CHAPTER 27

NUTRITION AND DIGESTION

Outline

Concepts

1. Animals are heterotrophic organisms that use food to supply both raw materials and energy. Nutrition includes all of those processes by which an animal takes in, digests, absorbs, stores, and uses food to meet its metabolic needs.
2. Digestion is the chemical and/or mechanical breakdown of food into particles that individual cells of an organism can absorb. Digestion can occur either inside a cell (intracellular), outside a cell (extracellular), or in both places.
3. Most animals must work for their nutrients. The number of specializations that have evolved for food procurement (feeding) and extracellular digestion are almost as numerous as the number of animal species. Some examples include continuous versus discontinuous feeding, suspension feeding, deposit feeding, herbivory, predation, surface nutrient absorption, and fluid feeding.
4. Intracellular digestion occurs in some invertebrates (e.g., in sponges); others (e.g., some cnidarians and molluscs) utilize both intracellular and extracellular digestion; and most higher invertebrates (e.g., insects) have evolved variations in extracellular digestion that allow them to exploit different food sources.
5. In primitive, multicellular animals, such as cnidarians, the gut is a blind (closed) sac called a gastrovascular cavity. Its one opening is both entrance and exit; thus, it is an incomplete digestive tract. The development of an anus and complete digestive tract in the aschelminths was an evolutionary breakthrough. The many variations of the basic complete digestive tract correlate with different food-gathering mechanisms and diets.
6. Vertebrate digestive systems have evolved into assembly lines where food is first broken down mechanically and then chemically by digestive enzymes. The simple sugars, fats, triglycerides, amino acids, vitamins, and minerals that result are then taken into the circulatory systems for distribution throughout the animal's body and are used in maintenance, growth, and energy production.

Nutrition includes all of those processes by which an animal takes in, digests, absorbs, stores, and uses food (nutrients) to meet its metabolic needs. **Digestion** (L. *digestio*, from + *dis*, apart + *gerere*, to carry) is the chemical and/or mechanical breakdown of food into particles that individual cells of an animal can absorb. This chapter discusses animal nutrition, the different strategies animals use for consuming and using food, and various animal digestive systems.

This chapter contains evolutionary concepts, which are set off in this font.

EVOLUTION OF NUTRITION

Nutrients in the food an animal consumes provide the necessary chemicals for growth, maintenance, and energy production. Overall, the nutritional requirements of an animal are inversely related to its ability to synthesize molecules essential for life. The fewer such biosynthetic abilities an animal has, the more kinds of nutrients it must obtain from its environment. Green plants and photosynthetic protists have the fewest such nutritional requirements because they can synthesize all their own complex molecules from simpler inorganic substances; they are **autotrophs** (Gr. *auto*, self + *trophe*, nourishing). Animals, fungi, and bacteria that cannot synthesize many of their own organic molecules and must obtain them by consuming other organisms or their products are **heterotrophs** (Gr. *heteros*, another or different + *trophe*, nourishing). Animals such as rabbits that subsist entirely on plant material are **herbivores** (L. *herba*, plant + *vorare*, to eat). **Carnivores** (L. *caro*, flesh), such as hawks, are animals that eat only meat. **Omnivores** (L. *omnius*, all), such as humans, bears, raccoons, and pigs, eat both plant and animal matter. **Insectivores,** such as bats, eat primarily arthropods.

Losses of biosynthetic abilities have marked much of animal evolution. Once an animal routinely obtains essential, complex organic molecules in its diet, it can afford to lose the ability to synthesize those molecules. Moreover, the loss of this ability confers a selective advantage on the animal because the animal stops expending energy and resources to synthesize molecules that are already in its diet. Thus, as the diet of animals became more varied, they tended to lose their abilities to synthesize such widely available molecules as some of the amino acids.

THE METABOLIC FATES OF NUTRIENTS IN HETEROTROPHS

The nutrients that a heterotroph ingests can be divided into macronutrients and micronutrients. **Macronutrients** are needed in large quantities and include the carbohydrates, lipids, and proteins. **Micronutrients** are needed in small quantities and include organic vitamins and inorganic minerals. Together, these nutrients make up the animal's dietary requirements. Besides these nutrients, animals require water.

