).

# Acidity and alkalinity: Ecology – Environments



Frying Pan Hot Spring (Yellowstone Park, USA). Johnson (2009)



Dallol dome hot springs (Ethiopia) Belilla et al. (2019)



Yellowstone mud volcano(USA)

*Geothermal features: Hotsprings, fumaroles, solfataras, and mud volcanoes*

- ✓ **Hot springs:** spring with water at temperatures substantially higher than the air temperature of the surrounding region due to the heat generated by shallow intrusions of magma in volcanic areas.
- ✓ **Fumaroles:** vent in the Earth's surface from which steam and volcanic gases are emitted ( $\text{CO}_2$ ,  $\text{SO}_2$  and  $\text{H}_2\text{S}$ ). The mixture of steam and gas is erupted from vents and fissures in the ground surrounding rock forming viscous pools of bubbling mud (mud volcanoes).
- ✓ **Solfataras:** a type of fumarole in which sulfur gases are the dominant constituent along with hot water vapour.



Pozzuoli Solfatara (Di Donar Reiskoffer, CC BY-SA 3.0, <https://commons.wikimedia.org/w/index.php?curid=238345>)



Hyperacidic crater lake at Kawah Ijen (Java, Indonesia)

# Acidity and alkalinity: Ecology – Environments



Frying Pan Hot Spring (Yellowstone Park, USA). Johnson (2009)



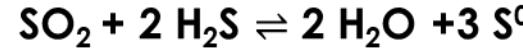
Dallol dome hot springs (Ethiopia) Belilla et al. (2019)



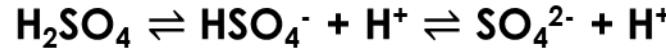
Yellowstone mud volcano(USA)

Geothermal features: Hotsprings, fumaroles, solfataras, and mud volcanoes

$S^0$  can form in geothermal areas through the condensation of  $SO_2$  and  $H_2S$  according to this reaction:



Acidophilic bacteria and archaea then oxidize  $S^0$  to produce  $H_2SO_4$



Pozzuoli Solfatara (Di Donar Reiskoffer, CC BY-SA 3.0, <https://commons.wikimedia.org/w/index.php?curid=238345>)



Hyperacidic crater lake at Kawah Ijen (Java, Indonesia)

# Acidity and alkalinity: Ecology – Environments



Kupferschiefer deposits (central Europe)



Sao Domingo mine (Portugal)



Gossans

Acid production is often limited by the physical nature of the unweathered rock, restricting its exposure to both oxygen and water

# Acidity and alkalinity: Ecology – Environments

The oxidative dissolution of pyrite by acidophilic bacteria and its role in generating acidic, metal rich pollution, such as acid mine drainage waters, can be seen through the equation:



- ✓ Net acid-generating reaction.

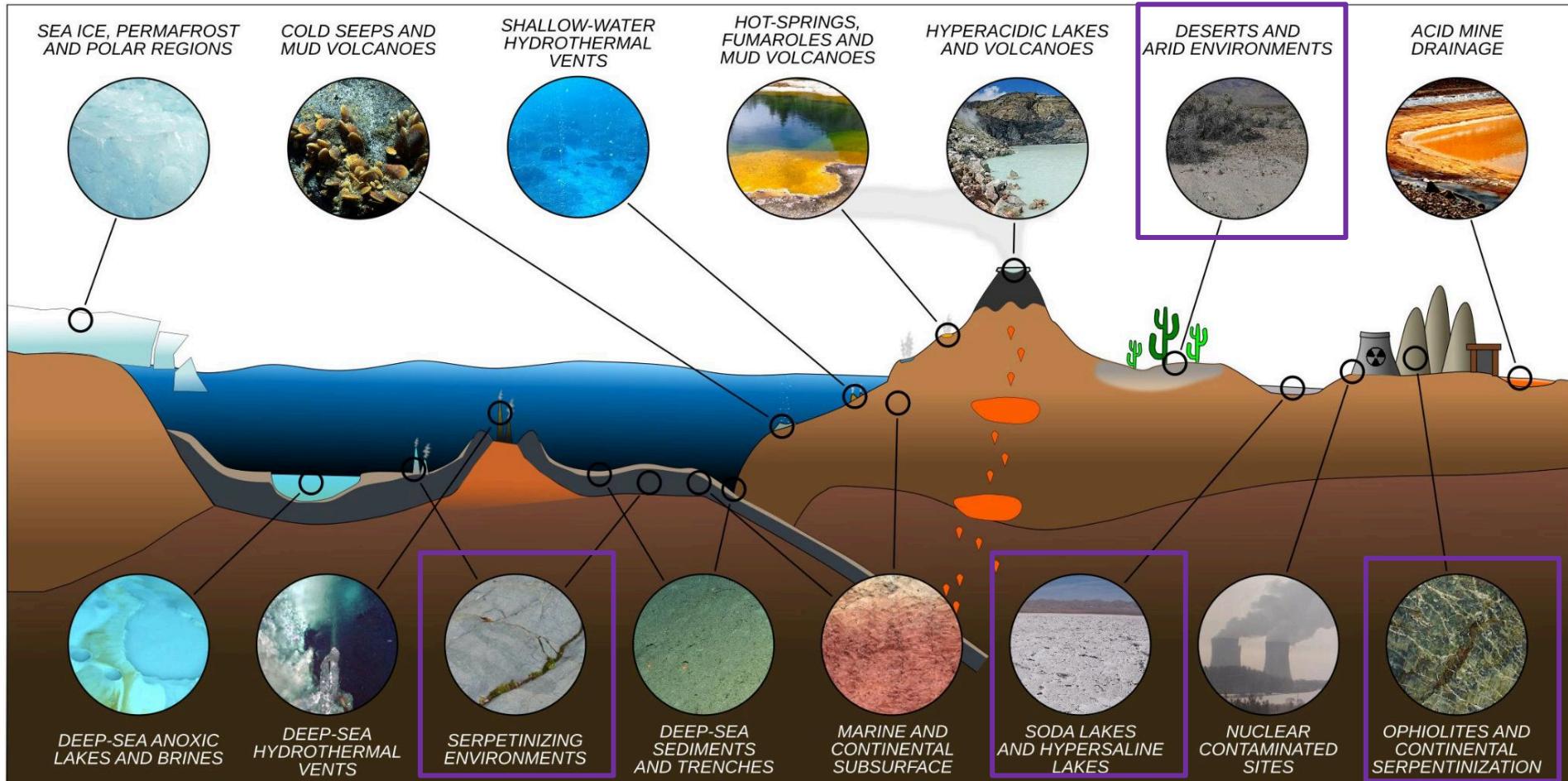
the Rio Tinto (SW Spain) maintains a pH of between ~ 2.2 and 2.8 throughout its 100 km length due to this reaction.



General view of Rio Tinto (Spain). Aguilera (2013)

# Acidity and alkalinity: Ecology – Environments

## ALKALINE ENVIRONMENTS



# Acidity and alkalinity: Ecology – Environments



Lake Magadi (Kenya)



Wadi el Natrun (Egypt)

Stable alkaline environments:

Climatic + geological + geographical conditions

pH > 10

Two types: low  $\text{Ca}^{2+}$  and high  $\text{Ca}^{2+}$



Mono lake(USA)



Soda lake of Kulunda Steppe (Russia)

# Acidity and alkalinity: Ecology – Environments



## Stable alkaline environments:

*Low  $\text{Ca}^{2+}$  soda lakes and deserts:*

- ✓ High amount of  $\text{NaCO}_3$  due to evaporative concentration
- ✓ In the absence of Ca and Mg, groundwater enriched with  $\text{HCO}_3^-$  is present
- ✓ Evaporative concentration of ions leads to a shift in the  $\text{CO}_2/\text{HCO}_3^-/\text{CO}_3^{2-}$  equilibrium
- ✓ The concentration of other salts, like  $\text{NaCl}$ , gives rise to environments both saline and alkaline



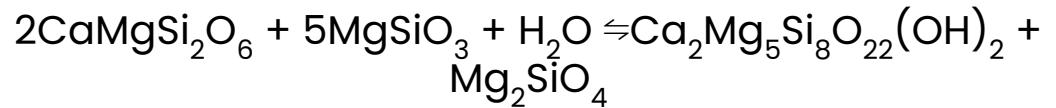
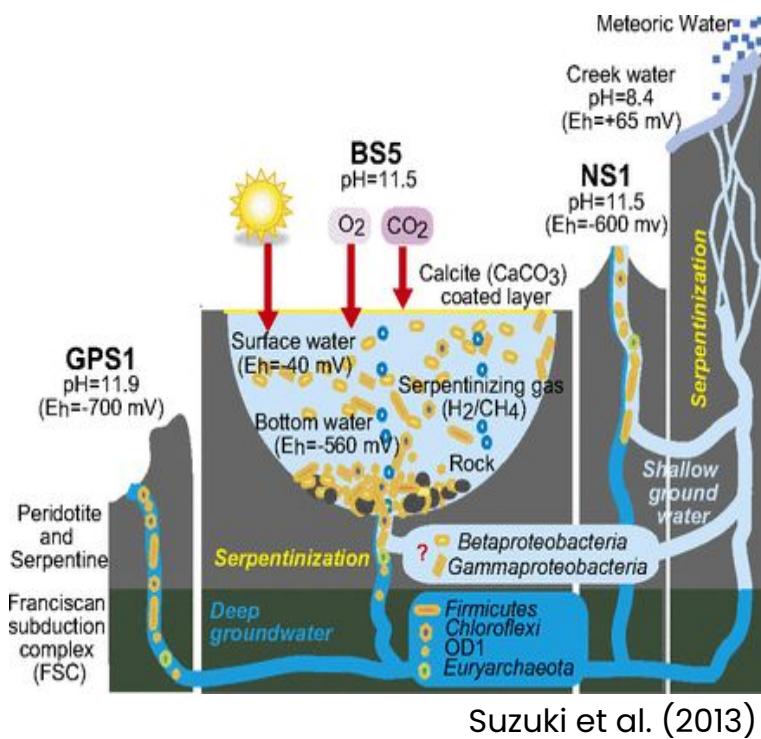
# Acidity and alkalinity: Ecology – Environments

## Stable alkaline environments:

High  $\text{Ca}^{2+}$  alkaline environments ( $\text{pH} \geq 11$ ):

Developed in areas where low temperature weathering of ultramafic (Olivine, Pyroxenes and Clinopyroxenes) minerals is possible .

Olivines (Ol) and pyroxenes (Px) decompose when exposed to waters enriched with  $\text{CO}_2$  releasing  $\text{Ca}^{2+}$  and  $\text{OH}^-$  into the solution.



$\text{Mg}^{2+}$  and  $\text{Fe}^{2+}$  are removed by precipitation of the mineral phases: Brucite, Magnesite or Dolomite, while  $\text{Ca}^{2+}$  remains in the solution.

In these type of environments («The Cedars» subduction zone) Suzuki et al. (2014) isolated Betaproteobacteria *Serpentinomonas* spp.

# Acidity and alkalinity: Ecology – Environments

Transient alkaline environments:  
pH values rarely over 9.5

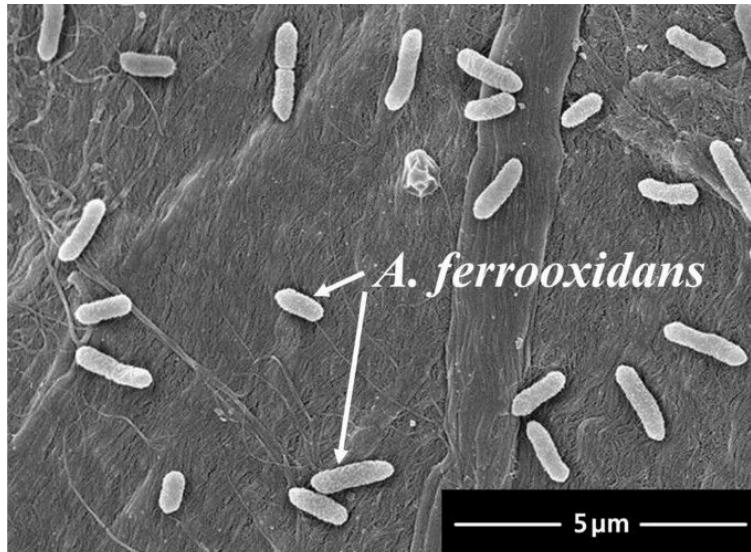


- ✓ Soil microhabitats due to ammonification and sulfate reduction
- ✓ Alkaline hot springs in volcanic areas generated through silicate decomposition

# Acidity and alkalinity: Taxonomy of acidophiles

## *Acidithiobacillus ferrooxidans*

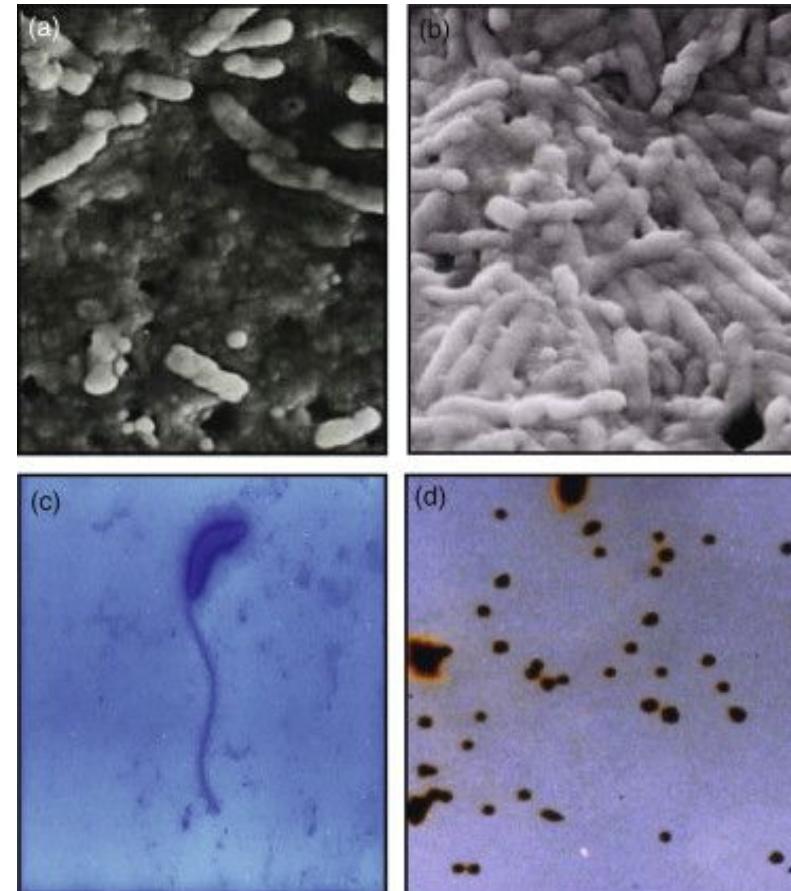
- *A. ferrooxidans* is a **Gram negative** rod shaped bacterium that is commonly found in **deep caves** or **acid mine drainage**, such as coal waste.
- Optimal **pH level of 1.5 – 2.5** where they convert insoluble metals to their soluble state. Even low concentrations (ppm) of these metallic ions would be extremely toxic to other bacteria.
- *A. ferrooxidans* is a **chemolithoautotrophic** bacterium which can use many different electron donors to support growth.
- In **aerobic conditions**, electron donors may include **ferrous ions or sulfur compounds** which are oxidized into ferric iron and sulfuric acid, respectively, yielding high energy. However, during **anaerobic conditions** **ferric ions** can replace oxygen as the electron acceptor with multiple substrates donating an electron.
- *A. ferrooxidans* can fix atmospheric **CO<sub>2</sub>** as a **carbon source** essential for biomass. Nitrogen is a common limiting nutrient scarce in the environment; however, *A. ferrooxidans* can fix atmospheric nitrogen into ammonia (NH<sub>3</sub>) essential for nucleotides and amino acids.



