

Is our heart a well-designed pump? The heart along animal evolution

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Received 4 February 2014; revised 14 April 2014; accepted 7 May 2014; online publish-ahead-of-print 10 June 2014

A carrier system for gases and nutrients became mandatory when primitive animals grew larger and developed different organs. The first circulatory systems are peristaltic tubes pushing slowly the haemolymph into an open vascular tree without capillaries (worms). Arthropods developed contractile bulges on the abdominal aorta assisted by accessory hearts for wings or legs and by abdominal respiratory motions. Two-chamber heart (atrium and ventricle) appeared among mollusks. Vertebrates have a multi-chamber heart and a closed circulation with capillaries. Their heart has two chambers in fishes, three chambers (two atria and one ventricle) in amphibians and reptiles, and four chambers in birds and mammals. The ventricle of reptiles is partially divided in two cavities by an interventricular septum, leaving only a communication of variable size leading to a variable shunt. Blood pressure increases progressively from 15 mmHg (worms) to 170/70 mmHg (birds) according to the increase in metabolic rate. When systemic pressure exceeds 50 mmHg, a lower pressure system appears for the circulation through gills or lungs in order to improve gas exchange. A four-chamber heart allows a complete separation of systemic and pulmonary circuits. This review describes the circulatory pumping systems used in the different classes of animals, their advantages and failures, and the way they have been modified with evolution.

Keywords

Animal evolution • Heart anatomy • Haemodynamics

Translational perspective

To assess if our heart is a good pump, we should study the heart along the animal evolution. From the worms, through the arthropods, the mollusks, and the reptiles to the vertebrates and the birds, the heart has followed a logical evolution which brought it to our own complex physiology. This evolution allowed the passage from submarine to terrestrial life and offered different cardiovascular solutions to complex adaptive problems.

Facing ventricular failure, we might wonder if our heart is really a good pump! A possible answer to this question can be found by looking back at animal evolution. Nature has experimented many different circulatory systems. By comparing human heart with these various achievements, we might evaluate the pump inherited from our animal ancestors.

The tree of evolution

The animal evolution is classically represented as a tree rooted on the first eukaryotic cells appeared 1.5 billion years ago (Figure 1).^{1,2} After ~700 million years, emerged organized animals with a radial symmetry (sponges, jellyfish), followed by creatures with a bilateral symmetry and a dorsoventral axis. These Bilateria gave two divergent branches: Protostoma (invertebrates) and Deuterostoma (vertebrates).³ The first tubular heart appeared probably in Bilateria.⁴

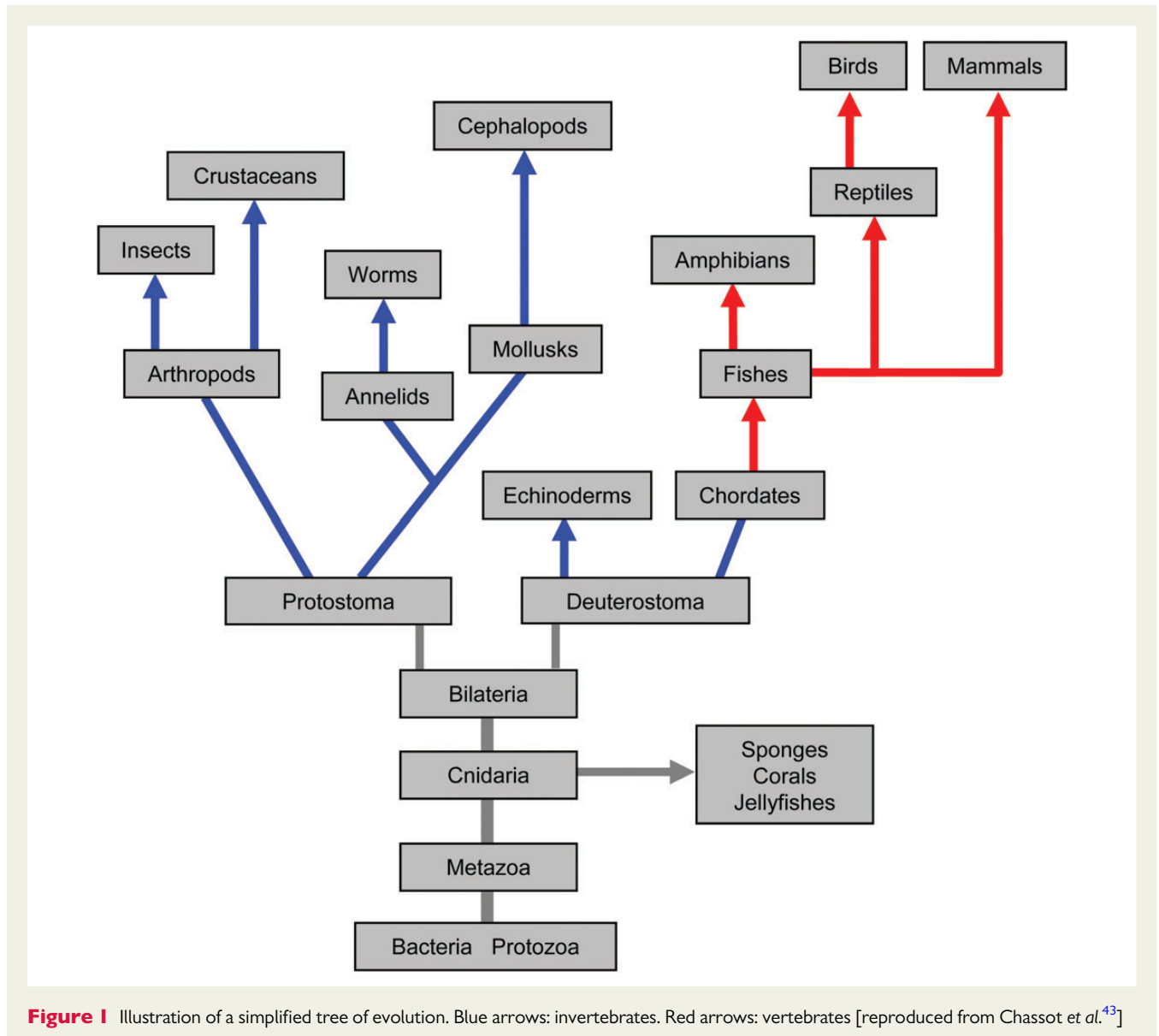
The embryogenesis shows that animals share a common step consisting in a primary cardiac tube derived from mesodermal precursors converging at the midline,⁵ with peristaltic movements pushing fluid into pericellular spaces without vessels.³

As long as living beings were only small clusters of cells, simple diffusion was adequate. But as soon as the organisms grew in size, a carrying system became mandatory to transport O₂ and nutrients, and to remove waste products. There are two possible configurations.

