On the Evolution of Arterial Vascular Patterns of Tetrapods

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ABSTRACT The factors that explain the diverse arrangement of the major arteries of tetrapods are not known. Here, I aim to illuminate some of the underpinnings of these patterns. I review the variation in the sauropsid left, right, and dorsal aortae regarding the origin of the gastrointestinal blood vessels and the relative diameters of left and right aortae where they join together to form the dorsal aorta. I focus on these features because the quality of blood that flows through these aortae can vary depending on the state of cardiac shunting and the size of the vessel can provide insight into the quantity of blood borne by the vessels. I then place the information in a phyletic, historical, and ecological context. The plesiomorphic pattern is for the gastrointestinal vessels to arise as segmental arteries from the dorsal aorta, which is formed from the confluence of left and right aortae with similar diameters. The pattern is well conserved with only two major variations. First, in several clades of reptiles (testudines, crocodilians, lizards of the genera *Varanus* and *Hydrosaurus*) a substantial portion of the gastrointestinal arteries arises from the left aorta, leaving the diameter of the left aorta smaller than the right at their confluence. I hypothesize that this vascular arrangement facilitates growth by allowing more alkaline blood to flow to the somatic (body wall) and appendicular circulations, which may promote bone deposition and inhibit resorption, whereas hypercapnic, acidic blood flows to the digestive viscera, which may provide CO_2 as a substrate for the synthesis of gastric acid, bicarbonate, fatty acids, glutamine, purine rings, as well as glucose from lactate. Second, in some snakes and lizards with snake-like body forms, such as Amphisbaenidae, the diameters of left and right aortae are asymmetrical at their confluence with the left aorta exceeding the right, but in members of the amphibian order Gymnophiona the right generally exceeds the left. This condition is associated with asymmetrical development of the lungs. J. Morphol. 000:000–000, 2011.

KEY WORDS: cardiovascular; heart; aorta; artery; amphibian; reptile; shunt; digestion; growth

INTRODUCTION

The cardiovascular system of tetrapods is intriguing because the arrangement of the major arteries and the cardiac ventricles varies considerably between clades, but the reasons underlying this variation are poorly understood. The major arterial vessels are not responsible for blood flow to a particular muscle, bone, or organ, but to large and general regions of the body and so modifications in their arrangements should not be brought about by slight changes in body components, but by large shifts in body form and life history. Because the architecture of the heart determines how blood is distributed into these major arteries, the evolution of the heart and the main arterial trunks are united by this common function and the topography of the major arteries should functionally intertwine with the cardiac anatomy, yet few studies have examined this putative structure–function relationship. Functional studies are especially lacking among the clade with the most highly variable vessels, the caecilians. In sauropsids, the group that includes all extant and extinct amniotes except those of the synapsid lineage (e.g., mammals), the structure of the cardiac ventricle underpins their ability to shunt blood and thereby vary the quality of the blood ejected into the major arteries (Hicks, 1998; Starck, 2009). Therefore, the vascular patterns may determine the usefulness of shunting. It is possible that this anatomy has no functional basis, but Barcroft (1938) and Ewer (1950) have pointed out that it is unwise in biological inquiries to assume a structure or phenomenon is useless; adaptation is the rule rather than the exception. Even if a function is not obvious, it is more profitable to carefully consider all possibilities than to pronounce the structure or phenomenon worthless, which will lead nowhere. Incorrect hypotheses can be refined or disposed of by subsequent experimental work. As Darwin pointed out in *The Descent of Man*,"...false views, if supported by some evidence, do little harm, for everyone takes a salutary pleasure in proving their falseness: and when this is done, one path towards

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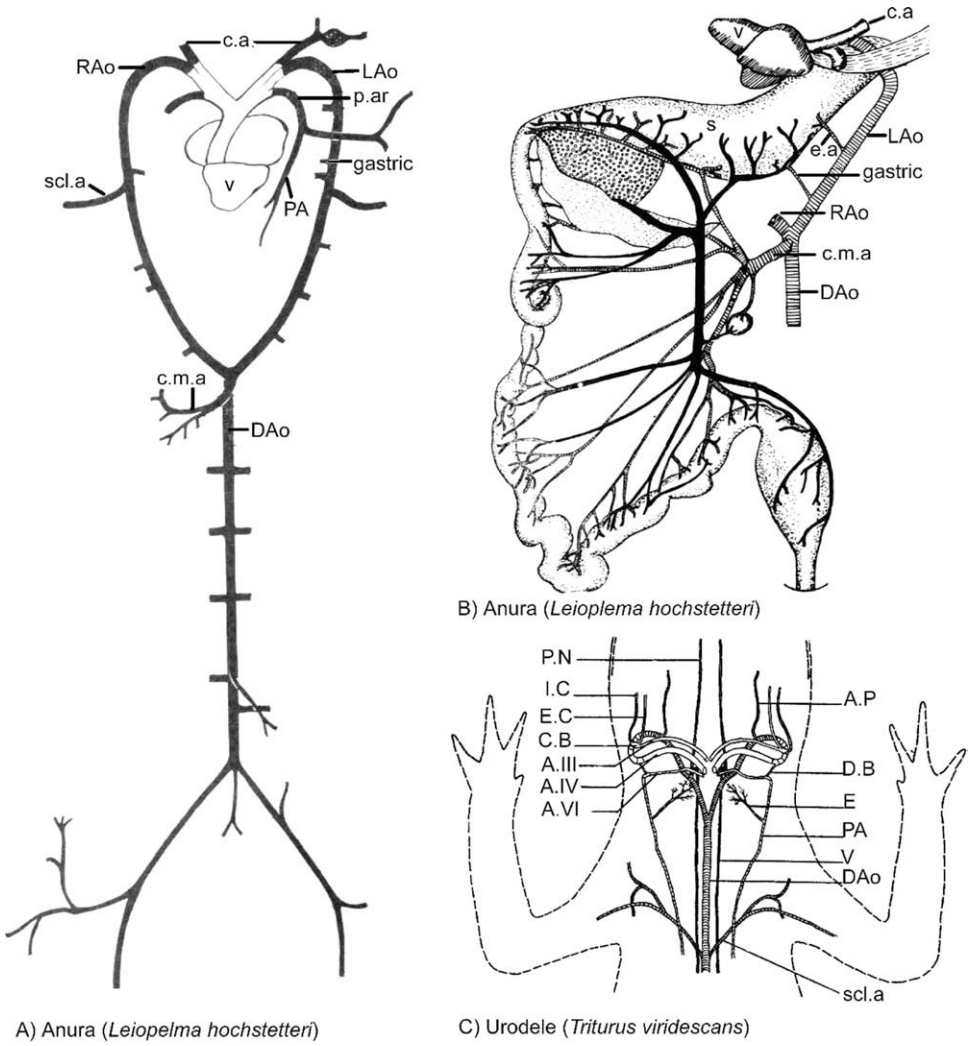

Fig. 1. Arterial vessels of anurans and urodeles. **A**: Ventral diagrammatic view of the arterial vessels of the frog *Leiopelma hochstetteri* Fitzinger from Elsie and Stephenson (1947). **B**: Arteries (stippled) and veins (solid black) of the alimentary canal of *Leiopelma* (from Elsie and Stephenson, 1947). Abbreviations for part A and B: c.m.a, coeliaco-mesenteric artery; DAo, dorsal aorta; e.a, esophageal artery; LAo, left aorta; PA, pulmonary artery; p.ar, pulmo-cutaneous arch; RAo, right aorta; s, stomach; scl.a, subclavian artery; v, cardiac ventricle. **C**: Ventral view of the arterial vessels of the urodele *Triturus viridescans* (from Darnell, 1949). The heart is not illustrated. c.a, carotid artery; A.III, carotid arch; A.IV, systemic arch; A.VI, pulmonary arch; A.P., ascending pharyngeal; C.B., carotid bulb; D.B., Ductus Botalli; E., esophageal; I.C., internal carotid; E.C., external carotid; PA, pulmonary; P.N., palatino-nasal; scl.a, subclavian; V., vertebral.

error is closed and the road to truth is often at the same time opened (Darwin, 1871)."

Because little is known about when shunts are employed and whether their use varies depending on phylogeny, it is difficult to interpret the functional significance of these patterns of blood flow. Some insight might be gained by integrating data about when shunts occur with information on the topography of the major arteries. Therefore, the aim of this manuscript is to shed new light on old data by the following means. I review the organization of the major arteries in amphibians and sauropsids. In several lineages of lepidosaurs, I could not find adequate descriptions of this vasculature and so I dissected specimens to elucidate this anatomy. Second, I map the patterns onto a phylogeny, so that the polarity can be determined. Finally, I integrate this information with data on shunts and on life history to illuminate possible functions that may underlie the patterns. Sauropsids provide an extraordinary opportunity to study how the cardiovascular system might be tailored to a variety of needs because the natural history of this group is remarkably diverse, providing a rich context in which to study the evolution of the cardiovascular system.

THE AORTIC ARCHES OF LISSAMPHIBIA

Anura and Urodela

The arrangement of the arterial arches of the three orders of Lissamphibia, Anura (Salientia), Urodela (Caudata), Gymnophiona (Apoda), varies depending on order and ontogeny (Darnell, 1949; Kolesova et al., 2007) but little is known about variability in cardiac structure. As in air-breathing fishes (*Polypterus*, *Amia*, the Dipnoi) and amniotes, the sixth arch in the Lissamphibia forms the pulmonary artery (Goodrich, 1958; Kolesova et al., 2007) [but see Ramaswami (1944) for a discussion about the fifth arch forming the pulmonary artery in some Gymnophiona and Darnell (1949) for discussion of the arches of caudata]. The remaining arches are more variable between orders and, in the Gymnophiona, between genera. The following overview focuses on the manner in which the gastrointestinal arteries arise.

