Part XIII

Animal Form and Function

Some species of lizard breathe better than others. The savannah monitor lizard *Varanus exanthematicus* breathes more efficiently than some of its relatives by pumping air into its lungs from the gular folds over its throat.

Why Some Lizards Take a Deep Breath

Sometimes, what is intended as a straightforward observational study about an animal turns out instead to uncover an odd fact, something that doesn't at first seem to make sense. Teasing your understanding with the unexpected, this kind of tantalizing finding can be fun and illuminating to investigate. Just such an unexpected puzzle comes to light when you look very carefully at how lizards run.

A lizard runs a bit like a football fullback, swinging his shoulder forward to take a step as the opposite foot pushes off the ground. This produces a lateral undulating gait, the body flexing from side to side with each step. This sort of gait uses the body to aid the legs in power running. By contracting the chest (intercostal) muscles on the side of the body opposite the swinging shoulder, the lizard literally thrusts itself forward with each flex of its body.

The odd fact, the thing that at first doesn't seem to make sense, is that running lizards should be using these same intercostal chest muscles for something else.

At rest, lizards breathe by expanding their chest, much as you do. The greater volume of the expanded thorax lowers the interior air pressure, causing fresh air to be pushed into the lungs from outside. You expand your chest by contracting a diaphragm at the bottom of the chest. Lizards do not have a diaphragm. Instead, they expand their chest by contracting the intercostal chest muscles on both sides of the chest simultaneously. This contraction rotates the ribs, causing the chest to expand.

Do you see the problem? A running lizard cannot contract its chest muscles on both sides simultaneously for effective breathing at the same time that it is contracting the same chest muscles alternatively for running. This apparent conflict has led to a controversial hypothesis about how running lizards breathe. Called the axial constraint hypothesis, it states that lizards are subject to a speed-dependent axial constraint that prevents effective lung ventilation while they are running.

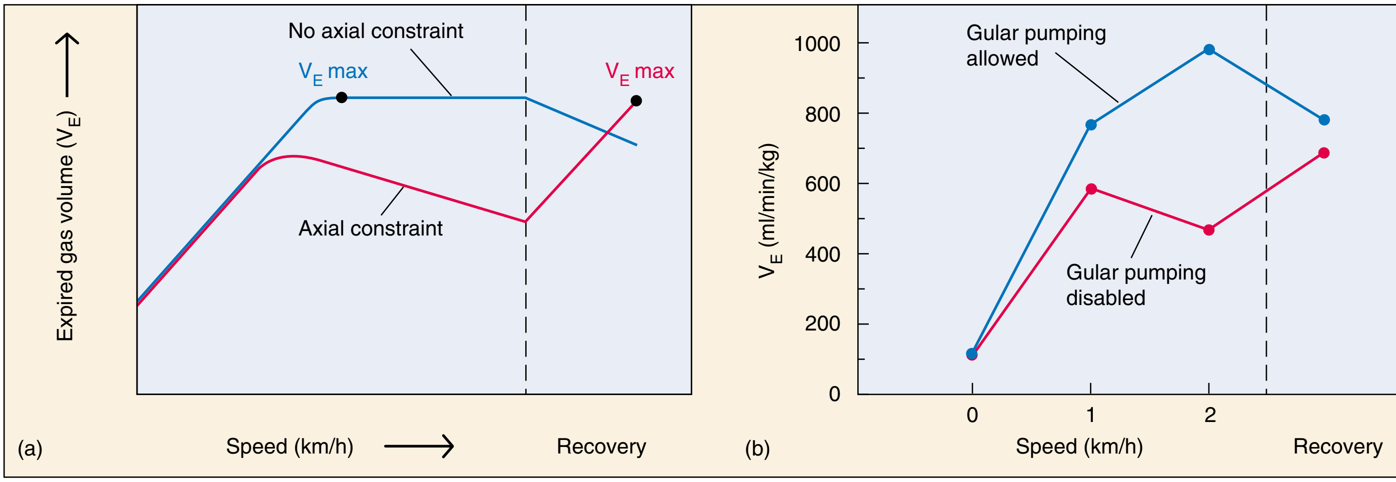
This constraint, if true, would be rather puzzling from an evolutionary perspective, because it suggests that when a lizard needs more oxygen because it is running, it breathes less effectively.

Dr. Elizabeth Brainerd of the University of Massachusetts, Amherst, is one of a growing cadre of young researchers around the country that study the biology of lizards. She set out to investigate this puzzle several years ago, first by examining oxygen consumption.

Looking at oxygen consumption seemed a very straightforward approach. If the axial constraint hypothesis is correct, then running lizards should exhibit a lower oxygen consumption because of lowered breathing efficiency. This is just what her research team found with green iguanas (*Iguana iguana*). Studying fast-running iguanas on treadmills, oxygen consumption went down as running proceeded, as the axial constraint hypothesis predicted.

Unexpectedly, however, another large lizard gave a completely different result. The savannah monitor lizard (*Varanus exanthematicus*) exhibited *elevated* oxygen consumption with increasing speeds of locomotion! This result suggests that something else is going on in monitor lizards. Somehow, they seem to have found a way to beat the axial constraint.

How do they do it? Taking a more detailed look at running monitor lizards, Dr. Brainerd's research team ran a series of experiments to sort this out. First, they used videoradiography to directly observe lung ventilation in monitor lizards while the lizards were running on a treadmill. The X-ray negative video images revealed the monitor's trick: the breathing cycle began with an inhalation that did not completely fill the lungs, just as the axial constraint hypothesis predicts. But then something else kicks in. The gular cavity located in the throat area also fills with air, and as inhalation proceeds the gular cavity compresses, forcing this air into the lungs. Like an afterburner on a jet, this added air increases the efficiency of breathing, making up for the lost contribution of the intercostal chest muscles.



Effects of gular pumping in lizards. (*a*) THEORY: The axial constraint hypothesis predicts that, above a threshold speed, ventilation, measured by expired gas volume (V_E), will decrease with increasing speed, and only reach a maximum during the recovery period after locomotion ceases. Without axial constraint, ventilation should reach its maximum during locomotion. (*b*) EXPERIMENT: Monitor lizards typically show no axial constraint while running. Axial constraint is evident, however, if gular pumping of air is disabled. So, it seems that some species of monitor lizards are able to use gular pumping to overcome the axial constraint on ventilation.

The Experiment

Brainerd set out to test this gular pumping hypothesis. Gular pumping occurs after the initial inhalation because the lizard closes its mouth, sealing shut internal nares (nostril-like structures). Air is thus trapped in the gular cavity. By contracting muscles that compress the gular cavity, this air is forced into the lungs. This process can be disrupted by propping the mouth open so that, when the gular cavity is compressed, its air escapes back out of the mouth. The lizards were trained to run on a treadmill. A plastic mask was placed over the animal's mouth and nostrils and air was drawn through the mask. The mask permitted the measurement of oxygen and CO_2 levels as a means of monitoring gas consumption. The expired gas volume (V_E) was measured in the last minutes of locomotion and the first minute of recovery at each speed. The speeds ranged from 0 km/hr to 2 km/hr. The maximum running speed of these lizards on a treadmill is 6.6 km/hr.

To disable gular pumping, the animal's mouth was propped open with a retainer made of plastic tubing. In parallel experiments that allow gular pumping, the same animals wore the masks, but no retainer was used to disrupt the oral seal necessary for gular pumping.

The Results

Parallel experiments were conducted on monitor lizards with and without gular pumping:

1. *Gular pumping allowed.* When the gular pumping mechanism was not obstructed, the V_E increased to a maximum at a speed of 2 km/hr and decreased during the recovery period (see blue line in graph *b* above). This result is predicted under conditions where there is no axial constraint on the animal (see graph *a* above).

2. *Gular pumping disabled.* When the gular pumping mechanism is obstructed, V_E increased above the resting value up to a speed of 1 km/hr. The value began to decrease between 1 and 2 km/hr indicating that there was constraint on ventilation. During the recovery period, V_E increased as predicted by the axial constraint hypothesis, because there was no longer constraint on the intercostal muscles. V_E increased to pay back an oxygen debt that occurred during the period of time when anaerobic metabolism took over.

Comparing the V_E measurements under control and experimental conditions, the researchers concluded that monitor lizards are indeed subject to speed-dependent axial constraint, just as theory had predicted, but can circumvent this constraint when running by using an accessory gular pump to enhance ventilation. When the gular pump was experimentally disrupted, the speed-dependent axial constraint condition became apparent.

Although the researchers have not conducted a more complete comparative analysis using the methods shown here, they have found correlations between gular pumping and increased locomotor activity. Six highly active species exhibited gular pumping while six less active species did not exhibit gular pumping in lung ventilation. It is interesting to speculate that gular pumping evolved in lizards as a means of enhancing breathing to allow greater locomotor endurance. The gular pumping seen in lizards is similar to the breathing mechanism found in amphibians and air-breathing fish. In these animals, the air first enters a cavity in the mouth called the buccal cavity. The mouth and nares close and the buccal cavity collapses, forcing air into the lungs. The similarities in these two mechanisms suggest that one might have arisen from the other.

To explore this experiment further, go to the Virtual Lab at www.mhhe.com/raven6/vlab13.mhtml

49

Organization of the Animal Body

Concept Outline

49.1 The bodies of vertebrates are organized into functional systems.

Organization of the Body. Cells are organized into tissues, and tissues are organized into organs. Several organs can cooperate to form organ systems.

