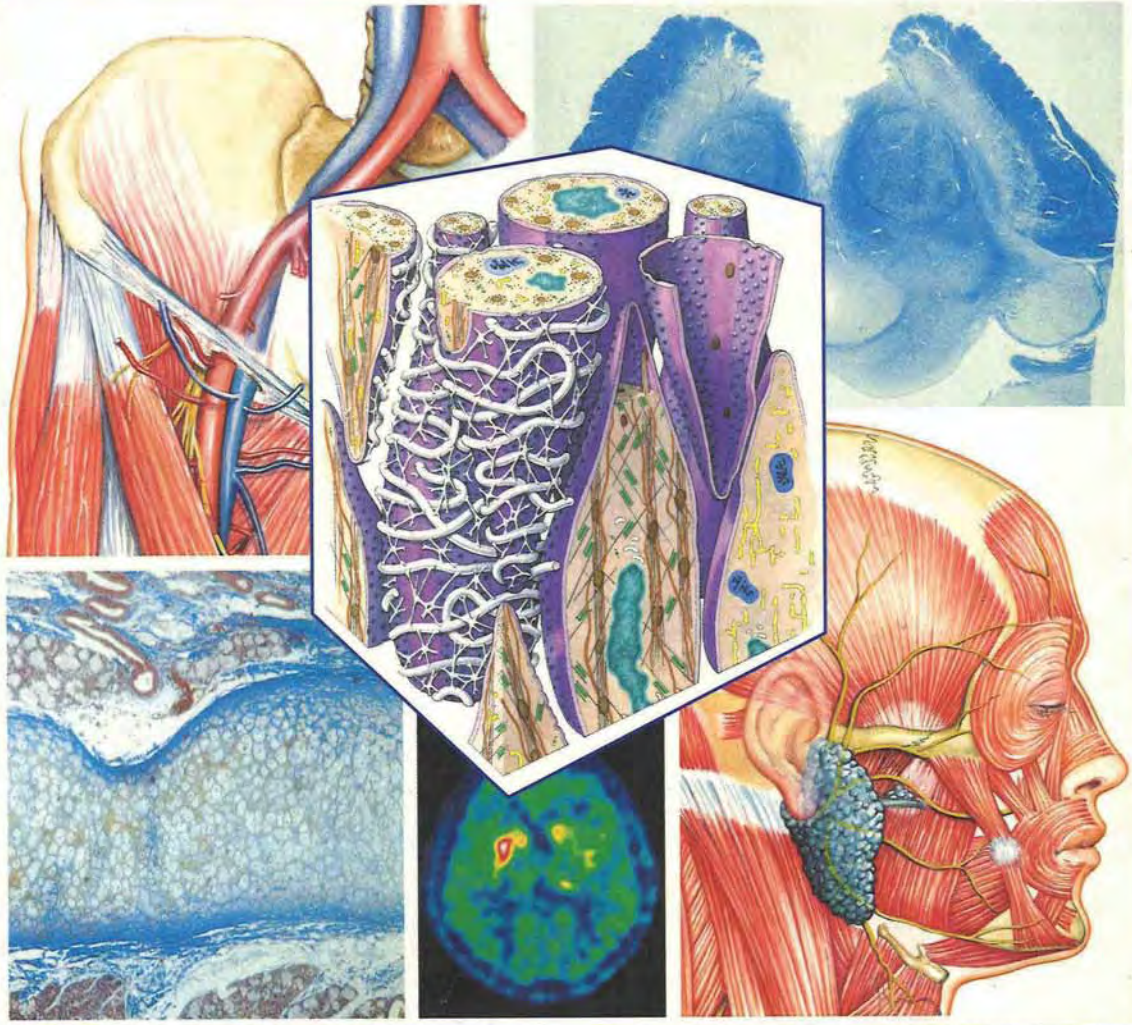
Henry Gray

THIRTY-EIGHTH EDITION

GRAY'S ANATOMY



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GRAY'S ANATOMY

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CARDIOVASCULAR

Section Editor: Giorgio Gabella

With contributions from Professor Robert Anderson, MD, Mr Julian Dussek FRCS, Dr Susan Evans, PhD, Mr Adrian Marston, FRCS and Dr Marta Perry, MUDr, PhD, Professor Anderson was responsible for the revision of the Heart and contributed all the colour photographs of the heart and the diagrams **10**.22, 43, 44, 57, 62, 63, 64. Dr Evans revised the General Introduction on the evolutionary aspects of cardiac morphology. The section on the pulse and central venous access were prepared by Mr Julian Dussek. Mr Marston advised on arteries and veins of the abdomen **10**.116, 117, 120, 125–127, and Dr Perry wrote the essay on leucocyte-endothelial cell interaction.

BLOOD VESSELS

INTRODUCTION

Movement and exchange of materials in the watery medium of living tissues takes place by diffusion, most commonly along chemical gradients. A vital requirement in large and complex organisms, however, is a fast, widespread, high-capacity system for continuously transporting to and from every single part of the body a large number of specific components, ranging from ions and small molecules to whole cells. This is the main function served by the vascular or circulatory system.

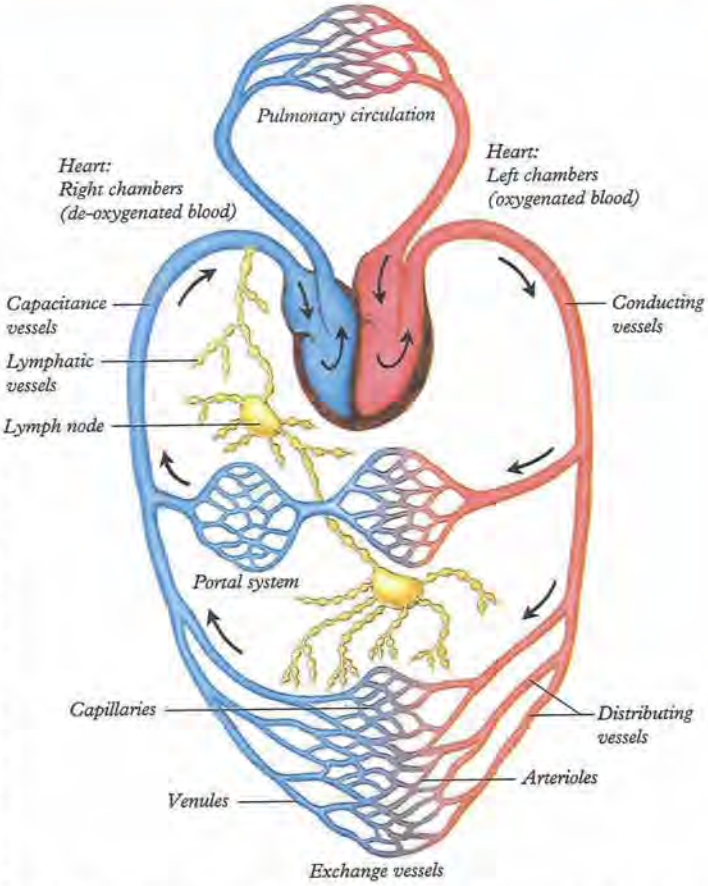
- Blood (see section 9) is the vehicle which maintains a vast chemical traffic through the body, moving hormones, oxygen, nutrients, antibodies, catabolites, red and white blood cells, as well as infestants and toxic compounds. In addition, in ectotherms, blood redistributes and disperses heat, and, because of the pulse pressure, it also has mechanical effects, such as maintaining turgidity of tissues and counteracting certain effects of gravity.
- The circulatory system is fast and has high capacity, for several reasons: because of the rheological properties of blood, because of the large volume of blood, and because of the mechanical properties of the heart and muscular arteries.
- The circulatory system is made up of the heart—a central pump and the main motor of the system—and by a vast array of tubes which lead away from the heart (as arteries) and carry the blood to the 'periphery' of the body; at the periphery, that is within organs and tissues, the tubes loop back and (as veins) reach the heart again where the blood eventually returns.

Schematically, one can envisage the vascular system as made up of long loops which are centred on the heart (at which level both arteries and veins are largest) and are much reduced in size and extremely arborized at the periphery (capillaries) (**10**.1). There are, in fact, not one but two such loops, because the heart is a **pair** of muscular pumps, one feeding a minor loop (pulmonary circulation), which serves the lungs, the other feeding a major loop (systemic circulation), which serves all the rest of the body. The two loops are also referred to as the *greater* and *lesser circle*.

With limited exceptions, which will be discussed in due course, each loop is a closed system of tubes, so that blood per se does not usually leave the circulation. As William Harvey discovered in the seventeenth century, blood is pumped away from the heart but it all returns to the heart after circulation through the body. Arteries are the vessels that carry the blood away from the heart, and veins are the vessels that carry it back to the heart.

From the centre to the periphery, the vascular tree shows three main changes:

- The arteries increase in number by repeated division and by the issuing of side branches, in both the systemic and the pulmonary circulation.
- The arteries also decrease in diameter, although not to the same extent as they increase in number, so that a notional cross-section of all the vessels at a given distance will have the greatest area the furthest away it is from the heart. As a result, blood flow is faster near the heart than at the periphery.
- Among other structural changes, the wall of the arteries decreases in thickness, although this is not as substantial as the reduction of the vessel diameter. In consequence, in the smallest arteries (arterioles) the thickness of the wall represents about half the outer radius of the vessel, whereas in a large vessel it represents between one-fifteenth and one-fifth. For example, in the thoracic aorta the radius is about 17 mm and the wall thickness 1.1 mm (Wolinsky & Glagov 1967a). From a functional viewpoint, while **size** is a fundamental parameter of a blood vessel, **position** of the vessel in the body and **structure of the vessel wall** are also very important characteristics, which dictate the properties of the vessel. Furthermore, whereas microcirculation vessels are remarkably similar in animal species of very different body size, equivalent large vessels vary greatly not only in size but also in wall thickness in mammals of different body size—an important consideration when data obtained on laboratory animals are extrapolated to man. As a first approximation, comparative studies show that in corresponding large arteries, the ratio between inner diameter and wall thickness is constant and is independent of body size (Caro et al 1978).



10.1 Diagrammatic drawing of the cardiovascular and lymphatic system. The nomenclature of the main vessel types is indicated; in red are the vessels carrying oxygenated blood, in blue those carrying un-oxygenated blood and in yellow the lymphatic structures.

VASCULAR SYSTEM

VESSEL NUMBER

The aorta, the single systemic artery emerging from the heart, gives origin by successive branching to hundreds of arteries of progressively smaller calibre; by further branching these produce about 4×10^6 arterioles and four times as many capillaries. A similar number of venules converge onto each other forming a progressively smaller number of veins of increasingly larger size; eventually, two veins only, which are also the largest of the body, the superior and the inferior vena cava, open into the heart from the systemic circulation. A similar pattern is found in the pulmonary circulation (lesser circle). In the lesser circle, however, the vascular loop is shorter and has therefore fewer branching points; consequently, the number of vessels is smaller than in the greater circle.

VESSEL SIZE

At the emergence from the heart the aorta of an adult man has an

outer diameter of about 30 mm (sectional area of nearly 7 cm^2). The diameter decreases along the arterial tree until it is as little as 10 μm in arterioles (sectional area of about 80 μm^2) (Rothe 1983). However, given the enormous number of arterioles, the total cross-sectional area at this level is about 150 cm^2, more than 200 times larger than at the level of the aorta (Wiedeman et al 1976); a further increase of the extent of the vascular bed takes place at the level of the capillaries and venules. In a 13-kg dog, the aorta had a cross-sectional area of 0.8 cm^2 and the capillaries (estimated at 1.2×10^9) had a total cross-sectional area of 600 cm^2 (Green 1950). Veins leading back to the heart grow progressively larger and fewer in number. As with the arteries, a cross-sectional area of all veins at a given level is smaller the nearer this is to the heart. Veins are a little larger than the corresponding arteries. The reduction in diameter along the vascular tree occurs when a vessel divides or issues collateral branches; in the absence of branches, the shape of a segment of any vessel is not a truncated cone but a cylinder.

The size of the vessels increases during development, while there are substantial changes in the structure of their wall. In old age, vessels generally become enlarged. In animal species, the size of comparable vessels is related to body size; so, while in a mouse the ascending aorta measures less than 2 mm in diameter, the same vessel in a blue whale measures over 30 cm, large enough for a human baby to swim through. In spite of these enormous differences in size there are no qualitative differences in the structure of the constitutive materials: similar types of cell and of extracellular material are found in corresponding vessels ranging in linear size over more than three orders of magnitude.

BRANCHING PATTERNS

When an artery divides into two branches of roughly equal size, these are called terminal branches, as that artery ceases to exist at this point. Branches issued along the course of an artery, before its termination, are usually of smaller size than terminal branches and are called collateral (or side) branches.

The angle of branching is related to the calibre of the vessels and it conforms to theoretical predictions based on the principle of minimum work (namely, in this context, the highest efficiency in blood flow) or the minimum 'cost' of the bifurcation (Woldenberg & Horsfield 1986), although there are many exceptions.

The *total cross-sectional area* of the daughter vessels is invariably greater than the cross-sectional area of the parent vessel. For example, the terminal portion of the abdominal aorta has an internal diameter of 13.8 mm, while each of the common iliac arteries has an internal diameter of about 9.7 mm, so that the bifurcation produces a 1.5-fold increase in total cross-sectional area. It has been calculated that vessels arising by equal bifurcation have a diameter 0.76 of that of the parent vessel (Green 1950).

ANASTOMOSIS

Arteries can be joined to each other by anastomosis, which makes them able to feed each other's territory. An *end-to-end anastomosis* occurs when two arteries open directly into each other (for example, the vaginal and the ovarian artery, the right and the left gastro-epiploic arteries, the ulnar artery and the superficial palmar branch of the radial artery). Anastomosis by *convergence* occurs when two arteries converge and merge, as in the case of the vertebral arteries forming the basilar artery. A *transversal* anastomosis occurs when a short arterial vessel links two large arteries transversely; examples are found in the anastomosis between the two anterior cerebral arteries, that between the posterior tibial artery and the peroneal artery, and that between radial and ulnar arteries at the wrist.

RELATIONS OF BLOOD VESSELS

Arteries are usually more deeply situated than veins, although there are several superficial or subcutaneous arteries, such as the occipital, temporal and frontal arteries and the epigastric artery.

In the proximity of the joints of limbs arteries are located on the flexor surface, but, characteristically, there are many transverse vessels which provide a collateral circulation over the lateral parts of the joint.

Arteries are usually separated from bones by muscles and fasciae. When they are in contact with bone tissue they leave an imprint or vascular groove, for example the subclavian artery on the first rib.

Large arteries (thoracic aorta, subclavian, axillary, femoral and popliteal) lie close to a single vein which drains the same territory supplied by the artery. The other arteries are usually accompanied by two veins, satellite veins (*venae comitantes*), lying on either side of the artery. Such venae comitantes flank an artery, with numerous cross-connections, the whole assembly being enclosed in a single connective tissue sheath. The artery and the two satellite veins are often associated with a nerve; when they are surrounded by a common connective tissue sheath they form a vasculo-nervous fascicle.

The close association between the larger arteries and veins in the limbs allows the counterflow exchange of heat to take place: this mechanism promotes heat transfer from arterial to venous blood, and thus helps to preserve body heat. Counterflow heat exchange apparatuses are found in other organs, for example in the testis, where the pampiniform plexus of veins surrounds the testicular artery: with this arrangement, not only is body heat conserved, but also the temperature of the testis is kept below average body temperature (Evans 1949; Grant & Wright 1971; see also p. 1854). Counterflow exchange mechanisms involving ions are found in the microcirculation, as exemplified by the arterial and venous sinusoids which exist in the vasa recta of the renal medulla where countercurrent exchange retains sodium ions at a high concentration in the medulla (p. 1824), efferent venous blood transferring sodium ions to the afferent arterial supply.

CLASSIFICATION OF VESSELS

Arteries and veins are identified and classified according to their anatomical position. A large part of this section (p. 1824) deals with the distribution, position and other systematic aspects of individual blood vessels. Furthermore, vessels can be classified anatomically according to their size and wall structure (**10.2**). Arteries can be divided into elastic and muscular: although muscle cells and elastic tissue are present in all arteries, while the relative amount of elastic material is largest in the largest vessels, the relative amount of musculature increases progressively towards the smallest arteries. Classifications of arteries are often presented or referred to; these classifications, however, are vague at best, because the changes of the structural and functional parameters are usually continuous rather than discrete. The gradual change of most parameters does not favour any firm classification, if one was needed. There is also considerable variability in vessel properties between individuals, based on heredity, individual history and age.

Functionally, arteries are often subdivided into conducting, distributing and resistance vessels. (In simplified functional terms some authors distinguish only three classes of vessels: *resistance vessels*, or arteries, *exchange vessels*, or microcirculation vessels, and *capacitance vessels*, or veins.)

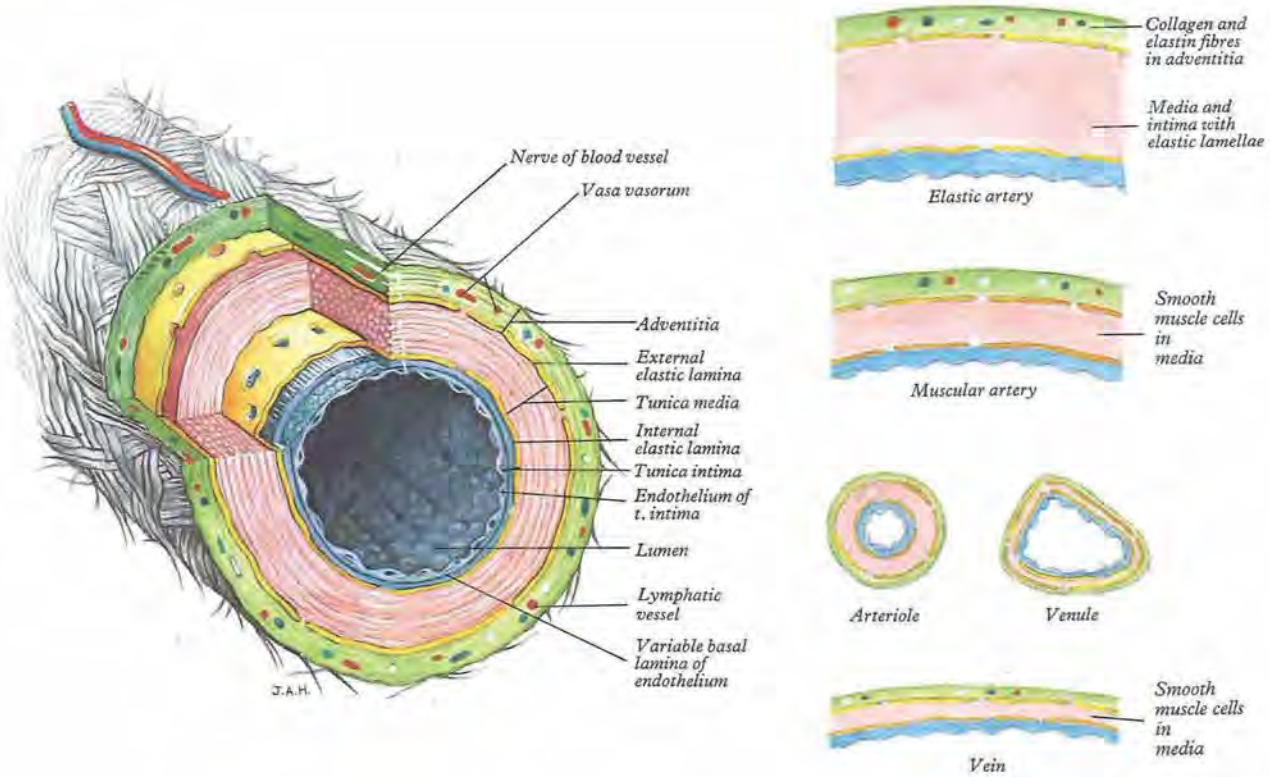
Conducting vessels. The large arteries arising from the heart and their main branches, these are characterized by the predominantly elastic properties of the wall.

Distributing vessels. These are smaller arteries reaching the individual organs and branching into them, and their wall is characterized by a conspicuous muscular component.

Resistance vessels. Mainly arterioles; because of their small size and abundant musculature, these are the main source of the peripheral resistance to blood flow, and they cause a marked drop in the pressure of blood.

Exchange vessels. This is the collective term for capillaries, sinusoids and postcapillary venules. Their wall allows or favours exchange between blood and the tissue fluid surrounding the cells, the essential function of circulatory systems. The exchange includes oxygen, carbon dioxide, nutrients, water and inorganic ions, vitamins, hormones, metabolic products, antibodies and defensive cells of various kinds. Arterioles, capillaries and venules constitute the *microvascular bed*, the site of the *microcirculation*.

Capacitance or reservoir vessels. Larger venules and veins form a coextensive but variable, large-volume, low-pressure array of these vessels conveying blood back to the heart. The high capacitance of these vessels is due to the distensibility (compliance) of their wall, so that the content of blood is large even at low transmural pressures.



10.2 Schematic drawing showing the principal structural features of the larger blood vessels. On the left the major layers and associated features of a muscular artery are depicted. On the right the particular features of an elastic artery, a muscular artery, an arteriole, a venule and a vein are shown, as they appear in transverse sections of these vessels.

Because of the large relative volume of veins, this part of the vascular bed contains the largest amount of blood.

BLOOD CIRCULATION

The cardiovascular or circulatory system provides a continuous circulation of the blood, in a system which is virtually closed. The heart itself is a large, muscular, valved vessel, and has four chambers: right atrium, left atrium, right ventricle and left ventricle. (These somewhat misleading names are discussed on p. 1474.) Each atrium leads into a corresponding ventricle, the right and left chambers being separated by septa. The right and left sides of the heart are thus twin pumps, topographically combined in a single organ but interposed in series in the vascular system, which through their connections they separate into a systemic and a pulmonary circulation (constituting the so-called double circulation typical of birds and mammals, see p. 1472). The course of blood from left ventricle through the body at large to the right atrium forms the systemic circulation, its passage from the right ventricle via the lungs to the left atrium being the pulmonary circulation. The relatively short pulmonary system offers much less peripheral resistance than the systemic circulation, as is reflected in the lower pressures in the pulmonary distribution vessels and in the thinner walls of the right ventricle (p. 1480). The average output volume of blood from the right and left sides of the heart must, of course, be the same. The superior and inferior venae cavae return to the right atrium blood which has become deoxygenated, has taken up carbon dioxide and been otherwise modified during circulation through the tissues of the body. This blood then enters the right ventricle, which expels it via the pulmonary trunk to the lungs. In the pulmonary capillaries blood is brought into close proximity to the inspired air, releasing some carbon dioxide and acquiring oxygen. This oxygenated blood, returned by the pulmonary veins to the left atrium, enters the left ventricle, which pumps it into the aorta for general distribution.

Blood traversing the spleen, pancreas, stomach and intestines is not carried back directly to the heart but passes through the portal vein to the liver. This vein divides like an artery, ending in the hepatic sinusoids intimately associated with the laminae of hepatocytes; the sinusoids are drained by the hepatic veins to the inferior vena cava, whence blood is conveyed to the right atrium. This route is the *portal circulation*; its essential feature is that the blood supplied to abdominal viscera, such as the spleen, pancreas, stomach and intestine traverses not one but **two** sets of capillaries before returning to the heart. One set of capillaries originates from the coeliac and mesenteric vascular bed and provides oxygenated blood to the above-mentioned organs. These are drained into the portal vein, which gives rise to the second set of capillaries, the hepatic sinusoids. The sinusoids carry through the liver unoxygenated blood rich in absorption products from the intestine. The conspicuous musculature of the hepatic portal vein helps to propel the blood through the second microvascular bed. Passage through these two sets of capillaries enables the blood to transfer the products of digestion directly from the alimentary canal to the cells of the liver. Another venous portal circulation connects the median eminence and infundibulum of the hypothalamus with the pars distalis of the adenohypophysis (p. 1884) (Akmayev 1971). A venous portal system is present in the kidney of non-mammalian vertebrates. In essence, a venous portal system is a capillary network that lies between two veins, instead of between an artery and a vein, as in standard circulation. In other situations a capillary network is interposed between two arteries, notably in the renal glomeruli (see p. 1826).

Another circulation in the body is provided by the system of lymphatic vessels and lymph nodes, which conduct the lymph from the interstitial spaces between cells to the large veins of the thorax. Other, more restricted, circulations are those of the cerebrospinal fluid (CSF), perilymph, various endocochlear fluids, ocular aqueous humour, synovial fluid and the fluids of the coelomic spaces, namely the pericardial, pleural and peritoneal cavities.

Dynamic aspects of circulation

Propulsive force is generated not only by the heart, but also by the musculature of arteries and veins, and by the compression of vessels, especially veins, exerted by contracting skeletal muscles and by taut fasciae and ligaments. Other factors influencing the mechanical behaviour of the system are the elasticity of arteries, the viscosity of blood, and the friction between blood and the surface of vessels. The last factor is the origin of laminar flow (or its disruption, as in turbulent flow).

There is a marked influence of gravity on the cardiovascular system, expressed as *hydrostatic pressure*, which, of course, is influenced by the position of the body, whether upright or lying down for example. (In contrast, gravity has very limited effect on the physiology of viscera.) The *hydraulic pressure* is that generated to overcome the resistance offered by the arteries and by the viscosity of blood.

Blood pressure and blood-flow velocity are not steady or constant but pulsatile. Approximately one-quarter of the blood resides in the lesser circulation and the rest in the greater circulation. Three-quarters of the total volume of blood is in veins, especially in small veins of less than 1 mm diameter.

The total cross-section of the vascular network varies with the distance from the heart. It is minimal in the aorta, and it is maximal (and about 4000 × larger) at the level of the venules. The blood pressure, generated to a greater extent by the cardiac musculature and to a lesser extent by vascular musculature, falls progressively but not linearly along the arterial tree. Major falls of pressure occur immediately beyond the arterioles, where the smooth musculature ends, and at the entry into the venules, because of the sudden expansion of the vessel size.

Tissue tethering: an isolated vein can fully collapse and expel the blood it contains, whereas a vessel in situ, especially a vein, a microvessel or a lymphatic, may never collapse completely even when compressed in vivo because of the restraints imposed by tissue tethering.

METHODS OF STUDY OF VESSEL STRUCTURE

The course of large and medium-sized blood vessels can be studied by dissection; injection of coloured tracers may help to identify the vessels. (It is salutary to remember how many centuries it took to work out the essence of the vascular system, even when the necessary means of observation were fully available.) Measurements of vessel size cannot normally be carried out on the cadaver. They can be carried out in vivo or in vessels fixed in situ by lumenal perfusion of the fixative at physiological pressure.

Vascular casts are prepared by injecting under pressure a fluid, coloured resin into the vascular bed of an organ, letting the resin polymerize and digesting away with acid all the tissue. The cast reproduces all the vascular spaces in the injected organ, and, in the case of the microcirculation, can be studied in a scanning electron microscope. The lumenal surface of the endothelium can be studied by scanning electron microscopy after covering it with an ultra-thin layer of metal (**10.7**A, 8A), while freeze-fracture preparations reveal the internal structure of the cell membrane (**10.7**B). To view intrinsic features of the vessel wall by scanning microscopy requires micro-dissection and chemical digestion of collagen and elastic materials, for example with collagenase or strong alkali (**10.8**B).

Histological sections are the method of choice to study the structure of vessel walls: transverse sections are orthogonal to the vessel's long axis, longitudinal sections are parallel to this axis and ideally should pass through the middle of the vessel. Since great structural distortion is produced by the collapse of the vessel, fixation under controlled conditions of distension or pressure is paramount for structural analysis.

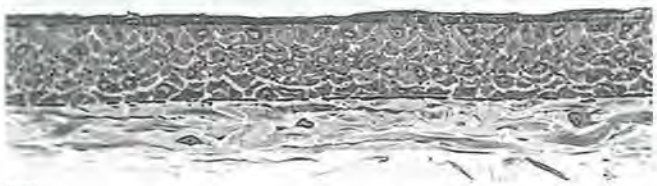
HISTOLOGY OF THE VESSEL WALL

In cross-section a blood vessel has a circular profile and, with few exceptions, a wall of uniform thickness. Small but appreciable differences in wall thickness are found in very curved vessels such as the aorta arch: on the inner curve, where the wall stress is greater, the wall is thicker than on the outer curve. The diameter of the vessel and thickness of the wall are greatly affected by contraction of the wall; great caution must be exerted in evaluating these parameters in histological sections, especially in postmortem material. On the other hand, these two structural parameters are essential to establish the mechanical properties of any vessel. For the structural analysis of blood vessels, irrespective of size, and with the exception of capillaries and venules, three concentric parts or layers (or tunicae) are recognized in the vessel wall (**10.2**):

- the intima (strictly speaking the tunica intima), or innermost layer, whose main component, the endothelium, lines the entire vascular tree.
- the media (tunica media), made of muscle tissue, elastic fibres and collagen; while it is by far the thickest layer in arteries, the media is absent in capillaries and is comparatively thin in veins.
- the adventitia (tunica adventitia), the outer wrapping of the vessel, made of connective tissue nerves and capillaries. The adventitia links the vessels to the surrounding tissues.

The main histological components of the vessel wall are therefore an endothelium, elastic tissue, muscle tissue, collagen and connective tissue (**10.3**). With the exception of the endothelium, the general features of the various tissues have already been described in sections 2 and 9.

A



B

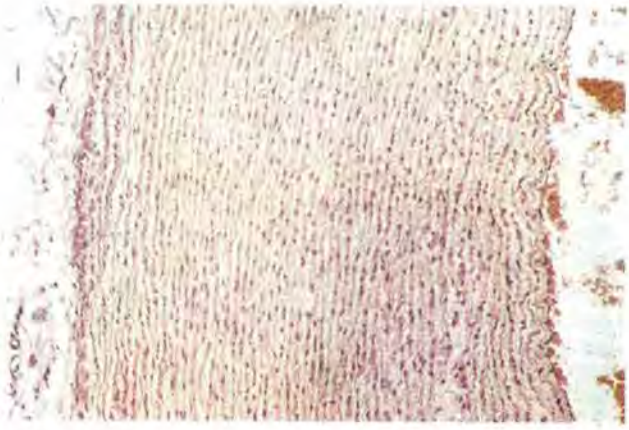
C

10.3 Histological sections of a muscular artery, fixed in situ in a condition of physiological distension. A. The artery is sectioned transversely, and the muscle cells of the media are cut longitudinally. Magnification × 510. B. The artery is sectioned longitudinally, and the muscle cells are cut transversely. Magnification × 510. C. At higher magnification, the endothelial cells can be seen, somewhat elongated in the direction of the blood flow; the dark line beneath the endothelium is the inner elastic lamina, which shows fenestration, and is straight in this preparation because it was fixed while distended. The tunica media is made of five or six arrays of muscle cells, which are transversely sectioned. The tunica adventitia displays collagen fibres and fibroblasts. Magnification × 510.

ENDOTHELIUM

The endothelium is a monolayer of flattened polygonal cells which extend continuously over the luminal surface of the entire vascular tree (**10**.4, 5, 6, 11). Its structure includes specific features in different regions of the vascular bed. The endothelium is a key component of the vessel wall because it serves several major physiological roles, as listed below.

- Because of their position, endothelial cells influence blood flow.
- They regulate the diffusion of substances and of cells, out of and into the circulating blood, across cell junctions and through their cytoplasm.
- They participate in the process of coagulation (see p. 1400), by secreting clotting factors, and in the process of fibrinolysis.
- They have selective phagocytic activity and extract substances from the blood, and have other metabolic activities; for example, the endothelium of the pulmonary vessels removes and inactivates several polypeptides, biogenic amines, bradykinin, prostaglandins and lipids from the circulating blood. Endothelium Derived Relaxing Factor (Ryan & Ryan 1984).
- Endothelial cells secrete substances (endothelium derived relaxing factor or nitric oxide, and endothelins) which affect vasomotility, and probably also substances which promote the growth of the endothelium itself, such as Basic Fibroblastic Growth Factor (b-FGF) (Schweigerer et al 1987).
- They are sensitive to the transmural stretch imposed by the pulse, via stretch-sensitive ionic channels in the cell membrane, thus endowing the vessel wall with a sensor or a sensory element.
- They can synthesize (and at least they do so in in vitro cultures) fibronectin, laminin, collagen, elastin and other components of the subendothelium (Ryan & Ryan 1984).
- They are capable of proliferating to provide new cells during the period of increasing size of a blood vessel, to replace damaged or exfoliated endothelial cells, and also to provide growing solid cords of cells which are the forerunners of new blood vessels (see angiogenesis, p. 470).

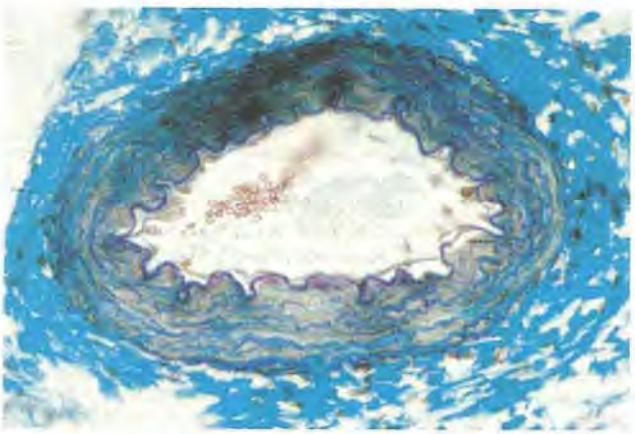


10.4A Part of a transverse section of the aorta of a monkey, stained with haematoxylin and eosin, showing the distribution of cell nuclei. Magnification × 100.

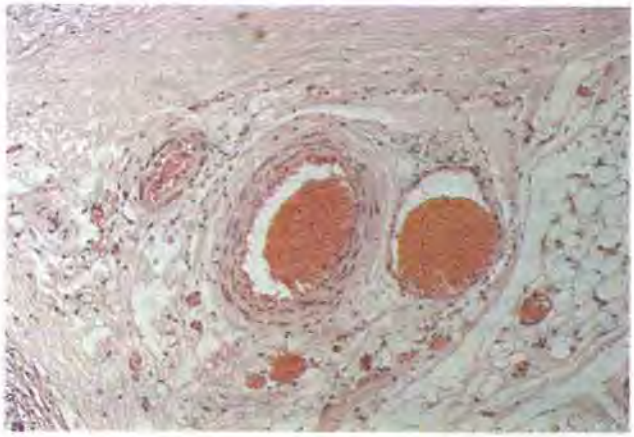
10.4B Part of a transverse section of a young human aorta stained with Verhoeff's stain for elastin. Note the density of the concentric fenestrated elastic lamellae. Magnification × 100.

Endothelial cells are wide and thin, tile-like and slightly curved to fit the curvature of the vessel. They are somewhat elongated in the direction of blood flow, especially in arteries (**10**.11). Endothelial cells firmly adhere to each other at their edges, so that the lining of the lumen presents no discontinuity (except in sinusoids, see p. 1466; **10**.4.) The thickness of endothelial cells is maximal at the level of their nucleus, where it can reach 2–3 μm, this part of the cell often bulging slightly into the lumen (**10**.3c). Elsewhere, the endothelial cell is thinner and laminar; in capillaries, these portions of the cell are very attenuated, often measuring as little as 0.2 μm in thickness (**10**.12).

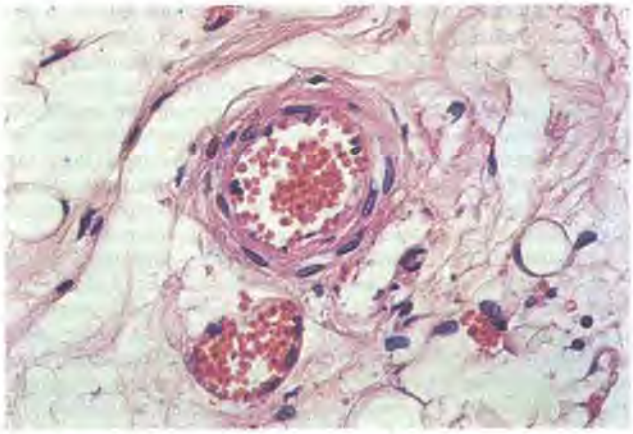
The *luminal surface* of the endothelium is relatively smooth. However, it is common to find endothelial laminar projections into the lumen, especially near the cell junctions. The cell surface is pitted by the numerous caveolae (**10**.7B) and the membrane is coated by a prominent glycocalyx (Luft 1966; Ryan & Ryan 1984). The glycocalyx is a highly-charged, polysaccharide-rich felt of glycoproteins,



10.4C Transverse section of a small muscular artery, stained with Verhoeff's stain for elastin and van Gieson stain for collagen. Note the prominent inner elastic lamina, which is heavily folded because the vessel was fixed postmortem when collapsed and virtually empty. Magnification × 200.



10.5 Transverse section of two small muscular arteries and a small vein, stained with haematoxylin and eosin. Numerous venules and capillaries are included but are indistinct at this magnification. (Supplied by D R Turner of the Department of Pathology, Guy's Hospital Medical School.)



10.6 Transverse section of a large arteriole and venule in loose connective tissue, stained with haematoxylin and eosin. (Source as **10.5.**)

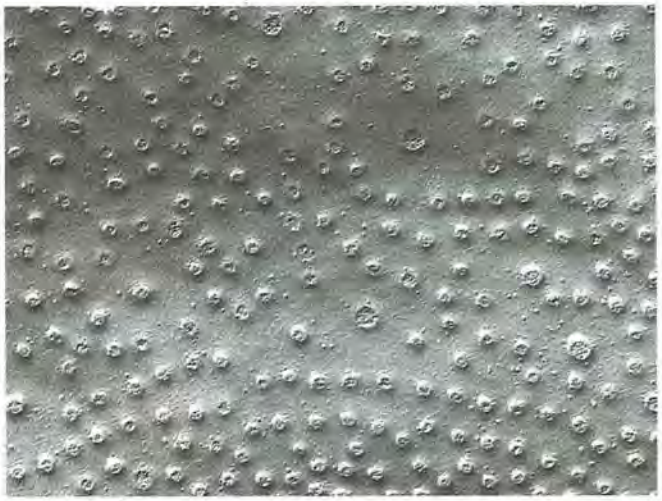
anchored to the cell membrane, which controls the transport of solutes and may mediate the mechanical effects of blood flow on the endothelial cells. Because of the high charge density the glycocalyx may contribute to the non-thrombogenic properties of the surface of the intact endothelium. The glycocalyx is not seen in standard electron micrographs of the endothelium, but can be visualized with electron-dense substances, such as ruthenium red, which bind specifically to glycoproteins. The abluminal surface is also pitted by caveolae and it rests over a basal lamina.

Caveolae are consistently observed in all endothelial cells. These invaginations of the cell membrane measure about 200 × 50 nm; their membrane is in continuity with the cell membrane proper and their cavity opens into the extracellular space through a narrow neck (**10.7B**, 12B). Their spatial density is of the order of several tens per square micron of cell surface; because of their large number, more than half of the plasma membrane at the cell surface is in the form of caveolae. Caveolae are regarded by several authors as manifestations of a process of transcytosis: the membrane is pinched in from **one surface** of the endothelial cell, and forms a caveola (which includes a tiny amount of extracellular fluid) that eventually detaches itself and becomes a free-moving spherical vesicle in the cytoplasm; the vesicle then merges with the membrane on the **other surface** of the cell, again forming a caveola (and again releasing its tiny amount of fluid into the extracellular space). In this interpretation, a 'shuttle' system, caveola–vesicle–caveola, transports material across the endothelial cell, in both directions. It is a 'bulk' transport because it is relatively non-selective and it involves a sizeable amount of extracellular fluid. There have been strong doubts about this form of transendothelial transport, mainly because of its lack of selectivity. Studies of serial sections of endothelial cells of capillaries have shown that even those structures which appear as free-floating vesicles in a single section are actually connected with the extracellular space; true vesicles seem to be exceedingly rare and the caveolae are constantly open to the extracellular space (Frokjaer-Jensen 1984). In other cell types, such as smooth muscle cells, caveolae are known to be stable structures, not involved in endocytosis (unlike coated pits and coated vesicles).

Cytoplasmic organelles of endothelial cells include mitochondria, granular and agranular endoplasmic reticulum, some free ribosomes and occasionally a pair of centrioles. In spite of the evidence of chemical factors being released by endothelial cells, cytological signs of secretion are not prominent. Bundles of microfilaments and intermediate filaments are also found. The former are made of actin and the latter are usually vimentin filaments. Filaments contribute to maintaining a certain shape of the cell and impart mechanical stability, and presumably they play an important role when the cell changes shape or migrates. Characteristic organelles of endothelial cells are the *Weibel-Palade bodies*, which are cytoplasmic vesicles, elongated, 0.2 × 2–3 μm, containing regularly spaced tubular structures parallel to the long axis which give rise to a striation. These organelles produce and store a large glycoprotein known as von Willebrand protein (or factor VIII), which mediates the binding of platelets to the extracellular matrix of the subendothelium after vascular injury. Von Willebrand protein is also produced, in larger amounts, by megakaryocytes and is stored in platelets.

Seen from the lumen, endothelial cells usually have a polygonal contour. At their edge they adhere to adjacent cells through an area of apposition where junctions of the adherens, communicans and occludens types are found (the so-called junctional complex). The area of apposition can be a straight line covering the shortest distance between luminal and abluminal aspects of the endothelium. More commonly, there is an oblique or a tortuous line of apposition, sometimes with overlap or interdigitation between endothelial cells. Often a laminar process from the edge of an endothelial cell projects into the lumen and seems to guard the area of apposition of the endothelial cells. The role of these projections, however, is unknown. A tight junction forms a belt (zonula occludens) around the contour

10.7A Inner surface of the endothelium of a basilar artery, examined by scanning electron microscopy. The lumenal surface is tessellated by endothelial cells which are tightly packed and elongated in the direction of the blood flow. Magnification × 1250. (Supplied by Masoud Alian of University College London.)



10.7B Freeze-fracture preparation of the plasma membrane of an endothelial cell. The E-face of the membrane shows innumerable caveolae fractured at the level of their neck. Magnification × 40 000.

of an endothelial cell, involving all the cells that are directly adjacent. These tight junctions are best visualized by freeze-fracture, and they vary in extent in different vascular regions. They provide a seal which blocks or restricts movement of fluids through the intercellular gaps of the endothelium; they also limit the lateral diffusion of membrane proteins and lipid between the luminal and the abluminal domains of the cell membrane. Gap junctions and, occasionally, intermediate junctions accompany the tight junctions between endothelial cells (Hüttner et al 1973); they invariably reside further away from the lumen than the tight junctions. The gap junctions are likely to allow the bi-directional and non-selective diffusion of ions and small molecules between endothelial cells. Cell contacts between endothelial cells and muscle cells are common in arterioles, where the separation between endothelium and media is reduced and the inner elastic lamina is very thin or absent.

Endothelial cells can synthesize and secrete collagen; thus they are regarded as contributing to the formation of the inner elastic lamina.

SMOOTH MUSCLE

This is invariably of the smooth type (see p. 738), with the exception of small segments of the pulmonary veins (p. 738) which, in the portion nearest to the heart, have striated musculature of the cardiac type. Smooth muscle cells are the only cell type found in the media of most arteries of mammals (**10.7A**, 11). One function of smooth muscle in blood vessels is to reduce, with their contraction, the vessel's lumen and hence the flow through it, an action which has the effect of raising the pressure on the proximal side. This role is particularly effective in small resistance vessels where the thickness of the wall is great relative to the diameter of the vessel. Another function of smooth muscle is to alter the stiffness of the wall, causing no constriction (isometric contraction) but affecting the distensibility of the wall and the propagation of pulse. The mechanics of the musculature of the media is complex for several reasons: because the structures involved have a concentric arrangement; because the tissue is incompressible and therefore of constant volume; because the spatial arrangement of muscle cells and fibrous extracellular materials is variable and not well understood; because materials of different mechanical properties and different spatial arrangement are tightly linked together. Properties of distensibility, strength, self-support, elasticity, rigidity, concentric constriction, are interrelated and finely balanced in the various regions of the vascular bed.

Muscle cells are responsible for the active motility of the vessel wall. These cells also synthesize and secrete elastin, collagen, mucopolysaccharides and other extracellular components which bear directly on the mechanical properties of the vessel. The muscle cells of the arterial media have been rightly labelled multifunctional mesenchymal cells (Wissler 1968). After damage to the endothelium, muscle cells migrate into the intima and proliferate, forming bundles of longitudinally oriented muscle cells (neo-intima; Fishman et al 1975). In pathological conditions, muscle cells with their fatty degeneration participate in the formation of atheromatous plaques.

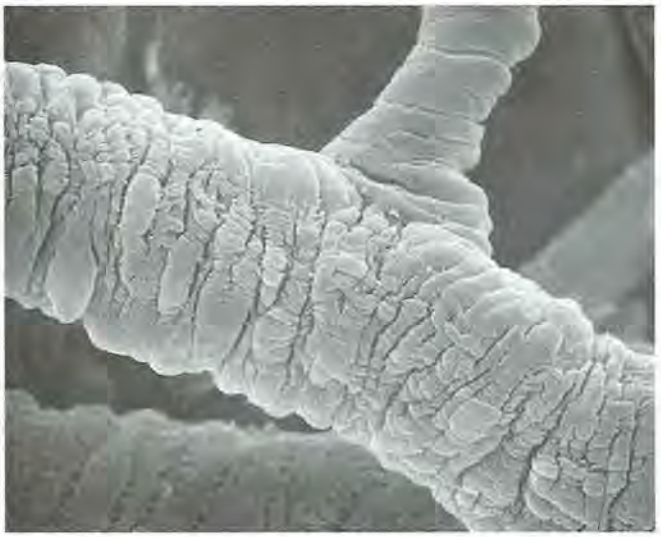
The vascular musculature is made of single, uninucleated muscle cells (vascular muscle cells) which have many common structural features with visceral muscle cells, but are also somewhat different (**10.4A**, 8, 11). The basic structural features of smooth muscles are described elsewhere (p. 771). In large arteries, where the blood pressure is high and the stress of the wall is high, the muscle cells are shorter (60–200 μm) and smaller in volume than in visceral muscles. The cell profile is very irregular and the cell membrane has many conspicuous dense bands where the contractile apparatus and the extracellular fibrous components are linked to each other. In arterioles and veins, smooth muscle cells resemble more closely visceral muscle cells.

The cells are packed with myofilaments and with elements of the cytoskeleton, including intermediate filaments. The latter, which are invariably of the desmin type in visceral smooth muscles, are made of vimentin or of vimentin and desmin in vascular muscle cells.

Cell-to-cell junctions are mainly of the adherens type and provide mechanical coupling between the cells (**10.11**). There is also a small number of gap junctions. Far more numerous than cell-to-cell junctions, especially in arteries, are the junctions between muscle cell and connective tissue matrix (*cell-to-stroma junctions*). Between adjacent muscle cells there are also interdigitations and extensive areas of apposition without apparent membrane specializations; they involve fusion or disappearance of the basal laminae and are likely to provide some adhesion between the two cells.

The orientation of muscle cells within the media has been the object of several investigations, and there is no conclusive account of this anatomical feature. In most arteries the orientation of the cells is approximately circumferential; over a wide range of vessel sizes the deviation from circumferential is minimal (Canham & Mullin 1978; Walmsley 1983), except for the occasional presence of a bundle of musculature of unexpected orientation within the media. In large vessels the musculature is divided into layers or into bundles and there are some variations even between adjacent lamellae. The circumferential arrangement appears more irregular when the vessel contracts and may be grossly disrupted in collapsed arteries. A helical orientation (as in a cylindrical spring) of muscle cells has

10.8A A small vessel approaching the surface of the brain, examined by scanning electron microscopy. The free surface of the endothelium is corrugated by the relief of the endothelial cells. Magnification × 750. (Source as **10.7A**.)



10.8B Arteriole isolated from the mesentery, freed of its adventitia by enzymatic digestion and examined by scanning electron microscopy. The muscle cells are contracted and are wound circumferentially in the vessel wall. Magnification × 1000. (Micrograph supplied by Professor Komuro, School of Human Sciences, Waseda University, Japan.)

been described in the lamellae of some large arteries. In the rat aorta, for example, where right- and left-handed helices may be present in successive lamellae (Rhodin 1962) has reported that the pitch increases during postnatal growth. In large elastic arteries, muscle cells often connect the elastic lamellae on either side, hence they have also a slightly spiral orientation (as in a two-dimensional spring, such as a watch spring). The spatial orientation of medial muscle cells is regarded as one of the anatomical factors affecting the mechanical properties of the vessel wall. It is possible, however, that the exact orientation of the muscle cells is not the most significant factor in this respect. Because of the cohesion of the media, the dense packing of cells and stroma, the vast number of cell-to-cell junctions and cell-to-stroma junctions and the lateral dislocation of volume when the cell shortens, a highly geometrical arrangement of the contracting cells is not a major requirement for an adequate functional performance.

In physiological conditions the intima of some large arteries contains a few smooth muscle cells, longitudinally arranged. In large arterioles some bundles of longitudinally oriented musculature are found near the adventitia. While in small arteries and arterioles the arrangement of the musculature becomes more regular and invariably circumferential (**10.8**B, 11), in veins the arrangement of the musculature is more variable (see p. 1466).

Even when they run circumferentially, muscle cells in the media of large arteries are only slightly curved, and many cell lengths are needed to make up the circumference of the vessel. In contrast, in arterioles the muscle cells are tightly coiled (see p. 1463).

COLLAGEN AND ELASTIC MATERIAL

A major constituent of the vessel wall are the extracellular materials, collectively known as the *stroma* or *matrix*. In large arteries and veins this constitutes more than half of the mass of the wall, and is mainly made of collagen and elastin (**10.11**). Other fibrous components, such as fibronectin microfibrils, and abundant amorphous or soluble materials are present in the extracellular spaces of the vessel wall.

Elastic material is found in all arteries and veins and it is especially abundant in elastic arteries (**10.11**A). Individual *elastic fibres* (0.1–1.0 μm in diameter) anastomose with each other forming net-like structures, which spread predominantly in a circumferential direction (**10.8**B). A more extensive degree of fusion produces lamellae of elastic material, which are usually perforated but separate layers of muscle cells, thus allowing the formation of lamellar 'units' (see p. 1463). A conspicuous elastic lamella occurs in arteries, between intima and media, the *inner elastic lamina*. This lamella is a tube of elastic material which allows the vessel to recoil after distension. When the intraluminar pressure falls below physiological limits, the inner elastic lamina is compressed sideways and it coils up into a regular corrugated shape (**10.4**C): in these conditions the lumen is much reduced but is not obliterated, and the profile of the artery remains circular. Fenestrations in the elastic lamina allow materials to diffuse between intima and media. An *outer elastic lamina*, similar in appearance but markedly less well developed than the inner elastic lamina, is situated at the outer aspect of the media at the boundary with the adventitia. Elastic fibres are less abundant in the adventitia.

Collagen fibrils (transversely banded cables of 30–50 nm diameter, see p. 81) are found in all three tunicae (**10.11**), and especially around the muscle cells of the media. Collagen is abundant in the adventitia where it forms large bundles of fibrils (*collagen fibres*) which increase in size from its innermost component near the media to its outermost component.

In general terms, collagen and elastic fibres in the media run parallel or at a small angle to those of the muscle cells, and therefore they are mainly circumferentially arranged. In contrast, the predominant arrangement of collagen fibres in the adventitia is longitudinal, and this imposes constraints on the elongation of large vessels under pressure. In large arteries, for example, the radial distension under the effect of the pulse far exceeds the longitudinal distension (Burton 1954). While the outer 'sheath' of collagen, i.e. that of the adventitia, limits the distensibility of the vessel, the collagen network of the media mainly provides attachment to the muscle cells and transmits force around the circumference of the vessel. While collagen fibres are inextensible, elastic fibres are very highly extensible. They provide ample attachment to the muscle cells, favouring a uniform spread of the muscle tension around the vessel wall; in a distended vessel, the elastic fibres store energy and, by recoiling, help to restore the resting length and calibre.

The extracellular material of the tunica media, including collagen and elastic fibres, is produced by the muscle cells during development. Its turnover is slow compared to that in other tissues, and this too is controlled by the muscle cells of the media. In the adventitia, collagen is synthesized and secreted by fibroblasts, as in other connective tissues. During development in postnatal life, while vessels increase in diameter and wall thickness, there is an increase in elastin and collagen content. Subsequent changes in vessel structure include an increase in the collagen-to-elastin ratio, with a reduction in vessel elasticity.

PERICYTES

In capillaries, where a proper adventitia is absent and where there are no muscle cells, other cells, the pericytes, are present at the outer surface of the vessel (**10.12**A). Pericytes, or cells of Rouget, are known under various other names and probably do not represent a uniform population of cells. They are elongated, have a bulging cell body and long laminar processes spread around the capillary endothelium. They do not form a continuous layer but their shape suggests a tight grip of the capillary and a mechanical supporting role. They (or some of them) may have a phagocytic role. It is possible that some pericytes are a source of new endothelial cells, to replace any which may become damaged in the endothelium, or of mesenchymal cells or of muscle cells. Their number and morphology are very variable. Because they contain some bundles of filaments, and they contain, as shown by immunohistochemistry, actin, myosin, tropomyosin and desmin (Uehara et al 1990), the pericytes are regarded by some authors as contractile cells (Rhodin 1962): the suggestion that they are a primitive type of muscle cell (Zimmermann 1923) is, however, purely speculative. Most pericytes have areas of close apposition with endothelial cells, occasionally forming adherens junctions (Forbes et al 1977). These are the only areas where a basal lamina does not coat the surface of the pericyte.

Leucocyte–endothelial cell interactions

INTRODUCTION

A remarkable feature of the immune system is the integration of functionally different organs and tissues by constant migration of lymphoid cells from one site to another along blood and lymphatic vessels. The migration of lymphocytes and the interactions of activated cells during immune responses are regulated by cell-surface molecules. Adhesive interactions between cells, and between cells and the extracellular matrix, are vital to all developmental processes and have a crucial role in a well-functioning immune system throughout life (Springer 1990).

Mature 'virgin' lymphocytes from the bone marrow and thymus, the sites of primary lymphoid organs, enter the blood circulation and reach secondary lymphoid organs such as lymph nodes, spleen, tonsils, Peyer's patches and appendix, as well as dispersed lymphoid tissues. The latter can be associated with skin ('skin associated lymphoid tissue' or SALT), or the mucosal surfaces of the gastrointestinal tract ('gut associated lymphoid tissue' or GALT), the respiratory tract

('bronchus associated lymphoid tissue' or BALT) and the urogenital tract (a part of the 'mucosa associated lymphoid tissue' or MALT). The secondary lymphoid organs and tissues guard the portals of entry for antigens and provide a favourable environment for the interactions of antigens with lymphocytes (Brandtzaeg 1984). Finally, using the efferent lymphatic drainage, both virgin and memory lymphocytes re-enter the venous limb of blood circulation via the lymphatic trunks and the thoracic duct and recirculate. This arrangement maximizes the probability of effective antigen–lymphocyte interaction throughout the body.

VASCULAR ENDOTHELIUM

The lumen of all blood vessels is lined by endothelial cells which maintain the fluidity of the blood, regulate the interactions of circulating cells and platelets with the vessel walls and form the interface between the bloodstream and extravascular tissues. Although the endothelium consists of a monolayer of cells it has, under normal conditions, two different surfaces that exhibit morphological as well as biochemical polarity: the luminal, non-thrombogenic surface, and the abluminal, adhesive surface (de Groot 1987). The abluminal surface faces the deeper layers of the vessel wall and is adhesive for platelets. In contrast, the luminal surface of endothelial cells can be considered blood cell-like, a haemocompatible interface. It represents a natural barrier capable of regulating the circulating levels of several vasoactive and platelet-active mediators and it does not support the adherence of leucocytes or platelets (Brown 1994). However, perturbation of endothelial cells induces the production of platelet-activation factor (PAF), which is a potent stimulus for platelet aggregation.

Many functions of human vascular endothelial cells are dynamic rather than fixed. For example, on endothelial injury, with the exposing of the subendothelial matrix, the nearby uninjured endothelial cells migrate across the denuded surface and can re-endothelialize a small defect within hours (Jarrell et al 1987).

LYMPHOCYTE CIRCULATION AND MIGRATION INTO LYMPHOID AND NON-LYMPHOID ORGANS

Under normal conditions there is a continuous flow of lymphocyte through secondary lymphoid organs. These organs are structurally analogous in that they all possess: first, a complex framework which provides ideal conditions for interactions between lymphocytes and antigen-presenting cells; second, separate domains which are more or less specific for T or B cells; and third, specialized segments of vasculature supporting the extravasation of circulating lymphocytes, known as the postcapillary or high endothelial venules (HEVs) (**10.9A**).

The bulk of the lymphocyte traffic is thought to pass through HEVs located in the parafollicular areas of lymph nodes, palatine and nasopharyngeal tonsils, Peyer's patches, appendix and the mucosal lymphoid tissue aggregates of MALT. There are no HEVs in the spleen, yet more lymphocytes migrate through this organ than through all lymph nodes (Pabst & Binns 1989). Although it has been proposed that the marginal sinus lining cells may be responsible for the initial arrest of blood lymphocytes in the splenic marginal zones, little is known about the mechanism of lymphocyte traffic through the spleen (Stevens & Lowe 1992; Picker & Butcher 1992).

The HEVs are also absent from primary lymphoid organs (bone marrow and thymus) and, normally, they are not present in non-lymphoid organs and tissues in spite of a continuous lymphocytic migration through them, in the course of general surveillance. Here, migration may occur through capillaries, sinusoids and possibly low endothelial venules. Pabst and Binns (1989) studied the migration route of lymphocyte subsets in pigs and sheep using suspensions of in vitro fluorescein isothiocyanate (FITC) labelled peripheral blood lymphocytes. Within the first few minutes 40% of lymphocytes were found in the lungs and 14–21% in the liver. Thus, similar to spleen, the lungs and the liver are not only sites for capturing effete cells but these non-lymphoid organs actively participate in recirculation of lymphocytes.

Interestingly, HEV-like vessels have been found at many sites of chronic inflammation where they are believed to support the extravasation of large numbers of leucocytes. Neutrophils, lymphocytes and monocytes migrate into inflamed tissue sites with class-specific kinetics: the relatively nonspecific neutrophils appear within minutes of stimulation while the antigen-specific T and B cells and monocytes arrive within hours but may remain for days (Osborn 1990). One of the best-documented examples of this phenomenon is the rheumatoid synovium (Freemont et al 1983; Koch et al 1991).

Some lymphocytes move from one secondary lymphoid organ to another via the blood and lymphatic vessels while others stay resident in these organs for a variable period of time. For example, antigen-specific lymphocytes are preferentially retained in those lymph nodes which drain the source of the antigen (Picker & Butcher 1992). Moreover, there is evidence for carefully regulated, non-random migration of lymphocytes to particular anatomical sites, referred to as 'homing' (Rosen 1989; Springer 1990; Picker & Butcher 1992). Thus, lymphocytes which home to the gut are thought to be transported selectively across gut specific microvasculature, while other populations of lymphocytes home in a similar manner to different target organs, such as the tonsils or peripheral lymph nodes. This tissue specificity for lymphocyte homing is thought to be relative rather than absolute and may be determined by a combination of multiple factors rather than by a single specific factor (Shimizu et al 1992).

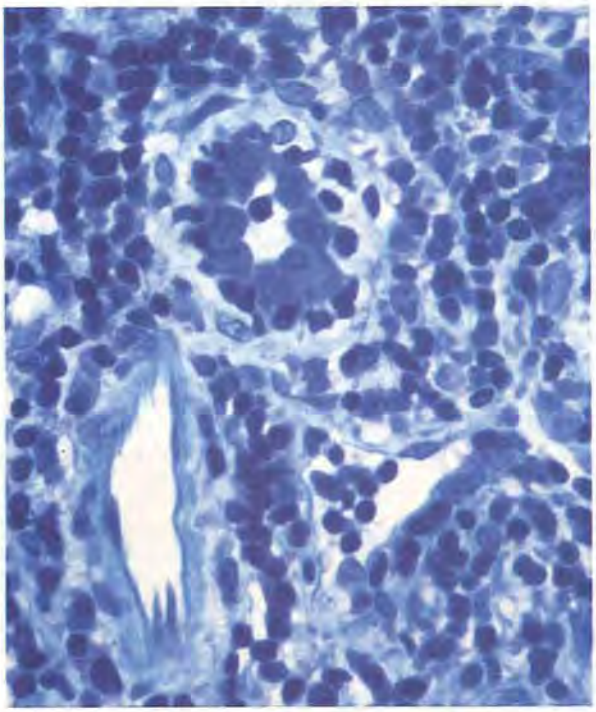
It has been now generally accepted that circulating lymphocytes are leaving the HEVs to home into the lymphoid compartments of secondary lymphoid organs and tissues, although in the past some researchers held the opposite view. In 1929 Ehrich proposed that in a lymph node 'small lymphocytes were immigrating into the vein lined with endothelium consisting of very high and crowded cells'. The physiological significance and the direction of transendothelial migration of lymphocytes had not been appreciated until the original autoradiographic experiments of Gowans and Knight (1964).

HIGH ENDOTHELIAL VENULES

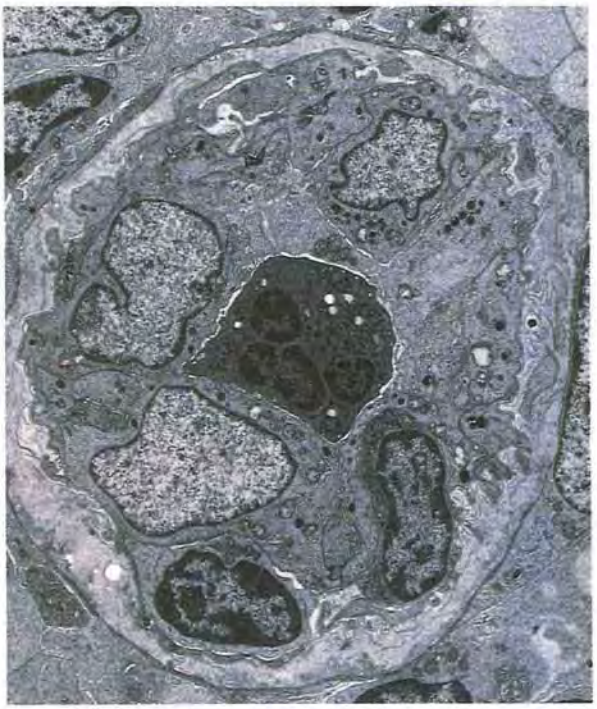
High endothelial venules are found in most mammalian species and recognized by the conspicuous plump endothelial lining associated with numerous luminal mural and extramural lymphocytes (**10.9A**). These vessels are located within the T cell domains, between and around lymphoid follicles in all secondary lymphoid organs and tissues, with the exception of the spleen. In the human palatine tonsil HEVs were also seen in the lower parts of reticulated crypt epithelium (Perry et al 1992). On account of their position and diameter of 7–30 μm, HEVs are also referred to as post-capillary venules. They begin at a junction of flat-walled venous capillary limbs, receive venules draining the surrounding lymphoid follicles and end as tributaries to larger veins (Ohtani et al 1989).

The luminal aspect of HEVs presents a so-called 'cobblestones' appearance covered with a prominent glycocalyx (Anderson & Anderson, 1975). The single layer of high endothelial cells (HECs) rests on endothelial basement membrane which is intimately related to pericytes. The pericytes, in turn, are surrounded by their basement membrane and a small amount of connective tissue (**10.9B**). The HECs are linked by discontinuous macular junctions at their apical and basal aspects, which may be circumnavigated by migrating lymphocytes (Anderson & Anderson 1976).

Ultrastructurally, HECs have the characteristics of metabolically active secretory cells. They contain large, rounded euchromatic nuclei with one or two nucleoli, prominent Golgi regions,



10.9A The height of the endothelium of transversely sectioned high endothelial venule (*HEV; upper field*), lined with columnar cells and associated with numerous dark blue stained lymphocytes, contrasts with the neighbouring low endothelial venule (*left lower field*) and lymphatic vessel (*right lower field*). Human palatine tonsil. Methylene blue/Azur II.



10.9B Transverse section of HEV in human palatine tonsil. The vessel lumen is occupied by a neutrophil completely surrounded by high endothelial cells. The electronlucent nuclei of three of these cells are present in the plane of this section. Pericyte (*right*) with its attenuated processes lies externally to the undulating endothelial basal lamina and a small amount of connective tissue. Note the position of the two mural (*right lower field*) and the extramural (*left upper field*) lymphocytes. TEM. Magnification × 3 000.

10.9C High endothelial cell in rheumatoid synovium containing many sectioned profiles of the microtubular Weibel-Palade bodies above and around the nucleus. TEM. Magnification × 20 000.

many mitochondria, ribosomes and pinocytotic vesicles. Typically, they also possess the microtubular Weibel-Palade bodies in which Factor VIII and P-selectin are stored (**10.9C**). Stimulation of the endothelium by thrombin, histamin or reactive oxygen species results in rapid translocation and redistribution of P-selectin to the endothelial surface (Hogg 1992; Cronstein & Weissmann 1993). The 10–12 μm high cuboidal or columnar cells protrude into the lumen and the rate of collision between circulating blood cells and vessel wall is increased. Subsequently collision attachment and migration of leucocytes can follow.

