Unit 3: Evolution, Genetics, and Development

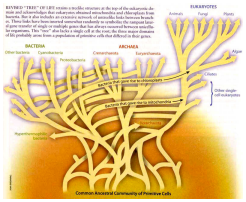
3. Bringing Back Development: Evolutionary-Developmental Biology (Evo-Devo)

The Prokaryote Challenge to the Synthesis

- The synthesis account works best for sexually reproducing organisms
  - In the late 19th century Weismann argued for the sharp distinction between germ cells that could figure in generating offspring and somatic cells that did not affect offspring
    - Mutations in somatic cells would not be passed on
    - Germ cells are, and they give rise to a vertical path from parents to offspring
- There is no germ/soma distinction in prokaryotes—they reproduce by dividing
  - Any change to genes will be passed on
- Moreover, prokaryotes are capable of acquiring DNA from other organisms—horizontal gene transfer
- As a result, a given prokaryote can get its DNA from many sources
  - If one bacterium has a mutation that helps deal with a challenge (a new drug we devise)
    - Other bacteria can borrow the solution
    - And even store it offline until they need it and move it to a place where it will be transcribed and translated into proteins

Problems for the Tree of Life

- It is common to view evolution as a tree developing from a single root
- But lateral gene transfer allows for passing material between lineages
- It also appears likely that eukaryotic cells (cells with internal organelles such as a nucleus and mitochondria) resulted from the combining of two prokaryotes (one becoming the mitochondrion or the chloroplast)
- These raise serious problems for understanding evolution as creating a tree of life



Clicker Question

What is meant by calling a biological trait an adaptation?

A. The trait serves to enable its bearer to leave more offspring
B. The trait serves to enable its bearer to live longer
C. The trait enables its bearer to better satisfy the constraints imposed by its local environment
D. The trait is present in current organisms as a result of being selected in previous generations

Challenging the Hardening of the Synthesis

- In 1979 Stephen J. Gould and Richard Lewontin issued a stinging critique of adaptationism
- Traits might be adaptive without being adaptations (i.e., without having been the object of natural selection)
- More generally, traits can evolve without being adaptations
  - As a result of being linked with other traits that are being selected
  - As conserved traits due to existing *bauplan*
  - As a result of developmental constraints
- Adaptationist explanations are often *just-so* stories
  - Typically they are not subjected to rigorous tests
  - When found to be false, they are quickly replaced with another purported adaptationist explanation

Discussion Question

Infidelity is a common characteristic of human relationships. What selection factors might have favored it? Pick your favorite story or propose another

A. It results in a more diverse range of combination of genes than if all relationships were monogamous
B. It provides opportunities for humans to re-evaluate their partner choice and find better fit partners with whom to have children
C. It helps promote a higher rate of reproduction given that people get tired of the same partner
D. Other

Spandrels of San Marco

- Spandrels are an inevitable consequence of mounting a dome on top of rounded arches
  - Once spandrels existed, they became places on which to present art
  - BUT, they were not included in the design as a place to put art
- Contention: biological traits are often spandrels, not products of selection

Lewontin and Gould's Analysis of Adaptationists' Mistakes

- Treating traits as typically atomic—each can be selected independently
  - some, features, like the chin, weren't objects of selection
  - many depend on others and cannot be promoted independently
- Treating all adaptive traits as adaptations
  - feathers are adaptive for flying but not adaptions for that activity (rather they were selected for temperature regulation)
- Ignoring other explanations
  - some traits are simply conserved, not undergoing selection
  - traits might be limited by constraints (trees limited in height)
- Failure to test adaptationist explanations
  - make new inferences from the hypotheses and investigate their truth

Bringing Development Back

- Before he developed the chromosomal theory of inheritance, Morgan's focus was on development (a project to which he returned late in his career)
- The evolutionary synthesis downplayed the significance of development for understanding evolution
  - Development is the unfolding of the organism according to the program laid out in the genes
  - Any noise in the expression of genes does not affect the genes themselves
- In pointing to developmental constraints Gould and Lewontin pointed to a potential relevance of development to evolution
- This has given rise to Evolutionary Developmental Biology (Evo-Devo) and the even more radical Developmental Systems Theory

Constraints: Limits and Possibilities

- The word “constraint” suggests limitation
  - If blood is constrained to flow through an blood vessel, then it cannot just spread out in all directions
- But constraints create possibilities
  - Without being constrained to a blood vessel, little blood would make it to the distant parts of an organism
- Biological structures in general constitute constraints
  - A skeleton limits how muscles can move, but enables an organism to exert forces and do things that would not otherwise be possible

Why Do No Centipedes Have 100 Legs?

