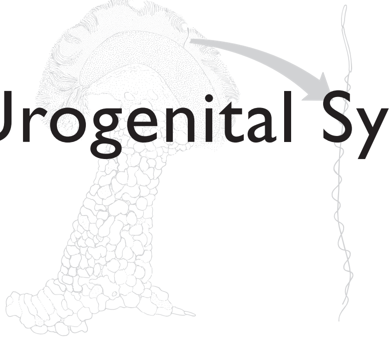
CHAPTER 14

The Urogenital System



Introduction

Evolutionary survival depends on doing many things successfully: escaping from predators, procuring food, adjusting to the environment, and so on. All of this comes down to reproducing successfully, which is the primary biological role of the genital system. On the other hand, the urinary system is devoted to quite different functions: namely, to the elimination of waste products, primarily ammonia, and to the regulation of water and electrolyte balance. Although urinary and reproductive functions are quite different, we treat both systems together as the urogenital system because both share many of the same ducts.

Anatomically, the urinary system includes the kidneys and the ducts that carry away their product, **urine.** The genital system includes the gonads and their ducts that carry away the products they form, **sperm** or **eggs.** Embryologically, urinary and reproductive organs arise from the same or adjacent tissues and maintain close anatomical association throughout the organism's life.

Urinary System

Structure of the Mammalian Kidney

The vertebrate kidneys are a pair of compact masses of tubules situated dorsal to the abdominal cavity. Urine produced by the tubules is ultimately released into the **cloaca** or its derivative, the **urogenital sinus.** We discuss the urinary ducts in some detail later in the chapter when

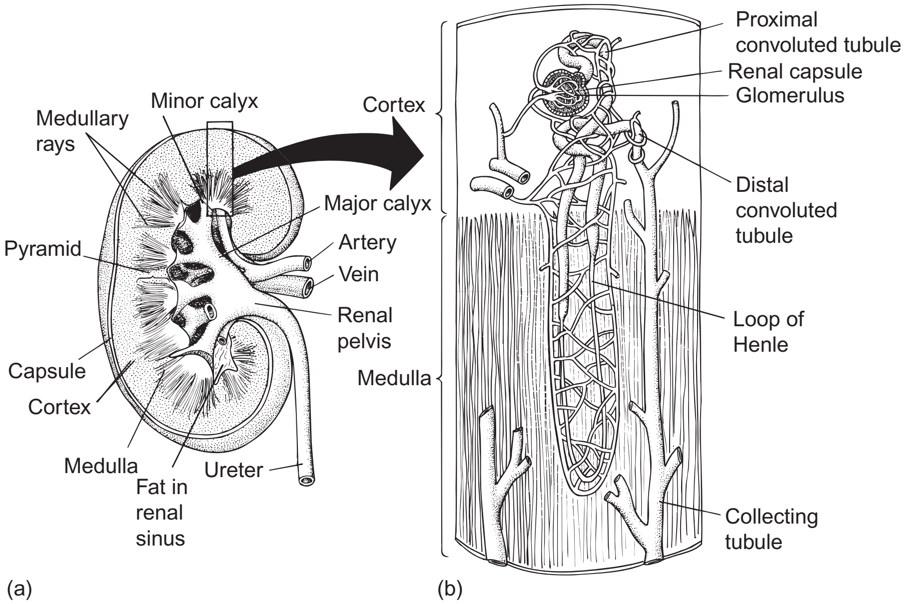


FIGURE 14.1 **Structure of the mammalian kidney.** (a) Section of kidney showing cortex, medulla, and departure of ureter. (b) The uriniferous tubule begins in the cortex, loops through the medulla, and then returns to the cortex, where it joins with the collecting tubule.

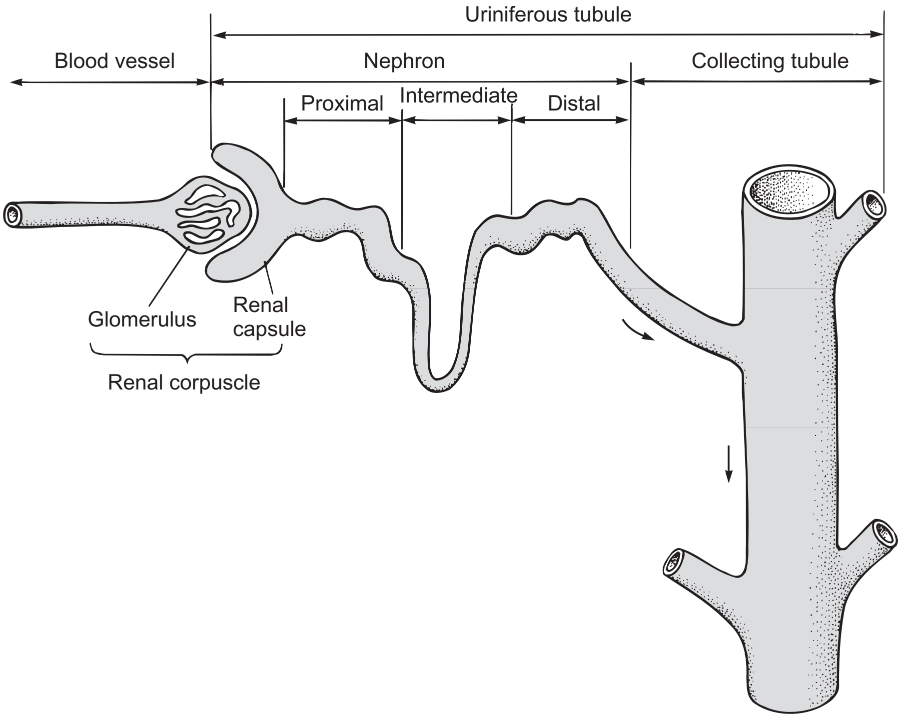


FIGURE 14.2 **Uriniferous tubule.** The nephron (nephric tubule) and collecting tubule make up the uriniferous tubule. In turn, the nephron comprises the renal (Bowman's) capsule and the proximal, intermediate, and distal tubules. The glomerulus is the capillary bed associated with the renal capsule. The excretory duct carries away waste products from several uriniferous tubules.

we consider the reproductive system. In this section, we examine the kidney using the mammalian kidney to introduce the terminology that describes the anatomical complexity of this organ.

A cutaway view of the mammalian kidney reveals the two regions: an outer **cortex** surrounding a deeper **medulla** (figure 14.1a). Urine produced by the kidney enters the **minor** and then the **major calyx,** which joins the **renal pelvis,** a common chamber leading to the **urinary bladder** via the **ureter.** Elimination of urine from the body occurs through the **urethra.** Within the kidney, the functional unit that forms urine is the microscopic **uriniferous tubule** (figures 14.1b and 14.2). The uriniferous tubule consists of two parts: the **nephron (nephric tubule)** and the **collecting tubule** into which the nephron empties. The number of uriniferous tubules varies from only a few hundred in the kidneys of cyclostomes to over a million per kidney in mammals, in whom the tubules of both kidneys combined constitute over 120 km of tubing. The nephron forms urine. The collecting tubule affects the concentration of urine and conveys it to the minor calyx, the beginning of the excretory duct.

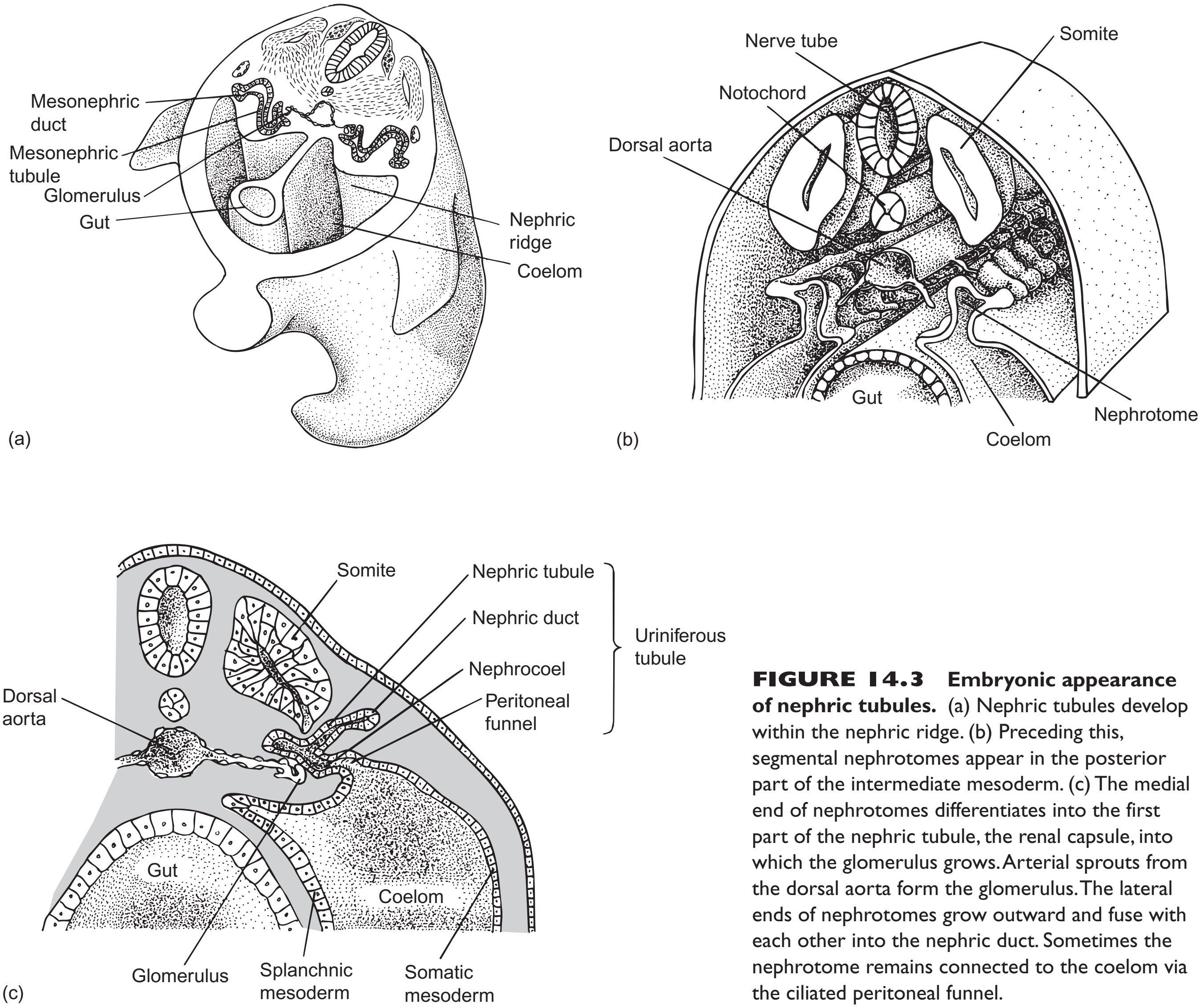


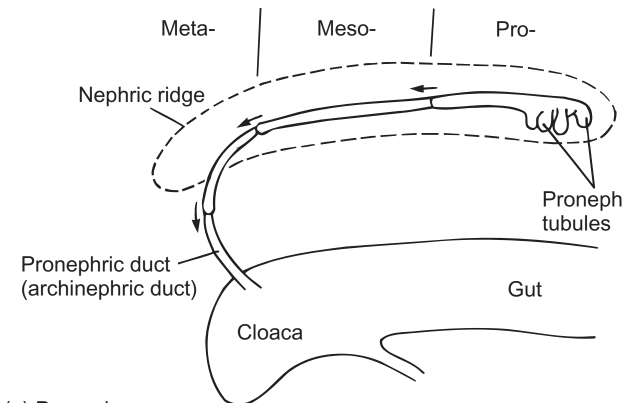
FIGURE 14.3 Embryonic appearance of nephric tubules. (a) Nephric tubules develop within the nephric ridge. (b) Preceding this, segmental nephrotomes appear in the posterior part of the intermediate mesoderm. (c) The medial end of nephrotomes differentiates into the first part of the nephric tubule, the renal capsule, into which the glomerulus grows. Arterial sprouts from the dorsal aorta form the glomerulus. The lateral ends of nephrotomes grow outward and fuse with each other into the nephric duct. Sometimes the nephrotome remains connected to the coelom via the ciliated peritoneal funnel.

The renal artery, one of the major branches from the dorsal aorta, delivers blood to the kidneys. Through a series of subsequent branches, it eventually forms tiny capillary beds known as **glomeruli,** each being associated with a **renal capsule (Bowman's capsule)** constituting the first part of the nephron. Collectively, the glomerulus and renal capsule form the **renal corpuscle.** An ultrafiltrate without blood cells and proteins is forced through the capillary walls and collects in the renal capsule before it passes through the **proximal** convoluted tubule, **intermediate** tubule, and **distal** convoluted tubule of the nephron, eventually entering the collecting tubules. During transit, the composition of the fluid is altered and water is removed. After circulating through the glomerulus, blood flows through an extended capillary network entwined about the rest of the uriniferous tubule (figure 14.1b). Thereafter, blood is collected in progressively larger veins that join the common renal vein leaving the kidneys.

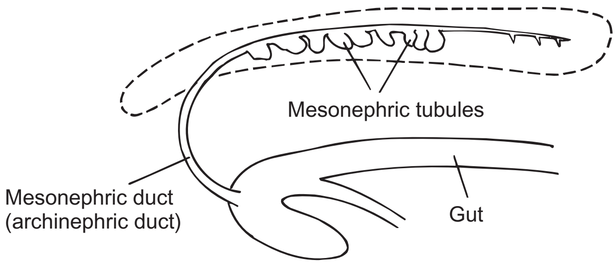
Embryonic Development

Nephrotome to Nephric Tubules

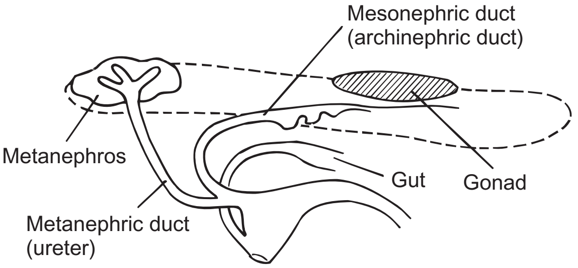
The kidneys form within the intermediate mesoderm located in the dorsal and posterior body wall of the embryo. At the onset of its differentiation, this posterior region of the intermediate mesoderm expands, forming a **nephric ridge** that protrudes slightly from the dorsal wall of the body cavity (figure 14.3a). The next structure to appear usually is the paired **nephrotome,** the embryonic forerunner of the uriniferous tubule (figure 14.3b). The nephrotome is often segmental and contains the **nephrocoel,** a coelomic chamber that may open via a ciliated **peritoneal funnel** to the coelom. Next, the medial end of the nephrotome widens into a thin-walled renal capsule into which grows the glomerulus, a tuft of arterial capillaries. The lateral end of the nephrotome grows outward. This outgrowth fuses with similar outgrowths from



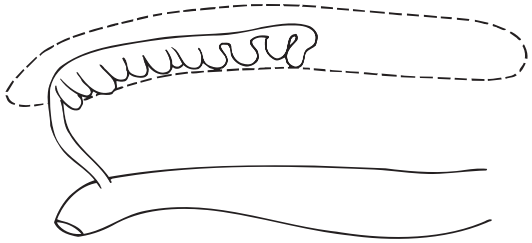
(a) Pronephros



(b) Mesonephros



(c) Metanephros



(d) Opisthonephros

FIGURE 14.4 **Embryonic origin of the kidneys.** Tubules forming the kidney arise in one of three regions of the nephric ridge: anterior (pro-), middle (meso-), or posterior (meta-). (a) Pronephros. Tubules arise in the anterior part of the nephric ridge. They produce a pronephric duct that grows posteriorly in the nephric ridge and empties into the cloaca. Of the three types of kidneys, the pronephros is the first to arise during embryonic development. It becomes the adult kidney in a few fishes but is usually replaced during embryonic development by the mesonephros. (b) Mesonephros. Tubules arise in the middle of the nephric ridge and tap into the existing pronephric duct, now appropriately renamed the mesonephric duct. The mesonephros is usually embryonic and transient.
(c) Metanephros. Sprouting from the mesonephric duct, the ureteric diverticulum (later the ureter) grows into the posterior section of the nephric ridge, where it stimulates differentiation of tubules that form the metanephros. In males, the mesonephric duct usually takes over the task of sperm transport and is called the vas deferens. In the female, the mesonephric duct degenerates. (d) Opisthonephros. Tubules arising from the middle and posterior nephric ridge form an extended kidney, the opisthonephros, that may develop into the adult kidney of fishes and amphibians.

successive nephrotomes to form the common **nephric duct** (figure 14.3c). From this point in embryonic development, the modified nephrotome is more properly called a uriniferous tubule. It may retain its connection with the coelom via the persistent peritoneal funnel.

Thus, the fundamental plan underlying the excretory system is envisioned to consist of paired and segmented uriniferous tubules that open on one end to the coelom and on the other end to the nephric duct, with a glomerulus in between. The ciliated peritoneal funnel seems to drive fluid from the coelom into the tubule, the associated glomerulus adds fluids from the blood, and the tubule itself modifies this collected fluid before it flows into the nephric duct. Although this structure represents the primitive or fundamental plan of excretory tubule organization, in fact, tubules opening to the coelom are rarely found in the kidneys of adult vertebrates. During embryonic development, the uriniferous tubule usually develops directly in the nephric ridge without ever establishing a direct opening to the coelom via a peritoneal funnel (figure 14.3a).

Tripartite Concept of Kidney Organization

Developmental and structural differences in the nephric tubules that arise within the nephric ridge inspired a view of kidney formation known as the **tripartite concept.** This concept envisions formation of nephric tubules in one of

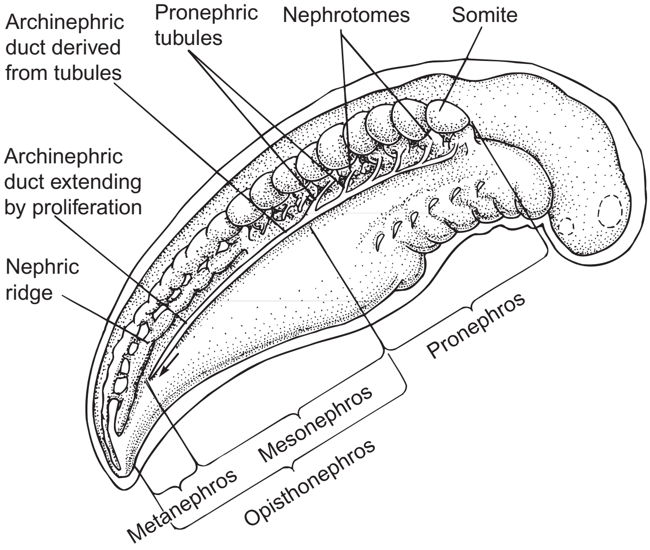


FIGURE 14.5 **Three-part kidney.** Within the nephric ridge, which is derived from intermediate mesoderm, up to three sets of tubules may arise. An extended adult kidney, drained by the mesonephric duct and composed of mesonephric and metanephric posterior tubules, is called the opisthonephros.

After Pough, Heiser, and McFarland.

three locations within the nephric ridge. Subsequent loss, merger, or replacement of these tubules constitutes the developmental basis for the definitive adult kidneys. Specifically, nephric tubules may arise within the anterior, middle, or posterior region of the nephric ridge, giving rise to a *pronephros*, *mesonephros*, or *metanephros*, respectively (figure 14.4a–c). In addition to positional differences, the three regions vary with respect to connections to the coelom. In the pronephros, tubules retain their connections to the coelom through the peritoneal funnel; however, tubules arising within the middle or posterior regions are not connected to the coelom.

Pronephros The anterior pronephros is usually only a transient embryonic developmental stage in all vertebrates. Tubules that appear within the anterior part of the nephric ridge are called **pronephric tubules**. These tubules join to form a common pronephric duct. This duct grows posteriorly in the nephric ridge, eventually reaching and opening into the cloaca (figure 14.4a). Glomeruli may protrude into the roof of the body coelom, and fluid filters from them into

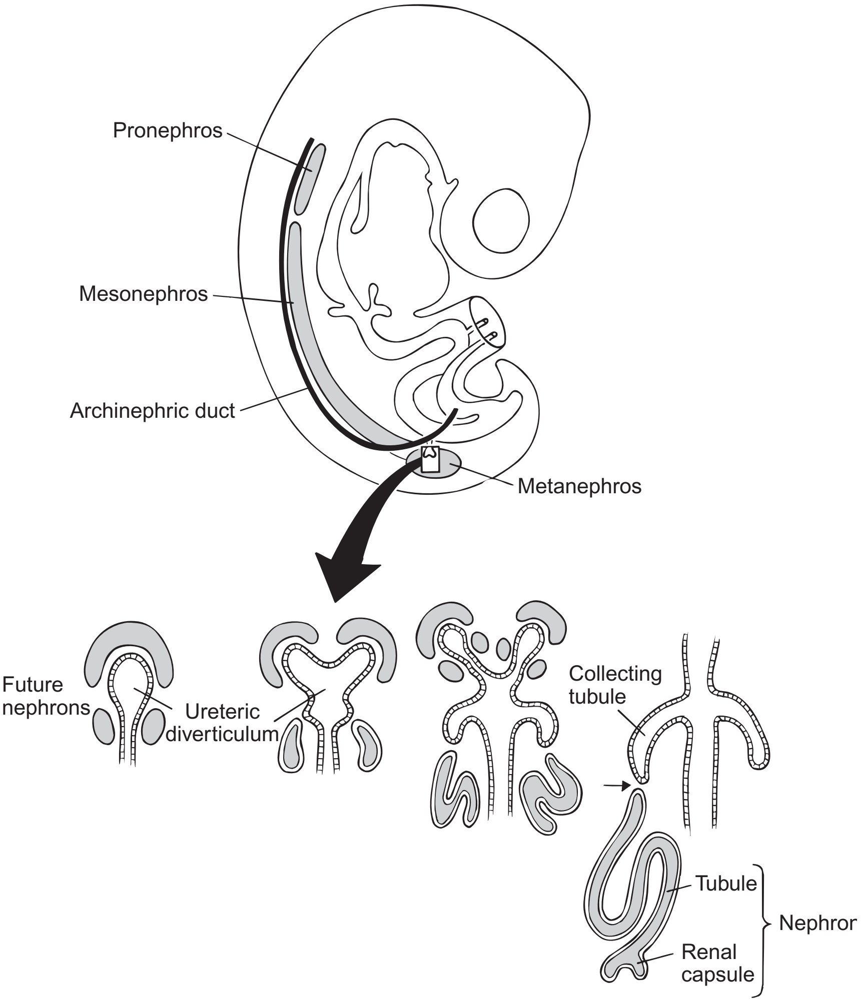


FIGURE 14.6 **Stages in formation of the amniote kidney.** Cross section of the forming metanephros shows that the ureteric diverticulum stimulates surrounding tissue in the nephric ridge to differentiate into nephrons. The ends of the ureteric diverticulum form the collecting tubules.

the body cavity. Pronephric tubules then take up this coelomic fluid through ciliated peritoneal funnels, act on it, and eventually excrete the fluid as urine. However, in most pronephric kidneys, glomeruli make direct contact with pronephric tubules.

Pronephric tubules become associated with glomeruli to form functional kidneys in larval cyclostomes, some adult fishes, and embryos of most lower vertebrates. Fluid filtered from the blood enters the tubules directly, and the peritoneal funnels may or may not remain open, depending on the species. In a few amniotes, usually only several pronephric tubules appear during embryonic development. They are not connected to the coelom and do not become functional. In most vertebrates, the embryonic pronephros regresses, and as it does, it is replaced by a second type of embryonic kidney, the mesonephros.

Mesonephros Tubules of the mesonephric kidney arise in the middle of the nephric ridge. These **mesonephric tubules** do not produce a new duct but instead tap into the preexisting **pronephric duct**. To be consistent, the pronephric duct is now properly renamed the **mesonephric duct** (figure 14.4b).

The mesonephros usually becomes functional in the embryo, but if it persists into the adult, it is modified by incorporation of additional tubules arising within the posterior nephric ridge. This extended mesonephric kidney with additional posterior tubules is termed the **opisthonephros** (figures 14.4d and 14.5). The opisthonephros is found in most adult fishes and amphibians. In amniotes, the mesonephros is replaced in later development by a third type of embryonic kidney, the metanephros.

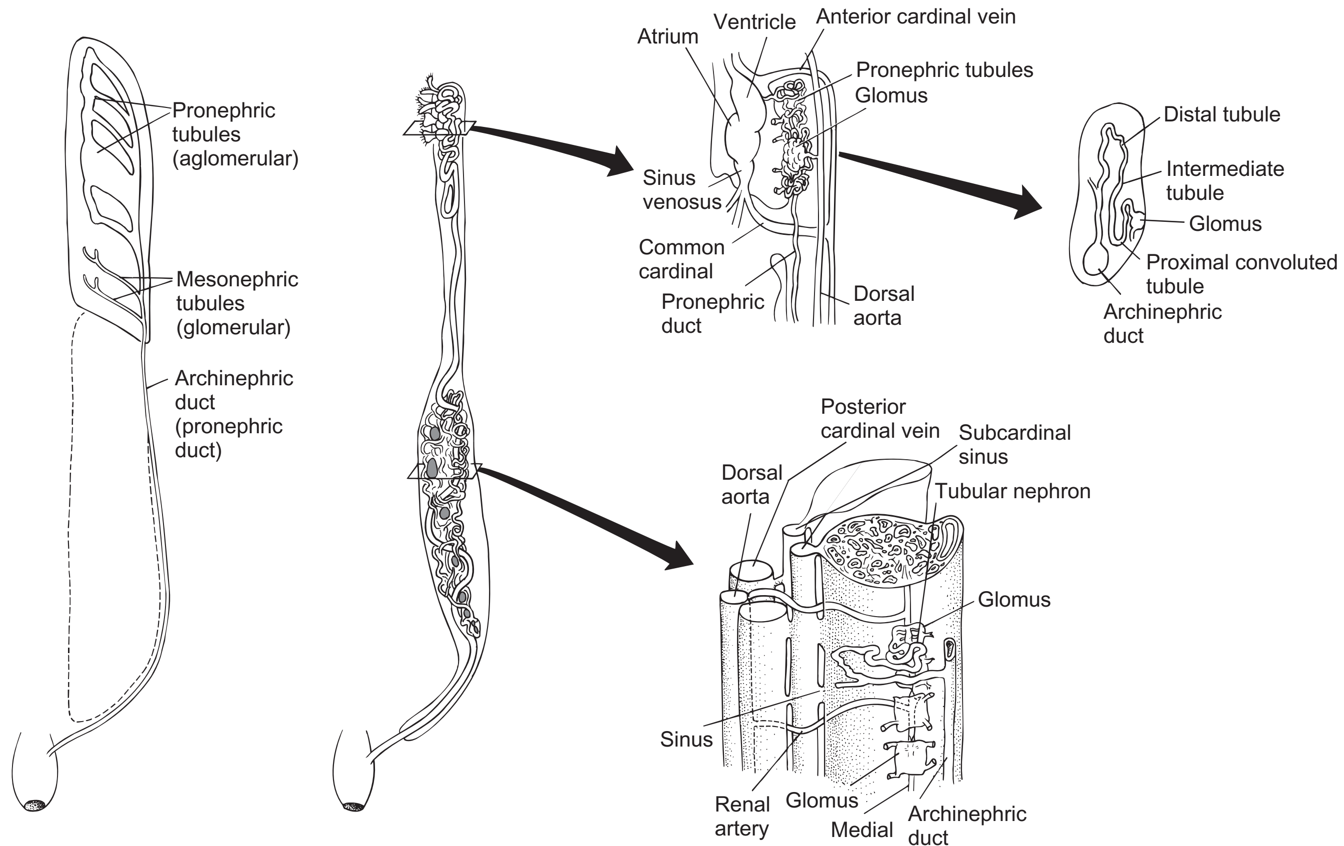
Metanephros The first embryonic hint of a metanephros is the formation of the metanephric duct that appears as a **ureteric diverticulum** arising at the base of the preexisting mesonephric duct. The ureteric diverticulum grows dorsally into the posterior region of the nephric ridge. Here it enlarges and stimulates the growth of **metanephric tubules** that come to make up the metanephric kidney. The metanephros becomes the adult kidney of amniotes, and the metanephric duct is called the ureter (figures 14.4c and 14.6).

Overview The nephric ridge is a **nephrogenic** region, meaning that it is the embryonic source of the kidneys and their ducts. Anterior, middle, or posterior parts of the nephric ridge may contribute to kidneys and ducts. Transient stages often yield to later urinary structures. The tripartite concept that we have used as the conceptual framework in which to discuss these events envisions development of the adult vertebrate kidney as stemming from one of the three regions of the nephric ridge. These three regions are treated as anatomically discrete, and the kidneys they yield as distinct types—pronephros, mesonephros, or metanephros. Additionally, the ontogenetic appearance of such kidneys seems to retrace their phylogenetic origins.

However, anatomical demarcations between these three regions of the nephric ridge are not always apparent, and the entire nephric ridge may be more a unit than composed of three parts. Consequently, many morphologists prefer to use an alternative conceptual framework to interpret kidney development and evolution. This alternative view stresses the unity of the entire nephric ridge and is termed the **holonephric concept.** Morphologists who take such a view emphasize that the three types of kidneys arise as parts of one organ, the **holonephros,** which produces tubules in anterior to posterior succession during development. There is no anatomical discontinuity marking separate kidney types. Thus, the holonephros is that part of the nephric ridge that produces the kidney.

Experimental embryology is provocative. For example, transplantation of mesonephros-forming or metanephric-forming mesoderm to the "pronephros" region of mesoderm results in differentiation of these transplanted tissues into pronephric tubules and not into what they would have become if left in place. This indicates that tissues within the nephric ridge are flexible and not committed to one type of kidney or another. Differentiation of the nephric ridge into pronephric, mesonephric, or metanephric tubules is induced by tissue location or by interactions with adjacent tissues and not by intrinsic regionalization within the intermediate mesoderm itself. Because the nephric ridge is nonspecific and developmentally pliable, it has the capacity to form different types of nephrons; therefore, some morphologists argue that the term *holonephros* should be used to describe the unity of the nephric ridge. A holonephric kidney seems to characterize the early development of some hagfishes, elasmobranchs, and caecilians. However, no adult vertebrate retains a holonephros. Absence of examples from adults seems contrary to what we would predict from the holonephric concept and leads other morphologists to retain the tripartite concept.