The arterial circulation of Anura (Fig. 1A,B) and Urodela (Fig. 1C) generally consists of symmetrical left and right arches that coalesce via the lateral dorsal aortae to give rise to a median dorsal aorta, from which spring the majority of the gastrointestinal blood vessels. Although the major gastrointestinal vessels of anurans arise from the dorsal aorta, it is interesting that in *Leiopelma*, a rather unique anuran with inscriptional ribs, there is an additional small gastric artery arising from the left aorta (Elsie and Stephenson, 1984), although this small vessel is not illustrated or noted by Szarski (1950) raising the possibility that the vessel identified by Elsie and Stephenson is an esophageal artery (Fig. 1A,B). Nevertheless, the largest vessel to the stomach is the coeliaco-mesenteric artery, which arises caudad to the confluence of the left and right aortae. The right and left subclavians generally also arise from the right and left aortae respectively (Ecker, 1889; Gibbons and Shadwich, 1991). In Urodela, the lateral dorsal aortae merge to form the dorsal aorta from which segmental arteries arise to irrigate both the gastrointestinal and somatic circulatory systems, as well as the forelimbs via the subclavian arteries (Fig. 1C). The position of the confluence of the left and right aortae is caudal to the apex of the ventricle in anurans but is variable in both Urodela and Gymnophiona, ranging from a caudal location relative to the ventricular apex to a cranial one (Ramaswami, 1944; Darnell, 1949).

Gymnophiona

The topography of the arterial trunks in the third order, the Gymnophiona (caecilians), is highly unusual and variable, indeed more variable than in any other group examined (Figs. 2, 3). Interestingly, some similar patterns are seen among sauropsids. Unlike amniotes, amphibians have a conus arteriosus from which the ventral aorta arises. However, caecilians differ from other amphibians because in many caecilians one of the lateral aortae, generally the right, is larger than the other at their confluence, which varies greatly in its cranial-to-caudal location relative to the heart (Ramaswami, 1944; Lawson, 1970). This is also seen in limbless sauropsids to differing degrees, but it is the left aorta that is larger than the right, and appears to correlate with reduction of one of the lungs (below this is more fully discussed). In Gymnophiona, a correlation with a diminished lung is not well supported. For example, both *Ichthyophis glutonosus* and *Dermophis gregorii* have diminutive left lungs (Butler, 1895) but the pattern of the aortic vessels in *Ichthyophis* is much more similar to the plesiomorphic tetrapod design in having lateral aortae with similar diameters converge caudal to the apex of the ventricle, whereas the confluence in *Dermophis* is cranial to the heart and the diameter of the right lateral aorta is very much greater than the left (Fig. 3).

The topography of the carotids and the lateral aortae are unusual in some clades of Gymnophiona. Studies of developing *Ichthyophis* led Ramaswami (1944) to propose that the third arch, which forms the carotids in other tetrapods, is lost in Gymnophiona and that the fourth enlarges into a systemico-carotid arch, the blood flowing cephalad through the ductus caroticus. In *Hypogeophis rostratus* (Lawson, 1970) and *Idiocranium russeli* (Wake, 1986), a single, large aorta leaves the truncus arteriosus, curves sharply over the apex of the right atrium, and gives rise to the pulmonary artery before continuing caudad as the dorsal aorta (Figs. 2, 3C). There is no confluence with another lateral aorta, evidently one aorta has been lost in this group (Lawson, 1970). The gastrointestinal vasculature arises from the dorsal aorta but the somatic vasculature arises from a combination of locations including the carotids and the dorsal aorta. Both the Old World and New World caecilians show considerable variation in the arrangement of the arterial trunks from the least specialized pattern where the arterial arches are symmetrical to one where either the right or left lateral components are greatly reduced or completely absent (Lawson, 1970). There are few data available on the quality of blood flowing through these vessels or on the ability of the animals to shunt blood within the ventricle, although it is clear caecilians can separate systemic venous and pulmonary venous streams (Toews and Macintyre, 1978). Are there functional underpinnings that can explain this variation? At the very least the diameters of the vessels suggest the volume of blood flowing through the vessels differs.

One hypothesis for the selective pressure driving the design of these circulatory systems is improved efficiency as the lineage underwent elongation of the body (Wilkinson, 1992). Two vessels running in parallel were proposed to have greater resistance to flow than one, larger diameter vessel because

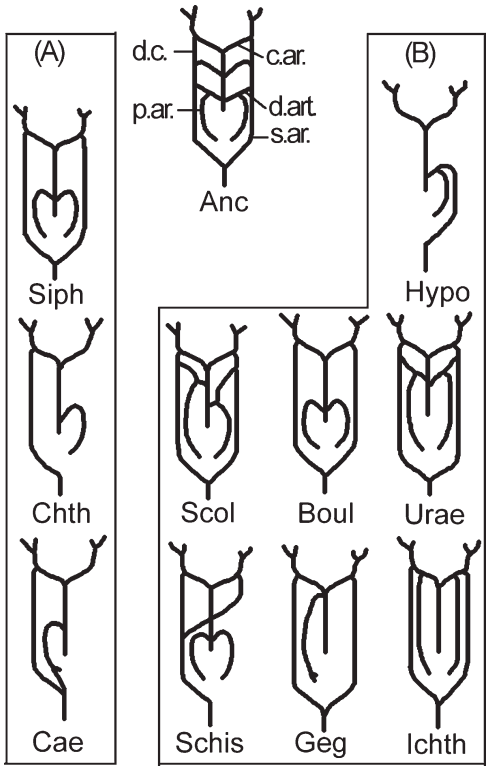

Fig. 2. Caecilian arterial vessels. Line drawings of the arterial arches in caecilians grouped into (**A**) Old-World Genera and (**B**) New-World Genera (after Lawson, 1970). Anc, "ancestral" form; Boul, *Boulengerula*; Cae, *Caecilia*; c.ar., carotid arch; Chth, *Chthonerpeton*; d. art., ductus arteriosus; d.c., ductus caroticus; Geg, *Gegeneophis*; Hypo, *Hypogeophis*; Ichth, *Ichthyophis*; p.ar., pulmonary artery; s.ar., systemic arch; Schis, *Schistometopum*; Scol, *Scolecomorphus*, Siph, *Siphonops*; Urae, *Uraeotyphlus.*

resistance is inversely proportional to the square of the diameter of the vessel. A caveat is that the reciprocal of the total resistance to vessels in parallel is the sum of the reciprocal of the resistance in each vessel. Thus, the capillary beds contribute less to total systemic resistance than the arteries and arterioles in spite of their small diameters because there are so many capillaries arranged in parallel. Nevertheless, Wilkinson (1992) proposed the loss of one of the systemic arches may improve efficiency by requiring less energy to propel the blood and fewer resources to construct the vessels. He reasoned by outgroup comparison that in the ancestral pattern the arterial and pulmonary arches run cephalad until they reach the pharyngeal region and then double back on themselves without giving rise to major anterior vessels and that it would be more efficient if the vessels simply doubled back near the point where they exit the pericardium, as is seen in *Hypogeophis* (Fig. 3).

However, other factors no doubt have influenced the evolution of this topography and some features of the caecilian cardiovascular system might be adaptations for dealing with the high pleuroperitoneal pressures generated during burrowing, which compound the normal stresses vertebrates experience in their arterial walls. Although there are both aquatic (e.g., *Typhlonectes natans*) and terrestrial caecilians (e.g., *Dermophis mexicanus*), all caecilians are specialized to some degree for burrowing; the ability to burrow using concertina locomotion probably arose in the common ancestor to these lineages and has been lost in the aquatic typhlonectids (Summers and O'Reilly, 1997). While burrowing, pleuroperitoneal pressures exceed 275 mmHg in *Dermophis* (O'Reilly et al., 1997), which might place unusual demands on the cardiovascular system (Dickerman et al., 1999; Dickerman et al., 2000; Hatzaras et al., 2007) and may determine whether one aorta functions better than two smaller aortae. The truncus arteriosus as well as the aortae store elastic energy (Gibbons and Shadwich, 1989, 1991) and their wall stresses are proportional to the diameters of the vessels (the law of Laplace). A single large diameter aorta has different biomechanical properties and elastic storage capacity than two smaller aortae. For a given transmural pressure, larger vessels have greater tension in the wall and greater potential to stretch and thereby store elastic energy, but also require relatively stronger walls. Understanding why one aorta was reduced or lost in Gymnophiona may provide insight into the evolutionary transition from two to one aorta that occurred among amniotes.

