CHAPTER 29

REPRODUCTION AND DEVELOPMENT

Outline

Concepts

1. All animals have the capacity to reproduce. The simplest form of reproduction is asexual. Asexual reproduction produces new individuals from one parent, but it does not produce new genetic combinations among offspring, as does sexual reproduction.
2. Almost all animals reproduce sexually, at least sometimes. Sexual reproduction involves mechanisms that bring sperm and egg together for fertilization and ensure that the fertilized egg has a suitable place to develop until the new animal is ready to function on its own.
3. Sexual reproduction evolved in aquatic environments, and its modification for organisms living on dry land entailed evolutionary innovations to prevent the gametes and embryos from drying out.
4. Mammalian fertilization and embryonic development are both internal.
5. Hormones coordinate the reproductive functions in both males and females. In female mammals, hormones also maintain pregnancy, and after childbirth, stimulate the production and letdown of milk from the mammary glands.

Reproduction is a basic attribute of all forms of life. Chapter 3 describes the general features of animal development and the control processes that allow a genotype to be translated into its phenotype. Although in modern zoology, development is "the center stage" in reproduction, the whole process includes the behavior, anatomy, and physiology of adults—whether protists, invertebrates, or vertebrates. This chapter begins with a comparative focus on the different reproductive strategies observed in protists, invertebrates, and the five major groups of vertebrates. The chapter concludes with a discussion of human reproduction, not only because of the subject's basic interest to everyone, but because scientists know more about the biochemistry, hormones, anatomy, and physiology of human reproduction than they do about any other species.

ASEXUAL REPRODUCTION IN INVERTEBRATES

In the biological sense, reproduction means producing offspring that may (or may not) be exact copies of the parents. Reproduction is part of a life cycle, a recurring frame of events in which animals grow, develop, and reproduce according to a program of instruction encoded in the DNA they inherit from their parents. One of the two major types of reproduction in the biological world is asexual reproduction.

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

The first organisms to evolve probably reproduced by pinching in two, much like the simplest organisms that exist today do. This is a form of **asexual reproduction,** which is reproduction without the union of gametes or sex cells. *In the first two billion years or more of evolution, forms of asexual reproduction were probably the only means by which the primitive organisms could increase their numbers. While asexual reproduction effectively increases the numbers of a species, those species reproducing asexually tend to evolve very slowly, because all offspring of any one individual are alike, providing less genetic diversity for evolutionary selection.*

Asexual reproduction is common among the protozoa, as well as among lower invertebrates, such as sponges, jellyfishes, flatworms, and many segmented worms. Asexual reproduction is rare among the higher invertebrates. The ability to reproduce asexually often correlates with a marked capacity for regeneration.

In the lower invertebrates, the most common forms of asexual reproduction are fission, budding (both internal and external), and fragmentation. Parthenogenesis, which is comparatively uncommon, also occurs in a few invertebrates.

FISSION

Protists and some multicellular animals (cnidarians, annelids) may reproduce by fission. **Fission** (L. *fissio*, the act of splitting) is the division of one cell, body, or body part into two (figure 29.1*a*). In this process, the cell pinches in two by an inward furrowing of the plasma membrane. Binary fission occurs when the division is equal; each offspring contains approximately equal amounts of protoplasm and associated structures. Binary fission is common in protozoa; for some, it is their only means of reproduction.

In fission, the plane of division may be asymmetrical, transverse, or longitudinal, depending on the species. For example, the multicellular, free-living flatworms, such as the common planarian, reproduce by longitudinal fission (figure 29.1*b*). Some flatworms and annelids reproduce by forming numerous constrictions along the length of the body; a chain of daughter individuals results (figure 29.1*c*). This type of asexual reproduction is called multiple fission.

BUDDING

Another method of asexual reproduction found in lower invertebrates is **budding** (L. *bud*, a small protuberance). For example, in the cnidarian *Hydra* and many species of sponges, certain cells divide rapidly and develop on the body surface to form an external bud (figure 29.1*d*). The bud cells proliferate to form a cylindrical structure, which develops into a new animal, usually breaking away from the parent. If the buds remain attached to the parent, they form a colony. A **colony** is a group of closely associated individuals of one species. Internal budding (as in the freshwater sponges) produces gemmules, which are collections of many cells surrounded by a body wall. When the body of the parent dies and degenerates, each gemmule gives rise to a new individual.

FRAGMENTATION

Fragmentation is a type of asexual reproduction whereby a body part is lost and then regenerates into a new organism. Fragmentation occurs in some cnidarians, platyhelminths, rhynchocoels, and echinoderms. For example, in sea anemones, as the organism moves, small pieces break off from the adult and develop into new individuals (figure 29.1*e*).

PARTHENOGENESIS

Certain flatworms, rotifers, roundworms, insects, lobsters, some lizards, and some fishes can reproduce without sperm and normal fertilization. These animals carry out what is called **parthenogenesis** (Gr. *parthenos*, virgin + *genesis*, production). (However, most parthenogenetic animals also can reproduce sexually at some point in their life history.) Parthenogenesis is a spontaneous activation of a mature egg, followed by normal egg divisions and subsequent embryonic development. In fact, mature eggs of species that do not undergo parthenogenesis can sometimes be activated to develop without fertilization by pricking them with a needle, by exposing them to high concentrations of calcium, or by altering their temperature.

Because parthenogenetic eggs are not fertilized, they do not receive male chromosomes. The offspring would thus be expected to have only a haploid set of chromosomes. In some animals, however, meiotic division is suppressed, so the diploid number is conserved. In other animals, meiosis occurs, but an unusual mitosis returns the haploid embryonic cells to the diploid condition.

Overall, animals that reproduce parthenogenetically have substantially less genetic variability than do animals with chromosome sets from two parents. This condition may be an advantage for animals that are well adapted to a relatively stable environment. However, in meeting the challenges of a changing environment, parthenogenetic animals may have less flexibility, which may explain why this form of reproduction is relatively uncommon.

Parthenogenesis also plays an important role in social organization in colonies of certain bees, wasps, and ants. In these insects, large numbers of males (drones) are produced parthenogenetically, whereas sterile female workers and reproductive females (queens) are produced sexually.

ADVANTAGES AND DISADVANTAGES OF ASEXUAL REPRODUCTION

The predominance of asexual reproduction in protists and some invertebrates can be partially explained by the environment in which they live. The marine environment is usually very stable. Stable environments may favor this form of reproduction because a combination of genes that matches the relatively unchanging environment is an advantage over a greater number of gene combinations, many of which do not match the environment. In other habitats, asexual reproduction is seasonal. The season during which asexual reproduction occurs coincides with the period

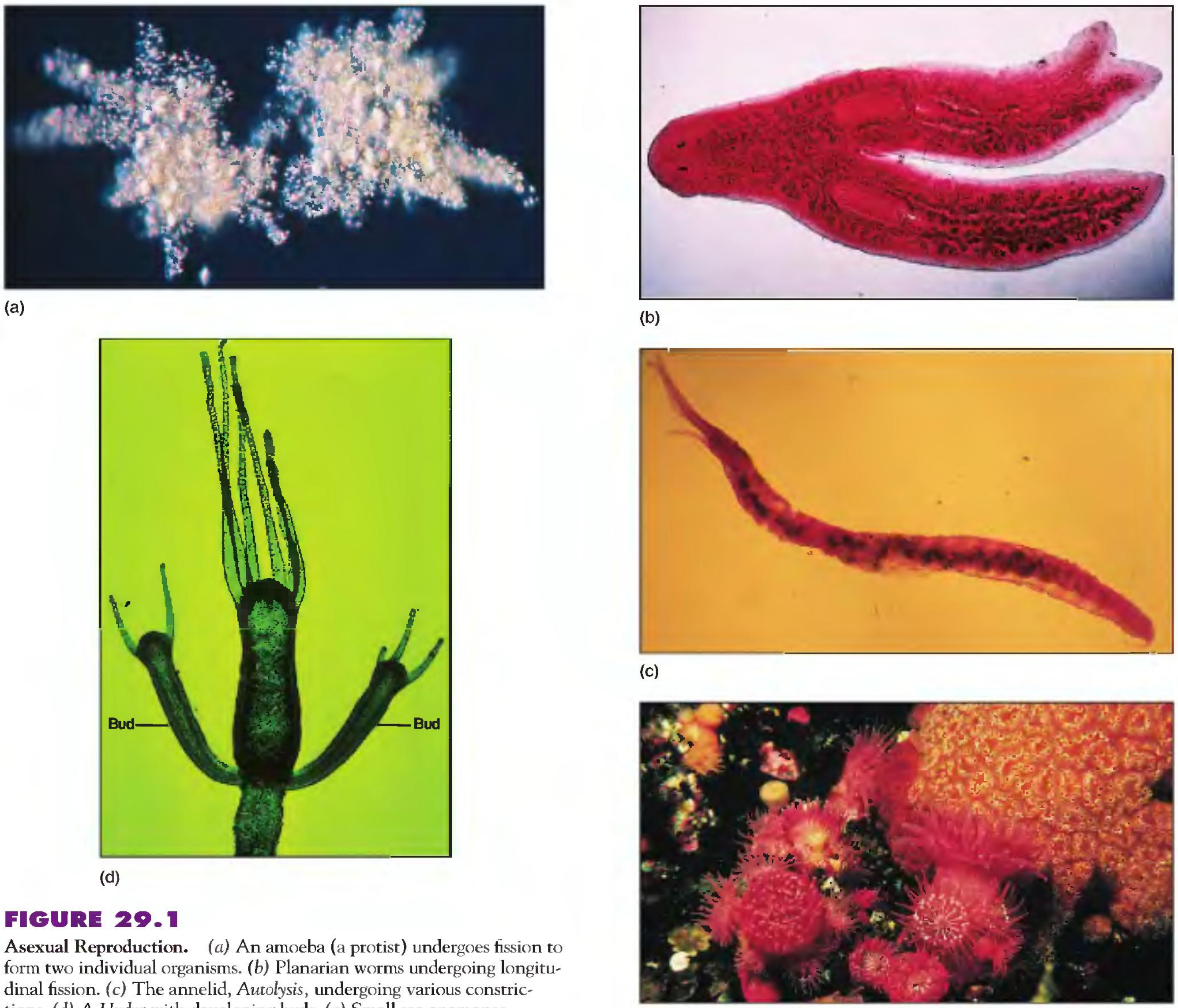


FIGURE 29.1

Asexual Reproduction. *(a)* An amoeba (a protist) undergoes fission to form two individual organisms. *(b)* Planarian worms undergoing longitudinal fission. *(c)* The annelid, *Autolysis*, undergoing various constrictions. *(d)* A *Hydra* with developing buds. *(e)* Small sea anemones produced by fragmentation.

when the environment is predictably hospitable. Under such conditions, it is advantageous for the animal to produce asexually a large number of progeny with identical characteristics. A large number of animals, well adapted to a given environment, can be produced even if only one parent is present.

