
REPTILIAN RENAL STRUCTURE AND FUNCTION

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ABSTRACT

This overview focuses on the urinary component of the urogenital system. Here I define terms, synthesize the relevant literature on reptilian renal structure, discuss structural – functional relationships, and provide comparisons to other vertebrate renal form and function.

The urinary and reproductive components of the urogenital system develop in conjunction with one another from two adjacent parts of the mesoderm. As development proceeds, ducts that drain nitrogenous wastes in the embryo are co-opted by the reproductive system or they regress (e.g., mesonephric ducts become the Müllerian ducts in females, pronephric ducts become the Ductus deferens in males) and new ducts (ureters) form to drain the kidneys.

Urogenital System Consists of Kidneys, Gonads and Duct Systems

- Urinary system is formed by the *kidneys*, including their *nephrons* (= nephric tubules) and *collecting ducts*. The collecting ducts drain products from the nephrons into to *ureters* that themselves drain to the cloaca via the (usually paired) *urogenital papillae* in the dorsolateral cloacal wall. A *urinary bladder* that opens in the floor of the cloaca may or may not be present depending upon species.
- The genital system (gonads and their ducts) forms later in development and is discussed here only when relevant to urinary function.

Kidney Form and Terminology

The literature includes a number of descriptive terms for the developing kidney that often confuse more than clarify the form of the kidney. Understanding the basics of kidney development should help.

The kidneys arise as paired structures from embryonic mesoderm. The mesonephric (nephrogenic) ridge mesoderm is located lateral and parallel the spine. During development the kidneys and their drainage ducts form in a cranial-to-caudal fashion, so that more cranial aspects tend to form earliest and the most caudal tend to form later. Three basic types of kidney structure (as well as some composite types) may form from these long, strip-like, mesonephric ridges. Pronephros, Mesonephros, Metanephros, Holonephros, and Opisthonephros all appear in the reptilian and amphibian renal literature. In theory, the Pronephros forms first, is more cranial in location, and its tubules connect to a pronephric duct that drains to the cloaca. The

Mesonephros forms next and is just caudal to Pronephros. The Metanephros forms last, is most caudally located and its nephric tubules drain into ureters which connect to the cloaca. However, the landmarks delineating where the pronephric region ends and the mesonephric region begins are not always distinct. Similarly, the mesonephric-metanephric margins are also indistinct. Hence, some morphologists simply acknowledge that the mesonephric ridge will give rise to kidney tubules in an anterior to posterior progression during ontogeny and call the whole structure a Holonephros. That somewhat common-sense distinction is not as common in the literature as designating three distinct forms of developing kidneys, however Holonephros may be the most accurate for reptiles. In comparison, the amphibian mesonephric ridge appears to develop and join the middle and posterior sections in the adult to form an Opisthonephros.^{15,17}

Who has what kind of kidney and at what stage? A Pronephros does not form fully in reptiles and is only transitory in embryonic amphibians.¹⁵ However, a pronephric duct forms. A functional Mesonephros forms in embryonic reptiles and amphibians and its tubules drain into the pronephric duct. This duct is renamed the mesonephric duct. A Metanephros forms toward the end of reptilian development and develops while the Mesonephros is still present. The Mesonephros and Metanephros may both function in neonate reptiles. The Metanephric form becomes the functional adult kidney in reptiles. In amphibians, kidney tubules from the middle to posterior part of the mesonephric ridge form the Opisthonephros in the adult.

Basic Components of Kidneys

The nephron is the functional unit of the kidney. The nephron (= nephric tubule) is composed of the renal (Bowman's) capsule, which is attached via a ciliated neck to a long proximal tubule segment that continues as a narrow, ciliated intermediate segment, followed by a short distal tubule segment. The intermediate tubule segment is short in reptiles and amphibians, in contrast to the elongated intermediate segment found in mammals (loop of Henle). *There is no loop of Henle in reptiles or amphibians.* The distal tubule drains into the collecting duct. Some recent histologic studies designate the terminal part of the distal segment as the connecting segment because it structurally and functionally distinct.¹⁶ The distal segment either drains directly or via the connecting segment into the collecting duct. In reptiles, the collecting ducts drain into the metanephric ducts or ureters. Each nephron interacts with the circulatory system at the renal corpuscle, which is formed of the glomerular arterioles and capillaries surrounded by the renal capsule (Figs. 1- 2). The surface area of the glomerulus tends to be greater in aquatic reptilian species than in terrestrial or marine species.⁷

Kidney Form and Tubule Function

- Filtration: water, nutrients, and wastes are removed from blood at the renal corpuscle.
- Reptile glomerular capillaries are large and few.^{4,7}
- Tubular reabsorption is limited in reptiles; some water and nutrients are absorbed back into the blood.
- Tubular secretion of large molecules such as protein-associated wastes are transported from the blood in the peritubular capillaries.^{4,7}
- Generally little water is reabsorbed by the intermediate and distal segments.

