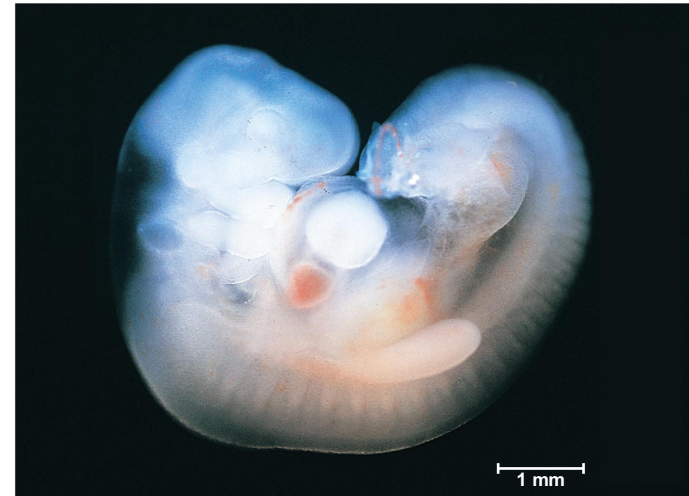


## Overview: A Body-Building Plan

- It is difficult to imagine that each of us began life as a single cell (**fertilized egg**) called a **zygote**.
- A human embryo at about 6–8 weeks after conception shows development of distinctive features.

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## How did this complex embryo develop from a single fertilized egg?



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- Development is determined by the zygote's genome and molecules in the egg cytoplasm called **Cytoplasmic determinants**.
- **Cell differentiation** is the specialization of cells in structure and function.
- **Morphogenesis** is the process by which an animal takes shape / form.
- **Model organisms** are species that are representative of a larger group and easily studied. Classic embryological studies use the sea urchin, frog, chick, and the nematode *C. elegans*.

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## After **fertilization**, embryonic development proceeds through **cleavage**, **gastrulation**, and **organogenesis**

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

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## Fertilization: sperm + egg = zygote $n + n = 2n$

- Fertilization brings the haploid nuclei of sperm and egg together, forming a diploid zygote.
- The sperm's contact with the egg's surface initiates metabolic reactions in the egg that trigger the onset of embryonic development:
  - Acrosomal Reaction
  - Cortical Reaction

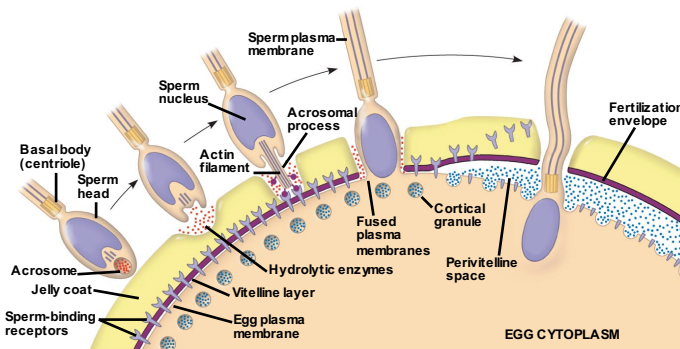
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## The Acrosomal Reaction

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

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## The acrosomal and cortical reactions during sea urchin fertilization



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## The Cortical Reaction

- Fusion of egg and sperm also initiates the **cortical reaction:**
- This reaction induces a **rise in  $Ca^{2+}$**  that stimulates **cortical granules** to release their contents outside the egg.
- These changes cause formation of a **fertilization envelope** that functions as a **slow block to polyspermy.**

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### Activation of the Egg

- The **sharp rise in  $Ca^{2+}$**  in the **egg's 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 sperm nucleus merges with the egg nucleus and cell division begins.

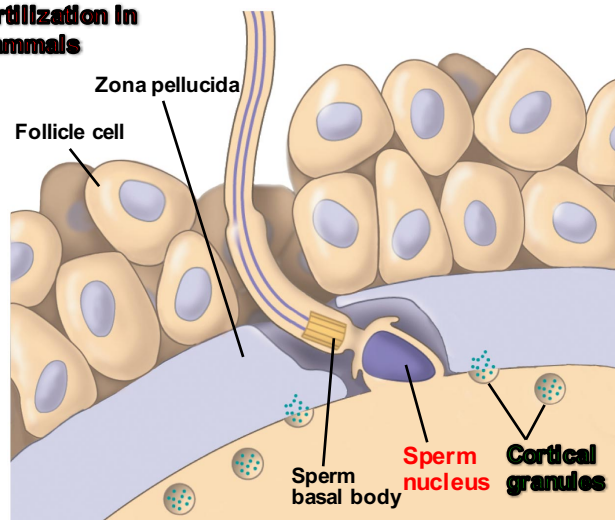
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### Fertilization in Mammals