Without the tremendous genetic variability bestowed by meiosis and sexual processes, however, a population of genetically identical animals stands a greatly increased chance of being devastated by a single disease or environmental insult, such as a long drought. A given line of asexually reproducing animals can cope with a changing environment only through the relatively rare spontaneous mutations (alterations in genetic material) that prove to be beneficial. Paradoxically, however, most mutations are detrimental or lethal, and herein lies one of the greatest disadvantages of asexual reproduction. All such mutations are passed on to every offspring along with the normal, unmutated genes. Consequently, the typical asexual animal may have only one "good" copy of each hereditary unit (gene); the one on the homologous chromosome may be a mutated form that is nonfunctional or potentially lethal.

SEXUAL REPRODUCTION IN INVERTEBRATES

In **sexual** (L. *sexualis*, pertaining to sex) **reproduction,** the offspring have unique combinations of genes inherited from the two parents. Offspring of a sexual union are somewhat different from their parents and siblings—they have genetic diversity. Each new individual represents a combination of traits derived from two parents because syngamy, or fertilization, unites one gamete from each parent.

Sexual reproductive strategies and structures in the invertebrates are overwhelming. What follows is an overview of some principles of reproductive structure and function. The coverage of each invertebrate phylum in chapters 9 through 17 provides more specific details.

EXTERNAL FERTILIZATION

Many invertebrates (e.g., sponges and corals) simply release their gametes into the water in which they live **(broadcast spawning),** allowing external fertilization to occur. In these invertebrates, the gonads are usually simple, often transient structures for releasing the gametes from the body through various arrangements of coelomic ducts, metanephridia, sperm ducts, or oviducts.

INTERNAL FERTILIZATION

Other invertebrates (from flatworms to insects) utilize internal fertilization to transfer sperm from male to female and have structures that facilitate such transfer (figure 29.2).

In the male, sperm are produced in the testes and transported via a sperm duct to a storage area called the seminal vesicle. Prior to mating, some invertebrates (e.g., arrow worms, leeches, some insects) incorporate many sperm into packets termed spermatophores. Spermatophores provide a protective casing for sperm and facilitate the transfer of large numbers of sperm with minimal loss. Some spermatophores are even motile and act as independent sperm carriers. Sperm or the spermatophores are then passed into an ejaculatory duct to a copulatory organ (e.g., penis, cirrus, gonopore). The copulatory organ is used as an intromittent structure to introduce sperm into the female's system. Various accessory glands (e.g., seminal vesicle) may be present in males that produce seminal fluid or spermatophores.

In the female, ova (eggs) are produced in the ovaries and transported to the oviduct. Sperm move up the oviduct, where they encounter the ova and fertilize them. Accessory glands (e.g., those that produce egg capsules or shells) may also be present in females.

As noted earlier, sexual reproduction usually involves the fusion of gametes from a male and female parent. However, some sexually reproducing animals occasionally depart from this basic reproductive mode and exhibit variant forms of sexual reproduction.

Hermaphroditism (Gr. *hermaphroditos,* an organism with the attributes of both sexes) occurs when an animal has both functional male and female reproductive systems. This dual sexuality is sometimes called the monoecious (Gr. *monos,* single + *oikos,* house) condition. Although some hermaphrodites fertilize themselves, most also mate with another member of the same species (e.g., earthworms and sea slugs). When this occurs, each animal serves as both male and female—donating and receiving sperm.

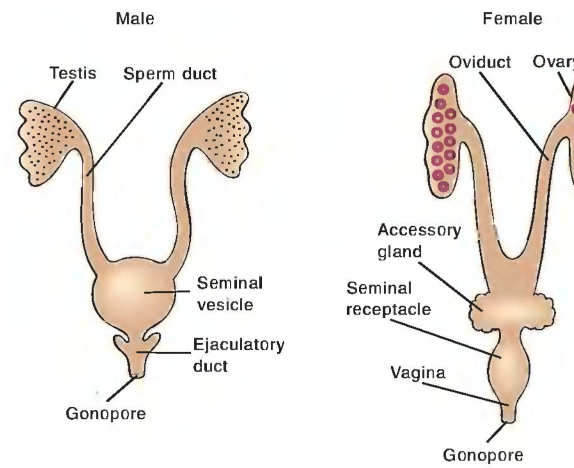


FIGURE 29.2

Stylized Male and Female Reprodutive Systems in Invertebrates. Sexual reproduction is possible via these systems.

Hermaphroditism is especially beneficial to sessile (attached) animals (e.g., barnacles) that may only occasionally encounter the opposite sex.

Another variation of hermaphroditism—**sequential hermaphroditism**—occurs when an animal is one sex during one phase of its life cycle and the opposite sex during another phase. Hermaphrodites are either **protogynous** (Gr. *protos,* first + *gyne,* women) or **protandrous** (Gr. *protos,* first + *andros,* man; **protandry**). In protandry, an animal is a male during its early life history and a female later in the life history. The reverse is true for protogynous animals. A change in the sex ratio of a population is one factor that can induce sequential hermaphroditism, which is common in oysters.

ADVANTAGES AND DISADVANTAGES OF SEXUAL REPRODUCTION

New combinations of traits can arise more rapidly in sexually reproducing animals because of genetic recombinations. The resulting genetic diversity or variability increases the chances of the species surviving sudden environmental changes. Furthermore, variation is the foundation for evolution. In contrast to the way asexually reproducing populations tend to retain mutations, sexually reproducing populations tend to eliminate deleterious and lethal mutations.

Sexual reproduction also has some disadvantages. For example, an animal that cannot reproduce asexually can never bequeath its own exact set of genetic material to its progeny. Sexual reproduction bestows on the progeny a reassortment of maternal and paternal chromosomes. Thus, the same mixing processes that create the adaptive gene combinations in the adult work to dismantle it partially in the offspring. In addition, many of the gametes that are released are not fertilized, leading to a significant waste of metabolic effort.

SEXUAL REPRODUCTION IN VERTEBRATES

Since the evolution of the first animals, the basic use of male and female gametes has been preserved. Vertebrate evolution has also given rise to the close link between reproductive biology and sexual behavior. The strong drive to mate or reproduce dominates the lives of many vertebrates, as illustrated by the salmon's fateful spawning run or the rutting of bull elk. Females of most mammal species come into heat or **estrus** (Gr. *oistros,* a most vehement desire; the period of sexual receptivity) about the same time each year. Genetic, hormonal, and nervous system controls usually time estrus so that the young are born when environmental conditions make survival most likely.

SOME BASIC VERTEBRATE REPRODUCTIVE STRATEGIES

Fishes are well known for their high potential fecundity, with most species releasing thousands to millions of eggs and sperm annually. Fish species have reproductive methods, structures, and an attendant physiology that have allowed them to adapt to a great variety of aquatic conditions.

The reproductive strategies in amphibians are much more diverse than those observed in other groups of vertebrates. In each of the three living orders of Amphibia (caecilians, salamanders, anurans) are trends toward terrestriality. The variety of these adaptations is especially noteworthy in anurans. These reproductive adaptations have been viewed as pioneering evolutionary experiments in the conquest of terrestrial environments by vertebrates. Noteworthy is the evolution of direct development of terrestrial eggs, ovoviviparity, and viviparity that have been important in the successful invasion of mountainous environments by amphibians.

The reproductive adaptations of reptiles, birds, and early mammals foreshadow changes evident in the reproductive systems of later mammals, including humans. The reptilian system includes shelled, desiccation-resistant eggs. These eggs had the three basic embryonic membranes that still characterize the mammalian embryo, as well as a flat embryo that developed and underwent gastrulation atop a huge yolk mass. The same process of gastrulation is still seen in mammalian embryos, even though the massive yolk mass has been lost.

The mechanisms for maintaining the developing embryo within the female for long periods of time evolved in the early mammals. During **gestation** (L. *gestatio,* from + *gestare,* to bear), the embryo was nourished with nutrients and oxygen, yet it was protected from attack by the female's immune system. After birth, the first mammals nourished their young with milk from the mammary glands, just as primates do today.

Female apes and monkeys are asynchronous breeders. Mating and births can take place over much of the year. Females mate only when in estrus, increasing the probability of fertilization. Human females show a less distinctive estrus phase and can reproduce throughout the year. They can also engage in sexual activity without reproductive purpose; no longer is sexual behavior precariously tied to ovulation. The source of this important reproductive adaptation may be physiological or a result of concomitant evolution of the brain—a process that gave humans some conscious control over their emotions and behaviors that hormones, instincts, and the environment control in other animals. *This separation of sex from a purely reproductive function has evolved into the long-lasting pair bonds between human males and females (e.g., marriage) that further support the offspring. This type of behavior has also resulted in the transmission of culture—a key to the evolution and success of the human species.*

With this background, the reproductive anatomy and physiology of selected vertebrate classes is now presented.

EXAMPLES OF REPRODUCTION AMONG VARIOUS VERTEBRATE CLASSES

Almost all vertebrates reproduce sexually; only a few lizards and fishes normally reproduce parthenogenetically. *Sexual reproduction evolved among aquatic animals and then spread to the land as animals became terrestrial.*

FISHES

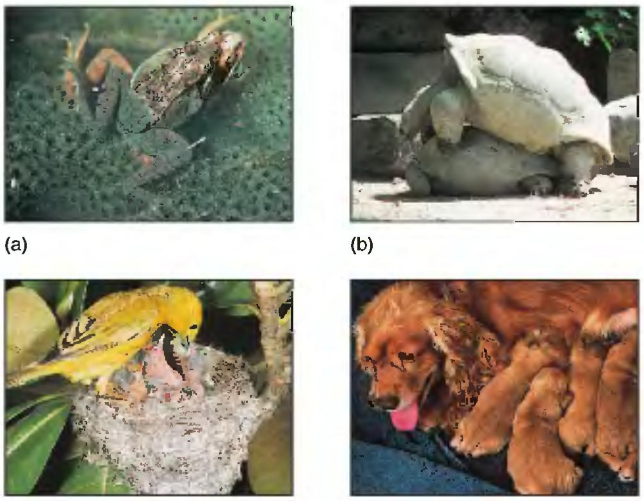
All fishes reproduce in aquatic environments. In bony fishes, fertilization is usually external, and eggs contain only enough yolk to sustain the developing fish for a short time. After this yolk is consumed, the growing fish must seek food. Although many thousands of eggs are produced and fertilized, few survive and grow to maturity. Some succumb to fungal and bacterial infections, others to siltation, and still others to predation. Thus, to assure reproductive success, the fertilized egg develops rapidly, and the young achieve maturity within a short time.