CALORIES AND ENERGY

The energy value of food is measured in terms of calories or Calories. A **calorie** (L. *calor*, heat) is the amount of energy required to raise the temperature of 1 g of water 1° C. A calorie, with a small c, is also called a gram calorie. A **kilocalorie,** also known as a **Calorie** or kilogram calorie (kcal), is equal to 1,000 calories. In popular usage, you talk about calories but actually mean Calories, because the larger unit is more useful for measuring the energy value of food. If an advertisement says that a so-called light beer contains 95 calories per 12 oz, it really means 95,000 calories, 95 Calories, or 95 kcal.

MACRONUTRIENTS

With a few notable exceptions, heterotrophs require organic molecules, such as carbohydrates, lipids, and proteins, in their diets. Enzymes break down these molecules into components that can be used for energy production or as sources for the "building blocks" of life.

Carbohydrates: Carbon and Energy from Sugars and Starches

The major dietary source of energy for heterotrophs is complex carbohydrates (figure 27.1*a*). Most carbohydrates originally come from plant sources. Various polysaccharides, disaccharides, or any of a variety of simple sugars (monosaccharides) can meet this dietary need. Carbohydrates also are a major carbon source for incorporation into important organic compounds. Many plants also supply cellulose, a polysaccharide that humans and other animals (with the exception of herbivores) cannot digest. Cellulose is sometimes called dietary fiber. It assists in the passage of food through the alimentary canal of mammals. Cellulose may also reduce the risk of cancer of the colon, because the mutagenic compounds that form during the storage of feces are reduced if fecal elimination is more frequent.

Lipids: Highly Compact Energy-Storage Nutrients

Neutral lipids (fats) or triacylglycerols are contained in fats and oils, meat and dairy products, nuts, and some fruits and vegetables high in fats, such as avocados (figure 27.1*b*). Lipids are the most concentrated source of food energy. They produce about 9 Calories (kcal) of usable energy per gram, more than twice the energy available from an equal mass of carbohydrate or protein (table 27.1).

Many heterotrophs have an absolute dietary requirement for lipids, sometimes for specific types. For example, many animals require unsaturated fatty acids (e.g., linoleic acid, linolenic acid, and arachidonic acid). These fatty acids act as precursor molecules for the synthesis of sterols, the most common of which is cholesterol. The sterols are also required for the synthesis of steroid hormones and cholesterol, which is incorporated into cell membranes. Other lipids insulate the bodies of some vertebrates and help maintain a constant temperature.

Proteins: Basic to the Structure and Function of Cells

Animal sources of protein include other animals and milk. Plant sources include beans, peas, and nuts. Proteins are needed for their amino acids, which heterotrophs use to build their own body proteins (figure 27.1c).

MICRONUTRIENTS

Micronutrients are usually small ions, organic vitamins, inorganic minerals, and molecules that are used repeatedly in enzymatic reactions or as parts of certain proteins (e.g., copper in hemocyanin

