A Body-Building Plan

- A human embryo at about 7 weeks after conception shows development of distinctive features

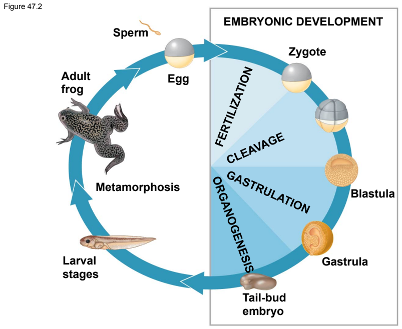
Figure 47.1

Figure 47.1a

- Biologists have long noted common features of early embryonic stages among animals
- Researchers have demonstrated specific patterns of gene expression that direct cells in a developing embryo to adopt distinctive fates

- Biologists use **model organisms** to study development, chosen for the ease with which they can be studied in the laboratory
- Development occurs at many points in the lifecycle of an animal
- Across a range of animal species, embryonic development involves common stages that occur in a set order

Figure 47.2



Concept 47.1: Fertilization and cleavage initiate embryonic development

- **Fertilization** is the formation of a diploid zygote from a haploid egg and sperm

Fertilization

- Molecules and events at the egg surface play a crucial role in each step of fertilization
  - Sperm penetrate the protective layer around the egg
  - Receptors on the egg surface bind to molecules on the sperm surface
  - Changes at the egg surface prevent polyspermy, the entry of multiple sperm nuclei into the egg

The Acrosomal Reaction

- The **acrosomal reaction** is triggered when the sperm meets the egg
- The **acrosome** at the tip of the sperm releases hydrolytic enzymes that digest material surrounding the egg

Figure 47.3-1

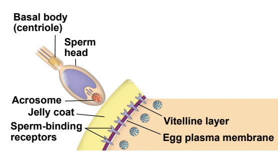


Figure 47.3-2

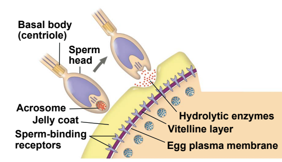


Figure 47.3-3

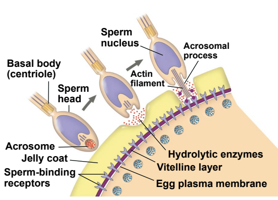


Figure 47.3-4

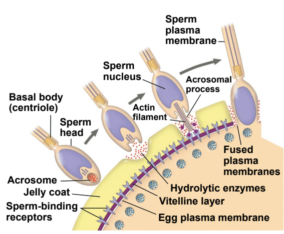
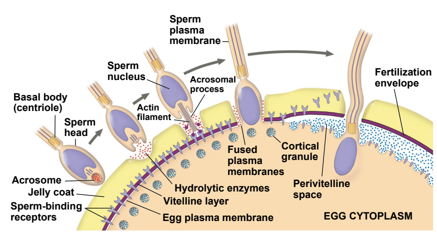


Figure 47.3-5



- 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
- Seconds after the sperm binds to the egg, vesicles just beneath the egg plasma membrane release their contents and form a fertilization envelope
- The fertilization envelope acts as the **slow block to polyspermy**

- The cortical reaction requires a high concentration of Ca^{2+} ions in the egg
- The reaction is triggered by a change in Ca^{2+} concentration
- Ca^{2+} spread across the egg correlates with the appearance of the fertilization envelope

Figure 47.4

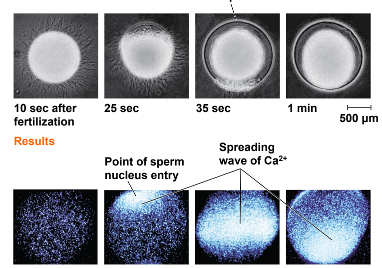


Figure 47.4a

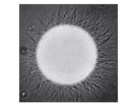


Figure 47.4b

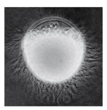


Figure 47.4c

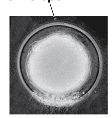


Figure 47.4d

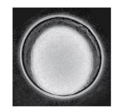


Figure 47.4e

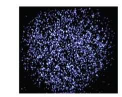


Figure 47.4f

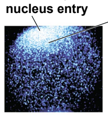


Figure 47.4g

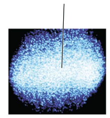
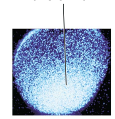
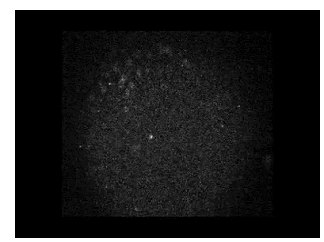


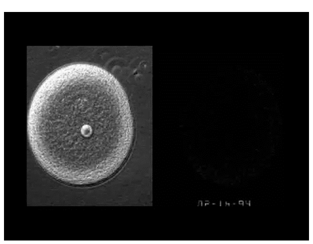
Figure 47.4h



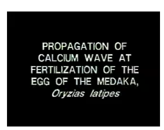
Video: Cortical Granule Fusion Following Egg Fertilization



