

EXTREMOPHILES

Concepts: environmental stresses and adaptation mechanisms, life in cold, dry, hot, acidic, basic, radioactive, sulfidic places, names for different extremophiles, animals in extreme environments

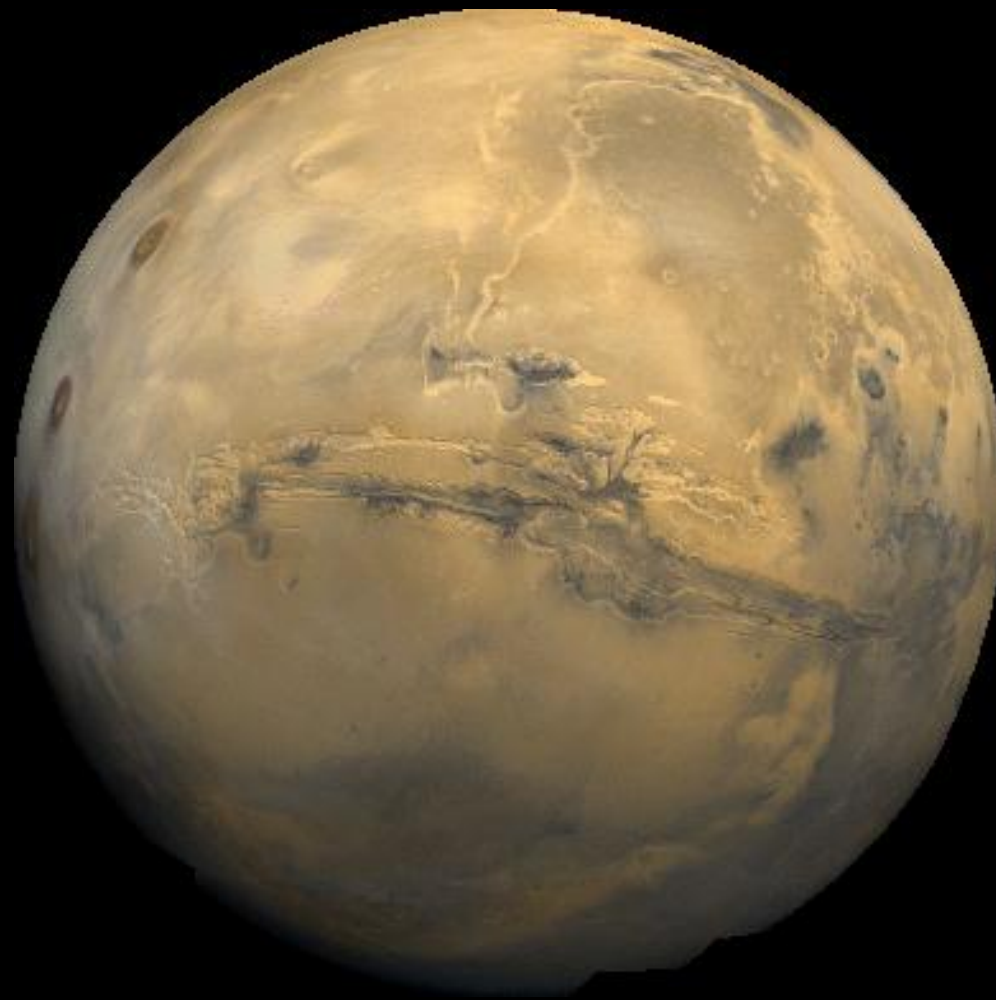
Reading: Rothschild and Mancinelli, *Nature*, 409, p 1092, 2001

What you should know

- Examples of 'extreme' environments
- Some concepts of what is 'extreme' and why
- A strategy for quantifying 'habitability'
- Strategies that allow organisms to survive 'extreme' environments
- Examples of pertinent research and its application to understanding limits of life in the solar system

Historical Perspective

- Most early attention given to hydrothermal systems
- 1881, first thermophile cultured
- 1903, Setchell notices “algae” in Yellowstone hot springs
- Very little attention given to “extreme” habitats prior to mid 20th C
- 1977, deep-sea hydrothermal vents first discovered
- 1977, the Archaea are “discovered” (Woese and Fox)
- 1980-1990, the Archaea are slowly recognized as a legitimate group; the 3 domain system is proposed
- 1985, PCR-based molecular methods first applied to hydrothermal systems
- 1998-present, Astrobiology “boom”; search for Earth analog systems fuels rapid increase in studies of “extreme” environments

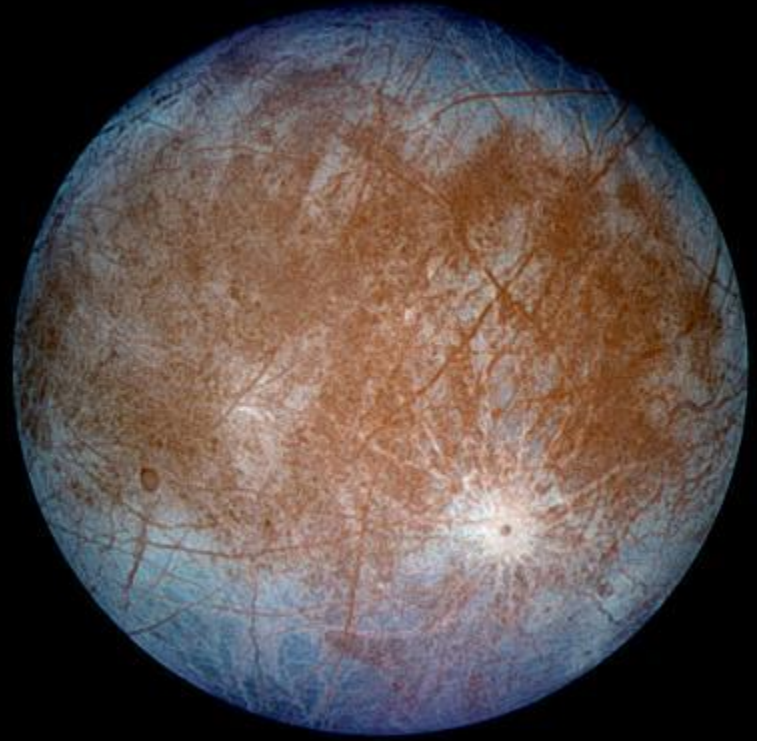
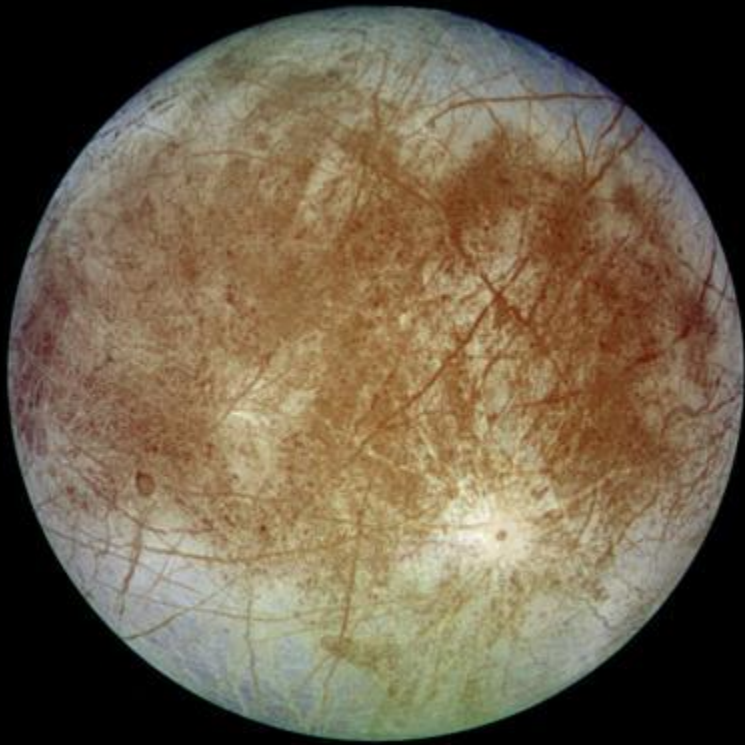


<http://photojournal.jpl.nasa.gov>



Curiosity at Gale Crater on Mars

Image courtesy of NASA.



<http://photojournal.jpl.nasa.gov>

Defining Extremes 1

- Temp: -20°C to 121°C → Arctic sea-ice / hydrothermal vents
- pH: <1 to 13 → acid mine drainage basaltic aquifers / groundwater
- “Toxins”: → Tutum Bay, PNG up to 70,000ppm Arsenic in vent sediments

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Junge et al., 2004



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Please see the image on Science cover at

<http://www.sciencemag.org/content/287/5459.cover-expansion>.

Bond et al, 2000

“acidophiles” in Iron Mountain

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Kashefi & Lovley, 2003

Strain “121”

Defining Extremes 2

- Saline environments
 - "0" to saturation
 - Dead Sea 2.5M

- UV exposure
 - Deinococcus: spacecraft returns

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Please see <http://www.jerichocosmetics.com/apage/33262.php>.

Image courtesy of NASA.

- Pressure:
seafloor HTV 40 MPa
Challenger Deep 124 MPa
*up to 1400 MPa (?)

Photograph of black smokers at a hydrothermal vent removed due to copyright restrictions.

Defining Extremes 3

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**Extremophiles alter or cope with environmental
“extremes”**

Defining Habitability

What makes an environment habitable?

The Earth-centric view includes availability of

Water

Energy

Carbon

Scaling Habitability



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Scaling Habitability



Image courtesy of D'Arcy Meyer-Dombard. Used with permission.

Photo: Meyer-Dombard

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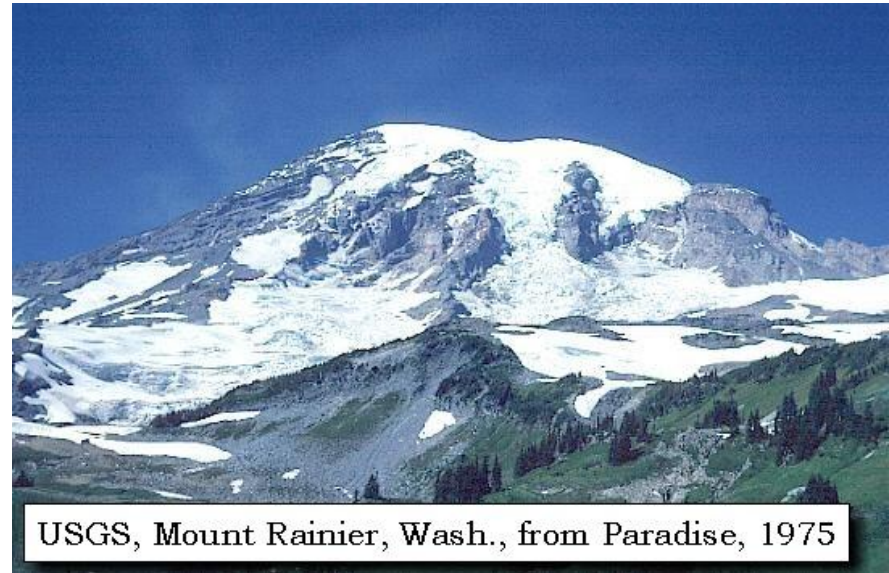


Image courtesy of USGS.

Scaling Habitability

Photograph of black smokers at a hydrothermal vent removed due to copyright restrictions.

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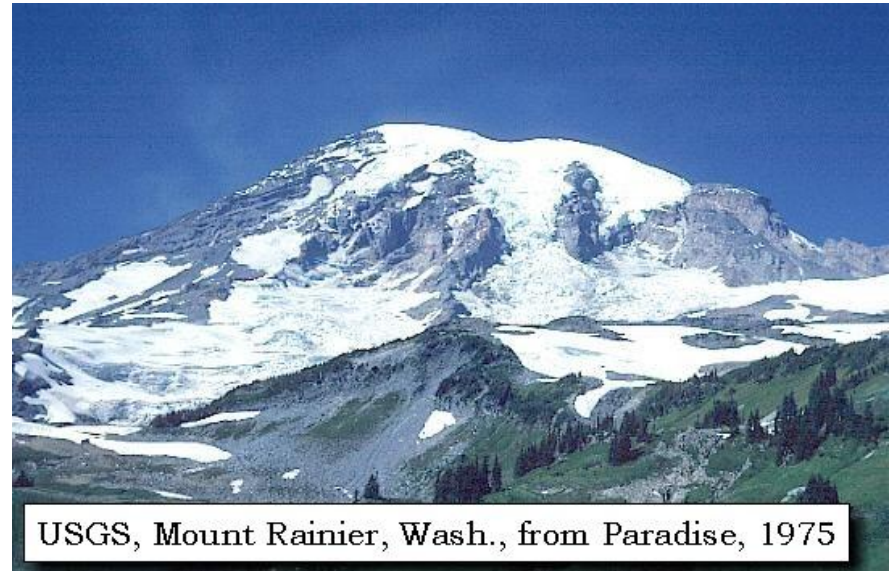


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Image courtesy of USGS.

Scaling Habitability

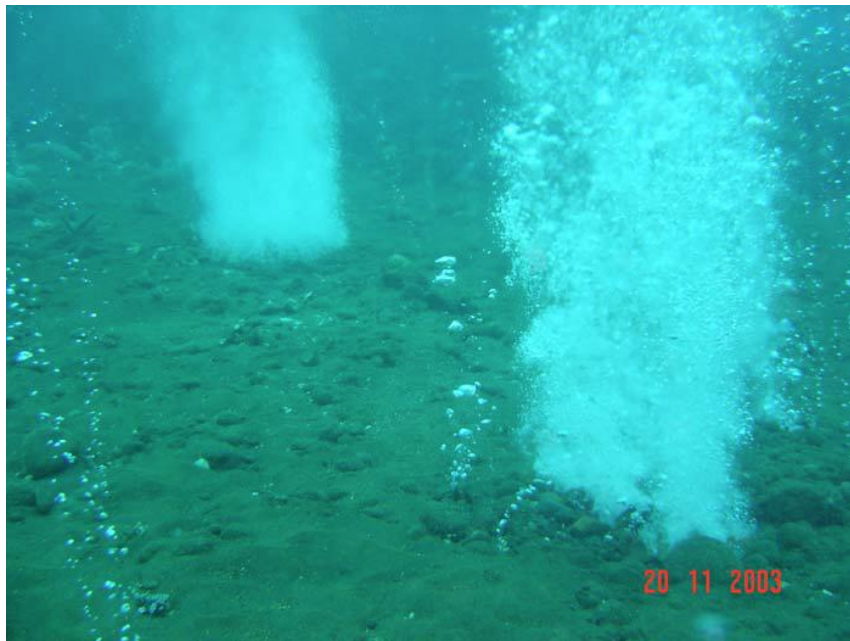


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Photo: Meyer-Dombard

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Photo: Meyer-Dombard

So what is Extreme?

cold

heat



Courtesy of NASA.



