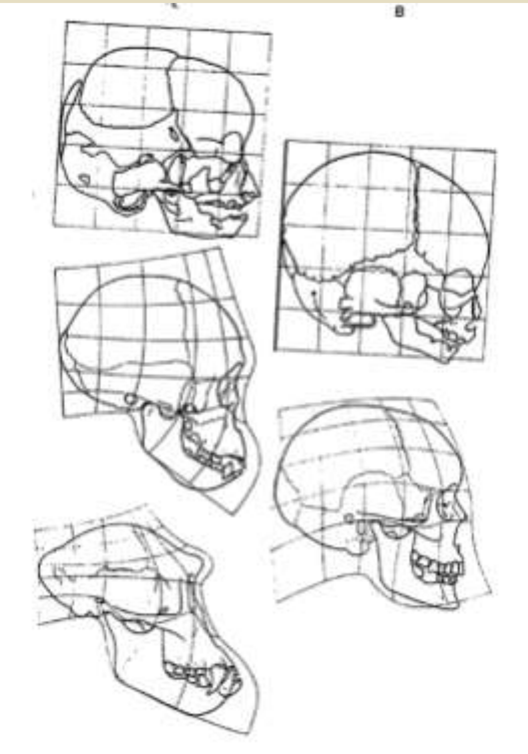
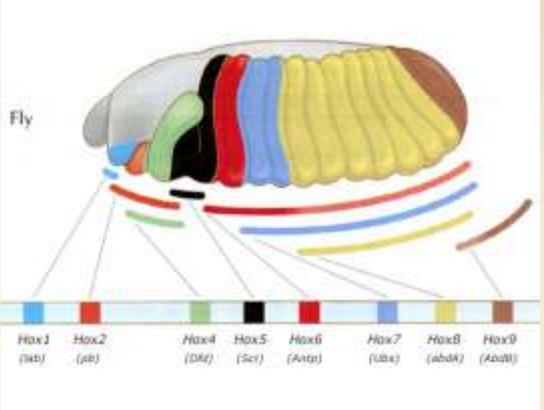
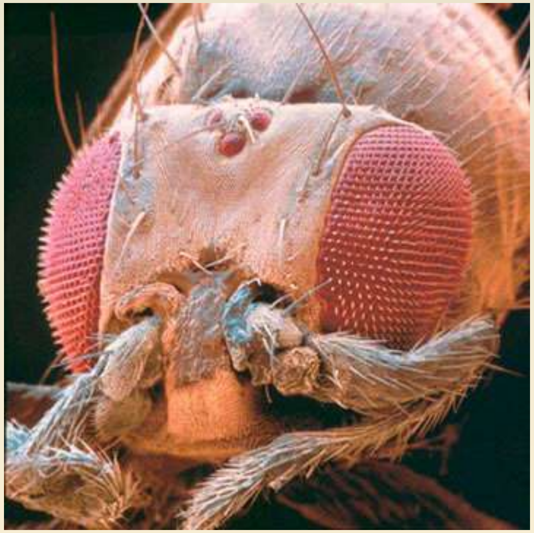
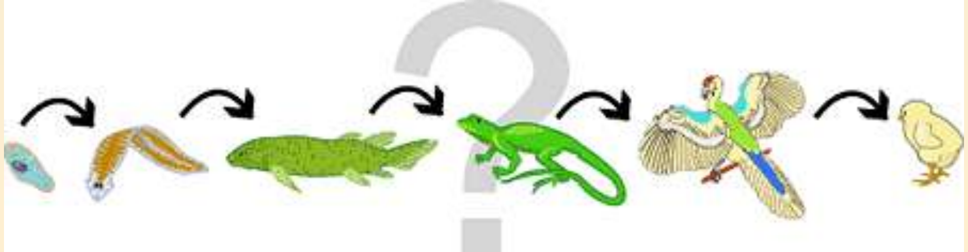
Evolution and Development

Evo-Devo









Darwin wrote a book on barnacles….

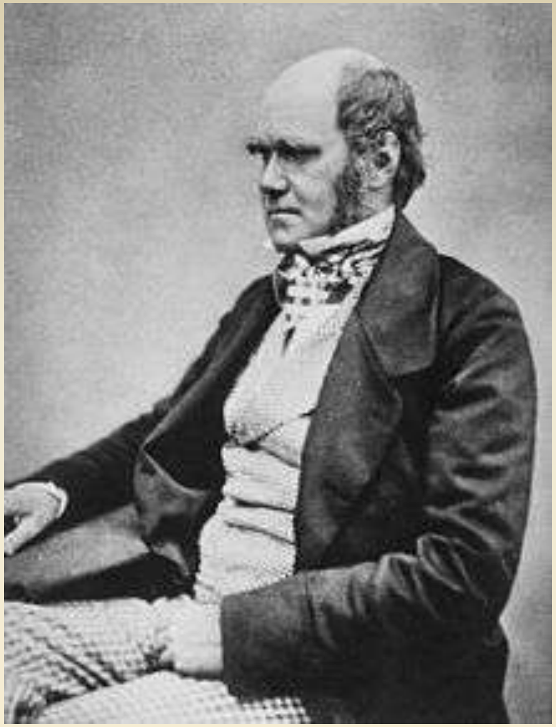


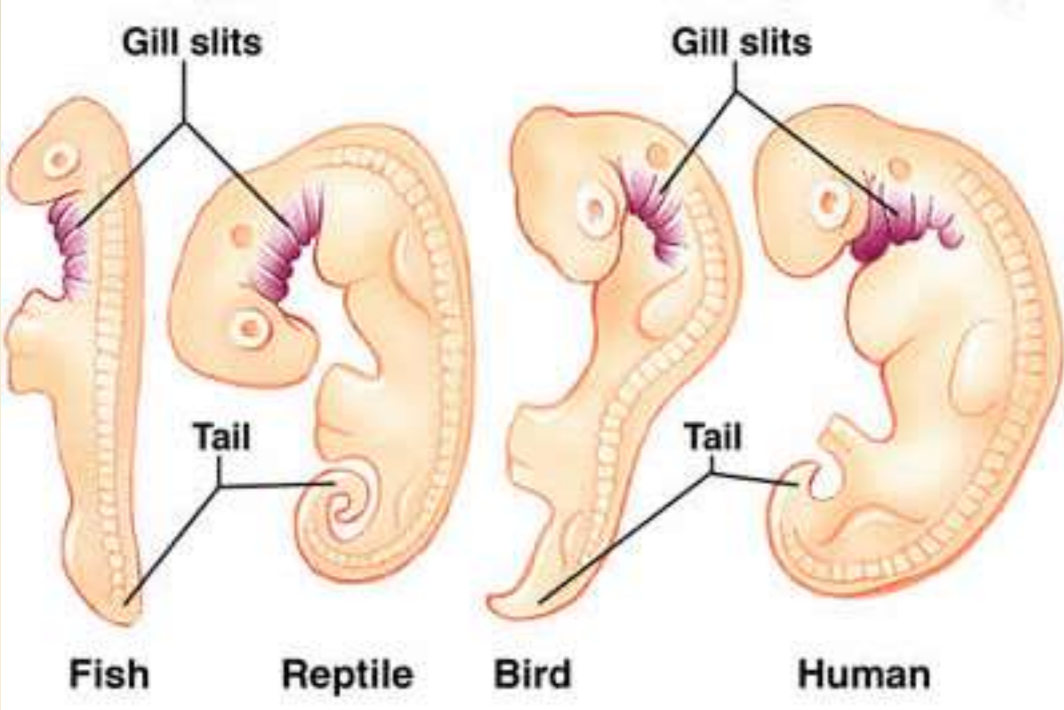
Plate 1 (Lepas), from “A monograph on the sub-class Cirripedia”, by Charles Darwin.

Comparative embryology

There is an obvious similarity between embryos of fish, amphibians, reptiles, birds and mammals.

All have tail and rudimentary “gill slits,” even though slits do not remain later in life, except in fish.

This may indicate a fundamental step that is common to all vertebrates and supports the idea of a common ancestor.

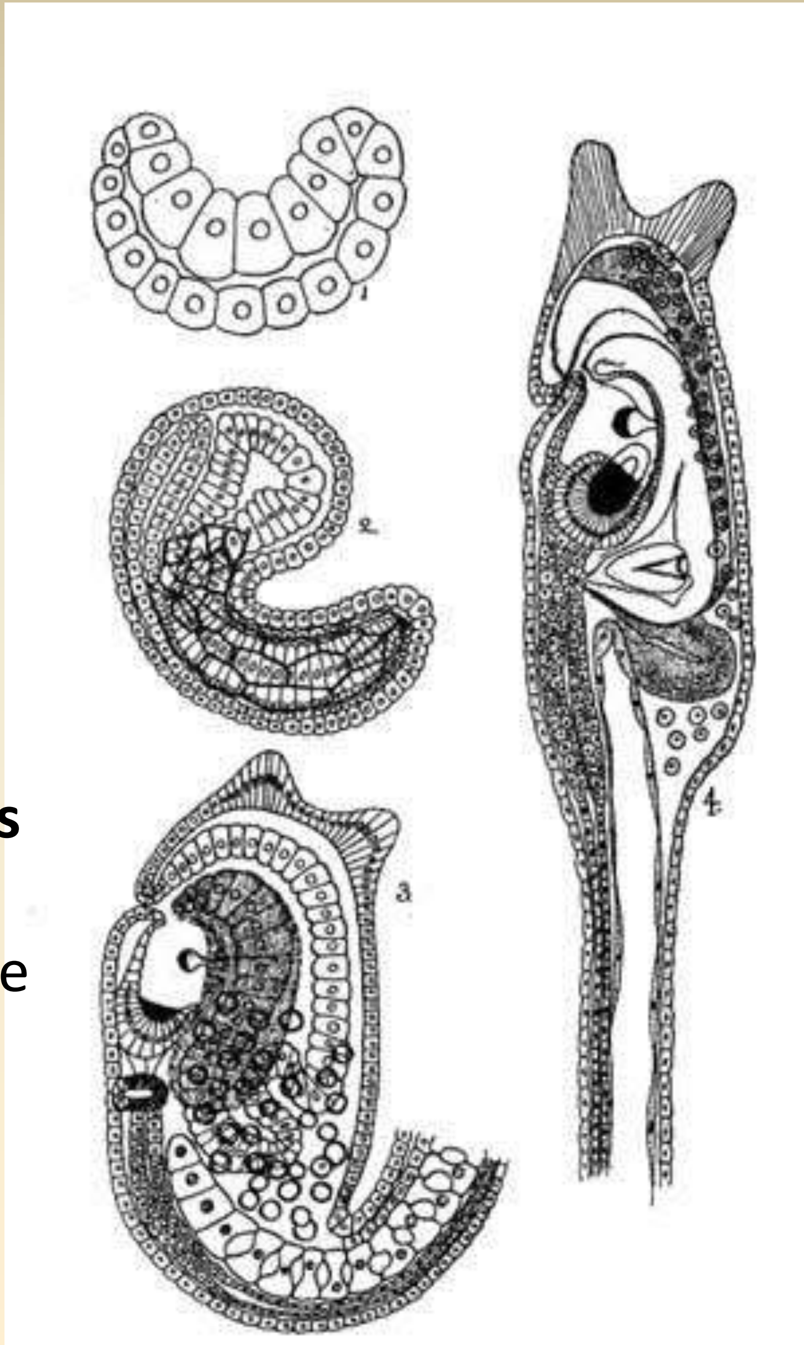


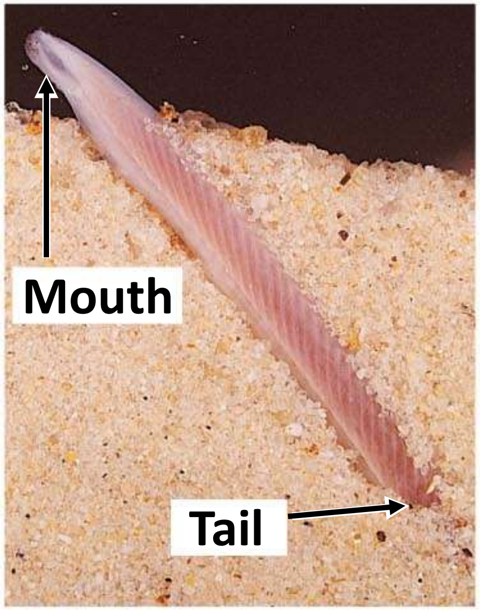
Alexander Kowalevsky

(1840-1901)

A Darwinian whose careful studies of invertebrate development and **efforts to find the nearest relatives of the vertebrates** (such as *Amphioxus)* were crucial to late 19th century phylogenetic debates.