- Open system (high output but low pressure, like a fan in a room), well performing over short distances, used in the peripheral circulation of worms or insects. Blood, lymph, and extracellular fluid are mixed together (*haemolymph*), flow from arteries into the interstitial space, and are directed into venous collectors. The volume of circulating fluid is large (20–50% of body weight) and its velocity is low.

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- Closed system moving blood rapidly over long distances inside arteries, capillaries, and veins lined with endothelial cells, used in cephalopods (octopus) and in all vertebrates. Blood volume is lower (6–8% of body weight), but pressure is higher.

The presence of an O₂-carrier pigment increases O₂ delivery 20–40 times. Haeme pigments are found in practically all classes of living beings. They evolved from enzymes such as cytochromes, primarily used to detoxify oxygen when it appeared in atmosphere with photosynthesis.⁶ Haemocyanin is a copper-containing molecule giving a greenish colour to the blood of mollusks, crustaceans, and some arachnids, existing only in solution, and transporting <4–5 vol% of O₂.⁷ Haemoglobin is more efficient. It is present in all vertebrates, but locked inside erythrocytes; this allows an increase in concentration and a decrease in toxicity.

Lower invertebrates

Worms have two peristaltic tubes, one dorsal, where the blood is pumped forwards, and one ventral, where it flows backwards.

Distally, the system is open with no capillaries. These vessels carry haemolymph between the tissues and the skin, where gas exchange takes place. The perfusion is slow (six to eight peristaltic waves per minute) and the pressure is low (10–20 mmHg). The most evolved among them have an iron-containing pigment and a peristaltic dorsal vessel pushing blood (pressure 20 mmHg) towards five pairs of lateral hearts in the five frontal segments. When they contract, these accessory hearts push blood into the ventral vessel at a pressure up to 70 mmHg.⁸

Arthropods

Insects have a series of pulsatile abdominal bulbs along the aorta. Their synchronized contraction (300–600 b.p.m.) initiated near the blind caudal extremity propels blood in the anterior direction at a low pressure (20/10 mmHg).⁹ The filling of these hearts in diastole is achieved by suction provided by the contraction of muscles attached to the shell pulling externally on the hearts wall. At the periphery, the blood flows freely into the interstitial space between the shell and the organs. It is directed by a network of membranes into

venous sinuses, which bring it slowly back to small lateral openings of the abdominal hearts (Figure 2A). This open peripheral system limits the size of insects and spiders, because the interstitial diffusion is efficient only over short distances. Although the lifespan of *Drosophila* is only a few weeks, their hearts show senescence: loss of performance, decrease in heart rate, arrhythmias, and myofibrils disorganization.¹⁰ The cardiomyocytes of insects have β -receptors and use cAMP as a second messenger, like the cardiomyocytes of all animals.^{4,8} They increase heart rate and contractility with adrenaline and decrease them with calcium-blockers.⁹

Insects have independent pulsatile accessory hearts (rate 200–300 min^{-1}) to assist the circulation in wings (flies) or limbs (locusts).¹¹ The accessory heart is a modification of the aorta

enclosed beneath the thoracic wall; the local contraction of this heart decreases the surrounding pressure inside the rigid housing, and aspirates the haemolymph from the wings or limbs. Respiration by expansion and contraction of the abdomen (rate 60 min^{-1}) has a major pumping effect on haemolymph, because the pressure raised by the abdominal contraction is higher than the pressure inside the aorta. The abdominal pump and accessory hearts are required to accelerate the flow during physical activity, because aortic hearts are too weak for this task.¹² Since the haemolymph percolates in an open system, the movements of the whole body participate in the flow propagation from and into the dorsal vessel. Haemolymph is not involved in oxygen transportation, since air is conveyed to the tissues by a network of small tracheoles.