49.2 Epithelial tissue forms membranes and glands.

Characteristics of Epithelial Tissue. Epithelial membranes cover all body surfaces, and thus can serve for protection or for transport of materials. Glands are also epithelial tissue. Epithelial membranes may be composed of one layer or many.

49.3 Connective tissues contain abundant extracellular material.

Connective Tissue Proper. Connective tissues have abundant extracellular material. In connective tissue proper, this material consists of protein fibers within an amorphous ground substance.

Special Connective Tissues. These tissues include cartilage, bone, and blood, each with their own unique form of extracellular material.

49.4 Muscle tissue provides for movement, and nerve tissue provides for control.

Muscle Tissue. Muscle tissue contains the filaments actin and myosin, which enable the muscles to contract. There are three types of muscle: smooth, cardiac, and skeletal.

Nerve Tissue. Nerve cells, or neurons, have specialized regions that produce and conduct electrical impulses. Neuroglia cells support neurons but do not conduct electrical impulses.

FIGURE 49.1
Bone. Like most of the tissues in the vertebrate body, bone is a dynamic structure, constantly renewing itself.

When most people think of animals, they think of their pet dogs and cats and the animals that they've seen in a zoo, on a farm, in an aquarium, or out in the wild. When they think about the diversity of animals, they may think of the differences between the predatory lions and tigers and the herbivorous deer and antelope, between a ferocious-looking shark and a playful dolphin. Despite the differences among these animals, they are all vertebrates. All vertebrates share the same basic body plan, with the same sorts of organs operating in much the same way. In this chapter, we will begin a detailed consideration of the biology of vertebrates and of the fascinating structure and function of their bodies (figure 49.1).

49.1 The bodies of vertebrates are organized into functional systems.

Organization of the Body

The bodies of all mammals have the same general architecture (figure 49.2), and are very similar to the general body plan of other vertebrate groups. This body plan is basically a tube suspended within a tube. Starting from the inside, it is composed of the digestive tract, a long tube that travels from one end of the body to the other (mouth to anus). This tube is suspended within an internal body cavity, the *coelom*. In fishes, amphibians, and most reptiles, the coelom is subdivided into two cavities, one housing the heart and the other the liver stomach, and intestines. In mammals and some reptiles, a sheet of muscle, the *diaphragm*, separates the **peritoneal cavity,** which contains the stomach, intestines, and liver, from the **thoracic cavity;** the thoracic cavity is further subdivided into the *pericardial cavity*, which contains the heart, and *pleural cavities*, which contain the lungs. All vertebrate bodies are supported by an internal **skeleton** made of jointed bones or cartilage blocks that grow as the body grows. A bony *skull* surrounds the brain, and a column of bones, the *vertebrae*, surrounds the dorsal nerve cord, or *spinal cord.*

There are four levels of organization in the vertebrate body: (1) cells, (2) tissues, (3) organs, and (4) organ systems. Like those of all animals, the bodies of vertebrates are composed of different cell types. In adult vertebrates, there are between 50 and several hundred different kinds of cells.

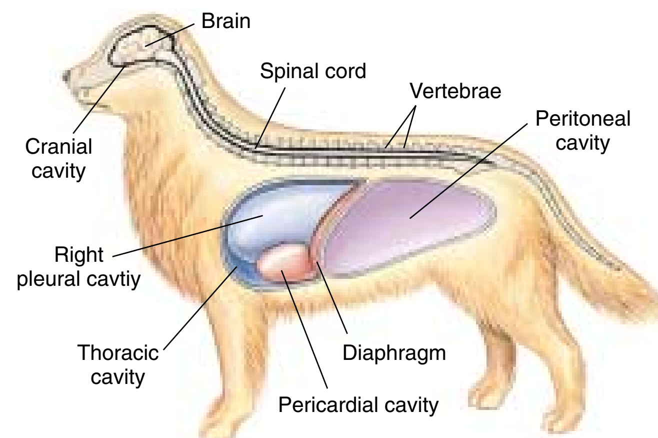


FIGURE 49.2
Architecture of the vertebrate body. All vertebrates have a dorsal central nervous system. In mammals and some reptiles, a muscular diaphragm divides the coelom into the thoracic cavity and the peritoneal cavity.

Tissues

Groups of cells similar in structure and function are organized into **tissues.** Early in development, the cells of the growing embryo differentiate (specialize) into three fundamental embryonic tissues, called *germ layers.* From innermost to outermost layers, these are the **endoderm, mesoderm,** and **ectoderm.** These germ layers, in turn, differentiate into the scores of different cell types and tissues that are characteristic of the vertebrate body. In adult vertebrates, there are four principal kinds of tissues, or *primary tissues:* epithelial, connective, muscle, and nerve (figure 49.3), each discussed in separate sections of this chapter.

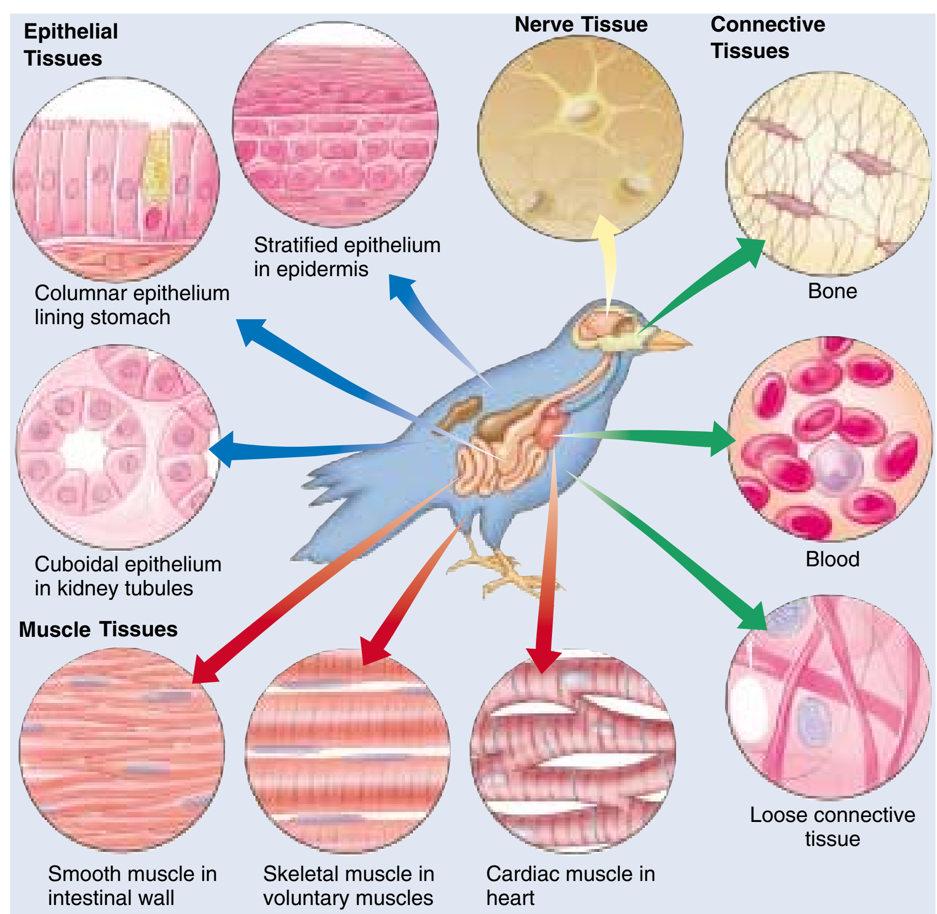


FIGURE 49.3
Vertebrate tissue types. Epithelial tissues are indicated by blue arrows, connective tissues by green arrows, muscle tissues by red arrows, and nerve tissue by a yellow arrow.

Organs and Organ Systems

Organs are body structures composed of several different tissues that form a structural and functional unit (figure 49.4). One example is the heart, which contains cardiac muscle, connective tissue, and epithelial tissue and is laced with nerve tissue that helps regulate the heartbeat. An **organ system** is a group of organs that function together to carry out the major activities of the body. For example, the digestive system is composed of the digestive tract, liver, gallbladder, and pancreas. These organs cooperate in the digestion of food and the absorption of digestion products into the body. The vertebrate body contains 11 principal organ systems (table 49.1 and figure 49.5).

The bodies of humans and other mammals contain a cavity divided by the diaphragm into thoracic and abdominal cavities. The body's cells are organized into tissues, which are, in turn, organized into organs and organ systems.

