UNIT 5

CIRCULATORY SYSTEM

Structure

5.1 INTRODUCTION

In the previous unit on Respiratory system you learnt about the various respiratory surfaces and organs that are involved in gas exchange in aquatic and terrestrial vertebrates. In this unit you will learn that the circulatory system of vertebrates consists of a heart, arteries, veins, capillaries and blood (the blood vascular system) and of lymph channels and lymph (lymphatic system).

Blood carries oxygen collected in respiratory organs, nutrients from extra embryonic membranes of embryos and from the adult digestive tract. It also carries hormones from endocrine tissues, substances associated with maintaining, immunity and disease. While flowing, it removes waste products of metabolism from the excretory organs. Lymph channels collect interstitial tissue fluids not taken up by the blood stream and emulsified fats absorbed in the small intestine. These lymph channels terminate in one or more of the large venous channels of the blood vascular system. Pressure differences that drive this flow of blood through the circulatory system are created by the pumping action of the heart.

Arteries carry blood away from heart. They have muscular elastic and fibrous walls capable of swelling with each intrusion of blood and of active constriction and dilation in response to nerve impulses. Arteries, thereby assist in regulating blood pressure. They terminate in capillary beds. Veins have proportionately less muscle and elastic tissue and more fibrous tissue and are therefore, capable of less dilation or constriction. They carry blood towards heart from capillary beds. Capillaries consist of endothelium only, with a lumen just large enough to accommodate red blood cells. In fact, the red cells must squeeze through and in so doing, become deformed. In vertebrates respiring by gills, blood is pumped from the heart to the gills, where external respiration takes place. From the gills it typically flows via arteries to capillaries throughout the body. Thus we see that the respiratory and circulatory systems work in tandem.

We begin by discussing the evolution of the vertebrate heart and aortic arches and see how the vertebrate circulatory system exhibits diverse adaptations across the radiation of vertebrates culminating in the highly specialized mammalian heart. Along with changes seen in the structure of the heart you can see the evolution of double circulation and its importance. You will realize that the structure and function of the circulatory system of each group of vertebrates has a vital role that benefits that particular group. We then go on to discuss the composition of blood and describe the lymphatic system.

Objectives

After studying this unit you should be able to:

- trace origin and evolution of the heart of vertebrates,
- trace origin and evolution of aortic arches,
- describe arterial and venous systems of vertebrates,
- describe composition of blood,
- describe lymphatic system, and
- explain the phenomenon of double circulation.

5.2 HEART

The vertebrate heart is really a modified blood vessel with highly muscular walls. There are valves to prevent backflow of blood. The heart consists of three layers:

1)	Endocardium	-	inner lining (endothelium and elastic tissue)
2)	Myocardium	-	between endocardium and epicardium (muscular layer)
3)	Epicardium	-	outer fibrous tunica, covered by visceral pericardium (subdivision of coelom).

Heart pulsates as a result of response of the muscle cells to electrolytes that infuse it. Evolutionary changes of the heart lead from a primitive, simple, straight tube in the protochordates through the sinuous multi chambered organ seen in fishes and the partially subdivided, but otherwise simple structure of early tetrapods, to the compact, highly efficient structure of birds and mammals. The evolution is summarized as follows:

i) the protochordate stage with alimentary pharynx,

ii) the piscine stage with branchial pharynx,

iii) the early tetrapod stage with primitive lungs,

iv) the late tetrapod stage of higher ectotherms and

v) the stage of endothermic tetrapods.

As implied by the names designating these stages, evolution of heart reflects changes in other structures, particularly respiratory organs.

5.2.1 Protochordate Heart

Protochordates (tunicates and *Amphioxus*) possess a simple, tubular heart that beats by peristaltic waves. Since arteries are more muscularised than veins, they may be taken as the primitive heart. Therefore, extensive muscularization of arteries has its functional significance in forcing blood into the smaller vessels (capillaries) from which blood may return back without special means of propulsion since it is passing from smaller into larger vessels.

The protochordate stage does not need, a more specialized heart, this can be explained on the basis of lack of proper respiratory function of the pharyngeal clefts. The pharyngeal clefts in protochordates primarily serve as a sieve to aid in capturing the food.

5.2.2 Early Vertebrate Heart

When pharynx is provided with capillary network, then in order to facilitate the gaseous exchange, a more efficient and specialized pump is required to force blood through to the dorsal aorta. The most primitive vertebrate heart is seen in agnathans. They have a circulatory system consisting of a main systemic heart and 3 accessory hearts (Fig.5.1). In the figure you can see the general arrangement of the circulatory system, the portal heart pumps blood from the intestines to the liver, the cardinal heart pumps blood from the head to the body, caudal heart pumps blood from the trunk and kidneys to the rest of the body. The agnathans have a different sinus venosus that is attached to the left side of the atrium. The circulatory system of hagfish has not changed in millions of years and since they are bottom feeders and dwellers they have adapted to a low arterial blood pressure and low cardiac output is sufficient.

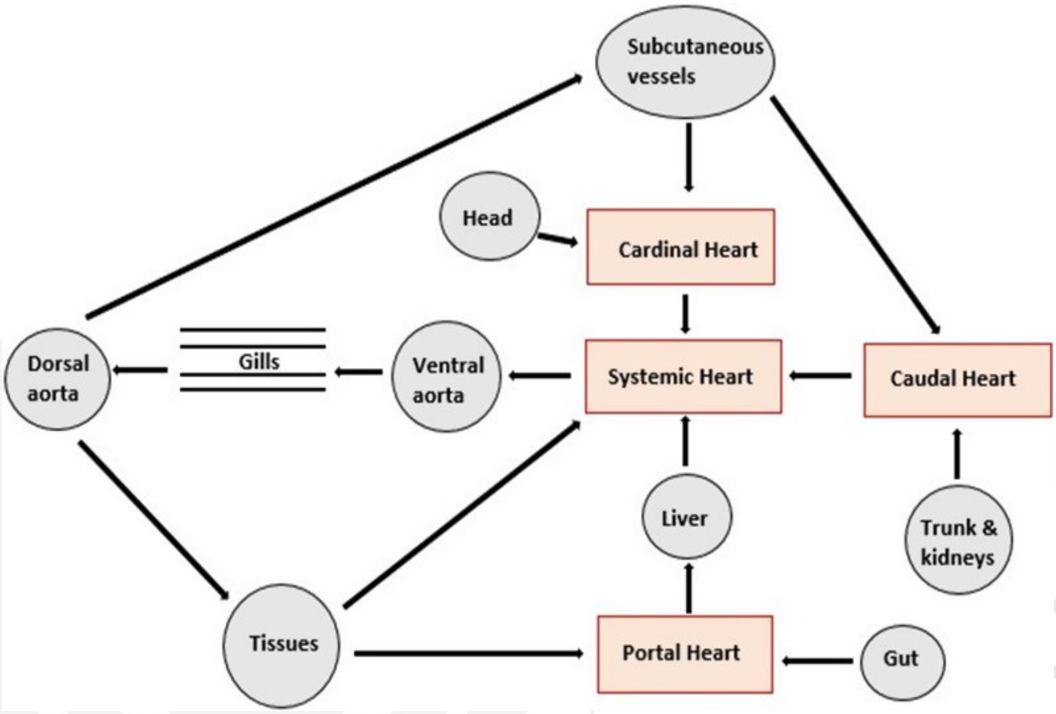


Fig. 5.1: Simplified view of the relationship between the main 'systemic (or brachial)' heart and the three accessory hearts of the hagfish (adapted from Jensen, 1965 and Jorgensen et al. 1998).

Thus a true heart is seen for the first time in fishes; a heart consisting of a series of specialized chambers to which the function of forcible propulsion of blood in arterial channels is restricted. The heart of fishes is known as the **branchial heart** as its main function is to provide deoxygenated blood through the ventral aorta into the gills. Basically there are two main chambers : the atrium and the ventricle; two other chambers the sinus venosus (SA) and conus arteriosus (CA) in lamprey, elasmobranchs and holosteans (Fig.5.2 & 5.3a). The same chamber in teleosts is known as bulbous arteriosus which is elastic and continues to form the ventral aorta (Fig.5.3b).

Actually two operations must be performed to carry out the cardiac function efficiently in a gill-respiring vertebrate. The blood must be first collected and then pushed along. Collecting chambers thus appear at the rear and propulsive chambers at the front. Fishes are provided with a posterior sinus venosus, followed by an atrium, then a ventricle, and finally a conus arteriosus in the anterior arranged in series (Fig. 5.2).

The sequence of beat is the peristaltic sequence; from the rear towards the front so the blood flows from posterior chambers to anterior chambers.

The sinus venosus is little more than an expansion of the junction of the primary somatic (common cardinal) and visceral (hepatic) veins. The walls are very thin and contain the pacemaker cells that initiate contraction. A slight negative pressure actually exists in this chamber, resulting from the integration of atrial contraction and action of the sinoatrial valve. The venous blood from the body fills the sinus venosus and through the sinoatrial valve blood passes with minimum cardiac assistance into the atrium. Because the S-shaped arrangement of the chambers in the fish heart (Fig. 5.2) places the thin-walled sinus venosus and atrium dorsal to the ventricle, the blood is forced by gravity and atrial contraction through the atrioventricular valve into the ventricle. The sinoatrial and atrioventricular valves prevent the back flow of the blood. The thickened walls of ventricle with cardiac muscle provide energy to move blood into the ventral aorta and gills.

Once received in the ventricle, blood passes through one or more series of semilunar valves (conal valves) in reaching the fairly rigid conus arteriosus, which adds still further push to the blood and smooths its flow on its way to the ventral aorta. The entrance into the latter is guarded by several rows of other semilunar valves. The semilunar valves are folds in the wall which prevent the back flow of blood and possibly help in distributing blood to the aortic arches (Fig. 5.2 & Fig. 5.3a).

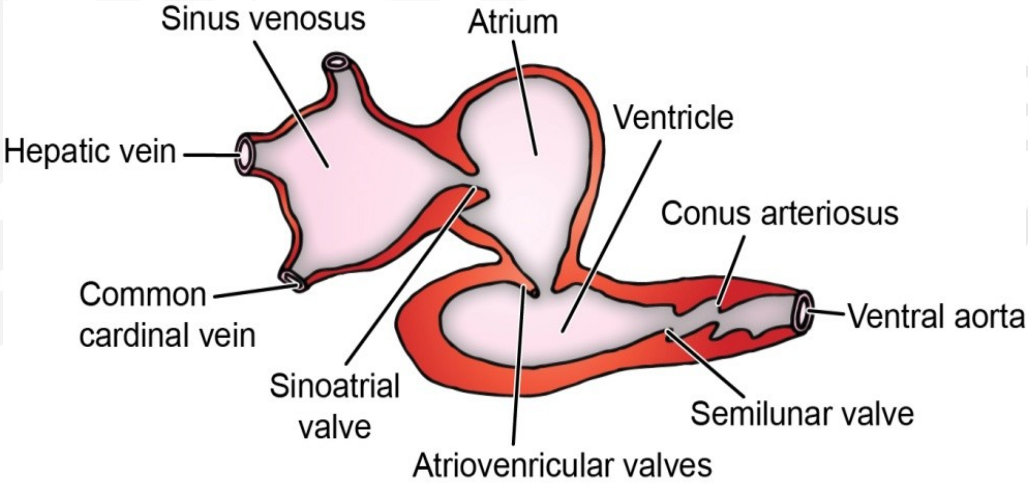


Fig. 5.2: Lamprey heart showing the chambers characteristic of most fishes.

In teleosts the blood flows from the ventricle into the bulbous arteriosus which is a unique structure, it is thin walled and elastic and expands each time the blood is pumped from the ventricle and connects to the ventral aorta. The blood pressure for this is generated in the ventricle which is much higher than what is required in the thin walled gills so the bulbous arteriosus regulates the pressure as it enters the gills. In fact the teleosts synchronize the opercular movement with the pulsation of the heart so that a steady flow of blood is maintained.

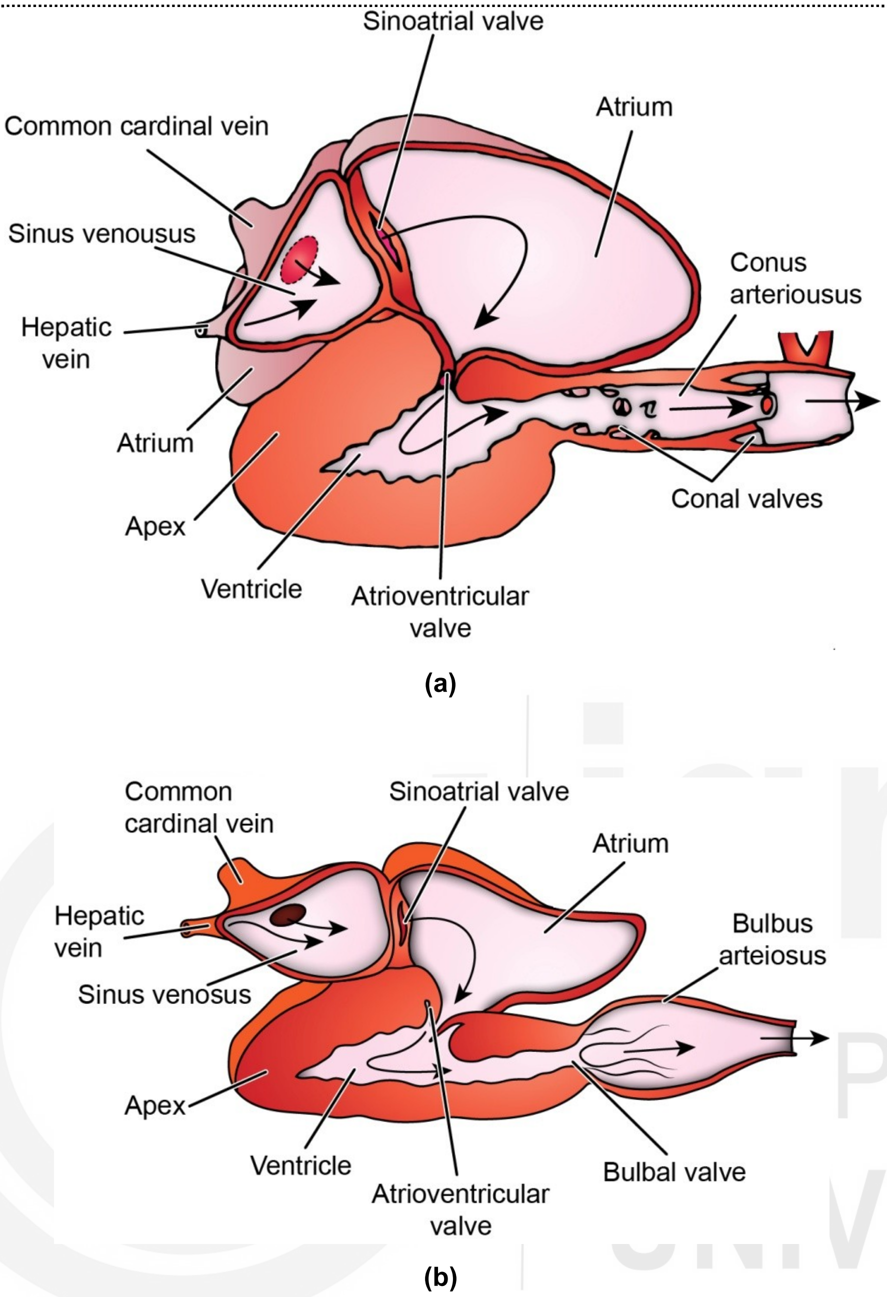


Fig. 5.3: Fish hearts, (a) Shark (b) Teleost. Blood leaves the shark heart through the muscular conus arteriosus, a chamber that is absent in teleost fishes. In the teleost heart, the base of the ventral aorta is swollen, creating the elastic, non contractile bulbus arteriosus. A single pair of bulbus valves prevent the back flow of blood into the ventricle.

5.2.3 Early Tetrapod Heart

This stage was initiated by the development of air bladder in pretetrapod ancestors for the perfection of aerial respiratory function in tetrapods. Gradually, the air bladder became specialised to serve the role in external respiration as seen in the present day lung fishes, the sarcopterygians. Lungfishes primarily use their gills for respiration but when they are outside water they adopt a vascularized lung supplied by two pulmonary arteries to assist in breathing air. The aerated blood does not supply the body directly but returns to the heart via a single pulmonary vein which opens on the left side of the atrium from where it is pumped into systemic circulation. The blood returning after circulation in the body comes back via the sinus venosus which has shifted to the right side of the heart. This modification forms the basis for dual circulation first seen in vertebrates which chiefly involved changes in the heart. First the atrium was subdivided into two chambers; a systemic chamber (right), receiving non-aerated blood from the sinus venosus, and a pulmonary chamber (left), receiving aerated blood from the pulmonary veins (Fig. 5.4).

