Animals develop throughout their lifetime. Development begins with changes that form a complete animal from a zygote and continue as progressive changes in form and function occur throughout life.

I. Early view of development

A. Preformation

1. the embryo contains all of its descendants as a series of successively smaller embryos within embryos-like nesting dolls

2. dissecting an egg, one would find smaller and smaller embryos as the dissection continued

- 3. popular in 18th century
- **B.** Epigenesis
 - 1. an embryo forms gradually from a formless egg

2. originally proposed by Aristotle

- 3. gained support in 19th century as improved microscopy permitted
- biologists to view embryos as they developed

II. Processes involved in Embryonic Development

- A. Cell division-increases number of cells
 - 1. all cells result from mitotic division beginning with zygote
 - 2. all cells have same exact DNA
- **B. Differentiation**

1. development of specialized cells that are organized into specialized tissues and organs

2. changes that result in 2 cells with same genes becoming 2 different types of cells depending on which genes are expressed (differential gene expression)

C. Morphogenesis

 physical processes that give shape to an animal's body and organs
 movement and arrangement of cells and tissues in the early embryo and production of characteristic 3D form of the organism

3. cell division, differentiation, and programmed cell death of certain cells are also part of morphogenesis

D. Four stages of growth and development

- 1. gametogenesis
- 2. embryonic development
- 3. processes leading to reproductive maturity (puberty)
- 4. aging process→death

III. Fertilization

→forms a diploid zygote from haploid sets of chromosomes from 2 individuals →triggers onset of embryonic development

A. Acrosomal reaction

→acrosome-part of sperm head with hydrolytic enzymes that will penetrate the egg

→our knowledge is based on studies of sea urchins

1. upon contact with the egg's jelly coat, the acrosomal vesicle in the head of the sperm releases hydrolytic enzymes via exocytosis

a. facilitates penetration of egg coverings

2. happens because of contact and recognition-sperm binds to special receptors on egg's vitelline layer and jelly coat (zona pellucida in humans)—outer layer that surrounds the plasma membrane

a. ensures that fertilization occurs only between male and female of same species

3. enzymes of acrosome digest vitelline layer allowing penetration

4. membranes of sperm and egg fuse, allowing sperm nucleus to enter egg

a. causes depolarization of plasma membrane which prevents the entrance of any other sperm

i. fast block to polyspermy

b. cortical reaction

i. slow block to polyspermy

B. Activation of egg

1. sperm penetration triggers meiosis II in egg, producing polar body, which is discharged through the plasma membrane

2. mature ovum forms from secondary oocyte

C. Fertilization

1. microvilli from egg pull whole sperm cell into egg cell

2. sperm cell's flagellar basal body divides and forms zygote's centrioles

3. nuclei fuse, forming zygote, which in humans, consists of 23 pairs of chromosomes-diploid

IV. Cleavage

 \rightarrow succession of rapid mitotic divisions following fertilization that produces a multicellular embryo, the blastula

 \rightarrow cells undergo S and M phases, but virtually skip the G₁ and G₂ phases-no growth

→cytoplasm is repeatedly divided into smaller cells called blastomeres, each with a nucleus-each nucleus contains same DNA as in zygote

A. Embryo polarity

 \rightarrow definite polarity is shown by eggs of most animals and planes of cleavage follow a specific pattern relative to poles of zygote

1. polarity is a result from the concentration gradients of cellular components, such as yolk, mRNA, proteins

a. yolk gradient is key factor in determining polarity 2. vegetal pole of animal has most yolk; therefore, it hangs to bottom of cell

3. animal pole, opposite vegetal pole, has lowest concentration of yolk and is site where polar bodies bud from cell

a. where anterior part of animal will form, because it stays on top 4. polar and equatorial cleavages

a. polar cleavages-early cleavages-divide egg into segments that divide egg from pole to pole

b. equatorial cleavages-later-cleavages-parallel to equator and perpendicular to polar cleavages

