Animal Development

Chapter 47

- Objectives
  - Describe the acrosomal reaction
  - Describe the cortical reaction
  - Distinguish among meroblastic cleavage and holoblastic cleavage
  - Compare the formation of a blastula and gastrulation in a sea urchin, a frog, and a chick
  - List and explain the functions of the extraembryonic membranes
  - Describe the process of convergent extension
  - Describe the role of the extracellular matrix in embryonic development

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- Describe two general principles that integrate our knowledge of the genetic and cellular mechanisms underlying differentiation
- Explain the significance of Spemann's organizer in amphibian development
- Explain pattern formation in a developing chick limb, including the roles of the apical ectodermal ridge and the zone of polarizing activity

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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

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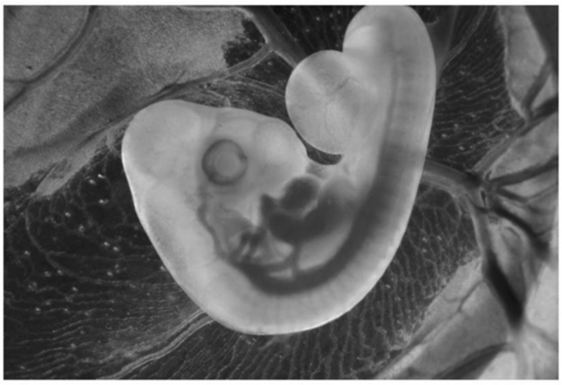

- The question of how a zygote becomes an animal has been asked for centuries
- As recently as the 18th century the prevailing theory was a notion called preformation
  - Preformation is the idea that the egg or sperm contains an embryo, a preformed miniature infant, or "homunculus," that simply becomes larger during development

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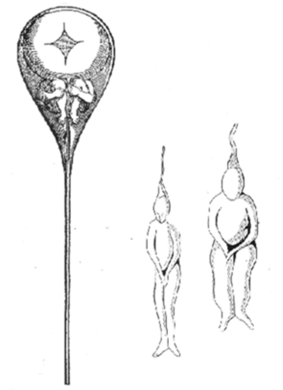

- The alternative view was epigenesis
  - Embryonic form emerges gradually from formless egg
    - First proposed by Aristotle
  - Microscopy confirmed that developing embryos developed in a stepwise fashion
- Preformation may have merit
  - The developmental plan in many species is in place in the egg

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- Development is determined by the zygote's genome and molecules in the egg called cytoplasmic determinants
  - Cell differentiation is the specialization of cells in their structure and function
  - Morphogenesis is the process by which an animal takes shape

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- Model organisms are species that are representative of a larger group and easily studied, for example, *Drosophila* and *Caenorhabditis elegans*
  - Classic embryological studies have focused on the sea urchin, frog, chick, and the nematode *C. elegans*

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The Four Stages of Development

- Important events regulating development occur during fertilization and each of the three successive stages that build the animal's body
  - After fertilization embryonic development proceeds through three stages:
    - Cleavage: cell division creates a hollow ball of cells called a blastula
    - Gastrulation: cells are rearranged into a three-layered gastrula
    - Organogenesis: the three layers interact and move to give rise to organs

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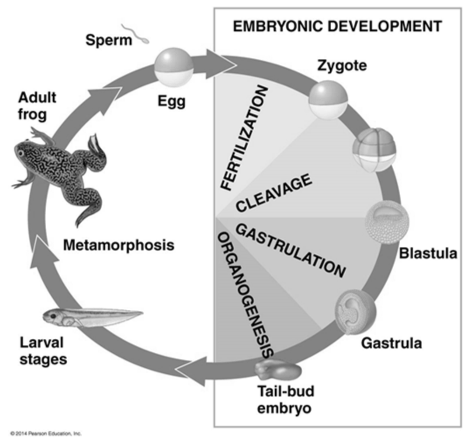

