Energy, Emergence & Evolution of Life

inspired by Nick Lane, The Vital Question (2015)

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23 April 2019

The Vital Question: Energy, Evolution, and the Origins of Complex Life. WW Norton & Co. 2015
for more information: www.nick-lane.net

Origin Stories

Where do we come from? What are we? Where are we going?





- **Garden of Eden**
- **Family histories**
- ***Cellular Evolution***

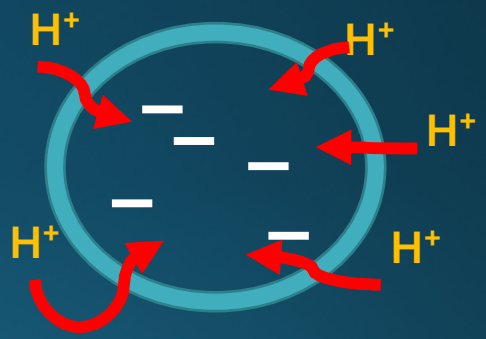
How did life emerge from inorganic chemistry?

Paul Gauguin (1897–98)
Boston MFA

2 Questions

Cellular Evolution . . .

1. **The Emergence of Complex Cells**
2. **The Origin of Life Itself**



. . . and a Revolution

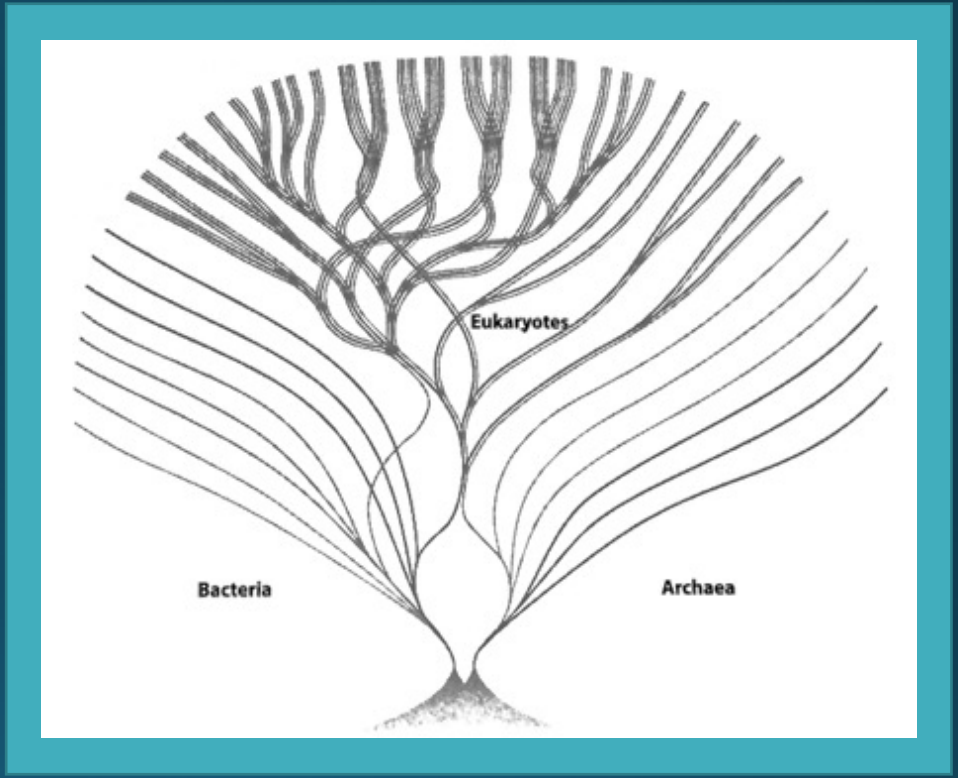
The Hydrogen Hypothesis:

All Life is powered by proton (H^+) gradients across membranes

P Mitchell, "chemiosmotic coupling" Nature 191:144-148, 1961
W Martin & M Müller "hydrogen hypothesis" Nature 392:37-41, 1998
W Martin & MJ Russell "alkaline hydrothermal vents" Phil Trans R Soc London B 358:59-85, 2003

Overview

1. How cells work
2. 3 Domains of Life
3. Earth's Timeline
4. Endosymbioses
5. Emergence



adapted from Martin, BioEssays 21:99-104, 1999

In the Beginning . . .

. . . Earth was a water world



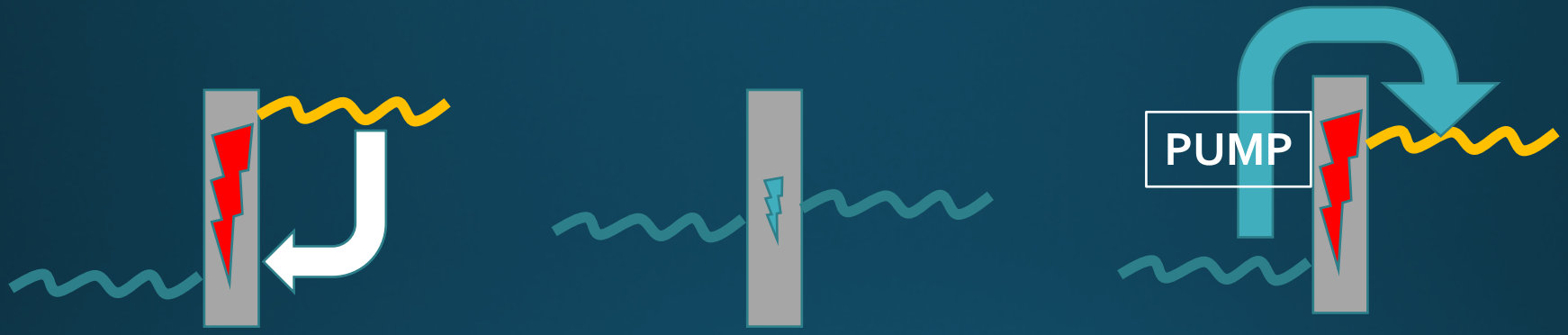
Image: © Simone Marchi

- **Acidic Oceans (pH 5-7)** ***rich in Iron & CO_2***
  - ✓ ***High CO_2 + Water Vapor -> Carbonic Acid***
  - ✓ ***No Free Oxygen (no atmospheric Ozone layer)***
- **Mantle rocks in the shallow seabeds react with seawater to form Alkaline fluids (pH 10-11)**
  - ✓ ***Sulfides and H_2 gas bubble up in ocean hydrothermal seeps***
- **Volcanic Activity &** ***Alkaline Hydrothermal Vents*** ***commonplace***

An inorganic "battery" between Ocean and Mantle created conditions for life to emerge in the ancient oceans

How do Cells work (1)?

