41

Animal Nutrition

▲ **Figure 41.1 How does a lean fish help a bear make fat?**

KEY CONCEPTS

OVERVIEW

The Need to Feed

Dinnertime has arrived for the Kodiak bear in **Figure 41.1** (and for the salmon, though in quite a different sense). The skin, muscles, and other parts of the fish will be chewed into pieces, broken down by acid and enzymes in the bear's digestive system, and finally absorbed as small molecules into the body of the bear. Such a process is what is meant by animal **nutrition**: food being taken in, taken apart, and taken up.

Although a diet of fish plucked from a waterfall is not common, all animals eat other organisms—dead or alive, piecemeal or whole. Unlike plants, animals must consume food for both energy and the organic molecules used to assemble new molecules, cells, and tissues. Despite this shared need, animals have diverse diets. **Herbivores**, such as cattle, sea slugs, and termites, dine mainly on plants or algae. **Carnivores**, such as sharks, hawks, and spiders, mostly eat other animals. Bears and other **omnivores** (from the Latin *omni*, all) don't in fact eat everything, but they do regularly consume animals as well as plants or algae. We humans are typically omnivores, as are cockroaches and crows.

The terms *herbivore*, *carnivore*, and *omnivore* represent the kinds of food an animal usually eats. Keep in mind, however, that most animals are opportunistic feeders, eating foods outside their standard diet when their usual foods aren't available. For example, deer are herbivores, but in addition to feeding on grass and other plants, they occasionally eat insects, worms, or bird eggs. Note as well that microorganisms are an unavoidable "supplement" in every animal's diet.

Animals must eat. But to survive and reproduce, they must also balance their consumption, storage, and use of food. Bears, for example, store energy, largely in the form of body fat, in preparation for winter sleep. Eating too little food, too much food, or the wrong mixture of foods can endanger an animal's health. In this chapter, we will survey the nutritional requirements of animals, explore some of the diverse evolutionary adaptations for obtaining and processing food, and investigate the regulation of energy intake and expenditure.

CONCEPT **41.1**

An animal's diet must supply chemical energy, organic molecules, and essential nutrients

Overall, an adequate diet must satisfy three nutritional needs: chemical energy for cellular processes, organic building blocks for macromolecules, and essential nutrients.

The activities of cells, tissues, organs, and whole animals depend on sources of chemical energy in the diet. This energy is used to produce ATP, which powers processes ranging from DNA replication and cell division to vision and flight. To meet the continuous requirement for ATP, animals ingest and digest nutrients, including carbohydrates, proteins, and lipids, for use in cellular respiration and energy storage.

In addition to providing fuel for ATP production, an animal's diet must supply the raw materials needed for biosynthesis. To build the complex molecules it needs to grow, maintain itself, and reproduce, an animal must obtain two types of organic precursors from its food. Animals need a source of organic carbon (such as sugar) and a source of organic nitrogen (such as protein). Starting with these materials, animals can construct a great variety of organic molecules.

The materials that an animal's cells require but cannot synthesize are called **essential nutrients**. Obtained from dietary sources, these nutrients include certain minerals and preassembled organic molecules. Some nutrients are essential for all animals, whereas others are needed only by certain species. For instance, ascorbic acid (vitamin C) is an essential nutrient for humans and other primates, guinea pigs, and some birds and snakes, but not for most other animals.

▲ **Figure 41.2 Storing protein for growth.** Penguins, such as this Adélie from Antarctica, must make an abundance of new proteins when they molt and grow new feathers. Because of the temporary loss of their insulating coat of feathers, penguins cannot swim—or feed—when molting. How, then, do they obtain amino acids for production of feather protein? Before molting, a penguin greatly increases its muscle mass. The penguin then breaks down the extra muscle protein, which supplies the amino acids for growing new feathers.

MAKE CONNECTIONS *Taking into account the examples in Figure 5.15, what generalization can you make about the circumstances under which animals commonly use proteins for amino acid storage?*

Essential Nutrients

There are four classes of essential nutrients: essential amino acids, essential fatty acids, vitamins, and minerals.

Essential Amino Acids

Animals require 20 amino acids to make proteins (see Figure 5.16). The majority of animal species have the enzymes to synthesize about half of these amino acids, as long as their diet includes sulfur and organic nitrogen. The remaining amino acids must be obtained from food in prefabricated form and are therefore called **essential amino acids**. Most animals, including adult humans, require eight amino acids in their diet (infants also need a ninth, histidine).

The proteins in animal products such as meat, eggs, and cheese are "complete," which means that they provide all the essential amino acids in their proper proportions. In contrast, most plant proteins are "incomplete," being deficient in one or more essential amino acids. Corn (maize), for example, is deficient in tryptophan and lysine, whereas beans are lacking in methionine. However, vegetarians can easily obtain all of the essential amino acids by eating a varied diet of plant proteins.

Some animals have adaptations that help them through periods when their bodies demand extraordinary amounts of protein. In penguins, for example, muscle protein provides a source of amino acids for making new proteins when feathers are replaced after molting **(Figure 41.2)**.

Essential Fatty Acids

Animals produce the enzymes to synthesize most, but not all, of the fatty acids they need. The **essential fatty acids**, the ones they cannot make, are certain fatty acids that contain one or more double bonds and are thus unsaturated (see Figure 5.11). For example, humans require linoleic acid to make some membrane phospholipids. Because seeds, grains, and vegetables in the diets of humans and other animals generally furnish ample quantities of essential fatty acids, deficiencies in this class of nutrients are rare.

Vitamins

As Nobel Prize winner Albert Szent-Györgyi pointed out, "A vitamin is a substance that makes you ill if you *don't* eat it." **Vitamins** are organic molecules that have diverse functions and are required in the diet in very small amounts. Vitamin B_2, for example, is converted in the body to FAD, a coenzyme used in many metabolic processes, including cellular respiration (see Figure 9.12). For humans, 13 vitamins have been identified. Depending on the vitamin, the required amount ranges from about 0.01 to 100 mg per day.

Vitamins are classified as water-soluble or fat-soluble **(Table 41.1)**. The water-soluble vitamins include the B vitamins, which are compounds that generally function as coenzymes, and vitamin C, which is required for the production of connective tissue. Among the fat-soluble vitamins are vitamin A, which is incorporated into visual pigments of the eye, and vitamin K, which functions in blood clotting. Another is vitamin D, which aids in calcium absorption and bone formation.

Table 41.1 Vitamin Requirements of Humans

Vitamin	Major Dietary Sources	Major Functions in the Body	Symptoms of Deficiency
Water-Soluble Vitamins			
B_1 (thiamine)	Pork, legumes, peanuts, whole grains	Coenzyme used in removing CO_2 from organic compounds	Beriberi (tingling, poor coordination, reduced heart function)
B_2 (riboflavin)	Dairy products, meats, enriched grains, vegetables	Component of coenzymes FAD and FMN	Skin lesions, such as cracks at corners of mouth
B_3 (niacin)	Nuts, meats, grains	Component of coenzymes NAD^+ and $NADP^+$	Skin and gastrointestinal lesions, delusions, confusion
B_5 (pantothenic acid)	Meats, dairy products, whole grains, fruits, vegetables	Component of coenzyme A	Fatigue, numbness, tingling of hands and feet
B_6 (pyridoxine)	Meats, vegetables, whole grains	Coenzyme used in amino acid metabolism	Irritability, convulsions, muscular twitching, anemia
B_7 (biotin)	Legumes, other vegetables, meats	Coenzyme in synthesis of fat, glycogen, and amino acids	Scaly skin inflammation, neuromuscular disorders
B_9 (folic acid)	Green vegetables, oranges, nuts, legumes, whole grains	Coenzyme in nucleic acid and amino acid metabolism	Anemia, birth defects
B_{12} (cobalamin)	Meats, eggs, dairy products	Production of nucleic acids and red blood cells	Anemia, numbness, loss of balance
C (ascorbic acid)	Citrus fruits, broccoli, tomatoes	Used in collagen synthesis; antioxidant	Scurvy (degeneration of skin and teeth), delayed wound healing
Fat-Soluble Vitamins			
A (retinol)	Dark green and orange vegetables and fruits, dairy products	Component of visual pigments; maintenance of epithelial tissues	Blindness, skin disorders, impaired immunity
D	Dairy products, egg yolk	Aids in absorption and use of calcium and phosphorus	Rickets (bone deformities) in children, bone softening in adults
E (tocopherol)	Vegetable oils, nuts, seeds	Antioxidant; helps prevent damage to cell membranes	Nervous system degeneration
K (phylloquinone)	Green vegetables, tea; also made by colon bacteria	Important in blood clotting	Defective blood clotting

Our dietary requirement for vitamin D is variable because we synthesize this vitamin from other molecules when the skin is exposed to sunlight.

For people with poorly balanced diets, taking vitamin supplements that provide recommended daily levels is certainly reasonable. It is much less clear whether massive doses of vitamins confer any health benefits or are, in fact, safe. Moderate overdoses of water-soluble vitamins are probably harmless because excesses of these vitamins are excreted in urine. However, excesses of fat-soluble vitamins are deposited in body fat, so overconsumption may result in accumulating toxic levels of these compounds.

Minerals

Dietary **minerals** are inorganic nutrients, such as iron and sulfur, that are usually required in small amounts—from less than 1 mg to about 2,500 mg per day. As shown in **Table 41.2** on the next page, minerals have diverse functions in animal physiology. Some are cofactors built into the structure of enzymes; magnesium, for example, is present in enzymes that split ATP. In contrast, sodium, potassium, and chloride are important in the functioning of nerves and in maintaining osmotic balance between cells and the surrounding body fluid. Vertebrates use one mineral—iodine—specifically to make thyroid hormones, which regulate metabolic rate. Vertebrates also require relatively large quantities of calcium and phosphorus for building and maintaining bone.

Ingesting large amounts of some minerals can upset homeostatic balance and impair health. For example, excess salt (sodium chloride) intake can contribute to high blood pressure. This is a particular problem in the United States, where the typical person consumes enough salt to provide about 20 times the required amount of sodium. Packaged (prepared) foods often contain large amounts of sodium chloride, even if they do not taste very salty. Excessive consumption of iron can also endanger health: Liver damage due to iron overload affects as much as 10% of the human population in some regions of Africa where the water supply is especially iron-rich.

Table 41.2 Mineral Requirements of Humans*

	Mineral	Major Dietary Sources	Major Functions in the Body	Symptoms of Deficiency
Greater than 200 mg per day required	Calcium (Ca)	Dairy products, dark green vegetables, legumes	Bone and tooth formation, blood clotting, nerve and muscle function	Impaired growth, loss of bone mass
	Phosphorus (P)	Dairy products, meats, grains	Bone and tooth formation, acid-base balance, nucleotide synthesis	Weakness, loss of minerals from bone, calcium loss
	Sulfur (S)	Proteins from many sources	Component of certain amino acids	Impaired growth, fatigue, swelling
	Potassium (K)	Meats, dairy products, many fruits and vegetables, grains	Acid-base balance, water balance, nerve function	Muscular weakness, paralysis, nausea, heart failure
	Chlorine (Cl)	Table salt	Acid-base balance, formation of gastric juice, nerve function, osmotic balance	Muscle cramps, reduced appetite
	Sodium (Na)	Table salt	Acid-base balance, water balance, nerve function	Muscle cramps, reduced appetite
	Magnesium (Mg)	Whole grains, green leafy vegetables	Enzyme cofactor; ATP bioenergetics	Nervous system disturbances
	Iron (Fe)	Meats, eggs, legumes, whole grains, green leafy vegetables	Component of hemoglobin and of electron carriers; enzyme cofactor	Iron-deficiency anemia, weakness, impaired immunity
	Fluorine (F)	Drinking water, tea, seafood	Maintenance of tooth structure	Higher frequency of tooth decay
	Iodine (I)	Seafood, iodized salt	Component of thyroid hormones	Goiter (enlarged thyroid gland)

*Additional minerals required in trace amounts are chromium (Cr), cobalt (Co), copper (Cu), manganese (Mn), molybdenum (Mo), selenium (Se), and zinc (Zn). All of these minerals, as well as those in the table, are harmful when consumed in excess.

Dietary Deficiencies

A diet that lacks one or more essential nutrients or consistently supplies less chemical energy than the body requires results in *malnutrition*, a failure to obtain adequate nutrition. Malnutrition resulting from either type of dietary deficiency can have negative impacts on health and survival.

Deficiencies in Essential Nutrients

Insufficient intake of essential nutrients can cause deformities, disease, and even death. For example, cattle, deer, and other herbivores may develop dangerously fragile bones if they graze on plants growing in soil that lacks phosphorus. Some grazing animals obtain otherwise missing nutrients by consuming concentrated sources of salt or other minerals **(Figure 41.3)**. Among carnivores, spiders have been found to adjust for dietary deficiencies by switching to prey that restores nutritional balance.

