

59

Sex and Reproduction

Concept Outline

59.1 Animals employ both sexual and asexual reproductive strategies.

Asexual and Sexual Reproduction. Some animals reproduce asexually, but most reproduce sexually; male and female are usually different individuals, but not always.

59.2 The evolution of reproduction among the vertebrates has led to internalization of fertilization and development.

Fertilization and Development. Among vertebrates that have internal fertilization, the young are nourished by egg yolk or from their mother's blood.

Fish and Amphibians. Most bony fish and amphibians have external fertilization, while most cartilaginous fish have internal fertilization.

Reptiles and Birds. Most reptiles and all birds lay eggs externally, and the young develop inside the egg.

Mammals. Monotremes lay eggs, marsupials have pouches where their young develop, and placental mammals have placentas that nourish the young within the uterus.

59.3 Male and female reproductive systems are specialized for different functions.

Structure and Function of the Male Reproductive System. The testes produce sperm and secrete the male sex hormone, testosterone.

Structure and Function of the Female Reproductive System. An egg cell within an ovarian follicle develops and is released from the ovary; the egg cell travels into the female reproductive tract, which undergoes cyclic changes due to hormone secretion.

59.4 The physiology of human sexual intercourse is becoming better known.

Physiology of Human Sexual Intercourse. The human sexual response can be divided into four phases: excitement, plateau, orgasm, and resolution.

Birth Control. Various methods of birth control are employed, including barriers to fertilization, prevention of ovulation, and prevention of the implantation.



FIGURE 59.1

The bright color of male golden toads serves to attract mates. The rare golden toads of the Monteverde Cloud Forest Reserve of Costa Rica are nearly voiceless and so use bright colors to attract mates. Always rare, they may now be extinct.

The cry of a cat in heat, insects chirping outside the window, frogs croaking in swamps, and wolves howling in a frozen northern forest are all sounds of evolution's essential act, reproduction. These distinct vocalizations, as well as the bright coloration characteristic of some animals like the tropical golden toads of figure 59.1, function to attract mates. Few subjects pervade our everyday thinking more than sex, and few urges are more insistent. This chapter deals with sex and reproduction among the vertebrates, including humans.

59.1 Animals employ both sexual and asexual reproductive strategies.

Asexual and Sexual Reproduction

Asexual reproduction is the primary means of reproduction among the protists, cnidaria, and tunicates, but it may also occur in some of the more complex animals. Indeed, the formation of identical twins (by the separation of two identical cells of a very early embryo) is a form of asexual reproduction.

Through mitosis, genetically identical cells are produced from a single parent cell. This permits asexual reproduction to occur in protists by division of the organism, or **fission**. Cnidaria commonly reproduce by **budding**, where a part of the parent's body becomes separated from the rest and differentiates into a new individual. The new individual may become an independent animal or may remain attached to the parent, forming a colony.

Sexual reproduction occurs when a new individual is formed by the union of two sex cells, or **gametes**, a term that includes **sperm** and **eggs** (or ova). The union of sperm and egg cells produces a fertilized egg, or **zygote**, that develops by mitotic division into a new multicellular organism. The zygote and the cells it forms by mitosis are diploid; they contain both members of each homologous pair of chromosomes. The gametes, formed by meiosis in the sex organs, or **gonads**—the **testes** and **ovaries**—are haploid (see chapter 12). The process of spermatogenesis (sperm formation) and oogenesis (egg formation) will be described in later sections. For a more detailed discussion of asexual and sexual reproduction, see chapter 12.

Different Approaches to Sex

Parthenogenesis (virgin birth) is common in many species of arthropods; some species are exclusively parthenogenic (and all female), while others switch between sexual reproduction and parthenogenesis in different generations. In honeybees, for example, a queen bee mates only once and stores the sperm. She then can control the release of sperm. If no sperm are released, the eggs develop parthenogenetically into drones, which are males; if sperm are allowed to fertilize the eggs, the fertilized eggs develop into other queens or worker bees, which are female.



(a)



(b)

FIGURE 59.2

Hermaphroditism and protogyny. (a) The hamlet bass (genus *Hypoplectrus*) is a deep-sea fish that is a hermaphrodite—both male and female at the same time. In the course of a single pair-mating, one fish may switch sexual roles as many as four times, alternately offering eggs to be fertilized and fertilizing its partner's eggs. Here the fish acting as a male curves around its motionless partner, fertilizing the upward-floating eggs. (b) The bluehead wrasse, *Thalassoma bifasciatum*, is protogynous—females sometimes turn into males. Here a large male, or sex-changed female, is seen among females, typically much smaller.

The Russian biologist Ilya Darevsky reported in 1958 one of the first cases of unusual modes of reproduction among vertebrates. He observed that some populations of small lizards of the genus *Lacerta* were exclusively female, and suggested that these lizards could lay eggs that were viable even if they were not fertilized. In other words, they were capable of asexual reproduction in the absence of sperm, a type of parthenogenesis. Further work has shown that parthenogenesis also occurs among populations of other lizard genera.

Another variation in reproductive strategies is **hermaphroditism**, when one individual has both testes and ovaries, and so can produce both sperm and eggs (figure 59.2a). A tapeworm is hermaphroditic and can fertilize itself, a useful strategy because it is unlikely to encounter another tapeworm. Most hermaphroditic animals, however, require another individual to reproduce. Two earthworms, for example, are required for reproduction—each functions as both male and female, and each leaves the encounter with fertilized eggs.

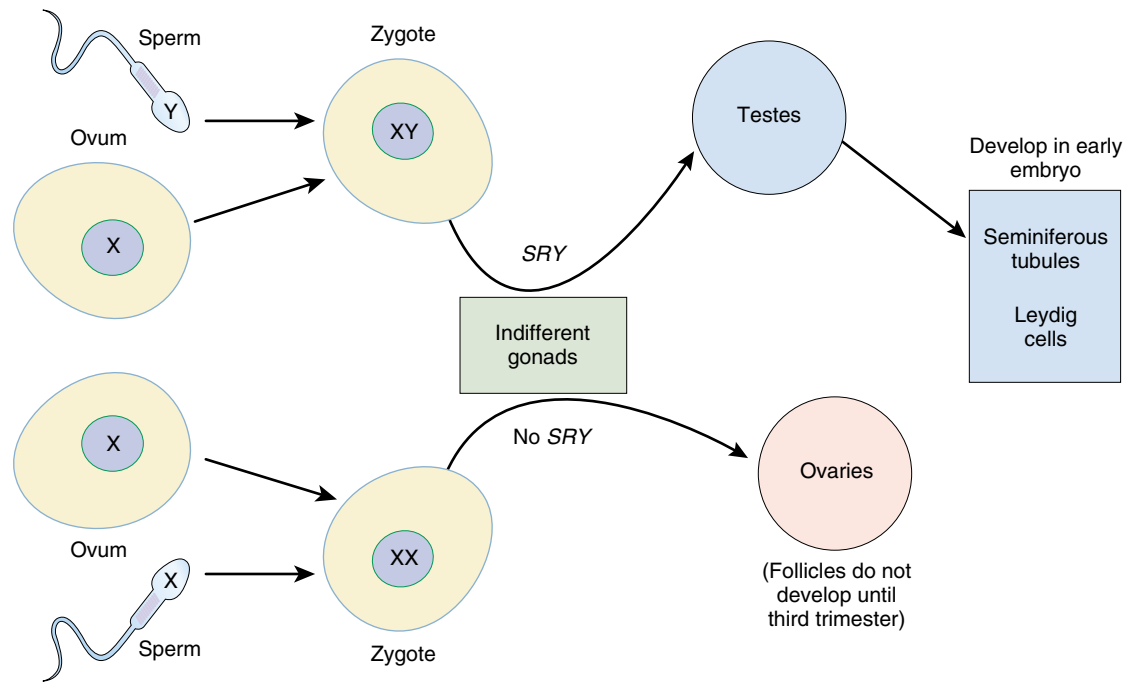


FIGURE 59.3 Sex determination in mammals is made by a region of the Y chromosome designated *SRY*. Testes are formed when the Y chromosome and *SRY* are present; ovaries are formed when they are absent.

There are some deep-sea fish that are hermaphrodites—both male and female at the same time. Numerous fish genera include species in which individuals can change their sex, a process called *sequential hermaphroditism*. Among coral reef fish, for example, both **protogyny** (“first female,” a change from female to male) and **protandry** (“first male,” a change from male to female) occur. In fish that practice protogyny (figure 59.2*b*), the sex change appears to be under social control. These fish commonly live in large groups, or schools, where successful reproduction is typically limited to one or a few large, dominant males. If those males are removed, the largest female rapidly changes sex and becomes a dominant male.

Sex Determination

Among the fish just described, and in some species of reptiles, environmental changes can cause changes in the sex of the animal. In mammals, the sex is determined early in embryonic development. The reproductive systems of human males and females appear similar for the first 40 days after conception. During this time, the cells that will give rise to ova or sperm migrate from the yolk sac to the embryonic gonads, which have the potential to become either ovaries in females or testes in males. For this reason, the embry-

onic gonads are said to be “indifferent.” If the embryo is a male, it will have a Y chromosome with a gene whose product converts the indifferent gonads into testes. In females, which lack a Y chromosome, this gene and the protein it encodes are absent, and the gonads become ovaries. Recent evidence suggests that the sex-determining gene may be one known as *SRY* (for “sex-determining region of the Y chromosome”) (figure 59.3). The *SRY* gene appears to have been highly conserved during the evolution of different vertebrate groups.

Once testes form in the embryo, the testes secrete testosterone and other hormones that promote the development of the male external genitalia and accessory reproductive organs. If the embryo lacks testes (the ovaries are nonfunctional at this stage), the embryo develops female external genitalia and sex accessory organs. In other words, all mammalian embryos will develop female sex accessory organs and external genitalia unless they are masculinized by the secretions of the testes.

Sexual reproduction is most common among animals, but many reproduce asexually by fission, budding, or parthenogenesis. Sexual reproduction generally involves the fusion of gametes derived from different individuals of a species, but some species are hermaphroditic.

59.2 The evolution of reproduction among the vertebrates has led to internalization of fertilization and development.

Fertilization and Development

Vertebrate sexual reproduction evolved in the ocean before vertebrates colonized the land. The females of most species of marine bony fish produce eggs or ova in batches and release them into the water. The males generally release their sperm into the water containing the eggs, where the union of the free gametes occurs. This process is known as **external fertilization**.

