ANKATOMY AND PHYSIOLOGY CARDIOPULMONARY SYSTEMS IN REPTILES

Jeanette Wyneken, PhD

Dept. of Biological Sciences, Florida Atlantic University, Boca Raton, FL  33431 USA

ABSTRACT

The cardiopulmonary anatomy of reptiles varies with taxon, behavior, ecology, and trophic level. However, the variations are superimposed upon just a few major functional anatomic themes. All reptiles have well developed atria and most have a partially compartmentalized ventricle. The extent of development of an intraventricular muscular ridge and the orientation of valves are responsible for directing blood flow toward systemic or systemic and pulmonary circulation. Crocodilians have a fully divided ventricle yet retain both systemic aortae and the pulmonary trunk. Generalist species that are large and active predators, as well as species that are aquatic divers tend to have particularly muscular hearts and more complex lungs. Less active species tend to have lungs with lower surface area, and often with less complexity. Recent advances in medical imaging technologies have significantly increased our understanding of the structural and functional relationships of cardiopulmonary anatomy in reptiles.

Cardiopulmonary Anatomy of Turtles, Lizards and Snakes

The hearts of turtles, lizards, and snakes are grossly similar. In ventral view it appears to be a three-chambered pump composed of two muscular atria and one ventricle. Looking dorsally reveals a large thin-walled sinus venosus. The sinus venosus, the structure responsible for initiating the heart beat, receives venous blood returning from the head, limbs, and body that then flows to the right atrium. From the right atrium, blood enters the ventricle, where it flows along at least two possible routes. The right atrium receives deoxygenated blood returning from the systemic circulation via the sinus venosus, a large chamber located on the dorsal surface of the atrium. The left atrium receives oxygenated blood from lungs via the left and right pulmonary veins. The solitary ventricle is divided into three subchambers: the cavum pulmonale, cavum venosum and cavum arteriosum (Fig 1). The cavum pulmonale is the most ventral chamber, which extends cranially to the pulmonary artery. The cavum arteriosum and cavum venosum are situated dorsal to the cavum pulmonale and receive blood from the left and right atria, respectively. The cavum arteriosum and cavum venosum are connected by an intraventricular channel, the interventricular canal.

During ventricular diastole, blood flows from the left atrium into the cavum arteriosum from the right atrium into the cavum venosum then, during late diastole, into the cavum pulmonale. The cavum venosum and cavum pulmonae are partially or completely separated from one another by the muscular ridge during ventricular systole when the ventricular walls approach one another.

Three great vessels, the left and right aorta and the pulmonary trunk emerge from the cranial
aspect of the ventricle. Blood leaving the ventricle tends to separate into either systemic and pulmonary outflows or just systemic outflow, directed flows passing along the muscular ridge in the ventricle and by the valve movement during ventricular contraction. The single cusped atrioventricular valves arise from the cranial aspect of the interventricular canal, and are anatomically aligned in such a fashion that they partially occlude the interventricular canal during atrial contraction (systole). They function during ventricular systole in the prevention of regurgitation of blood from the ventricle into the atria. In pythons, the left atrioventricular valve completely closes the interventricular canal during early ventricular diastole, effectively separating the cavum arteriosum and cavum venosum so that blood from the left atrium is directed into the cavum arteriosum exclusively.

**Crocodilians**

The crocodilians have a heart structure more similar to that of birds and mammals with the ventricle divided into pulmonary + systemic and systemic sides (Fig 2). They retain both left and right aortic arches. Structurally, the left aorta originates in the right ventricle with the pulmonary artery, and the right aorta drains the left ventricle. During normal ventilation, the pulmonary and systemic blood flows are separate. Crocodilians have a small aperture connecting the aortas, Foramen of Panizza, located just cranial to the ventricles. During apnea or diving, pulmonary flow is restricted by vasoconstriction of the pulmonary artery and some mixing of oxygenated and deoxygenated blood occurs both in the left aorta via the Foramen of Panizza and at the confluence of the left and right aortic arches.

