Cardiovascular dynamics in *Crocodylus porosus* breathing air and during voluntary aerobic dives

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Summary. Pressure records from the heart and outflow vessels of the heart of *Crocodylus porosus* resolve previously conflicting results, showing that left aortic filling via the foramen of Panizza may occur during both cardiac diastole and systole. Filling of the left aorta during diastole, identified by the asynchrony and comparative shape of pressure events in the left and right aortae, is reconciled more easily with the anatomy, which suggests that the foramen would be occluded by opening of the pocket valves at the base of the right aorta during systole. Filling during systole, indicated when pressure traces in the left and right aortae could be superimposed, was associated with lower systemic pressures, which may occur at the end of a voluntary aerobic dive or can be induced by lowering water temperature or during a long forced dive. To explain this flexibility, we propose that the foramen of Panizza is of variable calibre. The presence of a 'right-left' shunt, in which increased right ventricular pressure leads to blood being diverted from the lungs and exiting the right ventricle via the left aorta, was found to be a frequent though not obligate correlate of voluntary aerobic dives. This contrasts with the previous concept of the shunt as a correlate of diving bradycardia. The magnitude of the shunt is difficult to assess but is likely to be relatively small. This information has allowed some new insights into the functional significance of the complex anatomy of the crocodilian heart and major blood vessels.

Abbreviations: bpm beats per minute; *LAo* left aorta (aortic); *LV* left ventricle (ventricular); PA pulmonary artery; *RAo* right aorta (aortic); *RV* right ventricle (ventricular); SC subclavian artery.

Introduction

The anatomical peculiarities of the heart of extant crocodilians have attracted the interest and curiosity of functional morphologists for more than 150 years (Panizza 1833; Fritsch 1869; Sabatier 1873; Greil 1903). Alone among reptiles in having complete separation of left and right ventricles, such as seen in birds and mammals, they also possess two features which are uniquely crocodilian: the left systemic aorta derives not from the left ventricle, but from the right, alongside the main pulmonary arterial trunk, while the foramen of Panizza affords an opportunity for communication between the right and left aortae, at their bases. A detailed review of crocodilian cardiac anatomy in general, and of *Crocodylus porosus* in particular, was given by Webb (1979). The most recent reviews of functional interpretations of the cardiac anatomy are by White (1976), Johansen (1979, 1985), Johansen and Burggren (1980) and Burggren (1985).

Early functional interpretations of the crocodilian cardiovascular anatomy proposed that the left aorta would receive deoxygenated blood (Goodrich 1919) so that the dorsal aorta distal to the confluence of left and right would contain mixed blood. Functional interpretation based on physiological observations has revised substantially that early interpretation. White (1956) found in *Caiman crocodilus* that left and right systemic arches contained well-oxygenated blood, which implicated filling of the left aorta from the right aorta via the foramen of Panizza. Because he measured synchronous pressure events in both left aorta and right aorta, White (1956) considered that left aortic filling ocurred during systole. Comparisons of left and right aortic oxygenation led Greenfield and Morrow (1961) to the same conclusion about the origin of blood in the left aorta from right aorta via the foramen in *Alligator mississipiensis* also, but their pressure records led them to the conclusion that the left aorta is filled during diastole, the foramen being covered by the cusp of an open semi-lunar valve in the right aorta during ventricular systole. Concerning the significance of the anatomical origin of the left aorta from the right ventricle, they postulated that during diving or other breathholding, some output from the right ventricle could be diverted into the left aorta when the pulmonary oxygen store becomes depleted. They proposed that such a shunting arrangement would divert poorly oxygenated blood to the hindquarters, while the heart, brain and forequarters would continue to receive well oxygenated blood via the coronary, common carotid and subclavian arteries, all of which derive from the left aorta. The existence of this so-called right-left shunt (i.e. filling of the left aorta from the right ventricle) was demonstrated by White (1969). Whereas Greenfield and Morrow (1961) had studied animals supine and with the thorax open, White made chronic cannulations of major vessels and was able to make observations on intact animals. By force-diving alligators he showed that as bradycardia developed right ventricular pressure

rose until a right-left shunt occurred, under vagal control and originating in the pulmonary outflow tract (White 1970, 1976). The adaptive significance of the shunt remained unclear.

Whereas these studies have answered many questions, they have reported quite contradictory information about timing of the pressure events in left and right aortae, a dichotomy of views that has been drawn attention to by Webb (1979). The anatomy would seem to favour filling of the left aorta via the foramen of Panizza during diastole, such as proposed by Sabatier (1873), but further blood pressure data reported by White (1968) on *Alligator* confirmed synchronous left aortic and right aortic pressure events as he found earlier in *C. crocodilus* with little resistance to free flow through the foramen. Clearly more data are needed to clarify this dichotomy, particularly on short voluntary dives by unrestrained animals.

We present data which clarify some of the points raised, resolve the contradiction referred to by Webb (1979), address the question of the mechanism by which the left aorta is filled from the right aorta, and discuss the functional significance of crocodilian cardiac anatomy and 'right-left' shunting during aerobic dives.

Materials and methods

Eight *C. porosus* and a single *C. johnstoni,* ranging in weight from 1.7 to 7.6 kg, were used in the study. Surgery was performed under cold anaesthesia with ice, supplemented by local infiltration of xylocaine. Non-obstructive polyethylene cannulae were placed in the left aorta (LAo), right aorta (RAo) via the common carotid, left ventricle (LV) via the subclavian (SC) and the right ventricle (RV) directly through the ventricular wall. Cannulae were of equal length. Arterial cannulae were 0.58 mm i.d., attached to a cut off 23G needle. Ventricular cannulae were 0.97 mm i.d., to fit 19G needles. The main pulmonary artery (PA) was cannulated via a small anterior branch, and the cannula passed towards the heart so the tip lay within the main pulmonary trunk. A schematic of the anatomy showing cannula placement is given in Fig. 1. We often had difficulties in cannula management after closure of the chest wall. Hence, some observations were made before closure of the chest. This included observations on the effect on LAo pressure of its temporary ligation (see later). After closure with sutures, the incision was waterproofed by glueing a strip of rubber glove onto the skin with surgical glue.
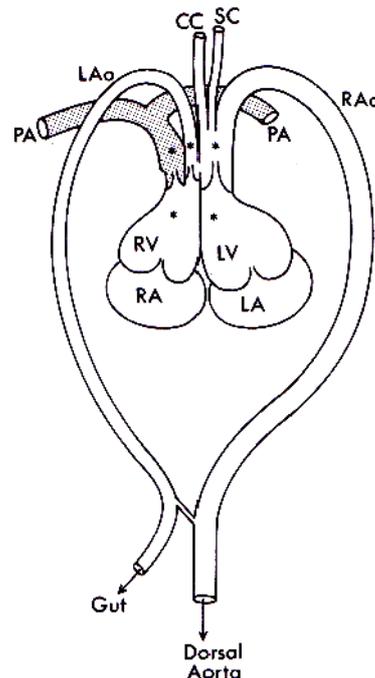

