Lesson 24

Lesson Outline:

- The Urogenital System
  - Urinary System
    - Embryonic Origins
    - Phylogenetic Trends
      - Function
  - Urinary Bladder
  - Implications for the Evolution of the Vertebrates
    - Freshwater or Seawater Origins?

Objectives:
At the end of this lesson you should be able to:

Describe the embryonic origins of the urinary system
Describe the phylogenetic trends seen in the design of kidneys and their ducts/tubules
Describe the significance of these trends
Describe the evolution of the urinary bladder
Describe the implications of these trends for the site of origin of the vertebrates

References:
Chapter15 : 351-386

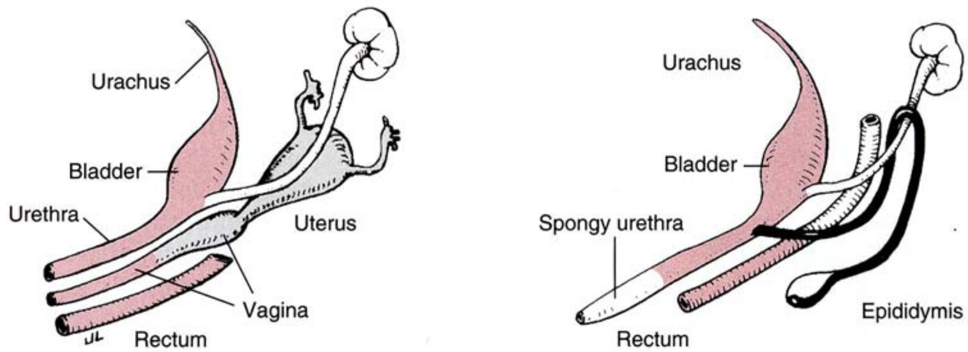
Reading for Next Lesson:
Chapter15 : 351-386

The Urogenital System

Urinary System

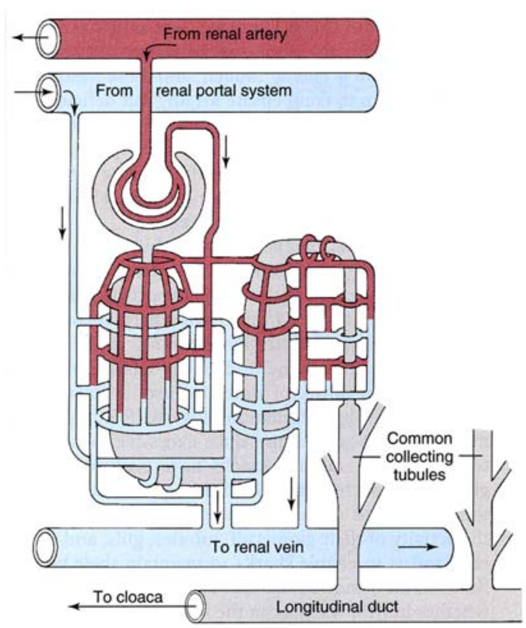
The kidneys develop as a complex arrangement of blood vessels and both secretory and absorbing tubules lying dorsal to the abdominal cavity. Their primary role is to excrete wastes.

There are two primary organs of excretion that fulfill very different roles. The rectum is the posterior end of the digestive system and excretes undigested wastes- material that was never sufficiently digested to enter into the body.



The kidneys excrete the waste products of cellular digestion, ions, amino acids, salts, etc. They also play a key role in water balance along with numerous other structures in different species living in different environments (i.e. gills, skin, salt glands). As a consequence, they also have very different superficial anatomy in different species living in different environments.

Their basic function is simple - excrete everything you can and absorb only what you want to keep. Remember - everything that enters the body must do so by crossing a cell membrane. Excretion takes advantage of the same principles. The capillary beds within the kidney are very permeable - very leaky. With the exception of large proteins and the red and white blood cells, virtually everything else within the plasma leaks out into the kidney tubules and would be excreted unless it is reabsorbed as it passes along the kidney tubules.

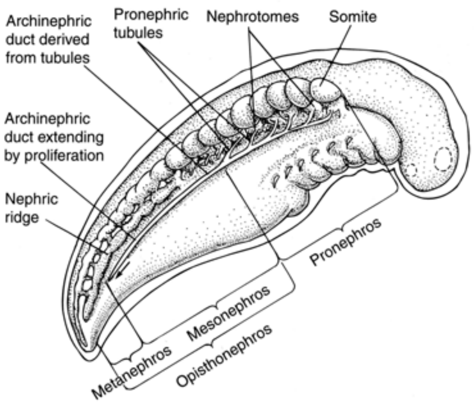


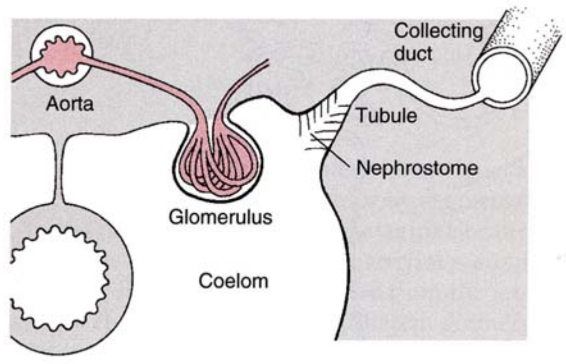
Why do things this way? The simple answer is that it is easier to evolve mechanisms to take up what you need than to evolve mechanisms to eliminate things you don't.