Video: Calcium Release Following Egg Fertilization



Video: Calcium Wave Propagation in Fish Eggs



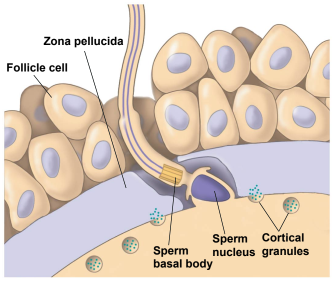
Egg Activation

- The rise in Ca^{2+} in the cytosol increases 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
- The proteins and mRNAs needed for activation are already present in the egg
- The sperm nucleus merges with the egg nucleus and cell division begins

Fertilization in Mammals

- Fertilization in mammals and other terrestrial animals is internal
- A sperm must travel through a layer of follicle cells surrounding the egg, before it reaches the **zona pellucida**, or extracellular matrix of the egg
- Sperm binding triggers a cortical reaction
- Overall, the process of fertilization is relatively slow in mammals; the first cell division occurs 12–36 hours after sperm binding in mammals

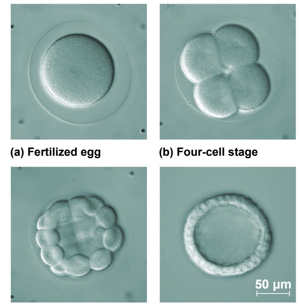
Figure 47.5



Cleavage

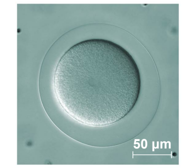
- Fertilization is followed by **cleavage**, a period of rapid cell division without growth
- Cleavage partitions the cytoplasm of one large cell into many smaller cells called **blastomeres**
- The **blastula** is a ball of cells with a fluid-filled cavity called a **blastocoel**

Figure 47.6



(a) Fertilized egg (b) Four-cell stage (c) Early blastula (d) Later blastula

Figure 47.6a

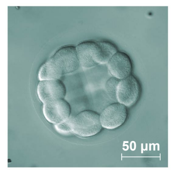


(a) Fertilized egg

Figure 47.6b

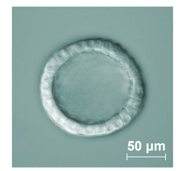
(b) Four-cell stage

Figure 47.6c



(c) Early blastula

Figure 47.6d



(d) Later blastula

Cleavage Pattern in Frogs

- In frogs and many other land animals, cleavage is asymmetric due to the distribution of **yolk** (stored nutrients)
- The **vegetal pole** has more yolk; the **animal pole** has less yolk
- The yolk greatly affects the pattern of cleavage

Figure 47.7-1

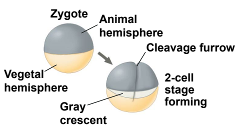


Figure 47.7-2

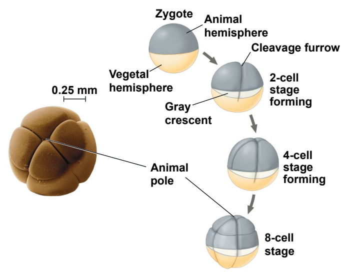


Figure 47.7-3

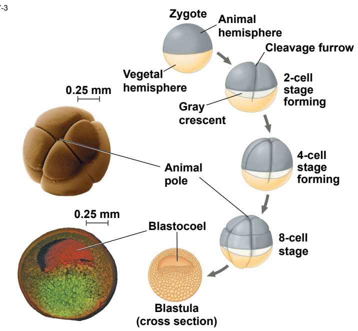
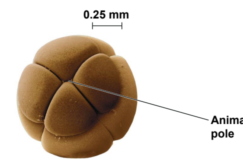
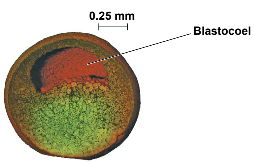


Figure 47.7a



8-cell stage (viewed from the animal pole)

Figure 47.7b



Blastula (at least 128 cells)

Video: Cleavage of a Fertilized Egg

- The first two cleavage furrows in the frog form four equally sized blastomeres
- The third cleavage is asymmetric, forming unequally sized blastomeres; this asymmetry is due to the yolk in the vegetal hemisphere

Cleavage Pattern in Other Animals

- **Holoblastic cleavage**, complete division of the egg, occurs in species whose eggs have little or moderate amounts of yolk, such as sea urchins and frogs
- **Meroblastic cleavage**, incomplete division of the egg, occurs in species with yolk-rich eggs, such as reptiles and birds

Regulation of Cleavage

- Initial development is carried out by RNA and proteins deposited in the egg during oogenesis
- After cleavage, the egg cytoplasm has been divided among many blastomeres, each of which can make sufficient RNA to program the cell's metabolism and further development

Concept 47.2: Morphogenesis in animals involves specific changes in cell shape, position, and survival

- After cleavage, the rate of cell division slows and the normal cell cycle is restored
- **Morphogenesis**, the process by which cells occupy their appropriate locations, involves
  - **Gastrulation**, the movement of cells from the blastula surface to the interior of the embryo
  - **Organogenesis**, the formation of organs

