Looking at evolution

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What is to be explained?

Existence and functioning of extremely improbable forms of matter

What should be the default option?

A suitable null model: Drift, Self-organisation; Mutations of major effect,...

What is the default option in practice?

Natural selection

(Levels of selection; Inclusive fitness)

Living Matter

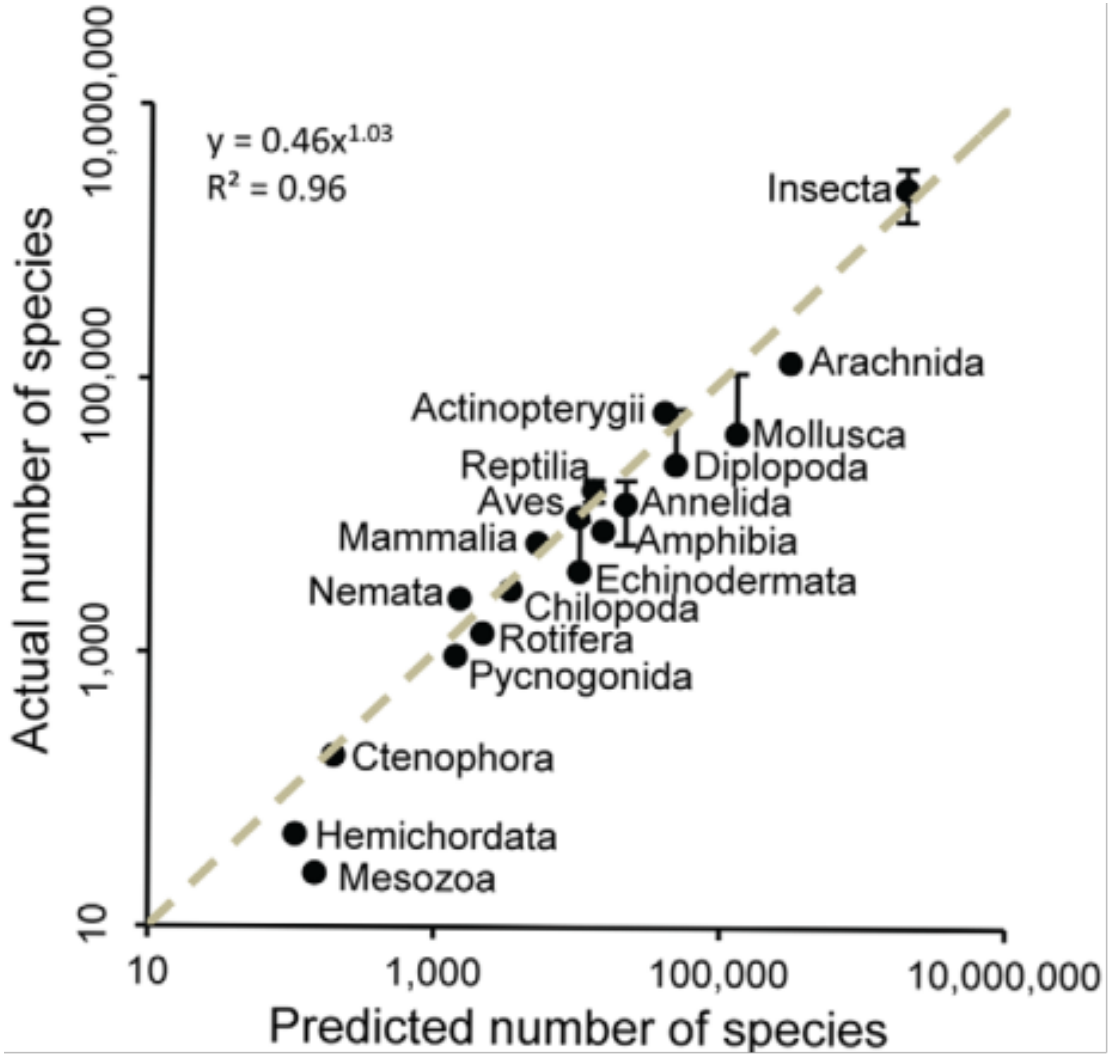
https://lanelester.com/the-history-of-life/

Observation, categories

Nested categories

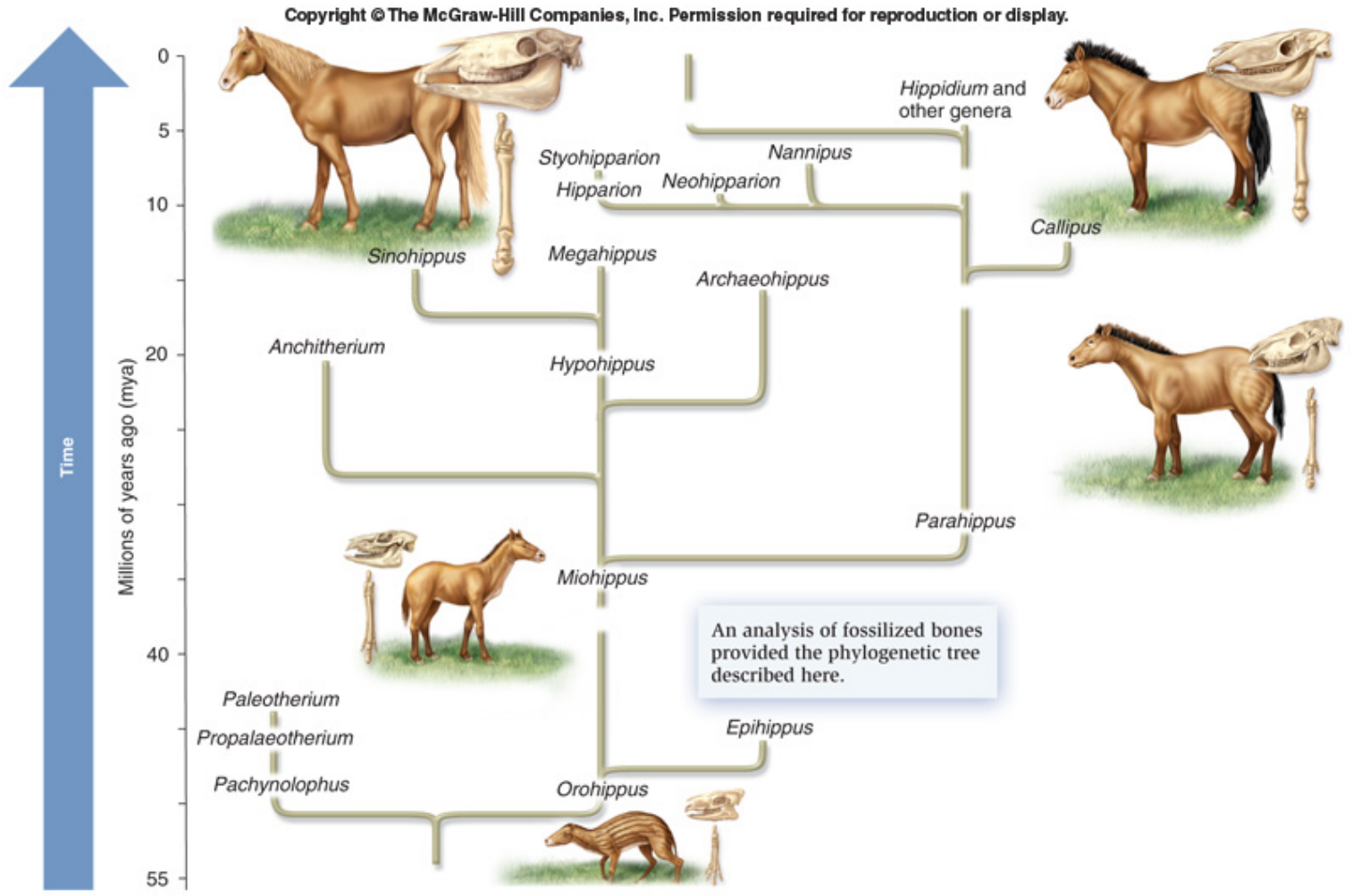
Individual, species, genus, ...phylum, supergroup, kingdom

How many forms?



Mora et al. PLoS Biol 9(8): e1001127, 2017

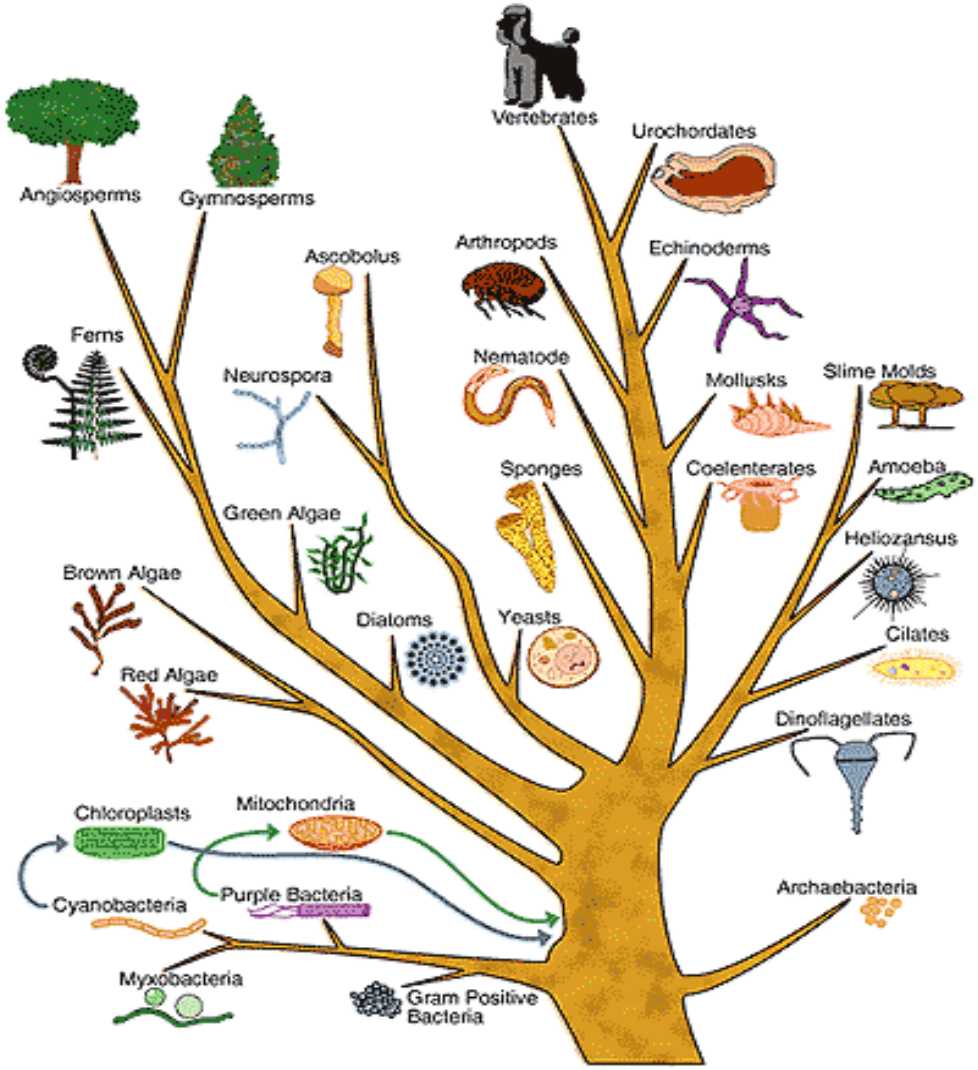
Fossil records → reconstruction of phylogenies



https://www.pinterest.com/pin/588212401301192383/

Categories seem to fall into a natural order:

Tree of Life



"Principle of Continuity"

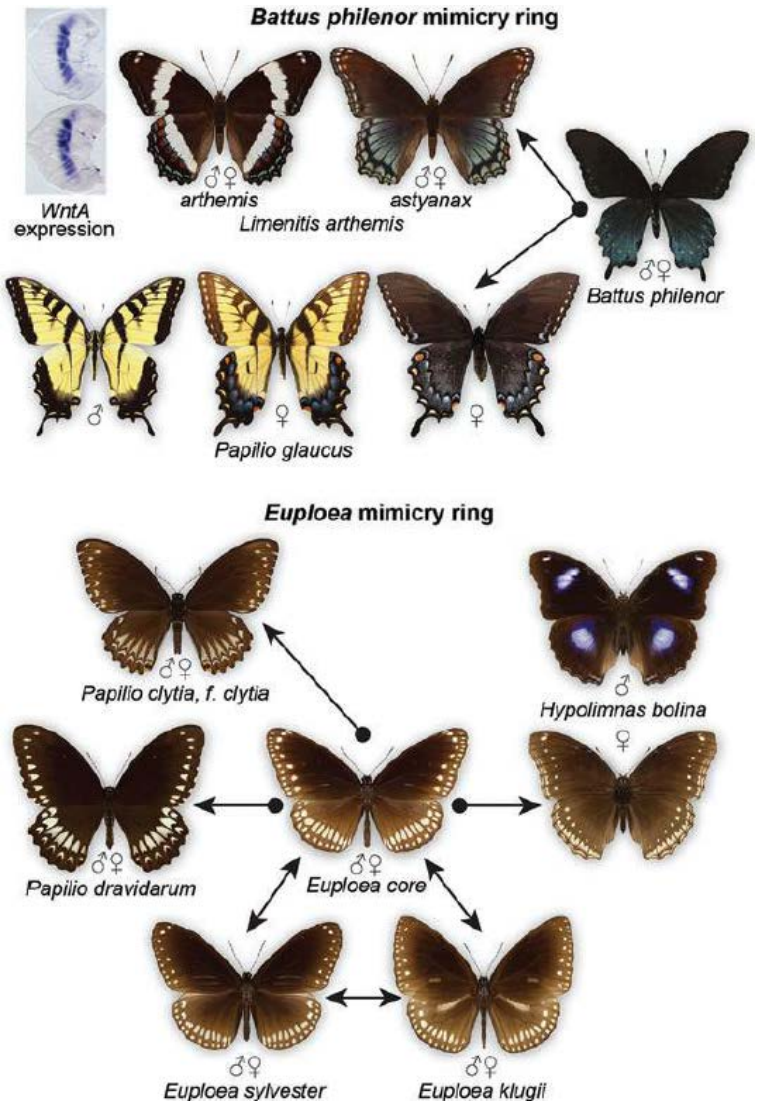
http://www.bio.miami.edu/dana/107/107F10_5print.html

