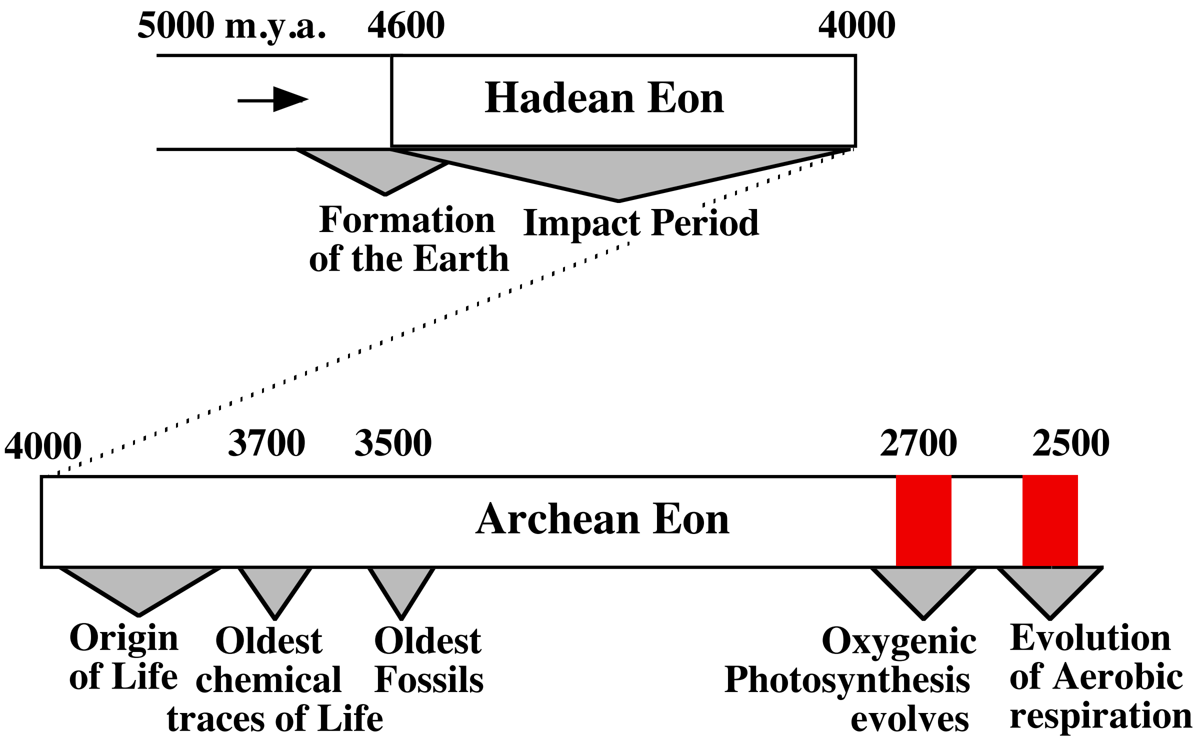
Alles Introductory Biology Lectures
An Introduction to Science and Biology for Non-Majors

Instructor David L. Alles
Western Washington University

Part Three: The Integration of Biological Knowledge

Life and Energy


5000 m.y.a.
4600
4000
Hadean Eon
Formation of the Earth
Impact Period
4000
3700
3500
2700
2500
Archean Eon
Origin of Life
Oldest chemical traces of Life
Oldest Fossils
Oxygenic Photosynthesis evolves
Evolution of Aerobic respiration

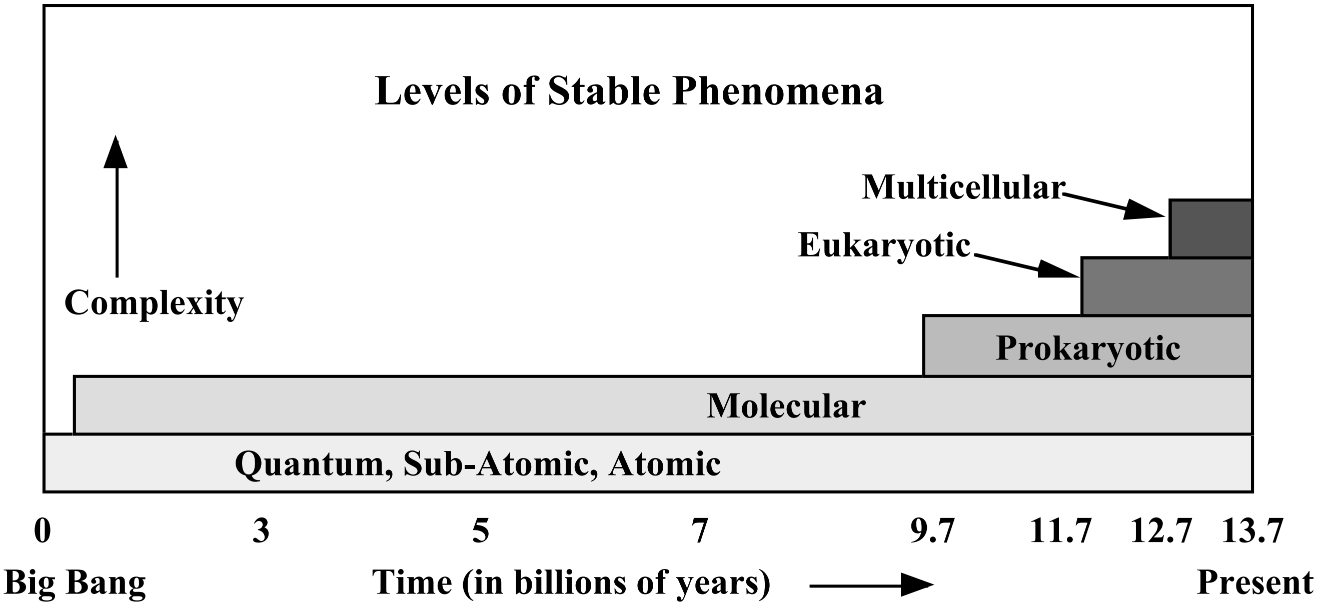
Life and the Exploitation of Energy

What has driven evolutionary change in the history of life? One answer is that life has evolved toward ever more complex ways of acquiring energy. This is by no means the only driving force behind evolution, environmental change is fundamentally important. But to understand life on Earth, we must understand something of the chemistry of life's energy.

