chapter 33

Descriptive Embryology

Outline

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- Egg Activation
- Metabolic and Nuclear Events

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- Cleavage Patterns

The Primary Germ Layers and Their Derivatives

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- The Chordate Body Plan
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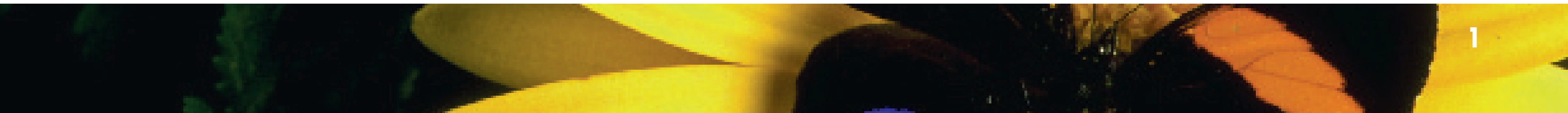
Concepts

1. Embryology is the study of an animal's development from the fertilized egg to the formation of all major organ systems. Descriptive embryology describes developmental stages of an animal, and experimental embryology examines the cellular controls for development.
2. Development of a new animal begins with a sperm fertilizing an egg. Fertilization events help ensure successful fertilization, help prevent multiple fertilization, and help prepare the egg for development.
3. Developmental patterns of different animals have important common themes. Some unique developmental patterns arise from differences in yolk distribution in animal eggs.
4. Echinoderm development illustrates how eggs with very little, evenly distributed yolk may develop.
5. Amphibian development illustrates how a moderate amount of unevenly distributed yolk influences development.
6. The embryos of reptiles, birds, and mammals require adaptations for long developmental periods in terrestrial environments.

This chapter contains evolutionary concepts, which are set off in this font.



How is the complexity of form and function in adult animals explained? Can all of this complexity arise from a single egg? Most biologists of the seventeenth and eighteenth centuries believed in **preformation,** the concept that gametes contain miniaturized versions of all of the elements present in the adult.

In the mid-eighteenth century, the competing theory of **epigenesis** (Gr. *epi,* on + L. *genesis,* birth) gained in popularity. Biologists who favored this theory maintained that the egg contains the material from which the embryo is gradually built—much like a carpenter builds a building from lumber, nails, bricks, and mortar. During the fourth century B.C., Aristotle described the essence of this theory, which depended on an unexplained "creative principle" to direct the assembly.

In separate experiments, Wilhelm Roux (1888) and Hans Driesch (1892) set out to determine whether epigenesis or preformation was correct. Both allowed a fertilized egg to divide to the two-cell stage. Roux, using amphibian embryos (frogs, toads, salamanders), killed one of the two cells with a hot needle. Driesch, using echinoderm embryos (sea stars, sea urchins, sea cucumbers), completely separated the divided cells. An entire animal developing from a single cell would support epigenesis. A portion of the animal developing would favor preformation. What was the result? Interestingly, Roux described the formation of a half embryo that he called a "hemiembryo" (figure 33.1*a*), and Driesch found that each cell retained the potential to develop into an entire organism (figure 33.1*b*). Biologists now know that Driesch was the more correct of the two and that the killed cell, still attached to Roux's developing amphibian embryo, probably altered the development of the untreated cell.

This episode in history marks an important turning point in **embryology** (Gr. *embryo,* to be full + *logos,* discourse), the study of animal development from the fertilized egg to the formation of all major organ systems. Early studies were descriptive in nature, documenting stages in embryological development. Such material is the subject of this chapter. The works of Roux, Driesch, and others were the beginning of experimental embryology (or developmental biology). Developmental biologists use the tools of molecular biology to investigate the genetic controls of development.

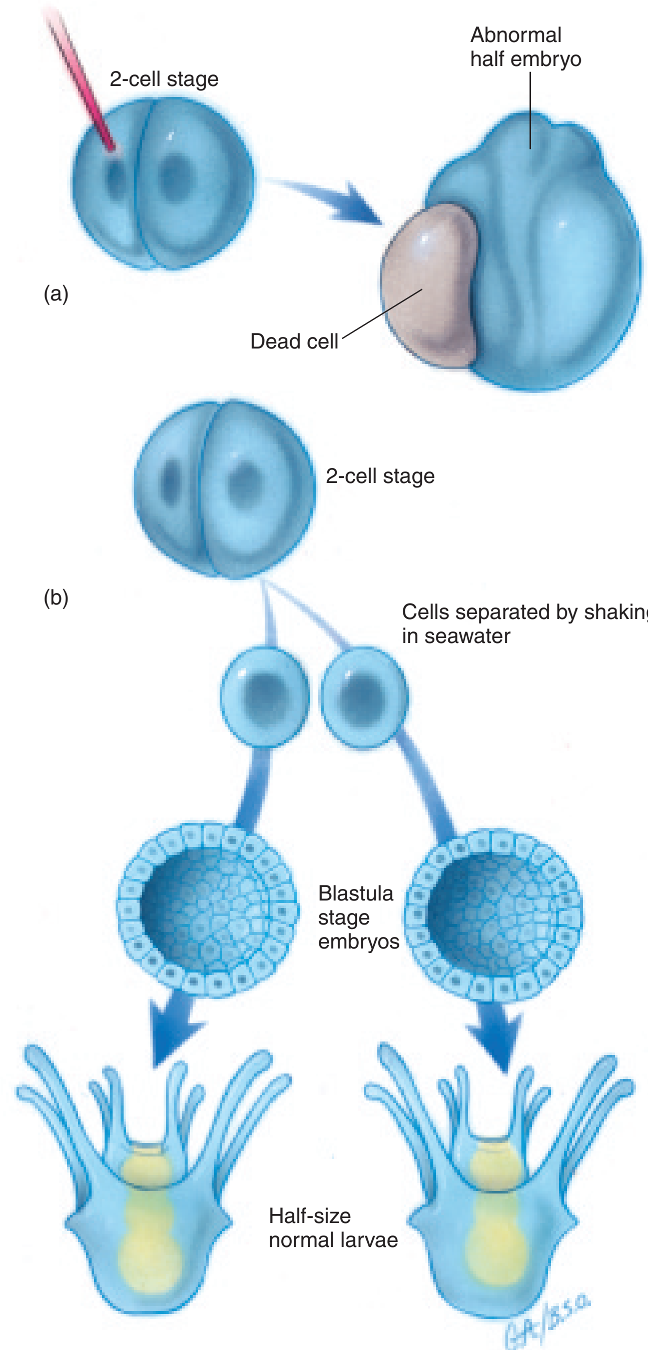


FIGURE 33.1

Experiments of Wilhelm Roux and Hans Driesch. *(a)* Wilhelm Roux produced a "hemiembryo" by killing one cell of a two-celled amphibian embryo. *(b)* Driesch found that separating cells of a two-celled echinoderm embryo resulted in the development of two small, but otherwise normal, larvae.

FERTILIZATION

Different animals use a variety of mechanisms to bring opposite sexes together and to induce the release of eggs and/or sperm. Similarly, once gametes have been released, different mechanisms increase the likelihood of fertilization.

