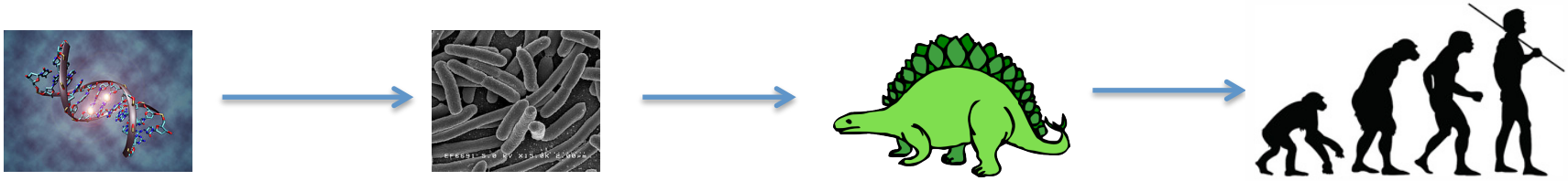
The evolution of complexity I

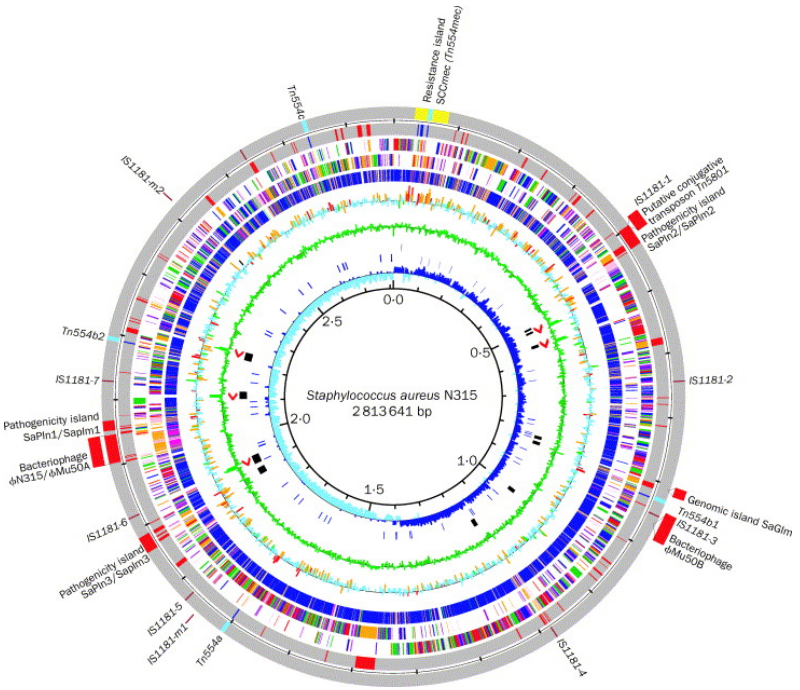
Iain Mathieson

There is no theoretical reason to expect evolutionary lineages to increase in complexity with time, and no empirical evidence that they do so. Nevertheless, eukaryotic cells are more complex than prokaryotic ones, animals and plants are more complex than protists, and so on. This increase in complexity may have been achieved as a result of a series of major evolutionary transitions. These involved changes in the way information is stored and transmitted.

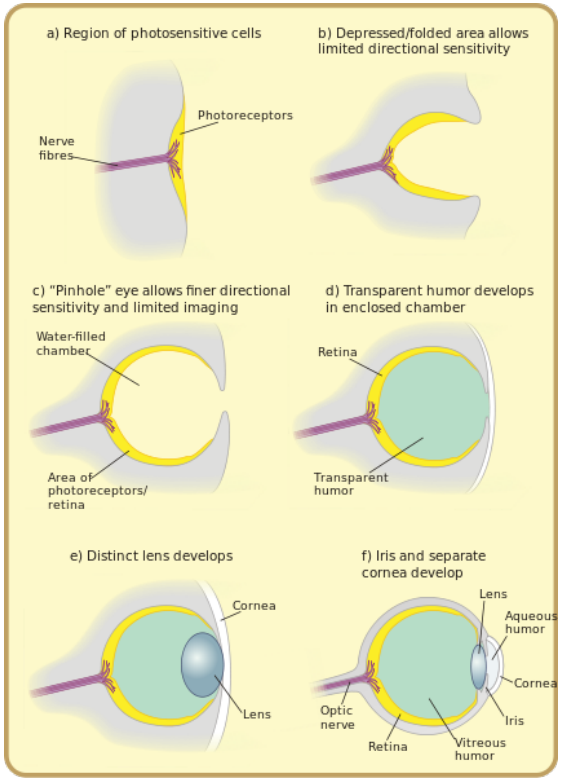
- SZATHMÁRY & MAYNARD SMITH. *Nature.* 1994

Complexity as progress:



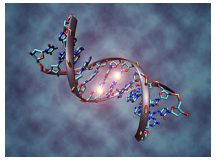


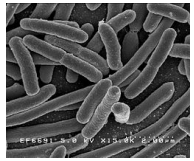
Kuroda et al.; *The Lancet*; 2001

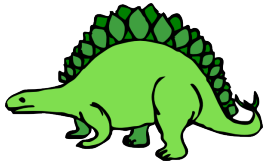


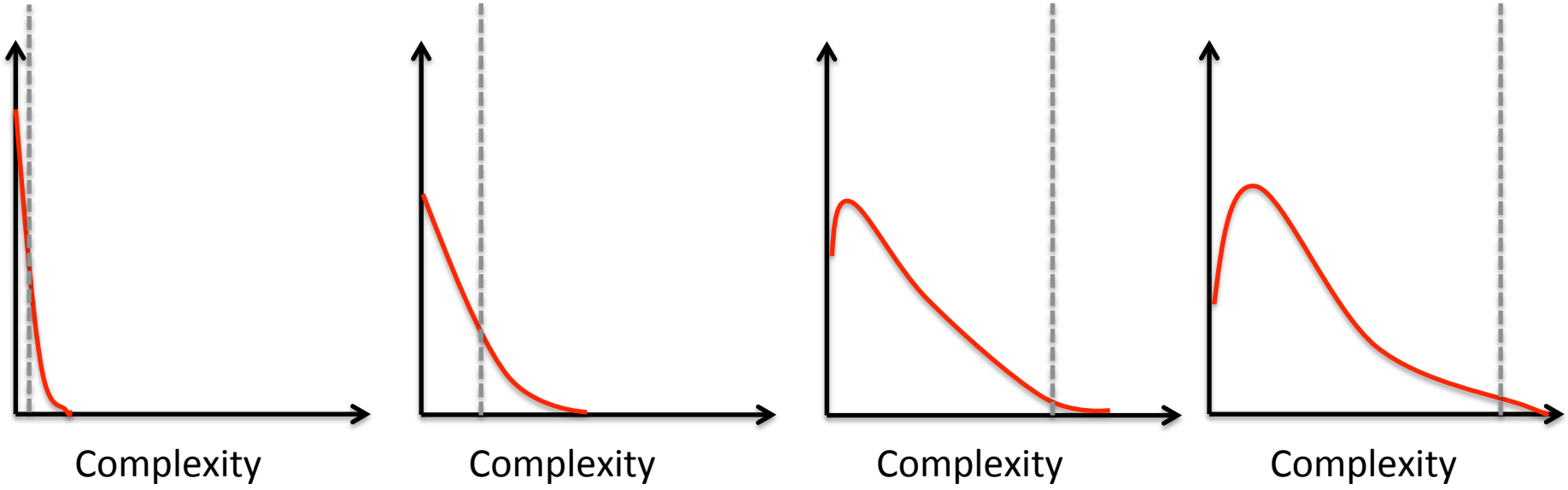
http://en.wikipedia.org/wiki/File:Diagram_of_eye_evolution.svg

Complexity as a random walk:



