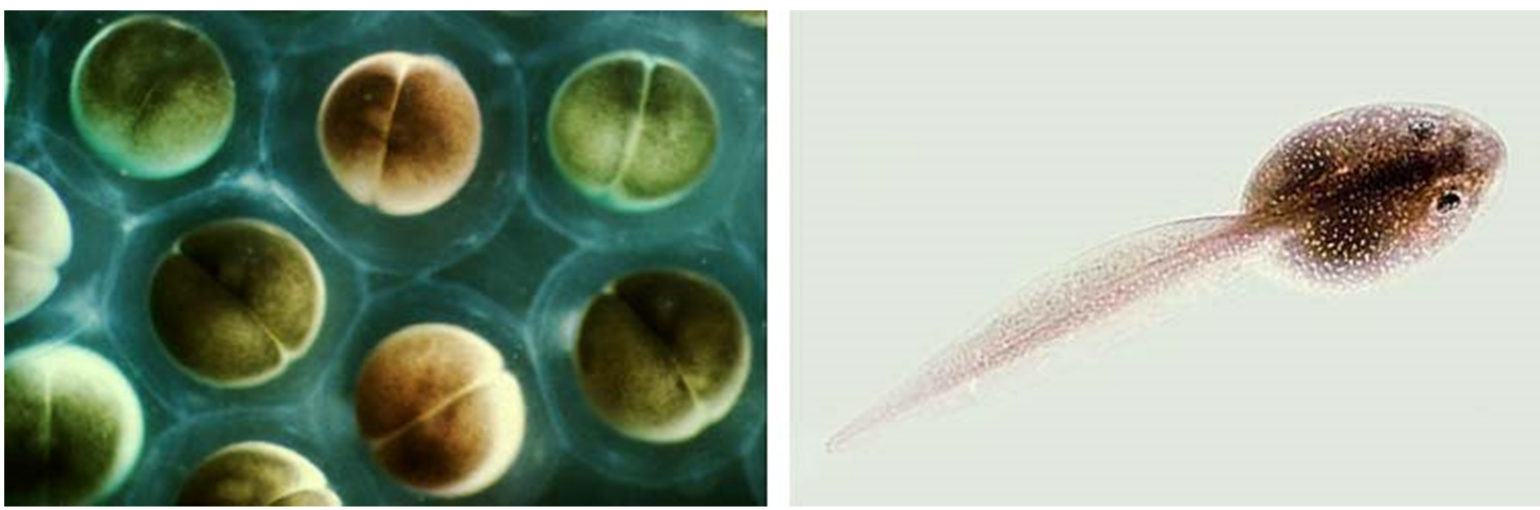
18.4 Embryonic development involves cell division, cell differentiation, and morphogenesis

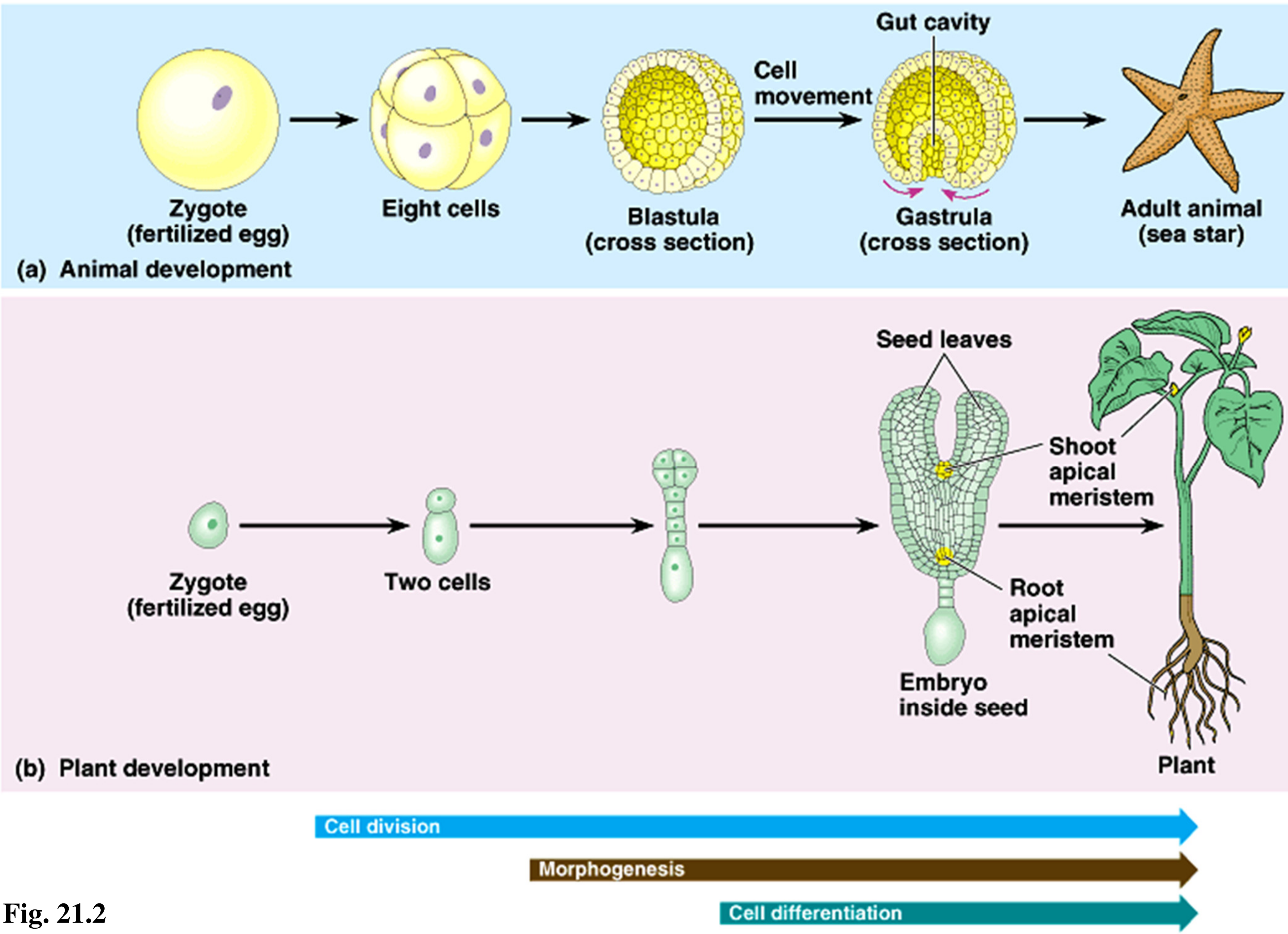
- An organism arises from a fertilized egg cell as the result of three interrelated processes: cell division, cell differentiation, and morphogenesis.
  - From zygote to hatching tadpole takes just one week.

