Thomas Mangelsen/Minden Pictures

An Alaskan brown bear *(Ursus arctos)* catching a sockeye salmon *(Oncornynchus nerka)*. Animals obtain nutrients by eating other organisms. Their digestive systems break down macromolecules in the food to produce simple organic molecules that are used for fuels and as building blocks for more complex molecules.

Study Plan

45 Animal Nutrition

Why It Matters

Invisible in the inky darkness, a deep-sea anglerfish (a member of the Order Lophiiformes) lies in wait, its gaping mouth lined with sharp teeth. Just above the mouth dangles a glowing lure suspended from a fishing-rod-like spine that projects from the fish's dorsal fin **(Figure 45.1).** The lure resembles a tiny fish; it even wiggles back and forth in imitation of swimming movements. Its glow is produced by bioluminescent bacteria that live symbiotically in the lure's tissues.

A hapless fish is attracted to the lure. As it comes within range, the anglerfish's mouth expands suddenly, creating a powerful suction that whips the prey in. The backward-angling fangs keep the prey from escaping. The strike takes only 6 ms (milliseconds), among the fastest of any known fishes.

Contractions of throat muscles send the prey to the anglerfish's stomach, which can expand to accommodate a meal as large as the anglerfish itself. In the fish's digestive tract, acids and enzymes dissolve the body of the prey, gradually breaking it into molecules small enough to be absorbed. In this function, the digestive system of the anglerfish is the same that of any other vertebrate, including humans—it provides nutrients that allow the animal to live. And the

David Shale/npl/Minden Pictures

Figure 45.1
A deep sea anglerfish, with its rod and lure lit and ready to attract prey.

anglerfish's adaptations for feeding, although bizarre to human sensibilities, are no more remarkable than those of many other animals.

Animal **nutrition**—which includes the processes by which food is ingested, digested, and absorbed into body cells and fluids—is the subject of this chapter. Our discussion begins with the basic categories of animal foods and **ingestion,** the feeding methods used to take food into the digestive cavity. Then we examine the process of **digestion:** the splitting of carbohydrates, proteins, lipids, and nucleic acids in foods into chemical subunits small enough to be absorbed into an animal's body fluids and cells. The chapter also presents the main structural and functional features of digestive systems, with special emphasis on humans and other mammals. The adaptations animals use to obtain and digest food are among their most strongly defining anatomical and functional characteristics.

45.1 Feeding and Nutrition

All organisms require sources of matter and energy for metabolism, homeostasis (maintaining their internal environment in a stable state; see Section 36.4), growth, and reproduction. For animals, meeting these nutritional requirements involves *feeding,* the uptake of food from the surroundings. Animals employ various feeding methods ranging from the ingestion of molecules in liquid solutions to eating entire organisms in one gulp. Once the food is ingested, digestive processes convert its molecules into absorbable subunits. In this section, we survey animal nutritional requirements and feeding methods as an introduction to animal digestive processes.

Animals Require both Organic and Inorganic Molecules for Nutrition

Plants and other photosynthesizers need only sunlight as an energy source and a supply of simple inorganic precursors such as water, carbon dioxide, and minerals to make all the organic molecules they require. In contrast, animals require a constant diet of organic molecules as a source of both energy and nutrients that they cannot make for themselves.

Animals are classified according to their sources of organic molecules. **Herbivores** such as antelopes, horses, bison, giraffes, kangaroos, manatees, and grasshoppers obtain organic molecules primarily by eating plants. **Carnivores**—cats, Tasmanian devils, penguins, sharks, and spiders, for example—primarily eat other animals. We say "primarily" because many herbivores eat animal matter at times, and a number of carnivores occasionally eat plant material. An antelope will eat insects as it grazes, and a grizzly bear, although primarily carnivorous, also eats berries. **Omnivores,** such as crows, cockroaches, and humans, eat both plants and animals and, in fact, any source of organic matter.

Organic molecules are the basis for two of the most fundamental processes of life: they act as fuels for oxidative reactions supplying energy and as building blocks for making complex biological molecules.

Energy supplies and requirements are usually described in terms of calories. A *calorie* (with a lowercase c) is the amount of heat energy required to raise 1 mL of pure water 1°C, from 14.5°C to 15.5°C. In animal nutrition, calories are usually considered in units of 1000 as kilocalories (kcal; the units listed on food packages in the United States) or Calories (with an uppercase C). One Calorie thus equals 1000 calories. Carbohydrates contain about 4.2 kcal per gram, fats about 9.5 kcal per gram, and proteins about 4.1 kcal per gram. At rest, a human female of average size expends about 1300 to 1500 kcal per day, and a human male about 1600 to 1800 kcal per day. Exercise and physical labor can increase these daily totals.

Carbohydrates and fats are the primary organic molecules used as fuels. Animals whose intake of organic fuels is inadequate, or whose assimilation of such fuels is abnormal, suffer from **undernutrition.** Undernutrition is a form of **malnutrition,** which is a condition resulting from an improper diet. **Overnutrition**, the condition caused by excessive intake of specific nutrients, is another main type of malnutrition.

An animal suffering from undernutrition essentially is starving for one or more nutrients, taking in fewer calories than needed for daily activities. Animals with chronic undernutrition lose weight because they have to use molecules of their own bodies as fuels. Mammals use stored fats and glycogen (animal starch) first. Once those stores have been used up, proteins are metabolized as fuels. The use of proteins as fuels leads to muscle wastage and, in the long term, to organ and brain damage and, therefore, eventually to death.

Organic molecules also serve as building blocks for carbohydrates, lipids, proteins, and nucleic acids. Animals can synthesize many of the organic molecules that they do not obtain directly in the diet by converting one type of building block into another. Typically, however, they cannot make certain amino acids and fatty acids from other organic molecules. These required organic building blocks are called **essential amino acids** and **essential fatty acids** because they must be obtained in the diet. If they are not obtained in the diet over a period of time, there may be serious consequences. For instance, protein synthesis cannot continue unless all 20 amino acids are present. In the absence of essential amino acids in the diet, the animal would have to break down its own proteins to provide them for new protein synthesis.

Animals must also take in **vitamins,** organic molecules required in small quantities that the animal cannot synthesize for itself. Many vitamins are *coenzymes,* nonprotein organic subunits associated with enzymes that assist in enzymatic catalysis (see Section 4.4).

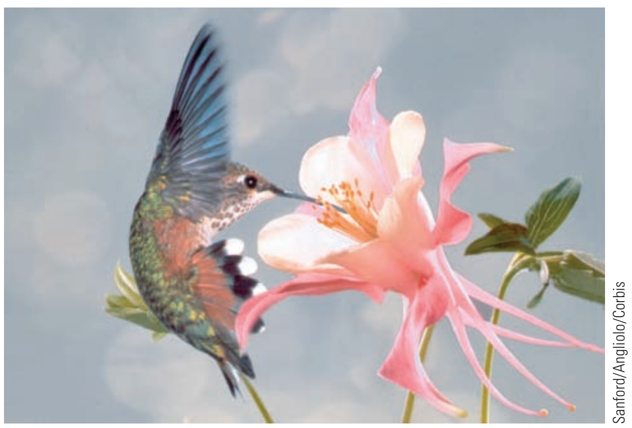
Individual species differ in the vitamins and essential amino acids and fatty acids they require. Various species also have differing dietary requirements for inorganic elements such as calcium, iron, and magnesium. These required inorganic elements are known collectively as **essential minerals.**

The essential amino acids, fatty acids, vitamins, and minerals are known collectively as an animal's **essential nutrients.** The list of essential nutrients differs from animal to animal. For domesticated animals, this means that specific feed formulations must be given to each type of animal. For instance, the essential nutrients for cats and dogs are different, which is why there are specific cat foods and dog foods, and why it is does not make good sense, nutritionally speaking, to feed cats and dogs human food.

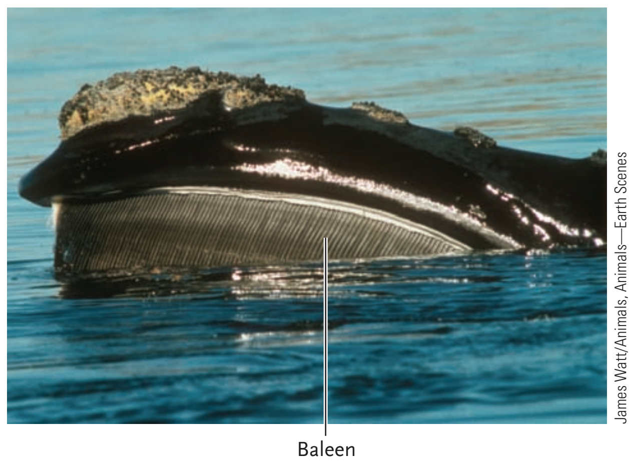
Animals Obtain Nutrients in Fluid, Particle, or Bulk Form

All animals display adaptations that allow them to obtain the food they need in particular environments. Although these adaptations are amazingly varied, animals can be classified into one of four groups according to overall feeding methods and the physical state of the organic molecules they consume. These four groups are fluid feeders, suspension feeders, deposit feeders, and bulk feeders **(Figure 45.2).**

a. Fluid feeder



b. Suspension feeder



c. Deposit feeder

d. Bulk feeder

Figure 45.2
Grouping of animals with respect to overall feeding methods and the physical state of the organic molecules they consume. **(a)** Fluid feeders, exemplified by a hummingbird, which obtains nectar from deep within a flower using its long bill and tongue. **(b)** Suspension feeders, exemplified by the northern right whale *(Balaena glacialis),* which gulps tons of water containing plankton into its mouth, pushes the water out through the sievelike baleen, and swallows the remaining plankton. **(c)** Deposit feeders, exemplified by a fiddler crab (*Uca* species), which sifts edible material from the sediment it takes into its mouth. **(d)** Bulk feeders, exemplified in an extreme way by a python, which ingests its prey (here, a gazelle) whole. Elastic ligaments connecting the jaws allow the snake's mouth to open wide enough to swallow large prey.

Fluid feeders obtain nourishment by ingesting liquids that contain organic molecules in solution. Among the invertebrates, aphids, mosquitoes, leeches, and spiders are examples of fluid feeders. Vertebrate fluid feeders include birds such as hummingbirds (see Figure 45.2a), which feed on flower nectar; parasitic fishes such as lampreys, which feed on body fluids of their hosts; and some bats, which feed on nectar or blood. Many fluid feeders have mouthparts specialized to reach the source of their nourishment. For example, mosquitoes, bedbugs, and aphids have needlelike mouthparts that pierce body surfaces. Nectar-feeding birds and bats have long tongues that can extend deep within flowers. Some fluid feeders use enzymes or other chemicals to liquefy their food or to keep it liquid during feeding. For example, spiders inject digestive enzymes that liquefy tissues inside their victim and then suck up the liquid. The saliva of mosquitoes, leeches, and vampire bats includes an anticoagulant that keeps blood in liquid form during a feeding by inhibiting the clotting reaction.

Suspension feeders ingest small organisms suspended in water, such as bacteria, protozoa, algae, and small crustaceans, or fragments of these organisms. Among the suspension feeders are aquatic invertebrates such as clams, mussels, and barnacles; many fishes; and even some birds and whales (see Figure 45.2b). These animals strain food particles suspended in water through a body structure covered with sticky mucus or through a filtering network of bristles, hairs, or other body parts. The trapped particles are then funneled into the animal's mouth. Bits of organic matter are trapped by the gills of bivalves such as clams and oysters, and plankton is filtered from water by the sievelike fringes of horny fiber hanging in the mouths of baleen whales (see Figure 45.2b).

Deposit feeders pick up or scrape particles of organic matter from solid material they live in or on. Earthworms are deposit feeders that eat their way through soil, taking the soil into their mouth and digesting and absorbing any organic material it contains. Some burrowing mollusks and tube-dwelling polychaete worms use body appendages to gather organic deposits from the sand or mud around them. Mucus on the appendages traps the organic material, and cilia move it to the mouth. The fiddler crab (*Uca* species) is also a deposit feeder (see Figure 45.2c). This animal has claws of markedly different sizes. The small claw picks up sediment and moves it to the mouth where the contents are sifted. The edible parts of the sediment are ingested, and the rest is put back on the sediment as a small ball. The feeding-related movement of the small claw over the larger claw looks like the crab is playing the large claw like a fiddle and hence gives the crab its name.

Bulk feeders are animals that consume sizeable food items whole or in large chunks. Most mammals eat this way, as do reptiles, most birds and fishes, and adult amphibians. Depending on the animal, adaptations for bulk feeding include teeth for tearing or chewing, claws and beaks for holding large food items, and jaws that are hinged or otherwise modified to permit a food mass to enter the mouth (see Figure 45.2d).

We now take up the processes by which animals, having fed, undertake the mechanical and chemical breakdown of food into absorbable molecular subunits.

Study Break

1. What are carnivores, herbivores, and omnivores?
2. What are essential nutrients, and are they the same for all animals?
3. What is the difference between deposit feeders and suspension feeders?

45.2 Digestive Processes

Digestive processes break food molecules into molecular subunits that can be absorbed into body fluids and cells. The breakdown occurs by **enzymatic hydrolysis,** in which chemical bonds are broken by the addition of H^+ and OH^-, the components of a molecule of water (see Section 3.2). Specific enzymes speed these reactions: *amylases* catalyze the hydrolysis of starches, *lipases* break down fats and other lipids, *proteases* hydrolyze proteins, and *nucleases* digest nucleic acids. Depending on the animal, the enzymatic hydrolysis of food molecules may take place inside or outside the body cells.

Intracellular Digestion Takes Place within Cells; Extracellular Digestion Occurs in an Internal Pouch or Tube

In **intracellular digestion,** cells take in food particles by endocytosis (described in Section 6.5). Inside the cell, the endocytic vesicle containing the food particles fuses with a lysosome, a vesicle containing hydrolytic enzymes. The molecular subunits produced by the hydrolysis pass from the vesicle to the cytosol. Any undigested material remaining in the vesicle is released to the outside of the cell by exocytosis (also discussed in Section 6.5). Only a few animals, primarily sponges and some cnidarians, break down food exclusively by intracellular digestion. In sponges, water containing particles of organic matter and microorganisms enter the animal's saclike body through pores in the body wall (see Figure 29.8). In the body cavity, individual *choanocytes* (collar cells) lining the body wall trap the food particles, take them in by endocytosis, and transport them to amoeboid cells, which digest them intracellularly.

Extracellular digestion takes place outside body cells, in a pouch or tube enclosed within the body. Epithelial cells lining the pouch or tube secrete enzymes that digest the food. Processing food in specialized compartments in this way prevents the animal from digesting its own body tissues.