Courtesy of NASA.

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Please see the image on <http://www.whoi.edu/page/live.do?pid=11916&tid=282&cid=988&print=this>.

salt



<http://www.flickr.com/photos/motorbikematt/4541461103/>
by Matthew Reyes

Research Paper

Quantitative Habitability

EVERETT L. SHOCK^{1,2} and MELANIE E. HOLLAND^{1,*}

ABSTRACT

A framework is proposed for a quantitative approach to studying habitability. Considerations of environmental supply and organismal demand of energy lead to the conclusions that power units are most appropriate and that the units for habitability become watts per organism. Extreme and plush environments are revealed to be on a habitability continuum, and extreme environments can be quantified as those where power supply only barely exceeds demand. Strategies for laboratory and field experiments are outlined that would quantify power supplies, power demands, and habitability. An example involving a comparison of various metabolisms pursued by halophiles is shown to be well on the way to a quantitative habitability analysis.

Key words: Habitability-Extreme environments-Net power-Power supplies-power demands-Halophiles. *Astrobiology* 7, 839-851.

Image by MIT OpenCourseWare.

Life on Earth

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Please see the image on:

http://www.astro.rug.nl/~schuiter/De_zoektocht_naar_leven/deelvraag1.php

Habitability Continuum?

extreme

habitable



energy available
to an organism
per unit time

Habitability Continuum?

extreme

habitable



Power (watts)

Quantifying Habitability?

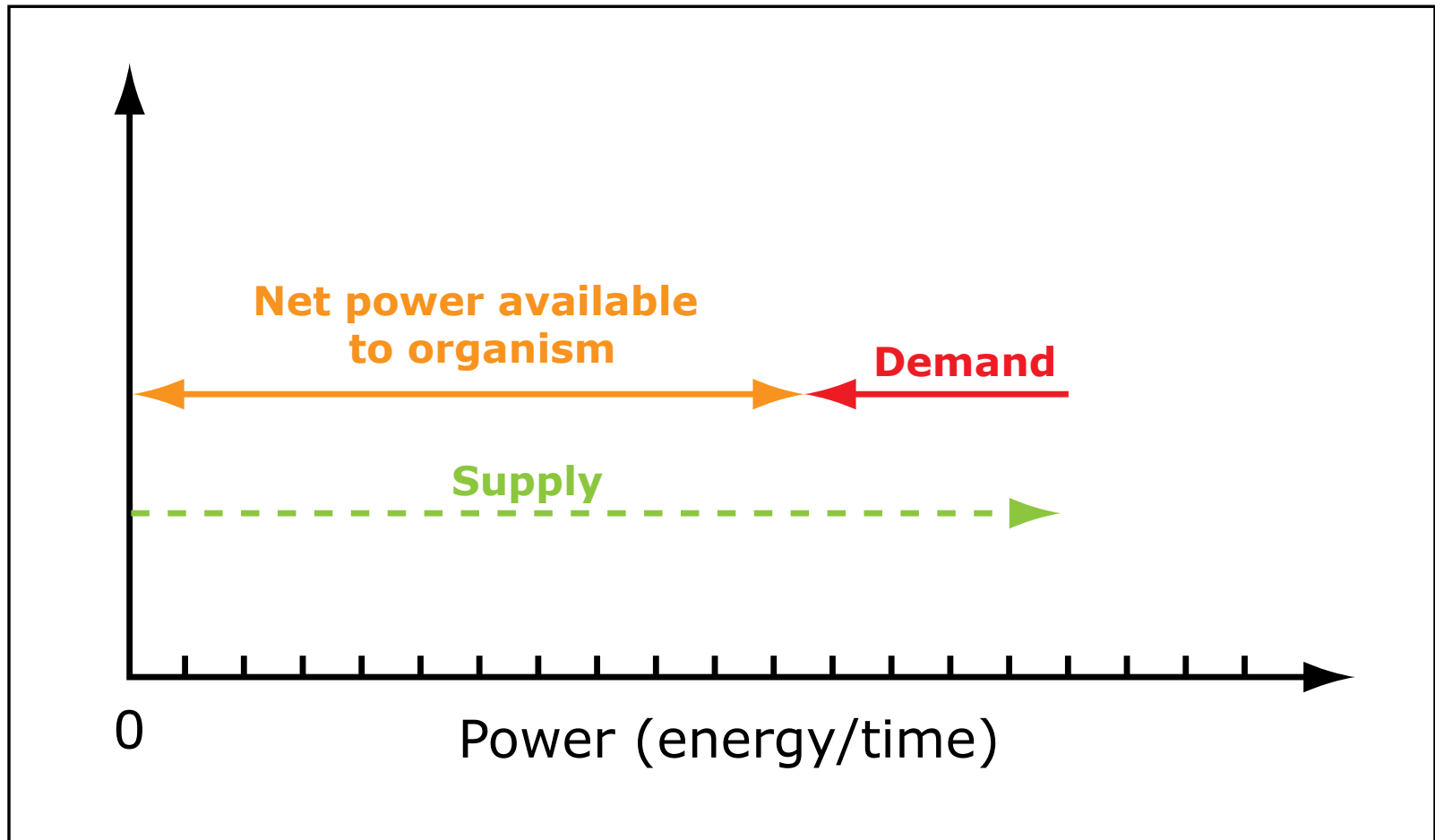


Image by MIT OpenCourseWare.

Quantifying Habitability?

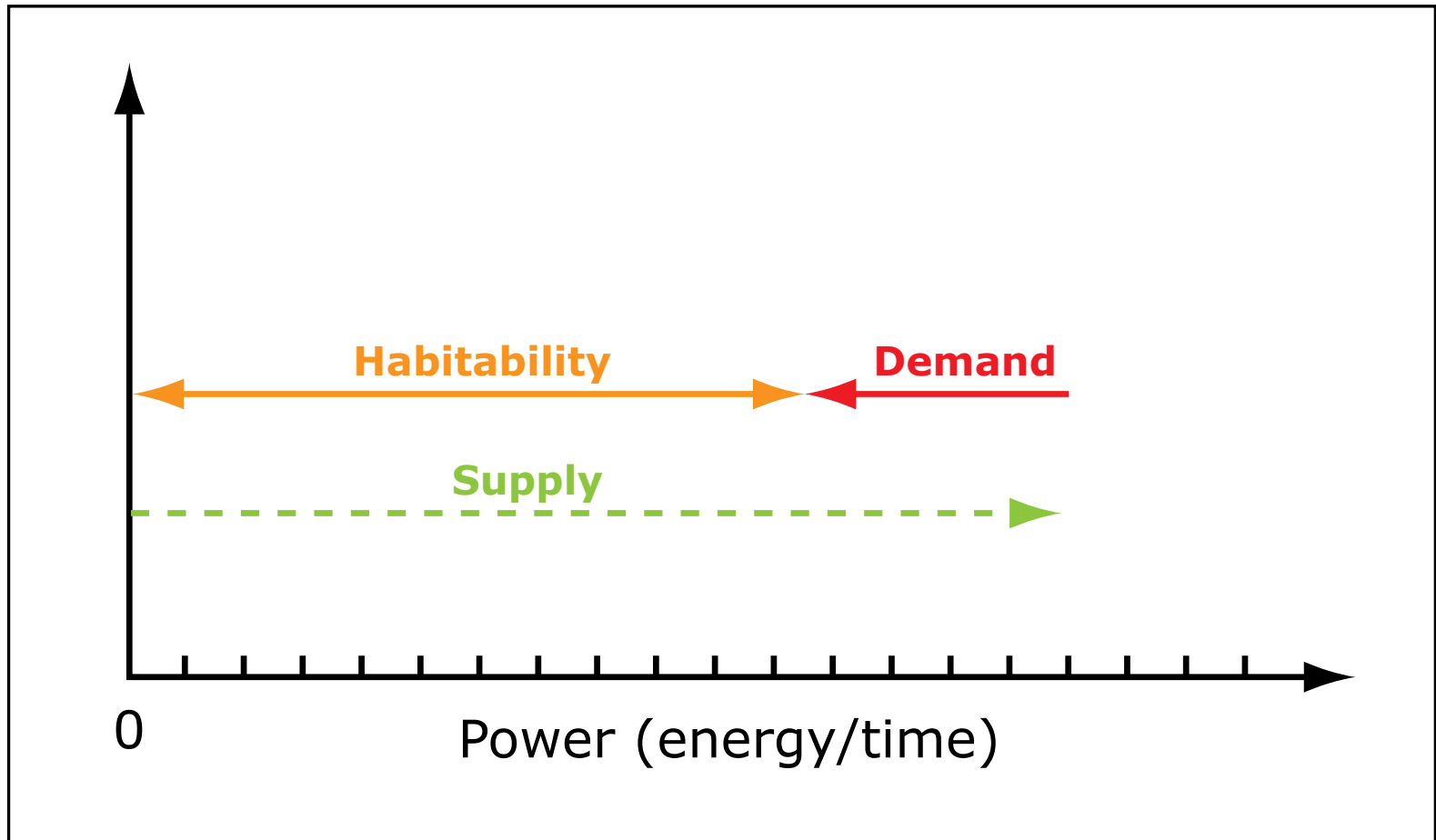


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Quantifying Habitability?

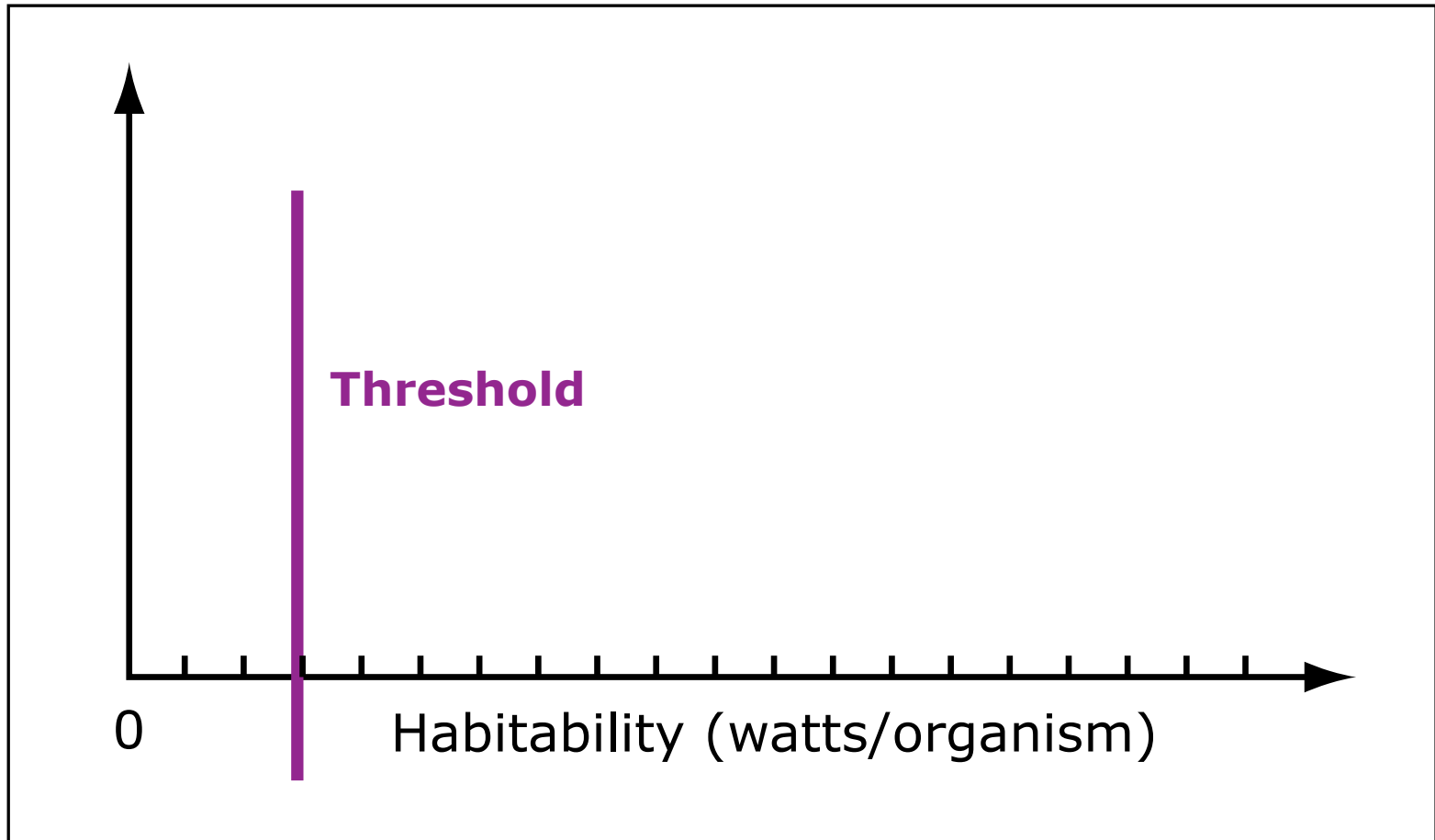


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Quantifying Habitability?