For fertilization to occur, a sperm must penetrate the gel coat of an egg, which consists of protein, or protein and polysaccharide (mucopolysaccharide). To penetrate this coating, the sperm of most animals possess enzymes called sperm lysins. These enzymes may be associated with a specialized organelle at the head of the sperm, called the **acrosome,** or with the plasma membrane of the sperm's anterior tip. When a sperm contacts the gel coat, the acrosome releases lysins that dissolve a pathway for the sperm (figure 33.2). In humans, even 80 million sperm per ejaculation often mean reduced fertility because sperm lysins from many sperm are required to dissolve the gel coat of an egg. The acrosome of some species reorganizes into an acrosomal process after releasing lysins. Just outside the egg plasma membrane is the vitelline layer (or zona pellucida). Egg binding proteins (bindins)

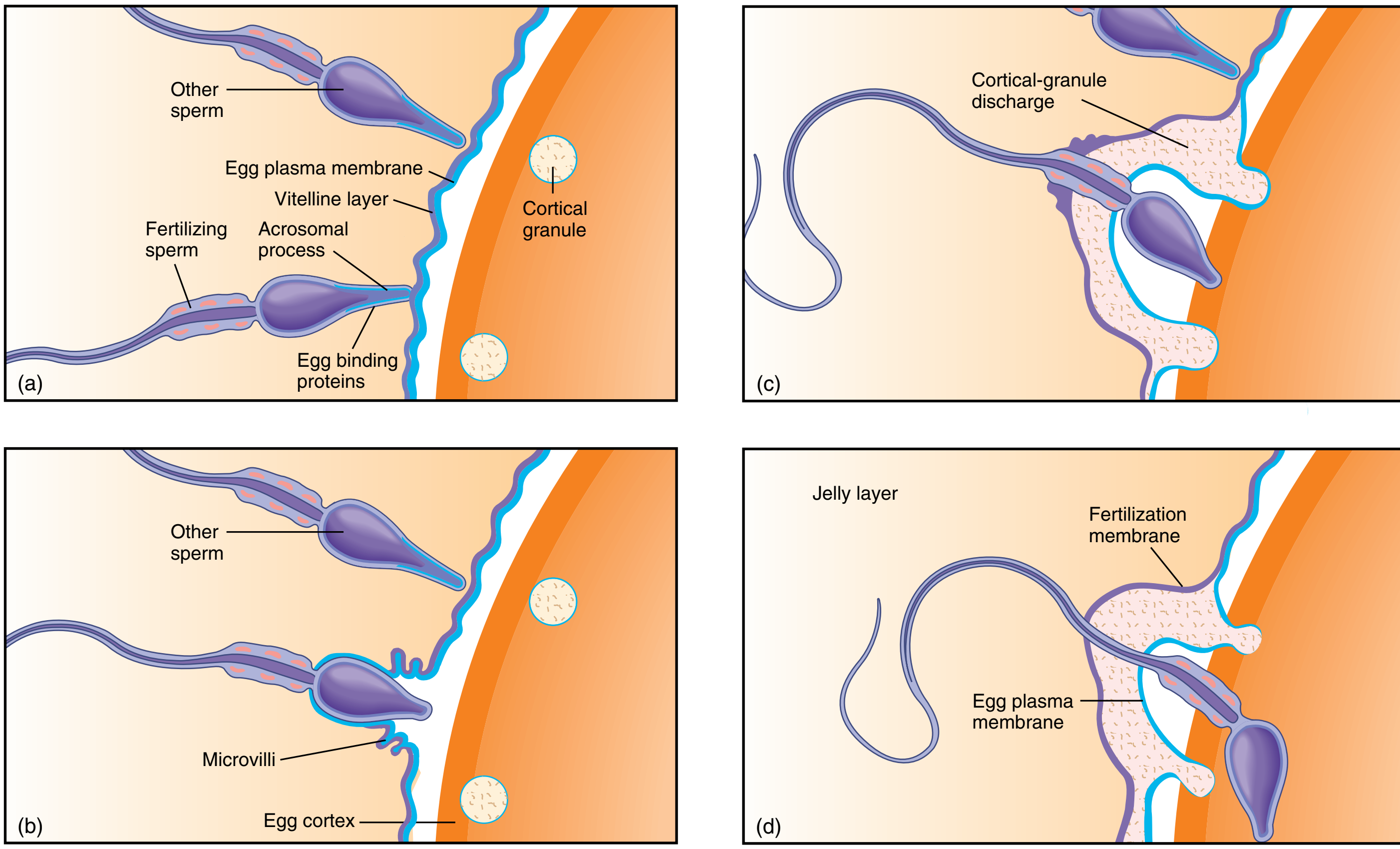


FIGURE 33.2

Fertilization of Echinoderm Eggs. *(a)* Acrosomal process contacts the vitelline membrane. *(b)* Sperm lysins create a hole in the vitelline membrane. Changes in the permeability of the plasma membrane to sodium ions initiate changes in the membrane that permit only a single sperm to enter. *(c)* Cortical granules discharge, and the vitelline membrane begins to rise off the egg plasma membrane. *(d)* The fertilization membrane forms.

on the surface of the acrosomal process bind to sperm attachment molecules on the vitelline layer of the egg plasma membrane (figure 33.3). Acrosomal and egg plasma membranes then fuse. Other parts of the sperm (e.g., the mitochondria, centrioles, and flagellum) may or may not enter the egg, depending on the species involved.

Egg Activation

The fusion of acrosomal and egg membranes is the beginning of egg activation. Egg activation is a series of biochemical changes in the egg that ensures the completion of fertilization and initiates embryonic development. Biologists have extensively studied the events of egg activation in echinoderms, and some of the findings of that work are discussed here.

Membrane and Cortical Events

Some of the earliest changes in the zygote occur at the plasma membrane and in the outer region of the cell cytoplasm (called the cortex). These early changes ensure fertilization by only a single sperm. Single-sperm fertilization is important because multiple fertilization usually results in genetic imbalances and a nonviable embryo.

After contact by sperm, microvilli from the plasma membrane of the ovum wrap around a single sperm. Contraction of microfilaments in the egg's cytoplasm then draws the sperm into the egg (*see figure 33.2*).

A second series of events defends against multiple fertilization. Within milliseconds of penetration by a sperm, ionic changes make the plasma membrane unresponsive to other sperm and initiate the formation of a protective envelope around the egg, called the **fertilization membrane.**

The fertilization membrane forms as granules in the cortex discharge into the region between the egg plasma membrane and the vitelline layer. The cortical granules release enzymes that loosen the vitelline layer's contact with the plasma membrane. The granules allow water to enter the space between the vitelline layer and the egg plasma membrane, causing the vitelline layer to lift off the egg. Proteins of the cortical granules thicken and strengthen the vitelline layer. All of these reactions are completed in 1 to 2 minutes following fertilization.

