Notes of a Geobiology Watcher, or How to Love Your Bacteria

Interactions Between Life Forms And The Earth's Physical And Chemical Systems

Prepared by Michael McGoodwin (MCM)
Autumn 2007

TABLE OF CONTENTS

Introduction and Disclaimers

This compilation of notes is built around transcription of the University of Washington Geobiology ESS313 lectures as presented in Autumn 2007. At the onset, Professor Roger Buick stated that there is no suitable textbook for this subject—the field is too new and rapidly evolving. As I became immersed in the fascinating subject matter of this multi-disciplinary course, it became apparent that this type of annotated document could serve as a useful tool—both for helping me to better learn the material, and for making the information available to other interested parties who might wish to explore some of the topics.

I am a retired physician—not a geobiologist, earth scientist, or biologist—and only audited[1] the course. These notes are not endorsed by the instructors. I have encountered occasional difficulties while

[1] My title for this document alludes to a genuine Biology Watcher, Lewis Thomas, whose enjoyable articles appeared in the *New England Journal of Medicine* during the 1970s.

taking notes on the lectures, but this is not necessarily a reflection on the quality of instruction. Where it seemed appropriate, I have provided corrections or clarifications—perhaps I missed or misunderstood what was said, the instructor erred, or there is legitimate scientific controversy about a subject for which opinions and even "facts" vary. Furthermore, I was unable to attend the labs, a significant part of the course where some of the lectures are given, so have missed hearing important information there. Corrections and comments would be welcome—send these to mcgoo at u period washington period edu [after converting this address to standard format].

The supplemental materials consist of hastily gathered excerpts from various Web resources including *Wikipedia*, but this does not imply any assumption of authoritativeness of any of these resources. If I could have spent more time, I would have made a more concerted effort to search out the respected primary sources. I find, however, that even imperfect and uneven Web resources like *Wikipedia* can help serve as quick entry points to relatively unfamiliar subject matter that is presented more definitively in the reference materials cited by the imperfect entry-level resources. In addition, *Wikipedia* materials may be quoted in detail so long as there is proper acknowledgement, as I have done here. Viewing this document in a Web browser or in a recent generation Adobe Acrobat Reader allows following the Web hyperlinks, just like with a normal Web page. In some instances, multiple separate sources are combined into one footnote (in which case the individual sources are demarcated by a bullet "• "). Regretfully, I have not included any images, although they are essential for assimilation of the material, in part to keep this document compact but more importantly to avoid potential copyright problems. However, I have stated in many cases which references provide especially useful images. The excellent PowerPoint presentations of Dr. Linda Reinink-Smith are especially replete with instructive images which cannot be included here out of respect and copyright concerns.

All Web resources were accessed in autumn 2007 unless otherwise stated, and would be expected to have a limited shelf life, as would these notes. Many of the issues raised however are timeless.

Instructors, Website, and Recommended Textbooks

Roger Buick, Ph.D.=RB (buick@ess.washington.edu)
Linda Reinink-Smith, Ph.D.=LRS (reininks@u.washington.edu)
TA: Sanjoy M. Som (http://students.washington.edu/sanjoy/, sanjoy@u.washington.edu)
Website: https://webcourse.ess.washington.edu:35131/moodle/login/index.php [requires password]
Textbooks mentioned in the syllabus but not required:
(1) Briggs, D.E.G. & Crowther, P. eds. *Palaeobiology: a Synthesis* (1990), Blackwell (1st edition) [MCM: a little long in the tooth]
(2) Briggs, D.E.G. et al. *Palaeobiology II* (2001), Blackwell (2nd edition) [MCM: Very substantive and dense but somewhat hit or miss, no color, not for the faint at heart; has a chapter by RB, p. 13-21. Referred to subsequently as PB2001]
(3) Kump, L.R. et al. *The Earth System* (2000), Prentice Hall [MCM: excellent resource, good diagrams. Referred to subsequently as *TES2000*]

Geobiology Journal

http://www.blackwellpublishing.com/journal.asp?ref=1472-4677&site=1:
Launched in 2003. Roger Buick is an editor for Ancient Earth Systems

[This first part of the course is given by Roger Buick, Ph.D.=RB]

LECTURE-RELATED MATERIALS

Definition of Geobiology and Course Emphases

(per RB lecture and supplemented, see also Glossary entry):
Term "Geobiology" in use for 10 years, a new cross-disciplinary field. It links the physical Earth's evolution and environment with the evolution of life.

From the course outline:
“Geobiology is 1) the effect that life has had on the Earth, its minerals, rock types, surface topography, ocean chemistry, and atmospheric composition; and 2) the effect that the Earth has had on the evolution, distribution and abundance of life. So, the objective of the course is to teach geobiological concepts fundamental to understanding the origin and evolution of life on Earth, the role that life has played in the formation of minerals and sedimentary rocks, and the interaction between life and its environment through time. In particular, the course will examine the inter-relationships between life and geological processes at scales ranging from the growth of individual crystals to global biogeochemical cycling between the atmosphere, oceans and land. The course will also examine critical moments in Earth history that have had a major impact on the diversification of life.”[2]

Also from the course outline:
“Within the course, five conceptual areas will be emphasized:
1) The three Domains of life (Archaea, Bacteria, Eucarya) arose in "extreme environments" on the early Earth, and still show influences from these origins;
2) Life through biogeochemical cycling has had a dominant role in the formation of the present-day atmosphere and controls many aspects of ocean chemistry;
3) The formation of many sedimentary rocks is mediated or controlled by the presence of life;
4) Life has influenced the formation of soil types, landforms, ore deposits and energy resources; and
5) The diversity of life today is the product of both evolutionary forces and environmental factors.

Topics of Study in Geobiology

(per RB lecture, supplemented with list from *Geobiology* journal):
1. Origins and evolution of life
2. Evolution of the atmosphere, hydrosphere and biosphere
3. Sedimentary rock record and geobiology of critical intervals
4. The Earth systems, paleobiology and evolutionary ecology
5. Environmental microbiology
6. Biogeochemistry and global elemental cycles
7. Geobiology of weathering—release of P, Ca etc.
8. Microbe-mineral interactions: metal binding, etc.
9. Biomarkers
10. Molecular ecology and phylogenetics
11. Astrobiology

Typical Geobiological Research Questions

(per RB lecture):
1. **Coral Reefs**: Can they control ocean composition?
2. **Global warming**: What will be the evolutionary effects?
3. **Global carbon cycle**: What if there were no green plants, would CO_2 increase leading to greater global warming? There would be less O_2 in the atmosphere, but still quite a bit… (why?)
4. **Venus**: It has no plate tectonics now, but may have had intermittent in the past? Only modest topological variation.[3] Plate tectonics recycles gases and water in atmosphere to mantle. Venus may have had plate tectonics 3 Ga (3 billion years ago).[4]

---

[2] **Geobiology**: ““Broadly defined, geobiology is an interdisciplinary field of scientific research that explores interactions between the biosphere and the lithosphere and/or the atmosphere. Investigators from numerous fields are involved in geobiologic research, including, but not limited to, such disciplines as: paleontology, paleobiology, microbiology, mineralogy, biochemistry, sedimentology, genetics, physiology, geochemistry (organic and inorganic), and atmospheric science. One major subdiscipline of geobiology is geomicrobiology, an area of study that focuses on investigating the interactions between microbes and minerals. Another related area of research is astrobiology, an interdisciplinary field that uses a combination of geobiological and planetary science data to establish a context for the search for life on other planets…”
http://en.wikipedia.org/wiki/Geobiology
[3] **Venus topography** (nice images, URL has been corrected)
http://www.windows.ucar.edu/tour/link=/venus/venus_il.html

5. **Coal**: Arose primarily in Carboniferous (359 - 306 MYA) and Permian (299 - 260 MYA) periods. Why not later?—in the Triassic 251 - 228 Ma (million years ago) etc.? May have been due to dinosaurs eating foliage and compacting the soils, changing forest dynamics?

What is Life?

(per RB lecture and supplemented, see Glossary entries also):
No simple universally accepted definition of Life. Worst answer is to say it is due to a special mysterious life force that animates organism (**vitalism** belief)—such a belief is not amenable to investigation and nonscientific. Linus Pauling said "In connection with the origin of life, I should like to say that it is sometimes easier to study a subject than to define it."[5] Chemists, biologists, astronomers, etc. all have differing definitions (physicists like to talk about entropy).

Some of the relevant issues and questions:

1. **Viruses, Prions, Rickettsia**, etc.: We are finding ever more simple forms of possible life on Earth, such as **viruses** and **prions** (proteinaceous infectious particle). **Rickettsiae** are obligate intracellular parasites, depending on entry into and growth and replication within the cytoplasm of eukaryotic host cells . Are these entities truly alive?
2. **Complex Molecules**: We are finding ever more complex organic molecules on Earth. When does a complex collection of molecules become alive? There is much extracellular DNA in the oceans[6]. **RNA** and **ribozymes** can catalyze reactions.
3. **Large Systems**: Ever more complex systems are being postulated as being alive. Does a living thing need to have a boundary? E.g., in the **Gaia hypothesis**, the whole planet [or its biota] is postulated (originally by James "Jim" Lovelock, also Lynn Margulis) to behave like a living entity, even regulating the environment and stabilizing climate to optimally support life.[7]
4. **Invented Inorganic Systems**: Some of these show characteristics of "life". Is life dependent on a particular chemical composition? E.g., are computer viruses that replicate, mutate, and transduce energy alive? Is the computer-based "Game of Life" alive?
5. **Ethical Dilemmas**: When does life begin and end. How much of a living system (organism) must remain alive in order for the system (organism) to be still considered alive? E.g., issues of brain death, Terry Schiavo, abortion.
6. **Searching for Extraterrestrial Life**: How will we recognize it? NASA has retooled all solar system exploration to search for existing and past extraterrestrial life. Is this a good use of tax dollars? Yes, if you are an astrobiologist.

---

[4] **Past Times and Time Intervals (Ga, b.y., Ma, and m.y.)**: In this document, I have tried (perhaps not consistently) to convert all specifications of past time to Ga and Ma terminology (except in quotations from outside sources), and time intervals to m.y. or b.y.:

- A point in past time of 4.4 billion years ago (where billion here signifies the "short billion" = 10^9 years), is abbreviated as **4.4 Ga** (**Gigaannum**).
- A time interval of 10 billion years is expressed as **10 b.y.** (where billion here signifies the "short billion" = 10^9).
- A point in past time of 10 million years ago (MYA) is expressed as **10 Ma**.
- A time interval of 10 million years is expressed as **10 m.y.**

[5] **Linus Pauling on Life**: http://www.ibiblio.org/jstrout/uploading/potter_life.html

[6] **Extracellular DNA**: "...Our global estimates indicate that up to 0.45 gigatons of extracellular DNA are present in the top 10 centimeters of deep-sea sediments, representing the largest reservoir of DNA in the world oceans. We demonstrate that extracellular DNA accounts for about one fifth of the total organic phosphorus regeneration and provides almost half of the prokaryotic demand for organic phosphorus. It therefore plays a key role in deep-sea ecosystem functioning on a global scale." Antonio Dell'Anno and Roberto Danovaro. "Extracellular DNA Plays a Key Role in Deep-Sea Ecosystem Functioning". *Science* 30 September 2005. Vol. 309. no. 5744, p. 2179

[7] **Gaia Hypothesis**: TES2000 p. 15.

Characteristics of Life as we know it:

1. **Organic**: Life is based on complex polymers of Carbon, etc. Only minimal amounts of inorganic (noncarbon) minerals are used, primarily for rigidity, protection, and some ions for electron transport.
2. **DNA (Deoxyribonucleic acid)**: Life is reproductive, and all living things (except certain RNA viruses) use DNA to reproduce. (see details in Glossary). Coding is similar to computer code—sequences of 3 bases (**codons**) that code for varying amino acids. There are 64 (4^3) possible codons. Coding for the 20 standard amino acids[8] is in most cases **redundant** (e.g., Leucine is coded by codons UUA, UUG, CUU, CUC, CUA, CUG, and Lysine is coded by AAG and AAA). Three codons serve as **stop codons** (UAA, UAG, UGA). The start codon is usually the first AUG codon (coding for methionine) in the mRNA sequence. Some organisms code for and incorporate two additional amino acids.[9]
3. **RNA (Ribonucleic acid)**: The base Uracil replaces DNA's Thymine, the sugar ribose replaces DNA's deoxyribose, and the molecule is single stranded. RNA is found as
   a. **Messenger RNA (mRNA)** used to copy DNA [as the complement of the **anti-sense** strand of DNA],
   b. **Transfer RNA (tRNA)** transfers the amino acids to the growing polypeptide being synthesized[10]
   c. **Ribosomal RNA (rRNA)** is the central component of the ribosome, whose function is to provide a mechanism for decoding mRNA into amino acids, etc."[11]
4. **Proteins**: Found in all living things. Include enzymes, which are the main catalytic molecules, allowing life to function out of thermodynamic equilibrium with respect to its environment. Proteins are complexly folded chains of up to many thousands of 20 distinct amino acids (out of hundreds of additional amino acids that can arise in abiotic synthesis—some bacteria can make 2 more amino acids). All **alpha amino acids** have an **amine** ($-NH_2$) group attached to the

---

[8] **Codons for the Standard 20 Amino Acids:** http://en.wikipedia.org/wiki/Codon

[9] **Nonstandard amino acids**: "In certain proteins, non-standard amino acids are substituted for standard stop codons, depending upon associated signal sequences in the messenger RNA: UGA can code for selenocysteine and UAG can code for pyrrolysine... Selenocysteine is now viewed as the 21st amino acid, and pyrrolysine is viewed as the 22nd..."
http://en.wikipedia.org/wiki/List_of_standard_amino_acids
"**Pyrrolysine** is a naturally-occurring genetically-coded amino acid used by some methanogenic archaea in enzymes that are part of their methane-producing metabolism..."
http://en.wikipedia.org/wiki/Pyrrolysine
"**Selenocysteine** is encoded in a special way by a UGA codon, which is normally a stop codon. The UGA codon is made to encode selenocysteine by the presence of a **SECIS element (SElenoCysteine Insertion Sequence)** in the mRNA. The SECIS element is defined by characteristic nucleotide sequences and secondary structure base-pairing patterns. In eubacteria, the SECIS element is located immediately following the UGA codon within the reading frame for the selenoprotein. In archaea and in eukaryotes, the SECIS element is in the 3' untranslated region (3' UTR) of the mRNA, and can direct multiple UGA codons to encode selenocysteine residues."
http://en.wikipedia.org/wiki/Selenocysteine

[10] **Transfer RNA** (tRNA): "first hypothesized by Francis Crick, is a small RNA chain (73-93 nucleotides) that transfers a specific amino acid to a growing polypeptide chain at the ribosomal site of protein synthesis during translation. It has a 3' terminal site for amino acid attachment. This covalent linkage is catalyzed by an aminoacyl tRNA synthetase. It also contains a three base region called the anticodon that can base pair to the corresponding three base codon region on mRNA. Each type of tRNA molecule can be attached to only one type of amino acid, but because the genetic code contains multiple codons that specify the same amino acid, tRNA molecules bearing different anticodons may also carry the same amino acid."
http://en.wikipedia.org/wiki/Transfer_RNA

[11] **Ribosomal RNA** (rRNA), "a type of RNA synthesized in the nucleolus by RNA Pol I, is the central component of the ribosome, the protein manufacturing machinery of all living cells. The function of the rRNA is to provide a mechanism for decoding mRNA into amino acids and to interact with the tRNAs during translation by providing peptidyl transferase activity."
http://en.wikipedia.org/wiki/Ribosomal_RNA

same C (the alpha carbon) as a **carboxyl** (-COOH) group and an organic substituent R.[12] Enzymes exhibit complex chain folding resulting in 3-D configuration in which the **active site** is positioned at the needed location to react on the **substrate** to lower the **activation energy** of the needed reaction. (Note that some RNA's called **ribozymes** can also catalyze or auto-catalyze reactions.) Mutations changing the amino acid sequence coded by DNA may be silent, or result in major disorders (such as in Sickle Cell Disease, in which Glutamic Acid is replaced with Valine at the 6th position of the beta chain of Hemoglobin).

5. **Lipids**: Fatty substances used for energy storage, cell membranes, etc.[13] **Cell membranes** are **lipid bilayers**.[14] They are unstable but held rigid by stiffening molecules, semipermeable, often capable of invagination and phagocytosis.
6. **Chirality**: All key biomolecules are constructed of only one form of **enantiomer**. Enantiomers are two stereoisomers that are related to each other by a reflection: they are **mirror images** of each other, which are non-superimposable.[15]
7. **Water** is used as a solvent, to aid catalysis, to facilitate hormonal signaling, etc.

What are the essential characteristics of life? (How could extraterrestrial life differ and still be life?)

1. **Organic?**: Carbon chemistry if very flexible and versatile, can form chains and rings, combine with many elements including N H O S P Se, etc.. **Silicon[16]** can form chains, but polymerizes well only at very low temperatures (c. -200°C) where reaction rates are low. It only forms single bonds easily. It bonds well with O but not well with other atoms. Its molecules are mostly solid—silicon dioxide, the analog of carbon dioxide, is non-soluble (sand, quartz, etc.) Complex long-chain silicone molecules are more unstable than their carbon counterparts. Conclusion: ORGANIC (CARBON-BASED): YES.
2. **Aqueous?**: Water is a highly remarkable liquid. It dissolves polar molecules well but also can organize and interact with **non-polar** molecules. Has high **specific heat** allowing energy storage and transport (as in the oceans). It has a high **heat of vaporization**, allowing dissipation of heat through evaporation. High surface tension allows molecules to accumulate. High **dielectric constant** allows proton pumping across cell membranes. Other potential solvents might include HCN (hydrogen cyanide), NH_3 (ammonia, is unstable over long periods). Conclusion: AQUEOUS: YES.
3. **Metabolic?[17]**: Do organisms need to take energy in and release it internally? All living things have greater internal order (lower **entropy**) than exists external to them. This requires energy

---

[12] **Amino Acids** http://en.wikipedia.org/wiki/Amino_acid

[13] **Lipids**: "The lipids are a large and diverse group of naturally occurring organic compounds that are related by their solubility in nonpolar organic solvents (e.g. ether, chloroform, acetone & benzene) and general insolubility in water."
http://www.cem.msu.edu/~reusch/VirtualText/lipids.htm
"The term lipid comprises a diverse range of molecules and to some extent is a catchall for relatively water-insoluble or nonpolar compounds of biological origin, including waxes, fatty acids, fatty-acid derived phospholipids, sphingolipids, glycolipids and terpenoids (e.g. retinoids and steroids)."
http://en.wikipedia.org/wiki/Biochemistry

[14] **Lipid Bilayers**: "The cell membrane consists of a thin layer of amphipathic [having both hydrophilic and hydrophobic properties] lipids which spontaneously arrange so that the hydrophobic "tail" regions are shielded from the surrounding polar fluid, causing the more hydrophilic "head" regions to associate with the cytosolic and extracellular faces of the resulting bilayer."
http://en.wikipedia.org/wiki/Cell_membranes

[15] **Chiral molecules**: "Many biologically-active molecules are chiral, including the naturally-occurring amino acids (the building blocks of proteins), and sugars. Interestingly, in biological systems most of these compounds are of the same chirality: most amino acids are L and sugars are D. Typical naturally occurring proteins, made of L amino acids, are known as left-handed proteins, while D amino acids produce right-handed proteins."
http://en.wikipedia.org/wiki/Chirality_%28chemistry%29

[16] **Silicon based life**: http://en.wikipedia.org/wiki/Alternative_biochemistry

[17] **Metabolism**: "Metabolism is the complete set of chemical reactions that occur in living cells. These processes are the basis of life, allowing cells to grow and reproduce, maintain their structures, and respond to their environments. Metabolism is usually divided into two categories. Catabolism yields

expenditure by metabolism—the organism must import energy, in normal life by using **redox (reduction/oxidation) reaction**[18]) gradients and reactions that yield energy. We cannot conceive of life that would have higher entropy than its surroundings, so therefore all life must metabolize. However, energy sources other than redox reactions might provide the energy—electrical, heat, radioactivity, mechanical such as wind-turbine, etc. Conclusion: METABOLIC: YES.

4. **Segregated?** Almost certainly must have a barrier between a life form and the external disordered environment, to maintain lower entropy and prevent energy escaping. Living things have bilayer lipid membranes (viruses have protein walls). Might conceivably have a steep environmental gradient instead. Could be a chemical barrier rather than a physical barrier. Hard to envision life without some kind of physical barrier, though possibly not a distinct membrane. Conclusion: SEGREGATED: YES.
5. **Homeostatic?**: Life maintains stable internal conditions by responding to external stimuli. We do it now by maintaining many chemical and electrical signaling channels across membranes, have the capability of growth and/or movement away or toward stimuli. Having senses and movement capability seems fundamental to concepts of life. Conclusion: HOMEOSTATIC: YES.
6. **Reproductive?** Most obvious feature of life is potential to replicate itself. (Viruses reproduce, but are they alive?) Not every individual of a species has this ability all the time (e.g., worker bees)—but the potential is there at some time under some circumstances for at least some of the members of the specific living comminuty. Conclusion: REPRODUCTIVE: YES
7. **Informative?** Reproduction should not occur at random, but should be controlled and regulated by an information system. To control all life processes, life needs to maintain and transmit information. Living things we know universally use a genetic code (of DNA or RNA). However, other life forms might not use DNA or RNA, or might use some other forms of DNA etc. (as has been tested in experiments) . Conclusion: INFORMATIVE: YES.
8. **Evolutionary?** Evolution is probably essential to any definition of life. Replication involving information transfer isn't always done with perfect fidelity. Homeostatic organisms interacting with their environments will undergo natural selection with respect to these variations in information quality, and evolution will necessarily occur in such a system. However, it may not be Darwinian but could follow some other pattern. Even organisms which reproduce usually with parthenogenesis or cloning sometimes revert to sexual reproduction using information transfer. Conclusion: EVOLUTIONARY: YES

Assessment: Do these mandatory criteria for life represent a satisfactory answer to "What Is Life?" No, not yet. We still can't be sure if viruses are alive. (Note that sentience and consciousness are not requirements for life—e.g., bacteria—these characteristics only occur in higher forms.) If there are alien life forms, they are most likely microorganisms [speaking probabilistically]. There is no set of mathematical equations (like the Maxwell equations) that define life—the science is still imperfect. It's hard to look for extraterrestrial life if we are not sure what it is.

Origin Of Life (How Did Life Start?)

[Past and current scientific theories of non-theistic abiogenesis]
(per RB lecture and supplemented, see also Glossary entries)

1. **Spontaneous Generation**: Arose in dirty underwear or dirt, slime, etc. Speculations by ancients including Anaximander, Aristotle. The 17C Belgian Jan Baptista van Helmont (1580 - 1644)[19] contended that mice arise from grains mixed with dirty underwear.

---

energy, an example being the breakdown of food in cellular respiration. Anabolism, on the other hand, uses this energy to construct components of cells such as proteins and nucleic acids."
http://en.wikipedia.org/wiki/Metabolism

[18] **Redox reduction/oxidation reactions**: "...describes all chemical reactions in which atoms have their oxidation number (oxidation state) changed."
http://en.wikipedia.org/wiki/Redox [see also Glossary]

[19] **Spontaneous Generation**: Jan Baptista van Helmont said c. 1620 "for if you press a piece of underwear soiled with sweat together with some wheat in an open mouth jar, after about 21 days the odor changes and the ferment coming out of the underwear and penetrating through the husks of the wheat, changes the wheat into mice. But what is more remarkable is that mice of both sexes emerge (from the wheat) and these mice successfully reproduce with mice born naturally from parents? But

Flaw: This view was refuted by various experiments, specifically [at least with respect to spontaneous generation of bacteria] by Louis Pasteur in 1862. His experiments with swan-necked flasks holding [sterile] nutrient broths showed that no [bacterial] growth occurs if the neck is intact [and therefore microorganisms and their spores cannot enter].

Key concept: Modern science however does agree with the presupposition that specific environmental conditions were required for life to arise—conditions which no longer exist but which did exist c. 3 Ga.

2. **Life Arose in A Warm Little Pond**: Charles Darwin 1871 wrote nervously only in private letters about this, but in an 1871 letter to J. D. Hooker[20] proposed specific conditions, which no longer exist, in which life might have formed in a warm pond.

   His statement presupposes that life's origin requires:
   a. Diversity of energy sources
   b. Diversity of simple chemical compounds as reactants
   c. Restricted environment capable of concentrating reactants
   d. Polymerization of simple compounds adding order to the system
   e. Polymers capable of increasing complexity—evolution!
   f. Conditions that do not exist now. (Life could not arise now—living organisms would consume the needed ingredients and products and/or molecular oxygen would oxidize them. The chemistry at the time of life's formation would have to have been different.)

3. **Life Arose In Dilute Oceans (Primordial Soup)**: The Soviet biologist **Aleksandr Oparin**[21] writing in 1924 considered the primordial atmosphere was "anoxic", contained hydrogen, [carbon dioxide], methane, and ammonia, but no molecular oxygen [as O_2 or O_3]. This would allow the formation of organic chemicals from light, lightning, and volcanic heat, which could accumulate by raining down on the oceans to form a hot dilute primordial soup. Independent development and additions to this concept of "**chemical evolution**" were made by **J. B. S Haldane**.[22] Haldane emphasized the importance of UV solar radiation in producing

---

what is even more remarkable is that the mice which came out were not small mice? but fully grown."
[http://wiki.cotch.net/index.php/Abiogenesis]
[20] **Darwin's Warm Pond**:
Charles Darwin's Letter to J.D. Hooker February 1, 1871:
"On the same subject my father [i.e., Frances Darwin's father Charles Darwin] wrote in 1871: "It is often said that all the conditions for the first production of a living organism are now present, which could ever have been present. But if (and oh! what a big if!) we could conceive in some warm little pond, with all sorts of ammonia and phosphoric salts, light, heat, electricity, &c., present, that a proteine compound was chemically formed ready to undergo still more complex changes, at the present day such matter would be instantly devoured or absorbed, which would not have been the case before living creatures were formed." "
Date of Charles Darwin's letter given in http://bevets.com/equotesd.htm
Text quotes a work edited by Darwin's son Frances Darwin found at http://darwin-online.org.uk/content/frameset?viewtype=text&itemID=F1452.3&pageseq=1)
[21] **Aleksandr Ivanovich Oparin** (1894-1980) "was a Soviet biologist and biochemist and was most famous for his research into the potential origins of life on Earth. He was the scientist who originally coined the term "primordial soup" to describe the organic molecules that were dissolved in water billions of years ago."
http://wiki.cotch.net/index.php/Aleksandr_Ivanovich_Oparin
[22] **John Burdon Sanderson Haldane** (1892-1964):
"… was a Professor of Genetics and Biometry at University College, London, and with Sewall Wright and Ronald Fisher, one of the principal architects of population genetics and the Modern Synthesis. Many people credit Haldane with the major contributions to defining "neo-Darwinism". He also anticipated the Miller-Urey experiments in abiogenesis.
[http://wiki.cotch.net/index.php/John_Burdon_Sanderson_Haldane]
"…[in] the 1920's, when Aleksandr Ivanovich Oparin and John Burdon Sanderson Haldane independently worked out scenarios of "chemical evolution". They concluded from various chemical grounds that the Earth had originally had hydrogen, ammonia, carbon dioxide, methane, and other

photochemical changes leading to organic synthesis.

These concepts presuppose:
a. An anoxic primordial atmospheric environment
b. Photochemical reactions caused by UV causing organic synthesis
c. Chemical evolution follows the fundamental laws of physics and chemistry.

Flaw: The theory is flawed because the oceans would be so dilute that needed chemical reactions are improbable.

4. **Life Began In A Thunderstorm (Spark Synthesis):** The **Miller-Urey experiments** began in 1953[23]. They found that **electrical discharges** in the proper anoxic conditions could lead to the formation of an organic-rich tar including amino acids, adenine and other of life's building blocks. These experiments have been extensively replicated and expanded, including successful organic syntheses using other energy sources such as UV, heat, sonic shock, x-rays, etc. The yields of relevant organic compounds in any of these experiments were substantial only in **reducing conditions**[24] (in which the gaseous medium reacted on contains H_2, NH_3,

---

simple compounds in its atmosphere -- but no oxygen molecules. And larger and larger molecules formed by various chemical processes until some of them succeeded in making copies of themselves, forming the first living things."
[http://wiki.cotch.net/index.php/Abiogenesis]
[23] **Miller-Urey experiment**: "The Miller-Urey experiment (or Urey-Miller experiment) was an experiment that simulated hypothetical conditions present on the early Earth and tested for the occurrence of chemical evolution. Specifically, the experiment tested Oparin and Haldane's hypothesis that conditions on the primitive Earth favored chemical reactions that synthesized organic compounds from inorganic precursors. Considered to be the classic experiment on the origin of life, it was conducted in 1953 by Stanley L. Miller and Harold C. Urey at the University of Chicago.

The experiment used water (H_2O), methane (CH_4), ammonia (NH_3) and hydrogen (H_2). The chemicals were all sealed inside a sterile array of glass tubes and flasks connected together in a loop, with one flask half-full of liquid water and another flask containing a pair of electrodes. The liquid water was heated to induce evaporation, sparks were fired between the electrodes to simulate lightning through the atmosphere and water vapor, and then the atmosphere was cooled again so that the water could condense and trickle back into the first flask in a continuous cycle.

At the end of one week of continuous operation Miller and Urey observed that as much as 10-15% of the carbon within the system was now in the form of organic compounds. Two percent of the carbon had formed amino acids, including 13 of the 22 that are used to make proteins in living cells, with glycine as the most abundant. Sugars, lipids, and some of the building blocks for nucleic acids were also formed. Nucleic acids (DNA, RNA) themselves were not formed. As observed in all consequent experiments, both left-handed (L) and right-handed (D) optical isomers were created in a racemic mixture. However, the experiment also produced a "toxic carcinogenic" substance, also known as tar, which, in a natural environment, would destroy any amino acids created."
http://en.wikipedia.org/wiki/Miller-Urey_experiment
[24] **Reducing Conditions in Early Atmosphere**:

"Chondrites are relatively unaltered samples of material from the solar nebula, According to Fegley, who heads [Washington University's] Planetary Chemistry Laboratory, scientists have long believed them to be the building blocks of the planets. However, no one has ever determined what kind of atmosphere a primitive chondritic planet would generate.

We assume that the planets formed out of chondritic material, and we sectioned up the planet into layers, and we used the composition of the mix of meteorites to calculate the gases that would have evolved from each of those layers," said Schaefer. "We found a very reducing atmosphere for most meteorite mixes, so there is a lot of methane and ammonia."

In a reducing atmosphere, hydrogen is present but oxygen is absent. For the Miller-Urey experiment to work, a reducing atmosphere is a must. An oxidizing atmosphere makes producing organic compounds impossible. Yet, a major contingent of geologists believe that a hydrogen-poor, carbon dioxide-rich atmosphere existed because they use modern volcanic gases as models for the early atmosphere. Volcanic gases are rich in water, carbon dioxide, and sulfur dioxide but contain no ammonia or methane."
Article reporting on experiment of Bruce Fegley, Ph.D. et al: "Origins of life: Calculations favor

CH_4, H_20, but lacks O_2, N_2, CO_2, or other oxidizing gases).[25] [26]

The key concepts include:
a. The origin of life can be studied experimentally
b. It is easy to create the building blocks of life in the right conditions.

Flaw: The flaw in this approach if that the early atmosphere was possibly not highly reducing (at least, volcanic gases are neutral, contain CO_2, N_2, not CH_4 or NH_3, and yields are low in these conditions. (But see discussion here[27]).

---

reducing atmosphere for early earth. Was Miller-Urey experiment correct?" [http://www.physorg.com/news6293.html]

[25] **Hydrogen as a Reducing Agent**: "Some compounds can act as either oxidizing agents or reducing agents. One example is hydrogen gas, which acts as an oxidizing agent when it combines with metals and as a reducing agent when it reacts with nonmetals." http://chemed.chem.purdue.edu/genchem/topicreview/bp/ch19/oxred_3.php#strong

[26] **Carbon dioxide as an Oxidizing Agent**: In the reaction 2 CO_2 + 2 H^+ + 2 e^- ==> $H_2C_2O_4$ (oxalic acid = HO_2CCO_2H), the oxidizing agent carbon is reduced when its oxidation state increases from -4 to -3 by the gain of an electron (since reduction is the gain of electrons). [MCM: But what is oxidized?—Is it the free electrons? The H ions/atoms maintain oxidation number +1 and the oxygens keep -2]. http://chemed.chem.purdue.edu/genchem/topicreview/bp/ch19/oxred_3.php#strong and http://en.wikipedia.org/wiki/Oxidizing_agent] , [http://en.wikipedia.org/wiki/Redox

[27] **Was Early Atmosphere Reducing?**

"There have been a number of objections to the implications derived from these [Miller-Urey] experiments. Scientists believe that Earth's original atmosphere might contain less of the reducing molecules than was thought at the time of Miller-Urey experiment. There is abundant evidence of major volcanic eruptions 4 billion years ago, which would have released carbon dioxide, nitrogen, hydrogen sulfide, and sulfur dioxide into the atmosphere. Experiments using these gases in addition to the ones in the original Miller-Urey experiment have produced more diverse molecules.

Originally it was thought that the primitive secondary atmosphere contained mostly NH_3 and CH_4. However, it is likely that most of the atmospheric carbon was CO_2 with perhaps some CO and the nitrogen mostly N_2. The reasons for this are (a) volcanic gas has more CO_2, CO and N_2 than CH_4 and NH_3 and (b) UV radiation destroys NH_3 and CH_4 so that these molecules would have been short-lived. UV light photolyses H_2O to H·and OH radicals. These then attack methane, giving eventually CO_2 and releasing H_2 which would be lost into space.

In practice gas mixtures containing CO, CO_2, N_2, etc. give much the same products as those containing CH_4 and NH_3 so long as there is no O_2. The H atoms come mostly from water vapor. In fact, in order to generate aromatic amino acids under primitive earth conditions it is necessary to use less hydrogen-rich gaseous mixtures. Most of the natural amino acids, hydroxyacids, purines, pyrimidines, and sugars have been produced in variants of the Miller experiment.

More recent results may question these conclusions. The University of Waterloo and University of Colorado conducted simulations in 2005 that indicated that the early atmosphere of Earth could have contained up to 40 percent hydrogen---implying a much more hospitable environment for the formation of prebiotic organic molecules. The escape of hydrogen from Earth's atmosphere into space may have occurred at only one percent of the rate previously believed based on revised estimates of the upper atmosphere's temperature. One of the authors, Prof. Owen Toon notes: "In this new scenario, organics can be produced efficiently in the early atmosphere, leading us back to the organic-rich soup-in-the-ocean concept... I think this study makes the experiments by Miller and others relevant again." Outgassing calculations using a chondritic model for the early earth, complement the Waterloo/Colorado results in re-establishing the importance of the Miller-Urey experiment.

Although lightning storms are thought to have been very common in the primordial atmosphere, they are not thought to have been as common as the amount of electricity used by the Miller-Urey experiment implied. These factors suggest that much lower concentrations of biochemicals would have been produced on Earth than was originally predicted (although the time scale would be 100 million years instead of a week). Similar experiments, both with different sources of energy and with different mixtures of gases, have resulted in amino and hydroxy acids being produced; it is likely that at least some organic compounds would have been generated on the early Earth.

However, when oxygen gas is added to this mixture, no organic molecules are formed. Opponents of Miller-Urey hypothesis seized upon recent research that shows the presence of uranium

5. **Life Began In Clay (Mineral Catalysis):** J. D. Bernal[28] first suggested this possibility in 1947[29]—his suggestion was ignored until the 1970s. Others have run experiments and elaborated on it. He favored clays because they have a specific regularly ordered molecular crystal structure, and some have surface charges which can bind simple organic molecules in an orderly manner. Thus some clays have catalytic surfaces that can facilitate the formation of polymers by allowing small molecules to be concentrated in an orderly manner and be polymerized. In particular, clays allow formaldehyde (CH_2O)—which is produced easily in spark experiments—to be polymerized into sugars, principally the 5-member ring sugars like those in DNA and RNA: ribose and deoxyribose. [MCM: In these sugars, there are 4 carbons

---

in sediments dated to 3.7 Ga and indicates it was transported in solution by oxygenated water (otherwise it would have precipitated out). These opponents argue that this presence of oxygen precludes the formation of prebiotic molecules via a Miller-Urey-like scenario, attempting to invalidate the hypothesis of abiogenesis. However, the authors of the paper are arguing that this presence of oxygen merely evidences the existence of photosynthetic organisms 3.7 Ga ago (a value about 200 Ma earlier than current values), a conclusion which while pushing back the time frame in which Miller-Urey reactions and abiogenesis could potentially have occurred, would not preclude them. Though there is somewhat controversial evidence for very small (less than 0.1%) amounts of oxygen in the atmosphere almost as old as Earth's oldest rocks, the authors are not in any way arguing for the existence of an oxygen-rich atmosphere any earlier than previously thought, and they state: ". . . In fact most evidence suggests that oxygenic photosynthesis was present during time periods from which there is evidence for a non-oxygenic atmosphere".

Conditions similar to those of the Miller-Urey experiments are present in other regions of the solar system, often substituting ultraviolet light for lightning as the driving force for chemical reactions. On September 28, 1969, the Murchison meteorite that fell near Murchison, Victoria, Australia was found to contain over 90 different amino acids, nineteen of which are found in Earth life. Comets and other icy outer-solar-system bodies are thought to contain large amounts of complex carbon compounds (such as tholins) formed by these processes, in some cases so much so that the surfaces of these bodies are turned dark red or as black as asphalt. The early Earth was bombarded heavily by comets, possibly providing a large supply of complex organic molecules along with the water and other volatiles they contributed.
[http://en.wikipedia.org/wiki/Miller-Urey_experiment]

[28] **John Desmond Bernal** (1901 - 1971)
• "was an Irish-born scientist (from Nenagh, County Tipperary), known for pioneering X-ray crystallography... "
[http://en.wikipedia.org/wiki/John_Desmond_Bernal]
• "The biologist John Desmond Bernal, coined the term Biopoesis for this process, and suggested that there were a number of clearly defined "stages" that could be recognised in explaining the origin of life.
Stage 1: The origin of biological monomers
Stage 2: The origin of biological polymers
Stage 3: The evolution from molecules to cell "
http://en.wikipedia.org/wiki/Origin_of_life
• "One of his pupils, the British biochemist and crystallographer Dorothy C. Hodgkin, received the Nobel Prize in chemistry in 1964 for X-ray studies of compounds, such as vitamin B12 and penicillin."
http://reference.howstuffworks.com/bernal-j-d-encyclopedia.htm
• MCM: Bernal is not listed as a Nobel Prize winner
http://en.wikipedia.org/wiki/List_of_Nobel_laureates

[29] **Bernal's Clay hypothesis**: "Montmorillonite, a clay mineral formed by the weathering of volcanic ash, may have played a central role in the evolution of life. Because of its structure, montmorillonite tends to adsorb organic compounds and this contributes to its ability to catalyze a variety of organic reactions critical to scenarios of life's origins. We have shown experimentally that RNA molecules bind efficiently to clays and that montmorillonite can catalyze the formation of longer molecules (oligomers), thus lending support to the RNA world hypothesis. This theory proposes that life based on RNA preceded current life, which is based on DNA and protein. More than half a century ago, Irish physicist John Desmond Bernal and Swiss geochemist Victor M. Goldschmidt independently proposed that clay minerals may have played an important role in prebiotic synthesis (Bernal 1949; Goldschmidt 1952)."
James P. Ferris "Mineral Catalysis and Prebiotic Synthesis: Montmorillonite-Catalyzed Formation of RNA". *ELEMENTS* , VOL . 1 , pp. 145-149. JUNE 2005
found at http://www.origins.rpi.edu/pdf/elemv1n3_145_150.pdf

plus one O as ring members—an additional (5th) C projects away from the ring.] Montmorillonite is a soft clay-forming mineral[30] which catalyzes the polymerization of sugars to short chains. After Miller-Urey, it could be explained how amino acids formed, but this new hypothesis provided a much-needed explanation for the formation of the sugars required by RNA or DNA and also required to provide energy for life forms. See also G. Cairns-Smith *Seven Clues to the Origin of Life: A Scientific Detective Story.* (1985).

Key concepts:
a. Surface chemistry (such as on clays) is important for making polymers. Gas and aqueous phases are not sufficient, must also have surface reactions.
b. Crystalline structure of clays impart order to the chemical forming on them of polymers.

Flaws:
a. It is very difficult to remove the molecules once they are bonded onto minerals.
b. There is no evidence of clay-like minerals participating as catalysts in modern (extant) life. Many enzymes have active centers resembling iron pyrite centers, but there is no evidence of silicate-related centers... (?).

6. **Life Began On A Polar Ice Cap (or On Interstellar Ice)**: Astronomy has revealed—using absorption spectroscopy—that simple organic molecules occur in interstellar dust clouds. Formaldehyde (CH_2O) was the first organic compound found in interstellar dust, and water, ammonia, HCN, and cyanoacetylene HCC-CN and many other molecules, ions, and radicals, etc. have been found[31] . Analysis of meteorites showed that cold planetary [MCM: or celestial] surfaces could be rich in organic molecules such as amino acids. Carbonaceous chondrite meteorites[32] have up to 5% organic content. Spectroscopy of comets showed that they were organic-rich snowballs. Experiments irradiating ice with UV have yielded amino acids and simple polymers.[33]

---

[30] **Montmorillonite**: "Montmorillonite is a very soft phyllosilicate mineral that typically forms in microscopic crystals, forming a clay. It is named after Montmorillon in France. Montmorillonite, a member of the smectite family, is a 2:1 clay, meaning that it has 2 tetrahedral sheets sandwiching a central octahedral sheet. The particles are plate-shaped with an average diameter of approximately 1 micrometre. It is the main constituent of the volcanic ash weathering product, bentonite."
http://en.wikipedia.org/wiki/Montmorillonite

[31] **Lists of molecules, radicals, etc. found in interstellar space**
• http://www-691.gsfc.nasa.gov/cosmic.ice.lab/interstellar.htm
• http://en.wikipedia.org/wiki/List_of_molecules_in_interstellar_space

[32] **Carbonaceous chondrite meteorites**: "A carbonaceous chondrite or a C-type chondrite is a type of chondritic meteorite which contains high levels of water and organic compounds, representing only a small proportion (~5%) of known meteorites. Their bulk composition is mainly silicates, oxides and sulfides, while the minerals olivine and serpentine are characteristic. The presence of volatile organic chemicals and water indicates that they have not undergone significant heating (>200°C) since they formed, so their composition is considered to be representative of the solar nebula from which the solar system condensed.

Carbonaceous chondrites are grouped according to distinctive compositions thought to reflect the type of parent body from which they originated. These are named after a prominent meteorite - often the first to be discovered - in the group...

The CM meteorite from Murchison, Victoria has over 70 extraterrestrial amino acids and other compounds including carboxylic acids, hydroxy carboxylic acids, sulphonic and phosphonic acids, aliphatic, aromatic and polar hydrocarbons, fullerenes, heterocycles, carbonyl compounds, alcohols, amines and amides."
http://en.wikipedia.org/wiki/Carbonaceous_chondrite

[33] **UV Irradiation of Ice**: "...Here we report a laboratory demonstration that glycine, alanine and serine naturally form from ultraviolet photolysis of the analogues of icy interstellar grains. Such amino acids would naturally have a deuterium excess similar to that seen in interstellar molecular clouds, and the formation process could also result in enantiomeric excesses if the incident radiation is circularly polarized. These results suggest that at least some meteoritic amino acids are the result of interstellar photochemistry, rather than formation in liquid water on an early Solar System body...
"Racemic amino acids from the ultraviolet photolysis of interstellar ice analogues. Max P. Bernstein et al. *Nature* Vol 416. 28 March 2002 (accessed thru UW online journals)

Key concepts:
a. Freezing provides a good concentrating mechanism for forming polymers.
b. Freezing dehydrates things, encouraging polymer formation. (Proteins are formed by linking amino acids in peptide bonds created by a dehydration synthesis reaction.)

Flaw: Cold temperature slows chemical reactions and immobilizes reaction products, for instance, in Carbonaceous chondrite meteorite.

7. **Life Began In A Hot Spring (Black Smoker)**: Discovery of submarine hydrothermal vents[34] ("black smokers") belching very reducing superheated solutions with highly concentrated metal ions, sulfides, etc. provided possible new possible site for formation of life. Early Earth must have had many similar environments given the high radiogenic heat flow from within.

   [MCM: the following paragraph is confusing and possibly mistranscribed.] Günter Wächtershäuser[35], a chemist and patent attorney, showed that pyrite precipitated [MCM: or

---

[34] **Black Smoker Hydrothermal Vents**: "Black smokers are a type of hydrothermal vent found on the ocean floor. The vents are formed in fields hundreds of meters wide when superheated water from below the Earth's crust comes through the ocean floor. It can also be known as a Sea Vent. T he superheated water is rich in dissolved minerals from the crust, most notably sulfides, which crystallize to create a chimney-like structure around each vent. When the superheated water in the vent comes in contact with the cold ocean water, many minerals are precipitated, creating the distinctive black color. The metal sulfides that are deposited can become massive sulfide ore deposits in time.

Black smokers were first discovered in 1977 around the Galápagos Islands by the National Oceanic and Atmospheric Administration. They were observed using a small submersible vehicle called Alvin. Today, black smokers are known to exist in the Atlantic and Pacific Oceans, at an average depth of 2100 meters. The temperature of the water at the vent can reach 400 °C, but does not usually boil at the seafloor due to the high pressure it is under at that depth. The water is also extremely acidic, often having a pH value as low as 2.8—approximately that of vinegar. Each year 1.4×10^{14} kg of water is passed through black smokers.

... Although life is very sparse at these depths, black smokers are the center of entire ecosystems. Sunlight is nonexistent, so many organisms—such as archaea and extremophiles—must convert the heat, methane, and sulfur compounds provided by black smokers into energy through a process called chemosynthesis. In turn, more complex life forms like clams and tubeworms feed on these organisms. The organisms at the base of the food chain also deposit minerals into the base of the black smoker, thus completing the life cycle."
http://en.wikipedia.org/wiki/Black_smokers

[35] **Wächtershäuser's Iron-Sulfur World**:
• "The iron-sulfur world theory is a hypothesis for the origin of life advanced by Günter Wächtershäuser, a Munich chemist and patent lawyer, involving forms of iron and sulfur. Wächtershäuser proposes that an early form of metabolism predated genetics. Metabolism here means a cycle of chemical reactions that produce energy in a form that can be harnessed by other processes. The idea is that once a primitive metabolic cycle was established, it began to produce ever more complex compounds.

A key idea of the theory is that this early chemistry of life occurred not in bulk solution in the oceans, but on mineral surfaces (e.g. iron pyrites) near deep submarine vents. This was an anaerobic, high-temperature (near 100°C), high-pressure environment. The first 'cells' would have been lipid bubbles on the mineral surfaces.

Wächtershäuser has hypothesized a special role for acetic acid, a simple combination of carbon, hydrogen, and oxygen found in vinegar. Acetic acid is part of the citric acid cycle that is fundamental to metabolism in cells...."
http://en.wikipedia.org/wiki/Iron-sulfur_world_theory
• In the editorial article sited below ("Life as We Don't Know It"), Günter Wächtershäuser refers to G. D. Cody et al., *Science* 289, 1337 (2000), and states:

"Pyruvic acid ... is one of the most crucial constituents of extant intermediary metabolism. It occurs in numerous metabolic pathways, notably the reductive citric acid cycle and the pathways that produce amino acids and sugars. It has been suggested that pyruvic acid or its anion pyruvate formed primordially by double carbonylation... Cody et al. provide experimental support for this suggestion. They show that pryuvic acid forms from formic acid in the presence of nonylmercaptane and iron pyruvate participated] in such settings and that pyrite [MCM: pyruvate?] could be the product of simple abiotic metabolism, releasing H, then catalyzing further reactions. He argues that these initially abiotic systems ["in which synthesis and polymerization of organic compounds took place on the surface of FeS and FeS_2"[36]] were subsequently taken over by organic molecules [MCM: or living systems]... Another model—metastable organic synthesis from dissolved gases in these environments, show simple redox metabolic systems are viable...(?)

John A. Baross, oceanographer at UW, has made important contributions in this origin of life topic.

[MCM: the following paragraph is confusing] Pyrite formation is highly exothermic[37] and gives off energy. Presence of S and metal can promote this reaction with energy release. Resembles metabolism. Excessive energy and reducing power could lead to biological takeover. ["The FeS/H2S combination is a strong reducing agent."[38]] May also be short-lived unstable reactive meta-stable organic compounds capable of undergoing redox reactions such as living organisms use for metabolism. A non-organic metabolism that would lead to organic (living) metabolism.

Key concepts:
a. Energy gradient is important for primitive metabolism.
b. Reducing micro-environments were common on the early Earth.

Flaw:
a. Heat rapidly destroys most organic polymers
b. Hydrothermal systems are very short lived, precipitated minerals plug up the vents within c.

---

sulfide at 250 [degrees] C and 200 MPa. Water is initially absent and forms only by the dehydration of the formic acid. This result poses fascinating thermodynamic and kinetic questions. Pyruvic acid is an extremely heat-sensitive compound that decomposes at. its boiling point of 165 [degrees] C. It appears paradoxical that at the very high temperature required for dehydration of formic acid, the relatively unstable pyruvic acid can form and exist at detectable concentrations. Moreover, it is astonishing that acetic acid is formed at a lower yield than pyruvic acid. The explanation may well lie in the very high pressure.

The work is particularly exciting because experience with organic synthesis in the high-pressure/high-temperature regime is very limited... It remains to be established whether such conditions are geophysically possible.

The new finding, if it holds, fills a critical gap in the experimental picture of the iron-sulfur world (see the figure)... The challenge will now be to overcome the discrepancies in the reaction conditions and to establish the right conditions for autocatalysis (reproduction) and evolution...

The reaction scheme in the figure is in substantial agreement with extant metabolism in terms of overall metabolic patterns, reaction pathways, and catalysts. The newly demonstrated formation of pyruvic acid by double carbonylation, however, has no analog in extant metabolism. It may have disappeared because of metabolic takeover...

Cody et al.'s results support the view that the primordial organisms were autotrophs feeding on carbon monoxide. But more importantly, the reactions shown in the figure can still occur today because the required conditions are in general still available on Earth, albeit at a lesser frequency....

It is occasionally suggested that experiments within the iron-sulfur world theory demonstrate merely yet another source of organics for the prebiotic broth. This is a misconception. The new finding drives this point home. Pyruvate is too unstable to ever be considered as a slowly accumulating component in a prebiotic broth. The prebiotic broth theory and the iron-sulfur world theory are incompatible..."
Günter Wächtershäuser "Life as We Don't Know It.(scientific theories on the origin of the earth)". *Science* 289.5483 (August 25, 2000): p1307.

[36] *PB2002* p. 5

[37] **Exothermic Pyrite Reactions**: "At standard conditions, the formation of pyrite [from Fe and 2S] is exothermic having an enthalpy value of -171.5 kJ-mol^{-1}.
Ladislav Cemič. *Thermodynamics in Mineral Sciences: An Introduction.* [year not stated]
"The low temperature oxidation of pyrite [FeS_2 to iron (II) sulfate $FeSO_4$] is exothermic."
James G. Speight. *The Chemistry and Technology of Coal.* p. 253

[38] *PB2002* p. 5.

1000 years or less.

8. **First Life Was a Smart Molecule (RNA)**: Walter "Wally" Gilbert argued that RNA was a key molecule because it could store, copy, and transport and translate information, so it could have constituted the first living entity , because primitive life required little else. Note that the HIV-AIDS retrovirus is an RNA virus. Thomas Cech[39], a Nobel Laureate in chemistry, showed that RNA molecules could also catalyze protein synthesis and cleavage (functioning as "ribozymes"), that some RNAs could catalyze their own splitting. Experiment shows that RNA can be forced to evolve to develop better catalytic properties.

   Key concepts:
   a. RNA can perform many of the major functions of life by itself
   b. The Last Common Ancestor Of All Life may have been considerably more complex than the first life, limiting what we can learn from modern biology about first life.

   Flaws: No known environment for synthesizing and polymerizing RNA. For example, where do the phosphate groups come from (phosphate is rare in geologic environments)? No supply of energy to power RNA world. Can make RNA-like molecules on clay, but not RNA itself.

   Nevertheless, this is the most popular paradigm for life's origin currently, some kind of RNA world.

9. **Life Began On A Beach**: Roger Buick is developing and advancing this theory. The Archean Earth shows complex environment and many energy sources, many organic sources, many catalytic surfaces, micro-environments allowing segregation. Seek a site with maximal environmental interface between atmosphere, hydrosphere, lithosphere, where catalytic minerals accumulate, dehydration is enhanced, energy supply and gradients are high (but not too high), conditions are variable but long-lived. This describes a Beach! But there was no land in Archean according to former dogma—a view now refuted.

   Key concepts:
   a. Maximize environmental diversity to allow best aspects of all models to contribute to formation of life.
   b. Based on realistic early Earth conditions

   Flaw: Roger says "It's my idea, so it probably is no good."

Extraterrestrial Life

(per RB lectures):
Is Earth the only inhabited astronomical body? Extraterrestrial (ET) life is the subject of **astrobiology**. This is a term that NASA has applied to the search for extant and extinct life, and to justify massive budget expenditures for this research, etc.

The key questions of astrobiology regarding ET life forms are:
1. Are they out there? (No ET life has been found so far).
2. Where might they live?
3. Is there any in our solar system?

---

[39] **Thomas Cech**: "Thomas Cech's main research area is that of the process of transcription in the nucleus of cells. He studies how the genetic code of DNA is transcribed into RNA. In the 1970s, Dr. Cech had been studying the splicing of RNA in the unicellular organism Tetrahymena thermophila when he discovered that an unprocessed RNA molecule could splice itself. In 1982, Dr. Cech became the first to show that RNA molecules are not restricted to being passive carriers of genetic information - they can have catalytic functions and can participate in cellular reactions. RNA-processing reactions and protein synthesis on ribosomes in particular are catalysed by RNA. RNA enzymes are known as ribozymes and have provided a new tool for gene technology. They also have the potential to provide new therapeutic agents - for example, they have the ability to destroy and cleave invading, viral RNAs." http://en.wikipedia.org/wiki/Thomas_R._Cech

4. What might they be like? Are they humanoid?
5. How can we find them?

Habitable Planets: Factors Predisposing to Habitability

(per RB lectures and supplemented)

Presumed Characteristics of Habitable Planets (and Moons)

(see **diagram** plotting the ratio of the mass of the star to the mass of the Sun against the orbital distance in AU, including a band designated as the "habitable zone" HZ, e.g. at http://en.wikipedia.org/wiki/Planetary_habitability. RB's diagram also included a plot of the tidal lock radius[40], which the Earth lies outside of).

The planetary characteristics thought to make a planet[41] in orbit around a host star potentially habitable include the following [note that additional needed stellar and galactic characteristics are listed further below]:

1. **Planet Not Too Close to a Gas Giant Planet[42]** : Otherwise gravity prevents the formation of small rocky planets (which are the most likely to support life).
2. **Planet Not Too Close To Its Host Star**. This is needed to avoid tidal locking (in which one side of the planet is always turned toward the start, e.g., Mercury—see Glossary). Tidal locking leads to severe persistent temperature extremes.
3. **Planet's Mass Falls In Appropriate Range**: The planet's mass should be less than that of a gas giant but still large enough to maintain an atmosphere and possess a magnetic field. Mercury has no atmosphere and Mars has only a trace currently [about 6-10 millibar or 0.6 - 1.0 kPa compared to c. 1013 millibar at Earth sea level[43]]. Mars's atmosphere is low due to lower gravity (0.376g) Earth is losing atmosphere slowly to space. Venus has a dense atmosphere—all gases in the surface rocks have outgassed, and there are no plate tectonics to help return these gases to the mantle. In contrast, Earth recycles some of its gases to the mantle through plate tectonics and subduction. Earth's magnetic field is produced by convection of liquid Fe in outer core. This provide shielding against influx of high energy charged particles. The surface of Mars has high rate of bombardment by high energy charged particles and ionizing radiation, due both to its thin atmosphere and low magnetic field, and would therefore be hazardous to astronauts[44].

---

[40] *TES2000* p. 385

[41] **Extrasolar planet (AKA exoplanet)**:
• a planet beyond the Solar System. The only directly imaged example is the brown dwarf 2M1207 and its planetary companion 2M1207b.
http://en.wikipedia.org/wiki/Extrasolar_planet
• List of Stars with confirmed extrasolar planets:
http://en.wikipedia.org/wiki/List_of_stars_with_confirmed_extrasolar_planets

[42] **Gas Giant Planet**: "A planet composed primarily of hydrogen gas with a mass between about 95 M_{EARTH} and 13 M_{JUP} ... Substellar objects more massive than 13 M_{JUP} are considered to be brown dwarfs rather than planets. Among the planets of the Solar System, Jupiter seems to be a typical gas giant, while Saturn is just above the dividing line between gas giant planets and the second most massive category, ice giants."
http://www.deepfly.org/TheNeighborhood/Glossary.html

[43] **Mars Atmospheric pressure**: http://en.wikipedia.org/wiki/Mars

[44] **Mars ionizing radiation**: "Mars has no global geomagnetic field comparable to Earth's. Combined with a thin atmosphere, this permits a significant amount of ionizing radiation to reach the Martian surface. The Mars Odyssey spacecraft carried an instrument, the Mars Radiation Environment Experiment (MARIE), to measure the dangers to humans. MARIE found that radiation levels in orbit above Mars are 2.5 times higher than at the International Space Station. Average doses were about 22 millirads per day (220 micrograys per day or 0.8 gray per year). A three year exposure to such levels would be close to the safety limits currently adopted by NASA. Levels at the Martian surface would be somewhat lower and might vary significantly at different locations depending on altitude and local magnetic fields."
http://en.wikipedia.org/wiki/Colonization_of_Mars

4. **Planet Has Nearly Circular Orbit (Low Eccentricity) and Little Variation in Relatively Low Axial Tilt**: These criteria also ensure that there will be relatively low seasonal or longer-term variation in temperatures. The Earth has 23.5° axial tilt. But Mars, currently tilted at 25.2°, varies in tilt[45] from 0° to 50° over long time periods [MCM: range estimates vary]. It also has significantly greater orbital eccentricity[46] [47]than Earth [causing the seasons to have much more unequal length]. Mars has had more widely fluctuating temperatures and migrating ice caps.
5. **Presence of a Distant ("Exterior") Gas Giant Planet**: It is desirable to have in the same planetary system a "good Jupiter" or "good gas giant"—not too close—that can protect the planet from intense bombardment by comets and asteroids by sweeping them up. The Kuiper Belt[48] and Oort Cloud[49] are zones of icy comets—these comets can be perturbed in their orbits

---

[45] **Mars' Axial Tilt (Inclination of equator to orbital plane, Axial Inclination, or Obliquity)**:
• "Both the tilt of Mars' equator is similar to that of Earth's: 25.1°; so Mars experiences seasons in much a similar way as Earth."
http://www.mira.org/fts0/planets/097/text/txt001x.htm
• "It is interesting to note that the axial tilt and eccentricity of Earth (or Mars) are by no means fixed, but rather vary due to gravitational perturbations from other planets in the solar system on a timescale of tens of thousands or hundreds of thousands of years."
http://en.wikipedia.org/wiki/Astronomy_on_Mars
• "Precession in the alignment of the obliquity and eccentricity lead to [Martian] global warming and cooling ('great' summers and winters) with a period of 170,000 years.
Like Earth, the obliquity of Mars undergoes periodic changes which can lead to long-lasting changes in climate. Once again, the effect is more pronounced on Mars because it lacks the stabilizing influence of a large moon. As a result the obliquity can alter by as much as 45°. Jacques Laskar, of France's National Centre for Scientific Research, argues that the effects of these periodic climate changes can be seen in the layered nature of the ice cap on the planets north pole. Current research suggests that Mars is in a warm interglacial period which has lasted more than 100,000 years"
http://en.wikipedia.org/wiki/Climate_of_Mars
• "Other planets may have a variable obliquity too, for example on Mars the range is believed to be between 15° and 35°"
http://en.wikipedia.org/wiki/Axial_tilt
• "The obliquity of Mars is still in a large chaotic region, ranging from 0° to 60°"
Nature 361, 608 - 612 (18 February 1993)
[46] **Orbital Eccentricity**: "In astrodynamics, under standard assumptions, any orbit must be of conic section shape. The eccentricity of this conic section, the orbit's eccentricity, is an important parameter of the orbit that defines its absolute shape. Eccentricity may be interpreted as a measure of how much this shape deviates from a circle..."
Eccentricity is calculated as

$(d_a-d_p)/(d_a+d_p)$

where
d_a = distance at **apoapsis** (generic name for farthest approach of orbiting body such as a planet with respect to the center of attraction or mass of the planetary system; formerly in planetary systems more specifically also called the **apastron**), and
d_p = distance at **periapsis** (closest approach of planet, formerly more specifically also called the **periastron**).
Eccentricity e for circular orbit = 0, for elliptic orbits $0<e<1$, for parabolic trajectory e = 1, and for hyperbolic trajectory e > 1.
"...The eccentricity of the Earth's orbit today is 0.0167. Through time, the eccentricity of the Earth's orbit slowly changes from nearly 0 to almost 0.05 as a result of gravitational attractions between the planets..."
http://en.wikipedia.org/wiki/Orbital_eccentricity
[47] **Mars Orbital Eccentricity**:
• "Its orbit is much less circular than Earth's, its distance to the Sun varies about 19%, from approximately 210 million kilometers to 250 million km (130-155 million miles).
http://www.mira.org/fts0/planets/097/text/txt001x.htm
• Mars eccentricity is 0.0934.
http://en.wikipedia.org/wiki/Table_of_planets_in_the_solar_system
[48] **Kuiper Belt**: The Kuiper belt (rhymes with "viper") "...is a region of the Solar System beyond the planets extending from the orbit of Neptune (at 30 AU) to approximately 55 AU from the Sun. It is similar to the asteroid belt, although it is far larger; 20 times as wide and 20–200 times as massive.

and be flung into the inner solar system. Comet Shoemaker-Levy 9[50], which impacted Jupiter, was presumably one such comet.

6. **Presence of Liquid Water and Sufficient "Metals"** (see below).
7. **Absence of High Radiation** (see below).

Like the asteroid belt, it consists mainly of small bodies (remnants from the Solar System's formation) and at least one dwarf planet – Pluto. But while the asteroid belt is composed primarily of rock and metal, the Kuiper belt objects are composed largely of frozen volatiles (dubbed "ices"), such as methane, ammonia, and water.

Since the first was discovered in 1992, the number of known Kuiper belt objects (KBOs) has increased to over a thousand, and more than 70,000 KBOs over 1 km in diameter are believed to reside there. The Kuiper belt is believed to be the main repository for periodic comets, those with orbits lasting less than 200 years. The centaurs, comet-like bodies that orbit among the gas giants, are also believed to originate there, as are the scattered disc objects such as Eris—KBO-like bodies with extremely large orbits that take them as far as 100 AU from the Sun. Neptune's moon Triton is believed to be a captured KBO. Pluto, a dwarf planet, is the largest known member of the Kuiper belt. Originally considered a planet, it has many physical properties in common with the objects of the Kuiper belt, and has been known since the early 1990s to share its orbit with a number of similarly sized KBOs, now called Plutinos.

The Kuiper belt should not be confused with the hypothesized Oort cloud, which is a thousand times more distant. The objects within the Kuiper belt, together with the members of the scattered disc and any potential Hills cloud or Oort cloud objects, are collectively referred to as **trans-Neptunian objects** (TNOs).
http://en.wikipedia.org/wiki/Kuiper_belt

[49] **Oort Cloud**: The Oort cloud "... is a postulated spherical cloud of comets situated about 50,000 AU from the Sun. This is approximately 1000 times the distance from the Sun to Pluto or nearly a light year. The outer extent of the Oort cloud places the boundary of our Solar System at nearly a quarter of the distance to Proxima Centauri, the nearest star to the Sun.

Although no confirmed direct observations of the Oort cloud have been made, astronomers believe it to be the source of all **long period** and **Halley-type comets** entering the inner solar system (some short-period comets, based on their orbits, may come from the Kuiper belt).

... According to the hypothesis, the Oort cloud contains trillions of comet nuclei, which are stable because the Sun's radiation is very weak at their distance. The cloud provides **a continual supply of new comets**, replacing those that are destroyed. In order for it to supply the necessary volume of comets, the total mass of comets in the Oort cloud must be many times that of Earth.

The Oort cloud is thought to occupy a vast space from the outer boundary of the Kuiper belt at 50 AU to as far as 50,000 AU from the Sun. It can be subdivided into spherical **outer Oort cloud** (20,000-50,000 AU) and doughnut-shaped **inner Oort cloud** (50-20,000 AU). The outer cloud is only weakly bound to the Sun and supplies the long period (and possibly Halley-type) comets to the inner part of the Solar System. The inner Oort cloud is also known as the Hills cloud, and may be the source of Halley-type comets. Some scientists think that the Hills cloud may contain much more material than the outer cloud. This hypothesis is employed to explain the continued existence of the Oort cloud over the course of billions of years.

... It is thought that other stars are likely to possess Oort clouds of their own, and that the outer edges of two nearby stars' Oort clouds may sometimes overlap, causing perturbations in the comets' orbits and thereby increasing the number of comets that enter the inner solar system. The interactions of the Oort cloud with those of neighboring stars, and its deformation by the galactic tide are thought to be the main triggers which send the long-period comets into the inner Solar System. This process also serves to scatter the objects out of the ecliptic plane, explaining the cloud's spherical distribution

The outer Oort cloud is commonly thought to contain several trillion individual comet nuclei larger than ~1.3 km, each tens of millions of kilometers apart. Its mass is not known with certainty, but is unlikely to be more than a few Earth masses. Earlier it was thought to be more massive (up to 380 Earth masses). However, the improved knowledge about the size distribution of the long period comets led to much lower values. The mass of the inner Oort cloud is not currently known.
http://en.wikipedia.org/wiki/Oort_cloud

[50] **Comet Shoemaker-Levy 9**: http://www2.jpl.nasa.gov/sl9/

Water and Ice Line

(per RB lectures and supplemented):
Life is thought to require liquid water, and water exists as a liquid only in a narrow region in the solar [or planetary] system in terms of distance from the Sun [or star]. Beyond the ice-line radius, water exists only as water ice.

Planets having liquid water don't originally form at their current position relative to the ice-line, but instead form beyond the ice-line[51] [52] (the distance from the host star beyond which water condenses as solid ice from the primordial gas cloud). Later, one or both of the following occurs[53] in planets that develop liquid water:

a. **Migration**: Planets with water ice migrate inwards due to a gravitational disturbance of their orbits that place them closer to the host star and thereby allow liquid water to exist. [This is the **endogenous theory of origin of water**.]

b. **Comets**: Water is delivered to the planet by comets (which are just "dirty snowballs") after the planet has cooled from the initial hot formative period in which water cannot be liquid. [This is the **Exogenous theory of origin of water**.] Comets and meteors collide with our planet, adding to or giving rise to the veneer of water. Much or all of the Earth's water may have come from these comets. We know little currently about the isotopic composition of comets—only a few have been measured (e.g., Halley comet, C/1999 S4[54] also known as "Comet LINEAR", etc.) Mercury lies inside the ice-line, and has no liquid water.[55] The narrow zone in the planetary system allowing for liquid water to exist

---

[51] **The Ice Line and the Birth of Planets**: "According to the 'primordial nebula' theory, the solar system formed from a cloud of gas and dust which, drawn inwards upon itself by its own mass, became a rotating disc. Water—present as ice and water vapour—was one of the prime constituents of this cloud. The 'ice line'—its position defined by the temperature of condensation of water and therefore at a fixed distance from the Sun—marked the boundary between the gaseous component of the protosolar material (the inner solar system) and the solid component (the outer solar system). It was one of the major factors in the differentiation of the planets into two very distinct groups: terrestrials and giants."
Thérèse Encrenaz. *Searching for Water in the Universe*. Springer New York. 2007 (http://www.springerlink.com/content/h1n8q2m528521850)

[52] **Ice-Line in a Planetary System**: "For any given star, the ice line is the radius outside of which freely orbiting particles of water ice can persist indefinitely in solid form without sublimation into vacuum. This boundary is also known as the snow line. The location of the ice line depends on the host star's luminosity. In the Solar System, the ice line is located at a radius of about 3 AU. This marks the boundary between the inner Solar System, which is dominated by rocky planets and asteroids, and the outer Solar System, which is dominated by the four giant planets, their icy moons, and the debris fields of the Kuiper Belt. For M dwarf stars, the ice line will be correspondingly closer to the host star, at about 0.4 AU, while for A stars it will be much farther, at about 20 AU...

The location of the ice line is a key variable in planetary system formation, since rocky planets like Earth and Mars must form within the ice line, while gas giants like Jupiter, Saturn, and most known extrasolar planets preferentially form just outside the ice line."
http://www.deepfly.org/TheNeighborhood/Glossary.html

[53] **The distribution of H_2O in protoplanetary systems**
http://astrobiology.ucla.edu/pages/res1d.html

[54] **Comet LINEAR**: "... was likely made up of water with the same isotopic composition as water found here on Earth. The finding supports a controversial idea that cometary impacts billions of years ago could have provided most of the water in Earth's oceans."
http://science.nasa.gov/headlines/y2001/ast18may_1.htm

[55] **Water on Mercury?**: "Despite the generally extremely high temperature of its surface, observations strongly suggest that ice exists on Mercury. The floors of some deep craters near the poles are never exposed to direct sunlight, and temperatures there remain far lower than the global average. Water ice strongly reflects radar, and observations reveal that there are patches of very high radar reflection near the poles. While ice is not the only possible cause of these reflective regions, astronomers believe it is the most likely.... The origin of the ice on Mercury is not yet known, but the two most likely sources are from outgassing of water from the planet's interior or deposition by impacts of comets."
http://en.wikipedia.org/wiki/Mercury_%28planet%29

helps to define the Circumstellar Habitable Zone (see below).

Circumstellar Habitable Zone

(per RB and supplemented, see also Glossary)
(see **diagram** plotting the ratio of the mass of the star to the mass of the Sun against the orbital distance in AU, including a band designated as the "habitable zone" HZ, e.g. at http://en.wikipedia.org/wiki/Planetary_habitability and in TES2000 p. 385).
The Sun was formerly less luminous at visible wavelengths though not in UV wavelengths.[56] The earlier Earth was (?) warmer [MCM clarification: The very early earth was probably "cooler" than now because the Sun was less luminous, but see discussion about Faint Young Sun.] The **Circumstellar Habitable Zone** [**ecosphere**] is defined partly by the presence of liquid water, and is dependent on matching an appropriate stellar luminosity with the mean orbital radius for the planet. (Note that other features listed above and below also play a role in planetary habitability.) Stars can't be too bright or too dull—for example, they should have relative masses of c. 0.75 to 1.5 M_{Sol} [multiples of the mass of our Sun], a range which includes spectral class K, G, and F stars[57,58]. For life to succeed, the

---

[56] **Solar variation**: Solar variations are changes in the amount of radiant energy emitted by our Sun. There are periodic components to these variations, the principal one being the 11-year solar cycle (or sunspot cycle), as well as fluctuations which are aperiodic. Solar activity has been measured via satellites during recent decades and through 'proxy' variables in prior times. Climate scientists are interested in understanding what, if any, effect variations in solar activity have on the Earth. Any such mechanism is referred to as "solar forcing". The variations in **total solar irradiance** (TSI) remained at or below the threshold of detectability until the satellite era, although the small fraction in ultra-violet wavelengths varies by a few percent. Total solar output is now measured to vary (over the last three 11-year sunspot cycles) by approximately 0.1% or about 1.3 W/m^2 peak-to-trough during the 11 year sunspot cycle. The amount of solar radiation received at the outer surface of Earth's atmosphere varied little from an average value of **1366 watts per square meter** (W/m^2). There are no direct measurements of the longer-term variation and interpretations of proxy measures of variations differ; recent results suggest about **0.1% variation** over the last 2000 years. The combination of solar variation and volcanic effects has very likely been the cause of some climate change, for example during the Maunder Minimum. A 2006 study and review of existing literature, published in Nature, determined that there has been no net increase in solar brightness since the mid 1970s, and that changes in solar output within the past 400 years are unlikely to have played a major part in global warming. It should be stressed, the same report cautions that "Apart from solar brightness, more subtle influences on climate from cosmic rays or the Sun's ultraviolet radiation cannot be excluded, say the authors. However, these influences cannot be confirmed, they add, because physical models for such effects are still too poorly developed.
http://en.wikipedia.org/wiki/Solar_variation

[57] **Main Sequence Stars**:
• http://en.wikipedia.org/wiki/Main_sequence
• K0 stars through K7 stars have relative masses of 0.83 to 0.56. G and F types extend this range to 1.6. The Sun is a G2 star.
http://www.io.com/~iareth/mainsequence.html
• See also *TES2000* p. 191

Star Spectral Classes:
• "Nine spectral classes are currently used to characterize stars and substellar objects. Each spectral class denotes a typical range of mass and luminosity. Listed in order of decreasing mass, the spectral classes are O, B, A, F, G, K, M, L, T. For classes O through M, each spectral class represents a successively more numerous population of stars -- in other words, stellar populations vary inversely according to mass. It is uncertain whether this mass/number relationship continues into the dimmest classes, L and T, which represent brown dwarfs.
In units of Solar mass, each spectral class spans a characteristic mass range:
O = 20+ M_{SOL} . . . B = 3 to 20 M_{SOL} . . . A = 1.6 to 3.0 M_{SOL}
F = 1.1 to 1.5 M_{SOL} . . . G = 0.85 to 1.2 M_{SOL} . . . K = 0.6 to 0.95 M_{SOL}
M = 0.1 to 0.5 M_{SOL}
http://www.deepfly.org/TheNeighborhood/Glossary.html
• "An orange-red star, of spectral type K. The spectra of K stars are dominated by the H and K lines of calcium and lines of neutral iron and titanium, with molecular bands due to cyanogen (CN) and titanium dioxide (TiO) becoming increasingly prominent at the cooler end of the range. K-type main

star's luminosity cannot change substantially over time, except perhaps slowly over long periods to allow for adaptation. If a star is more than 2 M_{Sol}, the time available for formation of liquid water is less than 1 billion years before the star becomes a red giant.[59] Our Sun will not be a red giant until 4-5 billion years more have passed, thus it is favorable to life formation. Humans have a narrow temperature tolerance range, but less complex organisms are not as picky. Stars like the Sun tend to increase in luminosity[60,61] with time as continuing fusion of H to He reduces internal pressure.

---

sequence stars (that is, K-type dwarfs) are intermediate in size and temperature between M-type red dwarfs and Sun-like stars (type G), with a mass of 0.5 to 0.8 M_{sun}, a temperature of 3900 to 5200 K (3600 to 4900°C), and a luminosity 0.1 to 0.4 L_{sun}."
http://www.daviddarling.info/encyclopedia/K/Kstar.html
• [The] "**Harvard one-dimensional (temperature) classification** scheme (based on hydrogen Balmer line strengths) was developed in Harvard College Observatory at about 1912 by Annie Jump Cannon and Edward C. Pickering." It includes common classes O B A F G K and M
There is also a **Yerkes spectral classification ("MKK")** comprising the following major classes: I supergiants, II bright giants, III normal giants, IV subgiants, V main sequence stars (dwarfs), VI subdwarfs (rarely used), and VII white dwarfs (rarely used).
http://en.wikipedia.org/wiki/Stellar_classification
[58] **Spectral Class of Stars for Habitable Planets**: "The spectral class of a star indicates its photospheric temperature, which (for main-sequence stars) correlates to overall mass. The appropriate spectral range for [stars suitable for planetary habitability] is presently considered to be "early F" or "G", to "mid-K". This corresponds to temperatures of a little more than 7,000 K down to a little more than 4,000 K; the Sun, a G2 star, is well within these bounds. "Middle-class" stars of this sort have a number of characteristics considered important to planetary habitability:
a. They live at least a few billion years, allowing life a chance to evolve. More luminous main-sequence stars of the "O," "B," and "A" classes [which are larger] usually live less than a billion years and in exceptional cases less than 10 million years.
b. They emit enough high-frequency ultraviolet radiation to trigger important atmospheric dynamics such as ozone formation, but not so much that ionisation destroys incipient life.
c. Liquid water may exist on the surface of planets orbiting them at a distance that does not induce tidal lock.
http://en.wikipedia.org/wiki/Planetary_habitability
[59] **Red Giant star**: "Red giants evolve from main sequence stars with masses in the range from about 0.5 solar masses to somewhere between 4 and 6 solar masses. Red giants are stars with radii hundreds of times larger than that of the Sun which have exhausted the supply of hydrogen in their cores and switched to fusing hydrogen in a shell outside the core. Since the inert helium core has no source of energy of its own, it contracts and heats up, and its gravity compresses the hydrogen in the layer immediately above it, thus causing it to fuse faster. This in turn causes the star to become more luminous (from 1,000 to 10,000 times brighter) and expand; the degree of expansion outstrips the increase in luminosity, thus causing the effective temperature to decrease. In stars massive enough to ignite helium fusion, an analogous process occurs when central helium is exhausted and the star switches to fusing helium in a shell, although with the additional complication that in many cases hydrogen fusion will continue in a shell at lesser depth—this puts stars onto the asymptotic giant branch. The decrease in surface temperature shifts the star's visible light output towards the red—hence red giant, even though the color usually is orange. Main sequence stars of spectral types A through K are believed to become red giants...

... The Sun is expected to become a red giant in about 4.5 billion years. It is calculated that the Sun will become almost sufficiently large to engulf the current orbits of some of the solar system's inner planets, including Earth. However, the gravitational pull of the Sun will have weakened by then due to its loss of mass, and all planets but Mercury will escape to a wider orbit. That said, Earth's biosphere will be destroyed as the Sun gets brighter while its hydrogen supply becomes depleted. The extra solar energy will cause the oceans to evaporate to space, causing Earth's atmosphere to become temporarily similar to that of Venus, before its atmosphere also gets driven off into space. Venus will become a burnt out planet; its atmosphere having long been driven off, and its rock will melt."
http://en.wikipedia.org/wiki/Red_giant
[60] **Increasing Solar Luminosity**: "Astronomers will sometimes refer to the "zero age main sequence", or ZAMS. This is a line calculated by computer models of where a star will be when it begins hydrogen fusion; its brightness and surface temperature typically increase from this point with age. Stars usually enter and leave the main sequence from about when they are born or when they are starting to

Faint Young Sun Paradox

(per RB and supplemented)
(See **diagram** in slide[62]): Temperature as the Y axis, going from 225 degrees Kelvin to 300 K, where the freezing point of water is 273 K. The X-axis was time in Ga going from c. 4.5 Ga to 0 (the present). T_e is the earth temperature considered as a "black body" (i.e. without the effect of an greenhouse atmosphere, thus colder), and T_s is the surface temperature of the Earth taking into account the greenhouse warming based on today's levels of atmospheric constituents. The diagram also shows a graph of relative solar luminosity variation over this same time period, rising from c. 0.7 to 1.0. This diagram shows a line for the freezing point of water, above which the T_s line eventually rises, but not until about 1.8 Ga.)

Stars like the Sun increase in luminosity as fusion of H to He reduces internal pressure. [MCM Clarification: The conversion of 4 H to 1 He nucleus would reduce core pressure all other things being held constant. However, "models predict … that the core contracts and heats up slightly as its helium content increases."[63]] Since 3.8 Ga, the Sun has become "30%" brighter[64] (in luminosity) [MCM: i.e., the initial value is estimated at c. 72% of current luminosity, or c. 30% less than current value.] For the Earth to have had liquid water with a temperature over 273 K as far ago as 3.8 - 4.4 Ga (when life was forming and yet the sun was cooler), there must have been a greenhouse effect greater than with today's atmosphere.[65]

---

die, respectively."
http://en.wikipedia.org/wiki/Main_sequence
[61] **Mid-Sized Stellar Evolution**: "A star of up to a few solar masses will develop a helium core supported by electron degeneracy pressure, surrounded by layers which still contain hydrogen. Its gravity compresses the hydrogen in the layer immediately above it [the helium core], thus causing it to fuse faster than hydrogen would fuse in a main-sequence star of the same mass. This in turn causes the star to become more luminous (from 1,000 – 10,000 times brighter) and expand; the degree of expansion outstrips the increase in luminosity, thus causing the effective temperature to decrease."
http://en.wikipedia.org/wiki/Stellar_evolution
[62] *TES2000* p. 232, derived from *Scientific American* 256:90, 1988. See also pp. 34-50 for quantitative discussion of blackbody radiation and greenhouse effect in general
[63] *TES2000* p. 14
[64] **Luminosity**:
• Defined as the amount of energy a body such as the Sun radiates per unit time, and thus measured in Watts. Subdivided into apparent (measuring visible light only) and bolometric (measuring all forms of radiant energy).
http://en.wikipedia.org/wiki/Luminosity
• For stars, the luminosity may be expressed as a ratio relative to the Sun's (in "**Solar Units**")
http://csep10.phys.utk.edu/astr162/lect/stars/magnitudes.html
• The solar luminosity … is a unit of luminosity (power emitted in the form of photons) conventionally used by astronomers to give the luminosities of stars. It is equal to the luminosity of the Sun, which is 3.827×10^{26} W, or 3.827×10^{33}ergs/s.
http://en.wikipedia.org/wiki/Solar_luminosity
[65] **Faint young Sun paradox**: "The faint young **Sun** paradox describes the apparent contradiction between observations of liquid water early in Earth's history and the astrophysical expectation that the **Sun**'s output would be only 70% as intense during that epoch as it is during the modern epoch.

The standard solar model describes the history and evolution of stars. An aspect of this model is that stars similar to the **Sun** should gradually brighten over their life time (excluding a very bright phase just after formation). This prediction is supported by the observation of lower brightness in young stars of solar type. However, with the predicted brightness 4 billion (10^9) years ago and with greenhouse gas concentrations the same as are current for the modern Earth, any liquid water exposed to the surface would quickly freeze solid. This contradicts geological observations of sedimentary rocks, which required the presence of flowing liquid water to form.

The tension between the two hypotheses stems from the incorrect assumption that atmospheric gas concentrations in the past were the same as today. First, before the advent of abundant life, the atmospheric oxygen concentrations were orders of magnitude lower than today. In the presence of oxygen, methane breaks down to carbon dioxide, so in the absence of oxygen the methane concentration could be much larger than currently observed. Methane is a more potent

Runaway Greenhouse Effect

(per RB and supplemented)
(see RB diagram plotting altitude in Venusian atmosphere y-axis against Temperature x-axis.).
1. If planets are too near to stars, they can get excess heating, vaporizing all water—even though they are inside the Water Ice Line, the water may be liquid or vapor
2. If temperature nears the boiling point of water, can get positive feedback (since water vapor is a strong greenhouse gas), causing more vaporization, thus more heat [infrared] trapping, thus more boiling, etc.
3. This phenomenon is called the "runaway greenhouse" effect and happened on Venus. In the Venusian atmosphere, the only zone potentially habitable with liquid water is possible in a band in the atmosphere [at about 50 to 70 km] where temperature drops from the c. 735 K at ground level to around 300 K.[66] This is near layers containing sulfuric acid clouds. The lowest temperature is at about 100 km, and temperatures increase above this altitude in the higher atmosphere up to 200 km.

Galactic Habitable Zone (GHZ)

(per RB and supplemented, see Glossary entries also)
This galactic zone is postulated to be determined by these galactic-level variables:

1. **Radiation Levels**: The region near the center of the galaxy has high ionizing radiation levels, lessening the likelihood of life, especially if the galaxy has a central black hole. These emissions arise from gamma ray bursters and supernovae, etc.
2. **Metallicity and Carbon Concentration**: The outer part of the galaxy has low "metallicity" (an astronomer's term meaning the relative concentration of elements heavier than H and He, regardless whether they are actually metals, see Glossary). Thus carbon concentration declines as one goes outward, decreasing the likelihood of carbon-based life.

The **Milky Way**[67] has its GHZ at 7 - 9 kparsec or kpc (23,000 - 29,000 light years) from its center. The Sun is estimated at 28,000 light years from the center, or 8.6 kpc [other estimates place it at 7.62

---

greenhouse gas than carbon dioxide, so the relative abundance of atmospheric methane throughout Earth's history must be considered when modeling the temperature.

Further, the inorganic version of the carbon cycle can be expected to provide negative feedback towards an Earth with liquid water. Carbon dissolved in liquid water can form carbonic acids, which can then interact with calcium to produce calcium carbonate. If rainfall were to cease and the oceans froze over, then this part of the inorganic carbon cycle would shut down. Periodic explosions from volcanoes would then cause a net increase in the atmospheric carbon dioxide and methane levels with no liquid water to absorb these emitted gases. Eventually the concentrations would become large enough that the surface temperature would rise due to the greenhouse effect. When the surface temperature became large enough for the oceans to melt and rainfall to resume the other half of the inorganic carbon cycle would turn on and moderate the greenhouse gas concentrations.

It is also noteworthy, that even though evidence of flowing water exists even from very early in Earth's history, there may still have been a number of examples of periods when the Earth's oceans froze over completely. The most recent such period may have been ~630 million years ago, and may have been instrumental in leading [to] the Cambrian explosion of new multicellular life forms."
http://en.wikipedia.org/wiki/Faint_young_sun_paradox

[66] **Venus Atmosphere Temperature Profile**:
• http://www.datasync.com/~rsf1/vel/1918vpt.htm
• http://en.wikipedia.org/wiki/Atmosphere_of_Venus
• For a comparable profile of Earth atmospheric temperature versus altitude, see http://www.ux1.eiu.edu/~cfjps/1400/atmos_origin.html

[67] **Milky Way size**: The Galactic Halo extends outward, but is limited in size by the orbits of the two Milky Way satellites, the Large and the Small Magellanic Clouds, whose perigalacticon is at ~180,000 light-years. [This determines the upper limit of Milky Way overall size.]...
...The Sun (and therefore the Earth and Solar System) may be found close to the inner rim of the Galaxy's Orion Arm, in the Local Fluff, at a hypothesized distance of 7.62±0.32 kpc from the Galactic

kpc].[68] See Glossary for more information about GHZ. (Guillermo Gonzalez, one of the initial proponents for GHZ, was denied tenure at Iowa State University due to his support for intelligent design. Was the circumstellar habitable zone and the galactic habitable zone divinely created?)

Potential Sites of Life in the Solar System

(per RB and supplemented, see Glossary entries also)
1. **Earth**
2. **Mars**. It was warmer and wetter before 3.5 GA. Are there possible biosignatures in a 4.5 GA Martian meteorite ALH84001?[69] There is a methane anomaly in Mars atmosphere, perhaps indicating subsurface extant life. (See further discussion on these topics below.)
3. **Europa** (moon of Jupiter)[70]: Europa has liquid salty ocean under ice cap [MCM: frozen upper crust or surface], so could harbor life. The icy crust exhibits magnesium sulfate line, sulfites, etc... Might conceivably get energy from deep ocean hydrothermal vents resembling black smokers.

Center."
http://en.wikipedia.org/wiki/Milky_Way

[68] **Milky Way Habitable Zone**:
"Our Sun is unusually metal-rich for a star of its age and type. Scientists aren't sure why. It could be that the Sun formed in a part of the Galaxy that had an abundance of metals, and then migrated to its present position...

Besides requiring a metal-rich star, a Galactic Habitable Zone excludes stars too close to the galactic center. Our Sun is a nice distance away from the galactic center, about 28,000 light years... Staying away from the galactic center has an additional advantage. The center of the Galaxy is awash in harmful radiation. Solar systems near the center would experience increased exposure to gamma rays, X-rays, and cosmic rays, which would destroy any life trying to evolve on a planet....
Keeping out of the way of the Galaxy's spiral arms is another requirement of the Galactic Habitable Zone...

The intense radiation and gravitation of a spiral arm would cause disruptions in our Solar System just as surely as if we were closer to the center of the Galaxy. Luckily, our Sun revolves at the same rate as the Galaxy's spiral-arm rotation. This synchronization prevents our Solar System from crossing a spiral arm too often...

The unusually circular orbit of our Sun around the galactic center also tends to keep it clear of the spiral arms. Most stars the same age as our Sun have more elliptical orbits...
Thus, thanks to a lot of unusual characteristics of our Sun, our Solar System is lucky enough to lie in a Galactic Habitable Zone. Gonzalez argues that these characteristics made it possible for complex life to emerge on Earth. More than 95 percent of stars in the Galaxy, says Gonzalez, wouldn't be able to support habitable planets simply because their rotation is not synchronized with the rotation of the galaxy's spiral arms."
http://www.spacedaily.com/news/life-01o.html

[69] **Meteorite ALH 84001**: ALH 84001 (Allan Hills 84001) is a meteorite found in Allan Hills, Antarctica in December 1984 by a team of US meteorite hunters from the ANSMET project. Like other members of the group of SNCs (shergottite, nakhlite, chassignite), ALH 84001 is thought to be from Mars. On discovery, its mass was 1.93 kg.... On August 6, 1996 ALH 84001 became newsworthy when it was announced that it was believed that the meteorite contained traces of life from Mars, as published in an article in Science by Dr. David McKay of NASA."
http://en.wikipedia.org/wiki/ALH84001

[70] **Europa**: "Europa is primarily composed of silicate rock, has an outer layer of ice with probably some liquid water, and likely has an iron core. At just over 3000 kilometers in diameter, it is slightly smaller than the Earth's moon and the sixth largest moon in the solar system. The satellite has a very tenuous oxygen atmosphere and one of the smoothest surfaces in the solar system. The young surface of the moon is striated by cracks and streaks, while craters are relatively infrequent. Due to a hypothesized water ocean beneath its icy surface, and an energy source provided by tidal heating, Europa has been cited as a possible host of extraterrestrial life. The heat energy ensures the ocean remains liquid and also drives geological activity

The intriguing character of Europa has led to a number of ambitious exploration proposals; to date, only flyby missions have visited the moon. The Galileo mission provided the bulk of current data on the satellite, while the abortive Jupiter Icy Moons Orbiter, cancelled in 2005, was the most ambitious planned spacecraft. Conjecture on extraterrestrial life has ensured a high profile for the moon and led to continued lobbying for future missions....

4. **Titan** (moon of Saturn)[71]: It has suspected hydrocarbon lakes and rains (including methane, ethane, etc.), so perhaps could have cold life.
5. **Enceladus** (moon of Saturn)[72]: Its South Pole exhibits water geysers. It is ice-covered but also thought to have a subsurface ocean warmed by tidal heating (as a result of its proximity to Saturn), so perhaps could harbor life there.

Europa's most striking surface feature is a series of dark streaks criss-crossing the entire globe. Close examination shows that the edges of Europa's crust on either side of the cracks have moved relative to each other. The larger bands are roughly 20 km (12 mi) across commonly with dark diffuse outer edges, regular striations, and a central band of lighter material…

Among the controversial hypotheses put forward to explain these features [Lineae], one states that they may have been produced by a series of volcanic water eruptions or geysers as the Europan crust spread open to expose warmer layers beneath. The effect would have been similar to that seen in the Earth's oceanic ridges. These various fractures are thought to have been caused in large part by the tidal stresses exerted by Jupiter; since Europa is tidally locked to Jupiter, and therefore always maintains the same approximate orientation towards the planet, the stress patterns should form a distinctive and predictable pattern. However, only the youngest of Europa's fractures conform to the predicted pattern; other fractures appear to have occurred at increasingly different orientations the older they are. This could be explained if Europa's surface rotates slightly faster than its interior, an effect which is possible due to the subsurface ocean mechanically decoupling the moon's surface from its rocky mantle and to the effects of Jupiter's gravity tugging on the moon's outer ice crust. Comparisons of Voyager and Galileo spacecraft photos serve to put an upper limit on this hypothetical slippage of no faster than once every 10,000 years for the surface relative to its interior….

The Galileo orbiter has also found that Europa has a weak magnetic field (about one quarter the strength of Ganymede's field and similar to Callisto's) which varies periodically as Europa passes through Jupiter's massive magnetic field. A likely explanation of this is that there is a large, subsurface ocean of liquid salt water. Spectrographic evidence suggests that the dark reddish streaks and features on Europa's surface may be rich in salts such as magnesium sulfate, deposited by evaporating water that emerged from within. Sulfuric acid hydrate is another possible explanation for the contaminant observed spectroscopically. In either case, since these materials are colorless or white when pure, some other material must also be present to account for the reddish color. Sulfur compounds are suspected.

It has been suggested that life may exist in this under-ice ocean, perhaps subsisting in an environment similar to Earth's deep-ocean hydrothermal vents or the Antarctic Lake Vostok. Life in such an ocean could possibly be similar to life on earth in the deep ocean. So far, there is no evidence that life exists on Europa but due to the likely presence of liquid water, there are proposals to send a probe there. Robert Pappalardo, an assistant professor within the University of Colorado's space department, said "We've spent quite a bit of time and effort trying to understand if Mars was once a habitable environment. Europa today, probably, is a habitable environment. We need to confirm this… but Europa, potentially, has all the ingredients for life… and not just four billion years ago… but today…"”
http://en.wikipedia.org/wiki/Europa_(moon)

[71] **Titan**: “Titan is primarily composed of water ice and rocky material. The dense atmosphere prevented understanding of Titan's surface until new information accumulated with the arrival of the Cassini–Huygens mission in 2004, including the discovery of liquid hydrocarbon lakes in the satellite's polar regions. These are the only large, stable bodies of surface liquid known to exist anywhere other than Earth. The surface is geologically young; although mountains and several possible cryovolcanoes have been discovered, it is relatively smooth and few impact craters have been discovered.

The atmosphere of Titan is largely composed of nitrogen and its climate includes methane and ethane clouds. The climate—including wind and rain—creates surface features that are similar to those on Earth, such as sand dunes and shorelines, and like Earth, is dominated by seasonal weather patterns. With its liquids (both surface and subsurface) and robust nitrogen atmosphere, Titan is viewed as analogous to the early Earth, although at much lower temperature. The satellite has thus been cited as a possible host for microbial extraterrestrial life or, at least, as a prebiotic environment rich in complex organic chemistry. Researchers have suggested a possible underground liquid ocean might serve as a biotic environment.”
http://en.wikipedia.org/wiki/Titan_(moon)

[72] **Enceladus**: “The Cassini spacecraft of the mid- to late 2000s acquired additional data on Enceladus, answering a number of the mysteries opened by the Voyager spacecraft and starting a few new ones. Cassini performed several close flybys of Enceladus in 2005, revealing the moon's surface

6. **Venus**: Perhaps had life before runaway greenhouse took over.

Martian Life

(per RB and supplemented, see Glossary entries also)
Is it or has it been inhabited? [MCM: This is a large topic for discussion and I have provided only modest annotations.]

Recent NASA missions to Mars have specifically sought water. **Phoenix** is a Mars lander [scheduled to land on Mars on May 25, 2008] at edge of polar ice cap.[73] Mars has much evidence of liquid water. Evidence for liquid water includes:

a. **Hematite**: Mars rover Opportunity found **hematite** concretions (Fe_2O_3)—spherical iron oxide growths arising within sediments." This form of hematite only forms from liquid water during diagenesis.[74] Grey hematite requires liquid water.[75] Remote sensing of gray hematite was the reason for the [Opportunity] rover mission.

---

and environment in greater detail. In particular, the probe discovered a water-rich plume venting from the moon's south polar region. This discovery, along with the presence of escaping internal heat and very few (if any) impact craters in the south polar region, shows that Enceladus is geologically active today. Moons in the extensive satellite systems of gas giants often become trapped in orbital resonances that lead to forced libration or orbital eccentricity; proximity to the planet can then lead to tidal heating of the satellite's interior, offering a possible explanation for the activity.

Enceladus is one of only three outer solar system bodies (along with Jupiter's moon Io and Neptune's moon Triton) where active eruptions have been observed. Analysis of the outgassing suggests that it originates from a body of sub-surface liquid water, which along with the unique chemistry found in the plume, has fueled speculations that Enceladus may be important in the study of astrobiology. The discovery of the plume has added further weight to the argument that material released from Enceladus is the source of the E-ring....

Thanks to data from a number of instruments on the Cassini spacecraft in 2005, **cryovolcanism**, where water and other volatiles are the materials erupted instead of silicate rock, has been discovered on Enceladus. The first Cassini sighting of a plume of icy particles above Enceladus' south pole came from images taken in January and February 2005"
http://en.wikipedia.org/wiki/Enceladus_(moon)

[73] **Phoenix Mars Lander Mission**:
• "Mars is a cold desert planet with no liquid water on its surface. But in the Martian arctic, water ice lurks just below ground level. Discoveries made by the Mars Odyssey Orbiter in 2002 show large amounts of subsurface water ice in the northern arctic plain. The Phoenix lander targets this circumpolar region using a robotic arm to dig through the protective top soil layer to the water ice below and ultimately, to bring both soil and water ice to the lander platform for sophisticated scientific analysis."
http://phoenix.lpl.arizona.edu/science.php
• "...Phoenix Landing Site: The Phoenix Mars Lander will touch down in the northern arctic plains of Mars at a site between 65° and 72° North, a region where the Mars Odyssey observed a reservoir of near-surface ground ice."
http://phoenix.lpl.arizona.edu/mars123.php
• http://en.wikipedia.org/wiki/Phoenix_(spacecraft)
• http://phoenix.lpl.arizona.edu/

[74] **Diagenesis**: "...diagenesis is any chemical, physical, or biological change undergone by a sediment after its initial deposition and during and after its lithification, exclusive of surface alteration (weathering) and metamorphism."
http://en.wikipedia.org/wiki/Diagenesis

[75] **Grey hematite and blueberries**:
• ""Grey hematite is a mineral indicator of past water," says Crisp. "It is not always associated with water, but it often is." Deposits of grey hematite are typically found in places where there has been standing water or mineral hot springs, such as those in Yellowstone. The mineral can precipitate out of water and collect in layers at the bottom of a lake, spring, or other standing water. But hematite can also occur without water, as the result of volcanic activity. Scientists have wanted to find out which of these processes created grey hematite on Mars since 1998, when Mars Global Surveyor spotted large concentrations of the mineral near the planet's equator... "

b. **Pseudomorphs**: Many concretions show crystals (pseudomorphs) of sulfate minerals. Opportunity rover found crystals and impressions (**pseudomorphs**)[76] of calcium, magnesium & iron sulfate minerals (gypsum, epsomite-keiserite, jarosite) on Martian surface. These contain water and form by precipitation from evaporating water (**evaporites**). Some minerals contain bound water, e.g. **jarosite**.[77]
c. **Polar ice caps:** Beneath carbon dioxide surface at polar ice caps water ice is found... The polar caps expand and contract.
d. **Geologic features**: River channels, Elongate islands, Ripple cross-bedding

Liquid water from comets etc. plus organic compounds from meteorites etc. may have provided conditions necessary for life.

Mars had a magnetic field >3.5Ga, protecting any life from high-energy ionizing radiation. May have had a thicker atmosphere, providing greenhouse effect to keep planet warmer. It was hit by large meteorites temporarily warming local areas.

The **meteorite ALH84001** was found in Antarctica 1984 (see earlier notes and footnote). It is thought to have come from Mars due to composition of trapped gases. Does it show evidence of fossil life? Lines of investigation included:
a. **"Nanofossils or Nanofossils"**: contains 30 nm worm-like structures resembling bacteria. These are smaller than known cellular life which is typically 250 nm, probably too small for DNA processes, etc. The smallest theoretical living cell is c. 100 nm. [Bacteria are typically 500 - 5000 nm, 0.5 - 5 microns).[78]]
b. **Pyrite** crystals or **sulfide** minerals consistent with sulfide metabolism by bacteria. But the sulfur isotopes are ambiguous in origin, and may be nonbiological.
c. **Polycyclic Aromatic Hydrocarbons PAH**: Said to be derived from living things (but are produced here by diesel exhaust). Other investigators thought these were probably contaminants from snowmobile exhaust, based on unexpected high ^{14}C suggesting recent origin.

---

http://marsrovers.nasa.gov/spotlight/hematite01.html
• "The spectral signature of hematite was seen on the planet Mars by the infrared spectrometer on the NASA Mars Global Surveyor ("MGS") and 2001 Mars Odyssey spacecraft in orbit around Mars. The mineral was seen in abundance at two sites on the planet, the Terra Meridiani site, near the Martian equator at 0° longitude, and the second site Aram Chaos near the Valles Marineris. Several other sites also showed hematite, e.g., Aureum Chaos. Because terrestrial hematite is typically a mineral formed in aqueous environments, or by aqueous alteration, this detection was scientifically interesting enough that the second of the two Mars Exploration Rovers was targeted to a site in the Terrra Meridiani region designated Meridiani Planum. In-situ investigations by the Opportunity rover showed a significant amount of hematite, much of it in the form of small spherules that were informally tagged by the science team "blueberries" (a term which is somewhat confusing, since in spectrally-correct color images they are, in fact, silver-grey in color). Analysis indicates that these spherules are apparently concretions formed from a water solution.
http://en.wikipedia.org/wiki/Hematite"
[76] **Pseudomorph**: "... a mineral compound resulting from a substitution process in which the appearance and dimensions remain constant, but the mineral which makes up the chief component of the compound is replaced by another."
http://en.wikipedia.org/wiki/Pseudomorph
[77] **Jarosite**: Jarosite was listed in RB slide as having formula $Fe_2(SO_4)(OH)_6$.
Alternate definitions: "Jarosite is a basic hydrous sulfate of potassium and iron with a chemical formula of $KFe^{3+}{}_3(OH)_6(SO4)_2$.... [Jarosite] is also a more generic term denoting an extensive family of compounds of the form $AM_3(OH)_6(SO_4)_2$, where A^+ = Na, K, Rb, NH_4, H_3O, Ag, Tl, and M^{3+} = Fe, Cr, V..."
http://en.wikipedia.org/wiki/Jarosite
[78] **Smallest bacteria**: "The smallest members of the domain bacteria known to date are found in the following phylogenetic groups: Proteobacteria, Chlamydia, gram-positive bacteria, spirochetes, and Verrucomicrobia. The spirochetes contain very thin bacteria with some species having cell diameters of about 0.1 to 0.15 microm that are at least 5 to 6 microm in length. Apart from this group, the author is not aware that any of other phylogenetic groups produce cells or buds that are less than 0.2 to 0.25 microm in diameter. Likewise, buds, baeocytes, resting, and dispersal stages such as spores and cysts are not known to be less than 0.25 microm in diameter.
http://www7.nationalacademies.org/ssb/nanopanel2staley.html

d. **Magnetite** crystals resembling inclusions found in magnetotactic bacteria (used by them for orientation). This is the only evidence that has not been readily refuted as nonbiological, and these may be biogenic. Magnetite tends to form octahedral crystals. The crystals found in magnetotactic bacteria are distinctive. But similar nonbiogenic magnetite crystals have been synthesized.

The solar system solid bodies formed c. 4.55 Ga, and this meteorite would have been formed only about 50 millions years afterward—thus very early in solar system history, probably before life would have had time to form. Thus the evidence for life presented by this meteorite has been largely discredited.

However, life on Mars has not been ruled out. Methane in atmosphere has been detected in certain areas, but may be nonbiogenic.[79] The thin atmosphere of Mars is mostly CO_2, and any methane should be rapidly oxidized. But the methane raises the question of methanogenic microbes (such as Archaea found on earth) living subsurface or under polar ice-caps. This methane should have a distinct $^{12}C/^{13}C$ ratio, enriched in ^{12}C.[80] However, methane can be generated by abiogenic processes such as serpentization of olivine. This ratio should be studied further[81], including by Phoenix lander. Such study can be done with robotic craft and does not require humans to be present.

---

[79] **Mars Methane**: However, "Methane can originate from both biotic and abiotic processes, the most plausible sources being emissions from subsurface methanogens or recent volcanic activity." http://www.lpi.usra.edu/meetings/lpsc2005/pdf/2303.pdf

[80] **Carbon Isotopes in Martian Methane**:
• "It has been proposed that with increasing molecular mass, the hydrocarbons become increasingly depleted in ^{13}C (due to the faster reaction rate of $^{12}CH_4$ relative to $^{13}CH_4$ to form chains) and enriched in ^{2}H (due to the preferential cleavage of the weaker ^{12}C-^{1}H relative to ^{12}C-^{2}H). However, there is at present very little laboratory verification of the isotopic fractionation factors involved in abiogenic hydrocarbon formation."
http://nai.nasa.gov/nai2005/abstracts/893%20-%20NAI%20abstract.doc.pdf
• "On Earth, biology sorts carbon-12 from carbon-13 differently than geological processes do. Therefore, if Martian methane has an excess of carbon-12 relative to carbon-13, it would suggest a Red Planet teeming with organisms."
http://www.skyandtelescope.com/news/3310651.html?page=1&c=y

[81] **Mars Methane**: Trace amounts of methane, at the level of several parts per billion, were first reported in Mars' atmosphere by Michael J. Mumma (NASA/Goddard Space Flight Center), whose team first detected Martian methane in 2003. In March 2004 the Mars Express Orbiter also suggested the presence of methane in the Martian atmosphere, with a concentration of about 10 ppb by volume. The presence of methane on Mars is very intriguing, since as an unstable gas it indicates that there must be (or have been within the last few hundred years) a source of the gas on the planet. It is estimated that Mars must produce 150 ton/year of methane. Volcanic activity, comet impacts, and the existence of life in the form of microorganisms such as methanogens are among possible but as yet unproven sources. The methane appears to occur in patches, which suggests that it is being rapidly broken down before it has time to become uniformly distributed in the atmosphere, and so it is presumably also continually being released to the atmosphere. Plans are now being made to look for other companion gases that may suggest which sources are most likely; in the Earth's oceans biological methane production tends to be accompanied by ethane, while volcanic methane is accompanied by sulfur dioxide.

