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VENTRICULAR HAEMODYNAMICS IN THE MONITOR LIZARD *VARANUS EXANTHEMATICUS*: PULMONARY AND SYSTEMIC PRESSURE SEPARATION

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SUMMARY

The haemodynamics of the anatomically undivided ventricle of the monitor lizard *Varanus exanthematicus* have been examined by measurements of blood pressure and flow. Central blood P_{O_2}, P_{CO_2} and pH were also measured.

Intracardiac pressure measurements show the ventricle to be functionally divided throughout systole into a high pressure pump (cavum arteriosum: 'mean' pressure 89 cm H_2O) perfusing the systemic circulation, and a low pressure pump (cavum pulmonale: 'mean' pressure 40 cm H_2O) perfusing the pulmonary circulation. Hypoxia produced by asphyxia or N_2 breathing changed systolic pressures in the ventricular cava, but never resulted in superimposable pressure waveforms which would have indicated a breakdown from ventricular division into two pressure pumps. Diastolic pressures were superimposable in the ventricular cava under all conditions.

Analysis of blood P_{O_2} and O_2 content revealed the potential for nearly complete separation of left and right atrial blood in the ventricle, but both left-to-right and right-to-left shunts of considerable magnitude could also develop.

The varanid heart with its systolic pressure separation allows the development of high blood pressure gradients capable of driving a large cardiac output through the high impedance systemic vascular beds. Concurrently, the low impedance pulmonary circuit is perfused at a much reduced blood pressure, circumventing filtration of plasma into the lungs and impairment of gas exchange. Haemodynamically this situation resembles that present in crocodilians and the homeothermic vertebrates.

INTRODUCTION

Within the Reptilia there exists a great variation in both cardiovascular anatomy and function. The most common pattern is typified by an anatomically incompletely divided ventricular pump (Chelonia, Ophidia, Rhynchocephalia and, with the known exception of the varanids, the Lacertilia). All three ventricular chambers are in

anatomical connection (see reviews by White, 1976; Webb, 1979; Johansen & Burggren, 1980) and a uniform systolic pressure develops throughout the ventricle (Shelton & Burggren, 1976; Burggren, 1977*a*, *b*). Blood is thus ejected into the base of both the systemic and pulmonary outflow vessels at nearly identical systolic pressures, unless constriction of a muscular sphincter at the base of the pulmonary artery produces a pressure drop along the pulmonary outflow tract (Burggren, 1977*a*, *b*; Smith & MacIntyre, 1979). Since the pulmonary and systemic circulation of these non-crocodilian reptiles are perfused in parallel, the distribution of the cardiac output between them is governed largely by the impedance balance between the two circulations (White & Ross, 1966; Shelton & Burggren, 1976). Holmes (1976), and Webb (1979) among others have suggested that the great similarities in ventricular anatomy in chelonians, squamates and rhynchocephalans may indicate that an undivided ventricular pump, developing a uniform pressure throughout, is the primitive condition in reptiles. The anatomically divided ventricle of the crocodiles, allowing separation of the ventricle into two distinct pumps, presumably represents a more recent evolutionary development.

The cardiac anatomy of the varanid lizards (see Fig. 1B) appears to occupy an intermediate position in this putative evolutionary scheme. The cavum arteriosum, which receives the oxygenated pulmonary venous return via the left atrium, is larger and more muscular than in other non-crocodilian reptiles, (Mathur, 1944; Meinertz, 1952, 1966; Webb, Heatwole & de Bavay, 1971; Webb, 1979) and perfuses the systemic arteries, a function which in other non-crocodilians is achieved by the cavum venosum. The varanid cavum venosum, in turn, is greatly reduced compared to other non-crocodilians, serving as a residual bridging chamber between cavum pulmonale and cavum arteriosum. In Webb's (1979) most recent scheme of the varanid heart, the reduced cavum venosum and the very much larger cavum pulmonale are considered together as a single functional chamber (the cavum pulmonale) receiving systemic venous return and perfusing the lungs, although this appears to be a simplification with a rationale based in nomenclature rather than haemodynamic function. This combined chamber is thus functionally analagous to the 'right' ventricle. Although there are considerable anatomical differences compared to other squamate ventricles, the varanid ventricle is still, nonetheless, anatomically undivided, so 'left-to-right' or 'right-to-left' intracardiac shunts can potentially develop, bypassing the systemic circulation or the lungs respectively.