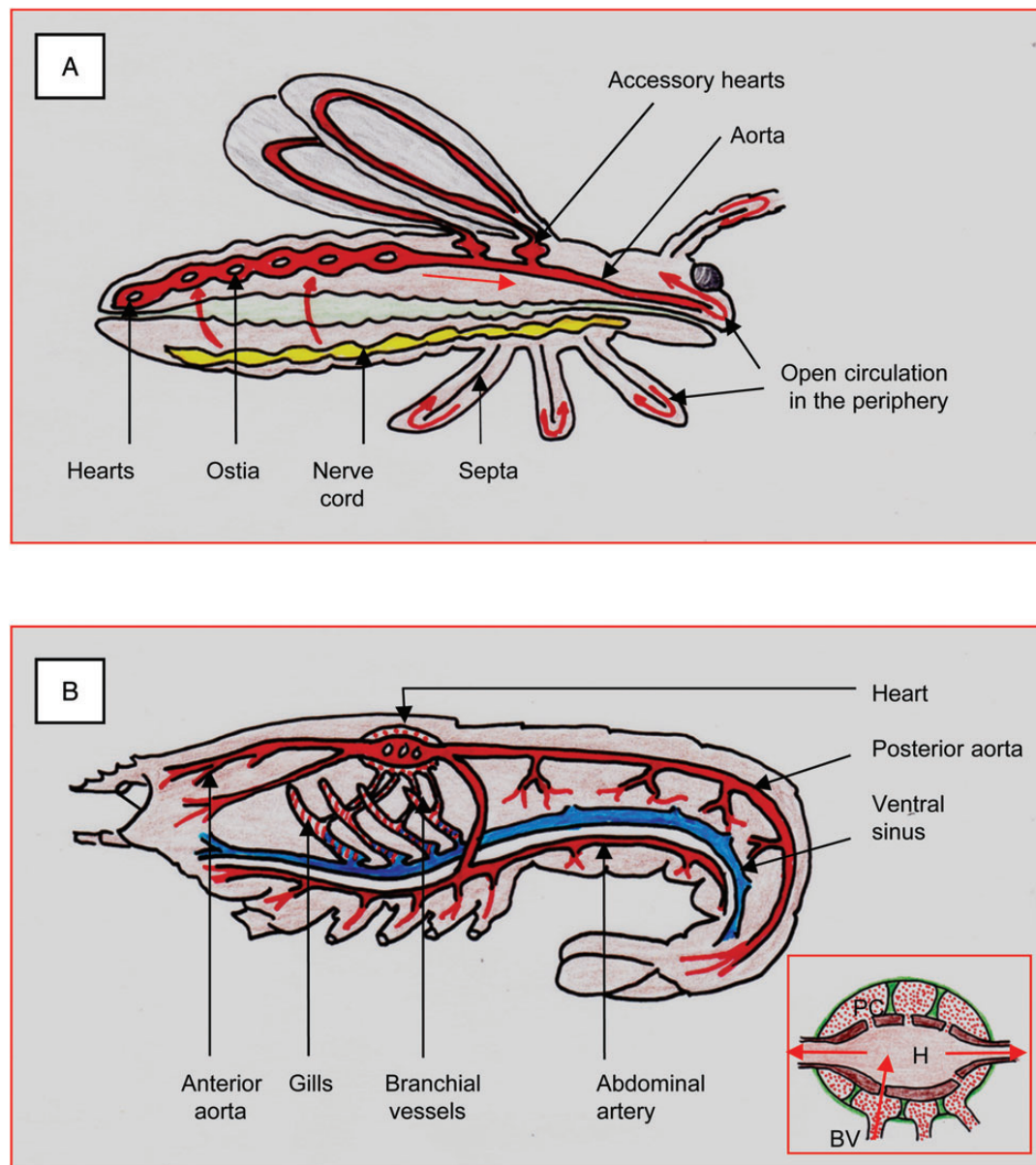


Figure 2 Cardiovascular system of arthropods. (A) Schematic drawing of a fly, with accessory hearts at the root of the wings. (B) Longitudinal slice of a lobster and its single heart (H). PC, pericardial cavity. BV, branchial vessels [reproduced from Chassot et al.⁴³]

Crustaceans present a wide spectrum of cardiovascular systems from primitive peristaltic conduits in small organisms of the plankton to complex pulsatile circulation with haemocyanin in decapods (crabs, lobsters). The latter have a single heart situated in the thorax, suspended inside a rigid pericardium by elastic ligaments, which provide diastolic expansion (Figure 2B).⁸ The venous blood returns inside the pericardium. In diastole, it enters the ventricular cavity through channels crossing the myocardial wall. In systole, the contraction closes these holes and blood is ejected into the anterior and posterior aortas. Gills are placed on the venous return to the heart, which is therefore perfused by arterial blood.⁸ Crustaceans have a sophisticated control of heart rate (average 70 b.p.m.) and stroke volume by nervous input from the cardiac ganglion, and by direct action of neurohormones on the cardiac muscle.¹³ The contraction or relaxation of muscular valves situated at the base of each of the five to seven arterial vessels originating from the heart allows the flow and the blood pressure (BP) (30–40 mmHg) of arteries vascularizing different organs to be controlled independently from each other. Large crabs have small arterioles ramifying within the tissues into a network of small channels as fine as capillaries, collecting fluid into venous sinuses. Brain and antennal glands have an uninterrupted continuity between arteries and veins.¹⁴

Mollusks

Gastropods (snails, mussels) appeared 500 millions years ago. They are the first animals with a two-chamber heart consisting of a ventricle and an atrium. The atrium acts as a buffering reservoir between the continuous venous return and the cyclic ejection; its contraction raises ventricular end-diastolic pressure without increasing the mean central venous pressure. The heart has an autonomous rhythm at 20 b.p.m. It provides a BP of 20–30 mmHg. Gas exchange takes place in gills or lungs placed on the venous circuit, bringing oxygenated blood to the heart. The O₂-carrier pigment is haemocyanin. Most mollusks have an open circulatory system in the periphery. Haemolymph and interstitial fluid are mixed together and constitute up to 50% of body weight, but are distributed to the different organs according to their O₂ consumption, not to their respective mass.¹⁵

Cephalopods (octopus, squids) are highly sophisticated mollusks. They have a closed system of arteries, capillaries and veins lined by endothelial cells, and a double-pressure circulation. A two-chamber heart collecting blood from the gills propels it into the systemic circulation at a high pressure (50–70 mmHg). Its output can be adapted to exercise by a two to three-fold increase in stroke volume and heart rate.^{7,15} Two accessory branchial hearts push the blood through the gills under a lower pressure (20 mmHg). This is the first appearance of a kind of 'pulmonary' flow at low pressure to facilitate gas exchange, and a 'systemic' circulation at high pressure to ensure efficient blood distribution according to increased activity. In a closed vascular tree, intravascular and interstitial fluids are separated; in cephalopods, they represent 6 and 15% of body weight, respectively.¹⁶

Vertebrates

Vertebrates are characterized by a multi-chamber heart, and a completely closed vascular system with capillaries, covered by endothelial cells. The blood contains erythrocytes with haemoglobin, blood cells,

and coagulation factors. The myocardial mass varies from 0.2% of body weight in fishes to 0.3–0.5% in reptiles, 0.6% in mammals, and 0.8–1.2% in birds.^{8,17} Vertebrates moved from an aquatic to a terrestrial environment 350 million years ago, where they had to breathe air and stand up against gravitational forces. Birds and mammals are homeotherms, which makes them independent from the surrounding temperature. These physiological challenges explain the wide variation in heart morphologies among vertebrates.

Anatomic evolution of the circulatory system

All vertebrates stem from a common chordate ancestor. Chordates (lancelets, sea squirts) are small marine animals looking like worms or anchovies. They have an open circulation and a peristaltic heart.⁴ This cardiac tube differentiated into five sequential segments, as during human embryogenesis: the *sinus venosus* and the atrium for the inflow, the atrio-ventricular canal, the ventricle, and the *conus arteriosus* for the outflow.¹⁸ The primary myocardium has a poor contractility and a slow electrical conductivity; it gives the AV canal and the heart valves. The inflow and outflow segments differentiated in the fast-conducting and well-contracting myocardium of the ventricular and atrial chambers.⁵ The heart modified progressively its shape among the different classes of vertebrates (Figure 3).^{2,18}

- Progressive displacement of the inflow structures from a caudal position to a dorsal (fishes) and cephalad (reptiles) position.
- Septation of the atrium in a right and a left cavity (amphibians).
- Development of the right ventricle (RV) from the proximal part of the conus arteriosus.
- Septation starting at the interventricular groove separating the left from RV (crocodiles).
- Development of a high-pressure left ventricle (LV) and a low-pressure RV.
- Disappearance of the sinus venosus and the conus arteriosus (birds and mammals).

The sinus venosus is important for providing an adequate pre-load when the venous pressure is very low (<4 mmHg in fishes and amphibians). The conus arteriosus smoothes the systolic pulsatility: in fishes, the gills are placed downstream of the heart. During human embryogenesis, the primitive tube loops on itself, the area between the primitive ventricle and the conus gives the RV, the septation divides the two chambers into four chambers (Figure 4).¹⁹ The fact that ontogenesis recapitulates phylogenesis means that all vertebrates share common precursors.¹⁸

Vertebrates have two types of contractile fibre arrangements.²⁰

- The trabeculated myocardium consists of randomly distributed fibres forming large trabeculations. It has the spongy appearance of the non-compacted myocardium encountered in some human congenital heart diseases. The O₂ supply is provided by diffusion through deep lacunae between trabeculations. It generates low blood BP (≤ 25 mmHg) but is an adequate volume pump.²¹ It predominates in fishes and amphibians, represents <50% of the ventricular wall in reptiles, and has disappeared in birds and mammals.
- The compact myocardium has well-organized fibre bundles able to develop high pressure. It is supplied by coronary vessels. It is present