MOLECULAR BASIS OF HOMING LEUCOCYTES

Cell adhesion molecules (CAMs) is a collective term for cell surface glycoproteins regulating the adhesion between cells. Endothelial adhesion molecules facilitate the attachment of free circulating leucocytes to the vessel walls. A rapid transition between adherent and non-adherent states of leucocytes is essential for the maintenance of their dual function of immune surveillance and responsiveness. However, fundamental changes occur on endothelium in the vicinity of an inflammatory response when inflammatory mediators such as lipopolysaccharide, interleukin-1 (IL-1), tumour necrosis factor alfa (TNF-α) or gamma interferon (γ-IFN) increase the adhesion but reduce the selectivity of extravasating leucocytes (Shimizu et al 1992).

Many of the adhesion molecules that mediate interactions between blood leucocytes and HEVs or cytokine-activated endothelium have been identified. These molecules can be divided into three general categories: the selectin family, the integrin family and the immunoglobulin supergene family. The selectin and integrin molecules are expressed on leucocytes and mediate adhesion of circulating cells to the endothelium, whereas selectins and members of the immunoglobulin supergene family are expressed on the endothelium and provide the 'sticky' substrate to which leucocytes can adhere (Springer 1990; Cronstein & Weissmann 1993).

Selectins

Three molecules have been identified so

far as members of the selectin family of adhesive proteins. They are the L-selectin (also known as lymphocyte homing receptor, CD62L, Leu-8, Mel-14, LAM-1), E-selectin (CD62E, ELAM-1) and P-selectin (CD62P, GMP-140, PADGEM). Selectins have a characteristic amino-terminal lectin domain, an epidermal growth factor-like domain and a variable number of complement regulatory domains. The selectin molecules bind to specific sialyated carbohydrates, including sialyl Lewis X, which is a unique feature among adhesive proteins (Polley et al 1991).

The L-selectin is expressed on most leucocytes and its endothelial ligand has been termed recently GlyCAM-1 (Imai et al 1993). Importantly, L-selectin mediates homing of lymphocytes to peripheral lymph nodes as well as accumulation of neutrophils and monocytes at sites of inflammation.

The E-selectin is a molecule which is only transiently expressed on endothelium. It is an inducible adhesion molecule which was first described as mediating adhesion of neutrophils to inflammatory cytokine activated endothelium (Bevilacqua et al 1989).

The P-selectin is rapidly mobilized to the endothelial surface by fusion from storage in Weibel-Palade bodies following stimulation of the endothelium. Since P-selectin is quickly endocytosed by the endothelial cells its expression is only short lived. P-selectin binds to ligands expressed on neutrophils, platelets, and monocytes and, similar to E-selectin, it tethers leucocytes to endothelium at sites of inflammation (Zimmerman et al 1992).

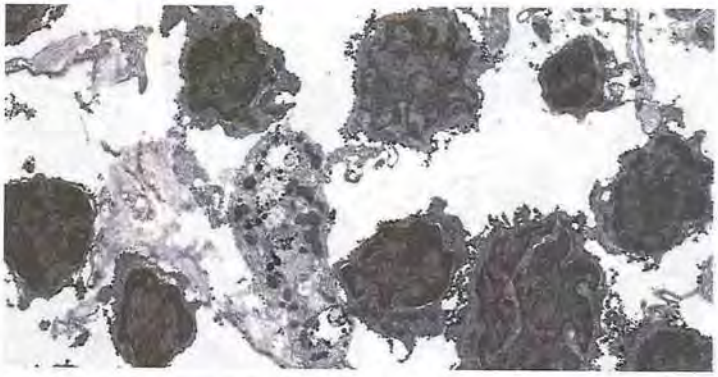
Integrins

The integrins are a large family of molecules mediating cell-to-cell adhesion as well as interactions of cells with intercellular substances. They are therefore essential in regulating spatial orientation and cell movement. Integrins represent a group of related heterodimeric adhesion proteins and each molecule comprises an α- and a β-subunit (β1, β2 and β3).

The β1 integrins are a subfamily of six molecules known as 'very late antigens' (VLAs) which function mainly as receptors for components of extracellular matrix. The VLA-1 and VLA-2 adhesion molecules were found to be expressed on lymphocytes only 2 to 4 weeks after antigenic stimulation in vitro and they bind to the extracellular matrix (Keelan & Haskard 1992). On the other hand the VLA-4 integrin ($\alpha 4\beta 1$, CD49d/CD29), which is present on resting lymphocytes, monocytes and eosinophils, binds also to its ligand on activated endothelium, the vascular cell adhesion molecule 1 (VCAM-1 CD106).

In contrast to β1 integrins the expression of β2 integrins is limited to white blood cells. Although the leucocyte integrins are not constitutively adhesive they become highly adhesive after cell activation and therefore play a key role in the events required for cell migration. The β2 subfamily comprises three molecules with common β2 subunit (CD18) and with chains of different molecular weight (CD11a, b, c) (Cronstein & Weissman 1993).

The CD11a/CD18 integrin molecule is known as the lymphocyte function-associated antigen 1 (LFA-1) and is present on the surface of all leucocytes (**10.9D**). The endothelial ligands for LFA-1 are the intercellular adhesion molecules 1 and 2 (ICAM-1 and ICAM-2) which belong to the immunoglobulin superfamily. The other two integrins of the β2 subfamily are CD11b/CD18 (Mac-1, CR3) and the less well-characterized CD11c/CD18. These molecules have more limited distribution on neutrophils, monocytes and natural killer cells and they mediate adhesion of leucocytes to endothelium by binding to ICAM-1. Recently, monoclonal antibodies directed against integrin-mediated adhesion have been administered in studies aimed to decrease inflammatory responses (Jasin et al 1992).

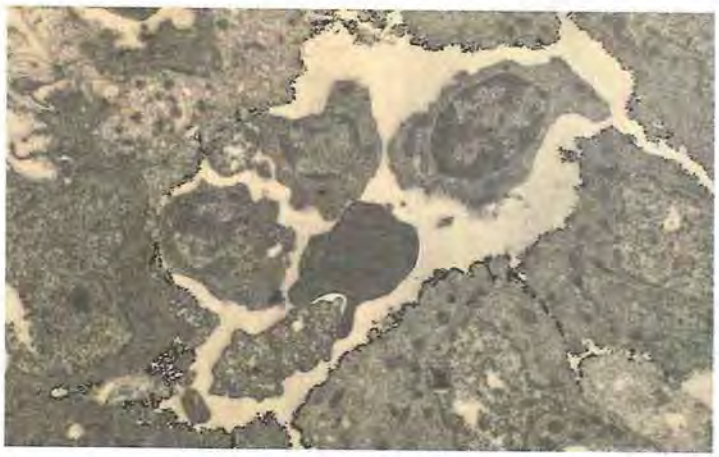


10.9D Lymphocytes in the interfollicular region of human palatine tonsil expressing LFA-1 (black dots) on their cellular membranes. Immunoelectron microscopy. Incubation with mAb to LFA-1. Magnification × 4 000.

Immunoglobulin supergene family

Three members of this large family of proteins are involved in leucocyte-endothelial adhesion. They are the integrin counter-receptors ICAM-1 (CD54), ICAM-2 and VCAM-1, found on the endothelial cell membrane.

The ICAM-1 has five immunoglobulin-like domains and the ICAM-2 has only two. Both the ICAM-1 and ICAM-2 are constitutively expressed on endothelium and ICAM-1 is also present on activated B cells and follicular dendritic cells in germinal centres (Springer 1990). The



10.9E Transversely sectioned tonsillar HEV stained strongly with anti-ICAM-1 antibody on luminal and lateral (black dots), but not on the abluminal, surfaces of high endothelial cells. Immunoelectron microscopy. Incubation with mAb to ICAM-1. Magnification × 5 000.

known ligands for ICAM-1 are LFA-1 and Mac-1 integrins, whereas the ICAM-2 binds only to LFA-1. Furthermore, the expression of ICAM-1 is readily upregulated by inflammatory cytokines (**10.9E**) resulting in an increased binding of circulating lymphocytes and monocytes to the stimulated endothelium.

The last member of the immunoglobulin superfamily is the VCAM-1 molecule containing either six or seven immunoglobulin-like domains. Its ligand on the leucocytes is the VLA-4 integrin (Cronstein & Weissmann 1993). Although VCAM-1 is absent from resting endothelium its expression can be induced by cytokines. Thus, VCAM-1 is thought to promote an accumulation of mononuclear cells at sites of inflammation (Shimizu et al 1992; Picker & Butcher 1992).

In addition, the widely expressed cell surface molecule CD44 has been identified as a homing receptor of haematopoietic cells. The CD44 molecule is a highly glycosylated protein and the major receptor for hyaluronic acid. It has been proposed by Günther et al (1991), that CD44 isoforms may play an important role in organ specific recognition, cell motility and invasion mechanisms.

In summary, the process of adhesion of leucocytes to endothelium is believed to involve multiple receptor–counterreceptor (ligand) interactions. This 'adhesion cascade' requires a co-ordinated sequence of adhesion molecules expression on both the leucocytes and the endothelium, from the time of the initial attachment to the final step of extravasation into the surrounding tissue (Shimizu et al 1992; Tanaka et al 1993).

The first step in this cascade is the loose binding, 'rolling' or 'tethering' of leucocytes, which is initiated via P- or E-selectin. Coexpression of tethering and 'signalling' molecules on activated endothelial cells, such as P-selectin and PAF and E-selectin and IL-8, augments this initial interaction (Zimmerman et al 1992). The second step is referred to as 'triggering', in which a signal delivered to leucocytes converts the functionally inactive integrin molecules into active adhesive configurations. The third step represents the establishment of strong adhesion mediated by integrins expressed on leucocytes, binding to their endothelial ligands. The fourth and last step is the migration of leucocytes into the surrounding tissue. This step requires reduction in adhesion and 'shedding' of some molecules from the surface of leucocytes, followed by cell movement. The precise mechanisms involved in this process are as yet unknown (Hogg 1992; Shimizu et al 1992; Tanaka et al 1993).

An understanding of molecules that mediate cellular interactions in homing of recirculating lymphocytes and during the initial stages of inflammation may eventually lead to the development of a new generation of anti-inflammatory agents.

STRUCTURE OF BLOOD VESSELS

Sharp distinctions of blood vessels based on the structure of the wall are to some extent arbitrary, because the variations along the vascular tree are continuous. Nevertheless a few basic patterns can be identified, and are described here as different vessel types.

LARGE ELASTIC ARTERIES (10.4A, B, 11A)

The intima is made of an endothelium, resting on a basal lamina, and a subendothelial layer. The endothelial cells are flat, measuring between 1.0 and 0.2 μm in thickness, polygonal in outline and elongated with the long axis parallel to the direction of blood flow. The subendothelial layer is well developed, contains elastic fibres and collagen fibrils and small cells identified as muscle cells or muscle cell precursors and fibroblasts. The orientation of subendothelial cells is irregular but predominantly longitudinal.

In the human aorta at birth, the endothelium adheres to the internal elastic lamina. After birth the intima grows in thickness with the appearance of a subendothelial layer (subendothelial intima), composed of delicate elastic fibres and smooth muscle cells running longitudinally, intermingled with abundant ground substance, a small amount of collagen and occasional fibroblasts. Splitting of the inner elastic lamina is not uncommon. The thickening of the intima progresses with age and is more marked in distal than in the proximal segment of the aorta. The cells of the subendothelial layer are thought to migrate from the media across the inner elastic lamina.

Between the intima and the media lies a prominent inner elastic lamina. This lamina is smooth, measures about 1 μm in thickness, and is stretched under the effect of the pulse, recoiling elastically afterwards; it coils up into a serpentine outline when the vessel is completely emptied, a condition that does not normally occur in vivo. Even when empty a large elastic artery does not completely collapse.

The media has a markedly layered structure, being made of layers of elastic material (elastic lamellae) alternating with interlamellar zones made of muscle cells, collagen and elastic fibres. The arrangement is very regular and each elastic lamella with an adjacent interlamellar zone is regarded as a 'lamellar unit' of the media. In the human aorta there are approximately 52 lamellar units, measuring about 11 μm in thickness. A similar arrangement exists in all mammals, and the number of lamellar units is roughly proportional to the vessel diameter in different species and vessels (Wolinsky & Glagov 1967b). Number and thickness of lamellar units increases during development. At birth the aorta has about 40 lamellar units. However, the developmental increase in vessel diameter far exceeds the increase in number of lamellae and in the thickness of the wall.

In the media of the largest arteries such as the aorta some authors distinguish an internal layer of musculature, situated externally to the inner elastic lamina, with muscle cells of various orientations intermingled with elastic fibres running longitudinally.

The adventitia is well developed. In addition to collagen and elastic fibres, it contains fibroblasts (which are flattened and have extremely long and thin laminar processes), macrophages and mast cells. The vasa vasorum are usually confined to the adventitia, where there are also nerve bundles, which do not come close to muscle cells, and lymphatic vessels.

MUSCULAR ARTERIES

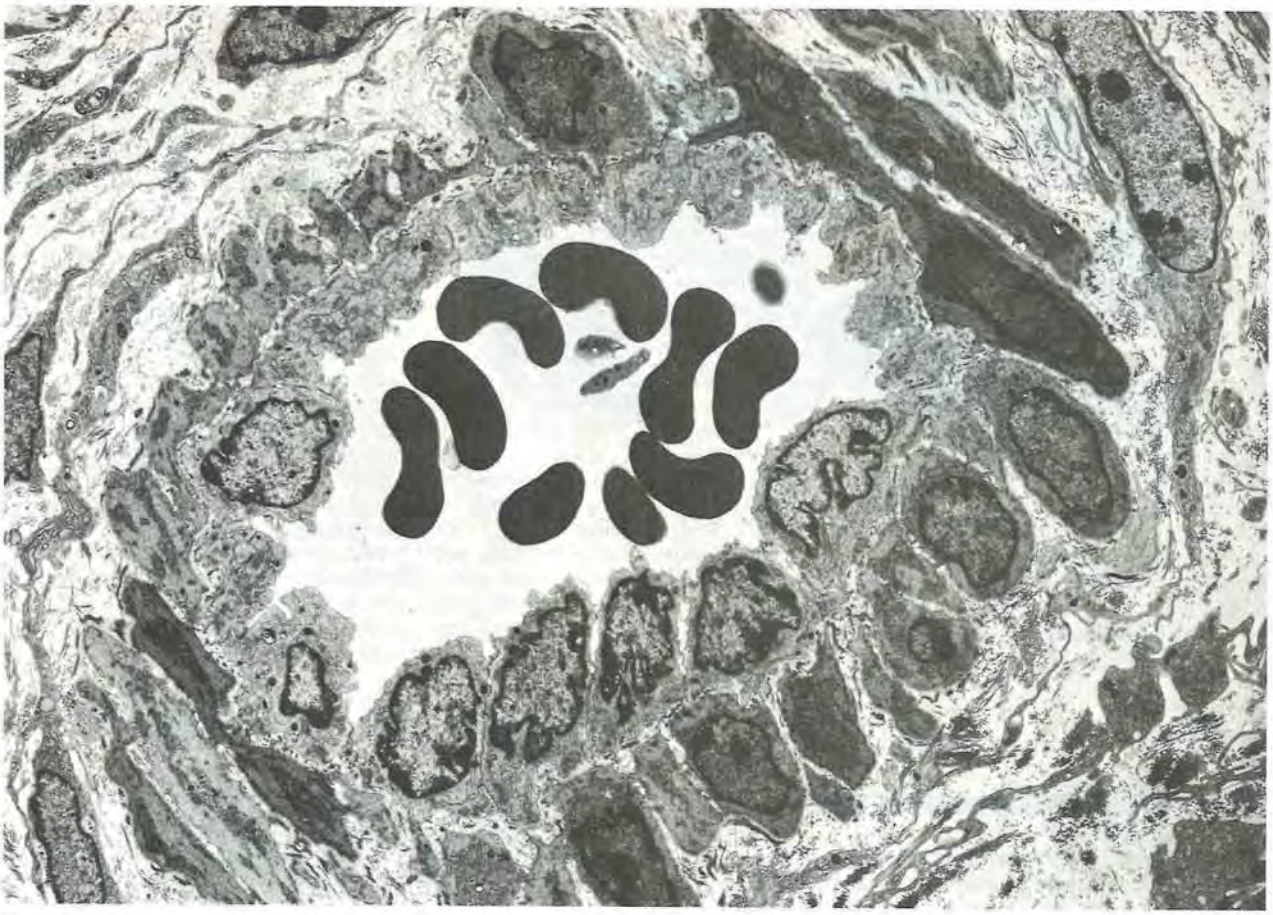
These include vessels of a large range of sizes, and they are characterized by the predominance of muscle in the media. The intima is made of an endothelium resting on a basal lamina (**10.5**, 11B). The inner elastic lamina is thin, and is occasionally absent. In the media about ¾ of the mass is represented by muscle cells. Therefore, the relative amount of extracellular space is less than in large arteries, but elastic fibres, running parallel to or at a very small angle with the muscle cells, remain prominent.

ARTERIOLES (10.10)

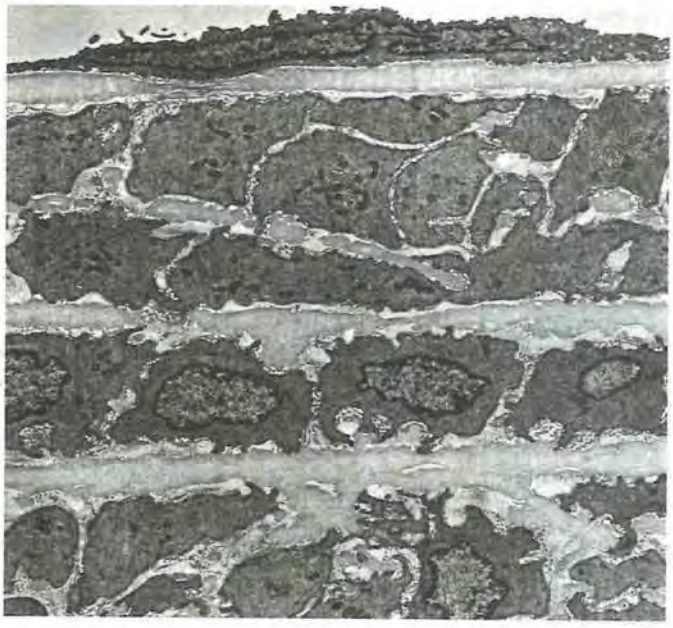
The endothelial cells are smaller than in large arteries; their nucleated portion is thicker and often projects markedly into the lumen. Even when fixed fully distended, the endothelium of arterioles has variable thickness and displays longitudinal grooves and ridges. The nuclei are elongated and oriented parallel to the vessel length and so is the long axis of the cell.

The abluminal surface of the endothelium is lined by a basal lamina, but an inner elastic lamina is absent or barely recognizable. When present, the elastic lamina is amply fenestrated and is traversed by cytoplasmic processes of muscle cells or of endothelial cells.

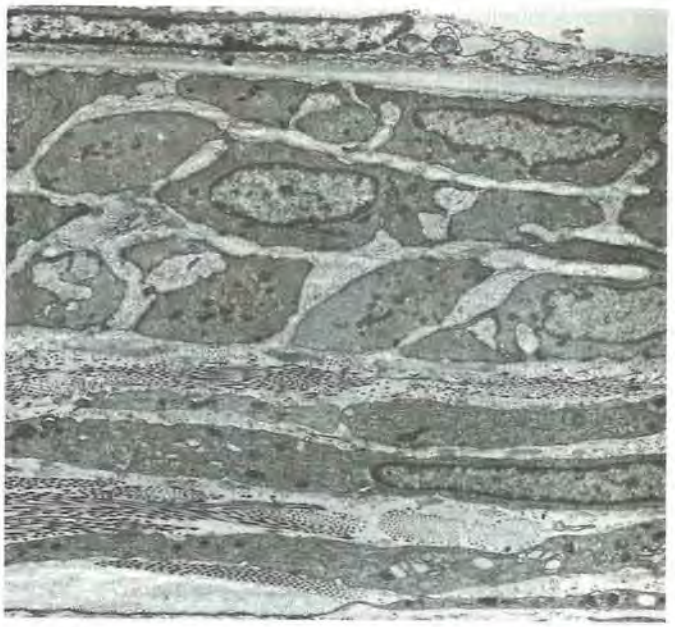
The muscle cells are larger in volume than those of large arteries and they form a layer one cell thick. They are arranged circumferentially and are tightly curved and wound around the endo-



10.10 Transmission electron micrograph of a partially contracted small arteriole in transverse section, showing an outer zone of non-striated myocytes and an inner lining of endothelial cells. Erythrocytes are visible within the lumen. The specimen is from the uterus of a rat. Magnification ×4000. (Supplied by Dr Gail ter Haar.)



10.11A Elastic artery sectioned longitudinally and examined by electron microscopy. Beneath the endothelium (*at top*) with the nucleated profile of a flat endothelial cell, is a thick inner elastic lamina. In the media (not shown in its full thickness) are several muscle cells profiles in transverse section, some nucleated, separated by large elastic fibres and elastic lamellae. Note the irregular, convoluted shape of the muscle cell surface. Magnification ×4500.



10.11B Muscular artery sectioned longitudinally and examined by electron microscopy. Beneath the endothelium (*at top*) with the nucleated profile of a flat endothelial cell, is an inner elastic lamina. In the media are several muscle cells profiles in transverse section; they are closer to each other than in the elastic artery, and the intervening spaces are occupied by collagen fibrils. In the bottom part of the micrograph is the tunica adventitia with fibroblasts and collagen fibrils. Magnification ×4500.

thelium (**10**.8). In the smallest arterioles each cell makes several turns, producing extensive apposition between parts of the same cell. The muscle cell profiles are asymmetric in that the region of the cell membrane nearest the adventitia bears most of the dense bands, hence most of the insertions of myofilaments.

The *precapillary arteriole* (strictly speaking, however, all arterioles are pre-capillary), or *precapillary sphincter*, has been variously defined in the literature. The most acceptable definition is that the precapillary sphincter is that part of the arteriole where the most distal muscle cell is found, before the vessel opens into the capillary network (Wiedeman et al 1976). The functional interest in the precapillary sphincters is that they appear to be mainly under myogenic, rather than under nervous control. Because of their position they are regarded not so much as sites of regulation of peripheral resistance but rather as sites where the blood flow into the capillary network is monitored (Wiedeman et al 1976).

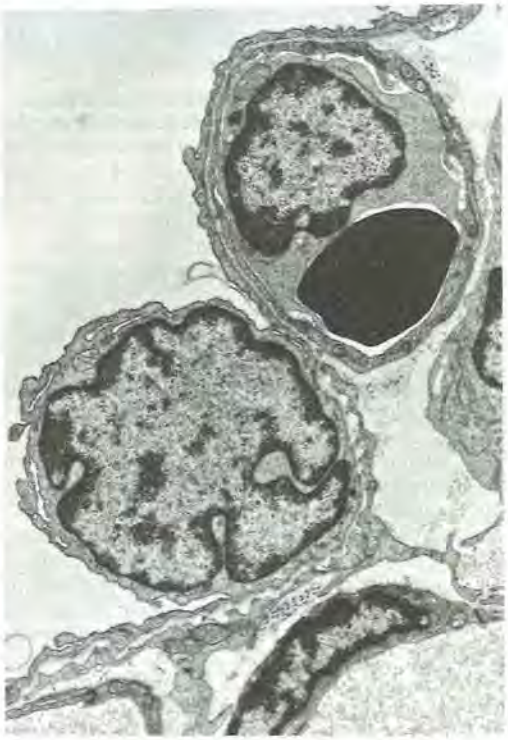
Arterioles are usually densely innervated by sympathetic fibres, via small nerve bundles containing axons expanded in varicosities and packed with axonal vesicles, mostly of the adrenergic type. The distance between axonal membrane and muscle cell membrane can be reduced to 50–100 nm and the gap is occupied by a single basal lamina. Ultrastructural studies with serial sections have shown that these contacts between adrenergic axons and muscle cells (autonomic neuromuscular junctions) are very common in arterioles (Luff et al 1987).

CAPILLARIES (**10**.12, 13)

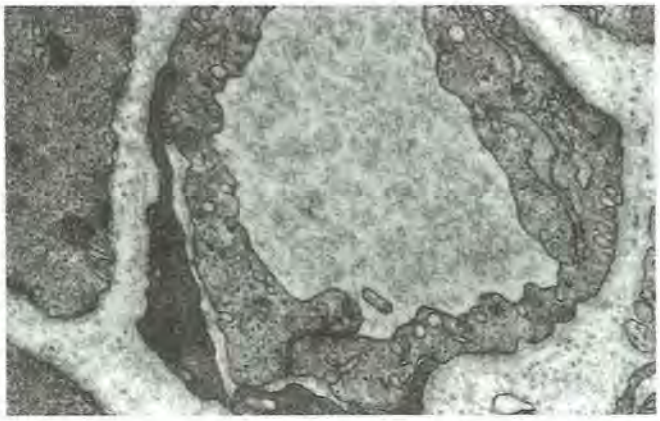
The wall of capillaries is made of an endothelium and its basal lamina, plus a few isolated pericytes (see p. 1459). The capillaries are the vessels closest to the tissue they supply and their wall is in intimate relation with the tissue. Their structure varies in different locations. They measure 5–8 μm in diameter (and much more in the case of sinusoids) and are hundreds of microns long. Their lumen is just large enough to let blood cells through, one at a time and with considerable deformation of their shape. It has been pointed out, however, that the vascular lumen is not at its narrowest in capillaries: the true bottleneck of the circulatory system is at the level of the arterioles (Cliff 1976), where muscle contraction can obliterate the lumen.

Commonly, a single endothelial cell forms the outline of a capillary and then the junctional complex (see p. 1457) occurs between laminar extensions of the same cell. In some capillaries, usually near their venous end, there are 'seamless' endothelial cells, i.e. the lumen is a large membrane-bounded canal through the cytoplasm (Bär et al 1984): in this case the lumen probably originated by fusion of several intracellular vacuoles (Wolff et al 1975).

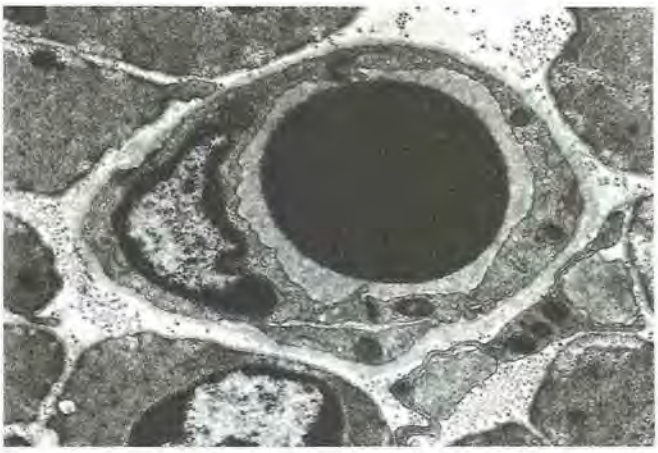
The structural characteristics of endothelial cells are discussed on page 1456. In capillaries the endothelium is at its thinnest: 2–3 μm at the level of the nucleus, and down to as little as one-fifth of a micron in certain regions. The endothelial cells of some capillaries have *fenestrations*, or pores, through their thinnest portions. Fenestrations are approximately circular, 50–100 nm in diameter, and at their edge the luminal and the abluminal membranes of the endothelial cell come into contact with each other. The fenestration, or fenestra, itself is usually occupied by a thin electron-dense diaphragm resembling in appearance a thin basal lamina. The chemical composition of endothelial fenestrae is still unknown. Permeability studies



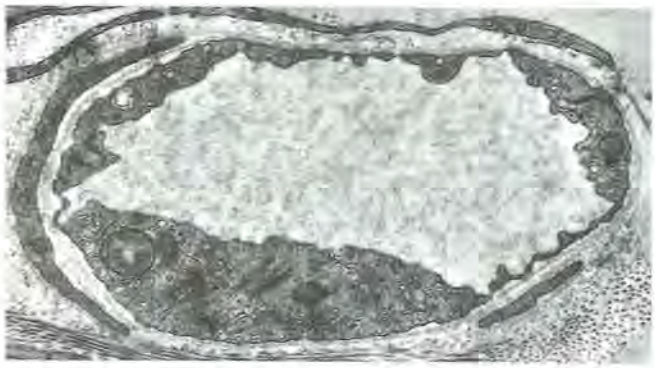
10.12A To the right a blood capillary in the wall of a pulmonary alveolus. The lumen of the capillary is occupied by a red blood cell and a lymphocyte. Lower centre is a Type I pneumocyte with its nucleus and with slender cytoplasmic processes fully lining the lumen of the air-filled alveolus (*top left*). Two other capillaries are partially visible at the bottom; their lumen is occupied by plasma. Magnification × 8 000.



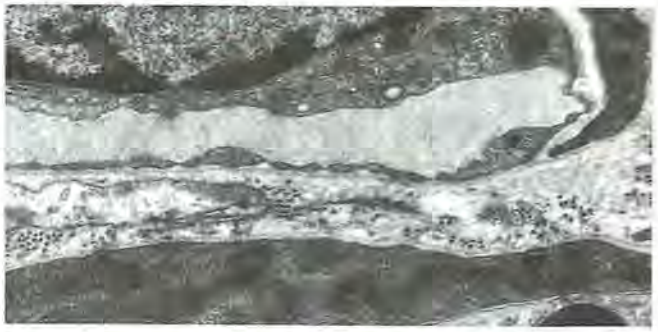
10.12B Intramuscular blood capillary. The endothelial cell to the left shows the nucleus; at top and bottom are junctions with another endothelial cell. The lumen of the capillary is occupied by a red blood cell and plasma. On the outer surface is a basal lamina and (*at bottom*) a slim process of a pericyte. Magnification × 10 000.



10.12C Intramuscular blood capillary. Caveolae are visible on both the lumenal and the ablumenal surfaces of the endothelial cell, together with endoplasmic reticulum, microtubules and bundles of microfilaments. The edges of the cell are in contact with each other at the bottom, and they form specialized junctions. Magnification × 29 000.



10.13A A fenestrated capillary, surrounded by a basal lamina, a laminar process of a pericyte (*left*) and collagen fibrils (*bottom*). The endothelial cell at top contains various organelles, including two centrioles, vesicles and Golgi complexes. Magnification × 18 000.



10.13B A fenestrated capillary in the intestinal mucosa. The fenestrations are close to the basal surface of the lining epithelium. Note the basal lamina on both the epithelial and the endothelial cell and the intervening collagen fibrils and fibroblastic process. Magnification × 30 000.

have shown that other components in addition to the diaphragm control the permeability of a fenestra (Levick & Smaje 1987). These capillaries are known as *fenestrated capillaries*, and they are found in renal glomeruli, in intestinal mucosa (**10.13**) and in endocrine and exocrine glands. Fenestrations are also almost invariably present in capillaries lying close to an epithelium, including skin (Imayama 1981).

Capillaries without fenestrations are known, somewhat inaccurately, as *continuous capillaries*. Capillaries in the brain, in striated and smooth muscles, in lung and in connective tissue are of this type. Capillary permeability varies greatly among tissues and can be correlated partly with the local type of endothelium. In tissues where large molecules pass easily (e.g. alimentary tract, endocrine glands) fenestrated endothelia exist, with numerous caveolae; intercellular junctions are either incomplete or 'leaky'. Where barriers to diffusion of large molecules occur (e.g. brain, thymic cortex and testis), endothelia are complete and not fenestrated, with efficient zonula junctions of the occludens type between cells; here, caveolae are somewhat fewer in number. Other tissues (e.g. skeletal muscle) show an intermediate condition.

Sinusoids. These are capillaries, large and irregular in shape, which have true discontinuities in their wall: blood can diffuse out of the circulation with only a minimal hindrance. A basal lamina may be found over these slits or holes in the endothelium, and other cell types may be found in the perisinusoidal space. Sinusoids occur in large numbers in the liver, spleen, bone marrow and adrenal medulla.

VENULES

Postcapillary venules are essentially tubes of flat, oval or polygonal endothelial cells supported by basal lamina and a delicate adventitia of collagen fibres mainly running longitudinally and fibroblasts (Rhodin 1968). They lack a distinct elastic lamina. Pericytes often accompany these venules. Postcapillary venules are sites of fluid exchange and leucocyte migration; in venules of lymphoid tissue of the gut and bronchi and in the lymph nodes and thymus, endothelial cells are taller and have intercellular junctions through which lymphocytes and other blood components can readily pass (see p. 1432). In other tissues these vessels are believed to be a major site of migration of neutrophils, macrophages and other leucocytes into extravascular spaces, and also a region of temporary endothelial attachment for neutrophils, forming marginated pools of these cells (see p. 1403).

The intracellular junctions of venules are sensitive to inflammatory agents which increase their permeability to fluids and defensive cells thus facilitating extravasation (see, e.g., Marchesi 1961, 1962). In general, the endothelium of venules has fewer tight junctions, and is more permeable. For example, in neurogenic inflammation venules are the primary site of extravasation of plasma.

When two or more capillaries converge the resulting vessel is larger (up to 30 μm), and is known as a *venule* (or a *postcapillary venule*). Venules do not acquire musculature until, after further convergence, they are about 30 μm in outer diameter, when they are known as *muscular venules* (**10.14**). The distinction is important because postcapillary venules are as permeable to solutes as capillaries, and are thus part of the microcirculatory bed. At the level of the postcapillary venule the cross-sectional area of the vascular tree is at its maximum, and there is a dramatic fall in pressure, from 25 mmHg in the capillary to about 5 mmHg (Rothe 1983). Muscular venules converge into *collecting venules* which lead to a series of veins of progressively larger diameter. Venules and veins are capacitance vessels (see p. 1453).

VEINS

Veins are characterized by a relatively thin wall in comparison with arteries of similar size and by a large capacitance. A small increase in lumenal pressure produces a large increase in volume, although the pressure–volume relation is not linear. The wall thickness is not exactly correlated to the size of the vein, but it varies in different districts: for example, the wall is thicker in veins of the leg than in veins of similar size in the arm (Kügelgen 1955).

The amount of muscle is considerably less than in arteries, while collagen and, in some veins, elastic fibres are the predominant components. In the cadaver the veins, even when collapsed, maintain their large diameter and they are more likely to be found full of blood than are the arteries. Furthermore, tethering of some veins to connective tissue fasciae and other surrounding tissues may prevent collapse of the vessel even with a negative transmural pressure.

Pressure within the venous system does not normally exceed 5 mmHg, it decreases centripetally as the veins grow larger and fewer in number, and it approaches zero in the proximity of the heart. Because of the small amount of musculature veins have limited influence on blood flow. However, during a sudden fall in blood pressure following a haemorrhage, elastic recoil and reflex constriction in veins compensate for the blood loss and tend to maintain venous return to the heart. Krogh (1959) stressed the importance of the active venous return by pointing to the fact that in man the heart is at a greater height above the feet than in any other mammal, except the elephant and the giraffe. Vasoconstriction in cutaneous veins in response to cooling is important in thermoregulation.

The structural plan of the wall is similar to that of other vessels, but the division into layers, especially media and adventitia, is often not clearly seen. The lumen is lined by an endothelium which lies over a basal lamina. A distinct inner elastic lamina is not found. The musculature is much thinner and has a more irregular distribution than in arteries. The orientation of muscle cells is not uniform and often variable and irregular. In most veins (for example those of the arm and leg) the musculature is arranged approximately circularly. Longitudinal musculature is present in the iliac vein,

10.14 A venule transversely sectioned and examined by electron microscopy. One of the endothelial cell profiles is nucleated and the lumen contains an erythrocyte. The tunica media consists of a single layer of muscle cells running almost circumferentially. To the bottom right is a nerve bundle. Magnification × 11 000.

brachiocephalic vein, superior vena cava, inferior vena cava, portal vein and renal vein. In the renal vein and in parts of the inferior vena cava, virtually all the musculature is arranged longitudinally (Kügelgen 1955). Large veins entering the heart are encroached upon for a short distance by myocardial tissue, and in the coronary sinus this covering is complete (Coakley & King 1959); in the transition areas smooth and cardiac muscle lie side by side. Muscular tissue is absent in certain veins: the maternal placental veins, the dural venous sinuses and pial veins, the retinal veins, the veins of trabecular bone and the venous spaces of erectile tissue. Such veins consist of endothelium supported by variable amounts of connective tissue.

In the outer layer of connective tissue there are few nerve fibres, vasa vasorum and abundant elastic fibres. Overall, collagen is the main component of the venous wall in man, accounting for more than half its weight. Walls of the larger veins, like the arteries, are supplied by vasa vasorum but these in veins may penetrate the wall deeply, perhaps because of the lower oxygen tension. Postganglionic sympathetic efferent and primary afferent nerves are distributed to the veins, as in arteries, but less abundantly.

Most veins have valves to prevent reflux of blood (**10.15**). A valve is composed of an inward projection of the tunica intima, strengthened by collagen and elastic fibres and covered by endothelium differing in orientation on its two surfaces. Surface cells which are juxtamural are transversely arranged whereas on the luminal surface, over which the main stream of blood flows, cells are arranged longitudinally in the direction of the current. Most commonly, two such valves lie opposite one another, especially in smaller veins or in larger ones where smaller tributaries join; occasionally three valves lie in opposition, sometimes only one is present. The valves are semilunar (cusps) and attached by convex edges to the venous wall; their concave margins are directed with the current and apposed to the wall as long as flow is towards the heart, but when blood flow reverses the valves close. Centripetal to each valvular flap the wall is expanded into a sinus, which fills when blood flow is reversed against a closed valve, giving a 'knotted' appearance to the distended veins, if these have many valves. In the limbs, especially the legs where venous return is against gravity, such valves are of great importance to venous flow, as blood is moved towards the heart by the intermittent pressure produced by contractions of the surrounding muscles. Valves are absent in very small and in very large veins and in many tissues are rare or absent. Valves are absent in veins of the thorax and abdomen.

Special features are found in some veins such as the portal vein, where there is a prominent musculature made of a thick outer layer arranged longitudinally and mixed with abundant connective tissue (Ferraz de Carvalho & Rodrigues 1978) and a thin inner layer arranged as a low-pitched helix that is almost circular.

VASCULAR SHUNTS

These are communications between arteries and veins found in many regions of the body where the capillary circulation is bypassed by wider channels. They may be classified according to their dimensions, site and complexity as:

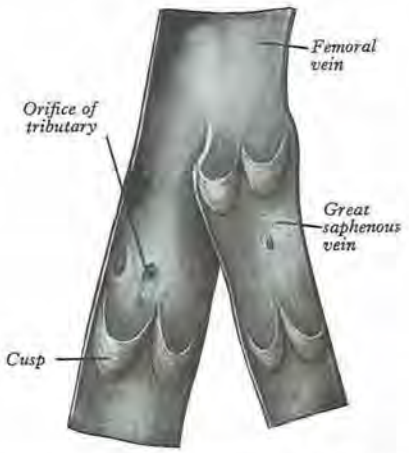
- preferential thoroughfare channels
- 'simple' arteriovenous anastomoses
- specialized arteriovenous anastomoses or *glomera*.

Preferential 'thoroughfare' channels

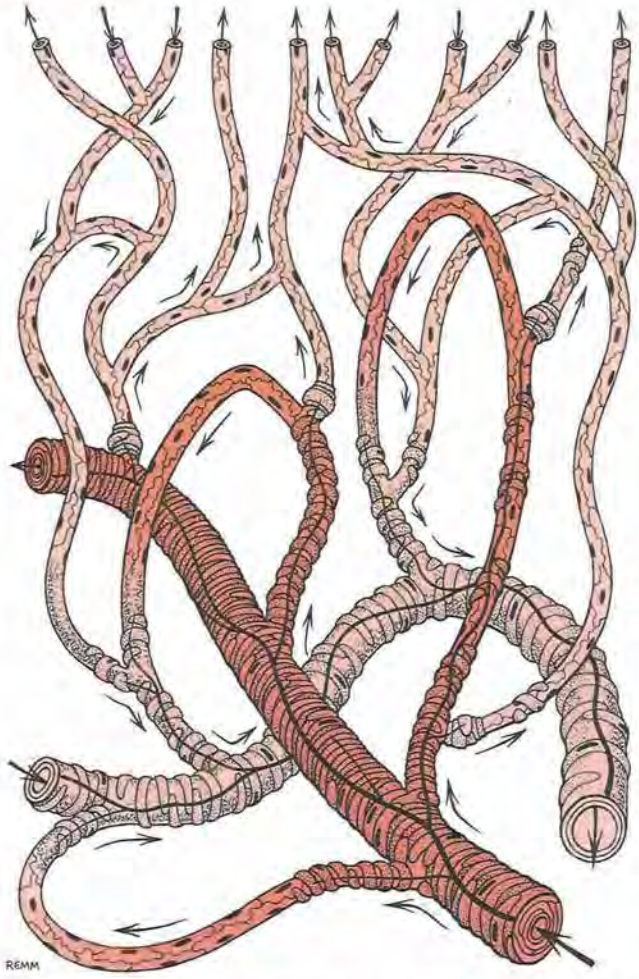
In many tissues true capillaries arise not only as direct side branches of terminal arterioles but also as side branches of a main or 'thoroughfare' channel connecting the terminal arteriole and the venule (Maggio 1965; Grant & Wright 1968, 1970; Zweifach 1973). This *thoroughfare channel* has a larger calibre than true capillaries and in ultrastructure resembles typical continuous capillaries, except that widely spaced smooth muscle cells spiral round the endothelium. Each capillary side branch has at its origin a precapillary sphincter. Such a channel and its capillaries form a functional *microcirculatory unit* (**10.16**). When functional demand is low, blood flow is largely limited to the bypass channel, with most precapillary sphincters closed. Periodic opening and closing of different sphincters may irrigate different parts of the capillary net. With increasing demand, blood flow may increase greatly following the opening of many sphincters. The size of the microcirculatory unit varies greatly, for example in skeletal muscle each channel gives rise to 20–30 true capillaries, but in some glandular tissues only one or two may be given off. Detailed investigations in the cremaster muscle and biceps femoris tendon of the rat (Grant & Wright 1968, 1970) have shown that in these sites, bypass channels are confined to perimuscular and peritendinous connective tissues and absent from the muscles itself. The form of the capillary net also varies with the tissue meshes being either round or elongated. Round or angular meshes are most common and prevail where networks are dense, as in the lungs, mucous membranes and skin. Elongated meshes occur in muscles and nerves, aligned parallel with their fibres. Sometimes capillaries are looped, as in the papillae of the skin and tongue. The number of capillaries and the size of their mesh determine the degree of vascularity; the smallest meshes occur in the lungs and the choroid of the eye.

Arteriovenous anastomoses (10.17)

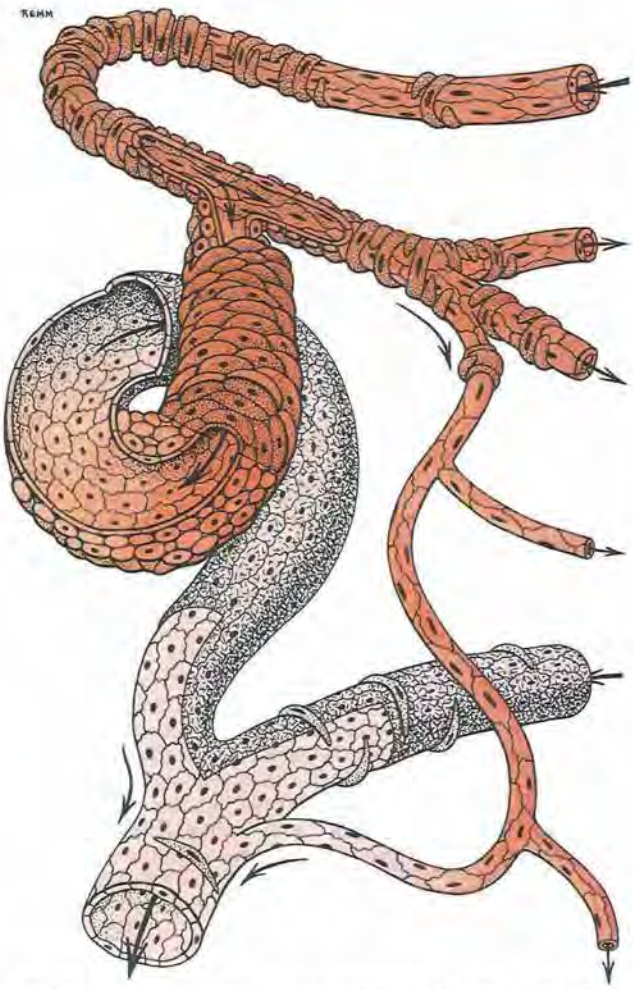
Arteriovenous anastomoses are direct connections between smaller arteries and veins (Grant & Bland 1931; Popoff 1934; Clark 1938). Connecting vessels may be straight or coiled, often possessing a thick muscular tunic and a narrow lumen, about 10–30 μm across. Under sympathetic control through abundant non-myelinated fibres in its wall, the vessel is able to completely close, circulation being then via



10.15 The upper portions of the femoral and great saphenous veins laid open to show the valves. About two-thirds of the natural size.



10.16 Diagram of a microcirculatory unit based upon descriptions in Zweifach (1959, 1961, 1973) and Reynolds and Zweifach (1959). Note the terminal arteriole, thoroughfare channels, capillaries and collecting venule. The distribution of smooth muscle cells and precapillary sphincters is shown.



10.17 Diagram of an arteriovenous anastomosis. Note the thick wall of the anastomotic channel composed of layers of modified smooth muscle cells.

the capillary bed. When patent, the vessel carries blood from artery to vein, partially or completely excluding the capillary bed from the circulation.

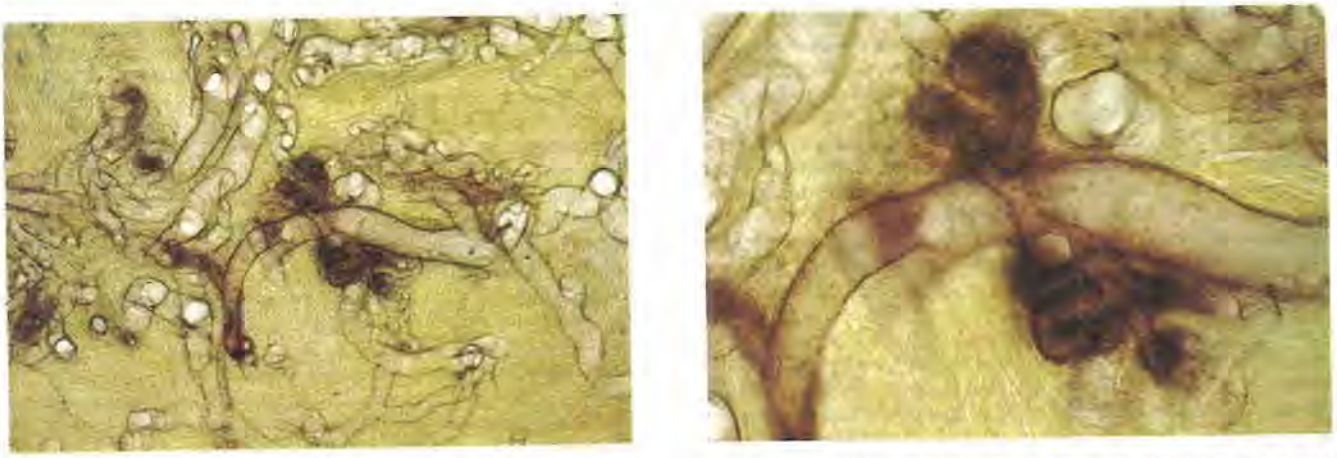
Arteriovenous anastomoses of relatively simple type occur in the nasal, labial and aural skin, nasal and alimentary mucous membranes, coccygeal body, erectile tissue, tongue, thyroid gland, sympathetic ganglia and probably elsewhere. Their ultrastructure has been investigated by Cauna (1970).

In the skin of the hands and feet (especially digital pads and nail beds) anastomoses form a large number of small units termed '*glomera*'. They are deep in the corium and each '*glomus*' has one or more afferent arteries, stemming from branches of cutaneous arteries approaching the surface (**10**.17, 18). These afferents arise at right angles from their parent vessels which then continue into the dermal papillary layer, ending in a capillary plexus. A short distance from its origin an afferent artery gives off a number of fine 'periglomeral' branches and then immediately enlarges, makes a sinuous curve and narrows again into a short funnel-shaped vein opening at right angles into a collecting vein. This vein commences on the deep aspect of the glomus, curving round its superficial surface, whence it retraces its course, receiving venules from the dermal papillary layer. Finally, it joins a deeper cutaneous vein.

In the newborn child arteriovenous anastomoses are generally few and poorly differentiated, but they develop rapidly during the early years of life. In old age they atrophy, sclerose and diminish in number.

The vessels concerned in digital arteriovenous anastomoses are unusual (**10**.18). Where these enlarge the afferent artery has small luminal endotheliomuscular projections but proximal to this structure it is typical. The connecting vessel has an endothelium supported by fine collagenous fibres but no internal elastic lamina. Longitudinal and circular muscle layers are not sharply differentiated but the muscular wall is thick; in sections myocytes appear pale and swollen, with central nuclei, and hence described as 'epithelioid'. The efferent vein has a thin wall lacking muscle but containing many elastic fibres which pass into the tunica adventitia of the collecting vein.

The mechanisms by which arteriovenous anastomoses regulate local flow are poorly understood. Where they have circular muscle in their walls, epitheliocytes may help to narrow the lumen; where it is absent closure may be due to swelling of these epithelioid cells. Cutaneous arteriovenous anastomoses are essential to the control of general and local body temperature. When a rabbit's ear is raised above 40°C, muscle in the walls of the connecting vessels relax and increased blood flow at body temperature results, with a consequent cooling. When the local temperature is lowered below 15°C, the connecting vessels again relax and increased flow at body temperature then helps to raise local temperature, unless artificial cooling is intensified. When the animal's overall **body** temperature is raised experimentally, a general opening of all subcutaneous arteriovenous anastomoses results, with an increase in heat radiation and consequent drop in body temperature (Grant 1930). The cooling effect of panting in dogs also involves the opening of lingual arteriovenous anastomoses. The paucity and immaturity of arteriovenous anastomoses in the newborn and marked reduction in subcutaneous



10.18 Human digital arteriovenous anastomoses prepared by intravascular perfusion of haematoxylin and subsequent clearing of a full thickness specimen of skin. The heavily stained, thick-walled, tortuous, anastomotic channels contrast with the central arterial stem and the thin-walled venous outflow channels. See text for further details. (The specimens were prepared and provided by R T Grant, Guy's Hospital Medical School.)

arteriovenous anastomoses with advancing years may be related to observed less efficient temperature regulation in these two extremes of age.

Arteriovenous anastomoses in alimentary mucous membranes fulfil a different function (Spanner 1932). An arteriole to a human villus has a direct connection with its corresponding venule and when absorption is in abeyance the connection is patent and helps to raise portal venous pressure; during alimentary absorption the anastomosis is closed and consequently blood traverses the capillary plexus.

Other suggested functions of arteriovenous anastomoses include regulation of blood pressure, secretion by epithelioid cells and pressor reception.

VASCULARIZATION OF BLOOD VESSELS

Some of the nourishment of the tissues of the vessel wall is provided by diffusion from the blood circulating in the vessel itself. In addition, large vessels have their own vascular supply, a network of small vessels, mainly microcirculatory vessels, the *vasa vasorum*. The wall thickness at which simple diffusion from the lumen becomes insufficient is about 1 mm (Kirk & Laursen 1955). The vasa vasorum originate from, and are drained into, adjacent vessels, which are peripheral branches of the vessel they supply. They are spread within the adventitia and, in the largest of arteries, penetrate into the outermost part of the media. The depth of penetration of capillaries into the media depends on the thickness of this tunica. Wolinsky and Glagov (1967b) in a comparative study of several mammals, found that only lamellar 'units' in excess of 29 are vascularized: if there are less than that number of units, the media remains avascular, and in the other cases the innermost 29 lamellae remain avascular.

INNERVATION OF BLOOD VESSELS

Blood vessels are innervated by efferent autonomic fibres, which regulate the contraction of the musculature, i.e. diameter and tone of the vessels, notably the arteries. In addition, most arteries also provide 'routes' along which nerves both travel to peripheral organs and arborize within them. These are *paravascular nerves* and they do not provide innervation to the vessel itself. They are parallel to the vessel but are situated at some distance from its adventitia and nerve and vessel are topographically but not physiologically related. In contrast, *perivascular nerves* run in the adventitia of the artery, where they branch and anastomose, forming a meshwork around the vessel. These nerves travel a long distance along the vessel, and they can provide innervation to its musculature. They are small bundles of axons, and the axons are almost invariably unmyelinated and typically *varicose*. Most of them are postganglionic fibres issuing from sympathetic ganglion neurons. However, some perivascular fibres originate from cranial parasympathetic ganglia and from ganglia of the enteric submucosal plexus, and some brain vessels are innervated by neurons of the central nervous system. The density of innervation varies in different vessels and in different areas of the body. The innervation is sparser in veins, where the musculature is consistently less well developed than in arteries, and the same is true of lymphatic vessels. But large veins with a conspicuous musculature, such as the portal vein, are richly supplied with nerves.

The principal site of action of nerves of blood vessels is on muscular artery and especially arterioles. The main effect of nerves is vasoconstriction and increase in vascular tone, and this role is particularly effective in arterioles, on account of their dense innervation and of the mechanical gain derived from the high ratio of wall thickness to vessel radius. *Adrenergic* fibres are vasoconstrictor and they act on adrenoceptors—of which several types are known—in the muscle cell membrane. Other substances are released with noradrenaline by the activated nerve endings, allowing for a complex regulation of the neurogenic control of vasomotility. The mechanical activity of vascular musculature is also under the influence of circulating factors such as hormones. In addition, there are factors, such as nitric oxide and endothelins, which are released from the endothelial cells and have a potent effect on vascular muscle cells. In this multiple control, while neurotransmitters reach the musculature from the adventitial surface of the media, the endothelial factors diffuse from its intimal surface. In some areas there are also sympathetic *cholinergic* fibres which inhibit muscle activity and induce vasodilatation. Afferent fibres from dorsal root ganglia are present in some vessels and can be identified either histochemically or with retrograde tracer studies. These afferent fibres usually end with a long chain of varicosities, but the physiology of their sensory transduction in the vessel wall is still obscure.

The terminal portions of the axons found in the vascular adventitia is varicose, i.e. it has a beaded appearance with expanded bulbous portions (up to 1.5 μm in diameter) and narrow intervaricose segments (about 0.2 μm in diameter). Varicosities contain mitochondria, microtubules, some neurofilaments and, above all, axonal vesicles, which transport and release the neurotransmitters. The intervaricose segments are occupied almost exclusively by a few microtubules.

All the perivascular fibres are confined to the adventitia of the vessel, where they run amid collagen fibres, fibroblasts and small vessels (lymphatics and vasa vasorum). Only in some large muscular arteries, small nerve fibres are occasionally found within the outermost layers of the musculature. As a general rule, nerve fibres do not penetrate into the media, and they are never found in the intima. (Nerve fibres are sometimes close to the wall of capillaries, and the possibility of a physiological interaction between nerve endings and

endothelial cells cannot be ruled out.) Because of their location in the adventitia, nerve fibres run at a considerable distance even from the nearest muscle cell. In large muscular arteries many varicosities lie more than 1 μm away from the nearest muscle cell and any neuromuscular transmission requires diffusion of neurotransmitters over a considerable distance. In smaller vessels, such as arterioles, however, where the elastic and collagen material is less abundant, axonal varicosities lie within a few tens of nanometres from muscle cells. These points of close apposition are regarded as proper neuromuscular junctions, and, when the tissue is examined in serial sections, they appear quite numerous (Luff et al 1987).

ANGIOGENESIS

Some tissues lack vascularization, for example cartilage, epithelia even when thick and stratified, the media of vessels themselves and elastic tissue in general. This may be partly due to an active inhibition of vascular growth by certain tissues.

Angiogenesis is the formation of new vessels starting from pre-existing vessels, during growth of an organ, both in development and in hypertrophy and also in pathological tissues as in tumours. The existence of diffusible angiogenic factors is well documented and some angiogenic polypeptides have been isolated and sequenced, including some growth factors (Folkman & Klagsbrun 1987). One of the trophic factors that stimulates migration and division in endothelial cells is b-FGF (Tsuboi et al 1990). Interestingly, the endothelial cells themselves express the b-FGF gene and release b-FGF; this raises the possibility that endothelium regulates its own growth via this trophic factor (Schweigerer et al 1987).

New capillaries originate from sprouting of small venules (Ausprunk & Folkman 1977); there is a local disruption of the basal lamina followed by migration of endothelial cells. The sprout is initially solid, but then becomes partly canalized, while it grows by division of the endothelial cells, until it joins another sprout and blood flow begins.

The importance of angiogenesis in human pathology stems from the possible role of blood vessels in the growth of tumours. Tumours implanted into isolated perfused organs in vitro fail to grow beyond a few millimetres in diameter; the same tumours reimplanted into donor mice grow to more than 1 cm^3 and kill their hosts (Folkman & Klagsbrun 1987). Since only the reimplanted tumours become vascularized (Folkman & Klagsbrun 1987), the tumour growth seems to be linked to capillary growth.

THORACIC CAVITY AND HEART

The thoracic skeleton is described on pages 545–546. The volume enclosed within the thoracic cavity does not correspond with that enclosed by the osseous thorax because the lower part of the space surrounded by the bony elements is encroached upon by the diaphragm and the mobile and distensible organs within the upper abdomen. The capacity of the thoracic cavity also varies with posture and respiration, both affecting the position and relations of the thoracic organs. Its arbitrary upper limit is usually taken as the oblique plane of its inlet at the first rib, but the pulmonary apices and pleural cavities extend above this level into the neck, reaching the level of the **neck** of the rib.

UPPER OPENING (INLET) OF THORAX

The boundaries are formed by the skeleton described on page 545. The structures passing through the opening can be divided into two groups:

- those in or near the medial plane
- those on each side closely related to the cervical parts of the lungs.

Near the midline: behind the manubrium of the sternum, the lowest parts of the sternohyoid muscles enter the thorax, and behind them are the sternothyroid muscles along with vestiges of the thymus gland and the inferior thyroid veins passing down to empty into the brachiocephalic veins. In children, particularly, the left brachiocephalic vein itself may be in the thoracic inlet. **Posteriorly**, the trachea and the oesophagus, with the left recurrent laryngeal nerves, pass through the median part of the opening. The thoracic duct also passes through the opening behind the left margin of the oesophagus. Anterior to the vertebral column are the prevertebral longus colli muscles and the anterior longitudinal ligament.

On each side: the upper part of the pleura and the pulmonary apex occupy the inlet. Between the pleura and neck of the first rib, mediolaterally, are found the sympathetic trunk, the superior intercostal artery and the ventral branch of the first thoracic nerve as it passes superolaterally to join the brachial plexus. Anteriorly, the internal thoracic artery enters the thorax between the pleura and the first costal cartilage while, medial to the artery, its vein leaves the thorax.

On the right (**10.26**): the brachiocephalic artery leaves the thorax between the trachea and pleura. The vagus nerve, having passed between subclavian artery and vein, is between the pleura and the brachiocephalic artery at the inlet. The right brachiocephalic vein enters the thorax anterolateral to its artery. The right phrenic nerve crosses the internal thoracic artery and is lateral to the brachiocephalic vein behind the first costal cartilage.

On the left (**10.26**): the left common carotid and subclavian arteries leave the thorax between the pleura and trachea, the left vagus nerve descending lateral to the interval between them. Anterolateral to this is found the left brachiocephalic vein. The left phrenic nerve passing inferomedially crosses anterior to the internal thoracic artery at a higher level than the right. At the inlet, the left phrenic nerve is found between the left brachiocephalic vein anterolaterally and the subclavian and common carotid arteries posteromedially.

LOWER OPENING (OUTLET) OF THORAX

This extensive opening is wider transversely and slopes obliquely down and backwards, so that the vertical extent of the cavity is much longer posteriorly than it is anteriorly. The diaphragm (p. 815) closes the opening and forms a convex floor for the cavity. It is flatter centrally than at its peripheral attachments. It is higher on the right and, in cadavers, this side of the floor reaches the level of the upper border of the fifth costal cartilage. On the left, the diaphragm reaches only to the level of the sixth cartilage. (See p. 816 for further information on diaphragmatic shape and levels.) From the summit of each side, the diaphragm slopes abruptly down to its sternal, costal and vertebral attachments. The muscle is short anteriorly, progressively longer laterally, and it is longest and with a much more marked slope posteriorly, where the space between the diaphragm and the posterior thoracic wall narrows rapidly as it extends inferiorly.

DIVISIONS OF THORACIC CAVITY

The thoracic cavity is divided by the *mediastinum*, itself formed by the mass of structures between the lungs which extend from the sternum to the vertebral column and from the thoracic inlet to the diaphragm. The heart is in the mediastinum, enclosed by the *pericardium*. The lungs occupy the right and left regions of the thorax, each covered by a serosal membrane, the *pleura*, which also lines the corresponding half of the thorax and the lateral aspect of the mediastinum (**10.21, 24**).

For description, the mediastinum is arbitrarily divided into superior and inferior parts. The *superior part* extends from the thoracic inlet to an oblique (*transverse thoracic*) plane passing through the lower edge of the manubrium of the sternum and lower border of the fourth thoracic vertebra. The *inferior part*, below this

plane, is subdivided into an *anterior* part in front of the pericardium, a *posterior* component behind this and the diaphragm, and a *middle* component, containing the pericardium and the heart together with the large vessels entering or leaving it. Detailed accounts of the mediastinal contents are included with descriptions of the respiratory organs (pp. 1636–1646); the heart (pp. 1474–1504); and the oesophagus (p. 1751).

PERICARDIUM

The pericardium contains the heart and the juxtacardiac parts of its great vessels. It consists of two components, the fibrous and the serosal pericardium. The *fibrous pericardium* is a sac made of tough connective tissue, fully surrounding the heart without being attached to it. This fibrous sac develops by a sequential process of cavitation of the embryonic body wall by expansion of the secondary pleural cavity (see p. 180); thus its lateral walls are clothed externally by *parietal mediastinal pleura*. The *serosal pericardium* consists of two sacs of serosal membrane, one inside the other, the inner (visceral) one adhering to the heart and forming its outer covering known as the *epicardium*, while the outer (parietal) one lines the internal surface of the fibrous pericardium. The two serosal surfaces are apposed and separated by a film of fluid, thus allowing movement of the inner membrane and the heart adhering to it, except at the arterial and venous areas of the pericardium where the two serosal membranes merge. The latter constitute two parietovisceral lines of serosal reflexion (see below). The separation of the two membranes of the serosal pericardium creates a narrow space, the *pericardial cavity*, which provides a complete cleavage between the heart and its surroundings thus allowing it some freedom to move and change shape.

Fibrous pericardium

The fibrous pericardium is roughly conical and clothes the heart. **Superiorly**, it is continuous exteriorly with the adventitia of the great vessels, while **inferiorly** it is attached to the central tendon of the diaphragm and a small muscular area of its left half. Above, the fibrous pericardium not only blends externally with the great vessels, but is continuous with the pretracheal fascia (p. 804). **Anteriorly** it is also attached to the posterior surface of the sternum by superior and inferior sternopericardial ligaments, although the extent of these 'ligaments' is extremely variable, the superior one often being undetectable. By these connections, the pericardium is securely anchored and maintains the general thoracic position of the heart, serving as the 'cardiac seat belt'.

