On the function and origin of the avian renal portal shunt and its potential significance throughout evolution

Buyse Kobe[1,*], Koen Stein[2], Ward De Spiegelaere[3], Pieter Cornillie[3], Marcus Clauss[4] and Geert P.J. Janssens[1]

[1]*Department of Veterinary and Biosciences, Faculty of Veterinary Medicine, Ghent University, Heidestraat 19, 9820 Merelbeke, Belgium*

[2]*Archaeology Environmental Changes and Geochemistry, Vrije Universiteit Brussel, 1000 Brussels, Belgium*

[3]*Laboratory of Morphology, Faculty of Veterinary Medicine, Ghent University, Salisburylaan 133, 9820 Merelbeke, Belgium*

[4]*Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich,Winterthurerstr. 260, 8057 Zurich, Switzerland*

[*]Author for correspondence (E-mail: Kobe.buyse@ugent.be; Tel.: +32479763315).

ABSTRACT

All birds possess a unique venous architecture surrounding the kidneys known as the renal portal system. In veterinary medicine, this system is well known for causing a first-pass effect when medication is administered parenterally *via* the leg veins, i.e. venous blood from the leg is filtered before entering general circulation thus possibly compromising adequate dosage. Additionally, bilateral valves are present in these veins, and it has been hypothesized that they play a crucial role in regulating flow through the kidneys to protect them against increases in blood pressure. While this hypothesis has been acknowledged, it has not been thoroughly explored. We propose that the function of the renal portal valve extends beyond its significance for kidney function, potentially impacting general hemodynamics. Examining anatomical similarities with extant non-avian reptiles, which lack the renal portal shunt with valve, could reveal additional functionalities of this system in birds. Given the endothermic metabolism and the energetically expensive locomotor activity of birds, the resistance of the hepatic and renal portal system might constrain the blood flow from splanchnic to non-splanchnic blood vessels necessary for (sustained) peak performance. Therefore, diverting blood from the renal portal system using the renal portal valve as a regulatory structure might represent a key adaptation to facilitate sustained peak performance. In addition, we hypothesize that this shunt and valve represents a very early adaptation in amniotes, possibly lost in extant non-avian reptiles but enhanced in birds, with a pivotal role in maintaining hemodynamic homeostasis to support the high metabolic rates characteristic of birds.

Key words: avian, renal portal system, function, evolution, comparative anatomy.

CONTENTS

I. INTRODUCTION

Experts in veterinary pharmacology have considered the avian renal portal system as an important structure, due to the so-called ‘first-pass effect’ when medication is administered *via* the hind limbs. In some circumstances, venous blood from the tail and legs passes through capillaries of the liver or kidneys, and hence blood constituents can be metabolized or waste products removed before this blood enters the general circulation (Coutant, Vergneau-Grosset & Langlois, 2018). It is in this practical context that the renal portal system has been studied extensively. Based on existing evidence, it has been hypothesized that the renal portal system protects the kidney against both pressure overloads and hypoperfusion (Wideman, 1988; Mirabella, Esposito & Pelagalli, 1996). Moreover, due to active secretion of uric acid from the portal veins, this system ensures the elimination of nitrogenous waste when glomerular filtration of arterial blood is reduced. Lastly, the renal portal circulation possesses a one-way valve in all birds investigated so far, yet its specific function is rarely stated in the literature. The renal portal valve has been considered to regulate blood flow into the kidneys and thus to protect the renal portal system against high pressures (Mirabella *et al*., 1996). In this review, we propose an expanded hypothesis for the function of the avian renal portal valve. We suggest that the valve not only represents a local adaptation relevant for the kidney, but also is an adaptation that may be able to regulate general whole-body hemodynamics.

We first compare birds with crocodiles; these taxa share a common kidney type, the metanephros, as well as a similar renal portal system (Holz, 1999). We then place the function of the renal portal system into the broader context of avian flight. The latter is reasonably well understood (Morrison *et al*., 2018), but knowledge of cardiovascular physiology during exercise is still limited (Butler, 2016). We propose an evolutionary scenario wherein the renal portal valve evolved as an adaptation to high metabolic activity. Our hypothesis can contribute to theories on the evolutionary transition from ectothermy to tachymetabolic endothermy.

II. THE RENAL PORTAL SYSTEM AND ITS FUNCTIONALITY

(1) Gross functional anatomy of the avian kidneys

To explore the blood flow pattern in the abdomen of birds, an understanding of the architecture and functionality of the avian kidneys and their similarities with those of reptiles is essential. In contrast to the cortical and juxtaglomerular nephron types in mammals, all of which have a loop of Henle, avian kidneys comprise two types of functional units: so-called ‘mammalian-like’ nephrons and ‘reptilian-like’ nephrons. The mammalian-like nephrons are located in medullary cones (Fig. 1). They are structurally similar to mammalian nephrons in that they contain a loop resembling the mammalian loop of Henle, enabling them to create a concentration gradient in the medullary cones that promotes the reabsorption of water. Unlike in mammals, the concentration gradient is created by NaCl instead of urea. This enables birds to concentrate urine independently of the presence of nitrogen (Wideman, 1988). The 'reptilian-like' nephrons resemble the nephrons of alligators (*Alligator mississippiensis*) (Moore *et al.*, 2009) and crocodiles (*Crocodylus acutus*) (Davis & Schmidt-Nielsen, 1967), amongst others. They are located in the cortical regions of the kidneys, and are more numerous than mammalian-like nephrons. Reptilian-like nephrons lack a loop of Henle and are less able to participate in creating a concentration gradient. Birds in environments with excess water have larger cortex regions with presumably more reptilian-like nephrons, whereas birds in arid environments have kidneys with more medullary mass containing the mammalian-like nephrons (McNabb, 1969; Casotti & Richardson, 1992; Casotti & Braun, 1996; Peña-Villalobos, Valdés-Ferranty & Sabat, 2013; Rezaei *et al.*, 2019). Therefore, the ratio of mammalian- and reptilian-like nephrons may affect the overall concentrating ability of the avian kidneys.

(1) Arterial pressure as the main driving force of glomerular filtration but not uric acid excretion

All avian nephrons and reptilian nephrons are characterized by a crude glomerular filter. This crude sieve allows larger molecules, such as proteins, to appear in the primary urinary filtrate and aid the suspension of uric acid (Casotti & Braun, 1996, 2004). In this crude glomerular sieve, the main driving force of glomerular filtration is the difference in hydrostatic pressure in the efferent arterioles because there is a negligible difference in osmotic pressure between plasma and the primary urinary filtrate. This is in contrast to mammals, in which both hydrostatic and osmotic pressure regulate filtration, as explained by the Starling principle (Michel, Woodcock & Curry, 2020). Indeed, birds regulate arterial blood flow to the kidney in response to water scarcity and thereby control glomerular filtration rate. Avian arterioles in the kidney cortex, i.e. those serving the reptilian-like nephrons, are sensitive to arginine vasotocin. Levels of this hormone typically increase during dehydration, eliciting arterial vasoconstriction, and thus limiting glomerular filtration and urine production, which results in water retention (Goldstein, 2006; Orosz & Echols, 2020).

The main nitrogenous waste product to be filtered is uric acid; however, uric acid can also be excreted by the renal tubuli. This enables birds and reptiles not only to filter out but also actively to excrete nitrogenous waste products, thus disconnecting uric acid excretion from water excretion. Therefore, even in water-deprived conditions and with limited glomerular filtration, birds and reptiles can eliminate nitrogenous waste products from the blood (Schmidt-Nielsen & Davis, 1968; Ventura *et al.*, 1989).

(2) The renal portal system as a solution to decreased arterial blood flow

Water excretion in the kidney relies mainly on arterial blood flow, which could pose perfusion problems in arid conditions: if the arterial blood supply to the kidneys ceased in order to save water, this would compromise nutrient deliver and waste product removal to and from the kidneys (Orosz & Echols, 2020). In order for the reptilian-like nephrons to function properly, a mechanism is needed to sustain kidney cortex tissue perfusion if arterial blood supply is limited.

To address this limitation, the reptilian-like nephrons are nested in a capillary network supplied by portal veins. A portal vein system is defined as blood coming from a capillary bed that flows into another capillary bed without first passing through the heart.

