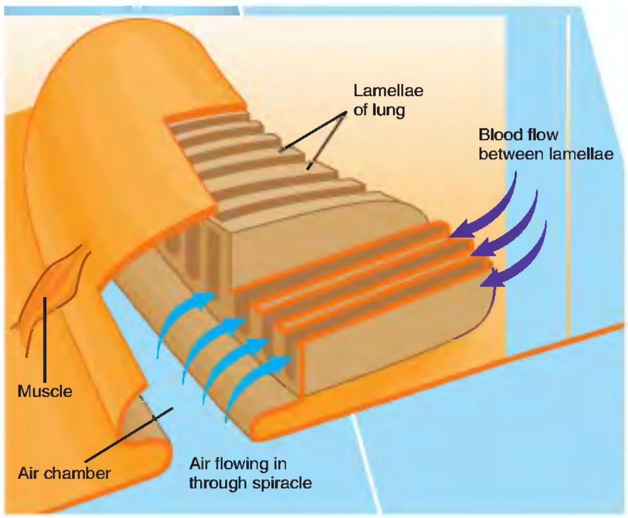

FIGURE 26.13

Invertebrate Respiration: A Book Lung. Structure of an arachnid (spider) book lung. Air enters through a spiracle into the air chamber by diffusion and by ventilation due to muscle contraction. Air diffuses from the air chamber into the lamellar spaces; hemolymph circulates through the blood lamellar spaces that alternate with air lamellar spaces. Small, peglike surface projections hold the lamellae apart. Due to this structural arrangement, air (blue arrows) and blood (purple arrows) move on opposite sides of a lamella in a countercurrent flow, allowing the exchange of respiratory gases by diffusion.

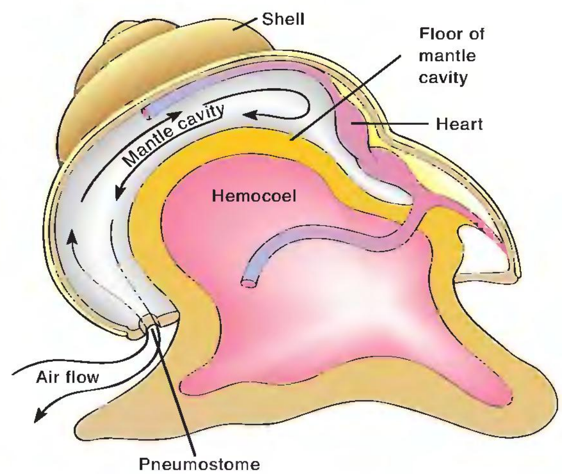

FIGURE 26.14

Invertebrate Respiration: The Pulmonate Lung. The mantle cavity of the pulmonate snail, *Lymnaea*, is highly vascularized and functions as a lung. Downward movement of the floor of the cavity increases the cavity's volume, so that air is drawn into the mantle cavity for respiration. Decreasing the volume of the mantle cavity expels the air. Air flows into and out of the lung through a single pore called the pneumostome. Black arrows indicate the direction of air flow.

cavity—which in other molluscs houses the gills and other organs. Some of the more primitive pulmonate snails are aquatic (freshwater) and close the pneumostome during submergence. When the snail surfaces to breathe air, the pneumostome opens. Most of the higher pulmonates are terrestrial and rely on their lungs for gas exchange. The lung may be ventilated by arching and then flattening the body, but most gas exchange occurs by diffusion through the pneumostome, which is open most of the time.

VERTEBRATE RESPIRATORY SYSTEMS

Aquatic vertebrates (fish, amphibians, and some reptiles) rely on one, or a combination of, the following surfaces for gas exchange: the cutaneous body surface, external filamentous gills, and internal lamellar gills. **Bimodal breathing** is the ability of an organism to exchange respiratory gases simultaneously with both air and water. A bimodal organism (e.g., some salamanders, crabs, barnacles, bivalve molluscs, and fishes [lungfishes]) uses gills for water breathing and lungs for air breathing. However, some gas exchange is always cutaneous, and some bimodal breathers are actually trimodal (skin, gills, and lungs). *Bimodal breathing was an important respiratory adaptation that made possible the evolutionary transition between aquatic and terrestrial habitats. Fundamental changes in the structure and function of the respiratory organs accompanied the transition from water to air breathing. In air-breathing terrestrial vertebrates (reptiles, birds, and mammals) lungs replaced gills.* These vertebrate surfaces and transitions are now discussed.