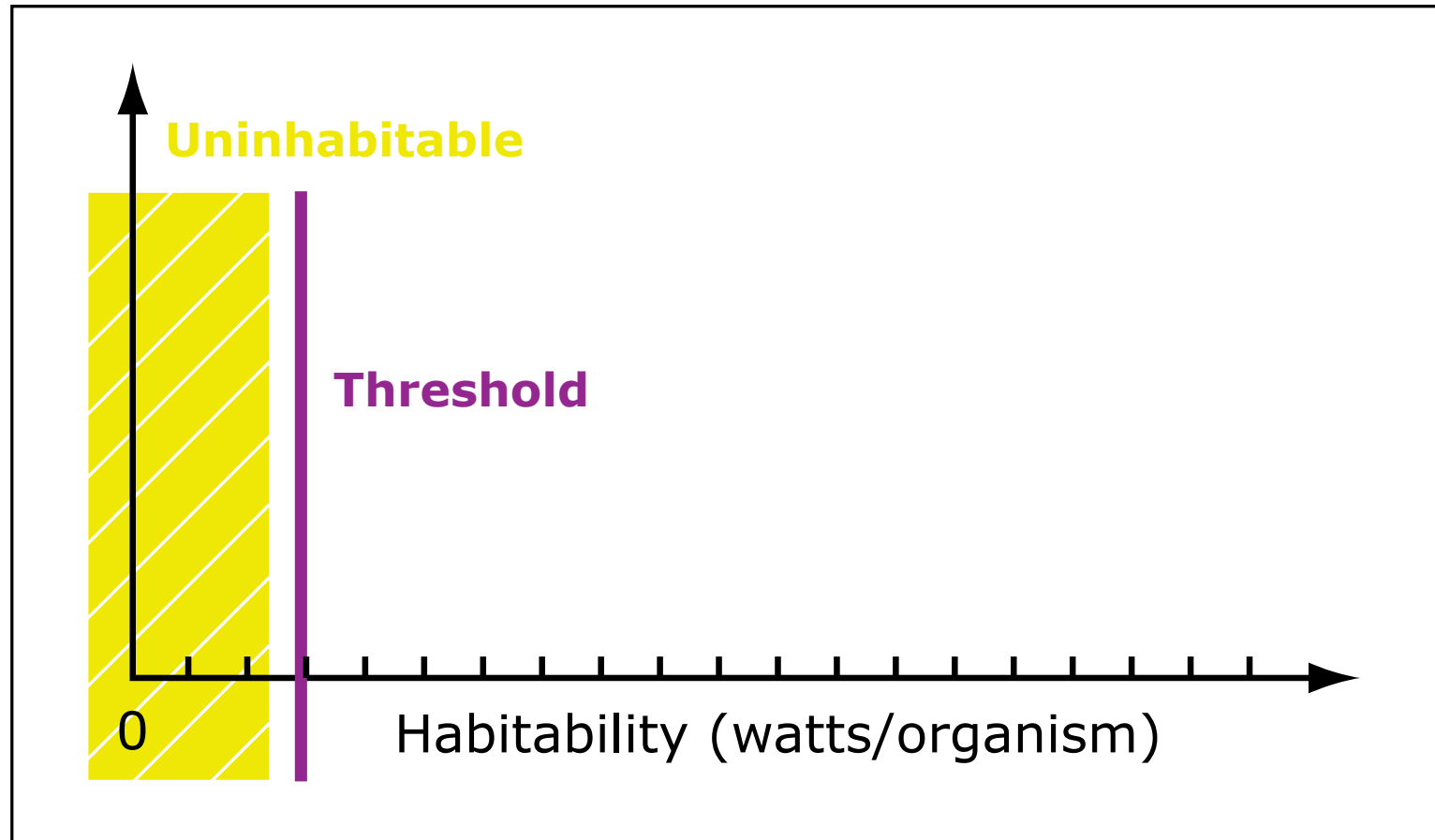


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Quantifying Habitability?

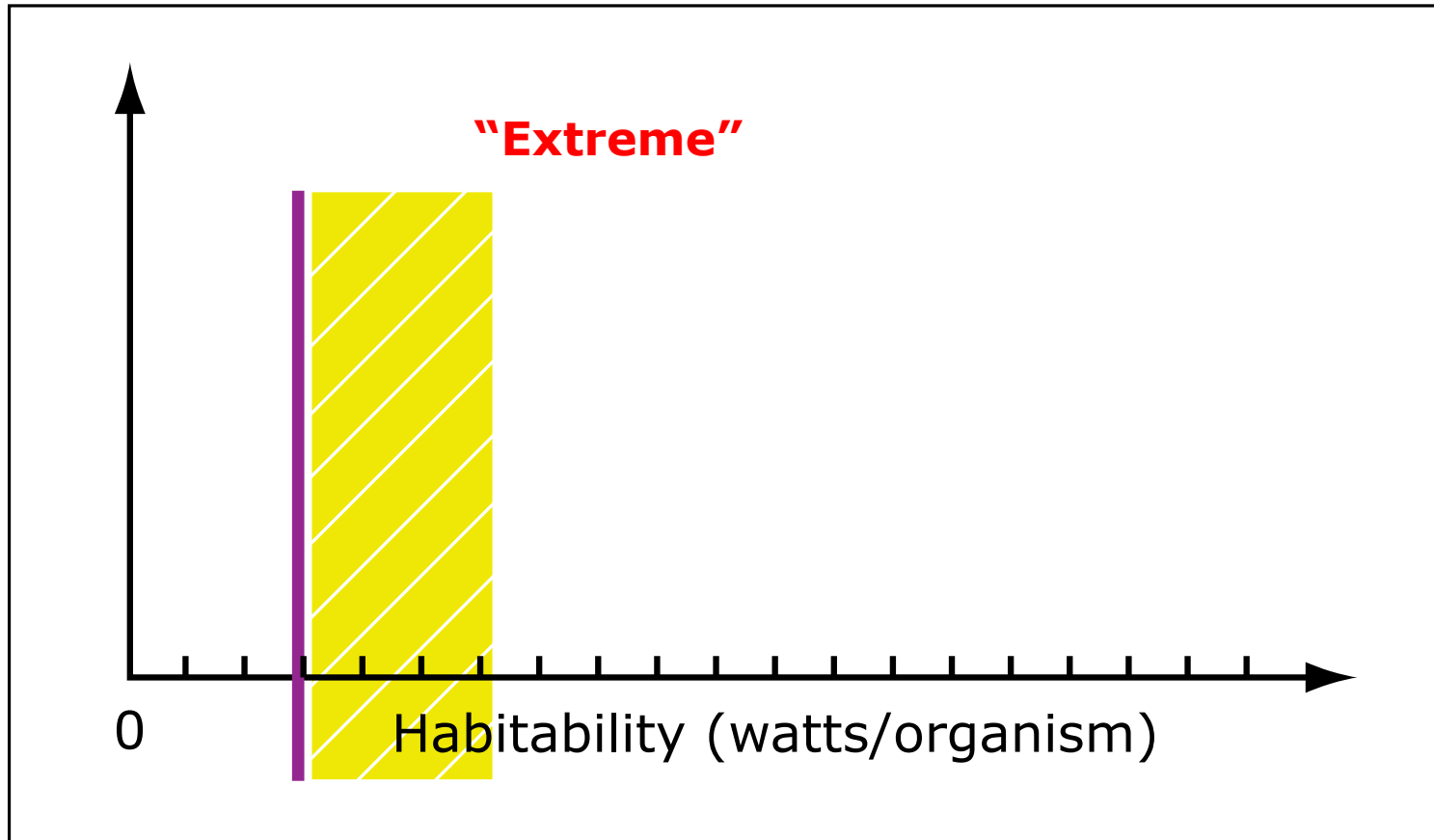


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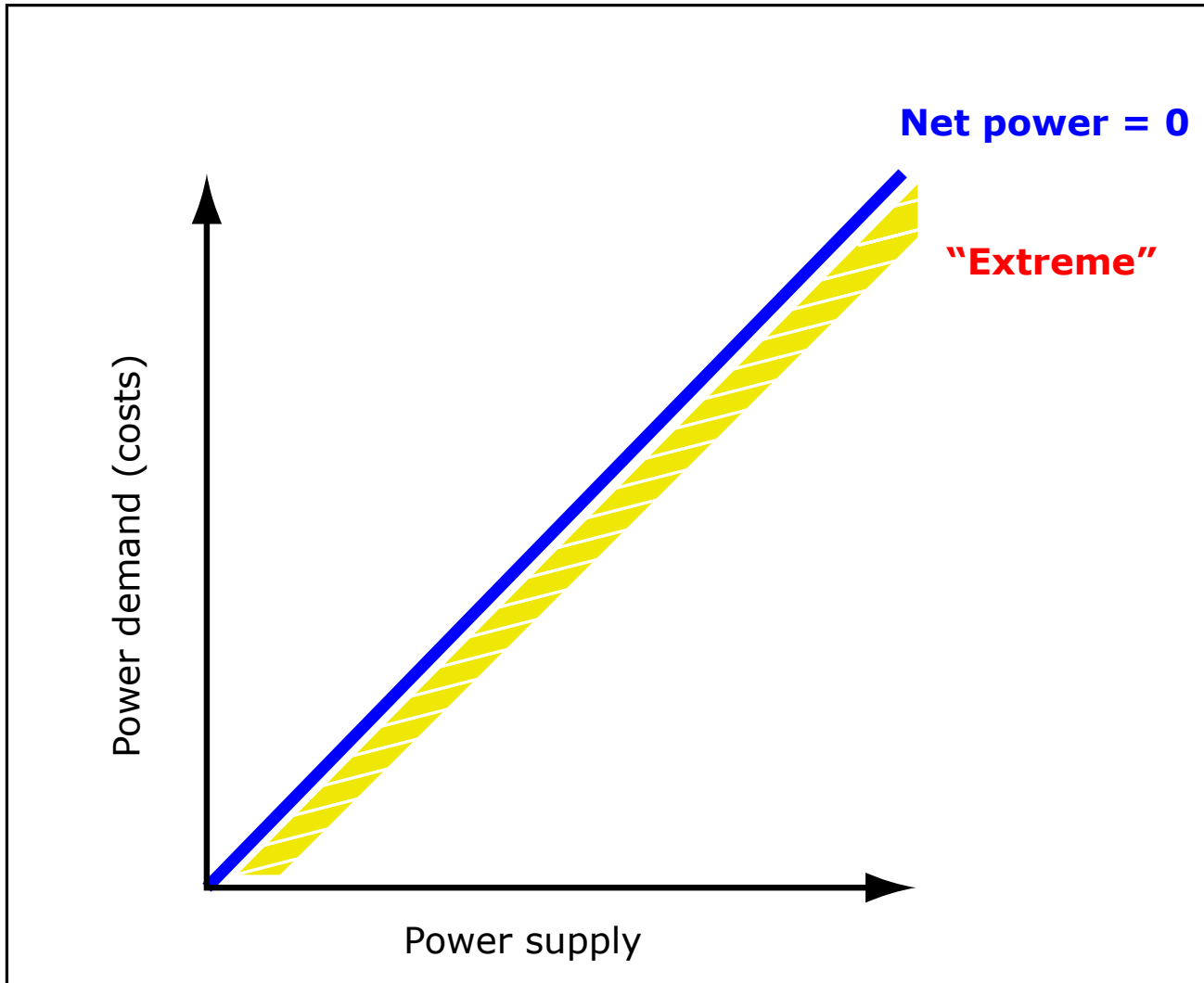


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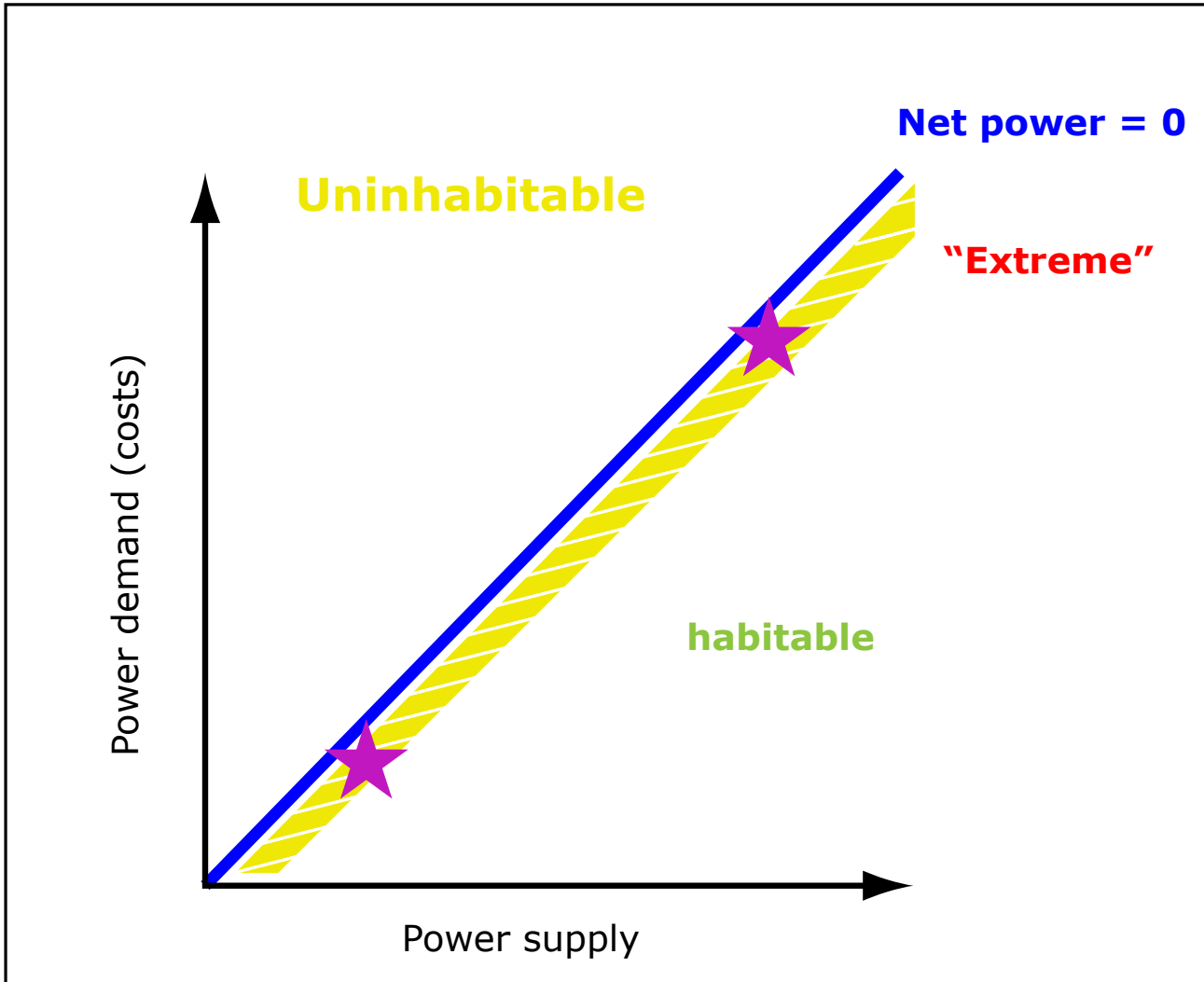


