

GENERALIZED PATTERN OF AORTIC ARCHES

VERTEBRATES

- (1) When the heart is forming in vertebrate embryos during development, a vessel, the VENTRAL AORTA, appears in the midline ventral to the pharynx.
- (2) It soon establishes a connection with the conus arteriosus.
- (3) At its anterior end the ventral aorta divides into two aortic arches which course dorsally in the mandibular region.
- (4) Dorsal to the pharynx, these are continued posteriorly, where they are known as the paired dorsal aortae.
- (5) Additional pairs of aortic arches then appear, forming connections between ventral and dorsal aorta on each side.
- (6) The aortic arches appear in sequence in an anterior-posterior direction, each coursing through the tissue between adjacent pharyngeal pouches.
- (7) The typical number of aortic arches to form in vertebrates is six pairs.
- (8) The first aortic arch is known as the mandibular aortic arch. The second is the hyoid aortic arch, the remainder being referred to as the third, fourth, fifth and sixth aortic arches respectively.
- (9) The paired dorsal aortae fuse posterior to the pharyngeal region so that only a single dorsal aorta ultimately is present. It is continued into the tail region as the caudal artery.
- (10) Various paired and unpaired vessels arise along the dorsal aorta to supply all the structures in the pharyngeal region. Anterior

COMPARATIVE ANATOMY OF AORTIC ARCHES IN VERTEBRATES

Although the arterial systems of various adult vertebrates appear to be different in arrangement, nevertheless 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 lower forms to the four-chambered organ of crocodilians, birds and mammals, is associated in part with the variations to be found in the blood-vascular system. Generalized pattern:

1. When the heart is forming in vertebrate embryos during development, a vessel, the VENTRAL AORTA, appears in the midline ventral to the pharynx.
2. It soon establishes a connection with the coronary arteriosus.
3. At its anterior end the ventral aorta divides into two aortic arches which course dorsally in the mandibular region.
4. Dorsal to the pharynx, these are continued posteriorly, where they are known as the paired dorsal aortae.
5. Additional pairs of aortic arches then appear, forming connections between ventral and dorsal aortae on each side.
6. The aortic arches appear in sequence in an anterior-posterior direction, each coursing through the tissue between adjacent pharyngeal pouches.
7. The typical number of aortic arches to form in vertebrates is six pairs.
8. The first aortic arch is known as the mandibular aortic arch the second is the hyoid aortic arch, the remainder being referred to as the third, fourth, fifth and sixth aortic arches respectively.
9. The paired dorsal aortae are posterior to the pharyngeal region so that only a single dorsal aorta ultimately is present. It is continued into the tail region as the caudal artery.
10. Various paired and unpaired vessels arise along the length of the dorsal aorta to supply all the structures of the body posterior to the pharyngeal region. Anterior continuations of the unpaired ventral aorta and the paired radicles

changes in the aortic arches:

A. CYCLOSTOMES

1. The ventral aorta in cyclostomes is continued forward from the heart for a considerable distance.
2. The number of aortic arches given off by the ventral aorta varies with the species and depends on the number of gill pouches.
3. They are most numerous among the Myxinoidea, Bdellostoma sp. have 15 pairs.
4. In the lamprey, Petromyzon natus, 7 pairs of gill pouches are present.
5. The ventral aorta leaves the heart as a single vessel which bifurcates at the level of the fourth gill pouch.
6. Four afferent branchial arteries arise from each of the paired anterior extensions, and four pairs are given off by the unpaired portion.

B. FISHES

1. Much variation is observed in the aortic arches of fishes. In general, there is a reduction in number within the superclass as the evolutionary scale is ascended.
2. The greatest variation occurs in certain primitive sharks in which the number is directly related to the number of gill pouches.
3. In sharks of the genus Heptanchus, which have seven pairs of gill clefts in addition to the spiracle, there are seven pairs of aortic arches in the adult. Six pairs are to be found in adult Selachians of the genus Hexanchus.
4. Although in the adult of the fishes and in members of the higher classes, the number of aortic arches is reduced or otherwise modified, practically all pass through a stage in embryonic development in which six pairs of aortic arches connect ventral and dorsal aortae.
5. In most fishes, each aortic arch, except the first or mandibular, consists of afferent and efferent branchial portions with an interarterial capillary network interposed. It is in the capillary network of the gill lamellae that aeration of the blood occurs.

6. In Protopterus, the third and fourth aortic arches pass directly to the dorsal aorta without interruption, no internal gills associated with these vessels.
7. In Sharks, other than those mentioned above, only five aortic arches persist, the first having been lost or modified.
8. In teleost fishes and most others, only the last four pairs of aortic arches remain, numbers 1 and 2 having disappeared or having been reduced to small branches of the third.
9. In Chondrostei and Synoi, a pulmonary artery arises from each sixth arch (or from the dorsal aorta) through which blood is carried to the swim bladder.
(refer Fig) * Anatomical peculiarities :-

(C) AMPHIBIANS

1. In amphibians and in the remaining vertebrates above, there is a further reduction in the number of aortic arches to three with a greater modification of the entire complex of vessels in the pharyngeal region.
2. The aortic arches do not break up into septum and efferent portions since in these higher forms internal gill lamellae do not develop.
3. In amphians aortic arches 1, 2, and 3 disappear.
4. The ~~radio~~ radius between arches 3 and 4 on each side gradually dwindles away.
5. The anterior continuations of the ventral aorta become the internal carotid arteries.
6. The third arch, together with the anterior portion of the radius of the aorta on that side, becomes the internal carotid artery.
7. A stapedial branch represents a remnant of the second aortic arch.
8. The portion of the ventral aorta from which the internal and external carotid arteries arise becomes the common carotid.
9. The fourth aortic arch persists to become the systemic arches, which unite posteriorly to form the dorsal aorta proper.
10. Arch 6 on each side sends a branch to the developing lung and to the skin, thus becoming the pulmo-cutaneous artery.

the portion of arch 6 between the pulmonary artery and the radix is called the ductus arteriosus, or duct of Botallus. It disappears at the same time of metamorphosis.

2. Slight differences from the above are to be found in urodeles. In certain salamanders, the fifth arch may persist in very much reduced form.

3. Frequently the radix between aortic arches, 3 and 4 fails to degenerate completely.

4. The ductus arteriosus also persists in urodeles.
(Refer Fig)

D) REPTILES

1. Just as in amphibians, reptiles retain aortic arches 3, 4 and 6. The fifth arch may also be retained in reduced form in certain lizards, and a remnant of the radix between arches 3 and 4 may persist on each side in certain snakes.

2. Further modifications consist chiefly of a splitting of the distal portion of the conus arteriosus and the ventral aorta into three vessels.

3. The fourth aortic arch on the left side, establishes a separate connection with the right side of the partially divided ventricle. It, together with a portion of the radix on the left side, becomes the left arch of the aorta.

4. The sixth arch on each side gives off a pulmonary artery to the lung and, most cases loses its connection (ductus arteriosus) with the radix.

5. The two pulmonary arteries arise from a common trunk, the pulmonary aorta, from the right side of the ventricle.

6. The right fourth aortic arch, together with a portion of the radix on that side, becomes the right arch of the aorta which joins the posterior continuation of the left arch to form the dorsal aorta proper.

7. The portion of the left aorta between the coeliac artery and the dorsal aorta proper is somewhat reduced since the major portion of the blood in the left aorta passes into the coeliac artery.

8. Right and left subclavian arteries arise from the right and

left aortae, respectively in those reptiles having pectoral units. Refer Fig.

Remarks: Since the right aorta bears mostly oxygenated blood and the left chiefly un氧ygenated blood, mixing occurs in the dorsal aorta proper where these two vessels become together. Mixing of oxygenated and un氧ygenated blood seems to be associated with the poikilothermic mode of life.

(E) BIRDS

1. The chief changes taking place in the aortic arches of birds correspond to those of reptiles.
2. In birds, the fourth arch and radix on the left side lose their connection with the dorsal aorta and finally disappear.
3. The ventral aorta splits into two portions, a systemic aorta and a pulmonary aorta or trunk.
4. The systemic aorta is connected to the left ventricle, and the pulmonary aorta to the right.
5. The fourth aortic arch on the right side bears the systemic aorta and by means of the radix, leads to the main arterial channel, or dorsal aorta proper. The latter supplies the entire body with oxygenated blood.
6. At its anterior end the systemic aorta gives rise to external and internal carotid arteries.
7. The fourth aortic arch on the left may possibly contribute to the left subclavian artery, but this vessel is usually a branch of the third aortic arch.
8. The right subclavian artery either arises off the right radix or off the third aortic arch on the right side.
9. The pulmonary aorta leading from the right ventricle gives off the pulmonary arteries, which are actually outgrowths of the sixth aortic arches.

(refer fig)



Source: Data from J. S. Kingsley, *Outline of Comparative Anatomy of Vertebrates*, 1920, The Blakiston Company, Philadelphia.

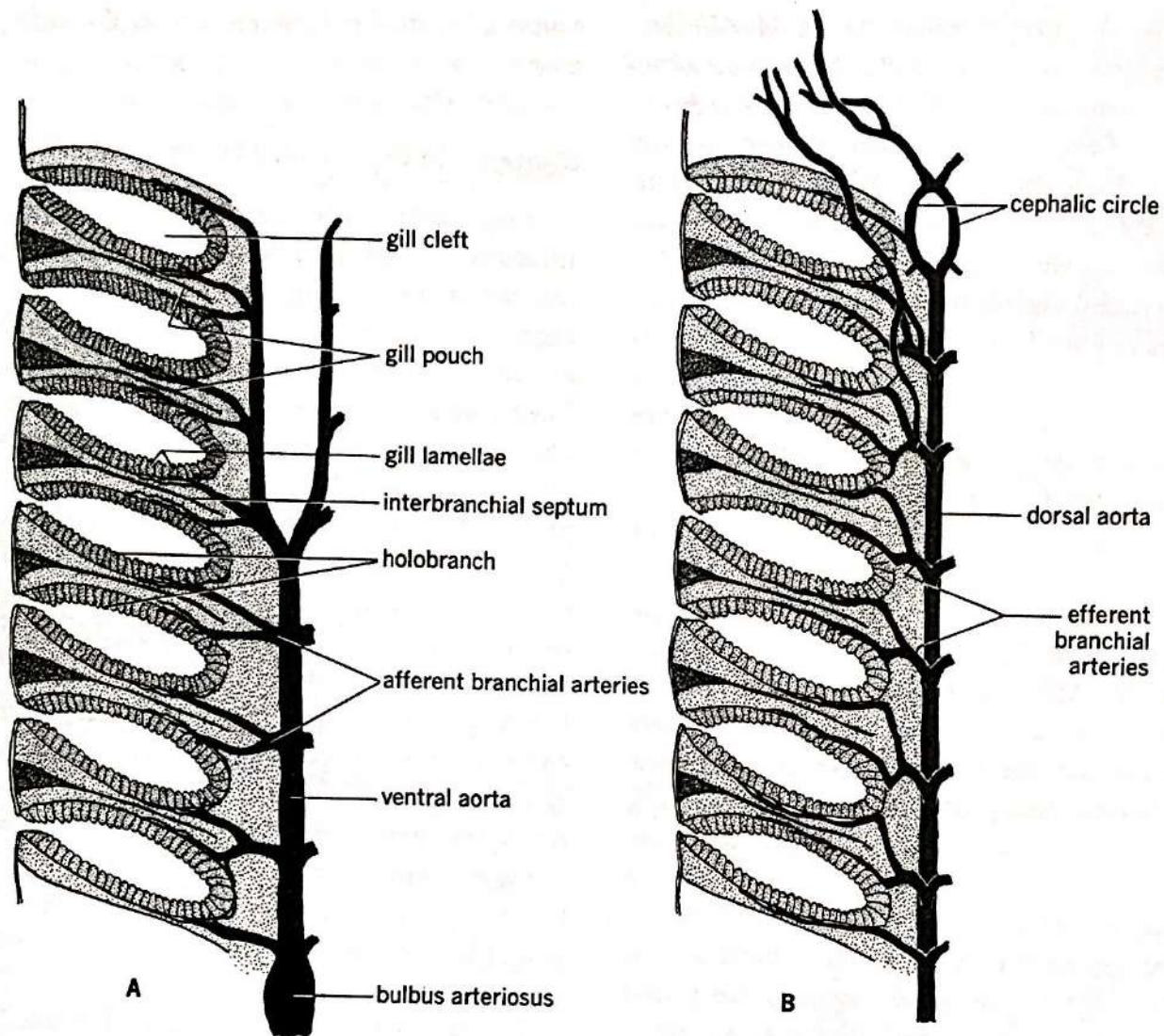


FIG. 12.14 Diagrams showing arrangement of arteries in gill region of lamprey *Petromyzon marinus*: *A*, ventral aorta and afferent branchial arteries; *B*, dorsal aorta and efferent branchial arteries.

some distance. The number of aortic arches which it gives off varies with the species and depends upon the number of gill pouches. In the lamprey *Petromyzon marinus*, which is representative, seven pairs of gill pouches are present. The ventral aorta leaves the heart as a single vessel which bifurcates at the level of the fourth gill pouch (Fig. 12.14*A*). Four afferent branchial arteries arise from each of the paired anterior extensions, and four pairs are given off by the unpaired portion. The most anterior of the eight pairs on each side

supplies the gill lamellae of the anterior hemibranch. The last furnishes blood to the most posterior hemibranch. Each of the remaining vessels arises at the level of an interbranchial septum and divides almost immediately to supply the lamellae on either side of the septum. Thus each holobranch is furnished with the two branches of an afferent branchial artery. Efferent branchial arteries, corresponding in position to the afferent vessels, collect blood from the gill lamellae (Fig. 12.14). They join the single, median dorsal

forms. The first is known as the *mandibular aortic arch*; the second is the *hyoid aortic arch*; the remainder are referred to as the third, fourth, fifth, and sixth aortic arches, respectively. Each lies anterior to the visceral cleft bearing the corresponding number. The two dorsal aortae soon fuse posterior to the pharyngeal region, so that only a single dorsal aorta ultimately is present. It is continued into the tail region as the *caudal artery*. Various paired and unpaired vessels arise along the length of the dorsal aorta, supplying all the structures of the body posterior to the pharyngeal region. Anterior continuations of the unpaired ventral aorta and of the paired *radices* (singular, *radix*) of the dorsal aorta supply the head and anterior branchial regions. Although the manner in which the dorsal aorta branches is fairly uniform throughout the vertebrate series, the aortic arches undergo profound modifications in different forms, the changes being similar in members of a given class. Blood, which is pumped anteriorly by the heart, passes through the ventral aorta to the aortic arches. These vessels carry the blood to the paired dorsal aortae, from which it goes anteriorly to the head or posteriorly to the single dorsal aorta, which distributes it to the remainder of the body. Veins return blood to the sinus venosus, at least during early stages of devel-

opment, or to the right atrium, as the case may be.