Kowalevsky first noted that young sea squirts come complete with a head, tail and a proto-spine in 1866.





Lancelet

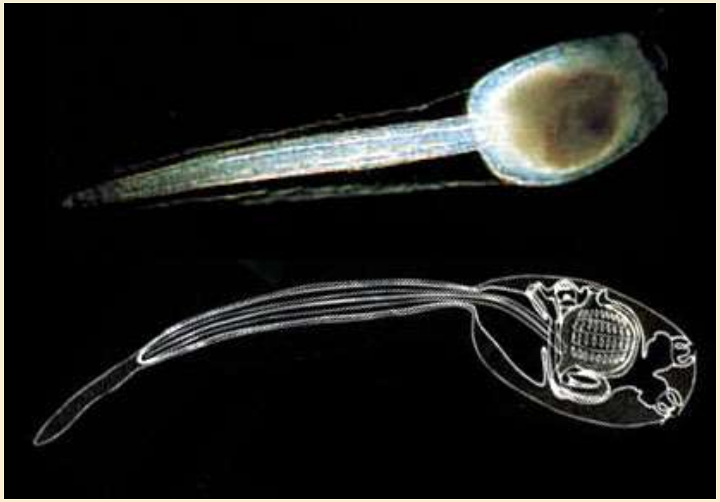
Tunicates

Figure 17.28

Development:

Similarities in developmental patterns may reveal evolutionary relationships.

The larvae of sea squirts has a notochord, which is also present in all vertebrates.

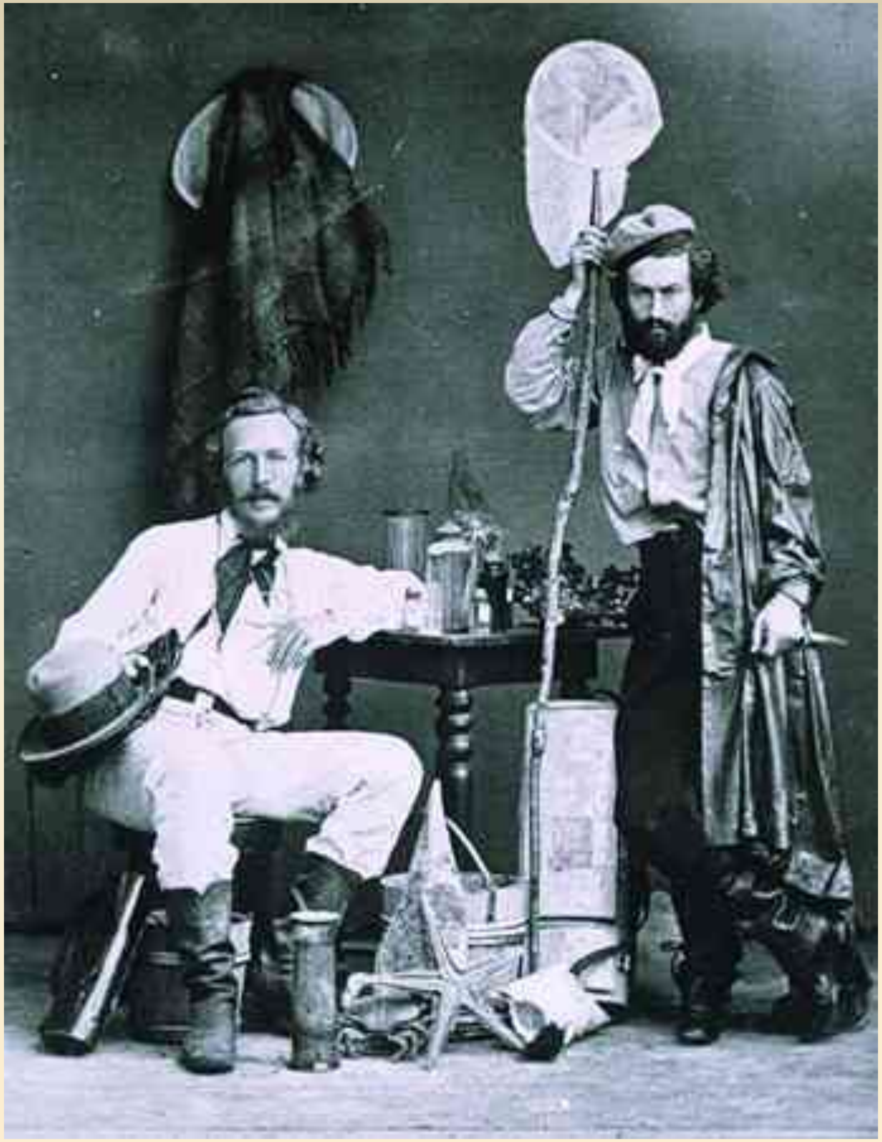


Larvae

Adult

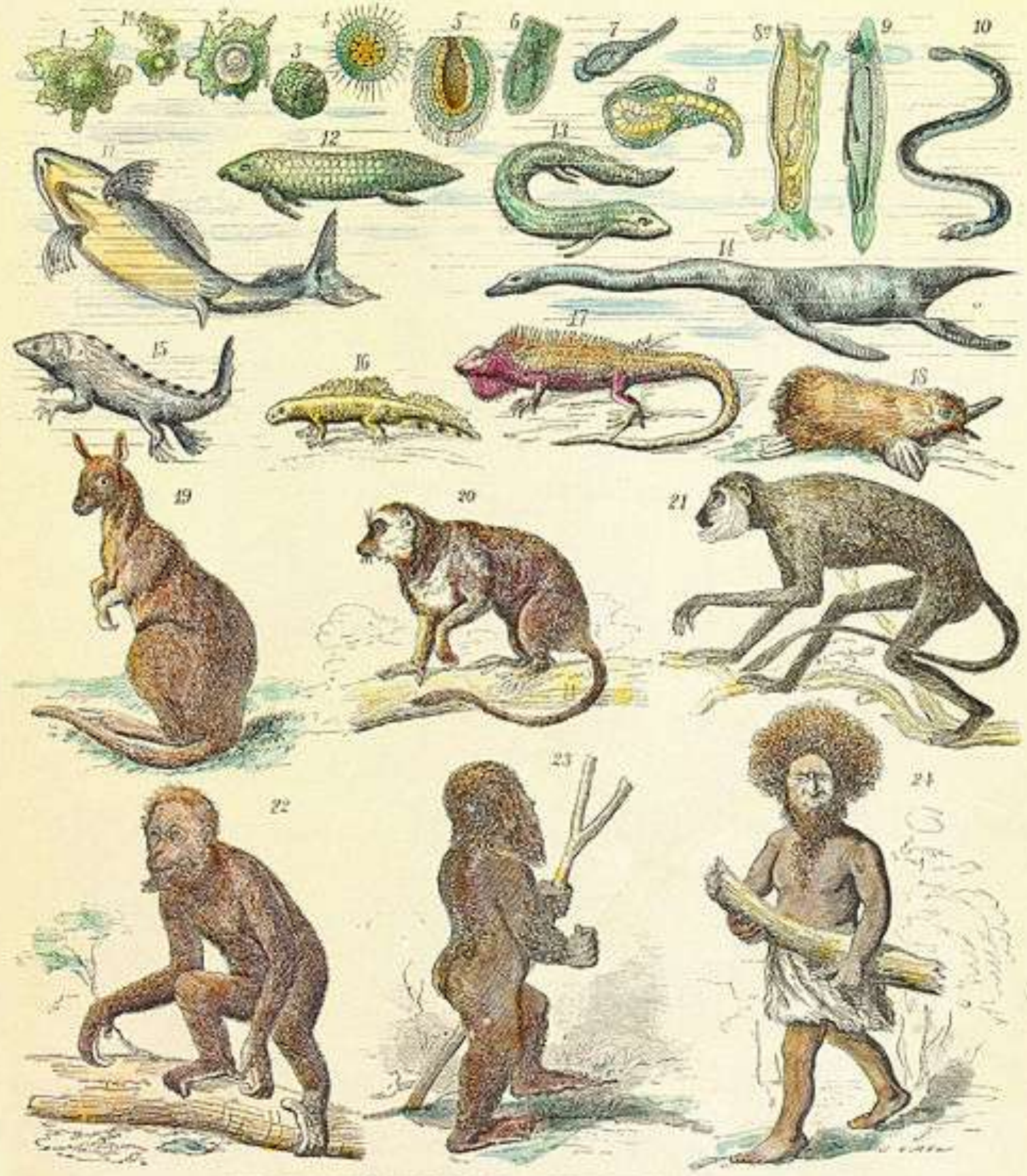
Ernst Haeckel - 1860s

Proposed Biogenetic Law - “ontogeny recapitulates phylogeny”



Ernst Haeckel - 1860s

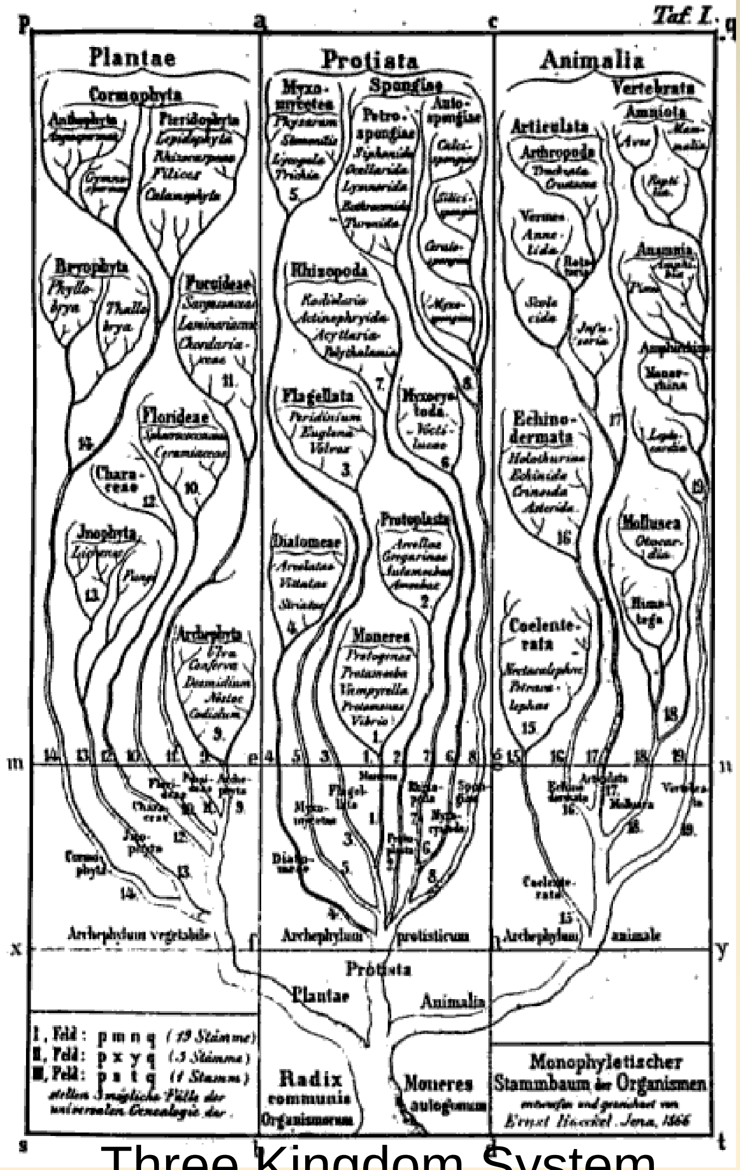
Biogenetic Law - ontogeny recapitulates
  phylogeny
(not really)