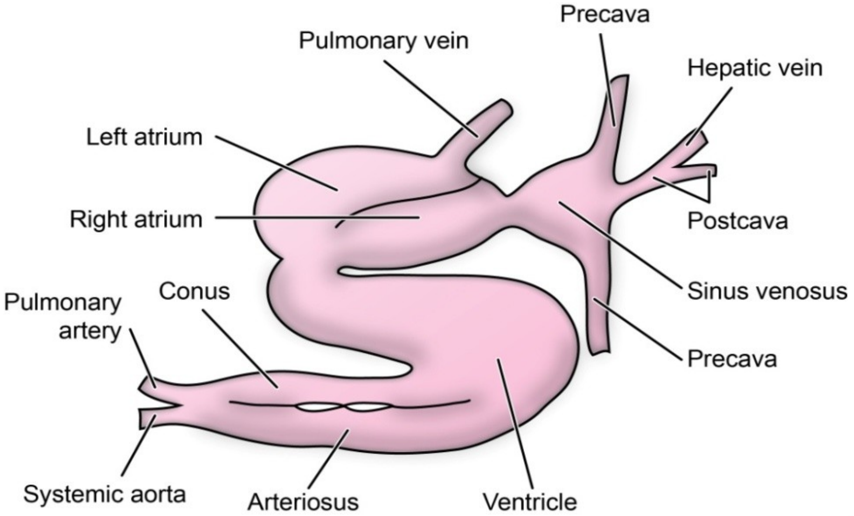


Fig. 5.4: The early tetrapod heart, ventral view with parts drawn to side instead of superimposed as in life.

A second related alteration involved a partial separation of two chambers in the conus arteriosus, serving apparently to direct the aerated blood (from the left side) chiefly into the anterior vessels of the ventral aorta, whereas the non-aerated blood (from the right side) was directed chiefly into the posterior pair of vessels bearing the pulmonary arteries. Thus we can recognize a pulmonary and a systemic chamber in the conus arteriosus. In amphibians that have functional lungs; the heart consists of 3 chambers:, atrium completely divided into right and left atria, a ventricle and a sinus venosus and conus arteriosus which is partially divided with the help of a spiral valve. In frogs, whose cardiovascular system is best studied, the conus arteriosus arises from the single trabeculate ventricle. Trabeculae are the projecting cones of the muscles that arise from the inner wall of myocardium of the ventricle creating deep recesses or compartments in the wall. As shown in Fig. 5.5 semilunar valves lie at the base of conus arteriosus and prevent the backflow of the blood into the ventricle. A spiral valve twisting almost through a complete rotation establishes chambers within the conus arteriosus that target blood to the systemic and pulmocutaneous arches, both of which arise from truncus arteriosus, a remnant of ventral aorta. The sources of oxygenated blood vary in amphibians; as for respiration they depend on the skin, on gills, on lungs or on all the three modes. It is for this reason the heart structure varies in different amphibians.

In lungless salamanders or the ones with reduced lung function the septum dividing the atrium as well as the spiral valve may be much reduced or entirely absent. In amphibians such as *Necturus* where gills dominate lungs as respiratory organs, the interatrial septum is reduced or perforated. The atrium is completely divided in modern anurans and in all living reptiles, birds and mammals.

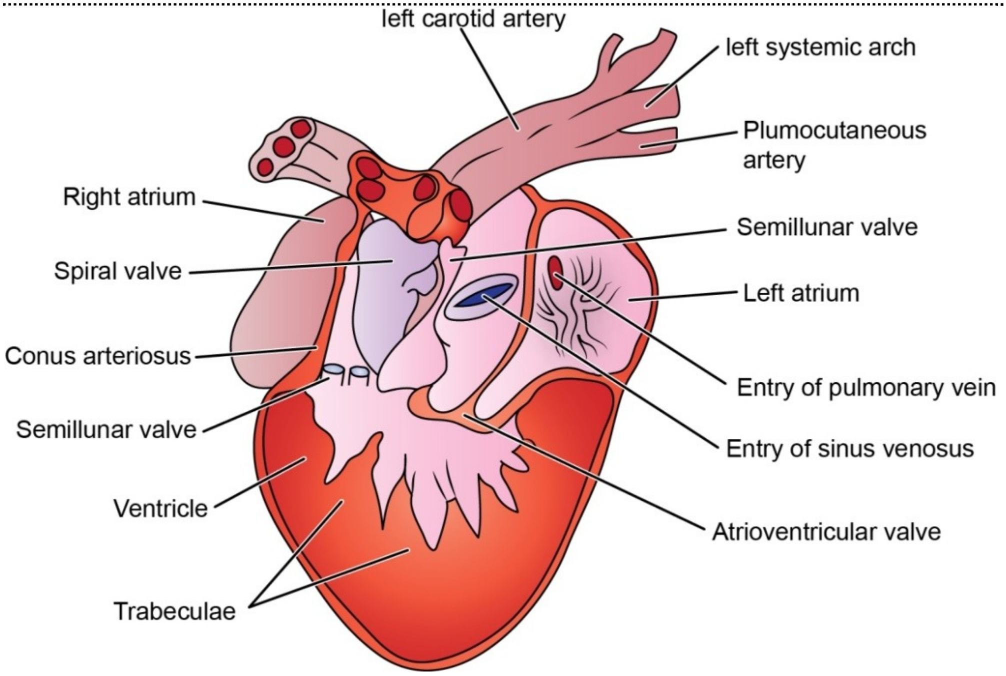


Fig. 5.5: Structure of the heart of a bull frog.

Another alteration in amphibian heart is the reduction of sinus venosus both in size and importance as a blood-gathering chamber. A large thin-walled heart chamber (sinus venosus), into which the blood can flow against an absolute minimum of resistance is essential for fishes. In land-dwelling vertebrates, subjected to the markedly lesser atmospheric pressure, such an elaborate collecting device is not essential; in later stages it is discarded completely.

In amphibians the deoxygenated and oxygenated blood streams returning from systemic and pulmonary circuits are kept separate as they pass through the heart. The deoxygenated blood is selectively directed to the lung via pulmonary artery and the oxygenated blood is directed to the systemic tissue via aortic arches. In frogs during the time of air breathing, the trabeculae in the ventricle separate the two different streams of blood in the heart. It is thought that as one stream enters the ventricle, it fills the compartments between the trabeculae, and then the second stream occupies the centre of the ventricle. Because of their different positions, the oxygenated and deoxygenated streams depart by different exits to reach appropriate set of arteries. Whenever a frog dives in the water, the lung collapses from the water pressure on the body wall. The blood flow is reduced in the lungs and increased in the skin. Thus, the loss of pulmonary respiration is somewhat compensated by increased cutaneous respiration in submerged frogs. Before we proceed further, try the following SAQ.

SAQ 1

Fill in the blanks with appropriate words.

i) The tubular heart of protochordates beats by ……………… .

ii) In the early tetrapod heart the …………… is divided into two chambers.

iii) Ventricle is ……………… in frogs.

iv) In *Necturus* the …………… ……………… is reduced or perforated.

v) In amphibians during diving the ……………… respiration is increased.

5.2.4 Late Ectotherm Heart

Living reptiles varied in cardiac structure though they exhibit uniformly a number of improvements over the early tetrapod heart (Fig.5.6). Since most reptiles are adapted to a fully terrestrial environment and have more active lifestyle, their cardiovascular system supports the accompanying higher metabolic rates and elevated levels of oxygen and carbon-dioxide transport. It is also capable of generating higher cardiac out-put, elevated blood pressures and more efficient separation of oxygenated and deoxygenated blood streams as compared to amphibians. Basically two types of reptilian hearts (one in chelonians and squamates and other in crocodiles) have been recognised.

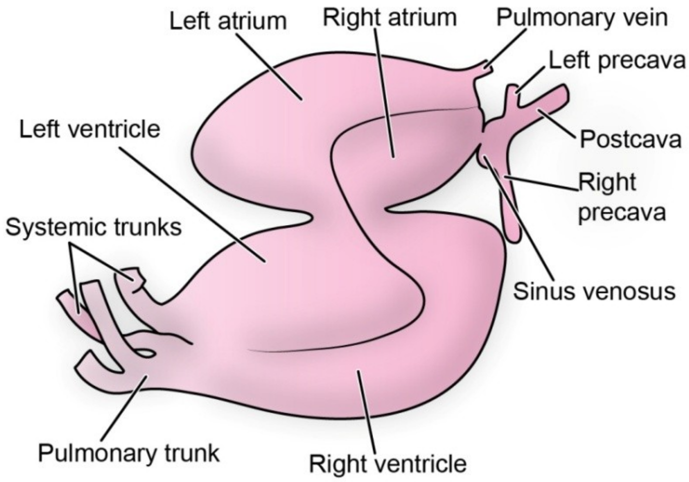


Fig. 5.6: Late ectothermic heart, ventral view with parts drawn to side instead of superimposed as in actual structure.

In chelonian/squamate heart, the sinus venosus is reduced in size as compared to that in amphibians and in advanced types ancestral to mammals, it has disappeared completely as a chamber, although it is present in all living reptiles. From the very first vertebrates, however, the sinus venosus served a function not only as a collecting chamber but also as a site of origin of heartbeat. Although its identity as a chamber may have been lost in at least some reptiles and certainly in birds and mammals, the function it formerly performed for initiation of heart beat still remains. The excitatory tissue remained embedded in the wall of the right atrium near the point of the entry of veins, that now with the loss of the sinus as a chamber, empty directly into the atrium. This myogenic center is the sinoatrial node, which serves in all amniotes lacking sinus venosus as the originator of each heartbeat. The conus arteriosus also disappeared, though it appears during early embryonic development, in adults it was subdivided to form the bases (trunks) of the three large arteries leaving the ventricle: the pulmonary trunk and the right and left aortic trunks (systemic trunks). This pairing of systemic trunk is seen in many reptiles, the right trunk connected with the left side of the heart, the left with the right side. Despite the loss of the role of the conus arteriosus as a cardiac chamber in reptiles, the semilunar valves that conus formerly possessed remained intact and unchanged. These persist at the bases of the pulmonary and systemic trunks in all amniotes, but are reduced into three valves in each vessel. Atrium is divided into right and left atria. Entry to the ventricle is guarded by the atrioventricular valves. Ventricle is partially divided internally resulting in a rather effective separation of venous and arterial blood. As you can see in Fig. 5.7, it has three interconnected compartments: cavum venosum, cavum pulmonale, cavum arteriosum. Cavum venosum and cavum pulmonale are separated from each other by a muscular ridge and cavum arteriosum is connected to the cavum venosum through an interventricular canal.

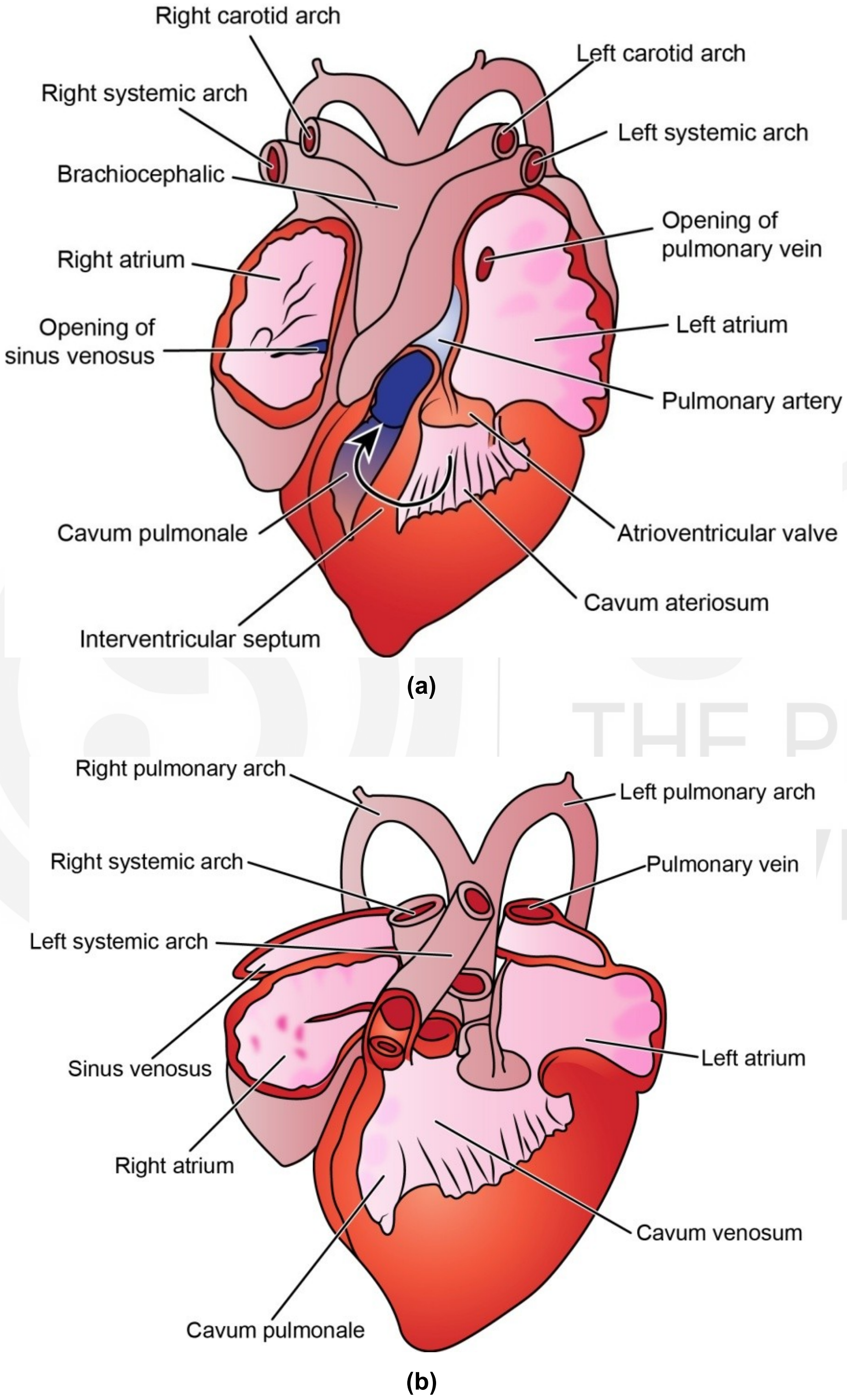
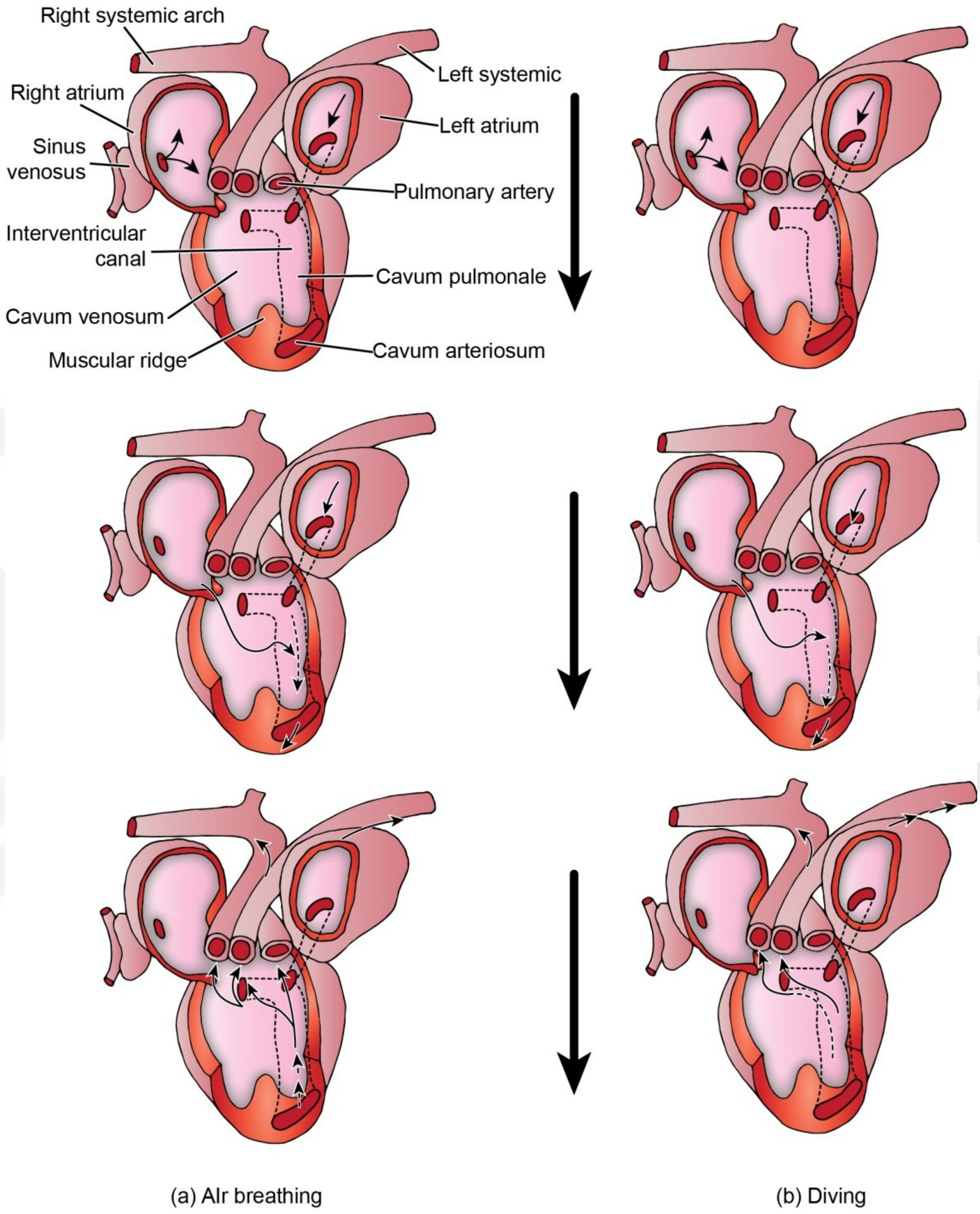


Fig. 5.7: Ventral view of the lizard heart. (a) Small part of the ventral wall has been removed. The arrow shows the direction of blood flow from cavum arteriosum to cavum venosum through interventricular canal. The blood goes to systemic arches from cavum venosum. (b) Structure of the heart after some more part of the ventral wall has been removed.

