Chapter 10

URINARY SYSTEM

External form of the kidney

In birds generally the kidneys lie symmetrically in bony depressions of the synsacrum, the renal fossae (Fig 4–10). They reach the lungs cranially and the end of the synsacrum caudally (Fig 6–10). In the adult domestic fowl they are about 7 cm long, and about 2 cm wide at their broadest point. The kidneys generally form over 1 per cent of the body weight in small species, and less than 1 per cent in large species. Extending between the kidneys and the pelvis are diverticula of the abdominal air sacs; because of this relationship the kidneys are removed during the postmortem processing of poultry in the slaughter plant if the abdominal air sacs are infected.

Each kidney is divided into cranial, middle and caudal divisions (Fig 10–1). These divisions are in no way homologous to the lobes of mammalian kidney. The boundaries between them are not always distinct, being formed by the external iliac artery and ischiadic artery as in Fig 10–1. In birds of most non-passerine orders, including the domestic fowl, the divisions are distinct, but in passerines the middle division is not well defined, being largely fused to the other two divisions, particularly the caudal one. Also, the relative sizes of the divisions vary greatly. Nevertheless the presence of the three divisions appears to be characteristic of birds in general. In many birds, including herons, puffins and penguins, but not the domestic fowl, the caudal divisions of the left and right kidneys are fused in the midline. Spinal nerves of the lumbar plexus and sacral plexus pass through the substance of the kidney.

The surface of each division is covered with small rounded projections, about 1–2 mm in diameter in the domestic fowl. These are renal lobules reaching the surface of the kidney (see Fig 10–1, left kidney). The architecture of the avian kidney is founded on renal lobules, the rough outlines of which can be identified without too much difficulty. It is also possible to recognize the presence of larger units, the renal lobes, but these are much less obvious. The lobes and lobules form areas of cortex and medulla. The general organization of all these components appears to be broadly similar in the domestic fowl and the other species which have been examined, the only differences being those of detail.
The renal lobule

In histological sections, which of course are only two-dimensional, an avian renal lobule is seen as a pear-shaped area of tissue wedged between the interlobular veins of the renal portal system (Fig 10-2). There are many such lobules in one kidney, some being superficial and many others buried deep below the surface. Each lobule is enclosed by its peritubular collecting tubules, as the staves enclose a barrel; the peritubular collecting tubules are therefore interlobular in position. The efferent vein which drains the lobule lies in the centre of the lobule, and is therefore the intralobular vein. The artery which supplies the lobule is also in the centre of the lobule, thus constituting the intralobular artery. (These relationships are therefore essentially the reverse of those in mammals, where the collecting tubules, as medullary rays, are intralobular and the arteries are interlobular.)

At the tapering stalk of the pear-shaped lobule, the collecting tubules converge to form a conical bundle of medullary collecting tubules. This conical stalklike part of the lobule is the medullary region or medullary cone of the lobule; in addition to collecting tubules it contains the nephronal loops (of Henle) belonging to the medullary types of nephron (Fig 10-2). The wide part of the pear is the cortical region of the lobule; it contains the nephrons of both the cortical and medullary types, except for the nephronal loops of the latter.

Three-dimensional preparations, as in cleared kidneys, show that the lobule is not really a simple pear-shaped object. It is more elongated, rather like a loaf of bread. The cortical part of the loaf actually drains not into only one medullary region but several. Furthermore, any one medullary region may...
receive contributions from the cortical regions of several lobules (Fig 10-3). Thus the renal lobule turns out to be much more complex than it appears to be at first sight. Nevertheless the lobule is still a convenient structural concept.

![Diagram of renal lobule](image)

**Fig 10-3** Renal lobules forming a renal lobe. Part of five lobules (1 to 5) belonging to one lobe are shown. Each lobule consists of a cortical region (CRL) and a medullary region (MRL), but the cortical regions of lobules 3 and 4 are omitted. The medullary regions of the five lobules converge into a single encapsulated cone-shaped assembly of medullary collecting tubules, cut in transverse section at X-X', which constitutes the medullary region of the renal lobe. This medullary region, and the lobules associated with it, form a complete renal lobe. The arrangement of the lobule is somewhat more complicated than the pear-shaped structure found in histological sections as in Fig 10-2. When seen in three-dimensional preparations the cortical region of the lobule is elongated. The elongated cortical region drains into several medullary regions, although this is not shown in the diagram. Furthermore, any one medullary region of a lobule may drain more than one cortical region; thus medullary region 5 drains the two independent cortical regions which adjoin each other at 'c'. Three nephrons are shown in lobule 1, the upper one being a cortical nephron and the lower two being medullary nephrons with nephronal loops contributing to the medullary region of the lobule. The two arrows show the direction taken by perilobular collecting tubules at 'a' as they enter the medullary region of lobule 2, where they combine to form increasingly larger ducts. From Johnson (1974), with kind permission of the editor of the Journal of Morphology.