The mechanisms by which this occur is the realm of physiology and is something that you will cover in detail in your physiology courses next year.

Embryonic Origin

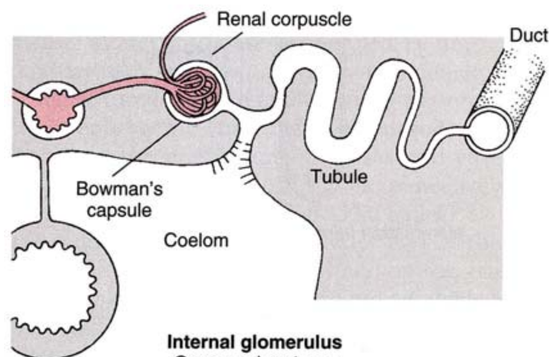
The kidneys form within the intermediate mesoderm in the embryo. This tissue expands forming a ridge, the nephric ridge, which protrudes slightly into the coelom formed by the differentiating hypomere below it.





External glomerulus

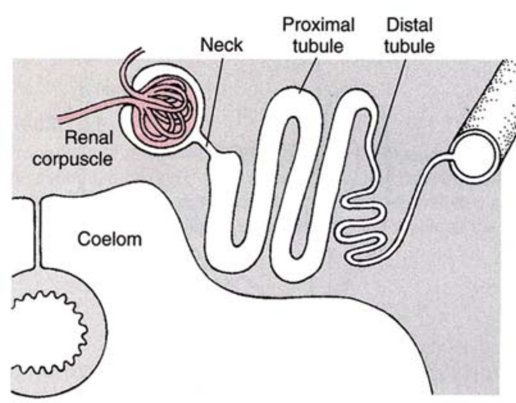
The tissue along this ridge becomes segmented under the influence of the epimere above it, forming neprotomes (paired) in each segment.



Internal glomerulus
Open nephrostome

The medial wall of the nephrotome receives a rich capillary supply from the dorsal aorta that forms the glomerulus. This is the site of urine formation. Initially, the glomerulus forms in the roof of the body coelom and the fluid filters from it into the body cavity.

The nephrotome develops to contain the nephrocoel, a coelomic chamber that initially is connected to the coelom by the peritoneal funnel.



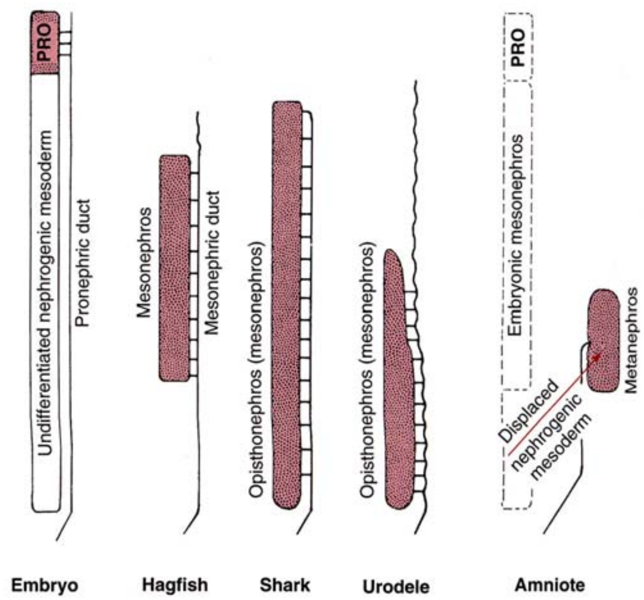
Internal glomerulus
Closed nephrostome

The roof of the coelom, containing the glomerulus, grows up and into the nephrocoel while the lateral end of the nephrotome grows out forming a tubule and the tubules from each segment unite to form a longitudinal duct, the nephric duct which runs the length of the trunk.

As a rule, the peritoneal funnel closes over.

Initially this occurs in each segment of the kidney along the nephric ridge, along the length of the body cavity. Not all of the segments remain active, however and this gives rise to a number of different kidneys and a number of different ducts or tubules.

The holonephric kidney produces tubules in anterior to posterior succession during development. Each segment gives rise to a pair of nephrotomes, each with a glomerulus and a nephrocoel and nephric tubule, all of which unite to form an archinephric duct. This type of kidney characterizes the early development of some hagfish, elasmobranches, and caecilians but is found in no adult vertebrate.



