hard surfaces (e.g., teeth) that powerful muscles manipulate. Invertebrates that evolved macroherbivory include molluscs, polychaete worms, arthropods, and sea urchins.

Many molluscs have a radula. A radula is a muscularized, belt-like rasp armed with chitinous teeth. Molluscs use the radula to scrape algae off rocks or to tear the leaves off terrestrial plants. Polychaetes have sets of large chitinous teeth on an eversible proboscis or pharynx that is used to scrape off algae. This toothed pharynx is also suitable for carnivory when plant material is scarce. Macroherbivory is found in almost every group of arthropods. For example, insects and crustaceans have large, powerful mandibles capable of biting off plant material and subsequently grinding and chewing it before passing the plant material to the mouth.

PREDATION

Predation (L. *praedator,* a plunderer, pillager) is one of the most sophisticated feeding strategies, since it requires the capture of live prey. Only a few generalizations about the many kinds of predation are presented here; discussions of various taxa are presented in their appropriate chapters.

Predators can be classified by how they capture their prey: motile stalkers, lurking predators, sessile opportunists, or grazers. Motile stalkers actively pursue their prey. Examples include ciliate protozoa, nemerteans, polychaete worms, gastropods, octopuses and squids, crabs, sea stars, and many vertebrates. Lurking predators sit and wait for their prey to come within seizing distance. Examples include certain species of praying mantises, shrimp, crabs, spiders, polychaetes, and many vertebrates. Sessile opportunists usually are not very mobile. They can only capture prey when the prey organism comes into contact with them. Examples include certain protozoa, barnacles, and cnidarians. Grazing carnivores move about the substrate picking up small organisms. Their diet usually consists largely of sessile and slow-moving animals, such as sponges, ectoprocts, tunicates, snails, worms, and small crustaceans.

SURFACE NUTRIENT ABSORPTION

Some highly specialized animals have dispensed entirely with all mechanisms for prey capture, ingestion of food particles, and digestive processes. Instead they directly absorb nutrients from the external medium across their body surfaces. This medium may be nutrient-rich seawater, fluid in other animals' digestive tracts, or the body fluids of other animals. For example, some free-living protozoa, such as *Chilomonas*, absorb all of their nutrients across their body surface. The endoparasitic protozoa, cestode worms, endoparasitic gastropods, and crustaceans (all of which lack mouths and digestive systems) also absorb all of their nutrients across their body surface.

A few nonparasitic multicellular animals also lack a mouth and digestive system and absorb nutrients across their body surface. Examples include the gutless bivalves and pogonophoran worms. Interestingly, many pogonophoran worms absorb some nutrients from seawater across their body surface and also supplement their nutrition with organic carbon that symbiotic bacteria fix within the pogonophoran's tissues.

FLUID FEEDERS

The biological fluids of animals and plants are a rich source of nutrients. Feeding on this fluid is called **fluid feeding.** Fluid feeding is especially characteristic of some parasites, such as the intestinal nematodes that bite and rasp off host tissue or suck blood. External parasites (ectoparasites), such as leeches, ticks, mites, lampreys, and certain crustaceans, use a wide variety of mouthparts to feed on body fluids. For example, the sea lamprey has a funnel structure surrounding its mouth (*see figure 27.6a*). The funnel is lined with over 200 rasping teeth and a rasplike tongue. The lamprey uses the funnel like a suction cup to grip its fish host, and then with its tongue, rasps a hole in the fish's body wall. The lamprey then sucks blood and body fluids from the wound.

Insects have the most highly developed sucking structures for fluid feeding. For example, butterflies, moths, and aphids have tubelike mouthparts that enable them to suck up plant fluids. Blood-sucking mosquitoes have complex mouthparts with piercing stylets.

Most pollen- and nectar-feeding birds have long bills and tongues. In fact, the bill is often specialized (in shape, length, and curvature) for particular types of flowers. The tongues of some birds have a brushlike tip or are hollow, or both, to collect the nectar from flowers. Other nectar-feeding birds have short bills; they make a hole in the base of a flower and use their tongue to obtain nectar through the hole.

The only mammals that feed exclusively on blood are the vampire bats, such as *Desmodus*, of tropical South and Central America. These bats attack birds, cattle, and horses, using knife-sharp front teeth to pierce the surface blood vessels, and then lap at the oozing wound. Nectar-feeding bats have a long tongue to extract the nectar from flowering plants, and compared to the blood-feeding bats, have reduced dentition. In like manner, the nectar-feeding honey possum has a long, brush-tipped tongue and reduced dentition.

DIVERSITY IN DIGESTIVE STRUCTURES: INVERTEBRATES

In primitive, multicellular animals, such as cnidarians, the gut is a blind (closed) sac called a **gastrovascular cavity.** It has only one opening that is both entrance and exit (figure 27.3*a*); thus, it is an incomplete digestive tract. Some specialized cells in the cavity secrete digestive enzymes that begin the process of extracellular digestion. Other phagocytic cells that line the cavity engulf food material and continue intracellular digestion inside food vacuoles. Some flatworms have similar digestive patterns (figure 27.3*b*).

The development of the anus and complete digestive tract in the aschelminths was an evolutionary breakthrough (figure 27.3c). A complete digestive tract permits the one-way flow of ingested food without mixing it with previously ingested food or waste. Complete digestive tracts also have the advantage of

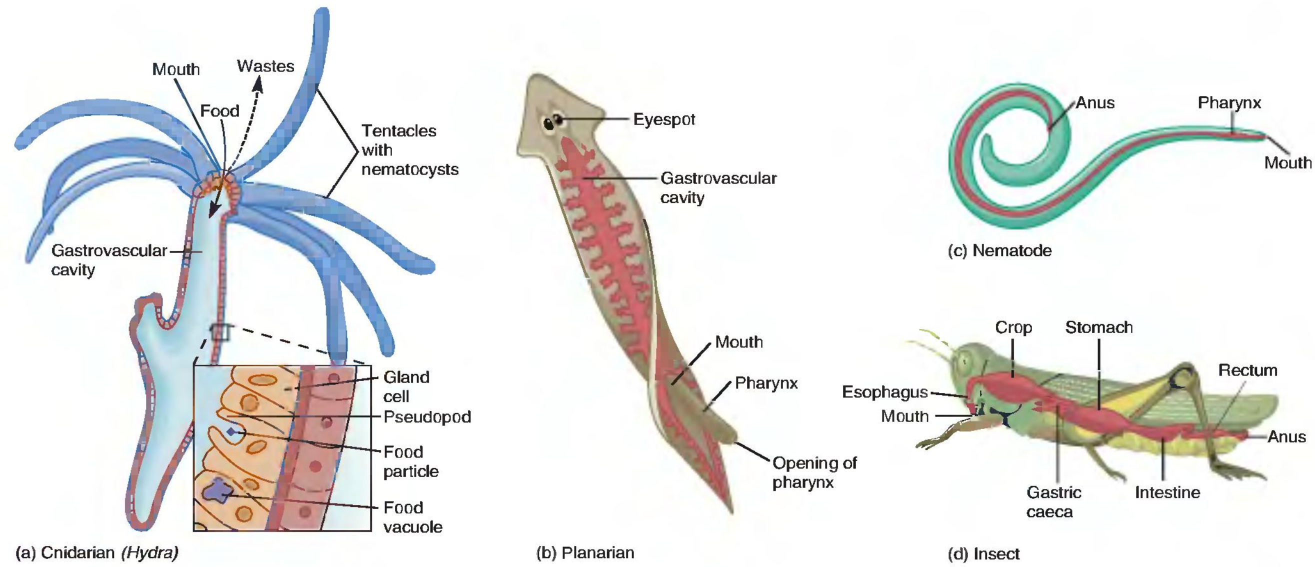

FIGURE 27.3

Various Types of Digestive Structures in Invertebrates. *(a)* The gastrovascular cavity of cnidarian *(Hydra)* is an incomplete digestive tract because its one opening, a mouth, must serve as the entry and exit point for food and waste. Extracellular digestion occurs in the gastrovascular cavity, and intracellular digestion occurs inside food vacuoles formed when phagocytic cells engulf food particles. *(b)* Even though the gastrovascular cavity in a platyhelminth (planarian) branches extensively, it is also an incomplete digestive tract with only one opening. When a planarian feeds, it sticks its muscular pharynx out of its mouth and sucks in food. *(c)* A nematode *(Ascaris)* has a complete digestive tract with a mouth, pharynx, and anus. *(d)* The complete digestive tract of an insect (grasshopper) has an expanded region called a crop that functions as a food storage organ.

progressive digestive processing in specialized regions along the system. Food can be digested efficiently in a series of distinctly different steps. The many variations of the basic plan of a complete digestive tract correlate with different food-gathering mechanisms and diets (figure 27.3*d*). Most of these have been presented in the discussion of the many different protists and invertebrates and are not repeated in this chapter. Instead, three examples further illustrate digestive systems in protozoa and invertebrates: (1) the incomplete digestive system of a ciliated protozoan is an example of an intracellular digestive system; (2) the bivalve mollusc is an example of an invertebrate that has both intracellular and extracellular digestion; and (3) an insect is an example of an invertebrate that has extracellular digestion and a complete digestive tract.