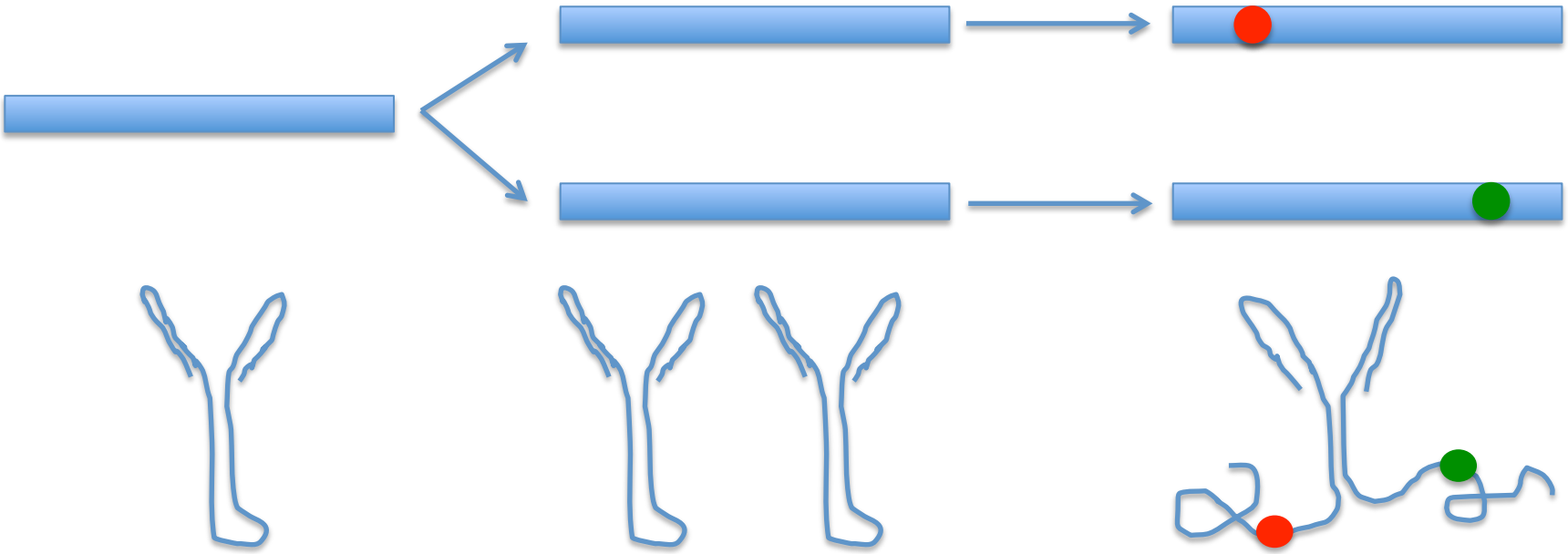






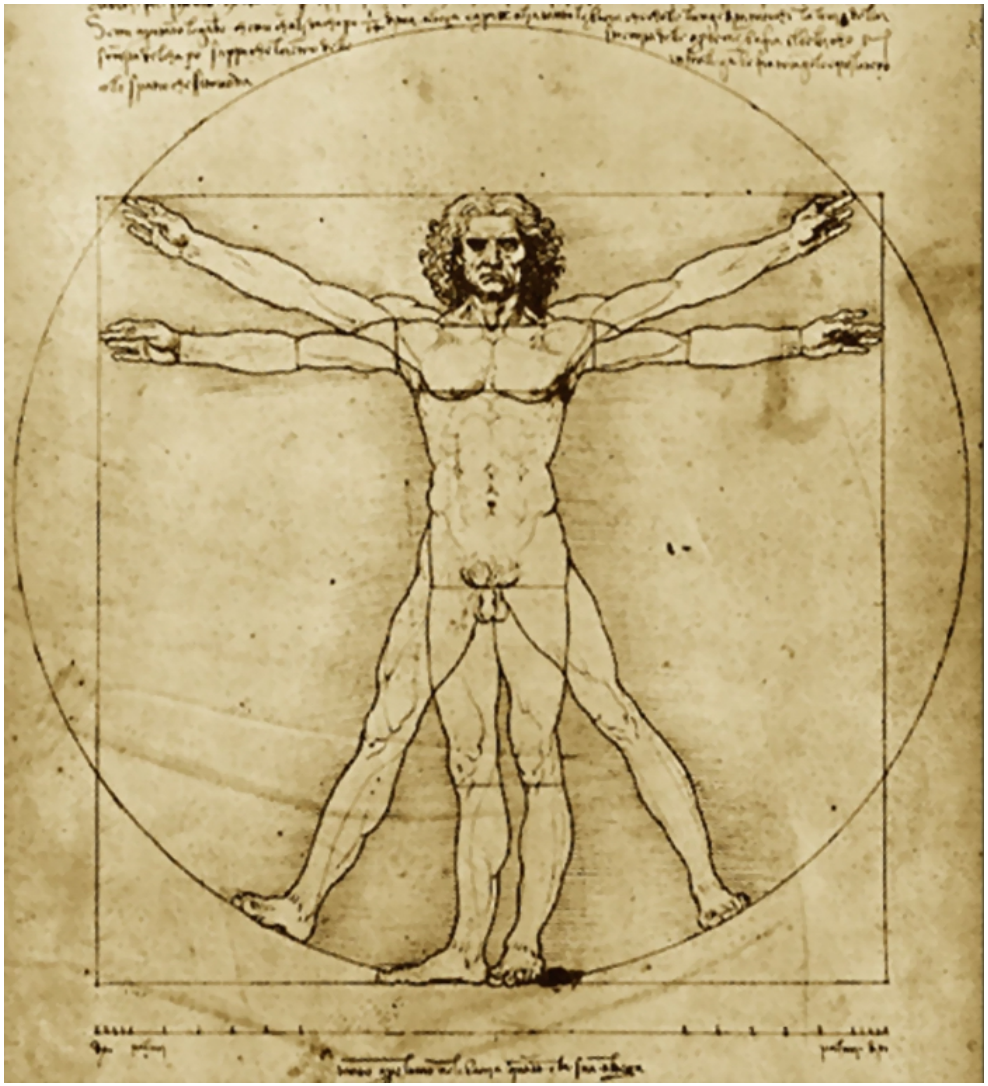
(Irreducible) Complexity as a ratchet:

Example: gene duplication



Ohno; *Evolution by gene duplication*; 1970
Force et al. *Genetics;* 1999
Finnegan et al. *Nature* 2012

I: Genomic complexity



Human genome size:

~ 3.2 Gbases
~ 760 Mbytes

Diffs, ~ 1/100 – 1/1000 bases

Human species ~ 5-50 Pbytes

~15 Pb/year

Composition of the human genome

"Junk" (64%)
44% transposable elements
9% viral DNA
9% intronic sequence (not included above)
1% pseudogenes

"Useful" (9%)
2% protein coding sequence (~20,000 genes)
2% regulatory RNA
2% centromeres
1% essential regulatory regions
2% other conserved regions

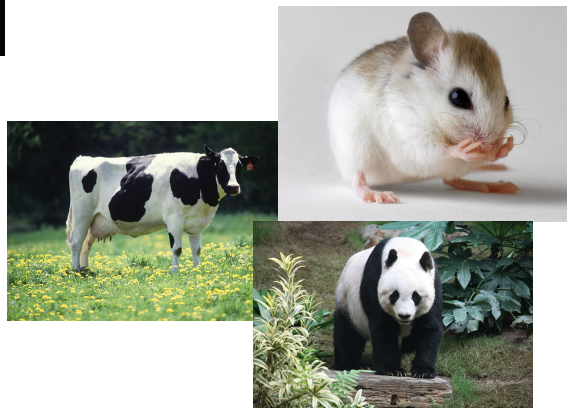
The rest:
~ 26% unknown but unconserved

Source: Laurence Moran

Other estimates of "Useful content" ~3-15%
See Ponting & Hardisson
Genome Research 2011

