

CHAPTER 26

CIRCULATION AND GAS EXCHANGE

Outline

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Lungs

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Concepts

1. Animal transport and circulatory systems move substances from one part of the body to another, and between the animal's external environment and extracellular fluid.
2. Some invertebrates have specific transport systems, such as gastrovascular cavities. The circulatory system of more complex animals consists of a central pumping heart, blood vessels, blood, and an ancillary lymphatic system.
3. Some invertebrates depend solely on gases, nutrients, and wastes diffusing between body surfaces and individual cells. Others have either open or closed circulatory systems for transporting gases, wastes, and nutrients.
4. Animals have five main types of respiratory systems: simple diffusion across plasma membranes, tracheae, cutaneous (integument or body surface) exchange, gills, and lungs.
5. Gas diffuses between the environment and cells of an animal's body from areas of higher concentration to areas of lower concentration. In large and active animals, respiratory pigments and ventilation—the active movement of air into and out of a respiratory system—increase gas exchange.

INTERNAL TRANSPORT AND
CIRCULATORY SYSTEMS

All animals must maintain a homeostatic balance in their bodies. This need requires that nutrients, metabolic wastes, and respiratory gases be circulated through the animal's body. Any system of moving fluids that reduces the functional diffusion distance that nutrients, wastes, and gases must traverse is an internal transport or circulatory system. The nature of the system directly relates to the size, complexity, and lifestyle of the animal in question. The first part of this chapter discusses some of these transport and circulatory systems.

TRANSPORT SYSTEMS IN INVERTEBRATES

Because protozoa are small, with high surface-area-to-volume ratios (see figure 2.3), all they need for gas, nutrient, and waste exchange is simple diffusion. In protozoa, the plasma membrane and cytoplasm are the media through which materials diffuse to various parts of the organism, or between the organism and the environment (see figure 26.11a).

Some invertebrates have evolved specific transport systems. For example, sponges circulate water from the external environment through their bodies, instead of circulating an internal fluid (figure 26.1a). Cnidarians, such as *Hydra*, have a fluid-filled internal

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

gastrovascular cavity (figure 26.1b). This cavity supplies nutrients for all body cells lining the cavity, provides oxygen from the water in the cavity, and is a reservoir for carbon dioxide and other wastes. Simple body movement moves the fluid.

The gastrovascular cavity of flatworms, such as the planarian *Dugesia*, is more complex than that of *Hydra*. In the planarian, branches penetrate to all parts of the body (figure 26.1c). Because this branched gastrovascular cavity runs close to all body cells, diffusion distances for nutrients, gases, and wastes are short. Body movement helps distribute materials to various parts of the body. One disadvantage of this system is that it limits these animals to relatively small sizes or to shapes that maintain small diffusion distances.

Pseudocoelomate invertebrates, such as rotifers, gastrotrichs, and nematodes, use the coelomic fluid of their body cavity for transport (figure 26.1d). Most of these animals are small, and movements of the body against the coelomic fluids, which are in direct contact with the internal tissues and organs, produce adequate transport. A few other invertebrates (e.g., ectoprocts, sipunculans, echinoderms) also depend largely on the body cavity as a coelomic transport chamber.

Beginning with the molluscs, transport functions occur with a separate circulatory system. A **circulatory or cardiovascular system** (Gr. *kardia*, heart + L. *vascular*, vessel) is a specialized system in which a muscular, pumping heart moves the fluid medium called either hemolymph or blood in a specific direction determined by the presence of unidirectional blood vessels.

The animal kingdom has two basic types of circulatory systems: open and closed. In an **open circulatory system**, the heart pumps hemolymph out into the body cavity or at least through parts of the cavity, where the hemolymph bathes the cells, tissues, and organs. In a **closed circulatory system**, blood circulates in the confines of tubular vessels. The coelomic fluid of some invertebrates also has a circulatory role either in concert with, or instead of, the hemolymph or blood.

The annelids, such as the earthworm, have a closed circulatory system in which blood travels through vessels delivering nutrients to cells and removing wastes (figure 26.1e).

Most molluscs and arthropods have open circulatory systems in which hemolymph directly bathes the cells and tissues rather than being carried only in vessels (figure 26.1f). For example, an insect's heart pumps hemolymph through vessels that open into a body cavity (hemocoel).

CHARACTERISTICS OF INVERTEBRATE COELOMIC FLUID, HEMOLYMPH, AND BLOOD CELLS

As previously noted, some animals (e.g., echinoderms, annelids, sipunculans) use coelomic fluid as a supplementary or sole circulatory system. Coelomic fluid may be identical in composition to interstitial fluids or may differ, particularly with respect to specific proteins and cells. Coelomic fluid transports gases, nutrients, and waste products. It also may function in certain invertebrates (annelids) as a hydrostatic skeleton (see figure 23.10).

Hemolymph (Gr. *haima*, blood + *lymph*, water) is the circulating fluid of animals with an open circulatory system. Most arthropods, ascidians, and many molluscs have hemolymph. In these animals, a heart pumps hemolymph at low pressures through vessels to tissue spaces (hemocoel) and sinuses. Generally, the hemolymph volume is high and the circulation slow. In the process of movement, essential gases, nutrients, and wastes are transported.

Many times, hemolymph has noncirculatory functions. For example, in insects, hemolymph pressure assists in molting of the old cuticle and in inflation of the wings. In certain jumping spiders, hydrostatic pressure of the hemolymph provides a hydraulic mechanism for limb extension.

The coelomic fluid, hemolymph, or blood of most animals contains circulating cells called **blood cells** or **hemocytes**. Some cells contain a respiratory pigment, such as hemoglobin, and are called erythrocytes or red blood cells. These cells are usually present in high numbers to facilitate oxygen transport. Cells that do not contain respiratory pigments have other functions, such as blood clotting.

