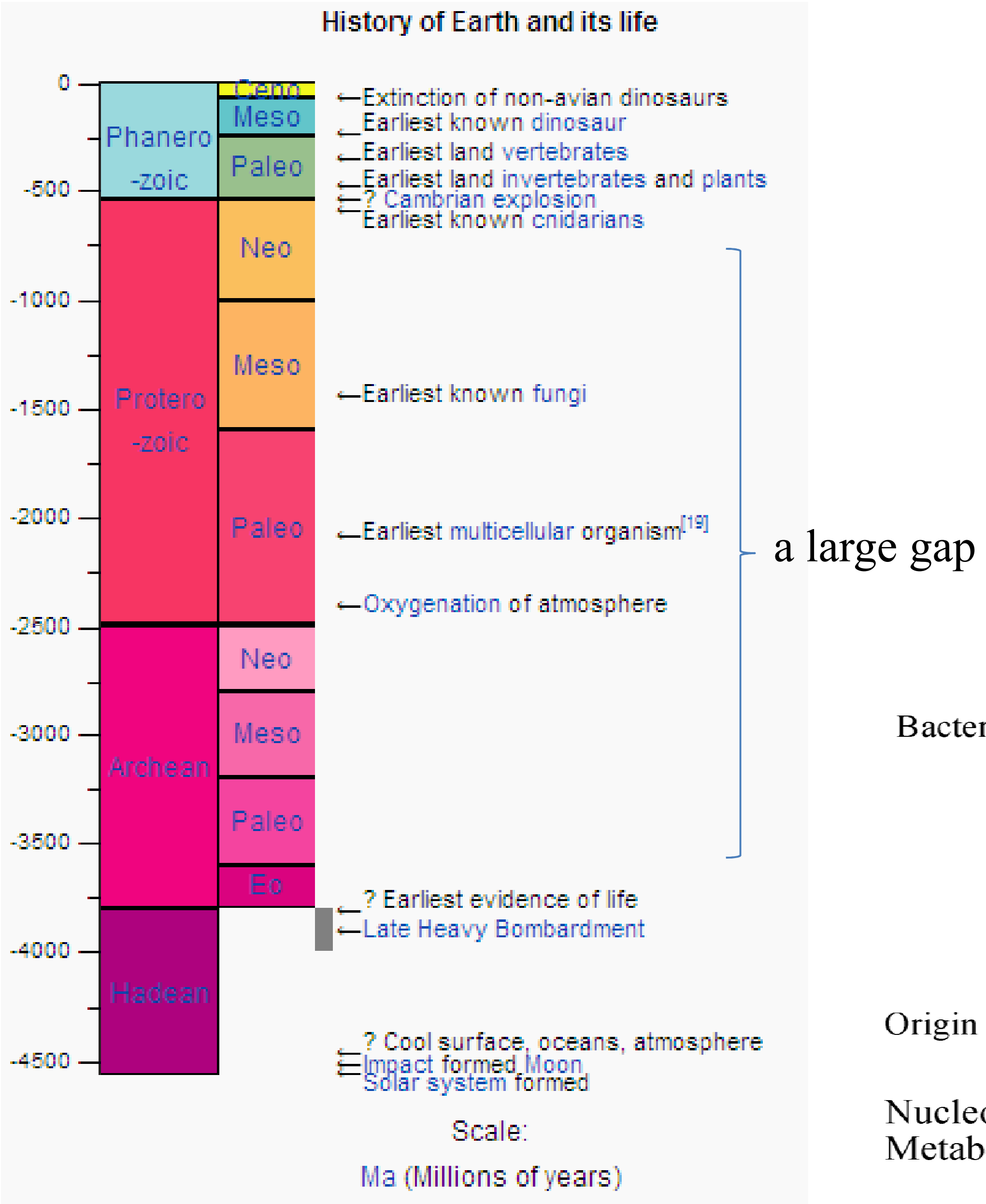
Evolution of eukaryotes (general concept?)
http://en.wikipedia.org/wiki/Eukaryote

Eukaryotes are closely related to archaea, at least in terms of nuclear DNA and genetic machinery. In other respects, such as membrane composition, they are similar to eubacteria. Three main explanations for this have been proposed:

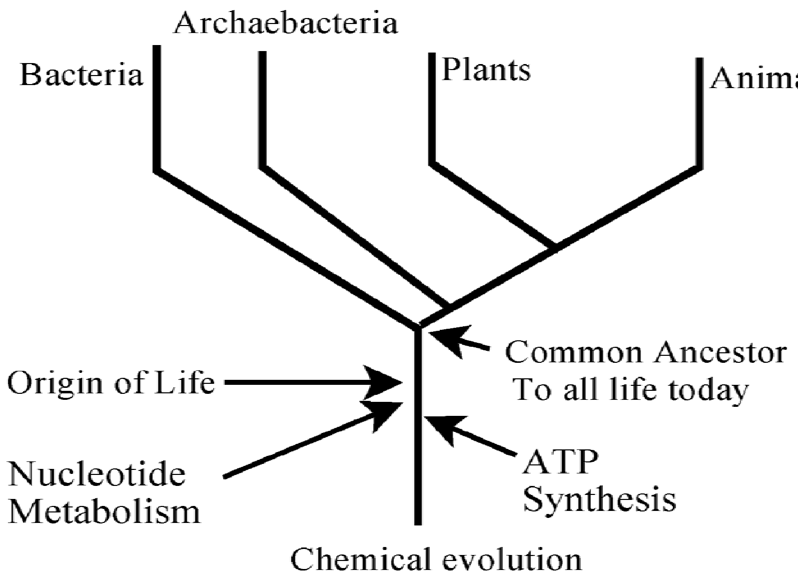
- Eukaryotes resulted from the complete fusion of two or more cells, the cytoplasm forming from a eubacterium and the nucleus from an archaeon (alternatively a virus).

- Eukaryotes developed from Archaea, and acquired their eubacterial characteristics from the proto-mitochondrion.

- Eukaryotes and Archaea developed separately from a modified eubacterium.



http://en.wikipedia.org/wiki/Evolutionary_history_of_life



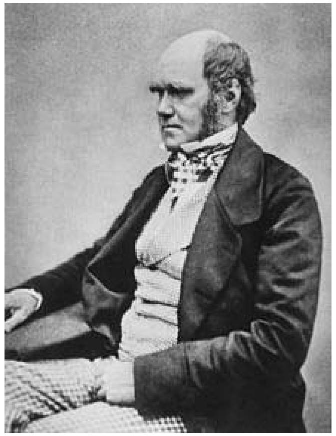
LUCA: the *last universal common ancestor*

Lamarck

1744-1829

heritability of acquired characteristics

Darwin



1809-1882

Mendel

1822-1884

Mendelian inheritance

Darwinism: evolution
by natural selection

Neo-Darwinism (modern evolutionary synthesis):
contemporary view of evolution

Gradualism: a gradual process of small random variation occurring in complex organisms
Punctuated equilibrium: a pattern of evolution where most speciation occurs relatively rapidly from a geological perspective through neo-Darwinian evolution
Saltation: speciation as a result of large mutation, early in the evolution of life

Microevolution: refers to smaller evolutionary changes (typically described as changes in allele frequencies) within a species or population
Macroevolution: "hopeful monster" theory
evolution on a scale of separated gene pools

Chap 1. Hopeful Monster (the first eukaryote)

The origin of the eukaryotic cell

The appearance of a chimeric cell containing mito

Only once, in spite of engulfing another is commonplace

What was so special?

The origin of life on earth

4 billion years ago by the estimates of molecular clock

The origin of eukaryote on earth

2.7 billion years ago by the presence of steranes (from wiki)

Late 1970s

finding of archaebacteria

living in excessively hostile conditions, like thermal vents

Evolution by the chance (of contingency) Stephen Jay Gould

vs

the necessity (of convergence) Conway Morris

convergence outweighs contingency (necessity overcomes chance)

life will keep converging on the best solutions

flight evolved independently no less than four times

Why is there a big temporal gap between the evolution of bacteria & eukaryote? → Chance rather than necessity?

What brake on evolution? (what was a chance event?)

- evolutionary flamboyance evolved in the last 600 million years
- primitive eukaryotic cells dates back to >3600 million years

Evolution of large multicellular creatures

- multicellular colony & multicellular organism
- cellular differentiation
- however, multicellular cooperation may not have been an obstacle

The evolution of eukaryotic cell

- evolved only once
- far more improbable than the evolution of multicelluar organism
- all eukaryotes either have, or once had, mito,
  - meaning the importance of mito in the evolution

***The birth of the nucleus: Science Aug 6, 2004

Part 1. The Deepest Evolutionary Chasm: The origin of eukaryotes

Bacterial colonies to true multicellular organisms
Lack of time or opportunity?