AMPHIBIANS

The vertebrate invasion of land meant facing for the first time the danger of drying out or desiccating; the tiny gametes were especially vulnerable. The gametes could not simply be released near one another on the land because they would quickly desiccate.

The amphibians were the first vertebrates to invade the land. They have not, however, become adapted to a completely terrestrial environment; their life cycle is still inextricably linked to water. Among most amphibians, fertilization is still external, just as it is among the fishes. Among the frogs and toads, the male grasps the female and discharges fluid containing sperm onto the eggs as she releases them into the water (figure 29.3*a*).

The developmental period is much longer in amphibians than in fishes, although the eggs do not contain appreciably more yolk. *An evolutionary adaptation present in amphibians is the presence of two periods of development: larval and adult stages.* The aquatic larval stage develops rapidly, and the animal spends much time eating and growing. After reaching a sufficient



(a) (b) (c) (d)

FIGURE 29.3

Vertebrate Reproductive Strategies. *(a)* A male wood frog (*Rana sylvatica*) clasping the female in amplexus, a form of external fertilization. As the female releases eggs into the water, the male releases sperm over them. *(b)* Reptiles, such as these turtles, were the first terrestrial vertebrates to develop internal fertilization. *(c)* Birds are oviparous. Their shelled eggs have large yolk reserves, and the young develop and hatch outside the mother's body. Birds may show advanced parental care. *(d)* A placental mammal. This female dog is nursing her puppies.

size, the larval form undergoes a developmental transition called metamorphosis into the adult (often terrestrial) form.

REPTILES

The reptiles were the first group of vertebrates to completely abandon the aquatic habitat because of adaptations that permitted sexual reproduction on land. *A crucial adaptation first found in reptiles is internal fertilization (figure 29.3b). Internal fertilization protects the gametes from drying out, freeing the animals from returning to the water to breed.*

Many reptiles are **oviparous** (L. *ovum*, egg + *parere*, to bring forth), and the eggs are deposited outside the body of the female. Others are **ovoviviparous** (L. *ovum*, egg + *vivere*, to live, + *parere*, to bring forth). They form eggs that hatch in the body of the female, and the young are born alive.

The shelled egg and extraembryonic membranes, also first seen in reptiles, constitute two other important evolutionary adaptations to life on land. These adaptations allowed reptiles to lay eggs in dry places without danger of desiccation. As the embryo develops, the extraembryonic chorion and amnion help protect it, the latter by creating a fluid-filled sac for the embryo. The allantois permits gas exchange and stores excretory products. Complete development can occur within the eggshell. When the animal hatches, it has developed to the point that it can survive on its own or with some parental care.

BIRDS

Birds have retained the important adaptations for life on land that evolved in the early reptiles. With the exception of most waterfowl, birds lack a penis. Males simply deposit semen against the cloaca for internal fertilization. Sperm then migrate up the cloaca and fertilize the eggs before hard shells form. This method of mating occurs more quickly than the internal fertilization that reptiles practice. All birds are oviparous, and the eggshells are much thicker than those of reptiles. Thicker shells permit birds to sit on their eggs and warm them. This brooding, or incubation, hastens embryo development. When many young birds hatch, they are incapable of surviving on their own. Extensive parental care and feeding of young are more common among birds than fishes, amphibians, or reptiles (figure 29.3c).

MAMMALS

The most primitive mammals, the monotremes (e.g., the duck-billed platypus and spiny anteater), lay eggs, as did the reptiles from which they evolved. All other mammals are viviparous.

Mammalian viviparity was another major evolutionary adaptation, and it has taken two forms. The marsupials developed the ability to nourish their young in a pouch after a short gestation inside the female. The other, much larger group—the placentals—retain the young inside the female, where the mother nourishes them by means of a placenta. Even after birth, mammals continue to nourish their young. *Mammary glands are a unique mammalian adaptation that permit the female to nourish the young with milk that she produces (figure 29.3d).* Some mammals nurture their young until adulthood, when they are able to mate and fend for themselves. *As noted at the beginning of this section, mammalian reproductive behavior also contributes to the transmission and evolution of culture that is the key to the evolution of the human species.*

THE HUMAN MALE REPRODUCTIVE SYSTEM

The reproductive role of the human male is to produce sperm and deliver them to the vagina of the female. This function requires the following structures:

1. Two testes that produce sperm and the male sex hormone, testosterone.
2. Accessory glands and tubes that furnish a fluid for carrying the sperm to the penis. This fluid, together with the sperm, is called semen.
3. Accessory ducts that store and carry secretions from the testes and accessory glands to the penis.
4. A penis that deposits semen in the vagina during sexual intercourse.

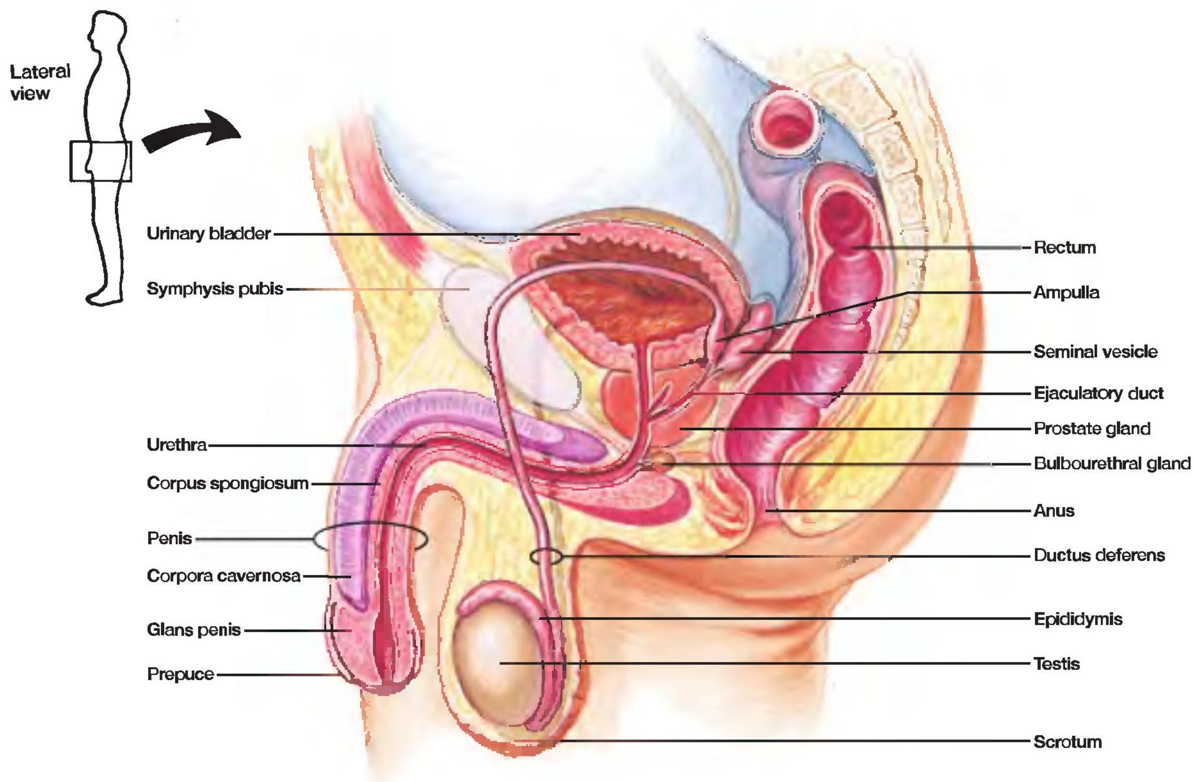


FIGURE 29.4

Lateral View of the Human Male Reproductive System. There are two each of the following structures: testis, epididymis, ductus deferens, seminal vesicle, ejaculatory duct, and bulbourethral gland.

PRODUCTION AND TRANSPORT OF SPERM

The paired **testes** (sing., testis) (L. *testis,* witness; the paired testes were believed to bear witness to a man's virility) are the male reproductive organs (gonads) that produce sperm (figure 29.4). Shortly after birth, the testes descend from the abdominal cavity into the **scrotum** (L. *scrautum,* a leather pouch for arrows), which hangs between the thighs. Because the testes hang outside the body, the temperature inside the scrotum is about 34° C compared to a 38° C core temperature. The lower temperature is necessary for active sperm production and survival. Muscles elevate or lower the testes, depending on the outside air temperature.

Each testis contains over eight hundred tightly coiled **seminiferous tubules** (figure 29.5*a,b*), which produce thousands of sperm each second in healthy young men. The walls of the seminiferous tubules are lined with two types of cells: spermatogenic cells, which give rise to sperm, and sustentacular cells, which nourish the sperm as they form and which also secrete a fluid (as well as the hormone inhibin) into the tubules to provide a liquid medium for the sperm. Between the seminiferous tubules are clusters of endocrine cells, called interstitial cells (Leydig cells), that secrete the male sex hormone testosterone.

A system of tubes carries the sperm that the testes produce to the penis. The seminiferous tubules merge into a network of tiny tubules called the rete testis (L. *rete,* net), which merges into a coiled tube called the epididymis. The epididymis has three main functions: (1) it stores sperm until they are mature and ready to be ejaculated, (2) it contains smooth muscle that helps propel the sperm toward the penis by peristaltic contractions, and (3) it serves as a duct system for sperm to pass from the testis to the ductus deferens. The ductus deferens (formerly called the vas deferens or sperm duct) is the dilated continuation of the epididymis. Continuing upward after leaving the scrotum, the ductus deferens passes through the lower part of the abdominal wall via the inguinal canal. If the abdominal wall weakens at the point where the ductus deferens passes through, an inguinal hernia may result. (In an inguinal hernia, the intestine may protrude downward into the scrotum.) The ductus deferens then passes around the urinary bladder and enlarges to form the ampulla (*see figure 29.4*). The ampulla stores some sperm until they are ejaculated. Distal to the ampulla, the ductus deferens becomes the ejaculatory duct. The urethra is the final section of the reproductive duct system.

