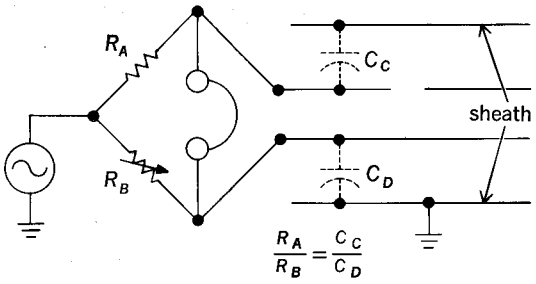

Fig. 5. Alternating-current capacitance bridge used in location of an open circuit in one conductor.

loop test except for the inclusion of the adjustable resistance R. The Varley loop (Fig. 4) is used for fault location in high-resistance circuits.

Open circuit. An alternating-current capacitance bridge can be used for locating an open circuit as shown in Fig. 5. One test terminal is connected to the open conductor and the other terminal to a conductor of known continuity in the cable. All conductors associated with the test are opened at a convenient point beyond the fault but at a known distance from the test connection. An audio oscillator supplies the voltage to the bridge, which is balanced by adjusting R_B for a null as detected by the earphones. Measured ratio R_A/R_B equals the ratio of capacitances between the lines and the grounded sheath. Because each capacitance is proportional to the length of line connected to the bridge, the location of the open circuit can be determined from Eq. (4).

$$R_A/R_B = C_C/C_D \tag{4}$$

For convenience in carrying out the tests for fault location, the fault location bridge has switches for setting up the various loop test circuits. Basically it is a bridge like other bridges used in circuit testing. *See* CIRCUIT (ELECTRICITY); OHMMETER; RESISTANCE MEASUREMENT; WHEATSTONE BRIDGE. [CHARLES E. APPLEGATE]

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Circulation

Those processes by which metabolic materials are transported from one region of an organism to another. Ultimately, the essential gases, nutrients, and waste products of metabolism are exchanged across cell membranes by diffusion. Diffusion is the movement of material, by random motion of molecules, from a region of high concentration to one of low concentration. The amount of material moved from one place to another depends on the difference in concentrations and on the distance between the two points. The greater the distance, the less movement of material per unit time for a given difference in concentration. Consequently, in all but the smallest animals, convection (or bulk circulation) of materials to the cell must be employed to supplement diffusion.

Protoplasmic movement aids diffusion at the intracellular level. In multicellular animals, however, either the external medium or extracellular body fluids, or both, are circulated. In sponges and coelenterates (Fig. 1*a* and *b*), water is pumped through definite body channels by muscular activity or, more often, by cilia or flagella on the cells lining the channels.

Coelenterates have a body wall derived from two cell layers; an outer ectoderm is separated from an inner endoderm by a noncellular gelatinous material (mesoglea). All higher animals have bodies consisting of three cell layers, with the ectoderm being separated from the endoderm by a cellular layer of mesoderm. The mesoderm proliferates and separates to develop a fluid-filled body cavity or coelom. The coelom separates the ectoderm (together with an outer layer of mesoderm) from the endoderm (which has an inner layer of mesoderm). Coelomic fluid is moved around by body movements or ciliary activity, but in larger animals this movement is usually inadequate to supply the metabolic requirements of the organs contained within the coelom. These needs are provided for by pumping a fluid, blood, to them through vessels, the blood vascular system (Fig. 1*c*–*e*). *See* BLOOD; LYMPHATIC SYSTEM.

OPEN AND CLOSED CIRCULATORY SYSTEMS

When the blood is in a separate compartment from the rest of the extracellular fluid, the vascular system is described as closed. In such a system, the blood is circulated by a pump, the heart, through special channels, blood vessels; it comes into close association with the tissues only in the capillaries, fine vessels with walls only one cell thick. In some tissues or regions, larger blood spaces may exist, called sinuses. A closed vascular system is found in most annelids (segmented worms and leeches), cephalopod mollusks (squids and octopods), holothurian echinoderms (sea cucumbers), and vertebrates (Fig. 1*c*–*e*).

