HEART

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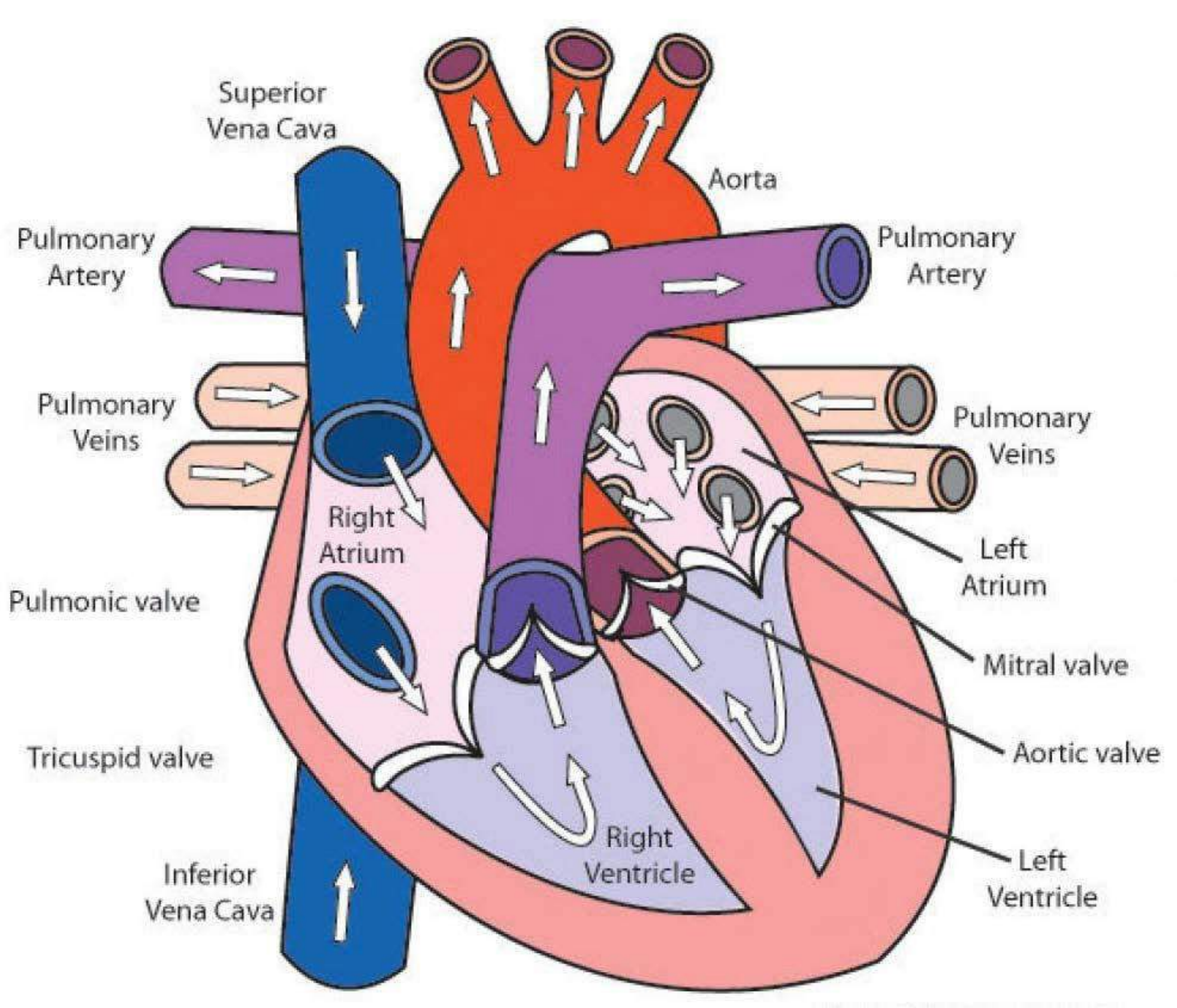
Comparative Anatomy of Heart in Vertebrates Evolution of Heart in Vertebrates

Chandrik Malakar



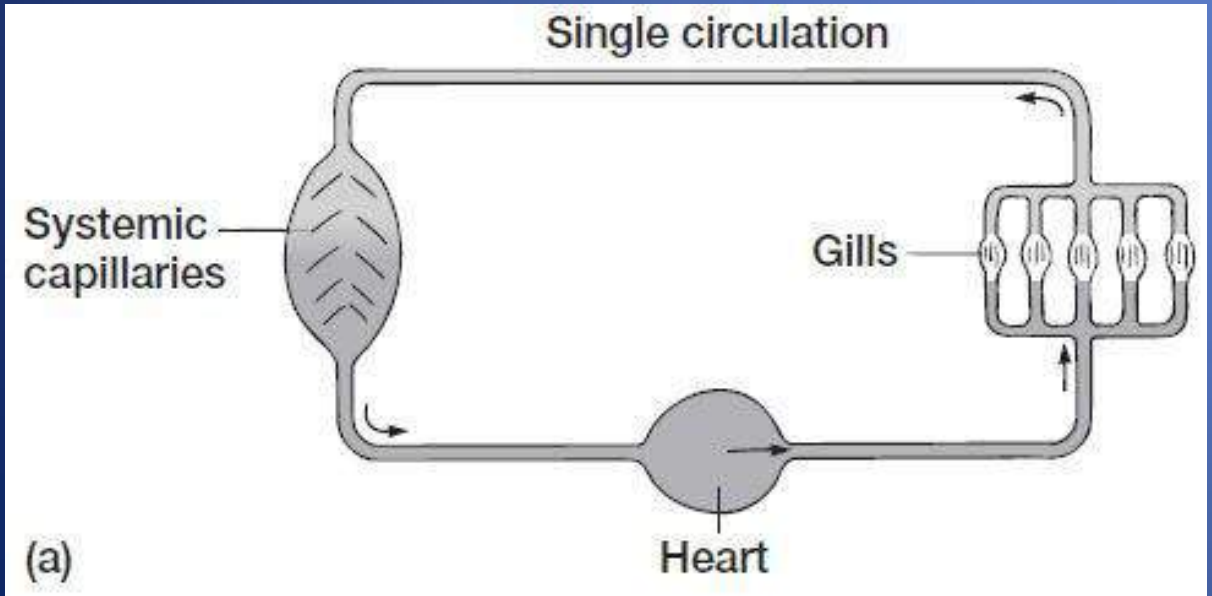
A mammalian heart

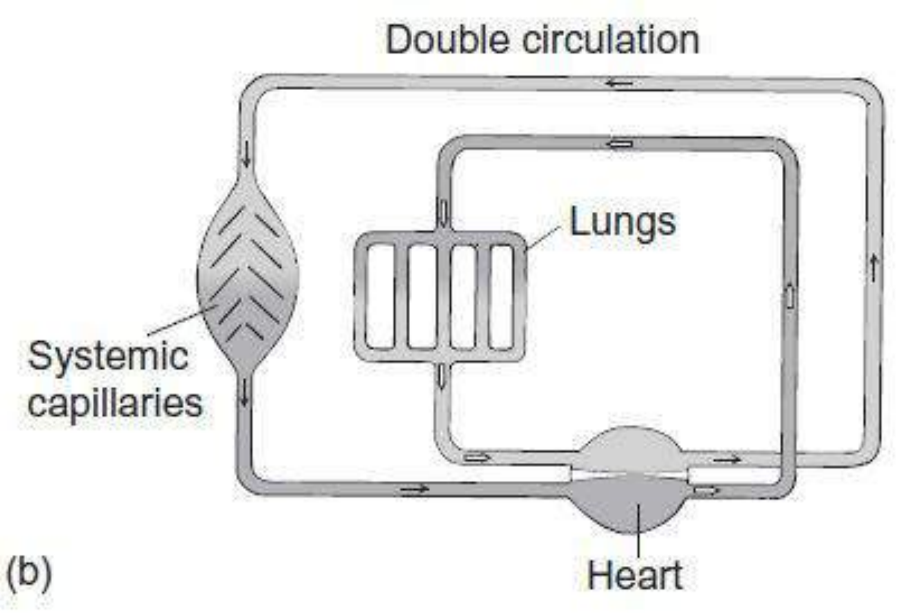
Single and Double Circulation

Blood travels in one of two general patterns.
Most fishes have a **single circulation (single-circuit)** pattern in which blood passes only once through the heart during each complete circuit. With this design, blood moves from the heart to the gills to the systemic tissues and back to the heart. The heart which pumps blood via ventral aorta directly to the gills (then to body) is called **branchial heart**.

Amniotes have a **double circulation (double-circuit)** pattern in which blood passes through the heart twice during each circuit, traveling from the heart to the lungs, back to the heart (**pulmonary** circuit), out to the systemic tissues, and back to the heart (systemic circuit) a second time.

Functional intermediates with characteristics of both conditions. The **intermediates include lungfishes, amphibians, and reptiles.**





Basic Vertebrate Heart

Phylogenetically, the heart probably began as a contractile vessel, much like those of amphioxus. The embryonic fish heart consists of four chambers in series, so that blood flows in sequence from the **sinus venosus,** to the **atrium,** to the **ventricle,** and finally to the fourth and most anterior heart chamber, the **bulbus cordis,** before entering the ventral aorta. The bulbus cordis is termed in the adult the **conus arteriosus** if its contractile walls possess cardiac muscle (and **conal valves** internally; eg chondrichthyans, holosteans, and dipnoans.), or **bulbus arteriosus** if its elastic walls lack cardiac muscle (teleost). The adult bulbus arteriosus, in some fishes, may also incorporate part of the adjoining ventral aorta as well.

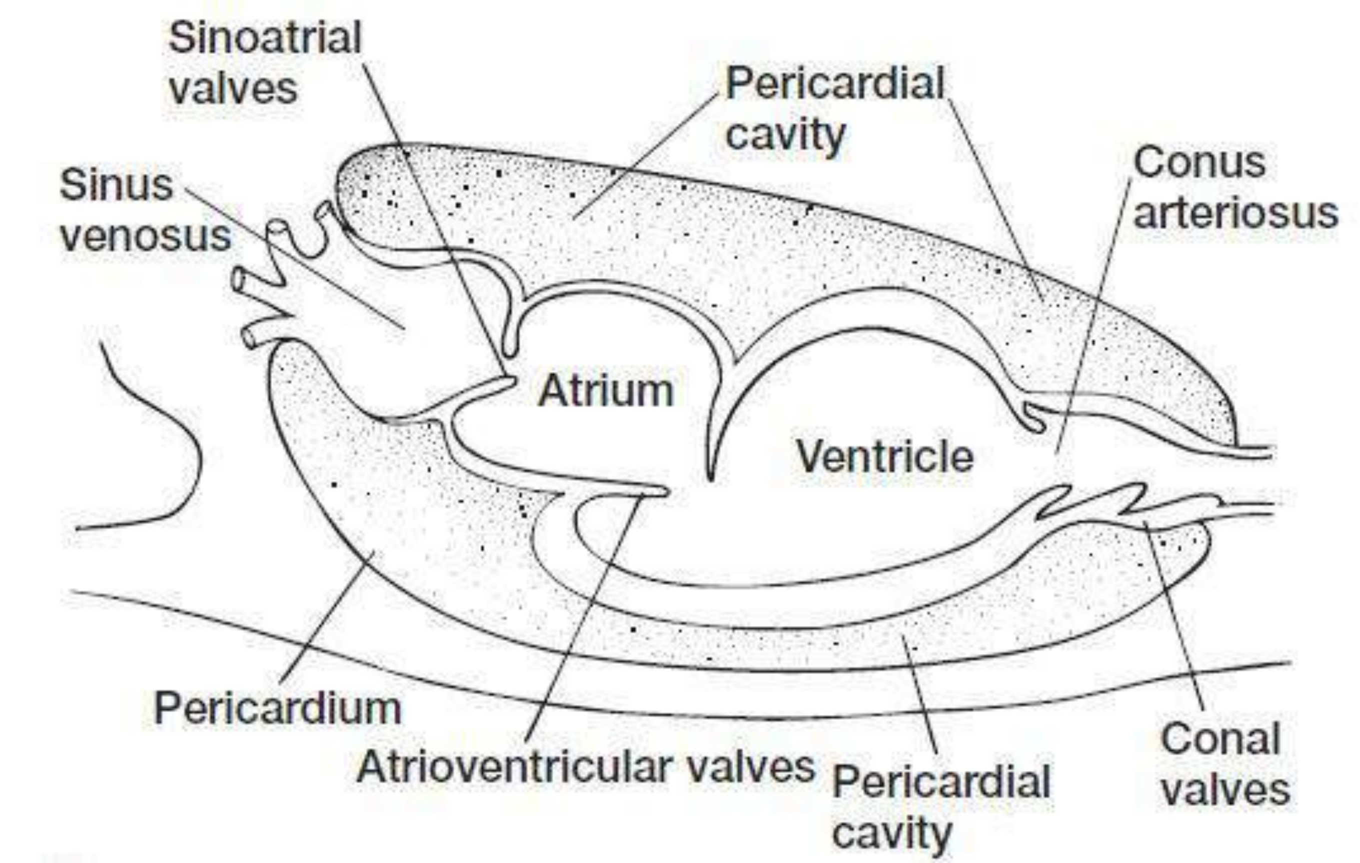
Besides conal valves, the endocardium develops the **sinoatrial (SA) valves** formed between the sinus venosus and the atrium, and the **atrioventricular (AV) valves** formed between the atrium and ventricle. Valves prevent retrograde blood flow.

The heart lies within the **pericardial cavity** lined by a thin epithelial membrane, the **pericardium.** In many fishes, the pericardial cavity lies within bone or cartilage.

[In tetrapods, the bulbus cordis divides into the bases of the aortae. Term **truncus arteriosus,** of the older literature, should apply only to the ventral aorta or its derivatives but not to any part of the heart proper. In birds and mammals both the atrium and the ventricle become divided into left and right compartments to produce four anatomically separate chambers.