After the ductus deferens passes around the urinary bladder, several accessory glands add their secretions to the sperm as they

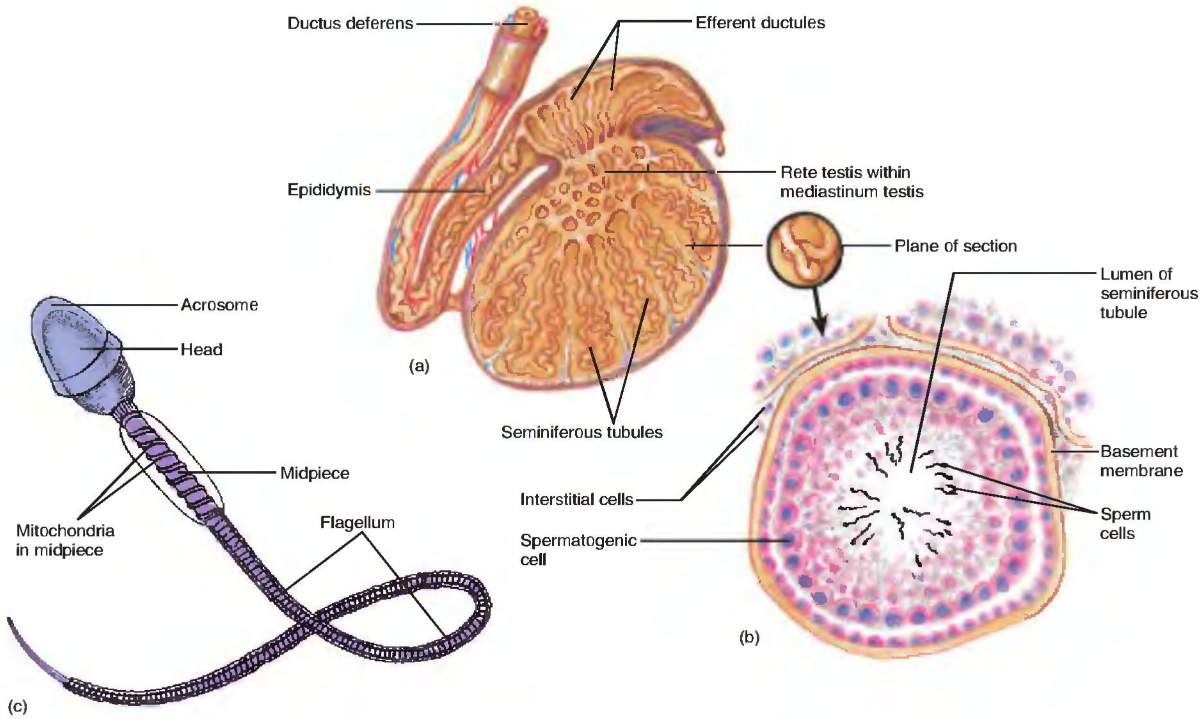


FIGURE 29.5

Human Male Testis. *(a)* Sagittal section through a testis. *(b)* Cross section of a seminiferous tubule, showing the location of spermatogenesis. *(c)* A mature sperm.

are propelled through the ducts. These accessory glands are the seminal vesicles, prostate gland, and bulbourethral glands *(see figure 29.4)*. The paired **seminal vesicles** secrete water, fructose, prostaglandins, and vitamin C. This secretion provides an energy source for the motile sperm and helps to neutralize the natural protective acidity of the vagina. (The pH of the vagina is about 3 to 4, but sperm motility and fertility are enhanced when it increases to about 6.) The **prostate gland** secretes water, enzymes, cholesterol, buffering salts, and phospholipids. The **bulbourethral glands** secrete a clear, alkaline fluid that lubricates the urethra to facilitate the ejaculation of semen and lubricates the penis prior to sexual intercourse. The fluid that results from the combination of sperm and glandular secretions is **semen** (L. *seminis*, seed). The average human ejaculation produces 3 to 4 ml of semen and contains 300 to 400 million sperm.

The penis has two functions. It carries urine through the urethra to the outside during urination, and it transports semen through the urethra during ejaculation. In addition to the urethra, the penis contains three cylindrical strands of erectile tissue: two corpora cavernosa and the corpus spongiosum *(see figure 29.4)*. The corpus spongiosum extends beyond the corpora cavernosa and becomes the expanded tip of the penis called the glans penis. The loosely fitting skin of the penis folds forward over the glans to form the prepuce or foreskin. **Circumcision** is the removal of the prepuce for religious or health reasons. Today, many circumcisions are performed in the belief that they lessen the likelihood of cancer of the penis.

A mature human sperm consists of a head, midpiece, and tail (figure 29.5*c*). The head contains the haploid nucleus, which is mostly DNA. The acrosome, a cap over most of the head, contains an enzyme called acrosin that assists the sperm in penetrating the outer layer surrounding a secondary oocyte. The sperm tail contains an array of microtubules that bend to produce whiplike movements. The spiral mitochondria in the midpiece supply the ATP necessary for these movements.

HORMONAL CONTROL OF MALE REPRODUCTIVE FUNCTION

Before a male can mature and function sexually, special regulatory hormones must come into play (table 29.1). Male sex hormones are collectively called **androgens** (Gr. *andros*, man + *gennan*, to produce). The hormones that travel from the brain and pituitary gland to the testes (and ovaries in the female) are called **gonadotropins.** As previously noted, the interstitial cells produce the male sex hormone **testosterone.** Figure 29.6 shows the negative feedback mechanisms that regulate the production and secretion of testosterone, as well as its actions. When the level of testosterone in the blood decreases, the hypothalamus is stimulated to

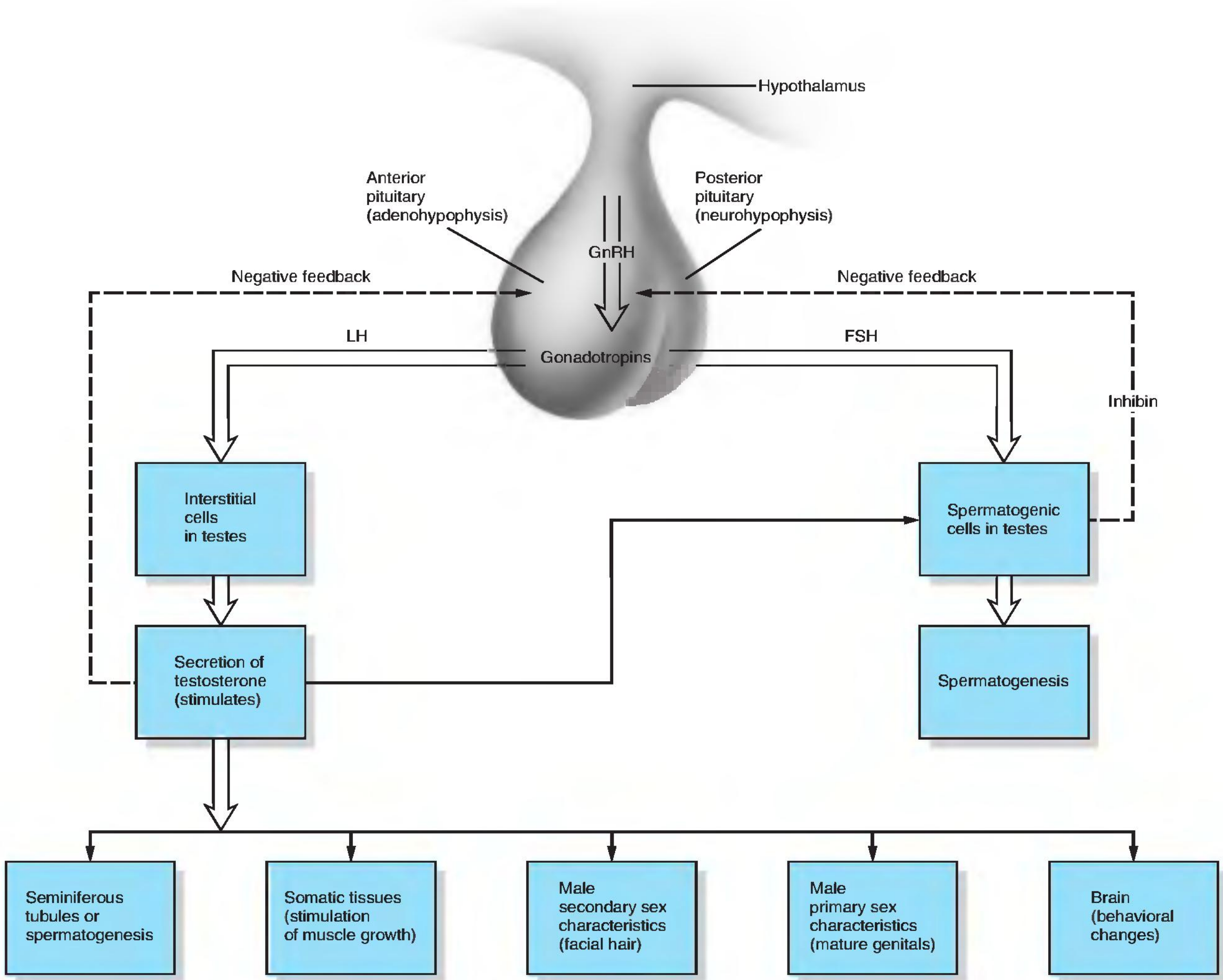


FIGURE 29.6

Hormonal Control of Reproductive Function in Adult Human Males. Negative feedback mechanisms by which the hypothalamus controls sperm maturation and the development of male secondary sexual characteristics. (GnRH = gonadotropin-releasing hormone; LH = luteinizing hormone; FSH = follicle-stimulating hormone.)