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Examining the chemotrophic 'buffet'

$$\Delta G_r = \Delta G_r^0 + RT \ln Q_r$$

↑
“activity product”

$$Q_r = \prod a_{(i,r)}^{V(i,r)}$$

$\Delta G_r < 0 \rightarrow$ energy yielding

- Example: $S^0 + H_{2(aq)} \rightarrow H_2S_{(aq)}$
- $Q_r = \frac{a_{H_2S(aq)}}{(a_{H_2(aq)})(a_{S^0})}$



http://visibleearth.nasa.gov/view_rec.php?id=2433

Endolithic Microorganisms in the Antarctic Cold Desert

E. Imre Friedmann

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Please see Figures 4, 5, and 7 on:

<http://www.sciencemag.org/content/215/4536/1045.full.pdf>

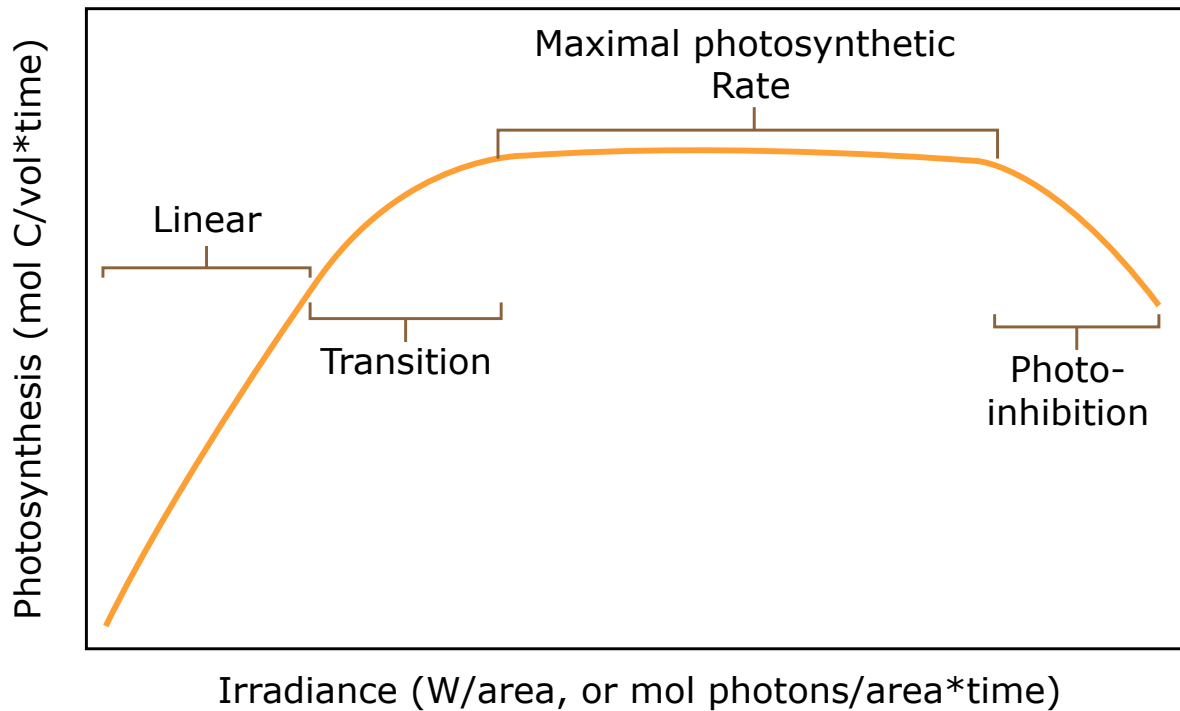
Endolithic Microorganisms in the Antarctic Cold Desert

E. Imre Friedmann

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<http://www.sciencemag.org/content/215/4536/1045.full.pdf>



Photosynthetic productivity as a function of irradiance, showing a linear dependence at low irradiance, followed by a transition to a maximal rate, which then transfers into a range of high irradiance at which photosynthesis becomes inhibited.

Image by MIT OpenCourseWare.

The Effects of Freezing and Desiccation on Photosynthesis and Survival of Terrestrial Antarctic Algae and Cyanobacteria

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Please see Figures 1 and 10 on:

<http://link.springer.com/article/10.1007%2FBF00238287#page-1>

Davey, 1989

Obligate psychrophile

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<http://webadventures.rice.edu/games/302/materials/Magazine-302.pdf>

Colwellia psychrerythraea

Photo: Richard A. Finkelstein / NCBI

Ice-active substances associated with Antarctic freshwater and terrestrial photosynthetic organisms

JAMES A. RAYMOND¹* and CHRISTIAN H. FRITSEN*

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ICE-NUCLEATION PROTEINS AND ANTIFREEZE SUBSTANCES

Antarctic Sea Ice-a Habitat for Extremophiles

D.N. Thomas and G.S. Dieckmann

The pack ice of Earth's polar oceans appears to be frozen white desert, devoid of life. However, beneath the snow lies a unique habitat for a group of bacteria and microscopic plants and animals that are encased in an ice matrix at low temperatures and light levels, with the only liquid being pockets of concentrated brines. Survival in these conditions requires a complex suite of physiological and metabolic adaptations, but sea-ice organisms thrive in the ice, and their prolific growth ensures they play a fundamental role in polar ecosystems. Apart from their ecological importance, the bacterial and algae species found in sea ice have become the focus for novel biotechnology, as well as being considered proxies for possible life forms on icecovered extraterrestrial bodies.

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Deinococcus radiodurans

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Please see the image on:

http://www.scifun.ed.ac.uk/card/images/facts/d_radiodurans.jpg

Fenton's Reaction



OR



$\text{OH}\cdot$ and $\text{OOH}\cdot$ promote relatively **non-specific** oxidation of all organic compound classes (in water)

Commonly used to clean glassware, wastewater, degrade pesticides etc

Fenton's Reaction

Radical Addition: $\text{OH}\cdot + \text{benzene} \rightarrow \text{phenol} + \text{H}\cdot$

Hydrogen Abstraction: $\text{OH}\cdot + \text{CH}_3\text{OH} \rightarrow \text{CH}_2\text{O} + \text{H}_2\text{O}$

Oxidation: $\text{OH}\cdot + [\text{Fe}(\text{CN})_6]^{4-} \rightarrow [\text{Fe}(\text{CN})_6]^{3-} + \text{OH}^-$

Radical Interaction: $\text{OH}\cdot + \text{OH}\cdot \rightarrow \text{H}_2\text{O}_2$

Photo-Fenton Reaction in Aqueous Solution

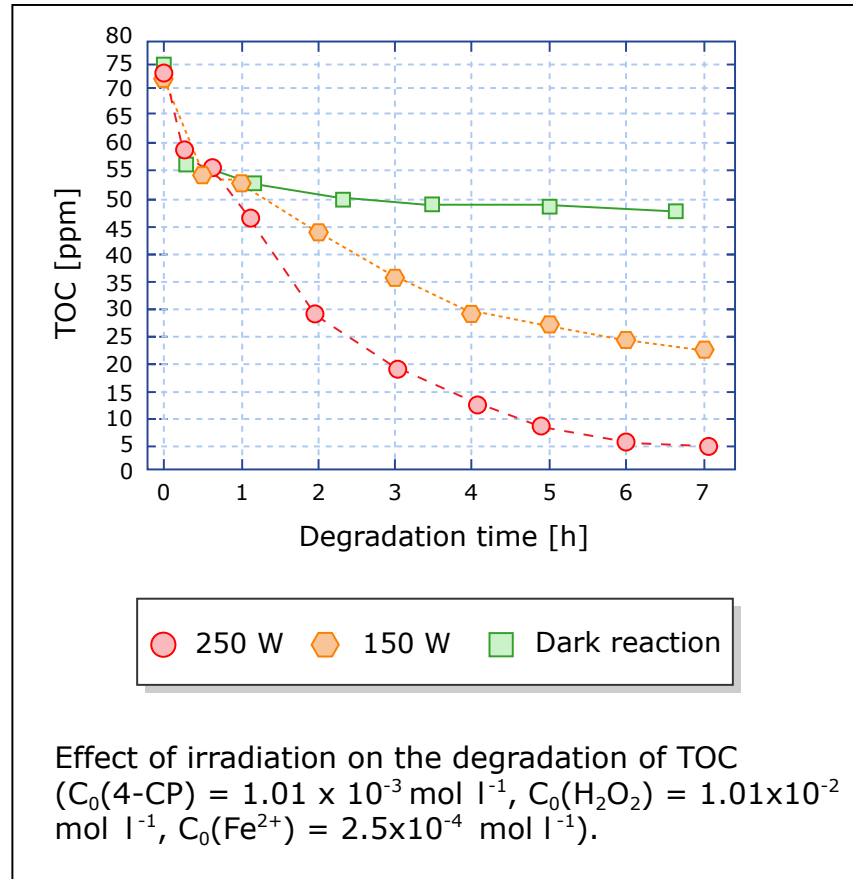


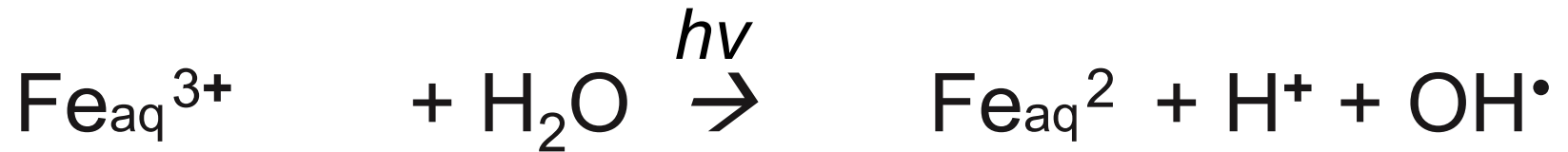
Image by MIT OpenCourseWare.

G. Ruppert, R. Bauer, G. Heisler

[The photo-Fenton reaction — an effective photochemical wastewater treatment process](#)

Journal of Photochemistry and Photobiology A: Chemistry, 73, 75-78 (1993)

Photo-Fenton Reaction in Adsorbed Water



A photo-Fenton-like process on mineral surfaces that releases hydroxyl radicals and, thus, that oxidize any organic molecules may be responsible for the lack of organics of meteoritic origin in martian soil of the upper surface, as was concluded from the results of Viking mission experiments.