The number and types of blood cells vary dramatically in different invertebrates. For example, annelid blood contains hemocytes that are phagocytic. The coelomic fluid contains a variety of coelomocytes (amoebocytes, eleocytes, lampocytes, linocytes) that function in phagocytosis, glycogen storage, encapsulation, defense responses, and excretion. The hemolymph of molluscs has two general types of hemocytes (amoebocytes and granulocytes) that have most of the aforementioned functions as well as nacreation (pearl formation) in some bivalves. Insect hemolymph contains large numbers of various hemocyte types that function in phagocytosis, encapsulation, and clotting (figure 26.2).

TRANSPORT SYSTEMS IN VERTEBRATES

All vertebrates have a closed circulatory system in which the walls of the heart and blood vessels are continuously contracted, and blood never leaves the blood vessels (figure 26.1g). Blood moves from the heart, through arteries, arterioles, capillaries, venules, veins, and back to the heart. Exchange between the blood and extracellular fluid only occurs at the capillary level.

CHARACTERISTICS OF VERTEBRATE BLOOD AND BLOOD CELLS

Overall, vertebrate blood transports oxygen, carbon dioxide, and nutrients; defends against harmful microorganisms, cells, and viruses; prevents blood loss through coagulation (clotting); and helps regulate body temperature and pH. Because it is a liquid, vertebrate blood is classified as a specialized type of connective tissue. Like other connective tissues, blood contains a fluid matrix called plasma and cellular elements called formed elements.

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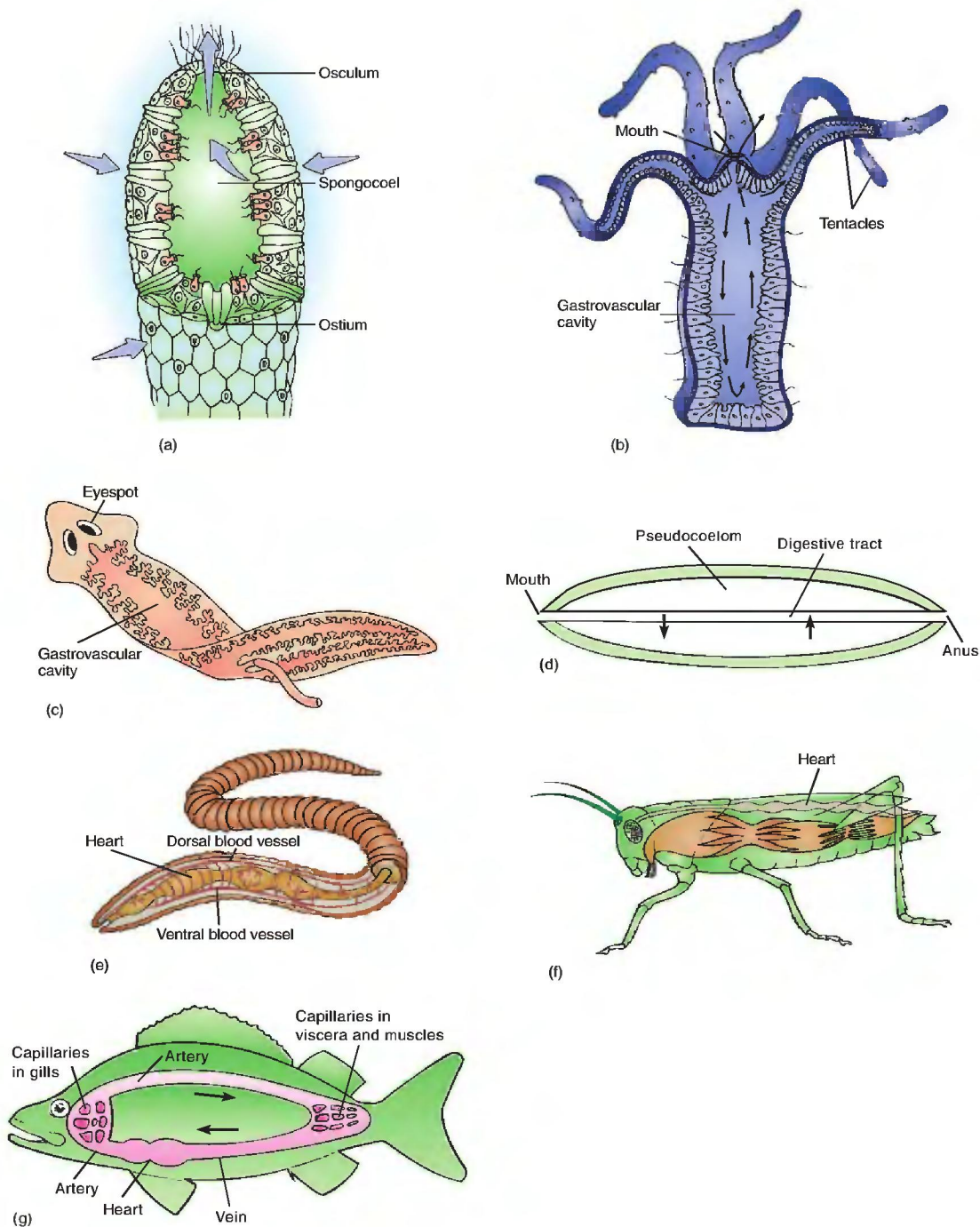


FIGURE 26.1

Some Transport and Circulatory Systems. (a) Sponges use water from the environment as a circulatory fluid by passing it through their bodies (blue arrows). (b) Cnidarians, such as this *Hydra*, also use water from the environment and circulate it (black arrows) through the gastrovascular cavity. Cells lining the cavity exchange gases and nutrients from the water and release waste into it. (c) The planarian's gastrovascular cavity is branched, allowing for more effective distribution of materials. (d) Pseudocoelomates use their body cavity fluid for internal transport from and to the digestive tract as the black arrows indicate. (e) The circulatory system of an earthworm contains blood that is kept separate from the coelomic fluid. This is an example of a closed circulatory system. (f) The dorsal heart of an arthropod, such as this grasshopper, pumps blood through an open circulatory system. In this example, blood and body cavity (hemocoelic) fluid are one and the same. (g) Octopuses, other cephalopod molluscs, annelids, and vertebrates, such as this fish, have closed circulatory systems. In a closed system, the walls of the heart and blood vessels are continuously connected, and blood never leaves the vessels. Black arrows indicate the direction of blood flow.