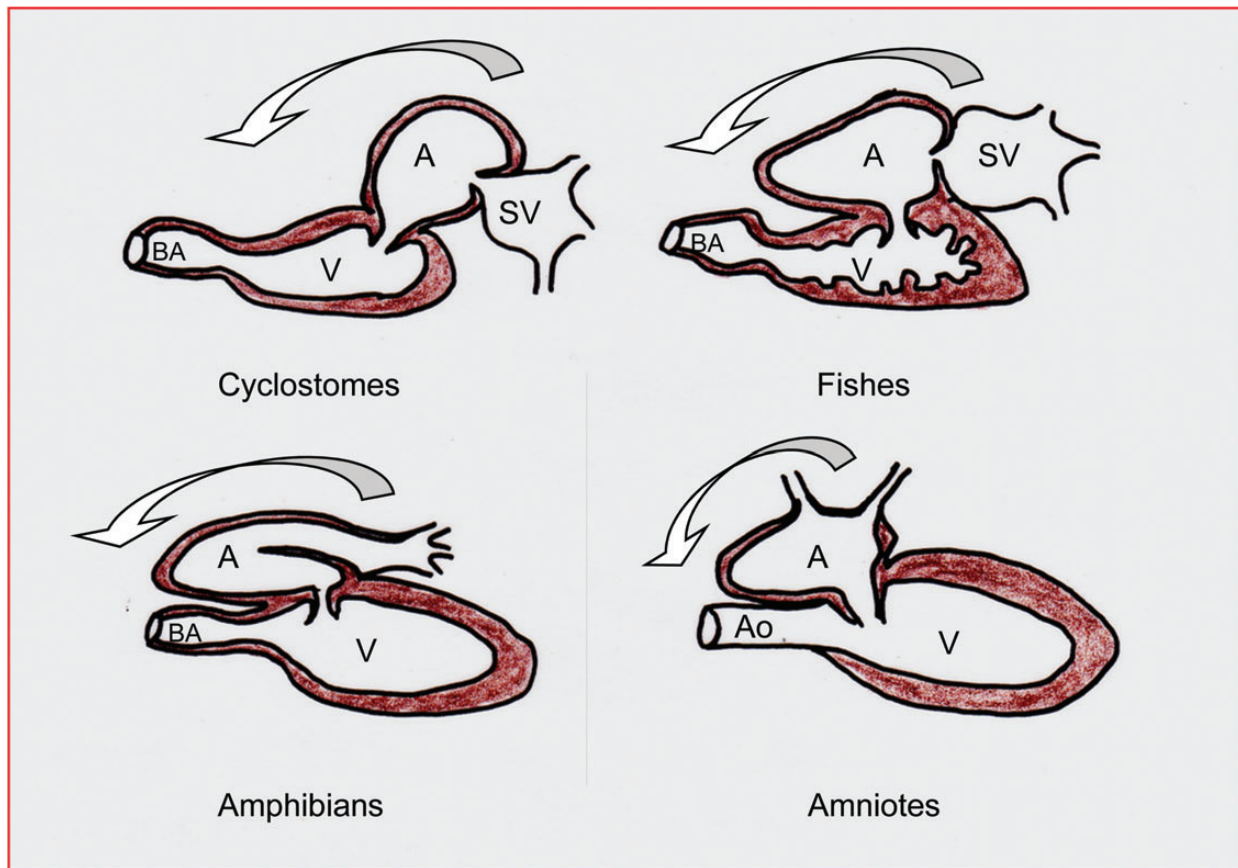


Figure 3 Progressive modification of the heart anatomy during evolution from the cyclostomes (primitive fishes) to the amniotes (reptiles, birds, and mammals). SV, sinus venosus; A, atrium; V, ventricle; BA, bulbus arteriosus; Ao, aorta [adapted from Simões-Costa et al.²]

in 15–35% of the wall thickness of active fishes, on most of the LV in reptiles, and in the totality of the ventricles in birds and mammals.²²

Intracardiac haemodynamics

In mollusks, the heart chambers are on a straight line with the vessels. The 'stop-and-go' flow during the alternation of systole and diastole represents a loss of energy. The atrio-ventricular orifice of fishes is almost at right angle with the direction of the inflow and of the outflow (Figure 5).² This 'S'-shaped flow establishes winding circuits in the atrium and the ventricle. In four-chamber hearts (birds and mammals), the diastolic filling flow makes a large vortex near the apex, pushing the blood volume around the edge of the anterior mitral leaflet towards the outflow tract. The inflow and the outflow are almost parallel ('U'-shaped flow). This continuous swirling preserves kinetic energy, maintains blood cells in motion, reduces dissipation of flow momentum, and redirects the volume for onward passage to the next cavity. This is particularly efficient at high heart rates, and enables the cardiac output to increase several fold.²³

The stress of gravity

Buoyancy in water provides practical weightlessness, but standing on the ground means resisting to gravitational forces. Terrestrial animals

have to maintain constant the perfusion of a brain positioned higher than the level of the heart, and to keep a normal venous return despite the lower position of the limbs. They have developed different adaptive measures against gravity.^{24,25}

- Increased BP. The giraffe has a systolic pressure of 260 mmHg in order to keep 100 mmHg in the brain.⁸ Since a high BP impairs gas exchange and increases transpulmonary filtration, the pulmonary circulation must be separated.
- Resistance to oedema. Tall birds and mammals have less compliant subcutaneous tissue and slender legs in order to resist the distending forces.
- Blood vessels. In mammals, vasoconstriction predominates in lower limbs, whereas autoregulated vasodilatation predominates in the brain to keep cerebral blood flow constant. Capillary basement membrane and medial smooth muscle are thicker in the legs compared with the neck.

Fishes

Fishes have a single circulation. An elastic arterial cone at the aortic root buffers the systolic pulsations before entering the gills situated downstream of the two-chamber heart. Unidirectional atrio-ventricular and outflow valves prevent backflow. Trabeculated