Hallmark of living forms: adaptation

Beak shapes in birds

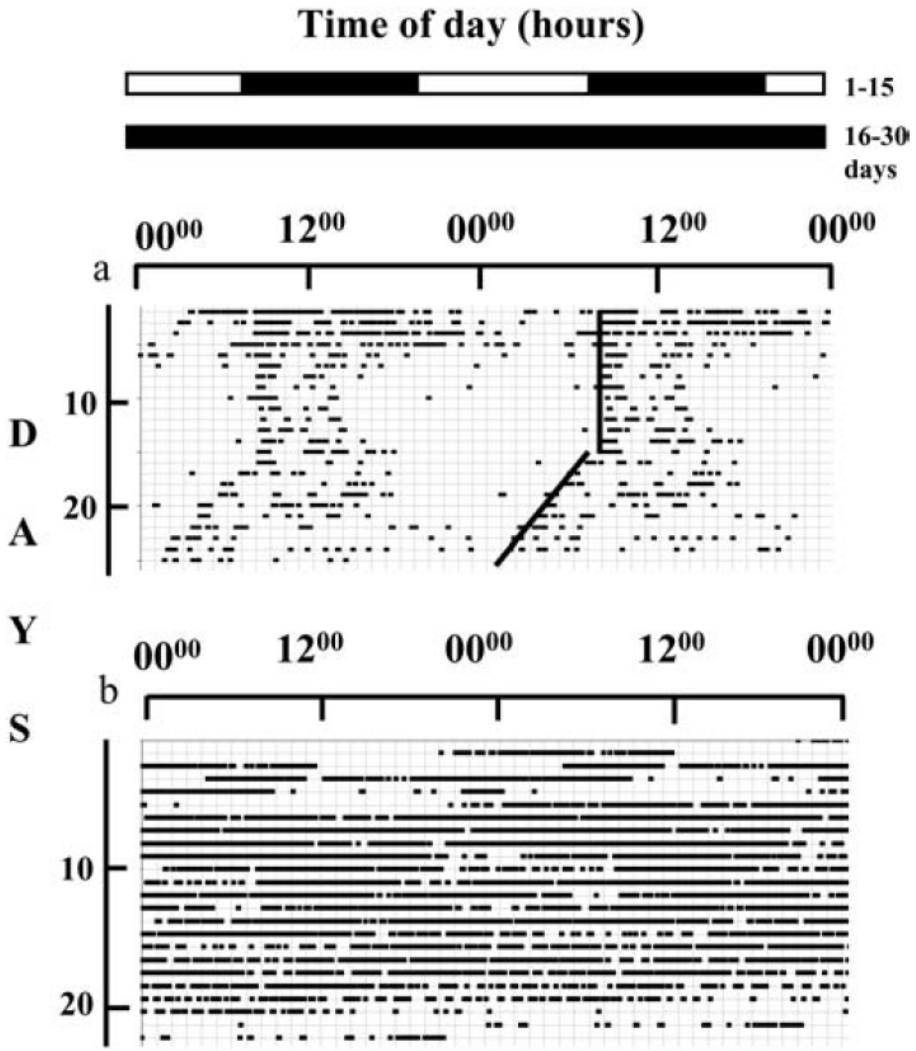
(http://www.agen.ufl.edu/~chyn/age2062/lect/lect_11/18_20.GIF)

Mimicry in butterflies



Deshmukh et al. *WIREs Dev Biol* 2017, e291. doi: 10.1002/wdev.291

Circadian rhythmicity in ants



Sharma et al. Naturwissenschaften (2004) 91:386–390

Explanations of the tree of life

One-time creation

Properties of matter (“Rational morphology”)

Multiple creations

Inner drive

Natural selection

Darwin-Wallace joint publication (1858)
to
Modern Synthesis (~1940?)

"Tree of life" based on inheritance with divergence

Descent with modification

Genes as vehicles for transmission of hereditary traits

DNA molecules + accessory proteins
are organised into chromosomes

Genes consist of strings of DNA

DNA codes for proteins

Proteins build bodies, catalyse transformations,
process signals, mediate movement, ... (“smart matter”)

Genes do NOT program development

Direction of flow of heritable information:
Nucleic acid to nucleic acid or nucleic acid to protein

"Central Dogma":

DNA → RNA → Proteins

Crick, F H C "**On protein synthesis Symp Soc Exp Biol** 12: 138-163, 1958.

Natural selection:
non-random differential survival or reproduction of phenotypically different individuals

Differential reproduction

based on heritable phenotypic variations

Phenotype proportions change

therefore genetic makeup changes

Simplest situation

Slowly varying environment

Invariant genotype→phenotype map

Additive effects ("mean field model")

Fixed fitnesses

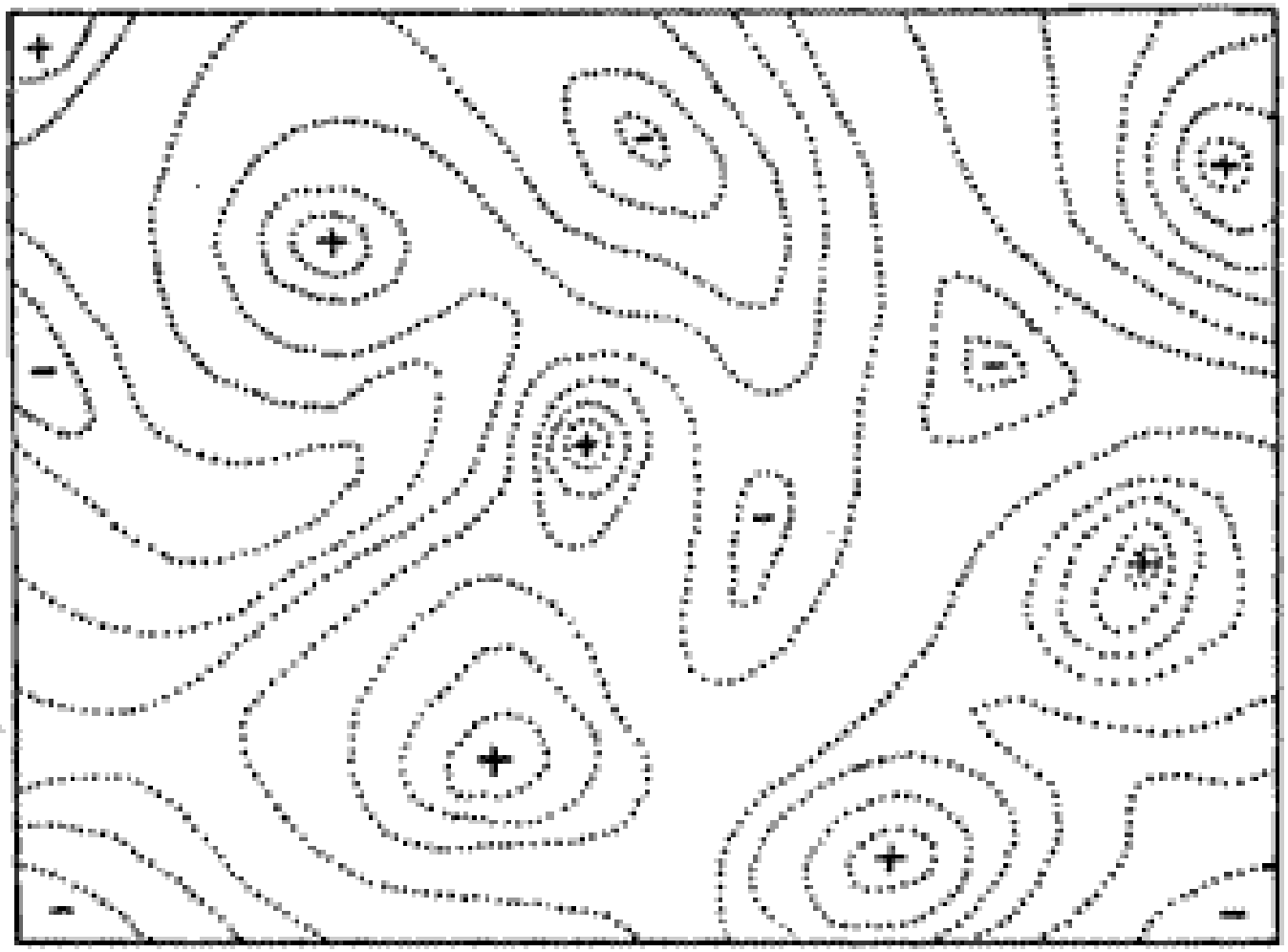
Pre-existing niches

Externalist view: 'Boundary-value problem'

The fitness landscape:

"Natural selection is like mountain climbing"

Must proceed slowly

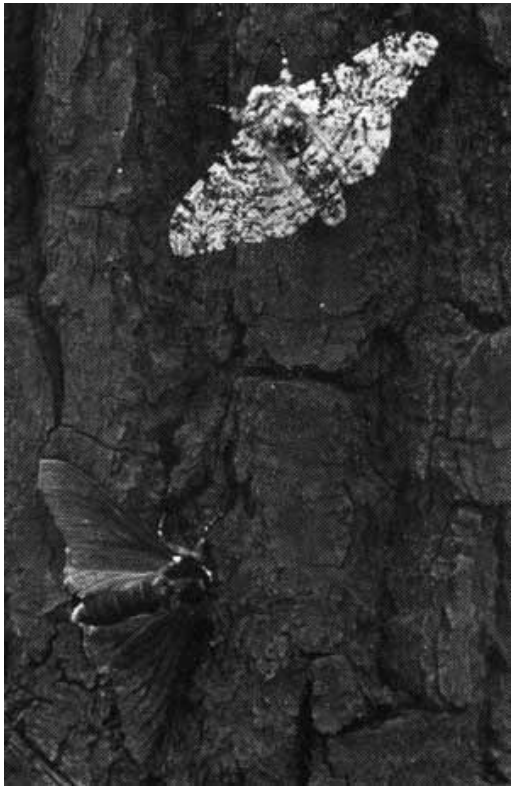


Wright, Proc. VI International Congress of Genetics: 1: 356-366, 1932

Evidence for natural selection

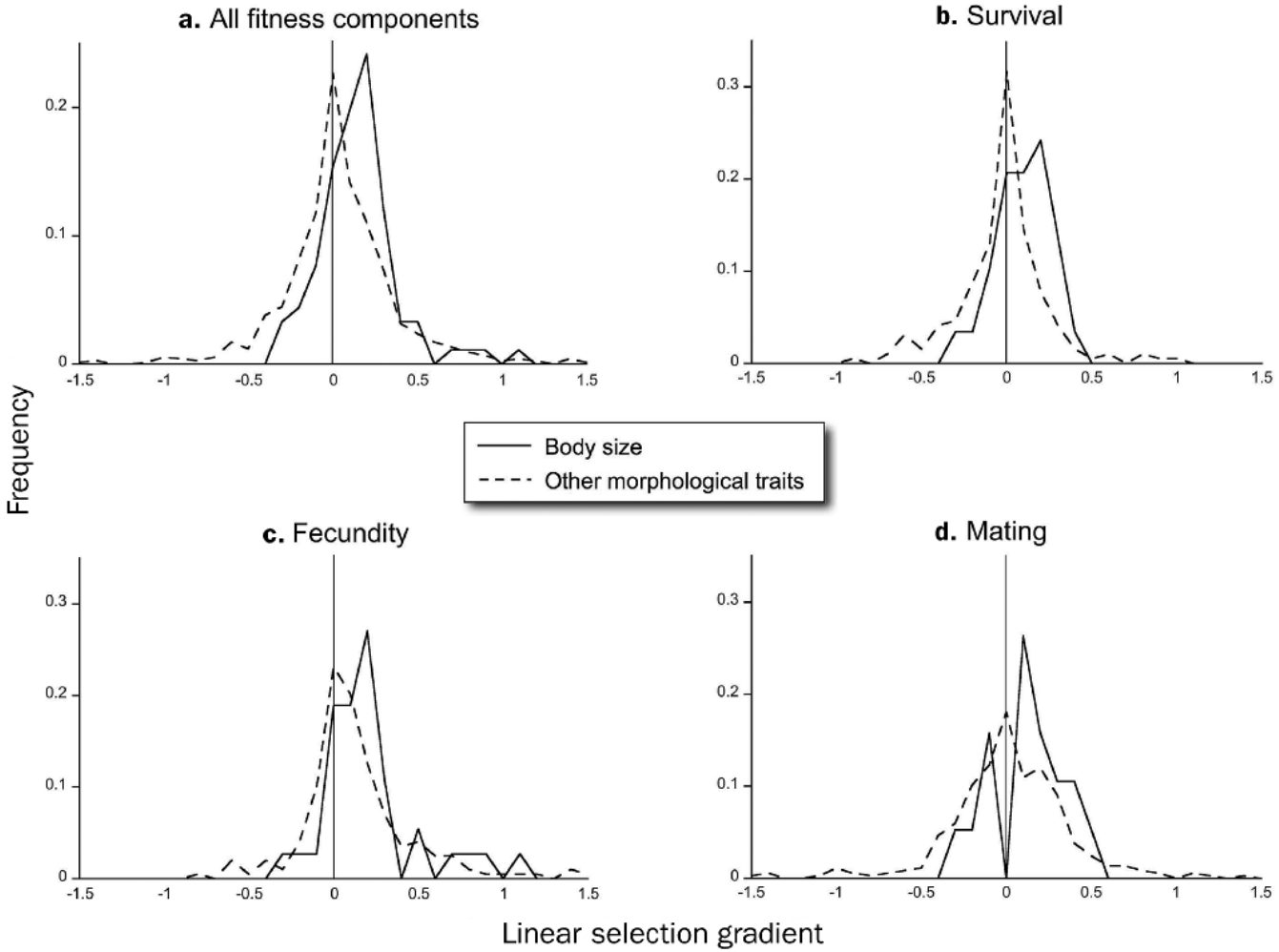
Natural selection in action: the peppered moth

Industrial melanism



Biston betularia (typica, melanica)
Unpolluted lichen covered trunk in Dorset (left), soot-covered trunk near Birmingham (right)
(Kettlewell, 1956, Heredity 10: 300).