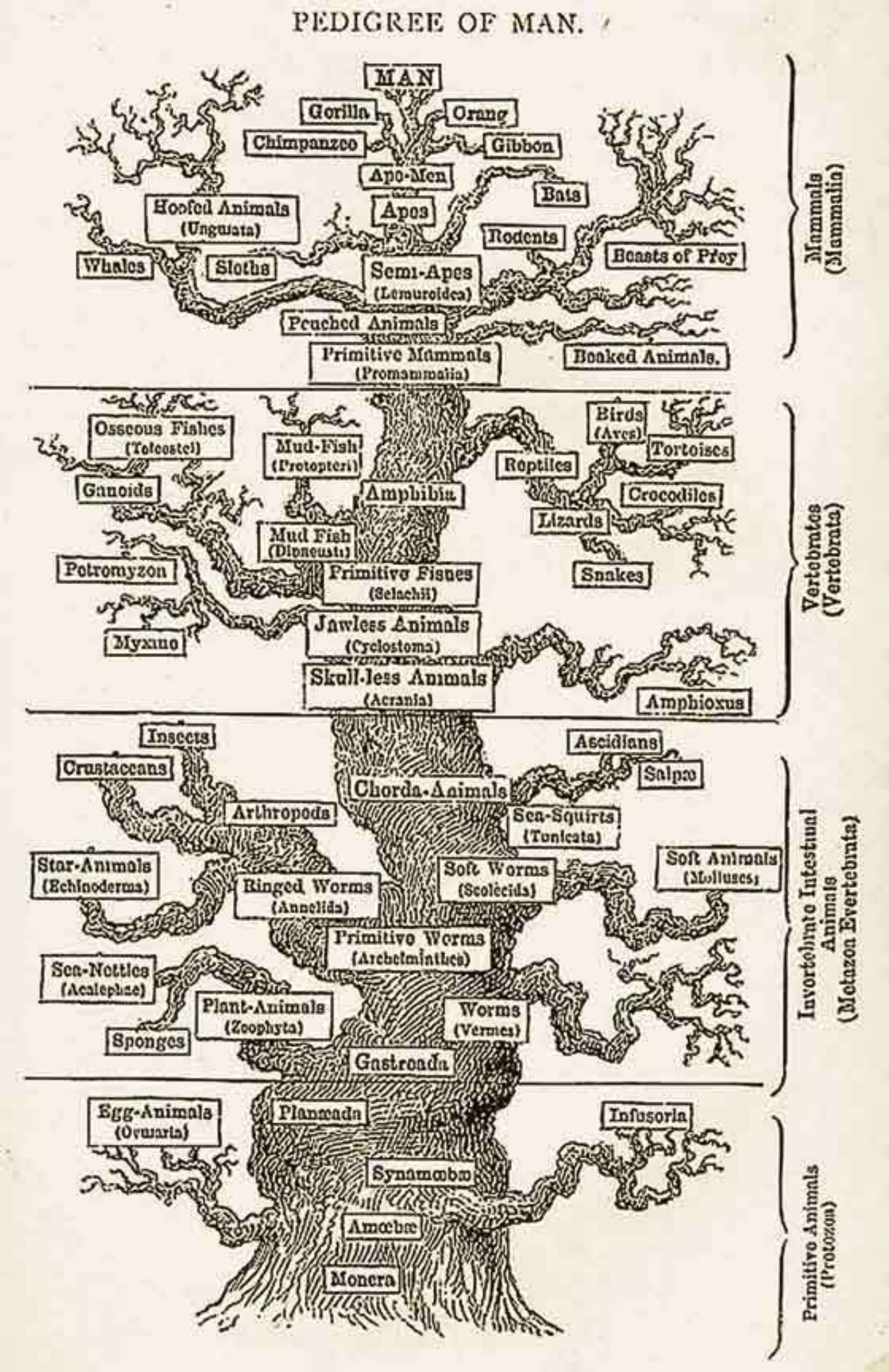
THE MODERN THEORY OF THE DESCENT OF MAN.

Ernst Haeckel Trees 1860s

Drew complete Tree of Life



Three Kingdom System



Neo-Darwinists - 1920s

Ronald Fisher, J.B.S. Haldane, Sewall Wright

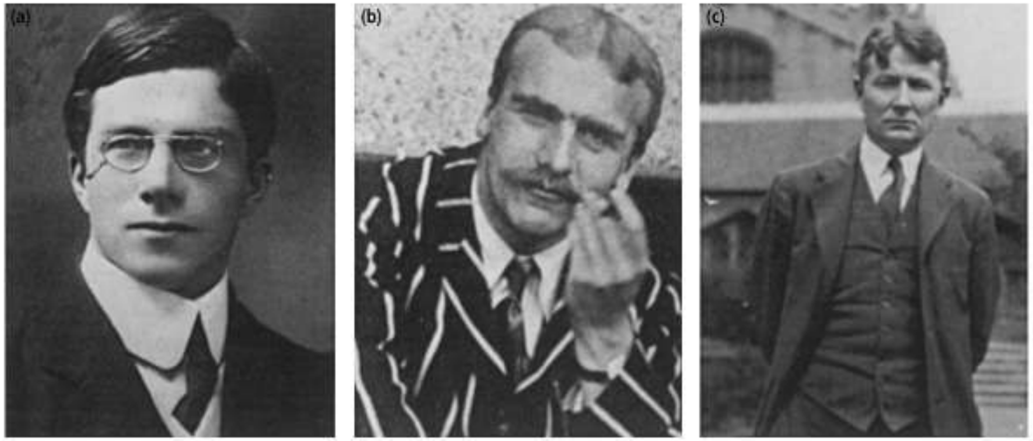
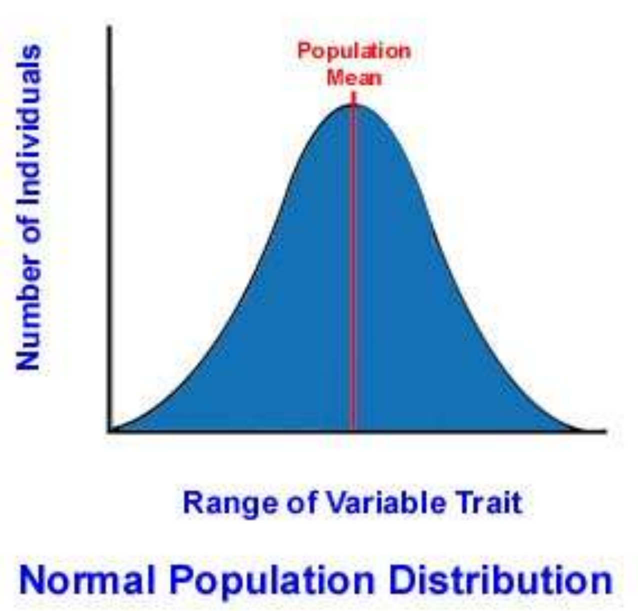


Figure 1.8
(a) Ronald Aylmer Fisher (1890–1962) in 1912, as a Steward at the First International Eugenics Conference.
(b) J.B.S. Haldane (1892–1964) in Oxford, UK in 1914.
(c) Sewall Wright (1889–1988) in 1928 at the University of Chicago.

Shift in emphasis from individuals to populations

Worked out the statistical foundation of population genetics



The morphologists’ complaint

- The modern synthesis, which has dominated much evolutionary thinking since the mid-20th Century, is a synthesis of Darwinian verbal argument and mathematic population genetics – it seeks to explain evolutionary change ultimately in terms of forces acting to change allele and genotype frequencies in populations
- Population genetics thinking does not, and cannot, explain much of what is interesting about evolution – particularly the evolution of morphology of multicellular animals

Morphology is *epigenetic*

- Morphology results from *interaction* between many gene products and between gene products and the environment and is expressed only through development (= ontogeny)
- We can’t understand the evolution of morphology simply by reference to forces that change allele and genotype frequencies in populations, or simply by understanding how a sequence of DNA nucleotides specifies a sequence of amino acids

“Evo-Devo”

- Animal body plans
- Formation of limbs in vertebrates and arthropods
- Evolution of the flower

Heterochrony

Heterochrony

Heterochrony is a **change in the timing of developmental events**. For example, a change in timing might slow down the development of the body, but not alter the maturation of the reproductive system. This change yields an adult organism with a form similar to the ancestral juvenile form.

© Greg Sievert

Salamanders go through a larval stage in which they have feathery, external gills (left). Most salamanders lose these gills when they metamorphose into adults (center). Because of heterochrony, axolotls now retain the juvenile external gills as fully reproductive adults (right).

Isometric Growth

Allometric Growth

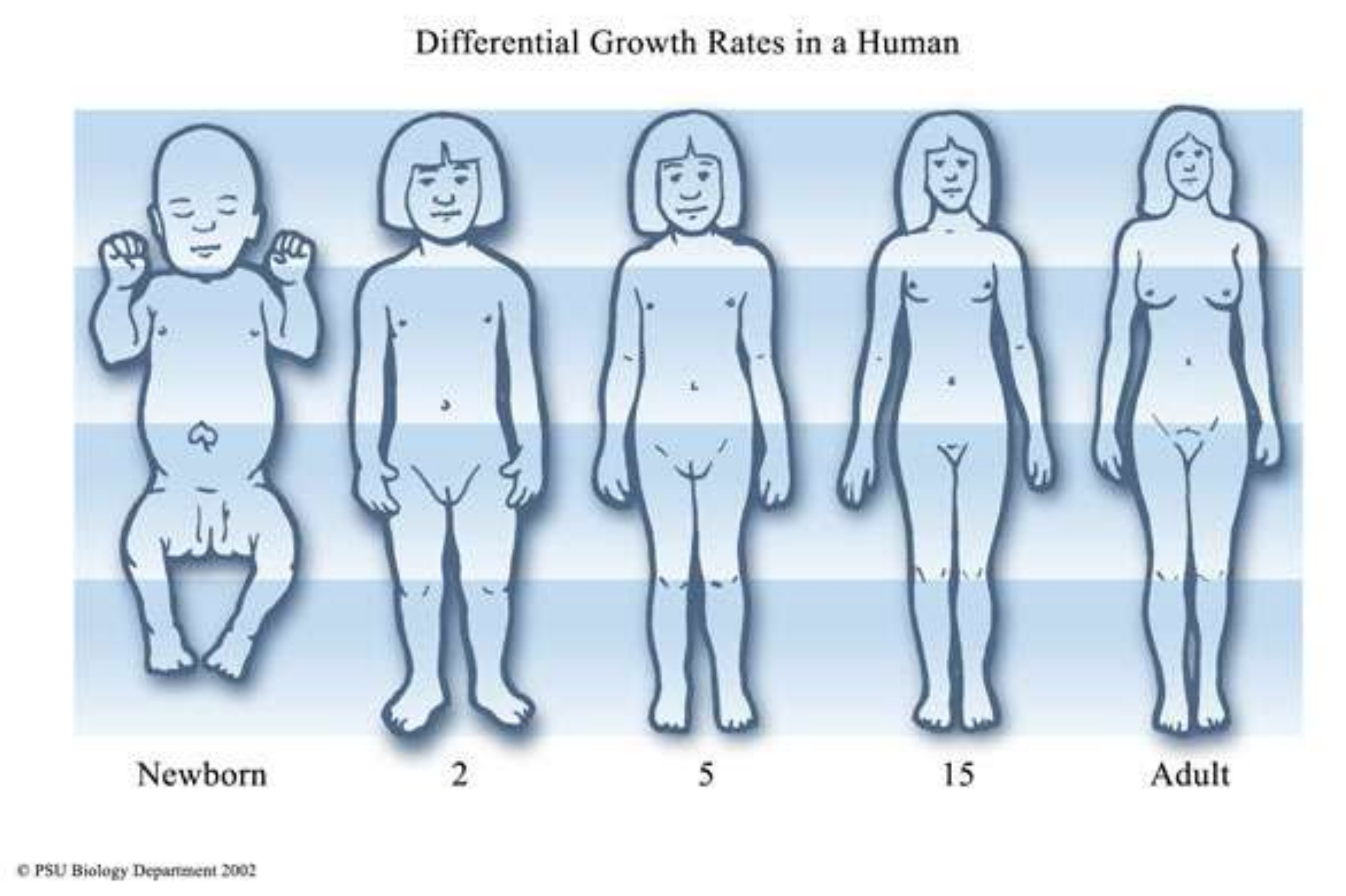
Allometric growth is a change in the rate of growth of a dimension or feature relative to other features.