Although seawater is not a hostile environment for gametes, it does cause the gametes to disperse rapidly, so their release by females and males must be almost simultaneous. Thus, most marine fish restrict the release of their eggs and sperm to a few brief and well-defined periods. Some reproduce just once a year, while others do so more frequently. There are few seasonal cues in the ocean that organisms can use as signals for synchronizing reproduction, but one all-pervasive signal is the cycle of the moon. Once each month, the moon approaches closer to the earth than usual, and when it does, its increased gravitational attraction causes somewhat higher tides. Many marine organisms sense the tidal changes and entrain the production and release of their gametes to the lunar cycle.

The invasion of land posed the new danger of desiccation, a problem that was especially severe for the small and vulnerable gametes. On land, the gametes could not simply be released near each other, as they would soon dry up and perish. Consequently, there was intense selective pressure for terrestrial vertebrates (as well as some groups of fish) to evolve **internal fertilization**, that is, the introduction of male gametes into the female repro-

ductive tract. By this means, fertilization still occurs in a nondesiccating environment, even when the adult animals are fully terrestrial. The vertebrates that practice internal fertilization have three strategies for embryonic and fetal development:

1. **Oviparity.** This is found in some bony fish, most reptiles, some cartilaginous fish, some amphibians, a few mammals, and all birds. The eggs, after being fertilized internally, are deposited outside the mother's body to complete their development.
2. **Ovoviviparity.** This is found in some bony fish (including mollies, guppies, and mosquito fish), some cartilaginous fish, and many reptiles. The fertilized eggs are retained within the mother to complete their development, but the embryos still obtain all of their nourishment from the egg yolk. The young are fully developed when they are hatched and released from the mother.
3. **Viviparity.** This is found in most cartilaginous fish, some amphibians, a few reptiles, and almost all mammals. The young develop within the mother and obtain nourishment directly from their mother's blood, rather than from the egg yolk (figure 59.4).

Fertilization is external in most fish but internal in most other vertebrates. Depending upon the relationship of the developing embryo to the mother and egg, those vertebrates with internal fertilization may be classified as oviparous, ovoviviparous, or viviparous.

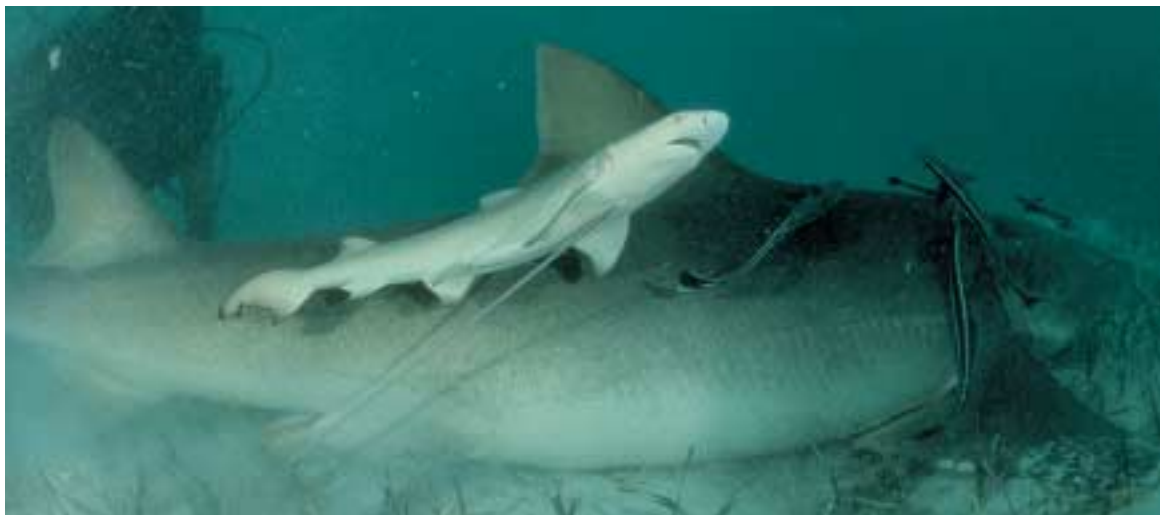


FIGURE 59.4
Viviparous fish
carry live, mobile young within their bodies. The young complete their development within the body of the mother and are then released as small but competent adults. Here a lemon shark has just given birth to a young shark, which is still attached by the umbilical cord.

Fish and Amphibians

Most fish and amphibians, unlike other vertebrates, reproduce by means of external fertilization.

Fish

Fertilization in most species of bony fish (teleosts) is external, and the eggs contain only enough yolk to sustain the developing embryo for a short time. After the initial supply of yolk has been exhausted, the young fish must seek its food from the waters around it. Development is speedy, and the young that survive mature rapidly. Although thousands of eggs are fertilized in a single mating, many of the resulting individuals succumb to microbial infection or predation, and few grow to maturity.

In marked contrast to the bony fish, fertilization in most cartilaginous fish is internal. The male introduces sperm into the female through a modified pelvic fin. Development of the young in these vertebrates is generally viviparous.

Amphibians

The amphibians invaded the land without fully adapting to the terrestrial environment, and their life cycle is still tied to the water. Fertilization is external in most amphibians, just as it is in most species of bony fish. Gametes from both males and females are released through the cloaca. Among the frogs and toads, the male grasps the female and discharges fluid containing the sperm onto the eggs as they are released into the water (figure 59.5). Although the eggs of most amphibians develop in the water, there are some interesting exceptions. In two species of frogs, for example, the eggs develop in the vocal sacs and stomach, and the young frogs leave through their mother's mouth (figure 59.6)!

The time required for development of amphibians is much longer than that for fish, but amphibian eggs do not include a significantly greater amount of yolk. Instead, the process of development in most amphibians is divided into embryonic, larval, and adult stages, in a way reminiscent of the life cycles found in some insects. The embryo develops within the egg, obtaining nutrients from the yolk. After hatching from the egg, the aquatic larva then functions as a free-swimming, food-gathering machine, often for a considerable period of time. The larvae may increase in size rapidly; some tadpoles, which are the larvae of frogs and toads, grow in a matter of weeks from creatures no bigger than the tip of a pencil into individuals as big as a goldfish. When the larva has grown to a sufficient size, it undergoes a developmental transition, or metamorphosis, into the terrestrial adult form.

The eggs of most bony fish and amphibians are fertilized externally. In amphibians the eggs develop into a larval stage that undergoes metamorphosis.



FIGURE 59.5

The eggs of frogs are fertilized externally. When frogs mate, as these two are doing, the clasp of the male induces the female to release a large mass of mature eggs, over which the male discharges his sperm.

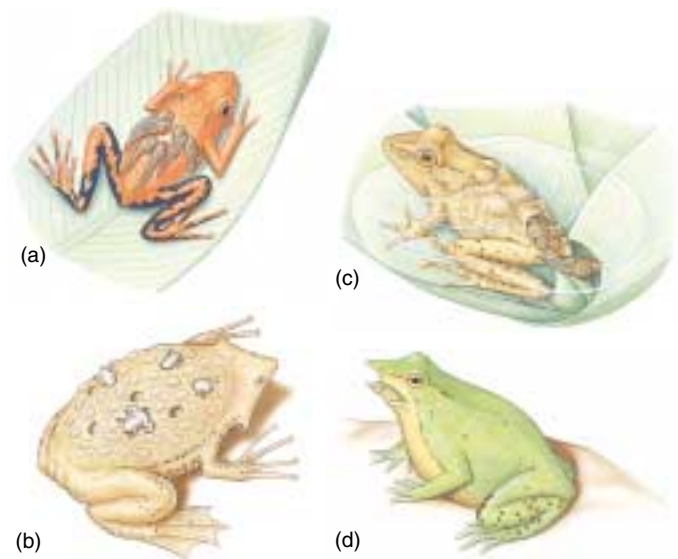


FIGURE 59.6

Different ways young develop in frogs. (a) In the poison arrow frog, the male carries the tadpoles on his back. (b) In the female Surinam frog, froglets develop from eggs in special brooding pouches on the back. (c) In the South American pygmy marsupial frog, the female carries the developing larvae in a pouch on her back. (d) Tadpoles of the Darwin's frog develop into froglets in the vocal pouch of the male and emerge from the mouth.

Reptiles and Birds

Most reptiles and all birds are oviparous—after the eggs are fertilized internally, they are deposited outside of the mother’s body to complete their development. Like most vertebrates that fertilize internally, male reptiles utilize a tubular organ, the penis, to inject sperm into the female (figure 59.7). The penis, containing erectile tissue, can become quite rigid and penetrate far into the female reproductive tract. Most reptiles are oviparous, laying eggs and then abandoning them. These eggs are surrounded by a leathery shell that is deposited as the egg passes through the oviduct, the part of the female reproductive tract leading from the ovary. A few species of reptiles are ovoviviparous or viviparous, forming eggs that develop into embryos within the body of the mother.

All birds practice internal fertilization, though most male birds lack a penis. In some of the larger birds (including swans, geese, and ostriches), however, the male cloaca extends to form a false penis. As the egg passes along the oviduct, glands secrete albumin proteins (the egg white) and the hard, calcareous shell that distinguishes bird eggs from reptilian eggs. While modern reptiles are poikilotherms (animals whose body temperature varies with the temperature of their environment), birds are homeotherms (animals that maintain a relatively constant body temperature independent of environmental temperatures). Hence, most birds incubate their eggs after laying them to keep them warm (figure 59.8). The young that hatch from the eggs of most bird species are unable to survive unaided, as their development is still incomplete. These young birds are fed and nurtured by their parents, and they grow to maturity gradually.

The shelled eggs of reptiles and birds constitute one of the most important adaptations of these vertebrates to life on land, because shelled eggs can be laid in dry places. Such eggs are known as amniotic eggs because the embryo develops within a fluid-filled cavity surrounded by a membrane called the amnion. The amnion is an extraembryonic membrane—that is, a membrane formed from embryonic cells but located outside the body of the embryo. Other extraembryonic membranes in amniotic eggs include the chorion, which lines the inside of the eggshell, the yolk sac, and the allantois. In contrast, the eggs of fish and amphibians contain only one extraembryonic membrane, the yolk sac. The viviparous mammals, including humans, also have extraembryonic membranes that will be described in chapter 60.



FIGURE 59.7

The introduction of sperm by the male into the female’s body is called copulation. Reptiles such as these turtles were the first terrestrial vertebrates to develop this form of reproduction, which is particularly suited to a terrestrial environment.



FIGURE 59.8

Crested penguins incubating their egg. This nesting pair is changing the parental guard in a stylized ritual.