Most invertebrates and all vertebrates digest food primarily by extracellular digestion. From an adaptive standpoint, extracellular digestion greatly expands the range of available food sources by allowing animals to digest much larger food items than single cells can take in. Extracellular digestion also allows animals to eat large batches of food, which can be stored and digested while the animal continues other activities.

Saclike Digestive Systems Have a Single Opening through Which Food Enters and Undigested Matter Exits

Some animals, including flatworms and cnidarians such as hydras, corals, and sea anemones, have a saclike digestive system with a single opening, a mouth, that serves both as the entrance for food and the exit for undigested material. In some of these animals, such as the flatworm *Dugesia,* the digestive cavity is called a **gastrovascular cavity** because it contributes to circulation as well as digestion. Food is brought to the mouth by a protrusible **pharynx** (a throat that can be stuck out) and then enters the gastrovascular cavity **(Figure 45.3);** glands in the cavity wall secrete enzymes that begin the digestive process. Cells lining the cavity then take up the partially digested material by endocytosis and complete digestion intracellularly. Undigested matter is released to the outside through the pharynx and mouth.

Digestive Tubes Typically Process Nutrients in Five Successive Steps

Most invertebrates and all vertebrates have a tubelike digestive system with two openings that form a separate mouth and anus; the digestive contents move in one direction through specialized regions of the tube, from the mouth to the anus. This type of digestive system is called a **digestive tube,** *gut, alimentary canal, digestive tract,* or *gastrointestinal (GI) tract.* Structurally, the inside of the digestive tube—called the **lumen**—is external to all body tissues. In other words, the lumen is *outside* of the body.

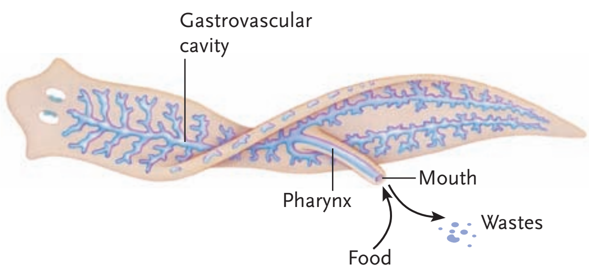


Figure 45.3
The digestive system of the flatworm *Dugesia.* The gastrovascular cavity (in blue) is a blind sac, with one opening to the exterior through which food is ingested and wastes are expelled.

In most animals with a digestive tube, digestion occurs in five successive steps, with each step taking place in a specialized region of the tube. The tube thus acts as a sort of biological disassembly line, with food entering at one end and passing through as many as five areas in which food processing occurs.

1. **Mechanical processing:** Chewing, grinding, and tearing breaks food chunks into smaller pieces, increasing their mobility and the surface area exposed to digestive enzymes.
2. **Secretion of enzymes and other digestive aids:** Enzymes and other substances that aid the process of digestion, such as acids, emulsifiers, and lubricating mucus, are released into the tube.
3. **Enzymatic hydrolysis:** Food molecules are broken down through enzyme-catalyzed reactions into absorbable molecular subunits.
4. **Absorption:** The molecular subunits are absorbed from the digestive contents into body fluids and cells.
5. **Elimination:** Undigested materials are expelled through the anus.

The material being digested is pushed along by muscular contractions of the wall of the digestive tube. During its progress through the tube, the digestive contents may be stored temporarily at one or more locations. The storage allows animals to take in larger quantities of food than they can process immediately, so that feedings can be spaced in time rather than continuous.

Digestion in an Annelid. The earthworm (genus *Lumbricus,* **Figure 45.4a**) is a deposit feeder. As it burrows, it pushes soil particles into its mouth. The particles pass from the mouth through a connecting passage, the **esophagus**, into the **crop**, an enlargement of the digestive tube where the contents are stored and mixed with lubricating mucus. This mixture enters the **gizzard,** which contains grains of sand, and is ground into fine particles by muscular contractions of the wall. The pulverized mixture then enters a long **intestine,** where the organic matter is hydrolyzed by enzymes secreted into the digestive tube. As muscular contractions of the intestinal wall move the mixture along, cells lining the intestine absorb the molecular subunits produced by digestion. The absorptive surface of the intestine is increased by folds of the wall called *typhlosoles.* At the end of the intestine, the undigested residue is expelled through the anus.

Digestion in an Insect. Herbivorous insects such as the grasshopper **(Figure 45.4b)** tear leaves and other plant parts into small particles with hard external

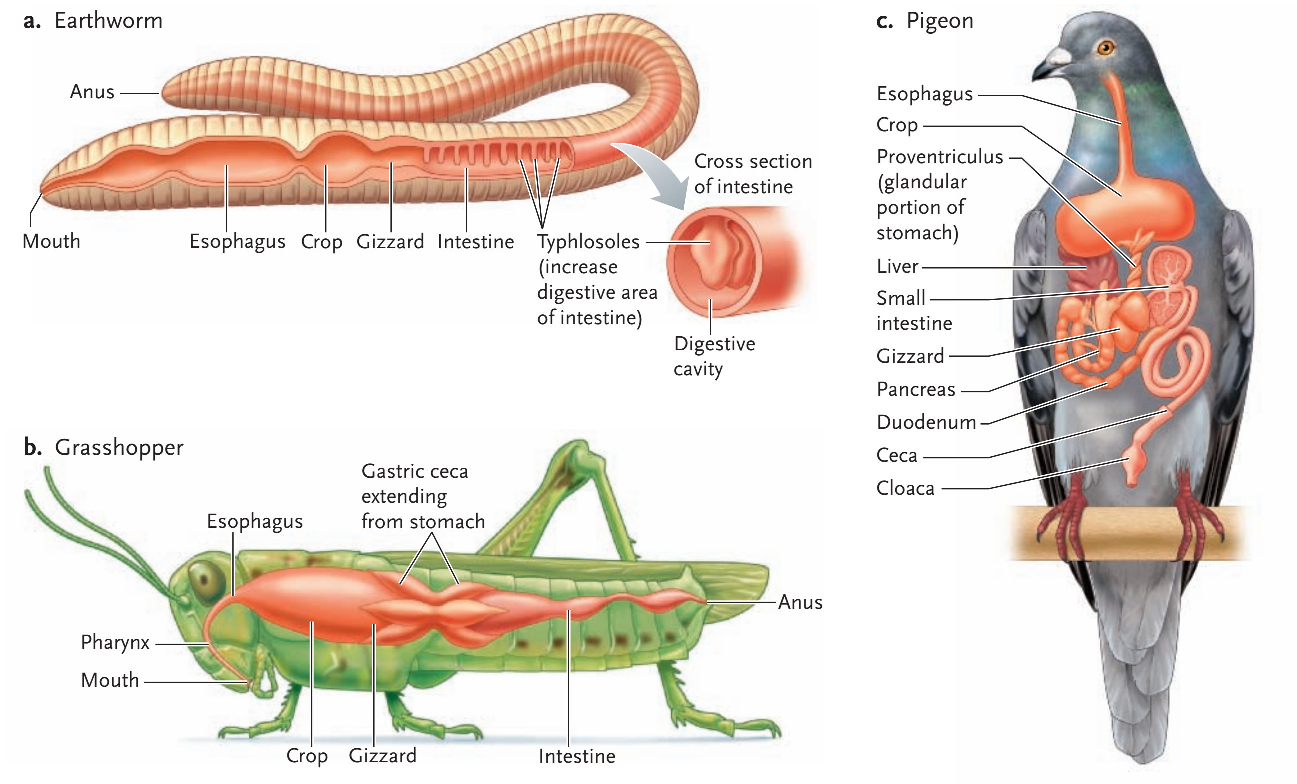


Figure 45.4 The digestive systems of an annelid, the earthworm **(a),** an insect, the grasshopper **(b),** and a bird, the pigeon *(Columba)* **(c).**

mouth parts. From the mouth, the food particles pass through the pharynx, where salivary secretions moisten the mixture before it enters the esophagus and passes into the crop. These secretions begin the process of chemical digestion. From the crop, the food mass enters the gizzard, which grinds it into smaller pieces. These food particles enter the **stomach,** in which food is stored and digestion begins. Insect stomachs have saclike outgrowths, the *gastric ceca* (*caecus* = blind), where enzymes hydrolyze the digestive contents; the products of digestion are absorbed through the walls of the ceca. The undigested contents then move into the intestine for further digestion and absorption. At the end of the intestine, water is absorbed from the undigested matter and the remnants are expelled through the anus. The digestive systems of other arthropods are similar to the insect system.

Digestion in a Bird. A pigeon (*Columba,* **Figure 45.4c**) picks up seeds with its bill. The bird's tongue moves the seeds into its mouth, where they are moistened by mucus-filled saliva and swallowed whole (birds have no teeth). The seeds then pass through the pharynx into the esophagus. (In some cases, birds crack open seeds with their bills and ingest seed kernels in a similar fashion.) The anterior end of the esophagus is tubelike; at the posterior end is the pouchlike crop, in which the bird can store large quantities of food. From the crop, the food passes into the anterior glandular portion of the stomach, called the *proventriculus,* which secretes digestive enzymes and acids. The posterior end is the gizzard, in which the seeds are ground into fine particles, aided by ingested bits of sand and rock. The food particles are released into the intestine, where the liver secretes bile and the pancreas adds digestive enzymes. The molecular subunits produced by enzymatic digestion are absorbed as the mixture passes along the intestine, and the undigested residues are expelled through the anus.

Many of the structures of the pigeon's digestive system, including the mouth, pharynx, esophagus, stomach, intestine, liver, and pancreas, occur in almost all vertebrates.

Study Break

1. Distinguish between extracellular digestion and intracellular digestion.
2. What are the five steps of food processing in a digestive tube?

45.3 Digestion in Humans and Other Mammals

Mammals digest foods using the same five steps as other animals with a digestive tube: mechanical processing, secretion of enzymes and other digestive aids, enzymatic hydrolysis, absorption of molecular subunits, and elimination. The mammalian digestive system is a series of specialized digestive regions that perform these steps, including the mouth, pharynx,

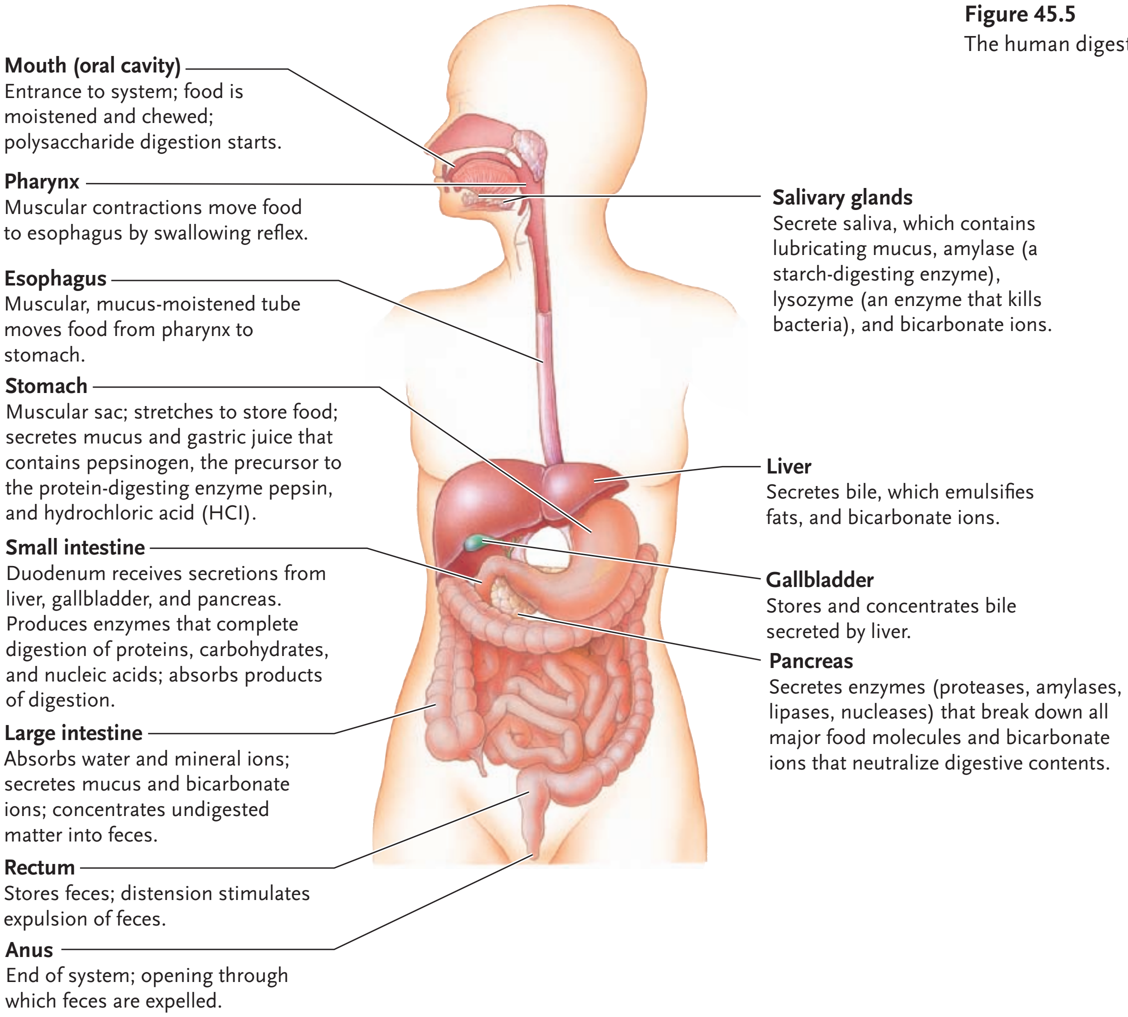


Figure 45.5
The human digestive system.

esophagus, stomach, small and large intestines, and anus **(Figure 45.5).** These regions are under the control of the nervous and endocrine systems.

Humans Require Specific Essential Amino Acids, Fatty Acids, Vitamins, and Minerals in Their Diet

The human digestive system meets our basic needs for fuel molecules and for a wide range of nutrients, including the molecular building blocks of carbohydrates, lipids, proteins, and nucleic acids. If the diet is adequate, the digestive system also absorbs the essential nutrients—the amino acids, fatty acids, vitamins, and minerals that cannot be synthesized within our bodies.