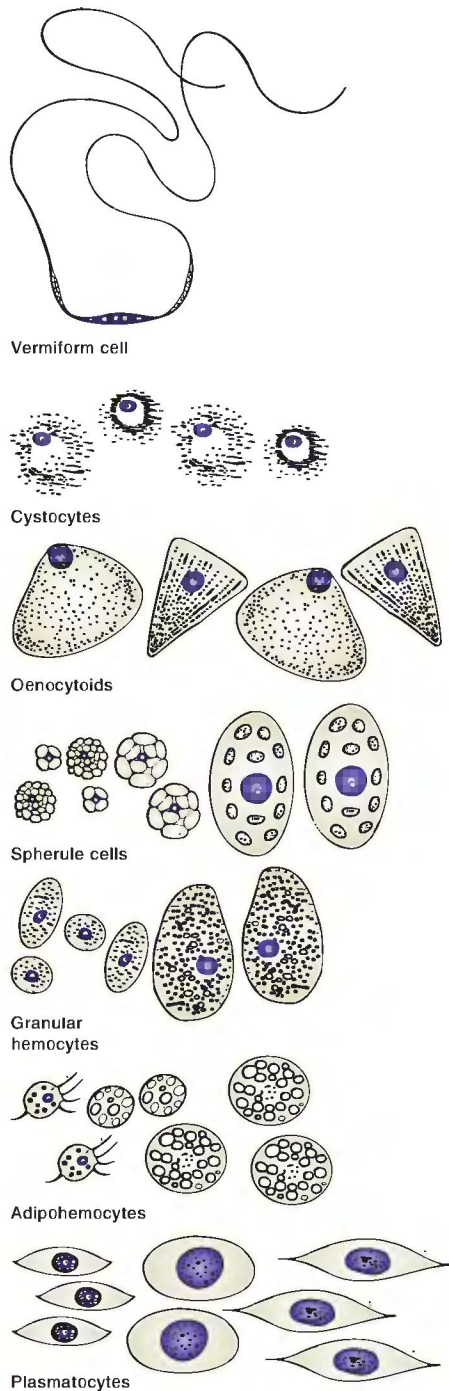


FIGURE 26.2

Examples of Invertebrate Hemocytes. These hemocytes are representative of those found in an insect. The different cells function in phagocytosis, agglutination, nutrient storage, wound repair, formation of connective tissue cells, and lipid transport.

Plasma

Plasma (Gr., anything formed or molded) is the straw-colored, liquid part of blood. In mammals, plasma is about 90% water and provides the solvent for dissolving and transporting nutrients. A group of proteins (albumin, fibrinogen, and globulins) comprises another 7% of the plasma. The concentration of these plasma proteins influences the distribution of water between the blood and extracellular fluid. Because albumin represents about 60% of the total plasma proteins, it plays important roles with respect to water movement. Fibrinogen is necessary for blood coagulation (clotting), and the globulins include the immunoglobulins and various metal-binding proteins. **Serum** is plasma from which the proteins involved in blood clotting have been removed. The gamma globulin portion functions in the immune response because it consists mostly of antibodies. The remaining 3% of plasma is composed of electrolytes, amino acids, glucose and other nutrients, various enzymes, hormones, metabolic wastes, and traces of many inorganic and organic molecules.