TABLE 29.1
MAJOR HUMAN MALE REPRODUCTIVE HORMONES IN AN ADULT

HORMONE	FUNCTIONS	SOURCE
FSH (follicle-stimulating hormone)	Aids sperm maturation; increases testosterone production	Pituitary gland
GnRH (gonadotropin-releasing hormone)	Controls pituitary secretion	Hypothalamus
Inhibin	Inhibits FSH secretion	Sustentacular cells in testes
LH (luteinizing hormone) or ICSH (interstitial cell–stimulating hormone)	Stimulates testosterone secretion	Pituitary gland
Testosterone	Increases sperm production; stimulates development of male primary and secondary sexual characteristics; inhibits LH secretion	Interstitial cells in testes

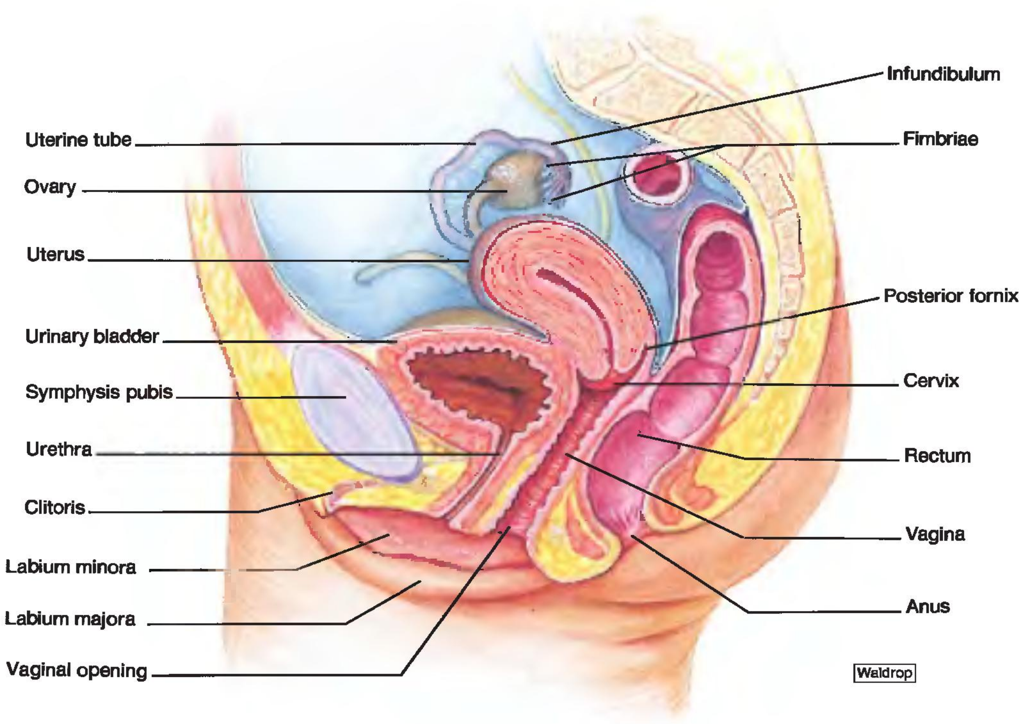


FIGURE 29.7

Lateral View of the Human Female Reproductive System. Two uterine tubes lead into the uterus and two ovaries.

secrete GnRH (gonadotropin-releasing hormone). GnRH stimulates the secretion of FSH (follicle-stimulating hormone) and LH (luteinizing hormone), also called ICSH (interstitial cell–stimulating hormone), into the bloodstream. (FSH and LH were first named for their functions in females, but their molecular structure is exactly the same in males.) FSH causes the spermatogenic cells in the seminiferous tubules to initiate spermatogenesis, and LH stimulates the interstitial cells to secrete testosterone. The cycle is completed when testosterone inhibits the secretion of LH, and another hormone, inhibin, is secreted. Inhibin inhibits the secretion of FSH from the anterior pituitary. This cycle maintains a constant rate (homeostasis) of spermatogenesis.

THE HUMAN FEMALE REPRODUCTIVE SYSTEM

The reproductive role of human females is more complex than that of males. Not only do females produce gametes (eggs or ova), but after fertilization, they also nourish, carry, and protect the developing embryo. After the offspring is born, the mother may nurse it for a time. Another difference between the sexes is the monthly rhythmicity of the female reproductive system.

The female reproductive system consists of a number of structures with specialized functions (figure 29.7):

1. Two ovaries produce eggs and the female sex hormones estrogen and progesterone.
2. Two uterine tubes, one from each ovary, carry eggs from the ovary to the uterus. Fertilization usually occurs in the upper third of a uterine tube.
3. If fertilization occurs, the uterus receives the blastocyst and houses the developing embryo.
4. The vagina receives semen from the penis during sexual intercourse. It is the exit point for menstrual flow and is the canal through which the baby passes from the uterus during childbirth.
5. The external genital organs have protective functions and play a role in sexual arousal.
6. The mammary glands, contained in the paired breasts, produce milk for the newborn baby.

PRODUCTION AND TRANSPORT OF THE EGG

The female gonads are the paired **ovaries** (L. *ovum*, egg), which produce eggs and female hormones. The ovaries are located in the pelvic part of the abdomen, one on each side of the uterus. A cross section of an ovary reveals rounded vesicles called follicles, which are the actual centers of egg production (oogenesis) (figure 29.8).

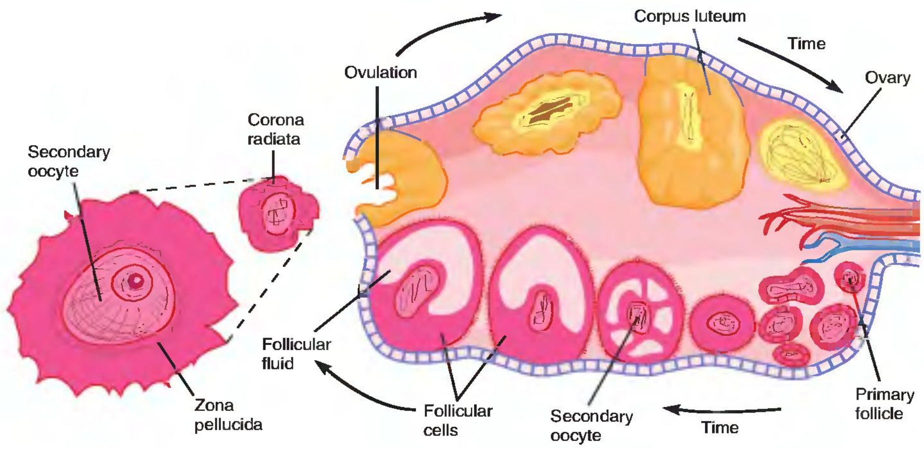


FIGURE 29.8

Cross Section through a Human Ovary. The events in the ovarian cycle proceed from the growth and maturation of the primary follicle, through ovulation (rupture of a mature follicle with the concurrent release of a secondary oocyte), through the formation and maintenance (during pregnancy) or degeneration (no pregnancy) of an endocrine structure called the corpus luteum. The positions of the oocyte and corpus luteum are varied for illustrative purposes only. An oocyte matures at the same site, from the beginning of the cycle to ovulation.

Each follicle contains an immature egg called a primary oocyte, and follicles are always present in several stages of development. After the release of a secondary oocyte (commonly called an egg) in the process called **ovulation,** the lining of the follicle grows inward, forming the corpus luteum ("yellow body"), which serves as a temporary endocrine tissue and continues to secrete the female sex hormones estrogen and progesterone.

The paired tubes that receive the secondary oocyte from the ovary and convey it to the uterus are called either the **uterine tubes** or **fallopian tubes** *(see figure 29.7)*. Feathery fimbriae fringe the part of the uterine tube that encircles the ovary. Each month, as a secondary oocyte is released, the motion of the fimbriae sweep it across a tiny space between the uterine tube and the ovary into the tube.

Unlike sperm, the secondary oocyte cannot move on its own. Instead, the peristaltic contractions of the tube and the waving motions of the cilia in the mucous membrane of the tube carry the secondary oocyte along (figure 29.9). Fertilization usually occurs in the uppermost third of the uterine tube. A fertilized oocyte (zygote) continues its journey toward the uterus, where it will implant. The journey takes four to seven days. If fertilization does not occur, the secondary oocyte degenerates in the uterine tube.

The uterine tubes terminate in the **uterus,** a hollow, muscular organ in front of the rectum and behind the urinary bladder (figure 29.10). The uterus terminates in a narrow portion called the cervix, which joins the uterus to the vagina. The uterus has three layers of tissues. The outer layer (perimetrium) extends beyond the uterus to form the two broad ligaments that stretch from the uterus to the lateral walls of the pelvis. The middle muscular layer (myometrium [Gr. *myo*, muscle + *metra*, womb]) makes up most of the uterine wall. The endometrium is the specialized mucous membrane that contains an abundance of blood vessels and simple glands.

The cervix leads to the **vagina,** a muscular tube 8 to 10 cm long. The wall of the vagina is composed mainly of smooth muscle and elastic tissue.

FIGURE 29.9

Cilia Lining the Uterine Tubes. The tiny, beating cilia on the surfaces of the uterine tube cells propel the secondary oocyte downward and perhaps the sperm upward (EM ×1000).

The external genital organs, or genitalia, include the mons pubis, labia majora, labia minora, vestibular glands, clitoris, and vaginal opening *(see figure 29.7)*. As a group, these organs are called the **vulva.** In most young women, the vaginal opening is partially covered by a thin membrane, the hymen, which may be

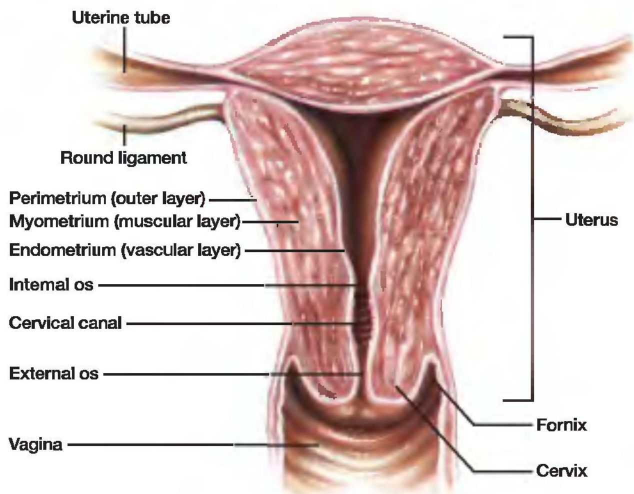


FIGURE 29.10

Human Female Uterus. This frontal section of a uterus shows the three major tissue layers. The outer layer is the perimetrium. The middle myometrium makes up the bulk of the uterine wall. It is composed of smooth muscle fibers. The innermost layer is composed of a specialized mucous membrane called the endometrium, which is deep and velvety in texture. Breakdown of the endometrium comprises part of the menstrual flow.

ruptured during normal strenuous activities or may be stretched or broken during sexual activity.

The **mammary glands** (L. *mammae*, breasts) are modified sweat glands that produce and secrete milk. They contain varying amounts of adipose tissue. The amount of adipose tissue determines the size of the breasts, but the amount of mammary tissue does not vary widely from one woman to another.

HORMONAL CONTROL OF FEMALE REPRODUCTIVE FUNCTION

The male is continuously fertile from puberty to old age, and throughout that period, sex hormones are continuously secreted. The female, however, is fertile only during a few days each month, and the pattern of hormone secretion is intricately related to the cyclical release of a secondary oocyte from the ovary.