How the portal blood flow is related to the nephrons is represented in Fig. 1. The kidney lobules are fed by arteries (a in Fig. 1) that form the glomerular filters (e in Fig. 1) ending in a sinusoid capillary network that resides in the cortical region (c in Fig. 1). This network is fed by drainage from the portal veins (14 in Fig. 2B) coming in from the periphery of each lobule (*Vena interlobularis*) (b in Fig. 1). All blood in this pool eventually drains into the centre of the lobule in the *Vena intralobularis* (d in Fig. 1) leading to the renal vein (13 in Fig. 2B) (Wideman, Braun & Anderson, 1981).

The gross anatomy of the avian renal portal system is well known (Sperber, 1949; Akester, 1964, 1967). Blood originating from the portal veins can enter different kidney divisions. Akester (1964) first hypothesized a bidirectional blood flow in the *Vena mesentarica caudalis* (coccygeomesenterial vein) (17 in Fig. 2B), later documenting that the flow in the renal portal veins indeed can change direction (Akester, 1967). Odlind (1978) reported the same observation. Both authors determined that the direction of blood flow in the portal veins and the influx of portal blood into the kidneys can change rapidly in a bird, but they did not determine the underlying physiological mechanisms (Akester, 1967; Odlind, 1978).

Kidney function tests showed that during reduced arterial pressure, such as in water-deprived birds, portal blood sustains kidney perfusion to the *Vas capillare sinusoideum* within the kidney lobule (c in Fig. 1) (Wideman & Gregg, 1988; Wideman, 1991; Glahn *et al.*, 1993). Dantzler (1989) suggested that a renal portal system was essential to sustain blood flow in the kidney to prevent ischemic necrosis of the kidney tubuli.

(4) Studies on the functionality of the renal portal system

One major dissimilarity between the gross anatomy of birds and crocodilians (Fig. 2) is the presence of a shunt with a valve between the portal veins and the major circulation (Miehle & Bauer, 1993; Holz, 1999). This renal portal valve is located in a vein segment between the *Vena portalis caudalis* (14 in Fig. 2) and the *Vena renalis caudalis* (13 in Fig. 2) called the *Vena iliaca communis* (18 in Fig. 2). In this review, we will refer to the latter as the renal portal shunt and its renal portal valve. Although only studied in few avian species, the valve shows a similar architecture and location among different bird species. In chickens (*Gallus gallus domesticus*) (Akester, 1964), penguins (Sphenisciformes) (Oelofsen, 1973), ducks (Mirabella *et al.*, 1996) and Cape vultures (*Gyps coprotheres*) (Havenga *et al.*, 2020), the valve is cone-shaped and has a round orifice facing the *Vena cava caudalis*. In Palaeognathae such as ostriches (*Struthio camelus*), this valve has three openings (Carvalho *et al.*, 2007). The absence of the renal portal shunt with a valve in crocodilians means that all blood originating from the hind limbs and tail is directed to the portal system of the liver or to the portal system of the kidneys (Gans & Harris, 1964). By contrast, the presence of a portal shunt, with a valve that can control the flow through this shunt, makes the avian circulation more flexible. It was first hypothesized that birds could open and close the renal portal valve, reversing blood flow in the *V. mesentarica caudalis* (Akester, 1964), enabling blood from the intestines to be directly shunted into the general circulation without passing through the liver. Nevertheless, the extent and functional relevance of these traits remained poorly understood (Akester, 1967; Bell & Freeman, 1971). Sturkie, Dirner & Gister (1978) argued that the importance of the renal portal valve was overemphasized and that it had little functional relevance. Yet, the renal portal valve in chickens and penguins contains smooth muscle fibres and densely packed nerve bundles described as autonomic nerves (Gilbert, 1961; Oelofsen, 1973), and the valve relaxed in response to noradrenaline/adrenaline and contracts when exposed to acetylcholine (Rennick & Gandia, 1954; Akester & Mann, 1969; Bennett & Malmfors, 1975; Sturkie *et al.* 1978; Burrows, Braun & Duckles, 1983; Palmore & Ackerman, 1985). A fast closing speed and large resistance to flow when the valve was closed was noted in response to applied pressure (Akester & Mann, 1969), and there was a high pressure difference across the valve (Mirabella *et al.*, 1996). It has been suggested by others that the valve appears to be a complex structure that plays an important role in avian hemodynamics (Burrows *et al.*, 1983).

Akester (1967) questioned whether shunting of blood between the portal systems reflected a change in metabolic status or whether it represented an anatomical relic without physiological significance, with the valve opening and closing in an arbitrary fashion. Most authors have concluded that this shunt and valve function as a flow-and-pressure regulator to protect the kidney against extreme pressures (Mirabella *et al.*, 1996; Braun, 2015).

No definitive evidence has been found to show that portal blood perfusion of the kidney is dependent on the functional status of the valve, but it is rather independent of intralobular arterial vasoconstriction and water balance (Akester, 1967; Dantzler, 1989). It is possible that the kidneys of both birds and reptiles partly autoregulate portal flow by increasing or decreasing arterial pressure in the kidney. Consequently, in comparison to the non-avian reptilian system, it is likely that the addition of a valve to one of the major blood vessels will have a crucial role in avian hemodynamics (Rennick & Gandia, 1954).

III. THE POSSIBLE EXTENDED FUNCTION OF THE RENAL PORTAL SHUNT IN AVIAN HEMODYNAMICS

The shunt with its valve could also affect the general venous blood flow. Although this may seem obvious, there are few reports on this functionality. In contrast to other extant sauropsids, birds are active, endothermic animals with a largely aerobic metabolism. This would require fundamentally different hemodynamics, including an increased blood flow, especially during periods of activity. We therefore postulate that the valve functions not only as a safety mechanism to prevent pressure overload in the kidney, but also facilitates a higher venous return and therefore a higher cardiac output at times of increased activity.

As in mammals, the circulatory system of birds could be explained by a two-compartmental model as defined by Krogh (1912). The model in mammals consists of splanchnic vessels, i.e. vasculature of the stomach, intestines, liver, spleen and other abdominal organs, and non-splanchnic vessels. In contrast to non-splanchnic blood flow, the splanchnic venous system is compliant, with a slow blood flow, and acts as a reservoir. At the onset of exercise, the arterial blood flow to the splanchnic tissues is reduced, and subsequently pressure and volume in the splanchnic veins decreases, resulting in a redistribution of blood towards the non-splanchnic circulation and increasing non-splanchnic venous return. Therefore, the contraction of splanchnic arterioles regulates the volume of blood currently in non-splanchnic circulation. This mechanism is reinforced by concerted contraction of the splanchnic veins due to their sensitivity to sympathetic stimulation. This is accompanied by dilatation of the arterioles in active muscles which increases the mean circulatory filling pressure and the non-splanchnic venous return (Gelman, Warner & Warner, 2008). In contrast to mammals, where the splanchnic compartment drains solely *via* the portal system of the liver into the general circulation, birds likely have additional drainage of their splanchnic veins into the renal portal system *via* the coccygeomesentarial vein (17 in Fig. 2B).

The avian body plan consists of different muscle groups called moduli (Gatesy & Dial, 1996). Running is mainly performed by the pelvic modulus, whilst flying makes use of pectoral and caudal moduli. In different bird species these muscle moduli are used to various degrees, depending on the main type of locomotory behaviour (Heers & Dial, 2015). To illustrate the role of the renal portal shunt and the renal portal valve on general hemodynamics, we consider three avian activity types, requiring different combinations of moduli: complete rest, take-off and active flight, and running or swimming.