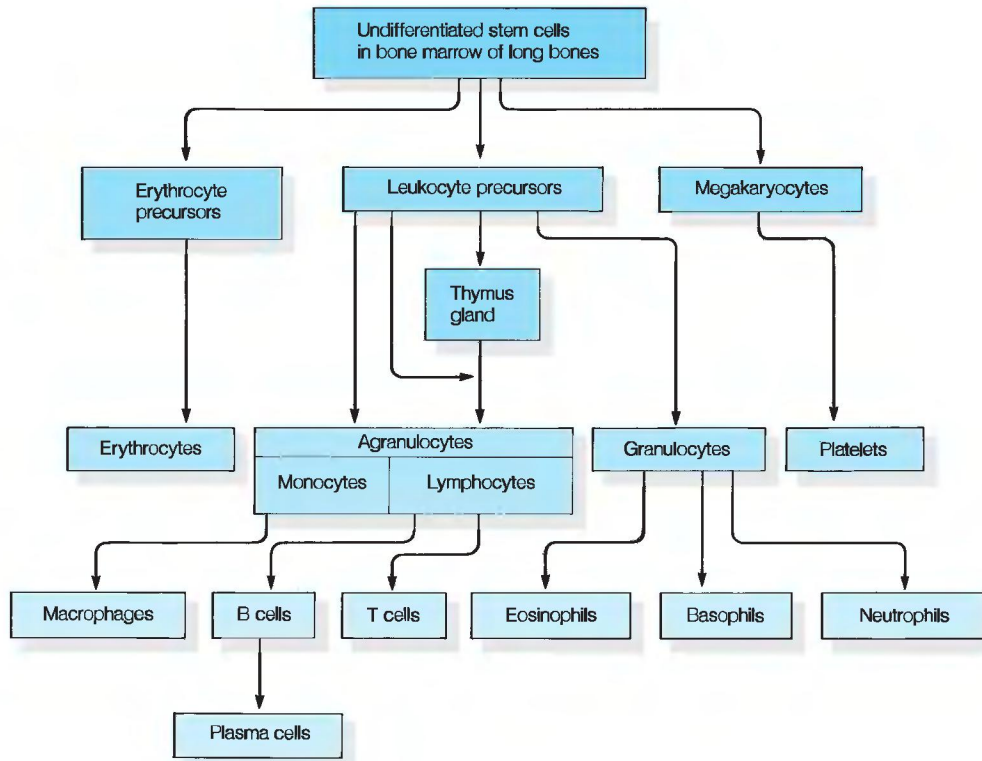
Formed Elements

The **formed-element fraction** (cellular component) of vertebrate blood consists of erythrocytes (red blood cells; RBCs), leukocytes (white blood cells; WBCs), and platelets (thrombocytes) (figure 26.3). White blood cells are present in lower number than are red blood cells, generally being 1 to 2% of the blood by volume. White blood cells are divided into agranulocytes (without granules in the cytoplasm) and granulocytes (have granules in the cytoplasm). The two types of agranulocytes are lymphocytes and monocytes. The three types of granulocytes are eosinophils, basophils, and neutrophils. Fragmented cells are called platelets (thrombocytes). Each of these cell types is now discussed in more detail.

Red Blood Cells Red blood cells (erythrocytes; Gr. *erythros*, red + cells) vary dramatically in size, shape, and number in the different vertebrates (figures 26.4 and 26.5a). For example, the RBCs of most vertebrates are nucleated, but mammalian RBCs are enucleated (without a nucleus). Some fishes and amphibians also have enucleated RBCs. Among all vertebrates, the salamander *Amphiuma* has the largest RBC (figure 26.4a). Avian RBCs (figure 26.4c) are oval-shaped, nucleated, and larger than mammalian RBCs. Among birds, the ostrich has the largest RBC. Most mammalian RBCs are biconcave disks (figure 26.5a); however, the camel (figure 26.4e) and llama have elliptical RBCs. The shape of a biconcave disk provides a larger surface area for gas diffusion than a flat disk or sphere. Generally, the lower vertebrates tend to have fewer but larger RBCs than the higher invertebrates.

Almost the entire mass of a RBC consists of **hemoglobin** (Gr. *haima*, blood + L. *globulus*, little globe), an iron-containing protein. The major function of an erythrocyte is to pick up oxygen from the environment, bind it to hemoglobin to form **oxyhemoglobin**, and transport it to body tissues. Blood rich in oxyhemoglobin is bright red. As oxygen diffuses into the tissues, blood becomes darker and appears blue when observed through the blood vessel walls. However, when this less oxygenated blood is exposed to

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**FIGURE 26.3**

Cellular Components of Vertebrate Blood. Hematopoiesis is the process of blood cell production. Notice that all blood cells initially begin their lives in the bone marrow of long bones within a vertebrate's body.

oxygen (such as when a vein is cut and a mammal begins to bleed), it instantaneously turns bright red. Hemoglobin also carries waste carbon dioxide (in the form of **carbaminohemoglobin**) from the tissues to the lungs (or gills) for removal from the body.

White Blood Cells White blood cells (leukocytes) (Gr. *leukos*, white + cells) are scavengers that destroy microorganisms at infection sites, remove foreign chemicals, and remove debris that results from dead or injured cells. All WBCs are derived from immature cells (called stem cells) in bone marrow by a process called **hematopoiesis** (Gr. *hemato*, blood + *poiesis*, to make; see figure 26.3).

Among the granulocytes, **eosinophils** are phagocytic, and ingest foreign proteins and immune complexes rather than bacteria (figure 26.5b). In mammals, eosinophils also release chemicals that counteract the effects of certain inflammatory chemicals released during allergic reactions. **Basophils** are the least numerous WBC (figure 26.5c). When they react with a foreign substance, their granules release histamine and heparin. Histamine causes blood vessels to dilate and leak fluid at a site of inflammation, and heparin prevents blood clotting. **Neutrophils** are the most numerous of the white blood cells (figure 26.5d). They are chemically attracted to sites of inflammation and are active phagocytes.

The two types of agranulocytes are the **monocytes** and **lymphocytes** (figure 26.5e,f). Two distinct types of lymphocytes are B cells and T cells, both of which are central to the immune response. **B cells** originate in the bone marrow and colonize the lymphoid tissue, where they mature. In contrast, **T cells** are associated with and influenced by the thymus gland before they colonize lymphoid tissue and play their role in the immune response. When B cells are activated, they divide and differentiate to produce **plasma cells**.

Platelets (Thrombocytes) **Platelets** (so named because of their platelike flatness), or **thrombocytes** (Gr. *thrombus*, clot + cells), are disk-shaped cell fragments that initiate blood clotting. When a blood vessel is injured, platelets immediately move to the site and clump, attaching themselves to the damaged area, and thereby beginning the process of blood coagulation.

VERTEBRATE BLOOD VESSELS

Arteries are elastic blood vessels that carry blood away from the heart to the organs and tissues of the body. The central canal of an artery (and of all blood vessels) is a lumen. Surrounding the lumen of an artery is a thick wall composed of three layers, or *tunicae* (L. *tunica*, covering) (figure 26.6a).