Very little data on the haemodynamics of the varanid heart have been published, in spite of its apparently intermediate and important position in a hypothetical pathway towards a divided circulation. Millard & Johansen (1974) reported that systemic arterial pressures greatly exceeded pulmonary arterial pressures in *Varanus niloticus*, suggesting that during systole the ventricle was functionally divided into a left, high-pressure pump and a right, low-pressure pump. Intracardiac shunting was considered to be unlikely except during the period of diastolic filling, and even then was considered to be minimal due to the small residual volumes presumed to remain in the ventricle after systemic ejection. However, Berger & Heisler (1977) subsequently used radioactively labelled microspheres in *Varanus exanthematicus* to measure a 16% right-to-left (r–l) and a 13% left-to-right (l–r) intracardiac blood shunt, values only

slightly less than in chelonian reptiles under similar conditions (Shelton & Burggren, 1976).

Our objective in the present study has been to undertake a detailed examination of the haemodynamics of ventricular outflow in a varanid lizard, in order to clarify the extent of pressure and flow division within the ventricle. Blood pressures have been measured in the cardiac chambers and systemic and pulmonary arteries with the pericardium intact in anaesthetized *Varanus exanthematicus*. Arterial blood flow has also been measured and the oxygenation of blood entering and leaving the heart has been determined to assess the extent of intracardiac mixing.

MATERIALS AND METHODS

Experiments were performed on 6 savanah monitor lizards, *Varanus exanthematicus*, weighing between 1·67 and 5·68 kg (mean weight 2·65 kg), transported from Kenya. They were maintained at Aarhus, Denmark, in an animal cage which provided a range of ambient temperatures from 30–40 °C, and were fed mice daily. All animals had been in captivity and in good health for over 1 year.

Anaesthetic and surgical procedures were identical for all lizards. After tracheal intubation, artificial ventilation was begun with a 2% halothane (Fluothane) air mixture provided by a Harvard Apparatus animal respirator connected in series with a Fluotec (Cyprane, Keighley, U.K.) vapourizer. After anaesthesia was induced, halothane levels were reduced to 1·5% for the duration of the experiment. Ventilation was adjusted to a tidal volume of 25–30 ml kg^{-1} at a frequency of 5–8 cycles min^{-1}, yielding a total ventilation of 125–240 ml kg^{-1} min^{-1}, approximating that measured directly in awake *Varanus exanthematicus* at this temperature (Wood, Johansen & Gatz, 1977).

The anaesthetized animal was placed ventral side up on a heated surgical pad. A thermistor was inserted 5–10 cm into the cloaca and the temperature of the pad was adjusted to yield a constant deep body temperature of 34–36 °C, which is the preferred temperature range of this species. A mid-ventral incision 15–20 cm long was made over the sternum, which was then split medially and retracted to reveal the underlying pericardial and pleural cavities. During this procedure, considerable attention was paid to cauterizing or ligating any blood vessels which had to be cut, and blood loss was invariably negligible. In most animals it was required that the lobes of the left and right lung be separated from each other before the underlying major arteries could be exposed.

Sites of blood vessel and cardiac cannulations and placement of electromagnetic blood flow probes are indicated in Fig. 1. Central arteries were non-occlusively cannulated in an upstream direction using 55–60 cm lengths of PE 60 (0·76 mm bore) or PE 50 (0·58 mm bore) polythene cannulae (see Shelton & Burggren (1976) for details of blood vessel cannulation). In some experiments, a cannula was carefully inserted into the pericardial chamber and tied into place, and in most animals varying combinations of the cavum pulmonale, cavum arteriosum and left and right atrium were cannulated without losing pericardial fluid or destroying the integrity of the pericardium. This was achieved by making 2–3 mm slits in the pericardium over the