Apnea, a condition of holding breathe occurs not only during diving. Most reptiles, while resting on land go for long intervals without taking a breath. As apnea continues, oxygen from the lungs becomes depleted and pulmonary perfusion declines until just before another breath.

As you can see in Fig. 5.8, the pattern of blood flow through the hearts of chelonian and squamates varies depending on whether they breathe air or hold their breath (a condition called apnea). For example, when turtle is air breathing on the land most of the deoxygenated blood returning from systemic tissues is directed to the lungs and most of the oxygenated blood from the lungs is directed to the systemic tissues via the aortic trunk. When the turtle dives in the water, the heart responds with a right to left cardiac shunt. Blood flowing in the cavum venosum is directed to the aortae rather than the pulmonary circuit. This shunting is controlled by the differences in the resistance of systemic and pulmonary circuits.

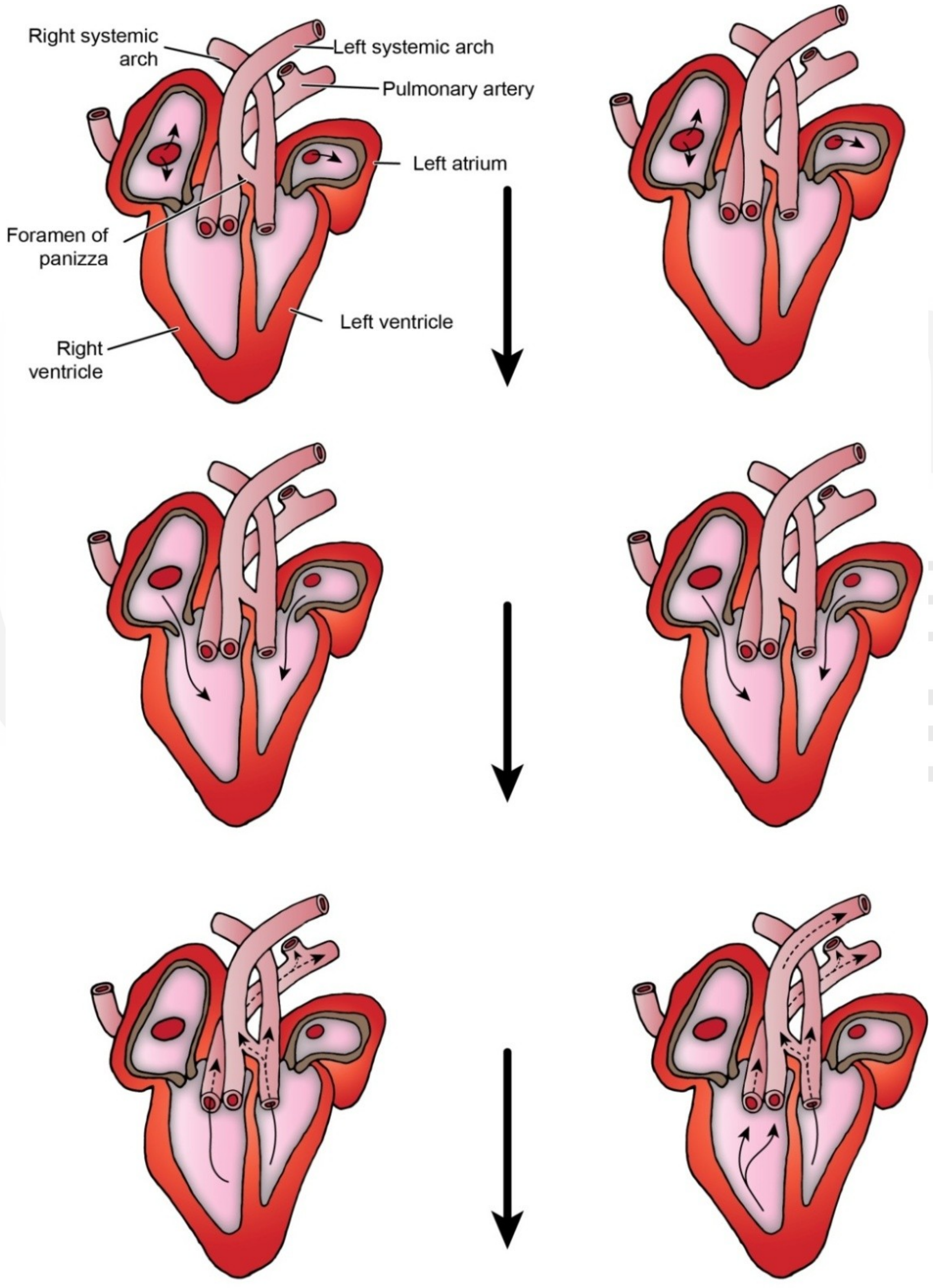


(a) Air breathing (b) Diving

Fig. 5.8: The path of blood flow in the squamate heart. (a) In the squamates breathing air, venous blood from the right atrium enters the cavum venosum, crosses the muscular ridge and fills the cavum pulmonale. When ventricle contracts, most of this blood flows in the pulmonary artery. Simultaneously, blood from the left atrium enters the deep cavum arteriosum. Upon contraction of the ventricle this blood passes through the interventricular canal to the left and right aortic arches. (b) On diving, due to the resistance to the pulmonary blood flow, the blood moves across the muscular ridge and departs mainly through the left aortic arch.

The heart of crocodiles shows structural variations in certain aspects. The ventricle is completely divided into right and left chambers by a complete interventricular septum. The pulmonary trunk and the left aortic arch opens off the right ventricle and the right aortic arch opens off the left ventricle.

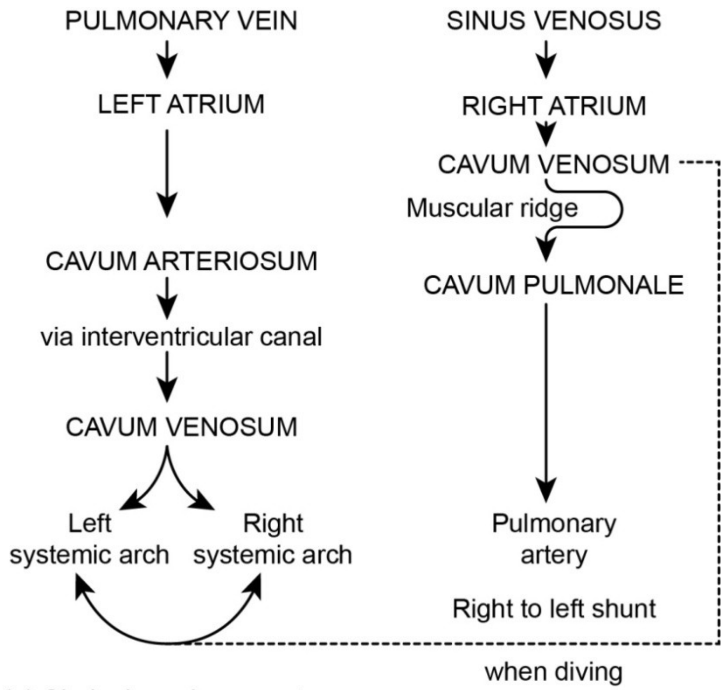
Curiously, the left arch does not receive blood directly from its own (right) ventricle, since the semilunar valves actually prevent flow from ventricle to aorta except under unusual stress situation. The left arch receives blood, through the foramen of Panizza that connects the right and left arches where they cross a short distance from the heart (Fig. 5.9). You can see in Fig. 5.10 the comparison of the path of blood flow in the hearts of chelonians / squamates and crocodiles.



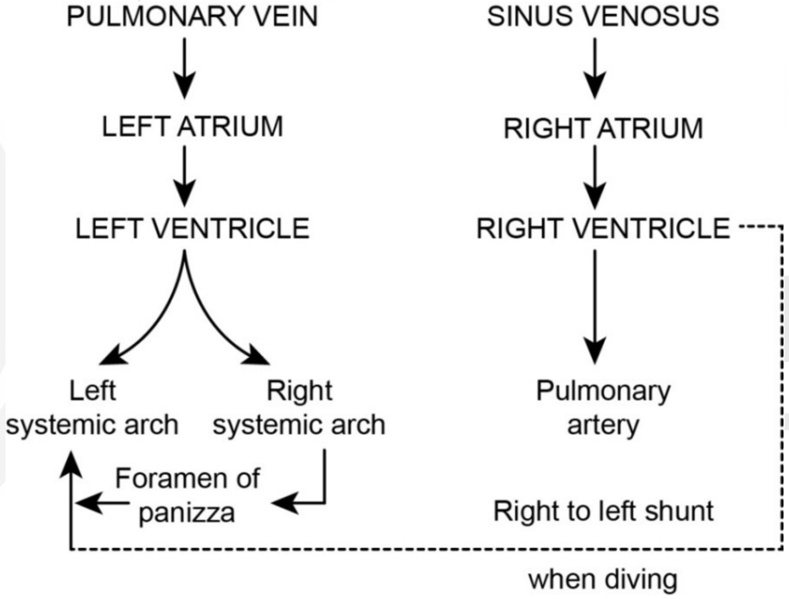
(a) Air breathing

(b) Diving

Fig. 5.9: Blood flow through the crocodile heart. (a) Systemic and pulmonary blood flow during air breathing period. (b) Internal changes that result in decreased pulmonary flow when the crocodile dives.



(a) Chelonia and squamates



(b) Crocodilians

Fig. 5.10: The flowchart comparing the blood flow patterns in the hearts of (a) chelonian and squamate, and (b) crocodiles. Dashed lines indicate the cardiac shunts that divert blood flow from pulmonary circuit to systemic circuit while diving. During this cardiac shunt resistance to pulmonary flow increases due to contraction of the sphincter at the base of pulmonary artery. In crocodiles the vasoconstriction of the vascular supply to the lungs also aids in this resistance.

So we can summarise that in the later ectothermic stage, out of the six occurring in the, preceeding stage, only three cardiac chambers remain. One of these three (the ventricle) is further subdivided so that in this stage there are four cardiac chambers at least partly separated from each other.

5.2.5 Endotherm Heart

Only a few, relatively slight alterations have occurred in endotherms to effect the maximum efficiency of the heart (Fig. 5.11).

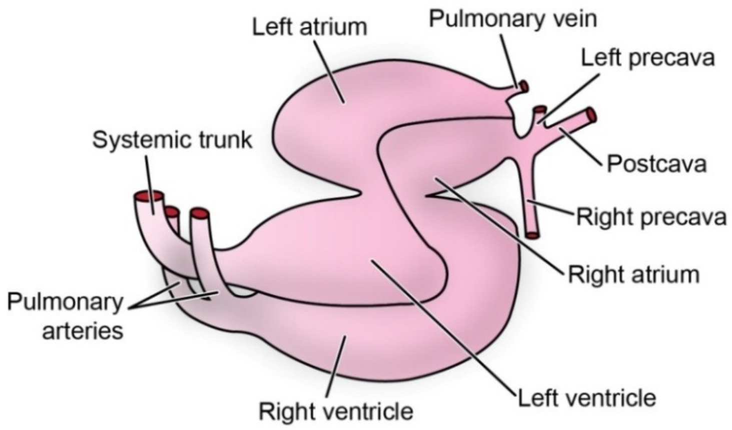


Fig. 5.11: Endothermic heart, ventral view with parts drawn to side.

Most important is the complete closure of the ventricular wall, rendering absolutely impossible any mixture of aerated and non-aerated blood. The trend towards double circulation in the heart was initiated certainly in the sarcopterygians. It attained perfection in endotherms. Closure of the ventricles along with simplification of the systemic aorta is the last step in reaching the greatest possible perfection in the cardiac link of the "forced draft" respiratory mechanism unique to birds and mammals and chiefly responsible for their endothermic condition.

In birds, though the sinus venosus is reduced, it still remains a small discrete area. The conus arteriosus is only transiently present in embryonic condition, that gives rise to the pulmonary trunk and a single aortic trunk (Fig. 5.12).

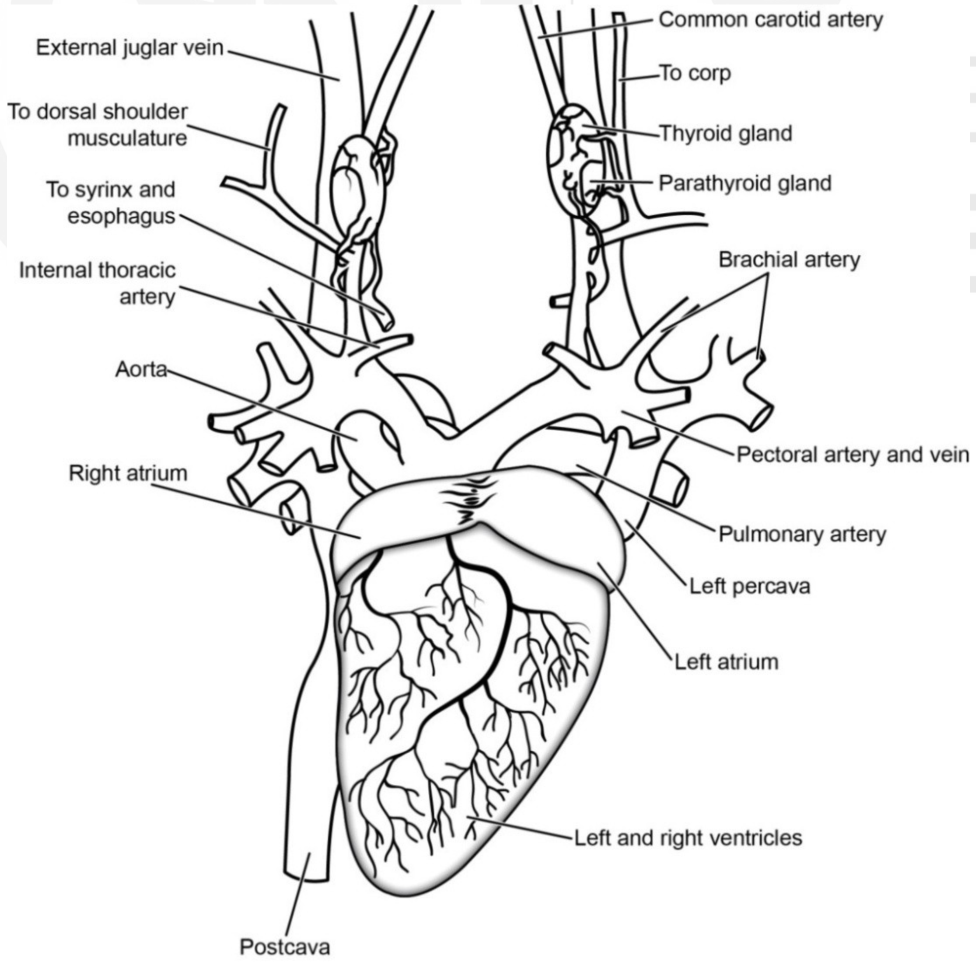


Fig. 5.12: The heart of a bird (ventral view).

In mammals the sinus venosus is reduced to a patch of Purkinje fibers (also called sinoatrial node) in the wall of right atrium. This node acts as a pacemaker, initiating the wave of contraction i.e. rhythmic heart beat that spreads across the heart like in all other vertebrates. Another mass of typical muscle fibers called as the atrioventricular node in the wall of right atrium in the four chambered heart, also acts as pacemaker under experimental conditions when the sinoatrial node is destroyed or prevented from functioning. Similar to that in birds the conus arteriosus during embryonic development splits to produce the pulmonary trunk and single aortic trunk of the adult (Fig. 5.13). The mammalian heart possesses only two of the three sets of valves present in piscine ancestors; the semilunar valves and the atrioventricular valves. The latter set is now divided into two, to which the names tricuspid valve and bicuspid or mitral valve are applied in mammals.

