

Replaying the tape: Is Evolution Predictable?

Lynn J. Rothschild NASA Ames Research Center Stanford University Brown University

Great moments in evolutionary history. Would they happen again?

Stephen Jay Gould. 1989. Wonderful Life: The Burgess Shale and the Nature of History. Pp. 289-90



"Invariant laws of nature impact the general forms and functions of organisms; they set the channels in which organic design must evolve. But the channels are so broad relative to the details that fascinate us! ... Charles Darwin recognized this central distinction between `laws in the background' and `contingency in the details' ".

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Simon Conway Morris. 1998. The crucible of creation: The Burgess Shale and the Rise of Animals. p. 205.



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"My own view is of a series of historical accidents, subject to engineering constraints on the one hand, and to the conservatism of development on the other".

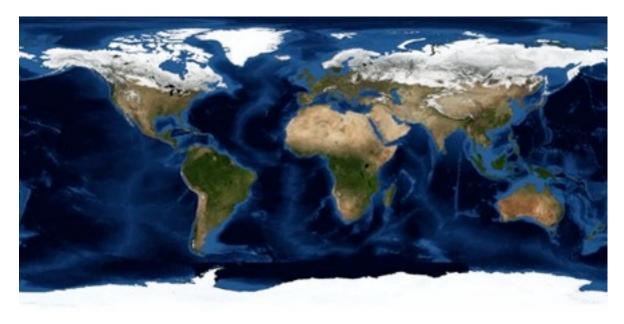
John Maynard Smith. The Problems of Biology. Oxford University Press, 1986.

Question for discussion:

- Is evolution PREDICTABLE based on the physical of biological environment, or contingent, that is a product of the quirks of history? That is, are there LAWS in evolution?
- This is pertinent to
 - Understanding **EVOLUTION**,
 - LIFE ELSEWHERE, and the
 - FUTURE OF LIFE on earth.



Using evolutionary "laws" to predict the future After Man: A Zoology of the Future



- Written by Dougal Dixon, and published in 1981, this book looks at the Earth 50 million years hence, assuming humans have gone extinct.
- Continents are similar, except South America is now an island.
- What has evolved to fill the niches left by our extinction? Based on evolutionary "laws" such as
 - Bergman's rule (related group, larger towards pole)
 - Allen's rule (related group, shorter limbs toward pole).



Big question #1:

How did we go from the Big Bang to Life?

What do we need for life? Thursday, August 5, 2010

Biogenic elements (C, H, O, N, S, P-and perhaps others?)

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What do we need for life?

Biogenic elements (C, H, O, N, S, P-and perhaps others?) Solvent (liquid water? implies temperature & pressure) Source of energy (Sun? Geothermal?) Solid surface (planet or moon?) Time (for origin of life and enough stability for evolution)

What do we need for life?

If we replayed the tape, would we still be organic chemists?

★ Discoveries in **astrochemistry**.

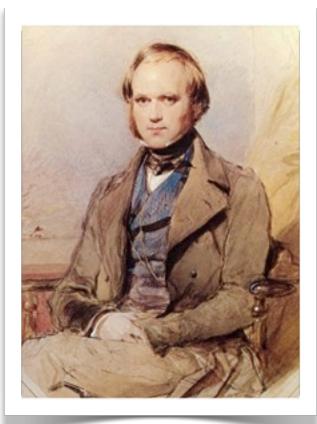
- ★ Punchline: an organic chemistry such as is found in life on Earth, appears to be THE language of chemistry in the universe.
- ★ Conclusion: if we "replay the tape", we would still be based on organic chemistry and likely to use amino acids, etc...and probably use water as solvent.
- **★ Implication**: don't bother to look for exotic aliens.

Big question #2:

How does life evolve?

Mechanisms of Evolution

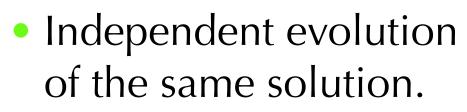
- Random (chance)
- Natural selection, which consists of:
 - Generation of heritable variability
 - Differential selection of offspring



- Can either be determined? Contingent?
- Is Natural Selection the only game in town?

Convergence

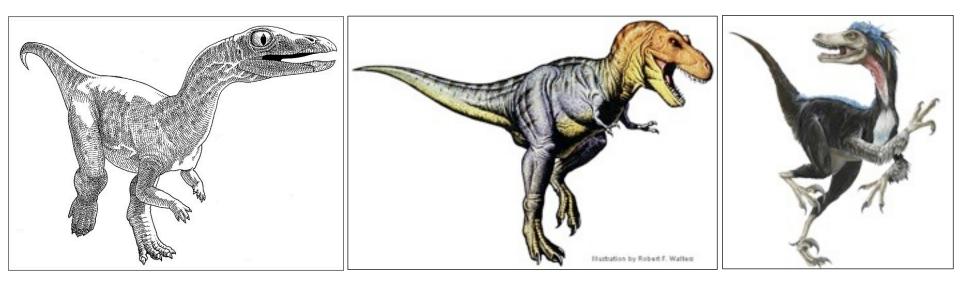




Example: protective thorns, wings



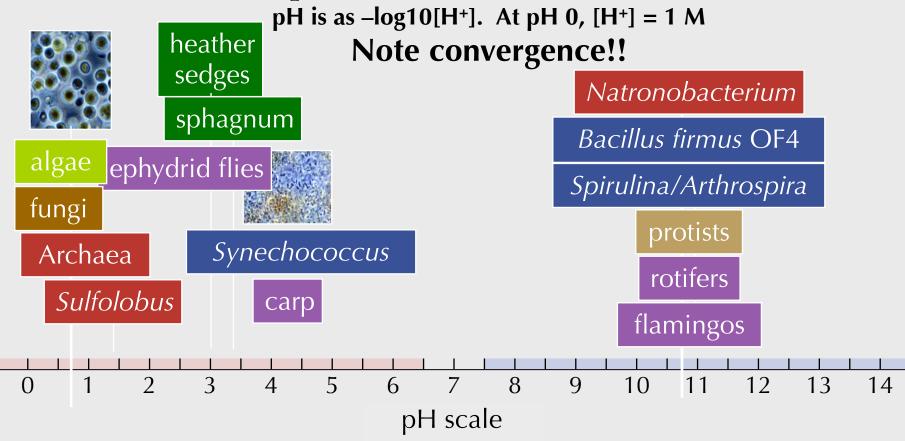
Convergence: Two-legged reptiles



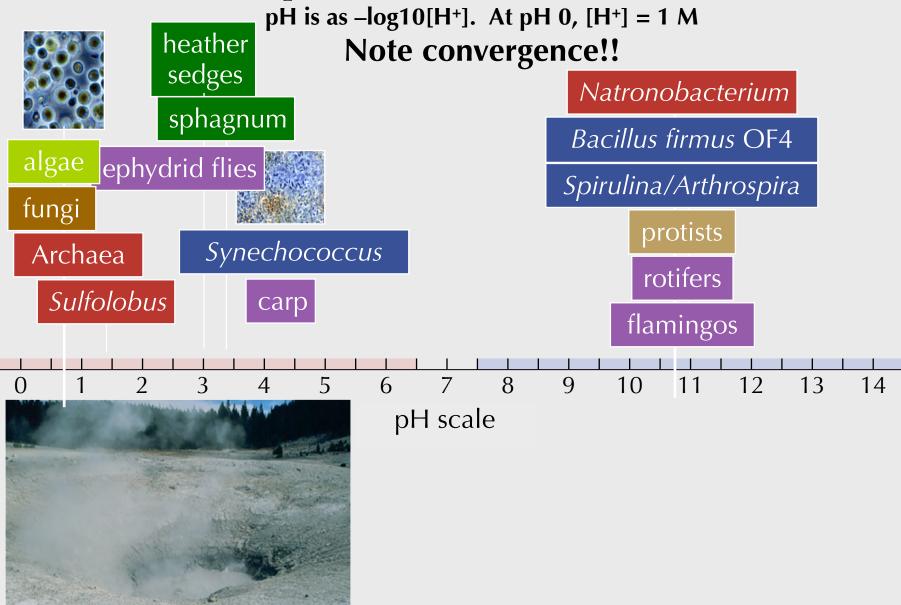
From left to right: crocodile, tyrannosaur, velocirapter

Scientists at the American Museum of Natural History have discovered a fossil in New Mexico that looks like a six-foot-long, two-legged dinosaur along the lines of a tyrannosaur or a velociraptor. But it is actually an 210-million year old relative of today's alligators and crocodiles.