It was also recently shown that methane could be produced by a non-biological process involving water, carbon dioxide, and the mineral olivine, which is known to be common on Mars. The required conditions for this reaction (i.e. temperature and pressure) don't exist on the surface, but likely exist within the crust. To prove this process is occurring, one could try detecting serpentine, a mineral by-product of the process.

The ESA found that the concentrations of methane in the martian atmosphere was not even, but rather that it coincided with the presence of water vapour. In the upper atmosphere these two gasses are uniformly distributed, but near the surface they concentrate in three equatorial regions, namely Arabia Terra, Elysium Planitia, and Arcadia Memnonia. Planetary scientist David H. Grinspoon (Southwest Research Institute) feels that the coincidence of water vapour and methane increases the chance of a biological source, but cautions that it is uncertain how life could have survived so long on a planet as inhospitable as Mars. Ultimately, to prove an organic nature for the methane, a future probe or lander hosting a mass spectrometer will be needed, since the isotopic proportions of C12 to C14 [MCM: this is wrong isotope, should be C13] can clearly distinguish between

Life Outside the Solar System

(per RB and supplemented)
Detection would require detection of radio waves. See **Search for Extra-Terrestrial Intelligence SETI**.[82] Uses radio telescopes to look at radio emissions for non-random transmissions from nearby sun-like stars at 1000-3000 MHz in 2 billion channels. Depicted in movie *Contact*. Not funded by US Government, private. Nothing found yet in 11 years of listening. The **Drake Equation**[83] of astronomer Dr. Frank Drake estimates the number of extraterrestrial civilizations in our Milky Way galaxy with which we might be able to communicate. The estimates range from Drake's original value in 1961 of 10 to current estimates ranging from much less than 1 to 5000.

RB: Drake equation etc. predict there are almost certainly other species. But evolution to our current state of development took 4.5 billion years. Currently, we have no evidence for life outside the Earth. The Fermi paradox asks: if ET life is so common, Where Are They? There are many factors which might prevent our detecting them—maybe they are too advanced, or too smart, or too alien, or in our midsts but invisible to us, or maybe the Earth is truly a Rare Earth.

Panspermia

[MCM: This was in slides but not discussed in class fully]
Microbial life might have originated often in the Universe. Microbial life is easier to evolve than technological organisms, and is longer lived because it can survive more extreme conditions than higher organisms. It can travel through space (microbes survive space exposure for months). There is the possibility of transfer between planets by meteorites or comets. If so, maybe microbes are widespread ("panspermia"[84])

How Did Earth Become Habitable? (Early Earth History)

(per RB and supplemented)

---

an inorganic and an organic (biologic - bacterial decay) origin of the methane.
http://en.wikipedia.org/wiki/Atmosphere_of_Mars

[82] **Search for Extra-Terrestrial Intelligence**:
• http://www.seti.org/
• http://en.wikipedia.org/wiki/SETI

[83] **Drake Equation**:
"The calculation considers the average rate of star formation in our galaxy (or number of stars in the galaxy), the fraction of those stars that have planets, the average number of planets that can potentially support life per star that has planets, the fraction of these that actually go on to develop life, the fraction of these that actually go on to develop intelligent life, the fraction of civilizations that develop a technology that releases detectable signs of their existence into space, and fraction of the planet's existence during which the communicating civilizations live (detectable signals are released into space)."
http://en.wikipedia.org/wiki/Drake_equation
• *TES2000* p. 386.

[84] **Panspermia**: "Panspermia is the hypothesis that "seeds" of life exist already in the Universe, that life on Earth may have originated through these "seeds", and that they may deliver or have delivered life to other habitable bodies. Exogenesis is a more limited hypothesis that proposes life on Earth was transferred from elsewhere in the Universe but makes no prediction about how widespread it is. Because the term "panspermia" is more well-known, it tends to be used in reference to what would properly be called exogenesis."
http://en.wikipedia.org/wiki/Panspermia

1. When did Earth form?[85]

The original Earth formed from chondritic material (such as forms stony meteorites or chondrites) by cold accretion. Nothing survives from the original formation of the Earth, due to effects of plate tectonics. Instead, we must extrapolate the date from other bodies in the solar system—e.g., meteorites that are too small to have tectonics and formed from the solar nebula. The primordial nearly spherical solar nebula of gas and dust condensed into a central Sun and a protoplanetary disk with myriad planetesimals including oblique orbits.[86] The planetesimals aggregated into planetary embryos, forming planets and asteroids. [Currently] accessible planetary bodies include meteorites derived from small asteroids. For example, the meteorites known as **chondrites**[87] are undifferentiated since their formation, have **chondrules** (see footnote). These chondrules include refractory **Ca-Al inclusions** (**CAls**), which are the oldest known solid structures in the universe at **4.55 Ga** [up to **4.567 Ga**] as determined by Uranium-Lead radiometric dating.[88]) **Carbonaceous chondrites**

---

[85] [**CM Solar System Timeline Summary** (compiled from various sources):

4.55 Ga	Chondrules form with CAIs that are incorporated into Meteorites; presumably the earliest Earth forms
4.52 - 4.50 Ga	Oldest Moon specimens, . indicating probable date of Giant Impact and new Earth size
4.46 Ga	Oldest minerals found in Moon rocks
4.3 - 4.4 Ga	Oldest native Earth minerals (zircons)

[86] **Solar Nebula Hypothesis**:
• http://en.wikipedia.org/wiki/Solar_nebula
• *TES2000* which has good discussion p. 188.

[87] **Chondrites**: "Chondrites are stony meteorites that have not been modified due to melting or differentiation of the parent body. They formed when various types of dust and small grains that were present in the early solar system accreted to form primitive asteroids. Prominent among the components present in chondrites are the enigmatic chondrules, millimeter-sized objects that originated as freely floating, molten or partially molten droplets in space; most chondrules are rich in the silicate minerals olivine and pyroxene. Chondrites also contain refractory inclusions (including Ca-Al Inclusions), which are among the oldest objects to form in the solar system, particles rich in metallic Fe-Ni and sulfides, and isolated grains of silicate minerals. The remainder of chondrites consists of fine-grained (micrometer-sized or smaller) dust, which may either be present as the matrix of the rock or may form rims or mantles around individual chondrules and refractory inclusions. Embedded in this dust are presolar grains, which predate the formation of our solar system and originated elsewhere in the galaxy.

Most meteorites that are recovered on Earth are chondrites: ~86% of witnessed falls are chondrites, as is the overwhelming majority of meteorites that are found. There are currently over 27,000 chondrites in the world's collections. The largest individual stone ever recovered, weighing 1770 kg, was part of the Jilin meteorite shower of 1976. Chondrite falls range from single stones to extraordinary showers consisting of thousands of individual stones, as occurred in the Holbrook fall of 1912, where an estimated 14,000 stones rained down on northern Arizona."
http://en.wikipedia.org/wiki/Chondrite

[88] **Uranium-Lead Radiometric Dating**:
• "Uranium-lead is one of the oldest and most refined radiometric dating schemes, with a routine age range of about 1 million years to over 4.5 billion years, and with routine precisions in the 0.1- 1 percent range. The method relies on the coupled chronometer provided by the decay of ^{238}U to ^{206}Pb, with a half-life of 4.46 billion years, and ^{235}U to ^{207}Pb, with a half-life of 704 million years. One of the advantages of uranium-lead dating is the two separate, chemically identical chronometers. Loss (leakage) of lead within the sample will result in a discrepancy in the two decay schemes, resulting in a different age determined by each decay scheme. This effect is referred to as discordance, and provides a check on the reliability of the age... Uranium-lead dating is usually performed on the mineral **zircon** ($ZrSiO_4$), though it can be used on other minerals such as monazite, titanite, and baddeleyite. Zircon incorporates uranium and thorium atoms into its crystalline structure, but strongly rejects lead. Undamaged zircon retains the lead generated by radioactive decay of uranium and thorium until very high temperatures (about 900 °C), though accumulated radiation damage within zones of very high uranium can lower this temperature substantially. Zircon is very chemically inert and resistant to mechanical weathering -- a mixed blessing for geochronologists, as zones or even whole crystals can survive melting of their parent rock with their original uranium-lead age intact..."
http://en.wikipedia.org/wiki/Uranium-lead_dating
• *TES2000* p. 189

(primitive meteorites) also contain water, c. 5% organic matter including amino acids, alcohols, carboxylic acids etc., so may have delivered the building-blocks of life to the Earth. The chondrites are only slightly younger than the chondrules they contain. The coagulation of the solar nebula by cold accretion happened rapidly, perhaps over a million years or less. The Earth's mass is growing by 40 kton/year, from infalling meteorites and **interplanetary dust particles** (**IDPs**, also called **Brownlee particles** after their discoverer). IDPs are identifiable at South Pole ice. We are also searching for IDPs in Archean sediments and in upper stratospheric studies. But what is the age of the Earth? [Indirectly it can be inferred that the original Earth formed around the same time as when the meteorite chondrules formed, therefore about **4.55 Ga**.] [Note: the oldest known Earth rock minerals of terrestrial origin are the **Jack Hills zircon crystals** with dates estimated radiometrically at **4.3 - 4.4 Ga**.[89]]

2. Moon Forming Impact (and Attainment of Final Earth Mass):

It is perhaps best to regard the age of the Earth as based on **the time when it gained the current mass and composition**. This occurred when [or soon after] a giant Mars-sized body [some call it **Theia**] is thought to have impacted[90] the Earth obliquely (**Giant Impact Hypothesis**), dislodging some of the earth's mantle and impactor materials into orbit, materials which eventually coalesced to become the Moon. Support for this hypothesis (rather than planetary capture or separate condensations) derives from the geochemical [and/or isotopic] similarity of Earth [crust] and Moon. The Earth was knocked off its normal [perpendicular] orbital axis [to the present tilt of 23.5 degrees] and became heavier due to addition of core from the impactor. The Earth's tilt is the greatest of the inner planets [not quite: Mercury 0°, Venus 177.3°, Earth 23.45°, Mars 25.1°][91]. The Earth is the densest[92] of the 4 inner planets [Mercury 5.43 gm/cm^3, Venus 5.24, Earth 5.515, Mars 3.94] because the impactor contributed proportionately more of its core to the Earth. The **oldest Moon rocks** are **4.46 Ga**, dating therefore before the oldest Earth rocks.[93] **Isotopic systematics** [radiometrically dated

---

[89] **Oldest Earth Minerals and Earth Age**:
• "In Western Australia, single zircon crystals found in younger sedimentary rocks have radiometric ages of as much as **4.3 billion years**, making these tiny crystals the oldest Earth materials to be found on Earth so far. The source rocks for these zircon crystals have not yet been found. The ages measured for Earth's oldest rocks and oldest crystals show that the Earth is at least 4.3 billion years in age but do not reveal the exact age of Earth's formation."
http://pubs.usgs.gov/gip/geotime/age.html
• "...Measurements of zircons indicate that the Earth is at least **4.404 billion years** old."
http://en.wikipedia.org/wiki/Age_of_the_Earth
• Graph of various modalities of assessing early solar system chronology, including **CAIs** at c. **4.567 Ga**.
http://ijolite.geology.uiuc.edu/02FallClass/geo433/papers/Gilmour_Solar_Sys_Clocks.pdf
[90] **Giant Impact Hypothesis**: "One hypothesis is that Theia formed at a Lagrangian point relative to Earth, that is, in about the same orbit and about 60° ahead or behind. When the protoplanet Theia had grown to about the size of Mars, it became too massive to reside stably in a Trojan orbit. As a result, its angular distance from Earth fluctuated, with the fluctuations growing larger until it hit the Earth. This is calculated to have occurred **4.533 billion years ago** (4.533 Ga); Theia is thought to have struck the Earth at an oblique angle, destroying Theia and ejecting most of Theia's mantle and a significant portion of the Earth's mantle into space, while Theia's core sank into Earth's core. Current estimates based on computer simulations of such an event suggest that some two percent of the original mass of Theia ended up as an orbiting ring of debris, about half of which coalesced into the Moon between one and 100 years after the impact..."
http://en.wikipedia.org/wiki/Giant_impact_hypothesis
[91] **Comparison of Solar System Planets Orbital Axis**:
http://en.wikipedia.org/wiki/Table_of_planets_and_dwarf_planets_in_the_Solar_System
[92] **Comparison of Solar System Planets Density**:
http://en.wikipedia.org/wiki/Table_of_planets_and_dwarf_planets_in_the_Solar_System
[93] **Moon Age**: [MCM: Age estimates vary and this topic is confusing].
• "The formation of the Moon is believed to have occurred **4.527** ± 0.01 billion years ago, about 30–50 million years after the origin of the solar system"
http://en.wikipedia.org/wiki/Moon
• "However, we found that the range of ages reported by the previous studies could be explained by subtle disturbance of the Sm-Nd isotopic compositions in plagioclase separated from the anorthosites,

minerals] of Moon specimens [presumably individual crystals embedded in rocks] go back to **4.52 Ga - 4.50 Ga**, probably indicating the age of the Moon-forming impact [and therefore the age of the current-sized Earth, occurring c. 30 - 50 million years after the initial Earth formation]. This impact would have "sterilized" the Earth [no life was expected to be present then], vaporized any oceans present up to that time, and blown away the atmosphere (the current atmosphere had to form later). The impact has been computer modeled, leading to hypotheses about the relative distributions of mantle and core components.[94] The moon quickly coalesced from the Earth/Impactor debris blown into orbit. Before the impact, the Earth was probably more homogeneous with (possibly) a chondritic composition. Afterwards the Earth was hot and became differentiated [core and mantle formed, etc.], with a composition enriched in **siderophile elements**[95] derived from the impactor core. The collision added to the angular momentum of the Earth.[96] The moon is slowly receding[97] from the Earth at 38 mm/yr and was once much closer.

---

and that the pyroxenes and olivines from these rocks defined an age of **4.46** ± 0.04 billion years (see graph below). This may represent a robust estimate for the primary crystallization age of the earliest lunar crust."
http://www.psrd.hawaii.edu/April04/lunarAnorthosites.html

[94] **Giant Impact Hypothesis: Chemical Distributions (Gregg Herres and William K. Hartmann)**:
a. "The Earth has a large iron core, but the moon does not. This is because Earth's iron had already drained into the core by the time the giant impact happened. Therefore, the debris blown out of both Earth and the impactor came from their iron-depleted, rocky mantles. The iron core of the impactor melted on impact and merged with the iron core of Earth, according to computer models.
b. Earth has a mean density of 5.5 grams/cubic centimeter, but the moon has a density of only 3.3 g/cc. The reason is the same, that the moon lacks iron.
c. The moon has exactly the same oxygen isotope composition as the Earth, whereas Mars rocks and meteorites from other parts of the solar system have different oxygen isotope compositions. This shows that the moon formed from material formed in Earth's neighborhood.
d. If a theory about lunar origin calls for an evolutionary process, it has a hard time explaining why other planets do not have similar moons. (Only Pluto has a moon that is an appreciable fraction of its own size.) Our giant impact hypothesis had the advantage of invoking a stochastic catastrophic event that might happen only to one or two planets out of nine."
http://www.psi.edu/projects/moon/moon.html

[95] **Siderophile Elements**: From Goldschmidt classification: "Au, Co, Fe, Ir, Mn, Mo, Ni, Os, Pd, Pt, Re, Rh, Ru. Siderophile elements are the high-density transition metals that tend to bond with metallic iron in the solid or molten state."
http://en.wikipedia.org/wiki/Siderophile

[96] **Earth Angular Momentum After Giant Impact**: "… A.G.W. Cameron and William R. Ward (Harvard University, Cambridge MA) pointed out that a collision with a body having at least the mass of Mars would be needed to give the Earth the present angular momentum of the Earth-Moon system…"
http://www.windows.ucar.edu/tour/link=/teacher_resources/impact_theory.html

[97] **Moon Receding From Earth**: "Data also indicate that ocean tides on Earth have a direct influence on the Moon's orbit. Measurements show that the Moon is receding from Earth at a rate of about 3.8 centimeters per year. "
http://sunearth.gsfc.nasa.gov/eclipse/SEhelp/ApolloLaser.html
"The tidal bulges on Earth are carried ahead of the Earth-Moon axis by a small amount as a result of the Earth's rotation. This is a direct consequence of friction and the dissipation of energy as water moves over the ocean bottom and into or out of bays and estuaries. Each bulge exerts a small amount of gravitational attraction on the moon, with the bulge closest to the moon pulling in a direction slightly forward along the moon's orbit, because the earth's rotation has carried the bulge forward. The opposing bulge has the opposite effect, but the closer bulge dominates due to its comparative closer distance to the moon. As a result, some of the Earth's rotational momentum is gradually being transferred to the Moon's orbital momentum, and this causes the Moon to slowly recede from Earth at the rate of approximately **38 millimetres per year**. Due to conservation of angular momentum, the Earth's rotation is gradually slowing, and the Earth's day thus lengthens by about **17 microseconds every year**." [i.e., 1.7 msec each century]
http://en.wikipedia.org/wiki/Orbit_of_the_Moon

3. Earth Differentiation[98]: When Did the Core Segregate From The Mantle?

The Earth's core formed [soon] after impact, dated by ^{182}Hf/^{182}W isotope systematics[99] with $t_{½}$ for ^{182}Hf being 9 M.y. Thus ^{182}Hf is a very short lived isotope. [MCM: it was presumably regenerated by seeding from nucleosynthesis in supernovas, etc.[100]] W is a **siderophile** (prefers mixing with Fe) whereas Hf is a **lithophile** (prefers mixing in silicate rocks), so mantle and crust only contain ^{182}W produced after core formation. [MCM: See footnotes for further specifics. There is no remaining ^{182}Hf today—it has long ago decayed away, and the testing here involves the relative distribution of stable isotopes of W including ^{182}W, ^{184}W, and ^{180}W]. The residual internal heat from the impact plus accumulating radiogenic heat from [long lived] radioisotopes (such as ^{40}K [with $t_{1/2} = 1.277 \times 10^9$ yr], U, Th, and Rb [MCM: but 87-Rb with half-life 4.92×10^{10} years is not generally described as being a significant source of radiogenic heating]) allowed melting very soon after the moon-forming impact. This led to segregation of metals from silicates. **Diapirs** of granite-like silicates moved up to help form the mantle, and "reverse diapirs" of metals (Fe, Ni, and a light element, perhaps S) melted and moved down to help form the metallic core. The mantle was probably initially a **magma ocean**, but quickly cooled because the first **crust** had formed by the time the Jack Hills zircons appeared in 4.40 Ga, only 10 million years or so from the giant impact. [MCM: The following is somewhat unclear and uncertain.] Zircons don't crystallize in mantle-derived basalt, big crystals suggest granitic crust. Zircon ($ZrSiO_3$) crystals are 1/3 mm in size. By 4.4 Ga, the mantle was cooling from the top down. It must have solidified and then remelted partially to allow the zircons to form. Zircons come from

---

[98] **Differentiation**: In planetary science, planetary differentiation is a process by which the denser portions of a planet will sink to the center; while less dense materials rise to the surface. Such a process tends to create a core, crust, and mantle.
http://en.wikipedia.org/wiki/Planetary_differentiation

[99] **Hafnium and Tungsten Dating of Time of Core Differentiation**:
• "Measurements of the isotopic composition of tungsten (W) show that lunar samples and Martian meteorites have an excess of tungsten-182 [compared to ^{184}W]. This was produced by the decay of hafnium-182 (Hf-182), an isotope with a half-life of only 9 million years. Because tungsten dissolves enthusiastically in metallic iron and hafnium does not, it is possible to use the abundance of W-182 in rocks formed by melting of the silicate mantle as an indicator of the timing of core formation…
http://www.psrd.hawaii.edu/Nov03/Hf-W.html
• "To determine the formation time of Earth's core, the two teams of researchers reexamined a standard radioactive-dating technique that uses the decay of the isotope hafnium-182 into its stable daughter product, tungsten-182. Hafnium and tungsten have distinctive locations in early Earth, says Thorsten Kleine of the University of Munster in Germany. Undecayed hafnium in Earth's mantle, the region that accumulated around the growing core, would have remained locked in minerals there. In contrast, tungsten produced in the mantle would have sunk into the molten core during the time that the core was forming. Any tungsten-182 now found in the mantle must have been produced by the decay of hafnium-182 after the core had finished forming and no longer interacted with the mantle. Therefore, the abundance of tungsten in rocks from Earth's mantle provides a measure of the core's age. Kleine and his colleagues, as well as a team led by Qingzhu Yin of Harvard University, measured the concentration of tungsten-182 in a variety of Earth rocks originally from the mantle. To date the rocks, the teams had to compare these numbers with the amount of tungsten-182 found in objects in the solar system that had never formed a core. Meteorites, the fragments of asteroids that have fallen to Earth, fit the bill. The measurements reveal that Earth's core—the bulk of the planet—formed in 30 million years…"
http://www.sciencenews.org/articles/20020831/fob1.asp
• "Revision of the ^{182}Hf–^{182}W parameters has far-reaching implications for the timing of terrestrial core formation and the origin of the Earth–Moon system. Most importantly, the bulk silicate Earth (BSE) has a clearly resolvable ^{182}Wexcess of 1.9 ε units relative to chondrites, and does not have a chondritic Wisotope composition as previously suggested. Using a Hf/W ratio of 17.7 for the BSE, core formation on Earth occurred 33 ± 2 Myr after the beginning of the Solar System.
Kleine, T., et al. 2002. "Rapid accretion and early core formation on asteroids and the terrestrial planets from Hf-W chronometry". *Nature* 418(Aug. 29):952-955.

[100] **Origin of Short-Lived Radioisotopes:** "On-going nucleosynthesis by a diversity of stars (supernovae, novae, AGB stars, etc.) in the Galaxy continuously replenishes the interstellar medium with freshly made SRs [short-lived radionuclides]."
Matthieu Gounelle. "The origin of short-lived radionuclides in the solar system". *New Astronomy Reviews* 50 (2006) 596–599

granite arising from partial remelting. Magma ocean must have formed before zircons formed.

4. *Crustal Differentiation*

[MCM: This all went by very fast and transcription is uncertain.] Crust was previously thought to [have arisen] at an Archean-Proterozoic boundary c. 2.5 Ga indicated by change in **rare earth elements patterns** (the REE patterns for sediments … were flat for Archean-like basalt, fractionated for Proterozoic-like granite…), but the sampling was probably biased. Granite rocks date back to 4.0 Ga—the oldest crustal granitic rocks include the **Acasta gneiss**[101] of 4.0 Ga age, arising at the Canadian Shield (craton) [MCM: these were not definitely subaerial, thus may have been subaqueous]. Granitic rocks require liquid water alteration of the melt source. Continental crust is thick, rigid, cool, buoyant, and felsic[102]. The oldest definitely continental [subaerial[103]] crusts date to **3.5 Ga**—data regarding the oldest **unconformity** involving **Coonterunah / Warrawoona**[104] in W. Australia was presented with a slide. Perhaps continental crust formed as early as **3.5 - 4.0** Ga [arising during the Hadean eon], therefore much earlier than the Archean eon-Proterozoic eon boundary. (But see Wilde et al 2001 on dating the Jack Hills zircons as early as 4.4 Ga).[105] Thus continental crust may be more

---

[101] **Acasta Gneiss**: "is a rock outcrop of Archaean tonalite gneiss in the Slave craton in Northwest Territories, Canada. It is the oldest known crustal rock outcrop in the world… The rock exposed in the outcrop formed just over four billion (4×10^9) years ago; an age based on radiometric dating of zircon crystals…"
http://en.wikipedia.org/wiki/Acasta_Gneiss

[102] **Felsic**: "is a term used in geology to refer to silicate minerals, magmas, and rocks which are enriched in the lighter elements such as silicon, oxygen, aluminium, sodium, and potassium. The term combines the words "feldspar" and "silica." " [MCM: thus is does not imply presence of Fe]
http://en.wikipedia.org/wiki/Felsic

[103] **Subaerial vs. Subaqueous**: "The term subaerial, mainly used in geology, describes events or structures located at the Earth's surface, "under the air". This is to be contrasted with submarine events or structures, those located under the sea. [MCM: or **subaqueous**=Found or occurring underwater.] A subaerial eruption of a volcano is one that ejects material into the air. Subaerial weathering is weathering by rain, frost, rivers etc. Subaerial materials are materials at the surface of the planet exposed to the air.
http://en.wikipedia.org/wiki/Subaerial

[104] **Coonterunah Warrawoona Group: "**In the Pilgangoora Belt the 3.517 Ga Coonterunah Group and 3.484-3.468 Ga Carlindi granitoids underlie the 3.458 Ga Warrawoona Group beneath an erosional unconformity, thus providing evidence for ancient emergent continental crust. (Green, 2001)."
http://en.wikipedia.org/wiki/Pilbara_craton

[105] **Jack Hills Zircon Age**: "No crustal rocks are known to have survived since the time of the intense meteor bombardment that affected Earth between its formation about 4,550 Myr ago and 4,030 Myr, the age of the oldest known components in the Acasta Gneiss of northwestern Canada. But evidence of an even older crust is provided by detrital zircons in metamorphosed sediments at Mt Narryer and Jack Hills in the Narryer Gneiss Terrane, Yilgarn Craton, Western Australia, where grains as old as ~ 4.276 Myr have been found. Here we report, based on a detailed micro-analytical study of Jack Hills zircons, the discovery of a detrital zircon with an age as old as 4,404 Myr—about 130 million years older than any previously identified on Earth. We found that the zircon is zoned with respect to rare earth elements and oxygen isotope ratios ($\delta^{18}O$ values from 7.4 to 5.0), indicating that it formed from an evolving magmatic source. The evolved chemistry, high $\delta^{18}O$ value and micro-inclusions of SiO_2 are consistent with growth from a granitic melt with a $\delta^{18}O$ value from 8.5 to 9.5. Magmatic oxygen isotope ratios in this range point toward the involvement of supracrustal material that has undergone lowtemperature interaction with a liquid hydrosphere. This zircon thus represents the earliest evidence for continental crust and oceans on the Earth."
http://www.geology.wisc.edu/%7Evalley/zircons/Wilde2001Nature.pdf (2001)
"No known rocks have survived from the first 500 m.y. of Earth history, but studies of single zircons suggest that some continental crust formed as early as 4.4 Ga, 160 m.y. after accretion of the Earth, and that surface temperatures were low enough for liquid water. Surface temperatures are inferred from high $\delta^{18}O$ values of zircons. The range of $\delta^{18}O$ values is constant throughout the Archean (4.4–2.6 Ga), suggesting uniformity of processes and conditions. The hypothesis of a cool early Earth suggests long intervals of relatively temperate surface conditions from 4.4 to 4.0 Ga that were conducive to liquidwater oceans and possibly life. Meteorite impacts during this period may have been less frequent than previously thought." [Includes graph Crystallization age (U-Pb) zircon age as x-axis and

ancient than formerly thought. Once formed, continental crust provided a more stable platform for the origin and early evolution of life: shallow water environments, diverse habitats, opportunity for heating and cooling, wetting and drying, dilute solutions, phosphate source, etc.

5. Where Did The Atmosphere Come From?

[MCM: This all went by very fast and transcription is uncertain.] The **modern atmosphere** is rich in oxygen, but this is almost entirely derived from photosynthesis produced by cyanobacteria enslaved by green plants. (A small amount of oxygen derives from nonbiogenic photolysis/photodissociation of water.) It is very different from early atmosphere. The **first atmosphere** was chondritic—i.e., it resembled the volatile composition of chondrites, [consisted probably of H_2 and He][106], was poor in H_2O and CO_2, and was blown away by impact forming the Moon. The **Archean atmosphere** in which life evolved was neither chondritic nor biogenic—it formed as a "late veneer" from bombardment by comets (which are 50% water) and carbonaceous chondrites (10% water). This bombardment was also rich in carbon[107], and added siderophile elements (PGE =platinum-group elements) to the Earth's mantle via "impact gardening". This occurred during the somewhat controversial "**Late Heavy Bombardment**"[108] c. 4.5 - 3.8 Ga, and is apparent as the heavily cratered Moon (thus is also referred to as the "Late Lunar Cataclysm"). This bombardment was heavy enough to form craters up to 1,000 km in diameter on the Moon and up to 2,000 km on Mars (Hellas, Argyre) [see also below]. Extra-terrestrial volatiles [presumably embedded by bombardments] degassed from the mantle during volcanism, so **Archean** atmosphere resembled modern volcanic gases, including H_20, N_2, H_2O, CO_2, CO, and SO_2 [plus S_2, Cl_2][109]. It was nearly neutral in redox capacity, not highly reducing like that required for Miller-Urey experiment. Comets and carbonaceous chondrites could have also supplied

---

and $\delta^{18}O$ for Archean magmatic zircons.]
Valley JW et al, http://www.geology.wisc.edu/zircon/Valley2002Cool_Early_Earth.pdf (2002)
Definition of $\delta^{18}O$ notation and Overview of Stable Isotopes In Research: [See Glossary for extended description.] "Results from environmental and agricultural studies using isotopically enriched tracers are usually reported in units of atom percent (At%). This value gives the absolute number of atoms of a given isotope in 100 atoms of total element... Studies examining stable isotopes at or near natural abundance levels are usually reported as delta [**δ**], a value given in parts per thousand or per mill ("‰"). Delta values are not absolute isotope abundances but differences between sample readings and one or another of the widely used natural abundance standards which are considered delta = zero (e.g. air for N, At%^{15}N = 0.3663033; ... At%13C = 1.1112328). Absolute isotope ratios (R) are measured for sample and standard, and the relative measure delta is calculated...[see formula images in article]
http://www.uga.edu/~sisbl/stable.html

[106] **He and H in Earliest Atmosphere**: http://www.ux1.eiu.edu/~cfjps/1400/atmos_origin.html

[107] **Chemical Forms of Carbon in Carbonaceous Chondrites**: "Most of the organic carbon in CI and CM carbonaceous chondrites is an insoluble complex material ... that is similar to the description for **kerogen**. The CM meteorite from Murchison, Victoria has over 70 extraterrestrial amino acids and other compounds including carboxylic acids, hydroxy carboxylic acids, sulphonic and phosphonic acids, aliphatic, aromatic and polar hydrocarbons, fullerenes, heterocycles, carbonyl compounds, alcohols, amines and amides."
http://en.wikipedia.org/wiki/Carbonaceous_chondrite

[108] **Late Heavy Bombardment**: "(commonly referred to as the **lunar cataclysm**, or LHB) is a period of time approximately 3800 to 4100 million years ago (Mya) during which a large number of impact craters are believed to have formed on the Moon, and by inference on Earth, Mercury, Venus, and Mars as well. The evidence for this event comes primarily from the dating of lunar samples, which indicates that most impact melt rocks formed in this very narrow interval of time. While many hypotheses have been put forth to explain a "spike" in the flux of either asteroidal or cometary materials to the inner solar system, no consensus yet exists as to its cause. One popular theory postulates that the gas giant planets migrated in orbit at this time, causing objects in either the asteroid belt or Kuiper belt to be put onto eccentric orbits that reached the terrestrial planets. Nevertheless, some argue that the lunar sample data do not require a cataclysmic cratering event near 3900 Mya, and that the apparent clustering of impact melt ages near this time is an artifact of sampling material affected by a single large impact basin."
http://en.wikipedia.org/wiki/Late_heavy_bombardment

[109] **Early Atmosphere Composition**: http://www.ux1.eiu.edu/~cfjps/1400/atmos_origin.html

organic monomers, e.g., amino acids, etc.

6. When Did The Oceans Condense?

[MCM: This all went by extremely fast and transcription is uncertain.] Initial earth was hot, degassed. If Earth formed dry, water may have been delivered to the Earth by bombardment by comets and carbonaceous chondrites. Water formed steam atmosphere. But clouds have high albedo, reflected lots of sunlight, so surface gradually cooled. Liquid water veneer then developed. It was once thought the oceans condensed late, and were kept hot by high radiogenic heat flow, and high greenhouse effect (cf. Venus). But first sedimentary rocks show evidence of liquid water as early as 3.8 Ga (**Isua**[110] metasediments). These are sedimentary conglomerates with round pebbles indicating liquid water. The **Acasta gneiss** 4.0 Ga contains metamorphosed granite, which requires liquid water altering melt source. The **Jack Hills zircons** 4.4 Ga have fractionated Oxygen isotopes [^{18}O vs. ^{16}O] indicating liquid water altered melt source—the mantle is +5.3% $\delta^{18}O$ ‰ [parts per thousand], enriched compared with modern oceans water. In ancient zircons the $\delta^{18}O$ is +6 to +8 implying that liquid water reacted with melt sometime at low temperature. [see also Article 2002 by Valley referenced in footnotes which says "High-$\delta^{18}O$ zircons and host magmas resulted from melting of protoliths that were altered by interaction with liquid water at low temperatures near surface of Earth"] Zircons and liquid water may have been present therefore as early as a few hundred million years from the formation of the Earth. If so, life could have originated in an aqueous site very early in Earth history. There **may have been liquid oceans as early as 4.4 Ga**. But did these oceans survive continuously, even the time of the Late Heavy Bombardment? Oxygen isotopes are fractionated by ocean vents etc….

7. Impact Frustration of Life

Heavy meteorite impacts (around 10x the current rate) occurred, culminating in the **Late Heavy Bombardment** (c. 3.8 - 3.9 Ga), forming cratered surfaces (discussed above) on Moon and Mars. Earth was also impacted, probably by even larger impactors. 1,000 km diameter impact craters on Moon include the largest, **Imbrium**[111] which formed 3.9 Ga. Craters up to 2,000 km formed on Mars (**Hellas, Argyre**). The energy released in the largest of these impacts could have vaporized all oceans and all subsurface ground water down to 0.5 km, creating a temporary steam atmosphere, killing any life present at the time, and disrupting all organic polymers. But clouds increase albedo and cooling would have rapidly occurred. And either

(a) Early life, if present prior to the Late Heavy Bombardment LHB, was very tough and able to survive the high temperatures in subsurface environments (such as hyperthermophilic organisms living at deep ocean black smokers, which have been found to survive temperatures at great as 125° C), or
(b) Life began anew after the 3.8 Ga LHB.

See the **Tree of Life diagram**[112], showing thermophiles and hyperthermophiles among the Archaea

---

[110] **Isua Greenstone Belt**: "an Archean greenstone belt in southwestern Greenland dated at 3.8-3.7 Ga and contains the oldest known, well preserved, metavolcanic (metamorphosed mafic volcanic), metasedimentary and sedimentary rocks on Earth. It consists of five tectonic domains…"
http://en.wikipedia.org/wiki/Isua_greenstone_belt

[111] **Imbrium**: "The outermost ring of mountains has a diameter of 1300 km"
http://en.wikipedia.org/wiki/Mare_Imbrium

[112] **Tree of Life Phylogenetic Diagram**:
• Shows **Archaea** positioned intermediate between Bacteria and Eukaryota.
http://en.wikipedia.org/wiki/Phylogenetic_tree
• "A highly resolved, automatically generated Tree Of Life, based on completely sequenced genomes".
http://upload.wikimedia.org/wikipedia/en/3/36/ITOL_Tree_of_life.jpg
• The original source of this circular TOL image is at the Interactive Tree of Life:
http://itol.embl.de/
• The source of data for this tree is described as follows: "We have developed an automatable procedure for reconstructing the tree of life with branch lengths comparable across all three domains. The tree has its basis in a concatenation of 31 orthologs [A gene in two or more species that has evolved from a common ancestor] occurring in 191 species with sequenced genomes…"
Francesca D. Ciccarelli, et al, "Toward Automatic Reconstruction of a Highly Resolved Tree of

(positioned between the bacteria and eukaryotes), which suggests primitive organisms were hyperthermophilic, so perhaps they could survive. A graph was projected showing Impact Energy (Joules) plotted against Time ago Ga—impact energy was highest for Hellas at c. 4 Ga (which could evaporate all water), lower for Argyre, and lower still for Imbrium, gradually tapered to lower values at present time. Water may have been delivered to the Earth subsequently by bombardment by comets, etc.

Archean Environment

(per RB and supplemented)
How and when did the Earth's surface become not just habitable but **equable** [i.e., having favorable conditions not varying much]?
[MCM: The Archean eon extended from 3.8 to 2.5 Ga. It is the eon in which simple single celled life—bacteria and possibly Archaea—arose.]

1. Was Surface Temperature Similar to Present?

Life is sensitive to temperature T°, most organism have only a 10° - 20° tolerance. We don't know early Earth T° well. The $\delta^{18}O$ system[113] is a "thermometer" that works well only for the last 100 M.y., because the substantial Oxygen in the atmosphere is constantly resetting the clock. Has the basal ratio [? $\delta^{18}O$] in seawater stayed the same? The "**Faint Young Sun paradox**" (MCM: see 1981 article by Gough, "Solar interior structure and luminosity variations") leads to the conclusions that the Sun has brightened with time—it had only 75% luminosity at 3.5 Ga, so surface T° of Earth should have been around minus 20 °C (were it not for a substantial greenhouse effect). But sedimentary evidence for liquid water, the absence of clear signs of glaciation before 2.3 Ga [RB: there might be some equivocal evidence at 2.9 Ga, even as far back as 3.4 Ga for glaciers] suggest there was about the same temperature [as modern]—there must have been substantial greenhouse gases raising the Archean temperature. Currently we experience about **30 °C warming** as a result of greenhouse effect. Atmospheric CO_2 is transparent to visible light but not to infrared IR. The

What were the **possible ancient greenhouse gases**?
[MCM: 2 tables of data were presented here that could not be fully transcribed. The following summarizes greenhouse and nongreenhouse atmospheric gases]:
a. **Water Vapor**: Water is a strong greenhouse gas, but it complicates the calculation of temperature by forming **clouds** that raise albedo and reflect light, partly canceling heating effect. The relative effects of these opposing (heating and cooling) factors are hard to quantify, and introduce considerable uncertainty into climatic modeling of effects of CO_2 on global temperatures.
b. **Carbon Dioxide CO_2**: This is the most "popular" Archean greenhouse gas. It is only a weak absorber of infrared, and therefore must have at nearly 1 bar (about current Earth atmospheric pressure) concentration at 3.5 Ga in order to keep surfaces from freezing. Would have needed 20% Archean CO_2 to maintain temperature. Prebiotic atmosphere had 30-90% CO_2, Archean was c. 10-20%, Modern CO_2 is only 380 ppm (0.038%). [But this table's data seems to be contradicted by what follows] However, CO_2 in large concentrations has pronounced effects on rock due to formation of carbonic acid and weathering. E.g.,
H_2CO_3 (carbonic acid) + $MgSiO_4$ (silicates) ➔ Mg^{2+} plus SiO_4 (quartz) + $2HCO_3^-$ (dissolved bicarbonate ion)
Thus we would expect to see extensively weathered rocks from high CO_2, and reaction of bicarbonate with Fe^{2+} to yield **siderite** ($FeCO_3$), yet large beds of siderite are not seen. [A course lab experiment looked at **paleosols**—ancient soils—and siderite.] Thus CO_2 was unlikely to have been the dominant

---

Life" *Science* 3 March 2006: Vol. 311. no. 5765, pp. 1283 - 1287 DOI: 10.1126/science.1123061, accessed 10/16/07 at http://www.sciencemag.org/cgi/content/abstract/311/5765/1283.
• See also *TES2000* p. 204
[113] **$\delta^{18}O$ Stable Isotope Standard Ratios**: $\delta^{18}O$ expresses $^{18}O/^{16}O$ comparing to one of the Oxygen standards:
a. **Vienna Standard Mean Ocean Water (VSMOW)** which has absolute isotope ratios R = 0.0020052
b. **Vienna Pee Dee Belemnite** (VPDB): R = 0.0020672
c. **Standard Light Antarctic Precipitation** (SLAP): R = 0.0018939
http://www4.nau.edu/cpsil/isotopes.htm

greenhouse gas. [MCM: a graph was presented with complex incompletely captured data extending from 4.5 Ga to 0.5 Ga showing required CO2 concentration in bars required to produce observed phenomena such as Huronian glaciation[114], late Precambrian glaciation.[115]]
c. **N_2**: not a greenhouse gas. The Prebiotic atmosphere was 10 - 80 % N_2, Archean 50 - 80 % N_2, and Modern 78% N_2.
d. **O_2**: not a greenhouse gas. [MCM: The Prebiotic atmosphere was c. 0 % O_2, Archean <1% O_2, and modern 21% O_2.]
e. **Volcanic gases during the Archean**: [MCM: in addition to H_20 and CO_2, these also included **SO_2**, **CO**, **S_2**, **Cl_2**, **H_2**, **NH_3** (ammonia), and **CH_4** (methane)][116], the latter further discussed here.
f. **Methane CH_4**: A relatively potent greenhouse gas[117], only need a few parts per thousand to produce 20 °C warming. It is stable and long-lived but can only exist when there is no atmospheric O_2 (otherwise gets oxidized to water and CO_2). Modern sources include natural and anthropogenic emissions.[118] The Prebiotic atmosphere was 10 - [?] 100 ppm, Archean 10^3 - 10^4 ppm, and Modern 1 - 6 ppm. Microbes affect the isotopic signature of light carbon by enriching ^{12}C relative to ^{13}C [i.e., depleting ^{13}C] yielding a $\delta^{13}C$ = -65 ‰ [parts per thousand, note minus sign, standard of comparison derives from a Cretaceous deposit c. 145 - 65 Ma.][119]. This enrichment of ^{12}C over ^{13}C is seen only as

---

[114] **Huronian glaciation**: "extended from 2400 mya [2.4 Ga] to 2100 mya [2.1 Ga], during the Siderian and Rhyacian periods of the Paleoproterozoic era. It was one of the most severe ice ages in geologic history and some geologists believe that it was very similar to the Snowball earth ice age that happened in the neoproterozoic era."
http://en.wikipedia.org/wiki/Huronian
[115] **Precambrian Glaciation**: "A number of glacial periods have been identified going as far back as the Huronian epoch, roughly 2200 Ma. The best studied is the Sturtian-Varangian glaciation, around 600 Ma [MCM: thus in late Precambrian, specifically the late Proterozoic, just prior to the Cambrian which began at 542 Ma], which may have brought glacial conditions all the way to the equator, resulting in a "Snowball Earth"."
http://en.wikipedia.org/wiki/Precambrian
[116] **Volcanic Gases including in Early Earth Atmosphere**:
http://www.ux1.eiu.edu/~cfjps/1400/atmos_origin.html
"Up to 40% of the gas emitted by a volcano during a subaerial volcanic eruption is carbon dioxide"
http://en.wikipedia.org/wiki/Carbon_dioxide
"The most abundant gas typically released into the atmosphere from [modern] volcanic systems is water vapor (H_20), followed by carbon dioxide ($C0_2$) and sulfur dioxide ($S0_2$). Volcanoes also release smaller amounts of others gases, including hydrogen sulfide (H_2S), hydrogen (H_2), carbon monoxide (CO), hydrogen chloride (HCL), hydrogen fluoride (HF), and helium (He)."
http://volcanoes.usgs.gov/Hazards/What/VolGas/volgas.html
[117] **Methane as Greenhouse Gas**:
• "Methane in the Earth's atmosphere is an important greenhouse gas... a 1 tonne methane emission will have 25 times the impact on temperature of a 1 tonne carbon dioxide emission during the following 100 years.... Early in the Earth's history—about 3.5 billion years ago—there was 1,000 times as much methane in the atmosphere as there is now. The earliest methane was released into the atmosphere by volcanic activity. During this time, Earth's earliest life appeared. These first, ancient bacteria added to the methane concentration by converting hydrogen and carbon dioxide into methane and water. Oxygen did not become a major part of the atmosphere until photosynthetic organisms evolved later in Earth's history."
http://en.wikipedia.org/wiki/Methane
• See also http://en.wikipedia.org/wiki/Greenhouse_gases
[118] **Sources of Methane in Modern Atmosphere**:
• See table summarized as follows
Natural Sources: Wetlands (incl. Rice agriculture) 225 Tg/a [Teragrams/annum], Termites 20, Ocean 15, Hydrates 10. Natural Total: 270 Tg/a
Anthropogenic Sources: Energy [presumably production and leakage] 110 Tg/a, Landfills [decaying waste] 40 , Ruminants (Livestock) 115, Waste treatment 25, Biomass burning 40. Anthropogenic Total 330 Tg/a
http://en.wikipedia.org/wiki/Methane
• MCM: microbial (Archaean) methanogenesis is the ultimate source of atmospheric methane from wetlands, landfills, livestock, etc.
[119] **Atmospheric $\delta^{13}C$ Stable Isotope Model and Standard**: [See also Glossary]
• Lists abundances of stable carbon isotopes ^{12}C and ^{13}C, defines $\delta^{13}C$ measured in per mil (‰), and

far back as c. 2.8 Ga, suggesting that before that time there were not strong methanogenic sources. [MCM: but nevertheless there was a lot more atmospheric methane in Archean times than currently.]
g. **Nitrous Oxide N_2O**: N_2O is even stronger greenhouse gas than methane.[120] It has left no geological record so far, however, and the search continues.

The $\delta^{18}O$ from 3.8 Ga chert (carbonates from the early Archean) suggest the ocean T° was 80-90 °C (assuming this chert precipitated from sea water). However, this high temp would have produced clouds... The chert texture shows it is hydrothermally silicified tuff (volcanic ash), so the $\delta^{18}O$ records hydrothermal temperature. $\delta^{18}O$ is unreliable > 100 Ma. Also, these cherts probably are tuff ... Thus this is an unreliable method for determining ocean temperatures.... The Earth's oceans probably did not get this hot [other than at hydrothermal vents]. **Evaporites** show Earth's past temperatures. A course lab dealt with **gypsum** ($CaSO_4 \cdot 2H_2O$), which is a good thermostat as it will not precipitate at > 20 °C in sea water—instead we will preferentially get precipitation of **anhydrite** ($CaSO_4$).[121] Handout says "3.5 Ga barite after evaporite gypsum indicates sea surface T° of ~20 °C." RB clarified subsequently this: barite later replaced Gypsum in rocks, but the implication is unchanged—the ancient oceans were probably around 20 °C, the same as now.

2. Were Day Length and Size of Tides Different in the Archean?

We know little about the ancient Earth's rotational history. We can look at coral growth lines—they add 1 layer per day. Devonian [416 to 359 Ma] corals exhibit 399 growth rings per year, indicating **399 days/year**.[122] [123] The Devonian day length was only about **21 hours**. The slowing rotation rate of

---

states the standard of comparison: "The standard was originally the carbon contained in calcite from fossils called belemnites from a particular limestone called the **Pee Dee Formation** (abbreviated as PDB)."
http://www.carleton.edu/departments/GEOL/DaveSTELLA/Carbon/c_isotope_models.htm
• "The international reference standard for carbon isotopes is **VPDB**, which is shorthand for "**Vienna Pee Dee Belemnite**". The original PDB sample was a sample of fossilized shells of an extinct organism called a [Cretaceous] belemnite (something like a shelled squid) collected decades ago from the banks of the Pee Dee River in South Carolina. The original sample was used up long ago, but other reference standards were calibrated to that original sample. We still report carbon isotope values relative to PDB but now use the term "VPDB" to indicate that the data are normalized to the values of that standard."
http://wwwrcamnl.wr.usgs.gov/isoig/projects/fingernails/results/interpretdata.html
• "$\delta^{13}C$sample = { ($^{13}C/^{12}C$ sample) / ($^{13}C/^{12}C$ standard) - 1} x 1000"
"For carbon, the international standard is Pee Dee Belemnite, a carbonate formation, whose generally accepted absolute ratio [R] of 13C/12C is 0.0112372. Materials with ratios of $^{13}C/^{12}C$ > 0.00112372 have positive delta values..." [This site also lists standard ratios for H, N, and S
http://www4.nau.edu/cpsil/isotopes.htm
[120] **Global Warming Potential GWP of a Greenhouse Gas**: Presents mathematical calculation Global Warming Potential of strong greenhouse gases compared to "a similar quantity" of carbon dioxide. "The global warming potential of a gas is defined as the "radiative forcing" (that is the additional radiative power that the gas is sending back to the ground) of a given quantity of gas, cumulated over a given period, generally 100 years." The reported values are: **CO_2 = 1; CH_4 = 25; N_2O = 298; Perfluorocarbons = 7,400 to 12,200; Hydrofluorocarbons = 120 to 14,800; Sulfur hexafluoride = 22,800.** Note that these calculations do take into consideration the stability of the gas in the atmosphere over the 100 year period on which the calculation is based.
"By definition, a kg of CO_2 is worth 0.2727 kg **carbon equivalent**, that is the weight of [just the] carbon in a kg of CO_2. For the other gases..., the **carbon equivalent in kg per kg gas** is definded as ... relative GWP x 0.2727" A table is given showing the GWP expressed as Carbon equivalent per kg of the greenhouse gas: For methane, the carbon equivalent per kg methane is 6.82 kg (compared to 0.2727 kg per kg for CO_2).
http://www.manicore.com/anglais/documentation_a/greenhouse/greenhouse_gas.html
[121] **The Gypsum-Anhydrite Equilibrium**: "The new data indicate that in seawater saturated with halite and gypsum should dehydrate above 18 °C. The scarcity of anhydrite in modern evaporite deposits is predicted by the present results."
http://www.minsocam.org/ammin/AM52/AM52_171.pdf
[122] **Devonian Coral Growth Rings**: "Dr. Wells' counts of daily growth rings on fossil coral from the Middle Devonian period turned up more than 365 per year. The specimens he studied were about 350 million years old and contained an average of 400 rings annually. Were there 400 days in a Devonian

the Earth can be measured [the day length increases 1.7 - 2.3 msec per century], and is responsible for the need to add leap seconds periodically.[124] **Tides** cause friction as Moon pulls on water, friction generates heat which dissipates rotational energy.[125] The Moon is slowly receding from Earth [**38**

---

year?"
http://query.nytimes.com/... 1982

[123] **Tidal Slowdown, Coral Growth and the Age of the Earth**: "Tides slow down the earth's rotation speed because of friction between the earth and the water under which it rotates. The effect is very small—a slowdown rate of about 0.0002 seconds per day per year. This means that as each year goes by, each day of the year lasts 2 hundred-thousandths of a second longer. Thus the length of the day changes by about 20 seconds every million years. Since the earth's rotation is slowing down, it took less time in the past for the earth to rotate on its axis than it does today. But the time for one complete rotation is the length of a day. So if the days were shorter in the past, then there were once more days in the year than there are now. This, of course, assumes that the length of the year has not changed. This is a reasonable assumption, since the year is the time (measured in unchanging units) it takes for the earth to go once around the sun, and there is no known mechanism to make any measurable changes in this period over a few billion years.... Suppose we want to know how many days made up a year in the Devonian period, estimated to have been some 400 million years ago. Each day was 20 sec shorter per million years x 400 million years = 8,000 seconds shorter. This means each day was only 21.8 hours long then, as opposed to 24 hours per day now. Since a year is 8799 hours long (24 hours/day x 365.25 days/year, using modern-length days) and this length has not changed, we can calculate the number of ancient days in a Devonian year by dividing 8766 hours/year by 21.8 hours/day, to get about **400 days/year**. A similar calculation for the Pennsylvanian period, beginning about 280 million years ago, gives 22.4 hours/day, or 390 days in the Pennsylvanian year.... The reason for choosing the Devonian and Pennsylvanian periods is that we can check to see if these calculations correspond to reality. In certain modern corals and shellfish, we find growth-bands that indicate yearly, monthly, and even daily growth, rather like the annual rings that trees produce. By counting these bands, we can determine how long a particular coral or shellfish lived just as we can for a tree by counting its rings. We can also see that there are ... about 365 daily bands per year for modern corals and shellfish. But careful analysis of the growth-bands of fossil corals and shellfish from the Devonian and Pennsylvanian has confirmed that years in these periods contained more days than years do now, and that the number of days per year for both these periods is remarkably close to the values calculated above."
http://ibri.org/DVD-1/Tracts/tidaltct.htm

[124] **Leap Seconds**: "A leap second is an intercalary, one-second adjustment that keeps broadcast standards for time of day close to mean solar time [UT1]. Broadcast standards for civil time are based on Coordinated Universal Time [UTC, a compromise derived from "coordinated universal time" and "temps universel coordonné"], a time standard which is maintained using extremely precise atomic clocks... Over long time periods, leap seconds must be added at an ever increasing rate... The name is based on the term "leap years", though in doing so it is a little inconsistent: leap seconds result in an extra second, while leap years result in an extra day, not an extra year... When a positive leap second is added at 23:59:60 UTC, it delays the start of the following UTC day (at 00:00:00 UTC) by one second, effectively slowing the UTC clock.... The solar day has gradually become **1.7 ms longer every century**, due mainly to the friction associated with tides"
http://en.wikipedia.org/wiki/Leap_second

[125] **Tidal Frictional Slowing of Earth Rotation**:
• "Currently the secular change in the rotation rate increases the length of day by some **2.3 milliseconds per day per century**... The tidal braking in the earth's rotation is actually caused primarily by friction in the oceans, where 'friction' may refer to any number of physical mechanisms which have yet to be determined definitively. For example, bottom friction, induced by tidal currents flowing across the seabed, various kinds of wave breaking, and scattering of tidal waves into oceanic internal waves are all thought to play a role. "
http://bowie.gsfc.nasa.gov/ggfc/tides/intro.html
• "Because the Moon's mass is a considerable fraction of that of the Earth (about 1:81), the two bodies can be regarded as a double planet system, rather than as a planet with a satellite. The plane of the Moon's orbit around the Earth lies close to the plane of the Earth's orbit around the Sun (the ecliptic), rather than in the plane perpendicular to the axis of rotation of the Earth (the equator) as is usually the case with planetary satellites. The mass of the Moon is sufficiently large and it is sufficiently close to raise tides in the Earth: the matter of the Earth, in particular the water of the oceans, bulges out along both ends of an axis passing through the centers of the Earth and Moon. The average tidal bulge

mm/year] as the Moon's orbital angular velocity increases and the Earth's rotational velocity decreases. Back-extrapolation predicted the "**Gerstenkorn Event**" (noted by astronomer Horst Gerstenkorn) c. 1.3 Ga, a time at which the Earth and Moon would have been in extremely close proximity. However there is no geologic record of such an event, which would have been accompanied by massive tides. Therefore we must assume that Earth is dissipating tidal energy now faster than in the past. The current higher rate is thought due to the intermediate sea level and moderate-sized polar ice caps we now have. If there were much more or much less ocean, there would be less tidal friction.

3. Tectonic Evolution: How Early Did Plate Tectonics Start?

(RB notes plus supplements)

Plate tectonics is important for life because it maintains **planetary homeostasis**: recycles atmospheric gases [particularly CO_2] and volatiles by subduction, [provides elevated land through mountain building and sediments through erosion], [?contributes] oceanic water, maintains equable temperatures, provides steady venting of radiogenic heating. On Earth, it is a slow and steady process, in contrast to Venus which undergoes catastrophic volcanic resurfacing[126] every few million years. Mars currently has no plate tectonics but has 6 large volcanoes, including the supergiant Olympus Mons, the largest volcano in the solar system [27 km high 550 km width, compared to the largest Earth volcano Mauna Loa, which is 9 km in height from seafloor]. Intense volcanism is not good for planetary homeostasis.

Evidence for earliest known plate tectonics: This is based on the distinctive rocks formed at plate boundaries.

Convergent Plate Boundaries CPB: Such boundaries can be oceanic/continental, continental/continental, or oceanic/oceanic. **Island arc volcanoes** form where both of the converging plates are made of oceanic crust, have distinct **chemistries**, particularly **boninites**[127], named after the

---

closely follows the Moon in its orbit, and the Earth rotates under this tidal bulge in just over a day. However, the rotation drags the position of the tidal bulge ahead of the position directly under the Moon. As a consequence, there exists a substantial amount of mass in the bulge that is offset from the line through the centers of the Earth and Moon. Because of this offset, a portion of the gravitational pull between Earth's tidal bulges and the Moon is perpendicular to the Earth-Moon line, i.e. there exists a [net] **torque** between the Earth and the Moon. This accelerates the Moon in its orbit, and decelerates the rotation of the Earth."
http://en.wikipedia.org/wiki/Tidal_acceleration

[126] **Venus Catastrophic Volcanic Resurfacing Controversy**: "VENUS WAS NOT CATASTROPHICALLY RESURFACED… Ribbon-terrain distribution… suggests that Venus' surface probably records a significantly longer history (>>1Ga) than previously appreciated, and that history does not include catastrophic volcanic resurfacing.
http://gsa.confex.com/gsa/2006AM/finalprogram/abstract_115427.htm"

[127] **Boninites**:
• "Boninite is a high magnesium mafic extrusive rock formed in back-arc environments, typically in seafloor spreading centres but also in terrestrial back-arc spreading centres. The rock is named for its occurrence in the Izu-Bonin arc south of Japan. Boninite is considered to be a primitive andesite derived from melting of metasomatised mantle…"
http://en.wikipedia.org/wiki/Boninite
• "Boninites, or high-magnesian andesites. These are unusual lavas, combining high Si with high Mg, Ni and Cr. They are thought to have formed by wet-melting of rather refractory lithosphere."
http://www.le.ac.uk/geology/art/gl209/lecture5/lecture5.html
• "The Bonin archipelago represents an uplifted fore-arc terrain [MCM: terrane] which exposes the products of Eocene supra-subduction zone magmatism. Chichijima, at the centre of the chain, represents the type locality for the **high-Mg andesitic lava termed boninite**."
http://petrology.oxfordjournals.org/cgi/content/abstract/35/3/577
• "The Ogasawara Islands were formed around 48 million years ago. They are a part of an island arc known geologically as a **fore arc**. They lie above a subduction zone between the Pacific Plate and the Philippine Plate. The Pacific Plate is subducting under the Philippine Plate, which creates an **oceanic trench** to the east of the islands. The crust of the **Ogasawara (Bonin) Islands** was formed by volcanic

Bonin islands formed at the convergence of Pacific and Mariana plates These contain high Mg, high Si basalts and andesites [or are high Mg andesites], and have distinctive trace elements. In the lab, the class studied an Archean basalt with pale color from Mg, but most basalts are not Si rich, though boninites are. They have been dated as early as **2.7-2.8 Ga** in specimens from Finland and Canada. In the past 6 months, a report from **Isua** Greenland[128] describes **3.8 Ga boninites** but this requires confirmation. **Blueschists and eclogites** (which are formed under high pressure metamorphosis at compressive convergent plate boundaries) would be the best evidence for ancient convergent tectonic boundaries, but none have been found in the Archean Eon, or before the Mesoproterozoic Era [begins 1.6 Ga].

One can also look for **physical evidence** of subduction. The descending slab of subducting cool ocean crust cause frictional heating and the formation of a **melting zone** in the mantle rock directly overlying the slab—this leads to expelling of water and volatiles, which rise to erupt at overlying volcanoes. Seismic tomographic traverses across the Canadian Shield N of Lake Huron show a major crustal **suture** associated with hanging slabs of dense **cold** (i.e., having slower seismic velocity) crust extending 70 km into the otherwise **anechoic mantle**. Is this a fossil "failed" Archean [3.8 - 2.5 Ga] subduction zone (one for which subduction stopped when the two colliding plates sutured together)?—dating it is not easily done! (Note: A craton[129] of stable continental crust is underlain by the **mantle root zone**, which is cooler than surrounding mantle for several hundred km, depleted ... and less melt-prone, preserves an old cooler subducting crust.)

Divergent Plate Boundaries DPB: Such boundaries can be **mid-ocean ridges** (or rift valleys). Best evidence for ancient mid-ocean ridges are characteristic rocks: **pillow basalts** above, a zone of **sheeted dike complexes** below and moving away from the ridge, **gabbros** (magma chambers), and below this mantle peridotites and distinct "**tectonized**" pattern... [lecture incompletely transcribed]..., and

---

activity when subduction began 45–50 million years ago, and is composed mostly of an **andesitic volcanic rock called boninite**, which is rich in **magnesium oxide, chromium, and silicon dioxide**. The Ogasawara Islands may represent the exposed parts of an ophiolite that has not yet been emplaced on oceanic crust. The rocks of the Volcano Islands are much younger; Iwo Jima is a dormant volcano characterized by rapid uplift and several hot springs."
http://en.wikipedia.org/wiki/Bonin_Islands

• "Late Archean subduction-related assemblages of the North Karelian [?Finland] greenstone belt, NE part of the Baltic Shield, Russia, reveal the oldest known boninite series occurring at least in two area of the belt. The first area referred to here as the Khizovaara structure shows apparent evidence of a late Archean ocean-island volcanic arc collage formed during two distinct tectonic episodes nearly **2.8 Ga** ago... These occurrences strongly suggest that late Archean subduction-related processes evolved boninite-hosting SSZ ophiolites have not changed substantially over the past 2.8 Ga."
http://adsabs.harvard.edu/abs/2001AGUFM.T52D..10K

[128] **Isua Greenstone Belt**: "The Isua Greenstone Belt is an Archean greenstone belt in southwestern Greenland dated at 3.8-3.7 Ga and contains the oldest known, well preserved, metavolcanic (metamorphosed mafic volcanic), metasedimentary and sedimentary rocks on Earth. It consists of five tectonic domains... It is thought that the recrystallized ultramafic bodies that occur in the belt are intrusions or komatiitic flows. Studies show that these komatiites are extremely similar to the 3.5 Ga Barberton basaltic komatiites of South Africa, and are both Archean equivalents of modern boninites produced by hydrous melting in subduction zones. The Barberton komatiites share some of the same geochemical characteristics with modern-day boninites..."
http://en.wikipedia.org/wiki/Isua_greenstone_belt

[129] **Craton**: "A craton (Greek kratos; "strength") is an old and stable part of the continental crust that has survived the merging and splitting of continents and supercontinents for at least 500 million years. Some are over 2 billion years old. Cratons are generally found in the interiors of continents and are characteristically composed of ancient crystalline basement crust of lightweight felsic igneous rock such as granite. They have a thick crust and deep roots that extend into the mantle beneath to depths of 200 km. The term craton is used to distinguish the stable interior portion of the continental crust from such regions as mobile geosynclinal troughs... The extensive central cratons of continents may consist of both shields and platforms, and the crystalline basement. A shield is that part of a craton in which the usually Precambrian basement rocks crop out extensively at the surface. In contrast, the platform of the basement is overlain by horizontal or subhorizontal sediments."
http://en.wikipedia.org/wiki/Craton

ophiolites[130] (**obducted**[131] or uprising ocean crust and upper mantle formed at spreading ridges). The oldest certain ophiolite is **2.0 Ga Cape Smith Fold Belt** in Canada [thus Paleoproterozoic]. Some Archean "greenstone belts" have been interpreted as ophiolite, but these lack distinctive **sheeted dike complexes** associated with continuously spreading ridges—thus we cannot be certain of their tectonic origin. In Isua are small outcrops at 3.8 Ga, but can't be sure if there is a sheeted dike complex. This is possible but unproven evidence of DPB.

We thus conclude regarding early plate tectonics:

(1) Plate tectonics of the modern style was certainly present by 1.6 Ga (Mesoproterozoic), probably present at 2.0 Ga (Paleoproterozoic), perhaps present in the late Archean.

(2) Early Archean: There was more radiogenic heat to vent then, so perhaps this was done faster and with smaller scale plate tectonics (with longer ridges or faster spreading), but the problem was initiating subduction. How to get lithosphere cool enough and dense enough to begin to sink? (The current pattern of plate tectonics is tens of millions of years old—it required [uncertain transcription] 70 million years to get crust cool enough to be dense enough to begin to subduct.) Perhaps a combination of plate tectonics and plume tectonics existed in the Archean eon, perhaps with more hotspots then than now.

(3) Perhaps life was not possible until plate tectonics was the dominant process—perhaps planetary homeostasis cannot exist without it.

---

[130] **Ophiolite**: "An Ophiolite is a section of the Earth's oceanic crust and the underlying upper mantle that has been uplifted or emplaced to be exposed within continental crustal rocks. Ophio is Greek for "**snake**", lite means "stone". The term ophiolite was originally used by Alexandre Brongniart (1813) for an assemblage of green rocks (serpentine, diabase) in the Alps; Steinmann (1927) later modified its use to include serpentine, pillow lava, and chert ("Steinmann's trinity"), again based on occurrences in the Alps. The term was little used in other areas until the late 1950's to early 1960's, with the recognition that this assemblage provided an analog for oceanic crust and the process of **seafloor spreading**. This recognition was tied to two events: (1) the observation of magnetic anomaly stripes on the seafloor, parallel to oceanic ridge systems, interpreted by Vine and Matthews (1963) to represent the formation of new crust at the oceanic ridge and its subsequent spreading away from that ridge, and (2) the observation of a **sheeted dike** complex within the Troodos ophiolite (Cyprus) by Gass and co-workers, which must have formed by 100% intrusion of new magma, since no older wall rocks are preserved within the complex (Gass 1968). Moores and Vine (1971) concluded that the sheeted dike complex at Troodos could only form by a process similar to the sea-floor spreading proposed by Vine and Matthews (1963). Thus, it became widely accepted that **ophiolites represent oceanic crust that had been emplaced on land**... Their great significance relates to their occurrence within mountain belts such as the Alps or the Himalayas, where they document the existence of former ocean basins that have now been consumed by subduction. This insight was one of the founding pillars of plate tectonics, and ophiolites have always played a central role in plate tectonic theory."
http://en.wikipedia.org/wiki/Ophiolite

[131] **Obduction**: "Obduction is the overthrusting of continental crust by oceanic crust or mantle rocks at a destructive plate boundary. It can occur during an orogeny... Obduction occurs where a fragment of continental crust is caught with resulting overthrusting of oceanic mafic and ultramafic rocks from the mantle onto the continental crust. Obduction often occurs where a small tectonic plate is caught between two larger plates with the crust, both island arc and oceanic, becoming attached as a new terraine [MCM: terrane] to an adjacent continent. When two continental plates collide obduction of the oceanic crust between is often a part of the resulting orogeny, or mountain building episode. New Caledonia is one example of recent obduction... The characteristic rocks of the obducted oceanic crust are the ophiolites; consisting of basalt, gabbro, peridotite, dunite, and eclogite. There are many examples of oceanic crustal rocks and deeper mantle rocks that have been obducted and exposed at the surface worldwide..."
http://en.wikipedia.org/wiki/Obduction

Mantle Plume Tectonics: A typical **mantle plume** tectonic feature is the Hawaiian-Emperor seamount chain[132], which has formed over a geologic hotspot. The newest island is **Loihi[133]**, which is a seamount 30 - 35 km off the coast of the Big Island.

More research is needed to help determine when Earth became potentially habitable.

First Signs of Life (When Did Life First Appear?)

(per RB and supplemented)

1. Difficulties in Detecting Earliest Life

There are numerous difficulties in resolving this key question regarding the Archean Eon [3.8 - 2.5 Ga]:

a. Archean rocks are **rare**[134], because they have been buried, metamorphosed, subducted, eroded, etc. Rocks > 3.0 Ga are found only in small scattered locations—**Pilbara** Australia, **Yilgarn** Australia, and **Kaapvaal** South Africa—and 2.5 - 3.0 Ga are uncommon. <1% of the Earth's surface. [MCM: The maps I found seem to show more widespread Archean rocks than were shown in the slide, but perhaps the slide depicted only accessible surface rocks.]
b. Archean rocks are **poorly preserved**, due to metamorphism, deformation, erosion, etc., especially ones 2.5 - 3.0 Ga.
c. High **radiogenic heat** flow means that most Archean rocks are volcanic, therefore contain few if any fossils. Most sediments suffered **hydrothermal alteration**—hydrothermal is a high temperature often high acid environment which destroys most fossils.
d. The earliest life forms were probably structurally **simple** in structure, so might be hard to recognize, like abiotic mimics.
e. The earliest life forms might have been fundamentally different in biochemistry compared to modern (extant) organisms, perhaps "failed evolutionary experiments", so could be unrecognizable.
f. **Contamination** during the long complex geologic history easily occurs, can confuse—especially bacteria of 1 micron size can pass through pores and be deposited in rocks.

---

132 **Hawaiian-Emperor seamount chain**: http://en.wikipedia.org/wiki/Hawaiian-Emperor_seamount_chain
133 **Loihi Seamount**: http://en.wikipedia.org/wiki/Loihi_Seamount
134 **Distribution of Archean Rocks:**
• **North America**: [In the Canadian Shield area]
http://nationalatlas.gov/articles/geology/legend/ages/archean.html etc.
• **Pilbara craton**: "The Pilbara craton (the Pilbara province in northwest Western Australia), along with the Kaapvaal craton (the Kaapvaal province of South Africa) are the only remaining areas of **pristine Archaean 3.6-2.7 Ga crust** on Earth. Similarities of their rock records, especially the similarities in the overlying Late Archean sequences of both these cratons, suggest that they were once part of the **Vaalbara supercontinent**, and then believed to have belonged to Ur continent."
http://en.wikipedia.org/wiki/Pilbara_craton
• **Yilgarn Craton**: "The Yilgarn Craton is a large craton which constitutes the bulk of the Western Australian land mass. It is bounded by a mixture of sedimentary basins and Proterozoic fold and thrust belts. Zircon grains in the Jack Hills, Narryer Gneiss Terrane have been dated at ~4.27 Ga, with one detrital zircon dated as old as 4.4 Ga."
http://en.wikipedia.org/wiki/Yilgarn_craton
• **Kaapvaal craton**: The Kaapvaal craton (Limpopo province of South Africa), along with the Pilbara craton of Western Australia, are the only remaining areas of pristine **3.6-2.5 Ga** crust on Earth...
http://en.wikipedia.org/wiki/Kaapvaal_craton
• **Vaalbara**: The name "Vaalbara" is given to Earth's theorized first supercontinent. According to radiometric data of the encompassing cratons that constituted Vaalbara, it is believed to have existed 3.3 billion years ago (3.3 Ga) and possibly even as far back as 3.6 Ga.
http://en.wikipedia.org/wiki/Vaalbara:

2. Microfossils

Finding the "dead bodies" (preserved remains) of life forms would be the best, most direct, most ideal evidence. To date, there are no preserved remains of macroscopic fossils older than 2.1 Ga. And microorganism are hard to find. They preserve poorly because they have no hard parts that preserve well. Preservation of microfossils only occurs when they are rapidly buried and entombed with rapid lithification. E.g., as evaporites in the Transvaal Supergroup (South Africa).

The **OLDEST CERTAIN MICROFOSSILS** are **2.5-2.6 Ga** [thus late Archaean] evaporites from Transvaal Supergroup (slide referenced Klein et al 1987 publ. Elsevier, article not yet found, see also Buick article 1990[135] and and *PB2001*.) Archean microbes are 2 micron to 19 microns, including ball (coccoid) and rod (bacilli) forms, filaments up to 200 microns in length. They contain **kerogen**[136] (organic material) sometimes encrusted with iron oxide.

Filamentous microorganisms have been reported, possibly as old as **3.2 Ga**, from the Pilbara craton, Sulphur Springs Group, Northwestern Australia.[137] The filaments are 1 micron in diameter and made of pyrite. There is no organic matter, but the distribution of the orientation ("behavior") of the pyritic filaments relative to the laminations, as well as their sinuous morphology and other features are somewhat suggestive microorganisms, but these remain **uncertain**. [MCM: These were described as "probably thermophilic chemotropic prokaryotes, which inhabited sub-sea-floor hydrothermal environments"—not as shallow water stromatolites.]

3.2 Ga Barberton South Africa samples also showed filaments and "coccoids", some appearing to be dividing. But no complex behavior seen and these remain uncertain microfossils.[138]

3.45 "Microfossils" from Apex Chert, Marble Bar[139], NW Australia, appear in textbooks. Carbonaceous microstructures in chert breccia. Contain kerogen. But they are pale, not black as expected, thus appear relatively unmetamorphosized despite metamorphosis of host rock peaking at 3.2 Ga, suggesting they are contaminants, prob. from 2.7 Ga, and may not even be microfossils. They occur within 20 m of an angular unconformity, an old weathering surface which commonly produce fissures and cracks. Roger believes these are not microfossils.

---

[135] **Oldest Microfossils**:
"Microfossil Recognition in Archean Rocks: An Appraisal of Spheroids and Filaments from a 3500 M.Y. Old Chert-Barite Unit at North Pole, Western Australia" Roger Buick *PALAIOS*, Vol. 5, No. 5 (Oct., 1990), pp. 441-459 (accessed via JSTOR).

[136] **Kerogen**: "Kerogen is a mixture of organic chemical compounds that make up a portion of the organic matter in sedimentary rocks. It is insoluble in normal organic solvents because of the huge molecular weight (upwards of 1,000) of its component compounds. The soluble portion is known as bitumen. When heated to the right temperatures in the Earth's crust, some types of kerogen release oil or gas, collectively known as hydrocarbons (fossil fuels). When such kerogens are present in high concentration in rocks such as shale, and have not been heated to a sufficient temperature to release their hydrocarbons, they may form oil shale deposits."
http://en.wikipedia.org/wiki/Kerogen

[137] **Oldest Stromatolites:** See Birger Rasmussen. "Filamentous microfossils in a 3,235-million-year-old volcanogenic massive sulphide deposit". *Nature* 405, 676-679 (8 June 2000) accessed 10/2007 at http://www.nature.com/nature/journal/v405/n6787/full/405676a0.html.

[138] **Barberton Microfossils**: Maud M. Walsh & Donald R. Lowe. "Filamentous microfossils from the 3,500-Myr-old Onverwacht Group, Barberton Mountain Land, South Africa". *Nature* 314, 530 - 532 (11 April 1985) accessed at
http://www.nature.com/nature/journal/v314/n6011/abs/314530a0.html.

[139] **Marble Bar ?microfossils**: "The Schopf Locality is located a brisk two-hour walk over rocky ground from the outskirts of **Marble Bar** in the **Pilbara area**. High on a hillside near Chinaman Creek is a chert barite dyke where material was collected. Dr Bill Schopf claimed that the material contained microfossils dating back into the early Archaean and a paper was published in the refereed journal *Nature* in 1993. Since then the matter has been the subject of an ongoing debate."
http://pilbara.mq.edu.au/wiki/Schopf_Locality

3. Stromatolites

[Some confusion in transcription for this section] These have been found throughout [much of] the Archean... They are ~trace fossils of microbial mats of accreted sediment (but not the organisms themselves), are laminated due to environmental cycles etc., have convex flexures due to microbes moving to light, etc. Late Archean stromatolites (<3.0 Ga) are uncontroversially biogenic. Older Archean stromatolites > 3.0 Ga are all controversial, sometimes dismissed as abiotic folds, precipitates, etc. There are many potential abiotic mimics of stromatolites, such as stalagmites, or folds in laminated sediments.

Stromatolites are rare in modern times because they are disrupted by burrowing or grazing animals such as crustaceans and snails.[140] However, they were abundant in Proterozoic times, and widespread in Archean especially after 2.5 Ga, though **scarce before 2.7 Ga**. For example, 2.72 Ga **Tumbiana** formation[141].... structure suggests fenestrae=gas-filled voids from trapped metabolic gases. These also show **filamentous palimpsests**, mineral filling in a void after organic microbe rotted away. [MCM: a palimpsest is defined in Merriam-Webster as "writing material (as a parchment or tablet) used one or more times after earlier writing has been erased".]

North Pole Warrawoona Group Australia stromatolites: (unpublished data of RB): RB has identified 3.46 - 3.49 Ga ("3.47 Ga") stromatolites with domical structure, layers thickening over flexure crests, alternating layers, kerogen rich and poor complex layers, flexing ... fragments and flakes eroded from apex and appearing in troughs... Several scales of laminae and flexures, moderate morphological inheritance, laminae thicken over flexures, desiccated fragments—have no abiotic explanation. These are the "**OLDEST VISIBLE SIGNS OF LIFE ON EARTH**" (**3.47 Ga**) according to RB. He has them, but is not quite ready to publish.

Stromatolites are characterized by [incomplete transcription]:
a. Layered mounds of sediment ascribed to microbial growth, movement, or metabolism.
b. Convex upward doming with layers of sediments thickening over flexure crusts.
c. Microbial mats baffle currents causing grain deposition, trapped sediments by overgrowth or precipitated cement-like calcium carbonate (calcite) formed during photosynthesis. (The calcite may be replaced eventually by chert SiO_2 quartz.)
d. Modern (extant) stromatolites are formed by cyanobacteria or diatoms or green algae, etc.

Only places to see modern stromatolites currently are:

---

140 **Stromatolites**: "Stromatolites are commonly thought to have been formed by the trapping, binding, and cementation of sedimentary grains by microorganisms, especially cyanobacteria..."
"...Cyanobacteria use water, carbon dioxide, and sunlight to create their food. The byproducts of this process are oxygen and calcium carbonate (lime). A layer of mucous often forms over mats of cyanobacterial cells. In modern microbial mats, debris from the surrounding habitat can become trapped within the mucous, which can be cemented together by the calcium carbonate to grow thin laminations of limestone. These laminations can accrete over time, resulting in the banded pattern common to stromatolites. The domal morphology of biological stromatolites is the result of the vertical growth necessary for the continued infiltration of sunlight to the organisms for photosynthesis..."
"...Modern stromatolites are mostly found in hypersaline lakes and marine lagoons where extreme conditions exclude animal grazing. One such location is Hamelin Pool Marine Nature Reserve, Shark Bay in Western Australia where excellent specimens are today observed, and another is Lagoa Salgada, Southeast Brazil, where modern stromatolites can be observed as bioherm (domal type) and beds. Fresh-water stromatolites can be found in Cuatro Ciénegas, a unique ecosystem in the Mexican desert."
http://en.wikipedia.org/wiki/Stromatolite

141 **Tumbiana formation**: "The Tumbiana Formation, about 2700 million years old, was largely deposited in ephemeral saline lakes, as judged by the unusual evaporite paragenesis of carbonate and halite with no sulfate. Stromatolites of diverse morphology occur in the lacustrine sediments, some with palimpsest fabrics after erect filaments. These stromatolites were probably accreted by phototropic microbes that, from their habitat in shallow isolated basins with negligible sulfate concentrations, almost certainly metabolized by ozygenic photosynthesis."
http://www.sciencemag.org/cgi/content/abstract/255/5040/74?ck=nck

1. **Shark Bay** (NW Australia), 1 m high with rippled sand between. This is a restricted desert embayment with high salinity. Have flagtail grunters—a type of fish—and a crustacean, but they don't eat the microbial carpet [uncertain transcription].
2. **Pink Lake**, Australia... sulfite...
3. [MCM: others sites mentioned on the Web include: Minnesota, Schooner Cays in the Bahamas, and Qatar]

4. Isotope Fractionation As Evidence of Archean Life:

(per RB lecture and annotated, see also detailed Glossary entry)
Microbial metabolism fractionates the stable isotopes of C—photosynthesis enhances the lighter ^{12}C relative to ^{13}C, and microbes also enhance ^{14}N and ^{32}S. The biotic [biogenic] fractionations [deviations from the standard ratios] are much larger than those found by abiotic processes, at least at low temperatures and pressures found in environments that could support life. Life "prefers" light isotopes such as ^{12}C over the heavier isotopes of the same element such as ^{13}C, because life is "lazy", and it is easier to move or diffuse the lighter isotopes around and easier to break bonds [why?]. Isotopic evidence is trapped in minerals and can survive thermal and mechanical trauma well, better than the microfossils themselves or stromatolites. To be sure of biogenic origin evidence from isotope fractionation, must have samples showing the ratios of the stable isotopes in both the reactant (parent precursor or host environment) and the product (biogenic result). If the parent precursor is unavailable, we can't be sure the product is biogenic.

Delta δ notation: The deviation from a standard ratio for 2 isotopes of an element is expressed numerically as δ, such as carbon $\delta^{13}C$, sulfur ($\delta^{34}S$), and N ($\delta^{15}N$).

$\delta^{13}C$ for a sample is defined as

$$\delta^{13}C = \{ ((^{13}C/^{12}C)_{sample}) \ / \ ((^{13}C/^{12}C)_{standard}) - 1\} \times 1000$$

expressed as parts per thousand or parts per mill and notated ‰

where $^{13}C/^{12}C$ is the absolute isotope ratio in the sample or standard of the number of atoms of the heavier isotope compared to the lighter isotope. The standard ratio for C is PDB (Pee Dee Belemnite).

The ocean has a $\delta^{13}C$ of about 0‰, the atmospheric CO_2 has $\delta^{13}C$ of about -6‰. (A chart was projected.) For organisms that convert CO_2 in photosynthesis, those that use the [older and ? more primitive] C3 pathway[142] yield values of $\delta^{13}C$ of about -32‰ to -24‰, whereas those that use the C4

---

[142] **C3 and C4 Carbon-Fixing Photosynthetic Pathways**:
• See updated details in http://www.mcgoodwin.net/pages/PlantPhysUW425.pdf
• "**C3 carbon fixation** is a metabolic pathway for carbon fixation in photosynthesis. This process converts carbon dioxide and Ribulose-1-5-biphosphate (RuBP, a 5-carbon sugar-related compound) into 3-phosphoglycerate [the first stable intermediate of the Calvin cycle] through the following reaction:

6 CO2 + 6 RuBP → 12 3-phosphoglycerate

This reaction [which is catalyzed by **rubisco]** occurs in all [green photsynthetic] plants as the first step of the Calvin cycle. In C4 plants, carbon dioxide is drawn out of malate and into this reaction rather than directly from the air. [MCM clarification: the first stable intermediates are malate- or aspartate-, both of which are 4 carbon acid compounds] Plants that survive solely on C3 fixation (C3 plants) tend to thrive in areas where sunlight intensity is moderate, temperatures are moderate, carbon dioxide concentrations are around 200 ppm or higher, and ground water is plentiful. The C3 plants, originating during Mesozoic and Paleozoic era, predate the C4 plants and still represent approximately 95% of Earth's plant biomass. C3 plants must be in areas with high concentrations of carbon dioxide because RuBisCO often incorporates an oxygen molecule into the RuBP, instead of a carbon dioxide molecule. This breaks the RuBP into a three-carbon sugar that can remain in the Calvin cycle, and two molecules of glycolate which is oxidized into carbon dioxide, wasting the cell's energy. High concentrations of carbon dioxide lowers the chance that RuBisCO incorporates an oxygen molecule. C4 and CAM plants have adaptations that allow them to survive in areas where the plant cannot take in a lot of carbon dioxide. The isotopic signature of C3 plants shows higher degree of 13C depletion than the C4 plants.
http://en.wikipedia.org/wiki/C3_carbon_fixation, article excerpt annotated by MCM
see further details in http://www.mcgoodwin.net/pages/PlantPhysUW425.pdf

pathway yield less negative values of -22‰ to -10‰. Algae are c. -3.5‰ to 12‰. Methanogenic bacteria (Archaea) have a wide range of values, recently found to be as great as -65‰ and extending down to +10‰. Cyanobacteria are -22‰ to -8‰. [MCM: Almost all these values are roughly estimated from viewing the slide graph—the source of slide data was not stated.]

Evidence for Early Archean Life based on Isotope Fractionation data:

(1) **Isua Greenland gneiss**. Examined $\delta^{13}C$ in graphite, found values of -20‰ in metamorphic shale. Dated to c. 3.85 to 3.7 Ga (~3.7 Ga average estimate). But no sedimentary carbonate parent available to determine extent of fractionation, so does not constitute certain evidence of life. This was found by Minik Rosing.[143]

(2) **Akilia Greenland gneiss**. [parts of transcription uncertain] ? c. 3.85 Ga. Cover of article in [1996] *Nature* billed this as "Oldest traces of Life on earth?" Small island off W. coast of Greenland. Examined $\delta^{13}C$ in **graphite grains**, found $\delta^{13}C$ values of -45 [?] to -20 ‰ in graphite inclusions within flakes/grains of apatite in ferruginous quartzite (?in a metamorphosized banded iron formation rock?—this aspect proved debatable) The apatite [general formula $Ca_5(PO_4)_3(OH,F,Cl)$, apatite does not contain carbon] was evidently of metamorphic origin, exposed to 600 degrees C, almost melted, c. 1.8 Ga. The host rock evidently was silicified igneous intrusion, not sediment—would not expect to find organisms in this. The graphite grains remain doubtful for evidence of early life.[144] Photo shows fission tracks, not microfossils. Specimen may be therefore 3.85 Ga to as recent as 1.8 Ga. Granite intrusions have zircons dated to 3.82 Ga, providing the dating of the host rock.

(3) **Coonterunah Group, NW Australia**: These are **3.52 Ga**. Unpublished data [except as abstract[145]] Kerogenous chert present is light in ^{13}C ($\delta^{13}C$ = -22 to -24 ‰), is imbedded in host rock of sedimentary

---

• "**C4 carbon fixation** is one of three biochemical mechanisms, along with C3 and CAM photosynthesis, functioning in land plants to "fix" carbon dioxide (binding the gaseous molecules to dissolved compounds inside the plant) for sugar production through photosynthesis. Along with CAM photosynthesis, C4 fixation is considered an advancement over the simpler and more ancient C3 carbon fixation mechanism operating in most plants. Both mechanisms overcome the tendency of RuBisCO (the first enzyme in the Calvin cycle) to photorespire, or waste energy by using oxygen to break down carbon compounds to CO2. However C4 fixation requires more energy input than C3 in the form of ATP. C4 plants separate RuBisCO from atmospheric oxygen, fixing carbon in the mesophyll cells and using oxaloacetate and malate to ferry the fixed carbon to rubisco and the rest of the Calvin cycle enzymes isolated in the bundle-sheath cells. The intermediate compounds both contain four carbon atoms, hence the name C4.... C4 plants have a competitive advantage over plants possessing the more common C3 carbon fixation pathway under conditions of drought, high temperatures and nitrogen or carbon dioxide limitation. C4 carbon fixation has evolved on at least 18 independent occasions in different groups of plants, so is an example of convergent evolution. Plants which use C4 metabolism include sugarcane, maize, sorghum, finger millet, amaranth, and switchgrass. C4 plants arose during the Cenozoic Era and did not become common until the Miocene Period. Today they represent about 5% of Earth's plant biomass and 1% of its known plant species. These species are concentrated in the tropics where the high air temperature contributes to higher possible levels of oxygenase activity by RuBisCO, which increases rates of photorespiration in C3 plants."
http://en.wikipedia.org/wiki/C4_carbon_fixation
see additional details in http://www.mcgoodwin.net/pages/PlantPhysUW425.pdf

[143] **Isua Greenland**: see for example: Minik T. Rosing "13C-Depleted Carbon Microparticles in >3700-Ma Sea-Floor Sedimentary Rocks from West Greenland". *Science* 29 January 1999: Vol. 283. no. 5402, pp. 674 - 676. Accessed at http://www.sciencemag.org/cgi/content/abstract/283/5402/674.

[144] **Akilia Greenland rocks**: "To my regret, the ancient Greenland rocks [at Akilia] have not yet produced any compelling evidence for the existence of life by 3.8 billion years ago.... true consensus for life's existence seems to be reached only with the bacterial fossils of the 1.9-billion-year-old Gunflint Formation of Ontario."
Stephen Moorbath. "Dating earliest life" *NATURE* VOL 434 10 MARCH 2005.
www.nature.com/nature

[145] **Coonterunah kerogen:** "However, in the 3.52 Ga Coonterunah Group of Australia, kerogens in low-grade sedimentary carbonates show fractionations consistent with autotrophy via the Calvin-Benson cycle, indicating that life started modifying geochemical"

carbonate (greenschist facies laminated limestones) having $\delta^{13}C$ = -2‰ to -1‰. The total fractionation value of $\delta^{13}C$ = -22‰ - 20‰ is typical for biologic carbon fixation. The rock is slightly metamorphosized. Both reactant (calcite) and product (kerogen) are present, satisfying this essential criterion. RB says this is the **OLDEST CERTAIN EVIDENCE OF LIFE: 3.52 Ga**.

Overall Implications for Development of Life: (slide)
a. The **prerequisites** for life have been present possibly as early as c. 4.4 Ga (core formation and magnetic field, crustal differentiation and P [phosphorus?] source, ocean condensation.
b. **Frustration of Life** due to Late Heavy Bombardment extended up to 3.8 Ga, including probably ocean vaporization.
c. **Definite signs of life** found by 3.52 Ga in Coonterunah kerogen, and in stromatolites soon thereafter c. 3.47 Ga.
d. Therefore, life arose and diversified rapidly.
e. Planets with early but short-lived habitable windows (e.g., Mars) could have evolved life.

Domains of Life

(per RB and supplemented)
The "Tree of Life" is a phylogeny[146] of all living organisms derived from relationships in nucleic acid sequences which has been claimed to represent the true history of life.

1. Construction of the Tree of Life (TOL)

It is possible to build a tree showing relationships among data of many types. For the phylogenetic Tree of Life, showing evolutionary relatedness, this was traditionally done using **physical features** (**morphology**), with specific features arbitrarily weighted for importance by particular researchers. Close relatives appear similar in location in the tree. However, a main difficulty is that one must decide which features and which variables affecting these features are the most important—e.g., eye color—in determining evolutionary relatedness, and these factors are often arbitrarily weighted. Physical features can be misleading regarding evolutionary relatedness [for example, **convergent evolution**[147]]. More recently, researchers use mathematical or computerized models for quantification in building trees, employing statistical tests to find best criteria.

Cladistics [see Glossary] has been used for fossils and for living organisms. Applied to physical features, count the number of shared characteristics (**synapomorphies**[148]) which (for comparing for example mammals) typically are more recently-evolved (such as opposable thumbs, binocular vision,

---

Roger Buick. "Earliest evidence of life on Earth" Goldschmidt Conference Abstracts 2007, http://www.goldschmidt2007.org/abstracts/A131.pdf
[146] **Phylogenetic**:
"A phylogeny, or evolutionary tree, represents the evolutionary relationships among a set of organisms or groups of organisms, called taxa (singular: taxon). The tips of the tree represent groups of descendent taxa (often species) and the nodes on the tree represent the common ancestors of those descendents. Two descendents that split from the same node are called sister groups... Evolutionary trees depict clades. A clade is a group of organisms that includes an ancestor and all descendents of that ancestor. You can think of a clade as a branch on the tree of life."
http://evolution.berkeley.edu/evolibrary/article/phylogenetics_02
"In biology, phylogenetics (Greek: phyle = tribe, race and genetikos = relative to birth, from genesis = birth) is the study of evolutionary relatedness among various groups of organisms (e.g., species, populations). Also known as phylogenetic systematics, phylogenetics treats a species as a group of lineage-connected individuals over time..."
http://en.wikipedia.org/wiki/Phylogenetic
[147] **Convergent evolution**: "In evolutionary biology, convergent evolution is the process whereby organisms not closely related (not monophyletic), independently evolve similar traits as a result of having to adapt to similar environments or ecological niches... On a molecular level, this can happen due to random mutation unrelated to adaptive changes...
http://en.wikipedia.org/wiki/Convergent_evolution
[148] **Synapomorphy**: In evolutionary biology, a synapomorphy is a derived character state shared by two or more terminal groups (taxa included in a cladistic analysis as further indivisible units) and inherited from their most recent common ancestor.

lack of a tail, etc.), but omit more primitive characteristics which evolved long ago (such as warm bloodedness, live birth, lactation, etc.) Then use computer program to find simplest tree showing relationships (the **most parsimonious**[149] solution).

[Modern extant organisms appear as the "**leaves**" in these diagrams, whereas the **inner nodes** or points of bifurcation may or may not correspond to a particular precursor organism. A **taxon** is a group of organisms that is given a name. A **natural taxon** is a group of organisms that exists in nature [and are related] as a result of evolution. A **monophyletic group** is a group of species that includes an ancestral species and all of its descendants. A **clade** is a monophyletic group, i.e., a natural taxon—a group of organisms that includes an ancestor [or bifurcation node] and all descendents of that ancestor.[150]]

When techniques for sequencing genes, RNA, and proteins were developed, it became possible to substitute this data for physical features in cladistics for building parsimonious trees. By comparing a number of differences in gene sequences, the more similar organisms compare in these gene sequences, the more closely related they are considered to be phylogenetically. For example, the gene for **casein**[151], (a milk protein unique to mammals [not an enzyme]), has been compared for multiple organisms. Small differences in the nucleotides CATG at fixed positions have been used to show a close relationship between cetaceans and hippopotami through a presumed common ancestor, compared to other mammals.

Such trees have been constructed for living organisms using chemical criteria, but others are working to construct a tree containing all fossil organisms, incorporating physical features (since DNA etc. is not available for almost all fossils).

Diagram of Tree of Life[152] slide projected, showing branching patterns into 3 main **domains**, the Bacteria [Eubacteria], Archaea, and Eukarya [also termed Eucarya, Eukarya, or Eukaryotes]. This diagram begins at a presumed common **root**, the "**Most Recent [or Last] Common [or Universal] Ancestor**" (MRCA or LCA) of all living organisms. Such diagrams are beloved by biologists, who think they truly represent the history of life. However, the existence of such a hypothetical single root organism is debated, and certain complexities cloud the picture (see below).

Potential Problems in Cladistics Trees (Cladograms):
(1) Require use of a distantly related **outgroup**[153] to serve as a standard of comparison. But what outgroup to use for the entire Tree of Life? No easy answer.
(2) Presume a **dichotomous (bifurcating or binary) branching pattern** (which may not always be true).
(3) Presume **linear descent** (no lateral gene transfer or exchange of genetic material), but this is not always the case, especially with microorganisms.
(4) Show only living organisms. **Extinction destroys genetic information**. There are only a few exceptions of preserved DNA: Neanderthal (bones in cold caves), mammoths (in permafrost). The oldest ice is only a few Ma. (Despite *Jurassic Park*, **amber** is a poor preservative because it admits O_2).

---

[149] **Parsimony**: "Maximum parsimony, often simply referred to as "parsimony," is a non-parametric statistical method commonly used in computational phylogenetics for estimating phylogenies. Under maximum parsimony, the preferred phylogenetic tree is the tree that requires the least number of evolutionary changes."
http://en.wikipedia.org/wiki/Maximum_parsimony
[150] **Clade vs. Taxon**: http://www.amnh.org/learn/pd/fish_2/pdf/compleat_cladist.pdf
[151] **Casein Phylogeny**: For example, John Gatesy, et al, "Evidence from Milk Casein Genes that Cetaceans are Close Relatives of Hippopotamid Artiodactyls", *Mol. Bid. Evol.* 13(7):954-963. 1996, accessed at http://mbe.oxfordjournals.org/cgi/reprint/13/7/954.pdf.
[152] **Tree of Life**: (see also other footnotes)
• http://en.wikipedia.org/wiki/Phylogenetic_tree
• http://www.tolweb.org/tree/
[153] **Outgroup**: "In cladistics, whenever three or more monophyletic groups of organisms are compared, and all but one of them are more closely related to each other than any single one of them is to the last, the latter group is known as the outgroup. The evolutionary conclusion from this is that the outgroup branched from the parent group before the other two groups branched from each other."
http://en.wikipedia.org/wiki/Outgroup

(5) Show the total length of branching paths indicating **evolutionary distance**, but not actual evolutionary time of divergence. Trees just give evolutionary order. Different branches evolve at different rates.
(6) Require preselection of a gene or molecule that is suitable in terms of its speed of evolution compared to the time scale being evaluated. If studying closely related species, should use a gene which evolves fast, whereas if studying distantly related phyla, use gene which is highly conserved and evolves slowly.

For constructing the entire Tree of Life, must evaluate a gene that is **universal** and fundamental, and ultra-conserved. But some organisms only have 500 different genes, and many are not shared by higher organisms. One suitable candidate is the gene coding for the **Small Subunit of Ribosomal RNA (SSU RRNA).**[154] [The small subunit is 30 - 40S whereas the other subunit, the Large subunit, is 50 - 60S. RB says there are 3 subunits but he may be adding in tRNA.] This gene is present in all organism that synthesize proteins using rRNA and has only slowly evolved.

2. Pattern of the Tree of Life: Three Domains

Before the advent of molecular phylogeny, all life was divided into **5 kingdoms**: Monera [bacteria and archaea], Protista[155], Fungi, Plantae, and Animalia.[156] But now the **3 Domain System**[157] dominates, consisting of the Bacteria [Eubacteria], Archaea, and Eukarya [also termed Eucarya, Eukaryota, or Eukaryotes]. The Bacteria and Archaea were previously lumped under the obsolete kingdom Monera, but are now collectively termed Prokaryotes. The Eucarya included the other 4 kingdoms.

Prokaryotes[158] are generally small organisms that

- are mostly unicelluar (though some, such as cyanobacteria, can form colonies of cells forming filaments, sheets, or balls, etc.[159])
- lack a membrane bound cell nucleus or any other membrane-bound internal organelles
- have only 1 loop of chromosomal DNA lacking **introns** and **operons** (except in some archaea)
- may have at most a primitive cytoskeleton
- have cell walls formed of a different molecule than **cellulose** found in some eukaryotes (and many eukaryotes have no cell wall at all):
    - Bacteria (Eubacteria): **peptidoglycan** which is **ester bond linked**
    - Archaea: **pseudopeptidoglycan** (AKA pseudomurein)[160] which is **ether bond linked**, or polysaccharides or other cell wall materials, etc.[161] in some archaea]

---

[154] **SSU rRNA**: "European ribosomal RNA database"
http://bioinformatics.psb.ugent.be/webtools/rRNA/ [no longer being updated]
See also
Ribosomal Database Project (RDP) II: http://rdp.cme.msu.edu/ and
Ribosomal RNA:
• http://en.wikipedia.org/wiki/Ribosomal_RNA
• http://www.his.se/upload/21749/Ribosomal%20RNA.pdf
[155] **Protista**: are a diverse group of organisms, comprising those eukaryotes that cannot be classified in any of the other kingdoms as fungi, animals, or plants... Protoctists (or protists) are a paraphyletic grade, rather than a natural, (monophyletic) group, and so do not have much in common besides a relatively simple organization..."
http://en.wikipedia.org/wiki/Protist
[156] **5 Life Kingdoms**: http://en.wikipedia.org/wiki/Kingdom_(biology)
[157] **3 Domain System:** Carl R. Woese, et al, "Towards a natural system of organisms: Proposal for the domains: Archaea, Bacteria, and Eucarya", *Proc. Nati. Acad. Sci.* USA Vol. 87, pp. 4576-4579, June 1990, accessed at http://www.pnas.org/cgi/reprint/87/12/4576.
[158] **Prokaryotes**: http://en.wikipedia.org/wiki/Prokaryote
[159] **Cyanobacteria**: http://en.wikipedia.org/wiki/Cyanobacteria
[160] **Peptidoglycan**:
• "Peptidoglycan, also known as murein, is a polymer consisting of sugars and amino acids that forms a mesh-like layer outside the plasma membrane of eubacteria... Some Archaea have a similar layer of pseudopeptidoglycan. Peptidoglycan serves a structural role in the bacterial cell wall, giving structural strength, as well as counteracting the osmotic pressure of the cytoplasm..."
http://en.wikipedia.org/wiki/Peptidoglycan

- have a cell membrane of lipid bilayer that is "stiffened" [or stabilized] by polycyclic isoprenoid[162] "hopanols" (**hopanoids**[163]). Hopanoids can give rise to **hopane** molecular fossils.

• **Pseudopeptidoglycan**: "Pseudopeptidoglycan (also known as pseudomurein) is a major cell wall component of some archaebacteria that chemically differs from but morphologically, functionally, and structurally resembles eubacterial peptidoglycan... Whenever pseudopeptidoglycan is present in an organism, lysozyme is ineffective."
http://en.wikipedia.org/wiki/Pseudopeptidoglycan
• **Ester vs. Ether Linkage**: "Archaeal membranes have features unlike those found in either eukaryotes or bacteria. The lipids in archaea have a different chemical make-up in the following way. Remember that lipids in bacteria are amphipathic molecules containing a backbone of glycerol connected to a hydrophilic head group and two hydrophobic long-chain fatty acids. In **eukaryotes and bacteria** the fatty acids are attached to the glycerol backbone by **ester bonds**, while in **archaea ether linkages** are used. Also, the stereochemistry of lipids from archaea is primarily of the S form, while that of bacteria and eukaryotes is of the R form. In some archaea the hydrophobic chains attached to the glycerol backbone are twice normal length and pass completely through the membrane, attaching to a second backbone on the opposite side. This adds extra stability to the membrane and these dual lipids are often found in archaea living in extreme environments."
http://www.microbiologytext.com/index.php?module=Book&func=displayarticle&art_id=73
• "Most bacteria and eukaryotes have membranes composed mainly of glycerol-ester lipids, whereas archaea have membranes composed of glycerol-ether lipids. "
http://en.wikipedia.org/wiki/Archaea
[161] **Archaea cell wall composition**: "Archaea have various chemical compositions [for their cell wall], including glycoprotein S-layers, pseudopeptidoglycan, or polysaccharides."
http://en.wikipedia.org/wiki/Cell_wall
[162] **Isoprene and Isoprenoids**:
• "Isoprene is a common synonym for the chemical compound 2-methylbuta-1,3-diene... Isoprene is formed naturally in animals and plants and is generally the most common hydrocarbon found in the human body... It is a common structural motif in biological systems. The terpenes (for example, the carotenes are tetraterpenes) are derived from isoprene, as are the terpenoids and coenzyme Q. Also derived from isoprene are phytol, retinol (vitamin A), tocopherol (vitamin E), dolichols, and squalene. Heme A has an isoprenoid tail, and lanosterol, the sterol precursor in animals, is derived from squalene and hence from isoprene."
http://en.wikipedia.org/wiki/Isoprene
• "The **terpenoids**, sometimes referred to as **isoprenoids**, are a large and diverse class of naturally occurring organic chemicals similar to terpenes, derived from five-carbon isoprene units assembled and modified in thousands of ways. Most are multicyclic structures which differ from one another not only in functional groups, but also in their basic carbon skeletons. These lipids can be found in all classes of living things, and are the largest group of natural products."
http://en.wikipedia.org/wiki/Diterpenoid
• "Archaeal lipids are based upon the **isoprenoid** sidechain. This is a five-carbon unit that is also common in rubber and as a component of some bacterial and eukaryotic vitamins. However, only the archaea incorporate these compounds into their cellular lipids, frequently as C-20 (four monomers) or C-40 (eight monomers) side-chains. In some archaea, the C-40 isoprenoid side-chain is long enough to span the membrane, forming a monolayer for a cell membrane with glycerol phosphate moieties on both ends. "
http://en.wikipedia.org/wiki/Archaea
[163] **Hopanoids**:
• "Hopanoids are pentacyclic compounds similar to sterols, whose primary function is to improve plasma membrane fluidity in prokaryotes. Cholesterol serves a similar function in eukaryotes (including humans)... In many bacteria hopanoids may play important roles in the adjustment of cell membrane permeability and adaptation to extreme environmental conditions."
http://en.wikipedia.org/wiki/Hopanoids
• "The presence of abundant 2alpha-methylhopanes, which are characteristic of cyanobacteria, indicates that oxygenic photosynthesis evolved well before the atmosphere became oxidizing."
Brocks JJ, Logan GA, Buick R, Summons RE. "Archean molecular fossils and the early rise of eukaryotes"
Science. 1999 Aug 13;285(5430):1033-6. Accessed at http://www.ncbi.nlm.nih.gov/
• "Hopanoids, which are amphiphilic, pentacylic triterpenoid lipids, condense membrane lipids

- may be **autotrophic** [primary producers of organic carbon] **or heterotrophic** [consumers of organic carbon]
- reproduce mostly by asexual **binary fission (cloning)** but sometimes can "swap" [transmit] DNA by **plasmids** (not a true form of sexual reproduction)

Eukaryotes, usually have larger cells than Prokaryotes and

- are complex-celled often **multicellular** organisms
- have a membrane bound **cell nucleus** containing discrete **chromosomes**
- have one or more **chromosomes** which include **introns** ("junk" DNA) and **operons**
- have a well-developed **cytoskeleton[164]** consisting of **actin, tubulin** [, and **Intermediate filaments**]. This is unique to eukaryotes—prokaryotes may have at most a primitive cytoskeleton with no actual actin.[165]
- **cell wall** is made of **cellulose** [MCM: plus hemicelluloses and pectins] (if present at all—in plants and fungi)
- have a flexible **cell membrane** "rigidified" by **sterols** such as **cholesterol.**[166] Sterols give rise to **sterane** molecular fossils exclusively in eukaryotes, such as **cholestane**. [MCM: I missed comments pertaining to phytane, but phytanes can be associated with "halophilic bacteria"[167]] Thus eukaryotes can have large cells, and membrane flexibility enables **phagocytosis**, even ingestion of whole organisms leading to **endosymbiosis**.[168]
- have **membrane-bound internal structures (organelles)** such as **chloroplasts**, **mitochondria**, plastids, ER, and Golgi bodies.
- metabolism is performed by **endosymbionts**
  - **mitochondria** (from proteobacteria) perform aerobic cellular respiration, creating ATP [by oxidizing the major products of glycolysis, pyruvate and NADH, that are produced in the cytosol[169]]. Certain protist eukaryotes lack mitochondria—are "amitochondriate"[170]—and may

---

therefore stabilizing the membranes in a similar way to which sterols do in higher organisms." http://microbewiki.kenyon.edu/index.php/Frankia

164 **Cytoskeleton**: "The cytoskeleton is a cellular "scaffolding" or "skeleton" contained within the cytoplasm. The cytoskeleton is present in all eukaryotic cells, and recent research has shown that prokaryotic cells possess a cytoskeleton too. It is a dynamic structure that maintains cell shape, and also has been known to protect the cell, enables cellular motion (using structures such as flagella, cilia and lamellipodia), and plays important roles in both intracellular transport (the movement of vesicles and organelles, for example) and cellular division... Eukaryotic cells contain these main kinds of cytoskeletal filaments: Actin filaments / Microfilaments... Intermediate filaments... Microtubules" http://en.wikipedia.org/wiki/Cytoskeleton

165 **Prokaryote cytoskeleton**: "The traditional cytoskeletal functions in bacteria are carried out by highly conserved external and periplasmic filaments (flagella, pili) and cell walls. In recent years, functional analogs of actin (MreB), tubulin (FtsZ) and intermediate filaments (crescentin) were found in prokaryotes.
http://content.karger.com/ProdukteDB/produkte.asp?Aktion=ShowEachType&ProduktNr=232105

166 **Cholesterol**: "In animal cells cholesterol is normally found dispersed in varying degrees throughout cell membranes, in the irregular spaces between the hydrophobic tails of the membrane lipids, where it confers a stiffening and strengthening effect on the membrane."
http://en.wikipedia.org/wiki/Cell_membrane

167 **Phytanes as molecular fossils**:
• Associated with halophilic bacteria.
http://www.oiltracers.com/chatable.html
• "The isoprenoids are derived from photosynthetic microbes with a possible contribution from isotopically light methanogenic Archaea, which are known to yield only small quantities of pristane and phytane relative to total biomass and no n-alkanes when pyrolyzed."
Jochen J. Brocks, Graham A. Logan, Roger Buick, Roger E. Summons. "Archean Molecular Fossils and the Early Rise of Eukaryotes". *Science* Volume 285, Number 5430 Issue of 13 Aug 1999, pp. 1033 - 1036 accessed at
http://cas.bellarmine.edu/tietjen/Evolution/archean_molecular_fossils_and_th.htm

168 **Evidence For Endosymbiosis**: http://en.wikipedia.org/wiki/Endosymbiotic_theory

169 **Mitochondrial aerobic cellular respiration**: "A dominant role for the mitochondria is the production of ATP, as reflected by the large number of proteins in the inner membrane for this task. This is done by oxidizing the major products of glycolysis: pyruvate and NADH that are produced in the cytosol. This process of cellular respiration, also known as aerobic respiration, is dependent on

represent a basal branch in the development of eukaryotes before endosymbiotic acquisition of mitochondria. Other organisms such as Giardia lamblia and Trichomonas tenax appear to have descended from a mitochondrial clade but no longer have mitochondria.[171]
    - **chloroplasts** (from cyanobacteria) which perform **photosynthesis**.
- most are **heterotrophic** (but green plants etc. are photolithotrophic autotrophs[172]).
- reproduce with cell division using **mitosis** and with sexual reproduction using **meiosis** and **fertilization**, sometimes with **asexual reproduction** in various forms

From the Most Recent Common Ancestor in the Tree of Life, the first split (bifurcation) leads on one side to a sister taxon comprising the Bacteria, while the other limb gives rise to both Archaea and Eucarya (which are therefore more closely related than Bacteria are to either). The basic tripartite pattern divided into Archaea, Eucarya, and Bacteria is replicated by molecular phylogenies derived from whole genomes and from many other fundamental strongly conserved single genes.