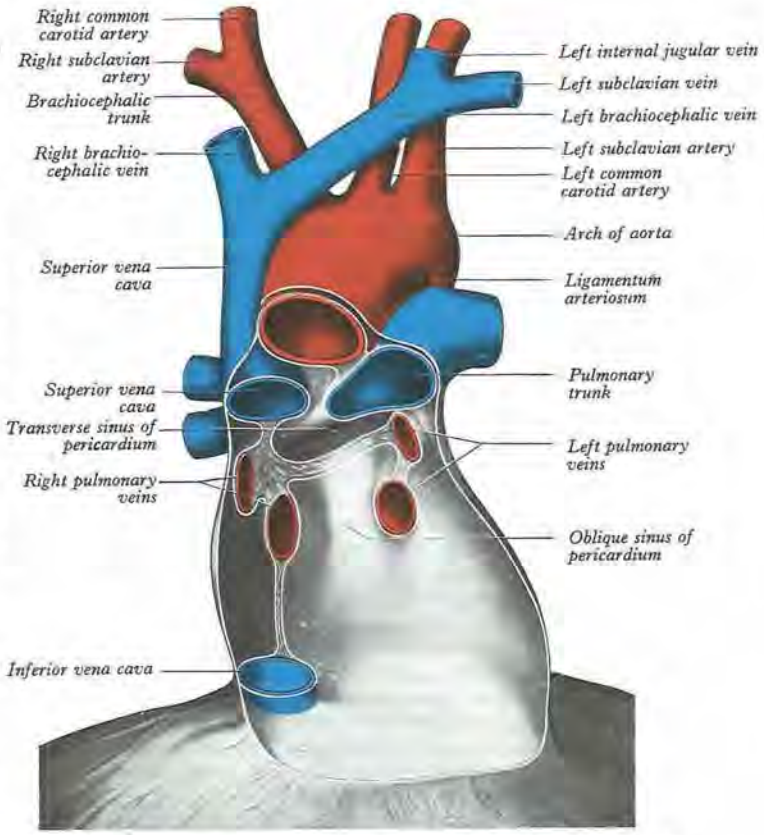
Anteriorly, the fibrous pericardium is separated from the thoracic wall by the lungs and the pleural coverings. However, in a small area behind the lower left half of the body of the sternum and the sternal ends of left fourth and fifth costal cartilages, the pericardium is in direct contact with the thoracic wall. Until it regresses, the lower end of the thymus is also anterior to the upper pericardium. **Posteriorly** are the principal bronchi, the oesophagus, the oesophageal plexus, the descending thoracic aorta, and the posterior parts of the mediastinal surface of both lungs. **Laterally** are the pleural coverings of the mediastinal surface of the lungs. The phrenic nerve, with its accompanying vessels, descends between the fibrous pericardium and mediastinal pleura on each side. **Inferiorly**, the pericardium is separated by the diaphragm from the liver and fundus of the stomach.

Vessels receiving extensions of the fibrous pericardium are the aorta, the superior vena cava, the right and left pulmonary arteries and the four pulmonary veins. The inferior vena cava, traversing the central tendon, has no such covering.

Serosal pericardium

The serosal pericardium is a closed sac within the fibrous pericardium, having a visceral and a parietal layer (**10.22**). The visceral layer, or *epicardium*, covers the heart and great vessels and is reflected into the parietal layer, which lines the internal surface of the fibrous pericardium. The reflexions of the serosal layer are arranged as two complex 'tubes', the aorta and pulmonary trunk being enclosed in one and the superior and inferior venae cavae and the four pulmonary veins in the other. The tube surrounding the veins has the shape of an inverted J (**10.19, 32**) and the cul-de-sac within its curve is behind the left atrium and is termed the *oblique sinus*. A passage between the two pericardial 'tubes' is the *transverse sinus* (**10.19**). This has the aorta and pulmonary trunk in front and the atria and great veins behind. The arrangement of the oblique and transverse sinuses, along with that of the main 'principal' cavity, is further affected by the development of complex three-dimensional pericardial recesses between adjacent structures. (For details, illustrations and bibliography see Vesely & Cahill 1986.) These recesses can be grouped according to the siting of their orifices or 'mouths'. From the principal pericardial cavity, the *postcaval recess* projects towards the left behind the atrial termination of the superior vena cava. It is limited above by the right pulmonary artery and below by the upper right pulmonary vein. Its mouth opens superolaterally to the right. The *right* and *left pulmonary venous recesses* each project medially and upwards on the back of the left atrium between the superior and inferior pulmonary veins on each side, indenting the side walls of the oblique sinus. The *superior aortic recess* extends from the transverse sinus. From its mouth, located inferiorly, it ascends posterior to, then right of, the ascending aorta to end at the level of the sternal angle. The *inferior aortic recess*, also extending from the transverse sinus, is a diverticulum descending from a superiorly located mouth to run between the lower ascending part of the aorta and the right atrium. The *left pulmonary recess*, mouth under the fold of the left vena cava, passes to the left between the inferior aspect of the left pulmonary artery and upper border of the superior left pulmonary vein. The *right pulmonary recess* lies between the lower surface of the proximal part of the right pulmonary artery and upper border of the left atrium.

A triangular fold of serosal pericardium is reflected from the left pulmonary artery to the subjacent upper left pulmonary vein as the *fold of the left superior vena cava*. It contains a fibrous ligament, a



10.19 Interior of the serosal pericardial sac after section of the large vessels at their cardiac origin and removal of the heart (seen from the front). See text for additional named recesses of the general serosal pericardial cavity and its transverse sinus.

remnant of the obliterated *left common cardinal vein* (left duct of Cuvier, p. 302). This descends anterior to the left pulmonary hilum from the upper part of the left superior intercostal vein to the back of the left atrium, where it is continuous with the *oblique vein of the left atrium* (p. 1576). The left common cardinal vein may persist as a left superior vena cava which then replaces the oblique vein of the left atrium and empties into the coronary sinus. When both common cardinal veins persist as right and left superior venae cavae, the transverse anastomosis between them, normally forming the left brachiocephalic vein, may be small or absent. When there is a left superior vena cava, it is joined by the left superior intercostal vein.

Vessels and nerves. The arteries of the pericardium are derived from the internal thoracic and musculophrenic arteries and the descending thoracic aorta. The veins are tributaries of the azygos system. The nerve supply is from the vagus together with phrenic nerves and the sympathetic trunks.

Structure. The fibrous pericardium is compact collagenous fibrous tissue. The serosal pericardium is a single layer of flat cells on a thin subserosal layer of connective tissue which blends with the fibrous pericardium in the parietal membrane and with the interstitial myocardial tissue in the visceral membrane. On the cardiac side, the subserosal layer contains fat, this being greatest along the ventricular side of the atrioventricular groove, the inferior cardiac border and the interventricular grooves. The main coronary vessels and their larger branches are embedded in this fat, its amount being related to the general extent of body fat and gradually increasing with age.

Pericardial puncture

Pericardial puncture can be performed either in the fifth or sixth left intercostal space near the sternum to avoid the internal thoracic artery, or at the left costoxiphoid angle, passing up and backwards into the pericardial sac. The serosal pericardium extends on the pulmonary trunk, anterior to the transverse sinus, as far as the arterial ligament (p. 1504, see **10.66**).

HEART

GENERAL INTRODUCTION

All triploblastic organisms, including chordates, overcome the limitations of diffusion over long distances by circulating a fluid from regions of high-oxygen tension and high concentration of nutrient substances to mesodermal and other cells remote from the external environment. The fluid, and its mode of circulation, vary amongst invertebrate phyla, but the majority (for example, annelid worms, arthropods and molluscs) are coelomates with closed vascular systems and some localized means of propelling 'blood' in a true circulation. The most common pattern consists of a dorsal pulsatile vessel (which may be valved and respond to muscular pacemakers under the influence of nerves), and one or more accessory structures which show varying degrees of development. Gas exchange is generally across gills and/or skin, although alternative systems (such as the tracheae of insects and lung books of spiders) occur in terrestrial groups. Echinoderms (sea urchins, starfish, etc.), the invertebrate group closest to chordates, display a unique water vascular system which takes over much of the role of the blood vascular system—a specialization which makes comparisons difficult.

Chordates possess a single heart (although accessory pulsatile vessels may be present) and the circulation is closed, but chordates differ from other coelomates in that the heart is ventral and not dorsal to the gut. In the primitive urochordates (tunicates or 'sea squirts'), the capillary beds are essentially in series, and flow of blood through the heart is bi-directional. In cephalochordates (including *Branchiostoma*, the familiar amphioxus), capillary networks are largely in parallel and blood flows through the unvalved tubular 'heart' in one direction (Randall & Davie 1980). This forms the starting point for the development of the vertebrate heart.

In tracing cardiac phylogeny, especially in deriving the mammalian heart, no direct palaeontological evidence is available. Comparison of existing arrangements in extant vertebrate groups, therefore, is the only source of information. Such comparison can be misleading. Many older textbooks, dwelling only on the degree of septation, give the impression of an orthogenetic evolution of the mammalian four-chambered heart through a series of imperfect (yet surviving) intermediates. This overlooks the fact that, in all vertebrates, the structure of the heart is intimately related to the nature of surfaces for gas exchange, to locomotion and lifestyle, and to metabolism. Hearts must function early in embryonic life, throughout development, and then in greatly changed postnatal conditions.

In its simplest form the vertebrate heart is a single pump consisting of a succession of three or four enlarged segments. These are, first, a sinus venosus draining principal veins; second, a pulsatile but thin-walled atrium; third, a thick-walled muscular ventricle; and either a so-called bulbus cordis or conus, with cardiac muscle in its wall (primitive jawless vertebrates, elasmobranchs and lungfish) or a bulbus arteriosus (the swollen proximal end of the ventral aorta) consisting of smooth muscle and elastic tissue (teleost fish). The chambers are separated one from another by valves which maintain a unidirectional flow and permit increased pressures to develop at the arterial outlet. The conus, or bulbus arteriosus when present, opens into a ventral aorta from which arise a series of aortic arches that supply the gills before joining to form a median dorsal aorta. The heart has its own coronary circulation (except in primitive jawless vertebrates like lampreys and hagfish) and is contained in a pericardial coelom, a separated part of the general body cavity. The pericardial cavity is semi-rigid in some fish (for example, elasmobranchs) and lies dorsal to the pectoral girdle. The resultant constancy of volume aids atrial filling by suction as the ventricle empties. This effect is largely lost in tetrapods because of caudal 'migration' of the heart and less massive bony girdles. The pulsatile rhythm of vertebrate hearts is basically myogenic, but is co-ordinated with systemic demands by a supply of nerves. With increasing specialization from fishes to birds and mammals, nodes and tracts of cardiac muscle differentiate as focuses initiating contraction and as rapid conductors for the dissemination of cyclic stimuli (at particular sites the conduction is much slower, introducing physiologically imperative delays).

In most vertebrates, the cardiac tube outgrows the length of its pericardial sac, developing a sinuous bend. The venous end (sinus venosus and atrium) then becomes dorsal to the arterial end (ventricle and conus). Moreover, the heart becomes asymmetrical in position with the change from symmetrical cardinal veins to asymmetrical venae cavae. In the lungfish (Dipnoi), the venous sinus opens into the right of a partly divided atrium, a condition persisting in subsequent vertebrate classes. In frogs, most salamanders and all amniotes (reptiles, birds and mammals), this asymmetry is coupled with absorption of some of the venous sinus and its vestiges into the atrium. With complete separation of atria, a right-sided systemic venous return is established. At the arterial end, the bulbar segment of the embryo persists as the contractile bulbus cordis (conus) of the adult and, in elasmobranchs, commonly has serial valvar flaps. From these may be derived the spiral valves in the conus of lungfish and amphibians. This development is linked with the greatest era of transformation in cardiac evolution, the long series of adaptations which allowed vertebrates to spread from an aquatic to a terrestrial habitat.

It is thought that the ancestors of tetrapods were fish which were chiefly dependent on gills but could breathe air using a pharyngeal diverticulum, the so-called 'swim bladder' or, later, lungs. We have a living model for such a lifestyle in the Australian lungfish *Neoceratodus*, a facultative air-breather which relies mainly on gills and cutaneous gas exchange, but uses its lung when the oxygen concentration in the surrounding water falls (Burggren & Johansen 1986). The other two living dipnoan genera (*Protopterus* from Africa

and *Lepidosiren* from South America) are more specialized and are fully dependent on air-breathing. An inherent duality is found in the circulation of dipnoans. They have a systemic 'portal' arterial circulation (through the gills) and also a parallel pulmonary 'portal' circulation (through the walls of the lung; the same system supplying the skin and the mucous membranes of the mouth and pharynx). The adoption of air-breathing, however, creates problems for the venous return. Blood leaving the lung capillaries lacks sufficient energy to perfuse the remaining body tissues effectively and must, therefore, be returned to the heart. If it simply joins the systemic venous return, there will be large-scale mixing of oxygenated and deoxygenated blood. Division of the atrial chamber, with pulmonary venous blood returning to a separate left atrium, is, therefore, a requirement for efficient air-breathing. Such circuits already return blood to discrete atria in dipnoans and, although the ventricle is only partly divided, perfusion studies have shown that obligate air-breathers have the ability to separate the different bloodstreams—partly by virtue of the highly trabecular internal ventricular surface. The ventricular output is divided into two streams by spiral valves in a large conus arteriosus. Oxygenated blood from the left side of the heart is directed preferentially to the head and dorsal aorta while blood from the right side is directed to the 'lungs' via the more caudal gill clefts (the passage through the gills being important for the removal of carbon dioxide).

The earliest tetrapods were in existence at least 360 million years ago in the Devonian Period of the Palaeozoic. From what we now know of them, it would seem that the first tetrapods were aquatic animals using, like the lungfish *Neoceratodus*, a combination of branchial, pulmonary and cutaneous gas exchange (Coates & Clack 1991). It may be, therefore, that no sudden change, either in structure or function, occurred in the slow adaptation from aquatic to terrestrial life. There was, instead, a change of balance between several coexistent modes of respiration. These respiratory changes, inseparable from cardiac circulatory modifications, were accompanied by changes in the locomotor system, with the evolution of limbs from fins, firstly as an aid to progression within an aquatic environment but then, with changes in the girdles and spine, to fully terrestrial locomotion.

In amphibians, the gills are usually lost at metamorphosis and the branchial capillary beds disappear. Gas exchange is mainly pulmonary and buccopharyngeal, with the skin becoming an important surface for the removal of carbon dioxide. In the heart, the atria are separate chambers (although the interatrial septum is perforated in most salamanders), but the ventricle is undivided (except in the salamanders *Siren* and *Necturus*). Despite this, perfusion studies have shown that several factors (a system of ventricular trabeculae, the spiral outlet valve, the position and volume of the returning blood) enable the streams of flow to be effectively separated when the animal is breathing. When the lungs are not in use, blood returning to the right atrium from the skin and buccopharyngeal region may contain more oxygen than the blood returning to the left atrium. The absence of the ventricular septum should not, therefore, be regarded as a primitive maladaptation but as a condition which permits an important flexibility in the cardiorespiratory pattern.

The earliest amniotes completed the transition to a terrestrial lifestyle with an egg that was capable of surviving out of water and a skin that was resistant to loss of water. Although some groups have returned to an aquatic or amphibious lifestyle, respiration is almost entirely pulmonary (some turtles and sea snakes are reported to use vascularized cloacal surfaces for limited gas exchange), and is linked with a complete interatrial septum and at least partial ventricular division.

The hearts of living reptiles are varied and complex and this is not a place for a detailed review (see references for further information). Reptilian hearts are unusual in having three incompletely separated ventricular compartments and a triple or quadruple arterial cardiac outflow with a pulmonary trunk, a right and a left aorta and, in turtles, a separate brachiocephalic trunk. The two aortae join dorsally to form a single median dorsal aorta. In lizards, snakes and turtles, all the outlet vessels arise from the right side of the heart (cavum venosum), although the pulmonary trunk issues from a more ventral compartment (cavum pulmonale). Blood from the left atrium flows into a left cavum arteriosum but no outflow vessels leave this compartment. The passages between the right and left ventricles, and between the two main compartments of the right ventricle, are at least partially separated one from another by valves which open and close in response to changes in pressure such that oxygenated and deoxygenated bloodstreams remain largely separated. As in amphibians the structure of the ventricle permits substantial right-to-left shunting (approaching pulmonary bypass) within the heart when the animal stops breathing (for example, when diving or, in the case of lizards, during sustained exercise—due perhaps to the disruptive effect of repeated lateral flexions of the body). In crocodiles, the arrangement is similar to that of lizards and snakes but there are two important differences. The first is the presence of a complete interventricular septum. The second is that, while the pulmonary trunk and left aorta arise from the right ventricle as usual, the right aorta leaves the left ventricle. An opening, the foramen of Panizza, permits a shunt from the right aorta into the left during breathing when little or no blood enters from the right ventricle. As in other reptiles, the system also permits a shunt in the opposite direction when the lungs are shut down in diving. Under these conditions, blood in the right ventricle passes preferentially into the left aorta due to the higher resistance of the pulmonary circuit.

The bird heart is closely similar to that of the crocodile except that degeneration of the left aortic arch (rarely present as a remnant), suppression of the interaortic septum and loss of the connection between the right ventricle and the aortic root has resulted in a fully divided heart with no possibility of right-to-left shunting. There is also a single right aortic arch. These changes probably occurred in the small, active bipedal dinosaurs which were ancestral to the first birds. In these animals, the upright posture and terrestrial lifestyle obviated the need for right-to-left shunts and permitted the continuous breathing required for a fully active lifestyle. Despite its four chambers, the bird heart differs from that of a mammal in several respects, most notably the retention of a right rather than left aortic arch and the presence of a flap-like muscular right atrioventricular valve which lacks either papillary muscles or tendinous chords (chordae tendineae).

Bird and mammal hearts have evolved independently to permit a lifestyle in which a high level of activity is maintained by a constant high metabolic rate, with all the demands that this makes on the system in terms of requirements for oxygen and energy supply. It is orthodox to derive mammals from 'reptiles', but it should be stressed that living reptiles are as far removed from such ancestral forms as are living mammals. Consequently, as we have seen, the hearts of living reptiles are specialized, and no extant reptile can provide a model for the ancestral mammalian heart. The earliest amniotes were derived from a lineage separate from that which gave rise to living amphibians. Similarly, the ancestors of mammals were primitive amniotes which separated at a very early stage (at least 300 million years ago) from the lineage which gave rise to modern reptiles and birds. We cannot easily predict, therefore, the structure of the heart in the amniotes which were ancestral to mammals. This heart seems likely to have shown full atrial and at least partial ventricular septation. Right-to-left shunting may have remained important until the limbs were brought under the body and lateral flexion of the trunk during walking no longer disrupted ventilation. The heart of the most 'primitive' living mammals, the egg-laying monotremes, is essentially mammalian, although there is reportedly some muscle within the right atrioventricular valve and its movements are regulated directly by papillary muscles without the intervention of tendinous cords.

In all mammals, including mankind, cardiac septation is complete but during embryonic life (p. 1501) stages occur that are rather like the final arrangements in some lower vertebrates. Abnormal development can lead to congenital defects resembling conditions in those forms. The resemblance is misleading because the heart must function effectively at all but its initial stages of development. The oval foramen, a feature of mammalian prenatal development, is a necessary shunt rather than an atavistic indication of earlier incomplete atrial septation. A persistently patent oval foramen, and other such cardiac abnormalities, are due to disturbed mammalian development rather than recapitulation. Equally, the functional fetal mammalian heart, with its elegant separation of blood flows within the right atrium by a combination of small valves, pressure differences and the positions of entry of the vessels, provides clear evidence that

the absence of discrete septa does not necessarily render a heart inefficient. For further details consult Embryology in this volume and the following references and their bibliographies: Foxon (1955), Johansen and Burggren (1980) and Lawson (1979).

There is no entirely logical progression in describing the heart. Whatever standpoint is used, subsequent details are presumed. The sequence adopted here is a compromise. General organization precedes external features, surface anatomy and radiology, and is then followed by internal structure, including accounts of valves, myocardium, fibrous 'skeleton', specialized conducting tissues and the cardiac cycle.

GENERAL CARDIAC ORGANIZATION

The human heart is a pair of valved muscular pumps combined in a single organ (**10**.20, 24). But, while the fibromuscular framework and conduction tissues of these pumps are structurally interwoven, each pump (the so-called 'right' and 'left' hearts) is physiologically separate, being interposed in series at different points in the double circulation. Despite this functional disposition in series, the two pumps are usually described topographically in parallel.

Of the four cardiac chambers, the two atria receive venous blood as weakly contractile reservoirs for final filling of the two ventricles, which then provide the powerful expulsive contraction forcing blood into the main arterial trunks.

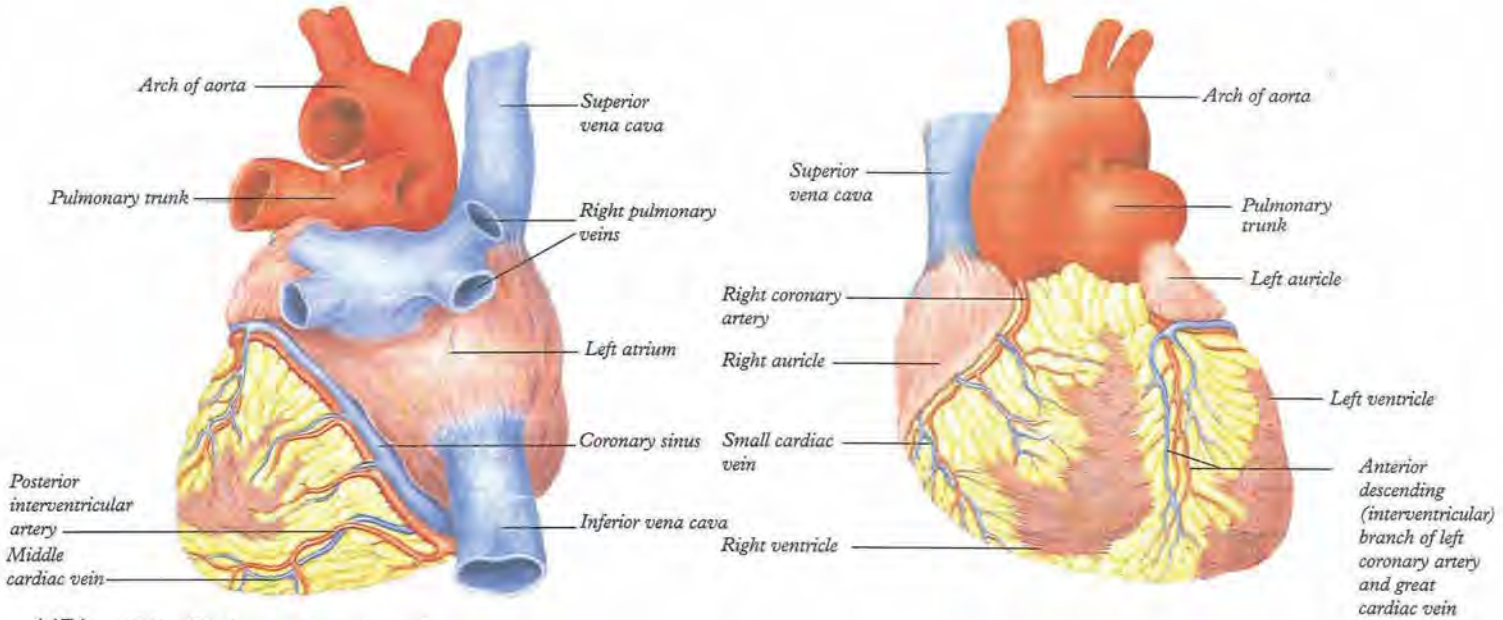
The **right heart** commences at the right atrium, and receives the superior and inferior venae cavae together with the main venous inflow from the heart itself via the coronary sinus. This systemic venous blood traverses the *right atrioventricular orifice*, guarded by the *tricuspid valve*, to enter the inlet component of the right ventricle. Contraction of the ventricle, particularly its apical trabecular component, closes the tricuspid valve and, with increasing pressure, ejects the blood through the muscular right ventricular outflow tract into the pulmonary trunk and thence to the pulmonary vascular bed, which has a relatively low resistance. Changes in pressure, time relations and valvar events are described below. Many structural features of the 'right heart', including its overall geometry, myocardial architecture and the construction and the relative strengths of the tricuspid and pulmonary valves, accord with this low resistance, being associated with comparatively low changes of pressure.

The **left heart** commences at the left atrium, which receives all the pulmonary inflow of oxygenated blood and some coronary venous inflow. It contracts to fill the left ventricle through the *left atrioventricular orifice* guarded by its *mitral valve*. The valve is the entry to the inlet of the left ventricle. Ventricular contraction rapidly raises the pressure in the apical trabecular component, closing the mitral valve and opening the aortic valve so that the ventricle can eject via the left ventricular outflow tract into the aortic sinuses, ascending aorta and thence to the whole systemic arterial tree, including the coronary arteries. This vast vascular bed presents a high peripheral resistance which, with large metabolic demands, especially the sustained requirements of the cerebral tissues, explains the more massive structural organization of the 'left heart'. The ejectional phase of the left ventricle is shorter than that of the right, but its fluctuations of pressure are very much greater.

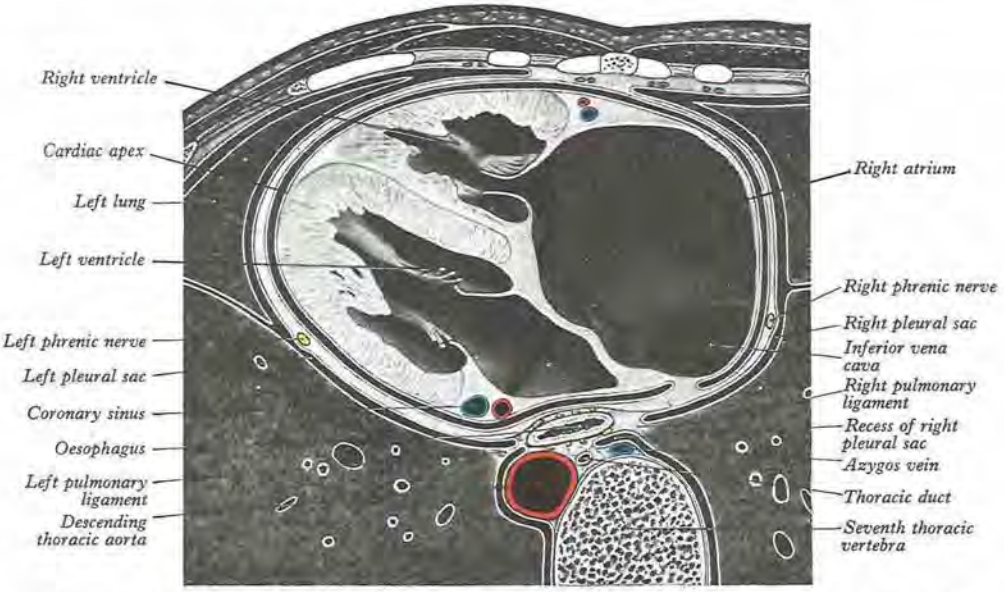
Because of its contrasting functional demands, the human heart is far from a simple pair of parallel pumps, structurally combined, even though the right and left ventricles must deliver more or less the same volume with each contraction. The heart has a complicated, spiralized, three-dimensional organization which is markedly skewed when compared with the planes of the body. Terms such as 'left' and 'right', 'anterior' and 'posterior', 'superior' and 'inferior', therefore, do not always assist the descriptions of cardiac anatomy. Another potential source of confusion is the usual study of isolated whole or dissected hearts, with the subsequent difficulty in relating details to the heart as it is positioned within the body. The following preliminary description emphasizes such difficulties so as to circumvent certain misconceptions before proceeding to an account of more detailed structure.

The principal features of cardiac anatomy can be illuminated by study of corrosion casts of normal hearts in which the two sides have been filled with resins of contrasting colours. Alternatively, similar information is obtained from horizontal mediastinal sections or scans taken at, or near, the seventh thoracic vertebral level (**10**.21, 25A, B).

The **right heart**, while forming the right aspect or 'border' (see p. 1476), follows a gentle curve and covers most of the anterior aspect of the left heart (except for a left-sided strip including the apex). Thus, the right heart forms the largest part of the **anterior** surface, its outflow tract ascending until it terminates on the **left** side of the outflow tract from the left ventricle. The sites of the tricuspid and pulmonary valves are widely separated and on different planes, the flat cavity of the right ventricle (crescentic in its section) splaying out between them. Conversely, the **left heart** (except the left-sided strip mentioned above) is largely **posterior** in position and is obscured when viewed from the front by the chambers of the right heart. The inlet to the left ventricle (containing the mitral valve) is very close to its outlet (the aortic valve), the two being embraced by the wide tract linking inlet and outlet components of the right ventricle. The



1474 **10**.20 The heart and great vessels.



10.21 Transverse section through the mediastinum at the level of the body of the seventh thoracic vertebra, viewed from above. Note the general disposition of cardiac cavities, their intervening septa (about 45° to sagittal and coronal planes) and, orthogonal to this, the plane of the atrioventricular valves. The oesophageal plexus of nerves is clear but not labelled.

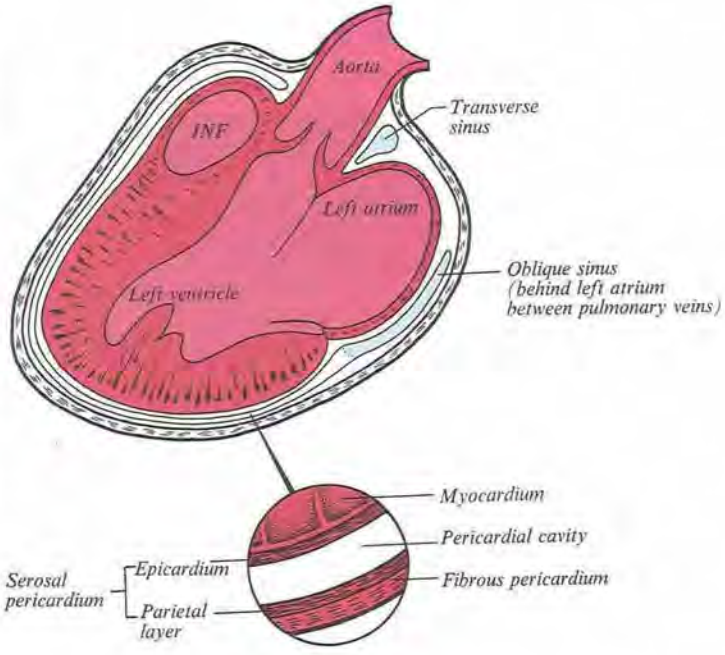
planes of the left ventricular orifices, though relatively inclined, are more nearly coplanar than those of the right. The left ventricular cavity is narrow and conical, with its tip occupying the cardiac apex. Most of the base of the heart is made up of the left atrium.

The heart is placed **obliquely** in the thorax (**10.28**). The atrial and ventricular septal structures are virtually in line but inclined forwards and to the left at about 45° to a sagittal plane. The planes of the mitral and tricuspid valves, though vertical and not precisely coplanar, are broadly at right angles to the septal plane. The right atrium, therefore, is not only to the right but also anterior and inferior to the left atrium. It is also partly anterior to the left ventricle, an important atrioventricular septum intervening. The right ventricle forms most of the anterior aspect of the ventricular mass (**10.27**), only its inferior end being to the right of the left ventricle, its upper left extremity (pulmonary orifice) being to the left and superior relative to the aortic valve. The left atrium forms most of the posterior aspect of the heart, while the left ventricle is only prominent inferiorly, running along the left margin to reach the apex. The atria are essentially right of and posterior to their respective ventricles. These general dispositions are of the greatest importance in planning or interpreting radiographs, scans, angiocardiograms and echocardiograms.

CARDIAC SIZE, SHAPE AND EXTERNAL FEATURES

The heart is a hollow, fibromuscular organ of a somewhat conical or pyramidal form, with a base, apex and a series of surfaces and 'borders'. Enclosed in the pericardium (**10.19, 21, 22**), it occupies the middle mediastinum between the lungs and their pleural coverings. It is placed obliquely behind the body of the sternum and the adjoining costal cartilages and ribs (**10.25A, B, 28**). Approximately one-third of the mass lies to the right of the midline.

An average adult heart is about 12 cm from base to apex, 8–9 cm at its broadest transverse diameter and 6 cm anteroposteriorly. Its weight varies from 280–340 g (average 300 g) in males and from 230–280 g (average 250 g) in females. Cardiac weight is said to be about 0.45% of body weight in males and 0.40% in females (Hudson 1965). Adult weight is achieved between the ages of 17 and 20 years. The oblique position of the heart may be emphasized by comparing it to a rather deformed pyramid, with the base facing posteriorly and to the right, and the apex anteriorly and to the left. A line from the apex to the approximate centre of the base, projected posterolaterally, emerges near the right midscapular line. Some surfaces of the cardiac 'pyramid' are flat, others more or less convex, these aspects merging along rather ill-defined 'borders'. Precise definition of surfaces and intervening 'borders' is, therefore, difficult. In the account which follows, official nomenclature (*Nomina Anatomica* 1989) and more generally used terms from clinical practice are given as alternatives. The heart is described as having a base and apex, its **surfaces** being designated as sternocostal (anterior); diaphragmatic (inferior); and right and left (pulmonary). Its borders are termed upper, inferior



10.22 The arrangement of the layers of the pericardium, and the location of the two sinuses within the pericardial cavity.

('acute' margin or border) and left ('obtuse' margin or border). Some name the right surface a 'border', despite its extent. One avoidable source of confusion is the use of 'posterior', which can be replaced with the unambiguous term 'diaphragmatic'. If posterior is to be used for a cardiac surface, it should be reserved for the base. But, compounding this difficulty, there are a number of different usages of the term 'cardiac base' (see below).

GROOVES ON THE CARDIAC SURFACES

The division of the heart into four chambers produces boundaries visible externally as grooves or sulci. Some are deep and obvious and contain prominent structures. Others are less distinct, even barely perceptible, and are sometimes obscured, in part, by the major structures crossing them. The *coronary*, or *atrioventricular, groove* (or *sulcus*) separates the atria from the ventricles. This groove, containing the main trunks of the coronary arteries, is oblique. It descends to the right on the sternocostal surface (**10.27**), separating the right atrium (and its auricular appendage) from the oblique right margin of the right ventricle and its infundibulum. Its upper left part is obliterated where it is crossed by the pulmonary trunk and, behind this, the aorta from which originate the coronary arteries. Continuing to the left, the groove curves around the 'obtuse margin' and descends to the right, separating the atrial base from the diaphragmatic surface of the ventricles (**10.32**). This diaphragmatic part of the coronary groove then curves around the 'acute margin' at its lower right end to become confluent with the sternocostal part. Thus, the groove passes from high on the left to low on the right, with the diaphragmatic part being a little to the left of the sternocostal. A section which includes the coronary groove is at about 45° to the sagittal plane and at a greater but variable angle to the transverse and coronal planes. It approximately traverses the lines of attachment of the atrioventricular valves and (even less precisely) those of the aortic and pulmonary valves. A line at right angles to the centre of this plane will descend forwards and leftwards to the cardiac apex.

Internally, the ventricles are separated by the septum (pp. 1480, 1483), the mural margins of which correspond to the anterior and inferior (diaphragmatic) interventricular grooves. The anterior groove, seen on the sternocostal cardiac surface, is near and almost parallel to the left ventricular obtuse margin. On the diaphragmatic surface, in contrast, the groove is closer to the midpoint of the ventricular mass. The interventricular grooves extend from the coronary groove to the apical notch on the acute margin. This is a little to the right of the true cardiac apex.

CARDIAC BASE, APEX, SURFACES, BORDERS

Posterior aspect of the heart. The true *cardiac base*, this is somewhat quadrilateral, with curved lateral extensions. It faces back and to the right, separated from the thoracic vertebrae (fifth to eighth in the recumbent, sixth to ninth in the erect posture) by the pericardium, right pulmonary veins, oesophagus and aorta. It is formed mainly by the left atrium, and only partly by the posterior part of the right atrium (**10.32**). It extends superiorly to the bifurcation of the pulmonary trunk and inferiorly to the posterior part of the atrioventricular groove containing the coronary sinus and branches of the coronary arteries (p. 1477). It is limited to the right and left by the rounded surfaces of the corresponding atria. These are separated by the shallow *interatrial groove*. The point of junction of the atrioventricular, interatrial and posterior interventricular grooves is termed the *crux of the heart* (**10.32**). Two pulmonary veins on each side open into the left atrial part of the base, while the superior and the inferior vena cava open into the upper and lower parts of the right atrial basal region. The area of the left atrium between the openings of right and left pulmonary veins forms the anterior wall of the oblique pericardial sinus (**10.19**). This description of the anatomical base reflects the usual position of the heart in the thorax. Some confusion is produced by other current usages of the term 'base'. It is often applied to the segment of the atrioventricular and ventriculo-arterial junctions seen after dissections through the coronary groove (**10.31**). This area is better termed the base of the ventricles. In clinical practice, auscultation in or near the parasternal parts of the second intercostal spaces is often described as occurring at the *clinical 'base'*, to make the contrast with the *clinical 'apex'*. Such descriptions, while less than perfect anatomically, will almost certainly persist.

Anatomical apex of the heart. This is the apex of the conical left ventricle, which is directed down, forwards and to the left. The left lung and pleura overlap it. It is located most commonly behind the fifth left intercostal space, near or a little medial to the midclavicular line.

Anterior, sternocostal surface of the heart (**10.26, 27**). Facing forwards and upwards, this has an acute right and a more gradual left convexity. It consists of an atrial area above and to the right, and a ventricular part below and to the left of the atrioventricular groove. The atrial area is occupied almost entirely by the right atrium. The left atrium is largely hidden by the ascending aorta and pulmonary trunk. Only a small part of the left appendage projects forwards to the left of the pulmonary trunk. Of the ventricular region, about one-third is made up by the left and two-thirds by the right ventricle. The site of the septum between them is indicated by the anterior interventricular groove. The sternocostal surface is separated by the pericardium from the body of the sternum, the sternocostal muscles and the third to the sixth costal cartilages. Owing to the bulge of the heart to the left, more of this surface is behind the left costal cartilages than behind the right ones. It is also covered by the pleural membranes and by the thin, anterior edges of the lungs, except for a triangular area at the cardiac incisure of the left lung. The lungs and their pleural coverings are variable in their degree of overlap of the heart.

Inferior, diaphragmatic surface of the heart (**10.32**). Largely horizontal, it slopes down and forwards a little towards the apex. It is formed by the ventricles (chiefly the left) and rests mainly upon the central tendon but also, apically, on a small area of the left muscular part of the diaphragm. It is separated from the anatomic base by the atrioventricular groove and is traversed obliquely by the posterior interventricular groove.

Left surface of the heart. Facing up, back and to the left, this consists almost entirely of the obtuse margin of the left ventricle, but has a small part of the left atrium and its auricle contributing superiorly. Convex and widest above, and crossed here by the atrioventricular groove, it narrows to the cardiac apex. It is separated by the pericardium from the left phrenic nerve and its accompanying vessels, and by the left pleura from the deep concavity of the left lung.

Right surface of the heart. A rounded surface is formed by the right atrial wall and is separated from the mediastinal aspect of the right lung by the pericardium and the pleural coverings. Its convexity merges below into the short intrathoracic part of the inferior vena cava and above into the superior vena cava. The *terminal groove* (*sulcus terminalis*) is a prominent landmark between the true atrial and the venous components of the right atrium, curving approximately along the junction of the sternocostal and right surfaces (**10.29**).

Upper border of the heart. This is atrial (mainly the left atrium). Anterior to it are the ascending aorta and the pulmonary trunk (**10.19**). At its extremity the superior vena cava enters the right atrium.

Right border of the heart. Corresponding to the right atrium, its profile is slightly convex to the right and it approaches the vertical.

Inferior border of the heart. Also known as the *acute margin* of the heart, it is sharp, thin and nearly horizontal. It extends from the lower limit of the right border to the apex and it is formed mainly by the right ventricle, with a small contribution from the left ventricle near the apex.

Left border of the heart. Also known as the *obtuse margin*, it separates the sternocostal and left surfaces. It is round and mainly formed by the left ventricle but, to a slight extent superiorly, is formed by the auricle of the left atrium. It descends obliquely, convex to the left, from the auricle to the cardiac apex.

CARDIAC CHAMBERS AND INTERNAL FEATURES

The right and left chambers of the heart will be described in sequence

in terms of their general form, their walls and their internal features. The two sides have much in common, such as the structure of valvar leaflets, tendinous cords, and papillary muscles of atrioventricular (inlet) valves, and the architecture of the cusps of the pulmonary and aortic (outlet) valves. Repetition, as far as possible, will be kept to a minimum.

RIGHT ATRIUM

General and external features

The *interatrial septum* (or *atrial septum*) is oblique, so the right atrium is anterior as well as to the right of the left atrium (**10.27**, 32), also extending inferior to it. Its walls form the right upper sternocostal surface, the convex right (pulmonary surface) and a little of the right side of the anatomic base. The superior vena cava opens into its dome and the inferior vena cava into its lower posterior part (**10.27**). An extensive muscular pouch, the *auricle* or appendage, projects anteriorly to overlap the right side of the ascending aorta. The auricle is a broad, triangular structure and has a wide junction with the true atrial component of the atrium (**10.23A**, 29). The junction between the venous part (*sinus venarum*) and the atrium proper is marked externally by a shallow groove, the *sulcus terminalis*, extending between the right sides of the openings of the two venae cavae. The sulcus terminalis corresponds, internally, to the terminal crest (*crista terminalis*) which is the site of origin of the extensive pectinate muscles arising serially at right angles from the crest (**10.33**). Posteriorly, the vertical interatrial groove descends to the crux.

Anteriorly, the right atrium is related to the anterior part of the mediastinal surface of the right lung, separated from it by pleura and pericardium. **Laterally**, the atrium is also related to the mediastinal surface of the right lung, but anterior to its hilum and separated from it by the pleura, right phrenic nerve and pericardiacophrenic vessels and pericardium. **Posteriorly** and to the left (**10.32**, 35), the atrial septum and the surrounding infolded atrial walls separate the right from the left atrium (the mural infolding being indicated by the extensive interatrial groove). Posteriorly and to the right are the right pulmonary veins. **Medially** are the ascending aorta and, to a lesser extent, the root of the pulmonary trunk and its bifurcation.

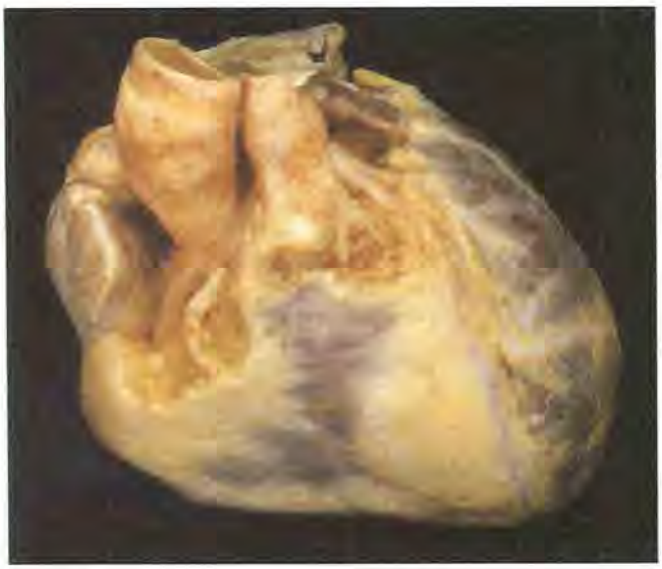
Interior surface of the right atrium (**10.24**, 34). The interior surface can be divided into three regions: a smooth-walled venous component, posteriorly, leading, anteriorly, to the vestibule of the tricuspid valve and the auricle. The wall of the vestibule is smooth, but its junction with the auricle is ridged all around the atrioventricular junction. The smooth-walled part receives the opening of the venae cavae and the coronary sinus. It represents the venous component ('sinus venosus') of the developing heart (p. 303). The wall of the vestibule has a ridged surface and that of the auricle is trabeculated; both are derived from the embryonic atrium proper.

Opening into the venous component are the *superior vena cava* returning blood from head, neck and upper limb through an orifice which faces infero-anteriorly and has no valve, and the *inferior vena cava*. The latter vessel is larger than its superior counterpart and returns blood from the lower part of the body into the lowest part of the atrium near the septum. Anterior to its orifice is a flap-like valve, the *Eustachian valve* or valve of the inferior vena cava (**10.33**). Of varying size, this valve is found along the lateral, or right, margin of the vein. When traced inferiorly, it runs into the sinus septum (see below) where it is contiguous with the valve of the coronary sinus (*Thebesius' valve,* also known as the *Thebesian valve*). The lateral part of the Eustachian valve becomes continuous with the lower end of the terminal crest. The valve is a fold of endocardium enclosing a few muscular fibres. It is large during fetal life, when it serves to direct richly oxygenated blood from the placenta through the oval foramen of the atrial septum into the left atrium. The valve varies markedly in size in postnatal life, sometimes being cribriform or filamentous but often being absent. A particularly prominent recess is seen postero-inferiorly relative to the orifice of the coronary sinus (see below). This is the *postEustachian sinus*.

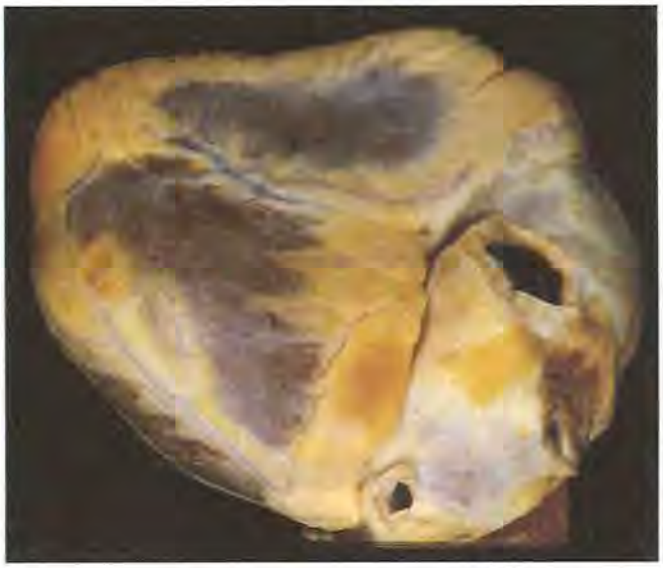
Also opening into the venous atrial component is the coronary sinus. This vessel returns the majority of blood from the heart itself, opening between the orifice or the inferior vena cava, the oval fossa and the vestibule of the atrioventricular opening (**10.33**). The coronary sinus is often guarded by a thin, semicircular valve which covers the lower part of the orifice (Thebesius' valve). The upper limb of this valve joins with the Eustachian valve and, from this commissure, a tendinous structure runs into the sinus septum (the septum between the coronary sinus and the oval fossa). The tendinous structure, called the *tendon of Todaro*, runs forwards to insert into the central fibrous body. It is one of the landmarks of the triangle of Koch (**10.36** see below).

The orifice of the coronary sinus forms a prominent landmark in the right atrium (**10.33**). The sinus itself, however, lies within the left atrioventricular groove (**10.32**). It is the conduit for return of most of the venous blood from the heart, although some atrial veins drain directly to the right or left atrial chambers. The coronary sinus commences at the point where the oblique vein of the left atrium joins. The sinus receives the middle and small cardiac veins close to its junction with the right atrium.

Multiple small venous orifices, draining the minimal atrial veins, are found scattered around the atrial walls. They return a small



10.23A. The anterior surface of the removed heart oriented so that it lies, as far as possible, in its position within the body.



B. The posterior surface of the removed heart, oriented to take its position within the body.

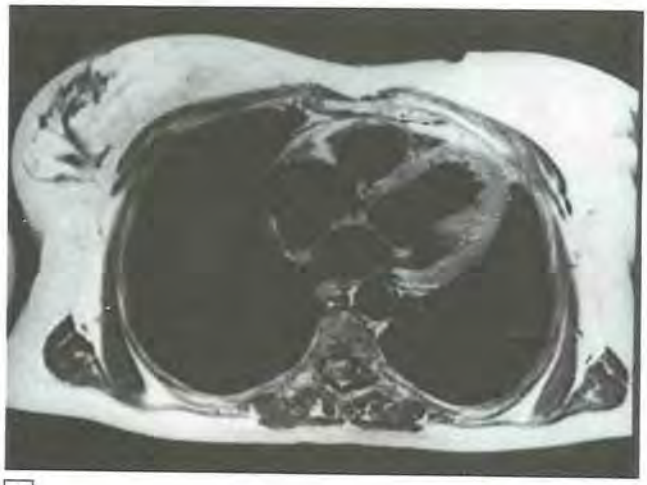
10.24 This dissection shows the crucial relation between subaortic outflow tract and ventricular inlet components, as shown in **10.25**. The non-coronary sinus of the aorta, with its corresponding aortic valvar cusp, has been removed.

fraction of blood from the heart (p. 1575), being most numerous on the septal aspect. The anterior cardiac veins and, sometimes, the right marginal vein may enter the atrium through larger orifices (p. 1576).

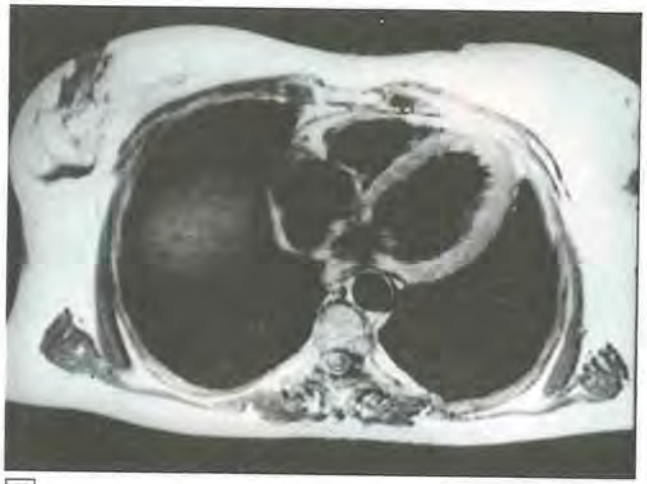
The atrium proper and the auricle are separated from the venous sinus by the *terminal crest* (*crista terminalis*). This smooth, muscular ridge begins on the upper part of the septal surface and, passing anterior to the orifice of the superior vena cava, skirts its right margin to reach the right side of the orifice of the inferior vena cava (**10.33**). It marks the site of the right venous valve of the embryonic heart (p. 303), and corresponds externally to the terminal groove (p. 1477). Within the superior part of the groove, lateral to, and extending below, the orifice of the superior vena cava, is found the sinus node (p. 1496).

The *pectinate muscles* (*musculi pectinati*), almost parallel muscular ridges, extend anterolaterally from the terminal crest and reach into the auricle, where they form multiple trabeculations.

The septal wall presents the *oval fossa* (*fossa ovalis*), an oval depression found above and to the left of the orifice of the inferior vena cava. Its floor is the *primary atrial septum*, the '*septum primum*' (p. 303). The rim of the fossa is prominent and, although often said to represent the edge of the so-called '*septum secundum*' (p. 304), in

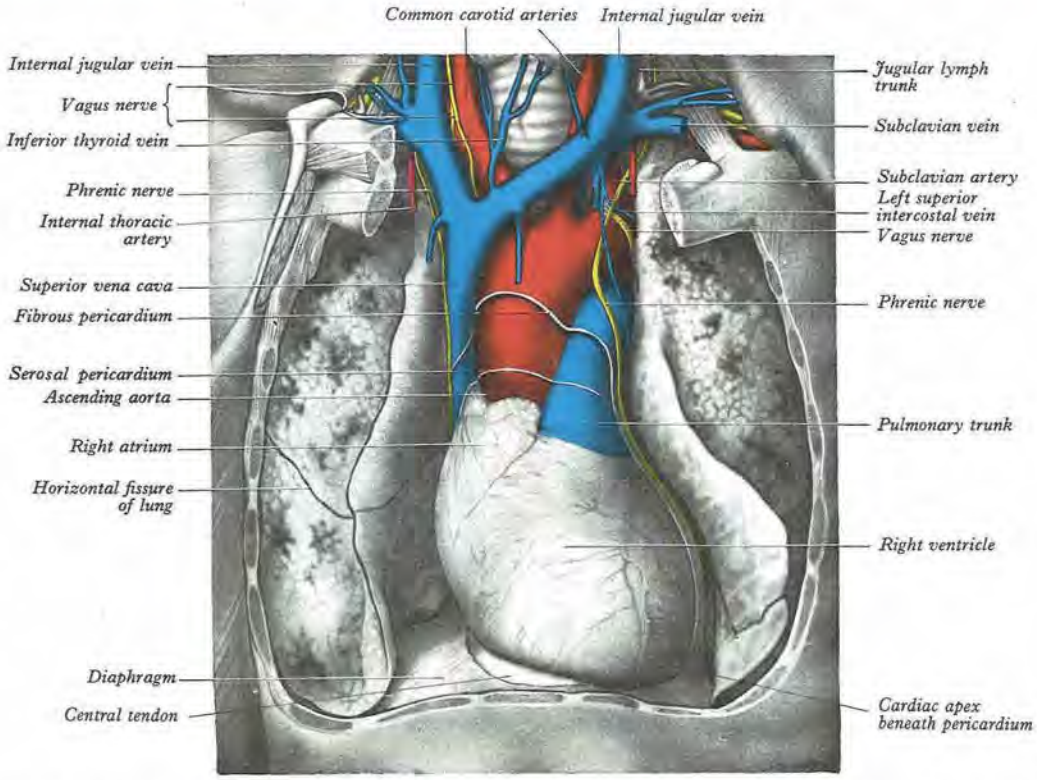


A



B

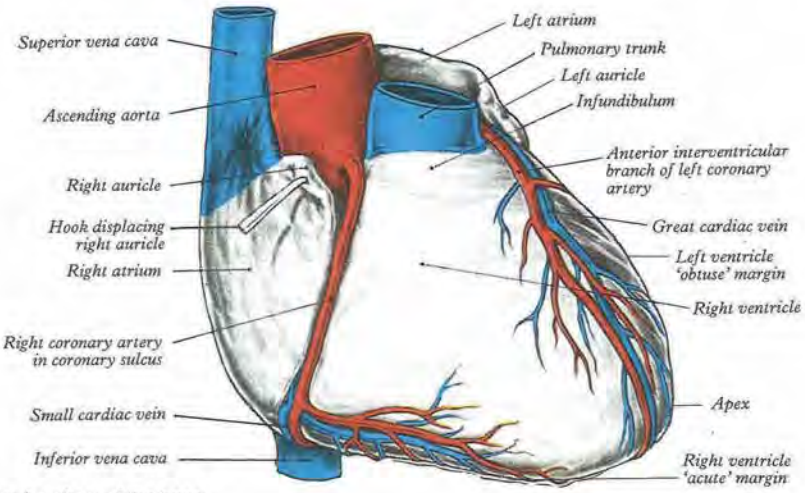
10.25 Computed tomograms of the thorax. A. Through the body of the seventh thoracic vertebra. B. Through the intervertebral disc between the seventh and eighth vertebrae. Note the overall disposition of the heart, its apex, base, oblique, interatrial and interventricular septa and, orthogonal to this, of the atrioventricular valves. Note also the atrioventricular septum, papillary muscles, trabeculae carneae, descending thoracic aorta and contrasting areas of right and left lungs and pleurae. (Provided by Shaun Gallagher, Guy's Hospital; photography by Sarah Smith.)



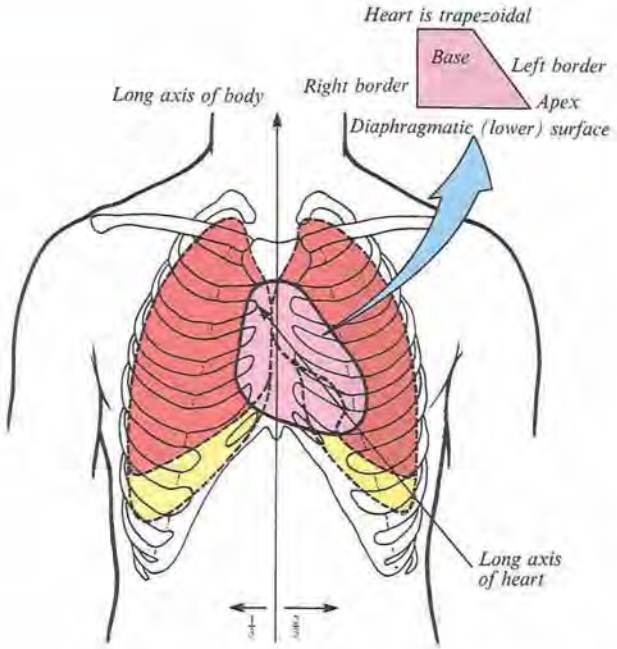
10.26 Dissection which displays the heart, the great vessels and the lungs in situ. The sternum and the sternal ends of the costal cartilages, together with the parietal pleura on each side, have been excised and the mediastinal pleura and parietal layer of the pericardium over the sternocostal surface of the heart have been removed. The lungs have been displaced to expose the heart and the epicardium dissected off the heart and roots of the great vessels. On the right side, the inferior cardiac branch of the vagus nerve descends between the brachiocephalic artery and the right brachiocephalic vein. On the left side, a communication descends from the left superior intercostal vein and crosses the aortic arch and the left pulmonary artery to become continuous with the oblique vein of the left atrium.

reality it is merely the infolded walls of the atrial chambers. It is most distinct above and in front of the fossa, usually being deficient inferiorly. A small slit is sometimes found at the upper margin of the fossa, ascending beneath the rim to communicate with the left atrium. This represents failure of obliteration of the fetal oval foramen, which remains patent in up to one-third of all normal hearts.

Antero-inferior in the right atrium is the large, oval vestibule leading to the orifice of the tricuspid valve. A triangular zone (the *triangle of Koch*, **10.36**) is found between the attachment of the septal leaflet of the tricuspid valve, the anteromedial margin of the orifice of the coronary sinus, and the round, collagenous, palpable, subendocardial tendon of Todaro. The triangle is a landmark of particular surgical import, indicating the site of the atrioventricular node and its atrial connections (p. 1499). Anterosuperior to the insertion of the *tendon of Todaro*, the septal wall is the **atrioventricular** component of the *membranous septum*, intervening between the right atrium and subaortic outlet of the left ventricle (**10.36**). The atrial



10.27 The anterior or sternocostal surface of the heart.



10.28 The front of the thorax, showing the surface relations of the bones, lungs (purple), pleurae (blue) and heart (red outline). Compare **10.46** for further cardiac detail.

10.29 Removal of the pericardium shows the right margin of the heart, made up mostly of the right atrium. Note the characteristic terminal groove (sulcus terminalis).

wall bulges anterosuperiorly above the membranous septum. This area is the aortic mound (*torus aorticus*) and marks the location of the non-coronary sinus of the aorta with its enclosed valvar cusp (p. 1488).

RIGHT VENTRICLE

The right ventricle extends from the right atrioventricular (tricuspid) orifice nearly to the cardiac apex. It then ascends to the left to become the *infundibulum*, or *conus arteriosus*, reaching the pulmonary orifice and supporting the cusps of the pulmonary valve. Topographically, the ventricle possesses: an inlet component, supporting and surrounding the tricuspid valve; a coarsely trabeculated apical component; and the muscular outlet or infundibulum surrounding the attachments of the cusps of the pulmonary valve (**10.37A**).

External features

The convex *anterosuperior surface* makes up a large part of the sternocostal aspect of the heart (**10.23A**), separated from the thoracic wall only by the pericardium. The left pleura and, to a lesser extent, the anterior margin of the left lung are interposed above and to the left. The *inferior surface* is flat and is related mainly, with the interposition of the pericardium, to the central tendon and a small adjoining muscular part of the diaphragm. The *left* and *posterior wall* is the ventricular septum. This is slightly curved and bulges into the right ventricle so that, in sections across the cardiac axis, the outline of the right ventricle is crescentic (**10.38**). A delicate collagenous band, the tendon of the infundibulum (conus ligament), is held by some to connect the pulmonary muscular infundibulum posteriorly to the root of the aorta. The wall of the right ventricle is significantly thinner (3–5 mm on average) than that of the left, the ratio usually being about 1 to 3.

Internal features

The inlet and outlet components of the ventricle, supporting and surrounding the leaflets of the tricuspid and pulmonary valves respectively, are separated in the roof of the ventricle (**10.31**) by the prominent *supraventricular crest* (*crista supraventricularis*). The crest is a thick, muscular, highly arched structure, extending obliquely forwards and to the right from a *septal limb* high on the interventricular septal wall to a *mural* or *parietal limb* on the anterolateral right ventricular wall. The posterolateral aspect of the crest provides a principal attachment for the anterosuperior leaflet of the tricuspid valve (see below). The crest's septal limb may be continuous with, or embraced by, the septal limbs of the septomarginal trabecula (see below). The inlet and outlet regions extend apically into and from the prominent coarsely trabeculated component of the ventricle. The inlet component is itself also trabeculated, whereas the outlet component (or infundibulum) has predominantly smooth walls. The trabeculated appearance is due to myriad irregular muscular ridges and protrusions, which are known collectively as *trabeculae carnae*, and are lined by endocardium. These protrusions and intervening grooves impart great variation in wall thickness. Protrusions vary in extent from mere ridges to trabeculae which are fixed at both ends but free in-between. Other conspicuous protrusions are the papillary muscles, which are inserted at one end onto the ventricular wall and are continuous at the other end with collagenous cords, the chordae tendineae, inserted on the free edge and elsewhere on the free aspect of the atrioventricular valves (p. 148). One protrusion in the right ventricle, the *septomarginal trabecula* or septal band, is particularly prominent. It reinforces the septal surface where, at the base, it divides into limbs which embrace the supraventricular crest. Towards the apex, it supports the anterior papillary muscle of the tricuspid valve and, from this point, crosses to the parietal wall of the ventricle as the 'moderator band' (this alternative name records an old idea that the septomarginal trabecula prevents overdistension of the ventricle). A further series of prominent trabeculae extend from its anterior surface and run onto the parietal ventricular wall. These are the septoparietal trabeculations (**10.37A**). The smooth-walled *outflow tract*, or *infundibulum* (*conus arteriosus*), ascends to the left

above the septoparietal trabeculations and **below** the arch of the supraventricular crest to the pulmonary orifice.

TRICUSPID VALVE

The atrioventricular valvar complex, in both right and left ventricles, comprises the following:

- the orifice and its associated annulus
- the leaflets
- the supporting *tendinous cords* (*chordae tendineae*) of various types
- the papillary muscles.

Harmonious interplay of all these, together with the atrial and ventricular myocardial masses (p. 1494), depends on the conduction tissues (p. 1495) along with the mechanical cohesion provided by the fibro-elastic cardiac skeleton. All parts change substantially in position, shape, angulation and dimensions during a single cardiac cycle.

Tricuspid valvar orifice

The largest valvar orifice (circumference of around 11.4 cm in males and 10.8 cm in females according to Silver et al 1971), it is best seen from its atrial aspect (**10.31**). It has a clear line of transition from the atrial wall or septum to the lines of attachment of the valvar leaflets. Its margins are not precisely in a single plane; at a near approximation it is almost vertical but at about 45° to the sagittal plane and slightly inclined to the vertical, such that it 'faces' (on its ventricular aspect) anterolaterally to the left and somewhat inferiorly (**10.46**). Roughly triangular, its margins are described as antero-superior, inferior and septal, corresponding to the lines of attachment of the valvar leaflets.

The *annulus* of the tricuspid valve is an ill-defined term used without uniformity. Elementary accounts often describe all four valvar orifices as surrounded by uniform rings of collagenous tissue, the rings interconnected by dense masses of collagen which, in the mitral and tricuspid valves, are situated precisely at the atrio-ventricular junctions (presumed also to separate the atrial and ventricular myocardial masses). Only some of these assumptions are true. The connective tissues around the orifice of the atrioventricular valves, while serving to separate atrial and ventricular myocardial masses completely except at the point of penetration of the atrio-ventricular bundle, vary in density and disposition around the valvar circumference. Extending from the right fibrous trigone component of the central fibrous body are a pair of curved, tapered, sub-endocardial tendons, or 'prongs' (*fila coronaria*) which partly encircle the circumference; the latter is completed by more tenuous, deformable fibroblastic sulcar areolar tissue. The extent of fibrous tissue also varies with sex and age (Walmsley & Watson 1978). Nevertheless, the tissue within the atrioventricular junction around the tricuspid orifice is less robust than similar elements found at the attachments of the mitral valve (p. 1485). Furthermore, in the tricuspid valve, the topographical 'attachment' of the free valvar leaflets does not wholly correspond to the internal level of attachment of the fibrous core of the valve to the junctional atrioventricular connective tissue. It is the line of attachment of the leaflet which is best appreciated in the heart when examined grossly, and this feature is also more readily discerned clinically.

Tricuspid valve leaflets

It is usually possible to distinguish three leaflets in the tricuspid valve, hence the name. They are located septally, antero-superiorly and inferiorly, corresponding to the marginal sectors of the atrio-ventricular orifice so named. Each is a reduplication of endocardium enclosing a collagenous core, continuous marginally and on its ventricular aspect with diverging fascicles of tendinous cords (see below) and basally confluent with the annular connective tissue. All leaflets of the atrioventricular valves display, passing from the free margin to the inserted margin, *rough*, *clear* and *basal zones*. The rough zone is relatively thick, opaque and uneven on its ventricular aspect where most tendinous cords are attached. The atrial aspect of the rough zone makes contact with the comparable surface of the adjacent leaflets during full closure of the valve. The clear zone is smooth and translucent, receives few tendinous cords and has a thinner fibrous core. The basal zone, extending about 2–3 mm from the circumferential attachment of the leaflets, is thicker, contains more connective tissue and is vascularized and innervated, containing the insertions of the atrial myocardium.

