Chapter 47

Animal Development

PowerPoint Lectures for
***Biology*, Seventh Edition**
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Lectures by Chris Romero

- Overview: A Body-Building Plan for Animals
- It is difficult to imagine
  - That each of us began life as a single cell, a zygote

- A human embryo at approximately 6–8 weeks after conception
  - Shows the development of distinctive features

Figure 47.1

- The question of how a zygote becomes an animal
  - Has been asked for centuries
- As recently as the 18th century
  - The prevailing theory was a notion called preformation

- Preformation is the idea that the egg or sperm contains an embryo
  - A preformed miniature infant, or “homunculus,” that simply becomes larger during development

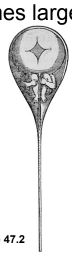


Figure 47.2

- An organism’s development
  - Is determined by the genome of the zygote and by differences that arise between early embryonic cells
- Cell differentiation
  - Is the specialization of cells in their structure and function
- Morphogenesis
  - Is the process by which an animal takes shape

- Concept 47.1: After fertilization, embryonic development proceeds through cleavage, gastrulation, and organogenesis
- Important events regulating development
  - Occur during fertilization and each of the three successive stages that build the animal's body

Fertilization

- The main function of fertilization
  - Is to bring the haploid nuclei of sperm and egg together to form a diploid zygote
- Contact of the sperm with the egg's surface
  - Initiates metabolic reactions within the egg that trigger the onset of embryonic development

The Acrosomal Reaction

- The acrosomal reaction
  - Is triggered when the sperm meets the egg
  - Releases hydrolytic enzymes that digest material surrounding the egg

- The acrosomal reaction

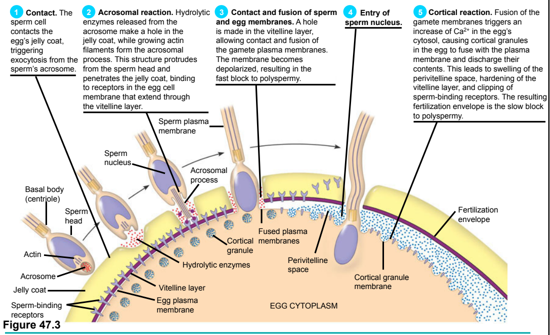


Figure 47.3

- Gamete contact and/or fusion
  - Depolarizes the egg cell membrane and sets up a fast block to polyspermy

The Cortical Reaction

- Fusion of egg and sperm also initiates the cortical reaction
  - Inducing a rise in Ca^{2+} that stimulates cortical granules to release their contents outside the egg

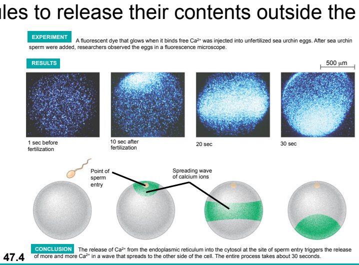


Figure 47.4

- These changes cause the formation of a fertilization envelope
  - That functions as a slow block to polyspermy

Activation of the Egg

- Another outcome of the sharp rise in Ca^{2+} in the egg's cytosol
  - Is a substantial increase in the rates of cellular respiration and protein synthesis by the egg cell
- With these rapid changes in metabolism
  - The egg is said to be activated

- In a fertilized egg of a sea urchin, a model organism
  - Many events occur in the activated egg

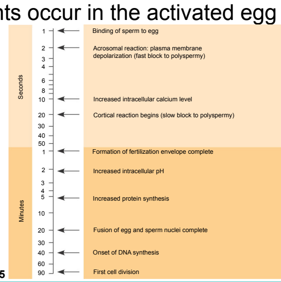


Figure 47.5

Fertilization in Mammals

- In mammalian fertilization, the cortical reaction
  - Modifies the zona pellucida as a slow block to polyspermy

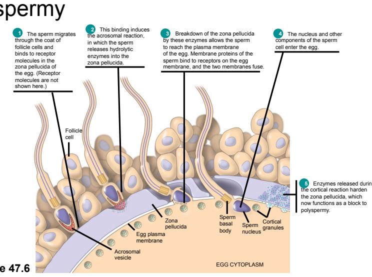


Figure 47.6

Cleavage

- Fertilization is followed by cleavage
  - A period of rapid cell division without growth

