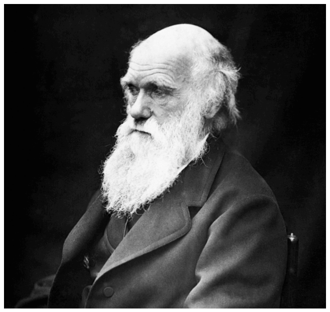
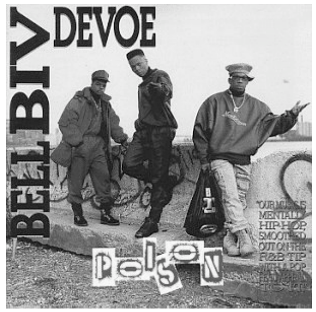
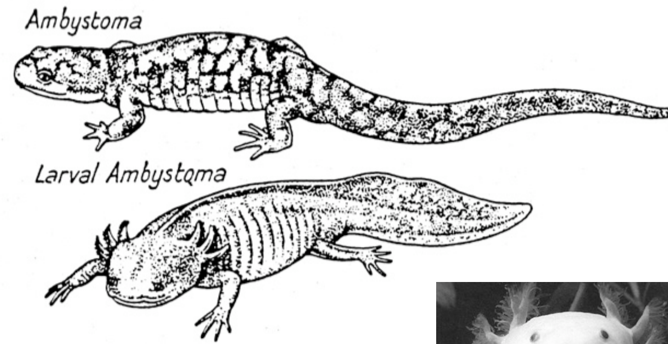
Evolutionary Developmental Biology

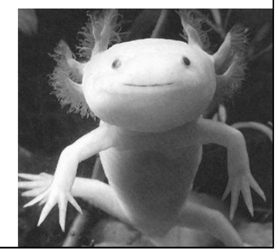


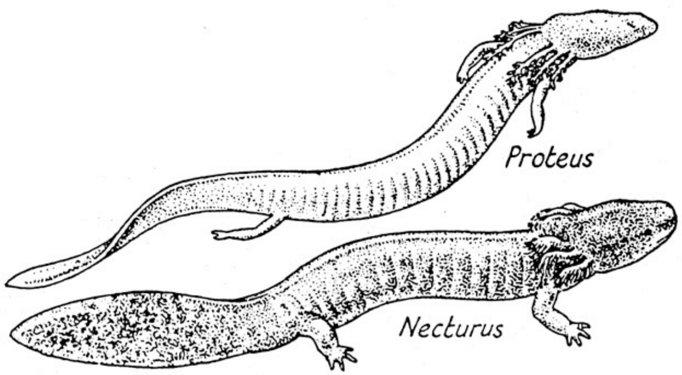


a.k.a. "EVO-DEVO"

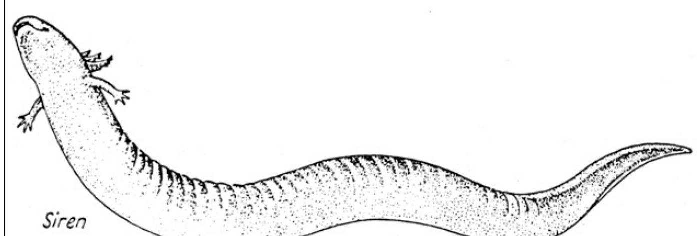


Top: adult tiger salamander.
Bottom: axolotl (paedomorphic tiger salamander)



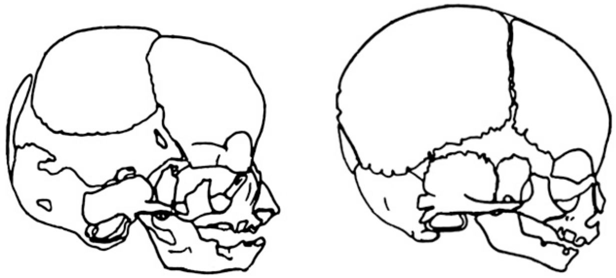


Paedomorphosis is common among salamanders. Note how this hellbender (top) and mudpuppy (bottom) both have gills, paddle tails, and weaker limbs. . .

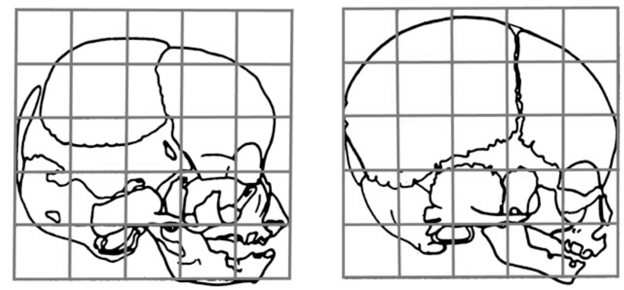


And then this aquatic salamander, *Siren*, is probably the champion paedomorphic salamander of all time! What's more, these *can't* be induced to metamorphose.

