#### The Evolution of Life on Earth

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#### Outline

- Introduction
- The origin of life from a genetic perspective
- The origin of life from an environmental perspective
- The evolution of eukaryotic cells
- The evolution of multicellular plants and animals
- Conclusions / implications

#### Lava flow, James Island



## Recent (100+ year old) lava flow, James Island



#### Landscape of Tower Island



#### Tower Island: can you see the owl now?



#### Galapagos short-eared owl, Tower Island



#### Galapagos hawk, inside Volcan Alcedo



#### Galapagos tortoise, inside Volcan Alcedo



## Frigate bird in flight, Tower Island



## Pelican, Seymour Island



#### Galapagos penguin, James Island





# Flamingos, James Island



#### Transposon subfamilies shared in common between the human and mouse genomes were independently predicted to be older than the divergence date in each genome considered separately

Table 6 Divergence levels of interspersed repeats predating the human-mouse speciation											
Interspersed repeat		Mouse				Human					
Family	Class	kb	Divergence	Range	JC	kb	Divergence	Range	JC	Substitution ratio	Adjusted ratio
L1MA6	LINE1	1,795	0.28	0.04	0.35	2,738	0.16	0.05	0.184	1.92	1.98
L1MA7	LINE1	789	0.28	0.04	0.35	3,502	0.16	0.04	0.181	1.92	1.96
L1MA8	LINE1	951	0.27	0.04	0.34	4,488	0.15	0.04	0.172	1.96	1.96
L1MA9	LINE1	1,032	0.28	0.04	0.35	6,468	0.18	0.05	0.201	1.74	1.86
L1MA10	LINE1	160	0.29	0.04	0.36	1,492	0.19	0.05	0.224	1.61	1.80
L1MB1	LINE1	627	0.29	0.04	0.36	2,947	0.18	0.05	0.211	1.71	1.87
L1MB2	LINE1	725	0.28	0.04	0.35	3,309	0.18	0.06	0.201	1.75	1.87
L1MC1	LINE1	1,389	0.28	0.04	0.36	7,221	0.17	0.05	0.198	1.80	1.92
MLT1A	MaLR	984	0.31	0.04	0.39	2,203	0.21	0.04	0.242	1.62	1.73
MLT1A0	MaLR	1,794	0.30	0.04	0.38	5,424	0.19	0.04	0.219	1.74	1.80
MLT1A1	MaLR	539	0.29	0.04	0.37	1,705	0.19	0.04	0.214	1.74	1.78
MLT1B	MaLR	73	0.28	0.03	0.35	4,482	0.18	0.04	0.203	1.73	1.73
MLT1C	MaLR	2,071	0.30	0.04	0.37	5,511	0.21	0.04	0.245	1.53	1.64
Looper	DNA	33	0.28	0.04	0.34	48	0.18	0.03	0.211	1.62	1.69
MER20	DNA	435	0.29	0.05	0.37	2,205	0.19	0.05	0.222	1.65	1.76
MER33	DNA	232	0.27	0.05	0.33	1,207	0.18	0.04	0.211	1.57	1.63
MER53	DNA	82	0.26	0.05	0.31	524	0.17	0.05	0.191	1.63	1.63
Tigger6a	DNA	97	0.29	0.03	0.37	190	0.18	0.06	0.211	1.77	1.85

Shown are the number of kilobases matched by each subfamily (kb), the median divergence (mismatch) level of all copies from the consensus sequence, the interquartile range of these mismatch levels (range), and a Jukes-Cantor estimate of the substitution level to which the median divergence level corresponds (JC). Notice that RepeatMasker found, on average, four- to fivefold more copies in the human than in the mouse genome, as a result of the higher DNA loss in the rodent lineage as well a failure to identify many highly diverged copies. The two right columns contain the ratio of the JC substitution level in mouse over human, and an adjusted ratio (AR) of the mouse and human substitution level after subtraction from both of the approximate fraction accumulated in the common human-mouse ancestor. For this fraction we have taken the difference between the ancestral repeat average substitution level and least diverged ancestral repeat family (L1MA8). See the Supplementary information for a discussion of the origin of the variance in the human and mouse ratios.