In vertebrates, a functional but anatomically closed connection exists between the extracellular spaces (between the cells) and the blood vascular system in the form of lymph channels. Lymph is derived from the noncellular component of blood (plasma), modified in its passage through the tissues, and is conducted to the veins by blind-ending lymphatic vessels, which are separate from blood vessels and coelomic space (Fig. 1*e*).

In most arthropods (crustaceans, insects), most mollusks (shellfish), and many ascidians (sea squirts), the extracellular spaces are confluent with the blood system. In these animals, blood is pumped through a limited network of vessels into a body cavity called a hemocoel (Fig. 1*d*). After bathing the tissues, blood (called hemolymph in these organisms) collects in sinuses and returns to the heart. This is the open vascular system. In animals with open circulatory systems, the coelom is much reduced.

DYNAMICS

A pump is required to circulate the blood in animals. The pump (usually called a heart) imparts propulsive energy to the blood, which flows from regions of high fluid energy to regions of low fluid energy (or down an energy gradient). The total energy of flowing blood consists of pressure energy, imparted by the pump, and energy contained in blood due to its motion (kinetic energy). Even in mammals, where blood flows very rapidly, the kinetic energy component is small compared with

(the pump-filling phase). Likewise, flow will be extremely pulsatile, often stopping between heartbeats.

In both open and closed circulatory systems, the volume of blood pumped by the heart must be the same volume as returns to the heart in any given time period. However, only in closed circulations does this have important consequences with regard to the rate at which blood flows through the vessels in the various regions of the vascular system. The velocity of blood flow at any part of a closed system depends on the cross-sectional area of the vessels in that part. Since the vessels that arise from or join to the heart must necessarily be about the same size, flow velocity in the veins is almost as rapid as in the arteries. Furthermore, since the cross-sectional area of the vessels within all the tissues is many times greater than vessels leaving the heart, the flow in the tissue vessels is very slow (usually less than 1 mm $\cdot$ s^{-1}), allowing plenty of time for exchange across cell walls.

COMPONENTS OF CIRCULATORY SYSTEMS

The two principal components of all circulatory systems are hearts and blood vessels.

Hearts. The circulatory pumps are the hearts, all of which operate by causing a wave of muscular contraction followed by a wave of relaxation (peristaltic wave) to travel over the walls of a tube. When the muscle contracts, the volume is reduced and fluid contents are expelled.

Tubular heart. If the heart persists in adult animals as a tube, such as the dorsal vessel of annelids or the dorsal heart of insects (Fig. 2*b*), it is called a tubular heart. The peristaltic wave passes along the tube in an anterior direction, pushing the blood before it in the same way the air in a balloon is squeezed down to one end by pulling the balloon through a cupped hand. Therefore, valves are unnecessary to ensure unidirectional flow of blood. In earthworms, the peristaltic waves travel up the dorsal vessel at rates of 2–4 cm $\cdot$ s^{-1} about 10 times each minute. Vessels in the gills of hagfishes and octopods also contract rhythmically and propel the blood.

Multiple and chambered hearts. In the majority of animals, the zone of propulsive activity is restricted to a localized region. Some animals have many hearts: earthworms have five pairs of lateral hearts connecting the dorsal and ventral vessels (Fig. 2*e*); octopods and squids have hearts which boost blood flow through the gas exchanger (gills) in addition to a main or central heart (Fig. 2*f*); sea cucumbers may have over 150 hearts between dorsal and ventral vessels (Fig. 2*i*). However, many animals have only one heart, and in order to pump a volume equivalent to that pumped by a long contractile vessel, the lumen is greatly enlarged and usually divided into a number of chambers (chambered heart). To ensure unidirectional flow of blood, chambered hearts require one-way valves. Valves are flaps of tissue situated around the edge of orifices between heart chambers or in vessels.