Essential Amino Acids and Fatty Acids. There are eight essential amino acids for adult humans: lysine, tryptophan, phenylalanine, threonine, valine, methionine, leucine, and isoleucine. Infants and young children also require histidine. The proteins in fish, meat, egg whites, milk, and cheese supply all the essential amino acids, provided those foods are eaten in adequate quantities. In contrast, the proteins of many plants are deficient in one or more of the essential amino acids. Corn, for example, contains inadequate amounts of lysine, and beans contain little methionine. Vegetarians, and especially vegans who eat a diet with no animal-derived nutrients, must choose their foods carefully to obtain all of the essential amino acids **(Figure 45.6).** Such diets typically include combinations of foods, each of which provides some amino acids, and that together contain all of the essential amino acids. An example is including in the diet rice or corn (low in lysine but high in methionine) with legumes such as lentils or with soybeans, perhaps in the form of tofu (low in methionine but high in lysine).

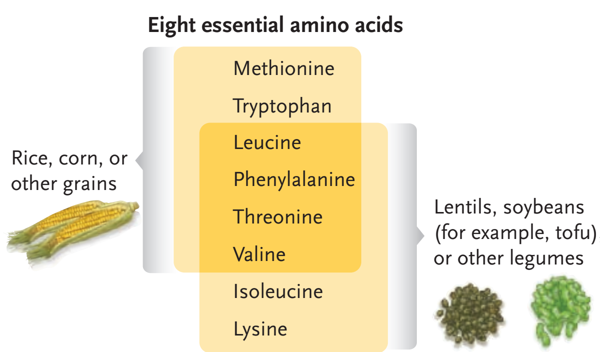


Figure 45.6
Obtaining essential amino acids in a human vegetarian diet.

If the diet lacks one or more essential amino acids, many enzymes and other proteins cannot be synthesized in sufficient quantities. The resulting protein deficiency is most damaging to the young, who must rapidly synthesize proteins for development and growth. Even mild protein starvation during pregnancy or for some months after birth can retard a child's mental and physical development.

Only two fatty acids, linoleic acid and linolenic acid, are essential in the human diet. Both are required for synthesis of phospholipids forming parts of biological membranes and certain hormones. Because almost all foods contain these fatty acids, most people have no problem obtaining them. However, people on a low-fat diet deficient in linoleic acid and linolenic acid are at serious risk for developing coronary heart disease. That is, there is an inverse correlation between the concentration of these essential fatty acids in the diet and the incidence of coronary heart disease. This is illustrated in the case of Hindu vegetarians from India. Their diet consists mainly of low-fat grains and legumes—clearly a low-fat diet—yet their rate of coronary heart disease is higher than that in the United States and Europe, where dietary fat content is higher.

Vitamins. Humans require 13 known vitamins in their diet. Many metabolic reactions depend on vitamins, and the absence of one vitamin can affect the functions of the others. These essential nutrients fall into two classes: **water-soluble** (hydrophilic) **vitamins** and **fat-soluble** (hydrophobic) **vitamins** (summarized in **Table 45.1**). The body stores excess fat-soluble vitamins in adipose tissues, but any amount of water-soluble vitamins above daily nutritional requirements is excreted in the urine. Thus, meeting the daily minimum requirements of water-soluble vitamins is critical. The body can tap its stores of fat-soluble vitamins to meet daily requirements; however, these stores are quickly depleted, so that prolonged deficiencies of the fat-soluble vitamins also become critical to health.

Most of us get all the vitamins we need through a normal and varied diet that includes meats, fish, eggs, cheese, and vegetables. Vitamin supplements are usually necessary only for strict vegetarians, newborns, the elderly, and individuals who are taking medication that affects the body's uptake of nutrients.

Vitamin D (calciferol) differs from other essential vitamins because humans can actually synthesize it themselves, through the action of ultraviolet light on lipids in the skin. However, many people are not exposed to enough sunlight to make sufficient quantities of the vitamin, and so must rely on dietary sources. And, although we cannot make vitamin K, much of our requirement for this vitamin is supplied through the metabolic activity of bacteria living in our large intestine. Vitamin K deficiency, therefore, is exceedingly rare in healthy persons. Vitamin K plays a role in blood clotting, so individuals with vitamin K deficiency will bruise easily and show increased blood clotting times. Vitamin K deficiency can be caused in persons on long-term antibiotic therapy because the antibiotics kill intestinal bacteria.

Other mammals have essentially the same vitamin requirements as humans, with some differences. For example, most other mammals, with the exception of primates, guinea pigs, and fruit bats, can synthesize vitamin C. So far as is known, no animal can synthesize B vitamins, but ruminants such as cattle and deer are supplied with these vitamins by microorganisms that live in the digestive tract (see Section 45.5).

Minerals. Many minerals are essential in the human diet **(Table 45.2).** Some of them, called **macronutrients,** are required in amounts ranging from 50 mg to more than a gram per day; others, such as zinc, are **micronutrients,** or **trace elements,** required only in small amounts, some less than 1 mg per day. All of the minerals, although listed as elements, are ingested as compounds or as ions in solution.

A normal and varied diet supplies adequate amounts of the essential minerals. Supplements may be required for those on a strict vegetarian diet, the very young, and the aged. Overdoses of some minerals can cause problems; ingesting excess iron, for example, has been linked to liver, heart, and blood vessel damage; too much sodium can lead to elevated blood pressure and excess water retention in tissues.

We now turn to the structures that extract nutrients from ingested foods. We begin with a survey of digestive structures common to all vertebrates.

Four Major Layers of the Gut Each Have Specialized Functions in Digestion

The wall of the gut in mammals and other vertebrates contains four major layers, each with specialized functions. These layers are shown for the stomach in **Figure 45.7.**

1. The **mucosa,** which contains epithelial and glandular cells, lines the inside of the gut. The epithelial cells absorb digested nutrients and seal off the digestive contents from body fluids. The glandular cells secrete enzymes, aids to digestion such as lubricating mucus, and substances that adjust the pH of the digestive contents.
2. The **submucosa** is a thick layer of elastic connective tissue that contains neuron networks and blood and lymph vessels. The neuron networks provide local control of digestive activity and carry signals between the gut and the central nervous system. The lymph vessels carry absorbed lipids to other parts of the body.

Table 45.1 **Vitamins: Sources, Functions, and Effects of Deficiencies in Humans**

Vitamin	Common Sources	Main Functions	Effects of Chronic Deficiency
Fat-Soluble Vitamins			
A (retinol)	Yellow fruits, yellow or green leafy vegetables; also in fortified milk, egg yolk, fish liver	Used in synthesis of visual pigments, bone, teeth; maintains epithelial tissues	Dry, scaly skin; lowered resistance to infections; night blindness
D (calciferol)	Fish liver oils, egg yolk, fortified milk; manufactured when body exposed to sunshine	Promotes bone growth and mineralization; enhances calcium absorption from gut	Bone deformities (rickets) in children; bone softening in adults
E (tocopherol)	Whole grains, leafy green vegetables, vegetable oils	Antioxidant; helps maintain cell membrane and red blood cells	Lysis of red blood cells; nerve damage
K (napthoquinone)	Intestinal bacteria; also in green leafy vegetables, cabbage	Promotes synthesis of blood clotting protein by liver	Abnormal blood clotting, severe bleeding (hemorrhaging)
Water-Soluble Vitamins			
B_1 (thiamine)	Whole grains, green leafy vegetables, legumes, lean meats, eggs, nuts	Connective tissue formation; folate utilization; coenzyme forming part of enzyme in oxidative reactions	Beriberi; water retention in tissues; tingling sensations; heart changes; poor coordination
B_2 (riboflavin)	Whole grains, poultry, fish, egg white, milk, lean meat	Coenzyme	Skin lesions
Niacin	Green leafy vegetables, potatoes, peanuts, poultry, fish, pork, beef	Coenzyme of oxidative phosphorylation	Sensitivity to light; contributes to pellagra (damage to skin, gut, nervous system, etc.)
B_6 (pyridoxine)	Spinach, whole grains, tomatoes, potatoes, meats	Coenzyme in amino acid and fatty acid metabolism	Skin, muscle, and nerve damage
Pantothenic acid	In many foods (meats, yeast, egg yolk especially)	Coenzyme in carbohydrate and fat oxidation; fatty acid and steroid synthesis	Fatigue, tingling in hands, headaches, nausea
Folic acid	Dark green vegetables, whole grains, yeast, lean meats; intestinal bacteria produce some folate	Coenzyme in nucleic acid and amino acid metabolism; promotes red blood cell formation	Anemia; inflamed tongue; diarrhea; impaired growth; mental disorders; neural tube defects and low birth weight in newborns
B_{12} (cobalamin)	Poultry, fish, eggs, red meat, dairy foods (not butter)	Coenzyme in nucleic acid metabolism; necessary for red blood cell formation	Pernicious anemia; impaired nerve function
Biotin	Legumes, egg yolk; colon bacteria produce some	Coenzyme in fat and glycogen formation, and amino acid metabolism	Scaly skin (dermatitis), sore tongue, brittle hair, depression, weakness
C (ascorbic acid)	Fruits and vegetables, especially citrus, berries, cantaloupe, cabbage, broccoli, green pepper	Vital for collagen synthesis; antioxidant	Scurvy, delayed wound healing, impaired immunity

3. In most regions of the gut, the **muscularis** is formed by two smooth muscle layers, a *circular layer* that constricts the diameter of the gut when it contracts and a *longitudinal layer* that shortens and widens the gut. The stomach also has an *oblique layer* running diagonally around its wall. The circular and longitudinal muscle layers of the muscularis coordinate their activities to push the digestive contents through the gut **(Figure 45.8).** In this mechanism, called **peristalsis**, the circular muscle layer contracts in a wave that passes along the gut, constricting the gut and pushing the digestive contents onward. Just in front of the advancing constriction, the longitudinal layer contracts, shortening and expanding the tube and making space for the contents to advance.
4. The outermost gut layer, the **serosa**, consists of connective tissue that secretes an aqueous, slippery fluid. The fluid lubricates the areas between the digestive organs and other organs, reducing friction between them as they move together as a result of muscle movement. Along much of the length of the digestive system, the serosa is continuous with the *mesentery,* a tissue that suspends the digestive system from the inner wall of the abdominal cavity.

Table 45.2 Major Minerals: Sources, Functions, and Effects of Deficiencies in Humans

Mineral	Sources	Functions	Effects of Deficiencies
Calcium (Ca)	Dairy products, leafy green vegetables, legumes, whole grains, nuts	Bone, tooth formation; blood clotting; neural and muscle action	Stunted growth; diminished bone mass (osteoporosis)
Chlorine (Cl)	Table salt, meat, eggs, dairy products	HCl formation in stomach, contributes to body's acid-base balance; neural function, water balance	Muscle cramps; impaired growth; poor appetite
Chromium (Cr)*	Meat, liver, cheese, whole grains, brewer's yeast, peanuts	Roles in carbohydrate metabolism	Impaired response to insulin; increases risk of type 2 diabetes mellitus
Cobalt (Co)*	Meat, liver, fish, milk	Constituent of vitamin B_{12} (required for red blood cell maturation)	Same as for vitamin B_{12} (see Table 45.1)
Copper (Cu)*	Nuts, legumes, seafood, drinking water, whole grains, nuts	Used in synthesis of melanin, hemoglobin, and some electron transport chain components in mitochondria	Anemia, changes in bone and blood vessels
Fluorine (F)*	Fluoridated water, tea, seafood	Bone, tooth maintenance	Tooth decay
Iodine (I)*	Marine fish, shellfish, iodized salt	Thyroid hormone formation	Goiter (enlarged thyroid), with metabolic disorders
Iron (Fe)	Liver, whole grains, green leafy vegetables, legumes, nuts, eggs, lean meat, molasses, dried fruit, shellfish	Component of hemoglobin, cytochrome, myoglobin	Iron-deficiency anemia
Magnesium (Mg)	Whole grains, green vegetables, legumes, nuts, dairy products	Required for action of many enzymes; roles in muscle, nerve function	Weak, sore muscles; impaired neural function
Manganese (Mn)*	Whole grains, nuts, legumes, many fruits	Activates many enzymes, including ones with roles in synthesis of urea, fatty acids	Abnormal bone and cartilage
Molybdenum (Mo)*	Dairy products, whole grains, green vegetables, legumes	Component of some enzymes	Impaired nitrogen excretion
Phosphorus (P)	Whole grains, legumes, poultry, red meat, dairy products	Component of bones and teeth, nucleic acids, ATP, phospholipids	Muscular weakness; loss of minerals from bone
Potassium (K)	Meat, milk, many fruits, vegetables	Muscle and neural function; roles in protein synthesis	Muscular weakness
Selenium (Se)*	Meat, seafood, cereal grains, poultry, garlic	Constituent of several enzymes; antioxidant	Muscle pain
Sodium (Na)	Table salt, dairy products, meats, eggs	Acid-base balance, water balance; roles in muscle and neural function	Muscle cramps
Sulfur (S)	Meat, eggs, dairy products	Component of body proteins	Same as protein deficiencies
Zinc (Zn)*	Whole grains, legumes, nuts, meats, seafood	Component of digestive enzymes and transcription factors; roles in normal growth, wound healing, sperm formation, taste and smell	Impaired growth, scaly skin, impaired immune function

*Required in trace amounts in diet

Powerful rings of smooth muscle called **sphincters** form valves between major regions of the digestive tract. By contracting and relaxing, sphincters control the passage of the digestive contents from one region to the next, and ultimately through the anus.

The specialized regions of the gut that perform the sequential processes of digestion in humans allow us to extract nutrients efficiently from the highly varied foods we ingest.