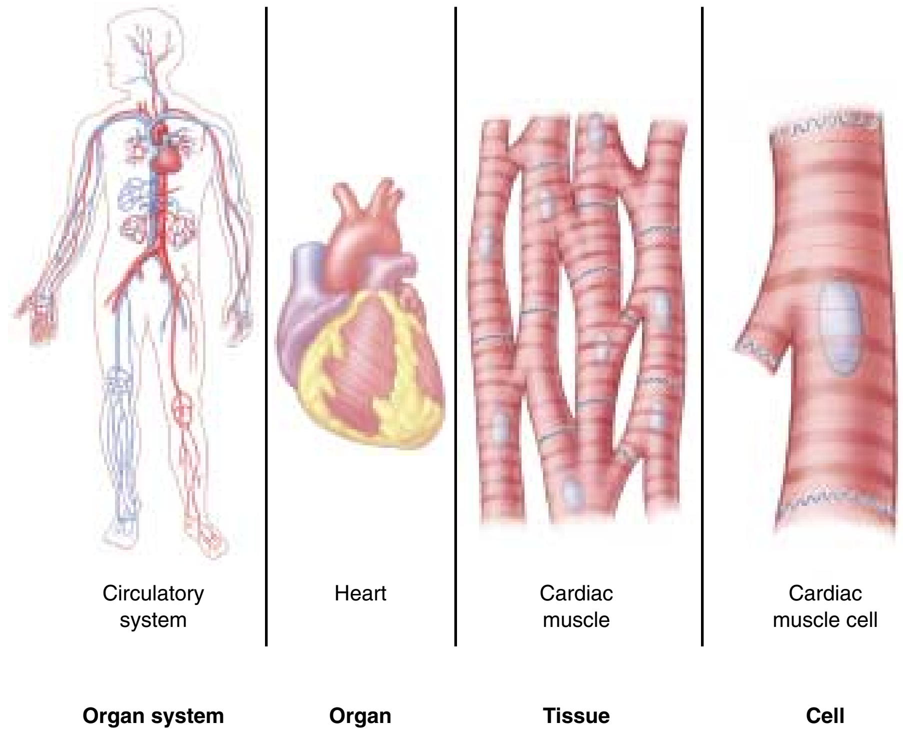


FIGURE 49.4
Levels of organization within the body. Similar cell types operate together and form tissues. Tissues functioning together form organs. Several organs working together to carry out a function for the body are called an organ system. The circulatory system is an example of an organ system.

Table 49.1 The Major Vertebrate Organ Systems

System	Functions	Components	Detailed Treatment
Circulatory	Transports cells, respiratory gases, and chemical compounds throughout the body	Heart, blood vessels, lymph, and lymph structures	Chapter 52
Digestive	Captures soluble nutrients from ingested food	Mouth, esophagus, stomach, intestines, liver, and pancreas	Chapter 51
Endocrine	Coordinates and integrates the activities of the body	Pituitary, adrenal, thyroid, and other ductless glands	Chapter 56
Integumentary	Covers and protects the body	Skin, hair, nails, scales, feathers, and sweat glands	Chapter 57
Lymphatic/ Immune	Vessels transport extracellular fluid and fat to circulatory system; lymph nodes and lymphatic organs provide defenses to microbial infection and cancer	Lymphatic vessels, lymph nodes, thymus, tonsils, spleen	Chapter 57
Muscular	Produces body movement	Skeletal muscle, cardiac muscle, and smooth muscle	Chapter 50
Nervous	Receives stimuli, integrates information, and directs the body	Nerves, sense organs, brain, and spinal cord	Chapters 54, 55
Reproductive	Carries out reproduction	Testes, ovaries, and associated reproductive structures	Chapter 59
Respiratory	Captures oxygen and exchanges gases	Lungs, trachea, gills, and other air passageways	Chapter 53
Skeletal	Protects the body and provides support for locomotion and movement	Bones, cartilage, and ligaments	Chapter 50
Urinary	Removes metabolic wastes from the bloodstream	Kidney, bladder, and associated ducts	Chapter 58

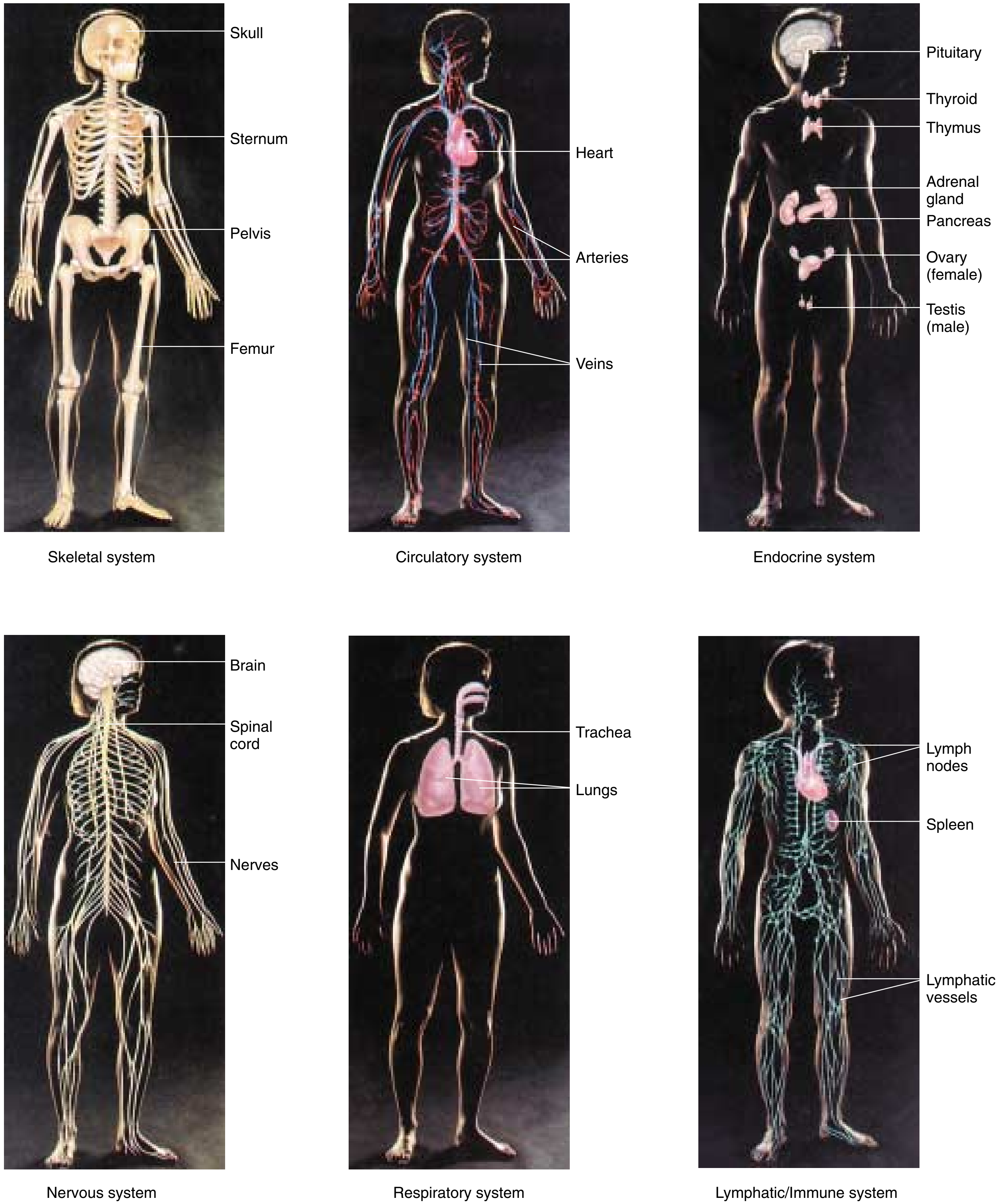


FIGURE 49.5
Vertebrate organ systems. The 11 principal organ systems of the human body are shown, including both male and female reproductive systems.

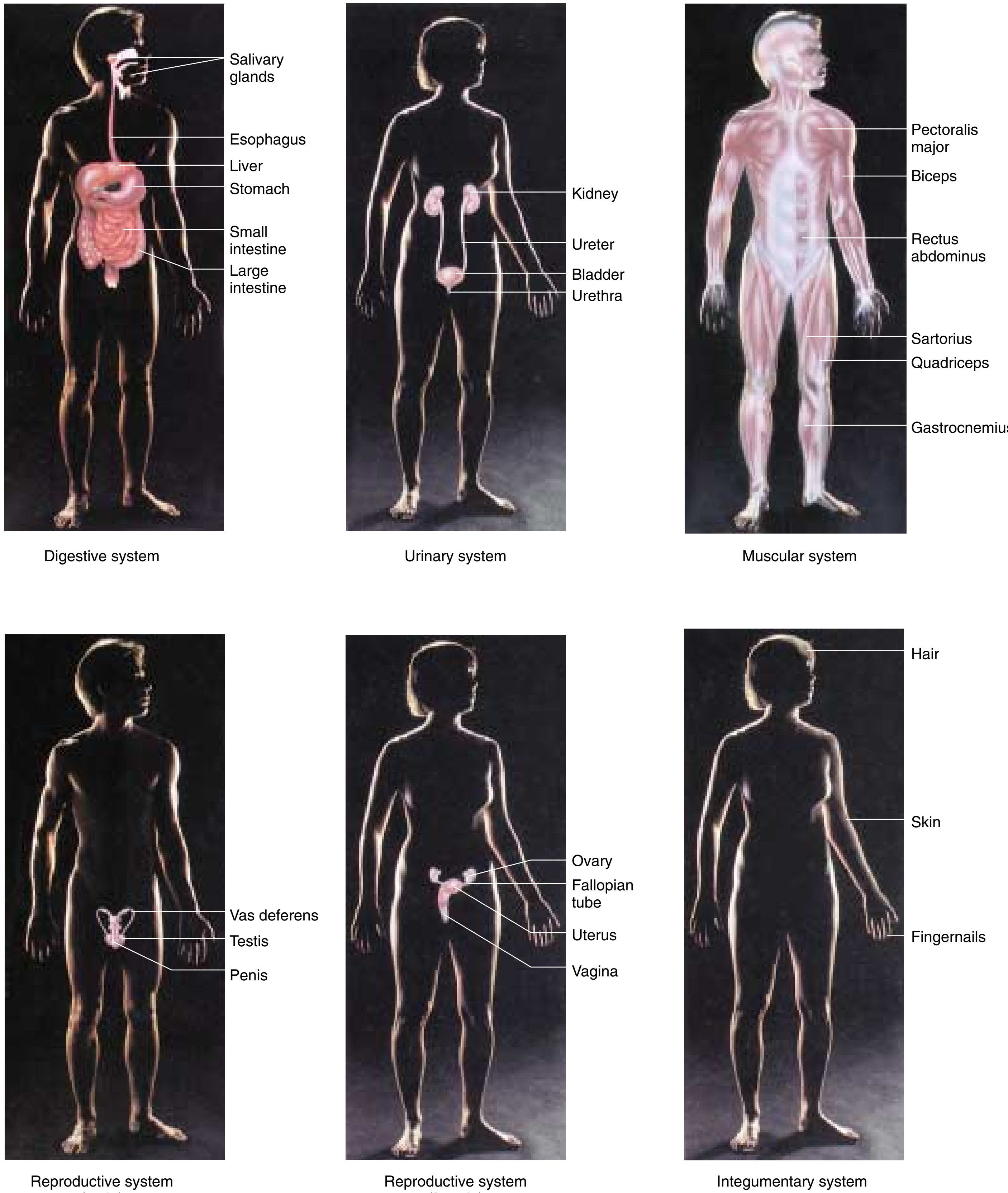


FIGURE 49.5 (continued)