# Acidity and alkalinity: Taxonomy of acidophiles

## *Leptospirillum ferrooxidans*

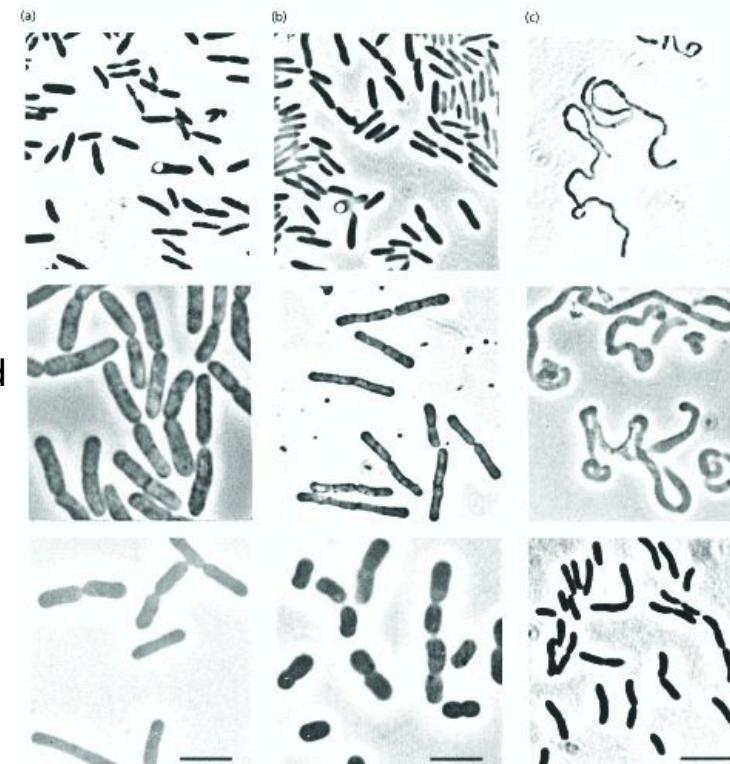
- *Leptospirillum* is a genus of **iron-oxidizing bacteria** which play an important role in industrial bioleaching (the conversion of metals to a soluble form) and biooxidation (the extraction of metals).
- They are **obligate aerobes** (require oxygen gas).
- Primary iron-oxidizers in industrial continuous-flow biooxidation tanks.
- Metabolically they are **strictly chemolithoautotrophic**, fixing carbon using ferrous iron as their electron donor and oxygen as the electron acceptor. Because of this, they are **some of the most metabolically-restricted** organisms known.
- *Leptospirilla* are also important contributors to the **acid mine drainage process**.



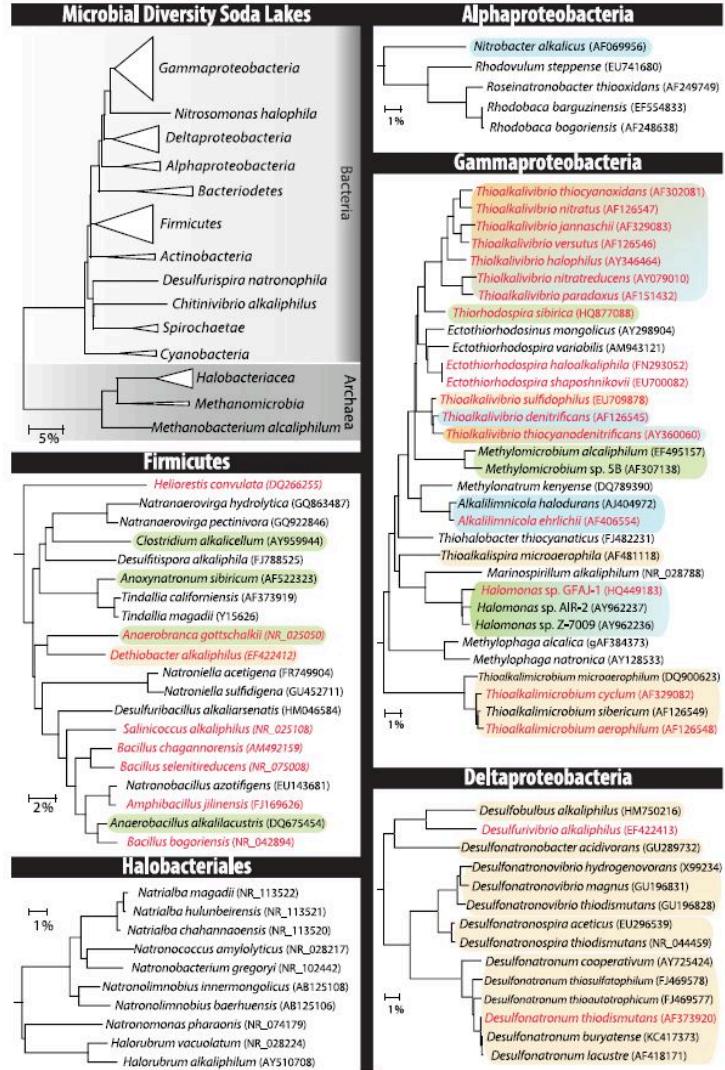
# Acidity and alkalinity: Taxonomy of acidophiles

## *Sulfobacillus thermosulfidooxidans*

- *Sulfobacillus thermosulfidooxidans* is a species of bacteria of the genus *Sulfobacillus*.
- ***S. thermosulfidooxidans*** is acidophilic and **moderately thermophilic**;
- All prefer environments around **pH 2.0** with optimal growth **temperatures ranging from 45 °C to 55 °C**;
- *S. thermosulfidooxidans* **is an iron- and sulfur-oxidizer**, capable of oxidation of elemental sulfur, tetrathionate, and sulfides;
- **Facultative chemolithotroph**;
- Also capable of **chemoorganoheterotrophic** growth;
- Widely distributed in both natural and artificial acidic environments, including hot springs and acid mine drainage;
- Used in biohydrometallurgical (biomining) approaches for the recovery of precious and non-ferrous metals.



# Acidity and alkalinity: Taxonomy of alkaliphiles



**Salt concentration** in the sedimentary pore water of **soda lakes** has a **strong influence** on the **in situ microbial community composition** and **negatively affects** the **diversity**

Phylogenetic tree of identified bacteria and archaea in soda lakes (Sorokin, 2014)

# Acidity and alkalinity: Taxonomy of alkaliphiles

## Serpentinomonas gen. nov.

- Serpentinomonas strains are **obligate alkaliphilic** and **facultative hydrogen-utilizing** bacteria.
- Serpentinomonas strains utilize **CaCO<sub>3</sub>** for carbon fixation, coupled with **hydrogen oxidation** at high pH.
- **Ca<sup>2+</sup>** released in the alkaline water appears to be a great **carbon-trapping** mechanism for the Serpentinomonas microbes.
- Serpentinomonas strains have **diverse metabolic abilities** in terms of organic carbon compounds and electron acceptor utilization.
- The most used **electron acceptor** is **oxygen**, so they mostly rely on Aerobic respiration.
- Some strains of Serpentinomonas can grow by fermenting sugars, such as glucose.

Table 2 | Summary of physiological characteristics of strains A1, B1 and H1.

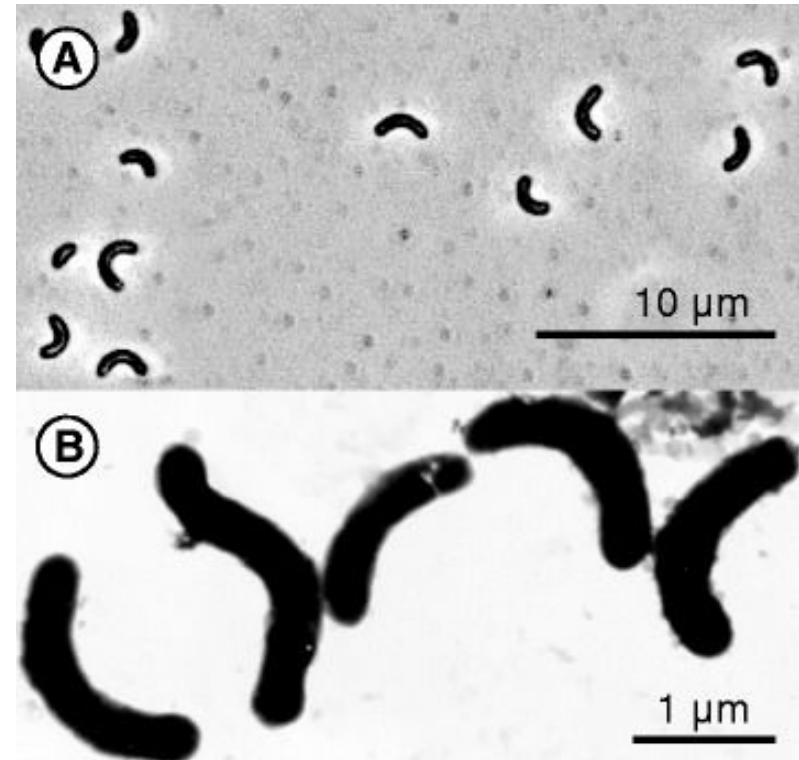
|   | Strain A1 | Strain B1 | Strain H1 |
|---|-----------|-----------|-----------|
| Temperature range (°C)                    | 18–37     | 18–37     | 18–37     |
| Optimum temperature                       | 26–30     | 30        | 30        |
| pH range                                  | 10.0–11.5 | 9.5–12.5  | 9–12      |
| Optimum pH                                | 11        | 11        | 11        |
| NaCl range (g l <sup>-1</sup> )           | 0–0.5     | 0–0.5     | 0–0.5     |
| Optimum NaCl                              | 0         | 0         | 0         |
| Flagella                                  | Polar     | Polar     | Polar     |
| Autotrophic growth                        |           |           |           |
| H <sub>2</sub> /CaCO <sub>3</sub> /Oxygen | ++        | ++        | ++        |
| Mixotrophic growth                        |           |           |           |
| Acetate                                   | +++       | +++       | +++       |
| Lactate                                   | +++       | +++       | +++       |
| Glucose                                   | +         | +++       | +++       |
| Cyclohexane                               | +++       | ±         | –         |
| Electron acceptor utilization             |           |           |           |
| Oxygen                                    | +++       | +++       | +++       |
| Nitrate                                   | –         | +++       | +++       |
| Sulphate                                  | –         | –         | –         |
| Thiosulphate                              | +++       | –         | –         |
| Fermentation                              |           |           |           |
| Glucose                                   | –         | +++       | +++       |

+, positive; –, negative.

# Acidity and alkalinity: Taxonomy of alkaliphiles

## *Desulfurivibrio alkaliphilus*

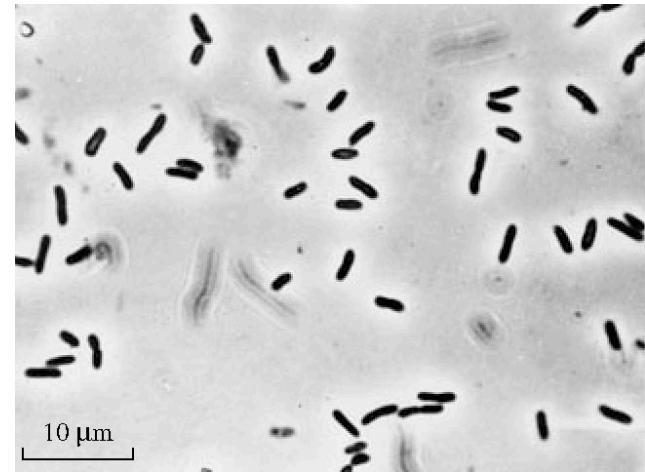
- *Desulfurivibrio alkaliphilus* are strictly anaerobic sulfidogenic haloalkaliphiles.
- The cells are **Gram-negative, non-motile, curved rods** that do not form spores.
- Members of this species are capable of chemolithoautotrophic growth through the disproportionation of elemental sulfur under alkaline conditions without iron oxides, which are normally required by neutrophilic sulfur disproportionators.
- *Desulfurivibrio alkaliphilus* **fixes inorganic carbon** thought the Acetyl-coA pathway.
- They can use H<sub>2</sub> as the electron donor and thiosulfate, elemental sulfur, polysulfide and nitrate as the electron acceptors



# Acidity and alkalinity: Taxonomy of alkaliphiles

## *Halomonas campisalis*

- An haloalkilophilic bacterium isolated from sediment samples taken from the salt plain of Alkali lake (USA).
- Members of this species have **rod-shaped** cells, and can use as **electron acceptors**: **oxygen, nitrate** and **nitrite** (capable of doing **denitrification**) and a variety of electron donors.
- Carbon sources include:Acetate, Lactate, Glycerol, Ethanol and Methanol.
- *Halomonas campisalis* is unable to grow fermentatively.
- They can grow at a wide range of temperature, ranging from **4 to 50 °C**, with **optimal growth at 30° C**.
- Due to its denitrification ability, broad carbon utilization range and high salinity tolerance, they can be used for the treatment of saline, alkaline waste.



# Acidophiles and alkaliphiles: Biotech Applications

Biotechnological potential of acidophiles and extremely acidophiles

Sulfate reduction for remediation of streams contaminated by mining or metallurgical industries

Known acidophilic sulfate reducing bacteria that can be used:

*Thermodesulfobium narugense*  
*Desulfosporosinus acidiphilus*  
*Desulfosporosinus acidurans*

Sulfur reduction for recovery of acid mine drainages

Acidophilic sulfur reducing bacteria used:

*A. ferrooxidans* (pH 1.8)  
*Acidilobus sulfurreducens* (pH 2)  
*Acidianus infernus* (pH 1.5)

Main advantage sulfur reducers can generally reduce elemental sulfur at pH values lower than the above mentioned sulfate reducers

Remediation of metal laden streams in metallurgical processes



[Biotechnology of Extremophiles](#): pp 215-241 | [Cite as](#)

Acidophilic Microbes: Biology and Applications

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Chapter

First Online: 28 April 2016

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# Acidophiles and alkaliphiles: Biotech Applications

## Biotechnological potential of alkaliphiles

| Sr. No. | Alkaliphile  | Isolation Site                                       | Product/Application                                      | Reference                 |
|---------|--|--|--|---------------------------|
| 1       | <i>Bacillus</i> sp.  | Alkaline soda Lake, Ethiopia                         | Xylanase   | Gessesse and Mamo (1999)  |
| 2       | <i>Exiguobacterium oxidotolerans</i>   | Fish processing plant, Hokkaido, Japan               | Catalase   | Yumoto et al. (2004)      |
| 3       | <i>Streptomyces tanashiensis</i>   | Loktak lake of Manipur, India                        | Antimicrobial activity                                   | Singh et al. (2009)       |
| 4       | <i>Halomonas</i> sp.   | Wheat straw black liquor                             | CMCase, xylanase, lipase, amylase, and pullulanase       | Yang et al. (2010)        |
| 5       | <i>Streptomyces aburaviensis</i>   | Saline desert of Kutch, India                        | Antimicrobial activity                                   | Thumar et al. (2010)      |
| 6       | <i>Acinetobacter</i> sp.   | Oil Spilling sites, Gujarat India                    | Synthetic chemistry                                      | Ahmed et al. (2010)       |
| 7       | <i>Chitinophaga pinensis</i>   | Cold desert, Antarctic (metagenomic library of soil) | Lipases/esterases  | Hu et al. (2012)          |
| 8       | <i>Bacillus cereus</i>   | Bani Salama Lake, Wadi El-Natron, Egypt              | Mannanase  | El-Sharouny et al. (2015) |
| 9       | <i>Streptomyces</i> sp.  | Arid soil, Boussaada, Algeria                        | Antifungal   | Souagui et al. (2015)     |
| 10      | <i>Bacillus</i> , <i>Corynebacterium</i> , <i>Micrococcus</i> , and <i>Actinomycetes</i> , <i>Flavobacterium</i> | Mangrove ecosystems, Goa, India                      | Biodegradation of aromatic hydrocarbons                  | Desai Gaokar (2015)       |
| 11      | <i>Bacillus marmarensis</i>  | —  | Biorefining of cellulose                                 | Wernick et al. (2016)     |
| 12      | <i>Bacillus infantis</i> SKS1  | Garden Soil, India                                   | Proteases  | Sagg and Mishra (2017)    |
| 13      | <i>Alkaliphilus namsaraevii</i>  | Steppe soda lake, Transbaikal Region, Russia         | Reducing activity against iron and sulfur in alkaline pH | Zakharyuk et al. (2017)   |

CMCase, carboxymethylcellulase.

***Halomonas aquamarina* and *Alteromonas macleodii***, suitable as biological systems for bioremediation of oily marine ecosystems.