Most reptiles and all birds are oviparous, laying amniotic eggs that are protected by watertight membranes from desiccation. Birds, being homeotherms, must keep the eggs warm by incubation.

Mammals

Some mammals are seasonal breeders, reproducing only once a year, while others have shorter reproductive cycles. Among the latter, the females generally undergo the reproductive cycles, while the males are more constant in their reproductive activity. Cycling in females involves the periodic release of a mature ovum from the ovary in a process known as ovulation. Most female mammals are “in heat,” or sexually receptive to males, only around the time of ovulation. This period of sexual receptivity is called **estrus**, and the reproductive cycle is therefore called an **estrous cycle**. The females continue to cycle until they become pregnant.

In the estrous cycle of most mammals, changes in the secretion of follicle-stimulating hormone (FSH) and luteinizing hormone (LH) by the anterior pituitary gland cause changes in egg cell development and hormone secretion in the ovaries. Humans and apes have menstrual cycles that are similar to the estrous cycles of other mammals in their cyclic pattern of hormone secretion and ovulation. Unlike mammals with estrous cycles, however, human and ape females bleed when they shed the inner lining of their uterus, a process called menstruation, and may engage in copulation at any time during the cycle.

Rabbits and cats differ from most other mammals in that they are induced ovulators. Instead of ovulating in a cyclic fashion regardless of sexual activity, the females ovulate only after copulation as a result of a reflex stimulation of LH secretion (described later). This makes these animals extremely fertile.

The most primitive mammals, the **monotremes** (consisting solely of the duck-billed platypus and the echidna), are oviparous, like the reptiles from which they evolved. They incubate their eggs in a nest (figure 59.9a) or specialized pouch, and the young hatchlings obtain milk from their mother’s mammary glands by licking her skin, as monotremes lack nipples. All other mammals are viviparous, and are divided into two subcategories based on how they nourish their young. The **marsupials**, a group that includes opossums and kangaroos, give birth to fetuses that are incompletely developed. The fetuses complete their development in a pouch of their mother’s skin, where they can obtain nourishment from nipples of the mammary glands (figure 59.9b). The **placental mammals** (figure 59.9c) retain their young for a much longer period of development within the mother’s uterus. The fetuses are nourished by a structure known as the placenta, which is derived from both an extraembryonic membrane (the chorion) and the mother’s uterine lining. Because the fetal and maternal blood vessels are in very close proximity in the placenta, the fetus can obtain nutrients by diffusion from the mother’s blood. The functioning of the placenta is discussed in more detail in chapter 60.

Among mammals that are not seasonal breeders, the females undergo shorter cyclic variations in ovarian function. These are estrous cycles in most mammals and menstrual cycles in humans and apes. Some mammals are induced ovulators, ovulating in response to copulation.



(a)



(b)



(c)

FIGURE 59.9

Reproduction in mammals. (a) Monotremes, like the duck-billed platypus shown here, lay eggs in a nest. (b) Marsupials, such as this kangaroo, give birth to small fetuses which complete their development in a pouch. (c) In placental mammals, like this domestic cat, the young remain inside the mother’s uterus for a longer period of time and are born relatively more developed.

59.3 Male and female reproductive systems are specialized for different functions.

Structure and Function of the Male Reproductive System

The structures of the human male reproductive system, typical of mammals, are illustrated in figure 59.10. If testes form in the human embryo, they develop *seminiferous tubules* beginning at around 43 to 50 days after conception. The seminiferous tubules are the sites of sperm production. At about 9 to 10 weeks, the Leydig cells, located in the interstitial tissue between the seminiferous tubules, begin to secrete testosterone (the major male sex hormone, or androgen). Testosterone secretion during embryonic development converts indifferent structures into the male external genitalia, the *penis* and the *scrotum*, a sac that contains the testes. In the absence of testosterone, these structures develop into the female external genitalia.

In an adult, each testis is composed primarily of the highly convoluted seminiferous tubules (figure 59.11). Although the testes are actually formed within the abdominal cavity, shortly before birth they descend through an opening called the inguinal canal into the scrotum, which suspends them outside the abdominal cavity. The scrotum maintains the testes at around 34°C, slightly lower than the core body temperature (37°C). This lower temperature is required for normal sperm development in humans.

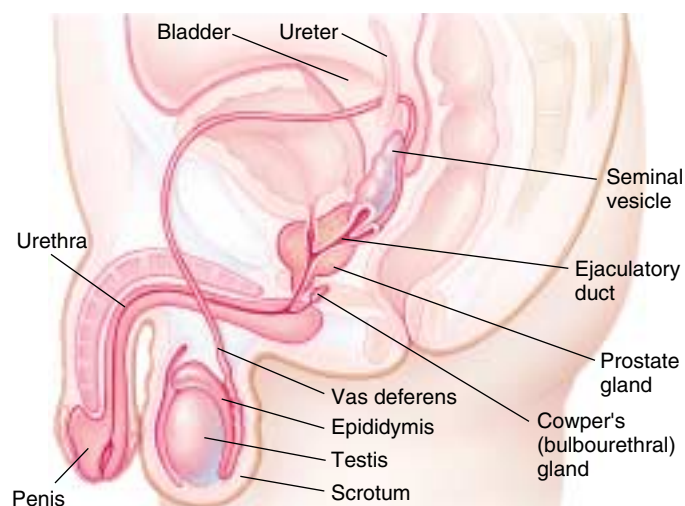


FIGURE 59.10
Organization of the human male reproductive system. The penis and scrotum are the external genitalia, the testes are the gonads, and the other organs are sex accessory organs, aiding the production and ejaculation of semen.

Production of Sperm

The wall of the seminiferous tubule consists of *germinal cells*, which become sperm by meiosis, and supporting *Sertoli cells*. The germinal cells near the outer surface of the seminiferous tubule are diploid (with 46 chromosomes in humans), while those located closer to the lumen of the tubule are haploid (with 23 chromosomes each). Each parent cell duplicates by mitosis, and one of the two daughter cells then undergoes meiosis to form sperm; the other remains as a parent cell. In that way, the male never runs out of parent cells to produce sperm. Adult males produce an average of 100 to 200 million sperm each day and can continue to do so throughout most of the rest of their lives.

The diploid daughter cell that begins meiosis is called a *primary spermatocyte*. It has 23 pairs of homologous chromosomes (in humans) and each chromosome is duplicated, with two chromatids. The first meiotic division separates the homologous chromosomes, producing two haploid *secondary spermatocytes*. However, each chromosome still consists of two duplicate chromatids. Each of these cells then undergoes the second meiotic division to separate the chromatids and produce two haploid cells, the *spermatids*. Therefore, a total of four haploid spermatids are produced by each primary spermatocyte (figure 59.11). All of these cells constitute the germinal epithelium of the seminiferous tubules because they “germinate” the gametes.

In addition to the germinal epithelium, the walls of the seminiferous tubules contain nongerminal cells known as Sertoli cells. The Sertoli cells nurse the developing sperm and secrete products required for spermatogenesis (sperm production). They also help convert the spermatids into *spermatozoa* by engulfing their extra cytoplasm.

Spermatozoa, or sperm, are relatively simple cells, consisting of a head, body, and tail (figure 59.12). The head encloses a compact nucleus and is capped by a vesicle called an acrosome, which is derived from the Golgi complex. The acrosome contains enzymes that aid in the penetration of the protective layers surrounding the egg. The body and tail provide a propulsive mechanism: within the tail is a flagellum, while inside the body are a centriole, which acts as a basal body for the flagellum, and mitochondria, which generate the energy needed for flagellar movement.

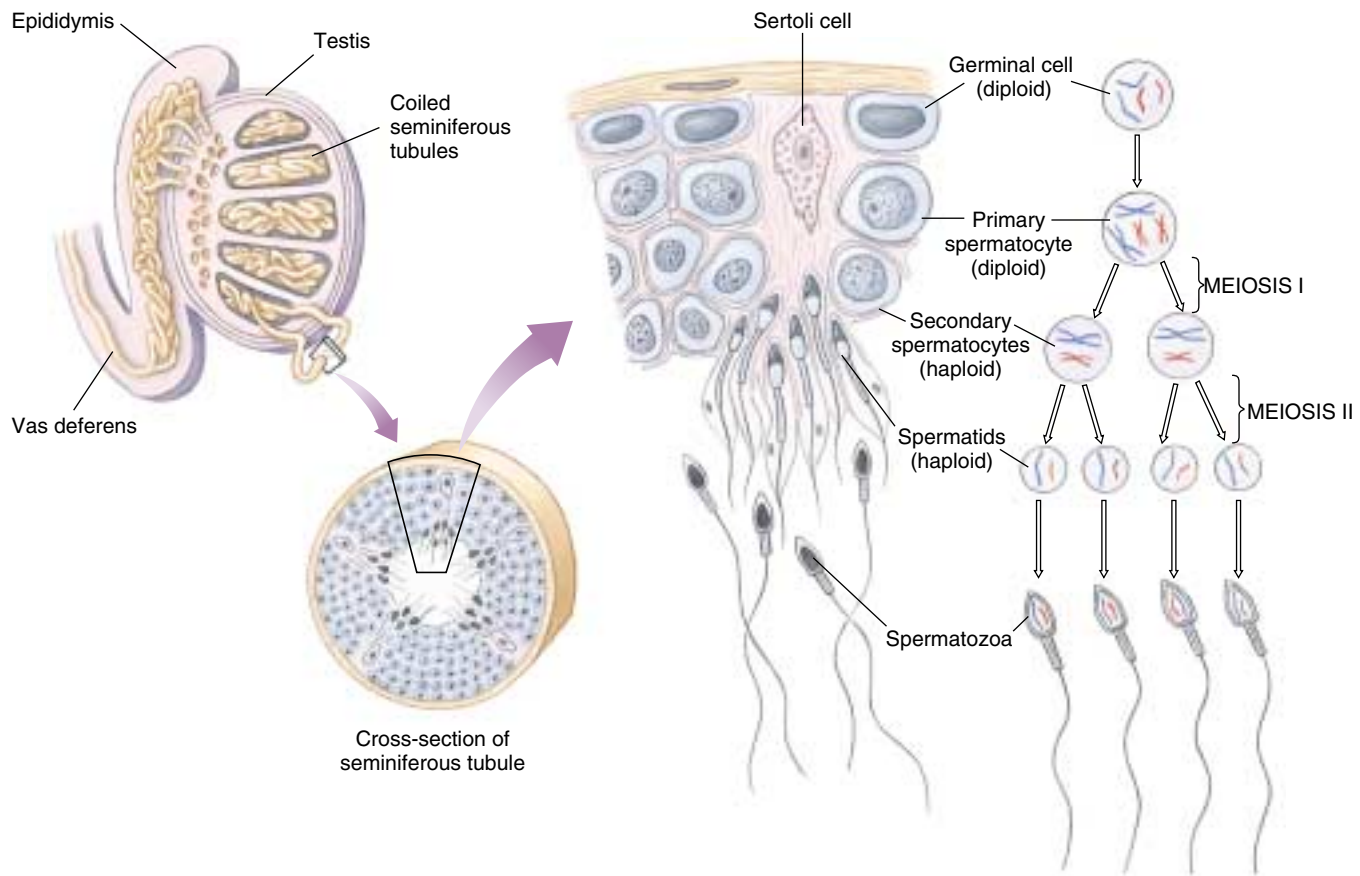
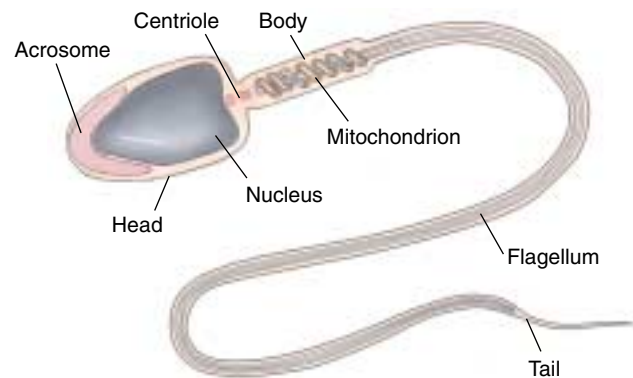