**The renal lobe**

As in Fig 10-2, the conical bundle of medullary collecting tubules at the stalk of a lobule joins several similar conical bundles from several other adjacent lobules. This group of several conical bundles of medullary collecting tubules eventually converges into a single cone-shaped assembly of collecting tubules encapsulated within a connective tissue sheath (cut transversely at X-X' in Fig 10-3). One such cone-shaped assembly therefore drains a group of several lobules; consequently it represents the medullary region of a renal lobe, and is probably homologous to the medullary pyramid of a mammalian multilobular kidney as in the ox. Together, the encapsulated cone-shaped assembly of collecting tubules and the cortical regions which drain into it form a renal lobe. It drains into a single large collecting duct (Fig 10-2). Several collecting ducts combine to form a secondary branch of the ureter (Figs 10-2 and 10-3).

**The renal cortex and medulla**

The cortex is formed by the wide cortical regions of the lobules, and the medulla by the tapering stalklike medullary regions of the lobules. However, the lobules, and therefore also the lobes, are embedded at varying depths in the kidney, and consequently the cortex and medulla do not form the continuous outer and inner strata respectively which typify the mammalian kidney. Instead, large areas of cortex enclose relatively small cone-shaped islands of medulla.

The number of these cone-shaped medullary regions per unit volume of kidney tends to be considerably greater in species which are particularly successful at conserving water (e.g. the salt marsh Savannah Sparrow). In such species each medullary region must drain a relatively small volume of cortex; this presumably implies a relatively high proportion of mammalian type nephrons (which have nephronal loops) and therefore suggests relatively good counter-current concentration.

**The nephron**

The avian kidney has two types of nephron. The cortical type of nephron, which forms the majority, is devoid of a nephronal loop (of Henle) and is confined to the cortical region of the lobule (Figs 10-2 and 10-3). These nephrons are reptilian in form. The medullary type has a nephronal loop which penetrates the conical medullary region of the lobule (Figs 10-2 and 10-3). These are mammalian in form.

Both types of nephron always begin with a *renal corpuscle*, which consists of the glomerular capsule (Bowman's capsule), deeply indented by the *glomerulus*, which is a tuft of capillaries. The renal corpuscles lie about midway between the inter- and intralobular veins (Figs 10-2 and 10-3). The cortical *nephron* has a convoluted proximal part (Fig 10-4) which tends to be localized at the periphery of the lobule and forms about half of the total length of the nephron. There is an ill-defined, short convoluted *intermediate segment*, followed by the *distal part* of the nephron which forms compact convolutions near the intralobular vein (Fig 10-4). Two zones can be distinguished in histological sections of the avian cortex, i.e. an outer zone which contains the convolutions of the proximal parts of the nephrons, and an inner zone which contains the convolutions of the distal parts of the nephrons surrounding the intralobular vein (Fig 10-4).

The *medullary nephron* has convoluted proximal and distal parts, like those
of the cortical nephron, but the intermediate segment forms a nephronal loop (nephronal ansa or loop of Henle) which descends usually within the medullary region of the lobule (Figs 10–2 and 10–3) but is quite often outside it. The avian nephronal loop is always like the short variety of loop in the mammal, the calibre enlarging before the bend (Fig 10–4). In passerines the medullary region of the lobule is relatively highly organized, with a ring of medullary collecting tubules which encloses the thin descending limbs of the nephronal loops and is in turn surrounded by layers of ascending thick limbs. In the domestic fowl and many other non-passerines there is a general intermingling of these medullary elements.

The collecting tubules (Fig 10–2) which lie superficially on the surface of the cortical region of the lobule are known as perilobular collecting tubules; those that pass within the medullary region of the lobule are named medullary collecting tubules. The medullary collecting tubules from one lobule typically combine into a single large vessel, the collecting duct (Fig 10–2). Several collecting ducts in turn combine to form a secondary branch of the ureter (Fig 10–2).