Like other animals, humans sometimes suffer from diets lacking in essential nutrients. A diet that provides insufficient amounts of one or more essential amino acids causes protein deficiency, the most common type of malnutrition among humans. For example, protein deficiency may arise if a child's diet shifts from consisting of breast milk to consisting solely of foods that provide almost all of their calories in the form of starch and other carbohydrates. Such children, if they survive infancy, often have impaired physical and mental development.

▲ **Figure 41.3 Obtaining essential nutrients.** A juvenile chamois (*Rupicapra rupicapra*), an herbivore, licks exposed salts and minerals in its rocky alpine habitat. This behavior is common among herbivores living where soils and plants provide insufficient amounts of essential nutrients, such as sodium, calcium, phosphorus, and iron.

Among populations subsisting on simple rice diets, individuals are often afflicted with vitamin A deficiency, which can cause blindness or death. To overcome this problem, scientists have engineered a strain of rice to synthesize beta-carotene, the orange-colored pigment that is abundant in carrots. Once absorbed into the body, beta-carotene is converted to vitamin A.

The potential benefit of this “Golden Rice” (see Chapter 38) is enormous because 1–2 million young children worldwide die every year from vitamin A deficiency.

Undernutrition

A diet that fails to provide adequate sources of chemical energy results in *undernutrition*. When an animal is undernourished, a series of events unfold: The body uses up stored carbohydrates and fat and then begins breaking down its own proteins for fuel; muscles begin to decrease in size; and the brain may become protein-deficient. If energy intake remains less than energy expenditures, the animal will eventually die. Even if a seriously undernourished animal survives, some of the damage may be irreversible.

Human undernutrition is most common when drought, war, or another crisis severely disrupts the food supply. In sub-Saharan Africa, where the AIDS epidemic has crippled both rural and urban communities, approximately 200 million children and adults cannot obtain enough food.

Sometimes undernutrition occurs within well-fed human populations as a result of eating disorders. For example, anorexia nervosa leads individuals, usually female, to starve themselves compulsively.

Assessing Nutritional Needs

Determining the ideal diet for the human population is an important but difficult problem for scientists. As objects of study, people present many challenges. Unlike laboratory animals, humans are genetically diverse. They also live in settings far more varied than the stable and uniform environment that scientists use to facilitate comparisons in laboratory experiments. Ethical concerns present an additional barrier. For example, it is not acceptable to investigate the nutritional needs of children in a way that might harm a child’s growth or development.

The methods used to study human nutrition have changed dramatically over time. To avoid harming others, several of the researchers who discovered vitamins a century ago used themselves as subject animals. Today, researchers typically rely on the study of genetic defects that disrupt food uptake, storage, or use. For example, a genetic disorder called hemochromatosis causes iron buildup in the absence of any abnormal iron consumption or exposure. Fortunately, this common disorder is remarkably easy to treat: Drawing blood regularly removes enough iron from the body to restore homeostasis. By studying the defective genes that can cause the disease, scientists have learned a great deal about the regulation of iron absorption.

Many insights into human nutrition have come from *epidemiology*, the study of human health and disease at the population level. In the 1970s, for instance, researchers discovered that children born to women of low socioeconomic status were more likely to have neural tube defects, which occur when tissue fails to enclose the developing brain and spinal cord (see Chapter 47). The English scientist Richard Smithells thought that malnutrition among these women might be responsible. As described in **Figure 41.4**, he found that vitamin supplementation greatly reduced the risk of neural tube defects. In other studies, he obtained evidence that folic acid (vitamin B_9) was the specific vitamin responsible, a finding confirmed by other researchers. Based on this evidence, the United States in 1998 began to require that folic acid be added to enriched grain products used to make bread, cereals, and other foods. Follow-up studies have documented the effectiveness of this program in reducing the frequency of neural tube defects. Thus, at a time when microsurgery and sophisticated diagnostic imaging dominate the headlines, a simple dietary change such as folic acid supplementation or consumption of Golden Rice may be among the greatest contributors to human health.

▼ Figure 41.4 **INQUIRY**

Can diet influence the frequency of birth defects?

EXPERIMENT Richard Smithells, of the University of Leeds, in England, examined the effect of vitamin supplementation on the risk of neural tube defects. Women who had had one or more babies with such a defect were put into two study groups. The experimental group consisted of those who were planning a pregnancy and began taking a multivitamin at least four weeks before attempting conception. The control group, who were not given vitamins, included women who declined them and women who were already pregnant. The numbers of neural tube defects resulting from the pregnancies were recorded for each group.

RESULTS

Group	Number of infants/fetuses studied	Infants/fetuses with a neural tube defect
Vitamin supplements (experimental group)	141	1 (0.7%)
No vitamin supplements (control group)	204	12 (5.9%)

CONCLUSION This study provided evidence that vitamin supplementation protects against neural tube defects, at least after the first pregnancy. Follow-up trials demonstrated that folic acid alone provided an equivalent protective effect.

SOURCE R. W. Smithells et al., Possible prevention of neural-tube defects by periconceptional vitamin supplementation, *Lancet* 315: 339–340 (1980).

INQUIRY IN ACTION Read and analyze the original paper in *Inquiry in Action: Interpreting Scientific Papers.*

WHAT IF? Subsequent studies were designed to learn if folic acid supplements prevent neural tube defects during first-time pregnancies. To determine the required number of subjects, what type of additional information did the researchers need?

CONCEPT CHECK 41.1

1. All 20 amino acids are needed to make animal proteins. Why aren't they all essential to animal diets?
2. **MAKE CONNECTIONS** Review the discussion of enzymes in metabolic reactions in Concept 8.4 (pp. 152–156). Then explain why vitamins are required in very small amounts in the diet.
3. **WHAT IF?** If a zoo animal eating ample food shows signs of malnutrition, how might a researcher determine which nutrient is lacking in its diet?

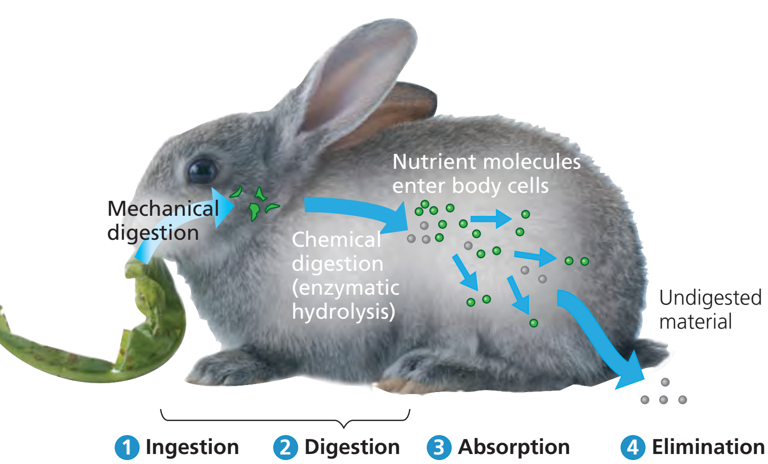
For suggested answers, see Appendix A.

CONCEPT 41.2

The main stages of food processing are ingestion, digestion, absorption, and elimination

In this section, we turn from nutritional requirements to the mechanisms by which animals process food. Food processing can be divided into four distinct stages: ingestion, digestion, absorption, and elimination **(Figure 41.5)**. The first stage, **ingestion**, is the act of eating or feeding. **Figure 41.6** surveys and classifies the principal feeding mechanisms that have evolved in animals. Given the variation in food sources among animal species, it is not surprising that strategies for extracting resources from food also differ widely. We will focus, however, on the shared processes, pausing periodically to consider some adaptations to particular diets or environments.

In **digestion**, the second stage of food processing, food is broken down into molecules small enough for the body to absorb. Mechanical digestion, such as chewing, typically precedes chemical digestion. Mechanical digestion breaks food into smaller pieces, increasing the surface area available for chemical processes. Chemical digestion is necessary because animals cannot directly use the proteins, carbohydrates, nucleic acids, fats, and phospholipids in food. One problem is that these molecules are too large to pass through membranes and enter the cells of the animal. In addition, the large molecules in food are not all identical to those the animal needs for its particular tissues and functions. When large molecules in food are broken down into their components, however, the animal can use these smaller molecules to assemble the large molecules it needs. For example, although fruit flies and humans have very different diets, both convert proteins in their food to the same 20 amino acids from which they assemble all of the proteins specific for their species.



▲ **Figure 41.5 The four stages of food processing.**

Recall from Chapter 5 that a cell makes a macromolecule or fat by linking together smaller components; it does so by removing a molecule of water for each new covalent bond formed. Chemical digestion by enzymes reverses this process by breaking bonds with the addition of water (see Figure 5.2). This splitting process is called *enzymatic hydrolysis*. A variety of enzymes catalyze the digestion of large molecules in food. Polysaccharides and disaccharides are split into simple sugars; proteins are broken down into amino acids; and nucleic acids are cleaved into nucleotides and their components. Enzymatic hydrolysis also releases fatty acids and other components from fats and phospholipids.

The last two stages of food processing occur after the food is digested. In the third stage, **absorption**, the animal's cells take up (absorb) small molecules such as amino acids and simple sugars. **Elimination** completes the process as undigested material passes out of the digestive system.

Digestive Compartments

In our overview of food processing, we have seen that digestive enzymes hydrolyze the same biological materials (such as proteins, fats, and carbohydrates) that make up the bodies of the animals themselves. How, then, are animals able to digest food without digesting their own cells and tissues? The evolutionary adaptation found across a wide range of animal species is the processing of food within specialized compartments. Such compartments can be intracellular, in the form of food vacuoles, or extracellular, as in digestive organs and systems.

Intracellular Digestion

Food vacuoles—cellular organelles in which hydrolytic enzymes break down food—are the simplest digestive compartments. The hydrolysis of food inside vacuoles, called *intracellular digestion*, begins after a cell engulfs solid food by phagocytosis or liquid food by pinocytosis (see Figure 7.22). Newly formed food vacuoles fuse with lysosomes, organelles containing hydrolytic enzymes. This fusion of organelles brings food in contact with the enzymes, allowing digestion to occur safely within a compartment

▼ Figure 41.6

Exploring Four Main Feeding Mechanisms of Animals

Suspension Feeders and Filter Feeders

Many aquatic animals are **suspension feeders**, which eat small organisms or food particles suspended in the water. For example, clams and oysters feed on tiny morsels of food in the water that passes over their gills; cilia sweep the food particles to the animal's mouth in a film of mucus. **Filter feeders** such as the humpback whale shown above move water through a filtering structure to obtain food. Attached to the whale's upper jaw are comblike plates called baleen, which strain small invertebrates and fish from enormous volumes of water.

Substrate Feeders

Substrate feeders are animals that live in or on their food source. This leaf miner caterpillar, the larva of a moth, is eating through the soft tissue of an oak leaf, leaving a dark trail of feces in its wake. Some other substrate feeders include maggots (fly larvae), which burrow into animal carcasses.

Fluid Feeders

Fluid feeders suck nutrient-rich fluid from a living host. This mosquito has pierced the skin of its human host with hollow, needlelike mouthparts and is consuming a blood meal (colorized SEM). Similarly, aphids are fluid feeders that tap the phloem sap of plants. In contrast to such parasites, some fluid feeders actually benefit their hosts. For example, hummingbirds and bees move pollen between flowers as they fluid-feed on nectar.

Bulk Feeders

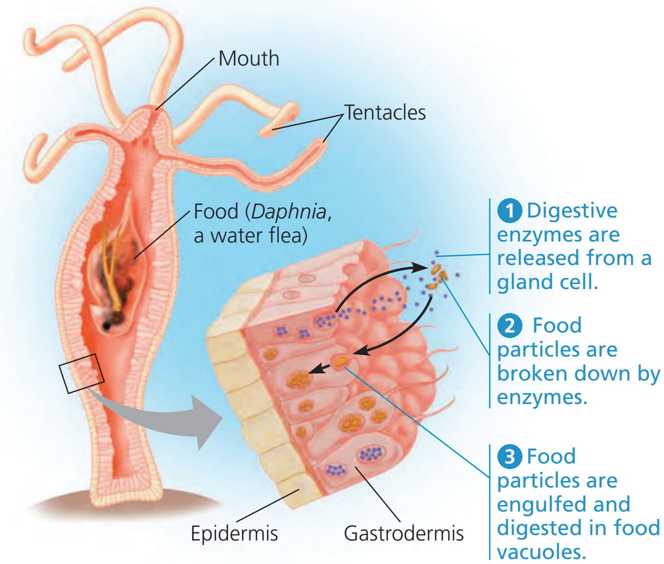
Most animals, including humans, are **bulk feeders**, which eat relatively large pieces of food. Their adaptations include tentacles, pincers, claws, poisonous fangs, jaws, and teeth that kill their prey or tear off pieces of meat or vegetation. In this amazing scene, a rock python is beginning to ingest a gazelle it has captured and killed. Snakes cannot chew their food into pieces and must swallow it whole—even if the prey is much bigger than the diameter of the snake. They can do so because the lower jaw is loosely hinged to the skull by an elastic ligament that permits the mouth and throat to open very wide. After swallowing its prey, which may take more than an hour, the python will spend two weeks or more digesting its meal.

enclosed by a protective membrane. A few animals, such as sponges, digest their food entirely by this intracellular mechanism (see Figure 33.4).