Gastrulation

- **Gastrulation** rearranges the cells of a blastula into a three-layered embryo, called a **gastrula**

- The three layers produced by gastrulation are called embryonic **germ layers**
  - The **ectoderm** forms the outer layer
  - The **endoderm** lines the digestive tract
  - The **mesoderm** partly fills the space between the endoderm and ectoderm
- Each germ layer contributes to specific structures in the adult animal

Gastrulation in Sea Urchins

- Gastrulation begins at the vegetal pole of the blastula
- Mesenchyme cells migrate into the blastocoel
- The vegetal plate forms from the remaining cells of the vegetal pole and buckles inward through invagination

Figure 47.8

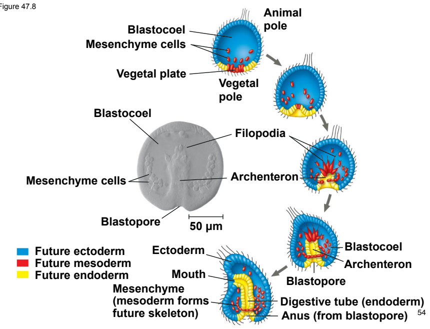


Figure 47.8a-1

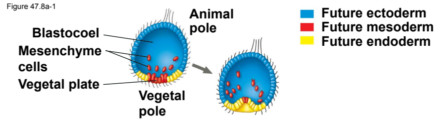


Figure 47.8a-2

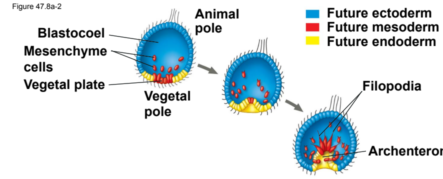


Figure 47.8a-3

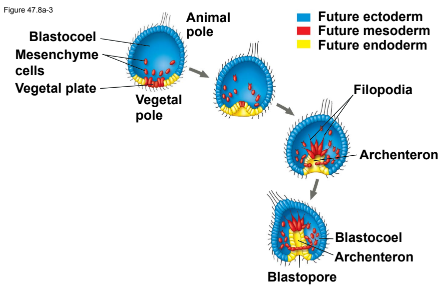


Figure 47.8a-4

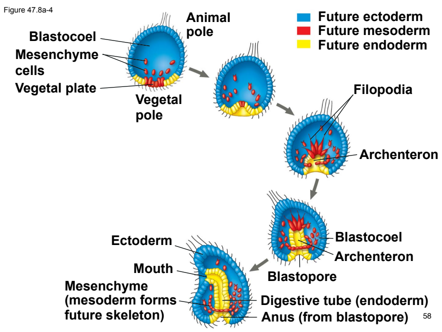
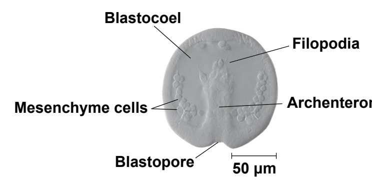
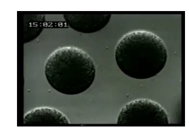


Figure 47.8b



Video: Sea Urchin Embryonic Development (Time Lapse)



- The newly formed cavity is called the **archenteron**
- This opens through the **blastopore**, which will become the anus

Gastrulation in Frogs

- Frog gastrulation begins when a group of cells on the dorsal side of the blastula begins to invaginate
- This forms a crease along the region where the gray crescent formed

- Cells continue to move from the embryo surface into the embryo by involution
- These cells become the endoderm and mesoderm
- Cells on the embryo surface will form the ectoderm

Figure 47.9

ECTODERM (outer layer of embryo)

- Epidermis of skin and its derivatives (including sweat glands, hair follicles)
- Nervous and sensory systems
- Pituitary gland, adrenal medulla
- Jaws and teeth
- Germ cells

MESODERM (middle layer of embryo)

- Skeletal and muscular systems
- Circulatory and lymphatic systems
- Excretory and reproductive systems (except germ cells)
- Dermis of skin
- Adrenal cortex

ENDODERM (inner layer of embryo)

- Epithelial lining of digestive tract and associated organs (liver, pancreas)
- Epithelial lining of respiratory, excretory, and reproductive tracts and ducts
- Thymus, thyroid, and parathyroid glands

Figure 47.10

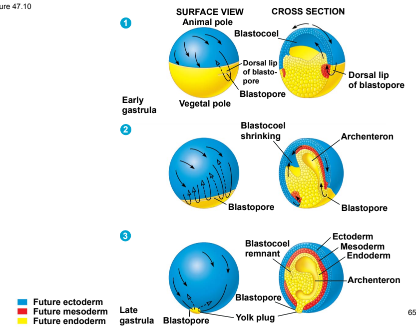


Figure 47.10a

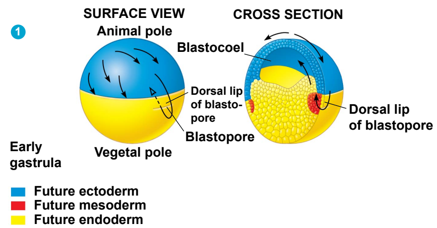


Figure 47.10b

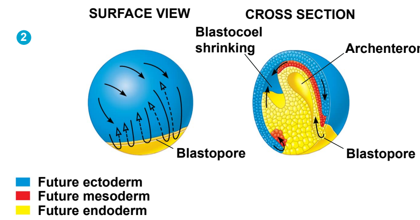
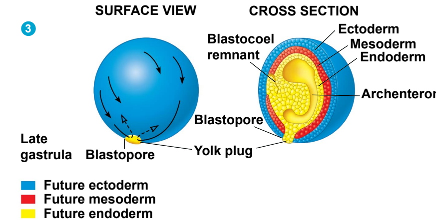