CUTANEOUS EXCHANGE

Some vertebrates that have lungs or gills, such as some aquatic turtles, salamanders with lungs, snakes, fishes, and mammals, use **cutaneous respiration** or integumentary exchange to supplement gas exchange. However, cutaneous exchange is most highly developed in frogs, toads, lungless salamanders, and newts.

Amphibian skin has the simplest structure of all the major vertebrate respiratory organs (*see figure 23.6*). In frogs, a uniform capillary network lies in a plane directly beneath the epidermis. This vascular arrangement facilitates gas exchange between the capillary bed and the environment by both diffusion and convection. A slimy mucous layer that keeps amphibian skin moist and protects against injury aids in this gas exchange. Some amphibians obtain about 25% or more of their oxygen by this exchange, and the lungless salamanders carry out all of their gas exchange through the skin and buccal-pharyngeal region.

GILLS

Gills are respiratory organs that have either a thin, moist, vascularized layer of epidermis to permit gas exchange across thin gill membranes, or a very thin layer of epidermis over highly vascularized dermis. Larval forms of a few fishes and amphibians have

FIGURE 26.15

Vertebrate Respiration: External Gills. This axolotl (*Ambystoma tigrinum*) has elaborate external gills with a large surface for gas exchange with the water.

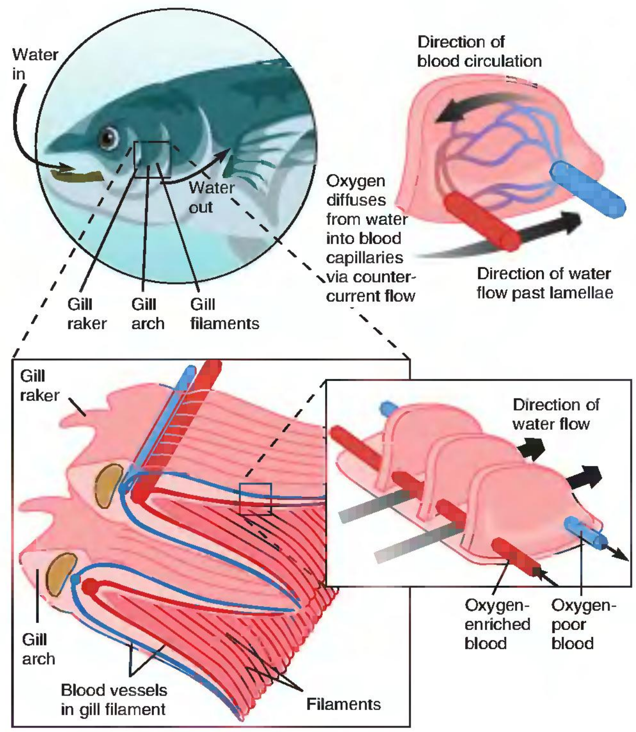

FIGURE 26.16

Vertebrate Respiration: Internal Gills. Removing the protective operculum exposes the feathery internal gills of this bony fish. Each side of the head has four gill arches, and each arch consists of many filaments. A filament houses capillaries within lamellae. Note that the direction of water flow opposes that of blood flow. This countercurrent flow allows the fish to extract the maximal amount of oxygen from the water.

external gills projecting from their bodies (figure 26.15). Adult fishes have internal gills.

Gas exchange across internal gill surfaces is extremely efficient (figure 26.16). It occurs as blood and water move in opposite directions on either side of the lamellar epithelium. For example, the water that passes over a gill first encounters vessels that are transporting blood with a low oxygen concentration into the body. Because the concentration (partial pressure) of the oxygen is lower in the blood than in the water, oxygen diffuses into the blood. Water then passes over the vessels carrying blood relatively high in oxygen from deep within the body. More oxygen diffuses inward because this blood still has less oxygen than the surrounding water. Carbon dioxide also diffuses into the water because its concentration (pressure) is higher in the blood than in the water. This countercurrent exchange mechanism provides efficient gas exchange by maintaining a concentration gradient between the blood and water over the length of the capillary bed.