- Fertilization in mammals and other terrestrial animals is internal.
- In mammalian fertilization, the cortical reaction modifies the **zona pellucida**, the **extracellular matrix** of the **egg**, as a **slow block to polyspermy**.
- 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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### Fertilization in mammals



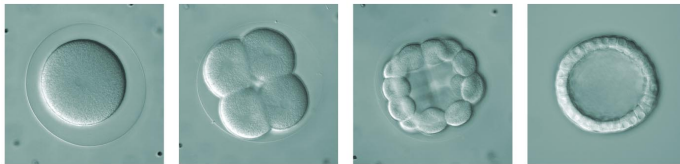
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### Cleavage = Rapid Mitosis / No Mass change

- 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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## Cleavage in an echinoderm embryo



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

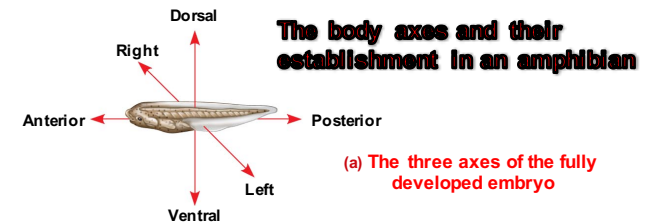
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- The **eggs** and **zygotes** of many animals, except mammals, have a definite polarity.
- The **polarity** is defined by distribution of **yolk** (stored nutrients).
- The **vegetal pole** has **more yolk**; the **animal pole** has less yolk.

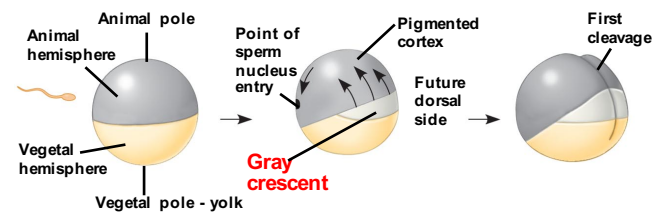
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- The three body axes are established by the egg's polarity and by a cortical rotation following binding of the sperm.
- Cortical rotation exposes a **gray crescent** opposite to the point of sperm entry.

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(a) The three axes of the fully developed embryo



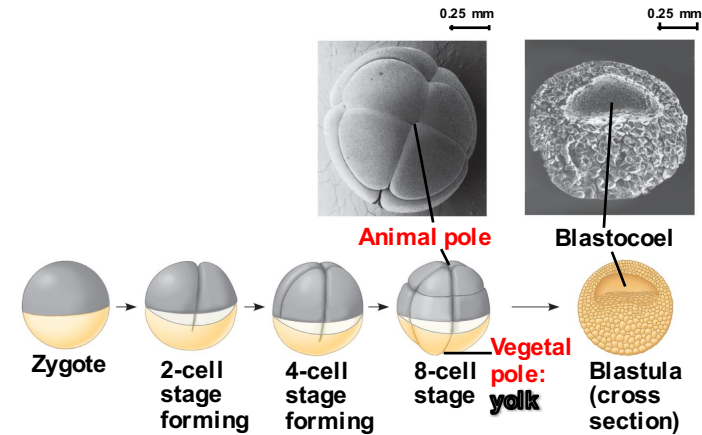
(b) Establishing the axes

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- Cleavage planes usually follow a pattern that is relative to the zygote's animal and vegetal poles.
- Cell division is slowed by yolk. *Yolk can cause uneven cell division at the poles.*
- **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.

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## Cleavage in a frog embryo



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## Gastrulation

- **Gastrulation** rearranges the cells of a blastula into a **three-layered embryo**, called a **gastrula**, which has a primitive gut.
- 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.

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## Gastrulation in the sea urchin embryo:

The blastula consists of a single layer of cells surrounding the blastocoel.

Mesenchyme cells migrate from the vegetal pole into the blastocoel.

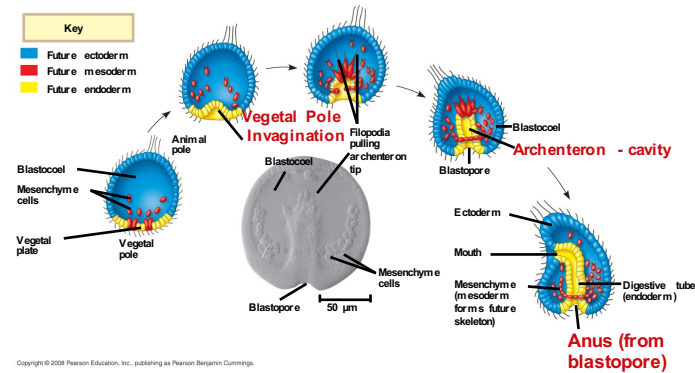
The **vegetal plate** forms from the remaining cells of the vegetal pole and buckles inward through **invagination**.

The newly formed **cavity** is called the **archenteron**.

This opens through the **blastopore**, which will become the **anus**.