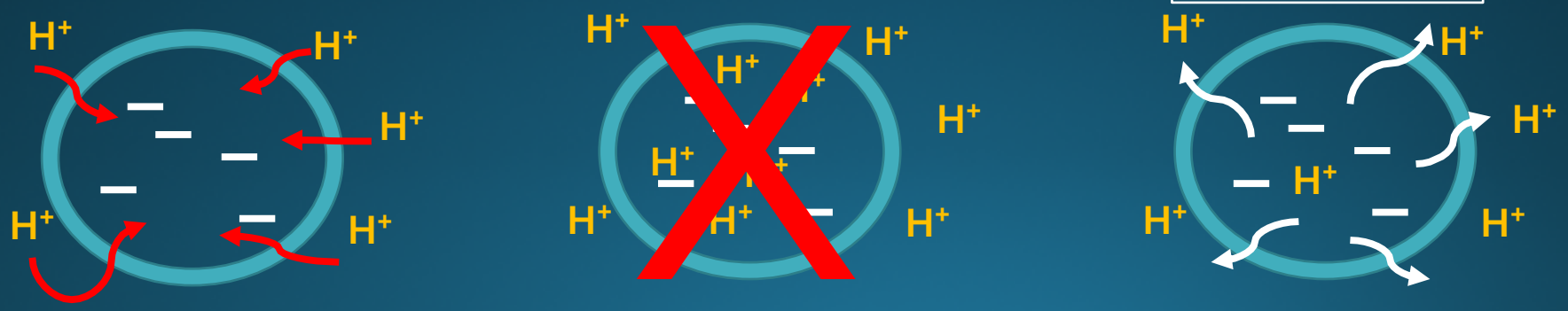
Like a hydroelectric reservoir pushes turbines to do work (electricity)



Disequilibrium

Equilibrium (no work)

Disequilibrium



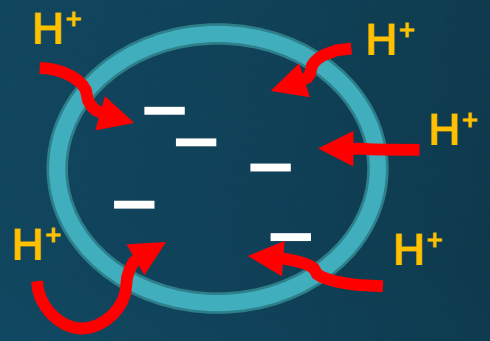
Cells are powered by proton (H+) gradients across membranes

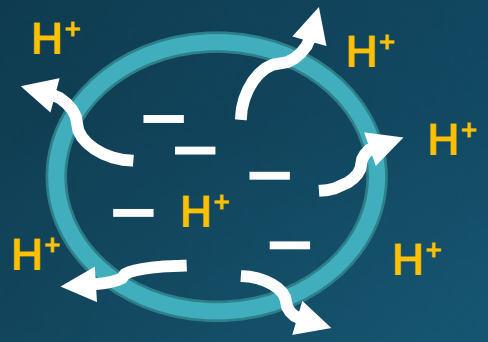
How do Cells work (2)?

Proton Gradients drive fundamental cell processes that sustain life such as

Energy Production & Storage

e.g., ADP + P = ATP



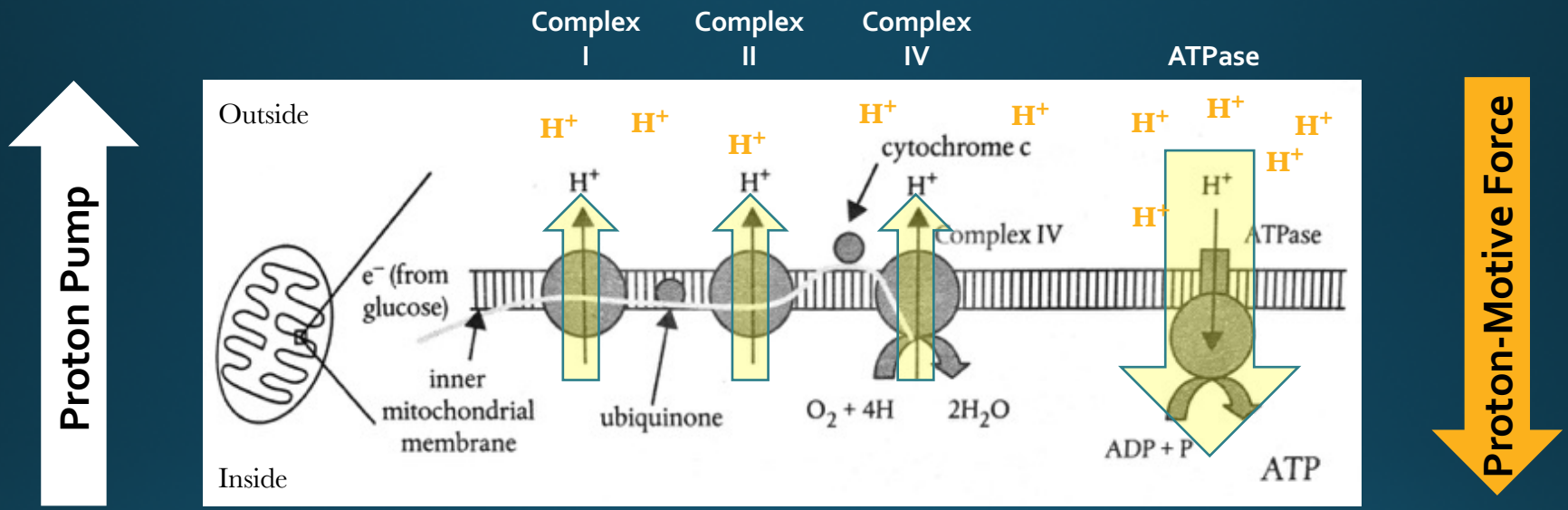


Proton Pumps require energy to maintain disequilibrium

Energy from food, sunlight, chemicals external to the cell

Adenosine triphosphate (**ATP**) is the power currency of the cell

Reduction-Oxidation Chain Respiration and the Proton Pump



the Respiration Chain in Mitochondria

From Glucose through successive redox reactions to ATP

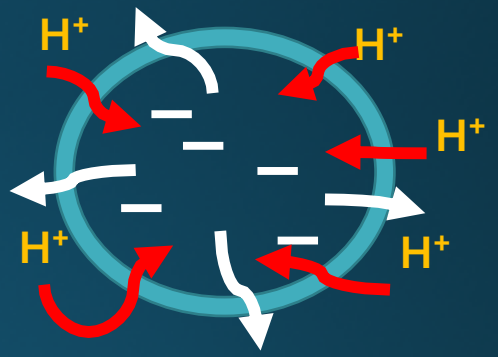
adapted from Nick Lane: Power, Sex and Suicide p 129, Fig 7 (2005)

How do Cells work (3)?

Proton Gradients are fundamental to ALL life

Supporting many functions such as

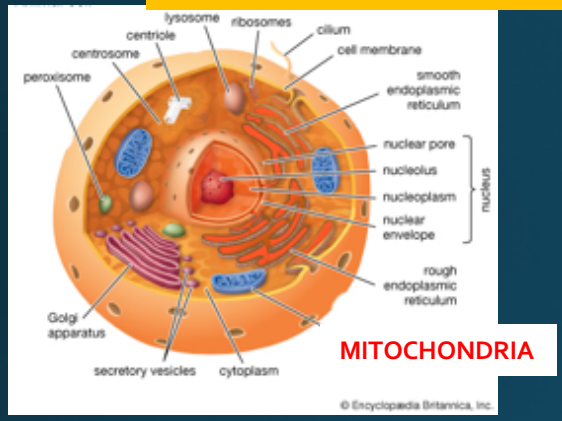
- ✓ *Energy storage, e.g., ATP*
- ✓ *Active transport of nutrients into cell & waste out of the cell*
- ✓ *Bacterial locomotion (flagella)*



Proton pumps must be ancient and ancestral

3 Domains of Life

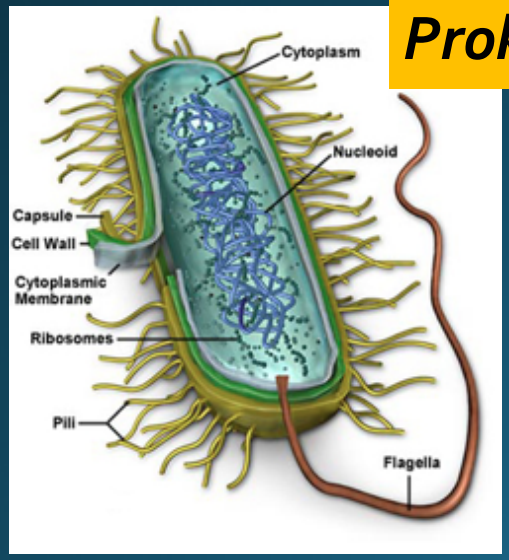
Eukaryotes: Plants, Algae, Fungi, Protists, Animals, People