LUNGS

A **lung** is an internal sac-shaped respiratory organ. The typical lung of a terrestrial vertebrate comprises one or more internal blind pouches into which air is either drawn or forced. The respiratory epithelium of lungs is thin, well vascularized, and divided into a large number of small units, which greatly increase the surface area for gaseous exchange between the lung air and the blood. This blind-pouch construction, however, limits the efficiency with which oxygen and carbon dioxide are exchanged with the atmosphere because only a portion of the lung air is ever replaced with any one breath. Birds are an exception in that they have very efficient lungs with a one-way pass-through system (*see figure 21.10*). For example, a mammal removes approximately 25% of the oxygen from air with each breath, whereas a bird removes approximately 90%.

The evolution of the vertebrate lung is related to the evolution of the swim bladder. The swim bladder is an air sac located dorsal to the digestive tract in the body of many modern fishes. Evidence indicates that both lungs and swim bladders evolved from a lunglike structure present in primitive fishes that were ancestors of both present-day fishes and tetrapods (amphibians, reptiles, birds, and mammals). These ancestral fishes probably had a ventral sac attached to their pharynx (*see figure 18.17*). This sac may have served as a supplementary gas-exchange organ when the fishes could not obtain enough oxygen through their gills (e.g., in stagnant or oxygen-depleted water). By swimming to the surface and gulping air into this sac, ancestral fishes could exchange gas through its wall.

Further evolution of this blind sac proceeded in two different directions (see figure 18.17). One adaptation is in the majority of modern bony fishes, where the swim bladder lies dorsal to the digestive tract. The other adaptation is in the form of the lungs, which are ventral to the digestive tract. A few

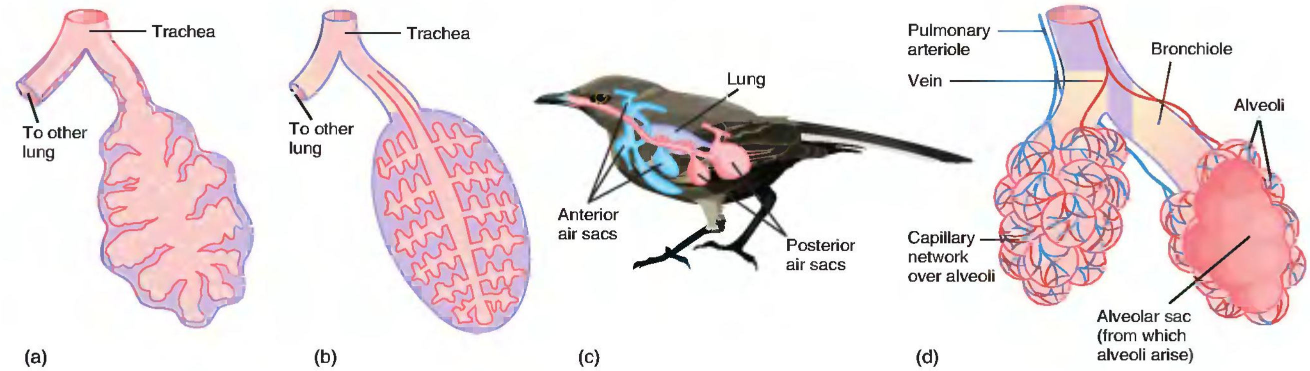

FIGURE 26.17

Vertebrate Respiration: Lungs. Evolution of the vertebrate lung, showing the increased surface area from *(a)* amphibians and *(b)* reptiles to *(c)* birds and *(d)* mammals. This evolution has paralleled the evolution of larger body size and higher metabolic rates.

