Revisiting Evolution in the 21st Century

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Disentangling basic issues in evolutionary debates

1. Origin of life & the first cells
   - still on the fringes of serious scientific discussion

2. Descent with modification of related living organisms
   - more convincing with each new technological advance (e.g. detailed protein and genome phylogenies)
   - but more complicated than simple vertical inheritance

3. The actual processes of evolutionary change over time
   - an ever growing number of distinct documented cellular and molecular events different from conventional predictions
   - novel molecular possibilities of genome reorganization as we learn more about how cells interact and control genome structure
Outstanding Questions Still at Issue in 21st Century Evolutionary Theory

• Where does novelty come from in evolution? (Nothing for selection to do with no differences.)

• Descent with modification: tree/web of life? how many cell types in the beginning? role of virosphere?

• Nature of heredity and hereditary change: vertical/horizontal transmission, passive/active variations, micro/macromutations, isolated/interactive germ plasm, Central Dogma still valid?

• Role of selection: positive/neutral/purifying?

• Relationship of evolutionary change to planetary, environmental & ecological events?
Major Points

1. The focus in biology has changed from mechanics to informatics. Cells are sensitive and communicative information-processing entities.

2. Cell-generated hereditary innovation is the source of new features in evolution.

3. Genome change is a cell-regulated process, not a series of accidents. (Genome as RW, not ROM, memory system)

4. The DNA record tells us that major steps in genome evolution have involved rapid genome-wide changes.

5. We know of molecular processes that allow us to think scientifically about complex evolutionary events – particularly about the rapid evolution of genomic circuits and multi-component adaptations.
Sensing, communication and information processing by cellular & intercellular networks: the sexually aroused yeast cell.
Revisiting the Central Dogma
(from genetic reductionism to systems biology)

Table I.1. Changing views of intracellular molecular information transfer


- (DNA -> 2X DNA) --> RNA --> Protein --> Phenotype


- DNA + 0 --> 0
- DNA + Protein + ncRNA --> chromatin/epigenetic markings (epigenotype)
- Chromatin + Protein + ncRNA --> DNA replication, chromatin maintenance/reconstitution
- Protein + RNA + lipids + small molecules --> signal transduction
- Signals + Chromatin + Protein --> RNA (primary transcript)
- RNA + Protein + ncRNA --> RNA (processed transcript)
- RNA + Protein + ncRNA --> Protein (primary translation product)
- Signals + chromatin + proteins + ncRNA + lipids --> nuclear/nucleoid localization
- Protein + nucleotides + Ac-CoA + SAM + sugars + lipids --> Processed and decorated protein
- DNA + Protein --> New DNA sequence (mutator polymerases, terminal transferases)
- Chromatin + Protein --> New DNA structure (DNA-based rearrangements)
- RNA + Protein + chromatin --> New DNA structure and sequence (retrotransposition, retroduction, retrohoming, diversity-generating retroelements)

- Protein + ncRNA + chromatin + signals + other molecules + structures <-> Phenotype & Genotype & Epigenotype
Key non-Darwinian Evolutionary Scientists in the 20th Century

- **William Bateson** (1861-1926) & **Hugo de Vries** (1848-1935): abrupt variation as a source of evolutionary novelty
- **Richard Goldschmidt** (1878-1958): altering developmental processes as a source of rapid evolutionary novelty (“hopeful monsters” and Evo-Devo)
- **Barbara McClintock** (1902-1992): genetic change as a biological response to danger and evolutionary novelty through genome restructuring resulting from “shocks”
- **G Ledyard Stebbins** (1906-2000): hybridization between species as a source of evolutionary novelty
- **Carl Woese** (1928- ): molecular phylogeny and the existence of at least three distinct cell kingdoms
- **Lynn Margulis** (1938- ): cell mergers/symbiogenesis as a source of evolutionary novelty
Four kinds of rapid, multi-character changes Darwin could not have imagined

• Horizontal DNA transfer in evolution;
• Multiple cell types and cell fusions (symbiogenesis) in evolution;
• Genome doublings at key steps of eukaryotic evolution;
• Built-in mechanisms of genome restructuring = natural genetic engineering
Evolution in real time using horizontal DNA transfer: Bacterial antibiotic resistance

Pssst! Hey kid! Wanna be a Superbug...?
Stick some of this into your genome...
Even *penicillin* won't be able to harm you...!