A complete juxtaglomerular complex is present in birds. It includes the macula densa which is a thickening of the epithelium of the beginning of the distal part of the nephron, where the latter comes into contact with the afferent arteriole. It also incorporates the secretory juxtaglomerular cells (modified myoepithelial cells) of the adjacent afferent arteriole. At the vascular pole of the glomerulus there is a third component, the juxtavascular insula (or extraglomerular mesangium) with its juxtavascular cells (or Polkissen cells). A vasopressor renin-like substance is present in the kidney of the domestic fowl; it may be formed in the juxtaglomerular cells and stored in the other components of the juxtaglomerular complex.

**The arteries of the kidney**

The cranial, middle and caudal renal arteries supply the cranial, middle and caudal divisions of the kidney respectively (Fig 10–5). Their branches eventually form the intralobular arteries (Fig 10–2), which pass towards the surface of the lobule lying about half-way between the inter- and intralobular veins. The intralobular arteries give rise to the very short afferent glomerular arterioles, each of which almost immediately forms its glomerulus (Fig 10–2). The capillary tufts of the glomerulus, which are much simpler and smaller than in mammals, consist of only two or three capillaries, and continue as the...
**The afferent or renal portal veins**

The cranial and caudal renal portal veins form a venous ring which encompasses both kidneys (Fig 10–5). The ring is completed at the cranial end by anastomosis of the left and right cranial renal portal veins with the internal vertebral venous sinus, and at the caudal end by anastomosis of the left and right caudal renal portal veins with the caudal mesenteric (coccygeomesenteric) vein. Portal blood can enter the ring, and hence the kidneys, via the external iliac veins, the ischiadic veins, the internal iliac veins and the caudal mesenteric vein. Many smaller veins, known as the **afferent renal branches**, arise from the ring (Fig 10–5) and penetrate the parenchyma of the kidney. Muscular sphincters at the roots of these branches control the volume of blood entering the renal parenchyma from the venous ring. Within the parenchyma of the kidney the smaller afferent (portal) branches become the **interlobular veins**, and these finally form the peritubular capillary plexus at the periphery of the lobule (Fig 10–2).

A conical valve, the **renal portal valve**, is so sited within the lumen of the common iliac vein (Fig 10–5) that when it is open it can divert the portal flow away from the tissues of the kidney and directly into the caudal vena cava. The smooth muscle of the valve is richly innervated by adrenergic and cholinergic fibres, and is inhibited by adrenaline and stimulated by histamine or acetylcholine. Nevertheless, the physiological mechanisms which control the valve in the live animal are not yet known. However, cineradiographic studies in the domestic fowl have shown that the portal blood can be shunted (a) through the portal valve into the caudal vena cava, (b) into the caudal mesenteric vein towards the liver, or (c) into the internal vertebral venous sinus within the neural canal. These shunts sometimes bypass the kidney completely, but usually only a part of the portal flow is diverted from the kidney and the rest enters it, eventually traversing the peritubular capillary network. The direction of flow in the caudal mesenteric vein is usually towards the kidney; reversal of this flow sends the blood into the hepatic portal circulation. The shunt through the portal valve directly into the caudal vena cava may be a part of a general physiological mechanism for increasing the venous return to the heart as in exercise. Or it may be part of a more specialized mechanism to allow an increase in the blood flow through the legs, to a higher level than that required by the kidneys, when the bird is running.

**The caudal renal vein and the cranial renal veins**

The caudal renal vein drains the middle and caudal divisions of the kidney (Fig 10–5). The initial tributaries are the intralobular veins (at the centres of the lobules), which drain the peritubular capillary network (Fig 10–2). The intralobular veins drain into efferent renal veins (efferent renal branches in Fig 10–5), which eventually empty into the caudal renal vein. This ends by opening into the common iliac vein, immediately on the heart side of the renal portal valve.