Fig. 21.1



- Cell division alone would produce only a great ball of identical cells.
- During development, cells become specialized in structure and function, undergoing **differentiation**.
- Different kinds of cells are organized into tissues and organs.
- The physical processes of **morphogenesis**, the "creation of form," give an organism shape.
- Early events of morphogenesis lay out the basic body plan very early in embryonic development.
  - These include establishing the head of the animal embryo or the roots of a plant embryo.

- The overall schemes of morphogenesis in animals and plants are very different.
  - In animals, but not in plants, *movements* of cells and tissues are necessary to transform the embryo.
  - In plants, morphogenesis and growth in overall size are not limited to embryonic and juvenile periods.



Gut cavity
Cell movement
Zygote (fertilized egg)
Eight cells
Blastula (cross section)
Gastrula (cross section)
Adult animal (sea star)
(a) Animal development
Seed leaves
Shoot apical meristem
Zygote (fertilized egg)
Two cells
Root apical meristem
Embryo inside seed
Plant
(b) Plant development
Cell division
Morphogenesis
Cell differentiation

Fig. 21.2

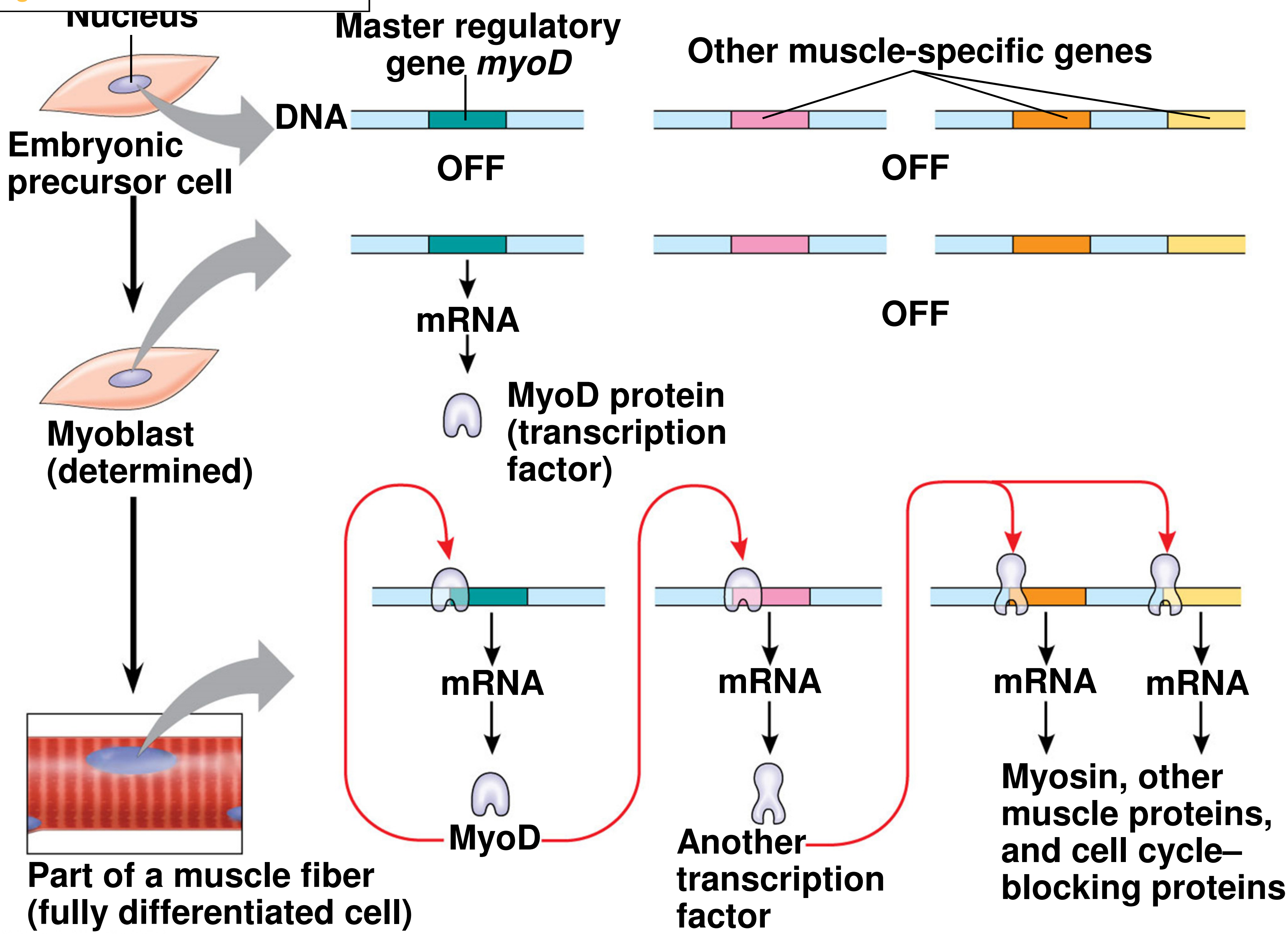
- **Apical meristems**, perpetually embryonic regions in the tips of shoots and roots, are responsible for the plant's continual growth and formation of new organs, such as leaves and roots.
- In animals, ongoing development in adults is restricted to the differentiation of cells, such as blood cells, that must be continually replenished.
- The importance of precise regulation of morphogenesis is evident in human disorders that result from morphogenesis gone awry.
  - For example, cleft palate, in which the upper wall of the mouth cavity fails to close completely, is a defect of morphogenesis.