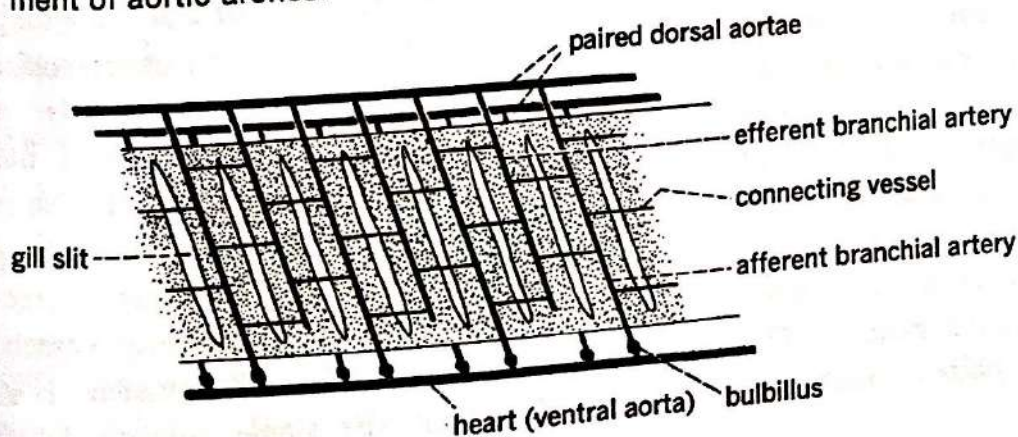
Changes in the Aortic Arches

Amphioxus The "heart" of amphioxus, sometimes called the *ventral aorta*, is a single contractile vessel lying ventral to the gill region. Lateral branches, the *afferent branchial arteries*, are given off on both sides alternately. They extend up into the primary bars of the pharynx. In an adult specimen 60 or more pairs of afferent branchial arteries may be present. Each bears a contractile *bulbillus* at its base. The afferent branchial arteries give off small branches, which connect with vessels in the secondary gill bars. The latter vessels have no direct connection with the ventral aorta, but those in both primary and secondary bars connect to the paired dorsal aortae by means of *efferent branchial arteries* (Fig. 12.13). The two aortae unite behind the pharynx to form a single median vessel which courses posteriorly. Oxygenation of the colorless blood takes place during its passage through the gill bars.

In amphioxus the aortic arches are much more numerous than in higher chordates.

Cyclostomes The ventral aorta in cyclostomes continues forward from the heart for

FIG. 12.13 Diagram of portion of pharyngeal region of amphioxus, showing arrangement of aortic arches.

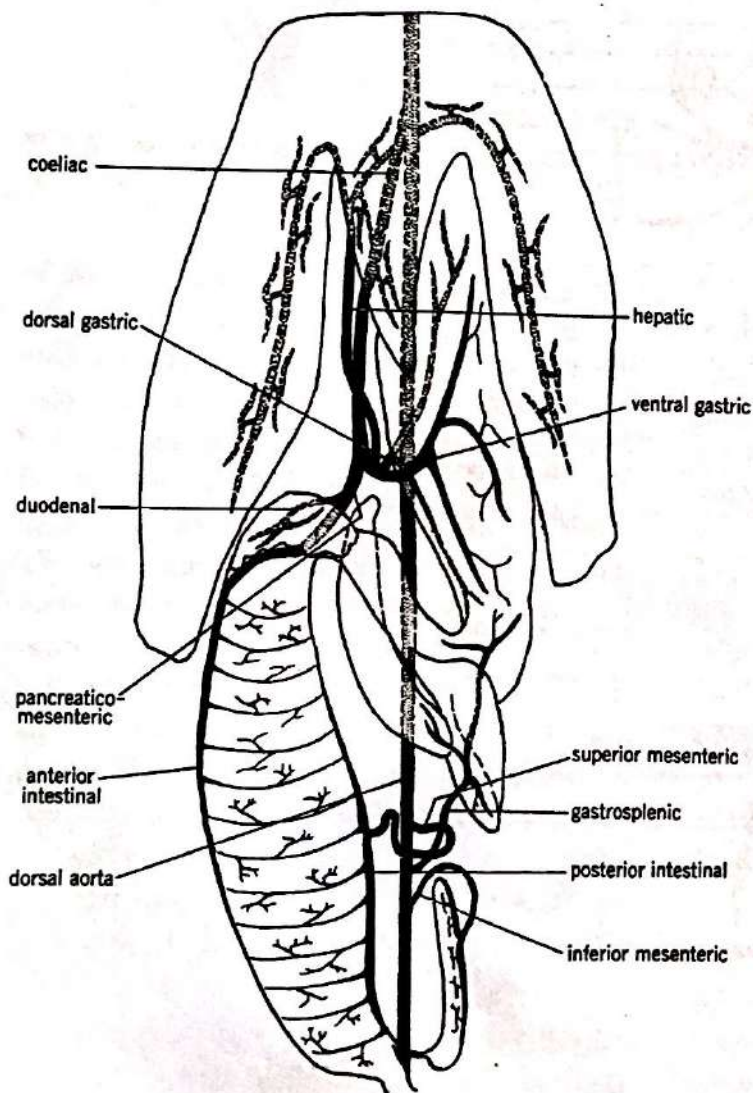


uted to the dorsal, or epaxial, musculature and vertebral column, where they are referred to as *parietal*, or *segmental*, *arteries*. Posterior branches pass through the intervertebral foramina into the neural canal to the spinal cord and its coverings. In higher forms, in which the body is divided into more or less definite regions, such terms as *intercostal*, *dorsolumbar*, and *sacral* are applied to these segmentally arranged vessels. Two or more segmental arteries may fuse, thus obscuring the fundamental metameric arrangement. The vessels going to the appendages, i.e., the *subclavians* to the pectoral appendages and the *iliacs* to the

pelvic, may be composed of a union of several segmental arteries, the number of vessels concerned corresponding to the number of somites involved in the formation of the limb. During development, rerouting of blood and shifting of vessels leading to the appendages occur, and the end result may show little evidence of metameric origin.

Visceral Arteries The arteries supplying the viscera are of two kinds, paired and unpaired. The paired arteries are segmentally arranged and supply portions derived from the embryonic mesomere from which the urogen-

FIG. 12.26 Diagram showing a portion of the dorsal aorta and its unpaired branches which supply the viscera of the dogfish *Squalus acanthias*, ventral view.





furnished with numerous small openings or a single, large aperture. This occurs in lungless salamanders and in those aquatic forms in which the lungs have been reduced in size and function. The sinus venosus may open into both right and left atria, and the left atrium may be reduced in size. The spiral valve may be reduced or is wanting in these forms in which no precise separation of the two bloodstreams occurs. Biologists are generally of the opinion that in its primitive condition (Paleozoic forms) the amphibian heart was three-chambered and capable of accommodating two separate bloodstreams. Other conditions, such as those mentioned above, are considered to be specializations.

A special coronary circulation, supplying and draining the muscular wall of the heart itself, is apparently lacking in many amphibians. In the frog the conus arteriosus receives a branch from the carotid artery bearing oxygenated blood. Blood is returned through two small veins entering the left brachiocephalic and anterior abdominal veins, respectively.

Reptiles Reptiles are the first of the chordates to become truly terrestrial. Except for certain aquatic turtles which at times utilize cloacal respiration, lungs are the only respiratory organs. In this group, as well as in birds and mammals, an efficient pulmonary circulation is a necessity. With its development, further changes have occurred in the structure of the heart.

Although a large sinus venosus is present in certain reptiles (turtles), it has, in general, been greatly reduced. Much of it is incorporated within the wall of the right atrium. Valves which are present where veins enter the right atrium represent vestiges of the sinus venosus. A complete interatrial septum separates the oxygenated blood in the left

atrium from the unoxygenated blood in the right.

All reptiles have a three-chambered heart except the crocodilians, which have a four-chambered heart. Even in the three chambered structure, however, the ventricle is partially divided by an incomplete *interventricular septum*, which extends from the apex toward the center. The conus arteriosus no longer exists as such. Its distal portion, as well as the ventral aorta, has split into three main trunks (Fig. 12.22), each of which has a row of semilunar valves at its base. One trunk is the *pulmonary trunk*, or *pulmonary aorta*, which gives off two pulmonary arteries going to the lungs. The pulmonary trunk leaves the right side of the ventricle. The two remaining *systemic trunks* are called the *left* and *right aorta*, respectively. The left aorta leads from the right side of the ventricle and crosses to the left side; the right aorta leads from the left side of the ventricle and crosses to the right side. A small aperture, the *foramen Panizzae*, is located at the point where right and left aortae cross each other and are in contact, so that their cavities are in communication. Even though the ventricle is only partially divided in most reptiles, an incomplete interventricular septum separates the two bloodstreams passing through the heart more effectively than in amphibians. In crocodilians, in which a complete interventricular septum appears for the first time, a true four-chambered heart is found. Some mixing of systemic blood occurs at the foramen Panizzae, however, as well as at the point where right and left aortae unite to form the dorsal aorta.

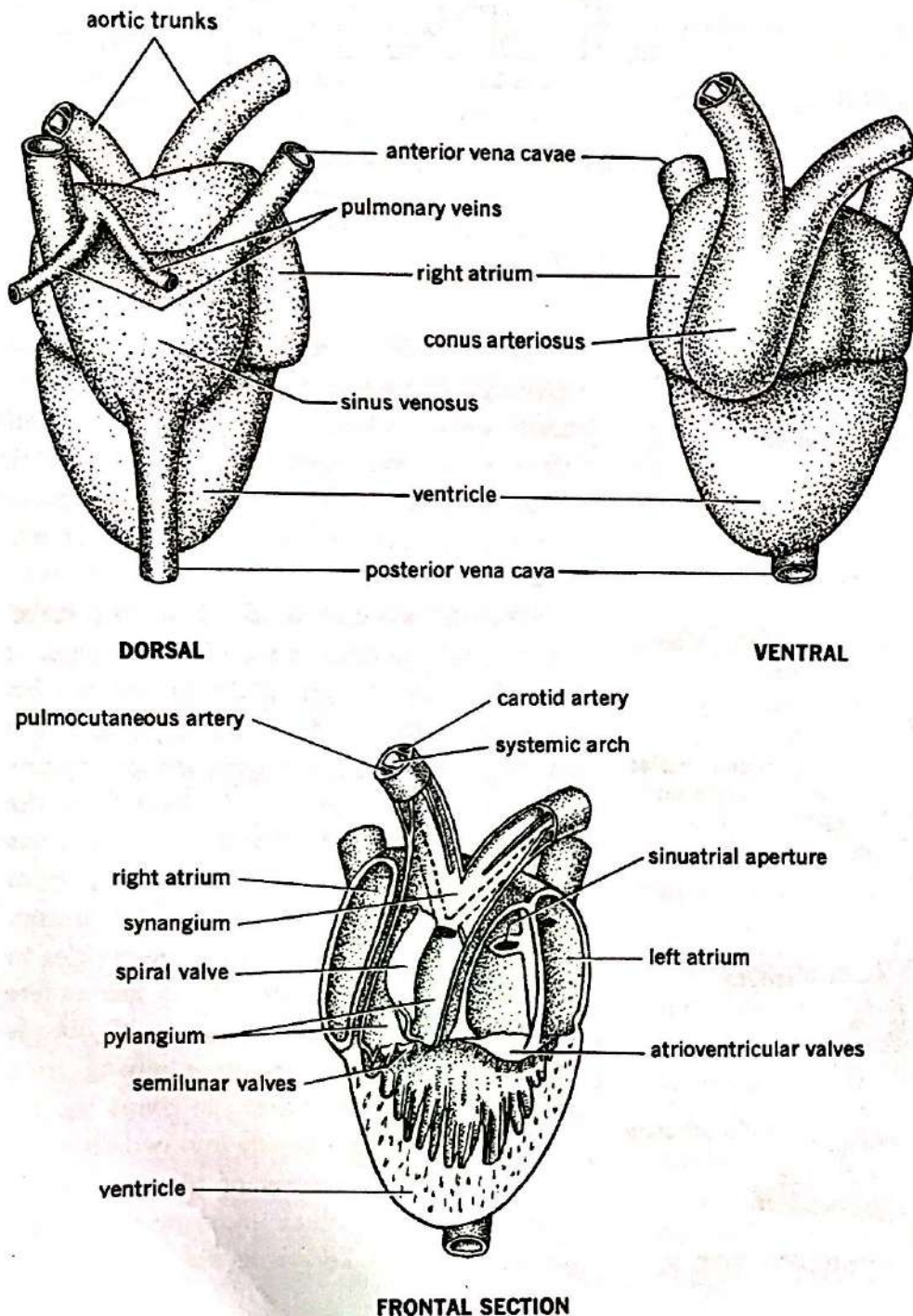
In reptiles the right aortic arch, carrying oxygenated blood from the left side of the ventricle, gives off a large *brachiocephalic artery*, which distributes blood to the anterior part of the body. At its base arise small coronary arteries, which pass to the walls of



circulation. The unoxygenated blood is sent to the posterior gill region and swim bladder, whereas the oxygenated stream goes to the dorsal aorta. It will be recalled that gill lamellae are lacking in the anterior gill region of *Protopterus*.