Fig. 1. Schematic diagram of the crocodilian heart and outflow tracts. Asterisks mark cannula locations. *LAo* left aorta; *RAo* right aorta; *PA* pulmonary aorta; *RV* right ventricle; LV left ventricle; CC common carotid; SC subclavian artery. The Foramen of Panizza is depicted as a gap in the common wall between LAo and RAo at their base

In the experimental tank, some animals remained at the surface unless disturbed, when they would submerge. Other animals remained on the bottom most of the time, surfacing briefly to breathe. We ensured minimum disturbance, to avoid `fright dives' (Gaunt and Gans 1969), knowing that short voluntary dives are typical of what occurs in the field (Grigg et al. 1985) and that such dives are aerobic (Wright 1985). Except where stated otherwise, observations were made at 25 °C, which is typical of water temperatures in the field (Messel et al. 1981). Blood samples were analysed on a Radiometer PHM 71 gas analyser and associated

electrodes, stabilized to 25 °C and calibrated with standard gas mixes. All samples were measured without delay. The order of measurement of samples drawn simultaneously was randomised to avoid introducing any bias. Oxygen partial pressure data were transformed to percentage saturation using a Hill coefficent of 2.7 and the relationship:

$\log P_{5O} = 0.4163 + 0.02\ T(°C) + 0.3763 \log P_{CO2}$ (Grigg and Cairncross 1980).

[These authors showed that, because of the high correlation between pH and PCO_2 and the small fixed acid Bohr effect in *C. porosus* (Grigg and Gruca 1979), it is unnecessary to take pH values into account additionally to P_{CO2} in this manipulation.]

Blood pressures were measured with Statham P23 ID Pressure Transducers actuating a four-channel Gilson Polygraph. The calibration and linearity of pressure transducers were checked against columns of water.

Table 1. Blood gas data in *C. porosus* and a single *C. johnstoni (F)*. Asterisks indicate O_2 values in the left aorta where coincident blood pressure data indicate pulmonary by-pass shunting. Values marked with a question mark are likely to be the result of shunting but pressure data are lacking

Croc #	Right aorta			Left aorta			Pulm. artery			Pressure indications	Measurement conditions
	PO_2	PCO_2	%S	PO_2	PCO_2	% S	PO_2	PCO_2	% S		
1	90	22.0	96.5	90	22.8	96.4	31	21.2	61.6	No shunt	Prone
1	95	21.9	97.0	91	21.5	96.7	36			No shunt	Prone
2	80	19.0	95.9	77	15.1	96.4	20	13.4	43.9	No data	Prone
2	92	16.9	97.4	? 79	14.0	96.8	21	17.3	40.8	No data	Prone
2	90	12.2	98.0	? 76	15.8	96.1	24	18.6	47.9	No data	Prone
4	71	32.0	90.8	? 61	26.0	89.0	24	32.5	34.2	No data	Making short repeated dives
4	86	34.0	94.0	? 76	30.0	92.7	27	30.5	43.3	No data	Making short repeated dives
4	65	34.0	88.0	? 60	32.5	86.1	19	30.5	22.8	No data	Making short repeated dives
4	76	34.0	91.8	? 71	30.5	91.2				No data	Early in a dive
4	47	32.5	76.2	*41	35.5	66.9	16	36.0	13.6	No data	9 min into 10 min dive
4	63	32.5	87.6	*51	27.5	82.5	26	35.0	37.5	Shunting	Just surfaced after 10 min dive
4	46	32.5	75.1	46	37.0	72.6	18	36.5	17.5	No shunt	8 min into 17 min dive (fright)
4	32	28.0	56.8	30	29.5	51.2				No shunt	16 min into 17 min dive (fright)
4	39	44.0	58.7	38	42.0	58.1	23	40.0	27.3	No shunt	Resting at surface
4	55	40.0	79.8	*44	36.0	70.7	24	34.0	33.2	Shunting	Resting at surface
5	91			? 84			17			No data	Resting on
S	82			? 71			15			No data	bottom
6	84	21.2	95.9	*57	19.5	90.0	41	18.9	79.3	Shunting	Supine
7	93	17.5	97.4	*47	16.3	86.6	30	19.0	62.1	Shunting	Supine
7	119			118						No shunt	Supine
8	67	25.5	91.4	*60	30.0	87.0	39	23.0	73.3	Shunting	Supine
8	44	36.5	70.4	44	36.0	70.7				No shunt	Supine
8	98	21.0	97.3	97	21.1	97.2	38	28.0	67.7	No shunt	Supine
8	43	33.0	71.2	*37	28.0	66.1	26	25.0	45.8	Shunting	19 min into 30 min dive
F	30			28			11			No data	Supine
F	33			28			10			No data	Supine

Results

Blood oxygen in the left and right aortae and the pulmonary artery

Systemic arterial oxygenation was high during air breathing and fell progressively during diving episodes. Hence it was possible to compare the relative oxygenation of blood in the pulmonary artery and in the left and right aortae over a wide range of oxygenation in the right aorta (Table 1, Fig. 2). All dives were known to be within the aerobic limit of the species (Wright 1985). Three observations can be made:

(a) Oxygenation in the left aorta is usually either as high or nearly as high as in the right aorta, confirming that in C. *porosus,* as in *Caiman sclerops* (White 1956) and A. *mississipiensis* (Greenfield and Morrow 1961) all or most of the blood in the left aorta derives from the right aorta. The oxygenation of blood in the left aorta may, however, be slightly less than and is sometimes substantially less than that in the right aorta. When one considers the shape of the oxygen equilibrium curve in *C. porosus* (Grigg and Cairncross 1980) it becomes clear that a slightly lower oxygen partial pressure in the left aorta makes little difference in oxygen content. This can be seen when the data are presented in terms of percentage saturation (Fig. 2b).