Food Begins Its Travel through the Digestive System in the Mouth, Pharynx, and Esophagus

The human digestive system in its normal contracted state in a living adult is about 4.5 m long. Fully relaxed, it is about twice as long. Food begins its travel through this tract in the mouth, where the teeth cut, tear, and crush food items into small pieces. While chewing is

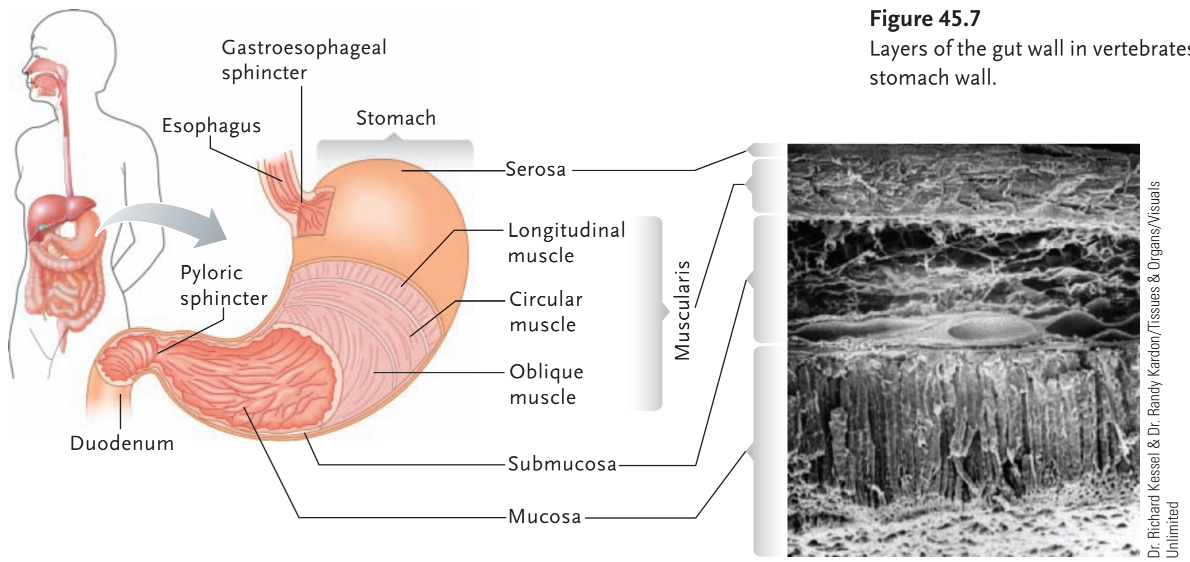
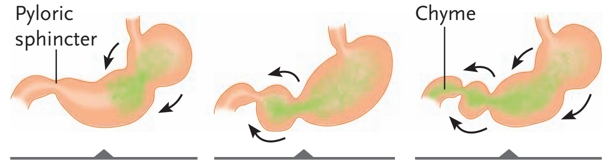


Figure 45.7
Layers of the gut wall in vertebrates, as seen in the stomach wall.

in progress, three pairs of **salivary glands** secrete saliva through ducts that open on the inside of the cheeks and under the tongue.

Saliva, which is more than 99% water, moistens the food. Saliva contains **salivary amylase,** which hydrolyzes starches to the disaccharide maltose. It also contains mucus, which lubricates the food mass, and bicarbonate ions (HCO_3^-), which neutralize acids in the food and keep the pH of the mouth between 6.5 and 7.5, which is the optimal range for salivary amylase to function. Another component of saliva is *lysozyme,* an enzyme that kills bacteria by breaking open their cell walls. Some 1 to 2 L of saliva are secreted into the mouth each day.

After a suitable period of chewing, the food mass, called a **bolus,** is pushed by the tongue to the back of the mouth, where touch receptors detect the pressure and trigger the *swallowing reflex* **(Figure 45.9).** The reflex is an involuntary action produced by contractions of muscles in the walls of the pharynx that direct food into the esophagus. Peristaltic contractions of the esophagus, aided by mucus secreted by the esophagus, propel a bolus towards the stomach. The passage of a bolus down the esophagus stimulates the *gastroesophageal sphincter* at the junction between the esophagus and



1 The circular layer of the muscularis contracts in a wave, constricting the gut and pushing the digestive contents onward.

2 The longitudinal layer contracts, shortening and expanding the gut and making space for the contents to advance.

3 Partially processed food (chyme) enters the small intestine.

Figure 45.8
The waves of peristaltic contractions moving food through the stomach.

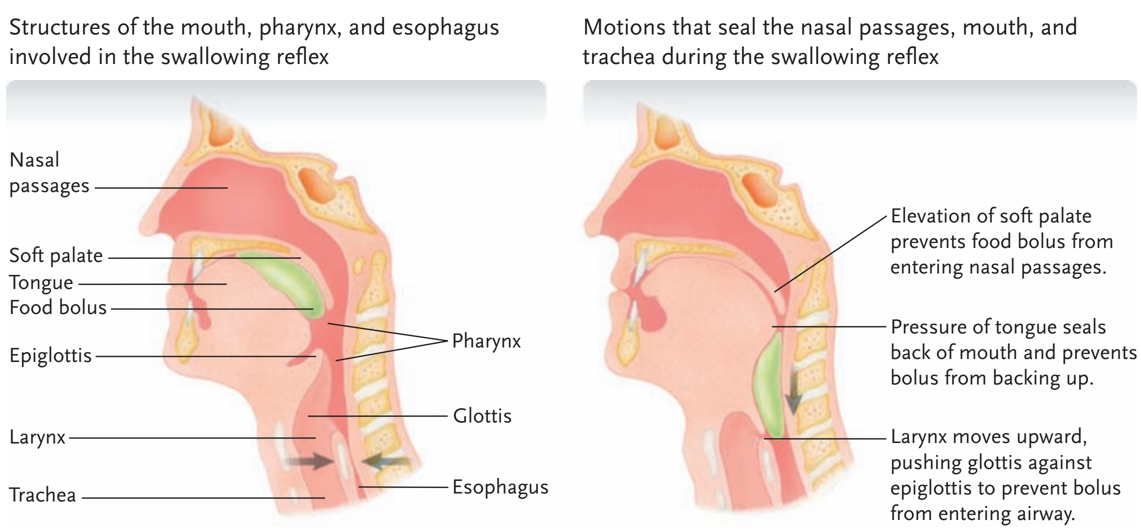


Figure 45.9
The swallowing reflex.

the stomach (see Figure 45.7) to open and admit the bolus to the stomach. After the bolus enters the stomach, the sphincter closes tightly. If the closure is imperfect, the acidic stomach contents can enter the esophagus and produce the irritation and pain we recognize as *acid reflux* or heartburn.

We can consciously initiate the swallowing reflex. However, once the swallowing reflex has begun, we cannot voluntarily stop it, as you might have noticed when you get that feeling of a piece of food or a pill being stuck in the throat or chest. This is because the muscles of the pharynx and upper esophagus are skeletal muscles, which you can control, while the muscles below are smooth muscles, which you cannot control.

Involuntary movements of the tongue and soft palate at the back of the mouth prevent food from backing into the mouth or nasal cavities. Entry into the trachea (the airway to the lungs) is blocked by closure of the *glottis* (the space between the vocal cords) and an upward movement of the *larynx* (the voice box) at the top of the trachea, which closes against a flaplike valve, the **epiglottis.** You can feel the larynx and the front of the epiglottis bob upward if you place your hand on your throat while you swallow. If these blocking mechanisms fail, touch receptors in the nasal passages and larynx trigger coughing and sneezing reflexes that clear these passages.

The Stomach Stores Food and Continues Digestion

The stomach is a muscular, elastic sac that stores food and adds secretions that further the process of digestion. The mucosal layer of the stomach is an epithelium covered with tiny *gastric pits* that are entrances to millions of *gastric glands.* These glands extend deep into the stomach wall and contain cells that secrete some of the products needed to digest food.

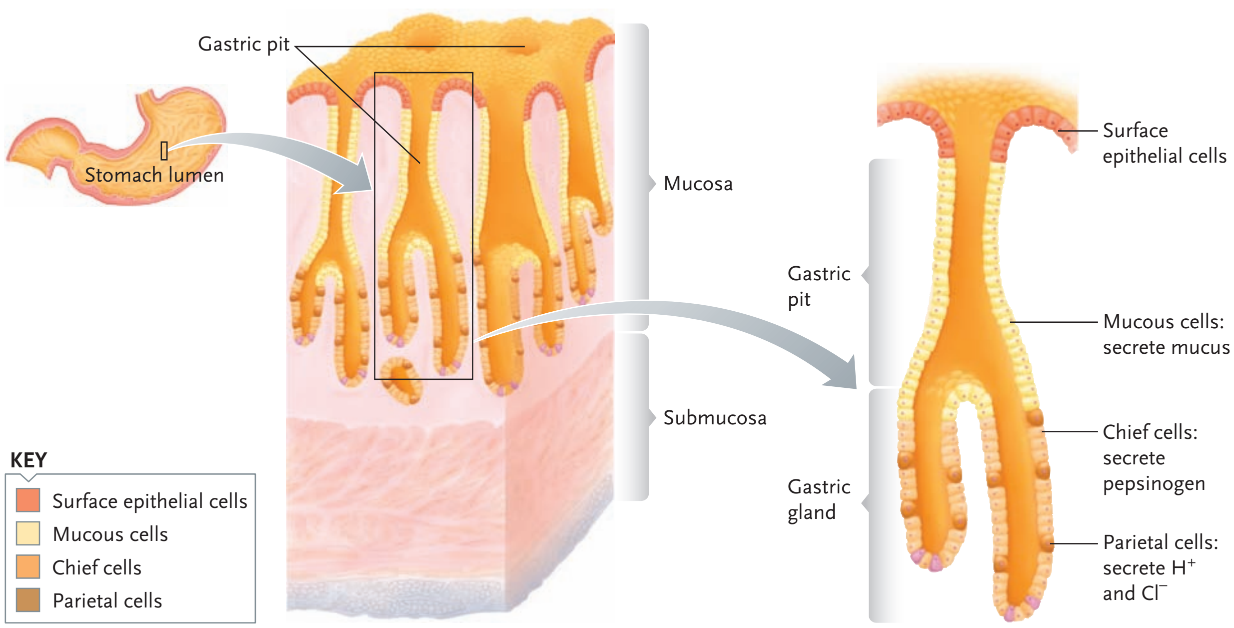
The entry of food into the stomach activates stretch receptors in its wall. Signals from the stretch receptors stimulate the secretion of **gastric juice (Figure 45.10),** which contains **pepsinogen,** the precursor for the digestive enzyme pepsin, hydrochloric acid (HCl), and lubricating mucus. The stomach secretes about 2 L of gastric juice each day.

Pepsinogen is secreted by *chief cells* in the gastric pits. It is an inactive precursor molecule that is converted to the digestive enzyme **pepsin** by the highly acid conditions of the stomach. Once produced, pepsin itself can catalyze the reaction that converts more pepsinogen to pepsin. Pepsin begins the digestion of proteins by introducing breaks in polypeptide chains. The activation of pepsinogen illustrates a common theme in the digestive system: powerful hydrolytic enzymes that would be dangerous to the cells secreting them are synthesized in the form of inactive precursors and are not converted into active form until they are exposed to the digestive contents.

Parietal cells secrete H^+ and Cl^-, which combine to form HCl in the lumen of the stomach. The HCl lowers the pH of the digestive contents to pH 2 or lower, the level at which pepsin reaches optimal activity. To put this pH in perspective, lemon juice is pH 2.4, and sulfuric acid or battery acid is approximately pH 1. The acidity of the stomach also helps break up food particles and causes proteins in the digestive contents to unfold, exposing their peptide linkages to hydrolysis by pepsin. The acid also kills most of the bacteria that reach the stomach and stops the action of salivary amylase.

A thick coating of alkaline mucus, secreted by *mucous cells,* protects the stomach's mucosal layer from attack by pepsin and HCl. Behind the mucous barrier, tight junctions between cells prevent gastric juice from seeping into the stomach wall. Even so, some break-

Figure 45.10
Cells that secrete mucus, pepsin, and HCl in the stomach lining.



down of the stomach's mucosal layer does occur. However, the damage is normally repaired quickly by the rapid division of mucosal cells. Even without damage, the rapid cell division leads to complete replacement of the stomach's mucosal layer.

Most bacteria cannot survive the highly acid environment of the stomach, but one, *Helicobacter pylori,* thrives there. In some people, the bacterium breaks down the mucous barrier, exposing the stomach wall to attack by HCl and pepsin. The resulting lesion, known as a *peptic* or *stomach ulcer,* causes bleeding and pain. If untreated, an ulcer can become so deep that it perforates the entire stomach wall, with potentially fatal consequences. Ulcers are treated by taking an antibiotic that kills *H. pylori.* Barry J. Marshall of the University of Western Australia and J. Robin Warren of Royal Perth Hospital received a 2005 Nobel Prize for their discovery that a bacterium is responsible for most human ulcers.

As part of the digestive process, contractions of the stomach walls continually mix and churn the contents, which can amount to as much as 2 L when the stomach is full. Peristaltic contractions of the stomach wall move the digestive contents toward the *pyloric sphincter* (*pylorus* = gatekeeper) at the junction between the stomach and small intestine. The arrival of a strong stomach contraction relaxes and opens the valve briefly, releasing a pulse of the stomach contents, now called **chyme,** into the small intestine (see Figure 45.8).

Depending on the volume and composition of the stomach contents, it can take from one to six hours for the stomach to empty after a meal. Feedback controls that regulate the rate of gastric emptying tend to match it to the rate of digestion, so that food is not moved along faster than it can be chemically processed. In particular, when chyme with high fat content and high acidity enters the first part of the small intestine, it stimulates the mucosal layer to secrete hormones that slow stomach emptying. Fat is digested more slowly than other nutrients, and it is digested only in the lumen of the small intestine. Therefore, further emptying of the stomach is prevented until the processing of fat has been completed in the small intestine. This is why a fatty meal, such as a greasy pizza, feels so heavy in the stomach. Highly acidic chyme must be neutralized by bicarbonate in the small intestine. Unneutralized stomach acid inactivates digestive enzymes secreted in the small intestine and, therefore, such acid inhibits further emptying of the stomach until it is neutralized.

The Small Intestine Completes Digestion and Begins the Absorption of Nutrients

No absorption of nutrients occurs in the mouth, pharynx, or esophagus; with the exception of a few substances, such as alcohol, aspirin, caffeine, and water, little absorption occurs in the stomach. Most absorption begins, and digestion is completed, as the contents move through the small intestine.

The "small" in the small intestine refers to its diameter, about 4 cm. It is roughly 6 m long and complexly coiled within the abdominal cavity. The lining of the small intestine folds into ridges that are densely covered by microscopic, fingerlike extensions, the **intestinal villi** (singular, *villus*). In addition, the epithelial cells covering the villi have a *brush border* consisting of fingerlike projections of the plasma membrane called **microvilli (Figure 45.11).** The intestinal villi and microvilli are estimated to increase the absorptive surface area of the small intestine to as much as 300 square meters, about the size of a doubles tennis court.

Secretions of the Pancreas, Liver, and Intestinal Mucosa. Digestion in the small intestine depends on enzymes and other substances secreted by the intestine itself and by the pancreas and liver. The secretions from the pancreas and liver enter a common duct that empties into the lumen of the first segment of the small intestine, a short region about 20 cm long called the **duodenum (Figure 45.12).**

In all, about 7 to 9 L of fluid from the stomach, liver, pancreas, and intestinal glandular cells enter the small intestine each day. About 95% of this amount is reabsorbed as water and nutrients as the digestive contents travel along the small intestine. Movement of the contents from the duodenum to the end of the small intestine takes about 3 to 5 hours.