Directional selection in nature



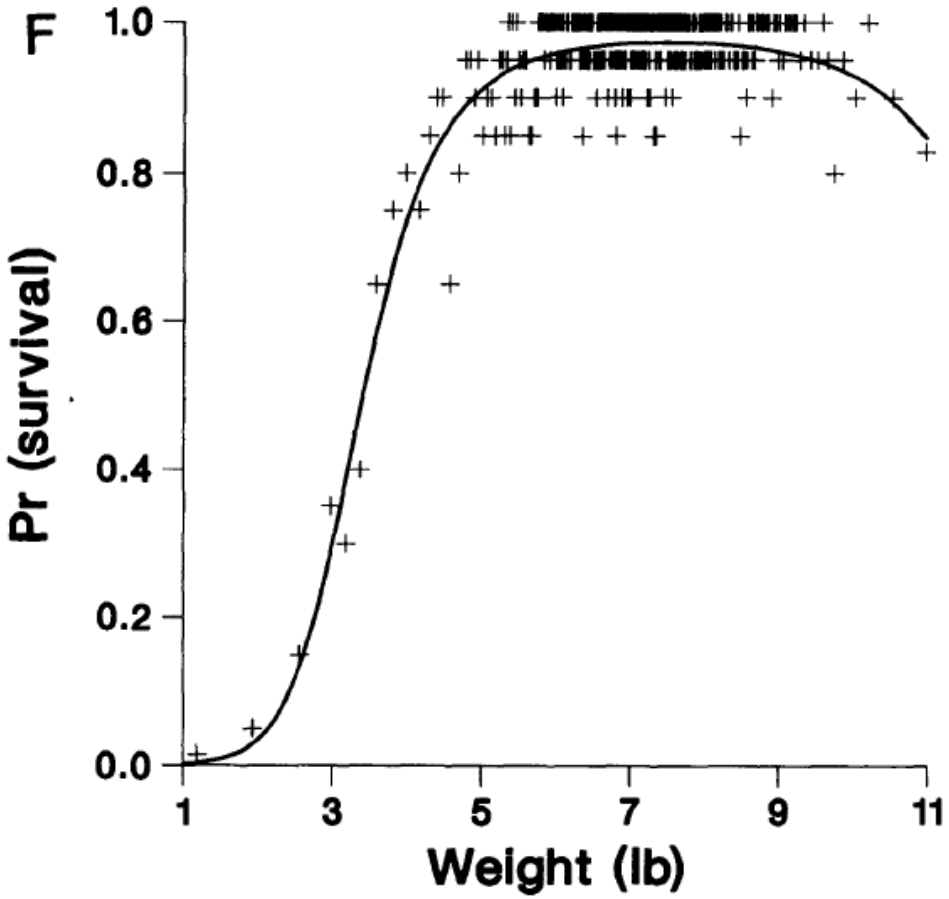
Continuous line = selection intensities for size

"Bigger is generally fitter"

KINGSOLVER and PFENNIG Bioscience *57 (7), 2007*

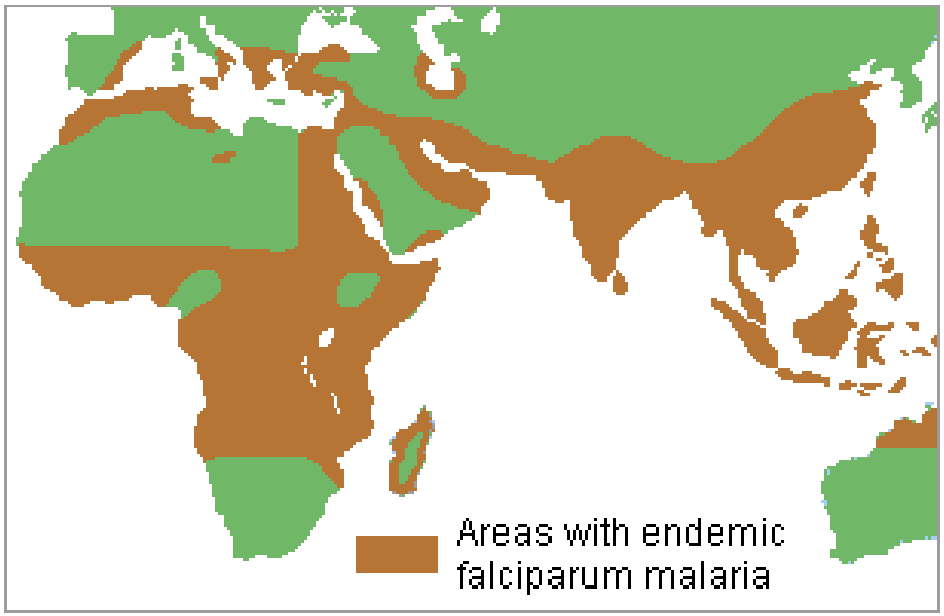
Natural selection → Stability.

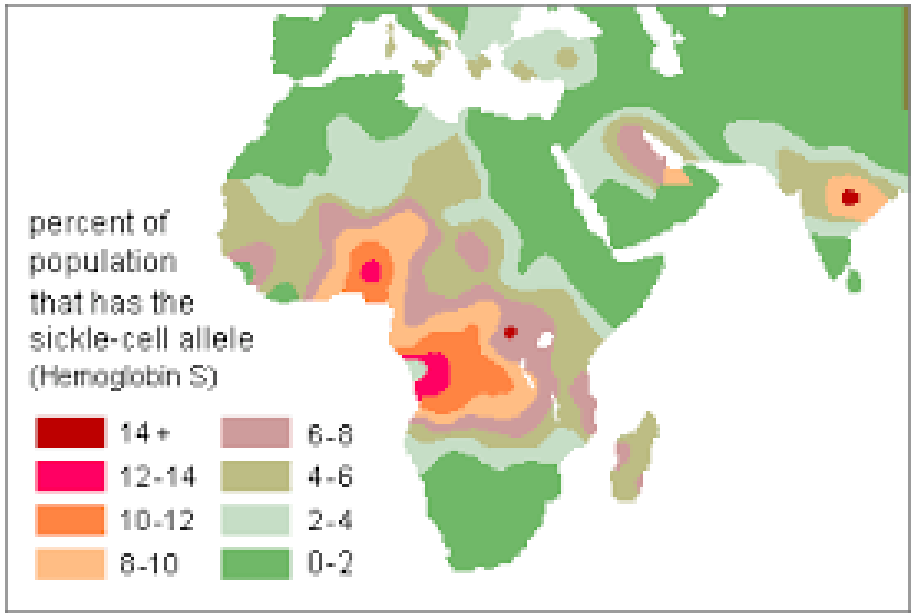
Human birth weights



Karn and Penrose, *Ann. Eugen. 16: 147–164;* Schluter, *Evolution,* 42(5), 849-861, 1988

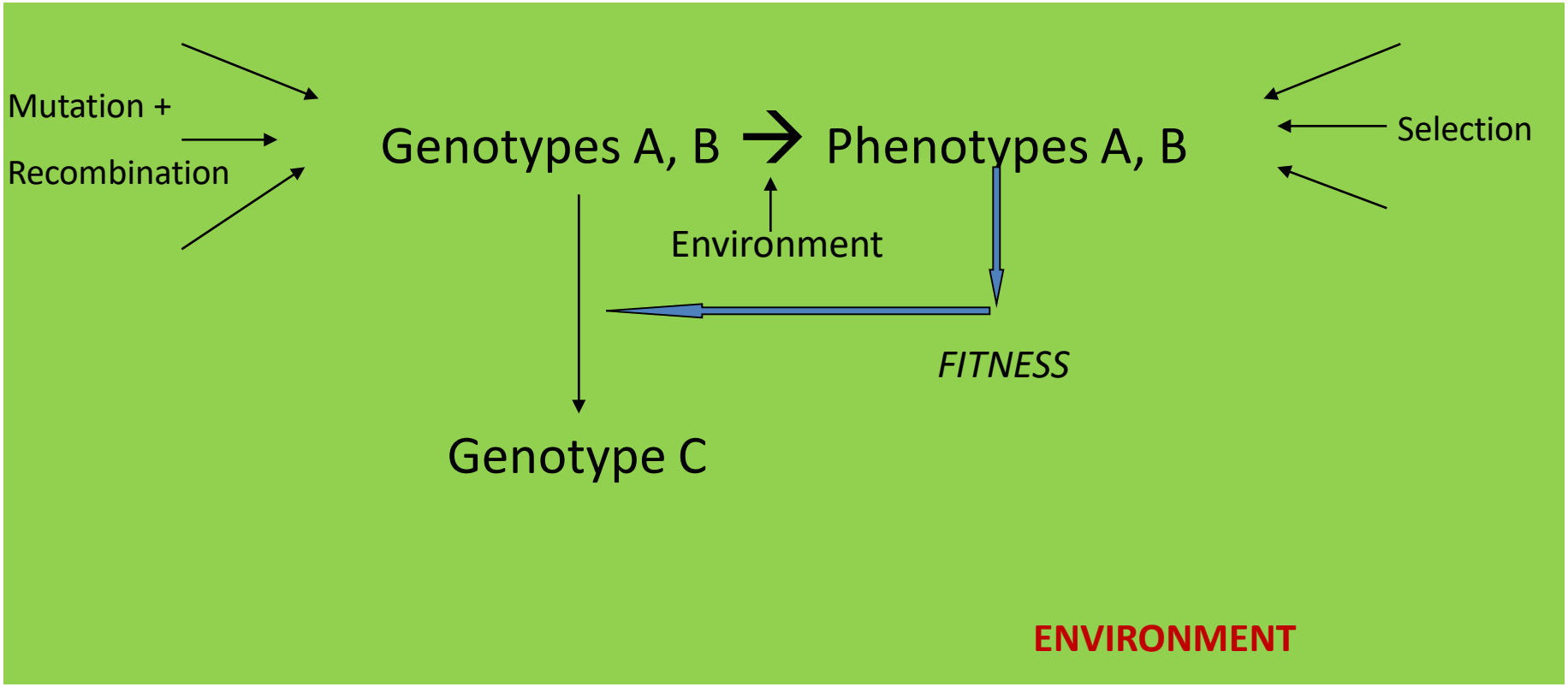
Natural selection → Stability:
Balanced polymorphism





http://anthro.palomar.edu/synthetic/synth_4.htm

Neo-Darwinian picture of evolution by natural selection



Genetic variants occur at random

Phenotypes of variants screened by environment

Heredity works through genes

Appearance of design through natural processes

Hard selection: stringent

Tiger can eat both; or both can get away

We cannot run faster than him!

Soft selection: less stringent

Tiger satisfied with one

I don't want to run faster than him; I want to run faster than *YOU!*

(cartoons from Houchmandzadeh; see Wallace, EVOLUTION 29:465-473. 1975)

Levels of selection

Traits that are socially beneficial but individually disadvantageous

Selection can act on an individual in favour of a trait that reduces its fitness and simultaneously benefits another individual.

One way for this to happen is through shared genes (kin selection)
(J. B. S. Haldane: Willing to lay down life for two brothers, or eight first cousins, or...)