(b) Oxygenation of the blood in the pulmonary artery (PA) was always very much less than that in the left aorta, during both surface air breathing and aerobic dives. Accordingly, we have no evidence from observations of blood oxygen that circumstances exist in which the left aorta is fed from the RV only.

(c) When blood pressure data showed evidence of the existence of a right-left shunt (see later), it is clear that the oxygenation of blood in the LAo is the result of mixing of blood from RAo and RV sources (Boxed points in Fig. 2 a, b).
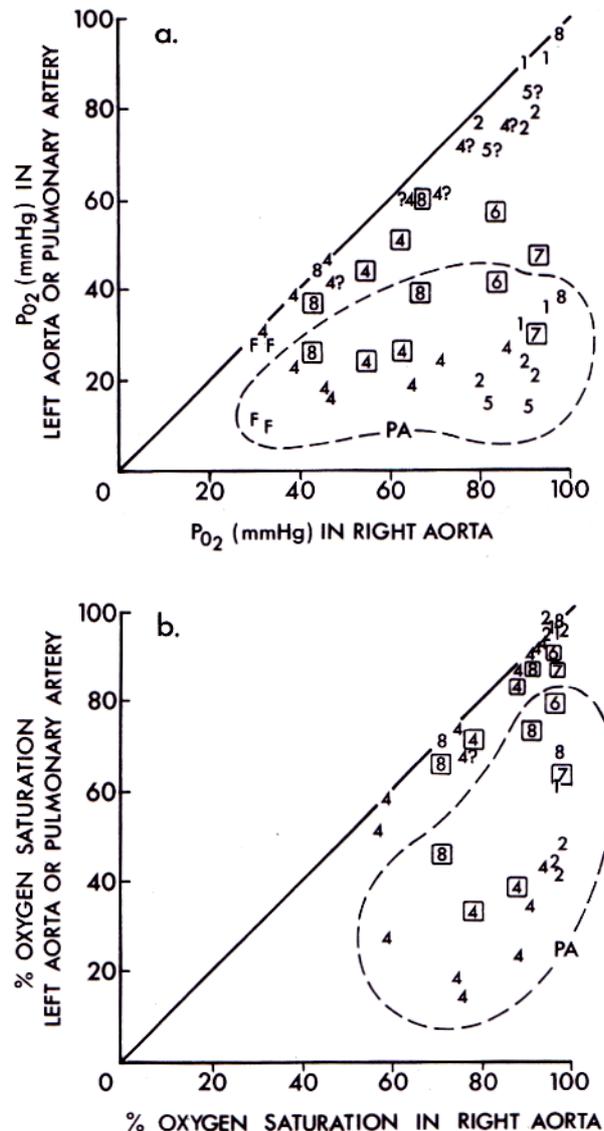
Fig. 2 a, b. Oxygen partial pressure (**a**) and percentage saturation (**b**) in left aorta and pulmonary artery (within dotted line) as a function of that in the right aorta. Numbers refer to crocodile number (Crocodylus porosus), F=*C. johnstonii*. Boxed points identify situations where pressure records indicate the operation of RV to LAo shunting. For those points marked with a question mark, shunt operation is likely but pressure records are lacking

In summary, blood oxygen data lead one inescapably to the conclusion that blood in the left aorta derives mainly from the right aorta. During aerobic dives a variable right-left shunt may or may not develop, in which the left aorta receives a contribution from the right ventricle also.

Blood pressures in the major vessels
We found no marked differences in blood pressures or in the shape of pressure traces between observations made on animals supine with the thorax open, during surgery, and those made subsequently on the same individuals, after release into the experimental tank. This is important because there have been challenges to the validity of some of the observations made by Greenfield and Morrow (1961) and because it means that observations we made under both circumstances are relevant.

Pressures in the right aorta were typically higher than those in the left aorta, which were in turn much higher than pressures in the pulmonary circuit (Table 2). Mean systolic pressures during air-breathing were 76.2 ± 9.5 (SD) mm Hg in RAo, 70.8 ±10:7 in LAo and 18.4 ± 3.9 in PA.

We observed a decrease in central systemic blood pressure in two circumstances; during cooling and well into voluntary dives. In crocodile # 8 RAo blood pressure fell from 62/42 mm Hg at 18 °C to 55/33 at 14 °C and 32/14 at 12 °C, with heart rates of 18.5, 16 and 12 beats per minute (bpm) respectively. During aerobic dives, RAo blood pressure fell with the gradual onset of bradycardia, increasing rapidly along with heart rate at each breathing episode. A typical pattern was seen in crocodile # 8 where RAo blood pressure was 58/40 (heart rate 12 bpm, left ventricle 58/2, left aorta 56/40) prior to surfacing for a breath after 10 min submerged. At surfacing, RAo pressure rose to 84/64 (20 bpm, left ventricle 84/4, LAo 77/ 63) associated with lung ventilation.