THE GREAT ARTERIES OF SAUROPSIDS

The arrangement of the great arteries of sauropsids deviates from the piscine and amphibian patterns in several ways. They directly connect to the cardiac ventricle rather than connecting indirectly through the conus arteriosus, so that blood can exit the ventricle through three separate ostia, each containing valves that are generally held in cartilaginous or ossified rings. These ostia lead to the following arteries (Fig. 4): the common pulmonary artery or pulmonary trunk, which typically subdivides into right and left pulmonary arteries and carries blood to the right and left lung, respectively; the left aorta, which usually traverses the left side of the body until it joins with its right moiety to form the dorsal aorta; a third vessel, often referred to as the brachiocephalic artery, that gives rise to the right aortic arch as well as numerous vessels that irrigate the cranial regions of the body. In general, the vascular arrangement of sauropsids is bilaterally less symmetrical than that of anurans and urodeles. For example, in frogs the left subclavian and left carotid arteries appear to receive their blood from the left arch and the right subclavian and right carotid arteries from the complex of the brachiocaphalic and right arch vessels (Fig. 1A). In contrast, in sauropsids the left carotids, left subclavians, and all

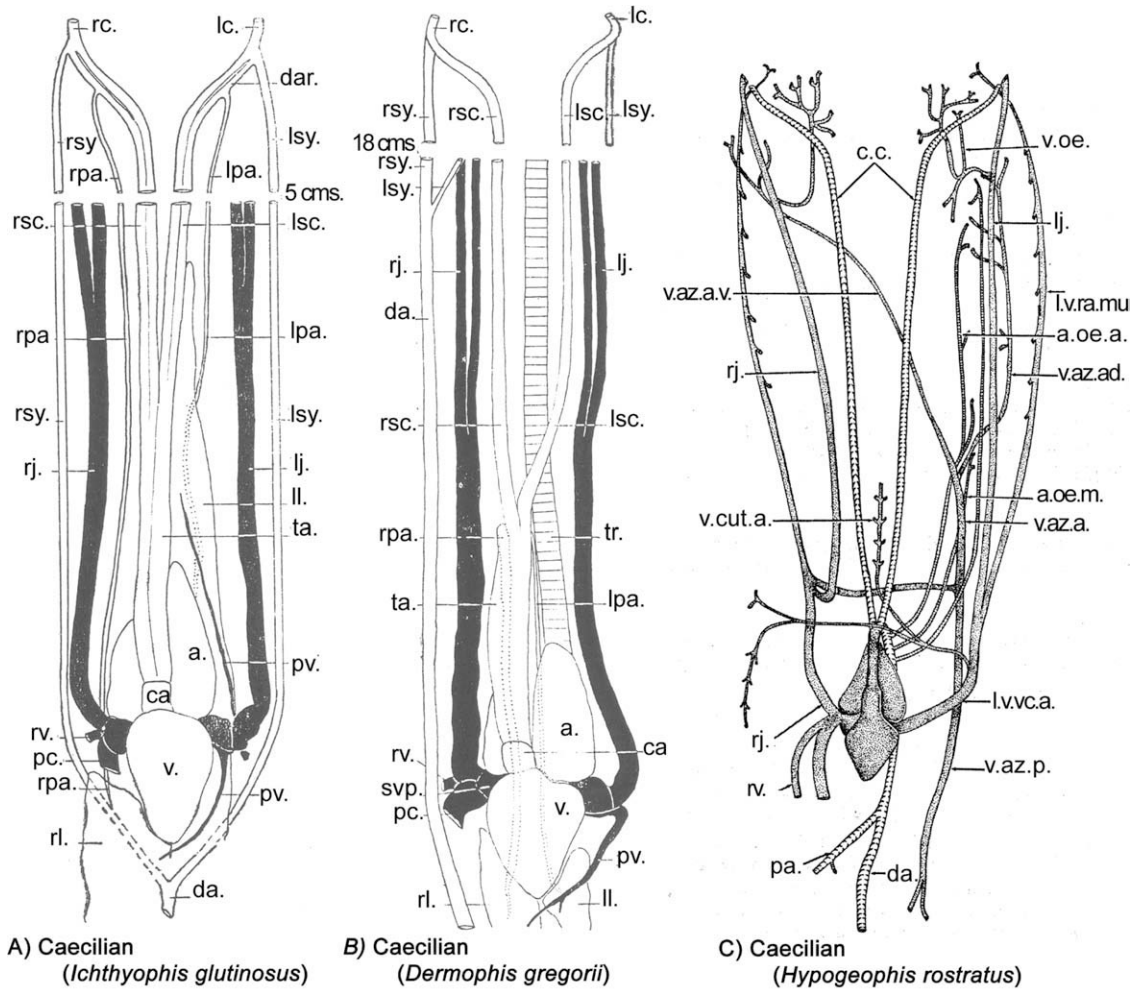

Fig. 3. Illustration of some of the variation that exists in the arterial arches of caecilians. **A**: *Ichthyophis glutinosus* (after Ramaswami, 1944); **B**: *Dermophis gregorii* (after Ramaswami, 1944); **C**: *Hypogeophis rostratus* (after Lawson, 1970). In *Ichthyophis*, the left and right systemic arches (lsy. and rsy.) are symmetrical and join together to form the dorsal aorta (da) caudal to the ventricle (V.). More derived patterns are found in *Dermophis*, in which the left systemic arches converges with the right cranial to the heart and the left arch is smaller than the right, and in *Hypogeophis* in which only one arch is seen. This arch gives rise to the pulmonary artery (pa.). a., atrium; a.oe.a., anterior oesophageal artery; a.oe.m., middle oesophageal artery; ca., conus arteriosus; c.c., common carotid artery; dar., ductus arteriosus; lc., left carotid artery; l.j., left common jugular vein; ll., left lung; lpa., left pulmonary artery; lsc., left subclavian artery; l.v.ra.mu., muscular ramus of left anterior vena cava; l.v.vc.a., left anterior vena cava; pa., pulmonary artery; pc., post caval vein; pv., pulmonary vein; rc., right carotid artery; rl., right lung; rpa., right pulmonary artery; rsc., right subclavian artery; rj., right jugular vein; rv., renal vein; ta., truncus arteriosus; tr., trachea; v., ventricle; v.az.a, anterior azygos vein; v.az.a.d., dorsal branch of anterior azygos vein; v.az.a.v., ventral branch of anterior azygos vein; v.az.p., posterior azygos vein; v.cut.a., vena cutana magna; v.oe., oesophageal vein.

arteries that ramify in the thoracic musculature and glands, such as the thymus, are usually associated with the complex of the brachiocephalic artery and right aorta (Fig. 4). However, some groups [e.g., *Sphenodon*, Iguanidae, Agamidae, Xantusiidae (personal observation)] retain a sizeable connection between the carotids and the systemic arches, the ductus caroticus (Figs. 4A, 5) but others have lost this connection (e.g., Varanidae and Helodermidae, Serpentes, Amphisbaenidae, Chamaeleontidae; Adams, 1953). Thus, in the groups that retain a sizeable ductus caroticus, blood could flow from the left aorta through the left ductus caroticus to reach the carotids, albeit physiological measurements are lacking, and it is not inconceivable that blood might flow the other way around, that is, from the carotids through the ductus caroticus into the left aorta.

In turtles, tuatara, and squamates, the cardiac architecture and the resistance of the outflow tracks underlie the ability of sauropsids to shunt blood, either from the systemic venous return back into the systemic arteries (the right-to-left shunt) or from the pulmonary venous return back into the pulmonary artery (the left-to-right shunt; Hicks, 1998).