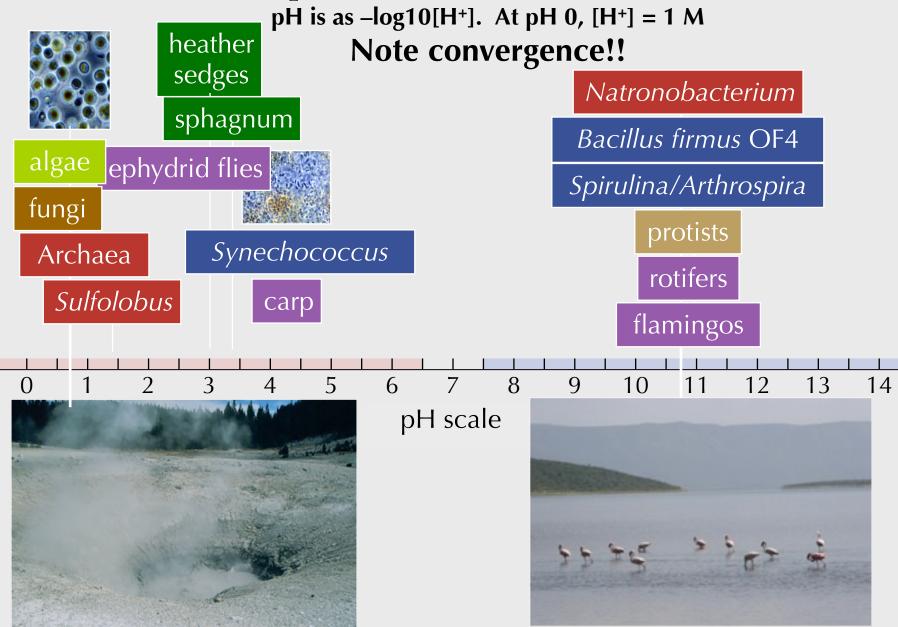
pH limits for life



pH limits for life

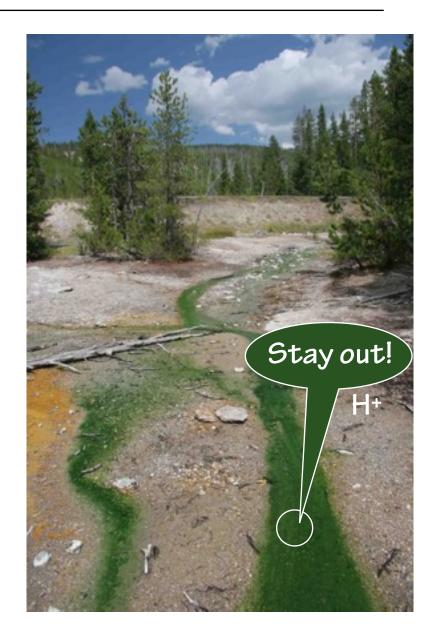


pH limits for life



pН

- pH is as -log10[H⁺]. At pH 0,
 [H⁺] = 1 M.
- Easiest is to keep internal pH near neutral.
- Acidophiles: maintain neutral pH. Strong proton pump or low proton membrane permeability.
- Alkaliphiles: internal pH 2⁺ units below medium. Need effective proton transport system. Serious problem if for membrane-bound ATP synthase system in bacteria.



The evolution of photosynthesis ...again?

Is photosynthesis convergent?

- Our sun is an essentially limitless source of power. 198 W/m² reaches earth's surface, but current global energy consumption is only 0.014% of this.
- With autotrophy, life was able to go beyond reliance on abiotically-produced organic carbon.
- Combining the two = photosynthesis.
 A great idea....but could it happen again?

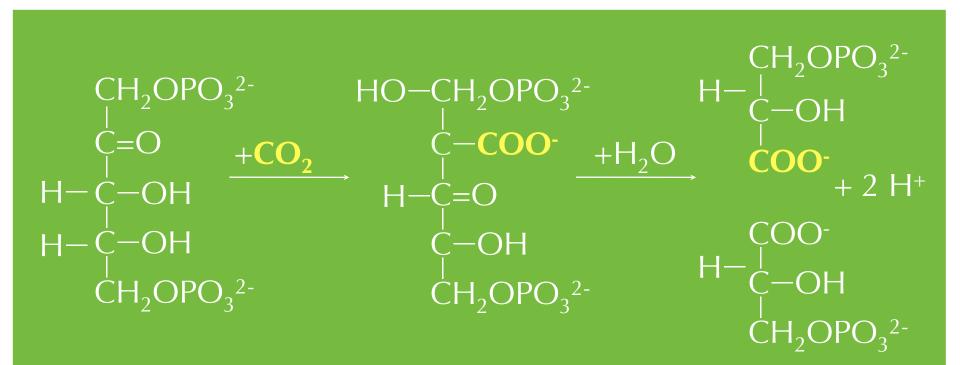
Plan of attack:

Autotrophy

- Photosynthesis, a specialized case of autotrophy
- How likely is photosynthesis to evolve?
 - Necessary ingredients
 - Evolutionary pressures
 - Suggestive evidence

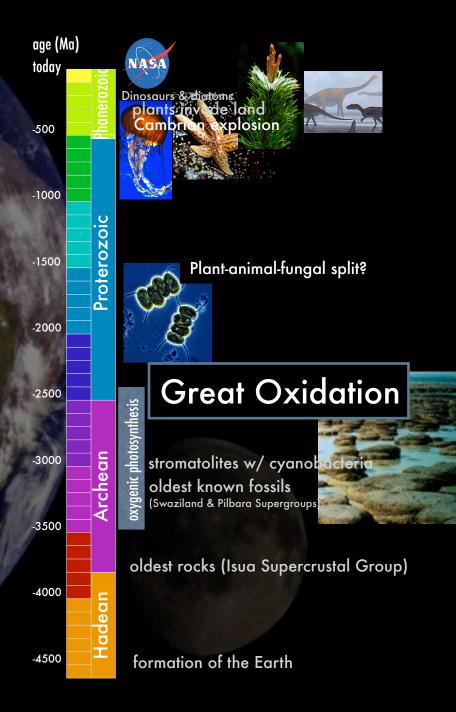
Autotrophs: organisms that can get some or all of their carbon from inorganic sources

Example: ribulose-1,5-bisphosphate carboxylase/ oxygenase, known to the cognicenti as RuBisCO



D-ribulose 1,5-bisphosphate

3-phosphoglycerate



When did

• Origin of life?

sua.

earlier?

autotrophy arise?

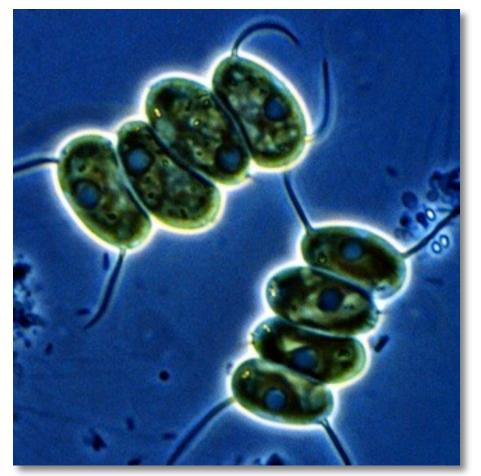
Oxygenic photosynthesis

very early, possibly by

• Photosynthesis later.

Chemolithoautotrophs

What are the pathways for autotrophy (carbon fixation)? #1. Calvin-Benson cycle (reductive pentose cycle)

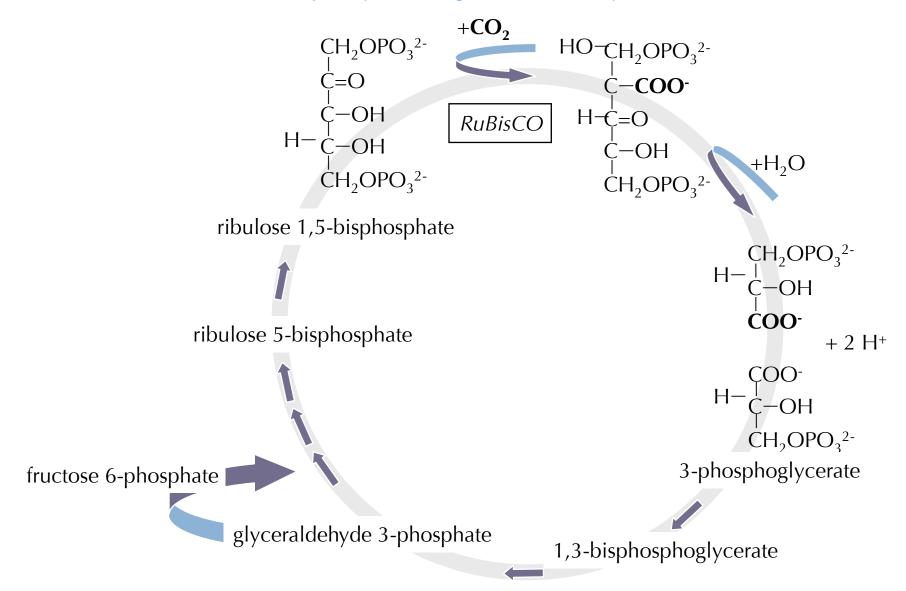


- Primary means of carbon fixation today.
- Plants, algae, cyanobacteria and purple photosynthetic bacteria, and most chemolithoautotrophs (e.g., hydrogen oxidizers)

Enzyme: Ribulose 1,5-bisphosphate carboxylase/oxygenase D-ribulose 1,5-bisphosphate + CO_2 + H_2O = 2,3-phospho-D-glycerate + 2 H⁺

Figure 1. Fixation of carbon dioxide by ribulose 1,5bisphosphate carboxylase/oxygenase (RuBisCO).

(Rothschild, L.J. 2008. The evolution of photosynthesis....again? Phil. Trans. Royal Soc. B. 363: 2787–2801.)