In humans, the **pancreas** is an elongated, flattened gland located between the stomach and duodenum (see Figures 45.5 and 45.12). Exocrine cells in the pancreas secrete bicarbonate ions ($H_2CO_3^-$) and digestive enzymes—*pancreatic enzymes*—into ducts that empty into the lumen of the duodenum. The bicarbonate ions neutralize the acid in the chyme, bringing the digestive contents to a slightly alkaline pH. The alkaline pH allows optimal activity of the enzymes secreted by the pancreas, which include proteases, an amylase, nucleases, and lipases. All of these enzymes act in the lumen of the small intestine. Like pepsin, the proteases released by the pancreas are secreted in an inactive precursor form; contact with the digestive solution activates them. Among the active forms of these enzymes are *trypsin,* which hydrolyzes bonds within polypeptide chains, and *carboxypeptidase,* which cuts amino acids from polypeptide chains one at a time.

The **liver** secretes bicarbonate ions and **bile,** a mixture of substances including *bile salts,* cholesterol, and *bilirubin.* Bile salts are derivatives of cholesterol and amino acids that aid fat digestion through their detergent action. They form a hydrophilic coating around fats and other lipids, which allows the churning motions of the small intestine to *emulsify* the fats—break them into tiny droplets called *micelles,* as in mixing oil and water in making a salad dressing. Lipase, a pancreatic enzyme,

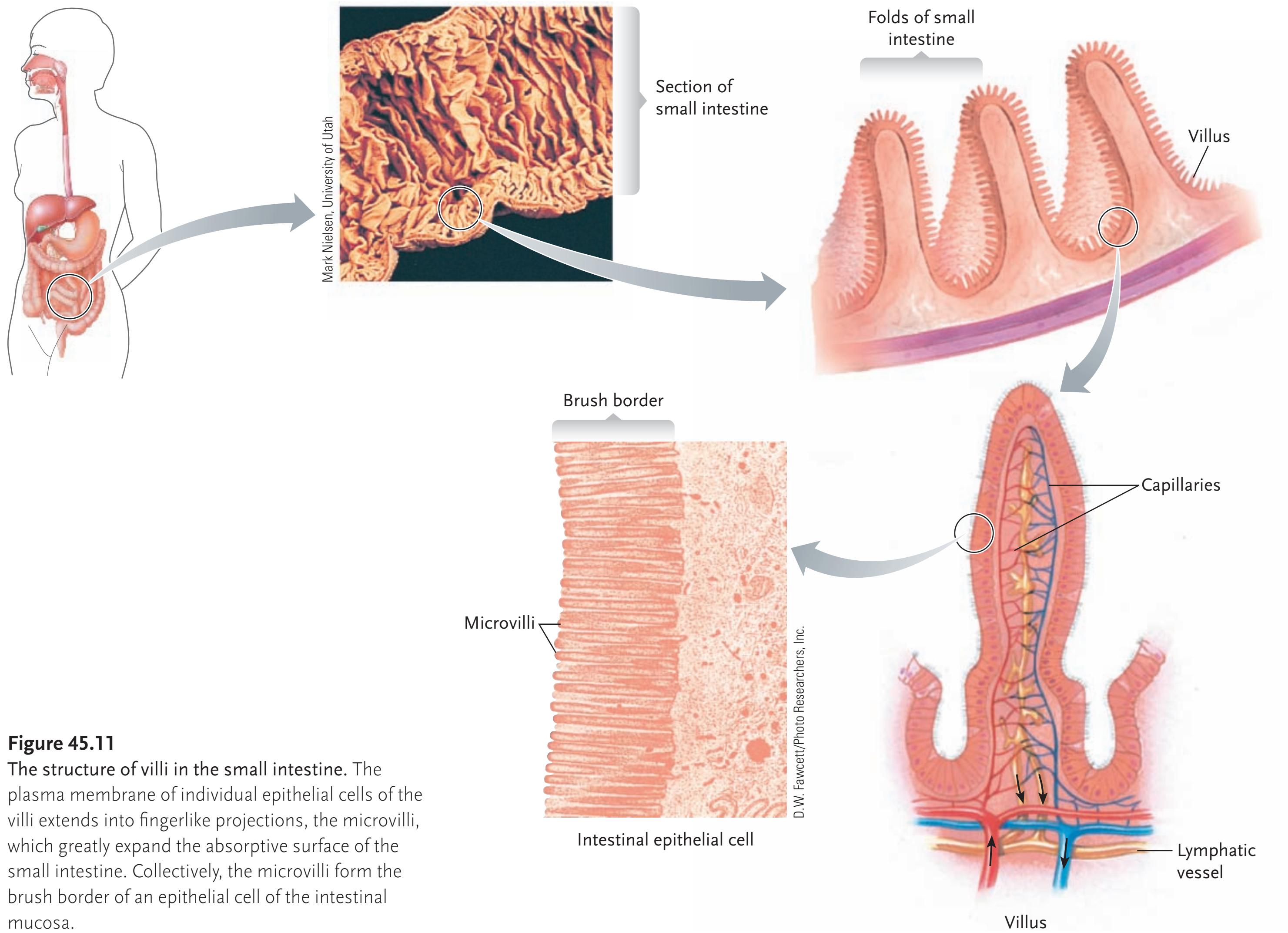


Figure 45.11
The structure of villi in the small intestine. The plasma membrane of individual epithelial cells of the villi extends into fingerlike projections, the microvilli, which greatly expand the absorptive surface of the small intestine. Collectively, the microvilli form the brush border of an epithelial cell of the intestinal mucosa.

can then hydrolyze the fats in the micelles to produce monoglycerides and free fatty acids. Bilirubin, a waste product derived from worn-out red blood cells, is the yellow pigment that gives the bile its color. Bacterial enzymes in the intestines modify the pigment, resulting in the characteristic brown color of feces.

The liver secretes bile continuously. Between meals, when no digestion is occurring, bile is stored in the **gallbladder**, where it is concentrated by the removal of water. After a meal, entry of chyme into the small intestine stimulates the gallbladder to release the stored bile into the small intestine.

Brush-border epithelial cells on the villi of the small intestine secrete water and mucus into the intestinal contents. They also produce enzymes that complete the digestion of carbohydrates, proteins, and nucleic acids. Substrates for those enzymes are breakdown products produced by enzyme activity elsewhere in the digestive system—disaccharides, large peptides, dipeptides, and nucleotides—that are transported across the plasma membranes of the brush-border epithelial cells **(Figure 45.13).** Different *disaccharidases* break maltose, lactose, and sucrose into individual monosaccharides. Two proteases complete protein digestion: an *aminopeptidase* cuts amino acids from the end of a polypeptide, and a *dipeptidase* splits dipeptides into individual amino acids. Nucleases and other enzymes digest the nucleic acids: *nucleotidases* break them down into nucleosides, and *nucleosidases* convert the nucleosides to nitrogenous bases, five-carbon sugars, and phosphates.

Many adults lose the capacity to synthesize lactase, the enzyme that breaks down the milk sugar lactose. The lactose remaining in the intestine is broken down by bacteria, producing excess methane and CO_2. The accumulating gases distend the large intestine, producing pain, discomfort, and other symptoms of *lactose intolerance*. For many people lactose intolerance can be relieved by taking tablets containing lactase before eating milk products. One estimate is that 70% of the world's population is lactose intolerant. In the United States, between 30 and 50 million people are lactose intolerant, with some ethnic and racial groups affected more than others. For instance, over 80% of Native Americans, up to 80% of African Americans, and over 90% of Asian Americans are lactose intolerant. Generally, lactose intolerance is far less common among people of northern European descent.

Absorption by the Brush-Border Cells of the Intestinal Mucosa. The water-soluble products of digestion enter the intestinal mucosa cells by active transport or facilitated diffusion **(Figure 45.14a),** and water follows by osmosis. The nutrients are then transported from the mucosal cells into the extracellular fluids, from where they enter the bloodstream in the capillary networks of the submucosa.

The micelles formed by bile salts assist in the absorption of fatty acids, monoglycerides, fat-soluble vitamins, and cholesterol and other products of lipid breakdown by lipase **(Figure 45.14b).** When a micelle contacts the plasma membrane of a mucosal cell, the hydrophobic molecules within the droplet penetrate through the membrane and enter the cytoplasm.

In the mucosal cells, the fatty acids and monoglycerides are combined into fats (specifically, triglycerides) and packaged into **chylomicrons**, small droplets covered by a protein coat. Cholesterol absorbed in the small intestine is also packed into the chylomicrons. The protein coat of the chylomicrons provides a hydrophilic surface that keeps the droplets suspended in the cytosol. After traveling across the mucosal cells, the chylomicrons are secreted into the interstitial fluid of

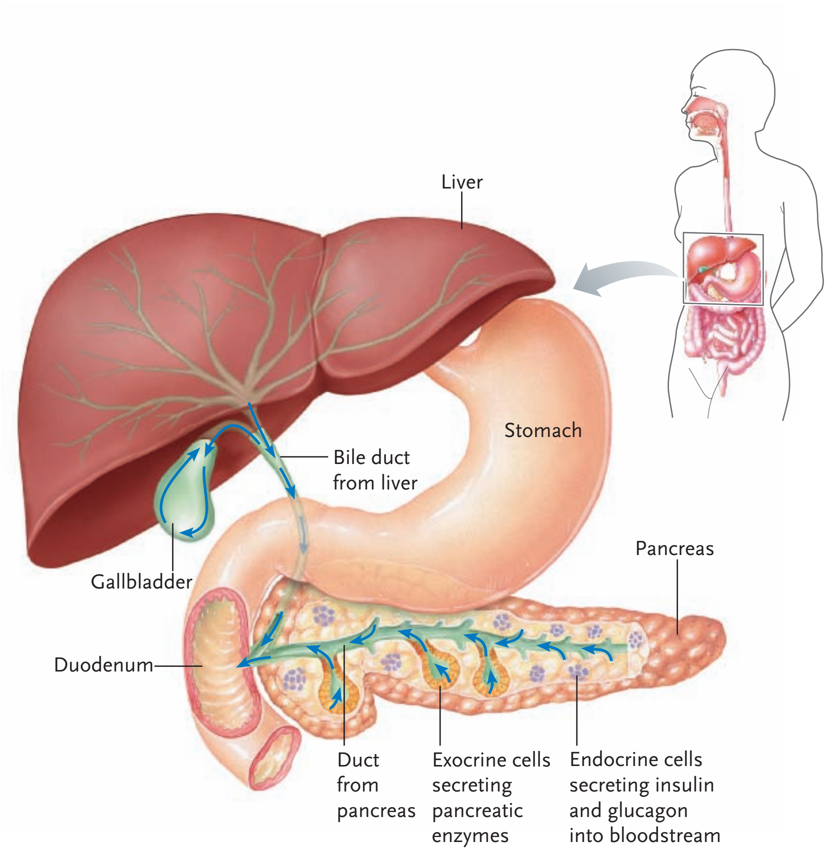
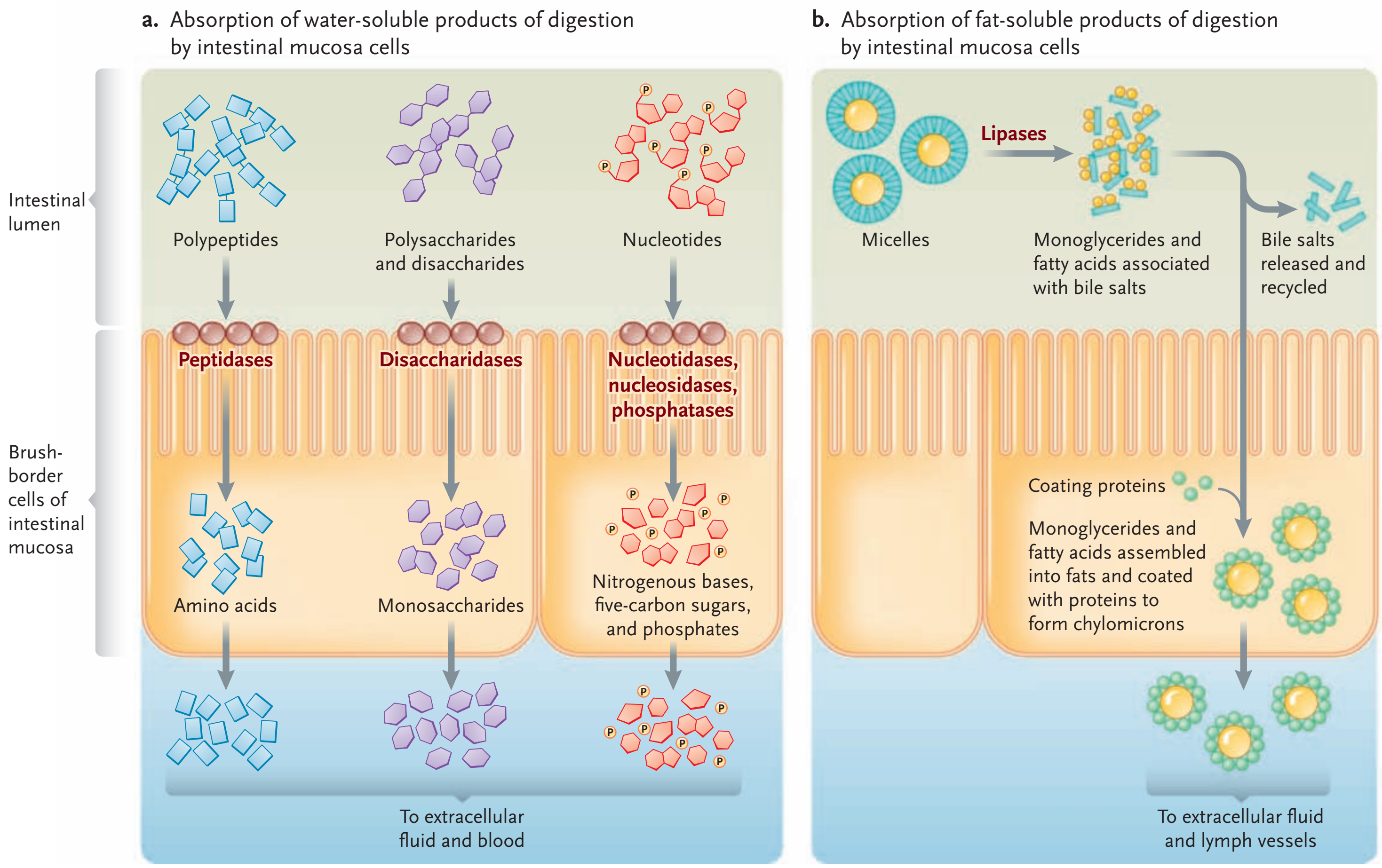


Figure 45.12
The ducts delivering bile and pancreatic juice to the duodenum of the small intestine.