Bat wings are basically paws with really long fingers and skin stretched between them.

In order for these wings to evolve, the rate of growth of finger bones must have increased relative to the growth of the rest of the bat's body.

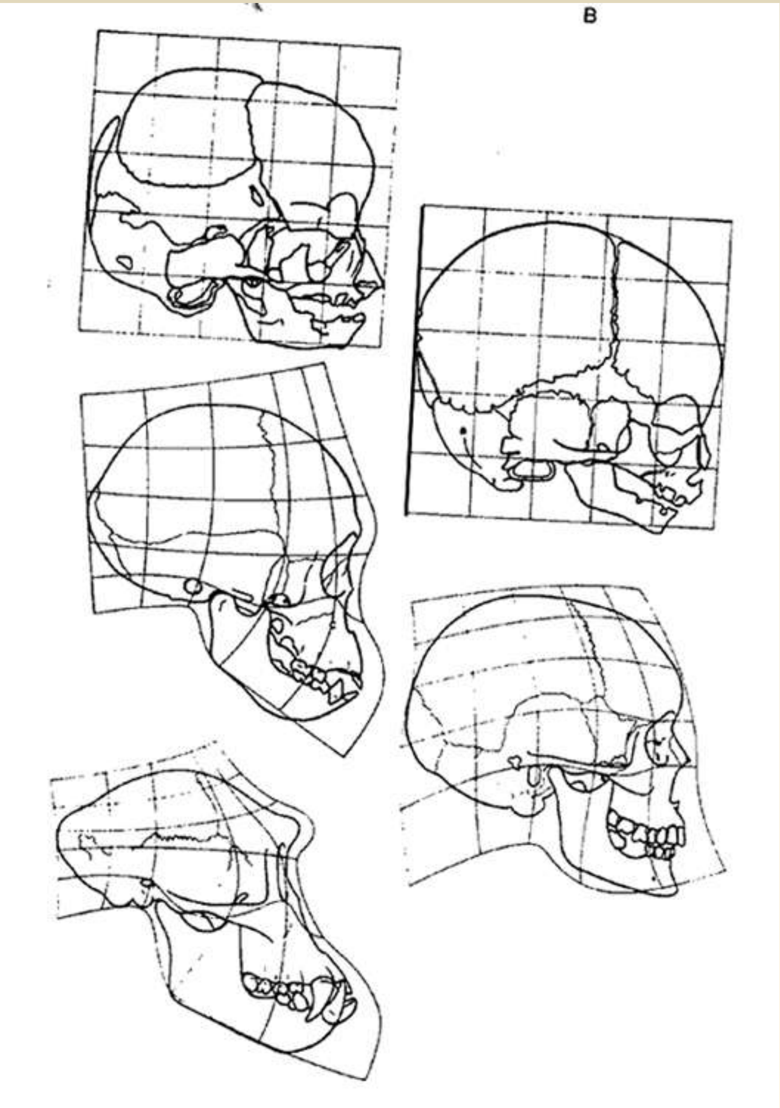
Or perhaps the rate of growth of the rest of the body decreased relative to the fingers. Either way, it is allometry

Allometric Growth



At birth the head is about 25% of the body's length, but at maturity it is about 12% (or less) of its length. Also, note that extremities grow disproportionately.

Homo sapiens, whose prolonged brain development period and relatively flat face reflect a prolonged juvenile period, relative to that of our closest relatives, the chimpanzees (*Pan paniscus* and *P. troglodytes*)



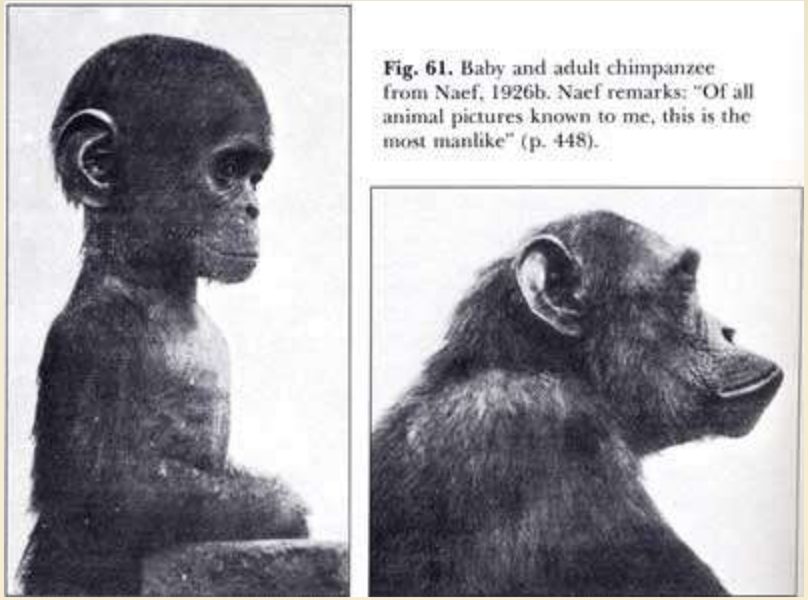


Fig. 61. Baby and adult chimpanzee from Naef, 1926b. Naef remarks: "Of all animal pictures known to me, this is the most manlike" (p. 448).

Paedomorphy

The mudpuppy is paedomorphic with respect to other salamander species: It retains its external gills as a reproductive adult.

Paedomorphy

Many domestic dog breeds (*Canis lupus familiaris*), derived from wolves (*Canis lupus*), exhibit paedomorphy with respect to adult wolves.

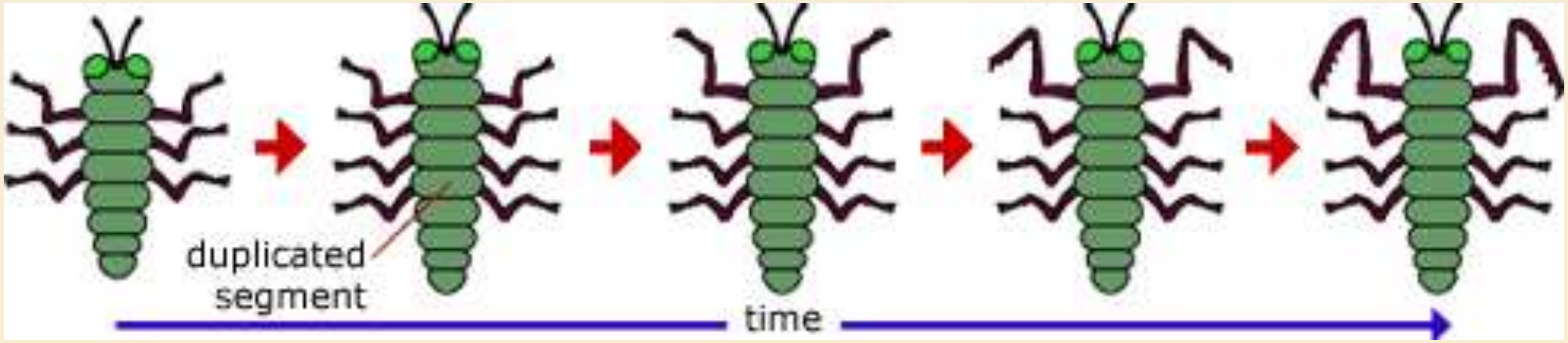
Developmental Constraints

Horses, sloths, and salamanders all develop through an embryonic stage with five-digit limbs — even though, the digits of the adult forms look quite different

Module duplication and adaptation

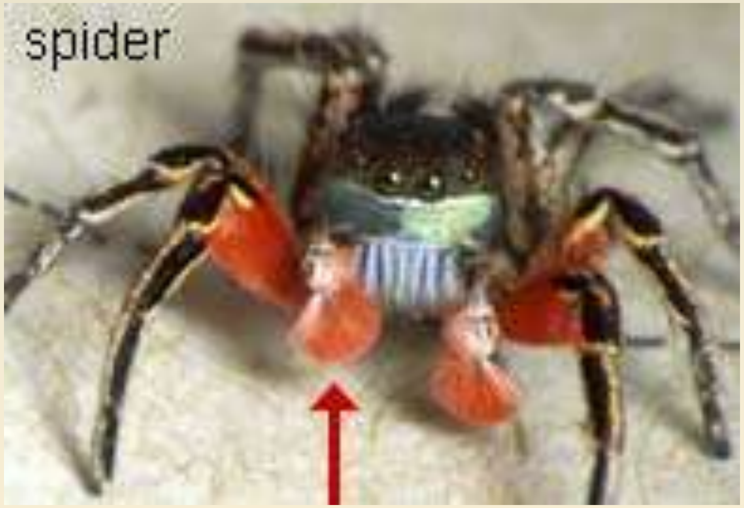
A module refers to a unit that can be duplicated and further adapted. For example, arthropods have various numbers of body segments.

Segment duplication and loss is a developmental change that probably occurred many times in the evolution of this clade.



Individualization

This is the modification of a particular module, usually when there is selection for a specialized function



One set of scorpions' appendages has evolved into pincers whereas the same appendage in many spiders has evolved into colorful pompoms used in mating rituals.

Hox Genes

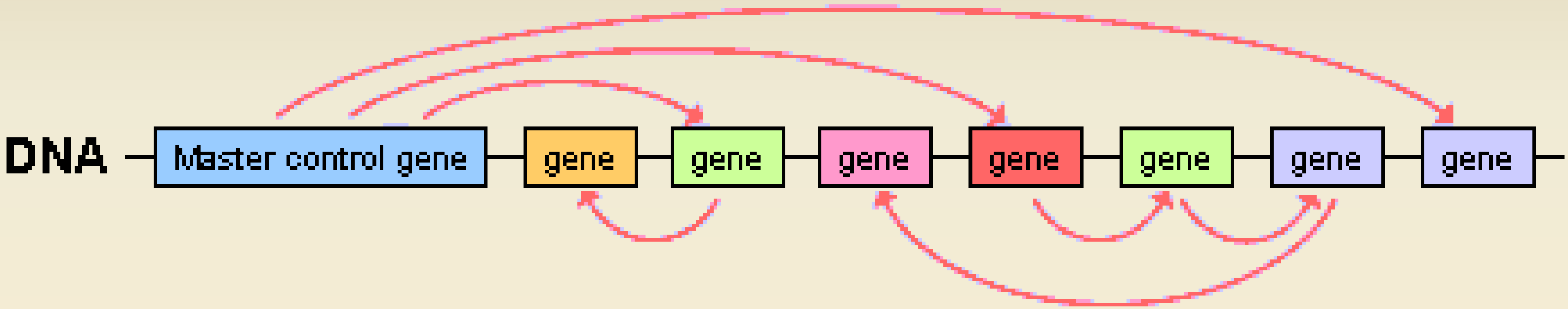
Homeotic genes and pattern formation

- Homeotic loci are genes that are responsible for telling cells where they are spatially in a developing 4 -dimensional embryo, for telling cells where they are in a developmental sequence, and for determining the fates of cells
- In animals, the key homeotic loci are called *Hox* (for "homeobox") or *HOM* genes – they are a gene family created by **gene duplication** events
- In plants, the key homeotic genes are the *MADS*-box genes
- Although there are *Hox* homologues in plants and *MADS*-box homologues in animals, *Hox* loci and *MADS*-box loci are not homologous to each other