International Biodeterioration & Biodegradation 64 (2010) 554–559

Contents lists available at ScienceDirect



International Biodeterioration & Biodegradation

journal homepage: [www.elsevier.com/locate/ibid](http://www.elsevier.com/locate/ibid)



Agarolytic bacteria with hydrocarbon-utilization potential in fouling material from the Arabian Gulf coast

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### ARTICLE INFO

#### Article history:

Received 10 May 2010  
Revised 10 June 2010  
Accepted 21 June 2010  
Available online 24 July 2010

**Keywords:**  
Agarolytic bacteria  
Hydrocarbon degradation  
Bioremediation  
Marine environment

### ABSTRACT

Fouling material adhering to a neglected navigation vehicle half-sinking in the coastal water of the Arabian Gulf harbored two agarolytic bacterial species, *Halomonas aquamarina* and *Alteromonas macleodii* with hydrocarbon-utilization potential. Both species were halophilic (optimum 2–5% NaCl, w/v), slightly alkaliphilic (optimum pH 8) and grew best at 25 °C. The oil and hydrocarbon consumption potential of both species was dramatically enhanced (2 fold or more) by the addition of agar powder to the liquid medium. Both organisms were able to grow on a nitrogen free medium. These results imply that such agarolytic bacteria could potentially be suitable biological systems for self-cleaning and bioremediation of oily marine ecosystems.

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# HALOPHILES

*halo-* + *-phile*: **salt loving**

The Voyage of the Beagle:

*“... Whether lakes of brine, or those subterranean ones hidden beneath volcanic mountains – warm mineral springs – the wide expanse and depths of the ocean – the upper regions of the atmosphere, and even the surface of perpetual snow – all support organic beings”.*

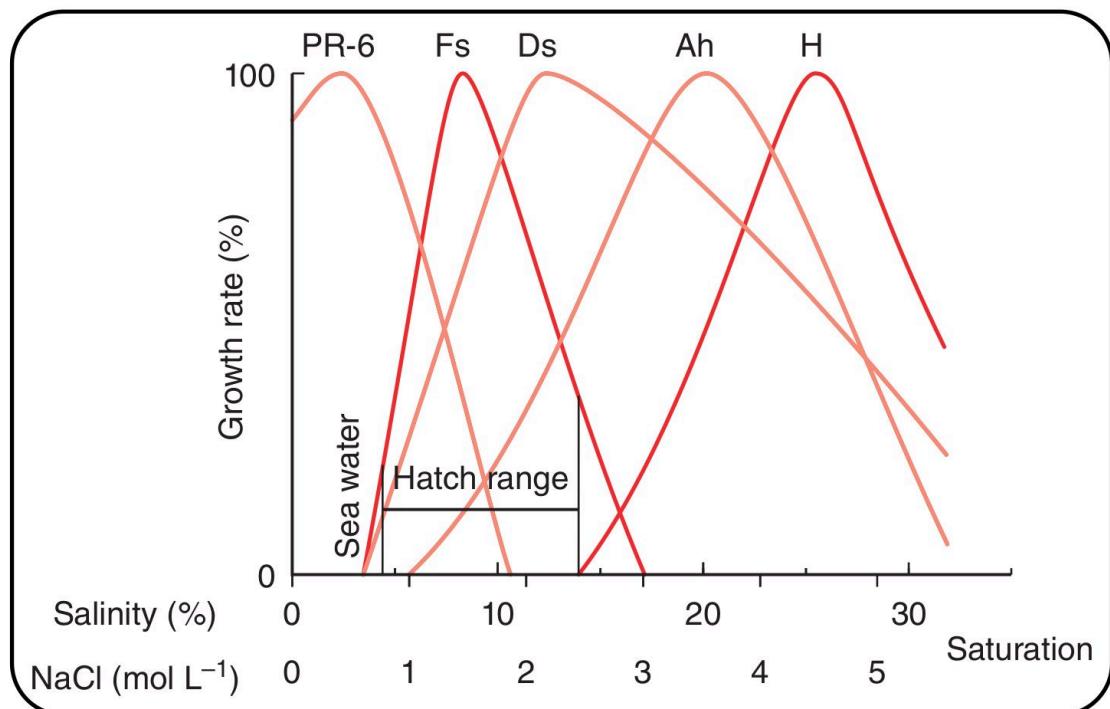
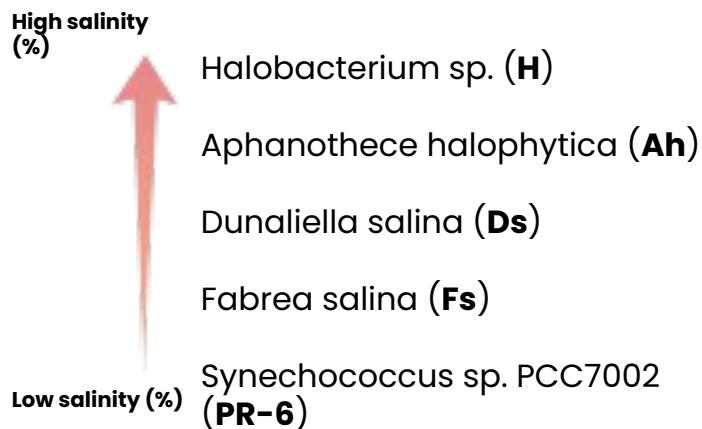
Charles Darwin (1809-1882)

# Range of life: Salinity

**TABLE 11.1** Classification of microorganisms based on response to salt.

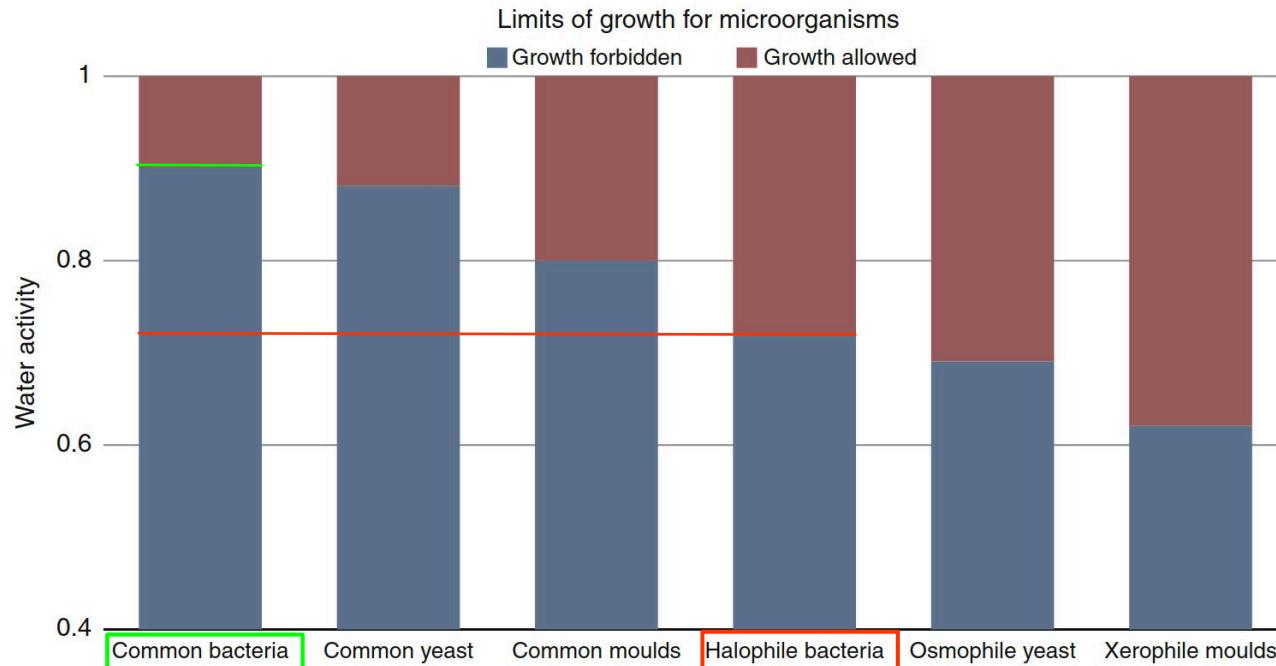
| Class of prokaryotes with respect to salinity   | Salinity conditions  | Examples  |
|---|--|---|
| Non-halophilic                                  | <0.2 M   | Bacteria thriving in freshwater   |
| Halotolerant                                    | Able to tolerate salt; if tolerates > 2.5 M, then considered as extremely halotolerant | <i>Staphylococcus</i> sp.   |
| Slight halophile                                | 0.2–0.5 M  | Bacteria constituting marine habitats   |
| Moderate halophile/borderline extreme halophile | 0.5–2.5 M/1.5–4.0 M  | <i>Salinivibrio costicola</i> , <i>Halomonas elongate</i> , <i>Tamilnaduibactersalinus</i> / <i>Halorhodospira halophila</i>  |
| Extreme halophile                               | 2.5–5.2 M  | Type species of genus <i>Halobacterium</i> , <i>Halobacterium salinarum</i> , <i>Halomarinaoriensis</i> , <i>Salinibacter ruber</i> (member of <i>Bacteroidetes</i> ) |

# Range of life: Salinity

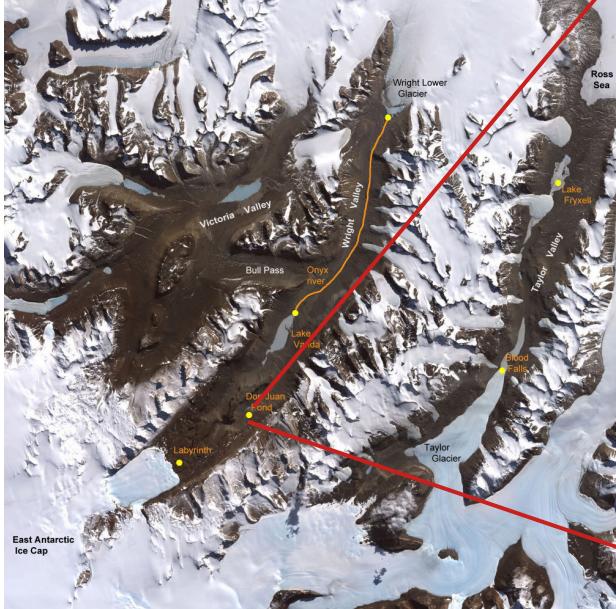


# Water activity

Water activity, **aw**, is a dimensionless parameter defined as the vapor pressure of water in a system (p) divided by that of pure water at the same temperature ( $p_0$ ). It correlates with the proportion of **water available for biological or chemical reactions** and is related to the energy status of the water molecules in a given system (pure distilled water has  $aw=1$ ).



# Water activity

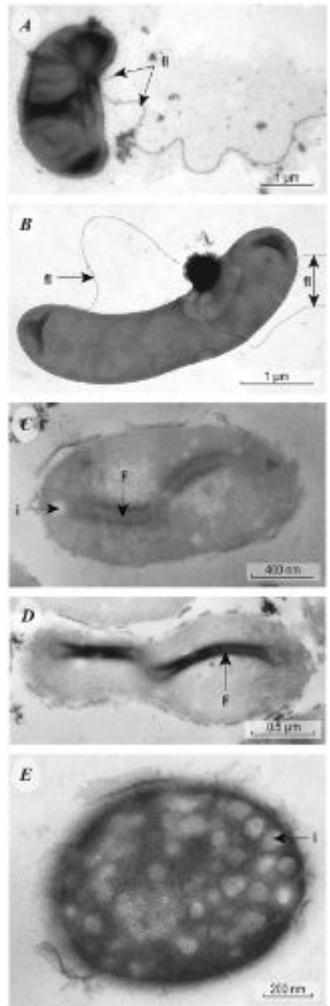


**Don Juan Pond:** unfrozen lake (Antarctica)

- a.  $\text{CaCl}_2$ - dominated brine: up to 474 g/L
- b. pH: 4.6
- c. Average depth: 11 cm
- d. Temperatures  $-36^\circ\text{C}$  ( $T_{\text{MAX}} \sim 20^\circ\text{C}$ )
- e. Water activity: 0.28 aw (25°C) to 0.61 aw (-50°C)

(Oren, 2013; Toner et al., 2017)

# Salinity loving extremophiles. Who are they? The “known” extremes

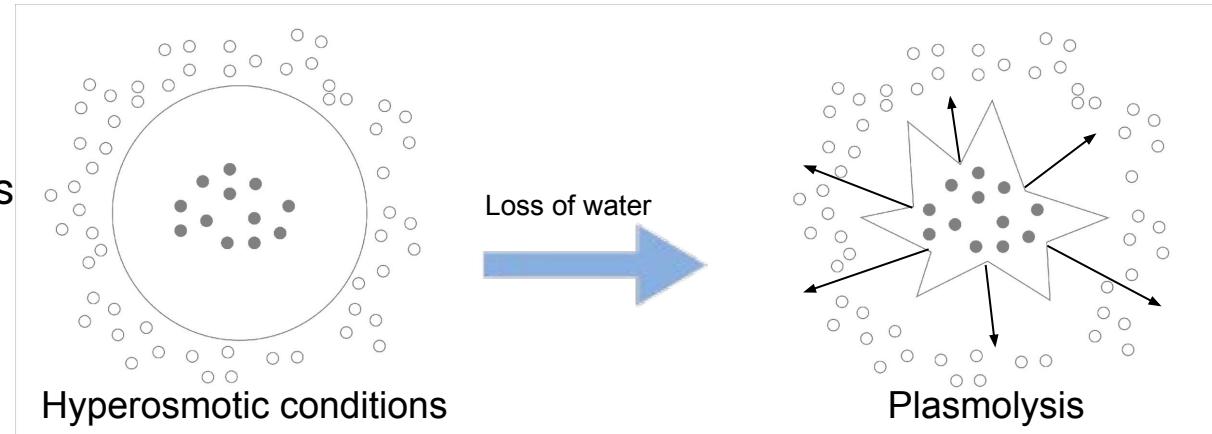


The organism that holds the record as capable of living at the highest salinity concentration is ***Halarsenatibacter silvermanii*** strain SLAS-1 growing at a **salinity optimum of 35% NaCl** isolated from the alkaline hypersaline Searles Lake (CA, USA).

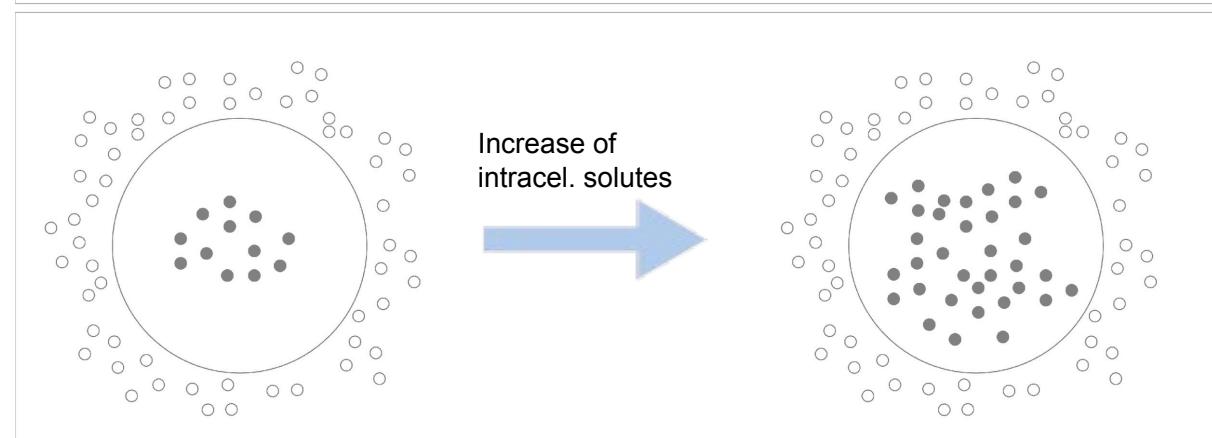


# Water activity and osmotic equilibrium

The survival of microorganisms in hypersaline environments requires the cells to **maintain** its **intracellular osmotic pressure**.



The regulation of lost water in the salt rich environment through the permeable biological membranes is **not energetically feasible** through active energy-dependent inward transport.