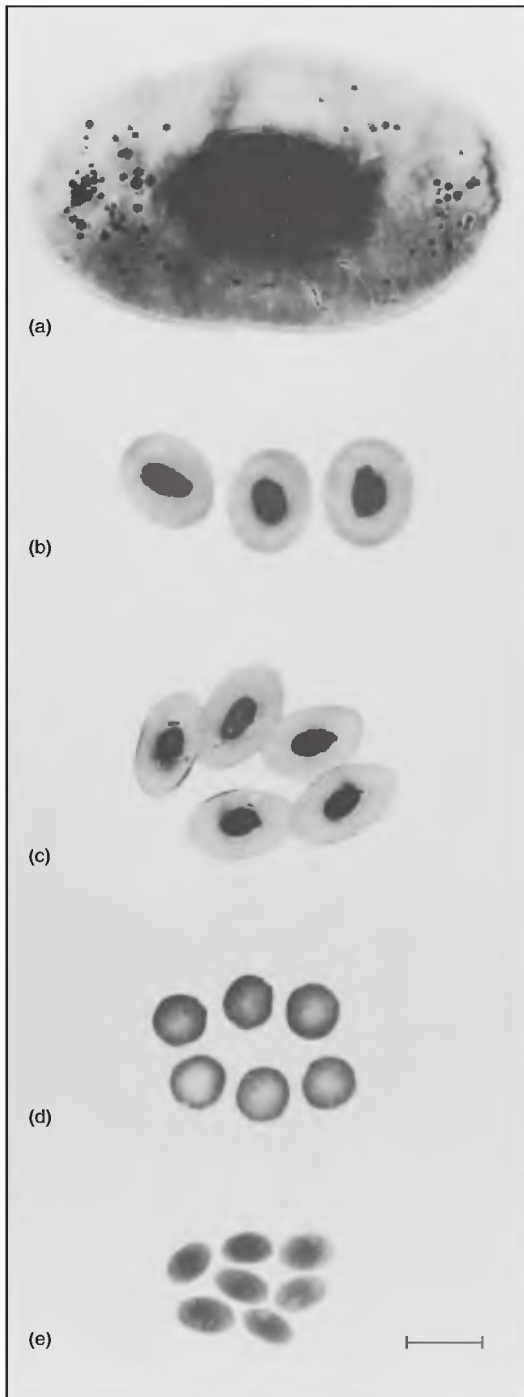


FIGURE 26.4

Comparison of Red Blood Cells from a Variety of Vertebrates. Light micrographs of (a) a nucleated cell from a salamander; (b) nucleated cells from a snake; (c) nucleated cells from an ostrich; (d) enucleated cells (biconcave disk) from a red kangaroo; and (e) enucleated cells (ellipsoid) from a camel (bar = 10 μm).

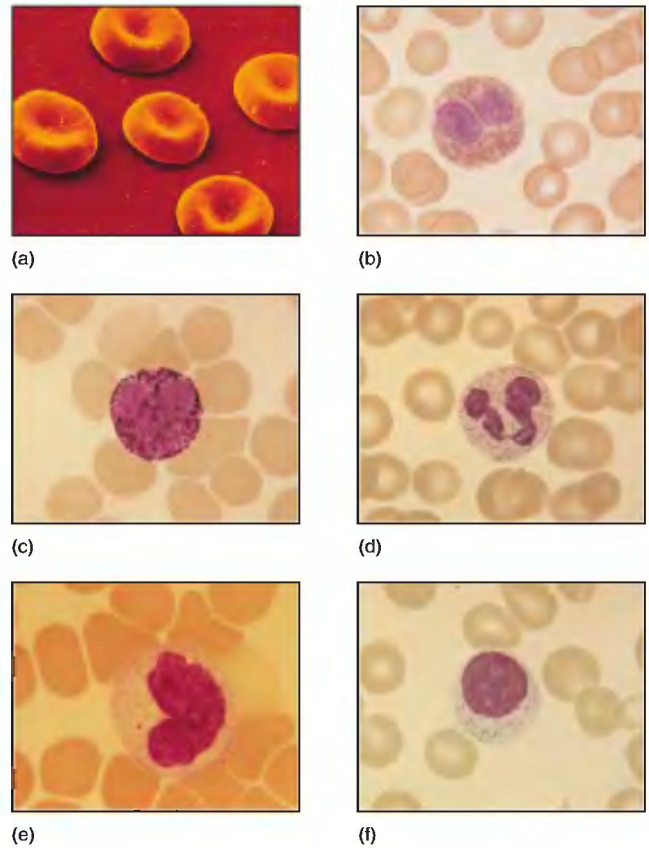


FIGURE 26.5

Blood Cells. (a) The biconcave shape of human erythrocytes (SEM $\times 1,500$). (b) Red-staining cytoplasmic granules characterize an eosinophil. (c) Blue-staining granules characterize a basophil. (d) Light-pink granules and a multilobed nucleus characterize a neutrophil. Cells in b–d are also known as granulocytes. The agranulocytes consist of large monocytes (e) and lymphocytes (f). (b–f are LM $\times 710$.)