(1) The portal valve during steady-state rest

During rest, the pectoral modulus at the front of the body is inactive, implying that these muscles consume little energy and require low levels of blood perfusion (Ellerby *et al.*, 2005). Arterial blood is, in this situation, most likely directed towards the intestinal organs to maximize digestion and nutrient absorption (Fig. 3A). Considering two extreme states of the renal portal valve, closed or completely open, a closed valve would prevent the flow of venous blood into the general circulation and direct it *via* the *Vena mesentarica caudalis* to the mesenteric veins to facilitate metabolization of its nutrients in the liver. By contrast, if the renal portal valve was open, we hypothesize that a fraction of venous blood originating from the mesenteric veins will take the path of least resistance *via* the *Vena mesentarica caudalis* through the renal portal shunt into the general circulation, which would limit the first-pass effect in the liver (Coutant *et al*., 2018). Thus, this situation would result in blood from the intestines passing into the general circulation and through the non-selective arterial glomerular filter in the kidneys, with the possible loss of absorbed nutrients such as proteins in the urine. In other words, a lack of nutrient assimilation in the liver and a loss of nutrients *via* renal excretion represent theoretical negative consequences of an open valve in a resting situation. Experimental evidence has shown that this valve can withstand high pressures from the build-up of blood in the compliant abdominal vein system (Akester & Mann, 1969). The vein most likely to serve as an abdominal capacitance vessel is the *Vena mesentarica caudalis* (17 in Fig. 2B). This vein drains little tissue, yet is a large autonomously enervated vein connecting the caudal part of the kidney portal system to the mesenteric veins close to the liver hilus (Maher, 2019). The situation with a closed valve resembles the blood flow of extant reptiles filtering all blood from the hind body and intestines through either the portal system of the kidney or liver without first entering the general circulation. In this case, the splanchnic compartment according to Krogh (1912) consists of the stomach, intestines, liver, spleen, kidneys, hindlimbs and tail, as all these systems are connected with and feed into the capacitance vessels; after passing through either the renal or the hepatic portal system the blood enters the general circulation (Fig. 3A).

(2) Take off and active flight

During take-off or active flight, muscle perfusion in the pectoral modulus has to increase to provide these groups with oxygen and nutrients, especially in the energy-consuming initial stages of flight (Peters, 2005; Biewener, 2011; Sakamoto *et al.*, 2013, Butler 2016). Consequently, blood vessels dilate in this muscle modulus and require a higher volume of blood perfusion (Fig. 3B). Flight muscles are densely packed with capillaries to accommodate high perfusion rates (Turner & Butler, 1988; Lundgren & Kiessling, 1988).

During the onset of activity most aerobic animals relocate blood pools in order to perfuse their muscles. In reaction to the onset of exercise, mammals recruit additional blood *via* contraction of the arterioles of the liver, spleen and skin vessels that act as reservoirs of venous blood (Krogh, 1912; Gelman *et al*., 2008; Rothe, 2011). In birds, casts of the venous system and radiographs (Akester, 1964; Oelofsen, 1973) show that significant amounts of blood can be located in abdominal capacitance veins such as the *Vena mesenterica caudalis* during rest. These veins can contract under sympathetic tonus, facilitating redirection of their blood towards active muscles (Gelman *et al*., 2008). Large veins in chickens, such as the *Vena mesentarica caudalis*, are well enervated with adrenergic receptors and contain smooth muscle fibres (Bennett & Malmfors, 1970; Bennet, 1974). However, the blood in these veins would still have to pass through the hepatic portal system, where the liver capillaries will exert resistance to passage of blood. In mammals, this is attenuated by dilating these veins by activating β-adrenergic receptors (Green, 1977). However, in birds, redirection of blood from the capacitance veins to active muscles might be more effectively facilitated by opening the renal portal valve and thus activating the renal portal shunt. Because of the large number of nerve endings around subendothelial cells in the valve, Mirabella *et al*. (1996) hypothesized that the valve contains sensory elements and therefore regulation could either originate locally or from baroreceptors in the carotid sinuses and the aortic arch in response to decreased pressure at these sites. Sympathetic tonus and release of noradrenaline would relax the renal portal valve (Rennick & Gandia, 1954; Akester & Mann, 1969; Bennett & Malmfors, 1975; Sturkie *et al.*, 1978; Burrows *et al.*, 1983; Palmore and Ackerman, 1985). Moreover, it was observed in isolated vein segments and valves of chickens that the iliac veins contract in response to the same stimulus that makes the valve relax (Burrows *et al.*, 1983). The combination of dilation of arterioles in active muscles, increased resistance in splanchnic arterioles, contracting capacitance veins and opening of the renal portal valve could improve the venous return, hence elevating cardiac output during the onset and duration of sustained activity. During the onset of flight, cardiac output increases 7.2-fold (Peters, 2005). In soaring flyers like vultures (*Gyps fulvus* and *Gyps himalayensis*), it was noted that heart rate increases only in the initial stage of flight (Duriez *et al*., 2014). However, it is likely that during sustained periods of flapping flight, such as during migration, requirements for an increased cardiac output might extend to longer time periods, making the renal portal shunt particularly valuable. Despite the scarcity of studies on venous return in avian subjects, a response of increased venous return to increase cardiac output is widely adopted across vertebrates (Joyce & Wang, 2021). However, the role of the renal portal shunt in facilitating venous return remains to be quantified.

(3) Running and swimming birds

Flight is just part of the locomotory spectrum of birds. Many birds rely on running or swimming compared to flying (Gatesy & Dial, 1996). Running and swimming using the legs , in contrast to swimming using wings (like penguins), make use of other muscle moduli and require different blood flow patterns compared to flight. As in the flight muscles of airborne birds, the arterioles in the leg muscles of cursorial birds dilate, causing higher perfusion of these muscles (Ellerby *et al.*, 2005). This leads to a different situation from flying: during flight, the legs are part of the splanchnic compartment according to Krogh (1912); during running, they will be part of the non-splanchnic compartment. Opening the renal portal valve would not only facilitate the drainage of the capacitance vessels, but would also be essential to direct venous blood from these muscles directly to the heart. The blood returns from the legs into the caudal portal vein *via* the *Vena ischiadica* and the *Vena iliaca externa* (19 and 6, respectively in Fig. 2B).

(4) Other considerations

Rest and onset of flight cover the extremes of the spectrum of avian activity. This is a dynamic system in which the renal portal valve can react flexibly to varying demands of blood flow allocation. The amount of blood that is recruited from the portal veins to perfuse flight muscles will depend on the pressure sensed in the general circulation. At the same time, this mechanism must ensure basal portal perfusion of the liver and kidney even during high activity. Flight is a metabolically demanding process and water intake is limited during long periods of flight. While the filtration rate caused by arteriolar perfusion did not significantly change during flight, tubular fractional water resorption due to portal perfusion became more important (Gerson & Guglielmo, 2013). Therefore, maintaining the portal circulation during long flights will be advantageous to maintain kidney function, reabsorb water and/or for efficient removal of nitrogenous waste products.

IV. THE RENAL PORTAL SHUNT AND THE VALVE IN AN EVOLUTIONARY PERSPECTIVE

(1) Similarities during embryological development

Above, we pointed out the similarities between the kidney and the central venous architecture of birds and reptiles. The main structure that makes birds unique among extant vertebrates with a portal system is the renal portal shunt between the hind limb circulatory system and the front of the body. While it may be advantageous to shunt blood from the hind body to the general circulation during peak activity, it remains unclear how this renal portal shunt evolved. The vein segment containing the renal portal valve is referred to as the *Vena iliaca communis* (Baumel, 1993), commonly known as the renal portal shunt. As this segment is in alignment with the *Vena iliaca externa* (6 in Fig. 2B), it could potentially be seen as its extension. However, we hypothesize that this small shunt may have other origins. During embryological development, many mammals have an abdominal vascular arrangement similar to that of adult reptiles and birds (Fig. 2C). The anatomical similarities between the arrangement in birds and 8-week-old human embryos suggest that the renal portal shunt could have the same origin as the human sub-supracardinal anastomosis (Huntington & McClure, 1920). If this is the case, this renal portal shunt may have been present in early amniotes. Early ancestors of both Sauropsida and Synapsida could have had a similar abdominal vascular architecture. The last common ancestor of mammals, reptiles and birds dates back to the early Amniota, around 312 million years ago (Benton, 1990; Laurin & Reisz, 1995). This group separated from amphibian reptiliomorphs by evolving, amongst other adaptations, a different type of kidney, the metanephros, and with it a different vasculature.