We can only compare extant life. The Tree of Life represents [begins at] the LCA of all extant life. It is derived by comparing duplicated [i.e., persistent] genes that arose before the LCA—for example, **Aminoacyl tRNA synthetase**.[173] tRNA's all arose from a single organism or gene. If we use tRNA as the outgroup, we get a phylogenetic tree as already depicted… Humans are not necessarily the most highly evolved species, at least as measured by the relative evolutionary distance from the LCA (this distance is not the same as evolutionary time). Some protists may in fact be greater in evolutionary distance from the LCA.

The Tree of Life does not show extinct life. The tree therefore has been "pruned" extensively. Paleontologists and paleobiologists are trying to add fossil extinct life forms to the tree. This very important problem sets a major research agenda for the next generation.

There are also some problems in the Tree of Life:

---

the presence of oxygen. When oxygen is limited, the glycolytic products will be metabolised by anaerobic respiration, a process that is independent of the mitochondria. The production of ATP from glucose has an approximately 13-fold higher yield during aerobic respiration compared to anaerobic respiration."
http://en.wikipedia.org/wiki/Mitochondrion

170 **Amitochondriate Eukaryotes**: "It is now widely accepted that the eukaryotes we call protists are far more diverse in cellular organization than the non-protist eukaryote groups—namely animals, plants and fungi. A variety of heterotrophic protists lack classical mitochondria, inhabiting low-oxygen environments such as the guts and tissues of animals, marine or freshwater sediments, and the lower reaches of stratified water bodies. Over the last two decades these 'amitochondriate' organisms have been of great interest to evolutionary biologists, as some may have diverged before the acquisition of the mitochondrion and consequently represent very early stages in the evolution of the eukaryotic cell. Some amitochondriate groups—particularly the largely parasitic trichomonads, diplomonads, and microsporidia— have indeed tended to form the most basal branches in evolutionary trees of eukaryotes, based on molecular sequence comparisons… "
http://www.mbari.org/seminars/1998/nov4_simpson.html

171 **Trichomonas and Giardia descended from mitochondrial eukaryotes**:
http://www.biolbull.org/cgi/reprint/196/3/389.pdf

172 **Phototroph**: "Photoautotrophs … are organisms that carry out photosynthesis. Using energy from sunlight, carbon dioxide and water are converted into organic materials to be used in cellular functions such as biosynthesis and respiration…. A **photolithotrophic autotroph** is an autotrophic organism that uses light energy, and an inorganic electron source (eg. H_2O, H_2, H_2S), and CO_2 as its carbon source. Examples include plants."
http://en.wikipedia.org/wiki/Phototroph

173 **Aminoacyl tRNA synthetase**: "In addition, most of the aaRSs of a given specificity display the so-called canonical phylogenetic pattern in which the enzymes are grouped by the three domains of life - Archaea, Bacteria, and Eukarya, and the root of the phylogenetic tree is present in between the Bacterial branch and the Archaeal/Eukaryal branch."
http://en.wikipedia.org/wiki/Aminoacyl_tRNA_synthetase

(1) **Lateral Gene Transfer**: "Housekeeping" genes that deal with biosynthesis or catabolism have been subject to lateral gene transfer.[174] Parasites share host genes, viruses transport genes, prokaryotes exchange genes via plasmids, etc. Hence, for some genes, the phylogenetic tree looks more like a cross-linked **trellis**.
(2) **Endosymbiosis**: Some organelles in eukaryotic cells have their own genetic material and represent enslaved bacteria, etc. For example, mitochondria are derived from the Proteobacteria and chloroplasts are derived from cyanobacteria. Some endosymbiont genes have been lost to the host, becoming part of the host DNA, further cross-linking the trellis of the TOL.

3. Bacteria Domain, Specific Additional Details

Bacteria (**eubacteria**) have prokaryotic organization (see above list of characteristics comparing prokaryotes and eukaryotes). Their cell size is c. 0.2 microns to 2 microns[175], though some are up to 750 microns in size. (The latter included certain sulfur-oxidizing bacteria[176] living in low oxygen zones.)

Bacteria and archaea can both exchange genes. Viruses and plasmids can serve as the intermediaries. For example, the gene for HMG-CoA reductase[177] (a cofactor) can be propagated between organisms that are not closely related (at least as determined by SSU rRNA analysis). Archaeoglobus fulgidus has an "archaeal body" but has incorporated a bacterial gene for HMG-CoA reductase.[178]

The endosymbiotic organelles in eukaryotes have lost [or transferred] much of their genetic material to the host eukaryote's nucleus, and are no longer able to survive on their own. (See discussion above) In this way, the host nucleus now contains some mitochondrial DNA, etc. Thus, bacterial genes have "infected" our eukaryotic genes. Thus the Tree of Life diagram, as based for example on SSU rRNA, is a gross oversimplification.

---

[174] **Horizontal gene transfer (HGT), also Lateral gene transfer (LGT)**: "... is any process in which an organism transfers genetic material to another cell that is not its offspring. By contrast, vertical transfer occurs when an organism receives genetic material from its ancestor, e.g. its parent or a species from which it evolved...
http://en.wikipedia.org/wiki/Horizontal_gene_transfer
[175] **Bacteria Size**: "Bacterial cells are about 10 times smaller than eukaryotic cells and are typically 0.5–5.0 micrometres in length. However, a few species–for example Thiomargarita namibiensis and Epulopiscium fishelsoni–are up to half a millimetre long and are visible to the unaided eye. Among the smallest bacteria are members of the genus Mycoplasma, which measure only 0.3 micrometres, as small as the largest viruses.
http://en.wikipedia.org/wiki/Bacteria
[176] **Largest Bacteria**: "Residing in the greenish ooze of ocean sediment off the coast of Namibia, the spherical bacteria have diameters ranging from 100 to 750 micrometers. Since the bacteria often form strands of a dozen or so cells and glisten white from light reflecting off sulfur inside them, scientists named the microbe Thiomargarita namibiensis, or sulfur pearl of Namibia.... The key to the new microbe's large size, and to its life, is a huge fluid-filled sac, or vacuole, that takes up about 98 percent of the bacterium's interior. Within this vacuole, the bacterium stores large quantities of nitrate, which it uses to oxidize sulfur and garner energy."
http://www.sciencenews.org/pages/sn_arc99/4_17_99/fob5.htm
[177] **HMG-CoA reductase** : HMG-CoA reductase (or 3-hydroxy-3-methyl-glutaryl-CoA reductase or HMGR) is the first enzyme ... of the HMG-CoA reductase pathway, the metabolic pathway that produces cholesterol and various other biomolecules.... In humans, the gene for HMG-CoA reductase is located on the long arm of the fifth chromosome... Related enzymes having the same function are also present in other animals, plants and bacteria... HMG-CoA reductase is also an important developmental enzyme. Inhibition of its activity and the concomitant lack of isoprenoids that yields can lead to morphological defects."
http://en.wikipedia.org/wiki/HMG-CoA_reductase
[178] **Archaeoglobus fulgidus**:
Yan Boucher, et al. "Bacterial Origin for the Isoprenoid Biosynthesis Enzyme HMG-CoA Reductase of the Archaeal Orders Thermoplasmatales and Archaeoglobales" **Molecular Biology and Evolution** 18:1378-1388 (2001)

Many antibiotics have mechanisms of action based on attacking the cell wall of the target bacteria [such as bacitracin, vancomycin, and penicillin[179]].

The cell membrane of bacteria is a lipid bilayer "stiffened" [or stabilized] by "hopanols" (hopanoids, see earlier footnotes). These **hopanoids** or hopanols persist as fossil "**hopanes**" and serve as geologic biomarkers[180] in old rocks. (An electron micrograph of fossil bacteria was shown.) Hopanols have a distinct 5-ring skeleton.

Bacteria grow by binary fission or budding, sometimes however by multiple fission. Bacteria can undergo binary fission as often as every 15 minutes, thus explaining how they can proliferate in disease so fast (e.g., Salmonella). Bacteria clone themselves usually, but on occasion resort to a type of sexual reproduction in which plasmids are exchanged [conjugation].[181] According to RB, the exchange of genetic information is "usually mutual" and each organism may receive useful new material [MCM: I did not find two-way simultaneous mutuality of transfer described in several references—there is usually a donor and a recipient.] Such exchange of information can help to overcome unfavorable genes resulting from constant cloning—these can be ill-adapted to the evolving environment, or actually damaged genes. RB states he does not know what conditions predispose to or precipitate bacterial plasmid gene exchange.

Bacteria come in various shapes (cocci, bacilli, spirilla) and are usually unicellular. However the cyanobacteria can form multicellular filaments, bunches of filaments, branching filaments, filaments more than one cell diameter in width, sheets, and hollow balls. They can form colonies living in a secreted sheath or layer of mucus and sediments. Some cyanobacteria can form differentiated (specialized) cells such as nitrogen-fixing heterocysts[182]—these contain no chlorophyll—and akinetes [spores capable of withstanding drying, found in Dermocarpa etc.]

---

[179] **Antibiotics Mode of Action**: http://www.tufts.edu/med/apua/Miscellaneous/mechanisms.html
[180] **Hopanes as Geologic Biomarkers**:
• "Over the years a number of chemicals have been discovered, which point to the presence of life millions of years ago. Specific classes of compounds, for which we have a reliable information base, include pentacyclic triterpane hydrocarbons, so called hopanes, which are the fossil remnants of hopanoids biosynthesized by numerous eubacteria. Further classes include steranes (derived from sterols) from eukaryotes, acyclic isoprenoids from various precursors but particularly from lipids of Archaea, and certain hydrocarbons derived from carotenoid precursors (Summons and Walter, 1990)." Jan Toporski And Andrew Steele, "From Microbial Fossils To Astrobiology" J. Seckbach (ed.), *Origins*, 593–605. © 2004 Kluwer Academic Publishers, p. 598 accessed at
http://www.springerlink.com/content/k402g1r0752587n2/fulltext.pdf
• Note: the paper cited by Toporski et al is Summons R.E. and Walter M.R (1990) "Molecular fossils and microfossils of prokaryotes and protests from Proterozoic sediments." *Am. J. Sci.*, 290, 212-244.
[181] **Bacterial genetic exchange**: "Bacterial conjugation is the transfer of genetic material between bacteria through direct cell-to-cell contact. Discovered in 1946 by Joshua Lederberg and Edward Tatum, conjugation is a mechanism of horizontal gene transfer—as are transformation and transduction—although these mechanisms do not involve cell-to-cell contact.

Bacterial conjugation is often incorrectly regarded as the bacterial equivalent of sexual reproduction or mating. It is not actually sexual, as it does not involve the fusing of gametes and the creation of a zygote, nor is there equal exchange of genetic material. It is merely the transfer of genetic information from a donor cell to a recipient. In order to perform conjugation, one of the bacteria, the donor, must play host to a conjugative or mobilizable genetic element, most often a conjugative or mobilizable plasmid or transposon. Most conjugative plasmids have systems ensuring that the recipient cell does not already contain a similar element.

The genetic information transferred is often beneficial to the recipient cell. Benefits may include antibiotic resistance, other xenobiotic tolerance, or the ability to utilize a new metabolite. Such beneficial plasmids may be considered bacterial endosymbionts. Some conjugative elements may also be viewed as genetic parasites on the bacterium, and conjugation as a mechanism was evolved by the mobile element to spread itself into new hosts."
http://en.wikipedia.org/wiki/Bacterial_conjugation
[182] **Cyanobacteria Cellular Differentiation Including Heterocysts**:
• "Cyanobacteria include unicellular and colonial species. Colonies may form filaments, sheets or even hollow balls. Some filamentous colonies show the ability to **differentiate** into several different cell types: **vegetative cells**, the normal, photosynthetic cells that are formed under favorable growing

How Do Bacteria Live and Adapt?
Many basal branches in the TOL are thermophilic, living above 60 C, and some live up to 125 C (possibly even higher—this is a topic of intense oceanographic research). They live by or in black smokers at 3000 m depth, thus at a pressure where boiling point of water is substantially elevated. Thermophiles are found in both the Bacteria and the Archaea, thus it is postulated by some that the original LCA was possibly a thermophile.

Bacteria have high tolerance to environmental variation, and live in a wide variety of habitats. Some are happy in brine pockets contained in frozen sea ice, or alongside volcanic vents, or at the newly formed face of a volcanic lava flow, or extreme desert conditions such as Atacama.[183] Most of the organic material produced in the oceans arises from bacteria.

Human **aerobic respiration**[184] is done by enslaved bacteria—mitochondria. Humans also ferment molecules [with **anaerobic respiration** or **lactic acid fermentation**[185]]. This is all eukaryotes can do [MCM: in the limited sense of mechanisms for obtaining biochemical energy]. But bacteria have up to 6 metabolic pathways [MCM: in the sense of creating energetic compounds and otherwise as well?]:

---

conditions; **akinetes**, the climate-resistant **spores** that may form when environmental conditions become harsh; and thick-walled **heterocysts**, which contain the enzyme nitrogenase, vital for nitrogen fixation. Heterocysts may also form under the appropriate environmental conditions (anoxic) wherever nitrogen is necessary. Heterocyst-forming species are specialized for nitrogen fixation and are able to fix nitrogen gas, which cannot be used by plants, into ammonia (NH_3), nitrites (NO_2^-) or nitrates (NO_3^-), which can be absorbed by plants and converted to protein and nucleic acids. The rice paddies of Asia, which produce about 75% of the world's rice, could not do so were it not for healthy populations of nitrogen-fixing cyanobacteria in the rice paddy fertilizer."
http://en.wikipedia.org/wiki/Cyanobacteria
• "Heterocysts are specialized nitrogen-fixing cells formed by some filamentous cyanobacteria, such as Nostoc punctiforme, Cylindrospermum stagnale and Anabaena sperica, during nitrogen starvation. They fix nitrogen from dinitrogen (N_2) in the air using the enzyme nitrogenase, in order to provide the cells in the filament with nitrogen for biosynthesis. Nitrogenase is inactivated by oxygen, so the heterocyst must create a microanaerobic environment."
http://en.wikipedia.org/wiki/Heterocysts
[183] **Atacama Desert**: "While cyanobacteria appear to be absent, the scientists did find small numbers of heterotrophic bacteria in some Atacama desert soils. Instead of producing their own energy through photosynthesis - as cyanobacteria do - heterotrophic bacteria gather their energy by feeding on other organisms. The scientists don't know what these Atacama bacteria are eating, or how they get their water. They are not even sure why some spots of the desert had the heterotrophic bacteria, while other areas seemed to be completely lifeless."
http://www.astrobio.net/news/modules.php?op=modload&name=News&file=article&sid=337
[184] **Aerobic Respiration**: "Aerobic respiration requires oxygen in order to generate energy (ATP). It is the preferred method of pyruvate breakdown from glycolysis and requires that pyruvate enter the mitochondrion to be fully oxidized by the Krebs cycle. The product of this process is energy in the form of ATP (Adenosine Triphosphate), by substrate-level phosphorylation, NADH and $FADH_2$.
Simplified Reaction: $C_6H_{12}O_6$ (aq) + $6O_2$ (g) → $6CO_2$ (g) + $6H_2O$ (l) ΔHc -2880 kJ
http://en.wikipedia.org/wiki/Cellular_respiration
[185] **Anaerobic Respiration:** "Without oxygen, pyruvate is not metabolized by cellular respiration but undergoes a process of fermentation. The pyruvate is not transported into the mitochondrion, but remains in the cytoplasm, where it is converted to waste products that may be removed from the cell. This serves the purpose of oxidizing the hydrogen carriers so that they can perform glycolysis again and removing the excess pyruvate. This waste product varies depending on the organism. In skeletal muscles, the waste product is lactic acid. This type of fermentation is called **lactic acid fermentation**. In yeast, the waste products are ethanol and carbon dioxide. This type of fermentation is known as **alcoholic or ethanol fermentation**. The ATP generated in this process is made by substrate phosphorylation, which is phosphorylation that does not involve oxygen."
http://en.wikipedia.org/wiki/Cellular_respiration

[MCM: The following was presented very rapidly and incompletely transcribed. This is a very large topic about which whole textbooks[186] have been written, and I need to learn more about it. See here[187] for a summary review. These metabolic pathways deal not just with obtaining energy but also the **Nitrogen Cycle** pathways. Although formaldehyde has the formula H_2CO, RB uses "CH_2O" here to mean "organic matter" or **carbohydrates** (which vary in formula but tend to have compositions close to $(C\bullet H2O)_n$]

Energy-Generating or Consuming Metabolic Reactions
1) **Aerobic respiration heterotrophy**[188]**:** oxidize CH_2O with O_2 to H_20 and CO_2. [MCM: Here the term heterotrophy is referring to the source of energy utilized, not the source of C for building purposes. Oxygen is consumed]
2) **Anaerobic respiration heterotrophy**: "oxidize organic matter CH_2O with Fe or Mn oxides, nitrates (NO_3^-), or sulfate SO_4^{2-}" These reactions include **heterotrophic methanogenesis**.[189]
3) **Anaerobic fermentation heterotrophy**: "breaks C-C bonds in organic matter".
4) **Aerobic [Oxygenic] Photosynthesis**: "uses light to react $CO_2 + H_2O \rightarrow CH_2O + O_2$" [$O_2$ is generated, thus "aerobic"]
5) **Anaerobic [Anoxygenic] Photosynthesis**: uses light to react $2CO_2 + H_2S + 2H_2O \rightarrow 2CH_2O + SO_4^{2-} + 2H^-$[MCM: formula revised; no O_2 is generated]
6) **Chemolithotrophy (Chemosynthesis)**[190]: "Reacts gas and [inorganic] minerals, e.g., oxidize H_2S to sulfur". There are many sorts of reactions, they use redox reactions of metals and gases to get energy.

---

[186] **Bacterial Metabolism**: Gerhard Gottschalk. *Bacterial Metabolism, 2nd Ed.* excerpts accessed at http://books.google.com/books
[187] **Microbial metabolism (Review)**: http://en.wikipedia.org/wiki/Microbial_metabolism
[188] **Heterotrophs and Autotrophs**:
• "A heterotroph (Greek heterone = (an)other and trophe = nutrition) is an organism that requires organic substrates to get its **carbon** for growth and development. A heterotroph is known as a consumer in the food chain. Contrast with **autotrophs** which use **inorganic carbon dioxide or bicarbonate** as sole carbon source. All animals are heterotrophic, as well as fungi and many bacteria. Some parasitic plants have also turned fully or partially heterotrophic, whereas carnivorous plants use their flesh diet to augment their nitrogen supply, but are still autotrophic." [MCM: Note that this definition refers to the source of C in the organism, not necessarily the means of energy generation.] http://en.wikipedia.org/wiki/Heterotroph
• **Autotroph**: "An autotroph (from the Greek autos = self and trophe = nutrition) is an organism that produces complex organic compounds from simple inorganic molecules and an external source of energy, such as light or chemical reactions of inorganic compounds. Autotrophs are considered producers in a food chain. Plants and other organisms that carry out photosynthesis are **phototrophs** (or **photoautotrophs**). Bacteria that utilize the oxidation of inorganic compounds such as hydrogen sulfide, ammonium or ferrous iron as an energy source are **chemoautotrophs** (some are known as **lithotrophs**)."
http://en.wikipedia.org/wiki/Autotroph
[189] **Methanogenesis**: "Methanogenesis in microbes is a form of anaerobic respiration. Methanogens do not use oxygen to breathe; in fact, oxygen inhibits the growth of methanogens. The terminal electron acceptor in methanogenesis is not oxygen, but carbon. The carbon can occur in a small number of organic compounds, all with low molecular weights. The two best described pathways involve the use of carbon dioxide and acetic acid as terminal electron acceptors... Methanogenesis is the final step in the decay of organic matter."
http://en.wikipedia.org/wiki/Methanogenesis
[190] **Chemosynthesis**: "is the biological conversion of 1-carbon molecules (usually carbon dioxide or methane) and nutrients into organic matter using the oxidation of inorganic molecules (e.g. hydrogen gas, hydrogen sulfide) or methane as a source of energy, rather than sunlight, as in photosynthesis. Large populations of animals can be supported by chemosynthetic primary production at hydrothermal vents, methane clathrates, cold seeps, and whale falls. Chemoautotrophs, organisms that obtain carbon through chemosynthesis, and are responsible for the primary production in oxygen-deficient environments, generally fall into four groups: methanogens, halophiles, sulfur reducers, and thermoacidophiles."
http://en.wikipedia.org/wiki/Chemosynthesis
See also *TES2000* p. 174

Use inorganic source of C. For example, the genus Beggiatoa[191] which lives around black smokers and metabolize $2H_2S$. + O_2 ➔ $2S^0 + 2H_2O$ ... etc. These reactions are thought to have contributed to forming the banded iron formations in which iron is oxidized Fe^{2+} ➔ Fe^{3+} They can also act on elements that did not occur in nature: Pu (atomic number 94)and Tc (atomic number 43). There can also be **autotrophic methanogenesis** by strictly anaerobic autotrophic archaea.

Nitrogen Metabolism Reactions:
7) **Nitrogen Fixation**: "incorporates atmospheric gas N_2 into organic matter". [MCM: The first step of nitrogen fixation[192] is conversion of N_2 to ammonia NH_3.] This requires enzyme **nitrogenase**, reactive metal cofactors (Fe^{2+}, Mo^{3+}) The metals are oxidized (increase in oxidation number) and the N is reduced (decrease in oxidation number to more negative values). Also, Fe Fe , Fe V[193] [may be used as cofactors (?)] ... Most nitrogen fixation is done by marine cyanobacteria (using heterocysts) and by [terrestrial] rhizobia[194] (bacteria contained in rhizomes of legumes that create a locally anoxic environment). [MCM: It also occurs in the atmosphere by photons and lightning.]
8) **Ammonification**: "Turns organic nitrogen [e.g., amino acids] into ammonia NH_3"[195] [MCM: But this term is also used to refer to the generation of NH_4^- by nitrogen fixing soil bacteria.] Ammonifiers are restricted to 2 terminal groups in proteobacteria and archaea, resp. Eukaryotes depend on ammonifiers [and nitrifying bacteria]. [See Nitrogen Cycle[196]]
10) **Nitrification**: "Turns ammonia NH_3 into nitrate NO_3^-" [MCM: with nitrite NO_2^- as an intermediary—often the two steps take place in different nitrifying organisms]
11) **Denitrification**: "Turns nitrate NO_3^- into nitrogen gas" [MCM: in some cases going through nitrite NO_2^- as an intermediary (occurs in anaerobic low oxygen conditions)

---

191 **Beggiatoa**: "Beggiatoa is a genus of colorless, filamentous proteobacteria. With cells up to 200 microns in diameter, species of Beggiatoa are among the largest prokaryotes. They are one of the few members of the chemosynthesizers, meaning that they can synthesize carbohydrates from carbon dioxide and water using energy from inorganic compounds." Includes formulas for reacting with H_2S. http://microbewiki.kenyon.edu/index.php/Beggiatoa
192 **Nitrogen Fixation**: "Nitrogen fixation is the process by which nitrogen is taken from its natural, relatively inert molecular form (N_2) in the atmosphere and converted into nitrogen compounds (such as, notably, ammonia, nitrate and nitrogen dioxide) useful for other chemical processes." http://en.wikipedia.org/wiki/Nitrogen_fixation
193 **Vanadium in Nitrogen Fixation**: "Nitrogen fixation is mediated in nature by a few N_2-fixing bacteria that express the enzyme nitrogenase, of which the most common and efficient form requires Mo as a cofactor. Mo is in very short supply in soils, and we are interested in understanding whether and how Mo availability controls nitrogen fixation in terrestrial ecosystems. **Vanadium** is another transition metal of interest because it is more abundant than Mo in soils, and can also be used to fix nitrogen in the alternative V-nitrogenase which is expressed by some microorganisms when Mo is unavailable. Both Mo and V form oxoanions in solution (molybdate and vanadate) and their environmental chemistry has been little studied compared to trace metals such as iron, zinc or copper which are present as cations in the environment." http://geoweb.princeton.edu/research/tracemetals/kraepiel/overview.html
194 **Rhizobia**: "Rhizobia (from the Greek words rhiza = root and bios = Life) are soil bacteria that fix nitrogen (diazotrophy) after becoming established inside root nodules of legumes (Fabaceae). The rhizobia cannot independently fix nitrogen, and require a plant host. Morphologically they are generally gram negative, motile, non-sporulating rods." http://en.wikipedia.org/wiki/Rhizobia
195 **Ammonification**: "Strictly speaking, ammonification refers to any chemical reaction that **generates ammonia** (NH_3) as an end product (or its ionic form, **ammonium**, NH_4^+). Ammonification can occur through various inorganic reactions or as a result of the metabolic functions of microorganisms , plants, and animals. In the ecological context, however, ammonification refers to the processes by which organically bound forms of nitrogen occurring in dead biomass (such as amino acids and proteins) are **oxidized into ammonia and ammonium**. The ecological process of ammonification is carried out in soil and water by a great diversity of microbes and is one of the many types of chemical transformations that occur during the decomposition of dead organic matter ." http://findarticles.com/p/articles/mi_km4455/is_200510/ai_n16263644
196 **Nitrogen Cycle**: Good general review of the multiple steps in this cycle. http://en.wikipedia.org/wiki/Nitrogen_cycle

Many of these processes take place in sediments—**diagenesis**. [Presumably thus in a relatively anoxic environment.]

Bacteria can evolve rapidly to defend against antibiotics or other environmental changes and threats. They can survive for long intervals. Bacteria have survived in the stomach of mammoths frozen in permafrost for 100,000 years. They can survive in extreme conditions. For example, Deinococcus radiodurans[197] thrives in Three Mile Island nuclear reactor core radiation. How can it protect its DNA? Deinococcus has multiple copies of its genome and rapid DNA repair mechanisms, etc. Other means of extremophile protection include histones that help to shield DNA from heat denaturation, etc... Streptococcus mitis[198] survived on the moon for several years (maybe). Even if only one in 10,000 survive, they may be able to persist in harsh conditions. As bacteria evolved, their internal mechanisms evolved while the outer appearance remained relatively unchanged (the "Volkswagen Phenomenon"). The phylogeny of bacteria is poorly resolved. [One source lists about 23 phyla.[199] [200]]

There are few fossilized bacteria known, other than cyanobacteria, which have preservable sheaths[201] and are well preserved in proterozoic chert dating back to 2.1 Ga.[202] [See earlier discussions regarding how certain the fossil evidence is at various ages in the past.] Cyanobacteria have formed fossil stromatolites, etc. Biomarkers (hydrocarbon molecular fossils) derived from membrane hopanols date back to **2.7 Ga to perhaps 3.2 Ga**, including **2α-methylhopanes**[203] derived from cyanobacteria in sediments.

4. Archaea Domain

[MCM: See above consolidated summary comparing bacterial, archaeal, and eukaryotic characteristics. Note that the domain of prokaryotic organisms which were originally called **Archaebacteria** is always spelled **Archaea** (with *chae*, singular **Archaeon**), but the Eon is preferentially spelled **Archean** (*che*), though it can also be spelled **Archaean** (*chea*).]

---

[197] **Deinococcus radiodurans**:
• "D. radiodurans is capable of withstanding an instantaneous dose of up to 5,000 Gy with no loss of viability, and an instantaneous dose of up to 15,000 Gy with 37% viability.... Deinococcus accomplishes its resistance to radiation by having multiple copies of its genome and rapid DNA repair mechanisms"
http://en.wikipedia.org/wiki/Deinococcus_radiodurans
• "Microorganisms in the reactor core after the Three Mile Island disaster grew at dose rates of 10 Gy/h [Gray/hour]." [MCM: this is equivalent to 1000 rad/hour]
Beth J. Pitonzo et al. Effect of Gamma Radiation on Native Endolithic Microorganisms from a Radioactive Waste Deposit Site. *Radiation Research*, Vol. 152, No. 1 (Jul., 1999), pp. 64-70. Found at JSTOR.
[198] **Streptococcus mitis on the moon**:
• "Space historians will recall that the journey to the stars has more than one life form on its passenger list: the names of a dozen Apollo astronauts who walked on the moon and one inadvertent stowaway, a common bacteria, Streptococcus mitis, the only known survivor of unprotected space travel."
http://science.nasa.gov/NEWHOME/headlines/ast01sep98_1.htm
• "It is widely claimed that a common bacterium from the human mouth, Streptococcus mitis, survived for two and a half years on the Moon inside the Surveyor 3 camera, to be detected when the camera was returned to Earth on board the Apollo 12 capsule. However, this claim cannot be sustained in the light of several lines of evidence..."
http://en.wikipedia.org/wiki/Reports_of_Streptococcus_mitis_on_the_moon
[199] **Bacteria Phyla**: http://en.wikipedia.org/wiki/Bacteria
[200] **The Taxonomic Outline of Bacteria and Archaea:**
http://www.taxonomicoutline.org/index.php/toba/issue/view/3
[201] **Cyanobacteria Sheaths**: "[Cyanobacteria] also possess a mucilaginous sheath of cellulose fibrils varying in thickness from one genus to another, which enables the filamentous forms to glide slowly in a longitudinal direction -- a motion which has not been fully explained. "
http://www.micrographia.com/specbiol/bacteri/bacter/bact0200.htm
[202] **Fossil cyanobacteria**: http://www.ucmp.berkeley.edu/bacteria/cyanofr.html
[203] **2α-methylhopanes**: **TES2000** p. 213

Archaea were recognized in c. 1990 [204] by genetic analysis [MCM: but first described in the 1970s], and appear to be prokaryotes that are distinctively different from Bacteria (eubacteria). They have a cell structure similar to bacteria but different chemistries especially in the cell wall. In some ways they are more closely related to eukaryotes [e.g., in genetic transcription and translation[205]].

Differences between archaea and other domains [all info in this paragraph is quoted from *The Microbial World*[206]]

- The RNA polymerase from Archaea is similar to RNA polymerase II from eukaryotes
- The ribosomes of Archaea are similar in structure to those of Bacteria.
- Lipids in membranes from Archaea are unique, containing **ether** linkages between the glycerol backbone and the fatty acids, **instead of ester linkages**.
- The **cells walls** of Archaea are chemically and structurally diverse, and do not contain peptidoglycan [found in bacterial cell wall].

"Archaea are considerably more diverse in the composition of their cell walls. They lack peptidoglycan, but some contain **pseudopeptidoglycan**... N-acetylalosaminuronic acid replaces N-acetylmuramic acid in the backbone of the molecule and each glycan unit is linked together using 1,3 glycosidic bonds, instead of the 1,4 glycosidic bonds seen in peptidoglycan. Many archaea do not contain a peptidoglycan molecule in any form, instead covering the outside of the membrane with proteins, glycoproteins or polysaccharides. Scientists refer to these cell walls as S-layers. In any case the function of the cell wall remains the same, containing the cytoplasm and giving the microbe its shape."

RB cites these additional distinctive features of archaea:

- **Unicellular**: Archaea never form multicellular organisms or differentiated cells (such as heterocysts found in cyanobacteria). Although they sometimes form coccoid, bacilloid, or filamentous chains, they remain unicellular in terms of cell differentiation and independence.
- **Cell Membrane**: The archaean cell membrane is rigidified by **ether**-linked isoprenoids (whereas bacteria have hopanols stiffening the cell membrane and **ester** linkages).
- **introns** ("junk" DNA): presence of this gene structure in archaea is more like eukaryotes
- **operons**: Genes coding consecutive or related steps of a pathway are spatially adjacent on the chromosome (whereas in bacteria the gene sequence is more random and operons are not found).
- **The sequence of genes** in the archaeal genome is more like eukaryotes.

Archaea mostly live in extreme environments, though some live in more normal (**mesophilic**) environments:

- **Hyperthermophiles** survive up to 115 C: (e.g., Pyrolobus fumarii lives near black smokers)[207]
- **Halophiles**[208] live in halite-saturated brine ponds. The archaeal **halobacteria**[209] use rhodopsin [or **bacteriorhodopsin**] to capture photons and **halorhodopsin** for production of energy from light (**photometabolism**).

---

[204] **Discovery of Archaea**:
• "In the late 1970s, Dr. Carl Woese ... spearheaded a study of evolutionary relationships among prokaryotes. Instead of physical characters, he relied on RNA sequences to determine how closely related these microbes were. He discovered that the prokaryotes were actually composed of two very different groups—the Bacteria and a newly recognized group that he called Archaea."
http://www.ucmp.berkeley.edu/archaea/archaeasy.html
• See also C. R. Woese, 1981. Archaebacteria. *Scientific American* (Jun): 98-122.
Woese CR, Fox GE. "Phylogenetic structure of the prokaryotic domain: the primary kingdoms." *Proc Natl Acad Sci U S A.* 1977 Nov;74(11):5088-90. PubMed PMID: 270744.
[205] **Archeal relatedness to Eukarya**: "Archaea are similar to other prokaryotes in most aspects of cell structure and metabolism. However, their genetic transcription and translation—the two central processes in molecular biology—do not show many typical bacterial features, and are in many aspects similar to those of eukaryotes. "
http://en.wikipedia.org/wiki/Archaea
[206] **Major differences between Archaea and other domains of life**:
Timothy Paustian and Gary Robert, *The Microbial World* .
http://www.microbiologytext.com/index.php?module=Book&func=displayarticle&art_id=73
[207] **Pyrolobus fumarii**:
http://www.ncbi.nlm.nih.gov/sites/entrez?cmd=Retrieve&db=PubMed&list_uids=9680332&dopt=AbstractPlus

- **Methanogens**[210] live in highly reducing anoxic environments and generate methane
- **Acidophiles**[211] live at highly acid pH of 2 or less [this term is sometimes spelled **Acidiphiles**]
- **Alkaliphiles**[212] live at highly alkaline pH >9

Though Archaeans have metabolisms similar to bacteria, including many with Sulfur metabolism, there are at least 2 unique pathways of **methanogenesis** found only in Archaeans:

- $CO_2 + 4H_2 \rightarrow CH_4 + 2\ H_2O$. This is possibly the simplest metabolic pathway known. It may possibly be the first autotrophic metabolism (in which organisms make their own organic carbon from inorganic substrate. This anaerobic pathway now occurs only in a narrow range of environments, since it requires free hydrogen which is scarce in nature.
- $2\ CH_2O \rightarrow CH_4 + CO_2$ [also written as $CH_3COOH \rightarrow CH_4 + CO_2$]. This anaerobic pathway is much more common. It is a type of fermentation. This type of methanogenesis is important in the cycling of organic carbon—for example, in landfills, marshes, and the guts of ruminants and humans.

Both methanogenic pathways yield a depletion of ^{13}C and **$\delta^{13}C$** values as negative as -65‰. This enrichment in ^{12}C to -40‰ or greater provides a characteristic biomarker of methanogenic archaea. (Note: **Methanotrophs**[213] are archaea that use anaerobic oxidation of methane as their source of carbon and energy—this is of potential interest in consuming the greenhouse gas methane.)

---

208 **Halophiles**: “Halophiles are extremophiles that thrive in environments with very high concentrations of salt (at least 2 M, approximately ten times the salt level of ocean water)…. Some halophiles are classified into the Archaea kingdom, but there are bacterial halophiles as well. Some well-known species give off a red color due to the carotenoid compounds. These species contain the photosynthetic pigment bacteriorhodopsin. Organisms are categorized either slight, moderate or extreme, by the extent of their halotolerance.”
http://en.wikipedia.org/wiki/Halophile

209 **Halobacteria**: “…The Halobacteria (also Halomebacteria) are a class of the Euryarchaeota, found in water saturated or nearly saturated with salt. They are also called halophiles, though this name is also used for other organisms which live in somewhat less concentrated salt water. They are common in most environments where large amounts of salt, moisture, and organic material are available. Large blooms appear reddish, from the pigment **bacteriorhodopsin**. This pigment is used to absorb light, which provides energy to create ATP. Halobacteria also possess a second pigment, **halorhodopsin**, which pumps in chloride ions in response to photons, creating a voltage gradient and assisting in the production of energy from light. The process is unrelated to other forms of photosynthesis involving electron transport; however, and halobacteria are incapable of fixing carbon from carbon dioxide.”
http://en.wikipedia.org/wiki/Halobacteria

210 **Methanogens**: “Methanogens are archaea that produce methane as a metabolic byproduct in anoxic conditions. They are common in wetlands, where they are responsible for marsh gas, and in the guts of animals such as ruminants and humans, where they are responsible for the methane content of flatulence… In marine sediments biomethanation is generally confined to where sulfates are depleted, below the top layers. Others are extremophiles, found in environments such as hot springs and submarine hydrothermal vents as well as in the "solid" rock of the earth's crust, kilometers below the surface. There are over 50 described species of methanogens, which are paraphyletic and all included among the Euryarchaeota.”
http://en.wikipedia.org/wiki/Methanogen

211 **Acidophiles**: “Acidophilic organisms are those that thrive under highly acidic conditions (usually at pH 2.0 or below) . These organisms can be found in different branches of the tree of life, including Archaea, Bacteria, and Fungus…”
http://en.wikipedia.org/wiki/Acidophile_%28organisms%29

212 **Alkaliphiles**: “Alkaliphiles are microbes classified as extremophiles that thrive in alkaline environments with a pH of 9 to 11 such as soda lakes and carbonate-rich soils. To survive, alkaliphiles maintain a relatively low alkaline level of about 8 pH inside their cells by constantly pumping hydrogen ions (H+) in the form of hydronium ions (H3O+) across their cell membranes into their cytoplasm.”
http://en.wikipedia.org/wiki/Alkaliphile

213 **Methanotrophs**: Katrin Knittel et al “Diversity and Distribution of Methanotrophic Archaea at Cold Seeps”. *Appl Environ Microbiol.* 2005 January; 71(1): 467–479.

Archaea may be extreme survivors, perhaps up to 250 M.y. in salt formations. This was proposed in Texas salt dome specimens of this age.[214] However, this conclusion is controversial, since salt is highly soluble and water can flow into a salt formation that then recrystallizes. The postulated ancient archaea were found to be within 1% in genetic similarity compared to modern extant archaea from the Dead Sea. Thus they may have a more modern origin than originally suggested.

The phylogeny of archaea is controversial and under intensive study. Three kingdoms[215] (or 5 phyla)[216] of archaea exist:

1) **Crenarchaeota[217]**—mostly thermophilic, Sulfur-metabolizing heterotrophs
2) **Euryarchaeota**—mostly mesophilic, methanogens and halophiles
3) **Korarchaeota**—recently discovered, cannot be cultured, are known only from DNA sequences, have early basal branching [i.e., arose early in the phylogenetic TOL, near the node separating bacteria from the archaea and eukaryotes].

There are no microfossils of archaea, only rock samples with low **$\delta^{13}C$** characteristic of archaean methanogenesis and dating as far back as **2.6 - 2.8 Ga**. (A graph was displayed with $\delta^{13}C$ plotted against Ga, showing specimens with low $\delta^{13}C$ beginning at about 2.8 Ga.)

Marine plankton include poorly identified archaea. Archaea in general are widespread and their systematic classification is not well worked out yet.

5. Eukaryote Domain

[MCM: See above consolidated summary comparing bacterial, archaeal, and eukaryotic characteristics.]

There are about 60 "kingdoms" of eukaryotes according to RB,[218] all on "long" branches, though the phylogeny is poorly resolved. There is a huge diversity of unicellular eukaryotes. Their deep history in unclear, as there was an explosive radiation. Animals and fungi are closely related. Multicellular eukaryotes don't all have a common eukaryotic ancestor.

Unlike bacteria and archaea, Eukaryotes have limited tolerance of environmental extremes, require temperature maximum < 60 C. Most use heterotrophic aerobic respiration with mitochonndria, thus they need access to oxygen, or use products anaerobically from aerobic organisms. Sterols can only be synthesized in an oxygen environment. Some eukarya like **Giardia lamblia**.[219] have degraded

---

214 **Long-lived Archaea**: Russell H. Vreeland, et al "Isolation of a 250 million-year-old halotolerant bacterium from a primary salt crystal" *Nature* Vol 407 19 October 2000 www.nature.com

215 **Kingdoms of Archaea**: http://www.tolweb.org/Archaea/4

216 "**Phyla" of Archaea**: Crenarchaeota, Euryarchaeota, Korarchaeota, Nanoarchaeota, ARMAN (Archaeal Richmond Mine Acidophilic Nanoorganisms)
http://en.wikipedia.org/wiki/Archaea

217 **Crenarchaeota**: "The kingdom Crenarchaeota has the distinction of including microbial species with the highest known growth temperatures of any organisms. Although they are microscopic, single-celled organisms, they flourish under conditions which would quickly kill most "higher" organisms. As a rule, they grow best between 80° and 100°C ... and several species will not grow below 80°C. Several species also prefer to live under very acidic conditions in dilute solutions of hot sulfuric acid. Approximately 15 genera are known, and most of the hyperthermophilic species have been isolated from marine or terrestrial volcanic environments, such as hot springs and shallow or deep-sea hydrothermal vents. Recent analyses of genetic sequences obtained directly from environomental samples, however, indicate the existence of low temperature Crenarchaeota, which have not yet been cultivated."
http://www.tolweb.org/Crenarchaeota/9

218 **Eukaryotic Lineages**: "To date, about 60 lineages of eukaryotes have been identified (Patterson 1999). The relationships among these are not clear."
http://tolweb.org/Eukaryotes

219 **Giardia metabolism**: "Giardia's main food source, glucose, is obtained by a process of diffusion or by pinocytosis. Like amoebae, they are aerotolerant anaerobes and require a reducing environment. Food reserves are stored in the form of glycogen. Glucose catabolism via the [anaerobic] glycolytic

mitochondria and live like parasites by anaerobic fermentation. This is probably the ancestral eukaryotic [energy-producing] metabolism—and only later were aerobic pathways added via endosymbiosis. Giardia cannot make sterols. Eukaryotes cannot survive in acid pH < 4.5 or alkaline pH [to what degree?]. They also don't like high methane concentration. Some eukaryotes are photosynthetic autotrophs, utilizing endosymbiotic chloroplasts.

The fossil record for eukaryotes is good once mineral skeletons evolved c. 500 Ma. Before that eukaryote fossils appear mostly as **acritarchs**[220]—typically cysts from photosynthetic algae with size up to 0.5 mm[221] and a tough persistent capsule. Some may be from dinoflagellates or fungi—we don't really fully know their origins. These date back to **1.8 Ga**. There are also fossil sterol derivatives (**steranes**)[222] in hydrocarbons dating back to **2.75 Ga**[223]—these may therefore provide evidence for eukaryotes arising early ("deep") in the Tree of Life.

Eukaryotes exhibit **endosymbiosis**. The organelles may be wrapped in multiple layers of cell membrane, suggesting secondary or **serial endosymbiosis**.[224] There can be as many as 8 membrane layers [4 bilayers] from tertiary serial endosymbiosis.

---

pathway results in production of the end products ethanol, acetate and carbon dioxide."
http://microbewiki.kenyon.edu/index.php/Giardia

[220] **Acritarchs**: "Acritarchs are small organic structures found as fossils. In general, any small, non-acid soluble (i.e. non carbonate, non-siliceous) organic structure that can not otherwise be accounted for is an acritarch. Most acritarchs are likely the remains of single-celled organisms, especially the planktonic algae. They are found in sedimentary rocks from the present back into the Precambrian... They are excellent candidates for index fossils used for dating rock formations in the Paleozoic Era and when other fossils are not available. Because most acritarchs are thought to be marine, they are also useful for palaeoenvironmental interpretation. Acritarchs include the remains of a wide range of quite different kinds of organisms - ranging from the egg cases of small metazoans to resting cysts of many different kinds of chlorophyta (green algae). It is likely that some acritarch species represent the resting stages (cysts) of algae that were ancestral to the dinoflagellates. The nature of the organisms associated with older acritarchs is generally not clear, though many are probably related to unicellular marine algae...

Acritarchs are known from 1400 million years ago, and had achieved considerable diversity 100 million years later... The acritarchs show their greatest diversity during the Cambrian, Ordovician, Silurian and Devonian. The nature of some acritarchs can be identified by their structure. A few can be tentatively identified by the presence of specific chemicals associated with the fossils."
http://en.wikipedia.org/wiki/Acritarchs

[221] **Acritarch size**: "most are between 20-150 microns across"
http://www.ucl.ac.uk/GeolSci/micropal/acritarch.html

[222] **Steranes as Eukaryote Fossils**:
• "Eukaryotic membranes contain a suite of distinct sterols with 26 to 30 carbon atoms. In the fossil record, these sterols are often preserved in the form of (C26) to (C30) hydrocarbon **steranes**. Their relative abundance is often characteristic of specific environments and geological periods in the Phanerozoic. We may expect particularly distinct sterane assemblages in the early history of eukaryote evolution.... Looking through the veil of contamination, we observe sterane assemblages in the interval 1,600 to 700 Ma ago that are distinct from anything observed later in Earth history."
http://adsabs.harvard.edu/abs/2005AGUFM.B12A..05B
• See also Kenneth E. Peters, Clifford C. Walters, J. Michael Moldowan. *The Biomarker Guide, 2nd Ed*, 2005. Univ. of Cambridge.

[223] **Fossil Steranes 2.7 Ga Old**: "Molecular fossils of biological lipids are preserved in 2700-million-year-old shales from the Pilbara Craton, Australia. Sequential extraction of adjacent samples shows that these hydrocarbon biomarkers are indigenous and syngenetic to the Archean shales, greatly extending the known geological range of such molecules. The presence of abundant 2alpha - methylhopanes, which are characteristic of cyanobacteria, indicates that oxygenic photosynthesis evolved well before the atmosphere became oxidizing. The presence of steranes, particularly cholestane and its 28- to 30-carbon analogs, provides persuasive evidence for the existence of eukaryotes 500 million to 1 billion years before the extant fossil record indicates that the lineage arose."
J Brocks, Roger Buick, et al. "Archean Molecular Fossils and the Early Rise of Eukaryotes": *Science* 13 August 1999: Vol. 285. no. 5430, pp. 1033 - 1036

[224] **Secondary Endosymbiosis**: "Primary endosymbiosis involves the engulfment of a bacterium by another free living organism. Secondary endosymbiosis occurs when the product of primary

Mitochondria are endosymbionts, create ATP, consuming a little ATP, but generating more than they consume.

Biochemical Cycles

(per RB and supplemented)
Concentrations of key biologic elements (C H O N P S) are controlled by metabolic redox reactions and geologic processes in the biosphere, lithosphere, hydrosphere, and atmosphere. These cycles keep the Earth's surface and biosphere habitable.

1. Characteristics of Biochemical Cycles

Biochemical cycles are described quantitatively by

Reservoirs (aka Compartments or Sinks): These are sinks where oxidized or reduced species reside. Also used to signify the amount of a species (e.g., Carbon in reduced or oxidized state) found in a particular location or (such as the atmosphere.
Fluxes: The rates of reservoir **inflow** (rate of material added to reservoir) and **outflow** (rate of material removed from reservoir)
Feedback: The negative effect (if reduce perturbabtion) and positive effect (if increase perturbabtion) on fluxes caused by perturbations of the species concentrations.
Turnover Time = (Mass)/(Total Flux Out) Or (Total Flux In). This is the time it would take to empty the reservoir. Also known as "**Flushing time**" or "**Renewal time**".
Average Residence Time: The average time spent by an atom or molecule in the reservoir. At steady state, Average residence time = Turnover time and is given by (Reservoir Size) / (Inflow or Outflow).

It is important to understand the Carbon Cycle. Other cycles include Sulfur Cycle (more complex, less well understood) and Nitrogen Cycle[225] (important for nutrients).

Cycles such as organic carbon can be broken into short-term and long-term components.

2. Carbon Cycles

[See Carbon Cycle diagram included here[226] and those presented by RB of short- and long-term as well as inorganic carbon cycles[227]—these diagrams are complex and cannot be fully summarized here. They include estimates of the reservoirs (see table below) but also the fluxes.]

[MCM: Carbon can exist in 9 **oxidation states**—{±4, ±3, ±2, ±1, 0}.[228]—though this concept is rarely used except in single C compounds and ions, usually with values of 2 or ±4.[229] Compounds include

---

endosymbiosis is itself engulfed and retained by another free living eukaryote. Secondary endosymbiosis has occurred several times and has given rise to extremely diverse groups of algae and other eukaryotes... Obligate secondary endosymbionts become dependent on their organelles and are unable to survive in their absence...
One possible secondary endosymbiosis in process has been observed by Okamoto & Inouye (2005). The heterotrophic protist Hatena behaves like a predator until it ingests a green algae, which loses its flagella and cytoskeleton, while Hatena, now a host, switches to photosynthetic nutrition, gains the ability to move towards light and loses its feeding apparatus."
http://en.wikipedia.org/wiki/Endosymbiotic_theory

[225] **Nitrogen Cycle**:
• http://en.wikipedia.org/wiki/Nitrogen_cycle
• http://essp.csumb.edu/esse/climate/climatefigures/Ncycle.html
• http://essp.csumb.edu/esse/climate/climatebiogeo.html

[226] **Diagrams of Carbon Cycle**: http://en.wikipedia.org/wiki/Carbon_cycle

[227] **Carbon Cycle Diagrams**: derived from *TES2000* p. 153, 160, 166.

[228] **Carbon Oxidation States**: http://en.wikipedia.org/wiki/Oxidation_state

[229] **Limited Use of Carbon Oxidation States**:
http://www.chemsoc.org/Viselements/pages/pdf/carbon.PDF

methane CH_4 {-4, most reduced}, C in diamond or graphite {0}, carbon monoxide CO {+2), carbon dioxide CO_2 {+4, most oxidized}, carbonate $(CO_3)^{2-}$ {+4, most oxidized}.]

The major reservoirs of C in the biosphere (expressed in **Giga metric tons** = **Gigatonnes Gt = Giga 1000 kilograms** = **10^{15} grams** = **petagrams Pg**) are as follows:[230]

Carbon Reservoir	**Quantity of Reservoir C in Gt or Pg**
Atmospheric CH_4	10
Living biomass (organic carbon "CH_2O")	600 - 610
Atmospheric CO_2	760
Oceanic dissolved CO_2	740
Oceanic carbonate ion CO_3^{2-}	1300
Organic carbon in soils and sediments [excluding biomass]	1600
Marine carbonate sediments	2500
Fossil fuels (i.e., underground oil, coal, natural gas)	4700 - 5000
Oceanic bicarbonate ion HCO_3^-	37,000
Organic carbon in sedimentary rocks [apparently other than fossil fuels]	10,000,000
Limestone in sedimentary rocks	40,000,000

Short Term Organic Carbon Cycle[231]

Key chemical reactions and some of their fluxes include [see diagram]
Photosynthesis: $CO_2 + H_2O \rightarrow CH_2O + O_2$ (60 GtC/yr removed from Atmosphere CO_2)
Aerobic Respiration: $CH_2O + O_2 \rightarrow CO_2 + H_2O$. (30 GtC/yr added to Atmosphere CO_2)
Methanogenesis: $2CH_2O \rightarrow CH_4 + CO_2$ (10 GtC/yr removed from Atmosphere CO_2)

Other Reactions and Fluxes:
Methane Oxidation: $CH_4 + 2O_2 \rightarrow CO_2 + 2\ H_20$ (0.5 GtC/yr added to Atmosphere CO_2)
Decomposition of Organisms (Aerobic): (29 GtC/yr added to Atmosphere CO_2)
Decomposition of Organisms (Anaerobic): (0.5 GtC/yr added to Atmosphere CO_2)
Death of Organisms: (30 GtC/yr added to Sediments)

The dominant form of C in the oceans is bicarbonate ion. C may be in reduced or oxidized forms, and currently the ocean oxidized species predominate.

The CO_2 exchange on land is simple: atmosphere → biomass → soil. But ocean is more complex with respect to organic carbon. In the oceans, photosynthesis by phytoplankton[232] "producers" [of organic

---

230 **Carbon Reservoirs in Pg or Gt(C)**:
• Main source is RB's diagram derived fr. TES2000 p. 150, but see also
• http://geography.berkeley.edu/ProgramCourses/CoursePagesFA2004/Geog40/L20Oct15.pdf
• http://science.hq.nasa.gov/oceans/system/carbon.html
231 **Carbon Cycles**:
http://www.carleton.edu/departments/geol/DaveSTELLA/Carbon/carbon_intro.htm
232 **Phytoplankton**: "Phytoplankton are the **autotrophic** component of plankton... Most phytoplankton are too small to be individually seen with the unaided eye. However, when present in high enough numbers, they may appear as a green discoloration of the water due to the presence of chlorophyll within their cells (although the actual color may vary with the species of phytoplankton present due to varying levels of chlorophyll or the presence of accessory pigments such as phycobiliproteins)... However, unlike terrestrial communities, where most autotrophs are plants, phytoplankton are a diverse group, incorporating protistan eukaryotes and both eubacterial and archaebacterial prokaryotes. There are about 5,000 species of marine phytoplankton... In terms of numbers, the most important groups of phytoplankton include the **diatoms**, **cyanobacteria** and **dinoflagellates**, although many other groups of **algae** are represented. One group, the

matter] consumes CO_2 in shallow water, creating organic matter incorporated into organisms. Photosynthesis can only occur in the **photic zone**,[233] which extends only as deep as 200 m, depending on turbidity, and yields O_2 plus organic material. Organic matter is consumed by "consumers", mostly zooplankton. All organisms eventually produce dead organic matter (carcasses and feces) which [along with inorganic calcium carbonate in shells] descends to deeper water. Most decomposition by respiration of metabolizing microorganisms of the descending dead organic matter takes place in the deeper ocean water column rather than in the sediments at the bottom or in the photic zone. CO_2 produced in this decomposition process of bacterial respiration upwells with nutrients. This cyclical sequence of carbon descent and upwelling maintains the **Marine Biological Pump**[234], whereby organic matter descends, and CO_2 produced in decomposition upwells [in the thermohaline circulation[235]]. This pump keeps the sources and sinks of ocean CO_2 at a steady state [at least prior to the onset of recent anthropogenic perturbations]. The relative concentrations in the deep ocean of the various key elements (nutrients including P and N) are maintained at stable **Redfield Ratios**.[236] These ratios are

---

coccolithophorids, is responsible (in part) for the release of significant amounts of dimethyl sulfide (DMS) into the atmosphere... In oligotrophic oceanic regions such as the Sargasso Sea or the South Pacific gyre, phytoplankton [are] dominated by the small sized cells, called **picoplankton**, mostly composed of **cyanobacteria** (Prochlorococcus, Synechococcus) and **picoeucaryotes** such as Micromonas."
http://en.wikipedia.org/wiki/Phytoplankton

233 **Photic Zone**: "The photic zone or euphotic zone (Greek 'well lit') is the depth of the water whether in a lake or an ocean, that is exposed to sufficient sunlight for photosynthesis to occur. The depth of the euphotic zone can be greatly affected by seasonal turbidity. It extends from the atmosphere-ocean interface downwards to a depth where light intensity falls to 1% of that at the surface (also called euphotic depth), so its thickness depends on the extent of light attenuation in the water column. Typical euphotic depths vary from only a few centimetres in highly turbid eutrophic lakes, to around 200 metres in the open ocean."
http://en.wikipedia.org/wiki/Photic_zone

234 **Biological Pump**: "In oceanic biogeochemistry, the biological pump is the sum of a suite of biologically-mediated processes that transport carbon from the surface euphotic zone to the ocean's interior... The organic carbon that forms the biological pump is transported primarily by sinking particulate material, for example dead organisms (including algal mats) or faecal pellets. However, some carbon reaches the deep ocean as dissolved organic carbon (DOC) by physical transport processes such as downwelling rather than sinking.

Carbon reaching the deep ocean by these means is either organic carbon or particulate inorganic carbon such as calcium carbonate ($CaCO_3$). The former is a component of all organisms, the latter only of calcifying organisms, for example coccolithophores, foraminiferans or pteropods. In reference to the different use of these materials in organisms, the organic carbon portion of this transport is known as the soft tissues pump, while the inorganic carbon portion is known as the hard tissues pump.

In the case of organic material, remineralisation (or decomposition) processes such as bacterial respiration, return the organic carbon to dissolved carbon dioxide. Calcium carbonate dissolves at a rate dependent upon local carbonate chemistry. As these processes are generally slower than synthesis processes, and because the particulate material is sinking, the biological pump transports material from the surface of the ocean to its depths.

As the biological pump plays an important role in the Earth's carbon cycle, significant effort is spent quantifying its strength. However, because they occur as a result of poorly-constrained ecological interactions usually at depth, the processes that form the biological pump are difficult to measure... "
http://en.wikipedia.org/wiki/Biological_pump

235 **Thermohaline circulation**:
• http://geography.berkeley.edu/ProgramCourses/CoursePagesFA2004/Geog40/L20Oct15.pdf
• See also *TES2000* p. 92

236 **Redfield Ratio**: "Redfield ratio or Redfield stoichiometry is the molecular ratio of carbon, nitrogen and phosphorus in phytoplankton. The stoichiometric ratio is C:N:P = 106:16:1. The term is named after the American oceanographer Alfred C. Redfield, who first described the ratio in an article in 1934. Redfield described the remarkable congruence between the chemistry of the deep ocean and the chemistry of living things in the surface ocean..."
http://en.wikipedia.org/wiki/Redfield_ratio

remarkably similar to the ratios of these elements measured in phytoplanktons. The normal relative ratios are:

C:106 N:16 P:1 Fe:0.01

When there are significant departures from these ratios, significant consequences result. For example, when N is raised from fertilizer runoff into the ocean. This causes a bloom of photosynthetic phytoplankton, which remove some of the CO_2. The bloom dies off, and the dead organisms are consumed (in the deeper zone) by heterotrophic respiring organisms which consume O_2. The resulting **anoxic dead zone** conditions[237] cause other organisms to die off (such as in Hood Canal or the Gulf of Mexico).

Fluxes:
The major **fluxes of Carbon dioxide with respect to the atmosphere** are as follows [consult diagrams cited for full data]:
Inflow: 60 Gt(C) / yr. through respiration and decomposition. [anthropogenic processes such as fossil fuel burning have increased this]
Outflow: 60 Gt(C) / yr. through photosynthesis.

Feedbacks:
(1) **Negative Feedback example**:
Chemical weathering of Silicate rocks consumes CO2, reducing atmospheric CO_2:

$CO_2 + H_2O \rightarrow H_2CO_3$

$CaSiO3 + 2\ H_2CO_3 \rightarrow Ca^{2+} + 2\ HCO_3 + SiO_2 + H_2O$]

Reduced atmospheric CO_2 leads to reduced greenhouse effect, leading to reduced temperatures and [MCM: reduced] hydrologic activity (including rainfall) leading to reduced silicate weathering.
(2) **Positive Feedback example**: This would include the **Runaway Greenhouse effect** (previously discussed).

[Average] Residence Times: This is the amount of time a molecular species spends on average in a particular reservoir. For steady state atmospheric CO_2, the previous values would yields a calculated value of :

Atmospheric CO_2 Residence Time = 760 Gt(C) / 60 Gt(C) /yr. = 12.8 years

If conditions are not steady-state, it is harder to estimate the Residence Time or Turnover Time.

The **isotopic fractionation** can assist in estimating which reactions are taking place:
Photosynthesis: $CO_2 + H_2O \rightarrow CH_2O + O_2$. This reaction yields a carbon isotopic fractionation incremental change $\delta^{13}C$ of -20‰ (e.g., changing prevailing value from -6 to --26)
Methanogenesis: $2CH_2O \rightarrow CH_4 + CO_2$. This reaction yields a carbon isotopic fractionation incremental change $\delta^{13}C$ of -40‰ (e.g., changing prevailing value from -26 to --66)
Most marine sediments are -26, indicating that photosynthesis predominates. In some sediments, values of -50‰ indicate more contribution by methanogens.

Long Term Organic Carbon Cycle:[238]

[MCM: Data presented was incompletely captured.]
This cycle adds to the short term organic cycle the effects of the relatively small flux ("leak") of carbon removed from the biosphere and entering the large reservoirs of **sediments** in the form of organism-derived **carbonate, kerogen**, etc. [The diagram show a flux of 0.05 GtC/yr resulting from

---

[237] **Anoxic dead zones**: "The cause of anoxic bottom waters is fairly simple: the organic matter produced by phytoplankton at the surface of the ocean (in the euphotic zone) sinks to the bottom (the benthic zone),where it is subject to breakdown by the action of bacteria, a process known as bacterial respiration. The problem is, while phytoplankton use carbon dioxide and produce oxygen during photosynthesis, bacteria use oxygen and give off carbon dioxide during respiration. The oxygen used by bacteria is the oxygen dissolved in the water, and that's the same oxygen that all of the other oxygen-respiring animals on the bottom (crabs, clams, shrimp, and a host of mud-loving creatures) and swimming in the water (zooplankton, fish) require for life to continue."
http://daac.gsfc.nasa.gov/oceancolor/scifocus/oceanColor/dead_zones.shtml
[238] **Long Term Carbon Cycle**:
http://www.carleton.edu/departments/geol/DaveSTELLA/Carbon/long_term_carbon.htm

sedimentaion and burial, and a return rate also of 0.05 from weathering.] The residence times for this C are much longer, measured in M.y.

Very little C gets buried, because much is recycled by respiration of ocean organisms… [MCM: The following is uncertainly transcribed.] Weathering [of silicate] consumes CO_2 and these products are carried to the ocean. Ocean organisms create downfalling organic and inorganic Carbon. Some of this C is buried in sedimentary ocean crust that eventually subducts. Some CO_2 is released from rocks undergoing metamorphosis. Old subducted C rises from the mantle and asthenosphere and is released (outgassed) as CO_2 at mid-ocean ridges. [MCM: Unclear sentence follows pertaining to maintaining atmospheric O_2 balance, slowing consumption of O_2 by weathering of Fe and S minerals… MCM: e.g., $4FeO$ (ferrous oxide) + $3O_2 \rightarrow 2Fe_2O_3$ (ferric oxide)] and oxidation of reduced volcanic gases (CO, H_2, [H_2S], and SO_2). At equilibrium, the rate of $C_{organic}$ generation from weathering equals the rate of $C_{organic}$ burial [from sedimentation and subduction]. Recent fossil fuel burning represent a non-equilibrium deviation in the past 300 years from previously stable pattern, causing increase of CO_2 in atmosphere by 50% (current value is c. 380 ppm, values from Vostok ice are as low as 180 ppm[239]), shortening of the usual 200 M.y. [buried fossil fuel] $C_{organic}$ residence time, a great speedup of weathering from increased carbonic acid.

Inorganic Carbon Cycle

[MCM: this data was incompletely captured.]

CO_2 diffuses between the atmosphere and ocean, dissolves in water and in part forms carbonic acid. The inorganic C components of sea water consists of dissolved CO_2, carbonic acid H_2CO_3, bicarbonate ion HCO_3^-, and carbonate ion CO_3^{2-} [collectively termed **dissolved inorganic carbon** or **DIC**[240]]:

$CO_2 + H_2O \Leftrightarrow H_2CO_3$ [carbonic acid] $\Leftrightarrow H^+ + HCO_3^-$ [bicarbonate] $\Leftrightarrow 2H^+ + CO_3^{2-}$

These reactions control ocean pH. Following **Le Chatelier's Principle** (applying to dynamic equilibria):

a. When ocean water becomes more alkaline (lower H^+ concentration), the reactions moves to the right to increase bicarbonate ion and (when pH > 7) increase carbonate ion concentrations.

b. When ocean water becomes more acidic (higher H^+ concentration), the reactions move to the left and increase undissociated carbonic acid and decrease biccarbonate and (when pH < 7) decrease carbonate.

Bicarbonate is the dominant form of C in the ocean sea water [MCM: i.e., 37,000 for HCO_3^-vs. 1300 for CO_3^{2-} and 740 for dissolved CO_2] at typical slightly alkaline pH of 8.1[241]

The oceans are gradually getting more acid. Rain in Seattle has a pH of c. 5.3 - 5.6[242], slightly acidic due to dissociated carbonic acid.

---

239 **Carbon dioxide concentration history**: http://www.aip.org/history/climate/co2.htm

240 **Dissolved Inorganic Carbon (DIC) and Solubility pump**: "Carbon dioxide, like other gases, is soluble in water. However, unlike many other gases …, it reacts with water and forms a balance of several ionic and non-ionic species (collectively known as dissolved inorganic carbon, or DIC… The balance of these carbonate species (which ultimately affects the solubility of carbon dioxide), is dependent on factors such as pH. In seawater this is regulated by the charge balance of a number of positive (e.g. Na^+, K^+, Mg^{2+}, Ca^{2+}) and negative (e.g. CO_3^{2-} itself, Cl^-, SO_4^{2-}, Br^-) ions. Normally, the balance of these species leaves a net positive charge. With respect to the carbonate system, this excess positive charge shifts the balance of carbonate species towards negative ions to compensate. The result of which is a reduced concentration of the free carbon dioxide and carbonic acid species, which in turn leads to an oceanic uptake of carbon dioxide from the atmosphere to restore balance. Thus, the greater the positive charge imbalance, the greater the solubility of carbon dioxide. In carbonate chemistry terms, this imbalance is referred to as **alkalinity**."
http://en.wikipedia.org/wiki/Solubility_pump

241 **Ocean pH**: "Between [years] 1751 and 1994 surface ocean pH is estimated to have decreased from approximately 8.179 to 8.104 (a change of -0.075)"
http://en.wikipedia.org/wiki/Ocean_acidification

242 **Rain pH**:

• "Generally, rain has a pH slightly under 6. This is because atmospheric carbon dioxide dissolves in the droplet to form minute quantities of carbonic acid, which then partially dissociates, lowering the pH. In some desert areas, airborne dust contains enough calcium carbonate to counter the natural acidity of precipitation, and rainfall can be neutral or even alkaline. Rain below pH 5.6 is considered

Weathering: H_2CO_3 formed in rain reacts with silicate and carbonate minerals (**weathering**):
(1) $CaSiO_3$ [a silicate mineral] + 2 H_2CO_3 ↔ Ca^{2+} + $2HCO^{3-}$ + SiO_2 [silica] + H_20
Here $CaSiO_3$ is a representative silicate mineral, namely **Wollastonite (Calcium Metasilicate)**. [Other silicate minerals containing cations such as Ca^{++}, Fe^{++}, and Na^{++} are also weathered in this manner.] Also,
(2) $CaCO_3$ [limestone etc.] + 2 H_2CO_3 ↔ Ca^{2+} + $2HCO^{3-}$
Here, $CaCO_3$ is rock in the form of limestone, calcite, aragonite, etc.

$CaCO_3$ Deposition: The reaction products wash into the ocean, and $CaCO_3$ is precipitated by organisms that form shells or coral skeletons, or evaporation:

Ca^{2+} + $2HCO^{3-}$ ↔ $CaCO_3$ + H_2CO_3

$CaCO_3$ is found as calcite or **aragonite**[243] (formed by mollusk shells and corals, etc). It becomes buried as carbonate in sediment (that forms limestones) if deposited on the ocean bottom above the **carbonate compensation depth (CCD)**[244], which lies at about **3 - 5 km** depth. (Below this level, the respiratory rate of organisms causing decomposition is high due to high availability of organic matter and relatively high O_2 levels (higher than found at the "**oxygen minimum zone**"[245] c. 1 km), so that higher CO_2 and carbonic acid levels (along with lower temperatures) lead greater solubility and dissolving of $CaCO_3$. Deep oceans have no $CaCO_3$ shells etc. on the bottoms.) Carbon therefore "leaks" to the ocean sediments at least above the CCD. The reservoir of Carbonate sedimentary rocks is very large, 40,000,000 Gt(C). Coral reefs assist in lowering atmospheric CO^2. Moreover, silicate weathering is the key negative feedback reducing atmospheric CO_2, maintaining climatic steady state over geologic time.

---

acid rain."
http://en.wikipedia.org/wiki/Rain
• ""Clean" or unpolluted rain has a slightly acidic pH of 5.6 [diagram shows 5.3 in Seattle area in 1992], because carbon dioxide and water in the air react together to form carbonic acid, a weak acid. Around Washington, D.C., however, the average rain pH is between 4.2 and 4.4."
http://pubs.usgs.gov/gip/acidrain/2.html
243 **Aragonite**: http://en.wikipedia.org/wiki/Aragonite
244 **Carbonate Compensation Depth:**
• "Carbonate compensation depth (CCD) is a level in the oceans below which the rate of supply of calcium carbonate (calcite and aragonite) equals the rate of dissolution, such that no calcium carbonate is preserved... Calcium carbonate is essentially insoluble in sea surface waters today, shells of dead calcareous plankton sinking to deeper waters are practically unaltered until reaching the lysocline where the solubility increases dramatically[—]by the time the CCD is reached all calcium carbonate has dissolved. Calcareous plankton and sediment particles can be found in the water column above CCD and, if the sea bed is above the CCD, bottom sediments can consist of calcareous sediments called calcareous ooze which is essentially a type of limestone or chalk. If the sea bed is below the CCD tiny shells of $CaCO_3$ will dissolve before reaching this level so there will be no carbonate sediment.

The exact depth of the CCD depends on the solubility of calcium carbonate which is determined by temperature, pressure and the chemical composition of the water - in particular the amount of dissolved CO_2 in the water. Calcium carbonate is more soluble at **lower temperatures** and at **higher pressures**. It is also **more soluble if the amount of dissolved CO_2 is higher** because some of this combines with water molecules to produce a weak acid.

At the present time the CCD in the Pacific Ocean is about 4,200 - 4,500 m except beneath the equatorial upwelling zone, where the CCD is about 5,000 m. In the temperate and tropical Atlantic Ocean the CCD is at approximately 5,000 m. In the Indian Ocean it is intermediate between the Atlantic and the Pacific. The CCD is relatively shallow in high latitudes.

The difference between CCD depths in different oceans today can largely be explained by variation in dissolved CO_2 content..."
http://en.wikipedia.org/wiki/Carbonate_Compensation_Depth
• "CCD is found deepest in the North Atlantic Ocean (50°N) at about **5,000** m moving upwards continuously in the water column to **3,000** m in the Atlantic sector of the Southern Ocean (60°S) and, in turn, CCD is found deepest in the Pacific sector of the Southern Ocean (60°S) at about **4,500** m moving upwards to **3,000** m in the North Pacific Ocean (50°N). "
http://www.enotes.com/earth-science/ccd-carbonate-compensation-depth
245 **Oxygen Minimum Zone**: *TES2000* p. 155

Adding the equations for weathering, etc. together, produces:

$CaSiO_3 + CO_2 \leftrightarrow CaCO_3 + SiO_2$.

This reaction would end up removing all atmospheric CO_2 in about 1 M.y., except that it is balanced by metamorphism releasing CO_2 which is released by volcanism, summed up as:

$CaCO_3 + SiO_2 \leftrightarrow CaSiO_3 + CO_2$

CO_2 rises in metamorphic water and is degassed in volcanoes, so overall there is a steady state of CO_2 subduction and degassing. Plate tectonics helps to maintain a stable CO_2 environment, and CO_2 is an essential greenhouse gas, required to keep Earth's temperature above freezing.

The diagram provided by RB showed several additional, long-term, carbon fluxes including:

Sedimentation and Burial: (0.20 GtC/yr added to Sedimentary Rocks)
Carbonate Weathering: (0.17 GtC/yr added to Ocean HCO_3)

These processes lead to a stable long-term isotopic balance:

$\delta^{13}C$ carb [probably inorganic carbonate] ≈ 0‰
$\delta^{13}C$ atmosphere ≈ -7‰
$\delta^{13}C$ organic ≈ -28‰

[Two charts were presented plotting time as the X-axis from 500 Ma to 4 Ga and $\delta^{13}C$ as the Y-axis. The first showed $\delta^{13}C$ [possibly for inorganic C as carbonate] with values centered around 0‰ all the way back to Coonterunah and Isua specimen. The 2nd chart showed $\delta^{13}C$ for organic carbon. These values centered on -28‰, with a more negative ancient spike reflecting a time of increased methanogenetic organisms. The source of these charts was not stated.] These graphs imply that there has been a reservoir of carbonate. Why has C stayed so stable? The graphs indicates that [MCM: unsure of this transcription] the [inorganic] carbonate burial rate and reservoir size has been historically 4 times that of the organic burial rate and reservoir size. There is some disturbance that makes this difference in ... [what?] The carbon cycle is very important. The effects of increasing CO_2 are difficult to predict.

3. Sulfur Cycle[246] [247]

[RB plus supplemented. This data was incompletely captured.]

In many amino acids, metabolically important, abundant in crust and seawater, oxidation of reduced sulfur acts as a sink for oxygen O_2, S oxidation causes acid rain. Ancient environment had more sulfur available. Sources of sulfur include basaltic pyrite, volcanic gases such as SO_2 and H_2S, hydrothermal vents H_2S.

Sulfur has complex atmospheric and oceanic chemistry. [MCM: It can exist in several oxidation states {0, −1, ±2, 4, 6} and forms such as sulfide S^{2-} {-2, most reduced state}, elemental sulfur {0}, thiosulfate $(S_2O_3)^{2-}$ {+2}, sulfite $(SO_3)^{2-}$ {+4}, sulfate $(SO_4)^{2-}$ {+6, most oxidized state} , etc.]

Microbial redox metabolisms shunt S through many valence states, consider only these 3:

(1) Photosynthetic sulfide oxidation: $H_2S + 2CO_2 + 2H_2O \rightarrow 2CH_2O + SO_4^{2-} + 2H^+$

This is done in 2 steps on sulfide (S_2^-, H_2S, FeS) with elemental S_0 as an intermediary, by photoautotrophic **purple bacteria**[248] **& green sulfur bacteria**[249], which use **Bacteriochlorophyll**[250], a

---

[246] **Sulfur Cycle**:
• http://en.wikipedia.org/wiki/Sulfur_cycle
• http://www.lenntech.com/sulfur-cycle.htm

[247] **Sulfur Cycle Diagram**:
• http://essp.csumb.edu/esse/climate/climatefigures/Scycle.html
• http://essp.csumb.edu/esse/climate/climatebiogeo.html

[248] **Purple bacteria**: "Purple bacteria or purple photosynthetic bacteria are proteobacteria that are phototrophic, i.e. capable of producing energy through photosynthesis. They are pigmented with bacteriochlorophyll a or b, together with various carotenoids. These give them colours ranging between purple, red, brown, and orange... Like most other photosynthetic bacteria, purple bacteria do not produce oxygen, because the reducing agent involved in photosynthesis is not water. In some, called purple sulfur bacteria, it is either sulfide or elemental sulfur. The others, called purple non-sulfur bacteria (aka PNSB), typically use hydrogen although some may use other compounds in small

simpler evolutionary precursor of chlorophyll. Strictly anaerobic (anoxic). Occurs in Black Sea and anaerobic dead zone of Hood Canal.

(2) Chemolithotrophic sulfide oxidation: $H_2S + 2O_2 \rightarrow SO_4^{2-} + 2H^+$

Also done in 2 steps through S_0, done by colorless Sulfide-metabolizing proteobacteria and many Archaea (Crenarchaeota), aerobic requiring O_2. Important process around modern hydrothermal vents (e.g., Beggiatoa[251] genus of proteobacteria), but less important in early Earth environments which had little O_2.

(3) Dissimilatory[252] **sulfate reduction:** $SO_4^{2-} + 2H^+ + 2CH_2O \rightarrow H_2S + 2CO_2 + 2H_2O$

Starts with sulfate, forms sulfide.[253] Imparts $\delta^{34}S$ = -20‰ isotopic fractionation where sulfate >1 mmol, records shows clear evidence back to 2.3 Ga, single instance at 3.45 Ga in sulfate oasis showing mesophilic bacterial S-reduction. Mostly in proteobacteria and Archaeoglobus[254] archaea. Organisms include genera Desulfovibrio and Desulfomonas.[255] [256]

---

amounts. At one point these were considered families, but RNA trees show the purple bacteria make up a variety of separate groups, each closer relatives of non-photosynthetic proteobacteria than one another." [Groups include] Rhodospirillales, Rhizobiales, Rhodobacteraceae, etc.]
http://en.wikipedia.org/wiki/Purple_bacteria

[249] **Green sulfur bacteria**: http://en.wikipedia.org/wiki/Green_sulfur_bacteria

[250] **Bacteriochlorophyll (Bacteriophyll):** "Bacteriochlorophylls are photosynthetic pigments that occur in various phototrophic bacteria. They are related to chlorophylls, which are the primary pigments in plants, algae, and cyanobacteria. Groups that contain bacteriochlorophyll conduct photosynthesis, but do not produce oxygen. They use wavelengths of light not absorbed by plants. Different groups contain different types of bacteriochlorophyll:"
http://en.wikipedia.org/wiki/Bacteriochlorophyll

[251] **Beggiatoa**: "Beggiatoa is a genus of colorless, filamentous proteobacteria. With cells up to 200 microns in diameter, species of Beggiatoa are among the largest prokaryotes. They are one of the few members of the chemosynthesizers, meaning that they can synthesize carbohydrates from carbon dioxide and water using energy from inorganic compounds. Beggiatoa are found in polluted marine environments, and can be seen by the naked eye as a white filamentous mat on top of the water as a sign of environmental deterioration...

Beggiatoa are evident in the marine environment as white filamentous mats on top of sulfide-rich sediments. They are found throughout the world's oceans, everywhere from shallow areas near land to the deep sea and around hydrothermal vents. In areas with overlapping sulfur and oxygen, sulfur bacteria perform diurnal vertical migrations, showing up at dark near the sediment surface. Mats tend to be 0.6 milimeters thick, but thickness varies depending on water movement. Beggiatoa tend to prefer areas that are rich in hydrogen sulfate, including water that has been contaminated with sewage. Because of this, the mats they form are good indicators of pollution in water."
http://microbewiki.kenyon.edu/index.php/Beggiatoa [see also other footnote]

[252] **Dissimilatory**: "Related to the conversion of food or other nutrients into products plus energy-containing compounds."
http://www.chemicool.com/definition/dissimilatory.html

Assimilation "designates the process of the transformation of external substances and materials into substances and materials internal to the body."
http://en.wikipedia.org/wiki/Assimilation_%28biology%29

[253] **Sulfate reduction III (dissimilatory) Metabolic Pathway**:
http://biocyc.org/META/NEW-IMAGE?type=PATHWAY&object=DISSULFRED-PWY

[254] **Archaeoglobus**: "... are hyperthermophiles that can be found in hydrothermal vents, oil deposits, and hot springs. They can produce biofilm when subjected to environmental stresses such as extreme pH or temperature, high concentrations of metal, or the addition of antibiotics, xenobiotics, or oxygen. These archaeons are known to cause the corrosion of iron and steel in oil and gas processing systems by producing iron sulphide. Their bioflims, however, may have industrial or research applications in the form of detoxifying metal contaminated samples or to gather metals in an economically recoverable form."
http://microbewiki.kenyon.edu/index.php/Archaeoglobus

[255] **Sulfate reduction**: "... is a relatively energetically poor process used by many Gram negative bacteria found within the δ-Proteobacteria, Gram positive organisms relating to Desulfotomaculum or the archaeon Archaeoglobus. Hydrogen sulfide (H2S) is produced as a metabolic end product... All sulfate reducing-organisms are strict anaerobes."
http://en.wikipedia.org/wiki/Microbial_metabolism#Sulfur_oxidation

RB displayed a graph plotting $\delta^{34}S$ as the Y-axis against Ga on the X-axis. The graph depicted a relative peak c. 1 Ga. Source not stated.

Sulfur Reservoirs: [RB presented a table, data incompletely captured here]
Reservoirs are expressed in 10^{18} g S:

Deep Ocean Rocks:	
Sedimentary	75
Mafic Rocks	2300
Sedimentary Rocks	
Sandstone	250
Shale	2000
Limestone	380
Evaporites	5100
Volcanoes	50
Connate water[257]	27
Atmosphere (SO2, H2S, DMS)	3.6
Freshwater	0.003
Ice	0.006

4. Nitrogen Cycle

[This topic was not presented in regular class lectures. Materials here are adapted from RB's handout and supplemented]

[**Nitrogen Oxidation States**: Nitrogen exists in several oxidation states {0, ±1, ±2, ±3, 4, 5}: Ammonia NH_3 {-3, most reduced}, Free N_2 {+0}, Nitrous Oxide (dinitrogen monoxide) N_2O {+1}, nitrogen (II) oxide NO {+2}, Nitrite $(NO_2)^-$ {+3}, dinitrogen tetroxide N_2O_4 {+4}, Nitrate $(NO_3)^-$ {+5, most oxidized}.]

Global N Reservoir:[258]

Reservoir/Pool Type	Metric Tons	% of Total
Biosphere	2.8×10^{11}	0.0002
Hydrosphere	2.3×10^{13}	0.014
Atmosphere	3.86×10^{15}	2.3
Geosphere	1.636×10^{17}	97.7
Crust	$0.13 - 1.4 \times 10^{16}$	0.78-8.4
Soils and Sediments	$0.35 - 4.0 \times 10^{15}$	0.21-2.4
Mantle and Core	1.6×10^{17}	95.6

[per RB handout, edited]:
N is in amino acids and nucleic acids, so N is a key nutrient, abundant in atmosphere but N_2 is not biologically usable by most organisms. The only abiotic fixation of N to nitric acid occurs in lightning, so availability is a major constraint on productivity, biosphere size. Like S, N exhibits complex atmospheric chemistry. Microbial redox metabolisms move N through many valence states—consider 4 reactions as most important:

1) Nitrogen fixation: $N_2 + 8H^+ + 8e^- \rightarrow 2NH_3 + H_2$

---

[256] **Enzymatic Basis For Assimilatory And Dissimilatory Sulfate Reduction**: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=279279

[257] **Connate fluids**: "The term connate fluids in the context of geology, and of sedimentology in particular, refers to the liquids that were trapped in the pores of sedimentary rocks as they were deposited. These liquids are largely composed of water, but also contain many mineral components as ions in solution. As rocks are buried, they undergo lithification and the connate fluids are usually expelled. If the escape route for these fluids is blocked, the pore fluid pressure can build up, leading to overpressure."
http://en.wikipedia.org/wiki/Connate_fluids

[258] **Nitrogen Reservoirs**: http://www.sws.uiuc.edu/nitro/nitrodesc.asp

By cyanobacteria, anaerobic photosynthetic bacteria, aerobic Azotobacter, anaerobic Clostridium, symbiotic Rhizobium, methanogenic Archaea, all use nitrogenase enzyme with Fe, Mo (rarely V) cofactors, doesn't work with oxygen present so cyanobacteria have special cells (heterocysts) or fix N nocturnally. This is a N reduction reaction.

2) Ammonification: Strip N from organic matter. (Turns organic nitrogen such as amino acids into ammonia NH_3.) Done by many heterotrophic bacteria

3) Nitrification: $NH_4^+ + 3O_2 \rightarrow 2NO_2^-$ (nitrite) $+ 2H_2O + 4H^+$ and $2NO_2^-$ (nitrite) $+ O_2 \rightarrow 2NO_3^-$ (nitrate)
Different bacteria for each step, e.g. *Nitrosomonas* to nitrite, *Nitrobacter* converts to nitrate, all are obligate aerobes.

4) Denitrification: $4NO_3^-$ (nitrate) $+ 5CH_2O + 4H^+ \rightarrow 2N_2 + 5CO_2 + 7H_2O$
Often stops before N_2 at NO, N_2O, large isotopic fractionation causing modern organic $\delta^{15}N$[259] to be +5‰ rather than 0‰ like atmosphere, many bacteria e.g. *Pseudomonas*, *Thiobacillus*.

Microbial Mineralization

(per RB and supplemented)
There are three main environmental events in Earth history which have geobiological causes:
1. **Oxygenation** of the oceans, atmosphere, and sediments. Caused by microbial metabolism, reflected in microbial mineralization and their direct or indirect sedimentary products. Will consider 3 forms of microbial mineralization to see how this reflects oxygen history: stromatolites, BIF, and sedimentary pyrite. The cyanobacteria were the only organisms producing large amounts of oxygen. Minimal free Oxygen is produced by UV-induced **photolysis** in upper atmosphere:

$$2\ H_2O\ [+\ h\nu] \Rightarrow \text{eventually } 2H_2 + O_2$$

but the Oxygen formed is unstable and tends to react and recombine with the free H also produced or with other elements.: This reaction yields only c. 10^{-20} of the current levels of atmospheric O_2. The same process occurs with CO_2 and SO_2.
2. **Skeletonization** enhancing carbonate, silicate, and phosphate deposition.
3. **Terrestrialization** or invasion of plants and animals onto land causing shift of organic productivity from sea to land.

1. Carbonate Precipitation in Stromatolites

Microbes can produce diagenetic carbonate inside deposited sediments. This is a small volume process—the carbonate acts like interstitial cement, not like a large limestone deposit. **Stromatolites** produce reefs, locking up much of the $CaCO_3$ in the crust. They begin as mounds of microbial mats and filaments which trap sediment. The mounds exhibit layers and fibrils, e.g., of the algae **Enteromorpha** [this is a nonmotile filamentous chlorophyte algae (seaweed), presumably therefore coexisting with the cyanobacteria.][260]. These organisms cause $CaCO_3$ precipitation after organism

---

[259] **Nitrogen Isotopic Fractionation (example)**: "The evolutionary success of reef-building corals in nutrient-poor tropical waters is attributed to endosymbiotic dinoflagellates. The algae release photosynthetic products to the coral animal cells, augment nutrient flux, and enhance the rate of coral calcification... Here we compare 17 species of symbiotic and nonsymbiotic corals to determine whether evidence for photosymbiosis appears in stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) of an organic skeletal compartment, the coral skeletal organic matrix (OM). Mean OM $\delta^{13}C$ in symbiotic and nonsymbiotic corals was similar (-26.08‰ vs. -24.31‰), but mean OM $\delta^{15}N$ was significantly depleted in ^{15}N in the former (4.09‰) relative to the latter (12.28‰), indicating an effect of the algae on OM synthesis and revealing OM $\delta^{15}N$ as a proxy for photosymbiosis. To answer an important paleobiological question about the origin of photosymbiosis in reef-building corals, we applied this proxy test to a fossil coral (Pachythecalis major) from the Triassic (240 million years ago) in which OM is preserved. Mean OM $\delta^{15}N$ was 4.66‰, suggesting that P. major was photosymbiotic. The results show that symbiotic algae augment coral calcification by contributing to the synthesis of skeletal OM and that they may have done so as early as the Triassic."
http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=547863
[260] **Enteromorpha and Green Algae**:
• http://www.sms.si.edu/irlspec/Entero_flexuo.htm
• http://en.wikipedia.org/wiki/Green_algae

decay inducing **lithification**, especially in conditions where local $CaCO_3$ is saturated. (See previous discussions and equations involving CO, carbonic acid, bicarbonate, and carbonate):

Ca^{2+} (dissolved Ca) + $2HCO^{3-}$ (bicarbonate)$\leftrightarrow$ $CaCO_3 + H_2CO_3$.

Addition of CO_2 from decaying organisms forces dissociation of H_2CO_3 forcing reaction toward formation of $CaCO_3$ and precipitation... There are many different forms of stromatolites [a complex diagram of unstated source was projected]: mounds, columnar and non-columnar forms, various attitudes and orientations, etc. The various forms may or may not reflect differing species versus simply environmental variations. The layering observed in stromatolites is seen at many scales. The microbes control the layering only at the lamellar scale.

Stromatolites were first **abundant** in the late Archean c. 2.7 Ga [Neoarchean] and had become ubiquitous by the PaleoProterozoic and MesoProterozoic. [See also previous discussion focused on stromatolites.] The greatest abundance was c. 1500 - 500 Ma. After the Cambrian [onset 542 Ma], they become scarce. What explains their NeoProterozoic [1000 - 542 Ma] decline, which began c. 1000 Ma? Possibly causes include:

1) **Grazing animals** eat them, preventing mats and mounds (but organisms persist at smaller scale).
2) **Crawling animals** disrupt the sediments and mats. But decline begins before first trace fossils[261] of relevant animals.
3) **Shells**: Animals remove $CaCO_3$ for use in shells and skeletons. But these animal forms occurred after onset of decline.
4) **Fecal**: Sediment supply is increased from animal fecal pellets, swamping carbonate precipitation. However, the decline began before the first fecal pellets. Note that fecal pellets change the composition of limestones and that amorphous stromatolites incorporate fecal pellets.
5) **Seaweeds** outcompeted microbial mats for space and light. This is the **most likely explanation for the decline**, since multicellular algae appeared c. 1.2 Ga, and radiate extensively by 0.8 Ga.

The rise in stromatolite abundance might reflect a rise in photosynthesis because carbonate precipitation is an indirect consequence photosynthesis and atmospheric O_2 caused by cyanobacteria. However, the converse is not suggested. [?exactly what converse]

2. Iron Precipitation in Banded Iron Formations (BIFs)

BIFs are laminated sediments consisting of Iron (Fe) oxide rich layers alternating with relatively iron-poor microcrystalline quartz (microquartz), chert, or shale. Formed by precipitation. The laminations vary widely in scale from 10μm-10m, reflecting cyclical environmental factors. The mechanisms of origin for BIFs are controversial.

On the largest scale, the variations may reflect the **Milankovitch (Milanković) cycles**.[262] [MCM: This is a complex astronomical subject barely touched on here.] These involve variations in or oscillations of

---

[261] **Trace Fossils**: "Trace fossils, also called **ichnofossils** ..., are structures preserved in sedimentary rocks that record biological activity. While we are most familiar with relatively spectacular, fossilized hard-part remains such as shells and bones (known as **body fossils**), trace fossils are often less dramatic, but nonetheless very important. Strictly defined, trace fossils must **reflect both the anatomy of their maker in some way, and be the result of behaviour**. Sedimentary structures made by empty shells rolling along the sea floor are thus excluded (as "**death marks**"), as are structures such as **stromatolites** that, although the result of behaviour, do not reflect the anatomy of their maker. Spun **coccoons** and **spiders webs** are considered to be trace fossils, as they are manipulated by their makers after secretion; egg cases, on the other hand, are not. Trace fossils include **burrows** (such as Chondrites), **borings**, **ichnites** (footprints and track marks), **Zoophycus feeding marks**, **trails** (such as Cruziana scratched by trilobites), **coprolites** (fossilized droppings) and other gut-derived objects, and **rhizoliths** or rhizocretions (the fossil remains of roots)." http://en.wikipedia.org/wiki/Trace_fossil

[262] **Milankovitch cycles**: "are the collective effect of changes in the Earth's movements upon its climate, named after Serbian civil engineer and mathematician Milutin Milanković. The eccentricity, axial tilt, and precession of the Earth's orbit vary in several patterns, resulting in 100,000 year ice age cycles of the Quaternary glaciation over the last few million years...

... The shape of the Earth's orbit varies from being nearly circular (low eccentricity of 0.005) to being mildly elliptical (high eccentricity of 0.058) and has a mean eccentricity of 0.028. The major

1) the **eccentricity** of the Earth's elliptical orbit (influenced by other planets, having major period components of roughly 100,000 and 400,000 years.)
2) the **general precession**[263] of the Earth's rotational axis (resulting from a combination of the precession of the spin axis, the precession of the perihelion, and certain planetary effects, the sum of which have major period components of c. 19,000 and 23,000 years)[264]
3) the Earth's **axial tilt or obliquity** (oscillating between 22.0° - 24.6°, with period of 41,000 years), and
4) the **Earth's orbital inclination** with respect to the **invariable plane** (with period of c. 100,000 years; Milankovitch did not study this item),
all having differing periodicities which sum together to affect local and overall insolation. Milankovitch postulated that cycles of the Quaternary glaciation were caused by the periodic astronomical variations. The effects can be measured in polar snowfall—e.g., when the orbit is more circular, there is less polar snowfall, whereas more elliptical leads to greater extremes and more polar snowfall. Changes in glacial melting and persistence also result. The variations at layering at micron and mm thickness scale can be traced (correlated) across horizontal distances of up to 500 km. The cause is unclear but might be due to orbital changes, even down to diurnal variations.

Banded Iron Formations[265] are present in the oldest sediments dating back to 3.8 Ga in Isua Greenland. [A graph plotting amount of BIFs vs. time, of unstated source, was projected by RB] They

---

component of these variations occurs on a period of 413,000 years (eccentricity variation of ±0.012). A number of other terms vary between 95,000 and 136,000 years, and loosely combine into a 100,000 year cycle (variation of -0.03 to +0.02). The present eccentricity is 0.017.

The angle of the Earth's axial tilt (obliquity) varies with respect to the plane of the Earth's orbit. These slow 2.4° obliquity variations are roughly periodic, taking approximately 41,000 years to shift between a tilt of 22.1° and 24.5° and back again…

Precession is the change in the direction of the Earth's axis of rotation relative to the fixed stars, with a period of roughly 26,000 years…

The inclination of Earth's orbit drifts up and down relative to its present orbit with a cycle having a period of about 70,000 years. Milankovitch did not study this three-dimensional movement."
http://en.wikipedia.org/wiki/Milankovitch_cycles
See also http://aa.usno.navy.mil/faq/docs/seasons_orbit.php

263 **Precession**: http://en.wikipedia.org/wiki/Precession_%28astronomy%29

264 **Precession**: *TES2000* p. 276

265 **Banded Iron Formations**: "Banded iron formations (also known as banded ironstone formations or BIFs) are a distinctive type of rock often found in primordial sedimentary rocks. The structures consist of repeated thin layers of iron oxides, either magnetite or hematite, alternating with bands of iron-poor shale and chert. Some of the oldest known rock formations, formed around three thousand million years before present (3 Ga), include banded iron layers, and the banded layers are a common feature in sediments for much of the Earth's early history…

The conventional concept is that the banded iron layers were formed in sea water as the result of oxygen released by photosynthetic cyanobacteria, combining with dissolved iron in Earth's oceans to form insoluble iron oxides, which precipitated out, forming a thin layer on the substrate, which may have been anoxic mud (forming shale and chert). Each band is similar to a varve. The banding is assumed to result from cyclic variations in available oxygen. It is unclear whether these banded ironstone formations were seasonal or followed some other cycle. It is assumed that initially the Earth started out with vast amounts of iron dissolved in the world's acidic seas. Eventually, as photosynthetic organisms generated oxygen, the available iron in the Earth's oceans was precipitated out as iron oxides. At the tipping point where the oceans became permanently oxygenated, small variations in oxygen production produced pulses of free oxygen in the surface waters, alternating with pulses of iron oxide deposition.

Until fairly recently, it was assumed that the rare later banded iron deposits represent unusual conditions where oxygen was depleted locally and iron-rich waters could form then come into contact with oxygenated water. An alternate explanation of these later rare deposits is undergoing much research as part of the Snowball Earth hypothesis—wherein it is believed that an early equatorial supercontinent (Rodinia) was totally covered in an ice age (implying the whole planet was frozen at the surface to a depth of several kilometers) which corresponds to evidence that the earth's free oxygen may have been nearly or totally depleted during a severe ice age circa 750 to 580 million years ago (mya)… Alternatively, some geochemists suggest that BIFs could form by direct oxidation of iron by (non-photosynthetic) autotrophic microbes. The total amount of oxygen locked up in the banded iron form commonly at moderate ocean depths below the photic zone, are abundant at moderate depths in the Archean [3.8 - 2.5 Ga] and early Paleoproterozoic, were forming maximally at c. 2.5 Ga (such as the Transvaal Supergroup), declined beginning c. 2.0 - 1.7 Ga, then disappeared. However, they anomalously reappeared at the 0.7 Ga Neoproterozoic Sturtian glaciation, a time which has been hypothesized to be a "Snowball Earth" time (or RB says maybe at least a slushy Earth).

[Oxides of iron[266] include:
Iron(II) oxide (FeO, wüstite) or **ferrous oxide**
Iron(III) oxide (Fe_2O_3, hematite or maghemite) or **ferric oxide**
Iron(II,III) oxide (Fe_3O_4, **magnetite** or **lodestone**) or **ferrous ferric oxide**
Rust[267] is typically hydrated iron(III) oxide ($Fe_2O_3.nH_2O$), and under wet conditions may include iron(III) oxide-hydroxide (FeO(OH)).]

Do BIFs imply low O_2 levels? Iron ion is only water soluble in the reduced ferrous Fe^{2+} state. [MCM: this could use clarification.] Sources of abundant iron in the oceans include:
1) **Weathering** of pyroxenes (e.g., $CaFeSi_2O_6$) and olivines (e.g., $CaFeSiO_4$) in anoxic conditions, producing soluble Fe^{2+} passing to the ocean.
2) **Hydrothermal Vents (Black smokers)**: erupting Fe^{2+} leached by hot water from basalts under the ocean.

If there is substantial O_2 in the atmosphere, the Fe^{2+} is highly oxidized to Fe^{3+} which is insoluble and precipitates to form magnetite and **redbeds**.[268] In the deep oceans, the iron from black smokers reacts with O_2 to form insoluble iron oxide [and iron sulfides].

Are BIFs biogenic or abiogenic? Here are some possible theories:
1) **UV radiation** can cause abiotic oxidation of Fe^{2+} (ferrous) to Fe_3O^4 with no O_2 involved. However, water absorbs UV so this mechanism cannot apply to deeper ocean levels.
2) **Anaerobic photosynthesis**: Some bacteria use Fe^{2+} in anaerobic photosynthesis. Thus they might create BIFs in an anaerobic process. But we should see their "dead bodies", and BIFs are not full of organic matter. Thus this mechanism is unlikely.
3) **Magnetotactic microbes**:[269] Microbes can also precipitate magnetite Fe_3O_4 [or greigite Fe_3S_4] in their cells under low oxygen or anoxic conditions. Magnetite forms distinctive octahedral crystals. BIFs don't have lots of these.

---

beds is estimated to be perhaps twenty times the volume of oxygen present in the modern atmosphere. Banded iron beds are an important commercial source of iron ore."
http://en.wikipedia.org/wiki/Banded_iron_formation
[266] **Iron Oxides**: http://en.wikipedia.org/wiki/Iron_oxide
[267] **Rust**: http://en.wikipedia.org/wiki/Rust
[268] **Red Beds**: "The term red beds usually refers to strata of reddish-colored sedimentary rocks such as sandstone, siltstone or shale that were deposited in hot climates under oxidizing conditions. The red color comes from iron oxide [hematite] in their mineral structure. Although they have been deposited throughout the Phanerozoic, they are most commonly associated with rocks deposited during the Permian and Triassic periods."
http://en.wikipedia.org/wiki/Red_bed
[269] **Magnetotactic bacteria**: "Magnetotactic bacteria (or MTB) are a class of bacteria discovered in the 1960s, that exhibit the peculiar ability to orient themselves along the magnetic field lines of Earth's magnetic field. The term magnetotaxis has been coined to describe the biological phenomenon upon which these microorganisms tend to move in response to the magnetic characteristics of the environment...

The sensitivity of magnetotactic bacteria to the Earth's magnetic field arises from the fact that the bacteria precipitate within their cells chains of crystals of magnetic minerals; all magnetotactic bacteria reported to date precipitate either magnetite or greigite. These crystals, and sometimes the chains of crystals, can be preserved in the geological record as magnetofossils...

Magnetite-producing magnetotactic bacteria are usually found in oxic-anoxic transition zones, the transition zone between oxygen-rich and oxygen-starved water or sediment. Many MTB are only able to survive in environments with very limited oxygen, and some can only exist in completely anaerobic environments. "
http://en.wikipedia.org/wiki/Magnetotactic_bacteria

BIFs need:
1) Fe^{2+} in solution from vents and rivers.
2) Low O_2 conditions such as in the photic [?] and deep ocean zones of the Archean and early Proterozoic. [needed to prevent immediate precipitation of Fe^{2+}as iron oxide]
3) Mixing in the photic zone with O_2 from cyanobacteria, producing Fe oxides which precipitate.

These conditions were satisfied in the Archean and PaleoProterozoic, but not the MesoProterozoic (too much oxygen and not enough dissolved iron). It has been hypothesized that the spike in the Neoproterozoic was due to extensive cooling and ocean freezing, stopping O_2 production from photosynthesis, and continued inputs of iron from black smokers, etc.

But some BIFs are huge and are important sources of iron ore. The 2.5 Ga Hamersley Australia banded iron formation in the Pilbara NW Australia is 500 km x 500 km, 200m thick), have 2α-methylhopane biomarkers of cyanobacteria, so associated with O_2 production.

Therefore, a popular model for BIFs origin:
1) Hydrothermal or weathering provide source for Fe^{2+} in solution
2) Anoxic deep-sea and atmosphere, some photosynthetic O_2 in shallow water. [The banding is assumed to result from cyclic variations in available oxygen, with more precipitation occurring when oxygen level is higher.]
3) After ~2.0 Ga atmosphere and deep-sea have more oxygen from photosynthetic O_2, so no more dissolved Fe^{2+} available

3. Sedimentary pyrite

[This topic was not presented in class—source of info is RB handout with modifications]
FeS_2 (iron pyrite or iron persulfide)[270] was formed by microbial sulfate reduction in reducing [anoxic] settings where Fe^{2+} is present.[271] Pyrite may coat microbes, often forms clusters of tiny cubic crystals (**framboids**)[272], leaves light ~-20‰ $\delta^{34}S$ isotopic fractionation[273] if sulfate > 1mmol. [RB has previously noted that pyrite formation is exothermic.]