Fertilization

- 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

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The Acrosomal Reaction

- The acrosomal reaction is triggered when the sperm meets the egg
  - The acrosome releases hydrolytic enzymes that digest material surrounding the egg
- Gamete contact and/or fusion depolarizes the egg cell membrane and sets up a fast block to polyspermy

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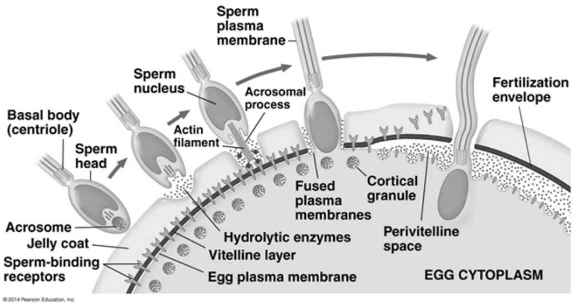

The Cortical Reaction

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

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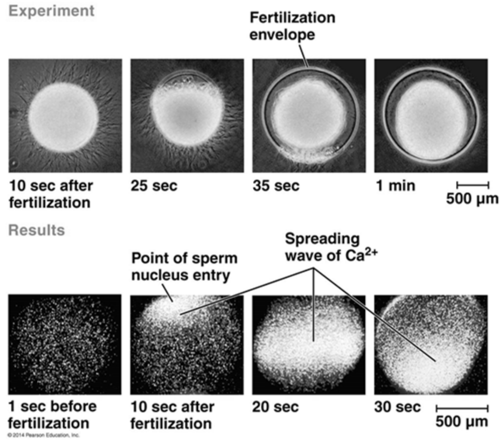

Activation of the Egg

- 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

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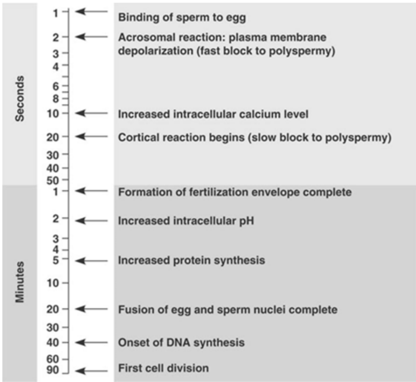

Fertilization in Mammals

- Fertilization in mammals and other terrestrial animals is internal
- In mammalian fertilization, the cortical reaction modifies the zona pellucida as a slow block to polyspermy

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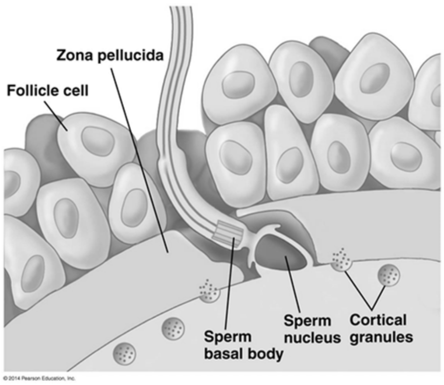

- In mammals the first cell division occurs 12–36 hours after sperm binding
- The diploid nucleus forms after this first division of the zygote

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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

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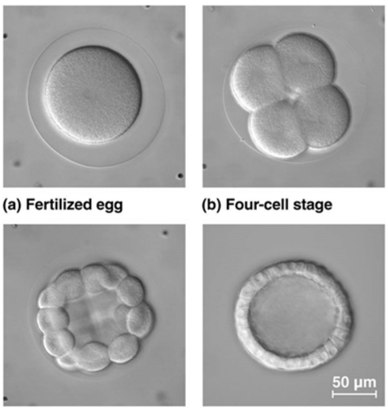

(a) Fertilized egg (b) Four-cell stage (c) Early blastula (d) Later blastula

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

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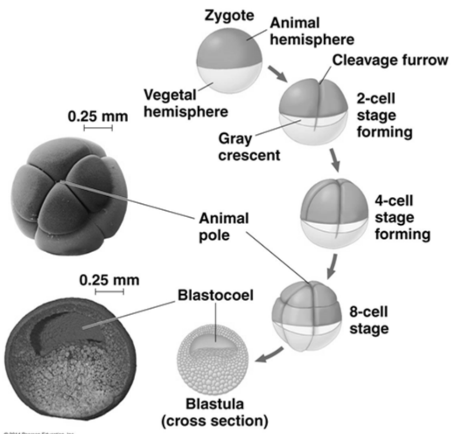