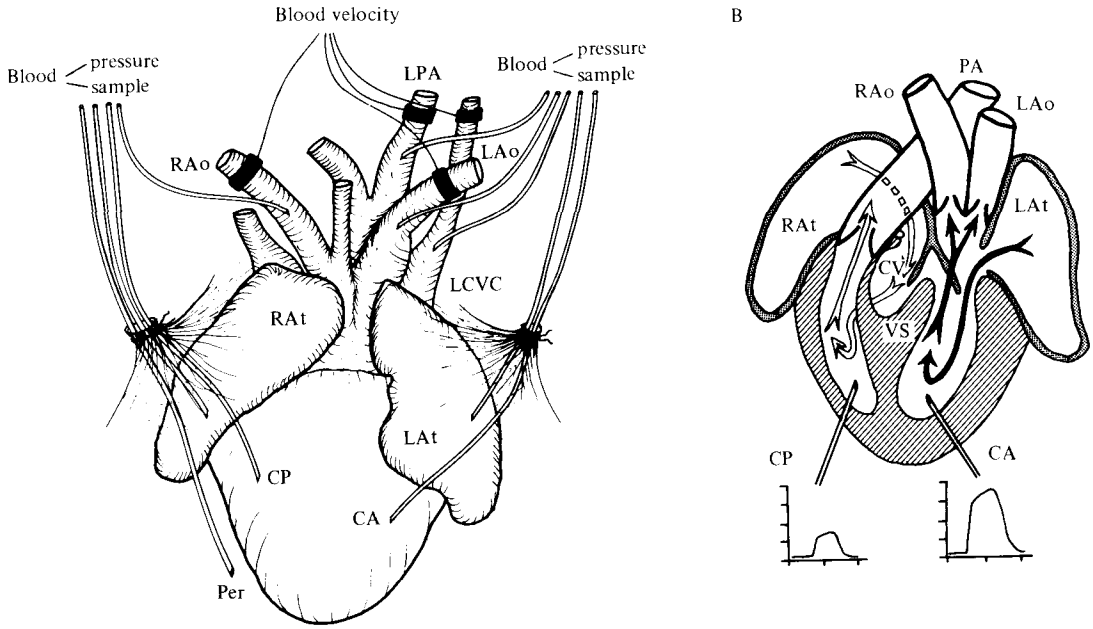

Fig. 1. (A) Diagrammatic illustration of the heart and major blood vessels of *Varanus exanthematicus*, showing placement of blood pressure cannulae and electromagnetic blood flow transducers. (B) Highly schematic drawing of the ventricular chambers. The black arrows indicate the major route of oxygenated blood from the lungs, while the open arrows indicate the major route of deoxygenated blood from the body tissues. CA, cavum arteriosum; CP, cavum pulmonale; LAo, left aorta; LAt, left atrium; LCVC, left cranial vena cava; LPA, left pulmonary artery; Per, pericardium; RAo, right aorta; RAt, right atrium; VS, vertical septum.

appropriate chamber of the heart, taking care to avoid either loss of pericardial fluid or entrance of air bubbles into the pericardial space. The epicardium was carefully drawn to the incision, and a PE 60 cannula (atrial chambers) or a 0·90 mm bore catheter (ventricle) was inserted through the heart wall and tied to the epicardium with a purse string suture. The incision in the pericardium was then drawn around the emerging cannula and secured with a single ligature. Intracardiac and pericardial fluid pressures could thus be measured in a preparation with a functionally intact pericardium. The location of the tip of each cannula was confirmed by post-mortem dissection. All cannulae were filled with heparinized saline, and approximately 200 i.u./kg body weight of sodium heparin were injected into the lizard at the beginning of the experiment.

Cannulae were connected to Statham 23 Db or 23 V fluid pressure transducers, which were attached to a Gould Brush 260 6 channel amplifier/recorder system. The entire pressure recording system with PE 60 catheters had a resonant frequency of 30 Hz with 11% critical damping, while with PE 50 catheters the resonant frequency was 29 Hz with 28% critical damping. Heart rate was about 1 Hz, so both pressure recording systems were assumed to be adequate to record blood-pressure transients without significant phase lag or amplitude error. Pressure calibrations and zero levels were frequently applied to each transducer during the course of the experiments. Measurements of blood flow in the right or left aorta or pulmonary artery were made

Table 1. *Systemic and pulmonary arterial blood pressure in anaesthetized* Varanus exanthematicus

Animal	Body weight (g)	Systemic arterial pressures (cmH_2O) Systolic	Diastolic	Pulse	'Mean'	Pulmonary arterial pressures (cmH_2O) Systolic	Diastolic	Pulse	'Mean'
1	2634	116	95	21	102	65	39	26	48
2	1633	80	59	21	66	80	47	33	58
3	1671	142	96	46	111	70	34	36	46
4	2828	70	46	24	54	47	36	11	40
5	1424	123	90	33	101	32	17	15	22
6	5680	143	80	63	101	46	19	27	20
$\bar{x}$ = 1SD	2645±1594	112±31	78±21	35±17	89±23	57±18	30±12	25±10	40±13

with Statham SP 2202 blood flow meters with electrical, non-occlusive zero function. Periarterial flow probes with lumen diameters of 1·5–4·0 mm were used. Occlusive zero-flow readings as well as non-occlusive zeros were determined, where possible. All flow probes were calibrated *in vitro* using heparinized blood delivered from an elevated reservoir through an excised portion of artery.