Fugu rubripes 0.4Gb

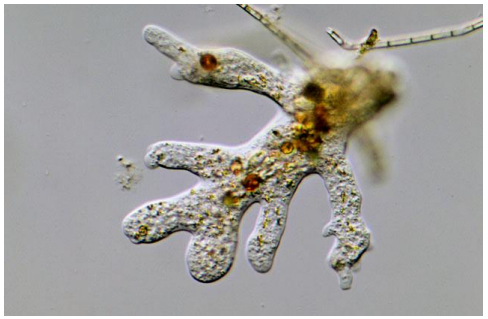
Lilium longiflorum 90Gb



Mammals ~3Gb

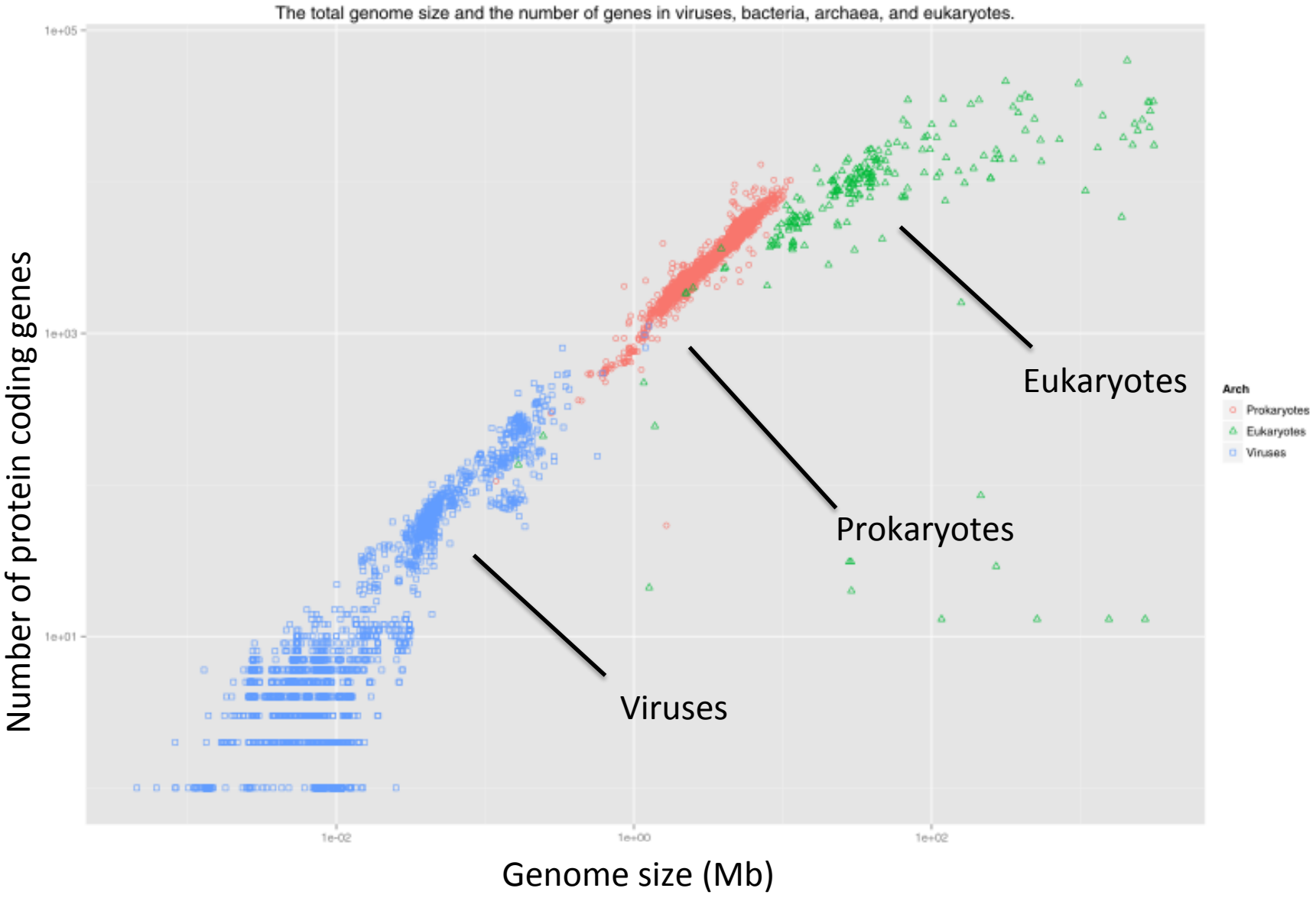
Necturus maculosus 50 Gb

Archilochus alexandri 0.9Gb

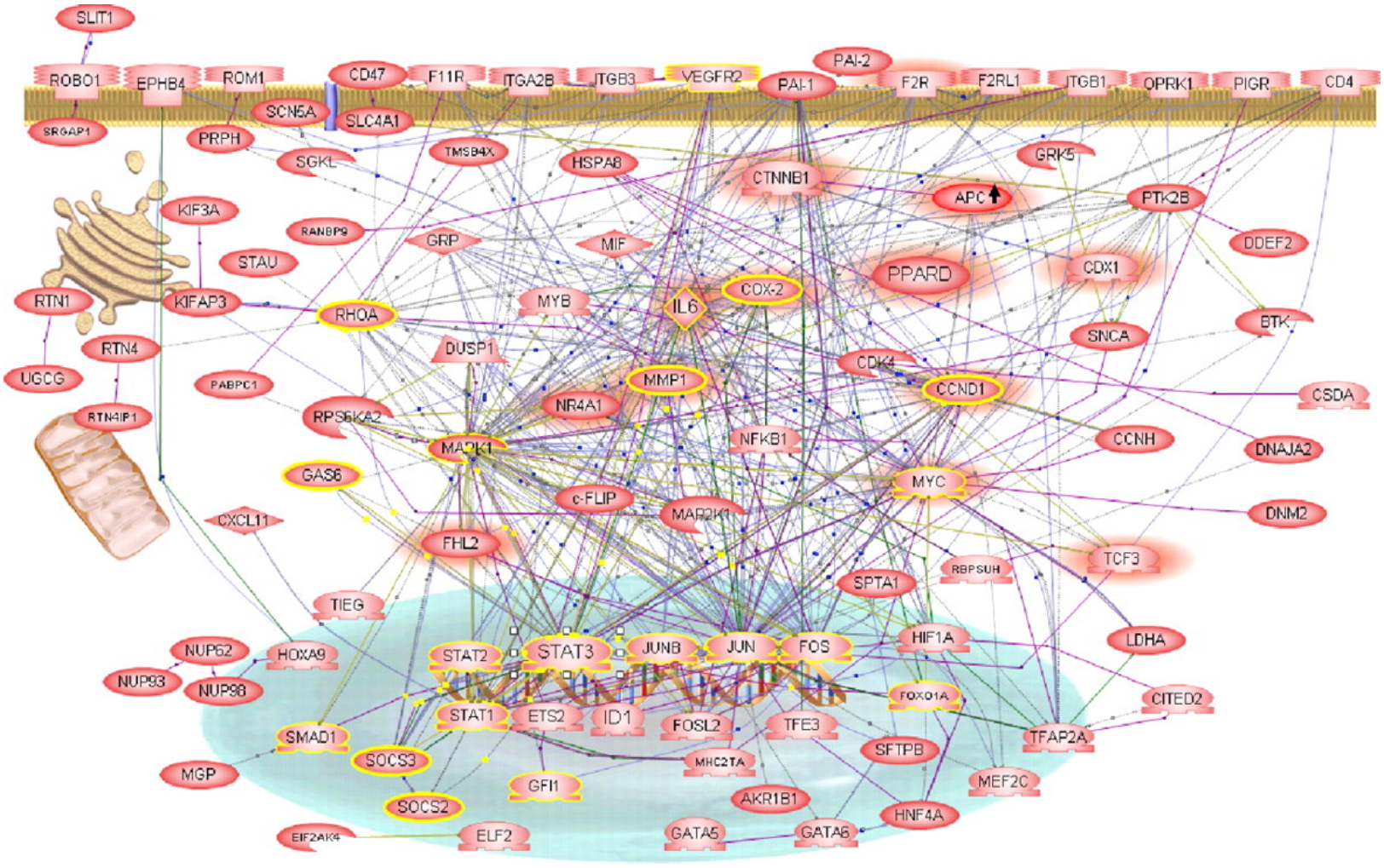


Polychaos Dubium “670Gb”