---

270 **Iron Pyrite**: "From the perspective of classical inorganic chemistry, which assigns formal oxidation states to each atom, pyrite is probably best described as $Fe^{2+}S_2^{2-}$. This formalism recognizes that the sulfur atoms in pyrite occur in pairs with clear S-S bonds. These persulfide units can be viewed as derived from hydrogen persulfide, H_2S_2. Thus pyrite would be more descriptively called iron persulfide, not iron disulfide."
http://en.wikipedia.org/wiki/Pyrite

271 **Microbial biogenesis of pyrite**: "Bacterial metabolism, involving redox reactions with carbon, sulfur, and metals, appears to have been important since the dawn of life on Earth. In the Archean, anaerobic bacteria thrived before the Proterozoic oxidation of the atmosphere and the oceans, and these organisms continue to prosper in niches removed from molecular oxygen… Heterotrophic anaerobes, which require organic carbon for their metabolism, catalyze a number of thermodynamically favorable reactions such as Fe-Mn oxyhydroxide reductive dissolution (and the release of sorbed metals to solution) and sulfate reduction. Bacterial sulfate reduction to H_2S can be very rapid if reactive organic carbon is present and can lead to precipitation of metal sulfides and perhaps increase the solubility of elements such as silver, gold, and arsenic that form stable Me-H_2S aqueous complexes… Bacteria may have been important contributors in some sedimentary ore-forming environments and could be important along the low-temperature edges of high-temperature systems such as those that form volcanogenic massive sulfides."
http://econgeol.geoscienceworld.org/cgi/content/abstract/100/6/1067 [2005]

272 **Framboids**: "Framboids are 0.5-100 µm-sized, raspberry-like, spheroidal accumulations of $10\text{-}10^9$ microcrystallites. These structures are predominantly composed of pyrite (FeS_2), although other minerals such as greigite (Fe_3S_4), magnetite (Fe_3O_4), and limonite ($FeO.OH.nH_2O$) have also been identified. Modern framboids are present in a variety of natural environments (soils, sediments, microbial mats), and can also be produced artificially in the laboratory. Even though numerous cases of framboids have been cited from the geological record, little is known about their mechanisms of formation, and biogenicity. Understanding the effects of the conditions of formation upon framboid characteristics from modern environments (e.g. size distribution, microtexture, composition, and mineralogy) will allow us to better understand what pyrite framboids can tell us about sediments from the geological record. The purpose of this project was to determine whether pyrite framboids can be

Light $\delta^{34}S$ is found back to 2.3 Ga, perhaps as far back as 2.7 Ga,[274] once at 3.5 Ga in sulfate oasis, suggest marine sulfate was low until 2.3 Ga, then rising O_2 levels allow higher levels. $\delta^{34}S < -30‰$ after 0.8 Ga, imply re-oxidation & re-reduction, another rise in O_2?

4. Oxygen History:

[This topic was not presented in class—source of info is RB handout with modifications, the following is somewhat unclear]
Almost all O_2 derives from microbial oxygenic photosynthesis, small amount from H_2O photolysis by UV in upper atmosphere. Accumulation of O_2 requires:

- burial of C_{org} to prevent O_2 consumption in respiration, should be marked by heavy (+10‰) "C_{carb}" [$\delta^{13}C$ in kerogen or carbonate?], evident in geologic record 2.4 - 2.0 Ga, 0.8 - 0.6 Ga;
- methane photolysis and H_2 escape in upper atmosphere, leaving O_2, should be marked by very light (-60‰) "C_{org}" [$\delta^{13}C$], evident 2.8-2.5 Ga. [MCM: See previous discussions of C^{12} enrichment by microbial methanogenesis]

Conditions for O_2 rise in late Archean-early Paleoproterozoic, much geologic evidence.
Model: no atmospheric O_2 before 2.4 Ga, little in upper ocean, rapid rise to 10% PAL [i.e., 10% Percent of Present Atmospheric Level] at 2.4 - 2.0 Ga, maybe further rise to 50% PAL 0.8-0.6 Ga.

Eukaryote Biomineralization (Shells, Skeletons, etc.)

[per RB and supplemented]
Eukaryotes use secretion to directly produce biomineralization from soluble seawater or environmental salts. In contrast, Prokaryotes produce mostly undirected extracellular or environmental mineralization as a result of metabolic byproducts, etc. Eukaryotes regulate seawater chemistry. This is a sudden major evolutionary change which rapidly propagated because of its evolutionary advantage. (In contrast, microbes have caused only one [?in what sense] major evolutionary change, the rise in O_2 occurring c. 2.4 - 2.0 Ga.) [MCM: The terms "Tests", "Shells", and "Skeletons" get used by RB and other authors somewhat confusingly and at times interchangeably for the various forms of eukaryotic biomineralized structures. I am uncertain what the best encompassing generic term is, so

---

used as a biosignature within ancient sediments. Microbial mats rich in pyrite framboids were collected from the Buncar Springs in Mangalia aquifer (Romania). The pyrite framboid rich microbial mats are formed underground at the anaerobic water-gas (90-95% methane, 5-10% CO_2) interface… "
http://adsabs.harvard.edu/abs/2003AGUFM.B51C0980S [2003]

[273] **Sulfur Isotopic Fractionation in Biogenic Pyrite**: "Coexisting dissolved sulfide and sulfate from hypersulfidic interstitial waters of a 380- m-long sediment core show a large isotopic difference of up to 72‰ caused by in situ microbial sulfate reduction. This is considerably larger than the assumed biological maximum of 46‰ derived from laboratory studies with pure cultures of sulfate-reducing bacteria. Similar high fractionations inferred from sedimentary metal sulfides have been previously explained by a multistage process, involving sulfide reoxidation and disproportionation of sulfur intermediates. Our data show that extreme isotopic differences between sulfate and the reduced sulfur species can also be generated during microbial single-step fractionation. This result indicates that the sulfate-reducing communities and/or their cellular metabolic activities in the deep biosphere may differ from those observed in near-surface sediments or the water column."
http://geology.geoscienceworld.org/cgi/content/abstract/29/7/647 [2001]

[274] **Archaean microbial Fe(III) and sulfate reduction**: "… Microbiological data indicate that sulfate and iron reduction are both among the earliest forms of microbial respiration, and direct evidence for the early origin of sulfate reduction comes from sulfur isotopic anomalies in ancient sediments. Fe isotope geochemistry potentially provides a new way of identifying microbial iron reduction early in Earth's history. We present Fe isotopic data for sedimentary pyrite from the 2.7 Ga Belingwe sedimentary basin in Zimbabwe. Isotopically light Fe and a remarkable covariation between Fe and S isotopes provide strong evidence for coexisting Fe and S reduction. Our results are consistent with an early origin for sulfate reduction and provide direct geochemical evidence for the antiquity of bacterial Fe reduction. The covariation of Fe and S isotopes may provide a useful new tracer of microbial evolution early in Earth history."
http://geology.geoscienceworld.org/cgi/content/abstract/34/3/153 [2006]

will use *skeleton* sometimes in a generic sense meaning “mineralized or unmineralized supporting or protective ridig hard parts including shells, exoskeletons, and endoskeletons”. Clearly, fossils usually derive mostly from mineralized hard parts.]

1. Calcium Carbonate Biomineralization

$CaCO_3$ occurs in 2 forms: **calcite** (trigonal-rhombohedral[275])) and **aragonite** (orthorhombic). Calcite can include up to 10% Mg. Aragonite can have no Mg but may contain Strontium. Aragonite is metastable[276] and converts to calcite over millions of years. But the Sr content in calcite can give evidence for previous aragonite form. Handout says “Mg-calcite (biogenic)” [MCM: this seems contradictory.] Prokaryotes also precipitate $CaCO_3$, but only as a byproduct of metabolism, whereas Eukaryotes do this “intentionally”. $CaCO_3$ can also form abiotically in saturated solutions to form **evaporites** (forming from the evaporation of bodies of surficial water), **ooids**[277], **stalagmites and stalactites**, and [sometimes] lamellated **tufas**[278]. In the current Earth, the dominant $CaCO_3$ precipitation is by skeleton/shell formation[279] by marine organisms. Most of the $CaCO_3$ in coral reefs is actually secreted by benthonic[280] “red and green algae” living on the sea floor [or by **Zooxanthellae** algae endosymbiotic within the coralline **anthozoans**[281]] so the reefs might be better termed coral-algal

---

[275] **Calcite**: “The carbonate mineral, calcite, is a chemical or biochemical calcium carbonate corresponding to the formula $CaCO_3$ and is one of the most widely distributed minerals on the Earth's surface. It is a common constituent of sedimentary rocks, limestone in particular. It is also the primary mineral in metamorphic marble. It also occurs as a vein mineral in deposits from hot springs, and also occurs in caverns as stalactites and stalagmites. Calcite is often the primary constituent of the shells of marine organisms, e.g., plankton (such as coccoliths [formed by coccolithophores] and [planktonic] foraminifera), the hard parts of red algae, some sponges, brachiopoda, echinoderms, most bryozoa, and parts of the shells of some bivalves, such as oysters and rudists. Calcite represents the stable form of calcium carbonate; aragonite will change to calcite at 470°C, and vaterite, or μ-$CaCO_3$, is less stable still.... Calcite crystals are trigonal-rhombohedral, though actual calcite rhombohedra are rare as natural crystals. However, they show a remarkable variety of habits including acute to obtuse rhombohedra, tabular forms, prisms, or various scalenohedra.”
http://en.wikipedia.org/wiki/Calcite
See also http://infohost.nmt.edu/~mruth/posters/crystal%20structure.pdf

[276] **Aragonite**: “Aragonite is thermodynamically unstable at standard temperature and pressure, and tends to alter to calcite on scales of 10^7 to 10^8 years.”
http://en.wikipedia.org/wiki/Aragonite

[277] **Ooids**: “... Ooids are small (< 2 mm), spheroidal, "coated" (layered) grains, usually composed of calcium carbonate, but sometimes made up of iron– or phosphate–based minerals. Ooids usually form on the sea floor, most commonly in shallow tropical seas (the Bahama Platform, for example), or in the Persian Gulf. After being buried under additional sediment, these ooid grains can be cemented together to form a sedimentary rock called an oolite. Oolites usually consist of calcium carbonate meaning they belong to the limestone rock family... An ooid forms as a series of concentric layers around a nucleus. The layers contain crystals arranged radially, tangentially or randomly. The nucleus can be a shell fragment, quartz grain or any other small fragment (including an aragonite/calcite amalgamation). Most modern ooids are aragonite... Some are composed of high-magnesium calcite, or are bimineralic (layers of calcite and layers of aragonite)... Ancient ooids are calcite, either originally precipitated as calcite, or formed by alteration (neomorphic replacement) of aragonite ooids (or aragonite layers in originally bimineralic ooids)... There are several factors that affect ooid growth: supersaturation of the water with respect to calcium carbonate, the availability of nuclei, agitation of the ooids, a constant location, water depth and the role of microbial organisms.”
http://en.wikipedia.org/wiki/Ooid

[278] **Tufa**: “Tufa is a rough, thick, rock-like calcium carbonate deposit that forms by precipitation from bodies of water with a high dissolved calcium content.”
http://en.wikipedia.org/wiki/Tufa

[279] **Origin of Calcite**: “The primary source of the calcite in limestone is most commonly marine organisms.”
http://en.wikipedia.org/wiki/Limestone

[280] **Benthonic**: “living on the bottom under a body of water”
http://www.wordreference.com/definition/benthonic

[281] **Organisms and Source of $CaCO_3$ in Coral Reefs**: “The building blocks of coral reefs are the generations of **reef-building corals**, and other organisms that are composed of calcium carbonate.

reefs. Planktonic[282] algae (**Coccolithophores**)[283] are unicellular algae which also precipitate $CaCO_3$. Some planktonic or benthonic protists including **foraminifera**[284] secrete Tests/Shells/Skeletons. Other benthonic or nektonic animals also secrete Tests/Shells/Skeletons: corals, mollusks including the nautilus, echinoderms including sea urchins and **Crinoids** ("sea lilies" or "feather-stars"), and sponges. Formerly prominent animals forming fossil Tests/Shells/Skeletons and flourishing in the Paleozoic included brachiopods, trilobites, and crinoid and blastoid echinoderms. Eukaryotic organisms actively control the precipitation of calcium carbonate by using an organic matrix, and actively pump $CaCO_3$ to the extracellular layer. Proteins direct the nucleation and crystal growth. The resulting structures tend to be complex. A sea urchin may create large single optically perfect crystals of calcite for its plates. Certain mollusks shells may exhibit 3 or more layers of differently oriented aragonite needles [sometimes with organic layers interposed].[285]

For example, as a coral head grows, it lays down a skeletal structure encasing each new polyp. Waves, grazing fish (such as parrotfish), sea urchins, sponges, and other forces and organisms break down the coral skeletons into fragments that settle into spaces in the reef structure. Many other organisms living in the reef community contribute their skeletal ... calcium carbonate in the same manner. **Coralline algae** [i.e zooxanthelate, filamentous algae] are important contributors to the structure of the reef in those parts of the reef subjected to the greatest forces by waves (such as the reef front facing the open ocean). These algae contribute to reef-building by depositing limestone in sheets over the surface of the reef and thereby contributing also to the structural integrity of the reef.

Reef-building or **hermatypir** corals are only found in the photic zone (above 50 m depth), the depth to which sufficient sunlight penetrates the water for photosynthesis to occur. The coral polyps do not photosynthesize, but have a symbiotic relationship with single-celled algae called **zooxanthellae**; these algal cells within the tissues of the coral polyps carry out photosynthesis... Because of this relationship, coral reefs grow much faster in clear water, which admits more sunlight. Indeed, the relationship is responsible for coral reefs in the sense that without their symbionts, coral growth would be too slow for the corals to form impressive reef structures. Corals can get up to 90% of their nutrients from their zooxanthellae symbionts.
http://en.wikipedia.org/wiki/Coral_reef
"**Zooxanthellae** ... are golden-brown intracellular endosymbionts of various marine animals and protozoa, especially **anthozoans** [Cnidarians that include the sea anemones and corals]. They are members of the phylum Dinoflagellata and are typically **dinoflagellate algae**, although algae such as diatoms can also be zooxanthellae."
http://en.wikipedia.org/wiki/Zooxanthellae

282 **Plankton and Planktonic versus Nekton and Nektonic**: "Plankton are any drifting organism that inhabits the pelagic zone of oceans, seas, or bodies of fresh water. It is a description of life-style rather than a genetic classification.... By definition, organisms classified as plankton are unable to resist ocean currents. This is in contrast to **nekton** organisms that can swim against the ambient flow of the water environment and control their position (e.g. squid, fish, and marine mammals)."
http://en.wikipedia.org/wiki/Plankton

283 **Coccolithophores**: ... are single-celled algae, protists and phytoplankton belonging to the class **haptophytes**. They are distinguished by special calcium carbonate plates (or scales) of unknown purpose called **coccoliths**, which are important microfossils. Coccolithophores are exclusively marine and are found in large numbers throughout the surface euphotic zone of the ocean. An example of a globally-significant coccolithophore is **Emiliania huxleyi**.

Due to their microscopic size and the broad distribution of many of their taxa, coccoliths (calcareous nannoplankton) have become very popular as index fossils for solving various stratigraphic problems. Nannofossils are sensitive indicators of changes in the temperature and salinity of the ocean and sea surface water. The quantitative analysis of calcareous nannoplankton assemblages is being employed to reveal such changes."
http://en.wikipedia.org/wiki/Coccolithophore

284 **Foraminifera** [not "foramenifera"]: "The Foraminifera ("Hole Bearers") or forams for short, are a large group of amoeboid protists with reticulating pseudopods, fine strands of cytoplasm that branch and merge to form a dynamic net. They typically produce a **test**, or shell, which can have either one or multiple chambers, some becoming quite elaborate in structure.... Most have calcareous tests, composed of calcium carbonate. In other forams the test may be composed of organic material, made from small pieces of sediment cemented together (agglutinated), and in one genus of silica. "
http://en.wikipedia.org/wiki/Foraminifera

285 **Nautilus Shell Structure**: R. Velázquez-Castillo et al. Nanoscale characterization of nautilus shell structure: An example of natural self-assembly. *J. Mater. Res.*, Vol. 21, No. 6, Jun 2006

Early Fossil History: First evidence of calcareous shells/tests is ~650 Ma [Neoproterozoic] in the Beck Spring Dolomite. Death Valley shows a calcifying encrusting benthic multicellular algae probably a red algae. The first known animal skeleton [or shell] is the ~550 Ma metazoan **Cloudina**[286], arising just before the Cambrian period [542 Ma]—it resembles stacked ice-cream cones and was abundant 10-20 M.y. before the Cambrian. Many additional PreCambrian species have been recently discovered. The earliest Cambrian examples were **small shelly fossils**[287], having test sizes up to 1mm (Tommotian age) and including Mollusks and brachiopods. Some of the fossils could be armor-plate called **sclerites** arising from worms. Then the rapid Cambrian radiation[288] [or "explosion"] occurs and extent and sizes increase, Large animal fossils are found within 10 M.y. in the Early Cambrian, coral reefs by mid-Cambrian [onset 513 Ma].

A graph was shown of unknown origin plotting the number of clades of organisms having carbonate, phosphate, and silicate skeletons against Time in Ma, beginning at 580 Ma. The values rapidly increased from c. 560 Ma to about 500 Ma and then attain fairly stable plateaus.

Why was the Cambrian explosion of marine fauna so sudden? Theories: [see also more complete discussion of this topic later]
1) **Environmental changes**: O_2 rise, Phosphorus upwelling, continental shelf increased area from continental breakup
2) **Biotic innovation**: a new capability conferring survival advantage (such as teeth) leading to predation, resulting arms race, rapid evolution). This is more likely.

The spatial distribution of calcareous skeletons is determined by solubility of $CaCO_3$. It is less soluble in warm water and in more saturated solutions—thus mineralization is favored in warm tropical water such as where coral reefs are concentrated. Also, deeper water has higher solubility due to rising CO_2 levels, (especially below the carbonate compensation depth CCD at c. 3 km), so calcareous skeletons are harder to form at greater depths.

The proportion of $CaCO_3$ [?in sediments, prokaryotic versus eukaryotic?, biogenic versus abiotic?] doesn't change much between the Proterozoic and [early] Phanerozoic [c. 542 Ga], but the rate [proportion] changes from inorganic or microbial origin to predominantly eukaryote by the mid-

---

[286] **Cloudina**: "Cloudinids are an early metazoan family containing the genus Cloudina, which became extinct at the base of the Cambrian period. They formed millimetre-scale conical fossils consisting of calcareous tubes nested within one another... Cloudina varies in size from a diameter of 0.3 to 6.5 mm, and 8 to 150 mm in length. Fossils comprise a series of stacked vase-like calcite tubes, whose original mineralogy is unknown."
http://en.wikipedia.org/wiki/Cloudina
[287] **Small Shelly Fauna or Fossils**:
• "the name given to an obscure collection of small hard-shelled fossils found worldwide in beds a bit older than the earliest trilobites and archeocyathids from the Nekamit-Daldynian and Tommotian stages (Lower Cambrian). The start of the Cambrian period had classically been set at the first appearance of small shelly fossils. Workers in a remote part of Siberia found very small hard-shelled fossils in slightly older beds in the 1980s. Similar fossils were later found in corresponding beds in many other parts of the world.... Common practice is to include the small shelly fauna in the earliest Lower Cambrian. The fauna and its relationship to more conventional later faunas is still poorly understood."
http://en.wikipedia.org/wiki/Small_shelly_fauna
• "These [fossils] are especially common in the Lower Cambrian all over the world. Many different groups of animals are found in these: Molluscs, brachiopods, coeloscleritophorans (Chancellorids and Sachitids), spicules, arthropods among others."
http://en.wikipedia.org/wiki/Small_Shelly_Fossil
[288] **Cambrian Explosion**: "The Cambrian explosion or Cambrian radiation describes the geologically sudden appearance of hard-bodied animals in the fossil record, around 530 million years ago. This is accompanied by a profound diversification of life on Earth. Prior to around 580 million years ago, organisms were on the whole simple, comprised of individual cells occasionally organised into colonies. Over the subsequent 70-80 million years, the rate of evolution would accelerate by an order of magnitude, and the diversity of life would begin to resemble today's..."
http://en.wikipedia.org/wiki/Cambrian_explosion

Cambrian. Deposits [of $CaCO_3$] become thicker faster, and become more purely $CaCO_3$ due to less mixing with organic and other sedimentary materials. Thus the Cretaceous [145 Ga] is named after extensive beds of chalk[289] (calcium carbonate deposited by the shells of marine invertebrates, principally coccoliths from coccolithophores, in [offshore] ocean basins [with seafloors lying above the CCD]).[290]

Limestone and calcareous sediments are now being subducted at some locations. As these plates descend, they undergo metamorphic formation of silicates and release of CO_2, which eventually makes it way to the surface and thereby recycles some of the carbon.

2. Apatite (Calcium Phosphate) Biomineralization

[One form of] apatite is written $Ca_5(PO_4)_3OH$[291] [Apatite, at least the three most common forms, is often written as $Ca_5(PO4)_3(OH, F, Cl)$]. Microcrytalline apatite is called **collophane**.[292] If biogenic, apatite

---

[289] **Chalk Formation**:
• "As discussed in Chalk Facts by C. S. Harris and Scholle et al. (1983), the Chalk Formation consists mostly of coccolith biomicrite. A biomicrite is a limestone composed of fossil debris ("bio") and calcium carbonate mud ("micrite"). The majority of the fossil debris comprising this chalk consists of the microscopic plates, which are called **coccoliths**, of microscopic green algae known as **coccolithophores** [such as Emiliania huxleyi]. In addition to the coccoliths, the fossil debris includes a variable, but minor, percentage of the fragments of **foraminifera**, **ostracods**, and **mollusks**. The coccolithophores lived in the upper part of the water column. When they died, the microscopic calcium carbonate plates, which formed their shells settled downward through the ocean water and accumulated on the ocean bottom to form a thick layer of calcareous ooze, which eventually became the Chalk Formation"
http://en.wikipedia.org/wiki/Chalk_Formation
• "Unlike any other plant in the ocean, coccolithophores surround themselves with a microscopic plating made of limestone (calcite). These scales, known as **coccoliths**, are shaped like hubcaps and are only [0.003 mm] in diameter. What coccoliths lack in size they make up in volume. At any one time a single coccolithophore is attached to or surrounded by at least 30 scales. Additional coccoliths are dumped into the water when the coccolithophores multiply asexually, die or simply make too many scales. In areas with trillions of coccolithophores, the waters will turn an opaque turquoise from the dense cloud of coccoliths. Scientists estimate that the organisms dump more than 1.5 million tons (1.4 billion kilograms) of calcite a year, making them the **leading calcite producers** in the ocean."
http://eobglossary.gsfc.nasa.gov/Library/Coccolithophores/
• **Emiliania huxleyi**:
http://www.noc.soton.ac.uk/soes/staff/tt/eh/

[290] **Cretaceous chalk**: "The Cretaceous (from Latin creta meaning 'chalk') as a separate period was first defined by a Belgian geologist Jean d'Omalius d'Halloy in 1822, using strata in the Paris Basin and named for the extensive beds of chalk (calcium carbonate deposited by the shells of marine invertebrates, principally coccoliths), found in the upper Cretaceous of continental Europe and the British Isles (including the White Cliffs of Dover)."
http://en.wikipedia.org/wiki/Cretaceous

[291] **Biologic Apatite Composition**:
• "Apatite is a group of phosphate minerals, usually referring to hydroxylapatite [not hydroxyapatite], fluorapatite, and chlorapatite, named for high concentrations of OH-, F-, or Cl- ions, respectively, in the crystal. The formula of the admixture of the three most common endmembers is written as $Ca_5(PO4)_3(OH, F, Cl)$, and the formulae of the individual minerals are written as $Ca_5(PO_4)_3(OH)$, $Ca_5(PO_4)_3F$ and $Ca_5(PO_4)_3Cl$, respectively.
Apatite is one of few minerals that are produced and used by biological micro-environmental systems. **Hydroxylapatite** is the major component of **tooth enamel**. A relatively rare form of apatite in which most of the OH groups are absent and containing many carbonate and acid phosphate substitutions is a large component of **bone** material."
http://en.wikipedia.org/wiki/Apatite
• "The primary tissue of bone, osseous tissue, is a relatively hard and lightweight composite material, formed mostly of calcium phosphate in the chemical arrangement termed calcium hydroxylapatite."
http://en.wikipedia.org/wiki/Bone
• "Seventy percent of bone is made up of the inorganic mineral hydroxylapatite. [Carbonated calcium-deficient] hydroxylapatite is the main mineral of which dental enamel and dentin are comprised."

usually has carbonate substituted for some of the phosphate groups [called **apatite carbonate**[293]], allowing recognition of its biogenic origin. The Phosphorus P comes from weathering of igneous rocks—such as chlorapatites and fluorapatities in granite basalts—and is found in nature as **phosphate** PO_4. Organisms need lots of phosphate P to make DNA, ATP, bones and teeth, etc.—it is an essential nutrient. It is liberated by decay of organic matter, upwells, and precipitates with calcium inorganically. Phosphate is also found in dung and **coprolites** (such as Cambridge was built on and once mined), an important source of phosphate fertilizer, and phosphate-containing minerals and deposits are extensively mined. (Major sites[294] include Florida, Morocco, Egypt, certain islands, etc.)

This form of biomineralization is mainly used by vertebrates to form bones and teeth. Cells in the skeleton secrete the crystals often in concentric layers. Some crustaceans such as **lobsters**, **myriapods**, and the fossil **trilobites** secrete [as part of their **exoskeleton**] a mixed apatite calcite containing **cuticle**.[295] Some **brachiopods** have apatite shells, such as in the class Lingulata[296] [formerly classified as brachiopods but under class Inarticulata][297,298]]

---

http://en.wikipedia.org/wiki/Hydroxylapatite
• "Chemical analyses and spectroscopic studies show that biogenic apatite is **Ca-deficient**, **nonstoichiometric**, and **contains carbonate ions** in its structure…"
http://www.minsocam.org/MSA/AmMin/TOC/Articles_Free/2003/Shi_p1866-1871_03.pdf
• "A rough estimate yields an **OH**– content of human cortical bone of about **20% of the amount expected** in stoichiometric hydroxyapatite."
http://www.sciencemag.org/cgi/content/abstract/300/5622/1123
[292] **Collophane**: "A massive, cryptocrystalline, carbonate-containing variety of apatite and a principal source of phosphates for fertilizers. Also known as collophanite."
http://www.answers.com/topic/collophane?cat=technology
[293] **Apatite Carbonate**: "Biogenic apatite, the mineral in living vertebrates contain relatively high concentrations of carbonate, sodium, and other ions. During fossilization the bioapatite composition changes from a meta-stable carbonate hydroxylapatite to a thermodynamically stable Fluorapatite incorporating fluoride, Rare Earth Elements (REE) and other trace elements during diagenesis."
http://gsa.confex.com/gsa/2006NE/finalprogram/abstract_100326.htm
[294] **Sources of Mined Phosphate**:
• "The largest rock phosphate deposits in North America lie in the Bone Valley region of central Florida, United States, the Soda Springs region of Idaho, and the coast of North Carolina. Smaller deposits are located in Montana, Tennessee, Georgia, and South Carolina near Charleston along Ashley Phosphate road. The small island nation of Nauru and its neighbor Banaba Island, which used to have massive phosphate deposits of the best quality, have been mined excessively. Rock phosphate can also be found [in] Egypt, Israel, Morocco, Navassa Island, Tunisia, Togo, and Jordan [—these] have large phosphate mining industries as well."
http://en.wikipedia.org/wiki/Phosphate
• See also http://www.mineralszone.com/minerals/apatite-rock-phosphate.html
[295] **Exoskeleton Mineralization**: "In addition to the chitino-proteinaceous composite of the cuticle, many crustaceans, some myriapods and the extinct trilobites further impregnate the cuticle with mineral salts, above all calcium carbonate, which can make up up to 40% of the cuticle. This can lead to great mechanical strength."
http://en.wikipedia.org/wiki/Exoskeleton
[296] **Lingulata**: "Lingulata shells are composed of a combination of calcium phosphate, protein and chitin. This is unlike most other shelled marine animals, whose shells are made of calcium carbonate. The Lingulata are inarticulate brachiopods, so named for the simplicity of their hinge mechanism. This mechanism lacks teeth and is held together only by a complex musculature. Both valves are roughly symmetrical."
http://en.wikipedia.org/wiki/Lingulata
[297] **Inarticulata**: Inarticulata was historically defined as one of the two classes of the phylum Brachiopoda and referred to those having no hinge. The other class was Articulata, meaning articulated – having a hinge between the dorsal and ventral valves. These classifications have now been superseded, see brachiopod classification."
http://en.wikipedia.org/wiki/Inarticulata
[298] **Treatise on Invertebrate Paleontology**:
http://en.wikipedia.org/wiki/Treatise_on_Invertebrate_Paleontology

Apatite is poorly soluble compared to calcium carbonate, thus it is well preserved in fossils such as dinosaur bones and trilobites. Fossil **teeth** first appear [in the Middle Cambrian 540 Ga] with the **conodonts**[299] [a type of chordate of controversial classification]. Fish with **jaws and teeth** were abundant by the Devonian[300] [416 - 360 Ga]. **Bony fish** (Osteichthyes)[301], having endochondral mineralized bone replacement, were also abundant in the Devonian and Permian, though they may have arisen in the Silurian.

The availability of phosphate is a critical limiting nutrient in living organisms, limiting the degree to which organisms can proliferate and fill the biosphere. Phosphate can combine with aluminum in muddy deposits to form aluminophosphate minerals which are very insoluble (e.g., florencite, goyazite, gorceixite), forming, along with bones and coprolites, a "sink" of available phosphate.[302] There may have been much more available phosphate in the Cambrian, perhaps contributing to the Cambrian "explosion".

---

299 **Conodonts**:
• "Conodonts are extinct chordates that form the class Conodonta. For many years, conodonts were known only from enigmatic tooth-like microfossils, which despite their common occurrence were always found in isolation, and were not associated with any other fossil. These phosphatic microfossils, now termed **conodont elements** to avoid confusion ... are widely used in biostratigraphy; they are also used as paleothermometers, because phosphate undergoes a predictable series of color changes as it experiences higher temperatures. It was not until early 1980s that the conodont teeth were found in association with fossils of the host organism... Once thought to only exist on the millimetre scale, a well-preserved and unusually large genus, Promissum, was found in 1994. It's now widely agreed that conodonts bore large eyes, fins with fin rays, chevron-shaped muscles and a notochord. The latter three are characteristic features of the phylum Chordata (ie., the vertebrates), leading to their current classification.... The conodont animal is considered to have been a herbivore: despite their ferocious appearance, the "teeth" were probably used to filter out plankton and pass it down the throat... [They are known] in rocks dating from the **Cambrian** to the Late Triassic"
http://en.wikipedia.org/wiki/Conodonta
• "Euconodonts have long been an enigmatic group of fossil marine animals, represented by minute, comb-shaped or claw-shaped denticles - the 'conodonts' - which were widely used by stratigraphers for dating and correlating geological formations. They are known from the **Middle Cambrian** (540 million years) to the Late Triassic (230 million years). These denticles, which are made of calcium phosphate, like the vertebrate bones and teeth, have been variously referred to [as] annelids, arthropods, molluscs, chaetognaths, and even plants, although it has been sometimes suggested that they were fish teeth. The clue came in 1983 when the first articulated "conodont animal" was discovered in the Carboniferous of Scotland. Later, yet another "conodont animal" was found in the Ordovician of South Africa. Both forms show an elongated body, with imprints of chevron-shaped muscles, a trace of the notochord, large paired eyes, and a caudal fin strengthened by radials. The conodont organs (i.e. the denticles) are situated in the head, presumably at the entrance of the pharynx. Recent histological studies on the euconodonts have brought to light a variety of hard tissues which recall the enamel, dentine and bone of the vertebrates, but their homology with vertebrate tissues remains controversial."
http://tolweb.org/tree?group=Euconodonta&contgroup=Vertebrata
300 **Onset of Jawed Toothed Fish**:
• "The ostracoderms [jawless fish] were joined in the mid-Devonian [397 - 385 Ga] by the first **jawed fishes**, and were declining in diversity and were being out competed by the jawed fish in both the sea and fresh water, [and also by] the great armored placoderms, as well as the first sharks and ray-finned fish."
http://en.wikipedia.org/wiki/Devonian
• "After the appearance of jawed fish (placoderms, acanthodians, sharks, etc.) about 400 million years ago [in the Devonian], most ostracoderm species underwent a decline, and the last ostracoderms became extinct at the end of the Devonian period."
http://en.wikipedia.org/wiki/Ostracoderms
• "The most ancient types of sharks date back to 450 million years ago [Silurian period], and they are mostly known from their fossilized teeth. The most common, however, are from the Cenozoic Era (65 million years ago)."
http://en.wikipedia.org/wiki/Shark_teeth
301 **Osteichthyes (Bony Fish)**: http://en.wikipedia.org/wiki/Osteichthyes
302 **Aluminophosphate minerals as phosphate sink**:
http://earth.geology.yale.edu/~ajs/1996/06.1996.02Rasmussen.pdf [Birger Rasmussen, 1996]

3. Silica Biomineralization

Silicon containing biominerals appear as **quartz** (SiO_2, stable) or as **opal** (hydrous silica, $SiO_2 \cdot nH_2O$, unstable).[303] Opal dehydrates with time, turning into **cristobalite** over c. 100 M.y. at temperatures > 50 ºC. The oldest opal fossil is mid-Jurassic [175 - 161 Ma]. Quartz [silica] precipitates at hydrothermal vents abiotically [MCM: RB handout states "less soluble at high pH"—he probably means that the acidic vent fluid contains dissolved silica that precipitates when it mixes with less acidic or alkaline seawater. Silica solubility is also greater at higher temperatures and pressures, so cold seawater can cause it to precipitate.[304]] Cherts also occurred in the Proterozoic and late Archean by evaporation of seawater, when seawater was saturated with silica [and also formed by primary sedimentation and diagenesis], forming [fossil bearing] cherts and limestones.[305] [MCM: The Apex chert from Marble Bar is dated to 3.45 Ga, therefore in the Paleo-Archaean, but the presence of fossil life dating to that age is doubted by RB.] The banded iron formations contain inorganic [abiotic] chert [but whether all BIFs are abiogenic is controversial].

Since the Cambrian period began, most silica precipitation has been biogenic[306] by Eukaryotic extraction of silica from below saturation seawater—particularly by
1) sponges (quartz, opal)[307],
2) radiolarians (quartz [MCM: or opal[308] initially according to other sources, transforming by diagenesis to quartz]), and

---

303 **Opal**: "The mineraloid opal is amorphous $SiO_2 \cdot nH_2O$, hydrated silicon dioxide, the water content sometimes being as high as 20% but is usually between three and ten percent."
http://en.wikipedia.org/wiki/Opal

304 **Hydrothermal Vent Precipitation of Silica**: Regarding the "The Lost City" vent system described by Deborah Kelley's team: "A ledge or flange made of carbonate juts out from the side of a 160-foot chimney in the Lost City hydrothermal vent field. The chimney and flange are made of carbonate minerals and silica dissolved in 160 F fluids that flow out of the seafloor and then precipitate when the fluids hit the icy cold seawater... Perhaps most surprising is that the venting structures are composed of carbonate minerals and silica, in contrast to most other mid-ocean ridge hot spring deposits, which are formed by iron and sulfur-based minerals. The low-temperature hydrothermal fluids may have unusual chemistries because they emanate from mantle rocks."
http://www.washington.edu/newsroom/news/2000archive/12-00archive/k121200.html

305 **Chert Mechanisms of Formation**: "Chert outcrops as oval to irregular nodules in greensand, limestone, chalk, and dolostone formations as a replacement mineral, where it is formed as a result of **diagenesis**. It also occurs in thin beds, when it is a **primary deposit**. Thick beds of chert occur in deep geosynclinal deposits. These thickly bedded cherts include the novaculite of the Ouachita Mountains of Arkansas, Oklahoma, and similar occurrences in Texas in the United States. The **banded iron formations** of Precambrian age are composed of alternating layers of chert and iron oxides."
http://en.wikipedia.org/wiki/Chert

306 **Modern Sources of Biogenic Silica**: "...The most abundant siliceous organisms in suspension are **diatomaceous algae**, the main producers of oceanic organic matter... The siliceous suspension belts coincide with the diatom suspension belts, which points to the dominant role of diatoms. [See map showing annual production of biogenic silica in the plankton of the world.]

The second major producers of suspended amorphous silica are **radiolarians**. They occur from the Arctic to the Antarctic, being most abundant in the equatorial zone...

Microscopic examination of suspensions also shows that the basic role in modern silica accumulation belongs to diatom algae, which comprise more than 70%, and sometimes over 90% of the suspended silica. Radiolarians are second in importance to diatoms. **Silicoflagellates** ... are the third most important silica-formers..."
http://www.radiolaria.org/index.htm?division=63

307 **Sponge silica and opal**: *Geology*; May 2003; v. 31; no. 5; p. 423-426, found at http://geology.geoscienceworld.org/cgi/content/abstract/31/5/423

308 **Radiolarian opal**:
• *Radiolarians in the Sedimentary Record.* By Patrick De Wever et al p. 55
• Emile A. Pessagno, Jr., R. Leo Newport. "A Technique for Extracting Radiolaria from Radiolarian Cherts" *Micropaleontology*, Vol. 18, No. 2 (Apr., 1972), pp. 231-234

3) diatoms (opal, since Jurassic times a major former of **frustules** [MCM: siliceous skeleton or test] of opaline silica).

Modern chert formation begins with deposition in cold deep water, often below the carbonate compensation depth CCD [so carbonate shells are dissolved], in lakes with abundant diatoms or in seawater, forming **diatomites** [**diatomaceous earth**]. Dissolved silica cements together the silica skeleton deposits.[309] There has been a shift in the location of chert deposition from shallow water to the deep sea since the onset of the Phanerozoic. This shift does not affect the size of the sedimentary silicon reserve. "However, dissolved silica concentration in seawater [is] markedly different, due to biological demand keeping it well below saturation during Phanerozoic."

Early Eukaryote Evolution

[per RB and supplemented]
It is bogus to presume "anthropic superiority", that eukaryotes represent a recently evolved and the most superior evolutionary branch [or that humans represent an evolutionary apex]. In fact, the cladistics data [SSU rRNA etc.] suggest that eukaryotes branched at the earliest [or one of the earliest] branching points of the Tree of Life. [This was previously discussed—the first node gives rise to a common root for Archaea + Eukarya on one side, and the bacteria on the other.]

Time of Origin: The key biomarker for eukarya are steranes in fossils (derived from sterols in living organisms). These are almost exclusively found in eukaryotes and are a key component of the cell membranes. (A few bacteria have simple sterols,[310] but probably not used in their cell membranes [nor are they related to fossil steranes].) This biomarker has been found with certainty as long ago as **2.7 Ga**[311], and possibly as long ago as **3.2 Ga** [source of data not stated]. There are four major evolutionary steps or innovations in early eukaryote evolution[312]

1. Phagocytosis

The development of the flexible cell membrane capable of **phagocytosis** is critical. Phagocytosis is a key feature that may precede other characteristics mentioned below. Phagocytosis consists of **pseudopodium** formation and/or **invagination**, membrane enclosure of the target prey, and **reattachment** (fusion) of the membrane opening and pinching off to form an internalized **phagosome**. This process is made possible by the presence of the lipid bilayer stabilized [or strengthened] by sterols.[313] Prokaryotic microbes have cell membranes that cannot do this, so must take up nutrients

---

309 **Silica oozes**: http://www.geol.umd.edu/~jmerck/geol100/lectures/31.html
310 **Sterols in Bacteria**: "Recently we detected sterol biosynthesis within the bacterial species **Gemmata obscuriglobus**, a member of the Planctomycetales. The sterols produced by Gemmata are structurally the most "primitive" set synthesized by any known organism. These bacterial sterols cannot explain the presence of complex steranes in ancient rocks."
A. Pearson, J. J. Brocks, And M. Budin (2003) Phylogenetic and biochemical evidence for sterol biosynthesis in the bacterium, Gemmata obscuriglobus. *Proc. Natl. Acad. Sci.* 100, 15,352-15,357.
311 **Earliest Eukaryotes**:
"Molecular fossils of biological lipids are preserved in 2700-million-year-old shales from the Pilbara Craton, Australia... The presence of steranes, particularly cholestane and its 28- to 30-carbon analogs, provides persuasive evidence for the existence of eukaryotes 500 million to 1 billion years before the extant fossil record indicates that the lineage arose."
Brocks JJ, Logan GA, Buick R, Summons RE. "Archean molecular fossils and the early rise of eukaryotes" *Science.* 1999 Aug 13;285(5430):1033-6. Accessed at http://www.ncbi.nlm.nih.gov/
312 **Eukaryotic Evolution**: Good review article of current conceptual and cladistic difficulties.
T. Martin Embley & William Martin. "Eukaryotic evolution, changes and challenges". *Nature* Vol 440 30 March 2006 doi:10.1038/nature04546.
313 **Role of Sterols in Cell Membrane**: "[Cholesterol molecules] immobilize the first few hydrocarbon groups of the phospholipid molecules. This makes the lipid bilayer less deformable and decreases its permeability to small water-soluble molecules. Without cholesterol (such as in a bacterium) a cell would need a cell wall…. Cholesterol [also] prevents crystallization of hydrocarbons and phase shifts in the membrane."
http://cellbio.utmb.edu/cellbio/membrane_intro.htm#Cholesterol

by absorption of single molecules, whereas eukaryotic cells can take in “solid food” in larger amounts [at a single gulp]. This capability leads to the possibility of eukaryotic cells being **larger in size**, since they can take in larger amounts of food more efficiently, and do not depend on slow molecular absorption. Eukaryote cells can be huge—e.g., the ostrich egg [or ovum] is one large cell. They can therefore store more food and go longer between “meals”.

Phagocytosis also makes possible ingestion of other organisms that may become endosymbionts. This key feature—phagocytosis—may have evolved before the **membrane-bound nucleus**, which itself resembles an endosymbiont.

2. Endosymbiosis

This second major evolutionary process requires phagocytosis. There are 2 obvious **organelles** that are thought to be endosymbionts based on their residual DNA (“**DNA phylogeny**”): **mitochondria** (for aerobic cell respiration, and derived from proteobacteria) and **plastids** especially **chloroplasts** (the latter are for photosynthesis, derived from cyanobacteria). Some, particularly biologist Lynn Margulis[314], have postulated that all organelles—such as flagellae, cilia, and nuclei—are endosymbionts. (She was on *Cosmos*, and the first wife of Carl Sagan.) However, there is little support for this more extreme position—discrete DNA evidence is lacking. Is the nucleus itself derived from a symbiotic membrane-bound organism? [Answer is unclear. If it is, the nuclear membrane is the only remaining eukaryotic feature, but see several possible theories in article here.[315]]

Plastids

Plastids are widespread in many groups [data including in a diagram not fully captured and classifications vary]:

- **Chlorophytes** (green algae), **Golden-brown algae** (chrysophytes and synurophytes), **Yellow-green algae** (xanthophytes), **Ochrophyta** (yellow green or brown algae and golden brown algae), and **Coccolithophores** (a kind of haptophytes) all have chloroplasts [some data missed]
- **Phaeophyta** (**brown algae**) have chloroplasts surrounded by four membranes.[316]
- **Euglenas** have chloroplasts.
- **Green plants** have chloroplasts.
- **Rhodophytes** (red algae) have **rhodoplasts** (**chromatophores**) which are photosynthetic and impart the red color
- **Glaucophytes** have photosynthetic **cyanelles**.[317]
- **Cryptomonads** are flagellates, most of which have chloroplasts or **leucoplasts[318]** (non-pigmented plastids found in various organisms).

---

[314] **Lynn Margulis**: http://en.wikipedia.org/wiki/Lynn_Margulis
[315] **Theories of Cell Nucleus Origin**:
(1) “Syntrophic model proposes that a symbiotic relationship between the archaea and bacteria created the nucleus-containing eukaryotic cell.”
(2) “Proto-eukaryotic cells evolved from bacteria without an endosymbiotic stage.”
(3) “Viral eukaryogenesis, posits that the membrane-bound nucleus ... originated from the infection of a prokaryote by a virus.”
(4) “Exomembrane hypothesis, suggests that the nucleus instead originated from a single ancestral cell that evolved a second exterior cell membrane; the interior membrane enclosing the original cell then became the nuclear membrane...”
http://en.wikipedia.org/wiki/Cell_nucleus#Evolution
[316] **Brown algae**: “Most brown algae contain the pigment fucoxanthin, which is responsible for the distinctive greenish-brown color that gives them their name”
http://en.wikipedia.org/wiki/Brown_algae
[317] **Cyanelle**: “Cyanelles are the primitive plastids of glaucocystophyte algae and are distinguished by the possession of a peptidoglycan wall. ”
http://www.ria.ie/cgi-bin/ria/papers/100023.pdf [2002]
[318] **Leucoplasts**: “They may become specialized for bulk storage of starch, lipid or protein and are then known as amyloplasts, elaioplasts, or proteinoplasts respectively. However, in many cell types, leucoplasts do not have a major storage function and are present to provide a wide range of essential biosynthetic functions, including the synthesis of fatty acids, many amino acids, and tetrapyrrole

- **Chromoplasts** (plastids responsible for pigment synthesis and storage) are found in fruit and floral petals, etc., and impart the characteristic colors.

Secondary or serial endosymbiosis is apparent when multiple concentric layers of membranes are present [as previously discussed]. For example, some **dinoflagellates** appear to have tertiary endosymbionts. The evidence of endosymbiosis keeps reappearing and turning up like stolen jewels. Complex diagram[319] showed proposed serial endosymbiosis steps: Eukaryote engulfs Cyanobacterium in primary endosymbiosis; this branches to:
(1) Chlorophyta, with secondary endosymbiosis forming **Chlorarachniophyta**, **Euglenophyta**, etc., and on to tertiary **Haptophyta** and **Dinophyta**
(2) Rhodophyta, with secondary or tertiary endosymbiosis forming Cryptophyta, **Heterokontophyta**, Haptophyta, **Apicomplexa**...

Mitochondria

These are the other major endosymbiotic organelle. The endosymbiotic event appears to have occurred only once in evolutionary history. All mitochondria are closely related, and derived from "same proteobacterium". Some of the DNA [from the putative proteobacteria] has migrated to the host cell nucleus [where it plays an essential role in the synthesis of the mitochondrion].

Mitochondria perform aerobic respiration ($CH_2O + O_2 \rightarrow CO_2 + H_2O$), yielding more energy per mole of organic material respired than any other process. The first eukaryotes could probably only ferment organic matter anaerobically. Then the more efficient aerobic metabolism was added by addition of these endosymbionts.

Some eukaryotes (which were once thought to be primitive and arising early in the eukaryote branch) appear to not have mitochondria (previously termed "**amitchondriate**"), but on further examination some have been found to have **mitosomes**[320] or **hydrogenosomes**[321] (which are degenerate forms of mitochondria), or else they are parasitic and have reverted to purely anaerobic metabolism in environments lacking oxygen. (In such environments, mitochondria would be of no benefit.) Such eukaryotes and their mitochondrial forms include:
1) parasites which can infect humans such as **trichomonads** (hydrogenosomes), **microsporidia** (lack mitochondria but have mitosomes, and include the potential human pathogen **Enterocytozoon**), **Entamoebae** (mitosomes), and **Giardia** (mitosomes). **Cryptosporidium**, another human pathogen, has mitosomes or "remnant" mitochondria that lack DNA[322]:
2) **Oxymonads** (have ?hydrogenosomes, live in the guts of wood-eating insects such as termites), and **anaerobic ciliates** (hydrogenosomes).

The origin of eukaryotes might have been an endosymbiotic event. The **Chimaera hypothesis** proposes formation of a chimaera (chimera) consisting of the union of an Archaean methanogen and a hydrogen [?producing] proteobacterium. However, neither has a sterol membrane, and it is unclear how this endosymbiosis could take place. But eukaryotes have genes derived from both groups—this

---

compounds such as haem. [heme?]"
http://en.wikipedia.org/wiki/Leucoplast
[319] **Serial Endosymbiosis**: Charles F. Delwiche 1999, "Tracing the Thread of Plastid Diversity Through the Tapestry of Life" *The American Naturalist* 1999.
[320] **Mitosome**: "an organelle found in some unicellular eukaryotic organisms...The mitosome has been detected only in anaerobic or microaerophilic organisms which do not have mitochondria... The mitosome was first described in Entamoeba histolytica, an intestinal parasite of humans. Mitosomes have also been identified in several species of Microsporidia and in Giardia intestinalis... Mitosomes are almost certainly derived from mitochondria. Like mitochondria, they have a double-wall membrane... A number of proteins associated with mitosomes have been shown to be closely related to those of mitochondria... Unlike mitochondria, mitosomes do not have genes... The genes for mitosomal components are contained in the nuclear genome."
http://en.wikipedia.org/wiki/Mitosome
[321] **Hydrogenosome**: "A hydrogenosome is a membrane-enclosed organelle of ciliates, trichomonads and fungi. It produces molecular hydrogen and ATP. This organelle is thought to have most likely evolved from mitochondria."
http://en.wikipedia.org/wiki/Hydrogenosome
[322] **Cryptosporidium**: http://en.wikipedia.org/wiki/Cryptosporidium

DNA could be ancestral in origin or partly derived from lateral gene transfer. A diagram projected of unknown source showed that for some genes (such as for argininosuccinate synthase), bacteria and eukaryota are more closely related than archaea, whereas for other genes (such as for adenylosuccinate synthase), archaea and eukaryota are more closely related than bacteria. A complex slide on the chimeric hypothesis was projected[323] that illustrates "models that propose the origin of a nucleus-bearing but amitochondriate cell first, followed by the acquisition of mitochondria in a eukaryotic host."

3. Multicellularity

This is the third major event in the evolution of eukaryotes. It allows occupation of a much more extensive habitat. Organisms can grow larger or higher to move into less crowded regions and/or exploit limited resources (such as light or water or other environmental gradients) more effectively. With **anchorages**, they can stay in a favorable habitat more effectively despite currents, etc. Multicellularity also sets the stage for the possibility of sex, since the latter requires differentiated cells and the ability to recognize self versus non-self (different) cells. (Breakdown of this capability can lead to cancer or autoimmune disorders.) Multicellularity also makes feasible the ability to control cell division for regular growth.

Some cyanobacteria are partly multicellular—they form multicellular filaments and exhibit a degree of cellular differentiation with heterocysts, but the cells in general are simply cloned and are not substantially differentiated. No archaeans are multicellular. The small genome of prokaryotes prevents differentiation into tissues. Similar prokaryote cells may group together to form 2-dimensional sheets (**tissues**) which perform simple functions, but they certainly cannot form **organs** (3-dimensional structures made of varying cells and capable of performing complex functions). Prokaryotes do not exhibit true sexual reproduction, whereas multicellular organisms can have specialized sex cells which allow sexual reproduction.

Grypania spiralis:[324] is the first [possibly] multicellular [possibly] eukaryote known. It makes a large coiled spiral, the size of a penny. Fossil evidence dates to 1.87 Ga Minnesota, but these cells do not

---

[323] **Eukaryotic Evolution and Chimaeral Hypothesis**: Figure 4 of
T. Martin Embley & William Martin. "Eukaryotic evolution, changes and challenges". *Nature* Vol 440 30 March 2006 doi:10.1038/nature04546.

[324] **Grypania spiralis and the Onset of Multicellularity**:
• "The oldest generally acknowledged carbonaceous compression is Grypania spiralis from the 1874±9 Ma Negaunee Iron-Formation, Michigan... However, the taxonomic affinity of Grypania is still in dispute... In general, Paleoproterozoic carbonaceous compressions are the simplest in morphology (filamentous, circular, or elongate; Grypania is an exception—it has a corkscrew shape)."
D.M. Lamb, S.M. Awramik, S. Zhu, "Paleoproterozoic Compression-Like Structures From The Changzhougou Formation, China: Eukaryotes Or Clasts?" *Precambrian Research*. 2007. Accessed at http://www.geol.ucsb.edu/faculty/awramik/pubs/LAMB07XX.pdf
• "A common palaeontological interpretation of the fossil record suggests that eukaryotes originated about 2000 million years ago... This view is based on the presence of some putative eukaryotic fossils, including the ca 1850 Myr old spirally coiled 'alga' Grypania (Hoffman 1987) and large acritarchs from the 1800–1900 Myr old Chuanlinggou Formation (Zhang 1986)... However, neither Grypania nor such [sterane] biomarkers can be unequivocally excluded from being of bacterial origin. A critical reassessment of these early fossils led Cavalier-Smith (2002a,b) to propose that eukaryotes originated only about 850 Myr ago, i.e. just before the Cryogenian glaciations..."
• Cédric Berney and Jan Pawlowski. "A molecular time-scale for eukaryote evolution recalibrated with the continuous microfossil record". *Proc Biol Sci.* 2006 August 7; 273(1596): 1867–1872. at http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1634798#bib20
"An important evolutionary innovation was multicellularity. The oldest known possible multicellular eukaryote is Grypania spiralis, a coiled, ribbon-like fossil two millimeters wide and over ten centimeters long. It looks very much like a coiled multicellular alga and has been described from banded iron formations in Michigan 2.1 billion years old. Grypania may not be a eukaryote, but another, unrelated colonial eukaryote, **Horodyskia**, is known from sedimentary rocks dated at **1.5** billion years in western North America and from rocks more than 1 billion years old in Western Australia... The earliest known occurrence of multicellular animals is the **Ediacaran fauna**, named for the Ediacaran hills of South Australia. Some of these Ediacaran animals resemble modern jellyfish

show differentiation and not unequivocally multicellular at that time, might be cyanobacterial colony. At 1.4 Ga India, there are clearly well-preserved [possibly] multicellular specimens [this seems to be somewhat in dispute]. Found in India, Minnesota [also Michigan, Montana]. Classification of Grypania remains uncertain.

Acritarchs: [see previous discussion; some data presented here was missed] are **organic walled** [unmineralized] microfossils [made of kerogen] c. 2 mm of unknown origin.[325] Appear 1.7 - 1.4 Ga [early to mid Proterozoic] as large ≤2 mm complex structures, of unknown origin—these earliest specimens are not unequivocally multicellular or eukaryotic. By 1.4 - 0.7 Ga [mid to late Proterozoic], **spiny ("acanthomorphic") acritarchs** appear, possibly representing multicellular fungi (such as **Tappania plana**)—some may be resting cysts of algae. The "spines" resemble the hyphae of fungi. Some believe that the spines would not be possible without a eukaryotic cytoskeleton.[326] By 0.7 Ga, **vase-shaped acritarchs** measuring c. 0.1 mm appear which closely resemble tests of **testate ameba** (unicellular protists)—they are clearly related to modern extant eukaryotes. These were found in the Grand Canyon.[327] Acritarchs may or may not represent eukaryotes.

Bangiomorpha: A fossil from Canada 1.2 Ga, almost identical in appearance to the modern extant red alga (Rhodophyta), **Bangia**.[328] Bangia is a multicellular, filamentous red alga, common in our Puget

---

and segmented worms, found in great numbers in the seas today. Others are unlike any known organisms and cannot be classified with certainty. All these early creatures lack the rigid, supporting skeletons and protective shells that characterize the first fossils of the Cambrian Period."
http://paleobiology.si.edu/geotime/main/htmlVersion/proterozoic3.html
• "Grypania spiralis was a coiled, spaghetti-like organism up to half a metre in length found in ~1300 Ma shales and slates from Montana, China and India. It is not known for certain what kind of organism this fossil represents, to which (if any) of the moden kingdoms it is most closely related, nor even if it was a large unicell – perhaps with many nuclei – or multicellular."
http://www.peripatus.gen.nz/paleontology/MaiLinEvo.html
• "Grypania is an early fossil tube from the Paleoproterozoic Era. The organism could possibly be a giant bacterium or unicellular algae. Grypania fossils start appearing from 2 bya in the Precambrian or more exactly the early Paleoproterozoic period. Grypania reproduced asexually."
http://en.wikipedia.org/wiki/Grypania
[325] **Acritarchs**: An extensive discussion with good microphotographs.
http://www.palaeos.com/Proterozoic/Proterozoic.htm
[326] **Spiny acritarchs**: "By the early Mesoproterozoic (Calymmian), the evidence for a eukaryotic grade of organization becomes more definite. This judgment is based on: "(1) wall structure and surface ornamentation (2) processes that extend from vesicle walls (3) excystment structures (openings through which cysts liberate their cellular contents) (4) wall ultrastructure and (5) wall chemistry." Javaux et al. (2004). In particular, large cells with processes extending beyond the wall (i.e. acanthomorphic acritarchs) are thought to be impossible without a eukaryotic cytoskeleton. "
http://www.palaeos.com/Proterozoic/Proterozoic.htm
[327] **Vase-shaped acritarchs**: Susannah M. Porter; Andrew H. Knoll. "Testate Amoebae in the Neoproterozoic Era: Evidence from Vase-Shaped Microfossils in the Chuar Group, Grand Canyon" *Paleobiology*, Vol. 26, No. 3. (Summer, 2000), pp. 360-385.
[328] **Bangiomorpha**:
• "Differential spore/gamete formation shows **Bangiomorpha pubescens** to have been sexually reproducing, the oldest reported occurrence in the fossil record. Sex was critical for the subsequent success of eukaryotes, not so much for the advantages of genetic recombination, but because it allowed for complex multicellularity. The selective advantages of complex multicellularity are considered sufficient for it to have arisen immediately following the appearance of sexual reproduction. As such, the most reliable proxy for the first appearance of sex will be the first stratigraphic occurrence of complex multicellularity.

Bangiomorpha pubescens is the first occurrence of complex multicellularity in the fossil record. A differentiated basal holdfast structure allowed for positive substrate attachment and thus the selective advantages of vertical orientation; i.e., an early example of ecological tiering. More generally, eukaryotic multicellularity is the innovation that established organismal morphology as a significant factor in the evolutionary process. As complex eukaryotes modified, and created entirely novel, environments, their inherent capacity for reciprocal morphological adaptation, gave rise to the "biological environment" of directional evolution and "progress." The evolution of sex, as a proximal cause of complex multicellularity, may thus account for the Mesoproterozoic/Neoproterozoic radiation

Sound area. They have cross-sections like the cross-section of an orange, and holdfasts, and at the end of the filament is a sporangium with spore-forming sex cells. [Similar structures are seen in Bangiomorpha.] Bangia has a complex life cycle on intertidal rocks. Can grow above mobile sediments to get more light—they represent the first evidence for this **tiering** behavior.[329]

4. Sexuality

[per RB and supplemented]
Sexual reproduction[330] consists of the following cellular mechanisms [This is a brief outline, and substantial variants exist in certain plants, fungi, and protists, etc., so that not all possibilities have been included.]:

Cellular Mechanisms Of Sexual Reproduction:

- **Somatic cells:** are the usual non-gamete cells in the body. They can reproduce by the cell division process called **mitosis**, which produces 2 cloned daughter somatic cells having the same number of chromosomes as the parent. They are usually **diploid** (sometimes **polyploid**), meaning that they have 2 (sometimes more) chromosomes of each type. Human somatic cells are usually **diploid—**the chromosomes are **paired** (each chromosome of a related pair is termed a **homologous** chromosome), though only one [gene] of the pair is usually expressed. Each of the paired chromosomes has 2 strands called **chromatids** which are linked by a centromere and have identical genetic information (the pairing of identical chromatids is not the same as the ploidy representing the pairing of homologous nonidentical chromosomes). In normal human somatic cells, there are 46 chromosomes, 23 pairs of homologous chromosomes (thus the somatic cell contains 92 chromatids, termed “4N”, seen discretely in anaphase 2 of meiosis).
- **Meiosis**:[331] In this process, (usually) **haploid gametes** are created from diploid germ cells. Gametes have (usually) half the number of chromosomes as in somatic cells. (In humans, there are 23 chromosomes in each gamete, each with only one chromatid, termed “1N”—the 23 chromatids can be seen immediately after meiosis.) The gametes are usually **male** (**spermatozoa** or **microspores**) and **female** (**ova** or **megaspores**), but may in some organisms be quite similar or identical in form. The gamete can end up with any combination of paternal or maternal chromosomes[332]—in humans there are 2^{23} possible combinations of how homologous chromosomes pass to a gamete. In addition, **chromosome crossing** or **chromosomal crossover**[333] usually occurs during meiosis between 2 non-sister and thus non-identical but homologous paired chromatids.[334] This assures a greater mixing of the genes with respect to

---

of eukaryotes.”
http://paleobiol.geoscienceworld.org/cgi/content/abstract/26/3/386
• “The oldest fossil identified as a red alga is also the oldest fossil eukaryote that belongs to a specific modern taxon. Bangiomorpha pubescens, a multicellular fossil from arctic Canada, strongly resembles the modern red alga Bangia despite occurring in rocks dating to 1200 million years ago”
http://en.wikipedia.org/wiki/Red_algae
[329] **Tiering**: “the height above or depths below the sediment-water interface at which animals live.” *PB2001* p. 432
[330] **Sexual Reproduction**: http://en.wikipedia.org/wiki/Sexual_reproduction
[331] **Meiosis**: http://en.wikipedia.org/wiki/Meiosis
Chromatids: http://en.wikipedia.org/wiki/Chromatids
[332] **Independent Assortment of Chromosomes**:
http://en.wikipedia.org/wiki/Independent_assortment
[333] **Chromosomal Crossover**: “Chromosomal crossover (or crossing over) is the process by which two chromosomes, paired up during prophase 1 of meiosis, exchange some portion of their DNA... During prophase I the four available chromatids are in tight formation with one another. While in this formation, homologous sites on two chromatids can mesh with one another, and may exchange genetic information.... The result of this process is an exchange of genes, called genetic recombination... Meiotic recombination allows a more independent selection between the two alleles that occupy the positions of single genes, as recombination shuffles the allele content between sister chromatids.”
http://en.wikipedia.org/wiki/Chromosomal_crossover
[334] **Chromosomal Crossover Between Nonsister Homologous Chromatids (diagram)**:
http://www.web-books.com/MoBio/Free/Ch8D2.htm

parental origin in each gamete, and ultimately contributes to even greater diversity through **genetic recombination**.
- **Fertilization**: Two gametes—one of each of the 2 types (opposite sexes)—fuse to produce a diploid **zygote** that subsequently divides and becomes the progeny organism.

Some organisms (plants, fungi, protists etc.) make use of **Alternation of Generations**,[335] which promotes species survival in varying environments. The two phases consist of:
- a free-living organism or **gametophyte[336]**, which is genetically haploid, and
- a **sporophyte**, which is genetically diploid.

Benefits Of Sexual Reproduction:
- **Promotes Rapid Diversification Through Increased Genetic Variation**: Sex increases the potential **evolutionary rate** by causing a shuffling of genes with every new generation (the "poker game of life"). In contrast, asexual species must depend on the much less frequent rate of random mutations (or have extremely rapid rates of reproduction) to create genetic diversity within their species. Although sex comes at a price for the individual organism (only 1/2 of individuals can actually bear offspring, and energy is spent finding and winning mates, etc.), the greater diversity in the species increases the chances of successful adaptation—by at least some members of a species—to new or unfavorable environments. Rapid changes in diversity may help to compete against rapidly changing threats, such as a varying exposures to a range of parasites. A diversified species may be able to extract food more completely from the environment than a set of cloned organisms, because each organism might adapt to a slightly different niche. The process of Alternation of Generations mentioned above may add survival value to a species.
- **Genetic Repair**: Provides a means for removing bad mutations and deleterious genes. Recombination of chromosomes and genes confers the possibility of reconstituting individuals lacking a particular deleterious mutation, even though one of the parents may carry the deleterious gene mutation. Moreover, some organisms will end up with a statistical lower combination of multiple mildly deleterious genes, the composite result being a greater survivability compared to individuals with more of these mildly deleterious genes.
- **Species Differentiation**: Sex is integral to the segregation of organisms into distinct **species** consisting of similar organisms that can interbreed.
- **Multicellularity**: Sex is needed to maintain multicellularity over long periods of time. Without sex, there are too many bad mutations which accumulate and cannot be purged.

Sexual differentiation is first seen with **Bangiomorpha** at 1.2 Ga. At the end of its filament is a spore forming sporangium which produces many gametes. After Bangiomorpha, we see a rapid radiation in multicellular eukaryotes over the next 400 M.y. probably due to sexuality. By 750 Ma, brown and green algae are seen differing in size, shape, and behavior. **Proterocladus**[337] is a 750 Ma green alga like modern **Cladophora**.

---

[335] **Alternation of Generations**:
• Thomas N. Taylor, Hans Kerp, and Hagen Hass. "Life history biology of early land plants: Deciphering the gametophyte phase" *PNAS* April 19, 2005 Vol. 102 No. 16 accessed at http://www.pnas.org/cgi/reprint/102/16/5892.pdf
• See also http://en.wikipedia.org/wiki/Alternation_of_generations

[336] **Gametophyte**: "In plants that undergo alternation of generations, a **gametophyte** is the structure, or phase of life, that contains only half of the total complement of chromosomes:
—The **sporophyte** produces spores, in a process called meiosis. These spores develop into a gametophyte. These spores and the resulting gametophyte have only half of the total complement of chromosomes.
—The gametophyte produces male or female **gametes** (or both), in a process called **mitosis**. The fusion of male and female gametes produces a **zygote** which develops into the **sporophyte**.
In mosses (bryophytes) the gametophyte is the commonly known phase of the plant... In most other plants the gametophyte is very small (as in ferns) or even reduced as in flowering plants (angiosperms), where the female form (**ovule**) is known as a **megagametophyte** and the male form (**pollen**) is called a **microgametophyte**."
http://en.wikipedia.org/wiki/Gametophyte

[337] **Proterocladus**: Cédric Berney and Jan Pawlowski. "A molecular time-scale for eukaryote evolution recalibrated with the continuous microfossil record". *Proc Biol Sci.* 2006 August 7; 273(1596): 1867–1872. at http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1634798#bib20

Sex allows morphology to dominate over metabolism in evolution. [MCM: This is a confusing statement, and might seem to apply better to other eukaryotic features named above which allow cells to be larger and more specialized. However, the rapid evolution conferred by sexual reproduction may have led to more rapid beneficial morphological changes.]

Possible Environmental Constraints On Eukaryotic Development

[per RB and supplemented, this material was presented very rapidly and some data missed.]

1. Oxygen

Some O_2 is needed—at least c. 1% of Present Atmospheric Level (PAL)—in surface water and the photic zone for sterol synthesis to take place in eukaryotes. This level has existed probably since the onset of photosynthesis in the Archean. The multicellular radiation coincides with the late c. 800 Ma O_2 rise to greater than 10% PAL based on $\delta^{34}S$ data. Greater than 10% PAL O_2 is needed for survival of [aerobic eukaryotic] organisms having **organs**, otherwise the [concentration and] diffusion rate of oxygen are too low to oxygenate these thick tissues. [A complex diagram was shown which I could not read or capture, dealing with evolution of oxygen levels in Archean, Mesoproterozoic, and Phanerozoic times. See here[338] for a simpler diagram of hypothetical O_2 evolution.]

2. Canfield Ocean

Was animal evolution inhibited in Mesoproterozoic (1850 - 1250 Ma) due to [anoxic conditions] and toxic H_2S [sulfidic environment] in deep ocean? A diagram was shown illustrating ocean levels of Fe and Mo in the ocean water column in Archean, Meso-Proterozoic (1850 - 1250 Ma), and Phanerozoic times. [See Canfield and RB articles[339]]

---

[338] **Oxygen Evolution**: “While photosynthetic life reduced the carbon dioxide content of the atmosphere, it also started to produce oxygen. The oxygen did not build up in the atmosphere for a long time, since it was absorbed by rocks that could be easily oxidized (rusted). To this day, most of the oxygen produced over time is locked up in the ancient "banded rock" and "red bed" rock formations found in ancient sedimentary rock. It was not until ~1 billion years ago that the reservoirs of oxidizable rock became saturated and the free oxygen stayed in the air.”
http://www.globalchange.umich.edu/globalchange1/current/lectures/samson/evolution_atm/

[339] **Canfield Ocean**:
• “In the first half of Earth history, ~4.5 to 2.3 billion years (Ga) ago, the world's oceans and atmosphere were almost entirely devoid of oxygen. Surprisingly, for the following interval of 1.5 billion years, the state of the oceans remains mysterious... However, recent hypotheses published in Nature and Science (Anbar and Knoll, 2002; Canfield, 1998) have suggested that ... the oceans were widely oxygen-deficient and partly euxinic (anoxic and sulphidic) well into the Neoproterozoic (1.0 to 0.54 Ga). If the world oceans really were anoxic and sulphidic in Earth's middle age (~1.8 – 0.8 Ga), then our understanding of more than 20% of the planet's history would radically change; textbooks would have to be rewritten.... Conclusive evidence for either scenario - mostly oxygenated or mostly euxinic - is still missing.”
http://shrimp.anu.edu.au/people/jjb/Res%20Canfield%20Ocean_frame.html
• “Because animals require oxygen, an increase in late-Neoproterozoic oxygen concentrations has been suggested as a stimulus for their evolution. The iron content of deep-sea sediments shows that the deep ocean was anoxic and ferruginous before and during the Gaskiers glaciation 580 million years ago and that it became oxic afterward. The first known members of the Ediacara biota arose shortly after the Gaskiers glaciation, suggesting a causal link between their evolution and this oxygenation event. A prolonged stable oxic environment may have permitted the emergence of bilateral motile animals some 25 million years later.”
Don E. Canfield, Simon W. Poulton, Guy M. Narbonne. Late-Neoproterozoic Deep-Ocean Oxygenation and the Rise of Animal Life. January 2007 Vol 315 Science WWW.Sciencemag.Org
• See also R. Buick (2007). Did the Proterozoic ‘Canfield Ocean’ cause a laughing gas greenhouse? *Geobiology* 5 (2), 97–100 Not yet available as online article at UW.

3. Snowball Earth

At c. 750 Ma [**Sturtian,** during the **Cryogenian period (850 to 630 Ma)** of the NeoProterozoic], the first of two [or more] postulated "Snowball Earth" events occurred: glaciation initially extended to within 40° of the equator, crossing the albedo threshold, reflecting so much light into space that the temperature further drops and the oceans freeze completely, sea ice is > 100 m thick, photosynthesis ceases, and oxygen becomes depleted in oceans. The second "Snowball Earth" occurred at c. 630 or 620 to 600 Ma [**Marinoan**].[340] [A third "Snowball Earth" at c. 2.2 or 2.3 Ga, the "**Makganyene**", is also postulated by some authors.] The **Gaskiers Ice Age** occurred at c. 580 Ma—it may or may not have been a snowball Earth.

These are postulated to have ended when slow volcanic CO_2 emission leads to accumulation because no photosynthetic consumption of CO_2. Rising CO_2 causes greenhouse warming, "snap" melting of ice, and deposition of "**cap carbonates**"[341] from rising CO_2, as well as BIFs from rising O_2 from photosynthesis. Such a global freeze should kill multicellular eukaryotes (since they have no long-lived resting cysts, etc.), and it is hard to explain how they could have survived such extreme conditions, certainly not a total global freeze. Low-latitude glaciation and anoxic deep ocean seem likely, but predicted order of melting events from completely frozen Earth is not seen in Australia (we expect massive **diamictite**[342] → laminated **tillite** with drop-stones → carbonate crystal crusts → BIF). Moreover, models of global climate have difficulty producing freezing oceans at the equator. Data and models therefore suggest at best a **Slush-ball Earth** rather than a snowball, maybe non-frozen within ±30° of the equator. The melting process perhaps led to a stratified ocean with fresher, less dense surface water from ice-melt on top (like in glacial fjords). If so, unlikely to have affected photosynthetic eukaryotes much.

---

[340] **Snowball Earth**:
• "Near the beginning and end of the Proterozoic Eon, circa 2220 Ma ("**Makganyene**"), circa 710 Ma ("**Sturtian**") and circa 640 Ma ("**Marinoan**")."
http://www.snowballearth.org/when.html
• "The Snowball Earth hypothesis states that the Sturtian [about 710 million years ago (Ma)] and Marinoan glaciations (about 635 Ma) were of global extent and lasted for several million years each. A variation of this hypothesis, called the Slushball Earth, requires milder conditions without substantial equatorial sea ice"
Bernd Bodiselitsch, Christian Koeberl, Sharad Master, Wolf U. Reimold. "Estimating Duration and Intensity of Neoproterozoic Snowball Glaciations from Ir Anomalies" *Science* 8 April 2005
• See also http://en.wikipedia.org/wiki/Snowball_Earth

[341] **Cap Carbonates**: "Cap carbonates are continuous layers of limestone ($CaCO_3$) and/or dolostone ($Ca0.55Mg0.45CO_3$) that sharply overlie Neoproterozoic glacial deposits, or sub-glacial erosion surfaces where the glacial deposits are absent."
http://www.snowballearth.org/capcarbs.html

[342] **Diamictite**: "Diamictites ... are non-sorted conglomerates with a wide range of clasts with up to 25% gravel sized (greater than 2 mm). They are composed of coarse, poorly sorted, angular to well rounded sedimentary clastic fragments, or other type of fragments (igneous and metamorphic rocks) supported by a typically argillaceous (clay sized) matrix. Diamictites are usually interpreted as having a glacial or ice sheet origin. The deposits are interpreted as originating as either unsorted end moraine glacial till or ice rafted sediments carried into marine environments and deposited by rapidly disintegrating ice sheets. The main characteristics of diamictite is the matrix that supporting the fragment, a phenomenon that only can be deposited by glacial or ice sheet origin. There are two Neoproterozoic diamictites layer in Namibia called Chuos and Ghaub Formation which extensively studied in support of the snowball earth hypothesis. Chuos diamictite is marked the Sturtian glaciation around 710 Mya, while Ghaub is the result of Marinoan glaciation (630 Mya). Both diamictites are deposited within continuous carbonate formation that only deposited in the tropical marine environment. It is postulated that thick ice-sheet was developed during two phases in Neoproterozoic that cover almost the entire earth, including the tropical seas."
http://en.wikipedia.org/wiki/Diamictite

Precambrian Life

Earliest Animal Forms (Late PreCambrian)

[per RB and supplemented, see also additional section below; addidtional material added from LRS slides]
Trails and burrows of muscular motile animals are found in sandstones shortly before and during the Ediacara period, as discussed above. Thus, animals certainly appeared before the "Cambrian Explosion". Other large traces of possible animals date as far back as **1.6 Ga** in India, c. **1.7 Ga** in (?Stirling Range) Australia, along with the more recent Ediacaran impressions. RB believes they are **worm trails**. Perhaps then animals are much older than generally believed. **Valkyria** 750 Ma in the form or an organic film, from Spitsbergen, may be an animal. [MCM: I could not find this animal described in detail on the web.]

The earliest certain animal fossils [other than trace fossils—see earlier discussion] are found in the c. 570 Ma [late NeoProterozoic, within the Ediacaran Period] **Doushantuo Formation**, China. These are phosphatized spheroidal embryos[343] showing complex cell division pattern including **spiral cleavage** and up to **128 or even 256 embryonic cells**. Interpreted by most as true animals. Some however argue that 2-16 "cell" forms are just giant sulfur bacteria with vacuoles. LRS: "The organic matter is replaced by apatite ($CaPO_4$). Identified as animals by distinctive cell division; thus complex programs of **cell division** machinery had developed by the Ediacaran". An image of one embryo is described as follows : "The image above is a volume rendering of a 31-celled animal embryo from the Doushantuo Formation. Models of individual cells were generated by scanning the embryos with a microfocus X-ray CT-scanner, and generating polygon models that correspond to compositional variations in each cell membrane boundary"

Ediacara Fauna (or Biota)

[per RB and supplemented]
Soon after the end of the **Gaskiers Ice Age** or **Glaciation** [c. 590 or 580 Ma], we see large multicellular nonphotosynthetic **Ediacara "fauna"**, impressions and body casts in sandstone (trace fossils) of large long organisms thought to be animals such as worms and cnidaria. Includes **Charniodiscus** (resembles a cnidarian [appearing at 565 to 555 Ma][344]) and **Dickinsonia costata** (a ?worm [time range 560-541 Ma][345]). These were initially found in 1946 in Ediacara Hills of S. Australia. They are highly diverse, with c. 20 genera. This fauna almost completely disappears at [or just past] the Proterozoic-Cambrian boundary (542 Ma), thus this biota extends c. 580 - 543 Ma. [MCM: Note that the USGS chart of the Ediacaran Period extends from 630 Ma to 542 Ma, but many of the fauna first appear later than 630 Ma. This approximate period—650 to 542 Ma—was also called the **Vendian**.)
Adolf Seilacher[346] observed that the symmetry of the Ediacaran fauna was not bilateral symmetry, not even radial (as seen with some animals such as Cnidarians), and that they were [mostly] nonmotile, thus not ideal for being called animals. He suggested the Ediacara fauna was a failed evolutionary experiment in multicellularity, perhaps a biota neither animals or plants as we now define them. [Some specific organisms are more extensively explored below.]

The Three Great Evolutionary Marine Faunas (ala Sepkoski)

[At this point lecturing is by Linda Reinink-Smith, Ph.D.=LRS. Some text below quotes her slides. Supplemental info added by MCM]

The Cambrian now starts at c. 544-542 Ma, and the span of the Cambrian duration has gradually shrunk. Names of epochs etc. are in transition—the [Precambrian] Ediacaran period was formerly called the **Vendian**. The Cambrian is divided into Lower (Early), Middle, and Upper (Late), and is also subdivided by region according to various regional faunal stages. For example, the Russian-

---

[343] **Doushanto Embryos**: *Geology*, Feb. 2007. p. 115–118, found at http://www.amherst.edu/~jwhagadorn/publications/XiaoHagadorn2007.pdf
[344] **Charniodiscus**: http://en.wikipedia.org/wiki/Charniodiscus
[345] **Dickinsonia**: http://en.wikipedia.org/wiki/Dickinsonia
[346] **Adolf Seilacher**: http://en.wikipedia.org/wiki/Adolf_Seilacher

Kazakhian region includes the **Tommotian stage**[347] began 530 million years ago and lasted for only about 3 million years, and is not included in the North American region.[348]

There are three principle evolutionary fossil marine faunas of the Phanerozoic according to the article by **Jack Sepkoski 1981**.[349] He used "Q-mode factor analysis" to cluster fossil families and quantitate diversity. LRS: "The three evolutionary faunas are broad assemblages of different phyla that at least in part have common environmental habitats… Each of the evolutionary faunas can be recognized by similar distributions in geological time and environmental space… Each successive fauna shows a higher level of maximum diversification than those preceding it. [Graphs exhibit] exponential decline of the previously dominant fauna… " He found [Sepkoski p. 49]
I. "a trilobite-dominated **Cambrian** fauna" [Trilobita, Polychaeta, Monoplacophora, Inarticulata]
II. "a brachiopod-dominated later **Paleozoic** [Ordovician to Permian] fauna", [Articulata, Crinoidea, Ostracoda, Cephalopoda, Anthozoa, etc.] and
III. "a mollusc-dominated **Mesozoic-Cenozoic**, or "modern" fauna" [Mollusks, Gastropoda, Bivalves, Osteichthyes, Echinoidea, etc.]
Diagram (Figure 5 from his article p. 49) was shown, which plots number of families in each of the 3 faunas as a function of time from 600 Ma and the Cambrian to the present. The rising number of families in recent times may be partly due to observer bias and greater preservation. [MCM: this article uses a complex technical method which I have not yet studied, but it looks impressive.] The graphs shows the contribution from each of the factors I, II, and III. A thin band at top is the "**Residual Diversity**", the amount of diversity that cannot be attributed to the first 3 factors and must be caused by the remaining factors.

Lagerstätten
(singular: Lagerstätte[350]) are important fossil sites with abundant well-preserved fossils. Examples include Burgess Shale, [Ediacara Hills, Doushantuo Formation,] and Chengjiang [Maotianshan shales].

---

[347] **Tommotian Age**: "…began approx. 530 million years ago… is an early part of the Cambrian period and lasted for only about 3 million years… The Tommotian saw the rise of diversified metazoans with skeletons, small shelly fauna, the first archaeocyathids, primitive molluscs - monoplacophorans, Lapworthella, and inarticulate brachiopods. Archaeocyaths are sponges with a simple morphology. Their calcareous skeleton consists of an inner and an outer wall that are variably connected. The small shelly fauna consists of various calcareous (also some silica, some calcium phosphate) fossils some 1-5 mm long. They represented a variety of organisms: sponges, molluscs, annelids, lobopods, and other forms that do not seem to belong to any recent phylum. Many of these organisms were recognized either as of unknown affinity or as representatives or groups that became extinct before the end of the Cambrian. The most primitive stage is marked by characteristic elements, such as anabaritids, tommotiids, and hyolithellids, also known as the "Tommotian fauna"." http://en.wikipedia.org/wiki/Tommotian
[348] **Cambrian Period Subdivisions by Regions**: http://en.wikipedia.org/wiki/Cambrian
[349] **Three Major Faunas by Factor Analysis**: "Only three factors are needed to account for more than 90% of the data. These factors are interpreted as reflecting the three great "evolutionary faunas" of the Phanerozoic marine record: **a trilobite-dominated Cambrian fauna**, a **brachiopod-dominated later Paleozoic [fauna**, and a **mollusc-dominated Mesozoic-Cenozoic, or "modern," fauna**. Lesser factors relate to slow taxonomic turnover within the major faunas through time and to unique aspects of particular taxa and times." The 3 faunas are further summarized:
"I. A Cambrian fauna that dominates the Cambrian fossil record but decays rapidly in importance during the post-Cambrian portion of the Paleozoic Era;
II. A Paleozoic fauna that is present during the Cambrian Period but grows in importance primarily during the Ordovician and remains dominant until the Permian extinctions at the close of the Paleozoic Era;
III. A Mesozoic-Cenozoic, or "modern," fauna that first attains appreciable diversity during the Ordovician radiations, grows slowly in importance throughout the remainder of the Paleozoic Era, and then ascends rapidly to dominance with the Permian extinctions; this is still the dominant evolutionary fauna in the oceans today
Sepkoski, J.J., Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology*, 7: 36–53.
[350] **Lagerstätten**: "…singular **Lagerstätte**; literally place of storage, resting place, are sedimentary deposits that exhibit extraordinary fossil richness or completeness. Palaeontologists distinguish two

Ecology
[quoted from LRS]
• The evolutionary faunas dominated different marine habitats as they succeeded one another through time.
• The ecology of these communities were different in terms of diversity and their use of ecologic resources.
•The initial diversity increases were accommodated by opening up additional ecological niches by specialization and tiering behavior.

Classification of marine environments
[MCM: A 3D diagram showing "Classification of marine environments" (or "**substrate niches**") was shown, depicting ocean depth and various habitats I don't fully understand this diagram, which requires more study. It derives from Levin *The Earth Through Time* fig. 4-30, a book with 7th ed. publ. 2003]:
Zones: Supratidal, Intertidal, Neritic [overlying shelf], and Oceanic
Benthic Provinces (Sea bottom): littoral (in intertidal zone), sublittoral (in Neritic zone), bathyal (along continental slope), abyssal (floor at 4,000 - 6,000m), hadal (trenches)
Pelagic Provinces (Water column): **Epipelagic** [0 - 200 m below surface, photic zone], **Mesopelagic** (200 - 1000), **Bathypelagic** (c. 1,000m - 2,000 to 4000m), **Abysso-pelagic** (c. 4000 - 6000), and **hadalpelagic** (deep sea trench, between 6,000m and 10,000m)

Ediacara Period Faunas (More Details)

[per LRS and supplemented]
These fauna have soft bodies, ? are they animals? Some resemble sea pens (a kind of cnidarian), but not sure if these are animals. Are they anchored to the sea floor or mobile? Are they a failed evolutionary experiment as Adolf Seilacher suggested, a Kingdom Vendobionta?. They show no signs of movement, and strange symmetry. LRS: "Others suggestions: Marine lichens, giant algae, flat organisms that absorbed nutrients from water or used symbiotic algae for photosynthesis. No agreement: some say animals, others say creatures not related to animals; perhaps both"
[Some of the fauna items below were added by MCM]:

- **Ediacaria**:[351] Posibly a microbial colony.
- **Spriggina floundersi**:[352] Was it crawling or anchored? May not be an animal. Is it a vendobiont, annelid or arthropod? [It may be a trilobite precursor.] Sprigginais is curved like a comma with a

---

kinds:
(1) Konzentrat-Lagerstätten (concentration Lagerstätten) are deposits with a particular concentration of disarticulated organic hard parts, such as a bone bed…
(2) Konservat-Lagerstätten (conservation Lagerstätten) are deposits known for the exceptional preservation of fossilized organisms, where the soft parts are preserved in the form of impressions or casts. This is caused by incompleteness of biological recycling, for example where anoxic conditions, as in oxygen-free mud, has suppressed common bacterial decomposition long enough for the initial casts of soft body parts to register… The individual taphonomy of the fossils varies with the sites. Conservation Lagerstätten are crucial in providing answers to important moments in the history and evolution of life, for example the Burgess Shale of British Columbia is associated with the Cambrian explosion, and the Solnhofen limestone with the earliest known bird, Archaeopteryx…" http://en.wikipedia.org/wiki/Lagerst%C3%A4tte
[351] **Ediacaria**: "Ediacaria is a fossil genus dating to the Ediacaran Period of the Neoproterozoic Era. Unlike most Ediacaran biota which disappeared almost entirely from the fossil record at the end of the Period, Ediacaria fossils have been found dating from 555 to 501 million years ago, well into the Cambrian Period. Ediacaria consists of concentric rough circles, radial lines between the circles and a central dome, with a diameter from 1 to 70 cm… Ediacaria was often classified as a jellyfish (a Scyphozoan Cnidarian), and has also been interpreted in many of the categories postulated to house the Ediacaran biota. A conspicuous filamentous microstructure preserved in some pyritised specimens appears to conclusively prove that it was in fact a microbial colony, which disrupted the surrounding microbial mat to create the distinctive pattern (Grazhdankin, in press)." http://en.wikipedia.org/wiki/Ediacaria

boomerang-shaped head and its body is divided into dozens of segments. It is not truly bilaterian with bilateral symmetry, but rather exhibits a **glide reflection** (shifted by 1/2 segment).

- **Kimberella quadrata**[353] possibly showed signs of **motion**. c. 550 Ma. A possible ancestor to mollusks. Ruffled border resembled the mantle of mollusks. "Claimed to be an Ediacaran—complex bilaterally symmetrical "invertebrate animal"with rigid parts. Interpreted (by some) as the first animal known to have a real body cavity with a digestive tract and internal organs." An algal mat scratcher
- **Cyclomedusa**:[354] a disc shaped fossil. Is it a jellyfish or a holdfast scar? It is the most common or conspicuous EF fossil. It might also be a result of **microbial colonies**.
- **Charniodiscus**: up to 1 m in length, resembled sea pen (Pennatulacea). "Some of these "jelly fish" were also thought to represent the anchoring holdfasts of colonial, soft corals."
- **Charnia**:[355] resembled a sea pen (Pennatulacea)
- **Trichophycus pedum**:[356] This trace fossil is used to define the Proterozoic-Cambrian boundary [542 Ma]. Consists of tube casts and burrows, no shells or other body fossils have been found.

---

[352] **Spriggina**: "Spriggina was an organism of the Ediacaran period, fossils of which have been found in the Ediacara Hills of Australia. The organisms grew to around three centimetres in length. The shape of Spriggina is roughly oblong, and segmented looking... Some researchers have claimed that the symmetry is not exactly bilaterean but is a glide reflection. "
http://en.wikipedia.org/wiki/Spriggina

[353] **Kimberella quadrata**:
• "Kimberella, one of the most fascinating Vendian fossils, has received a great deal of attention lately. It was hypothesized to be a box jellyfish (cubozoan) until new information came to light... Fedonkin and Waggoner have shown that Kimberella was a bilaterally symmetric animal that had rigid parts. Specimens of Kimberella from the White Sea are found as relatively deep depressions on the undersides of siltstone slabs. Fedonkin and Waggoner reasoned that Kimberella probably had a tough shell-like covering that rigidly stood up into the sediment when the animals were buried. Thus, Kimberella appears to be somewhat like a mollusc. Nevertheless, it is still uncertain which group of modern animals is most closely related to this interesting animal."
http://www.ucmp.berkeley.edu/vendian/kimberella.html
• "This fossil varies from 3 mm to 10 cm in size...Kimberella has been found in association with a trace fossil called Radulichnus, which appears to show the scrapes made by a mollusk-type radula on the sea floor. This association supports the molluscan affinities of Kimberella. There are also long trails from Ediacaran strata that may be the trace of Kimberella.
http://en.wikipedia.org/wiki/Kimberella

[354] **Cyclomedusa**: "is a circular fossil of the Ediacaran biota; it has a circular bump in the middle and as many as five circular growth ridges around it. Many specimens are small, but specimens in excess of 20cm are known...Cyclomedusa was originally thought to be a jellyfish..., but some specimens seem to be distorted to accommodate adjacent specimens on the substrate, apparently indicating a benthic (bottom-dwelling) creature. The markings do not match the musculature pattern of modern jellyfish. The fossils have been conjectured to represent a holdfast for some stalked form—possibly an octacorallian, or something else entirely. Cyclomedusa is widely distributed in Ediacaran strata, with a number of species described... It is now suggested that Cyclomedusa was a microbial colony (Grazhdankin, in press); D. Grazhdankin reinterprets the concentric rings and radial structures as comparable to those seen in modern-day microbial colonies exposed to homogeneously distributed environmental conditions."
http://en.wikipedia.org/wiki/Cyclomedusa

[355] **Charnia**: "Charnia is the genus name given to a frond-like Precambrian lifeform with segmented ridges branching alternately to the right and left from a zig-zag medial suture. There are two species, Charnia masoni ... and Charnia wardi... It was originally interpreted as an alga (Ford) and a sea pen (Glaessner). One modern interpretation favoured by Seilacher and McMenamin is that Charnia is a Vendazoan built with unipolar iterations of one cell family."
http://en.wikipedia.org/wiki/Charnia

[356] **Trichophycus pedum**: (or **Treptichnus pedum**; formerly Phycodes pedum) is regarded as the earliest wide-spread complex trace fossil. Its earliest appearance, which was contemporaneous with the last of the Ediacaran biota, is used to define the dividing line between the Ediacaran and Cambrian Periods. However, it has since been discovered below the originally defined GSSP... Trichophycus produced a fairly complicated and distinctive burrow pattern: along with a central, sometimes sinuous or looping burrow. It made successive probes upward through the sediment in search of nutrients, generating a trace pattern reminiscent of a fan or twisted rope. It is considered

Cambrian Period Marine Faunas (and Sepkoski Factor I Evolutionary Fauna)

[per LRS and supplemented]
Cambrian Period[357] is characterized by deposit feeders and grazers, low epifaunal or infaunal[358] **tiering**. There was "considerable internal turnover; rapid changes during initial radiation". Diversification slowed when an equilibrium level of ~85 families was approached[359]... [MCM: Trilobites, inarticulate brachiopods, archaeocyathid sponges, and eocrinoid faunas dominated according to Sepkoski].

Precambrian/Cambrian boundary:

---

more complex than earlier Ediacaran fauna; and its trace fossils, which occur worldwide, are usually found in strata above them. Since it lacked any hard anatomical features, such as shells or bones, no fossilized remains of Trichophycus (besides its burrows) have been found. Its morphology and relationship to modern animals is therefore unknown, and some dispute even its inclusion into the animal kingdom."
http://en.wikipedia.org/wiki/Trichophycus_pedum

[357] **Cambrian Period**: "The Cambrian is a major division of the geologic timescale that begins about 542 ± 1.0 Ma (million years ago) at the end of the Proterozoic eon and ended about 488.3 ± 1.7 Ma with the beginning of the Ordovician period (ICS, 2004). It is the first period of the Paleozoic era of the Phanerozoic eon. The Cambrian is named for Cambria, the classical name for Wales, the area where rocks from this time period were first studied. The Cambrian is the earliest period in whose rocks are found numerous large, distinctly fossilizable **multicellular organisms that are more complex than sponges or medusoids**. This sudden appearance of **hard body fossils** is referred to as the **Cambrian explosion**... The lower boundary of the Cambrian was traditionally set at the earliest appearance of early arthropods known as **trilobites** and of primitive reef-forming animals known as **archeocyathids**... Exactly at the [lower] Cambrian boundary there is a marked fall in the abundance of carbon-13, a "reverse spike" that paleontologists call an excursion. It is so widespread that it is the best indicator of the position of the Precambrian-Cambrian boundary in stratigraphic sequences of roughly this age. One of the places that this well-established carbon-13 excursion occurs is in **Oman**. Amthor (2003) describes evidence from Oman that indicates the carbon-isotope excursion relates to a mass extinction: the disappearance of distinctive fossils from the Precambrian coincides exactly with the carbon-13 anomaly.... Cambrian continents are thought to have resulted from the breakup of a Neoproterozoic supercontinent called **Pannotia**... "
http://en.wikipedia.org/wiki/Cambrian

[358] **Infauna**: "Benthic animals that live in the substrate of a body of water, especially in a soft sea bottom. Infauna usually construct tubes or burrows and are commonly found in deeper and subtidal waters. Clams, tubeworms, and burrowing crabs are infaunal animals."
http://www.thefreedictionary.com/infaunal

[359] **Cambrian Fauna**:
• "Aside from a few enigmatic forms that may or may not represent animals, all modern animal phyla with any fossil record to speak of (except bryozoans) appear to have representatives in the Cambrian, and of these most except sponges seem to have originated just after or just before the start of the period. However, several modern phyla, primarily those with small and/or soft bodies, have no fossil record, in the Cambrian or otherwise. Many extinct phyla and odd animals that have unclear relationships to other animals also appear in the Cambrian. The apparent "sudden" appearance of very diverse faunas over a period of no more than a few tens of millions of years is referred to as the "**Cambrian Explosion**". Also, the first possible tracks on land, such as **Protichnites** and **Climactichnites**, dating to about 530 mya and found in Ontario, Canada, and northern United States, appeared at this time. The **conodonts**, small predatory primitive chordates known from their fossilised teeth, also appeared during the Furongian epoch of the Cambrian period. The conodonts thrived throughout the Paleozoic and the early Mesozoic until they completely disappeared during the Late Triassic period when the first mammals were evolving."
http://en.wikipedia.org/wiki/Cambrian
• "Some important groups [of the Cambrian]: Trilobites, Brachiopods, Echinoderms, Conodonts (appear in Late Cambrian), and Other vertebrates (jawless "fish"):
http://www.geol.umd.edu/~tholtz/G102/102epal2.htm [edited]

A possible division of the time scale around the Precambrian/Cambrian boundary [MCM: times listed here are estimated by viewing the graph projected and LRS PDF p. 11; classifications vary. See diagram also here[360]]:

Tonian (late NeoProterozoic) 1000 Ma
Cryogenian (late NeoProterozoic) 850
Ediacaran ~630 Ma - 542 Ma.

- New data suggests that the Ediacaran may extend back to 635 Ma...
- LRS slide shows the youngest Ediacaran fossil dates to 533 Ma, thus extending into the Cambrian.
- Doushantou embryos? End of glaciations 580
- Ediacaran Fossils (570 Ma - early Cambrian)
- First Bilaterian Trace Fossils c. 555 Ma

Cambrian 543 - 490

- Lower Cambrian c. 543 - 490 Ma
  - Nemakit-Daldynian to 530 Ma
  - Tommotian 530 - 520. First arthropod trace fossils at c. 530
  - Atdabanian 520 - 515. First echinoderms and trilobites at c. 520
  - Botomin/Toyonian 515 - 510
- Middle Cambrian 510 - 500 [includes Burgess Shale 505]
- Upper Cambrian 500 - 490

1. Tommotian Fauna[361]

[c. 530 Ma, or c. 543 Ma per LRS] This is the time of **Small Shelly Fauna SSF**, 1-2 mm hard shells which begin to appear just before the start of the Cambrian [before 542 Ma, on LRS diagram at c. 550 Ma] and end c. 533 Ma or 540 Ma per LRS. [MCM: Tommotian and SSF do not appear to exactly correspond, according to some sources.] LRS: “Problematic skeletal taxa of the earliest Cambrian, high diversification, and rapid evolutionary turnover.” The SSF included **Cloudina**, “possibly a tube-dwelling annelid worm” [this organism was previously discussed as a late Proterozoic organism, having a calcareous shell resembles stacked ice-cream cones]. It exhibited [among the] first hard parts in animal world. Some resemblance with brachiopods (?) Many specimens are “of unknown affinity”, such as a collection displayed from the Görlitz fauna, Germany.

---

360 **Diagrams of Precambrian-Cambrian boundary, Burgess Shale**, etc.: good quality diagrams, some used by LRS, found in
Harold L. Levin. *The Earth Through Time, Eighth Edition*,
http://higheredbcs.wiley.com/legacy/college/levin/0471697435/chap_tut/chaps/chapter12-02.html
361 **Tommotian Fauna**:
• “The Tommotian Age, which began about 530 million years ago, is a subdivision of the early Cambrian. Named for rock exposures in Siberia, the Tommotian saw the first major radiation of the animals, or metazoans, including the first appearance of a great many mineralized taxa such as brachiopods, trilobites, archaeocyathids, molluscs, echinoderms, and more problematic forms. Soft-bodied members of many other phyla were also appearing and diversifying at this time.”
http://www.ucmp.berkeley.edu/cambrian/tommotian.html
• “The Tommotian saw the rise of diversified metazoans with **skeletons**, **small shelly fauna**, the first **archaeocyathids**, primitive **molluscs** - monoplacophorans, Lapworthella, and inarticulate brachiopods. Archaeocyaths are sponges with a simple morphology. Their calcareous skeleton consists of an inner and an outer wall that are variably connected. The small shelly fauna consists of various calcareous (also some silica, some calcium phosphate) fossils some 1-5 mm long. They represented a variety of organisms: **sponges**, **molluscs**, **annelids**, **lobopods**, and other forms that do not seem to belong to any recent phylum. Many of these organisms were recognized either as of unknown affinity or as representatives or groups that became extinct before the end of the Cambrian. The most primitive stage is marked by characteristic elements, such as anabaritids, tommotiids, and hyolithellids, also known as the "Tommotian fauna".
The origin of the many kinds of skeletons during this time was a major evolutionary development. The rapid evolution of a variety of external skeletons was probably in response to the evolution of advanced predators.”
http://en.wikipedia.org/wiki/Tommotian_fauna

2. Chengjiang Fauna and Biota:

These were found in the 1980s in China [**Maotianshan Hill** in Chengjiang County, Yunnan Province] Anomalocarids also found in Canada and Greenland. Occurred c. 15 - 25 m.y. after Proterozoic-Cambrian boundary, in latter part of Early Cambrian. Includes algae, sponges, corals, trilobites, cnidaria, echinoderms, annelids, arthropods, early chordates (earlier than the Burgess Shale). Examples include:

- **Waptia ovata**: An arthropod (crustacean-like organism), its carapace is a common fossil, similar to Burgess Shale Waptia.[362]
- **Fuxianhuia protensa**:[363] ?arthropod. Not otherwise found—not in Burgess Shale. LRS: "The exceptional preservation of early animals from this biota is similar to the Middle Cambrian fossils of the Burgess Shale. The systematic position of Fuxianhuiais still under debate, with some considering it a basal euarthropod."
- **Microdictyon sinicum**:[364] Like **Velvet worm** (**onychophorans**), sclerites look like compound eyes (?). Modern velvet worms exist. Had clawed feet—might have been an ectoparasite clinging to other organisms. LRS: "Six named genera of velvet worms (onychophorans), each with a single species, are known from the Chengjiang biota, making it the richest source of fossils of the type on Earth. It has nine pairs of trunk sclerites which have been likened to the compound eyes of arthropods!"
- **Myllokunmingia fengjiaoa**:[365] **First vertebrate fish**, resembles a lamprey larva. LRS: "Features that favor a placement with vertebrates include notochord, V-shaped musculature, a relatively complex skull, gill supports, and fin supports." Probably agnathan (**jawless**). Up to 3 cm. Can't say if it had eyes, brain, or single heart. Previous oldest fish was in Burgess Shale. May have been a parasite. Dates to c. 530 Ma from the Lower Cambrian of South China.
- **Anomalocaris saron**: an Anomalocarid, predator.

---

[362] **Waptia**: "Waptia fieldensis was a small, shrimp-like stem group crustacean. Many Cambrian crustaceomorphs such as Waptia lack the mouthparts to be classified as crown group crustaceans that lived during the Middle Cambrian about 510 million years ago."
http://en.wikipedia.org/wiki/Waptia

[363] **Fuxianhuia protensa**: "is a Lower Cambrian fossil arthropod known from the Chengjiang Fauna in China. Its purportedly primitive features have led to its playing a pivotal role in discussions about the euarthropod stem group. Nevertheless, despite being known from many specimens, disputes about its morphology, in particular its head appendages, have made it one of the most controversial of the Chengjiang taxa, and it has been discussed extensively in the context of the arthropod head problem.... Complete Fuxianhuia specimens are approximately 4 centimetres long."
http://en.wikipedia.org/wiki/Fuxianhuia

[364] **Microdictyon**: "Microdictyon is an extinct "armored worm" coated with dot-like scleritic scales, known from the Early Cambrian Maotianshan shale of Yunnan China. Microdictyon is sometimes included in a somewhat ill-defined Phylum – Lobopodia – that includes several other odd worm-like and segmented free-swimming animals that do not appear to be arthropods or worms. The phylum includes Microdictyon, Onychodictyon, Cardiodictyon, Luolishania, Paucipodia, as well as the Anomalocarids. The isolated sclerites of Microdictyon are known from other Lower Cambrian deposits. (The famous Hallucigenia from the Cambrian-age Burgess Shales was once considered to belong to the family Lobopodia, but is now recognized as an Onychophoran, a relative of the velvet worms. Microdictyon sinicum ... is typical."
http://en.wikipedia.org/wiki/Microdictyon

[365] **Myllokunmingia fengjiaoa**: "is a primitive, probably agnathan (jawless) fish from the Lower Cambrian Maotianshan shales of China, thought to be a vertebrate.... It somewhat resembles hagfish, which live today. It is described as 28 mm long and 6 mm high. It is the oldest vertebrate known, found in rocks of the Cambrian period (530 Ma old). It appears to have a skull and skeletal structures made of cartilage (like lampreys, which are also vertebrates). There is no sign of mineralization of the skeletal elements (biomineralization). The holotype was found in the Yuanshan member of the Qiongzhusi Formation in the Eoredlichia Zone near Haikou at Ercaicun, Kunming City, Yunnan, China... There are 25 segments (myomeres) with rearward chevrons in the trunk. There is a notochord, a pharynx and digestive tract that may run all the way to the rear tip of the animal. The mouth can not be clearly identified... There is one species - Myllokunmingia fengjiaoa...
http://en.wikipedia.org/wiki/Myllokunmingia

3. Burgess Shale Fauna[366]

This important lagerstätte was found in B.C. near Field B.C., west of Kicking Horse Pass, in the **Middle Cambrian** [c. 505 Ma]. The Stephen Formation is exposed at the Walcott Quarry on Mt. Wapta and at the Mt. Stephen Fossil Beds. Discovered by Charles Walcott in 1906. These are mostly black carbon imprints in shale. Includes arthropods like trilobites, sponges, onychophorans (velvet worms), crinoids, mollusks, worms, possibly corals, possibly chordates, and various unclassifiable species. The Burgess Shale was a well-preserved slump [turbidity flow] from the top of a submerged algal reef. It carried the shallow water organisms over the wall of the reef into an anoxic deeper environment, where they were buried by sediments. Fauna examples include:

- **Aysheaia**:[367] an invertebrate called on **onycophoran** or velvet worm—"it is of special interest because it appears to be intermediate in evolution between segmented worms and arthropods."
- **Leanchoila superlata**: [of unknown phylum within Crustacea Arthropod]
- **Wiwaxia corrugata**:[368] Has scales, perhaps molted its upper body? May be an ancestor to annelid worms (the polychaete annelid worms, also called bristle worms) or mollusks. LRS: "The upper (dorsal) body is covered with small, flat, overlapping hard plates, termed sclerites. Each of these little scales is attached with a root-like base and it is assumed Wiwaxia grew by molting the plates. Because of the sclerites, some researchers have attempted to place Wiwaxia with the annelids, thus, it may be ancestral or closely related to the segmented worms. The polychaete annelid worms are spiny with chaetae that are mineralized."