(2) Metabolism in early amniotes and cursorial dinosaurs

In an extensive review, Grigg *et al*. (2022) postulated that tachymetabolic endothermia could be older than the divergence between Sauropsida and Synapsida, thus questioning the paradigm of parallel evolution of endothermy in birds and mammals. Endothermy may therefore be an early synapomorphy, subsequently lost in extant reptiles. Early archosaurian reptiles evolved the capacity for running and potentially a higher metabolic rate (Persons & Currie, 2017). The erect position of the leg bones and development of the *Musculo* *caudofemoralis* complex removes Carrier’s constraint, i.e. the constraint to run and breathe simultaneously due to lateral position of the limbs and sideways flexing of the body. Its removal is believed to aid in prolonged activity and a higher metabolic rate (Carrier, 1987; Persons & Currie, 2017). The removal of Carrier’s constraint and prolonged activity enabled early dinosaurs to evolve bipedality, as this further removed the constraint of front limbs whilst running (Persons & Currie, 2017). Recent work suggests that some dinosaurs and their archosaur ancestors had elevated basal metabolic rates, and were capable of retaining heat (Desmond, 1976; Grady *et al.*, 2014; Legendre *et al.*, 2016). Endothermy in theropods was suggested based on locomotory dynamics (Pontzer, Allen & Hutchinson, 2009), similarities of bone histology with extant endothermic species, and the presence of feathers (Benton, 2014. A high cardiac output and high mean arterial pressure in dinosaurs also has been proposed, based on the size of the foramen nutritium in dinosaur bones (Seymour, 2016). One could suggest, therefore, that these adaptations in osteology and subsequently musculature would also lead to adaptations in the cardiovascular system to fuel increased performance. The portal systems of the liver and kidneys would potentially limit cardiac performance, as venous return would be impaired if dinosaurs had a venous architecture like today’s reptiles. Therefore, in cursorial dinosaurs, it is plausible that a sub-supracardinal anastomosis present in embyros would be retained into adult life to form a renal portal shunt similar to that seen in extant birds. This would enable improved venous return from exercising muscles of the hind limbs and tail to the *Vena cava caudalis* and therefore a greater cardiac output (Fig. 4). Blood from the legs and tail could be directed to this renal portal shunt by a vein segment similar to the hindlimb anastomosis in reptiles (10 in Fig. 2A). Modern avian species could have inherited this venous arrangement, although anatomical adaptations, such as reduction of the heavy tail (Rashid *et al.*, 2014), led to further changes to the venous system in extant birds.

(3) Extant non-avian reptiles without a renal portal shunt

In modern reptiles, a direct renal portal shunt is absent, with venous return from the hind limbs and intestines only entering the general circulation by means of the two capillary beds in the kidneys and liver (Gans & Harris, 1964; Holz, 1999). Terrestrial ectothermic animals have a slower metabolism and a musculoskeletal arrangement that relies on anaerobic metabolism, and therefore can not support a highly intensive cursorial lifestyle (Carrier, 1987). The low cardiac output of these animals enables this system to function well without a shunt and with continuous portal circulation. An increased cardiac output requiring a higher venous return would be difficult to achieve, as blood must pass through the capillary portal systems of the kidneys and the liver (Berlin & Bakker, 2014).

There is evidence that the ancestors of modern-day crocodiles were once mesothermic animals that moved in a fully erect quadrupedal position (Reilly & Elias, 1998; Seymour *et al.*, 2004). Crocodiles then evolved secondary ectothermy as an adaptation to a lifestyle with a slow metabolism and seasonal fluctuations in climate and food availability (Pough, 1980; Grigg *et al*., 2022). This implies that the early ancestors of crocodilians may also have possessed a renal portal shunt to sustain high venous return, which was lost together with other changes in their cardiovascular system when they became secondarily ectothermic (Grigg *et al*., 2022). Ectothermic metabolism requires a low cardiac output, and separation of the hind body circulation maximized the continuous use of the portal circulatory systems of the liver and kidneys. This hypothesis could be tested with comparative studies of the ontogeny of vein systems in reptile and avian embryos.

(4) The addition of a valve in the renal portal shunt

The renal portal valve has, to our knowledge, a similar morphology in all avian species except paleognath birds. In paleognaths, this valve is reported as having three orifices instead of one as in other birds (Carvalho *et al.*, 2007). A recent study used tinamous (Tinamidae) to investigate the role of the cardiovascular system in the evolution of flight and supported the ‘ground up’ paradigm, i.e. that flight evolved in running rather climbing ancestors (Altimiras *et al*., 2017). Despite the different anatomy of the renal portal valve in paleognaths and the dissimilar metabolic demands between running and flying based on the legs being part of the splanchnic compartment in birds (Grubb, Jorgensen & Conner, 1983), it is likely that both forms of exercise would require a functional valve, and that this valve was retained during the evolution of flight.

One report tentatively mentions a putative valve in a turtle, the red-eared slider (*Trachemis scripta elegans*) (Holz *et al.*, 1997). However, this valve is found at a different location (in the abdominal veins), mainly consists of connective tissue, and would only direct venous blood into either the portal system of the liver or the portal system of the kidneys, but would not facilitate shunting to the non-splanchnic venous circulation.

Modern avian species evolved from cursorial archosaurs into highly active animals with arboreal and aerial lifestyles requiring high metabolic rates. Consequently, a higher basal cardiac output, stroke volume and heart mass was needed to sustain this lifestyle (Dzialowski & Crossley, 2015). High activity requires a high input of nutrients, water conservation and, in cases of long flight bouts, the recovery of metabolites. The presence of a renal portal valve in the renal portal shunt renders this system versatile, facilitating the recruitment of blood when necessary, yet directing intestinal blood to the liver to metabolize and recover nutrients when possible. It is unknown whether the renal portal valve was already present in the early ancestors of birds. We speculate that among other adaptations, this valve may have been advantageous and could have evolved into a highly intricate structure when bipedal dinosaurs began to use their front legs for activities such as climbing or gliding, to protect portal flow to the liver and kidneys while enabling higher cardiac output when needed.

V. CONCLUSIONS

(1) Modern birds have many anatomical and physiological similarities to extant non-avian reptiles. Yet, birds have one major structure that is absent in the latter, the renal portal shunt with a renal portal valve.

(2) It has long been stated that this shunt regulates portal flow in the kidney and protects the kidneys against increases in venous pressure. However, based on the similarities between birds and reptiles in kidney anatomy and the surrounding venous architecture, we hypothesize that the renal portal shunt could have other functions. A renal portal shunt could improve venous return and cardiac output during increased activity.

(3) A closed shunt, directing blood to the liver and kidneys, would be advantageous in recovering and metabolizing nutrients and filtering waste products originating from the intestines and hind limbs as occurs in reptiles. An open shunt would allow blood to bypass these systems and enter the general circulation. Hence, the presence of a renal portal valve to regulate the flow between systems depending on metabolic status makes the overall circulatory system more versatile. Recent ideas on endothermy in early amniotes and cursoriality and mesothermy in dinosaurs lead us to hypothesize that a high cardiac output was needed early in amniote evolution and therefore a direct venous link between the hind body and general circulation was advantageous. If early amniotes were indeed endothermic, we propose that an anastomosis between the portal system and the general circulation could have persisted, eventually being lost in extant reptiles.

(4) This hypothesis provides new insights into the importance of the renal portal valve as a vital structure in bird metabolism, rather than simply functioning as a pressure valve to regulate renal portal flow. The renal portal valve enables birds to sustain a high cardiac output similar to that of mammals, whilst profiting from nutrient-recovery portal systems similar to

those of reptiles and amphibians. Measurements of venous return in birds at the onset of flight or during sustained flapping flight would clarify the importance of blood flow through the renal portal shunt.

(5) Comparative studies on the ontogenesis of blood vessels in birds and reptiles could provide further insights and illuminate the early development of this structure in both clades.

VI. REFERENCES

ALTIMIRAS, J., LINDGREN, I., GIRALDO-DECK, L. M., MATTHEI, A. & GARITANO-ZAVALA, Á. (2017). Aerobic performance in tinamous is limited by their small heart. A novel hypothesis in the evolution of avian flight. *Scientific Reports* **7(1)**, 15964.

AKESTER, A.R. (1964). Radiographic studies of the renal portal system in the domestic fowl (*Gallus domesticus*). *Journal of Anatomy* **98**, 365–376.