The *anterosuperior leaflet* is the largest component of the tricuspid valve (**10.37B**). It is attached chiefly to the atrioventricular junction on the posterolateral aspect of the supraventricular crest, but extends along its septal limb to the membranous septum, ending at the *anteroseptal commissure*. One or more notches often indent its free margin. The attachment of the *septal leaflet* passes from the *inferoseptal commissure* on the posterior ventricular wall across the muscular septum and then angles across the membranous septum to the anteroseptal commissure. The *inferior leaflet* is wholly mural in attachment and guards the diaphragmatic surface of the atrio-ventricular junction; its limits are the inferoseptal and *antero-inferior commissures*.

Tendinous cords (chordae tendineae)

The tendinous cords are fibrous collagenous structures supporting the leaflets of the atrioventricular valves. *False chordae* connecting papillary muscles to each other or to the ventricular wall including the septum, or passing directly between points on the wall (and/or septum), are irregular in numbers and dimensions in the right ventricle. The true chordae usually arise from small projections on the tips or margins of the apical thirds of papillary muscles, but sometimes from the bases of papillary muscles or directly from the ventricular walls and the septum. They are attached to various parts of the ventricular aspects or the free margins of the leaflets. They were classified by Tandler (1913) into first, second and third order chordae according to the distance of the attachment from the margins of the leaflets. Subsequent authors have usually followed this classification, although the scheme has little functional or morphological merit. According to their morphology, nonetheless, it is possible to distinguish several patterns (Lam et al 1970; Silver et al 1971).

Fan-shaped chordae have a short stem from which branches radiate to attach to the margins (or the ventricular aspect) of the zones of apposition between leaflets and to the ends of adjacent leaflets (**10.37A, B**). *Rough zone chordae* arise from a single stem which usually splits into three components which attach to the free margin, the ventricular aspect of the rough zone and to some intermediate point on the leaflet, respectively. *Free edge chordae* are single, threadlike and often long, passing from either the apex or the base of a papillary muscle into a marginal attachment, usually near the midpoint of a leaflet or one of its scallops. *Deep chordae*, also long, pass beyond the margins and, branching to various extents, reach the more peripheral rough zone or even the clear zone. *Basal chordae* are round chordae or flat ribbons, long and slender or short and muscular. They arise from the smooth or trabeculated ventricular wall and attach to the basal component of a leaflet.

Papillary muscles

The two major papillary muscles in the right ventricle are located in anterior and posterior positions; a third, smaller muscle has a medial position along with several smaller, and variable, muscles attached to the ventricular septum. The *anterior papillary muscle* is largest. Its base arises from the right anterolateral ventricular wall below the antero-inferior commissure of the inferior leaflet and it also blends with the right end of the septomarginal trabecula. The *posterior*, or *inferior, papillary muscle* arises from the myocardium below the inferoseptal commissure. It is frequently bifid or trifid. The *septal*, or *medial, papillary muscle* is small but typical, and arises from the posterior septal limb of the septomarginal trabecula. All the major papillary muscles supply chordae to **adjacent** components of the leaflets they support. A feature of the right ventricle, however, is that the septal leaflet is tethered by individual tendinous chordae directly to the ventricular septum. Such septal insertions are never seen in the left ventricle. When closed, the three leaflets fit snugly together, the pattern of the zones of apposition confirming the trifoliate arrangement of the tricuspid valve.

PULMONARY VALVE

The pulmonary valve, guarding the outflow from the right ventricle,

surmounts the infundibulum and is situated at some distance from the other three cardiac valves (**10.51, 52**). Its general plane faces superiorly to the left and slightly posteriorly. It has three *semilunar leaflets* or *cusps* attached by convex edges partly to the infundibular wall of the right ventricle and partly to the commencement of the pulmonary trunk; the line of attachments is curved, rising at the periphery of each cusp near their zones of apposition (the *commissures*) and reaching the sinutubular ridge of the pulmonary trunk (**10.43A**). Removal of the cusps shows that the fibrous semilunar attachments enclose three crescents of infundibular musculature within the pulmonary sinuses, while three roughly triangular segments of arterial wall are incorporated within the ventricular outflow tract beneath the apex of each commissural attachment (**10.43A**). There is, thus, no proper circular 'annulus' supporting the leaflets of the valve, the *fibrous semilunar attachment* being an essential requisite for snug closure of the nodules and lunules of the cusps (see below) during ventricular diastole. It is difficult precisely to name the cusps and corresponding sinuses of the pulmonary valve and trunk according to the co-ordinates of the body since the valvar orifice is obliquely positioned. The official nomenclature (*Nomina Anatomica* 1989) refers to an *anterior*, a *posterior* and a *septal* cusp, based on their position in the fetus. The position changes with development and in the adult there are two *anterior* cusps, *right* and *left*, and a *posterior* one.

Each cusp is a fold of endocardium, with an intervening, and variably developed, fibrous core. The core is substantial along both the free edge and the semilunar attached border, and the latter is particularly thickened at the deepest central part (nadir) of the base of each cusp (thus never forming a simple complete fibrous ring). Central in the free margin of each cusp is a localized thickening of collagen, the *nodule of Arantius*. Perforations within the cusps close to the free margin and near the commissures are frequently present but of no functional significance. Each semilunar cusp is contained within one of the three sinuses of the pulmonary trunk. Except for differences in relations of timing and pressures, opening and closure of the pulmonary valve has much in common with that of the aortic valve (see p. 1487, **10.55**).

LEFT ATRIUM

Though smaller in volume than the right, the *left atrium* has thicker walls (3 mm on average). Its cavity and walls are largely formed by the proximal parts of the pulmonary veins, incorporated into the atrium during development (p. 303). The only clear derivative of the left part of the embryonic atrium is the auricle, along with the vestibule of the mitral valve. The left atrium is roughly cuboidal and extends behind the right atrium, separated from it by the obliquely positioned septum (**10.25A, B**). Thus, the right atrium is in front and anterolateral to the right part of the left atrium. The left part is concealed anteriorly by the initial segments of the pulmonary trunk and aorta, with part of the transverse pericardial sinus between it and these arterial trunks. Antero-inferiorly, and to the left, it adjoins the base of the left ventricle at the orifice of the mitral valve (see below). Its posterior aspect forms most of the anatomical base of the heart and is approximately quadrangular, receiving the terminations of (usually) two pulmonary veins from each lung. It forms the anterior wall of the oblique pericardial sinus (**10.19**). This surface ends at the shallow vertical interatrial groove that descends to the cardiac crux. The left atrial auricle is constricted at its atrial junction and all the pectinate muscles of the left atrium are contained within it. It is characteristically longer, narrower and more hooked than the right auricle, its margins being more deeply indented. It turns forwards to the left of the pulmonary trunk, overlapping its origin (**10.30, 39**).

Interiorly, the four *pulmonary veins* open into the upper postero-lateral surfaces of the left atrium, two on each side. Their orifices are smooth and oval, the left pair frequently opening via a common channel. The *left atrioventricular orifice* is fully described below. Some minimal cardiac veins return blood directly from the myocardium to the cavity of the left atrium. The left atrial aspect of the septum has a characteristically rough appearance, bounded by a crescentic ridge, concave upwards, which marks the site of the oval foramen (p. 304).

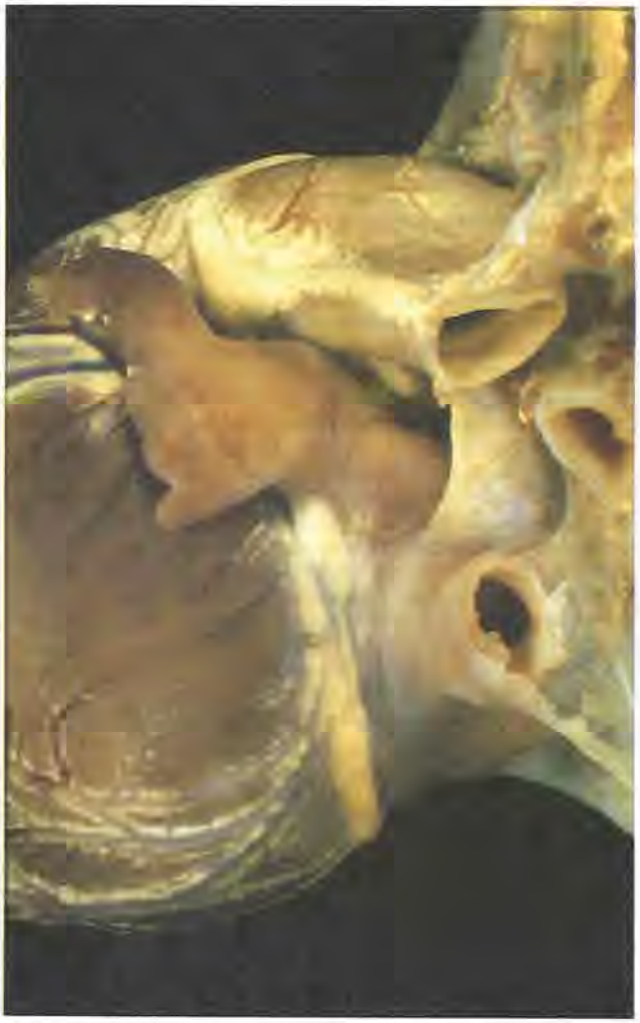
LEFT VENTRICLE

General and external features

The left ventricle is constructed in accordance with its role as a powerful pump needed to sustain pulsatile flow in the high-pressured systemic arteries. Variously described as half-ellipsoid or cone-shaped, it is longer and narrower than the right ventricle, extending from its base in the plane of the coronary groove to the cardiac apex. Its long axis descends forwards and to the left. In transverse section, at right angles to the axis, its cavity is oval or nearly circular, with walls about three times thicker (8–12 mm) than those of the right ventricle. It forms part of the sternocostal, left and inferior (diaphragmatic) cardiac surfaces. Except where obscured by the aorta and pulmonary trunk, the base of the ventricular cone is superficially separated from the left atrium and atrial auricle by part of the atrioventricular groove, the coronary sinus running in the posterior aspect of the groove to reach the right atrium (**10.30, 32**). The anterior and posterior interventricular grooves indicate the lines of mural attachment of the ventricular septum and the limits of the left and right ventricular territories. The sternocostal surface of the ventricle curves bluntly into its left surface at the obtuse margin.

Internal features

Like the right, the left ventricle has an inlet region, guarded by the mitral valve (*ostium venosum*), an outlet region, guarded by the aortic valve (*ostium arteriosum*), and an apical trabecular component



10.30 The characteristic morphology of the left atrial appendage (compare with **10.29**, the right appendage from the same heart).

10.31 This section of the heart is taken to either side of the oblique atrioventricular groove, but is then laid horizontal and photographed from the atrial aspect. It shows the interrelationships of the four cardiac valves at the so-called base of the heart. Note the central location of the aorta.

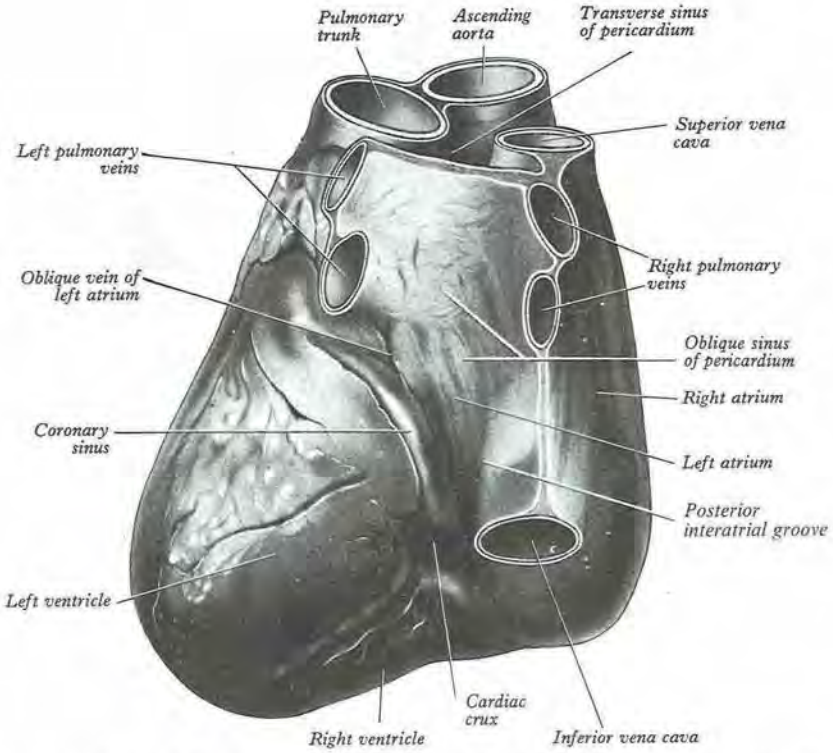
(40A, B, C). The left atrioventricular orifice, with its mitral valve, admits atrial blood during diastole, flow being towards the cardiac apex. After closure of the mitral leaflets, and throughout the ejection phase of systole, blood is expelled from the apex through the aortic orifice. In contrast to the orifices within the right ventricle, those of the left ventricle are in close contact, with fibrous continuity between the leaflets of the aortic and mitral valves (the subaortic curtain; **10**.42). The inlet and outlet turn sharply round this fibrous curtain (**10**.40C, 51).

The anterolateral wall is the concavo-convex *ventricular septum*, a muscular wall whose convexity is the posteromedial profile of the right ventricle as seen in section. It thus completes the circular outline of the left ventricle. Towards the aortic orifice, the septum becomes the thin, collagenous interventricular component of the *membranous septum*, an oval or round area below and confluent with the fibrous triangle separating the right and the non-coronary cusps of the aortic valve (p. 1488).

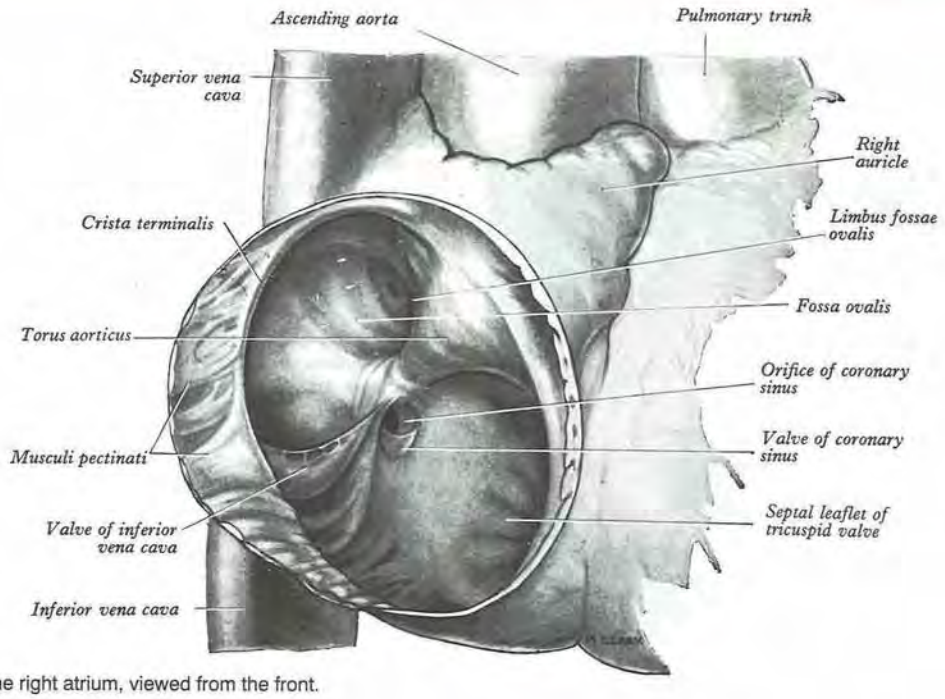
Between the lower limits of the free margins of the leaflets of the mitral valve and the apex of the ventricle, the muscular walls are deeply trabeculated. These *trabeculae carneae* are finer and more intricate than those of the right ventricle, but similar in structure (p. 1480, **10**.40A, B). Trabeculation is characteristically well developed near the apex, whereas the upper reaches of the septal surface are smooth (**10**.42).

MITRAL VALVE

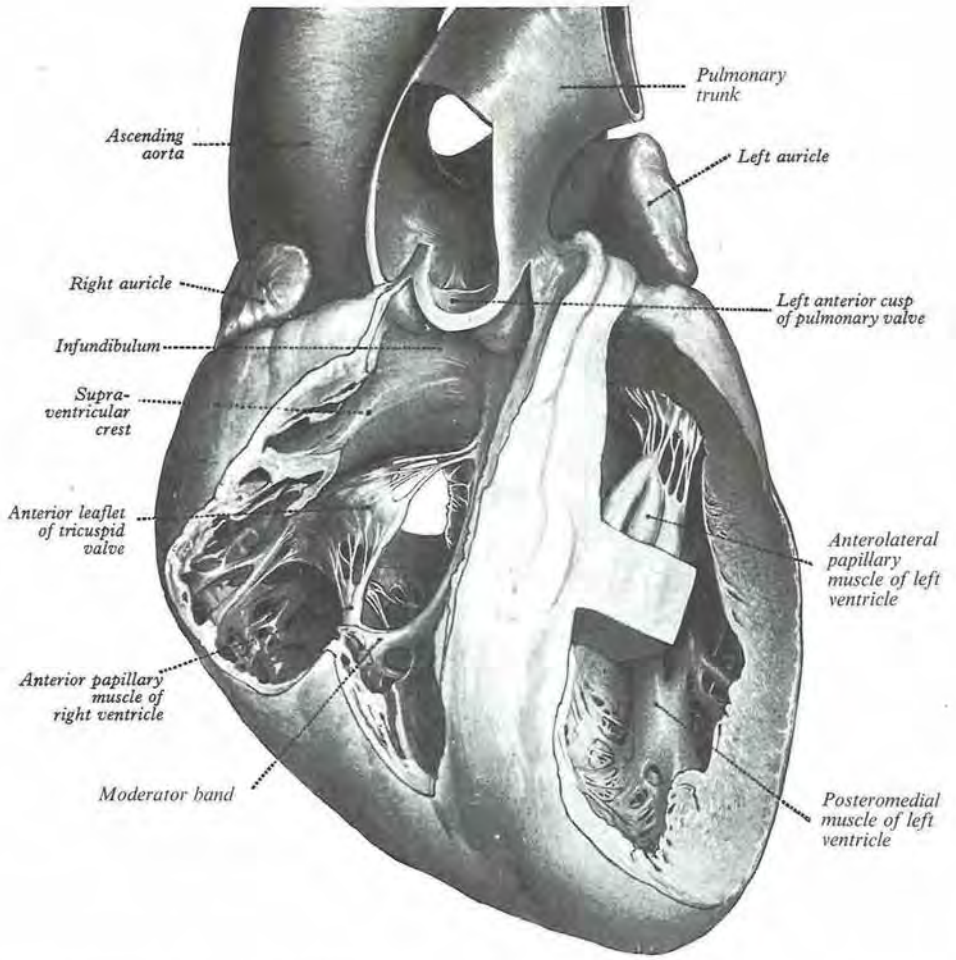
The general comments already made in respect to the tricuspid valve apply equally to the mitral. As expected, therefore, the valve has an orifice with its supporting annulus, leaflets, a variety of tendinous chordae and papillary muscles.



10.32 The base and the diaphragmatic surface of the heart. The serosal pericardium is in situ and its cut edge is seen around the great vessels; its disposition is highly schematic (recesses omitted). See text for additional details. The cardiac crux results from the confluence of the posterior interatrial groove, the posterior atrioventricular groove and the posterior interventricular groove.



10.33 The interior of the right atrium, viewed from the front.



 10.34 A dissection opening the ventricles, viewed from the front.

10.35 The surfaces of the right atrium are separated by the deep interatrial groove (Waterston's groove) from the left atrium. This groove forms the anterosuperior margin of the atrial septum (the oval fossa). Note the solitary line of coaptation of the leaflets of the mitral valve.

Mitral orifice

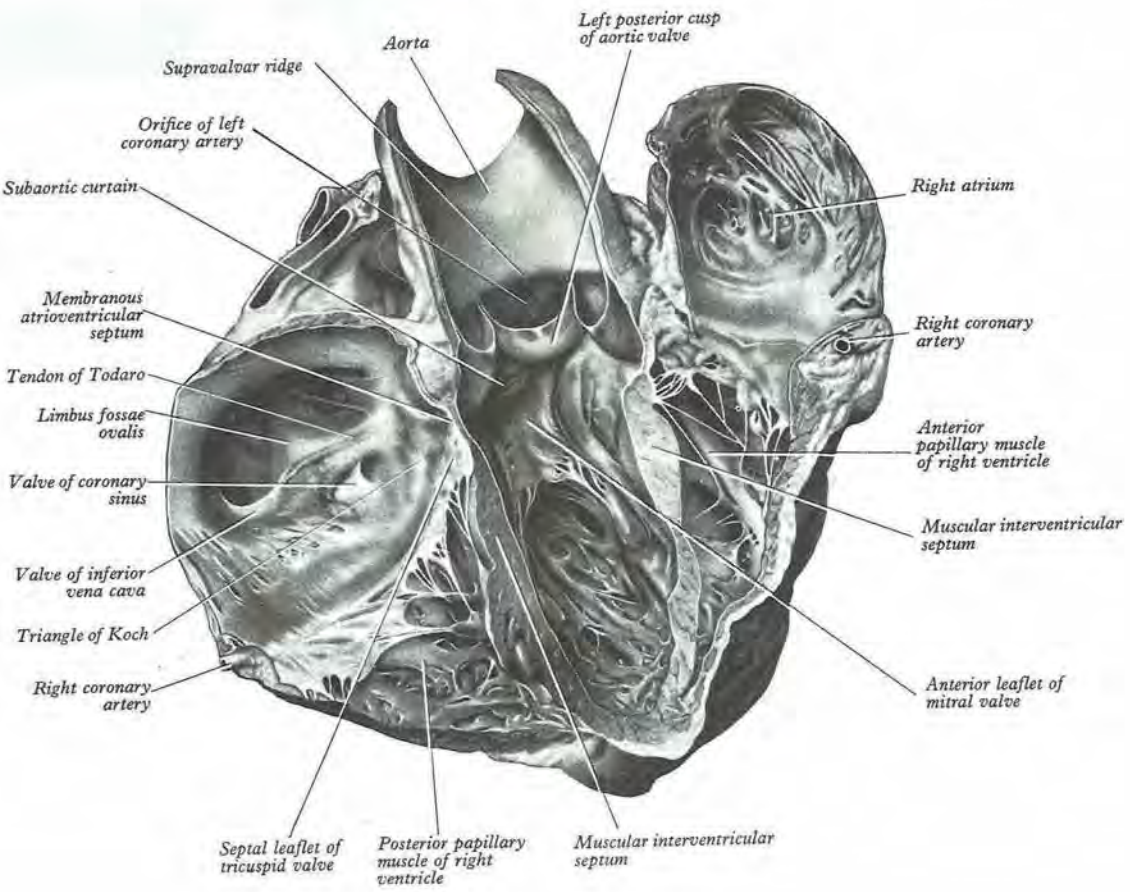
The mitral orifice is a well-defined transitional zone between the atrial wall and the bases of the leaflets (**10.40B**). It is smaller than the tricuspid orifice (mean circumference: 9.0 cm in males, 7.2 cm in females, according to Ranganathan et al 1970). The approximately circular orifice is almost vertical in diastole and at 45° to the sagittal plane but with a slight forward tilt. Its ventricular aspect faces anterolaterally to the left and a little inferiorly towards the left ventricular apex. It is almost coplanar with the tricuspid orifice but posterosuperior to it, whereas it is postero-inferior and slightly to the left of the aortic orifice. The mitral, tricuspid and aortic orifices are intimately connected centrally at the *central fibrous body* (p. 1493). When the leaflets of the mitral valve close, they form a single zone of coaptation, termed by some the *commissure* (**10.35**).

The *annulus* of the valve is not a simple fibrous ring, but comprises fibrocollagenous elements of varying consistency from which the fibrous core of the leaflets take origin. These variations allow major changes in the shape and dimensions of the annulus at different stages of the cardiac cycle and ensure optimal efficiency in valvar action.

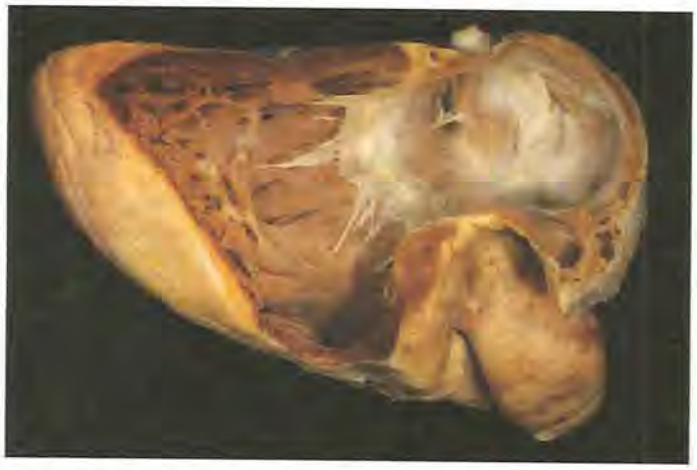
The annulus is strongest at the internal aspects of the left and right fibrous trigones (**10.51**). Extending from these structures, the anterior and posterior coronary prongs (tapering, fibrous, subendocardial tendons) partly encircle the orifice at the atrioventricular junction (**10.51, 52**). Between the tips of the prongs, the atrial and ventricular myocardial masses are separated by a more tenuous sheet of deformable fibro-elastic connective tissue. Spanning anteriorly between the trigones, the fibrous core of the central part of the anterior aortic leaflet of the mitral valve is a continuation of the fibrous *subaortic curtain* which descends from the adjacent halves of the left and non-coronary cusps of the aortic valve (**10.42**).

Mitral valvar leaflets

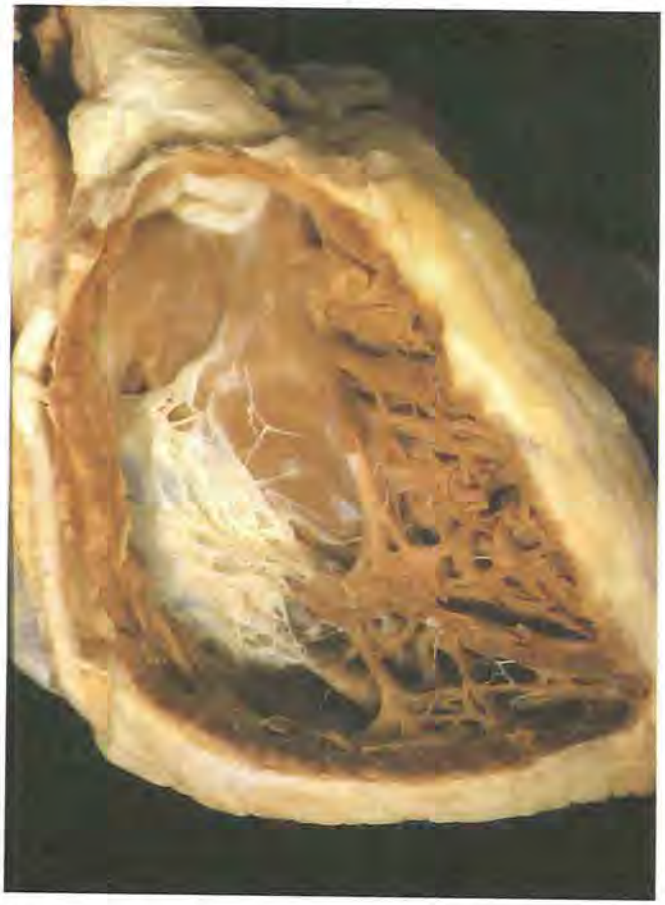
Since the earliest descriptions, these leaflets have been described as paired structures. Hence, the name 'bicuspid valve' is more explicit, though erroneous (the leaflets are not cuspid, or peaked, in form) and surely less picturesque than the clinical term 'mitral'. Confusion, controversy and difficulties in quantitation have arisen, however, because small accessory leaflets are almost always found between



10.36 The interior of the heart revealed by incising it along its right and lower surfaces and excising the pulmonary trunk and infundibulum. The rest of the front of the heart has been turned over to the left.



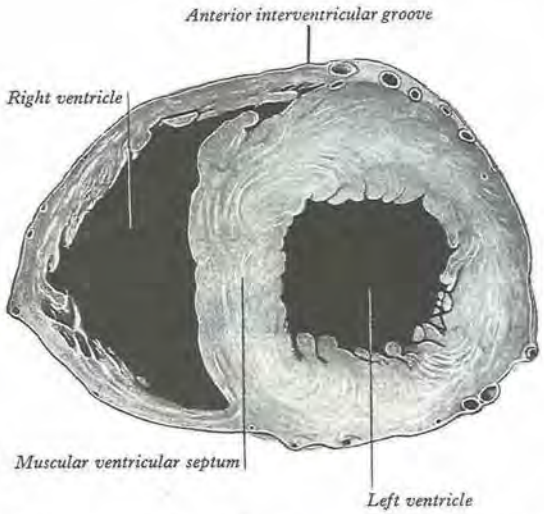
10.37A. Removal of the sternocostal parietal surface of the heart shows the components of the right ventricle. Note the supraventricular crest separating the attachments of the tricuspid and pulmonary valves.



10.37B. This anterior view through a window into the right ventricle shows the extent of the supraventricular crest. Note the relatively smooth-walled infundibulum, the prominent spetomarginal trabecule and the extensive septoparietal trabeculation.

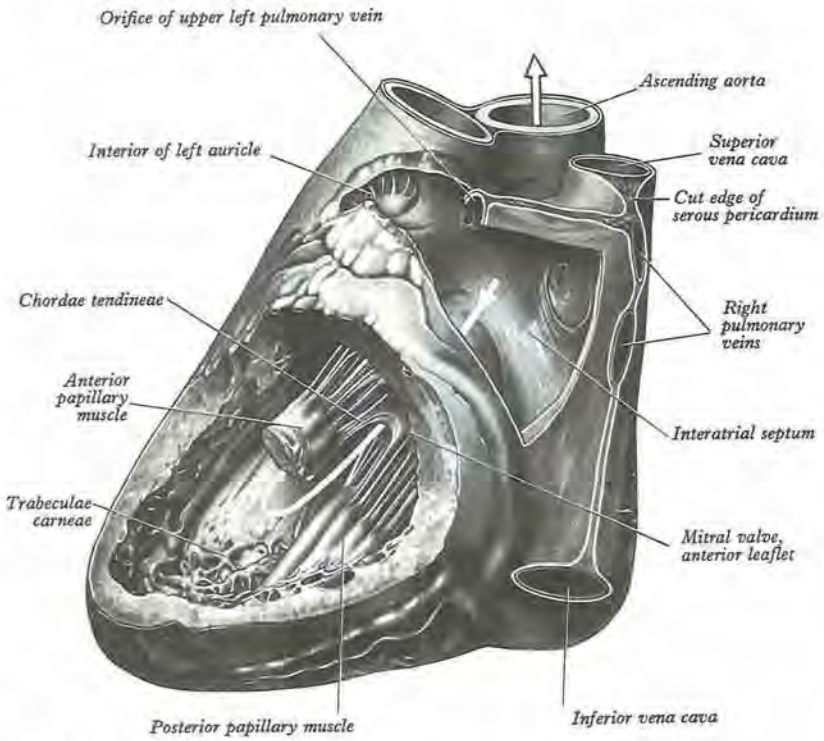
the two major leaflets. These problems can be resolved if the mitral valve is described as consisting 'of a continuous veil attached around the entire circumference of the mitral orifice' (Harken et al 1952). Its free edge bears several indentations, two being sufficiently deep and regular to be nominated as the ends of a solitary and oblique zone of apposition, or *commissure* (**10.31**, 35). It is more usual, nonetheless, for these anteromedial and posterolateral extremities themselves to be designated as two commissures, each positionally named as indicated. The official names for these leaflets, anterior and posterior, though simple, are somewhat misleading because of the obliquity of the valve.

When the valve is laid open (**10.40B**), its *anterior leaflet* (aortic, septal, 'greater' or anteromedial) is seen to guard one-third of the circumference of the orifice and to be semicircular or triangular, with few or no marginal indentations. Its fibrous core (*lamina fibrosa*) is continuous on the outflow aspect, beyond the margins of the fibrous subaortic curtain, with the right and left fibrous trigones (**10.31**, 36, 43B, 51). Between these, it is continuous with the fibrous curtain itself and, beyond the trigones, with the roots of the annular fibrous prongs (**10.52**). The leaflet has a deep crescentic rough zone receiving various tendinous chordae (see below). The ridge limiting the outer margin of the rough zone indicates the maximal extent of surface contact with the mural leaflet in full closure. A clear zone is seen between the rough zone and the valvar annulus which is devoid of attachments of chordae, though its fibrous core carries extensions from chordae attached in the rough zone. The anterior leaflet has no basal zone, continuing instead into the valvar curtain. Hinging on its annular attachment, and continuous with the subaortic curtain, it is critically placed between the inlet and the outlet of the ventricle. During passive ventricular filling and atrial systole, its smooth atrial surface is important in directing a smooth flow of blood towards the body and apex of the ventricle. After the onset of ventricular systole and closure of the mitral valve, the ventricular aspect of its clear zone merges into the smooth surface of the subaortic curtain which, with the remaining fibrous walls of the subvalvar aortic vestibule, forms the smooth boundaries of the ventricular outlet.



10.38 Transverse section through the ventricles of the isolated heart, viewed from below. Note that in this illustration the heart is not positioned as it would be in situ: in the latter position the crescentic 'right' ventricle overlaps most of the anterior surface of the 'left' ventricle.

The *posterior leaflet* (mural, ventricular, 'smaller' or posterolateral) has usually two or more minor indentations. Lack of definition of major intervalvar commissures has previously led to disagreement and confusion concerning the territorial extent of this leaflet and the possible existence of accessory scallops. Examination of the valve in closed position, however, shows that the posterior leaflet can conveniently be regarded as all the valvar tissue posterior to the anterolateral and posteromedial ends of the major zone of apposition with the aortic leaflet. Thus defined, it has a wider attachment to the annulus than does the anterior leaflet, guarding two-thirds of the circumferential attachments. There are further indentations usually dividing the mural leaflet into a relatively large middle 'scallop' and smaller anterolateral and posteromedial commissural 'scallops'. Each scallop has a crescentic, opaque rough zone, receiving the attachment of the chords on its ventricular aspect which define the area of valvar apposition in full closure. From the rough zone to within 2–3 mm of its annular attachment is a membranous clear zone devoid of



10.39 Dissection showing the interior of the left side of the heart. The white arrow indicates the course of blood flow from the left atrium through the left ventricle to the aorta.

chordae. The basal 2–3 mm is thick and vascular, and receives basal chordae. The ratio of rough to clear zone in the anterior leaflet is about 0.6. In the middle 'scallop' of the posterior leaflet, it is 1.4. Thus, much more of the mural leaflet is in apposition with the aortic leaflet during closure of the mitral valve.

Mitral chordae tendineae (tendinous cords)

These cords resemble those supporting the tricuspid valve (**10.40**A, B). False chordae (trabeculae carneae **10.39**, 40A, B), are also irregularly distributed as in the right ventricle. They occur in about half of all human left ventricles and often cross the subaortic outflow. Many contain extensions from the ventricular conduction tissues. Such left ventricular bands can often be identified by cross-sectional echocardiography. Their role, if any, has still to be determined. True chordae of the mitral valve may be divided into interleaflet (or commissural) chordae, rough zone chordae, including the special strut chordae, so-called 'cleft' chordae, and basal chordae. Most true chordae divide into branches from a single stem soon after their origin from the apical third of a papillary muscle, or proceed as single chordae dividing into multiple branches near their attachment. Basal chordae, in contrast, are solitary structures passing from the ventricular wall to the mural leaflet.

There is such marked variation between the arrangement of the chordae in individual normal hearts that any detailed classification loses much of its clinical significance. Suffice it to say that, in the majority of hearts, the chordae support the entire free edges of the valvar leaflets together with varying degrees of their ventricular aspects and bases. There is some evidence to suggest that those valves with unsupported areas of the free edge become prone to prolapse in later life.

Papillary muscles

The two muscles supporting the leaflets of the mitral valve also vary in length and breadth and may be bifid. The *anterolateral muscle* arises from the sternocostal mural myocardium, the *posteromedial* from the diaphragmatic region. Tendinous chordae arise mostly from the tip and apical third of each muscle, but sometimes take origin near their base. The chordae from each papillary muscle diverge and are attached to corresponding areas of closure on **both** valvar leaflets (**10.40**B).

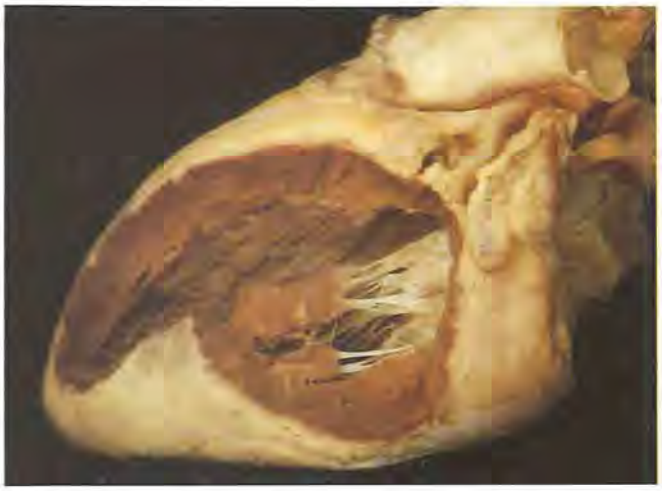
Opening of the mitral valve

At the onset of diastole, opening is passive but rapid, the leaflets parting and projecting into the ventricle as left atrial pressure exceeds left ventricular diastolic pressure. Passive ventricular filling proceeds as atrial blood pours to the apex, directed by the pendant aortic leaflet of the valve. The leaflets begin to float passively together, hinging on their annular attachments, partially to occlude the ventricular inlet. Atrial systole now occurs, jetting blood apically and causing re-opening of the leaflets. As maximal filling is achieved, the leaflets again float rapidly together. Closure is followed by ventricular systole, which starts in the papillary muscles and continues rapidly as general contraction of the walls and septum. Co-ordinated contraction of the papillary muscles raises the tension in the chordae and promotes joining of the corresponding points on opposing leaflets, preventing their eversion. With general mural and septal excitation and contraction, left ventricular pressure rapidly rises (**10.55**). The leaflets 'balloon' towards the atrial cavity and the atrial aspects of the rough zones come into maximal contact. Precise papillary contraction, and increasing tension in the chordae, continues to prevent valvar eversion and maintains valvar competence.

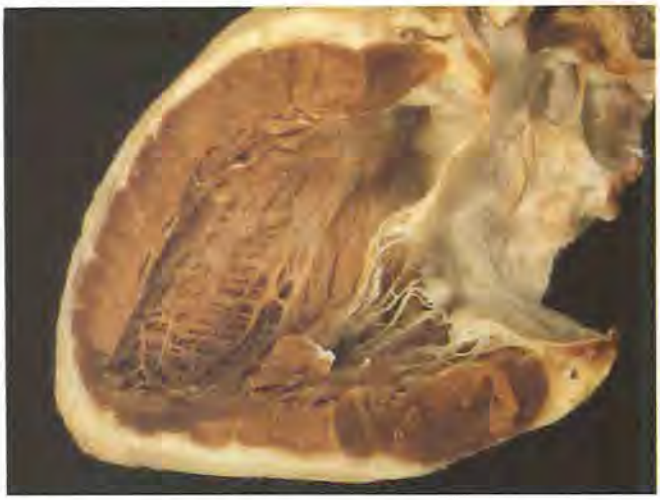
The orifices and the leaflets of both atrioventricular valves undergo considerable changes in position, form and area during a cardiac cycle (**10.50**). Both valves move anteriorly and to the left during systole, and reverse their motion in diastole. The mitral valve reduces its orificial (annular) area by as much as 40% in systole. Its shape also changes from circular to crescentic at the height of systole, the annular attachment of its aortic leaflet being the concavity of the crescent. The attachment of its mural leaflet, although remaining convex, contracts towards the anterior wall of the heart.

AORTIC VALVE

The smooth left ventricular outflow tract, or aortic vestibule, ends at the leaflets of the aortic valve. Although stronger in construction, the aortic valve resembles the pulmonary (**10.42**, 43, 44, 45) in



10.40A This dissection shows the papillary muscles of the left ventricle in their natural position. The cords from each muscle diverge to support the leaflets.



10.40B The left ventricle has been dissected by removing the obtuse margin so as to reveal its inlet, apical trabecular and outlet components.

10.40C This detail of the heart shown in B emphasizes the area of fibrous continuity between the leaflets of the aortic and mitral valves.

possessing three semilunar leaflets, the *cusps*, supported within the three aortic sinuses of Valsalva. Although the aortic valve, like the pulmonary valve, is often described as possessing an annulus in continuity with the fibrous skeleton, there is no complete collagenous ring supporting the attachments of the leaflets. Instead, again as with the pulmonary valve, the anatomy of the aortic valve is dominated by the fibrous semilunar attachment of the cusps (**10.43B**).

Cusps

The cusps are, in part, attached to the aortic wall and in part to the supporting ventricular structures. The situation is more complicated than in the pulmonary valve, because parts of the cusps also take origin from the fibrous subaortic curtain, being continuous with the aortic leaflet of the mitral valve (**10.42**). This area of continuity is thickened at its two ends to form the right and left fibrous trigones (**10.51**). But, again as with the pulmonary valve (**10.43B**), the semilunar attachments incorporate segments of ventricular tissue within the base of each aortic sinus. These sinuses and leaflets are conveniently named as being *right*, *left* and *non-coronary* according to the origins of the coronary arteries (**10.43B**). The semilunar attachments also incorporate three triangular areas of aortic wall within the apex of the left ventricular outflow tract. Since these triangular areas are part of the aortic wall rather than the left ventricle, interposing between the bulbous aortic sinuses, they separate the cavity of the left ventricle from the pericardial space. Removal of the triangles in an otherwise intact heart is instructive in demonstrating the relationships of the aortic valve, which can justly be considered as the keystone of the heart. The base of the triangle between the non-coronary and the left coronary cusps is continuous inferiorly with the fibrous aortic-mitral curtain. The apex of this triangle 'points' into the transverse pericardial space. The triangle between right and non-coronary cusps has, as its base, the membranous components of the interventricular septum and thus 'faces' the right ventricle, whereas its apex 'points' towards the transverse pericardial space behind the origin of the right coronary artery. The third triangle, between the two coronary cusps, has its base on the muscular ventricular septum. Its apex 'points' to the plane of space found between the aortic wall and the free standing sleeve of right ventricular infundibular musculature which supports the cusps of the pulmonary valve. Although the basal attachments of each leaflet are thickened and collagenous at their ventricular origins, there is no continuous collagenous skeleton supporting, in circular fashion, all the attachments of the cusps of the aortic valve. Valvar function depends primarily upon the semilunar attachments of the cusps.

The cusps themselves are folds of endocardium with a central fibrous core. With the valve half-open, each equals slightly more than a quarter of a sphere, an approximate hemisphere being completed by the corresponding sinus. Each cusp has a thick basal border, deeply concave on its aortic aspect, and a horizontal free margin. The latter is only slightly thickened except at its midpoint where it has an aggregation of fibrous tissue, the valvar *nodule of Arantius*. Flanking each nodule, the fibrous core is tenuous, forming the *lunules* of translucent and occasionally fenestrated valvar tissue (**10.42**). Such fenestrations are of no functional significance. The aortic surface of each cusp is rougher than its ventricular aspect.

Three sets of names currently exist for the aortic cusps. Official terms in the *Nomina Anatomica* (1989) refer to presumed fetal positions before full cardiac rotation has occurred. They are *posterior*, *right* and *left*. Corresponding terms based on the approximate positions in maturity are *anterior*, *left posterior* and *right posterior*. But, as already indicated, widespread clinical terminology links both cusps and sinuses to the origins of the coronary arteries. Thus, the anterior is the *right coronary* structure, left posterior is *left coronary*, and right posterior is *non-coronary*. These clinical terms are preferable since they are simple and unambiguous.

Aortic sinuses (of Valsalva)

The aortic sinuses are more prominent than those in the pulmonary trunk. The upper limit of each sinus reaches considerably beyond the level of the free border of the cusp and forms a well-defined complete circumferential *sinutubular ridge* when viewed from the aortic aspect (**10.43B**). Coronary arteries usually open near this ridge within the upper part of the sinus, but are markedly variable in their origin. The walls of the sinuses are largely collagenous near the

attachment of the cusps, but the amount of lamellated elastic tissue increases with distance from the zone of attachment. Strands of myocardium may enter this fibro-elastic wall. At the midlevel of each sinus, its wall is about half the thickness of the supravalvar aortic wall and less than one-quarter of the thickness of the sinutubular ridge. At this level, the mean luminal diameter of the beginning of the aortic root is almost double that of the ascending aorta. All such details are functionally significant in the mechanism of valvar motion.

The mechanism of valvar motion

During diastole, the closed aortic valve supports an aortic column of blood at high but slowly diminishing pressure. Each sinus and its cusp form a hemispherical chamber. The three nodules are apposed and the margins and lunular parts of adjacent cusps are tightly apposed on their ventricular aspects. From the aortic aspect, the closed valve is tri-radiate, three pairs of closely compressed lunules radiating from their nodules to their peripheral commissural attachments at the sinutubular junction (**10**.41, 45). As ventricular systolic pressure rises, it exceeds aortic pressure and the valve is passively opened. The fibrous wall of the sinuses nearest the aortic vestibule is almost inextensible but, in the upper parts of sinuses, the wall is fibro-elastic. Under left ventricular ejection pressure, the radius here increases about 16% in systole. Hence the commissures move apart, making the orifice triangular when fully open. The free margins of the cusps then become almost straight lines between peripheral attachments. But they do not flatten against the sinus walls, even at maximal systolic pressure, which is probably an important factor in subsequent closure. During ejection, most blood enters the ascending aorta, but some enters the sinuses, forming vortices which help to maintain the triangular 'midposition' of the cusp during ventricular systole and probably initiate their approximation with the end of systole. Tight and full closure ensues with the rapid drop of ventricular pressure in diastole.

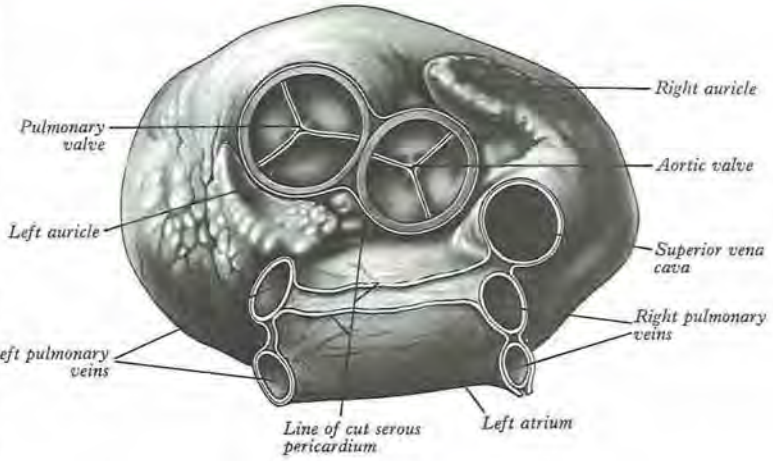
Commissures narrow, nodules aggregate and the valve reassumes its triradiate form. Experiments indicate that about 4% of ejected blood regurgitates through a valve with normal sinuses, while 23% regurgitates through a valve without them (Bellhouse & Bellhouse 1968). The normal structure of the aortic sinuses also promotes non-turbulent flow into the coronary arteries.

Similar events occur in the pulmonary valve, albeit more leisurely, the pressure profiles being less extreme (**10**.55) and the valvar structure less substantial.

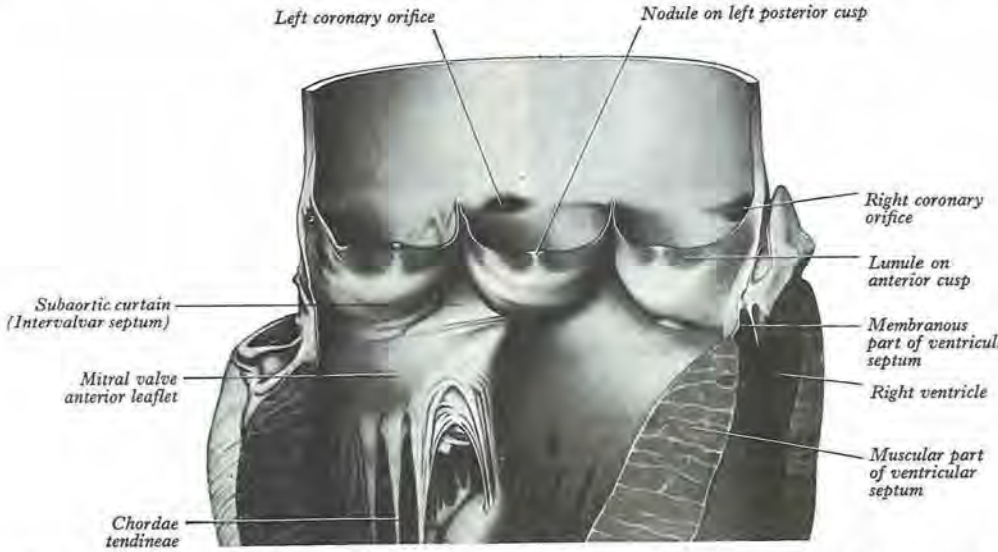
SURFACE ANATOMY OF THE HEART

The surface projections to be described below apply to an average adult. They are considerably modified by age, sex, stature and proportions, respiration and posture. The projections of the position of the valves to the surface are not the best sites for their auscultation (**10**.46). The cardiac apex almost corresponds to the apex beat, which is usually visible and always palpable in the fifth intercostal space, slightly medial to midclavicular line, about 9 cm from midline in average adult males. The apex beat is the most inferolateral point at which a pulsation can be felt. The true cardiac apex, however, is a short distance further inferolaterally. It does not contact the thoracic wall in systole.

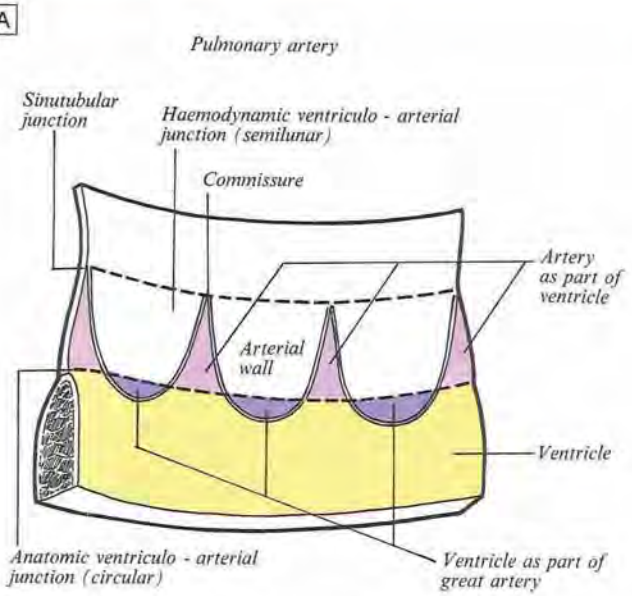
The cardiac sternocostal surface, projected to the anterior thoracic wall, is a trapezoid (**10**.29, 46). Its right border corresponds to a line from the superior border of the right third costal cartilage, about 1 cm from the sternal margin, to the sixth costal cartilage. The line is convex to the right and is maximally distant from the midline (about 3–4 cm) in the fourth intercostal space. It represents the



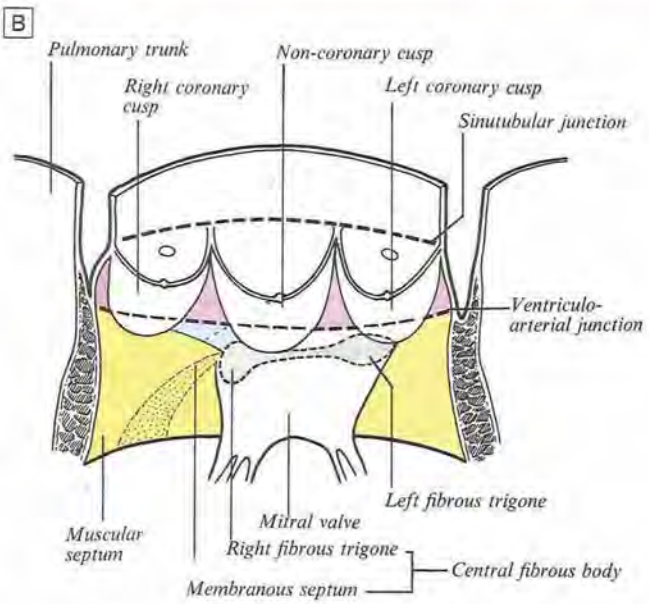
10.41 The heart viewed from above. The two continuous white lines which enclose the pulmonary trunk and aorta on the one hand and the pulmonary veins and the superior vena cava on the other, indicate the continuation of the parietal layer of the serous pericardium with the serous epicardium. The floor of the transverse sinus is seen from above, with the left coronary artery running in it. This diagram, from an earlier edition, has been retained for its pericardial details. However, in some respects it is misleading: the aortic and pulmonary valves are not, as shown, coplanar; the pulmonary valve is distinctly higher than the aortic valve; furthermore the planes of the valves 'face' approximately at right angles to each other.



10.42 The aortic orifice opened from the front to show the cusps of the aortic valve, their nodules, lunules, commissures and the triple-scalloped line of annular attachment. Also shown is the continuity of the subaortic curtain with the mitral anterior leaflet (i.e. 'aortic baffle') and the coronary orifices.



10.43A. In this diagram of the aortic root (compare with B the cusps have been resected at the attachment to the aortic wall. Note the relation of the cusp insertions and the ventriculo-arterial junction.



10.43B. The root of the aorta cut open and distended, to show the insertion of the semilunar cusps. The diagram illustrates the structure of the zone of fibrous continuity between the cusps of the aortic valve and the leaflets of the mitral valve and their relation with the fibrous trigones. It also shows the semilunar attachment of the leaflets (compare with **10.43A**)

10.43C. A heart opened to show the aortic root as illustrated diagrammatically in figure **10.43A**.

lateral profile of the right atrium. An upward continuation of this line marks the right border of the superior vena cava while a downward continuation corresponds to the border of the inferior vena cava. The lower border of the surface projection is a line joining the lower end of the right border to the apex beat. Corresponding largely to the lower (acute) margin of the right ventricle, it crosses over the xiphisternal joint to include the apical part of the left ventricle. The left border of the heart is marked by a line from the apex beat to the lower border of the left second costal cartilage approximately 1 cm from the sternal margin. It is convex upwards and to the left, corresponding to the obtuse margin of the left ventricle and to the left atrial appendage above. The border is completed superiorly by a sloping line joining the upper ends of the right and left borders, approximating to the upper limits of the atria. The left and right borders can be identified by heavy percussion.

The surface projection of the anterior part of the *atrioventricular groove* is an oblique line joining the sternal ends of the third left and sixth right costal cartilages. This line separates the atrial and ventricular areas. Although in different planes, the projections of the cardiac valves are also sited along or close to this line (**10.46**).

The *pulmonary orifice* is partly behind the superior border of the left third costal cartilage, and partly behind the left third of the sternum, being represented by a horizontal line, 2.5 cm long, crossing cartilage and sternum. Parallel lines from the ends of this line, up to the left second costal cartilage, indicate the site of the pulmonary trunk.

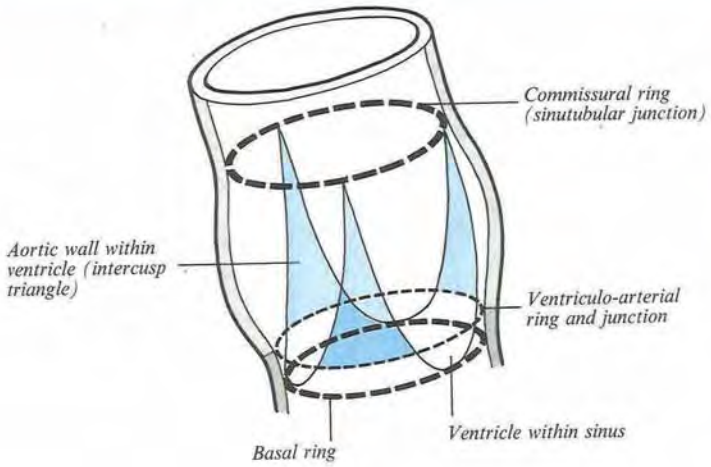
The *aortic orifice* is below and a little right of the pulmonary, marked by a line 2.5 cm long running from the medial end of the left third intercostal space downward to the right. Two parallel lines from the ends of this line, slanting up to the right half of the sternal angle, outline the location of the ascending aorta.

The *tricuspid valvar orifice* is represented by a line, 4 cm long, commencing near the midline just below the level of the fourth right costal cartilage and passing down and slightly to the right. The centre of this line should be level with the middle of the right fourth intercostal space.

The *mitral orifice* is behind the left half of the sternum opposite the fourth left costal cartilage and is represented by a line, 3 cm long, descending to the right.

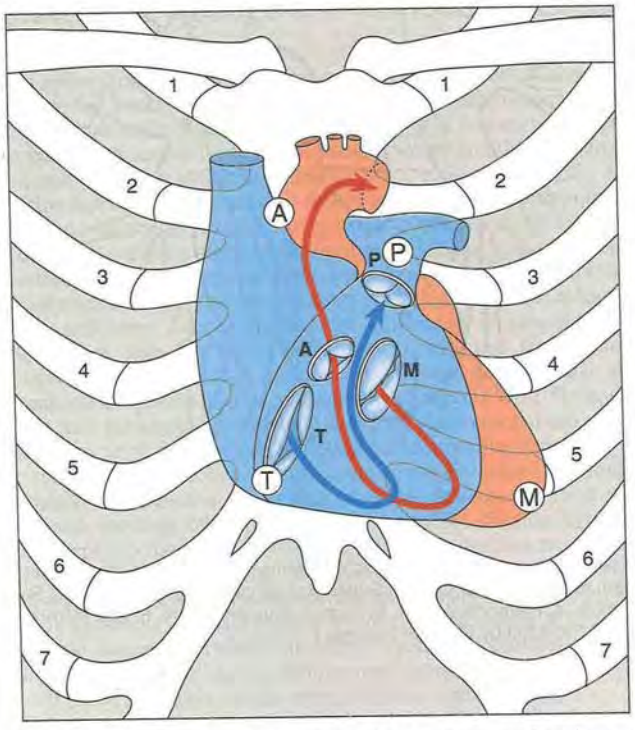
Auscultation. As stated the foregoing are the approximate surface projections of the cardiac valves: they do **not** correspond to the sites for optimal auscultation of the contribution of each valve to the heart-sounds. To understand the latter an appreciation of the **position** and **plane** of each valve (the oscillator) must be combined with the geometry of its associated column of blood (in the ascending aorta, pulmonary trunk, right and left ventricles), which maximally carries the acoustic waveforms to the chest wall. Thus convenient sites to apply the stethoscope bell or diaphragm are:

- The *pulmonary area*, the sternal end of the second left intercostal space
- the *aortic area*, the sternal end of the second right intercostal space
- the *mitral* area, near the *cardiac apex*
- the *tricuspid area*, over the *centre* of the lower part of the *sternal body*, at the level of the fifth intercostal spaces.

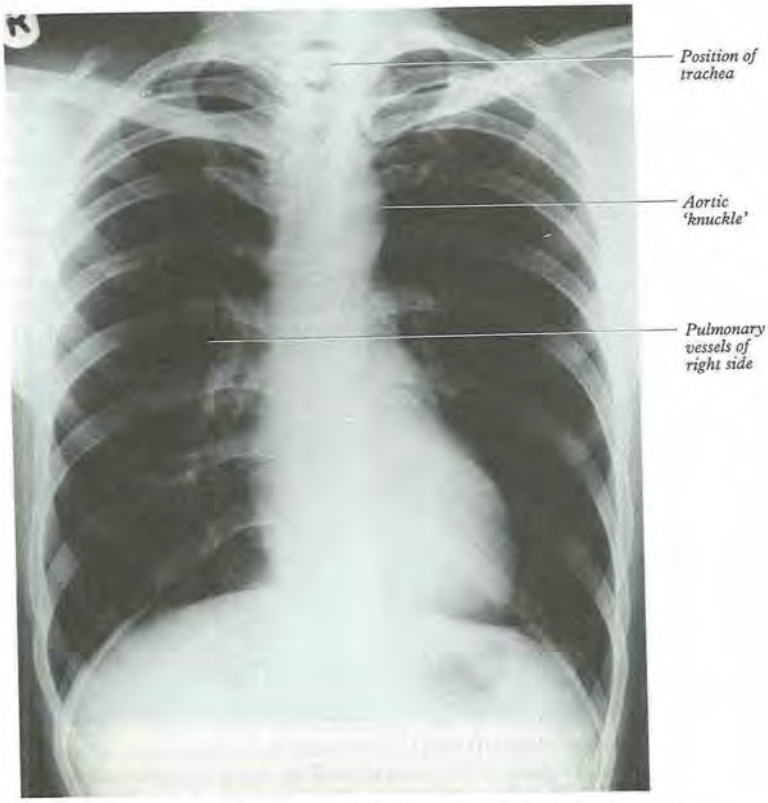


10.44 Diagram showing how the structure of the aortic root is best conceptualized in terms of a three-pronged coronet. There are at least three rings within this coronet, but none support the entirety of the attachments of the valvar leaflets (see also **10.43B**).

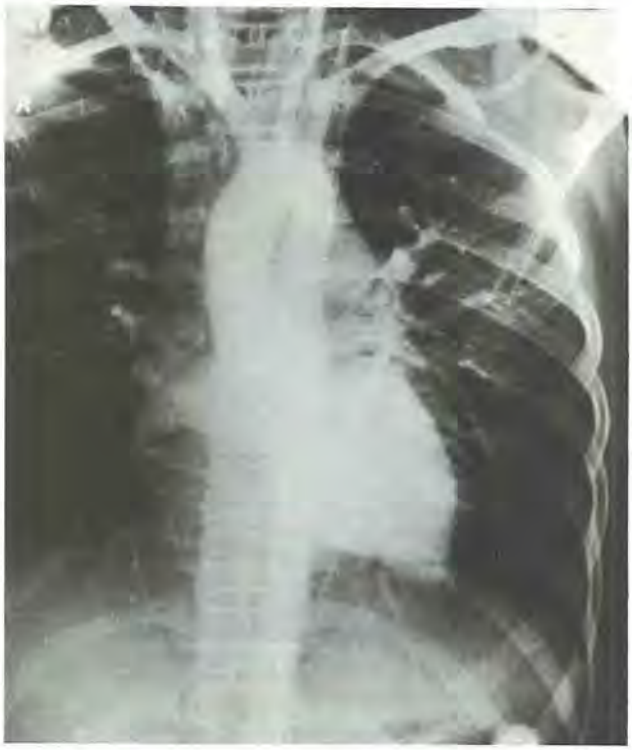
10.45 The arterial view of the aortic valve in its closed position shows the snug fit between its component leaflets.

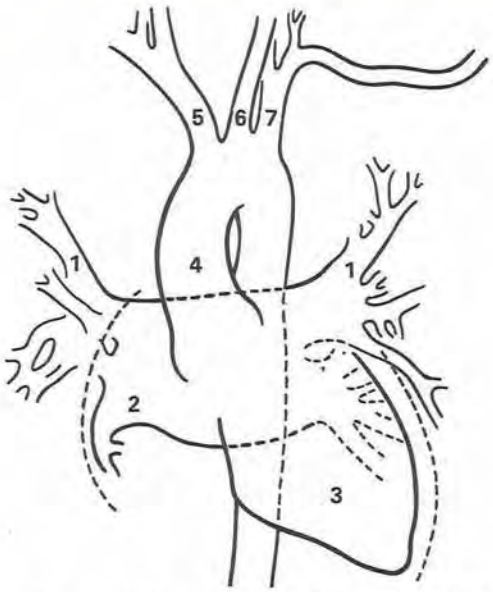


10.46 Diagram illustrating the relation of the sternocostal surface and valves of the heart to the thoracic cage. The right heart is blue, the arrow denoting the inflow and outflow channels of the right ventricle; the left heart is treated similarly in red. The positions, planes and relative sizes of the cardiac valves are shown. The position of the letters, A, P, T and M indicate the aortic, pulmonary, tricuspid and mitral auscultation areas of clinical practice. Note that, for purpose of illustration, the orifices of the aortic, mitral and tricuspid valves are shown with some separation between them. In reality, the leaflets of the three valves are in fibrous continuity (see **10.52**).