It was on a short-cut through the hospital kitchens that Albert was first approached by a member of the Antibiotic Resistance.
Transmissible Antibiotic Resistance

PROKARYOTES AND EUKARYOTES are fundamentally different at the structural level, as is shown by these schematized drawings of a typical prokaryotic cell (left) and eukaryotic cell (right). The prokaryote is by far the smaller cell. Little subcellular structure is seen even at the scale revealed by the electron microscope; a single circular strand of the genetic material DNA lies loose in the cytoplasm. Both the archaeabacteria and the eubacteria are prokaryotes and share prokaryotic structural properties. The eukaryotic cell is much larger and has a number of discrete subcellular structures. Its DNA, complexed with proteins, is organized into chromosomes within a membrane-bounded nucleus. Mitochondria carry out cellular respiration; in a plant cell there are chloroplasts, which conduct photosynthesis. The Golgi apparatus is a secretory organelle; the endoplasmic reticulum is a membrane system along parts of which some of the cell’s ribosomes (on which genetic information is translated into protein) are arrayed. All cells more complex than the bacteria are eukaryotes.
Tree of life idea

1844 letter from Darwin to Joseph Hooker

Carl R. Woese
Archaeabacteria.
Scientific American
16S ribosomal RNA - molecular basis for phylogenies

165 RIBOSOMAL RNA is the molecule whose nucleotide sequences in a number of organisms have been compared in order to establish phylogenetic relations. The molecule is a component of the ribosome, the molecular machine that synthesizes proteins; the designation 16S refers to the speed with which the molecule sediments in a centrifuge, measured in Svedberg units. The RNA molecule is a long chain of the subunits called nucleotides, each of which is characterized by one of four bases: adenine (A), uracil (U), guanine (G) or cytosine (C). The first two bases and the last two are complementary: they can be linked by hydrogen bonds to form pairs, A pairing with U and G pairing with C. Base pairing determines what is called the secondary structure of the molecule, or the way in which it initially folds, by forming some 50 short double-strand structures in which the bases are paired (barred regions). The drawing shows secondary structure of the 16S RNA of the eubacterium Escherichia coli, full sequence of which was determined by Harry F. Noller, Jr., of the University of California at Santa Cruz.

Carl Woese, molecular phylogeny, and three cell kingdoms (1977)

<table>
<thead>
<tr>
<th></th>
<th>Archaea</th>
<th>Eubacteria</th>
<th>Eukaryotes</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cell size</strong></td>
<td>About 1 micrometer</td>
<td>About 1 micrometer</td>
<td>About 10 micrometers</td>
</tr>
<tr>
<td><strong>Cellular organelles</strong></td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
</tr>
<tr>
<td><strong>Nuclear membrane</strong></td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
</tr>
<tr>
<td><strong>Cell wall</strong></td>
<td>Variety of types; none incorporates muramic acid</td>
<td>Variety within one type; all incorporate muramic acid</td>
<td>No cell wall in animal cells; variety of types in other phyla</td>
</tr>
<tr>
<td><strong>Membrane lipids</strong></td>
<td>Ether-linked branched aliphatic chains</td>
<td>Ether-linked straight aliphatic chains</td>
<td>Ether-linked straight aliphatic chains</td>
</tr>
<tr>
<td><strong>Transfer RNAs</strong></td>
<td>Thymine in 'common' arm</td>
<td>Present in most transfer RNAs of most species</td>
<td>Present in most transfer RNAs of most species</td>
</tr>
<tr>
<td><strong>Dihydrofolate reductase</strong></td>
<td>Absent in all but one genus</td>
<td>Present in most transfer RNAs of all species</td>
<td>Present in most transfer RNAs of all species</td>
</tr>
<tr>
<td><strong>Amino acid carried by initiator transfer RNA</strong></td>
<td>Methionine</td>
<td>Formylmethionine</td>
<td>Methionine</td>
</tr>
<tr>
<td><strong>Ribosomes</strong></td>
<td>30S, 50S</td>
<td>30S, 50S</td>
<td>40S, 60S</td>
</tr>
<tr>
<td><strong>Approximate length of 16S (18S) RNA</strong></td>
<td>1,500 nucleotides</td>
<td>1,500 nucleotides</td>
<td>1,800 nucleotides</td>
</tr>
<tr>
<td><strong>Approximate length of 23S (25-28S) RNA</strong></td>
<td>2,900 nucleotides</td>
<td>2,900 nucleotides</td>
<td>3,500 nucleotides or more</td>
</tr>
<tr>
<td><strong>Translation elongation factor</strong></td>
<td>Reacts with diphtheria toxin</td>
<td>Does not react with diphtheria toxin</td>
<td>Reacts with diphtheria toxin</td>
</tr>
<tr>
<td><strong>Sensitivity to chloramphenicol</strong></td>
<td>Insensitive</td>
<td>Sensitive</td>
<td>Insensitive</td>
</tr>
<tr>
<td><strong>Sensitivity to ansomycin</strong></td>
<td>Sensitive</td>
<td>Insensitive</td>
<td>Sensitive</td>
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<tr>
<td><strong>Sensitivity to kanamycin</strong></td>
<td>Insensitive</td>
<td>Sensitive</td>
<td>Insensitive</td>
</tr>
<tr>
<td><strong>Messenger RNA binding site nucleotide at 3' end of 16S (18S) RNA</strong></td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
</tr>
</tbody>
</table>

