The Physiological and Evolutionary Significance of Cardiovascular Shunting Patterns in Reptiles

James W. Hicks

Department of Ecology and Evolutionary Biology, University of California at Irvine, Irvine, California 92697

The morphology of the reptilian heart results in the mixing of oxygenated and deoxygenated blood (cardiac shunts). In birds and mammals cardiac shunts are detrimental, but in reptiles this condition is often considered a derived trait, conveying important physiological functions and favored by natural selection. Alternative views are advanced suggesting that, in reptiles, cardiac shunts represent either an ancestral condition or an embryonic trait.

The primary function of the cardiovascular system is to provide an adequate delivery of oxygen and nutrients to the metabolizing tissues while ensuring the removal of carbon dioxide and other metabolic waste products. In vertebrates, this goal is achieved through a variety of circulatory and cardiac designs that is often portrayed as the evolutionary progression from the two-chambered heart of fish to the completely divided, four-chambered heart of birds and mammals (Fig. 1).

Historically, the hearts of amphibians and reptiles were viewed as intermediate phylogenetic steps, functionally inefficient compared with the near-”perfect” circulation of birds and mammals (9). This view became antiquated in the latter half of the 20th century, when many studies indicated that the mixing of blood within the reptilian ventricle varied with physiological state and was probably regulated (see Refs. 6 and 11 for review of relevant literature). In contrast to the negative physiological consequences of cardiac shunts in “higher vertebrates,” the ability to control the mixing of oxygen-rich and oxygen-poor blood within the reptilian ventricle is hypothesized to provide many physiological benefits (Table 1).

Although there is little experimental evidence to support these hypotheses (11), the perception that cardiac shunts represent an adaptive phenotypic trait permeates much of the comparative physiological literature. This view is underscored by the notion that the cardiovascular system of reptiles is a “highly derived condition that provides reptiles with the ability to regulate the intracardiac shunt to their advantage, depending on respiratory needs” (7).

In comparative biology, adaptationist “storytelling” frequently influences arguments concerning the evolutionary significance of many phenotypic traits. These arguments are usually based on the belief that most, if not all, phenotypic features are adaptive. For reptiles, one underlying assumption has been that, if cardiac shunts were not adaptive, why would reptiles maintain their unique cardiac morphology and shunt blood? However, before cardiac shunts can be considered an adaptive trait, it is important not only to establish the patterns and physiological consequences of shunts but, more importantly, to provide strong evidence that the absence of cardiac shunting reduces physiological performance and/or reproductive fitness. Without such evidence, cardiac shunts should not be viewed as a derived trait but as rather more likely an ancestral condition or embryonic character that does not negatively impact the animal’s physiology.

This purpose of this article is to briefly review the anatomic and physiological basis of cardiac shunting in the reptilian heart, illustrate the usefulness of the comparative method for investigating the evolutionary significance of cardiac function in reptiles, and finally to propose alternative hypotheses that explain cardiac shunting in these interesting vertebrates.

Cardiac anatomy and shunting patterns in reptiles

The class Reptilia is made up of the testudines (turtles), squamates (lizards and snakes), and crocodilians (crocodiles, alligators, and caiman). The hearts of turtles, snakes, and lizards consist of two atrial chambers, separated by a complete septum and a single ventricle. The most distinctive feature of the ventricle is the muscular ridge (MR) or Muskelleiste (15). It originates from the ventral ventricular wall and runs from apex to base, dividing the ventricle into two major chambers. These include a smaller, right ventrolateral chamber, the cavum pulmonale, and a larger, left dorsolateral chamber. This latter chamber is subdivided into the smaller cavum venosum and larger cavum arteriosum (Fig. 2; Ref. 15). The dorsolateral border of the MR is free, resulting in potential communication between the ventricular subchambers during all phases of the cardiac cycle. In all reptiles, three great vessels arise from the ventricle: the pulmonary artery, the right aortic arch (RAo), and the left aortic arch (LAo). The pulmonary artery originates from the cavum pulmonale, and the two aortae emerge from the cavum venosum (15).