P_{O_2}, P_{CO_2}, and pH of 0·4 ml blood samples drawn from implanted cannulae were determined in a Radiometer BMS3 Mk2 blood gas system. Blood oxygen content and capacity were determined by the method described by Tucker (1967).

RESULTS

Arterial blood pressures and flows

Blood pressures measured in the systemic arteries (right and left aorta) were very high compared to those known for other reptiles, with an average 'mean' systemic arterial pressure ($\frac{1}{3}$(systolic pres. + 2 diastolic pres.)) of 89 cm H_2O (Table 1). Systolic and diastolic pressures were very similar in the left and right aorta (Fig. 2). There was considerable variation between lizards in systemic systolic pressure, in spite of identical levels of anaesthesia and surgical preparation. However, within any particular animal, systemic pressure varied little during the typical 4–5 h of pressure measurement.

In five out of six *Varanus* examined, systolic, diastolic, pulse and 'mean' blood pressures in the left pulmonary artery were about half those in the systemic arterial circulation ('mean' pulmonary pressure 40 cm H_2O, Table 1). During no part of the cardiac cycle did blood pressure in the systemic arteries follow a similar time course as pressure in the pulmonary arteries. In one lizard (no. 2, Table 1), the systemic and pulmonary arterial pressure wave forms were identical during ventricular systole, when pulmonary arterial pressures had risen to as high as 80 cm H_2O.

Ventricular ejection into the pulmonary artery usually began concurrent with or slightly in advance of the initiation of flow in the systemic arteries. However, systemic blood flow reached maximum rates within 50 ms of the opening of the valves, and well before maximum systemic systolic pressure was achieved, while pulmonary flow peaked much later and concurrent with peak systolic pressure (Figs. 2, 3A). There was invariably no systemic arterial flow recorded during diastole, but pulmonary arterial

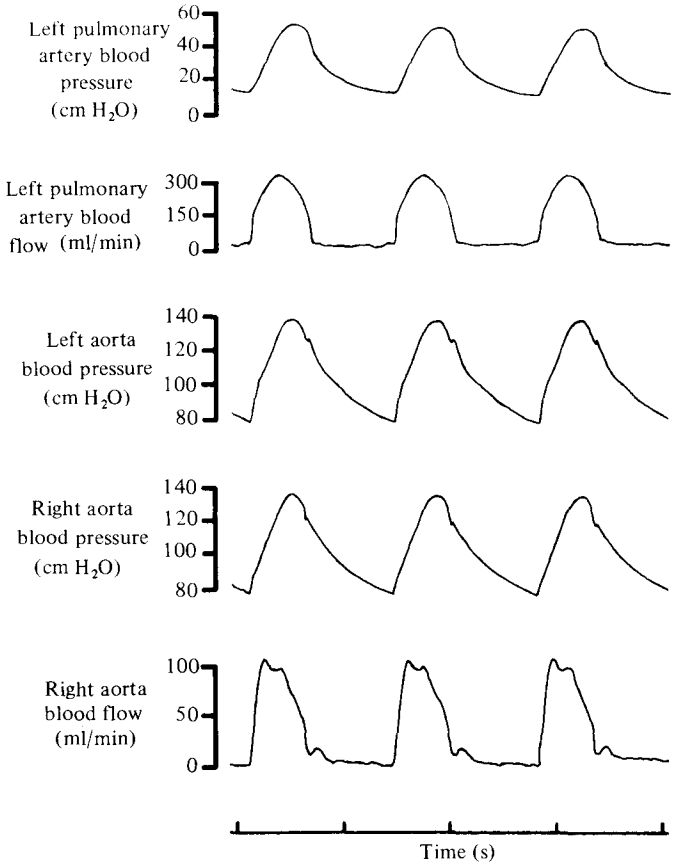

Fig. 2. Pulmonary and systemic arterial blood pressures and flows recorded in a 5680 g *V. exanthematicus*. In this particular preparation the right aortic cannula was implanted in a downstream direction 8 cm from the heart, while the left aortic cannula was implanted upstream 5 cm from the heart.

flow usually continued at measureable levels throughout the diastolic period. Stroke flow in the right aorta, distal to the origin of the common carotid artery, varied between 30% and 60% of stroke flow in the left pulmonary artery, which ranged from 10–20 ml kg^{-1} min^{-1}.