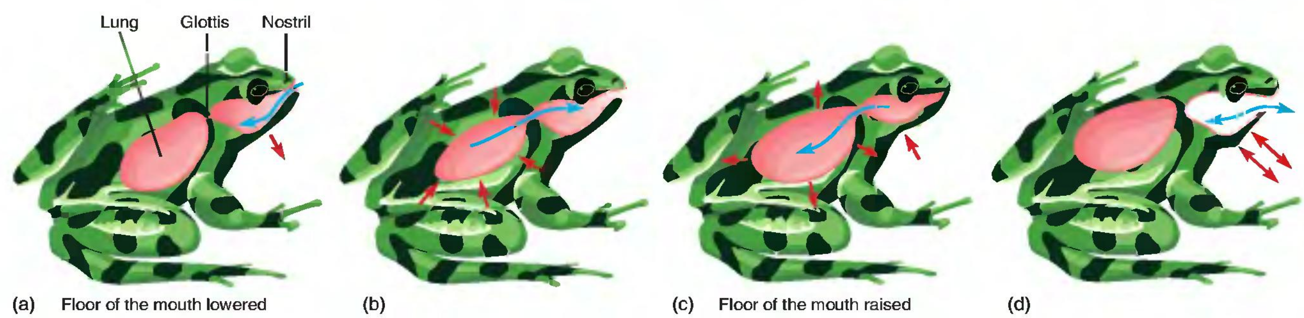

FIGURE 26.18

Ventilation in Amphibians. The positive pressure pumping mechanism in a frog *(Rana)*. The breathing cycle has several stages. *(a)* Air is taken into the mouth and pharynx by lowering the floor of the mouth. Notice that the glottis is closed. *(b)* The glottis is then opened, and air is permitted to escape from the lungs, passing over the air just taken in. *(c)* With the nostrils and mouth firmly shut, the floor of the mouth is raised. This positive pressure forces air into the lungs. *(d)* With the glottis closed, fresh oxygenated air can again be brought into the mouth and pharynx. Some gas exchange occurs in the mouth cavity (buccopharyngeal respiration), and frogs may repeat this "mouth breathing" movement several times before ventilating the lungs again. Red arrows indicate body wall movement, and blue arrows indicate air flow.

present-day fishes and the tetrapods have ventral lungs. The evolution of the structurally complex lung paralleled the evolution of the larger body sizes and higher metabolic rates of endothermic vertebrates (birds and mammals), which necessitated an increase in lung surface area for gas exchange, compared to the smaller body size and lower metabolic rates of ectothermic vertebrates (figure 26.17).

LUNG VENTILATION

Ventilation is based on several physiological principles that apply to all air-breathing animals with lungs:

1. Air moves by bulk flow into and out of the lungs in the process called ventilation.
2. Oxygen and carbon dioxide diffuse across the respiratory surface of the lung tissue from pulmonary capillaries.
3. At systemic capillaries, oxygen and carbon dioxide diffuse between the blood and interstitial fluid in response to concentration gradients.
4. Oxygen and carbon dioxide diffuse between the interstitial fluid and body cells.

Vertebrates exhibit two different mechanisms for lung ventilation based on these physiological principles. Amphibians and some reptiles use a positive pressure pumping mechanism. They push air into their lungs. Most reptiles and all birds and mammals, however, use a negative pressure system; that is, they inhale (breathe in) by suction.

Figure 26.18 shows the positive pressure pumping mechanism of an amphibian. The muscles of the mouth and pharynx create a positive pressure to force air into the lungs.

Most reptiles (e.g., snakes, lizards, crocodilians) expand the body cavity with a posterior movement of the ribs to ventilate the lungs. This expansion decreases pressure in the lungs and draws air

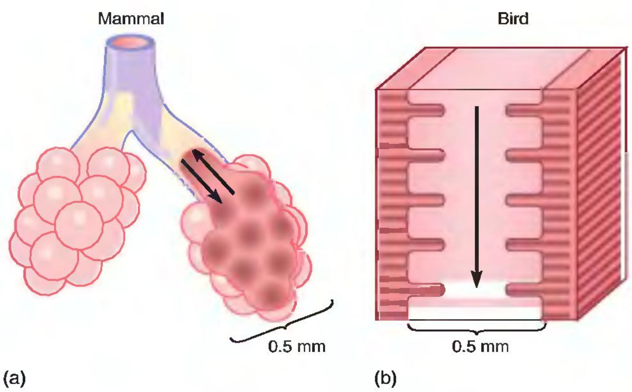

FIGURE 26.19

Gas Exchange Surfaces in Mammals and Birds. *(a)* The gas exchange surfaces in a mammal's lung are in saclike alveoli. Ventilation is by an ebb-and-flow mechanism (arrows), and the air inside the alveoli can never be completely replaced. *(b)* The smallest diameter passages in a bird lung are tubes that are open at both ends. Ventilation is by one-way flow (arrow), and complete replacement of air in the tubes is continuous.