In *Branchiostoma*, in stead of a true heart, a part of ventral aorta below pharynx becomes muscular and contractile; considered as a **single-chambered heart** by some.

In fish, Internally, each chamber may contain various numbers of **conal valves**. In some fishes, most notably in teleosts, the bulbus arteriosus is thin walled with smooth muscle and elastic fibers, but it lacks both cardiac muscle and conal valves.**]**



Basic heart structure: The four chambers of the fish heart are enclosed within the pericardial cavity. One-way valves between each chamber prevent reverse flow of blood as successive chambers contract.

[In many fishes and primitive tetrapods, there is a direct respiratory gas exchange between the myocardium and blood passing through its lumen. In others, the **coronary vessels** perfuse the heart wall (usually only the outer part of the myocardium), especially **in elasmobranchs, crocodiles, birds, and mammals**. In fishes, the coronary arteries are derived from the efferent arches or collecting loops of the gills, which carry oxygenated blood. The coronary veins enter the sinus venosus.]

Progressive modification of heart from primitive to higher chordates (vertebrates) occurs on the following lines:

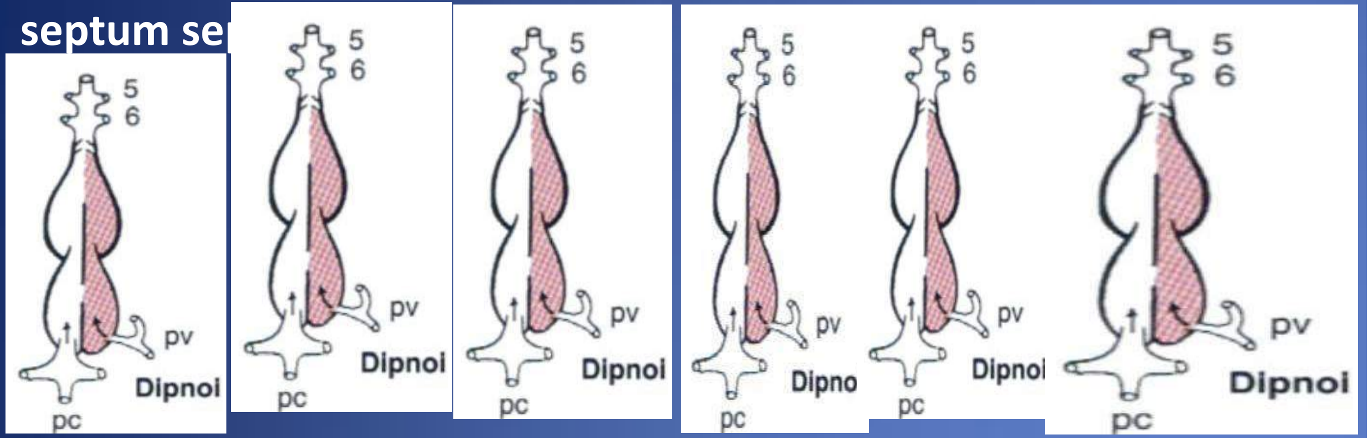
-Cardiac tube forms chambers due to constrictions

-Each chamber tends to divide into two separate chambers due to formation of partitions

-Subsequent folding of the tubular heart twists the heart into different configurations, but the internal sequence of blood flow remains the same.

-Heart gradually shifts from just behind head (fishes, amphibians) near gills into thoracic cavity (amniotes) with elongation of neck and development of lungs.

Fig: **Evolution of heart in vertebrates**. A, atrium or auricle; LA, left auricle; RA, right atrium; V, ventricle; LV, left ventricle; RV, right ventr SV, sinus venosus; 1 to 6 are aortic arches. Shaded chambers contair mainly oxygenated blood. **Note: In dipnoan, draw AV plug and IV septum se**



1. In *Branchiostoma*, a contractile muscular thickening of ventral aorta below pharynx is often treated as a *single-chambered heart.*

2. Cyclostomes and fishes (except dipnoans) have 2-chambered, single circuit, venous and branchial hearts:

Hagfish has 3- “chambered” heart; lamprey heart also has the 4th chamber - bulbus arteriosus having semilunar valves.

Fish heart has typical 4 chambers. Elasmobranch heart is S-shaped, auricle lying dorsal to ventricle. Teleost has bulbus arteriosus having a single pair of bulbar valves.

3.Dipnoan, amphibians and reptiles (except crocodiles) have 3-chambered transitional hearts. In crocodiles 4-chambered.

4.Birds and mammals have 4-chambered, double circuit

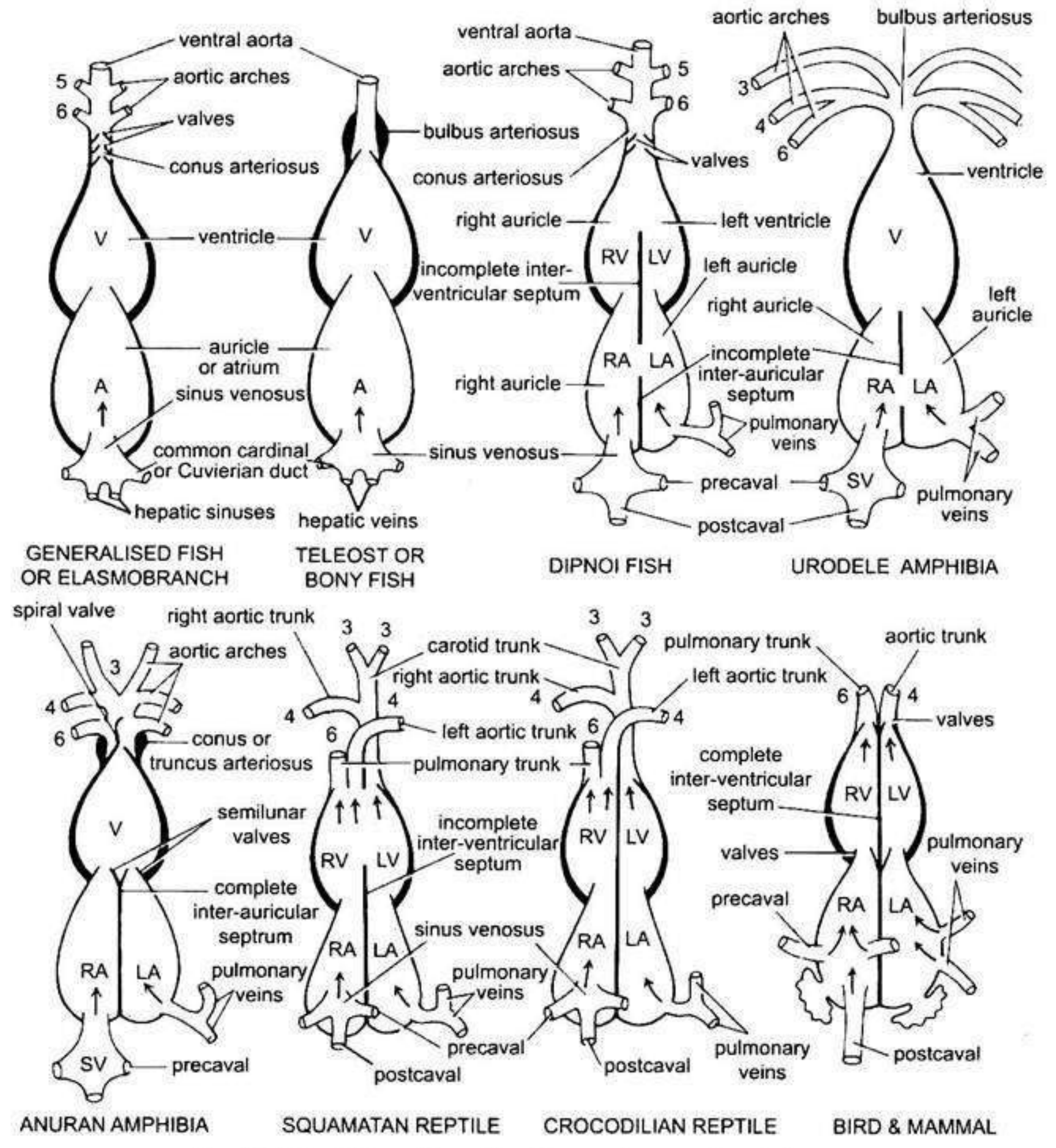
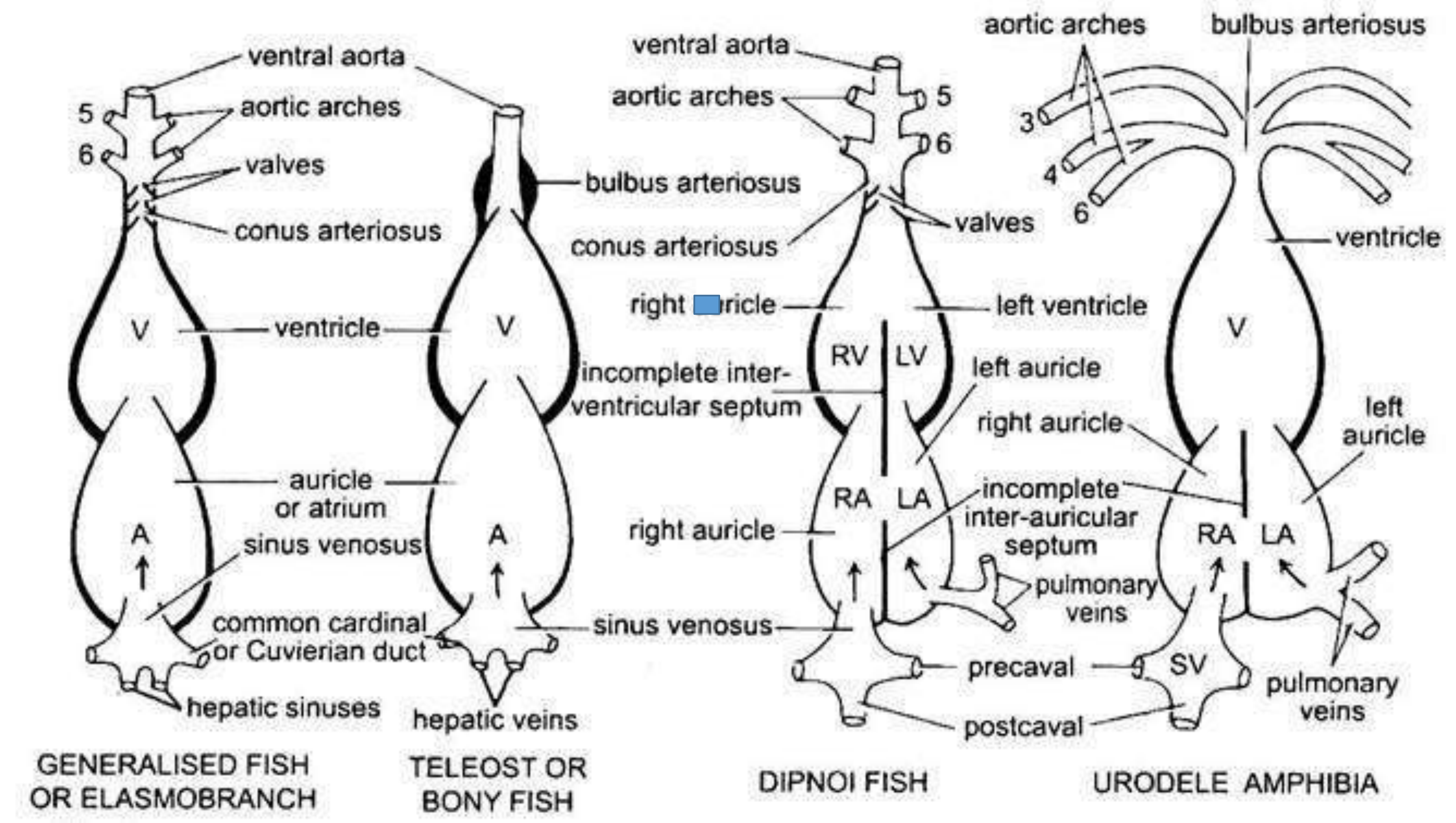


Fig. 45.4. Evolution of heart in different classes of vertebrates.


ventral aorta
5
6
aortic arches
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sinus venosus
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hepatic sinuses
bulbus arteriosus
hepatic veins
ventral aorta
aortic arches
5
6
valves
conus arteriosus
right ricle
left ventricle
RV
LV
incomplete inter-
ventricular septum
left auricle
RA
LA
right auricle
sinus venosus
pulmonary
veins
precaval
postcaval
incomplete
inter-auricular
septum
aortic arches
bulbus arteriosus
3
4
6
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right auricle
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GENERALISED FISH
OR ELASMOBRANCH
TELEOST OR
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DIPNOI FISH
URODELE AMPHIBIA