Amphibians A double type of circulation very similar to that of *Protopterus* is characteristic of adult amphibians. Two streams of blood, one oxygenated and the other partially oxygenated, enter the heart (Fig. 12.9). The oxygenated stream coming from the lungs (or

FIG. 12.9 Heart of bullfrog, enlarged. (After Storer, "General Zoology," 5th ed., McGraw-Hill Book Company, New York, by permission; drawn by R. Speigle.)



the heart itself. A coronary vein returns blood to the right atrium.

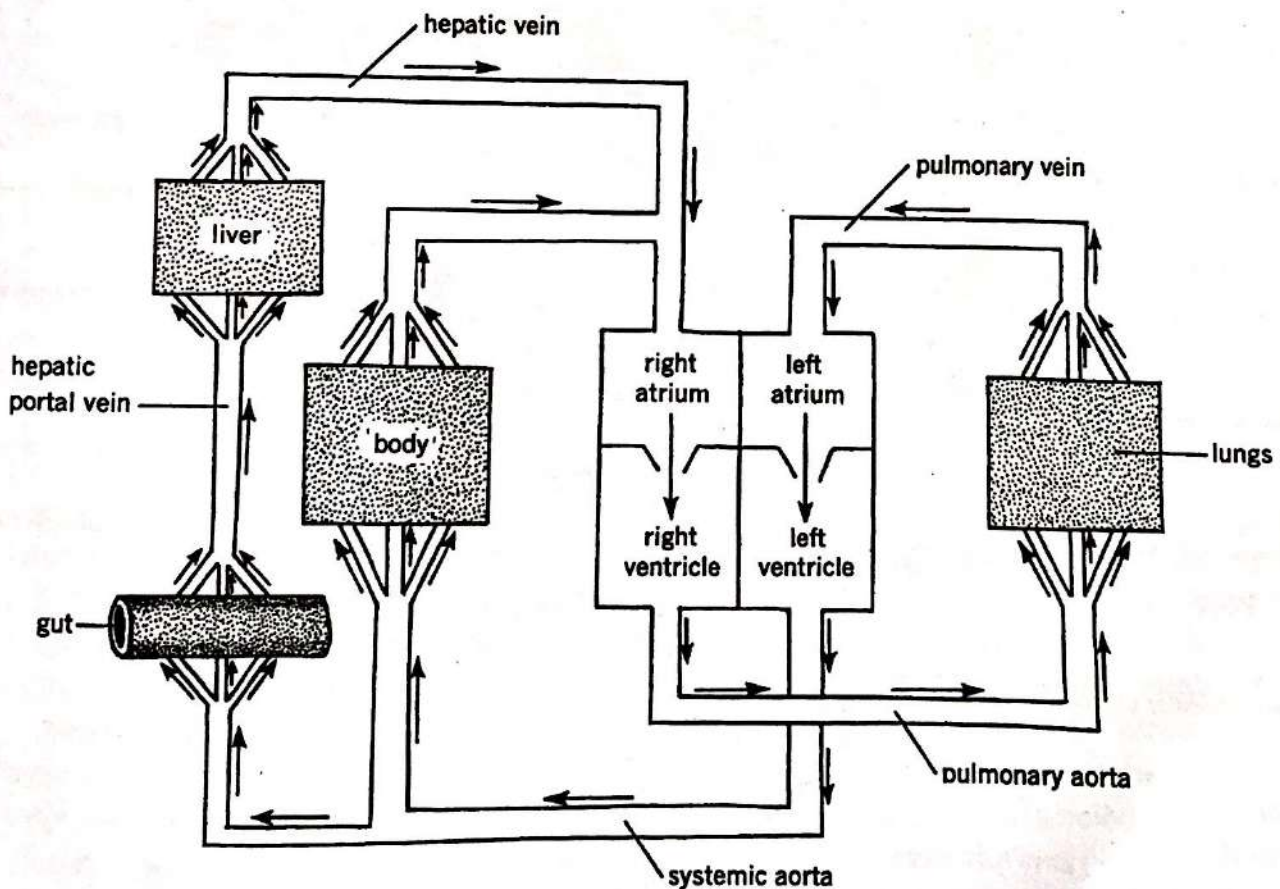
Birds A *complete* double circulation (Fig. 12.10) occurs in birds for the first time, since at no point is there any opportunity for oxygenated and unoxygenated blood to mix. The sinus venosus has disappeared, and three large veins, two precavae and one postcava, enter the right atrium directly (Fig. 12.35). Pulmonary veins return oxygenated blood from the lungs to the left atrium. The heart in birds is relatively much larger and more compact than in forms previously discussed. Both atria are thin-walled. The ventricles are completely separated, as in crocodilians, the muscular wall of the left ventricle being much heavier than the right. A single valve separates

right atrium from right ventricle. Two valves, however, known together as the *bicuspid valve*, are present at the left atrioventricular aperture. Chordae tendineae, attached to the atrioventricular valves, are anchored at their other ends to the lining of the ventricle by heavy projections called *papillary muscles*.

The main advance shown by the heart of the bird over the four-chambered crocodilian heart lies in the elimination of the left aorta. Only two vessels leave the heart in birds: a pulmonary trunk from the right ventricle and a systemic aorta, corresponding to the right aorta of reptiles, from the left. A single set of three semilunar valves is present at the base of each.

In birds the circulating blood passes from the left ventricle to all parts of the body. It is

FIG. 12.10 Diagram of double type of circulatory system in a vertebrate having a four-chambered heart, ventral view.



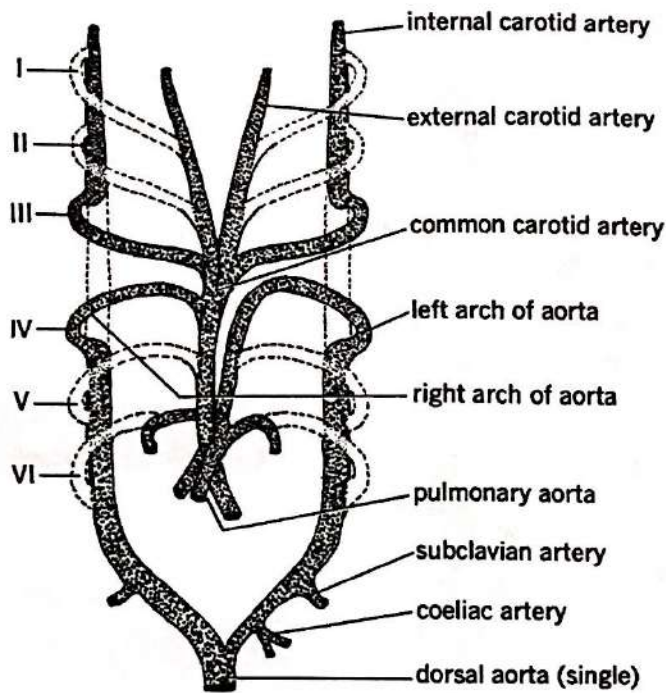


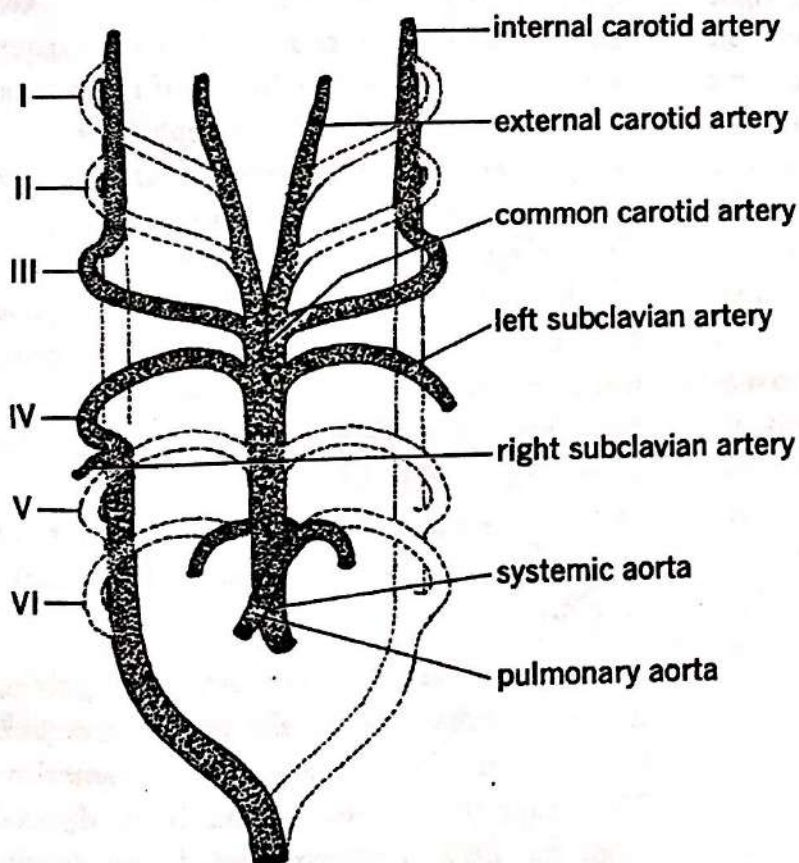
FIG. 12.22 Diagram showing modification of the aortic arches as found in reptiles, ventral view. The ventral aorta (truncus arteriosus) has split into three vessels: right and left systemic aortae and a pulmonary trunk, or aorta.

arch on the right side leaves the systemic aorta and, by means of the radix, leads to the dorsal aorta proper. The latter supplies the entire body with oxygenated blood.

The pulmonary trunk leading from the right ventricle gives off the pulmonary arteries, which are actually outgrowths of the sixth aortic arches. Until the time of hatching there is a ductus arteriosus on the right side, representing the portion of aortic arch VI between the pulmonary artery and the right radix. This serves as a shunt from the right ventricle to the dorsal aorta at a time before the lungs are functioning. It closes at the time of hatching, and all blood from the right ventricle is then sent to the lungs for aeration. A cord of connective tissue on the right side, the *ligamentum arteriosum*, is all that remains of the former arterial shunt.

Mammals The changes in the aortic arches of mammals are rather similar to those

FIG. 12.23 Diagram showing modification of aortic arches as found in birds, ventral view.



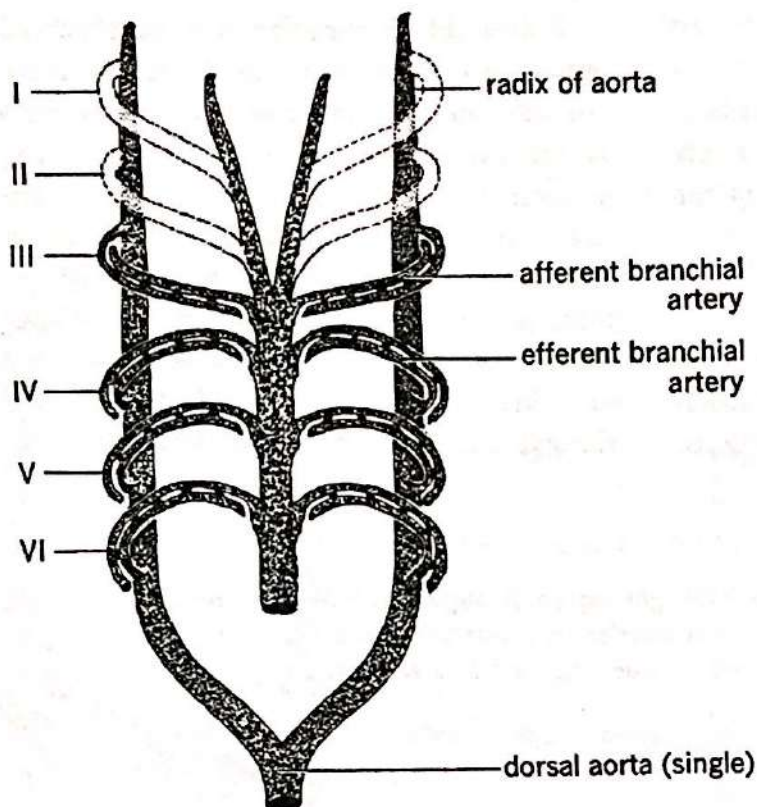


FIG. 12.16 Diagram of aortic arch region as found in most teleost fishes, ventral view. Arches I and II have degenerated. Each of the remaining arches is divided into afferent and efferent branchial arteries connected with each other by gill capillaries.

which six pairs of aortic arches connect dorsal and ventral aortae (Fig. 12.12). Six, then, should be thought of as the primitive number for vertebrates, whose ancestors undoubtedly possessed a greater number. The anterior continuations of the paired dorsal aortae (*radices*) give rise to the *internal carotid arteries*, supplying the brain. The jaws and face are supplied by an artery running ventroanteriorly from the efferent gill artery. In most fishes each aortic arch except the first, or mandibular, consists of afferent and efferent branchial portions with an interarterial capillary network interposed between. It is in the capillary network of the gill lamellae that aeration occurs. The afferent branchial arteries, unlike those in cyclostomes, course *through* the interbranchial septa. In cyclostomes the afferent vessels divide and pass

between the pouchlike structure, sending a branch to the adjacent halves of the neighboring pouches. In *Protopterus*, which is exceptional, the third and fourth aortic arches pass directly to the dorsal aorta without interruption.