49.2 Epithelial tissue forms membranes and glands.

Characteristics of Epithelial Tissue

An epithelial membrane, or **epithelium,** covers every surface of the vertebrate body. Epithelial membranes are derived from all three germ layers. The epidermis, derived from ectoderm, constitutes the outer portion of the skin. The inner surface of the digestive tract is lined by an epithelium derived from endoderm, and the inner surfaces of the body cavities are lined with an epithelium derived from mesoderm.

Because all body surfaces are covered by epithelial membranes, a substance must pass through an epithelium in order to enter or leave the body. Epithelial membranes thus provide a barrier that can impede the passage of some substances while facilitating the passage of others. For land-dwelling vertebrates, the relative impermeability of the surface epithelium (the epidermis) to water offers essential protection from dehydration and from airborne pathogens (disease-causing organisms). On the other hand, the epithelial lining of the digestive tract must allow selective entry of the products of digestion while providing a barrier to toxic substances, and the epithelium of the lungs must allow for the rapid diffusion of gases.

Some epithelia become modified in the course of embryonic development into glands, which are specialized for secretion. A characteristic of all epithelia is that the cells are tightly bound together, with very little space between them. As a consequence, blood vessels cannot be interposed between adjacent epithelial cells. Therefore, nutrients and oxygen must diffuse to the epithelial cells from blood vessels in nearby tissues. This places a limit on the thickness of epithelial membranes; most are only one or a few cell layers thick.

Epithelium possesses remarkable regenerative powers, constantly replacing its cells throughout the life of the animal. For example, the liver, a gland formed from epithelial tissue, can readily regenerate after substantial portions of it have been surgically removed. The epidermis is renewed every two weeks, and the epithelium inside the stomach is replaced every two to three days.

There are two general classes of epithelial membranes: simple and stratified. These classes are further subdivided into squamous, cuboidal, and columnar, based upon the shape of the cells (table 49.2). Squamous cells are flat, cuboidal cells are about as thick as they are tall, and columnar cells are taller than they are wide.

Types of Epithelial Tissues

Simple epithelial membranes are one cell layer thick. A *simple, squamous epithelium* is composed of squamous epithelial cells that have an irregular, flattened shape with tapered edges. Such membranes line the lungs and blood capillaries, for example, where the thin, delicate nature of these membranes permits the rapid movement of molecules (such as the diffusion of gases). A *simple cuboidal epithelium* lines the small ducts of some glands, and a *simple columnar epithelium* is found in the airways of the respiratory tract and in the gastrointestinal tract, among other locations. Interspersed among the columnar epithelial cells are numerous *goblet cells*, specialized to secrete mucus. The columnar epithelial cells of the respiratory airways contain cilia on their apical surface (the surface facing the lumen, or cavity), which move mucus toward the throat. In the small intestine, the apical surface of the columnar epithelial cells form fingerlike projections called *microvilli*, that increase the surface area for the absorption of food.

Stratified epithelial membranes are several cell layers thick and are named according to the features of their uppermost layers. For example, the epidermis is a *stratified squamous epithelium*. In terrestrial vertebrates it is further characterized as a *keratinized epithelium*, because its upper layer consists of dead squamous cells and filled with a water-resistant protein called *keratin*. The deposition of keratin in the skin can be increased in response to abrasion, producing calluses. The water-resistant property of keratin is evident when the skin is compared with the red portion of the lips, which can easily become dried and chapped because it is covered by a nonkeratinized, stratified squamous epithelium.

The glands of vertebrates are derived from invaginated epithelium. In **exocrine glands,** the connection between the gland and the epithelial membrane is maintained as a duct. The duct channels the product of the gland to the surface of the epithelial membrane and thus to the external environment (or to an interior compartment that opens to the exterior, such as the digestive tract). Examples of exocrine glands include sweat and sebaceous (oil) glands, which secrete to the external surface of the skin, and accessory digestive glands such as the salivary glands, liver, and pancreas, which secrete to the surface of the epithelium lining the digestive tract.

Endocrine glands are ductless glands; their connections with the epithelium from which they were derived are lost during development. Therefore, their secretions, called *hormones*, are not channeled onto an epithelial membrane. Instead, hormones enter blood capillaries and thus stay within the body. Endocrine glands are discussed in more detail in chapter 56.

Epithelial tissues include membranes that cover all body surfaces and glands. The epidermis of the skin is an epithelial membrane specialized for protection, whereas membranes that cover the surfaces of hollow organs are often specialized for transport.

Table 49.2 Epithelial Tissue

Simple Epithelium

SQUAMOUS

Typical Location

Lining of lungs, capillary walls, and blood vessels

Function

Cells very thin; provides thin layer across which diffusion can readily occur

Characteristic Cell Types

Epithelial cells

CUBOIDAL

Typical Location

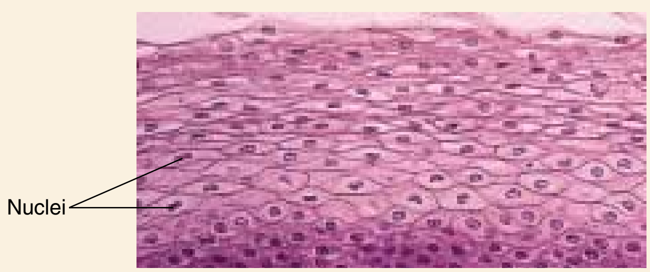
Lining of some glands and kidney tubules; covering of ovaries

Function

Cells rich in specific transport channels; functions in secretion and absorption

Characteristic Cell Types

Gland cells



COLUMNAR

Typical Location

Surface lining of stomach, intestines, and parts of respiratory tract

Function

Thicker cell layer; provides protection and functions in secretion and absorption

Characteristic Cell Types

Epithelial cells

Stratified Epithelium

SQUAMOUS

Typical Location

Outer layer of skin; lining of mouth

Function

Tough layer of cells; provides protection

Characteristic Cell Types

Epithelial cells

PSEUDOSTRATIFIED COLUMNAR

Typical Location

Lining parts of the respiratory tract

Function

Secretes mucus; dense with cilia that aid in movement of mucus; provides protection

Characteristic Cell Types

Gland cells; ciliated epithelial cells

49.3 Connective tissues contain abundant extracellular material.

Connective Tissue Proper

Connective tissues are derived from embryonic mesoderm and occur in many different forms (table 49.3). These various forms are divided into two major classes: **connective tissue proper,** which is further divided into loose and dense connective tissues; and **special connective tissues** that include cartilage, bone, and blood. At first glance, it may seem odd that such diverse tissues are placed in the same category. Yet all connective tissues do share a common structural feature: they all have abundant extracellular material because their cells are spaced widely apart. This extracellular material is generically known as the **matrix** of the tissue. In bone, the extracellular matrix contains crystals that make the bones hard; in blood, the extracellular matrix is plasma, the fluid portion of the blood.

Loose connective tissue consists of cells scattered within an amorphous mass of proteins that form a **ground substance.** This gelatinous material is strengthened by a loose scattering of protein fibers such as *collagen* (figure 49.6), *elastin*, which makes the tissue elastic, and *reticulin*, which supports the tissue by forming a collagenous meshwork. The flavored gelatin we eat for dessert consists of the extracellular material from loose connective tissues. The cells that secrete collagen and other fibrous proteins are known as *fibroblasts*.

Loose connective tissue contains other cells as well, including *mast cells* that produce histamine (a blood vessel dilator) and heparin (an anticoagulant) and *macrophages*, the immune system's first defense against invading organisms, as will be described in detail in chapter 57.

Adipose cells are found in loose connective tissue, usually in large groups that form what is referred to as *adipose tissue* (figure 49.7). Each adipose cell contains a droplet of fat (triglycerides) within a storage vesicle. When that fat is needed for energy, the adipose cell hydrolyzes its stored triglyceride and secretes fatty acids into the blood for oxidation by the cells of the muscles, liver, and other organs. The number of adipose cells in an adult is generally fixed. When a person gains weight, the cells become larger, and when weight is lost, the cells shrink.