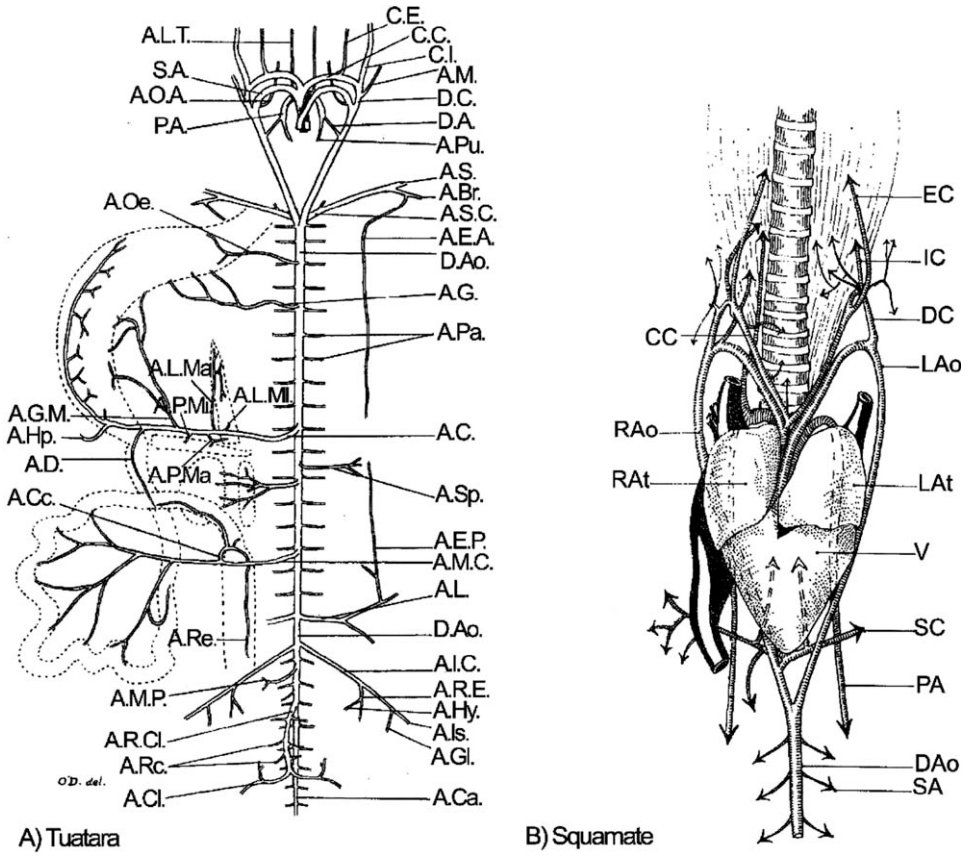

Fig. 4. Illustration of the arterial circulation in limbed sauropsids. **A**: Tuatara (from O'Donoghue, 1919). The left and right aortae are symmetrical, the subclavians (A.S.) are associated with the right aorta and gastrointestinal arteries arise from the dorsal aorta. A.Br., arteria brachialis; A.C., arteria coeliaca; A.Ca., arteria caudalis; A.Cc., arteria coecalis; A.Cl., arteria cloacalis; A.D., arteria duodenalis; A.E.A., arteria epigastrica anterior; A.E.P., arteria epigastrica posterior; A.G., arteria gastrica; A.Gl., arteria glutea; A.G.M., arteria gastrica media; A.Hp., arteria hepatica; A.Hy., arteria hypogastrica; A.I.C., arteria iliaca communis; A.Il.E., arteria iliaca externa; A.Is., arteria ischiadica; A.L., arteria lumbalis; A.L.Ma., arteria lienalis major; A.L.Mi., arteria lienalis minor; A.L.T., arteria laryngeotrachealis; A.M., arteria muscularis cervicis; A.M.C., arteria mesenterica communis; A.M.P., arteria mesenterica posterior; A.O.A., arteria oesophagea anterior; A.Oe., arteria oesophagea; A.Pa., arteria parietalis; A.P.Ma., arteria pancreatica major; A.P.Mi., arteria pancreatica minor; A.Pu., pulmonary arch; A.Rc., arteria recti; A.R.Cl., arteria renocloacalis; A.Re., arteria renales; A.S., arteria scapularis; A.S.C., arteria subclavia; A.Sp., arteria spermatica; C.C., carotis communis; C.E., carotis externa; C.I., carotis interna; D.A., ductus arteriosus (Botalli); D.Ao., dorsal aorta; D.C., ductus caroticus; P.A., pulmonary arch; S.A., systemic arch. **B**: Illustration of a generalized squamate, after Renous (1985). As with the tuatara, the right and left aortae are symmetrical, converge caudal to the ventricle to form the dorsal aorta, which gives rise to the splanchnic vasculature. The subclavians and carotids are associated with the right aorta. However, note the very large diameter of the ductus caroticus connecting the left aorta to left carotid. It is unknown which way blood flows through this duct. CC, common carotid; DAo, dorsal aorta; DC, ductus caroticus; EC, external carotid; IC, internal carotids; LAo, left aorta; LAt, left atrium; PA, pulmonary artery; RAo, right aorta; RAt, right atrium; SA, segmental artery; SC, subclavian artery; V, ventricle.

Furthermore, many of these sauropsids appear to have a capacity to send a large fraction of right-to-left shunted blood, which is oxygen-poor, hypercapnic, and acidic, into the left aorta, and more highly saturated blood into the right aorta (Tucker, 1966; Grigg and Johansen, 1987; Johansen et al., 1987; Ishimatsu et al., 1988; Hicks and Comeau, 1994; Hicks, 1998; Farmer and Hicks, 2002; Farmer et al., 2008). Sauropsids may use their ability to send blood of differing qualities to regions of the body whose biochemical needs differ. For example, the heart and brain are generally intolerant of hypoxia, or at least less tolerant than other tissues (Driedzic and Gesser, 1994; Hochachka et al., 1996). Commonly, the parent artery of the coronaries and the carotids is the brachiocephalic artery or its branches (MacKinnon and Heatwole, 1981). Thus, the brain and the coronaries, the forelimbs, the thymus, the muscles and bones of the thorax may receive less acidic, better oxygenated blood than the viscera, hindlimbs, and tail, which may receive blood containing more carbon dioxide, more acid, and less oxygen.

Several interesting trends in arrangement of the major arteries of sauropsids exist that may relate to this capacity to shunt. First, in limbless sauropsids

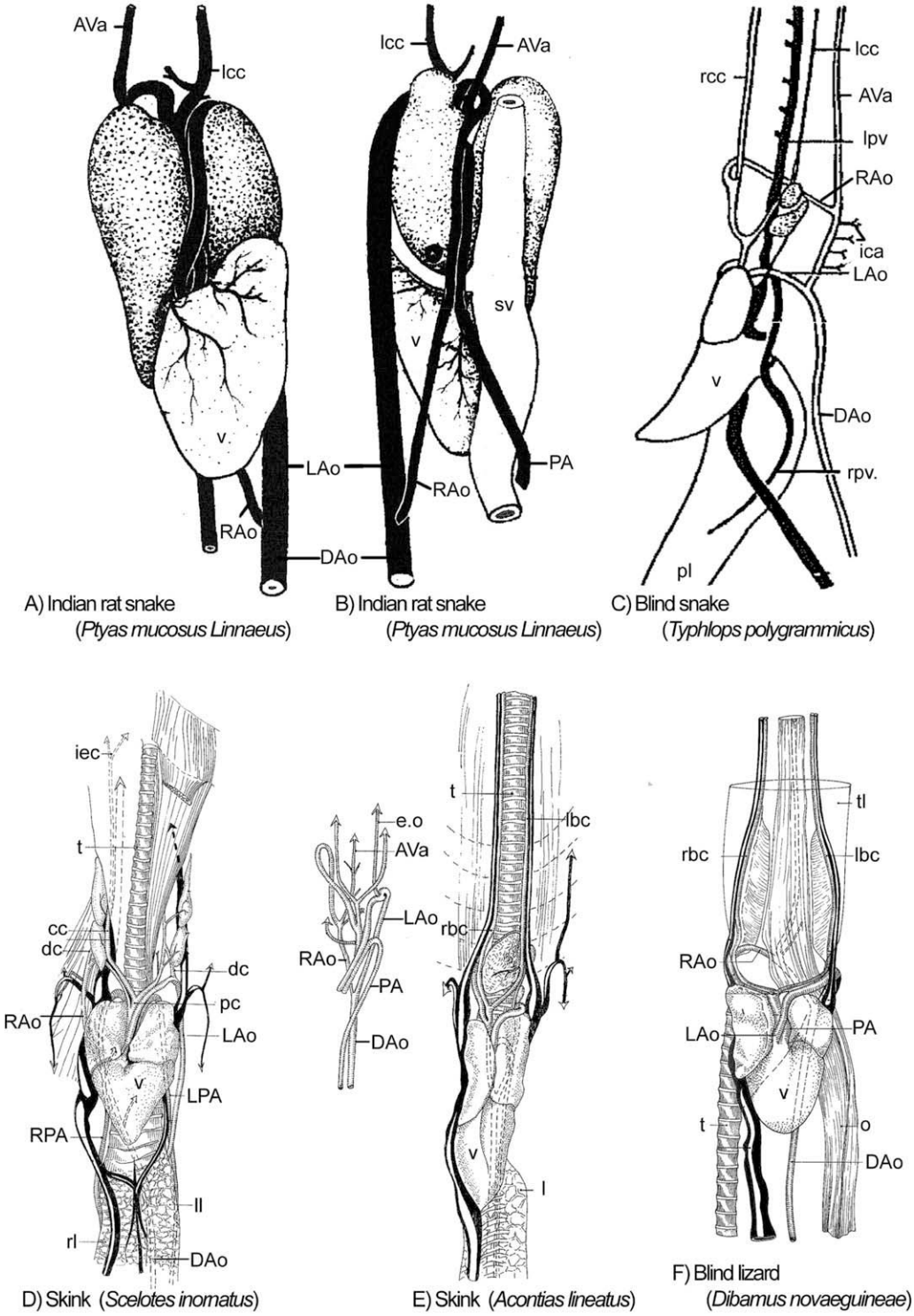

Fig. 5. Arterial circulation in limbless sauropsids (squamates). (**A**) Ventral and (**B**) dorsal views of the arteries of the Indian rat snake, both images were modified from Ray (1934). In this snake the right lung and right pulmonary artery persists but there is no trace of the left pulmonary artery. Furthermore, there is a pronounced asymmetry in the diameters of the left and right aortae at their confluence. (**C**) Ventrolateral view of the heart and arches of the blind snake *Typhlops polygrammicus*, after Robb (1960). The left and right aortae are illustrated as similarly sized vessels and Robb suggests that both lungs are present, the right having shifted cephalad and the left caudad. (**D**) Ventral view of the skinks, *Scelotes inornatus*, after Renous (1985) and (**E**) *Acontias lineatus*, after Renous (1985). *Scelotes* has two lungs of similar size and the left and right aortae are also of similar size whereas *Acontias* has asymmetrical aortae and lungs. The vessels of *Acontias* are also illustrated by the inset with the heart and other organs removed for clarity. (**F**) Ventral view of the limbless blind lizard *Dibamus novaeguineae* after Renous (1985). Like *Typhlops* the right lung may have shifted to lie cephalad to the left lung, but both lungs were perhaps retained. The left and right aortae have similar diameters. AVa, anterior vertebral artery; cc, common carotid; pc, primary carotid; dc, ductus caroticus; e.o., esophageal artery; DAo, dorsal aorta; ica, intercostal arteries; iec, internal and external carotids; l, lung; ll, left lung; LAo, left aorta; lbc, left brachiocephalic; lcc, left common carotid; LPA, left pulmonary artery, lpv, left pulmonary vein; o, esophagus; PA, pulmonary artery; pl, posterior lung; RAo, right aorta; rbc, right brachicephalic; rcc, right common carotid; rl, right lung; RPA, right pulmonary artery; rpv, right pulmonary vein; sv, sinus venosus; t, trachea; tl, tracheal lung; v, ventricle.