Ventricular haemodynamics

(1) *Pressure relationships between the ventricular compartments*

Intracardiac pressures were measured simultaneously with systemic and pulmonary arterial pressures in all 6 specimens studied. Blood pressure in the cavum arteriosum followed an identical time course to that in the cavum pulmonale during most of diastole (Fig. 3). Atrial contraction typically caused a brief 5–10 cm H_2O increase in CP pressure as the atrio-ventricular valves opened, followed within approximately 100 ms by a very sharp rise (dp/dt = 250 cm H_2O/s) in CA pressure during the period of isovolumetric contraction of this chamber. Importantly, isovolumetric contraction of the cavum pulmonale lagged 55–100 ms behind that in the cavum

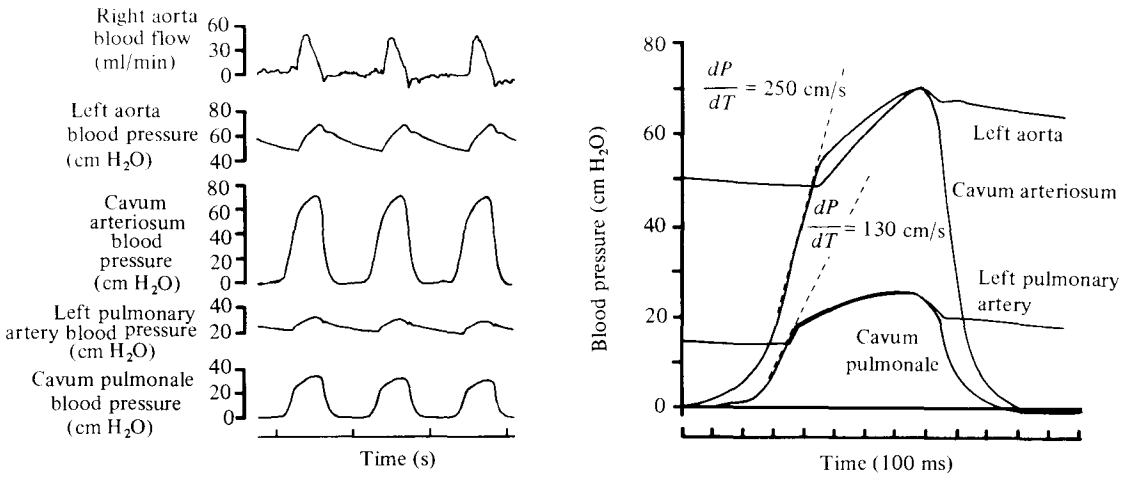

Fig. 3. Simultaneously recorded arterial and ventricular blood pressures and arterial blood flows in a 1671 g *V. exanthematicus*. In A are shown the original tracings, while in B the pressure profiles have been redrawn with a common abscissa. Also indicated by dashed lines are the rates of pressure rise and fall (dP/dT) in the cavum pulmonale and cavum venosum during periods of the cardiac cycle.

arteriosum, and the rate of pressure rise in the CP was only 130 cm H_2O/s, or about half that of the CA. Isovolumetric contraction of the CA continued for about 100 ms longer than in the CP until the much higher diastolic pressures of the aortae were exceeded. Thus although the cavum arteriosum was first to begin contraction, the pulmonary valves were first to open. Most significantly, there was no indication of the beginning of ejection into the pulmonary artery in the pressure profile recorded in the CA, nor were pressure and flow events in the CA detectable in the CP. Similarly, the closing of the systemic arterial valves was not reflected in the CP pressure, nor was any indication of the termination of pulmonary outflow evident in the CA pressure. Only at the beginning of ventricular diastole did pressure profiles recorded in the CP and CA once again follow the same time course. The conclusion from these data is that these two ventricular chambers, perfusing the systemic vascular bed and the lungs, are functionally entirely separate during systole.