Dense connective tissue contains tightly packed collagen fibers, making it stronger than loose connective tissue. It consists of two types: regular and irregular. The collagen fibers of **dense regular connective tissue** are lined up in parallel, like the strands of a rope. This is the structure of *tendons*, which bind muscle to bone, and *ligaments*, which bind bone to bone. In contrast, the collagen fibers of **dense irregular connective tissue** have many different orientations. This type of connective tissue produces the tough coverings that package organs, such as the *capsules* of the kidneys and adrenal glands. It also covers muscle as *epimysium*, nerves as *perineurium*, and bones as *periosteum*.

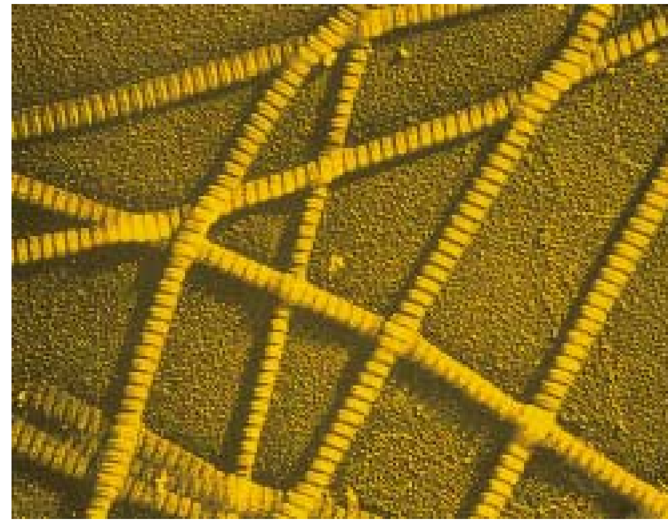


FIGURE 49.6
Collagen fibers. Each fiber is composed of many individual collagen strands and can be very strong under tension.

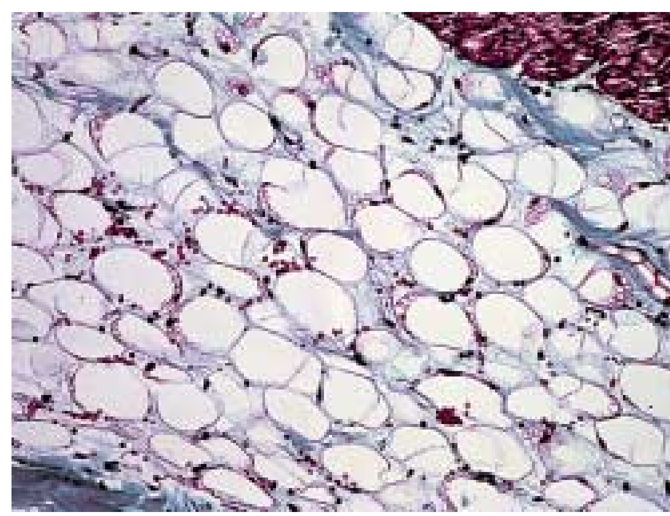
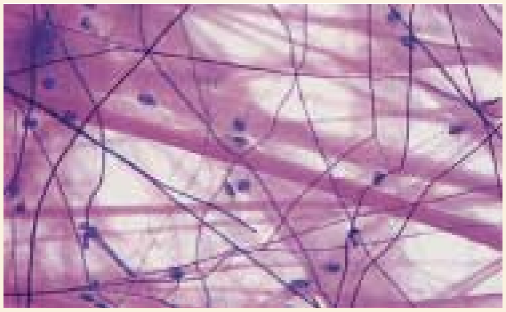


FIGURE 49.7
Adipose tissue. Fat is stored in globules of adipose tissue, a type of loose connective tissue. As a person gains or loses weight, the size of the fat globules increases or decreases. A person cannot decrease the number of fat cells by losing weight.

Connective tissues are characterized by abundant extracellular materials in the matrix between cells. Connective tissue proper may be either loose or dense.

Table 49.3 Connective Tissue



LOOSE CONNECTIVE TISSUE

Typical Location

Beneath skin; between organs

Function

Provides support, insulation, food storage, and nourishment for epithelium

Characteristic Cell Types

Fibroblasts, macrophages, mast cells, fat cells

DENSE CONNECTIVE TISSUE

Typical Location

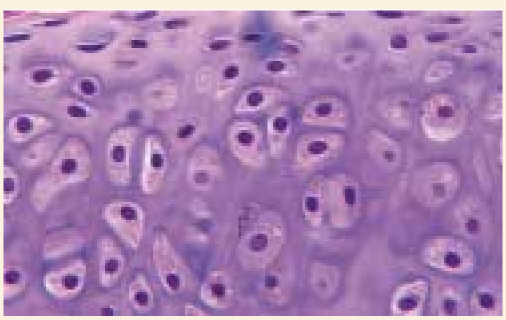
Tendons; sheath around muscles; kidney; liver; dermis of skin

Function

Provides flexible, strong connections

Characteristic Cell Types

Fibroblasts



CARTILAGE

Typical Location

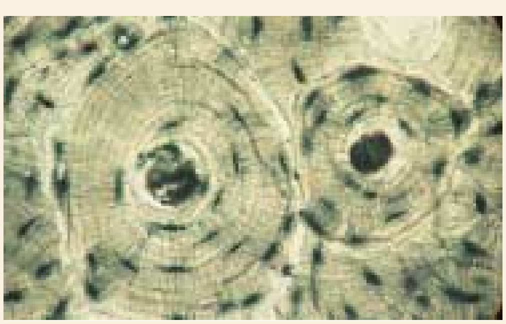
Spinal discs; knees and other joints; ear; nose; tracheal rings

Function

Provides flexible support, shock absorption, and reduction of friction on load-bearing surfaces

Characteristic Cell Types

Chondrocytes



BONE

Typical Location

Most of skeleton

Function

Protects internal organs; provides rigid support for muscle attachment

Characteristic Cell Types

Osteocytes

BLOOD

Typical Location

Circulatory system

Function

Functions as highway of immune system and primary means of communication between organs

Characteristic Cell Types

Erythrocytes, leukocytes

Special Connective Tissues

The special connective tissues—cartilage, bone, and blood—each have unique cells and extracellular matrices that allow them to perform their specialized functions.

Cartilage

Cartilage (figure 49.8) is a specialized connective tissue in which the ground substance is formed from a characteristic type of glycoprotein, and the collagen fibers are laid down along the lines of stress in long, parallel arrays. The result is a firm and flexible tissue that does not stretch, is far tougher than loose or dense connective tissue, and has great tensile strength. Cartilage makes up the entire skeletal system of the modern agnathans and cartilaginous fishes (see chapter 48), replacing the bony skeletons that were characteristic of the ancestors of these vertebrate groups. In most adult vertebrates, however, cartilage is restricted to the articular (joint) surfaces of bones that form freely movable joints and to other specific locations. In humans, for example, the tip of the nose, the pinna (outer ear flap), the intervertebral discs of the backbone, the larynx (voice box) and a few other structures are composed of cartilage.

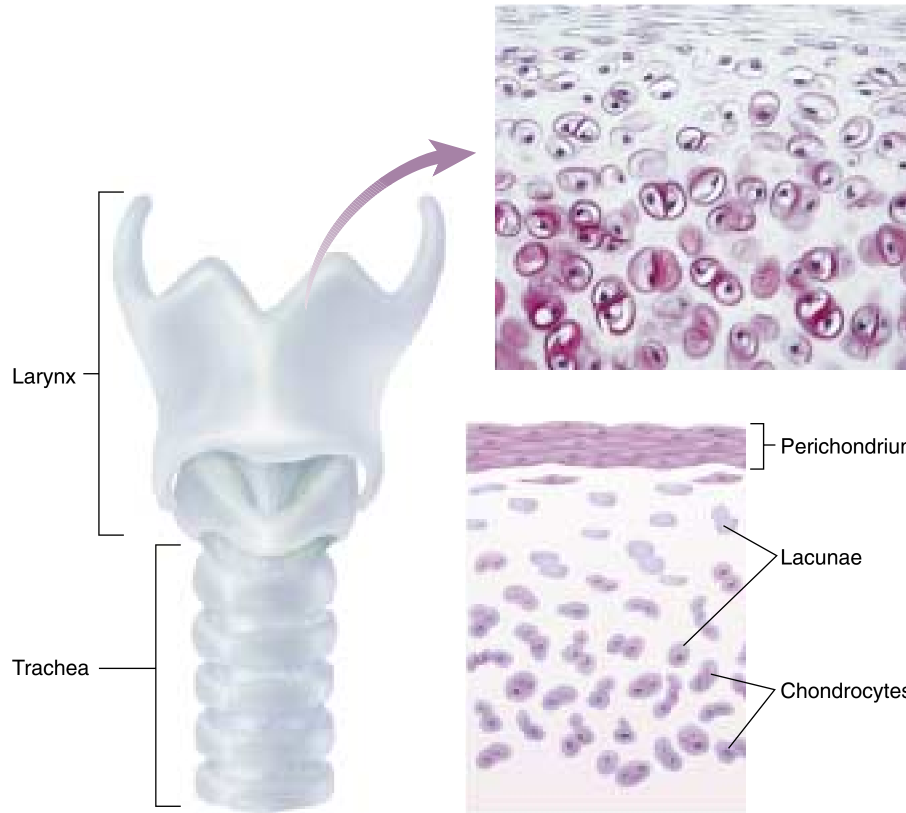


FIGURE 49.8
Cartilage is a strong, flexible tissue that makes up the larynx (voice box) and several other structures in the human body. The larynx (*a*) is seen under the light microscope in (*b*), where the cartilage cells, or chondrocytes, are visible within cavities, or lacunae, in the matrix (extracellular material) of the cartilage. This is diagrammed in (*c*).