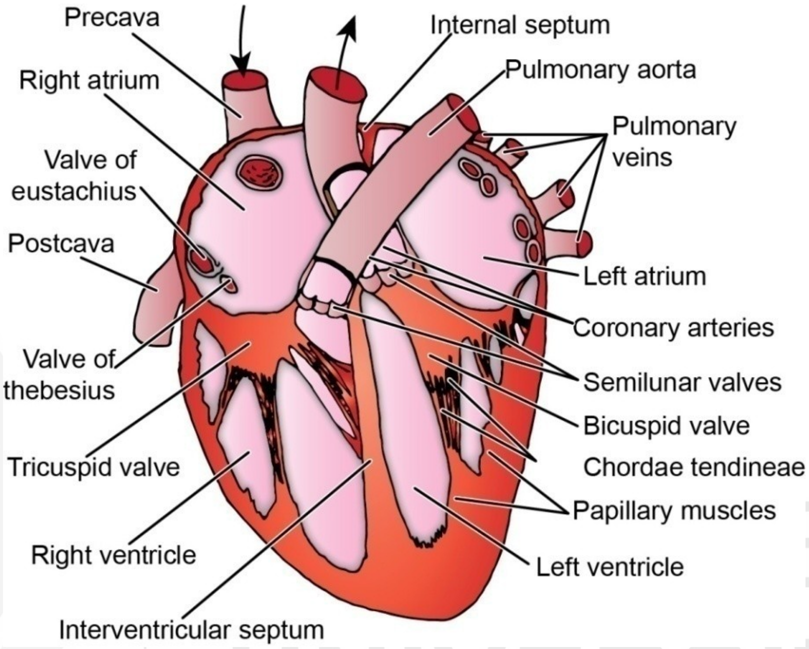


Fig. 5.13: Ventral view of the mammalian heart.

Although the structure of avian and mammalian heart is similar they both have evolved from different reptilian groups. This difference is reflected in their embryonic development. Both these hearts also function similarly as both consist of parallel pumps with double circulation circuits. The right side of the heart gathers deoxygenated blood from the systemic tissues and pumps it in pulmonary circuit. The left side of the heart pumps oxygenated blood from the lungs through the systemic circuit. There is no cardiac shunting as hearts of birds and mammals are divided into right and left chambers.

In single circulation pattern the blood passes only once through the heart during each complete circle as seen in most of the fishes (Fig. 5.14a). Amniotes have double circulation pattern in which blood passes twice through the heart in every circuit (Fig. 5.14b). From the heart the blood goes to the lungs, back to heart out to systemic tissues and again back to the heart. The major evolutionary event was addition of pulmonary circuit in the circulatory pattern. The intermediates that have characteristics of both the conditions include lung fishes, amphibians and reptiles. The evolution of this type of circulatory system design is the adaptive advantage of the transitional forms that came onto land.

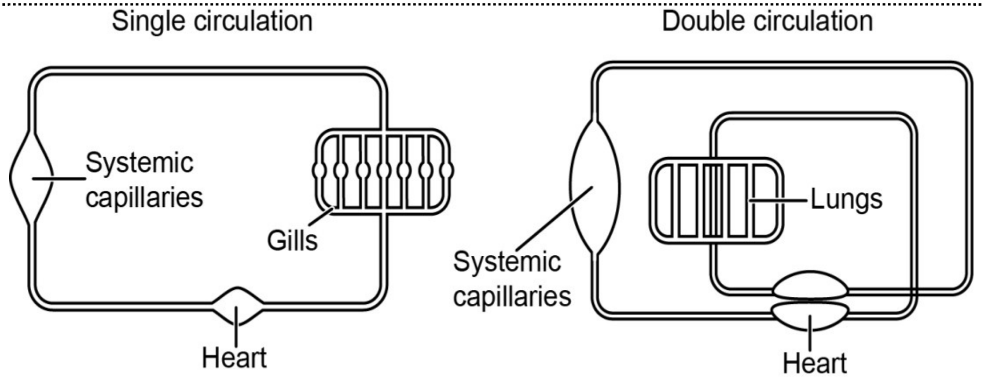


Fig. 5.14: Diagrammatical representation of single circulation (a) and double circulation (b).

You have finished studying about the evolution and structure of heart. In order to judge your progress attempt the following SAQ.

SAQ 2

i) Fill in the blanks with appropriate words.

a. Sinus venosus is ……………. in size in chelonian heart.

b. Pacemaker or sinoatrial node ……………. the heart beat.

c. The ventricle is …………….divided in squamates and is ……………. divided in crocodiles.

d. The systemic trunk is paired in ……………. and ……………. .

e. Double circulation in heart was initiated in ……………. .

f. Tricuspid and bicuspid valves are present in the ……………. heart.

ii) What is rhythmicity of heart beat in mammals?

5.3 ARTERIAL SYSTEM

Although arterial system in different vertebrates appears to be different in arrangement, a study of development reveals that all are built upon the same fundamental plan. The increasing complexity of the heart from the simple two chambered structure of the lower forms to the four-chambered organ of crocodilians, birds and mammals is associated with certain variations to be found in the blood vascular system. Modifications of the embryonic pattern, which occur during later ontogeny are of such a nature that they adapt the aortic arches for respiration either by gills or by lungs.

5.3.1 Aortic Arches-Overview

Early chordates evolved blood vessels that were retained as aortic arches in vertebrates. During embryonic development in all vertebrates the anterior end of the ventral aorta divides into two arches called aortic arches, which course dorsally into the mandibular region. Dorsal to the pharynx these are continued posteriorly where they are known as paired dorsal aortae. Additional pairs of aortic arches then appear in an anterio-posterior sequence, forming connections between ventral and dorsal aortae on each side (Fig5.15). Each travels through the tissue between the adjacent pharyngeal pouches. The typical number of aortic arches that are taken as basic embryonic pattern in vertebrates is six pairs, although there are certain exceptions among lower forms, such as, eight in lamprey, fifteen in hagfishes and ten or twelve in some species of shark. The first is known as mandibular aortic arch and the second is hyoid aortic arch. The remainder are referred to as the third, fourth, fifth and sixth aortic arches, respectively and all are designated by roman numerals (Fig. 5.15). Each aortic arch lies anterior to the visceral cleft bearing the corresponding number. The two dorsal aortae soon fuse posterior to the pharyngeal region, so that ultimately only a single dorsal aorta is present. It is continued in the tail region as a caudal artery. Blood which is pumped anteriorly by the heart, passes through the ventral aorta to the aortic arches. These vessels carry blood to the paired dorsal aortae, from which it goes anteriorly to the head and posteriorly to the single dorsal aorta which distributes it to the remainder of the body. Veins return blood to the sinus venosus, atleast during early stages of development. As we go up the vertebrate series we find that the number of aortic arches decreases from 6 in fishes to 3 in amniotes. As you read why this decrease happens you will be able to correlate it with the complexity in heart structure seen from fishes to amniotes and also the transition from an aquatic life to terrestrial seen in vertebrates. Let us learn about these changes in the aortic arches in different groups of animals.

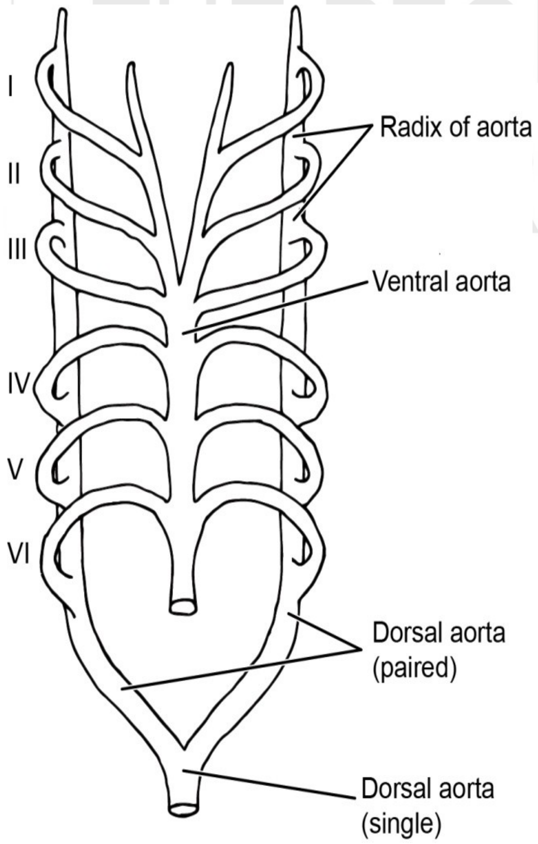


Fig. 5.15: Diagram illustrating the basic pattern of aortic arches in vertebrate embryos. Ventral view. Six pairs of arches connect ventral and dorsal aortae.

5.3.2 Fishes

The aortic arches of gill bearing vertebrates are primarily for bringing blood from the heart via the ventral aorta and afferent arteries through the gills where the blood is oxygeneated in a capillary bed and drained via the efferent arteries into the dorsal aorta for circulation in the body. Fish embryos have six pair of arteries corresponding to the six arches but in the adult fishes there is a reduction in the number of aortic arches within the superclass. The greatest number occurs in certain primitive sharks, where it is directly related to the number of gill pouches. The first pair is generally lost or modified. The IInd arch is present in elasmobranchs but lost in many other fish (Fig. 5.16). The anterior continuation of the paired dorsal aortae gives rise to the internal carotid arteries supplying to the brain; those arising from the ventral aorta form the external carotid arteries which supply blood to jaws and face.

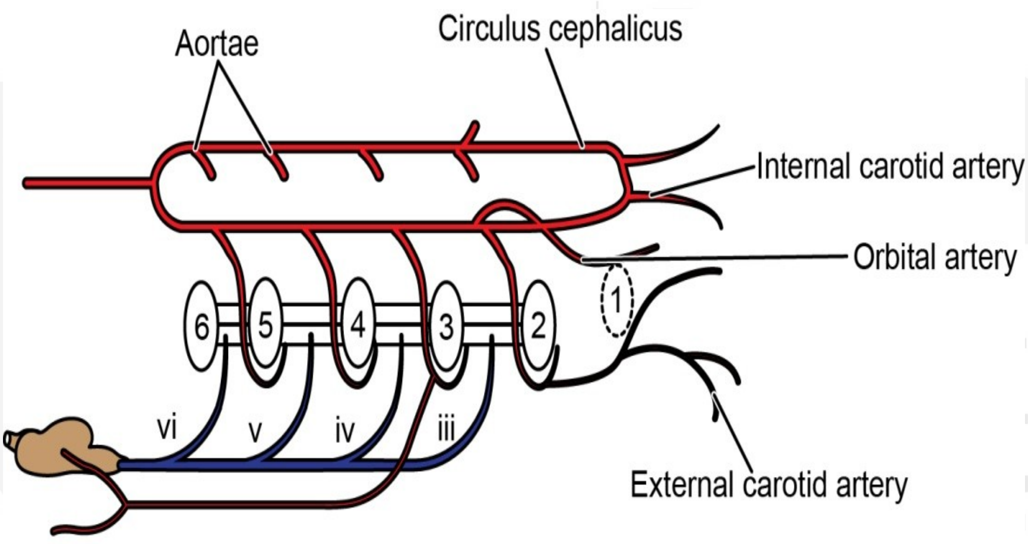


Fig. 5.16: Diagram of aortic arch region as found in most teleost fishes : ventral view. Arches I and II have degenerated. Each remaining arch is divided into afferent and efferent branchial arteries that are connected by gill capillaries.

Lungfishes have both gills and lungs and depend on their lungs for respiration, thus they have lost the capillary beds associated with arches III and IV (Fig. 5.17).The corresponding arches (III and IV) are uninterrupted vessels. When arches I and II are lost then the anterior extension of dorsal aorta from arch III continues and the internal carotid artery to the head. Fifth and VI have capillary networks and pulmonary arteries arise from the VI arch and go to the lungs of lungfishes and to the swim bladder of coelacanths.

Pulmonary veins bring back blood from the lungs to the heart via the left atrium. This is not a very efficient system but has some ability to shunt blood to regions of the body where oxygenated blood is necessary.

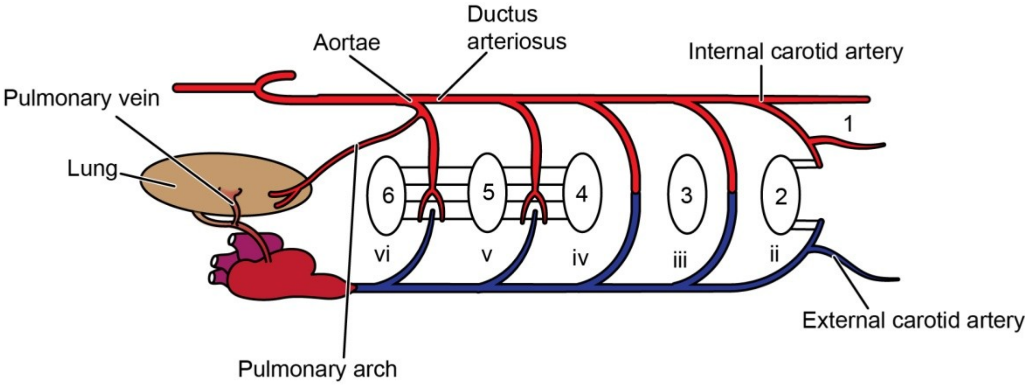


Fig. 5.17: Aortic arches of *Protopterus* (lung fish).

5.3.3 Amphibians

Since amphibians rely on lungs for respiration, the gills are no longer important for adults. Amphibians possess external gill filaments, atleast during early development but they are not homologous with the internal gill lamellae of fishes, nor are they supplied with blood in the same manner. In amphibians, generally the first two aortic arches (I, II) disappear early in the development. The pattern of remaining arches differs between larvae and metamorphosed adults. The frog larva has last four aortic arches (III-VI) that deliver blood to the internal gills. The embryonic pulmonary artery buds from the arch VI. During metamorphosis the gills and arch V are lost in anurans but is present in some urodeles (salamander) leaving arches III, IV and VI intact (Fig. 5.18). Dorsal link between III and IV becomes thin in urodeles but is lost in anurans.

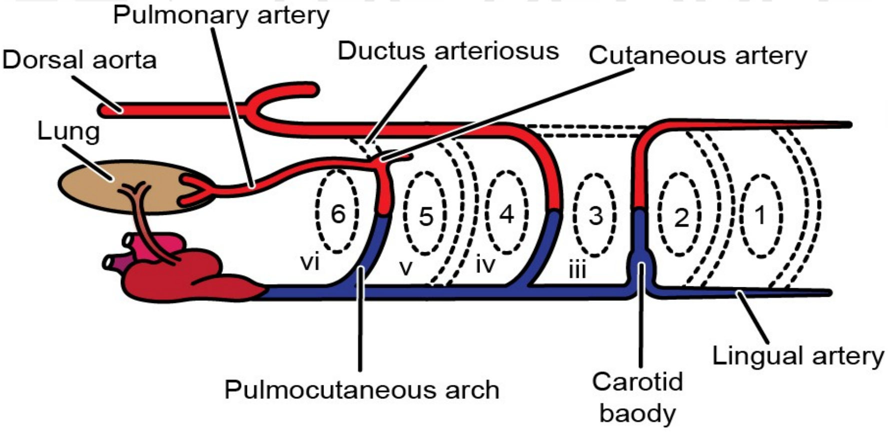


Fig. 5.18: Diagram showing modification of aortic arches as found in adult frog.

The anterior continuation of the ventral aorta becomes external carotid artery. The third arch becomes the internal carotid artery, and both of these carotid arteries arise from the common carotid which is the section of ventral aorta that lies between III and IV arches. At the base of the internal carotid lies the carotid body which is an enlarged portion of the carotid arteries and is formed at the point of branching of carotid arteries.

The fourth aortic arch persists to become the systemic arches which unite posteriorly to form the dorsal aorta. Arch VI on each side sends a branch to the developing lung and another branch to the skin, thus becoming the pulmocutaneous artery. Fig. 5.19 shows the arterial system of the adult frog.