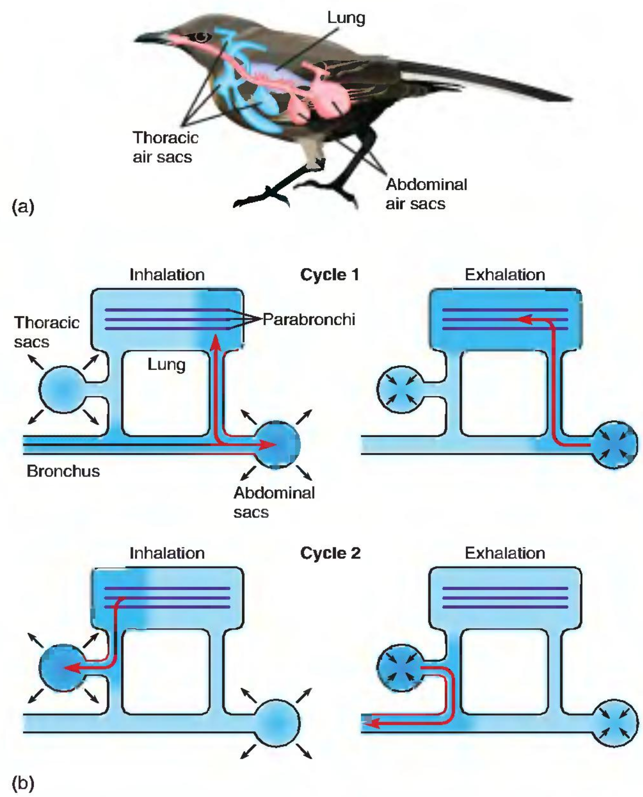

FIGURE 26.20

Gas Exchange Mechanism in Birds. *(a)* Birds have a number of large air sacs. Some of them (abdominal) are posterior to the small pair of lungs, and others (thoracic) are anterior to the lungs. The main bronchus (air passageway) that runs through each lung has connections to air sacs, as well as to the lung. In *(b)*, abdominal and thoracic air sacs are sketched as single functional units to clarify their relationship to the lung and bronchus. *(b)* Air flow through the bird respiratory system. The darker blue portion in each diagram represents the volume of a single inhalation and distinguishes it from the remainder of the air in the system. Two full breathing cycles are needed to move the volume of gas taken in during a single inhalation through the entire system and out of the body. This system is associated with one-way flow through the gas exchange surfaces in the lungs. Black arrows indicate expansion and contraction of air sacs. Red arrows indicate movement of air.

into the lungs. Elastic recoil of the lungs and the movement of the ribs and body wall, which compress the lungs, expel air. The ribs of turtles are a part of the shell *(see figure 20.5)*; thus, movements of the body wall to which they attach are impossible. Turtles exhale by contracting muscles that force the viscera upward, compressing the lungs. They inhale by contracting muscles that increase the volume of the visceral cavity, creating negative pressure to draw air into the lungs.

Because of the high metabolic rates associated with flight, birds have a greater rate of oxygen consumption than any other vertebrate. Birds also use a negative pressure system to move air into and out of their lungs in an ebb and flow breathing pattern similar to mammals. However, birds also have a special lung ventilation mechanism that permits one-way flow over gas exchange surfaces. This mechanism makes bird lungs more efficient than mammalian lungs (figure 26.19). This is also why bird lungs are smaller than the lungs of mammals of comparable body size. Bird lungs have tunnel-like passages called parabronchi, which lead to air capillaries in which gas exchange occurs. The arrangement and functioning of a system of air sacs make one-way flow possible. These air sacs ramify throughout the body cavity, are collapsible, and open and close as a result of muscle contractions around them. Inhaled air bypasses the lungs and enters the abdominal (posterior) air sacs. It then passes through the lungs into the thoracic (anterior) air sacs. Finally, air is exhaled from the thoracic air sacs. This whole process requires two complete breathing cycles (figure 26.20).