In 3 specimens the tips of arterial catheters were repeatedly advanced towards the specimen's heart through the arterial-ventricular valves and into the cavum pulmonale (pulmonary arterial catheter) or cavum arteriosum (aortic catheter), and then withdrawn past the valves back into the artery. Fig. 4 illustrates such an experiment on the pulmonary side in the aberrant lizard which showed identical pressure profiles from the cavum arteriosum and cavum pulmonale during the entire cardiac cycle. Presumably, any significant pulmonary outflow tract impedance in this animal with a pulmonary systolic pressure of 80 cm H_2O would cause an easily measurable pressure drop in blood leaving the ventricle. No such impedance to blood flow could be found in either the pulmonary or systemic outflow tracts in this, or in any other of the more typical lizards which were examined.

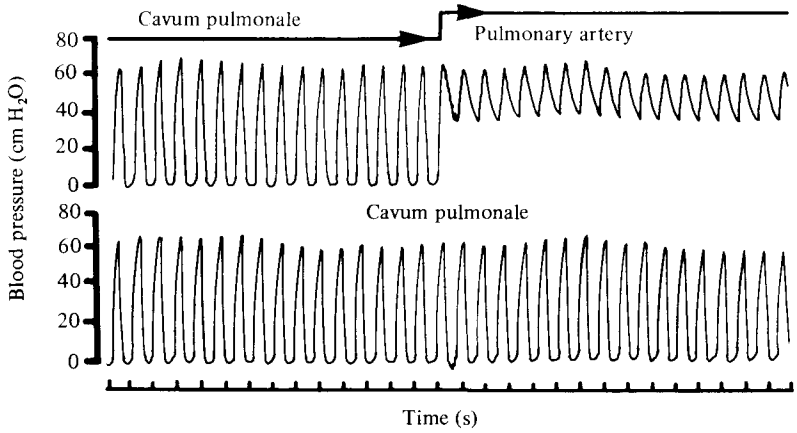

Fig. 4. The effect of withdrawing the tip of a mobile pressure cannula (upper trace) from the cavum pulmonale through the pulmonary valves into the pulmonary artery. The lower trace shows pressure in the cavum pulmonale measured with a pressure cannula implanted directly through the ventricular wall. Animal weight 1633 g.

(2) *Factors affecting intraventricular pressures*

Since artificial ventilation on anaesthetized lizards was employed in all experiments, the influence of spontaneous, intermittent breathing on cardiovascular function could not be examined. Increasing or decreasing the tidal volume of the artificial ventilation, with reciprocal changes in ventilation frequency to maintain total lung ventilation at control levels, had no effect on intraventricular pressure relationships, nor on systemic or pulmonary arterial pressures. Ventilation with hypoxic (P_{O_2} 75 mmHg) or anoxic gas mixtures, or asphyxia produced by stopping the artificial ventilation, similarly had no effect on the functional pressure division of the ventricle. Anoxic or asphyxic periods longer than 4 min usually produced a sharp fall in both systemic and pulmonary arterial pressures, but systolic pressure separation in the ventricle persisted even when a severe bradycardia or arrhythmia began to develop (Fig. 5). Clearly, the pressure division of the ventricle is not disrupted by alterations in the ventilatory pattern, blood gas composition, or blood pH.

Blood gases and intraventricular blood admixture

Table 2 presents mean values for blood gases and pH from four *Varanus*. P_{CO_2} and pH were consistent with data from other studies on this species at 34–36° (Wood, Glass & Johansen, 1977). Because all lizards were constantly ventilated, changing blood oxygenation patterns frequently associated with intermittent breathing in other reptiles (Burggren & Shelton, 1979) were not evident, and blood gases were constant for an individual. As evident in Table 2, blood oxygenation was highest in the left atrium, progressively decreasing in the right aorta, left aorta, pulmonary artery and right atrium. While the mean values convey the overall pattern of blood oxygenation, two individual lizards were noteworthy. In the first, concomitant with a 60 cmH_2O difference in systolic pressure between cavum pulmonale and cavum arteriosum, the following blood O_2 contents were measured; l. atrium = 12·6 vol.%, r. aorta = 12·6

