# 43 PRINCIPLES OF ANIMAL REPRODUCTION AND DEVELOPMENT

## *Sex and the Mammalian Heritage*

Sex and romance! Reinforcement of the contrived linkage between the two starts early and often in Western cultures. The idea of sex is used to sell everything from underwear and flowers to automobiles and erectile dysfunction drugs—and it trivializes the mammalian reproductive heritage.

Victoria's Secret aside, the breasts of a female mammal function to nourish offspring that are too vulnerable to survive on their own. Any mammalian mother that bonds with offspring is committing herself to protect it through an extended time of dependency and learning. Extended care helps the new individual survive until it is old enough to survive on its own. We can expect that such behavior is a result of natural selection, for it increases the odds of reproductive success in the next generation.

We see this behavior among all mammals. Less than four months after mating, a lioness typically gives birth to no more than a few small, blind cubs (Figure 43.1). She hides them in marshes or rock outcroppings. She nurses them for six or seven months before leading them to nearby kills. The cubs will remain dependent on her for at least sixteen months. Even with protection, 80 percent will die before then, primarily as a result of starvation.

Males alone have a thick, showy, protective mane, and they are much larger and twice as heavy as females. This pronounced sexual dimorphism is one outcome of severe reproductive competition. Males often form coalitions to battle for the chance to monopolize the females. Once they succeed, they have about two years to perpetuate their genes before younger, stronger lions challenge them.

The intense competition may explain the infanticidal behavior among male lions that take over a pride. The first thing they do is kill all cubs they can catch. The lionesses fight fiercely to protect the cubs. When they fail, they often become hyperactive sexually without becoming pregnant. Is the delay a form of natural birth control that gives the strongest males time to turn back more takeover attempts and assume dominance? Possibly. Four or five months after the initial takeover, all the females in the pride ovulate, get pregnant, and bear cubs together. When one females hunts, others even nurse her cubs.

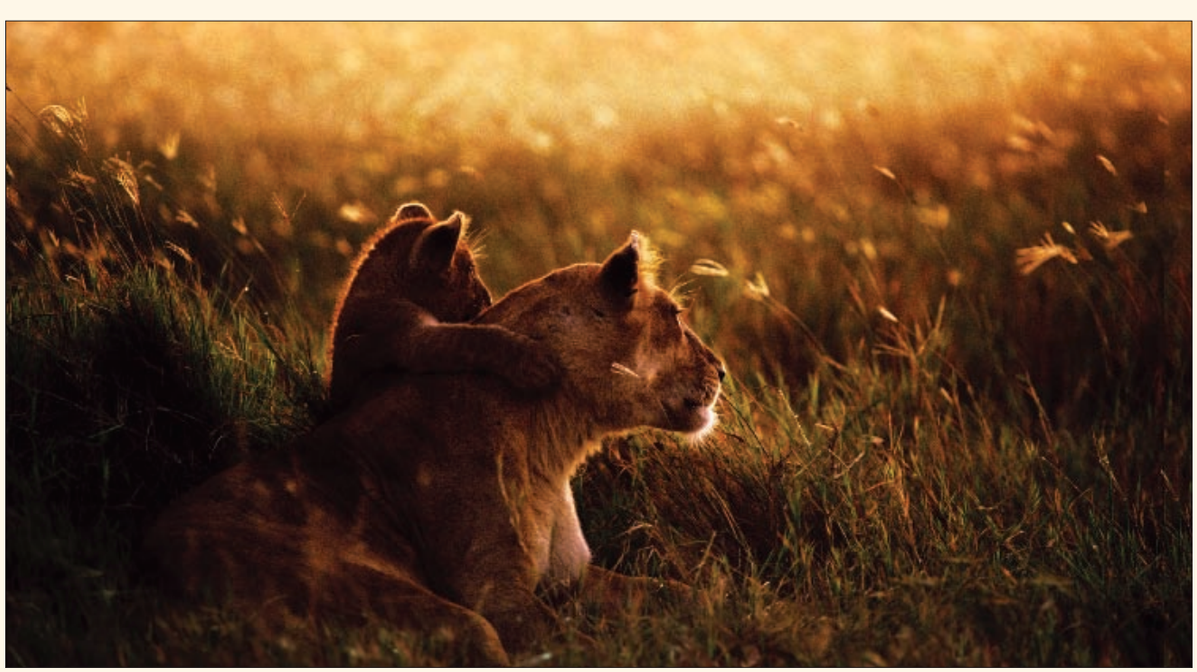
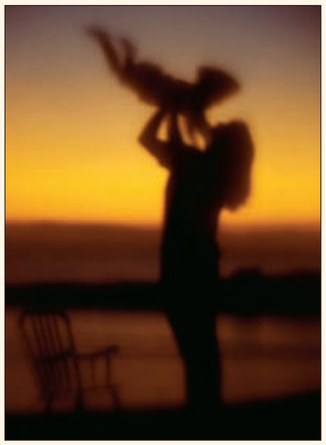


**Figure 43.1** Glimpses into maternal care. This complex form of behavior has become most highly developed among mammals. The offspring of these sexually reproducing species require an extended period of development, dependency, and learning.

## IMPACTS, ISSUES



In such ways, synchronization improves the chances of reproductive success for the males as well as females.

The point is this: In nature, the main function of sex is not recreational but rather the perpetuation of one's genes. And so, with this example, we turn to one of life's great dramas—the reproduction and development of complex animals in the image of their parents. *How does a single fertilized egg of a lion or frog, a bird or human, become transformed into all of the specialized cells and structures of the adult form?* Some answers will start to emerge through this chapter's survey of basic principles that guide animal life cycles, from the time of reproduction, through embryonic and postnatal development, and on to aging and eventual death. More answers will emerge in the next chapter, which offers a case study of human reproduction and development.

### How Would You Vote?

*Sanitation and medical advances have greatly extended the average human life span, especially in developed countries. Some researchers are now looking for ways to extend the human life span even further. Do you think research into life extension should be supported by federal research funding? See BiologyNow for details, then vote online.*

### Key Concepts

#### COSTS AND BENEFITS OF SEXUAL REPRODUCTION

Biologically, separation into sexes is far more costly than asexual reproduction. But sexual reproduction expands the capacity for fast, adaptive responses to abiotic and biotic conditions. That capacity may be present in the range of variation among offspring, so that at least some have a better chance to survive and reproduce. Section 43.1

#### SIX STAGES IN ANIMAL LIFE CYCLES

Animal life cycles typically proceed through six stages of reproduction and development: gamete formation, fertilization, cleavage, gastrulation, formation of organs, and growth and tissue specialization. Section 43.2

#### FORMATION OF THE EARLY EMBRYO

Different cell lineages in an embryo set out on different developmental roads. Their fate is partly sealed by cleavage, when daughter cells receive different instructions that were localized in different parts of the fertilized egg's cytoplasm. Then cells in the embryo start signaling and responding to one another. Cell differentiation and morphogenesis are outcomes of the interactions. Sections 43.3, 43.4

#### FILLING IN DETAILS OF THE BODY PLAN

The cytoplasmic localization and then inductive interactions among classes of master genes map the basic body plan. Gene products specify where and how body parts develop. Like beacons, they help cells assess their position in the embryo and how they will differentiate. Section 43.5

#### AGING IN THE LIFE CYCLES

All species of multicelled animals that show extensive cell differentiation undergo aging. Cell structure and function gradually decline, which leads to the decline of tissues, organs, and eventually the body. Sections 43.6, 43.7

### Links to Earlier Concepts

This chapter builds on the Chapter 10 introduction, which invited speculation on the costs and benefits of having separate sexes. You will be drawing on your knowledge of mitosis (Section 9.3), cleavage (9.4), and meiosis, gamete formation, and fertilization (10.3,10.5). You will be revisiting the nature of cell differentiation and the role of master genes in laying out the basic body plan (13.4, 15.1–15.3, 17.8). You will take a closer look at the primary tissue layers that give rise to all tissues and organs of adult animals (25.1, 33.5).

# 43.1 Reflections on Sexual Reproduction

LINK TO CHAPTER 10 INTRODUCTION

*Sexual reproduction dominates the life cycle of most animals, even those that also can reproduce asexually. We therefore can expect that the benefits of sexual reproduction outweigh the costs. What are they?*

## SEXUAL VERSUS ASEXUAL REPRODUCTION

In earlier chapters, we considered the genetic basis of **sexual reproduction**. Again, meiosis and the formation of gametes typically occur in two prospective parents. At fertilization, a gamete from one parent fuses with a gamete from the other and forms the first cell of the new individual—the zygote. We looked at **asexual reproduction**, whereby a single organism—just one parent—produces offspring. We turn now to examples of the structural, behavioral, and ecological aspects of these two modes of animal reproduction.


Think about a fragment torn away from a sponge body. It may well grow, by mitotic cell divisions, into a new sponge. Or think of a flatworm that splits spontaneously in two. If its body constricts at its midsection, the part below grips a substrate and starts a tug-of-war with the front. It splits off a few hours later. Then both parts go their separate ways and each grows what is missing, thus becoming a whole flatworm (Figure 43.2*a*).

Mutation aside, by *asexual* reproduction, one parent has all of its genes represented in the next generation; its offspring are all genetically identical. Phenotypic uniformity from one generation to the next helps when gene-encoded traits are adapted to fairly consistent abiotic and biotic conditions. In such circumstances, drastic variations in an adaptive gene package could be disastrous.

Most animals live where opportunities, resources, and danger are variable. They reproduce sexually, and their offspring inherit mixes of maternal and paternal alleles. Remember the Chapter 10 introduction? The capacity for rapid, adaptive responses to abiotic and biotic conditions is typically present in the expressed range of variation, so at least some offspring have a better chance to survive and reproduce.