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Alkane degradation pathway

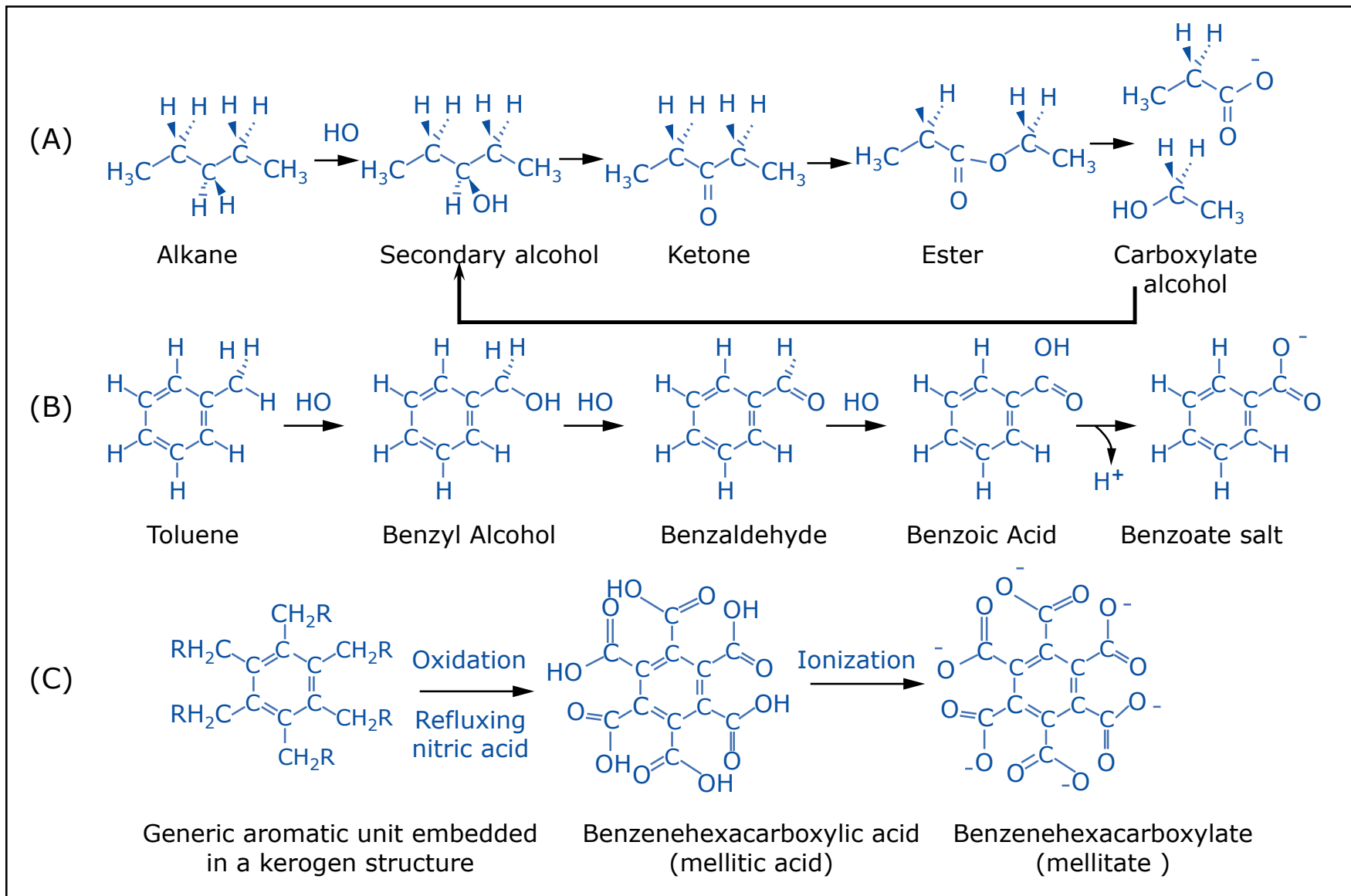
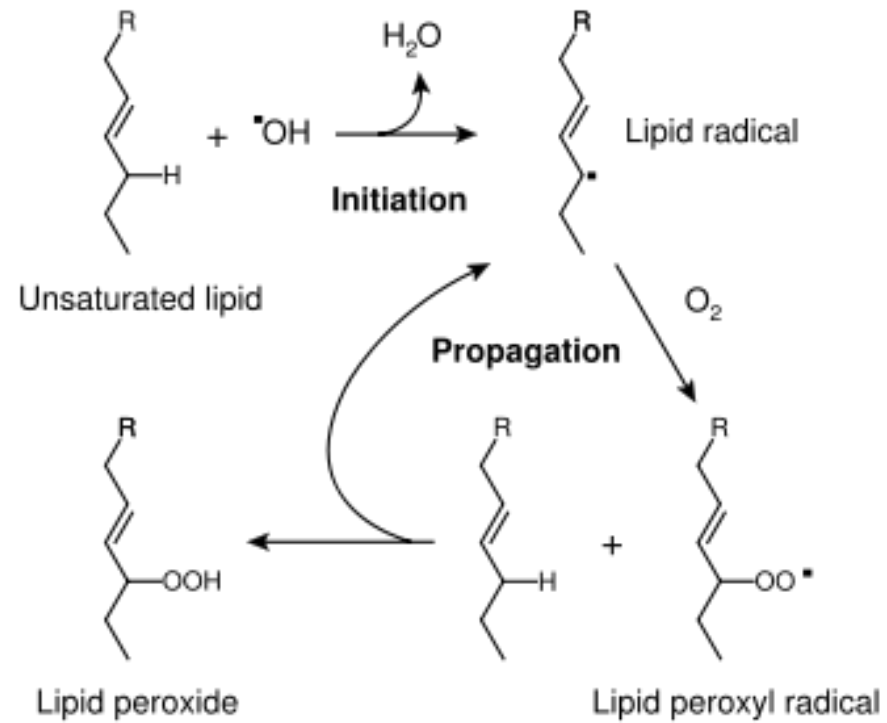


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From Benner et al, 2000

Lipid radical formation



Accumulation of Mn(II) in *Deinococcus radiodurans* Facilitates Gamma-Radiation Resistance

D10 Survival values and intracellular Mn and Fe levels (12).

Strains	Radiation dose yielding 10% CFU survival	Desiccation dose yielding 10% CFU survival	⁵⁹ Fe accumulation, atoms/cell	⁵⁴ Mn accumulation, atoms/cell	Total Fe: ICP-MS/nmol Fe/mg protein	Total Mn: ICP-MS/nmol Mn/mg protein	Intracellular Mn/Fe (ICP-MS) concentration ratio
<i>D. radiodurans</i>	16 kGy	>30 days	2.7×10^3	1.08×10^5	1.49 (± 0.39)	0.36 (± 0.11)	0.24
<i>Deinococcus geothermalis</i>	10 kGy	>30 days	7.7×10^3 ($\pm 1.1 \times 10^3$)	2.17×10^5 ($\pm 3.7 \times 10^3$)	1.7 (± 0.39)	0.78 (± 0.15)	0.46
<i>Enterococcus faecium</i>	2.0 kGy	>30 days	ND	ND	6.3 (± 2.8)	1.1 (± 0.21)	0.17
<i>E. coli</i>	0.7 kGy	8 days	7×10^5 (16)	3.8×10^4 (16)	2.72 (± 0.63)	0.0197 (± 0.0027)	0.0072
<i>Pseudomonas putida</i>	0.25 kGy	1 day	ND	ND	6.8 (± 0.70)	<0.001	<0.0001
<i>S. oneidensis</i>	0.07 kGy	<1 day	2.7×10^4	$<5 \times 10^2$	4.98 (± 0.40)	0.0023 (± 0.00005)	0.0005
<i>D. radiodurans</i> low-Mn DMM	10 kGy	ND	ND	ND	2.1	0.7	0.33
<i>D. radiodurans</i> high-Mn DMM	ND	ND	ND	ND	1.6	3.9	2.5

Image by MIT OpenCourseWare.

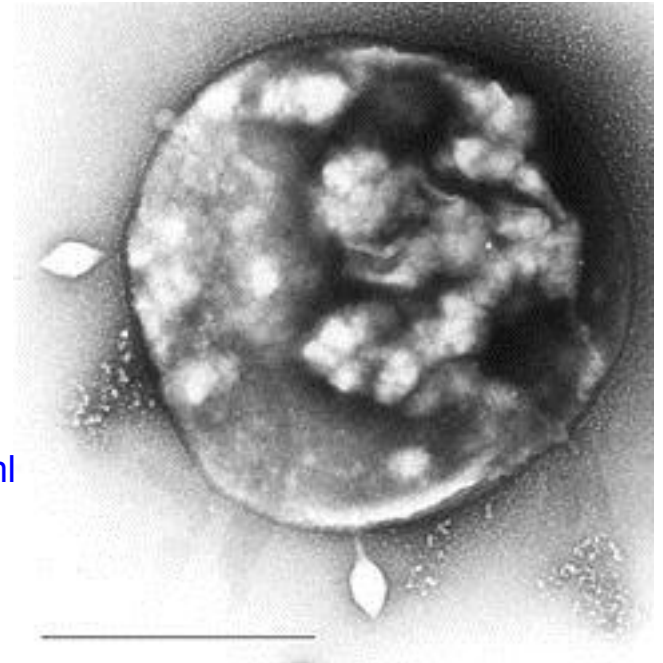
M. J. Daly, *et al.* 2008

Life in hot springs

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Sulfolobus solfataricus

pH 3, 80°C

Rothschild and Mancinelli, 2001

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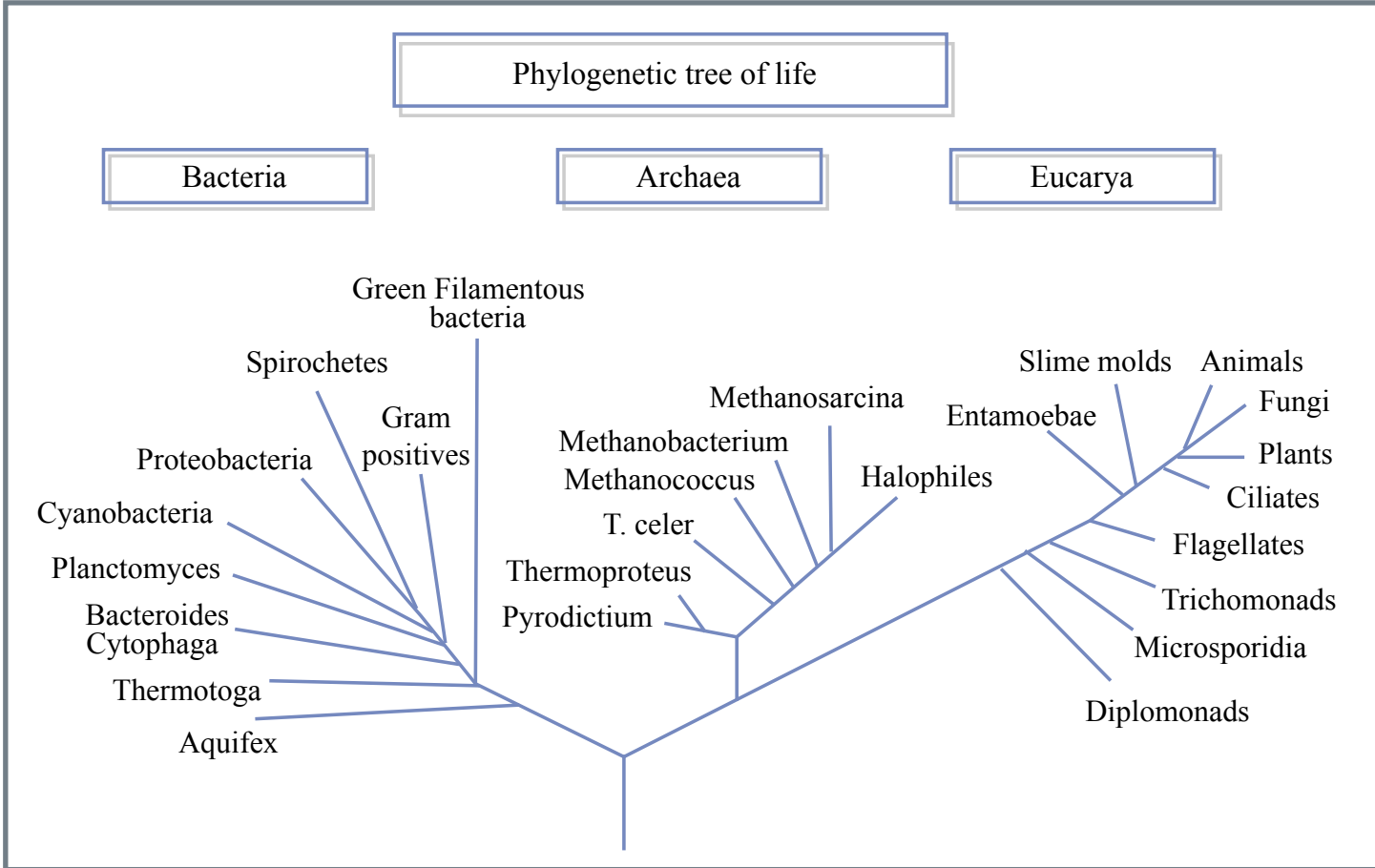


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Intact Microbial Lipids

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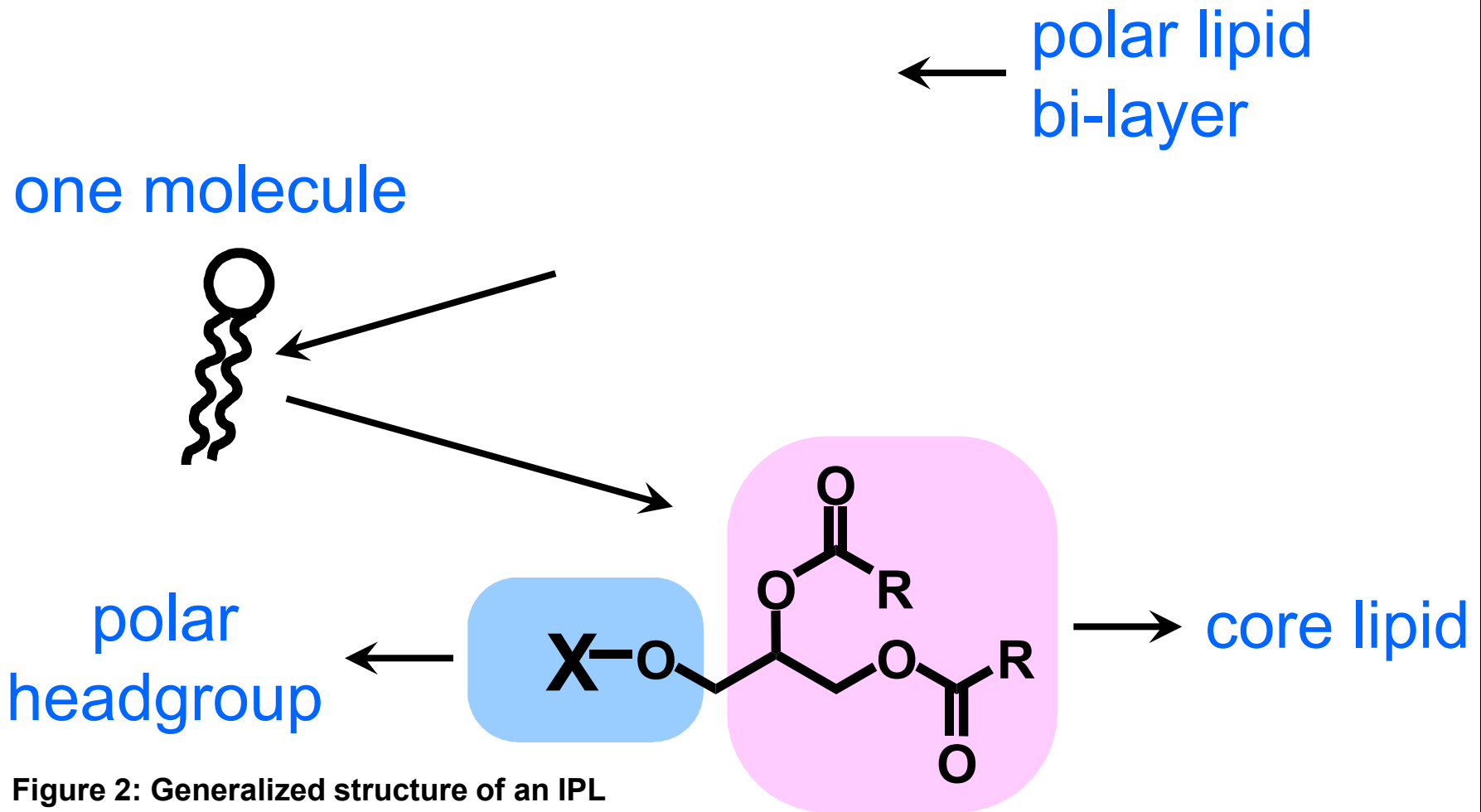


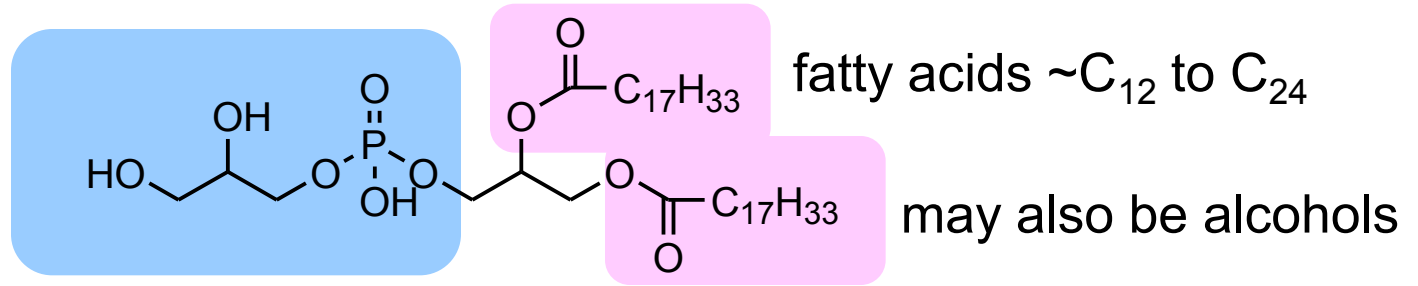
Figure 2: Generalized structure of an IPL

IPL variety analyzed by HPLC-ESI-MS

bacterial

10+ different headgroups identified...