Extracellular Digestion

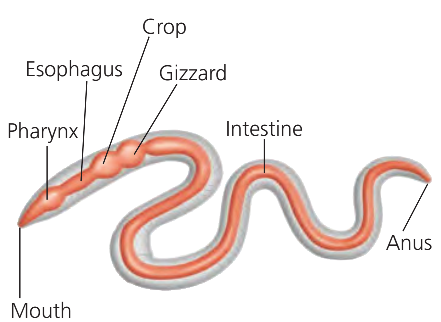
In most animal species, at least some hydrolysis occurs by *extracellular digestion*, the breakdown of food in compartments that are continuous with the outside of the animal's body. Having one or more extracellular compartments for digestion enables an animal to devour much larger pieces of food than can be ingested by phagocytosis.

Many animals with relatively simple body plans have a digestive compartment with a single opening **(Figure 41.7)**. This pouch, called a **gastrovascular cavity**, functions in digestion as well as in the distribution of nutrients throughout the body (hence the *vascular* part of the term). The carnivorous cnidarians called hydras provide a good example of how a gastrovascular cavity works. A hydra uses its tentacles to stuff captured prey through its mouth into its gastrovascular cavity. Specialized gland cells of the hydra's gastrodermis, the tissue layer that lines the cavity, then secrete digestive enzymes that break the soft tissues of the prey into tiny pieces. Other cells of the gastrodermis engulf these food particles, and most of the hydrolysis of macromolecules occurs intracellularly, as in sponges. After a hydra has digested its meal, undigested materials that remain in the gastrovascular cavity, such as exoskeletons of small crustaceans, are eliminated through the same opening by which food entered. Many flatworms also have a gastrovascular cavity with a single opening (see Figure 33.10).

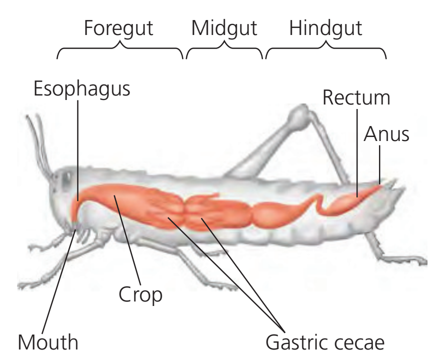


▲ **Figure 41.7 Digestion in a hydra.** Digestion begins in the gastrovascular cavity and is completed intracellularly after small food particles are engulfed by specialized cells of the gastrodermis.

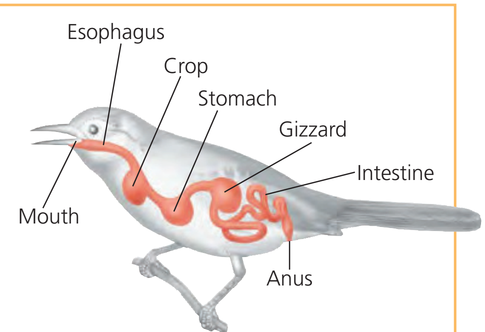
In contrast with cnidarians and flatworms, most animals have a digestive tube extending between two openings, a mouth and an anus **(Figure 41.8)**. Such a tube is called a *complete digestive tract* or, more commonly, an **alimentary canal**. Because food moves along the alimentary canal in a single direction, the tube can be organized into specialized compartments that carry out digestion and nutrient absorption in a stepwise fashion. An animal with an alimentary canal can ingest food while earlier meals are still being digested, a feat that



(a) Earthworm. The alimentary canal of an earthworm includes a muscular pharynx that sucks food in through the mouth. Food passes through the esophagus and is stored and moistened in the crop. Mechanical digestion occurs in the muscular gizzard, which pulverizes food with the aid of small bits of sand and gravel. Further digestion and absorption occur in the intestine.



(b) Grasshopper. A grasshopper has several digestive chambers grouped into three main regions: a foregut, with an esophagus and crop; a midgut; and a hindgut. Food is moistened and stored in the crop, but most digestion occurs in the midgut. Pouches called gastric cecae (singular, *ceca*) extend from the beginning of the midgut and function in digestion and absorption.



(c) Bird. Many birds have a crop for storing food and a stomach and gizzard for mechanically digesting it. Chemical digestion and absorption of nutrients occur in the intestine.

▲ **Figure 41.8 Variation in alimentary canals.**

is likely to be difficult or inefficient for animals with gastrovascular cavities. In the next section, we'll explore the spatial and functional organization of an alimentary canal.

CONCEPT CHECK 41.2

1. Distinguish the overall structure of a gastrovascular cavity from that of an alimentary canal.
2. In what sense are nutrients from a recently ingested meal not really "inside" your body prior to the absorption stage of food processing?
3. WHAT IF? Thinking in broad terms, what similarities can you identify between digestion in an animal body and the breakdown of gasoline in an automobile? (You don't have to know about auto mechanics.)

For suggested answers, see Appendix A.

CONCEPT 41.3

Organs specialized for sequential stages of food processing form the mammalian digestive system

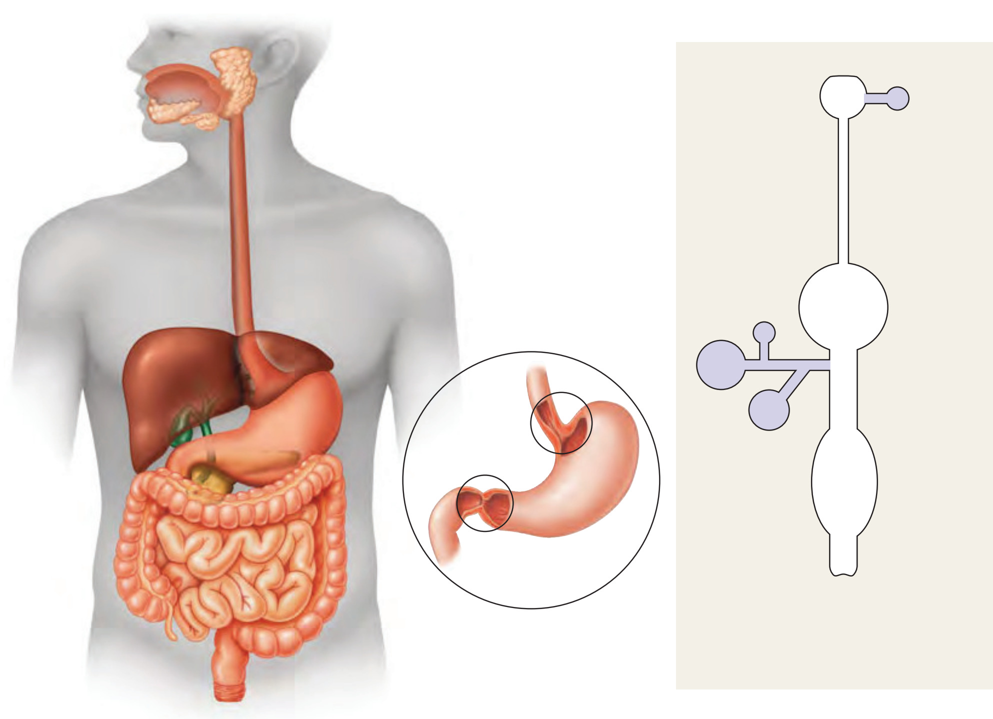
Because most animals, including mammals, have an alimentary canal, we can use the mammalian digestive system as a representative example of the general principles of food processing. In mammals, the digestive system consists of the alimentary canal and various accessory glands that secrete digestive juices through ducts into the canal **(Figure 41.9)**. The accessory glands of the mammalian digestive system are three pairs of salivary glands, the pancreas, the liver, and the gallbladder.

Food is pushed along the alimentary canal by **peristalsis**, alternating waves of contraction and relaxation in the smooth muscles lining the canal. At some of the junctions between specialized compartments, the muscular layer forms ringlike valves called **sphincters**. Acting like drawstrings to close off the alimentary canal, sphincters regulate the passage of material between compartments.

Using the human digestive system as a model, let's now follow a meal through the alimentary canal. As we do so, we'll examine in more detail what happens to the food in each digestive compartment along the way.

The Oral Cavity, Pharynx, and Esophagus

Ingestion and the initial steps of digestion occur in the mouth, or **oral cavity**. Mechanical digestion begins as teeth of various shapes cut, mash, and grind food, making the food easier to swallow and increasing its surface area. Meanwhile, the presence of food stimulates a nervous reflex that causes the **salivary glands** to deliver saliva through ducts to the oral cavity. Saliva may also be released before food enters the mouth, triggered by a learned association between eating and the time of day, a cooking odor, or another stimulus.



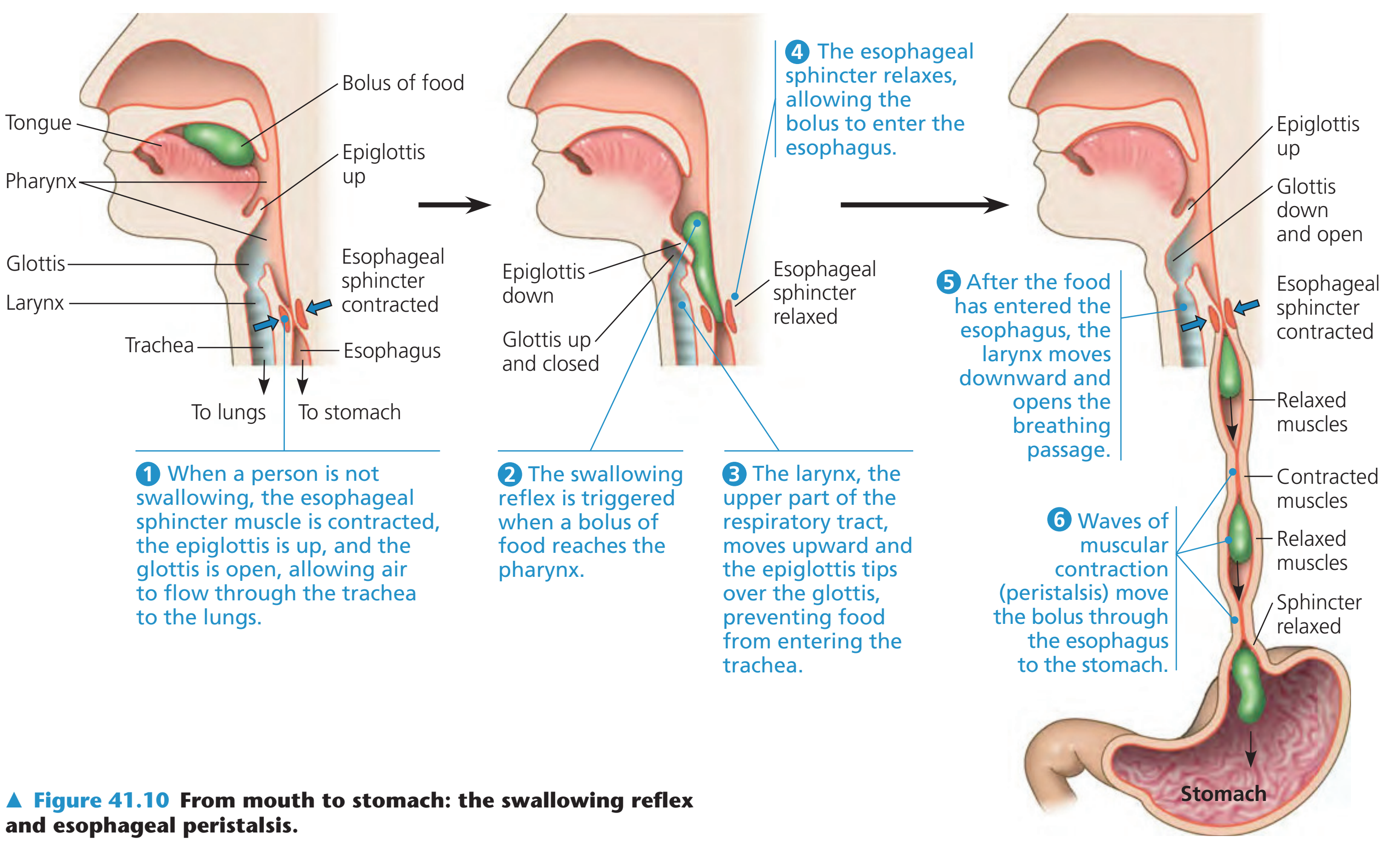
◀ **Figure 41.9 The human digestive system.** After food is chewed and swallowed, it takes 5–10 seconds for it to pass down the esophagus and into the stomach, where it spends 2–6 hours being partially digested. Final digestion and nutrient absorption occur in the small intestine over a period of 5–6 hours. In 12–24 hours, any undigested material passes through the large intestine, and feces are expelled through the anus.