PROTOZOA

As presented in chapter 8, protozoa may be autotrophic, saprozoic, or heterotrophic (ingest food particles). Ciliated protozoa are good examples of protists that utilize heterotrophic nutrition. Ciliary action directs food from the environment into the buccal cavity and cytostome (figure 27.4). The cytostome opens into the cytopharynx, which enlarges as food enters and pinches off a food-containing vacuole. The detached food vacuole then moves through the cytoplasm. During this movement, excess water is removed from the vacuole, the contents are acidified and then made alkaline and a lysosome adds digestive enzymes. The food particles are then digested within the vacuole and the nutrients

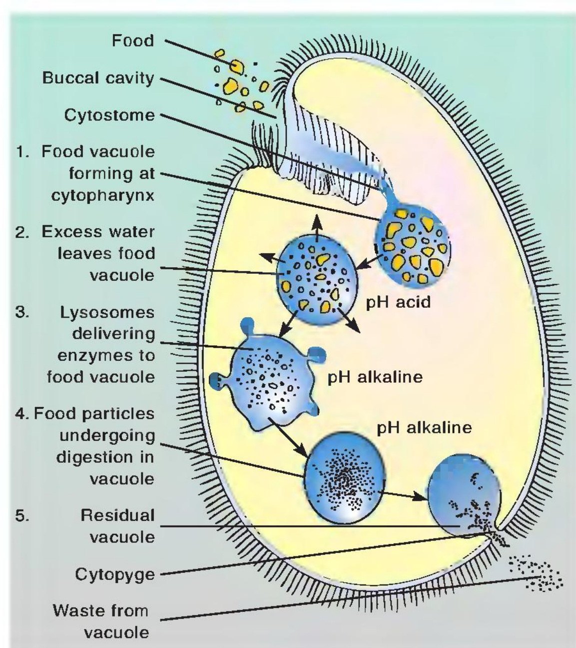

FIGURE 27.4

Intracellular Digestion in a Ciliated Protozoan. Cilia direct food toward the cytostome ("mouth"). The food enters the cytopharynx, where a food vacuole forms and detaches from the cytopharynx. The detached vacuole undergoes acidic and alkaline digestion, and the waste vacuole moves to the cytopyge ("anus") for excretion.

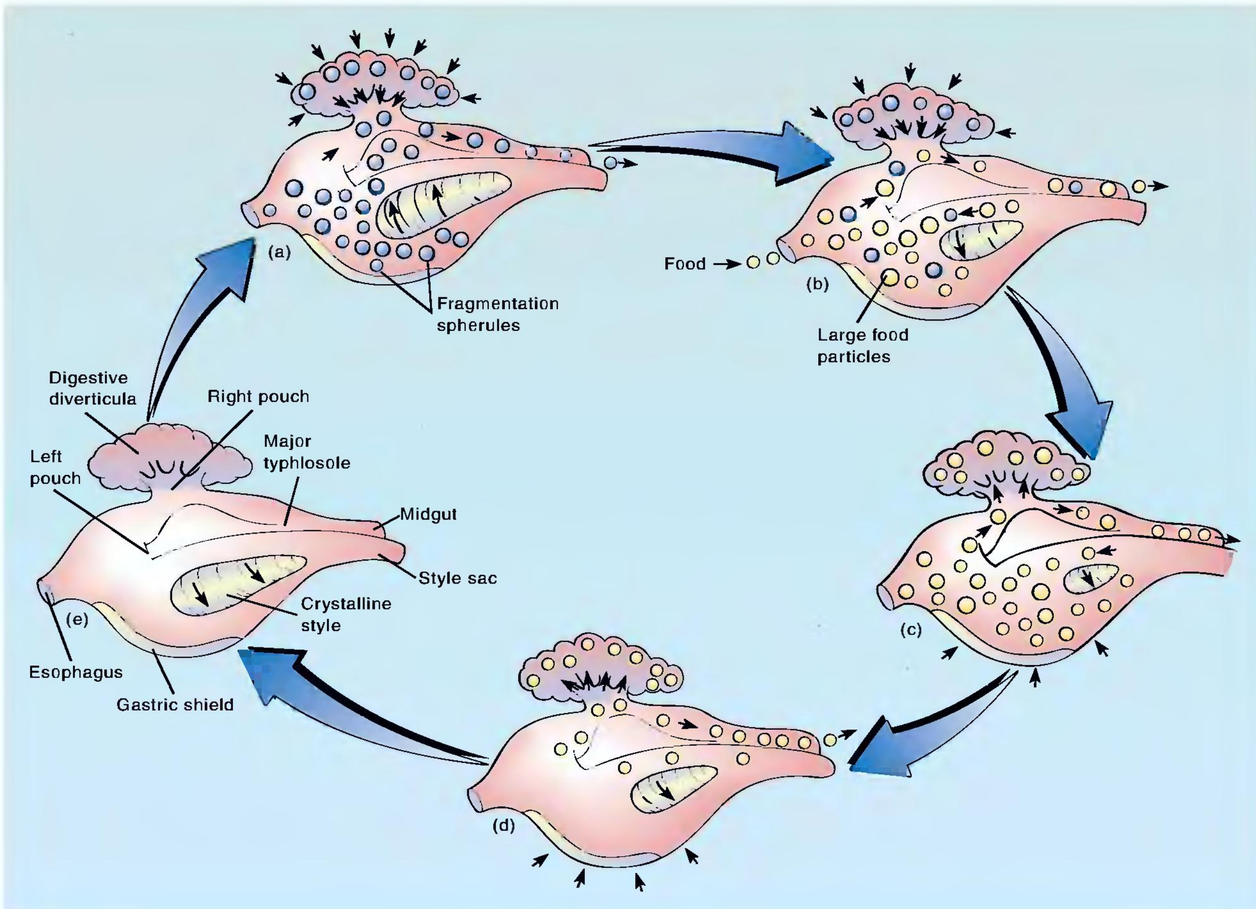

FIGURE 27.5

Extracellular and Intracellular Digestion in a Bivalve Mollusc. *(a)* Extracellular digestion begins before food ingestion by the dissolving of the crystalline style and the formation of fragmentation spherules in the stomach. *(b)* As food enters the stomach, the rotating style and the enzymes released by the gastric shield mechanically and enzymatically break it down. *(c)* The small food particles then move into the digestive diverticulae for intracellular digestion. *(d)* A progressive passage of food particles from the stomach to the digestive diverticulae follows cessation of feeding. *(e)* During this resting phase, the stomach empties and the style reforms, while intracellular digestion in the diverticulae is completed, and fragmentation spherules begin to form again. The movement of fragmentation spherules starts the next feeding cycle.

absorbed into the cytoplasm. The residual vacuole then excretes its waste products via the cytopyge.

BIVALVE MOLLUSCS

Many bivalve molluscs suspension feed and ingest small food particles. The digestive tract has a short esophagus opening into a stomach, midgut, hindgut, and rectum. The stomach contains a crystalline style, gastric shield, and diverticulated region. These diverticulae are blind-ending sacs that increase the surface area for absorption and intracellular digestion. The midgut, hindgut, and rectum function in extracellular digestion and absorption (figure 27.5).

Digestion is a coordination of three cycles: (1) feeding, (2) extracellular digestion, and (3) intracellular digestion. The resting phase is preparative for extracellular digestion. The mechanical and enzymatic breakdown of food during feeding provides the small particles for intracellular digestion. Intracellular digestion releases the nutrients into the blood and produces the fragmentation spherules that both excrete wastes and lower the pH for optimal extracellular digestion. These three cycles are linked to tidal immersion and emersion of the mollusc.

INSECTS

The grasshopper is a representative insect with a complete digestive tract and extracellular digestion (*see figure 27.3d*). During feeding, the mandibles and maxillae first break up (masticate) the food, which is then taken into mouth and passed to the crop via the esophagus. During mastication, the salivary glands add saliva to the food to lubricate it for passage through the digestive tract.

Saliva also contains the enzyme amylase, which begins the enzymatic digestion of carbohydrates. This digestion continues during food storage in the crop. The midgut secretes other enzymes (carbohydrases, lipases, proteases) that enter the crop. Food passes slowly from the crop to the stomach, where it is mechanically reduced and the nutrient particles sorted. Large particles are returned to the crop for further processing; the small particles enter the gastric cecae, where extracellular digestion is completed. Most nutrient absorption then occurs in the intestine. Undigested food is moved along the intestine and passes into the rectum, where water and ions are absorbed. The solid fecal pellets that form then pass out of the animal via the anus. During this entire feeding process the nervous system, the endocrine system, and the presence of food exert considerable control over enzyme production at various points in the digestive tract.

DIVERSITY IN DIGESTIVE STRUCTURES: VERTEBRATES

The complete vertebrate digestive tract (gut tube) is highly specialized in both structure and function for the digestion of a wide variety of foods. The basic structures of the gut tube include the buccal cavity, pharynx, esophagus, stomach, small intestine, large intestine, rectum, and anus/cloaca. In addition, three important glandular systems are associated with the digestive tract: (1) the salivary glands; (2) the liver, gallbladder, and bile duct; and (3) the pancreas and pancreatic duct.

Because most vertebrates spend the majority of their time acquiring food, feeding is the universal pastime. The oral cavity (mouth), teeth, intestines, and other major digestive structures usually reflect the way an animal gathers food, the type of food it eats, and the way it digests that food. These major digestive structures are now discussed to illustrate the diversity of form and function among different vertebrates.