"Initial sequencing and comparative analysis of the mouse genome." R. H. Waterston *et al.* (2002) (> 100 co-authors) *Nature* **420**, 520-562.

#### What is Evolutionary Biology?

- The unifying model is descent with modification.
- Molecular Evolution is based on DNA and protein sequencing experiments on living and extinct organisms, plus statistical analysis.
- Origin of Life studies are based on geological and astronomical observations of environmental conditions on the early earth, chemical experiments that simulate prebiotic conditions, and computational simulations of early molecular evolution.
- **Paleontology** is based on experimental analysis (chemical, morphological, and geological) of fossils and rock layers.
- **Systematic biology** combines the methods of molecular evolution and paleontology to analyze the evolutionary origin of organisms.
- Evolutionary Ecology combines physiological, anatomical and genetic laboratory experiments with field studies to analyze the evolutionary adaptations of living and extinct organisms.



Fig. 3. Composite amino acid usage bias across universal ribosomal tree. Bias values reflect the geometric mean distances (normalized as SD) between observed and expected amino acid usages. Increased bias across the archaeal domain is largely due to widespread thermophily, halophily, and nucleotide composition bias. Aside from branches associated with haloarchaea, the branch leading to the bacteria (the bacterial root) contains the greatest bias.

#### What is life (as we know it)?

- DNA and RNA
- The central dogma of molecular genetics
- The genetic code
- Amino acids and proteins
- The Krebs cycle (TCA cycle)
- Energy sources (aerobic vs. anaerobic, photosynthesis, etc).
- What is the likelihood of other chemistries of life on earth? On other planets?
- What are the prerequisites for building a multicellular organism?

## Primary structure of RNA and DNA



From Snustad & Simmons (2009) Principles of Genetics 5th ed.



= Carbon

From Snustad & Simmons (2009) Principles of Genetics 5th ed.

#### What about "arsenic based life"?

- Bacteria have recently been discovered that are extremely resistant to arsenic poisoning, and continue to be viable when arsenic is incorporated into their DNA in place of phosphate.
- However, these bacteria prefer phosphate to arsenic. They grow faster on phosphate media, and even in the presence of high concentrations of arsenic (and zero added phosphate), approximately half their DNA contains arsenic.
- Genetic studies show that these bacteria have the same genetic code as we do and clearly represent a small branch of a well -known group of bacteria.
- They are not "arsenic-based life".

#### The "central dogma" of molecular genetics

#### **The Central Dogma**

Flow of genetic information:

1. Perpetuation of genetic information from generation to generation



## mRNAs are "translated" by a "universal" genetic code

**TABLE 12.1** The Genetic Code<sup>a</sup> Second letter U С A G U UUU UAU UGU บсบไ Tyr (Y) Cys (C) Phe (F) UAC UGC UUC UCC с U Ser (S) UUA UCA UAA Stop **UGA Stop** A Leu (L) (terminator) (terminator) UUG UCG UAG Stop UGG Trp (W) G (terminator) U CUU CCU CAU CGU His (H) CAC CCC CGC С CUC C Leu (L) Arg (R) Pro (P) CGA A CUA CCA CAA Third (3') letter First (5') letter Gln (Q) CUG CGG G CCG CAG AUU ACU AAU AGU U Asn (N) Ser (S) AUC > Ileu (I) ACC AAC AGC C A Thr (T) AUA ACA AAA AGA A Lys (K) Arg (R) AGG ACG AAG Met (M) G AUG (initiator) U GCU GAU GGU GUU Asp (D) GCC GAC GGC С = Polypeptide chain GUC G Val (V) Ala (A) Gly (G) initiation codon GCA GGA A GAA GUA Glu (E) = Polypeptide chain GCG GAG GGG G GUG termination codon <sup>a</sup>Each triplet nucleotide sequence or codon refers to the nucleotide sequence in mRNA (not DNA) that specifies the incorporation of the indicated amino acid or polypeptide chain termination. The one-letter symbols for the amino acids are given in parentheses after the standard three-letter abbreviations.