- Cleavage partitions the cytoplasm of one large cell
  - Into many smaller cells called blastomeres

(a) Fertilized egg. Shown here is the zygote shortly before the first cleavage division, surrounded by the fertilization envelope. The nucleus is visible in the center.
(b) Four-cell stage. Remnants of the mitotic spindle can be seen between the two cells that have just completed the second cleavage division.
(c) Morula. After further cleavage divisions, the embryo is a multicellular ball that is still surrounded by the fertilization envelope. The blastocoel cavity has begun to form.
(d) Blastula. A single layer of cells surrounds a large blastocoel cavity. Although not visible here, the fertilization envelope is still present; the embryo will soon hatch from it and begin swimming.

Figure 47.7a–d

- The eggs and zygotes of many animals, except mammals
  - Have a definite polarity
- The polarity is defined by the distribution of yolk
  - With the vegetal pole having the most yolk and the animal pole having the least

- The development of body axes in frogs
  - Is influenced by the polarity of the egg

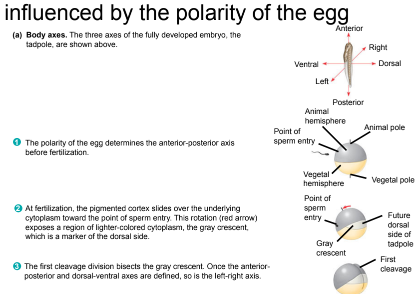


Figure 47.8a, b (b) **Establishing the axes.** The polarity of the egg and cortical rotation are critical in setting up the body axes.

- Cleavage planes usually follow a specific pattern
  - That is relative to the animal and vegetal poles of the zygote

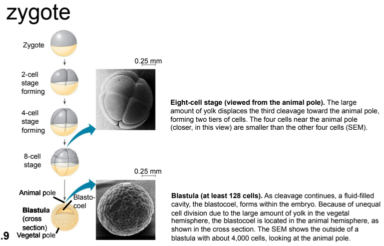


Figure 47.9

- Meroblastic cleavage, incomplete division of the egg
  - Occurs in species with yolk-rich eggs, such as reptiles and birds

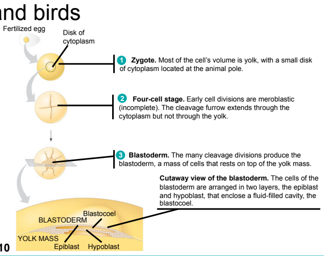


Figure 47.10

- Holoblastic cleavage, the complete division of the egg
  - Occurs in species whose eggs have little or moderate amounts of yolk, such as sea urchins and frogs

Gastrulation

- The morphogenetic process called gastrulation
  - Rearranges the cells of a blastula into a three-layered embryo, called a gastrula, that has a primitive gut

- The three layers produced by gastrulation
  - Are called embryonic germ layers
- The ectoderm
  - Forms the outer layer of the gastrula
- The endoderm
  - Lines the embryonic digestive tract
- The mesoderm
  - Partly fills the space between the endoderm and ectoderm

- Gastrulation in a sea urchin
  - Produces an embryo with a primitive gut and three germ layers

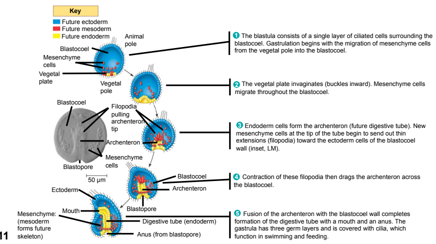


Figure 47.11

- The mechanics of gastrulation in a frog
  - Are more complicated than in a sea urchin

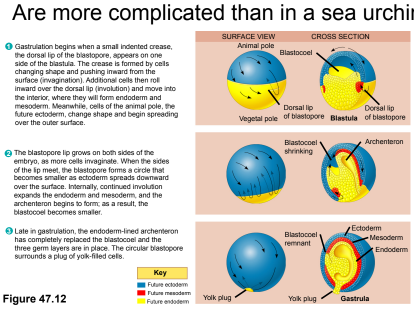


Figure 47.12

- Gastrulation in the chick
  - Is affected by the large amounts of yolk in the egg