5. radial and spiral cleavages

a. deuterostomes-early cleavages are radial

i. forms cells at animal and vegetal poles that are aligned together

ii. top cells are directly above bottom cells

iii. cleavage planes are parallel or perpendicular to vertical axis of the egg

b. protostomes-early cleavages are spiral

i. cells on top are shifted with respect to those below them

ii. planes of cleavage are diagonal to vertical axis of

embryo

6. indeterminate and determinate cleavages

a. indeterminate cleavages

i. each cell produced by early cleavage divisions retains the capacity to develop an entire embryo

ii. make human twins (identical multiple births) possible

b. determinate cleavages

i. mostly in protostomes

ii. rigidly casts development of each embryonic cell very early

7. morula

a. continuation of cleavage produces a solid ball of cells

8. blastula

a. blastocoel, a fluid-filled cavity, develops within morula as cleavage continues

b. changes morula into a hollow ball of cells called the blastula

V. Gastrulation

 \rightarrow extensive arrangement of cells which transfers the blastula, a hollow ball of cells, into the 3 layered embryo called the gastrula

1. cells invaginated (move inward) into the blastula, forming a 2 layered embryo

2. 3 germ layers form

 \rightarrow a third cell layer forms between the outer and inner layers of the embryo

a. ectoderm-outermost layer

i. will develop into nervous system and outer layer of skin b. endoderm-lines the archenteron (central cavity formed by gastrulation that will become the alimentary canal)

i. will become the lining of the digestive tract and accessory organs (ex: liver, pancreas)

ii. blastopore-opening of the archenteron

a. in protostomes becomes the mouth

b. in deuterostomes becomes the anus

c. mesoderm-middle layer

i. becomes the kidneys, heart, muscles, inner layer of skin, and most of the other organs

The stages of development, as summarized so far, are those of a sea urchin. There are variations among other animals, as follows:

A. Frog

1. Cleavage-zygote of frog forms the 2 poles, animal and vegetal, with different coloration in the two

a. animal hemisphere is gray due to melanin granules and vegetal hemisphere is pale yellow due to the yolk

b. at fertilization, the cytoplasm of the amphibian egg is rearranged

i. when sperm enters egg, outer cytoplasm rotates toward point of sperm entry

ii. seen as a gray crescent in light colored region due to the movement of the cytoplasm

iii. Hans Speeman-separated cells formed at early cleavagesshowed that each individual cell could develop into a normal frog, only if it contained a portion of the gray crescent

c. as development continues, the blastula forms

i. cleavage in the animal hemisphere is more rapid than in the vegetal hemisphere

ii. cells in the vegetal hemisphere contain much more yolk (moderately telolecithal); therefore, forms an embryo with different sized cells

iii. animal cells are smaller

iv. in most animals, the blastomeres, cells of the blastula, are \sim equal in size due to small amounts of yolk

v. here though, this makes a disproportionate blastula

2. Gastrulation

a. also results in 3 germ layers with archenteron that opens through a blastopore

b. more complicated because of large yolk ladened cells in vegetal hemisphere and presence of more than 1 layer of cells in the blastula cell wall

c. steps:

i. invagination (internally) of cells produces a 'tuck' called a dorsal lip (upper edge) of the blastopore-where gray crescent was originally present

ii. involution occurs-cells on the upper surface of the embryo roll over dorsal lip and move the embryo's interior away from the blastopore

iii. migrating internal cells form endoderm and mesodermarchenteron forms from the endoderm

iv. these movements produce a 3-layered embryo

v. more and more cells involute, resulting in a wider blastopore lip-which surrounds a group of large, fluid-filled cells from the vegetal pole called the yolk plug

vi. ectoderm forms from cells remaining on surface, except for yolk plug

B. Bird

1. Cleavage

a. yolk is not involuted in cleavage

b. cleavages occur in a blastula that consists of a flattened, disc-shaped region that sits on top of the yolk-birds have a large amount of yolk (highly telolecithal) surrounding the embryo-not in cells

c. this is called the blastodisc (meroblastic cleavage)

2. Gastrulation

a. invagination occurs along a line, rather than a circle, called the primitive streak

b. as cells invaginated along the primitive streak, crevice becomes an elongated blastopore, rather than a circular one

C. Humans

1. Cleavage

 \rightarrow embryo in the blastula stage is called the blastocyst-consists of 2 parts a. outer ring of cells called the trophoblast: functions:

i. accomplishes implantation by embedding into the endometrium of the uterus

ii. produces hCG to maintain progesterone production in corpus luteum-will retain the endometrium

iii. later, will form the chorion and embryonic membranes that together with maternal tissues forms the placenta

b. embryonic disc

i. within cavity, formed by the trophoblast, bundle of cells called inner cell mass (ICM) clusters at one pole and flattens into the embryonic disc (like the blastodisc of birds)
ii. develops the primitive streak and continues on with gastrulation