In most sharks only five aortic arches persist, the first having been modified. Although five afferent branchial arteries are present on each side, there are usually but four pairs of efferent vessels (Fig. 12.15).

In teleosts and most other fishes only the last four pairs of aortic arches remain, numbers I and II having been modified or reduced to small branches of the third (Fig. 12.16). In *Polypterus* and dipnoans, a pulmonary artery arising from each sixth arch (or from the dorsal aorta) carries blood to the swim bladder.

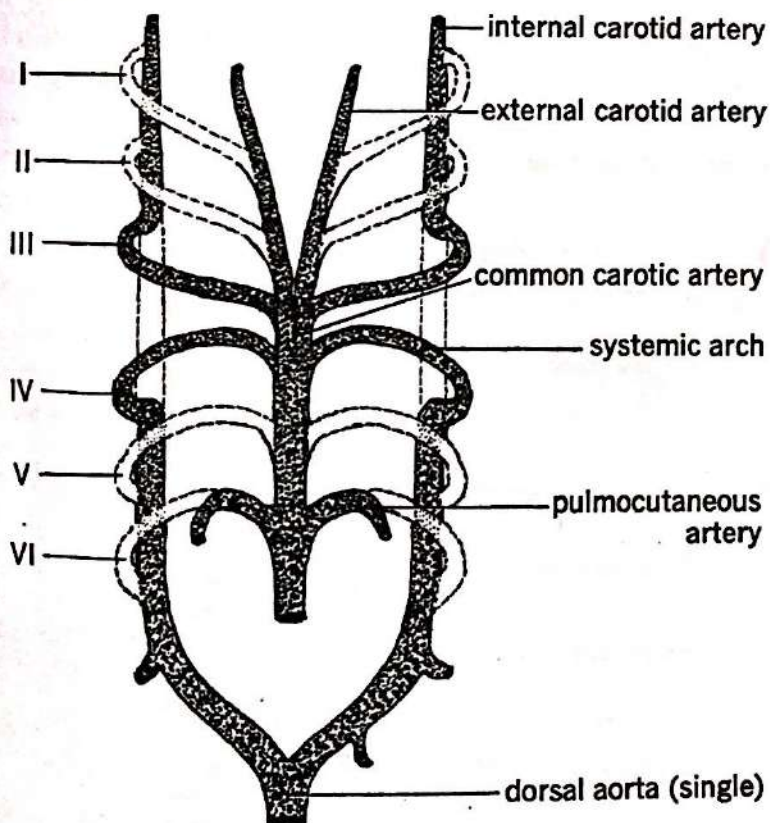
Amphibians In amphibians and in the remaining vertebrate classes there is a further reduction in the number of aortic arches, together a greater modification of the entire complex of vessels in the pharyngeal region. The aortic arches do not break up into afferent and efferent portions, since in these higher forms internal gill lamellae do not develop. To be sure, amphibians possess external gill filaments, at least during early development, but these are not homologous with the internal gill lamellae of fishes, nor are they supplied with blood in the same manner (pages 220 and 351).

In anurans (Fig. 12.17), aortic arches I, II, and V disappear. The radix between arches III and IV on each side is greatly reduced and may degenerate completely. The anterior continuations of the ventral aorta become the ex-

ternal carotid arteries. The third arch, together with the anterior portion of the radix on that side, becomes the internal carotid artery. The portion of the ventral aorta from which the internal and external carotids arise becomes the common carotid. The fourth aortic arches persist to become the systemic arches, which unite posteriorly to form the dorsal aorta proper (Fig. 12.18). Arch VI on each side sends a branch to the developing lung and to the skin, thus becoming the pulmocutaneous artery. The portion of arch VI present at first between the pulmonary artery and the radix is the *ductus arteriosus*. It disappears at the time of metamorphosis.

Slight differences from the above are to be found in urodeles (Fig. 12.19). In some salamanders the fifth arch may persist in very reduced form. Frequently the radix between

FIG. 12.17 Diagram showing modification of aortic arches as found in anuran amphibians, ventral view.



ital organs and their ducts arise. Although the mesomere is, for the most part, unsegmented, the arteries supplying its derivatives show pronounced evidences of metamerism, particularly in regard to the manner in which they supply the pronephric, opisthonephric, and mesonephric kidneys. Such terms as *renal*, *genital*, *ovarian*, *spermatic*, and *urogenital* arteries are applied to the paired visceral arteries. Renal and genital arteries are numerous in the lower vertebrates, but the number is greatly reduced in higher forms.

The unpaired visceral arteries supplying the spleen and the digestive tract and its derivatives course through the dorsal mesentery of the gut. They branch profusely, the method of branching showing great variation even in members of the same species. There are usually three unpaired visceral arteries in vertebrates. The most anterior of these is the *coeliac 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 coeliac artery. Branches of the superior mesenteric at its anterior end also supply a portion of the pancreas. The remainder of the vessel is distributed to the cecum and upper half of the large intestine. The third unpaired artery is the *inferior mesenteric*, supplying the posterior part of the large intestine and rectum.

Variations from the above may be accounted for by fusions or separations. For example, in frogs and other amphibians, the coeliac and superior mesenteric arteries have united into a single *coeliacomesenteric artery*. In the dogfish *Squalus acanthias* an unpaired *gastro-splenic artery* arises directly from the aorta just posterior to the origin of the superior

mesenteric, to supply the spleen and posterior part of the stomach (Fig. 12.26). It actually represents a branch of the superior mesenteric which has become secondarily connected with the aorta.

VENOUS SYSTEM

As in the case of the arterial system, a comparison of the veins in the various vertebrate groups shows that they are arranged according to the same fundamental plan and that the variations encountered form a logical sequence as the vertebrate scale is ascended. In its development the venous system of higher forms passes through certain stages common to the embryos of lower forms.

There is some difference in the formation of the earliest veins which appear in an embryo, according as a yolk sac is present or absent. In forms without a yolk sac a pair of *subintestinal veins* appears in the splanchnic mesoderm ventral to the gut. These veins soon fuse, except in the region of the anus, around which they form a loop, only to unite posteriorly, where they continue on into the tail as the *caudal vein*. In animals having a yolk sac, a pair of *vitelline veins* draining the yolk sac joins the posterior end of the heart. Indeed, their fusion is primarily responsible for heart formation. The part of the heart which the vitelline veins enter is destined to become the *sinus venosus*. The vitelline veins are concerned with obtaining nourishment used by the embryo during its development. Even though the yolk sac in mammals contains no yolk, vitelline veins (and arteries) are present. Each vitelline vein is joined posteriorly by a subintestinal vein arranged in a manner similar to that in forms lacking a yolk sac.

Before long, two additional pairs of veins, *anterior cardinals*, from the dorsal side of the head region, and *posterior cardinals*, from the

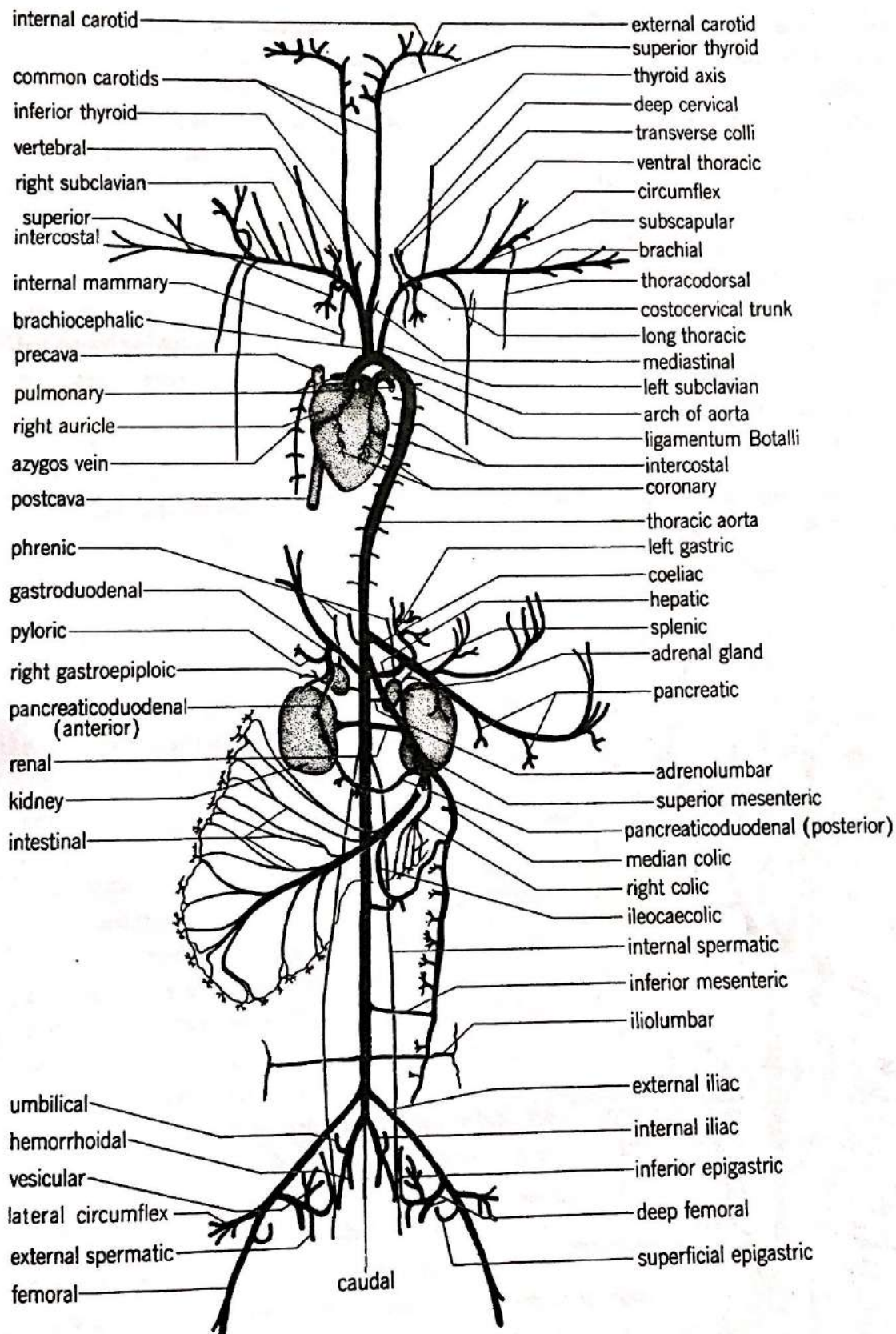


FIG. 12.25 Diagram of arterial system of cat, ventral view.

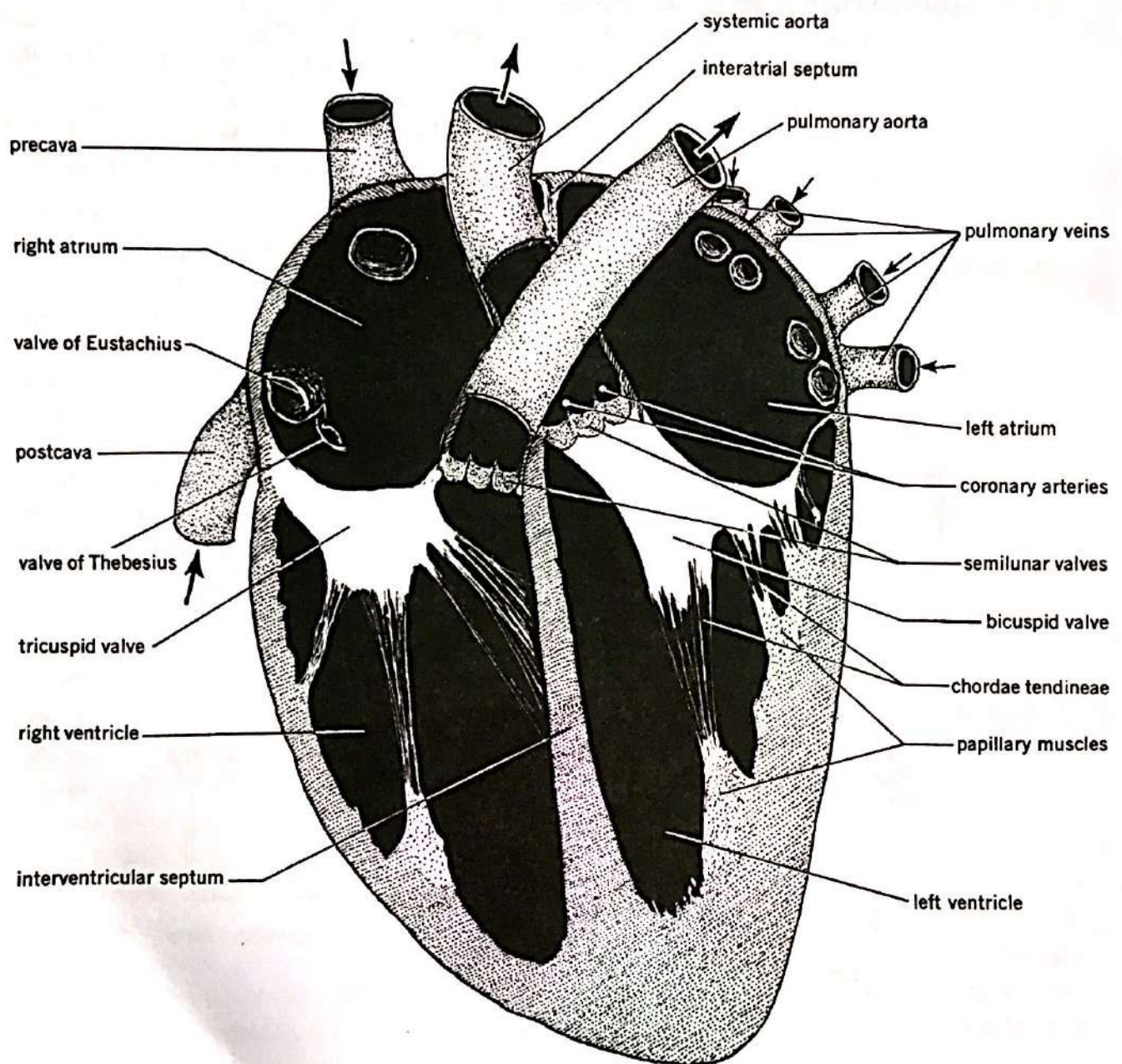
collected by the two precavae and the single postcaval vein and enters the right atrium. From here it passes to the right ventricle, which sends it to the lungs for aeration. Oxygenated blood is returned to the left atrium, which sends it past the bicuspid valve into the left ventricle.