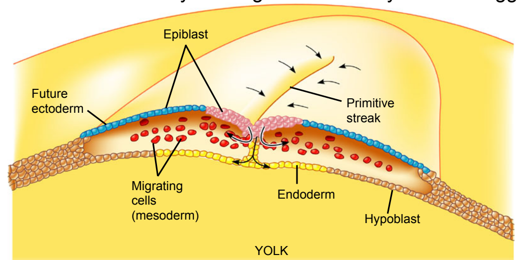


Figure 47.13

Organogenesis

- Various regions of the three embryonic germ layers
  - Develop into the rudiments of organs during the process of organogenesis

- Early in vertebrate organogenesis
  - The notochord forms from mesoderm and the neural plate forms from ectoderm

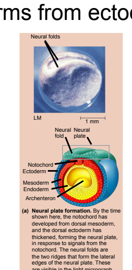
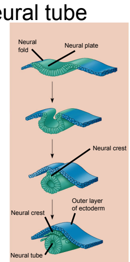


Figure 47.14a

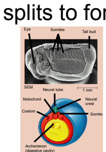
- The neural plate soon curves inward
  - Forming the neural tube



(b) Formation of the neural tube. Infolding and pinching off of the neural plate generates the neural tube. Note the neural crest cells, which will migrate and give rise to numerous structures.

Figure 47.14b

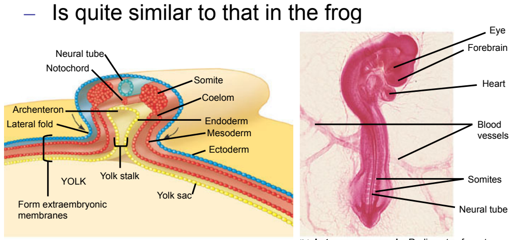
- Mesoderm lateral to the notochord
  - Forms blocks called somites
- Lateral to the somites
  - The mesoderm splits to form the coelom



(c) Somites. The drawing shows an embryo after completion of the neural tube. By this time, the lateral mesoderm has begun to separate into the two tissue layers that line the coelom; the somites, formed from mesoderm, flank the notochord. In the scanning electron micrograph, a side view of a whole embryo at the tail-bud stage, part of the ectoderm has been removed, revealing the somites, which will give rise to segmental structures such as vertebrae and skeletal muscle.

Figure 47.14c

- Organogenesis in the chick
  - Is quite similar to that in the frog



(a) Early organogenesis. The archenteron forms when lateral folds pinch the embryo away from the yolk. The embryo remains open to the yolk, attached by the yolk stalk, about midway along its length, as shown in this cross section. The notochord, neural tube, and somites subsequently form much as they do in the frog.

(b) Late organogenesis. Rudiments of most major organs have already formed in this chick embryo, which is about 56 hours old and about 2–3 mm long (LM).

Figure 47.15a, b

- Many different structures
  - Are derived from the three embryonic germ layers during organogenesis

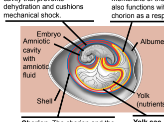
ECTODERM	MESODERM	ENDODERM
• Epidermis of skin and its derivatives (including sweat glands, hair follicles) • Epithelial lining of mouth and rectum • Sense receptors in epidermis • Cornea and lens of eye • Nervous system • Adrenal medulla • Tooth enamel • Epithelium or pineal and pituitary glands	• Notochord • Skeletal system • Muscular system • Muscular layer of stomach, intestine, etc. • Excretory system • Circulatory and lymphatic systems • Reproductive system (except germ cells) • Dermis of skin • Lining of body cavity • Adrenal cortex	• Epithelial lining of digestive tract • Epithelial lining of respiratory system • Lining of urethra, urinary bladder, and reproductive system • Liver • Pancreas • Thymus • Thyroid and parathyroid glands

Figure 47.16

Developmental Adaptations of Amniotes

- The embryos of birds, other reptiles, and mammals
  - Develop within a fluid-filled sac that is contained within a shell or the uterus
- Organisms with these adaptations
  - Are called amniotes

- In these three types of organisms, the three germ layers
  - Also give rise to the four extraembryonic membranes that surround the developing embryo



Amnion. The amnion protects the embryo in a fluid-filled cavity that prevents dehydration and cushions mechanical shock.