TONGUES

A tongue or tonguelike structure develops in the floor of the oral cavity in many vertebrates. For example, a lamprey has a protrusible tongue with horny teeth that rasp its prey's flesh (figure 27.6*a*). Fishes may have a primary tongue that bears teeth that help hold prey; however, this type of tongue is not muscular (figure 27.6*b*). Tetrapods have evolved mobile tongues for gathering food. Frogs and salamanders and some lizards can rapidly project part of their tongue from the mouth to capture an insect (figure 27.6*c*). A woodpecker has a long, spiny tongue for gathering insects and grubs (figure 27.6*d*). Ant- and termite-eating mammals also gather food with long, sticky tongues. Spiny papillae on the tongues of cats and other carnivores help these animals rasp flesh from a bone.

TEETH

With the exception of birds, turtles, and baleen whales, most vertebrates have teeth. Birds lack teeth, probably to reduce body weight for flight. Teeth are specialized, depending on whether an animal feeds on plants or animals, and on how it obtains its food. The teeth of snakes slope backward to aid in the retention of prey while swallowing (figure 27.7*a*), and the canine teeth of wolves are specialized for ripping food (figure 27.7*b*). Herbivores, such as deer, have predominantly grinding teeth, the front teeth of a beaver are used for chiseling trees and branches, and the elephant has two of its upper, front teeth specialized as weapons and for moving objects (figure 27.7*c–e*). Because humans, pigs, bears, raccoons, and a few other mammals are omnivores, they have teeth that can perform a number of tasks—tearing, ripping, chiseling, and grinding (figure 27.7*f*).

SALIVARY GLANDS

Most fishes lack salivary glands in the head region. Lampreys are an exception because they have a pair of glands that secrete an anticoagulant needed to keep their prey's blood flowing as they feed. Modified salivary glands of some snakes produce venom that is injected through fangs to immobilize prey. Because the secretion of oral digestive enzymes is not an important function in amphibians or reptiles, salivary glands are absent. Most birds lack salivary glands, while all mammals have them.

ESOPHAGI

The esophagus (pl., esophagi) is short in fishes and amphibians, but much longer in amniotes due to their longer necks. Grain- and seed-eating birds have a crop that develops from the caudal portion of the esophagus (figure 27.8*a*). Storing food in the crop ensures an almost continuous supply of food to the stomach and intestine for digestion. This structure allows these birds to reduce the frequency of feeding and still maintain a high metabolic rate.

STOMACHS

The stomach is an ancestral vertebrate structure that evolved as vertebrates began to feed on larger organisms that were caught at less frequent intervals and required storage. Some zoologists believe that the gastric glands and their production of hydrochloric acid (HCl) evolved in the context of killing bacteria and helping preserve food. The enzyme pepsinogen may have evolved later because the stomach is not essential for digestion.

GIZZARDS

Some fishes, some reptiles such as crocodilians, and all birds have a gizzard for grinding up food (figure 27.8*a*). The bird's gizzard develops from the posterior part of the stomach called the ventriculus. Pebbles (grit) that have been swallowed are often retained in the gizzard of grain-eating birds and facilitate the grinding process.

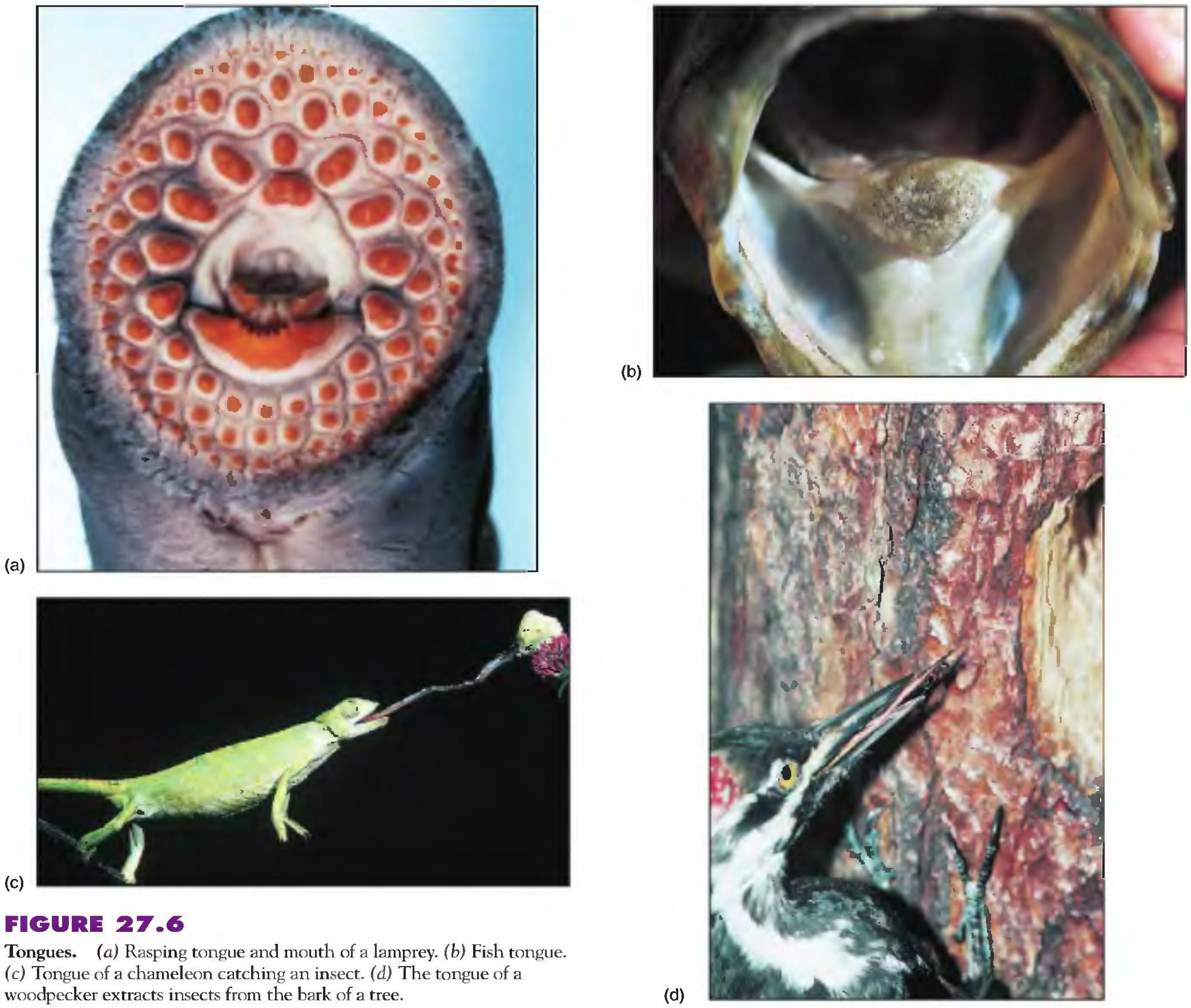
(a) (b) (c) (d)

FIGURE 27.6

Tongues. *(a)* Rasping tongue and mouth of a lamprey. *(b)* Fish tongue. *(c)* Tongue of a chameleon catching an insect. *(d)* The tongue of a woodpecker extracts insects from the bark of a tree.

RUMENS

Ruminant mammals—animals that "chew their cud," such as cows, sheep, and deer—show some of the most unusual modifications of the stomach. ***This method of digestion has evolved in animals that need to eat large amounts of food relatively quickly, but can chew the food at a more comfortable or safer location.*** More important though, the ruminant stomach provides an opportunity for large numbers of microorganisms to digest the cellulose walls of grass and other vegetation. Cellulose contains a large amount of energy; however, animals generally lack the ability to produce the enzyme cellulase for digesting cellulose and obtaining its energy. Because gut microorganisms can produce cellulase, they have made the herbivorous lifestyle more effective.

In ruminants, the upper portion of the stomach expands to form a large pouch, the rumen, and a smaller reticulum. The lower portion of the stomach consists of a small antechamber, the omasum, with a "true" stomach, or abomasum, behind it (figure 27.9). Food first enters the rumen, where it encounters the microorganisms. Aided by copious fluid secretions, body heat, and churning of the rumen, the microorganisms partially digest the food and reduce it to a pulpy mass. Later, the pulpy mass moves into the reticulum, from which mouthfuls are regurgitated as "cud" (L. *ruminare*, to chew the cud). At this time, food is thoroughly chewed for the first time. When reswallowed, the food enters the rumen, where it becomes more liquid in consistency. When it is very liquid, the digested food material flows out of the reticulum and into the omasum and then the glandular region, the abomasum. Here the digestive enzymes are first encountered, and digestion continues.