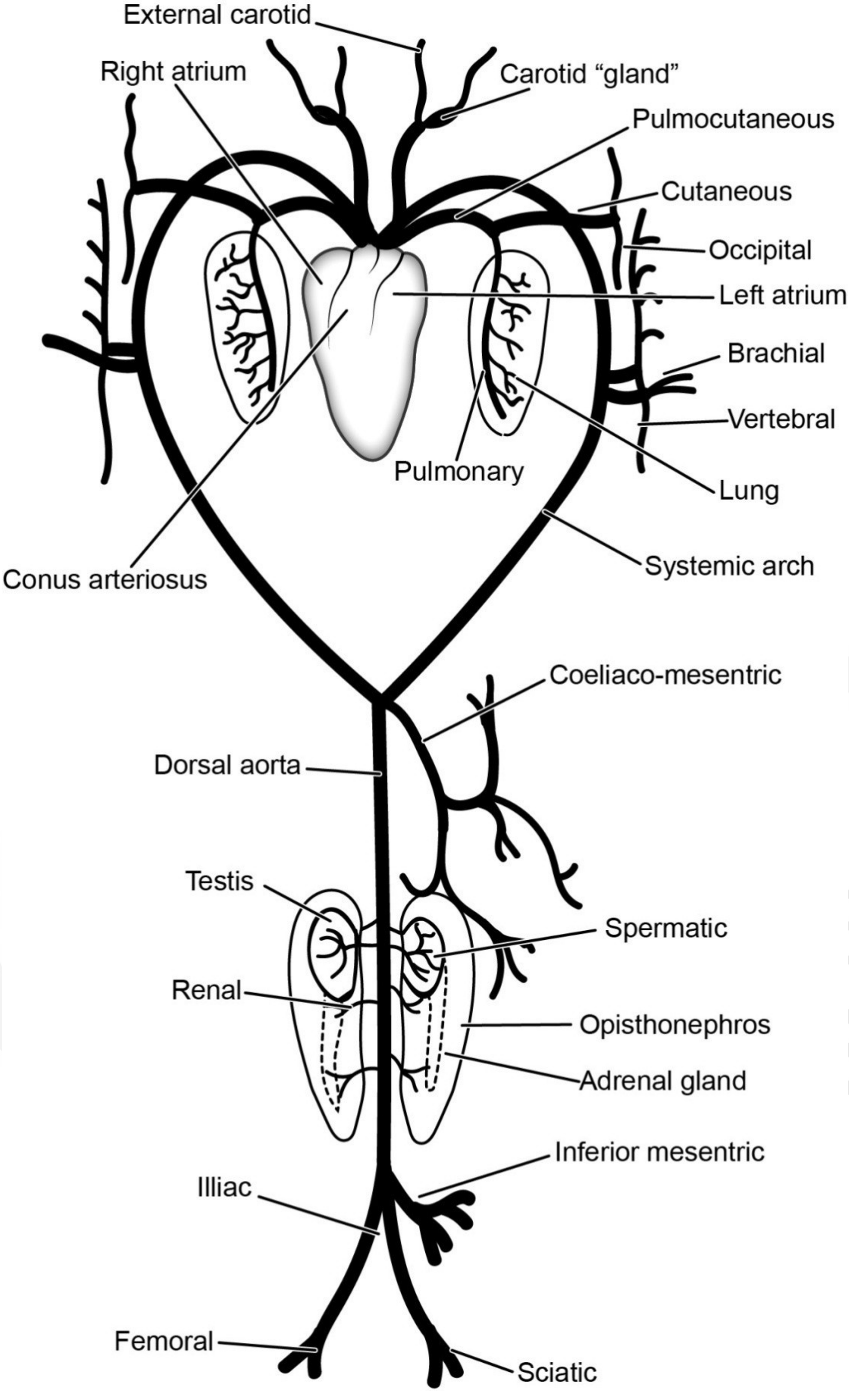
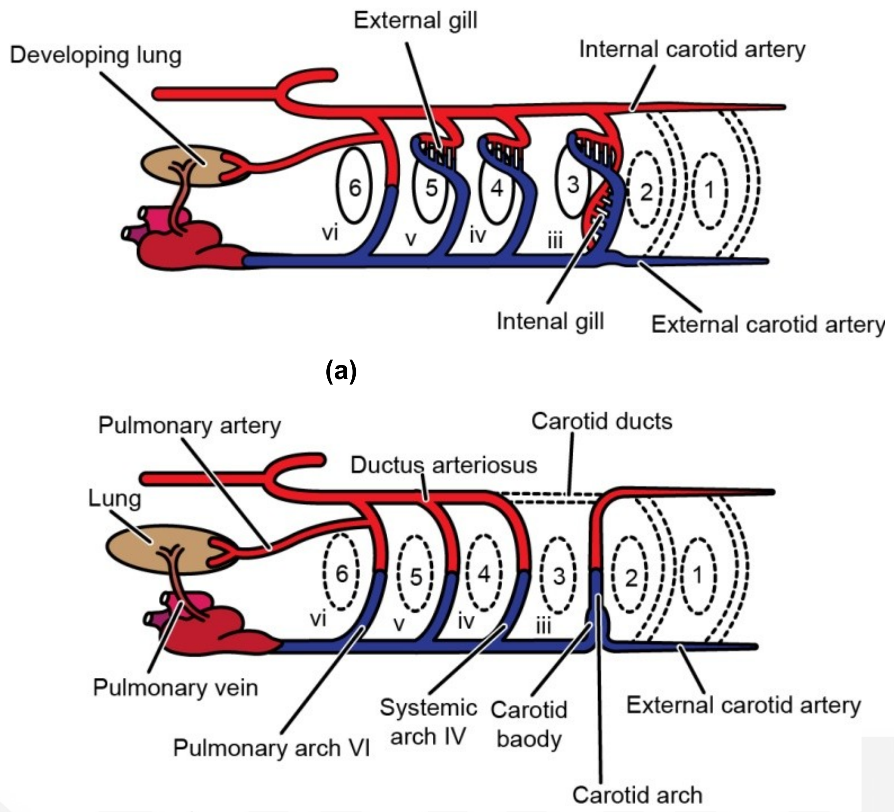


Fig. 5.19: Diagram of arterial system of adult frog (ventral view).

In salamanders (Caudates) the fifth arch may persist in a very reduced form. Frequently the radix or the lateral aorta between arches III and IV fails to degenerate completely. The ductus arteriosus also persists in caudates.

The external gills of larval caudates are supplied with vascular loops connected to aortic arches. In caudates, at the end of metamorphosis gills degenerate and atrophy of the vascular loops i.e. capillary net work surrounding the gill lamellae and collecting loop occurs (Fig. 5.20).



(a)

(b)

Fig. 5.20: Diagram showing modification of aortic arches as found in most caudate amphibians, (a) Salamander (larval); (b) Salamander (adult).

Certain caudates, such as neotenic salamander *Necturus* are called perenni branchiates since they retain gills throughout life and fail to metamorphose. In this amphibian, the fifth aortic arch persists and the pulmonary artery arises from the fifth arch rather than the sixth, the ventral portion of which is lacking. Blood going to the lungs in *Necturus* has already been oxygenated. The lungs, therefore, under normal conditions are unable to function as respiratory organs, and the gills are retained. Now try the following SAQ to assess your understanding.

SAQ 3

Match the items given in column I with those in column II.

	Column I		Column II
i)	Basic embryonic pattern in vertebrates	a)	Supply blood to jaws and face
ii)	External carotid artery	b)	Generally in amphibians
iii)	Reduction/modification of I and II aortic arches	c)	Occurs in caudates
iv)	Disappearance of I and II aortic arches during early development	d)	Characteristic of teleosts
v)	Atrophy of vascular loops at the end of metamorphosis	e)	Six pairs of aortic arches

5.3.4 Reptiles

Since reptiles are fully terrestrial, gills are totally absent and replaced by lungs. Just as in amphibians, reptiles retain aortic arches III, IV and VI. The fifth arch may also be retained in reduced form in certain lizards, and a remnant of the radix between arches III and IV may persist in some snakes.

In most reptiles, further modifications occur in the aortic arches (Fig. 5.21). Arches I, II and V are lost. Dorsal connection between III and IV disappears. Arch III forms a part of the internal carotid arteries and forward extensions of the ventral aorta form the external carotid arteries. Other important changes are splitting of the distal portion of the conus arteriosus and part of the ventral aorta into three vessels - left systemic arch, right systemic arch derived from the IV arch and the pulmonary trunk.

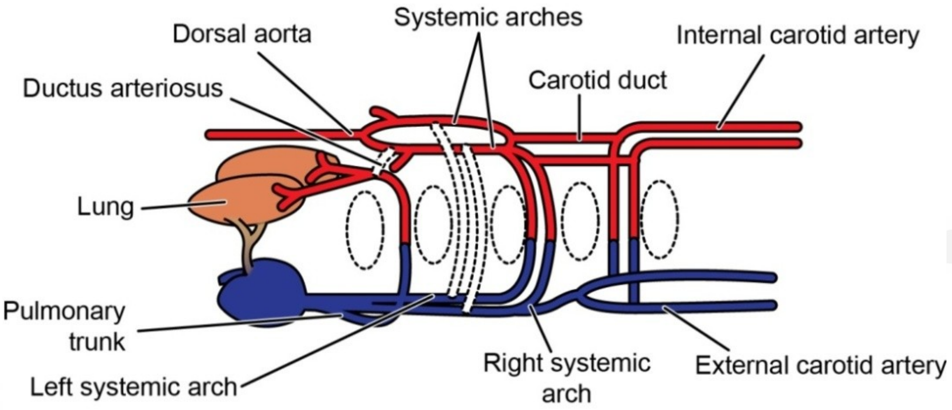


Fig. 5.21: Diagram showing modification of the aortic arches as found in reptiles. The ventral aorta has split into three vessels.

The right systemic arch arises from the left side of the ventricle carrying oxygenated blood to the carotid arch (IIIrd) to be sent to the head. Left systemic arch arises from the right side of the ventricle carrying mixed blood to the body through the dorsal aorta some mixing may also occur through the foramen of Panizza. Mixing of oxygenated and deoxygenated blood seems to be associated with the poikilothermal mode of life. (Poikilotherms are those animals which cannot adapt themselves to the changing temperature e.g. fishes and amphibians). The sixth arch on each side gives off a pulmonary artery carrying deoxygenated blood to the lung. The two pulmonary arteries, therefore, arise from a common trunk, the pulmonary aorta, coming from the right side of the ventricle. Thus, the modifications of the aortic arches give rise to one pulmonary circuit and two systemic circuits each of which arise independently from the heart.

5.3.5 Birds

Though 6 arches are present in the embryo; only II, IV and VI are retained in the adults. The ventral aorta splits into two portions, a systemic aorta and a pulmonary trunk or aorta. The systemic aorta is connected to tile left ventricle, and the pulmonary aorta to the right. The fourth aortic arch on the right side leaves the right systemic aorta and together with the radix, leads to the dorsal aorta proper, which supplies the entire body with oxygenated blood. The left systemic aorta does not develop fully. The pulmonary trunk leading from the right ventricle gives off the pulmonary arteries, which are actually outgrowths of the sixth aortic arch.

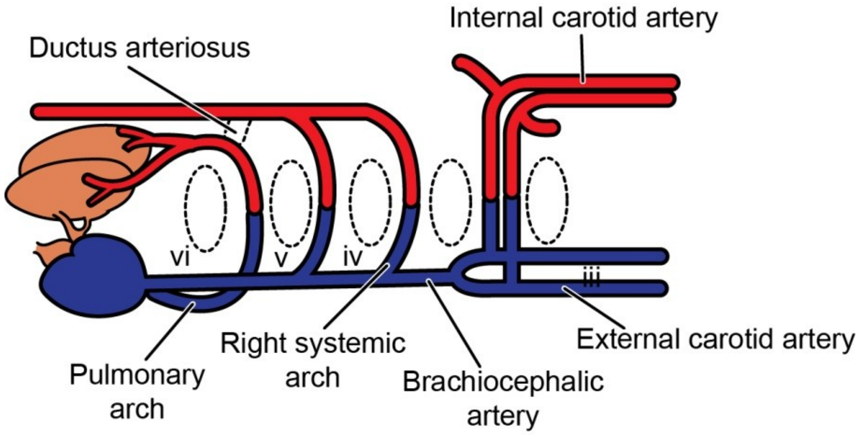


Fig. 5.22: Diagram showing modification of aortic arches as found in birds.

Until the time of hatching there is a ductus arteriosus on each side, representing the portion of sixth aortic arch between pulmonary artery and radix (Fig. 5.22). These serve as shunts from the right ventricle to the dorsal aorta until the lungs become functional. They close at the time of hatching, and the blood from the right ventricle is then sent to the lungs for aeration.

5.3.6 Mammals

Changes in the aortic arches of mammals are rather similar to those of birds. Only III, IV and VI arches are retained in the adult. The IV aortic arch on the left side together with its radix becomes the arch of the definitive aorta and therefore, is the left systemic arch in mammals. The IV arch on the right and a portion of the right radix together become the right subclavian artery. The left subclavian develops as an enlargement of one of the intersegmental arteries coming off the aorta (left systemic arch) in this region (Fig. 5.23). From the right subclavian emerges the right common carotid going to the neck and head. The VI arch gives rise to the pulmonary aorta that divides in right and left pulmonary arteries going to the lungs. In mammalian embryos there is at first a ductus arteriosus on each side, but the one on the right persists for only a short time. The left one, which serves as a shunt between pulmonary and systemic aortae, persists until birth, when it finally becomes occluded. The carotid arteries are formed from the paired third arch.

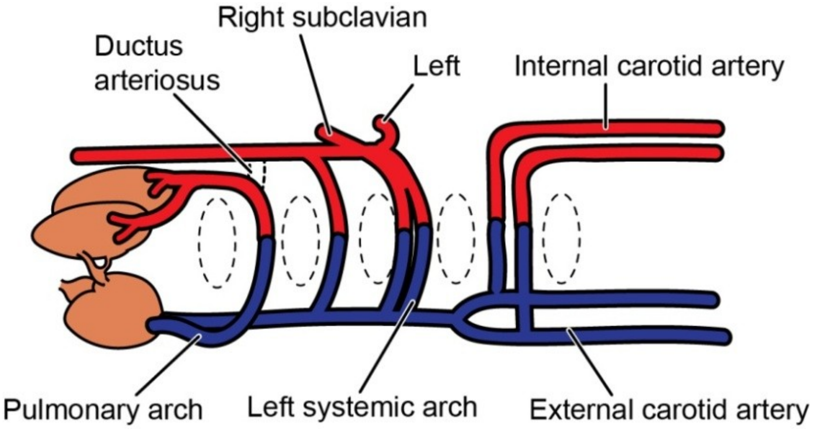


Fig. 5.23: Diagram showing modification of aortic arches as found in mammals.

5.3.7 Evolution of Aortic Arches

Till now you have studied about structure of aortic arches in different vertebrates. Let us now summarise their evolution in vertebrates.

The aortic arches in most of the fishes deliver the deoxygenated blood to the respiratory surfaces of the gills and from there distribute the oxygenated blood to the head region through carotid arteries and to the rest of the body through the dorsal aorta. In lung fishes and tetrapods the aortic arches form two types of circuits – arterial circuit to lungs through pulmonary arch and arterial circuit to rest of the body through systemic arches. Blood to the head in tetrapods is supplied by carotid arteries that arise from the systemic arch. The left and right arches are present in reptiles also. However, these are reduced to single systemic arch, the right arch in birds and left arch in mammals. You can see the evolution of aortic arches in Fig. 5.24.

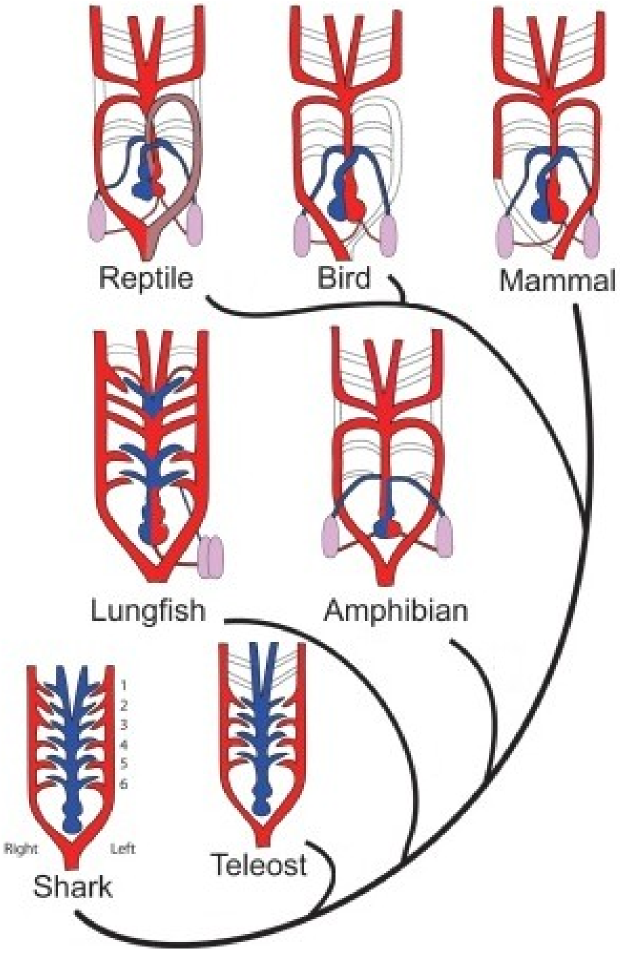


Fig. 5.24: The evolution of aortic arches in vertebrates. Hypothetical ancestor with 6 aortic arches corresponding to 6 pairs of gill pouches. Primitive fishes, represented by sharks, also have six paired gill arches. In teleosts, the 1st and 2nd gill arch arteries are absent and only four pairs are seen in the caudal branchial arches. Lungfish have both gills and a pulmonary circulation with the gill arches corresponding to arches two, five, and six. During air respiration, the blood is shunted through arches three and four, while the ductus arteriosus in arch six shunts oxygen-poor blood away from the gills and to the lungs. In adult amphibians, the gill arches are lost and the aortic arch vasculature remains bilaterally symmetrical. Oxygenated and de-oxygenated blood enter the ventricle through the right and left atrium and leaves the heart through a single outflow tract containing a spiral valve. In reptiles such as the turtle, aortic arch artery four remains bilateral but is divided at the base of the outflow tract. The outflow tract is divided into three arteries: right and left aortic arch arteries and the pulmonary artery. In mammals, the fourth aortic arch arteries become bilaterally asymmetrical and the outflow tract separates into two distinct outflow vessels. Birds also have a completely divided outflow tract with asymmetrical aortic arch arteries.

5.3.8 Types of Arteries

Most of the vertebrate body is supplied with blood through branches of the aorta which for convenience sake may be grouped under two divisions: somatic arteries supplying the body proper, and visceral arteries, distribute blood to various portions of the digestive tract and associated structures,

1) **Somatic arteries:** They supply portions of the body derived from the embryonic epimere, being distributed to the dorsal musculature and vertebral column, where they are referred to as parietal, or segmental arteries. In higher forms in which the body is divided into more or less definite regions, terms such as intercostal, dorsolumbar, and sacral are used. The vessels going to the pectoral appendage are called subclavians and those to the pelvic are iliacs, which may be composed of a union of several segmental arteries.