The cyclical production of hormones controls the development of a secondary oocyte in a follicle (figure 29.11; table 29.2). Gonadotropin-releasing hormone (GnRH) from the hypothalamus acts on the anterior pituitary gland, which releases follicle-stimulating hormone (FSH) and luteinizing hormone (LH) to bring about the oocyte's maturation and release from the ovary. These hormones regulate the **menstrual cycle,** which is the cyclic preparation of the uterus to receive a fertilized egg, and the **ovarian cycle,** during which the oocyte matures and ovulation occurs. This monthly preparation of the uterine lining for the fertilized egg normally begins at puberty. When a female reaches 45 to 55 years of age, the ovaries lose their sensitivity to FSH and LH, they stop making normal amounts of progesterone and estrogen, and the monthly menstrual cycle ceases in what is called the **menopause** (Gr. *men*, month + *pausis*, cessation).

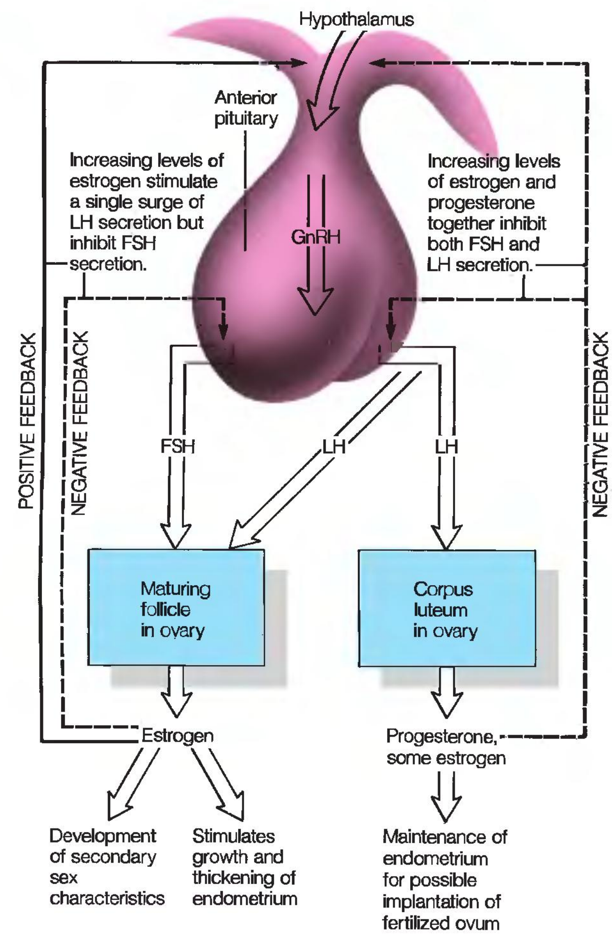


FIGURE 29.11

Hormonal Control of Reproductive Functions in an Adult Human Female. Feedback loops involve the hypothalamus, anterior pituitary, and ovaries. Gonadotropin-releasing hormone (GnRH) stimulates the release of both follicle-stimulating hormone (FSH) and luteinizing hormone (LH). Two negative feedback systems and a positive feedback system (one of the few in the human body) control the ovarian cycle.

One way to understand the hormonal pattern in the normal monthly cycle is to follow the development of the oocyte and the physical events in the menstrual cycle (figure 29.12; table 29.3). On average, it takes 28 days to complete one menstrual cycle, although the range may be from 22 to 45 days. During this time, the following events take place:

1. The controlling center for ovulation and menstruation is the hypothalamus. It releases, on a regular cycle, GnRH, which stimulates the anterior pituitary to secrete FSH and LH *(see figure 29.11)*.
2. FSH promotes the development of the oocyte in one of the immature ovarian follicles.
3. The follicles produce estrogen, causing a buildup and proliferation of the endometrium, as well as the inhibition of FSH production.

TABLE 29.2
MAJOR HUMAN FEMALE REPRODUCTIVE HORMONES

HORMONE	FUNCTIONS	SOURCE
Estrogen	Stimulates thickening of uterine wall, maturation of oocyte and development of female sexual characteristics; inhibits FSH secretion; increases LH secretion	Ovarian follicle, corpus luteum
FSH (follicle-stimulating hormone)	Causes immature oocyte and follicle to develop; increases estrogen secretion; stimulates new gamete formation and development of uterine wall after menstruation	Pituitary gland
GnRH (gonadotropin-releasing hormone)	Controls pituitary secretion	Hypothalamus
hCG (human chorionic gonadotropin)	Prevents corpus luteum from disintegrating; stimulates corpus luteum to secrete estrogen and progesterone	Embryonic membranes and placenta
Inhibin	Inhibits secretion of FSH from the anterior pituitary gland	Ovaries
LH (luteinizing hormone)	Stimulates further development of oocyte and follicle; stimulates ovulation; increases progesterone secretion; aids in development of corpus luteum	Pituitary gland
Oxytocin	Stimulates uterine contractions during labor and milk release during nursing	Pituitary gland
Prolactin	Promotes milk secretion by mammary glands after childbirth	Pituitary gland
Progesterone	Stimulates thickening of uterine wall	Corpus luteum
Relaxin	Increases flexibility of pubic symphysis during pregnancy and helps dilate uterine cervix during labor and delivery	Placenta and ovaries

TABLE 29.3
SUMMARY OF THE MENSTRUAL CYCLE EVENTS

PHASE	EVENTS	DURATION IN DAYS*
Follicular	Follicle matures in the ovary; menstruation (endometrium breaks down); endometrium rebuilds	1–5
Ovulation	Ovary releases secondary oocyte	6–14
Luteal	Corpus luteum forms; endometrium thickens and becomes glandular	15–28

*Using a 28-day menstrual cycle as an example.

4. The elevated estrogen level about midway in the cycle triggers the anterior pituitary to secrete LH, which causes the mature follicle to enlarge rapidly and release the secondary oocyte (ovulation). LH also causes the collapsed follicle to become another endocrine tissue, the corpus luteum.
5. The corpus luteum secretes estrogen and progesterone, which act to complete the development of the endometrium and maintain it for 10 to 14 days.
6. If the oocyte is not fertilized, the corpus luteum disintegrates into a corpus albicans, and estrogen and progesterone secretion cease.
7. Without estrogen and progesterone, the endometrium breaks down, and **menstruation** occurs. The menstrual flow is composed mainly of sloughed-off endometrial cells, mucus, and blood.
8. As progesterone and estrogen levels decrease further, the pituitary renews active secretion of FSH, which stimulates the development of another follicle, and the monthly cycle begins again.

HORMONAL REGULATION IN THE PREGNANT FEMALE

Pregnancy sets into motion a new series of physiological events. The ovaries are directly affected because, as the embryo develops, the cells of the embryo and placenta release the hormone human chorionic gonadotropin (hCG), which keeps the corpus luteum from disintegrating. The progesterone that it secretes is necessary to maintain the uterine lining. After a time, the placenta takes over progesterone production, and the corpus luteum degenerates. By the end of two weeks following implantation, the concentration of hCG is so high in the female's blood, and in her urine as well, that an hCG immunological test can check for pregnancy. As the embryo develops, other hormones are secreted. For example, prolactin and oxytocin induce the mammary glands to secrete and eject milk after childbirth. Oxytocin and prostaglandins also stimulate the uterine contractions that expel the baby from the uterus during childbirth.

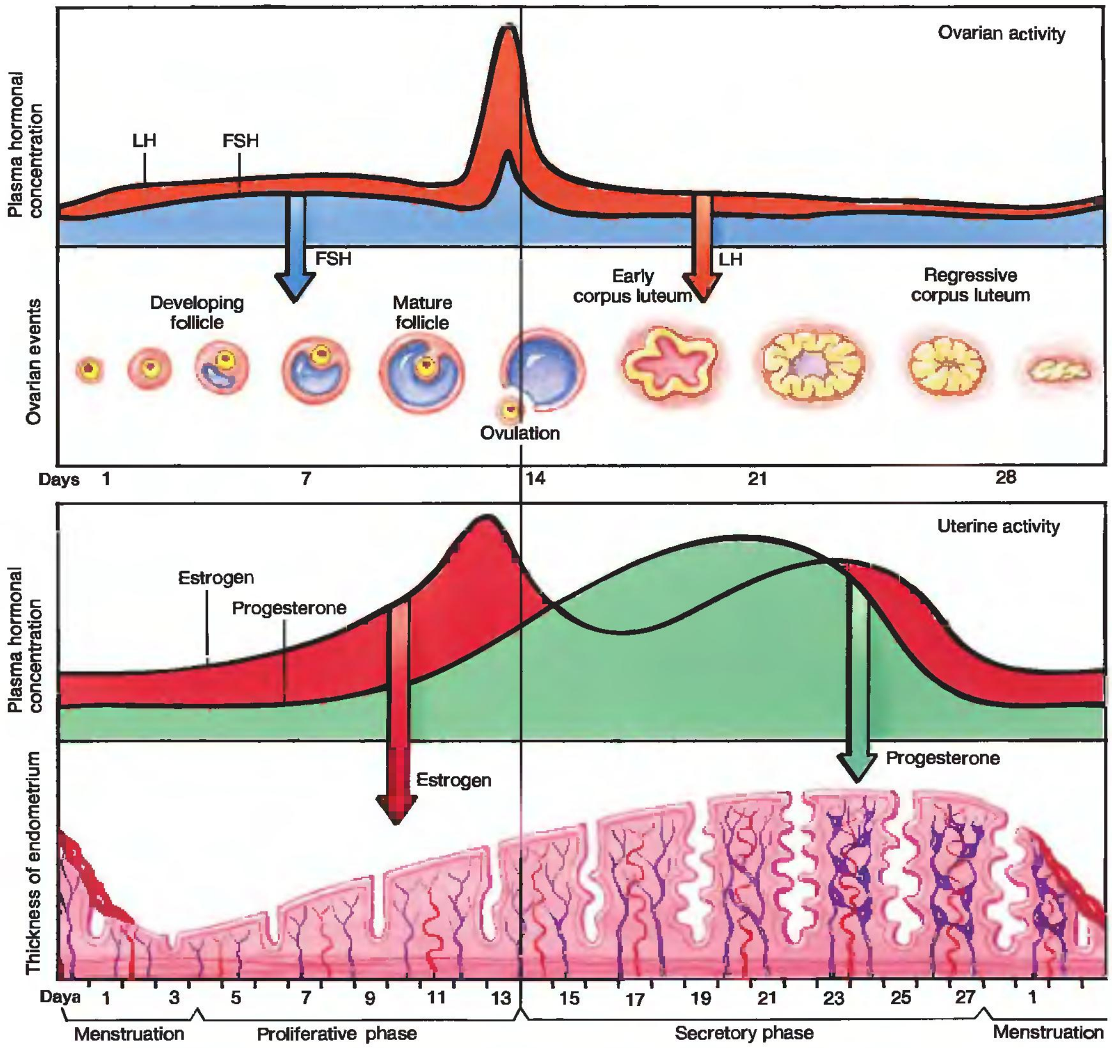


FIGURE 29.12

Major Events in the Female Ovarian and Menstrual Cycles. The two charts correlate the gonadotropins, ovarian hormones, follicle development, ovulation, and changes in uterine anatomy during the cycles.