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## Gastrulation in a sea urchin embryo



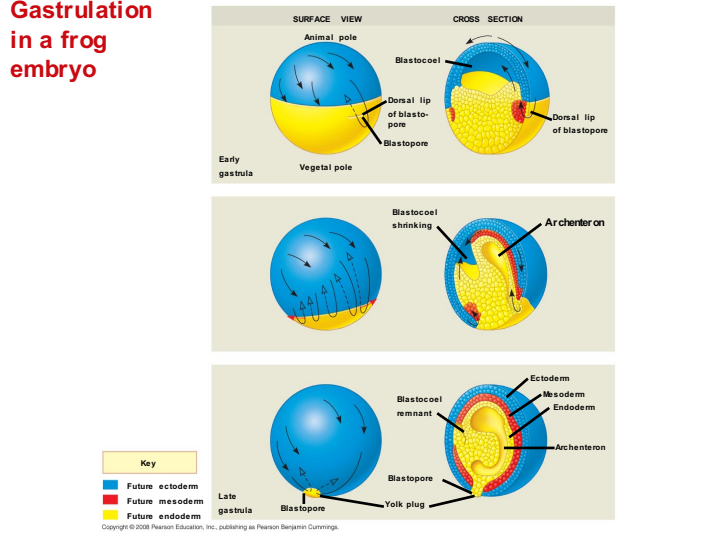
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## Gastrulation in the frog

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

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## Gastrulation in a frog embryo

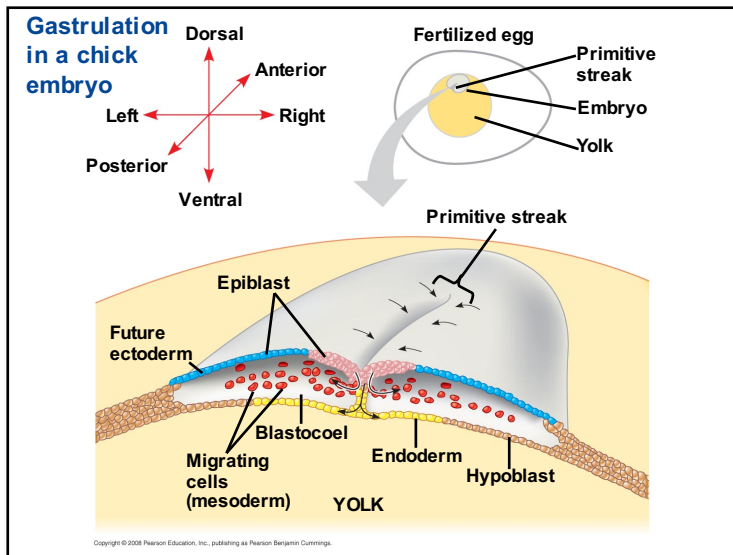


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## Gastrulation in the chick

- 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.

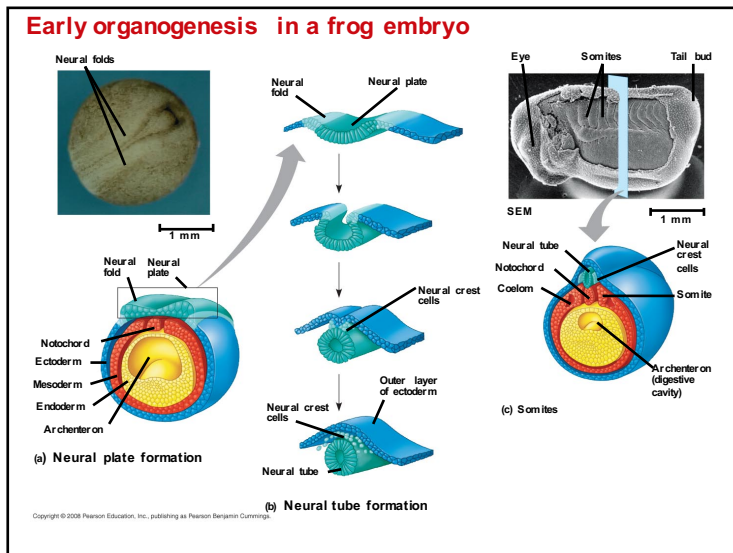
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## Organogenesis

- During **organogenesis**, various regions of the germ layers develop into rudimentary organs.
- The frog is used as a model for organogenesis.
- Early in vertebrate organogenesis, the **notochord** forms from mesoderm, and the **neural plate** forms from ectoderm.