	Carbohydrates	Proteins	Fats	Nucleic acids
Mouth	Polysaccharides → **Salivary amylase** → Smaller polysaccharides, disaccharides			
Stomach		Proteins → **Pepsin** → Peptides		
Lumen of small intestine	Polysaccharides → **Pancreatic amylase** → Disaccharides	Proteins → **Trypsin, chymotrypsin** → Peptides; Large peptides → **Carboxypeptidase** → Amino acids	Triglycerides and other lipids → **Lipase** → Fatty acids, monoglycerides	DNA, RNA → **Pancreatic nucleases** → Nucleotides
Epithelial cells (brush border) of small intestine	Disaccharides (maltose, sucrose, lactose) → **Disaccharidases** → Monosaccharides (for example, glucose)	Large peptides → **Amino-peptidase** → Amino acids; Dipeptides → **Dipeptidase** → Amino acids		Nucleotides → **Nucleotidases, nucleosidases, phosphatases** → Nitrogeneous bases, five-carbon sugars, and phosphates

Figure 45.13
Enzymatic digestion of carbohydrates, proteins, fats, and nucleic acids in the human digestive system.



Water-soluble molecules are broken into absorbable subunits at brush borders of mucosal cells and transported inside; the subunits are transported on the other side to extracellular fluid and blood.

Micelles (fats coated with bile salts) are digested to monoglycerides and fatty acids, which penetrate into cells and are assembled into fats. The fats are coated with proteins to form chylomicrons, which are released by exocytosis to extracellular fluids, where they are picked up by lymph vessels.

Figure 45.14 Absorption of digestive products by the brush-border cells of the intestinal mucosa.

the submucosa, where they are taken up by lymph vessels. Eventually, they are transferred with the lymph into the blood circulation.

The small intestine reabsorbs all but about 1 L of the 7 to 9 L of fluid released from the stomach. By the time the digestive contents reach the large intestine, almost all nutrients have been hydrolyzed and absorbed.

Many Nutrients Absorbed in the Small Intestine Are Processed in the Liver

The capillaries absorbing nutrient molecules in the small intestine collect into veins that join to form a larger blood vessel, the **hepatic portal vein**, which leads to capillary networks in the liver. In the liver, some of the nutrients leave the bloodstream and enter liver cells for chemical processing. Among the reactions taking place in the liver is the combination of excess glucose units into glycogen, which is stored in the liver cells. This reaction reduces the glucose concentration in the blood exiting the liver to about 0.1%. If the glucose concentration in the blood entering the liver falls below 0.1% during a period of fasting between meals, the reaction reverses. The reversal adds glucose to return the blood concentration to the 0.1% level before it exits the liver.

The liver also synthesizes the lipoproteins that transport cholesterol and fats in the bloodstream, detoxifies ethyl alcohol and other toxic molecules, and inactivates steroid hormones and many types of drugs.

As a result of the liver's activities, the blood leaving the liver has a markedly different concentration of nutrients than the blood carried into the liver by the hepatic portal vein. From the liver, blood is carried to the heart and then pumped by the heart to deliver nutrients to all parts of the body.

The Large Intestine Primarily Absorbs Water and Mineral Ions from Digestive Residues

From the small intestine, the contents move on to the large intestine. A sphincter at the junction between the small and large intestines controls the passage of material and prevents backward movement of the contents. The large intestine is several times larger in diameter than the small intestine, but it is relatively short, about 1.2 m long in humans, as compared with the 6 m length of the small intestine. The inner surface of the large intestine is relatively smooth and contains no villi.

The large intestine has several distinct regions **(Figure 45.15).** At the junction with the small intestine, a part of the large intestine forms a blind pouch called the **cecum.** A fingerlike sac, the **appendix,** extends from the cecum. The appendix is on average 100 mm long and 7 mm in diameter; it is a vestigial structure with no known function. It certainly has no function in digestion, but it does contain patches of lymphoid tissue, suggesting that at one time it may have functioned as part of the immune system. The cecum merges with the **colon,** the main part of the large intestine, which forms an inverted U. At its distal end, the colon connects with the final segment of the large intestine, the **rectum.**

The large intestine secretes mucus and bicarbonate ions and absorbs water and other ions, primarily sodium and chloride. The absorption of water condenses and compacts the digestive contents into solid masses, the **feces.** Normally, by the time the fecal matter reaches the rectum, it contains less than 200 mL of the fluid entering the digestive tract each day. Diarrhea, by contrast, is an abnormal condition in which the fecal matter is highly fluid. The most common cause of diarrhea is a higher-than-normal rate of movement of materials through the small intestine, which does not leave adequate time for absorption of water to occur. The higher rate of movement can occur as a result of irritation of the small intestine wall in bacterial and viral infections, or because of emotional stress.

About 30% to 50% of the dry matter of feces in humans and other vertebrates consists of more than 500 species of bacteria that live as essentially permanent residents in the large intestine. Most common is the bacterium *Escherichia coli,* which also lives in the intestine of many other mammals. Intestinal bacteria metabolize sugars and other nutrients remaining in the digestive residue, and produce useful fatty acids and vitamins (such as vitamin K, the B vitamins, folic acid, and biotin), some of which are absorbed in the large intestine. Their activity also produces large quantities of gas—*flatus*—primarily CO_2, methane, and hydrogen sulfide. Most of the gas is absorbed through the intestinal mucosa, and the rest is expelled through the anus in the process of *flatulence*. The amount and composition of the gas produced depends on the type of food being ingested and the particular population of bacteria present in the large intestine. Some foods, such as beans, contain carbohydrates that humans cannot digest but that can be metabolized by the gas-producing intestinal bacteria. After eating such foods, humans may produce more gas than usual, and flatulence is more likely.

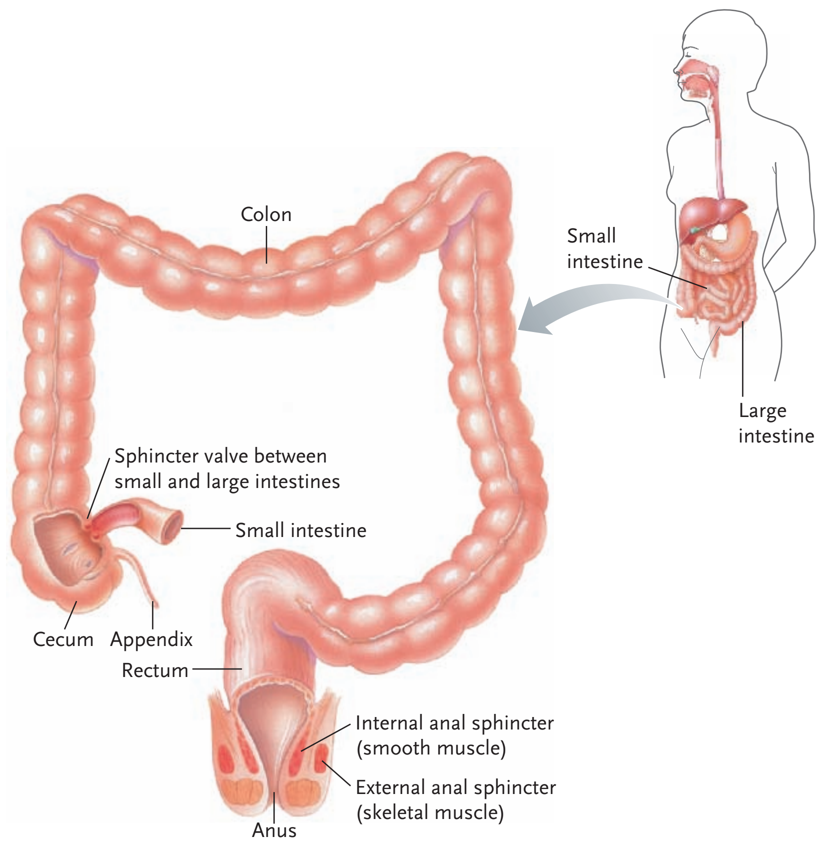


Figure 45.15
The human large intestine.

When feces enter the rectum, they stretch the rectal wall. The stretching triggers a *defecation reflex* that opens the *anal sphincter* and expels the feces through the anus. Because the anal sphincter contains rings of voluntary skeletal muscle as well as involuntary smooth muscle (see Figure 45.15), we can resist the defecation reflex by voluntarily tightening the striated muscle ring.

Having completed the journey of ingested food through the digestive tract, we now turn our attention to the mechanisms that regulate the activities of the digestive system. These mechanisms coordinate one region of the digestive tract with another, and help match the production of nutrients with the body's needs.

Study Break

1. What are the two classes of vitamins? Which of the two types is more critical in the diet and why?
2. What are the four layers of the mammalian gut? Which layer is responsible for peristalsis?
3. How is pepsin produced? What is its function?
4. Distinguish between the functions of the small and large intestines in digestion.

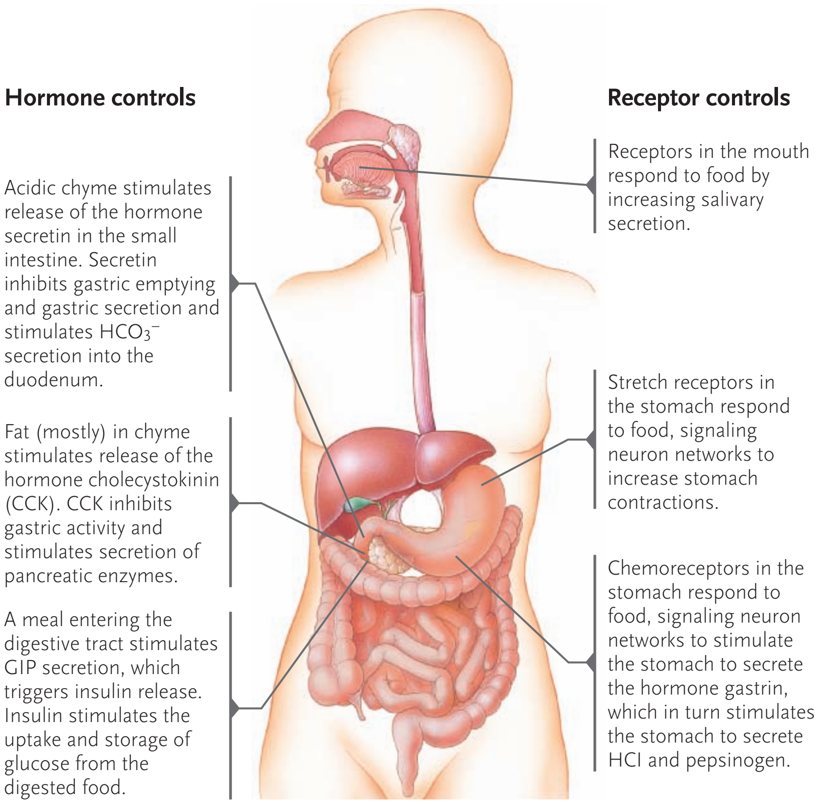


Figure 45.16 Control of digestion by receptors and hormones in the digestive system.

45.4 Regulation of the Digestive Process

The digestive process is regulated and coordinated at many steps by controls that are largely automated. The autonomic nervous system, local neuron networks in the gut wall, and endocrine glands interact in these controls, in response to sensory information gathered by receptors in the digestive tract. The integration of the controls speeds or slows digestion to produce maximum efficiency in the breakdown of food molecules and the absorption of the products.

Much of the control of the digestive system originates in the neuron networks of the submucosa. Other controls, particularly those regulating appetite and oxidative metabolism, originate in the brain, in control centers forming part of the hypothalamus.

The Digestive Tract Itself Has a Number of Control Systems

The movement of food through the digestive system is controlled by receptors in and hormones secreted by various parts of the system **(Figure 45.16).** Control starts with the mouth. Saliva is secreted constantly into the mouth. The presence of food activates receptors that increase the rate of salivary secretion by as much as 10-fold.

Swallowed food expands the stomach and sets off signals from stretch receptors in the stomach walls. Chemoreceptors in the stomach respond to the presence of food molecules, particularly proteins. Signals from these two types of receptors are integrated in neuron networks in both the stomach and the autonomic nervous system to produce several reflex responses. One is an increase in the rate and strength of stomach contractions. Another is secretion of a hormone, *gastrin,* into the blood leaving the stomach. After traveling through the circulatory system, gastrin returns to the stomach, where it stimulates the secretion of HCl and pepsinogen. These molecules are then used in the digestion of the protein that, as part of the swallowed meal, was responsible for their secretion. Gastrin also stimulates stomach and intestinal contractions, activities that serve to keep the digestive contents moving through the digestive system when a new meal arrives.

Three hormones secreted when food is present in the duodenum also participate in regulating the digestive processes. When chyme is emptied into the duodenum, its acidic nature stimulates the release of the hormone *secretin*. Secretin inhibits further gastric emptying to prevent further acid from entering the duodenum until the newly arrived chyme is neutralized. It also inhibits gastric secretion to reduce acid production in the stomach, and it stimulates HCO_3^- secretion into the lumen of the duodenum to neutralize the acid. If the acid is not neutralized, the duodenal wall will become damaged.

Fat, and to a lesser extent protein, in the chyme entering the duodenum stimulates the release of the hormone *cholecystokinin (CCK)*. CCK inhibits gastric activity, thereby allowing time for nutrients in the duodenum to be digested and absorbed. It also stimulates the secretion of pancreatic enzymes, used to digest the macromolecules in the chyme.

The hormone *glucose-dependent insulinotrophic peptide (GIP)* acts primarily to stimulate insulin release by the pancreas. When a meal is ingested, the body must change its metabolic state to use and store the new nutrients absorbed. Those activities are mostly under the control of insulin. Therefore, when a meal enters the digestive tract, GIP secretion is stimulated to trigger the release of insulin. Insulin is particularly important in stimulating the uptake and storage of glucose and so, not surprisingly, glucose in the duodenum causes an increase in GIP secretion.

The Hypothalamus Exerts Overall Controls

The hypothalamus contains two interneuron centers that work in opposition to control appetite and oxidative metabolism. One center stimulates appetite and reduces oxidative metabolism; the other center stimulates the release of a peptide hormone called *α-melanocyte-stimulating hormone (α-MSH),* which inhibits appetite.