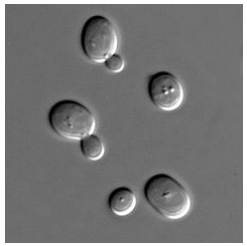
Images: Wikipedia



http://commons.wikimedia.org/wiki/File:Genome_size_vs_number_of_genes.svg

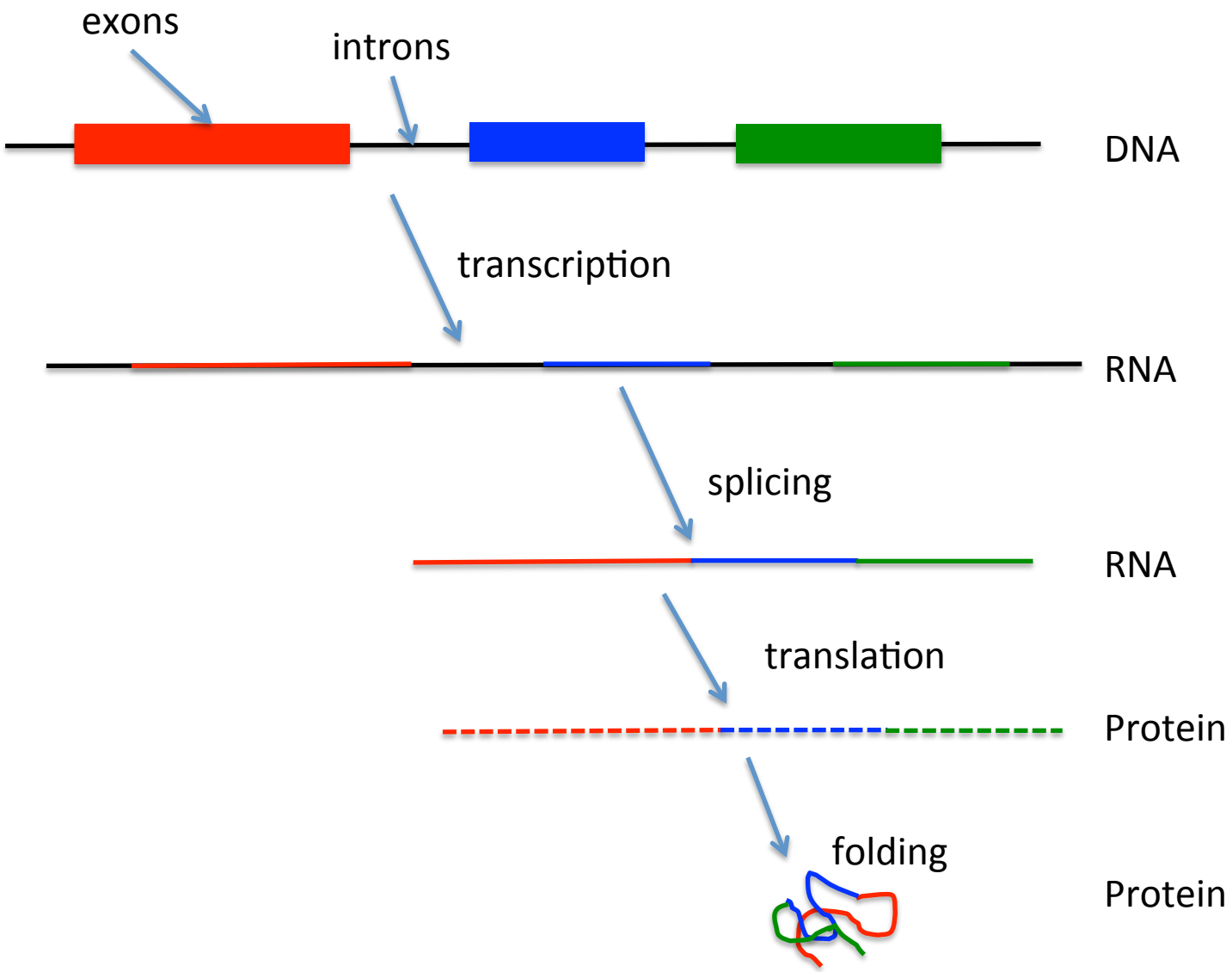


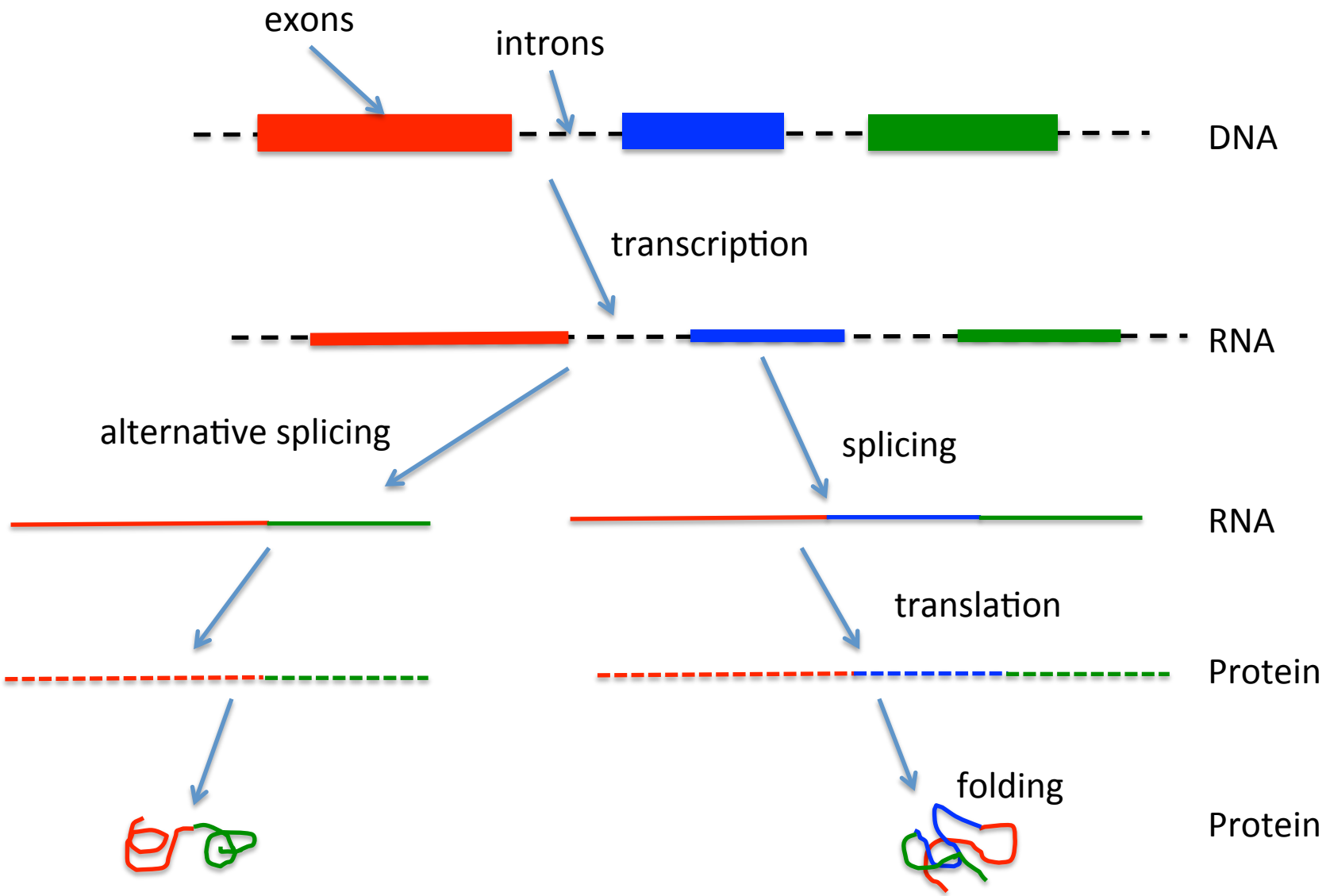
Abdollahi et al. *PNAS* 2007

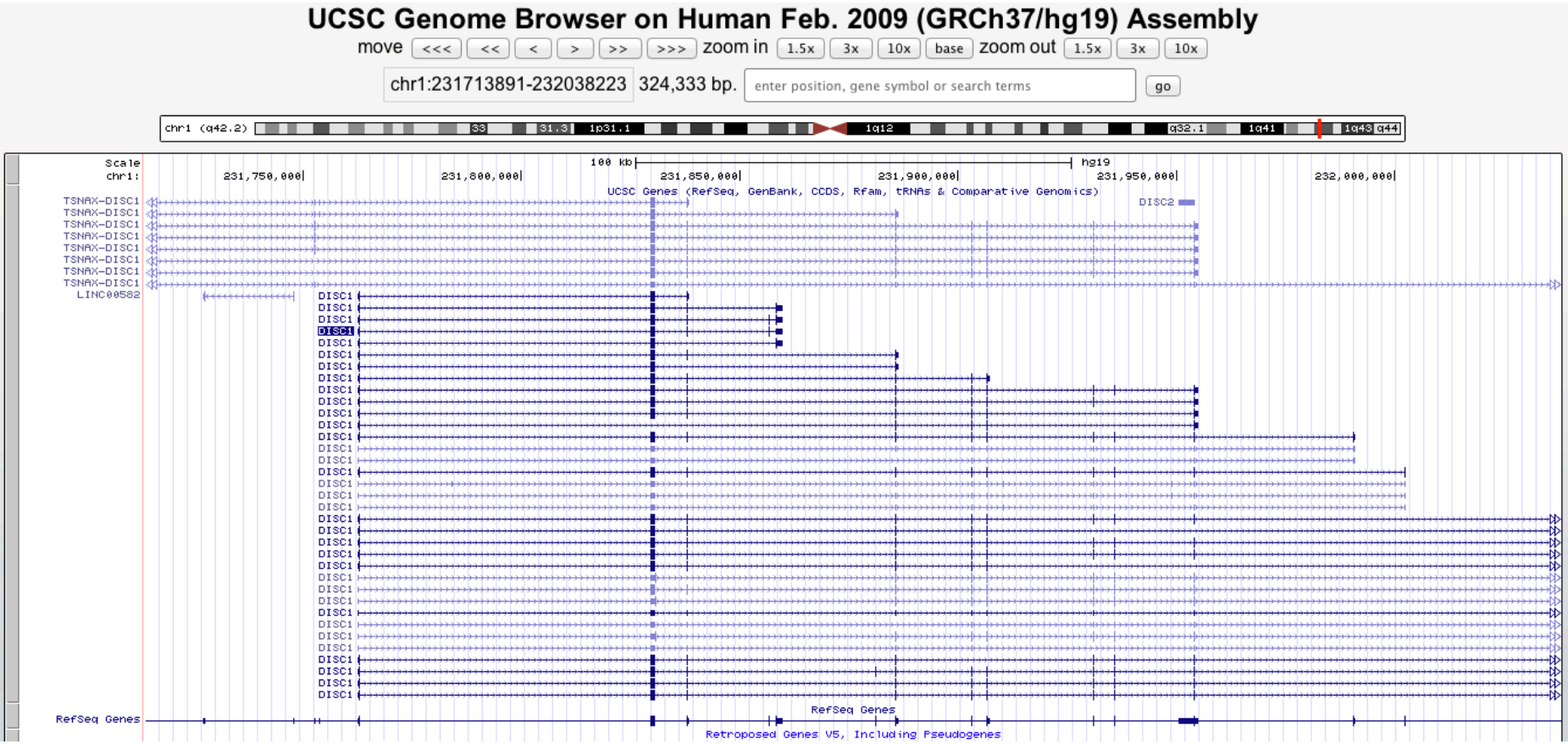


Genome size	3 Gb	137 Mb	100Mb	12 Mb
Number of genes	24,000	16,000	21,000	6,200
Mean exonic length/kb	1.3	1.7	1.3	1.44
Mean intronic length/kb	32	2.9	0.64	0.02
Mean regulatory/kb	2.0	1.4	0.43	0.11

Data: Lynch; *The evolution of genome architecture*; Chapter 3


exons
introns
DNA
transcription
RNA
splicing
RNA
translation
Protein
folding
Protein


exons
introns
DNA
transcription
RNA
alternative splicing
splicing
RNA
translation
Protein
folding
Protein


UCSC Genome Browser on Human Feb. 2009 (GRCh37/hg19) Assembly
move <<< << < > >> >>> zoom in 1.5x 3x 10x base zoom out 1.5x 3x 10x
chr1:231713891-232038223 324,333 bp.
enter position, gene symbol or search terms
go
chr1 (q42.2)
Scale
chr1:
231,750,000
231,800,000
100 kb
231,850,000
231,900,000
hg19
231,950,000
232,000,000
UCSC Genes (RefSeq, GenBank, CCDS, Rfam, tRNAs & Comparative Genomics)