We seem to be a long way from resolving the disparity between these competing concepts of kidney development and structure. Unfortunately, even basic descriptions of kidney anatomy vary between morphologists from the two camps. Our understanding of kidney morphology is profoundly affected by our intellectual framework. In comparative anatomy, as elsewhere in biology, the concepts we use to interpret what we see can themselves influence how we understand the world around us. Our consideration of kidney structure reminds us that the preconceived views we bring to a subject can affect our interpretation of our anatomical observations. As a practical matter, in this book we use the descriptive richness of the tripartite concept to examine the evolution of vertebrate kidneys. To characterize the kidney, I use terms that indicate which sections of the nephric ridge contribute to its formation. Middle and posterior regions form the opisthonephros. If the kidney forms just from the anterior region, it is a pronephros; if it forms just from the middle, it is a mesonephros; and if it is formed just from the posterior region, it is a metanephros.



(a) Hagfish (b) Lamprey

FIGURE 14.7 **Cyclostome kidneys.** (a) Hagfish. The adult kidney includes aglomerular anterior tubules and a few posterior glomerular tubules. (b) Lamprey. The adult kidney includes a posterior opisthonephros. In some species, a few anterior pronephric tubules with peritoneal funnels may persist. Several pronephric tubules share a glomus, and each can be composed of proximal, intermediate, and distal sections.

(b) After Goodrich; Youson and McMillan.

Kidney Phylogeny

Fishes

The most primitive vertebrate kidneys are found among cyclostomes. In the hagfish *Bdellostoma*, pronephric tubules arise in the anterior (cranial) part of the nephric ridge during embryonic development. These tubules unite successively with one another, forming the urinary or pronephric duct (figure 14.7a). Anterior tubules lack glomeruli but open to the coelom via peritoneal funnels, whereas posterior tubules are associated with glomeruli but lack connection to the coelom. In the adult, anterior aglomerular tubules together with several persisting posterior glomerular tubules become the compact pronephros. Although the adult pronephros may contribute to formation of coelomic fluid, the mesonephros is considered to be the functional adult kidney of hagfishes. Each paired mesonephros consists of 30 to 35 large glomerular tubules arranged segmentally along the excretory duct (pronephric duct) and connected to it by short tubules.

In lampreys, the early larval (ammocoete) kidneys are pronephric, consisting of three to eight coiled tubules served by a single compacted bundle of capillaries called a **glomus.** A glomus differs from a glomerulus in that each vascular glomus services several tubules. Each pronephric tubule opens to the coelom through a peritoneal funnel and empties into a pronephric duct. The pronephros is the sole excretory organ of the young larva. Later in larval life, it is joined by additional mesonephric tubules posteriorly. Upon metamorphosis, additional tubules are recruited from the hindmost part of the nephric ridge, yielding an opisthonephros that becomes the functional adult kidney. The pronephros degenerates, although a few tubules appear to persist into the adult in some lamprey species (figure 14.7b).

In larval fishes, the pronephros often develops initially and for a time may become functional, but it is usually supplemented by a mesonephros. In most fishes, the pronephros degenerates as more tubules are added caudal to the mesonephros to form a functional ophisthonephric kidney in the adult. In a few teleost species, the pronephros persists as the functional adult kidney.

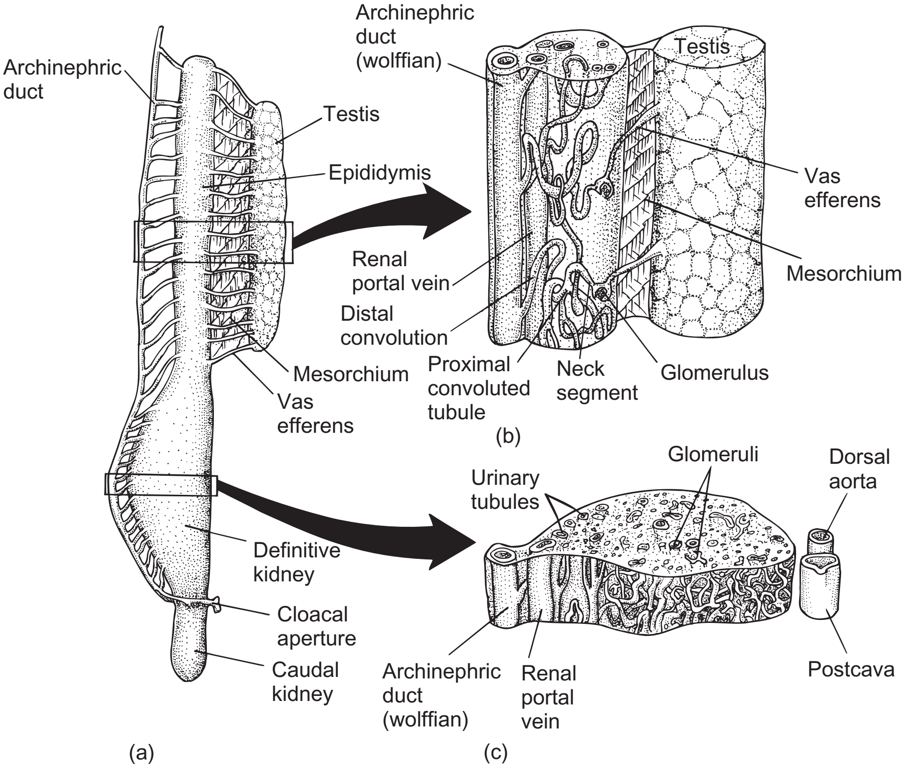


FIGURE 14.8 Urogenital organs of a male siren salamander. (a) Whole kidney and testis with associated ducts. (b) The anterior kidney contains tubules that drain the testis in addition to excretory nephrons. Both reproductive and urinary tubules enter the archinephric duct. (c) The posterior kidney is involved in urine formation and is drained by the archinephric duct.

After Willett.

Tetrapods

Among amphibians having active, free-living larvae, a pronephros may develop and become functional for a time. One or two pronephric tubules may contribute to the adult kidney as well. In caecilians, as many as a dozen pronephric tubules have been reported in the adult kidney. However, the early embryonic pronephros is usually succeeded by the larval mesonephros, which upon metamorphosis is replaced by an opisthonephros in most amphibians. Nephrons within the opisthonephros tend to differentiate into proximal and distal regions before joining the urinary ducts. In amphibians, as in many sharks and teleosts with opisthonephric kidneys, the anterior kidney tubules transport sperm, illustrating again the dual use of ducts that serve both genital and urinary systems (figure 14.8a–c).

In amniotes, the anterior end of the nephric ridge rarely produces pronephric tubules. When present, these are few in number and without excretory function. The predominant embryonic kidney is a mesonephros, but in all amniotes, it is supplemented in late development and completely replaced in the adult by the metanephros drained by a new urinary duct, the ureter. Metanephric tubules tend to be long with well-differentiated proximal, intermediate, and distal regions. In mammals, in particular, the intermediate section of the tubules is especially elongated, constituting the major part of the **loop of Henle.** This term refers to both a positional and a structural feature of the nephron. Positionally, the loop includes the part of the nephron that departs from the cortex and dips into the medulla (the descending limb), makes a sharp turn, and returns to the cortex (the ascending limb). Structurally, three regions contribute: the straight portion of the proximal tubule, the thin-walled intermediate region, and the straight portion of the distal tubule (figure 14.1b). Notice that the terms *descending* and *ascending limbs* refer to the parts of the loop that are departing or entering the cortex, respectively. The terms *thick* and *thin* refer to the height of the epithelial cells forming the loop. Cuboidal cells are thick, and squamous cells are thin.

Loops of the nephron occur only in groups capable of producing concentrated urine. Among vertebrates, only the kidneys of mammals and some birds can produce urine in which solutes in the urine are more concentrated than in the blood, and only these two groups possess nephrons with loops. All mammalian nephrons have loops, specifically loops of Henle. Mammalian kidneys produce urine 2 to 25 times more concentrated than blood. Further, the ability to concentrate urine is correlated with loop length, and loop length is correlated with availability of water. The beaver has short loops and excretes urine only about twice the osmotic concentration of its blood plasma, but some desert rodents have long loops and can produce urine that is about 25 times as concentrated as their blood.

In a few species of birds, the kidneys contain some nephrons with short, distinct loop segments (figure 14.9). Although analogous to the loops of Henle in mammals, these short avian loops evolved independently. These avian kidneys exhibit a modest ability to produce concentrated

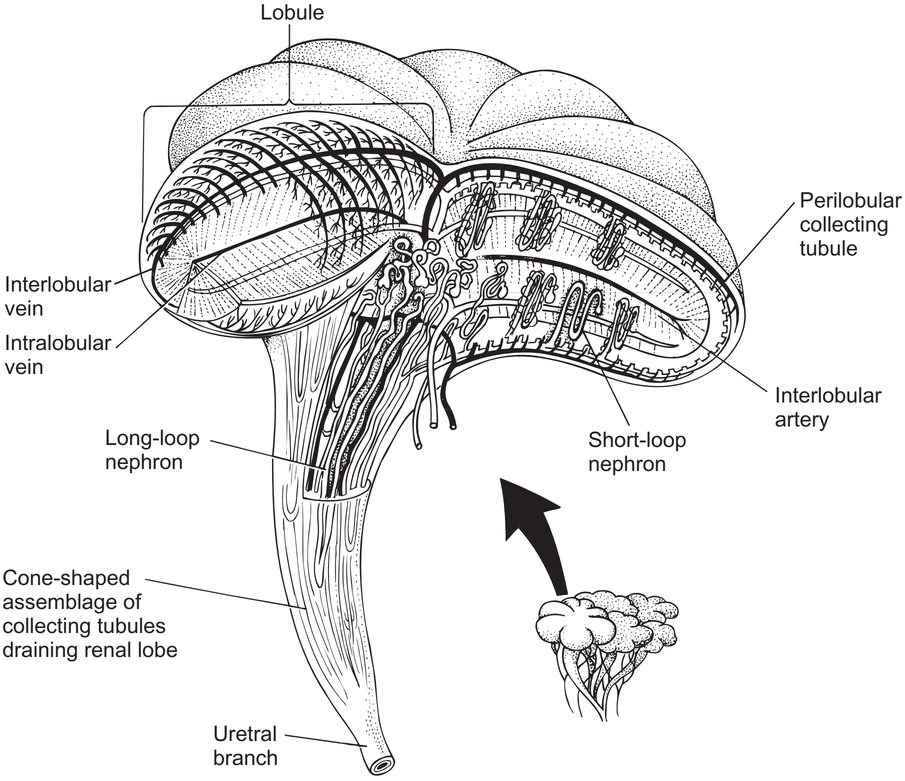


FIGURE 14.9 Avian kidney. A section of the kidney is enlarged and cut away to reveal the arrangement of nephrons within and the blood supply to the nephrons.

After Braun and Dantzler.

urine. Their product is about two to four times more concentrated than their blood. However, the nephrons of most birds do not have loops. In the absence of a loop, the avian nephron is similar to the nephron of reptiles.

Kidney Function and Structure

Nephron structure can be quite different from one taxonomic group to the next and may appear at first to have no obvious correlation with the phylogenetic position of the taxon. In hagfishes, the nephron is quite simple. A short tubule connects the renal capsule to the excretory duct (figure 14.10a). In lampreys and freshwater bony fishes, the nephron is more differentiated. It includes a renal capsule, proximal and distal tubules usually joined by an intermediate segment, and a collecting tubule (figure 14.10c). However, the nephron of saltwater teleosts is usually reduced because the distal tubule is lost, and in some, the renal capsule is lost (figure 14.10a). In amniotes, the nephron is again quite differentiated, and the intermediate segment that contributes to the loop of Henle in mammals is often elaborated (figure 14.10b).

To understand kidney design, the adaptive basis of its excretory and regulatory functions, and the evolution of the nephron, we must look at the demands placed on the kidneys. In general, the vertebrate kidney contributes to the maintenance of a constant, or nearly constant, internal environment, termed **homeostasis,** so that active cells (e.g., striated muscle, cardiac muscle, neurons) are not stressed by radical departure from optimum operating conditions. To accomplish this, the kidney performs two fundamental physiological functions, **excretion** and **osmoregulation.** Both are related to maintaining a constant internal environment in the face of accumulating metabolic by-products and perturbations in salt and water concentrations.

Excretion: Removing the Products of Nitrogen Metabolism

Most excreted components in the urine are metabolic by-products that collect within the organism and must be voided so they will not interfere with the organism's physiological balance.

Energy to support growth and activity comes from the metabolism of food. Carbon dioxide and water are end products of carbohydrate and fat metabolism, and both are easily eliminated. But metabolism of proteins and nucleic acids produces nitrogen, usually in the reduced form of ammonia (NH_3). Because ammonia is highly toxic, it must be removed from the body quickly, sequestered, or converted into a nontoxic form to prevent accumulation in tissues. Three routes of eliminating ammonia, sometimes in combination, exist in vertebrates. Direct excretion of ammonia is **ammonotelism.** Excretion of nitrogen in the form of uric acid is called **uricotelism.** The third route is **ureotelism,** excretion of nitrogen in the form of urea (figure 14.11). Ammonotelism is common in animals living in water. Ammonia is soluble in water, and a great deal of water is required to flush it from body tissues. For vertebrates living in an aqueous medium, water is plentiful. Thus, ammonia is

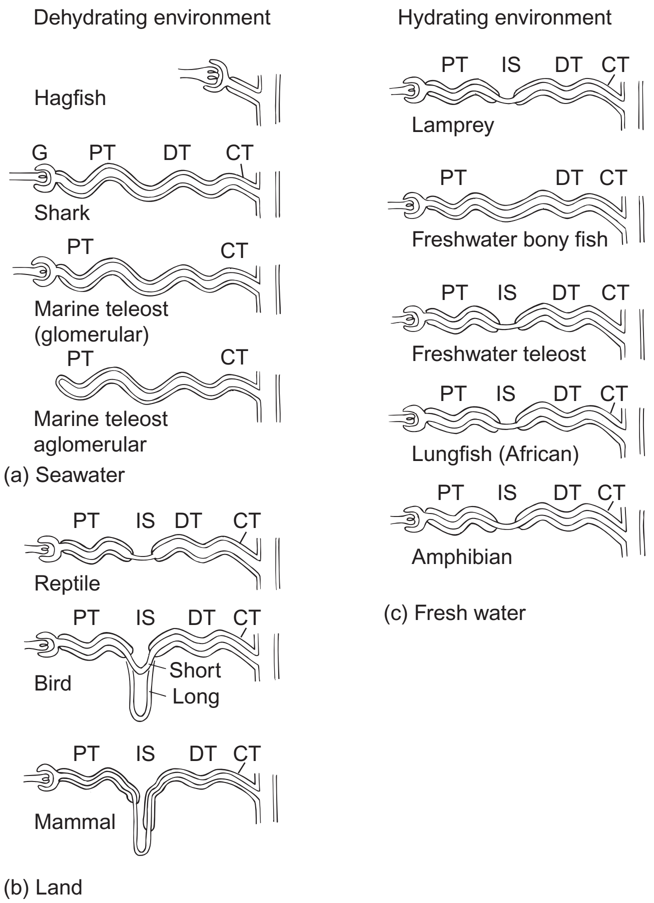


FIGURE 14.10 Nephrons from major groups of vertebrates. The segments contributing to the vertebrate nephron depend in large part on whether the animal lives in a dehydrating environment, such as seawater or land (a,b), or in a hydrating environment such as fresh water (c). Nephrons are diagrammed and not rendered to scale among groups. Abbreviations: collecting tubule (CT), distal tubule (DT), glomerulus (G), intermediate segment (IS), proximal tubule (PT).

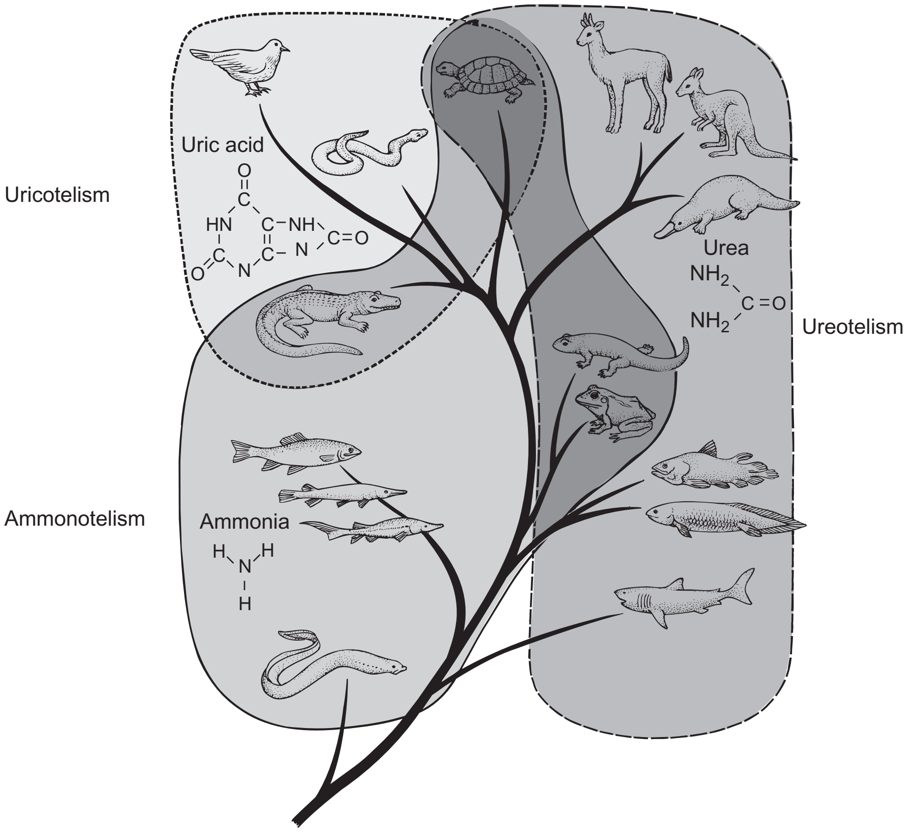


FIGURE 14.11 Mechanisms of eliminating nitrogenous wastes. Among many fishes, amphibians, and some reptiles, nitrogen is excreted in the form of ammonia (ammonotelism). Excretion of nitrogen as uric acid (uricotelism) occurs in some reptiles and all birds. In mammals and some amphibians and fishes, nitrogen is eliminated as urea (ureotelism).

After Schmidt-Nielsen.

BOX ESSAY 14.1 Mammals in Deserts, Frogs in the Sea

Dehydration threatens all vertebrates that venture onto land, but it is especially severe for animals living in hot, dry deserts. To manage dehydration, the kangaroo rat (*Dipodomys spectabilis*) has developed several physiological adaptations that allow it to inhabit desert habitats. Even rainwater is scarce for the kangaroo rat, so it doesn't depend on drinking water to replace water that is evaporated during the day. During lush springs, the vegetation it eats contains some water, but late in summer when the diet consists largely of dry seeds, food is not an important source of water. Instead, kangaroo rats depend on water produced as a by-product of carbohydrate and fat metabolism. When metabolized, food yields carbon dioxide and water. In fact, up to 90% of the kangaroo rat's water budget may come from the oxidation of food. On the other hand, less water is excreted in the urine than in most other mammals. The loops of Henle are elaborated in the kidneys of kangaroo rats. The long loops allow the production of a concentrated urine, up to four times as concentrated as that of humans. Thus, the kangaroo rat recovers some water from metabolism of its food and loses little in its urine. These adaptations allow it to maintain water balance even under desert conditions.

For amphibians moving from land to seawater, dehydration is also a problem. They are hyposmotic to the salty medium; therefore, water is drawn from their bodies. If water loss is not regulated, they will dehydrate and die. Most amphibians live in fresh water or on land. One of the few exceptions is the Southeast Asian frog, *Rana cancrivora*. At low tide, it ventures into saltwater pools to feed on crabs and crustaceans, a habit that has led to its common name, the crab-eating frog. It tolerates these salty conditions through an increase in blood concentrations of sodium and chloride ions and, especially, of urea, as in sharks. At least for short periods in tide pools, it is able to keep its blood levels hyperosmotic to seawater, thus preventing severe water loss and dehydration.

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eliminated through the gill epithelium, skin, or other permeable membranes bathed by water. However, in terrestrial vertebrates, water is often scarce, so water conservation becomes more critical. Because amniotes have lost gills, the gill epithelium is no longer a major route for ammonia excretion. Given these terrestrial constraints, ammonia is converted into urea or uric acid, both being nontoxic forms that address the immediate problem of ammonia toxicity. Furthermore, less water is required to excrete urea or uric acid, so water is conserved as well.

In advanced tetrapods, two evolutionary routes have been followed in addressing the related problems of water economy and nitrogen elimination. Birds and most living reptiles primarily depend on uricotelism. Uric acid, only slightly soluble in water, is formed in the kidneys and transported via the ureters to the cloaca. In the cloaca, uric acid joins with ions and forms a precipitate of sodium, potassium, and ammonium salts. The water not used diffuses through the walls of the cloaca back into the blood. A concentrated, nearly solid uric acid "sludge" forms, allowing nitrogen elimination with little accompanying loss of water.

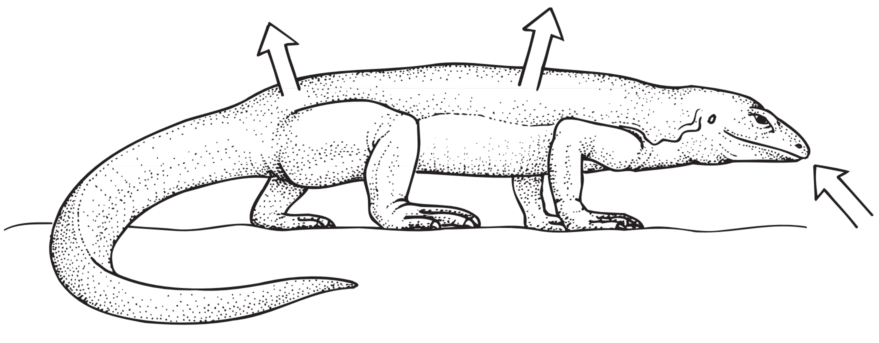
It is hypothesized that the synthesis of uric acid arose first as an embryonic adaptation, but because of its advantages in water conservation, it was carried over into the adult physiology. The cleidoic egg that first evolved in reptiles is usually laid in dry sites, making water conservation a factor in the embryo's survival. Embryonic adaptations that conserve water include (1) the eggshell, which retards water loss, (2) internal production of water through metabolism of stored yolk, and (3) uricotelism. Because uric acid precipitates out of solution, it does not exert osmotic pressure within the embryo; therefore, it is safely sequestered within the egg without requiring large volumes of water to remove it.

Mammals have followed a different evolutionary route in dealing with nitrogen elimination. They depend largely on ureotelism, the conversion of ammonia into urea. Mammalian kidneys accumulate urea and excrete it as a concentrated urine, thus also detoxifying ammonia and conserving water.

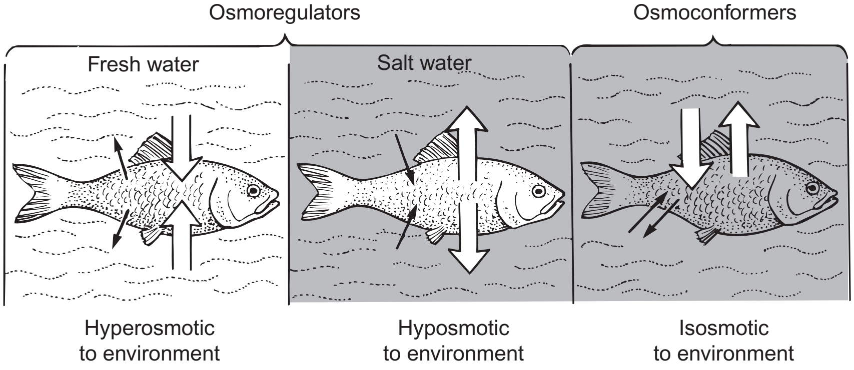
Within an individual, routes of nitrogen excretion can vary in relation to the availability of water. For example, the African lungfish excretes ammonia when it swims in rivers and ponds. But, during droughts, when ponds dry and the lungfish estivates, ammonia is transformed into urea, which can accumulate safely in the body during times of scarce water. With the return of rain, the lungfish rapidly takes up water and excretes the accumulated urea. Similarly, many amphibians eliminate ammonia in water and then excrete urea when they emerge onto land after metamorphosis. In alligators, both ammonia and uric acid are excreted. Turtles excrete primarily ammonia in aquatic habitats but eliminate urea or uric acid when on land (figure 14.11).

Osmoregulation: Regulating Water and Salt Balance

The second major physiological function of the kidneys is osmoregulation. Osmoregulation involves the maintenance of water and salt levels. The external world may vary considerably for an active vertebrate, but cells within see a relatively constant environment. A steady-state intracellular environment is maintained largely by exchange of solutes between the body fluids and the blood and lymph. In turn, the kidneys in large part regulate the constant volume and composition of blood and lymph in terrestrial vertebrates. In aquatic vertebrates, the



(a) Terrestrial environment



(b) Aquatic environment

FIGURE 14.12 Water balance. (a) In terrestrial vertebrates, the relatively dry surrounding environment tends to draw water from the body, posing the problem of dehydration. (b) In aquatic vertebrates, the tendency to gain, lose, or be in balance with the surrounding water depends on the relative concentration of solutes in the animal compared with those of the surrounding water. Osmoregulators control the concentrations of salt and water in their bodies. In fresh water, an animal is usually hyperosmotic to the medium, and the osmotic gradient leads to an influx of excess water. In salt water, most vertebrates are hyposmotic; therefore, water tends to flow from their bodies into the surrounding environment. As with terrestrial vertebrates, dehydration is the result. In both aquatic situations, the vertebrate must make physiological adjustments to eliminate or take up water in order to maintain homeostasis. In a third aquatic situation in which the level of solutes in body tissues rises to meet that of the surrounding salt water, no significant osmotic gradient develops. Such vertebrates are called osmoconformers because they are isosmotic to seawater and no net flux of water occurs. Open arrows represent net direction of water fluxes; solid arrows represent net direction of solute movement. Shading indicates relatively high concentration of solutes in water.

gill epithelium and digestive tract are as important as the kidneys in addressing problems of salt balance.

Water Balance Most vertebrates require physiological vigilance to maintain internal balance because the external world constantly intrudes. This is particularly true for water, which may be drawn from an organism and dehydrate it or seep inward across permeable surfaces and dilute body fluids. For example, a terrestrial vertebrate is usually in danger of losing water from its body. To counter dehydration, drinking can help replace lost water (figure 14.12a). Some groups, such as reptiles, control water loss with a thick integument that reduces the permeability of their skin to water. In addition, the kidneys, the cloaca, and even the urinary bladder are **water conservers,** meaning that they recover water before nitrogen is eliminated from the body.

On the other hand, an aquatic life presents other challenges in the management of **water fluxes.** Water may move in or out of the body. In freshwater fishes, the osmotic problem results from a net tendency for an *inward* flux of water. Relative to fresh water, the body of the fish is **hyperosmotic,** meaning that its body fluids are osmotically more concentrated (hence *hyper-*) than the surrounding water. Because fresh water is relatively dilute and the body is relatively salty, water flows into the body (figure 14.12b). If allowed to continue, the net influx of water would substantially dilute body fluids and thus create an imbalance in the extracellular environment. For freshwater fishes, the major homeostatic problem is ridding the body of this excess water. To address this problem, the kidneys are designed to excrete large quantities of dilute urine, about ten times the volume excreted by their marine counterparts.

For most saltwater fishes, the osmotic problem is just the reverse. There is a tendency for a net *outward* flux of water from the body tissues, dehydrating them. Relative to salt water, the bodies of most marine fishes are **hyposmotic,** meaning that the body is osmotically less concentrated (hence *hypo-*) than seawater. Water tends to be drawn from the body, and dehydration of the body will result if this condition is not controlled physiologically. In this respect, a fish in salt water faces a physiological problem much like that of a tetrapod on land, loss of body water to the environment (figure 14.12a). For marine fishes, osmoregulation is complex. They can drink to recover water, but if they do, they must excrete the excess salt ingested along with the seawater. To aid in water conservation, the kidneys are designed to excrete very little water, thus reducing water loss. To address the problem of excess salt, the gills and sometimes special glands become partners with the kidneys in the business of osmoregulation.

The body of some animals is **isosmotic,** meaning that the osmotic concentrations of the internal environment and surrounding seawater are approximately equal (hence *iso-*). Because of this balance, there is no net tendency for water to move in or out of the body, so the animal faces no special problems from excess water or dehydration (figure 14.12b). Dissolved molecules and ions, known as solutes, in the body increase in concentration until the osmotic concentration in the body equals that of the surrounding seawater. Such an animal is called an **osmoconformer.** Among vertebrates, hagfishes are osmoconformers. Concentrations of sodium and other ions are close to those of the surrounding seawater. Chondrichthyans and coelacanths (*Latimeria*) also have tissue fluids osmotically close to seawater, but this is due to elevated levels of the organic compound urea circulating in the blood. As a result, the osmotic concentration of the blood approaches that of seawater. Although this reduces the physiological problems of dealing with water fluxes, it requires that cells of hagfishes, elasmobranchs, and coelacanths operate efficiently in a fluid environment that is higher in osmotic concentration than that of other vertebrates. It is believed that such elevated concentrations may incur energetic costs in osmoregulation.

All vertebrates except for hagfishes, chondrichthyans, coelacanths, and some amphibians are **osmoregulators.** Despite fluctuations in external environmental osmotic levels, they maintain body fluids at constant osmotic levels through active physiological adjustments. Adjustments may involve conservation or elimination of body water to compensate for osmotically driven water loss or uptake relative to the external environment. Solutes also are regulated through excretion and uptake to maintain homeostasis of body fluids. Thus, osmoregulation involves adjustments of water *and* solutes. Next we meet structures designed to move both. Let us begin by looking at kidney adaptations that serve water balance. There are two problems that the environment imposes—water elimination and water conservation (figure 14.13).