Saliva initiates chemical digestion while also protecting the oral cavity. The enzyme **amylase**, found in saliva, hydrolyzes starch (a glucose polymer from plants) and glycogen (a glucose polymer from animals) into smaller polysaccharides and the disaccharide maltose. Much of the protective effect of saliva is provided by **mucus**, which is a viscous mixture of water, salts, cells, and slippery glycoproteins (carbohydrate-protein complexes) called mucins. Mucus in saliva protects the lining of the mouth from abrasion and lubricates food for easier swallowing. Additional components of saliva include buffers, which help prevent tooth decay by neutralizing acid, and antimicrobial agents (such as lysozyme; see Figure 5.18), which protect against bacteria that enter the mouth with food.

Much as a doorman screens and assists people entering a building, the tongue aids digestive processes by evaluating ingested material and then enabling its further passage. When food arrives at the oral cavity, the tongue plays a critical role in distinguishing which foods should be processed further. (See Chapter 50 for a discussion of the sense of taste.) After food is deemed acceptable and chewing commences, tongue movements manipulate the food, helping shape it into a ball called a **bolus**. During swallowing, the tongue provides further help, pushing the bolus to the back of the oral cavity and into the pharynx.

The **pharynx**, or throat region, opens to two passageways: the esophagus and the trachea (windpipe). The **esophagus** connects to the stomach, whereas the trachea leads to the lungs. Swallowing must therefore be carefully choreographed to keep food from entering and blocking the airway. When you swallow, a flap of cartilage called the *epiglottis* covers the *glottis*—the vocal cords and the opening between them. Guided by the movements of the *larynx*, the upper part of the respiratory tract, this swallowing reflex directs each bolus into the entrance of the esophagus (**Figure 41.10**, 1–4). If the swallowing reflex fails, food or liquids can reach the trachea and cause choking, a blockage of the trachea. The resulting lack of airflow into the lungs can be fatal if the material is not dislodged by vigorous coughing, a series of back slaps, or a forced upward thrust of the diaphragm (the Heimlich maneuver).

The esophagus contains both striated and smooth muscle (see Figure 40.5). The striated muscle is situated at the top of the esophagus and is active during swallowing. Throughout the rest of the esophagus, smooth muscle functions in peristalsis. The rhythmic cycles of contraction move each bolus to the stomach (see Figure 41.10, 6). As with other parts of the digestive system, the form of the esophagus fits its function and varies among species. For example, fishes have no lungs to bypass and therefore have a very short esophagus. And it will come as no surprise that giraffes have a very long esophagus.



▲ **Figure 41.10 From mouth to stomach: the swallowing reflex and esophageal peristalsis.**

Digestion in the Stomach

The **stomach**, which is located just below the diaphragm, stores food and begins digestion of proteins. With accordion-like folds and a very elastic wall, this organ can stretch to accommodate about 2 L of food and fluid. The stomach secretes a digestive fluid called **gastric juice** and mixes this secretion with the food through a churning action. This mixture of ingested food and digestive juice is called **chyme**.

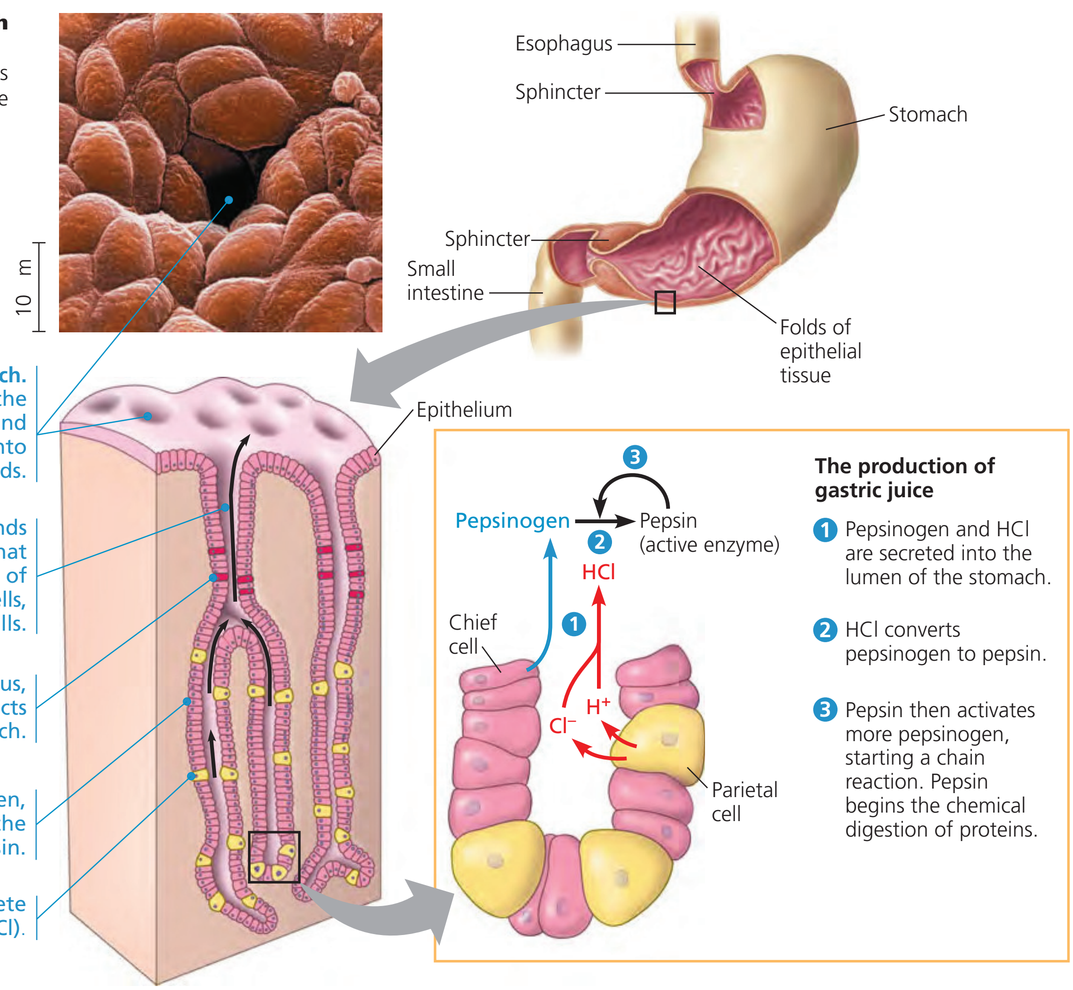
Chemical Digestion in the Stomach

Two components of gastric juice carry out chemical digestion. One is hydrochloric acid (HCl), which disrupts the extracellular matrix that binds cells together in meat and plant material. The concentration of HCl is so high that the pH of gastric juice is about 2, acidic enough to dissolve iron nails (and to kill most bacteria). This low pH denatures (unfolds) proteins in food, increasing exposure of their peptide bonds. The exposed bonds are attacked by the second component of gastric juice—a **protease**, or protein-digesting enzyme, called **pepsin**. Unlike most enzymes, pepsin works best in a strongly acidic environment. By breaking peptide bonds, it cleaves proteins into smaller polypeptides. Further digestion to individual amino acids occurs in the small intestine.

Why doesn't gastric juice destroy the stomach cells that make it? The answer is that the ingredients of gastric juice are kept inactive until they are released into the lumen (cavity) of the stomach. The components of gastric juice are produced by cells in the gastric glands of the stomach **(Figure 41.11)**. *Parietal cells* secrete hydrogen and chloride ions, which form HCl. Using an ATP-driven pump, the parietal cells expel hydrogen ions into the lumen. There, the hydrogen ions combine with chloride ions that diffuse into the lumen through specific membrane channels of the parietal cells. Meanwhile, *chief cells* release pepsin into the lumen in an inactive form called **pepsinogen**. HCl converts pepsinogen to active pepsin by clipping off a small portion of the molecule and exposing its active site. Through these processes, both HCl and pepsin form in the lumen of the stomach, not within the cells of the gastric glands.

After hydrochloric acid converts a small amount of pepsinogen to pepsin, pepsin itself helps activate the remaining pepsinogen. Pepsin, like HCl, can clip pepsinogen to expose the enzyme's active site. This generates more pepsin,

▶ **Figure 41.11 The stomach and its secretions.** The micrograph (colorized SEM) shows a gastric pit on the interior surface of the stomach, through which digestive juices are secreted.



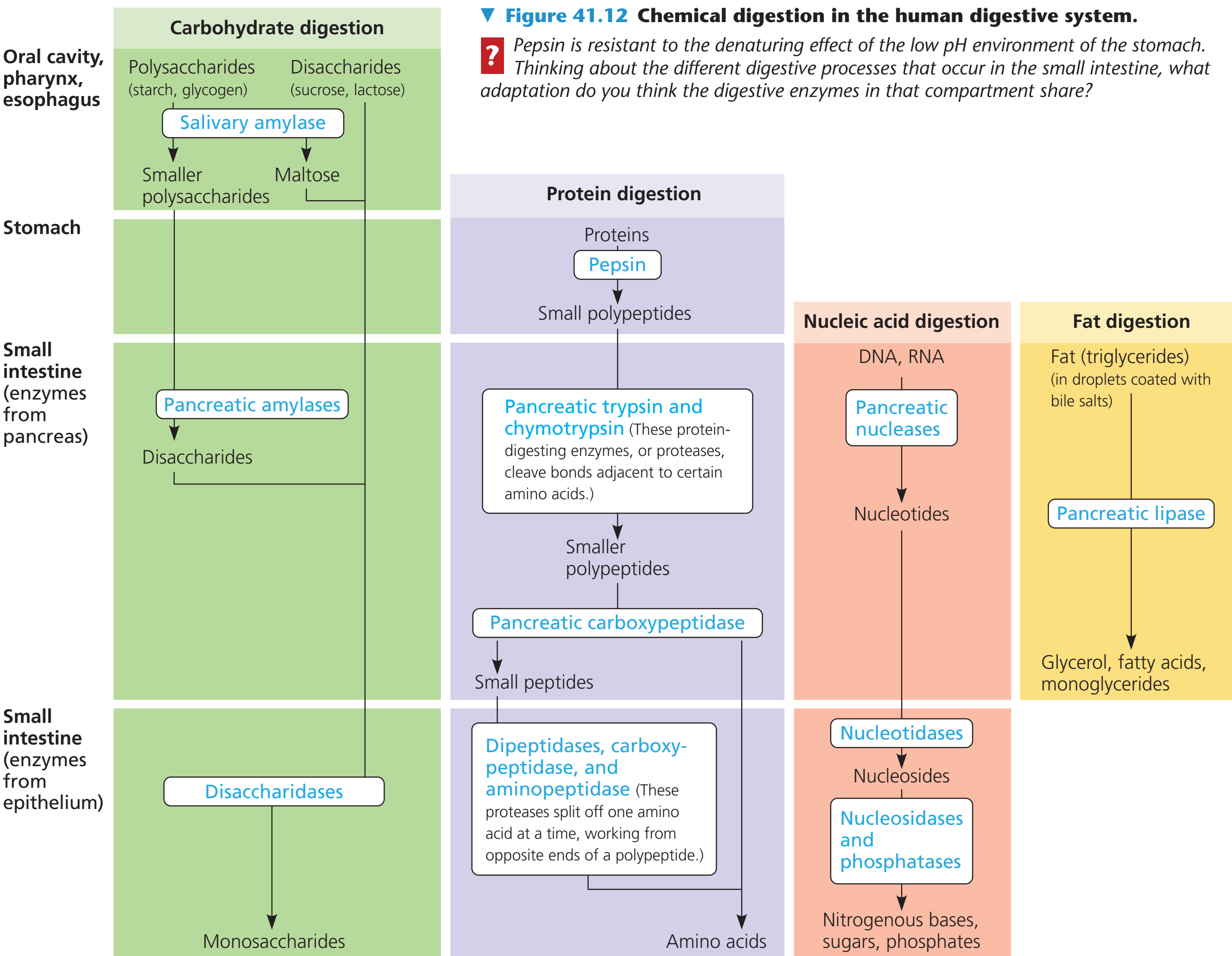
which activates more pepsinogen, forming more active enzyme. This series of events is an example of positive feedback, which amplifies the effect of an initially small input.