HUMAN RESPIRATORY SYSTEM

The structure and function of external respiration in humans are typical of mammals. Thus the human respiratory system is used here to describe those principles that apply to all air-breathing mammals.

Air-Conducting Portion

Figure 26.21 shows the various organs of the human respiratory system. Air normally enters and leaves this system through either nasal or oral cavities. From these cavities, air moves into the pharynx, which is a common area for both the respiratory and digestive tracts. The pharynx connects with the larynx (voice box) and with the esophagus that leads to the stomach. The epiglottis is a flap of cartilage that allows air to enter the trachea during breathing. It covers the trachea during swallowing to prevent food or water from entering.

During inhalation, air from the larynx moves into the trachea (windpipe), which branches into a right and left bronchus (pl.,

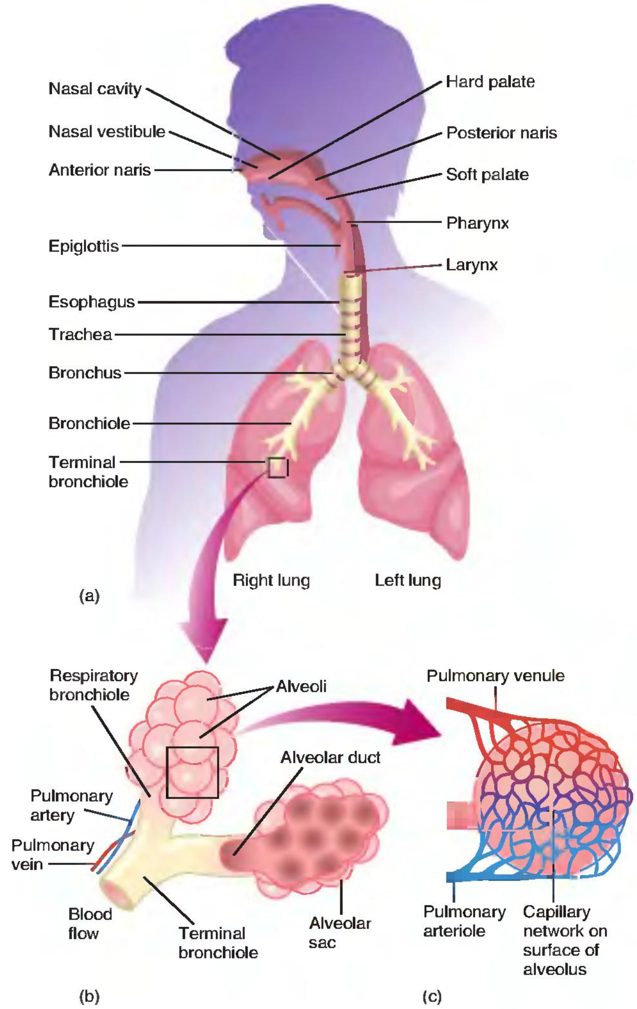

FIGURE 26.21

Organs of the Human Respiratory System. *(a)* Basic anatomy of the respiratory system. *(b,c)* The respiratory tubes end in minute alveoli, each of which is surrounded by an extensive capillary network.

bronchi). After each bronchus enters the lungs, it branches into smaller tubes called bronchioles, then even smaller tubes called terminal bronchioles, and finally, the respiratory bronchioles, which are part of the gas-exchange portion of the respiratory system.

Gas-Exchange Portion

Small tubes called alveolar ducts connect the respiratory bronchioles to grapelike outpouchings called **alveoli** (sing., alveolus) (L. *alveus*, hollow) (figure 26.21*b*). The alveoli cluster to form an alveolar sac. Surrounding the alveoli are many capillaries (figure 26.21*c*). Alveoli are the functional units of the lungs (gas-exchange portion). Passive diffusion, driven by a partial pressure gradient, moves oxygen from the alveoli into the blood and moves carbon dioxide from the blood into the alveoli (figure 26.22).