A major link in the control pathways is the peptide hormone *leptin* (*leptos* = thin), discovered in mice by Jeffrey Friedman and his coworkers at the

Insights from the Molecular Revolution

Food for Thought on the Feeding Response

A number of small proteins called *neuropeptides* regulate various physiological responses in humans and other mammals, including appetite and feeding, pain reception, and blood pressure regulation. They exert their effects by binding to receptors on the surfaces of neurons and other cells. For example, the neuropeptide NPY (neuropeptide Y) strongly stimulates appetite and food uptake when it binds to neurons in the hypothalamus and other locations in the brain.

A group of researchers at the Synaptic Pharmaceutical Corporation in New Jersey and at Ciba-Geigy in Switzerland was one of several teams that tried to identify the receptor binding NPY in the hypothalamus. The investigators extracted all the messenger RNAs made in the rat hypothalamus and converted them into DNA copies (cDNAs). The cDNAs were inserted into plasmid cloning vectors for cloning of the sequences in *E. coli*. Next, the plasmids were transferred into mammalian cells that do not normally make neuropeptide receptors, and the researchers screened for cells that were now able to bind the neuropeptide. The cells that did must have received an active gene encoding the receptor.

The investigators isolated the rat gene that encoded the receptor and obtained its sequence. The gene sequence showed that it encoded a previously unknown neuropeptide receptor, which they called Y5. An equivalent gene for this receptor was then identified in the human genome.

Next, different rat tissues were tested with a probe that could pair with the mRNA transcribed from the *Y5* gene. The result showed that *Y5* is expressed only in the brain, with the strongest expression in the hypothalamus and the amygdala, a center associated with emotional responses.

After testing the ability of various peptides to bind the Y5 receptor, and the effects of the binding on feeding behavior, the authors proposed that the binding of NPY initiates signals that stimulate hunger and the feeding response. Binding to receptors in the amygdala may add an emotional dimension to the craving for food. The authors conjectured that studies of Y5 could help further our understanding of eating disorders and perhaps aid in the development of drugs to combat those disorders.

Indeed, the Y5 receptor became a focus of considerable drug discovery efforts. However, a recent study has burst the bubble—drugs designed to inhibit the receptor are not going to be effective in combating obesity. In this study, Andrew Turnbull and his colleagues at AstraZeneca in the United Kingdom, tested whether one such drug affected feeding in rats. Unfortunately, the drug had no significant effect on the increase in food intake induced by NPY itself either in normal or genetically obese rats. Further, the drug had no effect on food intake or body weight in normal rats or in rats that were obese due to their diet. In short, the Y5 receptor is not a significant regulator of feeding behavior. The difference between these results and those of the previous study may reflect the experimental design—the compounds used in the earlier study may well have had other activities that were responsible for their effects on feeding behavior.

Rockefeller University. Fat-storing cells secrete leptin when the deposition of fat increases in the body. Leptin travels in the bloodstream and binds to receptors in both centers in the hypothalamus. Binding stimulates the center that reduces appetite and inhibits the center that stimulates appetite. At the same time, leptin binds to receptors on body cells, triggering reactions that oxidize fatty acids rather than converting them into fats. When fat storage is reduced, leptin secretion drops off, and signals from other pathways activate the appetite-stimulating center in the hypothalamus and turn off the appetite-inhibiting center.

These controls closely match the activity of the digestive system to the amount and types of foods that are ingested, and they coordinate appetite and oxidative metabolism with the body's needs for stored fats. *Insights from the Molecular Revolution* describes recent investigations identifying signal molecules and receptors that regulate appetite and feeding behavior in mammals.

Study Break

How does the hypothalamus regulate the digestive process?

45.5 Digestive Specializations in Vertebrates

Natural selection has modified the basic vertebrate digestive system into a multitude of structural and functional variations. The most common modifications are in the form of the mouth, teeth, and jaws; the structure and function of the esophagus, stomach, and cecum; and the length of the digestive tract. Vertebrates also vary in the types of enzymes secreted by the digestive system. For example, humans secrete an amylase into the saliva, but cats and pigs secrete a salivary lipase.

Teeth Are Adapted to Feeding Methods

To anthropologists and paleontologists, dentition (the number, kind, and arrangement of teeth) opens a window to an animal's diet and feeding method—and hence reveals a great deal about its habitat and life style. For example, snakes have sharp, pointed teeth that curve backward into the mouth, which helps to ensure that prey (dead or living) does not slip out of the animal's mouth as muscles contract to swallow. The dentition is combined with specializations in jaw structure; many snakes have jaws with elastic connections that allow them to open wide enough to swallow prey whole.

Tooth specialization is especially evident among mammals **(Figure 45.17).** Typically, mammals have four types of upper and lower teeth. **Incisors,** located at the front of the mouth, are flattened, chisel-shaped teeth used to nip or cut food. Horses use their prominent incisors to clip off blades of grasses. Pointed **canines** at the sides of the incisors are specialized for biting and piercing. Carnivores such as wolves and tigers use their long, sharp canines to pierce and kill prey, but the canines are minimally developed or absent in many herbivores. The blocky teeth at the sides of the mouth, the **premolars** and **molars,** have surface bumps, or *cusps,* that are used in crushing, grinding, and shearing food. Large premolars and molars with a ridged surface are characteristic of animals, such as deer, that consume fibrous plant material. The premolars and molars of some carnivores, such as cats, have sharp shearing surfaces that can slice meat efficiently. All four types of teeth are typically well developed in omnivores, such as humans.

The Length of the Intestine and Specializations of the Digestive Tract Reflect Feeding Patterns

There is a strong correlation between diet and the length of the digestive system **(Figure 45.18).** Vertebrates that feed primarily on nutrient-rich foods such as meat, blood, nectar, or insects, including carnivores (such as the dog), generally have a relatively short intestine. In contrast, herbivores (such as the rabbit) have a long intestinal tract and specializations of the esophagus, stomach, and cecum, or other structures that can store large volumes of plant material. Both the longer intestinal tract and greater storage capacity allow an herbivore to extract more nutrients from plant matter, which is relatively difficult to digest. Both types of intestine appear during the life cycle of frogs: frog tadpoles, which primarily eat algae, have a relatively long, coiled intestine; after metamorphosis, the adult frogs, which primarily eat insects, have a short intestine.

Symbiotic Microorganisms Aid Digestion in a Number of Organisms

Many herbivores use the hydrolytic capabilities of microorganisms such as bacteria, protists, and fungi to aid digestion of plant material, housing them in specialized structures of the esophagus, stomach, or cecum. Unlike vertebrates, the microorganisms can synthesize *cellulase,* the enzyme that hydrolyzes the cellulose of plant cell walls into glucose subunits. The arrangement is a classic example of symbiosis; the herbivores benefit from the digestive capabilities of the microorganisms, and the microorganisms benefit from an ideal habitat and an abundant supply of nutrients.

The most remarkable adaptations for symbiotic digestion of plant matter among vertebrates occur in the **ruminants,** which include cattle, deer, goats, sheep, and antelopes. These animals have a complex, four-chambered stomach **(Figure 45.19).** The first three chambers are derived from the esophagus. After the ruminant's teeth tear, cut, and grind plant matter, it is swallowed and arrives in the *reticulum.* In the reticulum, and in the next and largest chamber, the *rumen,* symbiotic microorganisms hydrolyze cellulose in the plant matter into fuels for fermentation reactions (the oxygen

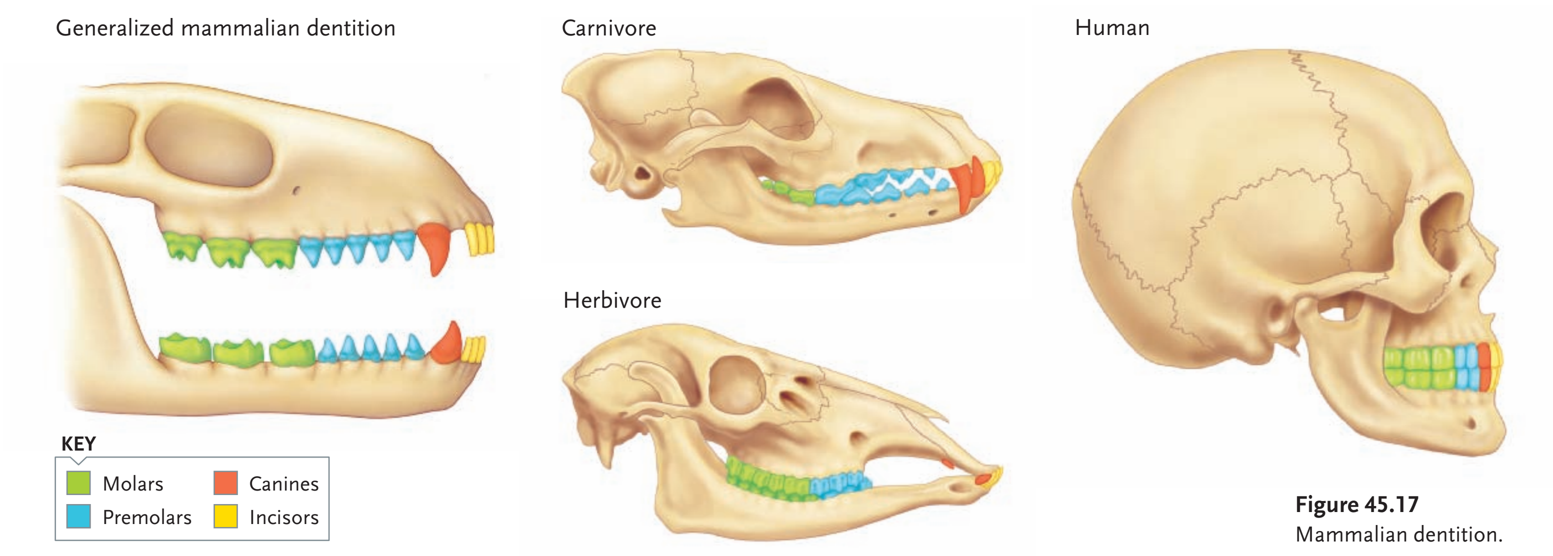


Figure 45.17
Mammalian dentition.

level in the chambers is too low to support mitochondrial reactions). The fermentations generate various products, including alcohols, amino acids, and fatty acids, which are used as nutrients by the ruminants. Methane, another product, collects in the fermentation chambers. Ruminants belch the gas in huge quantities; a cow potentially can release more than 400 L of methane per day. In fact, cattle are estimated to contribute 20% of the methane polluting our atmosphere.

As part of the digestive process, a ruminant "chews its cud"—it regurgitates material from the reticulum and rumen, rechews it, and swallows it again. This process crushes the plants into smaller fragments, exposing more surface area to the microbial enzymes, and gives the enzymes more time to act.

Matter that has been digested and liquefied by the microorganisms moves to the *omasum,* where water is absorbed from the mass, and then to the *abomasum* (the ruminant's true stomach). There, the addition of acids and pepsin to the food mass kills the microorganisms and starts the process of typical vertebrate digestion. As the food mass moves to the small intestine, the dead microorganisms, which are a rich source of proteins, vitamins, and other nutrients, are digested and absorbed along with other hydrolyzable molecules in the digestive contents.

Although the ruminant digestive system is uniquely specialized, many other vertebrate species also have esophageal or gastric chambers containing plant-digesting symbiotic microorganisms. These include the camel, sloth, and langur monkey, and marsupials such as kangaroos and wallabies. One bird, the South American hoatzin *(Opisthocomus hoazin),* is known to have a crop in which microorganisms break down plant matter.

Many vertebrates house symbiotic, plant-digesting microorganisms in the cecum. Horses, elephants, rhinos, rabbits, koalas, many rodents, and some reptiles and birds, including the iguana and chicken, are all examples. Even humans benefit from microbial symbionts living in the cecum. However, because the cecum and the remainder of the large intestine have little capacity to absorb nutrients, microbial digestion in the cecum is not as productive as microbial digestion in the stomach.

We have seen that animals use various strategies to extract the available nutrients from foods. These nu-

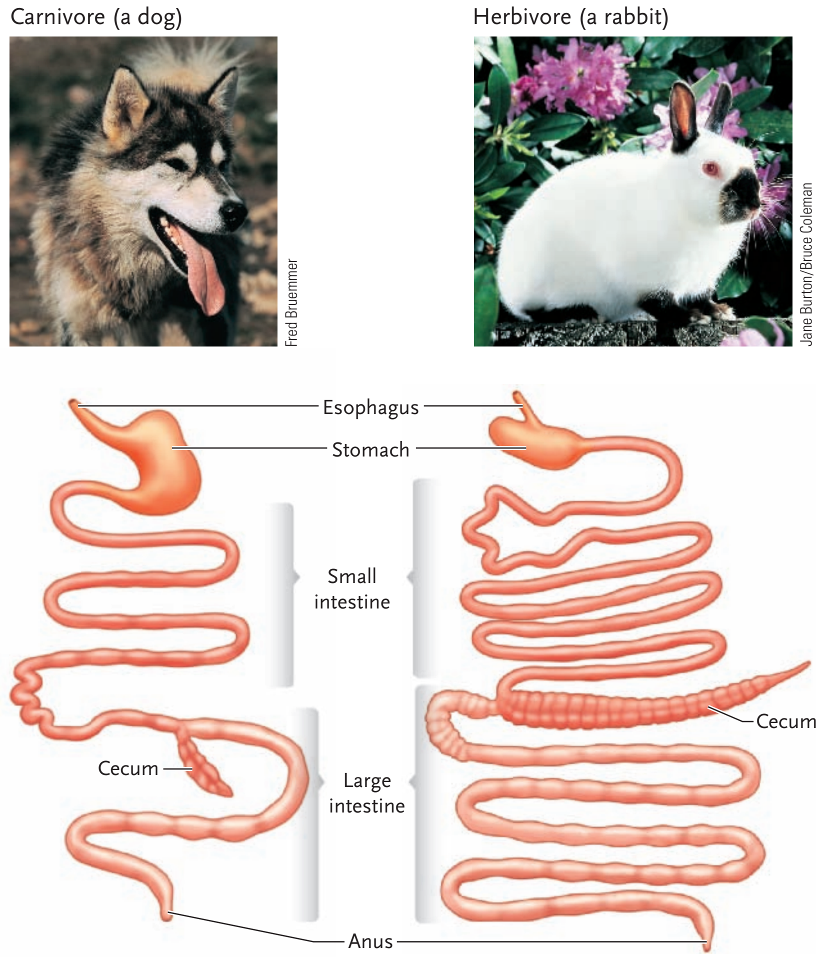


Figure 45.18
Comparison of the length of the digestive tract in a carnivore and an herbivore. The carnivore has a relatively short digestive tract, while the herbivore's digestive tract is much longer.