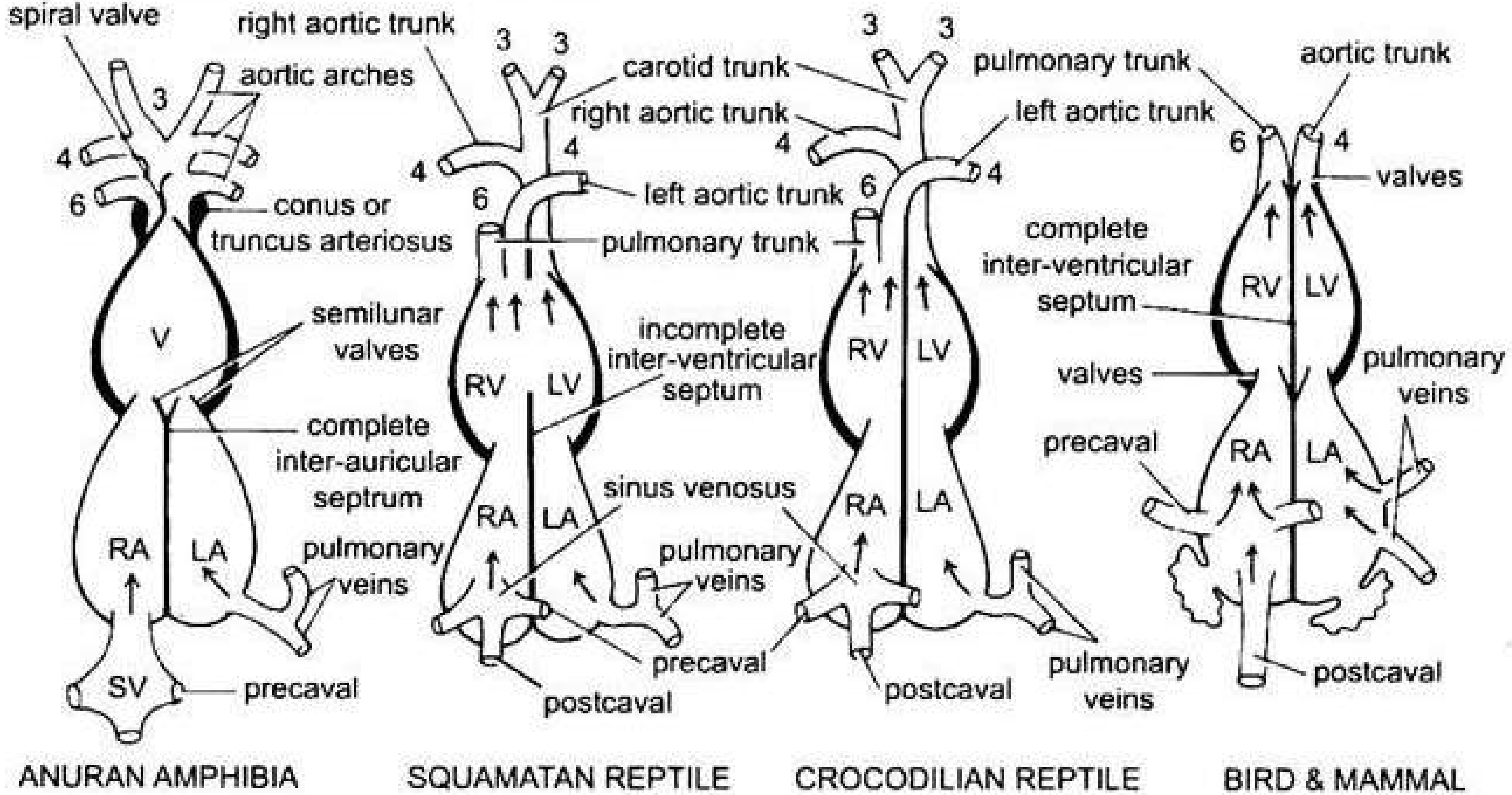


Fig. 45.4. Evolution of heart in different classes of vertebrates.

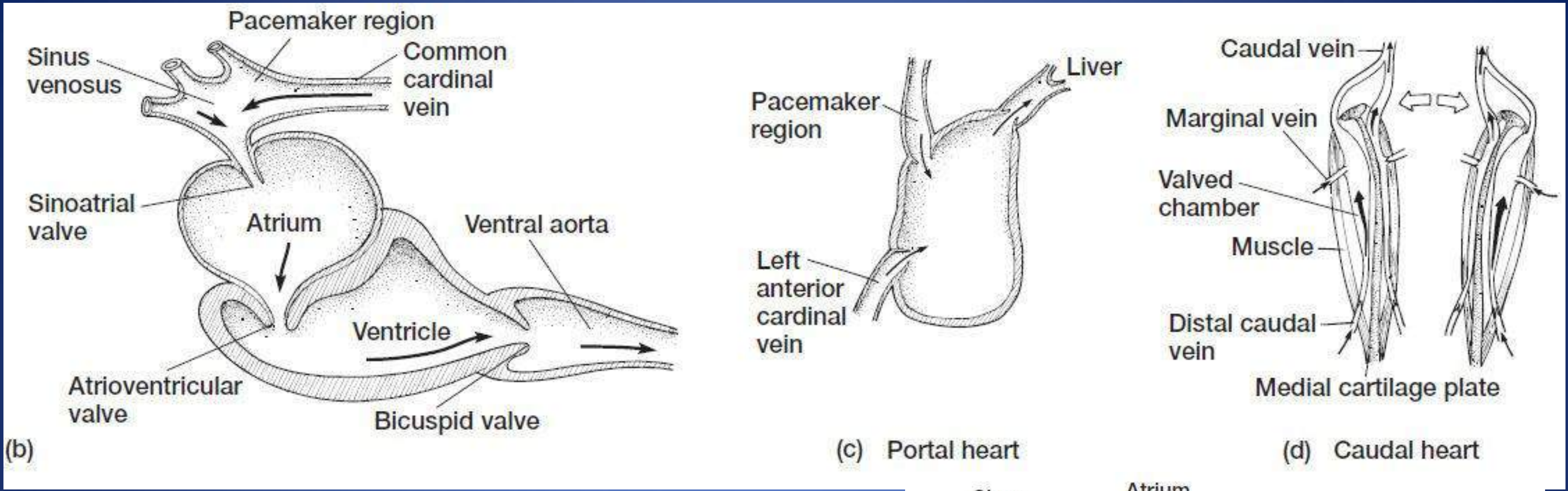
In ***Branchiostoma***, a contractile muscular thickening of ventral aorta below pharynx is often treated as a *single- chambered heart.*

Cyclostomes **(***2-chambered, single circuit, venous and branchial hearts***)**

Hagfishes The hagfish heart has **three chambers in series: the sinus venosus, the atrium, and the ventricle**.

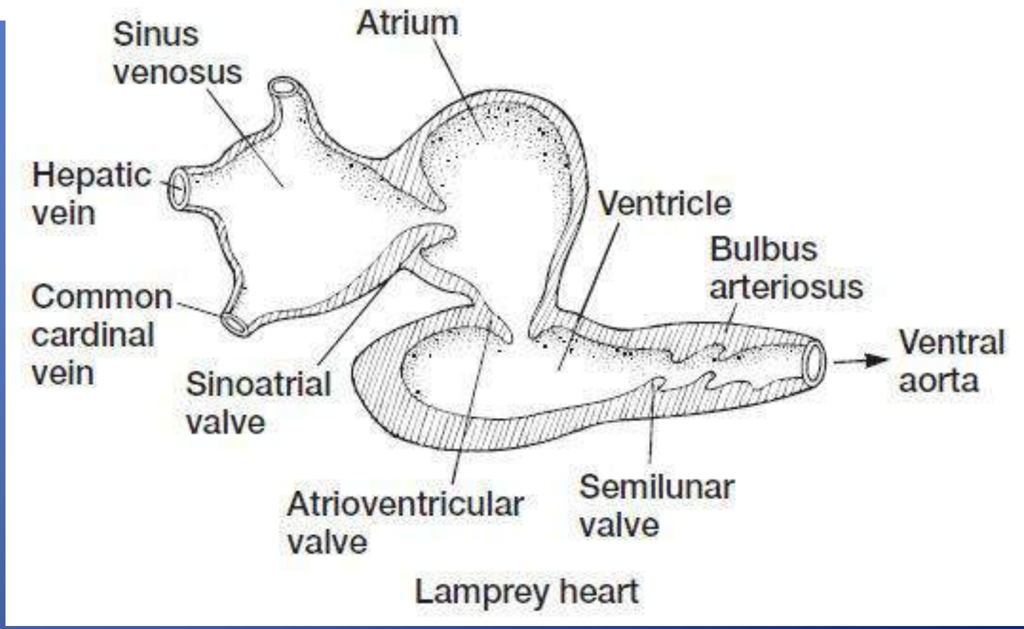
A slight microscopic **thickening** of the base of the ventral aorta is treated by some as a fourth compartment, **the bulbus arteriosus**. No major nerves innervate the hagfish heart to stimulate contraction. Instead, filling of the sinus venosus by returning blood elicits the **Frank-Starling reflex**. **Accessory 'hearts**' (contractile but lack cardiac muscle) like cardinal hearts, caudal hearts, portal heart (has cardiac muscles) are blood pumps in different parts of the circulation.

The **lamprey** heart (branchial heart) has four compartments - **sinus venosus, atrium, ventricle and bulbus arteriosus**. The luminal walls of the bulbus arteriosus are thrown into leaflets, collectively forming the **semilunar valves.** Unlike hagfishes, the heart is innervated and, further, the ventricle empties into the **bulbus arteriosus.**



Hagfish: (b) Branchial heart illustrating the three chambers. Accessory hearts. The walls of the cardinal (not shown) and portal hearts (c) pulsate to help drive blood. The caudal hearts (d) have paired striated muscles and a central flexible support.

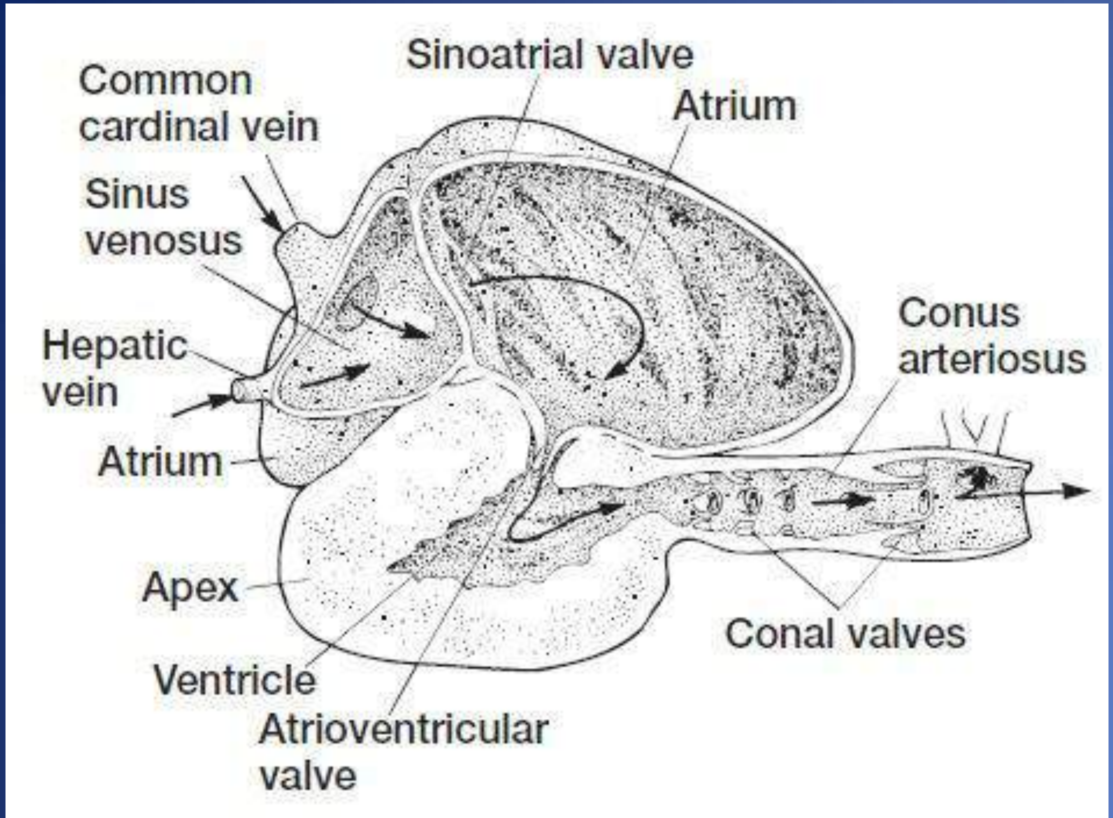
Lamprey heart. The four chambers characteristic of most fishes are present in the lamprey.



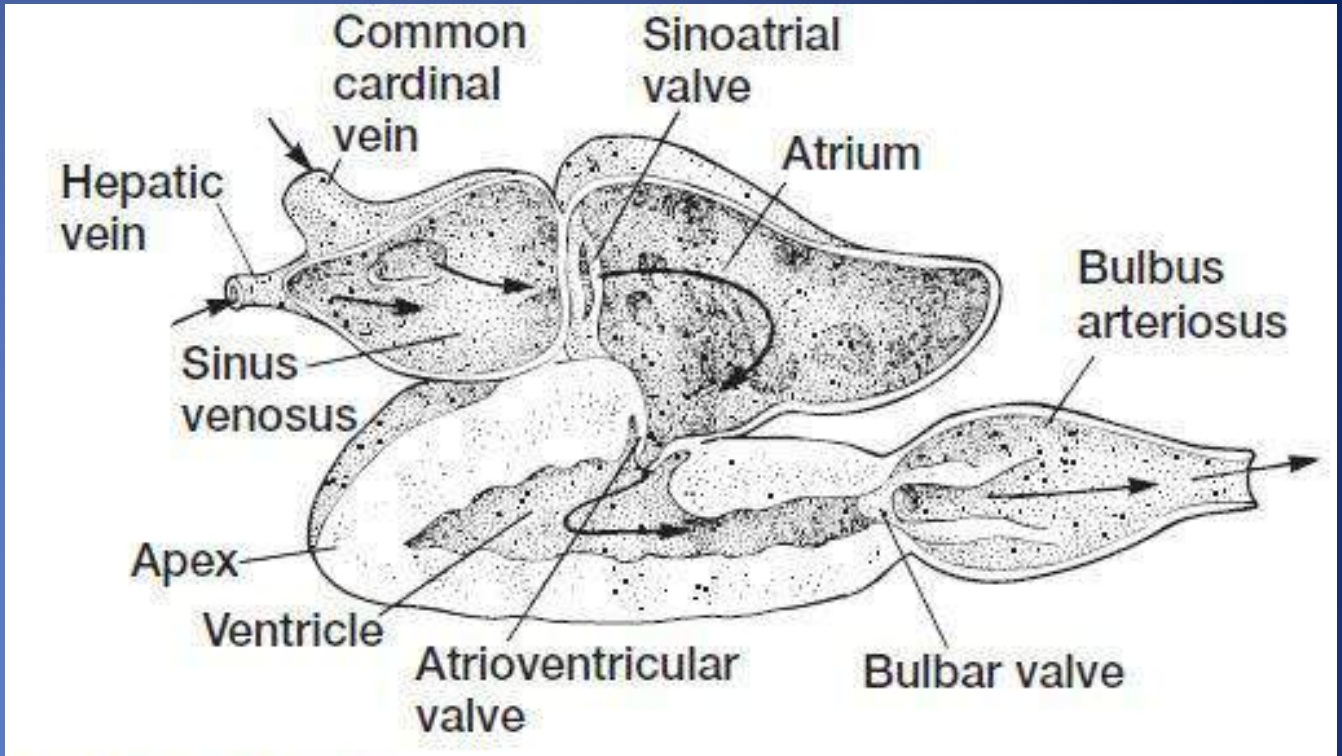
Fishes (*2-chambered, single circuit, venous and branchial hearts*)

The hearts of **chondrichthyans** and bony fishes consist of four basic chambers—sinus venosus, atrium, ventricle (with thick muscular wall is the actual pumping portion of the heart), and conus arteriosus (can contract and act as an auxiliary pump) (or bulbus arteriosus in teleost). One-way valves are stationed between compartments. Designation of fish hearts as “two-chambered” (not a definitive term) recognizes only atria and ventricles as chambers. The S-shaped arrangement of chambers in the fish heart places the thin walled sinus venosus and atrium dorsal to the ventricle, so that atrial contraction assists ventricular filling.