Terms and Definitions to Know

• Eubacteria	**• Archaebacteria**
• Heterotrophs	**• Autotrophs**
• Photoautotrophs	**• Chemoautotrophs**
• Aerobic	**• Anaerobic**
• Photosynthetic Bacteria	**• Stromatolites**
• Oxygenic Photosynthesis	**• Anoxygenic Photosynthesis**
• Cyanobacteria	**• Purple & Green Sulfur Bacteria**

(Note: Eubacteria and Archaebacteria are now commonly refer to simply as Bacteria and Archaea. They are classified as Domains, a larger, more fundamental taxonomic unit than Kingdoms.)



The Prokaryotic Level (origin ~ 4000 million years ago)

1) Scale in size—one millionth of human scale or 1 x 10 $^{-6}$ meter

2) Self Organization—organization of complex macro-molecules into a self-reproducing unit—the cell

3) Emergent Properties & Processes—**the origin of life**—Domains Bacteria & Archaea; natural selection; speciation; self-reproduction by binary fission; anaerobic and aerobic respiration; photosynthesis

Web References
http://microbewiki.kenyon.edu/index.php/Microbial_Biorealm

***Escherichia coli*, Domain Bacteria**

(Photograph by Dennis Kunkel courtesy of Microbeworld)

Web Reference
http://www.genome.wisc.edu/

***Halobacterium salinarum*, Domain Archaea**

The complete genomes of both *E. coli* and *H. salinarum* have been sequenced.

(Photograph courtesy of Microbial Biorealm, Kenyon College)

Web References
http://microbewiki.kenyon.edu/index.php/Halobacterium

http://www.pnas.org/cgi/reprint/97/22/12176.pdf

The sharp line across the center of this satellite image of Great Salt Lake, Utah, is caused by the restriction of water flow caused by a railroad causeway. The colors of the lake result because the lake is hypersaline, typically 3-5 times saltier than the ocean. North of the causeway salinities are higher, and the water turns purplish from the pigments of halophilic (salt loving) Archaea, such as *Halobacterium salinarum*. South of the causeway the greenish color is from photosynthetic Bacteria, such as cyanobacteria, and algae.

(May 31, 2001, MODIS/Terra image courtesy of NASA)

The Evolution of Photosynthesis

Photosynthesis exists in all the major taxonomic divisions of life. It occurs anywhere there's light energy, over a wide range of temperature, light and aeration conditions. Photoautotrophy occurs widely throughout the Eubacteria, and is an ancient trait. Fossil stromatolites in 3.5 billion year old rocks show that photoautotrophic prokaryotes evolved early in the history of life.

Photosynthesis is one of the most important biological processes on the planet. Besides producing almost all organic carbon on Earth, photosynthetic organisms completely transformed the planet to the way it is now. Early photosynthesis was anoxygenic (did not produce O_2 gas). When oxygenic photosynthesis evolved, our atmosphere as we know it was created, including the ozone layer which allowed life to evolve on land. (see also Leslie, 2009)

Anoxygenic Photosynthesis

- H_2S, or H_2, or organic compounds are used as hydrogen donors, and CO_2 and organic compounds as carbon donors
- Example organisms are purple and green sulfur bacteria.
- Purple sulfur bacteria use Photosystem II to make organic molecules.
- Green sulfur bacteria use the TCA cycle (Photosystem I) to make organic molecules.

Oxygenic Photosynthesis

- H_2O is used as the hydrogen donor, and CO_2 as carbon donor.
- Example organisms are cyanobacteria, algae, and plants.
- Oxygenic photosynthesis uses both Photosystem I & II, known as the Calvin-Benson cycle, to make organic molecules.