Figure 47.10c

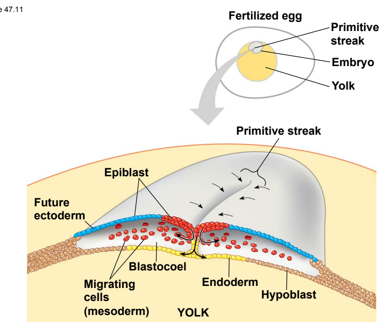


Gastrulation in Chicks

- Prior to gastrulation, the embryo is composed of an upper and lower layer, the epiblast and hypoblast, respectively
- During gastrulation, epiblast cells move toward the midline of the blastoderm and then into the embryo toward the yolk

- The midline thickens and is called the **primitive streak**
- The hypoblast cells contribute to the sac that surrounds the yolk and a connection between the yolk and the embryo, but do not contribute to the embryo itself

Figure 47.11



Gastrulation in Humans

- Human eggs have very little yolk
- A **blastocyst** is the human equivalent of the blastula
- The **inner cell mass** is a cluster of cells at one end of the blastocyst
- The **trophoblast** is the outer epithelial layer of the blastocyst and does not contribute to the embryo, but instead initiates implantation

- Following implantation, the trophoblast continues to expand and a set of **extraembryonic membranes** is formed
- These enclose specialized structures outside of the embryo
- Gastrulation involves the inward movement from the epiblast, through a primitive streak, similar to the chick embryo

Figure 47.12

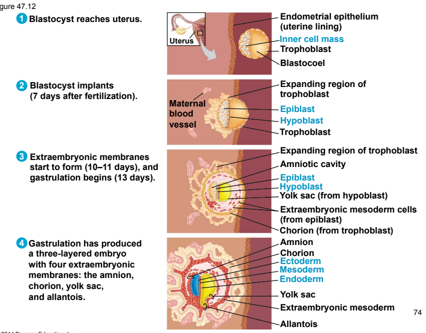


Figure 47.12a

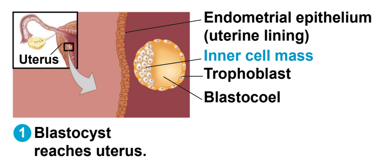


Figure 47.12b

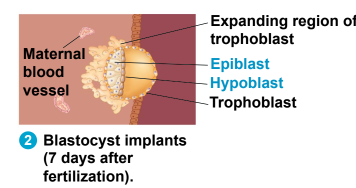


Figure 47.12c

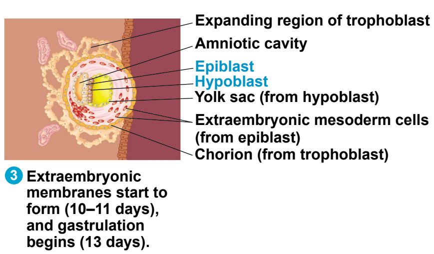
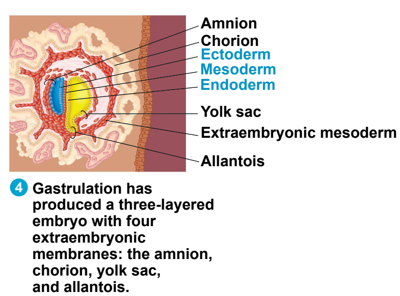


Figure 47.12d



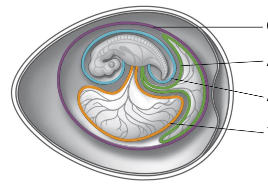
Video: Ultrasound of Human Fetus 1

Video: Ultrasound of Human Fetus 2

Developmental Adaptations of Amniotes

- Land vertebrates form four extraembryonic membranes: the chorion, allantois, amnion, and yolk sac
- These provide a life-support system for the further development of the embryo
- Reproduction outside of aqueous environments required development of
  - The shelled egg of birds, other reptiles, and the monotremes
  - The uterus of marsupial and eutherian mammals

Figure 47.13



- In both adaptations, embryos are surrounded by fluid in a sac called the amnion
- This protects the embryo from desiccation and allows reproduction on dry land
- Mammals and reptiles including birds are called **amniotes** for this reason

- The four extraembryonic membranes that form around the embryo
  - The chorion functions in gas exchange
  - The amnion encloses the amniotic fluid
  - The yolk sac encloses the yolk
  - The allantois disposes of waste products and contributes to gas exchange