# Proteins in living organisms contain a minimum of 20 different amino acids

#### 1. Hydrophobic or nonpolar side groups



#### 2. Hydrophilic or polar side groups



3. Acidic side groups



#### 4. Basic side groups





#### Proteins are built with peptide bonds



- Amino acids are joined by peptide bonds.
- The carboxyl group of one amino acid is covalently attached to the amino group of the next amino acid.

The Kreb's cycle burns sugar and oxygen -

and produces ATP, carbon dioxide and water



#### Gene duplication vs. horizontal transfer of genes

- Genomics has shown that genes in eukaryotes (like us) evolve primarily by gene duplication, while genes in bacteria evolve primarily by horizonal gene transfer.
- "Gene duplication" refers to any of several (very frequent) mutational processes in which an extra copy of one (or several) genes are produced. The extra copy is then free to evolve into a new (related) function, which if useful will be retained.
- Horizontal transfer" refers to any of several (very frequent) mutational processes by which a gene from another species can be taken up and incorporated into the host chromosome.
- Both processes have greatly facilitated the evolution of complex organisms.

#### 2. The origin of life - from a genetic perspective

- Which came first RNA, DNA, or protein?
- Which came first genes or metabolism?
- Hot start vs. warm start vs. cold start?
- How did the genetic code evolve?
- Which came first eubacteria or archaebacteria?
- What sort of organism was LUCA (the Last Universal Common Ancestor of living organisms)?

#### **RNA world**

RNA is both genetic material and the catalyst of metabolic reactions. Genes consist of short ds-RNA molecules. Chromosomes do not exist.

 $\downarrow$ 

#### **RNA/protein world**

Primitive genetic code allows the synthesis of proteins. This is essentially an extension of the catalytic abilities of RNA. Competition between cells (lipid vesicles) and virus probably exists at this stage.

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#### **U-DNA world**

Hydroxy group is removed from ribose on molecules used for information storage, providing increased thermal stability. Small chromosomes originate at this stage. Genetic code becomes more advanced (additional amino acids).

 $\downarrow$ 

#### **T-DNA world**

Methyl group is added to uracil on DNA, (but not RNA), allowing cytosine deamination to be repaired in DNA. Chromosomes grow larger, genetic code becomes more advanced.



**Figure 9:** Predicted structures of ribosomal RNA from (a) the archaeon *Halobacterium volcanii*, (b) the eukaryote baker's yeast, and (c) cow mitochondria. RNA is single-stranded, but, as in DNA, the letters can pair up to form bridges between two chains. In the case of RNA, a single chain doubles back on itself to form loops and hairpins (whereas the famous DNA double helix is in fact two distinct chains entwined in a helix). The 'bubbles' in this illustration are single-stranded RNA, in which the letters have not paired up. A comparison of the three ribosomal RNAs shows that the overall shape and structure of ribosomal RNA (its secondary structure) has been maintained throughout evolution. However, the actual sequence of letters has drifted substantially, and the sequence similarities are very low. The mitochondrial RNA structure is reminiscent of bacterial RNA, from which the mitochondria originated. Adapted with permission from Gutell *et al.*, and *Progress in Nucleic Acid Research and Molecular Biology*.

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Fig. 3. Composite amino acid usage bias across universal ribosomal tree. Bias values reflect the geometric mean distances (normalized as SD) between observed and expected amino acid usages. Increased bias across the archaeal domain is largely due to widespread thermophily, halophily, and nucleotide composition bias. Aside from branches associated with haloarchaea, the branch leading to the bacteria (the bacterial root) contains the greatest bias.

#### Some issues in the origin of life

- Which came first RNA, DNA, or protein?
- Ans: RNA (essentially unanimous), then protein, and DNA last.
- Which came first genes or metabolism?
- Ans: genes came first (majority view). Pre-existing energy flows were probably utilized by genetic systems at a very early stage.
- Hot start vs. warm vs. cold start?
- Ans: This is a controversial subject. Cold start is the most compatible with the storage of genetic information in RNA, a key point because of the overwhelming evidence for an "RNA world". On the other hand, important molecules and/or energy sources may have originated in undersea "black smokers" or "white smokers".