Hox genes in animals

- Found in all major animal phyla
- Occur in groups (gene duplication events) – the number of genes in each group and the total number of groups varies among phyla
- Perfect correlation between the 3’ – 5’ order of genes along the chromosome and the anterior to posterior location of gene products in the embryo. Genes at the 3’ end are also expressed earlier in development and in higher quantity than genes at the 5’ end – *spatial, temporal, and quantitative colinearity*
- Each locus within the complex contains a highly conserved 180 bp sequence, the **homeobox**, that codes for a DNA binding motif – *Hox* gene products are regulatory proteins that bind to DNA and control the transcription of other genes

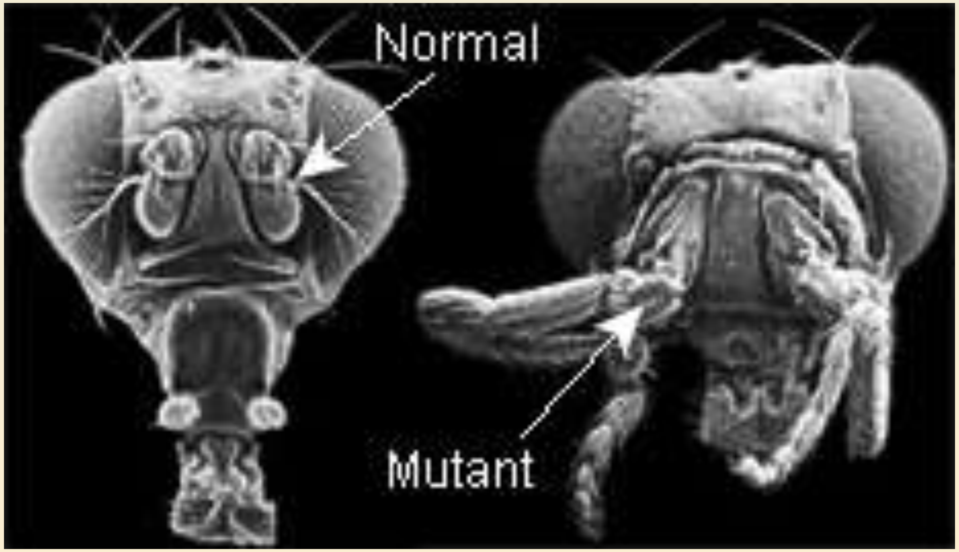
Master control genes regulate other genes, which in turn, regulate other genes



Homeotic Gene Mutation

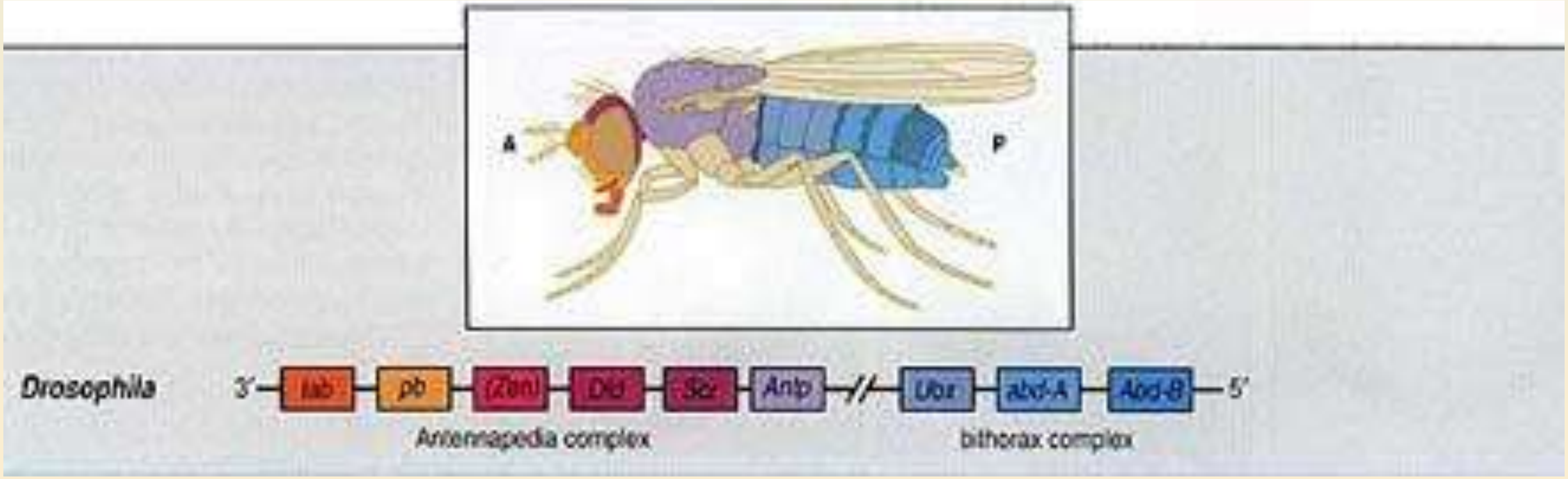
Mutations to *Hox* genes can produce 4-winged fly or put an entire leg where an antenna should sprout out, and produce other equally grotesque transformations.

Small changes in such powerful regulatory genes, or changes in the genes turned on by them, could represent a major source of evolutionary change



Hox genes in *Drosophila*

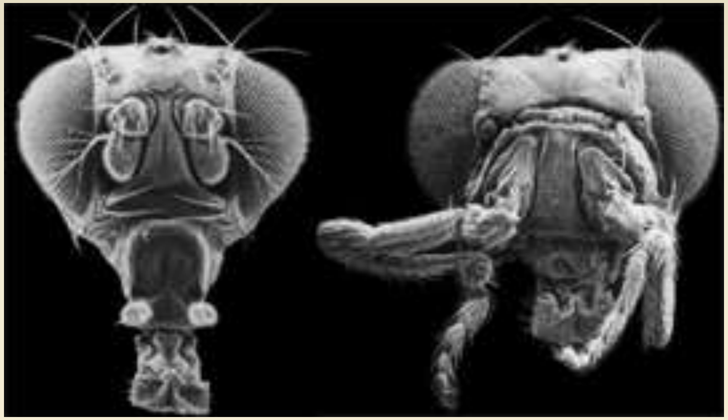
In the diagram below, you can see an array of 9 genes in the fly, from the orange *labial* (*lab*) gene on the left, or 3′ end of the DNA, to the blue *Abdominal-B* (*Abd-B*) gene on the right, or 5′ end. What’s really cool about this array is that it also corresponds to the spatial pattern of expression in the fly—the orange gene is turned on at the very front end of the fly, and the blue gene is turned on in the most posterior part.



Hox genes in *Drosophila*

- Two clusters – Antennapedia and bithorax
- Mutations in the Antennapedia genes affect the anterior of the developing embryo, mutations in bithorax genes affect the posterior
- Flies missing one or more *Hox* gene products produce segment-specific appendages such as legs or antennae in the wrong place
- Gene products from *Hox* loci demarcate relative positions in the embryo, rather than coding for specific structures – for example, they specify “this is thoracic segment 2” rather than “make wing”