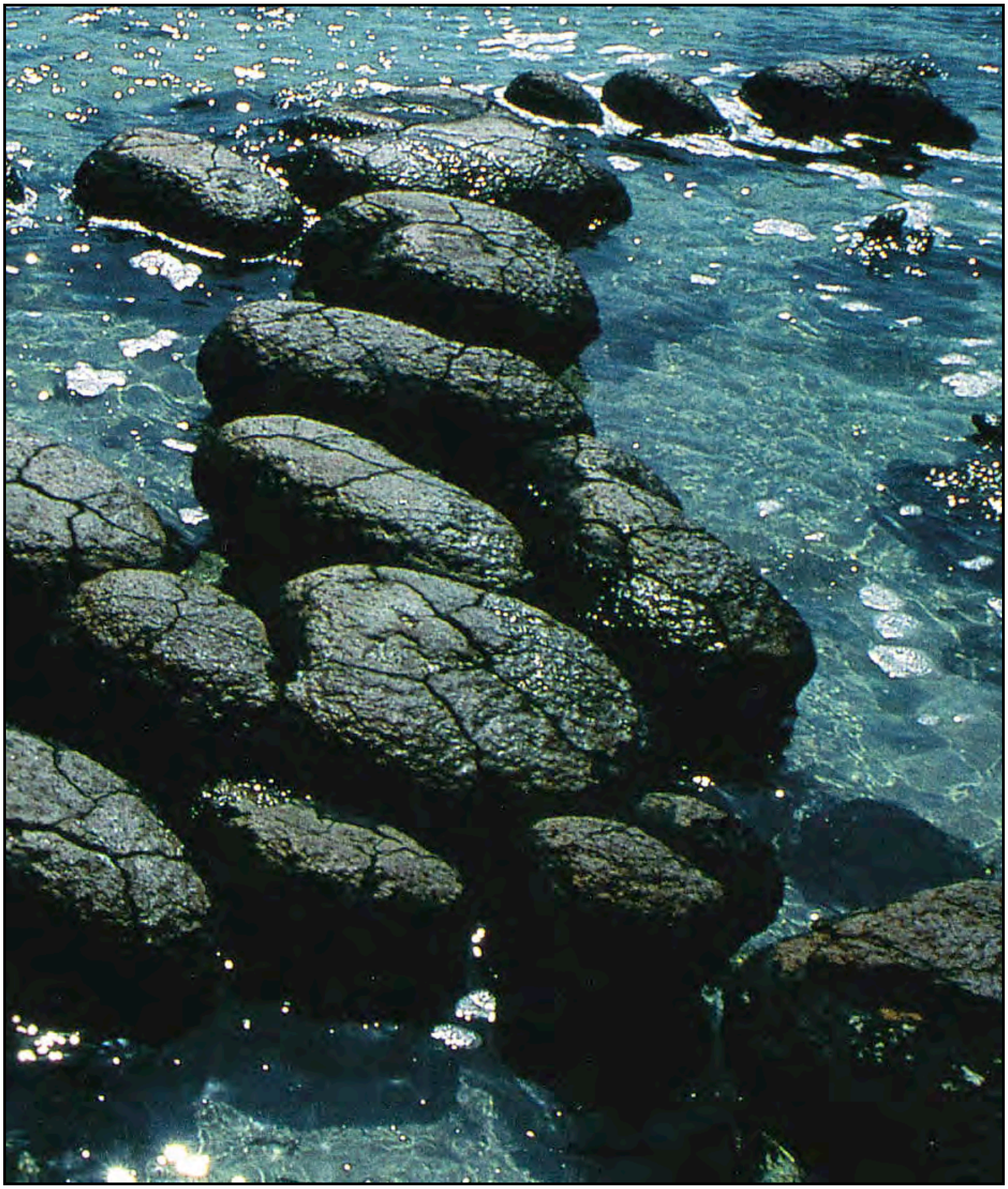
Purple and Green Sulfur Bacteria

Because of their unusual mechanisms for harvesting and using the energy of light, the purple and green sulfur bacteria are important in understanding the evolution and mechanisms of both photosynthesis and cellular energy metabolism. The ability to carry out photosynthesis in the absence of oxygen is particularly important to evolutionary studies because the early atmosphere of Earth had little oxygen. This is why scientists have suggested that the purple and green-sulfur bacteria were the first photosynthetic organisms. This has since been corroborated by genetic studies (Xiong, et al, 2000)

Green sulfur bacteria are widely distributed in aquatic environments where light reaches anoxic (low-oxygen) layers of water containing reduced sulfur compounds. When researchers analyzed the microbe's single circular chromosome, they identified numerous genes that play novel roles in photosynthesis or other processes that make use of the energy of light.

Green sulfur bacteria are also unique because their mechanism for capturing carbon dioxide differs from that of cyanobacteria and plants. The green sulfur bacteria use an unusual chemical cycle—called the reductive tricarboxylic acid (TCA) cycle—that differs from the Calvin Cycle that is used by cyanobacteria and plants. The TCA cycle uses hydrogen from hydrogen gas (H_2) or hydrogen sulfide (H_2S) to fix carbon dioxide; in contrast, the Calvin Cycle uses water (H_2O).

Archean Landscape Showing a Hydrothermal Spring and Stromatolites



Because of its high temperatures and salinity, stromatolites still flourish in Shark Bay, Australia, as they did throughout the globe 3500 million years ago. Taking up the top few inches, a velvety microbial mat grows in fine layers that include a crown of photosynthetic bacteria. There is a scientific consensus that stromatolites are the oldest macro-fossils of life (Simpson, 2003).

For more on Stromatolites go to:
http://fire.biol.wwu.edu/trent/alles/Stromatolites.pdf

Microbial mats, such as pictured above, are common in near shore aquatic habitats, and are similar to the mats that form stromatolites. Photosynthetic bacteria form the top layer with aerobic heterotrophic bacteria beneath them. Progressively as the layers move down, and further from oxygen in the air, they are formed by anaerobic bacteria.

(Photograph by Rolf Schauder)