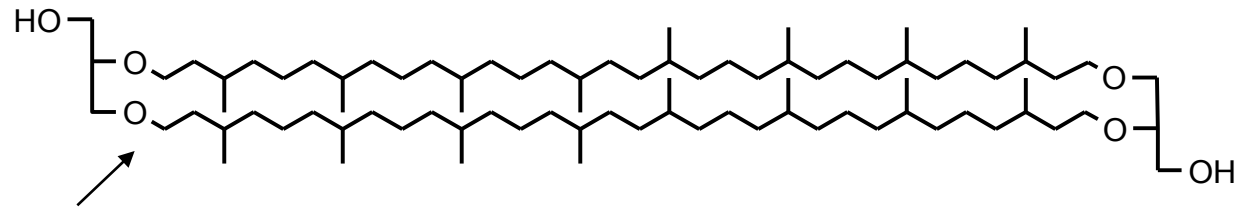
phospholipids & glycolipids, some highly specific



archaeal

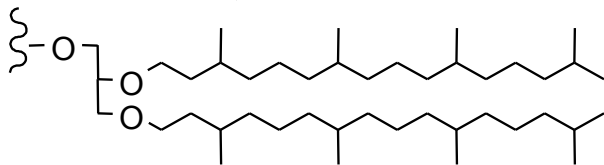
similar variety of headgroups but highly specific core lipids

2 basic types with some variations

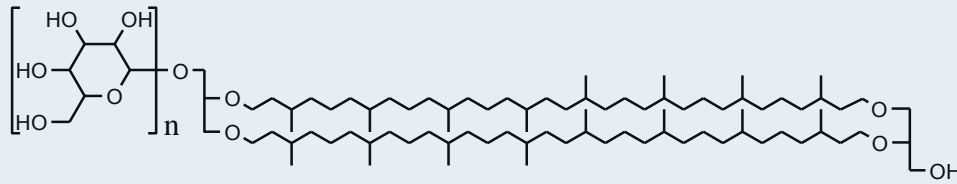


archaeol

caldarchaeol (GDGT: glycerol dialkyl glycerol tetraether)



Data on IPL distributions in biogeochemically relevant prokaryotes are very sparse

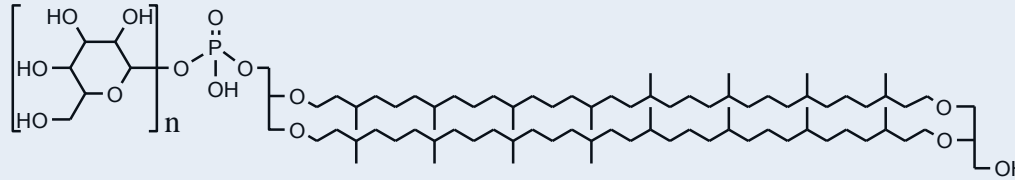


***n*G-GDGT**

$n = 1-4$

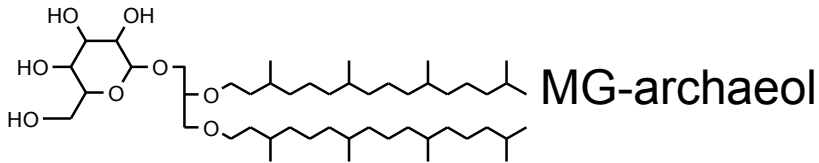
Glycosyl glycerol

dibiphytanyl glycerol tetraether

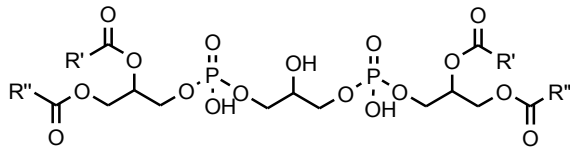


***n*G-PO₄-GDGT**

$n = 1-4$

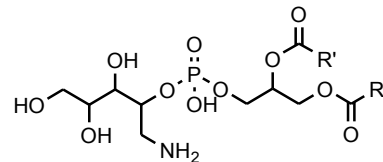


MG-archaeol



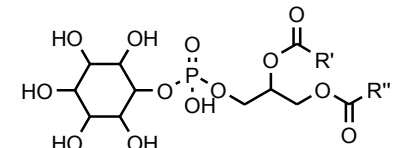
DPG

diphosphatidylglycerol



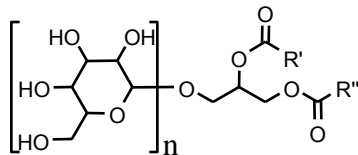
APT

aminopentane tetrol



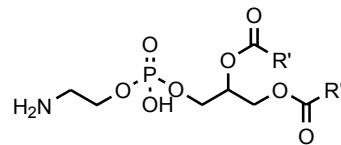
PI

inositol



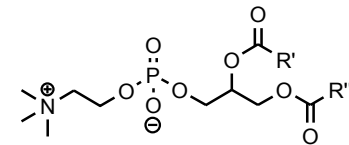
MGDG, DGDG

mono, di-glycosyl diglyceride



PE

ethanolamine



PC

choline

Life in hot springs

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Thermotoga

K. Stetter

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Aquifex

Please see:

<http://microbewiki.kenyon.edu/index.php/Image:Aquifex-pt1.jpg>

Please see:

http://microbewiki.kenyon.edu/index.php/File:Aquifex_environment.jpg

Historical Perspective

PSC -filamentous bacteria living at 89°C
Setchell, 1898

Filamentous bacteria colonised glass slide at 91°C
Brock, '67

Microbiology/Genomics

Reysenbach et al., 1994 → 16S rRNA sequences → limited diversity -
only 3 phylotypes of which
26/39 = Aquificales (EM17) → *T. ruber*
remainder Thermotogales (EM19) and an unknown group (EM3)

No Archaea detected

Thermocrinis ruber nov sp. isolated Huber, Eder et al. 1998

Chemosynthetic Zone Clone libraries

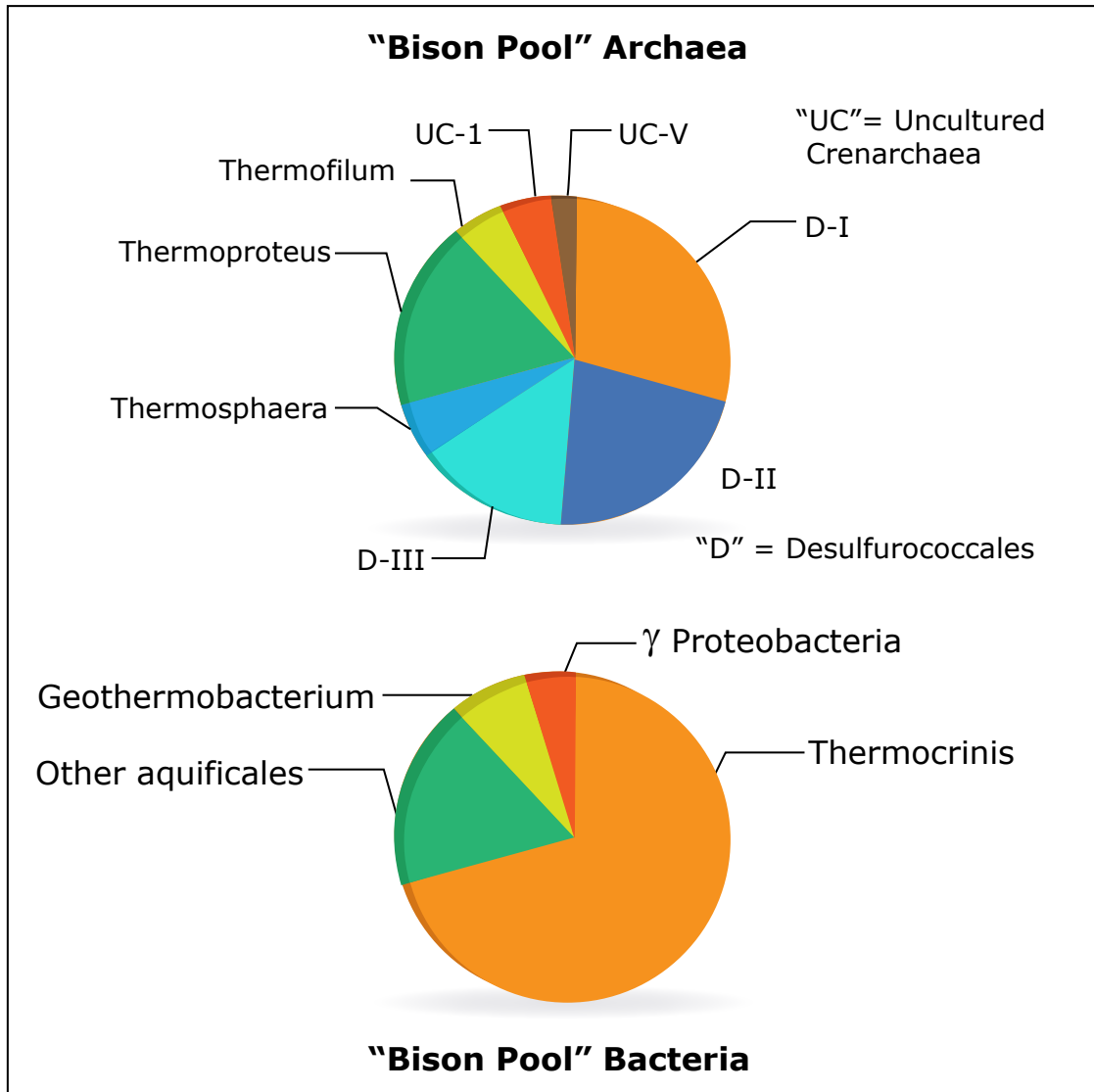


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Archaeal Clones
100% Crenarchaea

- 66% Desulfurococcales
- 27% Thermoproteales
- 7% Uncultured Crens

Bacterial Clones
71% Thermocrinis

Life in hot springs

Aquifex

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Photosynthetic extremophiles

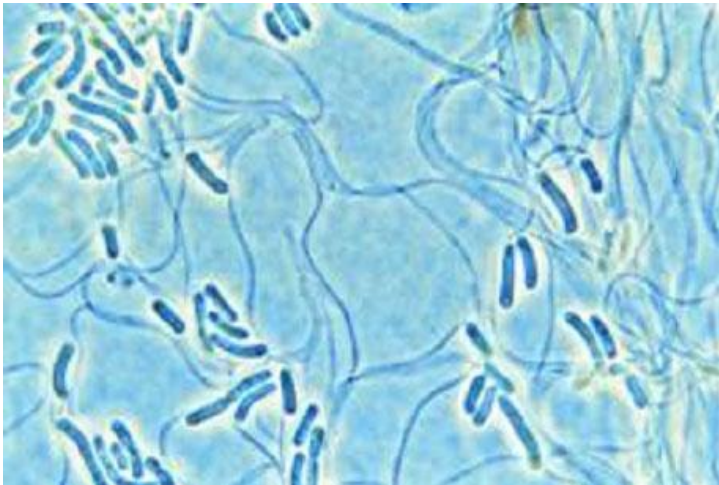
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Please see Figure 5 on:

<http://www.nature.com/nature/journal/v409/n6823/full/4091092a0.html>

Cyanidium – red alga that lives at $\text{pH} < 4$ and $T \sim 42^\circ\text{C}$

Rotschild and Mancinelli, 2001



Cyanobacteria (*Synechococcus*) are found at $\text{pH} > 4$

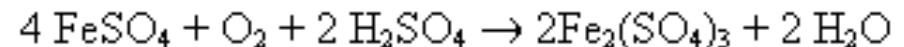
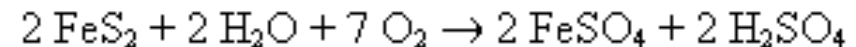
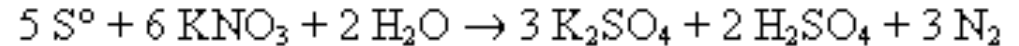
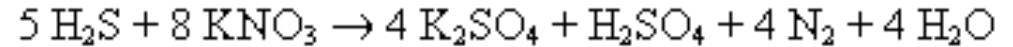
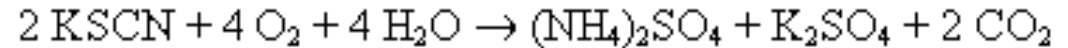
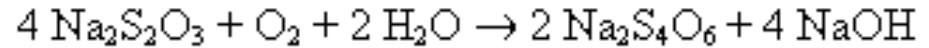
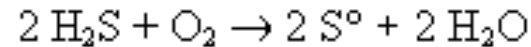
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Castenholz

Acid-mine drainage biota



Image courtesy of NASA.