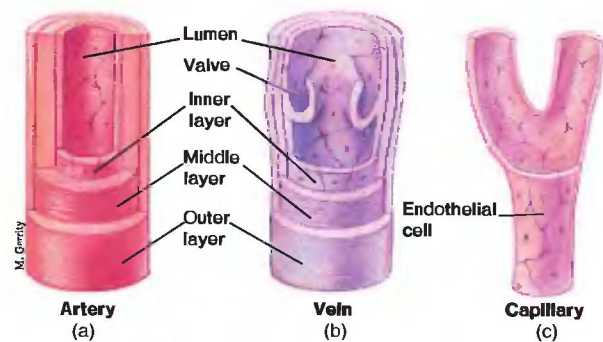
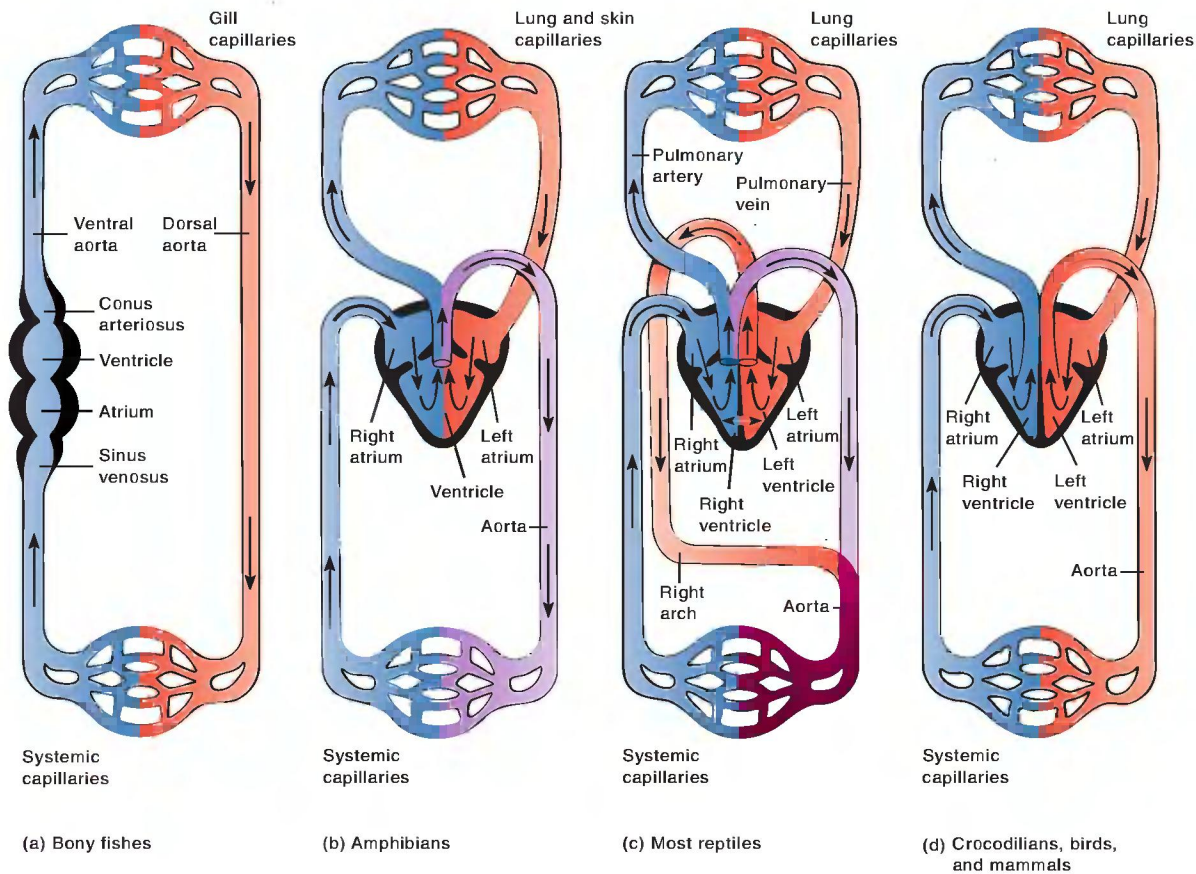


FIGURE 26.6

Structure of Blood Vessels. (a,b) The walls of arteries and veins have three layers (tunicae). The outermost layer consists of connective tissue, the middle layer has elastic and smooth muscle tissue, and the inner layer consists of a single layer of smooth endothelial cells (endothelium). Notice that the wall of an artery is much thicker than the wall of a vein. The middle layer is greatly reduced in a vein. (c) A capillary consists of a single layer of endothelial cells.

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**FIGURE 26.7**

Heart and Circulatory Systems of Various Vertebrates. Oxygenated blood is red; less oxygenated blood is blue; a mixture of oxygenated and less oxygenated blood is purple. (a) In bony fishes, the heart's two chambers (atrium, ventricle) pump in series. Respiratory and systemic circulations are not separate. (b) The amphibian heart has two atria and one ventricle. Blood from the lungs enters the left atrium, and blood from the body enters the right atrium. The blood from both atria empties into one ventricle, which then pumps it into the respiratory and systemic circulations. (c) Most reptiles exhibit a greater degree of anatomical division of the ventricle into two halves. (d) In crocodilians, birds, and mammals, the ventricle is completely divided, forming a four-chambered heart, with the blood flow through the lungs completely separated from the flow to other tissues. Black arrows indicate the direction of blood flow.

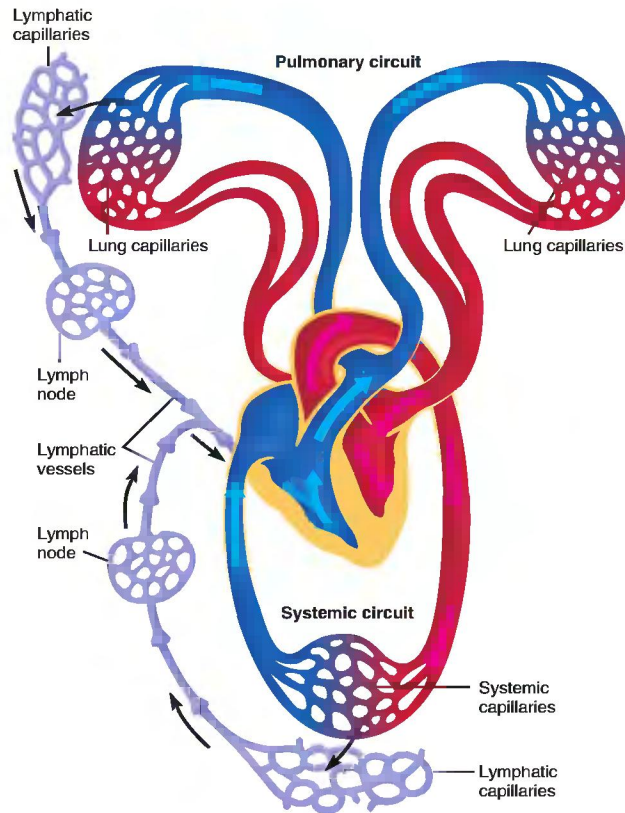
Most **veins** are relatively inelastic, large vessels that carry blood from the body tissues to the heart. The wall of a vein contains the same three layers (tunicae) as arterial walls, but the middle layer is much thinner, and one or more valves are present (figure 26.6b). The valves permit blood flow in only one direction, which is important in returning the blood to the heart.