Sequential Regulation of Gene Expression During Cellular Differentiation

- **Determination** commits a cell to its final fate
- Determination precedes differentiation
- Cell differentiation is marked by the production of tissue-specific proteins

- Myoblasts produce muscle-specific proteins and form skeletal muscle cells
- *MyoD* is one of several “master regulatory genes” that produce proteins that commit the cell to becoming skeletal muscle
- The MyoD protein is a transcription factor that binds to enhancers of various target genes

Figure 18.18-3



21.6. Homeotic genes direct the identity of body parts

- In a normal fly, structures such as antennae, legs, and wings develop on the appropriate segments.
- The anatomical identity of the segments is controlled by master regulatory genes, the **homeotic genes**.
- Discovered by Edward Lewis, these genes specify the types of appendages and other structures that each segment will form.

- Mutations to homeotic genes produce flies with such strange traits as legs growing from the head in place of antennae.
  - Structures characteristic of a particular part of the animal arise in the wrong place.

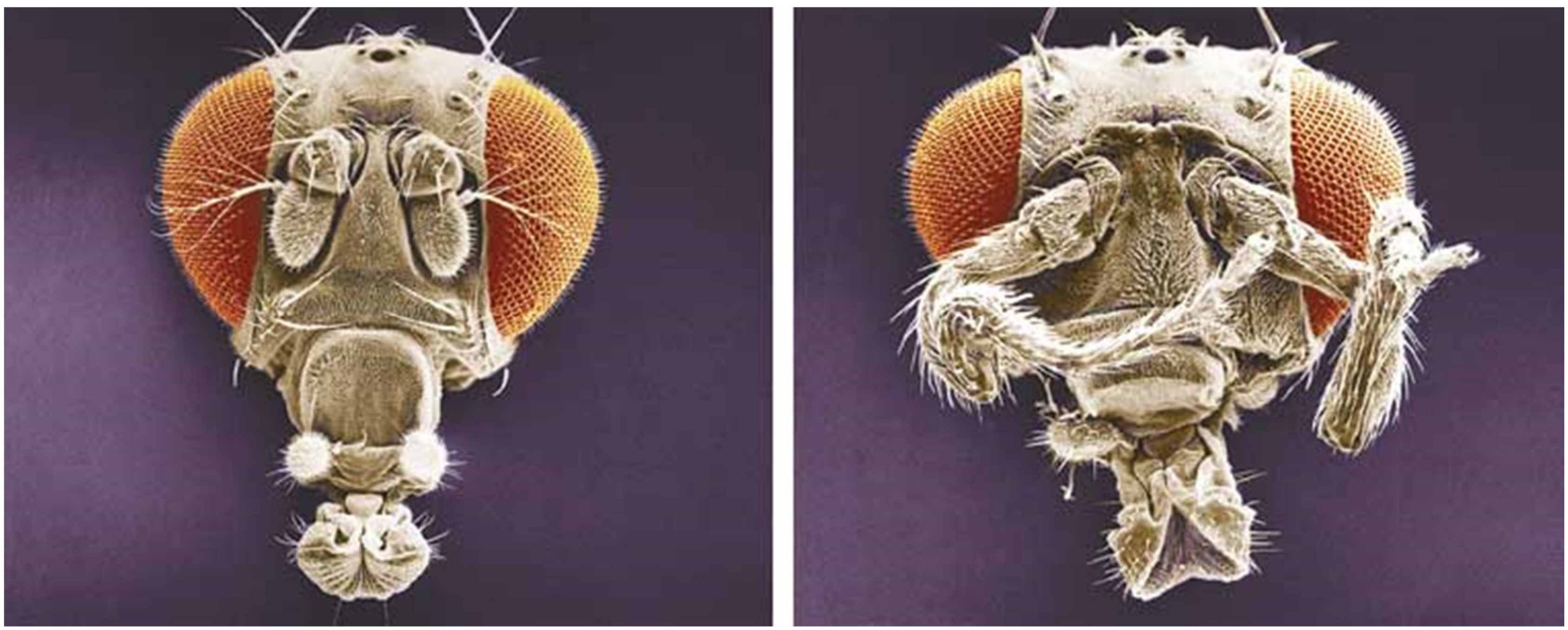


Fig. 21.14

- Like other developmental genes, the homeotic genes encode transcription factors that control the expression of genes responsible for specific anatomical structures.
  - For example, a homeotic protein made in a thoracic segment may activate genes that bring about leg development, while a homeotic protein in a certain head segment activates genes for antennal development.
  - A mutant version of this protein may label a segment as "thoracic" instead of "head", causing legs to develop in place of antennae.