Two hypothesis

1. Bottleneck thesis: Christian de Duve
    - populations of proto-eukaryotes
    - adaptation & expansion of the fittest under the selection pressure

However, competition (bottleneck) does not mean complete disappearance of the others
- there always a niche to survive
- example: birds & bats
    - methanogen & sulphate reducing bacteria, both competing for scarce H_2

2. A hopeful monster: Goldschmidt
    - micromutations
    - macromutations: not a succession of micromutations
        - speciation (?) to a hopeful monster through fusion of two whole genomes

Differences between bacteria & eukaryotes

Evolutionary root of eukaryotic cell structures

- bacteria barely changed in 4 billion yrs,
  - while eukaryotic cells showed complicated evolution
- two hypothesis
  - mergers between a variety of bacterial cells: Lynn Margulis
  - based on the features from within the group

Two theories of eukaryotic cell evolution

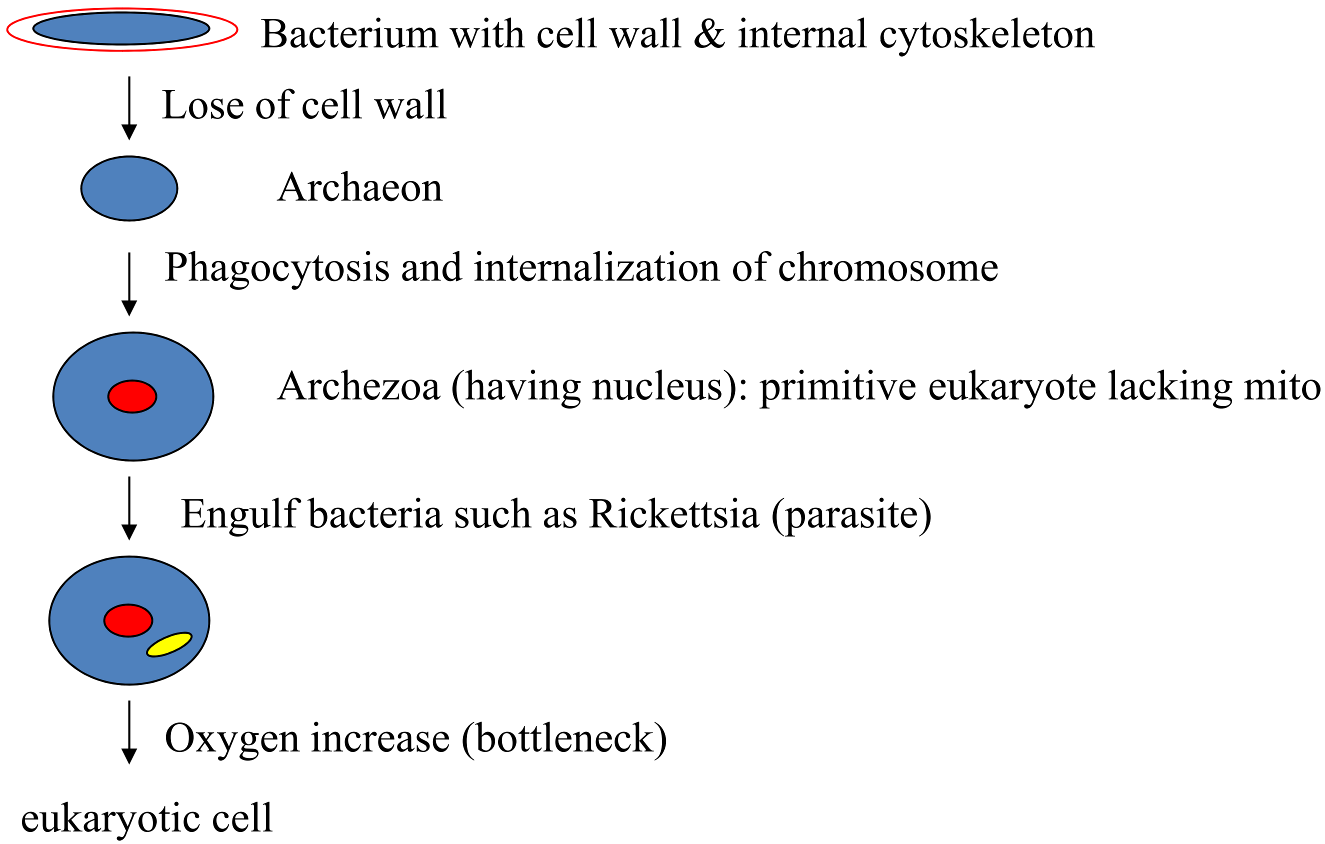
- Mainstream view (endosymbiotic or phagotrophic): Tom cavalier-Smith
  - nucleus first
  - morphological background
  - gradual transformation
- Hydrogen hypothesis (syntrophic): Bill Martin
  - mito first
  - biochemical background
  - nongradual transformation

Part 2. Quest for a progenitor: evolution of bacteria to eukaryote

Mainstream view (endosymbiotic theory)

a bacteria gradually transformed into a primitive eukaryotic cell

A scenario (p78)