A well-developed coronary system is present in birds. Coronary arteries arise from

the systemic aorta. A venous coronary sinus enters the right atrium near the entrance of the postcava.

Mammals The four-chambered mammalian heart (Fig. 12.11) is essentially similar to that of birds, the two sides of the heart being completely separated from each other by interatrial and interventricular septa. A thin

FIG. 12.11 Diagram showing internal structure of four-chambered mammalian heart, ventral view.



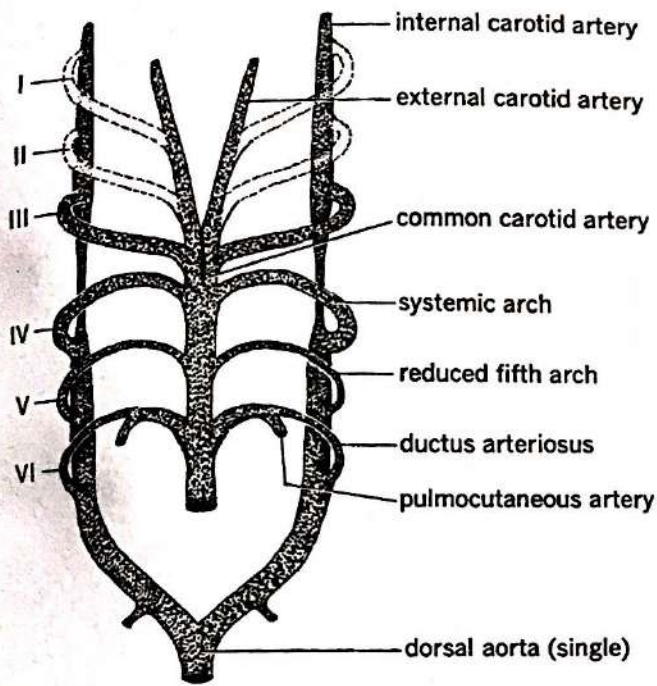


FIG. 12.19 Diagram showing modification of aortic arches as found in most urodele amphibians, ventral view.

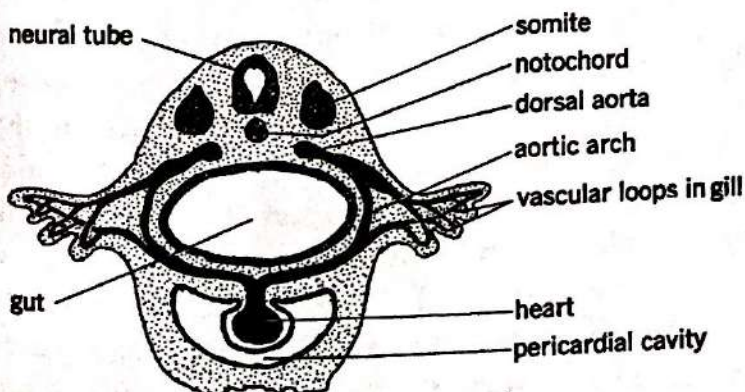
laries. They lie lateral to the aortic arches, the latter being located at the bases of the gills, each serving as a *gill bypass*. Blood may go directly through the aortic arches or through the adjacent loops. In urodeles at the time of metamorphosis the gills degenerate, and the vascular loops atrophy. The main aortic arch, which has maintained its integrity from the beginning, persists.

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 (Fig. 12.21). Blood going to the lungs in *Necturus* has already been oxygenated by passage through the gills. The lungs, therefore, under normal conditions are of little value as respiratory organs.

Reptiles 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. These consist mainly of splitting of the distal portion of the conus arteriosus and part of the ventral aorta into three vessels (Fig. 12.22). The fourth aortic arch on the left side establishes a separate connection with the right side of the partially divided ventricle. Together with a portion of the radix on the left side, it becomes the *left arch of the aorta*. The sixth arch on each side gives off a pulmonary artery to the lung and in most cases loses its connection with the radix. The two pulmonary arteries then arise from a common trunk, the *pulmonary aorta*, coming from the right side of the ventricle. The remaining vessel derived from the truncus arteriosus connects to the left side of the ventricle and as it courses forward gives off the fourth aortic arch on the right side, and finally divides into the two

FIG. 12.20 Diagrammatic cross section through gill region of early frog tadpole, showing relation of aortic arches to blood vessels in the external gills. (After Maurer.)





from the gills via the lungs in certain urodeles) enters the left atrium (via the sinus venosus) and thence passes to the left side of the posterior gill region and swim bladder, composed of unoxygenated blood from most of the body, mixed with oxygenated blood from the skin, enters the sinus venosus, from which it passes to the right atrium and thence to the right side of the ventricle.

The system of vessels coming from the lungs to the heart, and those leading from the heart to the lungs, is referred to as the *pulmonary circulation*. That which is distributed to the body in general and then returned to the heart is called the *systemic circulation*.

The *interatrial septum* is a thin membrane of connective tissue covered with endothelium. Perforations are frequently present in the interatrial septum of urodeles, but little mixing of the two bloodstreams occurs. The ventricle is not partitioned, but its lining is spongy and thrown into many pockets by muscular bands which, to a large extent, influence the blood flow, keeping the blood coming from the right atrium separate from that coming from the left. Chordae tendineae fastened to the atrioventricular valves prevent blood from being regurgitated into the atria when the ventricle contracts.

Despite the presence of a single ventricle, the two bloodstreams mix only to a slight degree. This, however, is not very important, since the systemic blood entering the right side of the ventricle has, to a considerable extent, been oxygenated in the skin and lining of the mouth. Both these areas in amphibians are important, since the animals utilize buccopharyngeal and cutaneous respiration in addition to pulmonary respiration.

Many amphibians have developed a rather complicated system of valves and partitions which ostensibly serve to keep the two bloodstreams well separated upon leaving the ventricle.

The conus arteriosus bears cardiac muscle fibers in its walls and is capable of contraction. In frogs it is made up of two regions. The part next to the ventricle is the *pylangium*. It is more muscular than the distal portion, which is referred to as the *synangium*. When viewed externally the anterior end of the synangium appears to divide into two trunks, each of which in turn separates into three arteries. The most anterior is the *carotid artery*, going to the head region; the second is the *systemic artery*, or *arch*, which gives off a few branches before the two systemic arches join each other posteriorly to form the *aorta*, which in turn distributes blood to the rest of the body; the third, or *pulmocutaneous artery*, leads to the lungs and skin. The latter actually connects with the pylangium.

The internal structure of the conus is rather complicated. Two sets of semilunar valves are present, one set at the base of the pylangium, the other at the junction of pylangium and synangium. In most amphibians one of the latter has become modified to form the *spiral valve*, which plays a role in separating the two bloodstreams as they leave the heart.

A spongy mass, the *carotid body* (sometimes incorrectly referred to as the carotid "gland"), located at the base of the carotid arch, aids in keeping the blood in the carotid vessels leading to the head at a rather constant pressure and gaseous content.

In such perennibranchiate salamanders as *Necturus*, blood is sent to the gills for aeration. Blood going to the lungs through pulmonary arteries has already been oxygenated in the gills. This would indicate that the lung has been reduced as a respiratory organ in such salamanders and may be used only in times of emergency.

Variations from the conditions described above are to be found in many amphibians. The interatrial septum may be incomplete or

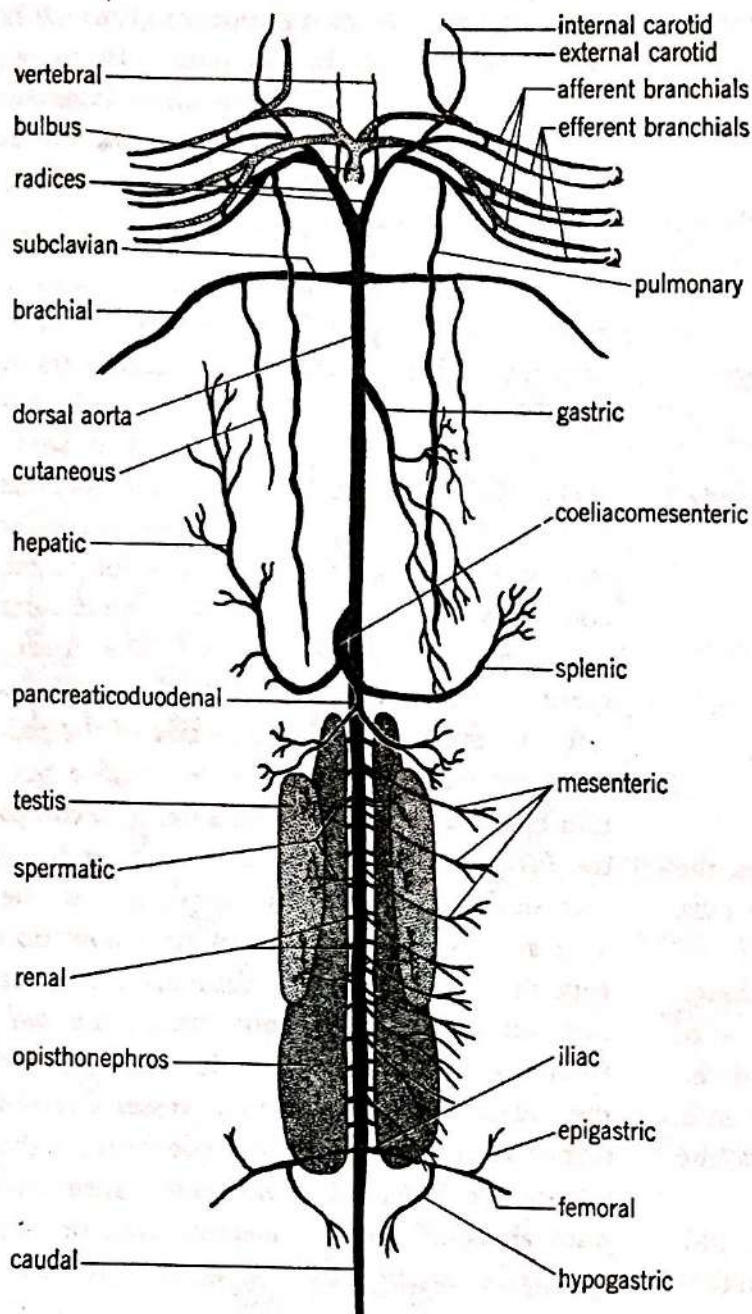


FIG. 12.21 Ventral view of arterial system of *Necturus*.

common carotid arteries with their external and internal branches. The right fourth aortic arch, together with a portion of the radix on that side, becomes the *right arch of the aorta*, which joins the posterior continuation of the left arch to form the dorsal aorta proper.

Birds The main changes taking place in

the aortic arches of birds correspond, in general, to those of reptiles. In birds, however (Fig. 12.23), the fourth arch and radix on the left side lose their connection with the dorsal aorta and finally disappear. The ventral aorta splits into two portions, a systemic aorta and a pulmonary trunk, or aorta. The systemic aorta is connected to the left ventricle, and the pulmonary aorta to the right. The fourth aortic

distinct from that inside the pulmonary arteries and veins. *Bronchial arteries and veins*, branches of certain systemic vessels close to the heart, function in this manner.

Rings of dense fibrous connective tissue furnish support and prevent excessive dilatation of certain regions of the heart when contraction occurs. Since the free ends of cardiac muscle fibers may insert on this tissue, it is sometimes called the "skeleton" of the heart. In some mammals cartilaginous or bony tissue may be associated with the fibrous rings.

RHYTHMICITY OF THE HEART-BEAT The "pacemaker" which regulates or initiates the rhythmic beat of the heart is a bundle of atypical muscle fibers located in the wall of the sinus venosus. It is called the *sinoatrial node*. In higher forms, in which the sinus venosus has been incorporated into the wall of the right atrium, the sinoatrial node lies embedded in the atrial wall. Another mass of atypical muscle fibers, the *atrioventricular node*, in the interatrial septum of the four-chambered heart, also acts as a pacemaker under experimental conditions when the sinoatrial node is destroyed or prevented from functioning. A bundle of tissue, the *bundle of His*, is distributed from the atrioventricular node to the ventricular walls via the *Purkinje fibers*. The two nodes, the bundle of His and the Purkinje fibers, are responsible for the rhythmic sequence of the various phases of the heartbeat. Except in hagfishes, the autonomic nervous system reaches the heart and may affect the rate of contraction.