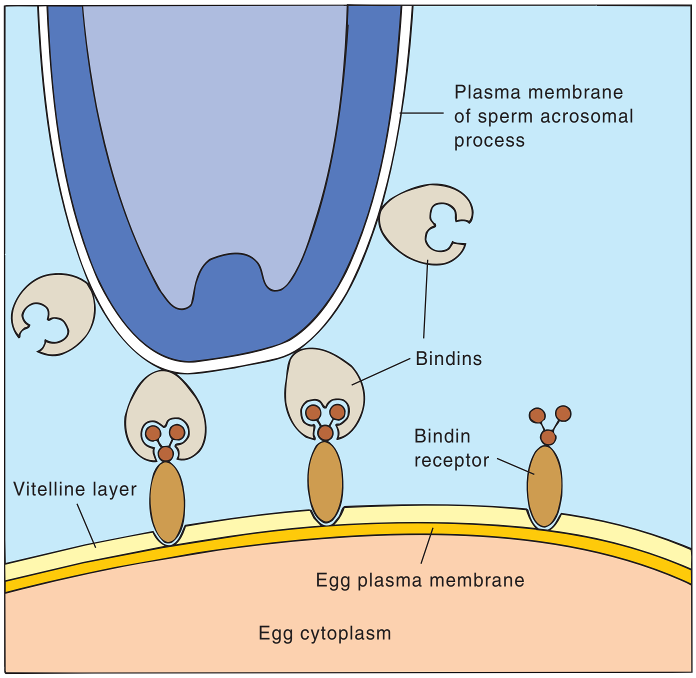


FIGURE 33.3

Sperm-Egg Adhesion Is Mediated by Species-Specific Macromolecules. Schematic drawing of bindin proteins covering the surface of the acrosomal process of a sea urchin sperm. The bindin proteins bind to specific bindin receptor molecules (a carbohydrate) associated with the vitelline layer of the egg. (Bindin proteins and receptors are drawn disproportionately large.)

Other important changes occur in the egg cortex. After sperm penetration, the cortical layer thickens, and rotational and sliding movements of the outer egg cytoplasm begin. In amphibians, these cortical changes result in the formation of a **gray crescent** on the egg, opposite the point of sperm penetration. The gray crescent has an important influence on later development.

Metabolic and Nuclear Events

Prior to nuclear fusion, other nuclear events usually occur. Postfertilization changes help prepare the zygote for the ensuing mitotic divisions. Ionic changes raise the intracellular pH and initiate changes in zygote physiology. DNA replication occurs, and in most species investigated, rates of protein synthesis increase. Rapid protein synthesis following fertilization meets the needs of new cells for enzymes and structural proteins that make up the mitotic spindle and contribute to chromosome structure. Little mRNA is synthesized in the zygote. Instead, existing maternal (egg) mRNA is activated, and it directs the formation of the bulk of the proteins synthesized in early stages of embryonic development. This influence is called maternal dominance.

The region of the egg referred to as the **animal pole** contains less yolk, more mitochondria, and more ribosomes, and is more metabolically active than the opposite, **vegetal pole** of the egg.

Embryonic Development, Cleavage, and Egg Types

Billions of cells that make up adult animals arise from the zygote. **Cleavage** refers to cell divisions that occur during embryonic development, and the cells that cleavage produces are **blastomeres** (Gr. *blasto*, sprout + *mero*, part). The first cell division of the zygote results in two daughter cells. These blastomeres divide in synchrony, producing a four-celled embryo. As more blastomeres are produced, divisions become asynchronous. Throughout early embryology, the embryo does not increase in overall size. Instead, blastomeres become smaller, and the proportion of DNA to cytoplasm increases.

Quantity and Distribution of Yolk

Egg sizes, cleavage patterns, and the length of embryonic periods of animal species are related to differences in the quantity and distribution of yolk in an egg. Yolk, a mixture of proteins, lipids, and glycogen, is the food reserve for the developing embryo. Animals with relatively small amounts of yolk—for example, echinoderms (sea stars and their relatives) and amphibians (frogs and their relatives)—often have larval stages that begin to feed after a brief period of embryological development during which yolk is entirely absorbed. Some animals with longer periods of embryological development (reptiles and birds) provide embryos with larger quantities of yolk. Other animals with long periods of embryological development (eutherian, or placental, mammals and some sharks) provide nourishment to embryos through a placenta or some other modification of the female reproductive tract.

Cleavage Patterns

The relative size of the blastomeres that result from cleavage and the rate of cleavage show how yolk influences cleavage patterns. Eggs with evenly distributed yolk usually have cleavage patterns that result in uniformly sized blastomeres. Eggs with unevenly distributed yolk have cleavage patterns that result in unequal blastomeres.

Cleavages that completely divide an egg are **holoblastic** (Gr. *holo*, whole + *blasto*, sprout). If cleavages cannot completely divide the embryo because of large quantities of yolk, the cleavages are **meroblastic** (Gr. *mero*, part). These embryos develop around, or on top of, the yolk (figure 33.4).

Other cleavage patterns result from differences in the orientation of the mitotic spindle during mitosis, and the degree to which the fate of early blastomeres is predetermined. Developmental differences are thought to reflect differences in the evolutionary history of the animal groups that possess them. For example, the pattern of cleavage where blastomeres are oriented directly over one another is characteristic of the evolutionary lineage leading to the echinoderms and chordates. Another pattern of cleavage, where an upper tier of blastomeres is twisted out of line with a lower tier of blastomeres, is characteristic of the lineage leading to the annelids (segmented worms) and arthropods (insects and their relatives). Chapter 7

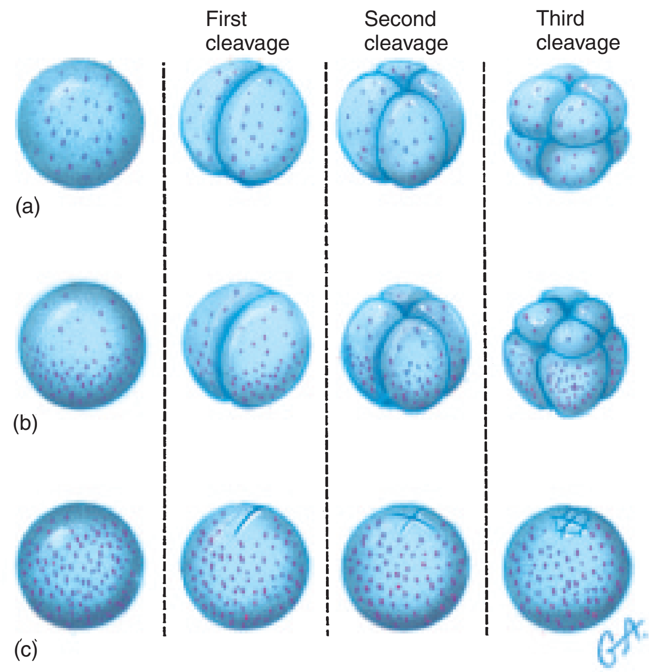


FIGURE 33.4

Early Cleavage Patterns. *(a)* Holoblastic cleavage of an embryo containing a small quantity of evenly distributed yolk results in uniformly sized blastomere (e.g., a sea urchin). *(b)* Holoblastic cleavage of an embryo containing moderate to large quantities of unevenly distributed yolk results in unequal blastomeres (e.g., an amphibian). *(c)* Meroblastic cleavage occurs when large quantities of yolk prevent the embryo from dividing completely (e.g., a reptile or bird).

compares cleavage patterns as well as other developmental differences in these two evolutionary lineages.