MITOCHONDRIA

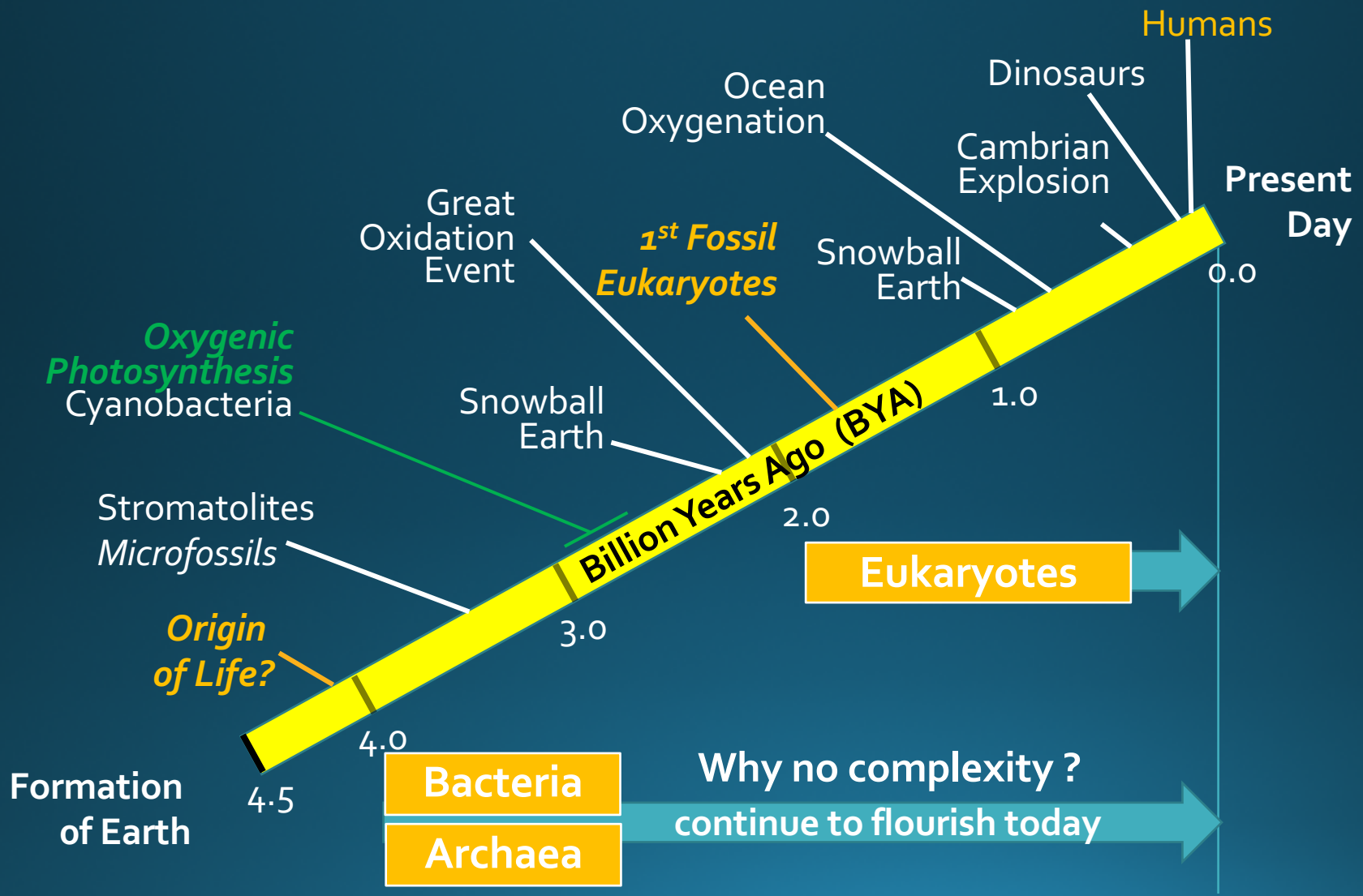
- Large Complex Genomes In Cell Nucleus
- Includes *ALL* multi-cellular organisms
- Descended from a single common ancestor
- Large cell volumes with *membrane-bound* organelles
- MITOCHONDRIA: Powerful energy production

Prokaryotes: Bacteria & Archaea



- Simple genome - No Nucleus – No Organelles
- Single Cells, simple morphology, a few microns wide
- Small cell volumes (10k-100k smaller volumes)
- NO *mitochondria:* Limited energy production
- Extensive penetration in many environmental niches

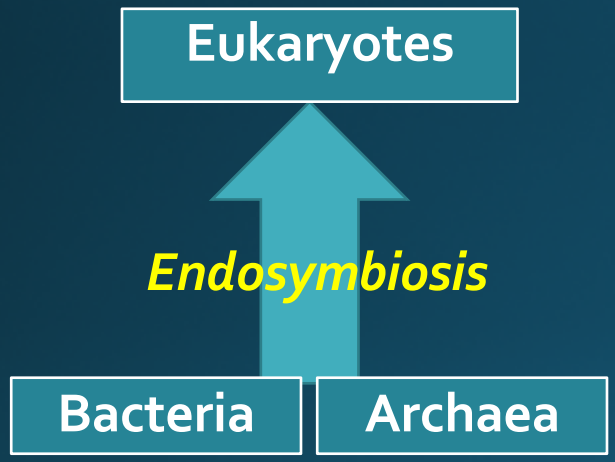
What came First? and When?



Eukaryotes: Prokaryote Endosymbiosis*

Symbiosis? Mutually beneficial, long-term relationship between two different species.

EndoSymbiosis: 2 cooperating species fuse within the same cell



Eukaryotes emerge from single event

- **Archaean host + H^2-producing Bacterium -> Mitochondria**
- **1.6 - 2 Billion Years Ago**
- **Many shared structures and traits**
- **Separate mitochondrial DNA - most genes migrate to central nucleus**
- **Enormous increase in energy production drives specialization and complexity**