## COSTS OF SEXUAL REPRODUCTION

Separation into sexes is costly. Energy and resources must be allocated to forming and nurturing gametes. Often, reproductive structures that can help deliver or accept sperm must be built. A potential mate might have to be courted. The timing of gamete formation and mating must be synchronized between the sexes.

Reflect on *reproductive timing*. How do the sperm in one individual mature at the same time that eggs are maturing in a different individual? Timing requires energy outlays to construct, maintain, and use neural and hormonal control mechanisms in both parents. It requires responsiveness to environmental cues, such as daylength, that signal the best time to start making gametes and to produce offspring.

For example, moose become sexually active only in late summer and early fall. This timing is adaptive; it means that the offspring will be born in spring, when weather is milder and food more plentiful.

Think about what it takes to find and recognize a likely mate. Many animals invest energy to produce sex attractants called pheromones or make receptors for them. They invest in visual signals such as richly colored and patterned feathers. Many males attract mates and fend off rivals, as with bonding rituals or claws, horns, or a larger body mass that may make a difference in territorial defense (Figure 43.2*b–d*).




**Figure 43.2** (**a**) Example of fast, easy, asexual reproduction. One of the flatworms (*Dugesia*) can reproduce asexually by spontaneous fission. If it divides into two pieces, each piece replaces what is missing, and each will be genetically identical to the original flatworm. All of the parent worm's genes are represented in both.

Biological costs associated with sexual reproduction. Reflect on the energy and raw materials directed into producing (**b**) sable antelope horns, (**c**) colorful feathers, and (**d**) the body mass of male northern elephant seals. The bulls are fighting for access to the far smaller female, lower right.

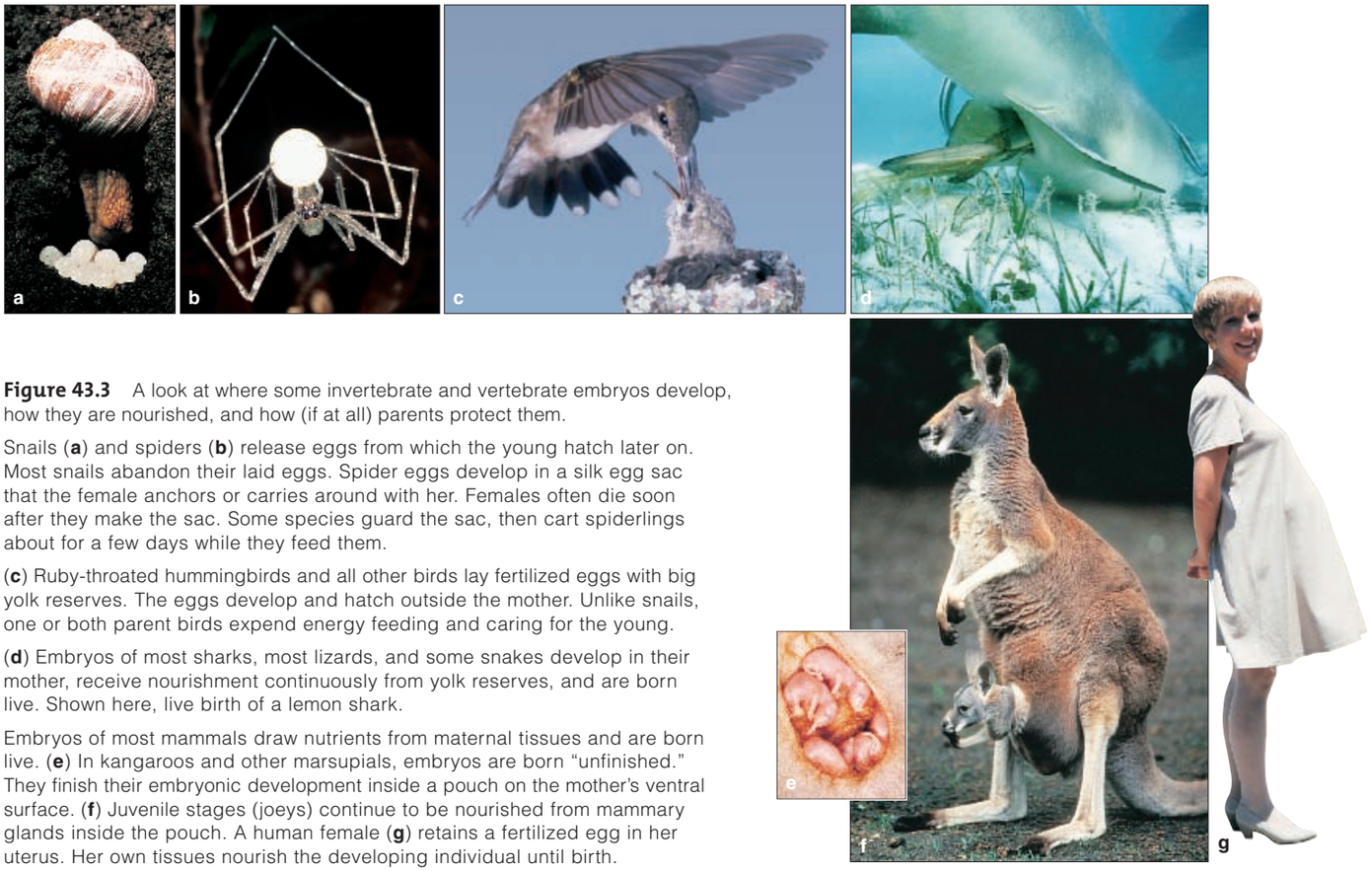



**Figure 43.3** A look at where some invertebrate and vertebrate embryos develop, how they are nourished, and how (if at all) parents protect them.

Snails (**a**) and spiders (**b**) release eggs from which the young hatch later on. Most snails abandon their laid eggs. Spider eggs develop in a silk egg sac that the female anchors or carries around with her. Females often die soon after they make the sac. Some species guard the sac, then cart spiderlings about for a few days while they feed them.

(**c**) Ruby-throated hummingbirds and all other birds lay fertilized eggs with big yolk reserves. The eggs develop and hatch outside the mother. Unlike snails, one or both parent birds expend energy feeding and caring for the young.

(**d**) Embryos of most sharks, most lizards, and some snakes develop in their mother, receive nourishment continuously from yolk reserves, and are born live. Shown here, live birth of a lemon shark.

Embryos of most mammals draw nutrients from maternal tissues and are born live. (**e**) In kangaroos and other marsupials, embryos are born "unfinished." They finish their embryonic development inside a pouch on the mother's ventral surface. (**f**) Juvenile stages (joeys) continue to be nourished from mammary glands inside the pouch. A human female (**g**) retains a fertilized egg in her uterus. Her own tissues nourish the developing individual until birth.

Producing enough offspring so that at least some survive is costly (Figure 43.3). Many invertebrates, the bony fishes, and frogs release sperm, eggs, or both into the environment. If each adult were to make only one sperm or egg each season, chances would not be good for fertilization. These animals invest energy in making many gametes, often thousands of them.

As another example, nearly all animals on land use internal fertilization, or the union of sperm and egg *within* the female body. They invest metabolic energy to construct elaborate reproductive organs, such as a penis and a uterus. A penis deposits sperm inside the female, and a uterus is a chamber in which an embryo develops inside certain mammalian females.

Finally, animals set aside energy in forms that can *nourish the developing individual* until it has developed enough to feed itself. Nearly all animal eggs contain **yolk**. This thick fluid has an abundance of proteins and lipids that nourish embryonic stages.

The eggs of some species have much more yolk than others. Sea urchins make enormous numbers of tiny eggs with little yolk. Each fertilized egg develops into a freely moving, self-feeding larva in less than a day. Very few escape predators. For sea urchins, then, reproductive success means allocating small amounts of energy and resources to making each egg.

Birds put a lot of energy and resources into making eggs with a lot of yolk, which has to nourish the bird embryo through an extended time inside an eggshell that forms after fertilization. *Your* mother placed huge strains on herself to nourish you through nine months of development from a nearly yolkless, fertilized egg. Physical exchanges with her bloodstream supported your embryonic development (Figure 43.3*g*).

Animals show great diversity in reproduction and development, as these examples suggest. However, as you will see in sections to follow, some basic patterns are widespread throughout the animal kingdom.

*Separation into male and female sexes requires special reproductive cells and structures, neural and hormonal control mechanisms, and forms of behavior.*

*A selective advantage—variation in traits among offspring—offsets biological costs related to separation into sexes.*

# 43.2 Stages of Reproduction and Development

LINKS TO SECTIONS 10.5, 25.1

*For animals more complex than sponges, the life cycle has six developmental stages, from gamete formation through growth and tissue specialization.*

Figure 43.4 is an overview of the six stages of animal reproduction and development. In *gamete formation*, the first stage, eggs or sperm develop inside parental reproductive tissues or organs, as outlined in Section 10.5. At *fertilization*, the first cell of a new individual—the zygote—forms when a sperm penetrates a mature egg and their nuclei fuse. *Cleavage* repeatedly cuts the fertilized egg by mitotic cell divisions. The number of cells grows, but the egg's original volume does not. This third stage is over when a ball of cells, a **blastula**, has formed. A blastula's cells are called **blastomeres**. They enclose a fluid-filled cavity, the blastocoel.