Table 2. Blood pressures and heart rates in a series of *C. porosus* measured under various conditions. Pressures are in mm Hg (systolic/diastolic) heart rate in beats per minute

Crocodile No. (weight)	Temp. (°C)	Pressure in			Heart rate (bpm)	Conditions of measurement
		Right aorta (mm Hg)	Left aorta (mm Hg)	Pulmonary artery (mm Hg)		
1 (3.5 kg)	25	84/68	79/66	12/ 5	34	Air breathing, supine
	25	83/67	80/66	-	32	Air breathing, prone
	25	82/65	77/63	-	32	Air breathing, in water
	25	48/33	48/32	-	7	Held under water
2 (2.1 kg)	25	70[49	-	16/ 9	47	Air breathing, supine
	25	68/45	-	23/18	43	Air breathing, supine
3 (1.7 kg)	25	80/60	73/52	-	21	Air breathing, supine
		76/51	60/49	-	29	Air breathing, in water
		68/45	58/43	-	25	At end of aerobic dive
4 (3.1 kg)	25	87/68	80/64	22/ 6	47	Air breathing, supine
		80/60	72/58	20/ 7	23	Air breathing, in water
		74/58	64/53	-	25	During aerobic dive
6 (4.5 kg)	25	68/50	60/48	20/ 6	28	Air breathing, in water
7 (7.6 kg)	19	54/42	48/40	14/ 6	26	Air breathing, supine
	25	54/30	48/30	-	12	During aerobic dive
8 (7.0 kg)	20	62/40	r+5/34	20/ 6	19	Air breathing, supine
	18	62/42	62/42	-	18	Air breathing, in water
	14	55/33	55/33	-	16	Air breathing, in water
	12	32/14	32/14	-	12	Air breathing, in water
	25	82/60	77/63	-	20	Air breathing, in water
	25	58/40	56/40	-	12	At end of aerobic dive

The pattern which emerges is that at lower central pressures and lower heart rates (e.g. during diving or cooling), LAo and RAo pressures coincide. Indeed, as we shall see later, pressure traces in LAo and RAo in such conditions are very similar, even completely indistinguishable (Figs. 3e, 4c). During air breathing, however, RAo systolic pressures usually exceeded LAo systolic pressures though diastolic pressures were often similar.

As a first step in illustrating the hemodynamic relations between the right and the left aortae we present a series of figures all gained from a single individual (# 8) over two days. Figure 3a represents a situation with the animal supine. Figures 3 b-e present data collected the following day with the animal unrestrained in a large tank in which it was free to float at the surface or dive at will.

In Fig. 3a, the upper part of the left ventricular pressure peak superimposes on the right aorta, trace on trace. The notches on the LV trace mark closures of the ventricular outflow valves. Blood is able to surge into the left aorta through the foramen just prior to this, as it becomes fully uncovered when the valve at the left ventricular outflow orifice begins to return to its diastolic position. From that point and through diastole, LAo and RAo pressures are equal, suggesting free communication between the two via the foramen of Panizza. This is the pattern described by Greenfield and Morrow (1961). Meanwhile, in Fig. 3a, RV pressure remains too low throughout the cycle to open the outflow valves into the left aorta. There is a large pressure gradient between the RV and the pulmonary PA artery, presumably the result of the constriction at the base of the pulmonary outflow tract where it exits from the RV (White 1969; Webb 1979). The second peak on the RV pressure trace begins to develop at subsequent to peak pressure in the PA, presumably coincident with the increased impedance of the pulmonary outflow tract either by peripheral vascular resistance or by active constriction at its base or both.

Figure 3b shows a similar pattern in the same individual on the following day, the animal having just submerged quietly on an aerobic dive. In another aerobic dive a few minutes later, evidence is seen of right-left shunting (Fig. 3c), RV pressure having increased enough to make an impact on LAo so that the LAo pressure trace shows a three-pulse cycle with the right ventricular surge interpolated between the 'initial' rise and the pressure surge associated with blood flowing in through the foramen. Note that PA pressures remain much the same. In this situation, some blood apparently exits from RV into LAo, a right-left shunt.

Another pattern is seen in Fig. 3d, collected during a dive in which there was little bradycardia. Here, no impact of the RAo is apparent on the LAo, whose pressure reflects the RV as its source. Both blood pressure and heart rate are comparatively high (RAo 70/48 mm Hg, LA 58/34, 17 bpm) and note that the pressure increase in RV precedes that in LV. In contrast, during a dive in which a bradycardia developed (to 7 bpm), blood pressures were low and essentially similar in both left aorta and right aorta (right aorta 50/25, left aorta 49/23, HR 7 bpm, Fig. 3 e). This is the sort of pattern described for *Alligator mississipiensis* by White (1969).
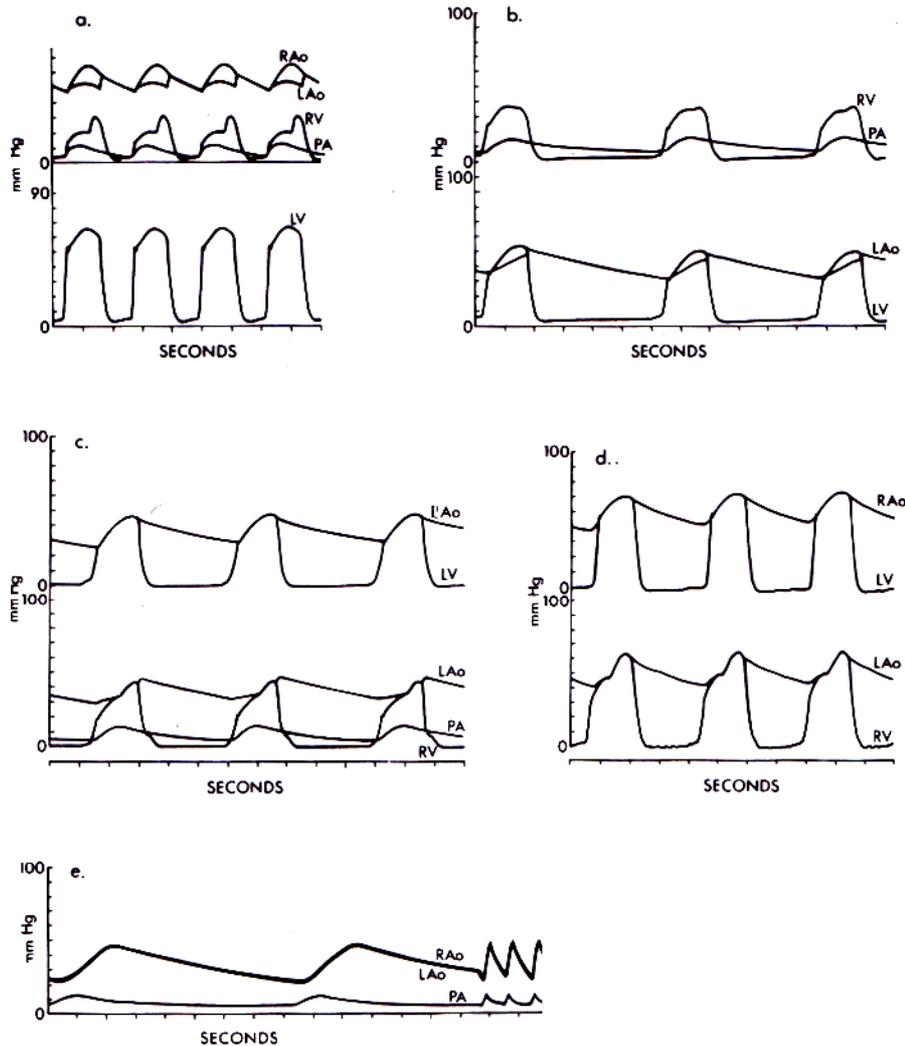
Fig. 3a-e. Pressure records in the heart and outflow vessels of a 7.0 kg *C. porosus* (# 8), **(a)** supine and **(b-e)** in water in a large tank, free to dive or surface at will. **b-e** were recorded during voluntary dives in which there was little bradycardia. In **a** and **b**, LAo fills from RAo via the foramen of Panizza. **c** and **d** show RV to LAo shunting. e recorded in a dive in which a severe bradycardia developed, shows coincidence between pressures in LAo and RAo. Symbols as in Fig. 1