In crocodilians, the cardiac anatomy is very different from other reptiles but similar to that of birds and mammals. The heart is completely divided into four chambers, except in crocodilians, which retain the dual aortic arch system found in all reptiles. In crocodilians, the LAo emerges from the right ventricle alongside the pulmonary artery, whereas the RAo emerges from the left ventricle (Fig. 2). This anatomic arrangement provides systemic venous blood with a potential bypass of the pulmonary circulation. An interesting feature of the crocodilian heart is that the RAo and LAo communicate at two distinct points. The first is a small opening, called the foramen

0886-1714/02 5.00 © 2002 Int. Union Physiol. Sci./Am. Physiol. Soc.
www.nips.org

News Physiol Sci 17: 241–245, 2002;
10.1152/nips.01397.2002

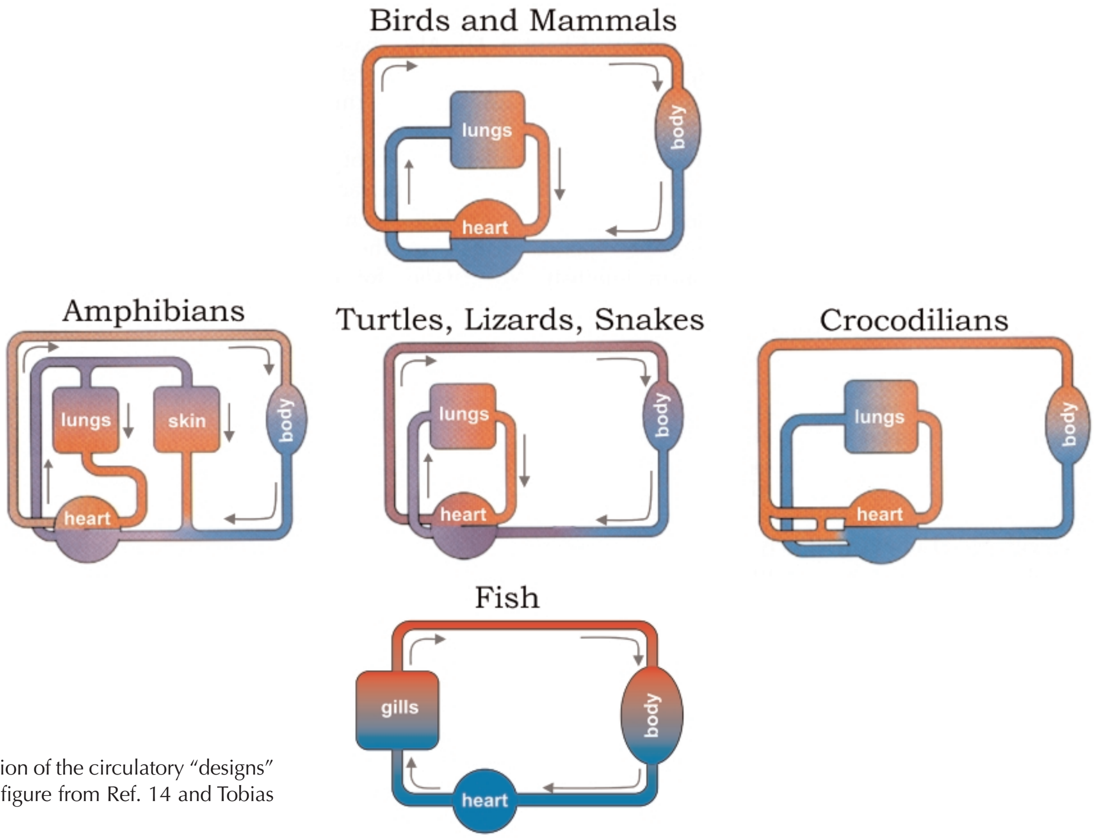

FIGURE 1. Schematic representation of the circulatory “designs” of vertebrates. Based on original figure from Ref. 14 and Tobias Wang (unpublished).

of Panizza, located near the base of the LAo and RAo, and the second point of communication is via an arterial anastomosis in the abdomen (Fig. 2). Beyond this anastomosis, the RAo continues as the dorsal aorta and the LAo becomes the celiac artery, which gives rise to smaller arteries that supply most of the blood flowing to the gut (2).