The blastula enters *gastrulation*. In this fourth stage, cells do not divide; they reorganize themselves into a **gastrula**. As you read in Sections 25.1 and 33.5, this early embryonic form has two or three primary tissue layers, or germ layers. Its cellular descendants give rise to all of the tissues and organs of the adult animal.

**Ectoderm**, the outermost primary tissue layer, forms first in all animal embryos. It is the forerunner of cell lineages that give rise to the nervous system and the outer part of the integument. Innermost is **endoderm**, the start of the gut's inner lining and organs derived from it. In most animal embryos, **mesoderm** forms in between the outer and inner primary tissue layers. It is the forerunner of muscles, most of the skeleton, the circulatory, reproductive, and excretory systems, and connective tissues of the gut and integument. For instance, in vertebrates, some mesoderm gives rise to **somites**: a longitudinal series of paired segments that are the source of most bones, skeletal muscles of the trunk and head, and most of the overlying dermis. Once again, mesoderm evolved hundreds of millions of years ago (Section 25.1). It was a key innovation in the evolution of nearly all large, complex animals.

After the primary tissue layers form, cells start to signal one another and interact in ways that result in distinct subpopulations of cells. These cells become specialized in composition, structure, and function. By orderly processes of *organ formation*, they form tissues and then organs in expected patterns.

*Growth and tissue specialization* is the sixth stage of animal development. The tissues and organs continue to grow, and they slowly take on their final sizes, shapes, proportions, and functions. This stage continues into adulthood.

Figure 43.5 has examples of the stages for one kind of vertebrate, the leopard frog (*Rana pipiens*). Take a moment to study this figure, for it reinforces an important principle: *Body structures that emerge during one developmental stage are a foundation for the stage that will come after it.* In the sections to follow, you will come across evidence that reinforces this principle.

*Most animal life cycles proceed through gamete formation, fertilization, cleavage, gastrulation, organ formation, and then growth and tissue specialization. Each stage builds on the stage that preceded it.*

**a** Eggs form and mature in female reproductive organs. Sperm form and mature in male reproductive organs.

**b** A sperm penetrates an egg. Their nuclei fuse. A zygote has formed.

**c** Mitotic cell divisions form a ball of cells, a blastula. Each cell gets regionally different parts of the egg cytoplasm.

**d** A gastrula, an early embryo that has primary tissue layers, forms by cell divisions, cell migrations, and rearrangements.

**e** Details of the body plan fill in as different cell types interact and form tissues and organs in predictable patterns.

**f** Organs grow in size, take on mature form, and gradually assume specialized functions.

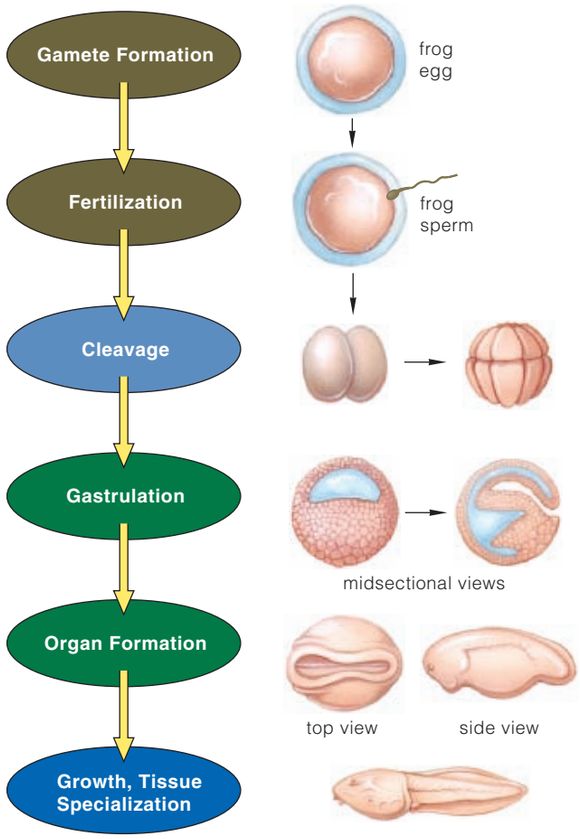



**Figure 43.4** Overview of the stages of animal reproduction and development. We use a few forms that appear during the frog life cycle as examples. The drawings are not to the same scale.

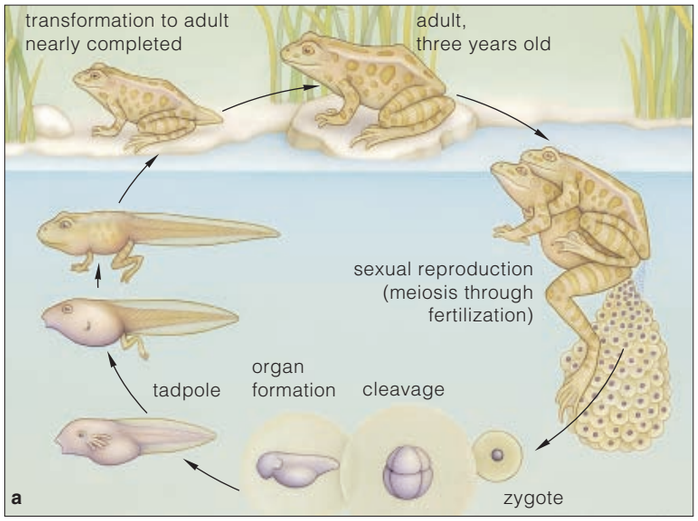



**Figure 43.5** ***Animated!*** Reproduction and development in the life cycle of the leopard frog, *Rana pipiens*.

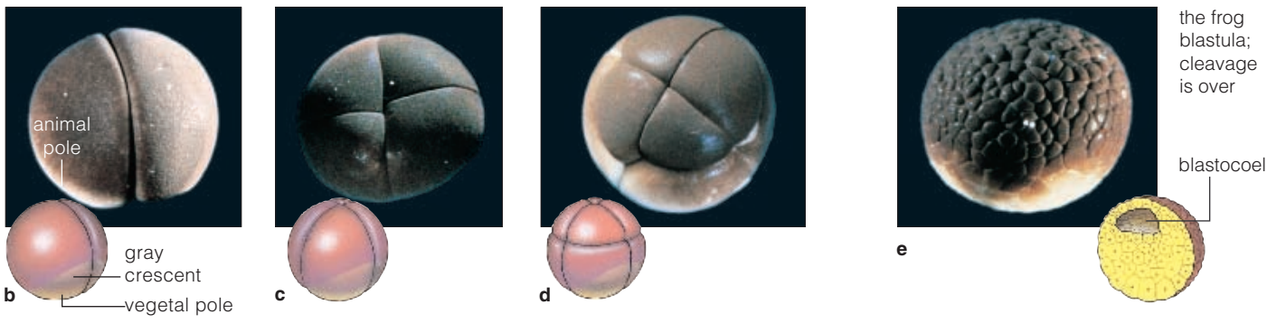
(**a**) We zoom in on the life cycle as a female releases her eggs into the surrounding water and a male releases sperm over the eggs. A frog zygote forms at fertilization. About one hour after fertilization, a surface feature called the gray crescent appears on this type of embryo. It establishes the frog's head-to-tail axis. Gastrulation will start here.

(**b**–**e**) Division planes of the first three cuts of cleavage and the blastula, formed by the end of cleavage. Gastrulation starts with this ball of cells, which contains a fluid-filled cavity (blastocoel).

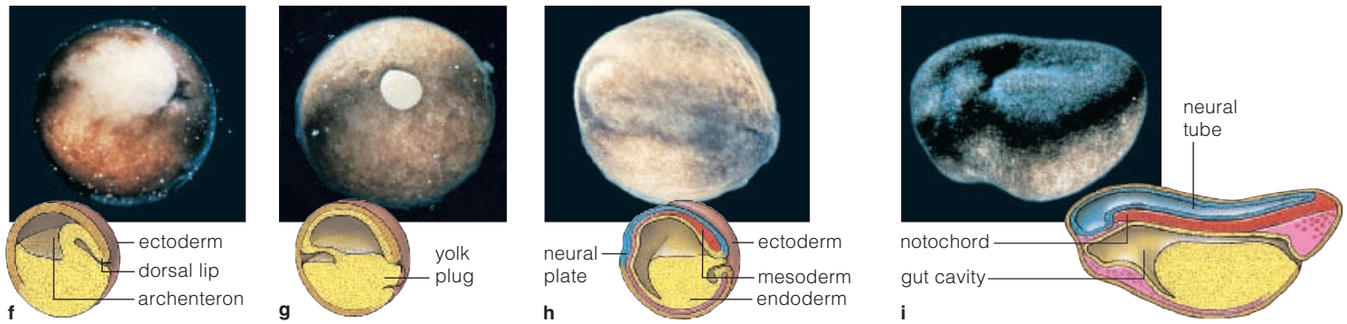
(**f**–**i**) Starting at gastrulation, part of the ectoderm folds inward at a site called the dorsal lip. Three primary tissue layers form by cell migrations and rearrangements. A primitive gut cavity opens up. A neural tube, notochord, and other organs form from the primary tissue layers.

(**j**–**l**) The embryo becomes a tadpole, which develops into an adult.