Finally, we present a variety of LAo and RAo pressure patterns from different animals with an interpretation of them(Figs. 4-5). Figure 4a (croc # 1) shows a typical pattern during breathing, with a large foramen 'spike' (i.e. a rapid pressure surge into LAo from RAo) on the LAo trace concurrent with the rapid decay of pressure in the RAo. In the same animal, the LAo trace shows a small foramen 'spike' six minutes into a forced dive (Fig. 4b). Sixteen minutes into the same forced dive, the record captures the gradual loss of the spike (Fig. 4c) and development of complete synchrony between LAo and RAo traces. Note that blood pressure has fallen by half during the dive, and heart rate from 36 to 7 bpm. Examples of a 'triplet' LAo trace are seen in Fig. 5a where, as in Fig. 3 c, RV is making an impact on the LAo trace. A record made from the same animal three days later (Fig. 5b) showed almost complete synchrony between LAo and RAo pressures, with a tiny foramen spike visible. This is a similar pattern to that seen in Fig. 4a, recorded during a forced dive yet it was made on an animal at rest and making short voluntary dives separated by brief surfacings. The relationship between RV, PA and LAo during air-breathing in *C. johnstoni* is seen in Fig. 6a. Note that the peak value of RV is reached while PA is declining. Despite the large RV peak, its timing and its level show that no RV-LAo shunting is occurring, the LAo showing signs of being fed only via the RAo, including a foramen 'spike'. A little later on, (Fig. 6b) an increase in RV pressure leads to its showing on the LAo, only to disappear again when RV pressure falls (latter part of Fig. 6b). Samples of left aortic and right aortic blood confirmed RV to LAo shunting (PA = 41 torr, LAo = 57, RAo = 84).
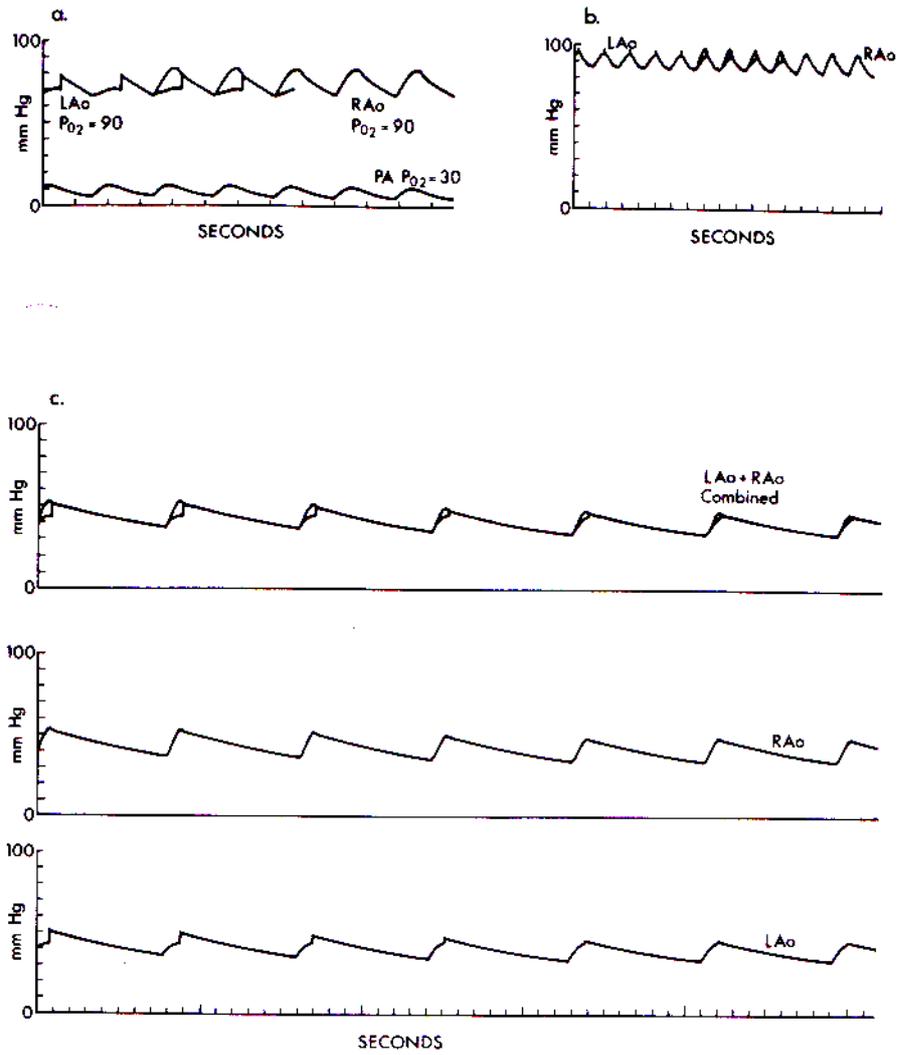
Fig. 4a-c. Pressure records in the heart and outflow vessels of a 3.5 kg *C. porosus* (# 1) air-breathing and at rest (**a**) and six (**b**) and sixteen (**c**) min into a forced dive in which a severe bradycardia developed. Symbols as in Fig. 1
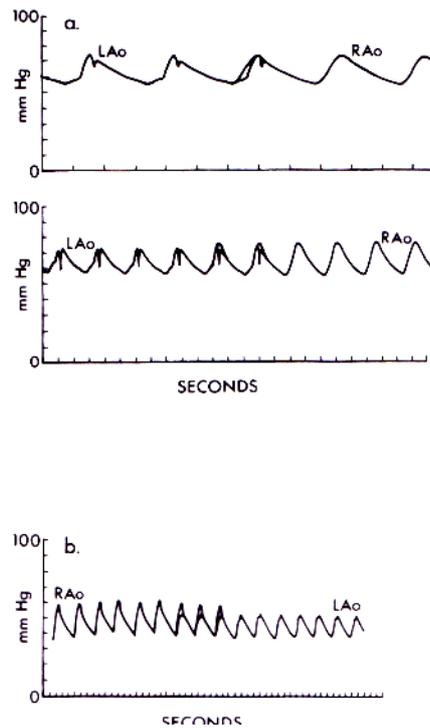
Fig. 5 a, b. Pressure records from the heart and outflow vessels of a 1.7 kg C. porosus (#3). **a** shows LAo and RAo, and the two superimposed, with a `triplet' pattern in LAo due to the impact of both RV (shunt pathway) and RAo (via the foramen of Panizza) on LAo trace. **b** recorded from an animal undertaking a short aerobic dive, shows pressure events in RAo and LAo almost in synchrony. Symbols as in Fig. 1
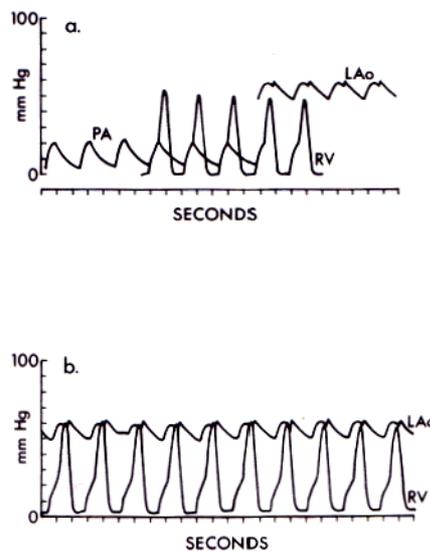