Mitochondria Required for Complex Life

**Lynn Sagan [Margulis]. J Theor Biol 14(3):255-274, 1967*

2 Seminal Endosymbioses

Only 2 Known Enduring Endosymbiotic Events

-> MITOCHONDRIA and CHLOROPLASTS

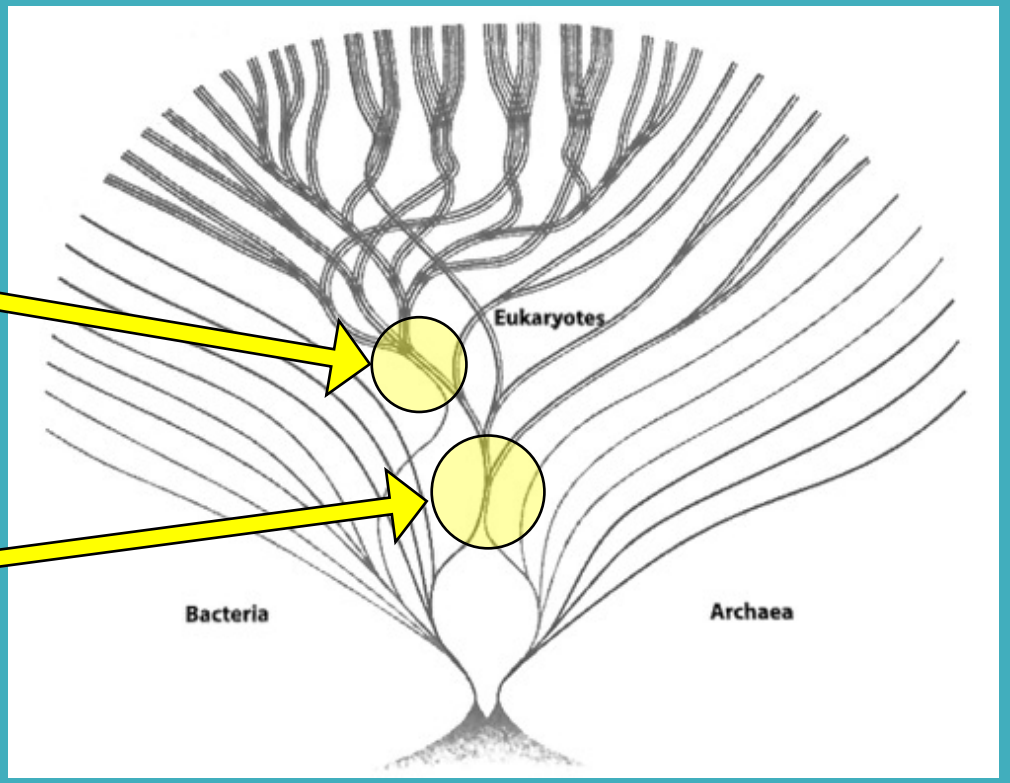
Plants
Algae

Endosymbiosis:
Chloroplasts

Eukaryotes

Endosymbiosis:
Mitochondria

Bacteria **Archaea**

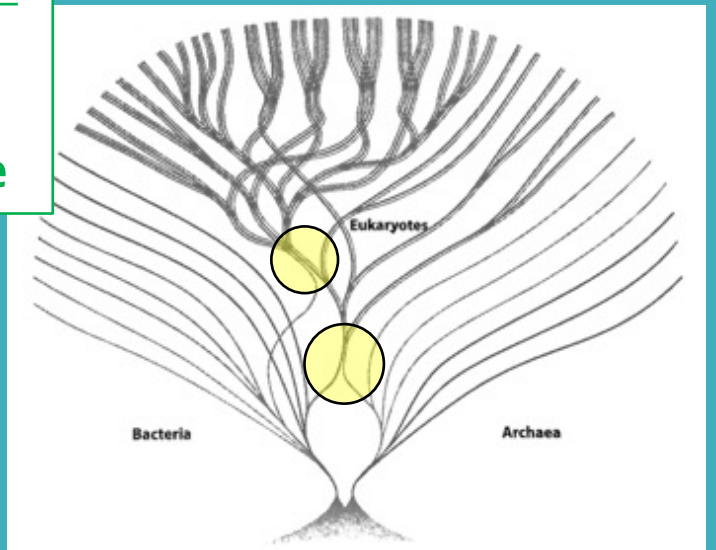


adapted Martin, BioEssays 21:99-104, 1999

"Family Tree" of Eukaryotes:
Chloroplast example

- **All Plants and Algae are Eukaryotes**
- **Only Plants and Algae have Chloroplasts**

✓ **Therefore Chloroplast Endosymbiosis more recent than Eukaryote emergence**



adapted from Martin, BioEssays 21:99-104, 1999

Vertical Descendence in Eukaryotes

Parent-Daughter Genome Transmission *BETWEEN* generations

- ***Traits transmitted* from progenitor cells**
- **Entire genome replicated**
- **Supports Darwin's "Family Tree" analysis**
- **Leads to a "Last Eukaryotic Common Ancestor"**

Where do we go from Eukaryotes ?

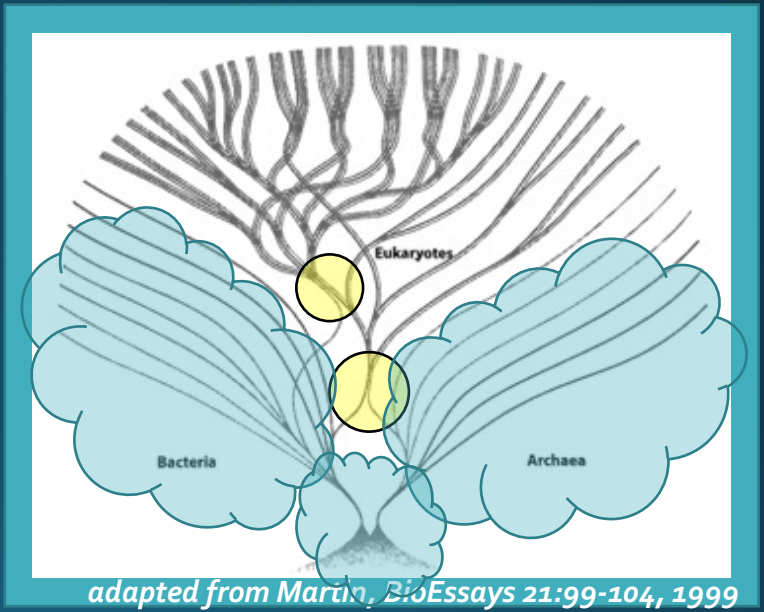
Archaea & Bacteria: Lateral Gene Transfer

Vertical Descendance alone cannot be used to track evolution in Prokaryotes

Lateral Gene Transfer in Prokaryotes

Gene Exchange *within* a generation

- *Fusion* between individuals or populations even across kingdoms



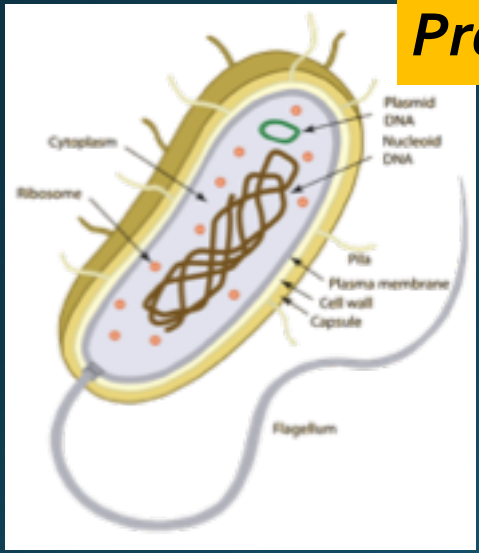
adapted from Martin, BioEssays 21:99-104, 1999

Need another way to track relatedness:
What do Bacteria and Archaea have in Common?
How are they Different?

Bacteria & Archaea Share Features

ALL CELLS across the 3 Domains of Life

- ***Generate energy from proton gradients across membranes***
- ***Use universal genetic code: DNA, RNA, protein assembly on ribosomes***



Prokaryotes: Bacteria & Archaea

- **Simple genome - No Nucleus – No Organelles**
- **Single Cells, simple morphology, a few microns wide**
- **Lipid external membranes – site of energy production**
- **Ribosomes/ circular DNA plasmids distributed freely throughout cytoplasm**
- **Lateral Gene Transfer common even across Kingdoms**

Indicating Common Evolutionary Ancestors

Bacteria & Archaea are Very Different

Similar size but distinct genes, structures, processes

Bacteria vs Archaea

- *Completely different ribosomal RNA (rRNA)*
  - ✓ *Ribosomes are location of protein production in all cells*
  - ✓ *Archaea defined as new Domain by rRNA (Woese, 1977)*
- *Different enzymes and mechanisms for DNA replication*
- *Different cell membrane composition and construction*
  - ✓ Last Universal Common Ancestor (LUCA) *may not have had a cell membrane !*



Indicating Different Evolutionary Ancestors

When, Where, and How did it all get started ?

Last Common Universal Ancestor: LUCA . . . or Two?