Web Reference
http://user.uni-frankfurt.de/~schauder/mats/microbial_mats.html

Cyanobacteria and Oxygenic Photosynthesis

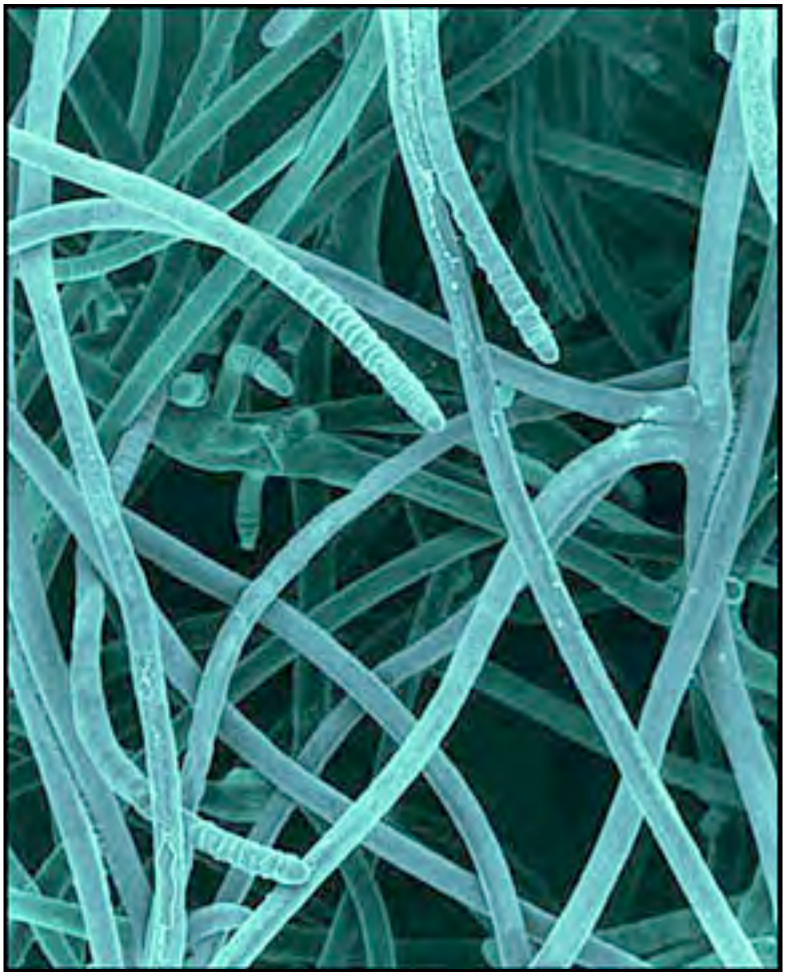
Carbon Hydrogen Oxygen

CO_2 H_20 $C_6H_{12}O_6$ O_2

Carbon dioxide and water plus sunlight produces carbohydrates and oxygen,
in the formula ratio of
six CO_2 + six H_2O —> plus energy —> one $C_6H_{12}O_6$ + six O_2

The problem with oxygenic photosynthesis is that

— oxygen gas is dangerously corrosive.



Cyanobacteria Growing in Long Filaments

(Photograph by Dennis Kunkel courtesy of Microbeworld)

The Oxygen Holocaust

"The oxygen holocaust was a worldwide pollution crisis that occurred about 2400 m.y.a.. Before this time there was almost no oxygen in the Earth's atmosphere. The Earth's original biosphere was as different from ours as that of an alien planet. But purple and green photosynthetic bacteria, frantic for hydrogen, discovered the ultimate resource, water, and its use led to the ultimate toxic waste, oxygen.

Our precious oxygen was originally a gaseous poison dumped into the environment. The appearance of oxygen-using photosynthesis and the resulting oxygen-rich environment tested the ingenuity of microbes, especially those producing oxygen and those non-mobile microorganisms unable to escape the newly abundant and reactive gas by means of motion. The microbes that stayed around responded by inventing various intracellular devices and scavengers to detoxify—and eventually exploit—the dangerous pollutant."—Margulis, 1986

The Great Oxygen Crisis 2700 to 2000 m.y.a.

Point 1 — It now seems clear that life could not have originated in the presence of oxygen.

Point 2 — Early life had to find a new source of energy as the early chemoautotrophs over-populated their ocean bottom world.

Point 3 — Early life had to adapt to the surface waters of the ocean to utilize sunlight as an energy source.

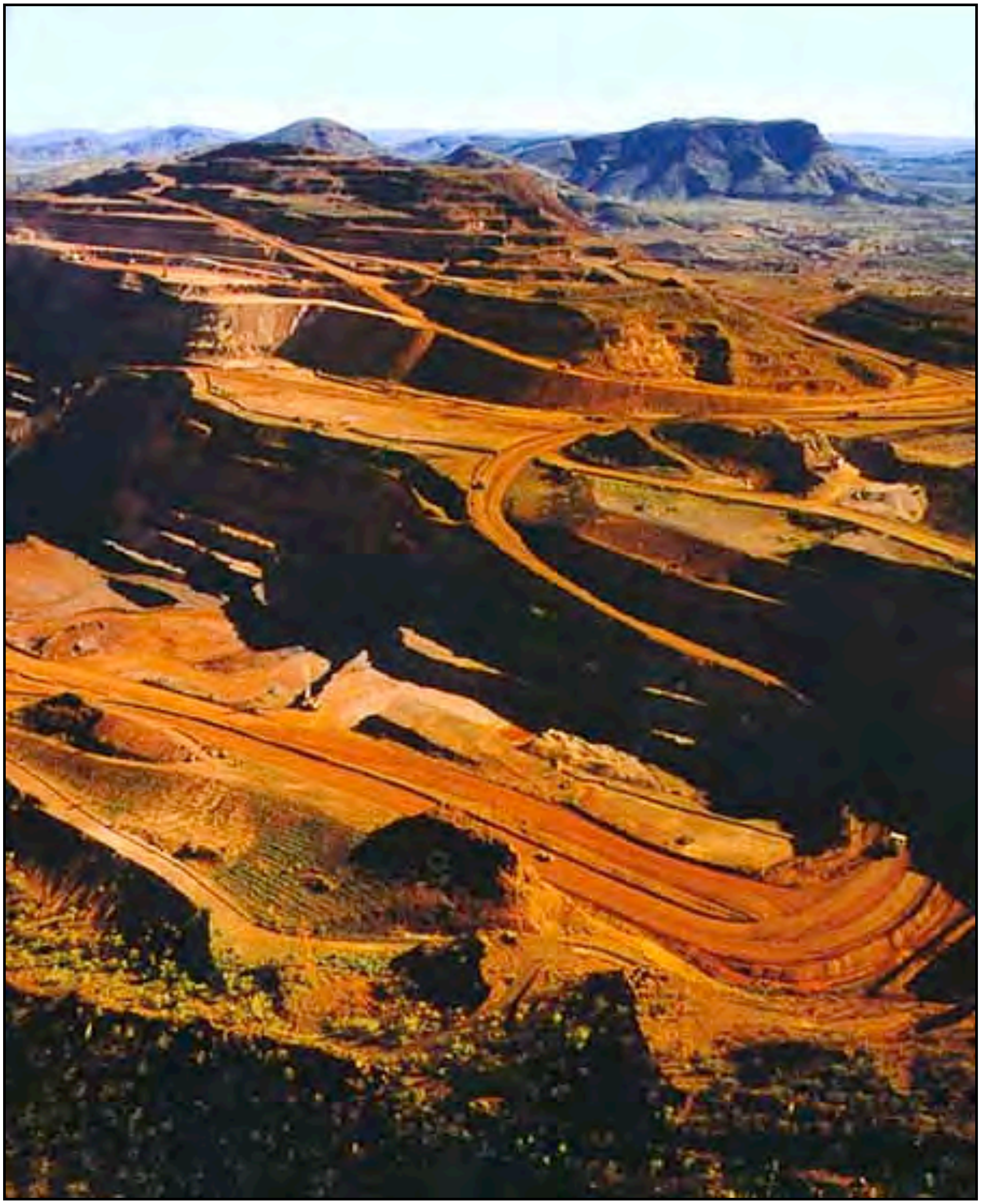
Point 4 — The first oxygenic photosynthetic bacteria had to neutralize the effects of the waste product of photosynthesis—oxygen.