AKESTER, A.R. (1967). Renal portal shunts in the kidney of the domestic fowl. *Journal of Anatomy* **101**, 569–594.

AKESTER, A.R. & MANN, S.P. (1969). Adrenergic and cholinergic innervation of the renal portal valve in the domestic fowl. *Journal Of Anatomy* **104**, 24–252.

AREY, L. B. (1974). *Developmental Anatomy 7th Ed.,* W.b. saunders, Philadelphia, NY.

BAUMEL, J.J. (1993). *Handbook Of Avian Anatomy: Nomina Anatomica Avium.* Publications of the Nuttall Ornithological Club (USA). no. 23.

BELL, D.J. & FREEMAN, B.M. (1971). *Physiology And Biochemistry Of The Domestic Fowl*. Volumes 1, 2, 3. Academic Press, London.

BENNET, T. (1974). The peripheral and autonomic nervous systems. *Avian Biology*, 1–46. Academic Press.

BENNETT, T. & MALMFORS, T. (1970). The adrenergic nervous system of the domestic fowl (*Gallus domesticus (L.)*). *Zeitschrift Für Zellforschung Und Mikroskopische Anatomie* **106**, 22–50.

BENNETT, T. & MALMFORS, T. (1975). Autonomic control of renal portal blood flow in the domestic fowl. *Experientia* **31**, 1177–1178.

BENTON, M.J. (1990). Phylogeny of the major tetrapod groups: Morphological data and divergence dates. *Journal Of Molecular Evolution* **30**, 409–424.

BENTON, M. J. (2014). Vertebrate palaeontology. John Wiley & Sons, Hoboken, NJ.

BERLIN, D.A. & BAKKER, J. (2014). Understanding venous return. *Intensive Care Medicine* **40**, 1564–1566.

BIEWENER, A.A. (2011). Muscle function in avian flight: achieving power and control. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 1496–1506.

BRAUN, E.J. (2015). Chapter 12 - Osmoregulatory Systems of Birds. *Sturkie's Avian Physiology 6th ed*. Academic Press, San Diego.

BURROWS, M.E., BRAUN, E.J. & DUCKLES, S.P. (1983). Avian renal portal valve: a reexamination of its innervation. *American Journal Of Physiology-Heart And Circulatory Physiology* **245**, H628–H634.

BUTLER, P. J. (2016). The physiological basis of bird flight. *Philosophical Transactions Of The Royal Society B: Biological Sciences* **371**(**1704**), 20150384.

CARRIER, D.R. (1987). The evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. *Paleobiology* **13**, 326–341.

CARVALHO, H. S. D., CIBOTO, R., BAITELO, C. G., DIAS, R. A., & CORTOPASSI, S. R. G. (2007). Anatomy of the renal portal system and its implications for the use of anesthetic agents in the restraint of ostriches (*Struthio camelus*). *Ciência Rural* **37**, 1688–1694.

CASOTTI, G. & BRAUN, E.J. (1996). Functional morphology of the glomerular filtration barrier of *Gallus gallus*. *Journal Of Morphology* **228**, 327–334.

CASOTTI, G. & BRAUN, E.J. (2004). Protein location and elemental composition of urine spheres in different avian species. *Journal Of Experimental Zoology Part A: Comparative Experimental Biology* **301A**, 579–587.

CASOTTI, G. & RICHARDSON, K.C. (1992). A stereological analysis of kidney structure of honeyeater birds (Meliphagidae) inhabiting either arid or wet environments. *Journal of Anatomy*, 180, 281–288.

COUTANT, T., VERGNEAU-GROSSET, C. & LANGLOIS, I. (2018). Overview of drug delivery methods in exotics, including their anatomic and physiologic considerations. *Veterinary Clinics: Exotic Animal Practice,* **21(2)**, 215–259.

DANTZLER, W.H. (1989). *Comparative Physiology Of The Vertebrate Kidney*. Springer-Verlag, Berlin.

DAVIS, L.E. & SCHMIDT-NIELSEN, B. (1967). Ultrastructure of the crocodile kidney (*Crocodylus acutus*) with special reference to electrolyte and fluid transport. *Journal Of Morphology* **121**, 255–276.

DESMOND, A.J. (1976). *The Hot-Blooded Dinosaurs: A Revolution In Palaeontology*. The Dial Press, New York.

DURIEZ, O., KATO, A., TROMP, C., DELL'OMO, G., VYSSOTSKI, A. L., SARRAZIN, F. & ROPERT-COUDERT, Y. (2014). How cheap is soaring flight in raptors? a preliminary investigation in freely-flying vultures. *PLoS One* **9(1)**, E84887.

DZIALOWSKI, E.M. & CROSSLEY, D.A. (2015). Chapter 11 - The Cardiovascular System. *Sturkie's Avian Physiology (6th ed.).* Academic Press, San Diego.

Ellerby, D.J., Henry, H.T., Carr, J.A., Buchanan, C.I. & Marsh, R.L. (2005). Blood flow in guinea fowl (*Numida meleagris*) as an indicator of energy expenditure by individual muscles during walking and running. *The Journal of Physiology* **564**, 631–648.

Gans, C. & Harris, V.A. (1964). *The Anatomy Of The Rainbow Lizard Agama agama L. Copeia*, 1964, 597.

Gatesy, S.M. & Dial, K.P. (1996). Locomotor Modules and the Evolution of Avian Flight. *Evolution* **50**, 331–340.

Gelman, S., Warner, D. S. & Warner, M. A. (2008). Venous function and central venous pressure: a physiologic story. *The Journal Of The American Society Of Anesthesiologists* ***108*(4),** 735–748.

Gerson, A.R. & Guglielmo, C.G. (2013). Measurement of glomerular filtration rate during flight in a migratory bird using a single bolus injection of FITC-inulin. *American Journal Of Physiology-Renal Physiology* **305**, F823–F829.

Gilbert, A.B. (1961). The innervation of the renal portal valve of the domestic fowl. *Journal of Anatomy* **95**, 594–598.1.

Glahn, R.P., Bottje, W.G., Maynard, P. & Wideman, R.F. (1993). Response of the avian kidney to acute changes in arterial perfusion pressure and portal blood supply. *American Journal Of Physiology-Regulatory, Integrative And Comparative Physiology* **264**, R428–R434.

Goldstein, D.L. (2006). Regulation of the avian kidney by arginine vasotocin. *General And Comparative Endocrinology* **147**, 78–84.

Grady, J.M., Enquist, B.J., Dettweiler-Robinson, E., Wright, N.A. & Smith, F.A. (2014). Evidence for mesothermy in dinosaurs. *Science* **344**, 1268–1272.

Green, J. F. (1977). Mechanism of action of isoproterenol on venous return. *American Journal Of Physiology-Heart And Circulatory Physiology* ***232*(2),** H152–H156.

GRIGG, G., NOWACK, J., BICUDO, J. E. P. W., BAL, N. C., WOODWARD, H. N. & SEYMOUR, R. S. (2022). Whole-body endothermy: ancient, homologous and widespread among the ancestors of mammals, birds and crocodylians. *Biological Reviews* ***97*****(2),** 766–801.

GRUBB, B., JORGENSEN, D. D. & CONNER, M. (1983). Cardiovascular changes in the exercising emu. *Journal Of Experimental Biology* ***104*****(1),** 193–201.

HAVENGA, L., NAIDOO, V., WOLTER, K., DUNCAN, N. & GROENEWALD, H.B. **(**2020). Does the renal portal valve exist in a raptor species? A study aimed at further evaluating the mechanism of toxicity of diclofenac in vultures. *Anatomia, Histologia, Embryologia* **49**, 836–841.

HEERS, A.M. & DIAL, K.P. (2015). Wings versus legs in the avian bauplan: Development and evolution of alternative locomotor strategies. *Evolution* **69**, 305–320.

HOLZ, P., BARKER, I.K., CRAWSHAW, G.J. & DOBSON, H. (1997). The Anatomy and Perfusion of the Renal Portal System in the Red-Eared Slider (*Trachemys scripta elegans*). *Journal Of Zoo And Wildlife Medicine* **28**, 378–385.