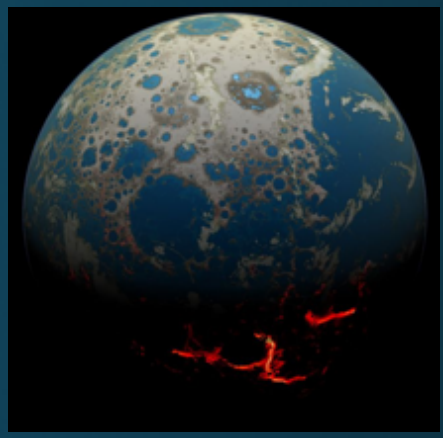


Image: © Simone Marchi

- **Ocean chemistry then and now**
- **Inorganic Energy Flow / Proton Gradients**
- **Organic Chemistry, Concentration, Self-replication**
- **Proliferation**

Early Ocean Chemistry

Early Earth was a waterworld – Not Hadean inferno

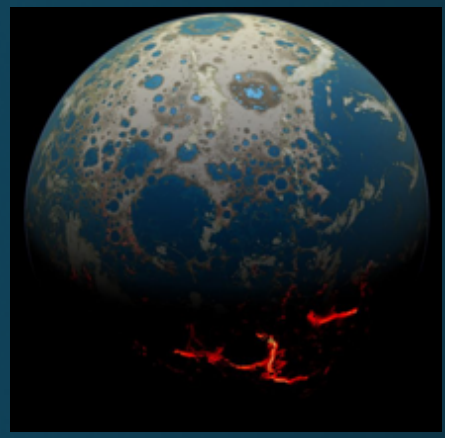


Image: © Simone Marchi

- Shallow oceans covered most of the earth
- Lots of CO_2 but no free Oxygen in the atmosphere or ocean: *Anaerobic*
- Oceans were *Acidic (H^+; pH 5-7)*
  - ✓ Seeded by terrestrial and underwater volcanism
  - ✓ Rich in minerals including Iron & Sulfur

Early Ocean Chemistry

Hydrothermal vents were common

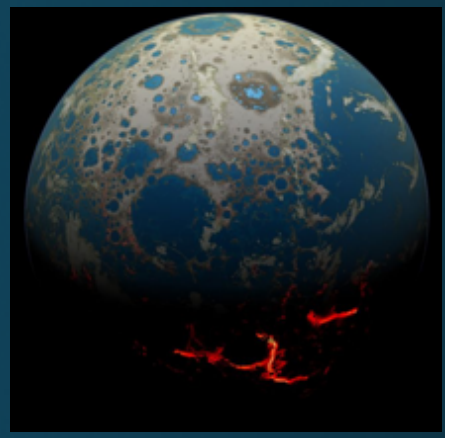
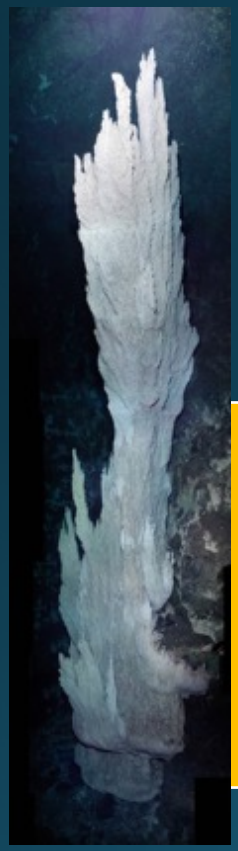


Image: © Simone Marchi



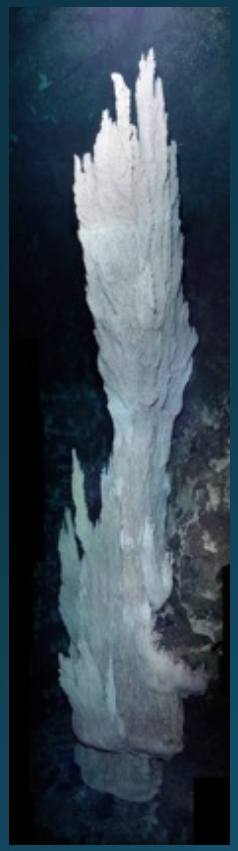
"Black Smokers" hydrothermal chimneys

- ✓ **Discovered in 1977 at Mid-Pacific Rise**
- ✓ **Hot (400°C), very acidic pH 2-5, turbulent conditions**
- ✓ **Large amounts of catalytic minerals like Iron & Sulfur**

"Lost City" Alkaline Hydrothermal Vents

- ✓ **Discovered in 2000 at Mid-Atlantic Ridge**
- ✓ **Warm (45-90°C), Alkali pH 10-11, 60-meters tall**
- ✓ **At least 120,000 years old. Stable environment!**

How Alkaline Hydrothermal Vents Form

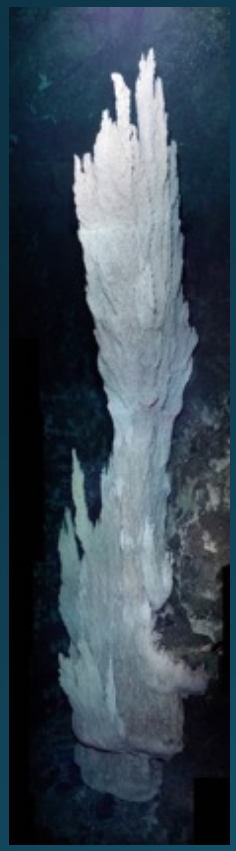


1. Subterranean mantle rock makes contact with seawater
2. ***Steady* flow of alkaline fluids emerges from seabed**
3. Stable, warm, large $CaCO_3$ structuress built up over time
4. **Iron-Sulfur minerals precipitate into bubbles** that could support evolution and concentration of organic chemistry

Inorganic Iron-Sulfur compartments could be precursors of cell walls and membranes in free-living prokaryotes

Alkaline Hydrothermal Vents

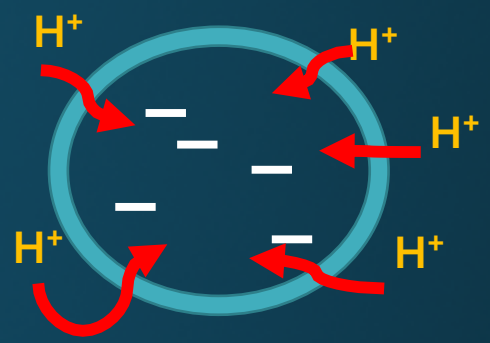
Proton gradients in alkaline hydrothermal vents create conditions for life in ancient oceans



- ✓ Plenty of CO_2 and H_2 to produce organic compounds
- ✓ Plenty of reactive minerals that can serve as biological catalysts like Iron, Sulfur
- ✓ Microporous compartments that segregate alkaline from acidic fluids
- ✓ Warm, stable, alkaline environment like a bioreactor