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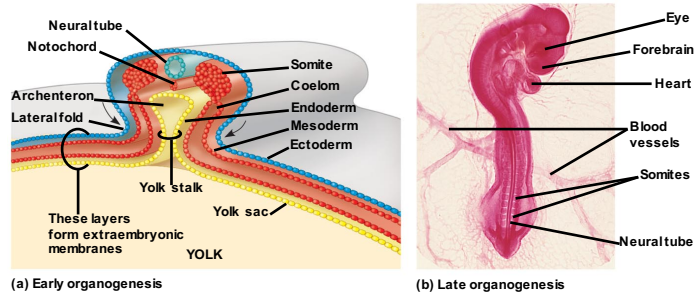


- The neural plate soon curves inward, forming the **neural tube**. The neural tube will become the central nervous system = brain and spinal cord.
- **Neural crest cells** develop along the neural tube of vertebrates and form various parts of the embryo: nerves, parts of teeth, skull bones ...
- Mesoderm 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 a chick embryo is similar to that in a frog



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### Adult derivatives of the three embryonic germ layers in vertebrates

ECTODERM	MESODERM	ENDODERM
<ul style="list-style-type: none"> <li>• Epidermis of skin and its derivatives (including sweat glands, hair follicles)</li> <li>• Epithelial lining of mouth and anus</li> <li>• Cornea and lens of eye</li> <li>• Nervous system</li> <li>• Sensory receptors in epidermis</li> <li>• Adrenal medulla</li> <li>• Tooth enamel</li> <li>• Epithelium of pineal and pituitary glands</li> </ul>	<ul style="list-style-type: none"> <li>• Notochord</li> <li>• Skeletal system</li> <li>• Muscular system</li> <li>• Muscular layer of stomach and intestine</li> <li>• Excretory system</li> <li>• Circulatory and lymphatic systems</li> <li>• Reproductive system (except germ cells)</li> <li>• Dermis of skin</li> <li>• Lining of body cavity</li> <li>• Adrenal cortex</li> </ul>	<ul style="list-style-type: none"> <li>• Epithelial lining of digestive tract</li> <li>• Epithelial lining of respiratory system</li> <li>• Lining of urethra, urinary bladder, and reproductive system</li> <li>• Liver</li> <li>• Pancreas</li> <li>• Thymus</li> <li>• Thyroid and parathyroid glands</li> </ul>

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### Developmental Adaptations of Amniotes

- **Embryos** of birds, other reptiles, and mammals develop in a **fluid-filled sac** in a shell or the uterus.
- Organisms with these adaptations are called **amniotes**.
- Amniotes develop **extra-embryonic membranes** to **support** the **embryo**.

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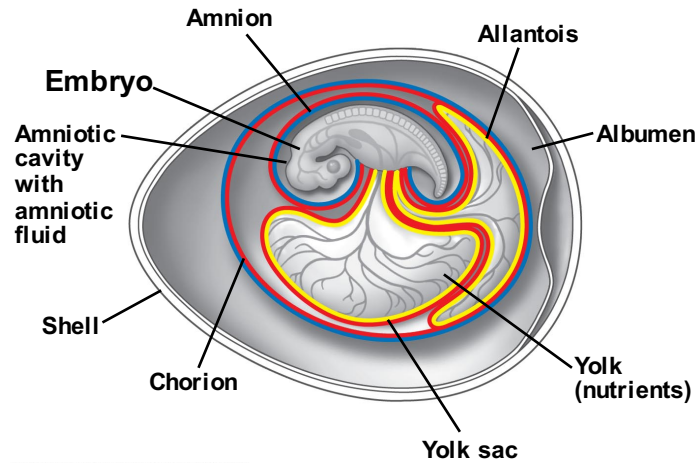
### Amniote ExtraEmbryonic Membranes

- During amniote development, four **extraembryonic membranes** form around the embryo:
  - The **chorion** *outermost membrane* / functions in gas exchange.
  - The **amnion** encloses the *amniotic fluid*.
  - The **yolk sac** encloses the yolk.
  - The **allantois** disposes of *nitrogenous waste* products and contributes to *gas exchange*.

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### ExtraEmbryonic Membranes In birds and other reptiles:



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### Mammalian Development

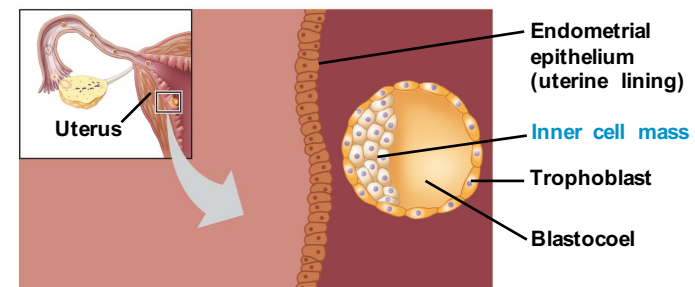
- The eggs of **placental mammals**
  - Are **small yolk** and store few nutrients
  - Exhibit **holoblastic cleavage**
  - Show **no obvious polarity**.
- Gastrulation and organogenesis resemble the processes in birds and other reptiles.
- Early cleavage is relatively slow in humans and other mammals.