Evidences

1. Catastrophic loss of the cell wall: a possible event & advantage
   Survival & subversion of the order of things

   Some bacteria having a cytoskeleton as well as a cell wall
   Some groups of archaebacteria don’t have cell wall
   All eukaryotes don’t have cell wall

cocci (spherical): default bacterial shape

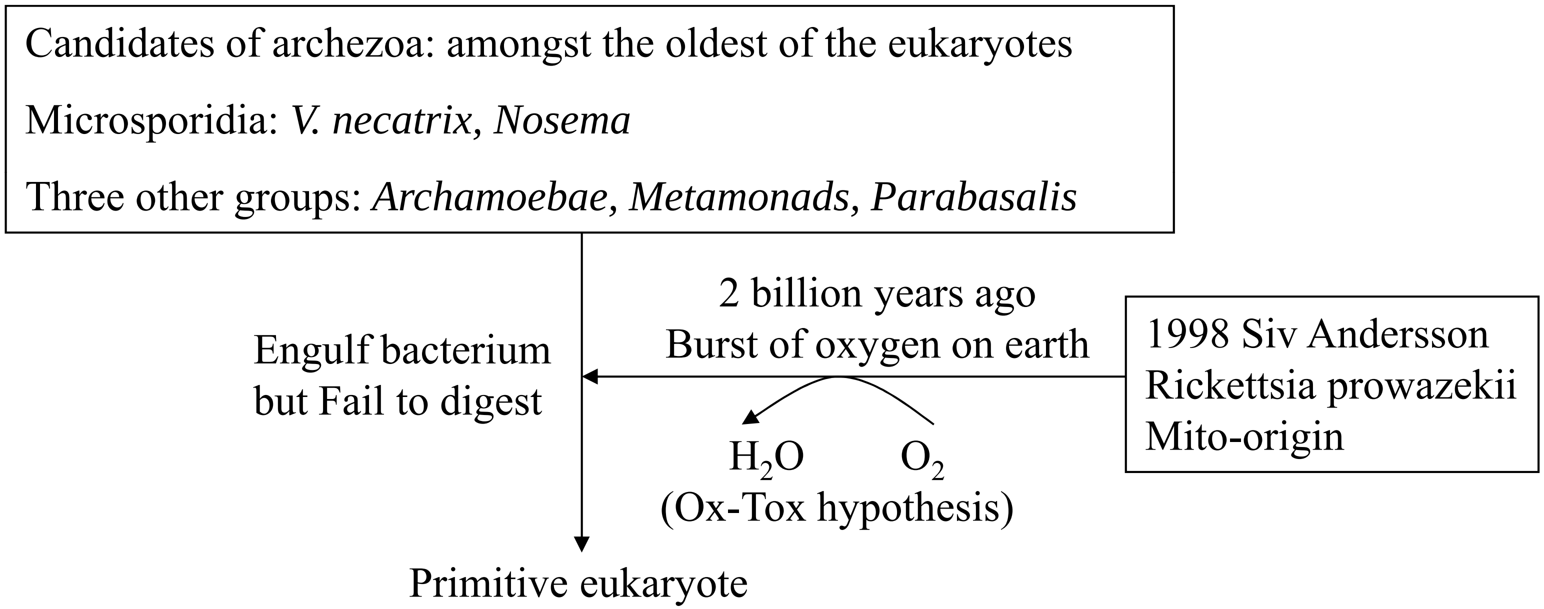
↑ Delete the encoding gene

bacilli (rod): require internal support (actin filament)

2. The archezoa: eukaryotes without mito

Some of the single celled eukaryotes resemble the earliest eukaryotes
>1000 species of the primitive eukaryotes have no mito
A few of them are primitive amitochondriate
thriving today by fermentation in low or absence of oxygen

Postulation of archaezoa, which never had mito
nucleus, dynamic cytoskeleton, phagocytosis



Reversal of a paradigm to "Mainstream view"

1. Genome sequence of archezoa
   - Entamoeba histolytica (a postulated progenitor of eukaryotic cells)
   - Less older than other which has mito

2. Evidence of mito trace in Entamoeba
   - mito gene transfer to nuclear genome
   - some oval organelle (might be remains of mito)
   - more evidence in other archezoa (Giardia)

3. Microsporidia
   - more close to the higher fungi

   Any remaining possibility to find real archaezoa?