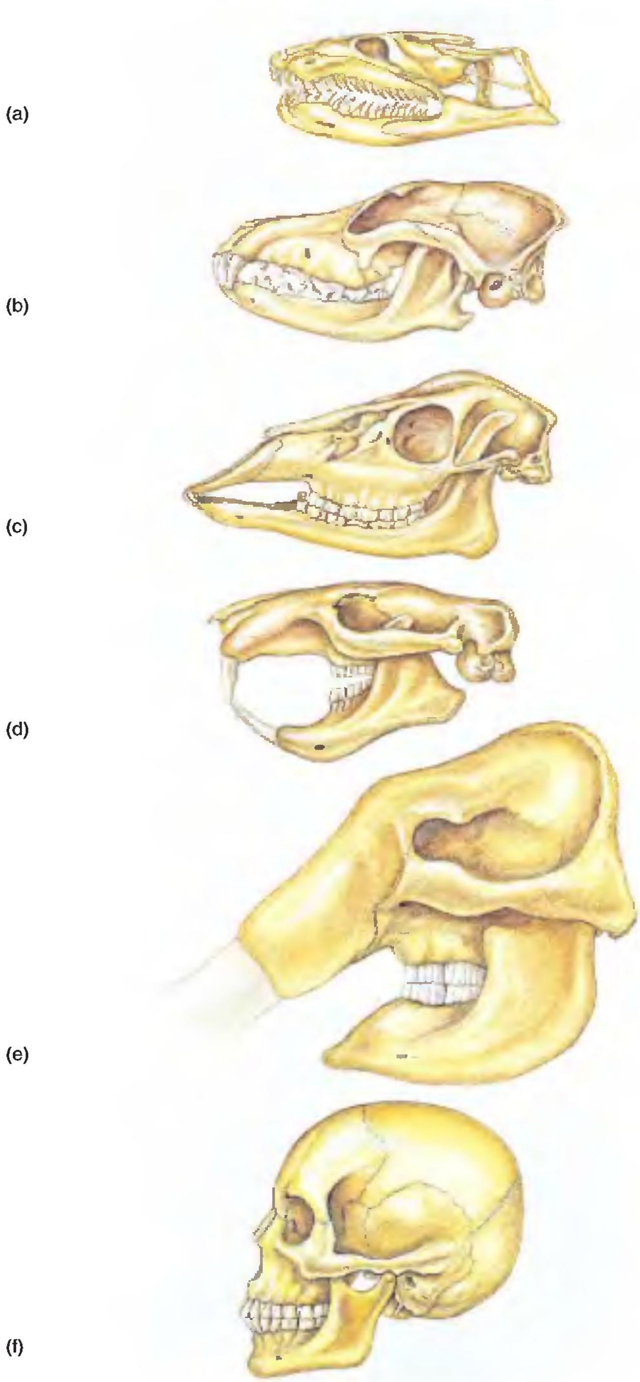

FIGURE 27.7

Arrangement of Teeth in a Variety of Vertebrates. *(a)* Snake. *(b)* Wolf. *(c)* Deer. *(d)* Beaver. *(e)* Elephant. *(f)* Human.

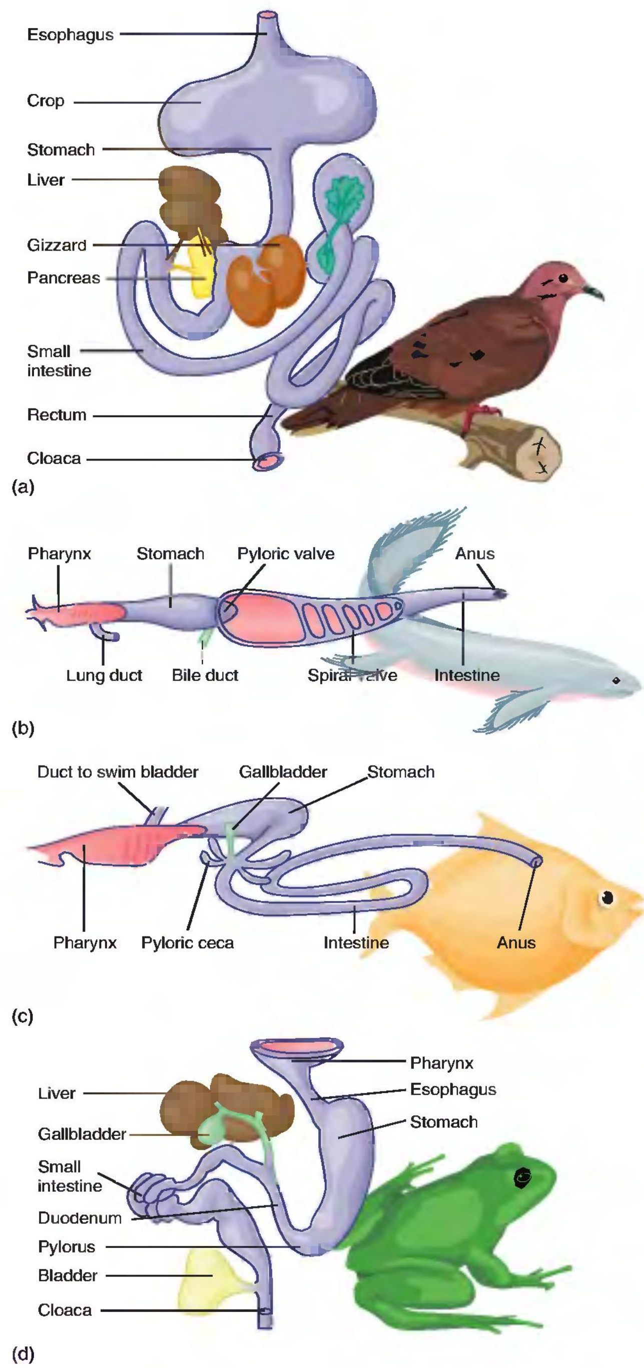

FIGURE 27.8

Arrangement of Stomachs and Intestines in a Variety of Vertebrates. *(a)* Pigeon. *(b)* Lungfish. *(c)* Teleost fish. *(d)* Frog.

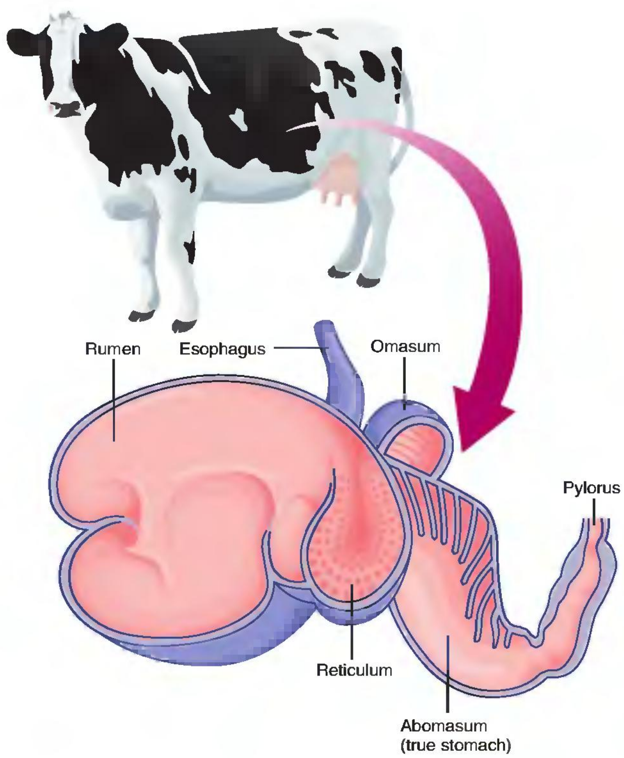

FIGURE 27.9

Ruminant Mammal. Four-chambered stomach of a cow, where symbiotic microorganisms digest cellulose.

CECA

Microorganisms attack the food of ruminants before gastric digestion, but in the typical nonruminant herbivore, microbial action on cellulose occurs after digestion. Rabbits, horses, and rats digest cellulose by maintaining a population of microorganisms in their unusually large cecum, the blind pouch that extends from the colon (figure 27.10). Adding to this efficiency, a few non-ruminant herbivores, such as mice and rabbits, eat some of their own feces to process the remaining materials in them, such as vitamins.

LIVERS AND GALLBLADDERS

In those vertebrates with a gallbladder, it is closely associated with the liver. The liver manufactures bile, which the gallbladder then stores. **Bile** is a fluid containing bile salts and bile pigments. Bile salts play an important role in the digestion of fats, although they are not digestive enzymes. They emulsify dietary fat, breaking it into small globules (emulsification) on the surface of which the fat-digesting enzyme lipase can function. Bile pigments result from phagocytosis of red blood cells in the spleen, liver, and red bone marrow. Phagocytosis cleaves the hemoglobin molecule, releasing iron, and the remainder of the molecule is converted into pigments that enter the circulation. These pigments are subsequently extracted from the circulation in the liver and excreted in the bile as bilirubin ("red bile") and biliverdin ("green bile").

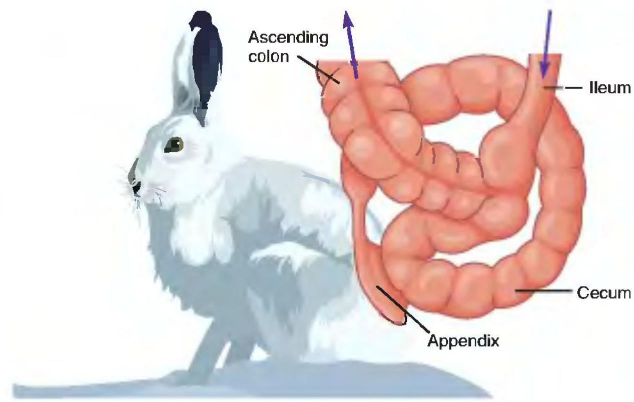

FIGURE 27.10

Extensive Cecum of a Nonruminant Herbivore, Such as a Rabbit. The cecum contains microorganisms that produce digestive enzymes (e.g., cellulase that helps break down cellulose).

Because of the importance of bile in fat digestion, the gallbladder is relatively large in carnivores and vertebrates, in which fat is an important part of the diet. It is much reduced or absent in bloodsuckers, such as the lamprey, and in animals that feed primarily on plant food (e.g., some teleosts, many birds, and rats).