The volume and osmolarity of urine in reptiles depends of the anatomy of the nephrons, the permeability of the nephric epithelium to water, volume flow rates (controlled by the numbers of nephrons), uric acid production, salt gland function, and large intestine function. Additionally, nephrons may collapse shutting down some glomerular filtration when hydration and flow is low.⁶ The presence of a loop in the nephron is associated with the ability to produce concentrated urine (restricted to mammals and a few birds). Reptiles and amphibians lack loops. Instead they excrete uric acid in a colloidal form with proteins. Uric acid excretion requires very little water. Urine from the ureters moves from the cloaca into the rectum by a reverse peristalsis.⁵ The proteins are then broken down into peptides and amino acids, which are absorbed in the rectum. The uric acid binds with ions and is eliminated as salts.

Kidney Structure and Location

Reptile and amphibian kidneys typically lack the distinct color and functional distinction of the mammalian cortex and medulla. The kidneys are paired, lobular (weakly so in some lizards), elliptical, pink or red structures that are located retroperitoneally (extracoelomically) in all reptiles and amphibians. In turtles, the kidneys are often lobed, wide flat structures between the peritoneum and the shell and positioned lateral and anterior to the ilia. Kidneys are posterior to the level of the ilial crest in most lizards and usually lack distinct lobes. Snake kidneys are distinctly lobed and elongated. They are found in the posterior third of the bodies of snakes with the right kidney occurring anterior (approximately 69 -77% of snout-vent length) to the left kidney (~74 – 82% of snout-vent length). In crocodilians, the kidneys are lobed and dorsoventrally flattened. They extend from approximately the level of the umbilical scar to the ilial crest. In amphibians, the kidneys are found in the central portion of the coelomic cavity, often extending from the level of the heart posteriorly.

The ureters extend from the kidney, through the coelomic membrane and empty into the dorsal cloaca on each side. Ureters are located on the ventral surface of each kidney. Each ureter enters the cloaca via a urinary papilla lateral to the genital opening in the urodeum portion of the cloaca. The urinary papillae are incorporated into the genital papillae in females of many species of turtles and snakes. They are small and located in the lateral walls of the urogenital papillae. The cloaca is the common chamber into which the ureters, gonadal ducts, rectum, and bladder (if present) empty. The cloaca leads to the outside of the body via the vent.

The Urinary Bladder

The urinary bladder is a highly elastic single sack-like structure located along the midline of the pelvis in most lizards and all turtles and most amphibians.^{3, 15} It opens via a single opening to the ventral floor of the cloaca. Because the bladder is located ventrally and both water and excretory products must enter via the cloaca, it is often contains materials that enter opportunistically. Turtles have two or more accessory urinary bladders, each located lateral to the neck of the urinary bladder and dorsal to the pubis. Both the urinary bladder and the accessory bladder may occupy a significant portion of the body cavity in turtles and tortoises.

Crocodylians and snakes lack urinary bladders; nitrogenous wastes are refluxed from the cloaca into the rectum where uric acid is stored and further ion reclamation may occur. However, the extent of sodium and chloride ion recovery by these structures appears to be limited.^{1,16} Several species of lizard lack urinary bladders or develop just a vestigial bladder; these lizards include some varanids, some agamids including *Pogona* spp., several *Crotophytus* spp., *Sceloporus* spp., teiids, and a few gekkonids.² Uric acid is sequestered in the rectum of these lizards until it is eliminated.^{5,6}

Overall Urinary Function

The kidney's function is maintaining homeostasis of the animal's internal environment. Its two main roles are in removal of nitrogenous wastes (excretion) and maintaining water and electrolyte balance (osmoregulation). The ureters transport nitrogenous wastes to the cloaca where it moves into the urinary bladder or the rectum and is eliminated. In reptiles and amphibians, the bladder, distal ureter and rectum² or may also function in some ion management and water conservation, as well as some urine storage.

The mechanisms for eliminating wastes are classified by their primary waste products. Animals that produce primarily uric acid are termed uricotelic. Those that produce primarily ammonia are ammonotelic and those that sequester wastes as urea or ureotelic. Amphibians are both ammonotelic and ureotelic. The skin and gills of amphibians also function in ammonia excretion. Reptiles tend to be primarily uricotelic, removing nitrogenous wastes primarily as uric acid, with small amounts of ammonia, urea, and water. Reptiles also differ from mammals and birds in that their kidneys cannot produce urine that is more concentrated than the plasma.

Renal Vascular Flow

The renal portal system (RPS) and ventral abdominal vein (VAV) are the major venous drainage systems of the caudal half of the body. They provide some redundancy in the routes blood may take when returning toward the heart. The blood in the RPS runs from sets of capillaries in the hind limbs, cloaca, distal parts of the reproductive tract (including hemipenes), caudal body wall and/or tail to the capillary beds of the kidneys without passing through the heart¹⁵. Functionally, the RPS and VAV provide low-pressure blood supply to the kidneys as well as routes of blood flow that bypass the kidneys. This low-pressure component of kidney circulation is probably important in tubular secretion, some water recovery, and electrolyte recovery.