4. Bioinformatics analysis of eukaryotic genes

Methanogens as mito origin

1. Maria Rivera in 1998 & 2004

    Comparative genome analysis of the organisms from the three domains of life

    Two distinct classses of genes in eukaryotes

        informational: from methanogens
        operational: from α-proteobacteria

2. John Reeve

    the structure of eukaryotic histones is related to methanogen histones
    the 3D structure of DNA-protein package is also similar

A hopeful monster (the first eukaryotic cell)
a merger between a methanogen and an α-proteobacteria

Hydrogen hypothesis

A symbiosis between

Methanogen and α-proteobacteria (ex. a parasite like Rickettsia)

Methanogen can tolerate the presence of oxygen

but can't generate any energy in its presence

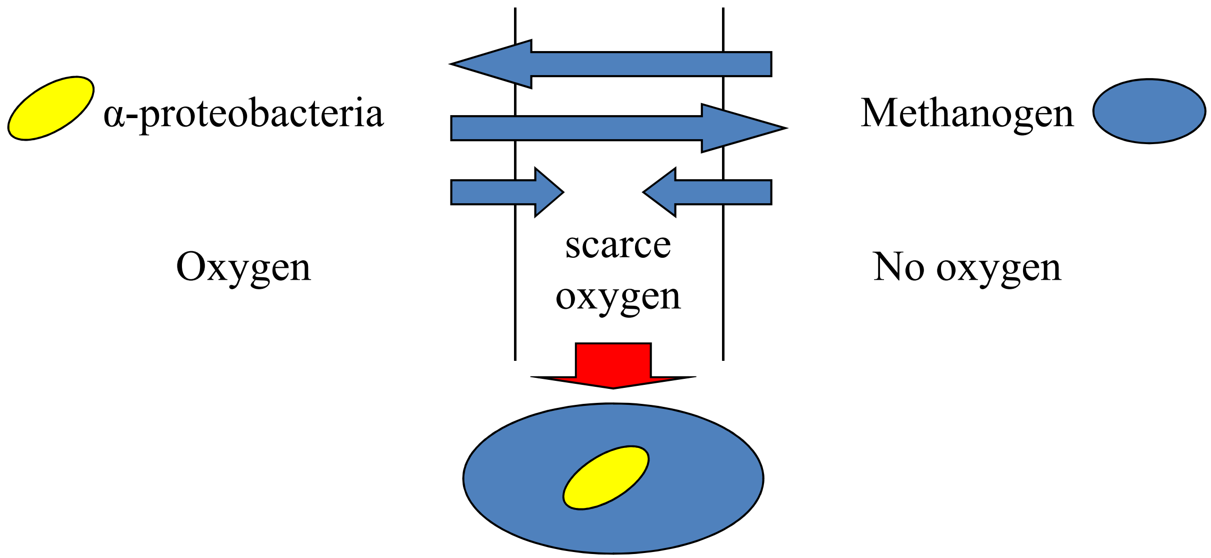
because they depend on hydrogen for fuel

Methanogen: oxygen hater

α-proteobacteria: oxygen lover

A paradox

How to jump the deep chasm?



Part 3. Hydrogen hypothesis

1998 Bill Martin & Miklós Müller
Hydrogenosomes mostly among primitive single celled eukaryotes
- mitochondria like
- energy production by releasing hydrogen gas

Also found were a number of tiny methanogens in them (Fig. 3)
Maintenance of a kind of metabolic wedlock in the absence of O_2
- methanogen: energy & organic compounds from CO_2 and H_2
- hydrogenosomes: release H_2 and CO_2

Anaerobic mitochondria in many single-celled eukaryotes

aerobic mitochondria, anaerobic mitochondria, hydrogenosomes

A common ancestor?
Hydrogenosome: An anaerobic mitochondrion that produces hydrogen