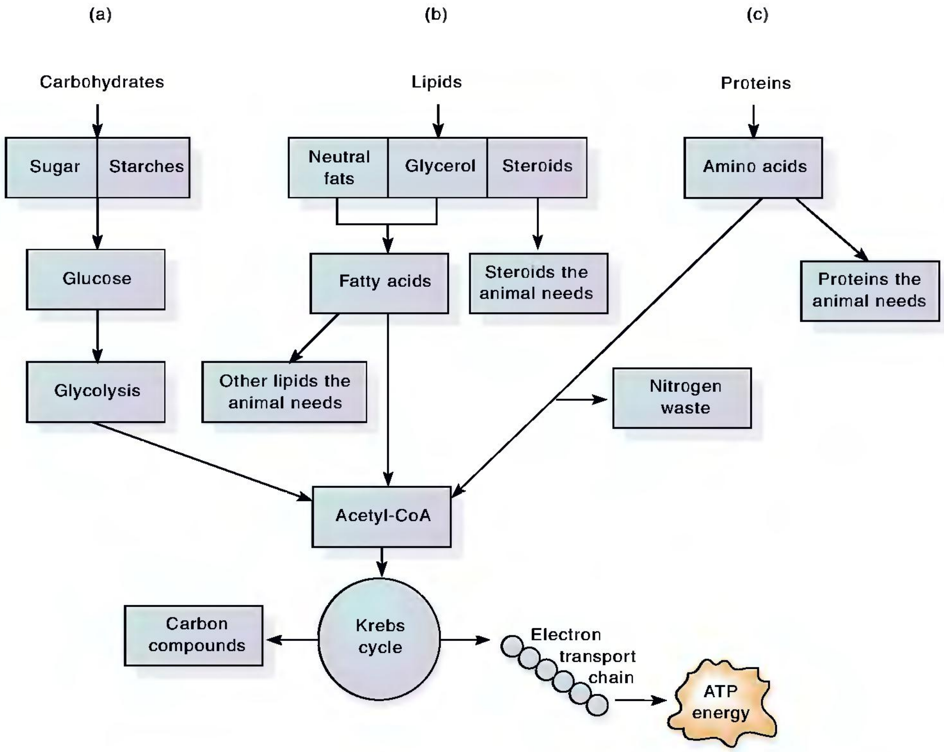

FIGURE 27.1

Macronutrients in the Diet. *(a)* Carbohydrate foods break down to their constituent sugars and starches, and ultimately into glucose. Individual cells use this sugar in glycolysis and aerobic respiration to create new carbon compounds or ATP energy. *(b)* Lipids (fats and oils) in the diet break down to neutral fats, glycerol, and steroids. These molecules can be modified and incorporated into the lipids or steroids the animal needs for storing fat or generating hormones, or they can be converted to acetyl-CoA and enter the Krebs cycle and electron transport chain for ATP production. *(c)* Proteins break down to amino acids, which are incorporated into new proteins or modified to enter the Krebs cycle and electron transport chain to produce ATP energy.

TABLE 27.1
THE AVERAGE CALORIC VALUES OF MACRONUTRIENTS

MACRONUTRIENT	CALORIES PER GRAM
Carbohydrates	4.1
Lipids	9.3
Proteins	4.4

and iron in hemoglobin). Even though they are needed in small amounts, animals cannot synthesize them rapidly (if at all); thus, they must be obtained from the diet.

Minerals

Some minerals are needed in relatively large amounts and are called essential minerals, or macrominerals. For example, sodium and potassium are vital to the functioning of every nerve and muscle in an animal's body. Animals lose large quantities of these minerals, especially sodium, in the urine every day. Animals that sweat to help regulate body temperature lose sodium in their sweat. A daily supply of calcium is needed for muscular activity and, with phosphorus, for bone formation. Table 27.2 lists the functions of the major essential minerals.

Other minerals are known as trace minerals, trace elements, or microminerals. Animals need these in only very small amounts for various enzymatic functions. Table 27.3 lists the function of some trace minerals.

Vitamins

Normal metabolic activity depends on very small amounts of more than a dozen organic substances called vitamins. **Vitamin** (L. *vita*, life) is the general term for a number of chemically unrelated, organic substances that occur in many foods in small amounts and are necessary for normal metabolic functioning. Vitamins may be water soluble or fat soluble. Most water-soluble vitamins, such as the B vitamins and vitamin C, are coenzymes needed in metabolism

TABLE 27.2
PHYSIOLOGICAL ROLES OF THE ESSENTIAL MINERALS (MACROMINERALS) ANIMALS REQUIRE IN LARGE AMOUNTS

MINERAL	MAJOR PHYSIOLOGICAL ROLES
Calcium (Ca)	Component of bone and teeth; essential for normal blood clotting; needed for normal muscle, neuron, and cellular function
Chlorine (Cl)	Principal negative ion in extracellular fluid; important in acid-base and fluid balance; needed to produce stomach HCl
Magnesium (Mg)	Component of many coenzymes; needed for normal neuron and muscle function, as well as carbohydrate and protein metabolism
Potassium (K)	Major constituent of bones, blood plasma; needed for energy metabolism
Phosphorus (P)	Major positive ion in cells; influences muscle contraction and neuron excitability; part of DNA, RNA, ATP, energy metabolism
Sodium (Na)	Principal positive ion in extracellular fluid; important in fluid balance; essential for conduction of action potentials, active transport
Sulfur (S)	Protein structure; detoxification reactions and other metabolic activity