**Cardiovascular Physiology**

The heart rate is dependent upon a number of variables, including body temperature, body size, metabolic rate, respiratory rate, and sensory stimuli. Heart rate is regulated by vagal tone. Temperature’s influence is well known. Reptiles that are warming up have higher heart rates than animals cooling down. Elevation of heart rate with peripheral vasodilation during warm basking periods tends to maximize heat gain. Peripheral vasoconstriction and the correlated reduction in heart rate slow heat loss as environmental temperatures drop.

The hearts of reptiles, and particularly chelonians are hypoxia resistant. Experimental studies have shown that reptiles hearts derives its oxygen and nutrient supply directly from the blood within the relatively thick, inner, spongy myocardium that surrounds ventricular cavity. The outer compact myocardium is thin and supplied by coronary arteries; it is resilient to loss of flow in the coronary arteries over several days. Transmyocardial blood supply may account for up to 30% of coronary perfusion in turtles and alligators. It is unknown if snake hearts derive such significant blood gas exchange and energy via this mechanism.

**Cardiopulmonary Circulation**

Unlike mammalian cardiopulmonary systems, the pulmonary and systemic blood flows are not completely separate. The extent of separation of the pulmonary and systemic circuits of flow
appears to be directed, in part by the muscular ridge within the heart of most reptiles. The details of the intraventricular structure differ with taxon; as a result so does the nature and extent of separation of flow streams. The degree of development of the ventricle’s muscular ridge is relatively low in freshwater turtle species, such as the red-eared slider *Trachemys scripta*, but is much more robust in animals that are active divers (sea turtles) and in large tortoises. Although a number of species have been studied generally (summarized by Farrell et al., 1998), relative few studies experimentally address the structural and functional relationships of the heart structure (summarized by Hicks, 1998), and fewer yet are comparative.

Circulation through the heart differs depending upon whether blood is shunted toward the lungs and the body or primarily toward the body. The extent of separation between the pulmonary and systemic circuits of flow differs somewhat across reptiles with the development of the ventricle’s muscular ridge. For example, in the leatherback turtle, *Dermochelys coriacea*, an active and somewhat endothermic species, the muscular ridge is exceptionally well developed when compared with other marine turtles. Dissected leatherback turtle hearts suggests that there is a nearly complete separation of systemic (body) and pulmonary (lung) circulation in the ventricle during ventricular contraction, but the physical separation is less well developed in other species. In some marine turtles and Galapagos tortoises, *Geochelone elephantopus* (= *G. nigra*), pulmonary artery walls are thickened near the lungs, similar to a muscular sphincter.

The aortae and pulmonary trunk receive vagal innervation. Vagal tone is correlated with development and regulation of L-R shunts. Studies of turtles show that whether blood is shunted toward or away from the lungs is a function of blood arterial gas levels.

**Cardiac Shunts**

Cardiac shunts (= central shunts) are associated with intraventricular flow and require an incomplete septum; these are found in noncrocodilian reptiles (turtles, snakes, and lizards). Shunts are often described as “right to left” (R-L) referring to the shift in blood from the pulmonary circulation to the body (the system), and “left to right” (L-R), referring to the shift of blood back toward the lungs and the body when physiologic conditions change. Large R-L shunts may be triggered by low systemic blood oxygen levels and may serve to regulate metabolism. However, several physiologic or environmental events (temperature, exercise, or digestion) that can increase metabolism, can reduce a R-L cardiac shunt and increase oxygen delivery. Farmer et al. (2008) showed that R-L shunts may be important in high H+ availability and in aiding digestion in crocodilians.

During normal respiration, the flow of blood tends to create a left-to-right shunt within the ventricle based upon pressure differentials. So blood flows to both the systemic and pulmonary circuits. During diving, apnea, or other instances in which the pulmonary resistance is elevated, a right-to-left-shunt occurs. This means that flow to the pulmonary circuit is reduced and most blood exiting the ventricle shifts to the systemic vessels (aortae).