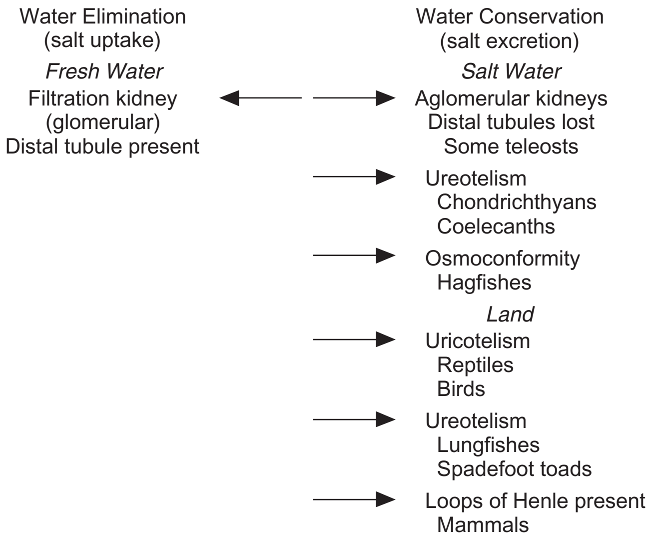


FIGURE 14.13 Summary of kidney adaptations to two environmentally imposed homeostatic problems: water elimination and water conservation. In fresh water, most vertebrates need to eliminate excess water. A filtration kidney with fully developed glomerular apparatus and distal tubules can produce copious amounts of dilute urine and rid the body of excess water. In salt water and in terrestrial environments, water-conserving kidneys are advantageous. In marine fishes, aglomerular kidneys that lack distal tubules, ureotelism resulting in elevated levels of blood solutes, and osmoconformity represent three different adaptive routes to water conservation. Vertebrates in terrestrial environments conserve water through structural changes in the nephron (loop of Henle) that promote recovery of water or through more economical means of ridding the body of nitrogen, such as uricotelism or ureotelism, that require less water than ammonotelism.

Water Elimination Water elimination is a problem for hyperosmotic vertebrates living in fresh water. The vertebrate mechanism of urine formation seems especially well suited to address such a problem. The kidneys of most insects and some other invertebrate animals are **secretion kidneys.** Urine is formed by secretion of constituents into the tubules along their length. However, vertebrate kidneys, like the kidneys of most crustaceans, annelids, and molluscs, are **filtration kidneys.** Large quantities of fluid and solutes pass immediately from the glomerulus into the renal capsule to form a **glomerular filtrate.** As this filtrate moves along the tubule, selective secretion adds constituents, but most of the initially filtered water and solutes are absorbed back into the capillaries entwined about the tubules. In humans, for example, each day the kidneys form about 170 liters (45 gallons) of glomerular filtrate in their 2 million renal capsules. This is four to

BOX ESSAY 14.2 Between Fresh and Salt Water

Most fishes are stenohaline; they can tolerate only a narrow range of salinities. A few fishes are euryhaline; they tolerate wide swings in salinity and may in fact migrate between fresh and salt water. **Anadromous** fishes hatch in fresh water, migrate to salt water where they mature, and then return to fresh water to spawn. Salmon are an example. Depending on species, anadromous fishes spend one to several years at sea, feeding and growing, then return to their natal stream, where they breed. **Catadromous** fishes migrate in the opposite direction, from salt to fresh water. European and American eels, *Anguilla,* are examples. They mature in streams and migrate to the ocean to breed.

Although euryhaline fishes pass part of their lives in fresh water and part in salt water, the transition from one to the other cannot be abrupt. A period of adjustment, usually involving several weeks in brackish water, is often required to allow acclimation. When these fishes swim into fresh water, the major physiological challenge is coping with salt loss across the gills. Marine stenohaline fishes placed in fresh water cannot compensate for the high permeability of their gills to salt. Salt continuously leaks out, and the fishes die. Euryhaline fishes develop reduced physiological permeability to salt and survive.

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five times the total volume of water in the body. If this volume were voided each day, there would be little time for anything else, to say nothing of the large volumes of water we would need to drink to replace water that was excreted. In fact, all but about 1 liter of filtrate is resorbed back into the blood along the uriniferous tubules.

In freshwater fishes and aquatic amphibians, the kidneys characteristically have large, well-developed glomeruli. Consequently, relatively large volumes of glomerular filtrate are produced. The prominent distal tubule absorbs solutes (salts, amino acids, etc.) from the filtrate to retain these in the body, but it absorbs only a third to a half of the filtered water. In this instance, a large proportion of the water is eliminated in the urine. Thus, the kidney is designed to produce large amounts of dilute urine and address the main osmotic problem of excess water in freshwater vertebrates.

Water Conservation As emphasized, water conservation is a problem not just for terrestrial vertebrates facing a hot, drying environment but also for vertebrates in salt water. A variety of structural and physiological adaptations have arisen to address the problems of desiccation in salt water and in terrestrial environments.

The filtration kidney is disadvantageous for hyposmotic fishes in seawater because it is designed to form large volumes of urine. These fishes must conserve body water, not eliminate it. Consequently, in many species of marine teleosts, parts of the nephron that contribute to water loss are absent, specifically the glomerulus and the distal tubule. Absence of the glomerulus and associated renal capsule reduces the quantity of tubular fluid that initially forms. These marine teleosts have **aglomerular kidneys** that, by not producing copious amounts of glomerular filtrate, never face the problem of resorbing it later. Essentially, aglomerular kidneys conserve water by eliminating the filtration process in the renal capsule.

Loss of the distal tubule also contributes to water conservation. The distal tubule absorbs salt from urine but allows water to be excreted. Loss of the distal tubule therefore favors water retention by the fishes. Without glomeruli and distal tubules, these teleosts depend largely on selective secretion of solutes into the aglomerular tubules to form a concentrated urine.

Terrestrial vertebrates have alternative adaptations to conserve water. In mammals, and to a lesser extent in birds, water conservation is based on modification of the loop of Henle. The loop creates an environment around the tubules that encourages the absorption of water before it can be excreted from the body. Consequently, urine becomes concentrated, and kidney design serves water conservation.

In the mammalian kidney, the relationship between tubule design and water conservation is complex. The first step in urine formation is formation of glomerular filtrate. Circulating blood cells, fat droplets, and large plasma proteins do not flow into the nephron, but most water and solutes from the blood plasma pass from the capillaries of the glomerulus into the renal capsule. Second, most of the sodium ions, nutrients, and water are reabsorbed in the proximal tubule. Absorption is facilitated by the large surface area of proximal tubule cells and depends on active transport of sodium. Usable proteins that were part of the glomerular filtrate are also absorbed in the proximal tubule. Third, the filtrate enters the intermediate tubule of the loop of Henle. Contrary to earlier theories, the loop of Henle is not an additional site in which water is extracted from the filtrate. Instead, the loop actively pumps sodium ions from the filtrate out into the interstitial space to create hyperosmotic interstitial fluid around the collecting ducts. Fourth, as collecting ducts carry the modified filtrate to the renal pelvis, they pass through a region that, thanks to the loops of Henle, is hyperosmotic to the filtrate. The osmotic gradient between surrounding tissue fluid and dilute urine entering the collecting ducts provides the driving force that moves water out of the collecting ducts and into the surrounding fluid. When the body is dehydrated, the permeability of cells of the collecting duct changes under hormonal influence and water is drawn from the tubular fluid into the surrounding interstitial fluid. Here

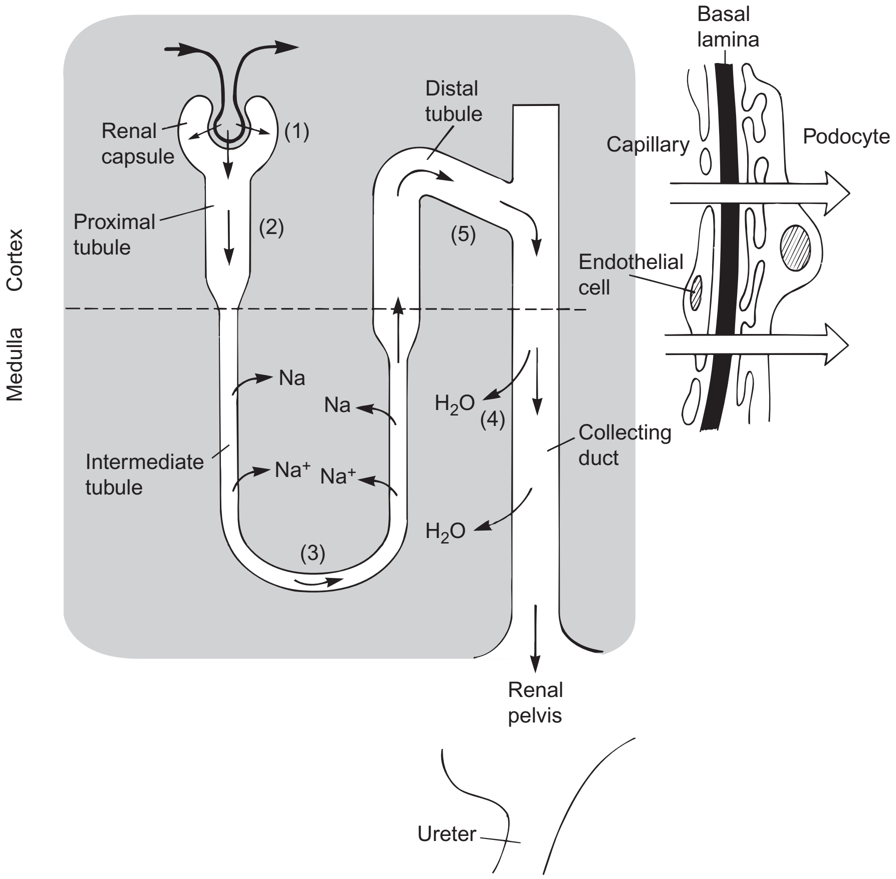

FIGURE 14.14 **Mammalian kidney function.** At the start of urine formation, high pressure in the glomerulus encourages fluid in the blood to flow from the capillaries into the renal capsule, forming a glomerular filtrate. (1) As the glomerular filtrate passes through the rest of the nephron, some constituents are added, but most of the water is absorbed back into the capillaries. In mammals (and birds), this absorption occurs primarily in the proximal tubule (2) and collecting ducts (4). The intermediate tubule of the loop of Henle produces a salty environment (3) in the kidney medulla. As urine flows in the collecting duct through the medulla (4), it is carried through this hyperosmotic region, and water follows the osmotic gradient out of the tubule into the surrounding tissue. Blood vessels of the vasa recta (not shown) take up this water and return it to the systemic circulation. This produces a concentrated urine in the collecting ducts that is excreted from the kidney via the ureter (5). The insert (upper right) is an enlarged view of the renal corpuscle showing the endothelial wall of the glomerulus, the specialized endothelial cell of the renal capsule (podocyte), and the thick basal lamina between these endothelial layers. Arrows indicate the direction of flow of fluid from the blood into the renal capsule to form glomerular filtrate.

blood capillaries, collectively termed the **vasa recta,** take up water, together with some solutes, and return them to the circulation. The urine that remains in the collecting ducts thus becomes concentrated before it flows into the renal pelvis and ureter (figure 14.14).

Blood flow to the uriniferous tubules is necessary for filtration and resorption to occur. The glomeruli sprout from the renal arteries, which branch directly from the dorsal aorta. Blood pressure is still high in the renal arteries; therefore, blood pressure in the glomeruli is high and promotes the flow of fluid into the renal capsules. On the other hand, pressure in the vasa recta is low, as these vessels arise from the arterioles beyond the glomeruli and pressure drops as blood flows through the glomeruli. The lower pressure in the vasa recta encourages uptake of the water that collects around the loops of Henle.

Notice that unlike the water-conserving kidney of aglomerular teleosts, the distal tubule is retained in the water-conserving kidney of mammals. In mammals, part of the distal tubule is incorporated into the loop of Henle, where its ability to absorb salts contributes to the production of a hyperosmotic interstitial environment around the collecting ducts. Thus, in aglomerular teleosts, water conservation is accomplished by elimination of parts of the uriniferous tubule that allow water loss, whereas in mammals, those homologous parts of the uriniferous tubule are retained but become incorporated into a totally different mechanism of concentrating urine.

Osmoconformers In a sense, one way to address the problem of water fluxes is to avoid the problem in the first place. This is the strategy of osmoconformers, whose body fluids have the same osmotic concentration as that of the surrounding

BOX ESSAY 14.3 Philosophers to Finals

The kidney seems to bring out the philosopher in all of us. Homer W. Smith, who spent a lifetime in the study of kidney physiology, produced the reflective book, *Man and His Gods,* examining the effects of religious and secular myths on human thought and human destiny. No less than Albert Einstein found it an intensely interesting book and wrote the foreword. Isak Dinesen, perhaps today best known for her book turned into a movie, *Out of Africa,* similarly reflected upon the kidney. In a 1934 collection of writing, *Seven Gothic Tales,* her character, an Arab sailor on deck of his ship cruising off the African coast, philosophizes as follows,

> *What is man when you come to think upon him, but a minutely set, ingenious machine for turning, with infinite artfulness, the red wine of Shiraz into urine?*

Urine comes from the Latin word, *urina,* entering into English usage about the fourteenth century. Before then, the French word "pissier" gave the English "piss," used comfortably by Geoffrey Chaucer (fourteenth century) and even by proper Elizabethan ladies and gentlemen. Not until Oliver Cromwell and puritanism (seventeenth century) did the term fall out of favor. Only recently has it enjoyed rediscovery and use once again in mixed company.

Urine has been put to a variety of household uses: as a hairdressing, as a fermentor of bread, to flavor cheese, and to macerate tobacco leaves. Wealthy French ladies of the seventeenth century could often be found in urine-enriched baths to beautify the skin. In various cultures it has been tried as a mouthwash and gargle. For centuries, it was considered proper and humane to wash battlefield injuries by urinating on the wounds of comrades (no more sterile nor antiseptic elixir was available). In the early nineteenth century, uroscopy, or "water casting," was in great vogue in the medical profession throughout North America and Europe. This involved inspection of the "piss pot," as Elizabethans called it, or urinal, and these medical devices were often elaborately decorated with flowers in middle-class households and by gold and silver in finer families. So prominent was nineteenth-century uroscopy that the urinal became an emblem of the medical profession.

Students too have come to appreciate their kidneys. When loading up with coffee and great thoughts the night before a final exam, or when celebrating with drink and great excuses after the exam, we are reminded of our kidneys and the volumes of urine they can produce when required. Although evolved for their water-conserving abilities, our kidneys possess the physiological flexibility to rid our bodies of excess water when we overindulge. The collecting ducts become impermeable to the egress of water (ADH, a pituitary hormone, changes its permeability), less moves from collecting ducts into the interstitial space, less is available to be absorbed by the vasa recta, and more fluid is left behind to be excreted in copious amounts. Drinking establishments around the world serve different beers, wines, coffees, and soft drinks, but all have restrooms.

Such inspiration between physiology and philosophy has made public watering holes the site where we celebrate our kidneys. Perhaps it was just such a homage to the human kidney that prompted Samuel Johnson, himself a legendary raconteur and heavy user of his kidneys, to observe,

> *There is nothing which has yet been contrived by man by which so much happiness is produced as by a good tavern or inn.*
>
> *Life of Dr. Johnson,* James Boswell

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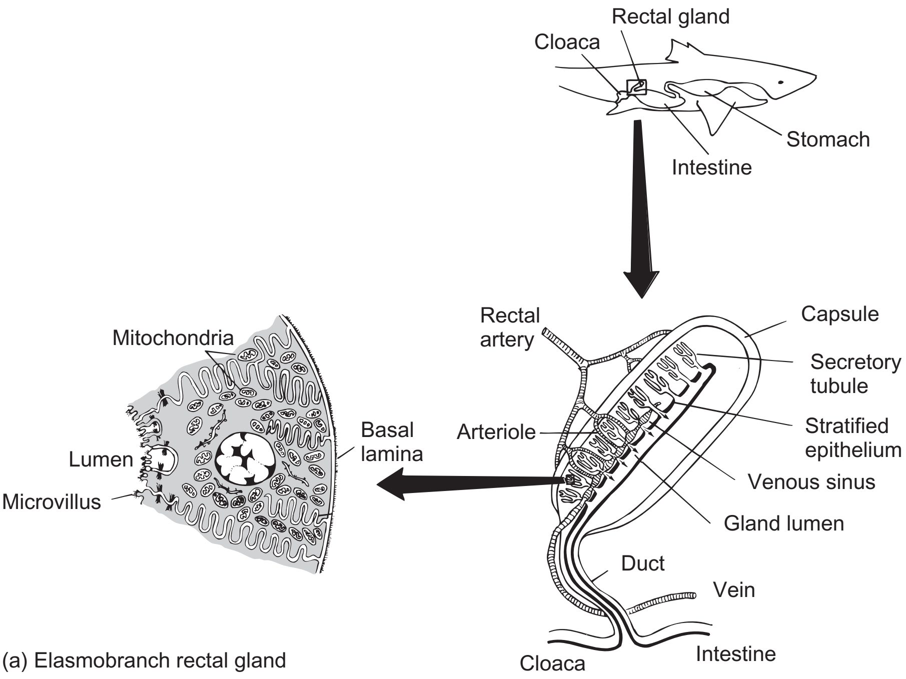
medium. Isosmotically balanced with their environments, osmoconformers do not have to cope with the problems of water entry or loss. Osmoconformer vertebrates are all marine. In hagfishes, unlike in the hyposmotic body fluids of most marine fishes, concentrations of Na^+ and Cl^- in blood and extracellular fluid are elevated, so they are close to those of seawater. Hagfish tissues tolerate these relatively high levels of solutes. Because the hagfish is in osmotic equilibrium with its environment, the nephron does not need to excrete large volumes of urine. Consequently, the nephron is reduced to little more than a renal capsule connected to the archinephric duct by a short, thin-walled duct (figure 14.10a). Surprisingly, the renal corpuscles are quite large. Because water elimination is not a problem for the hagfish, the well-developed renal corpuscle probably functions in regulating divalent ions such as Ca^{++} and SO_4^{--}.

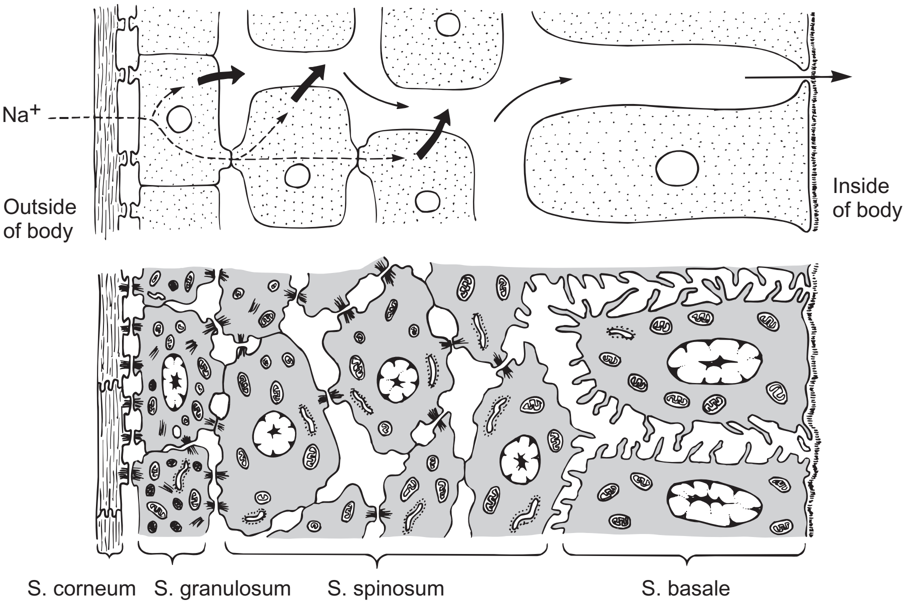
Elasmobranchs and the coelacanth *Latimeria* are also approximate osmoconformers, but this is achieved via ureotelism. Urea accumulates at high concentrations in the blood and elevates the blood osmolarity up to that of seawater. For these fishes, large fluxes of water do not occur, and maintenance of water balance presents no special problem. Excess salts that enter the body fluids from seawater are eliminated through special glands, such as the *rectal gland* of sharks, or through the gills.

Tolerance of Fluctuations Changes in kidney structure and osmoconformity are not the only ways of dealing with osmotic stress. Some aquatic vertebrates can tolerate wide variations in salinity. Those that are osmotically tolerant are **euryhaline** (*eury-*, wide; *haline*, salt) animals. Some euryhaline animals can move from marine to brackish water and even to fresh water. Other vertebrates that can withstand only a narrow range of environmental salinities are **stenohaline** (*steno-*, narrow; *haline*, salt) animals.

Salt Balance Although we have focused on renal mechanisms that eliminate or conserve water, striking an osmotic balance involves moving salts as well as water. Various structures are devoted to the task of regulating salt



(a) Elasmobranch rectal gland



(b) Amphibian integument

FIGURE 14.15 Regulating salt levels. (a) Rectal glands of sharks and other elasmobranchs. These glands have evolved to eliminate salts efficiently from the body without the expenditure of large volumes of water. The outer capsule of the elasmobranch rectal gland consists of connective tissue and smooth muscle. Blood enters via the renal artery, circulates around the secretory tubules, enters a venous sinus, and then flows into the renal vein. Salt collected by the secretory tubules passes into the lumen of the rectal gland and is then forced into the intestine to be eliminated with the feces. (b) Diagrammatic cross section of amphibian integument. Salt tends to diffuse from amphibians into fresh water. They have evolved the ability to take up replacement salts, especially sodium ions, through the skin by means of active transport. Sodium is taken up across the stratum granulosum and moved by active transport into the spaces between cells. Eventually it makes its way into capillaries within the dermis.

After Berridge and Oschman.

balance. As mentioned, the distal tubule within the kidney recovers salts from the urine. Gills address ion imbalances by pumping salts out of (marine bony fishes) or into (freshwater fishes) the body. The rectal gland of elasmobranchs also collects, concentrates, and rids the body of salts (figure 14.15a).

Marine reptiles and birds that eat salty foods or drink seawater to replace lost fluids also ingest high levels of salt. Because their kidneys cannot handle this excess salt, it is excreted by special **salt glands.** In response to a salt load, salt glands intermittently produce a highly concentrated secretion containing Na^+ and Cl^- primarily. In reptiles, these salt glands can be specialized nasal glands (in some marine lizards), orbital glands (in some marine turtles), sublingual glands (in sea snakes), or glands on the tongue's surface (in Asiatic saltwater crocodiles and North American crocodiles).

In marine birds, paired nasal salt glands are present. These large, specialized glands are usually located within shallow depressions on the dorsal surface of the skull and release their concentrated secretion into the nasal cavity. Marine mammals lack specialized salt glands. Their kidneys produce urine that is much more concentrated than seawater, so most salt is eliminated through the kidneys. Many terrestrial mammals have sweat glands in the integument primarily serving thermoregulation, but they also eliminate some salt.

In fresh water, the problem is totally different. Salt tends to be lost to the environment. Freshwater fishes absorb salts through their gills. In aquatic amphibians, the skin aids in the regulation of salt balance (figure 14.15b).

Balancing Competing Demands The cloaca, urinary bladder, and large intestine also aid in the regulation of both salt and water balances. Managing salt and water balance must be compromised with other demands. We have already seen that the demands of nitrogen excretion must sometimes be balanced with the need for water conservation. Furthermore, amniotes often incur a heat load if they live in hot climates or lead active lives. Birds pant and mammals sweat to help dissipate heat through the process of evaporative cooling. Water also is lost in this process. Although reptiles lack sweat glands, they possess a thick, water-resistant skin and exhibit only a modest panting mechanism, so they cannot regulate their body temperature through evaporative cooling. Instead, they move out of the sun (into the shade or into burrows) or become active at night. Behavioral thermoregulation and lower metabolic rates reduce evaporative water loss and contribute to water conservation in reptiles.

Evolution

Vertebrate kidneys illustrate preadaptation, a theme we have seen within other systems. But the preadaptation of the urinary system raises an issue we have not addressed—the freshwater origins of vertebrates.

Preadaptation

Excretion of urea or uric acid conserves water and is adaptive for life on land; however, conversion of ammonia into urea or uric acid probably arose well before vertebrates actually ventured onto land. In chondrichthyans and coelacanths, the formation of urea answers the problem of water balance by turning these fishes into osmoconformers. Detoxification of ammonia, by converting it to urea, allows lungfishes to address the immediate problem of surviving droughts. The amniote embryo, confined to a cleidoic egg, converts ammonia into uric acid so it can safely sequester nitrogenous wastes without requiring large quantities of water to flush them away. One or more of these conditions may have preceded life on land and been preadaptive. When vertebrates eventually ventured onto land, they entered an environment in which water was scarce, making water conservation especially important. But as such a transition occurred, the metabolic means of conserving water may already have been in place.

Origin of Vertebrates

Homer Smith, a physiologist, was the first person to notice that the vertebrate kidneys appeared to be better suited to life in fresh water than in salt water. In fact, he argued that the kidneys were so well designed for fresh water that vertebrates must have evolved in fresh water and only later entered salt water. His reasoning went like this: The kidneys of vertebrates are filtration kidneys that can produce large volumes of glomerular filtrate. Such a design would be a liability in marine environments in which water must be conserved, but it would be an asset in freshwater environments in which fishes must rid their bodies of influxes of excess water.

Marine invertebrates are osmoconformers. The levels of salts in their blood are close to those of seawater, making them isosmotic. They are in no danger of dehydration; however, this is not true for marine vertebrates. Compared with marine invertebrates, the levels of salt in the blood of marine vertebrates is almost two-thirds lower. Consequently, vertebrates are hyposmotic to seawater and can become dehydrated. To make matters worse, vertebrates have a filtration kidney capable of producing large volumes of water, not conserving it.

Such disadvantageous features of marine vertebrates can be explained, Smith reasoned, if vertebrates originated in fresh water. If vertebrate ancestors lived in fresh water, evolution of filtration kidneys and low solute levels would be adaptive to cope with water influxes an animal experienced in such an environment. However, when these vertebrates later radiated from fresh to salt water, their filtration kidney was disadvantageous and modifications were required. In chondrichthyans and coelacanths, solute levels rose in the blood to address this problem. Other fishes developed adaptations, such as drinking seawater, that recovered water, and salt glands and gills that eliminated excess salt along with loss of glomeruli and distal tubules. Smith felt that the fossil record available in 1931 also supported a freshwater origin for the earliest vertebrates.

Others have taken issue with Smith's hypothesis and favor instead a marine origin for vertebrates. First, the filtration kidneys of vertebrates are characteristically high-pressure kidneys that produce large volumes of glomerular filtrate. Large volumes of fluid moving from blood to kidney tubules give the kidneys a greater chance to act on the constituents within the circulating fluids of the body. A high-pressure system produces a high volume of filtrate, which aids in processing nitrogenous wastes. Thus, the filtration kidney could represent an efficient system for eliminating nitrogenous and other wastes by moving large volumes of filtrate through the kidney. Second, the filtration kidney is not unique to vertebrates. Crustaceans and many other invertebrates possess filtration kidneys, yet clearly they evolved from marine ancestors. Moreover, many are marine osmoconformers today. Finally, reexamination of early vertebrate fossil deposits suggests that they came from marine seas and not from freshwater habitats as Smith supposed. Contrary to Smith's views, the filtration kidney of the marine vertebrates was preadapted to fresh water, but it did not arise there.

In this debate, the hagfish poses a problem for everyone. Hagfishes are osmoconformers like most marine *in*vertebrates, but unlike most vertebrates. They are members of

BOX ESSAY 14.4

Water, Water, Everywhere, Nor Any Drop to Drink*

Adrift on the ocean, seamen who have survived the loss of their ships face an irony. Exposed to heat, they dehydrate. They are surrounded by water, yet to drink it would only make matters worse. The reason is that seawater is hyperosmotic to body fluids. If a person drinks seawater, the salt is absorbed, and blood osmotic levels rise. But to flush the excess salt from the body, the kidney must spend as much or more water than was originally gulped in by the thirsty castaway. The net result is to make the body even more dehydrated. Furthermore, there is another problem. Seawater also contains magnesium sulfate, an ingredient used in laxatives. It stimulates diarrhea, and hence even more fluid is lost via the digestive tract.

Many marine animals address this problem differently. They drink seawater but excrete the excess salt by active transport in special salt glands rather than by flushing it through the kidneys with water. This allows them to use the seawater but not fall behind like humans in their water balance.

**The Rime of the Ancient Mariner,* Samuel Taylor Coleridge.

the oldest surviving vertebrate group, the cyclostomes, and possess a filtration kidney, yet they live in salt water. If Smith were correct, then these primitive vertebrates would live in fresh water. They do not, of course. If the marine origin of vertebrates is to hold, then hagfishes should be osmoregulators like other vertebrates. Of course, they are not. Perhaps it is best to recognize that the hagfish, although a representative of the earliest group of vertebrates, is very ancient and may have diverged significantly in its physiology from an ancestral condition.

Reproductive System

The reproductive system includes the gonads, their products, hormones and gametes, and the ducts that transport gametes. Reproductive hormones facilitate sexual behavior and parental care, prepare the reproductive ducts to receive the gametes, support the zygote, and perform other functions that we turn our attention to in chapter 15 on the endocrine system. Now we look at the gametes and the ducts that provide a home for and convey gametes during reproduction. The eutherian mammal is used again to introduce the terminology applied to the reproductive system.

Structure of the Mammalian Reproductive System

In mammals, each ovary consists of an outer connective tissue capsule, the **tunica albuginea,** that encloses a thick **cortex** and deeper **medulla.** The **ova,** or eggs, occupy the cortex and are wrapped in layers of **follicle cells** derived from connective tissue. An ovum plus its associated follicle cells is termed a **follicle.** Some follicles remain rudimentary, never change, and never release their ova. Others pass through a series of growth, or **maturation,** stages, at the end of which the ovum and some of its clinging follicle cells are cast out of the ovary in the process of **ovulation,** and become ready for fertilization. If fertilization occurs, the ovum continues down the **oviduct** and becomes **implanted** in the wall of the prepared **uterus,** where subsequent growth of the embryo occurs. If fertilization does not occur, the undeveloped ovum continues down the oviduct and is flushed out of the uterus during the next menstruation (figure 14.16).

Embryonic implantation (p. 193)

Each mammalian testis also consists of an outer tunica albuginea, which encloses the **seminiferous tubules** that produce sperm. Within the walls of the seminiferous tubules, stem cells multiply and grow into sperm that eventually are released into the lumen. The coiled seminiferous tubules straighten, forming **tubuli recti** just before they join the **rete testis.** Via the **efferent ductules,** the rete testis joins the **epididymis,** where sperm are temporarily stored. Upon ejaculation, sperm travel along the **vas deferens (ductus deferens)** into the urethra. Along the way, three accessory sex glands, the **seminal vesicle, prostate,** and **bulbourethral** (Cowper's) **gland,** respectively, add their secretions as sperm move from the testes to the urethra. This fluid and the sperm it contains constitute **seminal fluid,** or **semen** (figure 14.17).