FIGURE 59.11

The testis and spermatogenesis. Inside the testis, the seminiferous tubules are the sites of spermatogenesis. Germinal cells in the seminiferous tubules give rise to spermatozoa by meiosis. Sertoli cells are nongerminal cells within the walls of the seminiferous tubules. They assist spermatogenesis in several ways, such as helping to convert spermatids into spermatozoa. A primary spermatocyte is diploid. At the end of the first meiotic division, homologous chromosomes have separated, and two haploid secondary spermatocytes form. The second meiotic division separates the sister chromatids and results in the formation of four haploid spermatids.



(a)



(b)

FIGURE 59.12

Human sperm. (a) A scanning electron micrograph. (b) A diagram of the main components of a sperm cell.

Male Accessory Sex Organs

After the sperm are produced within the seminiferous tubules, they are delivered into a long, coiled tube called the epididymis (figure 59.13). The sperm are not motile when they arrive in the epididymis, and they must remain there for at least 18 hours before their motility develops. From the epididymis, the sperm enter another long tube, the vas deferens, which passes into the abdominal cavity via the inguinal canal.

The vas deferens from each testis joins with one of the ducts from a pair of glands called the seminal vesicles (see figure 59.10), which produce a fructose-rich fluid. From this point, the vas deferens continues as the ejaculatory duct and enters the prostate gland at the base of the urinary bladder. In humans, the prostate gland is about the size of a golf ball and is spongy in texture. It contributes about 60% of the bulk of the semen, the fluid that contains the products of the testes, fluid from the seminal vesicles, and the products of the prostate gland. Within the prostate gland, the ejaculatory duct merges with the urethra from the urinary bladder. The urethra carries the semen out of the body through the tip of the penis. A pair of pea-sized bulbourethral glands secrete a fluid that lines the urethra and lubricates the tip of the penis prior to coitus (sexual intercourse).

In addition to the urethra, there are two columns of erectile tissue, the corpora cavernosa, along the dorsal side of the penis and one column, the corpus spongiosum, along the ventral side (figure 59.14). Penile erection is produced by neurons in the parasympathetic division of the autonomic nervous system. As a result of the release of nitric oxide by these neurons, arterioles in the penis dilate, causing the erectile tissue to become engorged with blood and turgid. This increased pressure in the erectile tissue compresses the veins, so blood flows into the penis but cannot flow out. The drug sildenafil (**Viagra**) prolongs erection by stimulating release of nitric oxide in the penis. Some mammals, such as the walrus, have a bone in the penis that contributes to its stiffness during erection, but humans do not.

The result of erection and continued sexual stimulation is ejaculation, the ejection from the penis of about 5 milliliters of semen containing an average of 300 million sperm. Successful fertilization requires such a high sperm count because the odds against any one sperm cell successfully completing the journey to the egg and fertilizing it are extraordinarily high, and the acrosomes of several sperm need to interact with the egg before a single sperm can penetrate the egg. Males with fewer than 20 million sperm per milliliter are generally considered sterile. Despite their large numbers, sperm constitute only about 1% of the volume of the semen ejaculated.

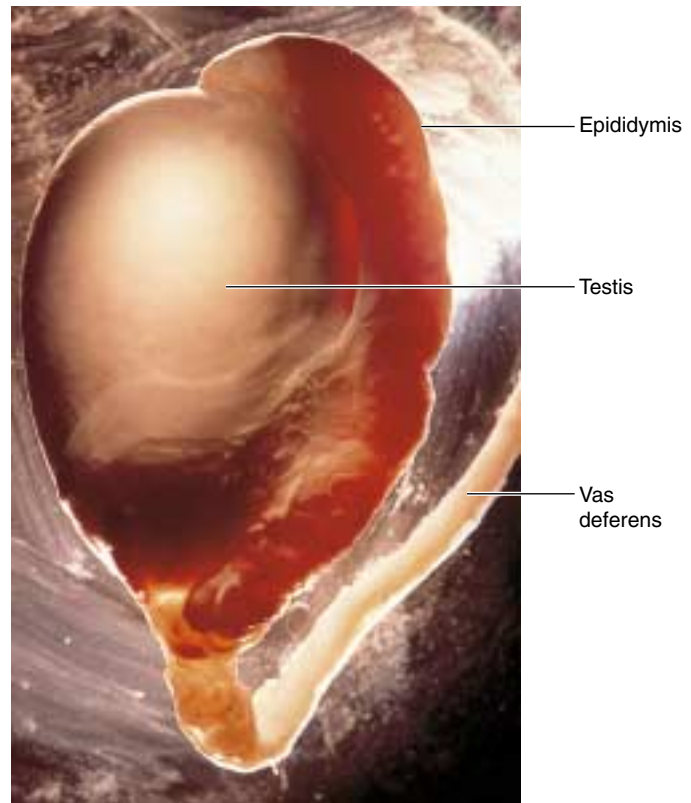


FIGURE 59.13
Photograph of the human testis. The dark, round object in the center of the photograph is a testis, within which sperm are formed. Cupped around it is the epididymis, a highly coiled passageway in which sperm complete their maturation. Mature sperm are stored in the vas deferens, a long tube that extends from the epididymis.

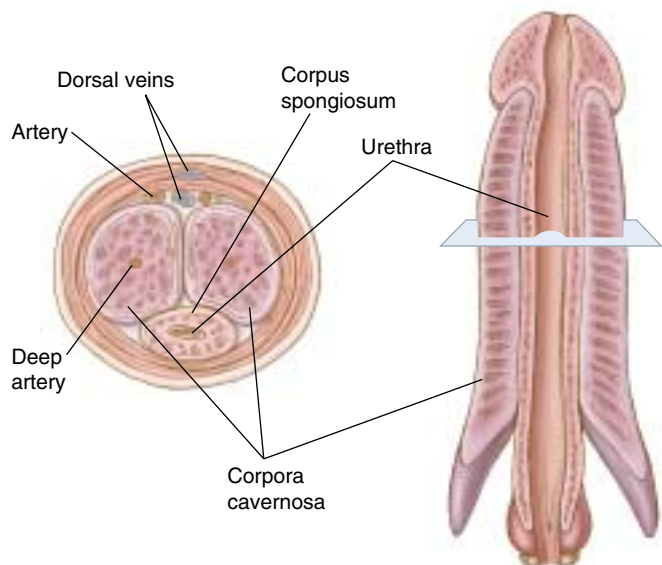


FIGURE 59.14
A penis in cross-section (left) and longitudinal section (right). Note that the urethra runs through the corpus spongiosum.

Table 59.1 Mammalian Reproductive Hormones**MALE**

Follicle-stimulating hormone (FSH)	Stimulates spermatogenesis
Luteinizing hormone (LH)	Stimulates secretion of testosterone by Leydig cells
Testosterone	Stimulates development and maintenance of male secondary sexual characteristics and accessory sex organs

FEMALE

Follicle-stimulating hormone (FSH)	Stimulates growth of ovarian follicles and secretion of estradiol
Luteinizing hormone (LH)	Stimulates ovulation, conversion of ovarian follicles into corpus luteum, and secretion of estradiol and progesterone by corpus luteum
Estradiol	Stimulates development and maintenance of female secondary sexual characteristics; prompts monthly preparation of uterus for pregnancy
Progesterone	Completes preparation of uterus for pregnancy; helps maintain female secondary sexual characteristics
Oxytocin	Stimulates contraction of uterus and milk-ejection reflex
Prolactin	Stimulates milk production

Hormonal Control of Male Reproduction

As we saw in chapter 56, the anterior pituitary gland secretes two gonadotropic hormones: FSH and LH. Although these hormones are named for their actions in the female, they are also involved in regulating male reproductive function (table 59.1). In males, FSH stimulates the Sertoli cells to facilitate sperm development, and LH stimulates the Leydig cells to secrete testosterone.

The principle of negative feedback inhibition discussed in chapter 56 applies to the control of FSH and LH secretion (figure 59.15). The hypothalamic hormone, gonadotropin-releasing hormone (GnRH), stimulates the anterior pituitary gland to secrete both FSH and LH. FSH causes the Sertoli cells to release a peptide hormone called inhibin that specifically inhibits FSH secretion. Similarly, LH stimulates testosterone secretion, and testosterone feeds back to inhibit the release of LH, both directly at the anterior pituitary gland and indirectly by reducing GnRH release. The importance of negative feedback inhibition can be demonstrated by removing the testes; in the absence of testosterone and inhibin, the secretion of FSH and LH from the anterior pituitary is greatly increased.

An adult male produces sperm continuously by meiotic division of the germinal cells lining the seminiferous tubules. Semen consists of sperm from the testes and fluid contributed by the seminal vesicles and prostate gland. Production of sperm and secretion of testosterone from the testes are controlled by FSH and LH from the anterior pituitary.