Thiobacillus ferrooxidans

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Please see the image on:

<http://www.torinoscienza.it/img/200x200/it/s00/00/0004/0000048c.png>

Life around black smokers

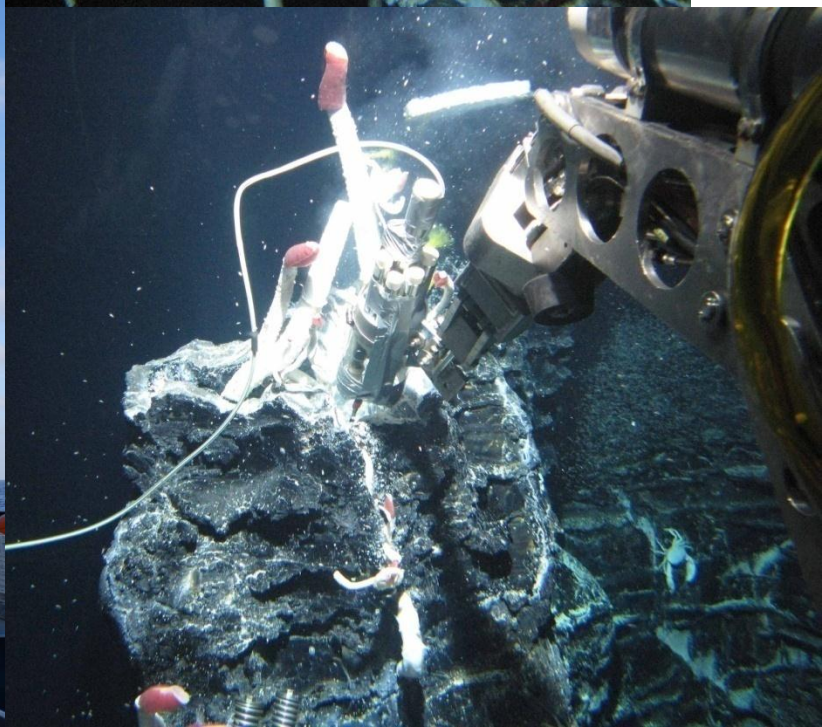
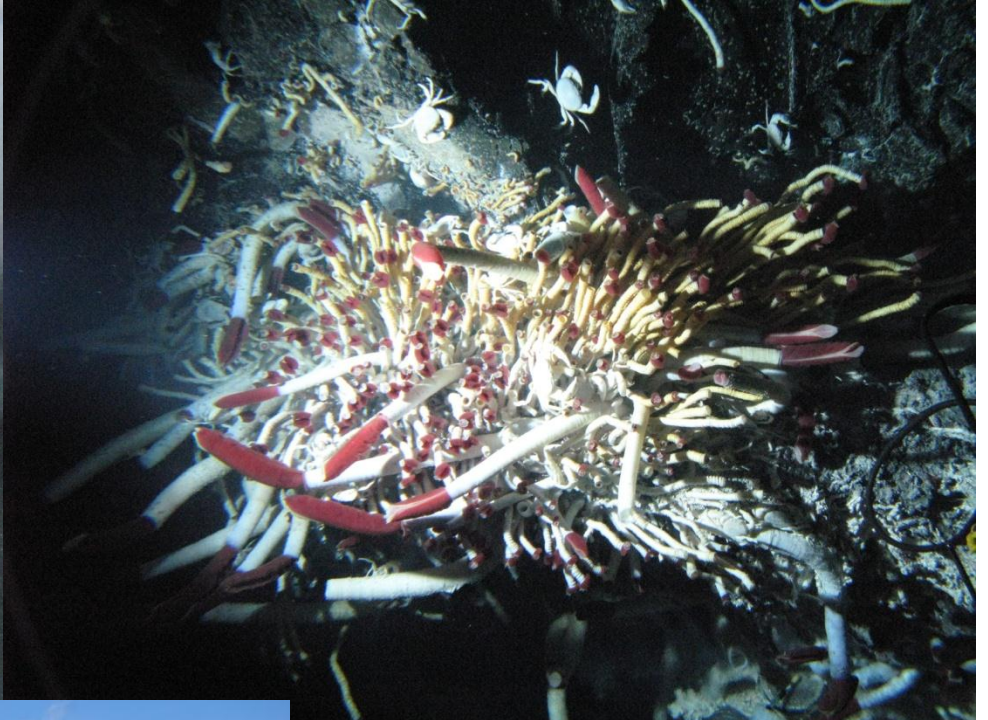
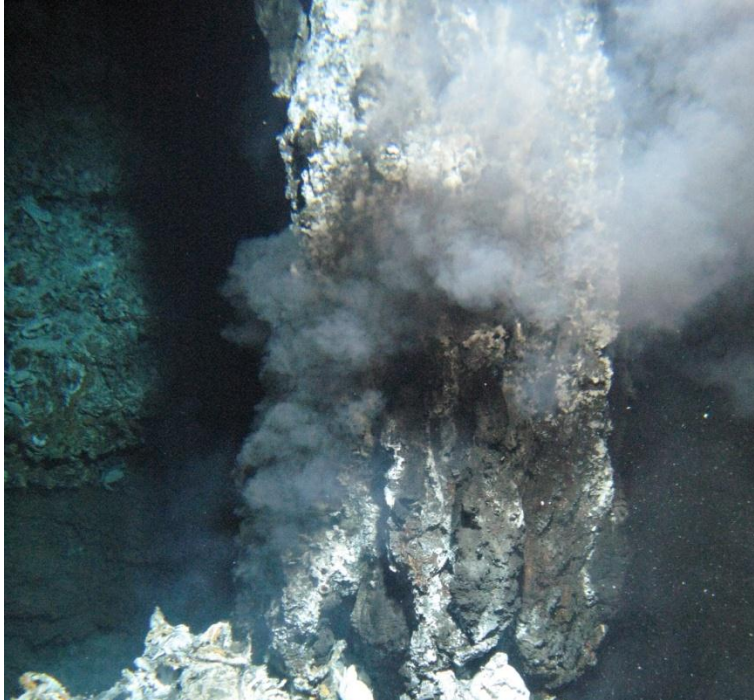
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Please see the animated image on:
<http://www.laszloart.com/Vents.htm>

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Please see the image on:
<http://diversehierarchy.wikispaces.com/Archaeobacteria+-+P.+fumarii>

Pyrolobus fumarii



More hyperthermophiles

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Please see the image on <http://commtechlab.msu.edu/sites/dlc-me/zoo/microbes/pyrococcus.html>.

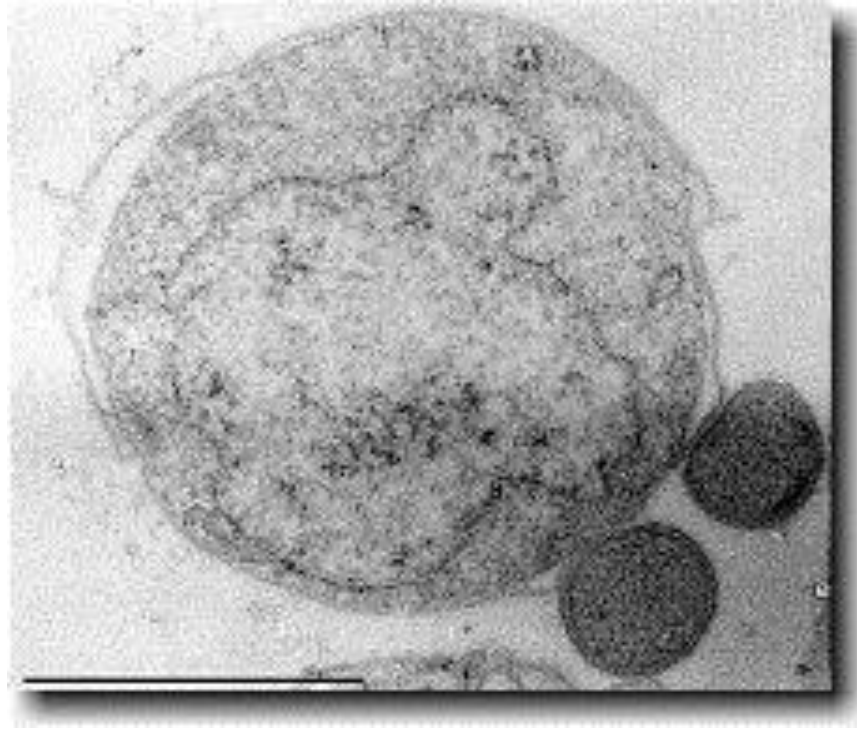


Pyrococcus furiosus

Thermus aquaticus

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Archean parasite at near-boiling temperatures



Nanoarchaeon equitans on *Ignicoccus*

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Life around black smokers

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Please see the image on:

<http://www.sciencedaily.com/images/2005/02/050223124700.jpg>

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Please see the images on:

<http://www.accessexcellence.org/BF/bf01/arp/bf01p3.php>

A Hot-Vent Gastropod with Iron Sulfide Dermal Sclerites

Anders Warén,^{1*} Stefan Bengtson,¹ Shana K. Goffredi,²
Cindy L. Van Dover³

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Please see Figure 1 on:

<http://www.sciencemag.org/content/302/5647/1007.full>

The new gastropod. (A) Retracted in shell; scales and shell are rusty from storage in low grade ethanol. (B) Shell removed; front view of head-foot. Scales are in their normal, black color. (C and D) Longitudinal sections of scales, viewed with light microscopy (C) and scanning electron microscopy (D) photos. Sul, sulfide layers [black in (C), light in (D)].

Vampire squid: life at depth and low O₂

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Please see the images on:

<http://www.pinterest.com/samurott/all-about-vampire-squids-book-project/>

<http://www.itsnature.org/sea/other/vampire-squid>

<http://www.seasky.org/deep-sea/deep-sea-menu.html>

Loriciferans: life at depth and low or zero O₂

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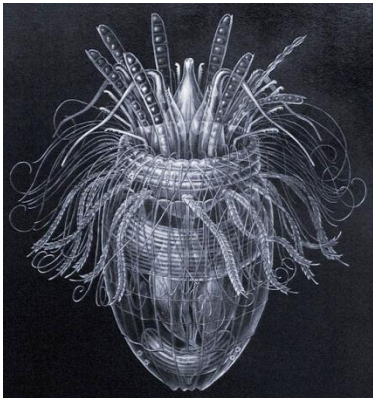
Please see the image on:

<http://culturingscience.files.wordpress.com/2010/04/snapshot-2010-04-07-14-39-34.jpg>

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Please see the second image on:

<http://www.benjamintseng.com/2010/06/life-without-oxygen/>



L'Atalante basin, a brine lake west of Crete in the Med. Sea

Image courtesy of NASA.

(Danovaro et al., 2010)

Tardigrades (waterbears or moss piglets): polyextremophiles

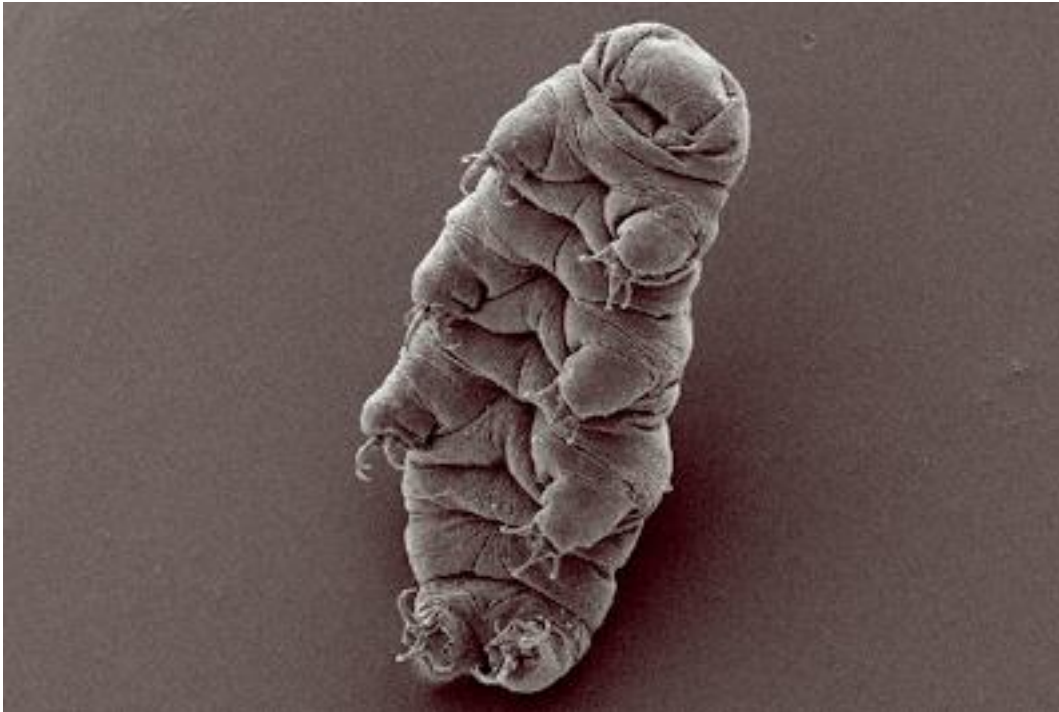
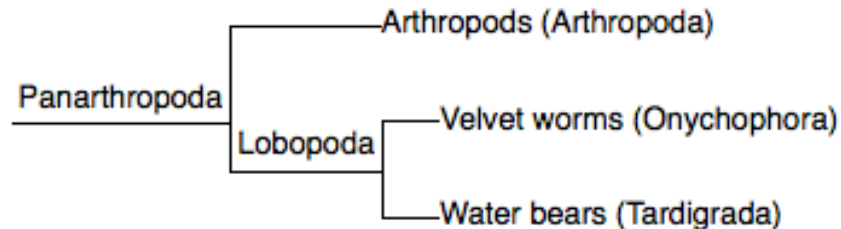


Image from
<http://en.wikipedia.org/wiki/Hypsibiidae>
by Bob Goldstein and Vicky Madden.