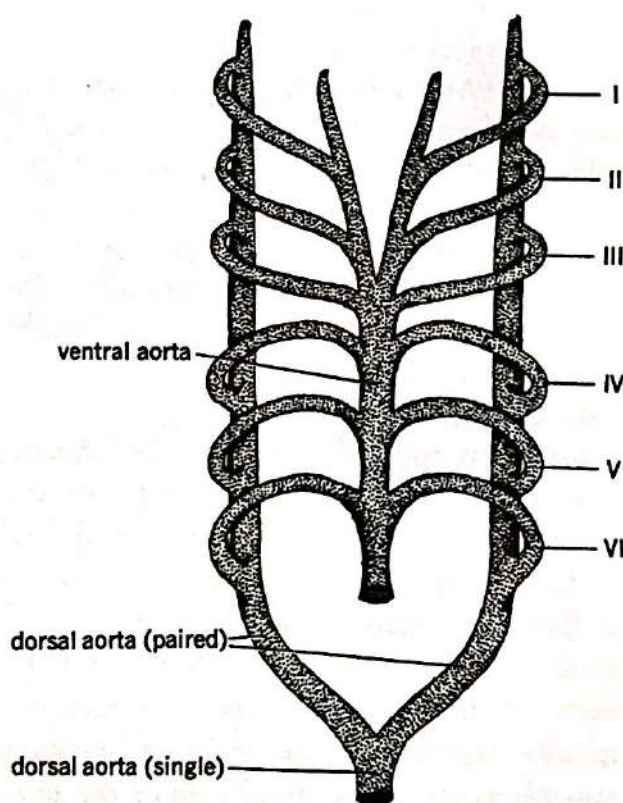
ARTERIAL SYSTEM

Although the arterial systems of various adult vertebrates appear 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 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.

During early development the anterior end of the ventral aorta divides into two *aortic arches*, which course dorsally in the mandibular region. Dorsal to the pharynx these are continued posteriorly, where they are known as the *paired dorsal aortae*. Additional pairs of aortic arches then appear in an anterior-posterior sequence, forming connections between ventral and dorsal aortae on each side. Each courses through the tissue between adjacent pharyngeal pouches. The typical number of aortic arches to form in vertebrates is six pairs (Fig. 12.12), although there are certain discrepancies among lower

FIG. 12.12 Diagram illustrating the typical condition of aortic arches in vertebrate embryos, ventral view. Six pairs of arches connect ventral and dorsal aortae.

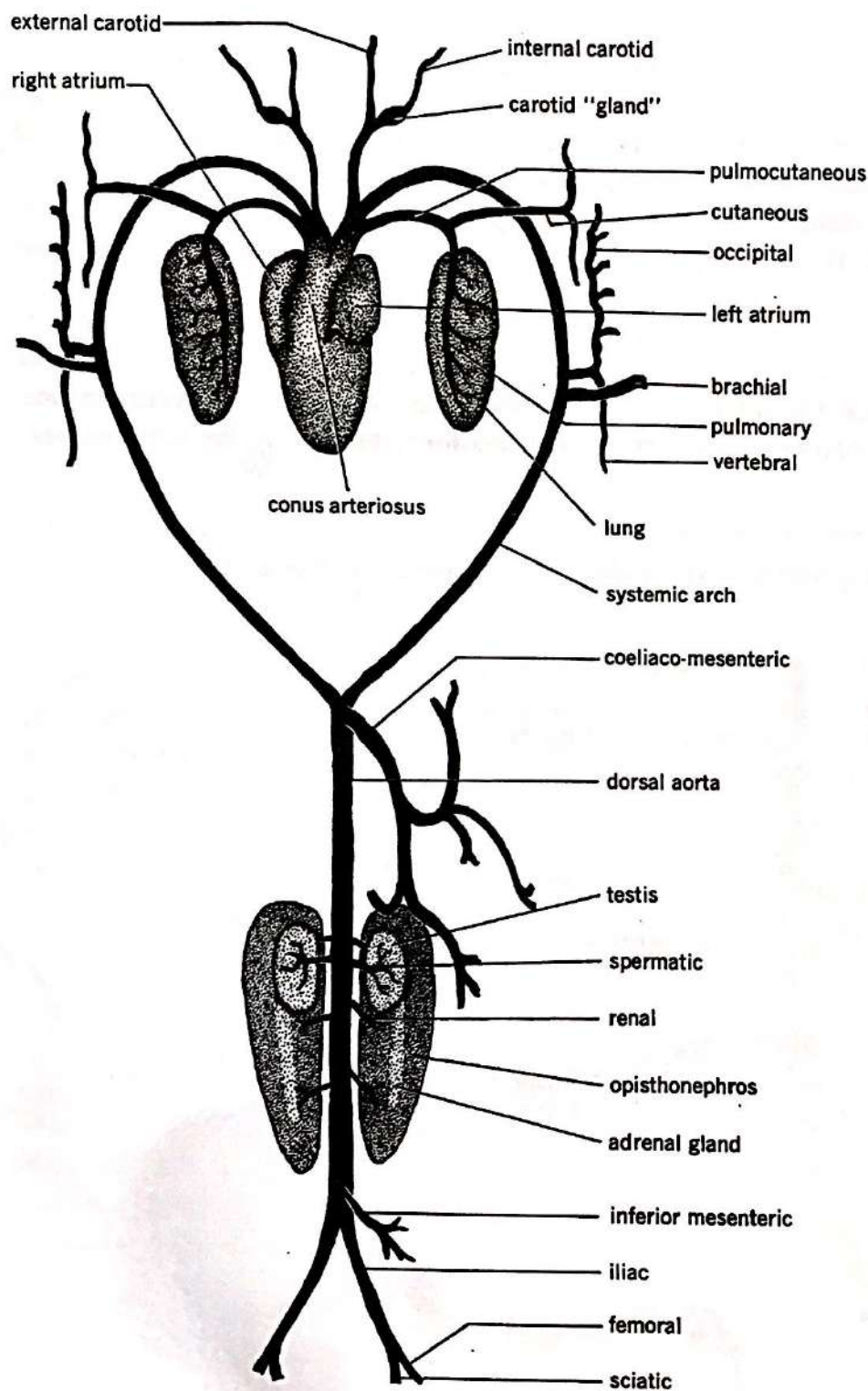


arches III and IV fails to degenerate completely. The ductus arteriosus also persists in urodeles.

The external gills of larval urodeles and

early anuran larvae are supplied with vascular loops connected to aortic arches (Fig. 12.20). The loops themselves are composed of afferent and efferent vessels connected by capil-

FIG. 12.18 Diagram of arterial system of adult frog, ventral view.



area, the *fossa ovalis*, in the interatrial septum represents the position of an opening, the *foramen ovale*, which is present during fetal life. A sinus venosus, present only during early embryonic development, is lacking in the fully formed mammalian heart, having been incorporated into the wall of the right atrium.

When the atria are in a contracted state, a flaplike projection of each may be observed extending for a short distance over the ventricle. These are the *auricular appendages*. Although the inner lining of the greater part of each atrium is smooth, that of the auricular appendages is ridged by muscular bands, the *musculi pectinati*.

Some variation exists among mammals in regard to the number of systemic veins entering the right atrium. A single postcava guarded by a *valve of Eustachius* is present in all, but there may be either a single precava, as in man and the cat, or two precavae, as in the rabbit, rat, and others. Pulmonary veins, returning oxygenated blood from the lungs, enter the left atrium. Their number varies in different species.

As in birds, a *bicuspid valve*, consisting of two membranous flaps, prevents blood in the left ventricle from being regurgitated into the left atrium. Monotremes are exceptional in that the left atrioventricular valve is tricuspid. In most mammals, a *tricuspid valve*, composed of three somewhat irregular flaps, is located between the right atrium and the right ventricle. Since a single valve is present in birds at this point, the presence of the tricuspid valve is a distinguishing feature of the mammalian heart. Chordae tendineae, attached to the irregular borders of the bicuspid and tricuspid valves, are connected at their other ends either directly to the inner walls of the ventricles and the interventricular septum, or indirectly to papillary muscles which are continuations of the mus-

cular ridges (*trabeculae carneae*) lining the inner surfaces of the ventricles. All are covered with endocardium.

In mammals, contrary to the condition in birds, the right aorta has been eliminated, so that only the left aorta persists. It arises from the left ventricle and distributes blood to all parts of the body. It is called the *systemic aorta*. The *pulmonary aorta* from the right ventricle carries unoxygenated blood to the lungs. A set of three semilunar valves is located at the bases of both pulmonary and systemic trunks.

A well-developed coronary system is present in the mammalian heart. Right and left coronary arteries arise from the systemic aorta as it leaves the left ventricle, just distal to the semilunar valves. During diastole there is a rebound of blood in the aorta. Semilunar valves prevent the blood from returning to the left ventricle. Some of the blood, however, is forced into the coronary arteries, which distribute it to the tissues of the heart itself. Deoxygenated coronary blood is returned through several vessels which converge to enter the right atrium through the *coronary sinus* guarded by the *valve of Thebesius*. Other small openings, the *foramina of Thebesius*, are openings of small veins, the *venae cordis minimae*, which return some blood directly from the heart muscle to the right atrium.

One form of heart failure, known as *coronary occlusion*, is caused by a blood clot or some other fragment blocking a coronary vessel. Death often results when the myocardium fails to receive its normal supply of metabolic substances.

Just as the walls of blood vessels are supplied with blood by the *vasa vasorum*, and the walls of the heart by the coronary vessels, the tissues making up the framework of the lungs, bronchi, and even the walls of the pulmonary vessels themselves receive a supply of blood

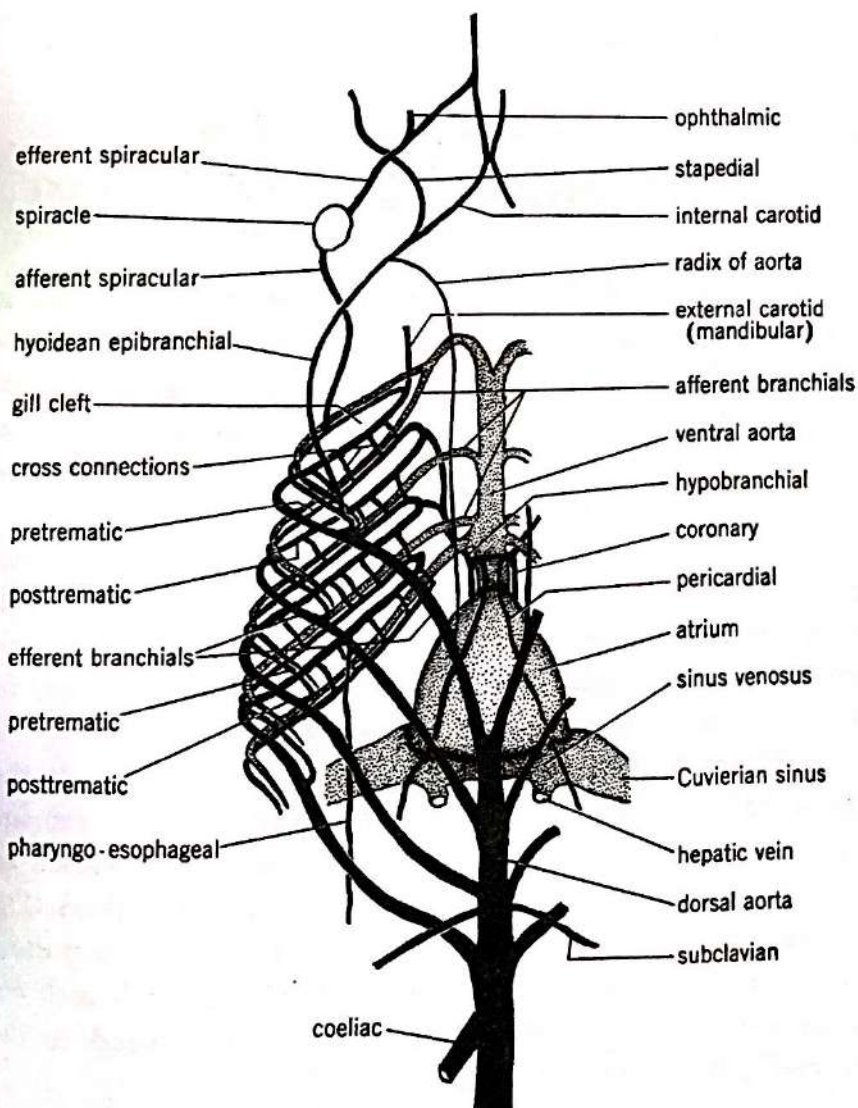


aorta. The anterior end of this vessel is paired for a short distance, but the two portions come together again, thus forming a *cephalic circle*. From this arise arteries which supply brain, eyes, tongue, and various parts of the head.

The salient features of the aortic arches in cyclostomes are (1) a reduction in number as compared with amphioxus; (2) the manner in which they break up into interarterial capillaries between afferent and efferent vessels.

Fishes Much variation is to be observed in the aortic arches of fishes. In general there is a reduction in number within the superclass as the evolutionary scale is ascended. The greatest number occurs in certain primitive sharks, in which the number is directly related to the number of gill pouches. Although in most fishes and in members of the higher classes the number of aortic arches is reduced or otherwise modified, practically all pass through a stage in embryonic development in

FIG. 12.15 Diagram showing arteries in the left gill region of dogfish *Squalus acanthias* as seen from the dorsal side. The length of the arteries at the anterior end has been exaggerated for clarity. Capillary connections between afferent and efferent arteries have been omitted. (Modified from Daniel.)