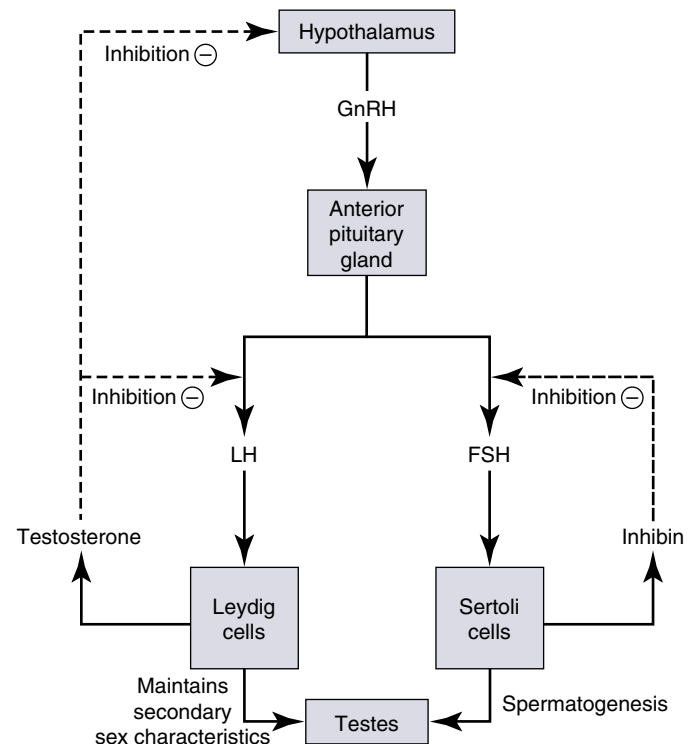


FIGURE 59.15
Hormonal interactions between the testes and anterior pituitary. LH stimulates the Leydig cells to secrete testosterone, and FSH stimulates the Sertoli cells of the seminiferous tubules to secrete inhibin. Testosterone and inhibin, in turn, exert negative feedback inhibition on the secretion of LH and FSH, respectively.

Structure and Function of the Female Reproductive System

The structures of the reproductive system in a human female are shown in figure 59.16. In contrast to the testes, the ovaries develop much more slowly. In the absence of testosterone, the female embryo develops a **clitoris** and **labia majora** from the same embryonic structures that produce a penis and scrotum in males. Thus clitoris and penis, and the labia majora and scrotum, are said to be *homologous structures*. The clitoris, like the penis, contains corpora cavernosa and is therefore erectile. The ovaries contain microscopic structures called **ovarian follicles**, which each contain an egg cell and smaller **granulosa cells**. The ovarian follicles are the functional units of the ovary.

At puberty, the granulosa cells begin to secrete the major female sex hormone estradiol (also called estrogen), triggering **menarche**, the onset of menstrual cycling. Estradiol also stimulates the formation of the **female secondary sexual characteristics**, including breast development and the production of pubic hair. In addition, estradiol and another steroid hormone, progesterone, help to

maintain the female accessory sex organs: the fallopian tubes, uterus, and vagina.

Female Accessory Sex Organs

The fallopian tubes (also called uterine tubes or oviducts) transport ova from the ovaries to the uterus. In humans, the uterus is a muscular, pear-shaped organ that narrows to form a neck, the cervix, which leads to the vagina (figure 59.17*a*). The uterus is lined with a simple columnar epithelial membrane called the endometrium. The surface of the endometrium is shed during menstruation, while the underlying portion remains to generate a new surface during the next cycle.

Mammals other than primates have more complex female reproductive tracts, where part of the uterus divides to form uterine “horns,” each of which leads to an oviduct (figure 59.17*b, c*). In cats, dogs, and cows, for example, there is one cervix but two uterine horns separated by a septum, or wall. Marsupials, such as opossums, carry the split even further, with two unconnected uterine horns, two cervixes, and two vaginas. A male marsupial has a forked penis that can enter both vaginas simultaneously.

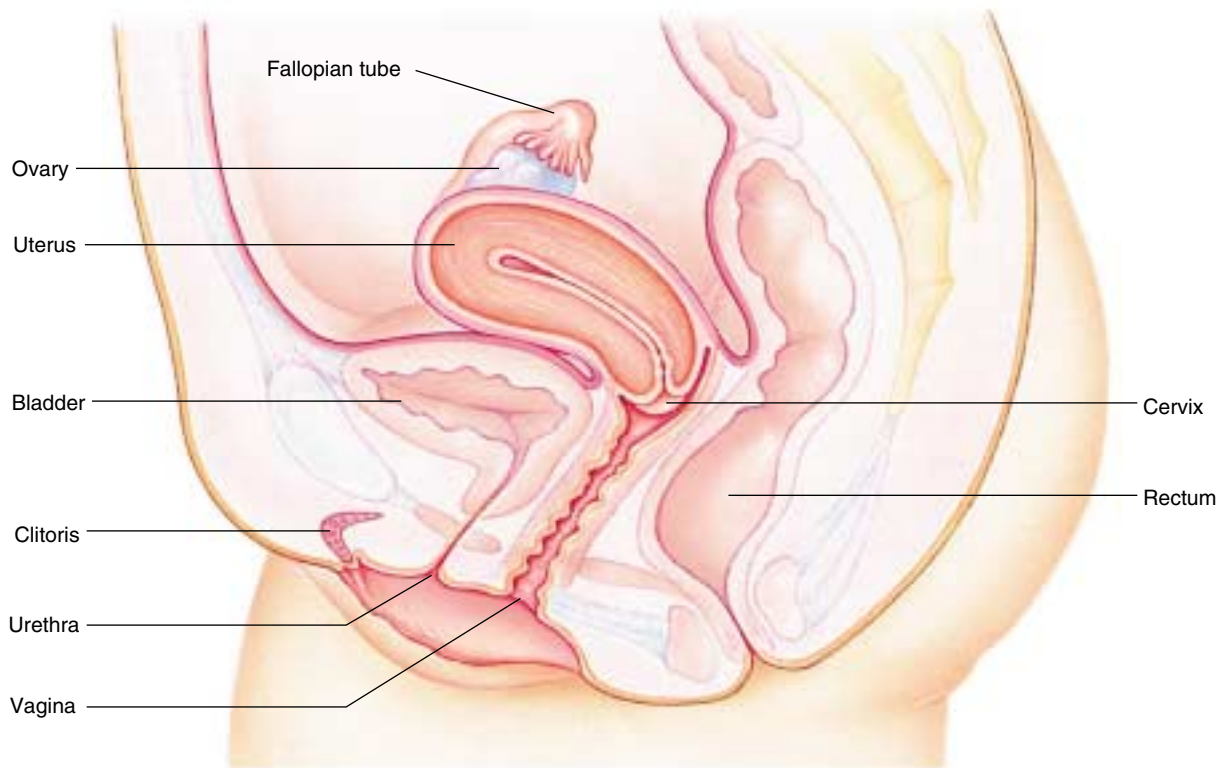


FIGURE 59.16

Organization of the human female reproductive system. The ovaries are the gonads, the fallopian tubes receive the ovulated ova, and the uterus is the womb, the site of development of an embryo if the egg cell becomes fertilized.

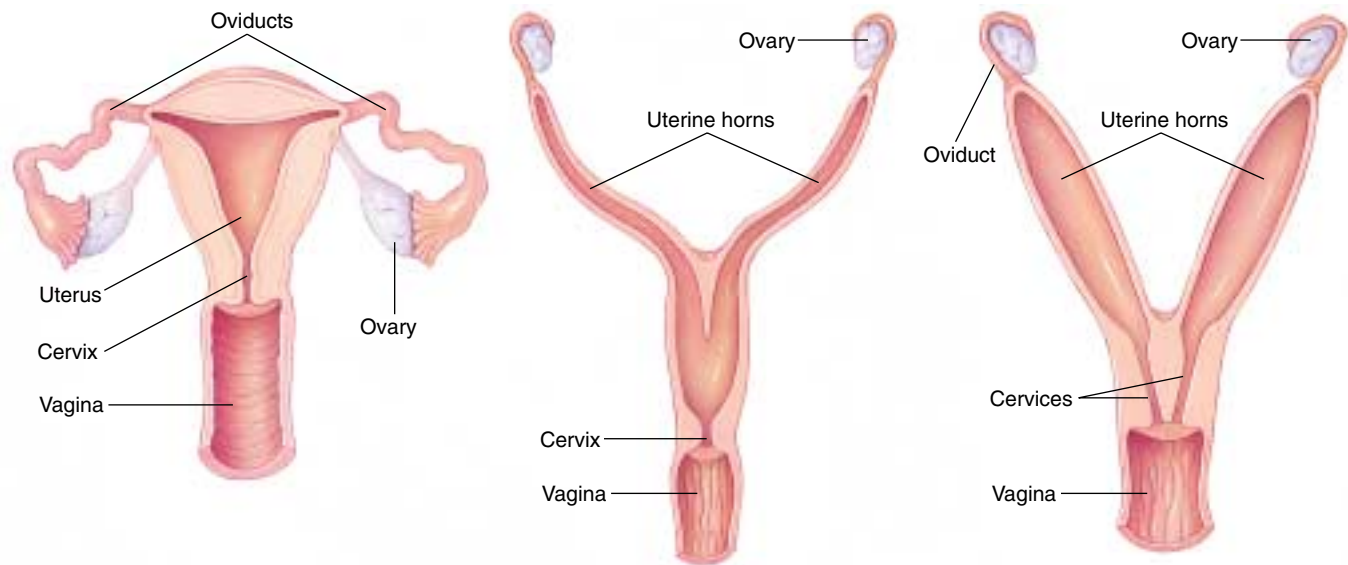


FIGURE 59.17
A comparison of mammalian uteruses. (a) Humans and other primates; (b) cats, dogs, and cows; and (c) rats, mice, and rabbits.

Menstrual and Estrous Cycles

At birth, a female's ovaries contain some 2 million follicles, each with an ovum that has begun meiosis but which is arrested in prophase of the first meiotic division. At this stage, the ova are called primary oocytes. Some of these primary-oocyte-containing follicles are stimulated to develop during each cycle. The human menstrual (Latin *mens*, "month") cycle lasts approximately one month (28 days on the average) and can be divided in terms of ovarian activity into a follicular phase and luteal phase, with the two phases separated by the event of ovulation.