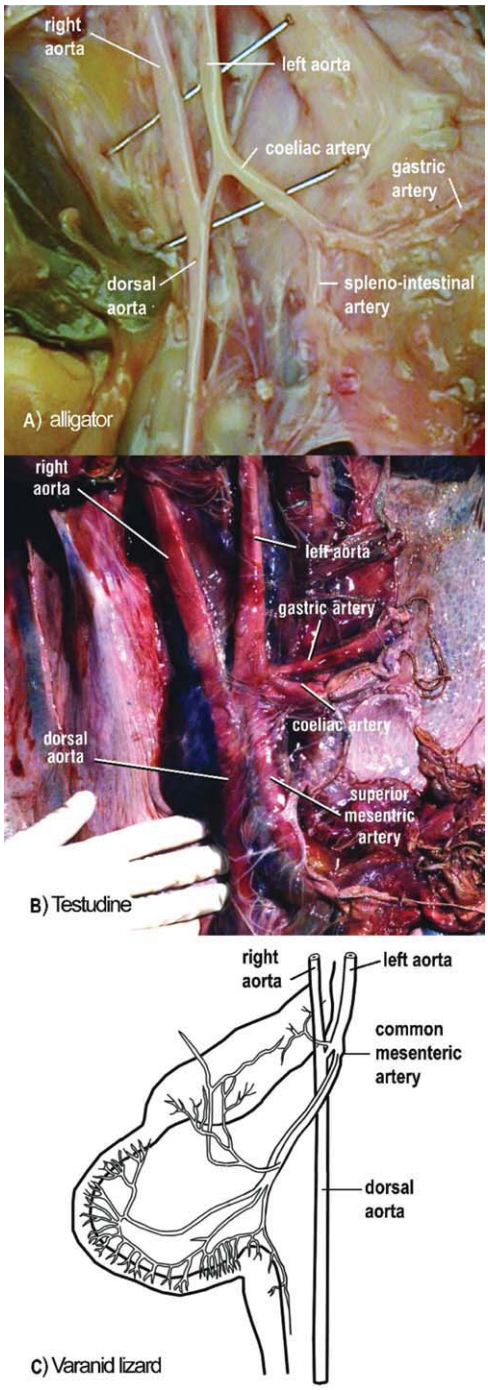

Fig. 6. Confluence of the left and right aortae in limbed sauropsids in which significant portions of the splanchnic vasculature arise from the left aorta. (**A**) crocodilian (*Alligator mississippiensis*); (**B**) testudine (from Wyneken, 2001); (**C**) varanid lizard (*Varanus niloticus*, from Hochstetter (1898); and (**D**) *Hydrosaurus*.

with asymmetrically developed lungs, the diameter of the left aorta is generally significantly greater than the right aorta at their confluence. Second, in at least three lineages of limbed sauropsids (crocodilians, chelonians, lizards of the genera *Varanus*, and to some extent in *Hydrosaurus*) much of the vasculature of the gastrointestinal system arises from the left aorta, rather than from the dorsal aorta (see online material for a list of species included in the analysis).

Limbless Squamates

Limblessness in squamate reptiles has evolved numerous times. Either complete limblessness or limb reduction to varying degrees is found in Serpentes, Pygopodidae, *Dibamus, Anelytropsis, Chasmaesaurus* (loss of forelimbs), Amphisbeanids, three lines of Anguids, and many lines of Gymnophthalmidae (Microteiidae; Gans, 1975). In lizards, limblessness is generally related to a fossorial lifestyle. In all cases, the loss of limbs is accompanied by the evolution of an elongate snake-like body form and often with the reduction or loss of one lung. As previously mentioned, limbless sauropsids repeatedly evolve vascular arrangements that are similar in some caecilians but not in limbed sauropsids. For example, in many limbless squamates the junction of left and right aortae is cranial to the base of the cardiac ventricle (Renous, 1985b; Robb, 1960). Combinations of these characters occur to varying degrees among these lineages, providing functional morphologists and evolutionary physiologists an opportunity to use the comparative method to sort out, which traits are most highly correlated and thereby gain some insight into functional relationships that may underlie this convergent evolution.

Many of these lineages have evolved a highly asymmetrical cardiovascular system (Fig. 6) with respect to the relative diameters of the left and right aortae at their junction, the left aorta being the greater (Renous, 1985b). The diameter of vessels may provide some information on the volume of blood that flows through the vessels; thus more blood appears to flow caudad through the left aorta than through the right. Furthermore, a relatively small pulmonary artery in conjunction with a large right atrium relative to the left atrium is a trait common even in limbed reptiles and gives the impression that less blood flows to the lungs than to the body. Cuvier made this point long ago stating, "The disposition of the heart in Reptiles is such, that at each contraction, a portion only of the blood it has received from the different parts of the body is transmitted to the lungs, the remainder returning to those parts without having passed through the pulmonary organs, and without having respired (Cuvier, 1831)." Ewer (1950) proposed the lungs are not capacious enough to handle the same volume of blood being circulated through the systemic circuit, and that the left aorta functions as an overflow vessel. Although she was referring primarily to the left aorta of crocodilians, her reasoning applies equally well to

other sauropsids, some of which are known to reduce pulmonary blood flow at times. As Baron Cuvier surmised, during periods of calm apnea sauropsids can develop a right-to-left shunt, where some of the systemic venous return is directed into the systemic aortas rather than into the pulmonary artery. For example, in resting pythons the systemic circulation receives about twice as much blood as the pulmonary circulation (Starck, 2009). In animals that can right-to-left shunt, the left aorta often receives more of the shunted blood than the right aorta (Tucker, 1966; Grigg and Johansen, 1987; Johansen et al., 1987; Ishimatsu et al., 1988; Hicks and Krosniunas, 1996).

The right-to-left shunt is thought to reduce pulmonary edema (Burggren, 1982) and thus the loss or reduction of one lung, without a compensatory increase in the vasculature of the other lung, would presumably increase the importance of the role of the left aorta as an overflow vessel. This hypothesis predicts that the diameter of left arch will exceed that of the right in such lineages, a prediction that has support among limbless forms. For example, the cardiopulmonary systems of boids, pythons, and *Xenopeltis* are more primitive than those of most other snakes in several respects, including the persistence of two lungs with lesser asymmetry in size than seen in other snakes, the retention of a left pulmonary artery and a right common carotid in the neck, and left and right aortae of similar diameters (Butler, 1895; Bellairs and Underwood, 1951). Greater asymmetry in both the development of the lungs and in the diameters of the aortae is seen in most other snakes, with the diameter of the left aorta measuring over three-fold greater than the right in some Colubridae and Crotalinae (Fig. 5; Beddard, 1904; Ray, 1934; Van Bourgondien and Bothner, 1969).

Blind snakes of the family Typhlopidae could corroborate or refute the general pattern just discussed. These are small animals that are specialized for a subterranean life and are considered by many to retain a number of primitive characters (Coates and Ruta, 2000). Although several authors state that Typhlopidae have only one lung (Butler, 1895; Waite, 1918), Robb (1960) argues convincingly that *Typhlops* have two functional lungs. Whereas in pythons the right and left lung have similar stoutness and lie side by side in the body cavity, Robb suggests the right lung of *Typhlops* has been displaced behind (caudal) the left (Robb, 1960). Robb furthermore notes that in lineages that have the left lung suppressed, the left pulmonary artery no longer exists, whereas the left pulmonary artery can be traced to the anterior lung and the right pulmonary artery to the posterior lung of *Typhlops*. Robb's illustration of the cardiovascular system of *T. polygrammicus* shows symmetrical aortae at the confluence, which occurs cranial to the ventricle. This correlation of two functional lungs and symmetrical aortae is consistent with the overflow hypothesis of Ewer (1950).

The positive correlation between reduction of a lung and an enlarged left aorta relative to the right occurs in limbless lizards, Amphisbeanidea, Rhineuridae, Bipedidae, Trogonophidae, and Dibamidae (Renous, 1985a,b). For example, Amphisbeanids are burrowing lizards with elongated body forms, generally without limbs or with greatly reduced limbs. They have a smaller right lung than left, which is unusual, in Gymnophiona, snakes, and most snake-like lizards there is a reduction in the left lung rather than the right (Butler, 1895). Butler examined 12 species of amphisbeanids and found the least asymmetry in the length of the lungs in *Trogonophis wiegmanni* with the right lung measuring 60% of the left. In most of the other species studied, and *Amphisbaena alba* and *Blanus cinereus* were among them, the right lung was rudimentary (Butler, 1895). *Trogonophis* also have a more symmetrical arrangement of the left and right aortae than do other amphisbeanids. Renous (1985) found that the differences among *Trogonophis wiegmanni*, *Rhineura floridana*, and the Amphisbaenidae (*Amphisbaena alba*, *Blanus cinereus*, *Cadea palirostrata*) are an increase in the asymmetry between the two aortic arches both in terms of their length and in terms of the difference in their diameters (the left is always the larger), and a cranial shift in the position of the point of junction from caudal to the heart to one dorsal to the cranial end of the left atrium (Renous, 1985a). Thus, in this lineage there again appears to be a trend for those members with a rudimentary lung to have a larger left aorta compared to the right at the point of their junction. An argument similar to that used for the snake *Typhlops* may apply to the lizard *Dibamus*, as the arrangement of the lungs is very similar (Greer, 1985). Although it is stated that *Dibamus* has but one lung, the left pulmonary artery runs cephalad to the lung, which is located on the left side of the body, whereas the right pulmonary artery runs caudad to the lung, which is located on the right side of the body, suggesting the left lung has been displaced in front of the right (Greer, 1985). In *Dibamus,* the pulmonary artery bifurcates into well developed and similarly sized left and right pulmonary arches and both the left and right systemic arches are reported to be well developed (Greer, 1985) and are illustrated to be similar in size (Renous, 1985a), again consistent with Ewer's suggestions. Lizards of the Scincidae family also appear to fit this pattern. For example, the burrowing skink, *Scelotes inornatus*, has both a well developed left and right pulmonary arch and left and right aortae with similar diameters at their confluence (Renous, 1985a) and, although I could find no information on the development of the lungs, a congener, *Scelotes bipes*, is reported to

possess nearly symmetrical lungs (Butler, 1895). Similarly, the striped legless skink, *Acontias lineatus,* is shown to have but one pulmonary arch and highly asymmetrical left and right aortae (Renous, 1985a) and a congener, *Acontias meleagris*, is reported to have highly asymmetrical lungs (Butler, 1895).