Fig. 6a, b. Pressure records from the heart and outflow vessels of a *C. johnstonii* breathing air **(a)** and during an aerobic dive **(b)** in which shunting developed and then ceased. The left half of **b** shows shunting, with RV making an impact on LAo. Then RV pressure falls slightly, and shunting apparently ceases. Symbols as in Fig. 1

Discussion

Oxygenation of blood in the right and left aortic vessels

This seems to be the first study to compare oxygenation of blood in right and left aortae of a crocodilian by measuring oxygen partial pressure rather than oxygen content. This is significant because, due to the shape of the oxygen equilibrium curve, PO_2 measurements are more likely to uncover differences in blood oxygen qualities not decipherable by content measurements when blood approaches full saturation. Hence, while we confirm for *C. porosus* the findings of Greenfield and Morrow (1961) in *Alligator* and of White (1956) in *Caiman crocodilus*, that both right and left aortae carry well-oxygenated blood which clearly derives from the

left ventricle, we found in *C. porosus* that O_2 partial pressures in the left aorta are commonly less than in the right (Table 1, Fig. 2 a). That this is the result of RV to LAo shunting is confirmed by pressure traces at the time of blood sampling in many instances (e.g. Fig. 3c,d). Where pressure trace data is lacking (Table 1) the operation of the shunt can be postulated.

The right-left shunt developed commonly, but not as an unvarying correlate, as heart rate and systemic arterial oxygenation gradually fell during a voluntary aerobic dive. It developed often with the chest open during surgery and was seen occasionally in crocodiles resting at the surface of the water. It did not seem to be associated with fright-induced sudden bradycardia or anaerobiosis (see later). It is worth noting that the mixed blood in the left aorta during shunting remains, nevertheless, highly oxygenated during aerobic dives.

Leaving right-left shunting aside for the time being, blood oxygen data confirms that in *C. porosus* breathing air, blood in the left aorta is supplied from the right aorta. The only anatomical communication by which this can occur is via the foramen of Panizza yet, as drawn attention to by several authors, the size and position of the foramen are such that it is not easy to see how such flow can be other than severely restricted. How does it work?

Blood flow through the foramen of Panizza
That blood reaches the left aorta from the right aorta via the foramen has been accepted for some time and our results reinforce this view. We must now address the question of how that supply is achieved. The crux of the problem is not only that the foramen is quite small but also that its location in the common wall between the left aorta and the right aorta is obscured deep within the pockets formed by the cusps of the respective aortic valves (at least in a dead specimen). Hence, the foramen would seem to be closed by valves on both sides during systole. Nevertheless, Fritsch (1869) considered that the flow from the RAo to the LAo occurred during systole, while Sabatier (1873) was adamant that the foramen would be closed by the aortic valves during ventricular systole, so that the LAo filling could occur only during diastole, from the RAo after the aortic valves closed. The earliest pressure measurements (White 1956, on *C. crocodi*lus) were made with both mercury and optical manometers and favoured Fritsch's interpretation, for pressure events in the LAo and the RAo were synchronous. White discussed in great detail the disposition of cartilages within the heart, whose effect was interpreted as holding open the foramen and stiffening the LAo semi-lunar valves to hinder the flow of RV blood into the LAo, while directing it into the pulmonary arch. Unfortunately White did not detail the role of cartilage in the RAo semi-lunar cusps. In later work, on *Alligator,* White (1968, 1969) again recorded essentially synchronous pressure events in the LAo and the RAo, attributing the minor differences observed to losses in potential energy in traversing the foramen. In contrast, Greenfield and Morrow (1961) found the LAo and RAo pressure events to be essentially asynchronous, favouring Sabatier's (1873) interpretation. This contradictory dichotomy of anatomical interpretations and experimental results was outlined by Webb (1979) who suggested that the pressure events in the LAo might be transmural, given that all cardiac outflow vessels lie within a common sheath of connective tissue, or the `remote possibility' that the membranous cusp in the right systemic arch is everted through the foramen during systole.