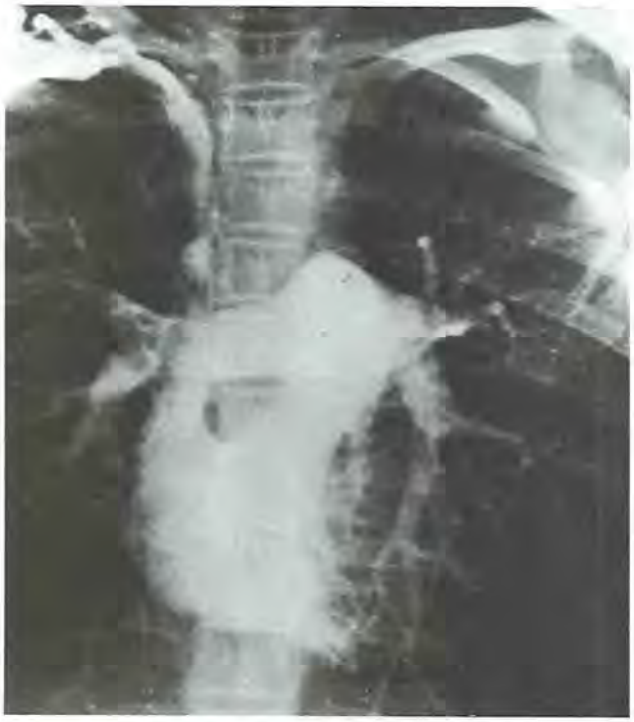


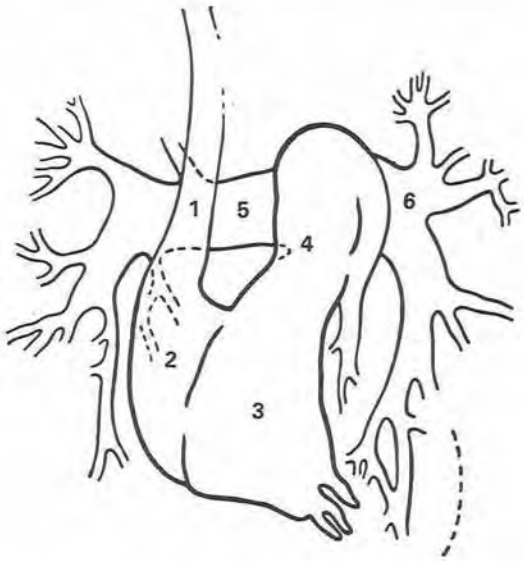
10.47 Radiograph of chest, postero-anterior view, of adult male. Note the difference in level of the right and left halves of the diaphragm. (Supplied by Shaun Gallagher, Guy's Hospital.)





10.48 Angiocardiogram showing the left side of the heart in a child of 11 years; anteroposterior view. 1. Upper pulmonary vein. 2. Left atrium. (Note that owing to the great obliquity of the atrial septum, the left atrium extends to the right behind the right atrium). 3. Left ventricle. 4. Ascending aorta. 5. Brachiocephalic trunk. 6. Left common carotid artery. 7. Left subclavian artery. The arms of the patient are raised above the head and as a result the distal end of the artery passes upwards. (Provided by Frances Gardner.)



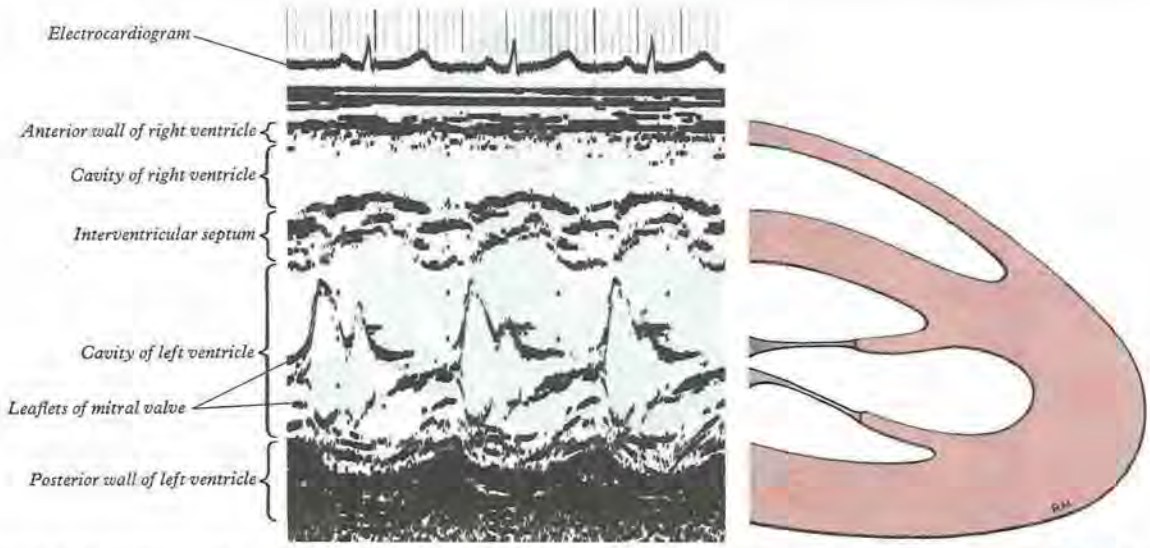


10.49 Angiocardiogram showing the right side of the heart in a child of 12 years; anteroposterior view. 1. Superior vena cava. 2. Right atrium. 3. Right ventricle. 4. Pulmonary trunk. 5. Right pulmonary artery. 6. Left pulmonary artery. (Provided by Frances Gardner.)

The area of superficial cardiac dullness as mapped out by light percussion is roughly triangular and corresponds to the area of the heart not covered by lung.

RADIOLOGICAL APPEARANCES OF THE HEART

The heart, being full of blood, casts a shadow, occupying the inferior mediastinum, which is in sharp contrast to those areas occupied by the air-filled lungs (**10.47**). In full inspiration, the apex is clear of the diaphragm, presenting a blurred outline in radiographs due to movement. The right border of the shadow is continuous with those of the venae cavae. Due to the attachment of the pericardium to the diaphragm, the heart elongates during inspiration and shortens during expiration. The cardiac shape also varies with stature and attitude (p. 1734). In lateral radiographs, the retrocardiac space is a translucent area between the heart and the vertebral column, occupied by the descending aorta and the oesophagus. Angiography was, and is, used routinely for detailed study of the cavities and larger



10.50 A standard M (motion) mode echocardiogram recorded from the parasternal window. This technique, now supplemented in clinical practice by so-called 2-D formats, shows the movement of the parietal walls, ventricular septum and mitral valvar leaflets as indicated in the accompanying diagram. Note the biphasic nature of closure of the mitral valve.

vessels (**10.48, 49**). Nowadays, nonetheless, use of angiography is, in some centres, being supplemented, and sometimes replaced, by non-invasive studies such as computerized tomography (CT), echocardiography (**10.50**), and magnetic resonance imaging (MRI). Interpretation of the images is unchanged and depends on knowledge of the location of the cardiac structures within the body.

CONNECTIVE TISSUES AND FIBROUS SKELETON OF THE HEART

From epicardium to endocardium, and from the orifices of the great veins to the roots of the arterial trunks, the intercellular spaces between contractile and conducting elements are everywhere permeated by connective tissue. The amount varies greatly in arrangement and texture in different locations.

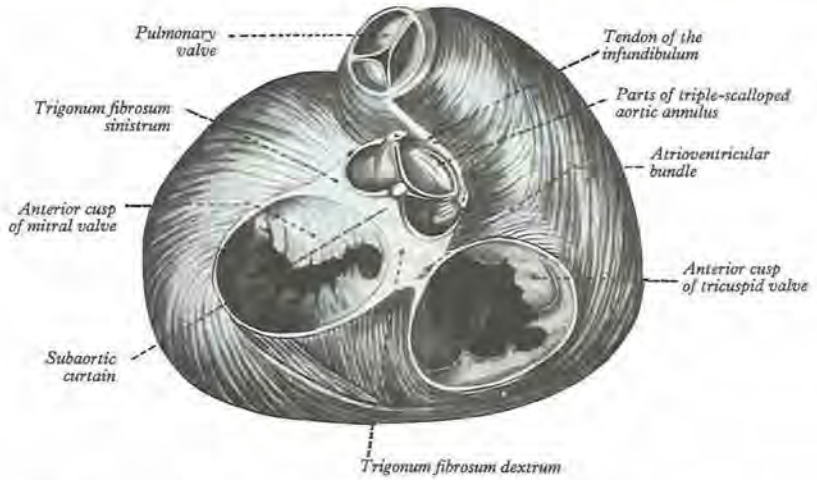
A fine layer of areolar tissue is found beneath the mesothelium of the serosal visceral epicardium over much of the heart (**10.23**). This accumulates *subepicardial fat*, the amount increasing with age, which becomes concentrated along the acute margin, the atrioventricular and interventricular grooves and their side channels. The coronary vessels and their main branches are embedded in this fat. The endocardium also lies on a fine areolar tissue, this time rich in elastic fibres. Fibrocellular components of these subepicardial and subendocardial layers blend on their mural aspects with the endomysial and perimysial connective tissue on the myocardium. Each cardiac myocyte is invested by delicate endomysium composed of fine reticular fibres, collagen and elastin fibres embedded in ground substance. This matrix is lacking only at desmosomal and gap junctional contacts of intercalated discs (p. 768). Similar arrangements apply to myocytes of the ventricular conduction tissues and their extensive contacts with the working myocardium. The connective tissue matrix itself is interconnected laterally to form bundles, strands or sheets of macroscopic proportions showing a complex geometric pattern (p. 1496). The larger myocardial bundles are surrounded by, and attached to, stronger perimysial condensations. The overall pattern is described in terms of struts and weaves.

The myocardial matrix, despite its importance, cannot be dissected grossly. Running at the ventricular base, nonetheless, and intimately related to atrioventricular valves and the aortic orifice, is a complex framework of dense collagen with membranous, tendinous and fibro-areolar extensions. The whole is sufficiently distinct to be termed the fibrous skeleton of the heart. (For detailed analyses see Zimmerman & Bailey 1962; Zimmerman 1966).

Although it is often stated that all four valves are contained within this skeleton, this is not the case. The cusps of the pulmonary valve are supported on a free-standing sleeve of right ventricular infundibulum which can easily be removed from the heart without disturbing either the fibrous skeleton or the left ventricle. The fibrous skeleton, rather, is strongest at the junction of aortic, mitral and tricuspid valves, the so-called *central fibrous body* (**10.51, 52**). Two pairs of curved, tapering, collagenous prongs (*fila coronaria*) extend from the central fibrous body, stronger on the left, passing partially around the mitral and tricuspid orifices, which are almost coplanar and incline to face the cardiac apex. The aortic valve, in contrast, faces up, right and slightly forwards. It is anterosuperior to and rightward of the mitral orifice. As already described, two of the cusps of the aortic valve are in fibrous continuity with the aortic leaflet of the mitral valve. This *aortic-mitral* or *subaortic curtain* (**10.43B, 51**) is also an integral part of the fibrous skeleton. The two ends of the curtain are strengthened as the *right* and *left fibrous trigones*, which are the strongest part of the skeleton. The *right trigone*, together with the membranous septum, then constitutes the *central fibrous body* (**10.51**). This important structure is penetrated by the mechanism for atrioventricular conduction (the bundle of His) while the membranous septum is crossed on its right aspect by the attachment of the tricuspid valve, dividing the septum into atrioventricular and interventricular components.

The functions of the fibrous skeleton are, first, to ensure electrophysiological discontinuity between the atrial and ventricular myocardial masses except at the site of penetration of the conduction tissue. Second, it functions as a stable but deformable base for the attachments of the fibrous cores of the atrioventricular valves.

The aortic root is central within the fibrous skeleton and, as discussed, is often described in terms of an '*annulus*' integrated within the fibrous skeleton. As with the pulmonary valve, nonetheless, the structure of the aortic root corresponds to the triple fibrous semilunar attachments of its cusps. Within this complex circumferential zone are three crucially important triangular areas which separate, on the ventricular aspect, the aortic bulbous sinuses which house the valvar cusps. As a whole, these three triangles can be conceptualized in terms of a three-pointed coronet (**10.44**). These triangular areas were termed the *subaortic spans* by Zimmerman (1959), Zimmerman and Bailey (1962), but were originally described as the intervalvular spaces by Henle (1876). Their triangular apices correspond to the tips of the valvar commissures. Their walls, significantly thinner than the sinuses, variously consist of collagen or admixed muscle strands and fibro-elastic tissue. They form the subvalvar extensions of the aortic vestibule. The interval between the non-coronary and left coronary sinuses is filled with the deformable *subaortic curtain*. The span between the non-coronary and right coronary sinuses is continuous with the anterior surface of the *membranous septum*. The



10.51 The base of the ventricles, after removal of the atria and the pericardium. Contrast the planes and positions of aortic and pulmonary valves. Contrast with **10.52**. (From Walmsley 1929.)

third subaortic span, namely that between the two coronary aortic sinuses, is filled with fibro-elastic tissue that separates the extension of the subaortic root from the wall of the free-standing subpulmonary infundibulum. Previously this was held to be the location of the *tendon of the infundibulum* (*conus ligament*). Similar fibrous triangles are found separating the sinuses of the pulmonary trunk, but these are significantly less robust.

The *mitral* and *tricuspid rings* (*annuli*) (pp. 1481, 1485), are also not simple and rigid collagenous structures but dynamic, deformable lines of valvar attachment that vary greatly at different peripheral points and change considerably with each phase of the cardiac cycle and with increasing age. The tricuspid attachments are even less robust than those of the mitral valve. At several sites it is only fibro-areolar tissue which separates the atrial and ventricular muscular masses.

ARCHITECTURE OF THE MYOCARDIUM

It has long been held that cardiac walls consist of 'fibres' transversely and longitudinally striated (p. 764) and intricately intermingled. They can be classed as atrial, ventricular, and conduction fibres (p. 1495). Atrial and ventricular muscle fibres are completely separated at the atrioventricular grooves, the only connection being via the axis of specialized myocardial cells responsible for atrioventricular conduction. The fibres of the working myocardium, atrial and ventricular, are aggregated by the fibrous matrix into well-organized rows and bundles (**10.53, 54**).

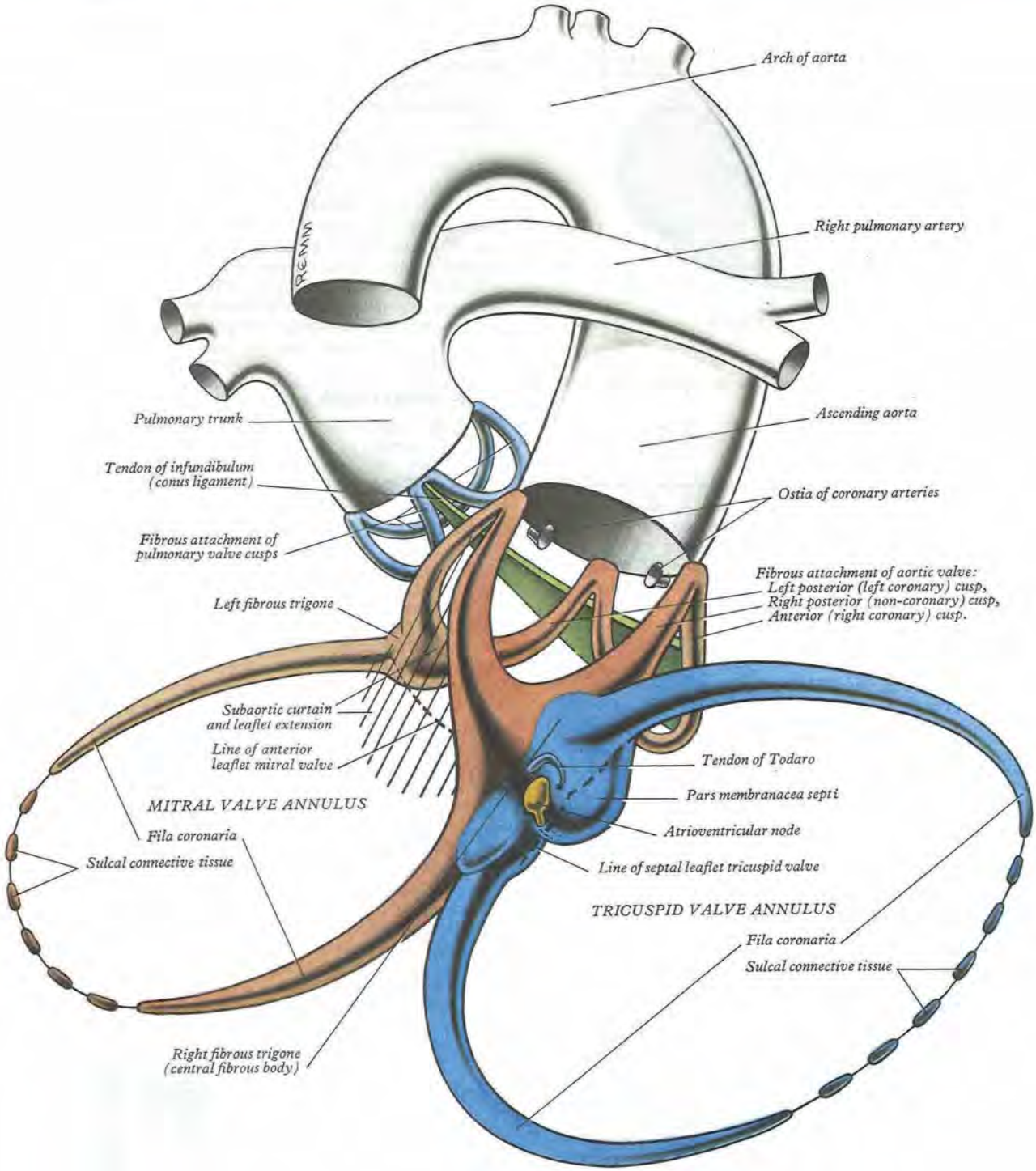
The *atrial fibres* are arranged in two layers: a superficial layer common to both atria and a deep layer proper to each. The *superficial fibres* are most distinct anteriorly where they cross the bases transversely as a thin, incomplete layer. Superiorly, the walls themselves are infolded to form the rim of the atrial septum. Deep fibres are looped and annular. The looped fibres pass over each atrium to its corresponding atrioventricular annulus, in front and behind, while annular fibres surround the appendages and encircle the openings of the venae cavae and the fossa ovalis. Further well-organized bundles are found within the terminal crest of the right atrium and its pectinate muscles.

The arrangement of the *ventricular fibres* within the ventricular mass is much more complicated, and has been the focus of many investigations over the years. Most of these have involved prior maceration or boiling of the hearts investigated, followed by dissection or tearing apart of the ventricular walls. Of necessity, these techniques are somewhat crude. Although they can produce remarkably photogenic specimens, they all suffer from the difficulty of distinguishing true tracts of fibres from artefactually induced pathways.

Combinations of dissections with study of orientations of fibres as measured in serial sections give a more accurate impression of the interrelationships of the musculature (Streeter et al 1969, 1979, 1980; Greenbaum et al 1981). These works have shown that earlier concepts, such as those espoused by MacCallum (1900) and Mall (1911), placed undue emphasis on the fibrous skeleton as the site of origin and insertion of the ventricular fibres. The heart is not to be compared with a skeletal muscle. Rather, it is a modified blood vessel. The myocardial fibres, in consequence, are attached to their neighbours and bound together by the fibrous matrix. The skeleton serves the purpose of anchoring the valves to the ventricular mass and, as discussed above, is significantly less well formed than is generally believed. Thus, concepts of the ventricular musculature being arranged in tracts which originate at the atrioventricular annulus and insert into the bases of the arterial trunks have little to support them in terms of anatomic fact. The dissections performed, which are backed up by histological studies, largely endorse the accounts of Pettigrew (1860, 1865).

The dissections show that the fibres can broadly be divided into subepicardial, middle, and subendocardial fibres. Simple inspection of the heart after the removal of the epicardium reveals the arrangement of the subepicardial fibres. By and large, these fibres run circumferentially around the right ventricle and longitudinally down the diaphragmatic surface of the left ventricle. Fibres cross over the posterior interventricular groove, and more complicated cross-over fibres are found at the anterior atrioventricular groove which continue into the free-standing subpulmonary infundibulum.

Superficial fibres also form vortices at the apices of both ventricles, turning in to form subendocardial fibres as well described by Mall (1911) (**10.53**). The middle fibres, arranged circumferentially, are confined to the left ventricle and the septum, the parietal wall of the right ventricle having only superficial subepicardial and deep subendocardial fibres. The greatest thickness of circumferential fibres is found at the base of the left ventricle, where they encircle the inlet and outlet components. This is the layer dubbed the *'bulbospiral' muscle* by earlier investigators. The subendocardial layers of both ventricles are continuous with the subepicardial fibres through the apical vortexes. These deep fibres form a thin layer in the left ventricle except where buttressed to form the papillary muscles. The fibres within the trabeculae run almost longitudinally, while those closer to the middle layer take an oblique course. The papillary muscles are less robust in the right ventricle. The septum belongs largely to the left ventricle, being formed for its greatest part by the circumferential layer of middle fibres (**10.36**). Since these circumferential fibres are lacking towards the ventricular apex, the apical septum is formed only by the co-apted subendocardial layers as they turn in from the ventricular apexes. There are major regional



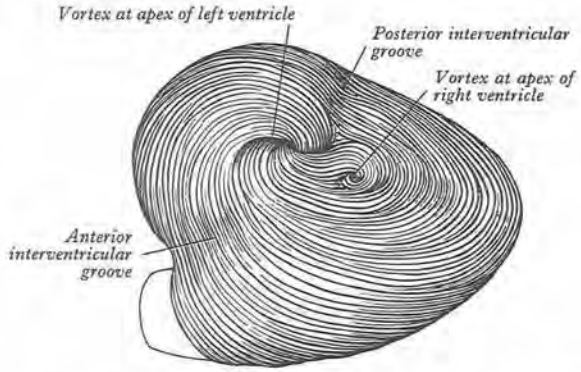
10.52 Principal elements of the fibrous skeleton of the heart: red = mitral and aortic 'annuli', blue = tricuspid and pulmonary 'annuli', green = tendon of the infundibulum. For clarity the view is from the right posterosuperior aspect. Note that due to perspective the pulmonary annulus appears smaller than the aortic annulus, whereas in fact the reverse obtains. Based in part on the work of Zimmerman (1966). Consult text for an extended discussion.

variations in the arrangement of the fibres from heart to heart. Even greater departures from this variable 'norm' are found in hearts diseased due to dilatation, hypertrophy, coronary arterial disease, or congenital malformations. Much more work remains to be done before the true organization of the ventricular fibres is elucidated.

That which has been accomplished in recent years simply underlines the potential dangers inherent in imposing procrustean and oversimplified ideas on a complex biological structure (Greenbaum et al 1981).

CO-ORDINATION OF CARDIAC ACTIVITY: CONDUCTION SYSTEM

The human heart beats ceaselessly at about 70 or so cycles every minute for many decades, maintaining perfusion of pulmonary and systemic tissues. The rate and stroke volume fluctuate in accord with prevailing physiological demands. The principal events in a cardiac cycle, including the electrical events recorded in the electro-



10.53 The two vortices in the myocardium at the apex of the heart (after Mall).

cardiogram (ECG), mechanical sequences of diastole, atrial systole, isovolumetric contraction, ejection and isovolumetric relaxation in ventricular systole, the acoustic phenomena recorded in the phonocardiogram, pressure profiles of right and left hearts and arterial trunks and the sequences of valvar events are summarized in **10.55**. Cardiac efficiency depends on precise timing of the operation in interdependent structures. Passive diastolic filling of the atria and ventricles is followed by atrial systole, stimulated by discharge from the sinus node, which completes ventricular filling. Excitation and contraction of the atria must be synchronous and finish prior to ventricular contraction. This is effected by a **delay** in the conduction of excitation from atria to ventricles. Thereafter, ventricular contraction proceeds in a precise manner, a specialized ventricular conduction system ensuring that closure of atrioventricular valves is followed rapidly by a wave of excitation and contraction spreading from the ventricular apices towards the outflow tracts and orifices, rapidly accelerating the blood during ejection.

Vertebrate cardiac contraction originates unequivocally in specialized myocytes, but neural influences are important in adapting the intrinsic cardiac rhythm to functional demands from the whole body. All cardiac myocytes (p. 764) are excitable, with autonomous rhythmic depolarization and repolarization of the cell membrane, conduction of waves of excitation via gap junctions to adjacent myocytes, and excitation-contraction coupling to their actomyosin complexes (p. 774). These properties are developed to different degrees in different sites and in different types of myocyte. The rate of depolarization and repolarization is slowest in the ventricular myocardium, intermediate in the atrial muscle, and fastest in the myocytes of the sinus node. The latter override those generating slower rhythms and, in the normal heart, are the locus for the rhythmic initiation of cardiac cycles. Conversely, conduction velocity is slow in nodal myocytes, intermediate in general 'working' cardiac myocytes and fastest in the myocytes of the ventricular conduction system.

The nodes and networks of the so-called specialized myocardial cells constitute the *cardiac conduction system* (**10.56**A, B, 57). The components of the system are the sinus node, the atrioventricular node, the atrioventricular bundle with its left and right bundle branches, and the subendocardial plexus of ventricular conduction cells (Purkinje fibres). Remnants of histologically specialized cells are also found at the insertions of right atrial myocardium into the atrioventricular junction. These are remnants of the more extensive conduction system found in the developing heart, and are described as *atrioventricular ring tissues*. Comprehensive accounts of the cardiac conduction system are found in Hudson (1965) and Anderson & Becker (1980).

Sinus node of Keith and Flack (1907)

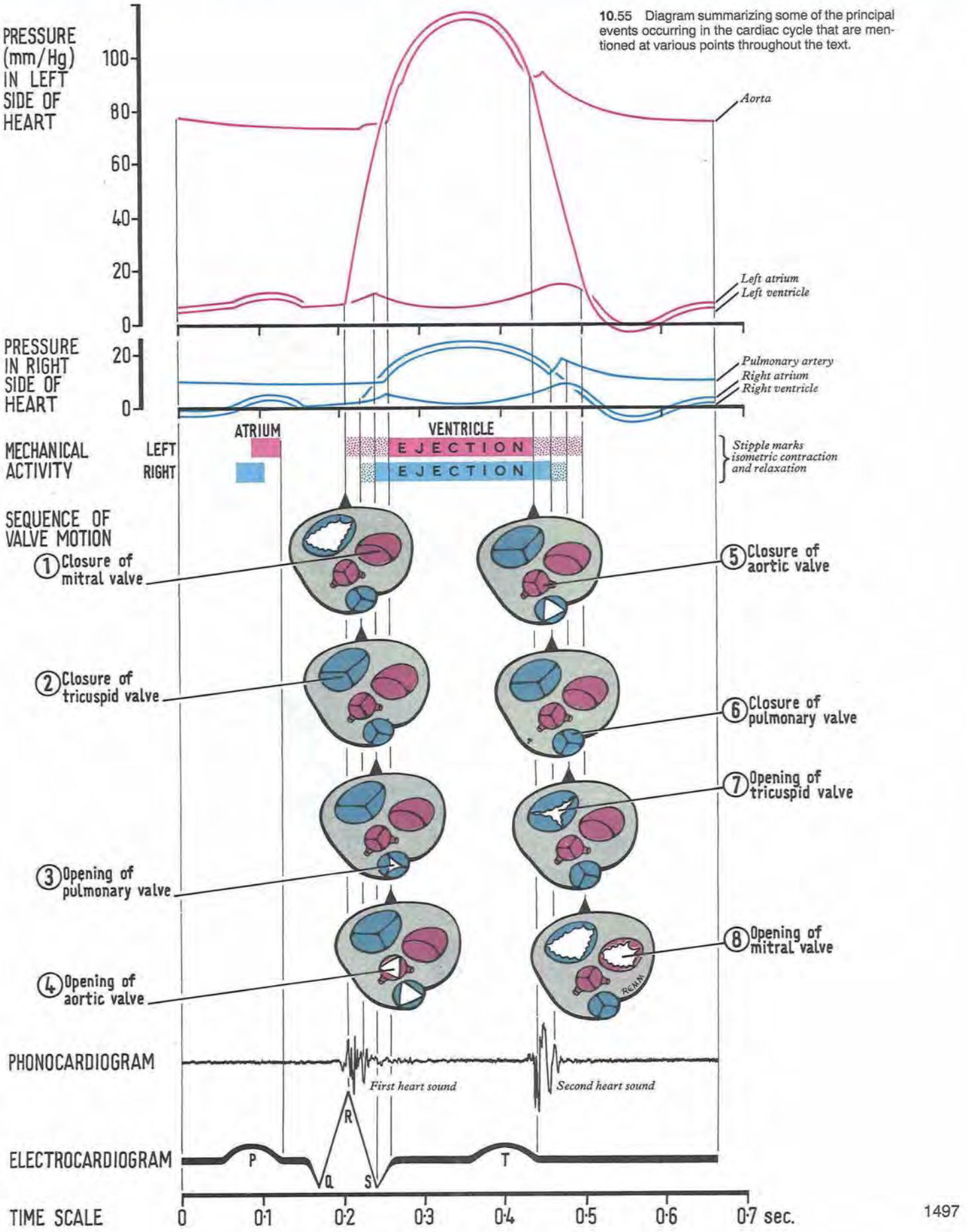
The cardiac 'pacemaker', it initiates (in some of its cells) each cardiac cycle. It is located at the junction between parts of the right atrium derived from the embryonic venous sinus and the atrium proper (**10.56**A, 57). The node is distinctive histologically, with very short transitional zones peripherally. Nodal tissue does not occupy the full thickness of the right atrial wall from epicardium to endocardium in humans, but rather sits as a wedge of specialized tissue subepicardially within the terminal groove. The node is often covered by a plaque of subepicardial fat, making it visible in some instances to the naked eye. It extends between 1 and 2 cm on the right from the crest of the right auricle and runs postero-inferiorly into the upper part of the terminal groove. In a small proportion of cases, about one-tenth, it extends in horse-shoe fashion across the crest of the auricle. An obvious feature of the node is its *central artery*. This has a surprisingly large calibre and takes its origin from either the right or the circumflex coronary arteries. Usually originating from the initial segments of these arteries, it rarely takes a more distal origin which then places it at risk during routine opening of the atrium in the course of cardiac surgery. Its adventitia merges into a dense collagenous reticulum which permeates the node and surrounds its myocytes. Its small lateral branches supplying nodal tissue are few, the vessel continuing beyond the node to ramify in the atrial myocardium. The *nodal myocytes* themselves are slender and fusiform. Such nodal myocytes themselves are confined to the nodal centre, circumferentially arranged around the nodal artery and more irregularly placed external to this. These cells are now considered the 'pacemakers'. They make functional contacts with each other and adjacent transitional myocytes, which are smaller than the general myocardial cells. There are only short transitional zones at the margin of the node, the junction with plain atrial myocardium being clear cut.

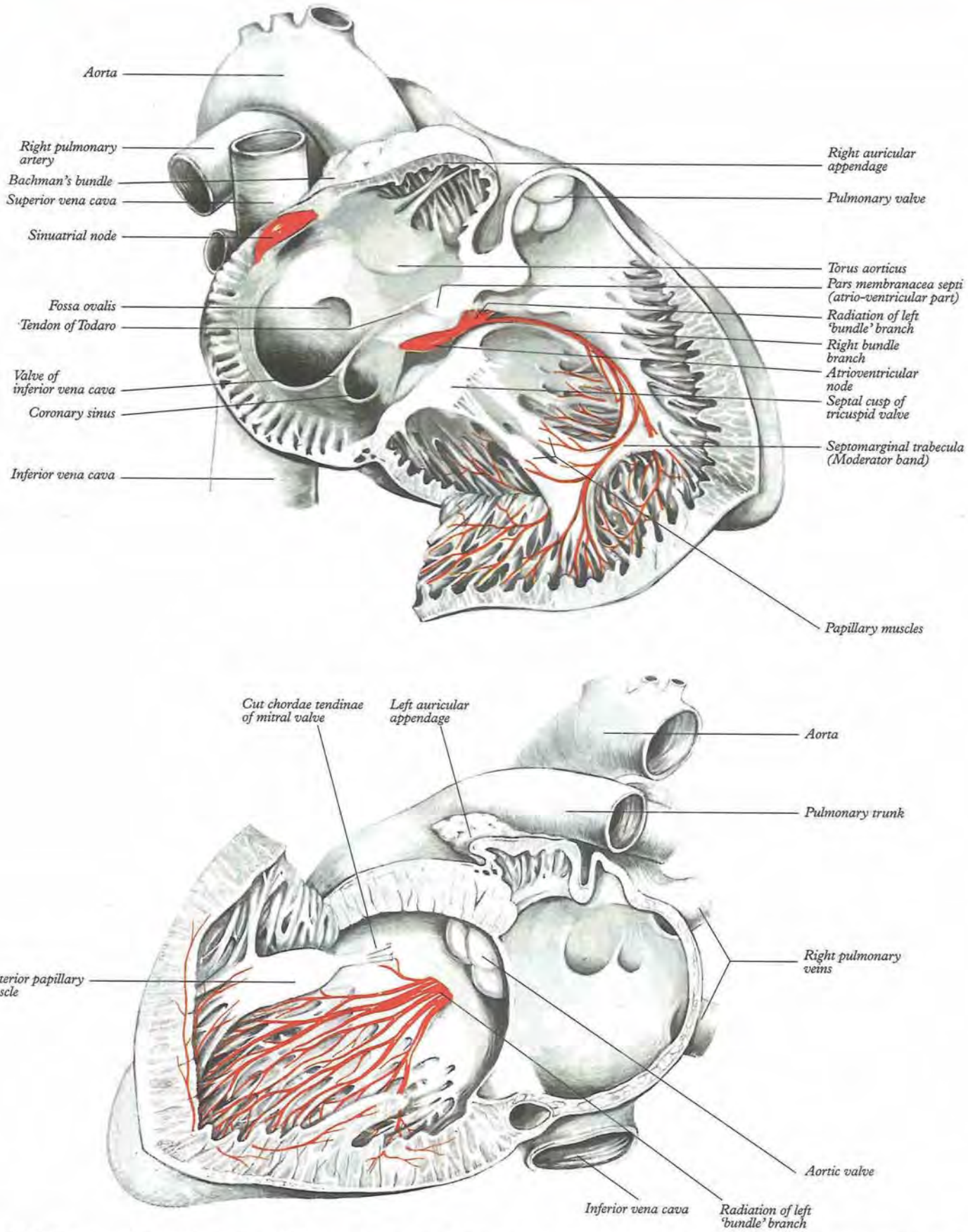

A


B

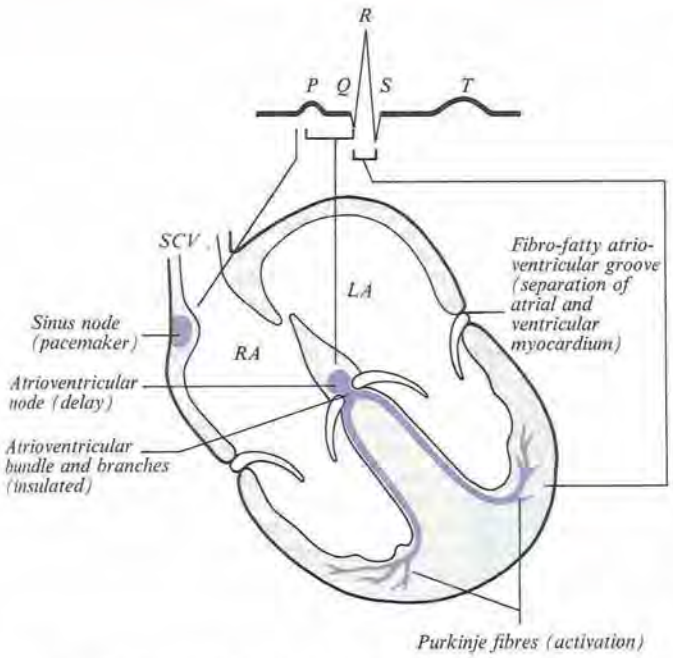
10.54A, B. These standard dissections of the ventricular mass show the superficial layer of fibres extending over the anterior surface of both ventricles (A). In B further dissection reveals the important middle layer of circumferential fibres (the 'bulbospiral muscle') which is confined to the left ventricle. Dissection made by Professor Damian Sanchez-Quintana, Badajoz, Spain, and reproduced by kind permission.

10.55 Diagram summarizing some of the principal events occurring in the cardiac cycle that are mentioned at various points throughout the text.





10.56 Diagrams of the conducting tissue of the heart as seen from the right (A) and left (B) aspects. The elements of the conducting system are shown in red. Note the conducting tissue accompanying fine trabeculae carneae and false chordae. Please note that in reality the radiation of the left bundle branch is directly related to the leaflets of the aortic valve.



10.57 A diagram illustrating the basic structure of the conduction system, and showing the relationship with the electrocardiogram.

Atrioventricular node (Tawara 1906)

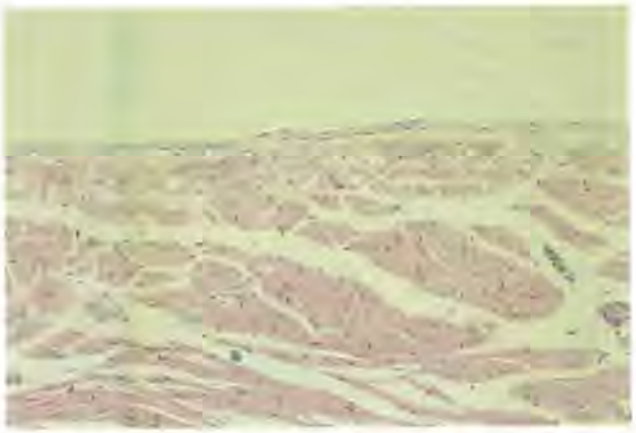
The atrioventricular node is an atrial structure which is at the root of an extensive tree of conduction tissue reaching the apex of the ventricles, the papillary muscles and other regions of the ventricles (**10.57**). The node, with its transitional zones, is located within the atrial component of the muscular atrioventricular septum, the anatomic landmarks being the boundaries of the triangle of Koch (**10.56A**). These are, inferiorly, the attachment of the septal leaflet of the tricuspid valve, basally the orifice of the coronary sinus and, superiorly, the tendon of Todaro. The compact node is a half oval set against the central fibrous body towards the apex of this triangle. Its atrial aspect is convex, being overlain by atrial myocardium. Its left margin is concave and abuts on the superior aspect of the central fibrous body. Its basal end projects into the atrial muscle while its antero-inferior end enters the central fibrous body to become the penetrating atrioventricular bundle. The node is pervaded by an irregular collagenous reticulum enmeshing the myocytes, but this is less dense than in the sinus node. Its arterial supply is from a characteristic vessel originating from the dominant coronary artery at the crux of the heart. The node has a well-formed compact zone made up of interlocking nodal cells which frequently show stratification. Superficially and posteriorly are found the transitional cell zones. The larger component of atrioventricular delay is probably produced in these transitional zones of the node.

Atrioventricular bundle

Originally described by His (1893) but clarified by Tawara (1906), the atrioventricular bundle is the direct continuation of the atrioventricular node, becoming oval, quadrangular or triangular in transverse sectional profile as it enters the central fibrous body (**10.56A**, p. 1493). Traversing the fibrous body, it branches on the crest of the muscular interventricular septum, the branching tract being sandwiched between the muscular and the membranous components of the septum. The *right branch* of the bundle (*crus dextrum*) is a narrow, discrete round group of fascicles which courses at first within the myocardium and then subendocardially towards the apex of the ventricle, entering the septomarginal trabecula to reach the anterior papillary muscle. It has few branches to the ventricular walls in its septal course, but, at the origin of the anterior papillary muscle, it divides profusely into fine subendocardial fascicles which diverge and embrace, first, the papillary muscle, then, recurving subendocardially to the remaining ventricular walls. The *left branch* (*crus sinistrum*) arises as numerous fine intermingling fascicles which leave the left margin of the branching bundle through much of its course along the crest of the muscular ventricular septum (**10.56B**). These fascicles form a flattened sheet down the smooth left ventricular septal surface. The sheet diverges apically and subendocardially across the left aspect of the ventricular septum, separating into anterior, septal and posterior divisions. Fine branches leave the sheets, forming subendocardial networks, which first surround the papillary muscles and then curve back subendocardially to reach all parts of the ventricle.

The principal branches of the bundle are insulated from the surrounding myocardium by sheaths of connective tissue (**10.58**). Functional contacts between ventricular conduction and working myocytes become numerous only in the subendocardial terminal ramifications. Hence, papillary muscles contract first, followed by a wave of excitation and ensuing contraction travelling from the apex of the ventricle to the arterial outflow tract. And, because the Purkinje network is subendocardial, muscular excitation proceeds from the endocardial to the epicardial aspect. In the developing heart, it can be shown that the bundle responsible for atrioventricular conduction is a much more extensive structure (Wessels et al 1992). Recent work using immunohistochemical markers has shown that the precursor of the system is a ring of cells which surrounds the inlet and outlet components of the developing ventricular loop (see p. 308). With septation of the ventricles, this ring becomes modified so that it encircles the right atrioventricular orifice and the aortic outlet from the left ventricle. With subsequent growth, only the septal components of this 'figure of eight' persist as the atrioventricular conduction tract. Careful study, nonetheless, reveals that part of the aortic ring can persist as a 'dead-end tract' (Kurosawa & Becker 1985).

The components initially surrounding the tricuspid orifice also persist to varying degree, and can be found by careful study in most human hearts. These nodes of unequivocally specialized tissue are identical to the structures described and illustrated by Kent at the turn of the nineteenth century (1893, 1913). Kent was convinced that these structures were the substrates for normal atrioventricular conduction, which, he argued, occurred at multiple points around the atrioventricular junction. This contention is incorrect, and the remnants found as atrioventricular ring tissue are always sequestrated by the fibrous insulation mechanism from the ventricular myocardium. Kent's findings, nonetheless, provided the stimulus for clinicians to explain the abnormal cardiac rhythm known as ventricular pre-excitation, specifically the variant known as the Wolff-Parkinson-White syndrome. It has now been shown that this syndrome is produced by abnormal small strands of otherwise unremarkable ventricular myocardium which connect the atrial and ventricular myocardial masses at some point around the atrioventricular junctions. Initially these muscular strands were described



10.58 Section of conducting, Purkinje fibres in the left ventricular wall. Note the paler, enlarged cells beneath the endocardium among normal (or 'working') myocytes. Haematoxylin and eosin. Magnification × 500.

as 'bundles of Kent', the belief being that they represented the multiple connections postulated by Kent. When the connections were identified histologically, it was seen that they bore no resemblance to the remnants of atrioventricular ring tissue initially described by Kent. Instead, they were strands of working myocardium running through the fibro-areolar tissue of the atrioventricular groove.

Sinus node, atrioventricular node and atrioventricular bundle constitute a well-defined anatomical system; in it the main pacemaker rhythm of the heart is generated (sinus), is influenced by nerves (sinus and its innervation) and is transmitted specifically from atria to ventricles (atrioventricular node and bundle) and, within the ventricles, to all their musculature. The spread of excitation is very rapid but not instantaneous: different parts of the ventricles are excited at slightly different times, with important functional consequences. Failure of the conduction system will not block cardiac contraction, but this will become poorly co-ordinated or uncoordinated; the rhythm will be slower as it then originates from a spontaneous (myogenic) activity in the working cardiac myocytes or in a subsidiary pacemaker in a more distal part of the diseased or disrupted conduction system.

One important question in this account of the role of the conduction system is: how does the excitation generated by the sinus reach the atrioventricular node? There has been considerable debate and controversy on this issue since the beginning of the century, when there were reports on the occurrence of bundles of specialized cardiac myocytes in the atria, connecting the sinus to the atrioventricular node and the right to the left atrium. Although only Thorel (1909) truly claimed to have distinguishd specialized tracts, two other tracts have been attributed to Wenckebach (1906) and Bachmann (1913). The latter workers, although describing tracts, made no claims concerning histological specialization. Furthermore, subsequent studies of the atrial walls have failed to show the existence of specialized muscle tissue, such as can be readily seen in the atrioventricular bundle. Modern authors, therefore, dismiss the occurrence of any specialized internodal and interatrial conduction pathways (Anderson et al 1974; Anderson 1975). In the absence of specialized internodal and interatrial conduction pathways, the excitation emanating from the sinus node spreads to the atrial musculature and to the atrioventricular node through ordinary atrial working myocardium. The studies of Spach and Kootsey (1983) have confirmed that there are no anatomically specialized pathways comparable with the ventricular system responsible for conduction. Instead, it is the packing and the geometric arrangement of fibres along well-organized atrial muscle bundles, such as the terminal crest and the rims of the oval fossa, which are responsible for conduction being marginally more rapid than elsewhere within the atrium. The muscle fibres responsible for such conduction, as far as can be judged with standard staining, are ordinary working atrial myocardial fibres (Janse & Anderson 1974).

NERVE SUPPLY TO THE HEART

Initiation of the cardiac cycle in vertebrates is myogenic, originating in the sinus node. The cardiac cycle initiated in this fashion is harmonized in rate, force and output by nerves of the autonomic nervous system operating on the nodal tissues and their prolongations, on coronary vessels and on the working atrial and ventricular musculature. This supply is autonomic, and has both efferent (sympathetic and parasympathetic) and afferent components. Parasympathetic fibres reach the heart through vagal branches (p. 1252), the sympathetic from the branches of the sympathetic trunk (p. 1303). Vagal preganglionic fibres proceed from origins within the brainstem, particularly the medulla, including the nucleus ambiguus (p. 1021), the reticular nuclei (p. 1073) and possibly the dorsal vagal nucleus (p. 1020). Preganglionic axons leave in the cardiac branches of both the right and the left vagus nerves to reach the cardiac plexus. Sympathetic preganglionic neurons are in the upper five or six segments of the intermediolateral column of the thoracic spinal cord (Kuntz 1953). These fibres end in the cervical and the third and fourth thoracic sympathetic ganglia (Mitchell 1953), from all of which postganglionic fibres proceed bilaterally to the heart (pp. 1252, 1306). (See also general comments and modern reservations concerning the simplification implicit in the terms pre- and postganglionic, p. 1293.)

The central connections of cardiac preganglionic neurons, parasympathetic and sympathetic, are described elsewhere (Reticular formation of the brainstem p. 1073, Hypothalamus p. 1141 and Cerebral cortex p. 1094). The existence and behaviour of these integrating influences can be deduced in terms of their function, but the precise locations of connecting pathways in the spinal cord, brainstem, and cerebrum are uncertain.

Nearing the heart, the autonomic nerves form a mixed cardiac plexus (p. 1306), usually described in terms of a superficial component found inferior to the aortic arch and between it and the pulmonary trunk, and a deep part between the aortic arch and tracheal bifurcation. These plexuses contain ganglion cells, with further ganglion cells found in the heart along the distribution of branches of the plexus (**10.59**). The branches of these cells are considered largely, if not exclusively, postganglionic and parasympathetic in nature. The advent of more reliable staining techniques for identification of cholinergic and adrenergic nerve cells and their ramifications has now helped clarify the distribution of cardiac autonomic components, although the discovery of additional neural transmitters which are neither truly cholinergic nor adrenergic has added a further complicating element (Corr 1992).

Cholinergic and adrenergic fibres, arising in or passing through the cardiac plexus, are distributed most profusely to the sinus and atrioventricular nodes, with a much less dense supply to the atrial and ventricular myocardium. Adrenergic fibres supply the coronary arteries and cardiac veins. Rich plexuses of nerves containing cholinesterase, adrenergic transmitters, and other peptides such as neuropeptide Y (NY) are found in the subendocardial regions of all chambers and in the leaflets of the valves. Complex endorgans have also been discovered in the subendocardium of the left atrium (Tranum-Jensen 1975).

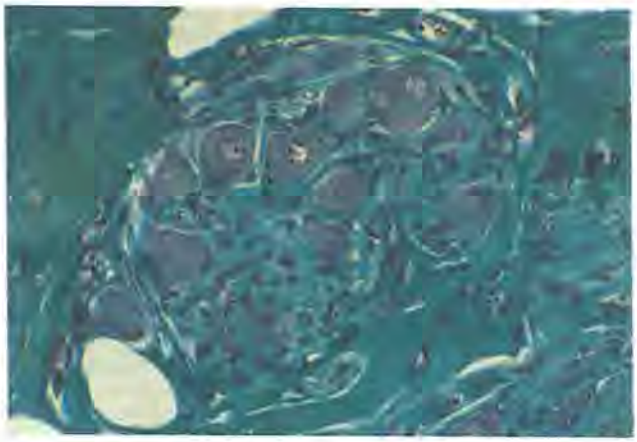
Ganglion cells, the source of vagal postganglionic fibres, are confined to the atrial tissues in man, with a preponderance adjacent to the sinus node. Some ganglion cells in the atrium have now been shown to contain adrenergic transmitters, and they also contain small, intensely-fluorescent chromaffin cells (SIF-cells, see p. 1299).

VESSELS OF THE HEART

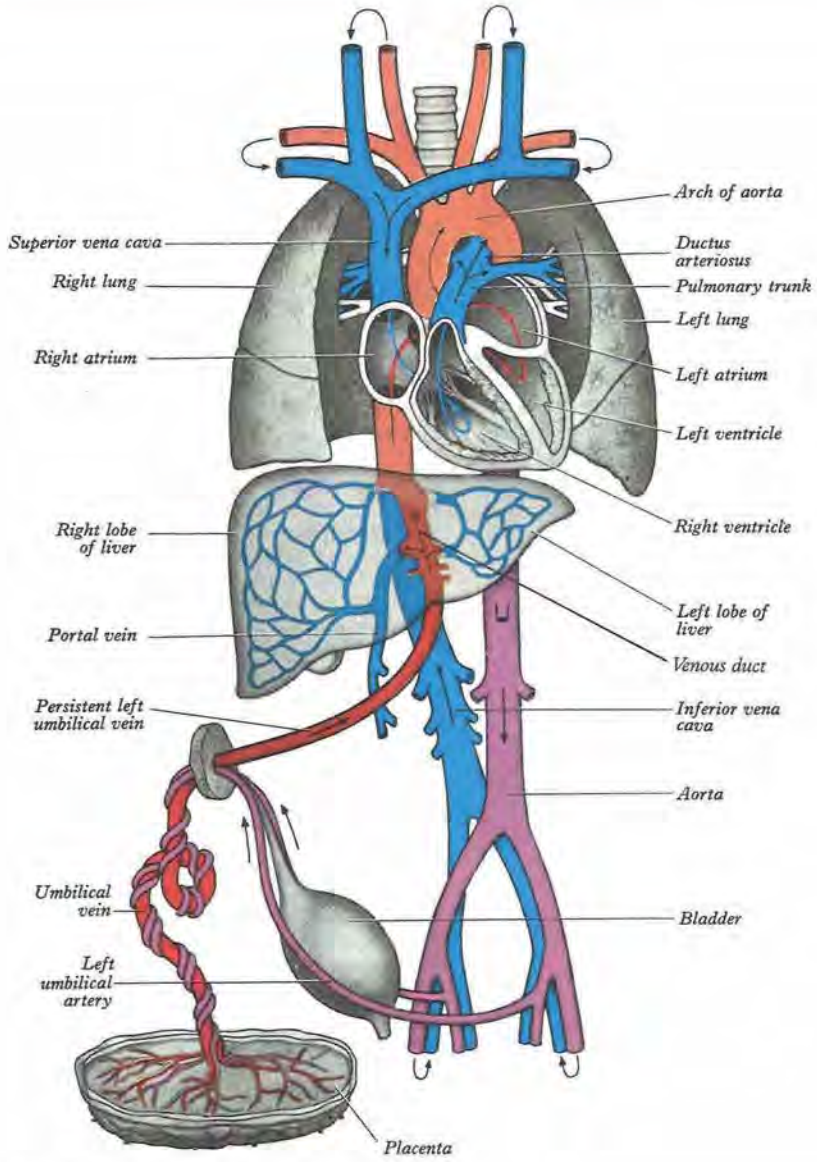
Arteries of cardiac supply, the aortic coronary branches, are described on pages 1495–1510, cardiac veins and the coronary sinus on pages 1575–1576 and lymphatic drainage on page 1625.

FETAL CIRCULATION

Fetal blood reaches the placenta via two umbilical arteries and



10.59 Small autonomic nerve ganglion in the wall of the left atrium (monkey). The ganglion lies within the atrial musculature; several ganglion neurons are grouped together, and each of them is surrounded by small satellite cells (glial cells). Masson trichrome stain. Magnification × 600.



10.60 Plan of the fetal circulation. The arrows indicate the direction of blood flow. The placenta is drawn to a greatly reduced scale.

returns in early fetal life by two umbilical veins (**10.60**). Later, the right one disappears (p. 324). The persisting left umbilical vein enters the abdomen at the umbilicus and traverses the edge of the falciform ligament to reach the hepatic surface of the liver. It then joins the left branch of the portal vein at the hepatic portal. Opposite the junction, a large vessel, the *venous duct* (*ductus venosus*), arises and ascends posterior to the liver to join the left hepatic vein near its termination in the inferior vena cava. (For a detailed developmental account, with illustrations, of the circumhepatic veins see p. 321.) The portal vein is small in the fetus compared with the size of the umbilical vein. Parts of its left branch, proximal and distal to their junctions, function as branches of the portal vein, carrying oxygenated blood to the right and left parts of the liver. Hence, blood in the left umbilical vein reaches the inferior vena cava by three routes:

- Some enters the liver directly and reaches the vena cava via the hepatic veins
- A considerable quantity circulates through the liver with portal venous blood before also entering by the hepatic veins
- The remainder is bypassed into the inferior vena cava by the venous duct.

Blood from the venous duct and hepatic veins mixes in the inferior vena cava with blood from the lower limbs and abdominal wall. It enters the right atrium and, guided by the valve of the inferior vena cava, passes mostly through the oval foramen into the left atrium, where it mingles with the limited venous return from the pulmonary veins. Some blood returning via the inferior vena cava, instead of traversing the oval foramen, joins blood from the superior vena cava and passes through the right atrium to reach the right ventricle. From the left atrium, blood enters the left ventricle and thence the aorta, by which it is probably distributed almost entirely to the heart, head and upper limbs, little reaching the descending aorta. Blood from the head and upper limbs returns via the superior vena cava to the right atrium, all of which traverses the right atrioventricular orifice, along with the small amount returned via the inferior vena cava. From the right ventricle, this blood enters the pulmonary trunk. The fetal lungs are largely inactive, so only a little of the blood from the right ventricle traverses the right and left pulmonary arteries, and this returns by the pulmonary veins to the left atrium. The greater part of the outflow through the pulmonary trunk is carried by the *arterial duct* (*ductus arteriosus*) directly to the aorta, where it mixes with the small quantity of blood passed from the left ventricle into this part of the aorta. The mixture descends

the aorta and is partly distributed to the lower limbs and the organs of the abdomen and pelvis. Most is returned via the umbilical arteries to the placenta.

In terms of function, it is the placenta which serves as the organ for fetal nutrition and excretion, receiving deoxygenated fetal blood and returning it oxygenated and detoxified. Most of the blood entering the left atrium comes from the right atrium, right atrial pressure being much higher than that in the left atrium. Hence, the flap-like valve of the primary septum (p. 304) is thrust to the left (3.168, 169, 170), allowing passage of blood from the right to the left atrium. The valve of the inferior vena cava is so placed as to direct nearly all the richly oxygenated blood from the umbilical vein to the oval foramen and left atrium, whereas most of the venous blood from the superior vena cava enters the right ventricle directly through the right atrioventricular orifice. The refreshed placental blood, therefore, mixed with blood from the portal vein and inferior vena cava, passes almost directly to the aorta for distribution to the head and upper limbs. In contrast, the blood which reaches the descending aorta through the ductus arteriosus is mostly the blood which has circulated through the head and upper limbs, with only a small amount coming from the pulmonary veins and left atrium. This blood is distributed to the abdomen and lower limbs, but principally returns to the placenta.

CHANGES IN THE VASCULAR SYSTEM AT BIRTH

At birth, as pulmonary respiration begins, increased amounts of blood from the pulmonary trunk traverse the pulmonary arteries to the lungs and return by the pulmonary veins to the left atrium. Consequently, pressure rises within the left atrium. A fall in pressure also occurs in the inferior vena cava due to reduction of venous return concomitant with occlusion of the umbilical vein and venous duct. Atrial pressures become equal and the valvar oval foramen is closed by apposition, and later fusion, of the primary septum to the rims of the foramen (p. 304). Contraction of the atrial septal muscle, synchronized with that in the superior vena cava, may assist this closure which occurs after functional closure of the ductus arteriosus. Sometimes fusion is incomplete, a potential atrial communication persisting throughout life. Almost always this has no functional effect, since the inequality of atrial pressures and the valve-like arrangement of the opening do not favour passage of blood. When the umbilical cord is ligated, arresting placental circulation, the umbilical vein thromboses, gradually becoming the ligamentum teres. Umbilical vessels are muscular but devoid of a nerve supply in their extra-abdominal course. They constrict in response to handling, stretching, cooling and altered tensions of oxygen and carbon dioxide. The venous duct (*ductus venosus*) shuts down by an unknown mechanism. It is already closed in about one-third of newborn infants (Rudolph et al 1961). Its fibrous remnant is the venous ligament (*ligamentum venosum*). After ligation of the umbilical cord, the umbilical (hypogastric) arteries also thrombose from the origin of their last branches (superior vesical arteries) to the umbilicus, subsequently becoming fibrous chordae (medial umbilical ligaments) in the extraperitoneal fat of the abdominal wall.

The ductus arteriosus contracts rapidly immediately after birth, although blood probably continues to flow intermittently through it for a week or so. Such flow, nonetheless, is reversed relative to that occurring in the fetal circulation. This is the consequence of the rise in systemic vascular resistance which results from exclusion of the placental circulation, and the fall in pulmonary resistance occurring with expansion of the lungs. Anatomic closure of the duct is due to endothelial proliferation but takes some months to complete. Initial constriction at birth has been attributed to raised oxygen tension. A neural factor may also be involved, the muscular wall having afferent and efferent nerve endings and responding to adrenaline and noradrenaline (Franklin 1939; Barcroft 1941; Barclay et al 1942). After closure, the duct becomes an impervious ligament connecting the left pulmonary artery (near its origin) with the aortic arch. (For morphological and biomechanical studies of the arterial ligament, consult Dohr et al 1986. For a general review of perinatal vascular changes, see Dawes 1969.)

CONGENITAL CARDIAC MALFORMATIONS

Congenital malformations of the heart are relatively common, amounting to about one-quarter of all developmental abnormalities. Their incidence is estimated at 8 per 1000 live births, but they are found in up to 2% of stillbirths. Only a small proportion of the anomalies are directly attributable to genetic or environmental factors, the majority being the result of multifactorial events.

ABNORMALITIES OF THE CARDIAC POSITION

The most severe abnormality of position is an extrathoracic heart, so-called *ectopia cordis*. The heart usually projects to the surface through the lower thoracic and upper abdominal wall, remaining covered in most instances by the fibrous pericardium. There is usually additional herniation of the abdominal contents. Another abnormality of position is for the heart to show a mirror-like reversal in shape and position, being found in the right hemithorax with its apex directed to the right instead of the left (*dextrocardia*). This arrangement may be part of a general mirror-like reversal (so-called general '*situs inversus*'). More usually an abnormal location of the heart is found with an arrangement known as *isomerism*, in which both sides of the thorax, including the atrial appendages, retain features of either morphological rightness or leftness. This is also usually associated with anomalous arrangement of the abdominal organs, *right isomerism* associated with absence of the spleen (*asplenia*) and left isomerism with multiple spleens (*polysplenia*). The heart can also be abnormally located when the rest of the body is normal. Such an abnormal location usually indicates presence of additional lesions within the heart but can simply be the consequence of abnormality of the lungs, the abnormally located heart being anatomically normal.

DEFECTS OF THE CARDIAC SEPTATION

Most anomalies can be placed in this group, with simple deficiencies of septation affecting the atrial septum, the atrioventricular septum, the ventricular septum or the arterial pole of the developing heart. More complex forms with abnormal septation represent failure of, or inappropriate, connection of the atria to the ventricles. In this set can be placed anomalies such as double inlet ventricle; absence of one atrioventricular connection (tricuspid or mitral atresia); and discordant atrioventricular connections (congenitally corrected transposition).

Atrial septal defects

Defects within the oval fossa. A persistent communication between the atrial chambers within the oval fossa is common, resulting from failure of fusion of the primary atrial septum (the flap valve) with the infolded muscular rims of the fossa. When the flap valve is still able to overlap the rims, the communication is of no functional significance as long as left atrial pressure is higher than right, which is usually the case. In contrast, when the flap valve is smaller than the fossa, or when it is perforate, there is a true atrial septal defect (10.61).

Other atrial communications. In normal development, the free edge of the primary septum fuses with the atrioventricular endocardial cushions, permitting subsequent formation of the atrioventricular septum. When this process fails to occur, the entire atrioventricular junction is malformed, with an atrioventricular septal defect being part of the complex anomaly. This defect can be found when the leaflets of the atrioventricular valves are fused to the crest of the ventricular septum (10.62), producing an interatrial communication at the expected site of the atrioventricular septum. This so-called '*ostium primum*' defect, therefore, is properly classed as an atrioventricular septal defect (see below). Other interatrial communications can be formed in the mouths of the venae cavae, most frequently the superior vena cava, and are usually associated with drainage of the right pulmonary veins into the cavo-atrial junction. Known as *sinus venosus defects* (10.61), their essential feature is a bi-atrial connection of the vena cava. An interatrial

communication can also occur through the mouth of the coronary sinus when there is a deficiency or absence of the wall usually separating the sinus from the left atrium.

Atrioventricular septal defects

Atrioventricular septal defects result from failure of fusion of the endocardial atrioventricular cushions, leaving a common atrioventricular orifice and deficiencies of the adjacent septal structures (**10.62**). The common orifice is guarded by a basically common valve, with superior and inferior leaflets bridging the scooped-out ventricular septum to be tethered in both right and left ventricles. Although the left component of the valve thus formed is often interpreted as a 'cleft mitral valve', in reality it bears no resemblance to the normally structured mitral valve, having three leaflets and with the 'cleft' forming the zone of apposition between the left ventricular components of the bridging leaflets. The defects show marked variation according to the attachments of the bridging leaflets of the common valve to each other and to the adjacent atrial and ventricular septal structures. Two major subgroups are identified. The more frequent pattern has a common atrioventricular orifice and the potential for shunting through the septal defect at both atrial and ventricular levels (**10.62**, middle). The minority of cases have separate right and left atrioventricular orifices with shunting possible only at atrial level. Although the latter defect is often described as an *ostium primum atrial septal defect*, it is, in reality, an atrioventricular septal defect.

Ventricular septal defects

The commonest defect of the ventricular septum is found in the environs of the expected site of the membranous septum in the right wall of the aortic vestibule, below the commissure between the non-coronary and right coronary leaflets of the aortic valve (**10.63**). The defect is closely related to the septal leaflet of the tricuspid valve, but can extend to open into the ventricular outlet beneath the supraventricular crest (p. 1480). It results from incomplete closure of the ventricular septum by its membranous component, often being associated with overriding of the crest of the muscular septum by the aortic orifice, along with pulmonary stenosis or atresia and hypertrophy of the right ventricle (*Fallot's tetralogy*). Rarely the pulmonary trunk can be normal or even dilated with this combination, giving the so-called *Eisenmenger complex*. Such perimembranous defects, so called because they have the remnant of the membranous septum as part of their perimeter, can also be found with abnormal ventriculo-arterial connections (see below). It is then often the pulmonary trunk which overrides the muscular septum, giving the so-called *Taussig-Bing syndrome*. In perimembranous ventricular septal defects, the atrioventricular bundle and its right and left branches are always found along the *postero-inferior margin* of the defect (Latham & Anderson 1972).

Less commonly, a septal defect can be found in the ventricular outflow tracts roofed by the conjoined facing leaflets of the aortic and pulmonary valves. Such juxta-arterial defects are doubly committed in that they open beneath the orifices of both aortic and pulmonary valves. They are due to failure of formation of both the outlet component of the muscular ventricular septum and the free-standing subpulmonary muscular infundibulum, but with appropriate septation at the ventriculo-arterial junction. They usually have a muscular postero-inferior rim which protects the atrioventricular bundle, but can extend to become perimembranous.

The third type of ventricular septal defect is made up of those enclosed within the musculature of the septum. Such muscular defects can occur in all parts of the septum, and can be multiple, producing a so-called '*Swiss-Cheese*' septum.

Defects within the inlet part of the septum are important because the atrioventricular bundle passes in their upper border, in contrast to perimembranous defects opening to the inlet of the right ventricle where the atrioventricular bundle is postero-inferiorly located.

Common arterial trunk

The essence of a common arterial trunk lesion is presence of an undivided arterial channel, guarded by a common arterial valve, positioned above and astride the free margin of the muscular ventricular septum (**10.64**). There is, therefore, a coexisting juxta-arterial deficiency of the ventricular septum. The right and left pulmonary arteries usually arise via a confluent segment but can take independent origin from the common arterial trunk, which continues as the ascending aorta. The common valve usually has three leaflets, but may have two, four, or more. The lesion is due to a failure of development of the aorticopulmonary septum, and is almost certainly linked to abnormal migration of cells into the heart from the neural crest.