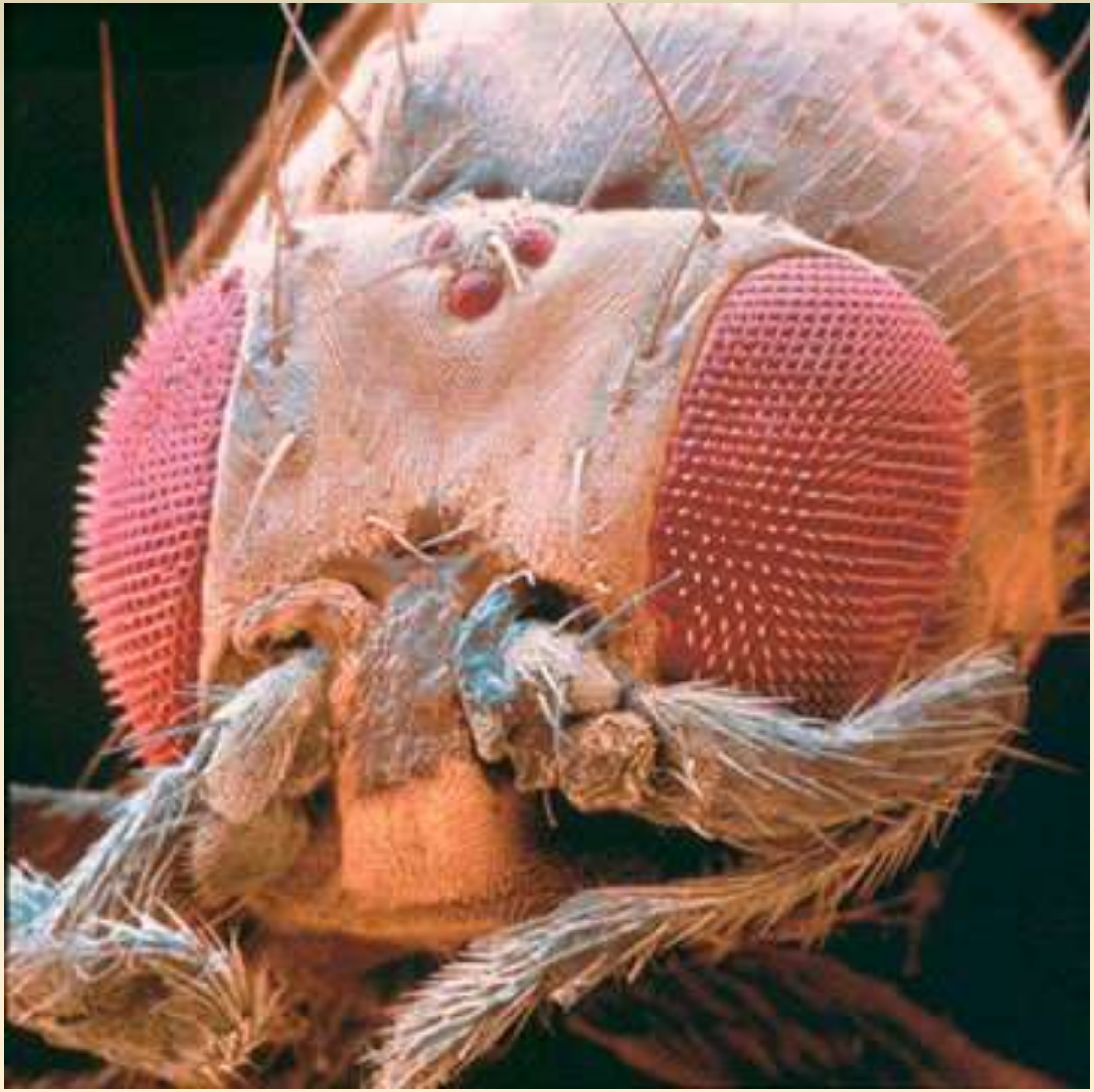
Hox gene mutant phenotypes



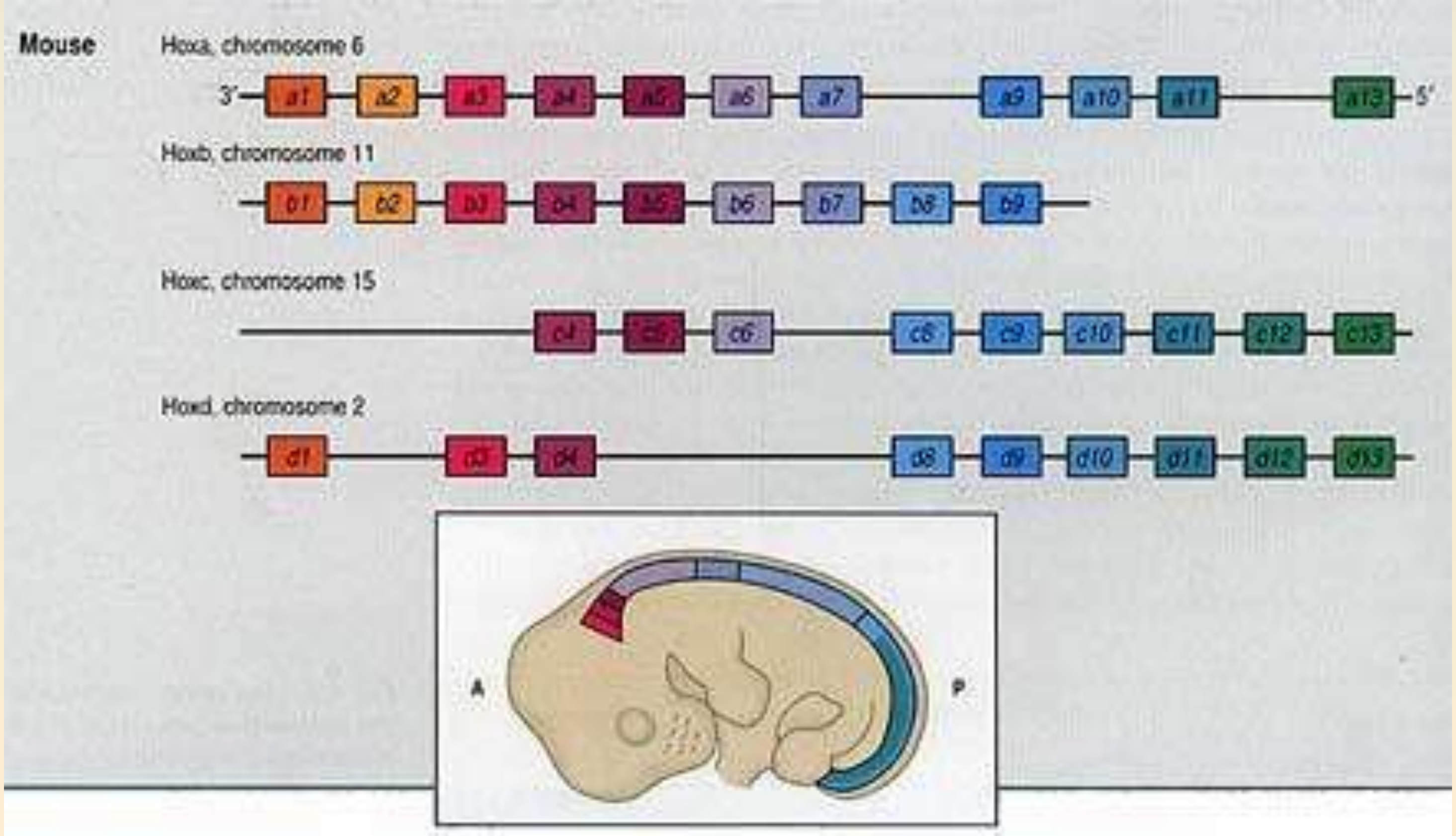
- Top: normal fly on left; antennapedia mutant phenotype on right

- Bottom: bithorax mutant phenotype

Colored electron micrograph of a fruit fly with legs instead of antennae



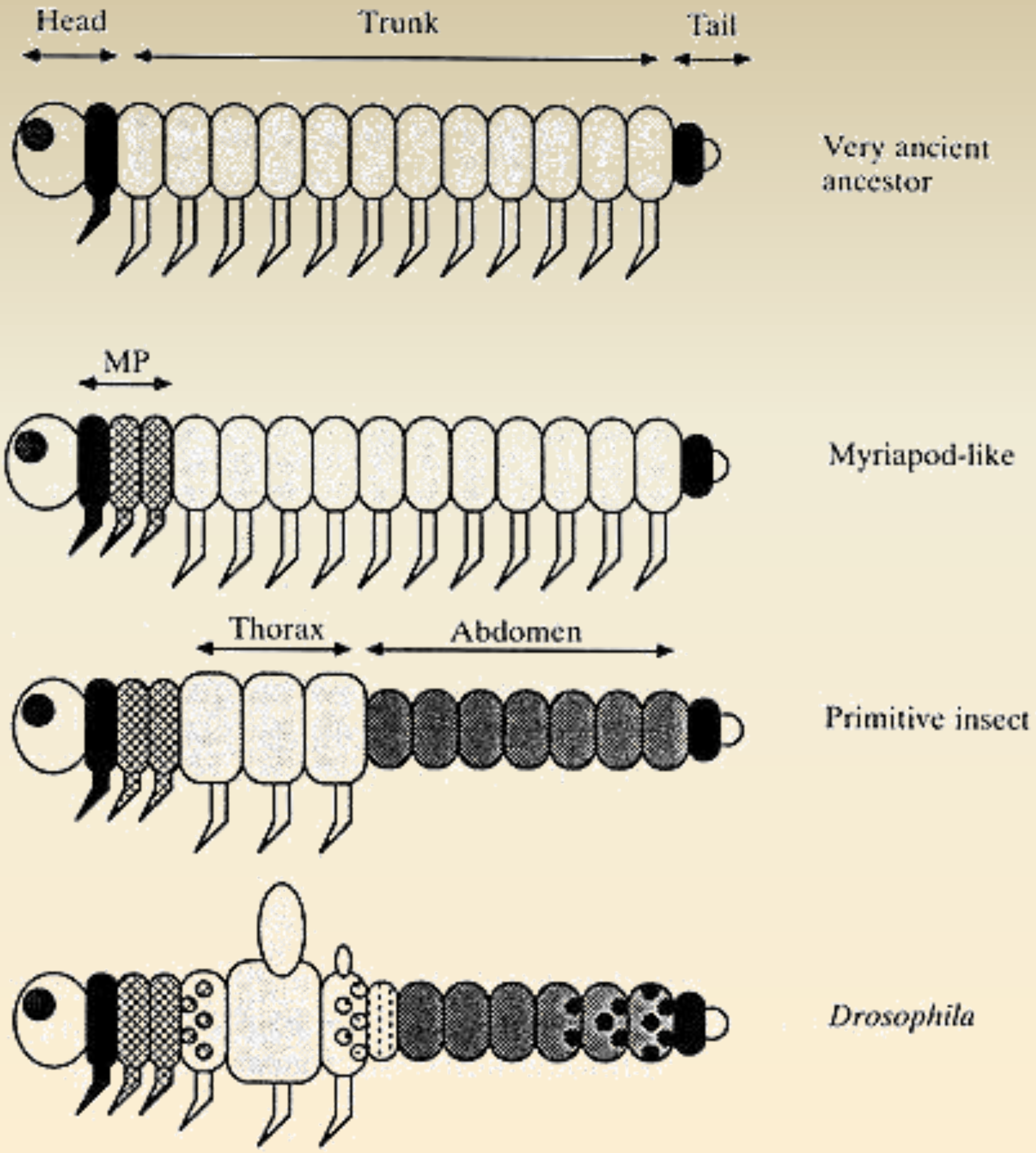
We vertebrates also have Hox genes, and they have the same properties: each gene contains a homeobox, and they are organized on the chromosome in the order of their expression from front to back. Here is a color-coded version of the homologous Hox genes in the mouse.

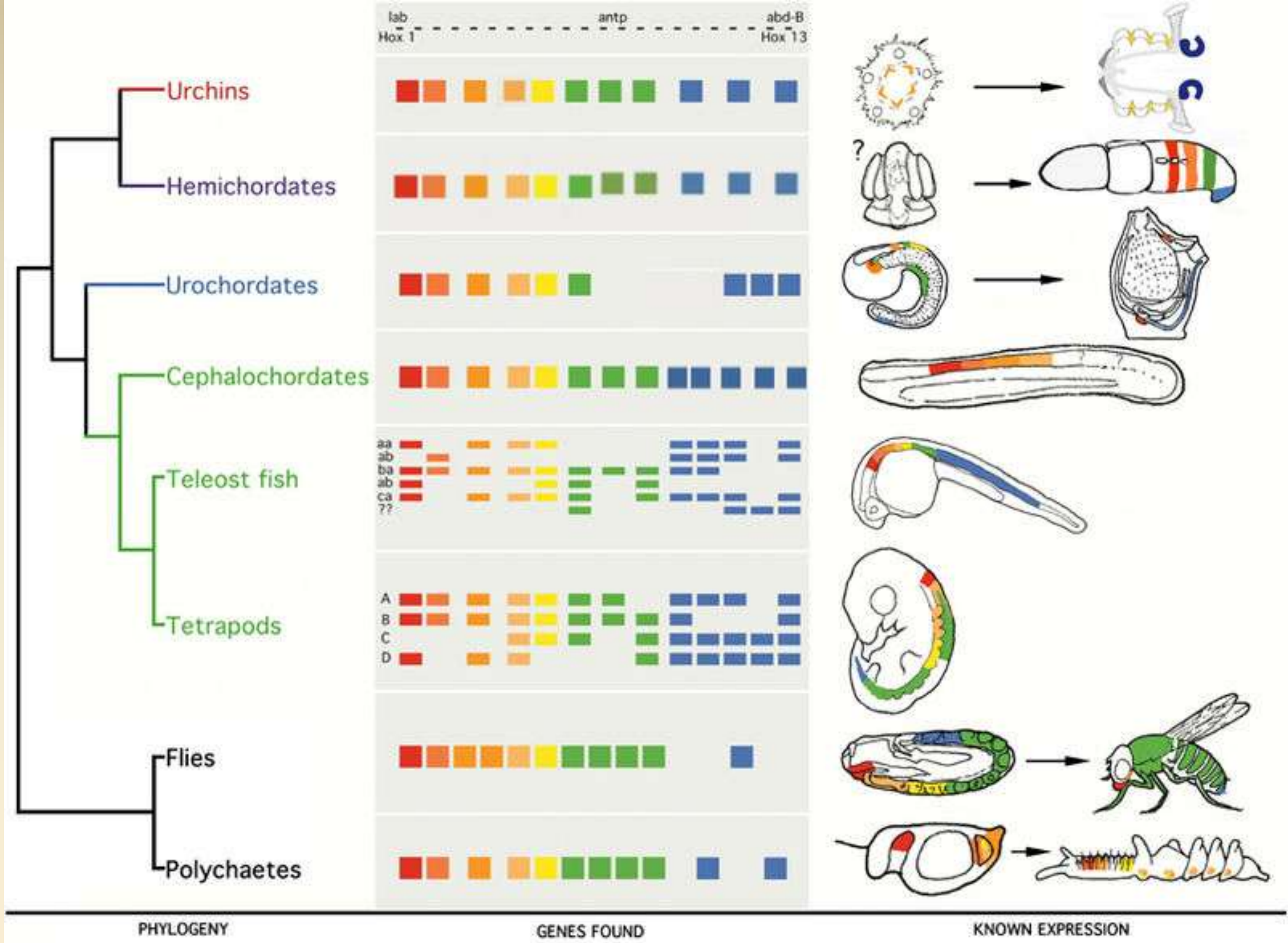


Duplication of *hox* genes can lead to differential regulation in different segments, and different phenotypes in different segments.

Each gene produces a DNA binding protein that turns on a set of genes...