Our results seem to resolve the controversy, for we found in *C. porosus* that LAo and RAo pressures may be synchronous (as Fritsch proposed and White found) or asynchronous (as Sabatier proposed and Greenfield and Morrow found) in the same individual within the period of a few minutes or less; see, for example Fig. 4c, 6c. Interestingly, we found the asynchronous pattern typically associated with higher heart rates and higher systolic blood pressures (> 50 mm Hg), the synchronous pattern typical of lower blood pressures. As pressures recorded by White were consistently < 50 mm Hg and lower than those reported by Greenfield and Morrow, our observations on *C. porosus,* extrapolated to their respective studies, would predict the patterns that each found. Typically, we found the asynchronous pattern to be associated with air breathing at normal temperatures and it usually showed a characteristic LAo pressure trace with a dramatic spike interpreted by us and by Greenfield and Morrow as corresponding to the major pressure surge through the foramen after semi-lunar valves retreat to expose the foramen at the end of systole. Typical examples of this are seen in Figs. 3a, b and 4a. Less typical traces which still show the foramen spike are seen in Figs. 4b, 5a,b, 6a and the early part of 4c. To accommodate these two patterns, we propose that the foramen of Panizza is of variable calibre.

How does blood flow through the foramen into the left aorta? Typically, the LAo trace shows two pressure events, an initial rise followed by a sharp rise, the 'foramen spike' (Figs. 3a, 4a). The initial rise occurs during ventricular systole, the latter during diastole. The source of the initial pressure rise in the left aorta is problematical. Three possibilities exist: transmission 'around the loop' via the dorsal confluence of the two aortae, transmural (remembering that all outflow vessels are bound within the same connective tissue sheath), or via the foramen from the left ventricle (which implies a partly exposed foramen during systole, in contrast to the anatomical relationship suggested by examination of dead specimens). The first possibility is rejected by direct observation, for ligation of the left aorta did not obliterate the initial pressure rise. It is rejected also by the indirectness of the dorsal connection between LAo and RAo (see Fig. 1). The latter two

possibilities are not mutually exclusive; the initial pressure rise could be a combination of transmural pressure and a flow from the right aorta before and during peak systole which is then augmented when the right aortic valve retreats, allowing a surge of blood through which causes the foramen spike: The timing and pattern of the early pressure rise is very variable (compare Figs. 3a, b, 4a, b, 5b and 6a) and it is likely that the variability reflects different relative components of transmural pressure and systolic flow through the foramen. We propose that this is consistent with the idea that the foramen is of variable calibre. This awaits further examination, but it would explain the observed events. Such a proposition must take into account the presence of the foraminal process of the central cartilage (White 1956) which sweeps around the distal margin of the foramen. Indeed, the cartilaginous support may be part of the mechanism by which opening of the foramen occurs. It seems that enlargement of the foramen is associated particularly with reduced systemic blood pressure, and may be a response to it (see later). Complete synchrony of pressure events in RV and LAo, as described by White (1956, 1969) and seen in our records also can be envisioned as being at one end of a continuum from the asynchronous pattern (Fig. 4a) in which the calibre of the foramen is small, the initial pressure rise is transmural and the foramen spike is the dominant LAo pressure event, to the synchronous pattern (Fig. 3e) in which the calibre is large, the initial and main pressure event is direct from the LV and the foramen spike is absent. Any alternative to the 'variable calibre' hypothesis must account for the great flexibility which is observed in the LAo pressure trace. The general support and stiffening of the heart in this region by cartilage would seem to be consistent with an interpretation that depends upon a certain three-dimensional structure during the cardiac cycle and its regulation in response to physiological needs. Resolution of the question depends upon gaining an understanding of the relative positions of the free margin of the RAo valve in relation to the position of the foramen in a living crocodile during synchronous and asynchronous filling of the two aortae.

'Right-left' shunting during aerobic dives

We found ample evidence from pressure records of the development of an RV to LAo (functionally a 'right-left' shunt) in *C. porosus,* occurring frequently as an aerobic dive progressed. The evidence is in the form of a visible impact of right ventricular pressure on the left aortic trace, such as in Figs. 3c, d, 5a and 6b, as discussed by White (1969) working on *Alligator.* Like White, we found that the shunt developed following an increase in right ventricular pressure (Fig. 3b, c) and ceased when right ventricular pressure decreased (Fig. 6 b).

The magnitude of the shunt is very difficult to assess. Tazawa and Johansen (in press) have presented a detailed analysis of central shunts in vertebrates, including crocodiles, taking a modelling approach. They show that to quantify the shunt in a two aorta system such as crocodiles have, one must know the oxygen content of 'mixed' systemic blood, i.e. of blood downstream of a junction between right and left aortas. In crocodiles, the anatomical arrangement at this junction is such that mixed systemic blood is no more than an abstract concept. Therefore, its oxygen content could be calculated only if one had data on relative blood flow as well as oxygen contents in the two aortas. Tazawa and Johansen estimated shunting in *Caiman crocodilus* using data from White (1956). However, they calculated the oxygen content of mixed systemic blood as the arithmetic mean of LAo and RAo oxygen contents, which assumes equal flows in both vessels. As LAo is at most half to two-thirds the diameter of RAo, with a similar length and similar pressure drop, a much smaller flow in LAo is certain. Estimating likely relative flows by Poiseuille's law and applying our data to the equation given by Tazawa and Johansen, it seems unlikely that the shunt in *C. porosus* would exceed 10%.