Allantois. The allantois functions as a disposal sac for certain metabolic wastes produced by the embryo. The membrane of the allantois also functions with the chorion as a respiratory organ.

Chorion. The chorion and the membrane of the allantois exchange gases between the embryo and the surrounding air. Oxygen and carbon dioxide diffuse freely across the egg's shell.

Yolk sac. The yolk sac expands over the yolk, a stockpile of nutrients stored in the egg. Blood vessels in the yolk sac membrane transport nutrients from the yolk into the embryo. Other nutrients are stored in the albumen (the "egg white").

Figure 47.17

Mammalian Development

- The eggs of placental mammals
  - Are small and store few nutrients
  - Exhibit holoblastic cleavage
  - Show no obvious polarity

- Gastrulation and organogenesis
  - Resemble the processes in birds and other reptiles

- Early embryonic development in a human
  - Proceeds through four stages

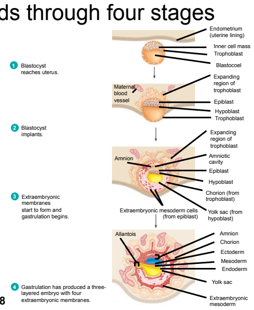


Figure 47.18

- At the completion of cleavage
  - The blastocyst forms
- The trophoblast, the outer epithelium of the blastocyst
  - Initiates implantation in the uterus, and the blastocyst forms a flat disk of cells

- As implantation is completed
  - Gastrulation begins
  - The extraembryonic membranes begin to form
- By the end of gastrulation
  - The embryonic germ layers have formed

- The extraembryonic membranes in mammals
  - Are homologous to those of birds and other reptiles and have similar functions

- Concept 47.2: Morphogenesis in animals involves specific changes in cell shape, position, and adhesion
- Morphogenesis is a major aspect of development in both plants and animals
  - But only in animals does it involve the *movement* of cells

The Cytoskeleton, Cell Motility, and Convergent Extension

- Changes in the shape of a cell
  - Usually involve reorganization of the cytoskeleton

- The formation of the neural tube
  - Is affected by microtubules and microfilaments

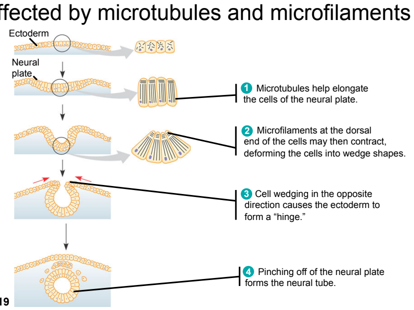


Figure 47.19

- The cytoskeleton also drives cell migration, or cell crawling
  - The active movement of cells from one place to another
- In gastrulation, tissue invagination
  - Is caused by changes in both cell shape and cell migration

- Cell crawling is also involved in convergent extension
  - A type of morphogenetic movement in which the cells of a tissue become narrower and longer

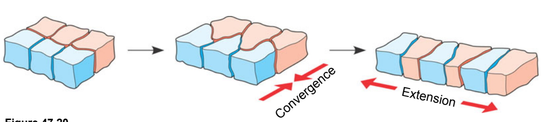


Figure 47.20

Roles of the Extracellular Matrix and Cell Adhesion Molecules

- Fibers of the extracellular matrix
  - May function as tracks, directing migrating cells along particular routes

- Several kinds of glycoproteins, including fibronectin
  - Promote cell migration by providing specific molecular anchorage for moving cells

EXPERIMENT Researchers placed a strip of fibronectin on an artificial underlayer. After positioning migratory neural crest cells at one end of the strip, the researchers observed the movement of the cells in a light microscope.

RESULTS In this micrograph, the dashed lines indicate the edges of the fibronectin layer. Note that cells are migrating along the strip, not off of it.

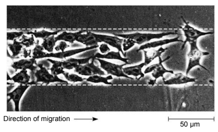


Figure 47.21 **CONCLUSION** Fibronectin helps promote cell migration, possibly by providing anchorage for the migrating cells.