PANCREATA

Every vertebrate has a pancreas (pl., pancreata); however, in lampreys and lungfishes it is embedded in the wall of the intestine and is not a visible organ. Both endocrine and exocrine tissues are present, but the cell composition varies. Pancreatic fluid containing many enzymes empties into the small intestine via the pancreatic duct.

INTESTINES

The configuration and divisions of the small and large intestines vary greatly among vertebrates. Intestines are closely related to the animal's type of food, body size, and levels of activity. For example, cyclostomes, chondrichthian fishes, and primitive bony fishes have short, nearly straight intestines that extend from the stomach to the anus *(see figure 27.8b)*. In more advanced bony fishes, the intestine increases in length and begins to coil *(see figure 27.8c)*. The intestines are moderately long in most amphibians and reptiles *(see figure 27.8d)* In birds and mammals, the intestines are longer and have more surface area than those of other tetrapods *(see figure 27.8a)*. Birds typically have two ceca, and mammals have a single cecum at the beginning of the large intestine. The large intestine is much longer in mammals than in birds, and it empties into the cloaca in most vertebrates.

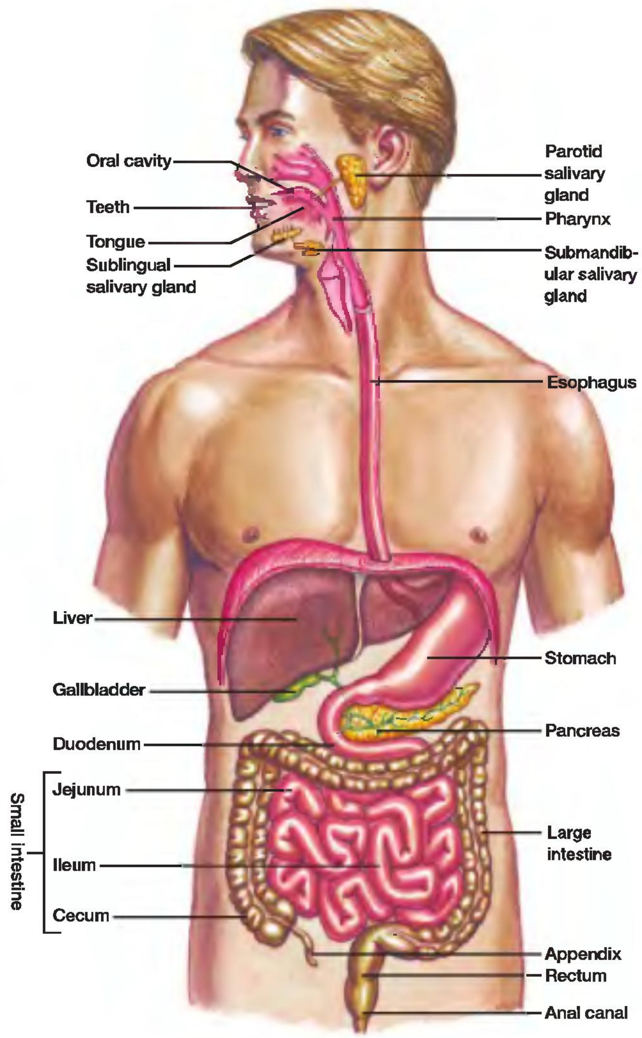

FIGURE 27.11

Major Organs and Parts of the Human Digestive System. Food passes from the mouth through the pharynx and esophagus to the stomach. From the stomach, it passes to the small intestine, where nutrients are broken down and absorbed into the circulatory and lymphatic systems. Nutrients then move to the large intestine, where water is reabsorbed, and feces form. Feces exit the body via the anal canal.

THE MAMMALIAN DIGESTIVE SYSTEM

Humans, pigs, bears, raccoons, and a few other mammals are omnivores. The digestive system of an omnivore has the mechanical and chemical ability to process many kinds of foods. The sections that follow examine the control of gastrointestinal motility, the major parts of the alimentary canal, and the accessory organs of digestion (figure 27.11).

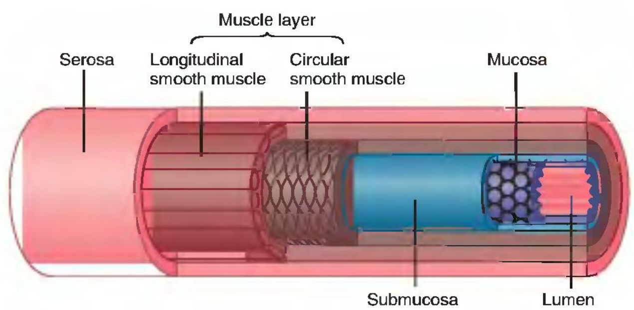

FIGURE 27.12

Mammalian Gastrointestinal Tract. Common structural layers of the gastrointestinal tract. The central lumen extends from the mouth to the anus.

The process of digesting and absorbing nutrients in a mammal includes:

1. Ingestion—eating
2. Peristalsis—the involuntary, sequential muscular contractions that move ingested nutrients along the digestive tract
3. Segmentation—mixing the contents in the digestive tract
4. Secretion—the release of hormones, enzymes, and specific ions and chemicals that take part in digestion
5. Digestion—the conversion of large nutrient particles or molecules into small particles or molecules
6. Absorption—the passage of usable nutrient molecules from the small intestine into the bloodstream and lymphatic system for the final passage to body cells
7. Defecation—the elimination from the body of undigested and unabsorbed material as waste

GASTROINTESTINAL MOTILITY AND ITS CONTROL

As with any organ, the function of the gastrointestinal tract is determined by the type of tissues it contains. Most of the mammalian gastrointestinal tract has the same anatomical structure along its entire length (figure 27.12). From the outside inward is a thin layer of connective tissue called the serosa. (The serosa forms a moist epithelial sheet called the peritoneum. This peritoneum lines the entire abdominal cavity and covers all internal organs. The space it encompasses is the coelom.) Next are the longitudinal smooth-muscle layer and circular smooth-muscle layer. Underneath this muscle layer is the submucosa. The submucosa contains connective tissue, blood, and lymphatic vessels. The mucosa faces the central opening, which is called a lumen.

The coordinated contractions of the muscle layers of the gastrointestinal tract mix the food material with various secretions and move the food from the oral cavity to the rectum. The two types of movement involved are peristalsis and segmentation.

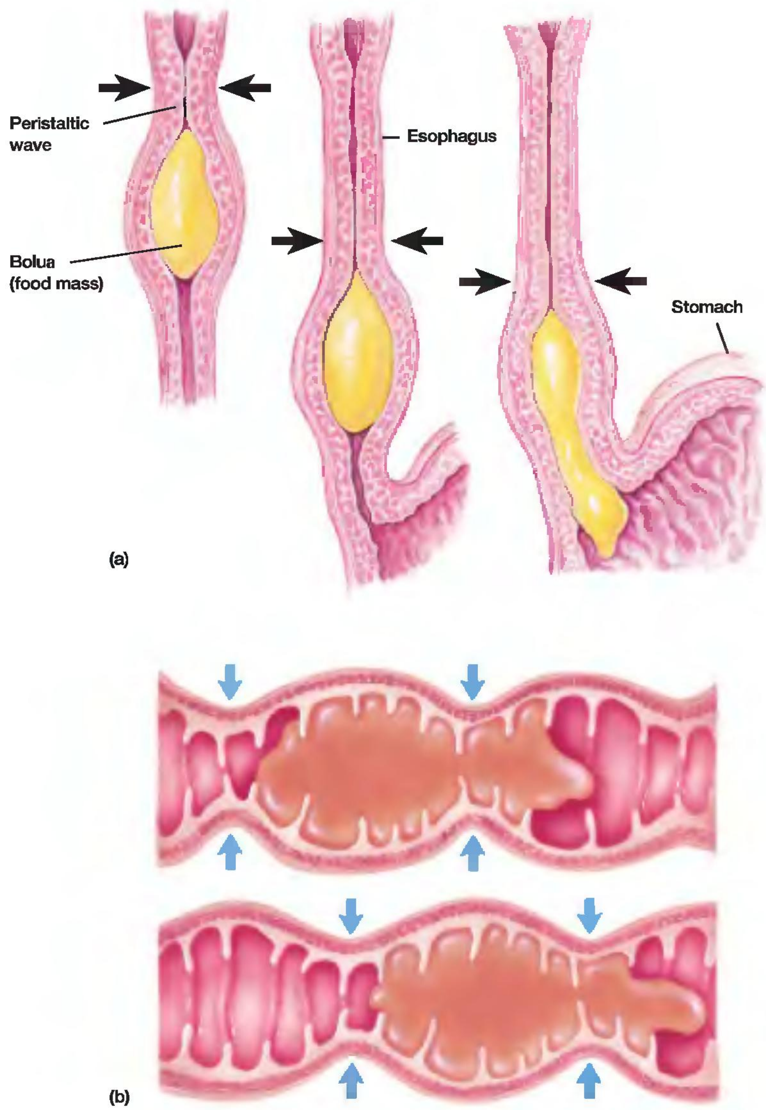

FIGURE 27.13

Peristalsis and Segmentation. *(a)* Peristaltic waves move food through the esophagus to the stomach. *(b)* In segmentation, simultaneous muscular contractions of many sections of the intestine (blue arrows) help mix nutrients with digestive secretions.