Chondrocytes, the cells of the cartilage, live within spaces called *lacunae* within the cartilage ground substance. These cells remain alive, even though there are no blood vessels within the cartilage matrix, because they receive oxygen and nutrients by diffusion through the cartilage ground substance from surrounding blood vessels. This diffusion can only occur because the cartilage matrix is not calcified, as is bone.

Bone

In the course of fetal development, the bones of vertebrate fins, arms, and legs, among others, are first "modeled" in cartilage. The cartilage matrix then calcifies at particular locations, so that the chondrocytes are no longer able to obtain oxygen and nutrients by diffusion through the matrix. The dying and degenerating cartilage is then replaced by living bone. Bone cells, or osteocytes, can remain alive even though the extracellular matrix becomes hardened with crystals of calcium phosphate. This is because blood vessels travel through central canals into the bone. Osteocytes extend cytoplasmic processes toward neighboring osteocytes through tiny canals, or *canaliculi* (figure 49.9). Osteocytes communicate with the blood vessels in the central canal through this cytoplasmic network.

It should be noted here that some bones, such as those of the cranium, are not formed first as cartilage models. These bones instead develop within a membrane of dense, irregular connective tissue. The structure and formation of bone are discussed in chapter 50.

Blood

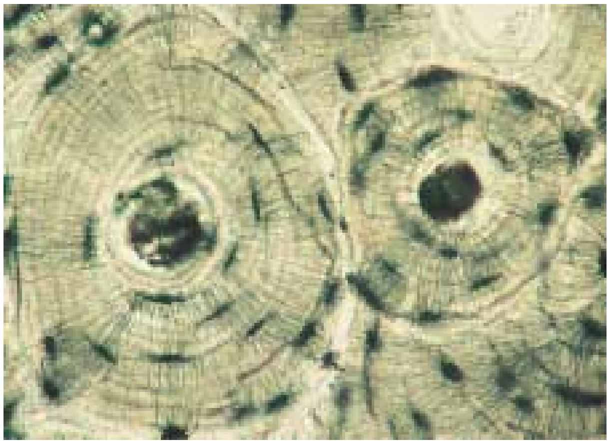
Blood is classified as a connective tissue because it contains abundant extracellular material, the fluid plasma. The cells of blood are erythrocytes, or red blood cells, and leukocytes, or white blood cells (figure 49.10). Blood also contains platelets, or *thrombocytes,* which are fragments of a type of bone marrow cell.

Erythrocytes are the most common blood cells; there are about 5 billion in every milliliter of blood. During their maturation in mammals, they lose their nucleus, mitochondria, and endoplasmic reticulum. As a result, mammalian erythrocytes are relatively inactive metabolically. Each erythrocyte contains about 300 million molecules of the iron-containing protein *hemoglobin*, the principal carrier of oxygen in vertebrates and in many other groups of animals.

There are several types of leukocytes, but together they are only one-thousandth as numerous as erythrocytes. Unlike mammalian erythrocytes, leukocytes have nuclei and mitochondria but lack the red pigment hemoglobin. These cells are therefore hard to see under a microscope without special staining. The names *neutrophils*, *eosinophils*, and *basophils* distinguish three types of leukocytes on the basis of their staining properties; other leukocytes include *lymphocytes* and *monocytes*. These different types of leukocytes play critical roles in immunity, as will be described in chapter 57.

The blood plasma is the "commons" of the body; it (or a derivative of it) travels to and from every cell in the body. As the plasma circulates, it carries nourishment, waste products, heat, and regulatory molecules. Practically every substance used by cells, including sugars, lipids, and amino acids, is delivered by the plasma to the body cells. Waste products from the cells are carried by the plasma to the kidneys, liver, and lungs or gills for disposal, and regulatory molecules (hormones) that endocrine gland cells secrete are carried by the plasma to regulate the activities of most organs of the body. The plasma also contains sodium, calcium, and other inorganic ions that all cells need, as well as numerous proteins. Plasma proteins include *fibrinogen*, produced by the liver, which helps blood to clot; *albumin*, also produced by the liver, which exerts an osmotic force needed for fluid balance; and *antibodies* produced by lymphocytes and needed for immunity.

Special connective tissues each have a unique extracellular matrix between cells. The matrix of cartilage is composed of organic material, whereas that of bone is impregnated with calcium phosphate crystals. The matrix of blood is fluid, the plasma.



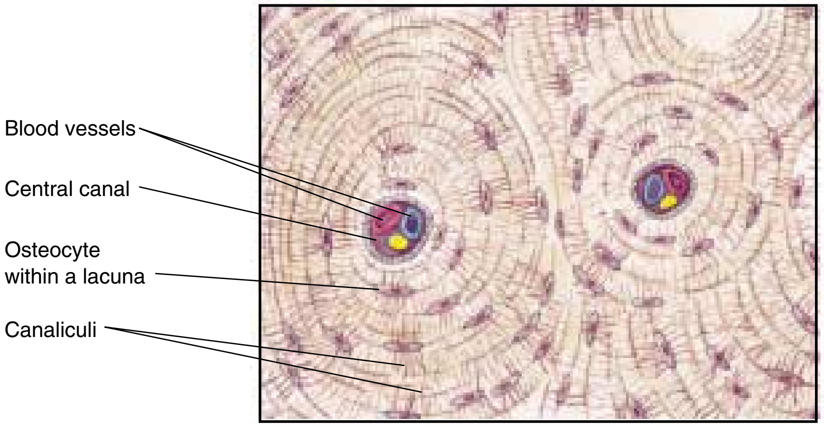


FIGURE 49.9
The structure of bone. A photomicrograph (*a*) and diagram (*b*) of the structure of bone, showing the bone cells, or osteocytes, within their lacunae (cavities) in the bone matrix. Though the bone matrix is calcified, the osteocytes remain alive because they can be nourished by blood vessels in the central cavity. Nourishment is carried between the osteocytes through a network of cytoplasmic processes extending through tiny canals, or canaliculi.

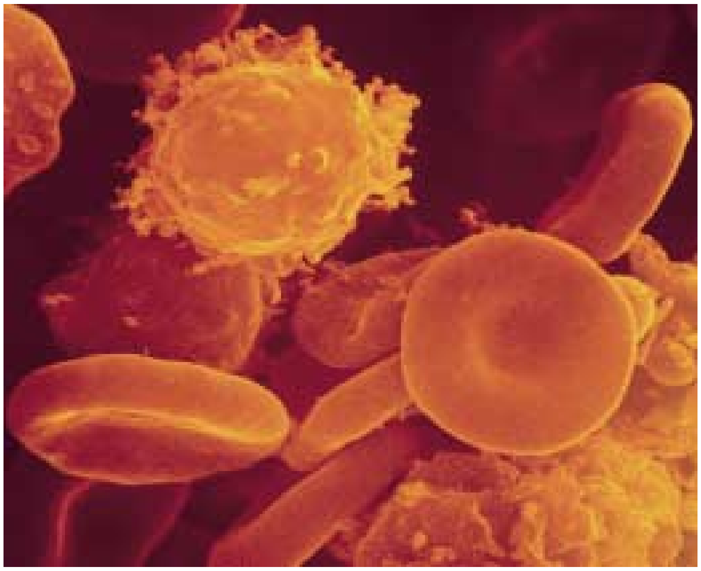


FIGURE 49.10
White and red blood cells (500×). White blood cells, or leukocytes, are roughly spherical and have irregular surfaces with numerous extending pili. Red blood cells, or erythrocytes, are flattened spheres, typically with a depressed center, forming biconcave discs.

49.4 Muscle tissue provides for movement, and nerve tissue provides for control.

Muscle Tissue

Muscle cells are the motors of the vertebrate body. The characteristic that makes them unique is the relative abundance and organization of actin and myosin filaments within them. Although these filaments form a fine network in all eukaryotic cells, where they contribute to cellular movements, they are far more common in muscle cells, which are specialized for contraction. Vertebrates possess three kinds of muscle: smooth, skeletal, and cardiac (table 49.4). Skeletal and cardiac muscles are also known as **striated muscles** because their cells have transverse stripes when viewed in longitudinal section under the microscope. The contraction of each skeletal muscle is under voluntary control, whereas the contraction of cardiac and smooth muscles is generally involuntary. Muscles are described in more detail in chapter 50.

Smooth Muscle

Smooth muscle was the earliest form of muscle to evolve, and it is found throughout the animal kingdom. In vertebrates, smooth muscle is found in the organs of the internal environment, or *viscera*, and is sometimes known as visceral muscle. Smooth muscle tissue is organized into sheets of long, spindle-shaped cells, each cell containing a single nucleus. In some tissues, the cells contract only when they are stimulated by a nerve, and then all of the cells in the sheet contract as a unit. In vertebrates, muscles of this type line the walls of many blood vessels and make up the iris of the eye. In other smooth muscle tissues, such as those in the wall of the gut, the muscle cells themselves may spontaneously initiate electric impulses and contract, leading to a slow, steady contraction of the tissue. Nerves regulate, rather than cause, this activity.