Recent use of computed tomography has increased our understanding of the extent and gross
architecture of the lung in vivo. Structural and functional magnetic resonance imaging also show promise in enhancing our understanding of the function of the cardiopulmonary system in unanesthetized animals in a noninvasive or minimally invasive manner. Ultrasonography adds further understanding of function. Together these medical imaging technologies have worked their way into both the basic research community and into private practice, enhancing our understanding of dissected and necropsy material. Several recent discoveries come from such work. First, our understanding of blood flow through the heart during rest and during digestion in pythons (Starck 2009). Second, flow in the pulmonary arteries of turtles intermittently perfuse the lung, whereas venous flow appears to be more constant. Finally, when shunting from the pulmonary to systemic systems occurs (L-R), several shunt sites may be involved (central or intracardiac shunts--blood movement within the ventricular chambers; from the pulmonary circuit to the systemic circuit; and at locations between the pulmonary arteries and veins), suggesting control of perfusion at several levels (Wyneken 2008). It is likely that further structural-functional relationships will be identified with further use of these noninvasive imaging tools.

**Blood Function**

Movement of blood is responsible for the transfer of heat, nutrients, waste products, blood gases, and probably assists digestion (at least in some species). Primary focus is on the oxygen capacity, a measure of the blood’s ability to carry oxygen per unit volume; which is dependent on the amount of hemoglobin in the nucleated red blood cells. The hemoglobin molecule is the compound responsible for the respiratory properties and color of the blood. Published oxygen capacities in reptiles typically range from 5-11% in turtles, 6-15% in crocodilians, and 7-8% in lizards (compared to 35-55% in exercised dogs). Reptiles with the broadest thermal tolerances tend to have the least variation in their oxygen capacities at different temperatures. Reported rise in oxygen capacity with an increase in size in gartersnakes (*Thamnophis spp.*)) is due to increases in hemoglobin concentration or hemoglobin form in erythrocytes.

Oxygen dissociation curves describe the functional relationships of blood and oxygen at differing temperatures and pH. They describe the pressures (measures of concentration) of oxygen that produce saturation or partial saturation of the hemoglobin. Oxygen dissociation curves effectively map how much oxygen is retained by the hemoglobin under specified conditions. The forms of the curves are subject to the effects of temperature, pH, carbon dioxide, metabolites of glycolysis (2,3-DPG), and the ions Na⁺, K⁺, Mg²⁺, Cl⁻ and SO₄⁻. Ontogenetic stage also can impact oxygen saturation. There is a general trend for oxygen dissociation curves of smaller homeotherms, with their usually high metabolic rates, to be shifted right (meaning that their blood has a lower oxygen affinity, making delivery of oxygen easier). In reptiles, the oxygen dissociation curves are highly variable because of the influences of variable temperature (and metabolic rate) and the ability to buffer blood, particularly in turtles, as well as the other factors listed above.

Oxygen affinity is a measure of how easily the hemoglobin gives up oxygen to tissues. Hemoglobins with higher affinities give up oxygen to tissues less readily; low affinity
hemoglobins give up oxygen to the tissues readily. Reptiles generally have a lower oxygen affinity than mammals. Theoretically, this allows reptiles to deliver oxygen to tissues even at very low blood oxygen levels, and hence gain oxygen delivery performance from their blood at relatively low hematocrit levels and at low energy costs.

Blood oxygen affinities of a number of lizard species have been measured. As expected, the more active species (e.g. teids, anguids) had lower oxygen affinities. Higher oxygen affinities are seen in the slower or “sit and wait” predator species (e.g. chameleontids, gekkonids). Iguanid lizards (including *Iguana iguana*, *Anolis* sp., *Ctenosaura* sp.) serve as the baseline for comparison. There is a reported positive relationship between body size and oxygen affinity in iguanid lizards, measured at their preferred body temperatures. However, this measure is confounded by behavioral differences in the species and may not be clinically relevant. In snakes and crocodilians, which are episodic feeders, oxygen affinity goes down when digesting prey (a process which can be metabolically demanding).