Pathways for autotrophy

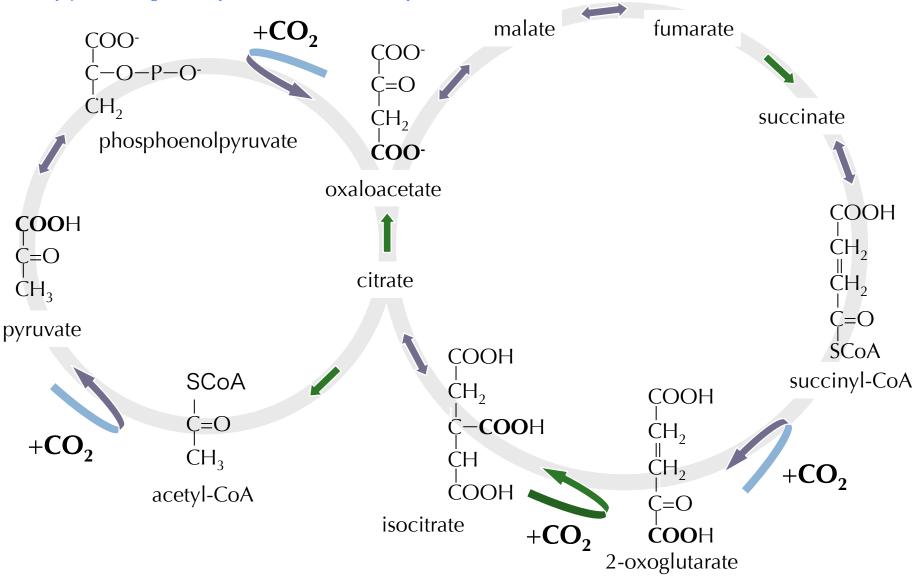
- Calvin-Benson cycle (reductive pentose cycle). *Plants, algae, cyanobacteria and purple photosynthetic bacteria, and most chemolithoautotrophs (e.g., hydrogen oxidizers)*
- Reverse (reductive) TCA cycle. Green sulfur bacteria, Sulfolobus, some deeply branching thermophilic chemolithoautotrophs (organisms that use energy from inorganic compounds to fix carbon)
- Hydroxypropionate pathway. *Chloroflexus*.
- Reductive acetyl-CoA pathway (Ljungdahl-Wood pathway). *Obligate anaerobic chemolithoautotrophs e.g., homoacetogens, methanogens*
- Ribulose monophosphate pathway. *Chemolithoautotrophs, e.g., several methanotrophs*
- Serine pathway. Chemolithoautotrophs, e.g., several methanotrophs

*Note: carbon monoxide (carboxidotrophs), methanol & formate (methylotrophs) are converted to CO_2 before assimilation in Calvin or other pathways. Formaldehyde and methane are used by several bacteria, but are not converted to CO_2 first but are assimilated by the serine or ribulose monophoshate pathway.

**Note 2: Crenarcheota alone have 3, possibly 4, of these pathways (Hügler et al., 2004).

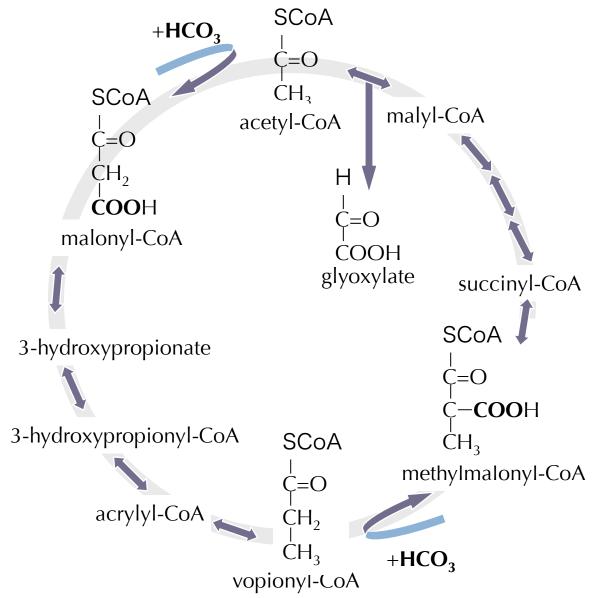
Figure 2. Reverse (reductive) TCA cycle.

May predominate over Calvin cycle in hydrothermal vents (Campbell and Cary, 2004). Green sulfur bacteria (a family of obligately anaerobic photoautotrophic bacteria), Sulfolobus, Aquifex, some deeply branching thermophilic chemolithoautotrophs.

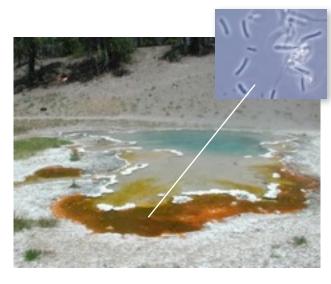


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Figure 3. Proposed 3-hydroxypropionate cycle of autotrophic CO₂ fixation in the phototrophic green non-sulfur bacterium *Chloroflexus aurantiacus*.



Evidence for a similar pathway of autotrophic CO₂ fixation in green non-sulfur bacteria, acidophilic archaebacteria of the phylum Crenarchaeota, such as Acidianus brierleyi, Metallosphaera sedula, and Sulfolobus metallicus

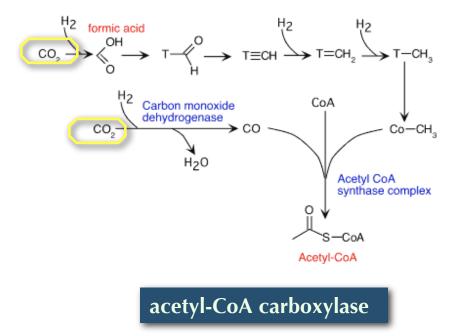


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Reductive acetyl-CoA pathway (Ljungdahl-Wood pathway).

- Unlike reverse TCA and Calvin cycles, reductive acetyl-CoA pathway is not cyclical.
- Obligate anaerobic chemolithoautotrophs e.g., homoacetogens, methanogens.

Reduces CO_2 to acetate, usually with H_2 as the electron donor. Reductive acetyl-CoA pathway results in the fixation of two *CO*² and the production of one molecule of acetyl-CoA. Another molecule of CO₂ can be fixed by the carboxylation of acetyl-coA to pyruvate. Pyruvate can be converted to phosphoenolpyruvate, which can enter gluconeogenesis, or can alternatively assimilate a fourth carbon dioxide molecule by carboxylation to oxaloacetate. This carboxylation is catalyzed by phosphoenolpyruvate Thursday, August 5, 2010



Plan of attack:

- Autotrophy: conclusion multiple pathways
- Photosynthesis, a specialized case of autotrophy
- How likely is photosynthesis to evolve?
 - Necessary ingredients
 - Evolutionary pressures
 - Suggestive evidence

Necessary ingredients: biotic carboxylation

Inorganic carbon
Reductant
Energy
Carboxylating enzymes

Necessary ingredients: biotic photosynthesis

Inorganic carbon
 Reductant
 Energy in form of light
 Carboxylating enzymes

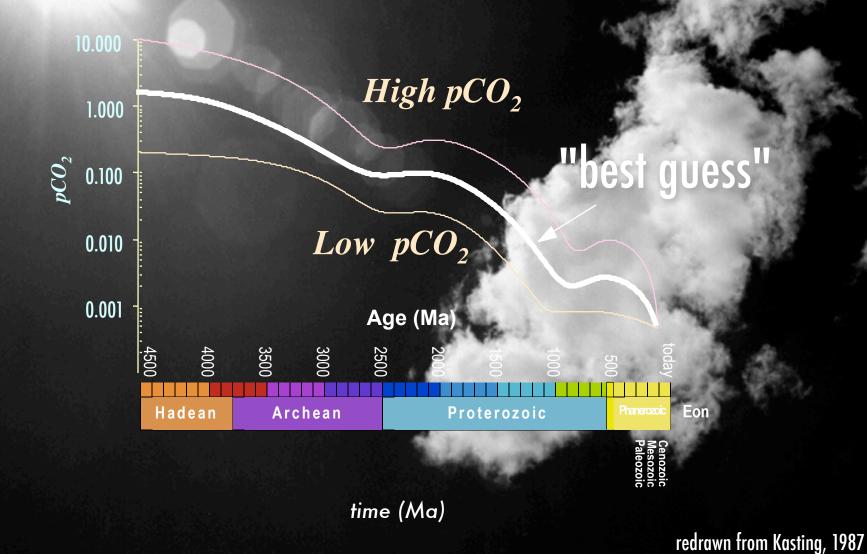
Plan of attack:

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Necessary ingredients for photosynthesis

Inorganic carbon - plenty of it!
Reductant
Energy in form of light
Carboxylating enzymes

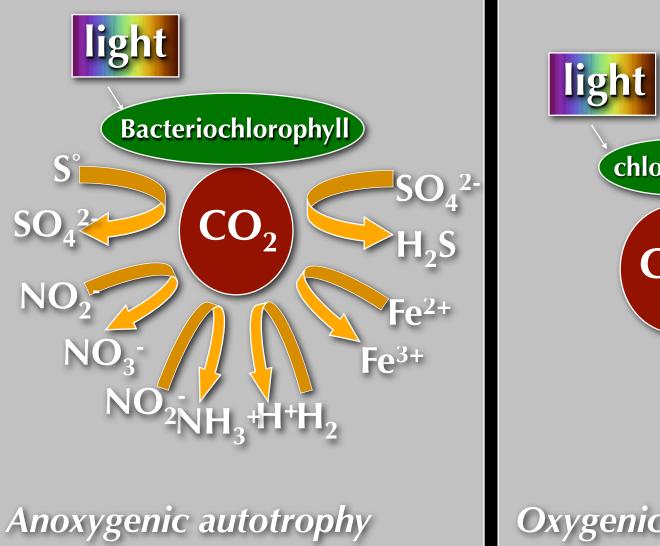
pCO₂ levels through time. How will these change?