Contractile chambers. The more powerful the heart muscle becomes, the faster the blood can be driven into the outflow vessels, but filling the heart then requires a greater force. In vertebrates, there is often enough energy in the fast-flowing venous blood to do this, but other chambers may be necessary to fill the main propulsive chamber (or ventricle) in stages. These chambers are auricles and must have sufficiently thin walls to be expanded by the energy of the inflowing blood, yet must be powerful enough to fill the ventricle when they contract.

Most animals with chambered hearts have a single auricle, but in mollusks there is one for each pair of gills, so there may be from one to four (Fig. 2*f* and *h*). Fishes have a single auricle, but in amphibians the auricle is divided into two atria. In birds and mammals, the ventricle often divides, giving two separate, parallel circulations: one to the body and the other to the lungs. Fishes and amphibians have an extra contractile chamber, the sinus venosus, which fills the auricle when it contracts. Elasmobranchs and amphibians also have an extra contractile chamber on the ventricular outflow pathway, the conus arteriosus. Its role has not been established, but it could be actively closing the outflow valves of the heart.

All vertebrate hearts, and many in invertebrates (such as mollusks and arthropods; Fig. 2*f* and *g*), are enclosed in a small portion of the coelom called the pericardial cavity. This cavity is fluid-filled and serves to prevent the heart from being buffeted by other body organs, but it can also aid in returning blood to the heart. If the pericardial wall is rigid, as in elasmobranchs and most mollusks and crustaceans, one chamber of the heart cannot contract unless another is expanding. If the ventricle starts to contract, the reduction in volume will tend to increase the volume of the pericardial cavity, and since it has rigid walls, the pressure inside it will be reduced. This suction pressure is transmitted through the thin auricular wall and draws blood in from outside the pericardium. This mechanism ensures successful filling of the heart even in open blood systems.

In tubular hearts, blood will tend to be sucked into the lumen when the muscle relaxes behind the wave of contraction. It has even been suggested that the major function of the dorsal contractile vessel in annelids is to prime the lateral hearts with blood. In insects, the tubular heart is suspended by alary or aliform muscles attached to the external skeleton, and when these contract the expansion of the lumen sucks blood through valved openings (ostia) into the heart (Fig. 2*b*).

Electrophysiology. The wave of contraction which passes across the heart is driven by an electrical impulse (action potential) which arises spontaneously, either in modified heart muscle cells, or in special nerve cells located on or near the heart. These cells form the pacemaker, which sets the heart rhythm. When nerve cells initiate the heartbeat, the pacemaker is called neurogenic. A pacemaker of muscle cells is called myogenic. Myogenic pacemakers are found in vertebrates, mollusks, echinoderms, and perhaps in some annelids. Neurogenic pacemakers are found in most arthropods. Many hearts have more than one pacemaker. In tunicates, the tubular heart pumps into the open circulation in two directions. After several hundred beats the rhythm slows and stops, and the direction of the wave of contraction reverses when the heart starts up again. Consequently, the tunicate heart must have at least two pacemakers. In frogs, heart contraction can be driven by electrical impulses arising in the sinus venosus, atria, or ventricle. Usually the sinus pacemaker beats fast-