Although diving episodes in crocodilians have been perceived as at least partly anaerobic events, often associated with bradycardia (Andersen 1961), it has become clear that severe bradycardia and lactate accumulation are more a response to 'fright' than to submergence when forced dives are employed in diving studies (Wright 1985; Gaunt and Gans 1969). Wright (1985) has shown in *C. porosus* that unrestrained animals of the same size range as those in the present study, diving voluntarily, do so aerobically without severe bradycardia, without building up muscle or plasma lactate and without nearly exhausting their oxygen stores. Smith et al. (1974) found by radio-telemetry of heart rate from a free-ranging *Alligator* that voluntary dives were not accompanied by severe bradycardia. Grigg et al. (1985) found that voluntary dives made by a free-ranging *C. porosus* in its familiar habitat were all well within the aerobic dive time. Comparing dive times, heart rates and blood gas values with other data from *C. porosus* (Wright 1985), it is clear that crocodiles diving voluntarily in our study were well within their aerobic limit.

What is the functional significance of the development of a right-left shunt? It is not immediately clear what advantage may derive from the ability to reduce the proportion of blood that goes to the lungs. Previous authors have suggested that a saving of cardiac energy is achieved (White 1970), there being little point in perfusing a lung that can no longer continue to supply oxygen, or needs to supply oxygen only at a reduced rate to meet the needs of a very much modified circulation (re-distribution of blood away from many peripheral tissues etc.). However, Burggren (1985) has pointed out that the metabolic cost of running

the heart is very low and the savings produced by even extreme right-left shunting are very small. Furthermore, in voluntary aerobic dives, *C. porosus* maintains its oxygen consumption at pre-dive rates and bradycardia develops slowly and is not severe (Wright 1985).

A more likely possibility is that the shunt enables crocodiles to match lung perfusion to oxygen requirements as the dive progresses, sequestering carbon dioxide away from the lungs and thus prolonging efficient oxygen uptake. As Wright (1985) has shown, oxygen consumption remains constant during the dive despite falling pulmonary oxygen stores and a slowing heart rate. This is achieved by an increase in arterio-venous difference. At lower blood oxygen partial pressures as the dive progresses, because of the steepening of the oxygen equilibrium curve, an increased a-v difference can be maintained with reduced perfusion of the lungs. Hence, lung perfusion may be matched to oxygen requirements with some independence from systemic flow, an option unavailable to mammals and birds. As a consequence, with systemic blood flow exceeding pulmonary flow, a CO_2 shunt may result as described by Ackerman and White (1979) and White (1985) in turtles. Relative decrease in the acidification of the blood in the pulmonary circulation would promote continued utilisation of the pulmonary oxygen store during breath holding, while the CO_2 retention and a right-shifted oxygen equilibrium curve in the systemic circulation would augment oxygen delivery to the tissues (Wood 1984). Systemic CO_2 retention would also favour tissue CO_2 storage and buffering.

Why is the crocodilian cardiovascular anatomy so complex?

Why do crocodilians have this unusual anatomical arrangement? Webb (1979) suggested that while the anatomy implies the capacity for substantial shunting, the behaviour and physiology of modern crocodilians is such that the need for right-left shunting is minimal. He suggested that the anatomy of extant crocodilians reflects the needs of more aquatic ancestors which relied extensively on anaerobic diving, whereas the modern crocodilia may no longer need this shunting capability. However, if use is any guide to need, the physiological advantages of a pulmonary by-pass shunt may be quite significant and are likely to be found in relation to aerobic diving as discussed above.

Would crocodilians survive equally well if their ventricle were undivided and the left systemic received blood directly from the left ventricle? Both of these unusual features seem to promote advantages for crocodiles. Certainly, if the ventricles were more typically reptilian the possibility of intra-cardiac right-left shunting would take care of adjusting relative flows in the two principal circuits. The drawback of that may be that the resulting mixed blood perfuses heart and brain as well as the rest of the circuit. In shunting de-oxygenated blood away from the lungs via the left aorta, it is only the posterior systemic circuit that can receive mixed blood, particularly the gut which is probably better able to cope with that than either brain or heart would be.

Another possible advantage of the arrangement as it stands is that crocodiles, by having a completely divided ventricle, have evolved a high pressure systemic circuit and a low pressure pulmonary circuit more reminiscent of mammals than of reptiles. Burggren (1982) has drawn attention to drawbacks associated with high pulmonary arterial pressure in reptiles.

From a physiological point of view therefore, functional advantage may be seen in all three peculiarities of the crocodilian heart, as follows:

1. Unlike in other reptiles there is a complete anatomical basis during both diastole and systole to enable equal flow in both pulmonary and systemic circuits if that is appropriate. At such times, valves between the RV and LAo remain closed because of the pressure gradient, left and right aortae must fill from the left ventricle and all blood entering the LAo must traverse the foramen of Panizza.

2. Like other reptiles, crocodiles possess an anatomical basis for a smaller pulmonary than systemic flow, via a right-left shunt. However, instead of the shunt being intra-cardiac, it is mediated via a single vessel (LAo) which, in originating from the right ventricle, diverts the low-oxygen (shunted) blood away from the brain and the coronary circulation and from most of the systemic circulation.

3. The unusually indirect junction between the left and right aortae at their dorsal confluence appears to be a further elaboration of the left aortic shunt pathway, taking advantage of the gastrointestinal tract's tolerance for low arterial oxygen.

4. Crocodilians, unlike other reptiles, are not at risk of recirculation of blood to the lungs.

5. Also unlike other reptiles, the division of the ventricle in crocodiles provides the anatomical basis for a low pressure pulmonary circulation and a high pressure systemic circulation, as in mammals. This reduces the threat of plasma filtration into the lung and allows greater left ventricular output and more efficient arterial distribution.

6. Because of the shape of the oxygen equilibrium curve, pulmonary blood flow can be reduced during an aerobic dive without there being a reduction in oxygen uptake.

7. The most important consequence of the shunt may be that, with systemic blood flow exceeding pulmonary flow, there will be facilitation of oxygen uptake in the lung, improved oxygen transfer to the tissues and enhanced potential in the tissues for CO_2 storage.

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