- Cell division is slowed by yolk
- Meroblastic cleavage, incomplete division of the egg, occurs in species with yolk-rich eggs, such as reptiles and birds
- Holoblastic cleavage, the complete division of the egg, occurs in species whose eggs have little or moderate amounts of yolk, such as sea urchins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

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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

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- 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

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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**

- Gastrulation in a sea urchin:
  - The blastula consists of a single layer of cells surrounding the blastocoel
  - Mesenchyme cells migrate from the vegetal pole into the blastocoel
  - The vegetal plate forms from the remaining cells of the vegetal pole and buckles inward through invagination
  - The newly formed cavity is called the archenteron
    - This opens through the blastopore, which will become the anus

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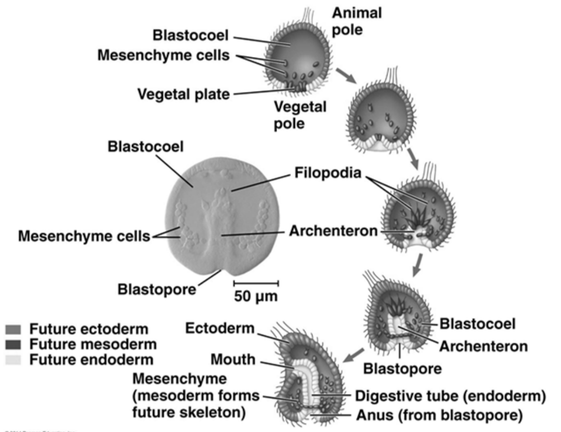

- Gastrulation in the frog
  - The frog blastula is many cell layers thick
  - Cells of the dorsal lip originate in the gray crescent and invaginate to create the archenteron
  - Cells continue to move from the embryo surface into the embryo by involution
    - These cells become the endoderm and mesoderm
  - The blastopore encircles a yolk plug when gastrulation is completed

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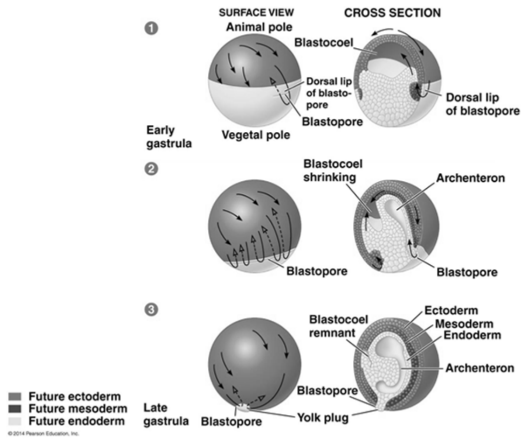
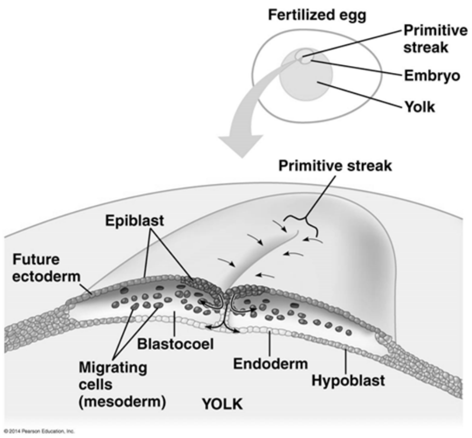
– The surface of the embryo is now ectoderm, the innermost layer is endoderm, and the middle layer is mesoderm



