CHAPTER 24
THE ORIGIN OF SPECIES

Section C: From Speciation To Macroevolution

1. **Most evolutionary novelties are modified versions of older structures**
2. **"Evo-devo": Genes that control development play a major role in evolution**
3. **An evolutionary trend does not mean that evolution is goal oriented**

Introduction

- Speciation is at the boundary between microevolution and macroevolution.
  - Microevolution is a change over the generations in a population's allele frequencies, mainly by genetic drift and natural selection.
  - Speciation occurs when a population's genetic divergence from its ancestral population results in reproductive isolation.
  - While the changes after any speciation event may be subtle, the cumulative change over millions of speciation episodes must account for macroevolution, the scale of changes seen in the fossil record.

1. Most evolutionary novelties are modified versions of older structures

- The Darwinian concept of "descent with modification" can account for the major morphological transformations of macroevolution.
  - It may be difficult to believe that a complex organ like the human eye could be the product of gradual evolution, rather than a finished design created specially for humans.
  - However, the key to remember is that that eyes do not need to as complicated as the human eye to be useful to an animal.

- The simplest eyes are just clusters of photoreceptors, pigmented cells sensitive to light.
- Flatworms (*Planaria*) have a slightly more sophisticated structure with the photoreceptors cells in a cup-shaped indentation.
  - This structure cannot allow flatworms to focus an image, but they enable flatworms to distinguish light from dark.
  - Flatworms move away from light, probably reducing their risk of predation.

- Complex eyes have evolved independently several times in the animal kingdom.
  - Examples of various levels of complexity, from clusters of photoreceptors to camera-like eyes, can be seen in mollusks.
  - The most complex types did not evolve in one quantum leap, but by incremental adaptation of organs that worked and benefited their owners at each stage in this macroevolution.

- The range of the eye complexity in mollusks includes (a) a simple patch of photoreceptors found in some limpets, (b) photoreceptors in an eye-cup, (c) a pinhole-camera-type eye in Nautilus, (d) an eye with a primitive lens in some marine snails, and (e) a complex camera-type eye in squid.

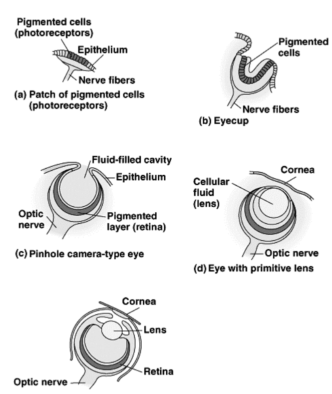


Fig. 24.18

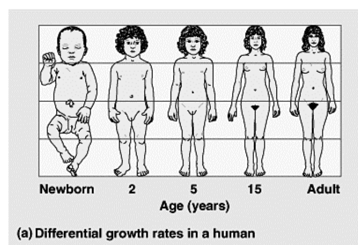
- Evolutionary novelties can also arise by gradual refinement of existing structures for new functions.
  - Structures that evolve in one context, but become co-opted for another function are **exaptations**.
- Natural selection can only improve a structure in the context of its current utility, not in anticipation of the future.

- An example of an exaptation is the changing function of lightweight, honey-combed bones of birds.
  - The fossil record indicates that light bones predated flight.
  - Therefore, they must have had some function on the ground, perhaps as a light frame for agile, bipedal dinosaurs.
  - Once flight became an advantage, natural selection would have remodeled the skeleton to better fit their additional function.

2. "Evo-devo": Genes that control development play a major role in evolution

- "Evo-devo" is a field of interdisciplinary research that examines how slight genetic divergences can become magnified into major morphological differences between species.
- A particular focus are genes that program development by controlling the rate, timing, and spatial pattern of changes in form as an organism develops from a zygote to an adult.

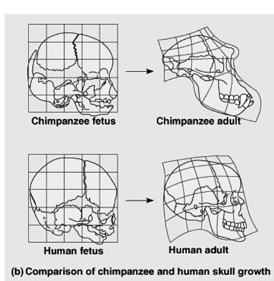
- **Allometric growth** tracks how proportions of structures change due to different growth rates during development.



(a) Differential growth rates in a human

Fig. 24.19a

- Change the relative rates of growth even slightly, and you can change the adult from substantially.
  - Different allometric patterns contribute to contrasting shapes of human and chimpanzee adult skulls from fairly similar fetal skulls.



(b) Comparison of chimpanzee and human skull growth

Fig. 24.19b

- Evolution of morphology by modification of allometric growth is an example of **heterochrony**, an evolutionary change in the rate or timing of developmental events.
- Heterochrony appears to be responsible for differences in the feet of tree-dwelling versus ground-dwelling salamanders.