Follicular Phase

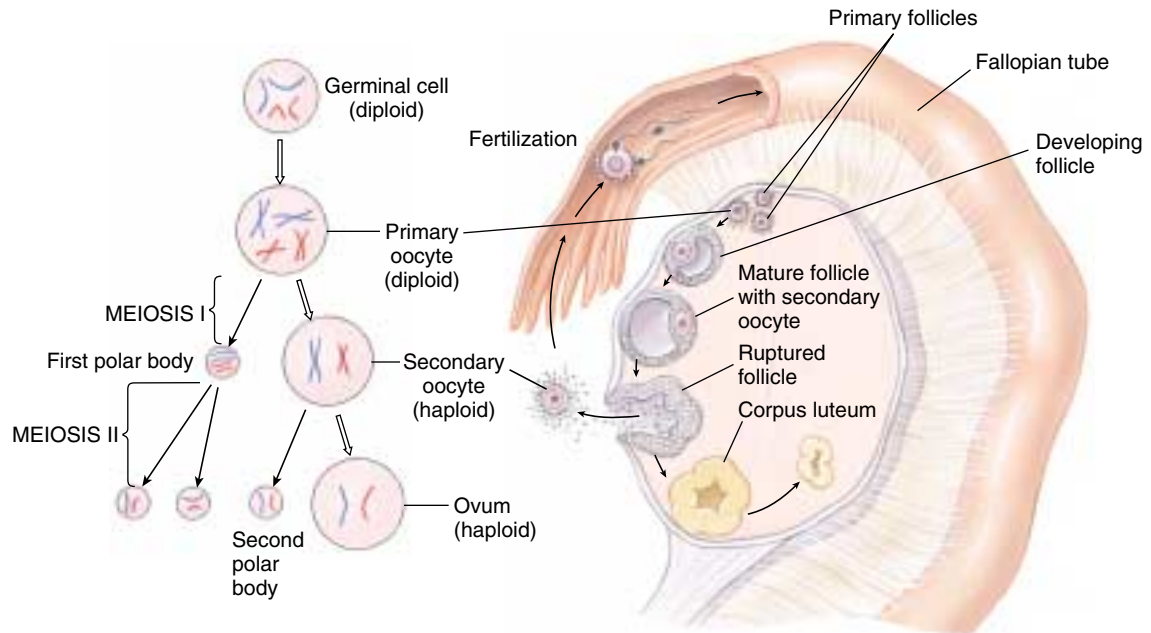
During the follicular phase, a few follicles are stimulated to grow under FSH stimulation, but only one achieves full maturity as a tertiary, or Graafian, follicle (figure 59.18). This follicle forms a thin-walled blister on the surface of the ovary. The primary oocyte within the Graafian follicle completes the first meiotic division during the follicular phase. Instead of forming two equally large daughter cells, however, it produces one large daughter cell, the secondary oocyte, and one tiny daughter cell, called a polar body. Thus, the secondary oocyte acquires almost all of the cytoplasm from the primary oocyte, increasing its chances of sustaining the early embryo should the oocyte be fertilized. The polar body, on the other hand, often disintegrates. The secondary oocyte then begins the second meiotic division, but its progress is arrested at metaphase II. It is in this form that the egg cell is discharged from the ovary at ovulation, and it does not complete the second meiotic division unless it becomes fertilized in the fallopian tube.



FIGURE 59.18
A mature Graafian follicle in a cat ovary (50 \times). Note the ring of granulosa cells that surrounds the secondary oocyte. This ring will remain around the egg cell when it is ovulated, and sperm must tunnel through the ring in order to reach the plasma membrane of the egg cell.

FIGURE 59.19

The meiotic events of oogenesis in humans. A primary oocyte is diploid. At the completion of the first meiotic division, one division product is eliminated as a polar body, while the other, the secondary oocyte, is released during ovulation. The secondary oocyte does not complete the second meiotic division until after fertilization; that division yields a second polar body and a single haploid egg, or ovum. Fusion of the haploid egg with a haploid sperm during fertilization produces a diploid zygote.



Ovulation

The increasing level of estradiol in the blood during the follicular phase stimulates the anterior pituitary gland to secrete LH about midcycle. This sudden secretion of LH causes the fully developed Graafian follicle to burst in the process of ovulation, releasing its secondary oocyte. The released oocyte enters the abdominal cavity near the fimbriae, the feathery projections surrounding the opening to the fallopian tube. The ciliated epithelial cells lining the fallopian tube propel the oocyte through the fallopian tube toward the uterus. If it is not fertilized, the oocyte will disintegrate within a day following ovulation. If it is fertilized, the stimulus of fertilization allows it to complete the second meiotic division, forming a fully mature ovum and a second polar body. Fusion of the two nuclei from the ovum and the sperm produces a diploid zygote (figure 59.19). Fertilization normally occurs in the upper one-third of the fallopian tube, and in a human the zygote takes approximately three days to reach the uterus, then another two to three days to implant in the endometrium (figure 59.20).

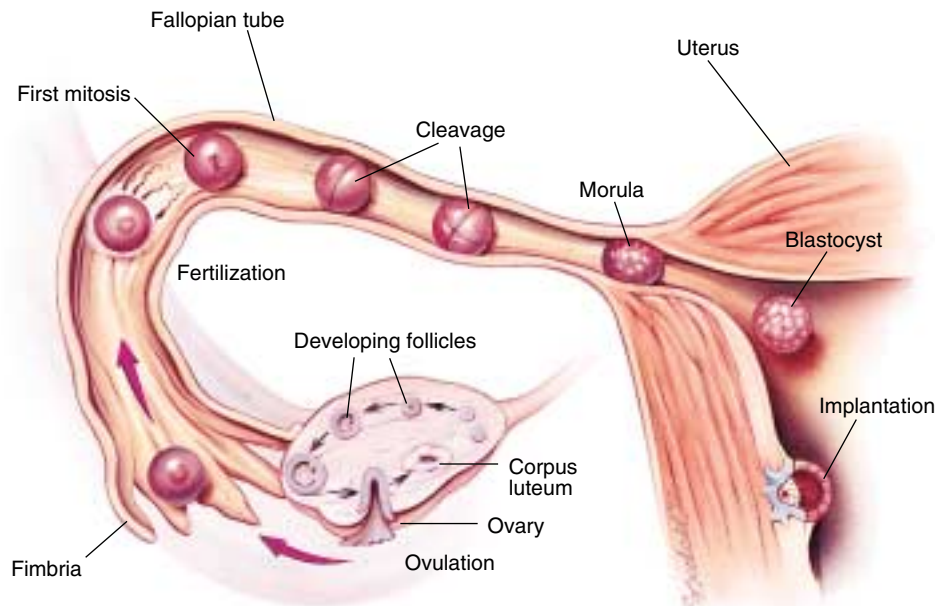


FIGURE 59.20

The journey of an egg. Produced within a follicle and released at ovulation, an egg is swept into a fallopian tube and carried along by waves of ciliary motion in the tube walls. Sperm journeying upward from the vagina fertilize the egg within the fallopian tube. The resulting zygote undergoes several mitotic divisions while still in the tube, so that by the time it enters the uterus, it is a hollow sphere of cells called a blastocyst. The blastocyst implants within the wall of the uterus, where it continues its development. (The egg and its subsequent stages have been enlarged for clarification.)

Luteal Phase

After ovulation, LH stimulates the empty Graafian follicle to develop into a structure called the corpus luteum (Latin, “yellow body”). For this reason, the second half of the menstrual cycle is referred to as the **luteal phase** of the cycle. The corpus luteum secretes both estradiol and another steroid hormone, progesterone. The high blood levels of estradiol and progesterone during the luteal phase now exert negative feedback inhibition of FSH and LH secretion by the anterior pituitary gland. This inhibition during the luteal phase is in contrast to the stimulation exerted by estradiol on LH secretion at midcycle, which caused ovulation. The inhibitory effect of estradiol and progesterone on FSH and LH secretion after ovulation acts as a natural contraceptive mechanism, preventing both the development of additional follicles and continued ovulation.

During the follicular phase the granulosa cells secrete increasing amounts of estradiol, which stimulates the growth of the endometrium. Hence, this portion of the cycle is also referred to as the **proliferative phase** of the endometrium. During the luteal phase of the cycle, the combination of estradiol and progesterone cause the endometrium to become more vascular, glandular, and enriched with glycogen deposits. Because of the endometrium’s glandular appearance, this portion of the cycle is known as the **secretory phase** of the endometrium (figure 59.21).

In the absence of fertilization, the corpus luteum triggers its own atrophy, or regression, toward the end of the luteal phase. It does this by secreting hormones (estradiol and progesterone) that inhibit the secretion of LH, the hormone needed for its survival. In many mammals, atrophy of the corpus luteum is assisted by luteolysin, a paracrine regulator believed to be a prostaglandin. The disappearance of the corpus luteum results in an abrupt decline in the blood concentration of estradiol and progesterone at the end of the luteal phase, causing the built-up endometrium to be sloughed off with accompanying bleeding. This process is called menstruation, and the portion of the cycle in which it occurs is known as the **menstrual phase** of the endometrium.

If the ovulated oocyte is fertilized, however, regression of the corpus luteum and subsequent menstruation is averted by the tiny embryo! It does this by secreting human chorionic gonadotropin (hCG), an LH-like hormone produced by the chorionic membrane of the embryo. By maintaining the corpus luteum, hCG keeps the levels of estradiol and progesterone high and thereby prevents menstruation, which would terminate the pregnancy. Because hCG comes from the embryonic chorion and not the mother, it is the hormone that is tested for in all pregnancy tests.

Menstruation is absent in mammals with an estrous cycle. Although such mammals do cyclically shed cells from the endometrium, they don’t bleed in the process. The estrous cycle is divided into four phases: proestrus, estrus, metestrus, and diestrus, which correspond to the proliferative, mid-cycle, secretory, and menstrual phases of the endometrium in the menstrual cycle.