Homeobox genes have been highly conserved in evolution

- All homeotic genes of *Drosophila* include a 180-nucleotide sequence called the **homeobox**, which specifies a 60-amino-acid *homeodomain*.
  - An identical or very similar sequence of nucleotides (often called *Hox* genes) are found in many other animals, including humans.
  - Related sequences are present in yeast and prokaryotes.
  - The homeobox DNA sequence must have evolved very early in the history of life and is sufficiently valuable that it has been conserved in animals for hundreds of millions of years.

- Proteins with homeodomains probably regulate development by coordinating the transcription of batteries of developmental genes.
  - In *Drosophila*, different combinations of homeobox genes are active in different parts of the embryo and at different times, leading to pattern formation.

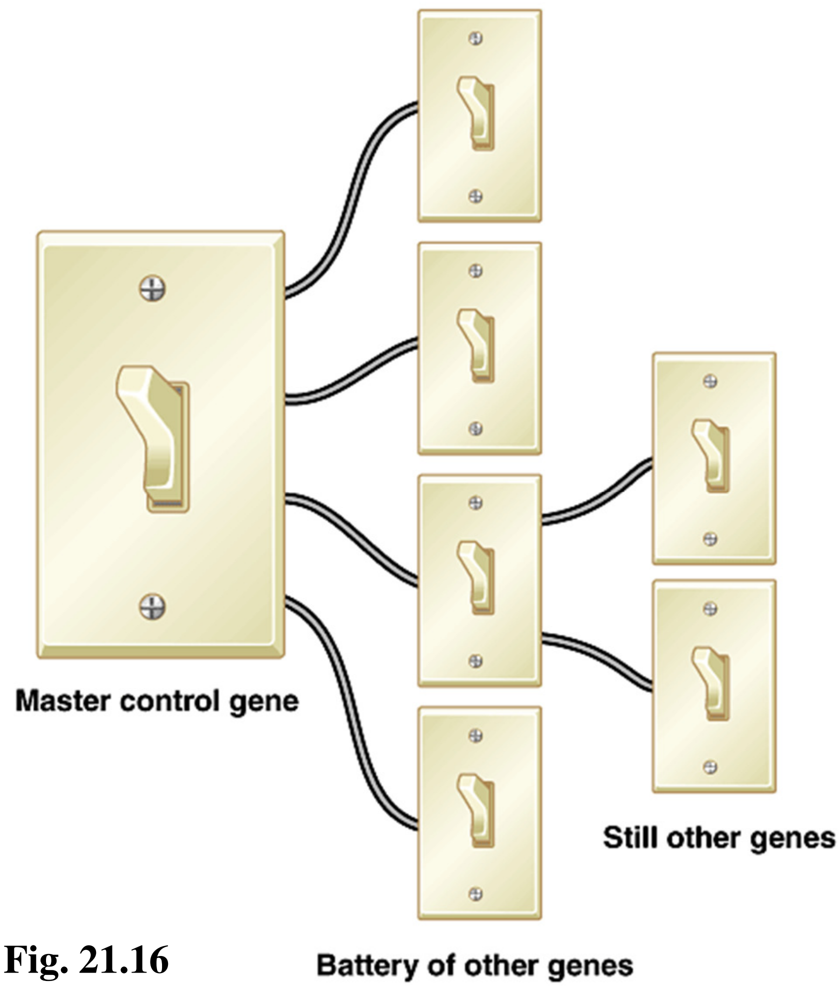


Fig. 21.16

- In fact, the vertebrate genes homologous to the homeotic genes of fruit flies have even kept their chromosomal arrangement.