ABNORMAL CONNECTIONS OF THE GREAT ARTERIES AND VEINS

Complete transposition is the condition in which the aorta arises from the right ventricle and the pulmonary trunk from the left. Better described as showing discordant ventriculo-arterial connections, such hearts can coexist with deficiencies of cardiac septation. They can also be found with discordant connections at the atrioventricular junction (congenitally corrected transposition). The developmental history of the discordant connections is still unknown.

Double outlet ventricle exists when the greater part of both arterial valves are attached within the same ventricle, almost always the right. For circulation to continue, it is then necessary for the ventricular septum to be deficient, although the septal defect can rarely close as a secondary event. The position of the septal defect serves for subclassification. It is usually beneath the aorta or the pulmonary trunk, but can be doubly committed or even non-committed.

Either the systemic or pulmonary veins can be anomalously connected. The commonest systemic anomaly is found when a persistent left superior vena cava drains into the right atrium through the enlarged orifice of the coronary sinus.

More rarely, the left vena cava may connect directly with the superior aspect of the left atrium, usually associated with unroofing of the coronary sinus, the orifice of the sinus then functioning as an interatrial communication. The commonest lesion of the inferior vena cava is for its abdominal course to be interrupted, with drainage to the heart via the azygos or hemiazygos venous system. This lesion is found most frequently with left isomerism.

The pulmonary veins can be connected to an anomalous site individually or in combination. Totally anomalous connection is of most significance. Usually the veins form a confluence behind the left atrium which then connects either to the superior vena cava, to the coronary sinus, or to the portal venous system having traversed the diaphragm.

A right aortic arch is found most frequently with tetralogy of Fallot or with common arterial trunk. It can also exist, together with a left arch, in various combinations known as arterial rings which compress the oesophagus, giving so-called dysphagia lusoria. Persistent patency of the ductus arteriosus (p. 1052) must be distinguished from delayed closure. The persistently patent duct can be an obligatory part of the circulation when associated with aortic or pulmonary atresia. Coarctation of the aorta can be found as an isolated lesion when the ductus arteriosus is closed, or with an open duct when it is more likely to be associated with additional lesions within the heart. Congenital cardiac malformations are often multiple and probably occur more frequently in siblings and in children of consanguineous marriages. There is a low correlation, however, among monozygotic twins. Ventricular septal defects are the commonest lesions, making up about 20% of all cases. This is followed by persistent patency of the ductus arteriosus, coarctation, pulmonary stenosis, Fallot's tetralogy, complete transposition, aortic stenosis, and hypoplastic left heart syndrome, each of these accounting for between 5% and 10% of all cases.

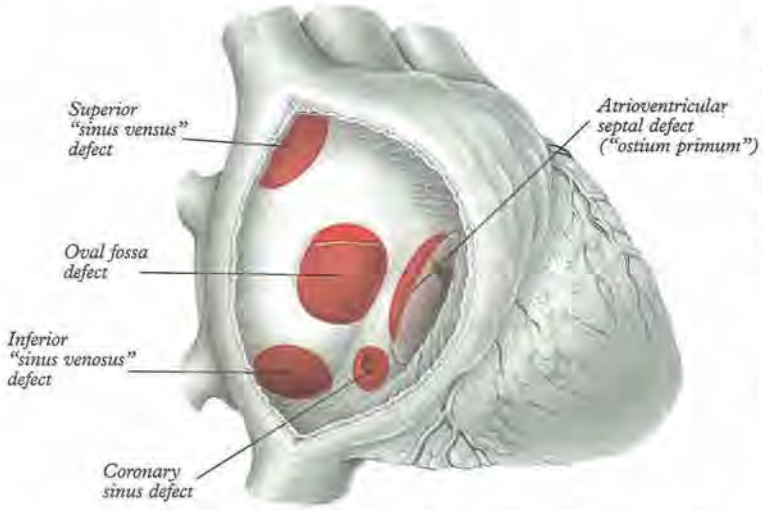
ARTERIAL SYSTEM

PULMONARY TRUNK

The pulmonary trunk, or pulmonary artery (**10.65, 66, 68**) conveys deoxygenated blood from the right ventricle to the lungs. About 5 cm in length and 3 cm in diameter, it is the most anterior of the cardiac vessels and it arises from the base of the right ventricle (from the pulmonary annulus surmounting the conus arteriosus) above and to the left of the supraventricular crest. It slopes up and back, at first in front of the ascending aorta, then to its left. Below the aortic arch it divides, level with the fifth thoracic vertebra and to the left of the midline, into the right and left pulmonary arteries of almost equal size. Thus the pulmonary trunk bifurcation lies **below, in front** and to the **left** of the tracheal bifurcation, which is also associated with the inferior tracheobronchial lymph nodes and the deep cardiac nerve plexus. In the fetus the pulmonary artery at the level of the bifurcation is connected to the aortic arch by the ductus arteriosus, which lies in the same direction as the pulmonary artery.

Relations

The artery is entirely within the pericardium, enclosed with the ascending aorta in a common tube of visceral pericardium; the fibrous pericardium gradually peters out in the adventitia of the pulmonary arteries. **Anteriorly** it is separated from the sternal end of the left second intercostal space by the pleura, left lung and pericardium. **Posterior** are at first the ascending aorta and left coronary artery, then the left atrium. The ascending aorta is finally on its right. An auricle and coronary artery are on each side of its origin. The superficial cardiac plexus is between the pulmonary bifurcation and the aortic arch; above, behind and right are the tracheal bifurcation, lymph nodes and nerves (see above).



10.61 This drawing shows the location of the defects which produce an interatrial communication. Only defects within the oval fossa are true atrial septal defects.

During fetal life, when blood pressure is similar in the pulmonary artery and the aorta, the structure of the vessels is similar. After birth, with the expansion of the lungs and dilatation of pulmonary arterioles, pulmonary vascular resistance falls while blood flow increases; the systolic pressure in the pulmonary artery falls and this is accompanied by a structural remodelling of the wall. The elastic material, which has originally a lamellar structure, becomes aggregated into star-shaped units which are linked to many muscle cells. The amount of musculature grows extensively after birth and it exceeds that found in the aorta; in the latter, however, the thickness of the wall is about twice that in the pulmonary artery.

Right pulmonary artery. Slightly longer and larger than the left artery, it runs horizontally to the right, behind the ascending aorta, superior vena cava and upper right pulmonary vein, then in front and below the tracheal bifurcation (see above) and thence in front of the oesophagus and right main bronchus to the right pulmonary hilum. It divides as it emerges from behind the superior vena cava into two large branches. A lymph node usually occupies the bifurcation. The superior branch, which is the smaller of the two, goes to the superior lobe and it usually divides into two further branches which supply the majority of that lobe. The inferior branch descends anterior to the intermediate bronchus and immediately posterior to the superior pulmonary vein. It gives off a small recurrent branch to the superior lobe and, at the point where the horizontal fissure meets the oblique fissure, this branch of the pulmonary artery then gives off anteriorly the branch to the middle lobe and posteriorly the branch to the superior segment of the inferior lobe. It then continues a short distance before dividing to supply the rest of the inferior lobe segments.

Left pulmonary artery. Shorter and smaller than the right, it runs horizontally in front of the ascending aorta and the left principal bronchus to the left hilum. It emerges from within the concavity of the aortic arch and descends anterior to the descending aorta to enter the oblique fissure. The branches of the left pulmonary artery are extremely variable. Usually its first and largest branch is to the anterior segment of the left superior lobe. Prior to reaching the fissure it gives off a variable number of other branches to the superior lobe. As it enters the fissure it usually supplies a large branch to the superior segment of the inferior lobe. Lingular branches arise within the fissure and the rest of the lower lobe is supplied by many varied branching patterns. It was a surgical aphorism of the late Lord Brock that when performing a left upper lobectomy 'There was always one more branch of the pulmonary artery than you thought!'.

10.62 This drawing shows how, depending on the attachment of the bridging leaflets, shunting across an atrioventricular septal defect can be atrial, ventricular or both levels.

AORTA

The aorta, the trunk of the arterial tree conveying oxygenated blood to the body, begins at the aortic annulus (pp. 1488, 1493), part of the base of the left ventricle, where it is about 3 cm in diameter. Passing up and right for about 5 cm, it arches upwards, backwards and to the left over the left pulmonary hilum and then descends in the thorax at first left of the vertebral column, then gradually inclining towards the midline, to enter the abdomen via the diaphragm's aortic hiatus. Diminished in size to about 1.75 cm. it ends a little left of

the midline, level with the lower border of the fourth lumbar vertebra, dividing into the right and left common iliac arteries. For convenience it is described as arbitrarily divided into *ascending*, *arch* and *descending thoracic* and *abdominal* parts.

ASCENDING AORTA

The ascending aorta (**10**.23A, 26, 65, 66, 67), about 5 cm long, begins at the base of the left ventricle, level with the third left costal cartilage's lower border; it ascends obliquely, curving forwards and right, behind the left half of the sternum to the level of the second left costal cartilage's upper border. At its origin, close to the aortic annulus, the sectional profile is larger and not circular because of three almost hemispherical outward bulges (sinuses of Valsalva), one posterior (non-coronary), one left and one right, which correspond to the three cusps of the aortic valve (p. 1488). Distal to the aortic annulus are three aortic sinuses, beyond which the vessel's calibre is slightly increased by a bulging of its right wall; this aortic bulb gives the vessel an oval section.

Relations

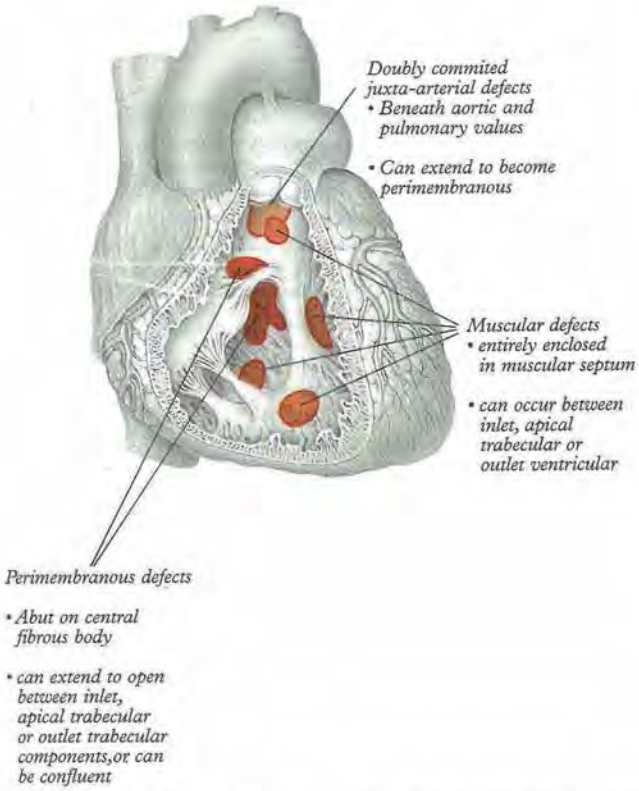
The ascending aorta is within the fibrous pericardium, enclosed in a tube of serosal pericardium with the pulmonary trunk (**10**.19). Anterior to its lower part are the infundibulum (p. 1480), the initial segment of the pulmonary trunk, and the right auricle; superiorly, it is separated from the sternum by the pericardium, right pleura, anterior margin of the right lung, loose areolar tissue and thymic remains; posterior are the left atrium, right pulmonary artery and principal bronchus; right lateral are the superior vena cava and right atrium, the former partly posterior; left lateral are the left atrium and, at a higher level, the pulmonary trunk.

At least two structures (reminiscent of the carotid arterial chemoreceptors and baroreceptors, p. 971) lie between the ascending aorta and the pulmonary trunk. The inferior aorticopulmonary body is near the heart and anterior to the aorta; the middle aorticopulmonary body is near the right side of the ascending aorta (Boyd 1961).

Branches form the right and left coronary arteries (**10**.67A–E), supplying the heart itself.

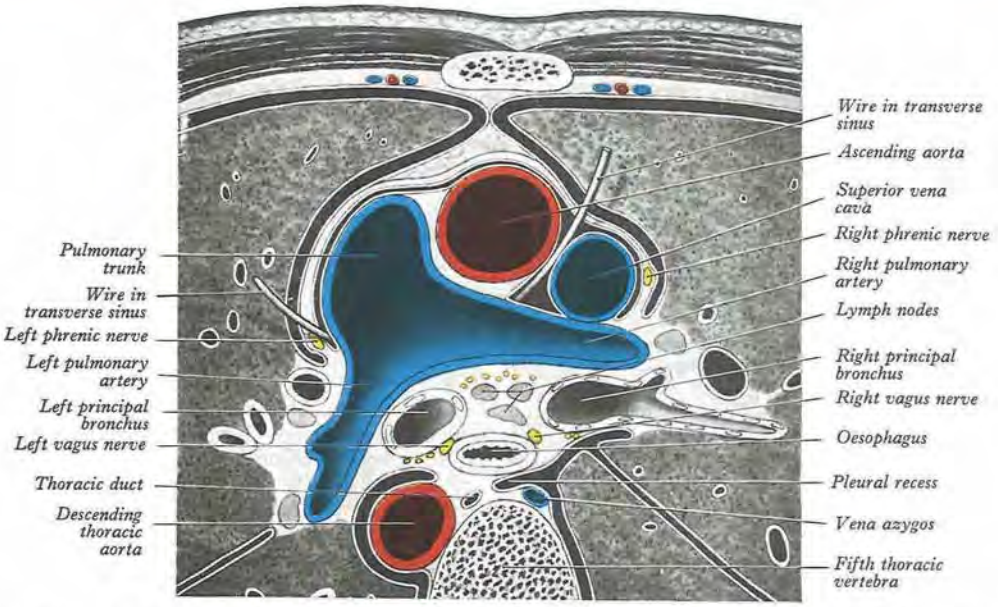
CORONARY ARTERIES

The right and left coronary arteries issue from the ascending aorta in its anterior and left posterior sinuses (**10**.65, 67A–E). Variations are rare but the two may start, separately or in common, from the same sinus; three or even four coronary arteries have been observed; the most common variation concerns a right coronary branch, *arteria coni arteriosi* or 'conus artery', which is usually (64%) its first branch but often arises separately in the anterior sinus (36%), as a third coronary artery. The left coronary opening may be double, leading into major initial branches, usually the circumflex and anterior interventricular; one may lead into a stem common to one such branch and a diagonal ventricular ramus. The levels of coronary orifices are variable; Thebesius (1708) appears to have started a view that aortic cusps obstruct them when fully spread in systole; but the coronary orifices are at a higher level, at or above cuspal margins, though below in about 10% (right coronary) and 15% (left). (Further, as detailed on p. 1486 et seq, it is now established that, even at the

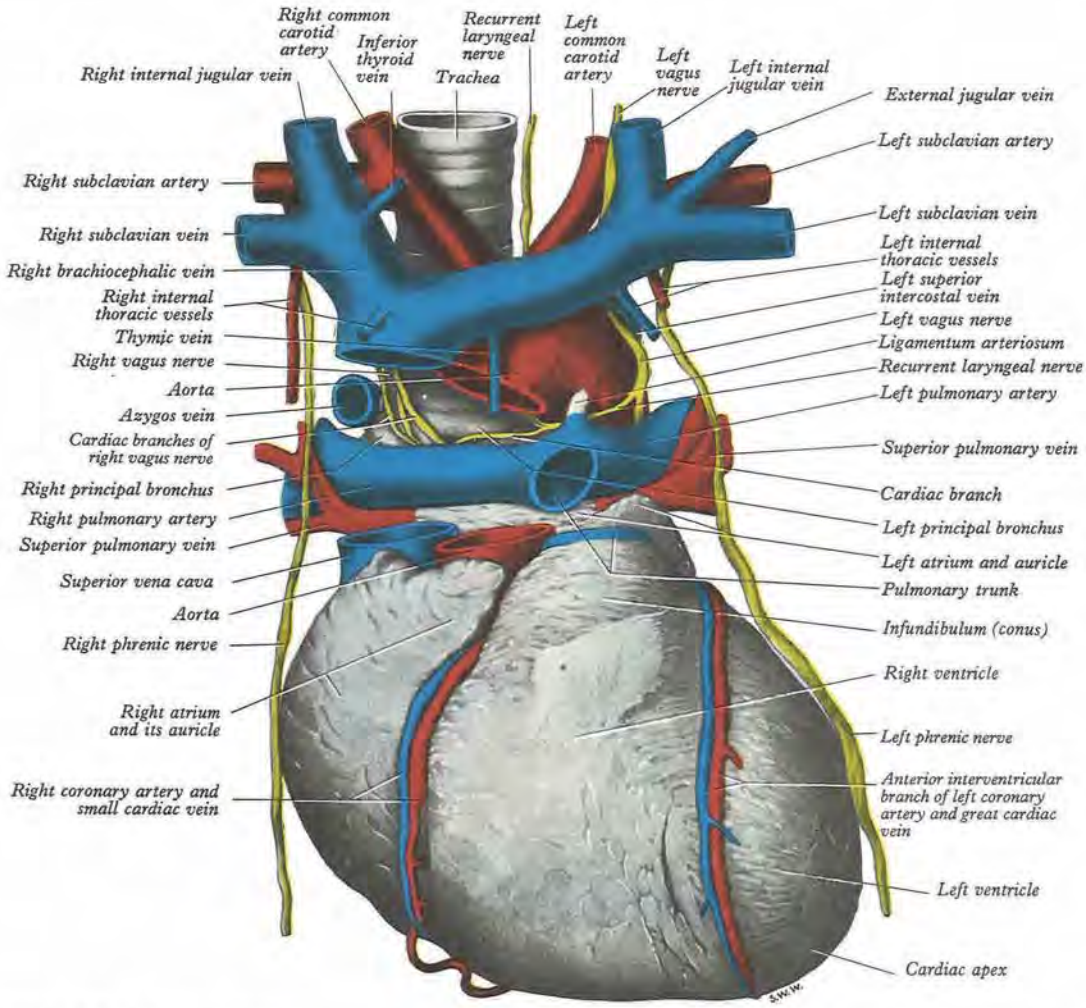


10.63 Diagram showing how, based on the structure of the anatomic borders seen from the right ventricle, ventricular septal defects can be placed into perimembranous, muscular or doubly committed groups.

10.64 This heart possesses a common arterial trunk, with a common truncal valve overriding a juxta-arterial deficiency of the ventricular septum. It is due to failure of septation of the arterial pole of the developing heart. (Specimen prepared by Dr Leon M Gerlis.)



10.65 Transverse section through the mediastinum at the level of the upper border of the fifth thoracic vertebra: superior aspect. Note nerve fibres of the deep cardiac and posterior pulmonary plexuses, inferior tracheobronchial and hilar lymph nodes.



10.66 The relations of the pulmonary arteries and primary bronchi seen from the front. Parts of the ascending aorta, pulmonary trunk and superior vena cava have been removed in the dissection. The right vagal trunk is uncoloured to avoid confusion.

height of the systole, the cusps do not 'flatten' against, i.e. co-apt to, the walls of their sinuses.)

The two arteries, as indicated by their name, form an oblique inverted crown, with an anastomotic circle in the atrioventricular sulcus connected by marginal and interventricular loops intersecting at the cardiac apex (**10.67**A–E). This is, of course, only an approximation; the degree of anastomosis is most variable and usually insignificant (see below). The main arteries and major rami are usually subepicardial but those in the atrioventricular and interventricular sulci are often deeply sited, occasionally hidden by overlapping myocardium or embedded in it. Myocardial strands may also cross atrial or ventricular branches; Pólaček (1961) found them in more than 80% of ventricles; Bloor and Lowman (1963) have emphasized their importance in interpretation of coronary arteriograms.

The term 'dominant' is used to refer to the coronary artery which gives the posterior interventricular branch, supplying the posterior part of the ventricular septum and often part of the posterolateral wall of the left ventricle. In 70% of people this is the left coronary artery, which is also invariably the larger of the two vessels. In the remaining cases the posterior interventricular branch is either bilateral, issuing from both the right coronary artery and the left circumflex artery, or absent and replaced by a network of smaller vessels from both right and left coronaries. Anastomoses between right and left coronary arteries are abundant during fetal life but are much reduced by the end of the first year of life. Anastomoses providing collateral circulation may become prominent in conditions of hypoxia and in coronary artery diseases. An additional collateral circulation is provided by small branches from mediastinal, pericardial and bronchial vessels.

The diameters of coronary arteries, both main stems and larger branches, have often been recorded; such figures are of limited value, since technique is not always stated, physiological state often ignored and measurement of external or internal diameters not clearly distinguished. Calibre is usually the basis, most measurements being made on arterial casts or angiograms. The maximum ranges recorded in major studies are 1.5–5.5 mm for coronary arteries at their origins. Baroldi and Scomazzoni (1967) give means of 4.0 and 3.2 mm. The left exceed the right in about 60% of hearts, the right being larger in 17%, the vessels approximately equal in 23%. Vogelberg (1957) considered that coronary diameters increase up to the thirtieth year.

Right coronary artery

Arising from the anterior ('right coronary') aortic sinus, the artery passes at first anteriorly and slightly to the right between the right auricle and pulmonary trunk, where the sinus usually bulges. Reaching the atrioventricular (coronary) sulcus it descends in this almost vertically to the right (acute) cardiac border, curving around it into the posterior part of the sulcus, where it approaches its junction with both interatrial and interventricular grooves, a region appropriately termed the *crux of the heart*. In about 60% of subjects the artery reaches the crux and ends a little left of it by variable anastomosis with circumflex branch of the left coronary. In a minority, the right coronary artery ends near the right cardiac border (c. 10%) or between this and the crux (c. 10%); more often (c. 20%) it reaches the left border, replacing part of the circumflex artery.

Branches of the right coronary supply both right atrium and ventricle and, variably, parts of the **left** chambers and atrioventricular septum. The first branch (arising separately from the anterior aortic sinus in 36% of cases) is the *conus artery* (sometimes a 'third coronary'); since a similar vessel comes from the left coronary, this is more correctly named the *right conus artery*. It ramifies anteriorly on the lowest part of the pulmonary conus and upper part of right ventricle; it commonly anastomoses with a similar left coronary branch to form the '*annulus of Vieussens*', a tenuous anastomotic 'circle' around the pulmonary trunk. Descriptions of the conus artery vary (Baroldi & Scomazzoni 1967), some regarding the right conus artery of significance in coronary arterial disease; some consider it to be the right coronary's first ventricular branch, supplying a variable region from the conus to the apex.

Anterior atrial and ventricular rami diverge from the so-called *first segment of the right coronary*, extending from its origin to the right margin of the heart. Both groups diverge widely, approaching a right angle in the case of ventricular arteries, in contrast to the more acute origins of the left coronary ventricular rami. The *right anterior ventricular rami*, usually two or three, ramify towards the cardiac apex, which they rarely reach unless the right marginal branch is included, as it is by some; this is then the largest right anterior ventricular ramus, greater in calibre and long enough to reach the apex in most hearts (93%; Baroldi & Scomazzoni 1967). When the right marginal artery is very large, the remaining anterior ventricular rami may be reduced to one, or may be absent. From the *second segment of the right coronary artery* (between the right border and crux) one to three small *right posterior ventricular rami*, commonly two, supply the diaphragmatic aspect of the right ventricle. Their size is inversely proportional to that of the right marginal artery, as in the anterior right ventricular supply, the right marginal usually extending to the cardiac diaphragmatic surface. Posterior right ventricular rami may be absent. As the right coronary approaches the crux, it produces one to three posterior interventricular rami but only one in the interventricular sulcus; this *posterior interventricular artery*, single in about 70%, is otherwise accompanied by parallel right coronary branches, to the right or left or on both sides of the sulcus. When these flanking vessels exist, branches of the posterior (descending) interventricular artery are small and sparse; when it exists alone it gives off a few branches, particularly to the right ventricle but also to the left. It is replaced in about 10% of cases by a left coronary branch.

The atrial rami of the right coronary artery are sometimes described as anterior, lateral (right or marginal) and posterior groups but are most frequently single, small vessels averaging 1 mm in diameter. The right anterior and lateral are occasionally double, very rarely triple, and supply chiefly the right atrium. The posterior ramus is usually single, distributed to the right and left atria; but in 40% or more a left posterior atrial branch of the right coronary exists. The artery of the sinuatrial node is an atrial branch, distributed largely to the myocardium of both atria, mainly the right. Its origin is variable: from the left coronary in about 35% (Hutchinson 1978), arising from its circumflex branch (see below); when it is a branch of the right coronary, it usually comes from its anterior stem, less often from its right lateral part, least often from its posterior atrioventricular part. This 'nodal' artery thus usually passes back in the sulcus between the right auricular appendage and aorta. Whatever its origin the artery usually branches around the superior vena cava's base, commonly as an arterial loop from which small rami supply the right atrium. A large '*ramus cristae terminalis*' (Spalteholtz 1924) traverses the sinuatrial node (**10.67**A–C); perhaps instead this ramus should be termed 'nodal artery', since most of the currently named vessel actually supplies the atria and is more appropriately named the 'main atrial branch' (Baroldi & Scomazzoni 1967).

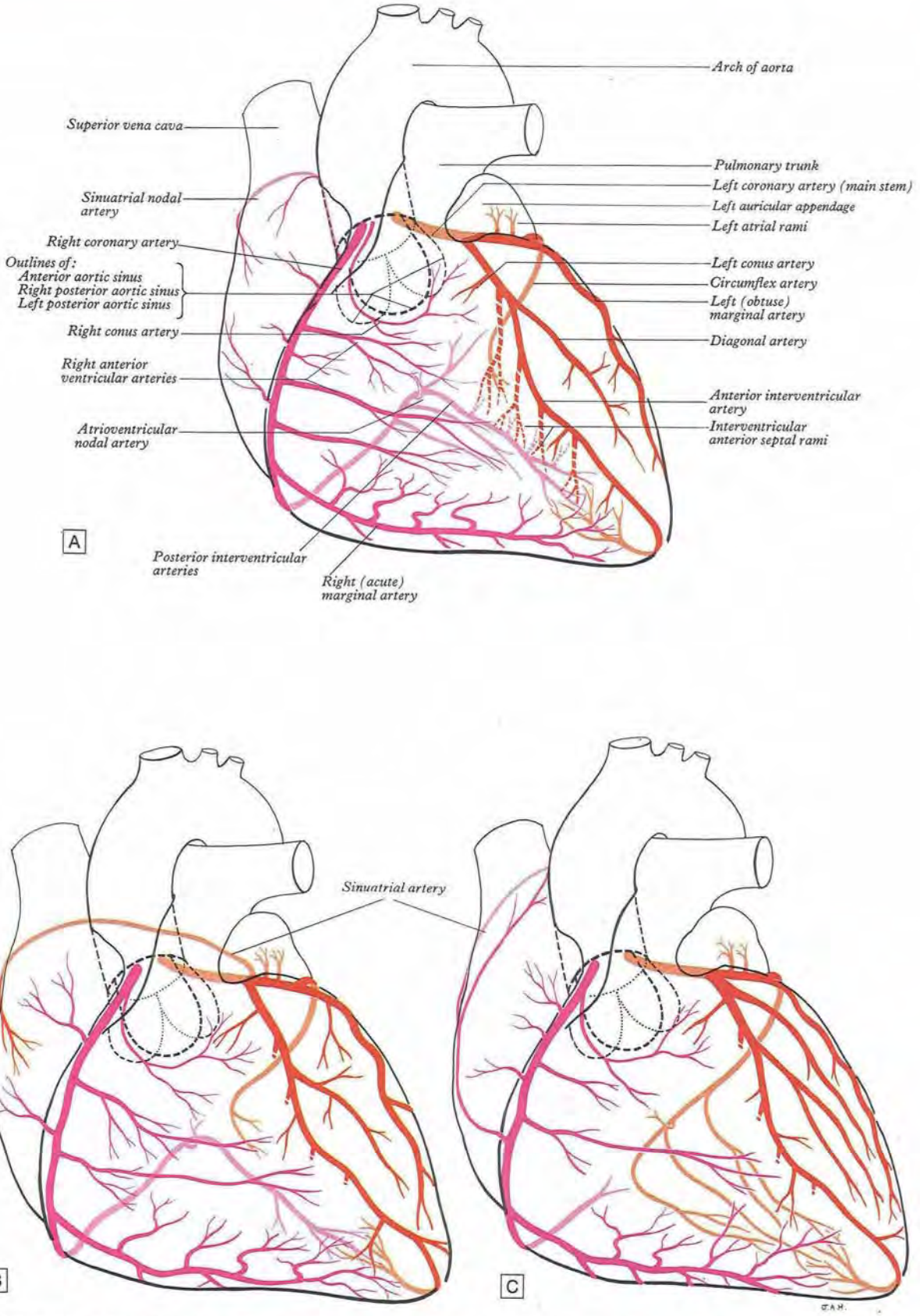
Right coronary septal rami are relatively short, leaving its posterior interventricular ramus to supply the posterior interventricular septum. They are numerous but do not usually reach the apical septal parts (supplied by terminal septal branches of the anterior interventricular).

The largest posterior septal artery, usually the first, is commonly from the inverted loop said to characterize the right coronary artery at the crux, where its posterior interventricular branch arises; this large posterior septal artery usually supplies the atrioventricular node—in 80% of hearts, according to Hutchinson (1978).

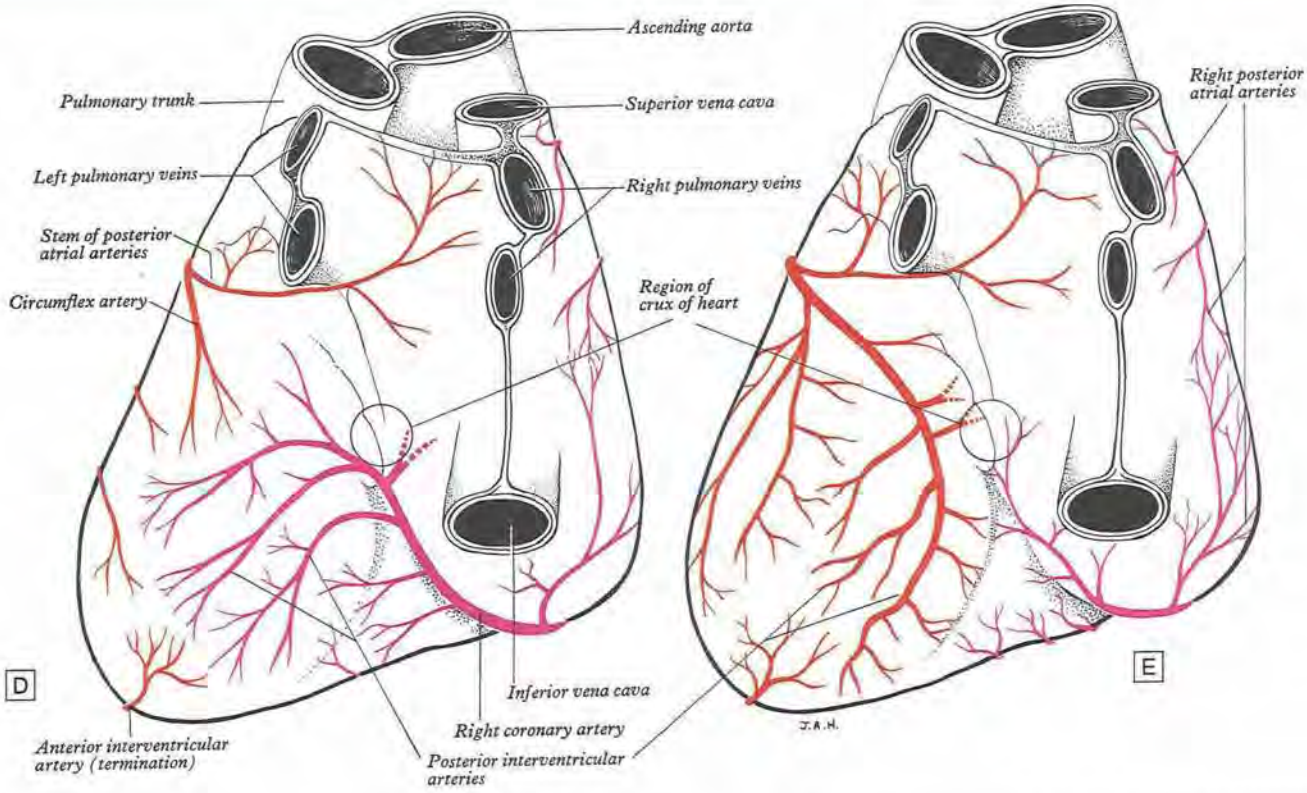
DiDio et al (1967) described the atrioventricular rami of the right coronary artery as consisting of small recurrent branches from each ventricular artery crossing the atrioventricular sulcus to supply the adjoining atrial myocardium, or ventricular twigs from the atrial arteries.

Left coronary artery

The left coronary artery is the larger in calibre, supplying a greater volume of myocardium, including almost all the left ventricle and atrium, except in so-called 'right dominance' where the right coronary partly supplies a posterior region of the left ventricle (**10.67**A–C). The left coronary usually supplies most of the interventricular septum. Its initial stem, between its ostium in the left posterior ('left coronary') aortic sinus and its first branches, varies in length from a few millimetres to a few centimetres. It lies between the pulmonary trunk and the left auricular appendage, emerging into the atrioventricular sulcus, in which it turns left; this part is loosely embedded in



10.67A–C Anterior views of the coronary arterial system, with the principal variations.
A The commonest arrangement.
B A common variation in the origin of the sinuatrial nodal artery.
C An example of left 'dominance' by the left coronary artery, showing also an uncommon origin of the sinuatrial artery.
Note that in **10.67**A–E the right coronary arterial tree is shown in magenta, the left in full red. In both cases posterior distribution is shown in a paler shade.



10.67D, E Postero-inferior views of the coronary arterial system.
D An example of the more normal distribution in right 'dominance'.
E A less common form of left 'dominance'.
N.B. In these 'posterior' views the diaphragmatic (inferior) surface of the ventricular part of the heart has been artificially displaced and foreshortening ignored to clarify the details of the so-called posterior (inferior) distribution of the coronary arteries.

subepicardial fat and usually has no branches; but a small atrial ramus may occur and, rarely, the sinuatrial nodal artery may arise from the left coronary artery (James 1961); but when it is a ramus of the left coronary it almost always comes from the circumflex branch. Reaching the atrioventricular or coronary sulcus, the left coronary divides into two or three main rami, its *anterior interventricular (descending) ramus* being commonly described as its continuation; this descends obliquely forward and left in the interventricular sulcus, sometimes deeply embedded or crossed by bridges of myocardial tissue and by the great cardiac vein and its tributaries. It reaches the apex almost always, terminating there in one-third of specimens, but more often turning round the apex into the posterior interventricular sulcus, in which it traverses a third to a half of its length, to meet the terminal twigs of the corresponding right coronary ramus.

The *anterior interventricular artery* produces right and left anterior ventricular, anterior septal and variable, corresponding posterior rami. Right anterior ventricular rami are small and rarely number more than one or two, the right ventricle being supplied almost wholly by the right coronary artery.

From two to nine large left *anterior ventricular arteries* branch at acute angles from the anterior interventricular to cross diagonally the left ventricle's anterior aspect, larger terminals reaching the rounded (obtuse) left border. One is often large and may arise separately from the left coronary trunk (which then ends by trifurcation); this left diagonal artery, reported in 33–50% or more cases, is occasionally duplicated (20%). A small left conus artery frequently leaves the anterior interventricular near its start, anastomosing on the conus with that of the right coronary and with the vasa vasorum of the pulmonary artery and aorta. The anterior septal rami leave the anterior interventricular almost perpendicularly, passing back and down in the septum, of which they usually supply about the ventral two-thirds. Small posterior septal rami from the same source supply the posterior septal third for a variable distance from the cardiac apex.

The *circumflex artery*, in calibre comparable to the anterior interventricular, curves left in the atrioventricular sulcus, continuing round the left cardiac border into the posterior part of the sulcus and ending left of the crux in most hearts, but sometimes continuing as a posterior interventricular artery. Proximally the left auricular appendage usually overlaps it. In about 90% a large ventricular branch, the *left marginal artery*, arises perpendicularly from it to ramify over the rounded 'obtuse' margin, supplying much of the adjacent left ventricle, usually to the apex. Smaller anterior and posterior rami of the circumflex artery also supply the left ventricle. *Anterior ventricular branches* (1–5, commonly 2 or 3) course parallel to the diagonal artery, when present, replacing it when absent. *Posterior ventricular branches* are smaller and fewer, the left ventricle being partly supplied by the posterior interventricular artery; when this is small or absent, it is accompanied or replaced by an interventricular continuation of the circumflex. Such a *left posterior interventricular artery* is frequently double or triple. Atrial rami, anterior, lateral and posterior, from the circumflex, supply the left atrium.

Inconstant branches of the circumflex artery require mention. The *artery to the sinuatrial node* is a branch in about 35% (Hutchinson 1978), usually from the anterior circumflex segment, less often the circummarginal. It passes over and supplies the left atrium, encircling the superior vena cava like a right coronary nodal ramus. It sends a large branch to (and through) the node but is predominantly atrial in distribution. The artery to the atrioventricular node, the terminal ramus in 20%, arises near the crux and then the circumflex usually supplies a posterior interventricular ramus, an example of so-called 'left dominance' (see below). *Kugel's anastomotic artery*, '*arteria anastomotica auricularis magna*,' was described by Kugel (1927) as a constant circumflex branch, usually from its anterior part, traversing the interatrial septum (near its ventricular border) to establish direct or indirect anastomosis with the right coronary. This anastomosis is controversial, apparently accepted by James (1978) but denied

by Baroldi and Scomazzoni (1967). James considered it an auxiliary supply to the atrioventricular node.

Details of coronary distribution require integration into a concept of total cardiac supply. Most commonly the right coronary supplies all the right ventricle (except a small region right of the anterior interventricular sulcus), a variable part of the left ventricular diaphragmatic aspect, the postero-inferior third of the intraventricular septum, the right atrium and part of the left, and the conducting system as far as the proximal parts of the right and left crura. Left coronary distribution is, of course, reciprocal, including most of the left ventricle (see above), a narrow strip of right ventricle (see below), the anterior two-thirds of the interventricular septum and most of the left atrium. As noted, variations (**10.67**A–E) chiefly affect the diaphragmatic aspect of ventricles residing in relative 'dominance' of supply by the left or right coronary artery. The term is misleading, since the left artery almost always supplies a greater volume of tissue. In 'right dominance' the posterior interventricular artery is from the right coronary, in 'left dominance' from the left. In the so-called 'balanced' pattern, branches of both run in or near the sulcus. Less is known of variation in atrial supply; the small vessels involved are not easily preserved in corrosion casts. From Hutchinson's results (1978) it is apparent that in over 50% the right atrium is supplied only by the right coronary, the rest receiving a dual supply. More than 62% of left atria are largely supplied by the left and about 27% by the right coronary; but in each group a small accessory supply from the other coronary exists, 11% being supplied almost equally by both. Sinuatrial and atrioventricular supplies also vary. According to James (1961) right and left coronary arteries supply the sinuatrial node respectively in 55% and 45%, corresponding values from Baroldi and Scomazzoni's study (1967) being 51% and 41% (8% receiving bilateral supply), and from Hutchinson (1978) 65% and 35%. For the atrioventricular node James's values are 90% (right coronary) and 10% (left coronary), Hutchinson's 80% and 20% respectively; Baroldi and Scomazzoni merely note that right coronary supply is common and left supply rare.

Coronary anastomosis

Anastomoses between branches of coronary arteries, subepicardial or myocardial, and between these arteries and extracardiac vessels are of prime medical import. Clinical experience suggests that anastomoses cannot rapidly provide collateral routes sufficient to circumvent sudden coronary obstruction. It is hence traditional to regard coronary circulation as end-arterial. Nevertheless, anastomosis has long been established particularly between the finer subepicardial rami. According to Gross (1921) such anastomoses may improve during individual life. Those who have investigated coronary arteries by radio-opaque perfusants (Vastesaeger et al 1957 in postmortem hearts; Laurie & Woods 1958 by in vivo coronary radiography), by perfusion with calibrated spherules (Prinzmetal et al 1947) or by subsequent corrosion casts of plastic resins (Baroldi et al 1956, James 1961) have almost all described anastomoses, and in vessels up to 100–200 μm in calibre. Baroldi and Scomazzoni (1967) have tabulated all results reported since 1880; no study denying anastomoses has been recorded since 1957. Some describe anastomoses only between branches of individual coronary arteries but the majority record intercoronary anastomoses. James (1978) considers the evidence conclusive for anastomoses at all levels: subepicardial, myocardial, and subendocardial; the most frequent sites of extramural anastomoses are the apex, the anterior aspect of the right ventricle, posterior aspect of the left ventricle, crux, interatrial and interventricular sulci and between the sinuatrial nodal and other atrial vessels. The functional value of such anastomoses must vary but they appear to become more effective in slowly progressive pathological conditions. Their structure is uncertain; most observations depend on corrosion casts, which suggest that anastomotic vessels are relatively straight in normal hearts, but much coiled in hearts subject to coronary occlusion. Little has been recorded of their microscopic structure; they appear little more than endothelial tubes, without muscles or elastic tissue

Extracardiac anastomoses may connect various coronary branches with other thoracic vessels via the pericardial arteries and arterial vasa vasorum of vessels linking the heart with systemic and pulmonary circulations. The classic study of Hudson et al (1932) showed that coronary injections of India ink could reach the diaphragm through the aortic vasa vasorum. Similar connections along pulmonary trunks reach the mediastinal and bronchial arteries and also exist along pulmonary veins and venae cavae. These results have been confirmed (Baroldi & Scomazzoni 1967) but the effectiveness of such connections as collateral routes in coronary occlusion is unpredictable.

Coronary arteriovenous anastomoses were reported by Nussbaum (1912). His evidence was indirect but Hirsch (1960) described glomeral structures with typical sphincteric appearances (p. 1468) in cardiac sulci; these must be regarded as at present unproven. Various other forms of 'arteriovenous' connections have been described; Wearn et al (1933) recorded numerous connections through the very thin-walled 'arterial' vessels between the coronary circulation and cardiac cavities, naming them 'myocardial sinusoids' and 'arterioluminal' vessels. They have been confirmed (Watanabe 1960) and indirect evidence of them, from perfusion experiments, dates back to Vieussens (1705). Their value in coronary disease is uncertain.

Histology of coronary arteries

The coronary arteries are highly muscular vessels, but rather variable in their structure, partly on account of their frequent branching and tortuous course. They differ in two respects from other vessels of similar size. The inner elastic lamina, discontinuous and poorly developed at birth, disappears during growth, and bundles of longitudinally oriented muscle are present in the outer part of the intima or the inner part of the media (a boundary between media and intima cannot be identified).

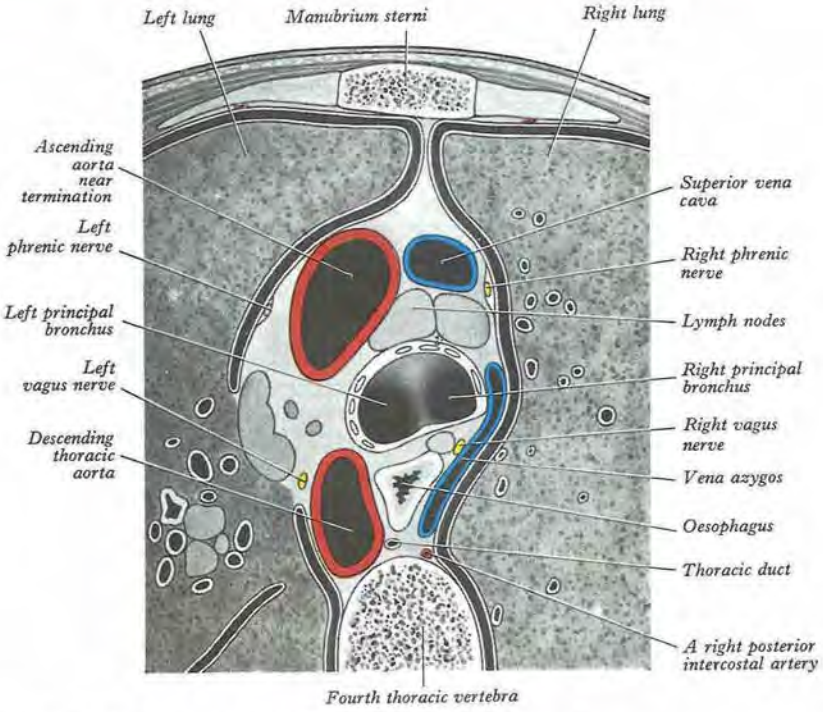
ARCH OF THE AORTA

The aortic arch (**10.65**, 70) continues the ascending aorta. Its origin, slightly to the right, is level with the upper border of the second right sternocostal joint. The arch first ascends diagonally back and to the left over the anterior surface of the trachea, then back across its left side and finally descends left of the fourth thoracic vertebral body, continuing as the descending thoracic aorta. Its end is level with the sternal end of the second, left costal cartilage (**10.28**). Thus, the aortic arch lies wholly in the superior mediastinum. It curves around the peduncle of the left lung, and extends upwards to the mid-level of the manubrium of the sternum. Its diameter at the origin is the same as in the ascending aorta, about 28 mm, but it is reduced to 20 mm at the end, after the issue of its large collateral branches. At the border with the thoracic aorta, a small stricture (aortic isthmus), followed by a dilatation, can be recognized. In fetal life the isthmus lies between the origin of the left subclavian artery and the opening of the ductus arteriosus.

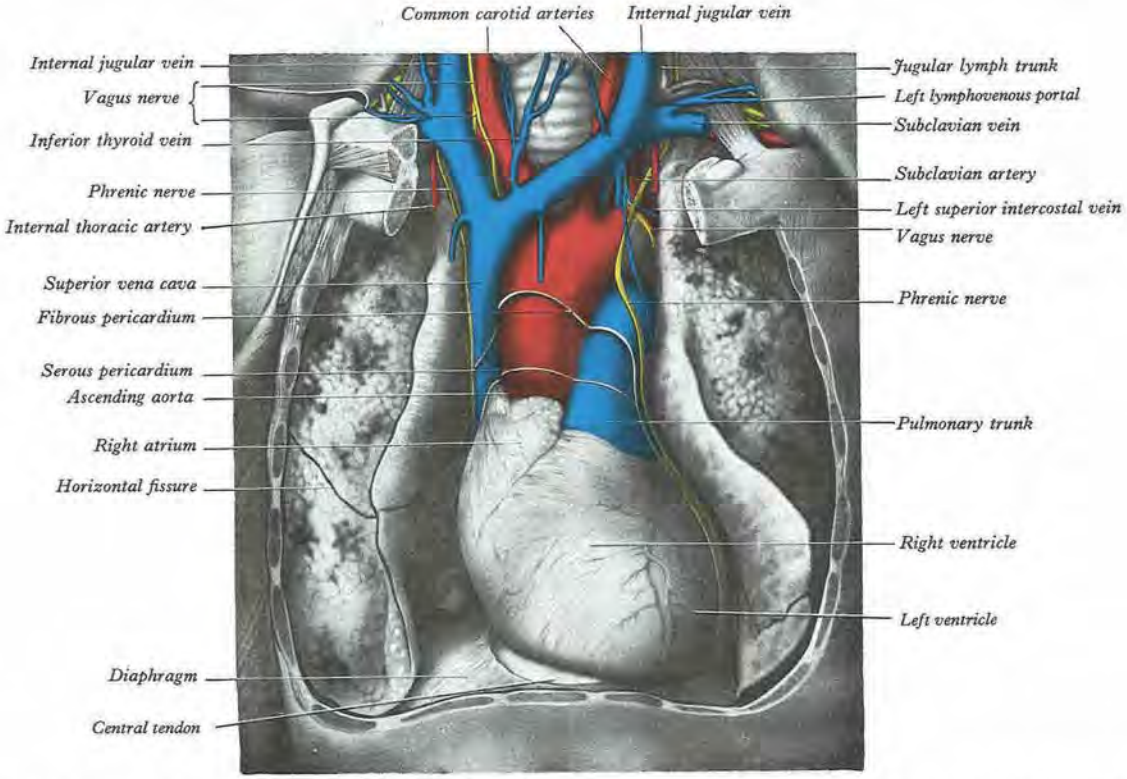
Relations

Anteriorly and to the left is the left mediastinal pleura, deep to which it is crossed by four nerves: the left phrenic, left lower cervical vagal cardiac branch, left superior cervical sympathetic cardiac branch and left vagus, in anteroposterior order. As the left vagus crosses the arch its recurrent laryngeal branch hooks below the vessel left and behind (developmentally caudal to) the ligamentum arteriosum and then ascends on the arch's right. The left superior intercostal vein ascends obliquely forwards on the arch, superficial to the left vagus, deep to the left phrenic nerve (**10.69**). The left lung and pleura separate all these from the thoracic wall. Posterior to the right are the trachea and deep cardiac plexus, the left recurrent laryngeal nerve, oesophagus, thoracic duct and vertebral column. Above, the brachiocephalic, left common carotid and left subclavian arteries arise from its convexity, crossed anteriorly near their origins by the left brachiocephalic vein. Below are the pulmonary bifurcation, left principal bronchus, ligamentum arteriosum (p. 1467), superficial cardiac plexus and left recurrent laryngeal nerve. (Best viewed from the left, the concavity of the aortic arch is the upper curved limit through which structures gain access or exit through the hilum of the left lung.)

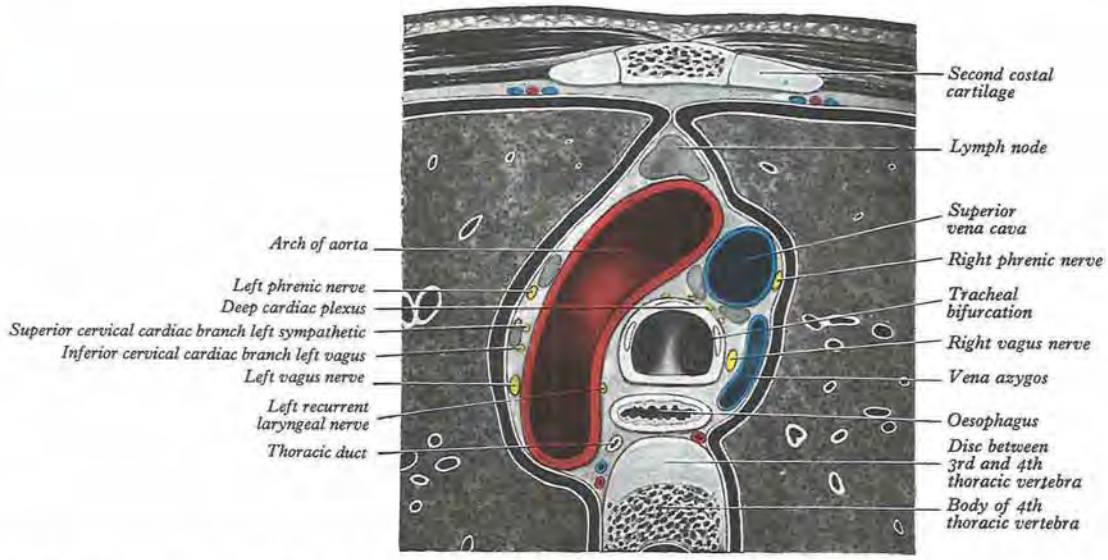
The fetal aortic lumen narrows between the origin of the left subclavian artery and the attachment of the ductus arteriosus, as the aortic isthmus; beyond the ductus arteriosus the vessel presents a fusiform aortic spindle, the junction of the two parts being marked inferiorly by an indentation; these features persist variably in adults.



10.68 Transverse section through the mediastinum at the level of the lower part of the body of the fourth thoracic vertebra, viewed from above. The deep cardiac plexus of nerves is omitted.



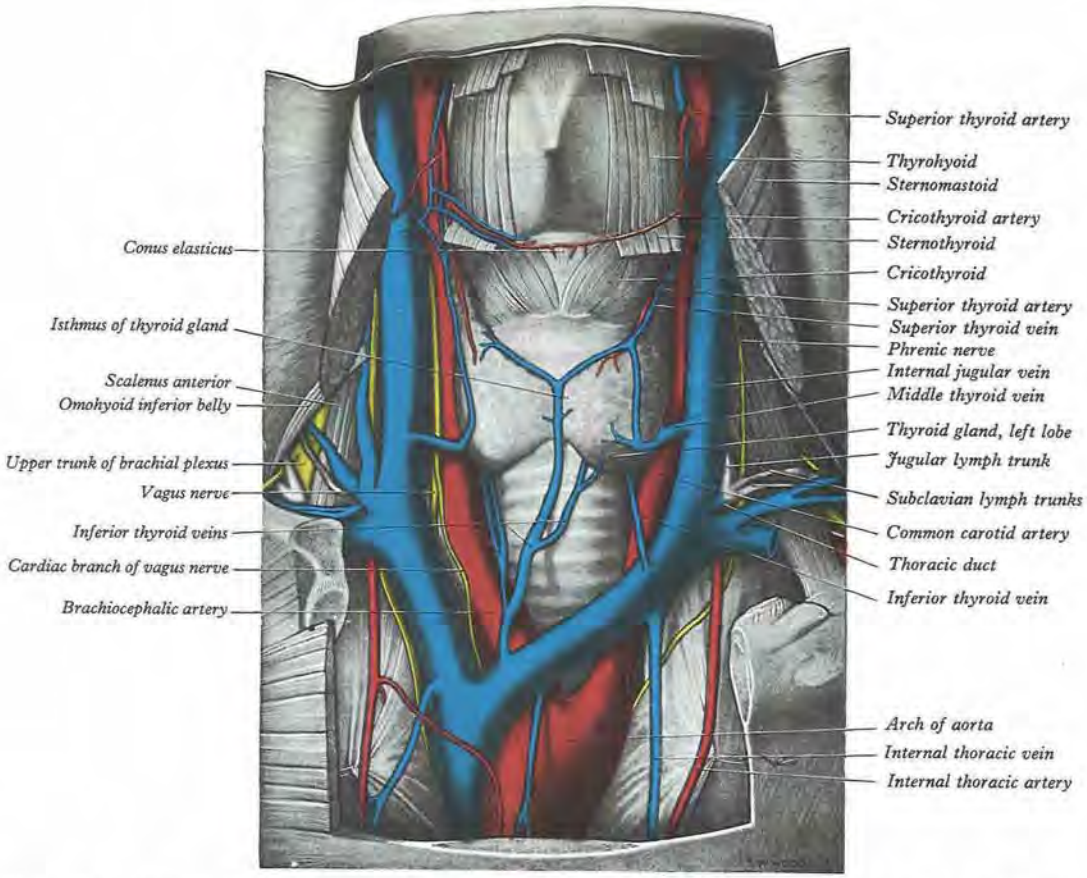
10.69 Dissection to display the heart, great vessels and lungs in situ. The sternum and the sternal ends of the costal cartilages, together with the parietal pleura on each side, have been excised and the mediastinal pleura and parietal layer of the pericardium over the sternocostal surface of the heart have been removed. The lungs have been displaced to expose the heart and the epicardium dissected off the heart and the great vessels.



10.70 Transverse section through the mediastinum at the level of the upper part of the body of the fourth thoracic vertebra, viewed from above.

Variations

The summit of the arch is usually about 2.5 cm below the superior sternal border but may diverge from this. In the infant it is closer to the upper border of the sternum; the same is often the case in old age, because of the dilatation of the vessel. Sometimes the aorta curves over the right pulmonary hilum descending right of the vertebral column, a condition normal in birds; there is usually transposition of thoracic and abdominal viscera. Less often, after arching over the right hilum, it passes behind the oesophagus to its usual position; this is not accompanied by visceral transposition.



10.71 Dissection of the lower part of the front of the neck and of the superior mediastinum. The manubrium sterni and the sternal ends of the clavicles and the first costal cartilages have been removed and the pleural sac and lung have been retracted on each side. In this specimen each superior thyroid artery arose from the common carotid artery.

The aorta may divide, as in some quadrupeds, into ascending and descending trunks, the former dividing into three branches to supply the head and upper limbs. Sometimes it divides near its origin, the two branches soon reuniting; the oesophagus and trachea usually pass through the interval between them; this is the normal condition in reptilia and is due to the persistence of a part of the right dorsal aorta which usually disappears (p. 312).

Radiological appearances

The shadow of the arch is easily identified in anteroposterior radiographs (**10**.48, 49) and its left profile is sometimes called the 'aortic knuckle'. The arch may also be visible in left anterior oblique views enclosing a pale space, 'the aortic window', in which shadows of the pulmonary trunk and its left branch may be visible.

Branches (10.69, 71)

Three branches spring from the vessel's convex aspect: the brachiocephalic trunk, left common carotid and left subclavian arteries (**10**.69, 71). They may branch from the beginning of the arch or the upper part of the ascending aorta; the distance between these origins varies, the most frequent being approximation of the left common carotid artery to the brachiocephalic trunk (Wright 1969). Primary branches may be reduced to one, more commonly two, the left common carotid arising from the brachiocephalic trunk (7%), or (more rarely) the left common carotid and subclavian arteries arising from a left brachiocephalic or right common carotid and subclavian arising separately, in which case the latter more often branches from the left end of the arch and passes behind the oesophagus (p. 314). The left vertebral artery may arise between the left common carotid and the subclavian. Very rarely, external and internal carotid arteries arise separately, the common carotid being absent on one or both sides; or both carotids and one or both vertebrals may be separate branches. When a 'right aorta' occurs, the arrangement of its three branches is reversed. The common carotids may have a single trunk, the subclavians separate, the right arising from the left end of the arch. Other arteries may branch from it, most commonly one or both bronchial arteries and the arteria thyroidea ima.

An analysis of variation in branches from 1000 aortic arches (Anson 1963) showed in 65% the usual pattern; in 27% a left common carotid shared the brachiocephalic trunk (contrast percentage quoted above); in 2.5% the four large arteries branched separately. The remaining 5% showed a great variety of patterns, the commonest (1.2%) being symmetrical right and left brachiocephalic trunks.

BRACHIOCEPHALIC ARTERY

The brachiocephalic (innominate) artery, the largest branch of the aortic arch, is from 4–5 cm in length (**10**.66, 71, 72), arising from the arch's convexity posterior to the centre of the manubrium sterni; it ascends posterolaterally to the right, at first anterior to the trachea, then on its right. Level with the right sternoclavicular joint's upper border it forks into the right common carotid and subclavian arteries.

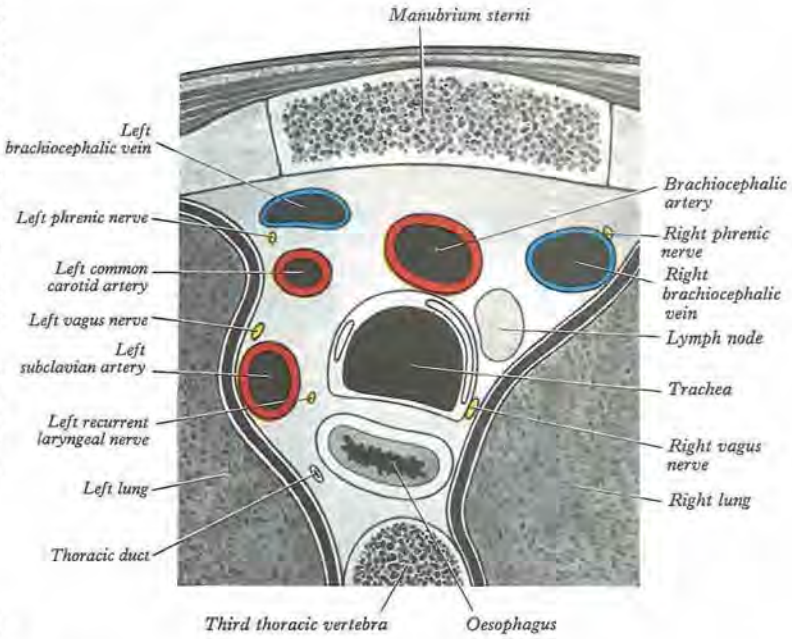
Relations

Anterior are sternohyoid and sternothyroid, the remains of the thymus, left brachiocephalic and right inferior thyroid veins, crossing its root, and sometimes the right vagal cardiac branches, all separating it from the manubrium. Posterior are the trachea below, right pleura above, where the right vagus is posterolateral before passing lateral to the trachea; right lateral are the right brachiocephalic vein, the upper part of the superior vena cava and pleura; left lateral are the thymic remains, the origin of the left common carotid artery, the inferior thyroid veins and the trachea at a higher level.

Branches

The brachiocephalic artery usually has only terminal branches but occasionally an arteria thyroidea ima arises from it, sometimes a thymic or bronchial branch.

Arteria thyroidea ima, small and inconstant, ascends on the trachea to the thyroid isthmus, in which it ends. It may arise from the aorta, right common carotid, subclavian or internal thoracic arteries.



10.72 Transverse section through the superior mediastinum at the level of the body of the third thoracic vertebra, viewed from above.

CAROTID SYSTEM OF ARTERIES

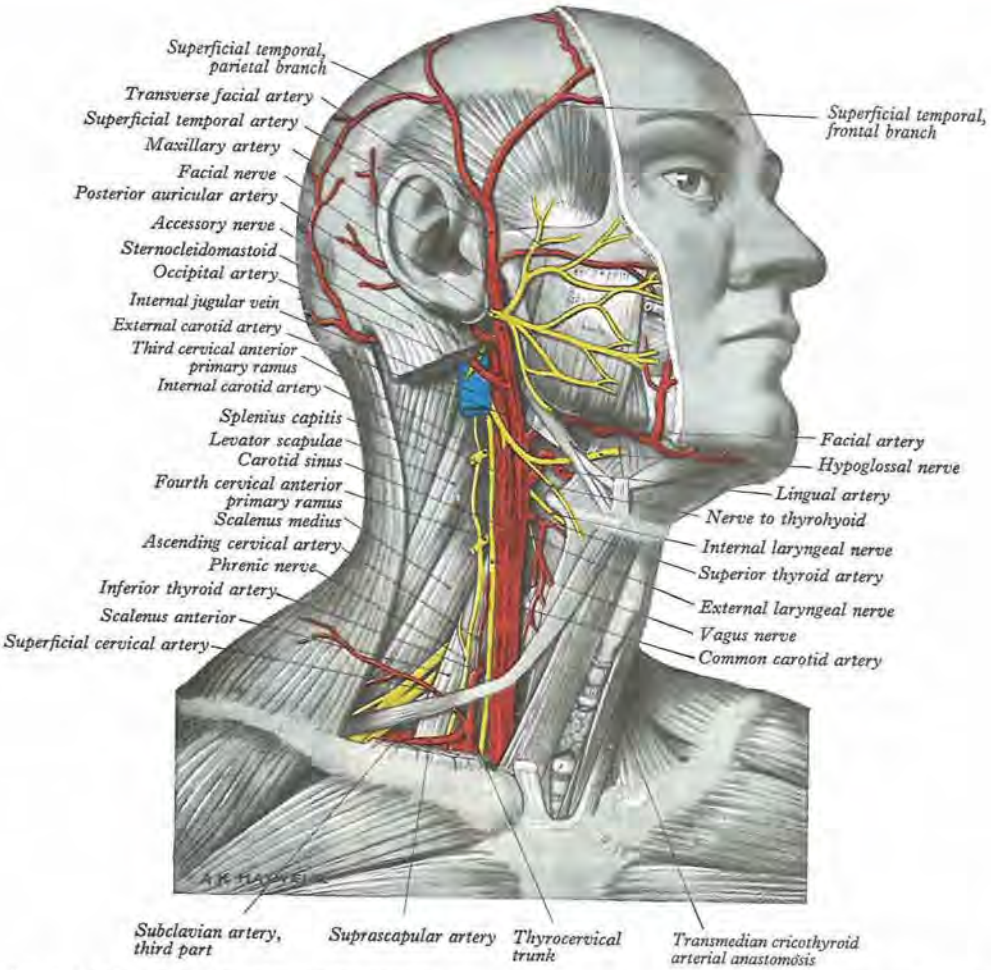
The common carotid artery is a large bilateral vessel supplying head and neck; it ascends to just above the level of the thyroid cartilage's upper border, where it divides into an external carotid, supplying the exterior of the head, face and most of the neck, and an internal carotid, supplying the cranial and orbital contents.

The common and internal carotid arteries, with veins and nerves accompanying them, lie in a cleft bounded posteriorly by cervical transverse processes and attached muscles, medially by the trachea, oesophagus, thyroid gland, larynx and pharyngeal constrictors, anterolaterally by the sternocleidomastoid with, at different levels, omohyoid, sternohyoid, sternothyroid, digastric and stylohyoid muscles.

COMMON CAROTID ARTERIES

The right and left carotid arteries differ in length and origin. The **right** carotid, exclusively cervical, originates from the brachiocephalic trunk behind the right sternoclavicular joint. The **left** carotid originates directly from the aortic arch immediately posterolateral to the brachiocephalic trunk and therefore has both thoracic and cervical parts.