In **teleosts**, the conus arteriosus may regress, leaving only remnants of a myocardial conus, or be replaced entirely by an elastic, noncontractile **bulbus arteriosus** (as in *Necturus* and some other perennibranchiate amphibians). A single pair of **bulbar valves** at the juncture of the bulbus arteriosus and the ventricle prevents retrograde flow. When receiving blood following ventricular contraction, the bulbus arteriosus stretches and then gently undergoes elastic recoil to maintain blood flow into the ventral aorta. The result is a **depulsation,** or dampening of the large oscillations in blood flow and pressure introduced by ventricular contractions. This has been proposed as a means of protecting the delicate gill capillaries up next in the circulation from exposure to sudden spurts of blood at high pressure that would otherwise occur.



(a) Shark heart

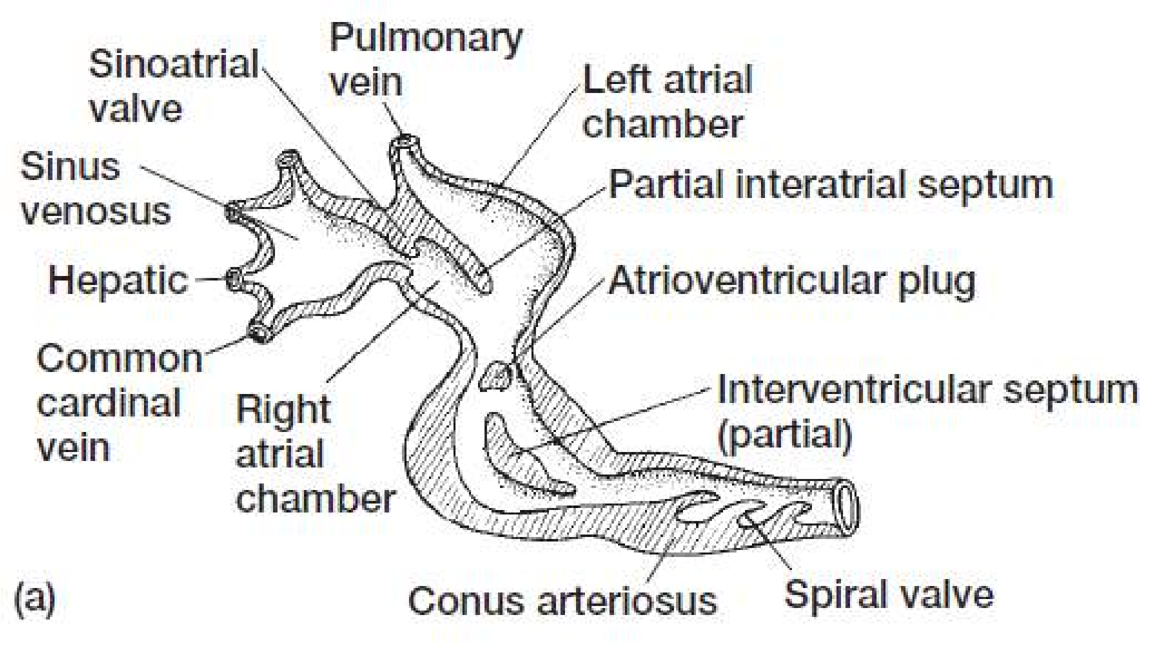


(b) Teleost heart

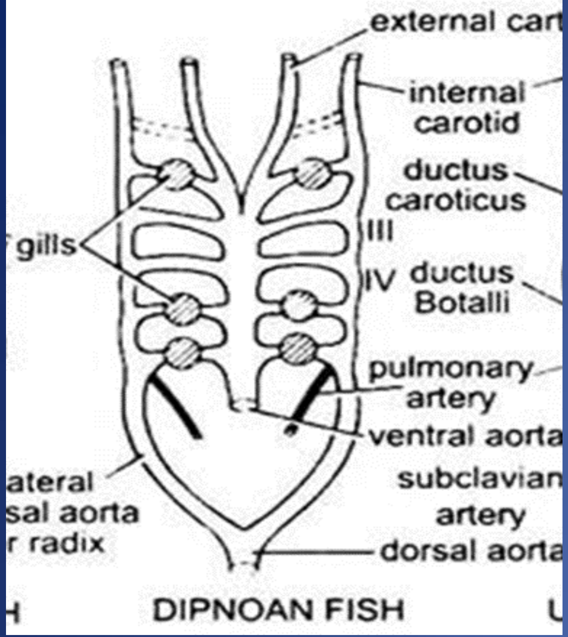
Dipnoans (Lungfishes): The single atrium is **partially divided** internally by an **incomplete interatrial septum** (IA septum, pulmonalis fold; Kotpal, with foramen ovale) that defines a larger **right** (receiving deoxygenated blood from **sinus venosus**) and smaller **left** (receiving **pulmonary vein**) **atrial chamber**. **Pulmonary veins** empty directly **into the left atrial** chamber (*Lepidosiren,* and *Protopterus* and tetrapods) or into the sinus venosus (only *Neoceratodus*). In place of AV valves is the **atrioventricular plug,** a raised cushion in the wall of the ventricle, to prevent retrograde flow. The ventricle is also divided **partially**, by an **interventricular septum** (also in *Siren*, a urodele)**.** Alignment of the IV septum, AV plug, and IA septum establishes a left channel (that tends to receive oxygenated blood returning from the lungs), and a right channel (that tends to carry deoxygenated systemic blood from the sinus venosus). The **spiral valve** (also in anurans) **internally divide the conus into two spiraling channels.** Thus, **despite the anatomically incomplete internal septation, the deoxygenated blood entering from the sinus venosus does not tend to mix with the oxygenated blood returning from the lungs**.

The left channel supplies the oxygenated blood, through aortic arches III and IV (which lack gills) to systemic tissues directly. The right channel supplies the deoxygenated blood through the V and VI arches to the gills and/or lungs. During aquatic respiration, gills oxygenate the blood and pass it on directly to the body, and only slightly to the lungs. When DO declines and lungfish rely on air, most of the deoxygenated blood is passed on to the lungs for oxygenation.

Air-breathing teleosts differ in that oxygenated blood returns to the systemic veins, resulting in mixing prior to arrival at the heart. In these taxa the aerial respiration is an accessory (secondary to the gill respiration) mechanism. But the **extant dipnoans and tetrapods are obligate air breathers**.



Heart of the African lungfish *Protopterus.* (a) Internal structure of the heart.



[In Dipnoi, III and IV aortic arches lack gills, and pulmonary artery arises from the efferent side of the VI arch. The oxygenated blood returning from the lung, via left side of the heart, is shunted through aortic arches III and IV, which lack gills, and flows to systemic tissues directly. Venous blood returning via sinus venosus and right side of the heart is shunted through the posterior arches, V and VI, and then diverted to the gills and/or lungs. During aquatic respiration, gills oxygenate the blood (and pass it on directly (i.e. without returning it back to heart again) to the body), and only few blood is passed on to the lungs. When DO declines and lungfish rely on air, most of the deoxygenated blood is passed on to the lungs for oxygenation, then it return to left auricle, and then supplied to the body via III and IV arches.

The **spiral valve** (also in anurans) **within the conus arteriosus** aids in separating oxygenated and deoxygenated blood. Apparently derived from conal valves, the spiral valve consists of two (a pair; in anurans a single flap) endocardial, longitudinal, typhlosolelike folds whose opposing free edges touch but do not fuse. The conus makes a couple of sharp bends and rotates about 270°, thus turning these folds into a spiral within its lumen. Although unfused, these twisting **folds internally divide the conus into two spiraling channels**. Because the conus is attached directly to the ventricle, oxygenated blood entering the left channel and deoxygenate blood entering the right channel tend to flow through different spiraling channels within the conus and remain separate.

The cardiac oxygenated and deoxygenated streams of blood enter different sets of aortic arches. The **oxygenated blood returning from the lung, via left side of the heart, is shunted through aortic arches III and IV, which lack gills**, and flows to systemic tissues directly. **Venous blood returning via sinus venosus and right side of the heart is shunted through the posterior arches, V and VI, and then diverted to the lung**. Oxygenated blood traveling through the left side of the heart is channeled along the opposite spiral of the conus to enter the anterior set (III and IV) of aortic arches.

When oxygen levels in the water decline, leaving little to diffuse across gills into the blood, the lungfish comes to the surface to gulp fresh air into its lungs. Under these deteriorating conditions, in *Protopterus,* deoxygenated
blood returning from systemic tissues tends to be diverted to the lungs (not to the gills), and about 95% of the oxygenated blood from the lungs tends to be directed via anterior aortic arches to the systemic tissues (not through the gills). The fraction of blood that passes from the lungs to the anterior arches steadily declines to about 65% just before the next breath, following which the fraction returns again to 95%.**]**

Amphibians (*3-chambered transitional hearts*)

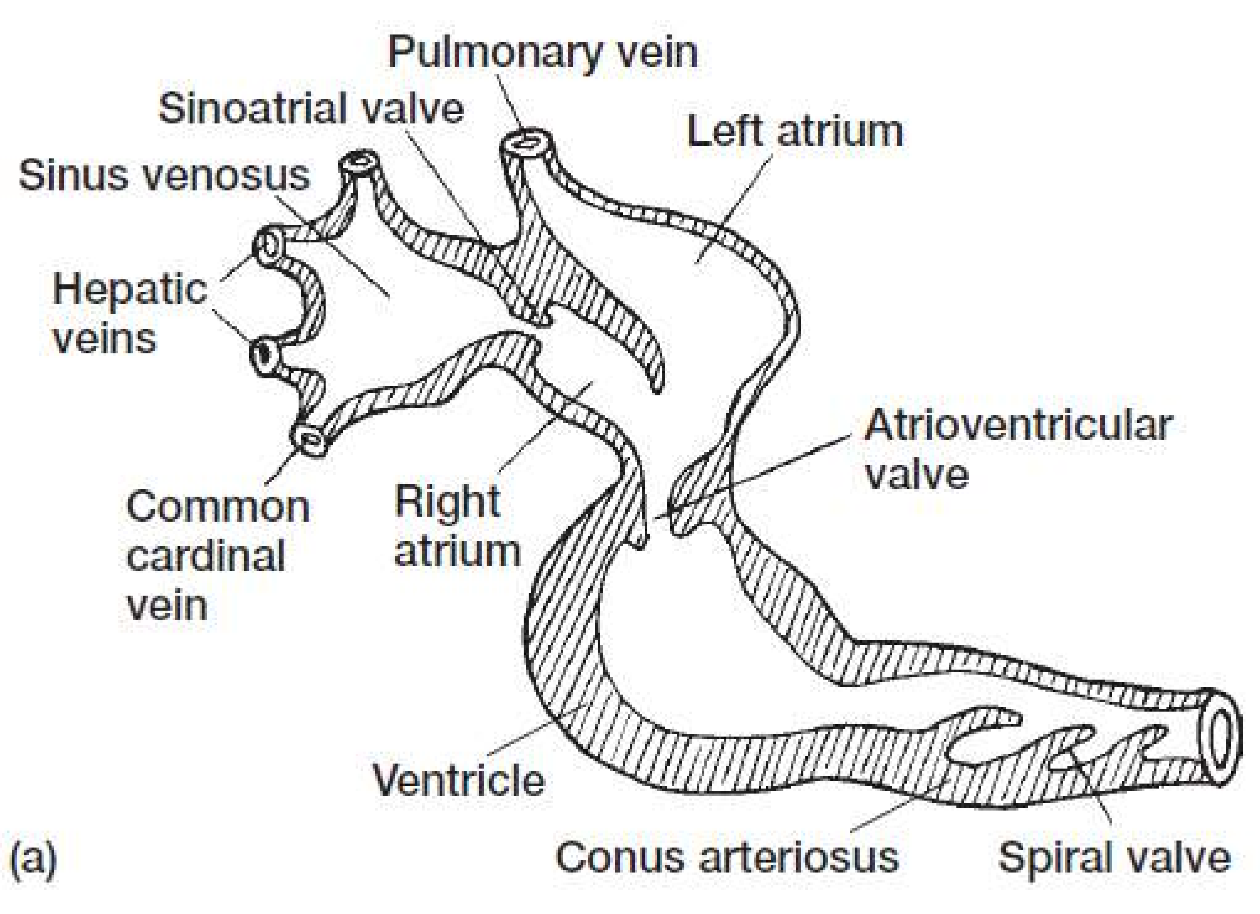
Amphibians rely on cutaneous gas exchange (**plethodontid salamanders lack lungs entirely**), on gills (many larval forms), on lungs (most toads and frogs), or on all three modes (most amphibians). Because the sources of oxygenated and deoxygenated blood vary, heart structure varies as well.