- Cell adhesion molecules
  - Also contribute to cell migration and stable tissue structure

- One important class of cell-to-cell adhesion molecule is the cadherins
  - Which are important in the formation of the frog blastula

EXPERIMENT Researchers injected frog eggs with nucleic acid complementary to the mRNA encoding a cadherin known as EP cadherin. This “antisense” nucleic acid leads to destruction of the mRNA for normal EP cadherin, so no EP cadherin protein is produced. Frog sperm were then added to control (noninjected) eggs and to experimental (injected) eggs. The control and experimental embryos that developed were observed in a light microscope.

RESULTS As shown in these micrographs, fertilized control eggs developed into normal blastulas, but fertilized experimental eggs did not. In the absence of EP cadherin, the blastocoel did not form properly, and the cells were arranged in a disorganized fashion.

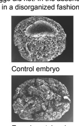


Figure 47.22 **CONCLUSION** Proper blastula formation in the frog requires EP cadherin.

- Concept 47.3: The developmental fate of cells depends on their history and on inductive signals
- Coupled with morphogenetic changes
  - Development also requires the timely differentiation of many kinds of cells at specific locations
- Two general principles
  - Underlie differentiation during embryonic development

- First, during early cleavage divisions
  - Embryonic cells must somehow become different from one another
- Second, once initial cell asymmetries are set up
  - Subsequent interactions among the embryonic cells influence their fate, usually by causing changes in gene expression

Fate Mapping

- Fate maps
  - Are general territorial diagrams of embryonic development

- Classic studies using frogs
  - Gave indications that the lineage of cells making up the three germ layers created by gastrulation is traceable to cells in the blastula

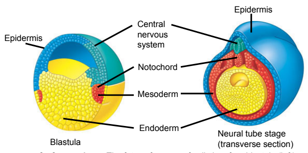


Figure 47.23a (a) **Fate map of a frog embryo.** The fates of groups of cells in a frog blastula (left) were determined in part by marking different regions of the blastula surface with nontoxic dyes of various colors. The embryos were sectioned at later stages of development, such as the neural tube stage shown on the right, and the locations of the dyed cells determined.

- Later studies developed techniques
  - That marked an individual blastomere during cleavage and then followed it through development

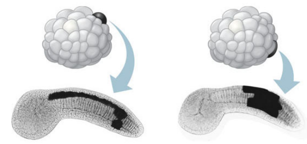


Figure 47.23b (b) **Cell lineage analysis in a tunicate.** In lineage analysis, an individual cell is injected with a dye during cleavage, as indicated in the drawings of 64-cell embryos of a tunicate, an invertebrate chordate. The dark regions in the light micrographs of larvae correspond to the cells that developed from the two different blastomeres indicated in the drawings.

Establishing Cellular Asymmetries

- To understand at the molecular level how embryonic cells acquire their fates
  - It is helpful to think first about how the basic axes of the embryo are established

The Axes of the Basic Body Plan

- In nonamniotic vertebrates
  - Basic instructions for establishing the body axes are set down early, during oogenesis or fertilization

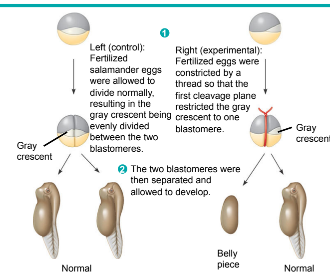
- In amniotes, local environmental differences
  - Play the major role in establishing initial differences between cells and, later, the body axes

Restriction of Cellular Potency

- In many species that have cytoplasmic determinants
  - Only the zygote is totipotent, capable of developing into all the cell types found in the adult

- Unevenly distributed cytoplasmic determinants in the egg cell
  - Are important in establishing the body axes
  - Set up differences in blastomeres resulting from cleavage

EXPERIMENT



RESULTS Blastomeres that receive half or all of the gray crescent develop into normal embryos, but a blastomere that receives none of the gray crescent gives rise to an abnormal embryo without dorsal structures. Spemann called it a "belly piece."

CONCLUSION The totipotency of the two blastomeres normally formed during the first cleavage division depends on cytoplasmic determinants localized in the gray crescent.