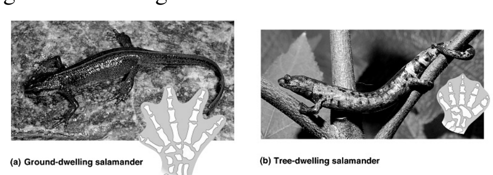


Fig. 24.20

- The feet of the tree-dwellers with shorter digits and more webbing may have evolved from a mutation in the alleles that control the timing of foot development.
  - These stunted feet may result if regulatory genes switched off foot growth early.
  - Thus, a relatively small genetic change can be amplified into substantial morphological change.

- Another form of heterochrony is concerned with the relative timing of reproductive development and somatic development.
- If the rate of reproductive development accelerates compared to somatic development, then a sexually mature stage can retain juvenile structures - a process called **paedomorphosis**.
- This axolotl salamander has the typical external gills and flattened tail of an aquatic juvenile but has functioning gonads.

Fig. 24.21

- Macroevolution can also result from changes in gene that control the placement and spatial organization of body parts.
  - Example: genes called **homeotic** genes determine such basic features as where a pair of wings and a pair of legs will develop on a bird or how a plant's flower parts are arranged.

- One class of homeotic genes, *Hox* genes, provide positional information in an animal embryo.
- Their information prompts cells to develop into structure appropriate for a particular location.

- One major transition in the evolution of vertebrates is the development of the walking legs of tetrapods from the fins of fishes.
  - The fish fin which lacks external skeletal support evolved into the tetrapod limb that extends skeletal supports (digits) to the tip of the limb.
  - This may be the result of changes in the positional information provided by *Hox* genes during limb development.

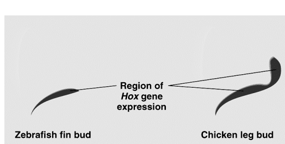


Fig. 24.22

- Key events in the origin of vertebrates from invertebrates are associated with changes in *Hox* genes.
  - While most invertebrates have a single *Hox* cluster, molecular evidence indicates that this cluster of duplicated about 520 million years ago in the lineage that produced vertebrates.
    - The duplicate genes could then take on entirely new roles, such as directing the development of a backbone.

- A second duplication of the two *Hox* clusters about 425 million years ago may have allowed for even more structural complexity.

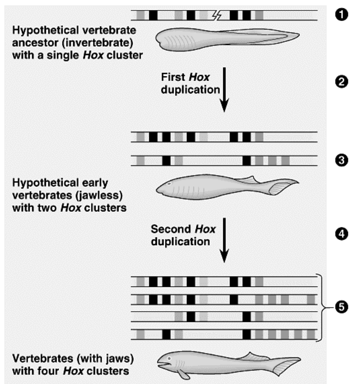


Fig. 24.23

3. An evolutionary trend does not mean that evolution is not goal oriented

- The fossil record seems to reveal trends in the evolution of many species and lineages.
- For example, the evolution of the modern horse can be interpreted to have been a steady series of changes from a small, browsing ancestor (*Hyracotherium*) with four toes to modern horses (*Equus*) with only one toe per foot and teeth modified teeth for grazing on grasses.
- It is possible to arrange a succession of animals intermediate between *Hyracotherium* and modern horses that shows trends toward increased size, reduced number of toes, and modifications of teeth for grazing.

- If we look at all fossil horses, the illusion of coherent, progressive evolution leading directly to modern horses vanishes.
  - *Equus* is the only surviving twig of an evolutionary bush which included several adaptive radiations among both grazers and browsers.

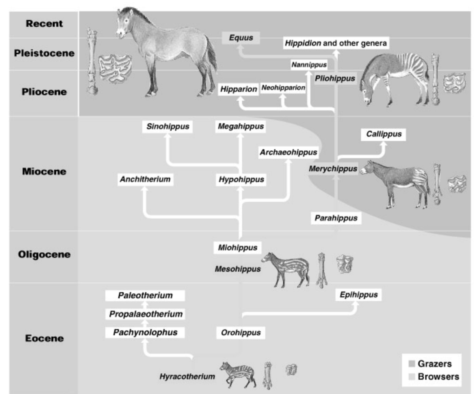


Fig. 24.24

- Differences among species in survival can also produce a macroevolutionary trend.
- In the **species selection** model, developed by Steven Stanley, species are analogous to individuals.
  - Speciation is their birth, extinction is their death, and new species are their offspring.
- The species that endure the longest and generate the greatest number of new species determine the direction of major evolutionary trends.

- To the extent that speciation rates and species longevity reflect success, the analogy to natural selection is even stronger.
  - However, qualities unrelated to the overall success of organisms in specific environments may be equally important in species selection.
  - As an example, the ability of a species to disperse to new locations may contribute to its giving rise to a large number of “daughter species.”

- The appearance of an evolutionary trend does not imply some intrinsic drive toward a preordained state of being.
  - Evolution is a response between organisms and their current environments, leading to changes in evolutionary trends as conditions change.