The **intralobular veins of the cranial division of the kidney drain into efferent renal veins which in turn form several cranial renal veins; the latter empty into either the common iliac vein (Fig 10–5) or the caudal vena cava directly.**

**The ureter**

The renal part of the ureter starts within the depth of the cranial division of the kidney but continues caudally in a groove on the ventral surface of the other two divisions (Figs 6–10, 9–2, 10–1). It receives a series of tributaries (about 17 in the domestic fowl), which are the primary branches of the ureter (Fig 10–1). Each primary branch receives about five or six secondary branches; each secondary branch in turn drains the medullary component of a renal lobe (Figs 10–2 and 10–3). In histological sections the lumen of the pelvic part of the ureter has a stellate shape and is lined mainly by a mucus-secreting, pseudostratified, columnar epithelium.

The pelvic part of the ureter (Fig 10–1) opens into the urethra (Fig 11–1). A ventral (allantoic) urinary bladder is absent in all birds. The Ostrich is sometimes said to have one, but the 'urinary bladder' of this species opens dorsally and is merely the cloacal bursa which has a very wide opening in the large flightless birds (ratites).

**Excretion**

Birds, like mammals, can produce a concentrated urine which is hypertonic to blood plasma. The concentrating power of the kidneys lies in the countercurrent medullary nephronal multiplier systems of the medullary nephronal loops. These systems are better developed in mammals than birds, and consequently birds have less ability than mammals to concentrate their urine.

Birds resemble reptiles in being uricotelic, that is they excrete the end product of nitrogen metabolism as uric acid. The uric acid is synthesized in the liver, and the kidney excretes it from the blood plasma partly by means of glomerular filtration and mainly by tubular secretion. The uric acid and the salts (urates) arising from it can form colloidal solutions with concentrations of up to 2 per cent, and this allows transport through the tubules and collecting ducts without precipitation. Precipitation could obstruct the collecting ducts. In the ureter the urine has been found to be viscous and stringy, and mucus
may be needed to lubricate the movement of precipitated urate down the ureter.

It is widely believed that the excretion of nitrogen as urate enables birds to economise on water by excreting a semi-solid urine instead of the much more watery solution of mammals. However, it has been calculated that the excretion of uric acid by an adult domestic fowl could entail the use of 200 ml of water per gram of nitrogen: to excrete urea a man could use 150 ml of water per gram of nitrogen. The advantages of uric acid probably lie more in overcoming the difficulties of the cloidoic (closed-box) egg, where the supply of water is strictly limited. The embryo bird stores its nitrogenous wastes in its allantois. Uric acid and its salts are less soluble than urea. In fact the urate is held in the avian allantois as a crystalline anhydrous deposit, which allows the transporting water to be reabsorbed and, because of its low solubility, is not toxic to the embryo. Moreover, if urea were the waste product it would hold water by osmotic forces, and would thereby reduce the availability to the growing embryo of the limited water supply inside the egg.

The renal portal system takes part in the secretion of urates. It achieves this by supplying venous blood to the peritubular capillary plexus at the periphery of the lobule (Fig 10–2), where the convoluted proximal parts of the nephrons are mainly situated (Fig 10–4). The proximal part of the nephron is responsible for the tubular secretion of urates. Tubular secretion can be demonstrated in the domestic fowl by injecting a dye into one leg; the dye appears first in the ureter on the same side of the body as the injection, and appears in the other ureter only after a further lapse of time.

Glomerular filtration also contributes to the elimination of urates, but is insufficient alone to account for urate clearance. It has been estimated that about two-thirds of the blood to the kidney is supplied by the renal portal veins. All of this blood goes to the peritubular capillaries and none to the glomeruli. It therefore seems likely that the renal portal system makes a major contribution to the elimination of urates.

The urine which leaves the ureter enters the urodeum and is then moved by peristalsis into the coprodeum and rectum, a small amount reaching ad

Further reading


Chapter 11

CLOACA AND VENT

The cloaca: external form

The cloaca is the chamber which receives the terminal parts of the digestive and urogenital systems and opens to the outside at the vent. Its basic organization seems to be fairly uniform throughout birds generally, the main variations being associated with the phallic region of the proctodeum. Externally the cloaca appears as a bell-shaped dilation of the end of the rectum (Figs 6–3, 6–10 and 11–1). In the adult domestic fowl it is about 2.5 cm long and 2.0–2.5 cm wide, although the size varies with the volume of faeces inside it. In the mature male the cloaca is in the midline, but in the mature female the enlarged left oviduct displaces it somewhat to the right; in immature birds the dorsally situated cloacal bursa is larger than the cloaca itself and compresses