Organogenesis

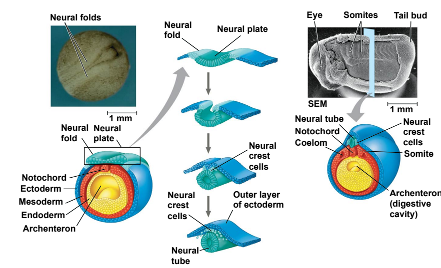
- During **organogenesis**, various regions of the germ layers develop into rudimentary organs
- Adoption of particular developmental fates may cause cells to change shape or even migrate to a new location in the body

Neurulation

- Neurulation begins as cells from the dorsal mesoderm form the **notochord**, a rod extending along the dorsal side of the embryo
- Signaling molecules secreted by the notochord and other mesodermal cells cause the ectoderm above to form the neural plate
- This is an example of **induction**, when cells or tissues cause a developmental change in nearby cells

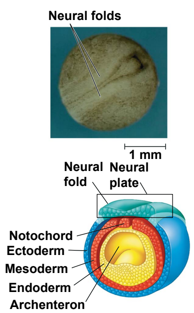
- The neural plate soon curves inward, forming the **neural tube**
- The neural tube will become the central nervous system (brain and spinal cord)
- The notochord disappears before birth, but contributes to parts of the discs between vertebrae

Figure 47.14



(a) Neural plate formation (b) Neural tube formation (c) Somites

Figure 47.14a



(a) Neural plate formation

Figure 47.14aa

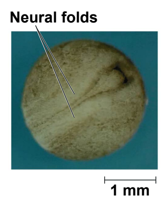
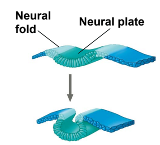
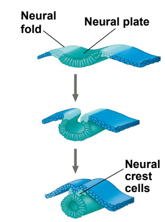


Figure 47.14b-1



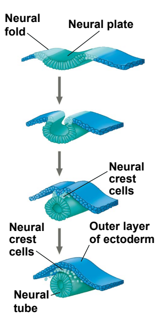
(b) Neural tube formation

Figure 47.14b-2



(b) Neural tube formation

Figure 47.14b-3

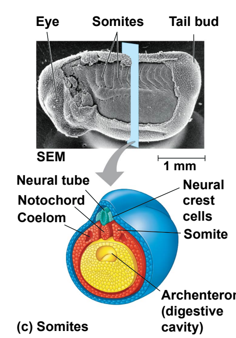


(b) Neural tube formation

Cell Migration in Organogenesis

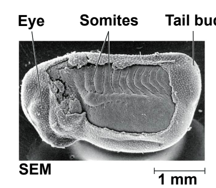
- **Neural crest cells** develop along the neural tube of vertebrates and migrate in the body, eventually forming various parts of the embryo (nerves, parts of teeth, skull bones, and so on)
- Mesoderm lateral to the notochord forms blocks called **somites**
- Parts of the somites dissociate to form mesenchyme cells, which migrate individually to new locations

Figure 47.14c

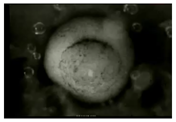


(c) Somites

Figure 47.14ca



Video: Frog Embryo Development



Organogenesis in Chick and Insects

- Early organogenesis in the chick is quite similar to that in the frog
- By the time the embryo is 3 days old, rudiments of the major organs are readily apparent
- Organogenesis in invertebrates is different, since invertebrate body plans diverge significantly from those of vertebrates
- The mechanisms of organogenesis—for example neurulation—are quite similar, however

Figure 47.15

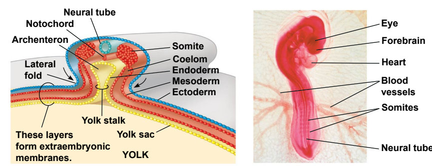
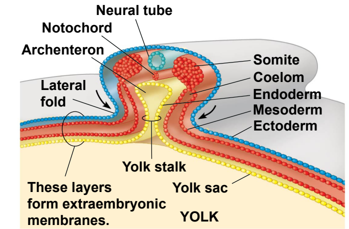
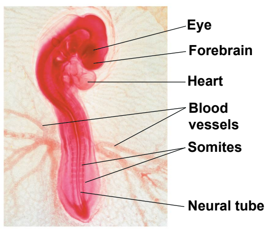


Figure 47.15a



(a) Early organogenesis

Figure 47.15b



(b) Late organogenesis

Mechanisms of Morphogenesis

- Morphogenesis in animals but not plants involves movement of cells
- In animals, movements of parts of a cell can bring about cell shape changes, or can enable a cell to migrate to a new location
- The microtubules and microfilaments of the cytoskeleton are essential to these events

The Cytoskeleton in Morphogenesis

- Reorganization of the cytoskeleton is a major force in changing cell shape during development
- For example, in neurulation, microtubules oriented from dorsal to ventral in a sheet of ectodermal cells help lengthen the cells along that axis