HOLZ, P.H. (1999). The Reptilian Renal Portal System - A Review. *Bulletin Of The Association Of Reptilian And Amphibian Veterinarians* **9**, 4–14.

HUNTINGTON, G. S. & MCCLURE, C. F. (1920). The development of the veins in the domestic cat (Felis domestica) with especial reference, 1) to the share taken by the supracardinal veins in the development of the postcava and azygos veins and 2) to the interpretation of the variant conditions of the postcava and its tributaries, as found in the adult. *The Anatomical Record* **20(1)**, 1–30.

JOYCE, W. & WANG, T. (2021). How cardiac output is regulated: August Krogh's proto-Guytonian understanding of the importance of venous return. *Comparative Biochemistry And Physiology Part A: Molecular & Integrative Physiology* ***253***, 110861.

KOENIG, H. E., KORBEL, R., LIEBICH, H. G. & KLUPIEC, C. (2016). *Avian anatomy: Textbook and colour atlas*. 5m Books Ltd, Lings, UK.

KROGH, A. (1912). The Regulation of the Supply of Blood to the Right Heart : With a Description of a new Circulation Model. *Skandinavisches Archiv Für Physiologie* **27(2)**, 227–248.

LAURIN, M. & REISZ, R.R. (1995). A reevaluation of early amniote phylogeny. *Zoological Journal Of The Linnean Society* **113**, 165–223.

LEGENDRE, L.J., GUÉNARD, G., BOTHA-BRINK, J. & CUBO, J. (2016). Palaeohistological Evidence for Ancestral High Metabolic Rate in Archosaurs. *Systematic Biology* **65**, 989–996.

LUNDGREN, B. O., & KIESSLING, K. H. (1988). Comparative aspects of fibre types, areas, and capillary supply in the pectoralis muscle of some passerine birds with differing migratory behaviour. *Journal Of Comparative Physiology B* **158**, 165–173.

MAHER, M.A. (2019). Descriptive Anatomy of Hepatic and Portal Veins with Special Reference to Biliary Duct System in Broiler Chickens (*Gallus gallus domesticus*): A Recent Illustration. *Brazilian Journal Of Poultry Science* **21**.

MCNABB, F.M.A. (1969). A comparative study of water balance in three species of quail 2. Utilization of saline drinking solutions. *Comparative Biochemistry And Physiology* **28**, 1059–1074.

MICHEL, C.C., WOODCOCK, T.E. & CURRY, F.R.E. (2020). Understanding and extending the Starling principle. *Acta Anaesthesiologica Scandinavica* **64**, 1032–1037.

MIEHLE, C.E. & BAUER, A.M. (1993). Visceral vasculature in the family Cordylidae (Reptilia: Squamata). *South African Journal Of Zoology* **28**, 146–154.

MIRABELLA, N., ESPOSITO, V. & PELAGALLI, G.V. (1996). The Valva Portalis Renalis in the Duck (*Anas platyrhynchos*). *Cells Tissues Organs* **157**, 151–158.

MOORE, B.C., HYNDMAN, K.A., COX, A., LAWLER, A., MATHAVAN, K. & GUILLETTE, L.J. (2009). Morphology and Histochemistry of Juvenile American Alligator (*Alligator mississippiensis*) Nephrons. *The Anatomical Record* **292**, 1670–1676.

MORRISON, M.L., RODEWALD, A.D., VOELKER, G., COLÓN, M.R. & PRATHER, J.F. (2018). *Ornithology: Foundation, Analysis, And Application*. JHU Press, Baltimore, MD.

ODLIND, B. (1978). Blood flow distribution in the renal portal system of the intact hen. A study of a venous system using microspheres. *Acta Physiologica Scandinavica* **102**, 342–356.

OELOFSEN, B.W. (1973). Renal function in the penguin (*Spheniscus demersus*) with special reference to the role of the renal portal system and renal portal valves. *African Zoology* 8, 41–62.

OROSZ, S.E. & ECHOLS, M.S. (2020). The Urinary and Osmoregulatory Systems of Birds. *Veterinary Clinics: Exotic Animal Practice* **23**, 1–19.

PALMORE, W.P. & ACKERMAN, N. (1985). Blood flow in the renal portal circulation of the turkey: effect of epinephrine. *American Journal Of Veterinary Research* **46**, 1589–1592.

PEÑA-VILLALOBOS, I., VALDÉS-FERRANTY, F. & SABAT, P. (2013). Osmoregulatory and metabolic costs of salt excretion in the Rufous-collared sparrow (*Zonotrichia capensis).* *Comparative Biochemistry And Physiology Part A: Molecular & Integrative Physiology* **164**, 314–318.

PERSONS, W.S. & CURRIE, P.J. (2017). The functional origin of dinosaur bipedalism: Cumulative evidence from bipedally inclined reptiles and disinclined mammals. *Journal Of Theoretical Biology* **420**, 1–7.

PETERS, G.W. (2005). Cardiorespiratory adjustments of homing pigeons to steady wind tunnel flight. *Journal Of Experimental Biology* **208**, 3109–3120.

PONTZER, H., ALLEN, V. & HUTCHINSON, J. R. (2009). Biomechanics of running indicates endothermy in bipedal dinosaurs. *PLoS One* **4(11)**, e7783.

POUGH, F. H. (1980). The advantages of ectothermy for tetrapods. *The American Naturalist* **115(1),** 92–112.

RASHID, D.J., CHAPMAN, S.C., LARSSON, H.C., ORGAN, C.L., BEBIN, A.-G., MERZDORF, C.S., BRADLEY, R. & HORNER, J.R. (2014). From dinosaurs to birds: a tail of evolution. *EvoDevo* **5**, 25.

REILLY, S.M. & ELIAS, J.A**.** (1998). Locomotion in alligator mississippiensis: kinematic effects of speed and posture and their relevance to the sprawling-to-erect paradigm. *Journal Of Experimental Biology* **201**, 2559–2574.

RENNICK, B.R. & GANDIA, H. (1954). Pharmacology of Smooth Muscle Valve in Renal Portal Circulation of Birds. *Proceedings Of The Society For Experimental Biology And Medicine* **85**, 234–236.

REZAEI, M., MASOUMI, Z., NABIPOUR, A., AZIZZADEH, M. & BEHNAM-RASOULI, M. (2019). Histological and Stereological Study on the Kidneys in Sparrows Living in Wet and Arid Zones. *Slovenian Veterinary Research* **56**, 105–114.

ROTHE, C. F. (2011). Venous system: physiology of the capacitance vessels. *Comprehensive Physiology*, 397–452.

SAKAMOTO, K.Q., TAKAHASHI, A., IWATA, T., YAMAMOTO, T., YAMAMOTO, M. & TRATHAN, P.N. (2013). Heart rate and estimated energy expenditure of flapping and gliding in black-browed albatrosses. *Journal Of Experimental Biology* **216**, 3175–3182.

SCHMIDT-NIELSEN, B. & DAVIS, L.E. (1968). Fluid Transport and Tubular Intercellular Spaces in Reptilian Kidneys. *Science* **159**, 1105–1108.

SEYMOUR, R.S. (2016). Cardiovascular Physiology of Dinosaurs. *Physiology* **31**, 430–441.

SEYMOUR, R.S., BENNETT-STAMPER, C.L., JOHNSTON, S.D., CARRIER, D.R. & GRIGG, G.C. (2004). Evidence for Endothermic Ancestors of Crocodiles at the Stem of Archosaur Evolution. *Physiological And Biochemical Zoology* **77**, 1051–1067.

SPERBER, I. (1949). Investigations on the circulatory system of the avian kidney. Almqvist & Wiksells.

STURKIE, P.D., DIRNER, G. & GISTER, R. (1978). Role of renal portal valve in the shunting of blood flow in renal and hepatic circulations of chickens. *Comparative Biochemistry And Physiology Part C: Comparative Pharmacology* **59**, 95–96.

TURNER, D.L. & BUTLER, P.J. (1988). The aerobic capacity of locomotory muscles in the tufted duck, *Aythya fuligula*. *Journal Of Experimental Biology* **135**, 445–460.