*Carving up the egg cytoplasm during cleavage:*




*Changes going on during gastrulation and organ formation:*




*Changes in body form during growth and tissue specialization:*

**j** Tadpole, a swimming larva with segmented muscles and a notochord extending into a tail.

**k** Metamorphosis to adult form under way. Limbs growing, tail tissues being resorbed.

**l** Sexually mature, four-legged adult leopard frog.

# 43.3 Early Marching Orders

LINKS TO SECTIONS 4.10, 9.4, 10.5, 25.2

*Why don't you have an arm attached to your nose or toes growing from your navel? The patterning of body parts starts with messages in immature, unfertilized eggs.*

## INFORMATION IN THE EGG

A **sperm**, recall, consists of paternal DNA and a bit of equipment that helps it reach and penetrate an egg. An **oocyte**, or immature egg, is much larger and more complex than the sperm (Section 10.5). As the oocyte is maturing, different numbers and kinds of enzymes, mRNA transcripts, and other factors are stockpiled in different parts of the cytoplasm. They are "maternal messages" for the forthcoming embryo. The messages are commonly used after fertilization, during the early rounds of DNA replication and mitotic cell divisions.

Also, remember how tubulin subunits assemble into microtubules (Section 4.10)? They become localized in specific parts of the egg cytoplasm—which establishes when microtubular spindles will form, and at which angles, for early cell divisions that follow fertilization. The amount of yolk affects how those divisions will cut up and parcel out cytoplasm, and its messages, to cells.

Some messages are "read" as early as fertilization. Most animal eggs show polarity, which establishes a front-to-back body axis for the embryo (Section 25.2).

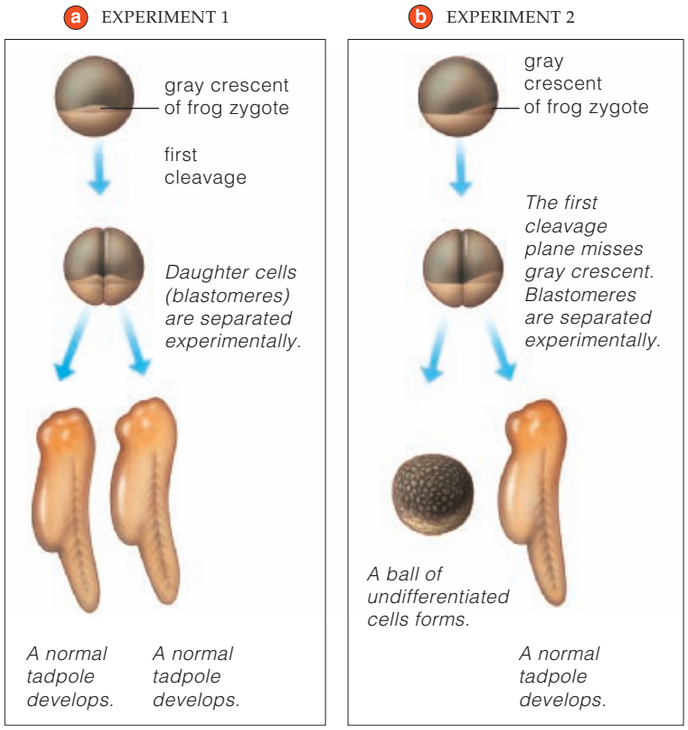
Consider the frog oocyte. A lot of yolk is concentrated near the *vegetal* pole; pigment granules are stockpiled by the *animal* pole, or closest to the nucleus. When a sperm enters the egg cytoplasm, it triggers structural reorganization of the cell cortex—a cytoskeletal mesh beneath the plasma membrane (Section 4.10). Part of the mesh shifts toward the site of penetration, which exposes a crescent-shaped, partially pigmented region near the cell midsection (Figure 43.6). This region, the **gray crescent**, establishes the anterior–posterior axis.

How do we know that a gray crescent is evidence of regional differences in maternal messages? Watch frog embryos develop, and you see that gastrulation normally starts here each time. Experiments of the sort shown in Figure 43.6 offer additional evidence.

## CLEAVAGE—THE START OF MULTICELLULARITY

Once an oocyte is fertilized, a zygote enters cleavage. By this process, recall, a ring of microfilaments just under the plasma membrane contracts and pinches the cell in two (Section 9.4). The zygote's cytoplasm does not grow in size during cleavage; the repeated cuts divide its volume into ever smaller blastomeres.

Simply by virtue of where the cuts are made, the blastomeres receive different maternal messages. This outcome of cleavage, called **cytoplasmic localization**, helps seal the developmental fate of each cell lineage. Cells of one lineage alone might inherit the cytoplasm with a protein that activates, say, a gene coding for a certain hormone. In most animal zygotes, those genes are silent through early cleavage; stockpiled maternal proteins and mRNAs control the cuts. In mammals,



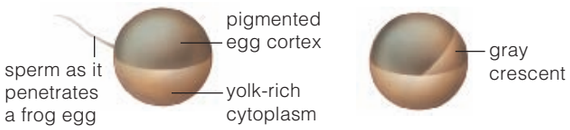
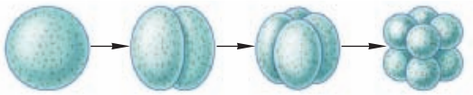



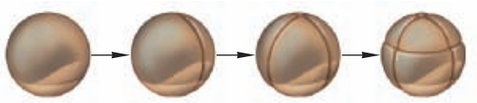

**Figure 43.6** ***Animated!*** Two experiments that showed the effect of cytoplasmic localization on the fate of a frog embryo. The frog egg cortex has granules of dark pigment concentrated near one pole. At fertilization, part of the granule-containing cortex shifts toward the point of sperm entry and exposes lighter colored, yolky cytoplasm, as a crescent-shaped gray area. Normally, the first cleavage puts part of the gray crescent in both of the first two blastomeres.

(**a**) In one experiment, the first two blastomeres were physically separated from each other. Each still gave rise to a whole tadpole.

(**b**) In another experiment, a fertilized egg was manipulated so the cut through the first cleavage plane missed the gray crescent. Only one of the first two blastomeres got the gray crescent. It alone developed into a normal tadpole. Deprived of maternal messages in the cytoplasm beneath the gray crescent, the other cell could not develop normally.



**a** Sea urchin egg, with little yolk. Radial cleavage complete and blastomeres similar in size.



**b** Frog egg, with moderate, localized concentration of yolk. Radial cleavage complete but blastomeres unequal in size.

**c** *Drosophila* egg with an abundance of centrally located yolk. Superficial cleavage, blastomeres form only from the cytoplasm's periphery.

**d** At right, a highly yolky fertilized egg of a zebrafish. Incomplete cleavage; the blastomeres form in a disk-shaped area on top of yolk.

**Figure 43.7** Examples of complete and incomplete cleavage patterns from different groups of animals.

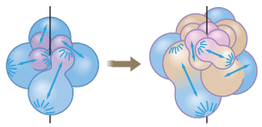
certain genes must be activated first; cleavage cannot be completed without their protein products.

Each species has a characteristic cleavage pattern. Differences start with the first cut, which determines whether the first two cells will be equal or unequal in size and the types and proportions of messages they will receive. The pattern depends in part on whether and how much yolk forms, and where. It depends also on the way the spindle forms, which is a heritable trait.

**Are the Cuts Complete or Incomplete?** When little yolk is present, the first cut divides all the cytoplasm. An abundance of yolk impedes the cut, so cleavage is incomplete. Sea urchin eggs do not have enough yolk to impede complete cuts, and blastomeres are similar in size (Figure 43.7*a*). Cleavage is complete for frogs and other amphibians, but concentrated yolk slows the cuts near the vegetal pole. Blastomeres form faster near the animal pole and are smaller than those carved from the yolky vegetal pole (Figure 43.7*b*). Cleavage is complete in the nearly yolkless eggs of mammals.

*Drosophila* and other insect eggs have a great deal of yolk concentrated in their center. Cuts are confined to the cytoplasm's periphery; cleavage is superficial (Figure 43.7*c*). Eggs of reptiles, birds, and most fishes are so yolky that cuts are exceedingly slow or blocked entirely, *except* in a small, disk-shaped region that has the least amount of yolk (Figure 43.7*d*).

**a** Early protostome embryo. Its four cells are undergoing spiral cleavage, *oblique to* the anterior–posterior axis:



**b** Early deuterostome embryo. Its four cells are undergoing radial cleavage, *parallel with* and *perpendicular to* the anterior–posterior axis:

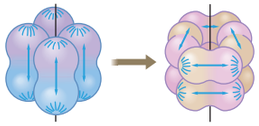


**Figure 43.8** Spiral and radial cleavage patterns.

**How Are the Cuts Oriented?** In Section 25.2, you read about a major divergence in animal evolution. The split into protostomes and deuterostomes arose by modifications in patterns of development. For instance, cleavage is *spiral* in the mollusks, annelids, arthropods, and other protostomes. The first bipolar spindles that form in the egg cytoplasm are angled with respect to the anterior–posterior axis, so all daughter blastomeres are tilted left to right (Figure 43.8*a*). Cleavage is *radial* in deuterostomes, which include the echinoderms and chordates. In these organisms, the first bipolar spindles that form are parallel with the main axis of the embryo, and later ones are perpendicular to it (Figure 43.8*b*).

There are many variations on these basic patterns. Mammals have the slowest cleavage rate of all; twelve to twenty-four hours pass between each cut. The first cut runs parallel with the anterior–posterior axis. Of the two blastomeres that form, one also is cut parallel, but the other gets cut sideways; the spindle orientation rotates by 90 degrees. Similar rotation occurs in some of the descendent cells. This is one type of a *rotational* cleavage pattern. Also, mammalian blastomeres do not all divide at the same time, so the blastula that forms may consist of an odd number of cells.

The next chapter considers how human embryos develop. For now, it is enough to know that the first cuts result in eight blastomeres with spaces between. Tight junctions hold the loose collection together. More cuts result in a hollow ball of cells. These outer cells secrete fluid that fills the ball's cavity; others huddle in a mass against the cavity wall. This type of blastula forms in all mammals, and it is called a **blastocyst**. The inner cell mass gives rise to the embryo proper.

