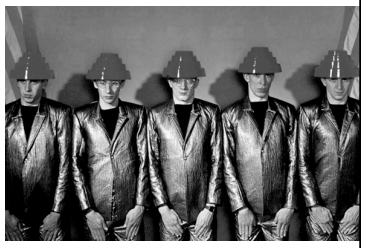
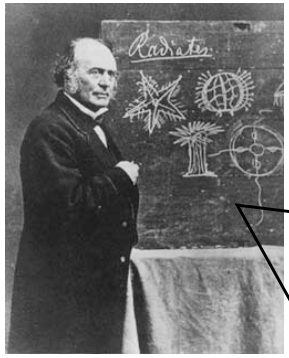
Evolutionary Developmental Biology



EVO DEVO

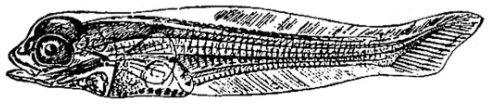
a.k.a. "EVO-DEVO"

It all started with the Swiss professor Louis Agassiz (1807-1873), who emigrated to the US and became a Harvard prof. . .

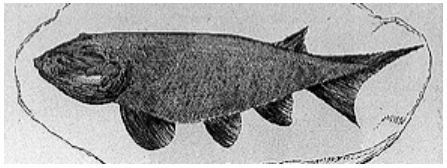


Hence, the embryos of different animals resemble each other more strongly in proportion as we examine them at an earlier period. . . . during almost the whole period of embryonic life, the young fish and the young frog differ scarcely at all: so it is with the young snake compared with the embryo bird.
—*Principles of Zoology* (1848)

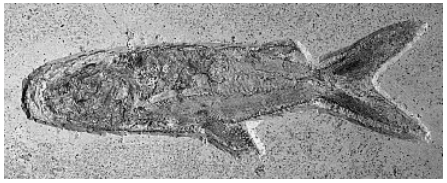
Agassiz had shown that embryonic fish go from a stage with an asymmetrical, *heterocercal* tail (top), to a stage with a symmetrical *homocercal* tail (bottom).



Heterocercal-tailed fish also appear earlier in the fossil record than homocercal-tailed fish. . .



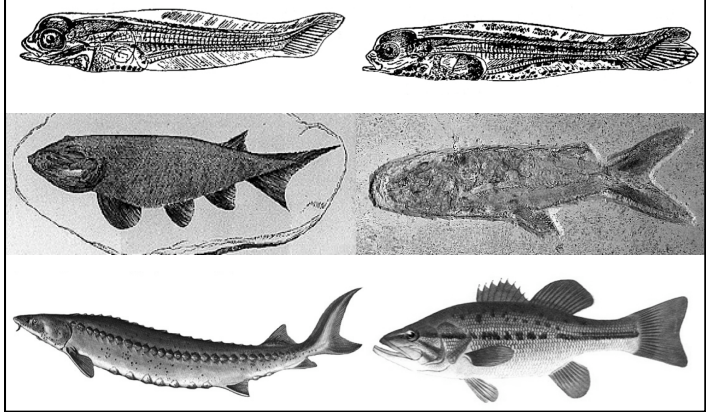
Cheirolepis
380 million years old



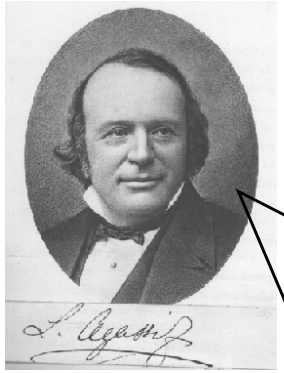
Caturus
180 million years old

This *also* seemed to parallel the "ladder of complexity": less complex fish, like the sturgeon (top), had heterocercal tails, while more complex fish, like bass (bottom), had homocercal tails. . .

This "threefold parallelism" seemed of crucial importance. . .
but what did it *mean?*



Agassiz certainly thought it was important!