Different hox genes produce different binding proteins, that stimulate different sets of genes



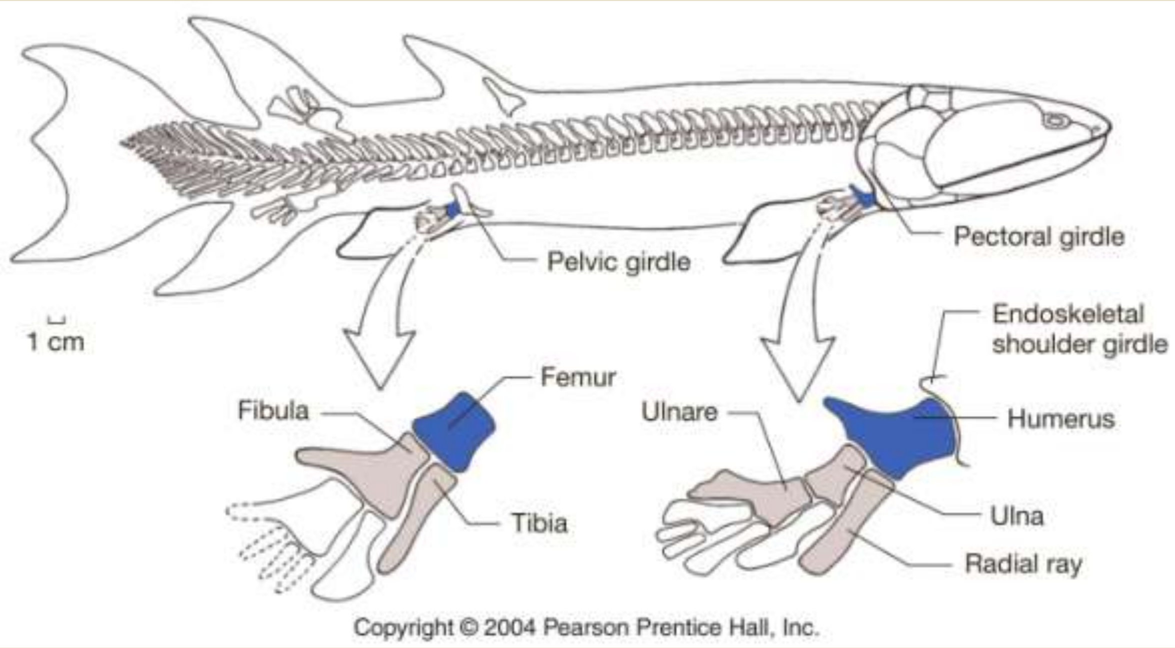


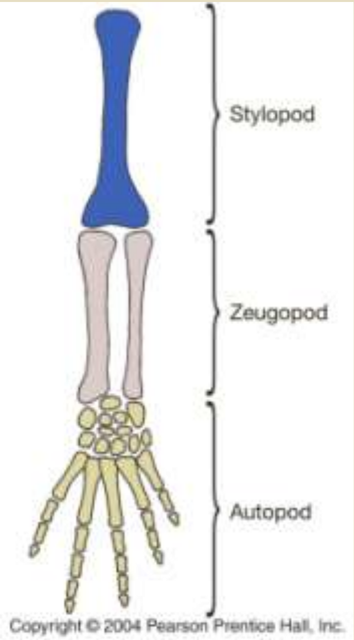
Hox gene clusters in several phyla. Each Hox gene is a colored box, and each organism has about 8 to over 40 Hox genes. The ancestral complement of Hox genes is likely similar to that in flies, polychaetes, and basal chordates, i.e. a single cluster consisting of 8-11 genes. The multiple copies of Hox genes in more derived vertebrates is due to the fact that this **single cluster was duplicated as a result of successive rounds of whole genome duplication** in the vertebrate lineage, with subsequent loss of some copies in various lineages

The origin of the tetrapod limb

- Phylogenetic and morphological analyses support the hypothesis that the tetrapod limb is derived from the fins of lobe-finned fish
- The first tetrapods (amphibians) appear in the late Devonian, about 365 mya
- Evolution of limb morphology in tetrapods may result from changes in the timing or level of expression of the pattern forming genes

Lobe-finned fish and the tetrapod limb





- *Eusthenopteron,* a lobe-finned fish from the Devonian (409-354 mya)

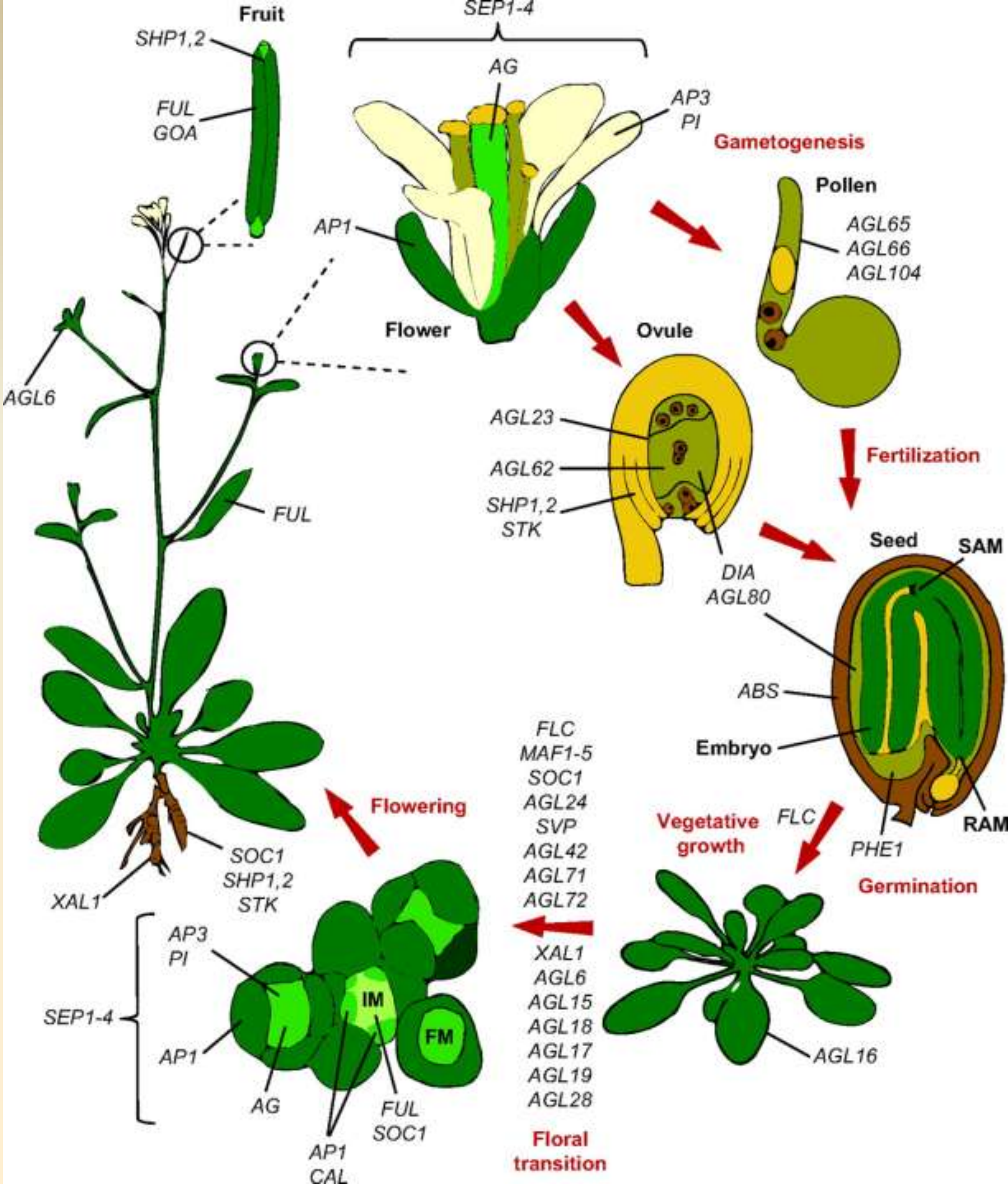
What about Flowering Plants?

MADS-box genes encode a family of **transcription factors** which control diverse developmental processes in flowering plants ranging from root development to flower and fruit development.

The MADS-box gene family got its name as an acronym referring to the four founding members.

- **M**CM1 from the budding yeast, *Saccharomyces cerevisiae*,
- **A**GAMOUS from the thale cress *Arabidopsis thaliana*,
- **D**EFICIENS from the snapdragon *Antirrhinum majus*,
- **S**RF from the human *Homo sapiens*.

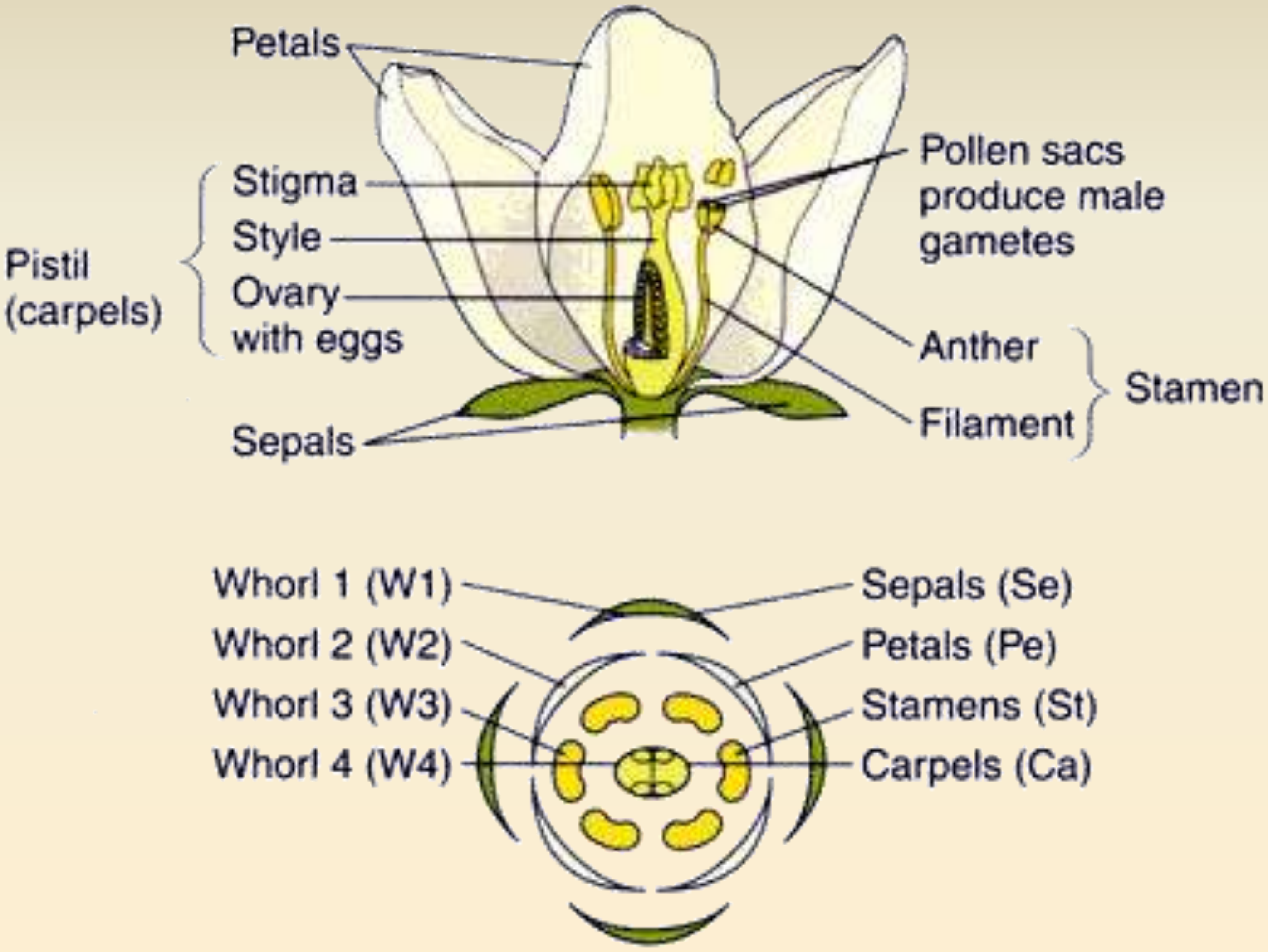
Functions of MADS-box genes throughout the life cycle of *Arabidopsis thaliana*.