To neutralize the effects of oxygen:

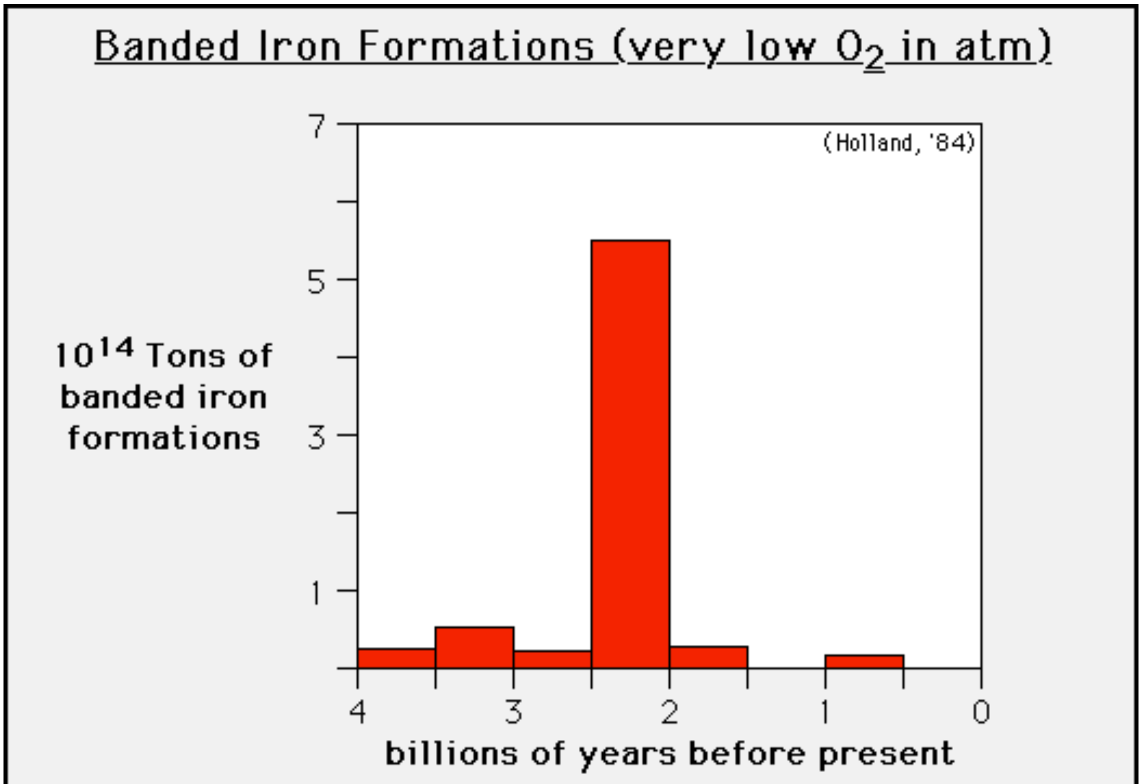
Plan A: have something get rid of the oxygen while you adapt to it.

Oxygen "sinks" and the Banded Iron Formations
Oxygen in the Sea 2700 to 2000 m.y.a.

Why did it take over a half billion years after the evolution of oxygenic photosynthesis for oxygen to begin accumulating in the atmosphere? One reason lies at the bottom of the ocean. Seawater once contained dissolved iron. When cyanobacteria took hold, the oxygen they generated reacted with the iron, which precipitated as rust onto the ocean floor. Over millions of years this created deep beds of banded rock. Shown above is a sample of Banded Iron Formation containing alternating bands of red jasper and black hematite.



The Hamersley iron resources, contained in Banded Iron Formations 2700 to 2400 million years in age, cover extensive areas of the Pilbara region of northwestern Australia.