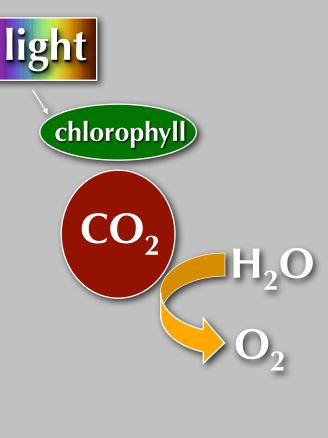


Necessary ingredients for photosynthesis

✓ Inorganic carbon Reductant - lots of possibilities, including water Energy in form of light Carboxylating enzymes

Alternate reductants



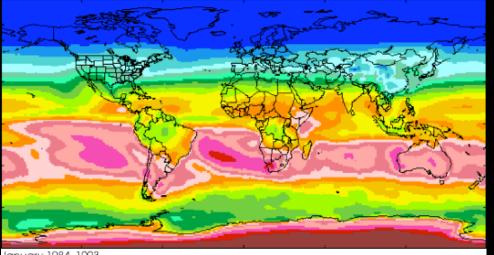


Oxygenic autotrophy

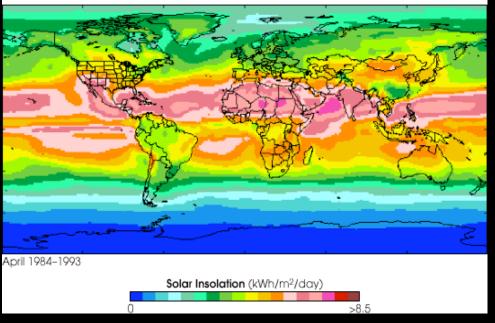
Necessary ingredients for photosynthesis

✓ Inorganic carbon ✓ Reductant Energy in form of light and a way to capture the energy Carboxylating enzymes

Light on planet Earth



anuary 1984–1993



- False-color images showing the average solar insolation, or rate of incoming sunlight at the Earth's surface, over the entire globe for the months of January and April. The colors correspond to values (kw hours m⁻² d⁻¹) measured every day by a variety of Earthobserving satellites and integrated by the International Satellite Cloud Climatology Project (ISCCP). NASA's Surface Meteorology and Solar Energy (SSE) Project compiled these data--collected from July 1983 to June 1993-into a 10-year average for that period.
- 1kWh = 3412 Btu = 3.6MJ = 859.8kcal
- Credit: Image courtesy Roberta DiPasquale, Surface Meteorology and Solar Energy Project, NASA Langley Research Center, and the ISCCP Project. http:// visibleearth.nasa.gov/view_rec.php?id=1683

Thursday, August 5, 2010

Necessary ingredients for photosynthesis

 Inorganic carbon ✓ Reductant Energy in form of light and a way to capture the energy Carboxylating enzymes

There are even more carboxylating enzymes than just the ones involved in autotrophy

- 1. *Pyruvic-malic carboxylase (1.1.1.38; 1.1.1.39; 1.1.1.40)*
- 2. Beta-ketoglutaric-isocitric carboxylase (aka isocitrate dehydrogenase) (1.1.1.41)
- *3.* Oxalosuccinate carboxylase (1.1.1.42)
- 4. 6-phosphogluconic carboxylase (1.1.1.44)
- 5. NADPH:2-(2-ketopropylthio)ethanesulfonate oxidoreductase/carboxylase (1.8.1.5)
- 6. Alpha-ketoacid carboxylase (aka Pyruvic decarboxylase) (4.1.1.1)
- 7. *Phosphoribosylaminoimidazole carboxylase(4.1.1.21)*
- 8. Phosphoenolpyruvate carboxylase (4.1.1.31)
- 9. Ribulose 1,5-bisphosphate carboxylase/oxygenase (4.1.1.39)
- 10. Urea carboxylase (6.3.4.6)
- 11. Biotin carboxylase (6.3.4.14)
- 12. Pyruvate carboxylase (6.4.1.1)
- 13. Acetyl-CoA carboxylase (6.4.1.2)
- 14. Propionyl-CoA carboxylase (6.4.1.3)
- 15. Methylcrotonoyl-CoA carboxylase (6.4.1.4)
- 16. Geranoyl-CoA carboxylase (6.4.1.5)
- 17. Acetone carboyxlase (6.4.1.6)
- *18. 2-oxoglutarate carboxylase (6.4.1.7)*

#7: Phosphoribosylaminoimidazole carboxylase:
5-amino-1-(5-phospho-D-ribosyl)imidazole + CO₂ = 5-amino-1-(5-phospho-Dribosyl)imidazole-4-carboxylate

#8: Phosphoenolypyruvate carboxylase: phosphoenolpyruvate + CO_2 + H_2O = phosphate + oxaloacetate

#9: RuBisCO:

D-ribulose 1,5-bisphosphate + CO_2 + H_2O = 2,3-phospho-D-glycerate + 2 H⁺

#10: Urea carboxylase: ATP + urea + **HCO**₃⁻ = ADP + phosphate + urea-1-carboxylate

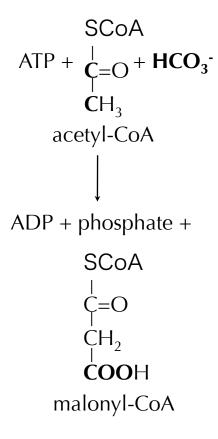
#11: Biotin carboxylase: ATP + biotin-carboxyl-carrier protein + **CO**₂= ADP + phosphate + carboxybiotin-carboxylcarrier protein

#12: Pyruvate carboxylase: ATP + pyruvate + **HCO**₃⁻ = ADP + phosphate + oxaloacetate

#13: Acetyl-CoA carboxylase: ATP + acetyl-CoA + $HCO_3^- \rightarrow ADP +$ phosphate + malonyl-CoA

#14: Propionyl-CoA carboxylase: ATP + propanoyl-CoA + **HCO₃** = ADP + phosphate + (S)-methylmalonyl-CoA.

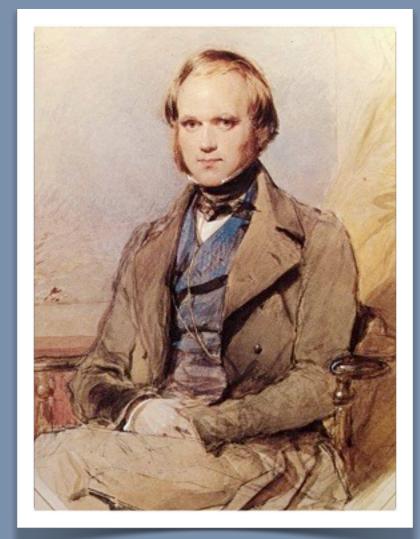
A carboxylase, acetyl-CoA carboxylase, catalyses the first step in fatty acid synthesis.





Necessary ingredients for evolution of photosynthesis Inorganic carbon - plenty of it! ✓ Reductant Energy in form of light Carboxylating enzymes Selection pressure

It is easy to envision an evolutionary scenario that includes strong selective pressure for organisms that evolve autotrophy, particularly photosynthesis.



The argument is as follows:

The facts:

Life on earth is based on organic carbon. This would likely occur again on earth and elsewhere because of the abundance of carbon, its chemical versatility and its ubiquity.

Most of the carbon in the universe is inorganic. Even on today's life-infested Earth, there are ~38,000 Gt carbon in contrast to 1000 Gt organic carbon in the oceans (Falkowski et al., 2000). On Mars, there is a large inventory of CO_2 in the atmosphere and as ice, but we have yet to detect organic carbon other than CH₄.

"Life is lazy" (efficient); necessary to maintain competitive edge.

Evolution uses what is available; "evolution as tinkerer" a la François Jacob. Parts are co-opted from within or from others. (Jacob, Evolution and tinkering. Science 1977; 196:1161-6.)

Contingency occurs. Asteroids, floods, atmospheric catastrophes and so on may change the rules substantially.

Key events in evolution

metabolism

- Selection of chemistry argument for carbonbased life (with water?)
- Eventually selection pressure for autotrophy.
 In many cases, photosynthesis efficient.
- Which should lead to herbivory...
- Leading to carnivory.



Is there evidence for this scenario?

Remember convergence in carboxylating enzymes?