# Physiological adaptation

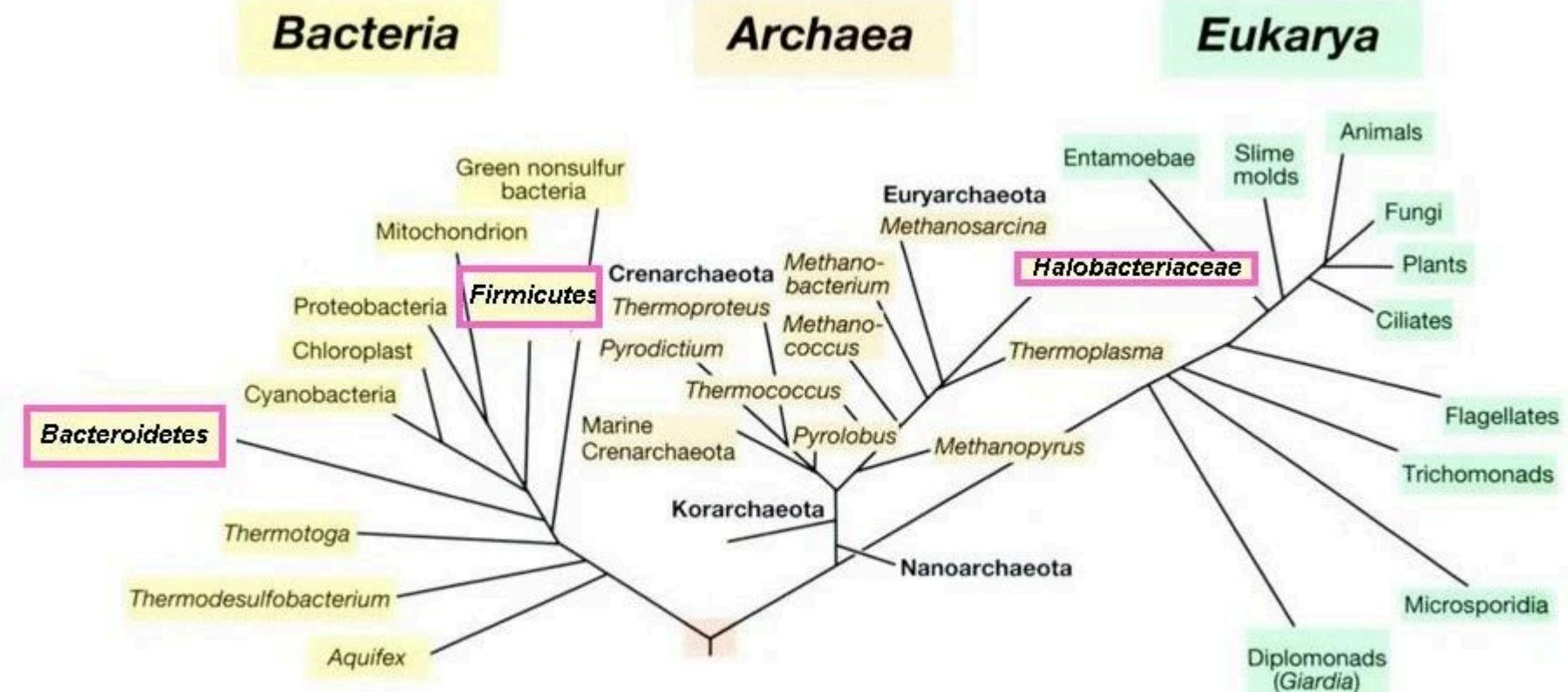
Two main **strategies**: "**HIGH SALT-IN**" and "**LOW SALT-IN/SALT-OUT**"

"**SALT-IN**": not widely used among the different phylogenetic and physiological groups of halophiles

**High salt content within the cell**



- Energetically **less costly to the cell** than the biosynthesis of large amounts of organic osmotic solutes;
- Involves **accumulation** of molar concentrations of **K<sup>+</sup>** and **Cl<sup>-</sup>** or other **inorganic solutes**;
- **Requires extensive adaptation** of the intracellular enzymatic machinery to the presence of salt.



**Distribution within the phylogenetic tree of microorganisms accumulating KCl as their sole or main osmotic solute.** Groups marked with purple boxes contain at least one halophilic representative (e.g. *Salinibacter ruber* within the *Bacteroidetes*). The group of the *Firmicutes* contains both microorganisms that use KCl for osmotic balance (the order *Halanaerobiales* within the low G+C branch, consisting of anaerobic fermentative organisms) and different halophilic aerobes (*Halobacillus* spp. and others) that accumulate inorganic solutes. High intracellular KCl concentrations are also found in the methanogenic halophiles, but these accumulate organic solutes as well.

# Physiological adaptation

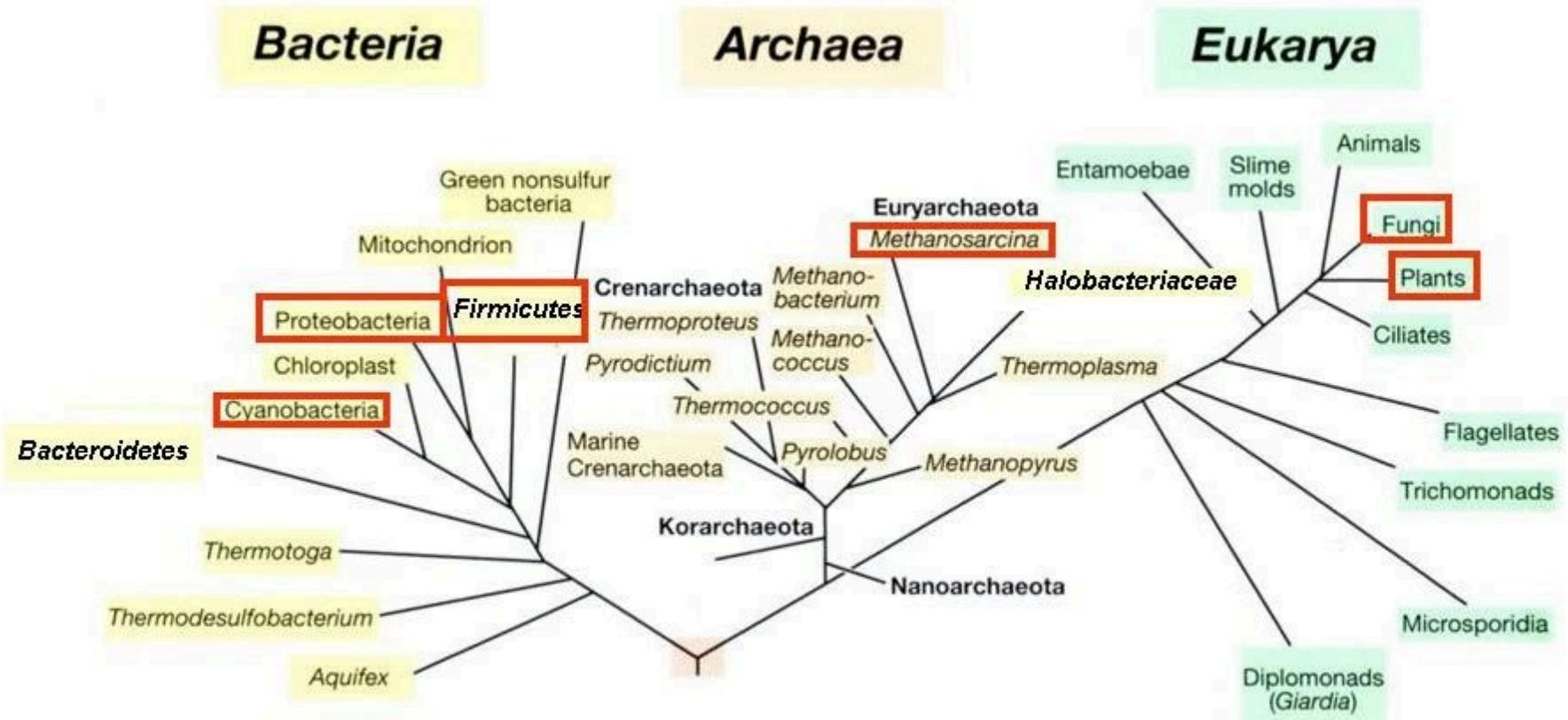
Two main **strategies**: "**HIGH SALT-IN**" and "**LOW SALT-IN/SALT-OUT**"

"**SALT-OUT**": most of halophilic and halotolerant Bacteria + methanogenic Archaea.

**Low** salt content within the cell



- **Organic compatible solutes** play a **key role** in osmotic balance;
- Cells **exclude salt from their cytoplasm** as much as possible;
- It requires few adaptations of the cells' proteome;
- The production of massive amounts of such solutes can be **energetically costly**, thus organisms have **optimized its metabolism to minimize** the energetic cost of osmotic adaptation



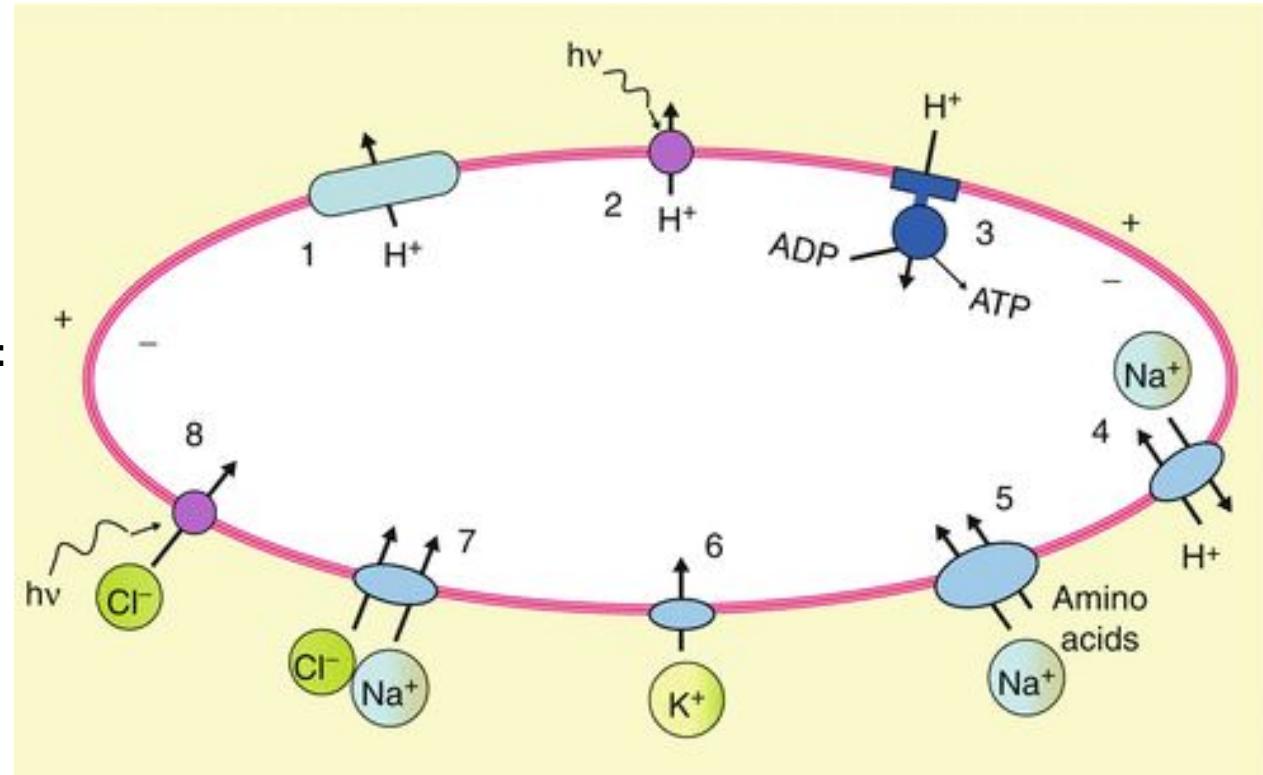
**Distribution within the phylogenetic tree of microorganisms accumulating organic solutes to provide osmotic balance.** Groups marked with red boxes contain at least some halophilic representatives in which de novo synthesis and/or accumulation of organic solutes has been demonstrated. The group of the Firmicutes contains both halophilic aerobes that accumulate organic solutes and anaerobic fermentative microorganisms (the order Halanaerobiales) that use KCl.

# Physiological adaptation: HIGH SALT-IN STRATEGY

*Halobacteriales* order

Pathways:

- 1 – 2: **Protons extrusion**
- 3: **ATP formation**
- 4 – 5: **Na<sup>+</sup> extrusion and syimport**
- 6: **K<sup>+</sup> accumulation**
- 7-8: **Cl<sup>-</sup> pumps**

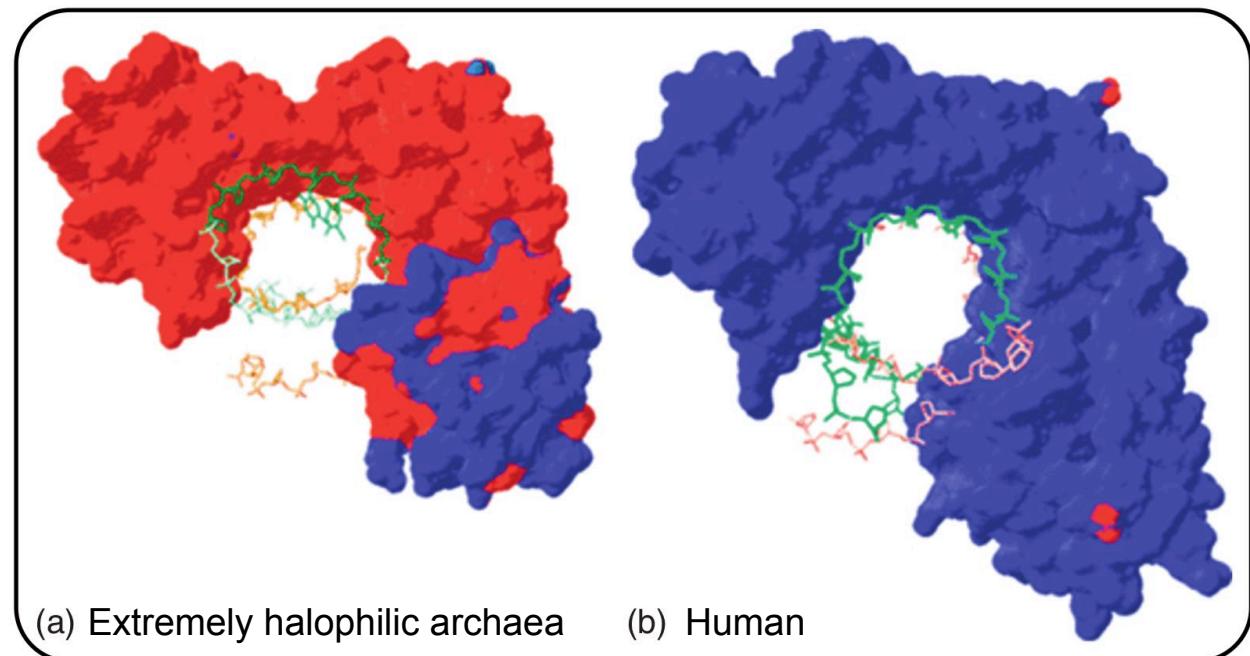


# Physiological adaptation: HIGH SALT-IN STRATEGY

*Halobacteriales* order

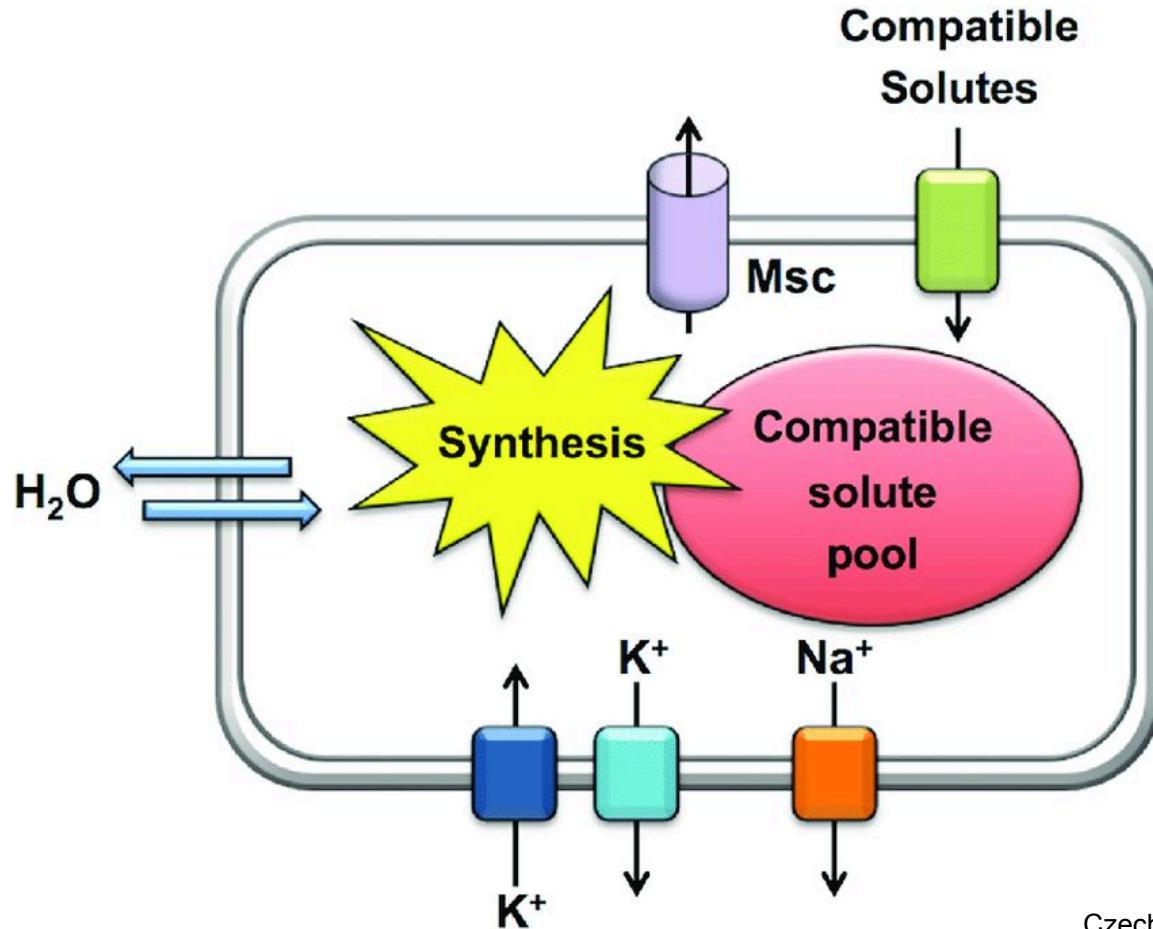
Protein–DNA complexes:  
transcription initiation  
complexes, surrounding the  
DNA double helix.