Thoracic part of the left common carotid artery (10.71, 72). This part ascends until level with the left sternoclavicular joint,



10.73 Dissection of the right side of the neck, showing the carotid and subclavian arteries and their branches. The parotid and submandibular glands have been removed together with the lower part of the internal jugular vein, most of the sternocleidomastoid and the upper parts of the stylohyoid and posterior belly of the digastric.

where it enters the neck. It is 20–25 mm long and it lies at first in front of the trachea, then it inclines to the left.

Relations. **Anterior** are the sternohyoid and sternothyroid, the anterior parts of the left pleura and lung, the left brachiocephalic vein and the thymic remnants, separating it from the manubrium; posterior are the trachea, left subclavian artery, left border of the oesophagus, left recurrent laryngeal nerve and thoracic duct. To the **right** are (below) the brachiocephalic trunk and (above) the trachea, inferior thyroid veins and thymic remains; to the **left** are the left vagus and phrenic nerves, left pleura and lung.

Cervical part of both common carotid arteries. Following a similar course (**10**.71–74), it ascends, diverging laterally from behind the sternoclavicular joint to the thyroid cartilage's upper border, where it divides into external and internal carotid arteries (**10**.73, 75). At its division the vessel has a dilatation, the *carotid sinus*, usually involving or restricted to the beginning of the internal carotid; the tunica media is thinner here and the tunica adventitia, relatively thick, contains many receptor endings of the glossopharyngeal nerve (p. 1250). The sinus is responsive to changes in arterial blood pressure, leading to reflex haemodynamic modification. Its position on the main artery of the brain accounts for its role as a baroreceptor in control of intracranial pressure. The *carotid body*, behind the common carotid bifurcation, a small, reddish-brown structure, is a 'chemoreceptor'. (See Adams 1958 for a comparative account and p. 971 for modern views on its ultrastructure and function.)

In the lower neck the common carotids are separated by a narrow gap into which projects the trachea; above this the thyroid gland, larynx and pharynx project between them. Each is contained in a carotid sheath (p. 804), continuous with the deep cervical fascia and of loose texture, though that actually around the artery is denser. This sheath encloses also the internal jugular vein and vagus nerve; the vein lies lateral to the artery, the nerve between them and posterior to both.

Relations. The artery is crossed **anterolaterally**, level with the cricoid cartilage, by the intermediate tendon (sometimes the superior belly) of the omohyoid. Below this muscle it is sited deeply, covered by skin, superficial fascia, platysma, deep cervical fascia, the sternocleidomastoid, sternohyoid and sternothyroid. Above the omohyoid it is more superficial, covered merely by skin, superficial fascia, platysma, deep cervical fascia and the medial margin of sternocleidomastoid and is crossed obliquely from its medial to lateral side by the sternocleidomastoid branch of the superior thyroid artery. In front of, or embedded in, the carotid sheath is the superior root of the ansa cervicalis, joined by its inferior root from the second and third cervical spinal nerves and crossing the vessel obliquely. The superior thyroid vein usually crosses near the artery's end, the middle thyroid vein a little below cricoid level; the anterior jugular vein crosses it above the clavicle, separated by sternohyoid and sternothyroid. **Posterior** are the fourth to sixth cervical transverse processes, and attached to them the longus colli and longus capitis and tendinous slips of scalenus anterior; the sympathetic trunk and ascending cervical artery are between the common carotid artery and the muscles. Below the level of the sixth cervical vertebra the artery is in an angle between the scalenus anterior and longus colli, anterior to the vertebral vessels, inferior thyroid and subclavian arteries, sympathetic trunk and, on the left, thoracic duct. **Medial** are the oesophagus, trachea, inferior thyroid artery and recurrent laryngeal nerve and, at a higher level, the larynx and pharynx; the

thyroid gland overlaps it anteromedially. **Lateral** is the internal jugular vein, which in the lower neck is also anterior to the artery; posterolaterally in the angle between artery and vein is the vagus nerve.

On the right, low in the neck, the recurrent laryngeal nerve crosses obliquely behind the artery; the right internal jugular vein diverges from it below but the left vein approaches and often overlaps its artery.

Variations

In about 12% the right common carotid artery arises above the level of the sternoclavicular joint or it may be a separate branch from the aorta; again it may arise with its fellow. The left common carotid artery varies in origin more than the right; it may arise with the brachiocephalic (see also p. 1513). Division of the common carotid may occur higher, near the level of the hyoid bone, more rarely at a lower level alongside the larynx. Very rarely it ascends without division, either the external or internal carotid being absent. Rarely, also, it is replaced by separate external and internal carotid arteries arising directly from the aorta, on one side or bilaterally.

The common carotid artery usually has no branches but the vertebral, superior thyroid (**10.71**) or its laryngeal branch, ascending pharyngeal, inferior thyroid or occipital may be branches of it.

EXTERNAL CAROTID ARTERY

This artery (**10.73–75**) begins lateral to the thyroid cartilage's upper border, level with the disc between the third and fourth cervical vertebrae. A little curved, and with a gentle spiral, it first ascends slightly forwards and then inclines backwards and a little laterally, to pass midway between the mastoid tip and the mandibular angle where, in the substance of the parotid gland behind the mandible's neck, it divides into the superficial temporal and maxillary arteries. It diminishes rapidly in calibre due to its many large branches. In children it is smaller than the internal carotid but in adults the two are of almost equal size. At its origin, it is in the carotid triangle (p. 1521) and lies anteromedial to the internal carotid but becomes anterior, then lateral to this as it ascends. At mandibular levels the styloid process and its attached structures intervene between the vessels, the internal carotid being deep and the external carotid superficial to the styloid. A finger tip placed at the carotid triangle perceives a powerful arterial pulsation: beneath the finger lie the termination of the common carotid, the origins of external and internal carotids and the stems of the external carotid's initial branches.

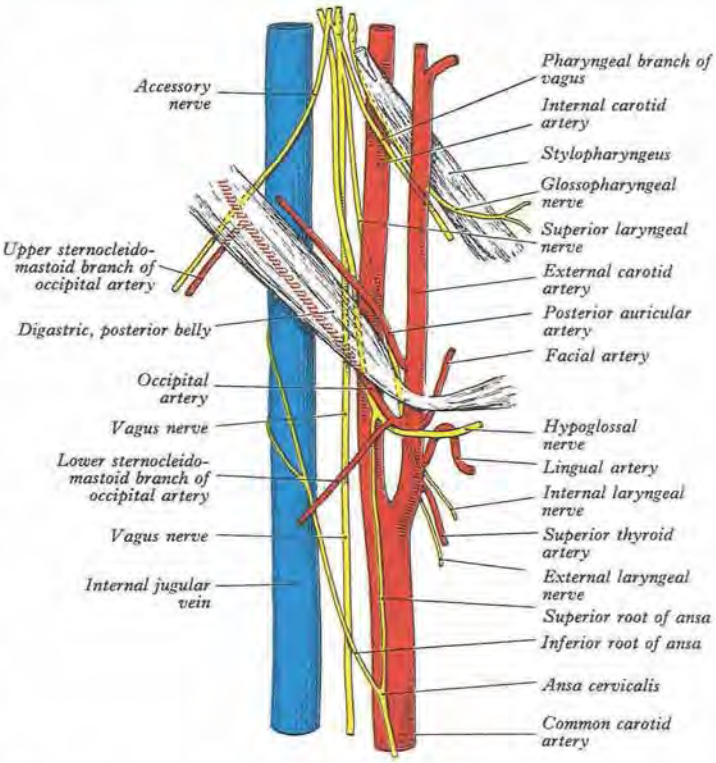
Relations. Superficial to the artery in the carotid triangle are: the skin, superficial fascia, the loop between the facial nerve's cervical branch and the transverse cutaneous nerve of the neck, deep fascia and the anterior margin of sternocleidomastoid; it is crossed by the hypoglossal nerve and its vena comitans and by the lingual (common), facial and sometimes the superior thyroid veins. Leaving the triangle it is crossed by the posterior belly of the digastric and stylohyoid and ascends between this muscle and the posteromedial surface of the parotid gland, which it enters, lying medial to the facial nerve and the junction of the superficial temporal and maxillary veins. **Medial** to the artery are at first the pharyngeal wall, superior laryngeal nerve and ascending pharyngeal artery; at a higher level the internal carotid artery is separated from the external by the styloid process, styloglossus and stylopharyngeus, glossopharyngeal nerve, pharyngeal branch of vagus nerve and part of the parotid gland (**10.74**). The relation of the artery to the parotid gland is controversial, many clinicians asserting that it is often medial to it rather than in it. It seems that both relations occur at about equal frequency (Guffarth & Graumann 1975).

Branches (**10.73, 74, 77**). These are:

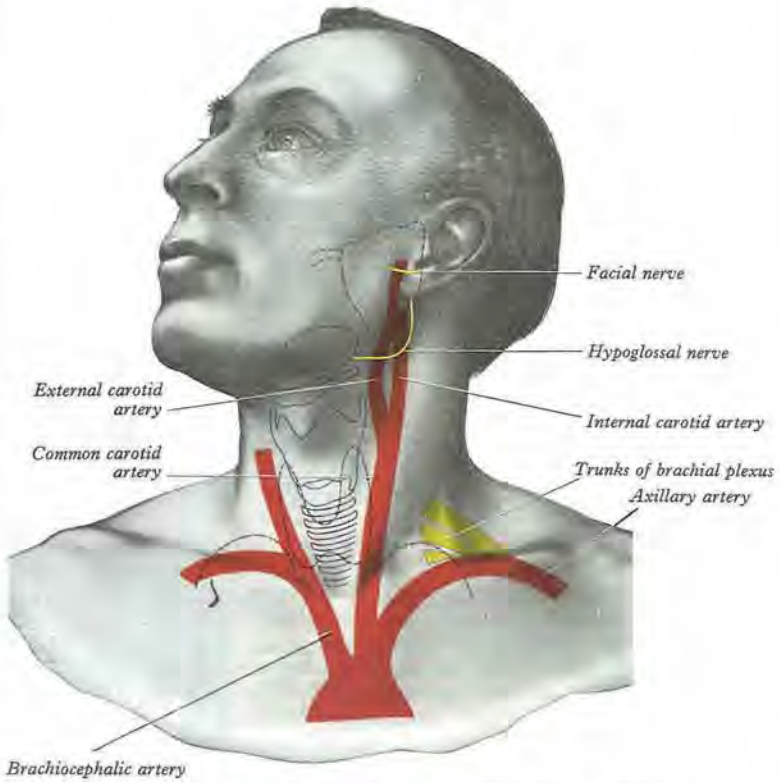
- Superior thyroid
- Ascending pharyngeal
- Lingual
- Facial
- Occipital
- Posterior auricular
- Superficial temporal
- Maxillary.

SUPERIOR THYROID ARTERY (10.73)

This arises from the front of the external carotid artery just below



10.74 The structures crossing the internal jugular vein and carotid arteries and those intervening between the external and internal carotid arteries.



10.75 The surface projection of some of the larger structures in the face and neck. Note that the parotid gland and duct, and submandibular and thyroid glands and the apices of the lungs are shown as interrupted outlines; the hyoid bone and the thyroid, cricoid and tracheal cartilages are indicated by continuous outlines.

the level of the greater cornu of the hyoid, dividing into terminal branches at the apex of the thyroid lobe, but it may issue from the common carotid (**10.71**).

Relations. From an origin under the sternocleidomastoid it descends forwards in the carotid triangle along the lateral border of the thyrohyoid, covered by skin, platysma and fasciae and then deep to the omohyoid, sternohyoid and sternothyroid. Medial are the constrictor pharyngis inferior and external laryngeal nerve; the nerve is often posteromedial.

Branches. The artery supplies the adjacent muscles and the thyroid gland; it anastomoses with its fellow and the inferior thyroid arteries. Glandular branches are anterior, along the medial side of the upper pole of the lateral lobe, supplying mainly the anterior surface, a branch crossing above the isthmus to anastomose with its fellow; and posterior descending on the posterior border, supplying the medial and lateral surfaces and anastomosing with the inferior thyroid artery. Sometimes a lateral branch supplies the lateral surface. The artery also has named branches: infrahyoid, superior laryngeal, sternocleidomastoid and cricothyroid.

Infrahyoid artery. This is small, runs along the lower border of the hyoid deep to thyrohyoid and anastomoses with its fellow. It can be replaced by two or more branches.

Sternocleidomastoid artery. Frequently arising from the external carotid, it descends laterally across the carotid sheath.

Superior laryngeal artery. Accompanying the internal laryngeal nerve deep to the thyrohyoid, it pierces the lower part of the thyrohyoid membrane, supplies the larynx and anastomoses with its fellow and the inferior laryngeal branch of the inferior thyroid.

Cricothyroid artery. A small artery, it crosses high on the cricothyroid ligament, communicating with its fellow.

ASCENDING PHARYNGEAL ARTERY

This, the smallest branch of the external carotid, is a long, slender vessel, arising posteriorly near the external carotid's origin and ascending between the internal carotid artery and pharynx to the cranial base (**10.84**); it is crossed by the styloglossus and stylopharyngeus, with longus capitis posterior to it; it anastomoses with the facial artery's ascending palatine branch. Its named branches are: pharyngeal, inferior tympanic and meningeal. Numerous small branches supply the longus capiti and longus colli, the sympathetic trunk, hypoglossal, glossopharyngeal and vagus nerves and cervical lymph nodes, anastomosing with branches of the ascending cervical and vertebral arteries.

Pharyngeal arteries. Three or four supply the constrictors and stylopharyngeus. A variable ramus supplies the palate and may replace the facial's ascending palatine branch; it descends forwards between the superior border of the superior constrictor and the levator veli palatini, accompanying the latter to the soft palate; it gives minute branches to the tonsil and one to the auditory tube.

Inferior tympanic artery. A small branch, it traverses the temporal canaliculus for the tympanic branch of the glossopharyngeal nerve to supply the tympanic cavity's medial wall.

Meningeal branches. These small vessels to the nerves, dura mater and adjacent bone enter the cranium through the foramen lacerum, jugular foramen and hypoglossal canal. They supply the nerves in these passages and their surrounding tissues. One of them, the *posterior meningeal artery*, which reaches the cerebellar fossa via the jugular foramen, is usually regarded as the terminal branch of the ascending pharyngeal artery.

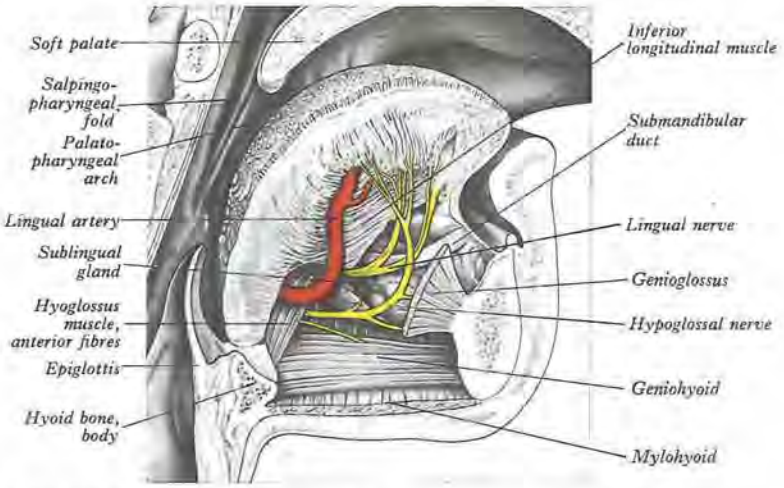
LINGUAL ARTERY

This vessel, bringing the chief supply to the tongue and buccal floor of the mouth, arises anteromedially from the external carotid opposite the tip of the hyoid's greater cornu, between the superior thyroid and facial arteries (**10.73, 74**). Ascending medially at first, it loops down and forwards, passes medial to the posterior border of the hyoglossus and horizontally forwards deep to it and, ascending again almost vertically, courses sinuously forwards on the tongue's inferior surface as far as its tip (**10.76**). Its relation to the hyoglossus naturally divides the vessel into descriptive 'thirds'.

Relations. In its *first part* the lingual artery is in the carotid triangle; superficial to it are the skin, fascia and platysma; the middle pharyngeal constrictor is medial. It ascends a little medially, then descends to the level of the hyoid bone, its loop crossed externally by the hypoglossal nerve. Its *second part* passes along the hyoid's upper border, deep to the hyoglossus, the tendons of digastric and stylohyoid, the lower part of the submandibular gland and posterior part of the mylohyoid; the hyoglossus separates it from the hypoglossal nerve and its vena comitans; here its medial aspect adjoins the middle constrictor and crosses the stylohyoid ligament; it is accompanied by lingual veins (p. 1580). The *third part* is the *arteria profunda linguae*, which turns upward near the anterior border of the hyoglossus, passing forwards close to the inferior lingual surface near the frenulum, accompanied by the lingual nerve. Medial to it is the genioglossus, lateral to it the longitudinalis linguae inferior, below it the lingual mucous membrane. Near the lingual tip it anastomoses with its fellow. Its named branches are suprahyoid, dorsal lingual and sublingual.

The lingual artery often arises with the facial or, less often, with the superior thyroid artery. It may be replaced by a ramus of the maxillary artery.

Suprahyoid artery. This is very small and runs along the hyoid's upper border to anastomose with the contralateral artery.



10.76 Dissection of the left half of the tongue from the medial side, exposing the end of the second part and the beginning of the third part of the left lingual artery and adjoining structures, in an edentulous subject.

Dorsal lingual arteries. Usually two or three small vessels, these arise medial to the hyoglossus, and ascend to the posterior part of the lingual dorsum to supply its mucous membrane, palatoglossal arch, tonsil, soft palate and epiglottis; they anastomose with the opposite vessels.

Sublingual artery. Arising at the anterior margin of hyoglossus, it goes forward between the genioglossus and mylohyoid to the sublingual gland, supplying this, the mylohyoid and the buccal and gingival mucous membranes. One branch pierces the mylohyoid and joins the submental branches of the facial artery; another courses through the mandibular gingiva to anastomose with its fellow. From this anastomosis issues a single artery which enters the lingual foramen of the mandible, situated in the midline on the posterior aspect of the symphysis, immediately above the genial tuberculus (McDonnell et al 1994).

FACIAL ARTERY

This artery (also known as *external maxillary*) arises anteriorly from the external carotid in the carotid triangle above the lingual artery and immediately above the greater cornu of the hyoid bone (**10.77**, 84). Medial to the mandibular ramus it arches upwards and grooves the posterior aspect of the submandibular gland; it then turns down again between the gland and the medial pterygoid. Reaching the surface of the mandible it curves round its inferior border, anterior to the masseter, to enter the face. Here it ascends forwards across the mandible and buccinator to traverse a cleft in the modiolus (p. 796) near the buccal angle. It then ascends the side of the nose and ends at the medial palpebral commissure, supplying the lacrimal sac and joining the dorsal nasal branch of the ophthalmic artery. The artery is very sinuous throughout: in the neck perhaps to adapt to the movements of the pharynx during deglutition and on the face to movements of the mandible, lips and cheeks. Distal to its superior branch it is termed the *angular artery*. Facial artery pulsation is most palpable where it crosses the mandibular base and, between thumb and finger, near the buccal angle.

Relations. In the neck, at its origin, the artery is superficial, covered by the skin, platysma and fasciae and often crossed by the hypoglossal nerve. It runs up and forwards, deep to the digastric and the stylohyoid and posterior part of the submandibular gland. At first on the middle pharyngeal constrictor, it may reach the lateral surface of the styloglossus, separated there from the tonsil only by this muscle and the lingual fibres of the superior constrictor. Thence it descends to the lower border of the mandible in a lateral groove on the submandibular gland. In the face, where, as noted, its pulse can be felt as it crosses the mandible, it is superficial and at first just beneath the platysma. It is covered by skin, the fat of the cheek and near the buccal angle by superficial modiolar muscles (p. 796). Deep to it are the buccinator and levator anguli oris; it may pass over or through the levator labii superioris. Terminally it is embedded in the levator labii superioris alaeque nasi. The facial vein is posterior, in a more direct course across the face; at the anterior border of the masseter the two are in contact; in the neck the vein is superficial. Branches of the facial nerve cross forwards over the artery, which supplies the muscles and tissues of the face, submandibular gland, tonsil and soft palate. Its branches are cervical and facial.

Cervical branches

Ascending palatine artery (**10.84**). Starting near the facial's origin, it ascends between the styloglossus and stylopharyngeus to the side of the pharynx, along which it ascends between the superior constrictor and the medial pterygoid towards the cranial base. Near the levator veli palatini it bifurcates: one branch follows this muscle, winds over the upper border of the superior constrictor, supplies the soft palate and anastomoses with its fellow and the greater palatine branch of the maxillary artery; the other branch pierces the superior constrictor to supply the tonsil and pharyngotympanic tube, joining with tonsillar and ascending pharyngeal arteries.

Tonsillar artery. The main supply to the tonsil, it sometimes arises from the ascending palatine, though is usually separate; it ascends between the medial pterygoid and styloglossus and at the latter's upper border it perforates the superior constrictor and ramifies in the tonsil and posterior lingual musculature.

Glandular branches. Three or four large vessels, they supply the submandibular salivary gland and lymph nodes, adjacent muscles and skin.

Submental artery. The largest cervical branch, it arises as the facial separates from the submandibular gland, turning forwards on the mylohyoid (**10.77**) below the mandible. It supplies the surrounding muscles and anastomoses with a sublingual branch of the lingual and mylohyoid branch of the inferior alveolar arteries; at the chin it ascends the mandible, dividing into superficial and deep branches which anastomose with the inferior labial and mental arteries, supplying the chin and lower lip.

Facial branches

Inferior labial artery (**10.77**). Arising near the buccal angle, it passes up and forwards under the depressor anguli oris, penetrates the orbicularis oris and runs sinuously near the lower lip's margin between the muscle and the mucous membrane. It supplies the inferior labial glands, mucous membrane and muscles, anastomosing with its fellow and the mental branch of the inferior alveolar artery.

Superior labial artery (**10.77**). Larger and more tortuous than the inferior, it has a similar course along the superior labial margin between the mucous membrane and the orbicularis oris; it anastomoses with its fellow, supplying the upper lip, a septal branch, which ramifies antero-inferiorly in the nasal septum, and an alar branch.

Lateral nasal artery (**10.77**). Branching from the facial as it ascends the side of the nose, it supplies the nasal ala and dorsum, anastomosing with its fellow, the septal and alar branches of the superior labial, dorsal nasal ramus of the ophthalmic and infraorbital branch of the maxillary artery. It may be replaced by several small branches or arise from the superior labial, diverging from its septal branch (as in **10.77**).

Facial anastomoses. These are numerous not only with corresponding contralateral branches but also: **in the neck**, with the sublingual branch of the lingual, ascending pharyngeal and palatine branch of the maxillary; **on the face**, with the mental branch of the inferior alveolar, transverse facial branch of the superficial temporal, infraorbital branch of the maxillary and dorsal nasal branch of the ophthalmic. The anastomoses in the lips are by main trunks, an important fact in labial injuries.

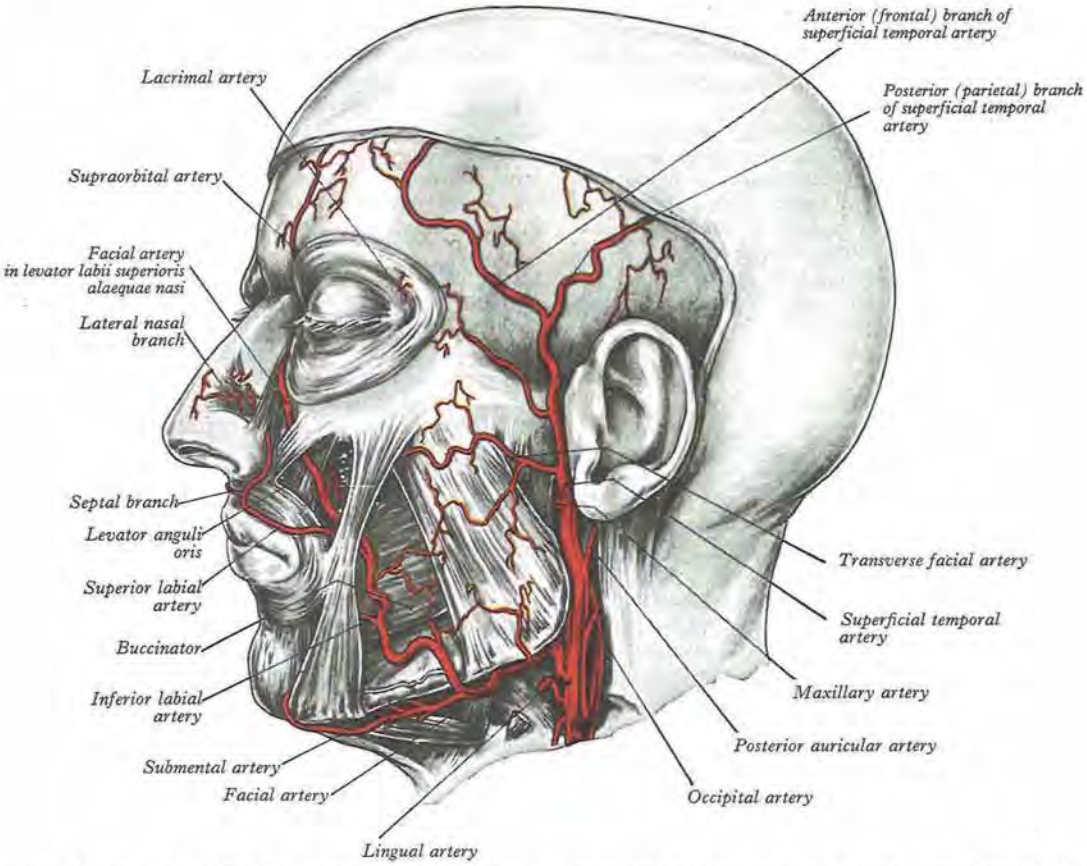
Variations. The facial artery may arise with the lingual, as a linguo-facial trunk. It varies in size and supply to the face: it may end as the submental artery and often extends only to the buccal angle. The deficiency is then filled by branches of neighbouring arteries. In 110 human fetuses a common linguo-facial trunk occurred in 43%; in 42% the facial did not reach the medial orbital angle, ending as a superior (20%) or inferior (22%) labial artery (Kozielec & Józwa 1977).

OCCIPITAL ARTERY

This artery arises posteriorly from the external carotid, about 2 cm from its origin; at first medial to the posterior belly of the digastric, it ends posteriorly in the scalp (**10.78**).

Course and relations. At its origin, the artery is crossed superficially by the hypoglossal nerve, winding round it from behind. It goes back, up and deep to the posterior digastric belly, crossing the internal carotid, internal jugular vein, hypoglossal, vagal and accessory nerves (**10.78**). Between the transverse process of the atlas and temporal mastoid process it reaches the lateral border of the rectus capitis lateralis. It then runs in the temporal bone's occipital groove, medial to the mastoid process and attachments of the sternocleidomastoid, splenius capitis, longissimus capitis and digastric, lying successively on the rectus capitis lateralis, obliquus superior and semispinalis capitis. Finally, accompanied by the greater occipital nerve, it turns up to pierce the fascia connecting the cranial attachments of the trapezius and sternocleidomastoid, ascends tortuously in the dense superficial fascia of the scalp and divides into many branches. Its branches are as follows.

Sternocleidomastoid branches. Two branches are usual, the **lower** arising near the origin of the occipital but sometimes directly from the external carotid. It descends backwards over the hypoglossal nerve and internal jugular vein, enters the sternocleidomastoid, and anastomoses with the sternocleidomastoid branch of the superior thyroid. The **upper** branch arises as the occipital crosses the accessory



10.77 The arteries of the left side of the face and their main branches. Many of the postmodiolar muscles and part of the modiolus (through which the facial artery passes) have been resected. Note the less usual origin of lateral nasal branch in this specimen.

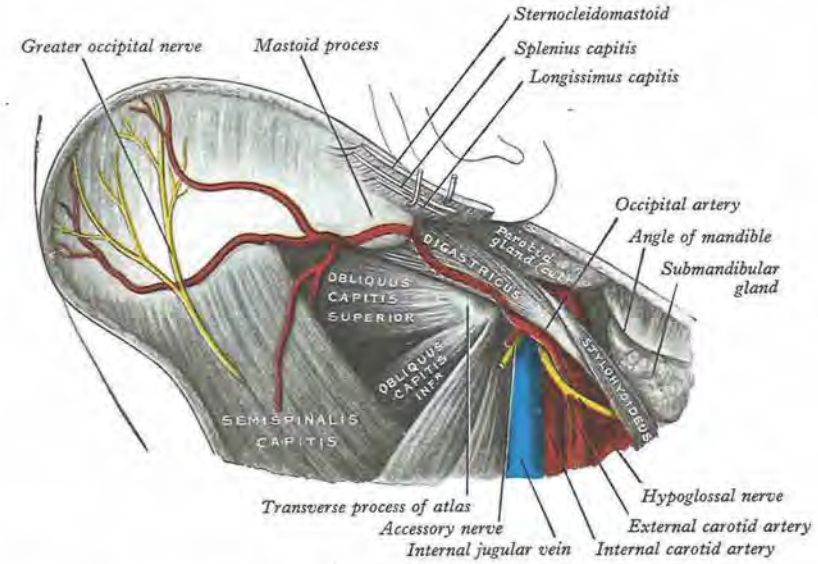
nerve, running down and backwards superficial to the internal jugular vein. It enters the deep surface of the sternocleidomastoid with the accessory nerve.

Mastoid artery. Small in size and sometimes absent, it enters the cranial cavity via the mastoid foramen, supplying the mastoid air cells and dura mater.

Stylomastoid artery. This branches from the occipital in two-thirds of subjects (p. 1520).

Auricular branch. It supplies the medial aspect of the auricle, anastomosing with the posterior auricular artery.

Muscular branches. These supply the digastric, stylohyoid, splenius, longissimus capitis and neighbouring muscles.



10.78 Dissection to show the course of the occipital artery. The upper and lower sternocleidomastoid branches of the artery have been transected and are not labelled.

Descending branch (10.78). This arises where the occipital adjoins the obliquus superior, dividing into superficial and deep branches. The superficial ramus passes deep to the splenius, anastomosing with the superficial branch of the transverse cervical artery; the deep ramus descends between the semispinales capitis et cervicis, anastomosing with both the vertebral and the deep cervical artery (from the costocervical trunk) (10.84).

Meningeal branches. They enter the cranium via the jugular foramen and condylar canal to supply the dura mater and bone of the posterior cranial fossa and the caudal four cranial nerves.

Occipital branches. Tortuous terminal branches distributed to the scalp as far as the vertex, they run between the skin and the occipital belly of the occipitofrontalis, anastomosing with the opposite occipital, posterior auricular and temporal arteries and supplying the occipital belly of the occipitofrontalis, skin and pericranium. There may be a meningeal lateral branch, traversing the parietal foramen.

POSTERIOR AURICULAR ARTERY

This small vessel branches posteriorly from the external carotid just above the digastric and stylohyoid (10.77). It ascends between the parotid gland and the styloid process to the groove between the auricular cartilage and mastoid process, dividing into auricular and occipital branches. As well as supplying the digastric, stylohyoid, sternocleidomastoid, and parotid gland, the posterior auricular artery has three named branches.

Stylomastoid artery. An indirect branch of the posterior auricular in about a third of subjects (Blunt 1954), it enters the stylomastoid foramen to supply the facial nerve, tympanic cavity, mastoid antrum and air cells, and semicircular canals. In the young its posterior tympanic ramus forms a circular anastomosis with the anterior tympanic artery (see below).

Auricular branch. Ascending deep to auricularis posterior, it ramifies on the cranial aspect of the auricle; some branches pierce this, others curve round it to supply its lateral aspect.

Occipital branch. It passes laterally across the mastoid process, turning back over the sternocleidomastoid to supply the occipital belly of the occipitofrontalis and scalp above and behind the ear; it anastomoses with the occipital artery.

SUPERFICIAL TEMPORAL ARTERY

This, the smaller terminal branch of the external carotid, begins in the parotid gland behind the mandible's neck, crosses the posterior root of the zygomatic process of the temporal bone and about 5 cm above this divides into anterior and posterior branches (10.73).

Relations. As it crosses the zygoma it is covered by the auricularis anterior; in the parotid gland temporal and zygomatic branches of the facial nerve cross it; in the scalp it is accompanied by corresponding veins, and just posterior to it lies the auriculotemporal nerve.

Branches. The superficial temporal supplies the parotid gland, temporomandibular joint and masseter and it also has several named branches.

Transverse facial artery (10.77). Arising before the superficial temporal emerges from the parotid gland, it traverses the gland, crosses the masseter between the parotid duct and the zygomatic arch, accompanied by one or two facial nerve branches, and divides into numerous branches supplying the parotid gland and duct, masseter and skin, anastomosing with the facial, masseteric, buccal, lacrimal and infraorbital arteries.

Anterior auricular branches. These are distributed to the lobule and anterior part of the auricle and the external acoustic meatus.

Zygomatico-orbital artery. Sometimes from the middle temporal, it skirts the upper border of the zygomatic arch between two layers of temporal fascia to the lateral orbital angle. It supplies the orbicularis oculi, and anastomoses with the lacrimal and palpebral branches of the ophthalmic artery.

Middle temporal artery. This branches just above the zygomatic arch, perforates the temporal fascia, supplies the temporalis and anastomoses with the deep temporal branches of the maxillary.

Frontal (anterior) branch. Meandering towards the frontal tuberosity, it supplies muscles, skin and pericranium in this region. It anastomoses with its fellow and the supraorbital and supratrochlear arteries.

Parietal (posterior) branch. Larger than the frontal, it curves up and back, superficial to the temporal fascia, anastomosing with its fellow and the posterior auricular and occipital arteries.

Variation

Variation in the superficial temporal artery is largely in the relative sizes of the frontal, parietal and transverse facial branches; the first two may be absent, the transverse facial may replace a shortened facial artery. Variations in fetal material have been described by Kozielec and Józwa (1976).

Clinical anatomy

Crossing the zygomatic process the artery is palpable through skin and fascia and is easily compressed here to control temporal haemorrhage. This vessel and other arteries supplying the scalp from below are well protected by dense tissue. Rarely are all implicated in a scalping injury and its branches anastomose so freely that a partially detached scalp may be replaced with reasonable hope of success as long as one vessel is intact. In craniotomy, incisions should be convex upwards to include the superficial temporal artery in the flap. In carotid angiograms branches of the superficial temporal and middle meningeal arteries are superimposed, but are distinguishable by the straighter course, lack of anastomoses and narrower calibre in the meningeal branches (Dominić-Stošić & Jeličić 1974).

MAXILLARY (INTERNAL MAXILLARY) ARTERY

This, the larger terminal branch of the external carotid, arises behind the mandibular neck, at first embedded in the parotid gland; it then passes medial to the mandibular neck and superficial or deep to the lower head of the lateral pterygoid to reach the pterygopalatine fossa, usually passing between the two heads of the lateral pterygoid (10.79). It has mandibular, pterygoid and pterygopalatine segments, related sequentially to bone, muscle and bone, a useful indication of its branches.

The **first, mandibular, part** is horizontal and passes between the mandible's neck and the sphenomandibular ligament, parallel with and slightly below the auriculotemporal nerve; it crosses the inferior alveolar nerve and skirts the lower border of the lateral pterygoid.

The **second, pterygoid, part** ascends obliquely forwards medial to the temporalis and superficial to the lower head of the lateral pterygoid; it is often deep to the latter, lying between it and branches of the mandibular nerve and it may then project as a lateral loop between the two parts of the lateral pterygoid.

The **third, pterygopalatine, part** passes between the heads of the lateral pterygoid and through the pterygomaxillary fissure into the pterygopalatine fossa, where it is situated anterior to the pterygopalatine ganglion.

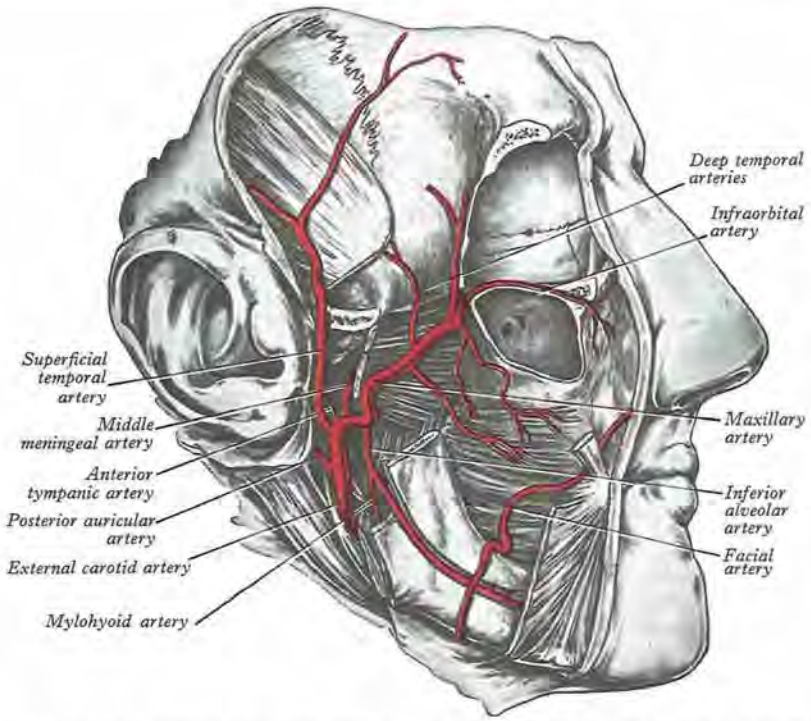
Branches. The artery is distributed to the mandible, maxilla, teeth, muscles of mastication, palate, nose and cranial dura mater. Its branches form three groups, corresponding with its parts.

Branches of the first part (10.79)

Deep auricular artery. Often arising with the anterior tympanic, it ascends in the parotid gland behind the temporomandibular joint, pierces the cartilaginous or osseous wall of the external acoustic meatus and supplies its cuticular lining, the exterior of the tympanic membrane and the joint.

Anterior tympanic artery. Ascending behind the temporomandibular joint, it enters the tympanic cavity through the petrotympanic fissure and ramifies on the interior of the tympanic membrane, forming a vascular circle around it with the posterior tympanic branch of the stylomastoid; it anastomoses with twigs of the artery of the pterygoid canal and caroticotympanic branches of the internal carotid artery in the mucosa of the tympanic cavity.

Middle meningeal artery. Largest of the meningeal arteries, it ascends between the sphenomandibular ligament and lateral pterygoid, passes between the roots of the auriculotemporal nerve and may lie lateral to the tensor veli palatini before entering the cranial cavity through the foramen spinosum. It then runs in an anterolateral groove on the squamous part of the temporal bone, dividing into frontal and parietal branches. The *frontal (anterior) branch*, the



10.79 The right maxillary artery. An extensive dissection has been carried out, involving the removal of the parotid gland, the zygomatic arch, part of the ramus of the mandible, the lateral walls of the orbit and maxillary sinus and the orbital contents.

larger, crosses the greater wing of the sphenoid, reaches a groove or canal in the parietal's sphenoidal angle and divides into branches between the dura mater and cranium, some ascending to the vertex, others to the occipital region. One ascending branch grooves the parietal bone about 15 mm behind the coronal suture, corresponding approximately to the precentral sulcus. The *parietal (posterior) branch* curves back on the squamous temporal bone, reaching the lower border of the parietal anterior to its mastoid angle and dividing to supply the posterior parts of the dura mater and cranium. These branches anastomose with their fellows and with the anterior and posterior meningeal arteries.

In the cranial cavity the artery has the following branches:

- Numerous *ganglionic branches* supply the trigeminal ganglion and roots.
- A *petrosal branch* enters the hiatus for the greater petrosal nerve and supplies the facial nerve, ganglion and tympanic cavity, anastomosing with the stylomastoid artery (p. 1519).
- A *superior tympanic artery* runs in the canal for the tensor tympani, supplying both muscle and the mucosa lining the canal.
- *Temporal branches* traverse minute foramina in the sphenoid's greater wing and anastomose with deep temporal arteries.
- An *anastomotic branch* (p. 1526) enters the orbit lateral in the superior orbital fissure, anastomosing with a recurrent branch of the lacrimal artery; enlargement of this anastomosis explains an occasional origin of the lacrimal from the middle meningeal artery.

Apart from these and a supply to the dura mater, the middle meningeal artery is predominantly periosteal, supplying bone and red bone marrow.

Surface anatomy (**10.79**). The middle meningeal artery enters the skull medial to the zygoma's midpoint, dividing 2 cm above this. From here the frontal branch runs first up and forwards to the pterion and then up and back towards a point midway between the inion and nasion. The parietal branch runs up and back towards the lambda.

Clinical anatomy. The middle meningeal artery may be torn in temporal fractures or by injuries separating the dura mater from the bone, followed by haemorrhage between them. Trephining may be necessary to reduce cerebral compression.

Accessory meningeal artery. This may arise from the maxillary or the middle meningeal. It enters the cranial cavity through the foramen ovale, supplying the trigeminal ganglion, dura mater and bone, but its main distribution is extracranial (Baumel & Beard 1961), principally the medial pterygoid, lateral pterygoid (upper head), tensor veli palatini, sphenoid bone (greater wing and pterygoid processes), mandibular nerve and otic ganglion. It is sometimes replaced by separate small arteries.

Inferior alveolar (dental) artery. Descending posterior to the inferior alveolar nerve, to the mandibular foramen, here it is between bone laterally and the sphenomandibular ligament medially. Before entering the foramen it has a mylohyoid branch, which pierces the sphenomandibular ligament to descend with the mylohyoid nerve in its groove on the mandibular ramus; it ramifies superficially on the muscle and anastomoses with the facial's submental branch. The inferior alveolar artery then traverses the mandibular canal with the inferior alveolar nerve and divides into the incisor and mental branches near the first premolar. The incisor branch continues below the incisor teeth to the midline, where it anastomoses with its fellow. In the canal the arteries supply the mandible, tooth sockets and teeth with branches entering the minute hole at the apex of the root to supply the pulp. The mental branch leaves the mental foramen, supplies the chin and anastomoses with the submental and inferior labial arteries. Near its origin the inferior alveolar artery has a lingual branch, which descends with the lingual nerve to supply the buccal mucous membrane.

Branches of the second part (10.79)

Deep temporal branches. Anterior and posterior, these branches ascend between the temporalis and bone, supplying mainly the former. They anastomose with the middle temporal artery. The anterior connects with the lacrimal by small branches perforating the zygomatic bone and greater wing of the sphenoid.

Pterygoid branches. Irregular in number and origin, these supply the pterygoid muscles.

Masseteric artery. This is small and with the masseteric nerve passes behind the tendon of temporalis through the mandibular incisure (notch) to the deep surface of masseter, in which it anastomoses with the masseteric branches of the facial and transverse facial arteries.

Buccal artery. Running obliquely forwards with the buccal nerve between the medial pterygoid and the attachment of the temporalis

it supplies the external surface of the buccinator (and through it the mucosa), anastomosing with branches of the facial and infraorbital arteries.

Branches of the third part

Posterior superior alveolar (dental) artery. Leaving the maxillary artery as it enters the pterygopalatine fossa, it descends on the maxilla's infratemporal surface. It then divides, some branches entering the alveolar canals to supply molar and premolar teeth and the maxillary sinus, others continuing over the alveolar process to supply the gingivae.

Infraorbital artery. Often arising with the posterior superior alveolar, it enters the orbit posteriorly through the inferior orbital fissure, to run in the infraorbital groove and canal with the infraorbital nerve, both emerging on the face via the infraorbital foramen, deep to the levator labii superioris. In the canal it has:

- *orbital branches*, which supply the rectus inferior, obliquus inferior and lacrimal sac
- *anterior superior alveolar (dental) branches*, which descend via the anterior alveolar canals to supply the upper incisor and canine teeth and the mucous membrane in the maxillary sinus.

On the face some branches ascend to the medial canthus and lacrimal sac, anastomosing with the terminal branches of the facial; others anastomose with a dorsal nasal branch of the ophthalmic artery and some descend between the levator labii superioris and levator anguli oris, anastomosing with the facial, transverse facial and buccal arteries.

The remaining branches arise in the pterygopalatine fossa.

Greater (or descending) palatine artery. This artery and nerve descend in their palatine canal; the artery gives off two or three lesser palatine arteries, transmitted through lesser palatine canals to supply the soft palate and tonsil, anastomosing with the ascending palatine. The main vessel emerges on the palate's oral surface by the greater palatine foramen and runs in a curved groove near the alveolar border of the hard palate to the incisive canal; it ascends this canal and anastomoses with a branch of the sphenopalatine artery. It supplies the gingivae, palatine glands and mucous membrane.

Pharyngeal artery. Very small, runs back through the pharyngeal (palatovaginal) canal with the pharyngeal branch of the pterygopalatine ganglion; it supplies the mucosa of the nasal roof, the nasopharynx, sphenoidal air sinus and auditory tube.

Artery of the pterygoid canal. Frequently from the greater palatine, it passes back in the pterygoid canal with the corresponding nerve, supplying its walls and contents and the mucous membrane of the upper pharynx, pharyngotympanic tube and tympanic cavity.

Relations. The pharyngeal artery is medial, that of the pterygoid canal lateral and the trunk of the maxillary artery passes anterior to the pterygopalatine ganglion.

Sphenopalatine artery. The termination of the maxillary, it traverses the sphenopalatine foramen into the walls of the nasal cavity posterior in the superior meatus. Here its *posterior lateral nasal branches* ramify over the conchae and meatuses, anastomosing with the ethmoidal arteries and nasal branches of the greater palatine, supplying the frontal, maxillary, ethmoidal and sphenoidal sinuses. Crossing anteriorly on the inferior sphenoid surface, the artery ends on the nasal septum as the *posterior septal branches*, which anastomose with the ethmoidal arteries; one branch descends on the vomer to the incisive canal to join the end of the greater palatine artery and septal branch of the superior labial.

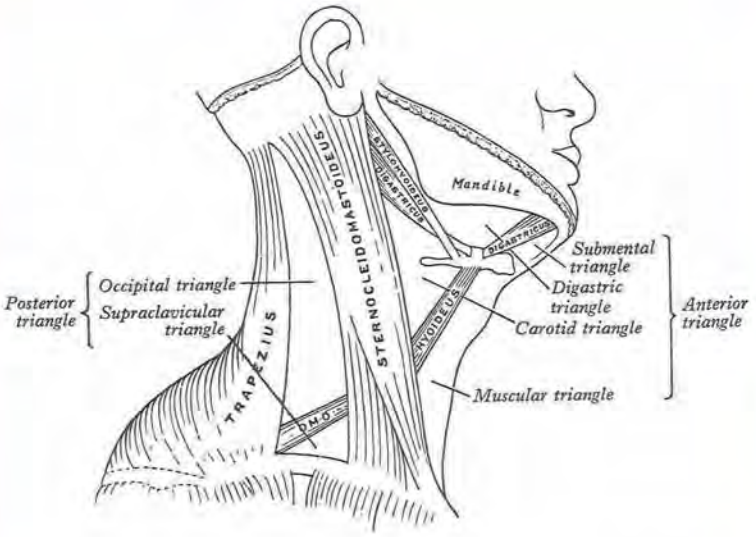
Collateral circulation

Collateral circulation, after interruption of one common carotid, is often established by the connections across the midline between the carotids, intra- and extracranial, and by enlargement of the subclavian branches. Chief extracranial connections are between superior and inferior thyroid arteries, the deep cervical and the descending branch of the occipital; the vertebral artery substitutes for the internal carotid in the cranium. Nevertheless symptoms of cerebral disturbance supervene in about 25% of cases.

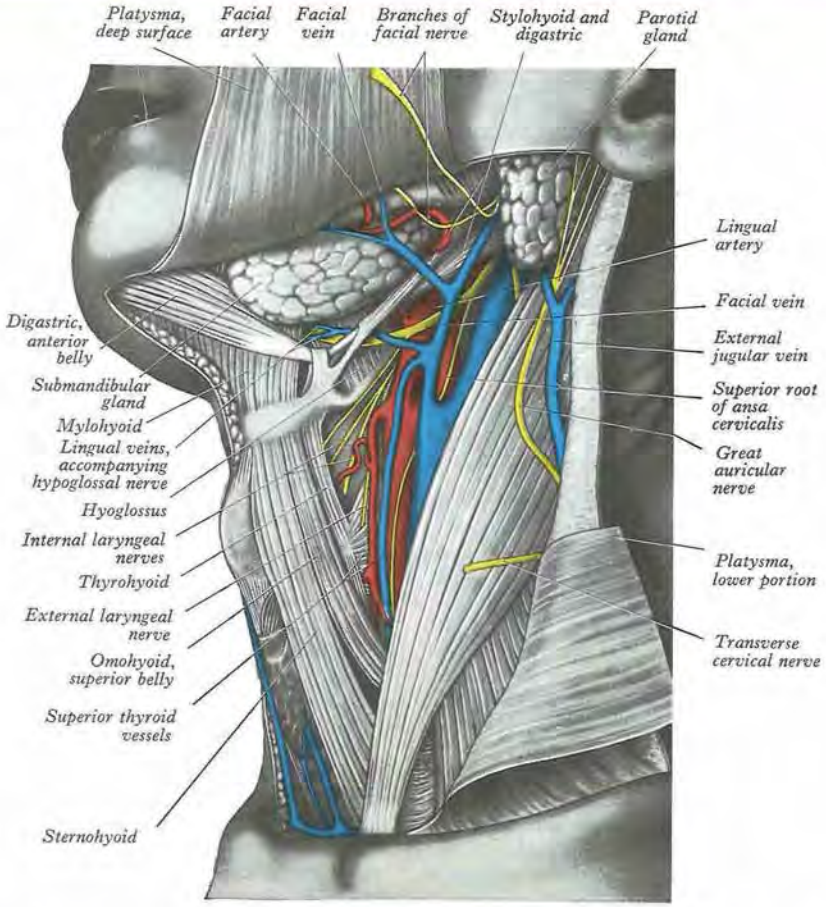
After interruption of the *external* carotid, circulation is maintained by anastomoses between most of its large branches (facial, lingual, superior thyroid, occipital) and their fellows, by their anastomoses with branches of the internal carotid and of the occipital with branches of the subclavian, etc.

Triangles of the neck

Anterolaterally the neck (10.80, 81) presents a somewhat quadrilateral area, limited **above** by the base of the mandible and a line continued from its angle to the mastoid process, **below** by the clavicle's upper border, **in front** by the anterior median line, **behind** by the anterior margin of trapezius. This region is divided by the sternocleidomastoid, ascending obliquely from the sternum and clavicle to the mastoid process and occipital bone. The area anterior to this is the *anterior triangle* and that behind it the *posterior triangle*. While these triangles and their subdivisions are emphasized by some as being purely arbitrary because many major structures (arteries, veins, lymphatics, nerves, some viscera) transgress their boundaries without interruption, nevertheless they have a topographical value in description. However, two further points should be made. Some of their subdivisions are easily identified by inspection and palpation and provide invaluable assistance in surface anatomical and clinical examination (see below). As the neck has a roughly cylindrical form, crossed obliquely by the sternocleidomastoid, the



10.80 The triangles of the right side of the neck: a highly schematic two dimensional representation of what in reality are non-planar trigones distributed over a waisted column. Submandibular would be an alternative name for digastric.



10.81 Dissection of the left anterior triangle. The platysma has been divided transversely; its upper part has been turned upwards on to the face, its lower part turned backwards, exposing the lower part of the sternocleidomastoid. Dominating the centre of the illustration is the carotid triangle, with many of its contents and surrounding structures.

names anterior and posterior are not particularly apt; the triangles are not plane (and coplanar as represented in a two-dimensional diagram such as **10.80**) but both are spiralized regions (trigones) on the surface of the column.

ANTERIOR CERVICAL TRIANGLE

This is bounded anteriorly by the median line, and posteriorly by the anterior margin of the sternocleidomastoid, its base being the inferior mandibular border and its mastoid extension noted above; its apex is at the manubrium. It may be subdivided into muscular, carotid, digastric and submental triangles.

Muscular triangle

The muscular triangle is bounded by the median line from the hyoid bone to the sternum, inferoposteriorly by the anterior margin of the sternocleidomastoid and posterosuperiorly by the superior belly of the omohyoid.

Carotid triangle

The carotid triangle is limited posteriorly by the sternocleidomastoid, anteroinferiorly by the superior belly of the omohyoid and superiorly by the stylohyoid and posterior belly of the digastric; in the living, except the obese, the triangle is usually a small visible triangular depression, sometimes best seen with the head and cervical vertebral column slightly extended and the head contralaterally rotated. Often the latter position is quite unnecessary; judicious oblique lighting (window or lamp) throws the hollow into relief.

It is covered by the skin, superficial fascia, platysma and deep fascia containing branches of facial and cutaneous cervical nerves. The hyoid bone forms its anterior angle and adjacent floor; its position can be located immediately on simple inspection, verified by palpation. Parts of thyrohyoid, hyoglossus and inferior and middle pharyngeal constrictors form its floor. It contains the upper part of the common carotid and its division into external and internal carotid arteries, overlapped by the anterior margin of the sternocleidomastoid; the external carotid is first anteromedial, then anterior to the internal. Branches of the external carotid are also encountered: the superior thyroid runs antero-inferiorly, the lingual anteriorly with its upward loop, the facial anterosuperiorly, the occipital posterosuperiorly and the ascending pharyngeal medial to the internal carotid. Massive arterial pulsation greets the examining finger. The veins correspond to the branches of the external carotid artery: superior thyroid, lingual, facial, ascending pharyngeal and sometimes the occipital, all ending in the internal jugular vein. The hypoglossal nerve crosses both carotid arteries, curving round the origin of the lower sternocleidomastoid branch of the occipital, where the superior root of the ansa cervicalis leaves it, descending anteriorly in the carotid sheath. Medial to the external carotid, below the hyoid bone, is the internal laryngeal nerve and, below this, the external laryngeal. Many structures in this region, such as all or part of the internal jugular vein, associated deep

cervical lymph nodes, vagus nerve, etc., may be variably obscured by the sternocleidomastoid and, pedantically, are thus 'outside the triangle'; much more importantly, their location is obvious during clinical examination.

Digastric triangle

The digastric triangle is bordered above by the base of the mandible (and its projection to the mastoid process), posteroinferiorly by the posterior belly of the digastric and stylohyoid and anteroinferiorly by the anterior belly of digastric. It is covered by the skin, superficial fascia, platysma and deep fascia, in which are branches of facial and transverse cutaneous cervical nerves. Its floor is formed by the mylohyoid and hyoglossus. Its anterior region contains the submandibular gland, superficial to which is the facial vein and deep to it the facial artery, crossing the lower border of the mandible at the anterior edge of the masseter; on the mylohyoid are the submental artery and mylohyoid artery and nerve. Variably related to the submandibular gland are the submandibular lymph nodes (p. 1612). Its posterior region contains the lower part of the parotid gland; the external carotid, passing deep to the stylohyoid, curves above the muscle and overlaps its superficial surface where it ascends deep to the parotid gland to enter it. The external carotid, which is superficial to the internal carotid, crosses it posterolaterally; deeper and separated from the external carotid by styloglossus, stylopharyngeus and the glossopharyngeal nerve, are the internal carotid artery, internal jugular vein and vagus nerve.

Submental triangle

The submental triangle, unpaired, is demarcated by both digastric muscles (anterior bellies); its apex is at the chin, its base the body of the hyoid and its floor the mylohyoid muscles. It contains lymph nodes and small veins uniting to form the anterior jugular.

POSTERIOR CERVICAL TRIANGLE

The posterior triangle is delimited anteriorly by the sternocleidomastoid, posteriorly by the anterior edge of trapezius, inferiorly by the middle third of the clavicle; its apex is between the attachments of the sternocleidomastoid and trapezius to the occiput and is often blunted, the 'triangle' becoming quadrilateral. It is crossed, about 2.5 cm above the clavicle, by the inferior belly of the omohyoid, which divides it into occipital and supraclavicular triangles.

Occipital triangle

The occipital triangle, the upper, larger part of the posterior triangle, has the same borders, except below where its limit is the omohyoid. Its floor is, from above down: splenius capitis, levator scapulae, and scaleni medius and posterior. (Sometimes semispinalis capitis appears at the apex.) It is covered by the skin, superficial and deep fasciae and below by the platysma. The accessory nerve pierces the sternocleidomastoid and crosses on the levator scapulae obliquely down and back to the deep surface of the trapezius; cutaneous and muscular branches of the cervical plexus emerge at the posterior border of the sternocleidomastoid; below, supraclavicular nerves, transverse cervical vessels and the uppermost part of the brachial plexus cross the triangle. Lymph nodes are arranged along the posterior border of the cleidomastoid from the mastoid process to the root of the neck.

Supraclavicular triangle

The supraclavicular triangle, the lower, smaller division, is bounded like the posterior triangle, except above where the omohyoid limits it. It corresponds in the living neck with the lower part of the deep, prominent hollow, the greater supraclavicular fossa (colloquially 'the salt cellar'). Its floor contains the first rib, scalenus medius and the first slip of serratus anterior. Its size varies with the extent of the clavicular attachments of the sternocleidomastoid and trapezius and also the level of the inferior belly of the omohyoid. The triangle is covered by the skin, superficial and deep fasciae and platysma and crossed by the supraclavicular nerves. Just above clavicular level the third part of the subclavian artery curves inferolaterally from the lateral margin of the scalenus anterior, across the first rib to the axilla. The subclavian vein is behind the clavicle and is not usually in the triangle; but it may rise as high as the artery and even accompany it behind scalenus anterior. The brachial plexus is partly above, partly behind the artery and closely related to it. The trunks of the brachial may easily be palpated here, the neck being contralaterally flexed and the examining finger drawn across the trunks at right angles to their length. With the musculature relaxed, pulsation of the subclavian artery may be felt or the arterial flow controlled by retroclavicular compression against the first rib. The suprascapular vessels pass transversely behind the clavicle; at a higher level are the transverse cervical artery and vein. The external jugular vein descends behind the posterior border of the sternocleidomastoid to end in the subclavian vein; it receives the transverse cervical and suprascapular veins, which form a plexus in front of the third part of the subclavian artery; occasionally it is joined by a small vein crossing the clavicle anteriorly from the cephalic vein. The nerve to the subclavius also crosses this triangle and some lymph nodes are contained in it.

INTERNAL CAROTID ARTERY

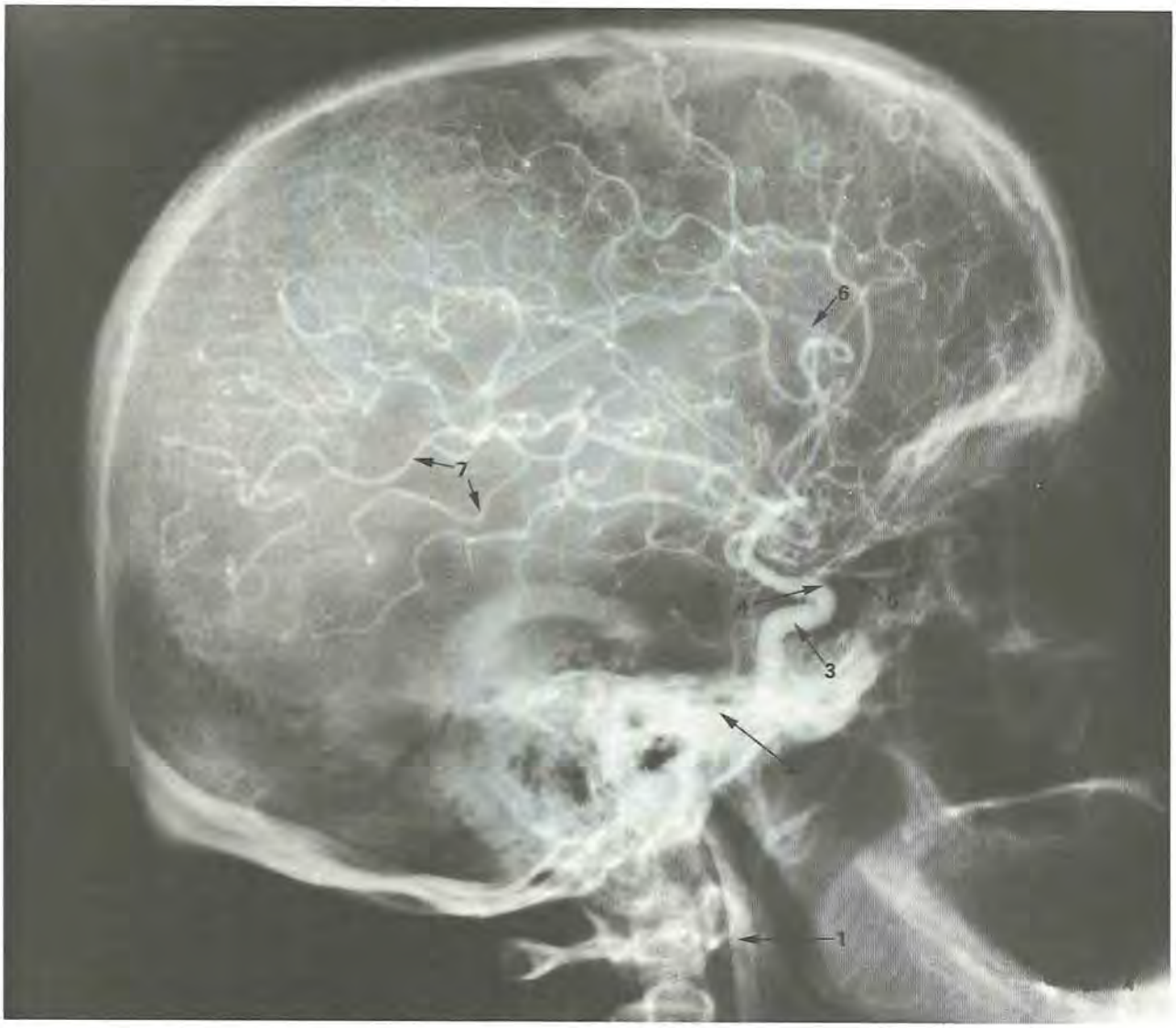
The internal carotid artery (**10.82–89**) supplies most of the ipsilateral cerebral hemisphere, eye and accessory organs, forehead and, in part, the nose. From the carotid bifurcation, where it usually has a carotid sinus (p. 1514), it ascends to the cranial base, enters the cranial cavity by the carotid canal and turns anteriorly through the cavernous sinus in the carotid groove on the side of the sphenoid body, ending below the anterior perforated substance by division into the anterior and middle cerebral arteries.

It may be divided conveniently into cervical, petrous, cavernous and cerebral parts. In the broadest outline its course is:

- **vertically upwards** in the neck
- curving **horizontally forwards** and **medially** in the petrous carotid canal
- **upwards** in the upper foramen lacerum
- **horizontally forwards** in the cavernous sinus
- **vertically upwards** medial to the anterior clinoid process
- looping a short distance **backwards** and **upwards** to its terminal division.

Cervical part

This section begins at the carotid bifurcation and ascends in front of the upper three cervical transverse processes to the inferior aperture of the carotid canal in the petrous temporal bone. It is superficial at first in the carotid triangle, then passes deeper, medial to the posterior belly of the digastric. Except near the skull, the internal jugular vein and vagus nerve are lateral; the external carotid is first anteromedial but then curves back to become superficial. The artery has many other relations. **Posteriorly** it adjoins the longus capitis, with the superior cervical sympathetic ganglion between them and the superior laryngeal nerve crossing obliquely behind it. **Medial** is the pharyngeal wall separated by fat and pharyngeal veins from the ascending pharyngeal artery and superior laryngeal nerve. **Anterolaterally** the artery is covered by the sternocleidomastoid; **below** the digastric, the hypoglossal nerve and superior root of the ansa cervicalis and the lingual and facial veins are superficial. **At the level of** the digastric it is crossed by the stylohyoid muscle and the occipital and posterior auricular arteries. **Above** the digastric it is separated from the external carotid by the styloid process, styloglossus and stylopharyngeus, glossopharyngeal nerve, vagal pharyngeal branch



10.82 Internal carotid arteriogram (right): lateral view, in adult male of 33 years. The following can be identified: parts of the internal carotid artery (and individual vessels): 1. Cervical. 2. Intrapetrous. 3. Cavernous. 4. Terminal. 5. Ophthalmic artery. 6. Anterior cerebral artery. 7. Branches of middle cerebral artery. Note the absence of radio-opaque injectant from the cerebellar vessels.

and the deeper part of the parotid gland. **At the base of the skull** the glossopharyngeal, vagus, accessory and hypoglossal nerves are between the internal carotid artery and the internal jugular vein, which here has become posterior.

Petrous part

The artery at first ascends in the carotid canal, curves anteromedially and then superomedially above the cartilage filling the foramen lacerum, to enter the cranial cavity, passing between the lingula and petrosal process. It is at first anterior to the cochlea and tympanic cavity, separated from the latter and the pharyngotympanic tube by a thin, bony lamella, cribriform in the young, partly absorbed in old age; anterior to this it is separated from the trigeminal ganglion by the thin roof of the carotid canal, often deficient. The artery is surrounded by a venous plexus and the carotid autonomic plexus derived from the internal carotid branch of the superior cervical ganglion.

