3/12&14/03 The Oxygen Revolution and Evolution of Eukaryotic Cells

The RNA World

Sterile Earth

Prebiotic syntheses (proteins and RNA made abiotically)

RNA

Self-replicating RNAs

Early cellular life (RNA as coding and catalytic molecule)

Lipoprotein vesicle

Proteins assume catalytic functions (RNA only as coding molecule)

Evolution of DNA from RNA

Modern cellular life (DNA replaces RNA as coding molecule leading to DNA → RNA → Protein)
Major landmarks in biological evolution. The positions of the stages on the time scale are approximate. Note that for the bulk of Earth’s history, only microbial forms existed.
<table>
<thead>
<tr>
<th>Era</th>
<th>Period</th>
<th>Myr</th>
<th>Major events/radiations</th>
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<tr>
<td>CENOZOIC</td>
<td>Quaternary</td>
<td>1.8</td>
<td>Flowering plants</td>
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<td>Tertiary</td>
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<td>MESOZOIC</td>
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<td>Jurassic</td>
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<td>PALAEOZOIC</td>
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<td>Devonian</td>
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<td>(365) Tetrapods</td>
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<td>Silurian</td>
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<td>(428) Cooksonia</td>
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<td>Ordovician</td>
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<td>(458) First land plants</td>
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<td>Cambrian</td>
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<td>(Sub-eras)</td>
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<td>Late Proterozoic</td>
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<td>(575-543) Ediacarans</td>
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<td>(610) Oldest radially symmetric impressions (animals)</td>
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<td>(750) Green algae</td>
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<td>Middle Proterozoic</td>
<td>1,600</td>
<td>(1,000-900) Multicellular algae radiation</td>
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<td>(1,200) Multicellular red algae</td>
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<td>Early Proterozoic</td>
<td>2,500</td>
<td>(1,900-1,700) Earliest eukaryotes</td>
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<td></td>
<td></td>
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<td>(2,000) Cyanobacteria</td>
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<td>ARCHAEAEN</td>
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<td>(2,750) Cyanobacteria-like filaments,biomarkers</td>
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<td>(3,500) Earliest microfossils</td>
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The Phanerozoic Eon

Paleozoic Era

550 M.y.a. 505 439 360 367 290 251 240


Cambrian Pikaia Fish Fish First First Reptiles
Explosion w/o with Amphibians Reptiles
jaws jaws

Mesozoic Era

240 208 205 180 150 138 65

Triassic Jurassic Cretaceous

First First First T. rex
Dinosaurs Mammals Birds

Cenozoic Era

65 54 38 25 5 1.65 0.01


Early First First Modern
Primate Apes Hominids Humans

Cantius

All dates are in millions of years ago, M.y.a.
The arrival of the cyanobacteria (oxygenic prokaryotic photosynthesizers) marked a point of no return in the history of life.

It was one of the most central events in the development of life on earth.

The relationship between changes in atmospheric oxygen and some of the major steps that occurred during the evolution of living organisms. Geological evidence suggests that there was a billion year delay between the rise of cyanobacteria (thought to be the first organism to release O\textsubscript{2}) and the time that O\textsubscript{2} levels began to accumulate in the atmosphere. This delay was probably due to the rich supply of ferrous iron in the oceans, which reacted with the released O\textsubscript{2} to form enormous iron deposits.
**Oxygen: the Great Destroyer**

- After all, these organisms had evolved under anaerobic conditions
- Oxygen was intensely toxic to all life forms existing at the time
- DNA is particularly sensitive to oxidative attack
- Other macromolecules (proteins, lipids, RNA are also sensitive)
- $O_2$ produces highly reactive compounds (such as $O_2^-$) that damage biological macromolecules (by oxidizing them) -- so increasing levels generated intense global stress
- Many organisms were immediately wiped out because of the oxygen toxicity