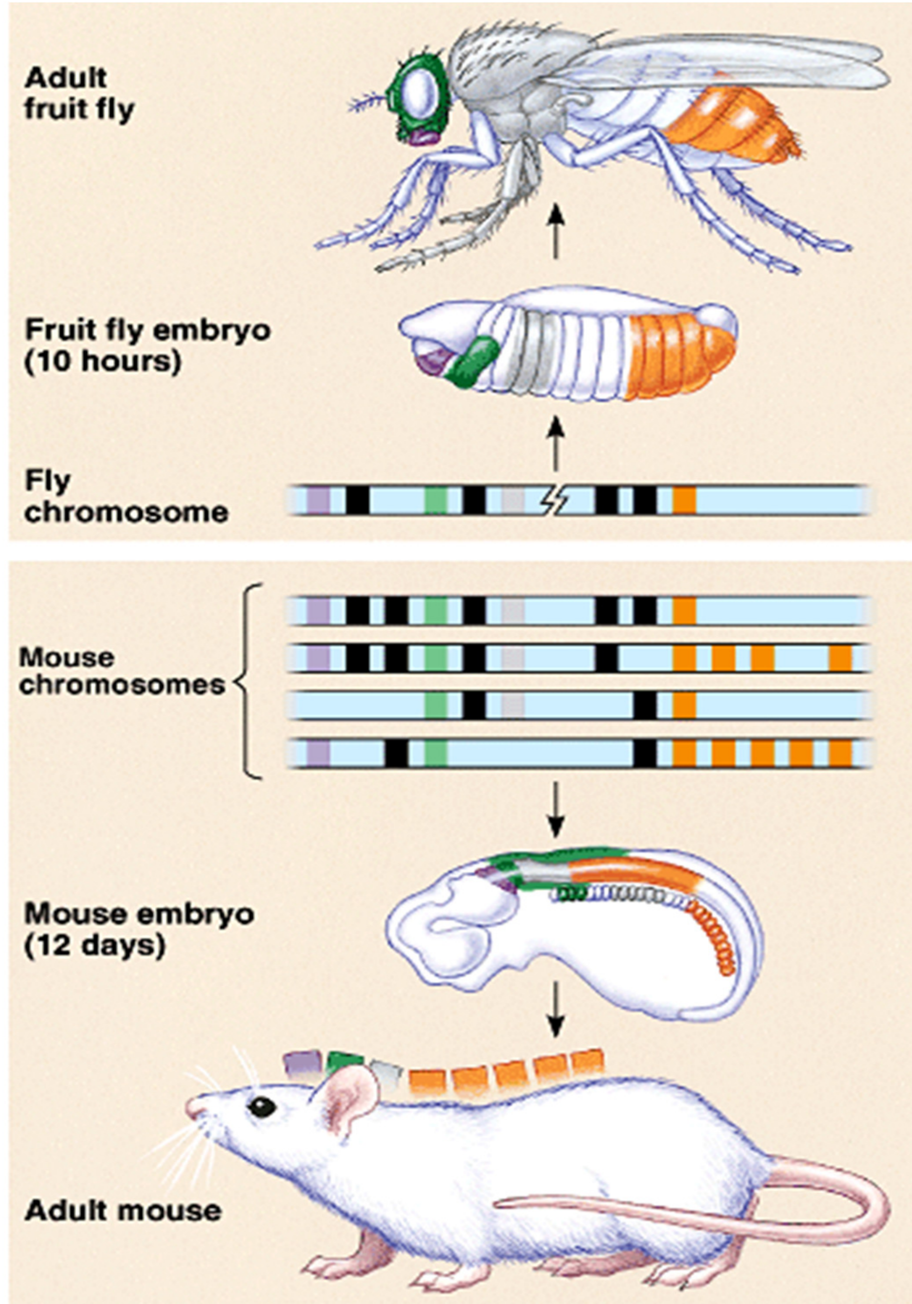


Fig. 21.15

- Most, but not all, homeobox-containing genes are homeotic genes that are associated with development.
    - For example, in *Drosophila*, homeoboxes are present not only in the homeotic genes but also in the egg-polarity gene *bicoid*, in several segmentation genes, and in the master regulatory gene for eye development.
- The polypeptide segment produced by the homeodomain is part of a transcription factor.
    - Part of this segment, an alpha helix, fits neatly into the major groove of the DNA helix.
- Other more variable domains of the overall protein determine which genes it will regulate.

- 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.

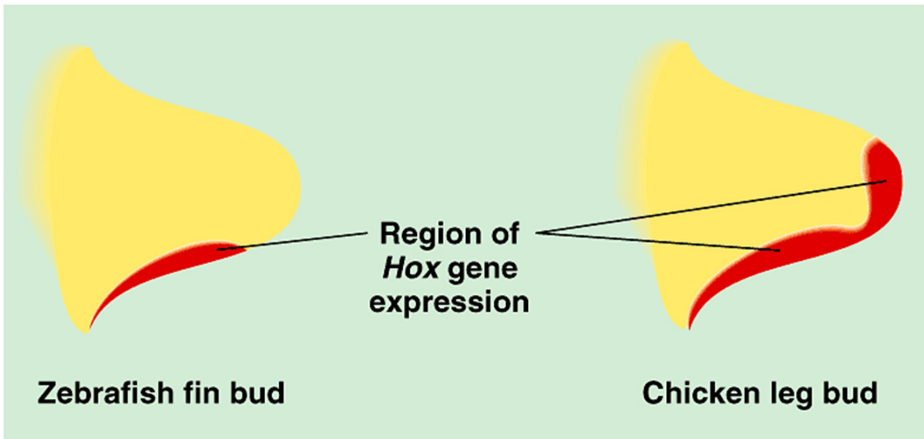


Fig. 24.22

- 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.