TSNAX-DISC1
DISC2
LINC00582
DISC1
RefSeq Genes
Retroposed Genes V5, Including Pseudogenes

Alternative splicing increases complexity, but is it adaptive?

- Cost of additional transcription.
- Damaging splicing errors.
- Larger target for damaging mutations.

An argument from population genetics….

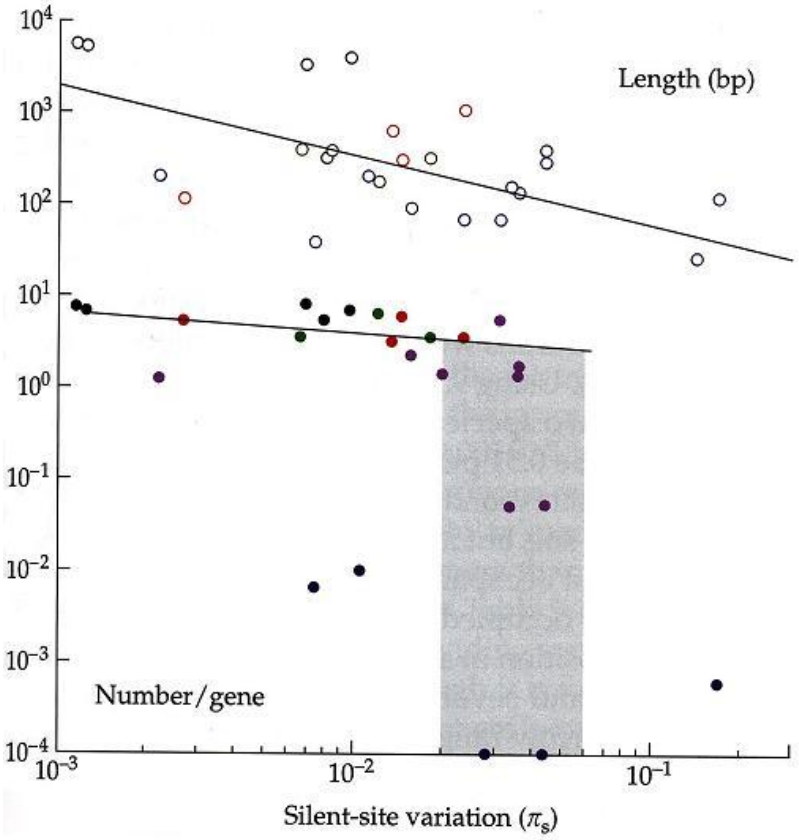


Figure 9.7 The relationship of the average number of introns per gene (solid points) and average intron length (bp, open points) to estimates of $2N_g u$ derived from levels of nucleotide variation at silent sites in protein-coding genes in eukaryotic species (see Chapter 4). All species-specific estimates of intron properties are based on surveys of the entire genome (black, vertebrates; red, invertebrates; green, land plants; purple, unicellular and oligocellular species). The shaded gray region denotes a rough transition between intron-rich and intron-poor taxa. (Data from Lynch 2006a and a few additional recent references.)

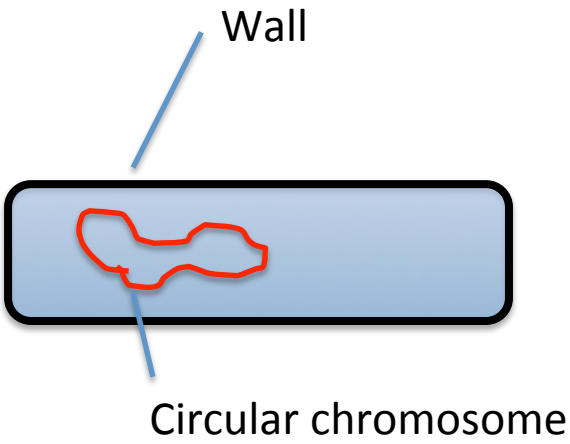
Figure: Lynch; *The evolution of genome architecture*; Chapter 9