**WHAT SORT OF STRATEGIES Could be USED TO SURVIVE IN THIS ENVIRONMENT?**

**Plan A: DETOXIFICATION AND EXPLOITATION**

- In one of the greatest coups of all time the cyanobacteria invented a metabolic system that required the very substance that had been a deadly poison: aerobic metabolism -- in other words that microcosm adapted

First primitive heterotroph used **ANAEROBIC FERMENTATION** to digest these compounds and derive energy

Glucose $\rightarrow$ ethyl alcohol + $CO_2$ + $H_2O$ + 2 ATP

Increase in oxygen in the atmosphere allowed the evolution of cells that respired aerobically

AEROBIC RESPIRATION
Glucose + $O_2$ $\rightarrow$ $CO_2$ + $H_2O$ + 34 ATP
Plan B: Detoxification

For the chemists: (about reactive oxygen species)
http://users.rcn.com/jkimball.ma.ultranet/BiologyPages/R/ROS.html

Some Reactive Oxygen Species:
O$_2^-$ Superoxide
Hydroxyl radical (OH with unpaired electron)

- the increase in atmospheric oxygen was slow at first and allowed a gradual evolution of protective devices
- The organisms that survived the exposure to O$_2$ evolved mechanisms to protect themselves from the toxic effects of O$_2$ (or learned to hide from it)

Enzymatic defenses: superoxide dismutase (SOD)
O$_2^-$ + O$_2^-$ + 2H+ -----> H$_2$O$_2$ + O$_2$
(superoxide)
(Hydrogen peroxide is metabolized by another enzyme)

Non-enzymatic defenses: compounds (vitamin C, vitamin E and others) that act as antioxidants to neutralize the highly reactive compounds produced by O$_2$ in biological tissues
Other implications of the rising levels of atmospheric O$_2$

Before the ozone layer developed, photosynthetic organisms probably protected themselves from UV by seeking filters such as

(i) developing pigments that absorbed harmful wavelengths
(ii) seeped under sand or other substances that filtered out UV light
(iii) evolved mechanisms to repair DNA damage that are still present in modern-day organisms
Eukaryotic cells evolved about 2(?) billion years ago

A late major development in the history of Precambrian life was the origin of the nucleated eukaryotic cell

How did the structurally complex eukaryotic cell arise from the structurally simple prokaryotic cell?

Two phases or eras of eukaryotic cell evolution
1. pre-endosymbiont era (between 3.5 and 1.5 billion years ago
2. post-endosymbiont era (from 1.5 bya to present)
Phase I: Pre-endosymbiont era:

- Larger, nucleated cell must have arisen first -- followed by endosymbiosis
- Cell wall must be lost-- some ancestral prokaryote lost ability to make the cell wall
- Cell enlarged- wall-less cell could invaginate its membranes and increase surface area for exchange
- Cytoskeleton acquired (no clues to the origin)
- Infoldings of the plasma membrane of the ancestral prokaryotic cell could have generated: nuclear envelope endoplasmic reticulum and golgi apparatus
Phase 2: A fateful meal

Endosymbiosis explanation for the origin of mitochondria and chloroplasts

**symbiosis**: an ecological relationship between organisms or two or more different species that live in direct contact

**endosymbiosis**: intracellular symbiosis

The endosymbiotic hypothesis of eukaryotic cell evolution proposes that mitochondria and chloroplasts evolved from symbiotic associations of smaller prokaryotic cells living inside larger nucleated cells (capable only of fermentation)

**Mitochondria**: intracellular organelle that allows the cell to carry out aerobic respiration is the evolutionary descendant of a free-living aerobic bacterium that became incorporated in a host cells early in the lineage of eukaryotes

ancestor of mitochondria: α proteobacteria (aerobic respiration)
Similarly, the chloroplast: intracellular organelle where photosynthesis takes place is derived from a free-living cyanobacterial ancestor that combined with a eukaryotic cell ancestor of chloroplasts: cyanobacteria capable of photosynthesis and respiration (chloroplasts later lost ability to respire)
A simplified diagram of the evolution of plants and animals, showing the two bacterial uptake events that established mitochondria and chloroplasts
How did these cellular precursors to mitochondria and chloroplasts come to reside inside a larger cell?