During **peristalsis** (Gr. *peri*, around + *stalsis*, contraction), food advances through the gastrointestinal tract when the rings of circular smooth muscle contract behind it and relax in front of it (figure 27.13*a*). Peristalsis is analogous to squeezing icing from a pastry tube. The small and large intestines also have rings of smooth muscles that repeatedly contract and relax, creating an oscillating back-and-forth movement in the same place, called **segmentation** (figure 27.13*b*). This movement mixes the food with digestive secretions and increases the efficiency of absorption.

Sphincters also influence the flow of material through the gastrointestinal tract and prevent backflow. Sphincters are rings of smooth or skeletal muscle at the beginning or ends of specific regions of the gut tract. For example, the cardiac sphincter is between the esophagus and stomach, and the pyloric sphincter is between the stomach and small intestine.

Control of gastrointestinal activity is based on the volume and composition of food in the lumen of the gut. For example, ingested food distends the gut and stimulates mechanical receptors in the gut wall. In addition, digestion of carbohydrates, lipids, and proteins stimulates various chemical receptors in the gut wall. Signals from these mechanical and chemical stimuli travel through nerve plexuses in the gut wall to control the muscular

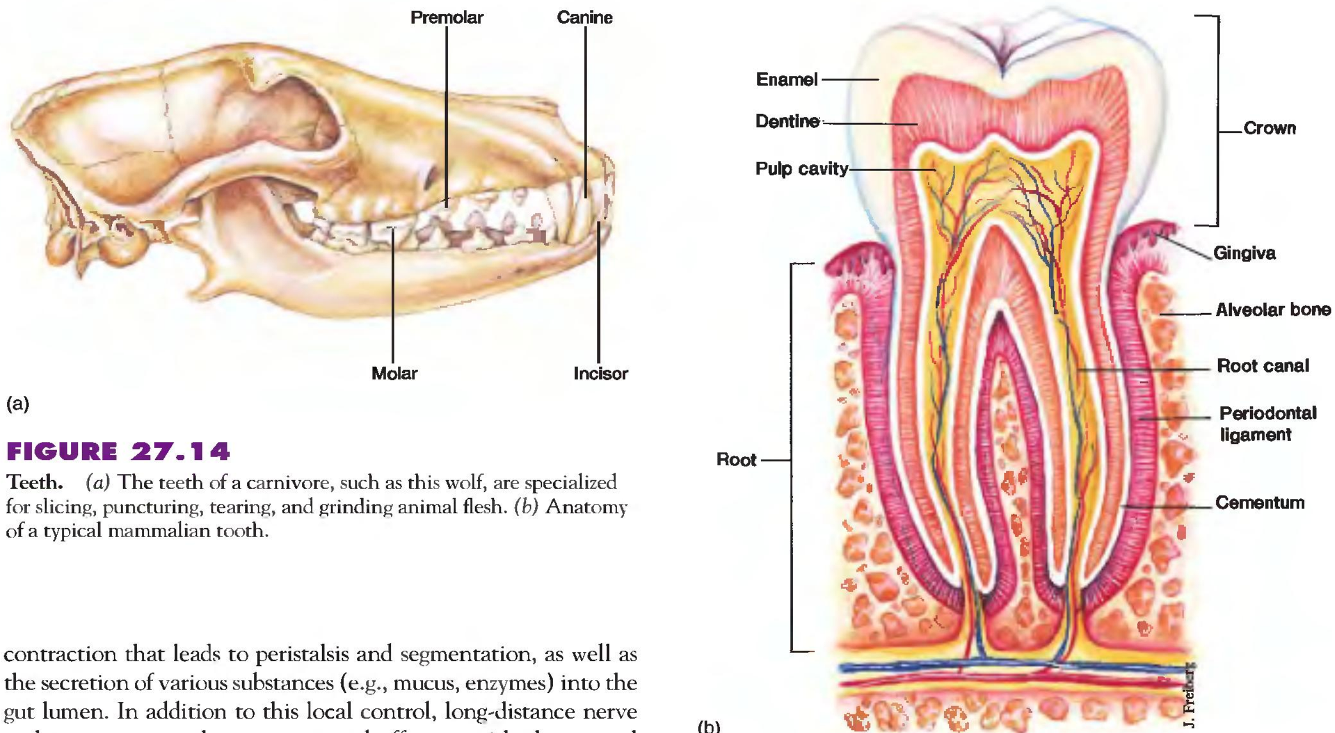

FIGURE 27.14

Teeth. *(a)* The teeth of a carnivore, such as this wolf, are specialized for slicing, puncturing, tearing, and grinding animal flesh. *(b)* Anatomy of a typical mammalian tooth.

contraction that leads to peristalsis and segmentation, as well as the secretion of various substances (e.g., mucus, enzymes) into the gut lumen. In addition to this local control, long-distance nerve pathways connect the receptors and effectors with the central nervous system. Either or both of these pathways function to maintain homeostasis in the gut. The endocrine cells of the gastrointestinal tract also produce hormones that help regulate secretion, digestion, and absorption.

ORAL CAVITY

A pair of lips protects the **oral cavity** (mouth). The lips are highly vascularized, skeletal muscle tissue with an abundance of sensory nerve endings. Lips help retain food as it is being chewed and play a role in phonation (the modification of sound).

The oral cavity contains the tongue and teeth (figure 27.14). Mammals can mechanically process a wide range of foods because their teeth are covered with enamel (the hardest material in the body) and because their jaws and teeth exert a strong force. The oral cavity is continuously bathed by **saliva,** a watery fluid that at least three pairs of salivary glands secrete. Saliva moistens food, binds it with mucins (glycoproteins), and forms the ingested food into a moist mass called a bolus. Saliva also contains bicarbonate ions (HCO_3^-), which buffer chemicals in the mouth, and thiocyanate ions (SCN^-) and the enzyme lysozyme, which kill microorganisms. It also contributes an enzyme (amylase) necessary for the initiation of carbohydrate digestion.

PHARYNX AND ESOPHAGUS

Chapter 26 discusses how both air and swallowed foods and liquids pass from the mouth into the **pharynx**—the common passageway for both the digestive and respiratory tracts. The epiglottis temporarily seals off the opening (glottis) to the trachea so that swallowed food does not enter the trachea. Initiation of the swallowing reflex can be voluntary, but most of the time it is involuntary. When swallowing begins, sequential, involuntary contractions of smooth muscles in the walls of the **esophagus** propel the bolus or liquid to the stomach. Neither the pharynx nor the esophagus contribute to digestion.

STOMACH

The mammalian **stomach** is a muscular, distensible sac with three main functions. It (1) stores and mixes the food bolus received from the esophagus, (2) secretes substances (enzymes, mucus, and hydrochloric acid [HCl]) that start the digestion of proteins, and (3) helps control the rate at which food moves into the small intestine via the pyloric sphincter (figure 27.15*a*).

The stomach is made up of an inner mucous membrane containing thousands of gastric glands (figure 27.15*b*). Three types of cells are in these glands. **Parietal cells** secrete a solution containing HCl, and **chief cells** secrete pepsinogen, the precursor of the enzyme pepsin. Both of the cells are in the pits of the gastric glands. The surface of the mucous membrane at the openings of the glands contains numerous **mucous cells** that secrete mucus that coats the surface of the stomach and protects it from the HCl and digestive enzymes. The surfaces of the upper gastrointestinal tract—the esophagus and mouth—have a much thinner mucous-cell layer

