Developmental Evolution

12 troublesome definitions
1. development
2. evolution
3. epigenetics
4. canalization
5. cryptic genetic variation / capacitance
6. genetic assimilation
7. evolvability
8. preadaptation
9. phenotypic plasticity
10. epistasis
11. modularity
12. developmental bias / constraint

Health and safety warning
"When I use a word, it means just what I choose it to mean – neither more nor less"
Humpty Dumpty

1. Development
- The process by which a genotype becomes a phenotype
- What about cell differentiation?
- What about λ lysis/lysogeny decision?

2. Evolution
- Evolution is sometimes defined in terms of changes in allele frequencies.
- Is this legitimate when Darwin described evolution without knowing what an allele frequency was?
- “Molecular evolution” can involve neutral drift only. Is this evolution in the Darwinian sense?
- Is evolution defined relative to phenotypes or genotypes?

3. Epigenetics
- Historical definition: The study of the processes involved in the unfolding development of an organism
- Modern definition: The study of heritable changes in gene function that occur without a change in the DNA sequence

Both definitions are still in use
4. Canalization
Conrad Waddington put development into evolution with the canalization metaphor
- Genotype and environment combined to form a high-dimensional epigenetic landscape
- Development is a ball rolling down the hill
- Evolution favors deep canals

Gene networks underlie epigenetic landscape

Canalization vs robustness
- **Canalization** explicitly includes development and evolution
- **Robustness** has engineering connotations
- **Redundancy** is a special case of robustness, in which specific functions are duplicated

Problems with canalization
Canalized relative to what organism or trait?
If all biological systems are canalized, then we have no negative control.
Canalized relative to what perturbation?
1. small vs large perturbations
2. genetic vs environmental perturbations
3. novel vs previously seen perturbations

Measuring canalization
- Can only measure variation, while canalization is about variability
- Fluctuating asymmetry is often used to look at perturbation by developmental noise (also some microenvironmental perturbation)
- Variation within inbred population looks at microenvironmental perturbation
- Variation between treatments looks at macroenvironmental perturbation

Internal selection
- External selection = the normal sort, some phenotypes are better than others
- Internal selection
  - different tissues need to develop and work together
  - developmental system has to be stable to fluctuations
  - requirement for stability can be separated for requirement for a particular outcome
Model development as transcriptional regulatory network

Internal selection is sufficient for phenotype to become canalized as a byproduct (Siegel & Bergman PNAS 2002)

5. Cryptic genetic variation / capacitance
- When the ball breaks out of a canal, there is a lot of cryptic genetic variation out there
- Mutants normally more variable than wild-type
- The process of storing and revealing cryptic genetic variation is known as evolutionary capacitance

6. Genetic assimilation: Waddington's experiment
- Crossveinless (cv) phenocopy appears at 40% in response to heat shock of Drosophila pupae.
- Select for cv under heat shock conditions.
- cv starts to appear even when heat shock is absent.
- Acquired phenotype has become inherited.

Definitions
Phenocopy:
Variant produced by environmental perturbation. Equivalent phenotype can be generated by mutation.

Genetic assimilation:
Phenocopy's loss of dependence on environmental perturbation for expression.
(functional definition)

Explanations for genetic assimilation
- Waddington: deepening of crossveinless canal
- Alternative: additive genetic variance for cv
- Lower cv expression threshold with heat shock
- Selection shifts the curve towards assimilation
- Nothing mysterious: explains phenomenon at genetic level

Natural eg.s of genetic assimilation: Waddington on ostrich callosities
- Ostriches sit on hot, hard ground and get calluses on their rump
- Selection ⇒ more sensitive to less stimulus
- Ostriches get calluses even as fetuses
- Genetic assimilation: an acquired phenotype has become inherited