*phagocytosis (cellular eating)*:
- ingestion of large particles (such as microorganisms and cellular debris) (>250nm in diameter)
- in present-day multicellular organisms performed only by specialized cells
- common in present-day protozoa, where it is a form of feeding

Phagocytosis by a neutrophil (a type of white blood cell)

Optional aside: phagocytes use burst of oxygen to kill microbes: [http://www.cellsalive.com/mac.htm](http://www.cellsalive.com/mac.htm)

**Interesting Stuff (from above web site):**
Macrophages and neutrophils must generate ROS (reactive oxygen species) in order to kill some types of bacteria that they engulf by phagocytosis.
What is the evidence for the theory?
1. What is the evidence that mitochondria and chloroplasts were once free-living cells?
2. What is the evidence that mitochondria and chloroplasts are related to prokaryotic cells?
3. What is the evidence for ancient engulfment events where a large nucleated cell engulfs a smaller prokaryotic cell?

What is the evidence that mitochondria and chloroplasts were once free-living cells?

(i) A symbiont originated as a free-living cell and therefore must have once been able to replicate its own DNA and make its own proteins--
- these organelles have their own genetic material
- have protein-synthesizing systems-- ribosomes, mRNA, tRNA etc. that produce proteins that participate in respiration or photosynthesis
- the organellar DNA and protein synthesizing system is still functional today
What is the evidence that mitochondria and chloroplasts are related to prokaryotic cells?

Molecular and biochemical characteristics of these organelle's protein synthesizing systems closely resemble those of bacteria and are quite distinct from the main system in the cell

• DNA in these organelles is a single piece of circular as is found in prokaryotes
• ribosomes in eukaryotes and prokaryotes differ in size: all cytoplasmic eukaryotic ribosomes are of a single size which is larger than a prokaryotic ribosome
• mitochondrial and chloroplast ribosomes are the same size as prokaryotic ribosomes
• antibiotics such as streptomycin that inhibit bacterial protein synthesis, also inhibit protein synthesis in mt and cp’s
• rRNA found in ribosomes: DNA sequence of the rRNA genes is very similar to that of bacteria and different from that of the eukaryotic cytoplasmic ribosomes
• Genome era sequence data: mitochondrial DNA sequences are much more closely related to the genomic sequences of α proteobacteria than to the nuclear DNA of the cell
What is the evidence for ancient engulfment events where a large nucleated cell engulfs a smaller prokaryotic cell?

1. double membraned structure of mt and cp organelles may reflect an ancient engulfment event

2. Non-compelling indirect evidence:
   • if a cellular organelle is acquired by symbiosis, there should be no organism containing intermediate intracellular stages of the organelle
   • the entire series of metabolic capabilities conferred on the host by the symbiont must be acquired together as a package

Is there any evidence for a missing link in the transition between eukaryotic and prokaryotic cells?

Are there any extant organisms that would provide support for the idea that the first eukaryote was anaerobic?

Previous research pointed to Giardia lamblia
   • a single-celled intestinal parasite
   • causes severe intestinal infections
   • obligate anaerobic eukaryote since it lacks mitochondria
   • Giardia engulfs extracellular objects by phagocytosis
   • Giardia was thought to have branched off from the main eukaryotic line more than 2 billion years ago before oxygen started appearing in the earth atmosphere

NOW KNOWN to be a degenerate eukaryotic form not an ancestral form

§ Present day giant ameoba Pelomyxa, which lives in mud ponds: lacks mitochondria

§ However this ameoba has a symbiotic relationship with two types of bacteria that provide the same function as a mitochondria