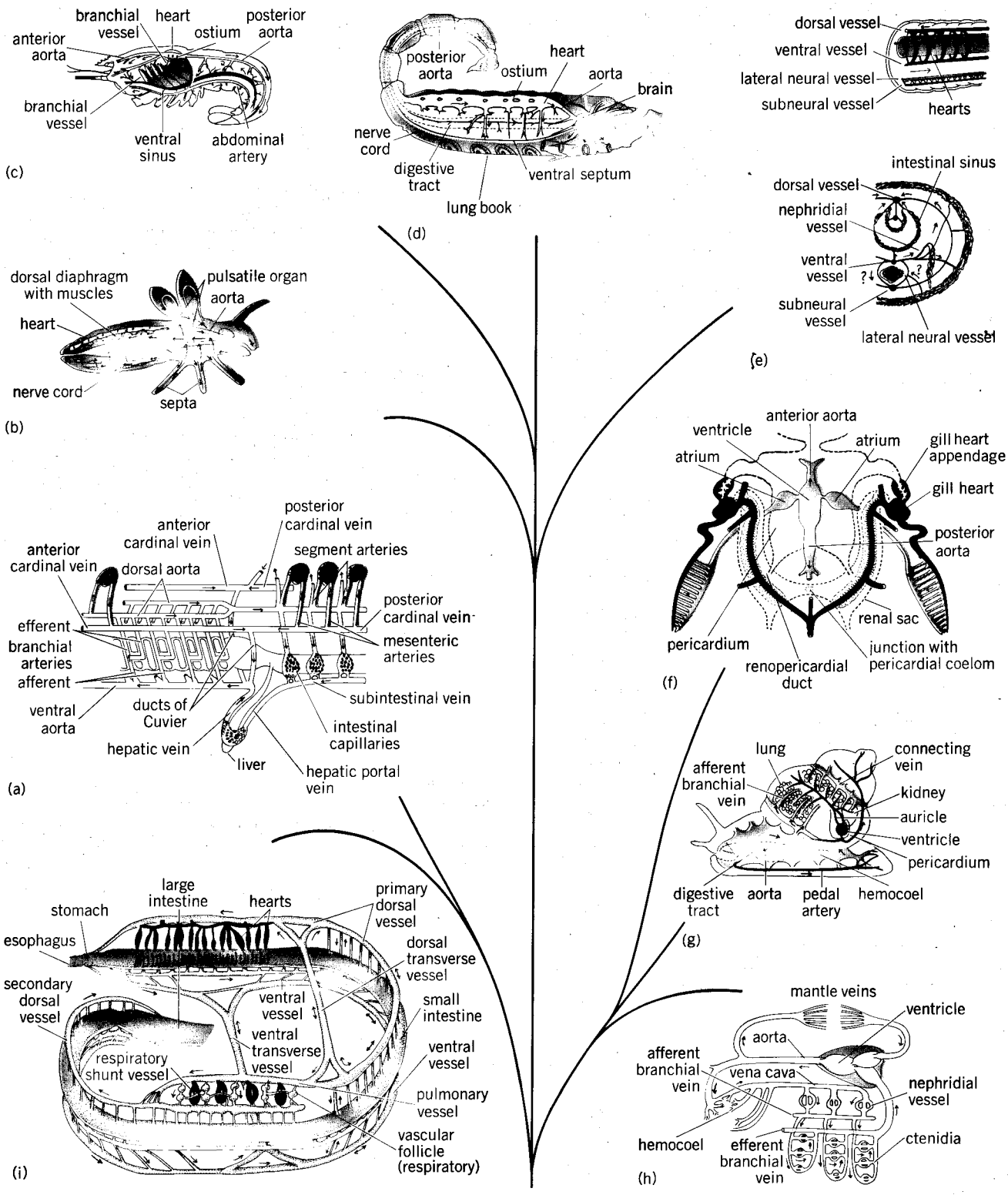

Fig. 2. Representative invertebrate and ancestral vertebrate circulatory systems on a schematic evolutionary tree. In all diagrams the arrows indicate the direction of blood flow. (*a*) Ancestral vertebrate, represented by *Amphioxus* (*from K. Johansen, Respiration and circulation, in A. J. Waterman et al., Chordate Structure and Function, MacMillan, 1971*). (*b*) Insect: a main dorsal vessel carries blood from the heart (*from K. Schmidt-Nielsen, Animal Physiology, 2d ed., Cambridge University Press, 1979*). (*c*) Crustacean: circulation in the lobster (*from K. Schmidt-Nielsen, 1979*). (*d*) Arachnid, represented by the scorpion *Bathus* (*from A. W. Martin and K. Johansen, Adaptations of the circulation in invertebrate animals, in W. F. Hamilton and P. Dow, eds., Handbook of Physiology, Section 2, Circulation, vol. 3, American Physiological Society, 1965*). (*e*) Annelid: cross section and longitudinal section (*from K. Schmidt-Nielsen, 1979*). (*f*) Cephalopod mollusk, represented by the closed circulation in the octopus (*from E. Florey. An Introduction to General and Comparative Animal Physiology, W. B. Saunders, 1966*). (*g*) Gastropod mollusk: an open circulation represented by the snail *Helix* (*from A. W. Martin and K. Johansen, 1965*). (*h*) Bivalve mollusk: an open circulation represented by the fresh-water mussel *Anodonta* (*from A. W. Martin and K. Johansen, 1965*). (*i*) Echinoderm represented by the sea cucumber, *Stichopus* (*from C. F. Herreid et al., Blood vascular system of the sea cucumber, Stichopus moebi, J. Morphol., 150:423, 1976*).