TABLE 1. Hypothesized physiological functions of cardiac shunting

Physiological Function	Direction of Shunt	Reference
Saves cardiac energy	R-L	6
"Meters" lung oxygen stores	R-L	5
Reduces CO_2 flux into the lungs	R-L	19
Reduces plasma filtration into lungs	R-L	6
Facilitates warming	R-L	3
Triggers hypometabolism	R-L	13
Facilitates stomach acid secretion and digestion	R-L	12
Facilitates CO_2 elimination into lung*	L-R	19
Minimizes V/Q mismatching*	L-R	20
Improves systemic O_2 transport*	L-R	11
Myocardial oxygenation*	L-R	8

R-L, right-to-left (pulmonary bypass); L-R, left-to-right (systemic bypass). *Hypothesized functions for L-R shunt apply only to turtles, snakes, and lizards. Crocodilian reptiles cannot develop L-R shunts due to anatomy; see text for details.

These morphological features result in cardiac shunts, which are typically defined by their direction, either as right-to-left (R-L) or left-to-right (L-R). A R-L shunt represents bypass of the pulmonary circulation and the recirculation of systemic venous blood (oxygen poor) back into the systemic arterial circulation. Since the shunted blood bypasses the lungs, it has no chance of being oxygenated and thus decreases the oxygen saturation of systemic arterial blood. In contrast, a L-R shunt represents the recirculation of pulmonary venous blood (oxygen rich) into the pulmonary circulation. It should be noted that in crocodilians the existence of a complete ventricular septum precludes a L-R shunt from developing. The potential flow patterns of oxygen-rich and oxygen-poor blood within the reptilian ventricle are summarized in Fig. 2.

The factors that control cardiac shunting have been studied in several species, with the monitor lizard *Varanus exanthematicus,* the freshwater turtle *Trachemys scripta,* and the crocodilians *Alligator mississipiensis* and *Crocodylus porusus* receiving the most attention (11). In some reptiles, the MR is relatively small and not well developed (11) and the ventricle functions as a single pressure pump during the entire cardiac cycle (6). Under these conditions, the direction and magnitude of shunt is determined by factors that control the vascular resistance of the pulmonary and systemic circulations (6, 11). In other reptiles, the MR is relatively large and well developed, almost forming a complete ventricular septum (11). In these animals, mixing of deoxygenated and oxygenated blood can occur during diastole. However, during