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- At completion of **cleavage**, the **blastocyst** forms.
- A group of cells called the **inner cell mass** develops into the embryo and forms the extraembryonic membranes.
- The **trophoblast**, the outer epithelium of the blastocyst, initiates **implantation in the uterus**, and the inner cell mass of the blastocyst forms a flat disk of cells.
- As **implantation** is completed, **gastrulation** begins.

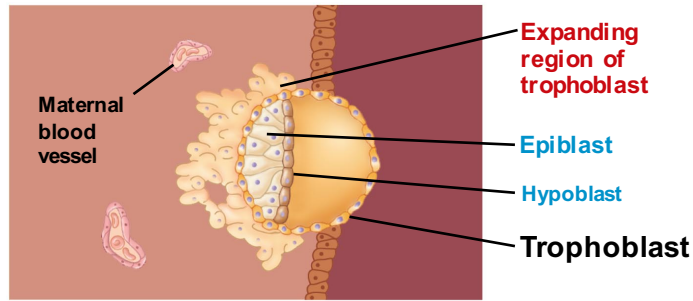
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### Early embryonic development of a human



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**Early embryonic development of a human**

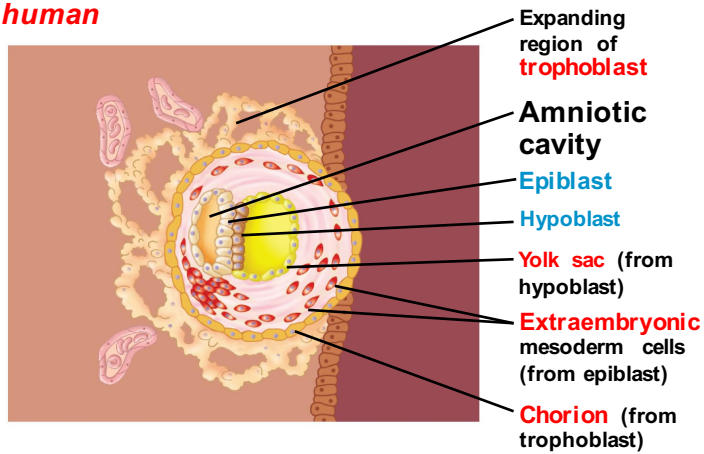


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- The epiblast cells **invaginate** through a primitive streak to form mesoderm and endoderm.
- The **placenta is formed** from the **trophoblast**, mesodermal cells from the epiblast, and adjacent endometrial tissue.
- The placenta allows for the exchange of materials between the mother and embryo.
- **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 develop in a similar way.

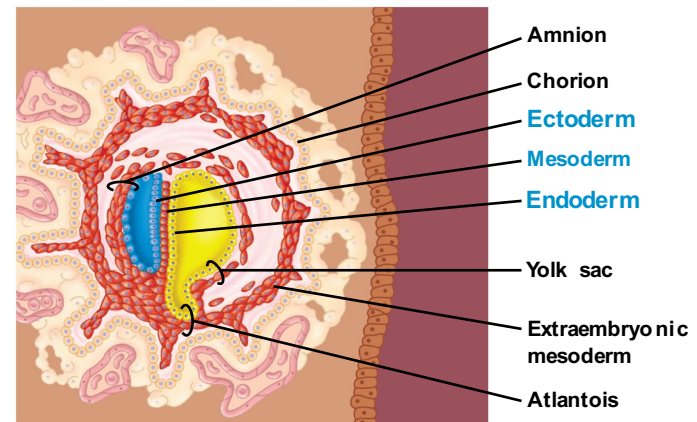
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**Early embryonic development of a human**



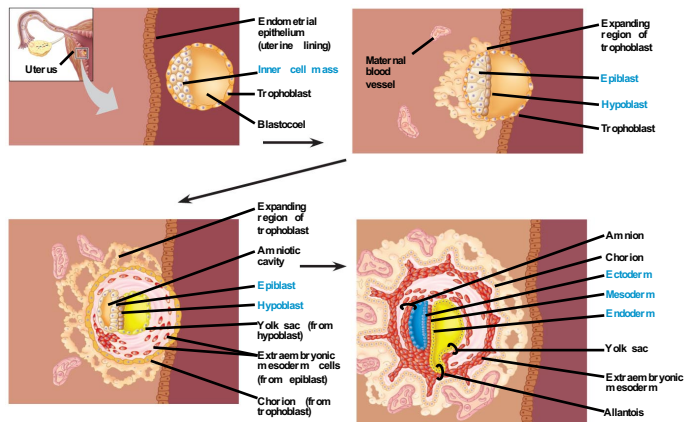
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**Early embryonic development of a human**



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### Four stages in early embryonic development of a human



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### Morphogenesis in animals involves specific changes in cell shape, position, and adhesion