2) **Visceral arteries:** The arteries supplying the viscera are of two kinds: paired and unpaired. The paired arteries are segmentally arranged and supply the body parts that are derived from the embryonic mesomere from which the urinogenital organs and their ducts arise. These are termed as renal, genital, ovarian, spermatic and urinogenital arteries. Renal and genital arteries are numerous in the lower vertebrates, but the number is much reduced in higher forms. The unpaired visceral arteries supplying spleen, and the digestive tract with its derivatives, are vessels which course through the dorsal mesentery of the gut. There are usually three unpaired visceral arteries in vertebrates. The most anterior of these is the celiac artery, supplying the anterior viscera, including stomach (gastric), spleen (splenic) pancreas (pancreatic), liver (hepatic), and duodenum (duodenal). The second unpaired visceral artery is the superior mesenteric, which supplies the entire length of the small intestine, with the exception of the pyloric end of the duodenum, which is taken care of by the celiac artery. The third unpaired artery is the inferior mesenteric, supplying to the posterior part of the large intestine and rectum.

SAQ 4

Give short answers to the following :

i) What is the major modification that occurs in reptilian aortic arches?

ii) What is the role of ductus arteriosus in bird's circulatory system'?

iii) How does right subclavian develop in mammals?

iv) Write difference between somatic and visceral arteries.

5.4 VENOUS SYSTEM

As in the case of the arterial system, a comparative account of veins in various vertebrate groups shows that they are arranged according to the same fundamental plan and that the variations form a logical sequence as the vertebrate scale is ascended. In its development, venous system of higher forms passes through certain stages common to the embryos of lower forms (Fig.5.25). Basically three major sets of paired veins are present in the early developmental stage – **vitelline veins** from the yolk sac, **cardinal veins** from the body of the embryo and **lateral abdominal veins** from the pelvic region.

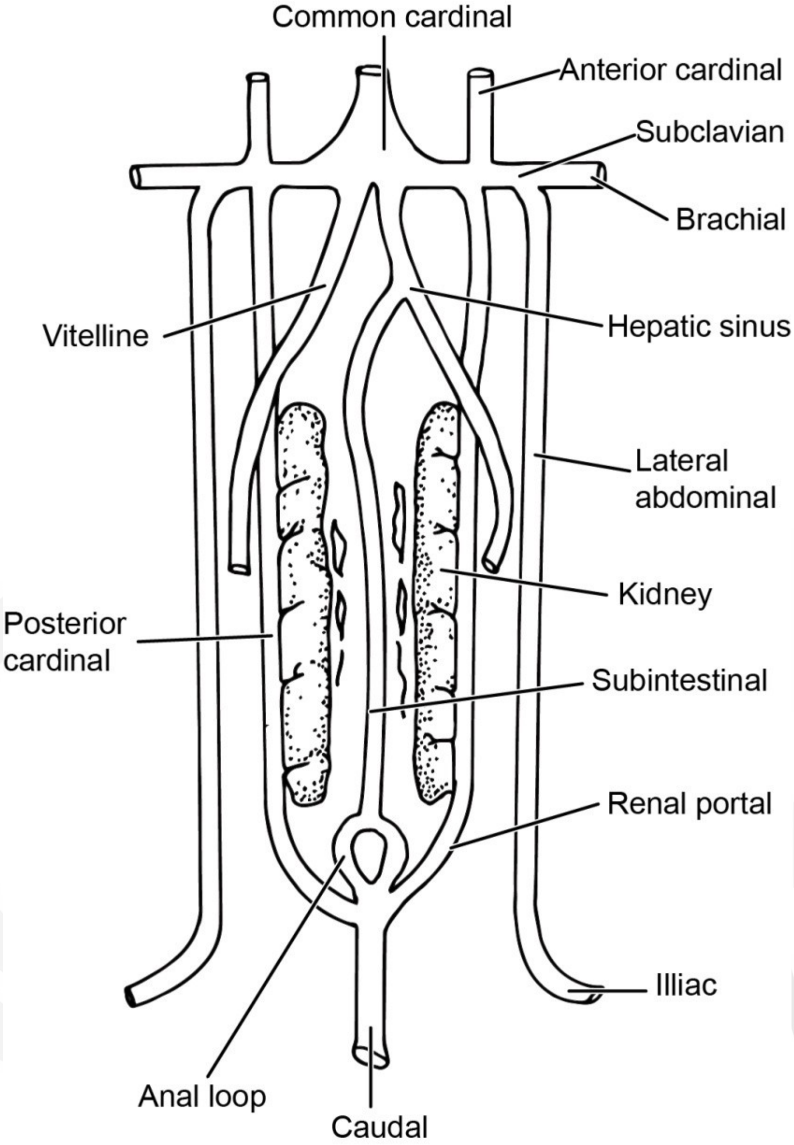


Fig. 5.25: Diagram of basic embryonic venous complex from which the venous system of vertebrates are derived.

Vitelline veins include the hepatic sinusoids and hepatic veins. Hepatic veins collect the blood from hepatic sinusoid network and enter the sinus venosus. The cardinal veins consist of anterior cardinal veins that collect the blood from the head region and, posterior cardinal vein that collects blood from the rest of the body of the embryo. Both these veins meet at common cardinal veins also called as duct of Cuvier that opens into sinus venosus. The lateral abdominal veins are present in fishes but are normally absent or merged in tetrapods. We will discuss about these veins while discussing the venous system of fishes. The vein that carries the absorbed end products of digestion from the digestive tract to the vascular sinusoids in liver is called the hepatic portal vein. It is present in all vertebrates and is developed from the embryonic subintestinal vein originating in the caudal vein. The subintestinal vein loops around the anus, extends along the ventral wall of intestine, passes through the liver and finally joins the left vitelline vein. The structural variations in the venous system of different vertebrates are described in further sub-sections.

5.4.1 Fishes

Many primitive features are retained by the venous system of fishes, but important advances over conditions in primitive chordates are evident (Fig. 5.26).

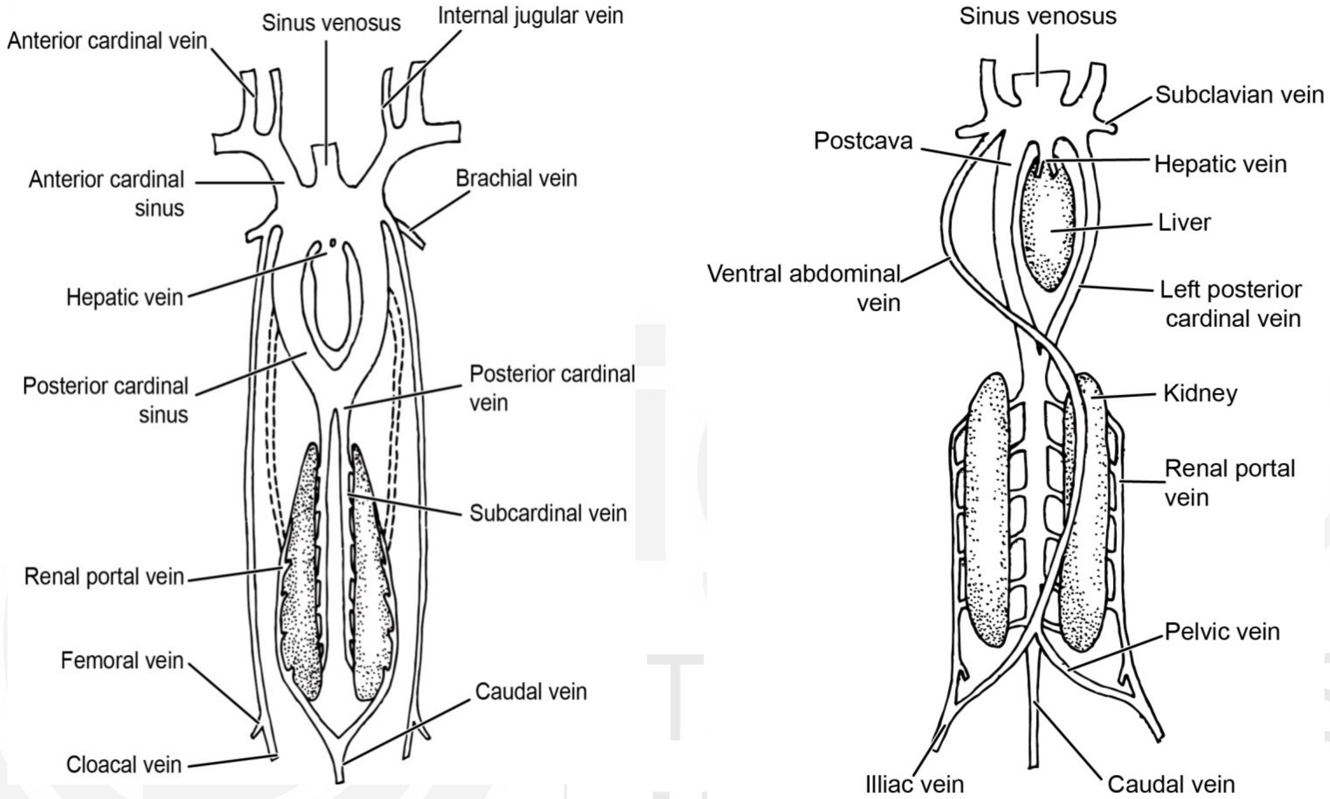


Fig. 5.26: Diagrams, a) shark and b) lungfish, illustrating the changes over the primitive condition which occur in the venous system of fishes.

The sinus venosus receives a duct of Cuvier on each side. An anterior cardinal, or jugular vein brings blood to the duct of Cuvier from the dorsal side of the head region. In many fishes a pair of inferior jugular veins from the ventrolateral part of the head also enters the common cardinal veins (Fig 5.26a). These are lacking in *Polypterus,* fused in *Lepisosteus*. Each common cardinal also receives a postcardinal vein from the posterior end of the body. Since fishes are the first vertebrates to possess paired appendages, subclavian and iliac veins, bringing blood from the pectoral and pelvic fins, respectively, make their appearance first in this group. The iliac veins join the lateral abdominals which course in the body wall to join the common cardinal. The posterior wall of the sinus venosus usually receives two hepatic veins, which return blood from the liver to the heart. The subintestinal vein has, in most cases, lost its connection with the caudal vein.

With the development of the opisthonephric kidneys (The adult kidney formed from the mesonephros and additional tubules from the posterior region of the nephric ridge. You will study more about this in the unit on Excretory System) and their posterior elongation, the postcardinals grow backward dorsal to the kidneys, ultimately to unite with the caudal vein. A pair of subcardinal veins develop ventral to the kidney, i.e. between opisthonephric kidneys. Small blood vessels connect the postcardinal and subcardinal veins. They are not associated with glomeruli, which receive arterial blood. Blood in the caudal vein has now two alternative routes through which it may pass on its way to the heart. It may either go into the postcardinals directly or indirectly through the subcardinals renal veins. The next advance seen in teleosts involves an interruption in the course of each postcardinal vein so that anterior and posterior portions are no longer continuous. Blood from the tail now travels only by one route. It passes through the kidneys, i.e. the renal portal veins to enter the subcardinal veins thus, establishing the renal portal system. The blood courses anteriorly via the postcardinals, which join the duct of Cuvier. The postcardinals usually receive veins from the gonads. The blood passing through the renal veins, flows in a direction reverse of that occurring during an early stage of development, after the renal portal circulation is established. These changes are evident upto elasmobranch fish stage.

In teleosts, lateral abdominal veins are not present. The subclavians enter the common cardinals, and the iliacs join the postcardinal. Veins from the swim bladder (derivative of the gut) usually join the hepatic portal vein. However, in certain forms the connection is with the postcardinal veins. In *Polypterus* they join the hepatic veins directly. In dipnoans, the pulmonary veins from the swim bladder enter the newly formed left atrium of the heart, and the double type of circulatory system appears for the first time.

Lung fishes show the characters that are connecting links between amphibians and fishes. In *Epiceratodus* a single, midventral; anterior abdominal vein, similar to that of amphibians, makes its appearance. The lateral abdominal veins have fused to form the anterior abdominal vein, which courses forward to enter the sinus venosus iliac joins with renal portal and the pelvic vein is a branch of iliac which joins the anterior abdominal. The right postcardinal, including its posterior portion, has become much larger than its counterpart on the left side. The connection with the caudal vein on both sides is retained. The larger vessel on the right side is now called the postcaval vein. It passes through the liver and enters the left duct of Cuvier. The venous system of *Protopterus,* except for the lack of an anterior abdominal vein, resembles more closely with that of amphibians than that of *Epiceratodus*.

5.4.2 Amphibians

In amphibians, the renal portal and hepatic portal systems are brought into close association, since blood from the hind limbs must pass through one or the other.

Pulmonary veins from the lungs enter the left atrium, as in *Dipnoi*. In lungless salamanders, of course, pulmonary veins are absent and the left atrium is reduced in size.

The ducts of Cuvier, which originally received the subclavian, jugular, and postcardinal veins, are further consolidated in amphibians and are now called the precaval veins. These enter sinus venosus on each side. The jugular vein has external and internal tributaries. Since cutaneous respiration has developed to a high degree in amphibians, exceptionally large cutaneous veins are present which join the subclavians to enter the sinus venosus.

Although both urodele (caudates) and anurans (salientians) are similar in the above respects, they exhibit certain differences in regard to the arrangement of the postcaval postcardinal complex. In most caudates and a few salientians the anterior portions of the postcardinals persist in reduced form connecting the middle portion of the postcava with the duct of Cuvier on each side. In most adult anurans however, the anterior portions of the postcardinals usually disappear and furnishes the only route through which blood from the kidneys and gonads may return to heart (Fig. 5.27).

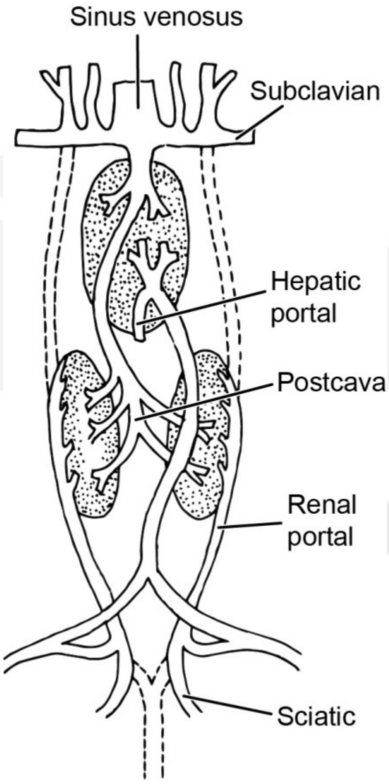


Fig. 5.27: Diagram of venous system of a typical anuran amphibian: ventral view.

SAQ 5

Answer the following questions in short.

i) What are the three sets of paired veins present in the early embryonic stage of vertebrates?

ii) What are the veins in fishes that bring blood from the fins?

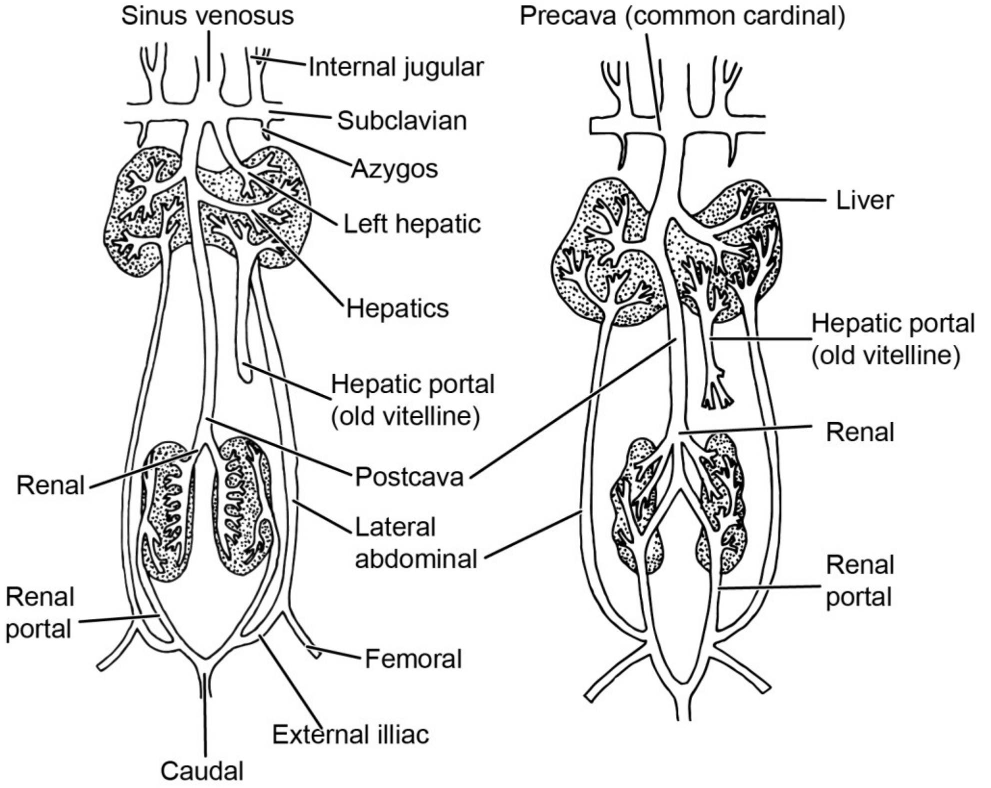
iii) What is the fate of lateral abdominal veins in teleosts and lung fishes?

iv) What are precaval veins?

v) Why are large cutaneous veins present in amphibians?