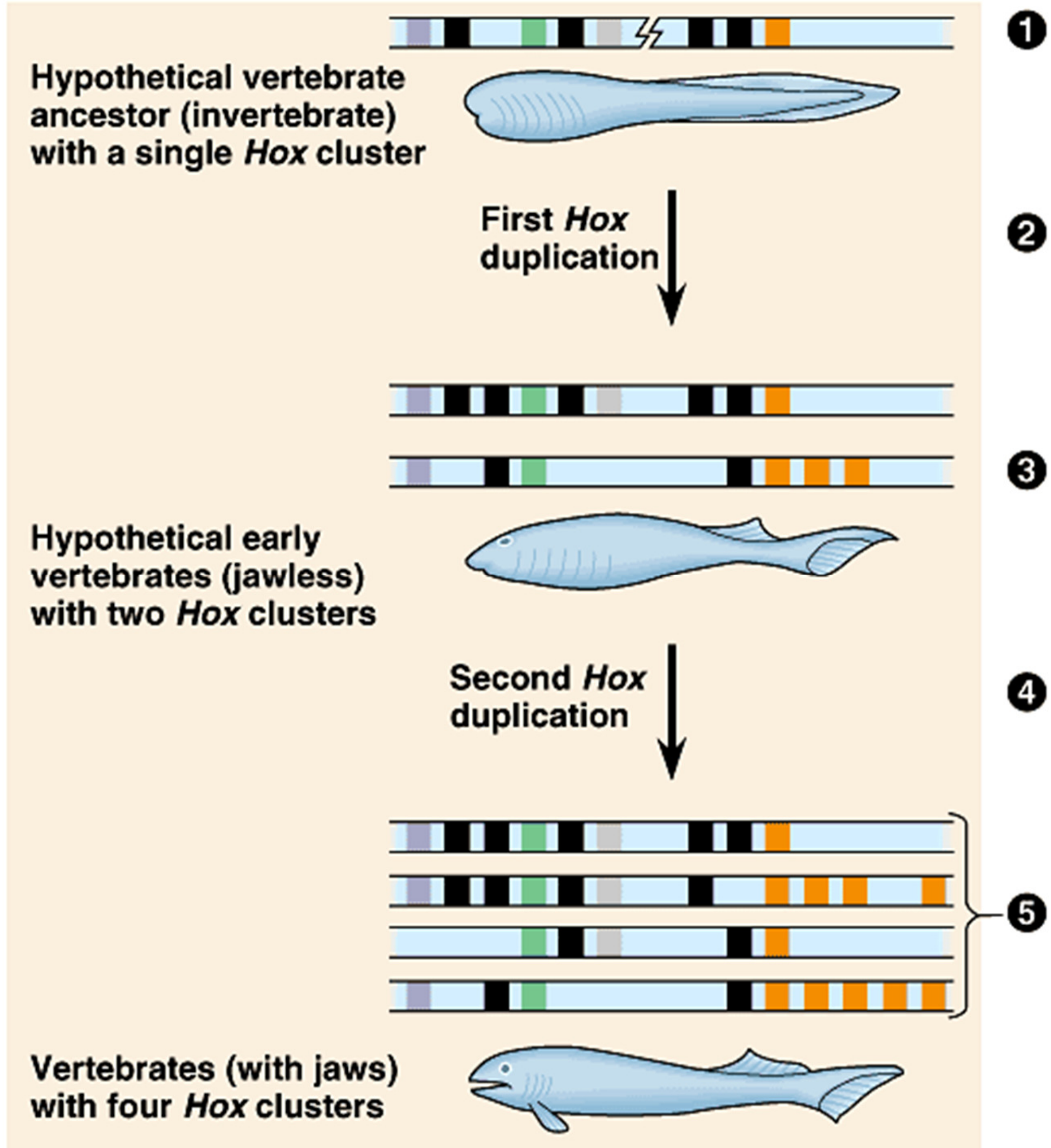


Fig. 24.23

Concept 25.5: Major changes in body form can result from changes in the sequences and regulation of developmental genes

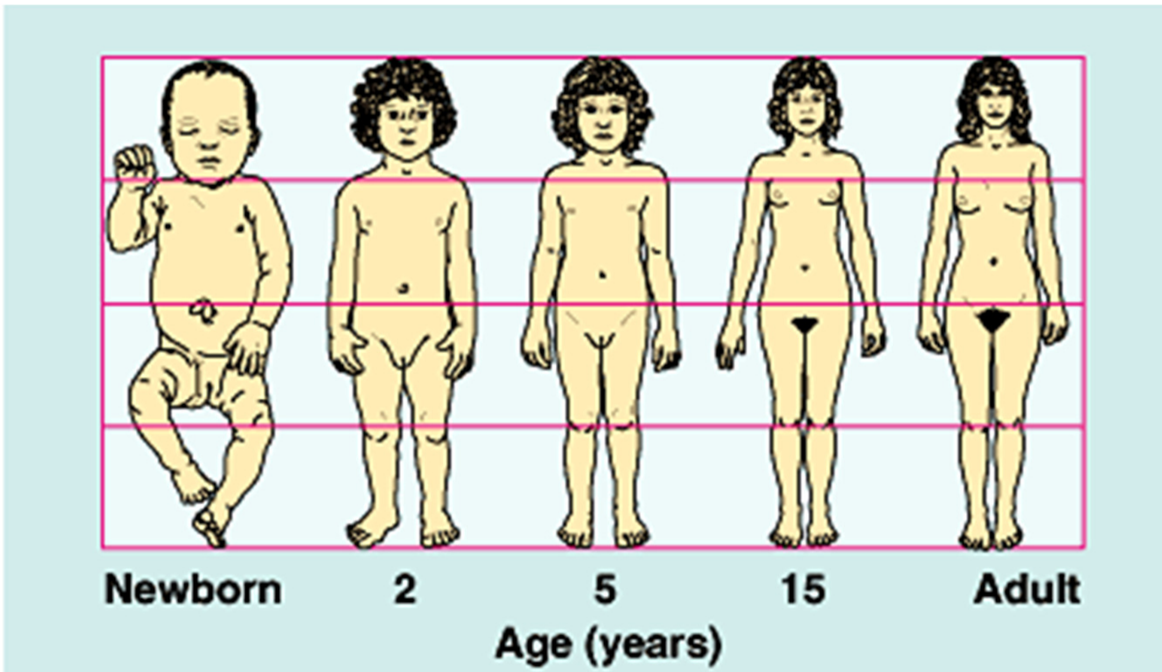
- “Evo-devo” is a field of interdisciplinary research that examines how slight genetic divergences can become magnified into major morphological differences between species.
- A particular focus are genes that program development by controlling the rate, timing, and spatial pattern of changes in form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

Changes in Rate and Timing

- **Heterochrony** is an evolutionary change in the rate or timing of developmental events
- It can have a significant impact on body shape
- The contrasting shapes of human and chimpanzee skulls are the result of small changes in relative growth rates

Animation: Allometric Growth
Right-click slide / select "Play"