- Despite their name, no centipedes have 100, or 92, 96, 104, 108, etc. legs
  - they have only an odd number of pairs of legs
    - although some centipedes go through a stage of development with an even number of pairs of legs
      - and these seem to function perfectly well

- The explanation identifies a two-stage process
  - one of doubling segments, resulting in an even number
  - endings with one that adds a segment between each existing segment, resulting in an odd number

Development and Constraints

- Multi-cellular organisms impose constraints on individual cells
  - In a biofilm, individual bacterial cells lose their ability to navigate freely
    - but gain the ability to rely on each other for nutrients, protection, etc.
    - individual bacteria can begin to specialize
  - In obligate multicellular organisms like us, individual cells are constrained to perform specific functions, allowing the whole organism to do things a single cell cannot do
    - the constraining structure must be built over time, and so offers different constraints at different points

Development and Constraints

- A complex multicellular organism goes through a process in which new constraints appear
  - limiting which structures can be developed next (also creating possibilities for new structures)
- An evolutionary change must alter an existing organism in a way that allows for the new organism to develop
  - it is easiest to make changes that do not alter early stages of development
    - those have many downstream consequences so messing with them may undermine the viability of the organism
  - any change must allow for an organism to function at all stages in its development

From Constraint to Evolvability

- In the decades after "Spandrels," proponents of a developmental perspective on evolution shifted from talk of constraints to talk of evolvability
  - "the ability of organisms to generate heritable and viable phenotypic variation" (Brigandt, 2015)
  - Development determines what can evolve
- Evolvability is not in opposition to selection, but characterizes a different dimension of the evolutionary process
  - "In every generation, heritable phenotypic variation is first generated—the manifestation of evolvability—and then natural selection acts on the available variation." (Brigandt)

Evolvability as an Evolutionary Force

- Selection is generally regarded as a force that determines the direction of evolution
- Evo-devo argues that evolvability is also a force determining what evolves
  - the possibilities for viable modifications of existing organisms direct what can evolve

Susan Oyama: Developmental Systems Theory

- Genes and Natural Selection are not sufficient to understand evolution
  - Rather, one should make the organism, and the developmental processes it undergoes, central
- "If development is to reenter evolutionary theory, it should be development that integrates genes into organisms, and organisms into the many levels of the environment that enter into their ontogenetic construction" (p. 113).
- Developmental System:
  - "a mobile set of interacting influences and entities" comprising "all influences on development" at all levels, including the molecular, cellular, organismal, ecological, social and biogeographical (p. 72).

Discussion Question

Which system do you think is most important for understanding what traits you exhibit today

A. Just my genes—I am what my genes made
B. My nuclear family
C. My neighborhood/village
D. My schools
E. Other

Genes Just Part of the Replicator Story

- Parity Thesis:
  - "any sense in which genes code for phenotypic traits, program development, or contain developmental information can be equally well applied to other factors required for development" (Griffiths and Gray, 2000)
- Intracellular resources required for development
  - Membranes to serve as templates for synthesizing new membranes from proteins
  - Mitochondria for energy
  - Chromatin marking system regulating transcription
  - Cytoplasmic chemical gradients

Discussion Question

What, besides genes, must be present for human development?

A. Nothing—genes do it on their own
B. The egg—it provides the resources for expressing genes
C. The family—it provides food and other resources needed for a baby to develop
D. The language community—it provides the opportunity to acquire a language
E. A social community—it is needed to develop attitudes needed to live

Genes Just Part of the Replicator Story - 2

- Extracellular resources required for development
  - Bush fires for eucalyptus trees
- But, according to orthodox Darwinism, these are not part of inheritance
- "In line with this theoretical role, developmental systems theory applies the concept of inheritance to any resource that is reliably present in successive generations, and is part of the explanation of why each generation resembles the last."
- Developmental system is a integrated system in which resources are made available to the developing organism

Niche Construction

- The standard view has been that the environment exists and selects among organisms that compete with each other
- But organisms can also modify environments in ways that create opportunities for themselves
- The selection forces operative in an environment are partly a product of the organisms' creation of a niche
  - not just something preset for the organism