Figure 47.16-1

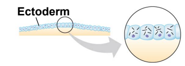


Figure 47.16-2

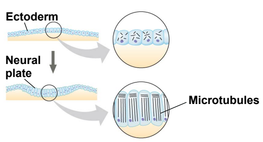


Figure 47.16-3

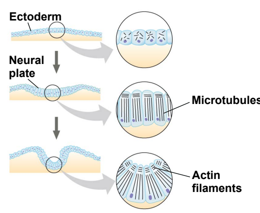


Figure 47.16-4

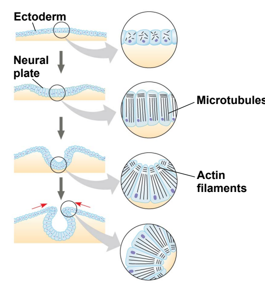
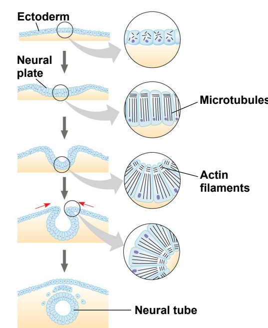
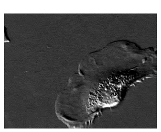


Figure 47.16-5

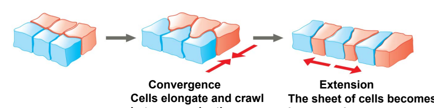


Video: Lamellipodia in Cell Migration



- The cytoskeleton also directs **convergent extension**, a morphogenetic movement in which a sheet of cells undergoes rearrangement to form a longer and narrower shape
- Cells elongate and wedge between each other to form fewer columns of cells

Figure 47.17



- The cytoskeleton also is responsible for cell migration
- Transmembrane glycoproteins called cell adhesion molecules play a key role in migration
- Migration also involves the extracellular matrix, a meshwork of secreted glycoproteins and other molecules lying outside the plasma membrane of cells

Programmed Cell Death

- Programmed cell death is also called **apoptosis**
- At various times during development, individual cells, sets of cells, or whole tissues stop developing and are engulfed by neighboring cells
- For example, many more neurons are produced in developing embryos than will be needed
- Extra neurons are removed by apoptosis

- In some cases a structure functions in early stages and is eliminated during later development
- For example, the tail of the tadpole undergoes apoptosis during frog metamorphosis

Concept 47.3: Cytoplasmic determinants and inductive signals contribute to cell fate specification

- **Determination** is the term used to describe the process by which a cell or group of cells becomes committed to a particular fate
- **Differentiation** refers to the resulting specialization in structure and function

- Cells in a multicellular organism share the same genome
- Differences in cell types are the result of the expression of different sets of genes

Fate Mapping

- **Fate maps** are diagrams showing organs and other structures that arise from each region of an embryo
- Classic studies using frogs indicated that cell lineage in germ layers is traceable to blastula cells

Figure 47.18

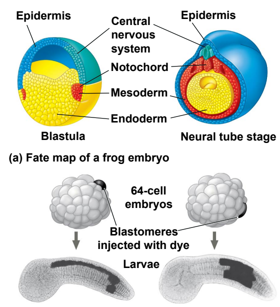
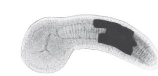


Figure 47.18a

Figure 47.18b



- Later studies of *C. elegans* used the ablation (destruction) of single cells to determine the structures that normally arise from each cell
- The researchers were able to determine the lineage of each of the 959 somatic cells in the worm

Figure 47.19

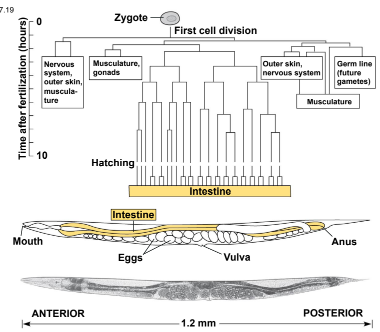
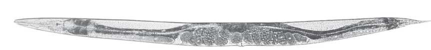
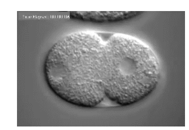


Figure 47.19a

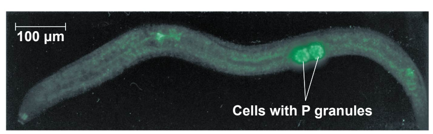


Video: *C. elegans* Embryo Development (Time Lapse)



- Germ cells are the specialized cells that give rise to sperm or eggs
- Complexes of RNA and protein are involved in the specification of germ cell fate
- In *C. elegans*, such complexes are called P granules, persist throughout development, and can be detected in germ cells of the adult worm

Figure 47.20



- P granules are distributed throughout the newly fertilized egg and move to the posterior end before the first cleavage division
- With each subsequent cleavage, the P granules are partitioned into the posterior-most cells
- P granules act as cytoplasmic determinants, fixing germ cell fate at the earliest stage of development

Figure 47.21

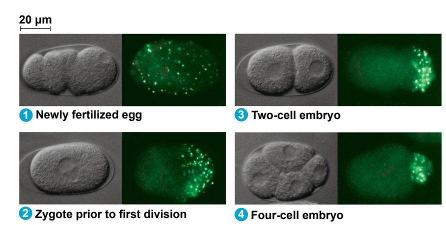
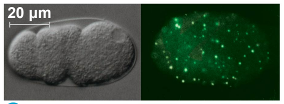
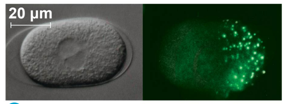