- Gastrulation in the chick
  - The embryo forms from a blastoderm and sits on top of a large yolk mass
  - During gastrulation, the upper layer of the blastoderm (epiblast) moves toward the midline of the blastoderm and then into the embryo toward the yolk
  - The midline thickens and is called the primitive streak
  - The movement of different epiblast cells gives rise to the endoderm, mesoderm, and ectoderm



Mammalian Development

- The eggs of placental mammals:
  - Are small and store few nutrients
  - Exhibit holoblastic cleavage
  - Show no obvious polarity
- Gastrulation resembles the processes in birds and other reptiles
- Early embryonic development in a human proceeds through four stages

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- 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 and the extraembryonic membranes begin to form

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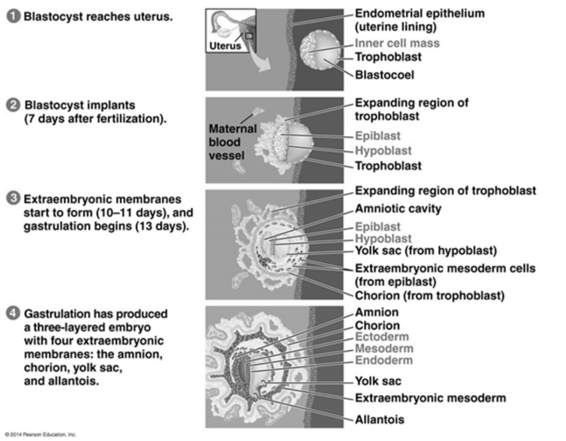

- By the end of gastrulation the embryonic germ layers have formed
- The extraembryonic membranes in mammals are homologous to those of birds and other reptiles and have similar functions

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
  - 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

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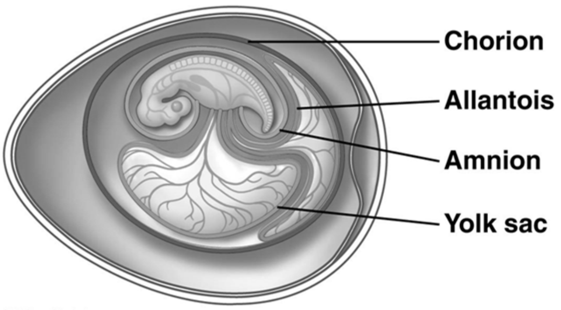

Organogenesis

- Various regions of the three embryonic germ layers develop into the rudiments of organs during the process of organogenesis
  - The frog is used as a model for organogenesis

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- Early in vertebrate organogenesis the notochord forms from mesoderm and the neural plate forms from ectoderm
  - The neural plate soon curves inward forming the neural tube
  - Mesoderm lateral to the notochord forms blocks called somites
  - Lateral to the somites the mesoderm splits to form the coelom

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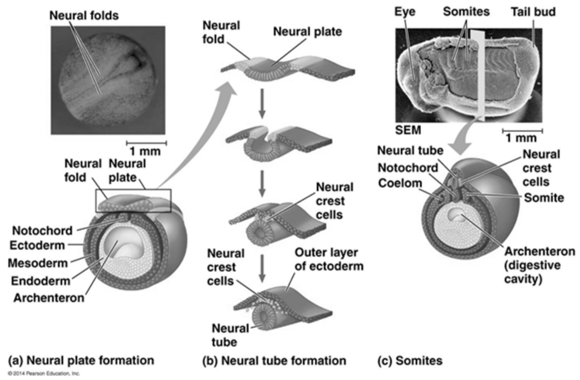

- Organogenesis in the chick is quite similar to that in the frog

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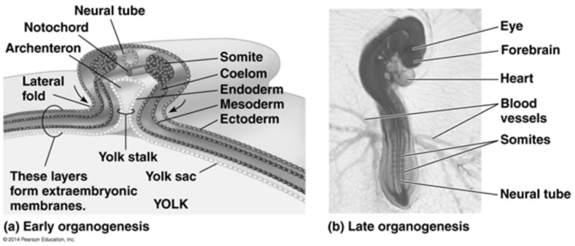