I have devoted my whole life to the study of Nature, and yet a single sentence may express all that I have done. I have shown that there is a correspondence between the succession of Fishes in geological times and the different stages of their growth in the egg, — that is all. It chanced to be a result that was found to apply to other groups and has led to other conclusions of a like nature.
—Lecture, 1869

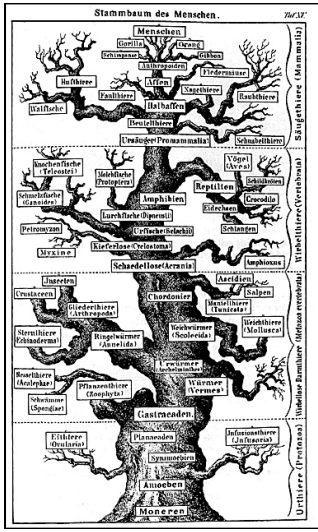
But Agassiz, the "last of the scientific creationists", refused to consider that this "threefold pattern" might have an evolutionary explanation. . .

In one word, all these facts in their natural connection proclaim aloud the One God, whom man may know, adore, and love; and Natural History must in good time become the analysis of the thoughts of the Creator of the Universe.

— "Essay on Classification" (1859)

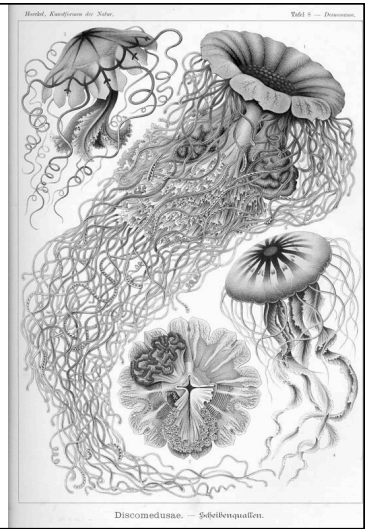
Darwin, however, thought that it could only make sense if you assumed some kind of evolutionary link among organisms!

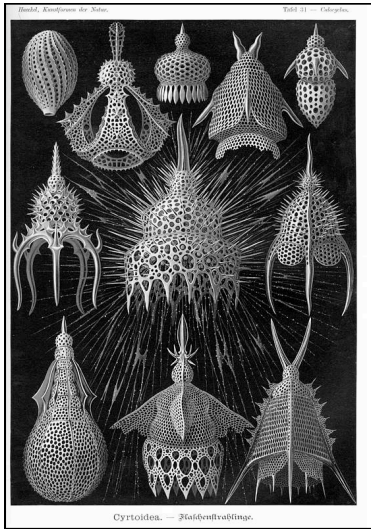
Agassiz insists that ancient animals resemble to a certain extent the embryos of recent animals of the same classes; or that the geological succession of extinct forms is in some degree parallel to the embryological development of recent forms. I must follow Pictet and Huxley in thinking that the truth of this doctrine is very far from proved. Yet I fully expect to see it hereafter confirmed. . .
For this doctrine of Agassiz accords well with the theory of natural selection.
—*Origin of Species*, chapter 10



"Darwin's Apostle to Germany", Ernst Haeckel (1834-1919) popularized Darwinian ideas in his native country. He's the one who drew up elaborate tree diagrams of how evolution had progressed (with man at the top, of course). . .

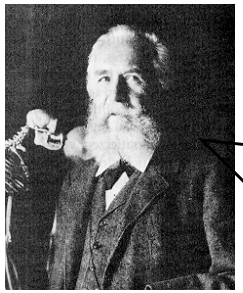
Haeckel was also a great invertebrate zoologist — he worked a lot on protists, sponges and jellyfish— and a gifted illustrator, even influencing the applied arts and design motifs of his time.





Here's another picture of his work—this illustrates the microscopic silica skeletons of some marine protists called *Radiolaria* —which I put in here for no other reason than that they look really cool. . .