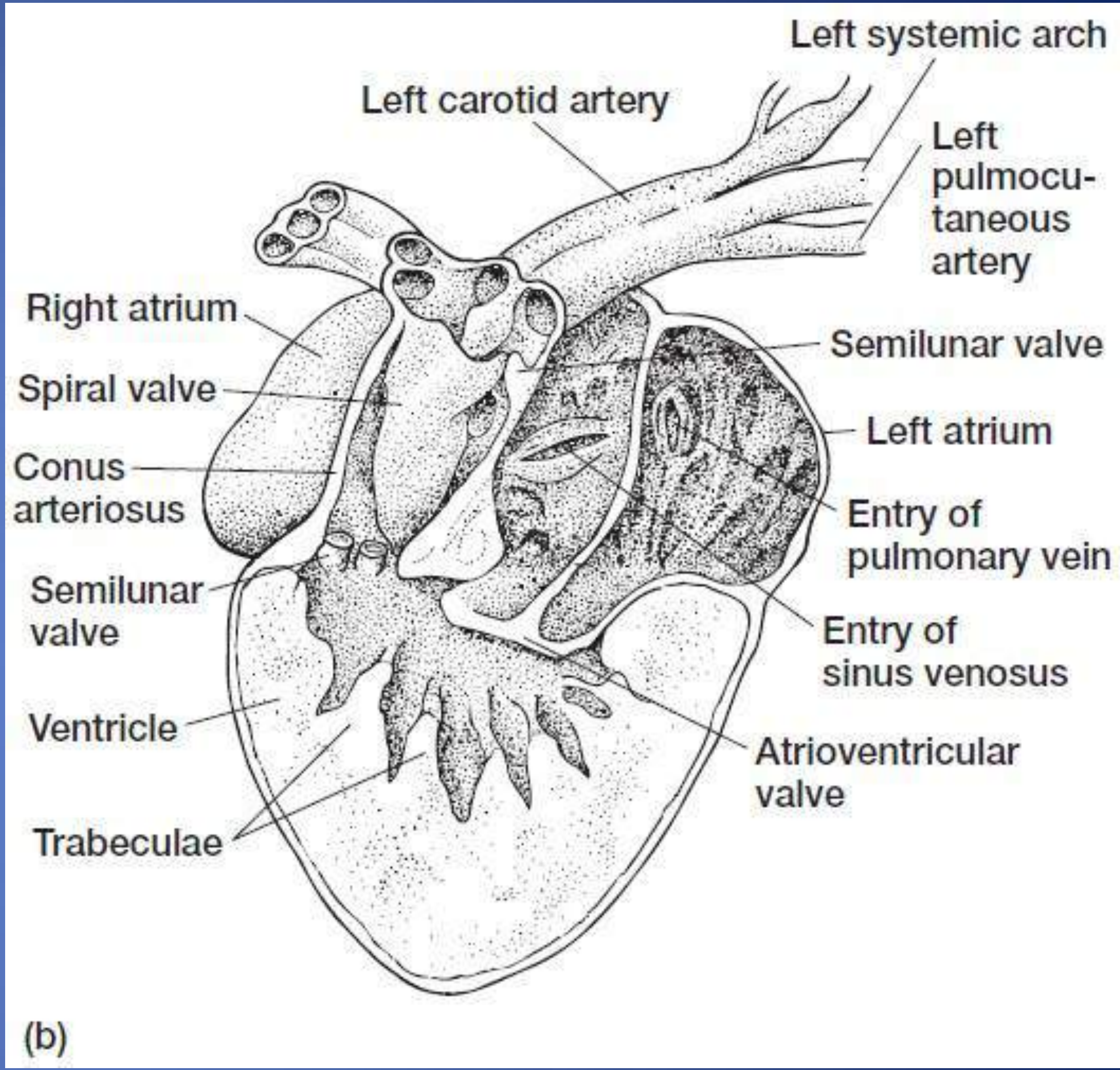
Urodela: In lungless salamanders or those with reduced lung function, the interatrial septum and spiral valve may be much reduced or absent entirely (so atrium remains totally undivided). **In the lungless plethodontids, left atrium is absent**. **Where gills predominate over lungs as respiratory organs (e.g., Necturus), the interatrial septum is reduced** or **perforated**. *Siren* (a salamander) have a partial interventricular septum.

Anura: Generally, in amphibians with functional lungs, the heart includes a **sinus venosus**, right and left atria divided by an anatomically **complete interatrial septum**, a **trabeculate ventricle** lacking any internal subdivision ((but trabeculae are thought to separate streams of blood that differ in oxygen tension)), and a **conus arteriosus** with a spiral valve (establishing separate channels for systemic and pulmocutaneous arches). Except for *Siren* (a salamander), which have a partial interventricular septum, amphibians are unique among air breathing vertebrates in lacking any internal division within the ventricle.

The two different streams of blood returning from the **systemic (deoxygenated) and pulmonary (oxygenated) circuits are kept mostly separate** as they pass through the heart.

When a **frog dives**, a sphincter at the base of the pulmonary artery constricts, resulting in reduced blood flow to the lung and increased flow to the skin. Thus, while a frog is submerged, loss of pulmonary respiration is somewhat offset by increased cutaneous respiration.





Amphibian hearts. (a) Diagram of typical amphibian heart. The atrium is divided into left and right chambers but the ventricle lacks an internal septum. Conus with spiral valves. (b) Bullfrog (*Rana catesbeiana*) heart. Although lacking internal septa, the wall of the ventricle folds into numerous **trabeculae** that aid in separating bloodstreams.

Amniota:

In amniotes, the right and left atria are completely separated by a **complete interatrial septum** (also in anurans) . However they are confluent during **embryonic** development via an **interatrial foramen, or foramen ovale**, which **closes near the time of hatching or at birth**. In adult mammals, the site of the obliterated foramen is marked by a depression, the **fossa ovalis**, in the medial wall of the right atrium.

Embryonic **conus arteriosus** (or bulbus cordis) **becomes divided in the adult to form the bases (trunks) of three** (or two) **aorta -** the **pulmonary trunk** and the **right** and **left systemic trunks.**

Reptiles

Two basic reptilian heart patterns are recognized.

1.3-chambered transitional hearts:

chelonians (turtles) and squamates (lizards and snakes),

2.4-chambered hearts: crocodilians.

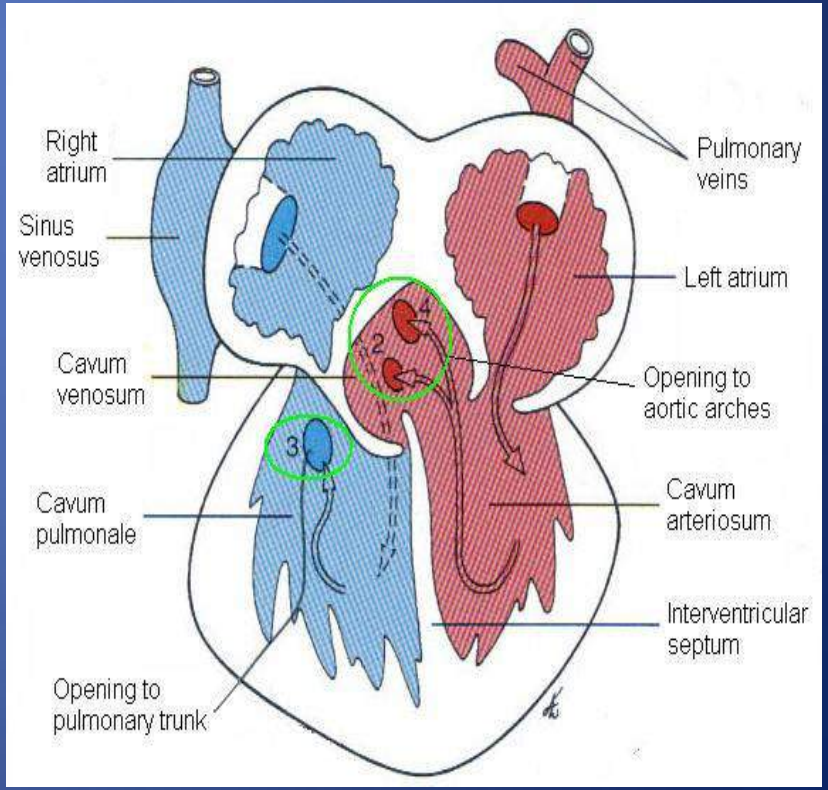


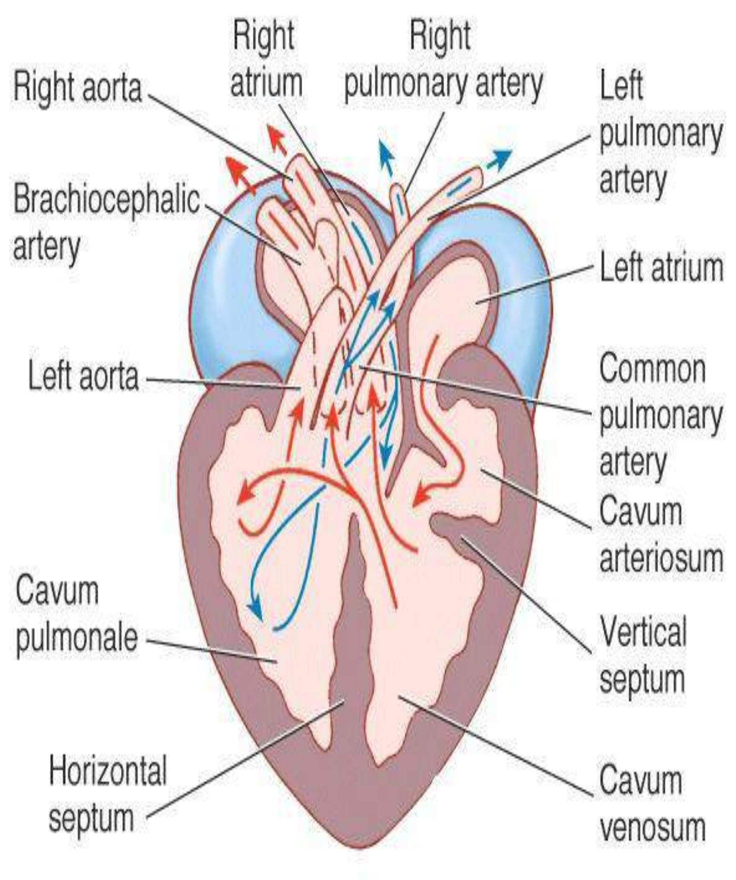
Figure. **Chelonian heart** chambers and circulation path

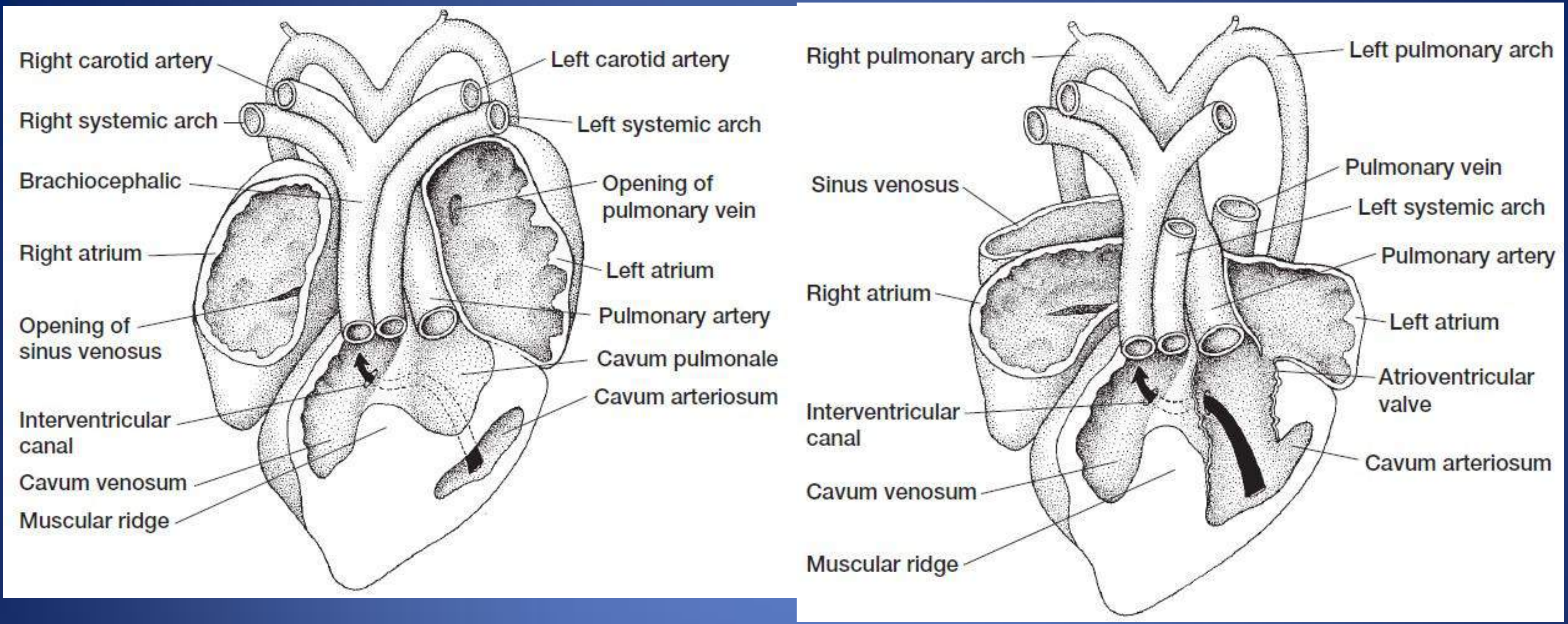
Chelonian/Squamate Hearts

-**sinus venosus reduced**.
-atrium completely divided into right and left atria by a complete interatricular septum.
-The embryonic **conus arteriosus** (or bulbus cordis) **becomes divided in the adult to form the bases (trunks) of three aorta**: the **pulmonary trunk** (from right side of ventricle) and the **right** and **left systemic trunks.** In **snakes, a valved interaortic foramen connects the bases of adjacent aortae**. But the shunting of blood made possible by this foramen has not been explored.
-**ventricle** single (IV septum incomplete) but has internally three interconnected compartments: the **cavum venosum** and the **cavum pulmonale** separated by a **muscular ridge,** and the **cavum arteriosum** connected to the cavum venosum via an **interventricular canal.**

-Normally the **cavum arteriosum receives oxygenated blood from the left atrium** and passes it on (through the interventricular canal) to the aortic arches (then to the body). Much of the **blood filling the cavum venosum is deoxygenated blood from the right atrium**. **Blood from the cavum venosum** moving across the muscular ridge **fills the cavum pulmonale** (to be passed on to lungs).