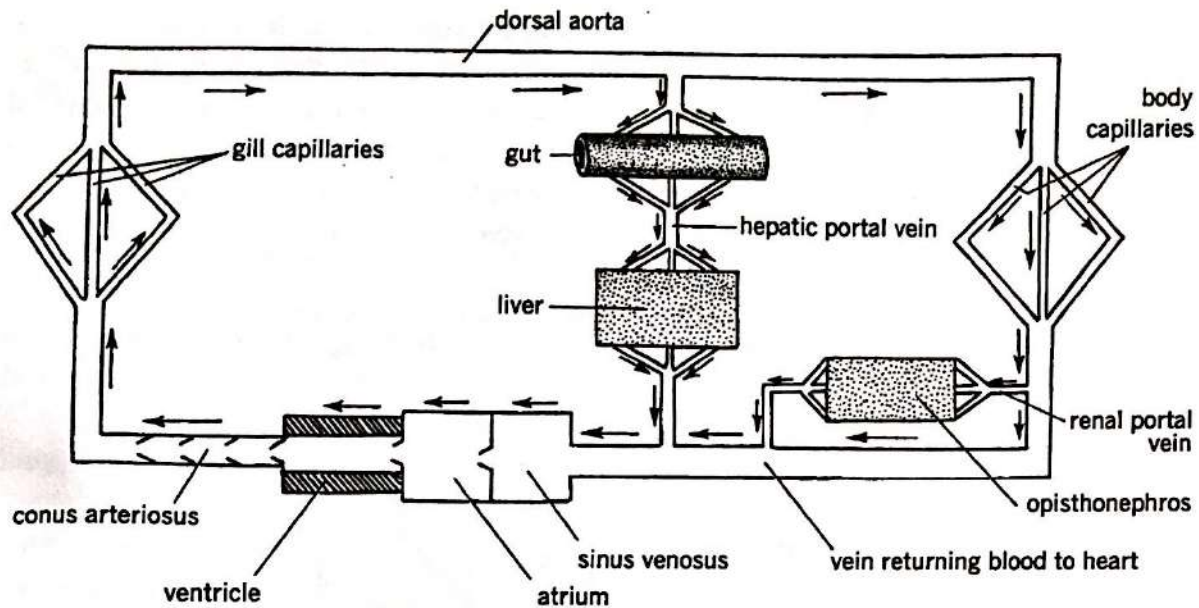
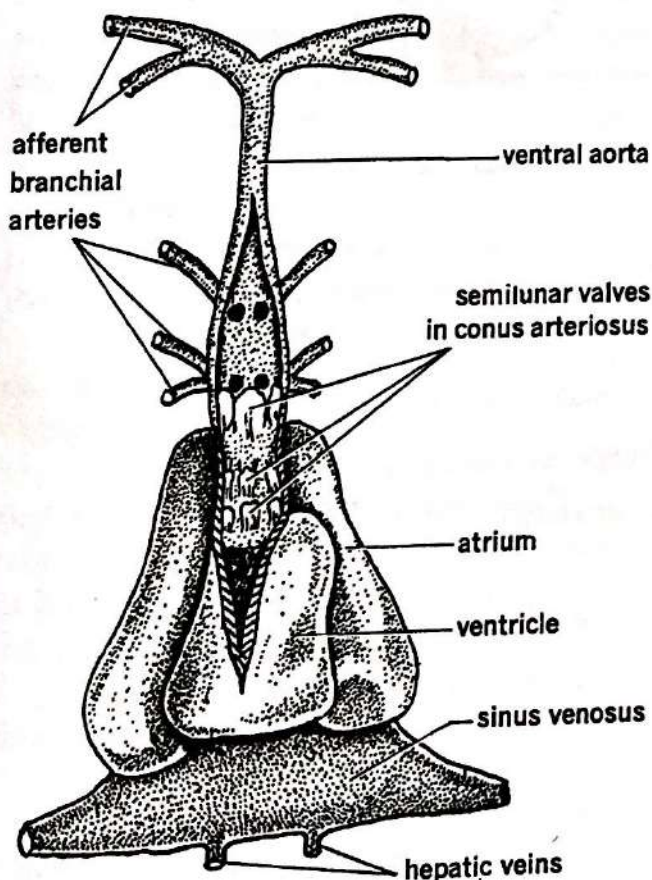


FIG. 12.7 Diagram of single type of circulatory system.

FIG. 12.8 Ventral view of heart of dogfish *Squalus acanthias*. The ventricle and conus arteriosus have been cut open to show the arrangement of the semilunar valves in the conus.



A coronary circulation, supplying and draining the walls of the heart itself, is particularly well developed in elasmobranchs. Similar vessels have been described in certain teleosts and other fishes, but in some a special coronary circulation does not seem to be evident.

The first advance from a two- to a three-chambered condition is seen in the Dipnoi, or lungfishes. In this group the atrium has become partially divided into right and left halves by an incomplete partition, or septum. In *Protopterus* unoxxygenated blood from the body enters the right chamber via the sinus venosus, but oxygenated blood coming from the swim bladder (lung) enters the left atrium. The ventricle possesses pocketlike cavities in its walls. These, together with an incomplete interventricular septum made up of fibrous and muscular tissues, prevent mixing to a large extent. In *Protopterus* the conus has become divided longitudinally into two channels so that the two streams of blood, one oxygenated and the other unoxxygenated, leave the heart. This is known as the *double type* of

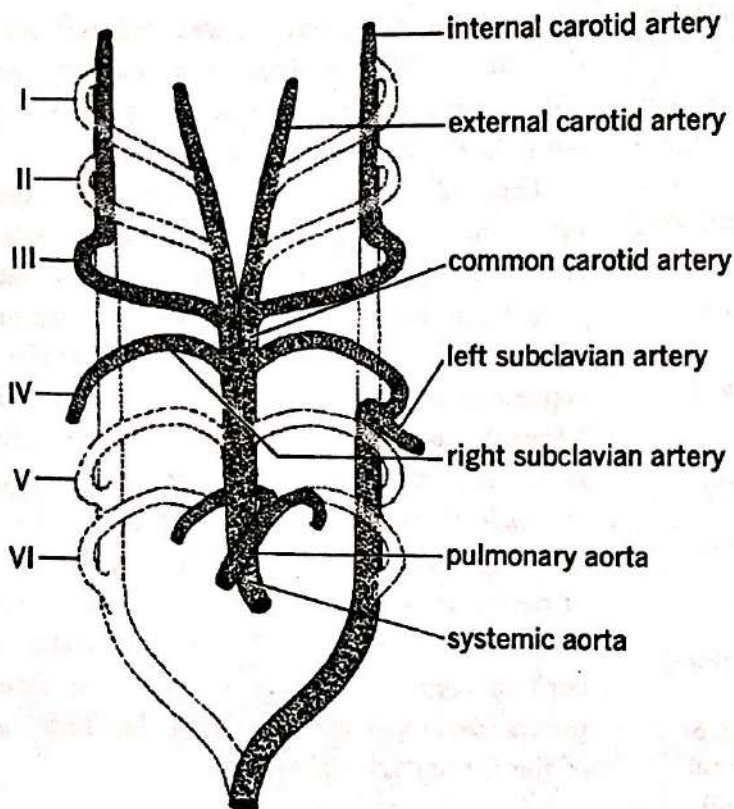


FIG. 12.24 Diagram showing modification of aortic arches as found in mammals, ventral view.

of birds except that the radix on the right side, rather than the left, loses its connection with the aorta (Fig. 12.24). The fourth aortic arch on the left side together with its radix becomes the arch of the definitive aorta. The fourth arch on the right and a portion of the right radix become the right subclavian artery. The left subclavian develops as an enlargement of one of the intersegmental arteries coming off the aorta in this region. 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. A ligamentum arteriosum is finally all that remains (Fig. 12.25).

REMAINDER OF THE ARTERIAL SYSTEM The arteries supplying the head

region are, for the most part, branches of the external and internal carotids. In some forms, branches of the fourth arches or of the subclavian arteries also pass to the cephalic region. Occipitovertebral and vertebral arteries are examples. The aorta continues posteriorly into the tail, where it becomes the *caudal artery*. Most of the vertebrate body is supplied with blood through branches of the aorta which may for convenience be grouped under two divisions, somatic arteries, supplying the body proper, and visceral arteries, distributed to the urogenital organs as well as to various portions of the digestive tract and associated structures.

Somatic Arteries The arteries supplying the body proper are usually paired structures which clearly show evidences of metamerism. They supply portions of the body derived from the embryonic epimere, being distrib-

tions of various kinds results in the formation of two-, three-, or four-chambered hearts.

Comparative Anatomy of the Heart

Amphioxus A single, median contractile vessel lies ventral to the pharynx in amphioxus. Some consider it to be a one-chambered heart. Usually, however, it is spoken of as the *branchial artery*, *endostylar artery*, or *truncus arteriosus*. The muscles in its walls contract more or less rhythmically from posterior to anterior ends. On either side of the vessel numerous lateral branches are given off which course through the primary gill bars. At the base of each lateral *afferent branchial artery* is a small contractile enlargement, the *bulbillus* (Fig. 12.28). A single contraction of the "heart" followed by contraction of the bulbilli is sufficient to force blood through the entire body. Since the primitive embryonic condition of the heart in vertebrates is that of a single tube, the "heart" of amphioxus is considered to correspond to an early stage of development of the heart of higher forms.

Cyclostomes The two-chambered heart of the lamprey consists of a large, thin-walled atrium which communicates with the ventricle by means of a small aperture guarded by an *atrioventricular valve*. The ventricle is smaller than the atrium and has thick muscular walls. The lining of the ventricle is irregular and is provided with tough cords, the *chordae tendineae*, which connect to the atrioventricular valve. The cords prevent the valves from being pushed into the atrium when the muscular ventricle contracts. Blood is forced from the ventricle through a poorly developed conus into the ventral aorta, which distributes it to the gills. A single set of two semilunar valves in the conus region prevents any backflow of blood. A small, thin-walled

sinus venosus, which lies in the crevice between atrium and ventricle, opens into the atrium through a slitlike aperture guarded by a pair of *sinuatrial valves*. The heart, which lies posterior to the last pair of gill pouches, is located in a pericardial cavity surrounded by a thick, tough pericardium. In the ammocoetes stage the pericardial cavity communicates with the rest of the coelom, but the connection disappears in the adult.

Only unoxygenated blood passes through the cyclostome heart, which sends blood to the gills, where exchange of gases takes place. This is known as the *single type of circulatory system* (Fig. 12.7), since but one stream of blood passes through the heart.

In hagfishes a secondary caudal "heart" assists in pumping blood forward.

Fishes The hearts of most fishes are essentially similar in structure to the two-chambered heart of the lamprey. The single type of circulation is the rule. Variations in the relative positions of atrium and ventricle occur but are of minor significance. The arrangement of veins entering the sinus venosus also varies. The feature which perhaps deserves the greatest attention is the number and arrangement of valves in the conus arteriosus (Fig. 12.8). These semilunar valves, which prevent backflow of blood into the heart, are most numerous in elasmobranchs and in the ganoid fishes. In these forms the valves are arranged in three longitudinal rows, one dorsal and two ventrolateral in position. Several valves are present in each row. In *Epiceratodus* eight sets of valves are present. Many elasmobranchs have six sets. The valves of the anterior set are the largest. There is a tendency among fishes toward a reduction in the number of valves in the conus. Teleosts are characterized by having a single set, although in a few species two sets are retained.

FIGURE 14.7

Heart of *Squalus acanthias* opened to show chambers and blood flow. Left lateral view.

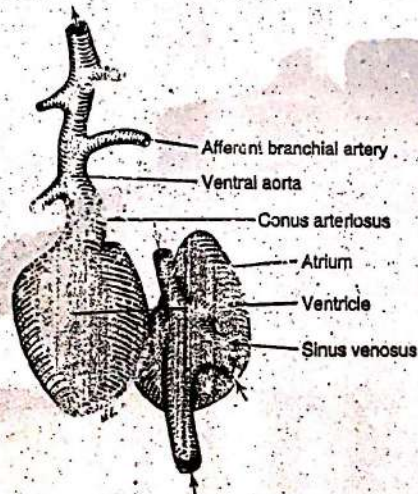
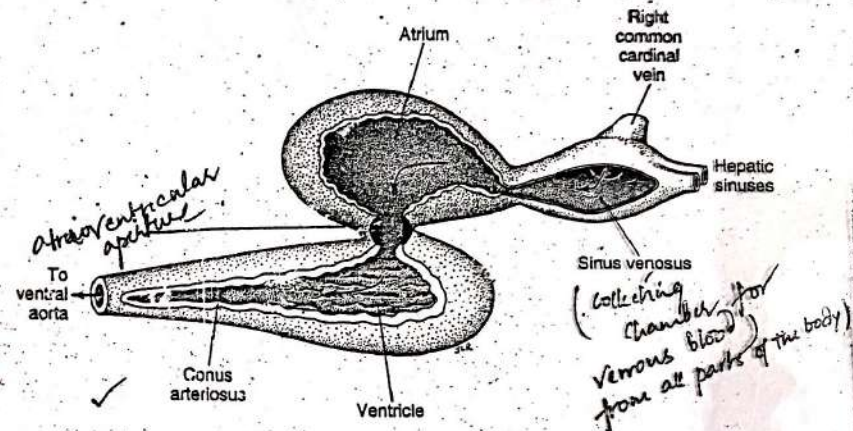


FIGURE 14.8

Heart and associated vessels of an agnathan, *Myxine glutinosa*, ventral view. Arrows indicate direction of blood flow.