Arteries lead to terminal **arterioles** (those closest to a capillary). The arterioles branch to form **capillaries** (L. *capillus*, hair), which connect to **venules** and then to veins. Capillaries are generally composed of a single layer of endothelial cells and are the most numerous blood vessels in an animal's body (figure 26.6c). An abundance of capillaries makes an enormous surface area available for the exchange of gases, fluids, nutrients, and wastes between the blood and nearby cells.

THE HEARTS AND CIRCULATORY SYSTEMS OF BONY FISHES, AMPHIBIANS, AND REPTILES

The heart and blood vessels changed greatly as vertebrates moved from water to land and as endothermy evolved. Examples of these trends are now presented.

The bony fish heart has two chambers—the atrium and ventricle (figure 26.7a). Blood leaves the heart via the ventral aorta, which goes to the gills. In the gills, blood becomes oxygenated, loses carbon dioxide, and enters the dorsal aorta. The dorsal aorta distributes blood to all of the body organs, and then blood returns to the heart via the venous system. Because blood only passes through the heart once, this system is called a single circulation

**FIGURE 26.8**

Circulatory Circuits. The cardiovascular system of a bird or mammal has two major capillary beds and transport circuits: the pulmonary circuit and systemic circuit. The lymphatic system consists of one-way vessels that are also involved in returning tissue fluid, called lymph, to the heart. The black arrows indicate the direction of lymph flow, and the colored (blue and pink) arrows indicate the direction of blood flow.

circuit. This circuit has the advantage of circulating oxygenated blood from the gills to the systemic capillaries in all organs almost simultaneously. However, the circulation of blood through the gill capillaries offers resistance to flow. Blood pressure and rates of flow to other organs are thus appreciably reduced. This arrangement probably could not support the high metabolic rates present in some birds and mammals.

In amphibians and reptiles, the evolution of a double circulatory circuit, in which blood passes through the heart twice during its circuit through the body, has overcome the slow blood-flow problem. Amphibians and most reptiles have hearts that are not fully divided in two. In amphibians, a single ventricle pumps blood both to the lungs and to the rest of the body (figure 26.7b). However, because most amphibians absorb more oxygen through their skin than through their lungs or gills, blood returning from the skin also contributes oxygenated blood to the ventricle. The blood pumped out to the rest of the body is thus highly oxygenated.

In the heart of most reptiles, the ventricle is partially divided into a right and left side (figure 26.7c). Oxygenated blood from the lungs returns to the left side of the heart via the pulmonary vein and does not mix much with deoxygenated blood in the right side of the heart. When the ventricles contract, blood is pumped out two aortae for distribution throughout the body, as well as to the lungs. The incomplete separation of the ventricles is an important adaptation for reptiles, such as turtles, because it allows blood to be diverted away from the pulmonary circulation during diving and when the turtle is withdrawn into its shell. This conserves energy and diverts blood to vital organs during the time when the lungs cannot be ventilated.

THE HEARTS AND CIRCULATORY SYSTEMS OF BIRDS AND MAMMALS

Even though the physiological separation of blood in left and right ventricles is almost complete in reptiles, the complete anatomical separation of ventricles occurs only in crocodylians, birds, and mammals (figure 26.7d). This facilitates the double circulation required to maintain high blood pressure. High blood pressure is important in the rapid delivery of oxygenated nutrient-rich blood to tissues with high metabolic rates.

Blood circulates throughout the avian and mammalian body in two main circuits: the pulmonary and systemic circuits (figure 26.8). The **pulmonary circuit** supplies the blood only to the lungs. It carries oxygen-poor (deoxygenated) blood from the heart to the lungs, where carbon dioxide is removed, and oxygen is added. It then returns the oxygen-rich (oxygenated) blood to the heart for distribution to the rest of the body. The **systemic circuit** supplies all the cells, tissues, and organs of the body with oxygen-rich blood and returns oxygen-poor blood to the heart.

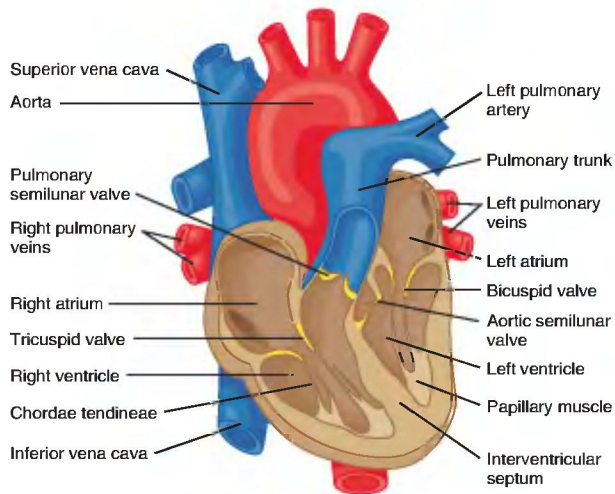
THE HUMAN HEART

The human heart is a hard-working pump that moves blood through the body. It pumps its entire blood volume (about 5 liters) every minute; about 8,000 liters of blood move through 96,000 km of blood vessels every day. The heart of an average adult beats about 70 times per minute—more than 100,000 times per day. In a 70-year lifetime, the heart beats more than 2.6 billion times without fatiguing.