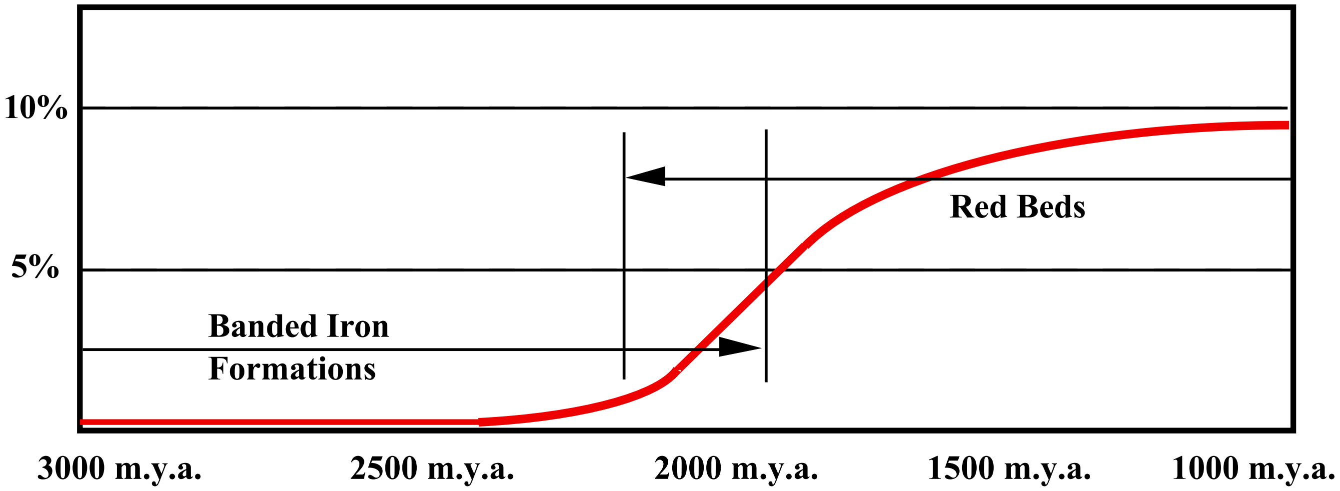
Very Large Fe Deposits

Continent	Area	Age (10^6 yrs)
Africa	Transvaal, S.A.	2100-2600
Australia	Hamersley Range	2400-2700
Eurasia	Krivoi Rog, Ukraine	1900-2600
North America	Labrador Trough, Canada	1900-2500
South America	Minas Gerais, Brazil	2000-2700

HJS/LP

In this chart, note that the predominate formation of Band Iron occurred between 2500 and 2000 m.y.a.. This is part of the evidence used to establish when oxygen first saturated the upper layers of the oceans and then began to build up in the atmosphere.

First Great Oxidation Event



The first rise of oxygen in the Earth's atmosphere began approximately 2400 m.y.a. and brought oxygen to about 10% of the atmosphere. It then stayed at this level for almost a billion years. The second great oxidation occurred approximately 700 to 600 m.y.a. and brought oxygen close to the current level of 20% of the atmosphere (Anbar & Knoll, 2002; Kerr, 2005).

Web Reference
http://www.astrobio.net/news/article541.html

Red Bed Iron Formations, such as these Permian sandstones from the desert southwest, are evidence of oxygen in the atmosphere from ~ 2200 m.y.a. to the present. A number of mineralogical and geochemical indicators of the oxidation state of the atmosphere suggest strongly that the level of O_2 rose dramatically about 2250 m.y.a.. Red beds and oxidized ancient soils call paleosols are among the most convincing of these indicators (Rye & Holland 1998).

The Missing Step

"The Proterozoic eon (2500 to 542 million years ago) marks the time between the largely anoxic world of the Archean (>2500 m.y.a.) and the dominantly oxic world of the Phanerozoic (<542 m.y.a.). The course of ocean chemistry through the Proterozoic has traditionally been explained by progressive oxygenation of the deep ocean in response to an increase in atmospheric oxygen around 2300 m.y.a.. This postulated rise in the oxygen content of the ocean is in turn thought to have led to the oxidation of dissolved iron, Fe(II), thus ending the deposition of banded iron formations (BIF) around 1800 m.y.a..

An alternative interpretation suggests that the increasing atmospheric oxygen levels enhanced sulphide weathering on land and the flux of sulphate to the oceans. This increased rates of sulphate reduction, resulting in Fe(II) removal in the form of pyrite as the oceans became sulphidic."—Poulton, S. W., et al., 2004

Plan B: evolve chemical defenses against oxygen.

Molecular Defenses against Oxidative Damage

A variety of molecular defenses in our cells prevent or repair molecular damage caused by free oxygen radicals.

• Antioxidants (macromolecules that neutralize free radicals or otherwise limit their activity)

• Vitamin E and beta carotene—react with free oxygen radicals preventing them from attacking cellular constituents; are fat soluble and so can protect membranes.

• Uric acid and Vitamin C—react with free oxygen radicals in the cytoplasm.

• Repair Systems (protein enzymes that degrade, repair or replace damaged molecules)

• Proteinases—cleave oxidized proteins.

• Peptidases—chop up products of protease activity; amino acids can then be recycled to make new proteins.

Point 5 — Meanwhile heterotrophic bacteria had two choices, retreat away from the growing oxygen environment, or also evolve adaptations to neutralize oxygen.

Point 6 — With oxygen present, heterotrophs could exploit a new way to extract energy from carbohydrates (the product of photosynthesis).

Oxygenic Photosynthesis

$6\ CO_2 + 6\ H_2O$ —> plus energy in —> $C_6H_{12}O_6 + 6\ O_2$

but the following is also chemically possible

$C_6H_{12}O_6 + 6\ O_2$ —> gives up energy —> $6\ CO_2 + 6\ H_2O$

The Evolution of Aerobic Respiration

Aerobic Respiration is the chemical "burning" of carbohydrates to obtain energy for living cells. "Burning" in this sense is chemical oxidation.

$$C_6H_{12}O_6 + 6\ O_2 \longrightarrow \text{gives up energy} \longrightarrow 6\ CO_2 + 6\ H_2O$$

Carbohydrates plus oxygen "burns" and forms carbon dioxide and water.

Aerobic respiration is the opposite of photosynthesis, but requires oxygen gas (O_2) in the water or air in order to exist. It could not evolve, therefore, until oxygen had first built-up in the oceans. Aerobic respiration evolved in both autotrophic and heterotrophic bacteria.

***E. coli* is an aerobic, heterotrophic bacteria.**

Summary of the Steps in the Evolution of Trophic Strategies

• Anaerobic Heterotrophs

The first life-forms had only the prebiotic soup to eat.