When HCl and pepsin form within the stomach lumen, why aren't the cells that line the stomach damaged? Actually, these cells are vulnerable to gastric juice as well as to acid-tolerant pathogens in food or water. However, the stomach lining protects against self-digestion by secreting mucus. In addition, cell division adds a new epithelial layer every three days, replacing cells eroded by digestive juices. Despite these defenses, damaged areas of the stomach lining called gastric ulcers may appear. For decades, scientists thought they were caused by psychological stress and resulting excess acid secretion. In 1982, however, Australian researchers Barry Marshall and Robin Warren reported that infection by the acid-tolerant bacterium *Helicobacter pylori* causes ulcers. They also demonstrated that an antibiotic treatment could cure most gastric ulcers. For these findings, they were awarded the Nobel Prize in 2005.

Stomach Dynamics

Chemical digestion by gastric juice is facilitated by the churning action of the stomach. This coordinated series of muscle contractions and relaxations mixes the stomach contents about every 20 seconds. As a result of mixing and enzyme action, what begins as a recently swallowed meal becomes the acidic, nutrient-rich broth known as chyme. Most of the time, the stomach is closed off at both ends (see Figure 41.9). The sphincter between the esophagus and the stomach normally opens only when a bolus arrives. Occasionally, however, a person experiences acid reflux, a backflow of chyme from the stomach into the lower end of the esophagus. The resulting irritation of the esophagus is commonly called "heartburn."

The contents of the stomach typically pass into the small intestine within 2–6 hours after a meal. The sphincter located where the stomach opens to the small intestine helps regulate passage into the small intestine, allowing only one squirt of chyme at a time.



▼ **Figure 41.12 Chemical digestion in the human digestive system.**

? *Pepsin is resistant to the denaturing effect of the low pH environment of the stomach. Thinking about the different digestive processes that occur in the small intestine, what adaptation do you think the digestive enzymes in that compartment share?*

Digestion in the Small Intestine

Although chemical digestion of some nutrients begins in the oral cavity or stomach, most enzymatic hydrolysis of the macromolecules from food occurs in the **small intestine** (**Figure 41.12**, on p. 886). Over 6 m (20 feet) long in humans, the small intestine is the alimentary canal's longest compartment. Its name refers to its small diameter, compared with that of the large intestine. The first 25 cm (10 inches) or so of the small intestine forms the **duodenum**. It is here that chyme from the stomach mixes with digestive juices from the pancreas, liver, and gallbladder, as well as from gland cells of the intestinal wall itself. As you will see in Concept 41.5, hormones released by the stomach and duodenum control the digestive secretions into the alimentary canal.

Pancreatic Secretions

The **pancreas** aids chemical digestion by producing an alkaline solution rich in bicarbonate as well as several enzymes. The bicarbonate neutralizes the acidity of chyme and acts as a buffer. Among the pancreatic enzymes are trypsin and chymotrypsin, proteases secreted into the duodenum in inactive forms (see Figure 41.12). In a chain reaction similar to activation of pepsin, they are activated when safely located in the lumen within the duodenum.

Bile Production by the Liver

Digestion of fats and other lipids begins in the small intestine and relies on the production of **bile**, a mixture of substances that is made in the **liver**. Bile contains bile salts, which act as emulsifiers (detergents) that aid in digestion and absorption of lipids. Bile is stored and concentrated in the **gallbladder**.

Bile production is integral to one of the other vital functions of the liver: the destruction of red blood cells that are no longer fully functional. In producing bile, the liver incorporates some pigments that are by-products of red blood cell disassembly. These bile pigments are then eliminated from the body with the feces. In some liver or blood disorders, bile pigments accumulate in the skin, resulting in a characteristic yellowing called jaundice.

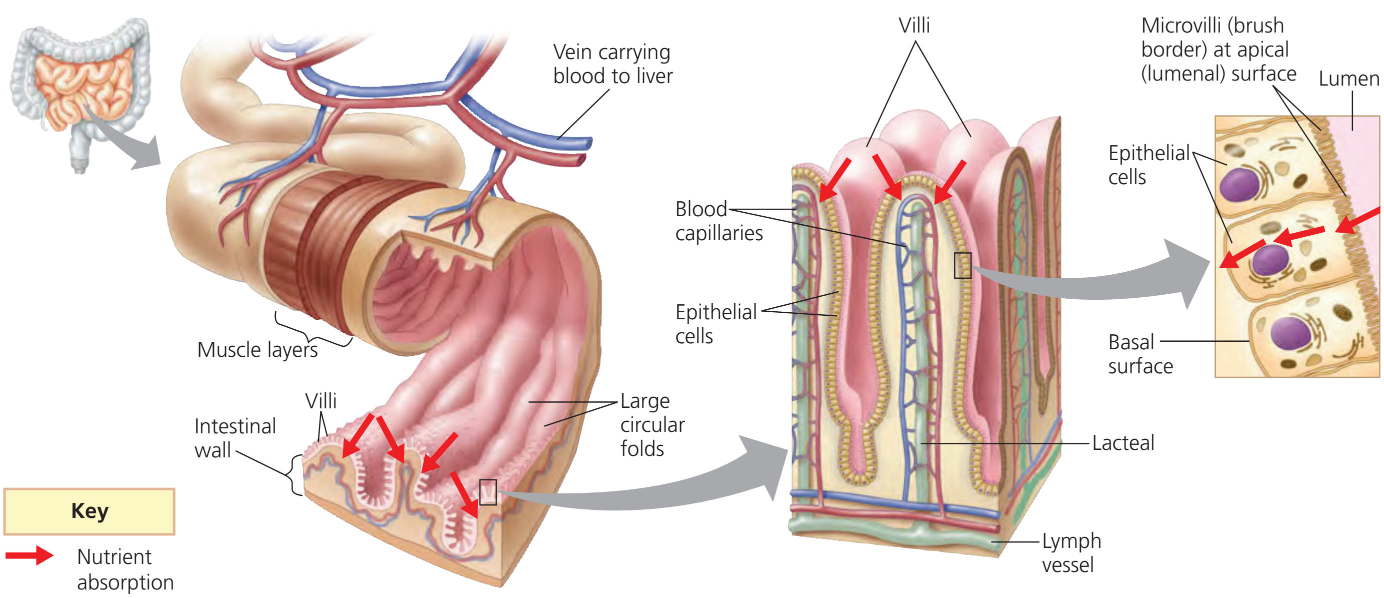
Secretions of the Small Intestine

The epithelial lining of the duodenum is the source of several digestive enzymes (see Figure 41.12). Some are secreted into the lumen of the duodenum, whereas others are bound to the surface of epithelial cells.

While enzymatic hydrolysis proceeds, peristalsis moves the mixture of chyme and digestive juices along the small intestine. Most digestion is completed in the duodenum. The remaining regions of the small intestine, called the *jejunum* and *ileum*, function mainly in the absorption of nutrients and water.

Absorption in the Small Intestine

To reach body tissues, nutrients in the lumen must first cross the lining of the alimentary canal. Most of this absorption occurs across the highly folded surface of the small intestine, as illustrated in **Figure 41.13**. Large folds in the lining encircle



▲ **Figure 41.13 Nutrient absorption in the small intestine.**

? *Tapeworms sometimes infect humans, anchoring themselves to the wall of the small intestine. Based on how digestion is compartmentalized along the mammalian alimentary canal, what digestive functions would you expect these parasites to have?*

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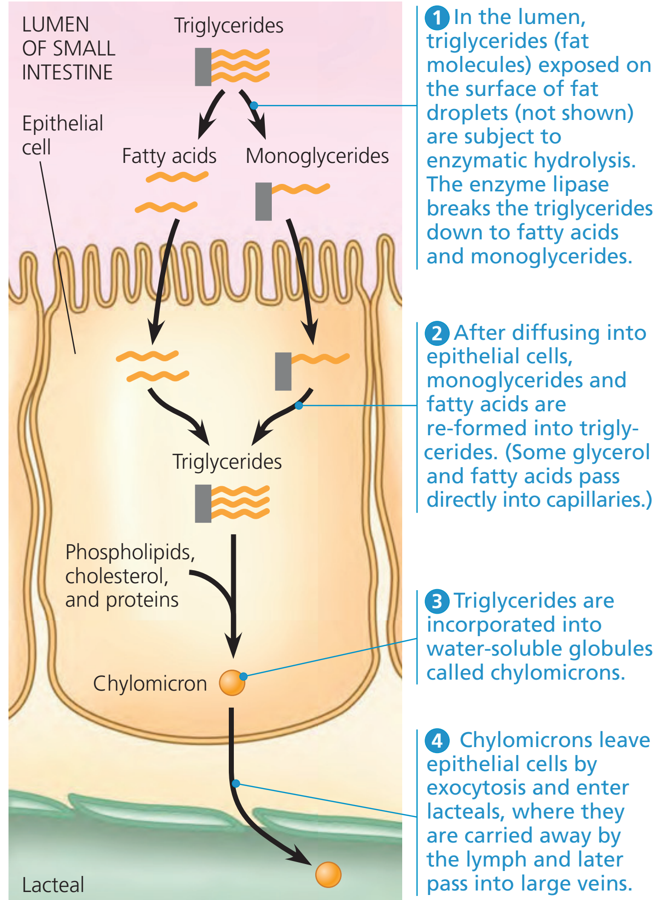
the intestine and are studded with finger-like projections called **villi**. In turn, each epithelial cell of a villus has on its apical surface many microscopic projections, or **microvilli**, that are exposed to the intestinal lumen. The many side-by-side microvilli give cells of the intestinal epithelium a brush-like appearance—reflected in the name *brush border*. Together, the folds, villi, and microvilli of the small intestine have a surface area of 300 m^2, roughly the size of a tennis court. This enormous surface area is an evolutionary adaptation that greatly increases the rate of nutrient absorption.

Depending on the nutrient, transport across the epithelial cells can be passive or active (see Chapter 7). The sugar fructose, for example, moves by facilitated diffusion down its concentration gradient from the lumen of the small intestine into the epithelial cells. From there, fructose exits the basal surface and is absorbed into microscopic blood vessels, or capillaries, at the core of each villus. Other nutrients, including amino acids, small peptides, vitamins, and most glucose molecules, are pumped against concentration gradients by the epithelial cells of the villus. This active transport allows much more absorption of nutrients than would be possible with passive diffusion alone.

The capillaries and veins that carry nutrient-rich blood away from the villi all converge into the **hepatic portal vein**, a blood vessel that leads directly to the liver. From the liver, blood travels to the heart and then to other tissues and organs. This arrangement serves two major functions. First, it allows the liver to regulate the distribution of nutrients to the rest of the body. Because the liver can interconvert many organic molecules, blood that leaves the liver may have a very different nutrient balance than the blood that entered via the hepatic portal vein. Second, the arrangement allows the liver to remove toxic substances before the blood circulates broadly. The liver is the primary site for the detoxification of many organic molecules, including drugs, that are foreign to the body.

Although many nutrients leave the intestine through the bloodstream, some products of fat (triglyceride) digestion take a different path. As shown in **Figure 41.14**, hydrolysis of fats by lipase in the small intestine generates fatty acids and monoglycerides (glycerol joined to a single fatty acid). These products are absorbed by epithelial cells and recombined into triglycerides. They are then coated with phospholipids, cholesterol, and proteins, forming water-soluble globules called **chylomicrons**.

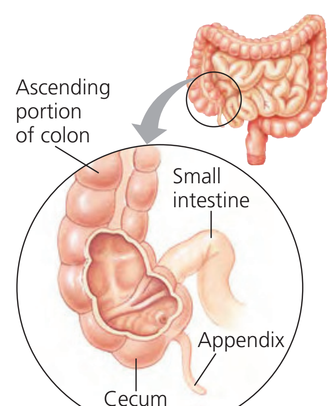
In exiting the intestine, chylomicrons are first transported from an epithelial cell into a **lacteal**, a vessel at the core of each villus (see Figures 41.13 and 41.14). Lacteals are part of the vertebrate lymphatic system, which is a network of vessels that are filled with a clear fluid called lymph. Starting at the lacteals, lymph containing the chylomicrons passes into the larger vessels of the lymphatic system and eventually into large veins that return the blood to the heart.



▲ **Figure 41.14 Absorption of fats.** Because fats are insoluble in water, adaptations are needed to digest and absorb them. Bile salts (not shown) break up large fat droplets and maintain a small droplet size in the intestinal lumen, exposing more of the fat at the surface for enzymatic hydrolysis. The fatty acids and monoglycerides released by hydrolysis can diffuse into epithelial cells, where fats are reassembled and incorporated into water-soluble chylomicrons that enter the lymphatic system.

Absorption in the Large Intestine

The alimentary canal ends with the **large intestine**, which includes the colon, cecum, and rectum. The small intestine connects to the large intestine at a T-shaped junction (**Figure 41.15**). One arm of the T is the 1.5-m-long **colon**, which leads to the rectum and anus. The other arm is a pouch called the **cecum**. The cecum is important for fermenting ingested material, especially in animals that eat large amounts of plant material. Compared with many other mammals,



▲ **Figure 41.15 Junction of the small and large intestines.**

humans have a small cecum. The **appendix**, a finger-like extension of the human cecum, has a minor and dispensable role in immunity.