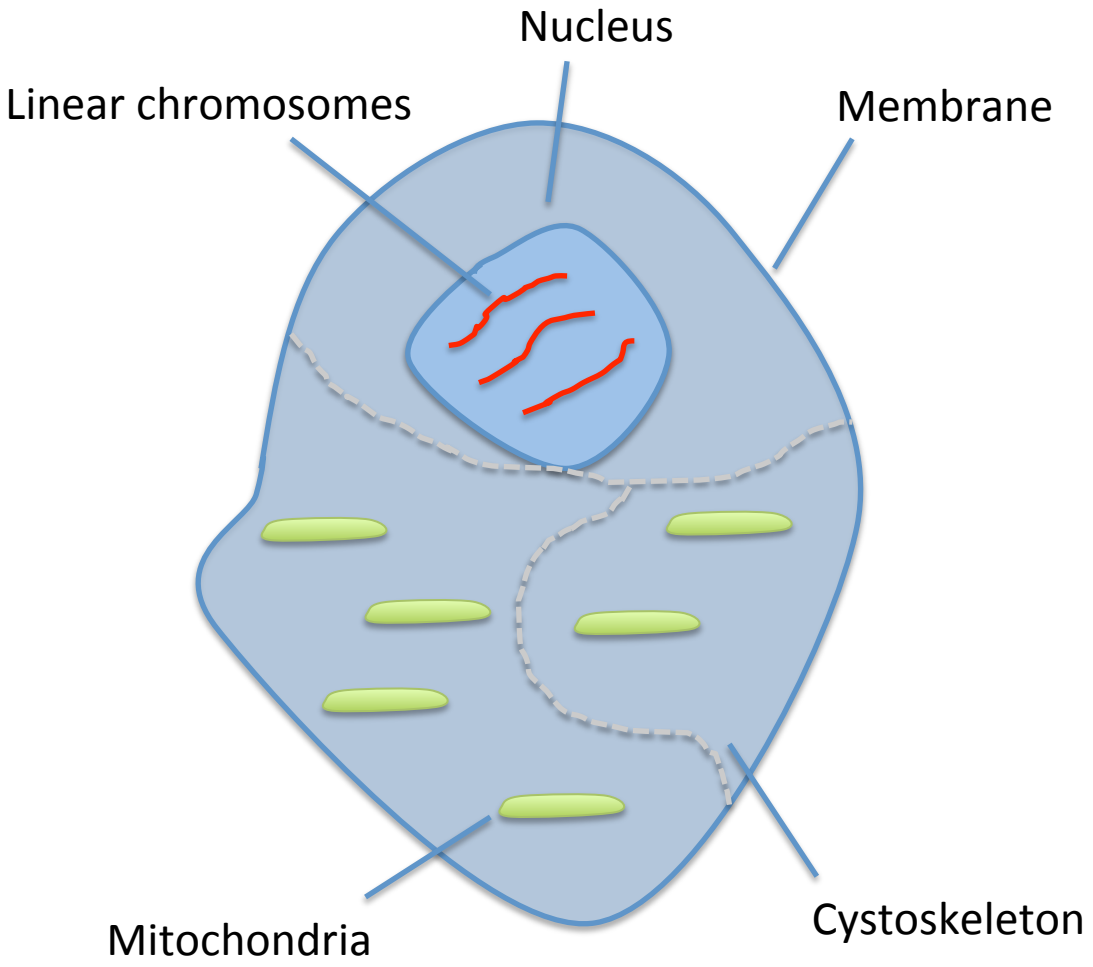
II: Organizational complexity

"The major transitions" – Maynard Smith and Szathmáry

1. Molecules ➔ Populations of molecules
2. Genes ➔ Chromosomes
3. RNA ➔ DNA
4. Prokaryotes ➔ Eukaryotes
5. Asexual ➔ Sexual
6. Protists ➔ Plants, animals and Fungi
7. Individuals ➔ Colonies
8. Primate societies ➔ Human societies