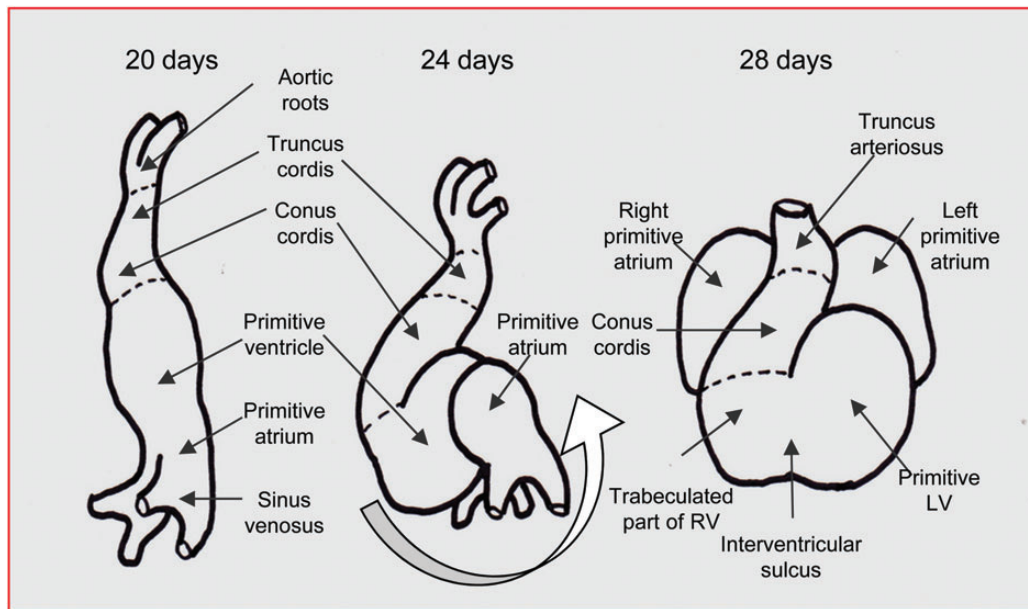


Figure 4 Progressive modification of the heart anatomy during human embryogenesis. At 20 days, the heart corresponds to the primitive cardiac tube. At 24 days, it looks like the heart of a fish. At 28 days, the configuration is close the three-chamber heart of amphibians and early reptiles [adapted from Kussman and Holzman¹⁹]

myocardium predominates in sedentary species. Compact myocardium, supplied by coronary vessels coming directly from the gills, is typical of active, pelagic species (tuna, sharks), where it represents up to 35% of the wall thickness and can develop pressure up to 80 mmHg.²⁶ The fish heart contracts in a posterior-to-anterior direction from sinus venosus to conus arteriosus. Pacemaker tissue is located in the inflow region and at the atrio-ventricular junction. The heart rate is proportional to the water temperature and inversely proportional to the animal size. At rest, it varies from 30 to 140 b.p.m. During exercise, it increases only by 25%; the increase in cardiac output is managed by a rise in stroke volume.¹⁸

Sharks have a cartilaginous pericardium filled with fluid. During systole, the volume of the ventricle decreases and the pressure inside the pericardium becomes negative (−1 to 3 mmHg). This phenomenon helps the filling of the atrium by a suction effect (Figure 6). Moreover, sharks can increase their stroke volume up to 40% by draining their pericardial fluid into the abdomen through a pericardioperitoneal canal, a mechanism acting like the decompression of a tamponade.²⁷

Lungfishes dwell in stagnant ponds frequently threatened by drought. They developed lungs made of numerous small air sacs, supplied by two pulmonary arteries (PA) branching after the gills. They have a beginning of septation inside the atrium and the ventricle. Oxygenated blood from the lungs flows with minimal mixing into the aorta, whereas desaturated venous blood goes mainly to the functional gills and to the lungs. When breathing air, the arterioles to the gills become partially vasoconstricted and the PA completely open. Since there is only one ventricle and one aorta, the BP is identical in the systemic and in the pulmonary circulation.¹⁸

Amphibians

Amphibians (frogs) have a three-chamber heart with two atria and one undivided ventricle made of trabeculated myocardium. The right atrium receives venous blood from the tissues. The left atrium receives oxygenated blood from the lungs. In the single ventricle, these two flows are parallel with practically no admixture, because of a longitudinal baffle inside the outflow tract.²⁰ The venous blood is ejected into the PA and the oxygenated blood into the aorta (Figure 7A). The PA gives branches to the skin (25% of pulmonary flow). The blood returning from the lungs and from the skin is saturated in oxygen (SaO_2 96%), but the latter is mixed with the systemic venous blood.

Amphibians are exclusive air-breathers. The major part of the respiration takes place in the lungs, but a significant part is performed through the moist skin. During diving, PA is vasoconstricted (vagal stimulation, acetylcholine), and its flow diverted towards the skin. This is sufficient to fulfil the low metabolic requirements of a frog hibernating in a cold swamp (PaO_2 30 mmHg). The increased O_2 consumption in summer is covered by the uptake through the lungs (PaO_2 100 mmHg).²⁸ The heart rate of amphibians (30–50 b.p.m.) decreases with hypothermia or diving. Since there is only one ventricle, the BP (40/20 mmHg) is identical in both pulmonary and systemic circulations.

Reptiles

Reptiles show a wide anatomical spectrum from a three-chamber heart with shunting and low arterial pressures (turtle), to functionally