*Unfertilized eggs contain maternal messages: localized regions with differences in the type and proportions of enzymes, mRNAs, tubulins, yolk, and other factors.*

*Cleavage divides a zygote into blastomeres. Simply by virtue of the cuts, each ends up with different maternal messages. Cleavage patterns differ among the major animal groups.*

# 43.4 How Do Specialized Tissues and Organs Form?

LINKS TO SECTIONS 13.4, 15.1, 22.12, 25.1. 28.5

*Nearly all animals have a gut that digests nutrients for absorption. They have surface parts that protect organs inside and detect what is going on outside. Most have organs in between that function in structural support, motion, and circulation. This three-layered body plan emerges after cleavage, as gastrulation gets under way.*

During gastrulation, the embryonic cells migrate and rearrange themselves into three primary tissue layers of the gastrula: ectoderm, endoderm, and mesoderm. Figure 43.9 shows an example. The first cavity to form in protostome gastrulas becomes a mouth, but it will become an anus in deuterostomes (Section 25.2). Also, the anterior–posterior body axis forms in gastrulas. In vertebrates, this main axis precedes the formation of a **neural tube**, the forerunner of the brain and spinal cord (Figures 43.10 and 43.11). These specializations arise through cell differentiation and morphogenesis.

## CELL DIFFERENTIATION

All cells of a normal embryo have the same number and kinds of genes, having descended from the same zygote. They all activate the genes for products that assure their survival, such as histones and glucose-metabolizing enzymes. But from gastrulation onward, **selective gene expression** occurs: Some cell lineages express different groups of genes than others do. This is the start of **cell differentiation**. By this process, cell lineages become specialized in composition, structure, and function (Section 15.1).

As an example, when your eye lenses formed, only one type of cell could activate the genes for crystallin proteins. Long, transparent crystallin fibers formed in the cells and forced them to lengthen and flatten. These differentiated cells impart unique optical properties to each lens. They are only 1 of 200 differentiated cell types in the human body.

As many experiments show, nearly all cells become differentiated with no loss of genetic information. For instance, John Gurdon stripped unfertilized frog eggs

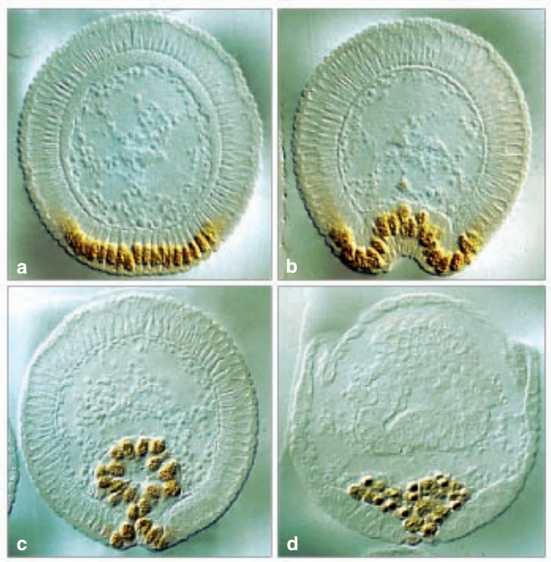



**Figure 43.9** Gastrulation in a fruit fly (*Drosophila*), cross-section. After cleavage, the blastula is transformed into a gastrula. Some cells (stained *gold*) migrate inward through an opening that forms at the surface of the ball of cells. Fruit flies are protostomes; this opening will become a mouth.

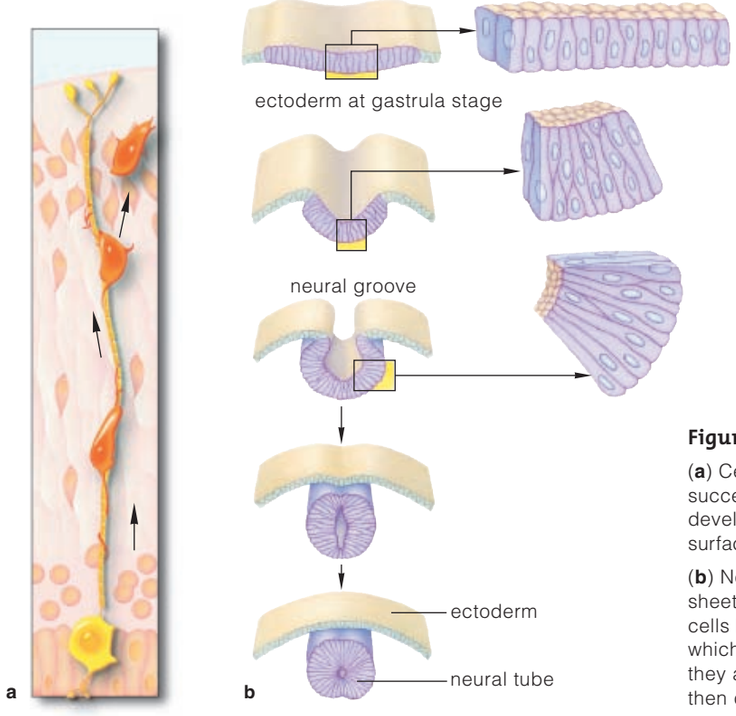



**Figure 43.10** ***Animated!*** Examples of what goes on during morphogenesis.

(**a**) Cell migration. The art shows the same embryonic neuron (*orange*) at successive times during its "climb" along cells that have already formed in developing brain tissue. The neuron is responding to chemical cues on the surface of a glial cell (*yellow*), which guide it to its destination in the embryo.

(**b**) Neural tube formation. By the end of gastrulation, ectoderm is a uniform sheet of cells. Along the axis of the future tube, microtubules in ectodermal cells lengthen. Rings of microfilaments constrict in some of these cells, which become wedge-shaped. The part of the ectodermal sheet where they are located folds back on itself, over the wedge-shaped cells, which then disengage from it as a separate tube.

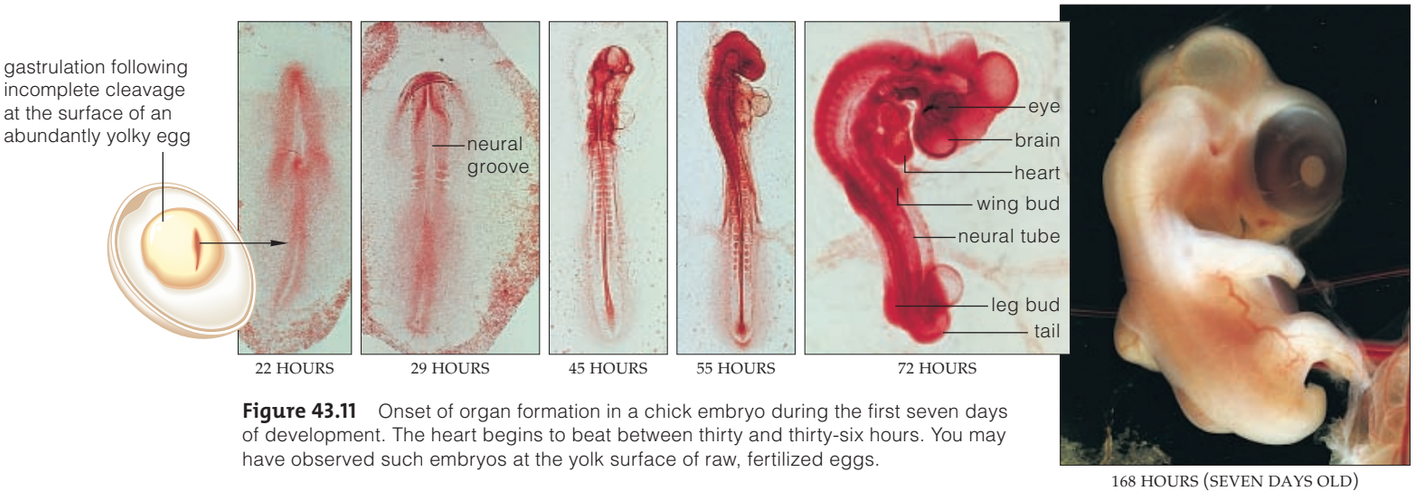



**Figure 43.11** Onset of organ formation in a chick embryo during the first seven days of development. The heart begins to beat between thirty and thirty-six hours. You may have observed such embryos at the yolk surface of raw, fertilized eggs.

of their nucleus. He ruptured the plasma membrane of intestinal cells from tadpoles of the same species. He left the nucleus and much of the cytoplasm of the fully differentiated cells intact and inserted them into the enucleated eggs. Some eggs developed into a frog. Intestinal cells still had the same number and kinds of genes as the zygote; its nucleus still had all the genes required to make all cell types that make up a frog.

Each cell in an early human embryo also retains the capacity to give rise to a whole individual. That is how identical twins arise (page 769). That is the basis of adult cloning methods, as Section 13.4 explains.

## MORPHOGENESIS

Tissues and organs of specific proportions, sizes, and shapes form by a program of orderly changes called **morphogenesis**. During this process, cells of different lineages divide, grow, disperse, and change in size. Tissues lengthen or widen and fold over. And some cells die in controlled ways at prescribed locations.

Think about active cell migration. *Cells send out and use pseudopods that move them along prescribed routes.* When they reach their destination, they connect with cells already there. Embryonic neurons migrate this way in a developing nervous system (Figure 43.10*a*).

How do these cells know where to move and when to stop? They respond to adhesive cues and chemical gradients. The cell migrations are coordinated by the synthesis, release, deposition, and removal of specific chemicals in the extracellular matrix.