Another is for group advantage to be stronger than individual disadvantage

A third is for altruistic acts to be reciprocated

Gadagkar, R. “Survival Strategies”, Universities Press, 2001

Levels of selection

Gene propagation without individual benefit

Transposable elements: Parasitic ("selfish") DNA

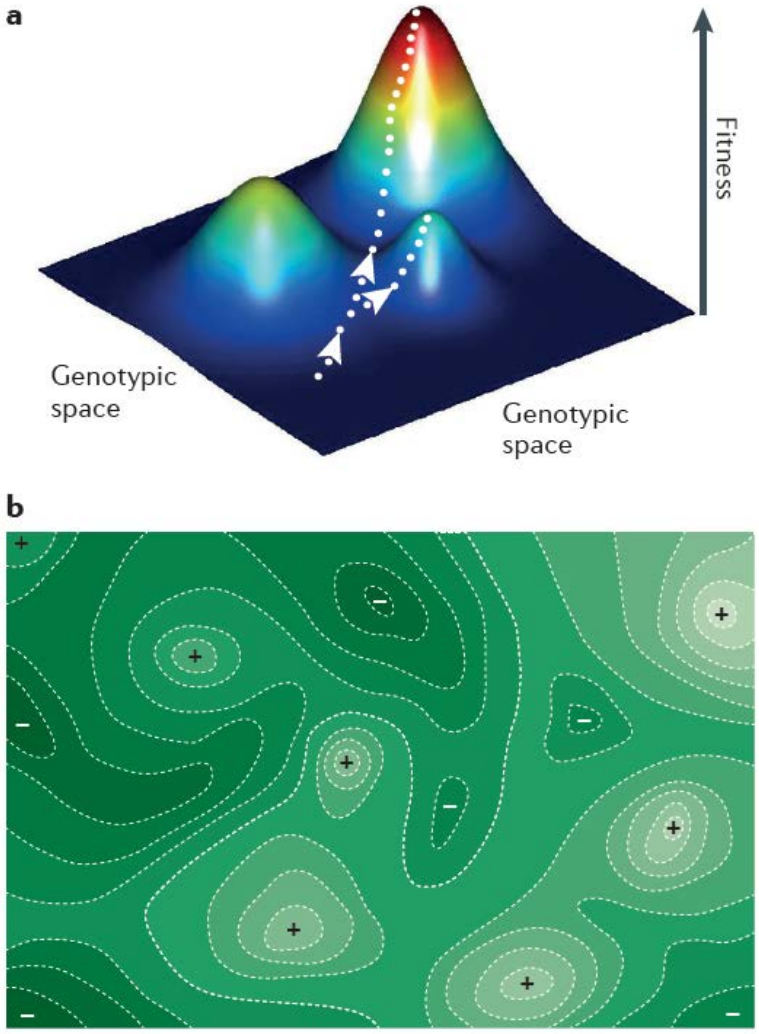
Restriction-modification complexes ("addiction modules")

Genes that violate the 50:50 rule of Mendelian segregation

Dawkins, R. "The selfish gene" (4th ed., 2016, Oxford University Press)

Interactions (epistasis) and Shifting Balance

Drift can help cross fitness valleys



De Visser, *Nature Reviews Genetics* | doi:10.1038/nrg3744, 2014

Mathematics and the Modern Synthesis

Population genetics
Gene frequencies

Quantitative genetics
Heritability,
Variance, Regression

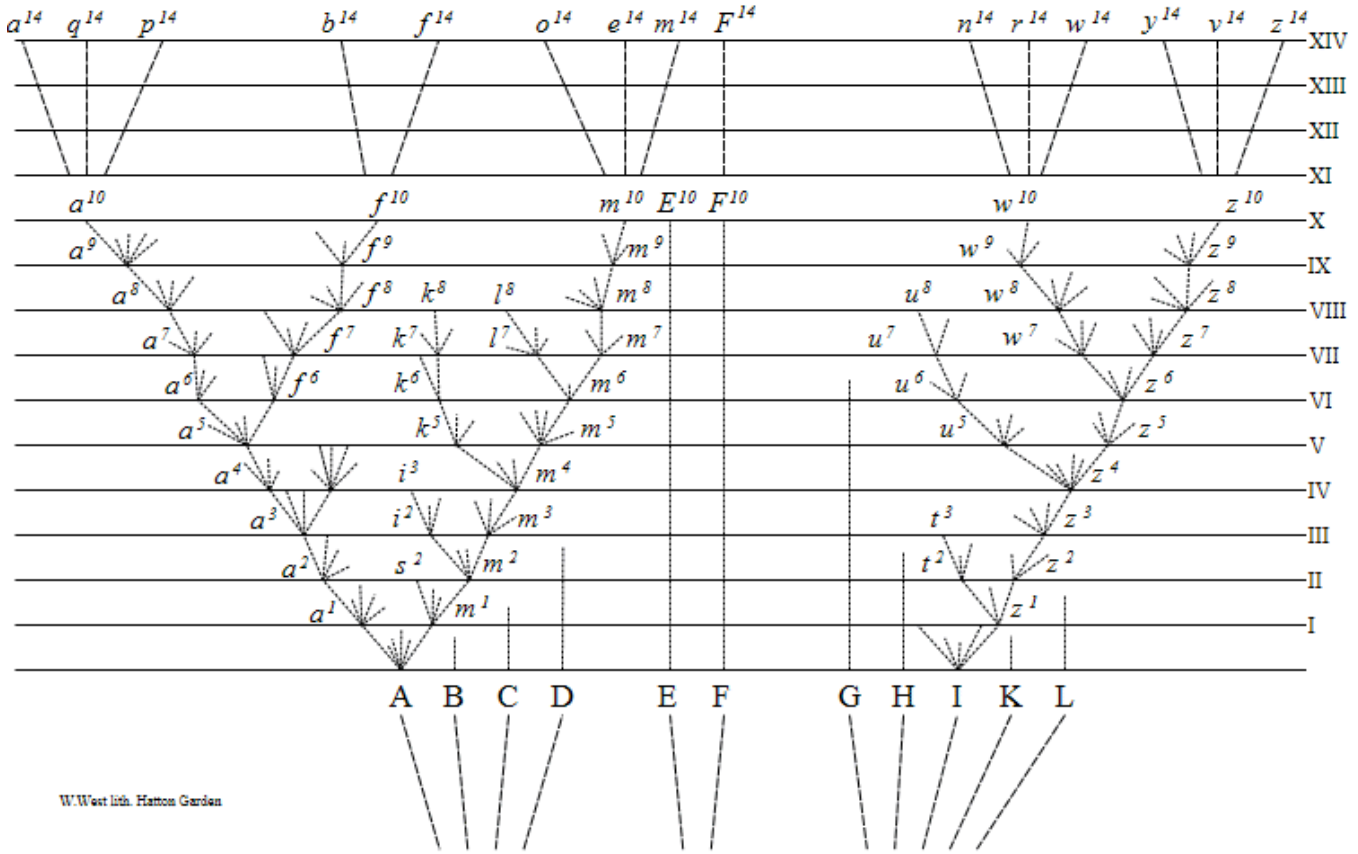
"Stat Mech"
Entropy,
Maximum likelihood

"Explain evolution in terms of known genetical causes"
(~Haldane, Wright, Chetverikov; *Deductive, Analytical*)

"Explain genetical phenomena in terms of known evolutionary causes"
(~Fisher; *Inductive, Statistical*)

How do species arise?

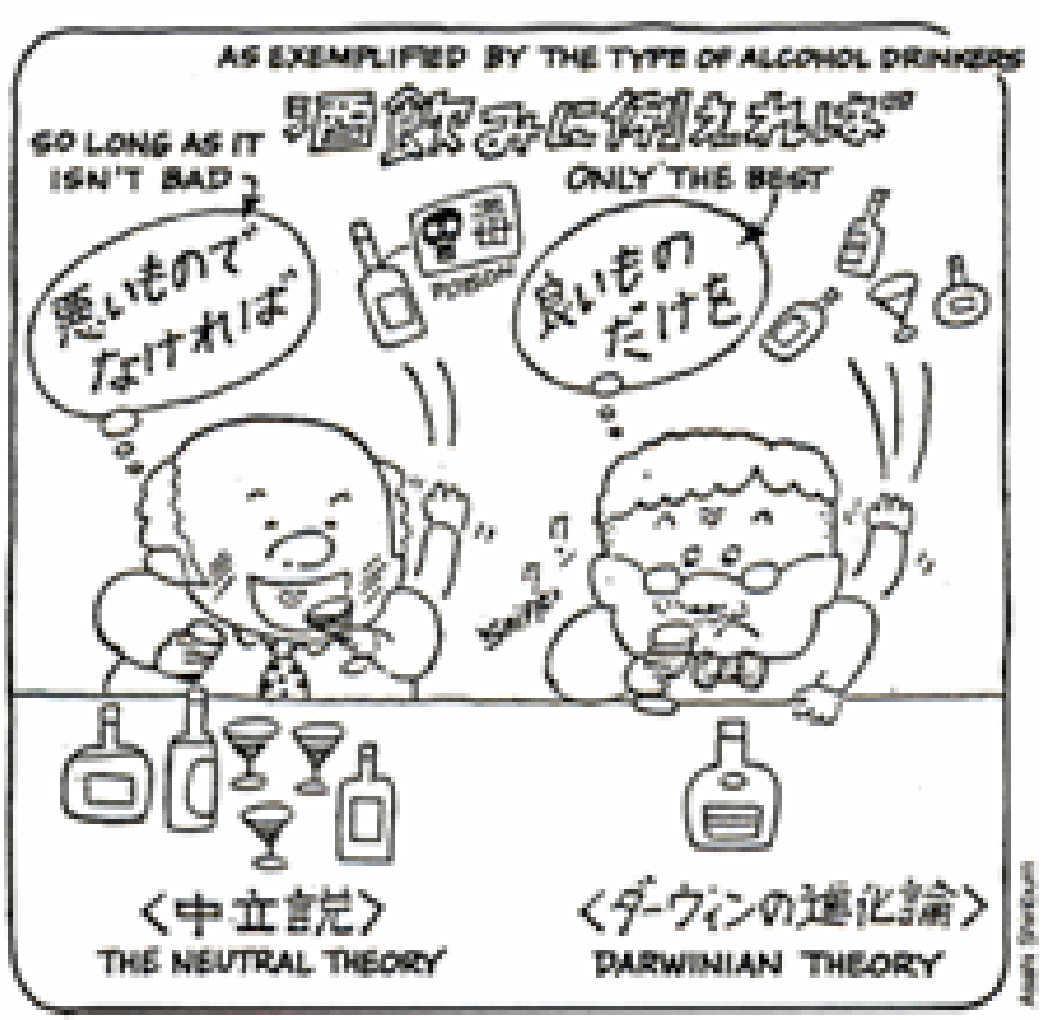
By successive diversifications,
members of two lineages can no longer mate successfully



Alternatives to natural selection

Neutral molecular evolution

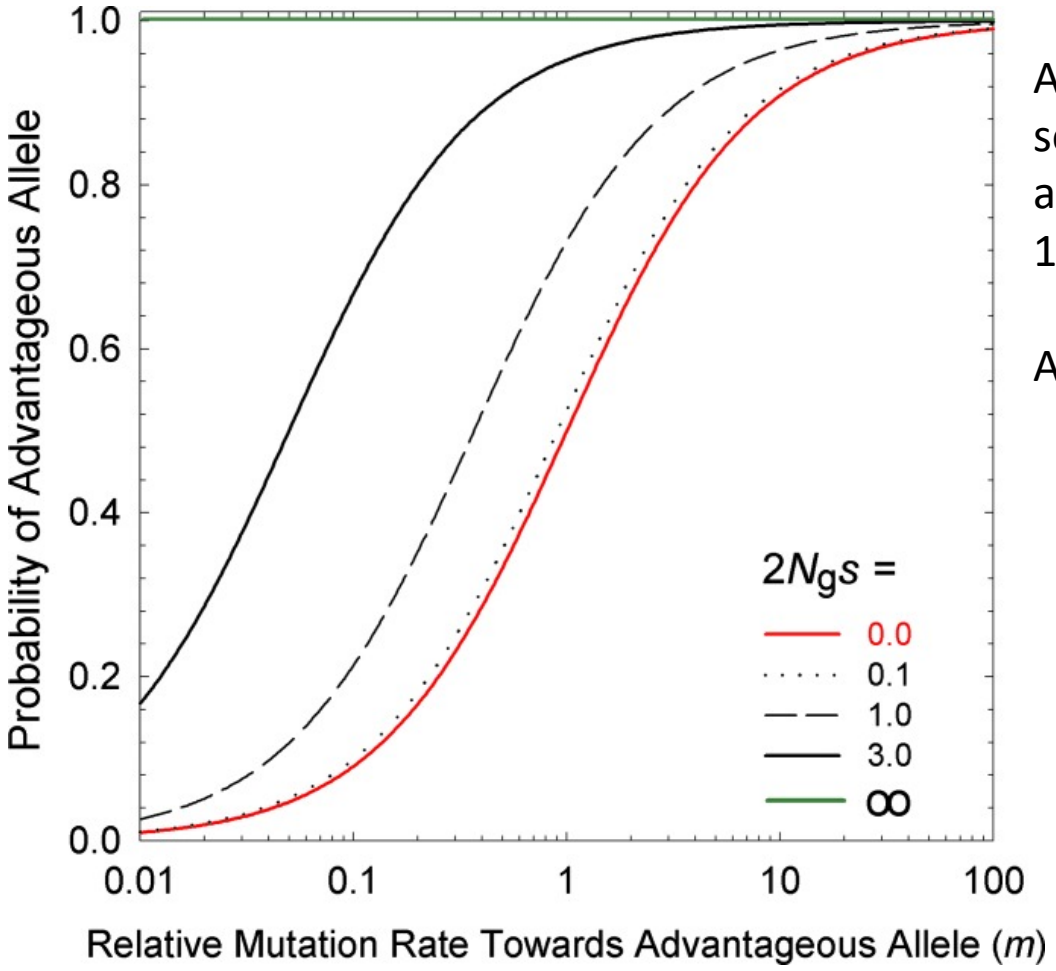
Random walks in gene space
(Kimura)