The Primary Germ Layers and Their Derivatives

Tissues and organs of animals arise from layers, or blocks, of embryonic cells called **primary germ layers.** Their development from a nondescript form in the early embryo to their form in late embryonic through adult stages is called **differentiation.** One layer, **ectoderm** (Gr. *ektos,* outside + *derm,* skin), gives rise to the outer body wall. **Endoderm** (Gr. *endo,* within) forms the inner lining of the digestive cavity. **Mesoderm** (Gr. *meso,* in the middle) gives rise to tissues between ectoderm and endoderm. Undifferentiated mesoderm (called **mesenchyme**) develops into muscles, blood and blood vessels, skeletal elements, and other connective tissues (table 33.1).

TABLE 33.1 The Primary Germ Layers and Their Derivatives in Vertebrates

Germ Layer	Derivative
Ectoderm	Nervous tissue Epidermis of the skin Sensory organs
Endoderm	Gut tract lining Digestive glands Respiratory tract lining

Mesoderm	Connective tissues
	  Circulatory system
	  Bones, tendons, ligaments
	  Dermis of the skin
	Excretory structures
	Reproductive structures
	Muscle

Echinoderm Embryology

Biologists have studied echinoderm embryology extensively. Echinoderms are easily maintained in laboratories, and the ease with which mature sperm and eggs are obtained makes them convenient models to illustrate principles of early animal development.

The eggs of echinoderms have relatively little yolk, and the yolk is evenly distributed throughout the egg (figure 33.5*a*). Cleavages are holoblastic and result in smaller blastomeres, but the overall size of the embryo remains relatively constant (figure 33.5*b–d*). In just a few hours, a solid ball of small cells, called the **morula** (L. *morum,* mulberry) is produced (figure 33.5*e*).

As cell division continues, cells pull away from the interior of the embryo. A fluid-filled cavity, the **blastocoel,** forms, and the cells form a single layer around the cavity. The embryo is now a hollow sphere called a **blastula** (figure 33.5*f*). In sea urchins, development through the blastula stage takes place within the fertilization membrane. When the cells of the blastula develop cilia, the blastula breaks out of the fertilization membrane and begins to swim. Late in the blastula stage, groups of cells break free of the animal end of the embryo and position themselves within the blastocoel. These cells, called primary mesenchyme, will form skeletal elements (called spicules) of the embryo.

The next series of events in echinoderm embryology is **gastrulation.** The first sign of gastrulation is the invagination of cells at a point in the vegetal half of the embryo (figure 33.5*g*). The point of invagination is the **blastopore,** which will eventually form the anal opening of the larva. During invagination, an embryonic gut, the **archenteron** (Gr. *archeo,* ancient + *enteron,* gut), elongates and reduces the size of the blastocoel (figure 33.5*h*).

During gastrulation, the embryo also begins to lengthen and assumes a pyramidal shape. Although adult echinoderms do not have head and tail ends, larvae have a preferred direction of movement. The end of an animal that meets the environment during locomotion is called the anterior end and is where the head of most animals is located. The opposite end is the posterior end.

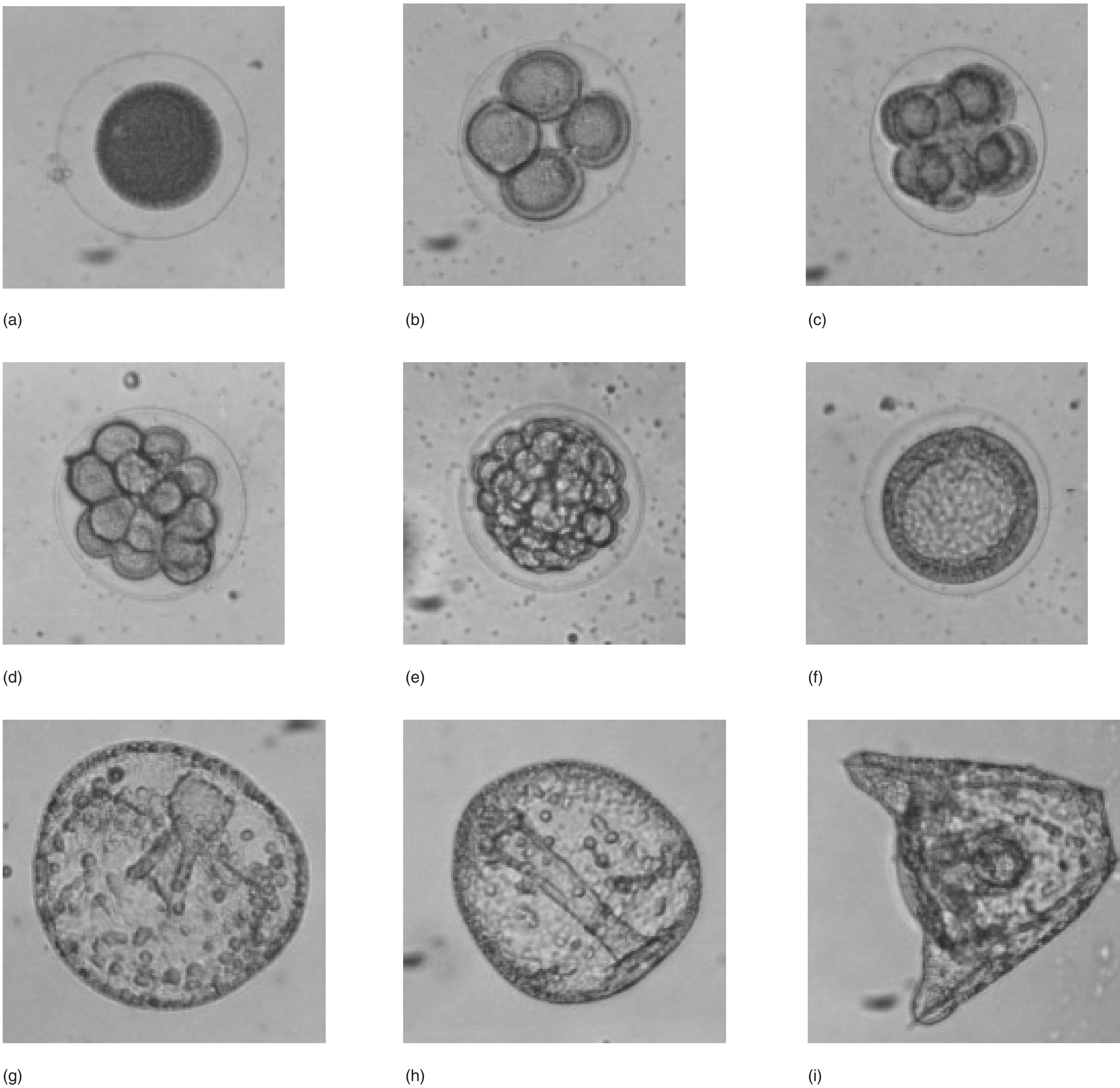


FIGURE 33.5

Stages in the Development of an Echinoderm. *(a)* The egg immediately after fertilization. Note the formation of the fertilization membrane. *(b)* The first two cleavages occur along the animal/vegetal axis. *(c)* The third cleavage occurs at right angles to the previous cleavages, midway between animal and vegetal poles. An eight-cell stage with approximately equal blastomeres results. *(d,e)* Subsequent cleavages result in the formation of the morula. *(f)* The blastula—a hollow sphere whose walls are a single cell layer thick. *(g)* Gastrulation begins with invaginations at a point on the surface of the blastula, and the archenteron forms. *(h)* As gastrulation continues, the archenteron enlarges. The gastrula breaks out of the fertilization membrane and is ciliated. *(i)* The pluteus is a pyramidal-shaped, free-swimming larva. Spicules can be seen in this scanning electron micrograph, and the gut is complete. (All photomicrographs are ×400.) Photographs © Stephen A. Miller.