PRENATAL DEVELOPMENT AND BIRTH

This section covers the main event in reproduction—the nine-month pregnancy period, during which time the human female's body carries, nourishes, and protects the embryo as it grows to a full-term baby.

EVENTS OF PRENATAL DEVELOPMENT: FROM ZYGOTE TO NEWBORN

The development of a human being can be divided into prenatal ("before birth") and postnatal ("after birth") periods. During the prenatal period, the developing individual begins life as a zygote, then becomes a ball of cells called a morula, and eventually becomes a blastocyst that implants in the endometrium. From two weeks after fertilization until the end of the eighth week of its existence, the individual is called an embryo. From nine weeks until birth, it is a fetus. During or after birth, it is called a newborn, or baby.

Pregnancy is arbitrarily divided into three-month periods called trimesters. The first trimester begins at fertilization, and during this time most of the organs are formed. The next two trimesters are mainly periods of growth for the fetus.

The First Trimester

After fertilization, usually in the upper third of the uterine tube, the zygote goes through several cleavages as it moves down the tube (figure 29.13). It eventually becomes a solid ball of cells called a **morula,** and by the fourth day, it develops into a 50- to 120-cell blastula stage called a **blastocyst.**

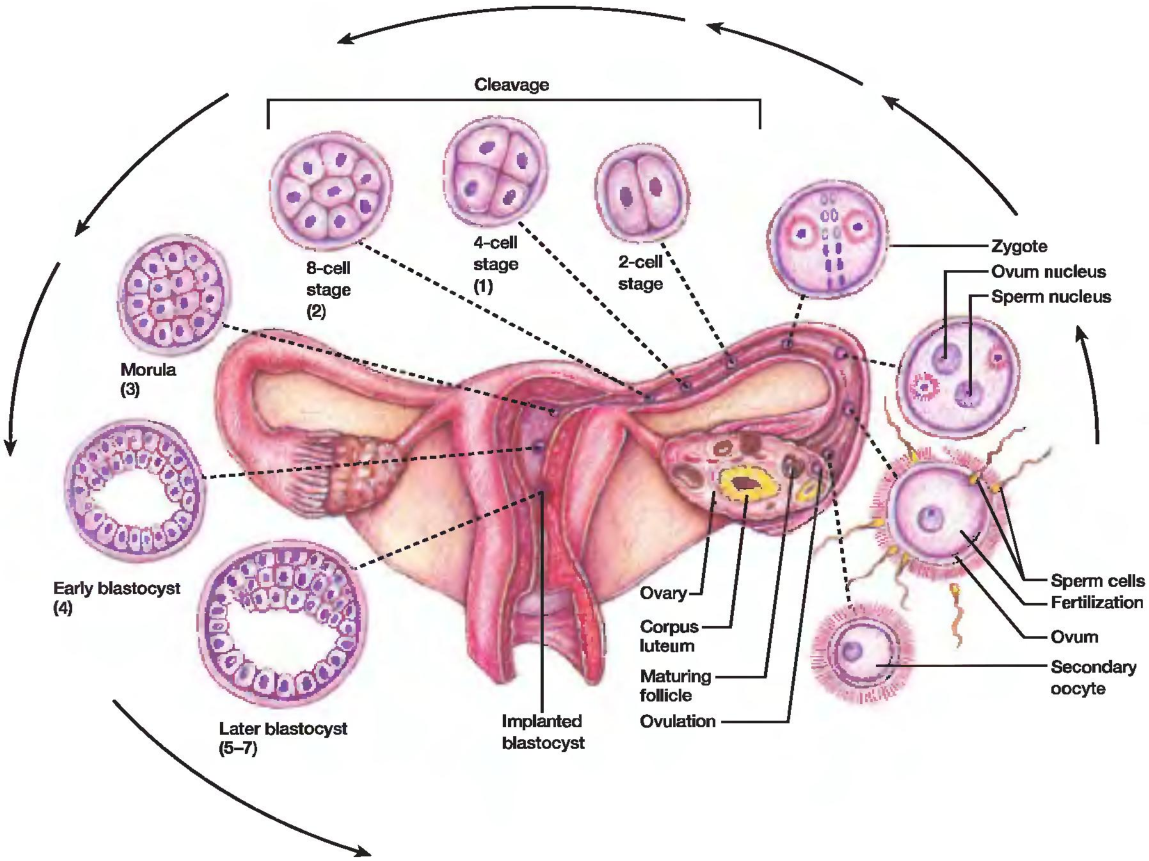


FIGURE 29.13

Early Stages in Human Development. The numbers in parentheses indicate the days after fertilization. The secondary oocyte is fertilized in the upper third of the uterine tube, undergoes cleavage while traveling down the tube, and finally implants in the endometrium of the uterus.

The next stage of development occurs when the blastocyst adheres to the uterine wall and implants. During implantation, the outer cells of the blastocyst, called the trophoblast, invade the endometrium. Implantation is usually completed 11 to 12 days after fertilization; from then on, the female is considered to be pregnant.

One of the unique features of mammalian development is that most of the cells of the early embryo make no contribution to the embryo's body, giving rise instead to supportive and protective membranes. Only the inner cell mass gives rise to the embryonic body. Eventually, these cells arrange in a flat sheet that undergoes a gastrulation similar to that of reptiles and birds.

Once gastrulation is completed, the rest of the first trimester is devoted to organogenesis and growth (figure 29.14). Regulatory events and inductive-tissue interactions shape most of the organ systems. By the middle of the first trimester, all of the major body systems have begun to develop.

The Second Trimester

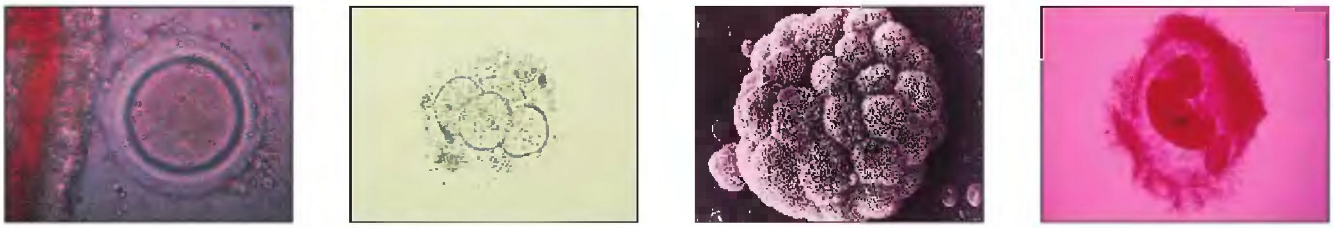
In the second trimester (fourth month), fetal growth is spectacular. By now, the pregnant mother is aware of fetal movements. The heartbeat can be heard with a stethoscope. During the sixth month, the upper and lower eyelids separate, and the eyelashes form. During the seventh month, the eyes open. During this period, the bones begin to ossify.

The Third Trimester

The third trimester extends from the seventh month until birth. During this time, the fetus has developed sufficiently (with respect to the circulatory and respiratory systems) to potentially survive if born prematurely. During the last month, fetal weight doubles.

THE PLACENTA: EXCHANGE SITE AND HORMONE PRODUCER

The lengthy pregnancy characteristic of mammals is possible, in part, because of the embryonic membranes that originated in the reptiles: the amnion, yolk sac, chorion, and allantois. The latter two gave rise to the embryonic parts of the placenta. The **placenta** is the organ that sustains the embryo and fetus throughout the pregnancy and through which gases, nutrients, and wastes are exchanged between the maternal and fetal systems (figure 29.15). The tiny,



(a) (b) (c) (d)

(e) (f) (g)

FIGURE 29.14

Human Embryonic Development. *(a)* A zygote. *(b)* The four-cell stage. *(c)* A blastula. *(d)* A 5-week-old embryo. *(e)* The embryo at 8 weeks. *(f)* The embryo at 10 weeks. *(g)* The fetus at about 3 months.

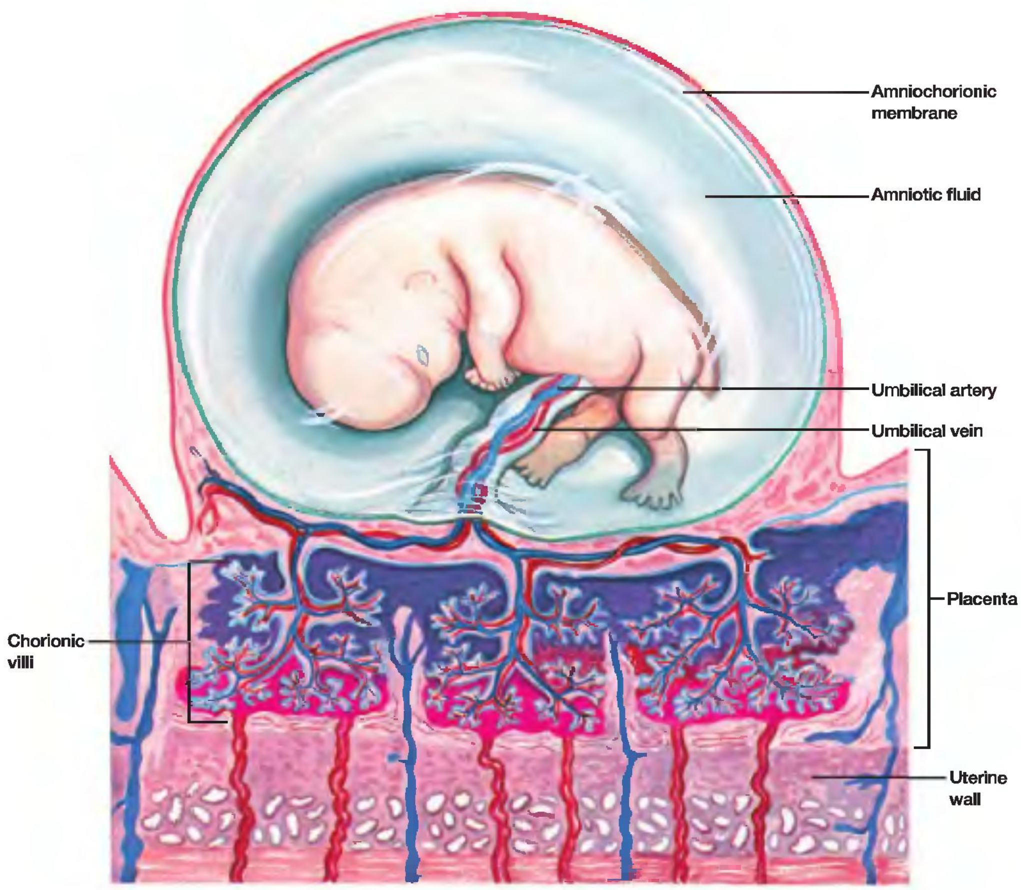


FIGURE 29.15

Fetus and Placenta at Seven Weeks. The circulations of mother and fetus are in close contact at the site of the chorionic villi, but they do not actually mix. Branches of the mother's arteries in the wall of her uterus open into pools near the chorionic villi. Oxygen and nutrients from the mother's blood diffuse into the fetal capillaries of the placenta. The fetal capillaries lead into the umbilical vein, which is enclosed within the umbilical cord. From here, the fresh blood circulates through the fetus's body. Blood that the fetus has depleted of nutrients and oxygen returns to the placenta in the umbilical arteries, which branch into capillaries, from which waste products diffuse to the maternal side.