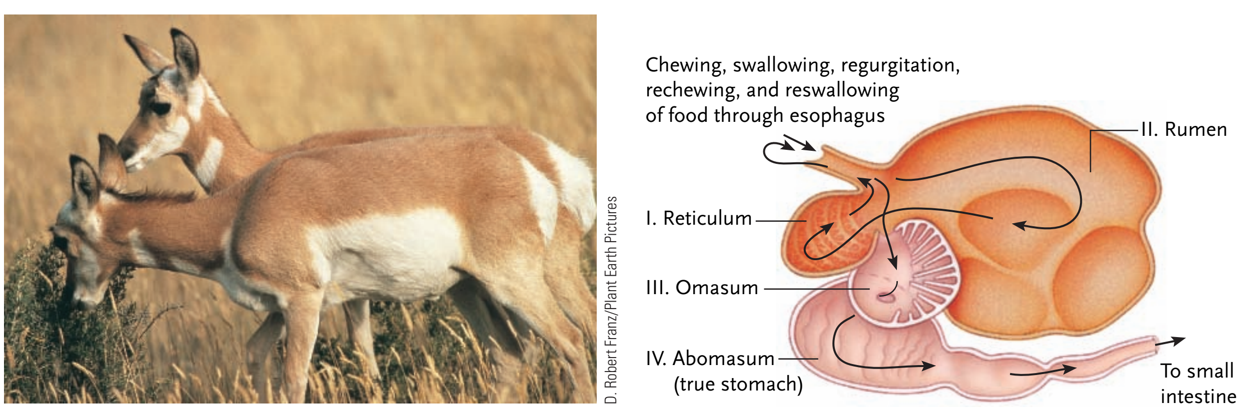


Figure 45.19
A ruminant, the pronghorn *(Antilocapra americanus)*, and its four-chambered system that digests plant matter with the aid of symbiotic microorganisms.

tritional strategies involve multiple steps combining both mechanical and chemical processing, which convert complex foodstuffs into the absorbable subunits that animals need to sustain life. Obtaining food is costly in terms of energy and risk, and animals have evolved many ways to make the most of it.

Study Break

1. How are the different types of teeth used in feeding?
2. What roles do symbiotic microorganisms play in digestion?

Unanswered Questions

How is energy partitioned in animals?

In this chapter you learned that ingested food molecules are broken down into smaller units that can be readily absorbed into body fluids and cells. The ingested energy is assimilated into the organism and partitioned into four main categories: maintenance metabolism, growth, reproduction, and storage. The top priority for energy allocation is maintenance metabolism—the energy required to seek and digest food and to support essential life processes. Researchers are studying the regulation of energy partitioning among the other categories when available energy exceeds that required for maintenance. The findings indicate that priorities for energy allocation vary between species as well as during an individual's life history. In the case of growth, for example, some species grow for a short period *(determinant growth)*, while other species grow throughout their lives *(indeterminant growth)*. Animal growth is controlled by genetic, environmental, and nutritional factors, but how such cues are integrated with each other and with other processes, such as reproduction and storage, remain to be determined. For example, the cues used to shut down growth and reproduction during fasting are not fully known. (In humans, malnourished juveniles become growth retarded and adult females stop menstruating.) The extent to which severe energy restriction may result in metabolic adaptation (reduced metabolic rate) also needs to be examined.

How are foraging and feeding regulated?

In this chapter you also learned about the control of appetite and oxidative metabolism. While some of the players are known—among them hunger centers in the brain, appetite-stimulating hormones such as neuropeptide Y, and appetite-suppressing or satiety hormones such as leptin—a number of questions remain. For example, how are various sensory inputs, such as smell, integrated to initiate feeding? Similarly, how are other inputs, such as gut contents or increasing nutrient concentration in the blood, integrated to terminate feeding? Also, how is an animal's feeding strategy matched to nutrient quantity and quality in the environment and to the animal's metabolic pattern: for example, sluggish or active (tortoise or hare)? Inevitably, a complex of integrating chemicals—produced by the brain, gut, fats cells, and other tissues—will prove to be involved. Knowledge of this complex system will provide insight not only into obesity but into eating disorders such as anorexia as well.

How are lipids taken up and utilized?

Adipose and other cells take up lipids (mostly triglycerides) that have been hydrolyzed from chylomicrons and very-low-density lipoprotein (VLDL) by the enzyme lipoprotein lipase (LPL). Low-density lipoproteins (LDLs) are VLDL remnants and are the major means of delivering cholesterol to tissues. Normally, LDLs are taken up by receptor-mediated endocytosis. Cholesterol can be scavenged by high-density lipoproteins (HDLs) through the action of the enzyme lecithin cholesterol acyltransferase (LCAT), taken up by the liver, and removed from the body. Researchers have found that defects in LPL, LCAT, and LDL disrupt normal lipid metabolism and lead to severe health risks. For example, genetic defects in the LDL receptor are associated with familial hypercholesterolemia, in which excess cholesterol is left in the blood and causes heart disease and other abnormalities. Continued research on lipid and lipoprotein metabolism will be important for understanding obesity, type 2 diabetes mellitus, and cardiovascular disease.

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Review

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45.1 Feeding and Nutrition

- Animals obtain organic molecules by eating other organisms. Herbivores primarily eat plants, carnivores primarily eat other animals, and omnivores eat animals, plants, and other sources of organic nutrients. The organic molecules are used as fuels for oxidative reactions providing energy and as building blocks for making complex biological molecules.
- Animals require essential substances in their diets—amino acids, fatty acids, vitamins, and minerals—that they cannot make for themselves.
- Animals may be classified with respect to feeding methods and the physical state of the organic molecules they eat. Fluid feeders ingest liquids containing organic molecules in solution. Suspension feeders eat small particles of organic matter or small organisms in suspension in fluids. Deposit feeders ingest small organic particles or organisms that are part of solid matter that the feeders live in or on. Bulk feeders consume large pieces of organisms, or entire large organisms (Figure 45.2).

45.2 Digestive Processes

- Digestion is the process of mechanical and chemical breakdown of food into molecular subunits small enough to be absorbed into body fluids and cells.
- Digestion may be intracellular or extracellular. Extracellular digestion allows food to be eaten in large batches, stored, and broken down while the animal carries out other activities.
- In animals with extracellular digestion, the digestive processes take place in an internal body cavity that is either a pouch or sac with one opening that serves as both mouth and anus, or a tube with two openings forming a mouth on one end and an anus on the other end (Figures 45.3 and 45.4).
- In animals with a digestive tube, digestion occurs in five stages: (1) mechanical processing, including chewing and grinding of food; (2) secretion of enzymes and other digestive aids into the digestive tract; (3) enzymatic hydrolysis of food molecules into molecular subunits; (4) absorption of the molecular subunits across cell membranes; and (5) elimination of undigested matter.
- Food particles and molecules are pushed through the digestive tube by muscular contractions of its wall. Storage of food at various locations in the tube allows animals to digest food while engaged in other activities.

  Animation: Examples of digestive systems

45.3 Digestion in Humans and Other Mammals

- Adult humans require eight essential amino acids, 13 vitamins (Table 45.1) and a large number of essential minerals (Table 45.2).
- The mouth, pharynx, esophagus, stomach, intestine, and anus are common to the digestive system of mammals, including humans, and most vertebrates (Figure 45.5).
- The wall of the vertebrate gut is formed from four layers of tissues: the mucosa, the submucosa, the muscularis, and the serosa (Figure 45.7).
- Coordinated contractions of the circular and smooth muscles produce peristaltic waves that move the digestive contents from the mouth to the anus (Figure 45.8).
- Digestion begins in the mouth, where the teeth break the food into smaller bits. Salivary amylase, an enzyme that digests starch, is secreted into the food in the mouth. After chewing, the food is swallowed and travels through the pharynx and esophagus to reach the stomach (Figure 45.9).
- In the stomach, hydrochloric acid, the protein-digesting enzyme pepsin, and mucus are added to the food mass. The stomach churns the acid contents into chyme, which is released in pulses into the small intestine (Figure 45.10).
- Absorption of nutrients begins in the small intestine. Specializations of the small intestine to optimize absorption are the intestinal villi and microvilli (Figure 45.11).
- In the small intestine, digestive juices from the pancreas and liver add enzymes and digestive aids to the food mass (Figure 45.12). The pancreatic juice contains digestive enzymes and bicarbonate ions that neutralize the acidity of the digestive contents. The liver secretion, bile, contains bile salts, which emulsify fats, cholesterol, bilirubin, and additional bicarbonate ions.
- The small intestine secretes enzymes that complete most digestion. The mucosal cells of the small intestine absorb the molecular subunits created by digestion (Figures 45.13 and 45.14).
- Absorbed nutrients are delivered to the liver, where excess glucose is converted into glycogen and fats, and some of the amino acids are converted into plasma proteins or sugars. The liver also synthesizes cholesterol from lipids, carbohydrates, and other substances.
- The large intestine absorbs water and mineral ions from the digestive contents. At the end of the large intestine the undigested remnants, the feces, are expelled from the anus (Figure 45.15).

  Animation: Human digestive system

  Animation: Peristalsis

  Animation: Structure of the small intestine

  Animation: Structure of the large intestine

  Animation: Vitamins

45.4 Regulation of the Digestive Process

- Digestion is regulated by signals from the autonomic nervous system, by the activity of neuron networks in the digestive tube wall, and by hormones secreted by the digestive system. The regulatory mechanisms operate in response to signals from sensory receptors that monitor the volume and composition of the digestive contents (Figure 45.16).

  Animation: Body mass index

  Animation: Caloric requirements

  Animation: Chronology of leptin research

45.5 Digestive Specializations in Vertebrates

- Common variations in vertebrate digestive systems include modifications of the teeth, length of the digestive tract, and structure and function of the stomach.
- Mammals have four basic types of teeth—incisors for cutting, canines for piercing, and premolars and molars for cutting, grinding, and smashing food (Figure 45.17).
- Carnivores and vertebrates that eat other nutrient-rich foods have a relatively short digestive tract. Herbivores, which eat nutrient-poor foods, typically have a relatively long digestive tract that includes extensive storage regions (Figure 45.18).
- Many herbivores have digestive chambers in which symbiotic microorganisms digest plant matter into molecules that can be absorbed by the host (Figure 45.19).

  Animation: Human teeth

  Animation: Ruminant stomach function

Questions

Self-Test Questions

1. Required molecules that animals cannot synthesize are called:
   a. nutrients.
   b. essential nutrients.
   c. enzymes.
   d. proteins.
   e. carbohydrates.
2. Which of the following accurately describes a feeding style?
   a. Deposit feeders obtain nutrients from organic molecules in solution.
   b. Deposit feeders scrape organic matter from solid material on which they live.
   c. Fluid feeders digest organisms suspended in water.

d. Fluid feeders strain food with networks of mucus or bristles and hairs.
e. Suspension feeders consume sizable food whole or in chunks.

3. The order of successive steps in digestion is:
   a. absorption follows enzymatic hydrolysis.
   b. secretion of enzymes follows absorption of digestive material.
   c. mechanical processing follows enzyme secretion.
   d. mechanical processing follows enzymatic hydrolysis.
   e. enzymatic hydrolysis precedes secretion of digestive aids.
4. The esophagus, crop, gizzard, and intestine are found in:
   a. birds and mammals.
   b. insects and mammals.
   c. flatworms and birds.
   d. earthworms and birds.
   e. sponges and cnidarians.
5. All of the following are essential nutrients in humans *except:*
   a. vitamin B.
   b. calcium.
   c. glycogen.
   d. linoleic acid.
   e. vitamin K.
6. A specialized region of the gut is/are the:
   a. submucosa formed by circular and longitudinal layers.
   b. serosa lining the gut for absorption.
   c. mucosa composed of thick elastic connective tissue for movement.
   d. muscularis, an outer layer that secretes a slippery material to prevent friction with other organs.
   e. sphincters, which form valves between major digestive organs.
7. If the fat in whole milk is ingested:
   a. the stomach, with its high pH, will stimulate cells of the duodenum to hasten stomach emptying.
   b. parietal cells in the stomach will absorb it.
   c. in the small intestine, bile salts emulsify the fats and then lipase hydrolyzes them.
   d. lactase deficiency in the small intestine would prevent its digestion.
   e. microvilli will absorb the fat in the form of chylomicrons directly into the blood of the hepatic portal vein.
8. The liver's role in digestion is to:
   a. synthesize aminopeptidase and dipeptidase to digest polypeptides.
   b. synthesize lipase to form free fatty acids.
   c. secrete trypsin to break the bonds in polypeptides.
   d. secrete bile and bicarbonate ions to help emulsify fats.
   e. store bile between meals.
9. Which of the following best describes regulation of digestion?
   a. GIP inhibits insulin release from the pancreas.
   b. Gastrin stimulates pancreatic secretion of HCl and pepsinogen.
   c. Secretin stimulates gastric emptying into the duodenum.
   d. CCK stimulates gastric activity to activate the duodenum.
   e. Leptin binds different hypothalamic receptors to stimulate or inhibit appetite.
10. An example of a digestive specialization is seen in:
   a. the long intestines characteristic of herbivores.
   b. the incisors being the dominant teeth in wolves.
   c. the canine teeth being the dominant teeth in deer.
   d. salivary lipase being made by humans.
   e. cellulose being made by humans.

Questions for Discussion

1. As a person ages, the number of cells in the body steadily decreases and their energy needs decline. If you were planning an older person's diet, what kind(s) of nutrients would you emphasize, and why? Which ones would you recommend less of? Include vitamins and minerals in your answer.
2. Formulate a healthy diet for a young, actively growing 7-year-old, and explain why you have included each part of the diet. Refer to Question 1, above, for some issues to consider.
3. A baby develops symptoms of protein deficiency, and the attending physician suggests the cause is a genetic defect leading to a nonfunctional enzyme associated with digestion. Name at least three enzymes that might be likely suspects, and for each one explain how the defect would result in a protein deficiency.

Experimental Analysis

Design experiments to test whether cigarette smoke affects the functioning of the various parts of the digestive system.

Evolution Link

What is the advantage of a tubelike digestive system over a saclike digestive system?

How Would You Vote?

Many nutritionists suspect that increasing consumption of "fast foods" is contributing to rising levels of obesity. Should fast-food labels carry consumer warnings, as alcohol and cigarette labels do? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.