5.4.3. Reptiles

In this group following further partitioning of the heart the large systemic veins entering heart have shifted more to right (Fig. 5.28). Two precavae are the original ducts of Cuvier, which receive jugular, subclavian, and postcardinal veins. The anterior portion of the jugular, subclavian, and postcardinal have degenerated into two small vertebral veins. In snakes the subclavians are lacking. More blood from the posterior part of the body now courses through the anterior abdominal vein which joins the hepatic portal veins anteriorly. The importance of the renal portal vein has diminished, and in some forms direct channels may even pass through the kidneys, connecting renal portal and postcaval veins. Since cutaneous respiration does not exist in reptiles, pulmonary circulation has assumed greater importance.



(a) Turtle **(b) Crocodile**

Fig. 5.28: Venous channels in reptiles a) turtle, b) crocodile. A strong branch of the renal portal vein in crocodilians continues directly to the postcava. The pelvic vein occurs in turtles but has been omitted to facilitate identification of the basic pattern.

Depending upon the degree of asymmetrical development of the respiratory organs, pulmonary veins from the two lungs show discrepancies in size in various forms. One pulmonary vein may even be entirely absent in certain snakes in which the left lobe of the lung is absent. The reptilian postcava, as in amphibians, is derived partly from the subcardinals and partly from the vitelline veins. The postcardinals have practically disappeared.

5.4.4 Birds

The sinus venosus has been incorporated in the wall of the right atrium, so that the two precavae and single postcava enter the right atrium directly. Each precava is formed by the confluence of subclavian and jugular veins. The original postcardinal connection is no longer in existence. The postcava is the chief pathway for the return of blood from the posterior part of the body. The posterior end of the postcava receives blood directly from the limbs via the renal portal veins. The hepatic veins of birds join the postcava as it nears heart. The caudal vein in birds is greatly reduced. A vein variously known as the inferior mesenteric, coccygeomesenteric, and caudal mesenteric, connects the caudal vein with the hepatic portal vein. A small epigastric vein carries blood from the great omentum to one of the hepatic veins (Fig. 5.29).

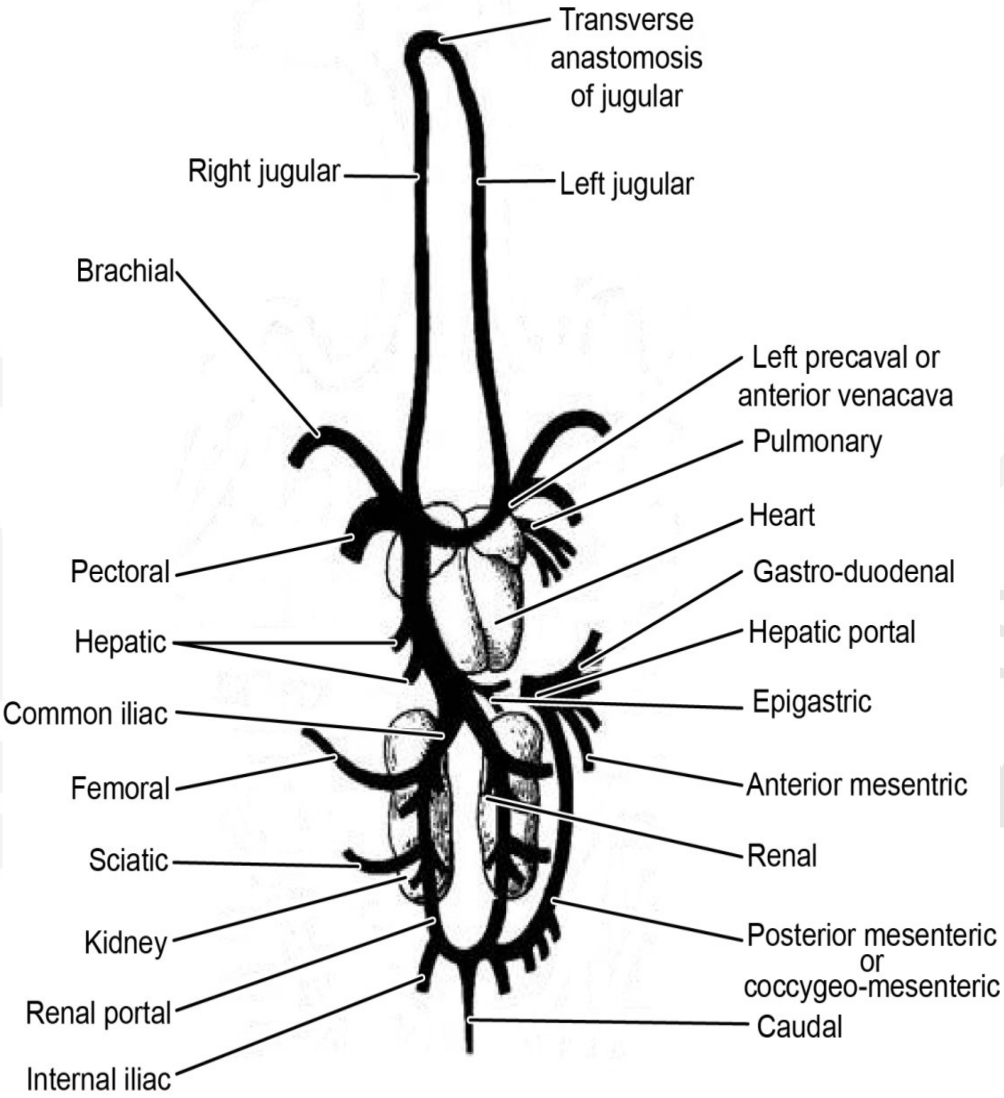


Fig 5.29: Diagram of venous system of bird, ventral view.

5.4.5 Mammals

The shifting of the main venous channels to right side is more clearly indicated in mammals than in other vertebrates. In some mammals two precavae are present, but in others they are joined. The vessel on each side which receives jugular and subclavian vein is then called the brachiocephalic (innominate) vein. In mammals a portion of the anterior end of the right postcardinal persists as the azygos vein. This drains the intercostal muscles and enters the precava. The greatest change in the venous system of mammals occurs in the postcava, which has become considerably simplified. No trace of a renal portal system is found in adults and all blood from the posterior end of the body is collected by the postcava. The anterior abdominal vein has disappeared in mammals, being found only in the monotreme, *Echidna.* Usually only the left umbilical vein persists, passing through the liver as the ductus venosus to join the postcava before it enters the heart. The hepatic portal vein usually referred to as the portal vein, is similar to the hepatic portal vein of lower forms (Fig. 5.30).

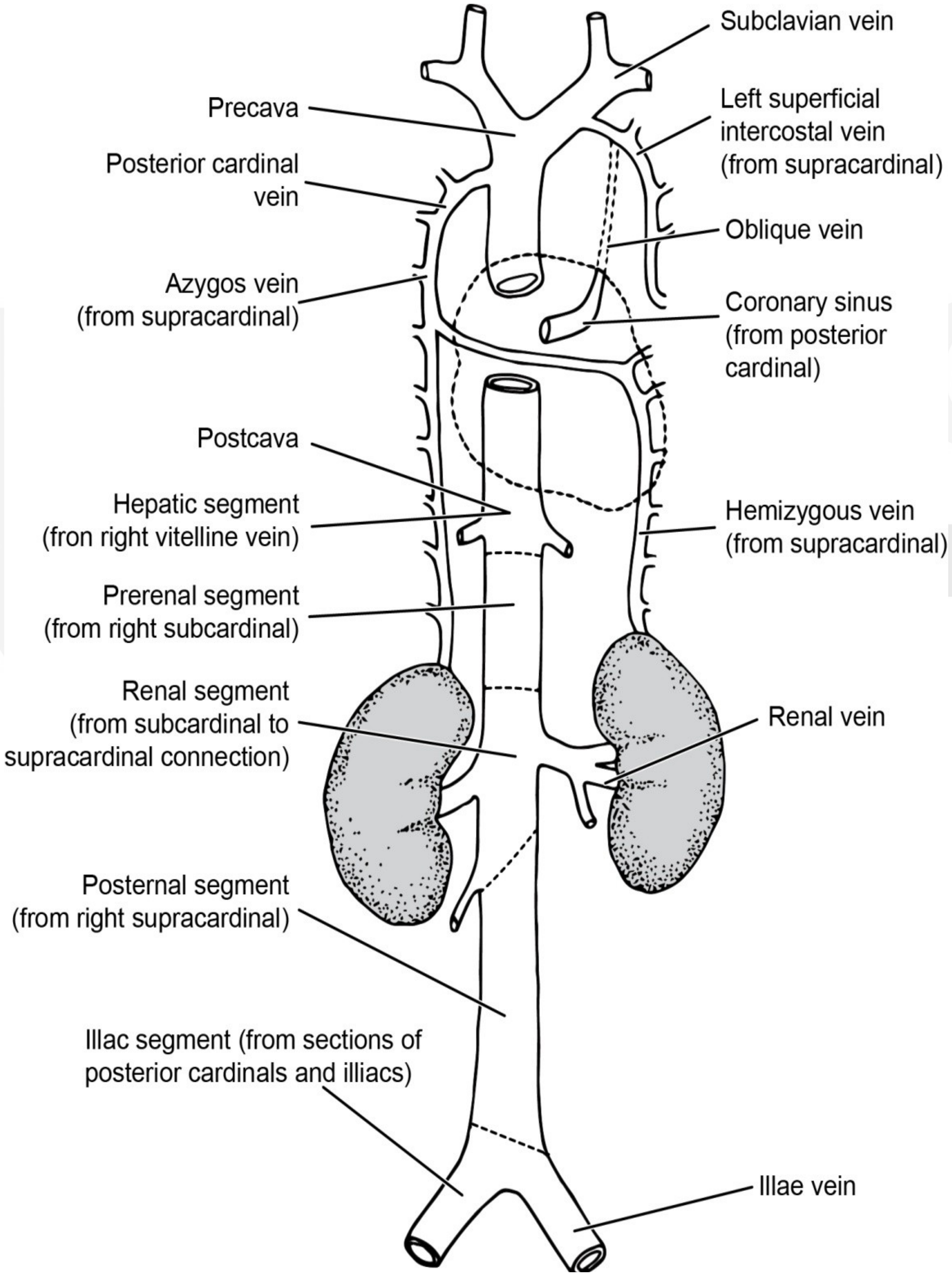


Fig. 5.30: Diagram of venous system of cat, ventral view.

SAQ 6

Fill in the blanks with appropriate words.

i) Subclavians are absent in ____________.

ii) The reptilian postcava is derived partly from ____________ and partly from ____________.

iii) The ____________ brings the blood from the posterior part of the body.

iv) The caudal vein is greatly reduced in ____________.

v) The ____________, ____________ transports blood from great omentum to hepatic vein.

vi) In ____________ the azygos vein brings the blood from intercostal muscles.

vii) The anterior abdominal vein has disappeared in mammals, except in ____________.

viii) ____________ is the process of formation of blood vessels.

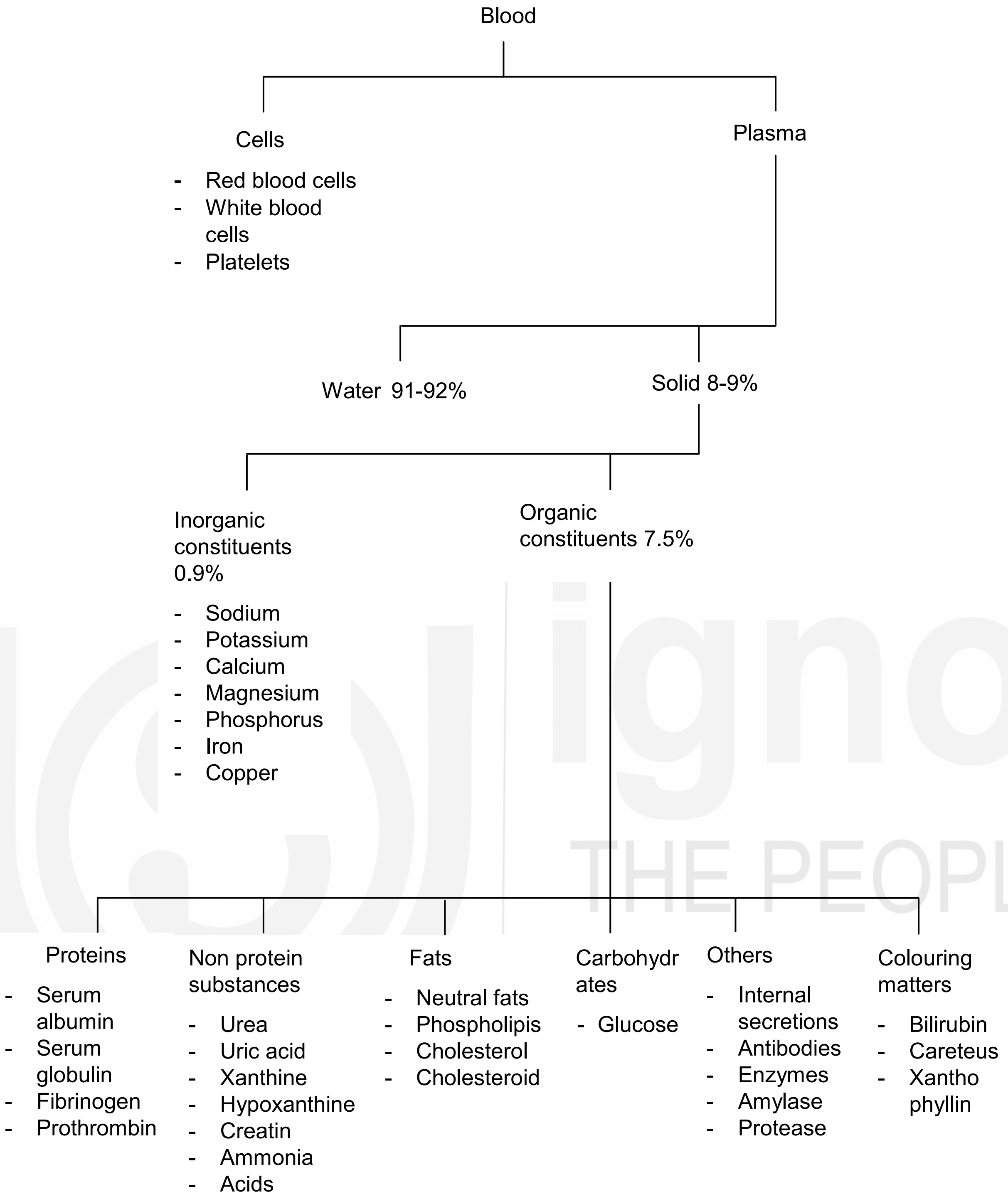
ix) The basic four chambered heart in most tetrapods is formed from ____________.

5.5 BLOOD

Blood may be described as a specialized connective tissue in which there is liquid intercellular substance known as plasma, and formed elements, the red blood cells, the white blood cells and the platelets suspended in the plasma.

5.5.1 Composition of Blood

The general composition of the whole blood is summarized below. Among the cellular components the red blood cells or erythrocytes are the containers of haemoglobin, the respiratory pigment. The erythrocytes in all the groups of animals, except for mammals have nuclei. Red blood cells vary in size for example, 8 μm in humans, 9 μm in elephants and 80 μm in some salamanders. The life of the erythrocytes is three to four months in the circulating blood before being broken down and replaced. White blood cells, the second major cellular component of the blood defend the body from infection and disease. The third type of blood cells are the platelets that help in the formation of clot at the site of tissue damage. Blood has important roles to play in body processes such as respiration, protection against diseases, nutrition, excretion, regulation of body temperature, maintenance of water balance, and transport of hormones.



5.5.2 Respiratory Pigment

Haemoglobin is the only respiratory pigment among vertebrates. This combines with far greater amounts of oxygen than any of the other respiratory pigment.

Haemoglobin is made up of an iron porphyrin compound associated with a protein, globin. This heme component of the molecule is a constant feature of all haemoglobins, but the globin portion varies in different vertebrates. The oxygen carrying capacity of haemoglobin in various vertebrates is given in Table 5.1.

Table 5.1: Haemoglobin and its oxygen carrying capacity in different vertebrate groups.