Embryonic Development

Gonads and Gametes

The paired gonads arise from the **genital ridge,** initially a thickening in the splanchnic mesoderm to which adjacent mesenchyme cells contribute (figure 14.18). The early gonad is little more than a swelling on the dorsal wall of the coelom with a thick outer cortex around a deeper medulla (figure 14.19a,b). Because the gonad shows neither unique male nor female characters at this early stage, it is termed an **indifferent gonad.** The gonads of both sexes initially contain **germ cells,** the future sperm or eggs. Surprisingly, germ cells themselves do not arise in the genital ridge nor even in the adjacent mesoderm. In fact, they do not arise in the embryo at all. They first debut in remote sites outside the embryo in the extraembryonic endoderm. From the extraembryonic endoderm, they undergo a journey that takes them eventually to the indifferent gonad, where they

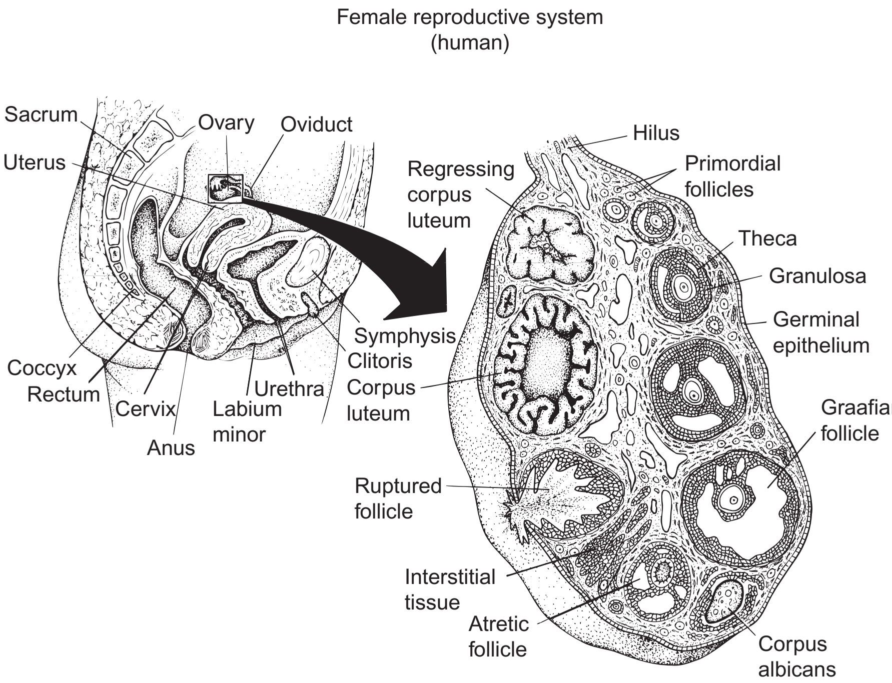


FIGURE 14.16 Female reproductive system (human). This sagittal section of the female pelvis shows the reproductive organs and their relationships to the urinary and digestive systems. The ovary is enlarged and sectioned at the right. The successive stages in follicle maturation, beginning with the primordial follicles and then clockwise to the Graafian follicle and corpus luteum, are summarized within the representative ovary. Atretic follicles and other regressing stages are included.

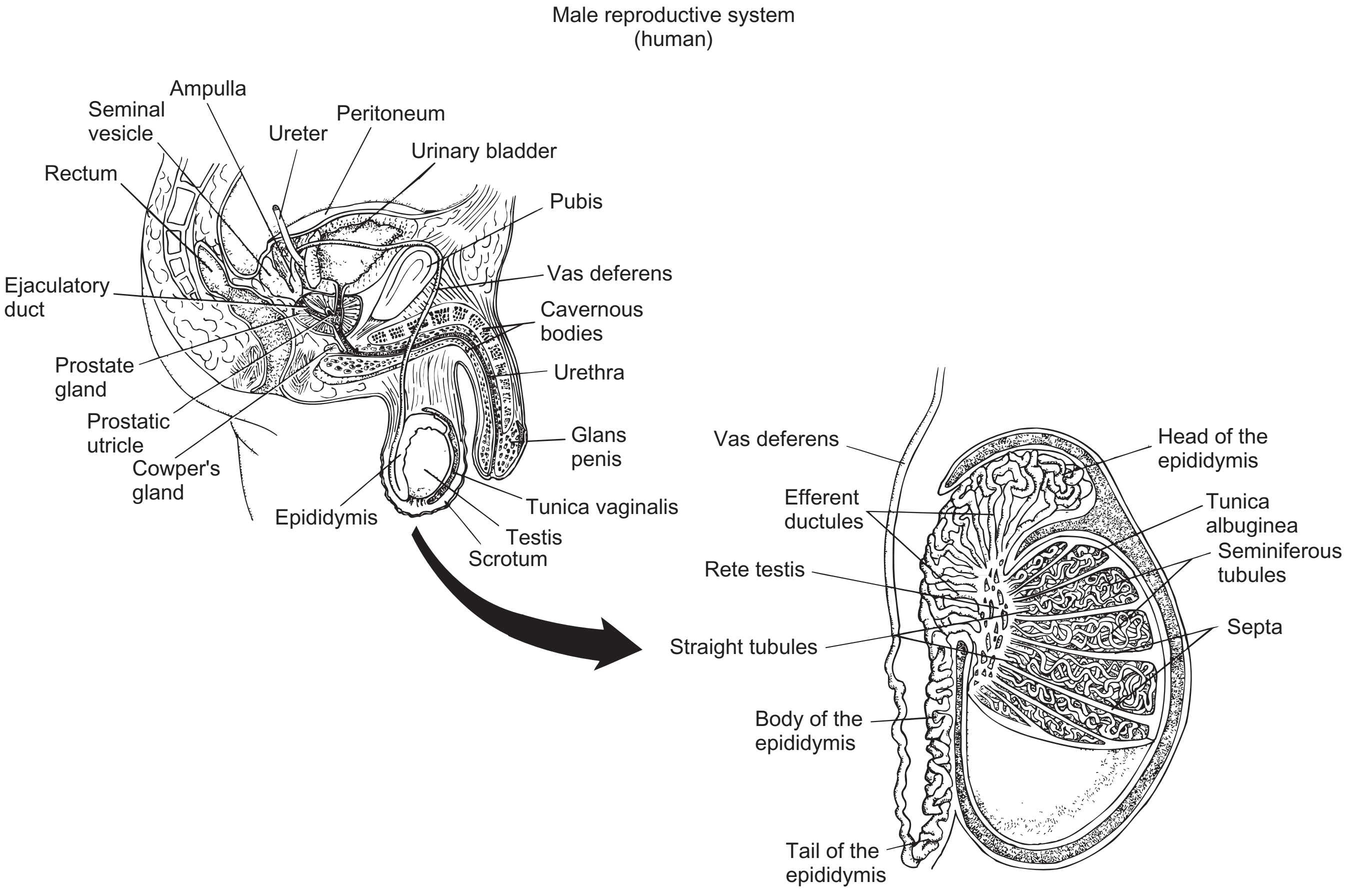


FIGURE 14.17 Male reproductive system (human). This sagittal section of the male pelvis shows the reproductive organs and their relationships to the urinary and digestive systems. The enlarged and cutaway view of the testis and its duct system is shown at the bottom. Spermatozoa produced in the seminiferous tubules eventually pass through the straight tubules into the rete testis and enter the epididymis. Fluid is added as spermatozoa are moved through the vas deferens by contractions of sheets of smooth muscle in its walls.

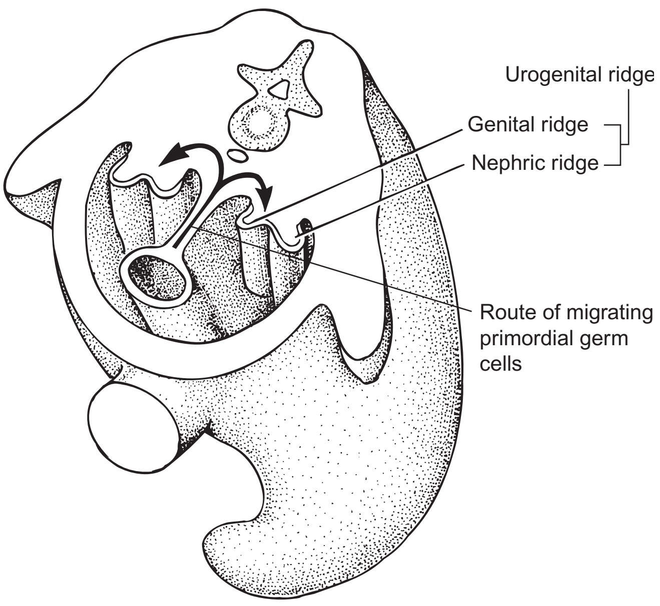


FIGURE 14.18 Urogenital ridge. In the posterior part of the developing embryo, paired urogenital ridges arise within the roof of the coelom. The medial ridges are the genital ridges and give rise to the gonads. The lateral nephric ridges give rise to the kidney and its ducts. Primordial germ cells that develop into eggs or sperm arise outside the gonads, migrate to them, and colonize the early gonad rudiments.

take up a permanent residence. In females, germ cells establish residence in the cortex. In males, arriving germ cells establish residence in the medulla, which develops into the seminiferous tubule (figure 14.19c,d).

Reproductive Tracts

Parts of the embryonic urinary system are salvaged by or shared with the genital system. In female mammals, the mesonephric duct **(wolffian duct)** drains the embryonic mesonephros, but it regresses later in development when the metanephros and its ureter become the kidney of the adult. However, a second parallel **Müllerian duct** arises next to the embryonic mesonephric duct before it regresses. The Müllerian duct, rather than the wolffian, forms the oviduct, uterus, and vagina (figure 14.20). A few mesonephric tubules may persist as the **Paroöphoron** and **Epoöphoron.** In male mammals, the mesonephric duct becomes the vas deferens. Mesonephric tubules and some of the associated ducts contribute to the epididymis. A rudimentary Müllerian duct occasionally arises in embryonic males but never assumes a significant role in the adult male (figure 14.20).

Overview

The urogenital system of vertebrates certainly does not heed the Shakespearean warning, "Neither a borrower nor lender be." Parts evolved first to serve the kidneys (e.g., pronephric duct) later ended up serving the testis in males (e.g., vas deferens). In some species, a given duct is shared between the urinary and reproductive systems. In others, the same duct functions in only one of these systems. Even within the same species, homologous parts perform different roles in opposite sexes. Keeping track of these anatomical differences is no simple matter. A prolific terminology that has developed to track these anatomical and functional differences can obscure the underlying unity of the system. In this book, we select a set of terms applicable throughout the vertebrate urogenital system (noting synonyms) and apply it consistently (figure 14.21). When we examine phylogeny, we use

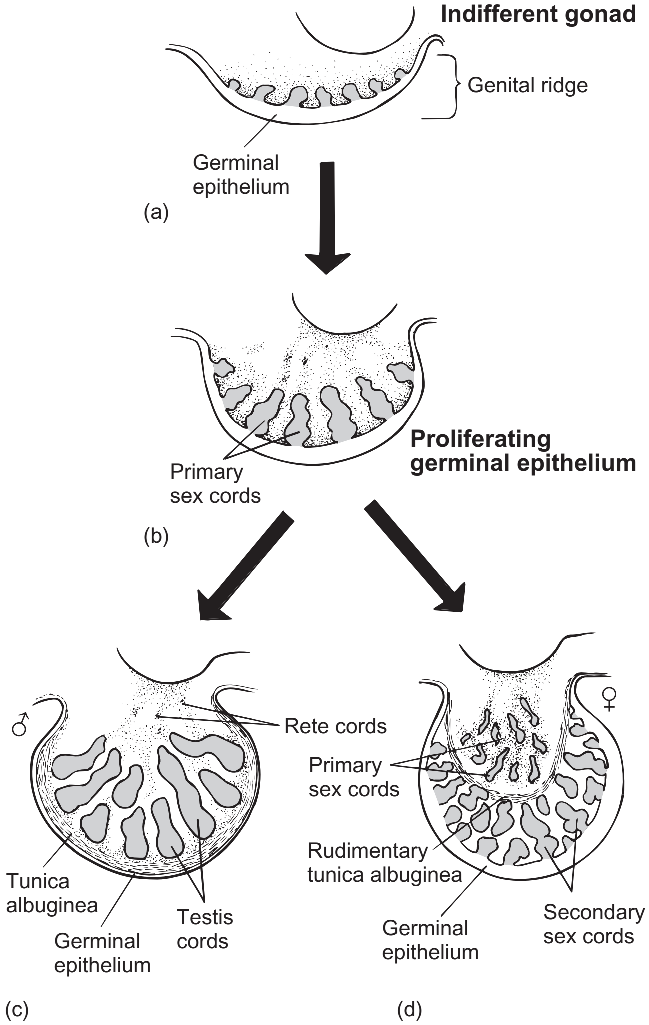


FIGURE 14.19 Embryonic formation of the gonad. (a,b) Thickening of the genital ridge and inward movement of adjacent mesenchymal cells give rise to a swelling, the genital ridge, from the roof of the coelom. Because this early developmental stage is similar in both sexes, it is referred to as the indifferent gonad, which includes cortex and medulla. Primordial germ cells arriving from distant locations outside the embryo usually take up residence in the indifferent gonad. (c) In males, the medulla enlarges to become the testis cords that will form the seminiferous tubules. (d) In females, the cortex expands, forming secondary sex cords that house the follicles.

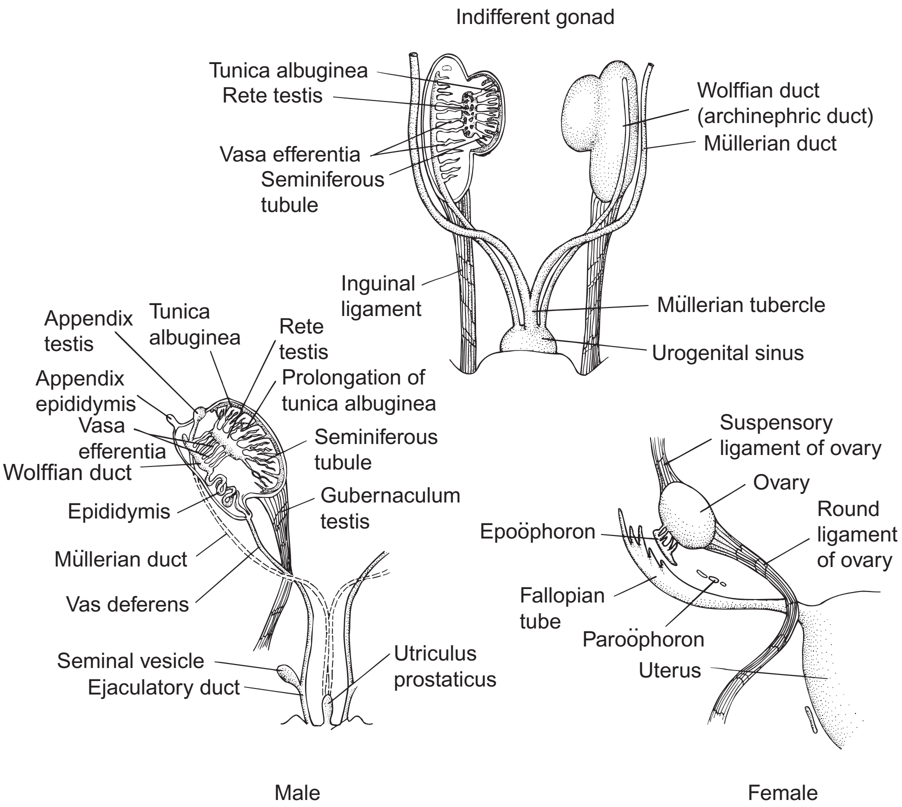


FIGURE 14.20 **Embryonic formation of the male and female genital systems in mammals.**

After Tuchmann-Duplessis and Haegel.

Ducts of the Urogenital System	
General term	*Alternative term*
Archinephric duct	Pronephric duct/mesonephric duct Wolffian duct Opisthonephric duct Ductus deferens (vas deferens)
Müllerian duct	Oviduct
Metanephric duct	Ureter

FIGURE 14.21 **Terminology of the urogenital system.** Associations of ducts change during evolution and development. Sometimes the same duct performs different roles in males and females. The result has been a proliferation of synonyms, which are summarized in this figure. The duct serving the early pronephros is the pronephric duct, but when the mesonephros replaces the pronephric kidney, this duct now serves the new mesonephros and is called the mesonephric duct. With the advent of the metanephros, this duct degenerates in the female but becomes the vas deferens of the testis in the male. Some authorities prefer the term *archinephric duct* or *wolffian duct* for this structure. Although the term *metanephric duct* might parallel the terms *pronephric* and *mesonephric* ducts, more often the term *ureter* is used for the metanephric duct.

terminology that applies to the homology of reproductive parts throughout vertebrates and place the more common or functional term for a given species and sex in parentheses.

As we saw earlier in our discussion of the kidney, the pronephric duct usually persists and drains the mesonephros or extended opisthonephros. It is renamed the mesonephric duct or the opisthonephric duct, respectively. In some males, this duct transports sperm and is called the vas deferens. In females, it is known embryologically as the wolffian duct. Because this duct plays different roles in different groups, the more general term **archinephric duct** is preferred. The **metanephric duct** is commonly called the ureter. In some males, the kidney divides its services between reproductive and excretory roles. To recognize this, it is common to speak of the **reproductive kidney** and the **uriniferous kidney.**

In females, the archinephric (mesonephric) ducts tend to function only within the urinary system. The Müllerian duct arises embryologically next to the archinephric (wolffian) duct. In males, the Müllerian duct regresses if it appears at all, but in females, the Müllerian ducts become the oviducts of the reproductive system. Released ova enter the oviduct through the **ostium,** which typically flares into a **funnel** (infundibulum) in many vertebrates. The fringed margins of the ostium are the **fimbria** that embrace the ovary. The ovary and ostium are sometimes enclosed in a common peritoneal sac, but usually the oviducts are not connected to the ovaries directly. Instead, the ciliated

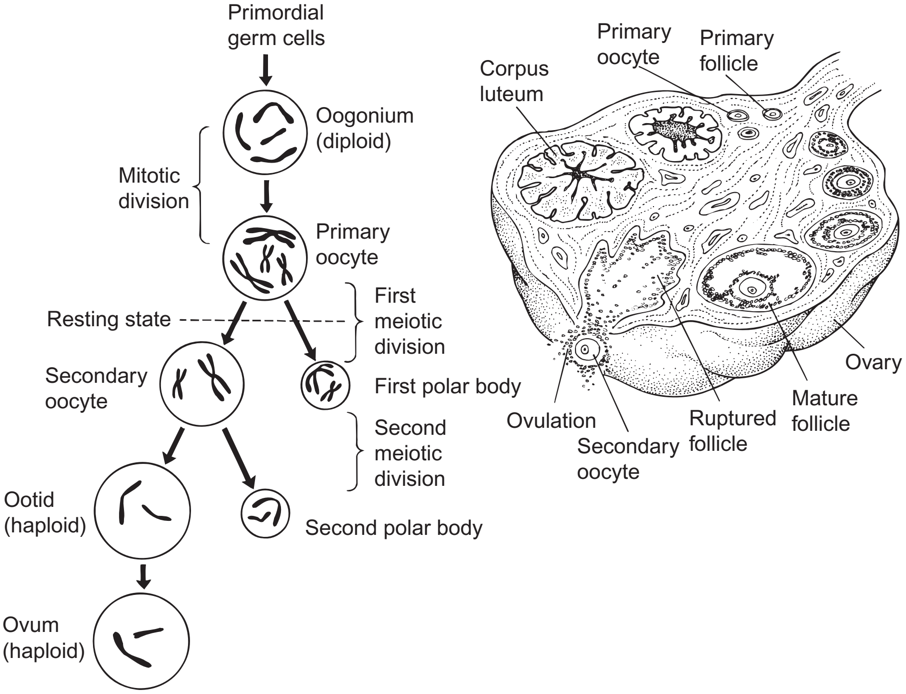


FIGURE 14.22 Oogenesis. Diploid primordial germ cells colonize the ovary of the embryonic female. When they arrive in the ovary, these germ cells are called primary oocytes. They gather around themselves a layer of connective tissue cells to form an ovarian follicle. Most oocytes begin meiosis but do not complete this process until ovulation or later, depending upon the species. Of the hundreds or thousands of oocytes residing in follicles within the ovary, only a few will ever mature, be released at ovulation (after which they are usually termed ova), and become fertilized.

fimbria and infundibulum gather released ova and move them into the oviduct. Fertilization, if it is internal, usually occurs soon after the ovum enters the oviduct. Shortly before their terminus, the oviducts may expand into the uterus, the organ in which an embryo is housed and nourished. If the fertilized egg is wrapped in a shell, **shell glands** or **shell-secreting regions** may be evident in the oviduct.

Female Reproductive System

Ovary

The ovary produces both hormones and mature ova (sing., *ovum*). **Oogenesis** is the process of egg maturation, which occurs from the time of its appearance in the ovary until it completes meiosis. Oogenesis is a complex process involving **mitotic** as well as **meiotic** cell division, growth in egg size, and changes in cytoplasmic composition (figure 14.22). Once germ cells take up residence in the ovary, they are called **oogonia.** The diploid oogonia undergo mitotic division, yielding diploid cells. At the end of this phase of development, they are **primary oocytes.** Primary oocytes then begin meiotic cell division for the first time. As a result of the first meiotic division, each ovum yields a first **polar body** and a **secondary oocyte.** Although the first polar body may divide again, its role in helping to reduce the chromosome number is complete; thereafter, it is of little importance. The secondary oocyte undergoes a second meiotic division, yielding a second polar body and a haploid ovum.

A capsule of supportive connective tissue cells termed *follicle cells* forms around the primary oocyte. Follicle cells and the oocyte they embrace form an **ovarian follicle.** The follicle cells contribute to nutritional support and help build up yolk within the ovum. During the breeding season, selected follicles and the oocytes they contain resume maturation under hormonal stimulation. As meiosis is completed, a **secondary oocyte** is formed. Release of the oocyte from the ovary is termed ovulation.

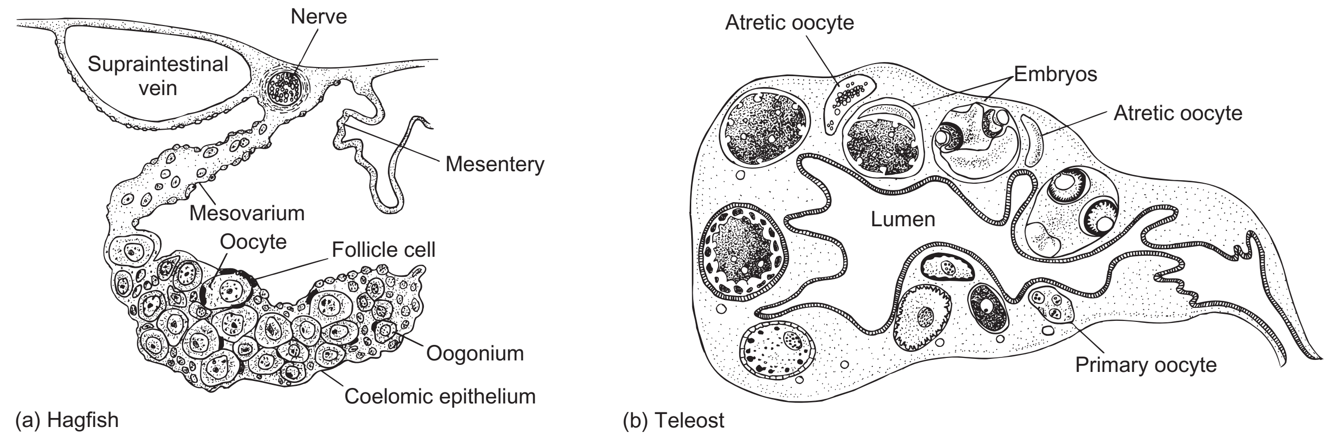
Much variation occurs during the time before meiosis takes place. These events of oogenesis may occur largely before or after sexual maturity, depending on the species. At the birth of a mammalian female, the primordial germ cells have already migrated into the ovary and started to undergo meiosis, but further oogenesis is usually arrested until the onset of sexual maturity. In fact, not all the primary oocytes mature. For example, the human female is born with half a million primary oocytes in her ovaries, but perhaps only several hundred of these complete oogenesis. The rest eventually degenerate. In some mammalian species, meiosis occurs before ovulation. In other species, it does not occur until after fertilization.

The ovary is suspended from the dorsal wall of the coelom by a mesentery, the **mesovarium** (figure 14.23). Except for cyclostomes, in which eggs escape through secondary pores in the body wall, vertebrate eggs travel through genital ducts after they are released from the ovaries. In most vertebrates, the ovaries are paired; however, in cyclostomes, some reptiles, most birds, the platypus, and some bats, only a single ovary is functional (table 14.1).

Oviparity, viviparity (p. 164)

Genital Ducts

Fishes In cyclostomes, the single large ovary is suspended from the middorsal wall. In lampreys, as many as 24,000 to over 200,000 ovarian follicles can develop

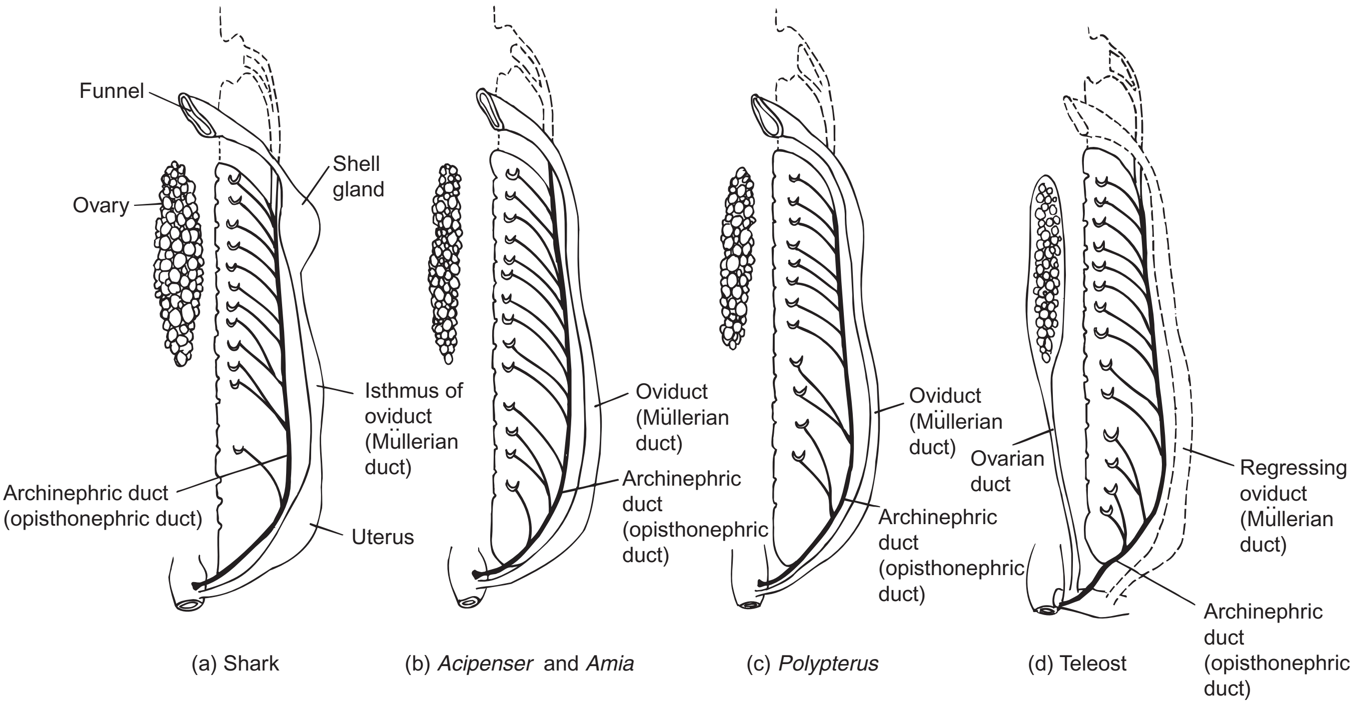


(a) Hagfish

(b) Teleost

FIGURE 14.23 **Fish ovaries.** (a) Hagfish. Oocytes and surrounding follicle cells are held within the ovary. (b) Teleost. Section of the ovary of the guppy *Poecilia reticulata*. Ova are fertilized while they are within the ovary, and they are retained well into embryonic development. There can be one to seven oocytes in progressive stages of development. Atretic oocytes that fail to develop and developing embryos are illustrated.

(a) After Hardisty; (b) after Lambert.



(a) Shark (b) *Acipenser* and *Amia* (c) *Polypterus* (d) Teleost

FIGURE 14.24 **Oviducts of female fishes.** (a) Shark. (b) Sturgeon and bowfin. (c) Bichir. (d) Teleost. The oviduct (Müllerian duct) arises adjacent to and parallel with the archinephric duct in most fishes. In teleosts, the oviduct is usually replaced by an ovarian duct that is derived separately.

in synchrony, and are ovulated during a single breeding season. Most lampreys spawn once and die shortly thereafter. Few follicles are present in hagfishes, and little is known about their reproductive behavior. Cyclostome ovaries lack ducts. Instead, eggs are shed into the coelom. From the coelom, they reach the cloaca (in lampreys) or anus (in hagfishes) through secondary pores. The archinephric ducts drain the kidneys exclusively.

In elasmobranchs, the ovaries are initially paired, but in some species, only one may develop. The Müllerian duct, or oviduct, differentiates into four regions: funnel, shell gland, **isthmus,** and uterus (figure 14.24a). The funnel collects the eggs shed from the ovary. Anterior ends of the paired oviduct may fuse into a single funnel, or asymmetric development may leave only one primary funnel. In some species, the shell gland (nidamental gland) stores sperm, but

TABLE 14.1 Vertebrates with One Functional Ovary

Species	Explanation for One-Ovary Condition
Agnatha	
Lampreys	Fusion of two gonads
Hagfishes	One gonad fails to develop
Osteichthyes	
Perches, *Perca*	Fusion of two gonads
Pike perch, *Lucia-Stizostedion* sp.	Fusion of two gonads
Stone loach, *Noemacheilus* sp.	Fusion of two gonads
European bitterling, *Rhodeus ararus*	Fusion of two gonads
Japanese ricefish, *Oryzias latipes*	One gonad fails to develop
Guppy, *Poecilia reticulata*	One gonad fails to develop
Chondrichthyes	
Sharks	
Scyliorhinus	Left ovary becomes atrophic
Pristiophorus	Left ovary becomes atrophic
Carcharhinus	Left ovary becomes atrophic
Galeus	Left ovary becomes atrophic
Mustelus	Left ovary becomes atrophic
Sphyrna	Left ovary becomes atrophic
Rays	
Urolophus	Left ovary functional
Dasyatis	Right ovary absent
Reptilia	
Blind worm snakes, *Typhlops*	Left ovary and oviduct absent
Aves	
Birds	Left ovary functional in most species; right ovary regresses in embryos
Mammalia	
Platypus *Ornithorhynchus anatinus*	Left ovary functional
Bats	
Miniopterus natalensis	Left ovary functional
Miniopterus schreibersi	Right ovary functional
Rhinolophus	Right ovary functional
Tadarida cyanocephala	Right ovary functional
Molossus ater	Right ovary functional
Mountain viscacha, *Lagidium peruanum*	Right ovary functional
Water buck, *Kobus defassa*	Left ovary functional

in most elasmobranchs, it secretes albumen and mucus. In oviparous species, the shell gland produces the egg case as well. In viviparous species, in particular, the shell gland may be indistinguishable. The isthmus connects the shell gland to the uterus. The uterus nutritionally supports embryos if they are held in the oviduct for an extended period. Oviducts may join before they enter the cloaca, or they may enter separately. The genital ducts of chimaeras are similar to those of sharks, except the oviducts always share a common funnel and each oviduct opens separately into the cloaca. The archinephric duct drains the female opisthonephric kidney.