Survive desiccation, vacuum and radiation in space, high and low temperatures



Capable of suspended metabolism: Cryptobiosis

Life at high pressures

Photobacterium profundum

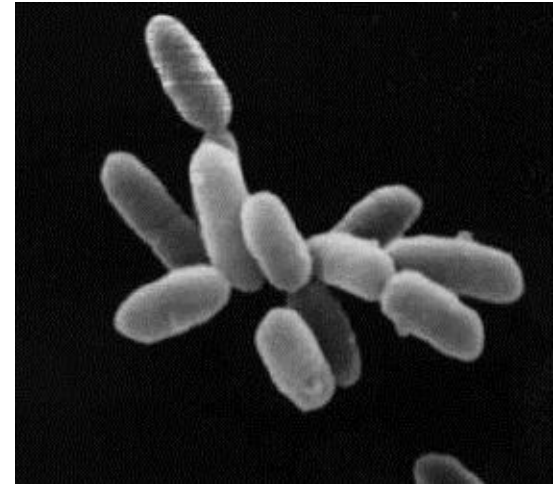
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Please see the image on:

http://microbewiki.kenyon.edu/images/e/e3/Photobacterium_profundum_flagella.JPG

Salt-loving organisms

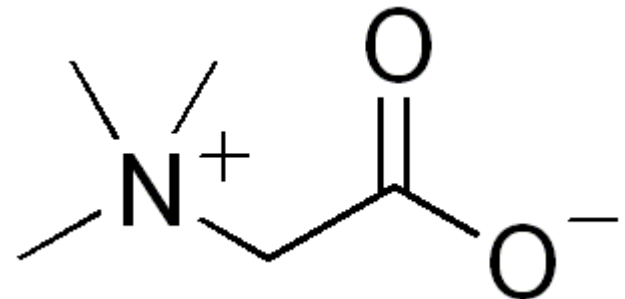
Photograph of an aerial view of a solar saltern facility removed due to copyright restrictions.



Halobacterium

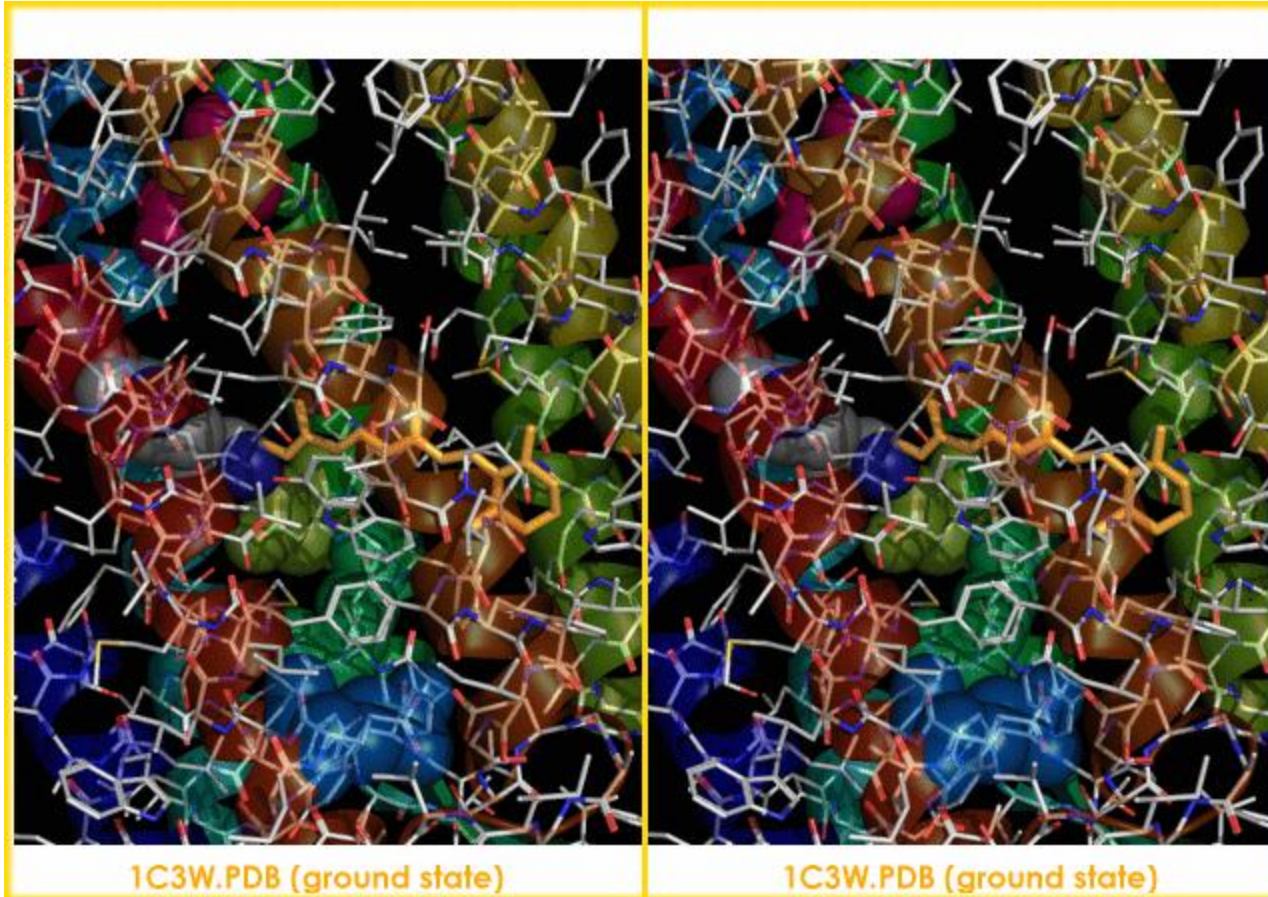
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<http://www.sas.upenn.edu/~pohlschr/>



Glycine betaine

Bacteriorhodopsin



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<http://www.nature.com/nature/journal/v409/n6823/full/4091092a0.html>

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Please see Table 3 on:

<http://www.nature.com/nature/journal/v409/n6823/full/4091092a0.html>

Rotschild and Mancinelli, 2001

Serpentinization

Photograph of a carbonate chimney venting removed due to copyright restrictions.

Lost City

<http://www.lostcity.washington.edu/file/Carbonate+chimney+venting+91%C2%B0C%2C+pH+11+fluids>

Biosignatures and Biogeochemical Processes at the Alkaline Hydrothermal Ecosystem at Lost City



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[http://commons.wikimedia.org/wiki/File:Lost_City_\(hydrothermal_field\)02.jpg](http://commons.wikimedia.org/wiki/File:Lost_City_(hydrothermal_field)02.jpg)

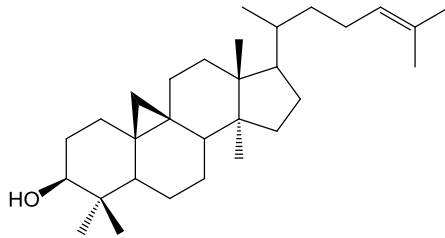
Overview

Overarching Goal: understand carbon cycling & microbial ecology in thermal environments

Approach: Apply tools of geochemistry and genomics



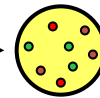
fluid
chemistry



lipid
structures

δ

stable
isotopes

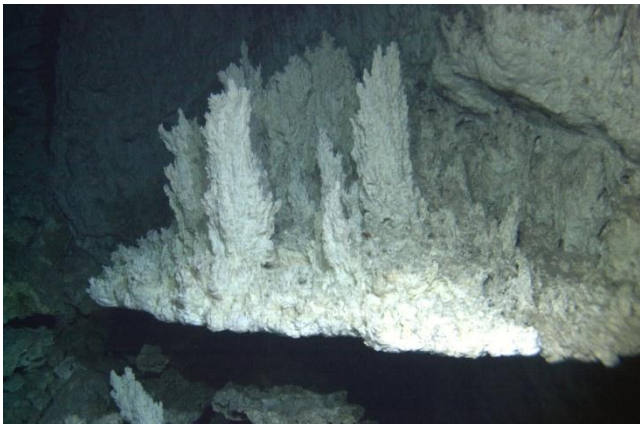


Sequence #1

Sequence #2

Sequence #3

environmental
DNA



Localities within
the Lost City
Hydrothermal
Field

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Serpentinization: source of H₂ and alkalinity

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Photograph of a carbonate chimney venting removed due to copyright restrictions.



Lost City Hydrothermal Field

Vent Fluids

Hydrogen – up to 15 mmol/kg

Methane – up to 2 mmol/kg

Calcium – up to 30 mmol/kg

pH – 9 to 11

**Low temp volatile production:
Proskurowski et al., Chem. Geology 2006**

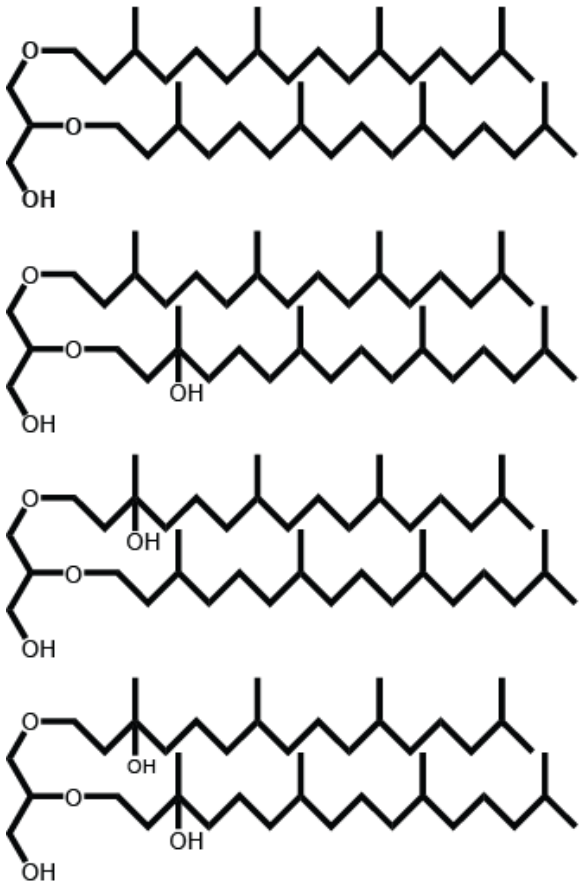
**Abiogenic Hydrocarbon Production at
Lost City Hydrothermal Field:
Proskurowski et al., Science 2006**

Photograph of a carbonate chimney venting
removed due to copyright restrictions.

Biomarkers at Lost City are dominated by diether lipids

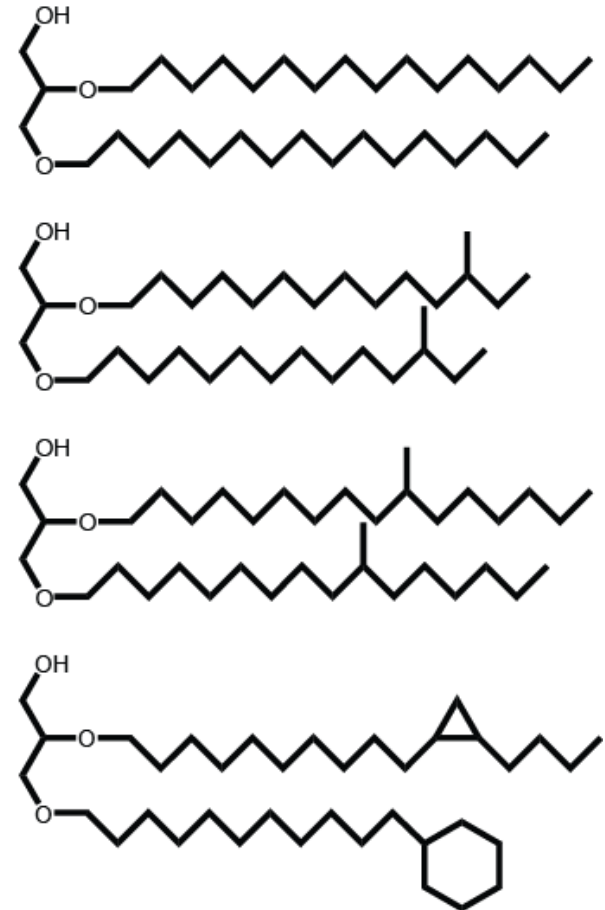
Archaeal diethers

Methanogens, ANME groups



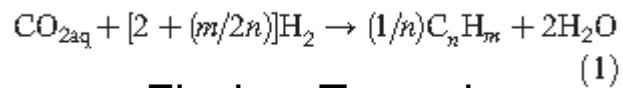
Bacterial diethers

Aquificales, *Ammonifex*,
Thermodesulfobacterium, δ -proteobacteria



Abiogenic Hydrocarbon Production at Lost City Hydrothermal Field

Giora Proskurowski,^{1,2*} Marvin D. Lilley,¹ Jeffery S. Seewald,² Gretchen L. Früh-Green,³ Eric J. Olson,¹ John E. Lupton,⁴ Sean P. Sylva,² Deborah S. Kelley¹



Fischer-Tropsch

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Please see Figure 1 on:

<https://www.sciencemag.org/content/319/5863/604.full>

Serpentinization in terrestrial environments: Cedars, CA

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Please see the images on:

http://www.supertopo.com/climbing/thread.php?topic_id=1410539

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12.007 Geobiology
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