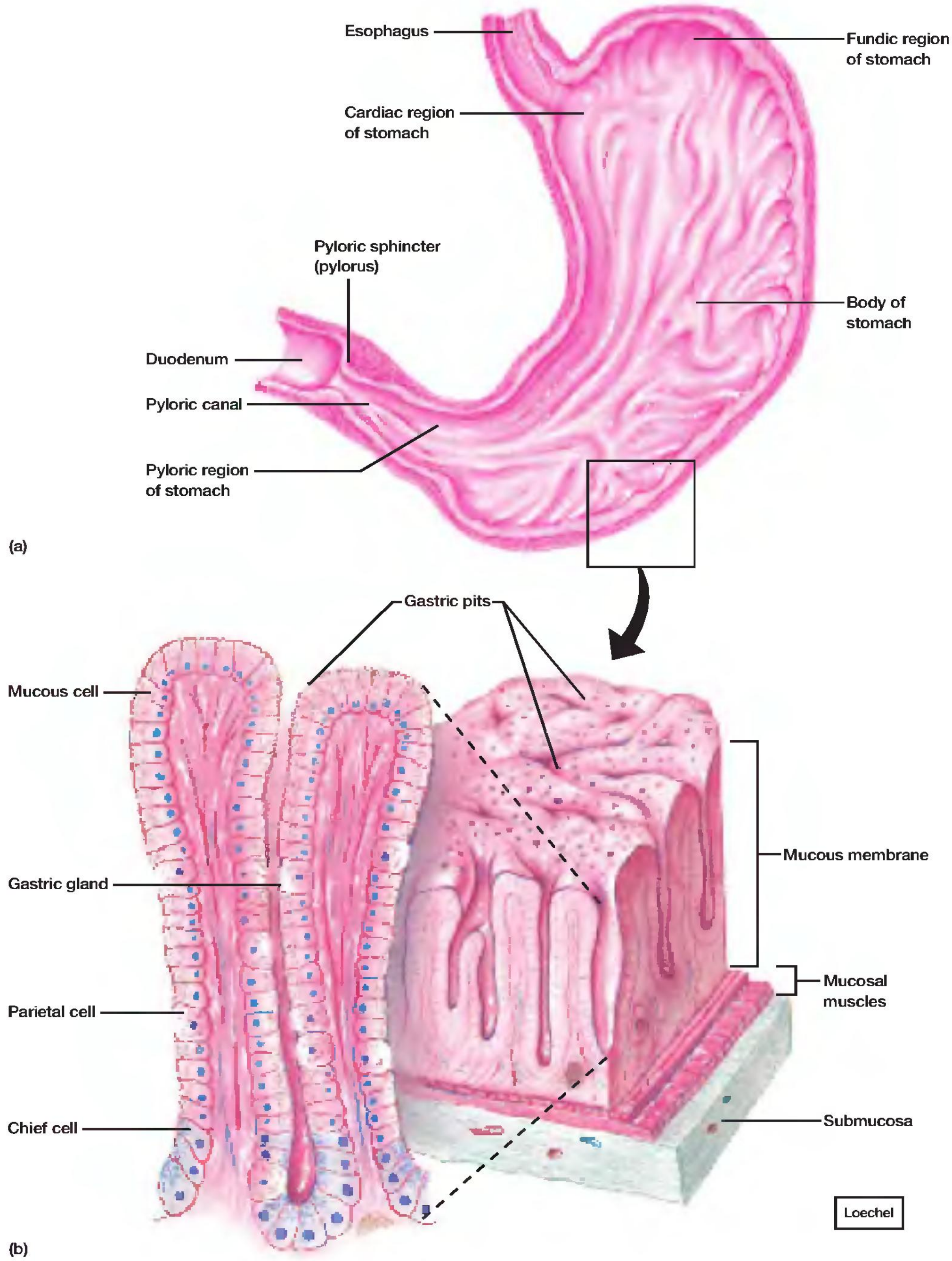

FIGURE 27.15

Stomach. *(a)* Food enters the stomach from the esophagus. *(b)* Gastric glands cover the mucosa of the stomach and include mucous cells, parietal cells, and chief cells. Each type produces a different secretion.

than the stomach, which is why vomiting can cause a burning sensation in the esophagus or mouth. Endocrine cells in one part of the stomach mucosa release the hormone gastrin, which travels to target cells in the gastric glands, further stimulating them.

When the bolus of food enters the stomach, it distends the walls of the stomach. This distention, as well as the act of eating, causes the gastric pits to secrete HCl (as H^+ and Cl^-) and pepsinogen. The H^+ ions cause pepsinogen to be converted into the active enzyme pepsin. As pepsin, mucus, and HCl mix with and begin to break down proteins, smooth mucosal muscles contract and vigorously churn and mix the food bolus. About three to four hours after a meal, the stomach contents have been sufficiently mixed and are a semiliquid mass called **chyme** (Gr. *chymos*, juice). The pyloric sphincter regulates the release of the chyme into the small intestine.

When the stomach is empty, peristaltic waves cease; however, after about 10 hours of fasting, new waves may occur in the upper region of the stomach. These waves can cause "hunger pangs" as sensory nerve fibers carry impulses to the brain.

SMALL INTESTINE: MAIN SITE OF DIGESTION

Most of the food a mammal ingests is digested and absorbed in the **small intestine.** The human small intestine is about 4 cm in diameter and 7 to 8 m in length (*see figure 27.11*). It is intermediate in length between the small intestines of typical carnivores and herbivores of similar size, and it reflects the human's omnivorous eating habits. The length of the small intestine directly relates to the total surface area available for absorbing nutrients, as determined by the many circular folds and minute projections of the inner gut surface (figure 27.16*a*). On the circular folds, thousands of fingerlike projections called **villi** (L. *villus*, tuft of hair) (sing. villus) project from each square centimeter of mucosa (figure 27.16*b*,*c*). Simple columnar epithelial cells, each bearing numerous microvilli, cover both the circular folds and villi (figure 27.16*d*). These minute projections are so dense that the inner wall of the human small intestine has a total surface area of approximately 300 m^2—the size of a tennis court.

The first part of the small intestine, called the duodenum, functions primarily in digestion. The next part is the jejunum, and the last part is the ileum. Both function in nutrient absorption.

The duodenum contains many digestive enzymes that intestinal glands in the duodenal mucosa secrete. The pancreas secretes other enzymes. In the duodenum, digestion of carbohydrates and proteins is completed, and most lipids are digested. The jejunum and ileum absorb the end products of digestion (amino acids, simple sugars, fatty acids, glycerol, nucleotides, water). Much of this absorption involves active transport and the sodium-dependent ATPase pump. Sugars and amino acids are absorbed into the capillaries of the villi, whereas free fatty acids enter the epithelial cells of the villi and recombine with glycerol to form triglycerides. The triglycerides are coated with proteins to form small droplets called **chylomicrons,** which enter the lacteals of the villi (figure 27.16*c*). From the lacteals, the chylomicrons move into the lymphatics and eventually into the bloodstream for transport throughout the body.

Besides absorbing organic molecules, the small intestine absorbs water and dissolved mineral ions. The small intestine absorbs about 9 liters of water per day, and the large intestine absorbs the rest.

LARGE INTESTINE

Unlike the small intestine, the **large intestine** has no circular folds, villi, or microvilli; thus, the surface area is much smaller. The small intestine joins the large intestine near a blind-ended sac, the **cecum** (L. *caecum*, blind gut) (*see figure 27.11*). *The human cecum and its extension, the **appendix,** are storage sites and possibly represent evolutionary remains of a larger, functional cecum, such as is found in herbivores* (see figure 27.10). The appendix contains an abundance of lymphoid tissue and may function as part of the immune system.

The major functions of the large intestine include the reabsorption of water and minerals, and the formation and storage of feces. As peristaltic waves move food residue along, minerals diffuse or are actively transported from the residue across the epithelial surface of the large intestine into the bloodstream. Water follows osmotically and returns to the lymphatic system and bloodstream. When water reabsorption is insufficient, diarrhea (Gr. *rhein*, to flow) results. If too much water is reabsorbed, fecal matter becomes too thick, resulting in constipation.

Many bacteria and fungi exist symbiotically in the large intestine. They feed on the food residue and further break down its organic molecules to waste products. In turn, they secrete amino acids and vitamin K, which the host's gut absorbs. What remains—feces—is a mixture of bacteria, fungi, undigested plant fiber, sloughed-off intestinal cells, and other waste products.

ROLE OF THE PANCREAS IN DIGESTION

The **pancreas** (Gr. *pan*, all + *kreas*, flesh) is an organ that lies just ventral to the stomach and has both endocrine and exocrine functions. Exocrine cells in the pancreas secrete digestive enzymes into the pancreatic duct, which merges with the hepatic duct from the liver to form a common bile duct that enters the duodenum. Pancreatic enzymes complete the digestion of carbohydrates and proteins and initiate the digestion of lipids. Trypsin, carboxypeptidase, and chymotrypsin digest proteins into small peptides and individual amino acids. Pancreatic lipases split triglycerides into smaller, absorbable glycerol and free fatty acids. Pancreatic amylase converts polysaccharides into disaccharides and monosaccharides. Table 27.6 summarizes the major glands, secretions, and enzymes of the mammalian digestive system.