Cavernous part

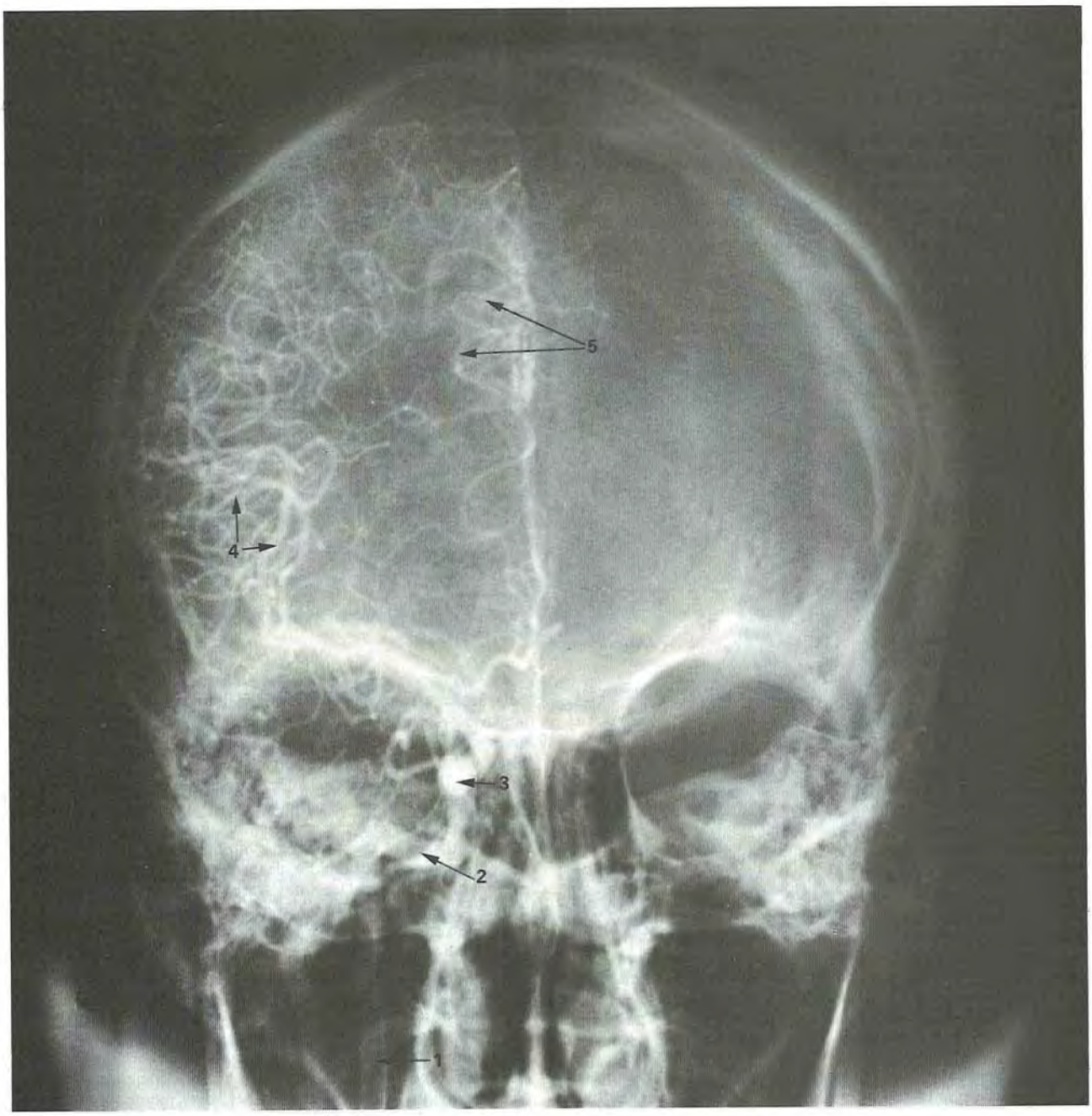
In the cavernous sinus the artery is covered by lining endothelium of the veins. It ascends to the posterior clinoid process, turns anteriorly to the side of the sphenoid and again curves up medial to the anterior clinoid process, emerging through the dural roof of the sinus; occasionally the two clinoid processes form a ring round the artery, which is also surrounded by a sympathetic plexus; the oculomotor, trochlear, ophthalmic and abducens nerves are lateral to it.

Cerebral part

Having traversed the dura mater the artery turns back below the optic nerve, passing between this and the oculomotor nerve to the anterior perforated substance at the medial end of the lateral cerebral sulcus, where it divides into anterior and middle cerebral arteries.

Variations. The length of the artery varies with the length of the neck and the point of carotid bifurcation. It may arise from the aortic arch and then be medial to the external carotid as far as the larynx but there crossing behind it. Its cervical part is normally straight but on occasion may be very tortuous, being nearer to the pharynx than usual and very near the tonsil. Its absence has also been recorded.

Surface anatomy. The internal carotid corresponds in position to a broad line from the termination of the common carotid to the back of the mandibular neck (**10.75**).



10.83 Internal carotid arteriogram (right): anteroposterior view of same subject as **10.82**. Parts of the internal carotid artery: 1. Cervical. 2. Intrapetrous. 3. Cavernous. 4. Branches of middle cerebral artery. 5. Branches of anterior cerebral artery. Note the lack of contrast medium on the left side.

Branches. The cervical part has no branches. Those from the other parts are:

From the petrous part

- Caroticotympanic
- Pterygoid

From the cavernous part

- Cavernous
- Hypophyseal
- Meningeal

From the cerebral part

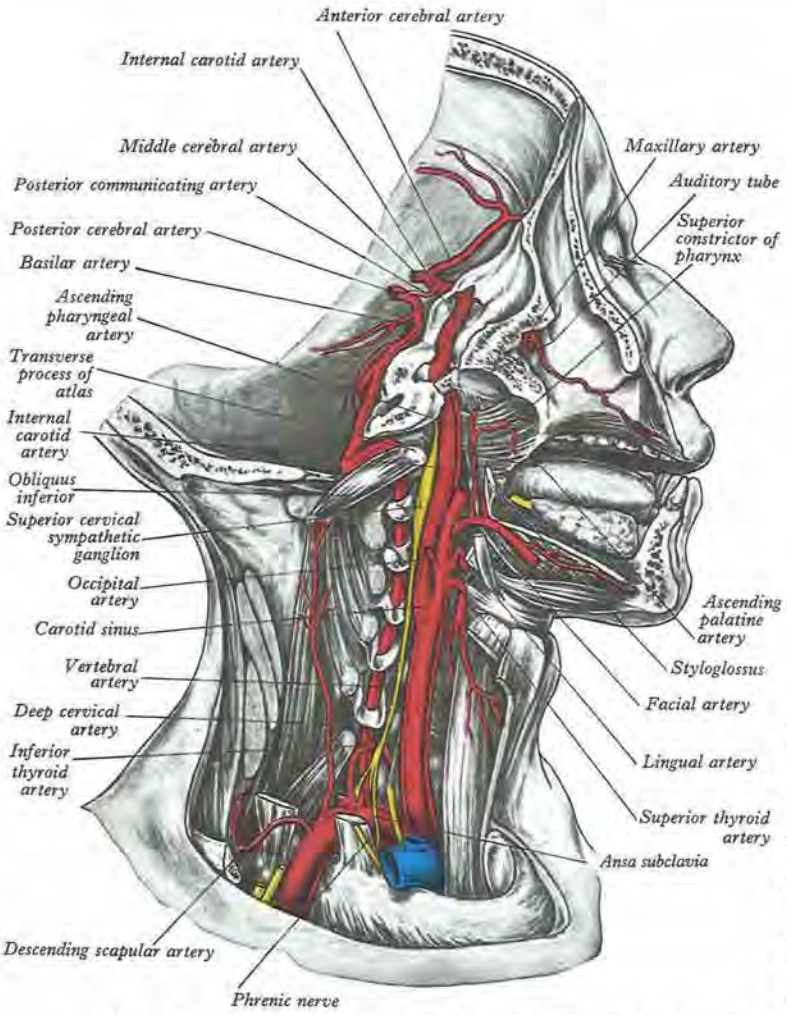
- Ophthalmic
- Anterior cerebral
- Middle cerebral
- Posterior communicating
- Anterior choroid.

Caroticotympanic artery. Small, occasionally double, it enters the tympanic cavity by a foramen in the carotid canal, anastomosing with the anterior tympanic branch of the maxillary artery and the stylomastoid artery.

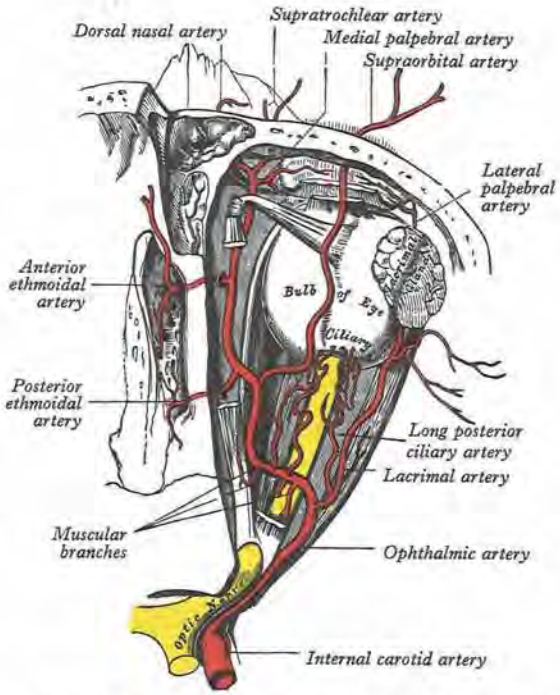
Pterygoid artery. Inconstant, it enters the pterygoid canal with the nerve of the same name, anastomosing with a (recurrent) branch of the greater palatine artery.

Cavernous branches. Numbers of these small vessels supply the trigeminal ganglion, walls of the cavernous and inferior petrosal sinuses and contained nerves. Some anastomose with middle meningeal branches.

Hypophyseal branches. Small but numerous, they are important vessels (for details see p. 1887).



10.84 Dissection to show the course of the right vertebral and internal carotid arteries and some of their branches.



10.85 The ophthalmic artery and its branches in the right orbit, as seen from above.

Meningeal branch. This is minute and passes over the lesser sphenoid wing to supply the dura mater and bone in the anterior cranial fossa; it anastomoses with a meningeal branch of the posterior ethmoidal artery.

Ophthalmic artery (10.85). It leaves the internal carotid as it quits the cavernous sinus medial to the anterior clinoid process; it enters the orbit by the optic canal, inferolateral to the optic nerve; for a short distance it is then lateral to the nerve, medial to the oculomotor and abducens nerves, ciliary ganglion and rectus lateralis. It crosses between the optic nerve and rectus superior to the medial orbital wall, runs between the obliquus superior and the rectus medialis to the medial end of the upper eyelid, dividing into *supratrochlear* and *dorsal nasal branches*. As it crosses the optic nerve with the nasociliary nerve it is separated from the frontal nerve by the rectus superior and levator palpebrae superioris; its terminal branch accompanies the infratrochlear nerve. In about 15% of subjects the ophthalmic artery is below the optic nerve. Its branches are as follows:

Central artery of the retina. A first and small branch, it begins below the optic nerve. For a short distance it is in the nerve's dural sheath; about 1.25 cm behind the eye it enters the nerve's inferomedial surface and runs to the retina along its axis. Its distribution is described on page 1347.

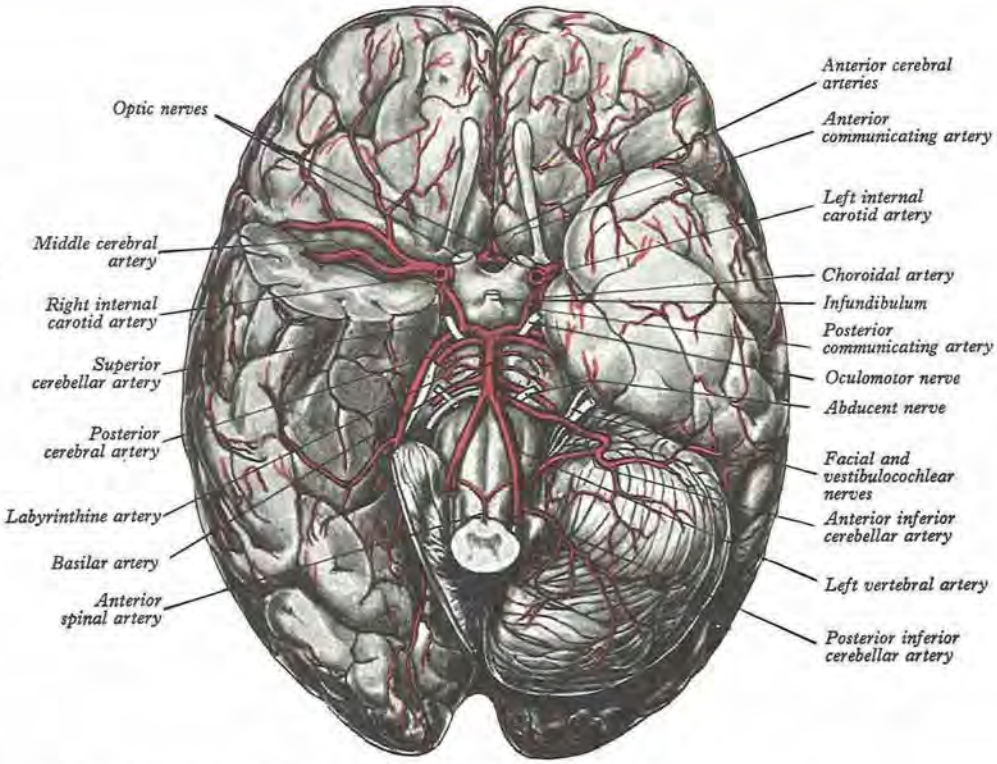
Lacrimal artery. Leaving the ophthalmic near its exit from the optic canal, it is a large branch, sometimes arising before the ophthalmic enters the orbit; a branch of the middle meningeal artery (p. 1520) may replace it. It accompanies the lacrimal nerve along the upper border of the rectus lateralis, supplying the lacrimal gland, after traversing which it ends in the eyelids and conjunctiva as *lateral palpebral arteries* running medially in the upper and lower lids to anastomose with the medial palpebral arteries. The lacrimal artery gives off one or two *zygomatic branches*: one reaches the temporal fossa via the zygomaticotemporal foramen, anastomosing with the deep temporal arteries; another reaches the cheek by the zygomaticofacial foramen, anastomosing with transverse facial and zygomatico-orbital arteries. A *recurrent meningeal branch* passes back via the lateral part of the superior orbital fissure to anastomose with a middle meningeal branch; enlargement of this anastomosis may provide an alternative lacrimal artery.

Muscular branches. These frequently spring from a common trunk but form superior and inferior groups, most accompanying branches of the oculomotor nerve. The inferior, more constant, contains most of the anterior ciliary arteries. Other muscular vessels branch from the lacrimal and supraorbital or the trunk of the ophthalmic artery.

Ciliary arteries. They are divisible into three groups: long and short posterior and anterior. *Long posterior ciliary arteries*, usually two, pierce the sclera near the optic nerve (p. 1132). About seven *short posterior ciliary arteries* pass around the optic nerve to the eyeball; dividing into 15–20 branches, they pierce the sclera around the optic nerve to supply the choroid and the ciliary processes. At the optic disc they anastomose with twigs of the central retinal artery and at the ora serrata with the long posterior and anterior ciliary arteries. *Anterior ciliary arteries* arise from muscular branches of the ophthalmic; reaching the eyeball on tendons of the recti to form a circumcorneal subconjunctival vascular zone, they pierce the sclera near the sclerocorneal junction and end in the greater arterial circle of the iris (p. 1132).

Supraorbital artery. Leaving the ophthalmic where it crosses the optic nerve, it ascends medial to the rectus superior and levator palpebrae superioris, meets the supraorbital nerve and runs with it between the periosteum and levator palpebrae superioris to the supraorbital foramen or notch; traversing this it divides into superficial and deep branches, supplying the skin, muscles and frontal periosteum, anastomosing with the supratrochlear artery, frontal branch of the superficial temporal and its fellow. It supplies the rectus superior and levator palpebrae and sends a branch across the trochlea to the medial canthus. At the supraorbital margin it often sends a branch to the diploe of the frontal bone and may also supply the mucoperiosteum in the frontal sinus.

Posterior ethmoidal artery. Entering the posterior ethmoidal canal,



10.86 The arteries at the base of the brain. The right temporal pole and most of the right hemisphere of the cerebellum have been removed. Variations in the pattern of these vessels are common.

it supplies the posterior ethmoidal air sinuses, enters the cranium, sends a meningeal branch to the dura mater and nasal branches descending into the nasal cavity via the cribriform plate, to anastomose with the sphenopalatine branches supplying bone.

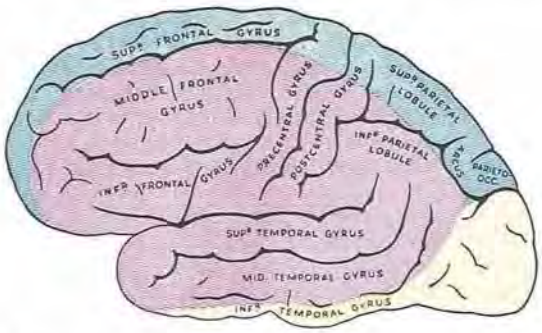
Anterior ethmoidal artery. Together, artery and nerve traverse their canal, the artery supplying anterior and middle ethmoidal and frontal air sinuses and, entering the cranium, giving a meningeal branch to the dura mater and nasal branches descending into the nasal cavity with the anterior ethmoidal nerve; they run in a groove on the deep surface of the nasal bone to supply the lateral nasal wall and septum; a terminal branch appears on the nose between the nasal bone and the upper nasal cartilage. Angiographic studies (Kuru 1967) show the meningeal branch extending to the falx; Müller (1977) has confirmed this in fetal and adult material; he also derives such '*falciate arteries*' from the recurrent meningeal branch of the lacrimal artery.

Meningeal branch. A small artery passing back by the superior orbital fissure to the middle cranial fossa, it anastomoses with the middle and accessory meningeal arteries, supplying bone.

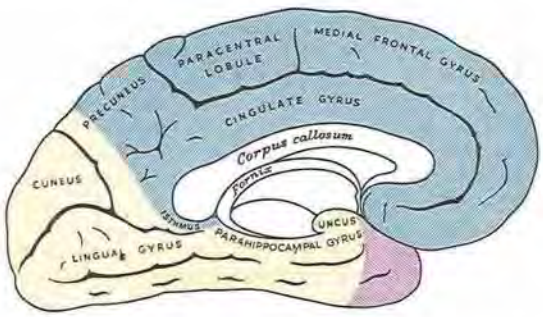
Medial palpebral arteries. Superior and inferior, they leave the ophthalmic below the trochlea, descending behind the lacrimal sac to enter the lids, where each divides into two branches coursing laterally along the tarsal edges, to form the superior and inferior arches, completed by anastomoses with branches of the supraorbital and zygomatico-orbital (superior arch) and palpebral branches of the lacrimal (both arches); the inferior arch also links with the facial artery, thus supplying the mucosa of the nasolacrimal duct.

Supratrochlear artery. A terminal branch of the ophthalmic, it leaves the orbit superomedially with the supratrochlear nerve, ascending on the forehead to supply the skin, muscles and pericranium, anastomosing with the supraorbital artery and with its fellow.

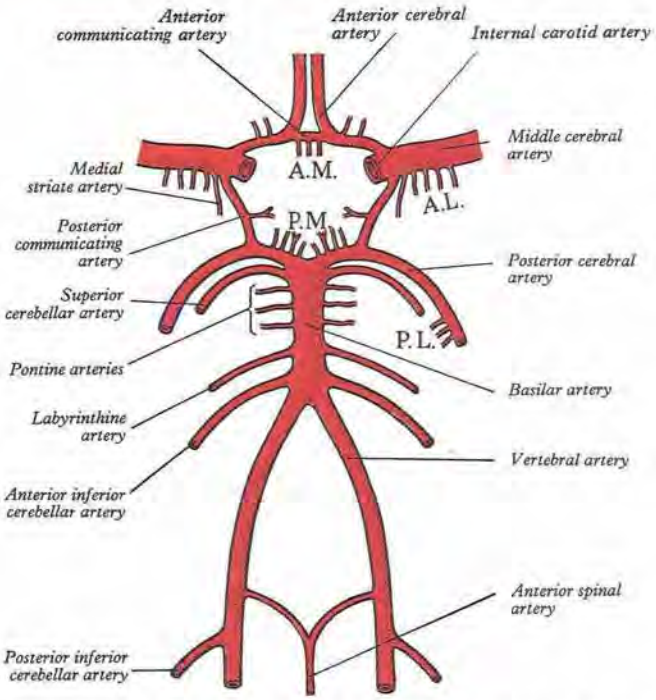
Dorsal nasal artery. The other terminal branch, it emerges from the orbit between the trochlea and medial palpebral ligament, gives a branch to the upper lacrimal sac and divides; one branch joins the terminal part of the facial artery, the other runs along the dorsum



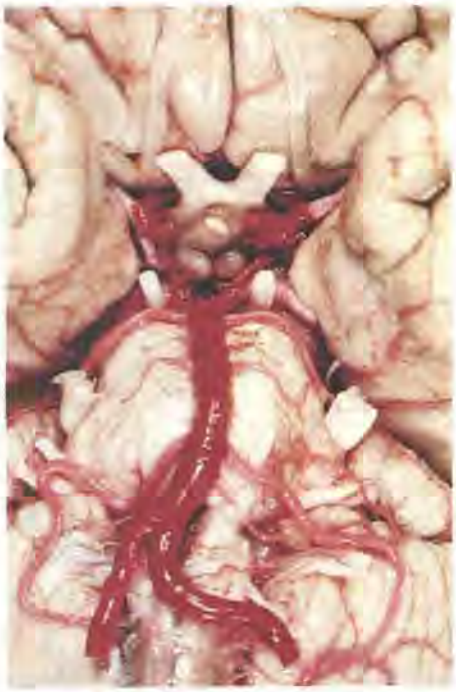
10.87A The lateral surface of the left cerebral hemisphere, showing the areas supplied by the cerebral arteries. In this and the next figure the area supplied by the anterior cerebral artery is coloured blue, that by the middle cerebral artery pink and that by the posterior cerebral artery is yellow.



10.87B The medial surface of the left cerebral hemisphere, showing the areas supplied by the cerebral arteries (see description of **10.86**).



10.88 Diagram of the arteries at the base of the brain, showing the constitution of the arterial circle. The arteries constituting this so-called arterial 'circle' are commonly asymmetrical and sometimes a constituent vessel is missing. AL = anterolateral central branches; AM = anteromedial central branches; PL = posterolateral central branches; PM = posteromedial central branches.



10.89 Resin cast of the arteries at the base of the brain, showing the components of the arterial circle. (Cast prepared by M C E Hutchinson and photographed by Kevin Fitzpatrick, Department of Anatomy, UMDS, Guy's Campus, London.)

of the nose supplying its exterior and joining its fellow and lateral nasal branch of the facial.

Anterior cerebral artery (10.86–89). The smaller terminal branch of the internal carotid, it starts at the medial end of the stem of the lateral cerebral sulcus and passes anteromedially above the optic nerve to the longitudinal fissure, where it connects with its fellow by a short transverse anterior communicating artery. The two arteries thence travel together in the fissure, curving round the genu of the corpus callosum and back along its upper surface to its posterior end, where they anastomose with posterior cerebral arteries. Occasionally they are a single vessel. There are central and cortical branches.

Anterior communicating artery. With an average length of 4 mm, it connects anterior cerebral arteries across the anterior end of the longitudinal fissure; it may be double. It has a few anteromedial central branches. According to Crowell and Morawetz (1977) its branches, from three to 13, supply the optic chiasma, lamina terminalis, hypothalamus, paraolfactory areas, fornix (anterior columns) and cingulate gyrus.

Central branches. These arise from the commencement of the anterior cerebral, entering the anterior perforated substance and lamina terminalis to supply the rostrum of the corpus callosum, septum pellucidum, the anterior part of the putamen of the lentiform nucleus and the head of the caudate nucleus. *Cortical branches* are named by distribution: two or three *orbital branches* ramify on the frontal lobe's orbital surface, supplying the olfactory lobe, gyrus rectus and medial orbital gyrus; *frontal branches* supply the corpus callosum, cingulate gyrus, medial frontal gyrus and paracentral lobule, sending twigs over the hemisphere's superomedial border to the superior and middle frontal gyri and upper part of the precentral gyrus (including the 'leg area' of the motor cortex, p. 1164); *parietal branches* supply the precuneus and the adjacent lateral surface.

Middle cerebral artery (10.86–89). The larger terminal branch of the internal carotid, it runs first in the lateral cerebral sulcus, then posterosuperiorly on the insula, dividing into branches distributed to this and the adjacent lateral cerebral surface. Its *central branches* are small and from its commencement they enter the anterior perforated substance, arranged in two sets: *medial striate arteries* ascend through the lentiform nucleus to supply it, the caudate nucleus and the internal capsule; *lateral striate arteries* ascend over the lower lateral aspect of the lentiform nucleus (in the external capsule) and turn medially to traverse it and the internal capsule to supply the caudate nucleus. One lateral branch, usually the largest, was termed by Charcot the 'artery of cerebral haemorrhage'. *Cortical branches* supply orbital branches to the inferior frontal gyrus and the lateral orbital surface of the frontal lobe; frontal branches supply the precentral, middle and inferior frontal gyri; two *parietal branches* are distributed to the postcentral gyrus, the lower part of the superior parietal lobule and the whole inferior parietal lobule. Two or three *temporal branches* supply the lateral surface of the temporal lobe. Cortical branches of the middle cerebral thus supply all the motor area (excluding the leg), the corresponding somaesthetic area (p. 1116) and the auditory area (p. 1204).

Posterior communicating artery (10.86, 88, 89). This runs back from the internal carotid above the oculomotor nerve, anastomosing with the posterior cerebral, a basilar branch. It is usually small but sometimes so large that the posterior cerebral appears to come from the internal carotid rather than basilar artery. It is often larger on one side. From its posterior half several small branches pierce the posterior perforated substance with others from the posterior cerebral to supply the medial thalamic surface and walls of the third ventricle (p. 1203).

Anterior choroidal artery. Small but constant, it leaves the internal carotid near its posterior communicating branch (Abbie 1933, 1934), passing back above the medial part of the uncus to cross inferior to the optic tract and reach and supply the crus cerebri. Turning laterally, it recrosses the optic tract, arrives lateral to the lateral geniculate body and supplies it with several branches. Finally it enters the inferior cornu of the lateral ventricle via the choroidal fissure to end in the choroidal plexus. It supplies: the globus pallidus, caudate nucleus and amygdaloid body, hypothalamus, tuber cinereum, red nucleus, substantia nigra, posterior limb of the internal capsule, the optic radiation, optic tract, hippocampus and the fimbria of the fornix.

Circle of Willis

Much of the brain is supplied by the two internal carotid arteries (p. 1523), and a central anastomosis, the Circle of Willis (also known as *circulus arteriosus*), exists between these and the two vertebral arteries (p. 1530) that supply the remainder. This 'circle', more polygonal than circular, is in the cisterna interpeduncularis, surrounding the optic chiasma, the neural infundibular stem of the hypophysis cerebri and other related neural structures in the interpendicular fossa (**10.88, 89**). **Anteriorly** the anterior cerebral arteries (from the carotids) are joined by the anterior communicating artery; **posteriorly** the basilar artery (p. 1534) divides into two posterior cerebral arteries, each joined to the ipsilateral internal carotid by a posterior communicating artery (**10.88**).

Vessels of this 'circle' vary in calibre, being often partially developed, sometimes even absent. About 60% of circles display 'anomalies'; the above description applies to a minority.

Variations

Variations have been much studied, from Windle's account in 1888 of 200 specimens to that of Puchades-Orts et al (1976) in 62 dissections, the largest series being the 700 dissections of Fawcett and Blachford (1906) and Riggs and Rupp's (1963) 994 dissections. Fields et al (1965) have summarized such studies. Cerebral and communicating arteries, anterior and posterior, may all be absent, variably hypoplastic, double or even triple. In about 90% there is, nevertheless, a complete 'circular' channel but in most one vessel is sufficiently narrowed to reduce its role as a collateral route. The haemodynamic 'balance' is usually disturbed by variation in the calibre of communicating arteries, often with variation in the segments of anterior and posterior cerebral arteries extending from their origins to their junctions with the corresponding communicating arteries. This is especially true in the case of the posterior cerebral artery and its anastomosis with the posterior communicating artery. Commonly the precommunicating part of the posterior cerebral artery has a diameter larger than the posterior communicating artery; in this case the blood supply to the occipital lobes is mainly from the vertebrobasilar system. Less commonly the diameter of the precommunicating part of the posterior cerebral artery is smaller than that of the posterior communicating artery, in which case the blood supply to the occipital lobes is mainly from the internal carotids via the posterior communicating arteries (Van Overbeeke et al 1991). The latter arrangement, whose frequency ranges according to different studies from 6% (McCormick 1969) to 40% (Zeal and Rhoton 1978), is sometimes referred to as the 'embryonic configuration' (as opposed to the standard 'adult configuration'), and according to Abbie (1933), Williams (1936) and Kaplan (1956) is accounted for by the ontogenetic and phylogenetic association of posterior cerebral and internal carotid arteries. However, a recent study has shown that the 'embryonic configuration' is not more common in human fetuses than in adults (Van Overbeeke et al 1991). Anterior in the arterial circle, agenesis or hypoplasia of the initial anterior cerebral segment is more frequent than anomalies in the anterior communicating, and hence a commoner cause of defective circulation. Angiographic evidence indicates such defective or absent circulation in about a third of individuals (Sedzmir 1959); existence of an effective arterial circle can never be assumed and surgical procedures involving its 'feeders' must be preceded by angiography. Radioopaque substances may be injected into the internal carotid or vertebral arteries in the neck for radiography of the condition of their intracranial branches (**10.82, 83, 93, 94**).

Further details of the distribution of cerebral arteries and veins appear on pages 1218 to 1220 and of intracranial venous sinuses on pages 1582 to 1589.

SUBCLAVIAN SYSTEM OF ARTERIES

The stem artery of the upper limb is single as far as the elbow, but its name changes in the regions traversed. From its origin to the outer border of the first rib it is *subclavian*; thence to the tendon of teres major it is *axillary*; and from this to its division at the elbow it is *brachial*.

SUBCLAVIAN ARTERY

The right subclavian arises from the brachiocephalic trunk, the left from the aortic arch. For description, each is divided into a *first part*, from its origin to the medial border of the scalenus anterior, a *second part* behind this muscle and a *third part* from the muscle's lateral margin to the first rib's outer border, where the artery becomes axillary. Each subclavian artery arches over the cervical pleura and pulmonary apex. Their first parts differ, the second and third parts are almost identical.

First part of right subclavian artery

The right subclavian, branching from the brachiocephalic trunk behind the upper border of the right sternoclavicular joint, passes superolaterally to the medial margin of the scalenus anterior (**10.66, 84, 90**). It ascends about 2 cm above the clavicle but this varies.

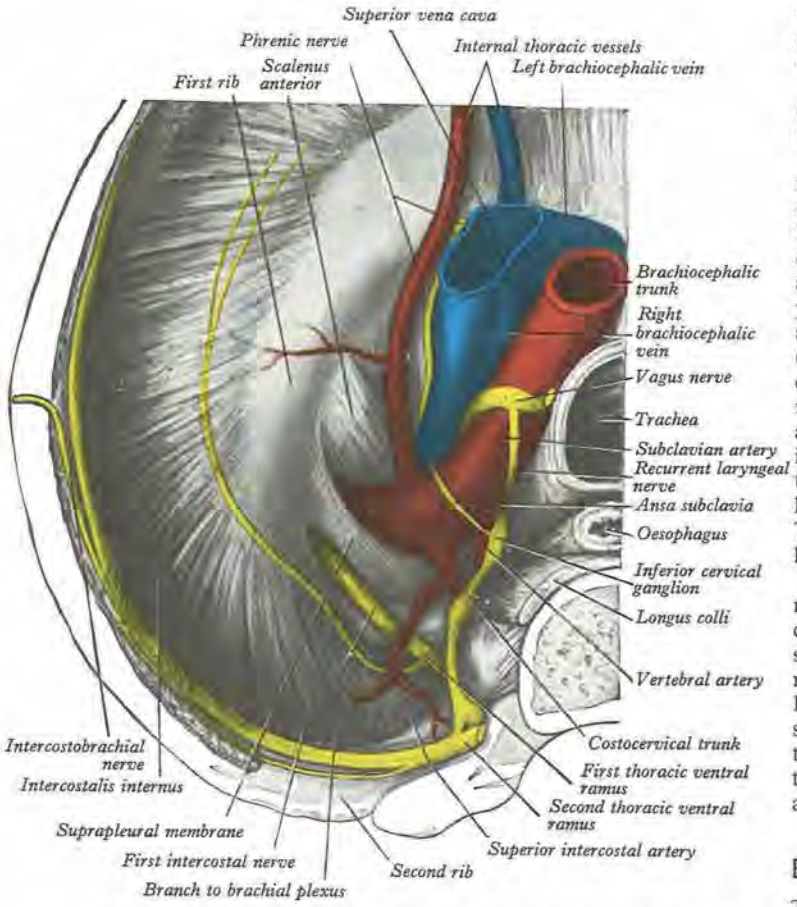
Relations. The artery is deep to the skin, superficial fascia, platysma, anterior supraclavicular nerves, deep fascia, clavicular attachment of the sternocleidomastoid, sternohyoid and sternothyroid. It is at first behind the right common carotid's origin; more laterally it is crossed by the vagus nerve, the cardiac branches of the vagus and the sympathetic chain and by internal jugular and vertebral veins; the subclavian sympathetic loop encircles it. The anterior jugular vein diverges laterally in front of it, separated by the sternohyoid and sternothyroid. Below and behind the artery are the pleura and pulmonary apex but separated by the suprapleural membrane (p. 1663), the ansa subclavia, an accessory vertebral vein (p. 1580) and the right recurrent laryngeal nerve (curving round inferoposterior to the vessel).

First part of left subclavian artery

This springs from the aortic arch, behind the left common carotid, level with the disc between the third and fourth thoracic vertebrae; it ascends into the neck, then arches laterally to the medial border of the scalenus anterior (**10.48, 66, 91**).

Relations. In the *thorax* it is related, **anteriorly** to the left common carotid artery and left brachiocephalic vein, separated by the left vagus, cardiac (p. 1253) and phrenic nerves. Superficial to these the anterior pulmonary margin, pleura, sternothyroid and sternohyoid are between the vessel and the upper left area of the manubrium sterni. **Posterior** are the left side of the oesophagus, the thoracic duct and longus colli; it is in contact posterolaterally with the left lung and pleura. **Medial** are the trachea, the left recurrent laryngeal nerve, oesophagus and thoracic duct. **Laterally** the artery grooves the mediastinal surface of the left lung and pleura which also encroach on its anterior and posterior aspects.

In the neck, near the medial border of the scalenus anterior, the artery is crossed anteriorly by the left phrenic nerve and the termination of the thoracic duct. Otherwise anterior relations are as



10.90 Structures related to the right cervical pleura, as seen from below.

previously described for the first part of the right subclavian artery. Posteriorly and inferiorly, the relations of both vessels are identical but the left recurrent laryngeal nerve, medial to the left subclavian artery in the thorax, is not directly related to its cervical part.

Second part of subclavian artery

This is behind the scalenus anterior; it is short and the highest part of the vessel (**10.73, 92**).

Relations. Anterior are the skin, superficial fascia, platysma, deep cervical fascia, sternocleidomastoid and scalenus anterior; the right phrenic nerve is often described as separated from the second part by the scalenus anterior, but crossing the first part on the left; Qvist (1977) stated that both nerves are anterior to the muscle. Postero-inferior are the suprapleural membrane, pleura and lung and the lower trunk of the brachial plexus; superior are the upper and middle trunks of the plexus; the subclavian vein is antero-inferior, separated by the scalenus anterior (**10.92**).

Third part of subclavian artery

This descends laterally from the lateral margin of the scalenus anterior to the outer border of the first rib, where it becomes axillary; it is the most superficial part of the artery and lies partly in the supraclavicular triangle (p. 1523), where its pulsations may be felt and it may be compressed.

Relations. Anterior are the skin, superficial fascia, platysma, supraclavicular nerves and deep cervical fascia (**10.68, 92**). The external jugular vein crosses its medial end and here receives the suprascapular, transverse cervical and anterior jugular veins, together often forming a venous plexus. The nerve to the subclavius descends between the veins and the artery; the latter is terminally behind the clavicle and subclavius, where it is crossed by the suprascapular vessels. The subclavian vein is antero-inferior and the lower trunk of the brachial plexus is postero-inferior, between the artery and the scalenus medius (and on the first rib). Superolateral are the upper and middle trunks of the brachial plexus (palpable here) and the inferior belly of the omohyoid. Inferior is the first rib.

Surface anatomy. The subclavian artery describes a broad line, convex superiorly, from the sternoclavicular joint to the midpoint of the clavicle (**10.75**).

Variations. The right subclavian may arise above or below sternoclavicular level; it may be a separate aortic branch and be the first or last branch of the arch; when first, it is in the position of a brachiocephalic trunk and when last it arises from the arch's left end, ascending obliquely to the right behind the trachea, oesophagus and right common carotid to the first rib. In this case the proximal part of the artery represents a persistent part of the right dorsal aorta, the right fourth aortic arch taking no part in its formation (p. 1510); hence the right recurrent laryngeal nerve hooks round the common carotid, derived from the third arch. Sometimes, when the right subclavian is the last aortic branch, it passes between trachea and oesophagus. It may perforate the scalenus anterior; very rarely it passes anterior to it. Sometimes the subclavian vein accompanies the artery behind the scalenus anterior. The artery may ascend as high as 4 cm above the clavicle or it may reach only its upper border. The left subclavian is occasionally combined at its origin with the left common carotid.

Clinical anatomy. The third part of the subclavian artery is the most accessible. Since the line of the posterior border of the sternocleidomastoid approximates to the (deeper) lateral border of the scalenus anterior, the artery is just lateral to the former and, as noted, can be felt in the antero-inferior angle of the posterior triangle. It can only be effectively compressed against the first rib; with shoulder depressed, pressure is exerted down, back and medially in the angle between the sternocleidomastoid and clavicle. The palpable trunks of the brachial plexus may be injected with local anaesthetic allowing major surgical procedures to the arm.

BRANCHES OF THE SUBCLAVIAN ARTERY

These branches are:

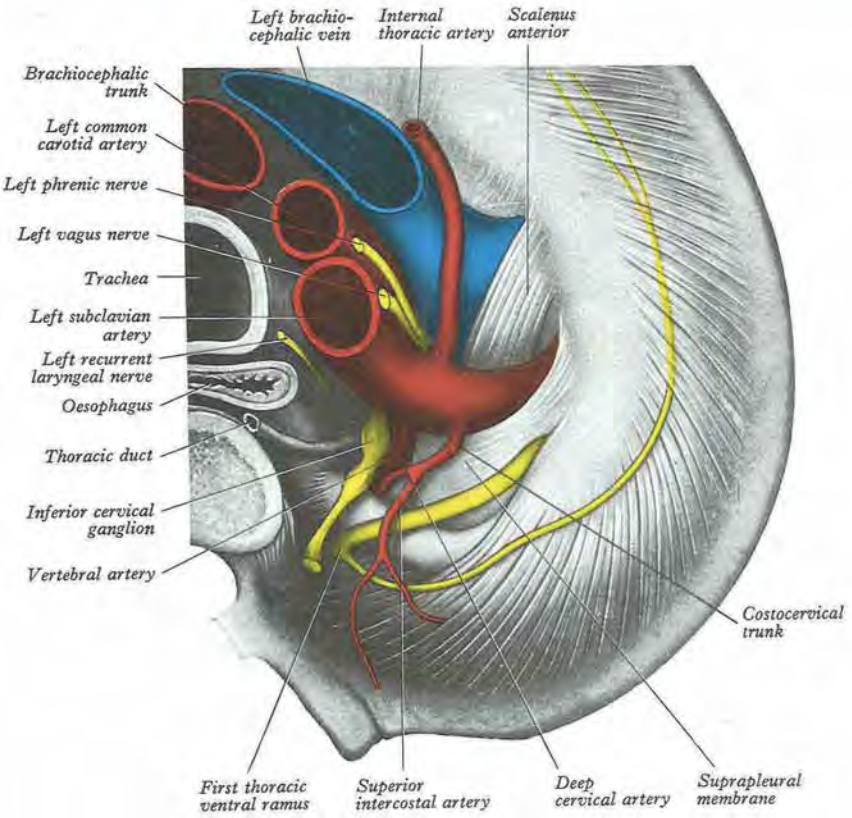
1. Vertebral
2. Internal thoracic
3. Thyrocervical
4. Costocervical
5. Dorsal scapular.

On the left all branches except the dorsal scapular arise from the first part; on the right the costocervical trunk usually springs from the second part. The origins of branches proceeding into the posterior triangle are variable but distributions are relatively constant.

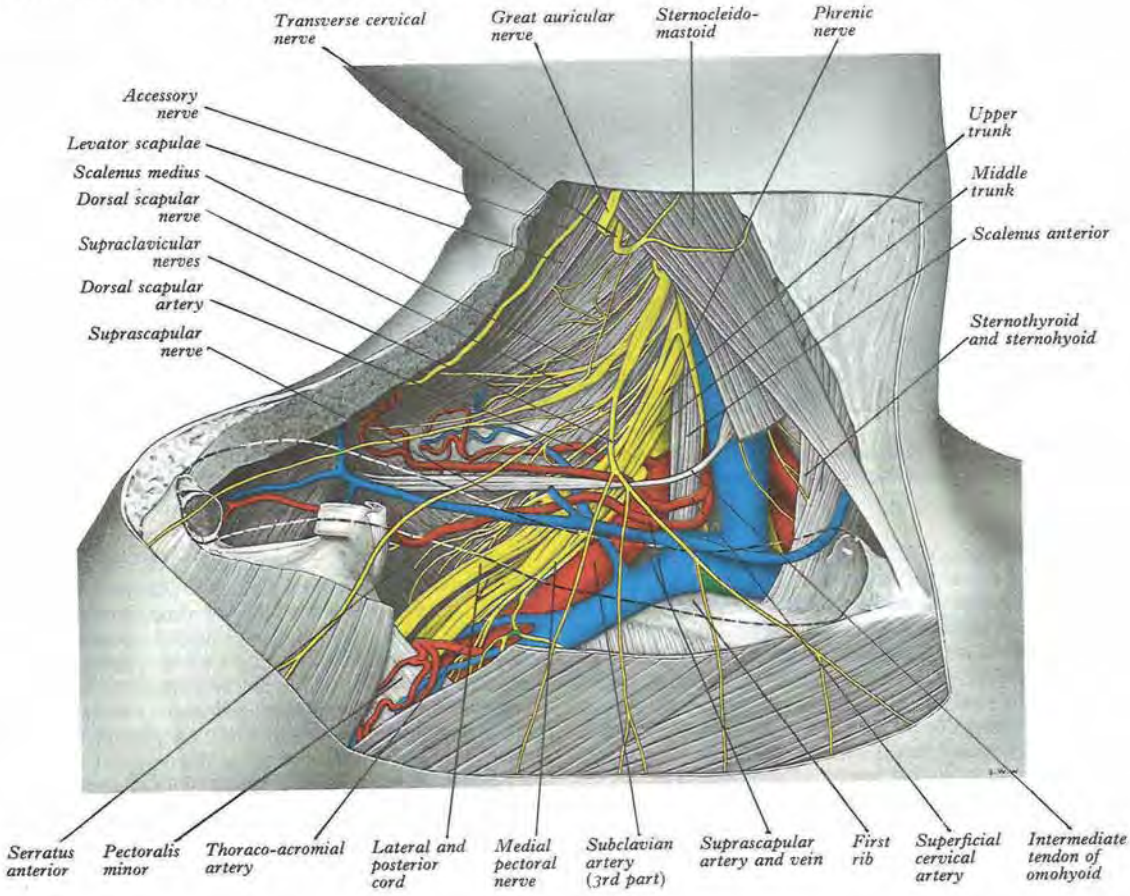
1. Vertebral artery

This artery arises from the superoposterior aspect of the subclavian, passes through the foramina of all cervical transverse processes except the seventh, curves medially behind the lateral mass of the atlas and then enters the cranium via the foramen magnum. At the lower pontine border it joins its fellow to form the basilar artery. Occasionally it may enter the bone at the fifth, fourth or seventh cervical transverse foramen (**10.83, 86, 88, 89, 90, 93, 94, 154**; p. 1510).

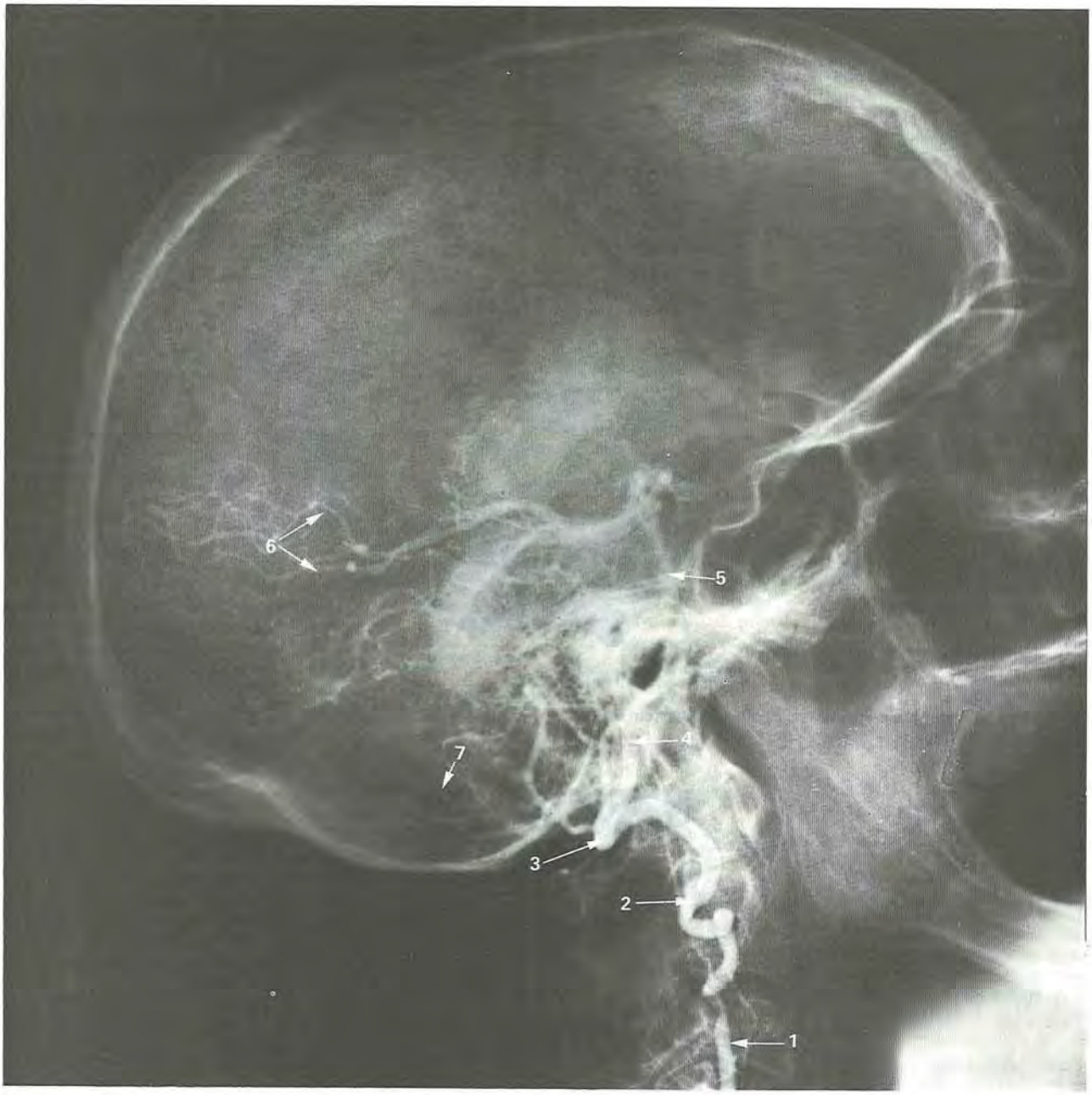
Relations. The *first part* ascends back between the longus colli and scalenus anterior, behind the common carotid artery and vertebral vein, and crossed by the inferior thyroid artery, and on the left also by the thoracic duct. **Posterior** are the seventh cervical transverse process, the stellate ganglion (**10.86, 89, 90, 91**) and ventral rami of the seventh and eighth cervical spinal nerves. The *second part* ascends through the transverse foramina, with a large branch from the stellate ganglion and a plexus of veins which form the vertebral vein low in the neck. It is anterior to the ventral rami of the cervical spinal nerves (C.2–C.6), ascending almost vertically to the transverse process of the axis, through which it turns laterally to the transverse foramen of the atlas; from here the *third part* issues medial to the rectus capitis lateralis, curving back and medially behind the lateral mass, the first cervical ventral spinal ramus being medial. It is then in a groove on the upper surface of the posterior arch of the atlas, entering the vertebral canal below the inferior border of the posterior atlanto-occipital membrane. This part,



10.91 Structures related to the left cervical pleura, as seen from below.



10.92 The lower part of the posterior triangle showing the relations of the third part of the right subclavian artery. Note the clavicle has been removed but its outline is indicated by a dashed line; the middle trunk of the brachial plexus gives an unusual contribution to the medial cord.



10.93 Vertebral arteriogram (left): lateral view. 1. Vertebral artery, ascending part. 2. Loop between transverse foramina of axis and atlas. 3. Suboccipital part. 4. Intracranial part. 5. Basilar artery. 6. Posterior cerebral branches. 7. Inferior cerebellar branches.

covered by the semispinalis capitis, is in the suboccipital triangle. The first cervical dorsal spinal ramus is between the artery and the posterior arch. The *fourth part* pierces the dura and arachnoid mater, ascends anterior to the hypoglossal roots (p. 1256) inclining anterior to the medulla oblongata where, at the lower pontine border, it unites with its fellow to form the midline basilar artery (**10.88, 89**).

Winckler (1972) has described variation in elastic and muscular tissue in the vertebral artery; in its first and third parts it appears adapted by increased elasticity to the greater mobility and lack of support in these regions.

Cervical branches of the vertebral artery

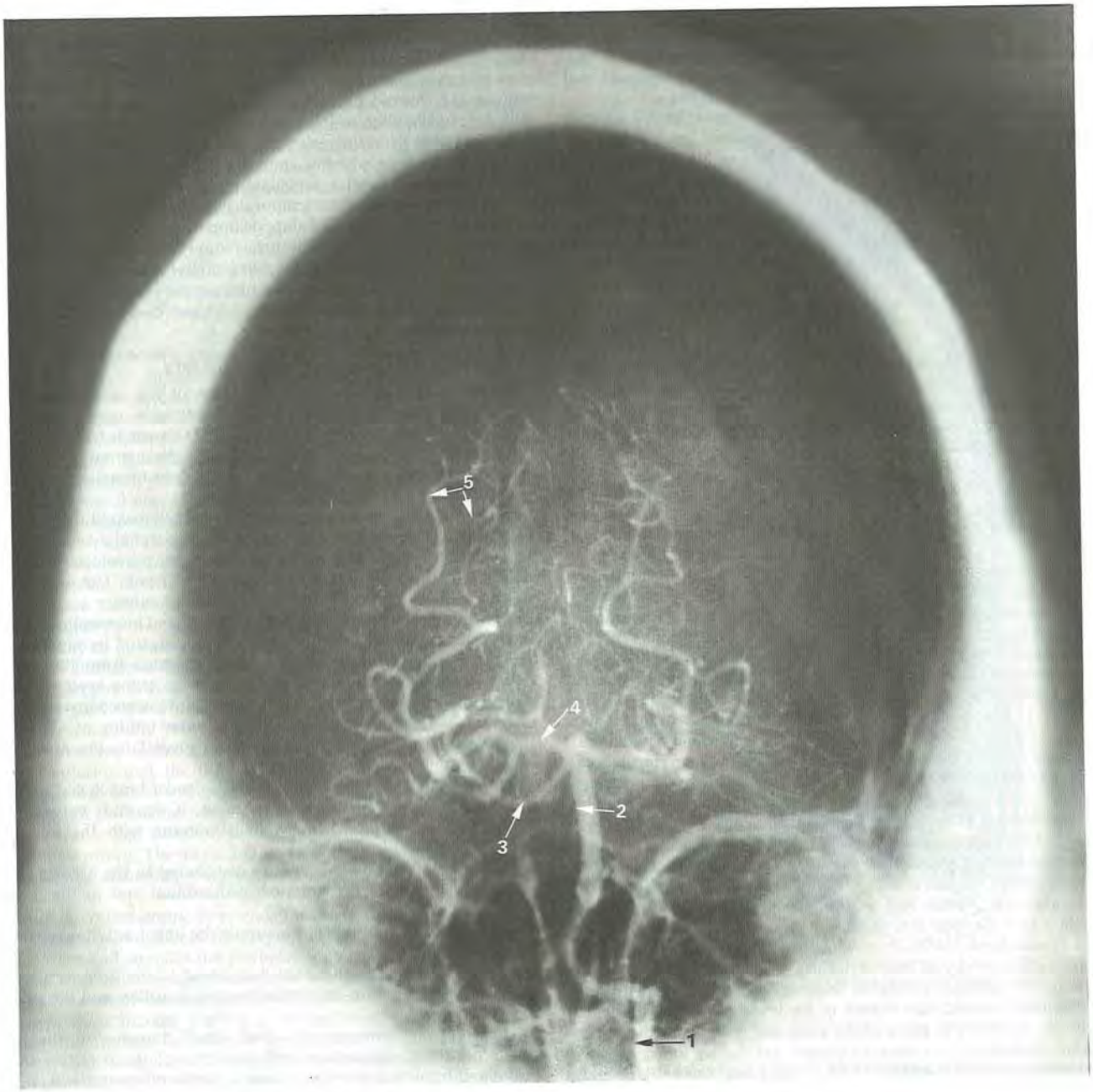
Spinal branches. These small branches enter the vertebral canal by the intervertebral foramina, supplying branches to the spinal cord and its membranes. They anastomose with other spinal arteries, which fork into ascending and descending rami, to unite with those above and below, forming two lateral anastomotic chains on the posterior surfaces of the vertebral bodies near the attachment of their pedicles. From these chains branches supply the periosteum and vertebral bodies, while others communicate with similar branches across the midline; from these connections small rami join similar ones above and below, forming a median anastomotic chain on the posterior surfaces of the vertebral bodies.

Muscular branches. Arising from the vertebral artery as it curves round the lateral mass of the atlas, they supply the deep muscles of this region and anastomose with the occipital, ascending and deep cervical arteries.

Cranial branches of the vertebral artery

Meningeal branches. One or two of these branches from the vertebral artery near the foramen magnum ramify between the bone and dura mater in the cerebellar fossa, supplying bone, diploë and the falx cerebelli.

Posterior spinal artery. This may arise from the vertebral near



10.94 Vertebral arteriogram (left): anteroposterior view. 1. Left vertebral artery. 2. Basilar artery. 3. Right superior cerebellar artery. 4. Right posterior cerebral artery. 5. Branches of right posterior cerebral artery.

the medulla oblongata but most frequently from its posterior inferior cerebellar branch (see below). It passes posteriorly, descending as two branches, anterior and posterior, to the dorsal roots of the spinal nerves; these are reinforced by spinal twigs from the vertebral, ascending cervical, posterior intercostal and first lumbar arteries, which reach the vertebral canal by the intervertebral foramina, sustaining the posterior spinal arteries to the lower spinal levels (8.329).

Anterior spinal artery. A small branch arising near the vertebral's end, it descends anterior to the medulla oblongata and unites with its fellow at midmedullary level. The single trunk then descends on the ventral midline of the spinal cord, reinforced by a succession of small spinal rami entering the vertebral canal through the intervertebral foramina from the vertebral, ascending cervical, posterior intercostal and first lumbar arteries. They unite by ascending and descending branches as a single anterior median artery, which reaches the lower spinal cord and filum terminale. This median artery is encased in the pia mater along the anterior median fissure; it supplies the spinal cord and inferiorly the cauda equina. Branches from the anterior spinal arteries and beginning of their common trunk pass into the medulla oblongata, with a central distribution sharply limited dorsally by the trigonum hypoglossi (p. 1218, 8.329).

Posterior inferior cerebellar artery (10.46). The largest branch, it is sometimes absent. Arising near the lower end of the olive, it curves back around it to ascend behind glossopharyngeal and vagal roots to the inferior border of the pons, where it curves and descends along the inferolateral border of the fourth ventricle. Finally it turns laterally into the cerebellar vallecula, dividing into medial and lateral branches. The *medial branch* runs back between the cerebellar hemisphere and inferior vermis, supplying both; the *lateral branch* supplies the inferior cerebellar surface as far as its lateral border, anastomosing with the anterior inferior and superior cerebellar

arteries (from the basilar artery). Its trunk supplies the medulla oblongata and choroid plexus of the fourth ventricle, sending up a branch lateral to the (cerebellar) tonsil to supply the dentate nucleus. The medullary area supplied is dorsal to the olivary nucleus and lateral to the hypoglossal nucleus and its emerging fila.

Clinical anatomy. The posterior inferior cerebellar artery supplies the lateral medulla. Thrombosis therefore causes loss of function ('lateral medullary syndrome') in the nucleus ambiguus, nucleus of the tractus solitarius, vestibular and cochlear nuclei, spinocerebellar tracts, the lateral spinothalamic tract, trigeminal spinal nucleus and tract. The anterior spinal artery supplies the medial medulla; thrombosis of it ('medial medullary syndrome') affects the hypoglossal nucleus and nerve, medial lemniscus and corticospinal tract.

Medullary arteries. These are minute vessels from the vertebral and its branches, distributed to the medulla oblongata.

Basilar artery

This median vessel, formed by the junction of the vertebral arteries, extends from the lower to the upper pontine borders in the cisterna pontis (10.86, 88). It adjoins a shallow, median groove on the ventral pontine surface, between the abducent nerves at the lower pontine border and the oculomotor at the upper pontine border, where it divides into two posterior cerebral arteries.

Pontine branches. These are numerous and leave the front and sides of the basilar to supply the pons and adjacent parts.

Labyrinthine (internal auditory) artery. Long and slender, it may branch from the lower part of the basilar but more often from the anterior inferior cerebellar artery (see below); it accompanies facial and vestibulocochlear nerves into the internal acoustic meatus and is distributed to the internal ear (p. 1376). In a radiographic study of this artery Wende et al (1975) identified the origins of 238. Only 38 (16%) were from the basilar; 108 (45%) were from the anterior inferior cerebellar. The superior cerebellar artery accounted for 58 (25%), the posterior inferior cerebellar for 13 (5%). The remaining 21 (9%) were reduplicated and were branches of the basilar and one or other of the cerebellar arteries. They found a unilateral artery in 24 of 316 subjects. Others have recorded different incidences. Cavatori (1908) observed a basilar origin for the labyrinthine artery in about 70% in Italians; Stopford (1916) and Adachi and Hasche (1928) recorded it as most often from a trunk common to it and one of the cerebellar arteries. Gillilan (1972) has indicated racial variation.

Anterior inferior cerebellar artery (10.86). This branches from the lower part of the basilar and runs posterolaterally usually ventral to the abducent, facial and vestibulocochlear nerves, commonly forming a variable loop into the internal acoustic meatus below the nerves (Sunderland 1945a), from which the labyrinthine artery often arises. Emerging from the meatus the artery supplies the anterolateral region of the inferior cerebellar surface, anastomosing with the posterior inferior cerebellar branch of the vertebral. A few branches supply the inferolateral parts of the pons and sometimes the upper medulla oblongata.

Superior cerebellar artery (10.86). Arising near the basilar's end, it passes laterally below the oculomotor nerve which separates it from the posterior cerebral artery and curves round the cerebral peduncle below the trochlear nerve; arriving at the superior cerebellar surface, it divides into branches ramifying in the pia mater to supply this cerebellar aspect and anastomose with branches of inferior cerebellar arteries. It also supplies the pons, pineal body, superior medullary velum and tela choroidea of the third ventricle.

Posterior cerebral artery (10.86, 88, 89). Frequently double, this is larger than the superior cerebellar, from which it is separated near its origin by the oculomotor nerve and, lateral to the midbrain, by the trochlear nerve. Passing laterally, parallel with the superior cerebellar, it receives the posterior communicating artery, winds round the cerebral peduncle and reaches the tentorial cerebral surface, where it supplies the temporal and occipital lobes. Its branches are central and cortical.

Central branches. Several small *posteromedial central branches* (10.88) from the beginning of the posterior cerebral, with similar branches from the posterior communicating artery, pierce the posterior perforated substance to supply the anterior thalamus, lateral wall of the third ventricle and the globus pallidus. *Posterior choroidal branches* vary (Abbie 1933); one or more course over the lateral geniculate body and supply it before entering the posterior part of the inferior cornu of the lateral ventricle via the lower part of the choroidal fissure. Others curl round the posterior end of the thalamus and traverse the transverse fissure, some going to the third ventricle's tela choroidea, some to traverse the upper choroidal fissure; they supply the choroid plexuses of the third and lateral ventricles and the fornix (Percheron 1977, p. 1220). Small posterolateral central branches arise from the posterior cerebral artery beyond the cerebral peduncle; they supply this and the posterior thalamus, colliculi, pineal gland and medial geniculate body.

Cortical branches. The temporal branches, usually two, are distributed to the uncus, parahippocampal, medial and lateral occipitotemporal gyri; occipital branches supply the cuneus, lingual gyrus and posterolateral surface of the occipital lobe; parieto-occipital branches supply the cuneus and precuneus. The posterior cerebral artery supplies the visual area (p. 1220) and other structures in the visual pathway.

2. Internal thoracic (mammary) artery

This arises inferiorly from the first part of the subclavian artery, about 2 cm above the sternal end of the clavicle, opposite the root of the thyrocervical trunk (10.90, 91, 95). It descends behind the first six costal cartilages about 1 cm from the lateral sternal border; level with the sixth intercostal space it divides into musculophrenic and superior epigastric branches.

Relations. At first it descends anteromedially behind the clavicle's sternal end, the internal jugular and brachiocephalic veins and the first costal cartilage. As it enters the thorax, the phrenic nerve crosses it obliquely from its lateral side, usually in front. The artery then descends almost vertically to its bifurcation; anterior to it are the pectoralis major, the first six costal cartilages and intervening external intercostal membranes and internal intercostals and terminations of the upper six intercostal nerves. It is separated from the pleura, down to the second or third cartilage, by a strong layer of fascia and below this by the transversus thoracis. It is accompanied by a chain of lymph nodes and venae comitantes uniting at about the third costal cartilage into a single vein medial to the artery. Its intermediate branches are as follows:

Pericardiacophrenic artery. A long, slender branch accompanying the phrenic nerve to the diaphragm, it descends between the pleura and pericardium, finally anastomosing with the musculophrenic and phrenic arteries.

Mediastinal arteries. These are distributed to the areolar tissue and lymph nodes in the anterior mediastinum and to the thymic vestiges.

Pericardial branches. These supply the upper anterior region of the pericardium.

Sternal branches. These are distributed to the transversus thoracis, the periosteum of the posterior sternal surface and the sternal red bone marrow.

The foregoing three groups, with small branches of the pericardiacophrenic, anastomose with branches of the posterior intercostal and bronchial arteries to form a *subpleural mediastinal plexus.*

Anterior intercostal branches. Distributed to the upper six intercostal spaces, two in each space, they pass laterally along the borders of the space to anastomose with the posterior intercostal arteries (and their collateral branches). They lie at first between the pleura and the internal intercostals, then between the intercostales intimi and the internal intercostals. They supply the intercostal muscles and send branches through them to the pectoral muscles, breast and skin.

Perforating branches. They traverse the upper five or six intercostal spaces with anterior cutaneous branches of the corresponding intercostal nerves. They enter the pectoralis major and, curving laterally, supply the muscle and skin. In the female the second to fourth branches supply the breast; during lactation they are enlarged.

Musculophrenic artery. This passes inferolaterally behind the seventh to ninth costal cartilages, traverses the diaphragm near the ninth and ends near the last intercostal space. It anastomoses with the inferior phrenic and the lower two posterior intercostal and ascending branches of the deep circumflex iliac arteries. Two anterior intercostal arteries branch from it for each of the seventh to ninth intercostal spaces, distributed like those in other spaces. The musculophrenic also supplies the lower part of the pericardium and the abdominal muscles.