#### More issues in the origin of life

- How did the genetic code evolve?
- Ans: It is generally agreed that the genetic code evolved in stages and caused the extinction of its competitors. Probably 1letter code (3 spacing) -> definitely 2-letter code -> 3-letter code.
- What were the genetic characteristics of the Last Universal Common Ancestor?
- Ans: LUCA was anaerobic, marine bacterium with 500-1000 genes. It definitely had the same genetic code as we do, and it may have been the first organism with this code.
- Which came first eubacteria or archaebacteria?
- Ans: LUCA was likely more similar to eubacteria (based on the molecular signature of the origin of the genetic code).
  Archaebacteria came later and then evolved into eukaryotes.



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3. The origin of life: from a geological perspective

#### The early earth

- 4.6 billion years ago, the early earth was entirely molten and had little or no atmosphere.
- The moon originated 4.5 billion years ago and shows evidence of a high rate of meteorite bombardment, which tapered off 4.0 to 3.5 billion years ago.
- The first solid rock on planet earth formed 4.4 billion years ago, but survives to the present only as tiny crystal grains (eroded sand) embedded within younger sandstones.
- The planet cooled enough to provide the first evidence of liquid water (marine sandstones) and stable rock formations 3.85 billion years ago. At this time, continents (small rafts of lighter rock) and shallow oceans likely were present.

#### The evolution of life

- The oldest surviving rocks exposed at the surface of the earth (marine sandstones, 3.85 billion years old) already unambiguous biomarkers of life as we know it (C<sup>12</sup> : C<sup>13</sup> stable isotope ratios)!!
- By 3.5 billion years ago, we have morphological fossil evidence of cyanobacteria (stromatolites).
- By 2.7 billion years ago, we have biomarkers of both cyanobacteria and eukaryotes (sterols, etc).
- At 2.3 billion years ago, we have clear evidence of the first "snowball earth", in which the earth was completely covered by glaciers and biomass deposition declined to zero.

#### Oxygen in the atmosphere

- The first living things on earth were anaerobic (did not use oxygen for respiration).
- Oxygen in the atmosphere gradually accumulated from two sources -- first the hydrolysis of water by UV light, and later the enzymatic production of oxygen by photosynthesis (and biomass deposition).
- Most of the oxygen produced by UV light was used up in the process of oxidizing iron-containing sediments (red rock and clay) exposed at the earth's surface.
- The excess oxygen produced by photosynthesis saved our oceans, by creating an ozone layer (to screen out UV light), and a way of recycling  $H_2$  gas (by reacting with  $O_2$  in the atmosphere).

#### Timeline of Earth history



Figure 1: Geological timeline from the formation of the Earth 4.6 billion years ago to the present day. Note the immense duration of the Precambrian era. The first plants and animals appeared around the time of the Cambrian explosion 543 million years ago. The extinction of the dinosaurs was about 65 million years ago.

# Increase in oxygen concentration during the Precambrian period



**Figure 2:** Geological timeline expanding the mid-Precambrian period (Archaean and early Proterozoic). Note the burst of evolutionary activity in the period 2.3 to 2 billion years ago, as oxygen levels rose to about 5–18% of present atmospheric levels.

+8+6+4Changes in carbon (%0 PDB) +2isotope ratios indicate 0 813C -2 rates of organic carbon Fe Fe burial, 1000 900 which correlate with rising oxygen levels



Figure 3: Changes in carbon isotope ratios during the late Precambrian and early Cambrian periods. The changes are given in parts per thousand (0/00)relative to the PDB standard. (The PDB standard is the carbon-13 level found in belemnite from the Pee Dee formation in South Carolina; belemnite is a form of limestone made from the calcification of an extinct order of molluscs related to squid, which were widespread in the Jurassic and Cretaceous periods.) The asterisk at the left-hand side shows the average present-day carbon-13 value. The peaks of carbon-13 (positive anomalies) indicate a substantial increase in the amount of organic-carbon burial (and therefore probably rising oxygen levels), whereas the troughs (negative anomalies) indicate virtually no organic-carbon burial. The negative troughs correspond to possible ice-ages or snowball Earths, of which the two most important were the Sturtian (750-730 million years ago) and the Varanger (610-590 million years ago). Fe indicates the presence of banded-iron formations. The cross marks a major extinction of microplankton that immediately predated the appearance of the Ediacaran fauna — the cushioned Vendobionts and the first worms. Adapted with permission from Knoll and Holland, and the National Academy of Sciences.