A major function of the colon is to recover water that has entered the alimentary canal as the solvent of digestive juices. About 7 L of fluid is secreted into the lumen of the alimentary canal each day, and about 90% of that is reabsorbed in the small intestine and colon. There is no mechanism for active transport of water. Instead, water is reabsorbed by osmosis when Na^+ and other ions are pumped out of the lumen of the colon.

The **feces**, the wastes of the digestive system, become increasingly solid as they are moved along the colon by peristalsis. It takes approximately 12–24 hours for material to travel the length of the colon. If the lining of the colon is irritated—by a viral or bacterial infection, for instance—less water than normal may be reabsorbed, resulting in diarrhea. The opposite problem, constipation, occurs when the feces move along the colon too slowly. An excess of water is reabsorbed, and therefore the feces become compacted.

A rich community of mostly harmless bacteria lives on unabsorbed organic material in the human colon, contributing approximately one-third of the dry weight of feces. One inhabitant, *Escherichia coli*, is so common in the human digestive system that its presence in lakes and streams is a useful indicator of contamination by untreated sewage. As by-products of their metabolism, many colon bacteria generate gases, including methane and hydrogen sulfide, which has an offensive odor. These gases and ingested air are expelled through the anus. Some bacteria produce vitamins, such as vitamin K, biotin, and folic acid, that supplement our dietary intake when absorbed into the blood.

Besides bacteria, feces contain undigested material, including cellulose fiber. Although it has no caloric value to humans, fiber helps move food along the alimentary canal.

The terminal portion of the large intestine is the **rectum**, where feces are stored until they can be eliminated. Between the rectum and the anus are two sphincters, the inner one being involuntary and the outer one being voluntary. Periodically, strong contractions of the colon create an urge to defecate. Because filling of the stomach triggers a reflex that increases the rate of contractions in the colon, the urge to defecate often follows a meal.

We have followed a meal from one opening (the mouth) of the alimentary canal to the other (the anus). Next we'll see how some digestive adaptations may have evolved.

CONCEPT CHECK 41.3

1. How does swallowed food reach the stomach of a weightless astronaut in orbit?
2. Explain why a proton pump inhibitor, such as the drug Prilosec, relieves the symptoms of acid reflux.
3. **WHAT IF?** If you mixed gastric juice with crushed food in a test tube, what would happen?

For suggested answers, see Appendix A.

CONCEPT 41.4

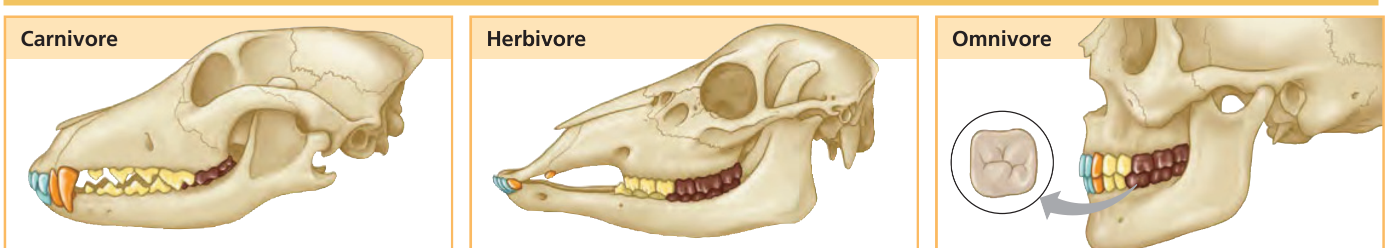
Evolutionary adaptations of vertebrate digestive systems correlate with diet

EVOLUTION The digestive systems of mammals and other vertebrates are variations on a common plan, but there are many intriguing adaptations, often associated with the animal's diet. To highlight how form fits function, we'll examine a few of them.

Dental Adaptations

Dentition, an animal's assortment of teeth, is one example of structural variation reflecting diet **(Figure 41.16)**. The evolutionary adaptation of teeth for processing different kinds of

▼ Figure 41.16 Dentition and diet.



Carnivores, such as members of the dog and cat families, generally have large, pointed incisors and canines that can be used to kill prey and rip or cut away pieces of flesh. The jagged premolars and molars crush and shred food.

Herbivores, such as horses and deer, usually have premolars and molars with broad, ridged surfaces that grind tough plant material. The incisors and canines are generally modified for biting off pieces of vegetation. In some herbivores, canines are absent.

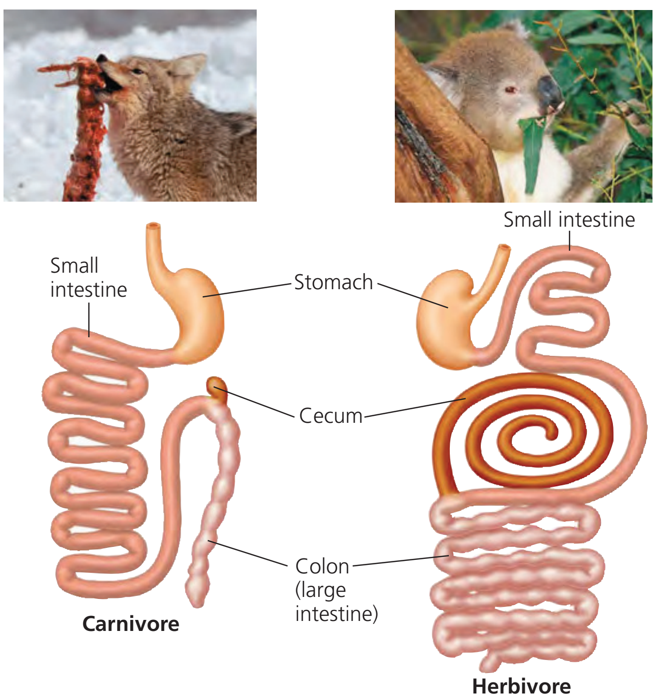
As omnivores, humans are adapted to eating both plants and meat. Adults have 32 teeth. From front to back along either side of the mouth are four bladelike incisors for biting, a pair of pointed canines for tearing, four premolars for grinding, and six molars for crushing (see inset, top view).

Key Incisors, Canines, Premolars, Molars food is one of the major reasons mammals have been so successful. Nonmammalian vertebrates generally have less specialized dentition, but there are interesting exceptions. For example, poisonous snakes, such as rattlesnakes, have fangs, modified teeth that inject venom into prey. Some fangs are hollow, like syringes, whereas others drip the poison along grooves on the surfaces of the teeth.

Stomach and Intestinal Adaptations

Large, expandable stomachs are common in carnivorous vertebrates, which may go for a long time between meals and must eat as much as they can when they do catch prey. A 200-kg African lion can consume 40 kg of meat in one meal!

The length of the vertebrate digestive system is also correlated with diet. In general, herbivores and omnivores have longer alimentary canals relative to their body size than do carnivores. Vegetation is more difficult to digest than meat because it contains cell walls. A longer digestive tract furnishes more time for digestion and more surface area for the absorption of nutrients. As an example, consider the koala and coyote in **Figure 41.17**. Although these two mammals are about the same size, the koala's intestines are much longer, enhancing the processing of fibrous, protein-poor eucalyptus leaves from which the koala obtains virtually all its food and water.



▲ **Figure 41.17 The alimentary canals of a carnivore (coyote) and herbivore (koala).** The koala's alimentary canal is specialized for digesting eucalyptus leaves. Extensive chewing chops the leaves into tiny pieces, increasing exposure to digestive juices. In the long cecum and the upper portion of the colon, symbiotic bacteria convert the shredded leaves to a more nutritious diet.

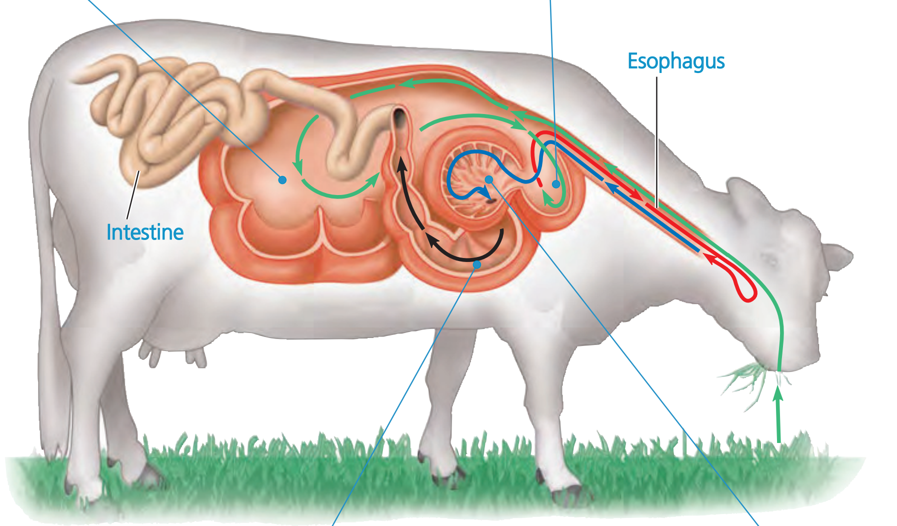
Mutualistic Adaptations

Some digestive adaptations involve mutualistic symbiosis, a mutually beneficial interaction between two species (see Chapter 54). For example, microorganisms help herbivores digest plants. Much of the chemical energy in herbivore diets comes from the cellulose of plant cell walls, but animals do not produce enzymes that hydrolyze cellulose. Instead, many vertebrates (as well as termites, whose wood diets consist largely of cellulose) house large populations of mutualistic bacteria and protists in fermentation chambers in their alimentary canals. These microorganisms have enzymes that can digest cellulose to simple sugars and other compounds that the animal can absorb. In many cases, the microorganisms also use the sugars from digested cellulose in the production of a variety of nutrients essential to the animal, such as vitamins and amino acids.

The location of mutualistic microbes in alimentary canals varies, depending on the type of herbivore. For example:

- The hoatzin, an herbivorous bird that lives in the South American rain forests, has a large, muscular crop (an esophageal pouch; see Figure 41.8) that houses mutualistic microorganisms. Hard ridges in the wall of the crop grind plant leaves into small fragments, and the microorganisms break down cellulose.
- Horses and many other herbivorous mammals house mutualistic microorganisms in a large cecum. The koala also has an enlarged cecum, where mutualistic bacteria ferment finely shredded eucalyptus leaves.
- In rabbits and some rodents, mutualistic bacteria live in the large intestine as well as in the cecum. Since most nutrients are absorbed in the small intestine, nourishing byproducts of fermentation by bacteria in the large intestine are initially lost with the feces. Rabbits and rodents recover these nutrients by *coprophagy* (from the Greek, meaning "dung eating"), feeding on some of their feces and then passing the food through the alimentary canal a second time. The familiar rabbit "pellets," which are not reingested, are the feces eliminated after food has passed through the digestive tract twice.
- The most elaborate adaptations for an herbivorous diet have evolved in the animals called **ruminants**, which include deer, sheep, and cattle **(Figure 41.18)**.

Although we have focused our discussion on vertebrates, adaptations related to digestion are also widespread among other animals. Some of the most remarkable examples are the giant tubeworms (over 3 m long) that live at pressures as high as 260 atmospheres around deep-sea hydrothermal vents (see Figure 52.16). These worms have no mouth or digestive system. Instead, they rely entirely on mutualistic bacteria to generate energy and nutrients from the carbon dioxide, oxygen,



◀ **Figure 41.18 Ruminant digestion.** The stomach of a ruminant has four chambers. Because of the microbial action in the chambers, the diet from which a ruminant actually absorbs its nutrients is much richer than the grass the animal originally eats. In fact, a ruminant eating grass or hay obtains many of its nutrients by digesting the mutualistic microorganisms, which reproduce rapidly enough in the rumen to maintain a stable population.

hydrogen sulfide, and nitrate available at the vents. Thus, for invertebrates and vertebrates alike, mutualistic symbiosis has evolved as a general strategy for expanding the sources of nutrition available to animals.

Having examined how animals optimize their extraction of nutrients from food, we will next turn to the challenge of balancing the use of these nutrients.

CONCEPT CHECK 41.4

1. What are two advantages of a longer alimentary canal for processing plant material that is difficult to digest?
2. What features of a mammal's digestive system make it an attractive habitat for mutualistic microorganisms?
3. **WHAT IF?** "Lactose-intolerant" people have a shortage of lactase, the enzyme that breaks down lactose in milk. As a result, they sometimes develop cramps, bloating, or diarrhea after consuming dairy products. Suppose such a person ate yogurt containing bacteria that produce lactase. Why would eating yogurt likely provide at best only temporary relief of the symptoms?

For suggested answers, see Appendix A.