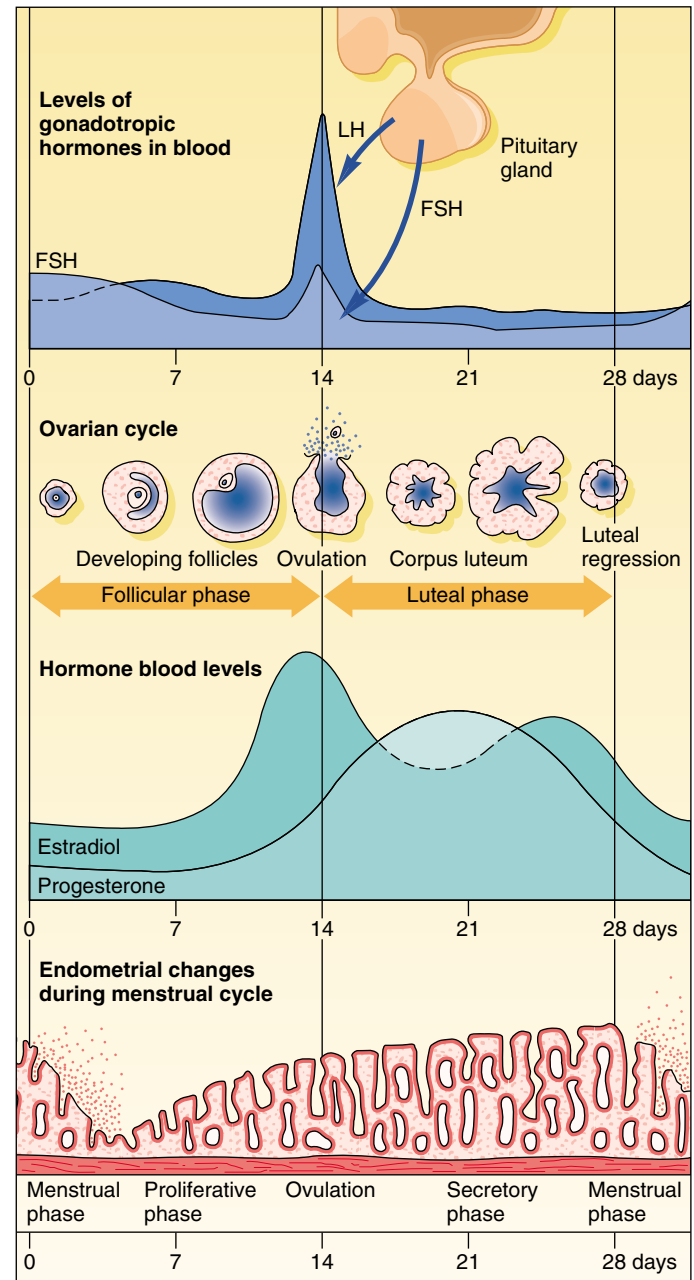


FIGURE 59.21

The human menstrual cycle. The growth and thickening of the endometrial (uterine) lining is stimulated by estradiol and progesterone. The decline in the levels of these two hormones triggers menstruation, the sloughing off of built-up endometrial tissue.

The ovarian follicles develop under FSH stimulation, and one follicle ovulates under LH stimulation. During the follicular and luteal phases, the hormones secreted by the ovaries stimulate the development of the endometrium, so an embryo can implant there if fertilization has occurred. A secondary oocyte is released from an ovary at ovulation, and it only completes meiosis if it is fertilized.

59.4 The physiology of human sexual intercourse is becoming better known.

Physiology of Human Sexual Intercourse

Few physical activities are more pleasurable to humans than sexual intercourse. The sex drive is one of the strongest drives directing human behavior, and as such, it is circumscribed by many rules and customs. Sexual intercourse acts as a channel for the strongest of human emotions such as love, tenderness, and personal commitment. Few subjects are at the same time more private and of more general interest. Here we will limit ourselves to a very narrow aspect of sexual behavior, its immediate physiological effects. The emotional consequences are no less real, but they are beyond the scope of this book.

Until relatively recently, the physiology of human sexual activity was largely unknown. Perhaps because of the prevalence of strong social taboos against the open discussion of sexual matters, no research was carried out on the subject, and detailed information was lacking. Over the past 40 years, however, investigations by William Masters and Virginia Johnson, as well as an army of researchers who followed them, have revealed much about the biological nature of human sexual activity.

The sexual act is referred to by a variety of names, including sexual intercourse, copulation, and coitus, as well as a host of informal terms. It is common to partition the physiological events that accompany intercourse into four phases—**excitement**, **plateau**, **orgasm**, and **resolution**—although there are no clear divisions between these phases.

Excitement

The sexual response is initiated by the nervous system. In both males and females, commands from the brain increase the respiratory rate, heart rate, and blood pressure. The nipples commonly harden and become more sensitive. Other changes increase the diameter of blood vessels, leading to increased circulation. In some people, these changes may produce a reddening of the skin around the face, breasts, and genitals (the sex flush). Increased circulation also leads to vasocongestion, producing erection of the male's penis and similar swelling of the female's clitoris. The female experiences changes that prepare the vagina for sexual intercourse: the labia majora and labia minora, lips of tissue that cover the opening to the vagina, swell and separate due to the increased circulation; the vaginal walls become moist; and the muscles encasing the vagina relax.

Plateau

The penetration of the vagina by the thrusting penis continuously stimulates nerve endings both in the tip of the penis and in the clitoris. The clitoris, which is now swollen,

becomes very sensitive and withdraws up into a sheath or "hood." Once it has withdrawn, the clitoris is stimulated indirectly when the thrusting movements of the penis rub the clitoral hood against the clitoris. The nervous stimulation produced by the repeated movements of the penis within the vagina elicits a continuous response in the autonomic nervous system, greatly intensifying the physiological changes initiated during the excitement phase. In the female, pelvic thrusts may begin, while in the male the penis reaches its greatest length and rigidity.

Orgasm

The climax of intercourse is reached when the stimulation is sufficient to initiate a series of reflexive muscular contractions. The nerve impulses producing these contractions are associated with other activity within the central nervous system, activity that we experience as intense pleasure. In females, the contractions are initiated by impulses in the hypothalamus, which causes the posterior pituitary gland to release large amounts of oxytocin. This hormone, in turn, causes the muscles in the uterus and around the vaginal opening to contract and the cervix to be pulled upward. Contractions occur at intervals of about one per second. There may be one to several intense peaks of contractions (orgasms), or the peaks may be more numerous but less intense.

Analogous contractions take place in the male. The first contractions, which occur in the vas deferens and prostate gland, cause *emission*, the peristaltic movement of sperm and seminal fluid into a collecting zone of the urethra located at the base of the penis. Shortly thereafter, violent contractions of the muscles at the base of the penis result in *ejaculation* of the collected semen through the penis. As in the female, the contractions are spaced about one second apart, although in the male they continue for only a few seconds and are almost invariably restricted to a single intense wave.

Resolution

After ejaculation, males rapidly lose their erection and enter a refractory period lasting 20 minutes or longer, in which sexual arousal is difficult to achieve and ejaculation is almost impossible. By contrast, many women can be aroused again almost immediately. After intercourse, the bodies of both men and women return over a period of several minutes to their normal physiological state.

Sexual intercourse is a physiological series of events leading to the ultimate deposition of sperm within the female reproductive tract. The phases are similar in males and females.

Birth Control

In most vertebrates, copulation is associated solely with reproduction. Reflexive behavior that is deeply ingrained in the female limits sexual receptivity to those periods of the sexual cycle when she is fertile. In humans and a few species of apes, the female can be sexually receptive throughout her reproductive cycle, and this extended receptivity to sexual intercourse serves a second important function—it reinforces pair-bonding, the emotional relationship between two individuals living together.

Not all human couples want to initiate a pregnancy every time they have sexual intercourse, yet sexual intercourse may be a necessary and important part of their emotional lives together. The solution to this dilemma is to find a way to avoid reproduction without avoiding sexual intercourse; this approach is commonly called birth control or contraception. A variety of approaches differing in effectiveness and in their acceptability to different couples are commonly taken to achieve birth control (figure 59.22 and table 59.2).

Abstinence

The simplest and most reliable way to avoid pregnancy is not to have sexual intercourse at all. Of all methods of birth control, this is the most certain. It is also the most limiting, because it denies a couple the emotional support of a sexual relationship.

Sperm Blockage

If sperm cannot reach the uterus, fertilization cannot occur. One way to prevent the delivery of sperm is to encase the penis within a thin sheath, or condom. Many males do not favor the use of condoms, which tend to decrease their sensory pleasure during intercourse. In principle, this method is easy to apply and foolproof, but in practice it has a failure rate of 3 to 15% because of incorrect use or inconsistent use. Nevertheless, it is the most commonly employed form of birth control in the United States. Condoms are also widely used to prevent the transmission of AIDS and other sexually transmitted diseases (STDs). Over a billion condoms were sold in the United States last year.

A second way to prevent the entry of sperm into the uterus is to place a cover over the cervix. The cover may be a relatively tight-fitting cervical cap, which is worn for days at a time, or a rubber dome called a diaphragm, which is inserted immediately before intercourse. Because



(a)



(b)



(c)



(d)

FIGURE 59.22

Four common methods of birth control. (a) Condom; (b) diaphragm and spermicidal jelly; (c) oral contraceptives; (d) Depo-Provera.

the dimensions of individual cervixes vary, a cervical cap or diaphragm must be fitted by a physician. Failure rates average 4 to 25% for diaphragms, perhaps because of the propensity to insert them carelessly when in a hurry. Failure rates for cervical caps are somewhat lower.

Sperm Destruction

A third general approach to birth control is to eliminate the sperm after ejaculation. This can be achieved in principle by washing out the vagina immediately after intercourse, before the sperm have a chance to enter the uterus. Such a procedure is called a douche (French, “wash”). The douche method is difficult to apply well, because it involves a rapid dash to the bathroom immediately after ejaculation and a very thorough washing. Its failure rate is as high as 40%. Alternatively, sperm delivered to the vagina can be destroyed there with spermicidal jellies or foams. These treatments generally require application immediately before intercourse. Their failure rates vary from 10 to 25%. The use of a spermicide with a condom increases the effectiveness over each method used independently.