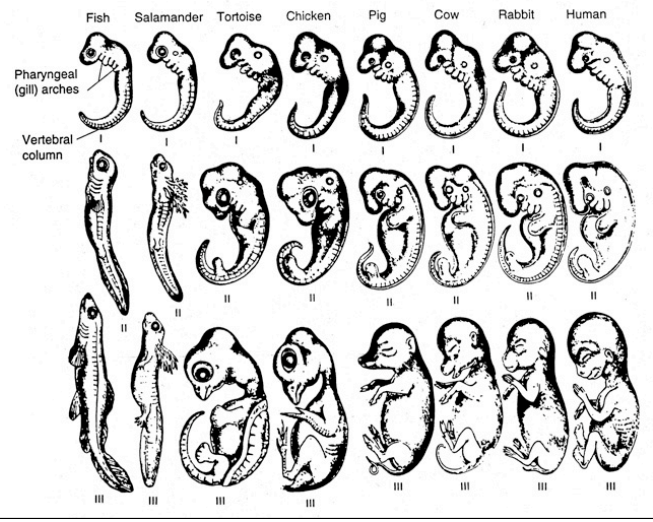
He was also a student of embryology, or *ontogeny*. He's often quoted as saying "Ontogeny recapitulates phylogeny", but what he actually said was:



The rapid and brief ontogeny is a condensed synopsis of the long and slow history of the stem (phylogeny). . .

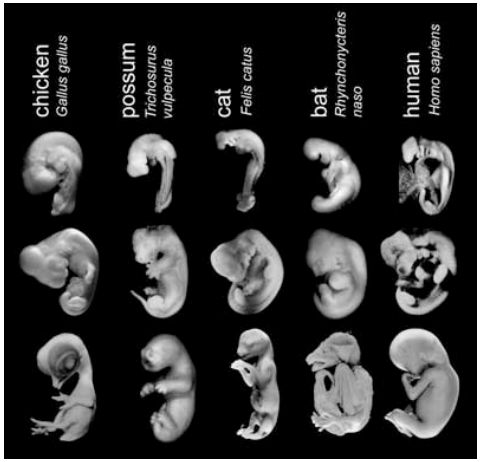
Haeckel reasoned thus:

- Evolution would add changes to the adult stages of the life cycle
  - This makes the most sense if you're a Lamarckian—and Haeckel did accept Lamarckian evolution!
- Previous adult stages would be "pushed backwards" in developmental time
  - Embryonic development was a record (often condensed and abridged and compressed) of an organism's past evolutionary history
- *"Ontogeny recapitulates phylogeny"*—Haeckel's "Biogenetic Law"



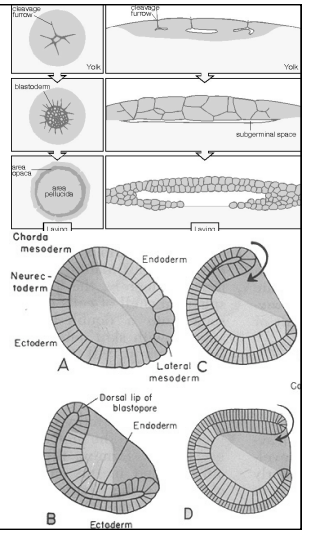
The truth turned out to be much more interesting. . .