Members of the Pygopodidae are largely nocturnal and fossorial, with no trace of forelimbs and atrophied or non-existant hindlimbs (Underwood, 1957). The vascular anatomy of this group has been partially described by Underwood (1957). Unfortunately, Underwood does not illustrate or comment on the relative sizes of the aortae, nor illustrate the point at which they join. However, it is noted that the length of the left lung varies with respect to the right depending on lineage (Underwood, 1957) and therefore it would be interesting to investigate whether there is a more marked asymmetry in the diameters of the aortae in species with more asymmetrical lungs.

Limbed Sauropsids

In general, the arterial topography of limbed sauropsids has the following features: 1) the diameters of the left and right aortae at their point of confluence are similar, and the confluence is located near or caudal to the apex of the cardiac ventricle; 2) the vessels that supply the gastrointestinal and posterior somatic circulations arise from the dorsal aorta (Supporting Information Table 1, Fig. 4). Although it is not uncommon for either the right or left aorta to give rise to small vessels that irrigate the esophagus and sometimes even offshoots of the pulmonary artery supply blood to the esophagus, the bulk of the digestive organs (e.g., stomach, liver, and intestine) are supplied from stout vessels originating from the dorsal aorta. However, in three lineages of limbed sauropsids a marked asymmetry was found in which a substantial portion of the vasculature that supplies regions of the digestive viscera, especially the stomach, liver, pancreas, spleen, and small intestine, arises from the left aorta rather than the dorsal aorta (Fig. 6). This pattern was observed in all testudines, all crocodilians, and all monitor lizards examined. It was not found in *Heloderma suspectum* (Beddard, 1906). I could not find information on the sole extant species of the genus *Lanthanotus*. The gastrointestinal vessels do not arise from left aorta in *Sphenodon* or in species from most squamate families examined (Table 1, Fig. 7), with the exception of one agamid, *Lophiura amboinensis* (Hochstetter, 1898). A current synonym for *L. amboinensis* is *Hydrosaurus amboinensis*. The pattern is not present in any of the descriptions of this vasculature of the other 19 agamids described by Hochstetter, and other studies of agamids report that the dorsal aorta gives rise to gastrointestinal vasculature (Duda, 1974). *H. amboinensis* is the largest of the agamid lizards, growing to over a meter in total length. Thus, among squamates this pattern appears unique to the genus *Varanus* and to one agamid.

Hypothesis for Why Varanids, Crocodilians, and Chelonians Differ from Other Sauropsids?

What functions could underlie the shift in the origin of the gastrointestinal arteries from the dorsal aorta to the left aorta in these three clades (crocodilians, chelonians, monitor lizards)? Do they share some feature of their life history that makes functional sense with the vascular pattern? Although many life-history correlates seem to fit two of the three clades, few fit all three. For example, a semiaquatic lifestyle immediately comes to mind when thinking about crocodilians and testudines, but it appears the direct ancestry of monitor lizards was terrestrial (Molnar, 2004). A caveat is that the fossil record of this lineage is not without gaps and so it is possible a direct aquatic ancestor existed but no remains have been discovered. Similarly, both crocodilians and some testudines lay heavily calcified eggs but monitors do not, and there are other squamates without the asymmetry that do.

The one life-history trait I can think of that is shared by all three clades is that some members of these lineages attain a relatively large body size and therefore grow quickly. Most lizards are small animals, for example 80% of extant lizard species weigh <20 g (Pough, 1980). The largest land living lizards all belong to one clade, Platynotans, containing three extant Genera: the North American Gila monsters and beaded lizards (family Helodermatidae, genus *Heloderma*); the earless monitor of Borneo (family Varanidae, genus *Lanthonotus*) and the monitors (family Varanidae, genus *Varanus*). Lizards of the genus *Varanus* vary greatly in size. For example, *V. brevicauda* are 20 cm in total length and weigh 8–10 g (Pianka, 2004). At the other end of the spectrum, the komodo dragon (*Varanus komodoensis*) is the largest of the living lizards weighing up to 70 kg and reaching 3 m, but an extinct member of the varanidae family, *Varanus prisca*, reached 7 m in length and is estimated to have weighed up to 620 kg, ~8–9 times the mass of the Komodo dragon (Rich et al., 1985). *Varanus sivalensis*, also extinct, reached a size similar to the Komodo dragon (Molnar, 2004). Furthermore, some of the marine platynotans, such as mosasaurs, were giants, reaching 15 m in length (*Hainosaurus*; Molnar, 2004). Although platynotans display a range of body sizes, the group contains many members that are considerably larger than other lineages of lizards and the direct ancestral lineage of monitors is thought to have been

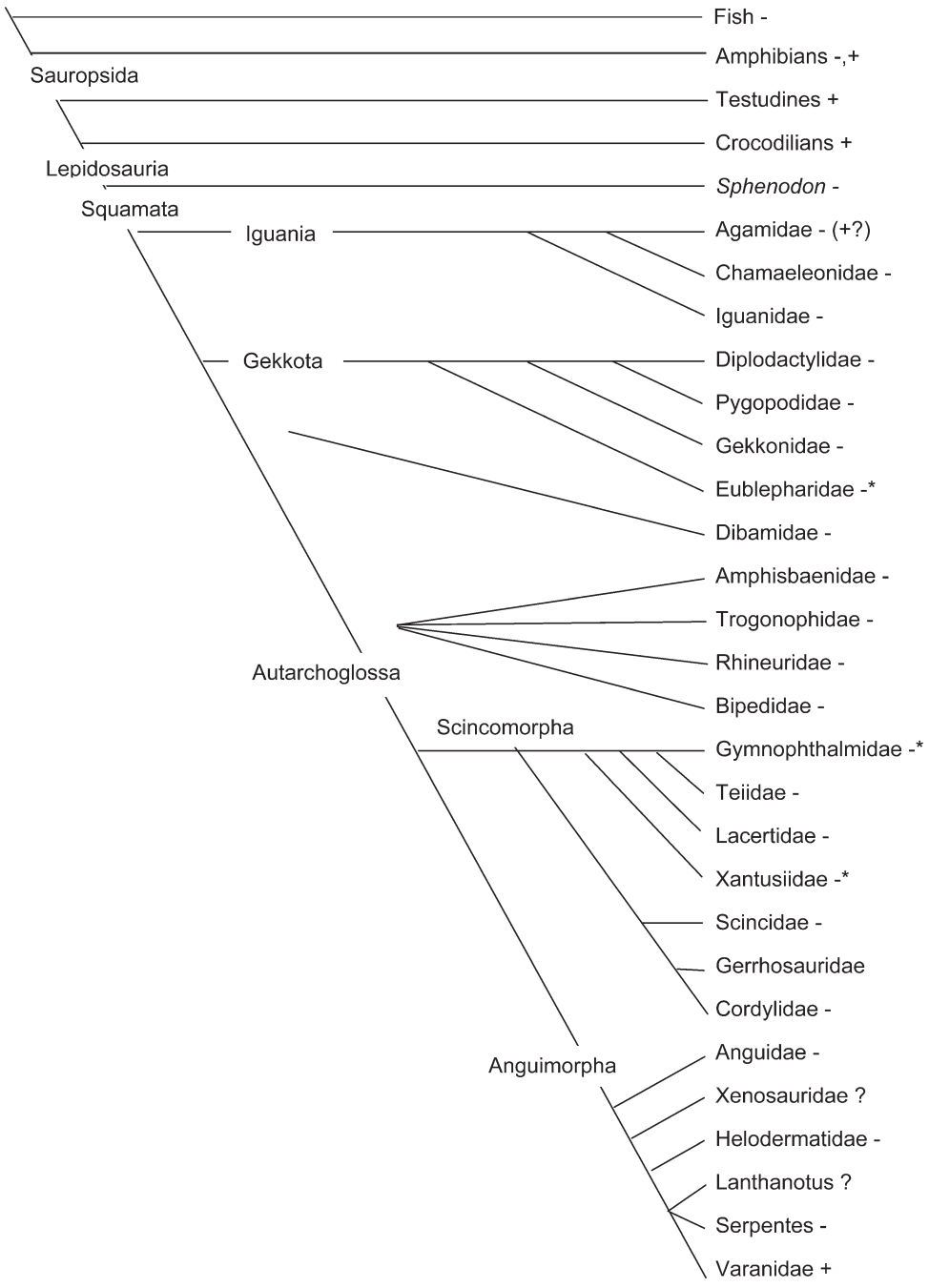

Fig. 7. Phylogenetic relationships of ectothermic sauropsids, modified from Pianka and Vitt (2003). +, substantial vessels arise from the left aorta and ramify in the gastrointestinal system other than the esophagus; −, splanchnic vasculature arises from the dorsal aorta. Sources are provided in Table 1.

relatively large (Pianka, 2004). As with platynotans, many testudines reach a large body size. The biggest leatherbacks are reported to reach 2.4 m in total length and weigh 916 kg (Eckert and Luginbuhl, 1988). However, *Archelon*, an extinct lineage, grew to 4.6 m and probably weighed as much as 2,700 kg (Wieland, 1896, 1904; Hay, 1908). Extinct crocodilians were also giants, for example, *Sarcosuchus imperator* is estimated to have been 11–12 m long and to weigh about 8,000 kg (Sereno, 2001). Thus, these lineages are distinct in attaining body sizes that are 4–5 orders of magnitude greater than most species of lizards. Could this vascular pattern enable or predispose these particular lineages to have evolved a body size larger than the 10–20 g commonly seen in lizards?