VENTURA, S.C., NORTHRUP, T.E., SCHNEIDER, G., COHEN, J.J. & GARELLA, S. (1989). Transport and histochemical studies of bicarbonate handling by the alligator kidney. *American Journal Of Physiology-Renal Physiology* **256**, F239–F245.

WIDEMAN, R.F., BRAUN, E.J. & ANDERSON, G.L. (1981). Microanatomy of the renal cortex in the domestic fowl. *Journal Of Morphology,* **168**, 249–267.

WIDEMAN, R.F. (1988). Avian kidney anatomy and physiology. *Critical Reviews In Poultry Biology* **1**, 133–176.

WIDEMAN, R.F. (1991). Autoregulation of avian renal plasma flow: contribution of the renal portal system. *Journal Of Comparative Physiology B* **160**, 663–669.

WIDEMAN, R.F. & GREGG, C.M. (1988). Model for evaluating avian renal hemodynamics and glomerular filtration rate autoregulation. *American Journal Of Physiology-Regulatory, Integrative And Comparative Physiology* **254**, R925–R932.

VII. ACKNOWLEDGEMENTS

The authors wish to acknowledge the reviewer, Jordi Altimiras, and the editors, John Welch and Alison Cooper, for their insightful feedback and thorough editing, which greatly enhanced the quality of this manuscript. This article was published with the support of the University Foundation of Belgium.

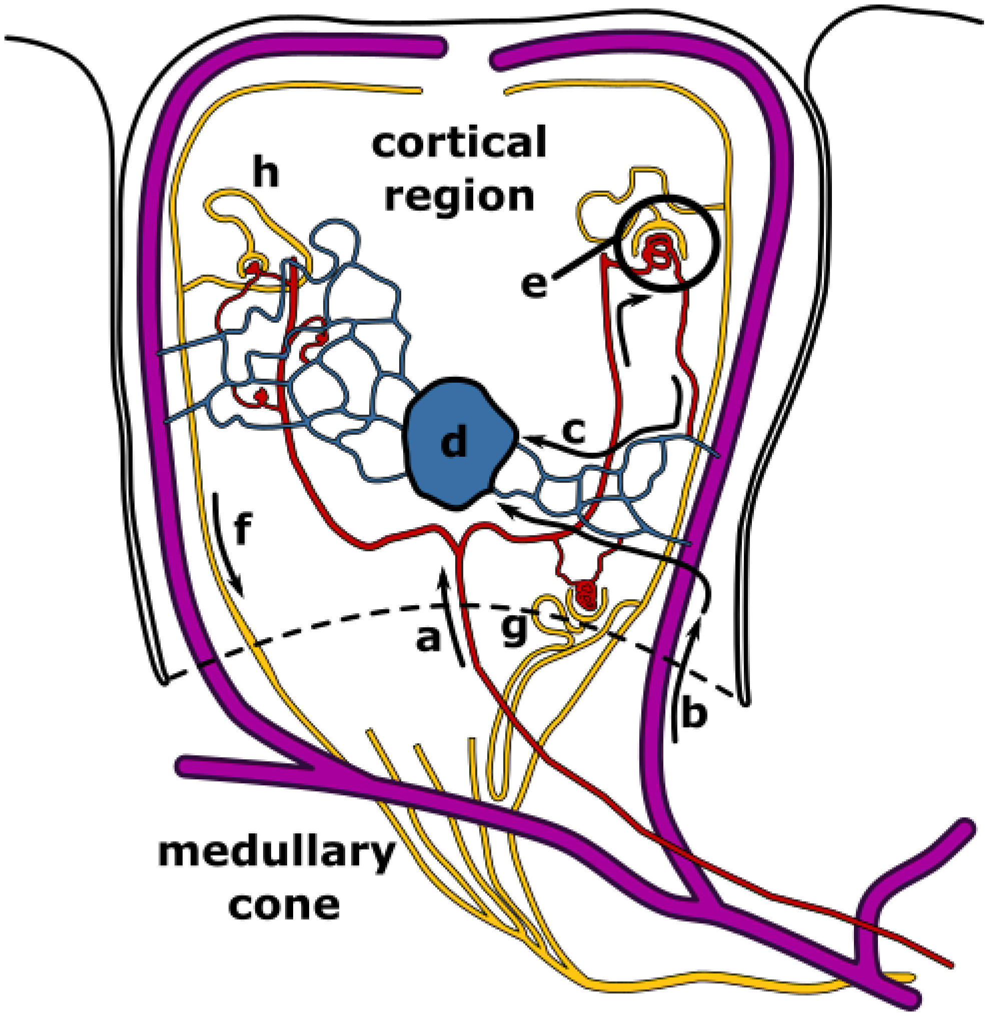

Fig. 1. Schematic representation of the architecture of the avian renal lobe (adapted from Koenig *et al*., 2016). a, *Arteria renalis* (arterial blood); b, *Vena interlobularis* (portal blood); c, *Vas capillare sinusoideum*; d, *Vena intralobularis* draining into the *Vena renalis*; e, glomerulus; f, urinary tubule; g, mammalian-like nephron; h, reptilian-like nephron. Arrows indicate direction of blood flow and urinary flow.