**Bacteria**

**Archaea**

**Eucarya**
REvised “tree” of life retains a treelike structure at the top of the eukaryotic domain and acknowledges that eukaryotes obtained mitochondria and chloroplasts from bacteria. But it also includes an extensive network of untreelike links between branches. Those links have been inserted somewhat randomly to symbolize the rampant lateral gene transfer of single or multiple genes that has always occurred between unicellular organisms. This “tree” also lacks a single cell at the root; the three major domains of life probably arose from a population of primitive cells that differed in their genes.
Mitochondria and chloroplasts are endosymbiotic bacteria inside eukaryotic cells.
What genomes teach: cell fusions at key places in eukaryotic evolution

GL Stebbins and interspecific hybridization

Nigra = black mustard
Juncea = mustard greens
Rapa = mizuna (turnip mustard)
Napus = rapeseed (canola)
Oleracea = wild cabbage
Carinata = Ethiopian mustard

www.answers.com/ topic/g-ledyard-stebbins
Whole genome duplications in vertebrate evolution

McClintock, B. 1941. The stability of broken ends of chromosomes in Zea Mays. Genetics 26:234-282. “If chromosomes are broken by various means, the broken ends appear to be adhesive and tend to fuse with one another 2-by-2. . . .

http://atlasgeneticsoncology.org//Deep/RingChromosID20030.html
“In the future, attention undoubtedly will be centered on the genome, with greater appreciation of its significance as a highly sensitive organ of the cell that monitors genomic activities and corrects common errors, senses unusual and unexpected events, and responds to them, often by restructuring the genome.”


Adaptive Mutation

Stimuli that Activate Natural Genetic Engineering and Disrupt Epigenetic Silencing

- Chromosome breaks (McClintock, 1944)
- Pheromones, hormones & cytokines
- **Starvation** (Shapiro, 1984)
- DNA damage (mutagens)
- Telomere erosion
- Antibiotics, Phenolics, Osmolites

- Oxidants
- Pressure, Temperature, Wounding
- Protoplasting & growth in tissue culture
- Bacterial or fungal infection & endosymbiosis
- Changes in ploidy & DNA content (genome doubling)
- Hybridization (interspecific mating)
Searching Genome Space by Natural Genetic Engineering: More Efficient than a Random Walk Guided by Gradual Selection

• combinatoric search using established functional modules (e.g., domain accretion and shuffling)

• activation when most biologically useful by “genome shock” (including starvation, infection, hybridization) ==> bursts of coordinated changes

• network adaptation after WGD, domain shuffling, establishment of novel interaction patterns

• molecular mechanisms for targeting coincident changes to functionally related locations (research agenda for the coming decades)
A 21st Century View of Evolution

1. Ecological disruption ==> changes in biota, food sources, adaptive needs & organismal behavior;
2. Macroevolution triggered by cell fusions & interspecific hybridizations (WGDs) leading to massive episodes of horizontal transfer, genome rearrangements;
3. Establishment of new cellular and genome system architectures; complex novelties arising from WGD and network exaptation;
4. Survival and proliferation of organisms with useful adaptive traits in depleted ecology; elimination of non-functional architectures; selection largely purifying;
5. Microevolution by localized natural genetic engineering after ecological niches occupied (immune system model).