Figure 47.24

- As embryonic development proceeds
  - The potency of cells becomes progressively more limited in all species

Cell Fate Determination and Pattern Formation by Inductive Signals

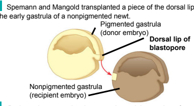
- Once embryonic cell division creates cells that differ from each other
  - The cells begin to influence each other's fates by induction

The "Organizer" of Spemann and Mangold

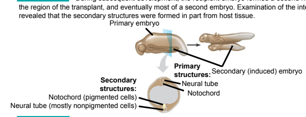
- Based on the results of their most famous experiment
  - Spemann and Mangold concluded that the dorsal lip of the blastopore functions as an organizer of the embryo

- The organizer initiates a chain of inductions
  - That results in the formation of the notochord, the neural tube, and other organs

EXPERIMENT Spemann and Mangold transplanted a piece of the dorsal lip of a pigmented newt gastrula to the ventral side of the early gastrula of a nonpigmented newt.



RESULTS During subsequent development, the recipient embryo formed a second notochord and neural tube in the region of the transplant, and eventually most of a second embryo. Examination of the interior of the double embryo revealed that the secondary structures were formed in part from host tissue.



CONCLUSION The transplanted dorsal lip was able to induce cells in a different region of the recipient to form structures different from their normal fate. In effect, the dorsal lip "organized" the later development of an entire embryo.

Figure 47.25

Formation of the Vertebrate Limb

- Inductive signals play a major role in pattern formation
  - The development of an animal's spatial organization

- The molecular cues that control pattern formation, called positional information
  - Tell a cell where it is with respect to the animal's body axes
  - Determine how the cell and its descendents respond to future molecular signals

- The wings and legs of chicks, like all vertebrate limbs
  - Begin as bumps of tissue called limb buds

(a) Organizer regions. Vertebrate limbs develop from protrusions called limb buds, each consisting of mesoderm cells covered by a layer of ectoderm. Two regions, termed the apical ectodermal ridge (AER, shown in this SEM) and the zone of polarizing activity (ZPA), play key organizer roles in limb pattern formation.

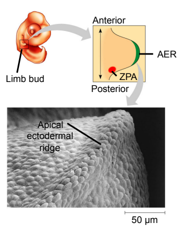


Figure 47.26a

- The embryonic cells within a limb bud
  - Respond to positional information indicating location along three axes

(b) Wing of chick embryo. As the bud develops into a limb, a specific pattern of tissues emerges. In the chick wing, for example, the three digits are always present in the arrangement shown here. Pattern formation requires each embryonic cell to receive some kind of positional information indicating location along the three axes of the limb. The AER and ZPA secrete molecules that help provide this information.

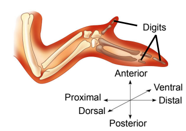
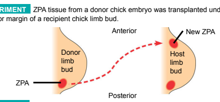


Figure 47.26b

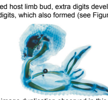
- One limb-bud organizer region is the apical ectodermal ridge (AER)
  - A thickened area of ectoderm at the tip of the bud
- The second major limb-bud organizer region is the zone of polarizing activity (ZPA)
  - A block of mesodermal tissue located underneath the ectoderm where the posterior side of the bud is attached to the body

- Tissue transplantation experiments
  - Support the hypothesis that the ZPA produces some sort of inductive signal that conveys positional information indicating "posterior"

EXPERIMENT ZPA tissue from a donor chick embryo was transplanted under the ectoderm in the anterior margin of a recipient chick limb bud.



RESULTS In the grafted host limb bud, extra digits developed from host tissue in a mirror-image arrangement to the normal digits, which also formed (see Figure 47.26b for a diagram of a normal chick wing).



CONCLUSION The mirror-image duplication observed in this experiment suggests that ZPA cells secrete a signal that diffuses from its source and conveys positional information indicating "posterior." As the distance from the ZPA increases, the signal concentration decreases and hence more anterior digits develop.

Figure 47.27

- Signal molecules produced by inducing cells
  - Influence gene expression in the cells that receive them
  - Lead to differentiation and the development of particular structures