Most of the human heart is composed of cardiac muscle tissue called myocardium (Gr. *myo*, muscle). The outer protective covering of the heart, however, is fibrous connective tissue called the epicardium (Gr. *epi*, upon). Connective tissue and endothelium form the inside of the heart, the endocardium (Gr. *endo*, inside). (Endothelium is a single layer of epithelial cells lining the chambers of the heart, as well as the lumen of blood vessels; see figure 26.6.)

The left and right halves of the heart are two separate pumps, each containing two chambers (figure 26.9). In each half, blood first flows into a thin-walled atrium (L. *antichamber*, waiting room) (pl., atria), then into a thick-walled ventricle. Valves are between the upper (atria) and lower (ventricles) chambers. The

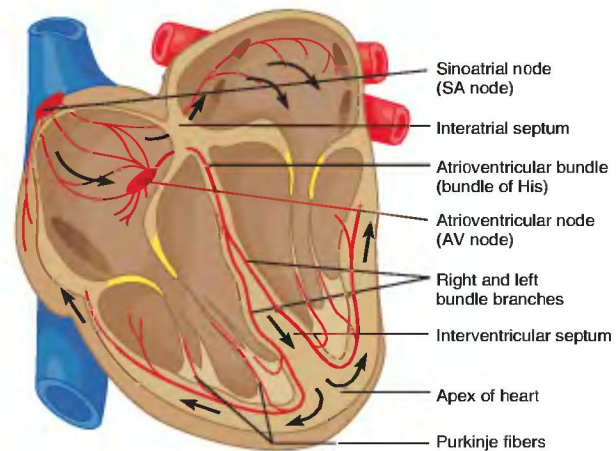
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**FIGURE 26.9**

Structures of the Human Heart. Less oxygenated blood from the tissues of the body returns to the right atrium and flows through the tricuspid valve into the right ventricle. The right ventricle pumps the blood through the pulmonary semilunar valve into the pulmonary circuit, from which it returns to the left atrium and flows through the bicuspid valve into the left ventricle. The left ventricle then pumps blood through the aortic semilunar valve into the aorta. The various heart valves are shown in yellow.

tricuspid valve is between the right atrium and right ventricle, and the bicuspid valve is between the left atrium and left ventricle. (Collectively, these are referred to as the AV valves—atrioventricular valves.) The pulmonary semilunar valve is at the exit of the right ventricle, and the aortic semilunar valve is at the exit of the left ventricle. (Collectively, these are referred to as the semilunar valves.) All of these valves open and close due to blood pressure changes when the heart contracts during each heartbeat. Like the valves in veins, heart valves keep blood moving in one direction, preventing backflow.

The heartbeat is a sequence of muscle contractions and relaxations called the cardiac cycle. A “pacemaker,” a small mass of tissue called the sinoatrial node (SA node) at the entrance to the right atrium, initiates each heartbeat (figure 26.10). (Because the pacemaker is in the heart, nervous innervation is not necessary, which is why a heart transplant without connection to nerves is possible.) The SA node initiates the cardiac cycle by producing an action potential that spreads over both atria, causing them to contract simultaneously. The action potential then passes to the atrioventricular node (AV node), near the interatrial septum. From here, the action potential continues through the atrioventricular bundle (bundle of His), at the tip of the interventricular septum. The atrioventricular bundle divides into right and left branches, which are continuous with the Purkinje fibers in the ventricular walls. Stimulation of these fibers causes the ventricles to contract almost simultaneously and eject blood into the pulmonary and systemic circulations.

**FIGURE 26.10**

Electrical Conduction System of the Human Heart. The SA node initiates the depolarization wave, which passes successively through the atrial myocardium to the AV node, the atrioventricular bundle, the right and left bundle branches, and the Purkinje fibers in the ventricular myocardium. Black arrows indicate the direction of the electrical current flow.

The action potential moving over the surface of the heart causes current flow, which can be recorded at the surface of the body as an electrocardiogram (ECG or EKG).

During each cycle, the atria and ventricles go through a phase of contraction called **systole** and a phase of relaxation called **diastole**. Specifically, while the atria are relaxing and filling with blood, the ventricles are also relaxed. As more and more blood accumulates in the atria, blood pressure rises, and the atria contract, forcing the AV valves open and causing blood to rush into the ventricles. When the ventricles contract, the AV valves close, and the semilunar valves open, allowing blood to be pumped into the pulmonary arteries and aorta. After blood has been ejected from the ventricles, they relax and start the cycle anew.

BLOOD PRESSURE

Ventricular contraction generates the fluid pressure, called **blood pressure**, that forces blood through the pulmonary and systemic circuits. More specifically, blood pressure is the force the blood exerts against the inner walls of blood vessels. Although such a force occurs throughout the vascular system, the term blood pressure most commonly refers to systemic arterial blood pressure.

Arterial blood pressure rises and falls in a pattern corresponding to the phases of the cardiac cycle. When the ventricles contract (ventricular systole), their walls force the blood in them into the pulmonary arteries and the aorta. As a result, the pressure in these arteries rises sharply. The maximum pressure achieved during ventricular contraction is called the **systolic pressure**. When the ventricles relax (ventricular diastole), the arterial pressure drops, and the lowest pressure that remains in the arteries before the next ventricular contraction is called the **diastolic pressure**.