At this time, 4 extraembryonic membranes form-in birds, reptiles, and mammals (all are considered to be amniote embryos)

 \rightarrow these membranes develop within a fluid filled sac within a shell or uterus 1. chorion-forms from the trophoblast

a. surrounds the embryo and other extra membranes

b. later, the chorion, together with maternal tissues forms the placenta,

where gases, nutrients, and wastes are exchanged with the mother

2. amnion

a. encloses embryo in fluid filled cavity (amniotic cavity)-cushions developing embryo

3. yolk sac-birds and reptiles

a. digests enclosed yolk

- b. blood vessels transfer nutrients to the developing embryo
- c. placental mammals
 - i. yolk sac is fluid filled with little yolk
 - ii. nutrition is carried out by the placenta

4. allantois

a. sac that buds off from the archenteron

- b. birds and reptiles
 - i. stores waste products in the form of uric acid
 - ii. later in development, it fuses with the chorion and together
 - they act as a membrane for gas exchange with blood vessels below
- c. in mammals

i. transports wastes to the placenta

ii. will form the umbilical cord, which will transport gases,

nutrients, wastes between embryo and placenta

D. Organogenesis

 \rightarrow forms the organs of the body from the 3 germ layers

→first evidence of organ development comes from morphogenic changes (folds, splits, condensation of cells) that occur in layered embryonic tissues

1. neural tube and notochord are the first organs to develop in frogs and other chordates

a. dorsal mesoderm above the archenteron condenses to form the notochord in chordates

b. ectoderm above rudimentary notochord thickens to form a neural plate that sinks below the embryo's surface and rolls itself into a neural tube-which will become the brain and spinal cord

c. notochord elongates ands stretches the embryo lengthwise, functions as the core around which the mesoderm cells and vertebrae gather

2. other organs and tissues develop from other germ layers

a. ectoderm-epidermis, epidermal glands, inner ear, and eye lens

b. mesoderm-notochord, coeloms lining muscles, skeleton, gonads,

kidneys, and most of the circulatory system

c. endoderm-digestive tract linings, liver, pancreas, and lungs

3. neural crest forms from ectodermal cells which develop along border where neural tube breaks off endoderm

a. these cells migrate to other parts of the body and form pigment cells in the skin, bones, and muscles of the skull, teeth, adrenal medulla, and parts of the PNS

Embryonic development can result in one of two situations:

1. embryo does not resemble adult form

a. ex: frogs-end of embryonic development is an aquatic, herbivorous tadpole

b. called larvae-young that do not resemble the adult form of the animals (pluteus in sea urchins)

c. must undergo additional development (metamorphosis) to transform larvae to adult

d. also happens in sea urchins and insects

2. embryonic development forms offspring that resembles the adult

a. in mammals-embryo development forms a fetus (embryo that resembles the adult form)

b. fetal development follows

Factors that influence development and differentiation of cells →all cells from zygote contain the same DNA

→what makes some cells express some genes and others express different ones? 1. Influence of egg cvtoplasm

a. cytoplasm is distributed unequally in cells during cleavage (ex: gray crescent in frogs)

b. these unequal cleavages will cause daughter cells to have unequal amounts of cytoplasm and cytoplasmic materials

c. these substances may have an effect on the development of cells

2. Embryonic induction

a. influence of one cell or a group of cells over neighboring cells

b. cells are called organizers-secrete chemicals that diffuse to

neighboring cells, influencing their development

c. ex: rudimentary notochord induces the dorsal ectoderm of a gastrula to form the neural plate

d. ex: amphibial eye-sequence of steps induce one cell than another in the development of the eye

3. Homeotic genes

a. control development by turning on and off genes that encode for substance that directly affects development

b. unique DNA segments~180 nucleotides long, called homeobox, found in most species, from fungi to humans

c. in fruit flies, homeotic genes specify type of appendages and other structure (antennae, wings) specific for that segment

d. products of homeotic genes are regulatory proteins that bind to DNA and affect selective gene expression for continuing development

Fate maps and analysis of cell lineages

1. often possible to develop lineage maps for embryos whose axes are defined early in development

2. made by tracing the fates of each cell during development

3. W. Vogt, 1920s-used vital dyes to color different regions of amphibian

blastula surface, then sectioned embryo to see where each color turned up 4. no, lineage maps of *C. elegans* (nematodes)

5. mark individual blastomeres cells during cleavage and follow as cell develops 6. every one of 959 cells of nematode can be traced back to egg