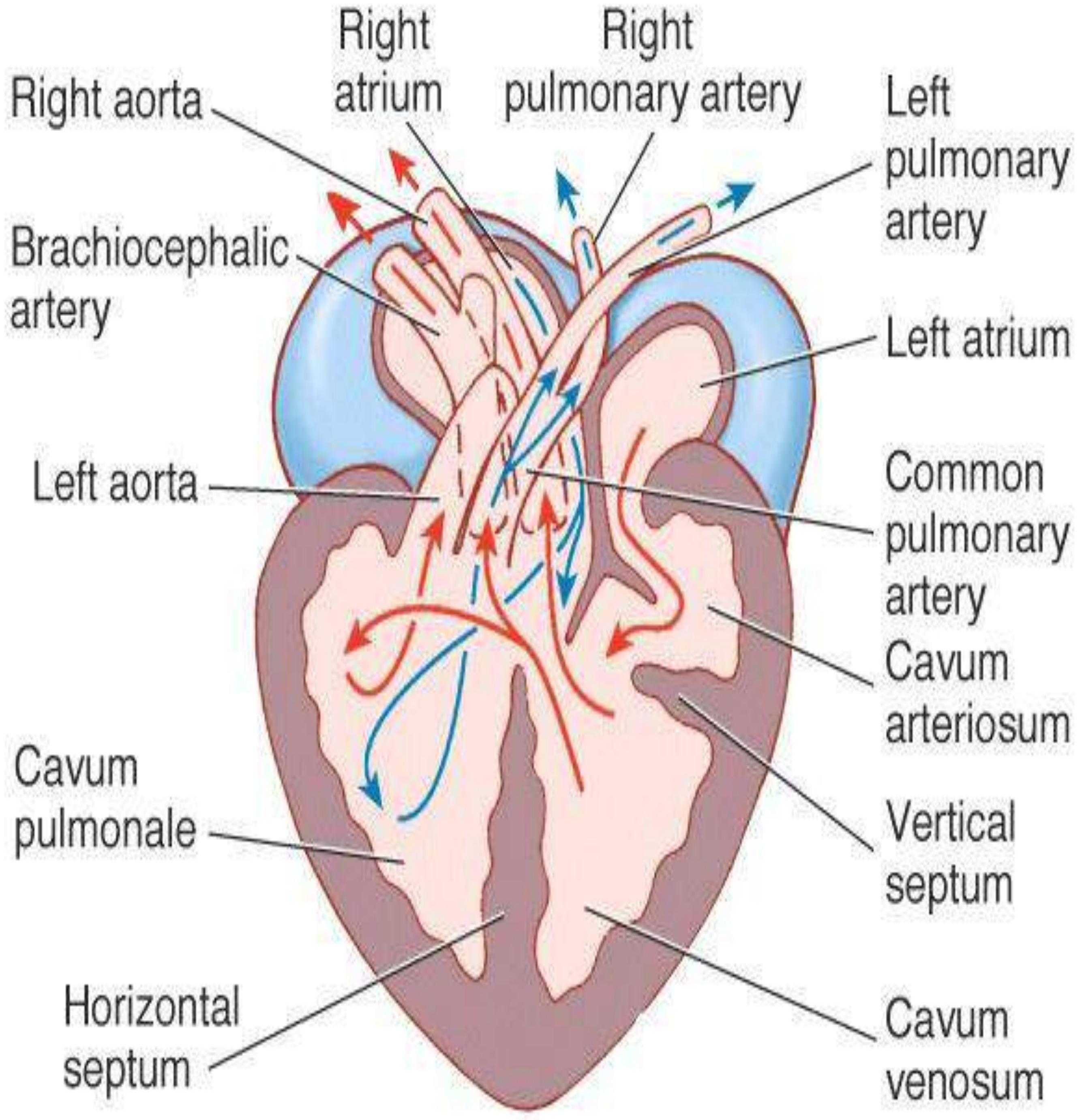
When the turtle dives beneath the water (lung is of little use), heart responds with a **right-to-left** or **cardiac shunt.** Here, **returning blood to the right side of the heart** (destined to go to lungs) **goes directly** (through the interventricular canal) **to the left side and departs for systemic tissues, thereby bypassing the lungs**.





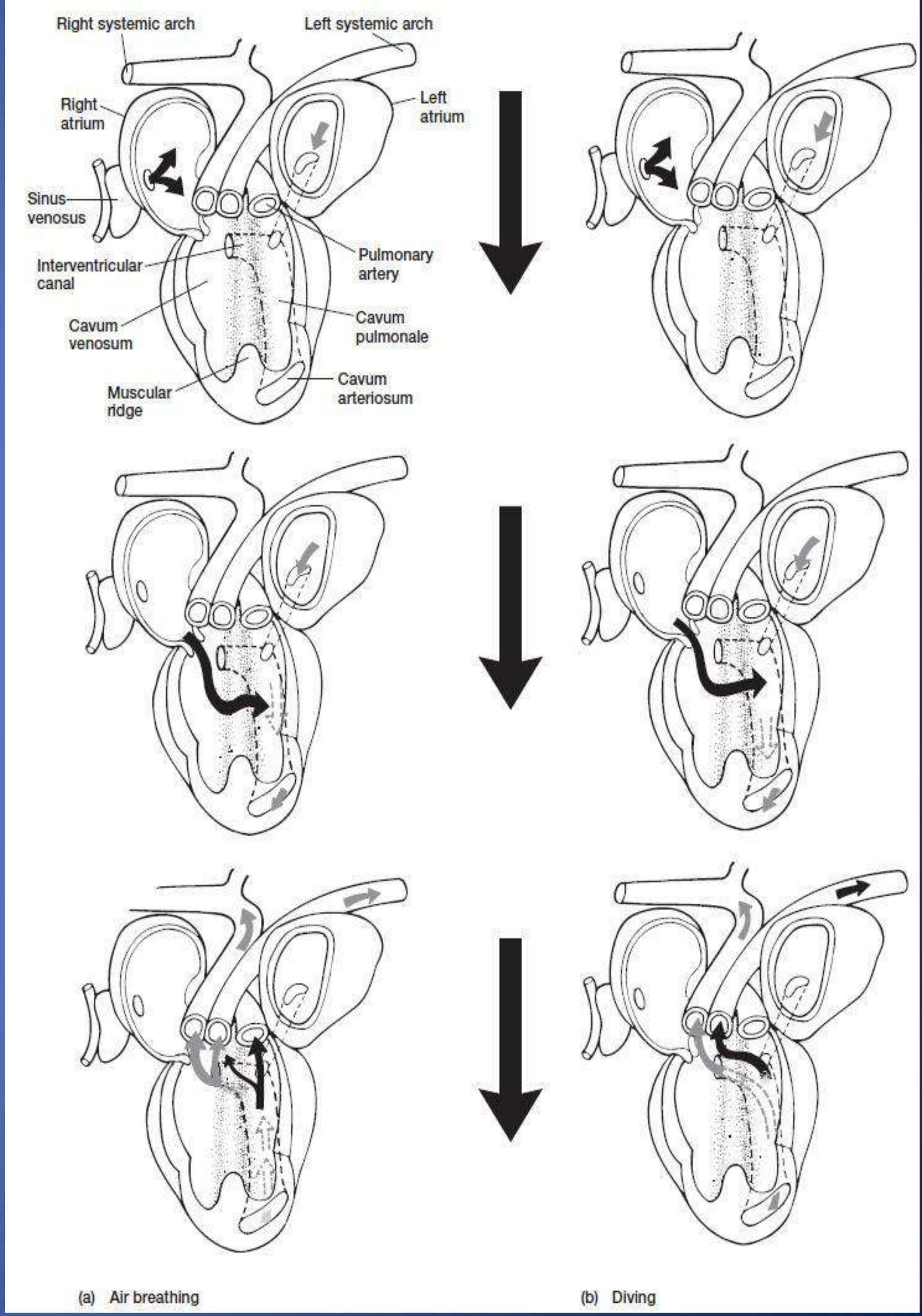
Lizard heart, ventral view. (a) Part of the ventral wall of the heart has been removed, as has the apex of the ventricle, to show its three interconnected compartments—cavum venosum separated by a muscular ridge from the cavum pulmonale, and deeper cavum arteriosum. The solid arrow indicates the route of blood flow from the cavum arteriosum via the interventricular canal into the cavum venosum entering at the bases of the aortic arches. **(b)** The wall of the **cavum pulmonale has been cut away to better reveal the deeper cavum arteriosum**. Trimming of the atria and left aortic arch permits better viewing of the sinus venosus and pulmonary artery.

The muscular ridge divides the cavum pulmonale and the cavum venosum. The vertical ridge divides the cavum venosum and cavum arteriosum. The cavum pulmonale receives blood from the right atrium through the cavum venosum and directs flow into the pulmonary circulation. The cavum arteriosum receives blood from the pulmonary veins and then directs oxygenated blood to the cavum venosum. The paired aortic arches arise from the cavum venosum



[**FIGURE. Blood flow through the squamate (and turtle) heart.** (a) When squamates breathe air on land, venous blood from the right atrium enters the cavum venosum of the ventricle and crosses a muscular ridge to fill the cavum pulmonale momentarily. Upon ventricular contraction, most of this blood exits via the pulmonary artery. Simultaneously, blood from the left atrium enters the deep cavum arteriosum. Contraction of the ventricle squirts this blood through the interventricular canal, and then the blood departs via the left and right systemic arches. (b) When squamates dive, resistance to pulmonary blood flow encourages blood that would normally exit to the lungs to move instead across the muscular ridge and depart primarily via the left aortic arch.

The pattern of blood flow through the hearts of Chelonia and squamates differs depending on whether they breathe air or hold their breath.
Specifically, **the deoxygenated blood in the right atrium flows into the cavum venosum and then across the muscular ridge to the cavum pulmonale**. Additionally, when opened, the right AV valves lie across the opening to the interventricular canal and temporarily close it. **Oxygenated blood, entering from left atrium into the cavum arteriosum**, temporarily remains there while the AV valves occlude the interventricular canal. When the ventricle contracts, the muscular ridge is compressed against the opposite wall to separate the cavum venosum from the cavum pulmonale, and the AV valves close (to prevent retrograde backflow into the atria). But in so doing, the right AV valve opens the interventricular canal and allows blood to flow through it. Thus, blood leaves the ventricle via the most accessible routes: **Deoxygenated blood in the cavum pulmonale exits primarily through the pulmonary artery to the lung, although some also squirts** across the muscular ridge **to enter the left aortic arch**; **oxygenated blood in the cavum arteriosum moves** through the interventricular canal **to reach the bases of the aortic trunks**, through which it then exits.
When the turtle dives beneath the water, heart responds with a **right-to-left** or **cardiac shunt.** Here, **returning blood to the right side of the heart instead goes directly to the left side and departs for systemic tissues, thereby bypassing the lungs**. The air held in its lungs is soon depleted of oxygen. The energy used to pump blood to the lungs would return no physiological benefit.]

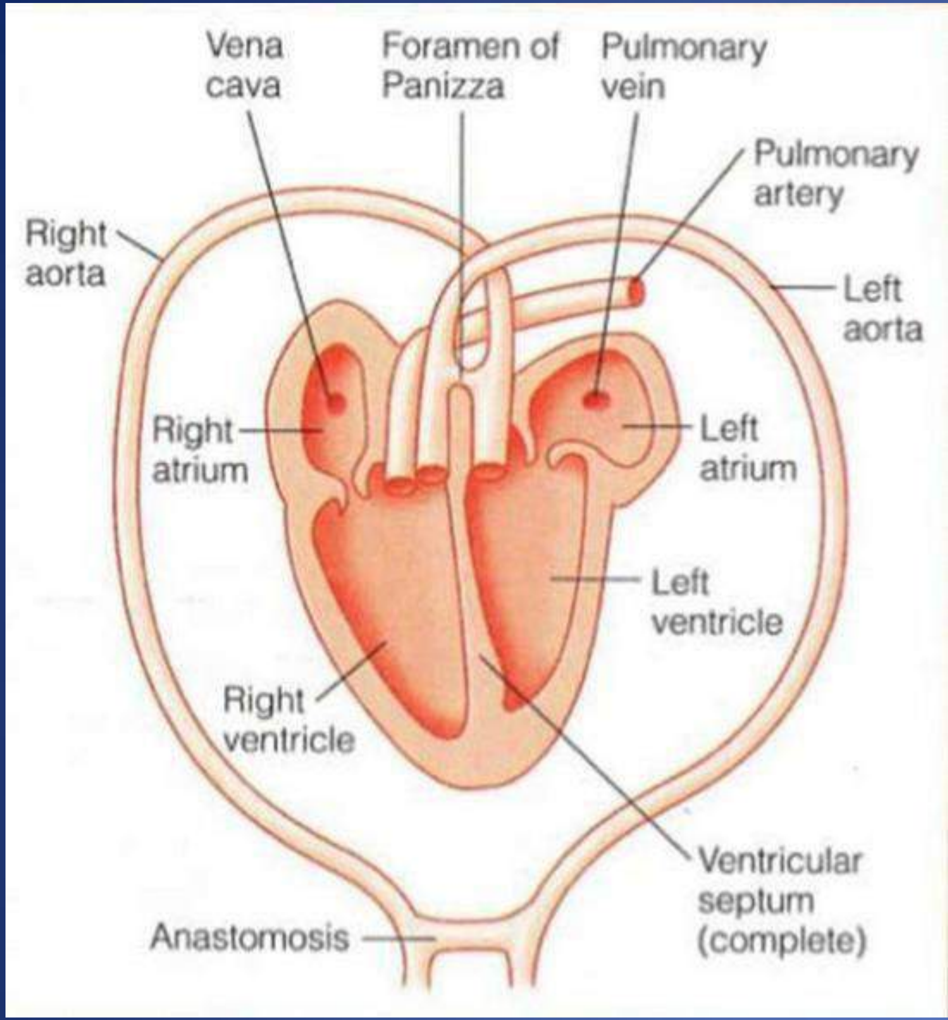


Crocodilian Hearts (*4-chambered*)
The pulmonary vein enters the left atrium in adults. In embryo, the pulmonary veins, one from each lung, unite as a single stem, the pulmonary vein, that enters the sinus venosus. As embryonic development proceeds, this part of the sinus venosus together with the associated pulmonary vein become incorporated into the developing left atrium.