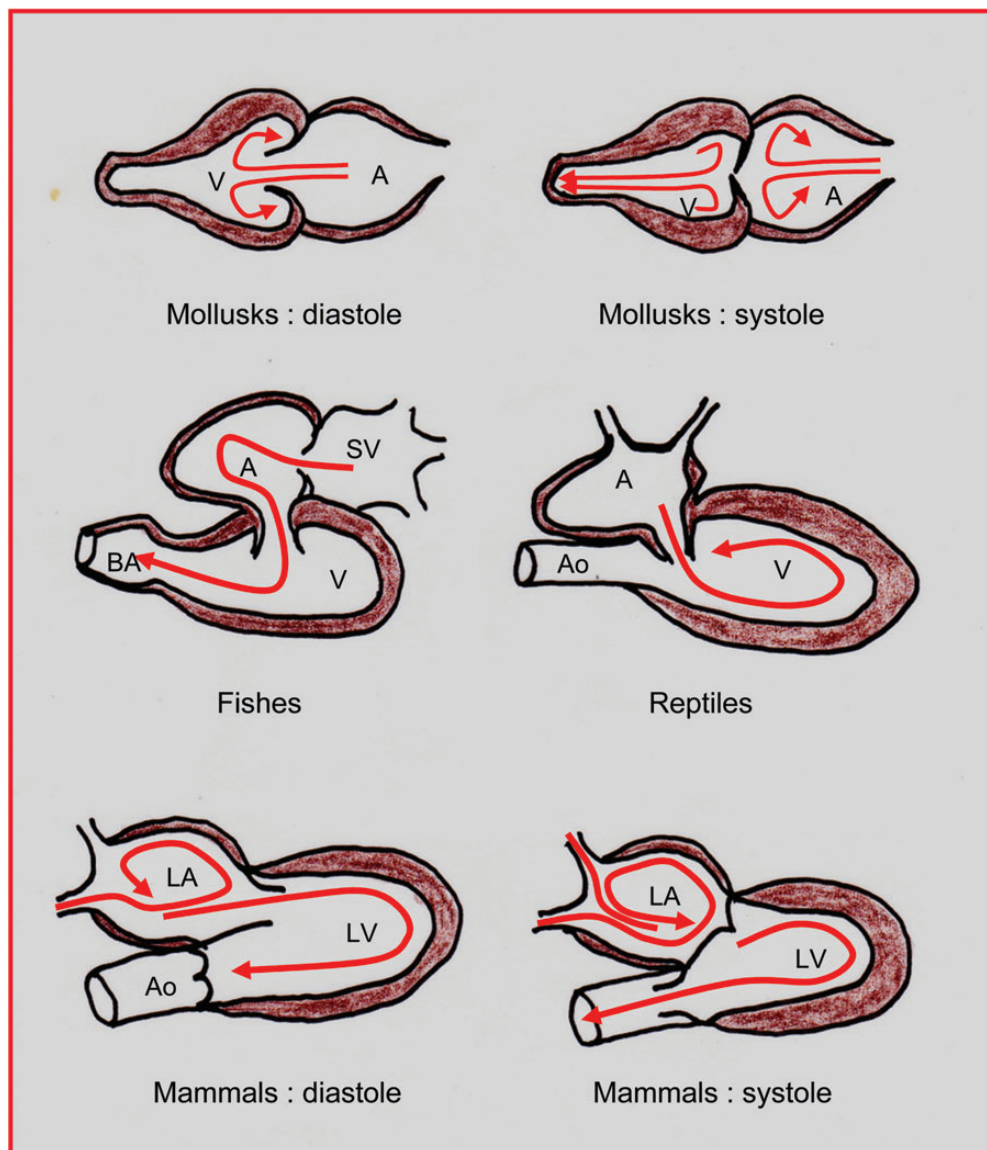


Figure 5 Modification of the intracardiac flow design in mollusks, fishes, reptiles, and mammals. A, atrium; V, ventricle; SV, sinus venosus; BA, bulbus arteriosus; Ao, aorta [reproduced from Chassot et al.⁴³]

separated circulations with high systemic arterial pressure (python) and to a four-chamber heart (crocodile). This evolution corresponds to the move from an aquatic to a terrestrial lifestyle, and from a low-speed locomotion to a high level of activity. Reptiles have one PA and two aortic arches, which bend dorsally and unite distally into a single descending aorta. They have some mixing of venous and arterial blood because the incomplete separation of the right and left ventricles behaves like a ventricular septal defect.²⁸ This has two major consequences (i) variations in resistance of the pulmonary or systemic arterial tree modify the pulmonary-to-systemic flow ratio, and induces L-to-R or R-to-L shunts; (ii) with the possibility of exchanging blood between right and left ventricles, the output of each ventricle can be dissimilar. At comparable body size, the O_2 consumption of the cool-blooded reptiles is 6–10 times lower than the consumption of the normothermic animals. Low metabolic requirement is an

advantage for diving because it prolongs the duration of apnoea, but it implies to rely on anaerobiosis during intense activity. Crocodiles can easily endure severe acidosis: their blood lactate levels rise to 20 mmol L^{-1} during exercise.²⁹

Turtles and most snakes have a three-chamber heart with two atria and one ventricle partially divided by a septum. The ventricle consists of three different parts: *cavum pulmonale*, corresponding to a thin RV, *cavum arteriosum*, corresponding to a thicker LV, and *cavum venosum*, which is a chamber situated at the level of the interventricular communication (IC), under the outflow tract towards the two aortic arches (Figure 7B).²⁰ The septum is surmounted by a muscular ridge, which contraction in systole decreases the size of the IC. Most of the ventricle is made of trabecular myocardium, but part of the *cavum arteriosum* contains layers of compact myocardium, particularly developed in pythons.³⁰ In turtles, the systemic BP is

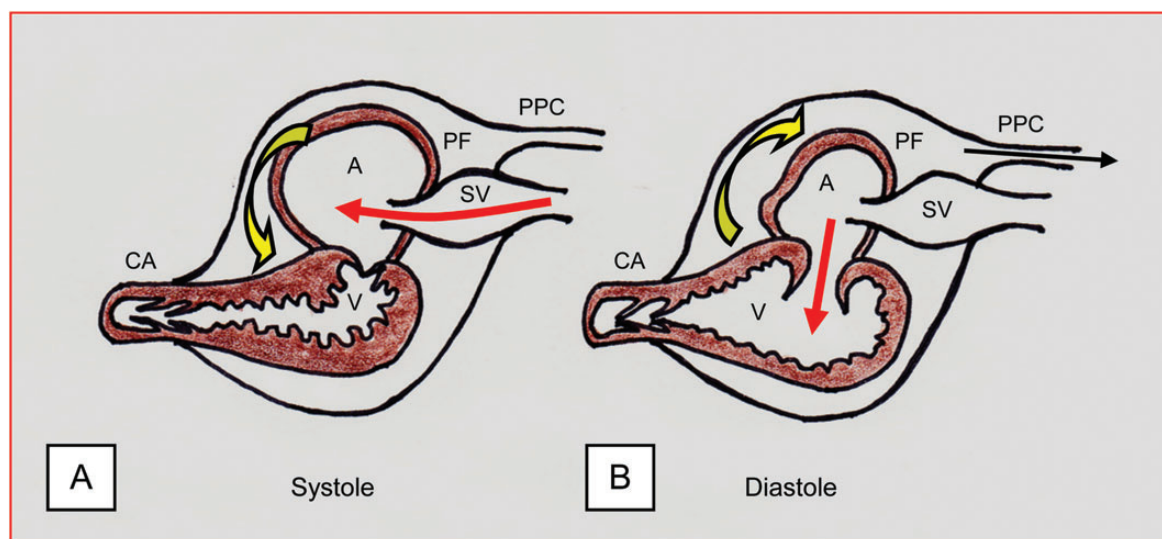


Figure 6 Elasmobranch heart. (A) Systole. (B) Diastole. Yellow arrows: push–pull mechanism induced on the atrial filling and emptying by the liquid-mediated coupling between the atrium and the ventricle. PPC, pericardioperitoneal canal; PF, pericardial fluid; A, atrium; V, ventricle; SV, sinus venosus; CA, conus arteriosus [reproduced from Chassot *et al.*⁴³]