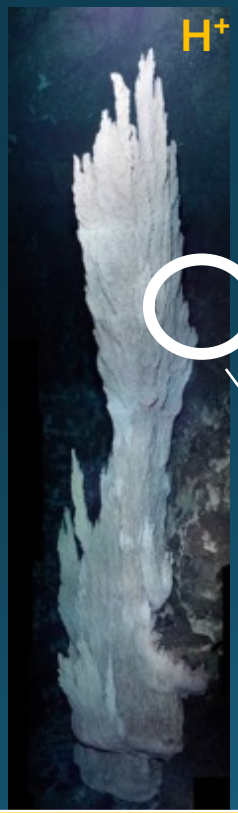
MJ Russell et al. Nature 336:117, 1988

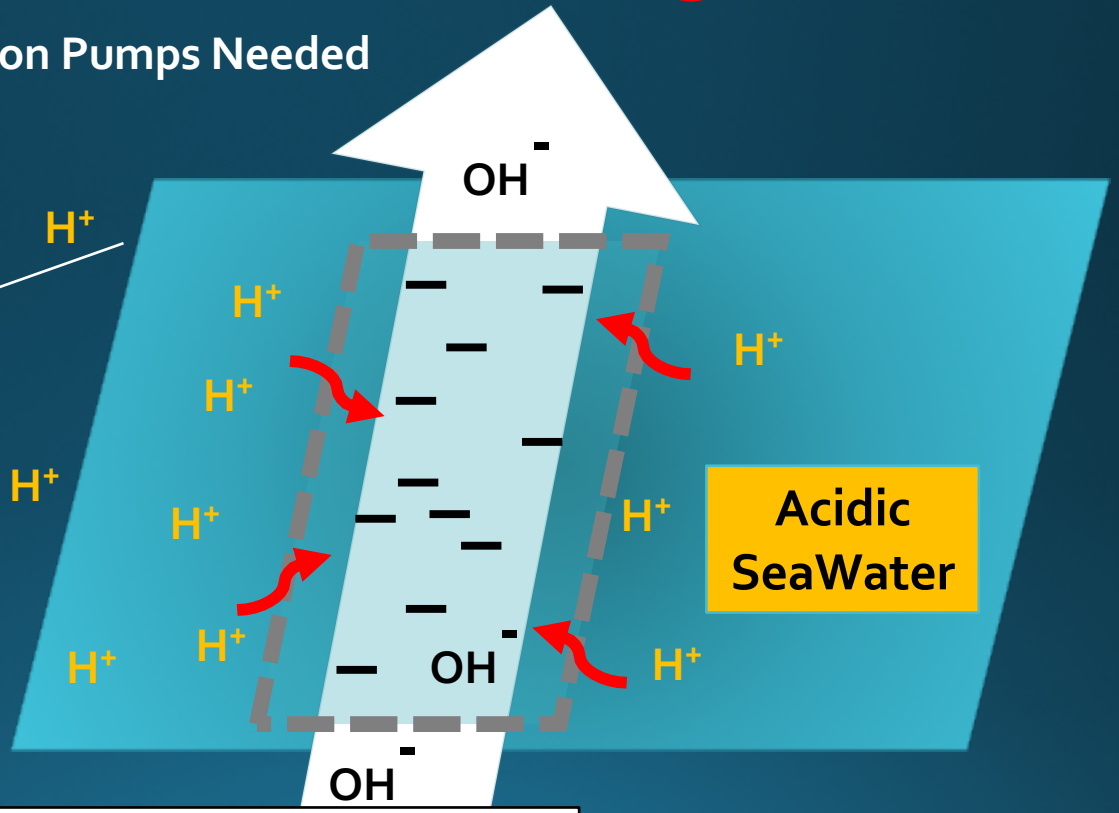
Inorganic Proton Gradients
in Alkaline Hydrothermal Vents



Acid and Alkaline fluids continuously replaced

No Proton Pumps Needed





Organic compounds / processes accumulate within cells

Last Universal Common Ancestor

LUCA common traits
formed basis of Bacterial and Archaeal emergence

1. **Emerged within the inorganic compartments of ancient alkaline hydrothermal vents**

2. **Powered by proton gradients across inorganic membranes**
   - ✓ **Did not have modern cell membrane**

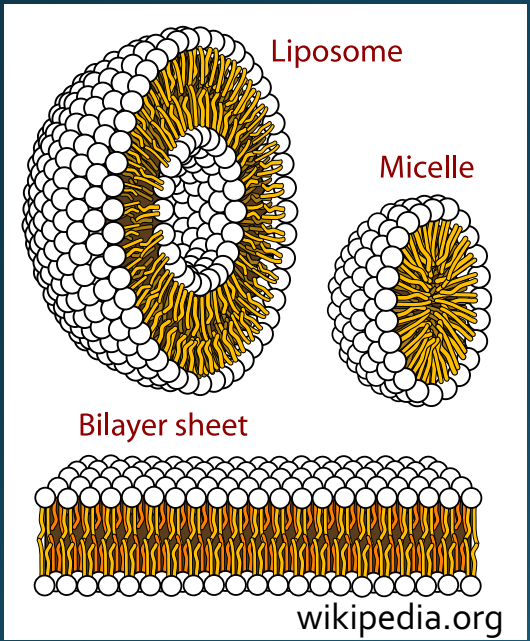
3. **Developed universal genetic code: DNA, RNA, Protein synthesis**
   - ✓ **But not modern DNA replication**

LUCA was not a free living cell with lipid membranes.
LUCA was confined to Iron-Sulfur compartments within alkaline hydrothermal vents.

How did independent cells develop modern cellular membranes?

Where do Cell membranes come from?

Lipid membranes and other organic compounds are created spontaneously within alkaline hydrothermal vents



Circles are the hydrophilic heads
Wavy lines are fatty acyl side chains

Phospholipids in Aqueous Solutions

spontaneously

- ✓ **Form bilayers**
- ✓ **Form spherical structures**
- ✓ **Split into daughter cells when critical size is reached**

Independent cells require lipid membranes and membrane pumps

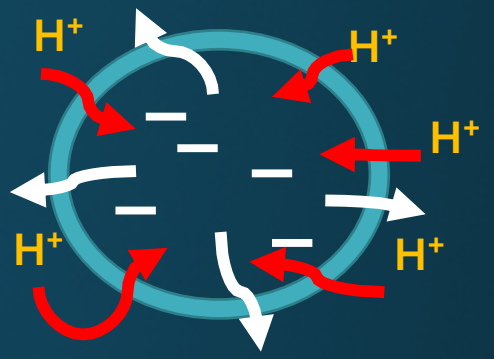
Organic Chemistry goes Mobile

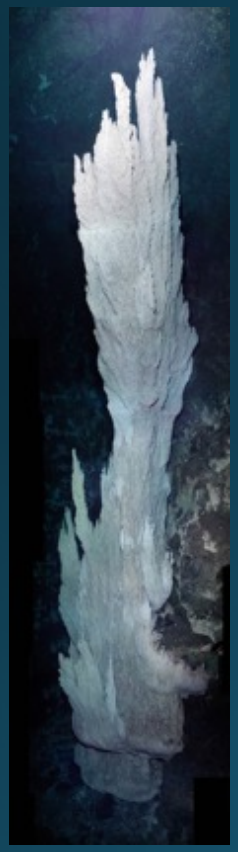
Membrane pumps enable independent Bacteria and Archaea to recreate conditions of alkaline hydrothermal vents in open ocean

1. **Organic molecules / processes accumulate & concentrate**
   - ✓ **DNA, RNA & protein synthesis, phospholipids, self-replication and energy metabolism created within inorganic compartments in alkaline hydrothermal vents**
2. **Bacterial and Archaean proto-membranes encompass organics enabling further concentration and evolution.**
3. **Biochemical Na+ pumps maintain disequilibrium, reducing reliance on natural proton gradients.**
4. **Newly independent archaea and bacteria escape anaerobic hydrothermal vents and exploit new ocean environments**

Summary

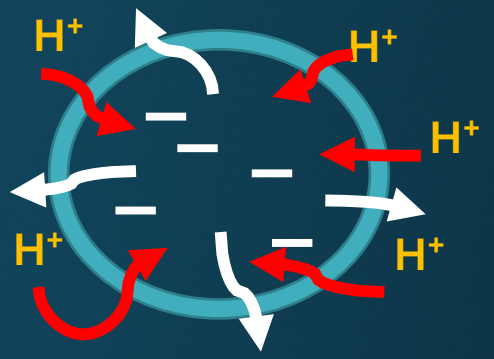
Proton Gradients across membranes power the emergence and evolution of Life





1. Proton gradients in alkaline hydrothermal vents created conditions for life in ancient oceans
2. Organic biological products and processes concentrated and evolved within inorganic Iron-Sulfur compartments
3. Bacteria and Archaea emerge independently from anaerobic environments with different cell membranes
4. Prokaryotes expand and exploit ecological niches
5. Single endosymbiosis creates Eukaryotes with mitochondria
6. Mitochondria enable evolution of complex life forms including us

Thoughts & Conclusions



1. Life emerged early in earth's history

2. Emergence of Simple Life in the universe is as likely as similar geology in other waterworlds

However . . .