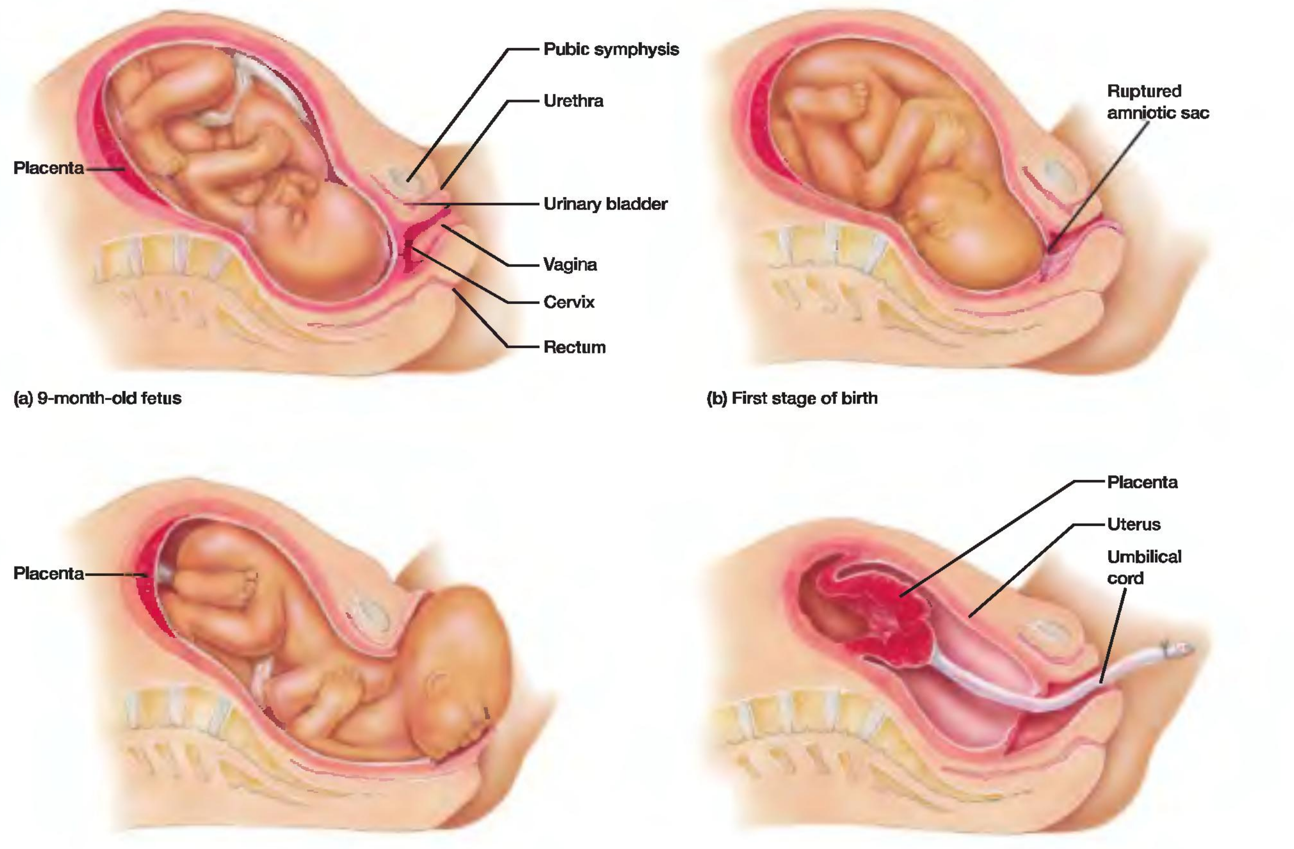


FIGURE 29.16

Stages of Labor and Parturition. *(a)* The position of the fetus prior to labor. *(b)* The ruptured amniotic sac and early dilation of the cervix. *(c)* The expulsion stage of parturition. *(d)* Passage of the afterbirth.

fingerlike projections that were sent out from the blastocyst during implantation develop into numerous chorionic villi, which contain embryonic blood vessels. These blood vessels do not merge with those of the mother; the two bloodstreams remain separate throughout the pregnancy. The **umbilical cord** connects the placenta to the abdomen of the fetus. Two fetal umbilical arteries and one fetal umbilical vein spiral about each other in the umbilical cord.

BIRTH: AN END AND A BEGINNING

About 266 days after fertilization, or 280 days from the beginning of the last menstrual period, the human infant is born. The birth process is called **parturition** (L. *parturire,* to be in labor). During parturition, the mother's uterine muscles begin to contract, and the cervix begins to dilate, or open. The hormone relaxin, produced by the ovaries and placenta, causes the mother's pelvic bones to slightly separate so that the baby can pass through the birth canal.

Changing hormone levels initiate parturition. When it is time for the baby to be born, its pituitary gland secretes adrenocorticotropic hormone (ACTH), which stimulates the adrenal glands to secrete steroids. These steroids stimulate the placenta to produce prostaglandins that, along with the hormone oxytocin from the mother's pituitary, cause the uterus to begin powerful muscular contractions. The contractions build in length and increase in frequency over a period that usually lasts from 2 to 18 hours. During that time, the cervix becomes fully dilated, and the amniotic sac ruptures. Usually within an hour of these events, the baby is expelled from the uterus (figure 29.16*a–c*). After the baby emerges, uterine contractions continue to expel the **afterbirth** (figure 29.16*d*). The umbilical cord is severed, and the newborn embarks on its nurtured existence in the outside world. (In mammals other than humans, the female bites through the cord to sever it.)

MILK PRODUCTION AND LACTATION

Lactation (L. *lactare,* to suckle) includes both milk secretion (production) by the mammary glands and milk release from the breasts. *(Mammary glands, a unique characteristic of mammals,* *evolved from sweat glands in the skin.)* During pregnancy, the breasts enlarge in response to increasing levels of the hormone prolactin. Before birth, placental secretions of estrogen and progesterone inhibit milk secretion from the breasts. After the placenta has been expelled from the uterus, the concentrations of estrogen and progesterone drop, and the breasts begin to produce copious amounts of milk.

The mother's breasts do not actually release milk until one to three days after the baby is born. During these first days, the suckling baby receives **colostrum,** a high-protein fluid present in the breast at birth. Colostrum contains an abundance of maternal antibodies and thus helps strengthen the baby's immune system. It also functions as a laxative, removing fetal wastes, called **meconium,** retained in the intestines. After about three days, the prolactin secreted from the pituitary stimulates milk production. The newborn's suckling stimulates the pituitary to release oxytocin as well as prolactin. Oxytocin triggers milk release from the mammary glands.

SUMMARY

1. Asexual reproductive processes do not involve the production and subsequent fusion of haploid cells, but rely solely on vegetative growth through mitosis.
2. Sexual reproduction involves the formation of haploid cells through meiosis and the subsequent fusion of pairs of those cells to produce a diploid zygote.
3. The forms of asexual reproduction in invertebrates are binary fission, budding (both external and internal), and fragmentation. Parthenogenesis also occurs in a few invertebrates.
4. Sexual reproductive strategies and structures in the invertebrates are numerous and varied.
5. Sexual reproduction first evolved in aquatic animals. The invasion of land meant facing the danger of the gametes and embryos desiccating. The five major groups of vertebrates have reproductive adaptations for the environment in which they reproduce.
6. The reproductive role of the human male is to produce sperm and deliver them to the vagina of the female. This function requires different structures. The testes produce sperm and the male sex hormone, testosterone. Accessory glands furnish a fluid, called semen, for carrying the sperm to the penis. Accessory ducts store and carry secretions from the testes and accessory glands to the penis. The penis deposits semen in the vagina during sexual intercourse.
7. Before a human male can mature and function sexually, special regulatory hormones (FSH, GnRH, inhibin, LH, and testosterone) must function.
8. The reproductive roles of the human female are more complex than those of the male. Not only do females produce eggs, but after fertilization, they also nourish, carry, and protect the developing embryo. They may also nourish the infant for a time after it is born. The female reproductive system consists of two ovaries, two uterine tubes, a uterus, vagina, and external genitalia. The mammary glands contained in the paired breasts produce milk for the newborn baby.
9. The human female is fertile for only a few days each month, and the pattern of hormone secretion is intricately related to the cyclical release of a secondary oocyte from the ovary. Various hormones regulate the menstrual and ovarian cycles.
10. Pregnancy sets a new series of physiological events into motion that are directed to housing, protecting, and nourishing the embryo.
11. The development of a human may be divided into prenatal and postnatal periods. Pregnancy is arbitrarily divided into trimesters.
12. The placenta is the organ that sustains the embryo and fetus throughout the pregnancy. The birth process is called parturition and occurs about 266 days after fertilization.
13. Lactation includes both milk secretion (production) by the mammary glands and milk release from the breasts.

SELECTED KEY TERMS

asexual reproduction (p. 475)
broadcast spawning (p. 477)
budding (p. 475)
estrus (p. 478)
fission (p. 475)
fragmentation (p. 475)
gestation (p. 478)
parthenogenesis (p. 475)
sequential hermaphroditism (p. 477)
sexual reproduction (p. 476)

CRITICAL THINKING QUESTIONS

1. Is the fertility of a woman affected by the length of a given menstrual cycle or whether the cycles are regular or irregular? Explain.
2. Looking at a variety of animals, what are the advantages to restricting reproduction to a limited time period? Why do so many animals have a sharply defined reproductive season during the year?
3. In most sexual species, males produce far more gametes than do females. Why does this occur when, in most cases, only one male gamete can fertilize one female gamete?
4. Why are the accessory glands of the male so important in reproduction?

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