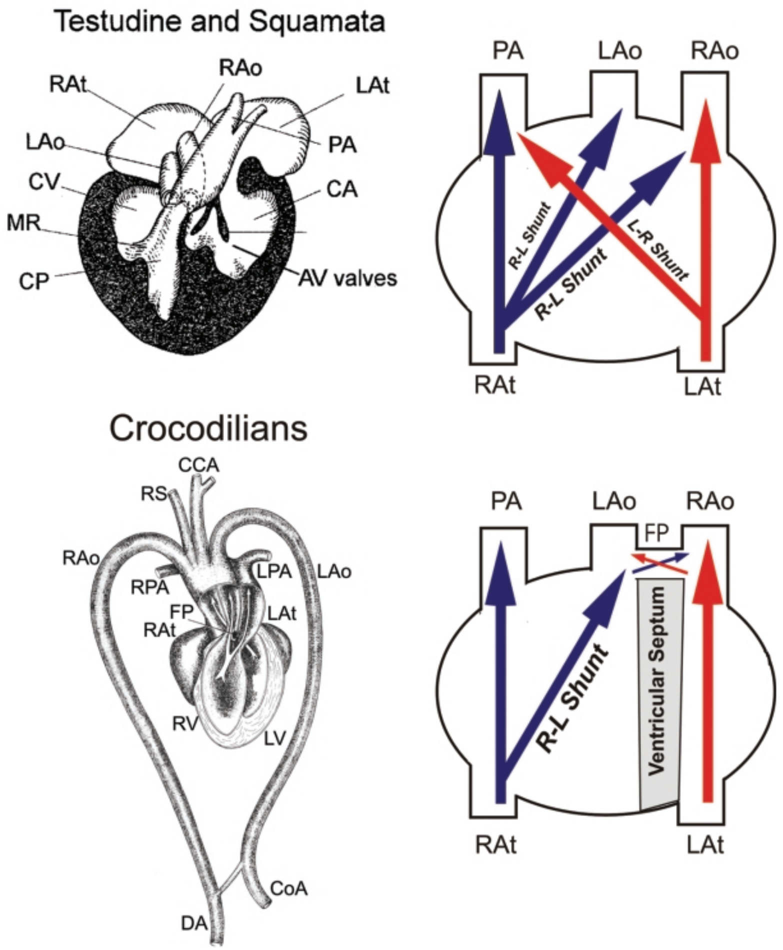

FIGURE 2. *Top*: diagrammatic illustration of the heart of noncrocodilian reptiles (*left*) and the potential blood flow patterns in the ventricle (*right*). The heart is shown in the ventral aspect. RAt, right atrium; LAt, left atrium; CP, cavum pulmonale; CA, cavum arteriosum; CV, cavum venosum; PA, pulmonary artery; LAo, left aortic arch; RAo, right aortic arch; MR, muscular ridge. Illustration is based on an original unpublished drawing by F. N. White. *Bottom*: diagrammatic illustration of the heart of *Caiman crocodylus* (*left*) and the potential blood flow patterns in the ventricle (*right*). LV, left ventricle; RV, right ventricle; LPA, left pulmonary artery; RPA, right pulmonary artery; RS, right subclavian artery; CCA, common carotid artery; DA, dorsal aorta; CoA, celiac artery, FP, foramen of Panizza. Reprinted from Ref. 1. For both panels, red arrows represent oxygenated blood and blue arrows represent deoxygenated blood.

systole the ventricle functions as a dual pressure pump (6). Consequently, the size and direction of the cardiac shunt are less affected by changes in pulmonary and systemic vascular resistance (11).

Regulation of pulmonary and systemic vascular resistances results from changes in autonomic tone and the release of neurohumoral factors. In addition, these combined factors also influence heart rate, ventricular contractility, and ventricular blood volumes, which together can contribute to the size and direction of the shunt (11). Changes in autonomic tone are partially generated within the central nervous system, but stimulation of pulmonary stretch receptors and vascular chemoreceptors may also be involved (17).

The patterns of cardiac shunting associated with environmental challenges or different physiological states have been investigated in relatively few animals. Obtaining these patterns requires chronic implantation of blood pressure and blood flow probes, thus limiting the studies to relatively large animals. However, these few studies have been informative and have provided insights into general patterns of cardiac shunting, particularly those associated with ventilatory state (11). In many reptiles, particularly many turtles and crocodilians, lung ventilation is intermittent, wherein brief ventilatory periods are interspersed among apneas of variable duration. These apneic periods can be associated with quiet breathing or with diving in semiaquatic species. During apnea there is a general increase in parasympathetic tone, resulting in a bradycardia and an increased pulmonary vascular resistance. These cardiovascular changes result in a reduction in pulmonary blood flow and the development of a R-L shunt. In contrast, periods of ventilation are characterized by tachycardia, decreased pulmonary vascular resistance, increase in pulmonary blood flow, reduction of R-L shunt, and development of a L-R shunt. Detailed information on the cardiac shunting patterns occurring during thermoregulation, diving, activity, feeding, and digestion remains virtually unknown, although a limited set of studies have investigated some blood flow patterns during these states (1, 16, 18). Recent advances in blood flow-measuring devices, computer-assisted data acquisition systems, and the potential advances in telemetry devices are making chronic measurements of blood flow in many sizes of animals increasingly possible; thus there remain many possibilities for advancing our understanding of the blood flow patterns associated with various physiological states in these vertebrates.