#### Likely scenario for the evolution of early life

RNA world T Anaerobic chemotrophic bacteria (LUCA) T Anaerobic chemotrophic bacteria, aided by primitive anaerobic photosynthesis (purple bateria) Accumulation of oxygen in the atmosphere, produced by ultraviolet light breakdown of water molecules T Evolution of biological defenses against oxygen toxicity (enzymatic metabolism of oxygen in many species) Evolution of aerobic photosynthesis (blue-green algae, stromatolites) Further accumulation of oxygen in the atmosphere, reaching levels of 1-4% Evolution of aerobic heterotrophs (conventional bacteria) Evolution of eukaryotic, aerobic organisms (diatoms, protozoa, us)

## 4. The origin of eukaryotic cells

- Eukaryotic cells originated when an archaebacterium (ancestor of our cell nuclei) engulfed a eubacterium (ancestor of our mitochondria).
- These two organisms continue their separate existence in our cells to this day, maintaining their separate chromosomes and separate gene expression apparatus.
- The mixing of these two genomes facilitated aerobic metabolism.
- This first eukaryotic cell is the common ancestor of all plants and animals on earth today.

# 5. The evolution of multicellular plants and animals

High rates of erosion after several "snowball earths" led to increases in atmospheric oxygen to modern levels, which made multicellular life possible



**Figure 4:** Geological timeline expanding the late Precambrian period and Cambrian explosion. Exactly when the first metazoans evolved is not known. Calculations from molecular clocks suggest a date of somewhere between 700 and 1200 million years ago. The succession of snowball Earths appears to have driven atmospheric oxygen up to atmospheric levels similar to those today.

Changes in atmospheric oxygen and carbon dioxide over the last 600 million years



Figure 5: Changes in atmospheric composition over the Phanerozoic period, from 600 million years ago, based on the models of Robert Berner. Oxygen levels (top graph) reached a peak of 35% in the late Carboniferous and early Permian, before falling to 15% in the late Permian. Oxygen levels peaked a second time at 25 to 30% in the late Cretaceous (K) before falling to present atmospheric levels in the Tertiary (T). Carbon dioxide levels (bottom graph) for 0.5% in the Silurian (S) to around 0.03% by the end of the Carbonferous. Reproduced with permission from Graham *et al.*, and *Nature*. Correlations between the body length of amphipods and water temperature (top), vs. dissolved oxygen concentrations (bottom).



**Figure 6:** Correlation between body length of amphipods in millimetres (given as an index of average length,  $TS_{95/5}$ ) and (a) temperature and (b) oxygen concentration. Lake Baikal, the Caspian Sea and the Black Sea are outliers from the temperature curve because they are brackish or freshwater, rather than saline. Oxygen dissolves more readily in freshwater, so the correlation is restored by plotting the length of amphipods against the dissolved oxygen concentration. Reproduced with permission from Chapelle & Peck, and *Nature*.

# Animals thrive without oxygen at sea bottom

Living exclusively oxygen-free was thought to be a lifestyle open only to viruses and single-celled microorganisms. A group of Italian and Danish researchers has now found three species of multicellular animal, or metazoan, that apparently spend their entire lives in oxygen-starved waters in a basin at the bottom of the Mediterranean Sea.

The discovery "opens a whole new realm to metazoans that we thought

was off limits", says Lisa Levin, a biological oceanographer at Scripps Institution of Oceanography in La Jolla, California.

Roberto Danovaro from the Polytechnic University of Marche in Ancona, Italy, and his colleagues pulled up the animals during three research cruises off the south coast of Greece. The species, which have not yet been



Some loriciferans live in anoxic sediments.

named, belong to a phylum of tiny bottom-dwellers called Loricifera. Measuring less than 1 millimetre long, they live at a depth of more than 3,000 metres in the anoxic sediments of the Atalante basin, a place so little explored that Danovaro likens his team's sampling to "going to the Moon to collect rocks".