Tokyo's Fleet Street tackles evolutionary theory

Probability that beneficial allele prevails

depends on chance and selection



Alleles A, a; the selection coefficient associated with A is 1+s. $S=2.N_g.s$

$A \underset{m}{\rightleftharpoons} a.$

Lynch, PNAS 104(Suppl 1): 8597–8604, 2007

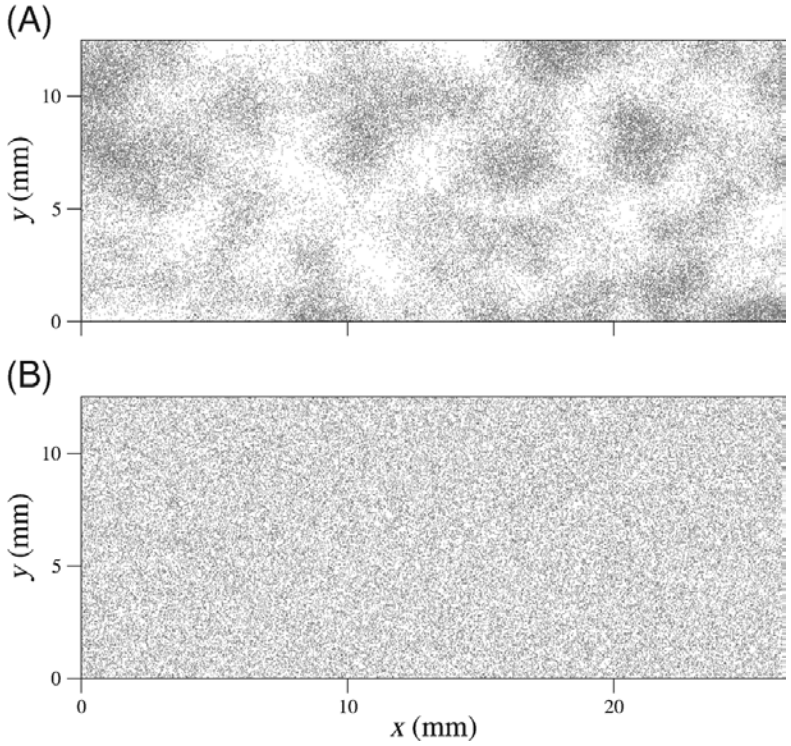
Selection ineffective in small populations

4. N_{eff}. s<< 1

➔

fixation of ‘sub-optimal’ alleles, invasion by parasitic DNA, baroque embellishments

Neutral clustering of cells or DNA sequences

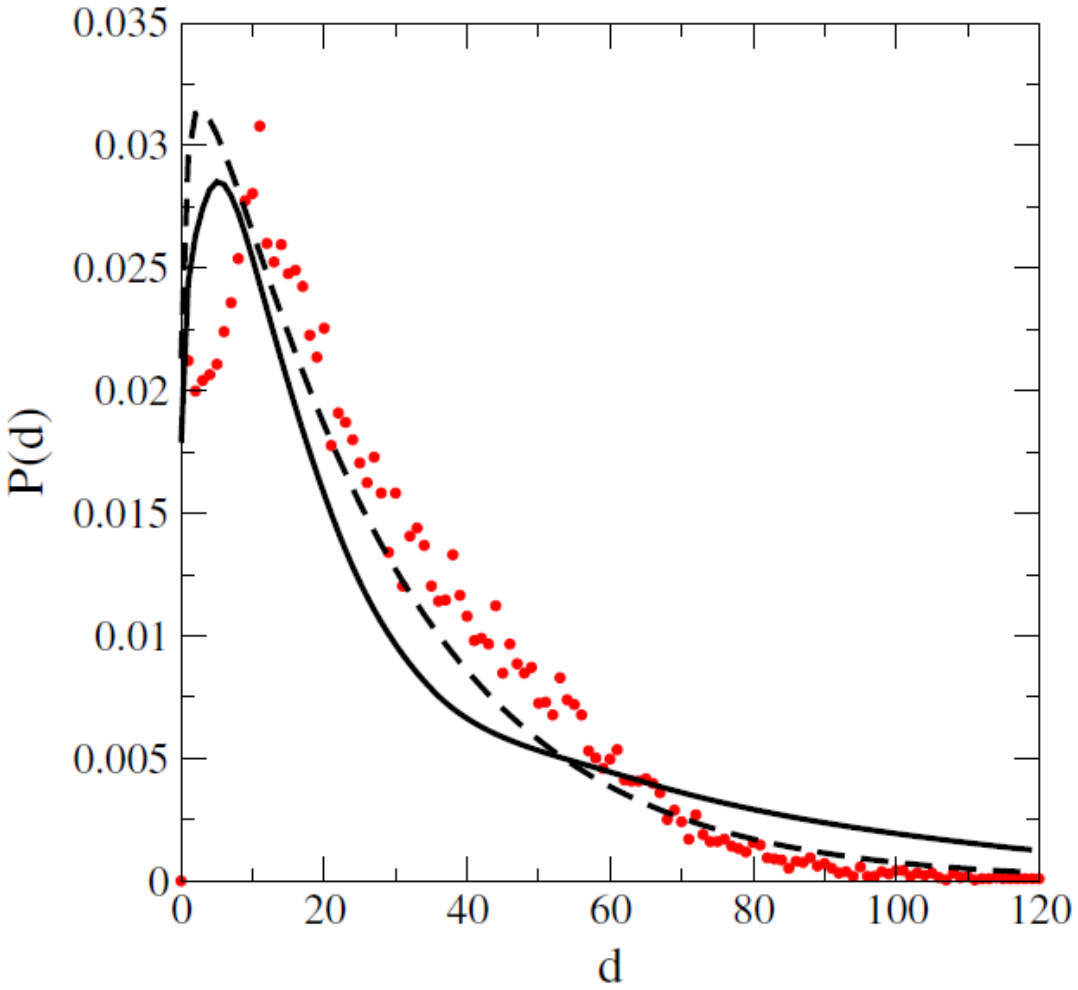


Houchmandzadeh, J. Biosci. 39 249–258, 2014

Neutral interaction networks

miRNA binding sites on mRNA

P(d) = Prob.(randomly chosen mRNA can bind d miRNAs)

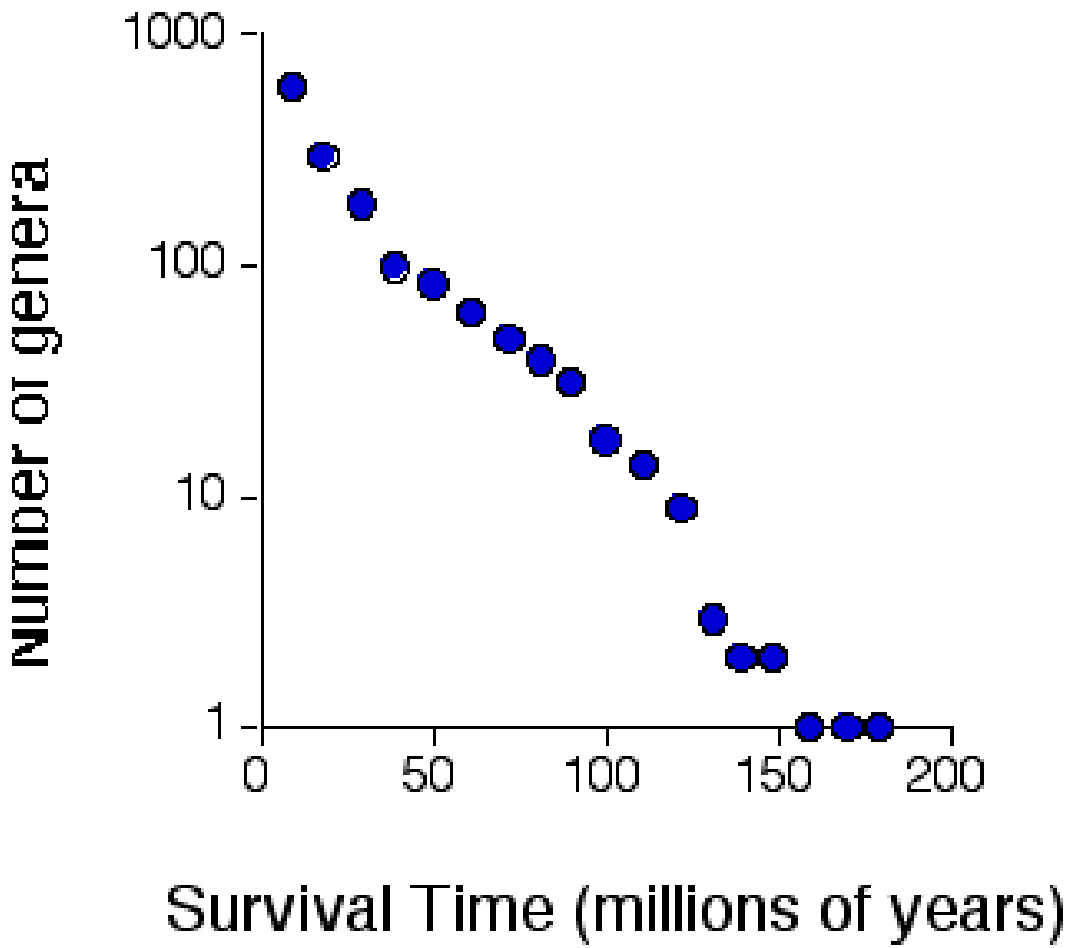


Red dots=exptl data, black line=computed, dashed line=sampled output

ARPAĞ and ERZAN J. Biosci. 39 259–280 2014

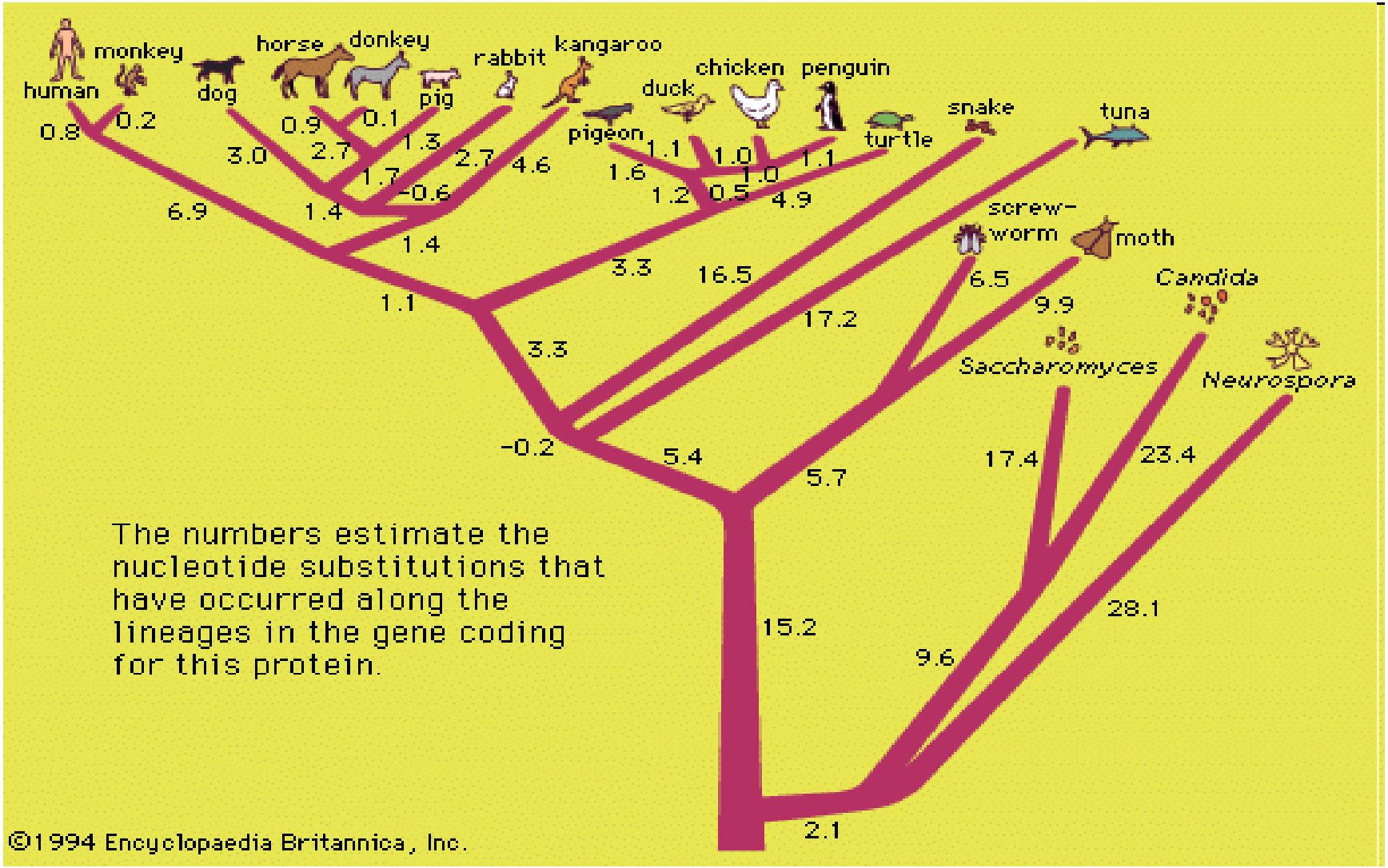
Neutral extinctions?