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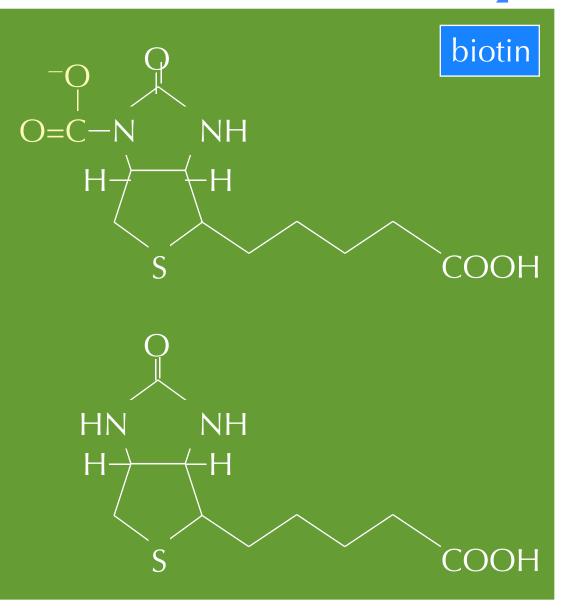
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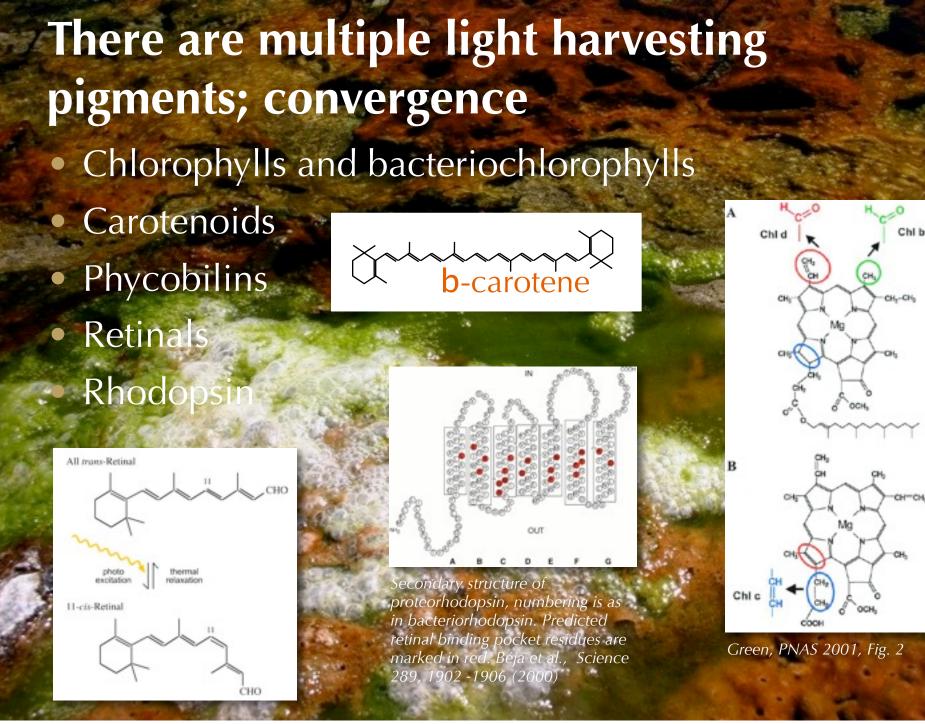
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OK, not all of them are completely convergent. Some use biotin: a mobile carrier of activated CO₂

- Biotin (vitamin B₇, vitamin H) is a cofactor for CO₂ transfer.
- The carboxyl terminus of biotin is linked to the amino group of a specified lysine residue by an amide bond.
- Carboxylating enzymes using biotin are: acetyl-CoA carboxylase alpha, acetyl-CoA carboxylase beta, methylcrotonyl-CoA carboxylase, propionyl-CoA carboxylase, pyruvate carboxylase (Nikolau et al., 2003)





Could photosynthesis evolve again?

Yes. Ingredients available, data from convergence, and evolutionary pressure present

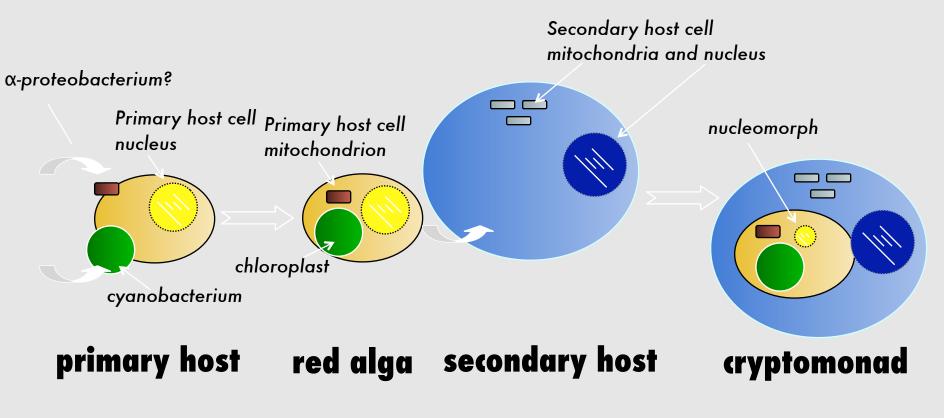
CONVERGENCE?

- Redundancy (genes, proteins, etc.)
- Symbiosis
- Multicellularity
- Transition to land and back to water
- Skin color
- Intelligence

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The origin of the eukaryotic cell by primary and secondary endosymbiosis.



Rothschild, JEM 2004

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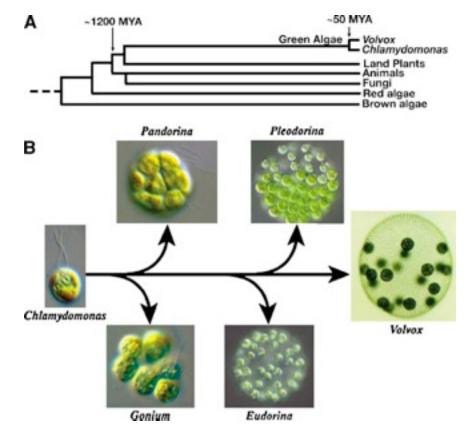
Advantages of "multicellularity"

- Size. Avoiding prey, faster movement, different scale sensing of environment.
- If large and "unicellular", have
 - diffusion problems (but could get around this geometrically to a certain extent)
 - co-ordination of self
- Senescence
- Sequestering germ line



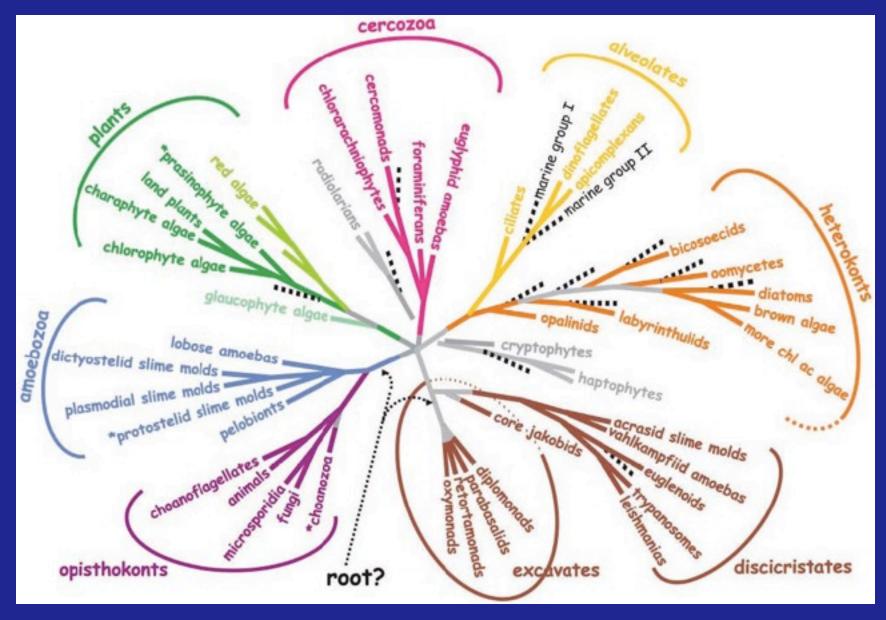
Multicellularity is convergent

- Widely accepted that the plants, animals, fungi, red and brown algae had independent origins from different unicellular ancestors >1 Ga.
- Multicellularity also arose independently in two different groups of cellular slime molds, in diatoms, in ciliates and in several other eukaryotic groups, as well as several groups of prokaryotes.
- The "most-repetitive invention of multicellularity" award goes to the Chlorophyceae (9 out of 11 orders) and sometimes it has arisen more than once in the order.

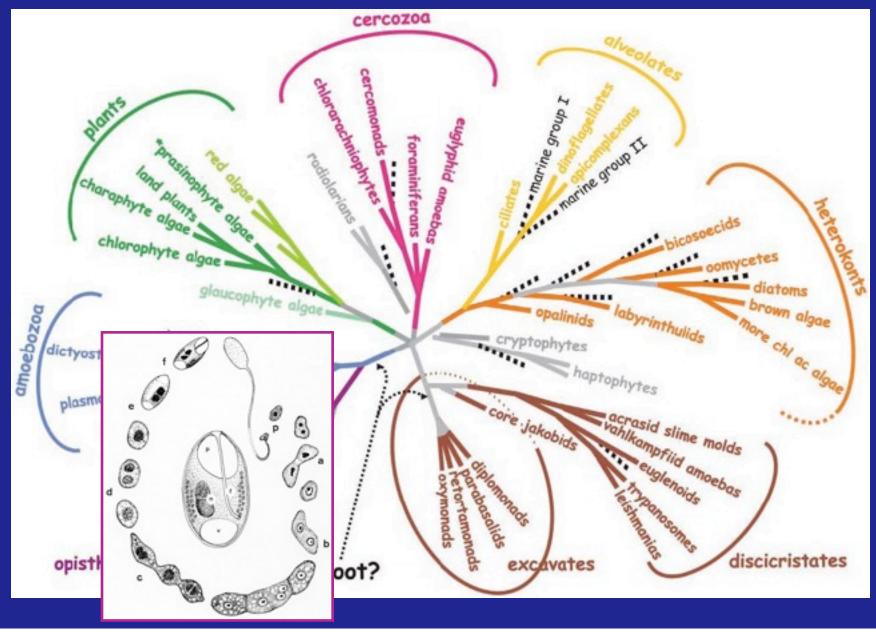


Kirk. 2005. A twelve-step program for evolving multicellularity and a division of labor. Bioessays 27:299-310.