TABLE 27.3
SOME PHYSIOLOGICAL ROLES OF TRACE MINERALS (MICROMINERALS) IN ANIMALS

MINERAL	PHYSIOLOGICAL ROLES
Cobalt (Co)	Component of vitamin B_{12}; essential for red blood cell production
Copper (Cu)	Component of many enzymes; essential for melanin and hemoglobin synthesis; part of cytochromes
Fluorine (F)	Component of bone and teeth; prevents tooth decay
Iodine (I)	Component of thyroid hormones
Iron (Fe)	Component of hemoglobin, myoglobin, enzymes, and cytochromes
Manganese (Mn)	Activates many enzymes; an enzyme essential for urea formation and parts of the Krebs cycle
Molybdenum (Mo)	Constituent of some enzymes
Selenium (Se)	Needed in fat metabolism
Zinc (Zn)	Component of at least 70 enzymes; needed for wound healing and fertilization

(table 27.4). The fat-soluble vitamins have various functions (table 27.5).

The dietary need for vitamin C and the fat-soluble vitamins (A, D, E and K) tends to be limited to the vertebrates. Even in closely related groups, vitamin requirements vary. For example, among vertebrates, humans and guinea pigs require vitamin C, but rabbits do not. Some birds require vitamin A; others do not.

DIGESTION

In some of the simplest forms of life (the protists and sponges), some cells take in whole food particles directly from the environment by diffusion, active transport, and/or endocytosis and break them down with enzymes to obtain nutrients. This strategy is called **intracellular** ("within the cell") **digestion** (figure 27.2*a*). Intracellular digestion circumvents the need for the mechanical breakdown of food or for a gut or other cavity in which to chemically digest food. At the same time, however, intracellular digestion limits an animal's size and complexity—only very small pieces of food can be used. Intracellular digestion provides all or some of the nutrients in protozoa, sponges, cnidarians, platyhelminths, rotifers, bivalve molluscs, and primitive chordates.

Larger animals have evolved structures and mechanisms for ***extracellular digestion:*** *the enzymatic breakdown of larger pieces of food into constituent molecules, usually in a special organ or cavity (figure 27.2b).* Nutrients from the food then pass into body cells lining the organ or cavity and can take part in energy metabolism or biosynthesis.

ANIMAL STRATEGIES FOR GETTING AND USING FOOD

As noted earlier, only a few protists and animals can absorb nutrients directly from their external environment via intracellular digestion. Most animals must work for their nutrients. The number of specializations that have evolved for food procurement (feeding) and extracellular digestion are almost as numerous as the number of animal species. What follows is a brief discussion of the major feeding strategies animals use.

CONTINUOUS VERSUS DISCONTINUOUS FEEDERS

One variable related to the structure of digestive systems is whether an animal is a continuous or discontinuous feeder. Many **continuous feeders** are slow-moving or completely sessile animals (they remain permanently in one place). For example, aquatic **suspension feeders,** such as tube worms and barnacles, remain in one place and continuously "strain" small food particles from the water.

Discontinuous feeders tend to be active, sometimes highly mobile, animals. Typically, discontinuous feeders have more digestive specializations than continuous feeders because discontinuous feeders take in large meals that must be either ground up