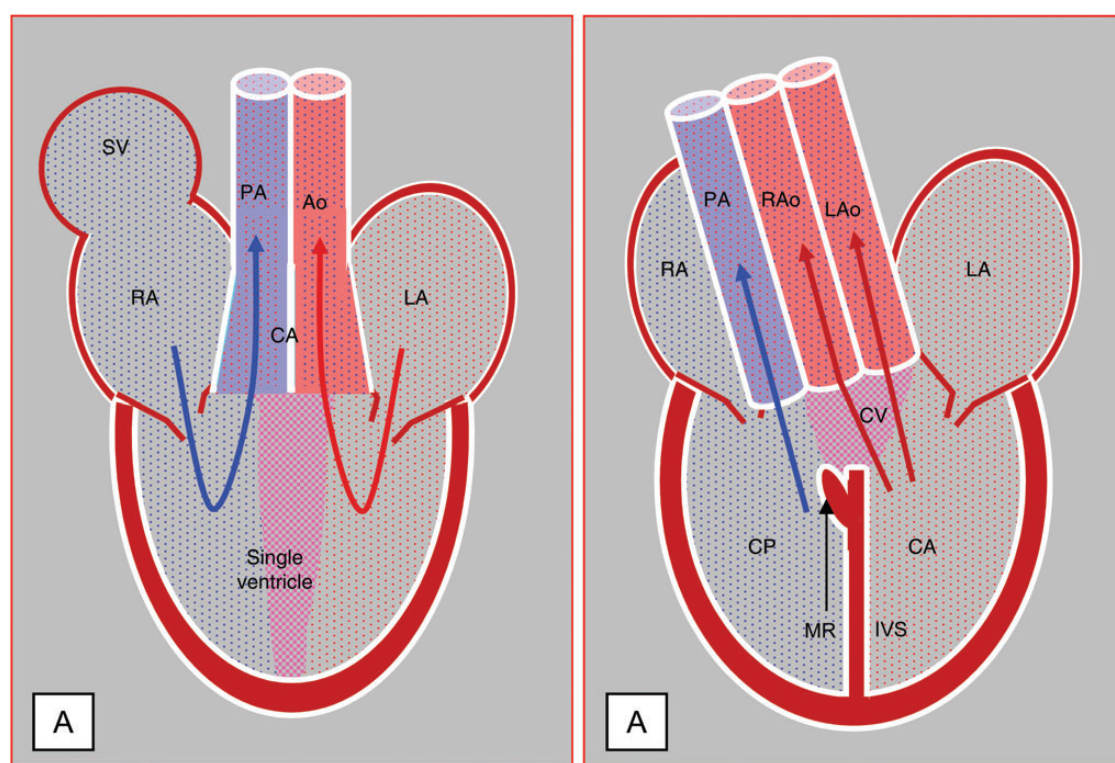


Figure 7 Schematic illustration of the three-chamber hearts. (A) Single ventricle of amphibians. (B) Partially divided ventricle of primitive reptilians (turtle). PA, pulmonary artery; Ao, aorta; SV, sinus venosus; CA, conus arteriosus; LAo, left aortic arch; RAo, right aortic arch; CV, cavum venosum; CP, cavum pulmonale; CA, cavum arteriosum; IVS, interventricular septum; MR, muscular ridge [reproduced from Chassot *et al.*⁴³]

30–40 mmHg; the pulmonary arterial pressure (PAP) is only slightly lower. During apnoea of diving, the heart rate and the pulmonary flow (Q_p) decrease by 50–80%, with a 150% increase in pulmonary resistance. The result is a $\geq 50\%$ R-to-L shunt.²⁰ During air breathing, heart rate and Q_p increase two- and three-fold, respectively. A net L-to-R shunt takes place. The heart rate of reptile is slow and depends on the temperature: 15–20 b.p.m. at 18° and 25–55 b.p.m. at 28°C.³¹

In pythons and varanid lizards, the separation between left and right circulations is almost complete. During diastole, the septal leaflet of the left atrio-ventricular valve is occluding the IC (Figure 8A).³⁰ In systole, the contraction of the muscular ridge separates the pulmonary from the systemic flow.^{31,32} There is only a non-significant R-to-L shunt due to the presence of O_2 -poor blood of the cavum venosum. This dynamic separation of pulmonary and systemic flows allows an increased systemic pressure up to 80 mmHg, whereas the pressure in the PA is 15–20 mmHg.³³

Crocodiles have a true four-chamber heart, but the interventricular septum inserts between the two aortic valves. The left aortic arch (LAo) and the PA exit from the RV, and the right aortic arch (RAo) from the LV (Figure 8B).¹⁷ At their root, the aortic arches communicate with each other through an opening (*foramen of Panizza*). The systolic pressure is 20–30 mmHg in the RV and 60 mmHg in the LV. During air-breathing, the LV pushes blood into the RAo and into the LAo through the foramen of Panizza. Since the pressure in the aortic roots is above the pressure in the RV, the valve of the LAo stays closed and there is no mixing of blood. During diving, blood flow to the lungs decreases because of the closure of a cog-tooth valve made of fibrous nodules situated in the RV subpulmonary outflow tract; this valve contracts with increased vagal tone and relaxes under adrenergic stimulation.³⁴ The pressure increase in the RV forces mixed venous blood into the LAo, whereas RAo continues to receive saturated blood from the LV. The main impact of the partial shunting in reptiles is the possibility to uncouple left and right ventricular outputs, which gives a wide margin of manoeuvre when pulmonary and systemic vascular resistances vary in opposite direction.³⁵

Birds and mammals

Birds and mammals maintain a constant body temperature $\sim 37^\circ\text{C}$: their activity is not affected by a cold or a warm surrounding. This advantage has a price: the increased basal metabolic rate requires a higher cardiac output and a higher BP. They have a four-chamber heart, with a septum inserted between the aortic and the pulmonary valves. This allows two completely separated circulations with different BPs.^{8,17}

- The average systemic BP is 120/60 mmHg in mammals and 150–170/70 mmHg in birds. This allows rapid transfer of oxygen and nutrients to the tissues and selective repartition of blood flow according to the needs (increased flow to the heart and muscles during hunting).
- The PAP is 25/15 mmHg in mammals and 20/10 mmHg in birds. This low pressure facilitates oxygen transfer from air to blood, allows thinner membranes, and prevents interstitial fluid leakage.

The major hindrance is the complete interdependence of both circulations. Left ventricle and RVs must have an equal flow per minute, even if the pre-load of each ventricle is reciprocally modified by ventilation in mammals. This requires a sophisticated system of haemodynamic regulation. Heart and lungs should be close together, because the pulmonary circulation has a pressure too low to accommodate the loss of pressure of long vessels. The ability to separate the pulmonary from the systemic circulation evolved independently in birds and mammals: the phylum of mammals took off from early terrestrial vertebrates 300 million years ago, whereas birds are descendants from reptiles.^{2,4}

The stroke volume of birds is similar to the stroke volume of mammals with the same body mass, but their cardiac output is three to six times higher because of a much higher heart rate at rest and during exercise, respectively, 85 and 335 min^{-1} in the swan, and 520–1260 min^{-1} in the hummingbird.³⁶

In mammals, the ratio between heart mass and body weight is 0.6%, man included: heart weight is 12 mg for a shrew (2–5 g) and 600 kg for a blue whale (100 t).³⁷ The resting heart rate is inversely proportional to the size (600 min^{-1} for shrews, 25 for elephants, and 6–12 for whales) and to the life-expectancy.³⁸ Large animals beat slowly and live longer, but the average number of heartbeats per lifetime is surprisingly constant (average 1.1 billion),³⁹ because the total O_2 consumed per bodyweight per lifetime is stable for all normothermic animals.³⁷