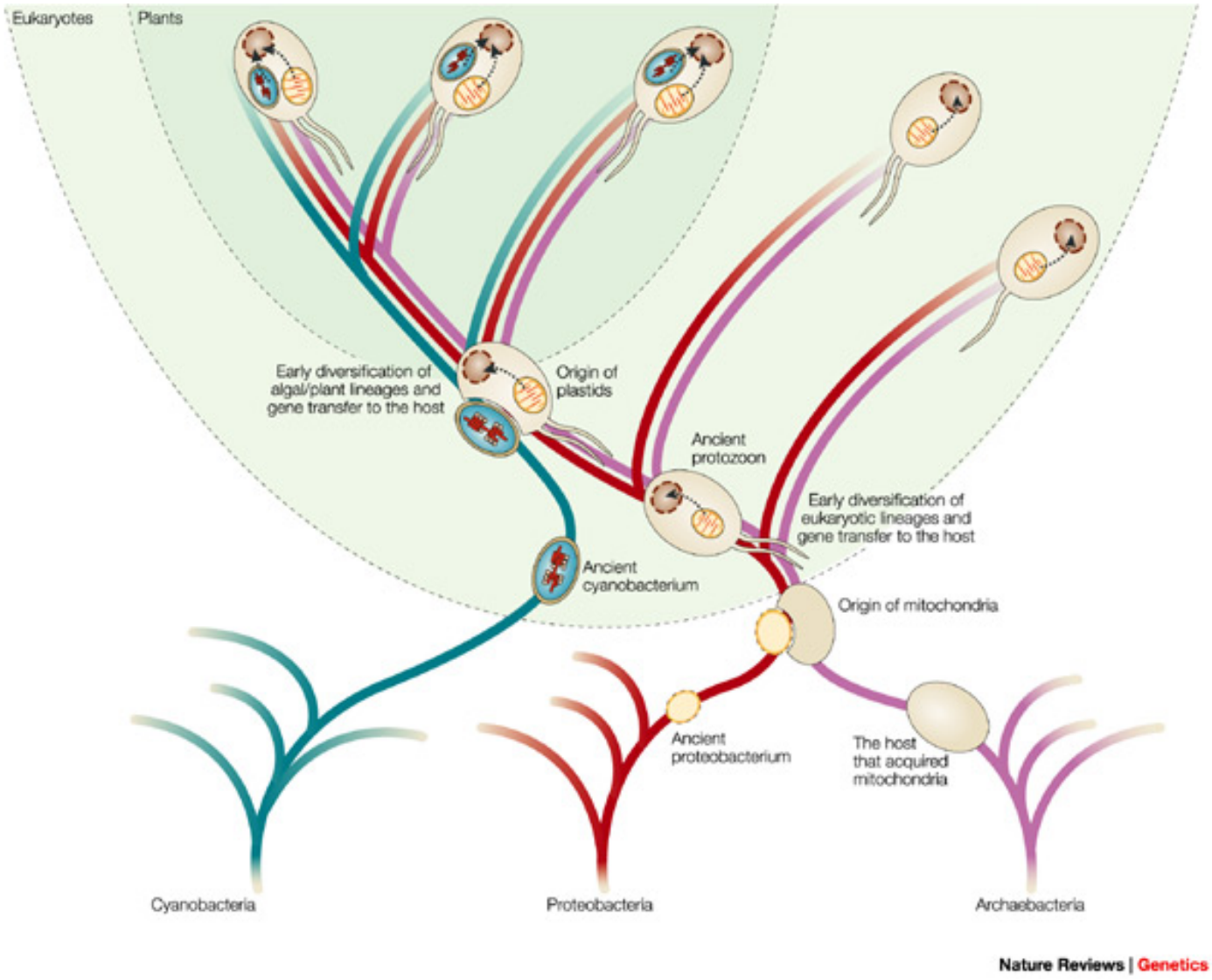
The evolution of eukaryotes





Prokaryote

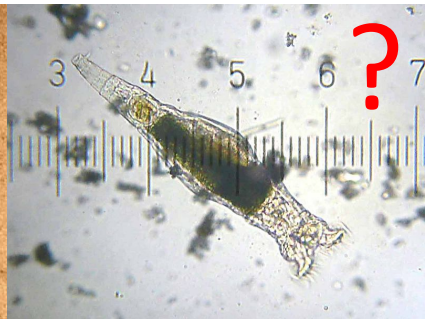
Eukaryote



Timmins et al. *Nature reviews genetics.* 2004

The evolution of sex and stuff

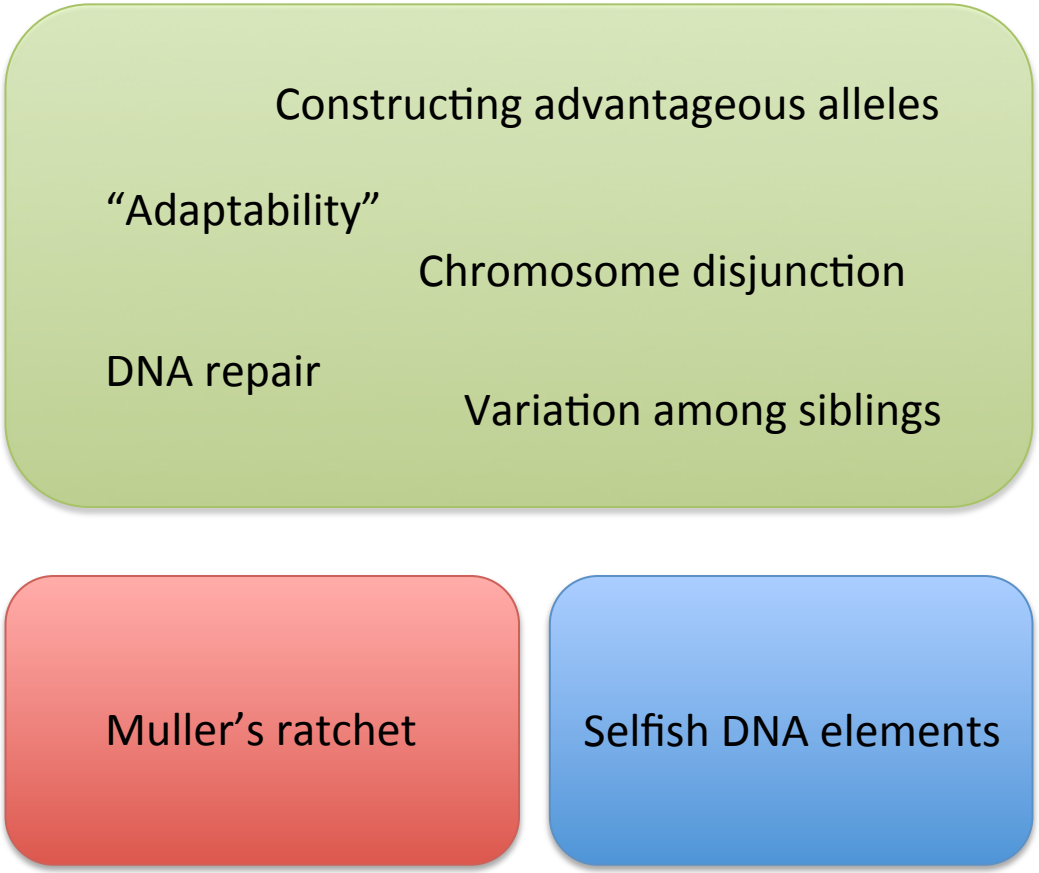
Asex



Facultative sex

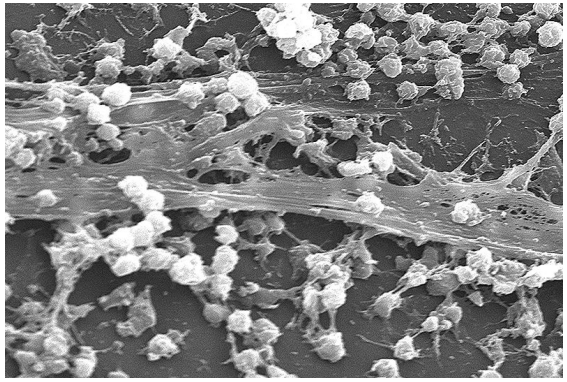
Obligate sex

Many explanations…



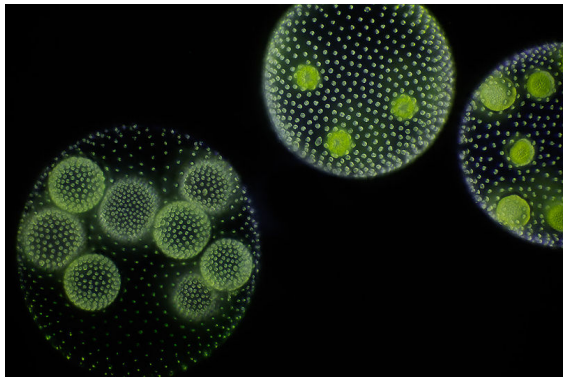
The evolution of multicellularity

Single cells



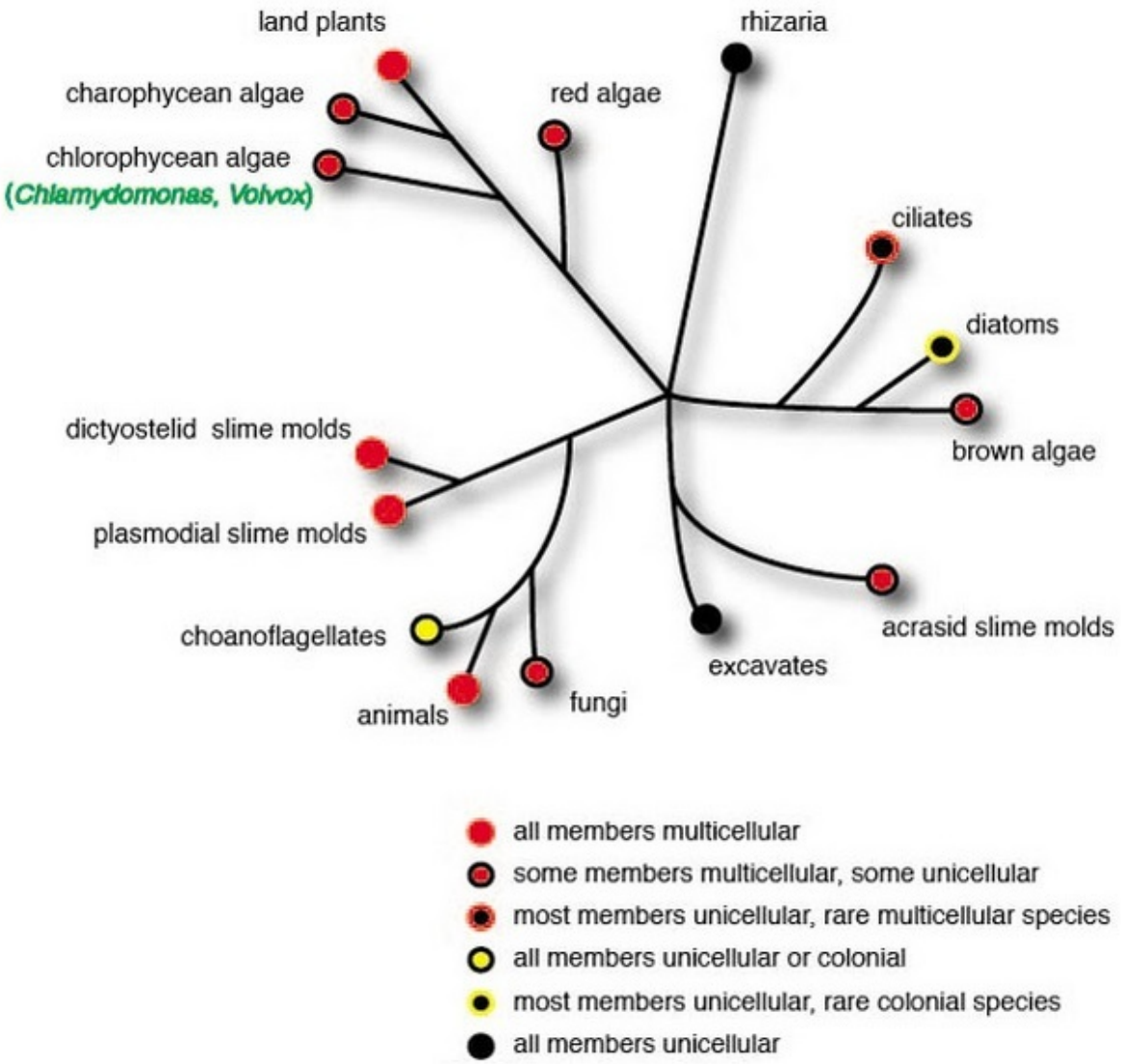
biofilms

Colonies



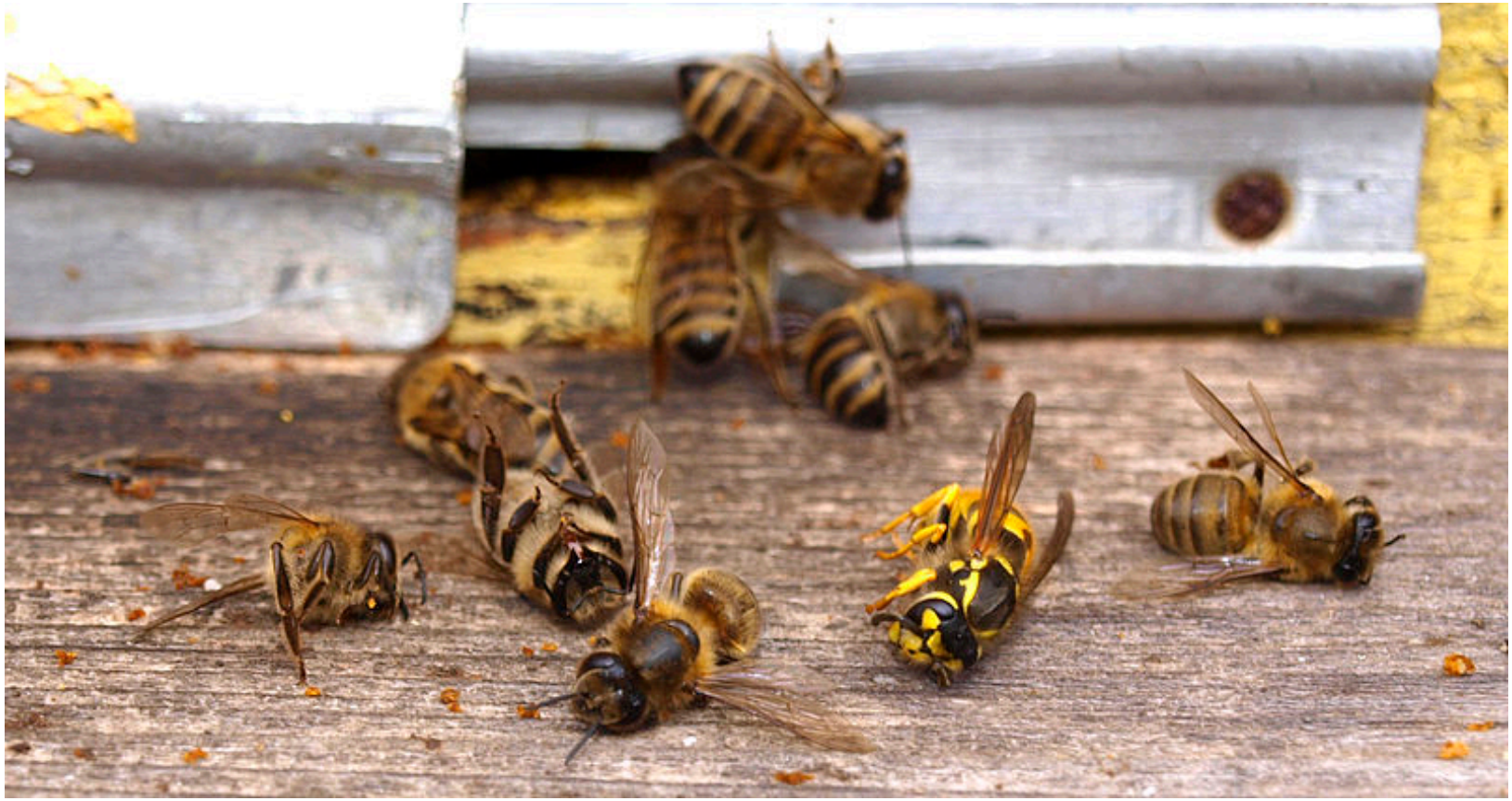
Volvox

Specialization



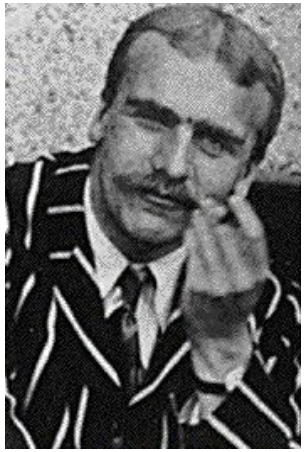
Nature Education 2010

Evolution of social behavior



http://en.wikipedia.org/wiki/File:Wasp_attack.jpg

Kin selection



Haldane: Lay down my life to save my brother?
"No, but I would to save two brothers or eight cousins."

Hamilton's rule: $rB > C$

Dawkins: "The selfish gene"

Multi-level selection

Ecosystems

Species

Social Groups

Individuals

Cells

Genes

Higher levels