Alternative approaches: the comparative method

Are cardiac shunts in reptiles really adaptations (that is, derived traits favored by natural selection) and, if so, what was or is their selective advantage? Strong experimental evidence supporting the hypothesis that cardiac shunts are an adaptive trait remains elusive. In the absence of such direct evidence, adaptive hypotheses could be strengthened through methods

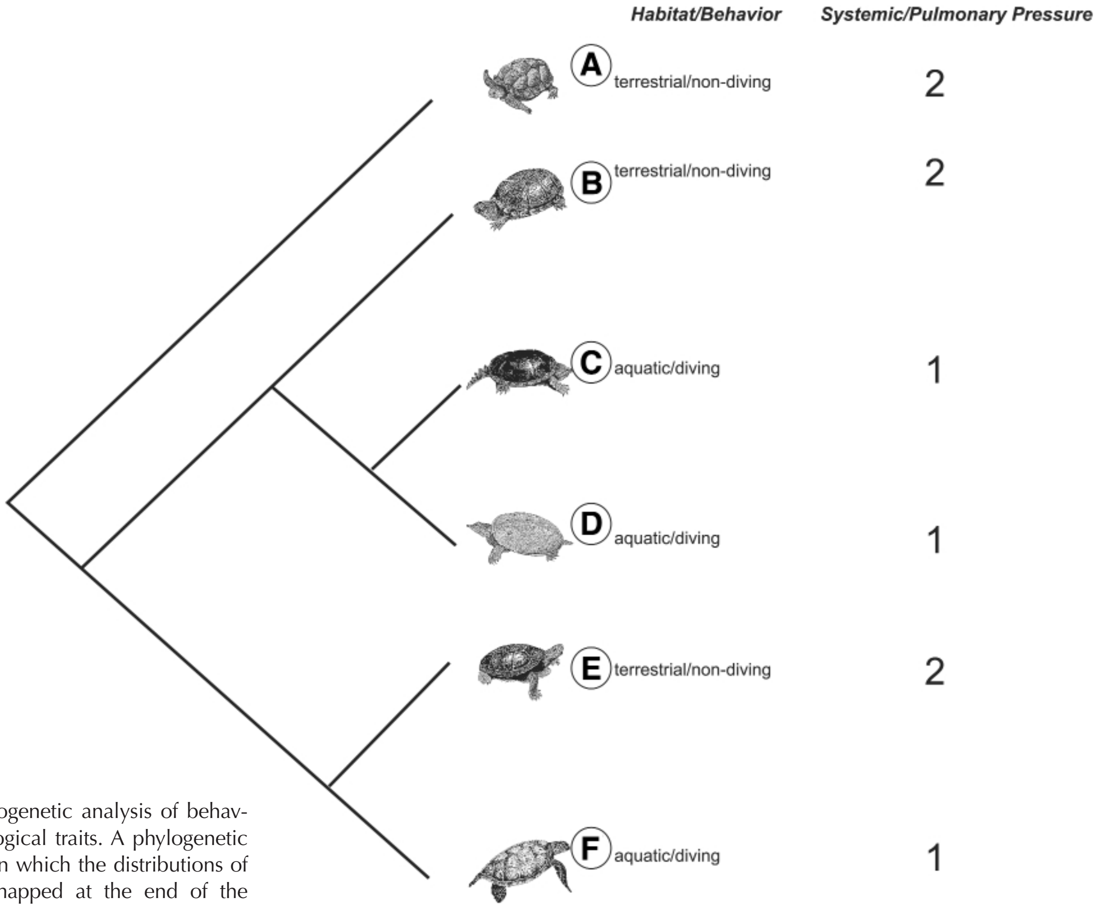

FIGURE 3. Comparative phylogenetic analysis of behavioral, ecological, and physiological traits. A phylogenetic tree for a hypothetical taxon in which the distributions of two sets of characters are mapped at the end of the branches is shown (see text for explanation).

that incorporate comparative phylogenetic analysis. Such an approach encompasses the mapping of phenotypic or ecological traits onto an independently derived phylogeny. The phylogeny represents the best estimate of the evolutionary history of the group being investigated. Analyses that combine both the historical patterns (phylogeny) with present-day character traits (phenotype) can provide insights into where specific phenotypic features arose, if the features arose more than once, and allows stronger inference about whether phenotypic traits are adaptations (4, 10)

A hypothetical analysis illustrates this approach. Figure 3 depicts a phylogenetic tree for a hypothetical taxon in which the distributions of two sets of characters are mapped at the end of the branches. One set of characters includes ecological and behavioral traits (aquatic vs. terrestrial, diving vs. nondiving), and the other set includes a physiological trait, in this case the ratio of peak systolic blood pressure in the systemic (S) and pulmonary (P) circulations, or S/P. The S/P reflects the capacity of the heart to separate blood pressure and may be related to the ability for altering the size and direction of the cardiac shunt (see above). In animals that have an S/P of 1, the heart functions as a single pressure pump and shunt direction and magnitude are varied by changes in pulmonary and systemic vascular resistances. In contrast in animals with an S/P of 2, the heart functions as a dual pressure pump and shunt direction and magnitude remain relatively fixed and not altered by changes in vascular resistances.