Red Queen



Echinoidea; Van Valen, L. 1973. Evol. Theory 1: 1-30;
Gingerich, www-personal.umich.edu

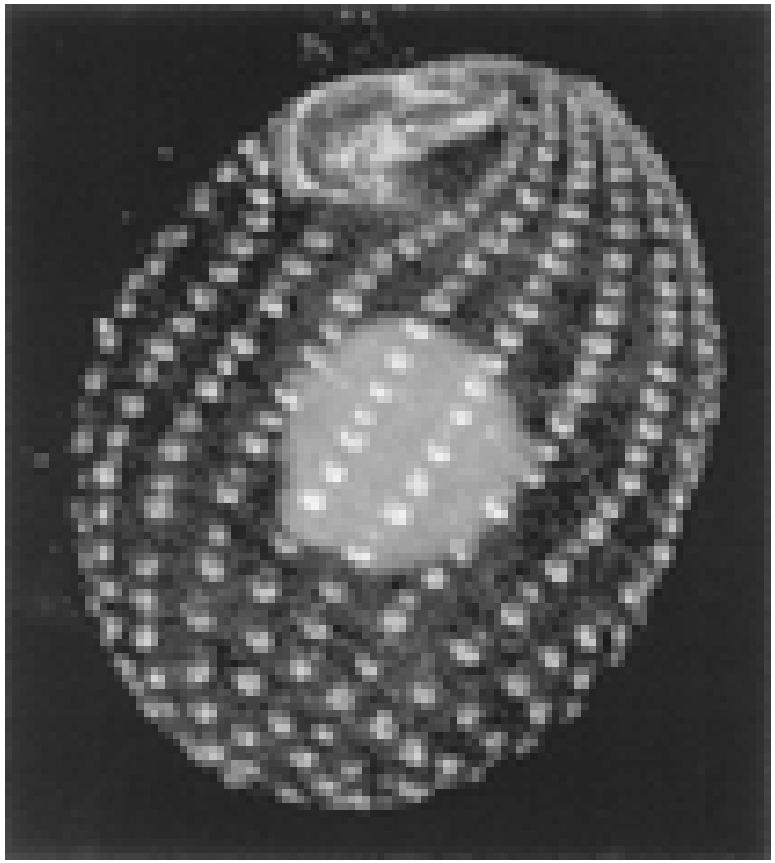
Trees based on neutrality assumption work



philosophy.wisc.edu

Neutral forms?

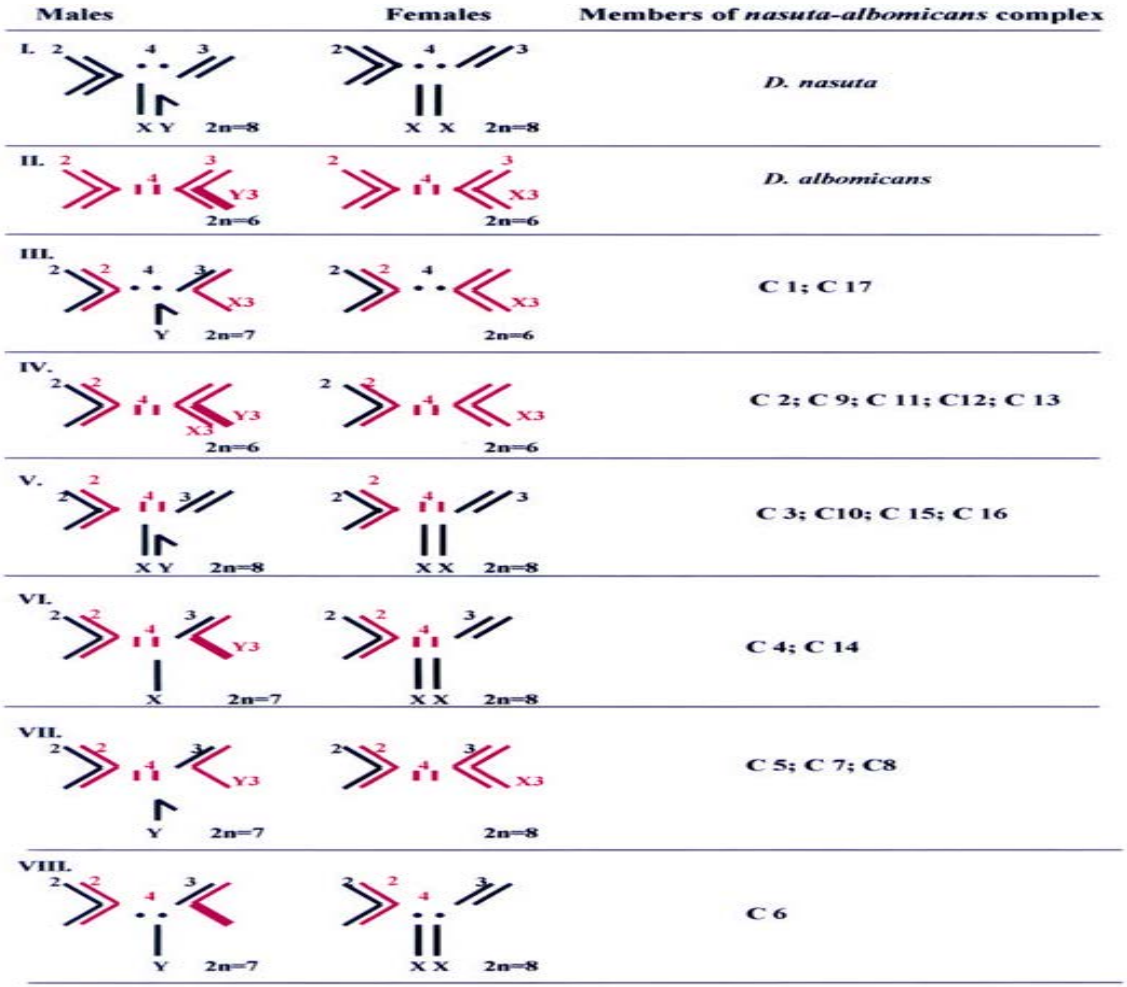
Epigenetic inheritance
primary DNA sequence unchanged



Ciliary row pattern in Tetrahymena
(http://www.bioone.org/na101/home/literatum/publisher/bioone/journals/content/)
Jablonka and Raz 2009, Q Rev Biol 84(2):131-176, Pfennig and Servedio

Chromosomal mutations

Large mutation not same as mutation of large effect



Ranganath and Aruna, *J. Genet*. **82**, 163–177, 2003

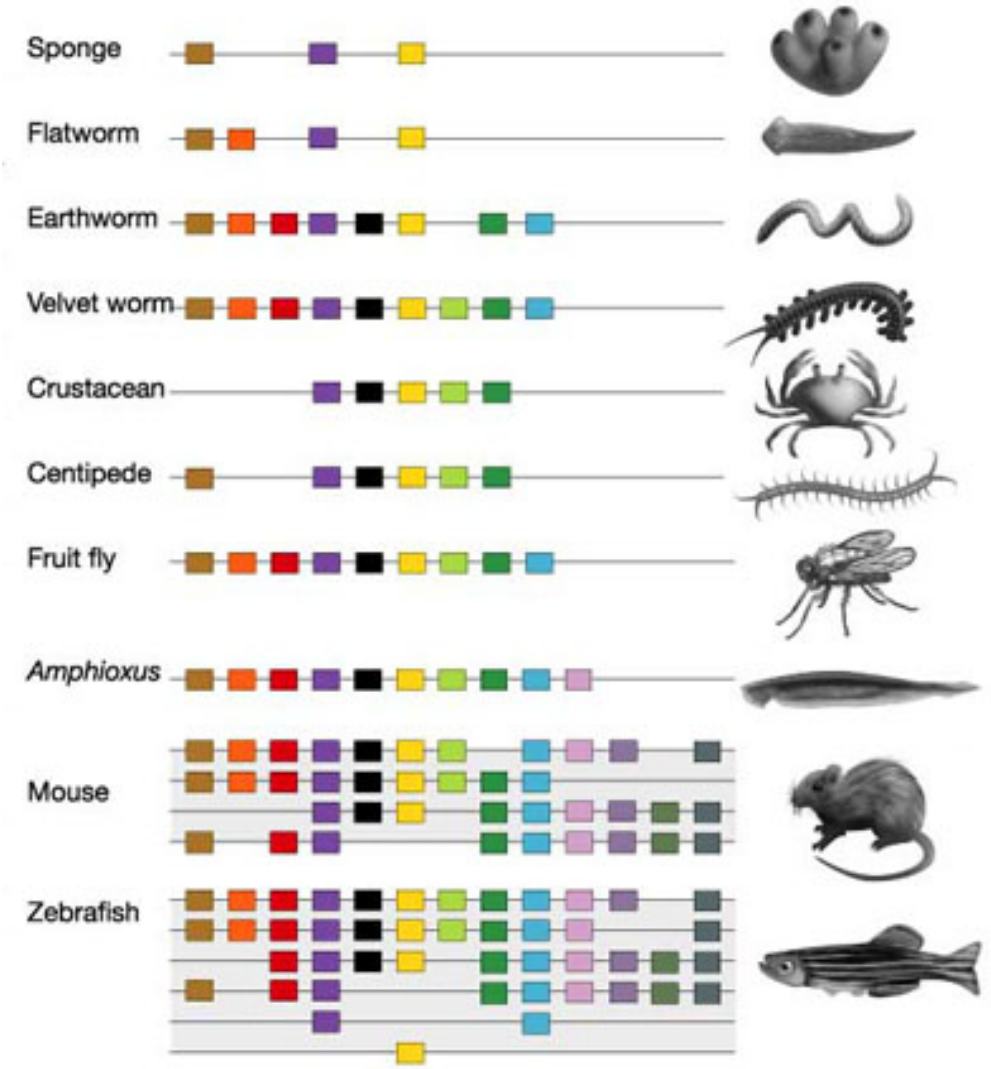
Reproductive barriers→ Incipient speciation?

Homogamic matings N (%)	Heterogamic matings N (%)	$\Sigma\chi^2$	Isolation index
73 (83·91)	14 (16·09)	38·66*	0·68
64 (73·56)	23 (24·44)	18·38*	0·49
92 (91·09)	09 (08·91)	66·58*	0·82
59 (73·75)	21 (26·25)	17·12*	0·47
70 (77·78)	20 (22·22)	26·68*	0·56

Tanuja et al. J Biosci 26(3):365-71, 2001.

Evolution via changes in gene regulation:

same DNA sequences work differently in different organisms



http://www.lorologiaiomiope.com/la-forma-il-caso-e-la-necessita/

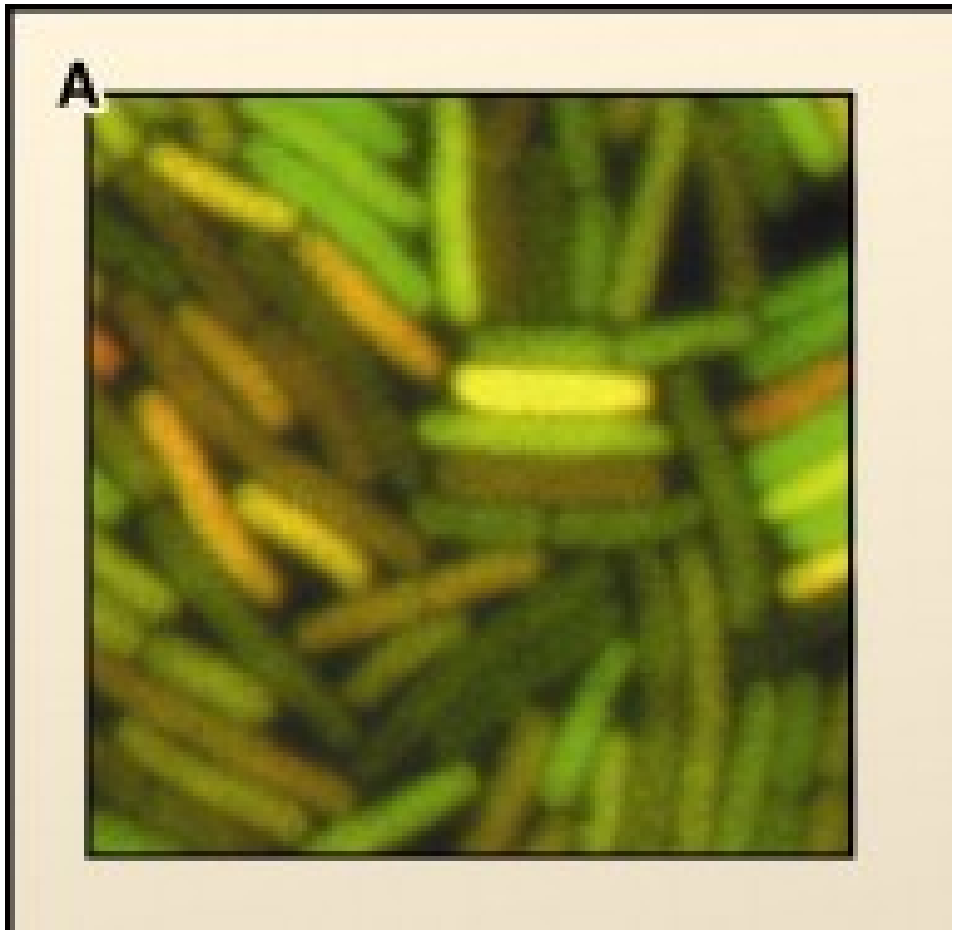
Horizontal gene transfer

Common in bacteria and archaea,

rare in eukaryotes

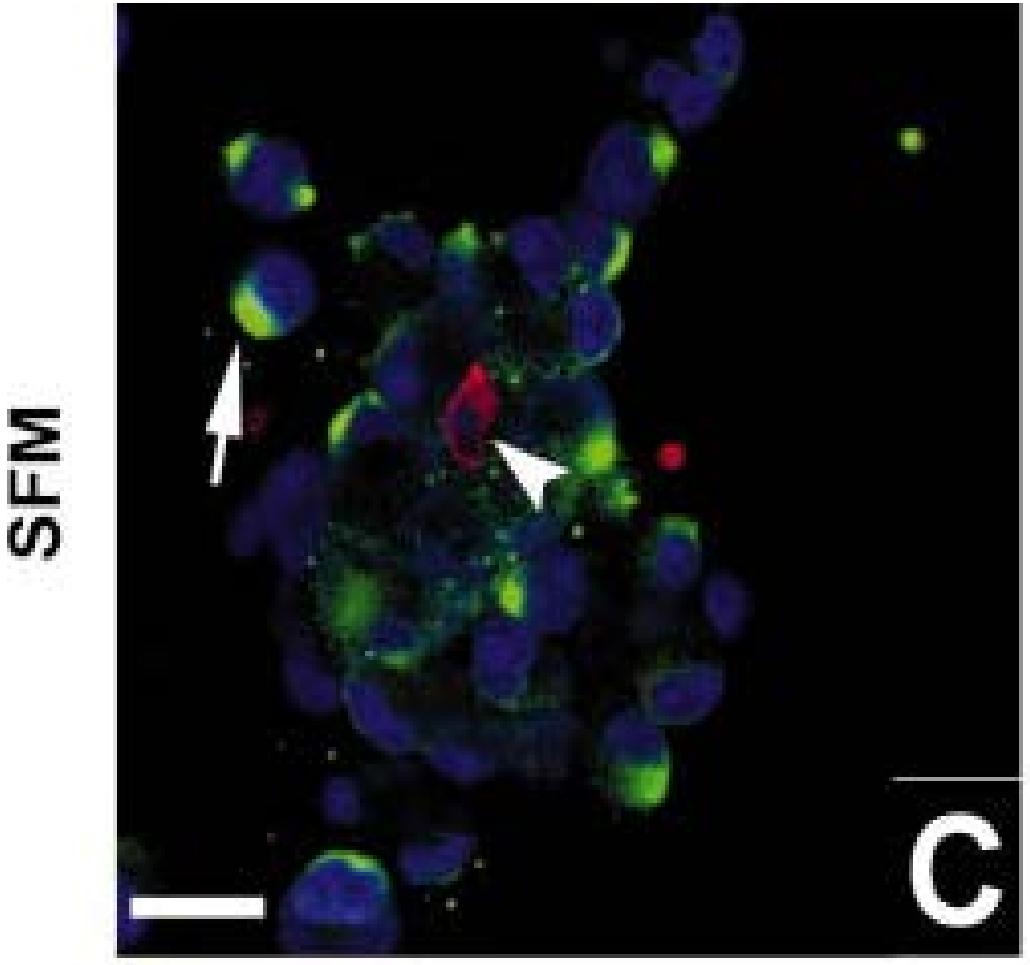
Stochasticity in gene expression

Genotype-phenotype map no longer 1-1



Novick and Weiner PNAS 43, 43: 553–566, 1957; Elowitz et al. Science 297: 1183–1186, 2002; Raj and van Oudenaarden CELL 135(2): 216–226, 2008

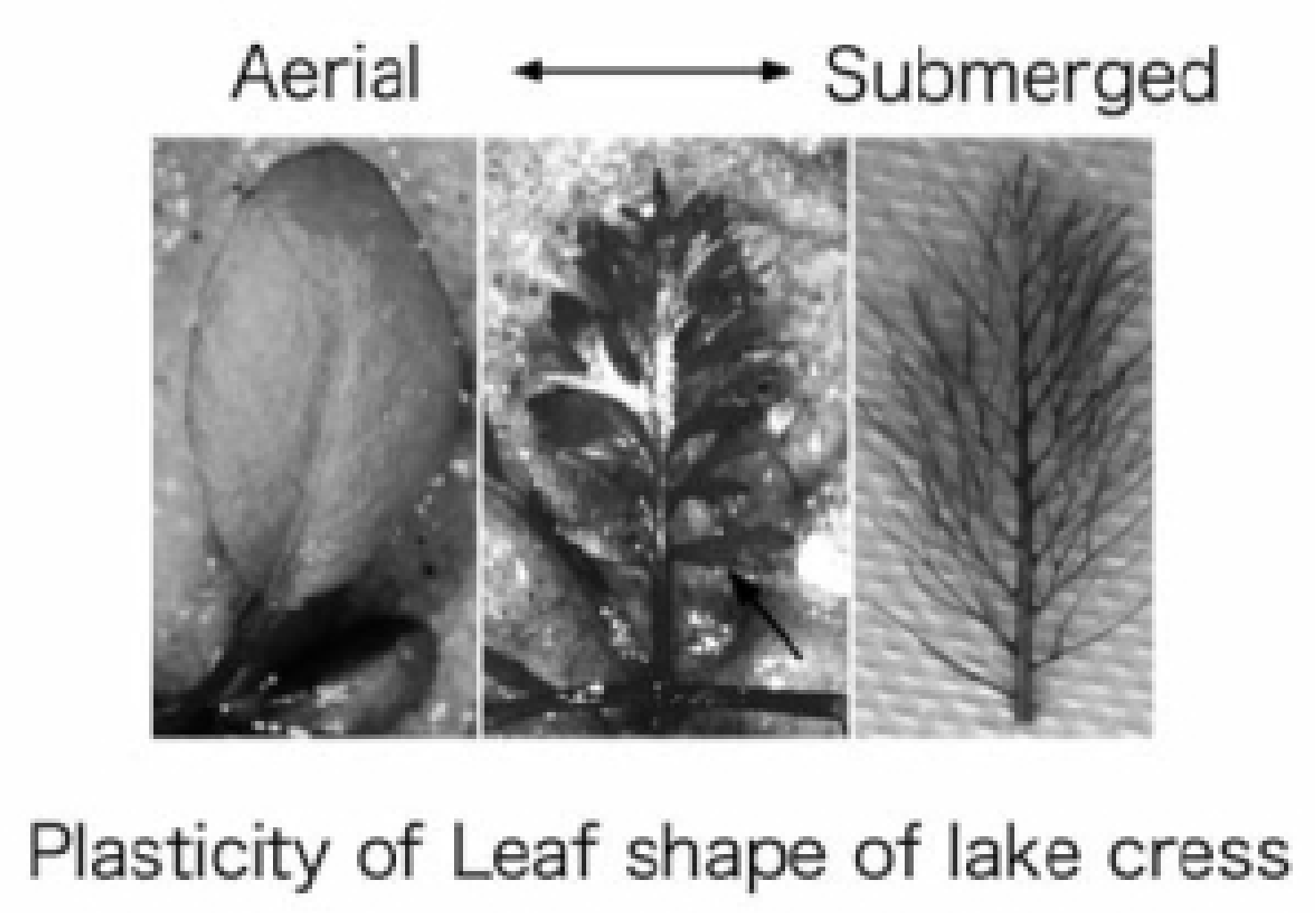
Functional consequences of stochasticity



Clone of PANC-1 cells expresses FGF-2 (red) or FGF-2 receptor (green), not both.
Hardikar et al. (2003) PNAS 100(12): 7117–7122

Environment imposes phenotype:

Phenotypic plasticity



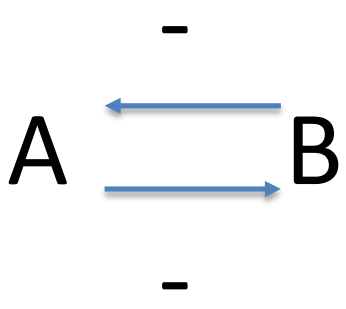
Plasticity of Leaf shape of lake cress

http://www.kyoto-su.ac.jp/english/department/graduate/g_eng/fm/kimura.html

Environmentally induced state can be inherited

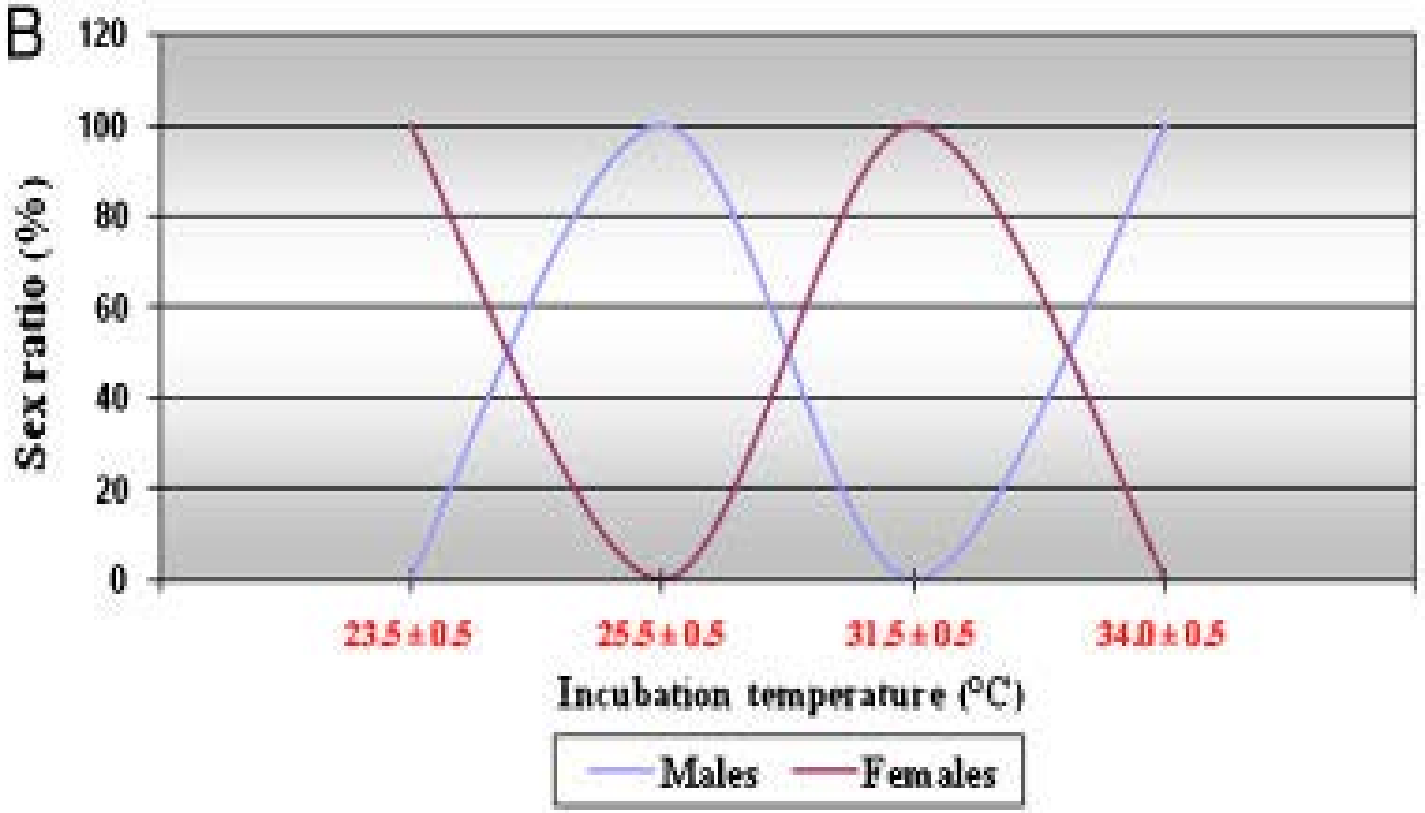
Two-state system,

states inhibit each other



A (on), B (off) and vice-versa are the only two stable outcomes.
An environmental fluctuation can induce a transition between them.
Either stable outcome can be inherited.