Figure 47.21a



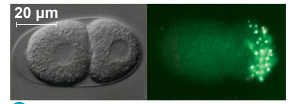
1 Newly fertilized egg

Figure 47.21b



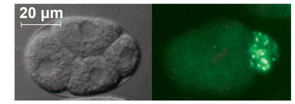
2 Zygote prior to first division

Figure 47.21c



3 Two-cell embryo

Figure 47.21d



4 Four-cell embryo

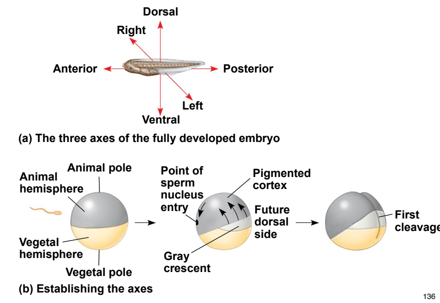
Axis Formation

- A body plan with bilateral symmetry is found across a range of animals
- This body plan exhibits asymmetry across the dorsal-ventral and anterior-posterior axes
- The right-left axis is largely symmetrical

- The anterior-posterior axis of the frog embryo is determined during oogenesis
- The animal-vegetal asymmetry indicates where the anterior-posterior axis forms
- The dorsal-ventral axis is not determined until fertilization

- Upon fusion of the egg and sperm, the egg surface rotates with respect to the inner cytoplasm
- This cortical rotation brings molecules from one portion of the vegetal cortex to interact with molecules in the inner cytoplasm of the animal hemisphere
- This leads to expression of dorsal- and ventral-specific gene expression

Figure 47.22



- In chicks, gravity is involved in establishing the anterior-posterior axis
- Later, pH differences between the two sides of the blastoderm establish the dorsal-ventral axis
- In mammals, experiments suggest that orientation of the egg and sperm nuclei before fusion may help establish embryonic axes
- In insects, morphogen gradients establish the anterior-posterior and dorsal-ventral axes

Restricting Developmental Potential

- Hans Spemann performed experiments to determine a cell's developmental potential (range of structures to which it can give rise)
- The first two blastomeres of the frog embryo are **totipotent** (can develop into all the possible cell types)

Figure 47.23-1

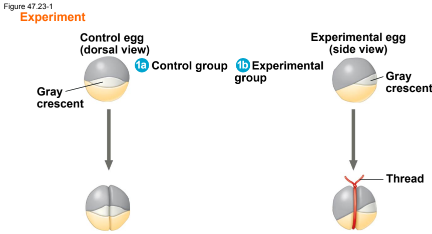
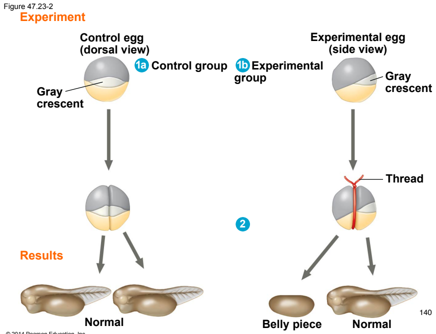


Figure 47.23-2



- In mammals, embryonic cells remain totipotent until the eight-cell stage, much longer than other organisms
- Progressive restriction of developmental potential is a general feature of development in all animals
- In general tissue-specific fates of cells are fixed by the late gastrula stage

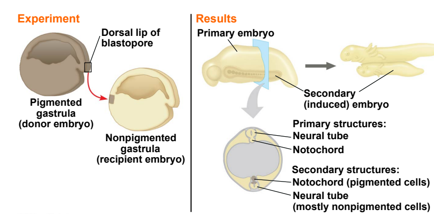
Cell Fate Determination and Pattern Formation by Inductive Signals

- As embryonic cells acquire distinct fates, they influence each other's fates by induction

The "Organizer" of Spemann and Mangold

- Spemann and Mangold transplanted tissues between early gastrulas and found that the transplanted dorsal lip of the blastopore triggered a second gastrulation in the host
- The dorsal lip functions as an organizer of the embryo body plan, inducing changes in surrounding tissues to form notochord, neural tube, and so on

Figure 47.24

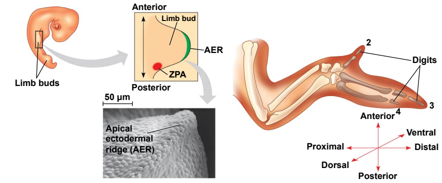


Formation of the Vertebrate Limb

- Inductive signals play a major role in **pattern formation**, development of spatial organization
- The molecular cues that control pattern formation are called **positional information**
- This information tells a cell where it is with respect to the body axes
- It determines how the cell and its descendants respond to future molecular signals

- The wings and legs of chicks, like all vertebrate limbs, begin as bumps of tissue called limb buds
- The embryonic cells in a limb bud respond to positional information indicating location along three axes
  - Proximal-distal axis
  - Anterior-posterior axis
  - Dorsal-ventral axis