TABLE 27.4
WATER-SOLUBLE VITAMINS

VITAMIN	CHARACTERISTICS	FUNCTIONS	SOURCES
Thiamin (vitamin B_1)	Destroyed by heat and oxygen, especially in alkaline environment	Part of coenzyme needed for oxidation of carbohydrates, and coenzyme needed in synthesis of ribose	Lean meats, liver, eggs, whole-grain cereals, leafy green vegetables, legumes
Riboflavin (vitamin B_2)	Stable to heat, acids, and oxidation; destroyed by alkalis and light	Part of enzymes and coenzymes needed for oxidation of glucose and fatty acids and for cellular growth	Meats, dairy products, leafy green vegetables, whole-grain cereals
Niacin (nicotinic acid)	Stable to heat, acids, and alkalis; converted to niacinamide by cells; synthesized from tryptophan	Part of coenzymes needed for oxidation of glucose and synthesis of proteins, fats, and nucleic acids	Liver, lean meats, poultry, peanuts, legumes
Vitamin B_6	Group of three compounds; stable to heat and acids; destroyed by oxidation, alkalis, and ultraviolet light	Coenzyme needed for synthesis of proteins and various amino acids, for conversion of tryptophan to niacin, for production of antibodies, and for synthesis of nucleic acids	Liver, meats, fish, poultry, bananas, avocados, beans, peanuts, whole-grain cereals, egg yolk
Pantothenic acid	Destroyed by heat, acids, and alkalis	Part of coenzyme needed for oxidation of carbohydrates and fats	Meats, fish, whole-grain cereals, legumes, milk, fruits, vegetables
Cyanocobalamin (vitamin B_{12})	Complex, cobalt-containing compound; stable to heat; inactivated by light, strong acids, and strong alkalis; absorption regulated by intrinsic factor from gastric glands; stored in liver	Part of coenzyme needed for synthesis of nucleic acids and for metabolism of carbohydrates; plays role in synthesis of myelin	Liver, meats, poultry, fish, milk, cheese, eggs
Folate (folic acid)	Occurs in several forms; destroyed by oxidation in acid environment or by heat in alkaline environment; stored in liver, where it is converted into folinic acid	Coenzyme needed for metabolism of certain amino acids and for synthesis of DNA; promotes production of normal red blood cells	Liver, leafy green vegetables, whole-grain cereals, legumes
Biotin	Stable to heat, acids, and light; destroyed by oxidation and alkalis	Coenzyme needed for metabolism of amino acids and fatty acids and for synthesis of nucleic acids	Liver, egg yolk, nuts, legumes, mushrooms
Ascorbic acid	Closely related to monosaccharides; stable in acids, but destroyed by oxidation, heat, light, and alkalis	Needed for production of collagen, conversion of folate to folinic acid, and metabolism of certain amino acids; promotes absorption of iron and synthesis of hormones from cholesterol	Citrus fruits, citrus juices, tomatoes, cabbage, potatoes, leafy green vegetables, fresh fruits

or stored, or both. Many carnivores, for example, pursue and capture relatively large prey. When successful, they must eat large meals so that they need not spend their time in the continuous pursuit of prey. Thus, carnivores have digestive systems that permit the storage and gradual digestion of large, relatively infrequent meals.

Herbivores spend more time eating than carnivores do, but they are also discontinuous feeders. They need to move from area to area when food is exhausted and, at least in natural environments, must limit their grazing time to avoid excessive exposure to predators. Thus, their digestive systems permit relatively rapid food gathering and gradual digestion.

TABLE 27.5
FAT-SOLUBLE VITAMINS

VITAMIN	CHARACTERISTICS	FUNCTIONS	SOURCES
Vitamin A	Occurs in several forms; synthesized from carotenes; stored in liver; stable in heat, acids, and alkalis; unstable in light	Necessary for synthesis of visual pigments, mucoproteins, and mucopolysaccharides; for normal development of bones and teeth; and for maintenance of epithelial cells	Liver, fish, whole milk, butter, eggs, leafy green vegetables, and yellow and orange vegetables and fruits
Vitamin D	A group of sterols; resistant to heat, oxidation, acids, and alkalis; stored in liver, skin, brain, spleen, and bones	Promotes absorption of calcium and phosphorus; promotes development of teeth and bones	Produced in skin exposed to ultraviolet light; in milk, egg yolk, fish-liver oils, fortified foods
Vitamin E	A group of compounds; resistant to heat and visible light; unstable in presence of oxygen and ultraviolet light; stored in muscles and adipose tissue	An antioxidant; prevents oxidation of vitamin A and polyunsaturated fatty acids; may help maintain stability of cell membranes	Oils from cereal seeds, salad oils, margarine, shortenings, fruits, nuts, and vegetables
Vitamin K	Occurs in several forms; resistant to heat, but destroyed by acids, alkalis, and light; stored in liver	Needed for synthesis of prothrombin; needed for blood clotting	Leafy green vegetables, egg yolk, pork liver, soy oil, tomatoes, cauliflower