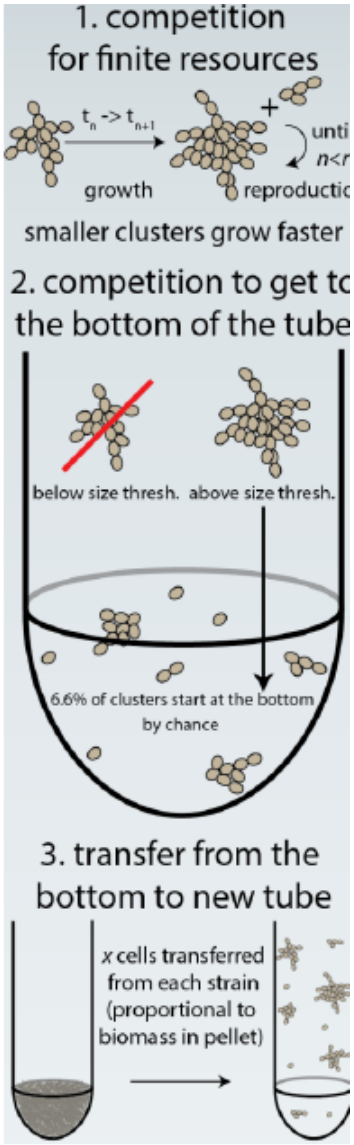
Environment imposes phenotype:
temperature-dependent sex



Temperature-dependent sex determination in *Calotes versicolor*;
Inamdar et al., J Exp Zool 317A (1) 32–46, 2012

Environmentally-induced multicellularity in yeast:

"throwing" cells together is enough to induce multicellularity



Ratcliff, in "Multicellularity" (Niklas and Newman, eds., MIT Press 2016)

Co-evolution

The individual" ➔ Many genomes

"Environment" co-evolves with "organism"; Holobiont

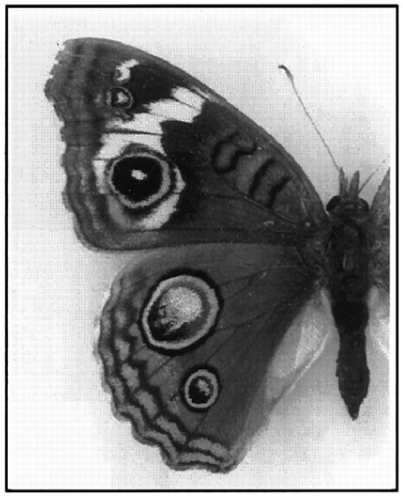
Egyptian plover and Nile crocodile
(http://bookbuilder.cast.org/bookresources/12/12710/46346_1.jpg)

Gilbert & Epel, Ecological Developmental Biology

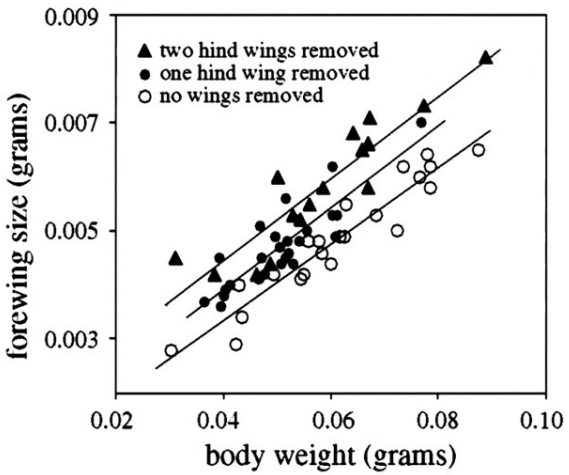
Correlations

Developmental constraints on evolution

a



b

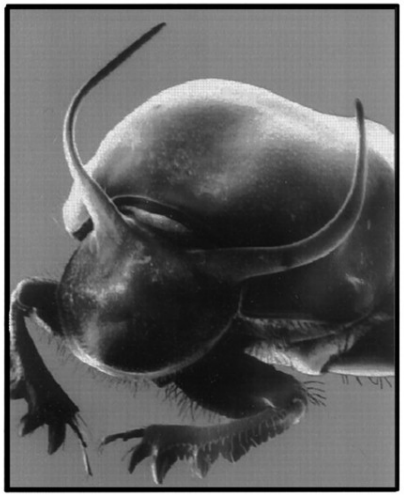


c

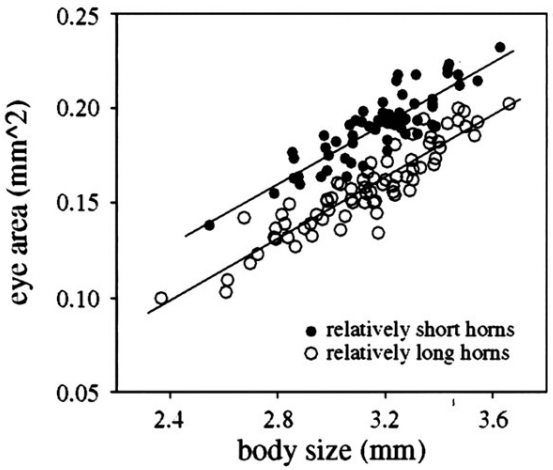
Compensatory response to a removal of hindwings during development:

body part	F	p
forewings	**51.010**	**0.0001**
thorax	**16.575**	**0.0001**
forelegs	**14.558**	**0.0003**
head	0.693	0.4084
abdomen	0.661	0.4193

d



e



f

Correlated response to artificial selection on male horn length:

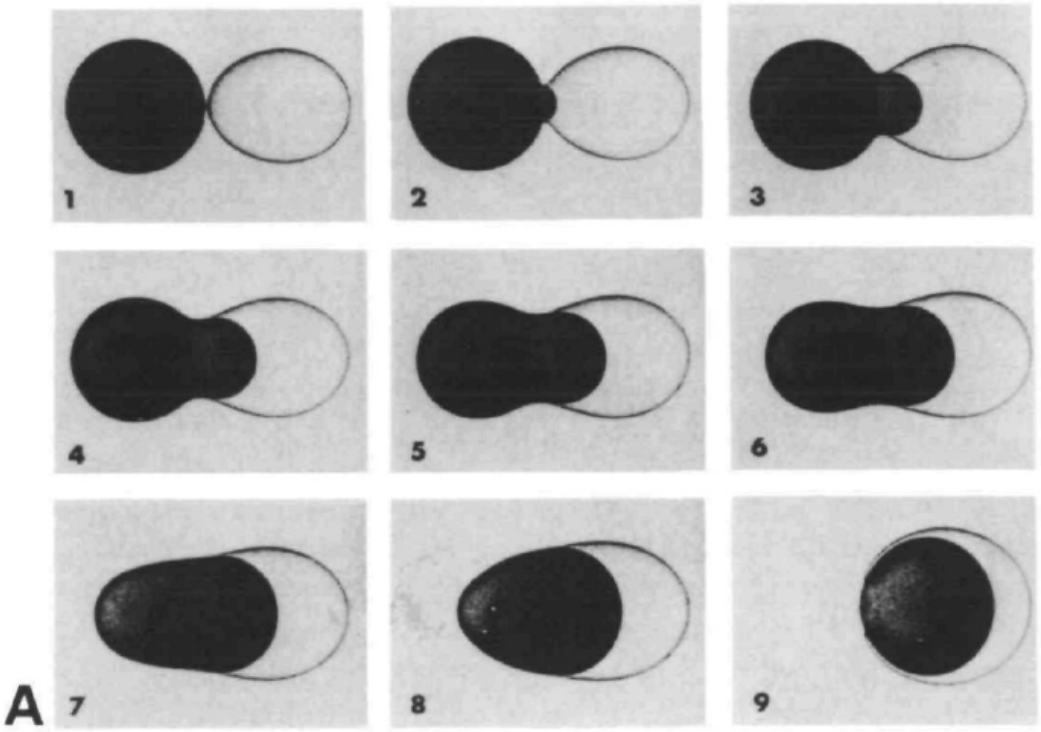
body part	F	p
eyes	**330.355**	**0.0001**
antennae	0.233	0.6302
palps	0.116	0.7341
forelegs	0.022	0.8825
wings	3.418	0.0671

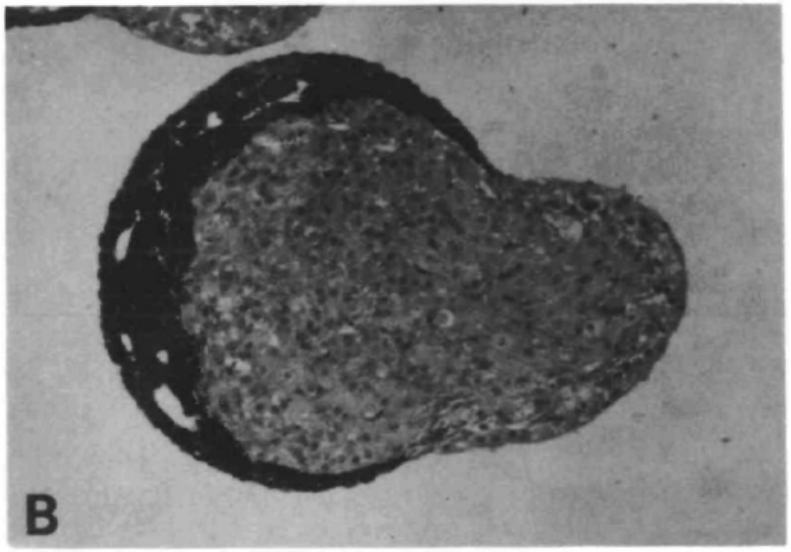
Nijhout and Emlen, PNAS 95 (7): 3685-3689, 1998

Form without genes:

Evolution facilitated by physics

(Haldane: “Even the Pope is 70% water”)





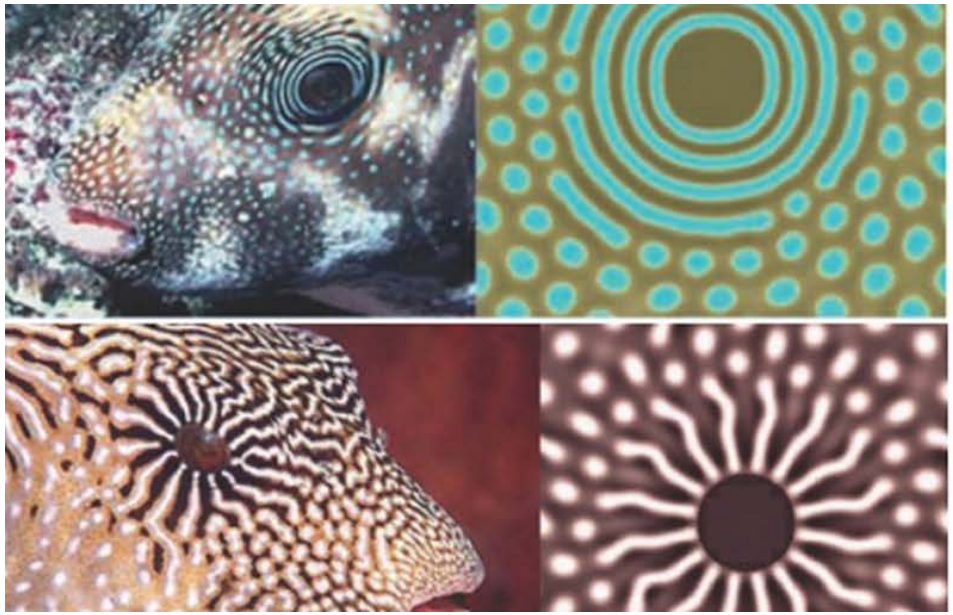
Water drop engulfs polyglcol; embryonic retina cells engulf embryonic heart;

Internalist view of form; variation in form *precedes* genetic change

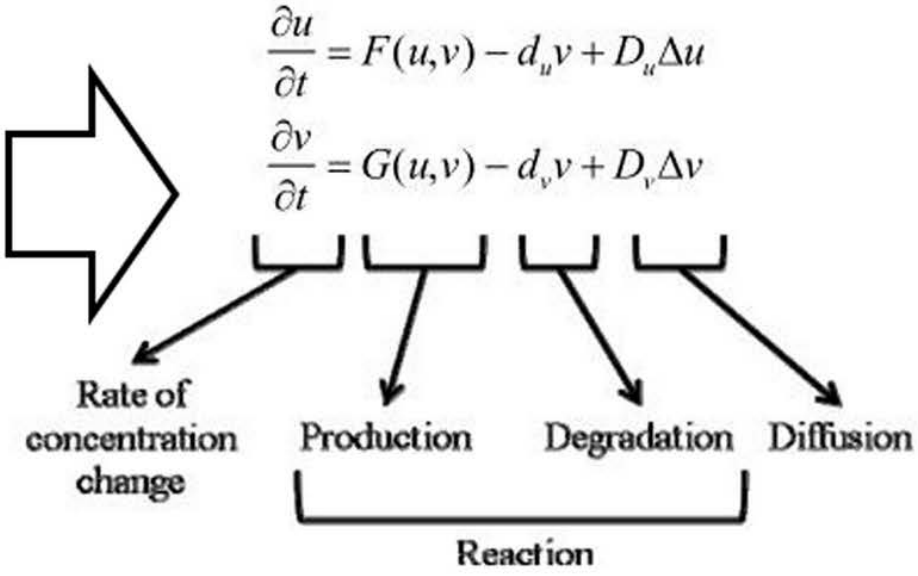
Newman and Comper, Development 110, 1-18 (1990)

Patterns via self-organisation (Turing)

Biology



Physics



Kondo; http://24.media.tumblr.com/tumblr_lhjkj7gN0j1qz8rhwo1_500.jpg

Reach of evolutionary thinking

1. Mathematics
2. History
3. Culture
4. Behaviour
5. Psychology

Suggested readings (besides those already given)

Darwin, The Origin of Species;

Jacob, The Possible and the Actual;

Maynard Smith, The theory of evolution

Futuyma and Kirkpatrick, Evolution;

Bateson et al., ”New trends in evolutionary biology: biological, philosophical and social science perspectives”, Interface Focus 2017 7 20170051; DOI: 10.1098/rsfs.2017.0051;

Nanjundiah, The Origin of Species after 150 Years (http://www.ias.ac.in/article/fulltext/reso/014/02/0124-0153).