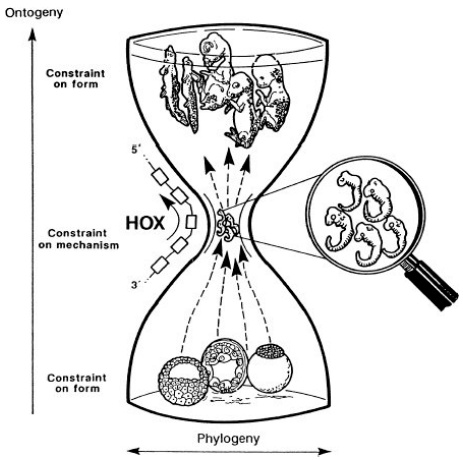
- Haeckel's "Biogenetic Law" doesn't work—organisms do not literally repeat their ancestral stages in any real sense
  - "Von Baer's Law," proposed by Haeckel's rival Karl von Baer, is more accurate: Generalized features, common to all members of a taxon, appear in development before the features of subgroups do.
  - . . . but evolution can and does modify any stage of an organism's life cycle, sometimes almost beyond recognition
- BUT. . . learning how evolution and development are interrelated has become a very fruitful area of research.



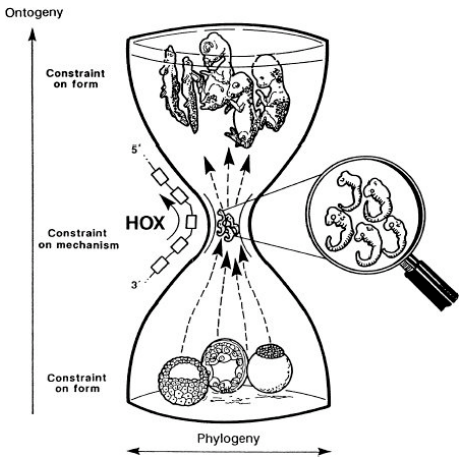
Vertebrate embryos do go through a stage—known as the *pharyngula*—at which they most closely resemble each other. Haeckel has been accused of faking his drawings, but the similarities at the pharyngula stage are real.

The ways that different vertebrates get to the pharyngula, however, vary a great deal—the early stages of chicken development (top) don't look anything like the early stages of frog, fish, or amphioxus development (bottom), largely because of the very different amounts of yolk in different eggs affecting the cells' ability to divide.





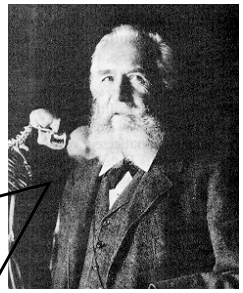
Development across the vertebrates may be diagrammed as an hourglass—very different early stages and adults, but a common *phylotypic* stage, the pharyngula, in between. Other phyla, such as arthropods, show a similar pattern.



We now know that embryos at the phylotypic stage are most similar, not only in shape, but in patterns of gene expression. Notice that at the phylotypic stage, a set of genes called *HOX* is transcribed and translated—more later on what they do!

Haeckel's "Law" isn't accepted today, but in some cases he was dead-on. . .

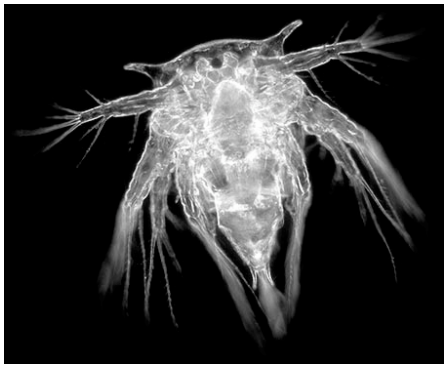
". . . this history of the embryo (ontogeny) must be completed by a second, equally valuable, and closely connected branch of thought— the history of race (phylogeny). Both of these branches of evolutionary science, are, in my opinion, in the closest causal connection; this arises from the reciprocal action of the laws of heredity and adaptation. . . '"



Embryos may show features that the adults have lost—this is another source of information for classification and phylogenetic studies.

These barnacles were once classified as molluscs. . .

. . . until their larvae were discovered to be very much like the larvae of crustaceans—which is what barnacles really are.