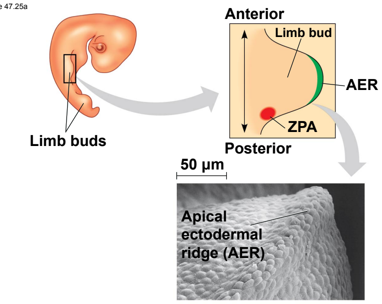
Figure 47.25



(a) Organizer regions

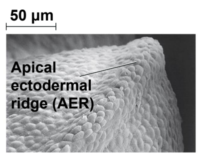
(b) Wing of chick embryo

Figure 47.25a



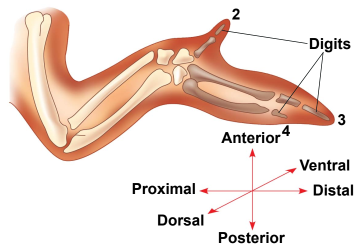
(a) Organizer regions

Figure 47.25aa



(a) Organizer regions

Figure 47.25b



(b) Wing of chick embryo

- One limb bud–regulating region is the **apical ectodermal ridge (AER)**
- The AER is thickened ectoderm at the bud's tip
- The second region is the **zone of polarizing activity (ZPA)**
- The ZPA is mesodermal tissue under the ectoderm where the posterior side of the bud is attached to the body

- The ZPA influences development by secreting a protein signal called Sonic hedgehog
- Implanting cells expressing Sonic hedgehog into the anterior of a normal limb bud results in a mirror image limb
- The same results are obtained when a ZPA is grafted there

Figure 47.26

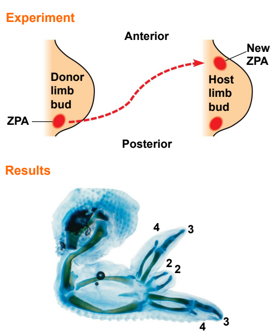
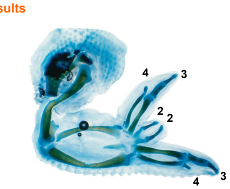


Figure 47.26a

Results



Cilia and Cell Fate

- Ciliary function is essential for proper specification of cell fate in the human embryo
- Motile cilia play roles in left-right specification
- Monocilia (nonmotile cilia) play roles in normal kidney development

- Insight into the role of motile cilia in development comes from identification of Kartagener's syndrome, a set of medical conditions that often appear together
- These include immotile sperm, infections of nasal sinuses and bronchi, and situs inversus, a reversal of normal left-right asymmetry
- All of the associated conditions result from a defect that makes cilia immotile

Figure 47.27

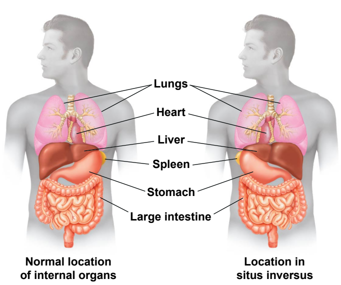
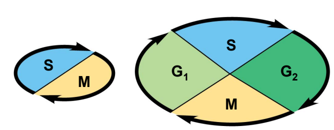


Figure 47.UN01a

	Nucleic Acid Synthesis (on scale of 0–100)										
DNA Toxin added	35	48	54	71	83	85	88	87	100	96	
DNA No toxin	10	24	28	31	47	49	49	53	55	55	55
RNA Toxin added			0		6		25	27		33	
RNA No toxin			0		3		14	22		27	
Time Point (every 35 min)	1	2	3	4	5	6	7	8	9	10	11

Figure 47.UN01b



Cell cycle during cleavage stage

Cell cycle after cleavage stage

Figure 47.UN02

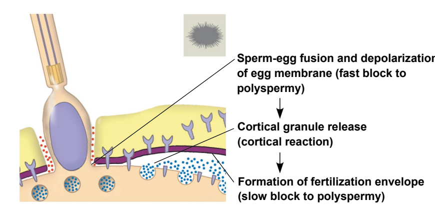


Figure 47.UN03

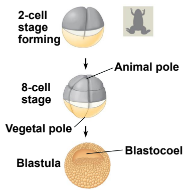


Figure 47.UN04

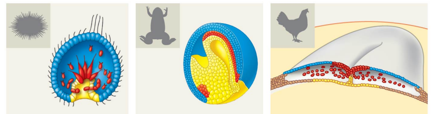


Figure 47.UN05

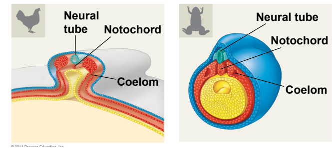


Figure 47.UN06

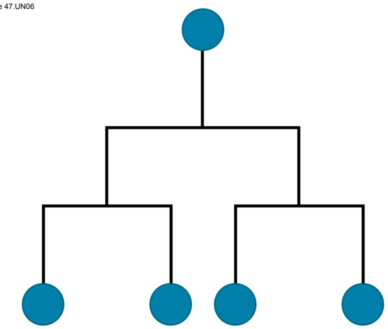


Figure 47.UN07