Large animals grow absolutely faster than small animals (Case, 1978) and so these lineages may have undergone more intense selection on the vascular topography to enhance rapid growth than smaller bodied sauropsids. Growth entails an increase in both bony and soft tissues, but the processes involved are distinct and the quality of blood that promotes the growth of bone can differ from that which promotes the formation of soft tissues. Whereas soft tissues grow through a multiplicative process, bones grow by accretion where new material is mineralized and cannot contribute to the formation of subsequent tissue; consequently soft tissue can grow much faster than bone (Cubo et al., 2008). There are several modes of bone growth, and the mode used by a lineage determines maximal rates of growth. In fast growing crocodilians and leatherback turtles a type of bone, a woven bone, is formed that is similar to bone found commonly in fetal and very young mammals (Enlow, 1962, 1969). In some animals accretional growth is achieved only at the external surface of the bone shaft, but in other cases there is also osteonal growth, that is, large cavities within the bone cortex grow centrifugally and become filled by centripetal apposition of bone to form primary osteons, for example, the femora of varanids and crocodilians (Cubo et al., 2008). Primary osteons are also found in the cortical bone of the carapace of large turtles (Scheyer and Sanchez-Villagra, 2007). Osteonal growth is more common in large, fast growing animals, and animals with a high resting metabolic rate (de Buffrénil et al., 2007; Cubo et al., 2008). The bones of lizards and snakes are notable because their compact bone is virtually nonvascular, and it has been suggested that avascular tissues are the result of slower rates of growth (Enlow, 1969). A study of cortical vascularization in 20 monitor species supports this view because bone cortical vascularization was lacking in all species with a snout vent length of $<$398 mm but larger species (460–1,170 mm snout vent length) had vascular canals, and beyond that threshold vascular density increased linearly with size (de Buffrénil et al., 2007; Cubo et al., 2008). De Buffrénil et al (2007) conclude that vascular density reflects absolute growth rates of bone cortices. However, this correlation may not be causative (Starck and Chinsamy, 2002).

The organization of the vasculature has considerable potential to relate to bone growth because extracellular pH and oxygen tension affect bone formation and resorption by several mechanisms (Jackson et al., 2000; Arnett, 2007, 2008). Low pH has a deleterious action on bone caused by a physicochemical dissolution of bone mineral. However, pH also appears to directly regulate bone resorption. Cell culture experiments in mice have shown that osteoclasts are nearly inactive at pH 7.4 but that their activity increases steeply with decreasing pH, reaching a plateau at about pH 6.8, and this sensitivity of osteoclasts to pH has also been documented in birds and humans. Changes in pH of only a few hundredths of a unit can double osteoclast activity (reviewed in Arnett, 2007). Furthermore, hypoxia profoundly stimulates osteoclast formation from precursor blood cells and inhibits the activity of osteoblasts. Thus, acidic, hypoxic blood, such as that returning to the heart in the systemic venous return, can inhibit the formation of bone, stimulate bone resorption (Arnett, 2007, 2008), and can even chemically dissolve bone (Jackson et al., 2000).

In contrast, systemic venous blood may aid a number of biosynthetic processes carried out by the liver, stomach, and other organs of digestion because it contains more carbon dioxide and bicarbonate ions than blood that has passed through the lung (Fig. 8). In the acid and base secreting cells of the gastrointestinal system, the enzyme carbonic anhydrase hydrates CO_2 to form a bicarbonate ion (HCO_3^-) and acid (H^+). In the stomach the H^+ is pumped into the gastric lumen whereas in base producing cells of the liver, pancreas, and small intestine the HCO_3^- enters the duodenal lumen to neutralize the acidic chyme. Although the acid and base secreting cells themselves are internally generating CO_2, it appears from both in vivo and in vitro studies that maximal rates of secretion of acid or base depend on an external (blood-borne) supply of CO_2 (Kidder and Montgomery, 1974; Flemström, 1980; Simson et al., 1981; Kuijpers et al., 1984; Schiessel et al., 1984; Grotmol et al., 1987; Holm et al., 1990; Glauser et al., 1995a,b; Flemström and Isenberg, 2001; Furukawa et al., 2005; Farmer et al., 2008). In addition, base secreting cells, such as the duodenal enterocytes, import HCO_3^- from the blood at their basolateral membrane by a Na^+–HCO_3^- cotransport mechanism and then export the HCO_3^- into the lumen by Cl^-–HCO_3^- exchange. Furthermore, base secretion, which has been studied in a wide range of species, seems to show very little variation with species (Flemström and Isenberg, 2001). Thus, broadly speaking, maximal rates of acid and base secretion in vertebrates rely on blood-borne CO_2 to supplement that being produced locally. Therefore, an important, and perhaps underappreciated, function of the cardiovascular system is to transport CO_2 from tissues where it is produced in excess, such as muscle, to organs where the CO_2 can be used for synthesis, such as the acid or base producing cells of the stomach and the liver. As previously mentioned, when sauropsids develop a right-to-left shunt where some of the systemic venous return is directed back into the systemic aortae instead of the pulmonary artery, there is a tendency for the left aorta to receive more of the shunted blood than the right. Thus, blood in the left aorta can be more acidic, contain less oxygen,

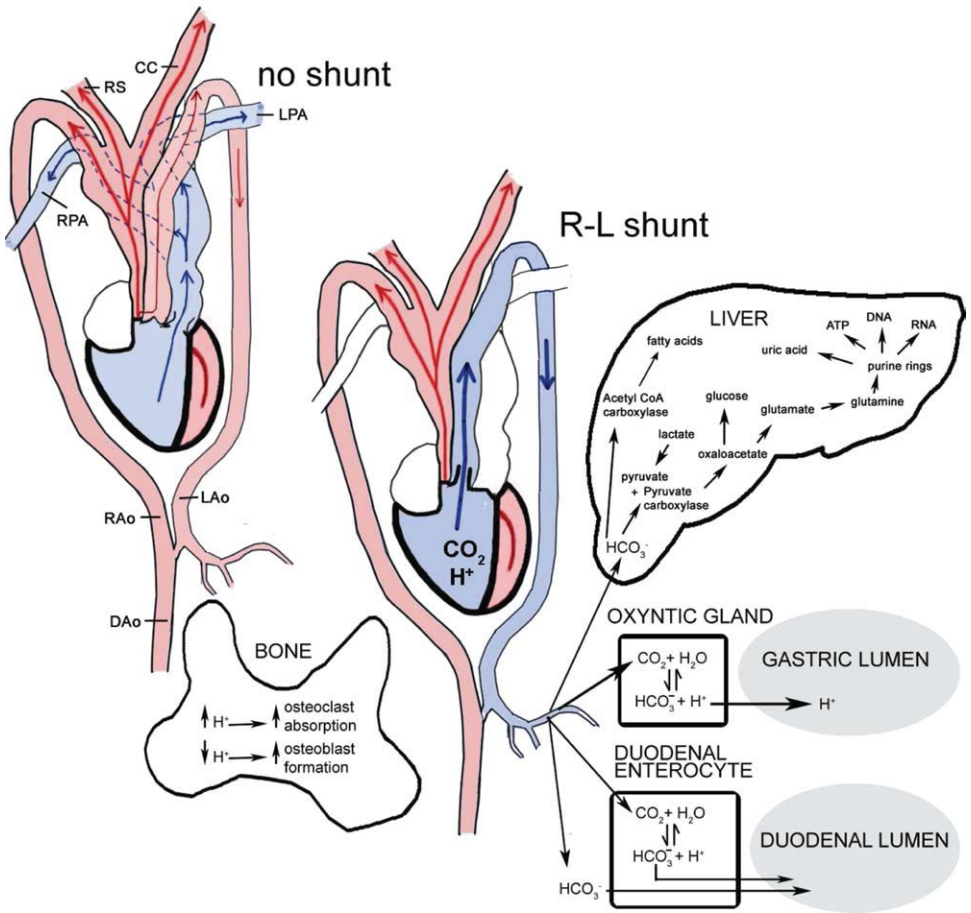

Fig. 8. Schematic of putative benefits of directing right-to-left shunted blood, which is more generally more acidic, hypercapnic, hypoxic blood than blood that has passed through the lung and undergone gas exchange, into the left aorta rather than into both systemic arches. If the left aorta is the parent vessel for most of the gastrointestinal vasculature, this blood may provide carbon dioxide as a substrate for the synthesis of gastric acid, base, fatty acids, glucose, and purine rings. In contrast, acidic hypoxic blood can dissolve bone, inhibit deposition, and stimulate resorption. Thus directing less acidic blood into the right aorta might facilitate bone formation in fast growing species. Common carotid, CC; dorsal aorta, DAo; left aorta, LAo; left pulmonary artery, LPA; right aorta, RAo; right pulmonary artery, RPA; right subclavian, RS.

have a greater tension of carbon dioxide, and contain a greater concentration of bicarbonate ions than blood in the right aorta. If right-to-left shunted blood is preferentially directed into the left aorta and thus to the gastrointestinal vasculature, then this anatomy may promote the formation of both acid and base.