est and drives all the others. *See* HEART (INVERTEBRATE).

In birds and mammals, the heart is large and generates high pressures. To prevent the pressure set up by the contraction of one part of the heart from stretching, and perhaps rupturing, the relaxed part, all of the ventricular muscle must be activated simultaneously. This is achieved by conveying the electrical impulse to all parts of the ventricle through specialized conduction pathways composed of modified muscle cells.

Chemical and mechanical excitation. Many hearts are innervated by nerves which regulate the beat. When these nerves are active, they liberate chemicals such as noradrenalin or acetylcholine from their terminals, and these neurotransmitters affect the cardiac muscles directly. In general, the pacemaker of myogenic hearts is inhibited by acetylcholine; excitation is produced by noradrenaline (vertebrates) or serotonin (mollusks). In neurogenic hearts, gamma aminobutyric acid (GABA) is inhibitory, whereas glutamic acid is excitatory. Neurotransmitters affect not only the rate, but also the strength of cardiac contraction. For example, noradrenaline increases the amount of blood pumped by a single ventricle (stroke volume) while acetylcholine decreases stroke volume. *See* ACETYLCHOLINE; ENDOCRINE MECHANISMS.

Mechanical factors may also affect rate and strength of heart contraction. In earthworms, mollusks, and some fishes, stretching the pacemaker region of the myocardium increases its rhythm. Moreover, in all vertebrates, and probably in all mollusks as well, the length of the muscle fibers in the heart at the end of diastole is directly proportional to the strength of the next muscle contraction (Starling's law of the heart).

Many animals, both vertebrate and invertebrate, take advantage of muscular activity in the body, such as during exercise, as an aid to circulation of the blood. In vertebrates, valved thin-walled veins run through blocks of skeletal muscle and are compressed when the muscle contracts, squeezing blood toward the heart (muscle pump). In other animals, the blood functions directly in locomotion. Spiders have no leg extensor muscles, so leg extension is brought about by forcing hemolymph into the leg at high pressure (50 kPa), which is generated by the contraction of lateral cephalothoracic muscles depressing the carapace. Backflow into the abdominal heart (which can generate pressures of only 13 kPa) is prevented by valves on the outflow vessels at the junction of the cephalothorax and abdomen. But there are no valves in the veins, and blood returns rapidly to the abdomen.

Caudal heart. Hagfishes have a unique caudal heart. A longitudinal rod of cartilage separates two chambers, and when body muscles on one side contract, the rod is bent to that side. The bend in the rod causes the volume of the chamber on the actively contracting side to expand so that it fills with blood, while the volume of the chamber on the other side is decreased, expelling blood. Valves at the inflow and outflow ends of the chambers ensure unidirectional flow of blood. *See* HEART (VERTEBRATE).

Blood vessels. Blood ejected from the heart is conveyed by vessels which are usually called arteries or aortas. In some animals, structural differences between outflow and inflow vessels are not obvious, and they are usually referred to simply as blood vessels. In closed systems, the arteries (ouflow vessels) divide and subdivide so that ultimately tubes only a few micrometers thick (capillaries) run between the cells of each organ.