---

[366] **Burgess Shale**:
• "In 1909, geologist Dr. Charles D. Walcott discovered fossils with fine details on Mount Burgess [in Yoho National Park]..."
http://en.wikipedia.org/wiki/Mount_Burgess
• "As the backdrop to Emerald Lake and Emerald Lake Lodge in Yoho National Park, Mount Burgess is a well known peak... The mountain lies between Emerald Lake and the Kicking Horse Valley... Mount Burgess was named in 1886 by Otto Klotz who discovered the fossil beds on Mount Stephen. "
http://www.peakfinder.com/peakfinder.ASP?PeakName=mount+burgess
• "Walcott's Quarry lies along a ridge on Mt. Wapta, across Burgess Pass from Mt. Burgess. Mt. Burgess has two peaks; the highest of these will officially be named "Walcott Peak" in honour of Dr. Charles Doolittle Walcott...
The fossil sites: (1) The hike to the Mt. Stephen Fossil Beds is a moderate 6-hour return trip. Elevation gain is 520 metres (1700 ft.). (2) The hike to Walcott's Quarry is a moderately difficult hike of 20 km. Elevation gain is 760 metres (2888 ft.).
http://www.pc.gc.ca/pn-np/bc/yoho/natcul/natcul15_E.asp"
• See also Map at http://www.pc.gc.ca/pn-np/bc/yoho/visit/visit9a_E.asp

[367] **Aysheaia pedunculata**: "was a soft-bodied, caterpillar-shaped organism average body length of 1-6 cm. They are known from fossils found in the middle Cambrian Burgess shale of British Columbia. Similar forms are known from the lower Cambrian Maotianshan shales of China. Aysheaia has ten body segments, each of which has a pair of spiked, annulated legs. The animal is segmented, and looks somewhat like a bloated caterpillar with a few spines added on -- including six finger-like projections around the mouth and two grasping legs on the "head." Based on its association with sponge remains, it is believed that Aysheaia was a sponge grazer and may have protected itself from predators by seeking refuge within sponge colonies. Aysheaia probably used its claws to cling to the sponge."
http://en.wikipedia.org/wiki/Aysheaia

[368] **Wiwaxia corrugata**: "is an extinct species of animal known only from fossils found in Canada's Burgess Shale deposits. The size of the larger reconstruction is 6-7cm. Although Wiwaxia resembles a mollusk in having a well developed radula, it does not really fit the conchifera because of its sclerites (armor of flattened, chitinous spines), but rather the class Aplacophora. The actual classification of Wiwaxia in the animal kingdom is still controversial.... Wiwaxia is now considered to be related to the slug-like Halkieria due to the recently discovered Burgess shale organism, Orthrozanclus reburrus. O. reburrus combines features of both Halkiera (scale mail sclerites and an anterior shell) and Wiwaxia (elongated, spine-like sclerites)."
http://en.wikipedia.org/wiki/Wiwaxia

- **Hallucigenia sparsa**:[369] from phylum ?Onychophora. Originally portrayed as walking on spines. May be the appendage of a larger creature not otherwise preserved. LRS: "The currently accepted arrangement of Hallucigenia is that proposed by Ramiskold and Hou Xingxuang, depicted by the 3D model (below). However, some believe that Hallucigenia may not be an independent creature at all but rather the appendage of a larger creature not preserved in the fossil record. Its very small size--averaging 3 cm —also contributes to this theory."
- **Opabinia regalis**:[370] Has 5 eyes, segmented body, nozzle trunk with spiny jaws or pincers which feeds mouth behind, paddle gills underneath. Hard to classify, features between annelid and arthropod. No modern similar organism.
- **Marrella splendens**:[371] a "lace crab", the most common fossil in the Burgess Shale, over 15,000 specimens have been collected from the Walcott Quarry. "The head shield had two pairs of large spines curving back over the body. Two pairs of antennae project forward and the body consists of a large number of segments bearing identically shaped limbs. Marrella presumably fed on small animals and organic particles as it moved over the surface of the sediment. It is a primitive type of arthropod that could have given rise to any of the three aquatic arthropod groups - crustaceans (shrimp, crab, lobster, etc.); chelicerates (scorpions and spiders); or trilobites."
- **Anomalocarids**:[372] The most spectacular of the Burgess Shale fauna, up to 2 m in length. Pincers were orig. found as isolated anterior appendages and thought to be kind of shrimp. Other parts

---

[369] **Hallucigenia**: "Hallucigenia is an extinct genus of animal found as fossils in the ... Burgess Shale. It was named by Simon Conway Morris when he re-examined Charles Walcott's Burgess Shale genus Canadia in 1979. Morris found that what Walcott had called one genus in fact included several quite different animals. One of them was so unusual that nothing about it made much sense. Since the species clearly was not a polychaete worm, Morris had to provide a new generic name to replace Canadia. Morris named the species Hallucigenia sparsa because of its "bizarre and dream-like quality" (like a hallucination)."
http://en.wikipedia.org/wiki/Hallucigenia

[370] **Opabinia regalis**: "Its sole species, Opabinia regalis, is known from the Middle Cambrian Burgess Shale of British Columbia... The discoverer of Opabinia, Charles Doolittle Walcott, named it after a local mountain, Opabin Peak in the Canadian Rockies. It is known from fewer than twenty good specimens. The animal was segmented and had an unmineralized exoskeleton. Total body length ranged from 40 to 70 millimeters. The head carried five stalked eyes that would have given their owner a range of vision of almost 360°, and a long, flexible, hose-like proboscis. At the end of the proboscis were grasping spines; these are theorised to have served as a grab to catch prey, which would then be brought to the mouth, which was located underneath the head, behind the base of the proboscis..."
http://en.wikipedia.org/wiki/Opabinia

[371] **Marrella splendens**: "is an unusual arthropod known from fossils found in only a single stratum of the ... Burgess Shale.... It is, however, the most common fossil in the Burgess Shale, with over 15,000 specimens catalogued. Marrella was the first fossil collected by Charles Walcott from the Burgess Shale. Walcott described Marrella informally as a "lace crab" and described it more formally as an odd trilobite. It was later reassigned to the now defunct class Trilobitoidea in the Treatise on Invertebrate Paleontology. In 1971, Whittington did a thorough redescription of the animal and, on the basis of its legs, gills and head appendages, concluded that it was neither a trilobite, nor a chelicerate, nor a crustacean.

Marrella itself is a small animal, 2 cm or less in length.... It's currently accepted that Marrella is a stem group arthropod—that is, it's descended from a common ancestor common to it and most or all of the major later arthropod groups. It is thought to have been a benthic (bottom-dwelling) marine scavenger living on detrital and particulate material. Marrella had a hard shell-like head that was not only hollow but like the shell of a crab. Taken with two other unexpectedly unique arthropods, Opabinia and Yohoia, Marrella has demonstrated that the soft bodied Burgess fauna were much more complex and diverse than anyone had previously suspected."
http://en.wikipedia.org/wiki/Marrella

[372] **Anomalocaris canadensis**: "Anomalocaris ("Anomalous shrimp") is an extinct genus of anomalocarids, which are, in turn, thought to be closely related to the Arthropoda. Anomalocaris was a swimming creature which possibly used flexible lobes on the sides of its body to propel itself through the water. Its large head had one pair of large, possibly compound, eyes, and a disk-like mouth that resembled a slice of pineapple. Two large 'arms' with barb-like spikes were positioned in front of the mouth; Anomalocaris probably used these to grab prey and bring it to its mouth. For the time in which it lived Anomalocaris was a truly gigantic creature, reaching lengths from an already large 60 cm (2 ft) to a staggering 2 m (6 ft 8 in). Anomalocaris has been misidentified several times. Its name

mistaken for whole organisms: the mouth of **Anomalocaris canadensis** mistakenly termed a jellyfish **Peytoia** by Walcott 1911, and the body, suspected of being a sponge. Anomalocarids include **A. saron** and **A. symbrachiata** (both Chengjiang), **Amplectobelua symbrachiata**, **Laggani cambria** (a filter feeder, Burgess Shale). 12 species. [MCM: The Anomalocarids were nektonic top predators.] "In 1892, Whiteaves described a spine-bearing segmented fossil from the Mt Stephen trilobite beds in the Canadian Rockies as the abdomen and tail of a crustacean. He called it Anomalocaris canadensis, "anomalous shrimp," since it showed no sign of a gut, and its ventral, spine-like "appendages" were unsegmented." Additional species displayed included:

- **Pikaia**:[373] Formerly the first proto-chordate, now preceded by **Myllokunmingia**. "Pikaia was regarded as one of the earliest known primitive representative of Phylum Chordata, until Myllokunmingia. It was about 40 mm in length and swam above the sea floor. Pikaia may have filtered may particles from the water. Only 60 specimens have been found to date. Pikaia has a [proto-]notochord near the dorsal surface but it is not a vertebrate. The rib-like features [in the image] are muscles."
- **Waptia**: An arthropod (crustacean-like organism), its carapace is a common fossil, related to Waptia of Chengjiang Fauna.
- **Eocrinoids**[374]: began in Lower Cambrian, so not unique to Burgess Shale.

4. Cambrian Explosion (Evolution's Big Bang [of Fauna])

This lasted 10 M.Y. All principle animal phyla except Bryozoa[375] (which appeared first in the Ordovician) apparently had appeared by c. 535 to 520 Ma in the Cambrian. Molecular evidence

---

originates from a description of a detached 'arm', mistaken for a separate creature. The mouth was mistaken for a jellyfish and called Peytoia, and the body was classified as a sponge named Laggania. According to ICZN rules, the oldest name takes priority, which in this case would be Anomalocaris. The name Laggania was later used for another genus of anomalocarid. "Peytoia" has been modified into Parapeytoyia, a genus of Chinese anomalocarid."
http://en.wikipedia.org/wiki/Anomalocaris
"**Anomalocarids** ("Strange shrimp") are a group of very early marine animals known from fossils found in Cambrian deposits in China, North America, and Australia. Anomalocarids are the largest Cambrian animals known (some Chinese forms grew up to **2 m**, and most of them were probably active carnivores (although recent thought posits one genus, Laggania, as a plankton-eating animal)."
http://en.wikipedia.org/wiki/Anomalocarid

[373] **Pikaia**: "Pikaia gracilens is an extinct animal known from the ... Burgess Shale... It was discovered by Charles Walcott and was first described by him in 1911. Based on the obvious and regular segmentation of the body, Walcott classified it as a Polychaete worm. It resembles a living chordate commonly known as the **lancelet** and perhaps swam much like an eel. During his re-examination of the Burgess Shale fauna in 1979, Paleontologist Simon Conway Morris placed P. gracilens in the chordates, making it perhaps the oldest known ancestor of modern vertebrates, because it seemed to have a very primitive, proto-notochord. Averaging about 1 1/2 inches in length(5 cm), Pikaia swam above the seafloor using its body and an expanded tail fin. Pikaia may have filtered particles from the water as it swam along. Only 60 specimens have been found to date."
http://en.wikipedia.org/wiki/Pikaia

[374] **Eocrinoids**: "Eocrinoids are among the earliest groups of echinoderms to appear, ranging from the Early Cambrian to the Silurian. This one [depicted], Gogia, is from the Middle Cambrian House Range of Utah. Despite the name ("dawn crinoids"), they are not directly ancestral to the true crinoids. Instead, various echinoderms in the Blastoidea appear to have evolved from eocrinoid ancestors; thus the Eocrinoidea is a paraphyletic or polyphyletic group... Most eocrinoids were sessile and fed with their long brachioles (the arm-like structures, which in this specimen are spirally twisted). The body was covered by plates; in early eocrinoids the holdfast was also covered by plates, but later eocrinoids evolved a stalk with columnals, like crinoids and blastoids. "
http://www.ucmp.berkeley.edu/echinodermata/eocrinoidea.html

[375] **Bryozoa**: "Bryozoans are tiny colonial animals that generally build stony skeletons of calcium carbonate, superficially similar to coral. They are also known as **moss animals** (which is the literal Greek translation) or **sea mats**. They generally prefer warm, tropical waters but are known to occur worldwide. There are about 5,000 living species, with several times that number of fossil forms known."
http://en.wikipedia.org/wiki/Bryozoans

suggests that branching of several phyla occurred at 1 Ga, but there are no fossils to confirm this however. Mollusks may have occurred c. 1 Ga. Annelids... [missed]. Cambrian Corals [missed] go back more [?, corals[376] first appear in the Cambrian]. All body parts are seen by end of Cambrian—maybe actually earlier, but no fossils to prove it. After the early Cambrian radiation, a Mid to Late Cambrian diversity "plateau" occurred. "Animals with skeletons appeared rather abruptly, although soft-bodied Ediacaran fossils are now found even above the first occurrence of typical Cambrian fossils (in Namibia). Basic body plans for all animals were established by the end of the Cambrian explosion." A complex chart was shown, listing major invertebrate phyla, classes, and orders and their stratigraphic ranges. The phyla from this list [subdivisions are not included here]:

- Protozoa: Cambrian to Recent
- Porifera: Cambrian to Recent
- Archaeocyatha: Cambrian
- Cnidaria: Cambrian to Recent
- Bryozoa: Ordovician to Recent
- Brachiopoda: Cambrian to Recent
- Mollusca: Cambrian to Recent
- Annelida: PreCambrian to Recent
- Arthropoda: Cambrian to Recent
- Echinodermata: Cambrian to Recent
- Hemichordata: Cambrian to Recent

Trilobites
Appear abruptly in the Cambrian and become the most ubiquitous element in the Cambrian environment—over 15,000 species in Cambrian. [Trilobites range in length from 1 - 720 mm.[377] The world's largest trilobite is Isotelus rex.] Diagram show of several different species. Have eyes or blind. Molted. Locomotion. Associated with **trace fossils**[378]:
• **Cruziana** ["tracks showing rather clearly defined edge furrows, probably created by a trilobite moving while partially buried through the mud"],
• **Rusophycus** [a "bi-lobed impression" formed while trilobite is at rest], and
• **Diplichnites** [formed "when a trilobite is walking or striding freely upon the surface, it leaves paired leg marks called Diplichnites, which can be reduced to rather widely-spaced impressions when the animal is striding at full speed across the substrate."].

Body sections were **Cephalon, Thorax, and Pygidum**. Trilobites however are named after longitudinal lobes: a central **axial lobe**, and two symmetrical **pleural lobes** [rather than the 3 body sections]. Trilobite eyes and vision[379] provided by single cornea over multiple lenses in contact with each other (**holochroal**) or separate corneas over each of several separated non-touching lenses (**schizochroal**). Could focus eye, lens made of calcite so rigid and could not accommodate, but ["instead, an internal doublet structure (two lens layers of different refractive indices acting in combination) corrected for focusing problems that result from rigid lenses."] LRS: "The trilobite had compound eyes and each of these had thick doublet lenses of oriented calcite to eliminate spherical aberration. The ability to focus gave it a huge advantage as it evolved in the Cambrian and Ordovician. The eye was made up of calcite, a mineral that has very unique optical properties. The calcite eye had two layers of lenses that had different optical properties, but worked together to help focus the image."

Brachiopods[380]

---

[376] **Corals**: http://en.wikipedia.org.offcampus.lib.washington.edu/wiki/Coral
[377] **Trilobites**:
• **General**: http://en.wikipedia.org/wiki/Trilobite
• **Size**: http://www.trilobites.info/lgtrilos.htm
[378] **Trilobite Trace Fossils**: http://www.trilobites.info/trace.htm
[379] **Trilobiate Vision**: http://www.trilobites.info/eyes.htm
[380] **Brachiopods**:
• "Apart perhaps from the trilobite, no other organism typifies the Age of Invertebrates more than the brachiopod. They were the first bilaterian animals to lose their mobility and encase their bodies in a solid external shell. Despite a superficially similar appearance to clams, they are actually completely different in their anatomy, belonging to the group known as the **Lophophorata**, which use a fringe of tentacles known as the lophophore to sweep food particles into their mouths. Brachiopods are rare

[See earlier notes and footnotes about Lingulata and Inarticulata.] Included **Inarticulata** like **Lingula** of Lingulata[381] (these are still found today). Small, 1 cm. Articulate brachiopods were present in Cambrian but became abundant in Ordovician. Both had a **pedicle** attached to the larger valve. LRS: "Brachiopods are marine bottom dwellers and filter feeders, and generally immobile. They have a soft body enclosed in two shells that can be opened to feed. Phylum Brachiopoda has two main branches, Articulata and Inarticulata. The articulates [such as **Terebratulina**] have a hard, calcareous, shell. The shell has two valves that are hinged at one end and thus "articulate" (rotate) around the hinge to open. The articulates are generally larger than the more primitive inarticulates" The **lophophore**[382]

---

today, but during the Paleozoic era (especially from the Middle Ordovician period onwards) they absolutely dominated every benthic (bottom-living) marine ecology, their shells accumulating in countless billions. Today their petrified remains are the most common of all fossils....
Bivalve mollusks generally have shells that are equal in size and shape (although mirror images of each other), whereas the two shells of brachiopods are of unequal size (the technical term is inequalvalved). The valve (shell) that has the attachment for the pedicle is the pedicle valve which is usually the lower and larger valve. This valve includes the pedicle opening. The valve that holds the a feeding tentacles - the lophophore or brachia - is called, naturally enough, the brachial valve. The brachidium, a long ribbon or loop-shaped calcified support for the lophophore, is attached to this shell. The brachial valve is usually, but not always, on the dorsal ("top") side of the organism.

... The interior of the shell is lined with a **mantle**, a membranous duplication of the body wall, through which respiration may occur and which secretes the shells. The shell is closed and opened by **adductor and diductor muscles** respectively. The scars of these muscles may be seen on the inside of the valves. The body of the animal occupies only about one-third of the interior of the shell. The rest is taken up by the **lophophore**, which is supported by a two-limbed, calcareous structure, the **brachidium**. The brachidium is variable in shape consisting in its simplest form of the loop of two short or moderately long, curved structures, and in its more complex form of two thin, spirally coiled ribbons or spires. The shape of the brachidium is very important in determining the classification of brachiopod types. The brachidium supports the **brachia**, the fleshy arm-like part of the lophophore which bear the **tentacles or cirri** that sweep food particles into the mouth." [includes good anatomic diagrams]
http://www.palaeos.com/Invertebrates/Lophotrochozoa/Brachiopoda/E0A0E0Brachiopoda.htm
• See also http://en.wikipedia.org/wiki/Brachiopoda

[381] **Lingulata**: "The only brachiopods to support a minor commercial fishery, lingulate brachiopods are also among the oldest of all brachiopods, and the most morphologically conservative, having lasted since the Cambrian with very little change in shape. The preserved specimen of a living lingulate shown here [image], Lingula, shows the typical tongue-shaped shell (hence the name Lingulata, from the Latin word for "tongue") with a long stalk, or pedicle, with which the animal burrows into sandy or muddy sediments.... Lingulate brachiopods radiated modestly in the Cambrian, but lost diversity in the Ordovician, and have never been particularly diverse."
http://www.ucmp.berkeley.edu/brachiopoda/lingulata.html [and related pages]

[382] **Brachiopod Lophophore and Lophophorata**:
• "...The common origin of the tentacle apparatus in Lophophorata from the postoral ciliary band of the larva is shown. The brachiopod lophophore is based on the brachial axis consisting of the brachial fold running along the row of tentacles. The brachial axis may be attached to the brachial (dorsal) mantle lobe (trocholophe, schizolophe, and ptycholophe lophophores) or extend freely into the mantle cavity to form coiling brachia (spirolophe, zygolophe, and plectolophe lophophores). The circulation of water flows through the mantle cavity in the brachiopods with attached and free lophophores is described. A new hypothesis on the sorting of particles suspended in water during filtration is proposed."
http://www.springerlink.com/content/v1857884111j3107/
• "Brachiopods are marine shelled invertebrates that look superficially very much like clams. They are actually quite different from clams in their anatomy, and they are not closely related to mollusks at all. In fact they belong to a (possibly polyphyletic) group known as the **Lophophorata**, because they feed by using a fringe of tentacles known as the **lophophore**. These tentacles sweep microscopic food particles in the water into the creature's mouth. Most species of brachiopods are attached to the substrate by a muscular stalk, known as the pedicle. There is however still a free-floating larval stage."
http://www.palaeos.com/Invertebrates/Lophotrochozoa/Brachiopoda/E0A0E0Brachiopoda.htm
• "**Lophophorata**: This group includes the **Phoronida** and **Entoprocta** (both small groups) as well as the **Bryozoa** ("moss" animals) and **Brachiopoda** (brachiopods), both of which have an extensive fossil

keeps water in circulation, distributes oxygen, and assists with feeding. Inarticulates had "chitinophosphate shell, lacked tooth and socket along hinge line."

Where Did These Cambrian Hard Parts Come From? [i.e., the mineralized parts such as calcareous shells and skeletons]
Theories[383] include [partly missed]:
1) **Detoxification** theories. Large amounts of toxic sedimentary **phosphate** [or toxic levels of **calcium**] were being deposited in the shallow shelf seas, and are eliminated from the organism as shell etc. Some bone has seasonal changes [MCM: how is this related?—perhaps reflects variations in levels of these components.]. [Vermeij believes detoxification is not a primary factor.]
2) **Biomechanical Locomotion** theories: Muscles need hard attachments to allow for more efficient dynamic action.
3) **Protection Against Predators** [felt by Vermeij to be the most important factor, and obviously is partly related to locomotion as well as passive shield-like protection.] Arose in the late Proterozoic and early Phanerozoic, first as skeletal parts and eventually evolved into continuous shells. Minerals included $CaCO_3$, $CaPO_4$, and SiO_2.
4) [**Rising oxygen levels**—Vermeij notes that rising body size and skeletons coincide with rising O_2 level, which makes them possible.]
5) **Protection Against UV and Desiccation** in an Intertidal environment**.**

What Caused The Cambrian Explosion of Fauna?
Much uncertainty persists, but theories (in addition to the **development of hard parts** and **preservation bias in the fossil record**), include:[384]
1) **Intrinsic Biotic Explanations**: Breakthrough in genetic control of development with **complex genomes**... **Homeotic** and **homeobox and Hox genes** which control segmentation and bilaterian developmental system...[385] LRS: "Genetic evidence now suggests that most phyla diversified before the Cambrian explosion."

---

record. The feature shared by this group is the **lophophore**, an unusual feeding appendage bearing hollow tentacles."
http://www.ucmp.berkeley.edu/phyla/lophotrochozoa.html
[383] **Origin of Calcareous Skeletons**: Geerat J. Vermeij. "The Origin of Skeletons" *Palaios*, Vol. 4, No. 6 (Dec., 1989), pp. 585-589
[384] **Causes of the Cambrian Explosion**:
• http://en.wikipedia.org/wiki/Cambrian_explosion
• http://palaeo.gly.bris.ac.uk/Palaeofiles/Cambrian/triggers/extrinsic/extrinsic.html
• Roberta Friedman. "The Cambrian Explosion: Tooth and Claw"
http://www.astrobio.net/news/modules.php?op=modload&name=News&file=article&sid=134
• Charles R. Marshall. "Explaining The Cambrian "Explosion" Of Animals" *Annual Review of Earth and Planetary Sciences*. Vol. 34: 355-384 (Volume publication date May 2006
http://arjournals.annualreviews.org/doi/abs/10.1146/annurev.earth.33.031504.103001?cookieSet=1&journalCode=earth [MCM: This is an exceptionally good review with excellent diagrams]
[385] **Homeotic and Homeobox Genes**:
• "Homeotic genes are **homeobox genes** that are responsible for **segment identity** in metazoan organisms. Inappropriate expression of homeotic genes will, in general, transform parts of the body into structures appropriate to other positions. An example would be the Antennapedia mutant of the fruit fly Drosophila, in which legs are found sprouting where antennae would normally be. Localized expression of homeotic genes is controlled by upstream maternal proteins, gap genes, and pair rule genes in the developmental cascade... Homeotic genes are evolutionarily highly conserved and generally encode transcription factors involved in the fate of developing regions of the body. Groups of homeotic selector genes determine how different regions of an organism develop. Homeotic genes are often homologous between different species; these genes are present in essentially all animals, humans included."
http://en.wikipedia.org/wiki/Homeotic_gene
• "A **homeobox** is a DNA sequence found within genes that are involved in the regulation of development (morphogenesis) of animals, fungi and plants. Genes that have a homeobox are called homeobox genes and form the homeobox gene family... A homeobox is about 129 base pairs long; it encodes **a protein domain (the homeodomain) which can bind DNA**... Homeobox genes encode transcription factors which typically switch on cascades of other genes, for instance all the ones needed to make a leg. The homeodomain binds DNA in a specific manner... However, the specificity of

2) **Extrinsic Environmental Or Forcing Events as Explanations**: Separation of the Pannotia[386] supercontinent (allowing more continental shelf and shallow sea areas), more equable climate (warming following prior Snowball Earth melting, perhaps assisted with greater greenhouse methane ["burps"] etc.), changes in ocean chemistry (rising P and S, facilitating development of hard parts, etc.), rising Oxygen level (which allows larger sized organisms, higher metabolic rates, and more complex body structures). LRS: "**Pannotia** (Gondwana plus Laurentia and Baltica), first described by Ian W. D. Dalzielin 1997, is a hypothetical supercontinent that existed from the Pan-African orogeny about 600-540 million years ago when it rifted apart. Pannotia is also known as the Vendian supercontinent. At about 750 million years ago, the previous supercontinent Rodinia rifted apart into the three continents that formed Pannotia."
3) **Ecological explanations:** [387]The proliferating phyla of animals are simply competing to occupy and fill for diverse ecological niches.

Shrinking Cambrian:
Diagram[388] show depicting "Changing views of late Neoproterozoic to earliest Ordovician time". This diagram [quoting date only as recent as 1998] shows that the onset of the Cambrian has moved from 590 Ma (before 1982) to 543 Ma (in 1998), and the end from 505 Ma to 490 Ma, thus the duration of the Cambrian has shrunk.

---

a single homeodomain protein is usually not enough to recognize only its desired target genes. Most of the time, homeodomain proteins act in the promoter region of their target genes as complexes with other transcription factors, often also homeodomain proteins. Such complexes have a much higher target specificity than a single homeodomain protein.... A particular subgroup of homeobox genes are the **Hox genes**, which are found in a special gene cluster, the Hox cluster (also called Hox complex). Hox genes function in patterning the **body axis**. Thus, by providing the identity of particular body regions, Hox genes determine where limbs and other body segments will grow in a developing fetus or larva."
http://en.wikipedia.org/wiki/Homeobox_genes
• "...Several workers point to the origin of the **bilaterian** developmental system, including the origin of the **Hox genes**, etc., as the primary cause of the "explosion" ..., and there can be little doubt that the origin of the bilaterian developmental system was critical to the Cambrian "explosion.""
Charles R. Marshall. "Explaining The Cambrian "Explosion" Of Animals" *Annual Review of Earth and Planetary Sciences*. Vol. 34: 355-384 (Volume publication date May 2006
http://arjournals.annualreviews.org/doi/abs/10.1146/annurev.earth.33.031504.103001?cookieSet=1&journalCode=earth
[386] **Pannotia**: "Pannotia, first described by Ian W. D. Dalziel in 1997, is a hypothetical supercontinent that existed from the Pan-African orogeny about 600 million years ago to the end of the Precambrian about 540 million years ago. It is also known as the Vendian supercontinent.... About 750 million years ago (750 Ma), the previous supercontinent **Rodinia** rifted apart into three continents: Proto-Laurasia (which broke apart and eventually re-formed as Laurasia), the continental craton of Congo, and Proto-Gondwana (all of Gondwana except the Congo craton and Atlantica). Proto-Laurasia rotated southward toward the South Pole. Proto-Gondwana rotated counterclockwise. The Congo craton came between Proto-Gondwana and Proto-Laurasia about 600 Ma. This formed **Pannotia**. With so much landmass around the poles, evidence suggests that there were more glaciers during this time than at any other time in geologic history."
http://en.wikipedia.org/wiki/Pannotia
[387] **Ecology as a Cause of the Cambrian Explosion**: "Several recent examinations of the Cambrian explosion have suggested that ecological diversification is the primary motor for the Cambrian explosion: even that the Cambrian explosion represents nothing more than ecological diversification. Given the evolution of multicellularity in heterotrophic organisms, it could be argued, a dynamic would be set up that would inevitably lead to the familiar food webs consisting of primary and secondary consumers, parasites, and (especially with the advent of mobility) deposit feeding and trophic recuperation. While it has been claimed that certain "key innovations"—most notably the origin of sight...were critical in driving the whole process decisively forward, most of these can themselves be seen as products of earlier ecological pressure... In this view, the Cambrian become the first and most spectacular "adaptive radiation"..."
http://en.wikipedia.org/wiki/Cambrian_explosion
[388] **Changing views of late Neoproterozoic to earliest Ordovician time (Diagram)**:
http://www.palaeontologie.uni-wuerzburg.de/Stuff/casu6.htm

Evolutionary Faunas, Various Topics Continued

[per LRS and supplemented]
See Sepkoski 1981 factor analysis article previously cited.

1. Sepkoski Factor II Evolutionary Marine Fauna (Paleozoic)

Factor II includes the fauna of the Paleozoic other than the Cambrian, from the Ordovician to Permian. There are 350 families including trilobites. These include filter feeders, macrozooplankton (jelly fish and shrimp, etc.) They are occupying a larger niche moving away [from benthic habitat] above the sea floor. This group begins to decline at Permian-Triassic boundary.

LRS:
• Paleozoic fauna takes over slowly
• Fauna reaches higher diversity than before
• Includes trilobites from the Cambrian fauna
• Includes filter feeders and macrozooplankton
• Increased niche space above seafloor
• Includes greater predator pressure
• Becomes dominant in the shelf environment
• By mid-Ordovician the second [Sepkoski Factor II] (Paleozoic) evolutionary fauna overtook the Cambrian faunal diversity;
• Survives mass extinctions at end Ordovician and end Devonian
• Massive decline at Perm-Triassic boundary, after which it is secondary to modern fauna

2. Ordovician Radiation

Includes **articulate brachiopods** which are common. **Nautiloids** [such as Endoceras measuring up to 3.5 meters] and other **cephalopods** are the dominant top predators (carnivores). Also **gastropods** (snails), **echinoderms** (especially stalked **crinoidea**[389]**, blastoids**, Starfish), Graptolites (**Graptolithina**), **Bryozoans**, **Rugose corals** (horn corals or tetracorals), **Tabulate corals**, Stromatoporoids (sponges), and **Ostracoderms** (jawless true vertebrate fish). [MCM: List compiled in part from outside sources[390]] ["The Ordovician radiation was manifested mainly by an unprecedented burst of diversification at lower taxonomic levels."[391]] LRS: "Ordovician radiations and the Silurian to Permian plateau; global taxonomic diversity tripled in 50 Ma reaching an equilibrium diversity of 350 families" [MCM: that is, there are 350 families from Factors I and II combined. The Sepkoski graph shows c. 450 families total during the mid-Paleozoic plateau. The LRS slide p. 55 however, shows 350 families but does not show from where the 350 families are derived, probably factors I and II.] Permian-Triassic extinction reduced global marine diversity dramatically."

The Ordovician fauna exhibits a higher level of **ecological complexity**, occupying **more ecological niches**, and exhibiting greater **ecological tiering** compared to the Cambrian. Food chain diagram projected shows, in addition to organisms named above, bacteria, phytoplankton, zooplankton,

---

[389] **Crinoids**: "Crinoids, also known as "sea lilies" or "feather-stars", are marine animals that make up the class Crinoidea of the echinoderms (phylum Echinodermata). They live both in shallow water and in depths as great as 6000 meters. Crinoids are characterized by a mouth on the top surface that is surrounded by feeding arms. They have a U-shaped gut, and their anus is located next to the mouth... Crinoids usually have a stem used to attach themselves to a substrate, but many live attached only as juveniles and become free-swimming as adults. There are only a few hundred known modern forms, but crinoids were much more numerous both in species and numbers in the past. Some thick limestone beds dating to the mid- to late-Paleozoic are entirely made up of disarticulated crinoid fragments... The earliest known crinoids come from the Ordovician. They are thought to have evolved from primitive echinoderms known as **Eocystoids**. Confusingly, another early group of echinoderms were also the **Eocrinoids**, but that group is currently thought to be an ancestor of **blastoids** rather than of crinoids...The largest fossil crinoid on record had a stem 40 m..." http://en.wikipedia.org/wiki/Crinoid
[390] **Ordovician Fauna**: http://www.geol.umd.edu/~tholtz/G102/102epal2.htm
[391] *PB2001* p. 49

benthic algae, filter feeders (including sponges, stromatoporoids,[392] corals, etc.), scavengers (such as trilobites) and grazers (including snails), skeletal borers (unnamed), and top predator cepahalopods.

3. Belemnites

[MCM: some authors do not include Belemnites as an Ordovician organism—instead, **orthoconic** [straight-coned] **nautiloids**[393] are seen then.]:

The Belemnite[394] is like a squid in a shell. **Neohibilites,** a small Cretaceous belemnite, is an ammonite-like nautilus [but with a straight guard]. Could go to 800 m, pressure resistant.

---

[392] **Stromatoporoidea**: "is an order of colonial aquatic invertebrates that until recently was believed to have gone extinct in the Devonian. The group was previously thought to be related to the corals and placed in the phylum Cnidaria. It is now thought to belong to the sponges (Porifera). There are numerous fossil forms, dating from the Cambrian to the Cretaceous periods, with spherical, branching or encrusting skeletons of lime. The living members of this order are recognized by the zoological society as sclerosponges but are identical to, what the paleontological community has identified as stromatoporoids. It is poor communication between these two groups that has caused inproper naming of this species and some confusion. Today stromatoporoids have been relegated to a marginal existence in areas intolerable to other reefing benthos."
http://en.wikipedia.org/wiki/Stromatoporoidea

[393] **Nautiloids**: http://en.wikipedia.org/wiki/Nautiloid

[394] **Belemnites**:

• "**Belemnites** (or **belemnoids**) are an extinct group of marine cephalopod, very similar in many ways to the modern squid and closely related to the modern cuttlefish. Like them, the belemnites possessed an ink sac, but, unlike the squid, they possessed ten arms of roughly equal length and no tentacles... Belemnites were numerous during the Jurassic and Cretaceous periods, and their fossils are abundant in Mesozoic marine rocks, often accompanying their cousins the ammonites. The belemnites become extinct at the end of the Cretaceous period along with the ammonites. The belemnites' origin lies within the bactritoid nautiloids, which date from the Devonian period; well-formed belemnite guards can be found in rocks dating from the Mississippian (or Early Carboniferous) onward through the Cretaceous. Other fossil cephalopods include baculites, nautiloids and goniatites.... Normally with fossil belemnites only the back part of the shell (called the **guard** or **rostrum** [MCM: note peculiar use of this word]) is found. The guard is elongated and bullet-shaped, being cylindrical and either pointed or rounded at one end. " Some belemnites (such as Belemnites) serve as index fossils, particularly in the Cretaceous Chalk Formation of Europe, enabling geologists to date the age the rocks in which they are found."
http://en.wikipedia.org/wiki/Belemnite

• "The earliest true belemnites (Belemnitida) date from the early Jurassic period and they became extremely widespread before their extinction at the end of the Cretaceous period, along with the ammonites. The early evolution of the belemnites is poorly understood, it appears that group may have derived from an earlier group known as the **Aulacocerida** which thrived from the Devonian to the early Jurassic. These in turn probably originated from the straight-shelled **orthoconic nautiloids** that dominated the seas as top predators in the Ordovician. The Aulacocerida display characteristics that seem transitional between the orthoconic nautiloids and the later belemnites. It is thought that the nautiloid shell slowly thickened and the phragmocone slowly expanded to reach the highly developed state in the belemnitida. This is particularly clear in the Triassic species Ausseites which has a phragmocone which very closely resembles the earlier nautiloids...

It is estimated that most belemnite species grew to around 300-500mm... The Early Cretaceous belemnite **Neohibilites** minimus has a rostrum about 30mm long implying the adult animal was probably around 100mm or so. On the other hand, there were also giants. The Jurassic Megateuthis is estimated to have reached a length of two to three metres and another example from Indonesia has a rostrum that was 46cm long. As this was only the posterior part of the animal, the whole belemnite may well have approached **four or five metres** in length depending on the length of the arms."
http://www.tonmo.com/science/public/belemnites.php

4. Ammonites[395]

Slide shown of anatomy of ammonite (including chambers) and an ammonite example (a Jurassic period Orthosphinctes), nautilus, and belemnites.

5. Sepkoski Factor III Evolutionary Marine Fauna

This is the fauna dominating the Mesozoic and Cenozoic Eras (Triassic through Neogene). It includes **Gastropoda** (incl. snails and slugs), Bivalvia (incl. scallops, clams, oysters and mussels), **Osteichthyes** (bony fish), Sharks and other **Chondrichthyes**, **Malacostraca** (various **crustaceans** like crabs, lobsters shrimp, krill, etc.), **Echinoidea** (Sea urchins), **Gymnolaemata** (class of bryozoa), **Demospongia** (sponges), ..., Cephalopoda, Anthozoa (sea anemones and corals etc.), Hydrozoa (Hydra, Obelia, Portuguese Man o' War etc.), Reptilia, marine **Mammalia**,[396] etc. [Partial list supplemented by Sepkoski article p. 44 and other sources.] Fossil record of Factor III includes abundant **duraphagous** (shell-crushing) predators on oysters, etc., as well as **infaunal** [burrowing into the seafloor] suspension- and deposit-feeders. This fauna factor exhibits the highest diversity, c. 650 families [in Factor III] by now. Early members of the modern fauna rise to dominance in very shallow habitats, then slowly expand into the shelf [deeper] region. LRS slide shows there are currently **1750 Metazoan**[397] **families**, whereas Sepkoski graph ends at c. 800, presumably because it includes only the marine environment.

6. Terrestrial Biotas

Terrestrial Vascular Plants (Flora) include:

- Silurian to Devonian Flora: early vascular plants (evolutionary end)
- Late Devonian to Early Carboniferous Flora: **Pteridophytes** (example: **ferns**), **lycopods** (clubmosses), **sphenopsids** (horsetails), and **progymnosperms** (ancestors of gymnosperms) [MCM: this factor continues to the present at low numbers according to LRS slide 61]

---

[395] **Ammonite**: “Ammonites are an extinct group of marine animals of the subclass Ammonoidea in the class Cephalopoda, phylum Mollusca. They are excellent index fossils, and it is often possible to link the rock layer in which they are found to specific geological time periods. Ammonites' closest living relative is probably not the modern Nautilus (which they outwardly resemble), but rather the subclass Coleoidea (octopus, squid, and cuttlefish). Their fossil shells usually take the form of planispirals, although there were some helically-spiraled and non-spiraled forms (known as "heteromorphs"). Their spiral shape begot their name, as their fossilized shells somewhat resemble tightly-coiled rams' horns. Plinius the Elder (died 79 A.D. near Pompeii) called fossils of these animals ammonis cornua ("horns of Ammon") because the Egyptian god Ammon (Amun) was typically depicted wearing ram's horns.... Originating from within the bactritoid nautiloids, the ammonoid cephalopods first appeared in the Late Silurian to Early Devonian (circa 400 million years ago) and became extinct at the close of the Cretaceous (65 m.y.a.) along with the dinosaurs.”
http://en.wikipedia.org/wiki/Ammonites

[396] **Post-Paleozoic Families Including Mammalia in Seposki Factor Analysis**: J. John Sepkoski, Jr.. “A Kinetic Model of Phanerozoic Taxonomic Diversity. III. Post-Paleozoic Families and Mass Extinctions” *Paleobiology*, Vol. 10, No. 2. (Spring, 1984), pp. 246-267.

[397] **Metazoan**:
• “Any member of the animal kingdom (Animalia or Metazoa) usually considered to include multicellular, heterotrophic eukaryotes in which (unlike plants) the cells lack cell walls. The term metazoan is less commonly used now than it was because it stems from a classification in which there were two main divisions within the animal kingdom: the multicellular animals, or metazoa, and the single-celled protozoa. The protozoa are no longer included in the animal kingdom, so only the metazoa remain.”
http://www.daviddarling.info/encyclopedia/M/metazoan.html
• “Animals are a major group of **multicellular** organisms, of the kingdom Animalia or Metazoa. Their **body plan becomes fixed** as they develop, usually early on in their development as **embryos**, although some undergo a process of **metamorphosis** later on in their life. Most animals are **motile** - they can move spontaneously and independently. Animals are **heterotrophs** - they are dependent on other organisms (e.g. plants) for sustenance.”
http://en.wikipedia.org/wiki/Animal

- Late Devonian to Mesozoic Flora: Gymnosperm dominated flora of seed plants [MCM: this factor obviously continues to present]
- Early Cretaceous to Present Flora: Angiosperm dominated flora

[MCM: this list of flora is based on some type of similar factor analysis, as shown in slide 61, but source not stated. There is extensive literature on biodiversification which I have not yet explored.]

LRS: "Evidence for declining speciation rates [of flora] and increasing species durations during each radiation. Each new radiation led to an increase in total global diversity while the diversity of the preceding floras declined. Angiosperms continue to diversify at high rates." [MCM: See here[398] for the APG II taxonomy of modern angiosperms.]

Terrestrial Tetrapoda Families:
Tetrapods are 4-limbed vertebrate animals including mammals. Diversification of Tetrapod Families appears to correspond to an exponential model of increase. [MCM: Factors follow but the origin of data not stated. Time periods stated are somewhat confusing, see the LRS graph slide 61]:
1: [MCM: Devonian to Triassic] (30-40 families): **Labyrinthodontia**[399] (amphibians, basal tetrapods), anapsids,[400] synapsids ("mammal-like" reptiles)
2: [MCM: Triassic to K/T boundary mass extinction[401]] (~100 families): **Diapsids**[402]**, dinosaurs, pterosaurs**

---

[398] **Angiosperm Taxonomy (Angiosperm Phylogeny Group APG II System)**:
• http://en.wikipedia.org/wiki/APG_II_system
• http://www.blackwell-synergy.com/links/doi/10.1046/j.1095-8339.2003.t01-1-00158.x/pdf
[399] **Labyrinthodontia**: "The Labyrinthodontia evolved from a bony fish group: the Crossopterygii rhipidistia. Nowadays only a few living representatives of these fish remains: two species of **coelacanth** and three species of **lungfish**... The most diverse group of the labyrinthodonts was the **Batrachomorpha**. Though these animals looked more like crocodiles, they most probably gave rise to the order Anura, the amphibians without tails, which include, in particular, the modern frogs. Batrachomorphs appeared in the Late Devonian, but they had worldwide distribution in the continental shallow basins of the Permian (Platyoposaurus, Melosaurus) and Triassic Periods (Thoosuchus, Benthosuchus, Eryosuchus). Some batrachomorphs existed until the end of the Cretaceous.
http://en.wikipedia.org/wiki/Labyrinthodont
[400] **Anapsid**: "an amniote whose skull does not have openings near the temples... While "anapsid **reptiles**" or "anapsida" are traditionally spoken of as if they were a coherent group, it has been suggested that several groups of reptiles that had anapsid skulls may be only distantly related: scientists still debate the exact relationship between the basal (original) reptiles which first appeared in the late Carboniferous, the various Permian reptiles which had anapsid skulls, and the **Testudines** (**turtles**, tortoises, and terrapins). Many modern paleontologists believe the Testudines are descended from diapsid reptiles which lost their temporal fenestrae, although that view is not generally accepted yet.... The only living reptiles with anapsid skulls are the Testudines. The earliest fossil testudines are from the Triassic, but they were already too like modern turtles to be near the start of their lineage - in particular they already had limb joints within the rib cage... Most of the other reptiles with anapsid skulls, including the millerettids, nyctiphrurets, and pareiasaurs, became extinct in the late Permian period by the Permian-Triassic extinction event. But the procolophonids managed to survive into the Triassic.
http://en.wikipedia.org/wiki/Anapsid
[401] **Mass Extinctions, List**:
1. **Present day**—the **Holocene** extinction event. 70% of biologists view the present era as part of a mass extinction event, possibly one of the fastest ever, according to a 1998 survey by the American Museum of Natural History. Some, such as E. O. Wilson of Harvard University, predict that man's destruction of the biosphere could cause the extinction of one-half of all species in the next 100 years...
2. **65 Ma**—at the Cretaceous-Paleogene transition (the **K/T or Cretaceous–Tertiary or End Cretaceous extinction** event) about 50% of all species became extinct. It has great significance for humans because it ended the reign of dinosaurs and opened the way for mammals to become the dominant land vertebrates. In the seas it reduced the percentage of sessile animals to about 33%...
3. **200 Ma**—at the **Triassic-Jurassic transition** [**End Triassic**] (the Triassic-Jurassic extinction event) about 20% of all marine families as well as most non-dinosaurian archosaurs, most therapsids, and the last of the large amphibians were eliminated.

3: [MCM: Triassic and beyond] (330 families): **Lissamphibia**[403] [including **Amphibia**], **turtles, crocodiles, lizards, birds, Mammalia**

Insects: Diversification increased exponentially through the Mesozoic, slowing somewhat in the Tertiary. This may indicate that insect diversity is approaching an equilibrium level now. There are 350,000 species of **Beetles**, representing 40% of insect diversity. Life on land today is apparently 5-6 times as diverse as life in the sea, largely because of the insects

7. Present Diversity Of Life:

- The number of living species ranges from 2 - 3 million to 30 - 100 million species.
- There are 1.9 million species of modern microbes, plants, and animals have been named so far by [a] systematist (a lower limit of current biodiversity).
- Each year, more than 7000 new insect species are named (versus 1 - 2 new mammals).
- Scientists find new species of microbes, fungi, parasites and deep-sea faunas wherever they look.
- A random soil sample may contain hundreds of previously unrecognized species—also applies to marine mud. Thus it is impossible to predict just how many species are to be found.

Present species diversity: there are 20 - 100 million species, of which only 1.9 million have been named.[404, 405]

---

4. **251 Ma**—at the **Permian-Triassic transition** [**End Permian**], Earth's largest extinction (the P/Tr or Permian-Triassic extinction event) killed 53% of marine families, 84% of marine genera, about 96% of all marine species and an estimated 70% of land species (including plants, insects, and vertebrate animals). The "Great Dying" had enormous evolutionary significance: on land it ended the dominance of mammal-like reptiles and created the opportunity for archosaurs and then dinosaurs to become the dominant land vertebrates; in the seas the percentage of animals that were sessile dropped from 67% to 50%. The whole late Permian was a difficult time for at least marine life—even before the "Great Dying", there was level of extinction large enough to be included in the "Big Five".
5. **360 Ma**—near the Devonian-Carboniferous transition (the **Late Devonian** extinction) a prolonged series of extinctions eliminated about 70% of all species. This was not a sudden event—it lasted perhaps as long as 20 MY, and there is evidence for a series of extinction pulses within this period.
6. **444 Ma**—at the **Ordovician-Silurian transition** [**End Ordovician**] two Ordovician-Silurian extinction events occurred, and together are ranked by many scientists as the second largest of the five major extinctions in Earth's history in terms of percentage of genera that went extinct.
7. **488 Ma**—a series of mass extinctions at the **Cambrian-Ordovician transition** [**End Cambrian**] (the Cambrian-Ordovician extinction events) eliminated many brachiopods and conodonts and severely reduced the number of trilobite species.

http://en.wikipedia.org/wiki/Extinction_event [MCM slightly edited]

[402] **Diapsid**: "Diapsids ("two arches") are a group of **reptiles** that developed two holes (temporal fenestra) in each side of their skulls, about 300 million years ago during the late Carboniferous period. Living diapsids are extremely diverse, and include all **crocodiles, lizards, snakes, tuatara, and possibly even turtles**. Under modern classification systems, even **birds** are considered diapsids, since they evolved from diapsid ancestors and are nested within the diapsid clade. While some diapsids have lost either one hole (lizards), or both holes (snakes), or even have a heavily restructured skull (modern birds), they are still classified as diapsids based on their ancestry. There are at least 7,925 species of diapsid reptile existing in environments around the world today (over 14,600 when birds are included). http://en.wikipedia.org/wiki/Diapsid" [supplemented]

[403] **Lissamphibia**: "The subclass Lissamphibia includes all recent amphibians.... Extant amphibians fall into one of three orders - the **Anura** (frogs, including toads), the **Caudata or Urodela** (salamanders, including newts), and the **Gymnophiona or Apoda** (the limbless caecilians). Although the ancestry of each group is controversial, all share certain common characteristics, which indicates they evolved from a common ancestor and so form a clade."
http://en.wikipedia.org/wiki/Lissamphibia

[404] **The Encyclopedia Of Life**: "Ultimately, the Encyclopedia will serve as an online reference source and database for every one of the 1.8 million species that are named and known on this planet, as well as all those later discovered and described. Encyclopedia of Life will be used as both a teaching and a learning tool, helping scientists, educators, students, and the community at large gain a better understanding of this planet and all who inhabit it."
http://www.eol.org/home.html

8. Mass Extinctions:

Diversification did NOT proceed smoothly however. See LRS slide 66 graph of Extinctions (number of genera) plotted against geologic time (derived from Levin *The Earth Through Time*, fig. 10-84)—this depicts diversity of marine animals compiled from a database recording first and last occurrence of more than 34,000 genera. The 5 extinctions include:

- Late or End Ordovician (Ordovician-Silurian)—c. 444 Ma
- Late Devonian—c. 360 Ma (the 2nd largest)
- Late or End Permian (Permian-Triassic)—c. 251 Ma, the largest
- Late or End Triassic—c. 200 Ma
- Late or End Cretaceous (Cretaceous-Tertiary)—c. 65 Ma

The Phanerozoic Fossil Record: Metazoan Effects On Sedimentation

Ichnofossils (Trace Fossils) and the Cambrian Substrate Revolution

[MCM: Edited slightly from verbatim text of LRS slides, lecture was missed as was given in lab, this is therefore a partial summary. I will not be able to post the slides PDF document, but if available to you see PDF document of slides, containing images which are essential for understanding this material.]

How do siliciclastic[406] sedimentary rocks derive their fabric?

(Fabric is the orientation or the lack thereof of the components [crystals and grains] of which a sedimentary rock is made.)

• Physical processes (original depositional fabric)
• Microbial processes (also produce primary sedimentary fabric)
• Geochemical processes play a minor role in producing fabric (except in carbonate fabric)
• **Bioturbation**[407] by metazoans (destroys primary fabric)

What is a trace fossil (ichnofossil)?

• In soft sediments: footprints, tracks, trails, and burrows
• In hard substrate: raspings, borings, etchings
• Left by animals: coprolites and fecal pellets

---

[405] **The Species 2000 & Integrated Taxonomic Information System (ITIS) Catalogue of Life**: "The Species 2000 & ITIS Catalogue of Life is planned to become a comprehensive catalogue of all known species of organisms on Earth by the year 2011. Rapid progress has been made recently and this, the seventh edition of the Annual Checklist, contains 1,008,965 species. Please note that this is probably just more than half of the world's known species. This means that for many groups it continues to be deficient."
http://www.catalogueoflife.org/info_about_col.php

[406] **Siliclastic**: "Siliciclastic rocks are clastic [fragmented] noncarbonate sedimentary rocks that are almost exclusively silica-bearing, either as forms of quartz or other silicate minerals."
http://en.wikipedia.org/wiki/Siliciclastic

[407] **Bioturbation**: "In oceanography and limnology, bioturbation is the displacement and mixing of sediment particles by benthic fauna (animals) or flora (plants). The mediators of bioturbation are typically annelid worms (e.g. polychaetes, oligochaetes), bivalves (e.g. mussels, clams), gastropods, holothurians, or any other infaunal or epifaunal organisms. Faunal activities, such as burrowing, ingestion and defecation of sediment grains, construction and maintenance of galleries, and infilling of abandoned dwellings, displace sediment grains and mix the sediment matrix. The sediment-water interface increases in area as a result of bioturbation, affecting chemical fluxes and thus exchange between the sediment and water column. Some organisms may further enhance chemical exchange by flushing their burrows with the overlying waters, a process termed bioirrigation. Benthic flora can affect sediments in a manner analogous to burrow construction and flushing by establishing root structures. Bioturbation is a diagenetic process and acts to alter the physical structure, as well as the chemical nature of the sediment."
http://en.wikipedia.org/wiki/Bioturbation

• Commonly also included: plant traces such as root penetration structures, algal mats, and **stromatolites** [this is a little controversial]

Trace fossils/Ichnofossils [examples image, technical names added, see more detailed definitions in footnotes]
A. Crawling traces (Repichnia, e.g., *Cruziana* made by trilobites)
B. Resting traces (Cubichnia, e.g., Rusophycus made by trilobite)
C. Dwelling traces (Domichnia, e.g., *Skolithos*)
D. Grazing traces (Pascichnia, made by grazing herbivores)
E. Feeding traces (Fodichnia)

Bioturbation examples:
Diplichnites trilobite trace
Ophiomorpha sp. burrow

The ichnofacies concept[408]
• Trace fossils do not occur in the oceans in random combinations, but in distinct communities related to water depth (Seilacher, 1964, 1967)
• Each of four main soft-substrate marine communities is named after a characteristic trace fossil:
  Littoral zone: named after **Skolithos** (U-burrows)
  Littoral zone to wave base: named after **Cruziana** (trilobite crawling traces in Lower Paleozoic sequences)
  Wave base to deep ocean: named after **Zoophycos** (complex feeding burrows)
  Deep ocean: named after **Nereites** (meandering traces)
• Other factors control trace-fossil distribution as well:
  Energy conditions at the depositional interface
  Substrate type
  Food availability
  Salinity and oxygen levels

Substrate niches (Levin diagram previously described)

Skolithos Ichnofacies:

---

[408] **Ichnofacies and Rock Facies**:
• "The concept of Ichnofacies was developed by Adolph Seilacher (1967)... This approach is used as a paleontological tool to analyze assemblages of trace fossils to determine ancient depositional settings and facies of sedimentary rocks. These facies were initially defined as assemblages of ichnofossils related by Seilacher (1967) to bathymetry. Since Seilacher's original publication he and like minded scientists have established that ichnofacies are also sensitive to sediment dynamics, coherence of the sediment, salinity, oxygen levels and predation..."
http://strata.geol.sc.edu/terminology/ichnofacies.html
• "The ichnofacies concept ... has become perhaps the best paleontological tool for interpreting ancient environments. Ichnofacies were originally defined as archetypal and recurring assemblages with reference to a bathymetric profile, but subsequent work has shown that water depth is only one facet of ichnofacies. Ichnofacies are named after one distinctive **ichnogenus** that is commonly (but not necessarily) present in the assemblage."
http://www.envs.emory.edu/faculty/MARTIN/ichnology/ichnofacies.htm
• **Sedimentary Rock facies**: "Sedimentary rocks tend to change in composition and nature laterally due to changes in depositional environment. Sediment can be deposited in different places at the same time, yet look very different because of a different depositional environment. Sedimentary facies reflect the characteristics of a particular depositional environment. These deposits each have a distinctive set of physical, chemical and biological attributes. Sea level fluctuations can result in a particular facies being deposited over wide areas."
http://www.geo.ua.edu/intro03/Seds.html
• "The term facies refers to all of the characteristics of a particular rock unit. For example, you might refer to a "tan, cross-bedded oolitic limestone facies". The characteristics of the rock unit come from the depositional environment."
http://gpc.edu/~pgore/geology/geo102/facies.htm

(images) The **Skolithos** Ichnofacies can be recognized by a low diversity of abundant **vertical domichnia** (domicile burrows)[409] (**Skolithos**, **Diplocraterion** and **Arenicolites**), **fodinichnia** (feeding traces[410]) (**Ophiomorpha**), and **fugichnia** (escaping/fleeing traces). All these traces typically indicate intertidal situations where the organisms have to be able to respond rapidly in stressful conditions. The Skolithos Ichnofacies was at first seen as occurring only in the intertidal zone, but it is also typical of other shifting sand environments, such as the tops of storm sand sheets and the tops of turbidity flows.

Cruziana Ichnofacies:
(image) The Cruziana Ichnofacies shows rich trace fossil diversity, with horizontal **repichnia** (walking or locomotion traces) (trilobite **Cruziana** and **Aulichnites**), **cubichnia** (resting traces, including Rusophycus, Asteriacites and Lockeia), and vertical burrows. This ichnofacies represents mid and distal continental shelf situations, below normal wave base, but may be affected by storm activity

(Image): Classic outcrops showing Skolithos pipe rock (in weakly deformed rock)
Cruziana trail showing the central paired leg grooves and the parallel furrows on the outside edges. The curved shape suggests a searching pattern.

(Image): One animal [a trilobite in this case] may, within minutes, produce several different trace fossils that are classified as belonging to different genera. Equally, the same trace fossil may be produced by several separate animals, such as the morphologically simple Trace fossil Planolites (Cruziana ichnofacies)

Rusophycus (Image): resting trace of a trilobite

Thalassinoides Cruziana ichnofacies (Image)

Zoophycos Ichnofacies (Image):
The Zoophycos Ichnofacies is characterized by complex **fodinichnia** (feeding trails) (**Zoophycos**, and sometimes other deep traces such as Thalassinoides) in tiered arrangements. The ichnofacies occurs in a range of water depths between the abyssal zone and the shallow continental shelf, in normal background conditions of sedimentation. The Nereites Ichnofacies may be a matching association found at similar water depths during times of turbidite (event) deposition.

Nereites Ichnofacies (Image)
The Nereites Ichnofacies is recognized by the presence of meandering **pascichnia** (**grazing trails**) (**Nereites**, Neonereites and Helminthoide), spiral pascichnia (Spirorhaphe), and **agrichnia** (farming traces, Paleodictyon and Spirodesmos). Vertical burrows are almost entirely absent. This ichnofacies indicates deep-water environments, including ocean floors and deep marine basins. The trace fossils occur in muds deposited from suspension, and in the mudstones and siltstones of distal turbidites.

Zoophycus traces; Zoophycus ichnofacies (Image)

Trace fossil left by Nereites in the Waterville Formation (Silurian). (Image)

The typical position of the major ichnofacies in marine and continental environments: (Image)
Cr -Cruziana; G -Glossifungites; N -Nereites; Ps -Psilonichnus; Sc -Scoyenia; Sk-Skolithos; Te -Teredolites; Tr-Tripanites; Z -Zoophycos
(after Benton & Harper, 1997)

Schematic diagrams of ichnofabric indices 1-5 for strata deposited in:
A) shelf environments;

---

[409] **Domichnia**: “burrows used principally for dwelling as opposed to feeding” http://www.geo.arizona.edu/geo3xx/geo308_fall2002/backup/cha3.html
[410] **Fodichnia**: “These are feeding structures, usually infaunal burrows made by deposit feeders that systematically mine the sediment for food. A typical feature found associated with these types of traces is called spreiten… Other fodichnial traces consist of complex burrows that form branching networks where the organism has tunneled systematically below the substrate (e.g. Chondrites).” http://www.geo.arizona.edu/geo3xx/geo308_fall2002/backup/cha3.html

B) high-energy nearshore sandy environments dominated by Skolithos;
C) high-energy nearshore sandy environments dominated by Ophiomorpha;
D) deep-sea deposits(Bottjer, 1993)
[Grading system]:
1. No bioturbation
2. ~10% disturbed bedding; discrete, isolated trace fossils
3. ~10-40% of original bedding disturbed
4. ~40-60% of bedding disturbed; last vestiges of bedding discernable
5. Bedding is completely obliterated but burrows are still discrete in places

Metazoan effects on lithic substrates
• Carbonates: limestone and hardgrounds, carbonate clasts, and reefs
  - Chemical and mechanical bioeroders
  - Diversity of trace fossils are high
• Calcite-cemented siliciclastic rocks
  - Bioerosion restricted to between grains—breaks down the rock
• Non-carbonates (igneous and metamorphic rocks)
  - Bioerosion by mechanical borers, including bivalves boring into granite, and crinoids excavating deep chambers within basalt

When did the first trace fossils appear?
• Despite reports to the contrary, there is no widely accepted trace fossil record from sediments older than about **560–555 Ma** (Jensen et al., 2003)
• The above conclusions place serious constraints on the time of appearance of bilaterian animals.
• The first Ediacaran traces are simple surface trails or horizontal burrows.

Neoproterozoic trace fossils (image):
600 -570 Ma trace fossils?
Ediacaran trace fossil

Neoproterozoic seafloors
• Well-laminated sedimentary layers
• Well-developed microbial (algal) mats
• Sharp water-sediment interface
• Poor/little development of vertically-oriented bioturbation (tiering)

History of tiering (vertical ecological structure) of shallow-water benthic marine Communities; the Cambrian fauna show little breadth or complexity in tiering Patterns; the Mesozoic shows maximum tiering breadth (diagram after Ausich and Bottjer(1991)

Agronomic and substrate revolutions!
• Proterozoic-Phanerozoic: Substrates on which marine benthos lived changed from being relatively firm matgrounds with a sharp sediment-water interface to having a high water content and blurry sediment-water interface = **agronomic revolution**
• The impact of this substrate transition, particularly the development of the mixed layer, on benthic metazoans = **Cambrian substrate revolution**.
• Microbial mats, once dominant on shallow marine Proterozoic seafloors, were relegated to stressed settings lacking intense metazoan activity.

Agronomic Revolution (diagram):
Conversion from Garden of Ediacara (with mat scratchers and mat encrusters) to Trophic Escalation
Sedimentary fabrics and processes affected by the agronomic revolution, which was driven by increased bioturbation

What organisms co-existed with the matgrounds?
• "**Mat encrusters**" were permanently attached to the mat
• "**Mat scratchers**" grazed the surface of the mat without destroying it
• "**Mat stickers**" were suspension feeders partially embedded in the mat
• "**Undermat miners**" burrowed beneath the mat and fed on decomposing mat material

Vendian mat scratcher: Kimberella (image)
Kimberella (~550 Ma)
Kimberella reconstructed as a bilaterally symmetrical, benthic animal with a non-mineralized, univalved shell, resembling a mollusk in many respects. Its ruffled borders may be a precursor to the mantle in mollusks

Vendian Mat Stickers: Cloudina: (Image) The earliest animal with a calcareous skeleton, built its shell by stacking vase-shaped "moltings," rather than by marginal accretion.
The Lower Cambrian **Volborthella** filled the apical part of its organic-walled conical shell rhythmically with agglutinated silt, except for a "siphuncular" canal in the center.

How did animals adapt to the Cambrian substrate revolution?
• Advances in organisms (infaunal burrowing, epifaunal grazers) eliminated algal matgrounds
• Many matground grazers accustomed to undisturbed substrate avoided the vertical bioturbation by retreating to the deep sea
• Loss of matground meant extinction for some groups (helioplacoids, for example)
• Mobile animals may have been immune to the changing substrate

Helioplacoid echinoderms (Image) were well-adapted for survival on typical Neoproterozoic-style substrates; they were **sediment stickers** on substrate with only horizontally directed bioturbation. They lacked typical Phanerozoic soft-substrate adaptations, such as hard substrate attachment abilities or a root-like holdfast.

How did organisms adapt to new substrate conditions? (diagram per Bottjer et al., 2000)
By the Late Cambrian, edrioasteroids and eocrinoids had evolved stems and lived attached to hard substrates, no longer as sediment stickers. This evolutionary response of Cambrian sessile suspension-feeding echinoderms is part of the Cambrian substrate revolution. Helicoplacoid echinoderms had gone extinct as it did not adapt.

How did other organisms adapt to the changing substrate?
Some (i.e. mollusks) may have migrated to "environmental refuges".
–Deep-sea substrate; the rate of bioturbation in today's deep-sea is about the same as on early Paleozoic shelves.
–Nearshore rocky coasts or reefs (can still scrape off microbial layers).

Onshore-offshore diagram:
showing environmental distribution of:
1)Late Neoproterozoic-Cambrian rasping traces from early soft-bodied mollusks
2)Cambrian grazing monoplacophorans and polyplacophorans
3)Modern monoplacophorans and polyplacophorans; the rate of bioturbation in today's deep sea is about the same as on early Paleozoic shelves.

Ediacaran (and following) complex organisms mix the sediments to hunt, eat, or hide. The oldest burrows may be found in Ediacaran sediments. However, only after the Cambrian radiation did bioturbation become effective in exchanging components between sediment and the water column (diagram, Bottjer et al., 2000). During the transition from Precambrian to Cambrian, Metazoans became dominant and behavioral complexity increased accordingly.

Cambrian: The positive feedback loop
Flow chart illustrating positive feedbacks related to metazoan activity (grazing and bioturbation) and their ability to alter the environment for further exploitation.

The horizontal burrow trace fossil, Trichophycus [Treptichnus pedum, formerly Phycodes pedum] defines the lower boundary of the Cambrian. (image)

Bioturbation and mass extinction
• Compilation of ichnogeneric diversity for the Phanerozoic does NOT (according to some scientists) show any of the mass extinctions evident in the body fossil record—not even for the Permian-Triassic boundary
• Why?

–Could be an artifact of an incompletely known trace fossil record
–A particular trace fossil pattern may be produced by more than one animal species; the behavior continues despite extinction

The levels of tiering above and below the sediment (Images) were greatly reduced after the end-Permian mass extinction (Ausich and Bottjer, 1982).

Onshore-offshore trends
• Many trace fossils did not have static environmental distribution through time
• May have originated in a shelf environment and migrated into deep water and other environments over time in an onshore-offshore pattern
• Increases in bioturbation moved from onshore to offshore through time as well

Ichnofacies Indices: (Diagram modified from Droser (1987))
Time-environment diagram showing average ii for Great Basin Cambrian and Ordovician carbonate shelf paleoenvironments
IS = Inner Shelf, MS = Middle Shelf, OS = Outer Shelf
LO: Late Ordovician.
MO: Middle Ordovician
EO: Early Ordovician
LC: Late Cambrian
MC: Middle Cambrian
TBEC: trilobite-bearing Early Cambrian
PTEC: pre-trilobite Early Cambrian

Ophiomorpha: (image)
• A branching burrow with a box-like networks; the burrow exterior is characterized by a knobby texture formed by a pelletal lining
• Interpreted as a combined dwelling and feeding burrow made by a shrimp-like animal

Zoophycos: (image)
• Lower Ordovician—inner shelf;
• early Silurian—slope and deep basin;
• Early Devonian-Permian—near-shore environments;
• Cretaceous-Oligocene—inner and middle shelf environments;
• Neogene-present—slope and deep basin Bottjer and Droser, 1994

Metazoan effects on freshwater environments
• The body fossil record of most freshwater burrowers does not extend back before the Mesozoic
• Aquatic sediments were probably not colonized by burrowers until or after the Permian-Triassic
• Compilation of published descriptions of biogenic structures in the Devonian through Triassic non-marine rocks supports this suggestion
• Conclusion: Bioturbation across the sediment-water interface was not operating until after (?) the Paleozoic in freshwater ecosystems

Erosion and deposition
1. The Proterozoic microbial mats would have: lowered erodability, i.e., stabilized sediments
2. The effect of bioturbation would have increased erosion and redeposition
3. Reduced surface–sediment shear strength caused an increased water content and irregular surface topology, resulting in re-suspension of sediments by currents

How did microbial mats respond to erosion?
By biostabilization, or by baffling and trapping the sediment. During calm dynamic conditions, microbial mat layers form by binding and growth.
(Diagram)
Biostabilization by benthic cyanobacteria:
A) Sedimentary grains are interwoven by cyanobacterial filaments, and fixed in their position. This either increases the resistance of the organic-rich sediment against erosion or permits flexible deformation.

B) Reduction of the surface roughness of the sandy deposits by the smoothing mucous-rich cyanobacterial cover (black).
C) Dense mat layer seals the sediment and gases become entrapped. The gas pressure increases over time and generates hollow cavities within the sands.

Trace-fossil diversity: Ediacaran-Lower Silurian (Diagram)
Graphs show mostly rising total trace fossil diversity and trace fossil diversity from strata deposited in deep-water settings from the Ediacaran through the Lower Silurian.
LC: Lower Cambrian; MC: Middle Cambrian; UC: Upper Cambrian; LO: Lower Ordovician; MO: Middle Ordovician; UO: Upper Ordovician; LS: Lower Silurian (source: Crimes et al. (1992))

Extent of bioturbation: Cambrian through Ordovician
(diagram, source Droser & Bottjer(1989)
Histogram of average extent of bioturbation from Cambrian through Ordovician strata deposited in carbonate shallow shelf settings.
Ichnofacies index 1 is no bioturbation.
Ichnofacies index 2 is up to 10% bioturbation;
Ichnofacies index 3 is 10-40%;
Ichnofacies index 4 is 40-60%;
Ichnofacies index 5 is 60-90%.
PTLC is pre-trilobite Lower Cambrian, TBLC is trilobite-bearing Lower Cambrian. All others are listed in previous slides.

Trace-fossil genera through the Phanerozoic (diagram of Precambrian through Triassic, Crimes, 1992)
Numbers of trace fossil genera increased rapidly through the Phanerozoic. Note, the similarity in compilation to Sepkoski's body fossil familial diversity, the three evolutionary faunas—except after the Paleozoic; lack complete understanding of the trace-fossil record.
Deep water forms tend to increase.
Bathymetrically independent forms tend to remain the same or decrease.
Shallow water forms tend to decrease.

Coccolithophore bloom (Image) reflects sunlight.
Acidification of the oceans may destroy many coccoliths [Coccolithophores] and contribute to global warming. Image of Coccolithophores, c. 5 micron diameter overall and with coccoliths of c. 2 micron.

The substrate revolution: Other effects on sedimentation
• Shallow water storm deposits of calcareous "flat-pebble" conglomerates are abundant in the Cambrian and lower Ordovician sediments
• No longer common after the Ordovician and the substrate revolution
• By the Cretaceous there are no layered marine sediments; they are all **bioturbated**. Today, storm layers are gone in a year. Need many storm layers in order to preserve layers.
• So, the trend through time is **increased burrowing**

Reefs and Climate

[MCM: Edited from verbatim text of LRS slides, not all material in the slides was discussed. I will not be able to post the slides document, but if available to you, see PDF document of slides, containing images which are essential for understanding this material.]

Reef topics (related to The Phanerozoic fossil record) include
- What is a reef?
- Reef structure
- Importance of reefs
- Controls in carbonate deposition
- Global distribution of reefs
- Climate and carbonate reefs; aragonite versus calcite seas
- Reefs through time

[Image] A healthy reef in Hawaii

Reef definitions

- Biologically produced three-dimensional bodies of sediments raised above the surrounding seafloor
- The direct or indirect result of organic activity [MCM: usually corals and coralline algae[411], also oysters]
- Aggregation of sessile epibenthic[412] marine organisms
- Results in higher rate of in-situ carbonate production than in surrounding sediments

[Image] Great Barrier Reef, Australia
[MCM: Reefs in the broadest sense can also be abiotic due to deposition of sand, or wave erosion planing down rock outcrops. See here [413] for **geologic reef definition including differentiation from mounds**.]

Reef responses to sea sea-level changes: Stages of Reef Growth [complex diagram from Longman, 1981]:

- **Falling sea-level or tectonic uplift** [MCM: youngest additions to reef occur on the edge of the reef (the **fore-reef**), where the material is deposited near the surface level, whereas the **reef crest** of **back reef** rises above sea level and is no longer a site of deposition.]
- **Stable sea level**: Reef grows by **lateral accretion**, while inner back-reef portion becomes a **lagoon**.
- **Rising sea level or tectonic subsidence with the reef keeping up** [MCM: If the rate of relative sea level rising is slow enough, the reef organisms keep up with **vertical accretion** at the peripheral reef crest, forming a lagoon centrally.]
- **Rising sea level with the submerged reef failing to keep up** and backstepping [MCM: A submerged reef may be left behind, and a new noncontiguous reef form just below the new much higher surface level.]

Reef Types include [images; definitions quoted are from here[414]]:

- **Atoll**: "rings of reef, often encircling an island"

---

[411] **Coralline Algae [or Calcareous Algae]**: "are red algae in the Family Corallinaceae of the order Corallinales characterized by a thallus that is hard as a result of calcareous deposits contained within the cell walls. Unattached specimens (maerl, rhodoliths) may form relatively smooth compact balls to warty or fruticose thalli. Many are typically encrusting and rock-like, found in tropical marine waters all over the world. They play an important role in the ecology of coral reefs. Colors are most typically pink or some other shade of red, but may be purple, yellow, blue, white or gray-green. Sea urchins, parrot fish, limpets (molluscs) and chitons molluscs feed on coralline algae.... A close look at almost any intertidal rocky shore or coral reef will reveal an abundance of pink to pinkish-grey patches, splashed as though by a mad painter over rock surfaces. These patches of pink paint are actually living algae: crustose coralline red algae. The red algae belong to the division Rhodophyta, within which the coralline algae form a distinct, exclusively marine order, the Corallinales. Coralline algae are widespread in all of the world's oceans, where they often cover close to 100% of rocky substrata. Many are epiphytic (grow on other algae or marine angiosperms), or epizoic (grow on animals), and some are even parasitic on other corallines..."
http://en.wikipedia.org/wiki/Coralline_algae

[412] **Epibenthic**: Living on the surface of the sea bottom, either freely moving or sessile. [modified from several sources]

[413] **Reefs**: "Geologists define reefs and related terms (for example, **bioherm**, biostrome, carbonate mound) using the factors of depositional relief, internal structure, and biotic composition. There is no consensus on one universally applicable definition. A useful definition distinguishes reefs from mounds as follows. Both are considered to be varieties of organosedimentary buildups: sedimentary features, built by the interaction of organisms and their environment, that have synoptic relief and whose biotic composition differs from that found on and beneath the surrounding sea floor. Reefs are held up by a **macroscopic skeletal framework**. Coral reefs are an excellent example of this kind. Corals and calcareous algae grow on top of one another and form a three-dimensional framework that is modified in various ways by other organisms and inorganic processes. By contrast, **mounds lack a macroscopic skeletal framework**. Mounds are built by microorganisms or by organisms that don't grow a skeletal framework. A microbial mound might be built exclusively or primarily by cyanobacteria. Excellent examples of **biostromes** formed by cyanobacteria occur in the Great Salt Lake of Utah (USA), and in Shark Bay, Western Australia."
http://en.wikipedia.org/wiki/Reef

[414] **Reef Types**: http://www.starfish.ch/reef/reef.html

- **Barrier reef**: "A coral reef growing parallel to the coastline and separated from it by a lagoon is called a barrier reef."
- **Fringing reef**: "Fringing reefs are relatively young. They can develop in shallow waters along the coast of tropical islands or continents. The corals grow upwards to sea level or just below and outwards towards the open ocean. Fringing reefs are generally narrow platforms a short distance from shore and don't contain a substantial lagoon."
- **Patch [Platform] reefs**: "Platform reefs usually lie in sheltered seas and quite far offshore. They are flat-topped with small and very shallow lagoons."

The **distribution of modern coral reefs** is mostly restricted to low-latitude areas, where the average water temperature exceeds 20°C throughout the year. [map image]

Reef facts

- Modern reefs consist of **zooxanthellate**[415] [zooxanthella-bearing] **scleractinian**[416] **corals**[417] (since about Jurassic)
- They first appeared in the Middle Triassic and replaced the ancient **tabulate**[418] and **rugose**[419] corals that went extinct at the end of the Permian.

---

[415] **Zooxanthella**: "Zooxanthellae ... are golden-brown **intracellular endosymbionts** of various marine animals and protozoa, especially anthozoans. They are members of the **phylum Dinoflagellata** and are typically dinoflagellate **algae**, although algae such as diatoms can also be zooxanthellae... Most are **autotrophs** and provide the host with energy in the form of translocated reduced carbon compounds derived from photosynthesis. Zooxanthellae can provide up to 90% of a coral's energy requirements. In return, the coral provides the zooxanthellae with protection, shelter, and a constant supply of the carbon dioxide required for photosynthesis. Their population in the host tissue is limited by available nutrients and incident light, and by expulsion of excess cells. However, zooxanthellae do not appear to be digested by their hosts."
http://en.wikipedia.org/wiki/Zooxanthella

[416] **Scleractinia**: "Scleractinia, also called **Stony corals**, are exclusively marine animals; they are very similar to sea anemones but generate a hard skeleton. They first appeared in the Middle Triassic and replaced tabulate and rugose corals that went extinct at the end of the Permian. Much of the framework of coral reefs is formed by scleractinians. There are two groups of Scleractinia:
[1] colonial corals found in clear, shallow tropical waters; they are the world's primary reef-builders.
[2] solitary corals are found in all regions of the oceans and do not build reefs.
Some live in temperate, polar waters, or below the photic zone down to 6000 meters."
http://en.wikipedia.org/wiki/Scleractinia

[417] **Corals**: "Corals are marine animals from the class Anthozoa and exist as small sea anemone-like polyps, typically in colonies of many identical individuals. The group includes the important reef builders that are found in tropical oceans, which secrete calcium carbonate to form a hard skeleton. A coral "head", commonly perceived to be a single organism, is actually formed of thousands of individual but genetically identical polyps, each polyp only a few millimeters in diameter. Over thousands of generations, the polyps lay down a skeleton that is characteristic of their species. A head of coral grows by asexual reproduction of the individual polyps. Corals also breed sexually by spawning, with corals of the same species releasing gametes simultaneously over a period of one to several nights around a full moon...Although corals can catch plankton using stinging cells on their tentacles, these animals obtain most of their nutrients from symbiotic unicellular algae called **zooxanthellae**. Consequently, most corals depend on sunlight and grow in clear and shallow water, typically at depths shallower than 60 m (200 ft). These corals can be major contributors to the physical structure of the coral reefs that develop in tropical and subtropical waters, such as the enormous Great Barrier Reef off the coast of Queensland, Australia. Other corals do not have associated algae and can live in much deeper water, such as in the Atlantic, with the cold-water genus Lophelia surviving as deep as 3000 m. Corals have also been found off the coast of Washington State and the Aleutian Islands in Alaska."
[This article also discusses coral reproduction and geologic history.]
http://en.wikipedia.org/wiki/Coral

[418] **Tabulate corals**: "forming the order Tabulata, are an extinct form of coral. They are almost always colonial, forming colonies of individual hexagonal cells known as corallites defined by a skeleton of calcite, similar in appearance to a honeycomb. Adjacent cells are joined by small pores. Their distinguishing feature is their well-developed horizontal internal partitions (tabulae) within each cell, but reduced or absent vertical internal partitions (septae). They are usually smaller than rugose

- Reef building corals evolved in tropical waters deficient in nutrients; **endosymbiosis** now provides the energy needed for maintenance, growth, and reproduction of these reef corals.
- Reefs are **sessile** (permanently attached [MCM: thus not able to move about—not used here in the sense of lacking a stalk]) and **colonial.**
- Sexual and asexual reproduction

[Image of Coral Spawning] Sexual Reproduction: Polyps release millions of eggs and sperm; hatch into larvae

Endosymbiosis
- Corals use CO_2, a product of respiration, and combine it with Ca^{2+} from seawater to form $CaCO_3$ skeletons.
- The energy required to do this comes from microscopic algae (zooxanthellae) living inside the coral's tissue (>1 million/cm^3).
- Photosynthesis by the algae provides the sugars, carbohydrates and fats necessary to support the coral's metabolism.
- The coral in turn, provides shelter and a constant supply of nutrients to the zooxanthellae, such as CO_2, nitrates and phosphates, which are waste products of the coral's own metabolism.

[Image: Coral polyps]

Coral Images:
- Brown zooxanthellae inside the tentacles of a coral polyp
- Soft coral polyps Lobophytum Compactum; green shows the polyp tissue, while red represents the zooxanthellae
- Zooxanthellae in the tissues of a coral polyp.
- Coral polyp (3 -56 mm)—anatomy diagram.

Structures of a typical reef
- **Primary framework growth**: Growth forms varies according to taxonomy and environment;
  - massive, encrusting forms and
  - delicate, open branched forms depending on water energy
- **Secondary framework** growth: **Calcareous, encrusting organisms** attach to the walls of cavities within the primary frame
  - The encrusting organisms have different light requirements
  - Bryozoans and encrusting red foraminifers can grow in nearly dark cavities

Examples of coral growth forms [images]
Encrusting corals:
• Spreading growth forms that usually adhere to hard rocky surfaces
• Growing larger in diameter versus upward
• Major advantage over branching corals [is the resistance to wave action]

---

corals, but vary considerably in shape, from flat to conical to spherical. Around 300 species have been described... Like rugose corals, they lived entirely during the Paleozoic, being found from the Ordovician to the Permian. With Stromatoporoidea and rugose corals, the tabulate corals are characteristic of the shallow waters of the Silurian to the Devonian. Sea levels rose in the Devonian, and tabulate corals became much less common. They finally became extinct in the Permian-Triassic extinction event."
http://en.wikipedia.org/wiki/Tabulate_coral

[419] **Rugose Corals**: "The Rugosa, also called the Tetracoralla, are an extinct order of coral that were abundant in Middle Ordovician to Late Permian seas. Solitary rugosans ... are often referred to as **horn corals** because of a unique horn-shaped chamber with a wrinkled, or rugose, wall. Some solitary rugosans reached nearly a meter in length. However, some species of rugose corals could form large colonies (e.g., Lithostrotion). When radiating septa were present, they were usually in multiples of four... Rugose corals have a skeleton made of calcite that is often fossilized. Like modern corals (Scleractinia), rugose corals were invariably benthic, living on the sea floor or in a reef-framework...The Rugosa is one of the most well-known of corals for its fossilized character. It's almost always in a cast because of its dead body sinking into sand and being filled in with clay and other inorganic particles."
http://en.wikipedia.org/wiki/Rugosa

Branching corals:
Branching corals are characterized by numerous branches. Image shows a large field of branching corals belonging to the family Acroporidae, from the French Frigate Shoals of the Northwestern Hawaiian Islands chain.

Erosion of reefs by physical and biological processes
- Affects mainly protruding portions of the primary framework
- Reef parts will fall into reef crevices; gets encrusted by both primary and secondary frame builders
- boring and grazing actions of organisms; may dislodge primary and secondary framework—major source of sedimentation
- Rates of boring may equal the rate of coral growth (~10 mm/year)
- Newly exposed surface will be colonized by secondary framework builders

Vertical cross cross-section through part of a Bermuda lagoonal patch reef, showing framework structure and internal processes [Image]:
Capital letter symbols indicate primary framework of scleractinian corals, here consisting of three genera (D, Diploria; M, Montastrea; P, Porites).
Secondary framework (laminated patterns) consists of coralline algae, bryozoa, and Agaricia coral. Encrusting foraminifera line the undersides of over over-hangs. Sediment infill is shown by horizontal stipple. Bioerosion is denoted in black, mainly by bivalves (larger holes) and sponges (smaller holes). (Scoffin, 1987)

Reefs—equivalent to the "canary in the mine"
- Reefs are reliable advance indicators of **mass extinction** phases—reefs have served as a global measure of productivity, just as the extent of tropical rainforests today do.
- Reefs generally vanished ~1 million years prior to a final extinction event.

Images: [1] Bleached coral with damsel fish, Great Barrier Reef Marine Park [2] Healthy coral

Reef extinction events
Reefs respond to global extinction events by:
- Reduction in size and areal extent
- Short-ranging taxa
- Ecological "dead zones"
- Switching their structural components to extinction resistant "disaster" species, such as cyanobacteria, calcareous [coralline] algae[420], bryozoans, and encrusting foraminifers

[Image] Ecological "dead zone"—dead corals in Belize's Barrier Reef.

Bryozoans [images]:
- **Archimedes**, Mississippian. In life the individual animals, "zooids", formed sheets that were attached to the central skeletal structure shown here. The whole structure would be attached to the seafloor or a shell.
- **Fenestrate Bryozoan**, Silurian
- **Staghorn Bryozoan** - Heteropora magna

Carbonate minerals
- All carbonate rocks form by combining divalent cations (Ca^{2+}, Mg^{2+}, Fe^{2+}, Sr^{2+}, Mn^{2+} Mn^{2+}, Ba^{2+}) combining with carbonate anions $(CO_3)^{2-}$
- Three carbonate minerals are abundant in the Earth crust: calcite, aragonite, and dolomite

---

[420] **Calcareous Algae [Coralline Algae]**: " are one of the most important reef formers, including the members of Cyanophyta, Rhodophyta, Chlorophyta and Phaeophyta. The main crystalline calcium carbonates of calcareous algae are calcite and aragonite forms. The basic requirement of calcification is an isolating environment. However, there are many hypotheses for calcification mechanisms, e.g., CO_2 utilization theory, HCO_3^- usage theory and organic matrix theory. Calcification is important to the adaptive significance of calcareous algae. The hermatypic roles of reef formers include cementers, structural element formers and sediment formers. Except the role of structural element formers is assigned to corals, the other two roles are calcareous algae."
http://www.mbi.nsysu.edu.tw/~fiddler/plant/alga_e.htm
[See other footnote about **Coralline algae]**

- **Calcite**: (trigonal rhombohedral) stable pseudomorph of aragonite
- **Aragonite**: (orthorhombic) less stable, a more open lattice (surrounded by 9 oxygens), cations can substitute for one another more easily (Sr^{2+}, Ba^{2+}, Pb^{2+})
- **Dolomite:** (trigonal-rhombohedral)

Controls in carbonate deposition

Ca^{2+} (aq) + $2HCO_3^-$ (aq. bicarbonate) $\leftrightarrow$ $CaCO_3$ (s) + CO_2 (aq) + H_2O

- Temperature increase (reaction moves to the right)
- Temperature decreases (reaction moves to the left)
- Pressure decreases (reaction moves to the right)
- Pressure increases (reaction moves to the left)
- Degree of agitation (pockets of low pressure; reaction moves to the right)

Sediment masking and clogging

Biological influences

- Direct precipitation of calcium carbonate by some organism
- Light effect on photosynthetic reef builders (symbiosis)

Carbonate compensation depth (CCD)

Carbonate (aragonite and calcite) compensation depth:

The rate of aragonite/calcite accumulation is balanced (compensated) by the rate of dissolution. [Graph from Scoffin, 1987] depicts:

- Degree of saturation of sea water with respect to aragonite and calcite in the Atlantic Ocean.
- The **ACD [Aragonite Compensation Depth]** is the depth below which no aragonite sediments can accumulate. [Below the ACD, the graphs shows that the degree of saturation of sea water with respect to aragonite is less than 1.0.]. This level is higher than the Calcite CCD and appears at c. 2 km.
- The **lysocline** marks the top of a zone of greatly increased rates of calcite dissolution. The degree of saturation is c. 1.0 with respect to calcite.
- The **CCD Calcite Compensation Depth** is the depth below which no calcite pelagic sediments can accumulate, and appears here to be c. 5.5 km [somewhat deeper than previous values mentioned]. The degree of saturation for calcite is < 1.0.

The importance of reefs through time

- Reefs and their associated carbonate sediments serve as long long-term storehouses of organic carbon
- Thus, reefs are regulators of atmospheric CO_2, and may influence climate
- Protect coastlines from erosion

Global distribution of reefs

- Has varied considerably through geologic time
- Distribution depends on:
  - Geochemical fluctuations (Ca/Mg)
  - Continental configurations
  - Climatic fluctuations
  - Sea level

[Map image of Earth in Early Devonian 390 Ma]

Geochemical fluctuations; aragonite versus calcite seas

Sandberg (1983) suggested that the world's oceans have alternated between:

- "**Aragonite seas**" (icehouse conditions, higher Mg-Ca ratio)
- "**Calcite seas**" (greenhouse conditions, lower Mg-Ca ratio)

Dominant groups of reef builders shift with the Mg Mg-Ca ratio

What drives the oscillation between calcite and aragonite seas? [images, Stanley and Hardie 1998,1999]

Aragonite Sea:

- Low [sea-floor] spreading rate—low [mid-ocean] ridge volume lowers the sea level.
- Low mid-oceanic brine flux
- The aragonite seas correlate with periods of decreased global volcanism.

- Mg is consumed at a low rate because of low spreading.
- The Mg/Ca ratio in seawater is high, promoting precipitation of **aragonite and high-Mg Calcite**.

Calcite Sea:
- High [sea floor] spreading rate—high [mid-ocean] ridge volume raises sea level
- High mid-oceanic ridge brine flux
- Cold sea water circulates more rapidly through fractures into hot, new, oceanic crust and reacts with pillow basalts and sheeted dikes.
- The Mg in the seawater reacts with these rocks and is removed from the seawater—Mg is consumed at a high rate, reducing its concentration in sea water.
- The Mg/Ca ratio in seawater is low, promoting precipitation of **low-Mg calcite**.

[MCM: See Stanley et al 2002 p. 15324 for a graph of Mg/Ca ratio, calcite, and aragonite in seawater, plotted against geologic time.[421] The current ocean is high Mg/Ca and therefore an “aragonite” sea. Modern scleractinian skeleton is composed of aragonite, but fossil carbonates have included low-Mg calcites.[422]]

Why high-Mg calcite?
- Two ions, Ca^{2+} and Mg^{2+}, have fluctuated through time, which changes the types of minerals (calcite versus aragonite) that have precipitated in reefs.
- Mg^{2+} can substitute for Ca^{2+} in many minerals. Mg^{2+} has the same charge and small differences in diameter (Ca = 0.100 nm; Mg = 0.072 nm).
- Thus, Mg can substitute for Ca in the crystal lattice of calcite, but it is too small [to properly fill out the crystal lattice space available] for aragonite (0.118 nm).

Icehouse and greenhouse climates
Produce dramatic differences in seawater temperature and chemistry and, thus, reef growth
- **Icehouse**:
  - Continents come together [to form supercontinents]; extensive polar ice caps [MCM: This is not currently the case.]
  - Sea level low due to lack of seafloor production [MCM: Current sea level is near its historic low]
  - Little limestone and few reefs form
  - Climate cooler, arid
  - Associated with Aragonite seas; high Mg/Ca ratio [MCM: Currently the case]
- **Greenhouse**:
  - Continents dispersed; climate warm and humid; no polar ice caps
  - Sea level high due to high seafloor production[423]
  - Relatively large amounts of CO_2 production at oceanic rifting zones
  - Large volumes of limestone and reefs form
  - Associated with Calcite seas; low Mg/Ca ratio

Latitudinal distribution of direct glacial evidence (tillites, striated bedrock, etc.) throughout the Phanerozoic (Diagram, Crowley, 1998):
This maps degrees of latitude for episodes of paleoglaciation, and correlates them with type of ocean. Depicts alternating major periods Icehouse and Greenhouse conditions:
Aragonite I (Late Proterozoic): Icehouse condition
Calcite I (Early and middle Paleozoic): Greenhouse condition
Aragonite II (Late Paleozoic): Icehouse condition
Calcite II (Jurassic through Eocene): Greenhouse condition
Aragonite III (Neogene to Present): Icehouse condition

---

[421] **Effects of the Mg/Ca ratio of seawater on the mineralogy of nonskeletal carbonate precipitates**: “Our results suggest that many taxa that produce high-Mg calcite today produced low-Mg calcite in Late Cretaceous seas.”
Steven M. Stanley, Justin B. Ries, and Lawrence A. Hardie. “Low-magnesium calcite produced by coralline algae in seawater of Late Cretaceous composition.”
PNAS November 26, 2002 vol. 99 no. 24 15323–15326. Found initially at http://www.pnas.org/cgi/content/full/99/24/15323/F1.
[422] **Modern Coral Aragonite**: http://en.wikipedia.org/wiki/Scleractinia
[423] **Sea Level Changes Through Geologic Time**: http://en.wikipedia.org/wiki/Sea_level

The major Carboniferous and Permian glaciation at c. 300 Ma [**Karoo**[424]] was during Icehouse conditions and Aragonite II.
Recent glaciations (Paleogene and Neogene) correlate with Aragonite III, etc.

The geological time scale illustrating major reef reef-related events. [Diagram]
This diagram shows type of reefs versus geologic time and aragonite versus calcite seas... It refers to bioherms.[425]

The most ancient reefs
Early Cambrian: Early **Archeocyathids**[426] (sponges) and microbial reefs, and **oolitic** carbonates prevailed but did not contribute a significant volume
[Photo and Diagram of Archeocyathids]

Reconstruction of a Lower Cambrian reef community [Diagram]:
1. **Renalcis** (calcified cyanobacterium)
2. branching archaeocyath sponges
3. solitary cup-shaped archaeocyath sponges
4. chancellorid (?sponge)
5. **radiocyath** (?sponge)
6. small, solitary archaeocyath sponges
7. cryptic ‘coralomorphs’
8. Okulitchicyathus (archaeocyath sponge)
9. early fibrous cement forming within crypts
10. microburrows (traces of a deposit-feeder) within geopetal sediment
11. cryptic archaeocyaths and coralomorphs
12. cryptic cribricyaths (problematic, attached skeletal tubes)
13. trilobite trackway
14. cement botryoid
15. sediment with skeletal debris. [per Wood, 1998]

Ordovician

---

[424] **Karoo Glaciation and Timeline of Glaciations**:
http://en.wikipedia.org/wiki/Timeline_of_glaciation
[425] **Bioherms**: “A lenslike to moundlike structure of strictly organic origin. This term involves two concepts: shape and organic internal composition. The term shape denotes original topographic relief above the sea floor as well as a three-dimensional quality: crudely conical (sugar loaf–shaped) or ellipsoidal (bread loaf–shaped). Such forms are massive or unbedded, their upbuilding resulting from the very rapid rate of accretion of organic carbonate once it starts in a favorable locality. There are size limitations: bioherms a meter or so in diameter are known, and some rise 300 ft (100 m) or more above the sea floor.”
http://www.answers.com/topic/bioherm?cat=technology
[426] **Archaeocyathids**:
• “The **Archaeocyatha** or archaeocyathids ("ancient cups") were sessile, reef-building marine organisms of warm tropical and subtropical waters that lived during the early (lower) Cambrian period. They are first known from the beginning of the Tommotian Age of the Cambrian, about 530 million years ago (mya), and quickly diversified into over a hundred families. They became the planet's very first reef building animals... The typical archaeocyathid resembled a hollow horn coral. Each had a conical or vase-shaped porous skeleton of calcite similar to that of a sponge. The structure appeared like a pair of perforated, nested ice cream cones.”
http://en.wikipedia.org/wiki/Archaeocyatha
• “The Archaeocyatha flourished briefly during the Early Cambrian period, then declined drastically, a few survivors straggling on until the end of the period. They are chiefly remembered for being the first Metazoan reef builders. They had calcareous skeletons and lived attached to the sea-floor. They sometimes formed colonies, but were more often solitary. After a long history of phylogenetic uncertainty, the present consensus is that they were sponges. However, their placement as stem demosponges is essentially arbitrary. The archaeocyath body typically consisted of two nested, perforate cones connected by a series of septa. Recent work on the biomechanics of water flow through this structure suggests that archaeocyaths operated much like other sponges.”
http://www.palaeos.com/Invertebrates/Porifera/Archaeocyatha.html

- Continents were to a large extent inundated by shallow seas
- Enormous carbonate platforms covered 50% or more of the tropical shelf regime
- First major diversification of sponges and corals (**tabulate and rugose**)
- Prolific sediment producers and sediment bafflers made up the reefs
- Reefs spread into latitudes as high as 45° - 60° (?)

Latitudinal distribution of distribution of modern and fossil organic reefs
[Histograms from McElhinny (1973)and Briden and Irving (1964)]
- Histogram of modern organic reefs within 10° bands of latitude [show concentration at latitudes less than 30°]
- Present latitudinal distribution of ancient organic reefs [show wider distribution including more northerly latitudes]
- Fossil organic reefs in paleolatitude determined from paleomagnetism; latitudes of the majority of fossil organic reefs are within 30° of the paleoequator, just like modern distribution.

Ordovician through middle Devonian time [image]
A Silurian-Devonian reef: Carbonate platforms were the major, and nearly only, global sedimentary reservoir for carbon. Reef builders during early Paleozoic were all made of calcite.
[Image 1] **Gyrfalcon Bluff**, an exhumed Devonian Stromatoporoid reef, Banks Island, Arctic Canada
[Image 2] Ordovician stromatoporoid (calcareous sponge), Ordovician

Images from Late Ordovician to Early Silurian
[Image] Tabulate and rugose corals, nautiloid, crinoids and brachiopods
[Image] **Calyces** of simple individual Rugose corals

Phylum Echinodermata, Class Crinoidea (Crinoids)
Images of crinoids showing stem or column arising from holdfast or root, crown with calyx, arm, and pinnules.

Devonian Reefs
- Space for Early Devonian reefs was greatly reduced due to major input of sediment from the continents in combination with sea-level lowstand(s)[427]
- A marked decline in reef development towards the end of the Devonian was probably caused by climatic deterioration from greenhouse to icehouse conditions.
- This climate change and rapid evolution of terrestrial ecosystems had a pronounced influence on sedimentation and biodiversity in the marine realm ("Devonian Change").

Carboniferous
Early Carboniferous: Mostly mud mounds containing calcareous mud of unknown origin, possibly baffled by crinoids and bryozoans. Rugose corals, calcified sponges, and brachiopods reappeared to colonize the mud.
[Image] **Devonian mud mounds**[428] [25 - 30 m high] of Morocco, Algeria, are the most spectacularly exposed carbonate buildups of the world.

---

[427] **Lowstands**: "The lowermost bathymetric position or depth reached by sea level during a specific period in geologic time."
http://www.maine.gov/doc/nrimc/mgs/explore/marine/seafloor/glossary.htm
[428] **Algerian Mud Mounds**: "The Devonian mud mounds of the northwestern Sahara (Morocco, Algeria) are the most spectacularly exposed carbonate buildups of the world... The aride climate has uncovered and exhibited these mounds as they were once standing on the sea floor...Generally, the mounds were established in a deeper subtidal environment as suggested by the lack of indications for ground-moving waves. Non-photic conditions are indicated by the absence of cyanobacterial activity (e.g. micritic envelopes) and calcareous algae. The mounds are reefs in the biological sense which means that they are autochthonous structures with a significant relief build by organisms. However, the typical Devonian reef builders, stromatoporoids and colonial rugose corals, are lacking. No rigid framework of organisms is present as that formed by the hermatypic scleractinian corals in modern reefs. The dominating faunal elements are crinoids, tabulate corals, brachiopods, trilobites, sponges, ostracods and bryozoans: thus mostly filter feeding organisms which preferred the exposed mound position because of better oxygenation and better food supply. But all these organisms are all mound

Mesozoic Era
- Permian-Triassic mass extinction: Limestones are missing from the rock record
- Carbonate buildups reappear in the Triassic and were simpler with fewer species than in the Permian
- **Hermatypic**[429] scleractinian corals made entirely of aragonite arose in the Triassic (end of Aragonite II world) and are also dominant today
- Late Triassic: Some shallow shallow-water scleractinian corals depended on zooxanthellae

[Image of modern Hermatypic scleractinian corals]

Reconstructions of an Upper Permian Reef [Images, Wood (1998)]:
Frondose bryozoan-sponge community (New Mexico)
1. Frondose bryozoans (Polypora sp.; Goniopora sp.)
2. Solitary sphinctozoan sponges
3. Archaeolithoporella (encrusting ?algae)
4. Microbial micrite
5. Cement botryoids
6. Sediment (grainstone-packstone)

Platy sponge community (Texas)
1. Gigantospongia discoforma (platy sponge)
2. Solitary and branching sphinctozoan sponges
3. Archaeolithoporella (encrusting ?algae)
4: Microbial micrite
5. Cement botryoids

Fusulinids[430] [images]
- The green arrows point to cross cross-sections of fusulinids, whose distinctive, living chambers were secreted by an extinct single-celled animal; from the Middle Pennsylvanian Keeler Canyon Formation, Inyo County, California.
- Fusulinids cover this limestone slab, collected from the Beil Limestone, Chautauqua County, Kansas.

Jurassic
Jurassic reef diversity during Calcite II was comparable to modern reefs: coral-stromatoporoid reefs, sponge-algal, sponge-bivalve and stromatolitic reef mounds as well as deep deep-water coral-sponge mounds dominated.

Cretaceous
- Cretaceous: Aragonite coral reefs were replaced by massive calcite **rudistids** (cone-shaped oysters)
- Water transparency might have been poor and rudistids may have trapped huge quantities of sediments
- Calcite seas may have favored the rudistids—higher concentration of CO_2 in atmosphere (aragonite more soluble)

---

dwellers, not mound builders. More than 80% of the mound volume is constituted of a fine-grained carbonate (micrite) whose origin is one of the main miracles of mud mounds. High accumulation rates (0.2-0.8 m/1000 a), purity of mound carbonates (> 95% $CaCO_3$) and homogeneous Mg-calcite mineralogy strongly argue for autochtonous (microbial?) carbonate production… But no direct evidences for calcimicrobes as the driving source of mud-mound formation have ever been found." http://www.uni-tuebingen.de/geo/gpi/mitarbeiter/kaufmann/mudmounds.htm

[429] **Hermatypic corals**: "are corals that contain and depend upon zooxanthellae (algae) for nutrients." http://en.wikipedia.org/wiki/Hermatypic_coral

[430] **Fusulinids**: "are an extinct group of foraminiferan protozoa. They produced calcareous shells, which are of fine calcite granules packed closely together; this distinguishes them from other calcareous forams, where the test is usually hyaline. Their fossils are so abundant that they have formed entire limestone formations. The fusulinid Cottonwood Limestone formation in Kansas is an example of this… Fusulinids appeared late in the Mississippian Period. They were a part of the Carboniferous and Permian marine communities. They are excellent guide fossils for Pennsylvanian and Permian rocks. However, fusulinids became extinct at the end of the Permian Period." http://en.wikipedia.org/wiki/Fusulinid

[Image] **Rudist bivalves**: Bouquet of bivalves: Durania cornupastoris at Abu Roash, Western Desert near Gizah, Egypt
[Diagram of Durania]

Cretaceous-Tertiary
- Cretaceous-Tertiary extinction: The most prolific carbonate-producing organisms became extinct because they thrive within narrow environmental limits
- Rudists became extinct
- A few species each of the coccolithophorids and planktonic foraminifera, that had been very common and gave the name to the Cretaceous, survived
- Scleractinian corals had adapted to deeper water and a few species survived

Foraminifera and Coccoliths [Images]
- **Planktonic foraminifera**: **Hantkenina alabamensis**, an unusual planktonic foraminifera from the late Eocene Pashuta Formation, Clarke County, Mississippi. Specimen is about 0.8 mm from spine tip to spine tip.
- Recent planktonic foraminifera: Young Neogloboquadrina pachyderma taken from sea ice, Arthur Harbor, Anvers Island, Antarctic Peninsula. Specimen is about I mm in size.
- Calcidiscus leptopous **coccolith**
- Emiliana huxleyi **coccolith**

Coccolithophores [Images]
- **Emiliania huxleyi** is only one of 5,000 or so different species of phytoplankton—freely drifting, photosynthesizing microscopic organisms that live in the upper, sunlit layers of the ocean.
- Satellite image of blooms [of **Coccolithophores**] off Newfoundland, July 1999,

How did the changes from calcite to aragonite seas affect the coral reefs?
- Deep-water **ahermatypic[431] corals** were unaffected—do not require symbiotic algae (no massive reefs)
- Hermatypic reef-building corals are very sensitive to changes in seawater chemistry and were especially affected by changes in Mg-Ca ratios
- Poor mechanism for regulating carbonate production
- Need zooxanthellae in their tissues to precipitate carbonate
- **Mollusks** (use both aragonite and calcite), brachiopods (low-Mg calcite), and echinoderms (high-Mg calcite) lived through these chemical changes without noticeable effect [Images]

Summary of reef building during the Phanerozoic
- Significant increases in bioerosion, debris , production, relative abundance of platform margin reefs, aragonitic and high-magnesium calcitic reef builders
- **Micrite** (lime mud, $CaCO_3$) and marine cement content significantly decrease

An idealized stratigraphic column showing the Phanerozoic history of bioherms [diagram]
This is a complex diagram depicting major reef builders from Precambrian to Tertiary [after Prothero and Schwab, 2004]: Archaeocyathids, Skeletal Algae, Stromatoporoids and Corals, Phylloid Algae, Sponges, Tubiphytes, Rudists, Bryozoa, etc.
A **Bioherm** is a moundlike form built by corals, echinoderms, gastropods, mollusks, and others; fossil calcareous algae are prominent in some bioherms. [MCM: Thus bioherm is an encompassing term which includes both reefs and mounds.]

Plant Evolution and World Productivity (Focus on Vascular Land Plants)

[MCM: Edited from verbatim text of LRS slides, not all material in the slides was discussed. I will not be able to post the slides document, but if available to you, see PDF document of slides, containing images which are essential for understanding this material. This presentation focuses primarily on

[431] **Ahermatypic coral**: Coral that do not contain zooxanthaellae and do not depend on their endosymbiosis.

vascular land plants or Tracheophyta[432] and their immediate land ancestors, not the less complex forms of plant life such as unicellular forms, algae, liverworts, hornworts, and mosses (bryophyta). This website[433] is a good overall resource on botany.]

Importance of [Vascular Land] Plants

- One of the major events in history[434]
- Opened new environments for animals to utilize
- Changed the nature of physical and chemical processes on earth.