Skeletal Muscle

Skeletal muscles are usually attached by tendons to bones, so that, when the muscles contract, they cause the bones to move at their joints. A skeletal muscle is made up of numerous, very long muscle cells, called *muscle fibers*, which lie parallel to each other within the muscle and insert into the tendons on the ends of the muscle. Each skeletal muscle fiber is stimulated to contract by a nerve fiber; therefore, a stronger muscle contraction will result when more of the muscle fibers are stimulated by nerve fibers to contract. In this way, the nervous system can vary the strength of skeletal muscle contraction. Each muscle fiber contracts by means of substructures called *myofibrils* (figure 49.11) that contain highly ordered arrays of actin and myosin myofilaments, that, when aligned, give the muscle fiber its striated appearance. Skeletal muscle fibers are produced during development by the fusion of several cells, end to end. This

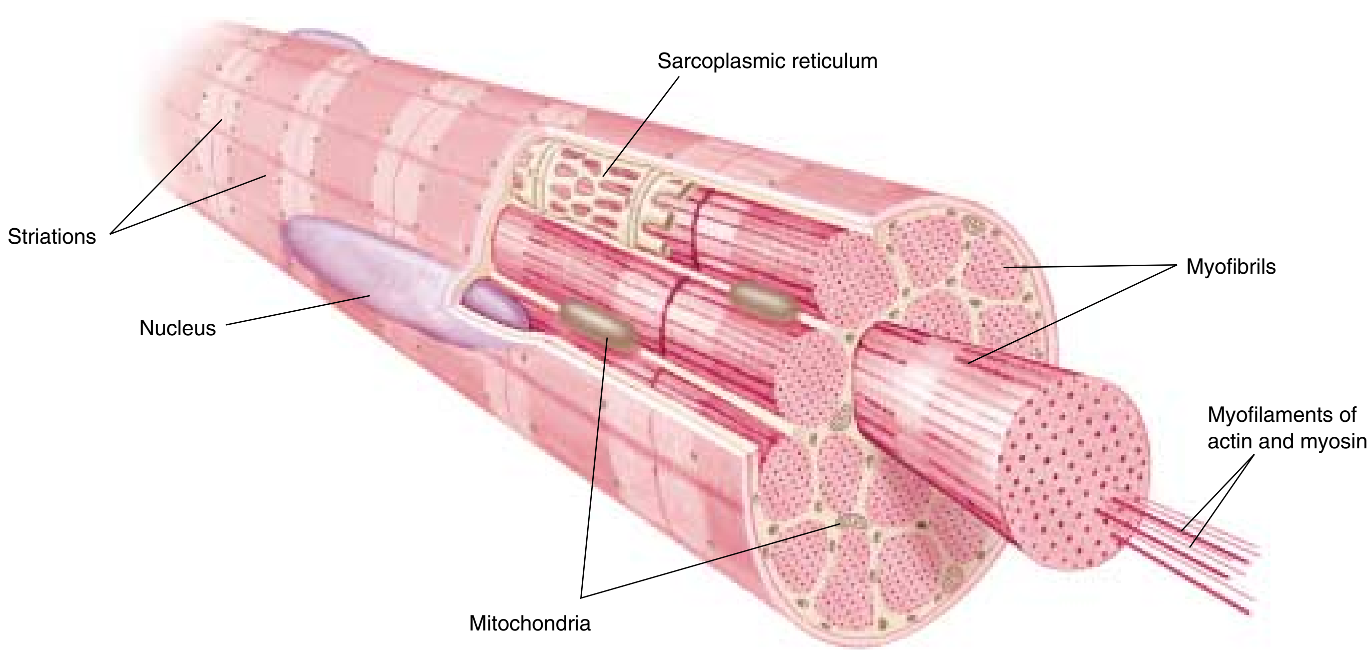
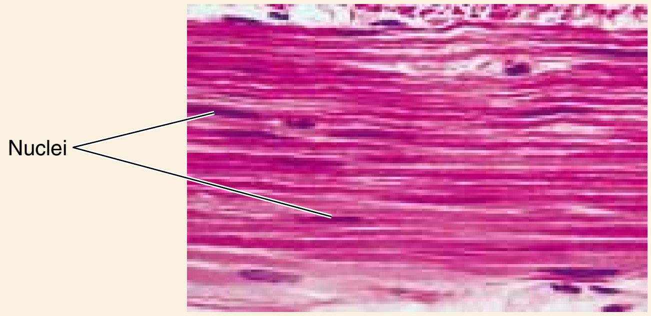
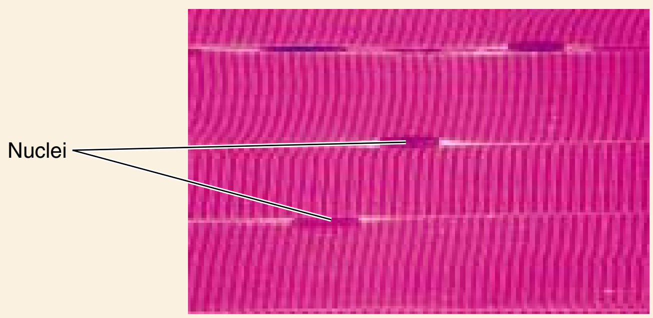
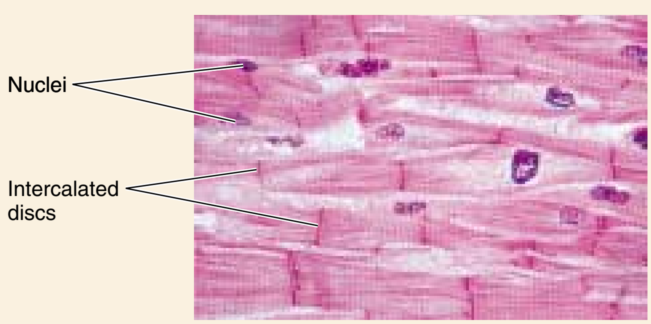


FIGURE 49.11
A muscle fiber, or muscle cell. Each muscle fiber is composed of numerous myofibrils, which, in turn, are composed of actin and myosin filaments. Each muscle fiber is multinucleate as a result of its embryological development from the fusion of smaller cells. Muscle cells have a modified endoplasmic reticulum called the sarcoplasmic reticulum.

Table 49.4 Muscle Tissue

	**SMOOTH MUSCLE** *Typical Location* Walls of blood vessels, stomach, and intestines *Function* Powers rhythmic, involuntary contractions commanded by the central nervous system *Characteristic Cell Types* Smooth muscle cells
	**SKELETAL MUSCLE** *Typical Location* Voluntary muscles *Function* Powers walking, lifting, talking, and all other voluntary movement *Characteristic Cell Types* Skeletal muscle cells
	**CARDIAC** *Typical Location* Walls of heart *Function* Highly interconnected cells; promotes rapid spread of signal initiating contraction *Characteristic Cell Types* Cardiac muscle cells

embryological development explains why a mature muscle fiber contains many nuclei. The structure and function of skeletal muscle is explained in more detail in chapter 50.

Cardiac Muscle

The hearts of vertebrates are composed of striated muscle cells arranged very differently from the fibers of skeletal muscle. Instead of having very long, multinucleate cells running the length of the muscle, cardiac muscle is composed of smaller, interconnected cells, each with a single nucleus. The interconnections between adjacent cells appear under the microscope as dark lines called *intercalated discs*. In reality, these lines are regions where adjacent cells are linked by *gap junctions*. As we noted in chapter 7, gap junctions have openings that permit the movement of small substances and electric charges from one cell to another. These interconnections enable the cardiac muscle cells to form a single, functioning unit known as a myocardium. Certain cardiac muscle cells generate electric impulses spontaneously, and these impulses spread across the gap junctions from cell to cell, causing all of the cells in the myocardium to contract. We will describe this process more fully in chapter 52.

Skeletal muscles enable the vertebrate body to move. Cardiac muscle powers the heartbeat, while smooth muscles provide a variety of visceral functions.

Nerve Tissue

The fourth major class of vertebrate tissue is nerve tissue (table 49.5). Its cells include neurons and neuroglia, or supporting cells. Neurons are specialized to produce and conduct electrochemical events, or "impulses." Each neuron consists of three parts: cell body, dendrites, and axon (figure 49.12). The cell body of a neuron contains the nucleus. Dendrites are thin, highly branched extensions that receive incoming stimulation and conduct electric events to the cell body. As a result of this stimulation and the electric events produced in the cell body, outgoing impulses may be produced at the origin of the axon. The axon is a single extension of cytoplasm that conducts impulses away from the cell body. Some axons can be quite long. The cell bodies of neurons that control the muscles in your feet, for example, lie in the spinal cord, and their axons may extend over a meter to your feet.

Neuroglia do not conduct electrical impulses but instead support and insulate neurons and eliminate foreign materials in and around neurons. In many neurons, neuroglia cells associate with the axons and form an insulating covering, a *myelin sheath*, produced by successive wrapping of the membrane around the axon (figure 49.13). Adjacent neuroglia cells are separated by interruptions known as *nodes of Ranvier*, which serve as sites for accelerating an impulse (see chapter 54).

The nervous system is divided into the central nervous system (CNS), which includes the brain and spinal cord, and the peripheral nervous system (PNS), which includes *nerves* and *ganglia*. Nerves consist of axons in the PNS that are bundled together in much the same way as wires are bundled together in a cable. Ganglia are collections of neuron cell bodies.

There are different types of neurons, but all are specialized to receive, produce, and conduct electrical signals. Neuroglia do not conduct electrical impulses but have various functions, including insulating axons to accelerate an electrical impulse. Both neurons and neuroglia are present in the CNS and the PNS.