(a) Early organogenesis (b) Late organogenesis

- The mechanisms of organogenesis in invertebrates are similar, but the body plan is very different
- Many different structures are derived from the three embryonic germ layers during organogenesis

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Morphogenesis and Development

- 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

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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

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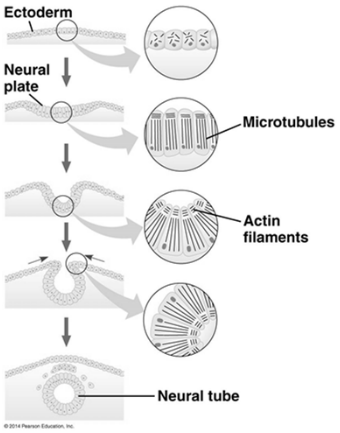

- The cytoskeleton also drives cell migration, or cell crawling the active movement of cells from one place to another
- In gastrulation, tissue invagination is caused by changes in both cell shape and cell migration
- Cell crawling is also involved in convergent extension a type of morphogenetic movement in which the cells of a tissue become narrower and longer

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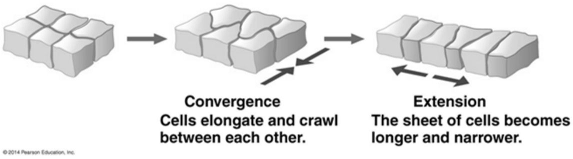

Roles of the Extracellular Matrix and Cell Adhesion Molecules

- 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

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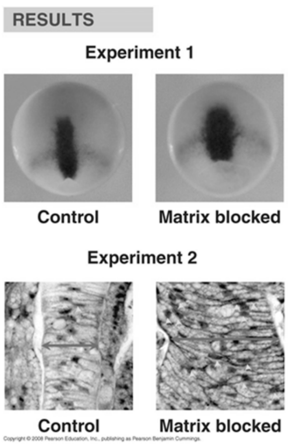

- Cell adhesion molecules also contribute to cell migration and stable tissue structure
  - One important class of cell-to-cell adhesion molecule is the cadherins which are important in the formation of the frog blastula

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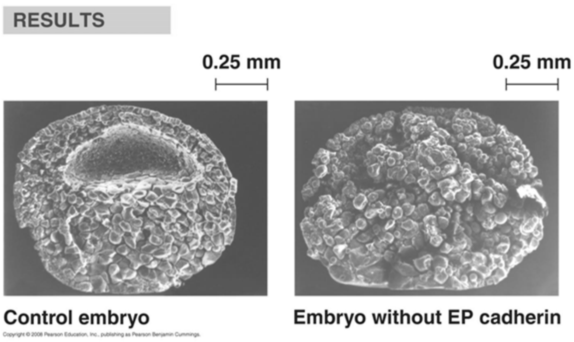

The Developmental Fate of Cells

- The developmental fate of cells depends on their history and on inductive signals
  - Cells in a multicellular organism share the same genome
  - Differences in cell types is the result of:
    - Determination – the process by which a group of cells become committed to a particular fate
    - Differentiation – the resulting specialization in structure and function that is the product of the expression of different genes

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- 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

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- First, during early cleavage divisions embryonic cells must somehow become different from one another
  - If the egg's cytoplasm is heterogenous, dividing cells vary in the cytoplasmic determinants they contain

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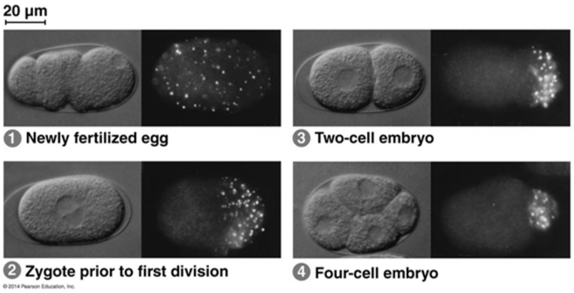