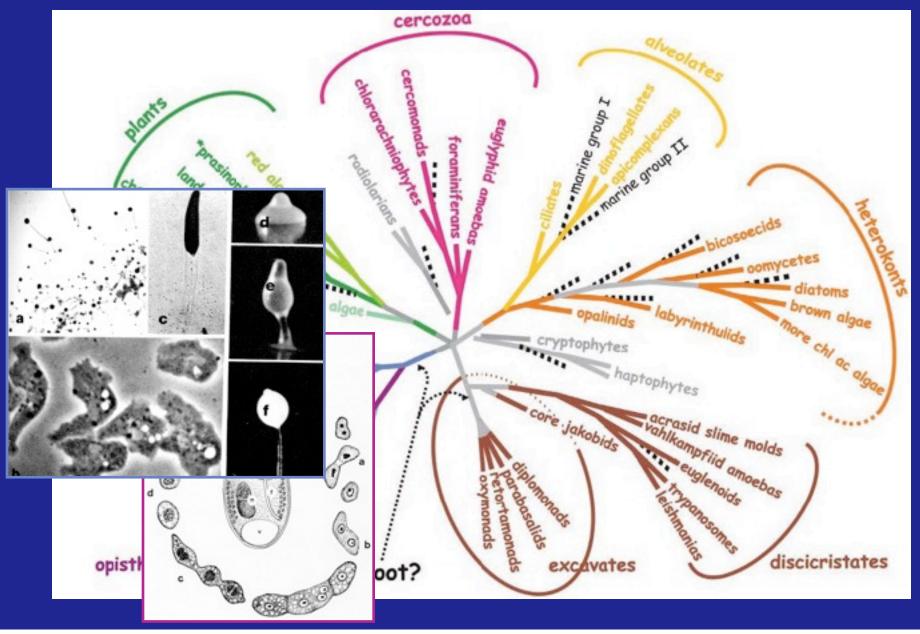
Multicells

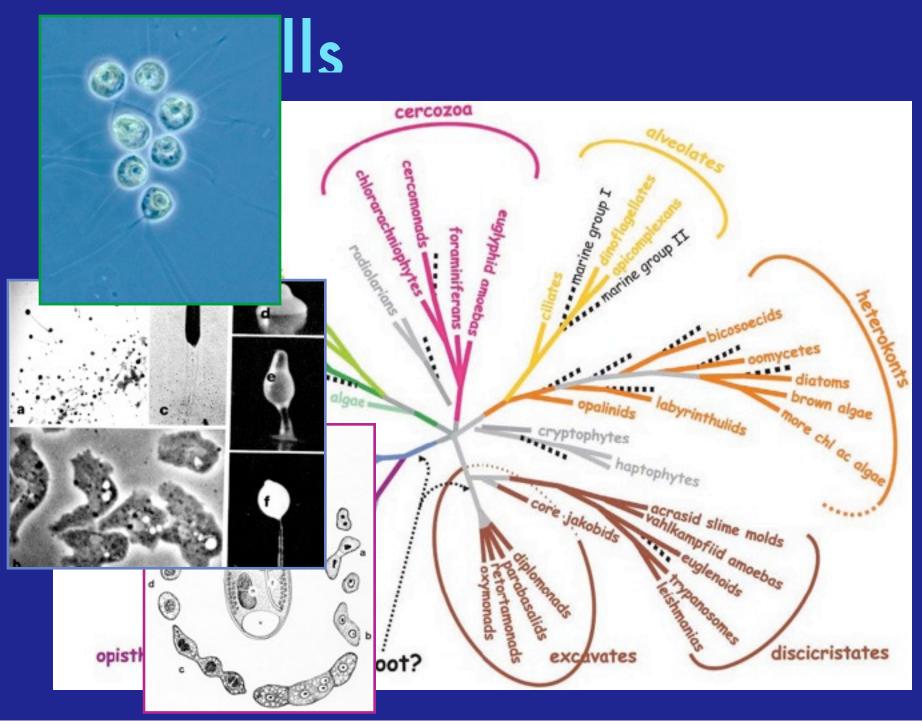


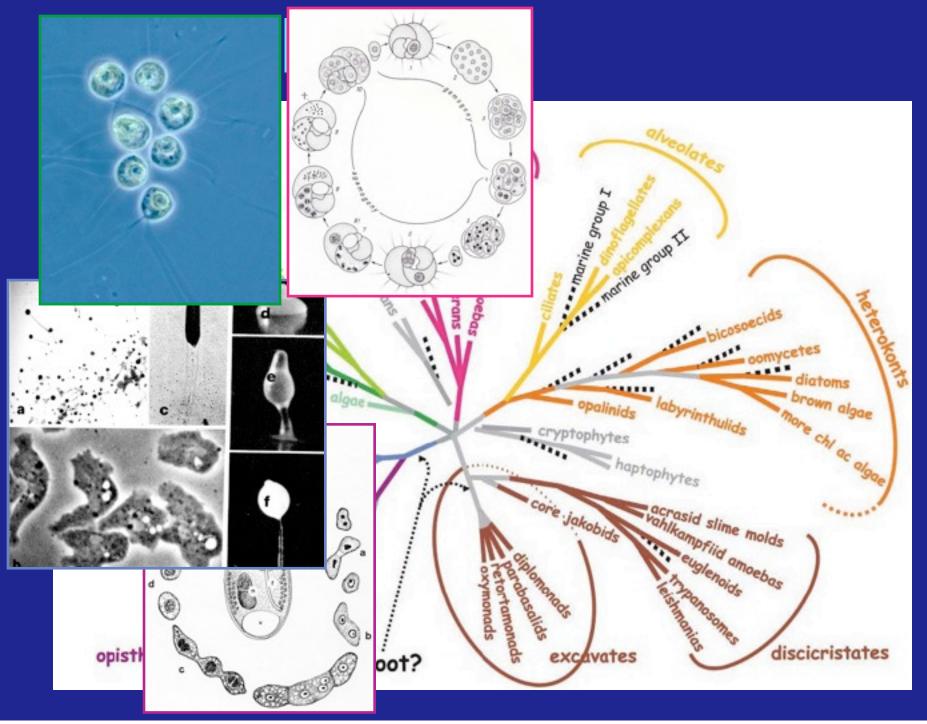
Multicells

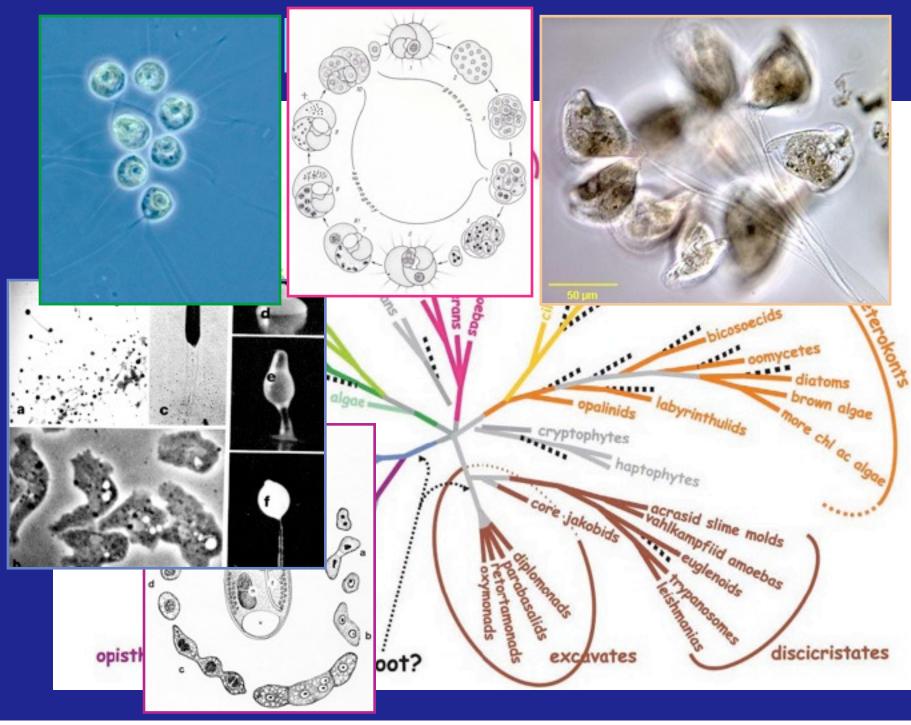


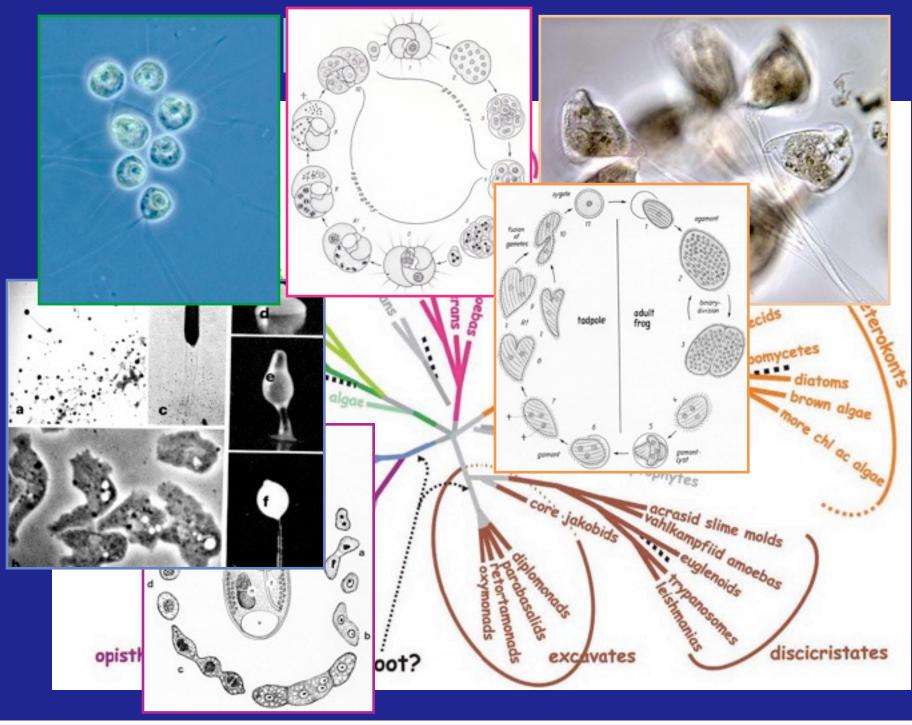
Multicells

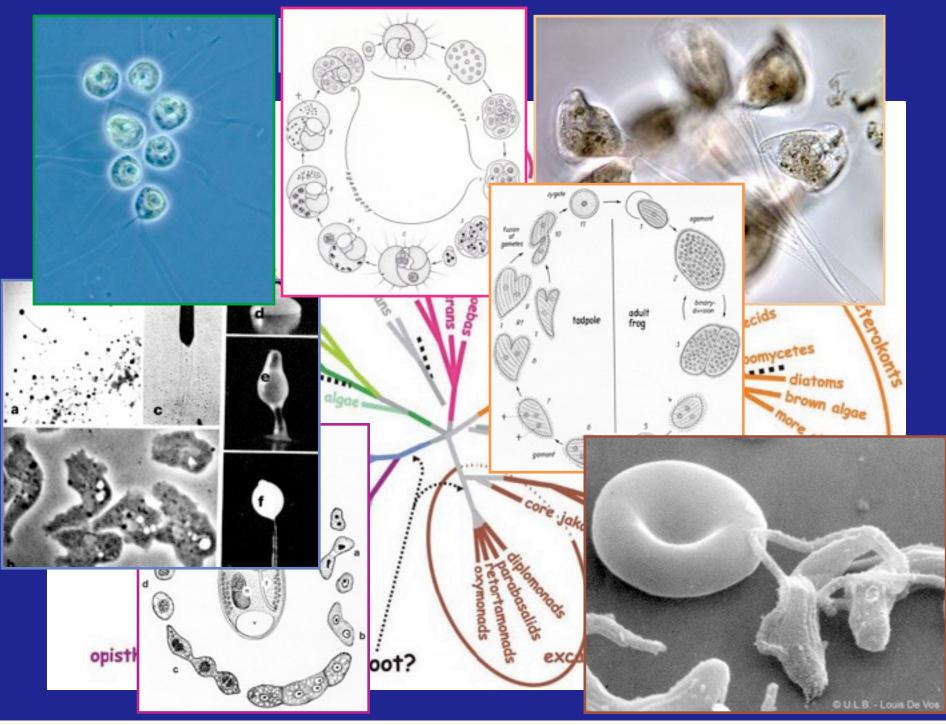


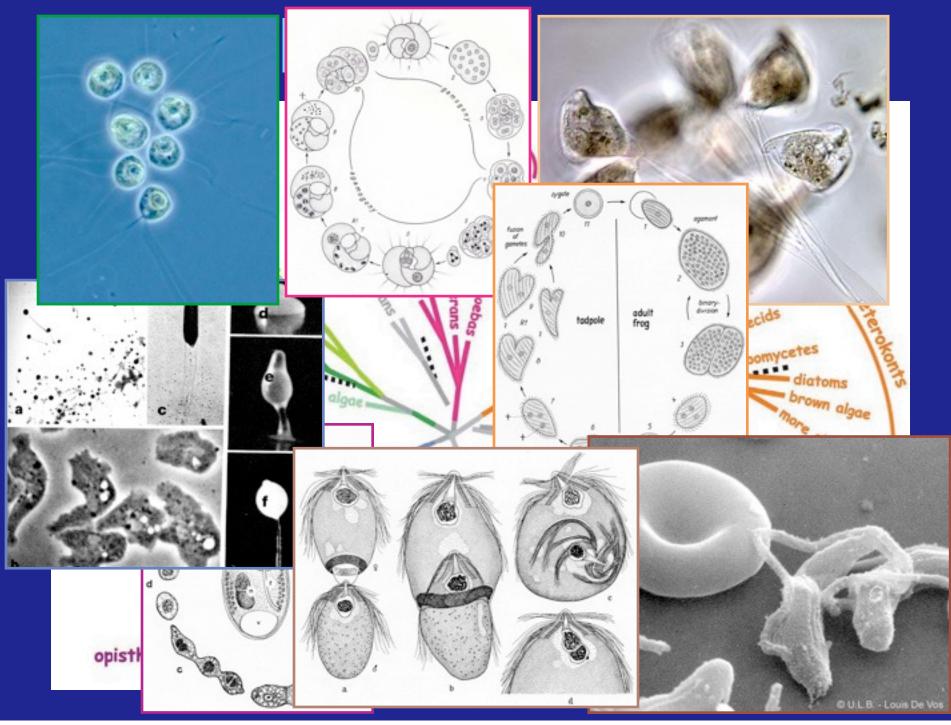












CONVERGENCE?

- Redundancy (genes, biochemistry, etc.)
- Symbiosis
- Multicellularity
- Transition to land, and back to water
- Skin color
- Intelligence

Was the adaptation to land COnvergent?

- Reasons to move from water to land:
 - Access to gases (CO₂ and O₂). This would be true at high temperatures and altitudes.
 - New niches
 - Escape predation
- Problems with moving to land
 - Desiccation
 - New predators



CONVERGENCE?

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Key events in evolution human skin color



"Skin color is an adaptation to the environment, not a badge of genetic identity," says Nina Jablonski, who has conducted more than a decade of in-depth research into the evolution of human skin color with her husband George Chaplin, a geographic information systems specialist also at Penn State.

"The earliest members of the hominid lineage probably had a mostly unpigmented or lightly pigmented integument covered with dark black hair, similar to that of the modern chimpanzee. The evolution of a naked, darkly pigmented integument occurred early in the evolution of the genus *Homo*. A dark epidermis protected sweat glands from UV-induced injury, thus insuring the integrity of somatic thermoregulation. Of greater significance to individual reproductive success was that highly melanized skin protected against UV-induced photolysis of folate, a metabolite essential for normal development of the embryonic neural tube. As hominids migrated outside of the tropics, varying degrees of depigmentation evolved in order to permit UVB-induced synthesis of previtamin D3. The lighter color of female skin may be required to permit synthesis of the relatively higher amounts of vitamin D3 necessary during pregnancy and lactation. Skin coloration in humans is adaptive and labile. Skin pigmentation levels have changed more than once in human evolution. Jablonski & Chaplin, 2000, The evolution of human skin coloration, *Journal of Human Evolution* **39**, 57–106)