• Chemoautotrophs

The first autotrophs may have evolved at hydrothermal vents on the ocean floor and may have used hydrogen sulfide as their source of hydrogen giving off sulfur as waste.

• Anoxygenic Photosynthesis

The first photoautotrophs were anaerobic using hydrogen sulfide (H_2S) as their source of hydrogen and, therefore, did not produce oxygen as a waste.

• Oxygenic Photosynthesis

The second type of photoautotrophs used water as their source of hydrogen producing oxygen as a waste and eventually made the transition to aerobic respiration as oxygen levels increased.

• Aerobic Heterotrophs

Heterotrophs also made the transition to aerobic respiration as oxygen levels increased.

Note that all of these major evolutionary events took place in the evolution of bacteria.

Aerobic Respiration and Mitochondria

"Aerobic respiration is on the order of 18 times more efficient in producing energy than anaerobic respiration. Because of mitochondria, all earthly beings made of nucleated cells—which, of course includes us and all organisms except bacteria—have remarkably similar metabolisms. Discounting the photosynthetic metabolism monopolized by plants and algae (which is virtually identical to that of cyanobacteria), in all its fundamental details eukaryote metabolism is the same.

Bacteria, by contrast, exhibit a far wider range of metabolic variation than eukaryotes. They indulge in bizarre fermentations, produce methane gas, "eat" nitrogen gas right out of the air, derive energy from globules of sulfur, precipitate iron and manganese while breathing, combust hydrogen using oxygen to make water, grow in boiling water and in salt brine, store energy by use of the purple pigment rhodopsin, and so forth.

As a group bacteria obtain their food and energy by ingenious methods, using every sort of plant fiber and animal waste as a starting material. (If they did not, we would be living in a mounting heap of garbage. Bacteria are the ultimate recyclers.) We, however, use just one of their many metabolic designs for energy production, namely that of aerobic respiration, the specialty of mitochondria."—Margulis, 1986

- Mitochondria are the decedents of free-living, aerobic, heterotrophic bacteria closely related to existing alpha-proteobacteria. Mitochondria are genetically most similar to the alpha-proteobacteria *Rickettsia prowazekii*. Because of the similarities of their genomes, rickettsias may be the closest living relatives to the ancestors of mitochondria.

Web References

http://microbewiki.kenyon.edu/index.php/Mitochondria

http://users.rcn.com/jkimball.ma.ultranet/BiologyPages/E/Eubacteria.html#Mitochondria_and_Chloroplasts

Octopus Springs, Yellowstone National Park

Hydrothermal springs still exist in many places in the world including Yellowstone National Park. Above is Octopus Springs, a hydrothermal pool located in the park. Hot water, greater than 90°C (194°F), comes up in the small pool to the right of the main, blue pool. Part of the water leaves immediately in a stream to the right, where pink streamers of bacteria can be found. The rest spills over in to the large blue pool, and then flows out to the upper right where microbial mats form.

Pink microbial filaments first appear in this channel ~2 meters downstream from the bubbling pool. The temperature measures 83°C (181°F). The filaments contain the bacteria *Aquifex* and *Thermotoga*. They live by using oxygen from the air to oxidize hydrogen gas (H_2) from the spring water. That is, they respire aerobically using O_2 from the air, and are chemoautotrophic drawing their nutrients from inorganic chemicals.

They get their energy by reacting oxygen from the air with hydrogen gas and/or sulfide in the water. They then use the energy to make carbohydrate (sugar) from atmospheric carbon dioxide and hydrogen in the water: $CO_2 + 2H_2 = CH_2O + H_2O$ (where CH_2O is part of a carbohydrate).

Bubbles at lower right show where the water comes up into the pool. The white deposits are silica sinter spring deposits. They grow out over the pool, and are fragile. Every year, several Park visitors step on and break through sinter like this, and are severely burned (poached).

As water flows away from the pool and cools down, the microbial mat communities change. The pink colonies of bacteria give way at ~60°C (140°F) to more familiar green of mats dominated by cyanobacteria. At lower temperatures, eukaryotic algae (green, brown, etc.) come to dominate.

Below the pool ~ 5 meters, reddish and greenish microbial mats grow in slow moving, cooler water outside the main channel. Here the temperature is ~60°C (140°F). The mats include a cyanobacterium (*Synechococcus*) that does oxygenic photosynthesis, and a green non-sulfur bacterium (*Chloroflexus*) that does anoxygenic photosynthesis.

In still water ~20 meters downstream from the spring, cyanobacteria forms cylinders and mushroom shapes instead of flat mats. These blobs resemble stromatolites, fossilized mounds that are found in rocks as old as 3.5 billion years.

(Photographs of and text about *Octopus Spring* courtesy of *Extremities: Geology and Life in Yellowstone National Park*, a field trip and workshop for 6th-12th grade teachers, July/August 2002, sponsored by The Lunar and Planetary Institute and NASA.)

Web Reference

http://www.lpi.usra.edu/education/EPO/yellowstone2002/index.html

Earth’s Co-evolutionary Ladder

Excerpts from Lenton, T. M., et al. (2004)