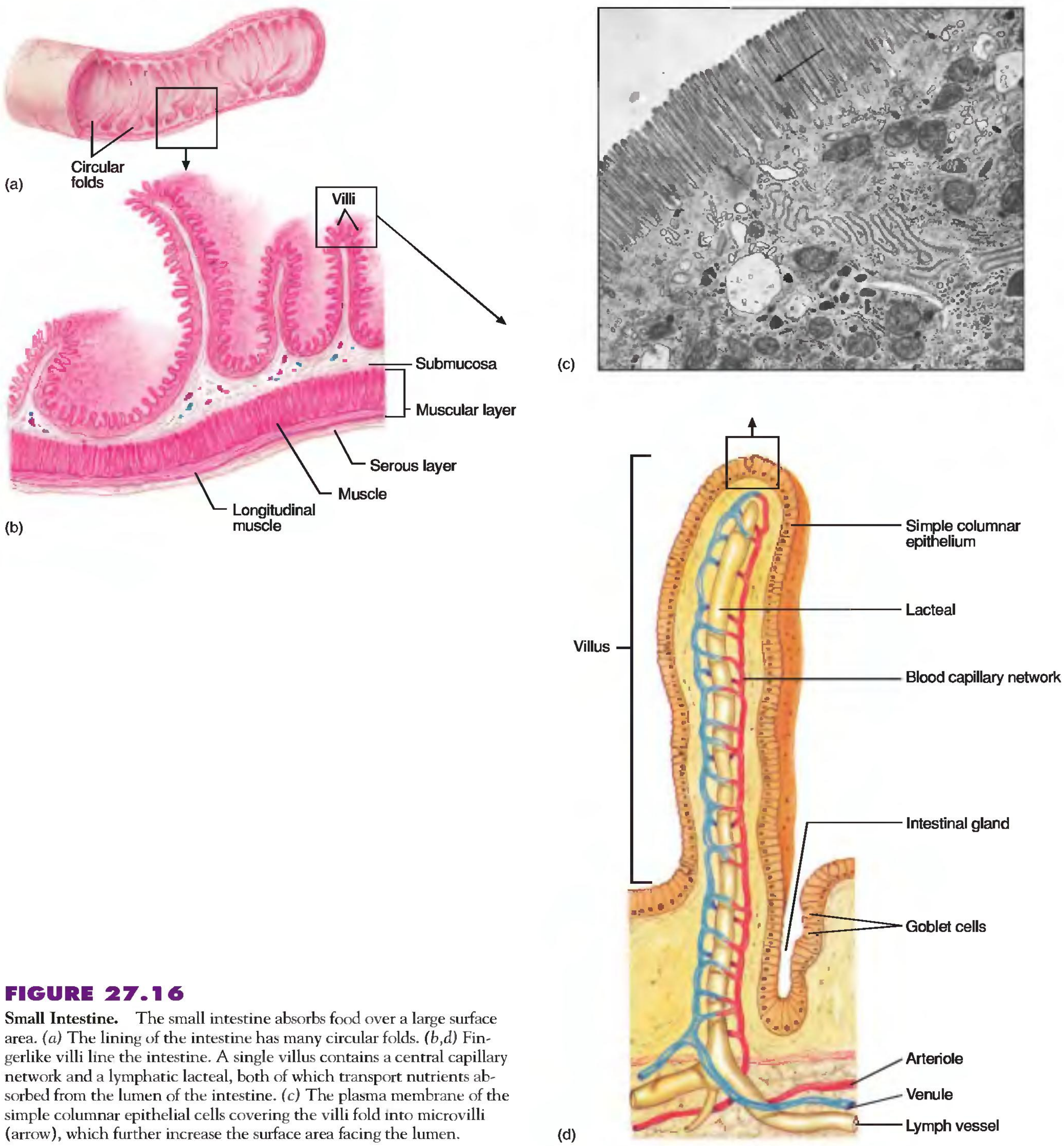

FIGURE 27.16

Small Intestine. The small intestine absorbs food over a large surface area. *(a)* The lining of the intestine has many circular folds. *(b,d)* Fingerlike villi line the intestine. A single villus contains a central capillary network and a lymphatic lacteal, both of which transport nutrients absorbed from the lumen of the intestine. *(c)* The plasma membrane of the simple columnar epithelial cells covering the villi fold into microvilli (arrow), which further increase the surface area facing the lumen.

TABLE 27.6
MAJOR DIGESTIVE GLANDS, SECRETIONS, AND ENZYMES IN MAMMALS

PLACE OF DIGESTION	SOURCE	SECRETION	ENZYME	DIGESTIVE FUNCTION
Mouth	Salivary glands	Saliva	Salivary amylase	Begins the digestion of carbohydrates; inactivated by stomach HCl
	Mucous glands	Mucus	—	Lubricates food bolus
Esophagus	Mucous glands	Mucus	—	Lubricates food bolus
Stomach	Gastric glands	Gastric juice	Lipase	Digests lipids into fatty acids and glycerol
			Pepsin	Digests proteins into polypeptides
	Gastric mucosa	HCl	—	Converts pepsinogen into active pepsin; kills microorganisms
	Mucous glands	Mucus	—	Lubricates
Small intestine	Liver	Bile	—	Emulsifies lipids; activates lipase
	Pancreas	Pancreatic juice	Amylase	Digests starch into maltose
			Chymotrypsin	Digests proteins into peptides and amino acids
			Lipase	Digests lipids into fatty acids and glycerol (requires bile salts)
			Nuclease	Digests nucleic acids into mononucleotides
			Trypsin	Digests proteins into peptides and amino acids
	Intestinal glands	Intestinal juice	Enterokinase	Digests inactive trypsinogen into active trypsin
			Lactase	Digests lactose into glucose and galactose
			Maltase	Digests maltose into glucose
			Peptidase	Digests polypeptides into amino acids
			Sucrase	Digests sucrose into glucose and fructose
	Mucous glands	Mucus	—	Lubricates
Large intestine	Mucous glands	Mucus	—	Lubricates

The pancreas also secretes bicarbonate (HCO_3^-) ions that help neutralize the acidic food residue coming from the stomach. Bicarbonate raises the pH from 2 to 7 for optimal digestion. Without such neutralization, pancreatic enzymes could not function.

ROLE OF THE LIVER AND GALLBLADDER IN DIGESTION

The **liver,** the largest organ in the mammalian body, is just under the diaphragm (*see figure 27.11*). In the liver, millions of specialized cells called hepatocytes take up nutrients absorbed from the intestines and release them into the bloodstream. Hepatocytes also manufacture the blood proteins prothrombin and albumin.

In addition, some major metabolic functions of the liver include:

1. Removal of amino acids from organic compounds.
2. Urea formation from proteins and conversion of excess amino acids into urea to decrease body levels of ammonia.
3. Manufacture of most of the plasma proteins, formation of fetal erythrocytes, destruction of worn-out erythrocytes, and synthesis of the blood-clotting agents prothrombin and fibrinogen from amino acids.
4. Synthesis of nonessential amino acids.
5. Conversion of galactose and fructose to glucose.
6. Oxidation of fatty acids.
7. Formation of lipoproteins, cholesterol, and phospholipids (essential cell membrane components).
8. Conversion of carbohydrates and proteins into fat.
9. Modification of waste products, toxic drugs, and poisons (detoxification).
10. Synthesis of vitamin A from carotene, and with the kidneys, participation in the activation of vitamin D.
11. Maintenance of a stable body temperature by raising the temperature of the blood passing through it. Its many metabolic activities make the liver the major heat producer in a mammal's body.
12. Manufacture of bile salts, which are used in the small intestine for the emulsification and absorption of simple fats, cholesterol, phospholipids, and lipoproteins.

13. Main storage center. The liver stores glucose in the form of glycogen, and with the help of insulin and enzymes, converts glycogen back into glucose as the body needs it. The liver also stores fat-soluble vitamins (A, D, E, and K), and minerals, such as iron, from the diet. The liver can also store fats and amino acids, and convert them into usable glucose as required.

The **gallbladder** (L. *galbinus*, greenish yellow) is a small organ near the liver (*see figure 27.11*). The gallbladder stores the greenish fluid called bile that the liver cells continuously produce. Bile is very alkaline and contains pigments, cholesterol, lecithin, mucin, bilirubin, and bile salts that act as detergents to emulsify fats (form them into droplets suspended in water) and aid in fat digestion and absorption. (Recall that fats are insoluble in water.) Bile salts also combine with the end products of fat digestion to form micelles. **Micelles** are lipid aggregates (fatty acids and glycerol) with a surface coat of bile salts. Because they are so small, they can cross the microvilli of the intestinal epithelium.

SUMMARY

1. Nutrition describes all of those processes by which an animal takes in, digests, absorbs, stores, and uses food (nutrients) to meet its metabolic needs. Digestion is the mechanical and chemical breakdown of food into smaller particles that the individual cells of an animal can absorb.
2. Losses of biosynthetic abilities have marked much of animal evolution. This tendency has led to the evolution of the following nutritional types: insectivores, herbivores, carnivores, and omnivores.
3. The nutrients that a heterotroph ingests can be divided into macronutrients and micronutrients. Macronutrients are needed in large quantities and include the carbohydrates, lipids, and proteins. Micronutrients are needed in small quantities and include the vitamins and minerals.
4. Only a few protists and animals can absorb nutrients directly from their external environment. Most animals must work for their nutrients. Various specializations have evolved for food procurement (feeding) in animals. Some examples include continuous versus discontinuous feeding, suspension feeding, deposit feeding, herbivory, predation, surface nutrient absorption, and fluid feeding.
5. The evolution and structure of the digestive system in various invertebrates and vertebrates reflect their eating habits, their rate of metabolism, and their body size.
6. The digestive system of vertebrates is one-way, leading from the mouth (oral cavity), to the pharynx, esophagus, stomach, small intestine, large intestine, rectum, and anus.
7. The coordinated contractions of the muscle layer of the gastrointestinal tract mix food material with various secretions and move the food from the oral cavity to the rectum. The two types of movement involved are segmentation and peristalsis.
8. Most digestion occurs in the duodenal portion of the small intestine. The products of digestion are absorbed in the walls of the jejunum and ileum. In the process of digestion, bile that the liver secretes makes fats soluble. The liver has many diverse functions. It controls the fate of newly synthesized food molecules, stores excess glucose as glycogen, synthesizes many blood proteins, and converts nitrogenous and other wastes into a form that the kidneys can excrete.
9. The large intestine has little digestive or nutrient absorptive activity. It functions principally to absorb water, to compact the material left over from digestion, and to be a storehouse for microorganisms.

SELECTED KEY TERMS

autotrophs (p. 434)
carnivores (p. 434)
digestion (p. 433)
herbivores (p. 434)
heterotrophs (p. 434)
macronutrients (p. 434)
micronutrients (p. 434)
nutrition (p. 433)
omnivores (p. 434)
suspension feeding (p. 438)
vitamin (p. 435)

CRITICAL THINKING QUESTIONS

1. What advantages are there to digestion? Would it not be simpler for a vertebrate to simply absorb carbohydrates, lipids, and proteins from its food and to use these molecules without breaking them down?
2. What might have been some evolutionary pressures acting on animals that led to the internalization of digestive systems?
3. Many digestive enzymes are produced in the pancreas and released into the duodenum. Why, then, has the mammalian stomach evolved the ability to produce pepsinogen?
4. Human vegetarians, unlike true herbivores, have no highly specialized fermentation chambers. Why?
5. Trace the fate of a hamburger from the mouth to the anus, identifying sites and mechanisms of digestion and absorption.