Possible candidates of a common ancestor

sophisticated bacteria: devolved

simple O_2-respiring bacteria (such as Rickettsia): evolved

Yet unproved, but several studies favoring a single origin for a few genes

in the anaerobic mitochondria and hydrogenosomes

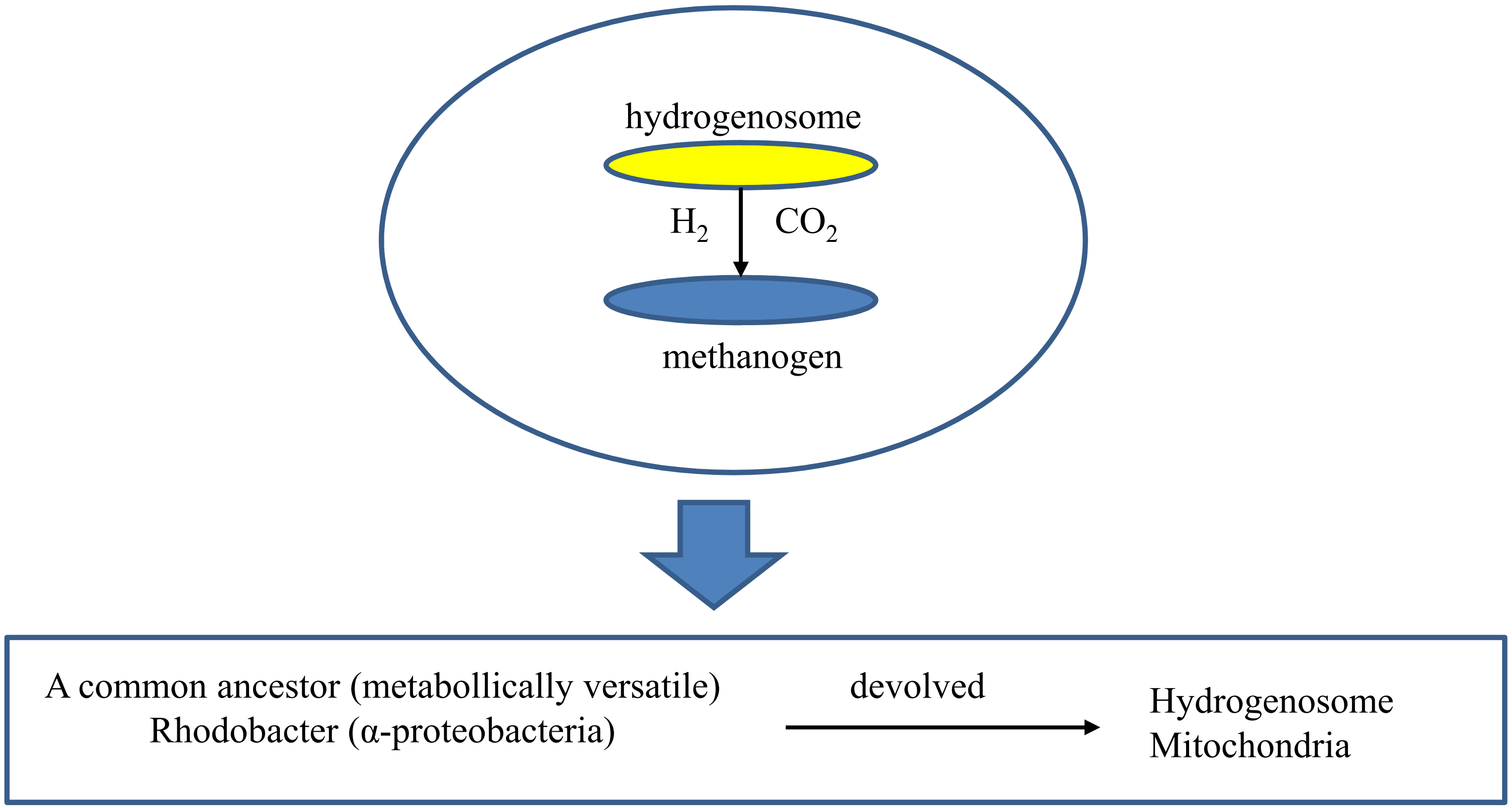
PFOR, ATP transporter, respiratory iron-sulfur protein

A metabolically versatile ancestor: Rhodobacter

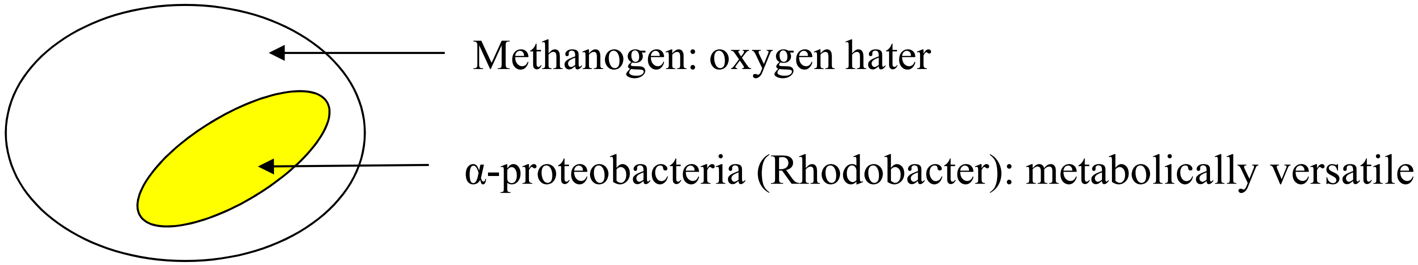
Why sequence similarity between mito and Rickettsia?

convergent evolution

Coexistence of hydrogenosome and methanogen in primitive single celled eukaryotes (anaerobic)



From addict to world-beater



How to gain entrance?
How to escape anaerobic environment?
How to keep oxygen-respiring genes in anaerobic environment?