In reptiles, as in birds, amphibians and fish, blood to the glomerulus is from a relatively high pressure system: the aorta and renal arteries and to the peritubular capillaries via the low pressure vasculature of the renal portal system.^{4,7} The RPS is often confusing because it has been defined in various ways^{8,11,14,15,17} and differently in different fields (in physiology, developmental biology and comparative anatomy). The broadest definition of the RPS includes the postcava, abdominal vein, renal portal vein, and external iliac veins and their drainage. Most narrowly, its definition is limited to the Renal Portal vein from the caudal body to the kidneys.

In general, blood arrives at the kidneys from the dorsal aorta via several renal arteries that branch many times within each kidney forming the glomerular capillary beds. Blood also enters the kidneys from the caudal body via caudal vein to the afferent renal veins (also termed renal portal veins or renal veins).¹³ Blood from these sources is supplied to the capillaries of the renal tubules. Venules leave the capillary beds of the renal tubules and coalesce to form the efferent renal veins, which drain into the postcava. The postcava runs anteriorly from the efferent renal veins of kidneys through the right lobe of the liver to emerge and enter the sinus venosus. Blood returning from the caudal vein and hind legs may take alternative routes and bypass the kidneys. In some pythons, the renal portal vein has branches to the abdominal veins.¹² Blood may shunt from the afferent renal veins to the mesenteric vein or enter the abdominal veins (in turtles and crocodilians). Other possible alternative routes vary with taxon.⁹

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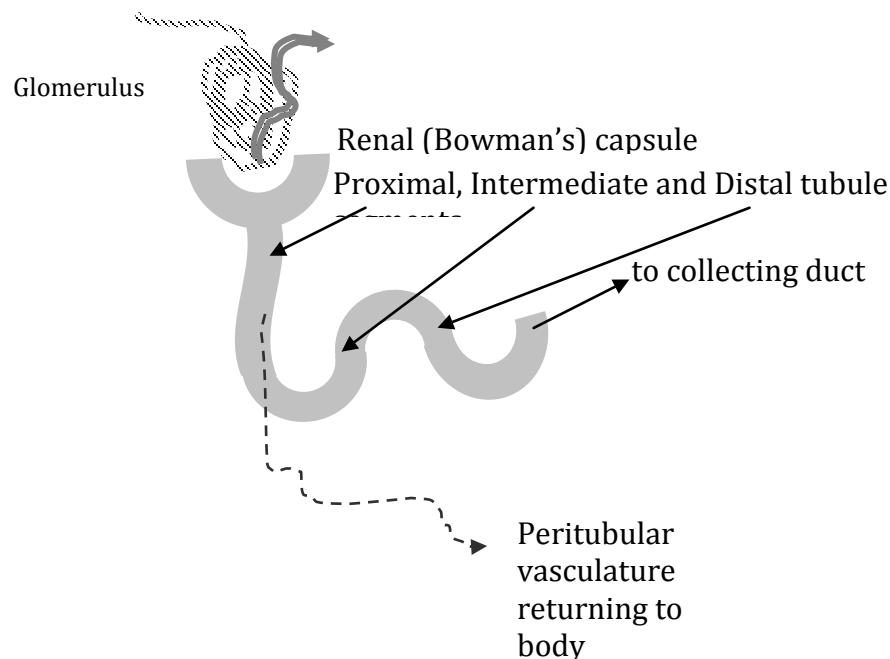


Figure 1. The functional components of the kidney. Blood arrives at the glomerulus from the aorta via the renal arteries (black and gray) and blood from the afferent renal veins (part of the renal portal system) arrives via the peritubular capillaries that intertwine with the nephric tubule and collecting duct. The nephron drains via collecting ducts into the ureters.

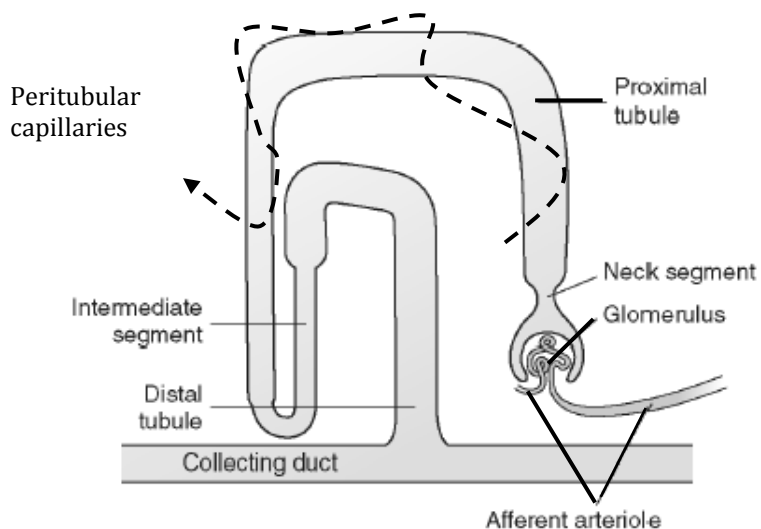


Figure 2. The reptilian nephrons drain into collecting duct, which themselves drain into the ureters. The intermediate tubule segment is thin and short in reptiles and amphibians; it does not form a loop of Henle (modified from Holtz¹⁰). In alligators the distal segment (tubule) is further specialized terminally as a connecting segment.¹⁶