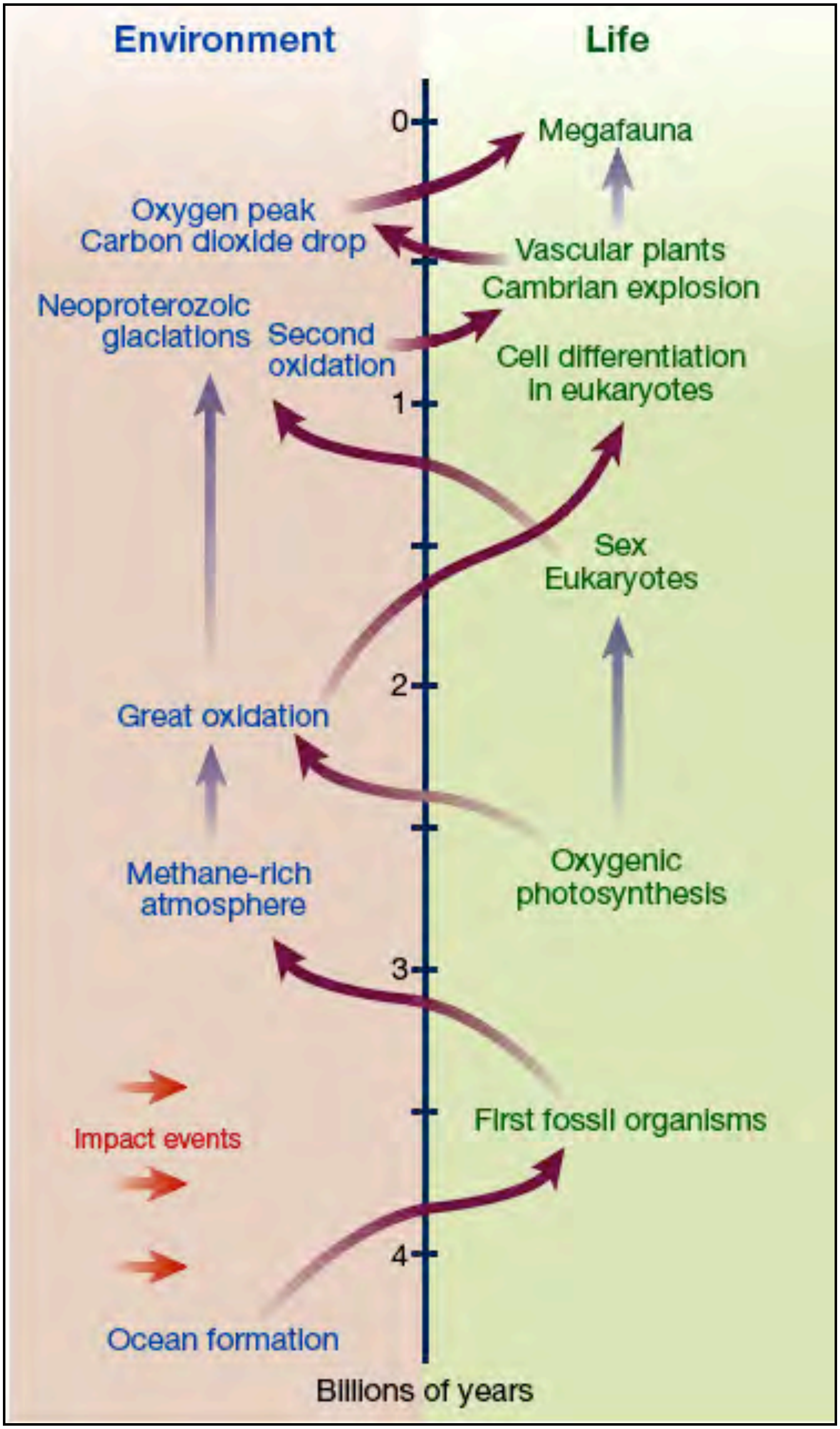
Co-evolution: Earth history involves tightly entwined transitions of information and the environment.

Entwined environment–information transitions, information processing (that is, active) life and force-driven (that is, passive) environment, have characterized Earth’s evolutionary history since its beginning some 4000 million years ago (m.y.a.). Life emerged remarkably soon after surface conditions became habitable, with the formation of oceans and cessation of sterilizing asteroid impacts. The first organisms would have drained the environment of energetically and structurally useful compounds and replaced them with degraded waste products, including methane. An ultimately dull fate for life, eking out a meager existence on a lifeboat Earth, was averted when closed recycling loops developed, in which one life form’s waste became another’s food. These loops are large-scale manifestations of the auto-catalytic nature of the cell, locked in as the core of the global ‘metabolism’ that is still with us.

Despite recycling, life remained energetically limited until the origin of oxygenic photosynthesis, sometime before 2700 m.y.a.. This breakthrough in metabolic evolution greatly increased the free energy supply to the biota, giving life a truly global environmental impact. It facilitated the great oxidation of the atmosphere around 2200 m.y.a., but—as the long time lag indicates—other factors were required. Perhaps oxidation had to await tectonically driven changes in Earth’s ‘anatomy’, including the appearance of shelf seas where reduced organic carbon could reach the sediments and be buried.

Although the energetic stage was now set for global dominance by eukaryotes, the emergence of a soft cell boundary membrane coupled to an internal skeleton and a means for cellular division were also required. These transitions are thought to have been especially difficult, as they required the fixation of thousands of rare mutations.

Eukaryotes may be implicated in the worst crisis of past co-evolution: the extreme Neoproterozoic glaciations of 800–600 m.y.a. that were accompanied by a second rise in oxygen. Whenever eukaryotes started to colonize the land surface, there would have been strong selection for traits that accelerated weathering to access rock-bound nutrients. Weathering of silicates would have inadvertently drawn down atmospheric carbon dioxide and cooled the planet, and weathering of phosphorus would have increased global productivity and contributed to oxygen rise. The latter opened the door for the diversification of larger, hard-shelled, animal life in the Cambrian explosion. After that, the triumph of vascular land plants, causing a further rise in oxygen and fall in carbon dioxide, played its part in creating the environmental conditions in which active megafauna (including ourselves) evolved.


Environment
Life
0
1
2
3
4
Megafauna
Oxygen peak
Carbon dioxide drop
Vascular plants
Cambrian explosion
Neoproterozoic glaciations
Second oxidation
Cell differentiation in eukaryotes
Sex
Eukaryotes
Great oxidation
Methane-rich atmosphere
Oxygenic photosynthesis
Impact events
First fossil organisms
Ocean formation
Billions of years

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