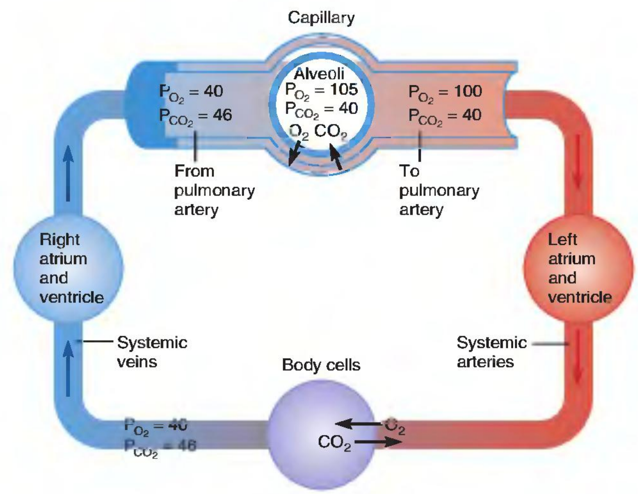

FIGURE 26.22

Gas Exchange between the Lungs and Tissues. Gases diffuse according to partial pressure (P) differences, as the numbers and arrows indicate.

Collectively, the alveoli provide a large surface area for gas exchange. If the alveolar epithelium of a human were removed from the lungs and put into a single layer of cells side by side, the cells would cover the area of a tennis court.

Ventilation

Breathing (also called pulmonary ventilation) has two phases: (1) inhalation, the intake of air; and (2) exhalation, the outflow of air. These air movements result from the rhythmic increases and decreases in thoracic cavity volume. Changes in thoracic volume lead to reversals in the pressure gradients between the lungs and the atmosphere; gases in the respiratory system follow these gradients. The mechanism of inhalation operates in the following way (figure 26.23):

1. Several sets of muscles, the main ones being the diaphragm and intercostal muscles, contract. The intercostal muscles stretch from rib to rib, and when they contract, they pull the ribs closer together, enlarging the thoracic cavity.
2. The thoracic cavity further enlarges when the diaphragm contracts and flattens.
3. The increased size of the thoracic cavity causes pressure in the cavity to drop below the atmospheric pressure. Air rushes into the lungs, and the lungs inflate.

During ordinary exhalation, air is expelled from the lungs in the following way:

1. The intercostal muscles and the diaphragm relax, allowing the thoracic cavity to return to its original, smaller size and increasing the pressure in the thoracic cavity.
2. Abdominal muscles contract, pushing the abdominal organs against the diaphragm, further increasing the pressure within the thoracic cavity.