Species-level diversity curves for vascular plants species over geological time. [Graph showing]:
1. Early land plants in small numbers in Silurian and Devonian
2. Spore producing plants (**pteridophytes**[435]) peaking in Carboniferous
3. Seed plants (**gymnosperms**[436]) peaking in Cretaceous
4. Flowering plants (angiosperms) rising from Cretaceous to the present

[MCM: note that there appear to be far too few species.]
[Graph] Rates of plant species turnover (origination minus extinctions) through geological time (Niklas, 1997)

---

[432] **Vascular Plants (Tracheophyta)**: "The vascular plants (also known as tracheophytes or higher plants) are those plants that have lignified tissues for conducting water, minerals, and photosynthetic products through the plant. Vascular plants include the ferns, clubmosses, flowering plants, conifers and other gymnosperms. Scientific names for the group include Tracheophyta and Tracheobionta, but neither name is very widely used."
http://en.wikipedia.org/wiki/Vascular_plant

[433] **Botany Online**: http://www.biologie.uni-hamburg.de/b-online/e00/contents.htm

[434] **Plant Evolution**: http://en.wikipedia.org/wiki/Evolutionary_history_of_plants

[435] **Pteridophytes**: "The pteridophytes do not form a monophyletic group but consist of several groups, the **Lycopodiophyta** (club mosses, spike mosses, and quillworts), the **Equisetophyta** (horsetails), the **Psilotophyta** (whisk ferns), the **Ophioglossophyta** (adder's tongues and grape ferns), and the **Pteridophyta** (true ferns). In addition to these living groups of pteridophytes are several groups now extinct and known only from fossils. These groups include the **Rhyniophyta**, **Zosterophyllophyta**, **Trimerophytophyta**, and the **progymnosperms**. Modern studies of the land plants agree that all the pteridophytes share a single common ancestor. However, they are not a clade (monophyletic group) because the seed plants are also descended from within this group -- probably close relatives of the progymnosperms."
http://en.wikipedia.org/wiki/Pteridophyte

[436] **Gymnosperms**: "(Gymnospermae) are a group of spermatophyte seed-bearing plants with ovules on the edge or blade of an open sporophyll, the sporophylls usually arranged in cone-like structures. The other major group of seed-bearing plants, the angiosperms, have ovules enclosed in a carpel, a sporophyll with fused margins. The term gymnosperm comes from the Greek word gumnospermos, meaning "naked seeds" and referring to the unenclosed condition of the seeds, as when they are produced they are found naked on the scales of a cone or similar structure. Gymnosperms are heterosporous, producing microspores that develop into pollen grains and megaspores that are retained in an ovule. After fertilization (joining of the micro- and megaspore), the resulting embryo, along with other cells comprising the ovule, develops into a seed. The seed is a sporophyte resting stage...

In early classification schemes, the gymnosperms (Gymnospermae) "naked seed" plants were regarded as a "natural" group. However, certain fossil discoveries suggest that the angiosperms evolved from a gymnosperm ancestor, which would make the gymnosperms a paraphyletic group if all extinct taxa are included. Modern cladistics only accepts taxa that are monophyletic, traceable to a common ancestor and inclusive of all descendants of that common ancestor. So, while the term 'gymnosperm' is still widely used for non-angiosperm seed-bearing plants, the plant species once treated as gymnosperms are usually distributed among four groups, which can be given equal rank as divisions within the Kingdom Plantae.

Molecular phylogenies of extant gymnosperms have conflicted with morphological datasets with regard to whether they comprise a monophyletic group or a paraphyletic one that gave rise to angiosperms. At issue is whether the Gnetophyta are the sister taxon to angiosperms, or whether they are sister to, or nested within, other extant gymnosperms."
http://en.wikipedia.org/wiki/Gymnosperm

Who were the plant ancestors?

- Eukaryotes resembling green and red algae appeared 1.4 billion [or more] years ago
- Many similarities especially of green algae with land plants:
  - Similar cell division (complex network of microtubules and membrane vesicles)
  - Carotenoids (natural fat-soluble pigments found principally in plants, algae, and photosynthetic bacteria)
  - Starch storage
  - Chlorophyll
  - Cellulose cell walls
  - Meiotic spore formation

[Image] Plant cellulose cell walls from the ragweed plant

Devonian Early Vascular Plants (409 - 363 Ma)

Four major groups dominated:

- **Rhyniophytes**[437]
- **Zosterophyllophytes**[438] (a group of early vascular plants, included in subsequent diagram within the Lycophytes)
- **Lycophytes**[439] (club mosses and scale trees)
- **Trimerophytes**[440] (early vascular plants, included in subsequent diagram within the Euphyllophytes)

---

[437] **Rhyniophyta**: "is a division of early vascular plants including the class Rhyniopsida. Its circumscription of included species has changed as additional information is revealed in the form of new fossils or new analysis. In particular, some specimens previously included in the group are now known to lack vascular tissue, and so cannot be included in the group if it is to be monophyletic. Currently, the group is reduced to include the genera Huvenia, Rhynia, and Stockmansella, all from the Devonian. One of the most important radiations for land plants occurred in the early Devonian (Pragian), when the first rhyniophytes appear in the fossil record, making this rich fossil discovery of major importance to paleobotany.

The general term "rhyniophytes" is also a name sometimes used for the assemblage of plants found in the Rhynie chert, Lagerstätte (rich fossil beds) in Aberdeenshire, Scotland. The Rhynie flora are unusual for their excellent preservation of very early fossils of primitive vascular plants, in addition to plants with uncertain vascular traces, and non-vascular plants…" http://en.wikipedia.org/wiki/Rhyniophyta

[438] **Zosterophylls**: "Evolving from a rhyniophyte-like ancestor around the beginning of the Devonian, the Zosterophyllophyta is an extinct taxon of small, rather unprepossessing Devonian plants. Zosterophylls occupy a key place in the evolution of land plants; several fossils show characters that are otherwise very typical of the lycophytes. Though the evolutionary relationships of the zosterophylls have not yet been worked out completely, several taxa traditionally placed in the Zosterophyllophyta appear to be close to the ancestry of the Lycophyta… The Zosterophyllophyta is probably a paraphyletic assemblage of early plants, including the ancestors and close relatives of the Lycophyta." http://www.ucmp.berkeley.edu/plants/lycophyta/zostero.html

[439] **Lycophytes** (**Club mosses and Scale trees)**: "The lycophytes are a small and inconspicuous group of plants today, but in the Carboniferous some lycophytes were forest-forming trees more than 35 meters tall. Lycophytes are the oldest extant group of vascular plants, and dominated major habitats for 40 million years. The club mosses (Lycopodiales) are usually evergreen, and have been used as Christmas decorations, though their flammable spores and increasing rarity has made this illegal in some states. Other lycophytes, such as Selaginella, may form extensive carpets in the understory of wet tropical forests. The most significant feature of lycophytes are microphylls, a kind of leaf which has arisen and evolved independently from the leaves of other vascular plants…" http://www.ucmp.berkeley.edu/plants/lycophyta/lycophyta.html

[440] **Trimerophytes**: "A number of fossil vascular plants of the Devonian are superficially similar to the "rhyniophytes" but show some features not found in the rhyniophytes. These plants are grouped together in the Trimerophytophyta, the "trimerophytes." This group is almost certainly paraphyletic; that is, it does not include all the descendants of a common ancestor. Nonetheless, trimerophytes are of great evolutionary interest, because they include fossils that are close to the common ancestry of prominent plant taxa, such as ferns, progymnosperms, and sphenophytes. The trimerophytes appear to form a sort of basal group close to the ancestry of these major taxa.

Like the rhyniophytes, trimerophytes lacked leaves and roots; most of the plant body consisted of branching stems that were photosynthetic throughout their length. Vascular tissue was present, First appearance of:

- **Progymnosperms**[441]—produce spores but have characteristics that resemble the future gymnosperms (example: **Archaeopteris**[442], the earliest tree)
- **Pteridosperms**[443] (**seed ferns** or **Pteridospermatophyta**—extinct gymnosperms)
- **Pteropsids**[444] (**ferns**[445], also variously categorized as **Pteridophyta**, **Filicophyta**, or **Polypodiopsida**)

Rapid radiation by the end of Devonian

[Diagram] **Early vascular plants**. The **rhyniophytes** diversified during the Silurian through the Middle Devonian into [or alongside] the two major trachaeophyte clades: **Lycophytes** [which have **microphylls**, which are not true leaves] and **Euphyllophytes**[446] (the "true leaf plants" having **megaphylls**).

Charophyceae (stoneworts)—an evolutionary link between green algae and land plants?

- A Silurian terrestrial thalloid (filamentous) plant, **Parka decipiens**, is very similar to modern **Coleochaete** (0.5 0.5-7 cm in diameter): It is classified as neither a bryophyte (non-vascular plants), nor a tracheophyte (vascular plants)
- Chemical analysis of Parka decipiens support the evolutionary-link suggestion: Starch, cellulose, and a range of hydrocarbon compositions are similar to present present-day green algae

[Image] Silurian-Devonian Parka decipiens

---

forming a solid central bundle in the center of the stem, or protostele...

Like the rhyniophytes, but unlike the superficially similar zosterophylls from the same time period, trimerophytes bore sporangia at the tips of branches..."
http://www.ucmp.berkeley.edu/plants/trimerophytophyta/trimero.html

[441] **Progymnosperms**: http://www.ucmp.berkeley.edu/seedplants/progymnosperms.html

[442] **Archaeopteris**: "is an extinct genus of tree-like plants with fern-like leaves that many scientists believe to be the **first tree**. A useful index fossil, this tree is found in strata dating from the Upper Devonian to Lower Carboniferous. Fossils are found in Europe, North America, and Morocco in North Africa. Some specimens have also been reported from Australia. Many scientists consider Archaeopteris to be the earliest known modern tree...

Because Archaeopteris reproduced by releasing spores rather than by producing seeds, paleobotanists suspect that modern trees come from a sibling line of plants they call the "**progymnosperms**". Archaeopteris is more like an ancient cousin than a direct ancestor."
http://en.wikipedia.org/wiki/Archaeopteris

[443] **Pteridospermatophyta**: "also called seed ferns, is an extinct spermatophyte group of the Plantae kingdom. Members of this division were predominant at the late Devonian, declined some 250 mya, and disappeared in the Cretaceous. The Pteridospermatophyta have not yet acquired a clear position in botanical systematics and indeed appear to be a paraphyletic form taxon. Some appear to be allied or ancestral to the gymnosperms."
http://en.wikipedia.org/wiki/Pteridosperms

[444] **Pteropsid**: refers to **Pteropsida**, a subdivision of vascular plants that is no longer in use. It includes all flowering plants and ferns and is divided into Filicinae, Gymnospermae, and Angiospermae.
http://en.wikipedia.org/wiki/Pteropsid

[445] **Ferns or Pteridophyta**: A fern is any one of a group of about 20,000 species of plants classified in the phylum or division **Pteridophyta**, also known as **Filicophyta**. The group is also referred to as **polypodiophyta**, or **polypodiopsida** when treated as a **subdivision of tracheophyta** (vascular plants). The study of ferns is called **pteridology**, and one who studies ferns is called a pteridologist. The term "**pteridophyte**" has traditionally been used to describe all seedless vascular plants, making it synonymous with "**ferns and fern allies**". This can be confusing since members of the fern phylum Pteridophyta are also sometimes referred to as pteridophytes... Ferns are vascular plants differing from the more primitive **lycophytes** by having true leaves (**megaphylls**), and they differ from seed plants (gymnosperms and angiosperms) in their mode of reproduction - lacking flowers and seeds."
http://en.wikipedia.org/wiki/Fern

[446] **Euphyllophytes**: "Euphyllophytes—the sister group to lycophytes—are characterized by euphylls (leaves with marginal or apical meristems and an associated leaf gap in the vascular stele), lateral branches that terminate in sporangia, and a distinctively lobed primary xylem strand."
http://www.amjbot.org/cgi/content/full/91/10/1582

[Image] Modern Coleochaete [appears quite similar]
The **thallus** is a multicellular plant body exhibiting little differentiation of tissues and lacking such organs as roots, stems and leaves. The thallus is derived from cell divisions occurring in more than two planes. Cells are arranged horizontally across the surface of a substrate. Disk-shaped structures found on some surfaces of the thallus are thought to be fossil remains of sporangia.

"The advantage of being algae"
- Do not have to worry about keeping water in; live in water—don't need cuticles
- Live in a buoyant medium—don't need to develop support
- Do not transpire—do not have to worry about desiccation
- Live in a similar environment top to bottom—don't need roots

[Image] Algae

Where did the earliest land plants occur?
- Near the seashore
- Algae would have been exposed to freshwater
- Alternating wet and dry environment
- Adaptations to survive drying out would have had strong survival value

Living on land required new complex strategies for survival
- Nutrient/water transport system
- Maintaining moisture/resisting desiccation
- Gas exchange/transpiration
- Structure/mechanical support
- Anchoring mechanism
- Reproduction

Nutrient/water transport system
- Early plants required specialized vascular conducting system to transport food and water
- Two types of vascularization exist: **phloem**[447] and **xylem[448]**

---

[447] **Phloem**:
• "In vascular plants, phloem is the living tissue that carries organic nutrients, particularly **sucrose**, a sugar, to all parts of the plant where needed. In trees, the phloem is the innermost layer of the bark, hence the name, derived from the Greek word φλοιος (phloios) for "bark". The phloem is mainly concerned with the transport of glucose and starch made during photosynthesis.... Unlike xylem (which is composed primarily of dead cells), the phloem is composed of still-living cells that transport sap. The sap is a water-based solution, but rich in sugars made by the photosynthetic areas. These sugars are transported to non-photosynthetic parts of the plant, such as the roots, or into storage structures, such as tubers or bulbs... [The companion cells in phloem include] transfer cells ... specialised in scavenging solutes from those in the cell walls which are actively pumped requiring energy.... Organic molecules such as sugars, amino acids, certain hormones, and even messenger RNAs are transported in the phloem through sieve tube elements."
http://en.wikipedia.org/wiki/Phloem
• See also details on plant vessesl in http://www.mcgoodwin.net/pages/PlantPhysUW425.pdf
[448] **Xylem**:
• "In vascular plants, xylem is one of the two types of transport tissue, phloem being the other one. The word "xylem" is derived from classical Greek ξυλον (xylon), "wood", and indeed the best known xylem tissue is wood, though it is found throughout the plant. Its basic function is to transport water... The xylem transports water from the root up the plant. The xylem is mainly responsible for the transportation of water and mineral nutrients throughout the plant. Xylem sap consists mainly of water and inorganic ions, although it can contain a number of organic chemicals as well. This transport is not powered by energy spent by the tracheary elements themselves, which are dead at maturity and no longer have living contents. Two phenomena cause xylem sap to flow: Transpirational pull... and Root pressure..."
http://en.wikipedia.org/wiki/Xylem
• "The lignified cell walls of the xylem elements will at the moment, rather simplifyingly, be called **wood**. They can last for thousands of years..."

- Various tubes and **tracheids** (primitive non-living cells of the xylem) appeared ~430 million years ago; provide water and minerals
- The greater the demand for water (tall plants), the more the tubes thickened—early tubes with thickening probably contained **lignin**

Nutrient/water transport system [Diagram]:
Xylem and phloem are often arranged in **vascular bundles**, surrounded by tissue called **cortex** (which lies inside the **epidermis**). The **cambium** in plants "is a layer of actively dividing cells between xylem (wood) and phloem (bast) tissues that is responsible for the secondary growth of stems and roots..."[449]
Phloem: Sieve elements for the transportation of dissolved carbohydrates: transport by diffusion (active transport) [MCM: Active transport is movement against a concentration gradient, requiring energy, not passive diffusion. The transport in phloem occurs in sieve vascular tissue tube elements[450].]
Xylem: Transports water and minerals away from roots; capillary action (passive transport)

Tracheids and **Vessel Elements**[451] **in Xylem**:

---

http://www.biologie.uni-hamburg.de/b-online/e06/06a.htm
• See also details on plant vessesl in http://www.mcgoodwin.net/pages/PlantPhysUW425.pdf
449 **Cambium**: http://www.britannica.com/eb/article-9018760/cambium
450 **Sieve tube element**:
• "In plant anatomy, **sieve vascular tissue tube elements**, also called **sieve tube members**, are a type of elongated parenchyma cells in **phloem** tissue. At the ends these cells are connected with other sieve elements, and together they constitute the sieve tube. The main function of the sieve tube is transport of carbohydrates in the plant (e.g., from the leaves to the fruits and roots). Unlike vessel elements, which are elongated cells that transport water and minerals in the xylem/wood that are dead when mature, and represent another kind of vascular tissue in the plant, sieve elements are living cells... At the interface between two sieve tube members in angiosperms are **sieve plates**, pores in the plant cell walls that facilitate the movement of liquid. Neighbouring each of the sieve tube elements is a minimum of one **companion cell**, connected by plasmodesmata (channels between the cells)."
http://en.wikipedia.org/wiki/Sieve_tube_element
• See also details on plant vessesl in http://www.mcgoodwin.net/pages/PlantPhysUW425.pdf
451 **Tracheids and Vessel Elements (Wood Vessels)**:
• "**Tracheids** are water conducting cell forming part of the plant xylem. Contains thick, lignified secondary cells walls, with no protoplast at maturity. Interconnects with neighbouring tracheids through pits, the end walls are not perforated."
http://www.biology-online.org/dictionary/Tracheids
• "**Tracheids** are elongated cells in the xylem of vascular plants, serving in the transport of water... Tracheids are one of two types of tracheary elements, **vessel elements** being the other. All tracheary elements will develop a thick lignified cell wall, and at maturity the protoplast has broken down and disappeared. The presence of tracheary elements is the defining characteristic of vascular plants to differentiate them from non-vascular plants. The two major functions that tracheids may fulfill are (1) as part of the transport system, (2) in structural support...In most cases, the prime function of tracheids is that of transporting water. They occur in vascular bundles throughout the non-woody parts of the vascular plant and provide water and minerals collected by the roots to leaves and other parts of the plant (stem, flowers, fruits etc). A good example of structural support is in softwoods where tracheids are the major cell type. Tracheids give softwood its strength."
http://en.wikipedia.org/wiki/Tracheid
• "A **vessel element** is one of the cell types found in xylem, the water conducting tissue of plants. Vessel elements are typically found in the angiosperms but absent from most gymnosperms such as the conifers. Vessel elements are the building blocks of vessels, which constitute the major part of the water transporting system in the plants where they occur..."
http://encyclopedia.thefreedictionary.com/Vessel+elements
• "In the more primitive conifers the xylem consists largely of spindle-shaped cells called **tracheids**, which have a diameter around 0.04 millimetre (0.0016 inch) and a length of about 3 millimetres (0.12 inch). Flowering plants have a more highly specialized xylem, in which the mechanical function and the water-conduction function have been separated during evolution. Tracheids, the primitive conducting cells, have evolved into **fibres** for mechanical strength and **vessels** for water conduction, particularly in angiosperms. **Vessel elements** are barrellike cells with widths of up to 0.5 millimetre (0.02 inch) in some plants. Vessel elements are arranged end to end; their end walls are partly or

Tracheids are nonliving cells found in the xylem of the more ancient plant types, seedless vascular plants (ferns, club mosses, and horsetails) and gymnosperms (cedar, pine, and cypress trees). Tracheids consist of single elongated cells with pointed [closed] ends and a secondary, cellulose wall thickened with **lignin**. The tracheid contains numerous pits [allowing interconnection between adjacent tracheids, and is closed at the ends]. At functional maturity, the cell is dead and empty. [**Vessel elements** are larger in diameter and found only in angiosperms.]
[Image of a Vascular Bundle from a Monocot—therefore an angiosperm]
[Image of tracheids]
[Diagram] Tracheid of extant vascular plant
[Diagram] Silurian tube [a tracheid?] (~440 Ma) with helical thickening on the inner surface; these tubes have measured ≤200 µm
[Diagram] Example of a cell wall of early tubes and tracheids in the fossil record—this one with annular-reticulate thickening (Willis and McElwain 2002)

Maintaining moisture/resisting desiccation
- Plants developed the cuticle (("skin"), a covering of cutin (wax and insoluble lipid polymers) in the epidermal cells to reduce water loss
- Seen first in the early Silurian (~430 Ma)
- The cuticle inhibits desiccation, protect against microbial attack, abrasion and mechanical injury
- Flaw: Initially prevented adequate flow of gases

Cuticle: A layer deposited on the cell wall, facing the environment, is embedded with waxes and fatty acids (**cutin**) to make the surface of the plant resistant to water loss and pathogen attack. Chemically, this layer has a number of components, comprising an organized structure that is not well understood, and which differ from plant to plant. (www.life.uiuc.edu)
[Cross Section Image] Shows surface wax, cuticle, cell wall, epidermis, and interior cells.

Gas exchange/transpiration
- Development of an imperforate, thin cuticle (allowed movement of gases by diffusion)
- Invention of **stomata**[452] (~408 Ma) to allow gases such as CO_2 and O_2 and H_2O in and out through the cuticle
- Fossil stomatal densities were closely related to the atmospheric CO_2 level

The stoma are valves (regulated holes) found on the surface of leaves and some stems, which allow the passage of gases (such as CO and O_2) into and out of plants otherwise blocked by cuticle. When investigating fossil stomatal densities, high stomatal densities occur at times of low atmospheric CO_2 densities and vice versa.
[Diagram] Shows excess water vapor flowing out through a stoma and CO_2 flowing in.

Structure/mechanical support
- Precursors to vascular plants may have grown horizontally along a rock substrate
- To attain height, plants needed a solid and/or thick-walled stem
- Early, thin, short stems with small internal diameter evolved into wider, longer stems with greater internal diameter
- Early plants had a photosynthetic "rind" just beneath the surface and hydrostatic tissue in the middle surface
- Thickening of the stem to attain height presented a physical barrier to photosynthesis—plant body compartmentalized

---

wholly dissolved, and rows of such cells thus form long **capillaries** (tubes) up to several metres in length. These tubes are the vessels."
http://www.search.eb.com.offcampus.lib.washington.edu/eb/article-73102
• See also details on plant vessesl in http://www.mcgoodwin.net/pages/PlantPhysUW425.pdf
[452] **Stoma**: "a "stoma" (also stomate; plural **stomata**) is a tiny opening or pore, found mostly on the underside of a plant leaf and used for gas exchange. The pore is formed by a pair of specialized sclerenchyma cells known as **guard cells** which are responsible for regulating the size of the opening. Air containing carbon dioxide enters the plant through these openings where it gets used in photosynthesis and respiration. Oxygen produced by photosynthesis in the parenchyma cells (parenchyma cells with pectin) of the leaf interior exits through these same openings. Also, water vapor is released into the atmosphere through these pores in a process called transpiration."
http://en.wikipedia.org/wiki/Stoma

[Image] Non-vascular plants Bryophyte: (Bryophyte (Porella) Mosses, liverworts, etc.

[Graph] **Relationship between stem diameter, stem height, and stelar[453] construction** (Niklas 1997)[454]
As stem diameter increases from 10^{-3} m to 1 m, plant height allowable by hydrostatic tissue support increases , but above a limiting height for any given stem diameter, there must be a tissue stiffening process other than hydrostatic stiffening. [MCM: Thinner stems have a hydrostatic core positioned centrally, the optimal location to prevent rupturing the vascular structures when the stem bends. As diameter and height increase, much more of the stem cross section must take on the roles both of water-conduction and mechanical stiffening.]

Anchoring mechanism

- Early plants needed a system to anchor them to the ground and enable them to obtain the mineral elements necessary for nutrition and water from soils
- Some of the first fossil evidence from early Devonian (~408 Ma)
- Early rooting structures were relatively undifferentiated from the aerial part of the plant—when the lower part of the plant was covered with mud, it eventually became specialized into a root system

[Diagram] **Root Systems**: Relative sizes, shapes, and penetration depths of root systems during the Early, Middle, and Late Devonian. Diagram shows invention of specialized below ground (root) tissues for nutrient transport, storage, and support.
1) Rhyniopsida (Aglaophyton)
2) Trimerophytes (Psilophyton)
3) early herbaceous lycopsid
4) early tree lycopsids (Lepidodendron)
5) progymnosperm (Archaeopteris)
6) early gymnosperm
7) filicopsid (fern)

Reproduction

- The development of the reproductive spore (~450 Ma) protected by **sporopollenin** was a key event in the spread of plant life on land
- Resistant spores may have been developed by semi-aquatic plants as a means of surviving periodic desiccation
- These spores may have provided a selective advantage to colonizing land–Neither the production nor dissemination of spores is reliant on water.

Spores[455] [Diagram]
Earliest, Ordovician (~450 Ma) spores were in a tetrahedral arrangement.
Single spores but with a distinctive trilete mark are found in the early Silurian (~430 Ma)
Trilete marks are seen in spores of some extant land plants: bracken and some bryophytes
Meiosis is a process that produces genetic variation.

---

[453] **Stele (**adj. **Stelar)**:
• "In a vascular plant, the stele is the **central part of the root or stem containing the vascular tissue** and occasionally a pith. The concept of the stele was developed in the late nineteenth century by French botanists P. E. L. van Tieghem and H. Doultion as a model for understanding the relationship between the shoot and root, and for discussing the evolution of vascular plant morphology…"
http://en.wikipedia.org/wiki/Stele_(biology)
• "The term Stele is applied to the tissues that develop from the Procambium… The location of the Stele represents an equilibrium between the location of strengthening and conducting cells. Engineering studies show that the ideal location for Strengthening Tissue is just beneath the surface of a cylindrical structure (Niklas 1997). The ideal location for Conducting Tissues is the center of the axis where they would be least likely to break when stems are bent by wind"
http://www.botany.hawaii.edu/faculty/Webb/BOT311/BOT311-00/Transition/invasion_landStele.htm
[454] **Graph of stelar diameter, height, and construction**:
http://www.botany.hawaii.edu/faculty/Webb/BOT311/BOT311-00/Transition/DIASTELE.jpg
[455] **Spores and Pollens**: http://www.ucl.ac.uk/GeolSci/micropal/spore.html

Diagram shows Meiotic division of a tetrahedral spore to single spores with distinctive trilete Y-shaped markings

Sporopollenin: Structure of the spore/pollen[456] wall
[Diagram of pollen wall] The **exine** of the pollen wall is divided into the outer **sexine** which may or may not be sculptured and an inner layer of **nexine** which is not sculptured. The sexine often exhibits a structure of "**columns**" that support an outer "**roof**" that may or not bear sculpture. The "roof" is called a **tectum** and the "columns" are called **columellae**. The tectum may be complete, partial, or absent.
[Image of pollen grains]

Late Silurian
Simple vascular plants
(Rhyniophyta) Cooksonia
Probably grew in swampy places
How was this plant attached to the substrate?
In many examples, no internal anatomy or cuticle features have been observed
Did they take up CO_2 through their "underground organs"?
[Image] Cooksonia caledonica (a Rhyniophyta) [This plant show regular branching pattern.]

[Image] Cooksonia: dichotomously branched (branch into two equal branches), plant body with sporangia (spore-bearing structures) at the end of each branch tip
[Drawing] Silurian landscape ~6 cm tall

Early Devonian
Rhyniophytes (Rhynia) date back ~400 Ma:
- Named after the Rhynie[457] chert beds in Scotland
- Simple vascular plants with true woody vascular tissue
- Has a cylindrical subterranean rhizome that bore upright, leafless, simply branches, aerial shoots
- No roots or foliar structures of any kind; instead rhizoids from the underside of the rhizome

[Image]: Cross section through an axis of Rhynie gwynne-vaughanii. A central stele (stem) consisting of water conducting cells [positioned most centrally] surrounded by a tissue that conducted assimilation products. Photosynthesis took place in an inner and outer cortex. The cortex is surrounded by a hypodermis and an epidermis covered by the cuticle.

---

[456] **Pollen**: "Pollen is a fine to coarse powder consisting of microgametophytes (pollen grains), which produce the male gametes (sperm cells) of seed plants... Each pollen grain contains vegetative cells (only one in most flowering plants but several in other seed plants) and a generative cell containing a tube nucleus (that produces the pollen tube) and a generative nucleus (that divides to form the two sperm cells). The group of cells is surrounded by a cellulose cell wall and a thick, tough outer wall made of **sporopollenin**. Pollen is produced in the **microsporangium** (contained in the **anther** of an **angiosperm flower**, **male cone** of a coniferous plant, or male cone of other seed plants). Pollen grains come in a wide variety of shapes, sizes, and surface markings characteristic of the species. Most, but certainly not all, are spherical. Pollen grains of pines, firs, and spruces are winged. The smallest pollen grain, that of the Forget-me-not plant (Myosotis sp.), is around 6 μm (0.006 mm) in diameter. The study of pollen is called **palynology** and is highly useful in paleoecology, paleontology, archeology, and forensics. In angiosperms during flower development the anther is composed of a mass of cells that appear undifferentiated, except for a partially differentiated dermis. As the flower develops, four groups of **sporogenous cells** form with in the anther, the fertile sporogenous cells are surrounded by layers of sterile cells that grow into the wall of the **pollen sac**, some of the cells grow into nutritive cells that supply nutrition for the microspores that **form by meiotic division** from the sporogenous cells. **Four haploid microspores** are produced from each diploid sporogenous cell called microsporocytes, after meiotic division. After the formation of the four microspores, which are contained by **callose walls**, the development of the pollen grain walls begins. The callose wall is broken down by an enzyme called callase and the freed pollen grains grow in size and develop their characteristic shape and form a resistant outer wall called the **exine** and an inner wall called the **intine**. The exine is made up of a resistant compound called **sporopollenin**; the intine is made up of cellulose and pectin. The exine is what is preserved in the fossil record."
http://en.wikipedia.org/wiki/Pollen
[457] **Rhynie Chert**: http://www.ucmp.berkeley.edu/devonian/rhynie.html

[Drawing] Rhynia ~18 cm tall, sporangia at tips, rhizome (underground horizontal stem)

Late Devonian
Early vascular plants: **Trimerophytes** (~395 Ma)
[Drawing] **Psilophyton**

- Improvement on Rhyniophyte design
- Are of great evolutionary interest; include fossils that are close to the common ancestry of ferns, progymnosperms, and sphenophytes (horsetails)
- Appear to form a sort of basal group close to the ancestry of these major taxa
- In contrast to rhyniophytes, branching was unequal forming a main stem, or axis, with several smaller lateral branches

[Image and Reconstruction] Trimerophyte Psilophyton
[Drawing] Psilophyton dawsonii

Late Devonian
Progymnosperms

- Ancestor of modern seed plants
- Gymnosperm-like stem anatomy but reproduces by spores like ferns and lycopods (club mosses)
- Grew as trees (~8 m in height)
- Thick trunks of wood
- Development of true, deeper rooting systems
- Archaeop**teris**: first "real" tree [not "Archeopteris"]

[Image] Archaeopteris
Archaeopteris is very widespread and has been reported from North and South America, Europe and Asia; several localities have yielded very large frond portions, e.g., Bear Island (Arctic), Kiltorkan (Ireland).
[Images] Archaeopteris hibernica, Upper Devonian, Kiltorkan, Ireland, and other Archaeopteris.

Carboniferous

- Great diversification of plants: Dominant flora consisted of ferns, progymnosperms, pteridosperms (seed ferns), lycopods (club mosses), sphenopsids (horsetails), and conifers
- Vast swamps on the continents formed on extensive poorly drained flatlands and large areas of coastal plains
- Coal fields of the Eastern U.S., Europe, and Northern China were primarily deposited during the Upper Carboniferous [Pennsylvanian 318-299 Ma]
- Even during the icehouse conditions of the Late Carboniferous, lush vegetation persisted in the world's tropical and cool temperate regions

[Image] Pteridosperm (seed fern)
[Image] The Pteridosperm seed fern Eusphenopteris sp. from the Upper Westphalian of the Piesberg near Osnabrück, Germany
[Image] Carboniferous seed fern Neuropteris, Graissesac, France
[Image] Sphenopsids: Annularia stellata, a small stem of a Carboniferous **calamite** from the Coal Deposits of France.
[Image] Sphenopsids: Modern horsetail
[Image] Sphenopsids: Sphenophyllum leaves of a late Carboniferous sphenopsid from the Coal Deposits of France.

Atmospheric CO_2 and average global temperature for the Phanerozoic [Graph[458]]

---

[458] **Graph of Atmospheric CO_2 and average global temperature for the Phanerozoic**: "Average global temperatures in the Early Carboniferous Period were hot- approximately 20° C (68° F). However, cooling during the Middle Carboniferous reduced average global temperatures to about 12° C (54° F)... This is comparable to the average global temperature on Earth today! Similarly, atmospheric concentrations of carbon dioxide (CO_2) in the Early Carboniferous Period were approximately 1500 ppm (parts per million), but by the Middle Carboniferous had declined to about 350 ppm -- comparable to average CO_2 concentrations today! Earth's atmosphere today contains about 380 ppm CO_2 (0.038%). Compared to former geologic times, our present atmosphere, like the Late Carboniferous atmosphere, is CO_2-impoverished! In the last 600 million years of Earth's history only the Carboniferous Period and our present age, the Quaternary Period, have witnessed CO_2 levels less

This graph shows low CO_2 and temperatures in Late Carboniferous and in current times (see footnote).

Significance of the spore versus seed

- Spores are easy to disperse, but they have few nutrient reserves. A spore contains only genetic material, completely undifferentiated
- A spore can develop into a new organism using mitotic division, producing a multicellular gametophyte, which will eventually go on to produce [haploid] gametes. Two gametes fuse [fertilization] to create a [zygote and then a] new [diploid] sporophyte.
- When a spore reaches a wet area, it germinates rapidly, and begins photosynthesizing straight away
- Thus spore-producing plants are limited to wet environments for at least part of their life cycle

[Diagram] Mitosis produces two daughter [diploid] cells that are identical to the parent cell.
[Diagram] When conditions are favorable, the spore can develop into a new organism using mitotic division.

- In comparison, seeds are the ripened ovules of flowering plants and contain a nutrient store. This means that seed plants (gymnosperms and angiosperms) can colonize areas with transient water as the young plant can establish itself extremely rapidly once it has germinated
- The evolution of the seed underpins the success of the gymnosperms and angiosperms

[Image] Mature seed

Vascular plants: Carboniferous-Permian environmental changes

- The rise of vascular land plants triggered a rise in atmospheric oxygen and an order of magnitude drop in carbon dioxide in the Carboniferous-Permian.
- The evolution of **lignin** resistant to biodegradation—leads to rise in atmospheric oxygen459 [?]
- Increased efficiency of phosphorus weathering from rocks [induced by vascular land plants]—leads to rise in atmospheric oxygen460

---

than 400 ppm... For example, during the Jurassic Period (200 mya), average CO_2 concentrations were about 1800 ppm or about 4.7 times higher than today. The highest concentrations of CO_2 during all of the Paleozoic Era occurred during the Cambrian Period, nearly 7000 ppm -- about 18 times higher than today. The Carboniferous Period and the Ordovician Period were the only geological periods during the Paleozoic Era when global temperatures were as low as they are today. To the consternation of global warming proponents, the Late Ordovician Period was also an Ice Age while at the same time CO_2 concentrations then were nearly 12 times higher than today-- 4400 ppm. According to greenhouse theory, Earth should have been exceedingly hot. Instead, global temperatures were no warmer than today. Clearly, other factors besides atmospheric carbon influence earth temperatures and global warming."
http://mysite.verizon.net/mhieb/WVFossils/Carboniferous_climate.html

[459] **Lignin and Atmospheric Oxygen**: "Jennifer Robinson of Pennsylvania State University, claims that lignin affected the composition of the atmosphere because it is difficult to degrade. The process of degrading - a form of combustion - uses oxygen, so at times in the past when lignin was common, oxygen that would have been used in degrading it would instead have built it up in the atmosphere. The carbon, on the other hand, would have gone into sediments."
http://www.newscientist.com/article/mg12717313.200-science-plant-material-may-have-controlled-oxygen-inatmosphere-.html

[460] **Phosporus weathering by plants and atmospheric oxygen**:
• "However, a new proposal that increases in oxygen suppress the biological amplification of rock weathering and hence the input of phosphorus to the Earth system provides the most effective oxygen regulation of all the mechanisms considered. A range of proxies suggests that the input of available phosphorus to the ocean may have been significantly reduced 40 Myr ago, suppressing new production and organic carbon burial in the model. With only ocean-based feedback, the atmospheric oxygen reservoir is predicted to have shrunk from c. 26% of the atmosphere 40 Myr ago."
http://www.agu.org/pubs/crossref/2000/1999GB900076.shtml
• "The evolution of vascular plants and their spread across the land surface, beginning c. 420 Ma, progressively increased the rate of weathering of phosphorus from rocks. This phosphorus supply promoted terrestrial and marine productivity and the burial of organic carbon, which has been the major source of O_2 over geological timescales. Hence, it is predicted that the rise of plants led to an increase in the O_2 content of the atmosphere from c. 12 vol %, 570–400 Ma to its present level of c. 21 vol % by c. 340 Ma... Such high concentrations are difficult to reconcile with the known persistence of forests, because rising O_2 increases the frequency and intensity of vegetation fires, tending to decrease

- Increased bulk silicate weathering possibly due to increased depth of the soil profile, rock-splitting by plant roots, and accelerated hydrological cycle—a reduction in carbon dioxide ($CO_2 + CaSiO_3 \rightarrow SiO_2 + CaCO_3$)

[Graph] **Levels of atmospheric O_2 and CO_2 during the Phanerozoic Era**
The vertical, dashed red line marks the Permian-Triassic boundary. The green line indicates the level of oxygen; the dashed green line at left, its present atmospheric level (PAL). The grey line indicates the level of carbon dioxide; the dashed grey line, its present atmospheric level. [O2 markedly rose and CO2 markedly fell during late Carboniferous and Early Permian, then moved oppositely at P-Tr boundary.

The existence of forests and atmospheric oxygen limits
- Even though forests have been widespread throughout the past 350 My, fires have never been so frequent as to prevent their regeneration
- However, a small increase in O_2 above 21 vol % causes a large decrease in the ignition energy required to start a fire, which generates a rapid increase in fire probability
- The continuous existence of forests sets an upper limit on O_2 to ~**25 vol %** (Lenton & Watson 2000), although others argue for a higher limit (Beerling et al. 1998).

Permian world
- Supercontinent **Pangea** (**Pangaea**[461]) formed in the early Permian
- Great environmental changes affected atmospheric and ocean circulations
- Still icehouse conditions in Early Permian
- Greenhouse conditions by mid-Permian
- Increased continentality caused widespread aridity and monsoonal climates by Late Permian
- Increased tectonic activity produced higher CO_2 levels, from levels similar to today (350 ppm) in mid-Carboniferous, to four times today's levels in the Triassic

[Image] Pangaea (Pangea) in late Permian 255 Ma

Permian flora
- Widespread glaciation in the southern hemisphere
- However, plants still grew in ice-free areas, among them the seed fern Glossopteris, which is known only from Gondwanaland
- In fact, the distribution of Glossopteris and other members of the Glossopteridales provided early evidence of continental drift.
- The seed ferns died out at the end of the Permian
- Conifers, cycads, and ginkgoes (all gymnosperms) began to replace the earlier forests, and were common across Pangaea during the Triassic.

Glossopteris as evidence for continental drift
[Image] Fossil Glossopteris leaf, Ellsworth Land, Antarctica
[Diagram] Glossopteris
[Diagram] Similar layers of rock (sandstone, shale, and coal) containing Glossopteris formed in Antartica, Australia, S. America, Africa, and India before Pangea broke apart.

[Image] **Dinosaurs** arose in the Triassic. In this scene, Plateosaurus (larger) spies two Yaleosaurus (left) and a smaller Coelophysus behind. **Cycads** were a dominant vegetative type.

Jurassic
- "The age of the cycads"

---

biomass and cause ecological shifts toward faster regenerating ecosystems. Rising O_2 also directly inhibits C3 photosynthetic carbon assimilation and increases the production of toxic reactive oxygen species in cells. These effects suppress plant-induced phosphorus weathering and hence organic carbon burial, providing a sensitive negative feedback on O_2. A revised model predicts that this mechanism could have regulated atmospheric O_2 within the range 15–25 vol % for the last 350 million years."
http://www.ingentaconnect.com/content/bsc/gcb/2001/00000007/00000006/art00429
[461] **Pangaea**: http://en.wikipedia.org/wiki/Pangaea

- The cycads[462] are seed [gymnosperm] plants in which true flowers have not been developed
- Jurassic cycads include tall trees with rough branches marked by the leaf bases of earlier growth and by crowns of leathery pinnate leaves
- Marked decline in the Late Cretaceous
- Few survived to present time—the sago palm is one of the survivors

[Image] Cycas revoluta, the **Sago Palm**

Jurassic and Cretaceous

- Gymnosperms, especially the cycads, remained the dominant land plants in the Jurassic.
- The Cretaceous saw the rise of the flowering plants (angiosperms) and their associated insect pollinators (an example of coevolution).
- There are around 235,000 species of angiosperms
- Angiosperms share a particular set of features: flowers, fruit, and a distinctive life cycle
- Therefore, angiosperms are assumed to be a monophyletic group (consists of a common ancestor and all its descendants).

[Image] Bee collecting pollen

Angiosperms[463]

---

[462] **Cycads**:
• "Cycads are a group of seed plants characterized by a large crown of compound leaves and a stout trunk. They are evergreen, gymnospermous, dioecious plants having large pinnately compound leaves... There are currently 305 described species, in 10-12 genera and 2-3 families of cycads."
http://en.wikipedia.org/wiki/Cycad
• "Propagation of Cycas revoluta is either by seed or by removal of basal offsets. As with other cycads, it is dioecious, with the males bearing cones and the females bearing groups of megasporophylls . Pollination can be done naturally by insects or artificially."
http://en.wikipedia.org/wiki/Cycas_revoluta

[463] **ANGIOSPERM FLOWER CHARACTERISTICS AND SIGNIFICANCE:**
1) **Flowers**: "The flowers of flowering plants are the most remarkable feature distinguishing them from other seed plants. Flowers aided angiosperms by enabling a wider range of evolutionary relationships and broadening the ecological niches open to them..." http://en.wikipedia.org/wiki/Angiosperm
2) **Stamens and Anthers**:
• "Stamens are much lighter than the corresponding organs of gymnosperms and have contributed to the diversification of angiosperms through time with adaptations to ... particular pollinators. Stamens have also become modified through time to prevent self-fertilization, again to increase diversity...."
http://en.wikipedia.org/wiki/Angiosperm
• The **stamen** consists of the **filament** (blade stalk) and the **anther** (consisting of two to four **microsporangia)**, and the stamens are positioned in one or two whorls collectively called the **Androecium**, the "male household".
[MCM fr. various sources]
3) **Reduced male parts**: "The reduced male **[micro]gametophyte** [**pollen**] in angiosperms may have evolved to decrease the amount of time from pollination, the pollen grain reaching the female plant, to the fertilization of the ovary." http://en.wikipedia.org/wiki/Angiosperm
4) **Closed carpel enclosing the ovules**:
• "The most important distinguishing feature separating flowering plants from gymnosperms is that the ovules of flowering plants are produced within **enclosed containers called carpels**."
http://www.search.eb.com.offcampus.lib.washington.edu/eb/article-76175
• "The closed carpel of angiosperms also allows adaptations to specialized pollination syndromes and controls to prevent self-fertilization, thereby maintaining increased diversity."
http://en.wikipedia.org/wiki/Angiosperm
• "A **carpel** is the basic unit of the female reproductive organ of a flower, the **gynoecium**. A flower may have zero, one, or more carpels. Multiple carpels may combine into a single **pistil**, or into multiple pistils."
http://en.wikipedia.org/wiki/Carpel
• "The **gynoecium** is composed of carpels [or pistils]. In more primitive families (e.g., Magnoliaceae) the carpels are spirally arranged, and in more advanced families they tend to be arranged in a single whorl."
http://www.search.eb.com.offcampus.lib.washington.edu/eb/article-73120
• "The **pistil** is "the female reproductive part of a flower. The pistil, centrally located, typically consists

- Evolution of the **flower** was important. The flower's pollen and nectar encourage pollinating insects to visit.
- After fertilization the **carpel** [specifically, the ovary which holds the ovules] and other parts of the flower are used to form fruit that aid dispersal of the seeds inside the fruit.
- The **xylem** vessels of angiosperms allow very rapid movement of water through the plant—thus, flowering plants can keep their stomata open through much of the day, achieving high photosynthetic rates; this "spare" photosynthetic capacity can support the development of fruit.
- The flowers of wind-pollinated angiosperms, e.g. grasses, are very much reduced in terms of size and complexity

[Image of stoma closing] When they are open, the **stomata** allow gas exchange, mainly CO_2 for photosynthesis and H_2O, between the leaf and the atmosphere. During a drought stress the plant has to close their stomata to limit water loss. [Closure is regulated by Abscisic Acid[464] (ABA).]

---

of a swollen base, the **ovary**, which contains the potential seeds, or **ovules**; a stalk, or **style**, arising from the ovary; and a pollen-receptive tip, the **stigma**, variously shaped and often sticky.

Differences in the composition and form of the pistil are useful in determining taxonomic relationships. There may be a single pistil, as in the lily, or several to many pistils, as in the buttercup. **Each pistil is constructed of from one to many enrolled leaflike structures, or carpels**. The carpel is a single megasporophyll, or modified seed-bearing leaf. A pistil then may be composed of one carpel (**simple pistil**), as in the sweet pea, or of two or more carpels (**compound pistil**) partially or completely joined, as in the mustard (two carpels) or lily (three carpels).

A flower that contains separate pistils (and therefore separate carpels) is termed **apocarpous**; if it contains a single pistil with two or more united carpels, it is **syncarpous**.

Pistils in the collective sense form the gynoecium, in distinction to the male reproductive parts, or androecium."
http://www.search.eb.com.offcampus.lib.washington.edu/eb/article-9060194
• "Each carpel of a gynoecium may either form a pistil of its own (**choricarpy** or **apocarpy**) or several carpels may be fused together to one pistil (**coenocarpy**)."
http://www.biologie.uni-hamburg.de/b-online/e02/02d.htm
• "The position of the ovary in relation to the other structures of a flower is an important taxonomical feature. It has to be distinguished between a **hypogynous** (the **perianth** [petals and sepals] is attached to the receptacle below the pistil), **perigynous** (perianth and stamens are borne on the rim of a concave structure in the depression of which the pistil is borne) or **epigynous** ovary (blossom seems to arise upon or above the ovary)."
http://www.biologie.uni-hamburg.de/b-online/e02/02d.htm
5) **Reduced female gametophyte:** The reduced female gametophyte, like the reduced male gametophyte may be adaptations allowing for more rapid seed set, eventually leading to such flowering plant adaptations as **annual herbaceous life cycles**....
6) **Endosperm**: Endosperm formation generally begins after fertilization and before the first division of the zygote. Endosperm is a highly nutritive tissue that can provide food for the developing embryo, the cotyledons, and sometimes for the seedling when it first appears."
http://en.wikipedia.org/wiki/Angiosperm
[464] **Abscisic acid (ABA) [dormin]**:
• "The plant hormone abscisic acid (ABA) is the major player in mediating the adaptation of the plant to stress... ABA mediates the conversion of the apical meristem into a **dormant bud**... It is important the seeds not germinate prematurely during unseasonably mild conditions prior to the onset of winter or a dry season. ABA in the seed enforces this **dormancy**... ABA also promotes **abscission** of leaves and fruits... The **dropping of leaves** in the autumn is a vital response to the onset of winter when ground water is frozen—and thus cannot support transpiration—and snow load would threaten to break any branches still in leaf... ABA is the hormone that triggers **closing of the stomata** when soil water is insufficient to keep up with transpiration."
http://users.rcn.com/jkimball.ma.ultranet/BiologyPages/A/ABA.html
• "When the roots begin to sense a water shortage in the soil, abscisic acid (ABA) is released. ABA binds to certain receptors in the guard cells' plasma membranes, which first raises the pH of the cytosol of the cells and cause the concentration of free Ca^{2+} to increase in the cytosol... chloride (Cl-) and inorganic ions ... stops the uptake of any further K+ ... The loss of these solutes causes a reduction in osmotic pressure, thus making the cell flaccid and so closing the stomatal pores."
http://en.wikipedia.org/wiki/Stoma
• See also http://en.wikipedia.org/wiki/Abscisic_acid

Groups of angiosperms

- Two major groups of angiosperms are the dicotyledons (dicots) and the monocotyledons (monocots—these include the grasses
- Grasses evolved in the Eocene, and this led in turn to the evolution of browsing mammals during the Oligocene.
- With a cooling Miocene these grasslands spread and the forests contracted; by the Pliocene deserts spread in many regions
- The fragmentation of forest habitats and spread of grasslands that accompanied this cooling trend are implicated in the evolution of humans.

Comparison of Monocotyledons (Monocots) and Dicotyledons (Dicots):[465]
Dicotyledons (Dicots) are a group of flowering plants whose seed typically contains two embryonic leaves or cotyledons. There are around 199,350 species within this group. Flowering plants that are not dicots are **Monocotyledons (Monocots)**, typically having one embryonic leaf.
[Image] Young castor oil plant showing its prominent two embryonic leaves (cotyledons), that differ from the adult

- **Flowers**: In monocots, flowers are **trimerous**[466] (number of flower parts in a whorl in threes) while in dicots the flowers are **tetramerous** or **pentamerous** (flower parts are in fours or fives).
- **Pollen Furrows or Pores**: In monocots, pollen has one furrow or pore while dicots have three.
- **Seed Cotyledons**: In monocots, the embryo has one cotyledon while the embryo of the dicot has two.
- **Stem Vascular Bundles**: In monocots, vascular bundles in the stem are scattered, in dicots arranged in a ring.
- **Adventitious Roots**: In monocots, roots are adventitious[467], while in dicots they develop from the radicle showing parallel veins
- **Leaf Veins**: In monocots, the major leaf veins are parallel, while in dicots they are reticulate.

---

[465] **Monocots vs. Dicots** [or **Eudicots**]: "Monocotyledons ... are one of two major groups of flowering plants (angiosperms) that are traditionally recognized, dicotyledons or dicots being the other.,, The APG II system recognizes a clade called "monocots" but does not assign it to a taxonomic rank... Monocots comprise the majority of agricultural plants in terms of biomass produced.... [Famililies include] **orchids**, **grasses** [of] family Poaceae (Gramineae), **palm** family (Arecaceae), **banana** family (Musaceae), **ginger** family (Zingiberaceae) and the **onion** family Alliaceae... many plants cultivated for their blooms are also from the monocot group, notably **lilies, daffodils, irises, amaryllis, orchids, cannas, bluebells and tulips**.
[Article also contains a comparison as above of monocots and dicots.]
http://en.wikipedia.org/wiki/Monocotyledon

[466] **Merosity In Flowers**: "The term merosity stands for the **number of parts within whorls** of floral organs, leaves, or stems. **Trimery** is considered to be a basic condition that arose through the cyclisation of a spiral flower. **Pentamery** is mostly derived from trimery by the repetitive fusion of two different whorls. **Dimery** is either directly derived from trimery, or through **pentamery** as an intermediate stage. Tetramery is linked with pentamery and should not be confused with dimery. Possible causes for a change in merosity are the reduction of the number of carpels and zygomorphy in flowers. Derivations of different merosities have important consequences for the arrangement of the androecium (the insertion of stamen whorls, their identifications, and their number). It is concluded that two main groups can be identified within the angiosperms: magnolialean and monocotyledonean taxa are mostly trimerous or dimerous; non-magnolialean dicots are mostly pentamerous or tetramerous."
L. P. Ronse Decraene and E. F. Smets. Merosity in flowers: Definition, origin, and taxonomic significance. *Plant Systematics and Evolution*. Volume 191, Numbers 1-2 / March, 1994.
http://www.springerlink.com/content/h2t895526v760733/

[467] **Adventitious Roots**: A "root developing from any part other than the radicle is called [an] adventitious root. Adventitious roots develop on stems, leaves and even old roots. The **radicle** or **primary root** and its **lateral roots** are the only nonadventitious roots. "
http://en.wikipedia.org/wiki/Adventitious

Soil formation through time(Evolution of Soils)

[MCM: Edited from verbatim text of LRS slides, not all material in the slides was discussed. I will not be able to post the slides document, but if available to you, see PDF document of slides, containing images which are essential for understanding this material.]

[Drawing of inhabited soil layers, soil ecosystem]
No soil, no terrestrial life!

What is a soil?
According To Soil Scientists: A medium of plant growth. (Then did soil formation start at Precambrian, Cambrian, or Silurian?)
According To Geologist: Soils forms by hydrolysis. (Did soil formation start in the Archean?)
According To NASA: Non-sedimentary modified surfaces of the Moon and Mars [and Earth?]. (Did soil formation start on planetesimals?)

Soil is not dirt!

- The fundamental resource of civilization and terrestrial life
- Highly active chemically, physically, and biologically, and also highly complex in its composition
- Supports a host of communities of living organisms endlessly exchanging energy and chemical resource
- Constantly changing its composition in response to changing conditions

How to distinguish a soil from sediments
[Diagram showing pie chart with percents]
Soil contains mineral particles 45%, air 25%, water 25%, and organic matter 5% (consisting of 80% humus [4% overall], 10% various types of organisms [0.5% overall], and 10% roots [0.5% overall]). The formation of a soil is influenced by organisms, climate, topography, parent material, and time.

Soil horizons[468]
[Drawing of Soil Horizons]
1. **Solum or True Soil**
   1.1. **Topsoil**
      1.1.1 **O Horizon**: Loose and partly decayed organic matter
      1.1.2 **A Horizon**: Mineral matter mixed with some humus. This layer **eluviates**[469] iron, clay, aluminum, organic compounds, and other soluble constituents.
      1.1.3 **E Horizon**: When eluviation is pronounced, a lighter colored "E" subsurface soil horizon is apparent at the base of the "A" horizon. This is the zone of eluviation and leaching.
   1.2 **Subsoil**
      1.2.1 **B horizon**. This layer accumulates (illuviates) iron, clay, aluminum and organic compounds from above.
      1.2.2 **C Horizon**: Partially altered parent material
2. **Unweathered Parent material**

---

[468] **Soil Horizons**:
• "A soil horizon is a layer, approximately parallel to the surface of the soil, distinguishable from adjacent layers by a distinctive set of properties produced by the soil-forming processes. The term **layer**, rather than horizon, is used if all of the properties are believed to be inherited from the parent material or no judgment is made as to whether the layer is genetic."
http://soils.usda.gov/technical/manual/contents/chapter3a.html#2
• http://en.wikipedia.org/wiki/Soil_horizon
• *USDA/NRCS Soil Taxonomy, A Basic System of Soil Classification for Making and Interpreting Soil Surveys, 2nd Ed.* 1999, amended 2000, 2002
ftp://ftp-fc.sc.egov.usda.gov/NSSC/Soil_Taxonomy/tax.pdf
[469] **Eluviation and Illuviation**: Eluviation is movement of humus, chemical substances, and mineral particles from the upper layers of a soil to lower layers by the downward movement of water through the soil profile. Illuviation is deposition of humus, chemical substances, and fine mineral particles in the lower layers of a soil from upper layers because of the downward movement of water through the soil profile.
http://www.physicalgeography.net/glossary.html

Detailed soil horizon [Diagram]
Oi: Organic, Slightly Decomposed
Oe: Organic, Moderately Decomposed
Oa: Organic, Highly Decomposed
A: Mineral mixed with humus, dark colored.
E: Horizon of maximum eluviation of silicates clays, Fe, Al oxides, etc.
EB : Transition to B, more like E than B
BE: Transition to B, more like B than E
B: Most clearly expressed portion of B Horizon
BC: Transition to C, more like B than C
CB: Transition to C, more like C than B
C: Zone of least weathering, accumulation of Ca and Mg carbonates, cementation, sometimes high bulk density.
R: Underlying bedrock

[Diagram] **Eluviation and illuviation under humid, semiarid and arid conditions.**
Humid: thick eluviation zone, illuviation zone begins deep
Semiarid: moderate eluviation zone, illuviation zone closer to surface
Arid: very thin or nonexistent eluviation zone, illuviation zone very close to surface
Eluviation Definition: The removal of inorganic and organic substances by leaching occurring in the A horizon.
Illuviation: Downward moving fine material accumulates in the B horizon. [Note 2 L's in Illuviation versus 1 L in Eluviation]

Soil classifications[470]
US comprehensive soil classification (Seventh Approximation [publ. 1960, are there more recent standards?]):
- Twelve major categories (orders)
- Subdivided into five more levels (and sub-levels) of classification into >12,000 soil series!

Advice: Use a reference book!

Twelve soil orders[471]
[lecture notes supplemented by text quoted from U Idaho website cited below]
Entisol (young soils without layering, recently deposited parent materials or rapid deposition).
"Entisols are soils of recent origin. The central concept is soils developed in unconsolidated parent material with usually no genetic horizons except an A horizon. All soils that do not fit into one of the other 11 orders are Entisols. Thus, they are characterized by great diversity, both in environmental setting and land use. Many Entisols are found in steep, rocky settings. However, Entisols of large river valleys and associated shore deposits provide cropland and habitat for millions of people worldwide. Globally Entisols are extensive, occupying ~16% of the Earth's ice-free land area. Only Inceptisols are more extensive. In the US, Entisols occupy ~12.3% of the land area."
Inceptisol (young soils; weakly developed layers, only moderate weathering and development)
"Inceptisols are soils that exhibit minimal horizon development. They are more developed than Entisols, but still lack the features that are characteristic of other soil orders. Inceptisols are widely distributed and occur under a wide range of ecological settings. They are often found on fairly steep

---

[470] **Soil Classification**:
• *Soil Classification: A Comprehensive System 7th Approximation* (book, 1960). [probably superceded]
• *USDA/NRCS Soil Taxonomy, A Basic System of Soil Classification for Making and Interpreting Soil Surveys, 2nd Ed.* 1999, amended 2000, 2002
ftp://ftp-fc.sc.egov.usda.gov/NSSC/Soil_Taxonomy/tax.pdf
• USDA/*NRCS Soil Survey Manual*, October 1993
http://soils.usda.gov/technical/manual/
[471] **Soil Orders**:
• http://soils.usda.gov/technical/soil_orders/
• Consise summary (cited in text above inside quotes):
http://soils.ag.uidaho.edu/soilorders/orders.htm
• Keys to Soil Taxonomy, Tenth Edition (2006) (3.9 MB):
http://soils.usda.gov/technical/classification/tax_keys/keys.pdf

slopes, young geomorphic surfaces, and on resistant parent materials. Land use varies considerably with Inceptisols. A sizable percentage of Inceptisols are found in mountainous areas and are used for forestry, recreation, and watershed."

Histosol (peat, bog-type soils, coal, moors, mucks, high content of organic matter) "Histosols are soils that are composed mainly of organic materials. They contain at least 20-30% organic matter by weight and are more than 40 cm thick. Bulk densities are quite low, often less than 0.3 g/cm^3."

Spodosol (coniferous forested areas; A-horizon leached of iron and organic matter, tend to be acid and infertile) "Spodosols are acid soils characterized by a subsurface accumulation of humus that is complexed with Al and Fe. These photogenic soils typically form in coarse-textured parent material and have a light-colored E horizon overlying a reddish-brown spodic horizon. The process that forms these horizons is known as podzolization."

Alfisol (forested areas; acid) "Alfisols are moderately leached forest soils that have relatively high native fertility. These soils are well developed and contain a subsurface horizon in which clays have accumulated. Alfisols are mostly found in temperate humid and subhumid regions of the world. Alfisols occupy ~10.1% of the global ice-free land area. In the US, they account for ~13.9% of the land area. Alfisols support about 17% of the world's population. The combination of generally favorable climate and high native fertility allows Alfisols to be very productive soils for both agricultural and silvicultural use."

Ultisol (pedalfer, laterite). "Ultisols are strongly leached, acid forest soils with relatively low native fertility. They are found primarily in humid temperate and tropical areas of the world, typically on older, stable landscapes. Intense weathering of primary minerals has occurred, and much Ca, Mg, and K has been leached from these soils. Ultisols have a subsurface horizon in which clays have accumulated, often with strong yellowish or reddish colors resulting from the presence of Fe oxides. The 'red clay' soils of the southeastern United States are examples of Ultisols. Ultisols occupy ~8.1% of the global ice-free land area and support 18% of the world's population. They are the dominant soils of much of the southeastern US and occupy ~9.2% of the total US land area. Because of the favorable climate regimes in which they are typically found, Ultisols often support productive forests."

Oxisol (more weathered than laterite) "Oxisols are very highly weathered soils that are found primarily in the intertropical regions of the world. These soils contain few weatherable minerals and are often rich in Fe and Al oxide minerals. Oxisols occupy ~7.5% of the global ice-free land area. In the US, they only occupy ~0.02% of the land area and are restricted to Hawaii. Most of these soils are characterized by extremely low native fertility, resulting from very low nutrient reserves, high phosphorus retention by oxide minerals, and low cation exchange capacity (CEC)."

Vertisol (swelling clays) "Vertisols are clay-rich soils that shrink and swell with changes in moisture content. During dry periods, the soil volume shrinks, and deep wide cracks form. The soil volume then expands as it wets up. This shrink/swell action creates serious engineering problems and generally prevents formation of distinct, well-developed horizons in these soils. Globally, Vertisols occupy ~2.4% of the ice-free land area. In the US, they occupy ~2.0% of the land area and occur primarily in Texas"

Mollisol (grasslands; rich in Ca) "Mollisols are the soils of grassland ecosystems. They are characterized by a thick, dark surface horizon. This fertile surface horizon, known as a mollic **epipedon**, results from the long-term addition of organic materials derived from plant roots. Mollisols primarily occur in the middle latitudes and are extensive in prairie regions such as the Great Plains of the US. Globally, they occupy ~7.0% of the ice-free land area. In the US, they are the most extensive soil order, accounting for ~21.5% of the land area. Mollisols are among some of the most important and productive agricultural soils in the world and are extensively used for this purpose."

Aridosol (arid climate - pedocal). "Aridisols are $CaCO_3$-containing soils of arid regions that exhibit at least some subsurface horizon development. They are characterized by being dry most of the year. Aridisols contain subsurface horizons in which clays, calcium carbonate, silica, salts, and/or gypsum have accumulated. Aridisols occupy ~11.8% of the Earth's ice-free land area and ~8.3% of the US. Aridisols are used mainly for range, wildlife, and recreation."

Gelisols (permafrost near surface) "Gelisols are soils of very cold climates that contain permafrost within 2 meters of the surface. These soils are limited geographically to the high-latitude polar regions and localized areas at high mountain elevations. Because of the extreme environment in which they are found, Gelisols support only ~0.4% of the world's population - the lowest percentage of any of the soil orders."

Andisols (volcanic soils) "Andisols are soils that have formed in volcanic ash or other volcanic ejecta. These soils differ from those of other orders in that they typically are dominated by glass and poorly crystalline colloidal materials such as allophane, imogolite, and ferrihydrite (andic properties). As a result, Andisols possess many unique chemical and physical properties that include high water-holding capacity and the ability to 'fix' (and make unavailable to plants) large quantities of phosphorus."

Geological range of soil features and soil orders recognized by the Soil Conservation Service of the US Department of Agriculture
[graph depicting ranges of geologic time over which various soil features and soil orders are found.]

Summary of soil types
[Table image; quotations included here are instead from Wikipedia[472]]
Pedalfer: Sandy, light-colored topsoil. "Pedalfer is a subdivision of the zonal soil order ... in which sesquioxides increase relative to silica during soil formation. Pedalfers usually occur in humid areas. It is not used in the current United States system of soil classification but the term commonly shows up in college geology texts. Pedalfers have three subdivisions of which one is **Lateritic** soils. Pedalfer is a formative element in the United States soil taxonomic system for the Alfisols soil order. **Alf** is the formative element in the Alfisol name, and refers to **aluminium (Al)** and **iron (Fe)**."
Pedocal: Commonly enriched in calcite, whitish. "Pedocal is a subdivision of the zonal soil order. It is a class of soil which forms in semiarid and arid regions. It is rich in calcium carbonate and has low soil organic matter. With only a thin A horizon (topsoil), and intermittent precipitation calcite, other soluble minerals ordinarily removed by water may build up in the B horizon (subsoil) forming a cemented layer known as **caliche**. It is not used in the current United States system of soil classification but the term commonly shows up in college geology texts."
Laterite: Enriched in iron and aluminum, brick-red color. "Laterite is a surface formation in hot and wet tropical areas which is enriched in iron and aluminium and develops by intensive and long lasting weathering of the underlying parent rock. Nearly all kinds of rocks can be deeply decomposed by the action of high rainfall and elevated temperatures. The percolating rain water causes dissolution of primary rock minerals and decrease of easily soluble elements as sodium, potassium, calcium, magnesium and silicon. This gives rise to a residual concentration of more insoluble elements predominantly iron and aluminium. Laterites consist mainly of the minerals kaolinite, goethite, hematite and gibbsite which form in the course of weathering. Moreover, many laterites contain quartz as relatively stable relic mineral from the parent rock. The iron oxides goethite and hematite cause the red-brown color of laterites..."

Importance of soil
Soil is a critical part in a number of the natural cycles and interactions on which all life depends:
- carbon cycle
- oxygen cycle
- moisture cycle
- nitrogen cycle
- mineral cycle

The study of soils
- Well studied subject—Best understood ecosystem
- But little is known of soil evolution through time
- Circumstantial evidence suggests that soils have existed since at least Middle Cambrian; evidence for Precambrian soils is growing

Why is little known?

[Graph] **Geological ranges of major soil**
Categories and first known appearance of important soil ecosystems
Graph show
- Microbial soils appearing at least by Cambrian, possibly much earlier.
- Bryophytic soils by Ordovician
- Rooted vascular soils by Silurian, etc.

---
[472] Pedalfer, Pedocal, Laterite:
• http://en.wikipedia.org/wiki/Pedalfer
• http://en.wikipedia.org/wiki/Pedocal
• http://en.wikipedia.org/wiki/Laterite

Soil in the Archean?
Abiotic soils:
- Products of physical and chemical processes
- The formation of early microbial soils were probably prevented by:

High levels of radiation
High or low temperatures
Adverse atmospheric conditions
No biologically available mineral elements (N, P, Fe, S)

Physical and chemical (hydrolysis) weathering
[Image] Modern example

Were Archean-Paleoproterozoic greenhouse paleosols biotic?
- Isotopic evidence suggest that methanogenic, hypersaline, normal, and decompositional microbes were present
- Mt. Roe paleosol (2,765 Ma), Western Australia have extremely depleted carbon isotopic compositions: $\delta^{13}C_{org}$ –40‰ (pond scum?)
- Microbial trace fossils in paleosols (1,300 Ma)
- Chemofossils (2,900 Ma)

The very oldest soils—Western Australia?
The oldest known paleosol (?) shows alteration to depths of 50 m on granites unconformably underlying the 3.5 Ga sedimentary succession of the Warrawoona Group in northwestern Western Australia
(Buick et al., 1995)
[Diagram]

Earliest biotic soil formation
- Prokaryotic and eukaryotic organisms would have been extremely important for soil formation
- Organic acids secreted by these organisms help breaking down the rock material and releasing Fe and P
- Vascular plants were not yet around to supply organic acids for weathering of the substrate to form soil

What was the order of microbial terrestrial colonization?
1. Cyanobacteria
2. Lichens (oxalic acid increases rock decomposition)
3. Microbial mats

But many uncertainties remain in understanding early microbial soil formation.
[Image] Thermophilic microbial mats at Octopus Geyser in Yellowstone National Park, Wyoming.

Gunflint Chert (2.51 Ga) microfossils
[Images]
Eoastrion, identical to the modern Metallogenium, a manganese-fixing bacteria [scale ~30 µm]
Eospheria
Animikiea, similar to the living algae Oscillatoria and Lyngbya
Kakabekia, similar to modern soil microbes
[Images] Some of the bacteria of the Gunflint Chert microflora is similar to modern soil microbes

Evidence for life in paleosols
2.2 Ga Waterval Onder clay paleosol of South Africa has trace fossils and features like modern rock varnish, associated with bacteria, algae, and fungi
In analysis of organic carbon and its isotopic composition, the common light carbon isotope is characteristic of photosynthetic organisms
[Image] Waterval Onder paleosol

Desert Rock Varnish
[Image] Blackened boulders of the Alabama Hills, Owens Valley, California, are coated with a black layer of clay and manganese oxide precipitated by colonies of bacteria living on the rock surface.

[Image] White House Anasazi ruins and wall with **desert varnish**. Canyon de Chelly National Monument, Arizona

Old microbial soils
One of the earliest biologically active soil: Cambrian phosphate horizons (supratidal or fully terrestrial?) in Georgia Basin, Australia, may be related to present day calcrete soils (contain calcified fungal tubes). These earliest terrestrial microbiota may have been cyanobacteria and chlorophytes
[Image] Calcified fungal tubes

Importance of early lichens
Lichens[473] are a symbiotic association between fungus and green algae or cyanobacteria
Lichen has the ability to colonize and weather rocks—contributing to soil formation
Could some Ediacaran fossil be lichen?? Controversial, but if true, the impact of lichens on early soil formation would have been significant
[Image] Dickinsonia costata, an Ediacaran organism of unknown affinity, with a quilted appearance—a lichen?

[Images of **Scaly lichen** and **Orange lichen**] Lichens consist of a symbiosis between an algae and a fungus. Algae contains chlorophyll which it uses during photosynthesis to produce carbohydrates. These are required by the algae itself but are also absorbed and used for growth by the fungus. Thus the fungus obtains nutrients from the algae, the fungal tissue in turn may provide shelter for the algae allowing it to grow in harsh conditions such as on rock surfaces where it would otherwise be destroyed.

Ordovician bryophite soils
Thin bryophite vegetation [existed] by the Ordovician; possible faunal colonization by microarthropods
[Diagrams of hypothetical organisms including Liverwort, millipede, etc.] Reconstructed ecosystem of the Late Ordovician Potters Mills paleosol from central Pennsylvania

What are bryophytes?
The group includes three quite distinct lineages (i.e., **mosses, liverworts**[474]**, and hornworts**[475])
More than 20,000 named species worldwide today
Are the most diverse group of land plants except for the flowering plants
Bryophytes clump as a "super-organism." Many mosses and some liverworts are essentially social organisms like a beehive. This results from the combination of clonal growth and external water conduction
[Image] Liverwort

Microarthropods (Mesobiota)
Mesobiota (0.1 to 2 mm in diameter): Include mainly micro-arthropods, such as pseudo-scorpions, protura, diplura, springtails, mites, small myriapods and the worm-like enchytraeids. Mesobiota have

---

473 **Lichen**:
• http://en.wikipedia.org/wiki/Lichen
• http://www.lichen.com/
474 **Liverworts**: "The Marchantiophyta ... are a division of bryophyte plants commonly referred to as hepatics or liverworts. Like other bryophytes, they have a gametophyte-dominant life cycle, in which cells of the plant carry only a single set of genetic information. It is estimated that there are 6000 to 8000 species of liverworts. Some of the more familiar species grow as a flattened leafless thallus, but most species are leafy with a form very much like a flattened moss. Leafy species can most reliably be distinguished from the apparently similar mosses by their single-celled rhizoids. Other differences are not universal for all mosses and all liverworts, but the occurrence of leaves arranged in three ranks, the presence of deep lobes or segmented leaves, or a lack of clearly differentiated stem and leaves all point to the plant being a liverwort."
http://en.wikipedia.org/wiki/Marchantiophyta
475 **Hornworts**: "Hornworts are a group of bryophytes, or non-vascular plants, comprising the division Anthocerotophyta. The common name refers to the elongated horn-like structure, which is the sporophyte. The flattened, green plant body of a hornwort is the gametophyte plant."
http://en.wikipedia.org/wiki/Hornwort

limited burrowing ability and generally live within soil pores, feeding on organic materials, microflora, microfauna and other invertebrates.
[Image[476] of many different mesobiota]

First well-established soils
By the end of Ordovician, well-established soil profiles had developed; evidence for:
- In situ oxidation of organic matter
- Deep-burrowing (millipede-like) organisms
- Both biological and non-biological processes
- Microbial organisms and lichens produced organic acids
- Weathering by acid rain

[Image] Soil microbes
[Image] Millipedes process soil by feeding on organic debris and humus

Silurian to Devonian soils
- Red clayey calcareous paleosols show a greater volume of roots and a decline in the density of animal burrows.
- These trends parallel the decline in atmospheric CO_2 determined from isotopic records of pedogenic[477] carbonate in these same paleosols.
- A paleosol (vertisol; swelling clays) in the Middle Devonian Aztec Siltstone of Victoria Land, Antarctica, is the most ancient known soil of well-drained forest ecosystems.

Rooted soils
- Diversification of vascular plants in the early Silurian
- True forests appeared in the late Devonian
- By the early Carboniferous, the soil ecosystem was similar to present day soils
- Grasses spread in the Tertiary

[Diagrams of Silurian and Devonian plants]

The advent of roots
[Diagram] Relative sizes, shapes, and penetration depths of root systems during the Early, Middle, and Late Devonian

What were the consequences of rooted soils?
Increased stability of the soil
Increased biomass
Thicker soils and humus
Dramatic increase in biochemical and biophysical weathering
Diverse soil types
Development of the rhizosphere
[Image] Modern rooted soil

Rhizosphere (root zone)
The rhizosphere is the zone that surrounds and includes the roots of plants.
[Diagram] **EndoRhizosphere** is root itself, **Ectorhizosphere** is root hairs, mucigel, and root cells that have sloughed off.
[Diagram] The root zone includes **mycorrhiza**[478], bacteria, and free living fungi, insects, nematodes, other animals, and SOM [soil organic matter].

---

[476] **Size Categories of Biota**:
Macrobiota—organisms generally >2 mm in diameter and visible to the naked eye.
Mesobiota are organisms generally ranging in size from 0.1 to 2 mm in diameter. [includes image]
Microbiota are the smallest organisms (<0.1 mm diam.),
http://www.fao.org/AG/agl/agll/soilbiod/soilbtxt.stm
[477] **Pedogenic**: "processes that add, transfer, transform, or remove soil constituents"
http://earthquake.usgs.gov/learning/glossary.php?term=pedogenic
[478] **Mycorrhiza**: "A mycorrhiza (Greek for fungus roots; typically seen in the plural forms mycorrhizae or mycorrhizas) is a symbiotic (occasionally weakly pathogenic) association between a fungus and the roots of a plant. In a mycorrhizal association the fungus may colonize the roots of a host plant either

Rhizosphere (root zone)

- A narrow zone of intensive biological activity of incredible complexity
- Microbial populations can be 10 - 100 times larger than the populations in the bulk soil.
- The chemistry and biology at the soil-root interface is governed by biotic (plant roots, microbes) and abiotic (physical and chemical) interactions.

[Image] The rhizosphere: wheat root (center root is 1 mm wide) with root hairs extending into rhizosphere soil.

Mycorrhizae (modern) from the rhizosphere

[Images] Mycorrhizal colonization of a root clump. Mycorrhizal fungi extend thread-like hyphae from inside cortex cells out into the soil for several millimeters. They **extend the feeding volume of the root by 10 to 1,000 times** or more for most plant species and extract and carry nutrients back to the root zone.
[Image] The images are about 3mm wide. Red fluorescing fungal filaments across the rhizosphere of spring wheat together with mainly red fluorescent bacteria.

Root-microbe symbiosis

- The plant grows microbes along the root surfaces. To do this, sunlight energy is channeled to the external root surface
- 12 to 40% (up to 80%) of plant energy is exuded as **mucigel**[479] into the **ectorhizosphere** as carbohydrates, amino acids, and other energy energy-rich compounds
- Billions of bacteria, fungi, algae, actinomycetes, protozoa, and other microbes feed upon this exudate

Exudate

- All rhizosphere soil microbes consume exudate
- In turn, the soil microbes may produce **acids to dissolve and chelate minerals**, **fix nitrogen**, **generate vitamins**, or **synthesize hormones** absorbed by the roots to stimulate additional growth and disease resistance
- Plants might adjust the quality of their exudates to encourage the growth of specific microbes that will most benefit the plant

[Image] Nitrogen-fixing bacteria cross section
[Image] Actinomycetes (filamentous bacteria)

---

intracellularly or extracellularly."
http://en.wikipedia.org/wiki/Mycorrhiza

[479] **Mucigel**:
• "Mucigel is a slimy substance that covers the rootcap of the roots of plants. It is a highly hydrated polysaccharide, most likely a pectin, which is secreted from the outermost (epidermal) cells of the rootcap. Mucigel is formed in the Golgi bodies of such cells, and is secreted through the process of exocytosis. The layer of microorganism-rich soil surrounding the mucigel is called the rhizosphere. Mucigel serves several functions, including: (1) Protection of of rootcap, prevents desiccation; (2) Lubrication of rootcap; allows root to more efficiently penetrate the soil; (3) Creation of symbiotic environment for nitrogen fixing bacteria (i.e. diazotrophs) and fungi (which help with water absorption); (4) Provision of a 'diffusion bridge' between the fine root system and soil particles, which allows for a more efficient uptake of water and mineral nutrients by roots in dry soils.
http://en.wikipedia.org/wiki/Mucigel
• " A complex polysaccharide containing sugars, organic acids, vitamins, enzymes, and amino acids, which is produced by cells in the root caps of plants. Mucigel has several functions:
(1) It protects roots from desiccation and contains compounds that diffuse into the soil and inhibit growth in other roots.
(2) It lubricates roots as they force their way between soil particles.
(3) Soil particles cling to mucigel, and increase the root's contact with the soil. These properties of mucigel help maintain the continuity between roots and soil water.
(4) Carboxyl groups in mucigel influence ion uptake, and organic acids in mucigel make certain ions more available to plants. Also, fatty acids, lectins, and sterols in mucigel may help establish beneficial symbioses with soil microbes."
http://www.daviddarling.info/encyclopedia/M/mucigel.html

Approximate number of *described* species in modern soil biota
Microorganisms: Bacteria and archaea 3,200; Fungi c. 35,000
Microfauna: Protozoa 1,500; Nematodes 5,000
Mesofauna: Mites 30,000; Springtails 6,500; Diplura 659; Symphyla 160; Pauropoda 500; Enchytraeids >600
Macrofauna: Root herbivorous insects c. 40,000; Millipedes 10,000; Isopods 2,500; Termites 2,000; Ants 8,800; Earthworms 3,627 Ants 3,627
[Image] Blind springtail is fungal -feeding and live deep in the soils

Effects of the first soils on the atmosphere
- Silurian to Devonian: Declining atmospheric levels of CO_2—increased consumption of atmospheric CO_2 by the increasing biosphere (evolution of life)
- High concentrations of CO_2 were maintained in soil pores as a result of decomposition and the metabolic activities of roots
- Organic acids formed as a result – chemical weathering increased
- High burial rates of carbon in limestone and organic matter

Atmospheric CO_2 and average global temperature for the Phanerozoic [Graph previously shown]

Plot of atmospheric oxygen level versus time for the Phanerozoic [Graph]
(past 550 million years, Berner, 1999)
Carbon consumption by accelerated weathering in forest soils and carbon burial in coals resulted in Late Paleozoic high atmospheric oxygen levels [peaking at c. 37% c. 300 Ma, at the start of Permian]

Devonian black shales
- Soil formed in the Devonian altered the amount and quality of nutrient material that flowed into the Devonian seas
- Marine sediments of the Devonian are unique in that they consist of black shales, which may have resulted from the influx of soil and organic plant materials [deposited in relatively anoxic reducing environments].

[Photo] This horizontal shale outcrop is part of the Devonian Exshaw Formation.

Effect of the first soils on the land
- Major changes in weathering and sedimentary processes
- Soils are a consequence of weathering, but also a factor in accelerating weathering.

Stabilizing weathered material
Decreased erosion
The binding effect allowed for greater decomposition

The benefits of high CO_2 in soil formation
- CO_2 favored increased growths of photosynthetically active organisms, which enriched soils with Fe and P and led to the growth of microbial mats
- Decomposition of these mats released inorganic nutrients back into the system
- High CO_2 precipitated more acid

Increased chemical decomposition of rocks
Promoted physical disintegration of rocks and soil formation

Can soils go extinct?
- Theoretically possible but the only known extinct soils are **green clay paleosols** of early Precambrian time

Green, clayey, alumina-rich paleosols developed on iron-rich basalt
Their composition may reflect lower oxygenation of the atmosphere; modern basalts weather to red, iron-rich soils (Rye and Holland, 1998)

Invasion of the Land—Tetrapods

[MCM: Edited from verbatim text of LRS slides, not all material in the slides was discussed. I will not be able to post the slides document, but if available to you, see PDF document of slides, containing images which are essential for understanding this material.]

The first land animals—arthropods?

- A discovery in the year 2000 of footprints of animals that scuttled about on sand dunes about 530 Ma [Lower Cambrian], might have been from arthropods, and resembled centipedes about the size of crayfish
- Thus arthropods may have invaded land long before tetrapods
- They probably didn't live on land, instead coming ashore to mate or evade predators
- At this time the only land plants might have been simple mosses

Invertebrates on land

- Of over 30 invertebrate phyla, only three have significant numbers of macroscopic terrestrial representatives: **Arthropods, mollusks, and annelids**
- None of these phyla originated on land
- Invertebrate species on land greatly exceeds that in the sea only because **insects** form 70% of all animal species on land today

Invasion of land

- Opened up new environments for animals to utilize
- Living on land required new strategies for survival; required profound changes in all aspects of life

[Drawing] Ordovician – empty land waiting for occupants

Problems in living on land—tetrapods

- Development of the jaw
- Gas exchange
- Support/structure
- Nutrient/water exchange
- Density differences
- Desiccation/maintaining moisture
- Reproduction
- Temperature variations
- Sensory differences

Simple fish classification[480] [Table]

Class Agnatha (jawless fish)

Early extinct members are ostracoderms

---

[480] **Fish Classification**: "Fish are a paraphyletic group: that is, any clade containing all fish also contains the tetrapods, which are not fish. For this reason, groups such as the "Class Pisces" seen in older reference works are no longer used in formal classifications. Fish are classified into the following major groups [MCM This classification differs substantially from LRS table]:

* Subclass Pteraspidomorphi (early jawless fish)
* Class Thelodonti
* Class Anaspida
* (unranked) Cephalaspidomorphi (early jawless fish)
    o (unranked) Hyperoartia
        + Petromyzontidae (lampreys)
    o Class Galeaspida
    o Class Pituriaspida
    o Class Osteostraci
* Infraphylum Gnathostomata (jawed vertebrates)
    o Class Placodermi (armoured fishes, extinct)
    o Class Chondrichthyes (cartilaginous fish)
    o Class Acanthodii (spiny sharks, extinct)
    o Superclass Osteichthyes (bony fish)
        + Class Actinopterygii (ray-finned fish)
        + Class Sarcopterygii (lobe-finned fish)
            # Subclass Coelacanthimorpha (coelacanths)
            # Subclass Dipnoi (lungfish)"

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

Class Acanthodii (first fish with jaws)
Class Placodermii (extinct armored jawed fish)
Class Chondrichthyes (cartilaginous fish including sharks, rays, skates and Holocephali)
Class Osteichthyes (bony fish)
    Subclass Actinopterygii (ray finned fish)
    Subclass Sarcopterygii (lobe-finned fish)
        Order Dipnoi (Lungfish etc.)
        Order Crossopterygii (Coelacanths including Latimeria etc.)
            Suborder Rhipidistia

Development of the jaw: Steps in the evolution of jaws by modification of gill arches
The evolution of jaws is an example of evolutionary modification of existing structures to perform new functions. Jaws are modified gill arches, and allowed the exploitation of new roles in the habitats: predators with powerful jaws.
[Diagrams]:
1. Jawless fishes (agnaths)
2. Early jawed fishes (placoderms)
3. Modern jawed fishes (cartilaginous and bony fish)

Placoderms
[Diagram] shows placoderms arise in Silurian, flourish and then go extinct in Devonian
[Drawings of Placoderms] Coccosteus (Middle Devonian), Campbellodus (Late Devonian), and Bothriolepis (Late Devonian)

Gas exchange
Several tasks had to be accomplished to create sufficient gas exchange and circulatory systems:
- Get O_2 into the animal; CO_2 out.
- Transport these gases to and from the tissues.
- Regulate rate of breathing (supply) and overall metabolism (demand)

Gas Exchange
[see fish classification Table previously shown]
    Subclass Actinopterygii (ray finned fish)
    Subclass Sarcopterygii (lobe-finned fish)
Gas exchange / circulatory system / air bladders → lungs

Circulatory system—Heart
- **Actinopterygians**: In most ray-finned fishes (actinopterygians), the heart is a single-sided two-chambered pump. Deoxygenated blood is pumped forward from the ventricle to the gills where O_2 and CO_2 are exchanged. The oxygenated blood then passes to the tissues, where it loses oxygen, and eventually returns to the heart, which it enters through the single atrium.
- **Sarcopterygian**: In the African **lungfish** (a sarcopterygian), two of the anterior gill arches have lost their gills, and their blood vessels deliver blood directly to the dorsal aorta from which it flows to the tissues. The lungfish has a partially divided atrium, which receives blood from the lung, as well as the tissues. This feature, in conjunction with a series of arterial valves allows the animal to breathe with either the gills or the lung.

Air bladders and lungs of various fishes and tetrapods (schematic)
A. Sturgeon and many Teleosts: Typical dorsal air bladder in actinopterygian (ray-finned) fishes. The primitive air bladder is dorsal to and connected to the pharynx by a pneumatic duct, which allows the animal to rise to the surface and gulp or discharge air, thereby adjusting its density
B. Lepidosteus and Amia
C. Erythrinus
D. Epiceratodus: Australian lungfish, a living sarcopterygian (lobe-finned fishes) with the bilobed lung rotated dorsally. The connection to the pharynx is ventral to ventral
E. Polypterus
F. Tetrapods: Tetrapod lung with complex lung internal structure

Developing support/structure

- For Fishes, support is not a big problem. An organism in the water is supported by buoyant forces acting equally over its entire body; density of the body is nearly equal to the density of the water surrounding it
- Tetrapods and Terrestrial vertebrates had to develop a new support structure to counteract gravity while allowing movement.

The density of air is only 1/1000 of water, so no longer have buoyant force
Body "hangs" off the spinal column
Legs support body weight
Rib cage helps support internal organs
[Diagrams] Body support
a) in fishes the surrounding water supports and buoys the weight of the body
b) in tetrapods the limbs support and the vertebral column suspends the weight of the body organs

Evolution of Fins to Feet
Crossopterygians → labyrinthodont amphibians (tetrapods)
The first tetrapods, labyrinthodont amphibians probably evolved from a crossopterygian ancestor [e.g., like the Coelacanth Latimeria]. As the lobe-fins of these fish evolved into stronger limbs, the first tetrapods appeared.
[Diagrams] Similarity between lobe-finned fish and early amphibian tetrapod (labyrinthodont amphibian)
[Diagrams] Lobe-finned fish (Sarcopterygian) extremity [e.g., lungfish] evolves to Primitive amphibian which evolves to Reptile.

Why did lobe lobe-finned fish evolve limbs?
All lobe-finned fish were initially marine and later invaded fresh water habitats. Why did the lobe-finned fish develop limbs to abandon the fresh water habitat? Hypotheses include:
1. **Climatic conditions**: Devonian red beds indicate severe drought. Fish left the ponds that dried up in search of water.
2. **Ecological conditions**: Appearance of wetlands at margins of lakes or estuaries meant abundant food for fish that could live in very shallow water. Limbs are adaptation for locomotion in shallow water.
3. **Dispersal of juveniles**: Juveniles would feed on terrestrial invertebrates and have fewer problems with gravity because of small size.
4. **Competition and predation in the aquatic habitats**: is that why they developed limbs?
5. **Stagnant Pools**: When the fresh water pools in which the lobe-finned fish lived became stagnant, did they crawl up the bank to breath air with their primitive lungs?

Developing land-based reproduction
- Amphibians had to return to an aquatic environment to lay their fish-like eggs, which produced larvae that (like fish) used gills for respiration
- With the reptiles came the amniote egg—one of the biggest steps in evolution towards living on land (Carboniferous)
- The reptile bypassed the need for a larval stage and emerged a "miniature adult"

[Image] Saltwater crocodile hatchling emerging from an egg

Amniote Egg
The egg contains several **extraembryonic membranes** that compartmentalize the interior and give it several different functions. The **chorion** provides a special hard covering that is permeable to respiratory gases (O_2 and CO_2) while being impermeable to water vapor. The allantois is a storage reservoir for waste products. The amnion is a fluid filled sac that acts as a cushion for the embryo and also prevents desiccation. The yolk sac contains food for the embryo, thus eliminating the need for a larval stage.
[Diagram] The **amniotic egg**—freedom from dependency on water, a BIG step in evolution!
[Components of bird egg anatomy[481] include **cuticle**, **shell**, **outer membrane** (just inside the shell and enclosing the **air cell**), the **inner membrane** encloses **albumin/albumen**, **chorio-allantoic**

[481] **Egg Anatomy**:
• http://people.eku.edu/ritchisong/avianreproduction.html
• http://ag.ansc.purdue.edu/poultry/images/embryo.GIF

membrane (fused **allantois** and **chorion**) encloses **allantoic cavity** and all embryonic structures, **amnion** secretes **amniotic fluid** and encloses the embryo. Also present in some eggs are **yolk sac** and **vitelline membrane**.]

Why did the amniote egg develop?

- Probably evolved from small non-amniote eggs that was laid on land
- To survive there would be an evolutionary pressure to improve or evolve a gaseous exchange system
- The presence of extra membranes meant that larger sized eggs could be supported
- The radiation of insects began at the same time. Insectivores and carnivores had an increasing food supply

Adjusting to temperature variations

- Water has high heat capacity, thus, most aquatic animals do not have problems with drastic temperature changes.
- Amphibians evade temperature changes by living only in moist, protected environments.
- Reptiles invented **keratin** (fibrous structural proteins) **scales** to protect the body and use many behavioral modifications to regulate their body temperature.
- Birds are **endothermic**[482] and modified the keratin scales to feathers which provide good insulation from temperature extremes.
- Mammals have layers of fat and hair to provide protection and insulation and also are endothermic.

[Photo] Iguana scales and spines
[Photo] Bird feathers

Bony fishes (Osteichthyes)
1) Ray-fin fish (Actinopterygii or actinopterygians)

- Fins are bony structures supported by bony rays

---

[482] **Endothermy and Warm Bloodedness**:
• "Both the terms "warm-blooded" and "cold-blooded" have fallen out of favor with scientists, because of the vagueness of the terms, and due to an increased understanding in this field. Body temperature types do not fall into simple either/or categories. Each term may be replaced with one or more variants... Body temperature maintenance incorporates a wide range of different techniques that result in a body temperature continuum, with the traditional ideals of warm-blooded and cold-blooded being at opposite ends of the spectrum...
Warm-bloodedness generally refers to three separate aspects of thermoregulation:
1. **Endothermy** is the ability of some creatures to control their body temperatures through internal means such as muscle shivering, fat burning, and panting ... Some writers restrict the meaning of "endothermy" to mechanisms which directly raise the animal's metabolic rate in order to produce heat. The opposite of endothermy is **ectothermy**.
2. **Homeothermy** is **thermoregulation** that maintains a stable internal body temperature regardless of external influence. This temperature is often higher than the immediate environment... The opposite is **poikilothermy**.
3. **Tachymetabolism** is the kind of thermoregulation used by creatures that maintain a high resting metabolism... Tachymetabolic creatures are, essentially, "on" all the time. Though their resting metabolism is still many times slower than their active metabolism, the difference is often not as large as that seen in **bradymetabolic** creatures. Tachymetabolic creatures have greater difficulty dealing with a scarcity of food.

A large proportion of the creatures traditionally called "warm-blooded" (mammals and birds) fit all three of these categories. However, over the past 30 years, studies in the field of animal thermophysiology have revealed many species belonging to these two groups that don't fit all these criteria. For example, many bats and small birds are poikilothermic and bradymetabolic when they sleep for the night, or day. For these creatures, another term was coined: **heterothermy**.

Further studies on animals that were traditionally assumed to be cold-blooded have shown that most creatures incorporate different variations of the three terms defined above, along with their counterparts (ectothermy, poikilothermy and bradymetabolism), thus creating a broad spectrum of body temperature types..."
http://en.wikipedia.org/wiki/Warm-blooded
• See also http://reptilis.net/cold-blood.html

- No nasal passage

2) Lobe-finned fish (**Sarcopterygii or sarcopterygians**): Important steps to the evolution of tetrapods

- Sturdy, fleshy lobe fins
- Openings in the roof of the mouth that led to nostrils
- From an evolutionary point of view, the Sarcopterygians were the last of the fishes of their kind.
- The next chordates to evolve were true tetrapods and thus were considered amphibians.
- Two major groups of Subclass sarcopterygians:

Order **Dipnoani** (Lungfishes)
Order **Crossopterygii**

- Suborder **Rhipidistia**

[MCM: The taxonomy is confusing and evolving. Another sources[483] list the following as subclasses of class Sarcopterygii: (1) **Dipnoi**; (2) **Coelacanthimorpha** (Coelocanths including modern Latimeria chalumnae and L. menadoensis), and (3) **Tetrapodomorpha** (Tetrapods). See note also on **Rhipidistia**[484] which are posited as the unranked ancestor of the tetrapods.]

[Diagram: Phylogeny of **Eusthenopteron**[485] linked to **Sensory Development**]
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Sarcopterygii
Subclass: Tetrapodomorpha
Superorder: Osteolepidida
Family: Tristichopteridae
Genus: Eusthenopteron

Comparison of Ray-fin and Lobe-fin breathing apparatus:
Ray Ray-fin: [Images] Lepidotes (Jurassic), Cheirodus (Carboniferous), and Ctenothrissa (Cretaceous)
Lobe -fin: [Images] Diplurus (Triassic), Eusthenopteron (Late Devonian) and Holoptychius (Late Devonian)

---

[483] **Sarcopterygii**: http://en.wikipedia.org/wiki/Sarcopterygii
[484] **Rhipidistia**:
• "The Rhipidistia were lobe-finned fishes that are the ancestors of the tetrapods. Taxonmists traditionally considered the Rhipidistia a subgroup of Crossopterygii that described a group of fish that lived during the Devonian consisting of the Porolepiformes and Osteolepiformes. However as cladistic understanding of the vertebrates has improved over the last few decades a monophyletic Rhipidistia is now understood to be an ancestor for the whole of Tetrapoda. Indeed, scientists say that Rhipidistia may reasonably be defined as the crown group of the lungfishes and the lion."
http://en.wikipedia.org/wiki/Rhipidistian
• See also http://www.palaeos.com/Vertebrates/Units/140Sarcopterygii/140.400.html
[485] **Eusthenopteron**:
• "was a genus of lobe-finned fish which has attained an iconic status from its close relationships to tetrapods. Early depictions of this animal show it emerging onto land, however paleontologists now widely agree that it was a pelagic animal... Anatomically, Eusthenopteron shares many unique features in common with the earliest known tetrapods. It shares a similar pattern of skull rooting bones with forms such as Ichthyostega and Acanthostega. "Eusthenopteron", like other tetrapodomorph fishes, had internal nostrils, (or a choana) which are found only in land animals and sarcopterygians. It also had labyrinthodont teeth, characterized by infolded enamel, which characterizes all of the earliest known Tetrapods as well... Eusthenopteron's notoriety comes from the pattern of its fin endoskeleton, which bears a distinct humerus, ulna, and radius (in the fore-fin) and femur, tibia, and fibula (in the pelvic fin). This is the characteristic pattern seen in tetrapods. It is now known to be a general character of fossil sarcopterygian fins."
http://en.wikipedia.org/wiki/Eusthenopteron
• "The small size of the external naris in Eusthenopteron suggests that the primary adaptive benefit of the choana was improved smelling capability; most respiration was would still have been conducted through the mouth."
http://ijolite.geology.uiuc.edu/00FallClass/geo143/lect/lect12.html

A canal connected the lungs with the outside of the body through openings termed external nares. While the lungs were not well developed, the much greater percentage of oxygen per volume of air made it possible for these organisms (Lobe-fins) to breathe.

[Drawing of a Lobe-finned fish emerging onto land] Lobe-finned fish: a group from which amphibians are thought to have evolved. **Eusthenopteron**, a rhipidistian crossopterygian [MCM: see alternative opinion in footnotes.]

[Photos and Drawing] **Latimeria**: A surviving lobe-finned fish (a Coelacanth)

[Diagram: Phylogeny of **Tiktaalik**]
Kingdom: Animalia
  Phylum: Chordata
    Subphylum: Vertebrata
    Class: Sarcopterygii
      Subclass:
        Tetrapodomorpha
          Genus: Tiktaalik
            Species: T. roseae

Missing link—Tiktaalik the "fishapod"

- **Tiktaalik**[486] (375 Ma), a genus of sarcopterygian (lobe-finned) fish from the late Devonian and an intermediate form between fish such as **Panderichthys**[487] (385 Ma), and early tetrapods such as **Ichthyostega**[488] (365 Ma) [both are depicted on previous diagram]
- It has many features similar to those of tetrapods

---

[486] **Tiktaalik**: ""Tiktaalik ... is a genus of extinct sarcopterygian (lobe-finned) fish from the late Devonian period, with many features akin to those of tetrapods (four-legged animals). It is an example from several lines of ancient sarcopterygian fish developing adaptations to the oxygen-poor shallow-water habitats of its time, which led to the evolution of amphibians.... Tiktaalik lived approximately 375 million years ago. Paleontologists suggest that it was an intermediate form between fish such as Panderichthys, which lived about 385 million years ago, and early tetrapods such as Acanthostega and Ichthyostega, which lived about 365 million years ago... Tiktaalik appears to be a transitional form between fish and amphibian. Unlike many previous, more fishlike transitional fossils, Tiktaalik 'fins' have basic wrist bones and simple fingers, showing that they were weight bearing. Close examination of the joints show that although they probably were not used to walk, they were more than likely used to prop up the creature's body, much like a pushup action. The bones of the fore fins show large muscle facets, suggesting that the fin was both muscular and had the ability to flex its fin like a wrist joint. These wrist-like features were speculated to evolve, if not from land excursions, then as a useful adaptation to anchor the creature to the bottom in fast moving current..." http://en.wikipedia.org/wiki/Tiktaalik

[487] **Panderichthys**: "is a 90–130 cm long fish from the Late Devonian period (Frasnian epoch) of Latvia. It has a large tetrapod-like head. Panderichthys exhibits transitional features between lobe-finned fishes and early tetrapods such as Acanthostega. The evolution from fish to land dwelling tetrapods required many changes in physiology, most importantly the legs and their supporting structure, the girdles. Well preserved fossils of Panderichthys clearly show these transitional forms, making Panderichthys a rare and important find in the history of life. Fish like Panderichthys were the ancestors of the first tetrapods, air-breathing, terrestrial animals from which the land vertebrates, including humans, are descended. The most notable characteristic of Panderichthys was its **spiracle**, a vertical tube used to breathe water through the top of its head, while its body was submerged in mud. This spiracle is a transitional organ that led, through evolution, to the development of the stirrup bone, one of the three bones (stirrup, hammer, and anvil) in the human middle ear." http://en.wikipedia.org/wiki/Panderichthys

[488] **Ichthyostega**: "Ichthyostega specimens were the first Devonian tetrapods to be found and described... Ichthyostega comes from the Upper Devonian (Famennian) of East Greenland and is widely featured in the literature as the first 'four-legged fish'. Reconstructions of the animal ... have been influential in ideas about what the earliest tetrapods were like, though more recent studies... have challenged more traditional interpretations.." [includes good anatomic images and detailed description]
http://tolweb.org/tree?group=Ichthyostega_stensioei&contgroup=Terrestrial_Vertebrates

- An excellent fossil was found in 2004 on Ellesmere Island in Nunavut, Canada
- One of its discoverers, Neil Shubin, characterizes Tiktaalik as a "fishapod"

[Image] Tiktaalik—bridging the evolutionary gap between animals of land and sea.

The lineage leading to modern tetrapods includes several fossil animals that form a morphological bridge between fishes and tetrapods. Five of the most completely known are **Eusthenopteron**; the transitional forms **Panderichthys** and **Tiktaalik**; and the primitive tetrapods **Acanthostega**[489] and **Ichthyostega**.
Tiktaalik

Adjusting sensory input (hearing)
- Fish developed an inner ear to detect vibrations; small bones of the jaw and gill apparatus were transformed to transmit sounds from the outside of the body to the inner ear
- On land this is not possible and there had to be a change in the hearing apparatus.
- A new theory is that the first step in the evolution of the middle ear may have had nothing to do with hearing. "Our forebears developed ears in order to breathe through them" (Per Ahlberg, Nature, 2006)

[Photo] Inner ear bones (**otoliths**[490]) from cod fish. Large morphological diversity among fish "hearing organs"

Developing hearing
- Instead of middle ears, fish have a little gill, the blow-hole, that is not covered by an eardrum but forms an open canal between the throat and the outside of the head
- Did the earliest land animals have a sound amplifying middle ear at all?

The earliest tetrapods, like Acanthostega had a stirrup that was in contact with the inner ear, but it appears not to have been connected to the eardrum.
- This combination of characteristics has led to the hypothesis that the earliest land animals still had open blow-holes and perhaps breathed through them.

[Image] Acanthostega

---

[489] **Acanthostega**: "Acanthostega gunnari (Jarvik 1952) is one of a small but increasing number of genera of stem-tetrapods known from the Upper Devonian, which are providing an expanding view of the appearance of tetrapods and the origin of limbs with digits... Acanthostega is represented by exceptionally well-preserved material. Notable features are the well-ossified gill arches combined with post-branchial lamina of the shoulder girdle, together suggesting retention of functional internal gills; paddle-like limbs with eight digits on each limb and a deep tail supported by finrays and accessory internal supports... It comes from the Celsius Bjerg Group of the Famennian of East Greenland, which date from about 360 mya.... Most phylogenetic analyses place Acanthostega as one of the most primitive known tetrapods, below Ichthyostega in most trees ... However, it may lie above the recently described Ventastega..."
http://www.tolweb.org/Acanthostega

[490] **Otoliths**: "Finfish (Osteichthyes) have three pairs of otoliths - the **sagittae** (singular sagitta), **lapilli** (singular lapillus), and **asterisci** (singular asteriscus). The sagittae are largest, found just behind the eyes and approximately level with them vertically. The lapilli and asterisci (smallest of the three) are located within the semicircular canals. The shapes and proportional sizes of the otoliths vary with fish species. In general, fish from highly structured habitats such as reefs or rocky bottoms (e.g. snappers, groupers, many drums and croakers) will have larger otoliths than fish that spend most of their time swimming at high speed in straight lines in the open ocean (e.g. tuna, mackerel, dolphinfish). Flying fish have unusually large otoliths, possibly due to their need for balance when launching themselves out of the water to "fly" in the air. Often, the fish species can be identified from distinct morphological characteristics of an isolated otolith.

Fish otoliths accrete layers of calcium carbonate and gelatinous matrix throughout their lives. The accretion rate varies with growth of the fish—often less growth in winter and more in summer—which results in the appearance of rings that resemble tree rings. By counting the rings, it is possible to determine the age of the fish in years... In addition, in most species the accretion of calcium carbonate and gelatinous matrix alternates on a daily cycle. It is therefore also possible to determine fish age in days. This latter information is often obtained under a microscope, and provides significant data to early life history studies..."
http://en.wikipedia.org/wiki/Otolith

Ichthyostega
One of the earliest tetrapods
Kingdom: Animalia
  Phylum: Chordata
Superclass: Tetrapoda
      Order: Ichthyostegalia
        Family: Ichthyostegidae
          Genus: Ichthyostega

Tetrapods (and arthropods) invade land
By the Devonian period two major animal groups dominated the land:
1. The tetrapods (4-legged terrestrial vertebrates):
The first tetrapods were amphibians such as Ichthyostega, and were closely related lobe-finned fish e.g., Eusthenopteron
2. The arthropods, including arachnids and wingless insects
[Image of Ichthyostega]

Crossopterygians
Because of the arrangements of bones in their muscular fins, the pattern of skull elements and the structure of their teeth, **crossopterygians** are considered the ancestors of the amphibians
[Drawing] Comparison of skulls and lower jaws of a crossopterygian and the Devonian amphibian Ichthyostega.
[Drawing Complexly Infolded enamel and dentine of the teeth of crossopterygian and "amphibian"
[Drawing] Ichthyostega reconstruction.]