The latest: UV radiation, not vitamin D, might limit multiple sclerosis symptoms. "MS incidence typically follows a latitudinal gradient in both hemispheres. In Europe and North America, MS is more common in the northern regions, whereas MS is more prevalent in the southern part of Australia" Becklund et al., 2010, UV radiation suppresses experimental autoimmune encephalomyelitis independent of vitamin D production, *PNAS March 22, www.pnas.org/cgi/doi/10.1073/ pnas.1001119107*

CONVERGENCE?

- Redundancy (genes, biochemistry, etc.)
- Symbiosis
- Multicellularity
- Transition to land and back to water
- Skin color
- Intelligence (also see Animal Intelligence and the Evolution of the Human Mind: Scientific American, Aug. 2008)

Key events in evolution

intelligence

- Heterotrophy requires movement and sensory ability.
- Prey need to avoid being eaten.
- Our strategy for dealing with an unpredictable environment was to evolve intelligence.



Convergence of intelligent mammals (Madsen et al., 2001; Nature 409:610)

Laurasiatheric Order Cetacea: Beluga whale



narihra

armad

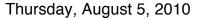
Order

huma

imates



Early Cretaceous (125-115 Ma)



Convergence of aquatic mammals (Madsen et al., 2001; Nature 409:610)

Laurasiatheric Order Cetacea: Beluga whale **Everchonta & Glires** (sciuld, mouse, rat, old World porcupine caviomorph, rabbit, pika, flying lemur, tree shrew, strepsirhine human)

Afrotheria Order Sirenia: Manatee

narihra

armadil

Early Cretaceous (125-115 Ma)

Convergence of fossorial mammals (Madsen et al., 2001; Nature 409:610) Euarchonta & Glires

Laurasiatheria Order Eulipotyphla: Mole

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(sciurid, mouse, rat, old World porcupine caviomorph, rabbit, pika, flying lemur, tree shrew, strepsirhine human)

Afroiheria Order Afrosoriciad: Golden mole

Early Cretaceous (125-115 Ma)

Convergence of ant-eating mammals (Madsen et al., 2001; Nature 409:610) Evarchonta & Glires

(sciurid, mouse, rat, old World porcupine caviomorph, rabbit, pika, flying lemur, tree shrew, strepsirhine human)

Afroiheria Order Tubulidentata: Aardvark



Early Cretaceous (125-115 Ma)

Lavrasiatheria

Order Pholidota: Pangolin

narihra

armadillo

Big question #3:

What is the role of the Environment?

In the beginning (and even later)...