In female bony fishes, like most other anamniote females, the archinephric ducts serve the kidneys, and the paired oviducts (Müllerian ducts) serve the paired ovaries (figures 14.24b–d and 14.25a–c). In some teleosts, such as salmonids, eggs released from the ovaries fill the body cavity. Eventually they reach short, funnel-like remnants of the oviducts situated at the posterior part of the coelom. However, in many teleosts, the oviducts regress entirely, leaving egg transport to new **ovarian ducts** (figure 14.26a–c). These ovarian ducts are not homologous to the oviducts (Müllerian ducts) of other vertebrates. Instead, they are derived from peritoneal folds that embrace each ovary and have grown posteriorly to form new ducts.

Most teleost fishes lay eggs, but some bear live young. Among these viviparous teleosts, maternal tissues may nourish the embryo. One extreme case is found in the family of teleosts that includes the guppy. In this group, fertilization occurs while the ova are still in the ovarian follicles. The ovary continues to hold the embryos during subsequent development until they are released as tiny fry. Oocytes that fail to reach a point in maturation where they can be fertilized usually undergo involution and are called **atretic oocytes** (figure 14.23b). Recycling of atretic tissue provides nutrition for the surviving oocytes.

Tetrapods Amphibian ovaries are paired, hollow structures that usually show a prominent cortex covered by germinal epithelium. The genital ducts of female amphibians are usually simple and consistent. The archinephric ducts serve the opisthonephric kidneys; the oviducts (Müllerian ducts) serve the ovaries.

In amniotes, remnants of the mesonephros may persist in larval stages, but adults have metanephric kidneys drained exclusively by new paired ducts, the ureters (metanephric ducts). In females, the archinephric ducts are rudimentary. The oviducts (Müllerian ducts) persist in their roles of transporting ova from the ovaries and supporting the embryo while it is in transit. The tubular oviducts (Müllerian ducts) of amniotes often have prominent sheets of smooth muscle within their walls and a lumen lined by a secretory mucosa. In oviparous amniotes, a shell gland may be prominent; in viviparous amniotes the uterus may be distinct (figures 14.27a–c and 14.28a–d).

Oviduct

After ovulation, the fimbria move the ovum into the oviduct. If fertilization is internal, the ovum and sperm meet almost immediately in the upper reaches of the oviduct. If fertilization is external, the smooth muscle and cilia lining the oviduct drive the ovum to the outside, where it is fertilized.

In addition to transporting the ovum, the oviduct in some vertebrates may add layers of membrane or a shell. In many species, parts of the oviduct are specialized as distinct shell glands that add these coats. Because membranes and shells are impervious to sperm, they are added

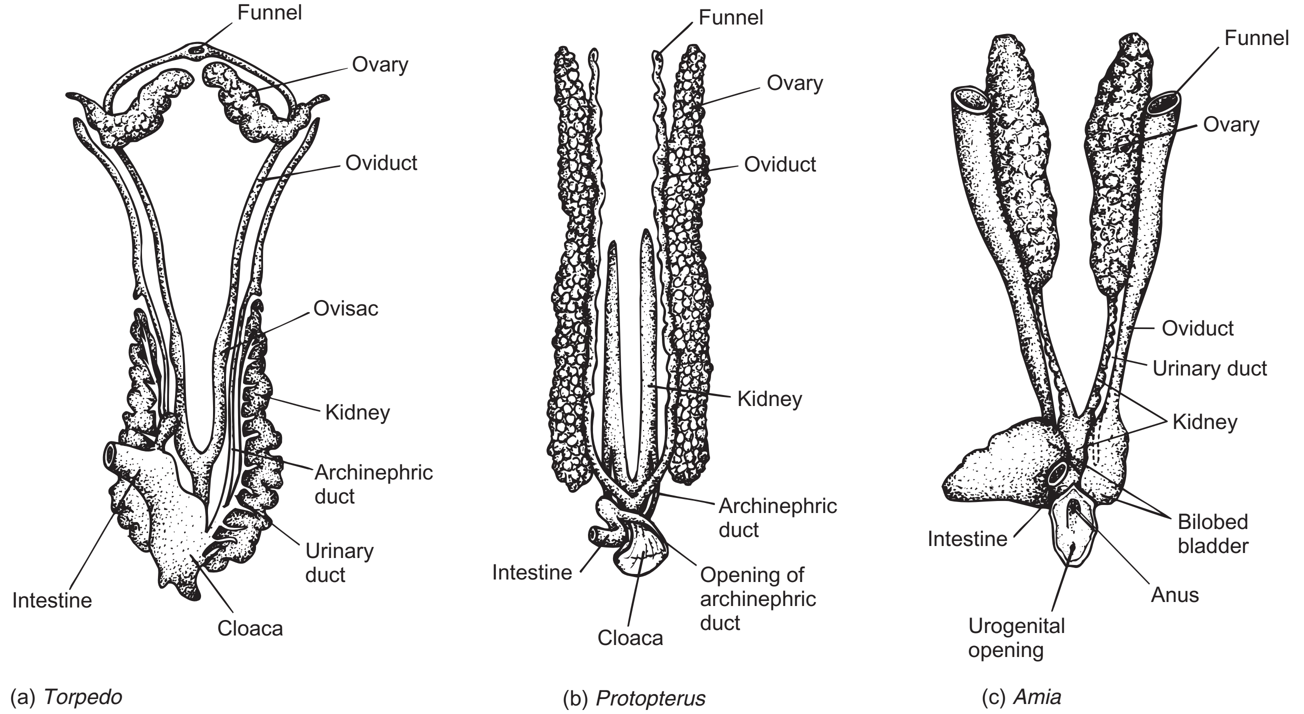


FIGURE 14.25 Urogenital systems of female fishes (a) Ray, *Torpedo.* (b) Lungfish, *Protopterus*. (c) Bowfin, *Amia.*

After Romer and Parsons.

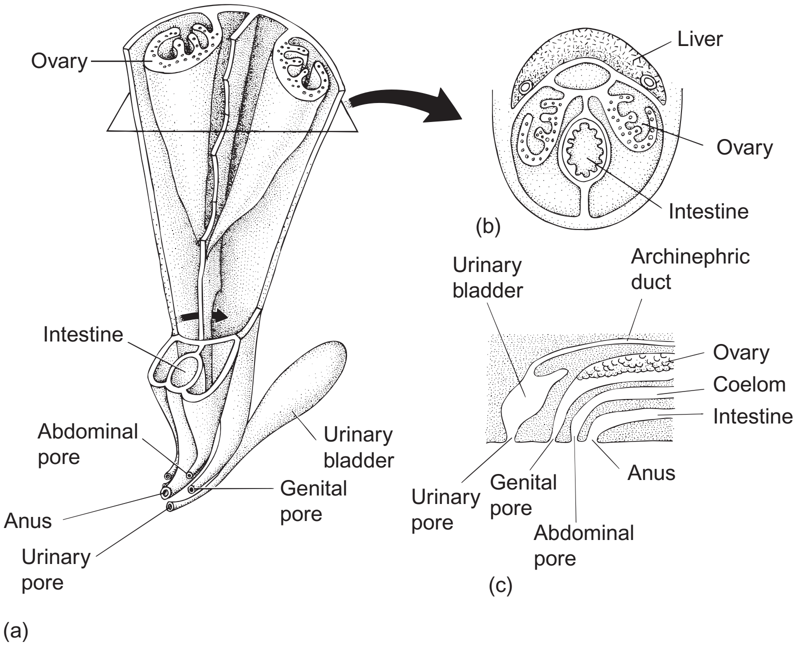


FIGURE 14.26 Urogenital system of a teleost female. (a) Ventral view, partially cut away, of the urogenital system in a generalized teleost fish. Ovaries are suspended from the dorsal wall, and release ova into the genital funnels formed from folds in the peritoneal wall. The coelom connects with the outside through abdominal pores. Feces are eliminated via the anus, and urine via the urinary pore of the bladder. (b) Cross section at the level of the ovaries. (c) Sagittal section.

after fertilization. In birds and egg-laying reptiles, a layer of albumen, and then a shell membrane, and finally a calcareous outer shell are added as the fertilized ovum slides along the oviduct (figure 14.29). The encapsulated egg is then held within the oviduct until a suitable environmental site in which to lay it is prepared.

Uterus

The uterus is the terminal portion of the oviduct. Shelled eggs waiting to be laid or embryos completing their development are held within the uterus. In eutherian mammals and a few other vertebrates, the walls of the uterus and extraembryonic membranes of the embryo establish a close vascular

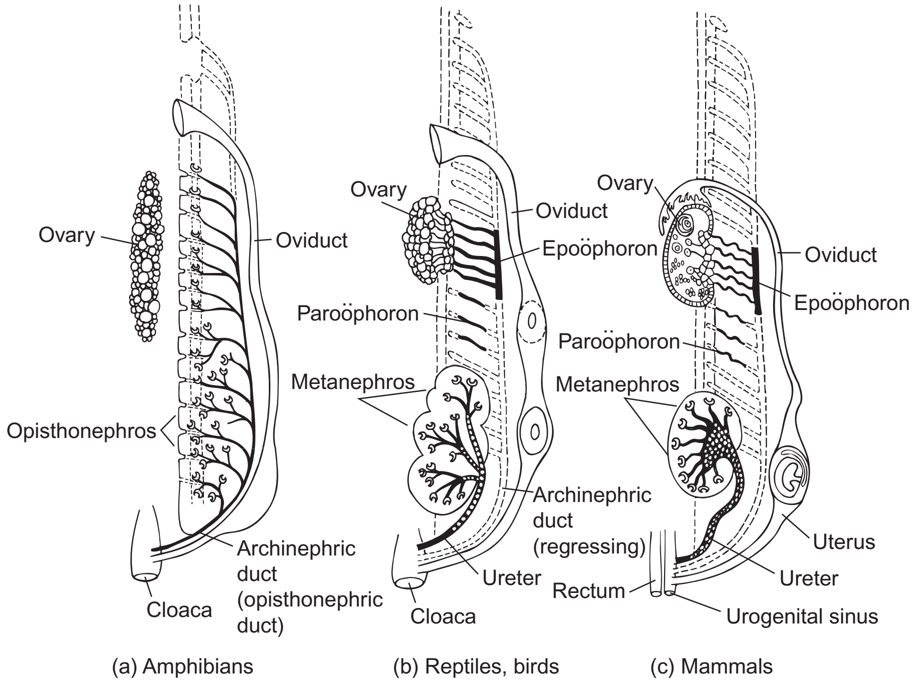


FIGURE 14.27 Urogenital anatomy of tetrapod females. (a) Amphibians. (b) Reptiles and birds. (c) Mammals.

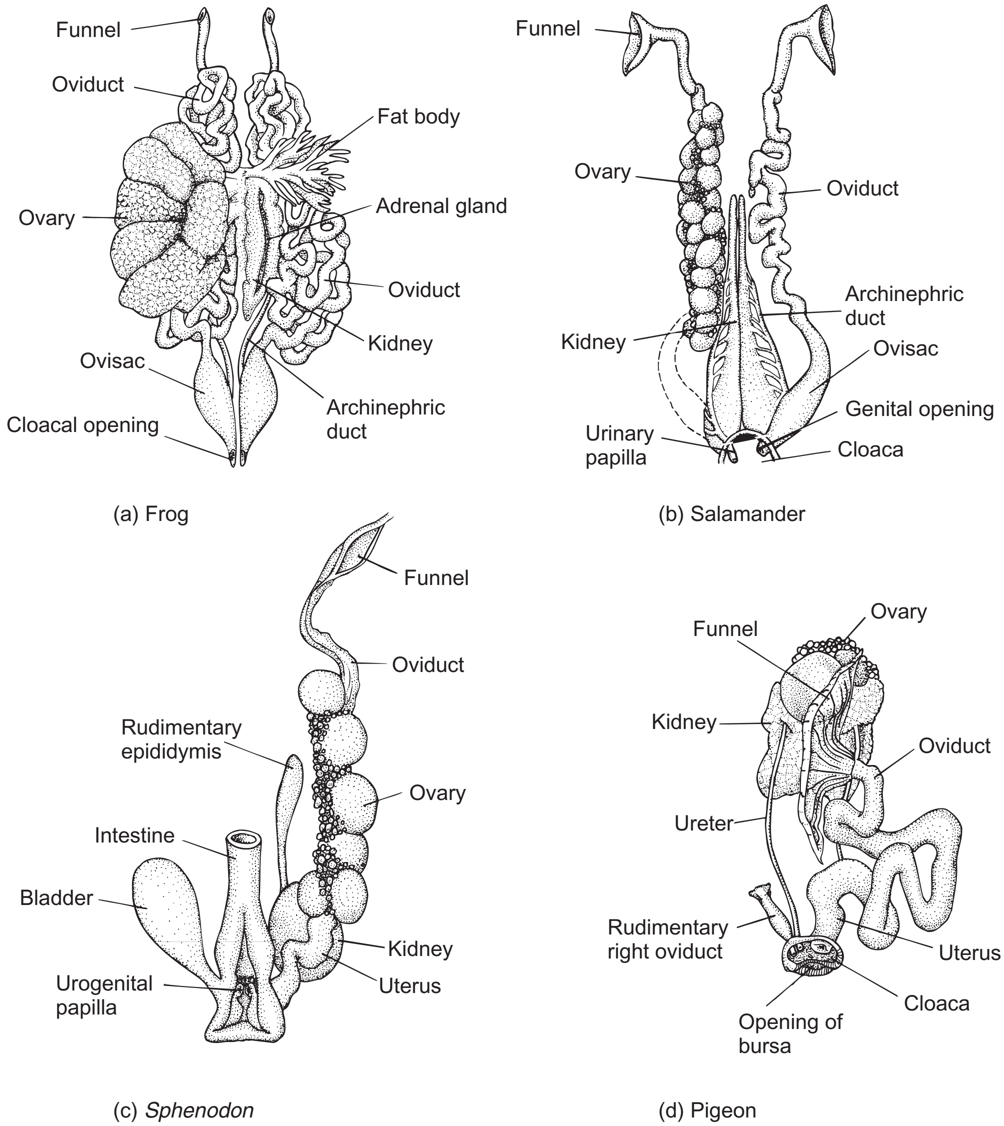


FIGURE 14.28 Urogenital systems of tetrapod females, ventral views. (a) Frog, *Rana*. The intestine, urinary bladder, and left ovary have been removed to reveal underlying structures. Urinary ducts of the right side are pulled away from the kidney to show their course. (b) Salamander, *Salamandra*. (c) Reptile, *Sphenodon*. (d) Bird, *Columba*.

After Romer and Parsons.

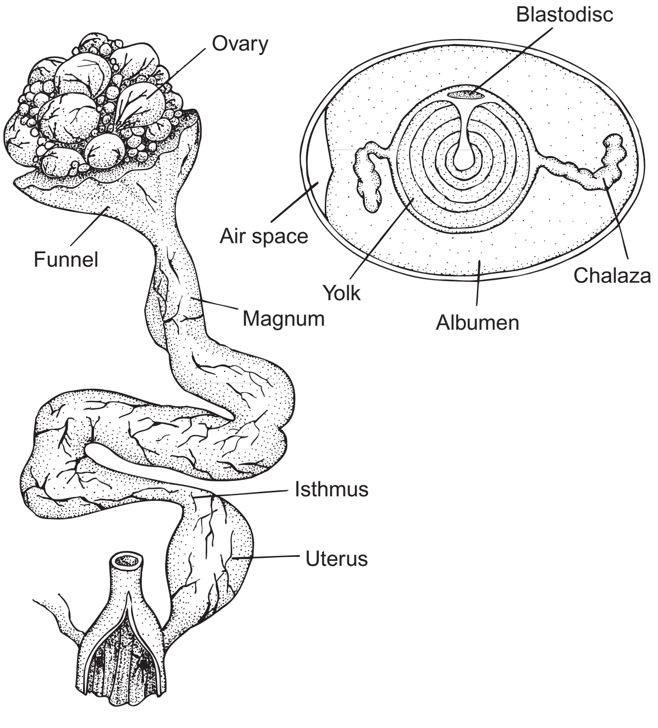


FIGURE 14.29 **Oviduct of a hen.** After ovulation, ova are gathered by the infundibulum of the oviduct. If egg membranes are to be added, fertilization occurs here in the upper reaches of the oviduct. The oviduct adds a coat of albumen, a shell membrane, and eventually a calcareous shell.

association through a **placenta.** Nutrients and oxygen are transported to the developing embryo, and carbon dioxide is given up to the maternal circulation via the placenta.

Placentae (p. 192)

In therian mammals, the terminal ends of the oviduct tend to merge into a single uterus and **vagina** that lie along the body's midline. The vagina receives the male penis or intromittent organ during copulation. The female homologue of the male penis is the **clitoris.** Unlike the penis, the clitoris participates neither in gamete transfer nor in urination.

Male Reproductive System

Testis

Except in cyclostomes and some teleosts, testes are paired, and each is suspended from the dorsal wall of the coelom by a mesentery, the **mesorchium.** The testes of vertebrates have two functions—sperm production and hormonal secretion. The hormones of the testes are steroids collectively called **androgens.** The principal androgen is **testosterone,** secreted primarily by the **interstitial cells** (Leydig cells) of the testes. Testosterone controls the development and maintenance of secondary sexual characteristics, elevates the sex impulse (or libido), and helps maintain the genital ducts and accessory sex organs. More will be said about the endocrine role of the testes in chapter 15.

During the breeding season, primordial germ cells in the testes begin the process termed **spermatogenesis,** whereby selected germ cells eventually become spermatozoa. Spermatogenesis (like oogenesis) involves both mitotic and meiotic divisions, as well as cytoplasmic reorganization (figure 14.30). In vertebrates, there are two general patterns of spermatogenesis, one in anamniotes and the other in amniotes.

Amniotes In reptiles, birds, and mammals, sperm form within the luminal wall of the seminiferous tubules, which lack subcompartments. Resident primordial germ cells, more commonly called **spermatogonia** at this stage, divide by mitosis. One member of the resulting pair of cells stays within the wall of the seminiferous tubule to propagate further spermatogonia, while the other grows in size. At the end of this growth, the diploid spermatogonium is called a **primary spermatocyte** and begins meiotic division. During meiosis, it briefly becomes a **secondary spermatocyte** and then a haploid **spermatid;** thereafter, it undergoes no further division. However, spermatids undergo cellular reorganization in which nuclear DNA condenses and excess cytoplasm and organelles are jettisoned to form sleek **spermatozoa,** or sperm.

For a time, **Sertoli cells** embrace and nutritionally support spermatids, perhaps promoting further maturation. Most sperm are stored in the lumina of the seminiferous tubules and in the connecting epididymis. At orgasm, sheets of smooth muscle in the walls of the ducts rhythmically contract, forcibly expelling sperm in the process of **ejaculation.** Sperm are transported in a thick, composite fluid secreted by accessory sex glands. In mammals, there are three such glands. The bulbourethral gland discharges mucus during erection and ejaculation. The prostate gland secretes an alkaline substance during ejaculation to protect the sperm from the acidity of any urine remaining in the male urethra. Finally, the seminal vesicle adds a thick secretion rich in the sugar fructose as a source of nutritional support for the sperm.

Anamniotes In fishes and amphibians, sperm are produced in clones, each located within a cyst or follicle, all of which are housed in separate tubular compartments within the testes (figure 14.31a,b). Generally, a spermatogonium is engulfed by one or several connective tissue cells, called (as in females) follicle cells, that become functional Sertoli cells as maturation proceeds. Proliferation of a spermatogonium within the follicle (Sertoli) cells produces a nested clone of many spermatogonia, sometimes called a spermatocyst. Cells within this **spermatocyst** undergo spermatogenesis in unison, eventually producing mature sperm.

Genital Ducts

Fishes In cyclostomes, the large unpaired testes are not served by any genital ducts. Sperm are shed into the coelom and exit via abdominal pores.

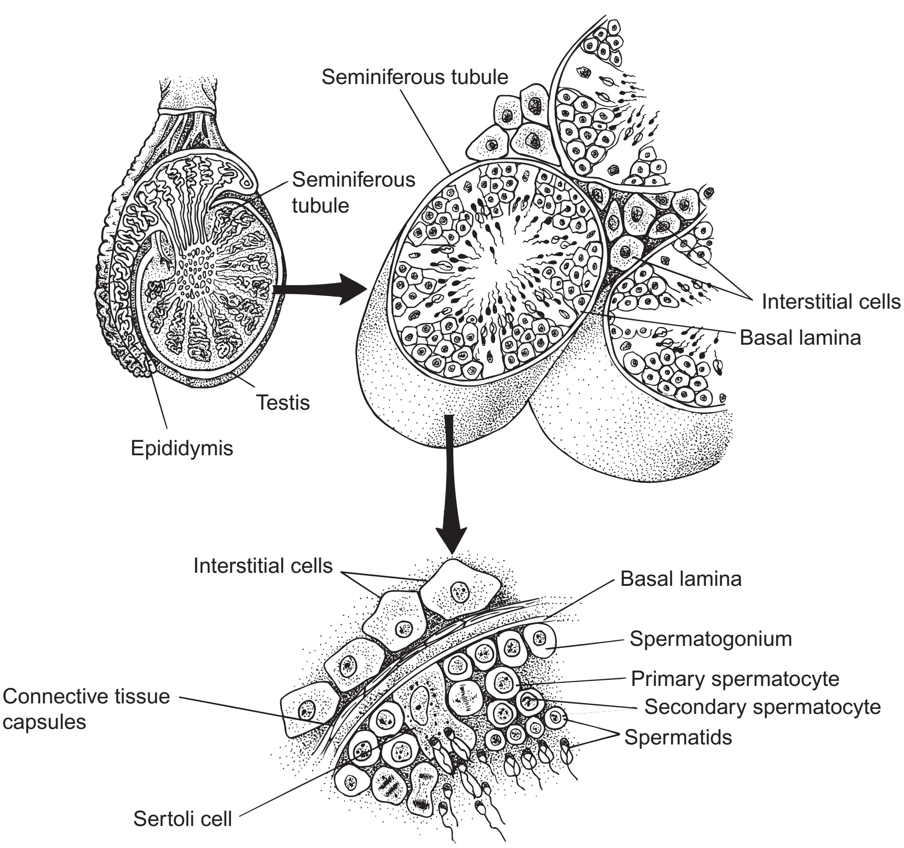


FIGURE 14.30
Spermatogenesis. Within the walls of the seminiferous tubules, spermatogonia divide, giving rise to cells that stay in place and preserve the population of spermatogonia as well as to cells that undergo meiotic and cytological reorganization. These become first primary and then secondary spermatocytes. Secondary spermatocytes undergo changes that transform them into spermatozoa. Sertoli cells hold spermatozoa and then release them into the lumen of the seminiferous tubules and connecting epididymis. Interstitial cells (cells of Leydig) lying between the seminiferous tubules secrete male hormones.

The archinephric ducts drain the kidneys exclusively (figure 14.32a). In elasmobranchs, the prominent Müllerian ducts of the female are rudimentary in the adult male (figure 14.32b). The **accessory urinary ducts,** distinct from the archinephric ducts, are usually present to service the posterior uriniferous kidney (figure 14.33a). Each anterior reproductive kidney has short tubules that join the testis to the archinephric duct, which because of its role in sperm storage and transport may be termed a vas deferens (figure 14.32b). These tubules within the anterior part of the kidney function as an epididymis, connecting the rete testis to the vas deferens and perhaps storing sperm. Adjacent Leydig cells in this cranial region secrete seminal fluid into the genital ducts.

In bony fishes, the archinephric ducts drain the kidneys and may receive sperm from the testes. However, the testes tend to develop separate sperm ducts and routes of exit (figure 14.33b,c). In most teleosts, this separate duct system forms a **testicular duct,** which is not homologous to the archinephric duct and may even establish its own opening to the exterior (figure 14.33d). Some teleosts, such as salmonids, lack sperm ducts entirely. Sperm are released into the body cavity and exit the body through pores near the posterior part of the coelom.

Tetrapods In male amphibians, several genital duct configurations can occur (figure 14.34a,b). In *Necturus* and a few other species, the archinephric ducts transport both sperm from the testes and urine from the uriniferous kidneys. However, this is likely a specialized condition of the paedomorphic *Necturus*. In general, this condition occurs only in larval salamanders. In some salamander families, new accessory urinary ducts service the caudal kidneys, and sperm are transported from the testes through tiny ducts in the cranial kidneys to the archinephric ducts (vas deferens) to be stored. In all frogs and a few species of salamanders, tiny ducts that reach directly from the testes to the archinephric ducts bypass the anterior part of the kidneys. Elimination from the uriniferous kidneys occurs exclusively via the accessory urinary ducts. Thus, in some adult amphibians, the archinephric ducts may have both reproductive and excretory roles, whereas in other species, these ducts may be involved exclusively in sperm transport and new accessory urinary ducts may drain the opisthonephros (figures 14.35a,b and 14.36a–c).

In male amniotes, the archinephric duct (vas deferens) transports sperm exclusively (figures 14.35c,d and 14.36c,d). Several mesonephric tubules of the embryonic kidney may contribute to the epididymis that connects each testis to a vas deferens (figure 14.37). Each amniote kidney is drained by a new duct, the ureter (metanephric duct).

In most vertebrate males, the testes reside within the abdomen; however, the testes of most mammals descend into the **scrotum,** a coelomic pouch suspended outside the body but connected to the abdominal coelom via an **inguinal**

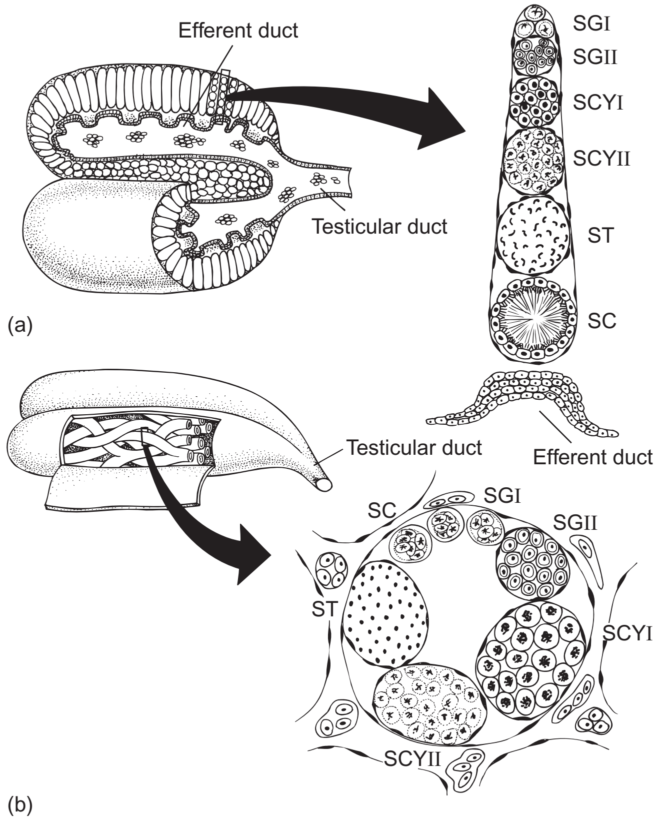
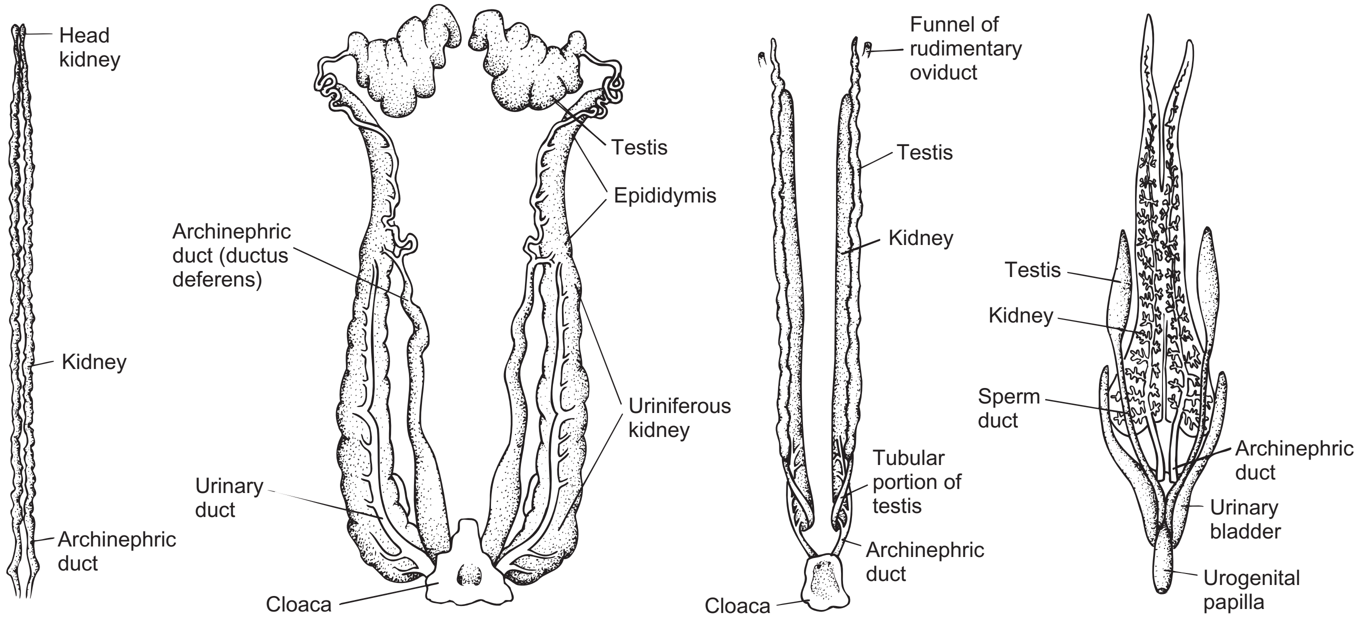


FIGURE 14.31 Sperm production in the teleost testis. Sperm may develop within compartments (a) or tubules (b). During copulation, mature sperm pass into the testicular duct. Primary spermatogonia (SGI) become, in succession, secondary spermatogonia (SGII), primary spermatocytes (SCYI), secondary spermatocytes (SCYII), and spermatids (ST). Sertoli cells (SC) form part of the epithelium lining the compartments or tubules.