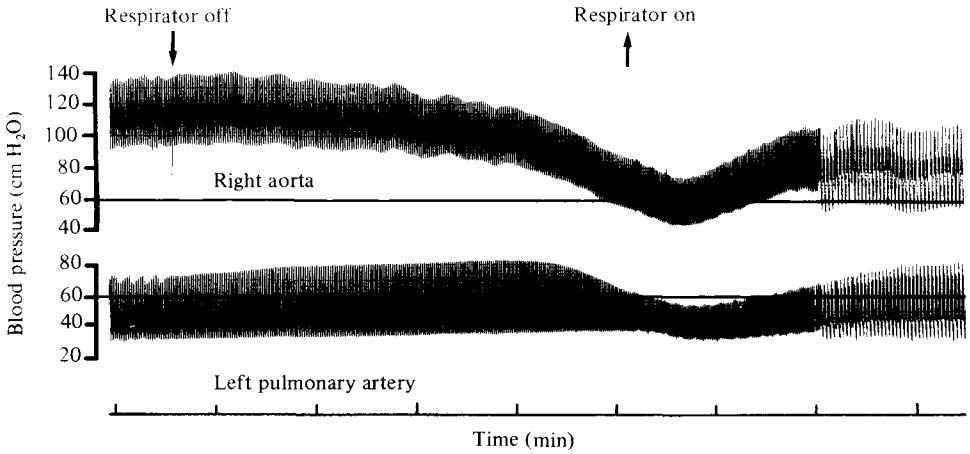

Fig. 5. Effects on systemic and pulmonary arterial blood pressures produced by a prolonged period of apnoea in a 1671 g *V. exanthematicus*. Arrows indicate termination and resumption of artificial ventilation.

Table 2. *Blood gas values in the atria and major arterial vessels of anaesthetized* Varanus exanthematicus *at* 34–36 °C (*Mean values* ± 1 *standard deviation are given*)

	Left atrium	Right aorta	Left aorta	Pulmonary artery	Right atrium
P_{a,O_2} (mmHg)	77 ± 44	73 ± 19	55 ± 4 ·	36 ± 17	31 ± 14
P_{a,CO_2} (mmHg)	25 ± 26	22 ± 9	29 ± 11	25 ± 15	24 ± 22
pH_a	7·562 ± 0·452	7·619 ± 0·209	7·513 ± 0·332	7·540 ± 0·261	7·841 ± 0·424
C_{O_2} (vol. %)	10·9 ± 2·4	9·5 ± 2·6	8·8 ± 0·6	5·7 ± 3·0	4·1 ± 1·4
$C_{O_2\,tot}$ (vol. %)	11·3 ± 2·8	10·9 ± 1·6	11·1 ± 1·7	10·9 ± 1·5	10·8 ± 2·3
O_2 sat. (%)	98 ± 2	85 ± 28	73 ± 8	52 ± 27	37 ± 10
No. of samples	2	7	5	8	2
No. of animals	1	3	2	4	1

vol.%, pul. artery = 5·4 vol.%, r. atrium = 5·2 vol.%. These data indicate that the shunt in either direction within this haemodynamically separated ventricle was almost negligible. In a second lizard however, which showed no evidence of a haemodynamically separated ventricle (i.e. identical pressures in cavum pulmonale and cavum arteriosum), nearly complete intracardiac admixture was affected by large r–l and l–r shunts.

DISCUSSION

Different pressure and flow characteristics occur in the systemic arterial (right and left aorta) and pulmonary outflow vessels from the heart of *Varanus*. These arise because of the distinctly different pressure relations in the cavum arteriosum and cavum pulmonale, both in magnitude and timing. We conclude that the ventricle of *V. exanthematicus* is functionally separated during ventricular systole into a high-pressure systemic pump and a low-pressure pulmonary pump. This is the first published evidence for a vertebrate ventricle having a double pumping action during systole, while the ventricular complex of subcompartments is in anatomical continuity during diastole.