MADS-box homeotic genes and development of flowers

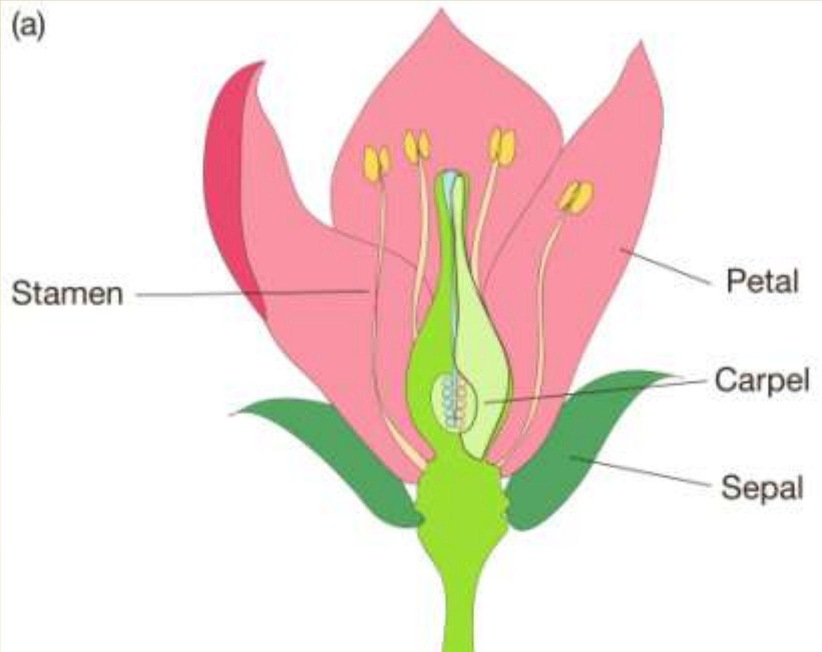
- Specify which floral organs appear where.
- Each locus encodes a DNA binding protein domain (*MADS* box) that is analogous to the DNA binding domain encoded by *Hox* genes.
- Mutations in specific *MADS*-box genes are associated with abnormal floral morphology.

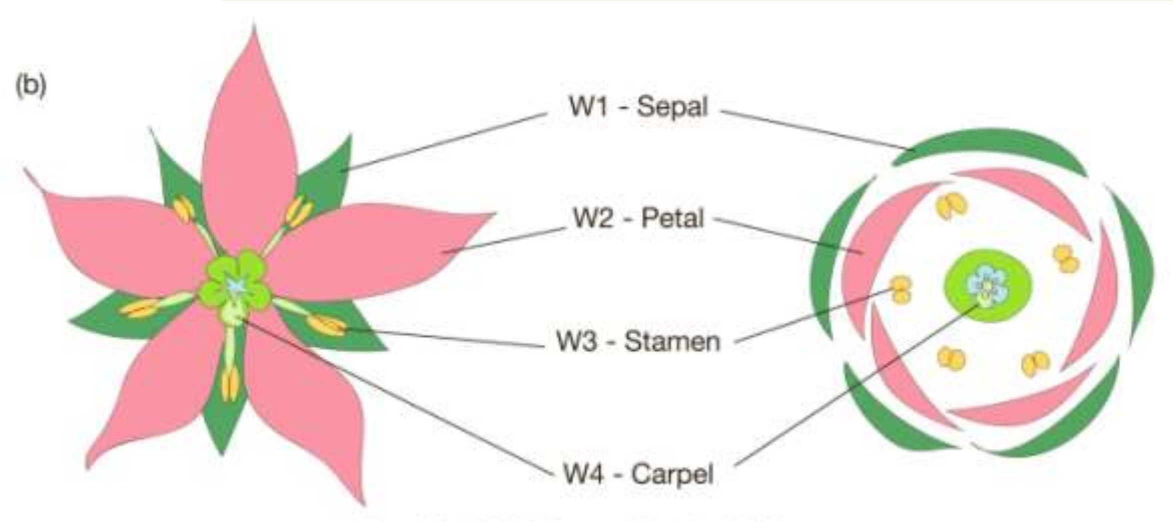
MADS-box Genes Control Parts of a flower



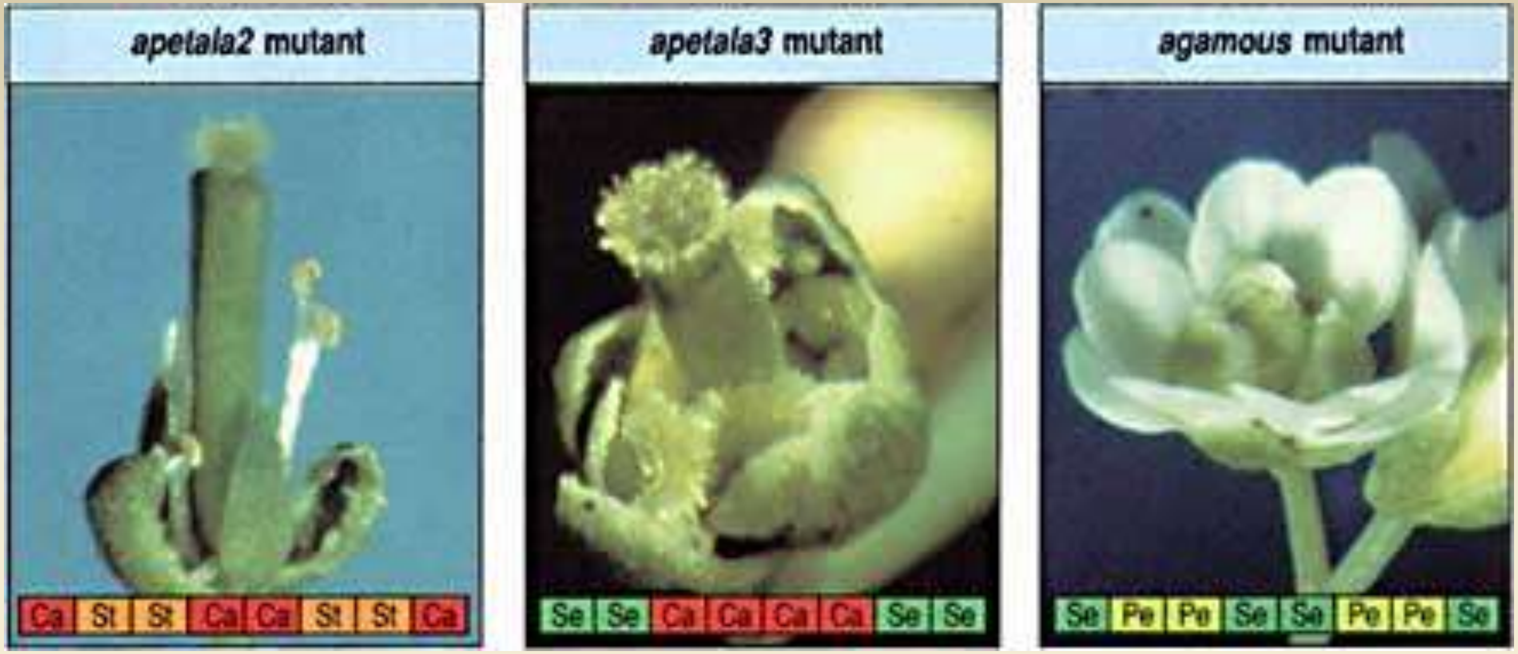
MADS-box Genes

Parts of a flower





Arabidopsis Flower Mutants

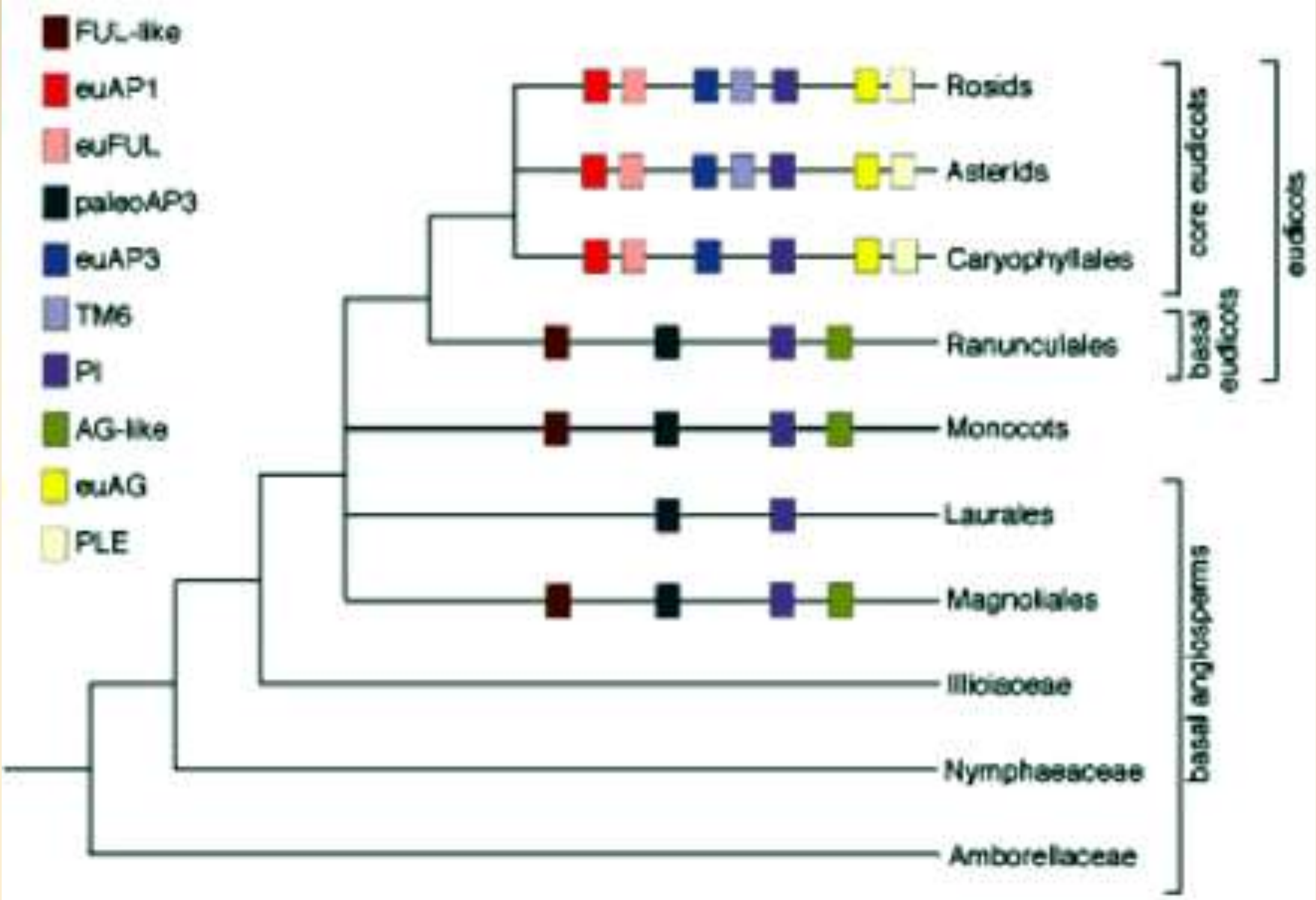


The *apetala2* mutant fails to make either sepals or petals—they are all transformed into stamens and carpels. That plant on the left has an excess of sex organs, and they are all hanging out there naked and unadorned.

The middle plant, the *apetala3* mutant, also lacks petals, and it also has no stamens, only sepals and carpels.

And on the right is the *agamous* mutant, a vegetable eunuch with no sex organs at all, only sepals and petals.

The homologies of specific MADS box genes can be used to map out a pattern of gene duplications during evolution



MADS box gene duplications. Genes corresponding to the different MADS box gene lineages are indicated in the clades where they have been identified.

Genes and development – summary

- The evo-devo research program of the last 20 years has done much to answer the criticisms of the modern synthesis that were made by developmental biologists and morphologists in the early 1980's
- We are now beginning to understand the genes and gene interactions that are responsible for the development and evolution of complex body plans and morphology in animals, and floral structures in plants.
- Macroevolutionary change in morphology can be understood in terms of changes in a set of genes common to all animals (or plants) – *deep homology* – and that are affected by microevolutionary processes – selection, drift, mutation, gene duplication

End