After van Tienhover, based on van den Hurk, 1975.



(a) *Bdellostoma* (b) *Torpedo* (c) *Protopterus* (d) *Hippocampus*

FIGURE 14.32 Urogenital systems of male fishes. (a) Hagfish, *Bdellostoma.* The single testis of the hagfish hangs in the dorsal body wall between the kidneys. (b) Elasmobranch, *Torpedo.* (c) Lungfish, *Protopterus.* (d) Teleost, sea horse *Hippocampus*.

After Romer and Parsons.

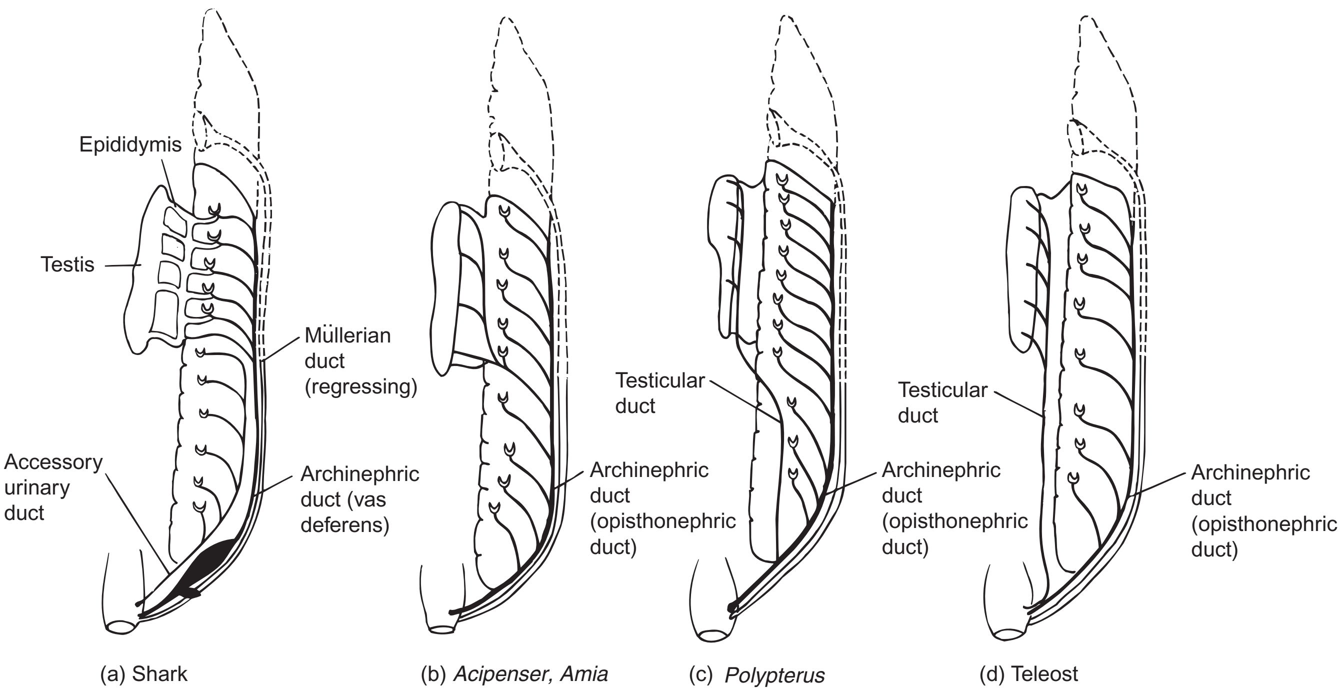


FIGURE 14.33 Urogenital ducts of male fishes. (a) Shark. (b) Sturgeon and bowfin. (c) Bichir. (d) Teleost. In sharks, an accessory urinary duct develops to drain the kidney, and the archinephric duct is concerned with sperm transport. In other groups, additional ducts that develop to drain the testis sometimes join the archinephric duct. In teleosts, these exit independently.

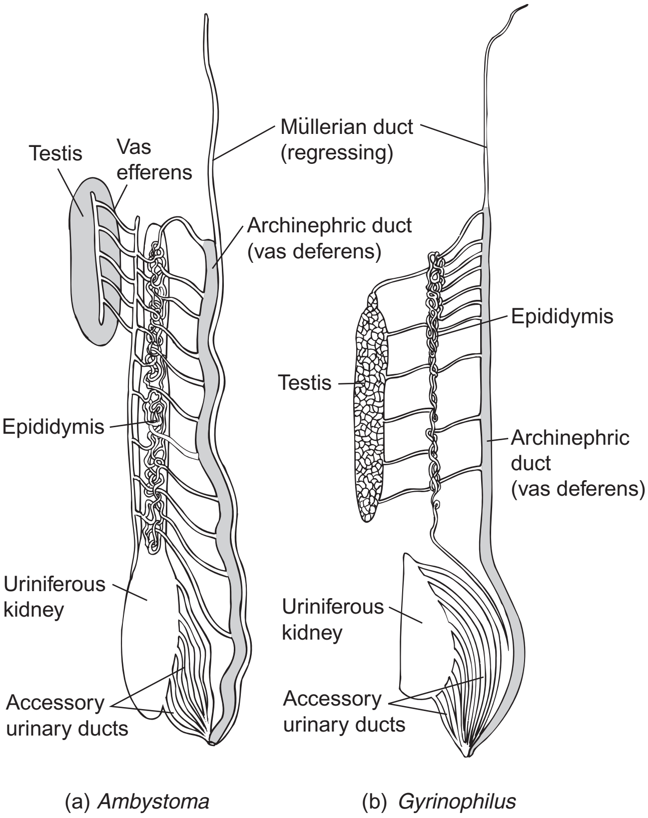


FIGURE 14.34 Urogenital systems of male amphibians. (a) Salamander, *Ambystoma*. (b) Salamander, *Gyrinophilus*.

(a) After Baker and Taylor; (b) after Strickland.

canal (figure 14.35d). In other mammals, the testes either remain in the body cavity (e.g., monotremes, some primitive insectivores, sirenians, elephants, sloths, cetaceans, armadillos) or descend into a muscular pouch but not a true coelomic scrotum (e.g., moles, shrews, many rodents, lagomorphs, pinnipeds, hyenas). Some mammals have testes that descend temporarily into the scrotum during the breeding season (e.g., chipmunks and squirrels, some bats, some primates). Absence of a scrotum in monotremes, as in sauropsids, means that testes are held internally within the abdominal cavity. This likely represents a primitive condition in monotremes. The presence of a scrotum in later therian mammals is a derived condition. Many marsupials have a scrotum, but it is prepenile, in front of the base of the penis. When present in eutherian mammals, it is postpenile. The functional significance of this difference is not known, nor is it known why some eutherian mammals lack a scrotum. However, absence of a scrotum in streamlined cetaceans is likely an adaptation to hydrodynamics. Although they are within their warm body cavity, the cetacean testes are cooled by special vascularization dedicated to the function. Most other eutherian mammals have testes that descend permanently, which typically occurs during embryonic development.

The testes migrate from the body cavity, through the abdominal wall via the inguinal canal, and into the scrotum where the temperature is cooler, often up to 8°C cooler than in the abdomen. The external cremaster muscles lift the testes closer to the body under cool conditions and allow them to descend under warm conditions, thus warming or

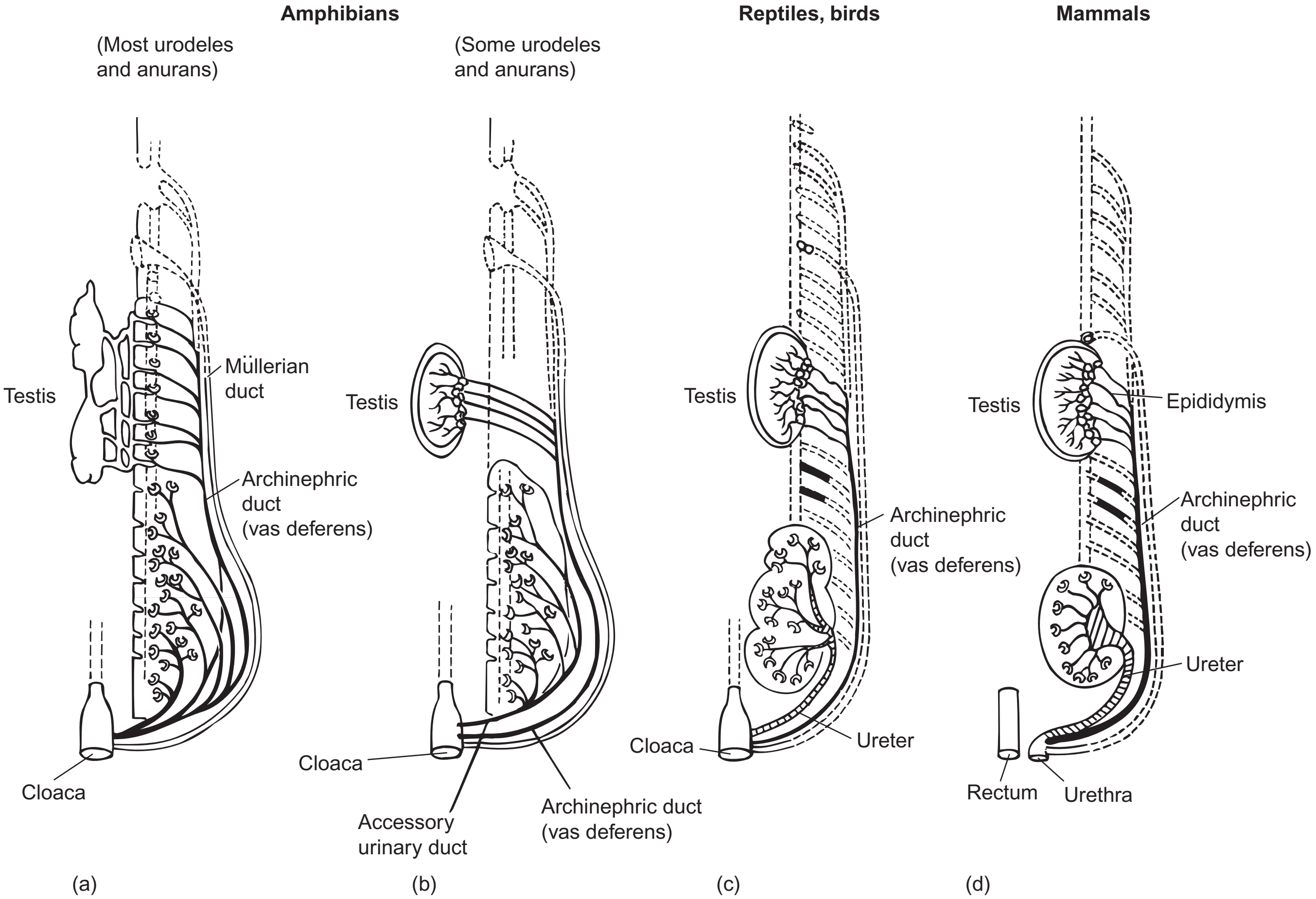


FIGURE 14.35 Urogenital ducts of tetrapod males. (a) Most urodeles and most anurans (adults). (b) Some urodeles and some anurans (adults). (c) Reptiles and birds. (d) Mammals.

cooling the testes as required. Further, arteries and veins entering and leaving the testes intermingle in a **pampiniform plexus,** a countercurrent exchange mechanism that serves as a heat block to the testes. If the testes fail to descend (a condition called **cryptorchidism**) or are artificially warmed in the scrotum, sperm production falls or even ceases in these species. Thus, the testes in mammals with scrotums seem to have lost the capacity to function at body temperature. However, why some mammals have evolved a scrotum and others have not is still not understood.

Copulatory Organs

In most water-dwelling vertebrates, fertilization is external. Eggs and sperm are shed simultaneously from the body into the water, where fertilization occurs. However, if the female uterus houses the embryo or if a shell seals an egg, sperm must fertilize the egg before it descends from the oviduct. In these instances, fertilization is internal. Sperm deposited within the female genital tract journey to the upper reaches of the oviduct to fertilize the egg. In many vertebrates, **copulation (coitus)** involves the direct, momentary apposition of the male and female cloacae to transfer sperm. Often, however, the male possesses external **intromittent organs** specialized to deliver sperm during coitus. In salamanders, sperm transfer is external and involves a **spermatophore,** but fertilization is internal.

In male sharks, rays, chimaeras, and some placoderms, the pelvic fins are specialized as **claspers** (figure 14.38a–c). During copulation, one clasper is inserted into the female cloaca and its terminal cartilages spread by muscle action to help hold the clasper in place. Sperm leave the male cloaca, enter a groove on the clasper, and are flushed by water squirted from siphon sacs within the body wall of the male into the female cloaca. In the killfish (*Fundulus*), a teleost, pelvic and anal fins interlock during spawning, holding male and female cloacae close together as gametes are released (figure 14.39a). In a few species of teleosts, the anal fin is fashioned into a grooved intromittent organ, termed a **gonopodium,** that deposits sperm into the female during copulation (figure 14.39b).

Fertilization in almost all frogs is external. The male grasps the female from above in a behavior called **amplexus** and releases sperm from his cloaca as eggs leave the female's cloaca. An exception among frogs is the tailed frog, *Ascaphus*.

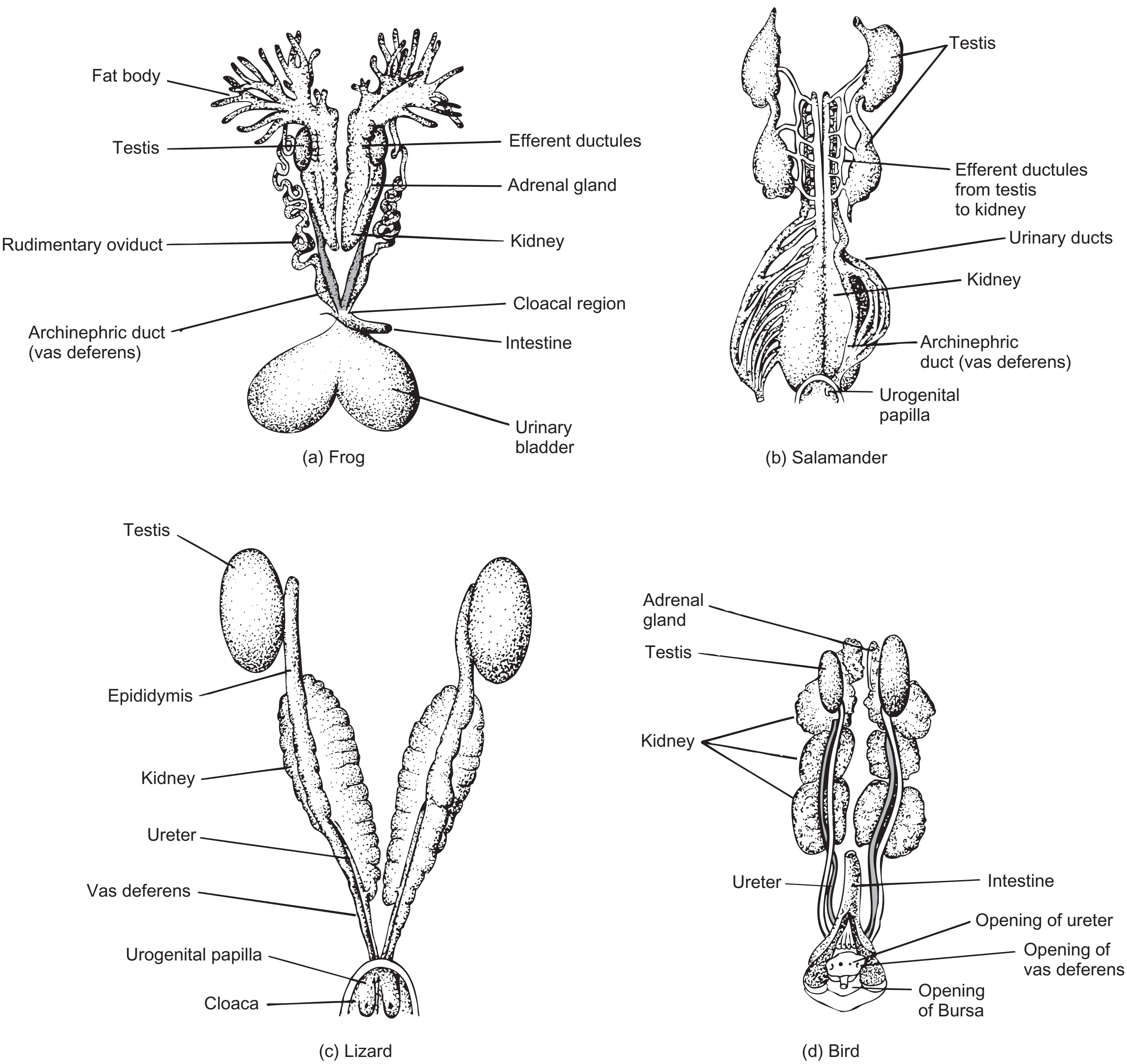


FIGURE 14.36 Urogenital systems of tetrapod males, ventral view. (a) Frog, *Rana.* (b) Salamander, *Salamandra.* (c) Lizard, *Varanus*. (d) Bird, *Columba.*

After Romer and Parsons.

The male possesses a short, grooved, tail-like extension of the cloaca used to transfer sperm directly into the cloaca of the female. The males of most salamander species produce a spermatophore, which consists of a cap of sperm on top of a gelatinous pedestal (figure 14.40a–c). The spermatophore is deposited in front of the female at the culmination of a stylized courtship. The female nips off the sperm cap with the lips of her cloaca to gather in the sperm (figure 14.41). Females of some species collect only a portion of each spermatophore sperm cap, but they sample from as many as 20 or 30 different spermatophores. Sperm are stored in a dorsal pocket of the cloaca, the **spermatheca,** until they are released to fertilize eggs internally as ova travel from the oviducts and out the cloaca. This method of reproduction decouples sperm transfer from fertilization. Thus, sperm transfer may occur at a time and place favorable to courtship but not to egg deposition. In caecilians, the male everts the posterior part of his cloaca through the vent and fits it into the female cloaca to aid sperm transfer.

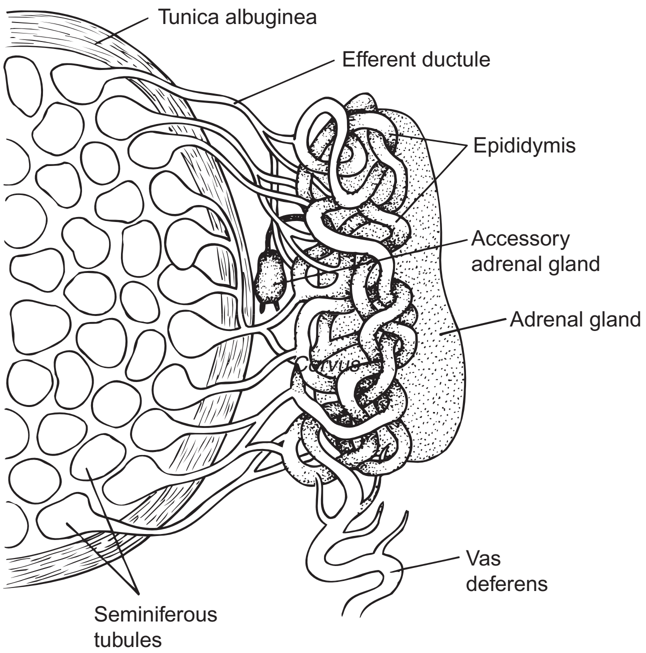


FIGURE 14.37 **Avian testis and epididymis in the jackdaw *Corvus*.**

After Lake.

Well-developed intromittent organs are absent in *Sphenodon*, although paired out-pouchings, supplied with thin strips of muscle, have been reported stationed at corners of the cloaca near the base of the tail. During courtship, the cloacae are pressed together and sperm are transferred directly. Some male birds and male turtles, crocodiles, and mammals have a single **penis,** an intromittent organ down the midline of the body (figure 14.42a–c). The evolutionary origin of the penis is unknown, but it seems to be a derivative of the cloaca. When not in use, the penis is usually flaccid and may be retracted into a sheath or returned to the cloacal chamber. It becomes engorged with blood or lymph that fills its specialized compartments and makes it erect. When the penis is erect, it penetrates the female and holds the channel open to ejaculate sperm. Erection achieved by blood infiltration is termed **hemotumescence.** In turtles, the midventral penis consists of two parallel bands of sinusoidal tissue, the **corpora cavernosa.** Between them lies a groove, the sulcus spermaticus (figure 14.42a,b). When engorged with blood, the corpora cavernosa enlarge, protrude the penis from the cloacal wall through the vent, and shape the sulcus spermaticus into a duct that receives and transfers sperm from each vas deferens. The females of some turtle species possess a homologue to the penis. Although this

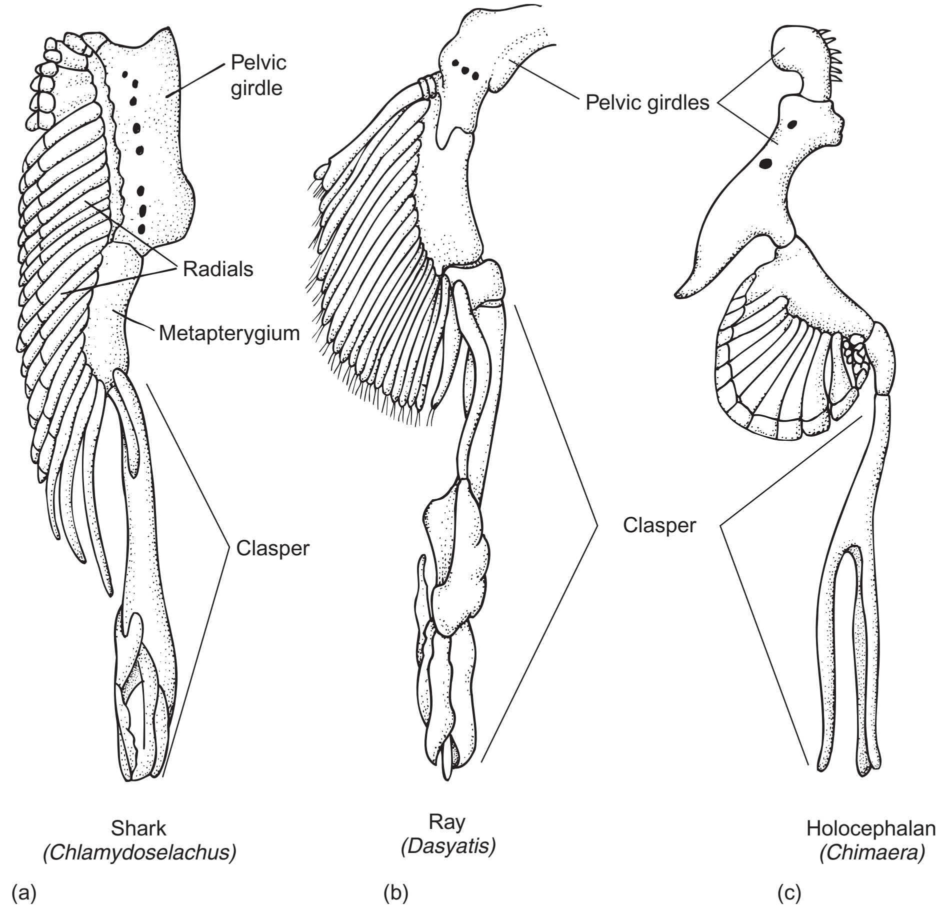


FIGURE 14.38 **Intromittent organs of chondrichthyans.** (a) Shark, *Chlamydoselachus*. (b) Ray, *Dasyatis*. (c) Holocephalan, *Chimaera*.

After van Tienhoven.

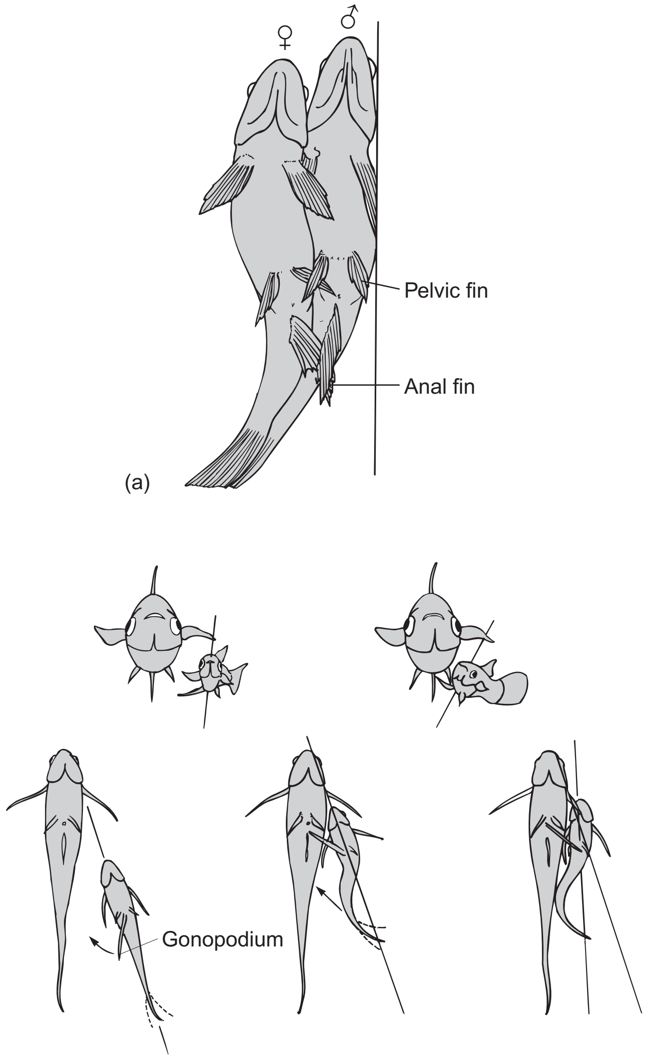


FIGURE 14.39 **Spawning in teleosts.** (a) Ventral view of interlocking anal and pelvic fins of *Fundulus*. (b) Gonopodium of male is inserted into anal region of female.

structure may be functionless, it possibly completes the other half of the male's sperm groove and therefore contributes to the sperm transfer channel.

The penis of male crocodilians is similar to that of turtles, except that it is relatively longer and the whole organ projects farther from the cloaca (figure 14.42c–e). Although the mechanism of erection is not clear, hemotumescence that defines a sulcus spermaticus seems to be involved. Female crocodilians also possess a rudimentary homologue of the male penis, but it remains within the cloaca and does not protrude.

In lizards and snakes, males possess a pair of intromittent organs, the **hemipenes.** Each hemipenis is usually grooved to allow for sperm transport. It is rough or spinous at its tip to ensure secure engagement when the male inserts it into the female's cloaca. A retractor muscle returns each hemipenis to the body by turning it outside in, a process called invagination. The retractor pulls it into a pocket located at the base of the tail, behind the vent. During erection, muscle action and hemotumescence force each hemipenis through the cloaca and balloon it out through the vent, turning it inside out—this is evagination (figure 14.43a,b). A sulcus spermaticus is defined in each hemipenis, which is sometimes Y shaped. During copulation, only one hemipenis is inserted in the cloaca of the female (figure 14.43c).

In birds, two types of intromittent organs are found. In the domestic turkey, little more than the edges of the cloaca swell during copulation (figure 14.44a). Male and female cloaca are pressed together at coitus. Semen flows between the lateral penile swellings of the male and is ejaculated into the female cloaca. Ostriches and some other groups have another intromittent organ. It is a true penis with an erectile shaft that the male inserts into the female cloaca. In the male ostrich, the erect penis is conical and widened at its base. It bears a sulcus spermaticus along its length (figure 14.44b). In ducks, the erect penis may be

BOX ESSAY 14.5 From da Vinci to Viagra

The Renaissance scientist, artist, and inventor Leonardo da Vinci (1452–1519) quietly dissected, at some risk of censure from religious voices, the bodies of the human deceased. This improved his art of human figures but also his understanding of biological function. Penises from men recently hung inspired his discovery of the basis of erection—the filling of blood sinuses produced erection. Perhaps from his own experiences, he observed that "the penis does not obey the order of its master, the penis erects freely while its master is asleep." In fact, episodes of nightly arousal also occur in women, usually during dreaming. Actually these arousals are presided over by central nervous system activity, but in complex ways. Excitatory nerves to the penis release chemicals that cause constricted arteries to the penis to relax, thus increasing blood flow to penis sinuses, which in turn fill and expand within, and the penis erects. Viagra works by slowing or preventing the breakdown of these natural relaxing chemicals; hence prolonging penile filling. As the penis fills, veins draining it are compressed, reducing emptying, and erection continues. An erection lasting over four hours is considered a medical emergency, because the turgid erection essentially deprives the penis of new blood carrying critical oxygen. Normally, after a man climaxes, other nerves limit blood flow, sinuses drain, and the penis becomes flaccid, and in cool weather experiences further "shrinkage," as the comedian Jerry Seinfeld made known to the world.