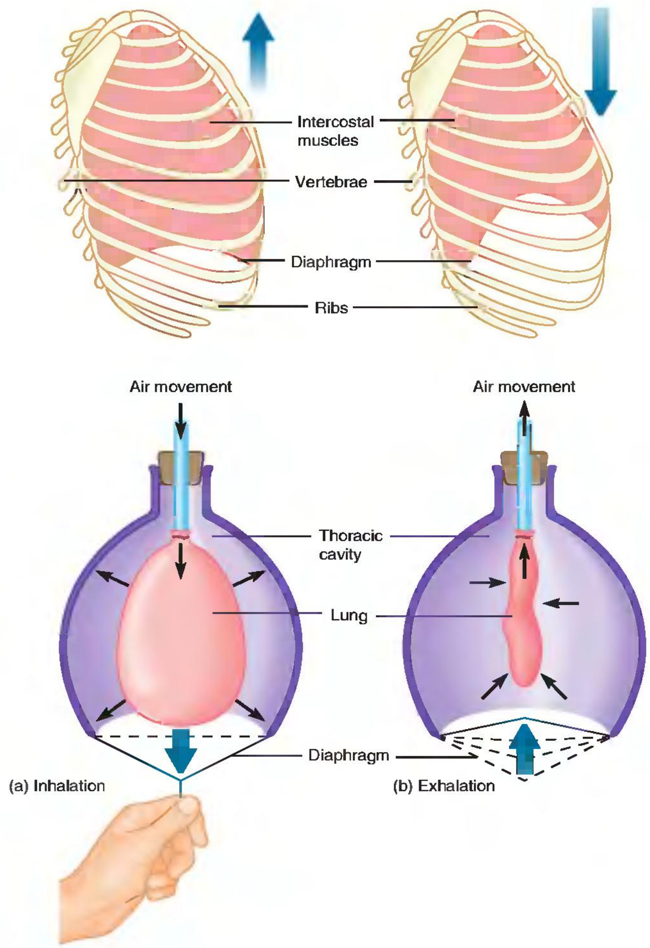

FIGURE 26.23

Ventilation of Human Lungs as an Example of Breathing in Mammals. *(a)* During inhalation, muscle contractions lift the ribs up and out (upper diagram arrows) and lower the diaphragm. These movements increase the size of the thoracic cavity and decrease the pressure around the lungs. This negative pressure causes more air to enter the lungs. *(b)* Exhalation follows the relaxation of the rib cage and diaphragm muscles, as the increased pressure forces the air out of the lungs. Arrows indicate the direction pressure changes take in the thoracic (lower diagrams) cavity during inhalation and exhalation.

3. The action in step 2 causes the elastic lungs to contract and compress the air in the alveoli. With this compression, alveolar pressure becomes greater than atmospheric pressure, causing air to be expelled (exhaled) from the lungs.

GAS TRANSPORT

As noted in the previous discussion, oxygen must be transported from the sites of environmental gas exchange to the cells of an animal's body. Various systems (e.g., tracheae, cutaneous exchange, gills, lungs) help accomplish this transport.

As animals became larger and acquired higher metabolic rates, simple diffusion became increasingly inadequate as a means of delivering oxygen to the tissues. Consequently, in most animals with high metabolic rates and tissues more than a few millimeters from respiratory surfaces, a specialized circulatory system circulates body fluids to aid in the internal distribution of oxygen (*see figure 26.1*). In general, more active animals have an increased demand for oxygen. However, simply creating a convection of a water-based body fluid does not in itself guarantee internal transport of sufficient oxygen to meet this increased demand. The reason is the low solubility of oxygen in water-based body fluids. *Thus, fluid-borne respiratory pigments specialized for reversibly binding large quantities of oxygen evolved in most phyla.* Respiratory pigments help the various transport systems satisfy this increased oxygen demand. In addition to oxygen transport, respiratory pigments may also function in short-term oxygen storage.

Respiratory pigments are organic compounds that have either metallic copper or iron that binds oxygen. These pigments may be in solution within the blood or body fluids, or they may be in specific blood cells. In general, the pigments respond to a high oxygen concentration by combining with oxygen and to low oxygen concentrations by releasing oxygen. The four most common respiratory pigments are hemoglobin, hemocyanin, hemerythrin, and chlorocruorin.

Hemoglobin is a reddish pigment that contains iron as the oxygen-binding metal. It is the most common respiratory pigment in animals, being found in a variety of invertebrates (e.g., protozoa, platyhelminths, nemerteans, nematodes, annelids, crustaceans, some insects, and molluscs), and with the exception of a few fishes, in all vertebrates. *This wide distribution suggests that hemoglobin evolved very early in the history of animal life.* Hemoglobin may be carried within red blood cells (erythrocytes; *see figure* 26.5a) or simply dissolved in the blood or coelomic fluid.

Hemocyanin is the most commonly occurring respiratory pigment in molluscs and certain crustaceans. Hemocyanin contains metallic copper, has a bluish color when oxygenated, and always occurs dissolved in hemolymph. Unlike most hemoglobin, hemocyanin tends to release oxygen easily and to provide a ready source of oxygen to the tissues as long as concentrations of oxygen in the environment are relatively high.

Hemerythrin contains iron and is pink when oxygenated. It is in nucleated cells, rather than free in body fluids or hemolymph. Sipunculans, priapulids, a few brachiopods, and some polychaetes have hemerythrin.

Chlorocruorin also contains iron but is green when associated with low oxygen concentrations and bright red when associated with high oxygen concentrations. Chlorocruorin occurs in several families of polychaete worms.

As just discussed, respiratory pigments raise the oxygen-carrying capacity of body fluids far above what simple transport in a dissolved state would achieve. Similarly, carbon dioxide concentrations in animal body fluids (and in seawater as well) are much higher than would be expected strictly on the basis of its solubility. The reason for this increased transport is that, in addition to being transported bound to hemoglobin and in the dissolved state,