The ventricle is divided by an anatomically **complete interventricular septum** into distinct left and right chambers. The **pulmonary trunk and *left* aortic arch open off the thick-walled *right* ventricle**. The ***right* aortic arch opens off the *left* ventricle**. A narrow channel called the **foramen of Panizza** connects the left and right aortic arches shortly after they depart from the ventricle.

At the moment of **systole, pressure is greatest in the left ventricle**. The oxygenated blood it holds enters the right aorta, and also into the left aorta via the foramen of Panizza. **High pressure in the left aorta keeps the lunar valves at its base closed, leaving only the pulmonary route of exit for blood in the right ventricle**. As a **result, both aortic arches carry oxygenated blood** to systemic tissues, and the pulmonary artery carries deoxygenated blood to the lungs.

When a crocodile dives, this pattern of cardiac blood flow changes because of a cardiac shunt. **Resistance to pulmonary flow increases** due to vasoconstriction of the vascular supply to the lungs and partial constriction of a sphincter at the base of the pulmonary artery. **Blood in the right ventricle now tends to exit through the left aortic arch** rather than through the pulmonary circuit, which presents high resistance to blood flow. **Diversion of blood in the right ventricle to the systemic circulation represents a right-to-left cardiac shunt.** Blood in the right ventricle, which would flow to the lungs in an air breathing crocodile, instead travels through the left aortic arch, joining the systemic circulation and **bypassing the lungs**. This lung bypass confers the same physiological advantages we have seen in turtles, namely, an increase in efficiency of blood flow while fresh air is unavailable.



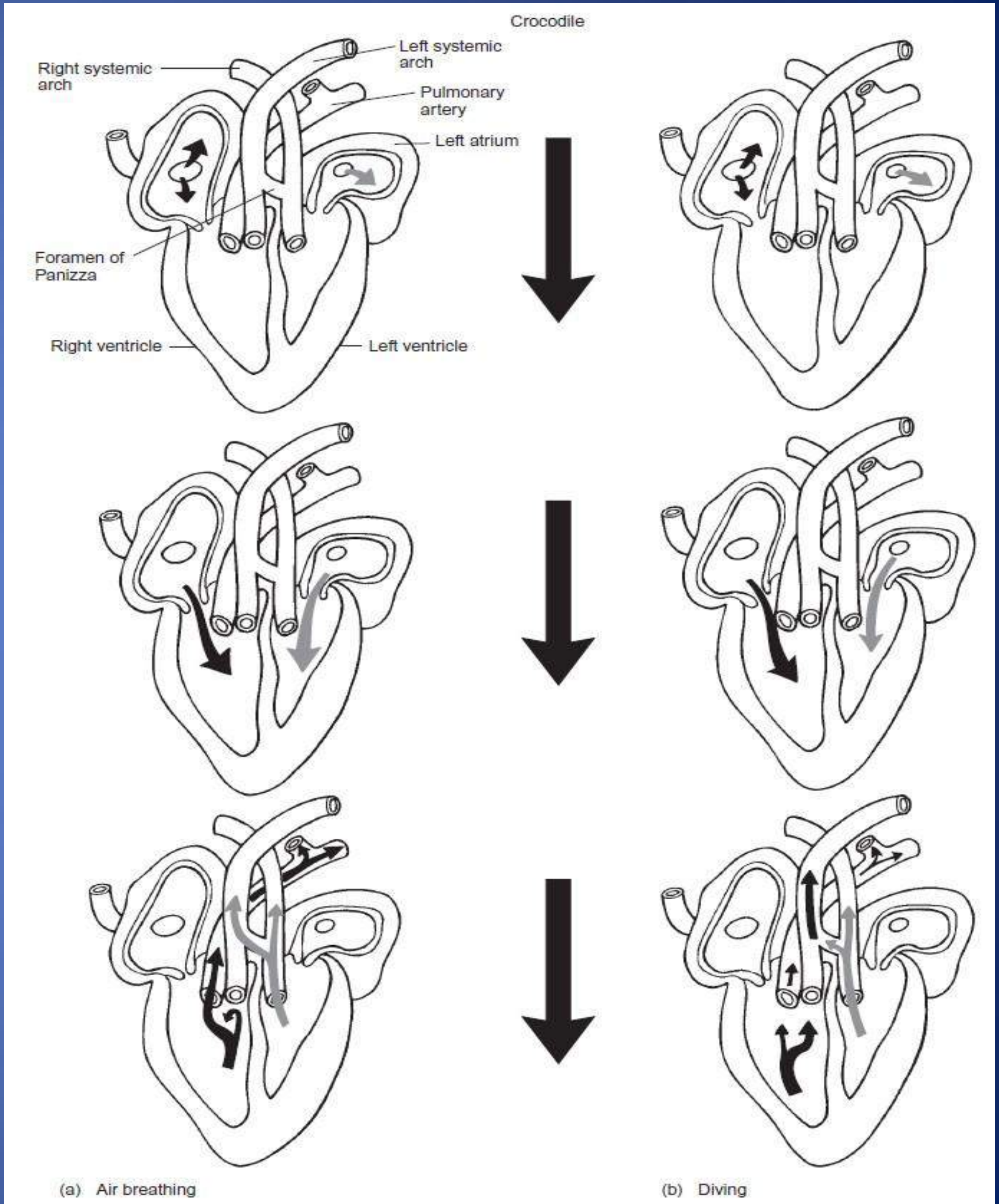


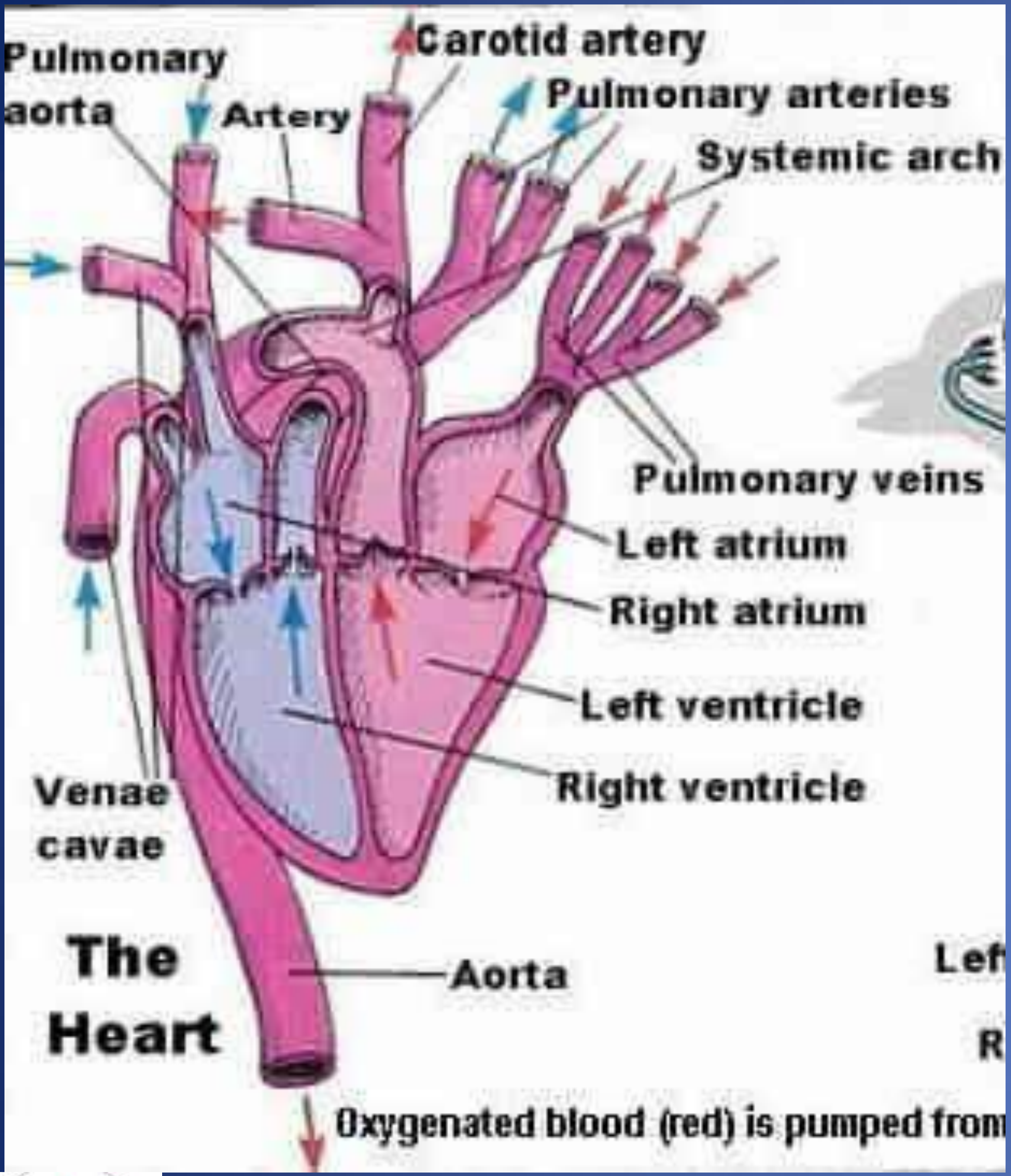
FIGURE. Blood flow through the crocodile heart. (a) Systemic and pulmonary blood flow when the crocodile breathes air. (b) Internal changes that result in decreased pulmonary flow when the crocodile dives.

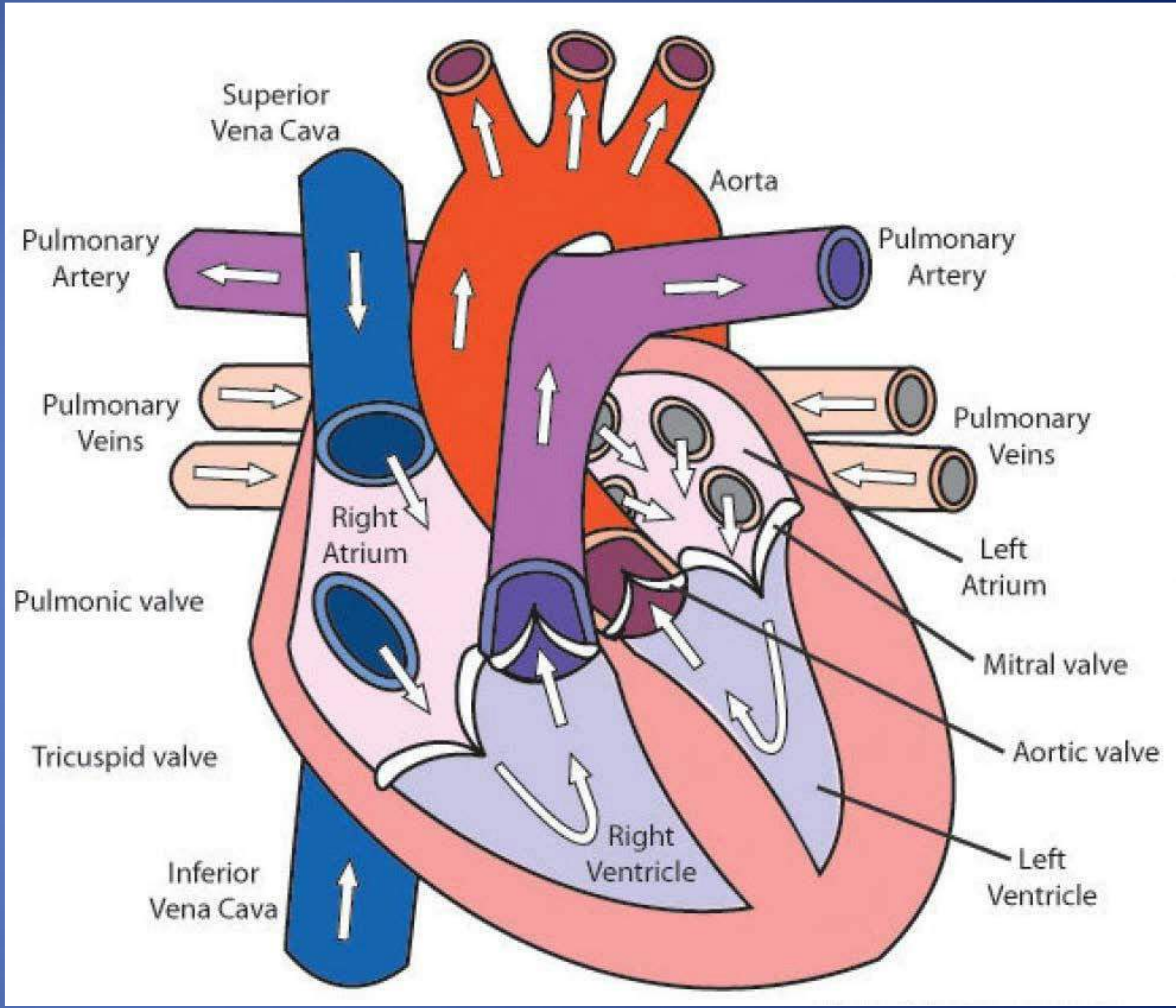
Birds and Mammals (*4-chambered, double circuit pulmonary hearts*)

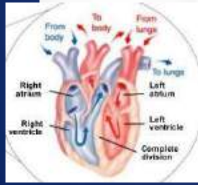
The hearts of birds and mammals have four chambers. In birds, the sinus venosus is reduced to a small but still anatomically discrete area. **In mammals, the sinus venosus is reduced to a patch of Purkinje fibers, or sinoatrial node (pacemaker), in the wall of the right atrium**. The embryonic **conus arteriosus (bulbus cordis) gives rise to the pulmonary trunk and a single aortic trunk (left in mammals while right in birds; in both cases it arises from left ventricle) in the adult**.