The neuron shown in Figure 43.10*a* is responding to gradients in the "stickiness" of its surroundings. Adhesion proteins on a patch of its plasma membrane stuck to proteins on the surface of a glial cell. Now, cytoskeletal elements in the neuron lengthen from the attachment site and push the cytoplasm forward. The neuron will migrate until its surface adhesion proteins reach the spot in the embryo that is stickiest to them. The capacity for adhesion arose early in the evolution of multicelled animals (Sections 22.12 and 25.1).

Also, *whole sheets of cells expand and fold inward and outward as their cells change in shape.* Within these cells, microtubules grow longer, and rings of microfilament constrict. The controlled assembly and disassembly of these cytoskeletal components cause the changes.

Figures 43.10*b* and 43.11 hint at what happens after three primary tissues form in vertebrate embryos. At the embryo's midline, some ectodermal cells elongate and form the neural plate, the start of nervous tissue. The plate sinks inward as cells lengthen and become wedge shaped. At the edges of the resulting groove in the surface, flaps of tissue fold over and meet at the midline, forming the neural tube.

Finally, *programmed cell death helps sculpt body parts*. By this process, called **apoptosis**, signaling molecules from some cells activate tools of self-destruction that are stockpiled in other, target cells. Remember how a human hand forms from a paddle-shaped body part? Programmed cell suicide was at work (Section 28.5).

*In cell differentiation, some cells selectively use certain genes that other cells do not use. Selective gene expression is the basis of cell differentiation. It results in cell lineages with characteristic structures, products, and functions.*

*Morphogenesis is a program of orderly changes in the size, shape, and proportions of developing tissues and organs.*

*Morphogenesis involves cell division, active cell migration, tissue growth and foldings, changes in cell size and shape, and programmed cell death, or apoptosis.*

# 43.5 Pattern Formation

LINKS TO SECTIONS 15.1, 15.3, 17.8

*Maternal messages in the egg cytoplasm guide the earliest stages of development. Later on, communication signals among embryonic cells cause tissues and organs to form according to a mapped-out body plan.*

## EMBRYONIC INDUCTION

In the developing embryo, cells divide, differentiate, and live or die. They migrate and stick to cells of the same type in tissues. They fill in details of the body plan in ordered patterns. Cells of frog embryos form a head at one end and a tail at the other, and so on.

Once locked in a tissue, an embryonic cell starts to selectively read its genes. Often it makes and secretes signaling molecules that affect its neighbors (Figure 43.12). *Signals diffusing through the neighborhood induce changes in the composition, structure, or both of all target cells*. They cause target cells to remember the roles that they—and their descendants—are supposed to play in the formation of tissues and organs.

We have experimental evidence of cell memory. In one case, researchers excised the dorsal lip of a normal axolotl embryo, then grafted it into a novel location in a different axolotl embryo. Gastrulation proceeded at the recipient's dorsal lip *and also at the graft*. A double embryo with two sets of body parts formed (Figure 43.13). The dorsal lip organizes this amphibian's front-to-back axis. It was the first embryonic signaling center discovered. Experiments with wing development also provide evidence of cell memory (Figure 43.14).

Thus, by **embryonic induction**, the developmental fates of embryonic cell lineages change when exposed to signals—gene products—from adjacent tissues. The signals are the basis of **pattern formation**, a sculpting of specialized tissues and organs from clumps of cells in the proper places in the embryo, in the proper order. These signals act on cells that start out as neighbors. They act on cells that meet up during gastrulation and other morphogenetic movements.

Many signals are short range, involving cell-to-cell contacts. For instance, signals that activate or inhibit genes for adhesion proteins and recognition proteins directly affect how cells interact in tissues and organs. Such proteins include cadherins and integrins, which affect how cells link up when the gastrula, then organs, are forming. Short-range signals also make cytoskeletal elements in a target cell lengthen in a specific direction. *Such signals can cause a given cell to stick to its neighbors, or break free and migrate to a different location, or become segregated from the cells of an adjoining tissue.*

Long-range signals act on control elements in the DNA of embryonic cells that are some distance away. Think about **morphogens**. These degradable molecules diffuse out of signaling centers, so their concentration weakens with distance. Each cell at a given point along a resulting gradient can chemically assess its position in the embryo, which affects how it will differentiate. *Differences in a signaling molecule's concentration induce lineages of cells positioned at different positions along the gradient to read different parts of the same genome.*

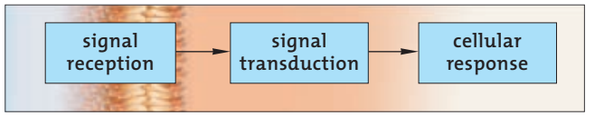
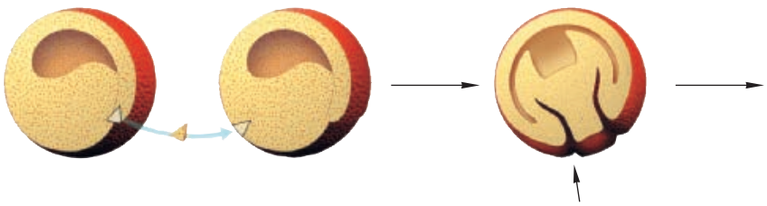



**Figure 43.12** Recap of signal transduction pathways. A signaling molecule docks at a membrane receptor. The signal then activates enzymes or other cytoplasmic components that cause changes in metabolism, gene expression, or cell membrane properties.

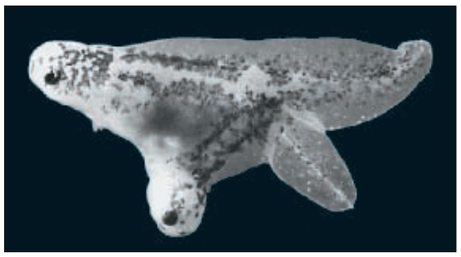
## A THEORY OF PATTERN FORMATION

The same kinds of genes are mapmakers for all major groups of animals. In Section 15.3, you saw how genes sculpt a *Drosophila* embryo into a series of segments.



a Dorsal lip excised from donor embryo is grafted to an abnormal site in another embryo.

b Graft induces a second site of inward migration.



c The embryo develops into a "double" tadpole. Most of its tissues originated from the host embryo.

**Figure 43.13** ***Animated!*** Experimental evidence that a dorsal lip controls amphibian gastrulation. A dorsal lip region of an axolotl embryo was transplanted to a different site in another axolotl embryo. It organized the formation of another set of body parts.

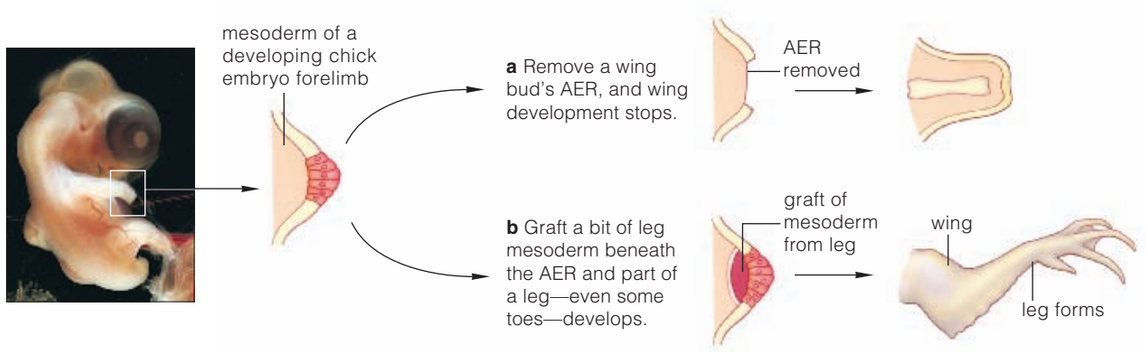



**Figure 43.14**
Experimental evidence of signaling between the mesoderm and ectoderm as a chick wing develops from a wing bud. AER is a narrow ridge of self-perpetuating cells at the apex of the two wing buds.

In Section 17.8, you read that genes map out the kind and number of legs, wings, and other appendages. Let us now put these examples in a broader context:

1. The formation of tissues and organs in ordered, spatial patterns starts with cytoplasmic localization, which equips cells with the molecular means to send and receive signals. Cell-to-cell contacts require short-range signals. Embryonic signaling centers also send long-range cues: chemical gradients that weaken with distance from the source. Embryonic cells at the start, middle, and end of a gradient are exposed to different chemical information and respond in different ways.

2. Morphogens and other inducer molecules diffuse through embryonic tissues, and they activate classes of **master genes** in sequence. The products of these genes interact with diverse control elements to lay the foundation for the basic body plan.

3. Products of **homeotic genes** and other master genes interact with control elements to map out the overall body plan. They form as blocks of genes are activated and suppressed in different cells along the anterior–posterior axis and dorsal–ventral axis of the embryo. Other gene products interact in ways that fill in the details of specific body parts.

Master genes and their products function in similar ways in all animal groups. When they fail in mapping out the overall body plan, results are disastrous, as when a heart forms in the wrong place. Once a plan is locked in, inductions can have only localized effects. If a lens fails to form, only the eye will be affected.

## EVOLUTIONARY CONSTRAINTS ON DEVELOPMENT

How long have master genes been around? The basic body plan for sponges, worms, flies, vertebrates, and all other major animal groups has not changed much for about 500 million years. All of the many millions of species are variations on a few dozen plans!