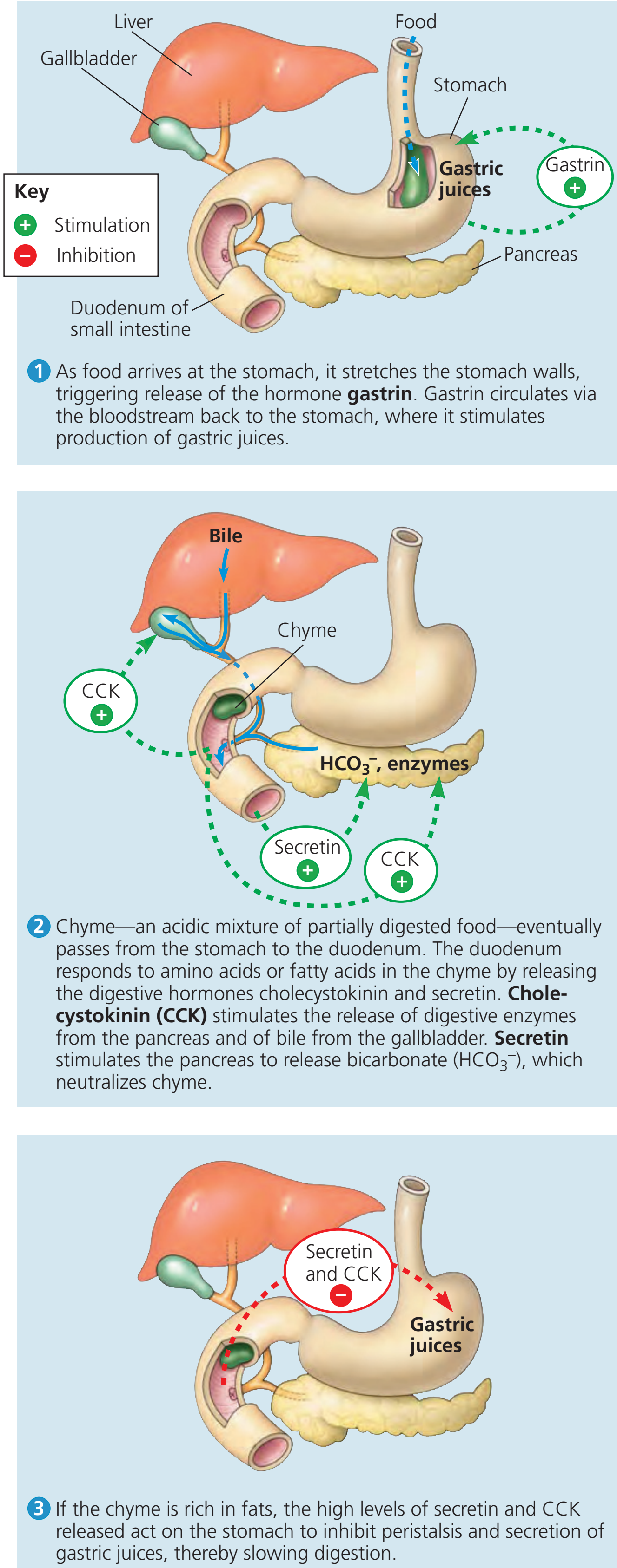
CONCEPT 41.5

Feedback circuits regulate digestion, energy storage, and appetite

Having examined the processes that enable an animal to obtain nutrients, we will finish our discussion of nutrition by considering how these processes are matched to circumstance and need.

Regulation of Digestion

Many animals go for long intervals between meals and do not need their digestive systems to be active continuously. Instead, each step in processing is activated as food reaches a new compartment in the alimentary canal. The arrival of food triggers the secretion of substances that promote the next stage of chemical digestion, as well as muscular contractions that propel food farther along the canal. For example, you learned earlier that nervous reflexes stimulate the release of saliva when food enters the oral cavity and orchestrate swallowing when a bolus of food reaches the pharynx. Similarly, the arrival of food in the stomach triggers churning and the release of gastric juices. A branch of the nervous system



1 As food arrives at the stomach, it stretches the stomach walls, triggering release of the hormone **gastrin**. Gastrin circulates via the bloodstream back to the stomach, where it stimulates production of gastric juices.

2 Chyme—an acidic mixture of partially digested food—eventually passes from the stomach to the duodenum. The duodenum responds to amino acids or fatty acids in the chyme by releasing the digestive hormones cholecystokinin and secretin. **Cholecystokinin (CCK)** stimulates the release of digestive enzymes from the pancreas and of bile from the gallbladder. **Secretin** stimulates the pancreas to release bicarbonate (HCO_3^-), which neutralizes chyme.

3 If the chyme is rich in fats, the high levels of secretin and CCK released act on the stomach to inhibit peristalsis and secretion of gastric juices, thereby slowing digestion.

▲ **Figure 41.19 Hormonal control of digestion.**

called the *enteric division*, which is dedicated to the digestive organs, regulates these events as well as peristalsis in the small and large intestines.

The endocrine system also plays a critical role in controlling digestion. As described in **Figure 41.19**, a series of hormones released by the stomach and duodenum help ensure that digestive secretions are present only when needed. Like all hormones, they are transported through the bloodstream. This is true even for the hormone gastrin, whose target (the stomach) is the same organ that secretes it.

Regulation of Energy Storage

As discussed in Chapter 40, when an animal takes in more energy-rich molecules than it needs for metabolism and activity, it stores the excess energy. In concluding our overview of nutrition, we'll examine some ways in which animals manage their energy allocation.

In humans, the first sites used for energy storage are liver and muscle cells. In these cells, excess energy from the diet is stored in glycogen, a polymer made up of many glucose units (see Figure 5.6b). Once glycogen depots are full, any additional excess energy is usually stored in fat in adipose cells.

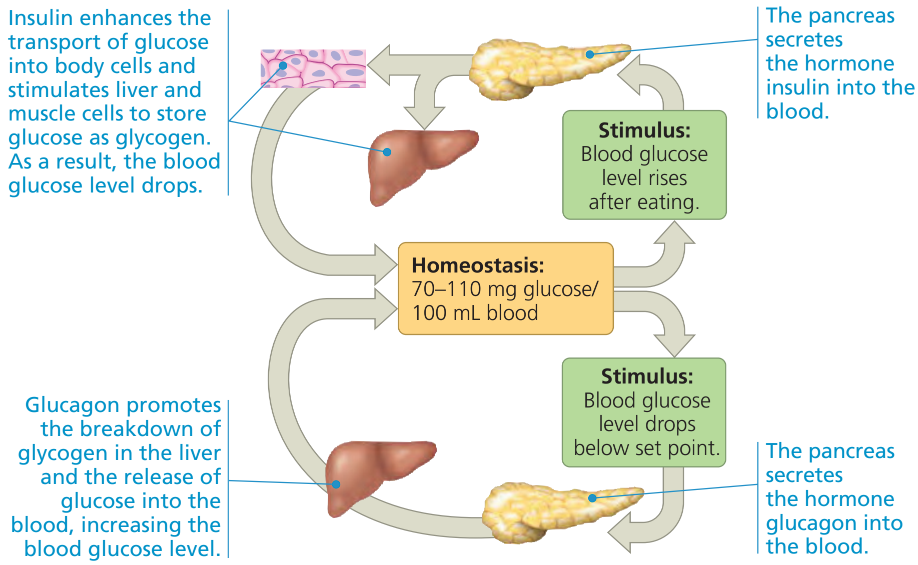
When fewer calories are taken in than are expended—perhaps because of sustained heavy exercise or lack of food—the human body generally expends liver glycogen first and then draws on muscle glycogen and fat. Fats are especially rich in energy; oxidizing a gram of fat liberates about twice the energy liberated from a gram of carbohydrate or protein. For this reason, adipose tissue provides the most space-efficient way for the body to store large amounts of energy. Most healthy people have enough stored fat to sustain them through several weeks without food.

Glucose Homeostasis

The synthesis and breakdown of glycogen is central not only to energy storage, but also to maintaining metabolic balance through glucose homeostasis. Tissues throughout the body rely on the generation of ATP by oxidation of glucose to fuel cellular processes (see Chapter 9). The pancreatic hormones insulin and glucagon maintain glucose homeostasis by tightly regulating the synthesis and breakdown of glycogen.

The liver is a key site for glucose homeostasis **(Figure 41.20)**. When insulin levels rise after a carbohydrate-rich meal, glucose entering the liver in the hepatic portal vein is used to synthesize glycogen. Between meals, when blood in the hepatic portal vein has a much lower glucose concentration, glucagon stimulates the liver to break down glycogen, releasing glucose into the blood. Through the combined action of insulin and glucagon, blood exiting the liver has a glucose concentration of 70–110 mg per 100 mL at nearly all times.

We will return to the mechanism of glucose homeostasis (and explore the consequences when it fails) in our discussion of the endocrine system in Chapter 45.



◀ **Figure 41.20 Homeostatic regulation of cellular fuel.** After a meal is digested, glucose and other monomers are absorbed into the blood from the digestive tract. The human body regulates the use and storage of glucose, a major cellular fuel.

MAKE CONNECTIONS *What form of feedback control does each of these regulatory circuits reflect (see Concept 40.2, p. 861)?*

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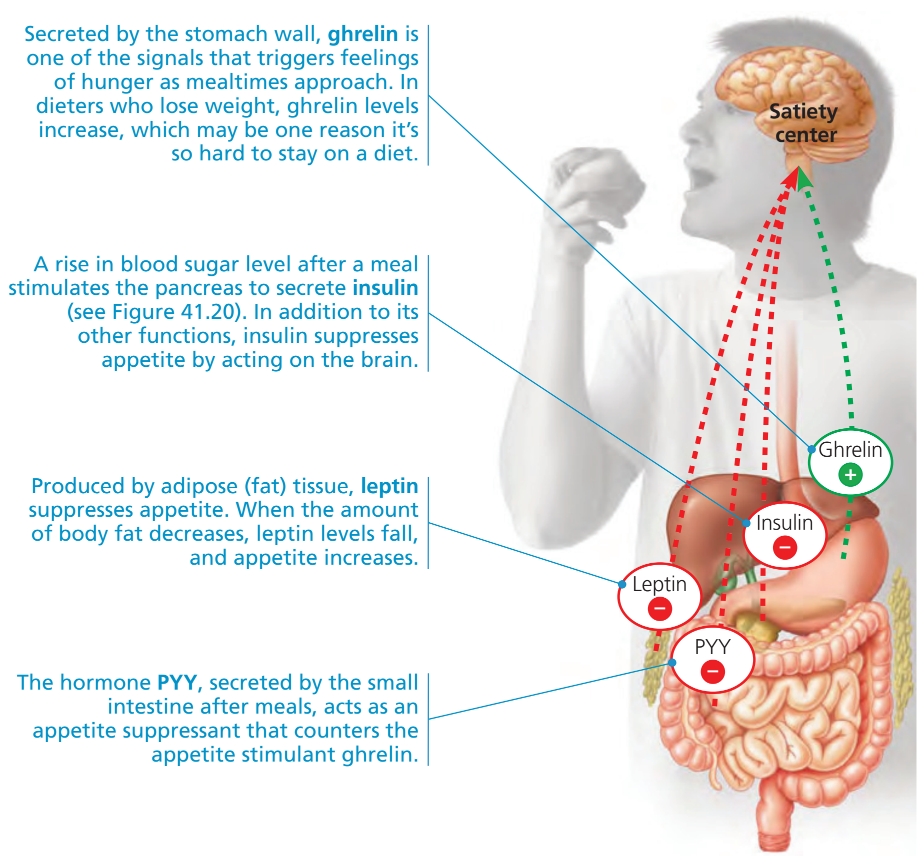
Regulation of Appetite and Consumption

Overnourishment, the consumption of more calories than the body needs for normal metabolism, causes obesity, the excessive accumulation of fat. Obesity, in turn, contributes to a number of health problems, including the most common type of diabetes (type 2), cancer of the colon and breast, and cardiovascular disease that can lead to heart attacks and strokes. It is estimated that obesity is a factor in about 300,000 deaths per year in the United States alone.

Researchers have discovered several homeostatic mechanisms that help regulate body weight. Operating as feedback circuits, these mechanisms control the storage and metabolism of fat. Several hormones regulate long-term and short-term appetite by affecting a "satiety center" in the brain **(Figure 41.21)**. In addition, a network of neurons relays and integrates information from the digestive system to regulate hormone release. To a large extent, this neuronal network functions independent of inputs from the central nervous system.

Mutations that cause mice to be chronically obese have played a key role in advancing our understanding of the satiety pathway. Mice with mutations in the *ob* or *db* gene eat voraciously and become much heavier than normal. Doug Coleman investigated how *ob* and *db* mutations disrupt normal



▲ **Figure 41.21 A few of the appetite-regulating hormones.** Secreted by various organs and tissues, the hormones reach the brain via the bloodstream. These signals act on a region of the brain that in turn controls the "satiety center," which generates the nervous impulses that make us feel either hungry or satiated ("full"). The hormone ghrelin is an appetite stimulant; the other three hormones shown here are appetite suppressants.