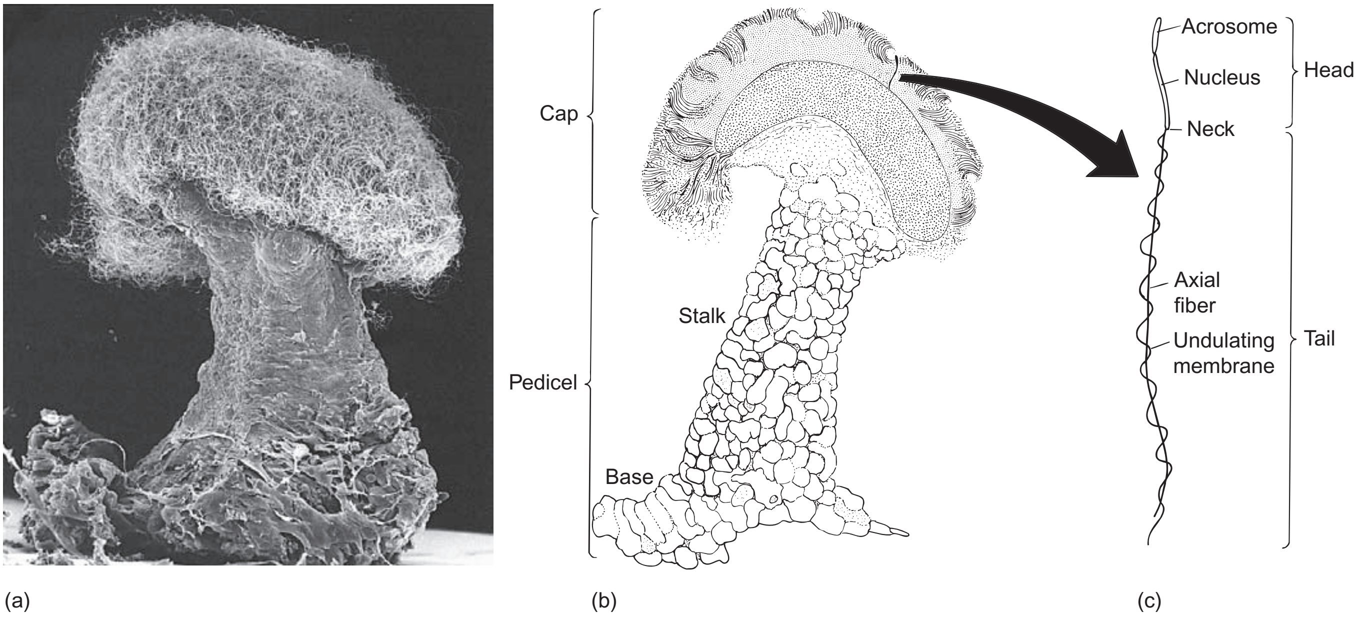
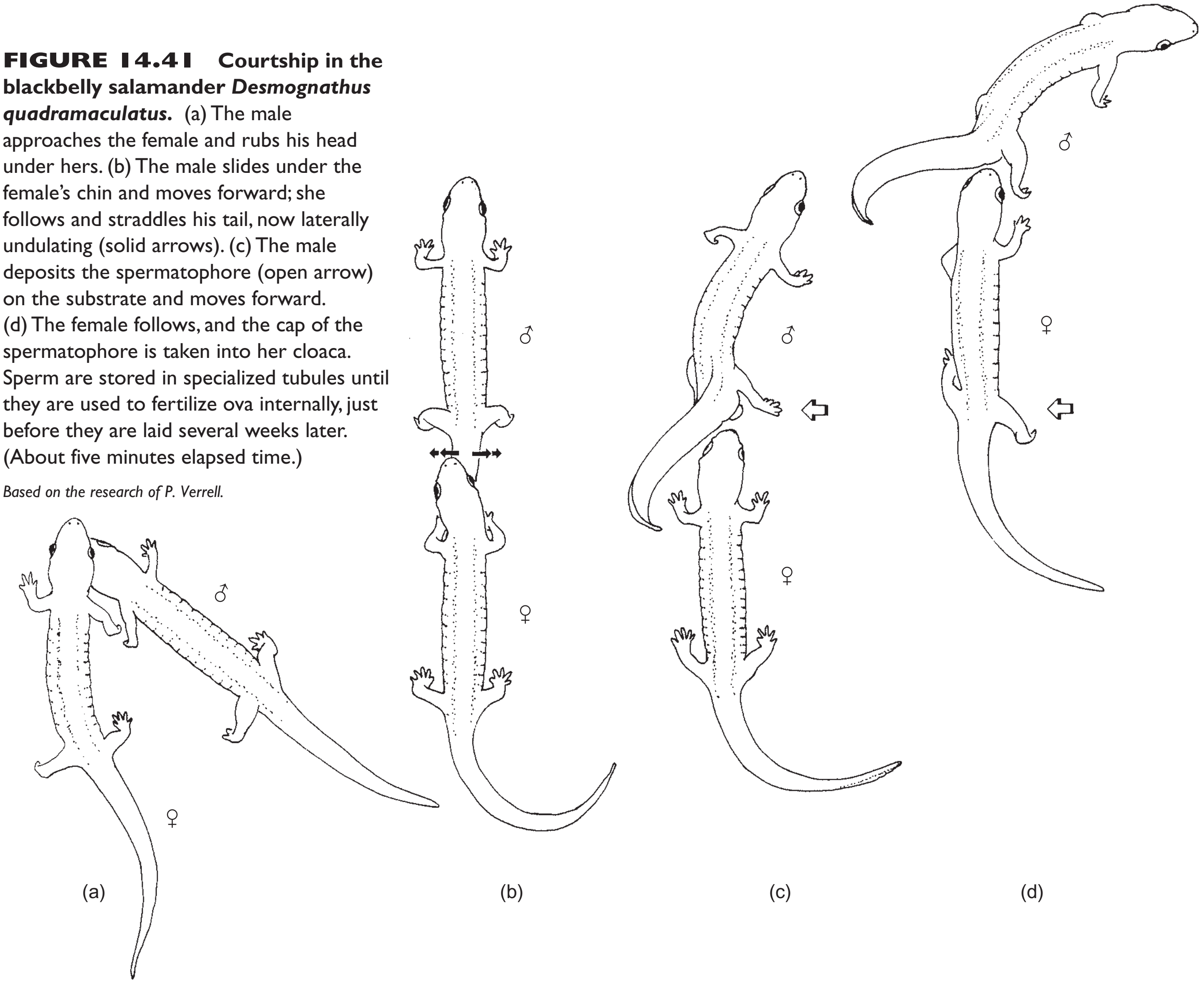


FIGURE 14.40 **Spermatophores of amphibians.** (a) Whole spermatophore deposited by male *Ambystoma macrodactylum.* (b) Longitudinal section of a spermatophore from *Ambystoma texanum.* Generally, sperm heads point outward, tails point inward. (c) An enlarged spermatozoon.

(a) Kindly supplied by E. Zalisko.

FIGURE 14.41 **Courtship in the blackbelly salamander *Desmognathus quadramaculatus.*** (a) The male approaches the female and rubs his head under hers. (b) The male slides under the female's chin and moves forward; she follows and straddles his tail, now laterally undulating (solid arrows). (c) The male deposits the spermatophore (open arrow) on the substrate and moves forward. (d) The female follows, and the cap of the spermatophore is taken into her cloaca. Sperm are stored in specialized tubules until they are used to fertilize ova internally, just before they are laid several weeks later. (About five minutes elapsed time.)

Based on the research of P. Verrell.



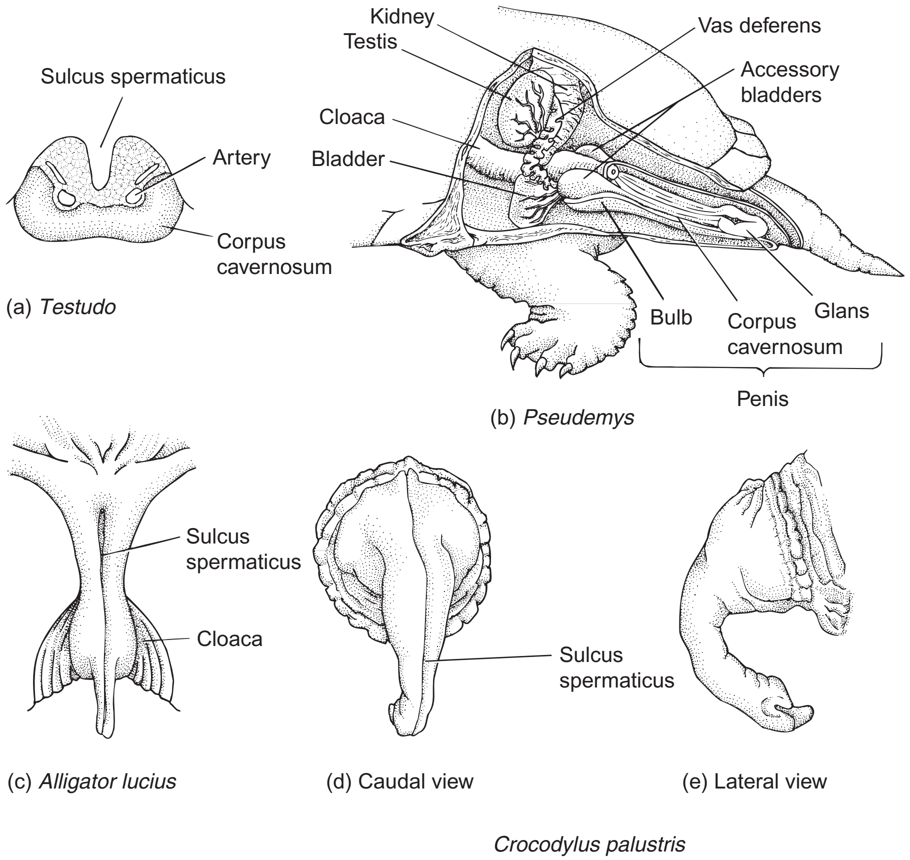


FIGURE 14.42 Penises of reptiles. (a) Turtle, *Testudo:* cross section of the penis within the cloaca. (b) Turtle, *Pseudemys:* sagittal section of the penis. (c) Alligator, *Alligator lucius* penis. Caudal (d) and lateral (e) views of the penis of the crocodile, *Crocodylus palustris*.

(a,c–e) After A. S. King; (b) after van Tienhoven.

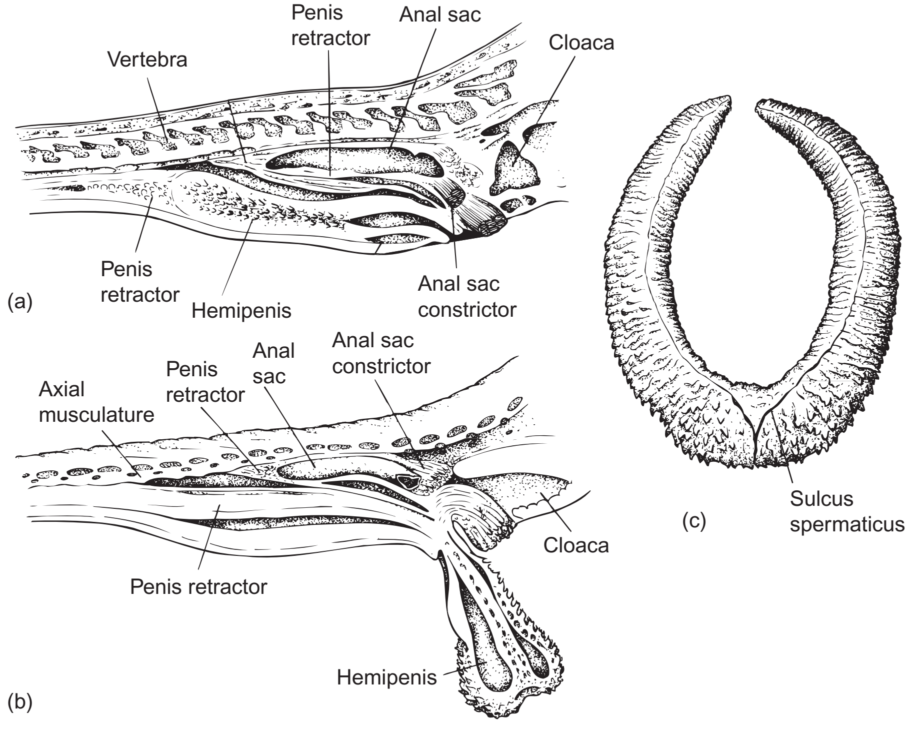


FIGURE 14.43 Hemipenis of a snake. Lizards and snakes have paired hemipenes, but usually only one is used during copulation. (a) The hemipenis is pulled back into the body by the retractor muscle (sagittal view). (b) When erect, the hemipenis's internal sinuses become engorged with blood, and it pops through the vent (sagittal view). During copulation, the male inserts its hemipenis into the cloaca of the female. Sperm travel down the sulcus spermaticus into the female. (c) One of the two hemipenes from the rattlesnake *Crotalus atrox* is shown everted. This single hemipenis is divided, which gives it a horseshoe shape. Note the divided sulcus spermaticus that runs along each arched branch of the hemipenis.

Modified from Dowling and Savage, 1960.

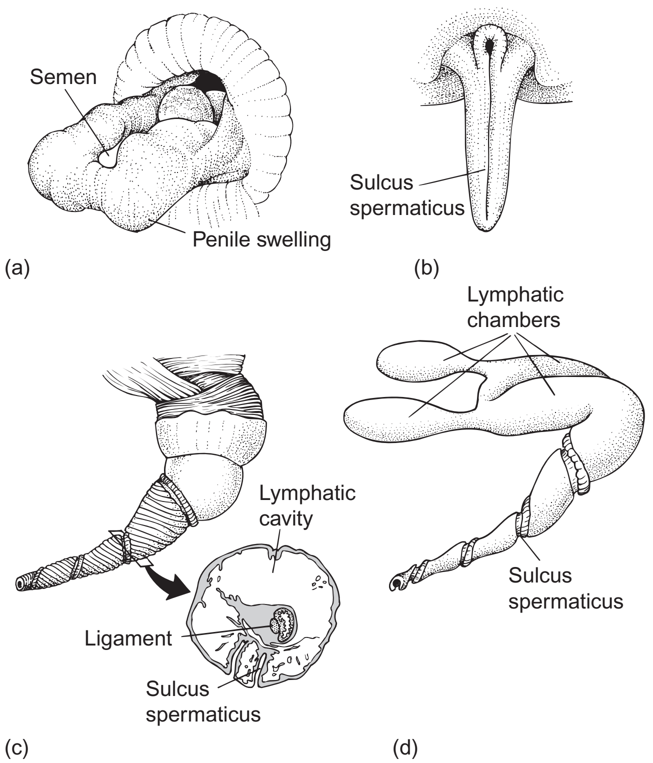


FIGURE 14.44 Intromittent organs of birds. (a) Domestic turkey with penile swellings. The margins of the cloaca form the central gully down which sperm flows during copulation. (b) Erect ostrich penis. (c) Erect duck penis with bird in standing position. Cross section shows lymphatic cavities thought to be responsible for eversion of the penis from the cloaca. (d) Diagrammatic lateral view of lymphatic chambers whose filling is thought to be responsible for penile erection.

After A. S. King.

quite elaborate, with the sulcus spermaticus spiraling along the tapering shaft. When relaxed, the penis is coiled and tucked within the cloaca along the ventral wall. Lymphatic channels within the penis connect to expanded chambers. The mechanism of erection is thought to involve filling of these internal chambers. As a result, the penis projects from the cloaca and bends forward (figure 14.44c,d).

All mammals copulate with a penis. In addition to the paired corpora cavernosa, a third sinusoidal tissue is present, the **corpus spongiosum** that surrounds the closed sulcus, or **cavernous urethra** (figure 14.45a). These spongy sinuses in the penis become engorged with blood and stiffen. In addition, insectivores, bats, rodents, carnivores, and most primates except humans have a **baculum** (os penis), a permanent bone located within the connective tissue of the penis to stiffen it. In these mammals, the already stiffened penis becomes engorged with blood into a fully erect position (figure 14.45b,c). The sensitive tip of the penis is the **glans penis.** The male penis is single in mammals, although in marsupials the tip is forked to fit into the two lateral vaginas of the female. As a result, ejaculated sperm move into each lateral vagina and then into the vaginal sinus, a chamber that receives both uteri (figure 14.51).

Cloaca

The cloaca has already been defined as a common chamber receiving products from kidneys, intestines, and often gonads. It opens to the outside through a cloacal opening or vent. (It is customary to point out that in Latin *cloaca* means "sewer.") The cloaca arises at some point during embryonic development in all vertebrates, but in many it becomes subdivided, lost, or incorporated into other adult structures (figure 14.46a–f). A well-developed cloaca occurs in adult sharks and lungfishes (figure 14.46b,d). But in teleosts, distinct urinary, anal, and genital openings are present, replacing the cloaca (figure 14.46f). Among tetrapods, a cloaca is present in amphibians, reptiles, birds, and monotremes. A shallow cloaca persists even in marsupials (figure 14.47a–k).

A cloaca is apparently a primitive vertebrate feature because it occurs in most primitive gnathostomes and persists in the embryos of almost all vertebrates. Its absence in chimaeras (Holocephali), ray-finned bony fishes (Actinopterygii), *Latimeria* (coelacanth), and most eutherian mammals may represent independent losses.

Embryologically, the cloaca arises from hindgut endoderm and proctodeal ectoderm. Structurally, three functions influence it: defecation, urination, and copulation. Each function tends to be associated with a compartment, and each compartment is controlled by muscles that regulate the entry and departure of products from the intestines, kidneys, and gonads. The most proximal compartment is the **coprodeum** into which the intestine empties. The **urodeum** receives products from urinary and genital ducts. The most distal compartment is the **proctodeum,** which functions in copulation and in many amniotes develops a penis (figure 14.47a). Many urogenital ducts, upon approach to the cloaca, inflate slightly to form an expanded **urogenital sinus.** These ducts often open into the cloaca via a small projection called the **urogenital papilla.**

Late in the nineteenth century, Hans Gadow suggested that each of the three cloacal compartments was separated from the other by folds in the mucosal wall: the **rectocoprodeal fold** between intestine and coprodeum, the **coprourodeal fold** between coprodeum and urodeum, and the **uroproctodeal fold** between urodeum and proctodeum. Although such folds occur in many vertebrates, they are low or absent in some, making it difficult to delineate boundaries between compartments of the cloaca. Gadow's terminology describing compartments and folds was based on tetrapods, but it is now applied to fishes as well. Unfortunately, there have not been any comparative studies of fishes in which a large sample of species was examined, so it is difficult to generalize about the presence or absence of these cloacal compartments within groups of fishes.

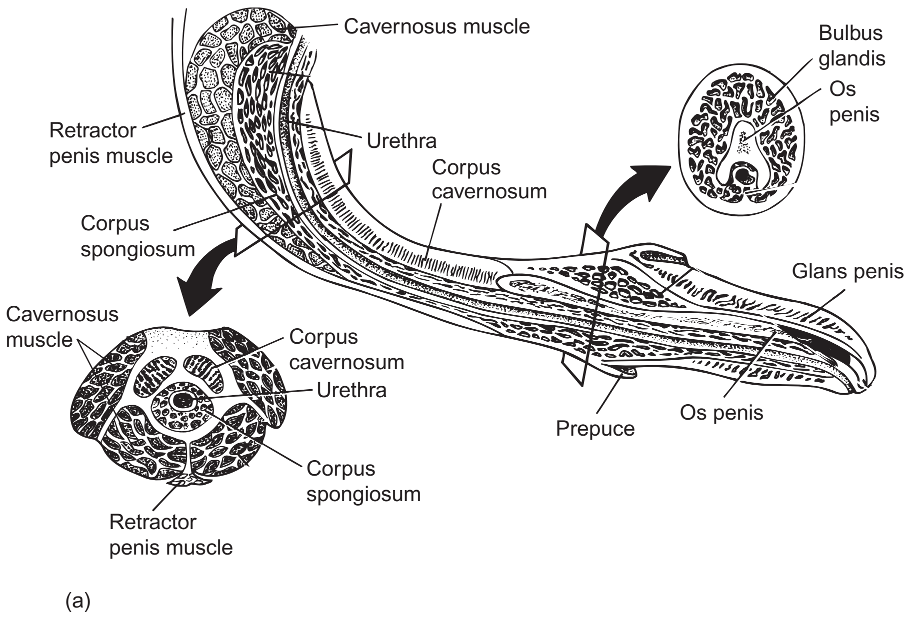
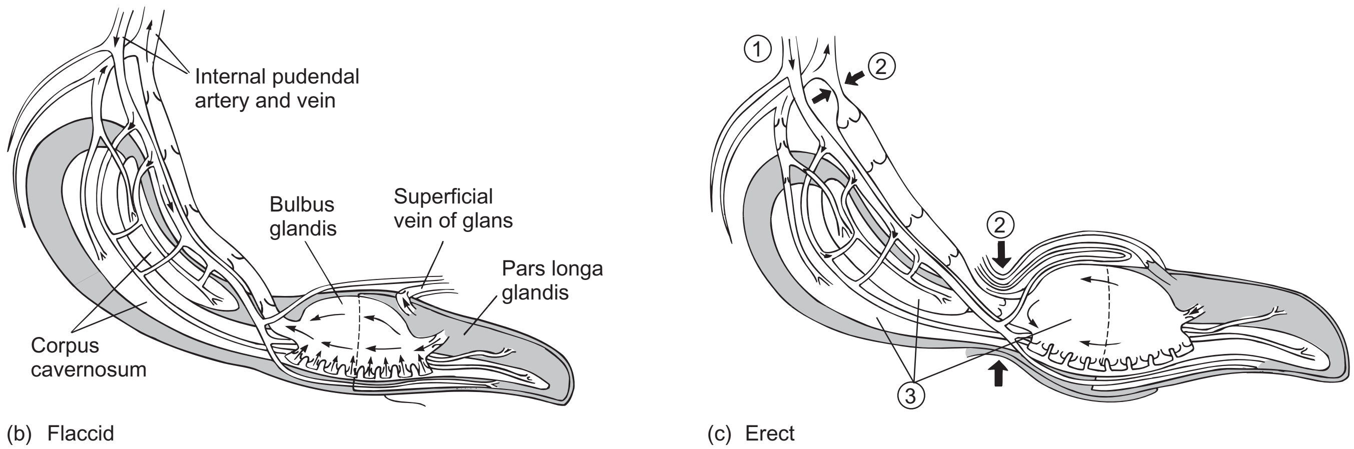


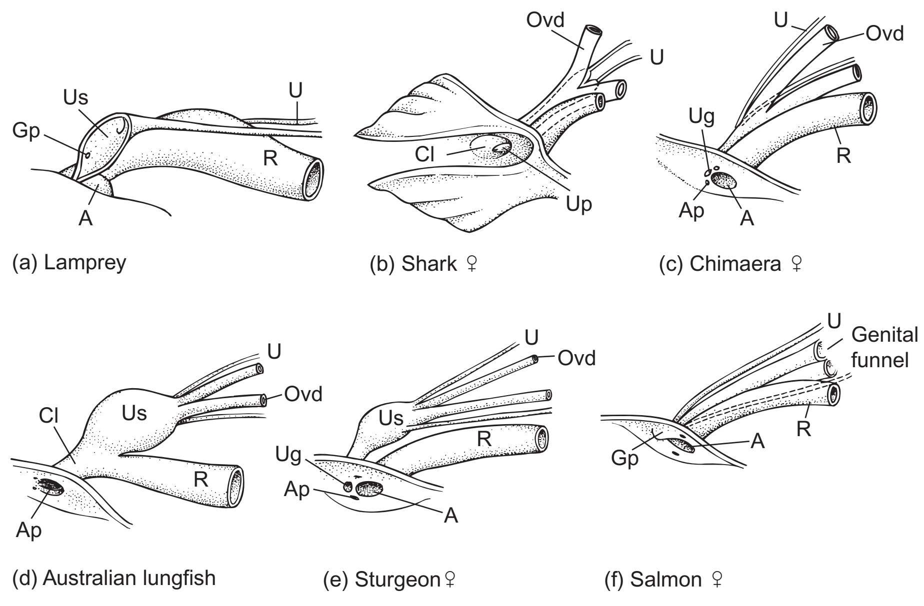
FIGURE 14.45 Penile erection in the dog. (a) Sagittal view and cross sections of the penis.
(b) Flaccid penis. Arterial blood enters the internal pudendal artery, circulates through capillaries of the penis, and flows from the penis through the pudendal vein.
(c) Erect penis. Stimulation of the nerves of erection causes increased blood flow to the penis (1). In addition, partial inhibition of venous drainage (solid arrows at 2) results in diversion of blood into the cavernous bodies (3) (corpus cavernosum and bulbus glandis), which fill, stiffen the penis, and result in erection. The os penis (baculum) also helps firm the penis.

After Miller, Christensen, and Evans.



(b) Flaccid

(c) Erect

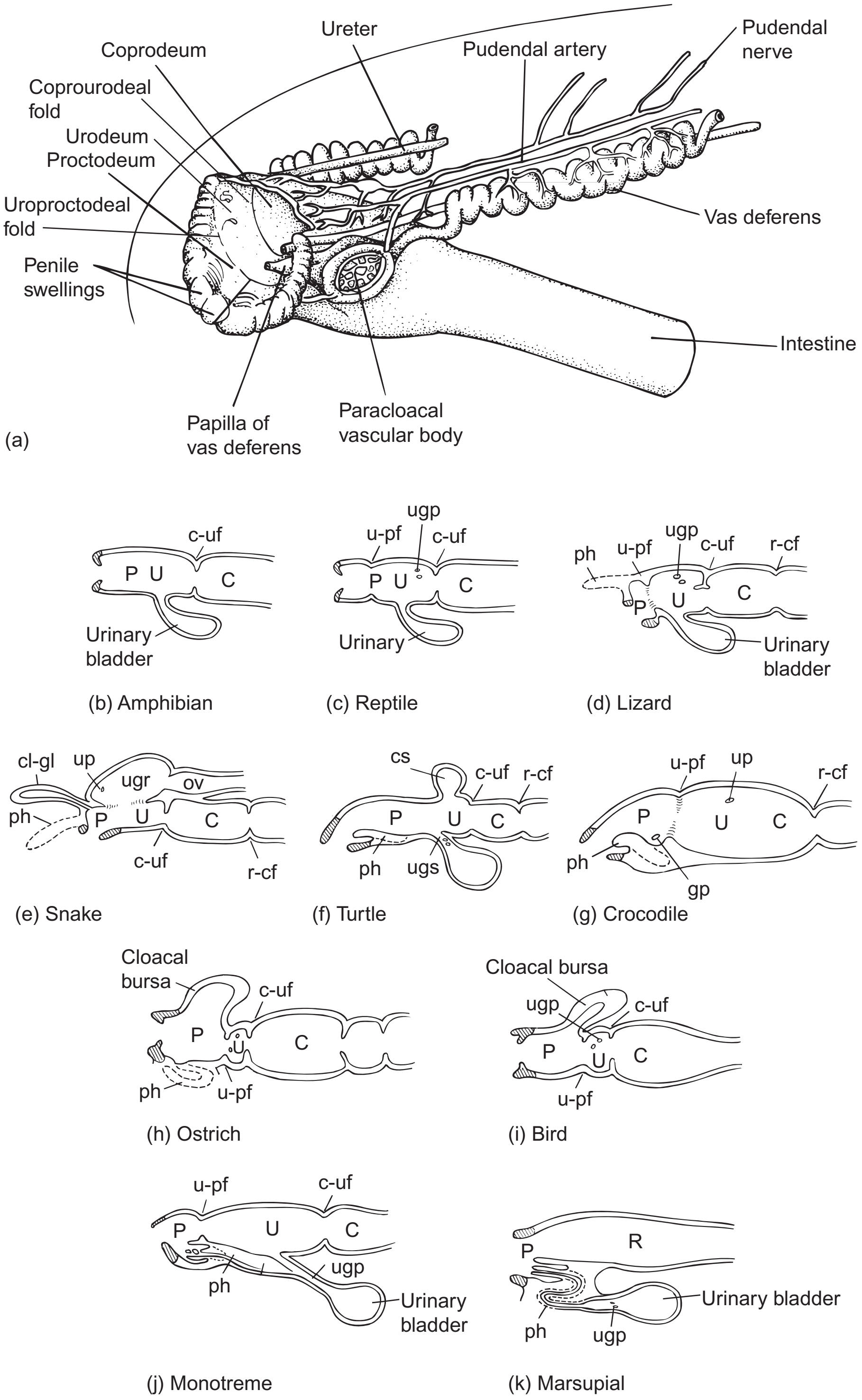


(a) Lamprey (b) Shark ♀ (c) Chimaera ♀

(d) Australian lungfish (e) Sturgeon♀ (f) Salmon ♀

FIGURE 14.46 Cloacal and anal regions of fishes. (a) Lamprey. (b) Female shark. (c) Female chimaera. (d) Australian lungfish. (e) Female sturgeon. (f) Female salmon. Structures of the urogenital system include the anus (A), abdominal pore (Ap), cloaca (Cl), genital pore (Gp), oviduct (Ovd), rectum (R), urinary ducts (U), urogenital opening (Ug), urogenital sinus (Us), and urinary papilla (Up).

After Romer and Parsons.



(b) Amphibian (c) Reptile (d) Lizard

(e) Snake (f) Turtle (g) Crocodile

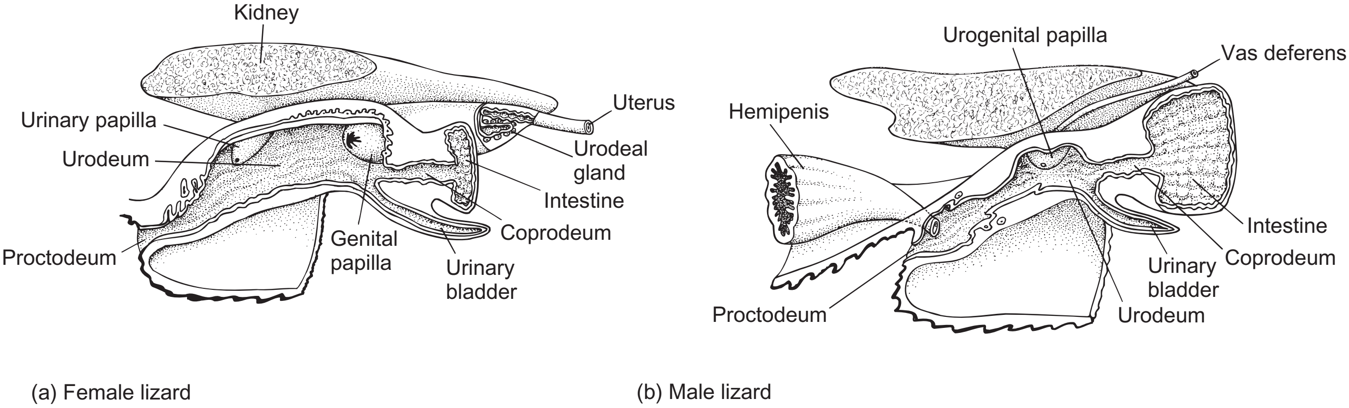
(h) Ostrich (i) Bird

(j) Monotreme (k) Marsupial

FIGURE 14.47 Diagrams of sagittal sections of tetrapod cloacae. (a) Bird cloaca with ducts and organs that open into each of the three chambers. (b) Amphibian. (c) Reptile, *Sphenodon.* (d) Lizard, *Lacerta.* (e) Snake, *Tropidonotus*. (f) Turtle, *Pseudemys*. (g) Crocodile. (h) Ostrich. (i) Bird. (j) Monotreme. (k) Marsupial. Parts of the cloacae include the coprodeum (C), proctodeum (P), rectum (R), and urodeum (U). Other abbreviations: coprourodeal fold (c-uf), cloacal gland (cl-gl), cloacal sac (cs), genital pore (gp), oviduct (ov), penis (ph), rectocoprodeal fold (r-cf), urinary pore (up), urogenital pores (ugp), uroproctodeal fold (u-pf), urogenital sinus (ugs), urogenital reservoir (ugr).