Why is this so? There are few new master genes, *so variations in form might be more of an outcome of how the control genes control each other*. Consider that insect, squid, and vertebrate eyes differ structurally, and yet genes governing eye formation are nearly identical in these groups. An *eyeless* gene controls eye formation in fruit flies (*Drosophila*). In humans, mutation of a nearly identical gene causes eyeless babies. The same gene controls the fate of cells that give rise to legs of fruit flies, crabs, and beetles, butterfly wings, sea star arms, fish fins, and mouse feet. These structures all start as buds from the main body axis (Section 17.8).

For a long time, we have known that body plans cannot change much because of *physical* constraints (such as the surface-to-volume ratio) and *architectural* constraints (as imposed by body axes). We now know there are *phyletic* constraints on change. These are the constraints imposed on each lineage by interactions of master organizer genes, which operate when organs form and control induction of the basic body plan.

That may be why we have so many species and so few body plans. Once the master genes evolved and started interacting in intricate ways, it would have been hard to change the basic parts without killing the embryo. Mutations have indeed added marvelous variations to animal lineages. But the basic body plans have prevailed through great spans of time, so maybe it simply proved unworkable to start all over again.

*Pattern formation is the ordered sculpting of embryonic cells into specialized tissues and organs.*

*Products that form through the orderly activation of classes of master genes map out the basic body plan. They specify where and how body parts develop. They are long-range as well as short-range beacons that help cells assess their position and how they will differentiate.*

*Physical, architectural, and phyletic constraints limit the evolution of animal body plans. Master genes are similar and sometimes identical among all major animal groups.*

# 43.6 Why Do We Age and Die?

LINKS TO PAGES 105, 206, SECTIONS 12.4, 12.8, 33.6

*As the years pass, all multicelled species undergo **aging**; tissues become harder to maintain and repair. Each species has a maximum life span—122 years for humans, 20 years for dogs, 12 weeks for butterflies, 35 days for fruit flies, and so on. The verifiably oldest human lived 122 years. We can expect that genes influence aging processes.*

## PROGRAMMED LIFE SPAN HYPOTHESIS

Do biological clocks influence aging? If so, an animal body might be analogous to a clock shop, with each type of cell, tissue, and organ ticking away at its own genetically set pace. Many years ago, Paul Moorhead and Leonard Hayflick tested this hypothesis. The two researchers cultured human embryonic cells—which divided about fifty times before dying out.

Hayflick also took cultured cells that were part of the way through the series of divisions and froze them for a few years. After he thawed the cells and placed them in a culture medium, they completed an *in vitro* cycle of fifty doublings and died on schedule.

No cell in a human body divides more than eighty or ninety times. You may well wonder: If an internal clock ticks off their life span, then how can *cancer* cells go on dividing? The answer provides us with a clue to why *normal* cells can't beat the clock.

Cells, remember, duplicate all chromosomes before they divide. Chromosomes have **telomeres**, or caps of DNA and proteins. Telomeres keep the chromosome ends from unraveling. Each time the nucleus divides, enzymes nibble off a bit of each telomere. When only a nub remains, cells stop dividing and die.

Cancer cells and germ cells are exceptions; both make telomerase, an enzyme that makes telomeres lengthen. Expose cells in culture to telomerase, and they go on dividing well beyond the normal life span.

## CUMULATIVE ASSAULTS HYPOTHESIS

Another hypothesis: Over the long term, aging is the outcome of cumulative damage at the molecular and cellular levels. Environmental assaults and failure of DNA repair mechanisms are at work here.

For example, the rogue molecular fragments called free radicals attack all biological molecules, including DNA. This includes DNA of mitochondria, the power plants of eukaryotic cells. Structural changes in DNA can skew the synthesis of enzymes and other proteins necessary for normal life processes.

Free radicals are implicated in many age-related problems, such as cataracts, Alzheimer's disease, and atherosclerosis. In one recent experiment, researchers extended the average life span of some roundworms by 50 percent simply by providing them with synthetic antioxidant enzymes.

Other studies suggest that extending the life span may come at a cost. Researchers were able to double the life span of roundworms by knocking out a single gene. However, the mutant worms were sterile.

What about DNA replication and repair problems? *Werner's syndrome*, an aging disorder, is linked with a mutation in a gene that specifies one of the enzymes that unwind nucleotide strands. The mutated helicase probably does not compromise replication of DNA; affected people do not die right away. They start aging fast in their thirties and die before age fifty. But the nonmutated gene may be vital for repairs. People with Werner's syndrome accumulate mutations at high rates. Sooner or later, the damage interferes with cell division. Like skin cells of the elderly, skin cells of Werner's patients just do not divide many times.

It may be that both hypotheses have merit. Aging may be an outcome of many interconnected processes in which genes, hormones, environmental assaults, and a decline in DNA repair mechanisms come into play. Consider how living cells of all tissues depend upon exchanges of materials with extracellular fluid. Also consider how collagen is a structural component of many connective tissues. If something shuts down or mutates collagen-encoding genes, then missing or altered gene products may disrupt flow of oxygen, nutrients, hormones, and so forth to and from living cells through every connective tissue. Repercussions from such a mutation would ripple through the body.

Similarly, if mutations cause altered self markers on the body's cells, do T cells of the immune system perceive them as foreign and attack? If autoimmune responses were to become more frequent over time, they would promote greater vulnerability to disease and stress associated with old age.

In evolutionary terms, reproductive success means living long enough to produce and raise offspring. Humans reach sexual maturity in fifteen years *and* help children reach adulthood. We don't *need* to live longer than we do. But we among all animals have the capacity to think about it, and most of us decide that we like life better than the alternative. Eventually, however, we may all learn to accept the inevitability of our mortality with wisdom and grace.

*Aging may be an outcome of time running out on internal biological clocks as well as cumulative, irreversible damage at the molecular and cellular levels.*

CONNECTIONS

## 43.7 Death in the Open

*As a leading cancer specialist, Lewis Thomas reflected with compassion on the fear of dying. Before Thomas himself died of cancer, he gave us this gift of insight.*

Everything in the world dies, but we only know about it as a kind of abstraction. If you stand in a meadow, at the edge of a hillside, and look around carefully, almost everything you catch sight of is in the process of dying, and most things will be dead long before you are. If it were not for the constant renewal and replacement going on before your eyes, the whole place would turn to stone and sand under your feet….

There are said to be a billion billion insects on the Earth at any moment, most of them with short life expectancies by our standards. Someone estimated that there are 25 million assorted insects hanging in the air over every temperate square mile, in a column extending upward for thousands of feet, drifting through the layers of atmosphere like plankton. They are dying steadily, some by being eaten, some just dropping in their tracks, tons of them around the Earth, disintegrating as they die, invisibly.

Who ever sees dead birds, in anything like the huge numbers stipulated by the certainty of the death of all birds? A dead bird is an incongruity, more startling than an unexpected live bird, sure evidence to the human mind that something has gone wrong. Birds do their dying off somewhere, behind things, under things, never on the wing.

Animals seem to have an instinct for performing death alone, hidden. Even the most conspicuous find ways to conceal themselves in time. If an elephant missteps and dies in an open place, the herd will not leave him there; the others will pick him up and carry the body from place to place, finally putting it down in some inexplicably suitable location. When elephants encounter the skeleton of an elephant in the open, they methodically take up the bones and distribute them, in a ponderous ceremony, over neighboring acres.

It is a natural marvel. All of the life on Earth dies all of the time, in the same volume as the new life that dazzles us each morning, each spring. All we see of this is the odd stump, the fly struggling on the porch floor of the summer house in October, the fragment on the highway. I have lived all my life with an embarrassment of squirrels in my backyard, they are all over the place, all year long, and I have never seen, anywhere, a dead squirrel.

I suppose it is just as well. If Earth were otherwise, and all the dying were done in the open, with the dead there to be looked at, we would never have it out of our minds. We can forget about it much of the time, or think of it as an accident to be avoided somehow. But it does make the process of dying seem more exceptional than it really is, and harder to engage in at the times when we must ourselves engage.

In our way, we conform as best we can to the rest of nature. The obituary pages tell us of the news that we are dying away, while birth announcements in finer print, off at the side of the page, inform us of our replacements, but we get no grasp from this of the enormity of the scale. There are now billions of us on the Earth, and all must be dead, on a schedule, within this lifetime. The vast mortality, involving something over 50 million each year, takes place in relative secrecy. We can only really know of the deaths in our households, among our friends. These, detached in our minds from all the rest, we take to be unnatural events, anomalies, outrages. We speak of our own dead in low voices; struck down, we say, as though visible death can occur only for cause, by disease or violence, avoidably. We send off for flowers, grieve, make ceremonies, scatter bones, unaware of the rest of the billions on the same schedule. All of that immense mass of flesh and bone and consciousness will disappear by absorption into the Earth, without recognition by the transient survivors.

Less than half a century from now, our replacements will have more than doubled in numbers. It is hard to see how we can continue to keep the secret, with such multitudes doing the dying. We will have to give up the notion that death is a catastrophe, or detestable, or avoidable, or even strange. We will need to learn more about the cycling of life in the rest of the system, and about our connection in the process. Everything that comes alive seems to be in trade for everything that dies, cell for cell. There might be some comfort in the recognition of synchrony, in the information that we all go down together, in the best of company.

— LEWIS THOMAS, 1973

## Summary

**Section 43.1** Compared with asexual reproduction, reproducing sexually takes more time and energy, in terms of the structures and behaviors required. Also, the genetic representation in the next generation of each parent is not as great. However, it might give the offspring a greater capacity to make faster adaptive responses to changing biotic and abiotic conditions.