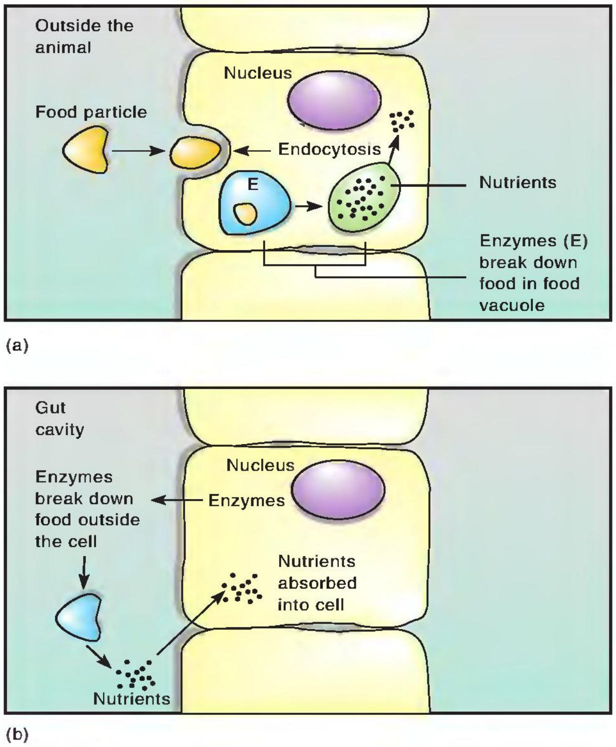

FIGURE 27.2

Intracellular and Extracellular Digestion. *(a)* A simple invertebrate, such as a sponge, has no gut and thus carries out intracellular digestion. Tiny food particles are taken into the body wall cells by endocytosis. Digestive enzymes in the vacuole then break the small particles into constituent molecules. *(b)* A dog, for example, has a gut and so can take in and digest (extracellularly) relatively large food particles. Cells lining the gut cavity secrete enzymes into the cavity. There, the enzymes break down food materials into constituent nutrients, and the nearby cells absorb these nutrients.

SUSPENSION FEEDERS

Suspension feeding is the removal of suspended food particles from the surrounding water by some sort of capture, trapping, or filtration structure. This feeding strategy involves three steps: (1) transport of water past the feeding structure, (2) removal of nutrients from the water, and (3) transport of the nutrients to the mouth of the digestive system. Sponges, ascidians, branchiopods, ectoprocts, entoprocts, phoronids, most bivalves, and many crustaceans, polychaetes, gastropods, and some nonvertebrate chordates are suspension feeders.

DEPOSIT FEEDERS

Deposit feeding involves primarily omnivorous animals. These animals obtain their nutrients from the sediments of soft-bottom habitats (muds and sands) or terrestrial soils. Direct deposit feeders simply swallow large quantities of sediment (mud, soil, sand, organic matter). The usable nutrients are digested, and the remains pass out the anus. Direct deposit feeding occurs in many polychaete annelids, some snails, some sea urchins, and in most earthworms. Other direct deposit feeders utilize tentacle-like structures to consume sediment. Examples include sea cucumbers, most sipunculans, certain clams, and several types of polychaetes.

HERBIVORY

Herbivory (L. *herba*, herb + *vorare*, to eat) is the consumption of macroscopic plants. This common feeding strategy requires the ability to "bite and chew" large pieces of plant matter (macroherbivory). Although biting and chewing mechanisms evolved within the architectural framework of a number of invertebrate lineages, they are often characterized by the development of

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

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

PREDATION

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

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

SURFACE NUTRIENT ABSORPTION

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

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

FLUID FEEDERS

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

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

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

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

DIVERSITY IN DIGESTIVE STRUCTURES: INVERTEBRATES

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

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