The mechanism by which the functional pressure separation of the ventricular compartments is achieved is not yet understood in detail, but is likely to involve the action of the large vertical septum acting to separate the cavum arteriosum and cavum pulmonale upon the start of ventricular shortening during systole. The vertical septum of *Varanus* is much larger and more muscular than in other squamates, and is directed more anteriorly towards the atrio-ventricular valves and the bases of the outflow arteries. The clearance between the anterior tip of the vertical septum and the atrio-ventricular valve complex is small, and the first shortening of muscle fibres in the ventricle during early systole may thrust the free edge of the vertical septum tightly against the anterior ventricular wall, thus effectively isolating the two ventricular pumps during ventricular contraction. This vertical septal partitioning must be firm enough to withstand the systolic 'trans-septal' pressures of up to 90 cm H_2O without opening and immediately reconnecting the cavum arteriosum and cavum pulmonale.

The cavum venosum is a much reduced compartment in varanids compared to other squamates, appearing as a small communicating channel between the cavum arteriosum and the cavum pulmonale (Fig. 1 B). A small anterior section of the cavum venosum will also bridge the connexion between the cavum arteriosum and the systemic outflow vessels during early systole. As ventricular shortening progresses during ejection, however, the vertical septum reaches the aortico-pulmonary septum, bringing the cavum arteriosum in direct contact with the right and left systemic arteries, exclusively. The cavum arteriosum thus receives blood directly from the left atrium while the cavum pulmonale receives right atrial blood. A low-pressure outflow from the cavum pulmonale to the pulmonary artery during systole is effectively separated from the high-pressure outflow from the cavum arteriosum by the temporary contacts of the vertical septum against the aortico-pulmonary septum and the dorsal aspect of the ventricular wall.

Why division of the ventricle into a high- and a low-pressure pump failed to occur in one specimen and appeared of variable magnitude in others is not clear. Presumably positioning of the vertical septum during the early phase of ventricular shortening may be very critical for the pressure division. This positioning in turn may depend on the pattern of excitation and contraction of the ventricular muscle fibres including the vertical septum. In chelonian reptiles the pattern of cardiac excitation and contraction of the ventricle is highly labile, depending among other factors on the pattern of lung ventilation (Burggren, 1978).

What physiological advantages might there be to the high- and low-pressure ventricular pumps in varanids, compared to other squamate and chelonian hearts operating with a single ventricular pump ? Varanids have higher metabolic scopes at their high preferred body temperature (36–38 °C) compared to other reptiles (Wood *et al.* 1977; Bennett, 1972). The very high systemic blood pressure of varanids may allow, for a given tissue mass, a larger number of capillaries to be perfused without a drop in capillary pressure, compared to a reptile with a systemic arterial blood pressure half or third of that in varanids. This may be a crucial factor in supplying the high skeletal muscle O_2 requirement during activity.

However, high pressure in pulmonary capillaries, which would occur if the ventricle was not separated into two pressure pumps, could compromise the gas-exchange

function of the lung by increasing plasma filtration across the gas-exchange surfaces (Burggren, 1981). Development of a separate low-pressure circulation to the gas-exchange organ would thus appear essential when systemic pressures rise, and is a common feature to all tetrapods with a very large circulatory demand.

If the extent of selective circulation through the heart is compared to the blood pressure values from the cavum arteriosum and cavum pulmonale for individual animals, a high degree of selective blood distribution can be seen to be associated with a marked separation of the pressure into high (CA) and low (CP) values. Our data on intraventricular blood pressure separation excludes that intraventricular mixing, when present, can occur during the systolic phase. Webb (1979) has suggested, based on anatomical deductions of cardiac valve function, that systolic shunting may exist, but the particular conditions of ventricular pressures under which Webb (1979) alleges such shunting would develop, simply do not occur (Fig. 3). Recirculation of the pulmonary and systemic venous returns may, however, be caused by intraventricular mixing during ventricular filling in diastole when the ventricular subcompartments are interconnected, or to a lesser extent during the iso-volumetric phase of ventricular systole.

The mechanism presently proposed for selective filling from the right and left atrium into the cavum pulmonale and cavum arteriosum, respectively, is based on contact made between the large atrioventricular valves and the vertical septum during ventricular filling (Webb, 1979). In varanids, as in other reptiles, the atrial contractions are the major filling agents for the ventricle (K. Johansen and W. Burggren, in preparation). Only slight differences in atrial pressure development and/or the distensibility of the ventricular compartments may influence the selective filling of cavum arteriosum and cavum pulmonale from the two atria. Also when the ventricular end diastolic volume has reached its maximum value, the juxtaposition of the a-v valve complex with the vertical septum may not be complete and some admixture may occur.

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