Capillaries. In vertebrates, each capillary consists of a single layer of endothelial cells surrounded by a basement membrane. In some echinoderms with well-developed circulatory systems (such as holothurians; Fig. 2*i*) capillary structure is similar to that in vertebrates, while in cephalopods (such as the octopus) capillaries are extremely small (1 μm in diameter) but are usually more than one cell thick. The total number of capillaries in a vertebrate is large, and in humans it is enormous: over 50,000,000,000 in the whole body. Therefore, although each capillary is small the total cross-sectional area of all capillaries is perhaps a thousand times greater than that of the main arterial vessels. Consequently, blood flows very slowly in the capillaries, about one-thousandth of the velocity in the aorta, allowing lots of time for exchange of materials with the cells.

In open circulations, after a greater or lesser number of branchings blood vessels ultimately open to the spaces between the cells. Even so, networks of fine blood pathways may occur, especially in gas-exchange organs, nephridia, and masses of nervous tissue (such as brains or ganglia). In animals with closed circulatory systems, a plexus of fine capillaries brings blood close to the external environment in skin (annelids, frogs), respiratory trees (holothurians), gills (fishes), and lungs. Similar close associations between blood and external media are seen in animals with open circulatory systems (Fig. 2*c* and *d*). For instance, gills of shrimp look similar to those of fish in all but the finest morphological details. Book lungs of spiders are unique structures in which blood is moved across rows of fine air tubes, stacked one on the other, in channels only a few micrometers in width. In insects, air is distributed directly to the body cells by way of the trachea, a system of tubes independent of the circulation. Fine blood channels are lacking in these animals.

Veins and portal systems. After traversing the capillaries, blood is collected into large vessels which return it to the heart. In cephalopods and vertebrates, these collecting vessels are called veins. In open circulations, channels returning blood to the heart exist, but the pattern is less precise than in closed systems. In insects and arachnids, longitudinal membranes impose some direction on blood movement (Fig. 2*b* and *d*).

In many vertebrates, venous blood is transported to another organ (such as the liver or kidney) on its way back to the heart. In these organs the veins divide into a capillary network supplying blood to the tissues at low pressure. This is a portal blood supply, and there are a large number of these in vertebrates. The hepatic portal system occurs in all vertebrates and serves to transport materials from the intestine, where they are absorbed, to the liver, where they are stored (Fig. 2*a*). Another prominent portal system is the renal portal system. It occurs in all vertebrates except mammals, and transports blood from the caudal parts of the body to the kidneys. The function of the renal portal system is not known. *See* KIDNEY; LIVER.

Contraction. Many blood vessels have muscular coats, the muscle cells being rhythmically contractile (myogenic rhythm). Contraction of blood vessels is found in the dorsal and ventral vessels and some capillaries of annelids, in the gill vessels of cephalopods and cyclostomes, and also in the fine vessels leading to the capillary beds in higher vertebrates. In these small vertebrate vessels (called arterioles, with a diameter of 50–200 μm), the muscles are in a continual state of activity, modulating the radius of the vessel and therefore the blood flow. This activity can be altered by nerves, by blood-borne agents such as adrenaline, and also at the local level by changes in the level of tissue metabolites (a fall in oxygen tension in the body tissues causes the muscles to relax).

Aortic elasticity. The aortas (or arteries leaving the heart) are fairly elastic in nearly all animals. In closed circulations, the stroke volume is stored by the elastic distension of the arteries and is fed to the periphery between cardiac ejections. This elastic reservoir (or Windkessel effect) is exemplified by the arterial vessels of vertebrates. In humans, the whole arterial tree participates in producing a Windkessel effect. In contrast, fishes have a very short ventral aorta, and only a very elastic bulb (bulbus cordis) just outside the ventricle provides a pressure reservoir, which smooths blood flow through the gills. Many mollusks with open circulatory systems have a similar elastic expansion of the aortic wall just beyond the ventricle. *See* BLOOD VESSELS.