The shape changes that occur during gastrulation establish the anteroposterior axis of the embryo.

Finally, a body cavity, or coelom, forms from outpockets of the archenteron, and the gut breaks through the anterior body wall. The opening thus produced is the mouth.

The cell movements that begin in gastrulation result from groups of cells changing their shapes simultaneously. Contractile microfilaments mediate these shape changes. These precise, coordinated changes transform a single-layered sphere of cells into an embryo with several layers of cells. The progressive development of an animal's form that begins in gastrulation is **morphogenesis.** In the sea urchin, these changes produce a pluteus larva that swims freely in the sea and feeds on even smaller plants and animals (figure 33.5*i*).

VERTEBRATE EMBRYOLOGY

Early stages of vertebrate (animals with a vertebral column or "backbone") development are similar to those described for echinoderms. The differences are the result of longer developmental periods and, for some vertebrates, adaptations for development on land.

THE CHORDATE BODY PLAN

Vertebrates are members of the phylum Chordata, and certain structures characterize all chordates. The endpoint of the study of vertebrate embryology is the point at which most of these characteristic structures have formed (figure 33.6).

The chordate nervous system develops from ectoderm, and is dorsal and tubular. The first evidence of a developing nervous system is the formation of the neural tube. Nervous tissue proliferates anteriorly into a brain.

The notochord is the primary axial structure in all chordate embryos, as well as many adults. It is flexible, yet supportive, and lies just beneath the neural tube. The notochord is mesodermal in origin and consists of vacuolated cells packed into a connective tissue sheath.

In addition to the notochord and the dorsal tubular nerve cord, all chordates possess pharyngeal slits or pouches and a postanal tail at some point in their life history.

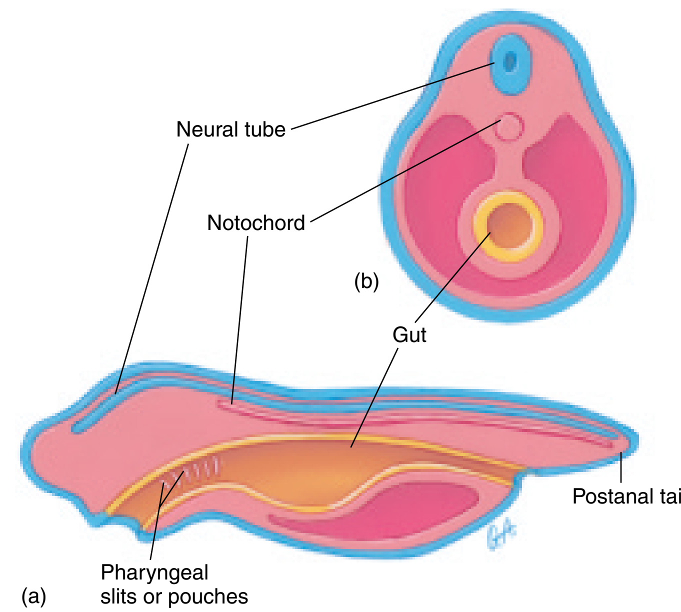


FIGURE 33.6

Chordate Body Plan. The development of all chordates involves the formation of a neural tube, the notochord, pharyngeal slits or pouches, and a postanal tail. Derivatives of all three primary germ layers are present. *(a)* Side view. *(b)* Cross section.

AMPHIBIAN EMBRYOLOGY

Most amphibians lay eggs in watery environments, and the eggs are fertilized as the female releases them (figure 33.7*a*). Frog eggs have a pigmented animal pole. Because the vegetal pole is heavily laden with yolk, the eggs rotate in their jelly coats so that the less dense, darkly pigmented animal pole is oriented up (figure 33.7*b*). This rather simple series of events has interesting adaptive significance. Amphibian eggs usually develop with little care or protection from the parents. The pigmentation helps camouflage developing embryos from predators. When viewed from below, the light color of the vegetal end of floating eggs blends with the sky above. When viewed from above, the dark color of the animal end blends with the bottom of the pond, lake, or stream. The dark pigment of the animal pole also absorbs heat from the sun, and the warming may promote development.

Initial Cleavages

The first cleavage of the amphibian embryo, like that of echinoderms, is longitudinal. It begins at the animal pole and divides the gray crescent in half. Because of the large amount of yolk in the vegetal end of the egg, cleavages are slower there than in the animal end. The amphibian morula, therefore, consists of many small cells at the animal end of the embryo and fewer, larger cells at the vegetal end of the embryo (figure 33.7*a–e*). The amphibian blastula forms in much the same way as the echinoderm blastula, except that the yolky vegetal cells cause the blastocoel to form in the animal half of the embryo (figure 33.7). Unlike that of echinoderms, the blastula wall of amphibians has multiple cell layers.

Gastrulation

The cells of the blastula that will develop into specific structures are grouped on the surface of the blastula. During gastrulation, some of these cells move into the interior of the embryo. Embryologists use dyes or carbon particles to mark the surface of the blastula and then follow the movements of these cells during gastrulation. Embryonic cells are designated according to their future development by "presumptive notochord," "presumptive endoderm," and so forth.