Researchers have previously found multicellular animals living in anoxic environments, but Danovaro

says that it was never clear whether those animals were permanent residents. The new loriciferans, which he and his team reported this week (R. Danovaro *et al. BMC Biol.* doi:10.1186/1741-7007-8-30; 2010), seem to "reproduce and live all their life in anoxic conditions", he says.

The researchers identified an adaptation

that helps these loriciferans to survive in their environment. Instead of mitochondria, which rely on oxygen, the creatures have organelles that resemble hydrogenosomes, which some single-celled organisms use to produce energy-storing molecules anaerobically.

Angelika Brandt, a deep-sea biologist at Germany's Zoological Museum in Hamburg, says that the work by Danovaro's group is "highly significant". The discovery of metazoans living without mitochondria and oxygen, she says, suggests that animals can occupy niches that once seemed too extreme. Janet Fang

#### Correction

The News Feature 'The human race' (*Nature* **464**, 668-669; 2010) misspelt the name of the architect of whole-genome shotgun sequencing. It should be Gene Myers. This error has been corrected online in the HTML and PDF versions of this story.

#### The "Cambrian explosion" of animal phyla

- Prior to the Cambrian period, the fossil record suggests only a few primitive soft-bodied animals.
- Then all 60 phyla of animals that have ever existed on earth originated within the Cambrian period!
- Actually, most of them originated within the first 8 million years (or less) at the very beginning of the Cambrian!!!
- A prerequisite for this rapid evolution was drastic rises in atmospheric oxygen levels.
- It was probably also partly due to genetic advances (tandem duplication and divergence of Hox genes).
- The result was a morphological "arms race" of predators and prey along shallow sea beds.

#### The extinction of the dinosaurs (and their precursors)

- It is now generally accepted that the extinction of the dinosaurs was caused by a large meteor that landed off the coast of southern Mexico 65.0 million years ago.
- The resulting mass extinctions wiped out approximately 90% of all species on earth (including diatoms in the ocean), and made possible the rise of the mammals (including us).
- The age of the dinosaurs also began with a mass extinction, and the end of the Permian, which may also have been associated with a large meteor collison (and/or catastrophic volcanic eruptions that covered Siberia 1-2 miles deep).
- This earlier catastrophe was worse, because it caused the extinction of at least 95% of all species on earth, and caused the entire world ocean to become anoxic (a "dead zone").

#### 6. Conclusions and implications

- At every stage, life has responded rapidly to changing environmental conditions, in part via gene transfer and gene duplication.
- The early evolution of photosynthesis was probably a key step that saved our oceans and atmosphere from the fate of Mars.
- Many environmental catastrophes have come close to wiping out life as we know it, but were also essential to "clear the decks" for the next stage in evolution.
- Evolution if not "progressive" in any sense. It gives rise to less complex organisms as often as more complex organisms.
- What does this imply for other planets??

#### Further reading

- Alvarez, W. (1997) T.rex and the crater of doom. Princeton University Press, Princeton, NJ.
- Benton, M. J. (2003) *When life nearly died: the greatest mass extinction of all time*. Thames & Hudson, NY.
- Erwin, D. H. (2006) *Extinction: how life on earth nearly ended 250 million years ago.* Princeton University Press, Princeton, NJ.
- Lane, N. (2002) *Oxygen: the molecule that made the world*. Oxford University Press, Oxford U.K.
- Lane, N. (2009) *Life ascending: the ten great inventions of evolution*. Norton, & Company NY.
- Ridley, M. (1999) *Genome: the autobiography of a species in 23 chapters.* Harper Collins, NY.
- Shubin, N. (2008) *Your inner fish: a journey into the 3.5-billion year history of the human body.* Random House, NY.
- Strickberger, M. W. (2000) Evolution (3rd edition). Jones & Bartlett, Sudbury, MA.
- Ward, P. (2004) *Gorgon: paleontology, obsession, and the greatest catastrophe in earth's history.* Viking Penguin, NY.
- Weinberg, S. (2001) A fish caught in time: the search for the coelacanth. Harper Collins, NY.
- Zimmer, C. (1999) *Fish with fingers, whales with legs, and how life came ashore but then went back to sea.* Touchstone, NY.