[If you don't know what a "gene" or a "genome" is by now, find out before you read this.]

Major Evolutionary Processes at the Genome Level

Basic ideas of inheritance, variation, and natural selection, the main features of traditional evolutionary theory, are still intact, just wildly elaborated. Primary difference is that the genome is much more dynamic than simple point mutations leading to gradual change. Instead, **genome evolution is dominated by *mobile elements***, like transposons, plasmids, and more. Those features of the genome are referred to as the "mobilome" (just as an organism's repertoire of proteins is called the "proteome"). The following list summarizes a few of the most important of these processes, starting with the most general features of the evolutionary process, then specific genome-level events.

Variation--today we know that the variation is genetic, caused partly by mutations due to DNA damage which is not repaired exactly. *Most* of these mutations are deleterious (not adaptive or beneficial). The big difference is that now it is understood that there are many sources of variation, involving much more dynamic processes of genome change, discussed below.

Punctuated equilibrium --in many cases rate of evolution has not been gradual as originally imagined, but in bursts and lulls ("stasis," long periods during which little evolution of a species occurs). *This is not a theory, just an observation of the fossil record--sometimes developments are rapid.* Some evolutionary biologists had a difficult time accepting this, but today it is not considered unusual, partly because of the more dynamic picture of the genome (below).

Sudden, often catastrophic, environmental changes --Giant impactors, Snowball Earth episodes, alternating glaciations and interglacials, variations in the ozone shield due to giant solar flares,, … Maybe related to punctuated equilibrium, but can't be the whole story (punctuated equilibrium is seen in laboratory bacterial evolution)

Neutral evolution --neutral mutations can occur, neither deleterious or beneficial, and which get "fixed" in a species is just a matter of chance ("genetic drift"). Kimura proposed that evolution was dominated by neutral mutations $\Rightarrow$ would be big blow to idea of natural selection. But now understood that genetic drift is just part of the story and natural selection is undoubtedly important in many or most cases.

Genome-level processes that control evolution:

Recombination-- partial strand of DNA is broken, then joined to another DNA. In Eukaryotes occurs during meiosis as pairs of chromsomes "cross over". Leads to offspring having different combinations of genes from their parents. This process is believed to be important in increasing complexity of organisms and avoiding a "mutational meltdown" by accumulated mutations. *Note:* In prokaryotes the enzyme that catalyzes recombination, the RecA protein, is also used to repair double strand break DNA damage. Think about it--the two broken DNAs have to join again. This implies that recombination, which is the essential feature of sex, can arise once an enzyme evolves for efficient DNA repair. We expect repair of damage to the genetic code to be universal, so ***recombination might be a convergent trait.***

Exaptation--change of function for some trait coded by some gene(s). E.g. wings in insects. May have once been thermal regulators, "blankets". Bird feathers apparently once served the same purpose. Note how this avoids many of the problems with seeing how complex traits like bird flight could have evolved gradually (what good is 5% of wings?)

Epistasis--Genes influence neighboring genes, either positively (e.g. a gene produces protein that activates neighbor gene) or negatively (e.g. gene codes for protein suppressing the expression of neighboring gene). Can no longer model gene evolution independently of other genes. Sexual populations predominantly negative epistasis, maybe as a way of eliminating deleterious mutations. See epistasis blog at epistasis.org.

Mutator genes, heat shock proteins, …-- organisms alter their mutaton rate (affecting diversity) in times of stress. At one time interpreted as "directed mutation," implying that environment affects genome, which violates the "central dogma" of molecular biology. Increases diversity by rampant mutations.

Lateral (or horizontal) transfer of genetic material between organisms (e.g. "viral transduction"). One of top three processes in prokaryotes, but incidence and significance in eukaryotes (or prokaryote-to-human!) has been controversial. A. M. Nedelcu et al. 2008 J. Evol. Biol. 21, 1852 found four cases of adaptive eukaryote-to-eukaryote lateral gene transfers in the closest unicellular relatives of animals, the choanoflagellates.

Transposable genetic elements --Transposons are sequences of DNA that can move around to different positions within the genome of a single cell. 2 types: "copy and paste" and "cut and paste." Results in *insertions, deletions, and translocations* (the terms mean just what they sound like). Can result in sudden and dramatic changes in genetic structure (first proposed by McClintock in 1970s, "jumping genes"). Retroviruses (involved in onset of cancer, HIV retrovirus,…) are specialized transposons, suggesting how they may have evolved. Now seen as insidious *mutagens* and *pathogens*, more like selfish DNA parasites, similar to viruses. Bacteria use *gene deletion* to remove transposons, while eukaryotes may have developed RNA interference mechanism to reduce transposon activity. But vertebrate immune system uses a similar mechanism to produce antibody diversity. And in bacteria they act as mutators, a source of diversity.

Gene duplication (and even genome duplication!)--could be the most important driver of evolution. The "spare copy" can mutate at a much higher rate, without consequences. So can result in rapid evolution. Can even have entire genome duplicated. E.g. wheat is a "hexaploid" with five copies of its genome. Plants are most prolific genome duplicators.

Gene loss -- among prokaryotes, this has turned out to be a major mode of evolutionary development; a recent detailed study (Koonin et al. 2008) has it three times as common as horizontal transfer. Insidious example: the *mycoplasma* bacterium (M. pneumoniae, M. genitalium, …): no cell wall, so unaffected by many common antibiotics; tiny, can change shapes radically,… Once thought to be extremely primitive because of very small genome, but now understood as product of extreme gene loss. Branched from Steptococci about 600 Myr ago, has been discarding genes ever since. *If this was a major mode of evolution, it does* ***not*** *support the idea that life "naturally" evolves into more complex forms!*

Introns, … we'll stop with gene loss.

The major question for us: How "random" of "chancy" or "unlikely" are these processes and the forms of life they led to? Just think of the mutators, churning out large numbers of random mutations, on the chance that one or more of them might adapt to the changing environmental conditions. Yet we speculated that recombination (sex) might be a convergent property because it basically just needs a DNA repair specialist, and any coding organism will have to repair.