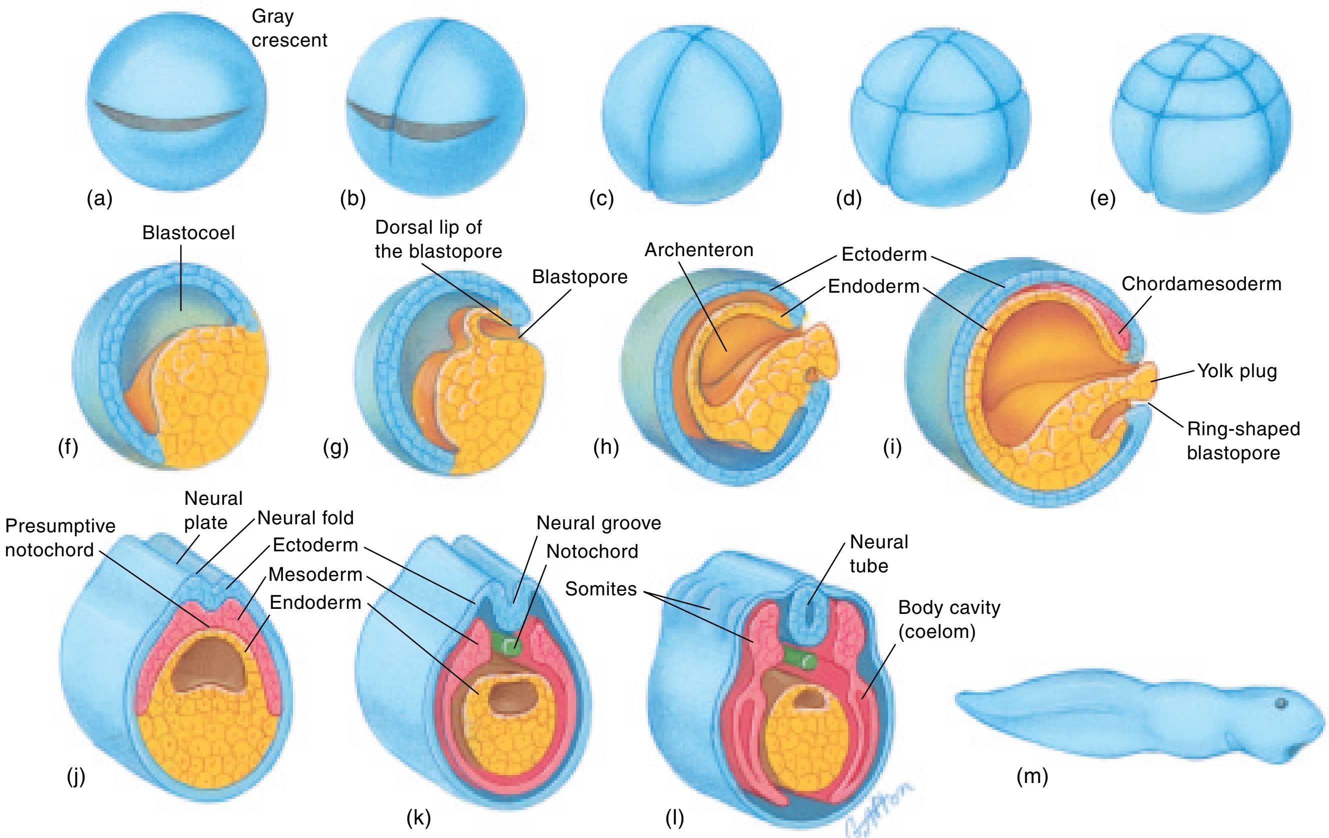


FIGURE 33.7

Stages in the Development of a Frog. *(a–c)* Early cleavages. The gray crescent is shown in *(a)*. The first and second cleavages usually begin at the animal pole and are at right angles to one another. The second cleavage begins before the first cleavage is completed. *(d)* The third cleavage is horizontal. Because of the dense, yolky cytoplasm at the vegetal pole, this third cleavage occurs closer to the animal pole and results in unequal blastomeres. *(e)* Morula. *(f)* Blastula. Note the blastocoel near the animal pole and the multiple cell layers of the blastula. *(g,h)* Gastrulation. Involution begins as cells move into the interior of the embryo, forming a slitlike blastopore. The blastopore extends to the sides and toward the vegetal pole. Ectodermal cells spread into a thin layer over the surface of the embryo, gradually covering the vegetal end. The ends of the blastopore join, forming a yolk plug, and the blastopore eventually closes. *(i)* Chordamesoderm begins forming the notochord and spreads laterally. *(j,k)* The embryo lengthens during gastrulation, and when gastrulation is complete, nerve cord formation begins. The neural plate develops, its edges upfold, and the neural tube forms. *(l)* The mesoderm proliferates, forming somites. Mesoderm along the sides of the embryo splits, forming the body cavity, or coelom. *(m)* The larval stage, or tadpole, gradually uses up the yolk stored in endodermal cells and begins to feed.

The first sign that gastrulation is beginning is the formation of a groove between the gray crescent and the vegetal region of the embryo. This groove is the slitlike blastopore. The animal-pole margin of the blastopore is the dorsal lip of the blastopore. Cells at the bottom of the groove move to the interior of the embryo, and the groove spreads transversely (figure 33.7*g*). This groove is similar to that which occurs during echinoderm blastopore formation. In amphibians, however, superficial cells begin to roll over the dorsal lip of the blastopore in a process called **involution** (to curl inward). Cells spread from the animal pole toward the blastopore and replace those moving into the interior of the embryo. In the process, the ends of the slitlike blastopore continue to spread transversely and downward toward the vegetal pole until one end of the slit meets and joins the opposite end of the slit. A ringlike blastopore now surrounds the protruding, yolk-filled cells near the vegetal end of the embryo. These protruding cells are called the **yolk plug** (figure 33.7*h,i*). Eventually, the lips of the blastopore contract to completely enclose the yolk. The blastopore is said to have "closed."

During the closing of the blastopore, two other movements occur. First, the spreading of cells from the animal pole toward the dorsal lip of the blastopore and the rolling of cells into the blastopore form the archenteron. As these mesodermal and endodermal cells roll into the interior of the embryo, the archenteron becomes larger, and the blastocoel becomes smaller (figure 33.7*g–i*). Because the large, yolk-filled cells of the vegetal end are less active in these movements, they ultimately make up the floor of the gut tract. Second, gastrulation results in a spreading and thinning of ectodermal cells toward the blastopore. In addition, ectoderm spreads over the entire embryo, a process called **epiboly.**

Mesoderm Formation

Some of the last cells to roll over the dorsal lip into the blastopore are presumptive notochord and presumptive mesoderm (figure 33.7*i*). Initially, these cells make up the dorsal lining of the archenteron near the blastopore. Later, they detach from the endoderm and move to a position between the endoderm and ectoderm in the region of the dorsal lip of the blastopore. This mesoderm, called **chordamesoderm,** spreads anteriorly (the embryo is now beginning to elongate) between ectoderm and endoderm. Chordamesoderm will differentiate into notochord (figure 33.7*j,k*). Lateral to the notochord, mesoderm spreads and thickens along the sides of the embryo. These thickenings, called **somites,** are visible externally as a row of bumps on either side of the embryo (figure 33.7*l*). As mesoderm continues to spread ventrally, it splits to form the body cavity (coelom) and the mesodermal lining of the body wall and gut.

Neural Tube Formation

During late gastrulation, external changes along the upper surface of the embryo begin to form the neural tube—a process called **neurulation.** After gastrulation is complete, an oval-shaped area on the dorsal side (the side that will become the animal's back) of the embryo marks the presumptive neural tube. This region is the neural plate. Microfilaments in neural plate cells flatten and thicken the neural plate. The edges of the neural plate roll up and over the midline of the neural plate. These longitudinal ridges, called neural folds, meet dorsally to form the neural tube (figure 33.7*j*). The portion of the neural tube that will become the brain is the last to close.