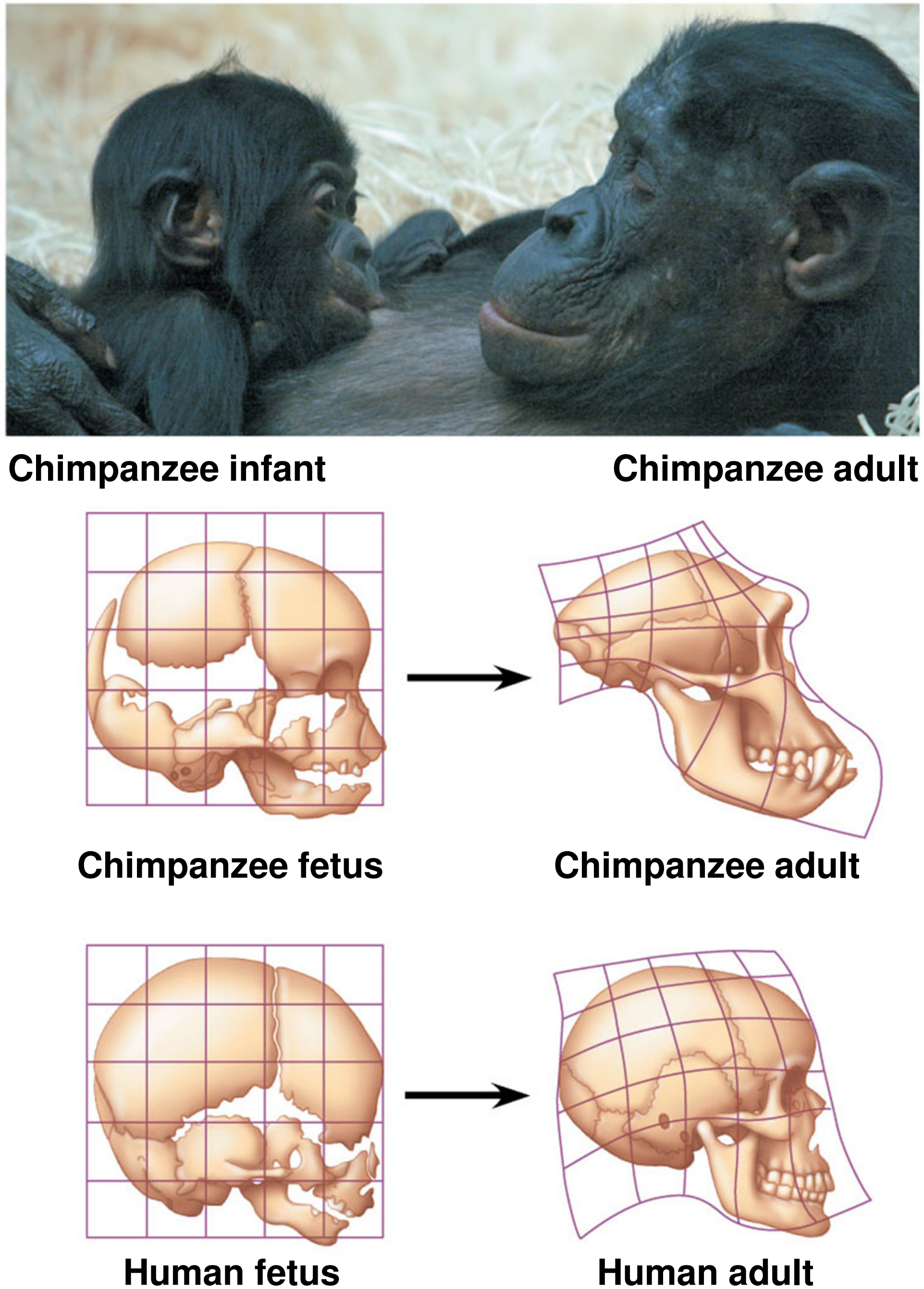
- **Allometric growth** tracks how proportions of structures change due to different growth rates during development.



(a) Differential growth rates in a human

Fig. 24.19a

Figure 25.21


Chimpanzee infant
Chimpanzee adult
Chimpanzee fetus
Chimpanzee adult
Human fetus
Human adult

- 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

- Heterochrony can alter the timing of reproductive development relative to the development of nonreproductive organs
- In **paedomorphosis**, the rate of reproductive development accelerates compared with somatic development
- The sexually mature species may retain body features that were juvenile structures in an ancestral species