3. Emergence of Complex Life is very unlikely
   - ✓ Only once in 4 billion years on Earth
   - ✓ Bacteria and Archaea never reach complexity of Eukaryotes

We may be alone in the Universe . . .

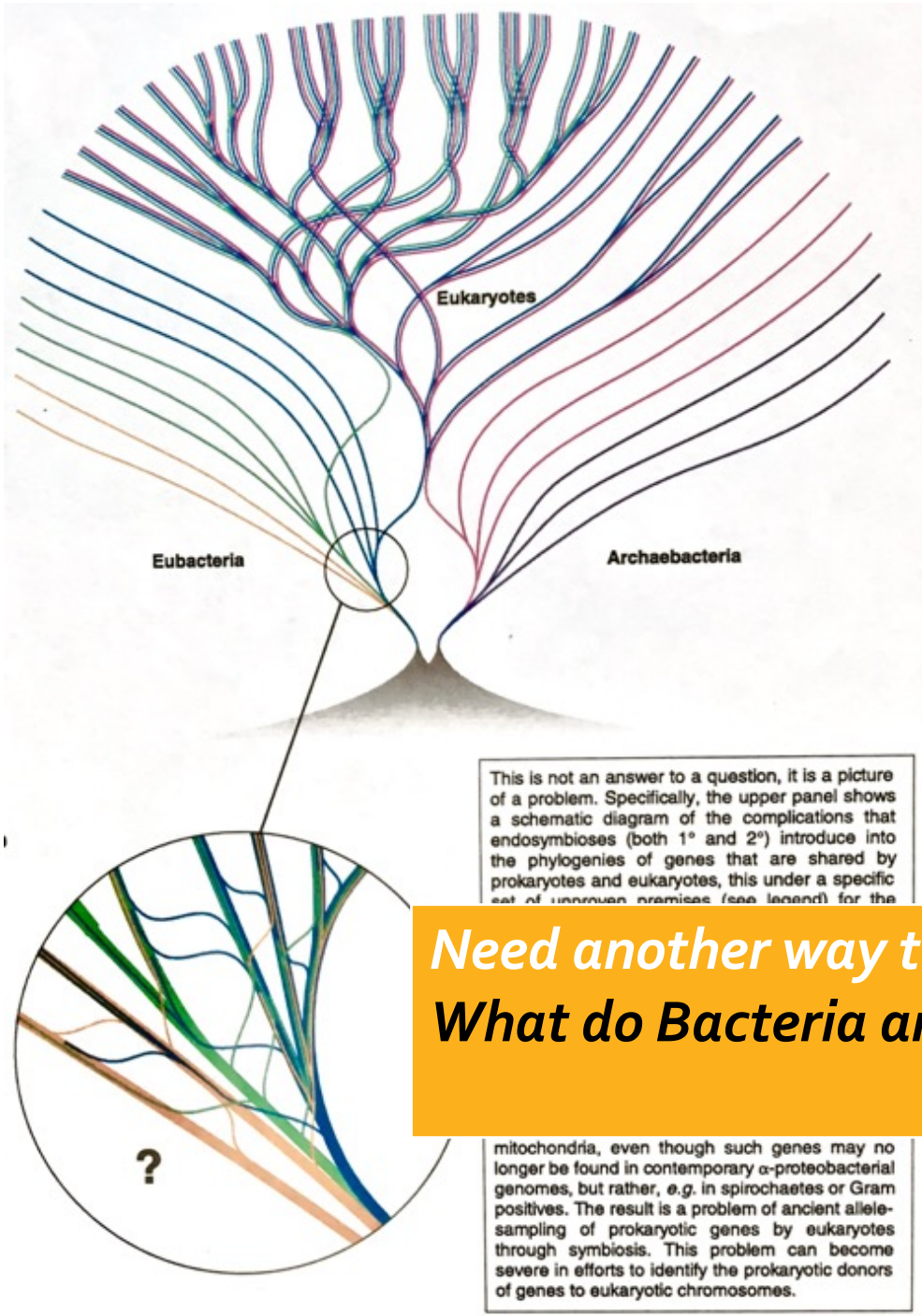




. . . but we'll keep looking



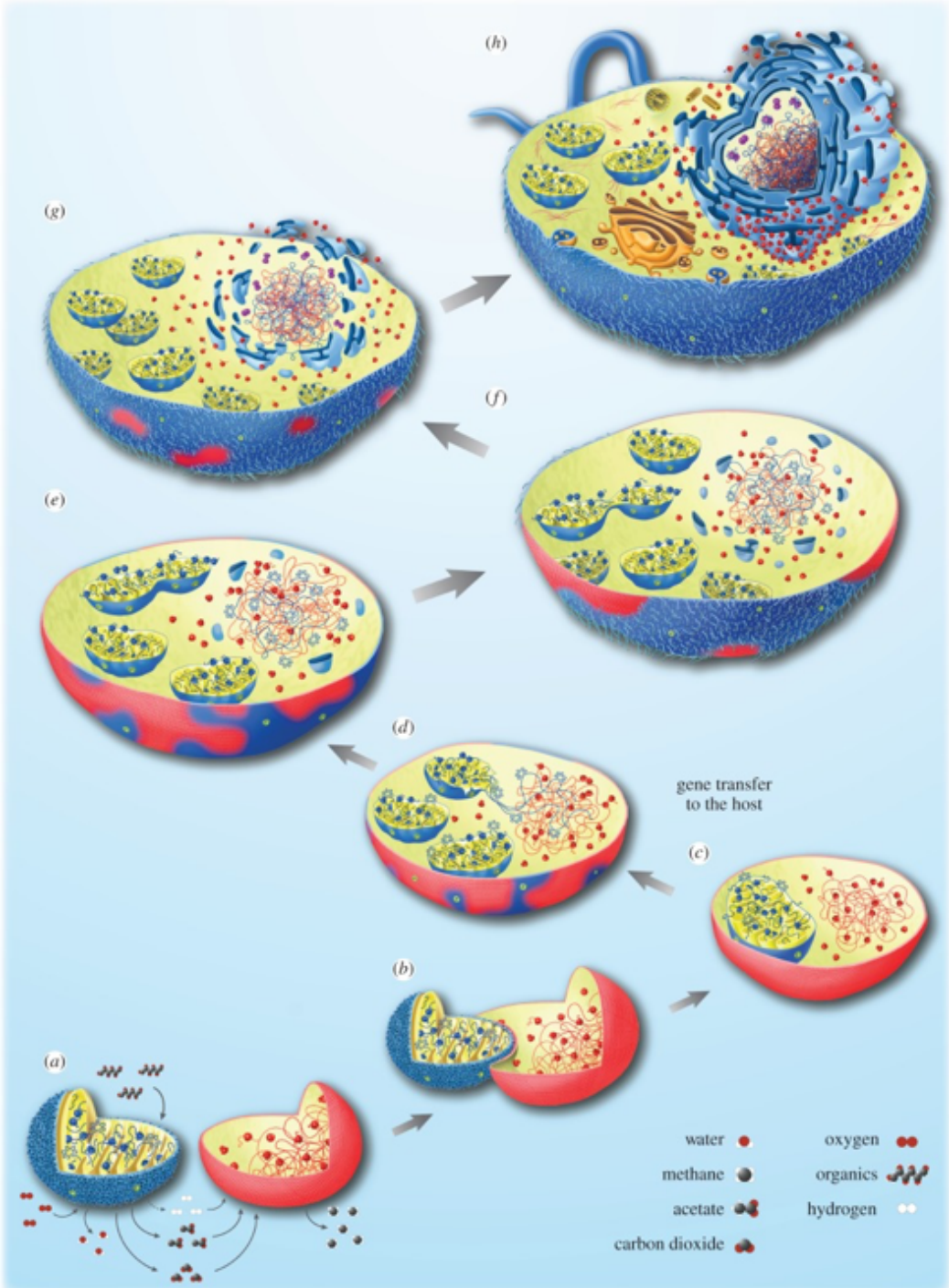
Lateral Gene Transfer in Prokaryotes



This is not an answer to a question, it is a picture of a problem. Specifically, the upper panel shows a schematic diagram of the complications that endosymbioses (both 1° and 2°) introduce into the phylogenies of genes that are shared by prokaryotes and eukaryotes, this under a specific set of unproven premises (see legend) for the mitochondria, even though such genes may no longer be found in contemporary α-proteobacterial genomes, but rather, *e.g.* in spirochaetes or Gram positives. The result is a problem of ancient allele-sampling of prokaryotic genes by eukaryotes through symbiosis. This problem can become severe in efforts to identify the prokaryotic donors of genes to eukaryotic chromosomes.

William Martin
Mosaic bacterial chromosomes:
a challenge en route to a tree of genomes.
BioEssays 21:99-104, 1999. Figure 2.

Need another way to track relatedness:
What do Bacteria and Archaea have in Common?
How are they Different?



Origin of Mitochondria from Prokaryote Endosymbiosis

WF Martin, S Garg, V Zimorski Endosymbiotic theories of eukaryote origin. **Philos Trans R Soc London B Biol Sci 370**, 2015. Figure 3.

Mitochondrial origin in a prokaryotic host. (*a*–*h*) Illustrations for various stages depicting the transition of a H_2-dependent archaeal host (in red) and a[n] anaerobic *α*-proteobacterium (in blue) to an eukaryote.

Most bacterium genes transfer to host nucleus.

Archaea / Bacteria Symbiosis



Methanogens / Hydrosomes within a living Eukaryote

- Methanogens (light grey) need H2
- Hydrogenosomes (dark grey) produce H2

H2 Hypothesis and Endosymbiosis

- ✓ *Archaeal Methanogens live in close proximity to H2-producing Bacterium*