Example: Nowak et al. *Nature*; 2010

Control mechansims

- Mitochondrial gene loss

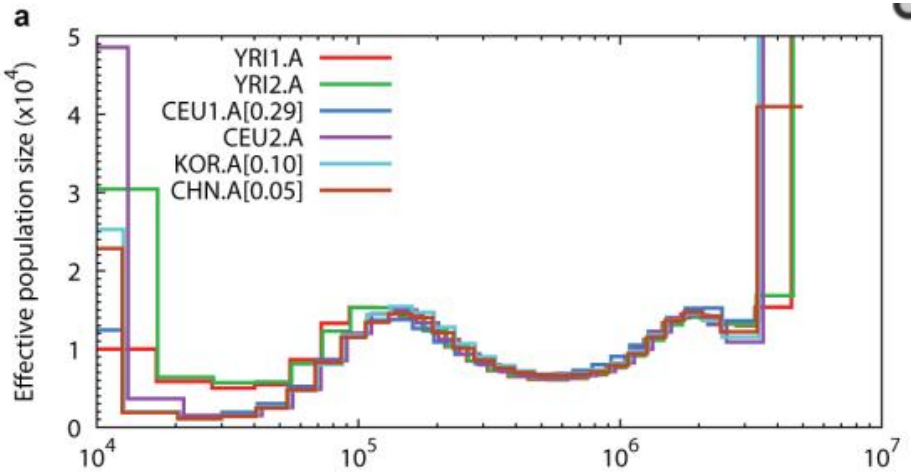
- Tumor suppressor genes

- Imprinting

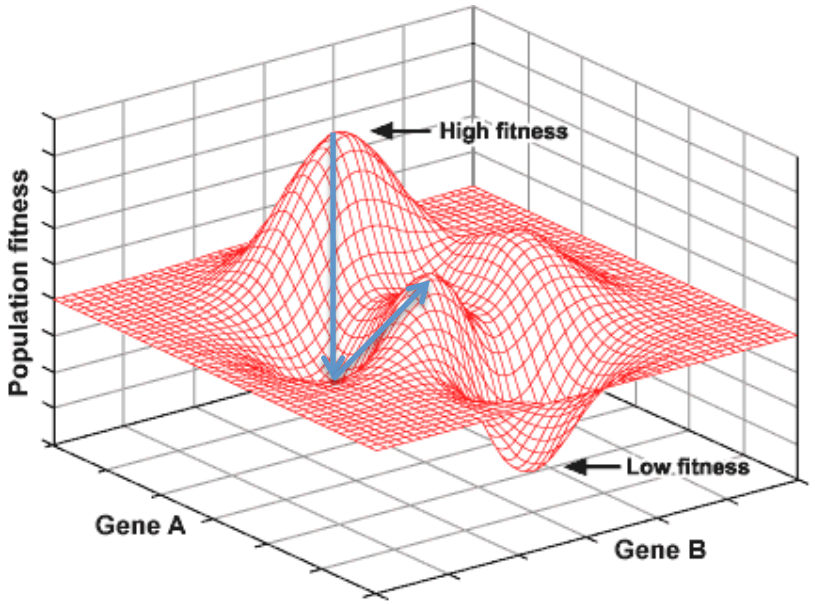
- Social punishment

Genetic drift

Remember, weakly deleterious alleles will still fix with $p \sim 1/2N_e$



Li & Durbin; 2011



http://evolution.berkeley.edu/

Insights from biological complexity:

- Rare, large and important jumps in qualitative complexity
- Complexity may increase when selection is relaxed –it's not necessarily directly adaptive.
- The mechanisms by which complexity is increased may not be the same ones which maintain it.
- Contingency is important. Eukaryotes only evolved once.

Questions about biological complexity:

- How should we measure the complexity of features, organisms and environments?
- How hard is it to drift across "fitness valleys"?
- Can we tell when a feature is adaptive?
- What's the relative role of different selective mechanisms in the evolution of different features?