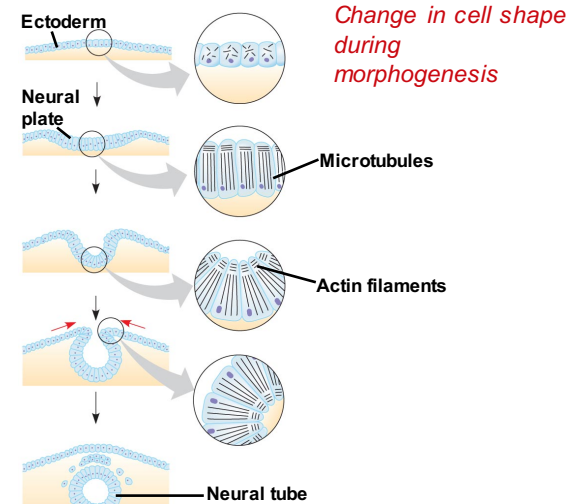
- Morphogenesis is a major aspect of development in plants and animals.
- *Only in animals does it involve the movement of cells.*

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### The Cytoskeleton, Cell Motility, and Convergent Extension

- Changes in cell shape usually involve reorganization of the cytoskeleton.
- Microtubules and microfilaments affect formation of the neural tube.

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

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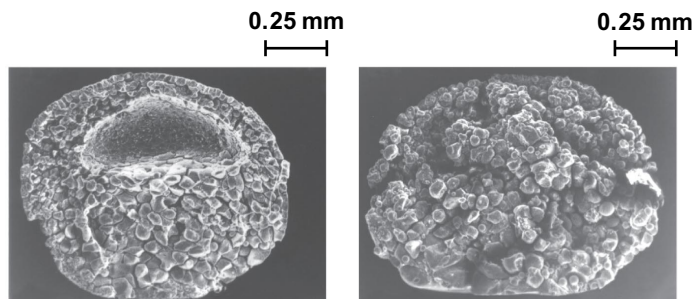
### Role of Cell Adhesion Molecules and the Extracellular Matrix

- **Cell adhesion molecules** located on cell surfaces contribute to cell migration and stable tissue structure.
- One class of cell-to-cell adhesion molecule is the **cadherins**, which are important in formation of the frog blastula.

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### *Cadherin is required for development of the blastula*

#### RESULTS



Control embryo

Embryo without EP cadherin

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### 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 differentiation, the expression of different genes = *differential gene expression*.

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## Two general principles underlie differentiation

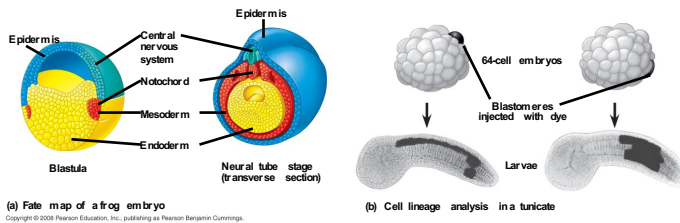
1. During early cleavage divisions, embryonic cells must become different from one another.
  - If the egg's cytoplasm is heterogenous, dividing cells vary in the **cytoplasmic determinants** they contain.
2. After cell asymmetries are set up, **interactions among embryonic cells influence** their fate, usually 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 maps** are general territorial diagrams of embryonic development.
- Classic studies using frogs indicated that cell lineage in germ layers is traceable to blastula cells.
- To understand how embryonic cells acquire their fates, think about how basic **axes** of the embryo are established.

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## Fate Mapping for two chordates



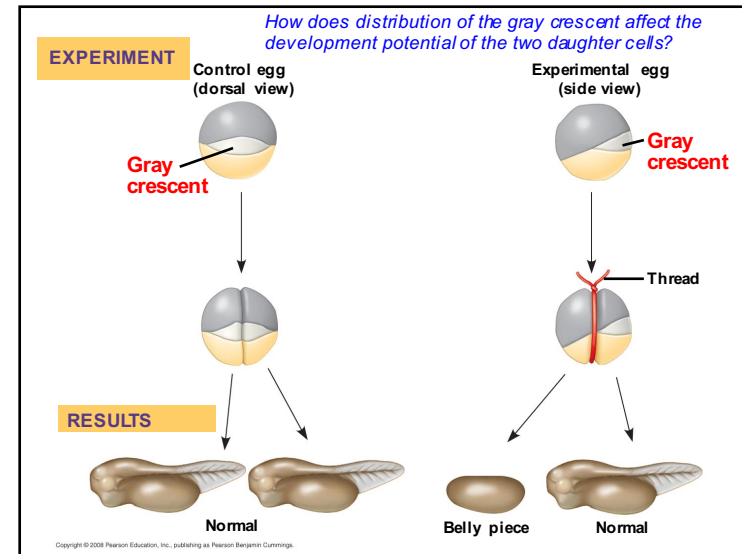
## The Axes of the Basic Body Plan

- 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 the body axes.
- In many species that have cytoplasmic determinants, only the zygote is **totipotent**.
- That is, only the zygote can develop into all the cell types in the adult.