During exercise or stress, reptiles can experience a metabolic acidosis resulting from lactic acid production. This change in blood pH reduces blood oxygen affinity through the Bohr effect, causing the blood to hold less oxygen. Species that typically live under hypoxic conditions (e.g., many turtles), or ventilate only when blood oxygen levels are nearly depleted appear to have blood-buffering mechanisms to resist the Bohr effect.

**Landmarks for the Heart and Airways**

The airways begin at the glottis, which is located in the floor of the oropharynx, often within caudal portion of the tongue. The glottis is the rostral (anterior-most) opening and “control valve” for the airway; it has both intrinsic muscles that control opening and closing as well as shape and extrinsic muscles, supported by the hyoid apparatus (the skeletal elements located between and behind the lower jaws), which control the position of the glottis in the oropharynx. The chelonian glottis is located at the base of the muscular, fleshy tongue. Within the shell, the trachea passes ventral to the esophagus as a single structure. In snakes and lizards, the glottis is located more caudally within the oropharynx but can be protruded rostrally in some species, most notably snakes and some monitor lizards. In crocodilians, the hard palate is complete so that the glottis is located much more caudally, and is protected by a fleshy flap, making it difficult to see in anaesthetized animals.

In most reptiles, the airways bifurcate cranially to the heart; the carina forms and bifurcates the airways well cranial of the formation of separate bronchi, which lead into the lungs. The two bronchi enter the proximal part of the lungs along with the dorsally positioned pulmonary arteries. The bronchi extend far into the lungs and have many openings. Lizards, pythons, chelonians and tuatara have two lungs. Most snakes have a single right lung, however boas and pythons have a long right lung and a reduced left lung. Other elongated reptiles such as legless (glass) lizards and amphisbaenians have just one lung or a normal lung along with a reduced lung.
Gloss lung structure is variable but well described by Perry (1998). Reptilian lungs often have complex or simple regions with clear vascular portions and nearly avascular, sac-like portions. In species with complex lungs such as crocodilians and marine turtles, cartilage-supported airways lead to cartilage-free airways.

The heart is often located near to or just caudal to the bifurcation of the bronchi. The exception is in snakes and some old-world tortoises. The elongated bodies of snakes reposition organs, and the heart is usually found cranial to the bronchial bifurcation. However it the position varies with ecology and behavior. It is located 15%–25% of total body length caudal to the snout in terrestrial and arboreal species but more caudally (at 25%–45% of total body length) in aquatic species snakes. In most lizards the heart is most often located at the level of the elbow then the forelimbs are extended along the side of the body. However in some short-necked species such as bearded dragons (*Pagona* spp.), the heart is located more cranially between the level of the shoulder joint and the elbow. In chelonians, the heart position varies slightly with taxon. In new world and marine species, the heart is often just caudal to the humeral-pectoral scute margins. In Testudo, the heart tends to be located more rostrally than in new world species. The shape and relative extent of the pectoral and humeral scutes vary sufficiently among species that they provide only rough landmarks. The cranial aspect of the heart is located approximately long a line drawn between the caudal most aspects of the shoulder joints.

References


Figure 1. Diagram of the heart and major pulmonary and systemic circulation of a lizard. (left: ventral; right: dorsal view). The hearts of other taxa are grossly similar in external structure. In snakes, the heart is more elongated in form. (Wyneken 2008)

Figure 2. Diagram of the heart and major pulmonary and systemic circulation of a crocodilian (left: ventral; right: dorsal view). The Foramen of Panizza is not shown in this diagram but is located as a small connection between the two aortae near their origin from the ventricle. (Wyneken 2008)