Although structurally similar, bird and mammal hearts arose independently from different groups of tetrapod ancestors. This **difference** is reflected in their embryonic development. Appearance of the interventricular and interatrial septa occurs quite differently in the two groups. **In mammals only, each atrium has an earlike flap, or auricle (with no known function),** within which is a blind chamber (Kent). In mammals, the muscular walls lining the **ventricular** chambers exhibit sturdy interanastomosing muscular ridges and columns, the **trabeculae carneae**. They strengthen the walls and increase the force exerted by them.

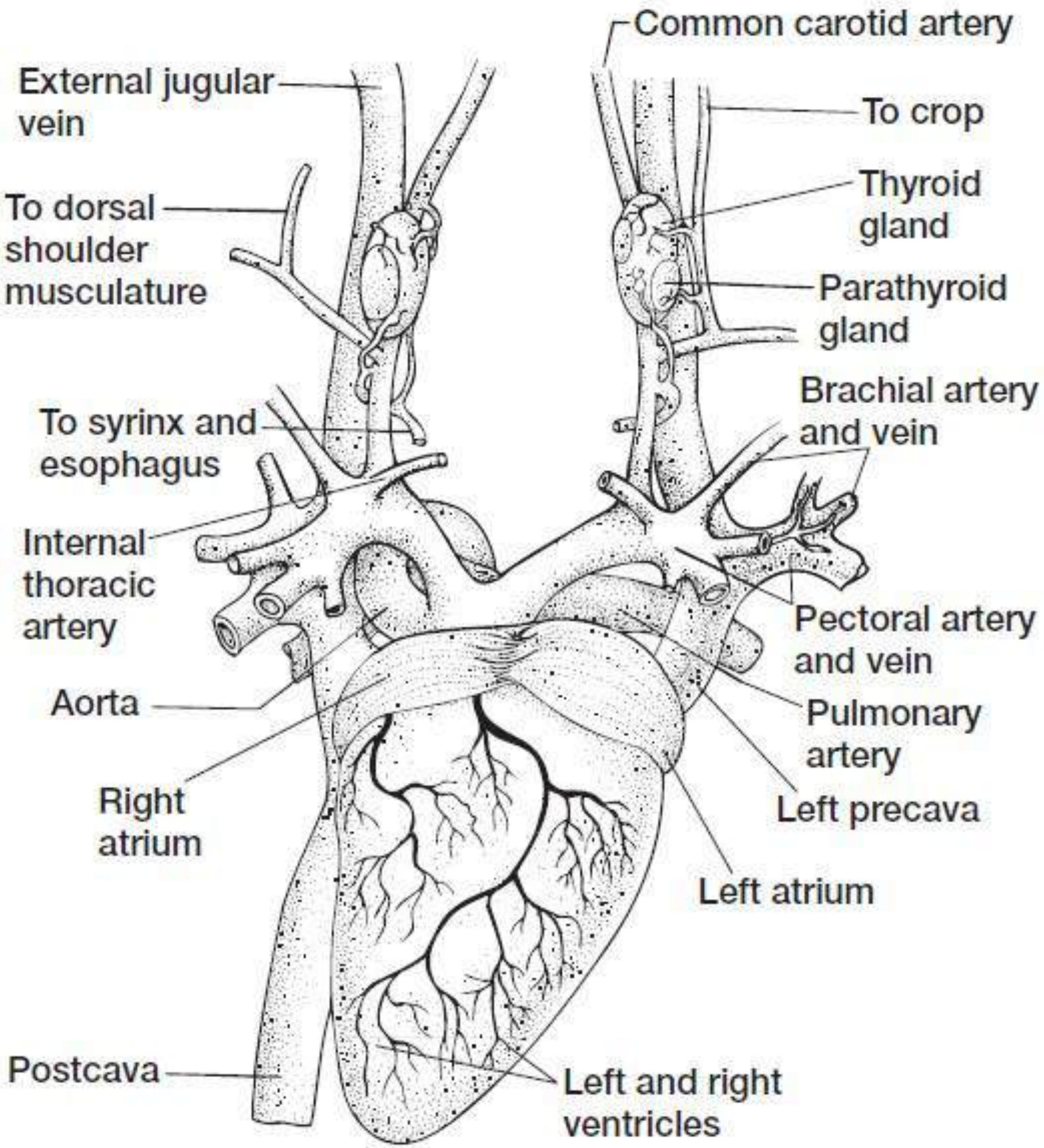
Due to anatomically divided left and right compartments, unlike in amphibians and reptiles, a cardiac shunt cannot be used to decouple perfusion of the lung and systemic tissues. Although the reasons are not well understood, some propose that endothermic animals (birds and mammals) may require complete anatomical separation of the cardiac chambers to prevent blood being sent to the lungs at the same high pressure as blood sent to systemic tissues.



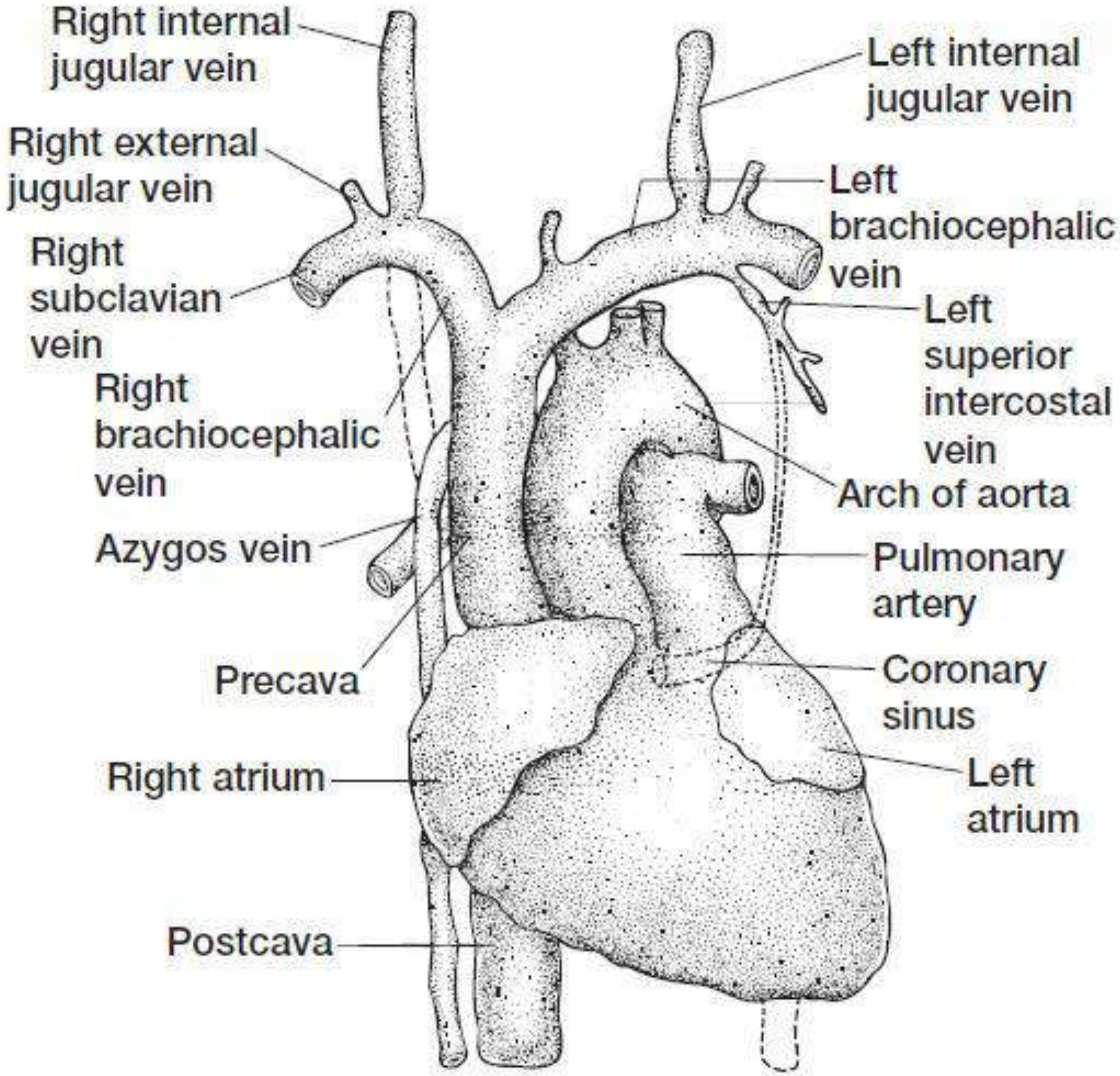




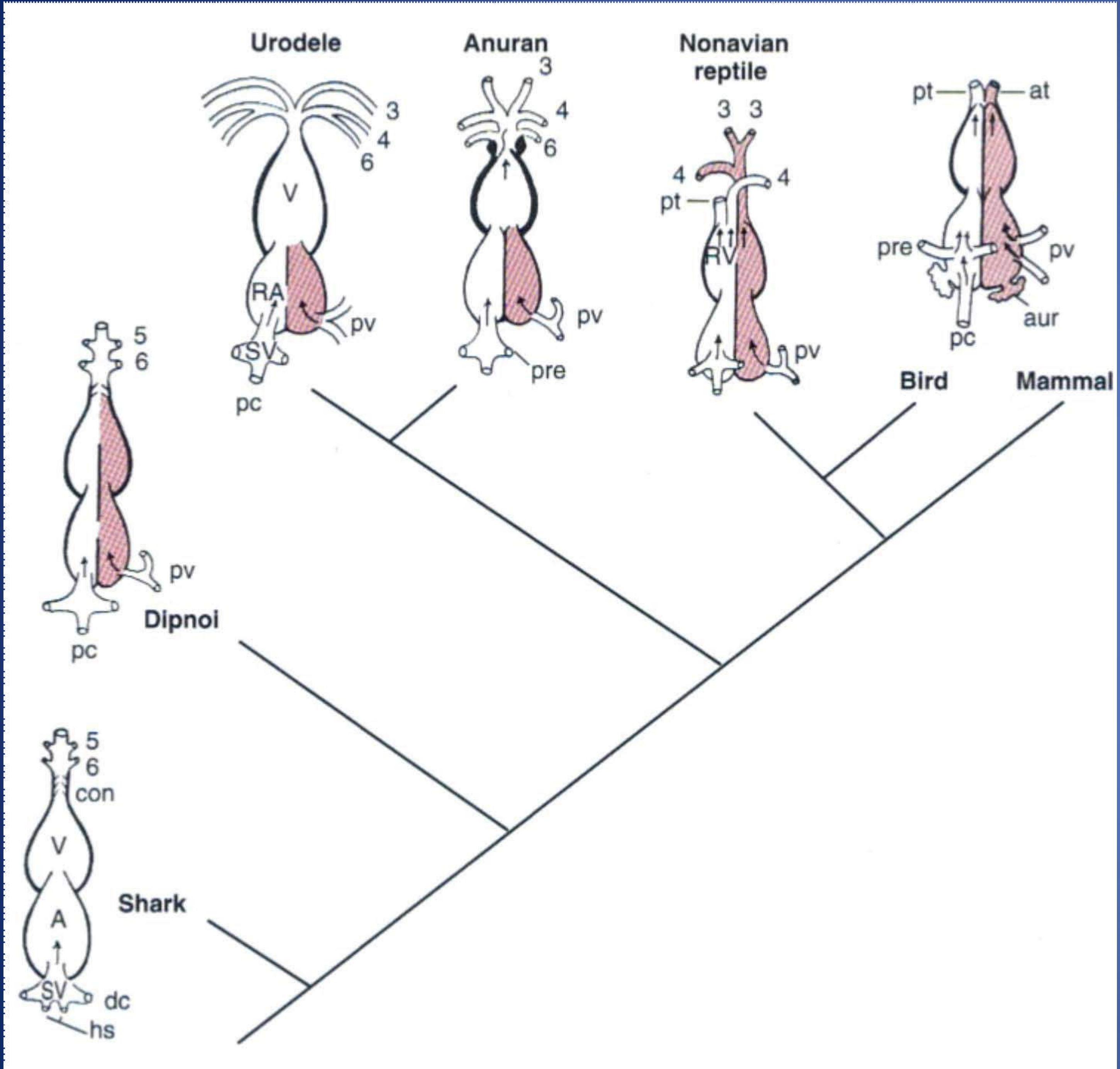
Heart of bird (left) and mammal (right). The **pulmonary trunk arise from right ventricle**. The single **aortic trunk (left in mammals while right in birds) arises from left ventricle**.



Avian heart
(ventral view)



Mammalian heart
(ventral view)



Heart chambers and oxygenated blood flow in some generalized vertebrates. 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; at, aortic trunk; dc, common cardinal vein; hs, hepatic sinus; pc, postcava; pre, precava (common cardinal vein); pt, pulmonary trunk; pv, pulmonary veins (Kent)