**Section 43.2** Most animal life cycles have six stages of embryonic development, and each must be completed successfully before the next begins:

Gamete formation. Oocytes (immature eggs) and sperm form in reproductive organs.

Fertilization. A sperm penetrates an egg cytoplasm; the sperm and egg nuclei fuse and form a zygote. This fertilized egg is the first cell of a new individual.

Cleavage. Mitotic cell divisions cut the egg cytoplasm into ever smaller blastomeres with no increase in volume.

Gastrulation. Two or three primary tissue layers (germ layers) form: ectoderm, endoderm, and often mesoderm. All tissues of the adult body develop from these layers.

Onset of organ formation. Different organs start developing by a tightly orchestrated program of cell differentiation and morphogenesis.

Growth and tissue specialization. Organs enlarge and acquire specialized chemical and physical properties.

Biology Now

*View the development of a frog with the animation on BiologyNow.*

**Section 43.3** As eggs mature, different types and proportions of enzymes, mRNAs, tubulins, and other maternal messages are stockpiled in different parts of the cytoplasm. After fertilization, cleavage puts these maternal messages in different daughter cells.

Cleavage patterns differ among animal groups. The cuts are complete in eggs with a sparse to moderate amount of yolk and may produce blastomeres of equal or unequal size. Cuts are incomplete in highly yolky eggs, and blastomeres form from all or part of the periphery of the cytoplasm only. How the cuts are oriented depends on the mitotic spindle's orientation, which is a heritable trait. Different maternal messages end up in different blastomeres, an outcome called cytoplasmic localization. Cleavage ends with the formation of a blastula, a tiny ball of cells with a fluid-filled cavity, the blastocoel.

Biology Now

*See a demonstration of the effects of cytoplasmic localization with the animation on BiologyNow.*

**Section 43.4** In cell differentiation, a cell selectively uses certain genes and synthesizes proteins not found in other cell types. The outcomes are subpopulations of specialized lineages of cells that differ from one another in their structure, biochemistry, and functioning.

Morphogenesis starts at gastrulation. By this program of orderly changes, tissues and organs of specific sizes, shapes, and proportions emerge. It involves cell divisions, migrations, enlargements, and programmed cell death, as well as the lengthening, widening, and folding of tissues.

Biology Now

*Learn about neural tube formation with the animation on BiologyNow.*

**Section 43.5** By embryonic induction, embryonic cell lineages become committed to developing a certain way when they are exposed to signals from adjacent tissues. The signals are the basis of pattern formation, a sculpting of specialized tissues and organs from clumps of cells in the proper places in the embryo, in the proper order. Signals act on cells that form together, as well as on cells that make contact during morphogenesis.

Products of master genes map out the basic body plan. Different products are short-range and long-range beacons, as when they form gradients from signaling centers that help cells assess their position in the embryo and how they will contribute to the formation of tissues and organs. Master genes are similar and in some cases identical among all major animal groups.

Biology Now

*See experimental evidence of embryonic induction with the animation on BiologyNow.*

**Sections 43.6, 43.7** Aging may be partly a result of time running out of internal biological clocks, which are genetically preset. Aging also may be partly an outcome of cumulative assaults on DNA and other biological molecules during the life cycle.

## Self-Quiz

*Answers in Appendix II*

1. Compared to an asexual reproducer, a male or female animal that reproduces sexually _____ .
   a. has spent more, biologically
   b. has fewer of its genes in the next generation
   c. gets variation in traits among offspring
   d. all of the above

2. A cell formed during cleavage is a _____ .
   a. blastula b. morula c. blastomere d. gastrula

3. Three primary tissue layers form during _____ .
   a. gametogenesis c. gastrulation
   b. implantation d. pattern formation

4. _____ distributes different maternal messages to different blastomeres.
   a. Gametogenesis c. Morphogenesis
   b. Cleavage d. Pattern formation

5. Primary tissue layers first appear _____ .
   a. in the egg cortex c. in the gastrula
   b. during cleavage d. in primary organs

6. During development, the formation of subpopulations of different cell types is the outcome of _____ .
   a. selective gene expression c. metamorphosis
   b. cell differentiation d. a and b

7. Homeotic genes map out the _____ .
   a. cleavage planes c. basic body plan
   b. primary tissue layer d. all of the above

8. _____ take part in pattern formation.
   a. Master genes
   b. Morphogens
   c. Regulatory proteins
   d. all of the above

9. The developmental fate of an embryonic cell lineage changes upon exposure to gene products from an adjacent tissue. This is a case of _____ .
   a. cleavage
   b. embryonic induction
   c. cytoplasmic localization
   d. apoptosis

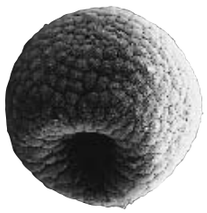
10. The cleavage pattern for *Drosophila* is _____ .
   a. superficial
   b. superfluous
   c. radial
   d. rotational

11. Match each term with the most suitable description.
   ____ gamete formation
   ____ fertilization
   ____ cleavage
   ____ gastrulation
   ____ cell differentiation
   ____ morphogenesis
   a. blastomeres form
   b. cellular rearrangements form primary tissues
   c. eggs and sperm form
   d. sperm and egg nuclei fuse
   e. tissues, organs of specific sizes and shapes emerge
   f. in most species, result of selectively using genes

*Additional questions are available on* Biology Now™

## *Critical Thinking*

1. The zebrafish (*Danio rerio*) is special to developmental biologists. This small freshwater fish is easily maintained in tanks. A female produces hundreds of eggs, which can develop and hatch in three days. The transparent embryos let researchers directly observe developmental events (Figure 43.15). Single cells can be injected with dye to see how they change position, or they can be killed or injected with genes to observe the outcome. In evolutionary terms, *D. rerio* is only remotely related to humans. Explain why researchers expect the early development of this fish to yield useful information about human development.



2. The photograph at left shows an early embryonic stage of a sea urchin (*Lytechinus*). Is it a blastula? Or a gastrula? How do you know?

3. Before an amphibian egg enters cleavage, you divide it so that the gray crescent is parceled out to only one of the two blastomeres that form first. You separate the two blastomeres. Only the one with the gray crescent gives rise to an embryo with an anterior–posterior axis, notochord, nerve cord, and dorsal muscles. The other blastomere gives rise to a shapeless mass of immature gut cells and blood cells. Would you expect cytoplasmic localization or embryonic induction to exert more influence in bringing about these results? Explain your answer.

4. In normal *Drosophila* larvae, a specific cluster of cells is the embryonic source of antennae on the head. When a larva has a certain mutant gene, it develops legs instead of antennae on its head, as in Section 15.4. Would you say that the mutated gene is first expressed during cleavage or during organ formation?

5. Four hundred million years ago, six-legged insect lineages arose from crustaceans that had far more jointed legs. Based on what you know about the constraints on drastic changes in morphology, formulate a hypothesis to explain why such a drastic reduction has persisted.

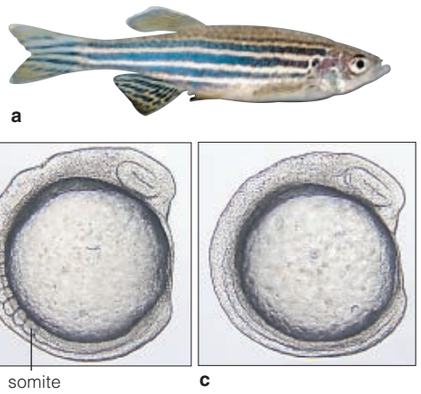



**Figure 43.15** (**a**) Adult zebrafish. (**b**) Normal embryo. Somites, a series of segments that give rise to bone and muscle, are clearly visible. (**c**) Mutant embryo that could not form somites. Changes in developmental steps show up clearly in these transparent embryos.

6. Once in a while in humans, the first two blastomeres, the inner cell mass, or the blastocyst splits in two. *Identical* twins, which have identical genes and are the same sex, may be the result. But identical offspring are the norm for the nine-banded armadillo (*Dasypus novemcinctus*), the state mammal of Texas and a common sight in the southeastern United States. Four offspring make up a normal litter. They formed from the same fertilized egg. After the second cleavage, the four blastomeres separated and each developed into an armadillo. Explain why this embryonic event reduces the genetic variability within an armadillo litter. In evolutionary terms, what might be some disadvantages of this event?

7. Sometimes mRNA transcripts cannot hang around in an embryonic cell after they have been used. For instance, some may have translated for an early developmental step that is over. How can the cell get rid of mRNA that is no longer needed and might cause problems in upcoming stages? In many eukaryotes, including roundworms, insects, fishes, and mammals, cells prevent transcription of unwanted mRNAs by *RNA interference*.

The process begins with the transcription of a gene that encodes a small interfering RNA (siRNA). The product is a long RNA sequence with a region complementary to the unwanted mRNA. A group of enzymes and other proteins attaches to a mature siRNA transcript. When the unwanted mRNA binds with the transcript, the proteins chop it up and destroy it.

How important are the siRNAs? One way to find out is to observe what happens if cells cannot make them. For example, you can inactivate Dicer, an enyzme that is required to produce mature siRNA. The results of such experiments suggest that siRNAS are essential for normal vertebrate development. When Dicer production was prevented in zebrafish, development was abnormal and stopped short of maturity. Attempts to breed Dicer-free mice have been unsucessful. Homozygous mutants do not survive to birth.

Genes encode siRNAs. We know that genes can mutate. So it is reasonable to assume that some mutations will produce defective siRNAs. Think about how particular genes are turned on during different developmental stages. What types of genes would you expect to be targeted by siRNAs during development? What might happen if the products of these genes remained available in cells longer than they should be?