The evolution of haemodynamics

Cardiac output increases from 25 $\text{mL min}^{-1} \text{kg}^{-1}$ in fishes to 75–100 $\text{mL min}^{-1} \text{kg}^{-1}$ in mammals, and 100–150 $\text{mL min}^{-1} \text{kg}^{-1}$ in birds, proportionally to the gradual increase in metabolic demand.⁸ This is accompanied by a steady increase of the systemic BP. However, gas exchanges in the respiratory organs are facilitated by a low BP, which must be provided by a different circulation. The differentiation between a low- and a high-pressure circulation appears first in octopus. It is most pronounced in birds. Animals with systemic pressure < 40 mmHg (mollusks, fishes, and amphibians) do not have a differentiated pulmonary circuit. A separate low-pressure circulation appears when the systemic pressure exceeds 50 mmHg (cephalopods, some reptiles, mammals, and birds). In humans, it is interesting to note that 50 mmHg is also the limit of PAP beyond which appear serious clinical problems. A pulsatile ventricle is the most common pumping system among animals, because it affords high output under high pressure, but pulsatility is a hindrance for capillaries, where flow must be as continuous as possible. Therefore, large arterial vessels have developed an increased elastin content to absorb systolo-diastolic pulsations.⁴ Relative hypertension might be the drawback of an increased activity, but birds live longer than same-weight mammals despite their higher BP, probably because their mitochondria produce less free radicals.^{37,40} Cardiovascular diseases seem evenly distributed among animals. Atherosclerosis is a genetic- and diet-dependent wear present in all mammals, but found also in birds (prevalence 6% in parrots), reptiles and fishes (tuna).⁴¹ Heart failure has been described in reptiles, birds and mammals (prevalence $\sim 1\%$).⁴²

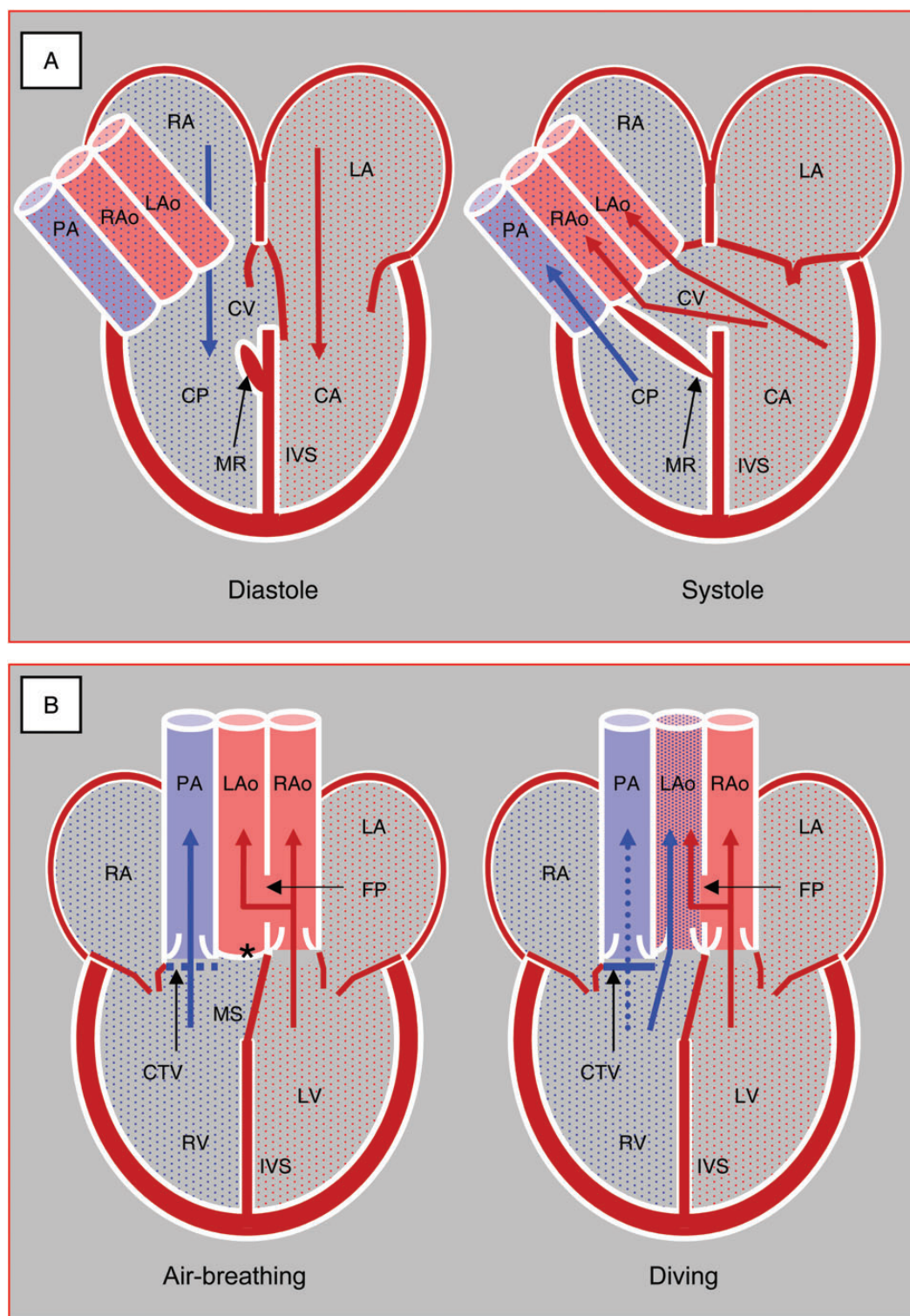


Figure 8 Schematic illustration of complex reptilian hearts. (A) Pythons. (B) Crocodiles. PA, pulmonary artery. CTV, cog-tooth valve. LAo, left aortic arch. *LAo valve closed. RAO, right aortic arch; CV, cavum venosum; CP, cavum pulmonale; CA, cavum arteriosum; IVS, interventricular septum; MS, membranous septum; MR, muscular ridge; FP, foramen of Panizza [reproduced from Chassot *et al.*⁴³]

Conclusions

All branches of the evolutionary tree, although independent from each other, tend to evolve in the same direction, a phenomenon called *convergence*.⁴ In each phylum, the improvements in the mechanical performance of the cardiovascular system continue towards the same goals of increased activity, increased metabolism, and independence from the surroundings. Each type of heart seems the best-fit for the needs of each phylum. The top performer is probably the bird's heart, but the human heart appears well-adapted for a medium-sized creature, which main achievement is its brain.

Conflict of interest: none declared.

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