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- Unevenly distributed **cytoplasmic determinants** in the egg cell help establish the body axes.
- These determinants set up differences in blastomeres resulting from cleavage.
- As embryonic development proceeds, potency of cells becomes more limited.
- After embryonic cell division creates cells that differ from each other, the cells begin to influence each other's fates **by induction signals**.

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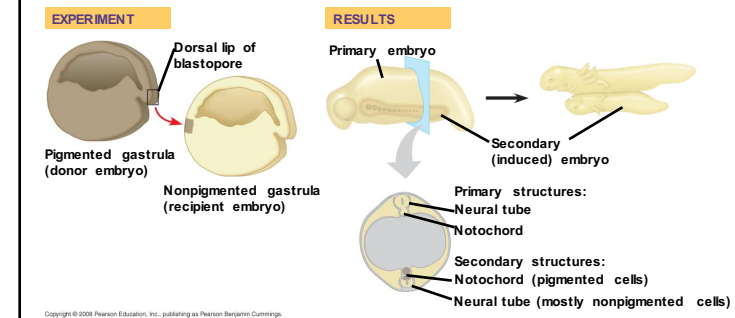


### The Dorsal Lip = “Organizer” of Spemann and Mangold

- Based on their famous experiment, Hans Spemann and Hilde Mangold concluded that the **blastopore’s dorsal lip** is an **organizer** of the **embryo**.
- The Spemann organizer **initiates inductions** that result in **formation of the notochord, neural tube, and other organs**.

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Can the **dorsal lip** of the blastopore **induce cells** in another part of the amphibian embryo to **change their developmental fate**?



## Formation of the Vertebrate Limb

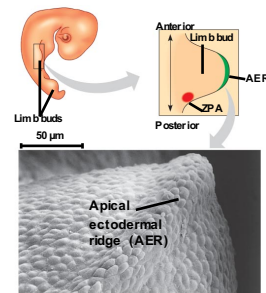
- Inductive signals play a major role in **pattern formation**, development of spatial organization.
- The molecular cues that control pattern formation are called **positional information**.
- This information tells a cell where it is with respect to the body axes.
- It determines how the cell and its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

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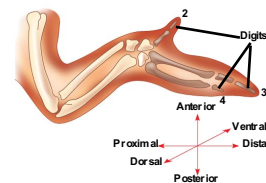
- The wings and legs of chicks, like all vertebrate limbs, begin as bumps of tissue called limb buds.
- The embryonic cells in a limb bud respond to positional information indicating location along three axes
  - Proximal-distal axis
  - Anterior-posterior axis
  - Dorsal-ventral axis

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## Vertebrate limb development