The most important morphological changes in amphibians
- The **limb and girdle bones** evolved to better hold the body above ground; bones and muscles get larger and more complex
- The **spinal column** was transformed into a sturdy but flexible bridge of interlocking elements. The force of gravity produces twisting forces on the animal's vertebral column. **Zygapophyses** form Zygapophysial (facet) joints, which resist the twisting forces evolved.
- A **three-chambered heart** developed to route the blood more efficiently to and from the lungs
- Improved **hearing** in air rather than under water

[Drawings] **Skeletons of rhipidistian fish and representative "labyrinthodonts"**
A. The Upper Devonian fish Eusthenopteron
B. The Upper Devonian amphibian Ichthyostega. The rear limb has since been shown to have 7 toes
C. The Carboniferous amphibian Crassiyyrinus
D. The embolomere Protorogyrinus (suborder of early amphibians)
E. The temnospondyl Caerorhachis (labyrinthodont amphibian)

Oldest Known Reptile: Hylonomus lyelli
• c. 30 cm in length, a **Protorothyrid** (small, short legged, lizard-like insectivores)
• Reconstruction and skeleton of one of the oldest known **reptiles** (Pennsylvanian), Nova Scotia, Canada. [Drawing]
• The oldest known amniote (300 Ma)
• Not on the evolutionary track to "mammal-like synapsids "
Phylum: Chordata
  Class: Sauropsida
    Order: Captorhinida
       Suborder: Captorhinomorpha
         Family: Protorothyrididae
           Genus: Hylonomus
             Species: lyelli

Evolutionary relationships
Amniotes (unranked)

Class **Synapsida**[491]: “mammal-like reptiles” etc. with one temporal fenestra per side
Order **Therapsida**: "mammal-like reptiles" etc.
Class **Mammalia**: mammals
Class **Sauropsida**: reptiles, dinosaurs, and birds with two temporal fenestrae per side
Subclass **Anapsida** (includes turtles)
(unranked) **Eureptilia** (true reptiles)
Subclass **Diapsida**[492] (various fossil reptiles, crocodiles, lizards, snakes)
(unranked) Euryapsida
Class Aves: birds
[MCM: somewhat confusing mixing of Class terminology]

Amniote skull types (Temporal Fenestrations)
[Drawings]
Diapsid (2 fenestrae): Lizards, snakes, crocodiles, flying reptiles, dinosaurs
Euryapsid (1 fenestra): Plesiosaurs, ichthyosaurs, and placodonts
Synapsids (1 fenestra): “Mammal-like reptiles”
Anapsids (0 fenestrae): Early reptiles and turtles
Temporal fenestration has long been used to classify amniotes (Osborn, 1903). Taxa such as Anapsida, Diapsida, Euryapsida, and Synapsida were named after their type of temporal fenestration. Temporal fenestra are large holes in the side of the skull. The function of these holes has long been debated but no consensus has been reached

Amniote phylogeny
Amniota is collective term for the classes Reptilia (reptiles), Aves (birds), and Mammalia (mammals) of the subphylum Vertebrata.
[Complex phylogenetic diagram]

Vertebrates Cladogram
Evolutionary tree of life showing relationships among premammalian land vertebrates.
As a hypothetical evolutionary process, the cladistic scheme traces evolutionary pathways. Cladistic analyses identify groups of species that all have traits that evolved as new features or “evolutionary novelties”.
Diagram starts with Sarcopterygii.

“Mammal-like reptiles ” Class Synapsida
- Actually mammal-like—not “mammal-like reptiles” not a subclass of reptilia as previously believed
- Cladistic analyses show that they diverged from ancestors completely different from Hylonomus [oldest known reptile] and true reptiles
- The first synapsids and the first reptiles appear at about the same time in the Early Pennsylvanian
- Some of the earliest amniotes were the pelycosaurs (“bowl lizards”, sailbacks); extended “sails” formed from vertebral spinous processes probably used as a heat regulator
- “Mammals” have become an arbitrary term with regards to synapsids

Evolutionary relationship among the Paleozoic amniotes
Phylum Chordata
Subphylum Vertebrata
(Unranked) Amniota—Tetrapoda
Class Synapsida

---

491 **Synapsida**: “Synapsids ('fused arch'), also known as Theropsids [**Therapsids**] ('beast face'), is a class of animals that includes mammals and everything closer to mammals than to other living amniotes. The non-mammalian members were traditionally described as '**mammal-like reptiles**', but are better referred to as "**stem-mammals**". Synapsids are one of the two major groups of amniote, the other being the **sauropsids**. They developed one opening in their skull (temporal fenestra) behind each eye, about 324 million years ago (mya) during the late Carboniferous Period.”
492 **Diapsida**: “Diapsids ("two arches") are a group of reptiles that developed two holes (temporal fenestra) in each side of their skulls, about 300 million years ago during the late Carboniferous period. Living diapsids are extremely diverse, and include all crocodiles, lizards, snakes, tuatara, and possibly even turtles.”
http://en.wikipedia.org/wiki/Diapsida

Subclass Therapsida
Subclass Pelycosauria

Cladistic analyses show that "mammal-like reptiles" should not be designated reptiles because they diverged from ancestors completely different from Hylonomus [oldest reptile]

Pelycosauria Dimetrodon [Pelycosauria Dimetron, 4 artists conceptions]

Therapsids[493]
Several mammalian traits
– Fewer bones in the skull than in reptiles
– Mammal-like enlargement of the lower jaw (dentary)
– A double-ball and socket had developed between the skull and neck
– Teeth show recognizable differentiation into incisors, canines, and cheek teeth
– The limbs were in a more vertical alignment beneath the body

Two Examples of Therapsids
Phylum: Chordata
Class: Synapsida
Order: Therapsida
Suborder: Cynodontia
Family: Cynognathidae
Genus: Cynognathus [carnivore]
Suborder: Anomodontia
[Infraorder: Dicynodontia]
Family: Kannemeyeriidae
Genus: Kannemeyeria [herbivore]
[Drawing] Cynognathus is a Permian - Triassic Carnivore.
[Drawing] Cynognathus Skull diagram shows Canines, Incisors
[Drawing] Herbivore Kannemeyeria

The cynodont radiation
- Cynodonts nearly have all the characteristics of mammals
- They were probably warm-blooded blooded, and some were covered in hair
- The cynodonts, or 'dog teeth', were the most successful , and one of the most diverse groups of **therapsids** (Permian and Triassic evolutionary radiation)
- Included large carnivorous and herbivores and small and extremely mammal-like **ictidosaurs**[494]
- The ictidosaurs are almost certainly close to the direct ancestry of the class Mammalia
- Thus, mammals are descended from a single group of cynodonts

Thrinaxodon liorhinus: a Triassic Cynodont, thus a therapsid with many mammal-like traits

---

493 **Therapsida**: "Therapsids, previously known as the "mammal-like reptiles", are an order of synapsids. Traditionally, synapsids were referred to as reptiles. However, when the term is used cladistically, the taxon also includes the mammals, which are descended from the cynodont therapsids.... Therapsids' temporal fenestrae were larger than those of the pelycosaurs. The jaws of therapsids were more complex and powerful and the teeth were differentiated into frontal incisors for nipping, large lateral canines for puncturing and tearing, and molars for shearing and chopping food. Therapsids' legs were positioned more vertically beneath their bodies than were the sprawling legs of reptiles and pelycosaurs."
http://en.wikipedia.org/wiki/Therapsid

494 **Ictidosaurs**: "The Trithelodontidae, also known as Ictidosaurs, were small to medium-sized cynodonts. They were extremely mammal-like, highly specialized cynodonts, although they still retained a very few reptilian anatomical traits. They descended from a basal Eucynodont therapsid, something more or less like Cynognathus. They were mainly carnivorous or insectivorous, though some species may have developed omnivorous traits. Their skeletons show that they had a close relationship to mammals. Some scientists feel that the Trithelodontidae stem or its closest relatives may have given rise to primitive mammals. The trithelodontids were one of the longest lived non-mammalian therapsids, living from the late Triassic to the Jurassic period..."
http://en.wikipedia.org/wiki/Ictidosaurs

Thrinaxodon liorhinus was a fairly small (total length about 50 cm) early cynodont, known from South Africa and Antarctica; a furry animal on the direct line to the mammals. Thrinaxodon fed on large invertebrates and smaller vertebrates, and gave rise to larger and more advanced forms like Cynognathus.

Kingdom: Animalia
  Phylum: Chordata
    Class: Synapsida
      Order: Therapsida
        Suborder: Cynodontia
          Family: Galesauridae
            Genus: Thrinaxodon

Morganucodon (first "real" mammal)

Morganucodon[495] was a tiny, rat-like quadruped that had 5-toed feet and a short tail. It was about 10 cm long, short legs, a long, narrow snout, and both sharp teeth and grinding molars. This early mammal belonged to the Order **Triconodont** (having 3 cups on molars). Its large eyes probably indicate that it was nocturnal. Morganucodon was probably was warm-blooded, but may have laid eggs, like other primitive mammals. Jurassic to early Triassic.

Diversity of terrestrial animals through time (Graph: Signor, 1990)

Romer's Gap

- Tetrapods began to invade land about 415 million years ago [Devonian]
- They nearly disappeared 360 million years ago [Lower Mississippian] (as did non-marine arthropods)
- The fossil record contains few examples of animals with backbones (or terrestrial arthropods) for the next 15-30 Ma, and then suddenly vertebrates show up again, this time for good [still Mississippian].
- The mysterious gap in vertebrate colonization of land is known as Romer's Gap, named for the paleontologist, Alfred Romer, who first recognized it
- Cause: precipitous drop in the oxygen ?

[Graph] A plot of atmospheric oxygen level versus time for the Phanerozoic: The data show a pronounced and extended rise in atmospheric O_2 over the period 375-275 Ma spanning the Carboniferous and Permian periods. The modeling shows that increased oxygen production caused by increased burial of organic carbon—the rise of the vascular plants (Berner, 1999) Romer's Gap occurs at a time O_2 is rising.

Graph showing proportion of tetrapod families by habitat

Initially all tetrapods lived in freshwater; later, they moved onto land, went back to the sea, or became gliders, fliers, arboreal or burrowers, etc. (Benton, 1990)

---

[495] **Morganucodon**: is an early mammalian genus which lived during the Upper Triassic. It first appeared about 205 million years ago. Unlike many other early mammals, Morganucodon is well represented by abundant and well preserved, though in the vast majority of cases disarticulated, material... There has been a long controversy about whether or not to classify it as a mammal at all and some authors prefer to include it in a protomammalian clade called Mammaliaformes. Morganucodon is regarded as very primitive, for its lower jaw retains some of the bones found in its reptilian ancestors in a very reduced form, rather than being composed solely of the dentary. Furthermore, the primitive reptilian jaw joint between the articular and quadrate bones, which in modern mammals has moved into the middle ear and become part of the ear ossicles as malleus and incus, is still to be found in Morganucodon. However, a consensus accepted by most scientists states that mammals as a group are defined by the possession of a special, secondarily evolved jaw joint between the dentary and the squamosal bones, which has replaced the primitive reptilian one between the articular and quadrate bones in all modern mammalian groups. Morganucodon is special in this respect, because apart from still having the primitive hinge, it has also evolved the derived mammalian one and thus features a double jaw joint. It is for this reason, and additional evidence pointing to diphyodonty and determinate growth, that Morganucodon is now usually considered a true mammal." http://en.wikipedia.org/wiki/Morganucodon

Graph showing proportion of tetrapod families by prey
From being all fish predators initially, tetrapods evolved to eat other tetrapods, insects, and herbage (browsing and grazing) (Benton, 1990)

Mass Extinctions, Part I: Evidence and Mechanisms for Events

[MCM: Edited from verbatim text of LRS slides, not all material in the slides was discussed. I will not be able to post the slides document, but if available to you, see PDF document of slides, containing images which are essential for understanding this material. See also earlier notes regarding mass extinctions.]

Possible Causes for extinction
1. Impact events
2. Climate change
3. Volcanism
4. Anoxic events
5. Plate tectonics
6. Astronomical events
7. Biological events
8. Press/pulse theory

1. IMPACT EVENTS[496]
• The impact of a large asteroid or comet could create "**mega-tsunamis**"(**iminami**[497]) and global forest fires, and simulate "nuclear winters" from the dust it puts in the atmosphere
• Taken together, these and other related effects might be sufficiently severe to disrupt the global ecosystem and cause extinctions
• Only for the End Cretaceous extinction is there strong evidence of such an impact
• Circumstantial evidence of such events is also given for the End Permian, End Ordovician, End Jurassic and End Eocene[498] extinctions.

Mega-Tsunamis
[Drawing] A "megatsunami" is associated with waves ranging from over 40 meters to giants over 100 m tall. Megatsunamis are caused by bolide impacts, explosive volcanism, or massive landslides.
[Drawing] A "megatsunami" as it would appear on the coast of Florida
Tsunamis can travel up to 965 km per hour, at the deepest point of the water, but slow as they near the shore, eventually hitting the shore at 48 to 64km per hour. The energy of the wave's speed is transferred to height and sheer force as it nears shore.
[Drawing] Normal wind generated waves exhibit circular-elliptical water movement pattern and do not flood higher areas.
[Drawing] Tsunamis run quickly over the land as a wall of water.

"Nuclear winter"
• Large quantities of aerosol particles dispersed into the atmosphere would
reduce the amount of sunlight that reached the surface
could potentially remain in the stratosphere for months or even years
• Assuming the impact is in the northern hemisphere, the ash and dust would be carried by the mid-latitude west-to-east winds, forming a uniform belt of particles encircling the northern hemisphere from 30°to 60° latitude

Impact Events Energy
[Graph] Frequency of impact plotted against energy, either in Joules or Megatons TNT equivalent.[499] Also indicated are a number of specific impact events. [The **Revelstoke** event was <10 Megatons TNT,

[496] **Impact Events**: http://en.wikipedia.org/wiki/Impact_events
[497] **Mega-Tsunami**: http://en.wikipedia.org/wiki/Megatsunami
[498] **End Eocene and other Extinction Events**: http://en.wikipedia.org/wiki/Extinction_event
[499] **Graph of Impact Event Energy vs. Frequency**: can be seen for instance in http://solarsystem.nasa.gov/scitech/display.cfm?ST_ID=345

the **Tunguska**[500] (Siberia) was 10-20 megatons, the **Meteor Crater** (**Barringer Crater**) was 50-100 megatons, the **Zhamanshin**[501] (Kazakhstan) was c. 10^5 megatons, and the K–T extinction event (Chicxulub Crater)[502] was c. 10^8 megatons.] Note an impact event with energy greater than the world's nuclear arsenal [c. 50,000 megatons] occurs on a time-scale of less than a million years.

2. CLIMATE CHANGE

• Rapid climate change may be capable of stressing the environment to the point of extinction, although convincing arguments are lacking that climate change alone causes major mass extinctions
• The recent cycles of ice ages are only believed to have had very mild impacts on biodiversity
• Climate change may cause slower increases in extinction rates than other causes
• Extinctions suggested to be causes by climate change include: End Ordovician, End Permian, Late Devonian, and others

Climate change and sea level regression

• The photic zone along the continental margins will shift
• Width of productive area will change drastically—reduction of habitat area
• Smaller habitat areas accommodate fewer taxa—lower diversity
• Lower diversity as extinction rates increase
increased competition
greater crowding

Why Do Marine regression and transgression[503] **not always result in (notable) mass extinction?**

• Regression followed by rapid transgression permit a sufficient number of organisms to survive (Quaternary regressions)
• Quaternary faunas were **eurytopic** (organisms that tolerate or adapt to a wide range of environmental conditions) survivors of the environmentally stressful Late Cenozoic times

3. VOLCANISM

• The formation of large igneous provinces, which can involve the outflow of millions of cubic kilometers of lava in a short duration
• Initially **sulfur aerosols and volcanic ash** would envelop the earth's atmosphere blocking out sunlight and sending surface temperatures plunging. These can cause a significant glaciation.
• The second major effect is the emission of greenhouse gases such as CO_2, methane and also water vapor. Heat reflected by the Earth cannot penetrate the atmosphere so it is retained
• This cause has been proposed for the End Cretaceous, End Permian, End Triassic, and End Jurassic extinctions.

Siberian traps

[Map showing range of Siberian Traps] The Siberian Traps[504] form a large igneous province in Siberia [covering 4 - 7 million km^2]. The massive eruptive event spans the Permian-Triassic boundary and

---

[500] **Tunguska Event**: http://en.wikipedia.org/wiki/Tunguska_event
[501] **Earth Impact Database including Zhamanshin**: http://www.unb.ca/passc/ImpactDatabase/
[502] **Cretaceous-Tertiary Extinction Event**: http://en.wikipedia.org/wiki/Cretaceous-Tertiary_extinction_event
[503] **Marine Regression and Transgression**: **Marine regression** is a geological process occurring when areas of submerged seafloor are exposed above the sea level. The opposite event, **marine transgression**, occurs when flooding from the sea covers previously exposed land. Evidence of marine regressions and transgressions occurs throughout the fossil record, and these fluctuations are thought to have caused (or contributed to) several mass extinctions, among them the Permian-Triassic extinction event ... and Cretaceous–Tertiary extinction event... At the time of the Permian or P/T extinction, the largest extinction event in the Earth's history, global sea level fell 250 meters, or more than 800 ft...

A major regression could, in and of itself, cause marine organisms in shallow seas to go extinct; yet mass extinctions tend to involve both terrestrial and aquatic species, and it is harder to see how a marine regression could cause widespread extinctions of land animals. Regressions are therefore seen as correlates or symptoms of major extinctions, rather than primary causes. The Permian regression might have been related to the formation of Pangaea... "
http://en.wikipedia.org/wiki/Marine_regression

was essentially coincident with the Permian-Triassic extinction event in what was one of the largest known volcanic events of the last 500 million years of Earth's geological history
[Image] **The Pu'u'O' fissure eruption, Hawaii, in July 1986**
This illustrates the type of eruption event that may have produced the Siberian flood basalts. However, the eruption volumes and rates would have been substantially greater in Siberia. Note the gas clouds (containing sulfur dioxide, carbon dioxide, and water vapor) issuing from the vent.

Volcanism and the formation of large igneous provinces [Diagram]
[This diagram shows how large eruptions lead to increased SO_2 emissions contributing to cooling and glaciation, increased Cl and F emissions contributing to acid rain and fungal proliferation, and increased CO_2 emissions contributing to long-term warming, increased weathering, marine anoxia, etc. The net effect is increased rates of extinction on land and in the ocean.]

Large igneous provinces
- When created, these regions often occupy a few million km^2 and have volumes on the order of 1 million km^3. In most cases, most of an igneous province's volume is emplaced in less than 1 Ma.
- Possible Causes of igneous provinces

Mantle plumes, where the excess heat and chemical differences lead to an extended period of volcanism
Rifting and, in particular, the divergence of newly formed continental rifts
It is possible that both theories may lead to the same results

Mantle Plumes [Drawing]
A 3-D view of a Mercator projection (scale is the same in every direction), around any position of the mantle, with orange surfaces surrounding warm blobs of mantle, rising as plumes.

Rifting
Laki is a volcanic system, belonging to Katla central volcano in Iceland, the origin of the biggest volcanic eruption on earth in historical times (1783), in the form of a flood basalt or "Large Igneous Province"
[Map] A map of Iceland astride the mid-Atlantic Ridge [between the North American Plate and the Eurasian Plate].

Large igneous provinces and extinctions [Graph[505]]
This graph shows the approximate correspondence of several extinctions and igneous provinces, including
Emeishan-Panjal and Siberian Traps: End Permian
CAMP [Central Atlantic Magmatic Province]: End Triassic
Deccan Traps: End Cretaceous

4. ANOXIC EVENTS[506]

---

[504] **Siberian Traps**:
• "The Siberian Traps ... form a large igneous province in Siberia. The massive eruptive event spans the Permian-Triassic boundary, about 251 to 250 million years ago, and was essentially coincident with the Permian-Triassic extinction event in what was one of the largest known volcanic events of the last 500 million years of Earth's geological history. The term 'traps' is derived from the Swedish word for stairs (trappa, or sometimes trapp), referring to the step-like hills forming the landscape of the region."
http://en.wikipedia.org/wiki/Siberian_traps
• "Milanovskiy (1976) estimated that the original extent of the [Siberian] Traps was about 4 $\times 10^6$ km^2, but there must be considerable latitude in this figure. Masaitis (1983), for example, has suggested that the Traps originally extended over a region of ~7 million km^2."
http://www.le.ac.uk/gl/ads/SiberianTraps/AreaVolume.html
[505] **Graph of Igneous Provinces and Extinctions**: see p. 157 of
http://www.tos.org/oceanography/issues/issue_archive/issue_pdfs/19_4/19.4_coffin_et_al.pdf
[506] **Anoxic Events**: "Oceanic anoxic events occur when the Earth's oceans become completely depleted of oxygen (O_2) below the surface levels. Although anoxic events have not happened for millions of years, the geological record shows that they happened many times in the past, and may have caused mass extinctions... Oceanic Anoxic Events occurred only during periods of very warm climate

• Climate change, brought on by heavy volcanic activity, warmed the oceans [e.g., increased CO_2], which led to anoxic conditions
• Surface temperatures were probably in excess of 25°C (Quaternary levels are 13°C)
• Killer greenhouse effect: The oceans became depleted in dissolved oxygen (close to 0% dissolved O_2) and enriched in hydrogen sulfide (H_2S)
• H_2S poisoned life on both land and sea, and destroyed the ozone layer
• Without the protective ozone, the sun's UV radiation killed off much of the life that still remained

Anoxia
• No polar ice caps—polar water is too warm to sink
• Ocean currents become weak and upwelling is absent
• The continental shelves may be flooded with anoxic water when flooded during a transgression [rising sea level]
• Productivity around the continental shelf is low
• The inhabitable shelf areas will be reduced in size (species-area effect)
• Black shales[507] are deposited [reflecting anaerobic decomposition of organic matter]
• An anoxic event may last for 3-4 Ma

Peter Ward Killer Greenhouse Effect Hypothesis
[Diagrams] These depict Increased volcanism and rising greenhouse gases, rapid global warming, warm ocean absorbs less O_2, anoxia destabilizes chemocline[508] [boundary between oxygenated and anoxic sea water permeated with H_2S from anaerobic bacteria] and it rises abruptly to the surface, upwelling H_2S entering troposphere results in destruction of ozone shield causing rising UV surface radiation, anaerobic organisms including green and purple sulfur bacteria flourish while aerobic organisms perish, H_2S kills land animals and plants.
[Quotation from article] See **"Impact from the Deep," Peter Ward (2006)**[509]

The best documented ocean anoxic events **OAEs** [Table]
The following are the best documented ocean anoxic events (OAE) [table data partially included here]: Maastrichtian 71.3 Ma, Campanian 83.5 Ma [OAE4, poorly studied], Santonian 85.8 Ma [OAE3, poorly studied], 2.3 Coniacian 89.9 Ma, Turonian 93.5 Ma [OAE2], Cenomanian 98.9 Ma, Albian 112.2 Ma and Aptan121 Ma [OAE1]; Barremian 127 Ma, Hauterivian132 Ma, Valanginian 137 Ma, and Berriasian 144.2
Earlier examples have been suggested to have occurred in the Jurassic, the late Triassic, Devonian, Ordovician and Cambrian. The Paleocene-Eocene Thermal Maximum, which was characterized by a global rise in temperature and deposition of organic-rich shales in some shelf seas, shows many similarities to OAE.

---

characterised by high levels of carbon dioxide (CO_2) and mean surface temperatures probably in excess of 25 °C (Quaternary levels are 13 °C)." [Includes discussion of possible mechanisms]
http://en.wikipedia.org/wiki/Anoxic_event
507 **Black Shales**: "A thinly bedded shale that is rich in carbon, sulfide, and organic material; formed by **anaerobic** decay of organic matter."
http://www.blackshale.com/
508 **Chemocline**: "A chemocline is the border region or interface between two contrasting and predominating chemistries within a body of water. A chemocline is analogous to a thermocline, the border at which warmer and cooler waters meet in an ocean, sea, lake, or other body of water. (In some cases, the thermocline and chemocline coincide.) Chemoclines most commonly occur where local conditions favor the formations of anoxic bottom water — deep water deficient in oxygen, where only anaerobic forms of life can exist. The Black Sea is the classic example of such a body, though similar bodies of water (classified as meromictic lakes) exist across the globe. Aerobic life is restricted to the region above the chemocline, anaerobic below. Photosynthetic forms of anaerobic bacteria, like green phototrophic and purple sulfur bacteria, cluster at the chemocline, taking advantage of both the sunlight from above and the hydrogen sulfide (H_2S) produced by the anaerobic bacteria below. In any body of water in which oxygen-rich surface waters are well-mixed (holomictic), no chemocline will exist. To cite the most obvious example, the Earth's global ocean has no chemocline."
http://en.wikipedia.org/wiki/Chemocline
509 **Impact from the Deep**: Ward, Peter. "Impact from the Deep" *Scientific American Magazine.* October, 2006. http://www.sciam.com/article.cfm?id=00037A5D-A938-150E-A93883414B7F0000&page=1

Present-day North Atlantic currents [diagram]
Since the Late Eocene, and the Antarctic glaciation, the oceans contain strong currents; this aerates the bottom waters (thus, most of the modern deep-sea fauna may be no older than Tertiary). [The Gulf Stream flows northward along Greenland etc. and warms the northern latitudes and replenishes the descending North Atlantic Deep water that returns south and continues along S. America.]

5. PLATE TECTONICS
• The opening and closing of seaways and land bridges may play a role in extinction events
• Large areas of shelf space may be lost during collision
• Previously isolated populations may be brought into contact and alter global diversity patterns
• However, tectonic changes are relatively slow in geological terms, while mass extinctions are relatively sudden
• A plausible mechanism for a trigger that suddenly fires a deadly "extinction bullet" is needed
• Plate tectonics is most frequently discussed in relation to the End Permian mass extinction.

Continents at the End Permian mass extinction 255 Ma [Map]
Previously shown, depicts Pangea etc.

6. ASTRONOMICAL EVENTS
• Nearby nova, supernova, or gamma ray burst. A nearby gamma ray burst (less than 6,000 light years distance) could sufficiently irradiate the surface of the Earth to kill organisms and destroy the ozone layer
• Extremely high-energy bursts of gamma-ray photons shine millions of times brighter that the Sun
• From statistical arguments, approximately 1 gamma ray burst would be expected to occur in close proximity to Earth in the last 540 million years
• This has been suggested as an explanation for the End Ordovician extinction event
• Another hypothesis: solar flare or variation in solar output

Gamma Ray bursts and Supernovae
[Drawings] **Gamma-ray bursts**[510] (GRBs) are the most powerful [luminous] events in the Universe. Two theories:
1) Most GRBs are thought to occur when a giant star "in the early universe" burns up its supply of fuel and the center of the star collapses into a black hole. A tremendous burst of gamma rays is released.
2) Two neutron stars collide, creating a black hole, and releasing a powerful blast of gamma rays.
[Drawing] **Life cycle of a massive star**
Stars which are 8 times or more massive than our sun end their lives as a **supernova**. A supernova explosion will occur when there is no longer enough fuel for the fusion process in the core of the star to create an outward pressure which combats the inward gravitational pull of the star's mass. [The star remnant becomes a neutron star or black hole.]

Solar flare or variation in solar output
[Image] This still image from an animation depicts the initiation of a **solar flare**. Magnetic field lines create an arch in the upper atmosphere of the sun, the corona. Some field lines shoot into space. Field lines recombine to flares. Particles, shown in hot white, accelerate down the field lines into the corona and downward towards the surface of the sun, not shown here. Young stars spin fast and flare more actively, and the early sun likely generated larger solar flares then at present.

7. BIOLOGICAL EVENTS
• Outdated hypothesis
• The spread of a new disease or simple out-competition following an especially successful biological innovation have also been considered as a cause for mass extinction
• The major mass extinctions in Earth's history are too sudden and too extensive to have resulted solely from biological events.

8. PRESS/PULSE THEORY
A new theory[511] (Ian West and Nan Crystal, 2006) suggests that co-occurrence of long-term stress and catastrophic disturbance led to the big extinctions

---

[510] **Gamma ray burst**: http://en.wikipedia.org/wiki/Gamma_ray_burst

• This theory postulates that the coincidence of press (e.g., continental flood volcanism) and pulse events (impact events) is required to produce the greatest extinctions
• Higher average extinction rates were recorded during press/pulse events than during either one or the other
• It is the combination of press and pulse events—a geologic one-two punch—rather than the magnitude of single events that explains Earth's greatest episodes of extinction

Press and pulse multiple events
• When an impact occurred during a flood basalt event, higher extinction rates occurred
• Flood basalts, especially, are considered press events because they release large amounts of greenhouse gases and can change Earth's climate
• Can today's extinction be seen as press and pulse?
Accelerating climate change (press)
Ongoing destruction of wild habitats worldwide (pulse)
• Paleontologists have claimed for years that the impact-kill hypothesis is all wrong. Impacts alone could not have been the killing mechanism for the End Cretaceous event (or any of the other major mass extinctions) •

Carbon 13 to Carbon 12 Ratios Evidence
Carbon 13 (^{13}C) isotopes found in geologic strata suggest longer-acting mechanisms behind two of three ancient extinction events. See three graphs of $\delta^{13}C$, at End Permian[512], End Triassic[513] Extinction, and End Cretaceous Extinction—these graphs do not exhibit identical patterns but show alterations in the relative abundance of ^{13}C that last for many hundreds of thousands of years. The graphs are annotated: "^{13}C is more abundant *in the atmosphere* when land and sea plants are thriving. [MCM: Because plants are preferentially extracting ^{12}C from the atmosphere, leaving more ^{13}C behind.] When plant life dies on a massive scale, ^{13}C drops as a proportion of atmospheric carbon. [MCM: Because plants are no longer preferentially extracting ^{12}C from the atmosphere.] Comparing ancient samples with a common carbon standard reveals multiple large drops in ^{13}C leading up to the End Permian [MCM: about 10 ‰] and End Triassic boundaries. The dips imply multiple extinction crises occurring over hundreds of thousands of years. In contrast, a ^{13}C plunge for the period around the Cretaceous-Tertiary boundary depicts one abrupt ecological cataclysm."

Mass Extinctions, Part II: Fossil Record

[MCM: Edited from verbatim text of LRS slides, not all material in the slides was discussed. I will not be able to post the slides document, but if available to you, see PDF document of slides, containing images which are essential for understanding this material.]

Definition
Jack Sepkoski's (1986) definition of a mass extinction: "A mass extinction is any substantial increase in the amount of extinction (i.e. lineage termination) suffered by more than one geographically widespread higher taxon [A taxon or taxonomic unit, is a grouping of organisms] during a relatively short interval of geological time, resulting in at least a temporary decline in their standing diversity."

---

511 **Press/Pulse Theory**: "Previous discussions of mass extinction mechanisms focused on events unique to the extinction they explain. To propose and test a general mechanism of mass extinction, we borrow a pair of concepts from community ecology: Press disturbances alter community composition by placing multigenerational stress on ecosystems; pulse disturbances are sudden, catastrophic, and can alter communities by causing extensive mortality. We hypothesize that the coincidence of press and pulse events is required to produce the greatest episodes of dying in Phanerozoic history…" Arens, Nan Crystal And West, Ian D. "Press/Pulse: A General Theory Of Mass Extinction?" http://gsa.confex.com/gsa/2006AM/finalprogram/abstract_111772.htm
512 **Carbon 13 Ratio and the End Permian Extinction:** http://www.peripatus.gen.nz/paleontology/extinction.html
513 **Carbon 13 Ratio and the End Triassic Extinction**: Peter D. Ward et al. "Isotopic evidence bearing on Late Triassic extinction events, Queen Charlotte Islands, British Columbia, and implications for the duration and cause of the Triassic/Jurassic mass extinction" *Earth and Planetary Science Letters* Volume 224, Issues 3-4, 15 August 2004, Pages 589-600.

[Graph[514]] **Apparent extinction intensity for Marine Genus Biodiversity**, i.e. the fraction of genera going extinct at any given time, as reconstructed from the fossil record. (Graph not meant to include recent epoch of Holocene extinction event). This graph shows spikes representing the End Permian, End Triassic, and K-T extinctions etc.
[Table] **Estimation of species extinction rate (%) during five major mass extinctions based upon extrapolation from family and genera data.**
[Family level extinction % / Family-based species / Genera level / Genera-based species]

End Ordovician:	26	84	60	85
Late Devonian:	22	79	57	83
End Permian:	51	95	82	95
End Triassic:	22	79	53	80
End Cretaceous:	16	70	47	76

After an extinction: Ecological recovery and Lazarus taxa
• Extinctions are followed by recovery
• The larger the extinction, the longer the recovery time, and the more the global ecosystem changes across the event
• During recoveries we sometimes see **Lazarus taxa**[515]: plants or animals that disappeared at the extinction are missing from the fossil record for a long time, only to reappear at a later time. Corals, for example, are absent after the Permian-Triassic extinction, and re-appear in the Middle Triassic
• The existence of Lazarus taxa implies that somewhere there must have been refuges for scattered survivors; only when they radiate away from the refuges do they appear again in the rock record

Is Sepkoski's statistical analyses of species turnover and diversity in the fossil record correct?
• It is quite feasible that the increase in diversity toward recent times is a result primarily of:
the greater volume of rock available from recent times
the greater amount of effort that has been put into studying these rocks.
• A number of studies have presented evidence showing that apparent diversity is closely correlated with the intensity with which different periods of geologic time have been sampled

[Graph] **Sepkoski (1981) History of the three evolutionary faunas**
This is the now familiar graph showing Total familial diversity through the Phanerozoic and the contributions by the 3 major "factors", residual diversity, etc.

Problems with time scale and sampling
• Quantifying pattern of survival is quite difficult—limited by biostratigraphic resolution
• **Signor-Lipps effect**[516] (Signor and Lipps, 1983) tends to "smear out" extinctions so they appear more gradual: When a collection of taxa are killed off simultaneously in a mass extinction, their last

---

514 **Graph of Marine Genus Biodiversity Extinction Intensity**:
http://en.wikipedia.org/wiki/Permian-Triassic_extinction_event
515 **Lazarus Taxon**: "Lazarus taxon (plural taxa) is a taxon that disappears from one or more periods of the fossil record, only to appear again later. The term refers to the New Testament story of Lazarus, in which Jesus miraculously raises Lazarus from the dead. Lazarus taxa are observational artifacts that appear to occur either because of (local) extinction, later resupplied, or as a sampling artifact. If the extinction is conclusively found to be total (global or worldwide) and the supplanting species is not a lookalike (an **Elvis species**), the observational artifact is overcome. [MCM: unclear] The fossil record is inherently imperfect (only a very small fraction of organisms become fossilized) and contains gaps not necessarily caused by extinction, particularly when the number of individuals in a taxon becomes very low. If these gaps are filled by new fossil discoveries, a taxon will no longer be classified as a Lazarus taxon."
http://en.wikipedia.org/wiki/Lazarus_taxon
516 **Signor-Lipps Effect**: "The Signor-Lipps effect is a paleontological principle proposed by Phil Signor and Jere H. Lipps which states that, since the fossil record of organisms is never complete, neither the first nor the last organism in a given taxon will be recorded as a fossil. The most spectacular example is the coelacanth, which was thought to have become extinct in the very late Cretaceous - until a live specimen was caught in 1938. But the Signor-Lipps effect is more important for the difficulties it raises in paleontology:
• It makes it very difficult to be confident about the timing and speed of mass extinctions, and this makes it difficult to test theories about the causes of mass extinctions. For example the extinction of

occurrences in the fossil record may nonetheless give the impression of a gradual extinction, due to the incompleteness of the fossil record
• Thus, actual time scale of an extinction is hard to pin down

The Precambrian and Vendian [Ediacaran] Mass Extinctions
• Both Paleoproterozoic and Vendian (Ediacaran) periods are believed to have hosted at least one mass extinction each
• About 650 million years ago, 70% of the dominant Neoproterozoic flora and fauna perished in the first great extinction. This extinction strongly affected stromatolites and acritarchs
• Probably caused by the Varanger-Marinoan glaciation (605-585 Ma); snowball earth
Continents were located at low and middle latitudes but not at the poles
Heat loss by reflection by highly reflective land surfaces, decline in atmospheric CO_2 by lichen and fungi

[Map at Late Proterozoic 650 Ma] **The break-up of the supercontinent, Rodinia**[517], which formed 1100 million years ago. The Neoproterozoic was an "Ice House World", much like the present-day.

Late Ordovician mass extinction
[Graph of number of genera show dip at Late Ordovician]
Late Ordovician extinction causes: Two pulses of extinction:
• In the first phase temperatures dropped throughout the world—glaciers spread on the Gondwana ice caps; tropical organisms were hit the hardest
• Sea level dropped and **epeiric seas**[518] disappeared
• In a second phase ice sheets melted and the sea level rose again
• Possibly circumstantial evidence for an impact event

[Map at time of Middle Ordovician 458 Ma] During the Ordovician, oceans separated the continents of **Laurentia**, **Baltica**, **Siberia** and **Gondwana**. The end of the Ordovician was one of the coldest times in Earth history. Ice covered much of the southern region of Gondwana.

Diagram of major Glaciations[519]
Paleoproterozoic [Huronian 2100 - 2400 Ma]
Neoproterozoic [Cryogenian or Sturtian-Varangian 800 - 635 Ma]

---

the dinosaurs was long thought to be a gradual process, but evidence collected since the late 1980s suggests it was abrupt, which is consistent with the idea that an asteroid impact caused it.
• The uncertainty about when a taxon first appeared makes it difficult to be confident about the ancestry of specific genera. For example if the earliest known fossil of genus X is much earlier than the earliest known fossil of genus Y and genus Y has all the features of genus X plus a few of its own, it is natural to suppose that X is an ancestor of Y. But this hypothesis could be called into question at any time by the finding of a fossil of Y that is earlier than any known fossil of X - unless an even older fossil of genus X is found, and so on."
http://en.wikipedia.org/wiki/Signor-Lipps_effect
[517] **Rodinia**: " (from the Russian ... "motherland") refers to one of the oldest known supercontinents, which contained most or all of Earth's then-current landmass. Paleomagnetic evidence provides clues to the paleolatitude of individual formations, but not to their longitude, which geologists have pieced together by comparing similar strata, often now widely dispersed... Geologic evidence suggests that Rodinia formed and broke apart in the Neoproterozoic, probably existing as a single continent from 1 billion years ago until it began to rift into eight smaller continents about 800 million years ago. It is thought to have been largely responsible for the cold climate of the Neoproterozoic era..."
http://en.wikipedia.org/wiki/Rodinia
[518] **Epeiric sea**: "An epeiric sea (also known as an **epicontinental sea**) is a large but shallow body of salt water that lies over a part of a continent. Epeiric seas are usually associated with the marine transgressions of the early Cenozoic and other eras. They can be warm or cold; indeed, several were present at the end of the last Ice Age, when sea level rose more rapidly than some areas could isostatically adjust. Modern examples are the Persian Gulf, the North Sea, and Hudson Bay." [MCM: Old examples include the Western Interior Seaway, Hudson Seaway, Labrador Seaway, Tyrrell Sea, etc.]
http://en.wikipedia.org/wiki/Epeiric_sea
[519] **Major Glaciations**: http://en.wikipedia.org/wiki/Timeline_of_glaciation

Ordovician-Silurian [450 - 420 Ma]
Carboniferous and Permian [360 - 260 Ma]
Quaternary

Late Ordovician: Impact of the first phase of extinctions
Warm-adapted species were wiped out:
• Planktonic and nektonic organisms, such as graptolities, acritarchs, nautiloids, and conodonts were severely reduced
• Benthic organisms such as trilobites, bryozoans, corals, and brachiopods were severely affected
[Drawing] **Graptolites** (Cambrian to mid-Carboniferous): A group of marine colonial animals that belong to the group Hemichordata. The animals lived in tiny cups arranged along slender stems. Most graptolites floated free in the oceans. As fossils most of the graptolites look like branches of saw blades.
[Drawings] **Conodonts**: A type of extinct worm-like animal with distinctive conical or multi-denticulate teeth made of apatite (calcium phosphate). The teeth of these animals are almost always the only parts preserved as fossils.
• Specimens of **Plectodina aculeata** teeth.
• Reconstruction of conodont animals—some may be juveniles.

Late Ordovician: Impact of the second phase of extinctions
Cool-adapted species were wiped out:
• Several trilobite groups that had survived the first phase were wiped out
• Corals, conodonts, and bryozoans were again severely reduced in diversity and numbers.
Thus, first warm-loving species were wiped out, followed by the cool-adapted species.

Illustration from Sepkoski's 1998 "Rates of speciation in the fossil record"—the end-Ordovician extinction[520]
• [Top right graph p. 320 shows "**sharp drop in standing diversity** of marine animal genera at the end of the Ordovician Period and then the long recovery of diversity to pre-extinction levels through the first half of the Silurian Period"]
• [Middle graph shows "the **peak of extinction** at the end of the Ordovician was sharp."]
• [Bottom graph shows "in contrast, that originations did not increase abruptly after the pulse of extinction, even though diversity began to recover; rather, origination rates increased [gradually] to the middle Silurian."]
• Sepkoski defines the **recovery** as the point at which the rate of new originations per taxon peak and begin to drop off.
• That point is the same as the one at which the taxon count reached pre-extinction levels
• The **origination rate** peaks about 20 million years after the peak in **extinction rates**
• Sepkoski considered this to be a long recovery period, and ascribed the length of the recovery to the enormity of the mass extinction event.

Late Devonian mass extinctions
[Graph of number of genera show dip at Late Devonian]

[Map depicting Earth at Early Carboniferous c. 356 Ma]
During the Late Devonian-Early Carboniferous, the Paleozoic oceans between Euramerica and Gondwana began to close. An ice cap grew at the South Pole and coal swamps were common near the equator.

Late Devonian extinction causes
• Occurred over a span of 20 Ma
• There are indications of climatic changes, and major changes in sea-level and ocean chemistry
• Possibly some sort of ecological crises like an explosive growth in algae—could result in anoxia, evidence may be seen in extensive tracts of **Devonian black shales**
• Continental glaciation again?—Glacial drift, erratics, and striations found in South America, which was located over the South Pole

[520] **Rates of speciation in the fossil record**: see p. 320 of J. J. Sepkoski. "Rates of speciation in the fossil record" *Phil.Trans. R. Soc. Lond. B* (1998) 353, 315-326

• Iridium anomalies, shocked quartz, and tektites are reported from China and Western Europe at or near the End Devonian boundary—impact?

Impact of Late Devonian extinctions
• One of the most devastating mass extinction for marine life in the Phanerozoic
• 40% of all marine genera disappeared
• 70% of all marine invertebrates disappeared
• Again, tropical areas was hardest hit:
Extensive Devonian reef communities were decimated, especially tabulate corals and stromatoporoids; only a few species of rugose corals survived
Brachiopods, goniatites, trilobites, conodonts, and placoderms were severely reduced
[Drawing] Goniatite [an ammonoid, a type of shelled cephalopods]

Late Permian mass extinctions
[Graph of number of genera show massive dip at Late Permian]

Late Permian mass extinctions—the mother of all mass extinctions!
• This was the greatest mass extinction of animal life of all time
• 90-95% of all marine species on Earth died out
• 80% of all life on Earth was wiped out
• Most losses probably occurred within one million years!

Late Permian extinction causes
Again, the tropics were hit especially hard:
• Pangea was complete—resulted in a rigid, cooling climate with temperature extremes
• No or limited epeiric seas
• Equatorial ocean circulation was blocked by Pangea
• Causes: Siberian traps (CO_2), glacial periods?
• Evidence also indicates a possible extraterrestrial cause, which may have triggered volcanism, anoxia, and destroyed the epeiric seas that remained

[Map depicting Earth at Late Permian c. 255 Ma]
Vast deserts covered western Pangea during the Permian. This Permian-Triassic mass extinction marked the end of the Paleozoic Era.

Late Permian mass extinctions
[Graph showing Carboniferous-Permian Glaciation, with Late Permian extinctions falling toward the end of this period.]

Permian anoxic event?
• The Siberian Traps may have produced large amounts of CO_2, which caused global warming; lowered O_2 with the result that the chemocline would have reached surface causing massive upwelling of H_2S [see previous discussion and illustrations of Peter Ward describing rising chemocline, etc.]
• Algae blooms of H_2S-consuming bacteria?
–H_2S was produced by upwelling anoxic water to produce extinctions both on land and in the oceans
–H_2S was produced at 2000 times the amount given off by volcanoes today
–H_2S may also severely have affected the ozone layer

Late Permian marine extinctions
• Tropical marine invertebrates experienced the most extensive losses; shallow marine invertebrates lost their shelf environments: Fusulinids, rugose corals, many families of crinoids, productid brachiopods (anchored to the substrate using spines on their valves), lacy bryozoans, and many groups of ammonoids became extinct
• Reefs eliminated—did not appear again for 12-14 Ma
[Image] **Fusulinid**: Fusulinids are foraminifera (Ordovician to Permian). Those at the end of the Permian were the largest that ever lived, some about the size of grains of rice; others a centimeter or more. Their skeletons are calcium carbonate. Most were benthic, though some species probably floated in the open water
[Image] **Productid brachiopod**

Late Permian terrestrial extinctions
• Spore-bearing ferns and other plants gave way to conifers, cycads, ginkgoes, and other gymnosperms—may have evolved in response to cooler drier climates
• Caused an ecological chain reaction: Many families of basal tetrapods, primitive reptiles, and synapsids disappeared
[Image] Ginkgo

Terminal Cretaceous extinction causes
Theories fall in two broad categories:
• Extraterrestrial interference
bolide impact
cosmic rays
• Extinction events originated on Earth
Volcanism
Global lowering of sea level

Bolide impact
Discoveries during the past few years have established beyond a reasonable doubt that an asteroid (~10 km wide) impacted with Earth prior to the Cretaceous-Tertiary mass extinctions.

Physical evidence for a bolide impact
• Luis Alvarez and son Walter Alvarez discovered **iridium** (a chemical element of the platinum group, At No = 77) in a thin clay layer in Italy, at the Cretaceous-Tertiary boundary [K-T boundary]
• This layer is also found in many other places in the world
• Iridium is very rare on Earth but common in meteorites

Facts about the boundary iridium-rich clay
• The boundary clays are similar in composition all over the world
• Composition differs between the iridium-rich layer and the surrounding sediments
[Image] This is an example of the iridium layer, which also includes soot particles from the after-impact fires
[Image] Iridium layer in boundary clay.
[Map of World] Distribution of Iridium-rich sedimentary layers
[Graph] Concentration of Iridium in ppb about Cretaceous-Tertiary boundary site in Italy. The graph show values below 0.1 ppb in Cretaceous and Tertiary, but a peak rising to about **10 ppb** in the boundary clay layer that is only 3-4 cm thick.
[Image] Stratigraphy of the Cretaceous-Tertiary boundary site in Italy. This cross-section of the strata containing the iridium-rich layer is on display at the Smithsonian Museum of Natural History. The thickness of the layer is ~ 3-4 cm.

Other physical evidence for an asteroid impact
• **Shocked quartz**[521]: **Coesite** and **stishovite** are pressure polymorphs with a different molecular structure than standard quartz; this structure can only be formed by intense pressure, but moderate temperatures. High temperatures would anneal the quartz back to its standard form
• **Tektites**[522] (spherical grains of molten ejecta): The tektites are in a 1meter layer in Mexico, 10 cm in Texas, and 5 cm in New Jersey
• **Microscopic diamonds**

---

[521] **Shocked Quartz—Coesite and Stishovite**:
• http://en.wikipedia.org/wiki/Shocked_quartz
• http://mineral.galleries.com/minerals/silicate/coesite/coesite.htm
• http://mineral.galleries.com/minerals/oxides/stishovi/stishovi.htm
[522] **Tektites**: "Tektites (from Greek tektos, molten) are natural glass objects, up to a few centimeters in size, which — according to most scientists — have been formed by the impact of large meteorites on Earth's surface. Tektites are among the "driest" rocks, with an average water content of 0.005%. This is very unusual, as most if not all of the craters where tektites may have formed were underwater before impact. Also, partially melted zircons have been discovered inside a handful of tektites. This, along with the water content, suggests that the tektites were formed under phenomenal temperature and pressure not normally found on the surface of the Earth."
http://en.wikipedia.org/wiki/Tektite

• **Soot residue** from plants that burned
• Coarse breccia beds and shelf erosion
• Major changes in plant types

Shocked quartz; stishovite, coesite (SiO_2 pressure polymorphs) [Images]
Shocked quartz has a microscopic structure that is different from normal quartz. Under intense pressure the crystalline structure will be deformed along planes inside the crystal. These planes are called **shock lamellae**. Planar deformation features are prominent shock effects in quartz of meteorite impact sites
[Diagrams] Stishovite forms at pressures so great [> c. 75 kbar] that silica tetrahedra break down and silicon assumes six-fold coordination. **Coesite** [forms at lower pressures and] consists of four-membered rings in chains, which in turn are cross-linked by other chains.
[Phase Diagram for Silica with respect to T and P]

Tektites
• Consist of SiO_2
• Low water content
• May contain coesite, nickel-iron spherules, and baddeleyite (a zircon oxide mineral)
• May show signs of spinning in the air
[Image] Tektites [sizes are c. 0.2 - 20 mm]
[Images] Thin section of spherule-bearing sediment of the original spherule layer (NE-Mexico). Both, well-rounded **spherules** (c. 0.4 mm) as well as glass-shards are freshly preserved, without any alteration features.
[Image] Scanning Electron Microscope picture of isolated, and well preserved spherule [c. 0.2 mm] from NE-Mexico
[Map] Localities with Cretaceous–Tertiary boundary sequences that contain vesicular altered impact glass spherules (microtektites and microkrystites) Keller et al., 2002. Map show many site in E Mexico, Brazos River in Texas, Belize area, etc.
[Global map] Tektite sites
Shows many sites in Europe, US, and sea floor etc. of areas that have not subducted since 65 Ma.

Microfossils
[Image including Foraminifera] There is a drastic change in marine microfossil across the cm thick clay layer rich in impact debris which marks the KT boundary

Plant extinctions
[Diagrams of Luis W. Alvarez] These compare the spike in Iridium versus pollen to spore ratios. The graphs demonstrate a sharp transient reduction in the pollen:spore ratio at the time of Ir spike, followed by a decline of spores from below the K-T boundary level suggesting fewer species of ferns.

Where is the crater?
• Chicxulub Crater[523] is just north off the Yucatan Peninsula in Mexico
• This crater is one of the largest impact structures in the last 4 Ga
• The asteroid struck at a low angle towards the north, 20° to 30° from the horizontal
[Maps] Showing location of impact and the shorelines of 65 million years ago at the end of the Cretaceous (green) vs. today's coastlines.
[Global map] The bull's eye marks the location of the Chicxulub impact site [not “Chixulub” according to most sources]
[Computer-generated gravity map image] Chicxulub Crater on Mexico's Yucatan Peninsula is 150-300 km in diameter. The buried impact structure may be much larger than scientists first suspected.

The Terminal Cretaceous Extinction: Fire Effects
[Drawing by Alfred Kamaj] An artist’s rendition of the Cretaceous Tertiary scene.
Many wild fires, especially in North America. A fiery vapor cloud would have moved northwest over North America. 75% of all flora in these areas died out (not seen in Australia and New Zealand).

Computer Models Of Chicxulub Impact Effects

[523] **Chicxulub Crater**: http://en.wikipedia.org/wiki/Chicxulub_Crater

[Diagrams] Computer model over the first few seconds of the Chicxulub impact showing the rising fireball and CO_2 plumes and ejecta material (from Alvarez, Claeys and Kieffer, 1995). The Chicxulub bolide struck a thick deposit of marine limestone ($CaCO_3$) and underlying gypsum ($CaSO_4$). This probably put large amounts of CO_2 and sulfuric acid into the atmosphere within minutes.

The Terminal Cretaceous Extinction: MegaTsunami
• The MegaTsunami is estimated to have been 50-100 meter high, flooding coastal areas
• Eroded sea floor
• Deposited coarse sediments (breccias)
• Redeposited skeletons, terrestrial material
• Probably not sufficient to have caused mass extinctions but would leave evidence
[Drawing] "Non-survivable view"

The Terminal Cretaceous Extinction: Effects
1) Perpetual night—darkness and dust would have lasted for several months; plants could not conduct photosynthesis
2) Cold winters for months, especially in interiors; possible indirect link to glaciation and sea-level fall
[Drawing of Triceratops on ash and/or snow-covered landscape]
3) After the cold—abnormal heat; greenhouse effect from water vapor trapped in the air (hundreds to thousands of years?)
4) Nitric acid (HNO_3) and sulfuric acid (H_2SO_4) (from SO_2) rain from atmospheric gases, vaporized limestone, and sulfate evaporites change pH of water, block incoming solar radiation, and destroys the ozone layer
5) Possible melting of glaciers and sea-level rise.

Graph summarizing durations of effects following K-T impact [after Kring 2000]
Fireball Radiation (Immediate)
Earthquakes (Immediate)
Tsunamis (Immediate)
Dust Loading (Months to Years)
NO_x effects: Acid Rain, ozone loss, cooling (Months to Years)
SO2 effects: Cooling and acid rain (Years)
Heavy Metal Poisoning (Years)
H_2O and CO_2 Greenhouse warming (Years to Decades)

Could there have been other causes?
• **Volcanic activity**: Carbon dioxide, spiked for only a very short time. **Deccan traps**[524] (large igneous province) a possible contender (68-60Ma; peak period of about 30,000 years 66 million years ago)
• **Magnetic reversals** prevented shielding from cosmic rays?
• **Supernova** blast?
• **Marine regression**
• **Environmental factors?**

Deccan Traps
[India Map] Present-day distribution of Deccan Traps basalts. Much of the original cover of lava has been lost to erosion. The Deccan Traps, which include Bombay, cover 500,000 square km with a volume of 1,000,000 cubic km.

- Created enough dust and soot to block out sunlight, contributing to climate change
- Caused food chains to collapse both on land and at sea by inhibiting photosynthesis
- Poisoned many plants and planktonic organisms with acid rain
- Source of iridium; can explain iridium spike (?)
- Source of tektites
- The Deccan Traps basalt flows imply a fairly gradual extinction

[Photo] **Deccan Plateau**
The Deccan Traps are/is one of the largest volcanic provinces in the world. They consists of >2,000 m of flat-lying basalt lava flows and covers an area of nearly 500,000 square km (roughly the size of the states of Washington and Oregon combined) in west-central India. Estimates of the original area covered by the lava flows are as high as 1.5 million square km.

---

524 **Deccan Traps**: http://en.wikipedia.org/wiki/Deccan_Traps

The Terminal Cretaceous Extinction And Volcanic Activity
• Aerosols enriched in iridium can be expelled from mantle rocks during flood basalt eruptions (over several 100,000 years)
• Contemporary explosive volcanism in other parts of the world could have produced shocked quartz
• Large quantities of sulfate aerosols were injected into the atmosphere—Resulting in acid rain, reduced alkalinity and pH of the surface ocean, global cooling, and ozone layer depletion
Flaw 1: Volcanic ejecta tend to have low iridium concentration
Flaw 2: How could the tektites (~1 cm) and shocked quartz have been distributed globally by volcanic activity?

Impact Of The Terminal Cretaceous Extinction
Uneven extinction: Why did different groups fare so differently?
• Large Reptiles: All dinosaurs and archosaurs, pterosaurs, plesiosaurs, and mosasaurs became extinct
• Non-dinosaurian reptiles (e.g., turtles, snakes, lizards, crocodiles), placental mammals, and amphibians appear to have got off relatively lightly
• Marsupials, birds, plankton, ray-finned fish, bivalves, snails, sponges, and sea urchins suffered heavy losses.
• In the sea: ammonites, belemnites, rudistid bivalves, entire families of echinoids, bryozoans, planktonic foraminifers, and calcareous phytoplankton disappeared
[Drawing] Belemnite (extinct cephalopod—related to modern cuttlefish and squid)

Was the end of the Cretaceous extinction a press-pulse event?
• Keller et al., 2004 suggest that the Chicxulub impact predated the end-Cretaceous mass extinction by about 300,000 years and did not cause the demise either of marine or terrestrial organisms
• The existence of an impact crater neither proves nor explains the demise of the dinosaurs, or the extinction of any other group
• The paleontological database amassed during the last 20 years lends little support to a sudden mass extinction at the K/T boundary, except for tropical-subtropical planktic foraminifera
• The impact probably coincided with major volcanism
Conclusion: The end of Cretaceous extinction was likely a progressive multi-event catastrophe (press-pulse theory)
[Cartoon of Dinosaur Lecturing On "Iridium Bomb"] Or have we got it all wrong…?

Biogenic Resources: Oil, Natural Gas, and Coal

[MCM: Edited from verbatim text of LRS slides, not all material in the slides was discussed. I will not be able to post the slides document, but if available to you, see PDF document of slides, containing images which are essential for understanding this material.]

[Diagrams showing oil drilling platform and progression of Peat to Lignite and then Coal, under influence of heat and pressure.]

Oil And Natural Gas

Differing origins of oil versus coal
• **Petroleum**[525] (**Crude Oil**) originates from kerogen derived from phytoplankton and bacteria

---

[525] **Petroleum**: "Petroleum … or crude oil is a naturally occurring liquid found in formations in the Earth consisting of a complex mixture of hydrocarbons (mostly **alkanes**) of various lengths. The approximate length range is C_5H_{12} to $C_{18}H_{38}$. Any shorter hydrocarbons are considered **natural gas** or natural gas liquids, while long-chain hydrocarbons are more viscous, and the longest chains are **paraffin wax**. In its naturally occurring form, it may contain other nonmetallic elements such as sulfur, oxygen, and nitrogen… Crude oil may also be found in semi-solid form mixed with sand, as in the Athabasca **oil sands** in Canada, where it may be referred to as **crude bitumen**.

Petroleum is used mostly … for producing fuel oil and gasoline (petrol), both important "primary energy" sources. 84% by volume of the hydrocarbons present in petroleum is converted into

• Most coals are remnants of terrestrial higher plants
• Oil is liquid and can migrate great distances (up to 300 km) from its **source rock** into **reservoir rocks** where it is trapped
• Coal is solid and is found at its site of deposition
• Most source rocks for oil were deposited in marine environments
• Most coal beds were deposited in terrestrial environments
[Image] Phytoplankton
[Image] Zooplankton feed off of Phytoplankton, making them the second link in the marine food chain.

Production and accumulation of organic matter
• Photosynthesis is the basis for mass production of organic matter, the food pyramid, and the evolution of higher life
• During the earth's history, the average **preservation rate of** the primary organic production (expressed as **organic carbon**) is <0.1%

Sedimentary processes and the accumulation of organic matter [Diagram]

- High production of organic-rich sediments (0.5% by weight of organic carbon) occurs along continental margins: swamps, lagoons, tidal flats, deltas, and estuaries.
- Preservation of high primary productivity and/or land-derived terrestrial plant material is enhanced (to ~4%) in deep basins having restricted circulation and scarce dissolved molecular oxygen.

What happens to organic matter after burial?—OIL

- [Diagram] Depicts life existing in an ancient sea hundreds of millions of years ago, and burial of organic matter in the sediments. The original organic material was mostly phytoplankton and zooplankton that lived in open seas, but much of it may have been derived from land plants and carried by streams to the site of deposition.
- [Diagram] Millions of years later, life still exists in a shallow sea and the sediments have increased in thickness. The organic matter is being altered into petroleum while buried **>1500 m** by sediments. Bacterial and chemical actions begin a long, complicated process of transforming the organic material to hydrocarbons—the process is poorly understood.
- [Diagram] The sea no longer exists. Pressure expels the petroleum from the source rock ("primary migration") to nearby porous and permeable rock, such as sandstone or limestone. If the petroleum enters a water-wet environment it will rise to the top of the porous layer, above the water. It will rise until it reaches **impermeable rock** above.
- [Diagram] The rocks have been folded. The petroleum is **trapped at the crest of the anticline**. If the rocks are tilted, the petroleum will continue to migrate up the sloping top of the bed until it reaches the surface or an **impermeable barrier** to its flow. If the petroleum reaches a surface outcrop it flows onto the surface as an oil or gas seep.

Diagenesis and Catagenesis [Diagram]
This diagram depicts the following sequential changes with depth:

---

energy-rich **fuels** (petroleum-based fuels), including gasoline, diesel, jet, heating, and other fuel oils, and liquefied petroleum gas.

Due to its high energy density, easy transportability and relative abundance, it has become the world's most important source of energy since the mid-1950s. Petroleum is also the raw material for many chemical products, including pharmaceuticals, solvents, fertilizers, pesticides, and plastics; the 16% not used for energy production is converted into these other materials.

Petroleum is found in porous rock formations in the upper strata of some areas of the Earth's crust. There is also petroleum in oil sands (tar sands). Known reserves of petroleum are typically estimated at around 140 km^3 (1.2 trillion barrels) without oil sands, or 440 km^3 (3.74 trillion barrels) with oil sands. However, oil production from oil sands is currently severely limited. Consumption is currently around 84 million barrels per day, or 3.6 km^3 per year. Because of reservoir engineering difficulties, recoverable oil reserves are significantly less than total oil-in-place. At current consumption levels, and assuming that oil will be consumed only from reservoirs, known reserves would be gone around 2039, potentially leading to a global energy crisis. However, this ignores any new discoveries, rapidly increasing consumption in China; India, and other developing nations, using oil sands, using synthetic petroleum, and other factors which may extend or reduce this estimate."
http://en.wikipedia.org/wiki/Petroleum

1) **Biogenic molecules**: Smaller fragments ➔ Humic substances [1-10 m] ➔ Kerogen and Methane [100m] ➔ Oil, Gas, and Dead Carbon [1,000 - 10,000 m]
2) **Major Constituents of Living Matter**: Biochemical and chemical degradation [millimeters] ➔ Condensation, Polymerization [1 m] ➔ Loss of CO_2, H_2O, NH_3 [10 - 100 m]➔ Thermal Maturation [1000 m] ➔ Cracking [10,000 m]
3) **Genesis Stages**: Life [surface] ➔ Diagenesis [to 100 m] ➔ Catageneis [100 - 10,000 m] ➔ Metagenesis [deeper than 10,000 m]

Diagenesis of organic matter
1. **Diagenesis**: The biological and physiochemical alteration of organic matter (and minerals), which occurs in sediments after deposition, but prior to changes caused by heat.
 - Main agents of transformation are microbial activity
 - Microorganisms degrade biopolymers (proteins, lipids, carbohydrates, and lignins) to geopolymers collectively called **kerogen**—the main organic material in ancient sediments.

[Image:] Atomic force EM of acritarch with reconstruction of kerogen[526] structure—amorphous platelets of polycyclic aromatic hydrocarbons [PAH] with no obvious resemblance to any familiar cell wall material have replaced an acritarch.

Kerogen and bitumen
- Kerogen is the component of organic matter that is insoluble in organic and inorganic solvents: example: $C_{215}H_{330}O_{12}N_5S$
- **Bitumen**[527] is the soluble component. [Note—spelled bitumen, not bitumin, but bituminous, not bitumenous]

---

[526] **Kerogen**:
• "Kerogen is a mixture of organic chemical compounds that make up a portion of the organic matter in sedimentary rocks. It is insoluble in normal organic solvents because of the huge molecular weight (upwards of 1,000) of its component compounds. The soluble portion is known as **bitumen**. When heated to the right temperatures in the Earth's crust, some types of kerogen release oil or gas, collectively known as hydrocarbons (fossil fuels). When such kerogens are present in high concentration in rocks such as shale, and have not been heated to a sufficient temperature to release their hydrocarbons, they may form oil shale deposits."
http://en.wikipedia.org/wiki/Kerogen
• "**Oil shales** and **tar sands** also contain significant amounts of hydrocarbon materials that might eventually prove to be important energy sources. Oil shales are fine-grained sedimentary rocks (shales) that contain hydrocarbons that are dispersed within the matrix of the rock. A ton of shale contains from 10 to 100 gallons of **kerogen**, a waxy material that breaks down to oils when heated in the absence of air. It is estimated that three states (Utah, Colorado, and Wyoming) contain shale bearing more oil than exists in all the proven [oil] reserves in the world. **Tar sands** are the extremely viscous petroleum deposits associated with sedimentary rocks. They are mixtures of clay, sand, and extremely viscous oils called **bitumens**. The utility of oil shales and tar sands is currently limited, because of problems having to do with hydrocarbon recovery and the disposal of large amounts of inorganic residues."
Thomson Gale Document Number: CX3400900201
[527] **Bitumen**: "Bitumen is a mixture of organic liquids that are highly viscous, black, sticky, entirely soluble in carbon disulfide, and composed primarily of highly condensed polycyclic aromatic hydrocarbons. Bitumen is the residual (bottom) fraction obtained by fractional distillation of crude oil. It is the heaviest fraction and the one with the highest boiling point, boiling at 525 degrees Celsius. In British English, the word 'asphalt' refers to a mixture of mineral aggregate and bitumen (or tarmac in common parlance). The word 'tar' refers to the black viscous material obtained from the destructive distillation of coal and is chemically distinct from bitumen. In American English, bitumen is referred to as 'asphalt' or 'asphalt cement' in engineering jargon. In Australian English, bitumen is sometimes used as the generic term for road surfaces. Most bitumens contain sulphur and several heavy metals such as nickel, vanadium, lead, chromium, mercury and also arsenic, selenium, and other toxic elements. Bitumens can provide good preservation of plants and animal fossils.... Bitumen is primarily used for paving roads. Its other uses are for general waterproofing products, including the use of bitumen in the production of roofing felt and for sealing flat roofs. It is also the prime feed stock for petroleum production from tar sands currently under development in Alberta, Canada. Bitumen from tar sands is projected to account for 80% of Canadian oil production by 2020..."
http://en.wikipedia.org/wiki/Bitumen

- Kerogen is the most abundant form of organic carbon on earth—it is 1000 times more abundant than petroleum + coal, and 50 times more abundant than bitumen.

Catagenesis of organic matter
2. Catagenesis: thermal alteration (at 100->1000 m depth [lower limit varies]) of organic matter by burial and [moderate] heating in the range of about 50 to 150°C, requiring millions of years
• Thermal degradation of kerogen
• Results in hydrocarbons, i.e., oil and gas

Biologic controls [or influences] on "petroleum systems": Source rock, Reservoir rock, and Seal
• Oil geologists speak of three important parts in "petroleum systems": source rock, reservoir rock, and seal. All three have strong biologic influences.
• Petroleum "source rocks" contain kerogen, which is derived from plants and bacteria.
• Some of the best petroleum "reservoir rocks" are in carbonate reefs with high porosity.
• The world's two largest hydrocarbon deposits (heavy oil "**tar sands**"[528] in Alberta and Venezuela) owe their existence to seals formed by biodegradation of oil that migrated hundreds of km in front of fold-thrust mountain belts. [see below]
• **Pinnacle reefs** make excellent oil reservoir rocks. Pinnacle reefs develop from patch reefs like these shown in an air photo of Great Barrier Reef, Australia

- Comprised of ancient coral structures.
- Associated with large coral reef systems; e.g., barriers and atolls.
- High porosity and permeability make them prolific oil-producing reservoirs.
- Highly prized and sought after by the oil industry.
- In 1982, near Rumsey, Alberta, Gulf Canada discovered a small pinnacle reef that averaged 4000 bbls/day and produced 3.7 million barrels of high gravity oil from 1 well.
- 90% of the oil from the Rumsey reef was recovered during first 3 years.

[Image] Living Pinnacle reefs

Modern coral barrier reef showing pinnacles growing to leeward [downwind] of barrier reef
[Diagram]
(From: *Geology of Petroleum*, A. I. Leverson)

Classic model of oil and natural gas formation [Diagrams]
Structural Traps include Anticline, Salt Dome, Faults, Reefs, Unconformity, and Pinch-Out.

---

[528] **Tar Sands (Oil Sands)**: "Tar sands is a common name of what are more properly called **bituminous sands**, but also commonly referred to as oil sands or (in Venezuela) extra-heavy oil. They are a mixture of sand or clay, water, and extremely heavy crude oil. The use of the word tar to describe these deposits is a misnomer, since tar is a man-made substance produced by the destructive distillation of organic material. Although it appears similar, the material in tar sands is a naturally-occurring, extremely heavy form of crude oil in which the lighter fractions of the oil have been lost, and the remaining fractions have been partially biodegraded by bacteria. As a result, the term "**oil sands**" is technically more accurate. Conventional crude oil is easily extracted from the ground by drilling wells into the formations, into which light or medium density oil flows under natural reservoir pressures, but tar sand deposits must be strip mined or made to flow into producing wells by in situ techniques which reduce the oil's viscosity using steam and/or solvents. These processes use a great deal of water and require large amounts of energy. The heavy crude oil or crude bitumen extracted from these deposits is a viscous, solid or semisolid form of oil that does not easily flow at normal ambient temperatures and pressures, making it difficult and expensive to process into gasoline, diesel fuel, and other products. Despite the difficulty and cost, oil sands are now being mined on a vast scale to extract the oil, which is then converted into synthetic oil by oil upgraders, or refined directly into petroleum products by specialized refineries. Many countries in the world have large deposits of oil sands, including the United States, Russia, and various countries in the Middle East. However, the world's largest deposits occur in two countries: **Canada and Venezuela**, both of which have oil sands reserves approximately equal to the world's total reserves of conventional crude oil. As a result of the development of these reserves, most Canadian oil production in the 21st century is from oil sands or heavy oil deposits, and Canada is now the largest single supplier of oil and refined products to the United States. Venezuelan production is also very large, but due to political problems its oil production has been declining since the start of the 21st century."
http://en.wikipedia.org/wiki/Tar_sands

Light blue in diagrams represents water-soaked porous rock, dark gray represents petroleum and light gray represents natural gas. All other colors represent impervious rocks.

How does oil migrate from source rocks to reservoir rocks?
[Geologic map and diagram] Inferred Brine Migrations(Bethke and Marshak, 1990). Alberta tar sands, Denver basin, Bighorn basin, Williston basin, etc. Migrations occur over many hundreds of km.

Theories of Forces Causing Oil Migration:
1) Tectonic compression "Squeegee" (Oliver,1986)
2) Topographically driven (Garven & Freeze, 1984)

Age of oil source rocks
[Complex diagram] Age distribution of the initial conventional oil in-place and heavy oil derived from the various geological periods. The age considered is that of the source rock. These ages are also compared with the major sea level changes and the abundance of phytoplankton. [MCM: The heavy oil is from the Devonian, Cretaceous, and Quaternary. The conventional oil has a broader distribution.]

The World's two largest hydrocarbon deposits are "**tar sands**" (**biodegraded oil**) at leading edge of long-distance oil migration
• In the absence of biodegradation, most of the migrating oil would have reached outcrops at the basin margin and would have been lost.
• Biodegradation increases viscosity, suppresses oil mobility, **forms an asphalt plug**, and prevents oil from escaping to the surface.
• Thus, heavy oils are self-sealing thanks to biodegradation.
One graph compares viscosity (centipoise) at 50 °C , sp. gr., and API Density [actually API Gravity]. Approximate values are:

Normal Oil:	10^2	0.93	22
Heavy Oil:	10^3	0.97	14
Tar Sands:	10^5	1.00	10

Athabasca tar sands[529], E. Alberta. Reserves = 1.7 trillion barrels
Orinoco tar sands[530], E. Venezuela. Reserves = 1.8 trillion barrels
These compared to worldwide reserves of conventional oil = 1.8 trillion barrels

Oils, bulk properties
• American Petroleum Institute **API Gravity**[531] = a USA measure related to specific gravity (SG) = arbitrary scale
• API Gravity (expressed in unitless "degrees") = (141.5 / SG @ 16°C) - 131.5 [Note that API decreases as SG rises]
• Water has API gravity 141.5–131.5 = 10°.
• Heavy oils are < 25°
• Medium oils are 25° to 35°
• Light oils are 35°to 45°
• Condensates are > 45°

[Distribution Maps] **Tar sand** is a combination of clay, sand, water, and bitumen. The bitumen is neither oil nor tar[532], but a semisolid, degraded form of oil which will not flow toward producing wells

---

529 **Athabasca (Alberta Canada) Oil Sands or Tar Sands**: http://en.wikipedia.org/wiki/Athabasca_tar_sands
530 **Orinoco (Venezuala) tar sands**: http://en.wikipedia.org/wiki/Orinoco_tar_sands
531 **API Gravity**: "Generally speaking 40 to 45 API gravity degree oils have a greatest commercial price and values outside this range have lower commercial price. Above 45 degrees API gravity the molecular chains become shorter and less valuable to a refinery. Crude oil is classified as light, medium or heavy, according to its measured API gravity. Light crude oil is defined as having an API gravity higher than 31.1 °API. Medium oil is defined as having an API gravity between 22.3 °API and 31.1 °API. Heavy oil is defined as having an API gravity below 22.3 °API." http://en.wikipedia.org/wiki/API_gravity
532 **Tar**: "Tar is a viscous black liquid derived from the **destructive distillation** of organic matter. Most tar is produced from **coal** as a byproduct of coke production, but it can also be produced from petroleum, peat or wood.... The word "tar" is used to describe several distinct substances. Naturally

under normal conditions, making it difficult and expensive to produce. Tar sands are currently found in about 70 countries around the world, including Canada, the former Soviet Union, and Venezuela. The United States contains scattered deposits of oil sands, mainly in Utah, Kentucky, Kansas.

Formation of Natural Gas[533]
There is a wide variety in natural gas occurrences.
- Composition and modes of gas formation may differ considerably
- Commonly measured as the **ratio of methane to total hydrocarbon** and the isotopic (carbon and hydrogen) composition

[Photo] Offshore gas production platform. West Africa.

Biogenic coalbed methane (CBM)
[Complex Cross-section Diagram] This diagram depicts Fruitland coal, northern San Juan Basin, Colorado. The San Juan Basin contains North America's largest accumulation of coalbed methane (CBM). In the northern basin, much of the CBM gas is biogenic in origin. Meteoric waters [i.e., from rain and snow] flowing downdip[534] through high permeability rocks introduced bacteria deep into the subsurface. These bacteria generated methane that was swept basinward to be trapped in the Fruitland coal fairway [underlying the Kirtland Shale], just north of the hinge line near the basin center. (Ayers, 2002)

The classic theory of biogenic origin of oil and gas
Buried biological debris decays into oil and natural gas, which migrates from its source rocks into reservoir rocks

---

occurring "tar pits" (e.g. the La Brea Tar Pits in Los Angeles) actually contain **asphalt**, not tar, and are more accurately known as **asphalt pits**. Tar sand deposits contain various mixtures of sand (or rock) with **bitumen** or heavy crude oil rather than tar... "Tar" and "pitch (resin)" are sometimes used interchangeably; however, pitch is considered more solid while tar is more liquid.... In English and French, "tar" is a substance primarily derived from coal. It was formerly one of the products of a gasworks. Tar made from coal or petroleum is considered toxic and carcinogenic because of its high benzene content, however, coal tar in low concentrations is used as a topical medicine. Coal and petroleum tar has a pungent odor."
http://en.wikipedia.org/wiki/Tar

[533] **Natural Gas**:
• "Natural gas is a gaseous fossil fuel consisting primarily of methane but including significant quantities of ethane, butane, propane, pentane, (heavy hydrocarbons removed later on as **condensate**) carbon dioxide, nitrogen, helium and hydrogen sulfide. [It is found in oil fields dissolved in oil ("**associated natural gas**"), in non-oil bearing natural gas fields ("**non associated natural gas**"), and in coal beds ("**coalbed methane**").] When methane-rich gases are produced by the anaerobic decay of non-fossil organic material, these are referred to as **biogas**. Sources of biogas include swamps, marshes, and landfills, as well as sewage sludge and manure by way of anaerobic digesters, in addition to enteric fermentation particularly in cattle. Since natural gas is not a pure product, when non associated gas is extracted from a field under supercritical (pressure/temperature) conditions, it may partially condense upon isothermic depressurizing—an effect called **retrograde condensation**. [MCM: Note the seemingly paradoxical condensation.] The liquids thus formed may get trapped by depositing in the pores of the gas reservoir. One method to deal with this problem is to reinject dried gas free of condensate to maintain the underground pressure [and to allow reevaporation and extraction of condensates]. Natural gas is often informally referred to simply as gas, especially when compared to other energy sources such as electricity. Before natural gas can be used as a fuel, it must undergo extensive processing to remove almost all materials other than methane. The by-products of that processing include ethane, propane, butanes, pentanes and higher molecular weight hydrocarbons, elemental sulfur, and sometimes helium and nitrogen." [MCM: entry somewhat edited]
http://en.wikipedia.org/wiki/Natural_gas
• See detailed discussion of natural gas processing including retrograde condensation and evaporation at http://www.schulich.ucalgary.ca/Chemical/class_notes/ench607/

[534] **Downdip**: "Located down the slope of a dipping plane or surface. In a dipping (not flat-lying) hydrocarbon reservoir that contains gas, oil and water, the gas is updip, the gas-oil contact is downdip from the gas, and the oil-water contact is still farther downdip. "
http://www.glossary.oilfield.slb.com/Display.cfm?Term=downdip

An alternative hypothesis (?):Thomas Gold's "The Deep Hot Biosphere" [1999[535]]
Hydrocarbons are not biology "reworked" but, rather, geology reworked by biology thus explaining the presence of all those biological signatures in oils.

Thomas Gold: abiotic origin of oil and gas?
• With increasing internal heat, liquid and gases are liberated in the crust
• Hydrocarbons move upward because they are less dense than rocks—accumulate in porous rocks
• Petroleum is, thus, [primarily] abiotic and a whole microbial, high-temperature biosphere is thriving [secondarily] on these deep resources
• Origin of Primordial hydrocarbons? Hydrocarbons are found in some meteorites (carbonaceous chondrites) and other primordial solar system debris.
• Hydrocarbons exist on other planets (e.g., methane and ethane on Titan), where there is unlikely to be biological activity.
[Photo] Surface of Titan Surface

Coal

[Photo of old time coal miners working underground]

Coal*[536]* Classification
Coal Type: A classification of coal distinguished on the basis of the constituent plant materials: **megascopic** classification is a "lithotype," **microscopic** classifications use "microlithotypes" and "macerals"[537].
Coal Grade: A classification of coal based on degree of **purity**—i.e., quantity of ash left after burning; dependent upon amount of mineral matter
Coal Metamorphic Rank: The classification of coals according to their degree of coalification (maturation) or metamorphism in the natural series:

> **Peat ➔ Lignite ➔ Sub-Bituminous (C, B, A) ➔**
> **High Volatile Bituminous (C, B, A) ➔ Medium Volatile Bituminous ➔ Low Volatile Bituminous ➔**
> **Semi-Anthracite ➔ Anthracite**

Major stages of the development from peat to meta-anthracite (**Coalification**) [Table, Taylor et al. 1998)
Table depicts characteristics of Coal Stages: Peat, Lignite[538], Bituminous[539], and Anthracite[540]

---

[535] **Thomas Gold**: http://en.wikipedia.org/wiki/Thomas_Gold
[536] **Coal**: http://en.wikipedia.org/wiki/Coal
[537] **Coal Macerals**: "Coal is an extremely complex heterogeneous material that is difficult to characterize. Coal is a rock formed by geological processes and is composed of a number of distinct organic entities called **macerals** and lesser amounts of inorganic substances - **minerals**. The essence of the petrographic approach to the study of coal composition is the idea that coal is composed **macerals**, which each have a distinct set of physical and chemical properties that contol the behavior of coal. The term was first introduced by Dr. Marie Stopes who said that 'These organic units, composing the coal mass I propose to call macerals, and they are the descriptive equivalent of the inorganic units composing rock masses and universally called minerals, and to which petrologists are well accustomed to give distinctive names.' There are three basic groups of macerals, the **vitrinite** group derived from coalified woody tissue, the **liptinite** group derived from the resinous and waxy parts of plants and the **inertinite** group derived from charred and biochemically altered plant cell wall material."
http://mccoy.lib.siu.edu/projects/crelling2/atlas/macerals/mactut.html
[538] **Lignite**: "Lignite, often referred to as brown coal, is the lowest rank of coal and used almost exclusively as fuel for steam-electric power generation. It is brownish-black and has a high inherent moisture content, sometimes as high as 66 percent, and very high ash content compared with bituminous coal. It is also a heterogeneous mixture of compounds for which no single structural formula will suffice. The heat content of lignite ranges from 10 to 20 MJ/kg (9 to 17 million Btu per short ton) on a moist, mineral-matter-free basis. The heat content of lignite consumed in the United States averages **13 million Btu/ton** (15 MJ/kg), on the as-received basis (i.e., containing both inherent moisture and mineral matter). When reacted with quaternary amine, amine treated lignite (ATL) forms. ATL is used in drilling mud to reduce fluid loss. Because of its low energy density, brown

- **Peatification**:
  Coal Rank range: Peat
  Predominant processes: maceration, humification, gelification, fermentation, and concentration of resistant substances. Physicochemical Changes: formation of humic substances and increase in aromaticity.
- **Dehydration**:
  Coal Rank range: Lignite [brown coal] to Sub-Bituminous
  Predominant processes: dehydration and compaction, expulsion of -COOH, CO_2, and H_20
  Physicochemical Changes: Dehydration and decreased O/C ratio, increased heating value.
- **Bituminization**:
  Coal Rank range: Upper Sub-Bituminous A to High Volatile A Bituminous
  Predominant processes: Generation and entrapment of hydrocarbons, depolymerization of matrix, increased hydrogen bonding.
  Physicochemical Changes: Increased vitrinite R_0[541] [reflectance], increased fluorescence, increased extract yields, decrease in density and sorbate accessibility, increased strength

---

coal is inefficient to transport and is not traded extensively on the world market compared with higher coal grades. It is often burned in power stations constructed very close to any mines, such as in Australia's Latrobe Valley and Luminant's Monticello plant in Texas. Carbon dioxide emissions from brown coal fired plants are generally much higher than for comparable black coal plants. The continued operation of brown coal plants, particularly in combination with strip mining and in the absence of emissions-avoiding technology like carbon sequestration, is politically contentious."
http://en.wikipedia.org/wiki/Lignite

[539] **Bituminous Coal**: "Bituminous coal is a relatively hard coal containing a tar-like substance called bitumen. It is of higher quality than lignite coal but of poorer quality than anthracite coal. Bituminous coal is an organic sedimentary rock formed by diagenetic and submetamorphic compression of peat bog material. Bituminous coal has been compressed and heated so that its primary constituents are the macerals vitrinite, exinite, etc. The carbon content of bituminous coal is around 60-80%; the rest is composed of water, air, hydrogen, and sulfur, which have not been driven off from the macerals. The heat content of bituminous coal ranges from **21 million to 30 million Btu/ton** (24 to 35 MJ/kg) on a moist, mineral-matter-free basis. Bituminous coal is usually black, sometimes dark brown, often with well-defined bands of bright and dull material. Bituminous coal seams are stratigraphically identified by the distinctive sequence of bright and dark bands and are classified accordingly as either "dull, bright-banded" or "bright, dull-banded" and so on. Bank Density is approximately 1346 kg/m³ (84 lb/ft³). Bulk density typically runs 833 kg/m³ (52 lb/ft³)."
http://en.wikipedia.org/wiki/Bituminous_coal

[540] **Anthracite Coal**: "Anthracite ... is a hard, compact variety of mineral coal that has a high luster. It has the highest carbon count and contains the fewest impurities of all coals, despite its lower calorific content. Anthracite coal is the highest of the metamorphic rank, in which the carbon content is between 92% and 98%. The term is applied to those varieties of coal which do not give off tarry or other hydrocarbon vapours when heated below their point of ignition. Anthracite ignites with difficulty and burns with a short, blue, and smokeless flame. Other terms which refer to anthracite are blue coal, hard coal, stone coal ... and black diamond... The moisture content of fresh-mined anthracite generally is less than 15 percent. The heat content of anthracite ranges from 22 to 28 million Btu per short ton (26 to 33 MJ/kg) on a moist, mineral-matter-free basis. The heat content of anthracite coal consumed in the United States averages **25 million Btu/ton** (29 MJ/kg), on the as-received basis... Anthracite coal may be considered to be a transition stage between ordinary bituminous coal and **graphite**, produced by the more or less complete elimination of the volatile constituents of the former; and it is found most abundantly in areas that have been subjected to considerable earth-movements, such as the flanks of great mountain ranges. Anthracite coal is a product of metamorphism and is associated with metamorphic rocks, just as bituminous coal is associated with sedimentary rocks... Structurally it shows some alteration by the development of secondary divisional planes and fissures so that the original stratification lines are not always easily seen. The thermal conductivity is also higher, a lump of anthracite feeling perceptibly colder when held in the warm hand than a similar lump of bituminous coal at the same temperature..."
http://en.wikipedia.org/wiki/Anthracite

[541] **Vitrinite and Vitrinite Reflectance**: "**Vitrinite** is one of the primary components of coals and most sedimentary kerogens. Vitrinite is a type of maceral, where "macerals" are organic components of coal analogous to the "minerals" of rocks. Vitrinite has a shiny appearance resembling glass (vitreous). It is derived from the cell-wall material or woody tissue of the plants from which coal was

- **Debituminization**:
  Coal Rank range: Uppermost High Volatile A Bituminous to Low Volatile Bituminous.
  Predominant processes: Cracking, expulsion of low MW hydrocarbons, especially methane.
  Physicochemical Changes: Decreased fluorescence, decreased MW of extract, decreased H/C ratio, decreased strength, cleat growth
- **Graphitization**:
  Coal Rank range: **Semi-Anthracite** To **Anthracite** To **Meta-Anthracite**[542]
  Predominant processes: Coalescence and ordering of pre-graphitic aromatic lamellae, loss of H, loss of N. Physicochemical Changes: Decrease in H/C ratio, stronger XRD [X-ray diffraction] peaks, increased sorbate accessibility, anisotropy, strength ring condensation, and cleat healing.

Major Stages in the Development of Coal From Peat [Diagram]. Shows effects of burial, pressure, heat, and time.

Humification
Humic substances[543] are compounds ubiquitous in waters, soils, sediments, peats and low-rank coals. They develop randomly from the decay of plant tissues, from microbial metabolism and/or catabolism. Humic substances comprise an extraordinary complex, amorphous mixture of highly heterogeneous, chemically reactive molecules. In spite of long-term intensive and extensive study, humic substances belong to nature's least understood materials. The amount of C on the Earth as humic acids (60×10^{11} metric tons) exceeds that which occurs in living organisms (7×10^{11} metric tons).
[Diagram] Depicts conversion of plant residues through several pathways including transformation by microorganisms to modified lignins, sugars, polyphenols, amino compounds, quinones, and finally humic substances.

Coal Metamorphic Rank and % of World Reserves
Rank increases with burial depth (depth ranges for formation are estimated below from the graph included), and determines utilization:
Peat: Shallow depths [used for domestic heating in Ireland, etc.]
Low Rank Coals (48%) have higher moisture, lower energy
  - Lignite (20%): for power generation. Depths to 5000 ft.
  - Sub-Bituminous (28%): for power generation and cement and other industrial uses. Depths 5,000 - 8,000 ft.

---

formed. Chemically, it is composed of polymers, cellulose and lignin…. The study of vitrinite reflectance is a key method for identifying the temperature history of sediments in sedimentary basins. The reflectance of vitrinite was first studied by coal explorationists attempting to diagnose the thermal maturity, or rank, of coal beds. More recently, its utility as a tool for the study of sedimentary organic matter metamorphism from kerogens to hydrocarbons has been increasingly exploited. The key attraction of vitrinite reflectance in this context is its sensitivity to temperature ranges that largely correspond to those of hydrocarbon generation (i.e. 60 to 120°C). This means that, with a suitable calibration, vitrinite reflectance can be used as an indicator of maturity in hydrocarbon source rocks. Generally, the onset of oil generation is correlated with a reflectance of 0.5-0.6% and the termination of oil generation with reflectance of 0.85-1.1%."
http://en.wikipedia.org/wiki/Vitrinite
542 **Meta-Anthracite**: "Anthracite coal containing at least 98% fixed carbon"
http://www.answers.com/topic/metaanthracite?cat=technology
543 **Humic Substances**: "Humic acid is one of the major components of humic substances which are dark brown and major constituents of soil organic matter humus that contributes to soil chemical and physical quality and are also precursors of some fossil fuels. They can also be found in peat, coal, many upland streams and ocean water. Humic substances make up a large portion of the dark matter in humus and consist of heterogenous mixtures of transformed biomolecules… Since the end of the 18th century, humic substances have been designated as either **humic acid, fulvic acid or humin**. These fractions are defined strictly on their solubility in either acid or alkali, describing the materials by operation only, thus imparting no chemical information about the extracted materials… The term 'humic substances' is used in a generic sense to distinguish the naturally occurring material from the chemical extractions named humic acid and fulvic acid, which are defined "operationally" by their solubility in alkali or acid solutions. It is important to note, however, that no sharp divisions exist between humic acids, fulvic acids and humins… "
http://en.wikipedia.org/wiki/Humic

Hard Coals (52%) have lower moisture, higher energy

- Bituminous (51%). Depths 8,000 - 19,000 ft.
  - Thermal (Steam coal): for power generation and cement and other industrial uses
  - Metallurgical (Coking coal): iron and steel manufacture
- Anthracite (1%): Domestic/industrial including smokeless fuel. Depths > 19,000 ft.

Macerals

Macerals are microscopic organic component of coal consisting of an irregular mixture of different chemical compounds. Macerals are analogous to minerals in inorganic rocks, but they differ from minerals in that they have no fixed chemical composition and lack a definite crystalline structure.
• Macerals change progressively both chemically and physically as the rank of coal advances
• Macerals for bituminous coal, are classified into three major groups: vitrinite, inertinite, and exinite (liptinite)
• **Vitrinite** is derived from woody plant tissue. Most coals have a high percentage of vitrinite
• **Inertinite** group is all rich in carbon (due to primary oxidation from mouldering or charring)
• **Exinite** from pollen spores, etc., is characterized by a high hydrogen content
[Image] Coal as seen under reflected light

Macerals and group macerals recognized in hard coals (Table, McCabe, 1984)
Lists Maceral Groups: Vitrinite (Huminite), Exinite (liptinite), and Inertinite. Presents morphology and origins of the various maceral types.

[Map] **Coal Fields of the Conterminous United States**, USGS[544]
[Map] **Geologic Age Of Coal In The United States**
[Diagram] **Geologic Age of Coal Deposits**—most derives from the Pennsylvanian and Permian

Climate And Coal Formation

- The warmer and wetter the climate, the more luxuriant is the flora and the more dominant forest swamps become over reed and moss swamps
- A tropical swamp will renew itself in 7 - 9 years and during this time trees can grow to heights of 30 m
- In contrast, trees in a temperate Alnus-swamp forest [alders] will grow 5-6 m in the same time
- With increasing warmth, also increasing rates of decomposition

Aerial view of a peat bog in Russia [Photo]
Geometry: Thickness and aerial [horizontal] extent of the coal deposit is controlled by the depositional environment; i.e. available space between active water courses or in ponded depressions.

The Earliest Coals

[Photos] Cyanophyta: Rivularia bullata and R. planktonica
First coals (?):The Middle Huronian (~2.4 Ga, Paleo-proterozoic) of Michigan; infrequent and impure coal. Microscopic structures of apparent biological remains are similar to the modern algae Rivularia.
• Lower Devonian: Submerged plants, **Taeniocrada decheniana** (are they Psilophytes?), grew in shallow lagoons, formed thin, coaly layers in Germany. Thin vitrinite layers are present
• Middle and Upper Devonian: Land plants spread over the continents rapidly in the Middle and Upper Devonian (Kazakhstan, etc.)

- Plants similar to Carboniferous vegetation formed true coal seams
- Some seams, however, still formed from Psilophytes[545]

---

[544] **Map of Coal Distrubution in US**: http://pubs.usgs.gov/of/1996/of96-092/
[545] **Psilophytes** [these may be related to modern **Psilotales, the Whisk ferns**]:
• "In very late Silurian time, the first Psilophytes came into existence. They were very basic vascular plants, from which all other vascular plants may have evolved. Their diversification and evolution happened so rapidly that, by the end of the Devonian time, forests are known to have already grown. Psilophytes probably evolved from fungi, although they had chlorophyll."
http://library.thinkquest.org/20886/psilophytes.htm
• "Extinct primitive plant: a primitive leafless vascular plant of the Silurian period with a horizontal stalk that grew beneath the ground sending up short vertical stems"
http://encarta.msn.com/dictionary_561533925/psilophyte.html
• "The **Psilotales** are the least complex of all terrestrial vascular plants, and were once believed to be

- Lower Carboniferous [Mississippian]: Important coal deposits did not form until the Lower Carboniferous (Russia).

[Drawing] **Taeniocrada decheniana** (Goeppert)—Lower Devonian plant similar to the Psilophyton habit of growth, but its exact relations are unknown
[Drawing] Early Devonian psilophytes
[Simulated image] Middle Devonian landscape. Laurentia (proto-North America) and Baltica collide, pushing up the Caledonides (background) which stretch from northern Norway through Britain and the eastern part of North America. The erosion of the Caledonides during the Devonian provides the first sediments in basins that later form the Norwegian continental shelf. These early sediments are represented here by the alluvial plains in the foreground. Vegetation consists of Eospermatopteris and Archaeopteris, the first tree-forming plants to evolve.

Most coal deposits formed during three major periods of coal formation
1. Late Carboniferous-Early Permian
2. Jurassic-Cretaceous
3. Tertiary

Late Carboniferous-Early Permian coals
• These form the bulk of coal reserves in the world
• Found on all continents
• Usually high rank but structurally deformed
• In the northern hemisphere, stretch from North America to Europe to the Far East
• In the southern hemisphere, form a broad band in the countries that were connected as Gondwanaland
• Condition of deposition in **Northern Hemisphere**:
  - Coal-bearing areas were situated near the equator
  - Humid, tropical and subtropical conditions dominated by **Lepidodendron**[546] [Scale tree], and **Sigillaria**[547] forests (no growth rings) and **Calamites**[548], reed-like aquatic plants that grew in stagnant swamps

---

remnants of an otherwise extinct Devonian flora. This is primarily because **psilophytes** are the only living vascular plants to lack both roots and leaves. Though they have been considered "primitive," recent developmental and molecular evidence suggests that the group may actually be reduced from fern-like ancestors. There is not universal agreement on this, but we here treat them with the ferns for that reason. Despite the uncertainty of their relationships, psilophytes do structurally resemble certain early vascular plants, and are used as a model for understanding the ecology of these plants... The psilophyte stem lacks roots; it is anchored instead by a horizontally creeping stem called a rhizome... "
http://www.ucmp.berkeley.edu/plants/pterophyta/psilotales.html

[546] **Lepidodendron**: "Lepidodendron (also known as the "Scale tree") is an extinct genus of primitive, vascular, arborescent (tree-like) plant related to the Lycopsids (club mosses). They sometimes reached heights of over 30 m, and the trunks were often over 1 m in diameter, and thrived during the Carboniferous period. Sometimes called "giant club mosses", this is actually not correct as they are actually closer to quillworts than to club mosses. Lepidodendron had tall, thick trunks that rarely branched and were topped with a crown of bifurcating branches bearing clusters of leaves. These leaves were long and narrow, similar to large blades of grass, and were spirally-arranged. The vascular system was a siphonostele with exarch xylem maturation..."
http://en.wikipedia.org/wiki/Lepidodendron

[547] **Sigillaria**: "a genus of extinct, spore-bearing, arborescent (tree-like) plants which flourished in the Late Carboniferous period but dwindled to extinction in the early Permian period. It was a lycopodiophyte, and is related to the lycopsids, or club-mosses, but even more closely to quillworts, as was its associate Lepidodendron. Sigillaria was a tree-like plant, with a tall, occasionally forked trunk that lacked wood. Support came from a layer of closely packed leaf bases just below the surface of the trunk, while the center was filled with pith. The old leaf bases expanded as the trunk grew in width, and left a diamond-shaped pattern, which is evident in fossils. The trunk had photosynthetic tissue on the surface, meaning that it was probably green.... It was associated with Lepidodendron, the scale tree, in the Carboniferous coal swamps."
http://en.wikipedia.org/wiki/Sigillaria

[548] **Calamites**: "a genus of extinct arborescent (tree-like) **horsetails** to which the modern horsetails (genus Equisetum) are closely related. Unlike their herbaceous modern cousins, these plants were

- Contains many broad bands of bright coal that arise from thick stems

[Drawings] Lepidodendron aculeatum; Part of a stem with leaf scars (Netherlands)
[Photo of U. Mich. Diorama] Trunk of Lepidodendron
[Drawing] Northern hemisphere Carboniferous forest
[Drawings] Sigillaria computer reconstructions
[Drawings] Calamites leaves and trunk; Sigillaria trunk;

• Condition of deposition in **Southern Hemisphere**:

- The coal-forming areas of Gondwanaland were around sub-arctic regions [?]
- The climate was mainly cold temperate
- Only during the late Permian did the climate become warmer
- Rich coal deposits dominated by a stunted, broad-leaved **Glossopteris**[549] forest
- Contains relatively little bright coal and may be finely detrital

[Drawings] Reconstruction of Glossopteris plant: (a) A Glossopteris tree; (b) the pollen producing organ (Eretmonia); (c) a seed-bearing organ attached to a Glossopteris leaf; (d-g) examples of different types of Glossopteris fructification.
[Photos] Glossopteris fossil leaves from the Triassic of Australia
[Map of Gondwanaland[550] showing formerly contiguous bands of fossils including Glossopteris]

Jurassic-Lower Cretaceous Coals
USA, China, and CIS (Commonwealth of Independent States, remnant of former USSR)

- Lignite to anthracite
- Most of the world's brown coal and black coal reserves [see here[551] for differeing opinion]
- Thick coals with minimal structural damage
- **Gymnosperms** (Ginkgophyta, Cycadophyta, and conifers) are the principal coal-forming plants

Ginkgophyta [Images]:
Ginkgo biloba leaves, plant morphology, and seeds [the name is often misspelled "Gingko"]
Cycadophyta [Images]:
Reconstructed Mesozoic cycad "flower" Cycadophyta
Cycad male cone, female seeds, plant, reconstructed Mesozoic cycad "flower"

Tertiary Coals
• Diverse angiosperm flora in swamps in North America, Europe, Japan,, and Australia
• Thick peat deposits with many different fabrics
• Tertiary peat
[Image] Tertiary peat
[Image] Paleocene coal basins in US West

---

medium-sized trees, growing to heights of more than 30 meters (100 feet). They were persistent minor component of coal swamps of the Carboniferous period.
http://en.wikipedia.org/wiki/Calamites

[549] **Glossopteris**: "is the largest and best-known genus of the extinct order of **seed ferns** known as Glossopteridales (or in some cases as Arberiales or Dictyopteridiales). Long considered a fern after its discovery in 1824, it was later assigned to the **gymnosperms**. The genus is placed in the division Pteridospermatophyta... Glossopteris was a woody, seed-bearing shrub or tree, some apparently reaching 30 m tall. They had a softwood interior that resembles conifers of the family Araucariaceae. Seeds and pollen-containing organs were borne in clusters at the tips of slender stalks partially fused (adnate) to the leaves.... They are interpreted to have grown in very wet soil conditions, similar to the modern Bald Cypress. The leaves ranged from about 2 cm to over 30 cm in length."
http://en.wikipedia.org/wiki/Glossopteris

[550] **Map of Gondwanaland and Reconstructed Bands of Fossils**:
http://pubs.usgs.gov/gip/dynamic/historical.html

[551] **Location of Major World Black and Brown Coal Reserves**: "The first [major period of coal formation] took place during the Late Carboniferous-Early Permian periods. Coals formed at this time now form the bulk of the black coal reserves of the world… The third major episode occurred during the Jurassic-Lower Cretaceous period… Tertiary coals form the bulk of the world's brown coal reserves… "
Larry Thomas. *Coal Geology*. Wiley 2002 p. 46.

Biogenic Metals Deposits

[MCM: Edited from verbatim text of LRS slides, not all material in the slides was discussed. I will not be able to post the slides document, but if available to you, see PDF document of slides, containing images which are essential for understanding this material.]

The principle metals under consideration here are **Manganese**, **Iron**, **Gold**, and **Aluminum**
[Image] Galionella [or Gallionella], an iron-oxidizing bacteria[552]

Bacteria and ore deposits
• Both aerobic and anaerobic bacteria have profound effects on the geochemistry of dissolved metals and metal-bearing minerals
• Bacterial metabolism can aid in the release of ore metals from rocks and minerals, as well as their transport and precipitation
• This process has the potential to play a significant role in **low-temperature ore formation** (e.g., deep-sea manganese nodules)
• Bacterially induced mineralization is being used for the bioremediation of metal-contaminated environments
• Bacteria can also change the permeability in rocks
[EM Image] Purple, non-sulfur bacterium, **Rhodospirillum**[553]

Flow chart to determine if a species is an autotroph, heterotroph, or a subtype
Chart sorts organisms out as Photoautotrophs, Chemoautotrophs, Autotrophs, Heterotrophs, Chemoheterotrophs, and Photoheterotrophs

How do bacteria interact with metals?
• Bacteria exhibit tremendous molecular and metabolic diversity and can alter the chemistry of their surroundings—often to their own benefit
• **Heterotrophic** bacteria require organic carbon for their metabolism; they couple the oxidation of organic carbon to CO_2 with the reduction of inorganic dissolved species of minerals
• **Autotrophic** (or **chemolithoautotrophic**) bacteria require only inorganic compounds for their metabolism (e.g., iron-, manganese-, and sulfur-oxidizing bacteria)

---

[552] **Galionella [Gallionella] bacteria photos in Red Mats**:
http://www.geo.utexas.edu/chemhydro/LowerKane/red_mats.htm
[553] **Rhodospirillum rubrum**:
• "is a purple nonsulfur bacterium that can grow aerobically or anaerobically. It has the ability to live through cellular respiration, fermentation, photosynthesis, or photoautotrophic growth."
http://microbewiki.kenyon.edu/index.php/Rhodospirillum
• "Rhodospirillum rubrum (R. rubrum) is a Gram-negative, purple-colored Proteobacterium, having a size of 800 to 1000 nanometer. As it can live both anaerobically and aerobically, it is therefore both heterotrophic and autotrophic. Under aerobic growth photosynthesis is genetically suppressed and R. rubrum is then colorless. After the exhaustion of oxygen, R. rubrum immediately starts the production of photosynthesis apparatus including membrane proteins, bacteriochlorophylls and carotenoids, i.e. the bacterium becomes photosynthesis active… The photosynthesis of R. rubrum differs from that of plants as it possesses not chlorophyll a, but bacteriochlorophylls. While bacteriochlorophyll a absorbs light having a maximum frequency of 800 to 925 nm, chlorophyll absorbs light having a maximum frequency of 660 to 680 nm. R. rubrum is a spiral-shaped bacterium (spirillum, plural form: spirilla). R. rubrum is interesting for biotechnology: 1) Quantitative accumulation of PHB (poly-hydroxy-butric-acid) precursors in the cell for the production of biological plastic, 2) production of biological hydrogen fuel and 3) model system for studying the conversion from light energy to chemical energy."
http://en.wikipedia.org/wiki/Rhodospirillum_rubrum

Manganese Nodules[554]

Distribution

- The highest concentrations are on vast abyssal plains in the deep ocean between 4,000 and 6,000 meters depth, in large fields often 1000s of km distant from the closest continent shores.
- Nodules lie on the seafloor, often partly buried; they vary greatly in abundance, in some cases covering more than 70 % of the bottom, or even paving the seafloor
- The total amount of nodules on the sea floor was estimated at 500 billion tons in 1981
- They are most abundant in oceanic regions where sedimentation rates are slow
- They are of economic interest, especially because of their high **copper, nickel and cobalt** content
- Metal abundances are particularly high where nodules are widely dispersed on the sea floor

[Image of manganese nodules almost covering ocean floor]

Chemical composition of Manganese Nodules

- The chemical composition of nodules varies according to the kind of manganese minerals and the size and characteristics of the core
- Those of greatest economic interest contain:
    - Manganese (27-30 %)
    - Iron (6 %)
    - Silicon (5 %)
    - Aluminum (3 %)
    - Nickel (1.25-1.5 %)
    - Copper (1-1.4 %)
    - Cobalt (0.2-0.25 %)
    - Small amounts of calcium, sodium, magnesium, potassium, titanium, and barium, along with hydrogen and oxygen.

Exploration of Manganese Nodules

[Photo] North-Central Pacific Ocean, 5157 m depth
Benthic infauna appears to redistribute sediments and help keep nodules on the surface
[Photos] Box core showing high density of manganese nodules. Box cores have the advantage of showing the character of undisturbed ocean bottom. Off of [vessel] OCEANOGRAPHER during DOMES project. (DOMES = Deep Ocean Mining Environmental Studies). NOAA Box coring operations during DOMES project.

Formation of Manganese Nodules

Several processes are involved in the formation of manganese nodules:

- **Hydrogenous**: Direct precipitation of metals from seawater
- **Diagenetic**: Formed under reducing conditions in organic-rich sediments where Mn is mobilized and reprecipitated near the sediment-water interface
- **Hydrothermal**: Metals are derived from submarine thermal solutions associated with volcanic activity
- **Halmyrolitic**: Mn is partially supplied by submarine weathering of basaltic debris
- **Biogenic**: Precipitation of metal hydroxides through the activity of microorganisms

Several of these processes probably operate concurrently or they may follow one another during the formation of a nodule, exactly how is not known.