(a) After Lake; (d–k) after A. S. King.

The cloaca of most amphibians is simple. Folds usually delineate the coprodeum and urodeum, but in the absence of an intromittent organ or a uroproctodeal fold, the proctodeum is not anatomically demarcated from the rest of the cloaca (figure 14.47b). Among reptiles, the cloaca of *Sphenodon* is subdivided by folds into three compartments; the proctodeum is simplified and lacks a penis. The cloaca of snakes and lizards also has three compartments, but the proctodeum is usually reduced (figures 14.47c–e and 14.48a,b). The internal subdivision of the cloaca is much less distinct in turtles (figure 14.47f), and in crocodilians the coprodeum and urodeum and, to a lesser extent, the proctodeum are more or less united into a single large chamber (figure 14.47g). In birds, the cloacal folds are quite variable. The ostrich cloaca has a rectocoprodeal fold (figures 14.47h and 14.49a,b), but this is apparently lacking in other groups

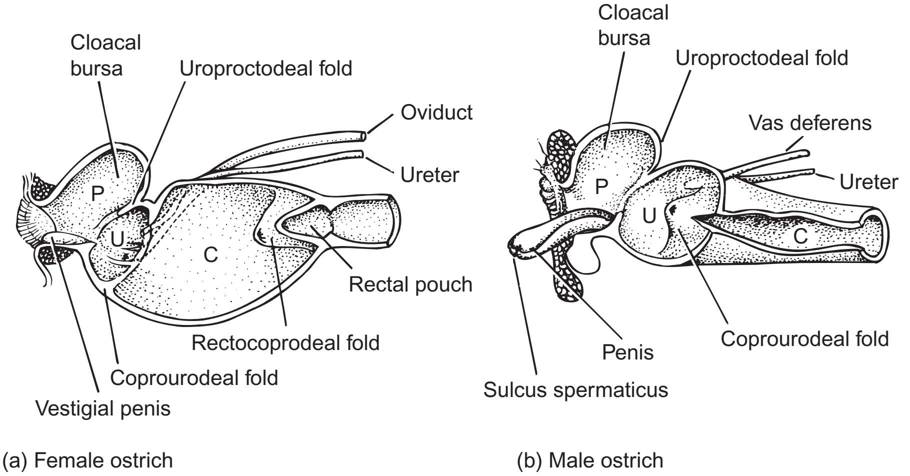


(a) Female lizard

(b) Male lizard

FIGURE 14.48 Cloaca of the lizard *Coleonyx*. (a) Female. (b) Male.

After Gabe and Saint-Girons.



(a) Female ostrich

(b) Male ostrich

FIGURE 14.49 Bird cloacae. (a) Female ostrich cloaca, longitudinal view. (b) Male ostrich cloaca. Chambers include coprodeum (C), proctodeum (P), urodeum (U).

After A. S. King.

(figure 14.47i). In birds, the proctodeum is associated with a **cloacal bursa** (bursa of Fabricius) that has an immune function.

The cloaca persists in monotremes, where distinct coprourodeal and uroproctodeal folds demarcate the urodeum from other compartments (figure 14.47j). The ureter and vas deferens open to a urogenital sinus, but urine flows directly into the urodeum, and semen flows through a sperm duct within the penis. Marsupials possess a reduced cloaca that is represented primarily by the proctodeum (figure 14.47k). The ectodermal part of the cloaca persists in some rodents and insectivores; however, in all other eutherian mammals, the cloaca divides in the sexually indifferent stage and forms separate orifices from the coprodeum and urodeum (figure 14.50a–c). Generally, the coprodeum becomes the rectal region of the digestive tract with an anal opening. The urodeum yields separate structures, depending on the sex. In the male, the urogenital sinus becomes the urethra that transports sperm and urinary products (figure 14.50d). In most eutherian mammals, the female urethra remains conjoined with the vagina to form a urogenital sinus. In others, the urogenital sinus divides again to produce a urethral opening for the urinary system and a vaginal opening for the reproductive system (figure 14.50c).

Two patterns are evident in the reproductive organs of marsupial females. In opossums, the oviducts enter a vaginal sinus that loops symmetrically around the viscera to form lateral vaginas (figure 14.51a). In kangaroos, the vaginal sinus, via an unpaired central vaginal canal, joins the lateral vaginal loops in the common urogenital sinus (figure 14.51b). In therian females, one end of each oviduct narrows into a slender fallopian tube, which receives the egg released from the ovary. At the other end, the oviducts expand into the uterus to support the young during their embryonic development. In some eutherian species, the oviducts join the vagina separately, forming a **duplex uterus.** In **bipartite** and **bicornuate uteri,** the uteri partially fuse. If the uteri fuse entirely, a **simplex uterus** is formed (figure 14.52).

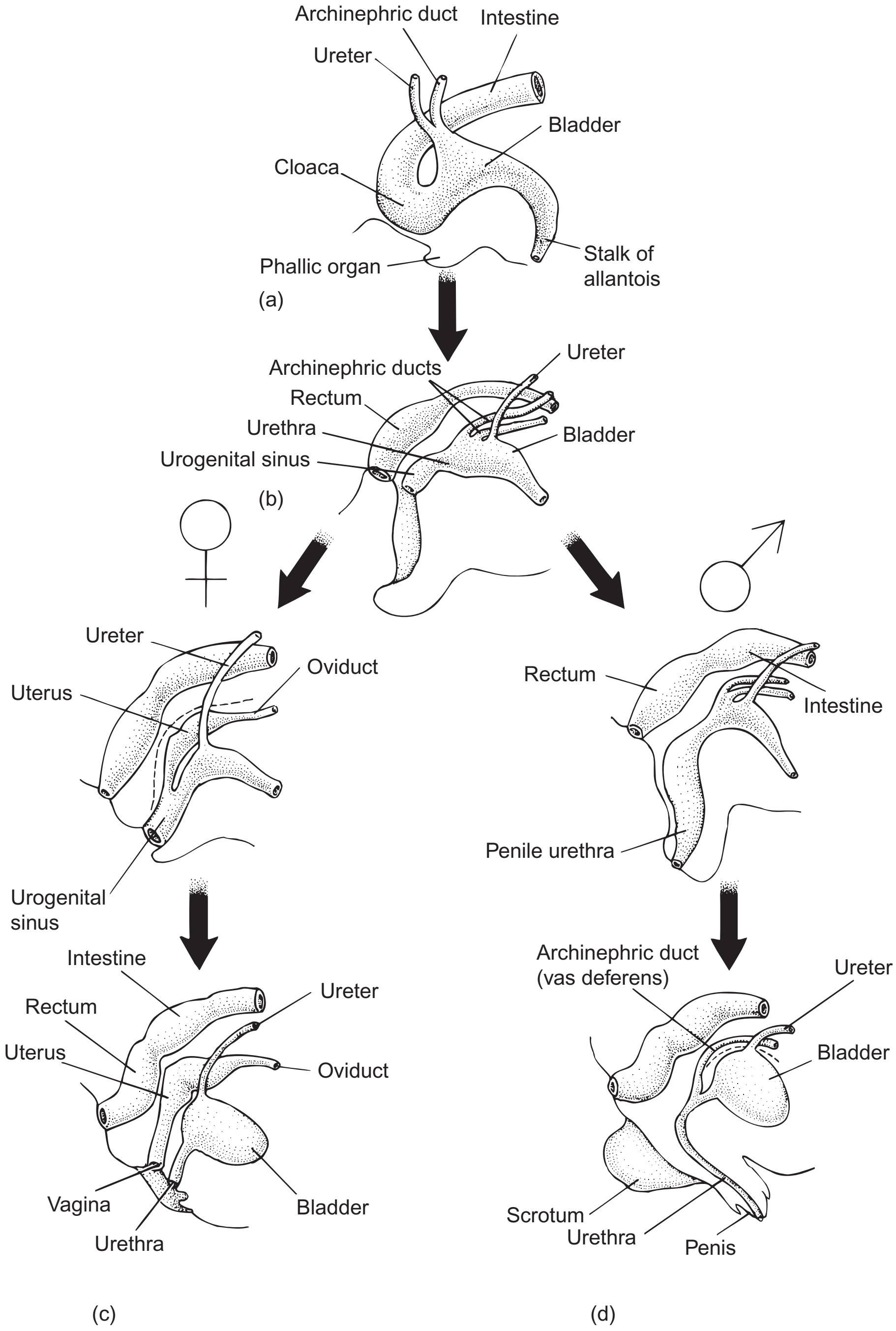


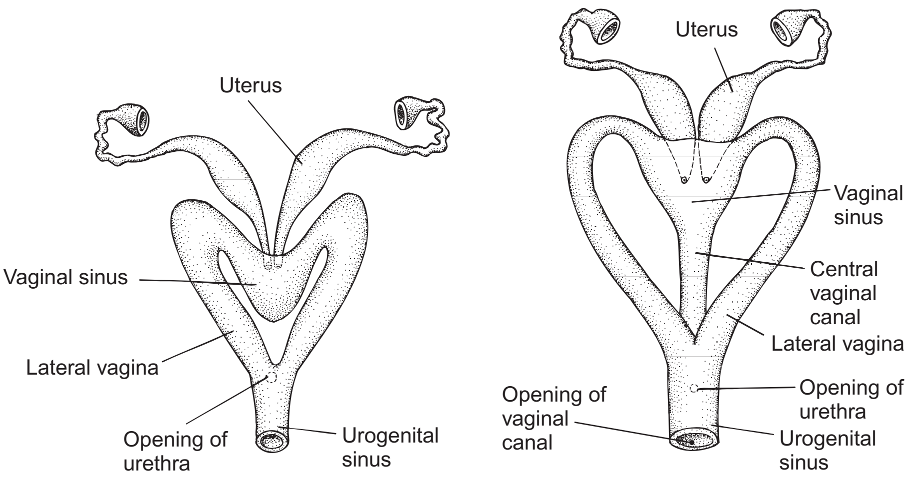
FIGURE 14.50 Embryonic derivatives of the urogenital sinus in some eutherian mammals. (a) In the indifferent stage, the cloaca is undivided. (b) The first step toward differentiation is separation of the urogenital sinus from the rectum. (c) In the female, the urogenital sinus divides to form the urethra and the vagina, both with separate external openings. (d) In the male, the urogenital sinus becomes the urethra of the penis and transports both sperm and urine.

Urinary Bladder

Before being excreted, urine is usually stored in specialized regions of the urogenital system. In this way, the vertebrate can void urine at opportune times rather than continuously as it is formed. If water conservation is important, the bladder sequesters the concentrated urine so that it does not create osmotic pressure that draws water out of the tissues of the animal.

In fishes, urine is usually stored within the ends of the urinary ducts where they join the cloaca or open to the outside. A urinary bladder of this type is mesodermal and noncloacal in origin. It is found among elasmobranchs, holocephalians, and most teleost fishes (figure 14.53a).

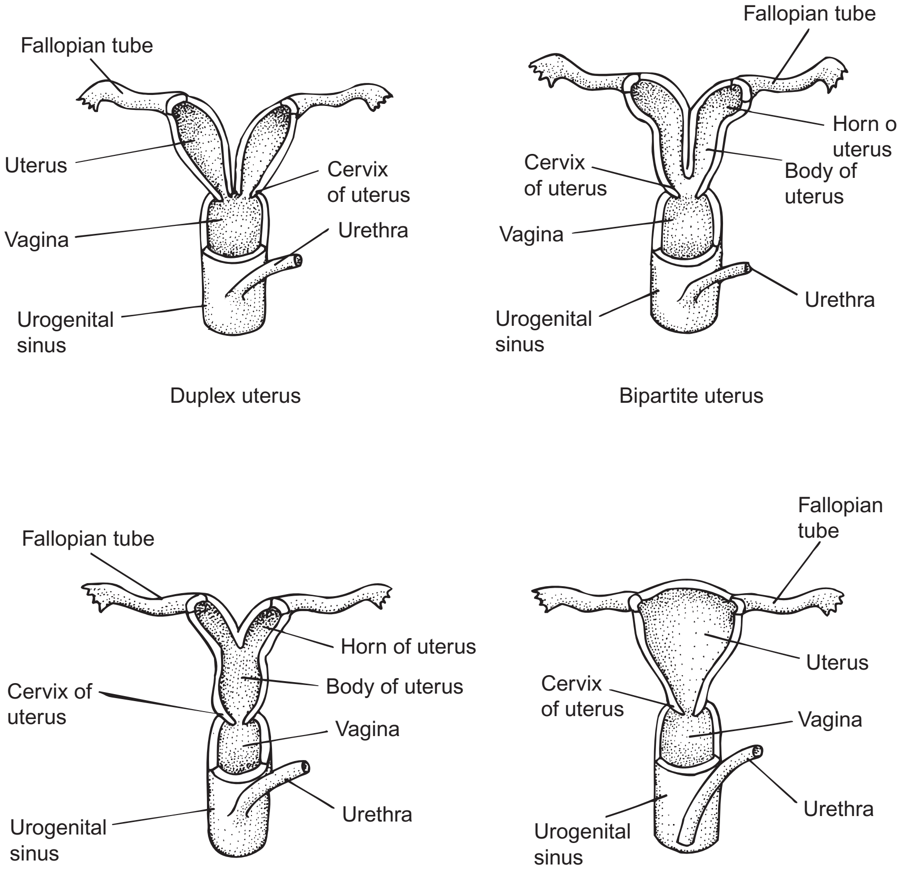
In tetrapods, the urinary bladder arises as an outpocketing of the cloaca. Urine flowing from the urinary ducts usually empties into the cloaca first and then fills



(a) Opossum

(b) Kangaroo

FIGURE 14.51 Reproductive organs of female marsupials. (a) Opossum. (b) Kangaroo.



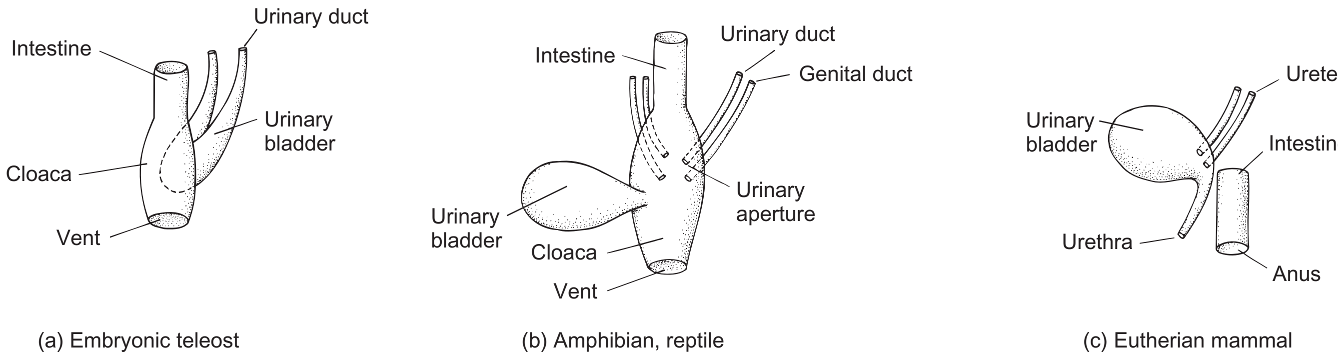
Duplex uterus

Bipartite uterus

Bicornuate uterus

Simplex uterus

FIGURE 14.52 Reproductive organs of female eutherian mammals. The uterus is characterized by the degree of fusion of the paired uteri.



(a) Embryonic teleost (b) Amphibian, reptile (c) Eutherian mammal

FIGURE 14.53 Evolution of the urinary bladder. (a) In teleosts, the intestine and urinary ducts establish separate exits, anus and urinary pores, respectively. As a consequence, the embryonic cloaca is lost in the adult. The teleost urinary bladder, when present, is formed from the expanded ends of the urinary ducts. (b,c) In tetrapods, the urinary bladder is an outgrowth of the cloaca. It empties into the cloaca in amphibians and reptiles (b) but exits via the urethra in mammals (c).

After M. Wake.

the baglike urinary bladder (figure 14.53b). In therian mammals, the urinary ducts (ureters) empty directly into the urinary bladder (figure 14.53c). The tetrapod urinary bladder appears first among amphibians and is present in *Sphenodon,* turtles, most lizards, ostriches among birds, and all mammals. The urinary bladder has been lost in snakes, some lizards, crocodilians, and all birds except the ostrich.

Function and Evolution

In most vertebrates, reproduction is seasonal. Courtship and copulation are usually restricted to a brief annual breeding season. During the breeding season, hormone-readied genital ducts receive and transport released eggs and sperm. Onset of reproductive readiness is called **recrudescence.** Only among humans is breeding a year-round affair.

Potency and Fertility

Fertility refers to the ability of the female to produce fertilizable eggs or of the male to produce sperm in sufficient numbers to achieve fertilization. A male producing insufficient numbers of sperm is **infertile** or **sterile.** In a human male, ejaculated semen can contain 200 million sperm. And although it just takes one sperm to fertilize an egg, a drop in the sperm count to 50 million may result in sterility. Although millions of sperm may be ejaculated into the vagina, the number of sperm that eventually survive the journey to the upper reaches of the oviduct rarely exceeds a few hundred. Considering that the spermatozoon is small in comparison to the volume of the oviduct, it is not surprising that only a very modest number of sperm arrive at the site of fertilization. Finally, many sperm interact to break through follicle cells or surface mucus clinging to the egg so that one sperm can penetrate the egg cell membrane. Thus, fertilization is performed by the fusion of a single spermatozoon with a single egg, but this comes after much attrition and cooperation among many sperm to promote penetration of the egg.

Potency refers to the ability of the male to engage in copulation. **Impotence** results from the failure to achieve an erection. Impotence is different from sterility. Castrated males are sterile because they lack testes and produce no sperm. However, if the testes are removed after puberty, there has often been enough time for androgens to masculinize the individual so that some secondary sexual characteristics, sex drive, and ability to engage in sexual intercourse (potency) are retained.

Spermatogenesis is under hormonal control. In a seasonal breeder, sperm are produced only certain times of the year. **Follicle-stimulating hormone (FSH),** a pituitary gonadotropic hormone, stimulates the multiplication of spermatogonia in the seminiferous tubules as the breeding season approaches. With advancing age, there may be a slow decline in the ability of the seminiferous tubules to produce mature sperm, but there is no abrupt cessation comparable to the female **menopause** that occurs in some mammals.

External and Internal Fertilization

External fertilization is common among invertebrates and primitive vertebrates. Eggs and sperm meet outside the body. However, many vertebrates live in environments in which external fertilization is disadvantageous. The tailed frog *Ascaphus,* for instance, lives and mates in fast-moving streams where swift currents might wash away eggs and sperm released into the environment. Internal fertilization via an intromittent organ increases the success of sperm transfer under these conditions.

But internal fertilization offers a further adaptive advantage. The events of courtship and fertilization can be separated from the events of egg deposition. Fertilization does not always occur in an environment that is also suitable for egg deposition. For example, some salamanders mate on land where courtship displays are visible, but dry land offers few favorable sites for the development of salamander eggs. In most salamanders, a spermatophore is taken up by the female during courtship, but eggs are not released at that time. Instead, the sperm are held in the spermatheca until she has found a suitable location for deposition. The eggs are fertilized as they are laid (figure 14.54a–c).

Physiological constraints can restrict the evolution of viviparity in some groups. Among amniotes, calcium for ossification of the embryonic skeleton can be stored in the yolk (e.g., squamates) or in the eggshell (e.g., turtles, crocodiles, and birds). In viviparity, the calcareous eggshell is lost, allowing for efficient exchange between fetal and maternal tissues. However, the shell's calcium reservoirs are lost as well. This may help explain why viviparity is absent among turtles, crocodiles, and birds, groups in which the eggshell is used for calcium storage. Viviparity is common among lizards and snakes that do not use the shell as a calcium reservoir.

In both oviparity and viviparity, the young are carried internally, extending the time between courtship and birth or egg deposition and giving the female a chance to seek safe sites for young to be born or hatch. In vertebrates that regulate their temperature internally or behaviorally, the females retain their embryos, allowing them to develop at a stable temperature. If an ectothermic reptile deposits her eggs under a rock, the eggs will be subjected to environmental fluctuation in temperature. But if she retains them in her body, she can shuttle between sites and on cool days bask in whatever warmth is available to elevate the temperature of the developing embryos within her body.

Delays in Gestation

Gestation lasts from conception to hatching or birth. It includes fertilization, implantation (in some species), and development. In some species of mammals, the onset of each stage may be prolonged or delayed. For example, **delayed fertilization** occurs in some bats. Copulation occurs in autumn just before hibernation, but females do not ovulate at that time. Instead, sperm are stored either in the uterus or the upper vagina. When bats emerge from hibernation several months later, eggs are released, sperm become active, and fertilization finally occurs. Young are born in early summer, a season that is usually characterized by an abundance of insects for food.

In **delayed implantation,** known only in mammals, fertilization and early development occur, but the embryo fails to implant in the uterus. Development is arrested for an extended period, until implantation finally occurs and gestation resumes. Delayed implantation occurs in many members of the weasel family (Mustelidae), bears (Ursidae), and a few other groups (figure 14.55). In most cases, delayed implantation is tied to the annual seasonal cycle. In some marsupials, such as kangaroos and wallabies, however, delayed implantation of the **blastocyst** is tied to the presence of a young kangaroo in the pouch, termed a joey. Suckling by an older joey in the pouch inhibits implantation of the next blastocyst, a type of delay referred to as **embryonic diapause.** In **delayed development,** known from several species of bats, fertilization and implantation occur on schedule, but subsequent growth of the embryo is slow.

Delay in fertilization, implantation, or development increases the time between mating and birth to ensure that young will not be born at an inopportune time (e.g., during migration) or when food is scarce (as in the middle of winter). Female caribou give birth immediately after their migration from winter forests to summer tundra. Many species of whales give birth after they migrate from polar seas and arrive in temperate or tropical oceans. Seals give birth when they reach their breeding beaches after an extended migration at sea.

Overview

The urinary and genital systems arise as neighbors from adjacent regions within the embryo and share some of the same ducts in the adult. Functionally, however, the two systems are quite distinct. The urinary system includes the kidneys and the ducts that carry away urine, a watery waste product. But urine is a by-product of the urinary system's primary function, the internal regulation of body fluid composition. Other organs may also participate—the skin, gills or lungs, alimentary canal, liver—but the kidneys are specialized for controlled maintenance of the internal fluid levels of water and solutes, osmoregulation, and for elimination of the waste products of metabolism, excretion. The functional unit of the kidney, the uriniferous tubule, collects in the renal capsule an ultrafiltrate of blood plasma diffusing in from the vascular glomerulus under favorable osmotic and hemodynamic pressures. As the ultrafiltrate moves along the tubule, regions of the tubule add and subtract fluid and solutes, eventually producing urine.

Organisms live in environments that may dehydrate them, critically lowering internal fluid levels, or in environments that result in an influx of fluid following an osmotic gradient, swelling tissues with excess fluid. By controlling the water composition of the ultrafiltrate, fluid may be recovered (producing a concentrated urine) or added (producing a dilute urine) to compensate for environmental stress upon internal fluid and solute balance. One end product of metabolism is nitrogen, usually in the form of ammonia, which can be toxic. Its elimination may be direct, usually via skin or gills (ammonotelism), or indirect, via the kidneys by first converting ammonia to uric acid and then eliminating (uricotelism) or to urea and then eliminating (ureotelism).

The genital system includes the gonads and the ducts that carry away their products, eggs and sperm. Therefore, the genital system is most directly involved in implementing successful reproduction, its primary biological role. Besides

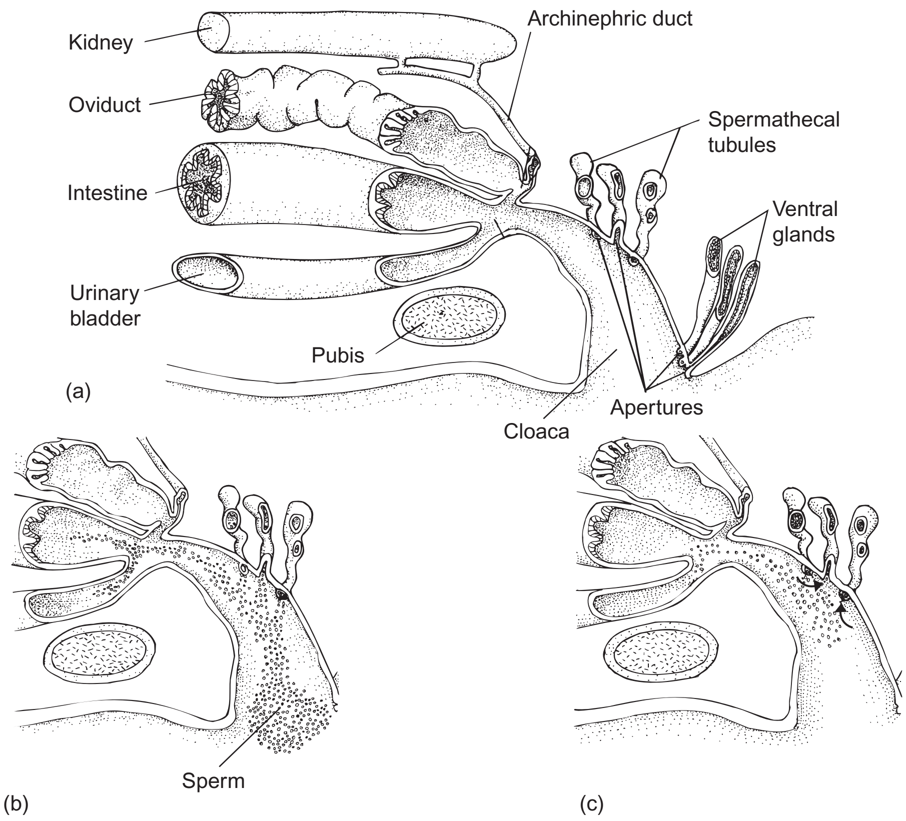
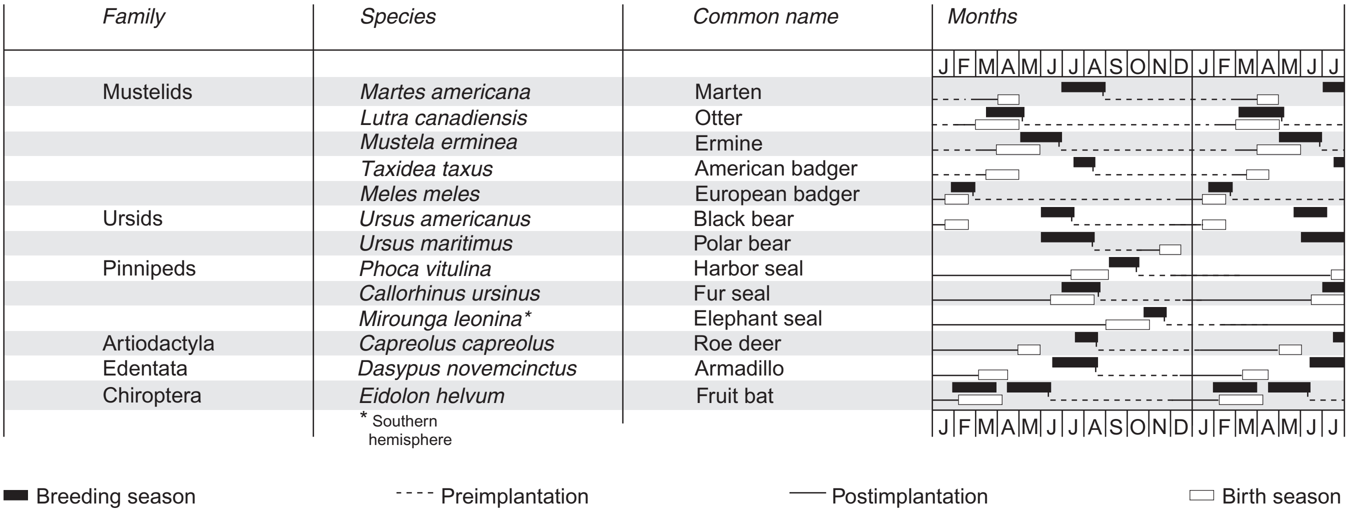


FIGURE 14.54 Sperm storage within the spermatheca of the salamander *Notophthalmus*. (a) Diagram of the urogenital system. A few hours after sperm enter the cloaca (b), they move into the spermathecal tubules (c), where they are stored. In this species, the ova are not released for several months. When they are released, stored sperm are discharged into the cloaca to fertilize the passing eggs.

After Hardy and Dent.



Family	Species	Common name
Mustelids	*Martes americana*	Marten
	Lutra canadiensis	Otter
	Mustela erminea	Ermine
	Taxidea taxus	American badger
	Meles meles	European badger
Ursids	*Ursus americanus*	Black bear
	Ursus maritimus	Polar bear
Pinnipeds	*Phoca vitulina*	Harbor seal
	Callorhinus ursinus	Fur seal
	*Mirounga leonina**	Elephant seal
Artiodactyla	*Capreolus capreolus*	Roe deer
Edentata	*Dasypus novemcinctus*	Armadillo
Chiroptera	*Eidolon helvum*	Fruit bat

* Southern hemisphere

FIGURE 14.55 Delayed implantation. Seasons of breeding, preimplantation, postimplantation, and birth for several species of mammals are shown. To ensure that young are born when resources are most likely available, many mammals have evolved methods to lengthen gestation beyond harsh seasons or times of migration so that birth occurs when conditions are favorable. Delayed implantation occurs following fertilization when the embryo does not immediately implant itself in the uterine wall. Instead, the embryo goes into a stage in which further development is slowed or arrested. Later, after implantation occurs, the pace of embryonic development picks up. Note that a few species give birth during the winter.

After Sadleir.

producing eggs and sperm, the gonads are endocrine organs that preside over the paced development of gametes, embryo, and breeding. They also initiate development of secondary sexual characteristics, prepare for pregnancy, maintain physiological support for the embryo, and activate accompanying reproductive behavior. Within amniotes, fertilization is usually internal, with sperm transfer occasionally aided by a male intromittent organ.

The vertebrate transition from water to land eliminated one convenient route of waste elimination, the gills, thereby increasing the role of the kidneys. As vertebrates became more terrestrial, water economy became more important during nitrogen elimination. Formation of uric acid, including resorption of water in the cloaca, is one answer. The other is formation of urea, a means of converting ammonia to a nontoxic form, and requiring less water in the process. The transition to land also initially favored internal fertilization as an alternative to spreading gametes externally in the surrounding aquatic environment. Internal fertilization permits decoupling in time of several reproductive activities—courtship, fertilization, and egg deposition. Thereby, these activities may occur at a time and in an environment most suited to each.

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