Protein surface charges:  
**Red** for **acidic** or negative;  
**Blue** for **basic** or positive.

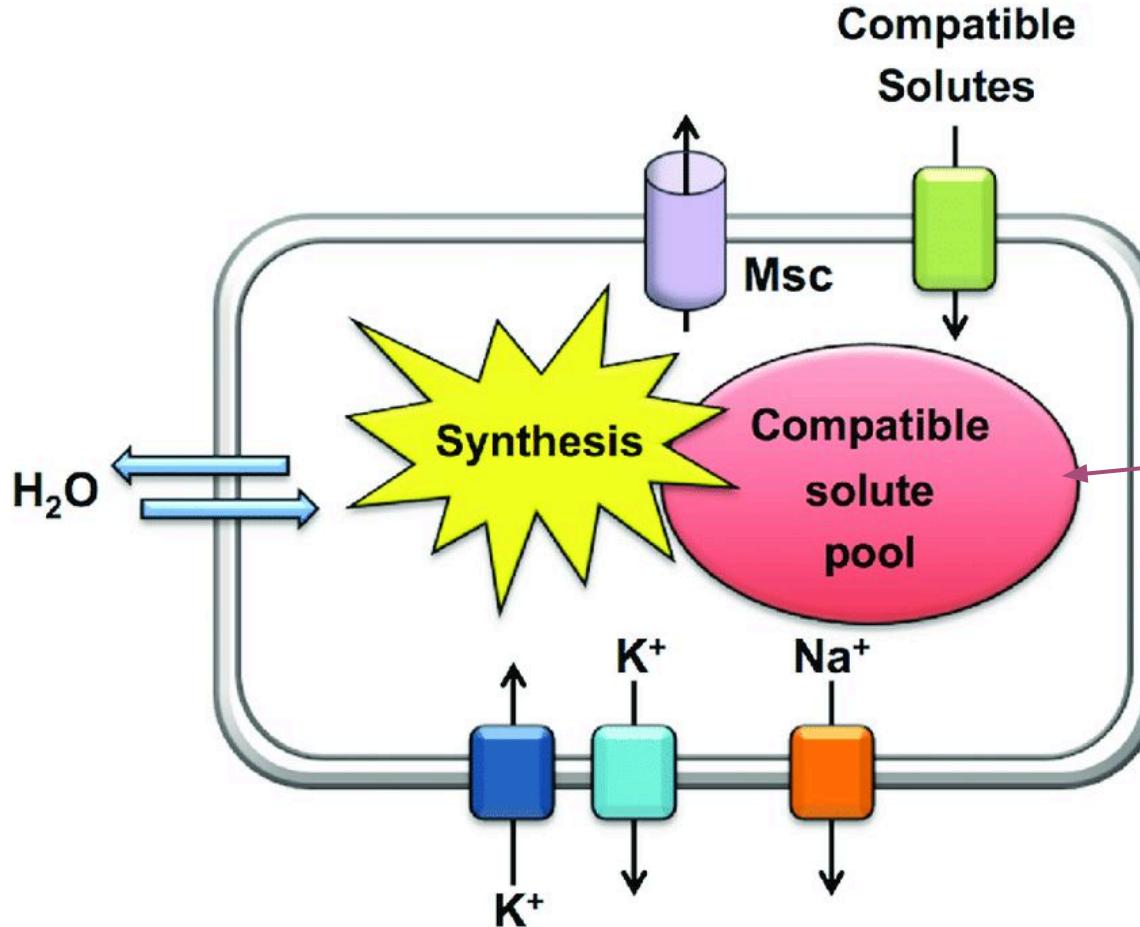


DasSarma and DasSarma (2017)

# Physiological adaptation: LOW SALT-IN/SALT-OUT STRATEGY

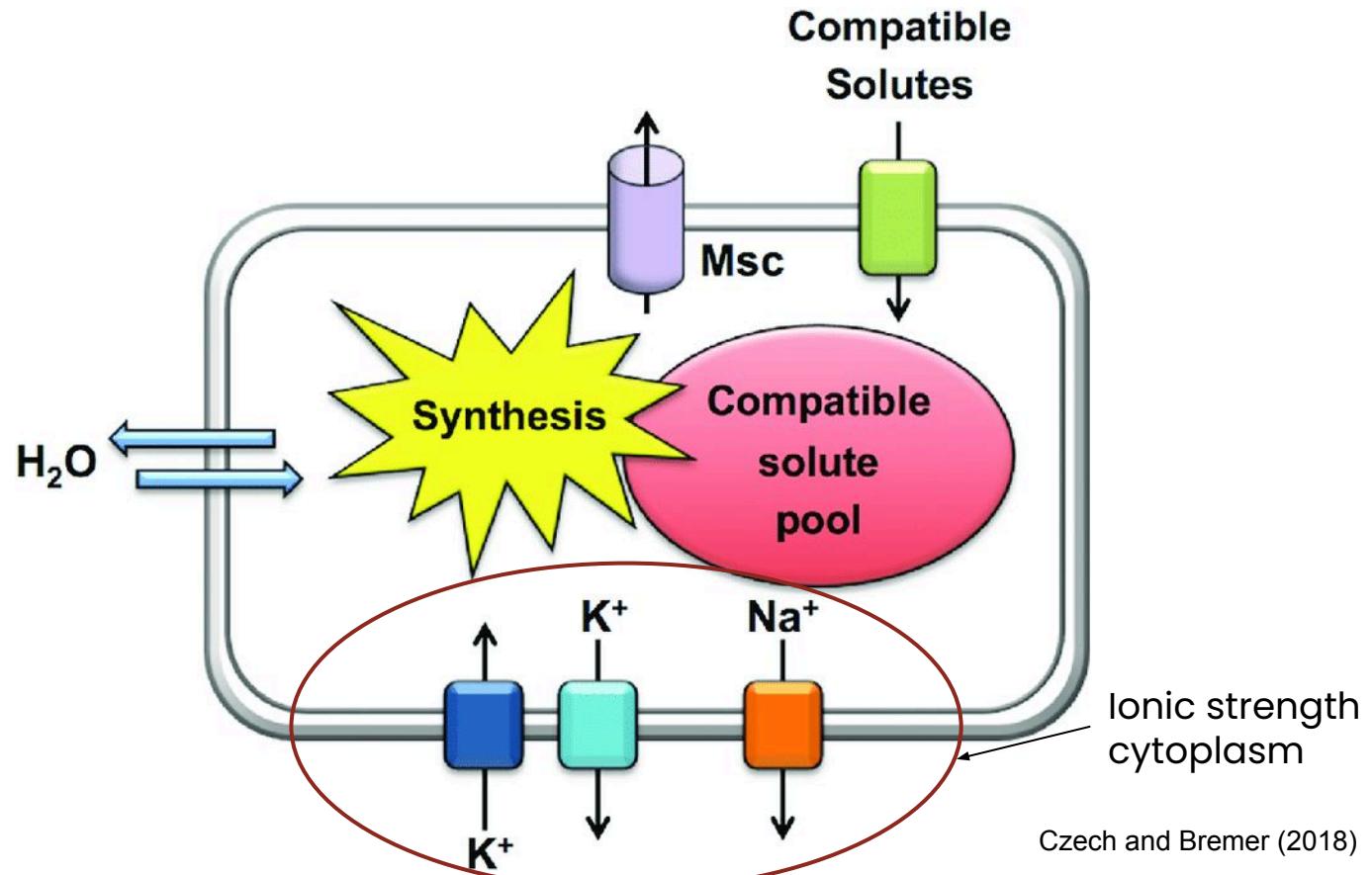


# Physiological adaptation: LOW SALT-IN/SALT-OUT STRATEGY

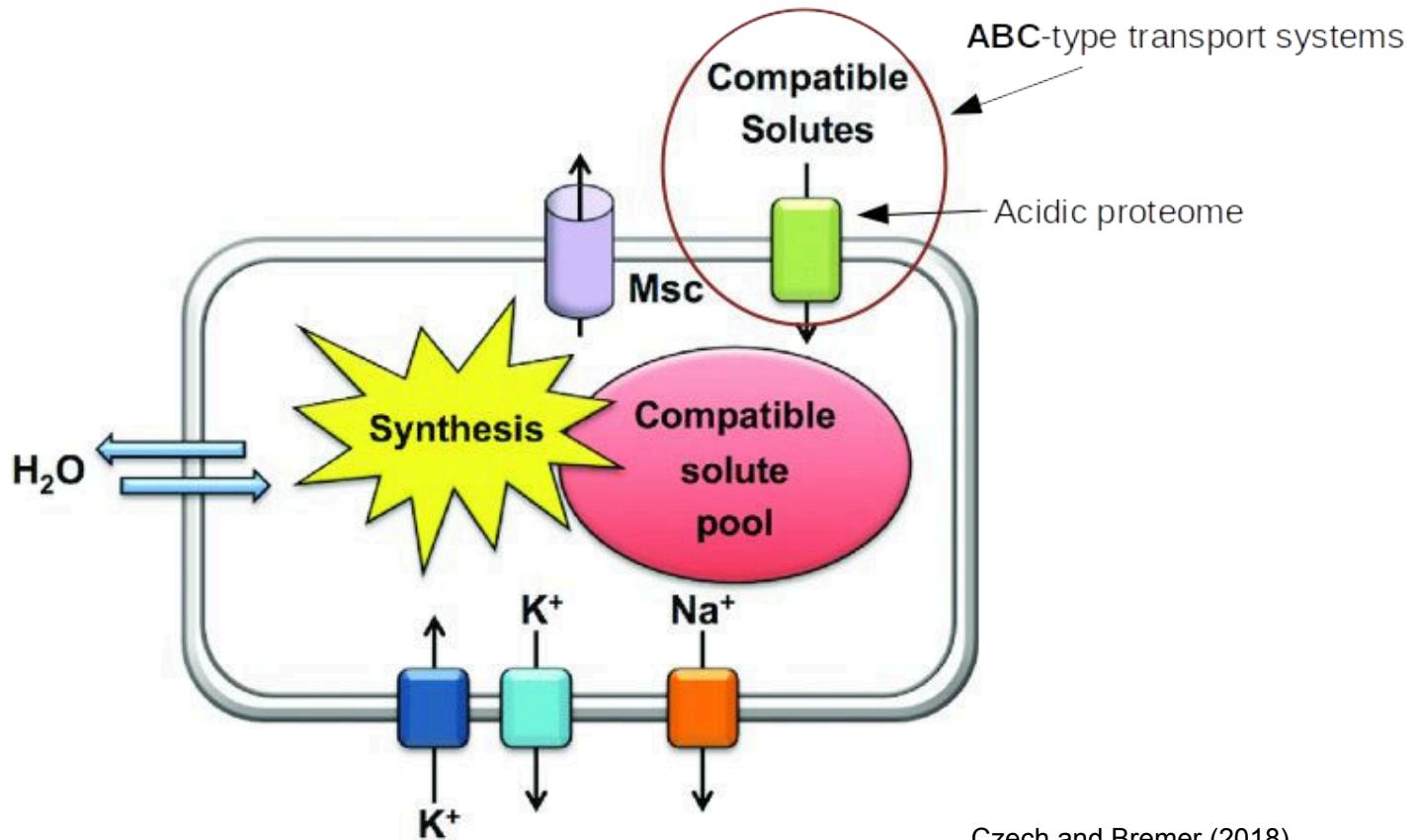


**Organic osmolytes** that can be amassed to exceedingly high cellular concentrations **without disturbing** vital biochemical and physiological processes. Many cells **contain cocktails of different compatible solutes** rather than relying on a single compound

# Physiological adaptation: LOW SALT-IN/SALT-OUT STRATEGY



# Physiological adaptation: LOW SALT-IN/SALT-OUT STRATEGY



Czech and Bremer (2018)

# Physiological adaptation: LOW SALT-IN/SALT-OUT STRATEGY

**TABLE 11.2** Structure and distribution of some zwitterionic organic osmolytes within the prokaryotes.

| Solute          | Distribution  |
|-----------------|---|
| Glycine betaine | Halotolerant and halophilic bacteria, phototrophic <i>Halorhodosporahalochloris</i> , aerobic chemoheterotrophic bacteria, methylotrophic bacteria, <i>Methylarcularterricola</i> , <i>Methylophaga</i> sp., <i>Sporosarcina pasteurii</i> , <i>Brevibacterium</i> sp., <i>Chromohalobacter</i> sp.   |
| Ectoine         | Halotolerant and halophilic bacteria, Heterotrophic Gammaproteobacteria ( <i>Vibrio cholera</i> , <i>Halorhodosporahalochloris</i> , <i>Halomonas elongate</i> , <i>H. variabilis</i> , <i>Chromohalobacter salexigens</i> , <i>C. israelensis</i> , <i>Methylophaga alcalica</i> , <i>Halobacillus halophilus</i> , <i>Micrococcus</i> sp., <i>Bacillus</i> spp., <i>Rhodovulum sulfidophilum</i> , <i>Brevibacterium</i> sp.) |