Manganese-oxidizing bacteria

---

[554] **Manganese nodules**: “Polymetallic nodules, also called manganese nodules, are rock concretions on the sea bottom formed of concentric layers of iron and manganese hydroxides around a core. The core may be microscopically small and is sometimes completely transformed into manganese minerals by crystallization. When visible to the naked eye, it can be a small test (shell) of a microfossil (radiolarian or foraminifer), a phosphatized shark tooth, basalt debris or even fragments of earlier nodules. Nodules vary in size from tiny particles visible only under a microscope to large pellets more than 20 centimeters across. However, most nodules are between 5 and 10 cm in diameter, about the size of potatoes…. Nodule growth is one of the slowest of all geological phenomena – in the order of a centimeter over several million years.” http://en.wikipedia.org/wiki/Manganese_nodule

• Various bacteria are present on and within the surface of nodules (100's to 10,000's per gram of nodule—probably underestimates)
• Divalent ions are concentrated on the nodules and Mn^{+2} serves as an energy source to Mn^{+2}-oxidizing bacteria that live on the nodules
• The nodules are, thus, a selective habitat for Mn^{+2} oxidizing bacteria, but also Mn^{+4} reducing bacteria
• Therefore, bacteria may play a role not only in nodule buildup but also in nodule breakdown
• Probably the Mn^{+4} reducing bacteria is active in-between growth periods—conditions appear not to be continually favorable for nodule growth
• The exact biogenic mechanism for nodule growth is not known
[Images] Scanning electron photomicrographs of bacteria attached to the surface of ferromanganese nodules from Blake Plateau, off the southern Atlantic coast of the United States. Note the slime strands anchoring the rod-shaped bacteria to the nodule surface (from Ehrlich, 2002)

Manganese Nodules Description: Exterior
• Nodules vary in size from microscopic particles to > 20 cm across
• Most nodules are between 5 -10 cm in diameter
• The surface is generally smooth, sometimes rough, knobby, or irregular.
[Photo] Manganese nodule from off the coast of Alaska
Manganese Nodules Description: Interior
• Manganese nodules are formed of concentric layers of iron and manganese hydroxides around a core
• The core can be a small test (shell) of a radiolarian or foraminifer, a shark tooth, basalt debris, meteor fragment, whale bone fragment, or even fragments of earlier nodules
• The core may be microscopically small and is sometimes completely transformed into manganese minerals by crystallization
[Image of ferromanganese nodule]

[Image] Manganese nodules and encrusting organisms
• Manganese-rich particles are associated with at least 20 species of benthic agglutinating foraminifers growing on the nodules
• Foraminifers are likely active in the physical construction of manganese deposits
[Image] **Archimerismus subnodosus** (Brady), and **Agglutinating foraminifer**. Intact specimen, aperture on top, South Barents Sea, modern mud
[Image] Arrangement of agglutinated particles near the aperture. South Barents Sea, modern mud. Example of an agglutinating foraminifer (but not from a Mn nodule)

Manganese conundrum
• Manganese nodules grow at extremely low rates (1-200 mm/million years)—growth rates are not constant—why?
• Average sedimentation in abyssal plains is approximately 1 mm per thousand years—sediment accumulation rates exceed nodule growth rates—why?
• Manganese nodules are rarely found below surface sediments—why ?
• Why do the nodules exist at all? They should be buried before they reach typical sizes observed in the ocean
[MCM speculation: are they being tended and farmed for some purpose by benthic organisms to stay exposed at the ocean bottom?]

Banded Iron Formations (BIFs)

Importance of Banded Iron Formations
• Speculations and studies abound as to the mechanism of deposition of BIFs: controversial origin [MCM: see extensive comments above on BIFs]
• BIFs play an important role in the study of oxygen concentrations of early earth
• The BIFs are especially interesting in that they were deposited concurrently with the early evolving biosphere

- Iron is used as a metabolic agent by numerous microorganisms; some of these, such as species of oxygenic and anoxygenic photoautotrophs and chemoferrotrophs, suggest that BIFs are at least in part, microbially mediated
- Evidence for a microbial role in Archean BIF deposition, however, is not conclusive

Formation of BIFs

In the presence of free oxygen, it has been speculated that oxidation of Fe^{2+} by chemolithoautotrophic microbial species such as **Gallionella ferruginea**[555] in an ocean with limited photosynthetic oxygen may have precipitated **ferric iron** over wide ocean areas:

$$6Fe^{2+} + 0.5O_2 + CO_2 + 16H_2O \rightarrow [CH_2O] + 6Fe(OH)_3 + 12H^+$$

Most models explaining the primary oxidation of Fe^{2+} to Fe^{3+} near the ocean surface have until recently focused on photochemical processes or inorganic reactions using photosynthesis-generated O_2

[Image] **Gallionella ferruginea**

Anoxygenic photosynthesis?

• Strong support now exists for iron-oxidizing anoxygenic phototrophs as a mechanism of deposition. Some strains of green sulfur, purple nonsulfur/sulfur bacteria can use ferrous iron, rather than water, as the electron donor in photosynthesis. Purple and green bacteria can evidently couple Fe^{2+} oxidation to the reduction of CO_2 during anoxygenic photosynthesis:

$$4Fe^{2+} + CO_2 + 11H_2O \rightarrow [CH2O] + 4Fe(OH)_3 + 8H^+$$

• This is now the most popular hypothesis used to explain iron deposition on early Earth, before free oxygen became widely available as an oxidant

BIF environments of deposition

• They are some of the oldest rocks on Earth; 90% of all iron formations were deposited between 3.8 Ga and 1.6 Ga

• BIFs are deposited in environments ranging from shelf and upper continental slope to the abyssal plain.

• Typically thin-bedded and/or finely laminated—why?

• Contain at least 15% iron of sedimentary origin, and commonly contain chert layers

• Can be carbonate-, silica-, and oxide-rich, believed to correspond to different water depths

[Photos] Finely lamellated Banded Iron Formations rock

[Photos] Banded Iron Formations. The dark bands in the close-up are iron oxides, and the red bands are **chert** stained with fine-grained iron oxides

Types of BIFs: Superior-type and **Algoma-type**

No all-inclusive BIF classification scheme exists. Some are based on mineralogical composition, tectonic setting, and depositional environment

1. Superior-type BIF: BIFs are large, and associated with depositional (sedimentary) environments along extensive rifted systems that formed during the early Proterozoic.

- • Extensive hydrothermal and volcanic activity developed along the fracture zones
- • BIFs deposited on shallow marine shelves of the resulting passive margins during transgressing seas
- • Can extend over more than 10^5 km^2

Western Australia BIFs (Superior-type)

• Thick, laterally extensive Proterozoic deposits of the 2.5 Ga Hamersley Group, Western Australia, formed on partially isolated, submerged platforms on the continental shelves of Archean cratons

• The BIF of the Hamersley Group are thought to have been precipitated by iron-oxidizing bacteria

[Photo] Banded iron formations, Karijini National Park, Western Australia (Superior-type) (Kirschvink, 2005)

[Photo] Hamersley Group BIFs

---

555 **Gallionella ferruginea** [not Galionella]: “Gallionella ferruginea is an iron-oxidizing, chemolithotrophic bacteria that lives in low-oxygen conditions. The bacteria oxidize and fix iron, but in order to get energy out of this process, they must live in a relatively specific environment that contains "reduced iron, the right amount of oxygen and sufficient amounts of carbon, phosphorus and nitrogen" (Halbach, Koschinsky, and Halbach 2001). G. ferruginea oxidizes dissolved iron, therefore removing it from the water and producing an insoluble precipitate of **ferric hydroxide**. In active, deep sea hydrothermal venting sites, most of the iron mineralizations that come from the emitted hydrothermal fluids are massive sulphides. Other iron hydroxide precipitates, such as jasper, also can be found in submarine hydrothermal fields that have relic filamental structures that indicate bacterial origin.”
http://microbewiki.kenyon.edu/index.php/Gallionella

Main sources of iron in Hamersley Group BIFs
• Midoceanic ridges and hotspots (and possibly additional continental drainage)
• The hydrothermal waters were brought onto the outer continental shelf by upwelling currents or plumes that lasted only years or decades
• Minerals subsequently precipitated uniformly throughout much of the depositional basin
[Photo] Mesoscale banding, banded iron formations, Western Australia. How did the alternating iron-rich and silica-rich bands form?

2. Algoma-type BIF iron formations are relatively small, and associated with submarine volcanic processes.

- Deposited in deep-water environments that are adjacent to volcanic arcs
- Associated with graywacke and turbidite sediments, carbon-bearing mudstones, and volcanic rocks.
- Age: Most of these deposits are Archean (>2.5 billion years).
- These are the oldest BIFs

Placer Gold Deposits[556]

Formation
• Gold nuggets or octahedral gold[557] crystals are commonly coated with secondary gold, which promotes the adhesion of smaller gold nuggets
• Precipitation of octahedral gold could be directly related to bacterial oxidation
• Weathering environments containing plant or bacterially derived organic material enhances the solubility of gold
• Weathering of gold-containing minerals under near surface conditions produce colloidal gold—the morphology of microscopic colloidal gold may reflect biological processes
• Careful documentation of the morphology will be needed to better understand the biogeochemistry of placer gold deposits
[Photo] Octahedral gold crystal
[SEM Photos of **Gold-forming bacteria**]
SEM color picture of gold forming bacteria **Pedomicrobium** showing branching and budding.
SEM photo of a bacterial gold-mat showing new bacterial formation on old specimen, Prophet Mine, Queensland, Australia (Gunther Bischoff)

Aluminum In Bauxite

Formation of Bauxite

---

[556] **Placer Deposits**: "In geology, a placer deposit or placer is an accumulation of alluvium or eluvium containing valuable minerals which is formed by deposition of dense mineral phases in a trap site. The name is from the Spanish word placer, meaning "sand bank". Typical locations for alluvial placer deposits are on the inside bends of rivers and creeks, in natural hollows, at the break of slope on a stream, the base of an escarpment, waterfall or other barrier, within sand dunes, beach profiles or in gravel beds."
http://en.wikipedia.org/wiki/Placer_deposit
[557] **Gold**: "Although gold is a noble metal, it forms many and diverse compounds. The oxidation state of gold in its compound ranges from -1 to 5+ but Au(I) and Au(III) dominate. Gold(I), referred to as the **aurous** ion, is the most common oxidation state with "soft" ligands such as thioethers, thiolates, and tertiary phosphines. Au(I) compounds are typically linear. A good example is $Au(CN)^{2-}$, which is the soluble form of gold encountered in mining. Curiously, aurous complexes of water are rare. The binary Gold Halides, such as AuCl, form zig-zag polymeric chains, again featuring linear coordination at Au. Most drugs based on gold are Au(I) derivatives…. Gold(III) ("**auric**") is a common oxidation state and is illustrated by gold(III) chloride, $AuCl_3$. Its derivative is chloroauric acid, $HAuCl_4$, which forms when Au dissolves in aqua regia. Au(III) complexes, like other d8 compounds, are typically square planar."
http://en.wikipedia.org/wiki/Gold

• Bauxite[558] is a product of weathering of aluminosilicate minerals (commonly from volcanic rocks) in warm and humid climates, and aided by microorganisms
• Vegetation provides cover that protects against erosion of the weathered rock, limits water evaporation, and is a source of nutrients for the microbiota that participate in the rock weathering
• Bauxite composition:
  45-50% Al_2O_3 (gibbsite, boehmite, diaspore)
  ~20% Fe_2O_3 (hematite, goethite
  ~3-5% silicates (kaolinite)
[Photo] Bauxite
[Photo] When mined, the bauxite is commonly in **pisolite** form
Bauxite is an aluminium (aluminum) ore which consists largely of the Al minerals **gibbsite** $Al(OH)_3$, **boehmite** and **diaspore** AlO(OH), together with the iron oxides **goethite** FeO(OH) and **hematite** Fe_2O_3, the clay mineral **kaolinite** $Al_2Si_2O_5(OH)_4$ and small amounts of anatase TiO_2.

Biological role in bauxite formation
1. Weathering of source rock and formation of "protobauxite"
   - The first stage, if aerobic, may be promoted by bacteria and fungus; if anaerobic, by anaerobic bacteria and facultative bacteria (adaptable to survive and multiply in either anaerobic or aerobic conditions)
   - Mobilization of Al, Fe, and Si from host rock and precipitation of these rock constituents as oxides, silica, and silicate minerals
2. Maturation of protobauxite to bauxite
   - The second stage is promoted by iron-reducing and fermentative bacteria under anaerobic conditions
   - Selective mobilization of iron oxides and silica/silicate enriching the solid residue in Al.

Human Impacts On Biodiversity: The Current Mass Extinction

[MCM: Edited from verbatim text of LRS slides, not all material in the slides was discussed. I will not be able to post the slides document, but if available to you, see PDF document of slides, containing images which are essential for understanding this material.]

Global Warming Effects

Effects On CO_2

[Graph of Atmospheric CO_2 labeled "Headed for Another Extinction?] Atmospheric CO_2 was high during ancient mass extinctions, supporting a role for global warming in those events. Today CO_2 stands at 385 ppm and is projected to climb by 2 to 3 ppm annually. If this trend continues, by the end of the next century [2200 CE], atmospheric CO_2 would approach 900 ppm—just below levels during the **Paleocene thermal extinction** (**Paleocene–Eocene Thermal Maximum**)[559] 54 million years ago.

---

[558] **Bauxite**: "Bauxite is the most important aluminium ore. It consists largely of the minerals gibbsite $Al(OH)_3$, boehmite γ-AlO(OH), and diaspore α-AlO(OH), together with the iron oxides goethite and hematite, the clay mineral kaolinite and small amounts of anatase TiO_2. It was named after the village Les Baux-de-Provence in southern France, where it was first discovered in 1821 by geologist Pierre Berthier."
http://en.wikipedia.org/wiki/Bauxite
[559] **Paleocene–Eocene Thermal Maximum [PETM] and Extinction**:
• "The end of the Paleocene (55.5 to 54.8 Mya) was marked by one of the most significant periods of global change during the Cenozoic Era. A sudden global climate change, the Paleocene-Eocene Thermal Maximum (PETM), upset oceanic and atmospheric circulation, leading to the extinction of numerous deep-sea benthic foraminifera and a major turnover in mammalian life on land that marked the emergence of mammalian lines recognizable today. In an event marking the start of the Eocene, the planet heated up in one of the most rapid and extreme global warming events recorded in geologic history, currently identified as the 'Paleocene-Eocene Thermal Maximum' or the 'Initial Eocene Thermal Maximum' (PETM or IETM). The same event has sometimes been termed the Late Paleocene Thermal Maximum (LPTM), depending upon a slightly different interpretation of the stratigraphic

Human activities and greenhouse warming: Atmospheric CO_2
• About ½ of CO_2 produced by human activities ends up in the atmosphere
• About ¼ ends up in the oceans
- Parts remain dissolved
- Parts are converted to biomass through photosynthesis by phytoplankton

• About ¼ is used for the expansion of forests; forests actually benefit from increased CO_2 (as long as there is forest around to benefit)

[Graph] **The increase in concentrations of carbon dioxide in the atmosphere since 1700** (After R.T. Watson et al., 1990).
Graph shows a steady rise from c. 280 in 1700 to c. 350 in 1990 [and subsequently levels have risen to c. 385]. (Prior to 1957, CO_2 samples are from the Antarctic ice. Since 1957, the samples are from the air.)

[Graph] **Increase in global average temperature predicted** in 1992 by the **Intergovernmental Panel on Climate Change** [**IPCC**]
Increase in CO_2 has elevated global temperature during the past century by ~1 °C [through 1992]. Predicted future temperatures are based on the premise that civilization will exercise no control over future CO_2. Actual increase "High" and "Low" are estimated ranges of uncertainty. [By 2100, the "High" estimate is > 5 °C, the "Low" is c. 2.5 °C.]

The Threat Of Methane "Eruptions"

• Methane has about 7.5 times more effect than CO_2 on greenhouse warming [over a 500 year period[560]]
• At present, it is found in low concentrations, but future increases are possible
• Huge quantities of methane CH_4 are frozen in soils (as **methane clathrates**[561]) deep beneath the tundra in high northern latitudes [MCM: Methane clathrates are also found in sediments on the ocean floor]

---

record. Sea surface temperatures rose between 5 and 8°C over a period of a few thousand years, and in the high Arctic, sea surface temperatures rose to a sub-tropical 23°C, or 73°F. In 1990, marine scientists James Kennett and Lowell Stott, both then at the University of California, Santa Barbara, reported analysis of marine sediments showing that, not only had the surface of the Arctic ocean heated up about 10 degrees at the beginning of the Eocene, but that the entire depth of the ocean had warmed, dramatically changing its chemistry. Oxygen content in deep sea waters was dramatically reduced, causing 30 to 40% of deep sea foraminifera to go extinct. Geologist Jim Zachos of the University of California, Santa Cruz connected the Eocene heat wave to drastic changes in ocean chemistry that caused the massive worldwide die-off."
http://en.wikipedia.org/wiki/Paleocene-Eocene_Thermal_Maximum
• See also graphs of climate change in the past 65 Ma based on $\delta^{18}O$ values in benthic foraminifera carbonate. http://en.wikipedia.org/wiki/Image:65_Myr_Climate_Change.png
[560] **Methane Global Warming Potential**: "Methane has an atmospheric lifetime of 12 ± 3 years and a GWP [global warming potential] of 62 over 20 years, 23 over 100 years and 7 over 500 years [compared to GWP = 1 for CO_2]. The decrease in GWP associated with longer times is associated with the fact that the methane is degraded to water and CO_2 by chemical reactions in the atmosphere."
http://en.wikipedia.org/wiki/Greenhouse_gases
[561] **Methane Clathrates:**
• "also called **methane hydrate** or **methane ice**, is a solid form of water that contains a large amount of methane within its crystal structure (a clathrate hydrate). Originally thought to occur only in the outer regions of the Solar System where temperatures are low and water ice is common, extremely large deposits of methane clathrate have been found under sediments on the ocean floors of Earth. Methane clathrates are common constituents of the shallow marine geosphere, and they occur both in deep sedimentary structures, and as outcrops on the ocean floor. Methane hydrates are believed to form by migration of gas from depth along geological faults, followed by precipitation, or crystallization, on contact of the rising gas stream with cold sea water. At higher pressures Methane clathrates remain stable at temperatures up to 18 °C. The average methane clathrate hydrate composition is 1 mole of methane for every 5.75 moles of water, though this is dependent on how many methane molecules "fit" into the various cage structures of the water lattice. The observed

- Contain 3,000 times as much CH_4 as is in the atmosphere
- Mostly produced by bacteria during Arctic summers

• Future global warming may release CH_4 gas from the tundra adding significantly to the greenhouse warming caused by CO_2.
• [MCM: Release of methane from clathrates in the ocean sediments could also be a major factor[562]]
[Image] Methane clathrate with flame from evolving methane.

A ticking time bomb in the Arctic tundra?
• The Arctic Council's recent report on the effects of global warming in the future is grim: global floods, extinction of polar bears and other marine mammals, collapsed fisheries
• A temperature increase of merely a few degrees would cause frozen CH_4 to volatilize and "burp" into the atmosphere, which would further raise temperatures, which would release yet more CH_4, heating the Earth and seas further, and so on.
• Once triggered, this cycle could result in **runaway global warming** the likes of which even the most pessimistic doomsayers aren't talking about.
• An apocalyptic fantasy concocted by hysterical environmentalists? Unfortunately, NO. Strong geologic evidence suggests something similar may have happened at least twice before—end of Permian and Paleocene-Eocene [PETM].

[Image of tundra and Mt. McKinley] There's 400 gigatons of methane locked in the frozen Arctic tundra—a temperature increase of only a few degrees is enough to start methane ‘burps’. The Arctic Council predicts it [i.e., such a temperature increase] is sufficient to melt all the methane clathrates and start a runaway global warming.

[Diagram] Methane clathrates may become an “important” [source of] greenhouse gas with a rise of the sea level
With sea levels low, gas clathrates imbedded in Arctic tundra are stable at Arctic temperatures.
With rising sea levels and warm water covering gas clathrates imbedded in Arctic tundra, melting occurs with release of methane into the atmosphere.

Effects on Water Supplies

• On the land, global warming will create severe problems of water supply for both natural and human communities.
• Water supply predictions take into account:

- Amount of precipitation
- Rate of water loss through evaporation and transpiration by plants

• Many uncertainties remain
[Graph] The proportion of total **runoff in California** that is occurring in late spring and early summer has declined over the last 100 years. Scientists say that's because more precipitation is falling as rain than as snow during the winter. [MCM by inspection of the graph: the average value for this proportion has decreased from c. 44% in 1910 to c. 34% in c. 1998] (Source: Pacific Institute for Studies in Development, Environment and Security)

---

density is around 0.9 g/cm^3. One liter of methane clathrate solid would therefore contain, on average, 168 liters of methane gas (at STP).”
http://en.wikipedia.org/wiki/Methane_clathrate
• “Clathrate hydrates (or alternatively gas clathrates, gas hydrates, clathrates, hydrates etc.) are a class of solids in which gas molecules occupy "cages" made up of hydrogen-bonded water molecules. These "cages" are unstable when empty, collapsing into conventional ice crystal structure, but they are stabilized by the inclusion of appropriately sized molecules within them. Most low molecular weight gases (including O_2, H_2, N_2, CO_2, CH_4, H_2S, Ar, Kr, and Xe), as well as some higher hydrocarbons and freons will form hydrate under certain pressure-temperature conditions. Clathrate hydrates are not chemical compounds. The formation and decomposition of clathrate hydrates are first order phase transitions, not chemical reactions.”
http://en.wikipedia.org/wiki/Clathrate_hydrate
[562] **Clathrate gun hypothesis**: http://en.wikipedia.org/wiki/Clathrate_Gun_Hypothesis

Effects On Sea Level Changes, Flooding, And Desertification

• Wet areas will become wetter because warm seas supply more water through evaporation than cold seas
• Monsoon rains will increase because seasonal warming will intensify; draws the monsoons inland
• Dry inland areas will become drier; high temperatures will cause evaporation to increase
[Map] Dry regions of the world; the dry grass lands are in danger of desertification, while wet areas are in danger of increased rain

Desertification
• Plants disappear
• Erosion increases
• Moisture is lost through reduction of plant and soil cover
• The system becomes even drier and the desertification process speeds up
[Photo of Sahel desert region S of the Sahara, Africa]

Rising sea levels
• By 2100, the sea level may have increased by 50 cm (4-10 cm in the past 100 years)
• Sea-level increases will be caused by:
  - Melting of glaciers
  - Heating up of the oceans—the water expands (may have the greatest effect)
• A 1-meter sea-level rise may:
  - Displace about 1 billion people
  - Endanger 1/3 of the world's crop-growing areas
• A 50 cm sea-level rise may:
  - Destroy Venice
  - Bangladesh would experience even more disastrous floods
  - Many of the world's wetlands would be lost because of human obstructions

Effects of sea level change is related to topography
Diagram shows width of shoreline shift is narrow with steeply sloping coast, but wide with gradually sloping coast.

The importance of ecosystems
• There are few studies in how any particular ecosystem functions in its totality—and how do particular assemblages of ecosystems interact at a global scale?
• Ecologists have been studying ecosystems for some time, but we still don't know exactly why species are being lost at such a high rate.
• The greatest rate of species loss today is found in the tropical forests.

Deforestation And The Global Carbon Cycle

• The plants and soil of tropical forests hold 460-575 billion metric tons of carbon worldwide, with each acre of tropical forest storing about 180 metric tons of carbon.
• When a forest is cut and burned, the carbon that was stored in the tree trunks (wood is about 50% carbon) joins with oxygen and is released into the atmosphere as CO_2.
• From 1850 to 1990, deforestation worldwide and decomposing debris (including in the United States) released 122 billion metric tons of carbon into the atmosphere [over this entire period].
• The current rate [of release from deforestation worldwide and decomposing debris] is ~1.6 billion metric tons of Carbon per year.
• In comparison, fossil fuel burning releases about 6 billion metric tons C per year,
• Thus, deforestation is an important contributor in the amount of CO_2 and other trace gases that go into the atmosphere.
[Satellite Images of progressive deforestation, including in the Amazon region taken from the Brazilian state of Para on July 15, 1986] If the current rate of deforestation continues, the **world's rain forests will vanish within 100 years**—causing unknown effects on global climate and eliminating the majority of plant and animal species on the planet!

Deforestation Figures for Brazil [Table and Map]

Map shows degree of Deforestation in the Brazilian Amazon[563] in 1986.
Table shows loss of 24,130 sq. km of forest in 2003, etc.
(All figures derived from official National Institute of Space Research (INPA) figures.)

Direct Causes Of Deforestation

• Most of the clearing is done for agricultural purposes, such as grazing cattle and planting crops—slash and burn agriculture. Large-scale (many km^2 at a time) intensive agriculture—large cattle pastures often replace rain forest to grow beef for the world market.
• Commercial logging, cutting trees for sale as timber or pulp.

- Selective logging where only the economically valuable species are cut
- Clear cutting, where all the trees are cut
- Commercial logging uses heavy machinery, such as bulldozers, road graders, and log skidders, to remove cut trees and build roads, which is just as damaging to a forest overall as the chainsaws are to the individual trees

• Fuel wood collection and charcoal making
• Mining and petroleum exploration
• Infrastructure development
[Photo] Slash and burn
[Photo] Northern Laos, slash and burn
[Photo] The haze carried by wind covered a big portion of South East Asian countries. Kuala Lumpur, thousands of kilometer away was covered in haze. The fires burned for 3 months and millions of hectares of virgin forest was destroyed. The fires were traced to a combination of new commercial agricultural projects, land clearing for tree and agricultural plantations, dry residues left in the forest after logging, and slash-and-burn agriculture. The situation was complicated by the very dry climatic conditions caused by the El Niño phenomenon. Eventually, Malaysia sent more than 2,000 firemen to help put out the fires.
[Photo] Huge forest fires burned in East Kalimantan, Borneo, Indonesia in 1997 and 1998.

Indirect Causes Of Deforestation

• Land access and land tenure: Unequal division of land that results in a small proportion of the population owning a very large fraction of the existing developed land
• Global market pressures
• Undervaluation of natural forests
• Weak government institutions
• Deliberate resettlement programs
• Growing population pressures (a crucial aspect of the problem)

Diagram of Causes of Deforestation

Proximate Forces: Fuelwood, Fodder, Farming, Logging, Mining
Driving Forces: Population Migration, Government Development Policy, International Contracting
Ultimate Causes: Population Growth, Inequality and Poverty, International Markets and Debts, Corruption

[Graphs] Between 1850 and 1980, 15% of the world's forests and woodlands were cleared
Some hope? Preliminary estimates show that between August 1, 2006 and July 30, 2007, some 3,707 square miles (9,600 square kilometers) of rainforest were cleared, a 31 percent drop from 2006.

World population and Deforestation

- Our [human] numbers are currently growing at the rate of 1,000 million new individuals every decade.
- The exact number of people who live by clearing the forest to plant subsistence crops is not known, but the accepted figure is at least 500 million or about 1 person in every 12 on the planet.
- Without a doubt, one of the most important predisposing conditions that underlies tropical deforestation (and many of the world's other problems related to achieving sustainable development) is our **growing population**

[Graph] Shows exponential growth in recent population.

Map of Habitat Loss

[563] **Deforestation in Brazil**: http://en.wikipedia.org/wiki/Deforestation_in_Brazil

Hotspots of habitat loss—areas with many endemic species that are in greatest danger of extinction as a result of human activity. These 25 hotspots comprise only 1.4% of Earth's land surface, yet contain almost half of all the world's species of vascular plants and 35% of all vertebrate species (excluding fish). Regions include: California Floristic Province, Brazil's Cerrado, Mesoamerica, Mediterranean Basin, Caucasus, Madagascar, etc.

Deforestation and Biodiversity
• Tropical rain forests cover only 7% of the total land surface of the Earth but hold over 50-90% all species
• Many of the rain forest plants and animals are endemic to small areas. If their habitat is destroyed, they may become extinct
• We do not know the exact rate of extinction, but estimates indicate that up to **137 species disappear worldwide** each day as a consequence of tropical deforestation.
• We are not only losing species that might show us how to prevent diseases, but other organisms are losing species they depend upon, and thus face extinction themselves
[Photo] Mountain Gorilla's Bwindi, Uganda

Decline Of Biodiversity and The Sixth Extinction

Why We Should Care About Biodiversity
• Intrinsic value of biodiversity
- It has value for its own sake regardless of whether we benefit from it or not
- All species have the same rights to exist that humans do
- Since humans dominate over nature and we are capable of moral and ethical judgments, these should include concerns for other species

[Photo showing BBC News 2003 article "Lions close to extinction"]
• Instrumental value of Biodiversity
- Defined as the degree to which the existence of a species benefits another species in some way
- We are normally the other species, and the value or benefit is typically economic

Biodiversity Instrumental Value
• **Medical Value**: Of all pharmaceuticals produced in the United States, 25% contain ingredients originally derived from native plants.
• **Scientific Value**: Much of what we know about evolution, ecology, and how natural systems work, has been derived from the study of species and ecosystems in their natural state.
• **Recreational And Aesthetic Value**
[Photo] Rosy periwinkle (Catharanthus roseus) from Madagascar may hold a cure to childhood leukemia
• **Commerce**
- Logging, commercial fishing, collection and sale of exotic plants and animal species
- Ecotourism

• **Agriculture, Forestry, Aquaculture, And Animal Husbandry**
- The existence and maintenance of our agricultural food supply is dependent on natural species

Ocean Ecosystems And Biodiversity: Coral Reefs
Coral reefs hold 25% of all marine species. Adverse impacts are from
• Global warming (increased El Niño events); reefs may be the first victims
• Natural damage—normally recovers quickly
• Now augmented by increasing water temperature, chemical pollution, sediment runoff, mining for coral rock, collecting coral specimens, damage by anchors and boats
• When reefs are stressed, they expel their zooxanthellae [endosymbiotic photosynthetic algae]

Is The Ocean Full Of Fish?
No. 70% of the world's fish species are either fully exploited or depleted.
[Diagram of how overfishing and wasteful practices are reducing fish populations.
- With **industrial fishing fleets**, companies and countries are competing for the world's fishes, and there is little incentive for any individual entity to catch fewer fish.
- Destructive fishing techniques worldwide destroys marine mammals and entire ecosystems.

- Predatory fish populations, including shark, tuna, and North Atlantic cod, continue to spiral downward, with many species dropping 90% or more in the past 40-50 years.

[Image] CNN.COM 2003 article shows 10% of big ocean fish remain.

Biodiversity And Agriculture

The problem with modern agriculture is its **uniformity** [lack of diversity]

- The object of modern agriculture is to reduce diversity as much as possible—to make a high-yield crop that is resistant to droughts, certain pests, and disease.
- Seed banks are very important when new genes are needed to combat disease.
- But seed banks represent the genetic diversity of plants at the time of the collecting.
- Pests and disease constantly evolve and mutate.
- When seeds from a seed bank cannot deal with a new disease, we have to go back to the wild "genetic home".
- Seed banks are too few (12) and are vulnerable to fire, war, or sabotage.

The Potato Blight

The Potato blight, caused by the fungus **Phytophthora infestans**, is one of the most important potato diseases in the world. It was responsible for the great Irish Potato Famine of the 1840's, leaving over 1 million people dead from famine-related diseases and resulting in the exodus of more than 1.5 million people from Ireland.

[Photos of Phytophthora infestans fungi and blighted potatoes]

Biodiversity And Stability

• Humans are not separate from the rest of Earth's biota; we are an integral part of the Earth system.

• Without the rest of the system in place we could not survive.

• The greater the number of species in an ecosystem, the healthier the ecosystem will be; the more diverse it is, the greater chance it can survive disruption.

• Productivity increases as biodiversity increases.

The Sixth Extinction?

[Graph showing a prominent peak in recorded extinction by 1950] The rate of historical extinctions of species for which information exists [1600-2000].

Rates of loss mount in the twentieth century. The apparent drop from 1950 to 2000 is not an indication of an improvement; the figures were recorded in 1990, and the full tally of species lost up to 2000 had not yet been calculated.

Extinctions Of Large Mammals And Birds

[Graphs of # of Living Species versus time, by Regions including North America, Australia, Africa, Madagascar, and New Zealand]

- The extinction of large mammals and birds correspond to the spread of human populations.
- Humans evolved first in Africa. They evolved with other animals there over millions of years. As a result, the curve for Africa is not as drastic.
- Humans arrived in New Zealand around A.D. 1000. Since then, 20 species of large land birds and 22 other species of flightless birds have been hunted to extinction. [Graph shows marked extinctions in New Zealand and Madagascar]
- The native Hawaiians (no graph included) extinguished 35 to 55 species of land birds. Fifty species remained when Captain Cook arrived in 1778, and one third of those are now extinct

Species facts

• 99% of all the species that ever lived are extinct, and only 1% of all species that ever lived have been preserved.

• Average lifetime of most species: 1 - 10 million years.

• 1.4 million modern species have been described (of those, 350,000 are beetles); 10 - 100 million species have not yet been discovered!

• There are more species today than at any single time in the past (?) [is this merely an investigational artifact?]

The Sixth Extinction: Human-Caused

• The rate of species loss due to human activity is equal to, or greater than, the rate of species loss in past mass extinctions!

• The implications of species loss can be harder to grasp than other, more tangible threats such as loss of ozone and climate change.
• We do not "see" species loss—so it is difficult to grasp the enormity.
[Image of 2002 BBC news article on "Quarter of mammals face extinction"

Species Loss Estimates
• 25% of all species on Earth may be extinct within the next 50 years.
• If 100 million species exist: 500,000 species a year go extinct
• If 10 million species exist: 50,000 species a year will go extinct
• We don't know exactly what the extinction rates are
• If this whole-sale species loss continues, restoring biodiversity may take 100 million years

We Are In The Middle Of A Mass Extinction
• Destruction of natural habitats
• Loss of biodiversity
• Whole ecosystems may become destroyed
• Many species are becoming extinct. Will this become another "Permian extinction?"
• Especially severe in tropical rainforests

Carrying Capacity—Overpopulation
• Carter Roberts, chief conservation officer for the World Wildlife Fund, said humans have already exceeded the planet's ability to sustain their level of consumption, known as **Earth's carrying capacity**, by about 20 percent
• That figure will climb steeply as more than 2 billion people living in India, China and other developing nations raise their standard of living.
• Climate change and industrialization will place enormous burdens on nations hoping to balance conservation and economic growth.

Human Extinction: Are We On The Same Path As Easter Island?
Ecosystem Collapse, Hypothesis I
• Polynesian people reached a green and forested Easter Island about 1500 years ago
• About 7000 people established a complex society, raising crops, chicken to supplement a fish diet
• Human population increased unchecked
• Forests were cleared and soil eroded; the resource base was destroyed
• The people could not build houses, boats, and did not have any fire wood
• Wars between villages became common as did slavery and cannibalism
• The society collapsed in just a few decades
Lesson: Limited resources cannot support an ever-growing human population—we are an isolated island in space.
[Photo] Almost 400 huge statues stand as mute monuments to the people who once lived on Easter Island in the Pacific Ocean's Polynesian archipelago. "Those who forget the past are condemned to repeat it."—Santayana
Ecosystem Collapse, Hypothesis II:
Europeans brought disease and took islanders away as slaves; and rats quickly multiplied after arriving with the first Polynesian settlers. The island's rat population spiked to 20 million from the years 1200 to 1300. Rats had no predators on the island other than humans, and they would have made quick work of the island's palm seeds. After the trees were gone, the island's rat population dropped off to a mere 1 million.
Modern analog: Are we the rats?

Urgent Message!
Hello…Hello…Helloooooooo…
Mass Extinction. Does it make any difference to you?
Endless studies? No action?
Does anyone hear ?
Does anyone care?
Draconian measures are needed!

[This ends LRS lectures]

Is Geobiology Important? (Course Conclusion)

[Per RB lecture rapidly delivered, no outline or slides available, mistranscription possible.]

The Past—Evolution

- Life would not have evolved on Earth at all but for geobiological interactions.
- Environmental evolution constrained what sort of life evolved and radiated.
- Microbial metabolism constrains greenhouse gas composition and therefore whether climate is equable and stable.
- Complex organisms require a narrow range of conditions.
- Terrestrial life changes planetary regulation and requires readjustment of biogeochemical changes.
- Evolution is contingent on chance environmental events [such as bolide impacts] that can cause mass extinctions and restructuring of the biota, providing opportunities for [previously non-dominant] groups such as mammals.
- Intelligent life needs a complex biosphere and stable but variable and diverse habitats in which to arise.
- Intelligent social organisms need a wide range of mineral and energy resources, many produced by geobiologic interactions.
- Were it not for geobiology, you wouldn't be here.

The Present—Society

- Agriculture depends on soil microbes…
- Fisheries depend on biogeochemical cycling of nutrients.
- Public health depends on microbial destruction of sewage and garbage.
- Coastal cities require stable sea level and therefore geobiologically regulated climate.
- Buildings, bridges, etc. are destroyed directly by organisms altering minerals including concrete, or indirectly by acids, acid rain, etc.
- Fresh water supply is regulated by plant transpiration and microbial contamination.
- Transport requires fuels (oil, gas, coal) which are geobiological products.
- Industry requires metals, many of which are concentrated by geomicrobiological processes.
- Were it not for geobiology, you wouldn't be sitting here as a group.

The Future—Environment

- The next ice-age is imminent, but may be postponed.
- Greenhouse gas products and global warming are mitigated or exaggerated by geobiological interactions.
- Toxic waste disposal is controlled by microbial degradation or enrichment.
- Size of human population is regulated by geobiological limits to productivity.
- Rapid microbial evolution produces novel pestilences which moderate the carrying capacity for humans.
- Future total nuclear war will either leave a sterilized planet or one with a prospect of an evolutionary future, depending on geobiological outcomes. For example, the radioresistant bacterium Deinococcus radiodurans.
- Long-term maintenance of atmospheric oxygen and CO_2 levels depends on geobiological controls, thus influences the future habitability of the Earth by humans in the face of an ever brightening Sun.
- In 0.5 to 1 billion years, the Sun will be so hot that large multicellular eukaryotic organisms will not be able to survive unless geobiological processes intervene.
- Without geobiology, your life as a species will be short.

Therefore, Geobiology *Is* Important.

End of Course Lectures

MCM Assessment

This course in geobiology presents important and extraordinarily diverse facts and concepts which draw on many previously established scientific disciplines—geology, evolutionary biology and phylogenetics, paleobiology and paleontology, astronomy and astrobiology, microbiology, genetics, organic and inorganic chemistry, biochemistry, mineralogy, atmospheric physics, oceanography, etc. Geobiology clearly covers a huge amount of intellectual territory, almost unlimited in its territorial claims. One might question whether the discipline is too broadly defined to be manageable or of practical scientific value. I suspect that many practitioners of some of the related disciplines named here might take exception with having their respected fields brought under the seemingly all-encompassing umbrella of geobiology. However, there is clear value in focusing specifically yet broadly on the interactions of life with the physical and chemical systems of Earth. Humans are heavily impacting and rapidly transforming our beloved planet's biosphere, generally for the worse. I believe that urgent and effective action is needed to avert global environmental and biological catastrophes, and to retard the rate of the mass extinction currently in progress. The multi-sector reforms required would surely benefit from a technically informed yet broad approach to understanding how we and other life forms interact with our planet. Thus I see the value of bringing together under one great tent these many distinguished disciplines for the purpose of saving our planet's habitability and life as we know it. Whether we term this gathering together of diverse disciplines "geobiology", or some more catchy name—perhaps *The Strategic Life Defense Consortium*—is probably unimportant.

My thanks to Professors Buick and Reinink-Smith for presenting such an informative and stimulating course.

GLOSSARY OF RELATED TOPICS

Abiogenesis

• http://en.wikipedia.org/wiki/Abiogenesis:
“Abiogenesis (Greek a-bio-genesis, "non biological origins") is the formation of life from non-living matter. Today the term is primarily used to refer to hypotheses about the chemical origin of life, such as from a 'primeval soup' or in the vicinity of hydrothermal vents, and most probably through a number of intermediate steps, such as non-living but self-replicating molecules (**biopoiesis**) [a term coined by J. D. Bernal]. The current models of abiogenesis are still being scientifically tested.”
• See also course notes above and http://en.wikipedia.org/wiki/Origin_of_life

Astrobiology

http://en.wikipedia.org/wiki/Astrobiology:
“Astrobiology ... is the interdisciplinary study of life in space, combining aspects of astronomy, biology and geology. It is focused primarily on the study of the origin, distribution and evolution of life. It is also known as exobiology (from Greek: ἔξω, exo, "outside"). The term "Xenobiology" has been used as well, but this is technically incorrect because its terminology means "biology of the foreigners". Some major astrobiological research topics include: What is life? How did life arise on Earth? What kind of environments can life tolerate? How can we determine if life exists on other planets? How often can we expect to find complex life? What will life consist of on other planets? Will it be DNA/Carbon based or based on something else? What will it look like?”

Chirality and Enantiomers

• http://en.wikipedia.org/wiki/Chirality_%28chemistry%29:
“The term **chiral** (pronounced [KAI ral]) is used to describe an object that is **non-superimposable** on its **mirror image**. In terms of chemistry, such objects are usually molecules.... The term non-superimposable distinguishes mirror images that are superimposable, such as the letter "A" and its mirror image, from those that are not [such as G]. Human hands are perhaps the most universally recognized example of chirality. The left hand is a non-superimposable mirror image of the right hand: no matter how the two hands are oriented, it is impossible for all the major features of both hands to coincide. This difference in symmetry becomes obvious if someone attempts to shake the right hand of a person using his left hand, or if a left-handed glove is placed on a right hand. Because this difference is universally known and easy to observe, many pairs of enantiomers are designated as "right- and left-handed....

The two "handednesses" (enantiomers) of a chiral molecule are sometimes referred to as **optical isomers**.

The symmetry of a molecule (or any other object) determines whether it is chiral. A molecule is **achiral** (not chiral) if and only if it has an axis of improper rotation; that is, an n-fold rotation (rotation by 360°/n) followed by a reflection in the plane perpendicular to this axis which maps the molecule onto itself. A simplified rule applies to **tetrahedrally**-bonded carbon...: if all four substituents are different, the molecule is chiral. A chiral molecule is not necessarily asymmetric, that is, devoid of any symmetry elements, as it can have, for example, rotational symmetry.

...An **optical isomer** [enantiomer] can be named by the spatial configuration of its atoms. The **D/L system** [of naming enantiomers] does this by relating the molecule to glyceraldehyde. Glyceraldehyde is chiral itself, and its two isomers are labeled D and L. Certain chemical manipulations can be performed on glyceraldehyde without affecting its configuration, and its historical use for this purpose ... has resulted in its use for nomenclature. In this system, compounds are named by analogy to glyceraldehyde, which generally produces unambiguous designations, but is easiest to see in the small biomolecules similar to glyceraldehyde. One example is the amino acid alanine: alanine has two optical isomers, and they are labeled according to which isomer of glyceraldehyde they come from. Glycine, the amino acid derived from glyceraldehyde, incidentally, has no optical activity as it is not chiral (achiral).

...For chemists, the **R [Rectus] / S [Sinistrus]** system is the most important nomenclature system... It does not involve a reference molecule...

An enantiomer can [also] be named by the direction in which it rotates the plane of **polarized light**. If it rotates the light clockwise (as seen by a viewer towards whom the light is traveling), that enantiomer is labeled (+). Its mirror-image is labeled (−).

• http://en.wikipedia.org/wiki/Enantiomer:

In chemistry, enantiomers ... are stereoisomers that are nonsuperimposable complete mirror images of each other, much as one's left and right hands are "the same" but opposite...

[D- vs. L- naming] is based on the actual geometry of each enantiomer, with the version synthesized from naturally occurring (+)-glyceraldehyde being considered the D- form."

• http://en.wikipedia.org/wiki/Racemic:

"A racemic mixture is one that has equal amounts of left- and right-handed enantiomers of a chiral molecule."

• http://en.wikipedia.org/wiki/Stereoisomer:

"Diastereomers are stereoisomers not related through a reflection operation. They are not mirror images of each other." [MCM: thus, not all steroisomers are chiral, and the term enantiomer rather than steroisomer should be used in the context of chirality.]

Cladistics

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

"Cladistics is the hierarchical classification of species based on evolutionary ancestry. Cladistics is distinguished from other taxonomic classification systems because it **focuses on evolution** (rather than focusing on similarities between species), and because it places heavy emphasis on objective, quantitative analysis. Cladistics generates diagrams called **cladograms** that represent the evolutionary tree-of-life. DNA and RNA sequencing data are used in many important cladistic efforts. **Computer programs** are widely used in cladistics, due to the highly complex nature of cladogram-generation procedures. A major contributor to this school of thought was the German entomologist Willi Hennig, who referred to it as **phylogenetic systematics** (Hennig, 1966). The word cladistics is derived from the ancient Greek κλάδος, klados, or "branch".

The starting point of cladistic analysis is a group of species and molecular, morphological, or other data characterizing those species. The end result is a tree-like relationship-diagram called a "**cladogram**". The cladogram graphically represents a hypothetical evolutionary process. Cladograms are subject to revision as additional data becomes available.

The term **evolutionary tree** is often used synonymously with cladogram. The term phylogenetic tree is sometimes used synonymously with cladogram, but others treat phylogenetic tree as a broader term that includes trees generated with a non-evolutionary emphasis.

Subtrees are Clades: In a cladogram, all organisms lie at the leaves. The two taxa on either side of a split are called sister taxa or sister groups. Each subtree, whether it contains one item or a hundred thousand items, is called a **clade**. [From en.wikipedia.org/wiki/Clade: A **clade** is a taxonomic group of organisms comprising a single common ancestor and all the descendants of that ancestor. Any such group is considered to be a **monophyletic group** of organisms, and can be represented by both a phylogenetic analysis, as in a tree diagram, and by a cladogram, or simply as a taxonomic reference.]

2-Way vs 3-Way Forks: Many cladists require that all forks in a cladogram be 2-way forks. Some cladograms include 3-way or 4-way forks when the data is insufficient to resolve the forking to a higher level of detail...

Depth of a Cladogram: If a cladogram represents N species, the number of levels (the "depth") in the cladogram is on the order of $\log_2(N)$. For example, if there are 32 species of deer, a cladogram representing deer will be around 5 levels deep (because $2^5=32$). A cladogram representing the complete tree of life, with about 10 million species, would be about **23 levels deep**. This formula gives a lower limit: in most cases the actual depth will be a larger value because the various branches of the cladogram will not be uniformly deep. Conversely, the depth may be shallower if forks larger than 2-way forks are permitted.

Extinct Species in Cladograms: Cladistics makes no distinction between extinct and non-extinct species, and it is appropriate to include extinct species in the group of organisms being analyzed. Cladograms that are based on DNA/RNA generally do not include extinct species because DNA/RNA samples from extinct species are rare. Cladograms based on morphology, especially morphological characteristics that are preserved in fossils, are more likely to include extinct species.

Time Scale of a Cladogram: A cladogram tree has an implicit time axis, with time running forward from the base of the tree to the leaves of the tree. If the approximate date (for example, expressed as millions of years ago) of all the evolutionary forks were known, those dates could be captured in the cladogram. Thus, the time axis of the cladogram could be assigned a time scale (e.g. 1 cm = 1 million years), and the forks of the tree could be graphically located along the time axis. Such cladograms are called **scaled cladograms**. Many cladograms are not scaled along the time axis, for a variety of reasons...

Cladistics compared with Linnaean taxonomy: Prior to the advent of Cladistics, most taxonomists used Linnaean taxonomy to organizing lifeforms. That traditional approach used several fixed levels of a hierarchy, such as Kingdom, Phylum, Class, Order, and Family. Cladistics does not use those terms, because one of the fundamental premises of Cladistics is that the evolutionary tree is very deep and very complex, and **it is not meaningful to use a fixed number of levels**. Linnaean taxonomy insists that groups reflect phylogenies, but (in contrast to cladistics) allows both monophyletic and paraphyletic groups as taxa. Although, since the early 20th century, Linnaeian taxonomists generally attempted to make genus- and lower-level taxa monophyletic (even though the word might not have been used). [See table for specifics]

Monophyletic groups encouraged: Many cladists discourage the use of **paraphyletic** groups because they detract from cladisitcs' emphasis on clades (monophyletic groups). In contrast, proponents of the use of paraphyletic groups argue that any dividing line in a cladogram creates both a monophyletic section above and a paraphyletic section below. They also contend that paraphyletic taxa are necessary for classifying earlier sections of the tree – for instance, the early vertebrates that would someday evolve into the family Hominidae cannot be placed in any other monophyletic family. They also argue that paraphyletic taxa provide information about significant changes in organisms' morphology, ecology, or life history – in short, that both paraphyletic groups and clades are valuable notions with separate purposes.

Each clade is distinguished by a set of characteristics that appear in its members, but not in the other forms from which it diverged. These **identifying characteristics of a clade are called synapomorphies** (shared, derived characters). For instance, hardened front wings (elytra) are a synapomorphy of beetles, while circinate vernation, or the unrolling of new fronds, is a synapomorphy of ferns. [A **synapomorphy** is present in the last common ancestor of a species group.]

Definitions

A **character state** that is present in both the **outgroups** and in the **ancestors** is called a **plesiomorphy** (meaning "close form", also called an **ancestral state** [i.e., a character state that was present before the last common ancestor of the species group]). A character state that occurs only in later descendants is called an **apomorphy** (meaning "separate form", also called a **"derived" state**) for that group. The adjectives **plesiomorphic** and **apomorphic** are used instead of "primitive" and "advanced" to avoid placing value judgments on the evolution of the character states, since both may be advantageous in different circumstances. It is not uncommon to refer informally to a collective set of plesiomorphies as a ground plan for the clade or clades they refer to.

A **homoplasy** is a character [such as "presence of wings"] that is shared by multiple species due to some cause other than common ancestry [and should be avoided in constructing cladograms].

Several more terms are defined for the description of cladograms and the positions of items within them. A species or clade is **basal** to another clade if it holds more plesiomorphic characters than that other clade. Usually a basal group is very species-poor as compared to a more derived group. It is not a requirement that a basal group be extant. For example, when considering birds and mammals together, neither is basal to the other: both have many derived characters.

A clade or species located within another clade can be described as **nested** within that clade.

A **clade** is an ancestor species and all of its decencents. A **monophyletic group** is a clade. A **paraphyletic group** is [an otherwise] monophyletic group that excludes some of the descendants (e.g. reptiles are sauropsids excluding birds). Most cladists discourage the use of paraphyletic groups. A **polyphyletic group** is a group consisting of members from two non-overlapping monophyletic groups (e.g. flying animals [birds and bats]). Most cladists discourage the use of polyphyletic groups.

There are three ways to define a clade for use in a cladistic taxonomy:

- **Node-based**: the most recent common ancestor of A and B and all its descendants.
- **Stem-based**: all descendants of the oldest common ancestor of A and B that is not also an ancestor of Z.
- **Apomorphy-based**: the most recent common ancestor of A and B possessing a certain apomorphy (derived character), and all its descendants. This definition is generally discouraged by most cladists.

Cyanobacteria

• http://en.wikipedia.org/wiki/Cyanobacteria:
"Cyanobacteria (Greek: κυανός (kyanós) = blue + bacterium) also known as Cyanophyta is a phylum (or "division") of Bacteria that obtain their energy through photosynthesis. They are often referred to as blue-green algae, although they are in fact prokaryotes, not algae. The description is primarily used to reflect their appearance and ecological role rather than their evolutionary lineage. The name "cyanobacteria" comes from the colour of the bacteria, cyan; the bacteria do not use or produce cyanide whose chemical prefix is cyano-.

Putative fossil traces of cyanobacteria have been found from around 3.8 billion years ago (Ga). See: Stromatolite. They are a significant component of the marine nitrogen cycle and an important primary producer in many areas of the ocean. Their ability to perform oxygenic (plant-like) photosynthesis is thought to have converted the early reducing atmosphere into an oxidizing one, which dramatically changed the life forms on Earth and provoked an explosion of biodiversity."
• http://tolweb.org/tree?group=Cyanobacteria&contgroup=Eubacteria:
Containing group: **Eubacteria**
[MCM: thus cyanobacteria are considered bacteria, not archaea]

DNA (Deoxyribonucleic Acid) and RNA (Ribonucleic Acid)

http://en.wikipedia.org/wiki/Dna:
"Chemically, DNA is a long polymer of simple units called **nucleotides**, with a backbone made of **sugars** and **phosphate groups** [that are] joined by ester bonds. Attached to each sugar is one of four types of molecules called **bases** [MCM: a purine A or G or pyrimidine C or T]. It is the sequence of these four bases along the backbone that encodes information. This information is read using the genetic code, which specifies the sequence of the amino acids within proteins. The code is read by copying stretches of DNA into the related nucleic acid RNA, in a process called transcription. Most of these RNA molecules are used to synthesize proteins, but others are used directly in structures such as ribosomes and spliceosomes....

DNA is a long polymer made from repeating units called **nucleotides**. The DNA chain is 22 to 26 Ångströms wide (2.2 to 2.6 nanometres), and one nucleotide unit is 3.3 Ångstroms (0.33 nanometres) long. Although each individual repeating unit is very small, DNA polymers can be enormous molecules containing millions of nucleotides. For instance, the largest human chromosome, chromosome number 1, is 220 million base pairs long.

In living organisms, DNA does not usually exist as a single molecule, but instead as a tightly-associated pair of molecules. These two long strands entwine like vines, in the shape of a **double helix**. The nucleotide repeats contain both the segment of the backbone of the molecule, which holds the chain together, and a base, which interacts with the other DNA strand in the helix. In general, a base linked to a sugar is called a **nucleoside** and a base linked to a sugar and one or more phosphate groups is called a **nucleotide**. If multiple nucleotides are linked together, as in DNA, this polymer is referred to as a **polynucleotide**.

The backbone of the DNA strand is made from alternating phosphate and sugar residues. The sugar in DNA is **2-deoxyribose**, which is a pentose (five carbon) sugar (whereas in RNA it is **ribose**).

The sugars are joined together by phosphate groups that form **phosphodiester bonds** between the third and fifth carbon atoms of adjacent sugar rings. [564] [565]

These asymmetric bonds mean a strand of **DNA has a direction**. In a double helix the direction of the nucleotides in one strand is opposite to their direction in the other strand. This arrangement of DNA strands is called **antiparallel**. The asymmetric ends of DNA strands are referred to as the **5′ (five prime)** and **3′ (three prime)** ends. One of the major differences between DNA and RNA is the sugar, with 2-deoxyribose being replaced by the alternative pentose sugar **ribose** in RNA.

The DNA double helix is stabilized by hydrogen bonds between the bases attached to the two strands. The four bases found in DNA are **adenine** (abbreviated A), **cytosine** (C), **guanine** (G) and **thymine** (T) [not thymidine]. These four bases ... are attached to the sugar/phosphate to form the complete nucleotide...

These bases are classified into two types; adenine and guanine are fused five- and six-membered heterocyclic compounds called **purines**, while cytosine and thymine are six-membered rings called **pyrimidines**. A fifth pyrimidine base, called **uracil** (U), usually **takes the place of thymine in RNA** and differs from thymine by lacking a methyl group on its ring. Uracil is not usually found in DNA, occurring only as a breakdown product of cytosine, but a very rare exception to this rule is a bacterial virus called PBS1 that contains uracil in its DNA. In contrast, following synthesis of certain RNA molecules, a significant number of the uracils are converted to thymines by the enzymatic addition of the missing methyl group. This occurs mostly on structural and enzymatic RNAs like transfer RNAs and ribosomal RNA."

Entropy and Free Energy, and Their Relationship To Life

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

"Much writing and research has been devoted to the relationship between the thermodynamic quantity entropy and the evolution of life. In 1910, American historian Henry Adams printed and distributed to university libraries and history professors the small volume A Letter to American Teachers of History proposing a theory of history based on the second law of thermodynamics and the principle of entropy. The 1944 book *What is Life?* by Nobel-laureate physicist Erwin Schrödinger served largely to stimulate this research. In this book, Schrödinger states that life feeds on negative entropy, or negentropy as it is sometimes called. Recent writings have utilized the concept of Gibbs free energy to elaborate on this issue....

Later, building on this premise, in the famous 1944 book *What is Life?*, Nobel-laureate physicist Erwin Schrödinger theorizes that life, contrary to the general tendency dictated by the Second law of thermodynamics, decreases or maintains its entropy by feeding on negative entropy. In a note to *What is Life?*, however, Schrödinger explains his usage of this term:

> "Let me say first, that if I had been catering for them [physicists] alone I should have let the discussion turn on free energy instead. It is the more familiar notion in this context. But this highly technical term seemed linguistically too near to energy for making the average reader alive to the contrast between the two things."

This is what is argued to differentiate life from other forms of matter organization. In this direction, although life's dynamics may be argued to go against the tendency of second law, which states that the entropy of an isolated system tends to increase, it does not in any way conflict or invalidate this law, because the principle that entropy can only increase or remain constant applies only to a closed system which is adiabatically isolated, meaning no heat can enter or leave. Whenever a system can exchange either heat or matter with its environment, an entropy decrease of that system is entirely compatible with the second law. The common justification for this argument, for example, according to renowned chemical engineer Kenneth Denbigh, from his 1955 book The Principles of Chemical

---

[564] **Esters** "are often derived from carboxylic acids. A carboxylic acid contains the -COOH group, and in an carboxylic acid ester the hydrogen in this group is replaced by a hydrocarbon group of some kind [MCM: so that the linkage is C-O-C]. The hydrocarbon group could be an alkyl group like methyl or ethyl, or one containing a benzene ring like phenyl."
http://www.chemguide.co.uk/organicprops/esters/background.html

[565] **Phosphodiester bonds**: "A phosphodiester bond is a group of strong covalent bonds between the phosphorus atom in a phosphate group and two other molecules over two ester bonds."
(http://en.wikipedia.org/wiki/Phosphodiester_bond)
[MCM: In DNA, the 5'-C projecting outside the ring of one deoxyribose connects to the 3'-C of an adjacent deoxyribose—the linkage is C-O-P-O-C.]

Equilibrium, is that "living organisms are open to their environment and can build up at the expense of foodstuffs which they take in and degrade."

In 1964, James Lovelock was among a group of scientists who were requested by NASA to make a theoretical life detection system to look for life on Mars during the upcoming space mission. When thinking about this problem, Lovelock wondered "how can we be sure that Martian life, if any, will reveal itself to tests based on Earth's lifestyle?" To Lovelock, the basic question was "What is life, and how should it be recognized?" When speaking about this puzzling issue with some of his colleagues at the Jet Propulsion Laboratory, he was asked, well what would you do to look for life on Mars? To this Lovelock replied: "I'd look for an entropy reduction, since this must be a general characteristic of life."

Thus, according to Lovelock, to find signs of life, one must look for a "reduction or a reversal of entropy."

Gibbs free energy

[see also http://en.wikipedia.org/wiki/Gibbs_free_energy]

"In recent years, the thermodynamic interpretation of evolution in relation to entropy has begun to utilize the concept of the Gibbs free energy, rather than entropy [S]. This is because biological processes on Earth take place at roughly constant temperature and pressure, a situation in which the Gibbs free energy is an especially useful way to express the second law of thermodynamics. The Gibbs free energy G is given by:

$\Delta G \equiv \Delta H - T^*\Delta S$

[H is the enthalpy (SI Units: joules), T is the temperature (SI Units: kelvins)]. The minimization of the Gibbs free energy is a form of the principle of minimum energy, which follows from the entropy maximization principle for closed systems. Moreover, the Gibbs free energy equation, in modified form, can be utilized for open systems when chemical potential terms are included in the energy balance equation. In a popular 1982 textbook Principles of Biochemistry by noted American biochemist Albert Lehninger, it is argued that the order produced within cells as they grow and divide is more than compensated for by the disorder they create in their surroundings in the course of growth and division. In short, according to Lehninger, "living organisms preserve their internal order by taking from their surroundings free energy, in the form of nutrients or sunlight, and returning to their surroundings an equal amount of energy as heat and entropy."

In 1998, noted Russian physical chemist Georgi Gladyshev, in his book Thermodynamic Theory of the Evolution of Living Beings, argues that evolution of living beings is governed by the tendency for quasi-equilibrium, semi-closed, hierarchical living systems to evolve in the direction that tends to minimize the Gibbs free energy of formation of each structure.[7][8] Variations of the Gibbs function of formation of a thermodynamic system at any stage of the evolution, for instance ontogenesis and phylogenesis, such as a social system, according to Gladyshev, "can be calculated by means of thermodynamic methods." Gladyshev calls this a form of sociological thermodynamics.

Similarly, according to the chemist John Avery, from his recent 2003 book Information Theory and Evolution, we find a presentation in which the phenomenon of life, including its origin and evolution, as well as human cultural evolution, has its basis in the background of thermodynamics, statistical mechanics, and information theory. The (apparent) paradox between the second law of thermodynamics and the high degree of order and complexity produced by living systems, according to Avery, has its resolution "in the information content of the Gibbs free energy that enters the biosphere from outside sources."

Extremophile

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

"An extremophile is an organism that thrives in and may even require physically or geochemically extreme conditions that are detrimental to the majority of life on Earth. Most extremophiles are microbes. The domain Archaea contains renowned examples, but extremophiles are present in numerous and diverse genetic lineages of both bacteria and archaeans. Furthermore, it is erroneous to use the term extremophile to encompass all archaeans, as some are mesophilic. Neither are all extremophiles unicellular; protostomes found in similar environments include the Pompeii worm, the psychrophilic Grylloblattodea (insects), Antarctic krill (a crustacean) and the water bear.

[Types of Extremeophiles include:]

Acidophile: An organism with an optimum pH level at or below pH 3.

Hyperthermophile: An organism that can thrive at temperatures between 80-121 °C, such as those found in hydrothermal systems.
Thermophile: An organism that can thrive at temperatures between 60-80 °C."

Gaia Hypothesis

• http://en.wikipedia.org/wiki/Gaia_hypothesis:
"The Gaia hypothesis is an ecological hypothesis that proposes that living and nonliving parts of the Earth are viewed as a complex interacting system that can be thought of as a single organism. Named after the Greek earth goddess, this hypothesis postulates that all living things have a regulatory effect on the Earth's environment that promotes life overall.

The Gaia hypothesis was first scientifically formulated in the 1960s by the independent research scientist Dr. James Lovelock, as a consequence of his work for NASA on methods of detecting life on Mars.[1][2] He initially published the Gaia Hypothesis in journal articles in the early 1970s[3][4] followed by a popularising 1979 book Gaia: A new look at life on Earth. He named this self-regulating living system after the Greek goddess Gaia, using a suggestion from the novelist William Golding, who was living in the same village as Lovelock at the time (Bowerchalke, Wiltshire, UK). The Gaia Hypothesis has since been supported by a number of scientific experiments[5] and provided a number of useful predictions,[6] and hence is properly referred to as the Gaia Theory.

Since 1971, the noted microbiologist Dr. Lynn Margulis has been Lovelock's most important collaborator in developing Gaian concepts[7].

Until 1975 the hypothesis was almost totally ignored. An article in the New Scientist of February 15, 1975, and a popular book length version of the theory, published as The Quest for Gaia, began to attract scientific and critical attention to the hypothesis. The theory was then attacked by many mainstream biologists. Championed by certain environmentalists and climate scientists, it was vociferously rejected by many others, both within scientific circles and outside them."

• MCM note: An interesting parallel can be seen with the alien planet Solaris envisioned in the novel by Stanisław Lem:
http://en.wikipedia.org/wiki/Solaris_%28novel%29:
"The planet, called Solaris, is covered with a so-called "ocean" that is really a single organism covering the entire surface. The ocean shows signs of a vast but strange intelligence, which can create physical phenomena in a way that science has difficulty explaining. The alien mind of Solaris is so inconceivably different from human consciousness that all attempts at communication are doomed (the "alienness" of aliens was one of Lem's favourite themes; he was scornful about portrayals of aliens as humanoid)."

Geologic Time Scales and Stratigraphy

• http://pubs.usgs.gov/fs/2007/3015/fs2007-3015.pdf:
The definitive publication on time scales "**Divisions of Geologic Time**" by the USGS, last updated 3/2007. "For consistency purposes, the USGS Geologic Names Committee (GNC...) and the Association of American State Geologists (AASG) developed **Divisions of Geologic Time**. The **Divisions of Geologic Time** is based on the time scale in STA7 ... ["**Stratigraphic Nomenclature And Description**". Hansen, 1991, http://www.nwrc.usgs.gov/lib/lib_sta.htm, p. 59] and updates it with the unit names and boundary age estimates ratified by the **International Commission on Stratigraphy** (ICS)... Advances in stratigraphy and geochronology require that any time scale be periodically updated. Therefore, the Divisions of Geologic Time is dynamic and will be modified as needed to include accepted changes of unit names and boundary age estimates."
• http://www.stratigraphy.org/gssp.htm:
Presents table called **Overview Of Global Boundary Stratotype Sections And Points** (GSSPs) with details of stratigraphic boundaries, Derivation of ages, Principal correlative events, etc., prepared by James Ogg of International Commission on Stratigraphy [ICS]), 2004.
• http://en.wikipedia.org/wiki/Geologic_time_scale:
This page also has excellent diagrams.
• http://www.stratigraphy.org/chron.htm:
Chronostratigraphic unit: A body of rocks that includes all rocks formed during a specific interval of geologic time, and only those rocks formed during that time span. Chronostratigraphic units are bounded by **synchronous horizons**.
[MCM: The following table derived from this article compares the chronostratigraphic unit with the

geochronologic Unit

Chronostratigraphic unit	Geochronologic unit
Eonothem	Eon
Erathem	Era
System	Period
Series	Epoch
Stage	Age
Substage	Subage or age]

"Position within a chronostratigraphic unit is expressed by adjectives indicative of position such as:basal, lower, middle, upper, etc.; position within a geochronologic unit is expressed by temporal adjectives such as:early, middle, late, etc."

Habitable Zone (Circumstellar and Galactic)

http://en.wikipedia.org/wiki/Habitable_zone:
"In astronomy a habitable zone (HZ) is a region of space where conditions are favorable for life as it can be found on Earth. There are two regions that must be favorable, one within a solar system and the other within the galaxy. Planets and moons in these regions are the likeliest candidates to be habitable and thus capable of bearing extraterrestrial life similar to our own. Astronomers believe that life is most likely to form within the circumstellar habitable zone (CHZ) within a solar system, and the galactic habitable zone (GHZ) of the larger galaxy (though research on the latter point remains nascent). The HZ may also be referred to as the "life zone", "Green Belt" or the "Goldilocks Zone" (because it's neither too hot nor too cold, but "just right"). In our own solar system, the HZ is thought to extend from a distance of 0.95 to 1.37 astronomical units.[566]

Gliese 581 c, the second planet of the red dwarf star Gliese 581 (approximately 20 light years distance from Earth), appears to be the best example of an extrasolar planet which orbits in the theoretical habitable zone of space surrounding its star."

Circumstellar habitable zone
(see the diagram plotting the ratio of the mass of the star to the mass of the Sun against the orbital distance in AU; plus formulas).
Within a solar system, it is believed a planet must lie within the habitable zone in order to sustain life. The circumstellar habitable zone (or ecosphere) is a notional spherical shell of space surrounding stars where the surface temperatures of any planets present might maintain liquid water. Liquid water may be vital for life because of its role as the solvent needed for biochemical reactions. In 1959, physicists Philip Morrison and Giuseppe Cocconi described the zone in a SETI research paper. In 1961, Frank Drake popularized the concept in his Drake equation."

The galactic habitable zone:
• http://en.wikipedia.org/wiki/Habitable_zone:
"The location of a solar system within the galaxy must also be favorable to the development of life, and this leads to the concept of a galactic habitable zone.

To harbor life, a solar system must be close enough to the galactic center that a sufficiently high level of heavy elements exist to favor the formation of rocky planets. Heavier elements must be present, since they form complex molecules of life, such as iron as the foundation for hemoglobin and iodine for the thyroid gland.

On the other hand, the solar system must be far enough from the galaxy center to avoid hazards such as impacts from comets and asteroids, close encounters with passing stars, and outbursts of radiation from supernovae and from the black hole at the center of the galaxy. The effect of radiation from supernovae on living organisms is not clear. Presumably, large amounts of radiation, which occur near the center of a galaxy, make formation of complex molecules more difficult.

Also, studies have shown that regions in which the level of heavy elements, or metallicity, is very high seem to be more likely to harbor massive planets orbiting close to their star. The gravitational tidal forces induced by such planets would distort the orbit and surface shape of any Earth-mass planets, which could destroy them before life has a chance to form.[citation needed] For these reasons, there are many uncertainties in determining where the habitable zone in a galaxy may lie.

---

[566] **Astronomical unit (AU)**: Equivalent to 93 million miles, the average distance of Earth from Sol (the Sun).

In our galaxy (the Milky Way), the GHZ is currently believed to be a slowly expanding region approximately 25,000 light years (8 kiloparsecs) from the galactic core, containing stars roughly 4 billion to 8 billion years old. Other galaxies differ in their compositions, and may have a larger or smaller GHZ – or none at all. Future technologies may enable us to determine the number and location of Earth-type planets in the Milky Way, greatly refining our understanding of the Galactic habitable zone."

• Guillermo Gonzalez, Donald Brownlee, Peter Ward. "The Galactic Habitable Zone: Galactic Chemical Evolution". *Icarus* 152, 185–200 (2001), accessed at http://isotope.colorado.edu/~astr5835/Gonzalez%20et%20al.%202001.pdf:

"We propose the concept of a "Galactic Habitable Zone" (GHZ). Analogous to the Circumstellar Habitable Zone (CHZ), the GHZ is that region in the Milky Way where an Earth-like planet can retain liquid water on its surface and provide a long-term habitat for animal-like aerobic life. In this paper we examine the dependence of the GHZ on Galactic chemical evolution. The single most important factor is likely the dependence of terrestrial planet mass on the metallicity of its birth cloud.We estimate, very approximately, that a metallicity at least half that of the Sun is required to build a habitable terrestrial planet. The mass of a terrestrial planet has important consequences for interior heat loss, volatile inventory, and loss of atmosphere. A key issue is the production of planets that sustain plate tectonics, a critical recycling process that provides feedback to stabilize atmospheric temperatures on planets with oceans and atmospheres. Due to the more recent decline from the early intense star formation activity in the Milky Way, the concentration in the interstellar medium of the geophysically important radioisotopes ^{40}K, $^{235;238}U$, and ^{232}Th has been declining relative to Fe, an abundant element in the Earth. Also likely important are the relative abundances of Si and Mg to Fe, which affects the mass of the core relative to the mantle in a terrestrial planet. All these elements and isotopes vary with time and location in the MilkyWay; thus, planetary systems forming in other locations and times in the MilkyWay with the same metallicity as the Sun will not necessarily form habitable Earth-like planets. As a result of the radial Galactic metallicity gradient, the outer limit of the GHZ is set primarily by the minimum required metallicity to build large terrestrial planets. Regions of the Milky Way least likely to contain Earth-mass planets are the halo (including globular clusters), the thick disk, and the outer thin disk. The bulge should contain Earth-mass planets, but stars in it have a mix of elements different from the Sun's. The existence of a luminosity–metallicity correlation among galaxies of all types means that many galaxies are too metal-poor to contain Earth-mass planets. Based on the observed luminosity function of nearby galaxies in the visual passband, we estimate that (1) the Milky Way is among the 1.3% most luminous (and hence most metal-rich) galaxies and (2) about 23% of stars in a typical ensemble of galaxies are more metal-rich than the average star in the MilkyWay. The GHZ zone concept can be easily extrapolated to the universe as a whole, especially with regard to the changing star formation rate and its effect on metallicity and abundances of the long-lived radioisotopes."

Planetary Habitability

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

"Planetary habitability is the measure of a planet's or a natural satellite's potential to develop and sustain life. As the existence of life beyond Earth is currently uncertain, planetary habitability is largely an extrapolation of conditions on Earth and the characteristics of the Sun and solar system which appear favorable to life's flourishing—in particular those factors that have sustained complex, multicellular organisms and not just simpler, unicellular creatures. Research and theory in this regard is a component of planetary science and the emerging discipline of astrobiology.

The only absolute requirement for life is an energy source, but the notion of planetary habitability implies that many other geophysical, geochemical, and astrophysical criteria must be met before an astronomical body can support life. In its astrobiology roadmap, NASA has defined the principal habitability criteria as "extended regions of liquid water, conditions favorable for the assembly of complex organic molecules, and energy sources to sustain metabolism."

The idea that planets beyond Earth might host life is an ancient one, though historically it was framed by philosophy as much as physical science.a The late 20th century saw two breakthroughs in the field. The observation and robotic exploration of other planets and moons within the solar system has provided critical information on defining habitability criteria and allowed for substantial geophysical comparisons between the Earth and other bodies. The discovery of extrasolar planets, beginning in the early 1990s and accelerating thereafter, has provided further information for the study of possible extraterrestrial life. Most importantly, it confirmed that the Sun is not unique among stars in hosting planets and expanded habitability research horizon beyond our own solar system."

This is an extensive article, which includes the key diagram relating solar size to planet's orbital radius.

Isotope Abundances, Isotope Fractionation, Delta Notation, and Reference Standards

• from *Atomic Weights Of The Elements/Review 2000: IUPAC Technical Report).* J. R. De Laeter et al [where IUPAC = International Union Of Pure And Applied Chemistry]:
"For each of the chemical elements, **E**, CAWIA [Commission on Atomic Weights and Isotopic Abundances] compiles atomic weights, $\boldsymbol{A_r}$**(E)**…**Abundances** of isotopes, $\boldsymbol{^i}$**E**, can be represented as **mole fractions**, $\boldsymbol{x}$**(^{i}E)**, where *i* is the mass number of the isotope. $A_r(^i\mathrm{E})$ is its relative mass." "… the decision by IUPAC and the International Union of Pure and Applied Physics (IUPAP), to adopt a new atomic-weight scale based on $\boldsymbol{A_r(^{12}C) = 12}$"… "as early as 1939, it was shown that the $\boldsymbol{n(^{13}C)/n(^{12}C)}$ ratios in various samples of C varied by up to 5 % of that ratio. The atomic weight of C is therefore dependent on the source of the material used in the analysis, and on the extent of C isotope fractionation in nature." "The **equilibrium isotope fractionation factor** is given by: $\boldsymbol{\alpha_{a/b} = R_a / R_b}$ where a and b are two chemical species in isotopic equilibrium and ***R* is the abundance ratio of two isotopes of an element** [$R = n(^i\mathrm{E})/n(^j\mathrm{E})$, where ^{i}E and ^{j}E typically are the heavier and lighter isotopes of an element, respectively]".... [MCM: note that this ratio does not have in the denominator all isotopes of the element.] "Because natural variations in the isotopic compositions of the elements commonly are small and because the differences commonly are more useful than the actual values, several different expressions have been used to amplify the differences and to obviate the need for "absolute" measurements for reporting purposes. Isotopic measurements of elements exhibiting isotope fractionation commonly are given with respect to a δ **(delta) scale** defined by: $\boldsymbol{\delta(^i\mathrm{E})_S = [R_S / R_{RM}] - 1}$ where R_S and R_{RM}, refer to the isotope-abundance ratios $n(^i\mathrm{E})/n(^j\mathrm{E})$ in a sample, S, and a **reference material, RM**, respectively.... Delta values commonly are reported in parts per thousand, or per mill (δ **x 1000 ‰**)"

"Isotope-abundance values that are free from all known sources of bias within stated uncertainties are referred to as **"absolute" isotope abundances**, and they can be determined by "calibrating" the mass spectrometer by means of gravimetrically measured, synthetic mixtures of materials in which an isotope is enriched (or depleted) by a known or measurable factor."

"For some elements, including many with low atomic numbers, the real isotope-abundance variations are much larger than the uncertainties of "absolute" isotope-abundance measurements. In such cases, the uncertainties in the standard atomic weights cannot be reduced by improved measurements."

"Relative measurements of variations in $n(^2H)/n(^1H)$ are made by comparison to the isotopic reference material **Vienna standard mean ocean water (VSMOW)**. A positive sign for $\delta(^2H)$ indicates that the sample is enriched in the isotope of higher mass compared to VSMOW."

HYDROGEN: "The currently accepted "best measurement" of the "absolute" isotopic composition of H from a single natural source was performed on **VSMOW** (distributed by the IAEA and NIST), the reference material endorsed by CAWIA as the basis of the delta (δ) scale for relative isotope-ratio measurements. According to this measurement, VSMOW has a mole fraction of ^{2}H = 0.000 155 74(5), corresponding to $A_r(H_{VSMOW})$ = 1.007 981 75(5)."

CARBON: "The ^{12}C isotope has served since 1960 as the scale-determining reference for the definition of the unified atomic mass unit and is the basis of all atomic weights. The zero value for the delta scale used in relative isotope-ratio measurements of C since the 1950s was based on a sample of fossil marine carbonate (**Belemnitella Americana**, **Peedee Formation**, Cretaceous Period, South Carolina, also known as **PDB**). Until 1990, the "best measurement" from a single natural source was attributed to Craig for an evaluation of a measurement by Nier on CO_2 from a Solenhofen limestone sample. For the "absolute" $n(^{13}C)/n(^{12}C)$ ratio in the PDB standard, Craig adopted a value of 0.011 2372(300), corresponding to a ^{13}C mole fraction of 0.01111(3) and an A_r(C) value of 12.011 15(3)…"

NITROGEN: “The primary reference material for the relative abundance measurements of N isotopes is **atmospheric N_2**, which is homogeneous with respect to analytical uncertainties and is assigned a δ ^{15}N value of 0 ‰... CAWIA subsequently recommended adoption of 272 exactly for the n(^{14}N)/n(^{15}N) ratio corresponding to a δ ^{15}N value of 0 ‰.

OXYGEN: “... The best “absolute” measurement of the complete isotopic composition of O in atmospheric O^2 is that of Nier, which yielded values of 0.997 587, 0.000 374, and 0.002 039 for the mole fractions of ^{16}O, ^{17}O, and ^{18}O, respectively. Those values correspond to A_r(O) = 15.999 376 when calculated with current atomic masses... The best measurement of the partial isotopic composition of O in water, according to CAWIA, is given by Baertschi, who obtained a value of 0.002 005 20(45) for n(^{18}O)/n(^{16}O) in the **VSMOW reference material**. For several years, the isotopic composition of VSMOW was obtained by combining Baertschi’s] n(^{18}O)/n(^{16}O) ratio with a value of 0.000 372(4) for n(^{17}O)/n(^{16}O), which was derived from Nier’s earlier data by assuming that the relative fractionation of the isotopes is governed by the relative mass differences, such that [n(^{17}O)/n(^{16}O)]s/[n(^{17}O)/n(^{16}O)]RM = {[n(^{18}O)/n(^{16}O)]$_s$/[n(^{18}O)/n(^{16}O)]$_{RM}$}$^{0.5}$, where s and RM refer to the sample and reference material, respectively. More recently, Baertschi’s n(^{18}O)/n(^{16}O) ratio has been combined with a new value of 0.000 3799(8) for n(^{17}O)/n(^{16}O), recommended by Li et al. [124] on the basis of new measurements, to obtain the “best measurement” of the total isotopic composition of O in a water sample (VSMOW).

• from http://www4.nau.edu/cpsil/isotopes.htm:
“Stable isotope abundances are expressed as the ratio of the two most abundant isotopes in the sample compared to the same ratio in an international standard, using the 'delta' (δ) notation. Because the differences in ratios between the sample and standard are very small, they are expressed as parts per thousand or 'per mil' (‰) deviation from the standard. For example, for carbon:

$$\delta^{13}C_{sample} = \{ [(^{13}C/^{12}C_{sample}) / (^{13}C/^{12}C_{standard})] - 1 \} \times 1000$$

By definition, the standard is defined as 0‰. For carbon, the international standard is **Pee Dee Belemnite**, a carbonate formation, whose generally accepted absolute ratio of ^{13}C/^{12}C is 0.0112372. Materials with ratios of ^{13}C/^{12}C > 0.00112372 have positive delta values, and those with ratios of ^{13}C/^{12}C < 0.00112372 have negative delta values. The table below shows the international standards and their absolute isotope ratios for the 5 environmental isotopes. Some elements, such as oxygen and hydrogen, have more than one international standard.

Element	δ Value	Ratio Measured (R)	International Standards	R, International Standards
Hydrogen	δ D [deuterium]	^{2}H / ^{1}H	Vienna Standard Mean Ocean Water (VSMOW)	0.00015575
	δ D	^{2}H / ^{1}H	Standard Light Antarctic Precipitation (SLAP)	0.000089089
Carbon	δ ^{13}C	^{13}C/^{12}C	Vienna Pee Dee Belemnite (VPDB) [originally a Cretaceous fossil]	0.0112372
Nitrogen	δ ^{15}N	^{15}N/^{14}N	Air	0.003676
Oxygen	δ ^{18}O	^{18}O/^{16}O	Vienna Standard Mean Ocean Water (VSMOW)	0.0020052
		^{18}O/^{16}O	Vienna Pee Dee Belemnite (VPDB)	0.0020672
		^{18}O/^{16}O	Standard Light Antarctic Precipitation (SLAP)	0.0018939
Sulfur	δ ^{34}S	^{34}S/^{32}S	Canyon Diablo Triolite (CDT) [a meteorite]	0.045005

• from http://www.uga.edu/~sisbl/stable.html:
Note that this source defines δ^{15}N slightly differently by including the sum of 2 or more isotopes in the denominator of the ratios employed. It defines

Atom Percent = At%^{15}N = (^{15}N/(^{14}N + ^{15}N) x 100

Delta δ^{15}N = (R_{sample} - R_{std})/R_{std}

where R = At%^{15}N / At%^{14}N

Metallicity (Astronomical)

http://en.wikipedia.org/wiki/Metallicity:
In astronomy and physical cosmology, the metallicity of an object is the proportion of its matter made up of chemical elements other than hydrogen and helium. (This terminology is used differently to the usual meaning of the word 'metal' - since on the grandest of scales the universe is overwhelmingly composed of hydrogen and helium, astronomers label all the heavier elements "metal"). For example, a nebula rich in carbon compounds would be called "metal-rich", even though carbon, oxygen & fluorine are not considered metals in other contexts.

The metallicity of an astronomical object may provide an indication of its age. When the universe first formed, according to the Big Bang theory, it consisted almost entirely of hydrogen which, through primordial nucleosynthesis, created a sizeable proportion of helium and only trace amounts of lithium. The first stars, referred to as Population III, had virtually no metals at all. These stars were incredibly massive and, during their lives, created the elements up to iron in the Periodic Table via nucleosynthesis. They subsequently died in spectacular supernovae which dispersed those elements throughout the universe. As of 2007, no Population III stars have been found; rather, their existence is inferred in current models of the origin of the universe. The next generation of stars was born out of those materials left by the death of the first. The oldest observed stars, known as Population II, have very low metallicities; as subsequent generations of stars were born they became more metal-enriched, as the gaseous clouds from which they formed received the metal-rich dust manufactured by previous generations. As those stars died, they returned metal-enriched material to the interstellar medium via planetary nebulae and supernovae, enriching the nebulae out of which the newer stars formed ever further. These youngest stars, including the Sun, therefore have the highest metal content, and are known as Population I stars.

Across the Milky Way, metallicity is higher in the galactic centre and decreases as one moves outwards. The gradient in metallicity is attributed to the density of stars in the galactic-centre: there are more stars in the centre of the galaxy and so, over time, more metals have been returned to the interstellar medium and incorporated into new stars. By a similar mechanism, larger galaxies tend to have a higher metallicity than their smaller counterparts. In the case of the Magellanic Clouds, two small irregular galaxies orbiting the Milky Way, the Large Magellanic Cloud has a metallicity of about forty per cent of the Milky Way, while the Small Magellanic Cloud has a metallicity of about ten per cent of the Milky Way.

... The metallicity of the Sun is approximately 1.6 percent by mass. For other stars, the metallicity is often expressed as "[Fe/H]", which represents the logarithm of the ratio of a star's iron abundance compared to that of the Sun [see article for formula]...

Meteorite Classification, Major Types

• per Roger Buick lab and supplemented:
The **Chondrites** are listed under **Undifferentiated Meteorites** [those that have undergone little change since their parent bodies originally formed], whereas the **Achondrites**, **Iron Meteorites**, and **Stony-Iron Meteorites** are listed under **Differentiated** [have a complex origin involving asteroidal or planetary differentiation].

• http://www.meteorlab.com/METEORLAB2001dev/clsschrt.htm (excerpted):
“Values presented in brackets represent the approximate known mass ... in kilograms...
Stone Meteorites [28,367kg, 9.88%]
 * **Ordinary Chondrites** [24,000kg, 8.36%]
 * **Carbonaceous Chondrites** [2,507kg, 0.87%]
 * **Enstatite Chondrites** [290kg, 0.10%]
 * **Rumuruti (R) Chondrites**
 * **Achondrites** [1,570kg, 0.55%]
Iron Meteorites [248,900kg, 86.44%]
Stony-Iron Meteorites [10,000kg, 3.48%]

• http://en.wikipedia.org/wiki/Meteorites_classification (excerpted):
I) **Stony meteorites**
 o **Chondrites**
  + **Carbonaceous chondrite** class
   # CI chondrite (Ivuna-like) group
   # CM-CO chondrite (mini-chondrule) clan

    # CV-CK chondrite clan
    # CR chondrite clan
  + **Ordinary chondrite** class
    # H chondrite group
    # L chondrite group
    # LL chondrite group
  + **Enstatite chondrite** class
    # EH chondrite group
    # EL chondrite group
  + **Other chondrite groups**, not in one of the major classes
o **Achondrites**
  + **Primitive achondrites**
    # Acapulcoite-lodranite clan
    # Brachinite group
    # Winonaite group
    # Ureilite group
  + **HED meteorite** clan (possibly from asteroid 4 Vesta)
    # Howardite group
    # Eucrite group
    # Diogenite group
  + **Lunar** meteorite group
  + **Martian** meteorite group (sometimes called "SNC meteorites")
    # Shergottites
    # Nakhlites
    # Chassignites
    # Other Martian meteorites, e.g., ALH84001
  + Angrite group
  + Aubrite group (enstatite achondrites)

II) **Stony-iron meteorites**
o Pallasites
o Mesosiderite group

III) **Iron meteorites**
o Magmatic iron meteorite groups
  + IC iron meteorite group
  + IIAB iron meteorite group
  + IIC iron meteorite group
  + IID iron meteorite group
  + IIF iron meteorite group
  + IIG iron meteorite group
  + IIIAB iron meteorite group
  + IIIE iron meteorite group
  + IIIF iron meteorite group
  + IVA iron meteorite group
  + IVB iron meteorite group
o Non-magmatic or primitive iron meteorite groups
  + IAB iron meteorite "complex" or clan (formerly groups IAB and IIICD)[1]
  + IIE iron meteorite group

Meteorites (specimens studied in the Labs, partial list)

(See classification scheme provided in the lab handout and also above.)

Cañon Diablo Siderite (a Fe-Ni or “Iron” meteorite):
• http://www.worldwideschool.org/library/books/geo/geography/ArizonaSketches/chap11.html:
“Ten miles southeast of Canon Diablo station on the Santa Fe Pacific Railroad, stands the Meteorite Mountain of Arizona, on a wide, open plain of the Colorado Plateau... It is not known positively just how or when the mountain was formed, but the weight of evidence seems to favor the meteorite theory, which is that at some remote period of time a monster meteorite fell from the sky and buried itself in the earth.”
• http://www.jjkent.com/articles/canon-diablo-meteorite.htm:

"The famous **Canon Diablo** meteorite possesses a surpassing mineralogical interest. In 1891, at the Tenth International Geologic Congress, Washington, D. C., the mineralogist Koenig announced that he had discovered some microscopic diamonds in this meteorite.... A mass of the iron weighing about 400 pounds was used by Professor Moissan; this was cut by means of a steel ribbon saw.... On close examination it became evident that the obstacles to the cutting consisted of round or elliptical nodules, of a dark gray to black hue, and enclosed in the bright iron. These nodules were mainly composed of **troilite** (iron protosulphide). After chemical treatment an insoluble residue remained, consisting of silica, amorphous carbon, graphite and diamond. Many of these very minute diamonds were black, but a few were transparent crystals, octahedrons with rounded edges. The presence of this diamond material in the interior of the iron mass of the meteorite indicates their formation from carbon by the combined agencies of high temperature and great pressure..."
• http://en.wikipedia.org/wiki/Siderite:
"**Siderite** is a mineral composed of iron carbonate FeCO3... Also, siderite is an obsolete term for a meteorite consisting principally of nickel and iron."

Allende Carbonaceous Chondrite (a Stony Meteorite):
• http://www.alaska.net/~meteor/AMinfo.htm:
"Landed in Pueblito de Allende, Chihuahua State, Mexico..." " Carbonaceous chondrites are thought to be the most primitive form of matter in the universe. Scientists theorize that if, at the beginning of time, the universe cooled and the dust clumped together and formed a rock, then the result would be something like a carbonaceous chondrite... The **matrix** or fine grained part of the Allende is primarily iron rich **olivine**. The total iron content is around 24 percent, but flecks of iron-nickel are only rarely found... Allende carbonaceous chondrites have another interesting feature. White clumps of white material--many with finger-like projections--are found throughout the meteorite. When analyzed these are mixtures of high temperature oxides and silicates of calcium, aluminum and titanium. They have been named **calcium-aluminum inclusions**, or CAIs for short. Scientists believe that these are among the first matter to have crystallized. They are older than the Earth itself.
• http://www.meteorlab.com/METEORLAB2001dev/allende.htm:
"Allende is a Type III (CV3) carbonaceous chondrite that fell in Allende, Mexico on February 8, 1969. This meteorite formed during the solar nebula phase of our solar system 4.56 billion years ago and contains interstellar grains (remnants of a prior star that lived out its life and exploded before the formation of our Sun) within calcium/aluminum-rich inclusions (CAIs). Allende represents some of the oldest known matter... To date, over two tonnes (2,000 kilograms) have been recovered, more than 80% of the total known carbonaceous chondrite material. Allende is the C-chondrite most commonly found in collections."

Lalande Meteorite (a Stony-Iron meteorite):
•
http://www.sciencemag.org/cgi/content/abstract/305/5684/657?siteid=sci&ijkey=nvGWiNYDebrzQ&keytype=ref:
"The lunar meteorite Sayh al Uhaymir 169 consists of an impact melt breccia extremely enriched with potassium, rare earth elements, and phosphorus [thorium, 32.7 parts per million (ppm); uranium, 8.6 ppm; potassium oxide, 0.54 weight percent], and adherent regolith. The isotope systematics of the meteorite record four lunar impact events at 3909 ± 13 million years ago (Ma), ~2800 Ma, ~200 Ma, and <0.34 Ma, and collision with Earth sometime after 9.7 ± 1.3 thousand years ago. With these data, we can link the impact-melt breccia to Imbrium and pinpoint the source region of the meteorite to the Lalande impact crater.
• http://www.astronomy.com/asy/default.aspx?c=a&id=2341:
"A meteorite found in Oman in 2002 can be traced back to the Imbrium basin and the crater **Lalande** on the lunar nearside. The meteorite's history may compel scientists to revise the Moon's early chronology... A fist-size meteorite named Sayh al Uhaymir 169 experienced three lunar impacts while on the Moon before a fourth ejected it and sent it earthward, says a team of planetary scientists who studied the meteorite's isotope chemistry. While the meteorite's lunar provenance has been known since it was found in early 2002, both its link to a specific crater and the history of its wanderings are new..."

Chihuahua Chondrite:

Tektite:
• http://www.answers.com/topic/tektite?cat=technology:

"Any of numerous generally small, rounded, dark brown to green glassy objects that are composed of silicate glass and are thought to have been formed by the impact of a meteorite with the earth's surface."
• Roger Buick lab:
"Tektites are produced when meteorites impact the Earth, blasting molten rock derived from both the impactor and the target crater out of the atmosphere and into orbit."

Kyancutta Octahedrite: (Iron Meteorite)
http://web.earthsci.unimelb.edu.au/TeachingSupport/meteorite.htm:
This is a medium octahedrite type IIIA. Found in 1932 at Kyancutta, Le Hunte Co, Eyre Peninsula, SA. Wt. = 689.5gm

Organic Chemistry vs. Inorganic Chemistry

• http://en.wikipedia.org/wiki/Organic_chemistry:
"**Organic chemistry** is a specific discipline within chemistry which involves the scientific study of the structure, properties, composition, reactions, and preparation (by synthesis or by other means) of chemical compounds consisting primarily of **carbon and hydrogen**, which may contain any number of other elements, including nitrogen, oxygen, halogens as well as phosphorus, silicon and sulfur.

The original definition of "organic" chemistry came from the misperception that organic compounds were always related to life processes. Not all organic compounds support life on Earth, but life as we know it also depends heavily on inorganic chemistry; for example, many enzymes rely on transition metals such as iron and copper; and materials such as shells, teeth and bones are part organic, part inorganic in composition. Apart from elemental carbon, **inorganic chemistry deals only with simple carbon compounds, with molecular structures which do not contain carbon to carbon connections** (its oxides, acids, carbonates, carbides, and minerals). This does not mean that single-carbon organic compounds do not exist (viz. methane and its simple derivatives). **Biochemistry mainly deals with the chemistry of proteins** (and other large biomolecules)....."

"Organic compounds are generally **covalently bonded**. This allows for unique structures such as long **carbon chains and rings**. The reason carbon is excellent at forming unique structures and that there are so many carbon compounds is that carbon atoms form very stable covalent bonds with one another (**catenation**). In contrast to inorganic materials, organic compounds typically melt, boil, sublimate, or decompose below 300 °C. Neutral organic compounds tend to be less soluble in water compared to many inorganic salts, with the exception of certain compounds such as ionic organic compounds and low molecular weight alcohols and carboxylic acids where hydrogen bonding occurs."
• http://en.wikipedia.org/wiki/Inorganic_chemistry:
"Inorganic chemistry is the branch of chemistry concerned with the properties and behavior of inorganic compounds. This field covers all chemical compounds except the myriad organic compounds (compounds containing C-H bonds), which are the subjects of organic chemistry. The distinction between the two disciplines is far from absolute, and there is much overlap, most importantly in the sub-discipline of **organometallic chemistry**."

Oxygen Catastrophe

http://en.wikipedia.org/wiki/Oxygen_Catastrophe:
"When evolving life forms developed oxyphotosynthesis about 2.7 billion years ago, molecular oxygen was produced in large quantities. The plentiful oxygen eventually caused an ecological crisis, as oxygen was toxic to the anaerobic organisms living at the time.... There was a time lag of about 300 million years between the time oxygen production from photosynthetic organisms started, and the Oxygen Catastrophe."

Phylogenetics

http://en.wikipedia.org/wiki/Phylogenetic:
"In biology, phylogenetics (Greek: phyle = tribe, race and genetikos = relative to birth, from genesis = birth) is the study of evolutionary relatedness among various groups of organisms (e.g., species, populations). Also known as phylogenetic systematics, phylogenetics treats a species as a group of lineage-connected individuals over time. Taxonomy, the classification of organisms according to similarity, has been richly informed by phylogenetics but remains methodologically and logically distinct.

… Cladistics provides a simplified method of understanding phylogenetic trees. There are some terms that describe the nature of a grouping. For instance, all birds and reptiles are believed to have descended from a single common ancestor, so this taxonomic grouping (yellow in the diagram) is called **monophyletic**. "Modern reptile" (cyan in the diagram) is a grouping that contains a common ancestor, but does not contain all descendents of that ancestor (birds are excluded). This is an example of a **paraphyletic** group. A grouping such as warm-blooded animals would include only mammals and birds (red/orange in the diagram) and is called **polyphyletic** because the members of this grouping do not include the most recent common ancestor. Although warm-blooded animals are all descended from a cold-blooded ancestor, warm-bloodedness evolved independently in both mammals and birds."

Prokaryotes

http://en.wikipedia.org/wiki/Prokaryotic:
"Prokaryotes … are a group of organisms that lack a cell nucleus (= karyon), or any other membrane-bound organelles. Most are unicellular, but some prokaryotes are multicellular organisms. The word prokaryotes comes from the Old Greek pro- before + karyon nut or kernel, referring to the cell nucleus, + suffix -otos, pl. -otes; it is also spelled "procaryotes" The prokaryotes are divided into two domains: the **bacteria** and the **archaea**. Archaea or Archaebacteria are a newly appointed [domain] of life. These organisms were originally thought to live only in inhospitable conditions such as extremes of temperature, pH, and radiation, but have since been found in all types of habitats."

Reduction/Oxidation (Redox) Reactions, Photosynthesis, And Cell Respiration

http://en.wikipedia.org/wiki/Redox:
"**Redox** (shorthand for reduction/oxidation reaction) describes all chemical reactions in which atoms have their oxidation number (oxidation state) changed.

This can be either a simple redox process such as the oxidation of carbon to yield carbon dioxide, or the reduction of carbon by hydrogen to yield methane (CH4), or it can be a complex process such as the oxidation of sugar in the human body through a series of very complex electron transfer processes.

The term redox comes from the two concepts of reduction and oxidation. It can be explained in simple terms:

Oxidation describes the loss of electrons by a molecule, atom or ion

Reduction describes the gain of electrons by a molecule, atom or ion

However, these descriptions (though sufficient for many purposes) are not truly correct. Oxidation and reduction properly refer to a **change in oxidation number** — the actual transfer of electrons may never occur. Thus, oxidation is better defined as an increase in oxidation number, and reduction as a decrease in oxidation number. In practice, the transfer of electrons will always cause a change in oxidation number, but there are many reactions which are classed as "redox" even though no electron transfer occurs (such as those involving covalent bonds).

Non-redox reactions, which do not involve changes in formal charge, are known as **metathesis** reactions.

… Substances that have the ability to oxidize other substances are said to be oxidative and are known as oxidizing agents, oxidants or oxidizers. Put in another way, the oxidant removes electrons from another substance, and is thus reduced itself. And because it "accepts" electrons it is also called an **electron acceptor**….

…The chemical way to look at redox processes is that the reductant transfers electrons to the oxidant. Thus, in the reaction, the reductant or reducing agent loses electrons and is oxidized and the oxidant or oxidizing agent gains electrons and is reduced. The pair of an oxidising and reducing agent that are involved in a particular reaction is called a redox pair.

In biology many important processes involve redox reactions. Cell **respiration**, for instance, is the oxidation of glucose to CO_2 and the reduction of oxygen to water…

… Much biological energy is stored and released by means of redox reactions. Photosynthesis involves the reduction of carbon dioxide into sugars and the oxidation of water into molecular oxygen. The reverse reaction, respiration, oxidizes sugars to produce carbon dioxide and water. As intermediate steps, the reduced carbon compounds are used to reduce nicotinamide adenine dinucleotide (NAD+), which then contributes to the creation of a proton gradient, which drives the synthesis of adenosine triphosphate (ATP) and is maintained by the reduction of oxygen. In animal cells, mitochondria perform similar functions…."

Ribozymes

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

"A ribozyme (from ribonucleic acid enzyme, also called **RNA enzyme** or **catalytic RNA**) is an RNA molecule that catalyzes a chemical reaction. Many natural ribozymes catalyze either their own cleavage or the cleavage of other RNAs, but they have also been found to **catalyze the aminotransferase activity of the ribosome**. Investigators studying the origin of life have produced ribozymes in the laboratory that are capable of catalyzing their own synthesis under very specific conditions, such as an RNA polymerase ribozyme... Before the discovery of ribozymes, enzymes, which are defined as catalytic proteins, were the only known biological catalysts... The functional part of the **ribosome**, the molecular machine that translates RNA into proteins, is fundamentally a ribozyme... If ribozymes were the first molecular machines used by early life, then today's remaining ribozymes—such as the ribosome machinery—could be considered living fossils of a life based primarily on nucleic acids. "

RNA World Hypothesis

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

The RNA world hypothesis is a theory which proposes that a world filled with RNA (ribonucleic acid) based life predates current DNA (deoxyribonucleic acid) based life. RNA, which can store information like DNA and catalyze reactions like proteins (enzymes), may have supported cellular or pre-cellular life. Some theories as to the origin of life present RNA-based catalysis and information storage as the first step in the evolution of cellular life.

The RNA world is proposed to have evolved into the DNA and protein world of today. DNA, through its greater chemical stability, took over the role of data storage while protein, which is more flexible in catalysis through the great variety of amino acids, became the specialized catalytic molecules. The RNA world hypothesis suggests that RNA in modern cells, in particular rRNA (RNA in the ribosome which catalyzes protein production), is the evolutionary remnant of the RNA world.

Three Domain Classification Of Life

http://en.wikipedia.org/wiki/Three-domain_system:

"The three-domain system is a biological classification introduced by Carl Woese in 1990 that emphasizes his separation of prokaryotes into two groups, originally called Eubacteria and Archaebacteria. Woese argued that, on the basis of differences in 16S rRNA [small subunit] genes, these two groups and the eukaryotes each arose separately from an ancestral progenote with poorly developed genetic machinery. To reflect these primary lines of descent, he treated each as a domain, divided into several different kingdoms. The groups were also renamed the Bacteria, Archaea, and Eukarya, further emphasizing the separate identity of the two prokaryote groups. [See phylogenetic tree diagram based on rRNA data, showing the separation of bacteria, archaea, and eukaryotes.]

Although the three-domain system was quickly adopted by most molecular systematists, biologists like Ernst Mayr criticized him for over-emphasizing the uniqueness of the archaebacteria and ignoring strong genetic similarities between the groups. Subsequent studies have confirmed that the archaea are unusual in the composition of their cell membrane and structure of their flagella. Other significant differences include archaeal systems for DNA replication and transcription which bear distinct similarity to those found in eukaryotes. For instance, archaeal RNA polymerase consists of up to 14 subunits, whereas most bacterial RNA polymerases have only 4 subunits...Nevertheless, a minority viewpoint suggests retaining the older **two-empire system** (**Prokaryota** and **Eukaryota**) and using the word bacterium in its earlier meaning of prokaryote.

Taxon

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

"A **taxon** (plural **taxa**), or **taxonomic unit**, is a name designating an organism or group of organisms. A taxon is assigned a rank and can be placed at a particular level in a systematic hierarchy reflecting evolutionary relationships. A distinction is to be made between taxa/taxonomy and classification/systematics. The former refers to biological names and the rules of naming. The latter refers to rank ordering of taxa according to presumptive evolutionary (phylogenetic) relationships.

A broad scheme of ranks in hierarchical order [MCM modified format]:

Domain > Kingdom > Phylum or Division > Class > Order > Family > Genus > Species

Note: "**Phylum**" applies formally to any biological domain but traditionally it was always used of animals whereas "**Division**" was traditionally often used of plants, fungi etc. A simple mnemonic phrase to remember the order is "Dignified Kings Play Chess On Fine Green Silk"...

A prefix is used to indicate a ranking of lesser importance. The prefix **super-** indicates a rank above, the prefix **sub-** indicates a rank below. In zoology the prefix **infra-** indicates a rank below sub-. For instance [MCM modified format]:

Superclass > Class > Subclass > Infraclass"

Tidal Locking

http://en.wikipedia.org/wiki/Tidal_locking:
"Tidal locking makes one side of an astronomical body always face another; for example, one side of the Earth's Moon always faces the Earth. A tidally locked body takes just as long to rotate around its own axis as it does to revolve around its partner. This synchronous rotation causes one hemisphere constantly to face the partner body. Usually, only the satellite becomes tidally locked around the larger planet, but if the difference in mass between the two bodies and their physical separation is small, both may become tidally locked to the other, as is the case between Pluto and Charon. This effect is employed to stabilize some artificial satellites."

The mechanism and a formula for estimating the time until locking are given, including the extremely strong dependence on orbital radius a (proportional to a^6).

Bodies affected include Mercury, our Moon, Phobos, Deimos, Io, Europa, and many other planetary moons.

"...Despite the Moon's rotational and orbital periods being exactly locked, we may actually observe about 59% of the moon's total surface with repeated observations from earth due to the phenomena of **librations** and parallax. Librations are primarily caused by the Moon's varying orbital speed due to the eccentricity of its orbit: this allows us to see up to about 6° more along its perimeter. Parallax is a geometric effect: at the surface of the Earth we are offset from the line through the centers of Earth and Moon, and because of this we can observe a bit (about 1°) more around the side of the Moon when it is on our local horizon."

Vitalism

http://en.wikipedia.org/wiki/Vitalist:
"Vitalism, as defined by the Merriam-Webster dictionary, is

1. a doctrine that the functions of a living organism are due to a vital principle distinct from physicochemical forces
2. a doctrine that the processes of life are not explicable by the laws of physics and chemistry alone and that life is in some part self-determining

Where vitalism explicitly invokes a vital principle, that element is often referred to as the "vital spark," "energy" or "élan vital," which some equate with the "soul." Vitalism has a long history in medical philosophies: most traditional healing practices posited that disease was the result of some imbalance in the vital energies which distinguish living from non-living matter. In the Western tradition, associated with Hippocrates, these vital forces were identified as the humours; Eastern traditions posited similar forces such as qi and prana. More recently, vitalistic thinking has been identified in the naive biological notions of children."