What might have happened? (Fig. 4)

1. close metabolic relation between methanogen and α-proteobacteria
2. physical contact and engulfment
3. lateral gene transfer to methanogen from dead α-proteobacteria
4. birth of a ‘prototype’ eukaryote without a nucleus (anaerobic mito)
5. escape to aerobic conditions (aerobic mito) & invention of ATP pumps

Step 1: close metabolic relation between methanogen and α-proteobacteria

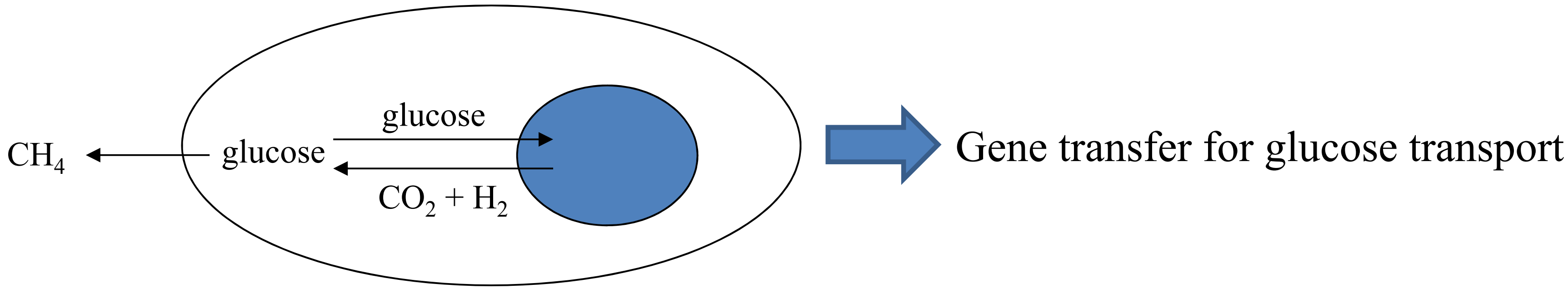
- methanogen: energy & organic compounds from CO_2 and H_2
- hydrogenosomes: release H_2 and CO_2
- evidence: described in the first slide

Step 2: physical contact and engulfment

- examples of bacteria living inside of others
- a predatory bacterium Bdellovibrio
- endosymbiont β-proteobacteria contain γ-proteobacteria inside

Step 3: lateral gene transfer to methanogen

- α-proteobacteria living inside of methanogen
- a problem of absorbing food
  - methanogen depends on H_2 and CO_2 from α-proteobacteria
  - α-proteobacteria depends on glucose (competition for glucose)
  - how methanogen absorbs glucose?



A scenario of lateral gene transfer

α-proteobacteria has all the genes for absorbing food
hand them over to the methanogen
however, methanogen uses glucose for biosynthesis

⬇

a competition for glucose between α-proteobacteria and methanogen

⬇

hand over more of its genes to methanogen

a population of cells: some thrive and some die
from loose relationship to closer relationship between methanogen and α-proteobacteria
more efficient transfer of H_2 to methanogen
suffocating free α-proteobacteria
more genes into environment
lateral gene transfer to methaogen
maintenance of α-proteobacteria as anaerobic mitochondria

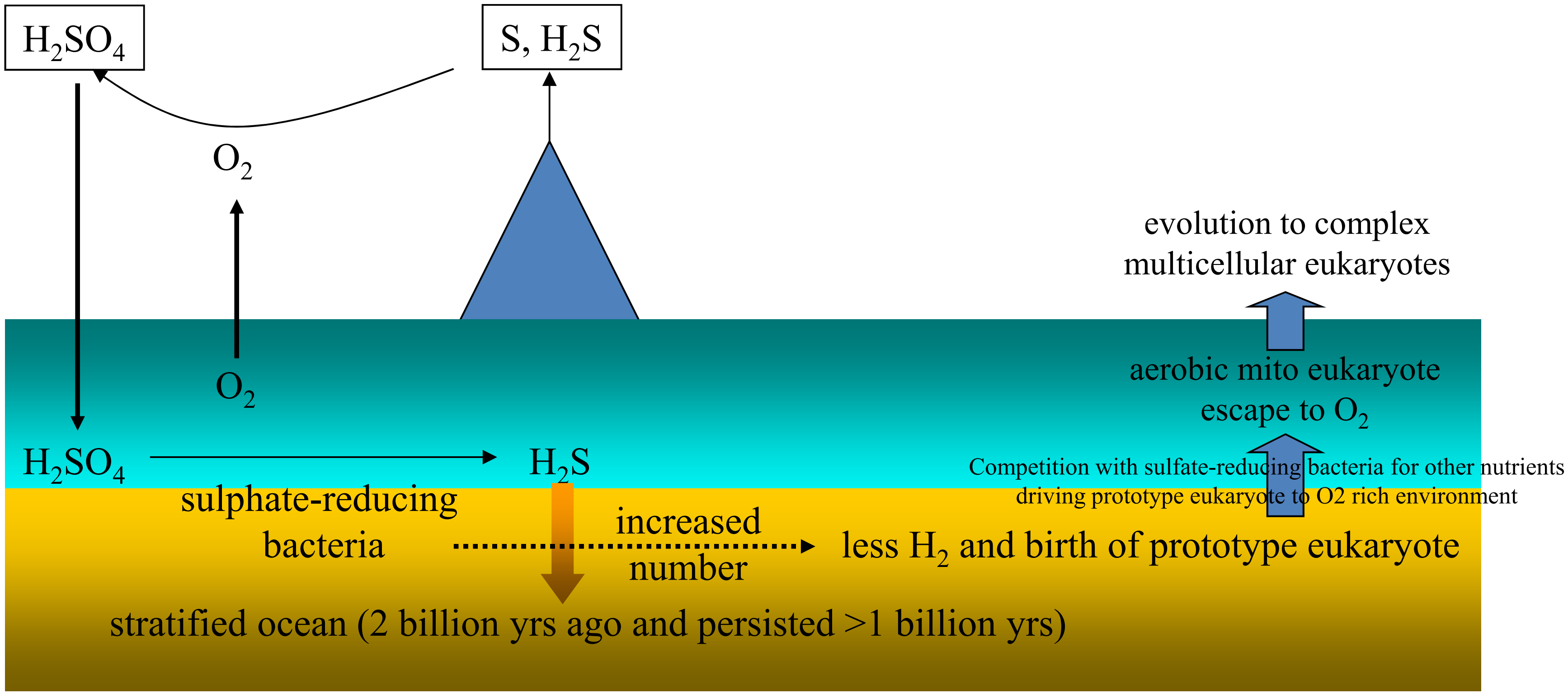
Step 4 & 5: birth of anaerobic 'prototype' eukaryote