The phylogenetic approach allows for interpreting the congruence of the physiological and morphological traits with the ecological traits and the evolutionary history. In this hypothetical example, the historical pattern (phylogeny) indicates that the ancestral state was terrestrial with an S/P of 2 (*species A*) and more interestingly that, each time lineage invaded an aquatic habitat and acquired diving behaviors (*species C*, *D*, and *F*), they also evolved an S/P 1 condition. Specifically, the heart became a single pressure pump, in which the direction and size of cardiac shunting is altered by changes in peripheral vascular resistances. A phylogenetic analysis results in stronger inferences for the evolution of a specific phenotypic trait, and, in this example, a more convincing case is made that specific physiological and morphological traits associated with the cardiovascular system are a derived and adaptive character. This type of analysis strengthens the hypothesis of adaptation and can focus the direction of future research by revealing the evolutionary patterns.

The comparative phylogenetic method is powerful but has limitations. First, it requires an independently derived phylogeny, which may not be available for the species being investigated. Second, it requires information on a specific phenotypic character, in this case some measure of cardiovascular performance. Such characters may be difficult to measure in a large number of species. However, as this hypothetical illustration shows, the power of the phylogenetic method lies in its ability to analyze and test patterns across species, correlating traits and features of the environment, life history, and natural history with evolution.

Alternative views of cardiac shunts

In the absence of experimental evidence or strong evolutionary inference, there is little reason, a priori, to assume that cardiac shunting in reptiles represents a trait that provides adaptive benefit. It is just as likely that the reptilian cardiac morphology results from a variety of other reasons, and thus a number of alternative hypotheses can be advanced. Studies on cardiac shunts have been limited to adult or subadult animals, excluding the possibility that shunts may be physiologically important in juveniles or during embryonic development. For example, during the embryonic stage, all amniotes (mammals, birds, and reptiles) possess central vascular shunts that bypass the nonfunctional lungs and provide a pathway for gas exchange via the chorioallantoic membrane or placenta. In endothermic vertebrates (mammals and birds) the continued presence of cardiac shunting in newborns and hatchlings is a maladaptive trait. This is because of the pronounced and detrimental effects that cardiac shunts have on systemic oxygen transport. However, ectothermic vertebrates have substantially lower tissue oxygen demands (~10-fold) and tolerate large deviations in many physiological variables that would prove detrimental to birds and mammals. The persistence of cardiac shunting in these animals may not be physiologically detrimental, and consequently there may not have been strong selection pressures for eliminating the cardiac shunt pathways. Under this scenario, the continued presence of cardiac shunts into the adult stage would not be considered an adaptation.

One argument against the above hypothesis is that in some reptiles cardiac shunting appears to be regulated, changing its size and direction with physiological state or environmental conditions. However, even if this is the case, such shunt patterns do not indicate that shunts are regulated per se but rather that regulation may be a simple consequence of regulating pulmonary and systemic vascular resistances. The primary function of the cardiovascular system is achieved by controlling the vascular resistance of the pulmonary and systemic circulations to match blood flow with tissue metabolic demands. These changes in vascular resistances can directly influence cardiac shunting patterns. Obviously, the resulting shunt patterns will alter blood gases and blood flow, but the physiological changes that result may well be within the range tolerated by reptiles and have little negative impact on physiological performance. Thus cardiac shunting occurs in reptiles not because it was selected for but rather because it was not selected against.