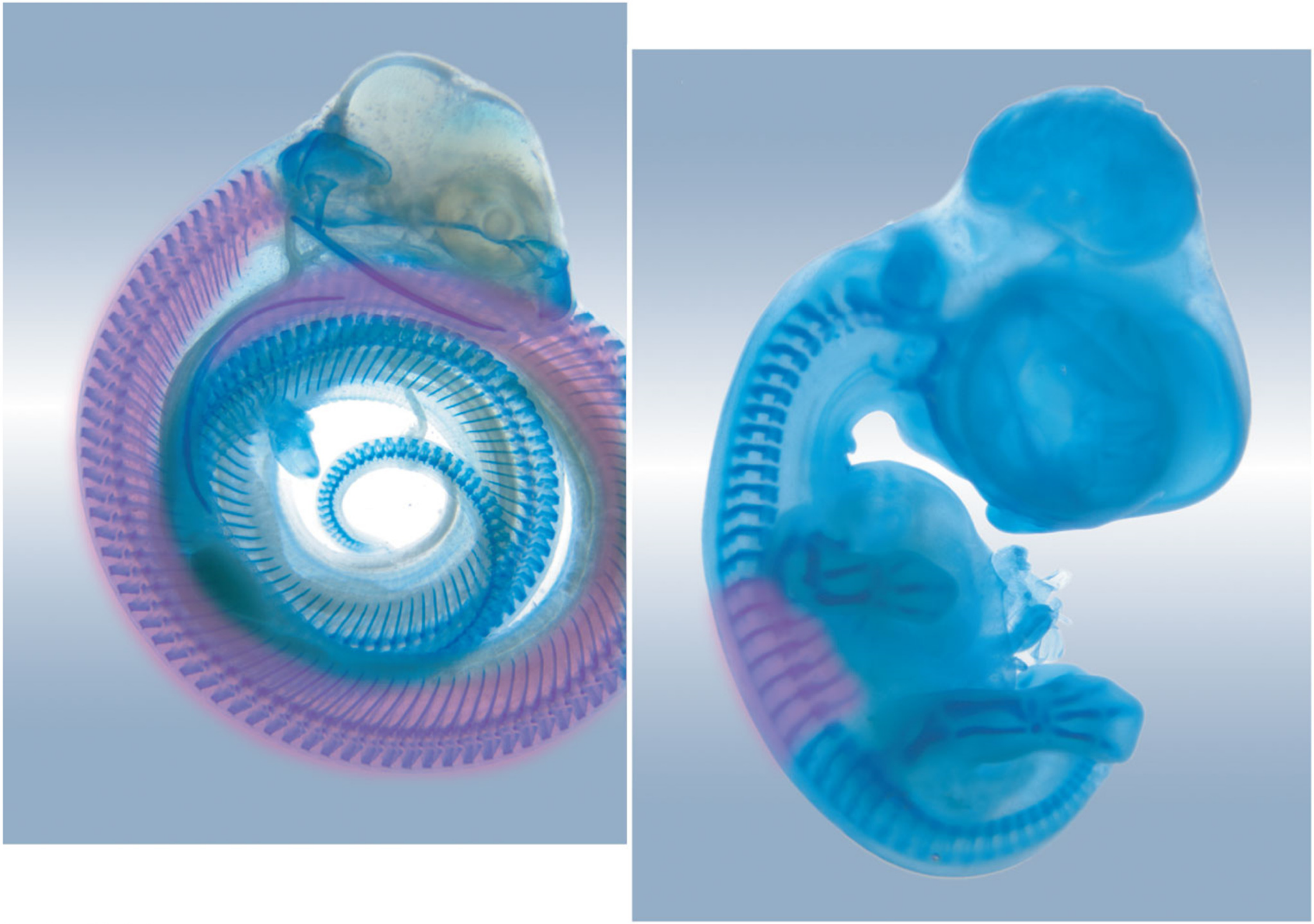
Figure 25.22

Changes in Spatial Pattern

- Substantial evolutionary change can also result from alterations in genes that control the placement and organization of body parts
- **Homeotic genes** determine such basic features as where wings and legs will develop on a bird or how a flower's parts are arranged

- *Hox* genes are a class of homeotic genes that provide positional information during development
- If *Hox* genes are expressed in the wrong location, body parts can be produced in the wrong location
- For example, in crustaceans, a swimming appendage can be produced instead of a feeding appendage

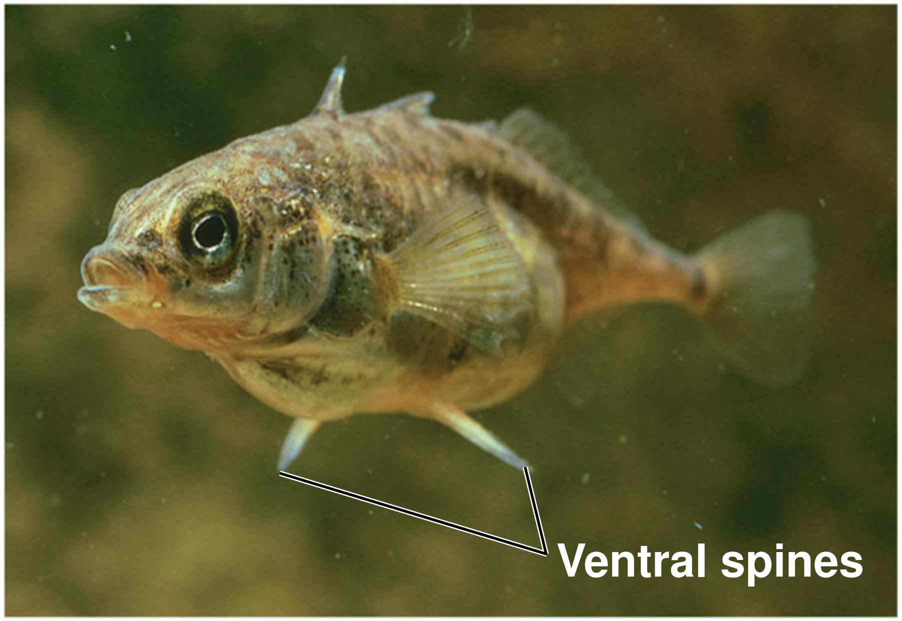
Figure 25.23



Changes in Gene Regulation

- Changes in morphology likely result from changes in the regulation of developmental genes rather than changes in the sequence of developmental genes
  - For example, threespine sticklebacks in lakes have fewer spines than their marine relatives
  - The gene sequence remains the same, but the regulation of gene expression is different in the two groups of fish

Figure 25.25a



Threespine stickleback
(*Gasterosteus aculeatus*)

Figure 25.25b

RESULTS

Test of Hypothesis A: Differences in the coding sequence of the *Pitx1* gene?

Result: No →

The 283 amino acids of the *Pitx1* protein are identical.

Test of Hypothesis B: Differences in the regulation of expression of *Pitx1?*

Result: Yes →

Pitx1 is expressed in the ventral spine and mouth regions of developing marine sticklebacks but only in the mouth region of developing lake sticklebacks.