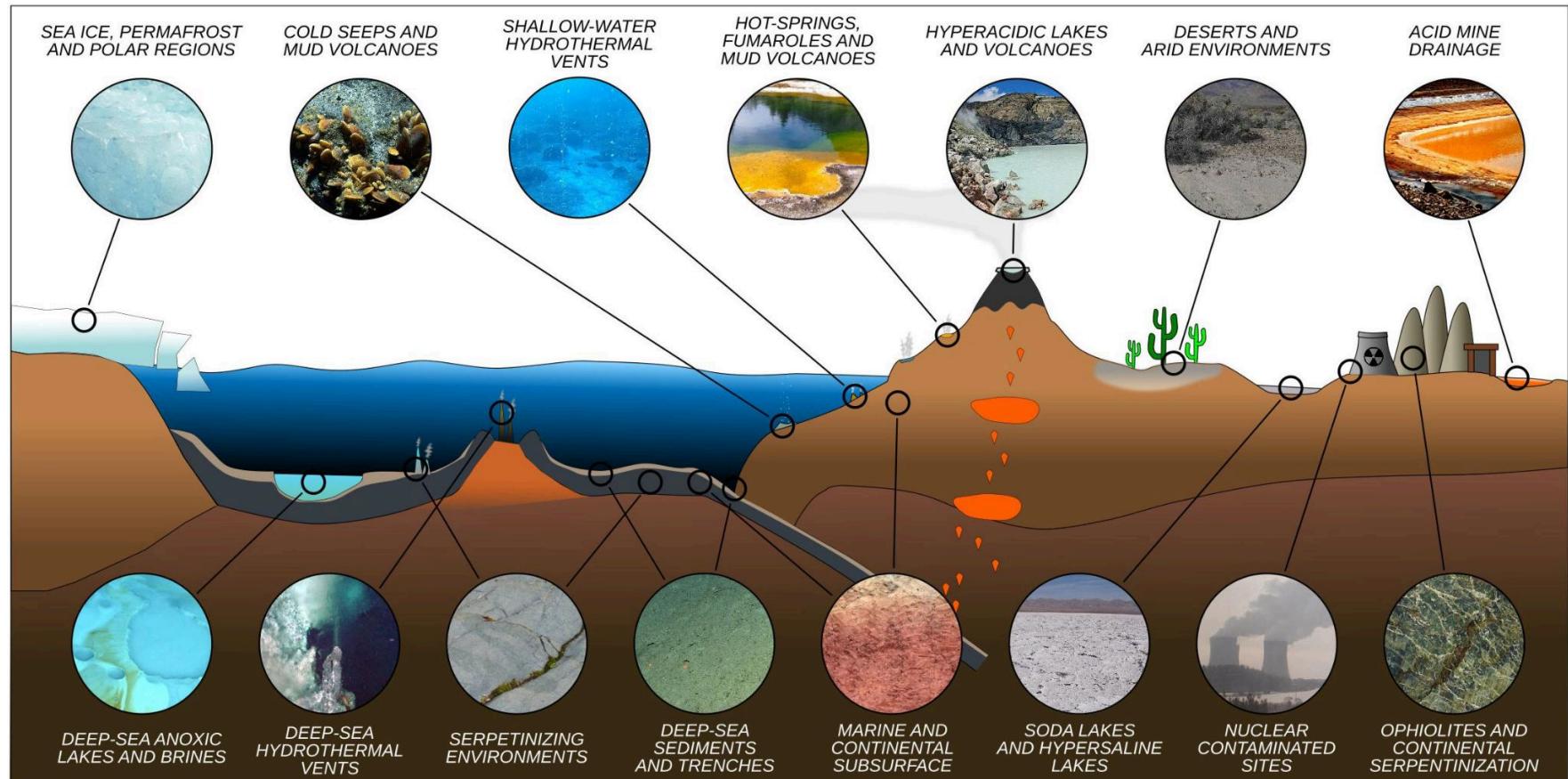
**TABLE 11.3** Structure and distribution of selected uncharged organic osmolytes within the prokaryotes.

| Solute                     | Distribution  |
|----------------------------|---|
| $\alpha$ -Glucosylglycerol | Marine and fresh water cyanobacteria ( <i>Pseudomonas mendocina</i> , <i>P. pseudoalkaligenes</i> , <i>Stenotrophomonas</i> , <i>Microcytis firma</i> )   |
| Trehalose                  | <i>Cyanobacteria</i> , <i>Halorhodospira</i> spp., <i>Sulfolobus solfataricus</i> , <i>Thermoproteus tenax</i> , <i>Rhodothermusobamensis</i> , <i>Desulfovibrio halophilus</i> , <i>Thermoplasma acidophilum</i> |
| Sucrose                    | <i>Cyanobacteria</i> , <i>Proteobacteria</i>  |

**TABLE 11.4** Structure and distribution of selected anionic organic osmolytes (carboxylates, phosphate, sulfate) within the prokaryotes.

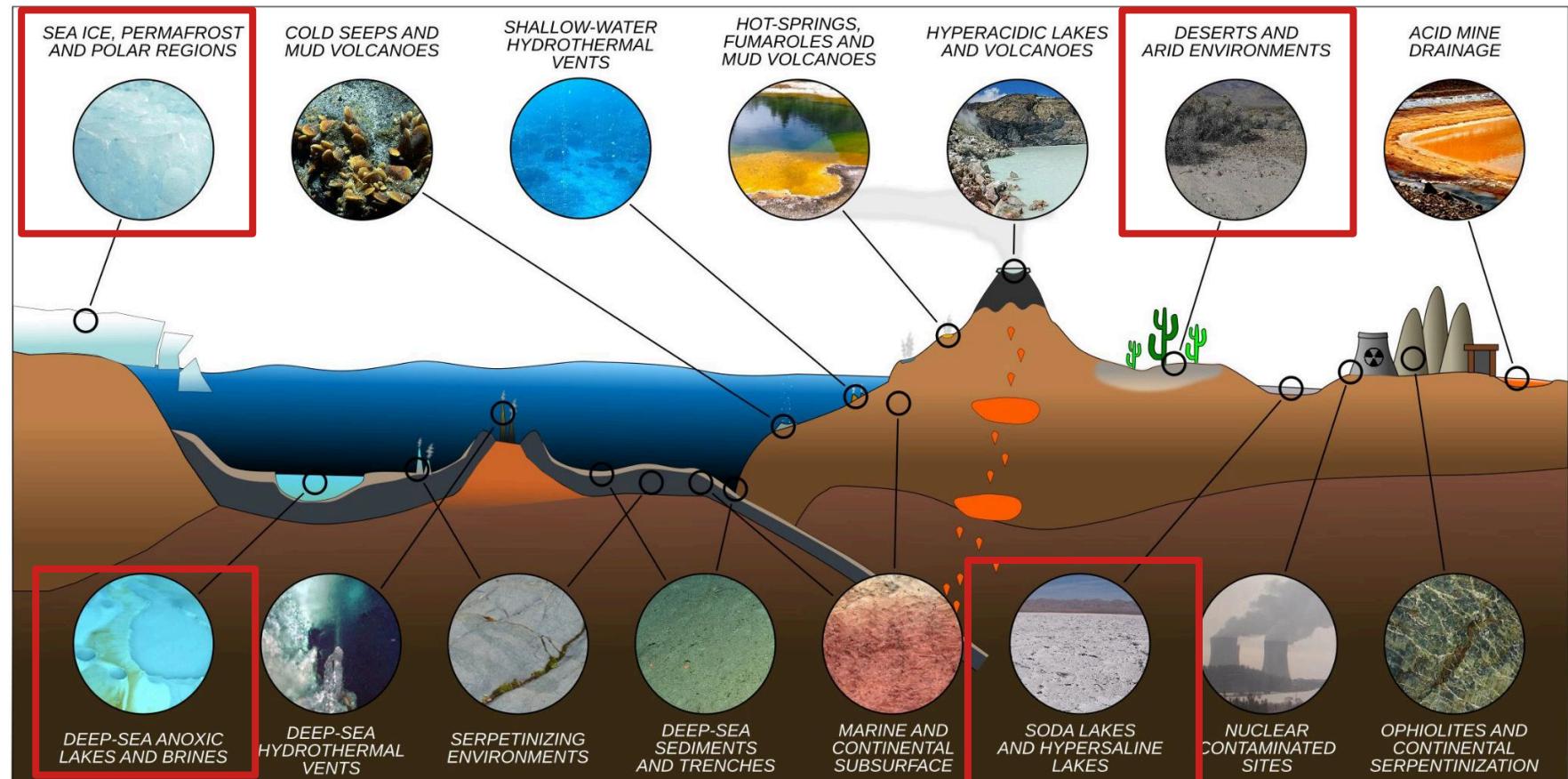
| Solute              | Distribution   | References |
|---------------------|--|------------|
| $\alpha$ -glutamate | Many halophilic bacteria and methanogens ( <i>Halomonas elongata</i> , <i>Halobacterium salinarum</i> , <i>Methanophilus portocalensis</i> ) | [88]       |
| $\beta$ -glutamate  | Methanogenic Archaea ( <i>Metanothermococcus thermolithotrophicus</i> )  | [88–91]    |

# Salinity: Ecology – Environments



Merino et al., 2019

# Salinity: Ecology – Environments

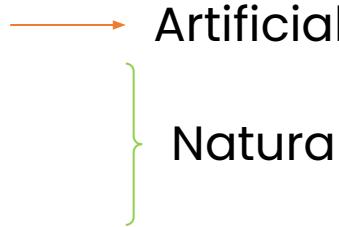


Merino et al., 2019

POLI- EXTREMOPHILES!!!

# Salinity: Ecology – Environments

## Types of saline environments:

1. **Based on the genesis of the environment:** Artificial or of natural origin.
  - a. *Solar salterns* ————— Artificial
  - b. *salt lakes*
  - c. *saline soils*
  - d. *deep-sea brines, ecc...*
2. **Based on the genesis of the salts present:** Thalassic and athalassic:
  - a. *Marine salts;*
  - b. *Non marine salts.*

# Salinity: Ecology – Environments

**ECOLOGY – ENVIRONMENTS:** artificial solar hypersaline environments

## Solar salterns

Multi pond solar salterns consist of a series of **interconnected shallow ponds** with increasing salinity, from sea water to NaCl saturation (~26% at 20°C).

**Succession** of different groups of microorganisms



# Salinity: Ecology – Environments

**ECOLOGY – ENVIRONMENTS:** artificial hypersaline environments

## Solar salterns

High presence of carotenoids  
in microbial community

Example:

***Salinibacter ruber***:  
photosynthesis antenna  
pigments



# Salinity: Ecology – Environments

## ECOLOGY – ENVIRONMENTS

**SODA LAKES:** most alkaline naturally occurring environments on Earth

### Alkaliphilic halophile

Dominant microbial community composed of:

Aerobic, organotrophic, halophilic and alkaliphilic bacterial and archaeal phyla

Anaerobic, alkaliphilic microbial community

Lake Natron, Tanzania.



# Salinity: Ecology – Environments

## ECOLOGY – ENVIRONMENTS

**DRY DESERT:** fluctuations in temperature, desiccation and radiation levels

### Xerotolerant halophile

Dominant microbial community:

Bacteria:

Cyanobacteria phylum  
Bacteroidetes phylum

Archaea:

Halobacteria class

**Primary production** represents the main source of carbon

Atacama Desert



Uritskiy et al., 2019

# Salinity: Ecology – Environments

## ECOLOGY – ENVIRONMENTS

**DRY DESERT:** fluctuations in temperature, desiccation and radiation levels

### Halophilic microbial community compositional shift after a rare rainfall in the Atacama Desert

[Gherman Uritskiy](#), [Samantha Getsin](#), [Adam Munn](#), [Benito Gomez-Silva](#), [Alfonso Davila](#), [Brian Glass](#), [James Taylor](#) & [Jocelyne DiRuggiero](#)

[The ISME Journal](#) 13, 2737–2749 (2019) | [Cite this article](#)

4177 Accesses | 20 Citations | 25 Altmetric | [Metrics](#)

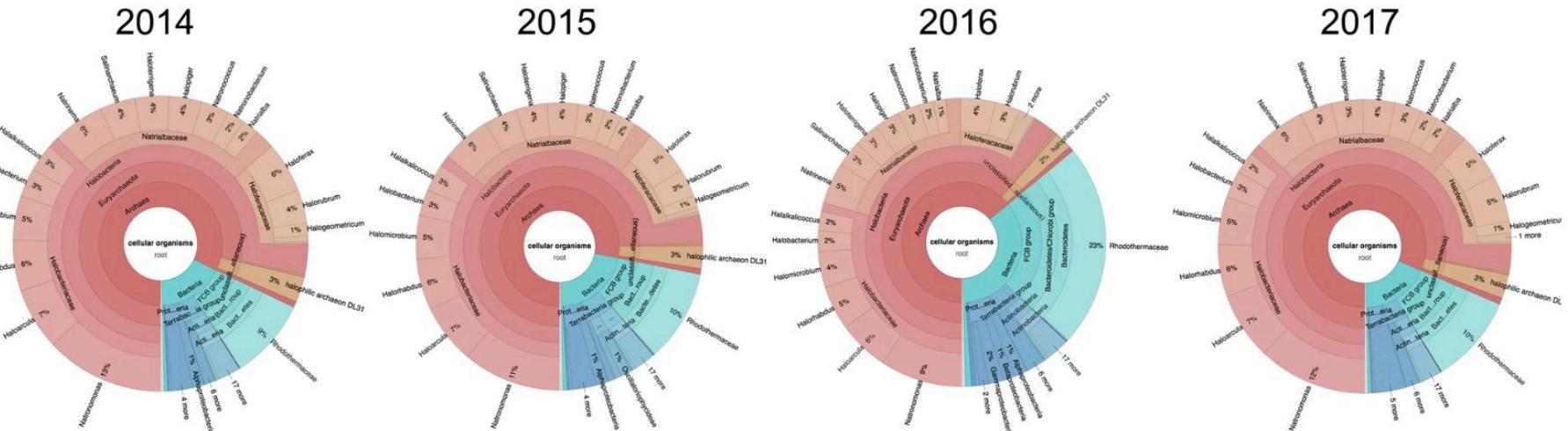
#### Abstract

Understanding the mechanisms underlying microbial resistance and resilience to perturbations is essential to predict the impact of climate change on Earth's ecosystems. However, the resilience and adaptation mechanisms of microbial communities to natural perturbations remain relatively unexplored, particularly in extreme environments. The response of an extremophile community inhabiting halite (salt rocks) in the Atacama Desert to a catastrophic rainfall provided the opportunity to characterize and de-conolute the

# Salinity: Ecology – Environments

## ECOLOGY – ENVIRONMENTS

**DRY DESERT:** fluctuations in temperature, desiccation and radiation levels



Average taxonomic composition of **halite** microbial communities from the same site, before (2014, 2015) and after (2016, 2017) the rain event.

Example of Ecosystem **resilience!!!**



# Salinity: Ecology – Environments

## ECOLOGY – ENVIRONMENTS

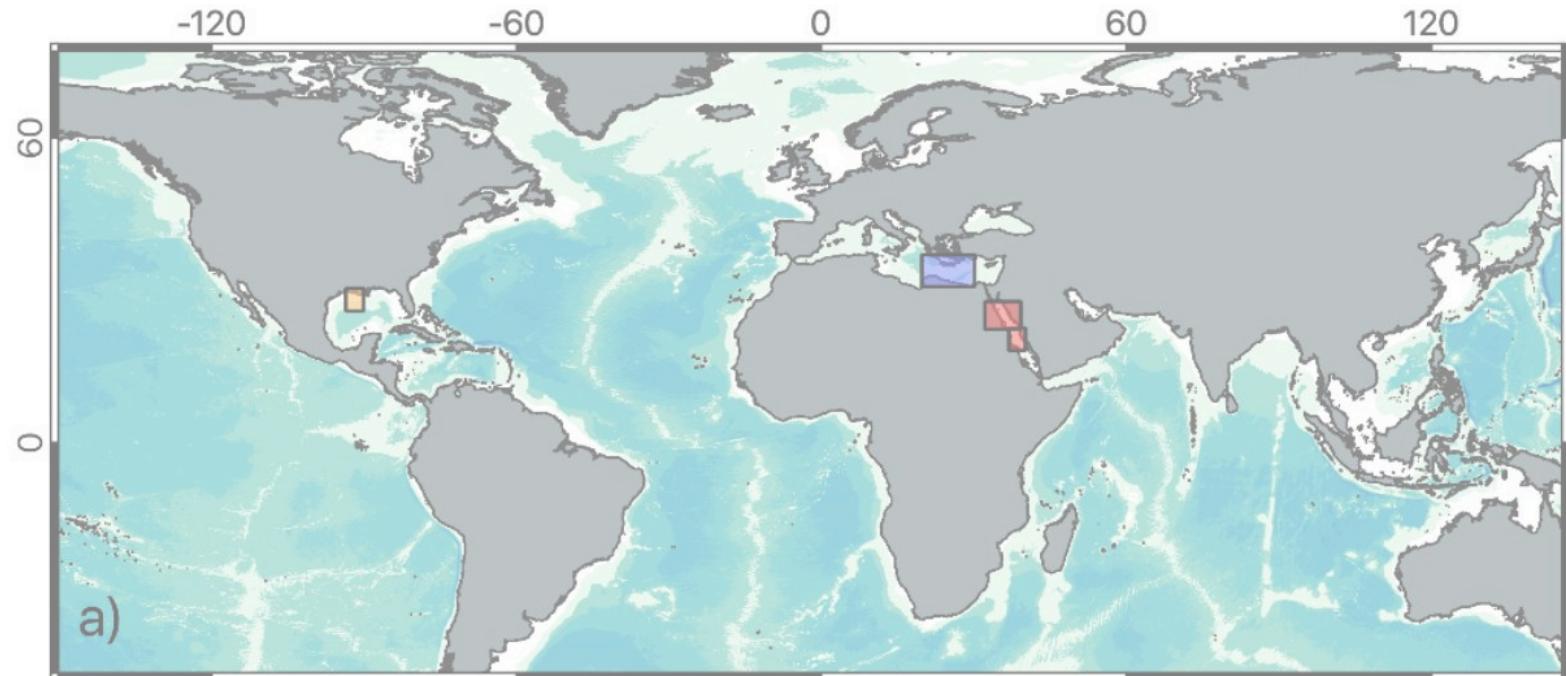
**DEEP-HYPERSALINE ANOXIC BASINS:** dense bodies of water that have a **salinity** that is **three to eight times** greater than the surrounding **ocean**.