EVOLUTION OF VERTEBRATE CIRCULATION

The evolution of an organ system which is not preserved in fossils can only be inferred from investigations of extant species. Thus, understanding must always be clouded by uncertainty. For example, a major pattern of increasing complexity, which emerges from comparative studies of circulatory systems, is related in vertebrates to life on land. More promising are investigations of the early stages of development of the heart and circulation. These show that all types of vertebrate circulations can be related to a common ancestral pattern (Fig. 2*a*). The ancestral pattern of circulation in vertebrates is for a ventral heart to pump blood anteriorly in a ventral vessel, connecting to the dorsal vessel through the gas exchanger (gills; Fig. 1*e*). The gills are situated on the high-pressure side of the circulation, and blood flows posteriorly in the dorsal vessel.

Annelid worms exhibit a superficial resemblance to the circulation in the ancestral vertebrate in the pattern of dorsal and ventral vessels (Fig. 1*c*), except that the heart is dorsal, flow in the dorsal vessels is anteriorly directed, and flow in the ventral vessel is posteriorly directed. More important, in most invertebrates the gas exchanger, when it exists as a discrete entity, is on the low-pressure side of the circulation. This arrangement limits metabolic scope, a problem which is solved in large, active invertebrates (such as cephalopods) by the development of high-pressure, prebranchial hearts.

Apparently, the chordate stock arose from ancestors in common with primitive echinoderms, a group with a very poorly developed circulation. Hence, the apparent similarities between the circulations in vertebrates and invertebrates are superficial and presumably arose as an evolutionary response to similar physiological demands. This is an example of convergent evolution due to common selection pressures, the circulatory systems in vertebrate and invertebrate groups being analogous rather than homologous. *See* CARDIOVASCULAR SYSTEM.

[DAVID R. JONES]

Circulation disorders

The function of the circulatory system is to transport and distribute substances either used or produced by cells or both. Excluded are those materials that are discharged directly from sweat glands, digestive glands, and renal tubule cells. Included, however, are nutritive and metabolic substances, hormones, waste products, water, and heat.

The circulating fluids are distributed between the heart, blood vessels, capillaries, intercellular spaces and lymphatics and within the cells. The blood and body fluids are in a constant state of dynamic equilibrium (Fig. 1). Blood flows through the vessels to the capillaries where some fluid passes through the endothelium to the intercellular spaces to bathe the cells. Fluid with contained electrolytes and metabolic substances can then pass into and out of the cells. At the distal end of the capillaries most of this fluid passes back into the vascular compartment. A portion of this fluid is returned to the circulation by way of the lymphatics.

Vascular disturbances. Disturbances in this pattern can either result in or from disease conditions. An example is edema, which is an abnormal accumulation of fluid in the cells, tissue spaces, or cavities of the body. There are three main factors in the formation of generalized edema and a fourth which plays a role in the formation of local edema. They are the permeability of the capillary wall, the colloid osmotic pressure of the plasma proteins, and the hydrostatic pressure in the capillaries. The fourth factor, which is of importance in local edema formation, is lymphatic obstruction. *See* CARDIOVASCULAR SYSTEM; LYMPHATIC SYSTEM.

An example of edema formation secondary to a decrease in the colloid osmotic pressure of the plasma proteins is nephrotic edema. In chronic Bright's disease there is a marked loss of urine albumin and the plasma protein level drops as a result.

Cardiac edema follows the generalized venous congestion of cardiac failure and is an example of edema formation resulting from increased hydrostatic pressure in the capillaries.

Increased permeability of the capillary walls plays an important role in the formation of inflammatory edema, the edema of severe infections, metabolic intoxications, asphyxia, anaphylactic reactions, secondary shock, and acute nephritis. *See* EDEMA.

Deficiencies. A deficiency of circulating blood volume, both cellular elements and fluid, is called oligemia. This may be the result of an acute blood loss or it may be of a chronic nature, such as an anemia combined with dehydration. Anemia, or oligochromemia, is a deficiency of circulating red cell volume or, more specifically, hemoglobin content. This is the oxygen-carrying component of the circulating red blood cell. The normal value for the adult human is 14–16 g/100 ml of blood. The norm