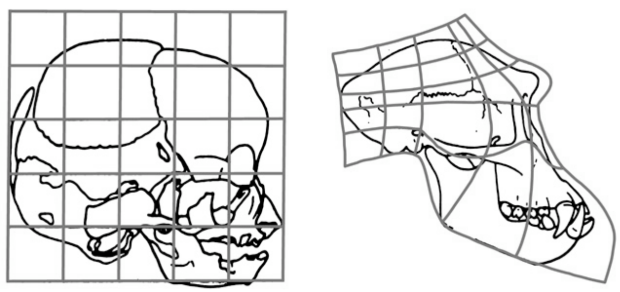
Case Study II



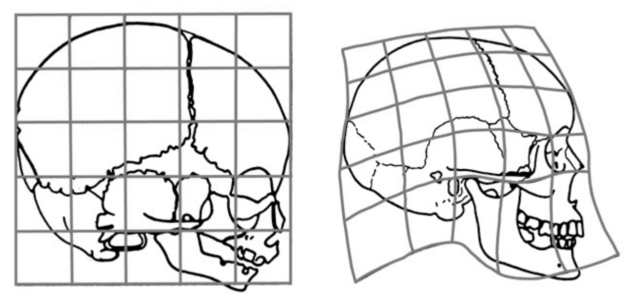
These are the fetal skulls of two closely related animal species. . .



To visualize how they change shape, imagine a grid of lines laid over them like so.



The first species changes a great deal—in particular, the jaw and face grow forwards.



The second species changes too—but much less than the first species did!

Heterochrony in Human Evolution

- Compared to our closest relatives, we humans are *paedomorphic* in many respects
- This is because the rate of physical maturation is, overall, greatly slowed down
  – But NOTE: Many human traits (such as the large brain) result from a longer growth period, which is *hypermorphosis*—which is technically a mode of *peramorphosis*, not paedomorphosis!
  – Human development compared to chimp development is actually a complex mix of changes in developmental rates—it can't be boiled down to a simple set of causes.

A side note on heterochrony:

- A paedomorphic appearance in mammals is often considered to be "cute" by humans.
  – High forehead
  – Large eyes
  – Small jaw
- It has been suggested that humans are behaviorally predisposed to react warmly to a paedomorphic appearance
  – Why? Well, someone who thought babies and children were hideous would not reproduce successfully very much (I would think, anyway). . .

This would seem to explain our feelings towards puppies and kittens. . .

. . . and it would also seem to explain a lot of anime!

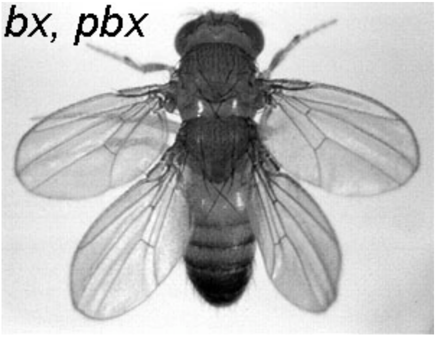
Evolution and Development

- Ernst Haeckel had proposed the "biogenetic law": good old "ontogeny recapitulates phylogeny."
  - Translation: An embryo passes through its own past evolutionary stages.
- As we discussed, this is not true in the literal sense.
  - Embryos don't literally pass through their own ancestral states. (You were never a fish.)
- But the question remains: *why* do embryos retain features like pharyngeal clefts, anyway?

Evolution and Development

- Molecular biology is now used to work out the details of how structures are built in embryos.
  - This is providing insights into the "nuts and bolts" of *how* single cells produce complex bodies. . .
  - . . . and *how* complex bodies can evolve.
- "Evo-devo" is one of the hottest fields in biology right now—an integration of evolution and development.