# Salinity: Ecology – Environments

## ECOLOGY – ENVIRONMENTS

### DEEP-HYPERSALINE ANOXIC BASINS:

**Gulf of Mexico – Mediterranean Sea – Red Sea**



# Salinity: Ecology – Environments

## ECOLOGY – ENVIRONMENTS

### DEEP-HYPERSALINE ANOXIC BASINS:

#### Origin: Salt tectonics

Shallow salty basin

Tectonic shifts

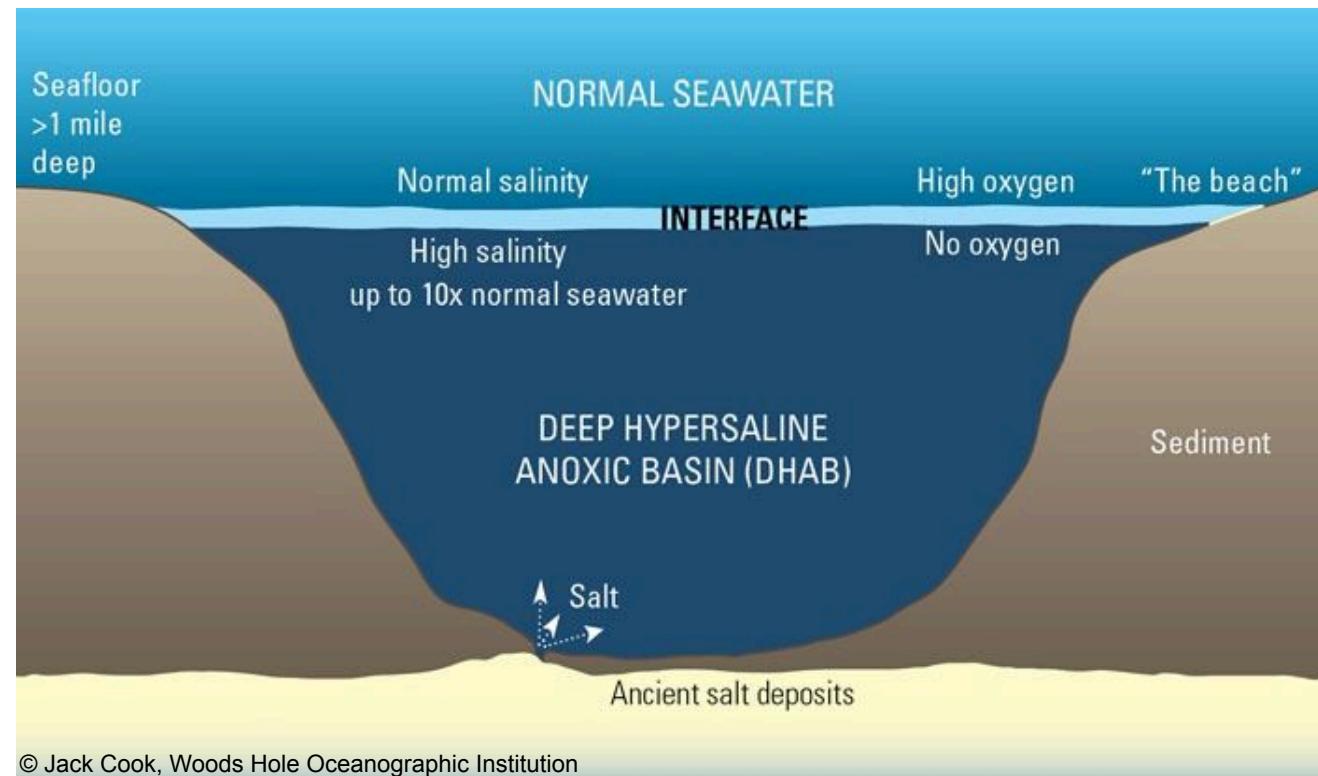
Lowering of the basin

Sediment buring

Crack of the salt dome

Salt rises and dissolves

Brine pool



# Salinity: Ecology – Environments

## ECOLOGY – ENVIRONMENTS

### DEEP-HYPERSALINE ANOXIC BASINS (DHABs):

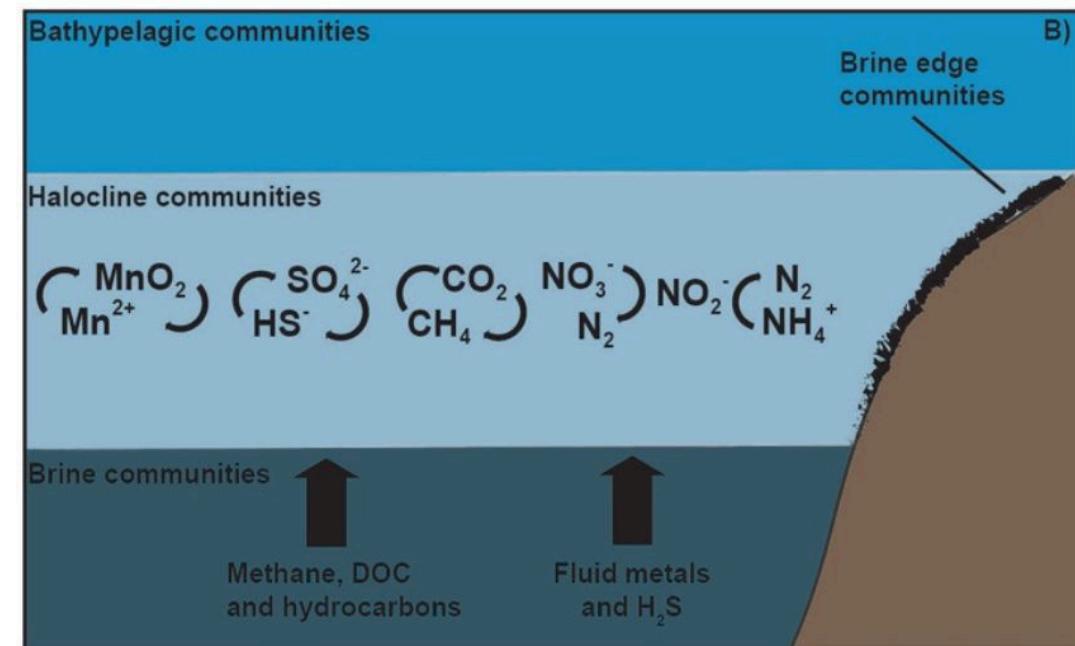
#### DHAB halophiles

Dominant microbial community:

Highly stratified community between brines and the seawater-brine interfaces;

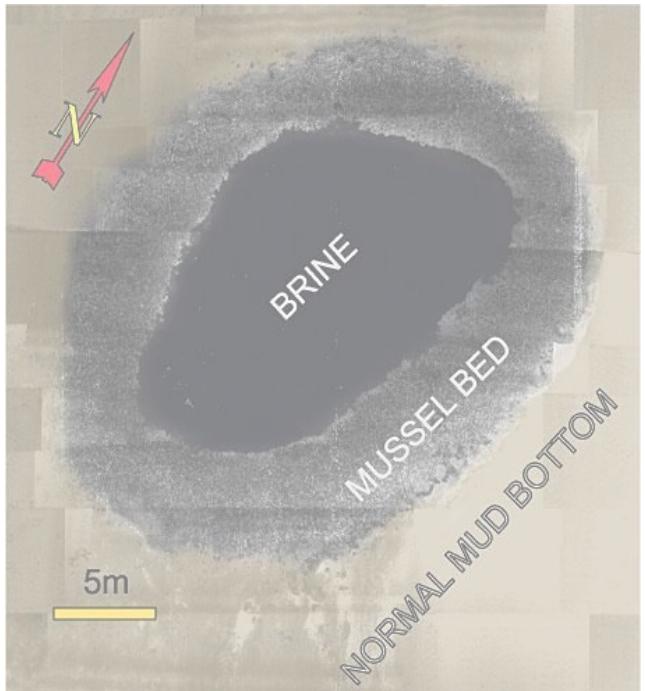
- *Delta-* and *Epsilonproteobacteria* sulfate-reducers (anaerobic oxidation of methane);
- *Gamma-* and *Epsilonproteobacteria* sulfide-oxidizer (sulfur-cycling);
- Top-down control made by viruses;

→ **Symbiosis** between microbes and mussels allows mussels to grow biomass thanks to the chemosynthetic, C fixing microbes located in their gill tissue



# Salinity: Ecology – Environments

## ECOLOGY - ENVIRONMENTS DEEP-HYPERSALINE ANOXIC BASINS:



© Dr. Ian McDonald, Texas A&M University



Photo credit: NautilusLive

# Water ice in crater at Martian north pole

Approximately:  
70.5° North and 103° East

The circular patch of bright material located at the center of the crater is **residual water ice**.

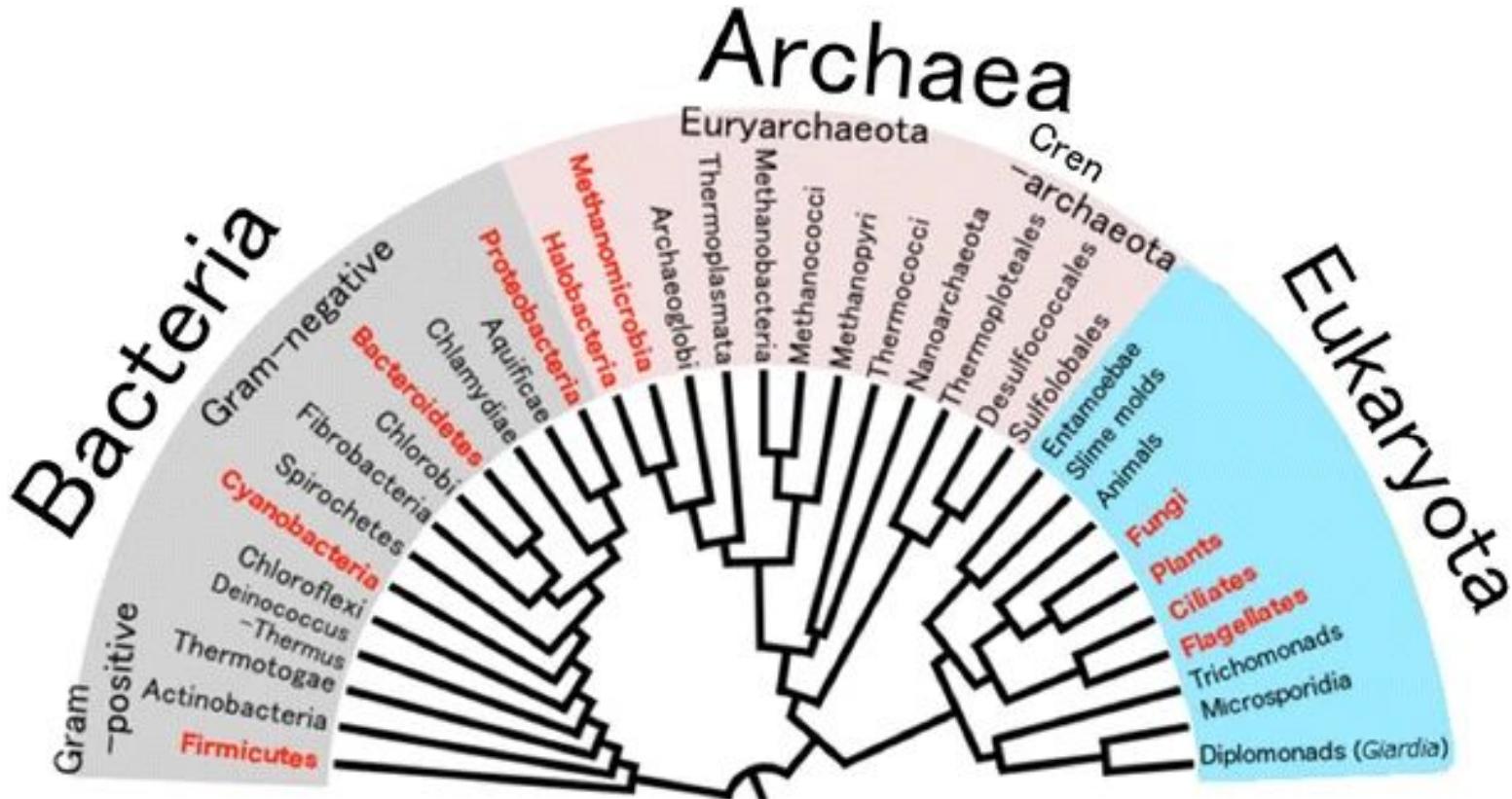
## Main hypothesis:

Halophiles are a leading group of microorganisms in the newly developing field of astrobiology and may be key to the search for life elsewhere in the universe. Discovery of recurring slope lineae has suggested the presence of freezing and thawing brine on Mars.

**Halophiles may expand the potential habitable zone** in our solar system and on extrasolar planets because of their ability to thrive under challenging conditions