- ✓ *Archaeon physically engulfs bacterium*

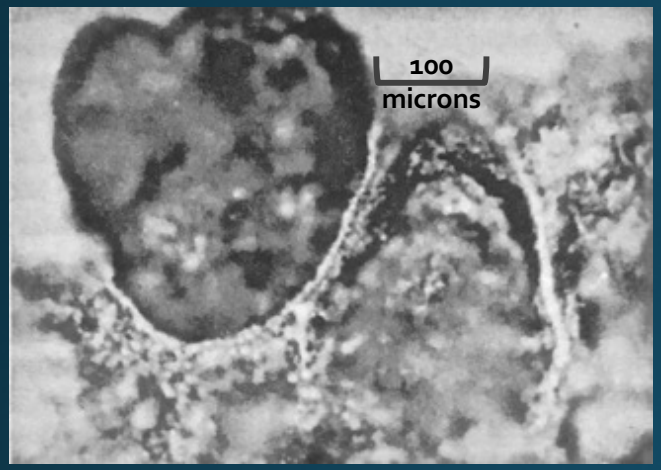
Bacterium provides H2 to power Archaean host

+ Archaea provide stability and organic fuel to Bacterium

Together, Eukaryotes can venture out into oxygen world

from Nick Lane: Power, Sex and Suicide p 81, Fig 3 (2005)
Courtesy of B Finlay, Queen Mary University of London.

Microporous Bubbles in Alkaline Hydrothermal Vents



Electron micrograph of Iron-Sulfur cells from Tynagh Ireland *

- ✓ **360 Million Years Old**

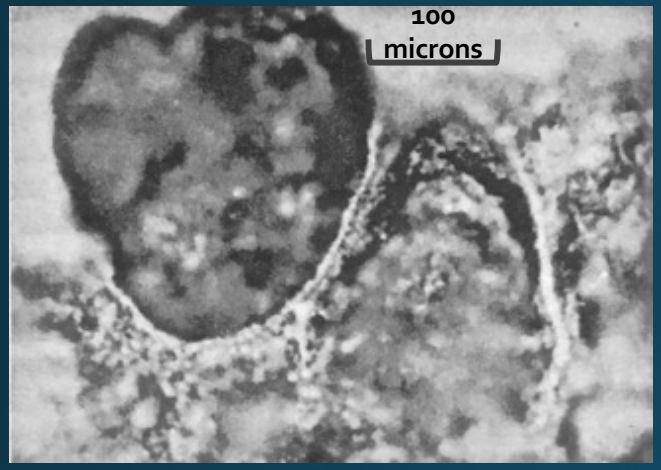
Inorganic Iron-Sulfur membranes

- ✓ Segregate Acid seawater and Alkali fluids i.e., maintain a proton gradient
- ✓ Enable flow of Protons (H^+) into cells
- ✓ Catalyze biochemical reactions and concentrate organic products
- ✓ Conduct electrons like iron-sulfur proteins in mitochondrial membranes

Inorganic Iron-Sulfur cells have been recreated in the lab

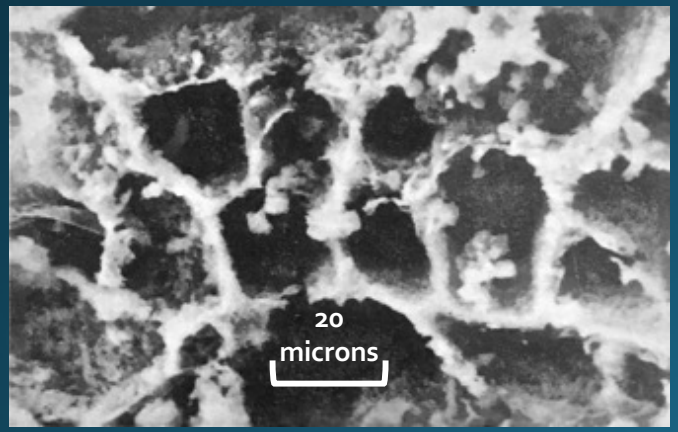
adapted from Martin & Russell. Philo Trans of Royal Society B 38:59-85, Fig 2,. 2003
**D Banks. Nature 313:128-131, 1985*

Primordial 'Cells' with Iron-Sulfide Membranes



Electron micrograph of Iron-Sulfur cells from Tynagh Ireland*

- ✓ **360 Million Years Old**



Electron micrograph of Iron-Sulfur cells created in the lab

- ✓ **Alkali-Acid reaction products of Sodium Sulfide + Iron Chloride**

adapted from Martin & Russell. Philo Trans of Royal Society B, Fig 2, 38:59-85, Fig 2. 2003

****D Banks. Nature 313:128-131, 1985***

What is Life ?

1. Segregation
2. Sustainment
3. Specialization
4. Replication
5. Socialization
6. Adaptation

1. ***Segregation:*** Inside vs outside environments
2. ***Sustainment:*** Maintaining internal materials and processes
3. ***Specialization:*** Interdependent functional differentiation
4. ***Replication:*** Propagation of self
5. ***Socialization:*** Interaction among individuals within and across populations
6. ***Adaptation:*** Mutation, competition and selection for specific environmental niches