Pigment	Colour	Site	Animals	Oxygen carrying capacity in volume per cent
Haemoglobin	Red	Corpuscles	Mammals	15-30
			Birds	20-25
			Reptiles	7-12
			Amphibians	3-10
			fishes	4-20

5.6 LYMPHATIC SYSTEM

Lymphatic system resembles the blood vascular system in that it consists of vessels, fluids in transit, and associated organs. A major difference is that lymph flows in only one direction that is towards the heart. The lymphatic system of all vertebrates consists of thin walled vessels called lymphatics or lymph vessels. The walls of lymphatics are like that of veins and like veins they also contain one way valves. The lymphatics penetrate nearly all the soft tissue of the body and commence as blind-end lymph capillaries that collect interstitial fluids. Once inside the lymph capillaries, the fluid is called lymph, a colourless or pale-yellow fluid containing metabolites and secretions, which constantly collect in the intercellular spaces. The lymph from any area mirrors the metabolic activities of that area from moment to moment.

Lymphatic system also includes lymphatic tissue which consists of connective tissue and free cells, the leucocytes, plasma cells and macrophages. Lymphatic tissue can be found almost anywhere in the body as diffusely distributed tissue, in patches or encapsulated in lymph nodes. A lymph node is a collection of lymphatic anastomosing lymph capillaries, macrophages, reticular cells and lymphocytes wrapped in capsule of fibrous connective tissue. Lymph nodes are located within channels of lymphatic vessels and occur in mammals and some water birds only. Lymph nodes have a crucial role in the immune system of mammals as they form check points for infections, bacteria and also intercept the cancer cells that migrate through the lymph nodes (the rapidly dividing cancer cells fill up the lymph nodes. If such a case is detected in the tests all the cancer affected nodes should be removed).

The lymphatics in the villi of the small intestine collect globules of fat absorbed from the intestine after a meal. If the meal has been particularly fatty, the lymph in these vessels is milky. For this reason, the lymphatics of the intestinal villi are called lacteals, and the lymph therein is called chyle.

Several factors that are instrumental in propelling the slow moving lymph through lymphatic vessels and nodes are as follows.

1) Muscular activity of various parts of the body.

2) Pressure built up in the smaller vessels by osmosis and absorption of tissue fluid.

3) The action of pulsating lymph hearts which consists of enlargements in lymphatic vessels with contractile walls, usually situated near a point where lymph enter the venous system. Lymph hearts are not true hearts because they lack cardiac muscles. The striated muscles in their walls slowly develop pulses of pressure to drive the lymph.

Let us discuss the lymphatic system in different vertebrates.

5.6.1 Fishes

Lymphatic vessels in fishes are extensively developed, peripherally located and extend into head, tail and fins. Deeper channels follow the course of some of the larger veins.

Lymph hearts are usually not present, but in some forms they are present near the point of junction of lymphatic vessels and veins. Eel has a lymph heart in the tall. The European catfish has two caudal lymph hearts. Lymph nodes are lacking in fishes.

5.6.2 Amphibians

Two main sets of lymphatic vessels are present in caudate amphibians. Superficial vessels beneath the skin carry lymph to cutaneous and postcardinal veins. Between 14 and 20 lymph hearts have been observed along their course in various forms. Deeper channels follow the dorsal aorta on each side and enter the subclavian artery. In anurans, with large lymph sacs, most of the lymph flows towards heart. Two pairs of lymph hearts are usually present in adult animals. First pair near the third vertebra, pumping lymph into the vertebral vein, and a second posterior pair, located near the end of the urostyle pumps blood into the transverse iliac vein. Lymph hearts are more numerous in larval and tadpole stages. More than 200 lymph hearts are present in caecilians, lying beneath the skin along the intersegmental veins.

5.6.3 Reptiles

The lymphatic system is well developed. A large subvertebral trunk divides anteriorly to enter the precaval veins. In snakes, lymphatic vessels and sinuses are exceptionally large and numerous. A posterior pair of lymph hearts pumps lymph into the iliac veins.

5.6.4 Birds

The lymphatic vessels of birds ultimately enter two thoracic lymph ducts which join the precaval veins. Transitory lymph hearts, not found in adult birds, may be observed in the pelvic region during embryonic development.

5.6.5 Mammals

Lymph hearts are altogether lacking in mammals. A main trunk, the thoracic duct drains all the lymphatic vessels of the posterior part of the body, as well as those coming from the left side of the head, neck and thoracic regions. In mammals nodes are numerous in superficial regions of the head and neck, axillae, and groin. Many lie within the body cavity, large and numerous in the mesentry of the intestine. In all those regions they serve to prevent the invasion of the body by bacteria (Fig. 5.31).

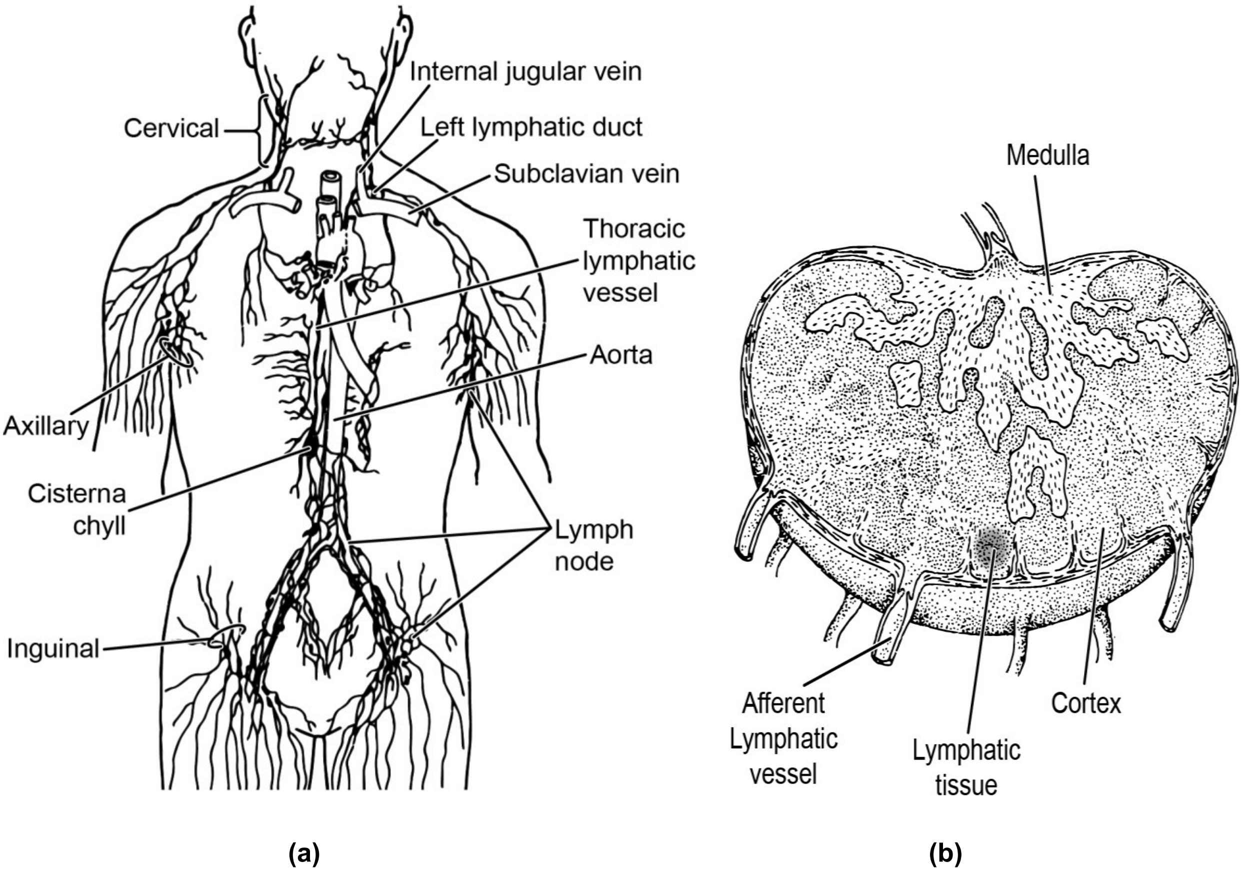


Fig. 5.31: Lymphatic circulation and lymph nodes. (a) Lymphatic vessels returning from all parts of the body join to form major lymphatic vessels, the largest being the thoracic duct, which empties lymph into the postcaval or subclavian, veins, (b) Cross section of a lymph node. These lymph nodes house lymphatic tissue, which functions to remove foreign materials from the lymph circulating through them. Lymph nodes have a cortex and medulla bound by a fibrous connective tissue capsule. Notice the entering and departing lymphatic vessels.

5.6.6 Other Lymphatic Organs

Some organs of pharyngeal origin usually considered to belong to lymphatic system include tonsils, adenoids and thymus glands. Tonsils and adenoids guard the body by forming antibodies against antigenic substances. They filter the tissue fluid and produce lymphocytes. Thymus gland has a role to play in some of the immunological reactions in the body. Peyer’s patches are nodules of lymphoid tissue in the small intestine especially numerous in the region of the ileum. Some other organs related to circulatory system in the body are as follows.

Hemolymph glands: These glands of the body closely resemble lymph glands except that they enclose blood vessels rather than lymphatic. Blood, rather than lymph, filters through them. They are also called hemal nodes. They are believed to play a role in the destruction of old and worn-out corpuscles and also erythrocyte formation. Ruminating mammals have numerous hemal-nodes but their occurrence in man is doubtful.

Spleen: The largest lymphoid organ in body is the spleen. It is sometimes considered to be a hemolymph gland since it is interposed in the blood stream rather than in lymphatic vessels. The blood vessels are peculiarly arranged in the spleen so that the, blood comes in contact with the phagocytes (macrophages) that engulf the fragments of disintegrating red corpuscles. Lymphocytes and plasma cells originating in thymus are later formed in large number in spleen. The spleen also serves as a storehouse for erythrocytes. Spleen also produces antibodies serving in the defence mechanism of the body.

Spleen enlargement is feature of malaria and in some other conditions in which the organ may assume relatively much larger size.

SAQ 7

i) a) Name two blood proteins .

b) Name two non-protein substances of blood.

c) Name three inorganic constituents of blood.

d) Describe the composition of respiratory pigment present in vertebrates.

ii) Match the items given in column I with those given in column II.

Column I	Column II
a) Arteries	i) Lymph
b) Unidirectional flow	ii) Blood
c) Collection of interstitial fluid	iii) Lacteals
d) Chyle	iv) Lymph capillaries
e) Absence of lymph nodes	v) Birds
f) Transitory lymph heart	vi) Mammals
g) Absence of lymph heart	vii) Fishes
h) Production of lymphocytes	viii) Tonsils
i) Lymphoid nodules in ileum	ix) Spleen
j) Phagocytosis of disintegrating red corpuscles	x) Peyer’s patches

5.7 SUMMARY

Let us symmarise whatever you learnt in this Unit:

- The circulatory system includes blood vascular and lymphatic systems. Blood vascular system consists of heart, arteries, capillaries, and veins. Lymphatic system is composed of lymphatics (including lacteals), lymph capillaries, lymph sinuses, lymph nodes in mammals and birds. Lymph hearts are present in lower vertebrates, but absent in birds and mammals. Lymph is transported from tissue spaces, and chyle, which is also a form of lymph, is transported from intestinal villi to certain major venous channels.

- An aortic arch is a blood vessel connecting the ventral and dorsal aortae and located, in the embryo at least, in a visceral arch. Typically, six pairs of aortic arches develop in each vertebrate embryo. During ontogeny the aortic arches are reduced in number, the most highly evolved vertebrates retaining fewest arches.

- A sinus venous occurs in fishes, amphibians, and reptiles. It is absent in adult birds and mammals, having been incorporated in the right atrial wall during embryonic development.

- There is no mixing of oxygenated and deoxygenated blood in fishes. Considerable mixing occurs in tailed amphibians, and less occurs in frogs and reptiles. Mixing occurs in fetal birds and mammals but not in adults.

- Major venous channels in the basic pattern of vertebrate circulation are anterior cardinal (internal jugular) veins from the head, postcardinal veins from the trunk and kidneys, and subclavian vein from the anterior appendages – all flow into common cardinal veins; abdominal veins from the hind limbs; renal portal system from the tail; and hepatic portal system from the chief digestive organs. Hepatic sinuses drain the liver, coronary veins drain the musculature of the heart, and pulmonary and postcaval veins are added in lung-breathing forms.

- The renal portal system drains only the tail in fishes. It acquires a connection (external iliac) with the hind limb drainage in amphibians and reptiles. In crocodilians and birds the connection may bypass the kidneys and go directly to the postcava. The renal portal system is absent in adult mammals, except monotremes, and the hind limbs and tail are drained solely by the postcava.

- Blood may be described as a specialized connective tissue in which there is intercellular substance known as plasma, and formed elements, the red blood cells, the white blood cells and the platelets suspended in the plasma. Specific gravity varies from 1.055 to 1.060.

- The lymphatic system of all vertebrates consists of thin walled lymphatics. In birds and mammals, the lymph nodes are interposed along the course of the lymphatics. The lymphatics penetrate nearly all the soft tissue of the body and commence as blind-end lymph capillaries that collect interstitial fluid which is pale yellow fluid containing metabolites and secretions which collect in the intercellular spaces.

- Lymphatic vessels in fishes are extensively developed. Peripherally located channels extend into head, tail and fins. Lymph hearts are present in amphibians in which two main sets of lymph vessels are present. In reptiles and birds, lymphatic system is well-developed. In mammals, there are no lymph hearts; but several lymph nodes are present. The largest lymphoid organ in body is spleen.

5.9 TERMINAL QUESTIONS

1. Write short note on the general structure of heart wall.
2. Name different stages in the evolution of heart.
3. What is pace-maker?
4. Write short note on foramen of Panizza.
5. Discuss lymphatic system in different vertebrates.

5.10 ANSWERS

Self-Assessment Questions

1. i) peristaltic waves

   ii) atrium

   iii) tuberculate

   iv) interatrial septum

   v) cutaneous

2. i) a) reduced

      b) initiates

      c) partially, completely

      d) squamates and crocodiles

      e) chondrichthyes

      f) mammalian

   ii) Heart beat originates in a bundle of typical muscle fibers located in the wall of the sinus. This is called as ‘Sinoauricular node’ (SA node). The heart beat further spreads to another as of a typical muscle fibers, in the wall of right atrium.

3. i - e

   ii - a

   iii - d

   iv - b

   v - c

4. i) Formation of right and left aortic arches, pulmonary trunk and a part of ventral aorta.

   ii) It serves as shunt from right ventricle to the dorsal aorta until the lungs become functional.

   iii) The fourth arch on the right and a portion of the right radix together become the subclavian artery.

   iv) Somatic arteries supply blood to the body parts derived from the embryonic epimere and visceral arteries supply to digestive tract and other organs derived from embryonic mesomere.

5. i) Vitelline veins from yolk sac, cardinal veins from the body of embryo and lateral veins from pelvic region.

   ii) Subclavian and iliac veins bring the blood from pectoral and pelvic fins, respectively.

   iii) Lateral abdominal veins are absent in teleosts but in lung fishes they fuse to form the anterior abdominal veins which enter the sinus venosus.

   iv) The ducts of Cuvier which originally received the subclavian, jugular and postcardinal veins are further consolidated in amphibians and are called precaval veins.

   v) It is because the cutaneous respiration has developed to the higher degree in amphibians.

6. i) snakes

   ii) subcardinals, vitelline veins

   iii) postcava

   iv) birds

   v) epigastric veins

   vi) mammals

   vii) *Echidna*

   viii) angiogenesis

   ix) splanchnic mesoderm

7. i) a) Fibrinogen, prothrombin

      b) Creatine, Urea

      c) Sodium, potassium, calcium

      d) Haemoglobin is made up of an iron porphyrin compound, hence associated with a protein, globin. The heme component is a constant feature of all haemoglobins, but the globin portion varies in different vertebrates.

   ii) a) ii; b) i; c) iv; d) iii; e) vii; f) v; g) vi; h) viii; i) x; j) ix.

Terminal Questions

1) Heart wall consists of 3 layers viz.

   a) Endocardium - the inner wall consisting of endothelium and elastic tissue.

   b) Myocardium - muscular portion in between endo- and epicardium.

   c) Epicardium - outer fibrous tunica, covered by visceral pericardium (subdivision of coelom).

2) Following are the different stages in the evolution of heart.

   a) The protochordate stage without alimentary pharynx.

   b) The piscine stage with branchial pharynx.

   c) The early tetrapod stage with primitive lungs.

   d) The later tetrapod stage of higher ectotherms.

   e) The stage of endothermic tetrapods.

3) The excitation tissue which is responsible for the initiation of the heartbeat and embedded in the wall of the right atrium is called sinoauricular (SA) node or sinuatrial node. This is also called the pacemaker (myogenic center) of the heart.

4) The crocodiles, which have a left aortic arch, do not receive blood from its own (right) ventricle, since the semilunar valves actually prevent flow from ventricle to aorta except under unusual stress situation. The left arch receives blood through a foramen of Panizza, connecting the right and left arches where they cross a short distance.

5) Refer to Sub Section 5.6.1 to 5.6.5.

Acknowledgement of Figures

Fig. 5.24: Source: modified from Keyte, Anna & Alonzo, Martha & Hutson, Mary. (2014). Evolutionary and Developmental Origins of the Cardiac Neural Crest: Building a Divided Outflow Tract. Birth Defects Research Part C: Embryo Today: Reviews. 102. 10.1002/bdrc.21076)


ignou
THE PEOPLE'S
UNIVERSITY