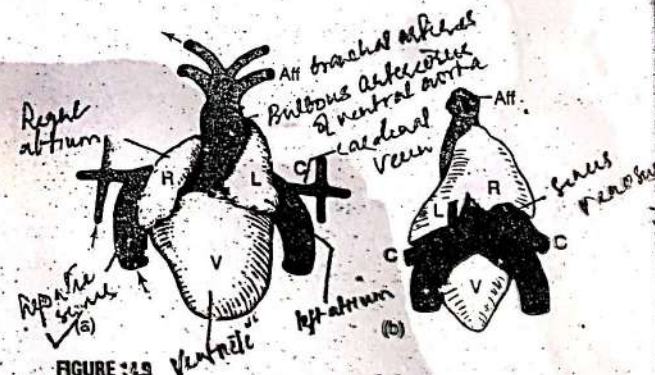


FIGURE 14.9

Heart and associated vessels of *Necturus*. (a) Ventral view. (b) Dorsal view. AH, common channel leading to fourth and fifth afferent branchial arteries (see fig. 14.18d); B, bulbous arteriosus of ventral aorta; C, common cardinal vein; H, hepatic sinus; L, left atrium receiving, in (b) the pulmonary vein; P, pulmonary vein; R, right atrium; SV, sinus venosus; V, ventricle. In (a), a short conus arteriosus connects the ventricle with the bulbous. Arrows show direction of blood flow. (Colors represent arteries (red) and veins (blue) but not necessarily oxygen content.)

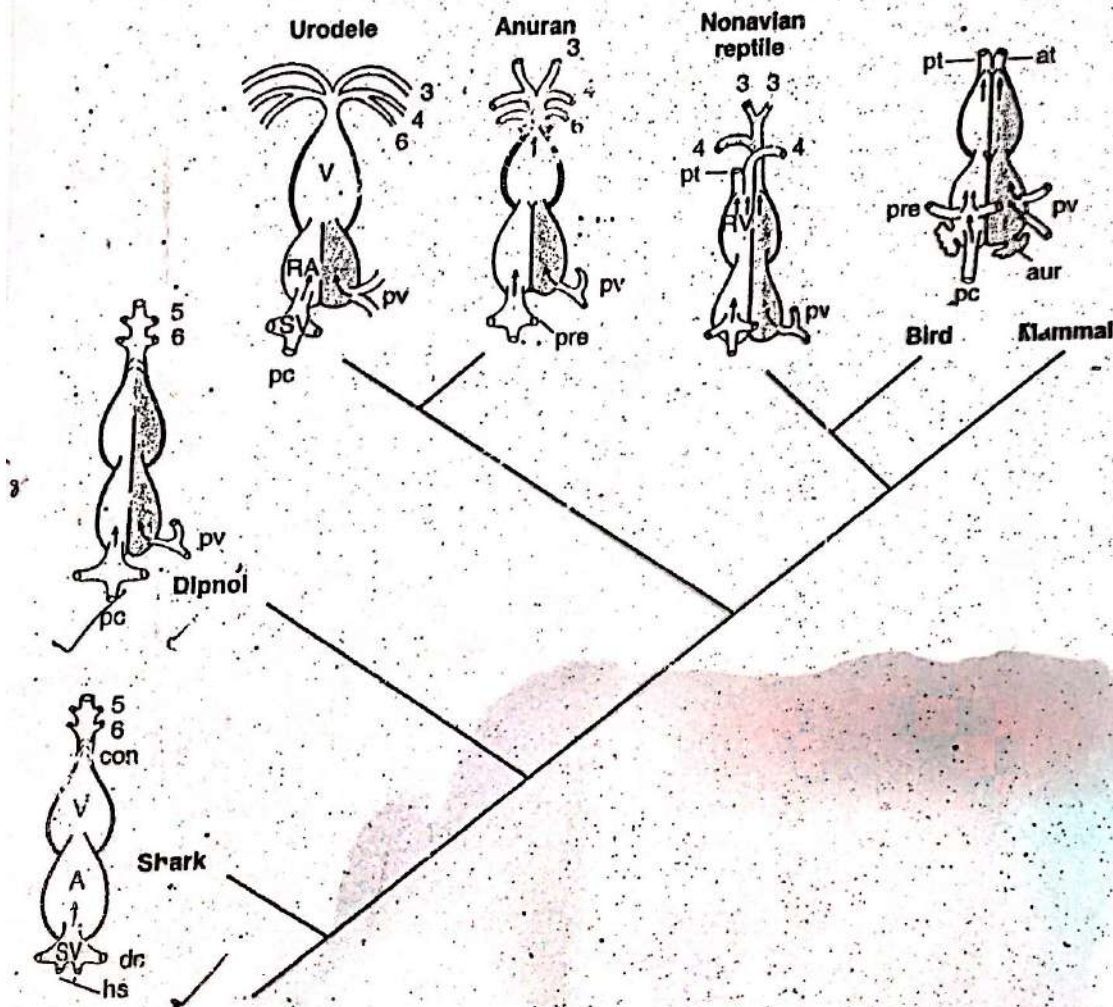


FIGURE 14.10

Heart chambers and oxygenated blood flow (red) in some generalized craniates. Distribution of oxygenated blood beyond the ventricle in dipnoi, urodele, and reptile depends on the species and the physiological needs of the organism. The parts of the heart shown are A, atrium; RA, right atrium; V, ventricle; RV, right ventricle; SV, sinus venosus; con, conus arteriosus; aur, auricle of mammalian heart. 3 to 6, third to sixth aortic arches. Other vessels are at, aortic trunk; dc, common dorsal cardinal vein; hs, hepatic sinus; pc, pre-cava; pre, pre-cava (common cardinal vein); pt, pulmonary trunk; pv, pulmonary veins.

Hearts of Dipnoans and Amphibians

1. Modifications in the heart and associated arteries in dipnoans and tetrapods are correlated with aerial respiration.
2. The modifications enable oxygenated blood returning from the swim bladders or lungs to be separated in the heart from deoxygenated blood returning from other organs.
3. One modification in dipnoans and amphibians was the establishment of a partial or complete interatrial septum so that there are partial or complete right and left atrial chambers. (Fig: Dipnoi, urodele, Anuran)
4. The Septum is complete in anurans and in some urodeles.
5. Except in Neoceratodus (Dipnoi), the veins from the swim bladder or lungs empty directly into the left atrium; therefore, the blood in this chamber is oxygen rich.
6. The sinus venosus empties into the right atrium; hence the blood in this chamber is low in oxygen.
7. In lungless urodeles, the atrium remains totally undivided.
8. A second modification is the formation of a partial interventricular septum (chiefly in dipnoans but also in Siren, a urodele) or of ventricular trabeculae (in amphibians).
9. Trabeculae are shelves or ridges projecting from the ventricular wall into the chamber.
10. Function of Interventricular septa and ventricular trabeculae: They maintain separation of oxygenated and unoxygenated blood that began in the left and right atria.
11. A third modification is formation of a spiral valve in the conus arteriosus in dipnoans and anurans.
12. The valve in dipnoans consists of a pair of longitudinal typhlosol-like folds of the lining of the conus.

13. In anurans, it is a single flap.
14. The valves direct oxygen-poor blood into aortic arches that lead to gills or lungs and they channelize oxygenated blood into arches that supply other organs.
15. A fourth modification shortened the ventral aorta so that it becomes practically non-existent as embryonic development progresses. As a result, blood moves from the conus arteriosus directly into appropriate vessels. Urodeles, however, retain a prominent ventral aorta.

REPTILES

1. The reptiles are the first group of chordates to become truly terrestrial.
2. In this group, lungs are the only respiratory organs, so an efficient pulmonary circulation is a necessity.
3. Although a large sinus venosus is present in certain reptiles (turtles), in many it has been greatly reduced. Much of it may be incorporated within the wall of the right atrium.
4. Valves which are present where veins enter the right atrium represent vestiges of the sinus venosus.
5. A complete interatrial septum separates the oxygenated blood entering the left atrium from the unoxygenated blood in the right.
6. All reptiles have a three-chambered heart except crocodiles and alligators, in which it is four-chambered.
7. Even in the three-chambered heart, however, the ventricle is partially divided by an incomplete interventricular septum which extend forward from the apex toward the center.
8. The conus arteriosus no longer exists as such.
9. Its distal portion as well as ventral aorta has split into three main trunks each of which has a single row of semilunar valves at its base.

10. One trunk is the pulmonary trunk, sometimes called the pulmonary aorta, which gives off two pulmonary arteries going to the lungs.
11. The two remaining systemic trunks are called the left and right aortae respectively.
12. An aperture, the foramen Panizzae, is located at the point where right and left aortae are in close contact and cross each other, so that their cavities are in communication.
13. In the Crocodilia, in which a complete interventricular septum appears for the first time, a true four chambered heart is found.

14. BIRDS

1. A completely double circulation occurs in birds for the first time, since at no point is there any opportunity for oxygenated and unoxygenated blood to mix.
2. The sinus venosus has disappeared, and three large veins, two precavae and one postcava, enter the right atrium directly.
3. Pulmonary veins return oxygenated blood from the lungs to the left atrium.
4. The heart in birds is relatively much larger and more compact than in forms previously discussed.
5. Both atria are thin walled. The ventricles are completely separated as in crocodilians.
6. Blood from the left ventricle is distributed over a considerable distance to all parts of the body.

7. A single muscular and very well-developed atrio-ventricular valve separates the right atrium from the right ventricle.
8. Two valves, known as, bicuspid valve, are present at the left atrioventricular aperture.
9. The main advance shown by the heart of the bird over the four-chambered heart of crocodiles lies in the elimination of the left aorta.
10. Only two vessels leave the heart in birds: a pulmonary trunk, or aorta, from the right ventricle, and a systemic aorta, corresponding to the right aorta of reptiles, from the left.
11. A single set of three semilunar valves is present at the base of each.

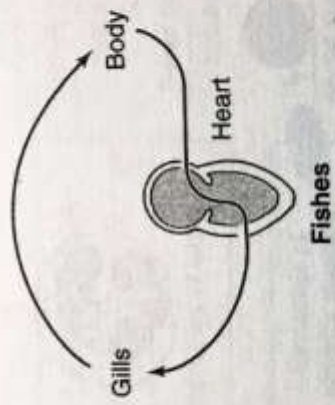
Remark: A well developed coronary system is present in birds. Coronary arteries arise from the systemic aorta. A venous, coronary sinus enters the right atrium near the entrance of the postcava.

MAMMALS

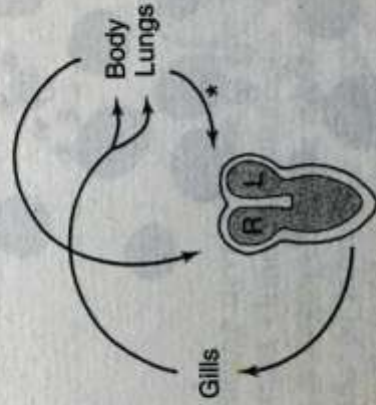
1. The four-chambered mammalian heart is essentially similar to that of birds, the two sides of the heart being completely separated from each other by interatrial and interventricular septa.
2. A thin area, the fossa ovalis, in the interatrial septum represents the position of an opening, the foramen ovale, which is present during fetal life.

3. A sinus venosus, present only during early embryonic development, is lacking in the fully formed mammalian heart, having been incorporated into the wall of the right atrium.
4. In placental mammals, the pulmonary veins open directly into the left atrium, but in monotremes and marsupials two pulmonary veins enter a common vestibule which in turn joins the left atrium.
5. When the atria are in a contracted state, a flaplike projection of each can be observed extending for a short distance over the ventricle. These are the atrial appendages, or auricles.
6. As in birds, a bicuspid, or mitral valve consisting of two membranous flaps, prevents blood in the left ventricle from being regurgitated into the left atrium. Monotremes are exceptions in that the left atrioventricular valve is tricuspid.
7. In most mammals a tricuspid valve, composed of three somewhat irregular flaps is located between the right atrium and ventricle.
8. Since a single valve is present in birds at this point, the presence of tricuspid valve is a distinguishing feature of the mammalian heart.
9. In mammals, contrary to the condition in birds, there has been an elimination of the right aorta, so that only the left aorta persists.
10. It arises from the left ventricle and distributes blood to all parts of the body.

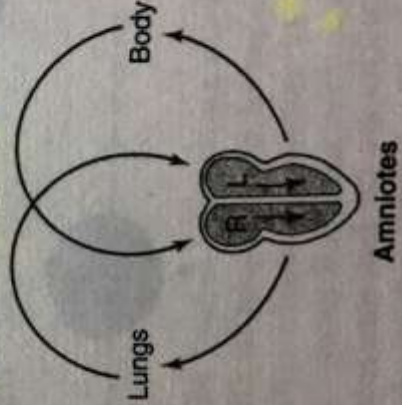
11. It is called the systemic trunk or aorta.
12. The pulmonary trunk, or aorta, from the right-ventricle carries un氧ogenated blood to the lungs.
13. A single set of three semilunar valves is located at the bases of both pulmonary and systemic aortae.
14. A well developed coronary system is present in the mammalian heart.
15. Right and left coronary system is present in the mammalian heart.
16. Right and left coronary arteries arise from the systemic aorta as it leaves the left ventricle and just distal to the semilunar valves.
17. ~~During~~ diastole there is ^x a retrograde of blood, in



Fishes



Gill-breathing amphibians



Amniotes