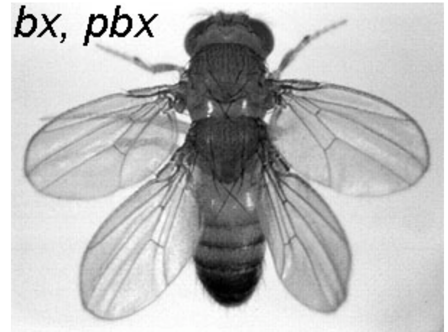
Case Study: Evolution of Insect Wings and Legs



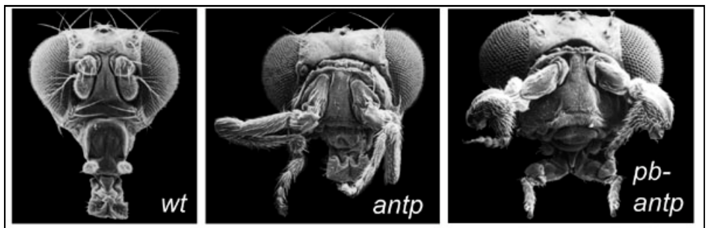
Homeotic Mutations

- Most insects have two pairs of wings.
- Normal fruit flies have one pair of wings and one pair of *halteres* (stubby organs used in balance and orientation in flight).
- In the 1930s, mutant flies were found in which the halteres were seemingly transformed into full-sized normal wings.
- Such mutations are called *homeotic mutations*.

This SEM of a housefly shows a club-like haltere posterior to the right wing. . .



. . . and this homeotic mutant fruit fly, *bithorax*, shows the transformation of a haltere to a second pair of wings.



Another example: Fly antennae and mouthparts could be transformed into completely normal legs.

The wild-type is at left. The center shows *antennapedia* (antennae replaced by legs). At right is a fly with both *antennapedia* and *proboscipedia* (mouthparts replaced by legs.)

Other animals may show homeotic mutations—William Bateson noticed them as early as 1894.

Bateson's drawing of a moth, *Zygæna filipendulae*, with a wing where one leg should be

"For the word 'Metamorphy' I therefore propose to substitute the term **Homoeosis**, which is also more correct; for the essential phenomenon is not that there has merely been a change, but that something has changed into the likeness of something else."

—*Materials for the Study of Variation* (1894)

Even plants have 'em—"double daffodils", for example, may have stamens converted to petals, or petals converted to sepals.

Homeotic Mutations

- Conclusion 1: Certain mutations can radically alter the phenotype
- Conclusion 2: Such mutations can provide evidence of homologies
  - On phylogenetic and structural grounds, it seems likely that halteres are homologous with wings
  - The fact that a single mutation converts one to the other suggests that there's a genetic basis for this hypothesis, too!
  - The same goes for antennae: it had already been proposed that antennae and mouthparts are modified legs.

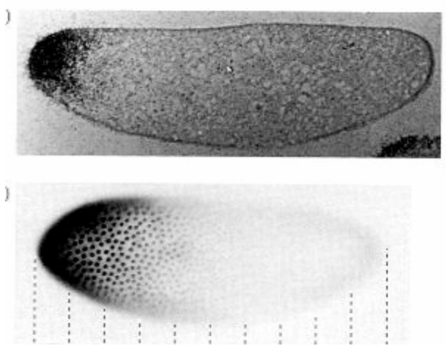
Homeotic Genes

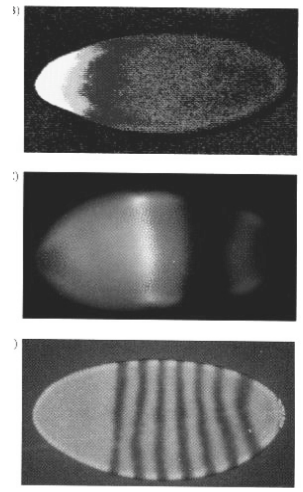
- The old "hopeful monster" theory of Richard Goldschmidt has been discredited. . . but it did encourage people to take a closer look at homeotic genes
- There are several classes of homeotic genes, organized into clusters on the chromosomes
- Homeotic genes are "master switches" of development: they code for transcription factors that activate whole complexes of genes.

Gene regulation in fruit flies

- *Maternal effect genes*, which are genes in the mother's genome for RNAs that are pumped into each egg cell, regulate. . .
- *gap genes*, which determine large areas of the embryo, and which regulate. . .
- *pair-rule genes*, which are expressed in alternating bands and specify the future segments of the embryo, and which regulate. . .
- *homeotic* genes, which determine segment identity, and which regulate. . .
- *realisator genes*, which cause segment differentiation

Drosophila egg, showing the location of the maternal mRNA *bicoid* (top) and the localization of the bicoid protein, forming a gradient from the future head end to the tail end





Maternal genes regulate *gap genes*; for example, *bicoid* (top) regulates *hunchback* (middle, shown in orange) and *Krüppel* (middle, shown in green). Gap genes regulate *pair-rule* genes such as *fushi tarazu* (bottom). Both gap and pair-rule genes regulate homeotic genes.

Just a part of the gene regulatory cascade, and we haven't even *got* to the homeotic genes yet. . .