adaptation to aerobic conditions & invention of ATP pumps

chance & necessity

under anaerobic conditions α-proteobacteria lose its gene for oxygen respiration

Changing chemistry of oceans: Ariel Anbar & Andrew Knoll (Science, 2002)

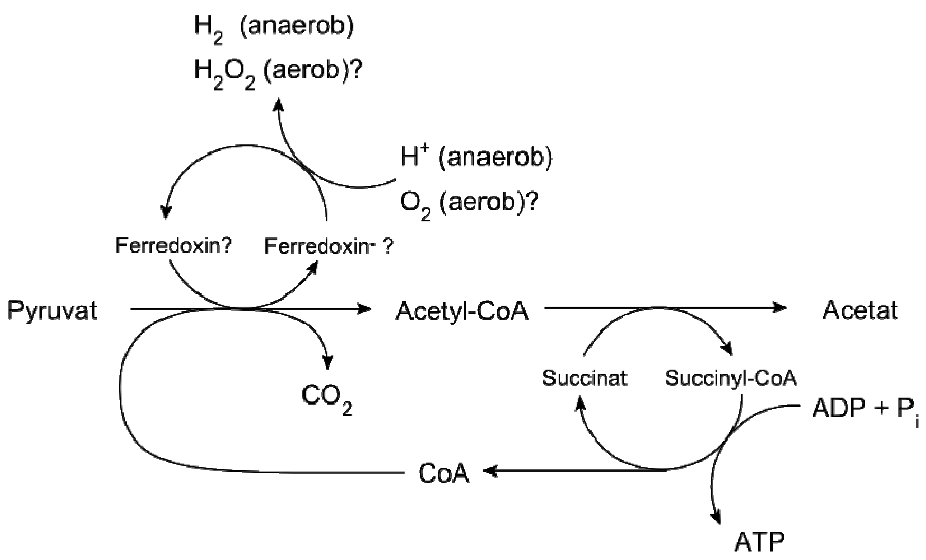


Hydrogenosomes are approximately 1 um in diameter and are so called because they produce H2.

Like mitochondria, they are bound by distinct double membranes and one has an inner membrane with some cristae-like projections.

A hydrogenosomal genome has been detected in Nyctotherus ovalis,and the stramenopile Blastocystis but not in Neocallimastix, Trichomonas vaginalis and Tritrichomonas foetus.

The similarity between Nyctotherus and Blastocystis, which are only distantly related, is believed to be the result of convergent evolution, and calls into question whether there is a clear-cut distinction between mitochondria, hydrogenosomes, and mitosomes (another kind of degenerate mitochondria).



The anaerobic ciliated protozoan Nyctotherus ovalis, found in the hindgut of several species of cockroach, has numerous hydrogenosomes that are intimately associated with endosymbiotic methane-producing archaea, the latter using the hydrogen produced by the hydrogenosomes. The matrix of N. ovalis hydrogenosomes contains ribosome-like particles of the same size as a numerous type of ribosome (70s) of the endosymbiotic methanogenic archaea. This suggested the presence of an organellar genome which was indeed discovered by Akhmanova .