• Second, once initial cell asymmetries are set up subsequent interactions among the embryonic cells influence their fate, usually by causing changes in gene expression
  – This mechanism is called induction, and is mediated by diffusible chemicals or cell-cell interactions

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

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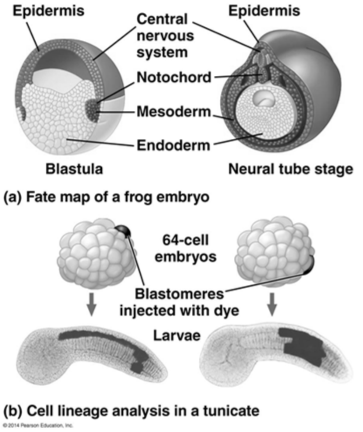
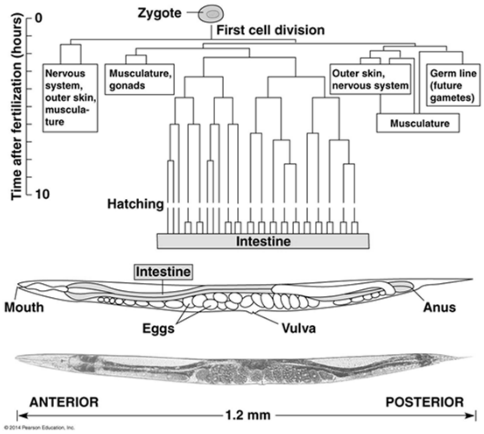


(a) Fate map of a frog embryo
(b) Cell lineage analysis in a tunicate



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
  - 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

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- The development of body axes in frogs is influenced by the polarity of the egg
  - The three body axes are established by the egg's polarity and by a cortical rotation following binding of the sperm
    - Cortical rotation exposes a gray crescent opposite to the point of sperm entry

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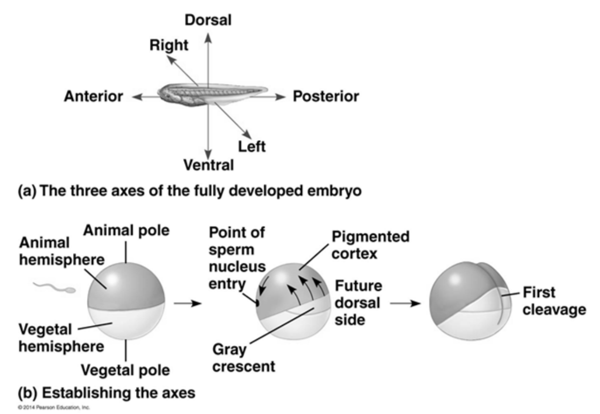

Restriction of Cellular Potency

- 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
  - This sets up differences in blastomeres resulting from cleavage

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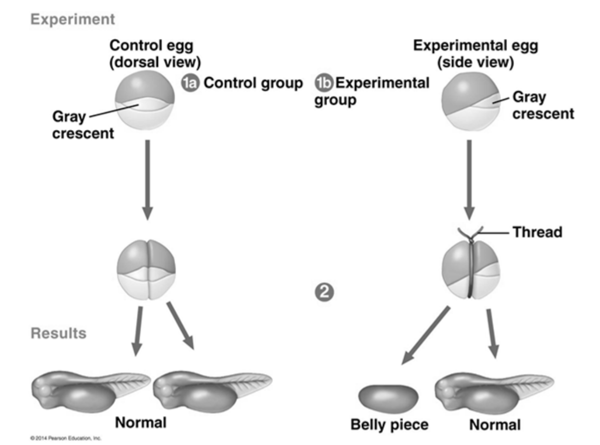

- As embryonic development proceeds the potency of cells becomes progressively more limited in all species

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Cell Fate Determination and Pattern Formation

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

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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