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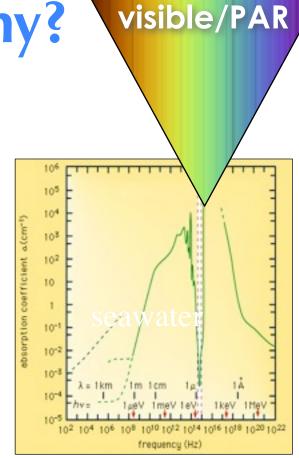
 The physical and chemical environment define the limits for life. The "struggle for existence" was just that: a struggle against the environment and entropy.

In the beginning (and even later)...

• The physical and chemical environment define the limits for life. The "struggle for existence" was just that: a struggle against the environment and entropy.

 Secondarily, there is biological competition, "nature red in tooth and claw". Eukaryotes and cyanobacteria use radiation from 400-700 nm for photosynthesis. Why? Visible/

- Window between infrared (which is not very energetic) and UV (which is damaging.)
- Or does it have to do with water chemistry?
- see also , "The Color of Plants on Other Worlds" (Nancy Kiang, Scientific American)

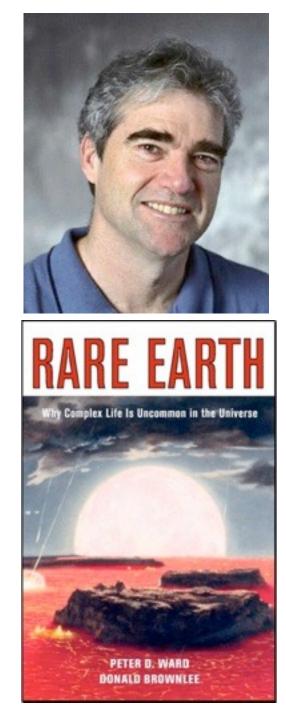


Biggest question:

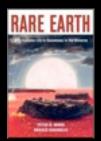
Does this mean life could arise elsewhere, and is predictable?

Rare Earth Hypothesis

"simple" (bacterial) life is very common in the universe; complex life (multi-cellular life forms, or animals -- let alone intelligent life) is very rare.



What do we need to take into account when looking for a planet with life?



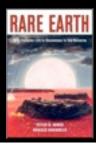
Proper distance from the star. *Distance from Sun helps determine presence of liquid water.*

Proper distance from the center of the galaxy. The density of stars near the center of the galaxy is so high, that the amount of cosmic radiation in that area would prevent the development of life.

- A star of a proper mass. A too-massive star would emit too much ultraviolet energy, preventing the development of life. A star that is too small would require the planet to be closer to it (in order to maintain liquid water). But such a close distance would result in tidal locking. In this case one side becomes too hot, the other too cold, and the planet's atmosphere escapes.
- **A proper mass.** A planet that is too small will not be able to maintain any atmosphere. A planet that is too massive would attract a larger number of asteroids, increasing the chances of life-destroying cataclysms.
- Oceans. Must have liquid water. On the other hand, too much water (i.e., a planet with little or no land) will lead to an unstable atmosphere, unfit for maintaining life.
- A constant energy output from the star. If the star's energy output suddenly decreases, all the water on the planet would freeze. This situation is irreversible, since when the star resumes its normal energy output, the planet's now-white surface will reflect most of this energy, and the ice will never melt. Conversely, if the stars energy output increases for a short while, all the oceans will evaporate and the result would be an irreversible greenhouse-effect disallowing the re-formation of the oceans.
 - **Successful evolution.** Even if all of these conditions hold, and "simple" life evolves (which probably happens even if some of these conditions aren't met), this still does not imply that the result is animal (multicellular) life.
- Avoiding disasters. Potential disasters include the supernova of a nearby star; a massive asteroid impact; drastic changes of climate; and so on.

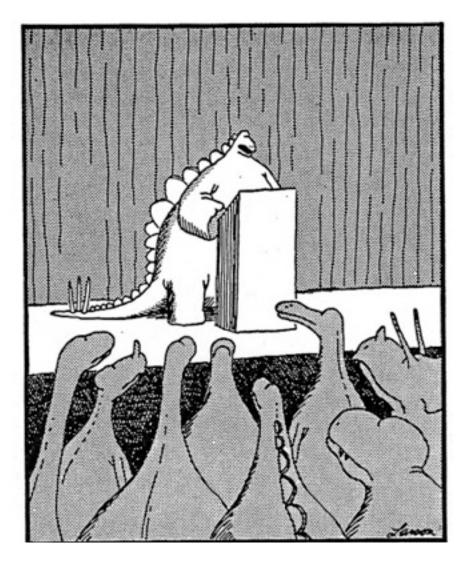
These seem reasonable, but what about these as well? Ward and Brownlee argue strongly for the importance of the following attributes

- **The existence of a Jupiter-like planet in the system.** Apparently, Jupiter's large mass attracted many of the asteroids that would have otherwise hit Earth. Could life evolve in a system with no Jovian planet? On the other hand, too many Jovian planets, or one that is too large, could lead to a non-stable solar system, sending the smaller planets into the central sun or ejecting them into the cold of space.
- **The existence of a large, nearby moon.** Apparently Luna, Earth's moon, is atypically large and close. Both of Mars's moons, for example, are minor rocks by comparison. What does this have to do with life? Well, it turns out that Luna kept (and still keeps) Earth's tilt stable. Without Luna, the tilt would have changed drastically over time, and no stable climate could exist. If the tilt would have stabilized on a too-large or too-small value, the results could also be disastrous; Earth's tilt is "just right".
- **Plate tectonics.** Surprisingly enough, it seems like plate tectonics are required for maintaining a stable atmosphere. Plate tectonics play an important role in a complex feedback system (explained in detail in the book) that prevents too many greenhouse gases from existing in the atmosphere. No other planet (except maybe for Jupiter's moon Europa) is known to have plate tectonics. Is this a rare phenomenon, but required for life?

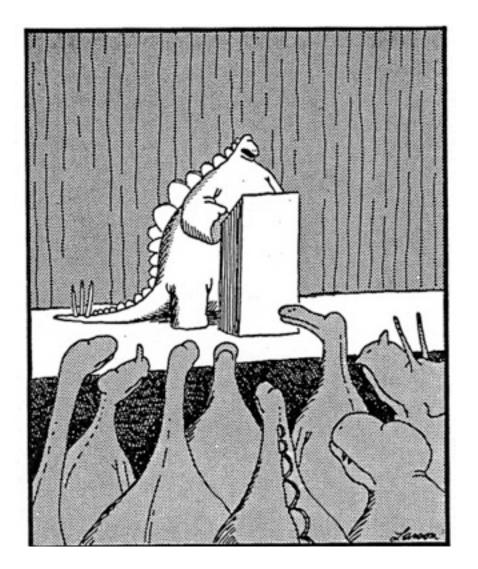


Suggestion

- An evolutionary trajectory based on metabolism is set in motion because we are carbon-based creatures.
- Evolution is a tinkerer that uses what is available and is constrained by physics, chemistry, development and history.
- Evolution makes its way to localized adaptive peaks (fine-tuning?)
- But if we stand back we can see the big mountains (coarse-tuning?) flowing from carbon-based life form.
- How life gets there may be contingent (allowing for developmental & engineering constraints and history), but the selective pressures will be to get there somehow.

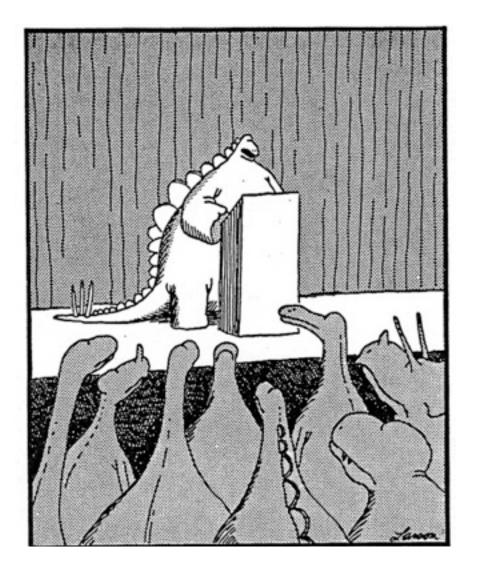


"The picture's pretty bleak, gentlemen...The world's climates are changing, the mammals are taking over, and we all have a brain about the size walnut."



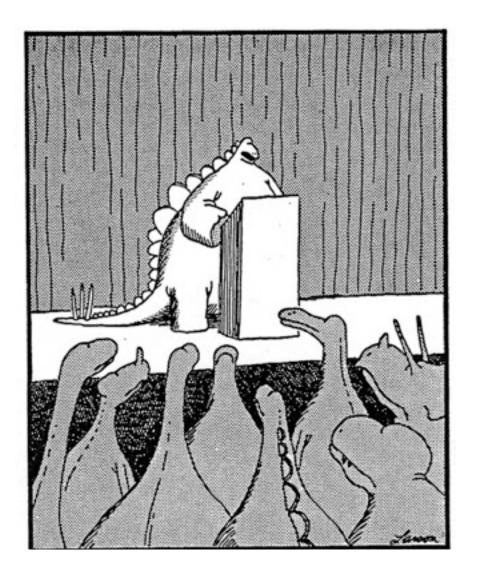
Environment

"The picture's pretty bleak, gentlemen...The world's climates are changing, the mammals are taking over, and we all have a brain about the size walnut."



EnvironmentCompetition

"The picture's pretty bleak, gentlemen...The world's climates are changing, the mammals are taking over, and we all have a brain about the size walnut."



EnvironmentCompetitionBiology

"The picture's pretty bleak, gentlemen...The world's climates are changing, the mammals are taking over, and we all have a brain about the size walnut."