Prevention of Ovulation

Since about 1960, a widespread form of birth control in the United States has been the daily ingestion of birth control pills, or oral contraceptives, by women. These pills contain analogues of progesterone, sometimes in combination with

Table 59.2 Methods of Birth Control

Device	Action	Failure Rate*	Advantages	Disadvantages
Oral contraceptive	Hormones (progesterone analogue alone or in combination with other hormones) primarily prevent ovulation	1–5, depending on type	Convenient; highly effective; provides significant noncontraceptive health benefits, such as protection against ovarian and endometrial cancers	Must be taken regularly; possible minor side effects which new formulations have reduced; not for women with cardiovascular risks (mostly smokers over age 35)
Condom	Thin sheath for penis that collects semen; “female condoms” sheath vaginal walls	3–15	Easy to use; effective; inexpensive; protects against some sexually transmitted diseases	Requires male cooperation; may diminish spontaneity; may deteriorate on the shelf
Diaphragm	Soft rubber cup covers entrance to uterus, prevents sperm from reaching egg, holds spermicide	4–25	No dangerous side effects; reliable if used properly; provides some protection against sexually transmitted diseases and cervical cancer	Requires careful fitting; some inconvenience associated with insertion and removal; may be dislodged during intercourse
Intrauterine device (IUD)	Small plastic or metal device placed in the uterus; prevents implantation; some contain copper, others release hormones	1–5	Convenient; highly effective; infrequent replacement	Can cause excess menstrual bleeding and pain; risk of perforation, infection, expulsion, pelvic inflammatory disease, and infertility; not recommended for those who eventually intend to conceive or are not monogamous; dangerous in pregnancy
Cervical cap	Miniature diaphragm covers cervix closely, prevents sperm from reaching egg, holds spermicide	Probably similar to that of diaphragm	No dangerous side effects; fairly effective; can remain in place longer than diaphragm	Problems with fitting and insertion; comes in limited number of sizes
Foams, creams, jellies, vaginal suppositories	Chemical spermicides inserted in vagina before intercourse that prevent sperm from entering uterus	10–25	Can be used by anyone who is not allergic; protect against some sexually transmitted diseases; no known side effects	Relatively unreliable; sometimes messy; must be used 5–10 minutes before each act of intercourse
Implant (levonorgestrel; Norplant)	Capsules surgically implanted under skin slowly release hormone that blocks ovulation	.03	Very safe, convenient, and effective; very long-lasting (5 years); may have nonreproductive health benefits like those of oral contraceptives	Irregular or absent periods; minor surgical procedure needed for insertion and removal; some scarring may occur
Injectable contraceptive (medroxy-progesterone; Depo-Provera)	Injection every 3 months of a hormone that is slowly released and prevents ovulation	1	Convenient and highly effective; no serious side effects other than occasional heavy menstrual bleeding	Animal studies suggest it may cause cancer, though new studies in humans are mostly encouraging; occasional heavy menstrual bleeding

*Failure rate is expressed as pregnancies per 100 actual users per year.

Source: Data from American College of Obstetricians and Gynecologists: Contraception, Patient Education Pamphlet No. AP005.ACOG, Washington, D.C., 1990.

estrogens. As described earlier, progesterone and estradiol act by negative feedback to inhibit the secretion of FSH and LH during the luteal phase of the menstrual cycle, thereby preventing follicle development and ovulation. They also cause a buildup of the endometrium. The hormones in birth control pills have the same effects. Because the pills block ovulation, no ovum is available to be fertilized. A woman generally takes the hormone-containing

pills for three weeks; during the fourth week, she takes pills without hormones (placebos), allowing the levels of those hormones in her blood to fall, which causes menstruation. Oral contraceptives provide a very effective means of birth control, with a failure rate of only 1 to 5%. In a variation of the oral contraceptive, hormone-containing capsules are implanted beneath the skin. These implanted capsules have failure rates below 1%.

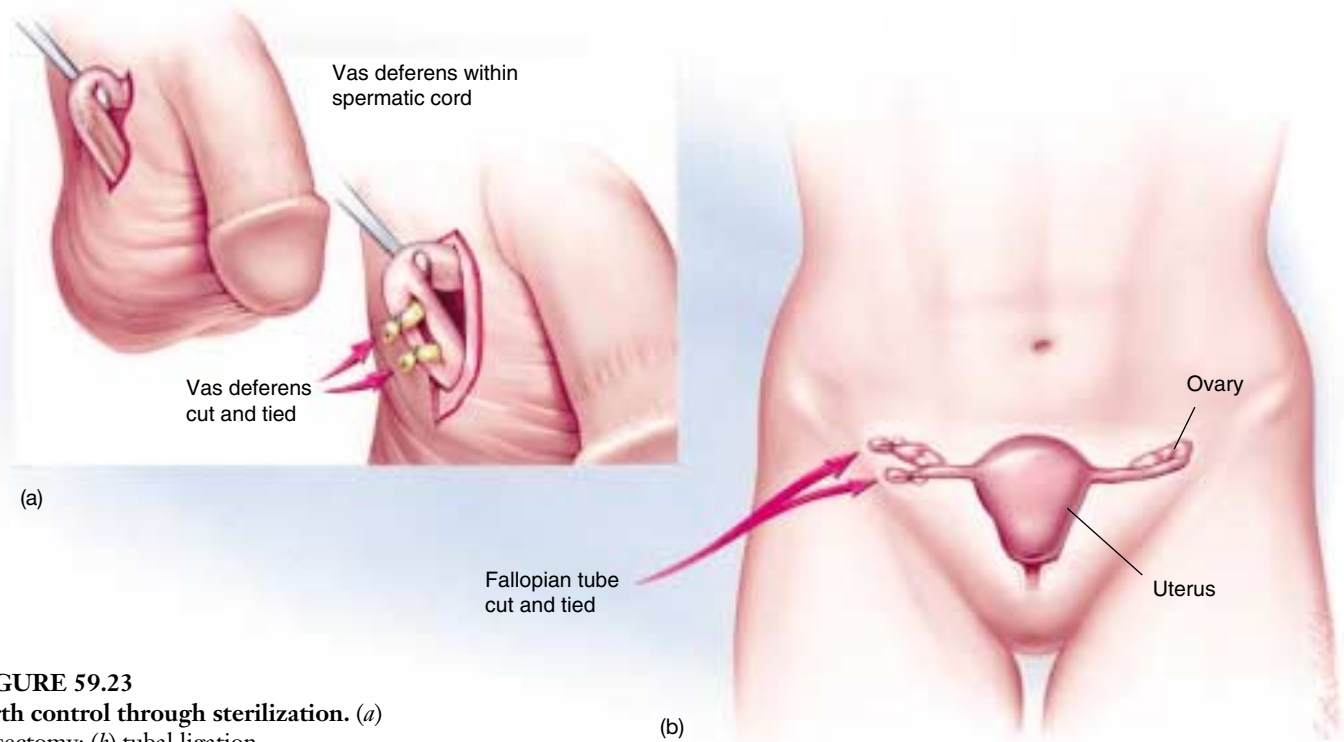


FIGURE 59.23
Birth control through sterilization. (a)
 Vasectomy; (b) tubal ligation.

A small number of women using birth control pills or implants experience undesirable side effects, such as blood clotting and nausea. These side effects have been reduced in newer generations of birth control pills, which contain less estrogen and different analogues of progesterone. Moreover, these new oral contraceptives provide a number of benefits, including reduced risks of endometrial and ovarian cancer, cardiovascular disease, and osteoporosis (for older women). However, they may increase the risk of contracting breast cancer and cervical cancer. The risks involved with birth control pills increase in women who smoke and increase greatly in women over 35 who smoke. The current consensus is that, for many women, the health benefits of oral contraceptives outweigh their risks, although a physician must help each woman determine the relative risks and benefits.

Prevention of Embryo Implantation

The insertion of a coil or other irregularly shaped object into the uterus is an effective means of birth control, because the irritation it produces in the uterus prevents the implantation of an embryo within the uterine wall. Such intrauterine devices (IUDs) have a failure rate of only 1 to 5%. Their high degree of effectiveness probably reflects their convenience; once they are inserted, they can be forgotten. The great disadvantage of this method is that almost a third of the women who attempt to use IUDs experience cramps, pain, and sometimes bleeding and therefore must discontinue using them.

Another method of preventing embryo implantation is the “morning after pill,” which contains 50 times the dose of estrogen present in birth control pills. The pill works by temporarily stopping ovum development, by preventing fertilization, or by stopping the implantation of a fertilized ovum. Its failure rate is 1 to 10%, but many women are uneasy about taking such high hormone doses, as side effects can be severe. This is not recommended as a regular method of birth control but rather as a method of emergency contraception.

Sterilization

A completely effective means of birth control is sterilization, the surgical removal of portions of the tubes that transport the gametes from the gonads (figure 59.23). Sterilization may be performed on either males or females, preventing sperm from entering the semen in males and preventing an ovulated oocyte from reaching the uterus in females. In males, sterilization involves a vasectomy, the removal of a portion of the vas deferens from each testis. In females, the comparable operation involves the removal of a section of each fallopian tube.

Fertilization can be prevented by a variety of birth control methods, including barrier contraceptives, hormonal inhibition, surgery, and abstinence. Efficacy rates vary from method to method.

**Summary****Questions****Media Resources****59.1 Animals employ both sexual and asexual reproductive strategies.**

- Parthenogenesis is a form of asexual reproduction that is practiced by many insects and some lizards.
- Among mammals, the sex is determined by the presence of a Y chromosome in males and its absence in females.

1. How are oviparity, ovoviviparity, and viviparity different?



- Introduction to reproduction

59.2 The evolution of reproduction among the vertebrates has led to internalization of fertilization and development.

- Most bony fish practice external fertilization, releasing eggs and sperm into the water where fertilization occurs. Amphibians have external fertilization and the young go through a larval stage before metamorphosis.
- Reptiles and birds are oviparous, the young developing in eggs that are deposited externally. Most mammals are viviparous, the young developing within the mother.

2. How does fetal development differ in the monotremes, marsupials, and placental mammals?



- *On Science* articles: Interactions
- Student Research: Reproductive biology of house mice
Evolution of uterine function

59.3 Male and female reproductive systems are specialized for different functions.

- Sperm leave the testes and pass through the epididymis and vas deferens; the ejaculatory duct merges with the urethra, which empties at the tip of the penis.
- An egg cell released from the ovary in ovulation is drawn by fimbria into the fallopian tube, which conducts the egg cell to the lining of the uterus, or endometrium, where it implants if fertilized.
- If fertilization does not occur, the corpus luteum regresses at the end of the cycle and the resulting fall in estradiol and progesterone secretion cause menstruation to occur in humans and apes.

3. Briefly describe the function of seminal vesicles, prostate gland, and bulbourethral glands.

4. When do the ova in a female mammal begin meiosis? When do they complete the first meiotic division?

5. What hormone is secreted by the granulosa cells in a Graafian follicle? What effect does this hormone have on the endometrium?



- Art Activities: Sperm and egg anatomy
Male reproductive system
Penis anatomy
Female reproductive system
Breast anatomy



- Spermatogenesis
- Menstruation
- Female reproductive cycle
- Oogenesis

59.4 The physiology of human sexual intercourse is becoming better known.

- The physiological events that occur in the human sexual response are grouped into four phases: excitement, plateau, orgasm, and resolution.
- Males and females have similar phases, but males enter a refractory period following orgasm that is absent in many women.
- There are a variety of methods of birth control available that range in ease of use, effectiveness, and permanence.

6. What are the four phases in the physiological events of sexual intercourse in humans? During the first phase, what events occur specifically in males, and what events occur specifically in females?

7. How do birth control pills prevent pregnancy?



- Penile erection
- Vasectomy
- Tubal ligation