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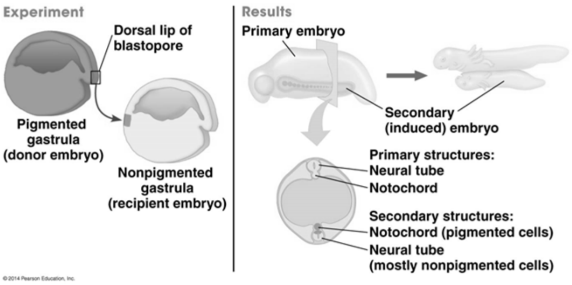
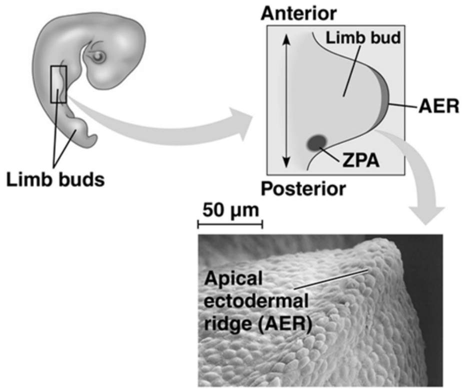


Formation of the Vertebrate Limb

- 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
  - This determines 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

- The embryonic cells within a limb bud respond to positional information indicating location along three axes
  - Proximal-distal axis
  - Anterior-posterior axis
  - Dorsal-ventral axis

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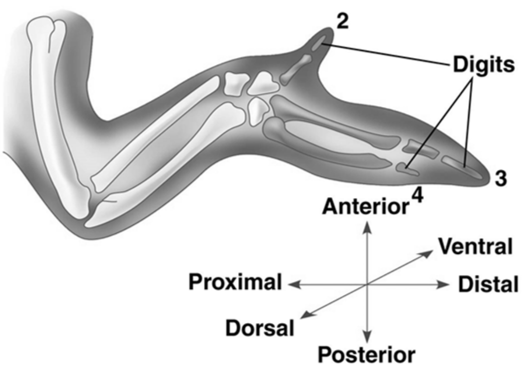

(b) Wing of chick embryo

- 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

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- Tissue transplantation experiments support the hypothesis that the ZPA produces some sort of inductive signal that conveys positional information indicating “posterior”

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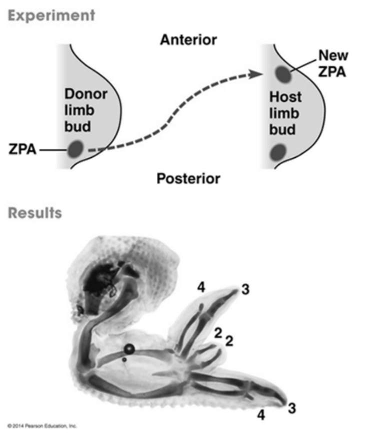

- Signal molecules produced by inducing cells influence gene expression in the cells that receive them
  - These signals lead to differentiation and the development of particular structures
- *Hox* genes also play roles during limb pattern formation

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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

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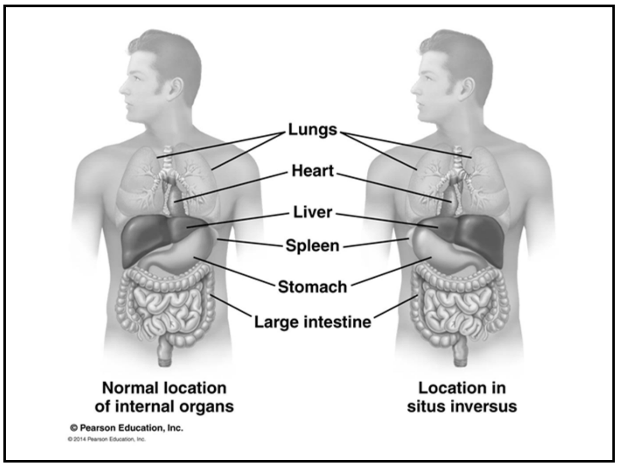
Lungs
Heart
Liver
Spleen
Stomach
Large intestine
Normal location of internal organs
Location in situs inversus
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