Besides acid and base formation, there are many other synthetic reactions of digestion and growth carried out in the gastrointestinal system that require either carbon dioxide or bicarbonate ions (Fig. 8). Some of these pathways are detailed below, but it is important to realize that what follows is not a comprehensive review of the role of CO_2 in synthetic pathways. It only highlights the importance of CO_2 in the syntheses and processing of amino acids, the synthesis of fatty acids, the synthesis of glucose from lactate, and the formation of purine rings, which are requisite for the production of ATP, RNA, DNA, hemoglobin, and uric acid. Two key regulatory enzymes, both biotin carboxylases and both found in abundance in the liver, require the binding of a bicarbonate ion to catalyze irreversible carboxylations; one is the committed step in the synthesis of fatty acids and the other is important in the synthesis of the intermediate oxaloacetate. The first enzyme, Acetyl-CoA carboxylase, must bind a bicarbonate ion to catalyze the irreversible carboxylation of acetly-CoA to form malony-CoA, a substrate in the biosynthesis of fatty acids (Wakil, 1989; Stryer, 1995). The second enzyme, pyruvate carboxylase, must bind bicarbonate to irreversibly catalyze the carboxylation of pyruvate to form oxaloacetate. Oxaloacetate is important in protein metabolism and in the synthesis of glucose.

After studying the composition of free amino acids in various tissues of the body before and after feeding Coulson and Henandez (1967) conclude, "In a young cayman growing rapidly, the demand

for essential amino acids for protein synthesis is almost insatiable." For example, after feeding total plasma free amino acids increased about 10-fold over fasting values and 85% of this increase was due to three amino acids: glutamine, glycine, and alanine (Coulson and Hernandez, 1967b). Furthermore, an even greater increase in these amino acids occurred in other tissues; in liver, glutamine increased 30-fold over fasting levels. Since the amino acid composition of fed and fasted crocodilians does not resemble that of the food eaten, synthesis is responsible for the amino acid composition that was measured subsequent to feeding (Coulson and Hernandez, 1967a, 1983a) and CO_2 plays an essential role in the synthesis of glutamine and glycine.

One of the most important reactions for the incorporation of CO_2 into tissue is the reaction of CO_2 with pyruvate to form oxaloacetate and the subsequent formation of α-ketoglutarate, which contains the assimilated carbon (Delluva and Wilson, 1946; Coulson and Hernandez, 1983b; Stryer, 1995). Alpha-ketoglutarate plays an important role in the processing of proteins; the α-amino group of many amino acids is transferred to α-ketogluterate to form glutamate. Glutamate can react with ammonia with the help of glutamine synthetase to yield glutamine. Coulsen and Hernandez (1983) report that the ability of the liver of lizards to convert CO_2 and pyruvate to glutamine is "without precedence" in that liver glutamine concentrations were increased 30-fold when the animals were given pyruvate. Furthermore, the reaction of CO_2 with pyruvate and the formation of oxaloacetate can be stopped in caiman and lizards by giving a carbonic anhydrase inhibitor; carbonic anhydrase is the enzyme that hydrates CO_2 to form a bicarbonate ion and water (Coulson and Hernandez, 1983b). Thus, the hydration of CO_2 is necessary for this reaction to occur in vivo in crocodilians. In addition, Coulson and Hernandez (1983) state that inhibition of carbonic anhydrase adversely affects the resynthesis of glucose from lactate by its inhibition of the formation of oxaloacetate. The amount of lactate generated by reptiles during exercise, and thus their need to convert lactate back to glucose, is positively correlated with body size (Bennett et al., 1985). Glutamine is an important player in integrative metabolism, serving acid-base homeostasis, in the synthesis of amino sugars, in intraorgan transport, red blood cell metabolism, and the formation of purine rings (Krebs, 1980; Campbell, 1991; Nihara et al., 1998). Purine rings are components of DNA, RNA, ATP and hemoglobin (Stryer, 1995) and CO_2 contributes to their formation, with the carbon of the carbon dioxide located at C6 of the purine ring (Stryer, 1995). Furthermore, uric acid synthesis is similar to the basic biosynthetic pathway for purines (Campbell, 1991).

In summary, although CO_2 is traditionally viewed as a waste product of metabolism and it is thought that the cardiovascular system functions to transport it from the tissues where it is produced to organs where it can be eliminated from the body (e.g., gills, skin, lungs), CO_2 is requisite to a number of biosynthetic processes—such as the synthesis of gastric acid, duodenal base, fatty acids, amino acids, purine rings, and glucose. The viscera (e.g., liver, stomach, small intestine) are important organs for this synthesis. During periods of digestion, it appears the needs of these organs for CO_2 cannot be met by the metabolism of their own cells and thus require the circulatory system to bring them CO_2 that has been produced by the metabolism of tissues elsewhere in the body, such as the skeletal muscle. Hence, the vascular pattern where the left aorta is the parent vessel for the major gastrointestinal arteries (e.g., testudines, crocodilians, and monitors) may facilitate growth by enabling animals in these lineages to direct blood with differing pH, carbon dioxide, and oxygen tensions to growing bones than to the gastrointestinal viscera (Fig. 8). Although it is true large snakes also grow rapidly, they of course no longer need to grow the femur and other bones of the appendicular skeleton, nor do they need to grow a carapace or plastron. Furthermore, I suspect fast growing sauropsids that experience large temperature fluctuations have the greatest need for this separation of bloodstreams.

The importance of temperature to the biochemical processes of digestion cannot be overstated and the effects of temperature may underpin the reason animals with a more constant body temperature, such as mammals and birds, do not need the capacity to direct venous blood to the gastrointestinal system, with the exception of the liver by means of the hepatic portal circulation. Temperature is important in three ways. 1) Temperature affects the rate of activity of enzymes as well as, albeit to a much lesser degree, the rate of non-enzymatically mediated chemical reactions. 2) Ectotherms have a low rate of CO_2 production. When measured at the same body temperature as a mammal of equal body size, ectotherms produce about an order of magnitude less carbon dioxide per gram of body tissue, and this metabolic rate drops even further with temperature (Coulson and Hernandez, 1959; Grigg, 1978). 3) Temperature has a pronounced effect on the driving force for diffusion of carbon dioxide. The carbon dioxide tension (PCO_2) in plasma decreases by about 1.8 mmHg for a drop in temperature of 1°C (Robin, 1962; Reeves, 1976). For example, in fasting America alligators a decrease in body temperature from 30°C, which is their preferred body temperature during digestion (Farmer et al., 2008), to 20°C caused arterial PCO_2 to decrease from 31 to 18 mmHg. The low driving force for CO_2 diffusion

may be particularly troublesome given the rapid synthesis of tissues seen in reptiles postprandially (Starck et al., 2007). Shunting hypercapnic blood to the gastrointestinal system could help compensate for this decrease in CO_2 tension with temperature. Thus fast growing ectotherms with constraints on their ability to maintain their preferred body temperature during digestion may have greater need to conserve CO_2 than slow growing ectotherms with a more equable body temperature. It has been hypothesized that the selective advantage of endothermy in birds and mammals is that being warm during periods of development and growth shortens the interval of time between when animals are conceived and when they reach sexual maturity (Farmer, 2000, 2001, 2003). The idea that the fastest growing lineages of sauropsids have specializations of the vasculature that may help them compensate for lowered body temperatures during periods of digestion, and that these specializations are not needed in both endothermic lineages, is consistent with the hypothesis that the selective benefit of endothermy is growth and reproduction.

CONCLUSION

The aims of this manuscript were to compile information on the organization of the major arteries of sauropsids, to frame working hypotheses about the possible interplay between shunts and this topography, and to highlight areas in need of further experimental work. A limitation of this study is the number of species examined relative to the total in existence. Observations of ~150 sauropsid species spanning 26 families where included in this analysis (see online material), but this number is small compared to the total number of extant sauropsid species in existence. Further observations on additional species might reveal variations on the themes I have discussed; thus descriptions of the vasculature of addition species are needed. Another limitation of the study is that any errors arising from the original descriptions of the vasculature or identification of species have been incorporated into my analysis. Finally, the anatomy has been used to formulate hypotheses about the factors that underlie the patterns observed, but now these hypotheses need testing. To test these hypotheses measurements are needed on the quality and quantity of blood ejected into the pulmonary artery, the right aorta, and the left aorta in a wide range of species and under different physiological states (fasting, while digesting, at different temperatures, while recovering from an exercise induced acidosis, etc.). Additionally, studies are needed of growth rates and bone formation that take into account this vasculature and patterns of blood flow.

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