With further development of the mesoderm, the amphibian embryo gradually takes on the form of a tadpole larva. Yolk in cells lining the floor of the gut is gradually depleted, and the larva begins feeding on algae and other plant material (figure 33.7*m*).

Development in Terrestrial Environments

Reptiles (class Reptilia), birds (class Aves), and mammals (class Mammalia) develop on land rather than in the water. Embryos that develop on land require protection from desiccation, which a series of extraembryonic membranes provides. The longer developmental periods of these animals reflect their lack of independent larval stages. (Larval stages, such as those of amphibians, allow individuals to achieve increased complexity in spite of short embryonic periods.)

Avian Embryology

Chicken development can be used to model the development of birds and reptiles. What is commonly referred to as the "egg" of a chicken is, in reality, the true egg, plus a variety of membranes that protect the egg. The yellow portion of the chicken egg is the single cell produced in the chicken ovary. This egg is released into the oviduct, where fertilization may occur. Following fertilization, membranes and fluids collect around the egg (figure 33.8*a*). A vitelline membrane covers the surface of the true egg. The "white" consists of water and a protein called albumen. This watery environment protects the egg from mechanical damage and drying. Albumen is a source of nutrients (in addition to the yolk of the egg) and is eventually consumed during development. Two denser strands of albumen (called chalazas) attach to the inside of the shell and to the egg, and suspend the egg in the center of the watery albumen. The shell is made of calcium carbonate impregnated with protein. Thousands of tiny pores (40 to 50 μm in diameter) in the shell permit gas exchange between the embryo and the outside. On the inside of the shell are two shell membranes. An air pocket forms between these membranes at the rounded end of the shell. The air pocket enlarges during development, as air moves through pores in the shell to replace water loss. As hatching approaches, the chick penetrates the air pocket with its beak, the lungs inflate, and the chick begins to breathe from the air sac, while still exchanging gases across vascular extraembryonic membranes.

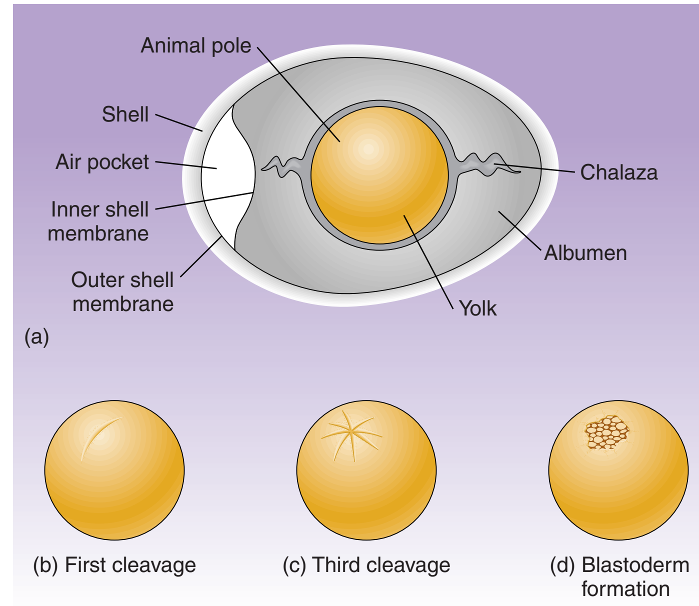


FIGURE 33.8

Structure and Early Development of the Chicken Egg. *(a)* Egg and egg membranes. Albumen is an accessory food source, and along with egg membranes, protects the embryo and prevents it from drying. *(b)* The first cleavage cannot pass through the massive yolk. *(c)* Third cleavage. *(d)* Blastoderm formation at the animal end of the egg.

Early Cleavages and Gastrulation

Cleavage of the chicken egg is meroblastic (figure 33.8*b–d*). A small disk of approximately sixty thousand cells at the animal end of the egg develops and is the **blastoderm.** The blastoderm is raised off the yolk, leaving a fluid-filled space analogous to the

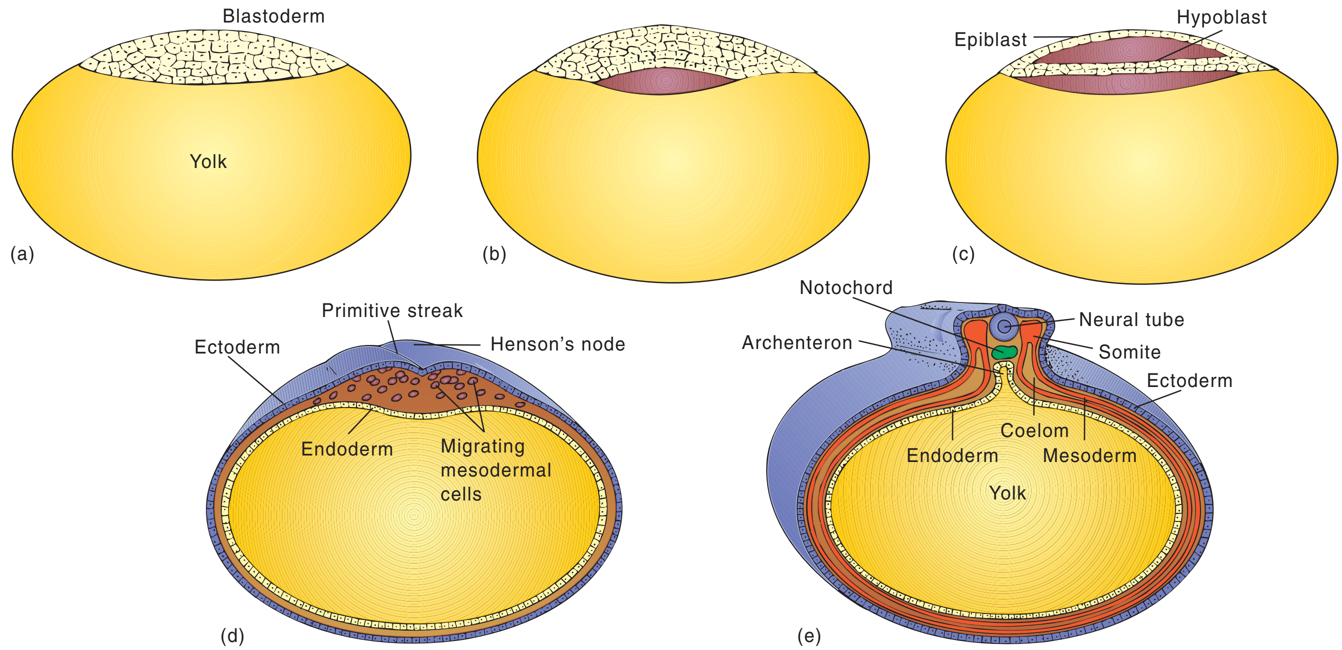


FIGURE 33.9

Gastrulation in the Chick Embryo. *(a,b)* Meroblastic cleavage results in blastoderm formation. *(c)* Cells of the blastoderm rise off the yolk and rearrange into two layers—epiblast and hypoblast. *(d)* Gastrulation results from the migration of epiblast cells into a longitudinal groove called the primitive streak. These migrating cells form mesoderm and endoderm, and cells remaining in the epiblast form ectoderm. *(e)* The embryo lifts off the yolk when the margins of the embryo grow downward and meet below the embryo.

blastocoel of the amphibian blastula. Proliferation and movement of blastoderm cells sort the cells into two layers. The **epiblast** (Gr. *epi,* upon + *blast*, sprout) is the outer layer of cells, and the **hypoblast** (Gr. *hypo,* below) is the inner layer (figure 33.9*a–c*). The movements of blastoderm cells are the beginning of gastrulation. The female reproductive tract releases the egg at about this time.