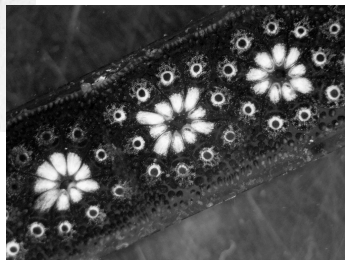


Even rhizocephalans—weird fungus-like parasites on decapod crustaceans such as crabs—have turned out to be crustaceans very close to the true barnacles, based on their larvae.

Another nifty example (which von Baer himself never believed): "Sea squirts", or *tunicates*, have blobby adult bodies, but larvae with chordate features.

"tadpole larva" of the tunicate
Botryllus schlosseri

adult colony of the tunicate
Botryllus schlosseri



Heterochrony

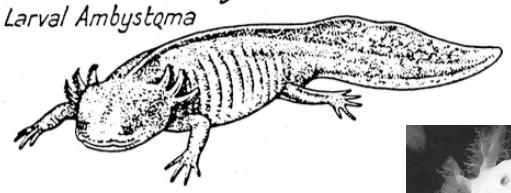
- "Different timing"—evolutionary change in the timing of a developmental event
  - May be global (affecting whole organism) or local (restricted to one part or organ)
- Heterochronic effects may be grouped into two broad classes:
  - *Paedomorphosis:* descendant is less developed / less mature than ancestor
  - *Peramorphosis:* descendant is more developed / more mature than ancestor

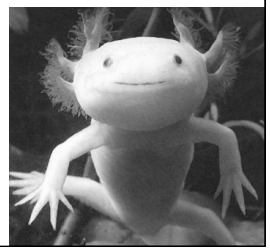
Modes of Heterochrony

- Paedomorphosis can be the result of:
  - **progenesis** (finishing early)
  - **neoteny** (slower growth rate)
  - **postdisplacement** (starting late)
- Peramorphosis can result from:
  - **hypermorphosis** (finishing late).
  - **acceleration** (greater growth rate)
  - **predisplacement** (starting early)
- These terms may apply to whole organisms (global heterochrony) or to parts of them (local heterochrony)

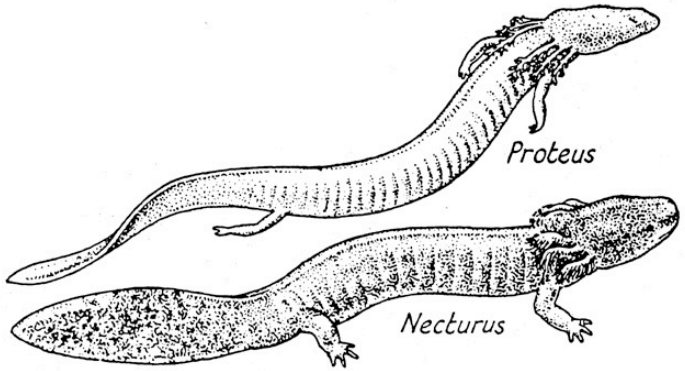
Case study: Axolotls

- The axolotl was first described as a bizarre aquatic salamander with external gills.
  - Gills are a feature of larval salamanders.
  - Yet axolotls reached sexual maturity, and bred.
- Iodine added to the water suddenly transformed axolotls into adult tiger salamanders (*Ambystoma tigrinum*)
  - Some populations of axolotls don't transform, or transform only rarely, when iodine is added. . .

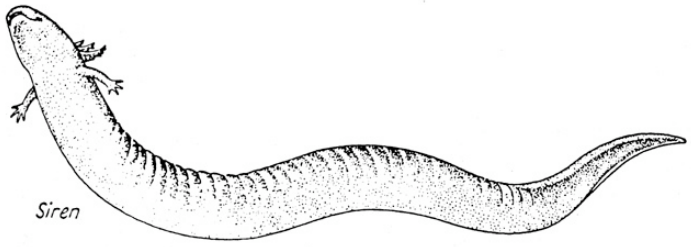




Top: adult tiger salamander.
Bottom: axolotl (paedomorphic tiger salamander)



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.