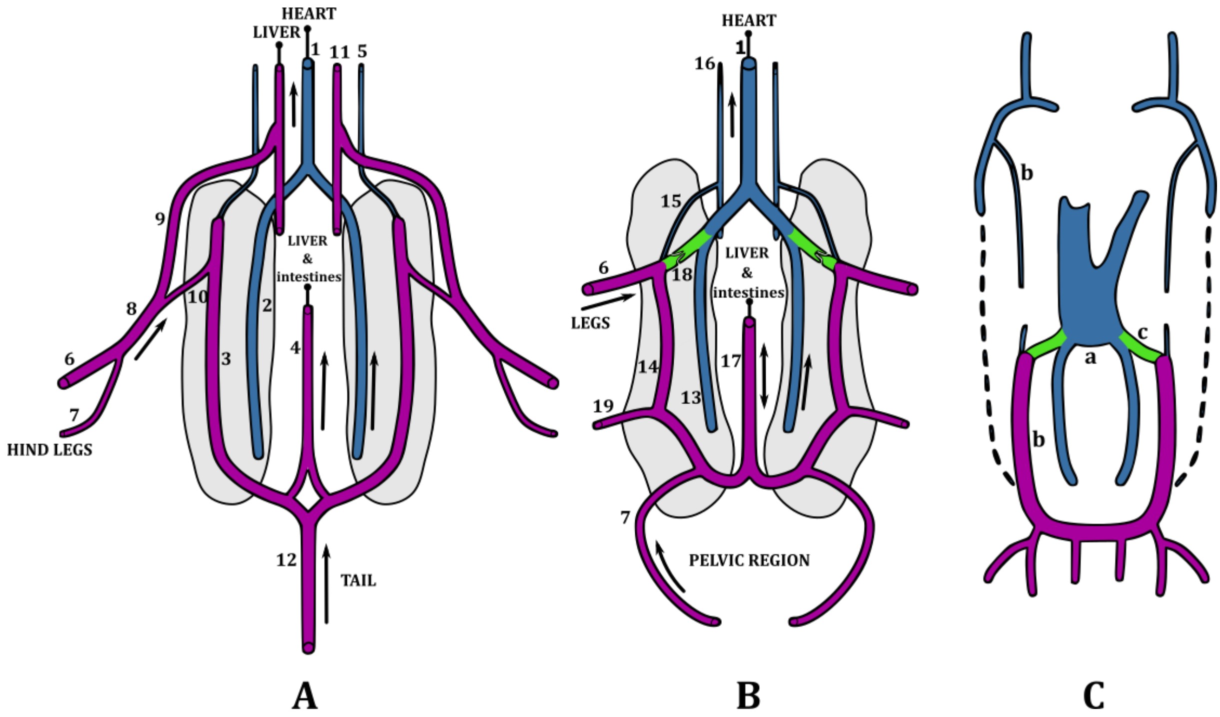

Fig. 2. (A) Arrangment of the veins surrounding the kidneys of Crocodilia (adapted from Holz, 1999). (B) Arrangement of the veins surrounding the kidneys of birds (adapted from Baumel, 1993). (C) Venous post-cardiac layout of the 8-week-old human embryo (adapted from Arey, 1974). 1, *Vena cava caudalis*; 2, *Vena renalis*; 3, *Vena portalis*; 4, *Vena mesenterialis*; 5, *Vena vertebralis*; 6, *Vena iliaca externa*; 7, *Vena iliaca interna*; 8, *Vena iliaca communis*; 9, pelvic vein; 10, hindlimb anastomosis: 11, bilateral abdominal vein; 12, *Vena caudalis*; 13, *Vena renalis caudalis*; 14, *Vena portalis caudalis*; 15, *Vena portalis cranialis*; 16, *Sinus venosus vertebralis*; 17, *Vena mesentarica caudalis* (*Vena coccygeomesenterica*); 18, *Vena iliaca communis* (renal portal shunt) with renal portal valve; 19, *Vena ichiadica*; a, subcardinal veins; b, supracardinal veins; c, sub-supracardinal anastomosis. Arrows indicate direction of blood flow. In crocodiles (A), blood from the hind legs (6,7) flows towards the abdominal vein (11) and subsequently to the liver or towards the renal portal system (3). In birds (B), from the legs (6,19) flows towards the renal portal system (14) and can be shunted to the caudal renal vein (13). In both species, blood from the tail (12) and pelvic region (7) flows towards the renal portal system. In crocodiles (A), the

renal portal system can also drain towards the liver and intestines (4); this can also occur in birds (17) although flow may be bidirectional. Blood originating from the kidneys *via* the renal veins (2 in A; 13 in B) drains towards the heart (1).

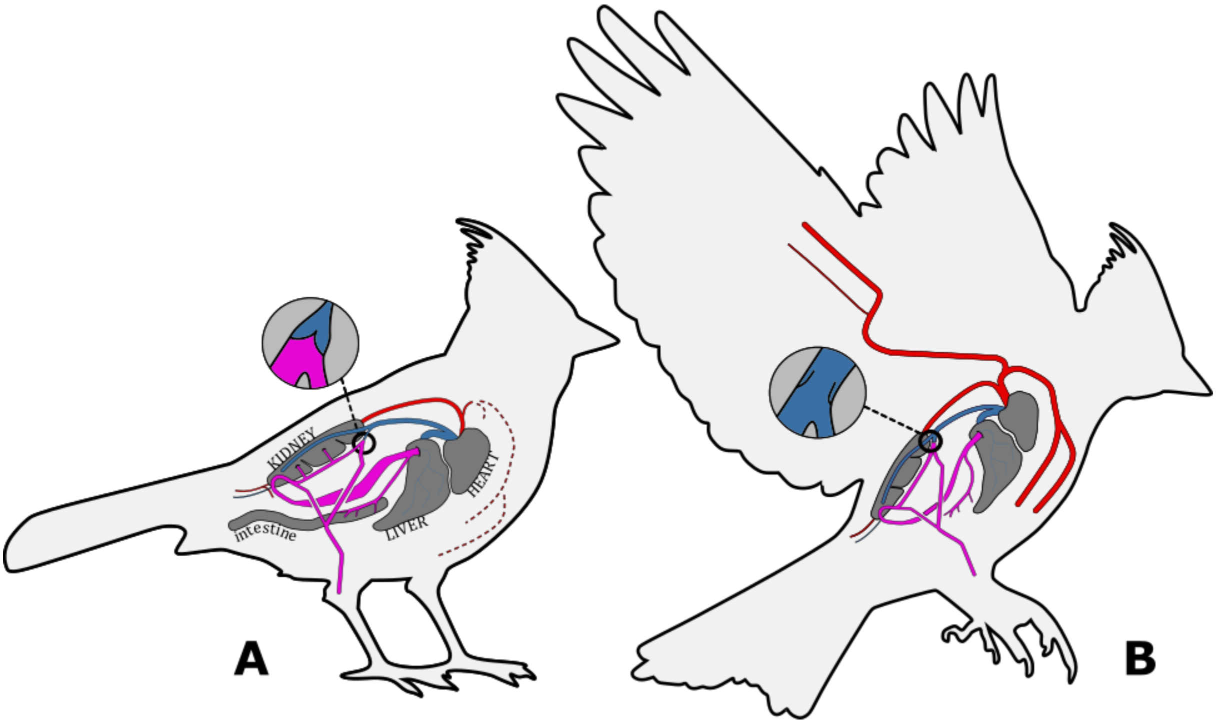

Fig. 3. A semi-anatomical representation of the redistribution of blood between a resting bird (A) and a bird at the onset of flight (B). The anterior resting muscle groups require minimal perfusion at rest (red dashed lines) but need higher perfusion rates during flight (red solid lines). Blood that is drained from the tail, hind limbs and abdominal organs resides in the abdominal capacitance veins behind a closed central valve in a resting bird (purple). This blood can either enter the portal circulation of the kidney or the portal circulation of the liver before entering the general circulation (blue). The blood in the abdominal veins (purple vein between intestines and kidneys) can be recruited to perfuse the flight muscle by opening the valve and contracting the abdominal veins.

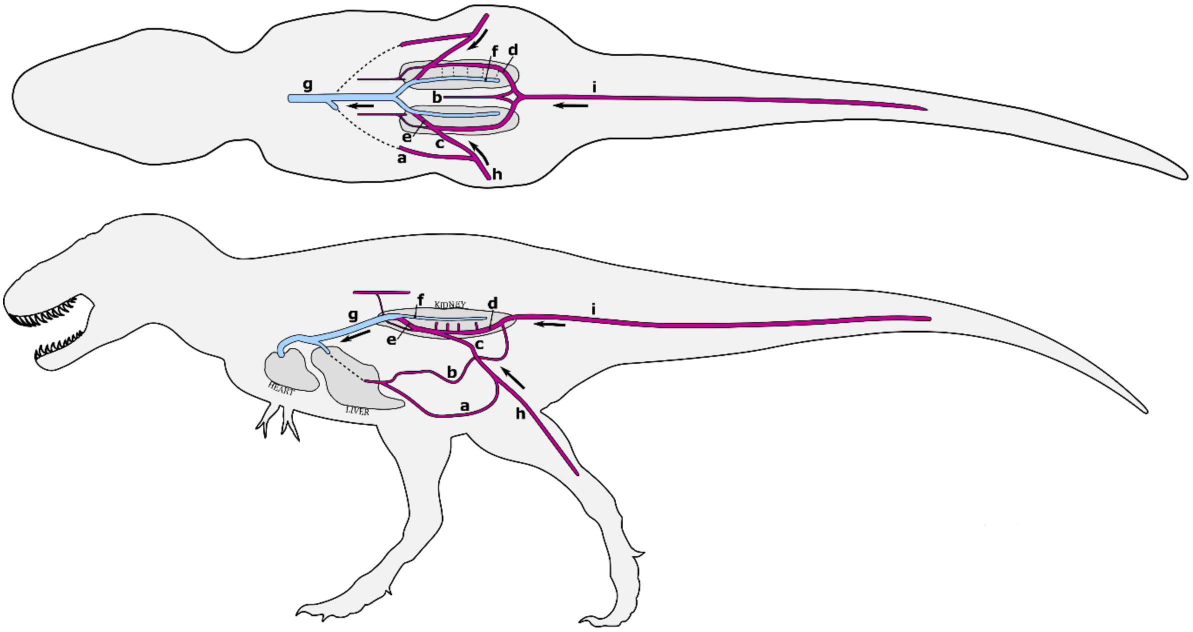

Fig. 4. Hypothetical anatomy of the vein system in theropods. This scheme is an adaptation of the basic non-avian reptile venous plan with the addition of a renal portal shunt. During running, leg and tail muscles require higher perfusion, necessitating a higher cardiac output with an adequate venous return. To aid this, blood could be directed directly to the heart from the hind body circulation (purple) to the general circulation (blue) without passing first through the portal capillaries of the kidney or liver. Arrows indicate blood flow from the legs (h) and tail (i) towards the portal vein (d), then shunted by the renal portal shunt (e) into the general circulation (g). a, abdominal veins; b, mesenteric vein; c, limb anastomosis; d, portal vein; e, renal portal shunt; f, renal vein; g, vena cava caudalis; h, iliac vein; i, caudal vein.