▼ **Figure 41.22** INQUIRY

What are the roles of the *ob* and *db* genes in appetite regulation?

Obese mouse with mutant *ob* gene (left) next to wild-type mouse.

EXPERIMENT Margaret Dickie, Katherine Hummel, and Doug Coleman, of the Jackson Laboratory in Bar Harbor, Maine, discovered that mice mutant for the *ob* gene (*ob ob*) or for the *db* gene (*db db*) eat voraciously and grow much more massive than mice with the wild-type (nonmutant) forms of both genes (designated ob^+ and db^+).

To explore further the roles of the two genes, Coleman measured the body masses of young mice with various genotypes and then surgically linked the circulatory system of each subject to that of another mouse. This procedure ensured that any factor circulating in the bloodstream of either mouse would be transferred to the other. After eight weeks, he again measured the mass of each subject.

RESULTS

Genotype pairing (red type indicates mutant genes)		Average change in body mass (g) of subject
Subject	Paired with	
ob^+ob^+, db^+db^+	ob^+ob^+, db^+db^+	8.3
ob ob, db^+db^+	*ob ob*, db^+db^+	38.7
ob ob, db^+db^+	ob^+ob^+, db^+db^+	8.2
ob ob, db^+db^+	ob^+ob^+, *db db*	−14.9*

*Due to pronounced weight loss and weakening, subjects in this pairing were reweighed after less than eight weeks.

CONCLUSION Because an *ob* mouse gains less weight when surgically joined with an ob^+ mouse than when joined with an *ob* mouse, Coleman concluded that the *ob* mouse fails to make a satiety factor but can respond to the factor when it is present. To explain the weight loss in an *ob* mouse that receives circulating factors from a *db* mouse, he reasoned that the *db* mutation blocks the response to the satiety factor but not its production, leading to an overproduction of the factor by the *db* mouse.

Subsequent molecular studies demonstrated the validity of both parts of Coleman's conclusion. The *ob* gene product is leptin, the satiety factor, whereas the *db* gene product is the leptin receptor. Thus, mice with the *ob* mutation cannot produce leptin, and mice with the *db* mutation produce leptin but cannot respond to it.

SOURCE D. L. Coleman, Effects of parabiosis of obese mice with diabetes and normal mice. *Diabetologia* 9:294–298 (1973).

MB See the related Experimental Inquiry Tutorial in MasteringBiology.

WHAT IF? Suppose you collected blood from a wild-type mouse and a *db* mouse over the course of a day. What changes would you expect in the concentration of leptin, the satiety factor, in each mouse? Explain your reasoning.

control of appetite **(Figure 41.22)**. Based on his experiments, Coleman deduced that the *ob* gene is required to produce the satiety factor, and the *db* gene is required to respond to the factor.

Cloning of the *ob* gene led to the demonstration that it codes for the hormone now known as **leptin** (from the Greek *lepto*, thin). The *db* gene encodes the leptin receptor. Leptin and the leptin receptor are key components of the circuitry that regulates appetite over the long term. Because leptin is a product of adipose cells, levels rise when the amount of body fat increases, cuing the brain to suppress appetite (see Figure 41.20). Conversely, loss of fat decreases leptin levels, signaling the brain to increase appetite. In this way, the feedback signals provided by leptin maintain body fat levels within a set range.

Our understanding of leptin may lead to treatments for obesity, but uncertainties remain. For one thing, leptin has complex functions, including a role in how the nervous system develops. Also, most obese people have an abnormally high leptin level, which somehow fails to elicit a response from the brain's satiety center. Clearly, there is much to learn in this important area of human physiology.

Obesity and Evolution

EVOLUTION The relationship between fat storage and evolutionary adaptation in animals is sometimes complex. Consider the plump offspring of the seabirds called petrels **(Figure 41.23)**. Their parents must fly long distances to find food. Most of the food that they bring to their chicks is very rich in lipids. The fact that fat has about twice as many calories per gram as other fuels minimizes the number of foraging trips. However, growing petrels need lots of protein for building new tissues, and there is relatively little in their oily

▲ **Figure 41.23 A plump petrel.** Too heavy to fly, the petrel chick (right) will have to lose weight before it takes wing. In the meantime, its stored fat provides energy during times when its parents fail to bring enough food.

diet. To get all the protein they need, young petrels must consume many more calories than they burn in metabolism, and consequently they become obese. Their fat depots nevertheless help them survive periods when their parents cannot find enough food. When food is plentiful, chicks at the end of the growth period weigh much more than their parents. The youngsters must then fast for several days to lose enough weight to be capable of flight.

Though fat hoarding in humans can be a health liability, it may have been an advantage in our evolutionary past. Our ancestors on the African savanna were hunter-gatherers who probably survived mainly on seeds and other plant products, a diet only occasionally supplemented by hunting game or scavenging meat from animals killed by other predators. In such a feast-or-famine existence, natural selection may have favored those individuals with a physiology that induced them to gorge on rich, fatty foods on those rare occasions when such treats were abundantly available. Individuals with genes promoting the storage of high-energy molecules during feasts may have been more likely to survive famines. Thus, our present-day taste for fats may be partly an evolutionary vestige of less nutritious times.

In the next chapter, we'll see that obtaining food, digesting it, and absorbing nutrients are parts of a larger story. Provisioning the body also involves distributing nutrients (circulation), and using nutrients for metabolism requires exchanging respiratory gases with the environment.

CONCEPT CHECK 41.5

1. Explain how people can become obese even if their intake of dietary fat is relatively low compared with carbohydrate intake.
2. After reviewing Figure 41.21, explain how PYY and leptin complement each other in regulating body weight.
3. **WHAT IF?** Suppose you were studying two groups of obese people with genetic abnormalities in the leptin pathway. In one group, the leptin levels are abnormally high; in the other group, they are abnormally low. How would each group's leptin levels change if both groups were placed on a low-calorie diet for an extended period? Explain.

For suggested answers, see Appendix A.

41 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

- Animals have diverse diets. **Herbivores** mainly eat plants; **carnivores** mainly eat other animals; and **omnivores** eat both. Animals must balance consumption, storage, and use of food.

CONCEPT 41.1

An animal's diet must supply chemical energy, organic molecules, and essential nutrients (pp. 875–880)

- Food provides animals with energy for ATP production, carbon skeletons for biosynthesis, and **essential nutrients**—nutrients that must be supplied in preassembled form. Essential nutrients include certain amino acids and fatty acids that animals cannot synthesize; **vitamins**, which are organic molecules; and **minerals**, which are inorganic substances.
- Animals can suffer from two types of malnutrition: an inadequate intake of essential nutrients and a deficiency in sources of chemical energy. Studies of genetic defects and of disease at the population level help researchers determine human dietary requirements.

? *Propose a reason why the diet of many mammals doesn't need to include vitamin C, a substance that is important for collagen synthesis.*

CONCEPT 41.2

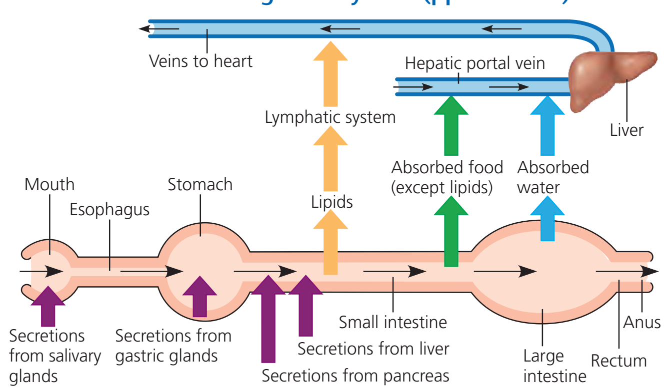
The main stages of food processing are ingestion, digestion, absorption, and elimination (pp. 880–883)

- Food processing in animals involves **ingestion** (eating), **digestion** (enzymatic breakdown of large molecules), **absorption** (uptake of nutrients by cells), and **elimination** (passage of undigested materials out of the body in feces).
- Animals differ in the ways they obtain and ingest food. Most animals are **bulk feeders**, eating large pieces of food.
- Compartmentalization is necessary to avoid self-digestion. In intracellular digestion, food particles are engulfed by endocytosis and digested within food vacuoles that have fused with lysosomes. In extracellular digestion, which is used by most animals, enzymatic hydrolysis occurs outside cells in a **gastrovascular cavity** or **alimentary canal**.

? *Propose an artificial diet that would eliminate the need for one of the first three steps in food processing.*

CONCEPT 41.3

Organs specialized for sequential stages of food processing form the mammalian digestive system (pp. 883–889)



? *What structural feature of the small intestine makes it better suited for absorption of nutrients than the stomach?*

CONCEPT 41.4

Evolutionary adaptations of vertebrate digestive systems correlate with diet (pp. 889–891)

- Vertebrate digestive systems display many evolutionary adaptations associated with diet. For example, dentition, which is the assortment of teeth, generally correlates with diet. In addition, herbivores usually have longer alimentary canals than carnivores, reflecting the longer time needed to digest vegetation. Many herbivores, including cows, also have fermentation chambers where microorganisms digest cellulose, a form of mutualism.

? *How does our anatomy indicate that our ancestors were not vegetarians?*

CONCEPT 41.5

Feedback circuits regulate digestion, energy storage, and appetite (pp. 891–895)

- Nutrition is regulated at multiple levels. Food in the alimentary canal triggers nervous and hormonal responses that control the secretion of digestive juices and that promote the movement of ingested material through the canal. The availability of glucose for energy production is regulated by the hormones insulin and glucagon, which control the synthesis and breakdown of glycogen.
- Vertebrates store excess calories in glycogen (in liver and muscle cells) and in fat (in adipose cells). These energy stores can be tapped when an animal expends more calories than it consumes. If, however, an animal consumes more calories than it needs for normal metabolism, the resulting overnourishment can lead to the serious health problem of obesity.
- Several hormones, including leptin and insulin, regulate appetite by affecting the brain's satiety center. The problem of maintaining a healthy weight may stem partly from our evolutionary past, when fat hoarding may have been important for survival.

? *Explain why your stomach might make growling noises when you skip a meal.*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Which of the following animals is *incorrectly* paired with its feeding mechanism?
a. lion—substrate feeder
b. baleen whale—suspension feeder
c. aphid—fluid feeder
d. clam—suspension feeder
e. snake—bulk feeder

2. The mammalian trachea and esophagus both connect to the
a. large intestine.
b. stomach.
c. pharynx.
d. rectum.
e. epiglottis.

3. Which of the following organs is *incorrectly* paired with its function?
a. stomach—protein digestion
b. oral cavity—starch digestion
c. large intestine—bile production
d. small intestine—nutrient absorption
e. pancreas—enzyme production

4. Which of the following is *not* a major activity of the stomach?
a. mechanical digestion
b. HCl secretion
c. mucus secretion
d. nutrient absorption
e. enzyme secretion

LEVEL 2: APPLICATION/ANALYSIS

5. After surgical removal of an infected gallbladder, a person must be especially careful to restrict dietary intake of
a. starch. b. protein. c. sugar. d. fat. e. water.

6. If you were to jog 1 km a few hours after lunch, which stored fuel would you probably tap?
a. muscle proteins
b. muscle and liver glycogen
c. fat stored in the liver
d. fat stored in adipose tissue
e. blood proteins

LEVEL 3: SYNTHESIS/EVALUATION

7. **DRAW IT** Make a flowchart of the events that occur after partially digested food leaves the stomach. Use the following terms: bicarbonate secretion, circulation, decrease in acidity, secretin secretion, increase in acidity, signal detection. Next to each term, indicate the compartment(s) involved. You may use a term more than once.

8. **EVOLUTION CONNECTION**
The human esophagus and trachea share a passage leading from the mouth and nasal passages, which can cause problems. After reviewing vertebrate evolution in Chapter 34, explain the evolutionary basis for this "imperfect" anatomy.

9. **SCIENTIFIC INQUIRY**
In human populations of northern European origin, the disorder called hemochromatosis causes excess iron uptake from food and affects one in 200 adults. Men are ten times as likely as women to suffer from iron overload. Devise a hypothesis for the difference in the disease between the two sexes.

10. **WRITE ABOUT A THEME**
Emergent Properties Hair is largely made up of the protein keratin. In a short essay (100–150 words), explain why a shampoo containing protein is not effective in replacing the protein in damaged hair.

For selected answers, see Appendix A.

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Make Connections Tutorial Fat Absorption (Chapter 41) and Fat Structure (Chapter 5)
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Tutorial Vitamins
Activities Digestive System Function • Hormonal Control of Digestion • The Digestion and Absorption of Food • Discovery Channel Video: Nutrition
Questions Student Misconceptions • Reading Quiz • Multiple Choice • End-of-Chapter

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