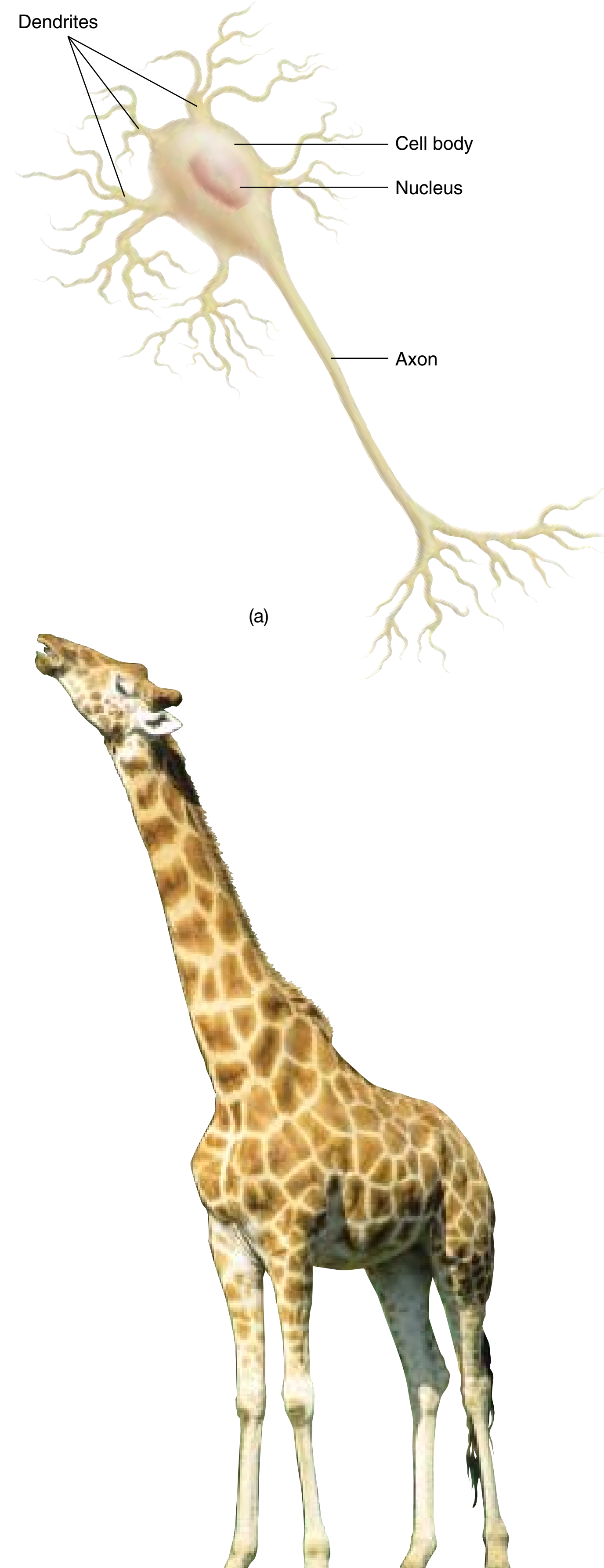
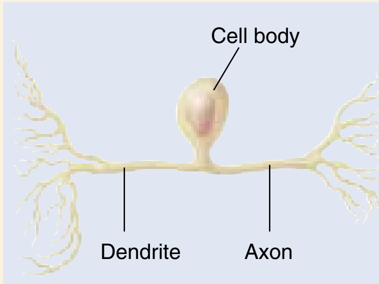


FIGURE 49.12
A neuron has a very long projection called an axon. (*a*) A nerve impulse is received by the dendrites and then passed to the cell body and out through the axon. (*b*) Axons can be very long; single axons extend from the skull down several meters through a giraffe's neck to its pelvis.

Table 49.5 Nerve Tissue



SENSORY NEURONS

Typical Location

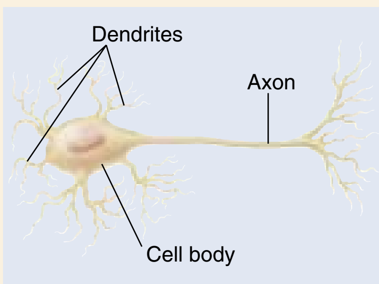
Eyes; ears; surface of skin

Function

Receive information about body's condition and external environment; send impulses from sensory receptors to CNS

Characteristic Cell Types

Rods and cones; muscle stretch receptors



MOTOR NEURONS

Typical Location

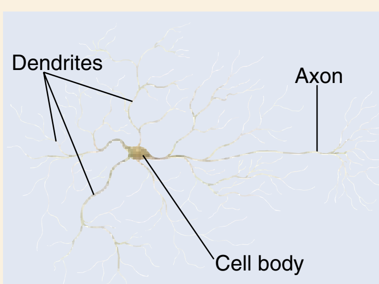
Brain and spinal cord

Function

Stimulate muscles and glands; conduct impulses out of CNS toward muscles and glands

Characteristic Cell Types

Motor neurons



ASSOCIATION NEURONS

Typical Location

Brain and spinal cord

Function

Integrate information; conduct impulses between neurons within CNS

Characteristic Cell Types

Association neurons

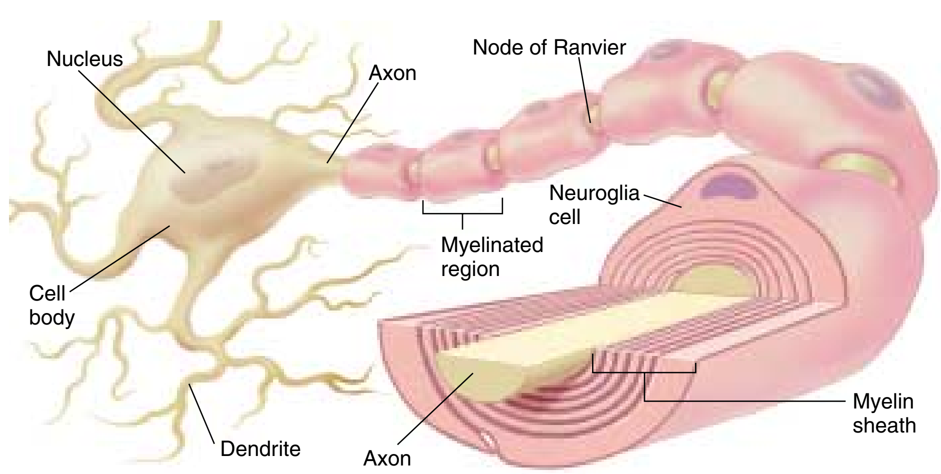


FIGURE 49.13
A myelinated neuron. Many dendrites arise from the cell body, as does a single long axon. In some neurons specialized for rapid signal conduction, the axon is encased in a myelin sheath that is interrupted at intervals. At its far end, the axon may branch to terminate on more than one cell.

Chapter 49

www.mhhe.com/raven6ch/resource28.mhtml

Summary	Questions	Media Resources

49.1 The bodies of vertebrates are organized into functional systems.

Summary

- The vertebrate body is organized into cells, tissues, organs, and organ systems, which are specialized for different functions.
- The four primary tissues of the vertebrate adult body—epithelial, connective, muscle, and nerve—are derived from three embryonic germ layers.

Questions

1. What is a tissue? What is an organ? What is an organ system?

Media Resources

- Art Activity: Mammalian body cavities

49.2 Epithelial tissue forms membranes and glands.

Summary

- Epithelial membranes cover all body surfaces.
- Stratified membranes, particularly the keratinized epithelium of the epidermis, provides protection, whereas simple membranes are more adapted for secretion and transport.
- Exocrine glands secrete into ducts that conduct the secretion to the surface of an epithelial membrane; endocrine glands secrete hormones into the blood.

Questions

2. What are the different types of epithelial membranes, and how do they differ in structure and function?

3. What are the two types of glands, and how do they differ in structure and function?

Media Resources

- Epithelial tissue
- Epithelial glands

49.3 Connective tissues contain abundant extracellular material.

Summary

- Connective tissues are characterized by abundant extracellular matrix, which is composed of fibrous proteins and a gel-like ground substance in connective tissue proper.
- Loose connective tissues contain many cell types such as adipose cells and mast cells; dense regular connective tissues form tendons and ligaments.
- Special connective tissues include cartilage, bone, and blood. Nutrients can diffuse through the cartilage matrix but not through the calcified matrix of bone, which contains canaliculi for that purpose.

Questions

4. What feature do all connective tissues share? What are the different categories of connective tissue? Give an example of each.

5. What is the structure of a ligament? How do cartilage and bone differ? Why is blood considered to be a connective tissue?

Media Resources

- Connective tissue

49.4 Muscle tissue provides for movement, and nerve tissue provides for control.

Summary

- Smooth muscles are composed of spindle-shaped cells and are found in the organs of the internal environment and in the walls of blood vessels.
- Skeletal and cardiac muscles are striated; skeletal muscles, however, are under voluntary control whereas cardiac muscle is involuntary.
- Neurons consist of a cell body with one or more dendrites and one axon. Neuron cell bodies form ganglia, and their axons form nerves in the peripheral nervous system.
- Neuroglia are supporting cells with various functions including insulating axons to accelerate an electrical impulse.

Questions

6. From what embryonic tissue is muscle derived? What two contractile proteins are abundant in muscle? What are the three categories of muscle tissue? Which two are striated?

7. Why are skeletal muscle fibers multinucleated? What is the functional significance of intercalated discs in heart muscle?

Media Resources

- Tissues
- Nerve tissue
- Nervous tissue
- Muscle tissue