Summary

Reptiles played a pivotal role in the evolution of mammals and birds, and although their cardiovascular system has been studied for almost 200 years, its unique morphology and function has remained an elusive mystery. By combining physiological investigations with comparative methods, it is possible that stronger inference can be made concerning the evolution of the reptilian cardiovascular system and the apparent functions of cardiac shunting. However, until such evidence is provided, there is no a priori reason to believe that shunts are an adaptive trait favored by natural selection. Rather, the unique cardiovascular system of reptiles may simply represent an ancestral condition and/or an embryonic character trait that does not negatively impact the primary function of the cardiovascular system.

References

1. Axelsson M, Fritsche R, Holmgren S, Grove DJ, and Nilsson S. Gut blood flow in the estuarine crocodile, *Crocodylus porosus*. *Acta Physiol Scand* 142: 509–516, 1991.
2. Axelsson M, Holm S, and Nilsson S. Flow dynamics of the crocodilian heart. *Am J Physiol Regul Integr Comp Physiol* 256: R875–R879, 1989.
3. Baker LA and White FN. Redistribution of cardiac output in response to heating in *Iguana iguana*. *Comp Biochem Physiol* 35: 253–262, 1970.
4. Brooks DR and McLennan DA. *Phylogeny, Ecology and Behavior: a Research Program in Comparative Biology*. Chicago: University of Chicago Press, 1991.
5. Burggren W, Smits A, and Evans B. Arterial O_2 homeostasis during diving in the turtle *Chelodina longicollis*. *Physiol Zool* 62: 668–686, 1989.
6. Burggren WW. Form and function in reptilian circulations. *Am Zool* 27: 5–19, 1987.
7. Burggren WW and Warburton SJ. Patterns of form and function in developing hearts: contributions from non-mammalian vertebrates. *Cardioscience* 5: 183–191, 1994.
8. Farmer C. Did lungs and the intracardiac shunt evolve to oxygenate the heart in vertebrates? *Paleobiology* 23: 358–372, 1997.
9. Foxon GEH. Problems of the double circulation in vertebrates. *Biol Rev* 30: 196–228, 1955.
10. Garland TJ and Adolph SC. Why not to do two-species comparative studies: limitations on inferring adaptation. *Physiol Zool* 67: 797–828, 1994.
11. Hicks JW. Cardiac shunting in reptiles: mechanisms, regulation and physiological function. In: *Biology of the Reptilia*, edited by Gans C and Gaunt AS. Ithaca, NY: Society for the Study of Amphibians and Reptiles, 1998, p. 425–483.
12. Hicks JW and Comeau SG. Vagal regulation of intracardiac shunting in the turtle *Pseudemys scripta*. *J Exp Biol* 186: 109–126, 1994.
13. Hicks JW and Wang T. Hypoxic hypometabolism in the anesthetized turtle, *Trachemys scripta*. *Am J Physiol Regul Integr Comp Physiol* 277: R18–R23, 1999.
14. Piiper J and Scheid P. Gas exchange in vertebrates through lungs, gills, and skin. *News Physiol Sci* 7: 199–203, 1992.
15. Van Mierop LHS and Kutsche LM. Some aspects of comparative anatomy of the heart. In: *Alfred Benzon Symposium 21; Cardiovascular Shunts; Phylogenetic, Ontogenetic and Clinical Aspects*, edited by Johansen K and Burggren W. Copenhagen: Munksgaard, 1985, p. 38–53.
16. Wang T, Abe AS, and Glass ML. Effects of temperature on lung and blood gases in the South American rattlesnake *Crotalus durissus terrificus*. *Comp Biochem Physiol A Physiol* 121: 7–11, 1998.
17. Wang T, Krosniunas EH, and Hicks JW. The role of cardiac shunts in the regulation of arterial blood gases. *Am Zool* 37: 12–22, 1997.
18. West NH, Butler PJ, and Bevan RM. Pulmonary blood flow at rest and during swimming in the green turtle, *Chelonia mydas*. *Physiol Zool* 65: 287–310, 1992.
19. White FN. Carbon dioxide homeostasis. In: *Comparative Pulmonary Physiology: Current Concepts*, edited by Wood SC. New York: Marcel Dekker, 1989, p. 439–462.
20. Wood SC. Cardiovascular shunts and oxygen transport in lower vertebrates. *Am J Physiol Regul Integr Comp Physiol* 247: R240–R247, 1984.