(a) Organizer regions



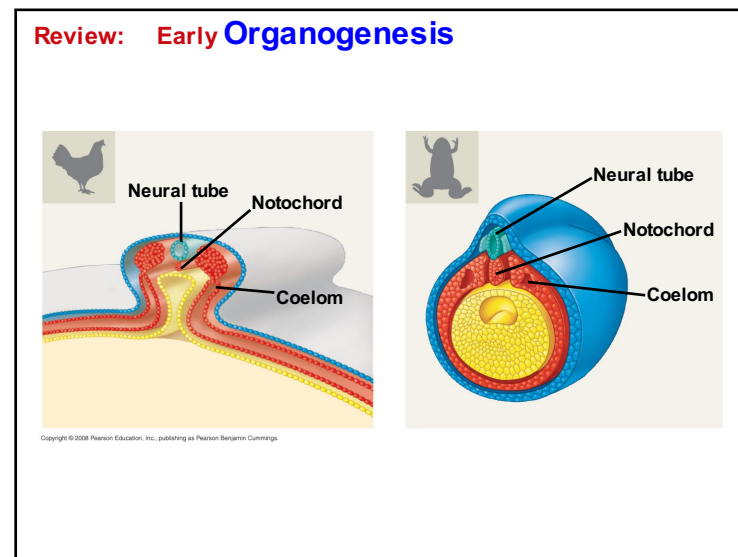
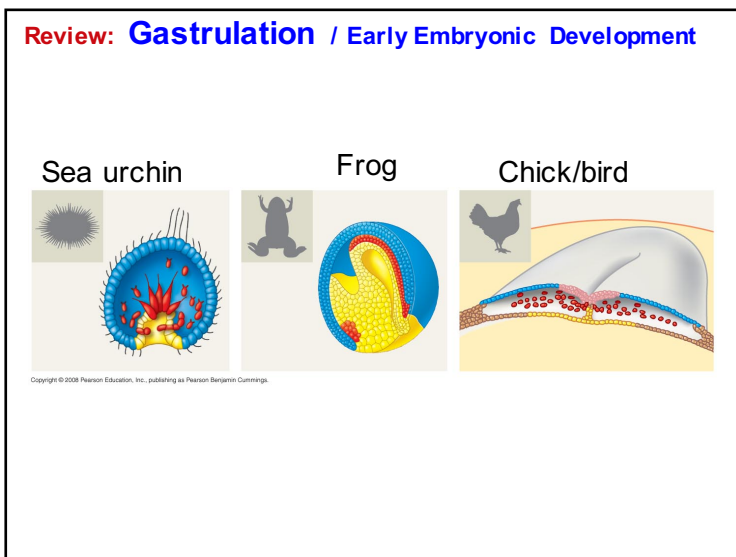
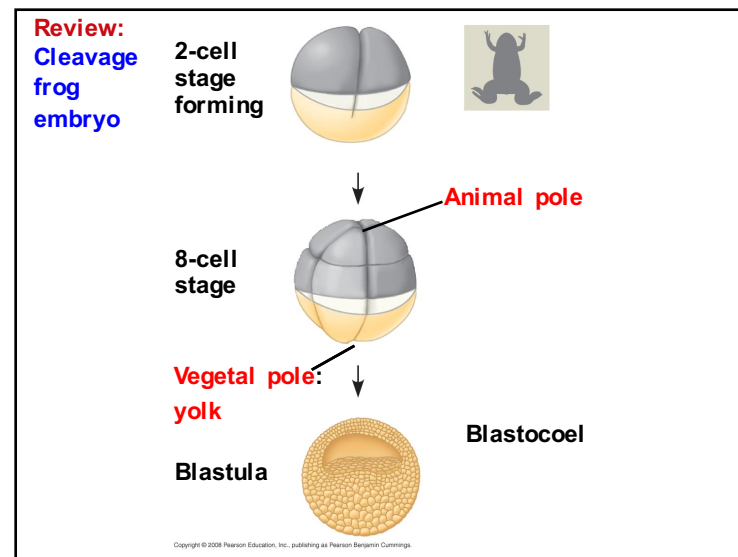
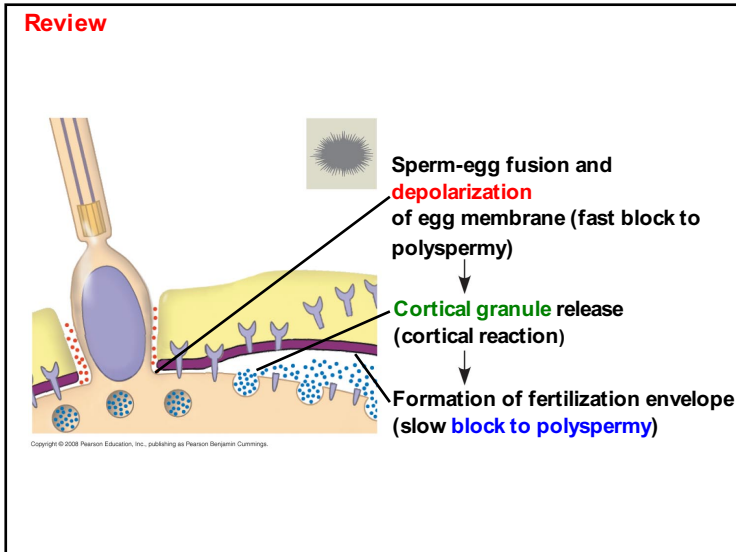
(b) Wing of chick embryo

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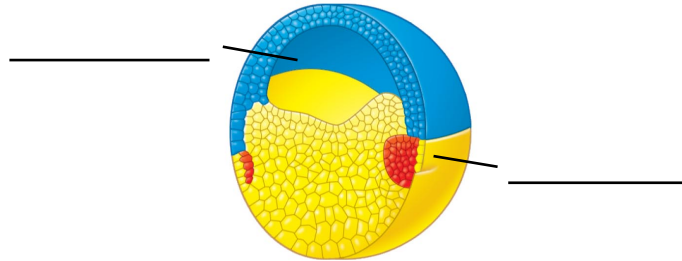
- **Signal molecules** produced by inducing cells **influence gene expression** in cells receiving them.
- Signal molecules **lead to differentiation** and the development of particular structures.
- **Hox genes** also play roles during **limb pattern formation**.

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Review: **Fate Map** of Frog Embryo



Species: \_\_\_\_\_

Stage: \_\_\_\_\_

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**You should now be able to:**

1. Describe the acrosomal reaction.
2. Describe the cortical reaction.
3. Distinguish among meroblastic cleavage and holoblastic cleavage.
4. Compare the formation of a blastula and gastrulation in a sea urchin, a frog, and a chick.
5. List and explain the functions of the extraembryonic membranes.

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6. Describe the role of the extracellular matrix in embryonic development.
7. Describe two general principles that integrate our knowledge of the genetic and cellular mechanisms underlying differentiation.
8. Explain the significance of Spemann's organizer in amphibian development.
9. Explain pattern formation in a developing chick limb.

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