A medial, linear invagination, called the **primitive streak,** gradually extends anteriorly (figure 33.9*d*). A depression, called Henson's node, forms at the anterior margin of the primitive streak and marks the beginning of an inward migration of epiblast cells, comparable to involution of the amphibian gastrula. The primitive streak is, therefore, analogous to the dorsal lip of the blastopore. This migration occurs during a dramatic posterior movement of Henson's node. Migrating cells form mesoderm, what is left of the epiblast on the surface of the embryo is the ectoderm, and the hypoblast forms the endodermal lining of the gut tract. The three germ layers are now arranged above the surface of the yolk.

Following gastrulation, notochordal cells separate from the overlying neural ectoderm, and the neural tube forms as described earlier for the amphibian embryo. In addition, mesoderm, which originally formed as solid blocks of cells, organizes into somites and splits to form the coelom.

The embryo lifts off the yolk when the margins of the embryo grow downward and meet below the embryo (figure 33.9*e*). A connection between the embryo and the yolk is retained and is called the yolk stalk. Blood vessels develop in the yolk stalk and carry nutrients from the yolk to the embryo.

The Development of Extraembryonic Membranes

Extraembryonic membranes of amniotes include the yolk sac, the amnion, the chorion, and the allantois (figure 33.10). Reptiles and birds have a large quantity of yolk that becomes enclosed by a **yolk sac.** The yolk sac develops from a proliferation of the endoderm and mesoderm around the yolk. The yolk sac is highly vascular and distributes nutrients to the developing embryo.

Following the neural tube stage, the ectoderm and mesoderm on both sides of the embryo lift off the yolk and grow dorsally over the embryo. As these membranes meet dorsally, they fuse and form an inner **amnion** and an outer **chorion.** The amnion encloses the embryo in a fluid-filled sac. This amniotic cavity protects against shock and drying. The chorion is nearer the shell, becomes highly vascular, and aids in gas exchange.

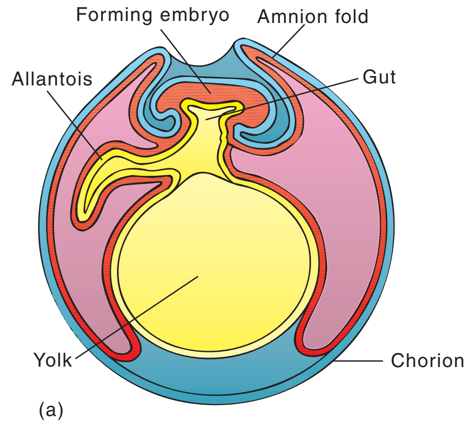


FIGURE 33.10

Formation of Extraembryonic Membranes. *(a)* The embryo lifts off the yolk as the hypoblast proliferates around the yolk to form the yolk sac. The amnion begins forming before the allantois. *(b)* Amnion folds fuse above the embryo, enclosing the embryo in the amnion and forming a continuous chorion on the inside of the shell. The allantois increases in size as uric acid accumulates. The yolk is absorbed and metabolized as the embryo grows.

Development in a closed environment presents a problem of waste disposal. Accumulation of nitrogenous waste products in the embryo, or unconfined in the shell, would be lethal for the embryo. The immediate breakdown product of proteins is highly toxic ammonia. This ammonia is converted to a less toxic form, uric acid, which is excreted and stored in the **allantois,** a ventral outgrowth of the gut tract. Uric acid is a semisolid, and thus, little water is wasted. The allantois gradually enlarges during development to occupy the region between the amnion and the chorion. In addition, the allantois becomes highly vascular and functions with the chorion in gas exchange.

The Fate of Mesoderm

Following gastrulation in birds, reptiles, and mammals, all three primary germ layers have formed. Of the three layers, the fate of mesoderm is the most complex. Mesoderm forms all of the supportive tissues of vertebrates, including connective tissues (bone, cartilage, and blood) and muscle. These supportive tissues are frequently associated with derivatives of other primary germ layers. For example, the inner lining of the gut is endodermal, but mesodermally derived structures, such as smooth muscle, blood, and blood vessels, make up the bulk of that system.

Summary

1. Embryology is the study of animal development from the fertilized egg to the formation of all major organ systems. Descriptive embryologists document these changes. Experimental embryologists study the cellular controls of development.
2. Fertilization is the process by which the union of two gametes forms a diploid zygote. A variety of mechanisms have evolved to ensure fertilization.
3. Contact with sperm activates the egg. Changes in the egg cytoplasm ensure that a singlΩe sperm penetrates the egg and that the cell is metabolically ready for mitosis.
4. The quantity and distribution of yolk influence cleavage patterns. Eggs that contain little yolk divide into equal-sized blastomeres. Eggs that contain larger amounts of yolk either do not divide completely or divide into unequal blastomeres.
5. One of the goals of embryology is the description of the formation and fates of the primary germ layers: ectoderm, endoderm, and mesoderm.
6. Echinoderm development is representative of the development of a zygote that contains little yolk. Cleavages are holoblastic and equal. Gastrulation occurs by invagination of the blastula. Mesoderm and the coelom form from simple outpockets of the archenteron.
7. Frog eggs have a large amount of unequally distributed yolk. As a result, their cleavage is holoblastic and unequal. The blastocoel forms near the animal pole, and gastrulation occurs by involution. Chordamesoderm forms between ectoderm and endoderm, and develops into somites, coelomic linings, and the notochord. Changes in the ectoderm include the formation of the neural tube.
8. The development of reptiles, birds, and mammals shows adaptations for living on land, including the formation of extraembryonic membranes.
9. The initial cleavages of a chicken egg result in the formation of a disk of cytoplasm, the blastoderm, at the animal end of the embryo. Gastrulation involves cells migrating toward a medial longitudinal groove, called the primitive streak.

Selected Key Terms

allantois
amnion
blastula
chorion
differentiation
ectoderm
embryology
endoderm
gastrulation
mesoderm
morula

Critical Thinking Questions

1. In what sense is fertilization a random event? Do you think random fertilization is adaptive for a species? Explain.
2. What mechanisms prevent fertilization of an egg by more than one sperm? Why is this important?
3. Practical applications often follow quickly on the heels of basic research. How could basic research into the process of fertilization be applied to problems of contraception and infertility?
4. Evaluate the following statement: “The primary differences between early cleavages of most animal embryos are the result of the quantity and distribution of yolk.”
5. The eggs of many terrestrial vertebrates are protected by a shell and have large quantities of yolk. Why do most mammalian eggs lack these features?