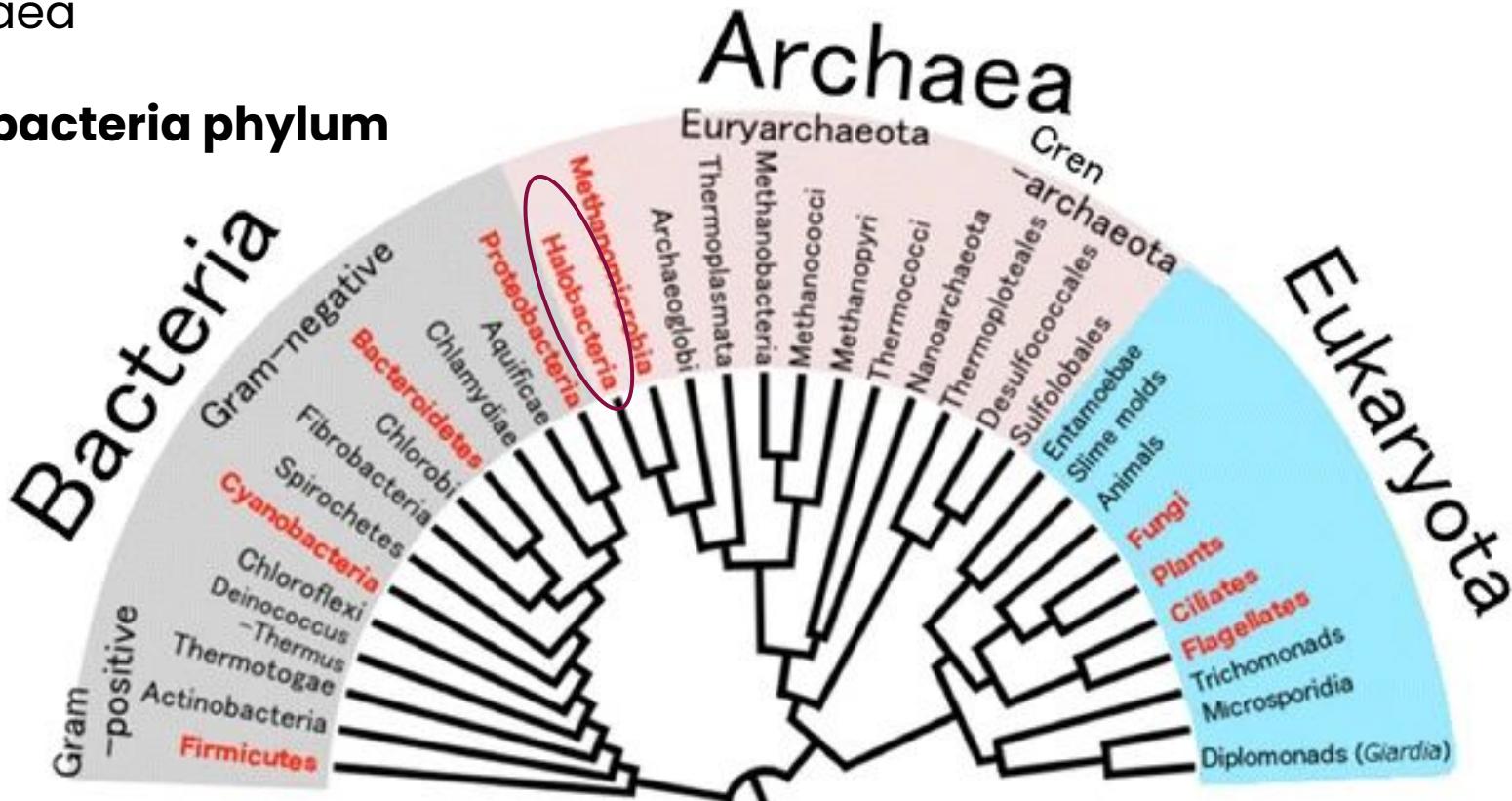
# TAXONOMY



# TAXONOMY

Archaea

**Halobacteria phylum**



# Salinity: Taxonomy of halophiles

Archaea

## Halobacteria phylum

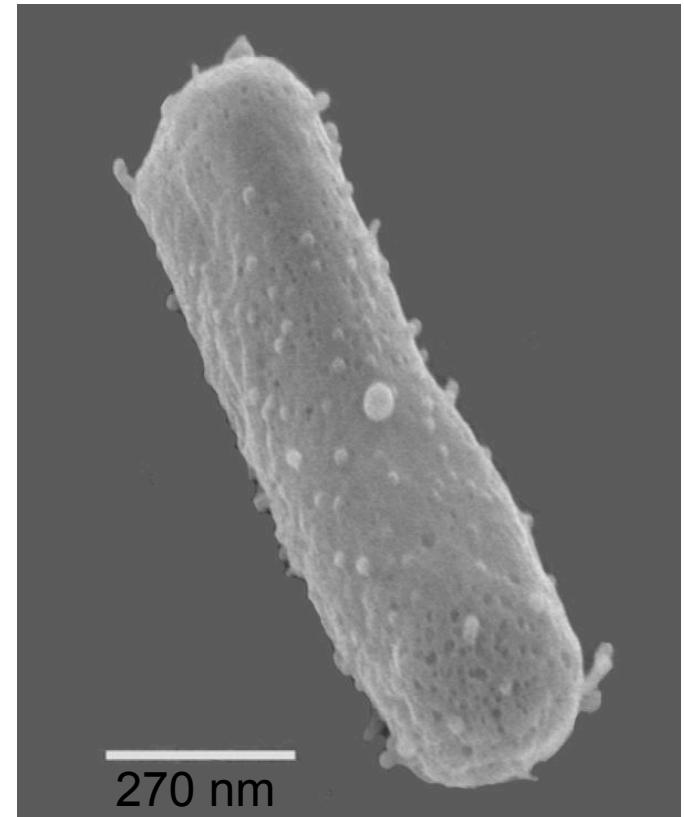
### *Halobacterium salinarum NRC-1*

**Energy** is obtained by **aerobic**, **anaerobic**, or phototrophic use of the energy of light;

**Multiple pathways** using organic molecules:  
**dissimilatory nitrate reduction** and **denitrification**,  
**fermentation** of different sugars, **breakdown** of **arginine** and  
the use of **light energy** mediated by **retinal pigments**.

**Bacteriorhodopsin** make purple membranes.  
The **membrane potential** generated by bacteriorhodopsin can be used to drive **ATP synthesis** and maintain phototrophic growth. **Halorhodopsin also contributes to phototrophic growth** because of its inwardly-directed light-driven chloride pump.

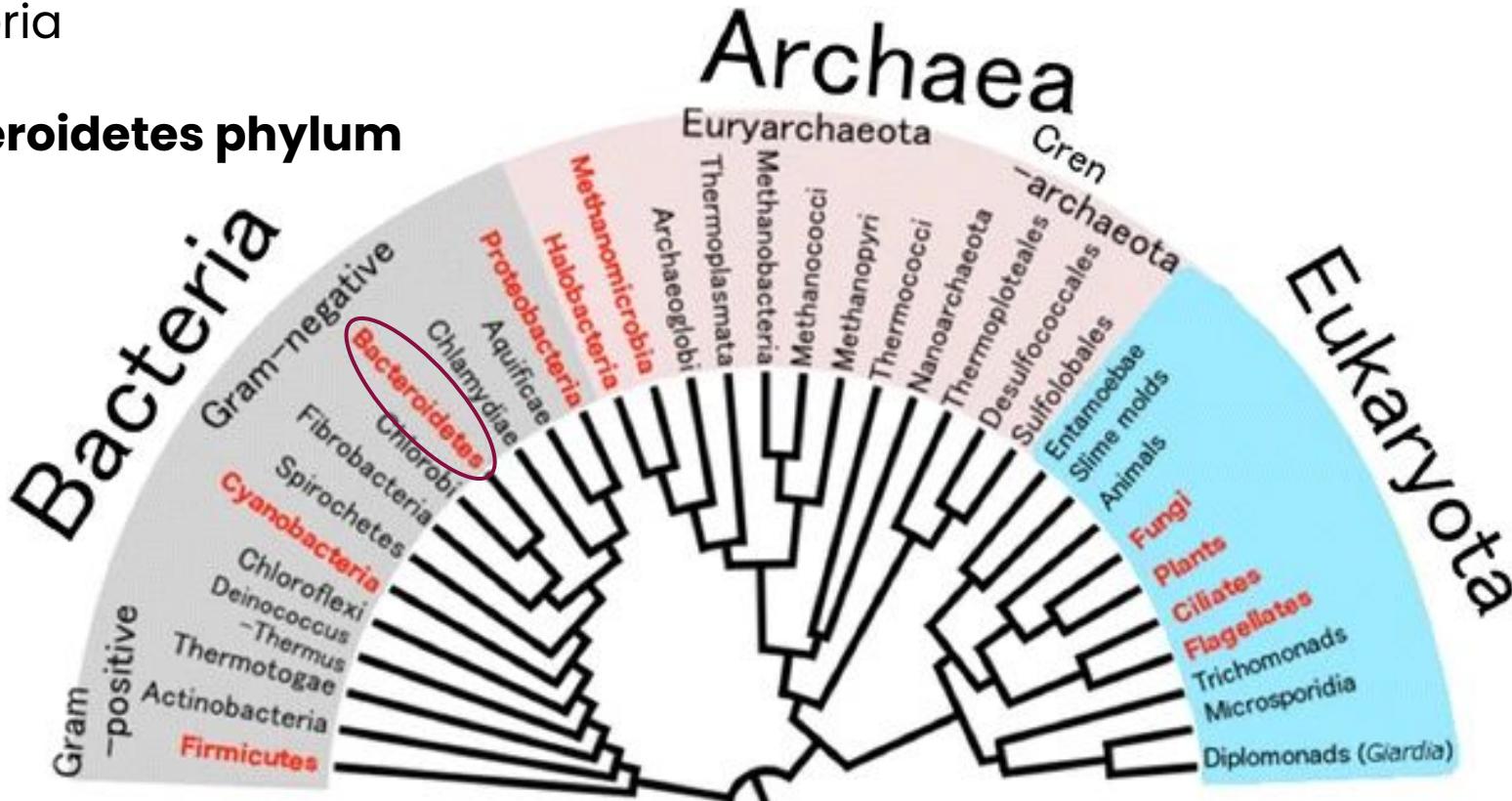
*H. NRC-1* is found to grow on either dimethyl sulfoxide (DMSO) or trimethylamine N-oxide (TMAO)



# TAXONOMY

Bacteria

**Bacteroidetes phylum**



# Salinity: Taxonomy of halophiles

## Bacteroidetes phylum

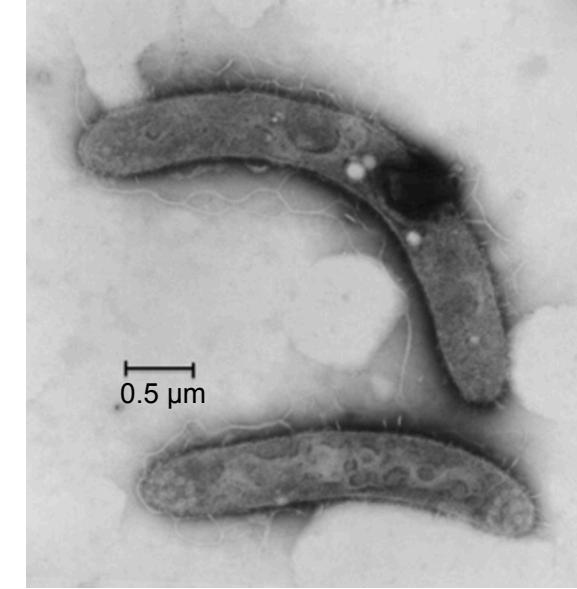
***Salinibacter ruber***: gram-negative aerobic heterotroph

*S. ruber* itself **cannot grow below 15% salt concentration**, with an **ideal concentration between 20–30%**.

Within the genome of *S. ruber*, there is a hypersalinity island, which is extremely crucial for survival in a halophilic environment. This cluster of 19 genes includes a K<sup>+</sup> uptake/efflux systems and cationic amino acid transporters.

*Salinibacter* produces an **unusual carotenoid**, salinixanthin that forms a light antenna and transfers energy to the retinal group of xanthorhodopsin, a light-driven proton pump.

*S. ruber* uses a modified **Entner–Doudoroff pathway** (phosphorylation step is delayed). **Glycerol** is abundantly used for growth, as it is one of the most common substrates in saltern lakes. **Glycerol metabolism** starts with the phosphorylation of glycerol by glycerol kinase, followed by dehydrogenation of glycerol 3-phosphate.



Electron micrograph of *Salinibacter ruber* strain Pola-18

## BIOTECHNOLOGICAL APPLICATIONS

They are notably able to produce **bacteriorhodopsin** used, for example, in **optical data processing**, as **light sensors** or in **holography**.

They also generate **exopolysaccharides** and **polyhydroxyalkanoates** that could advantageously **replace conventional petrol-derived plastics** in the future due to their **easy biodegradability**.

In addition, to compensate for the high osmotic pressure of their environments, a large diversity of **moderate halophiles and halotolerant** microorganisms **produce** high concentrations of **compatible solutes** such as **amino acids** (glycine and proline), glycine- and glutamate-betaines, choline, glycerol, trehalose, and **ectoines**, the latter being already commercially produced.

# Halophiles: Biotech Applications

[Plant-Microbe Interaction: An Approach to Sustainable Agriculture pp 297-325 | Cite as](#)

**Halophilic Bacteria: Potential Bioinoculants for Sustainable Agriculture and Environment Management Under Salt Stress**

**Authors** [Anjney Sharma](#), [Anukool Vaishnav](#), [Hena Jamali](#), [Anchal Kumar Srivastava](#), [Anil Kumar Saxena](#), [Alok Kumar Srivastava](#)

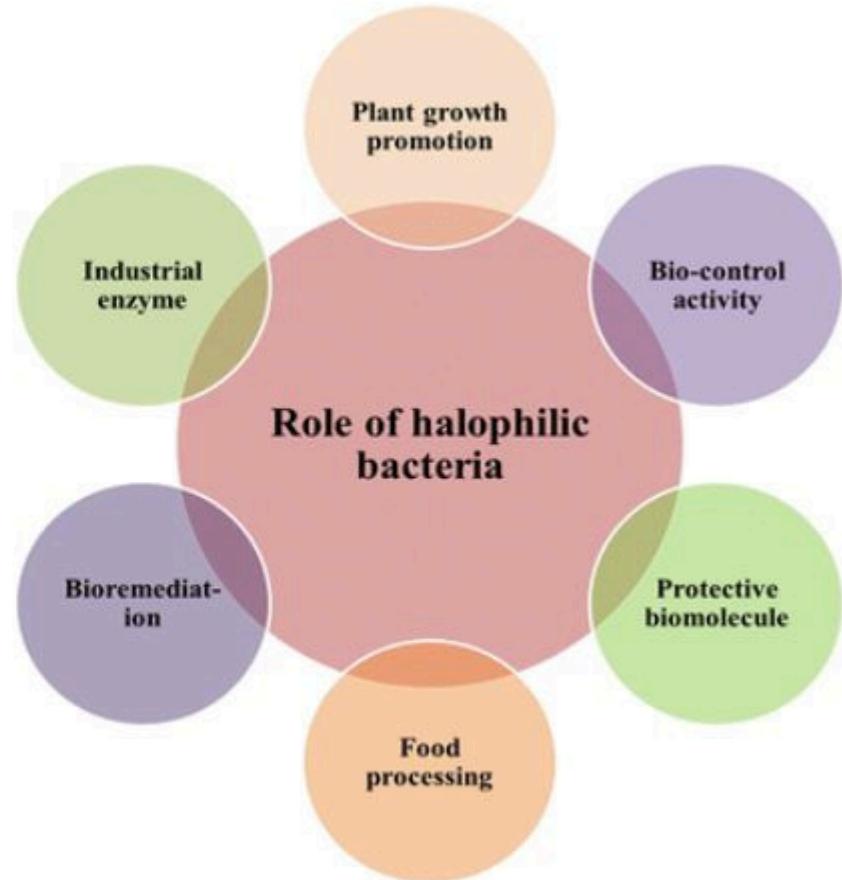
**Chapter** [First Online: 10 February 2017](#)

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[Others](#) [Downloads](#)

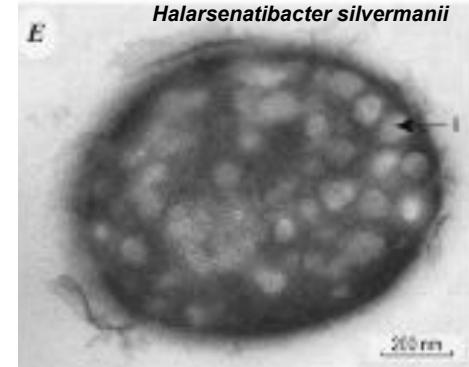
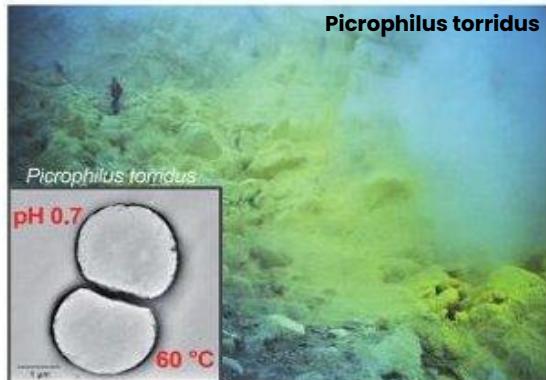
**Abstract**

Salinity is one of the most critical environmental constraints which cause soil degradation and hampering agricultural production throughout the world. In the present time, a total 831 million hectares of land is affected by salinity. The salinity affects the processes in plant life from its germination to maturation stage. Regulation of phytohormones, root/shoot development, nutrient uptake, and photosynthesis are severely affected by salt stress and ultimately reduce agricultural productions. The loss of agriculture production due to salinization is one of the major constraints to feed to the growing population. High salt levels in the soil limit its agroecological potential and represent a considerable ecological and socioeconomic threat to sustainable development. In this context, the use of halophilic bacteria



# SUMMARY

| Strain                                      | Domain   | Type of extremophile | Isolated from           | Temp. (°C) | pH                | Salinity (%) | References                           |
|---|----------|----------------------|-------------------------|------------|-------------------|--------------|--------------------------------------|
| <i>Picrophilus oshimae KAW 2/2</i>          | Archaea  | Hyper-acidophile     | Hot springs, Solfataras | 47-65      | <b>-0.06</b> -1.8 | 0-20         | Schleper et al. 1995, 1996           |
| <i>Serpentinomonas sp. B1</i>               | Bacteria | Hyper-alkaliphile    | Serpentining fluids     | 18-37      | <b>9-12.5</b>     | 0-0.5        | Suzuki et al. 2014; Bird et al. 2021 |
| <i>Halarsenatibacter silvermanii</i> SLAS-1 | Bacteria | Halo-alkaliphile     | Soda lake               | 28-55      | 8.7-9.8           | <b>20-35</b> | Oremland et al. 2005                 |



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