If the kidney forms from the anterior tubules only, it is a pronephric kidney or pronephros. If it forms from the middle it is a mesonephros, and if it forms from the posterior region only it is a metanephros or metanephric kidney.

Some kidneys form from both the middle and posterior regions and these are referred to as opisthonepric kidneys.

In the case of the pronephric kidney, the tubules from individual segments unite to form the pronephric duct. This grows back to join the cloaca and is referred to as the archinephric duct.

In the mesonephric kidney the tubules unite to form the mesonephric duct, which grows back to join the cloaca as the archinephric duct. The same is true of the opisthonephric kidney.

In the metanephric kidney, the tubules unite to form a metanephric duct. In this instance, it is the outgrowth of a ureteric diverticulum from the mesonephric or archinephric duct that grows up to meet the metanephros and because this duct originates in a slightly different way it is referred to as the ureter rather than as the archinephric duct.

Phylogenetic Trends

The most primitive vertebrate kidney was the holonephric kidney and was believed to have consisted of a series of nephrotomes arranged segmentally along the entire length of the trunk. Each gave rise to a tubule, which all joined together to form the archinephric (wolffian) duct on each side, which drained the kidney. The nephrotome in each segment also opened directly into the coelom via a peritoneal funnel. This is still found in hagfish larvae.

In adult hagfish, the most anterior tubules (the pronephros) remain while the more posterior tubules have regressed. This is a pronephric kidney. The more cranial portion may still open into the coelom via peritoneal funnels but the more posterior portions drain only by the archinephric duct.

In adult lamprey, the most anterior tubules (the pronephros) have disappeared. The remaining more posterior portion is the opisthonephric kidney. It does not open into the coelom at all but drains only by the archinephric duct. This kidney may have more than one tubule per segment.

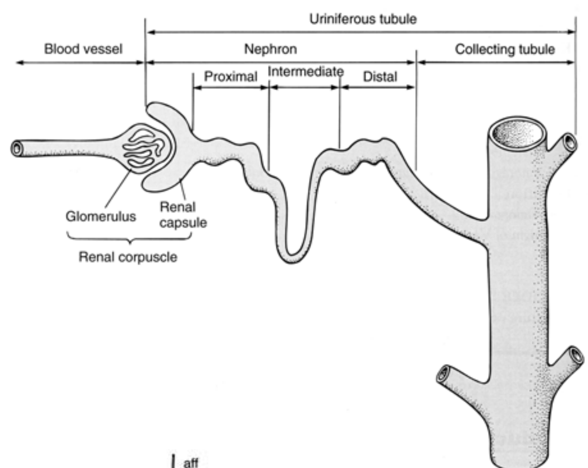
In adult female sharks, the arrangement is just as we have described it in the adult lamprey.

In adult male sharks, the more posterior portion of the kidney losses its segmentation and the number of tubules increases dramatically. These tubules now drain through a new structure, the accessory archinephric duct (urinary duct).

Thus another of the phylogenetic trends that we see is an increase in the number of nephrons in each body segment. As the number increases, it disrupts the primitive segmentation of the kidney.

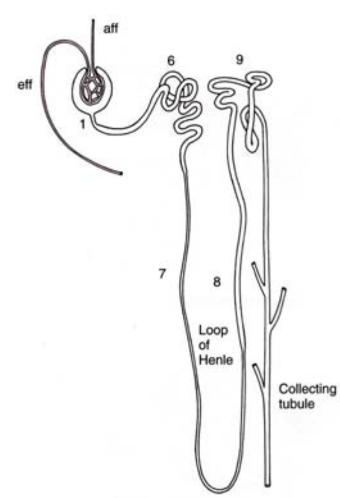
In some fish, a pronephric kidney persists. It is usually replaced during development with a mesonephric kidney. Most often, more tubules are added posterior to this to form an opisthonephric kidney. This is also true of most amphibians.

In all amniotes, during late development, a metanephric kidney develops, drained by ureters. The tubules in each segment arising from each glomerulus tend to be long with three distinct segments.



These are the proximal, intermediate and distal tubules.

In many mammals particularly, the intermediate tubule can become very elongate and form a long loop called the loop of Henle. The longer the loops, the greater the ability to concentrate urine and conserve water. The best mammalian kidneys can concentrate urine up to 25X plasma levels.



Mammalian nephron

In some birds we also see convergent evolution in the form of kidneys with short loops analogous to the loops of Henle in mammals. These loops give these species limited ability to concentrate urine.

Since birds can concentrate urine - even more than most mammals, this raises the question of how it is done. ????

Function
The glomerulus from the dorsal aorta delivers blood to the kidney where it is filtered into the kidney tubules. Everything is filtered out of the blood except blood cells and proteins too large to pass through the extremely permeable capillaries. The system is designed to excrete everything and then reabsorb all substances that are needed.

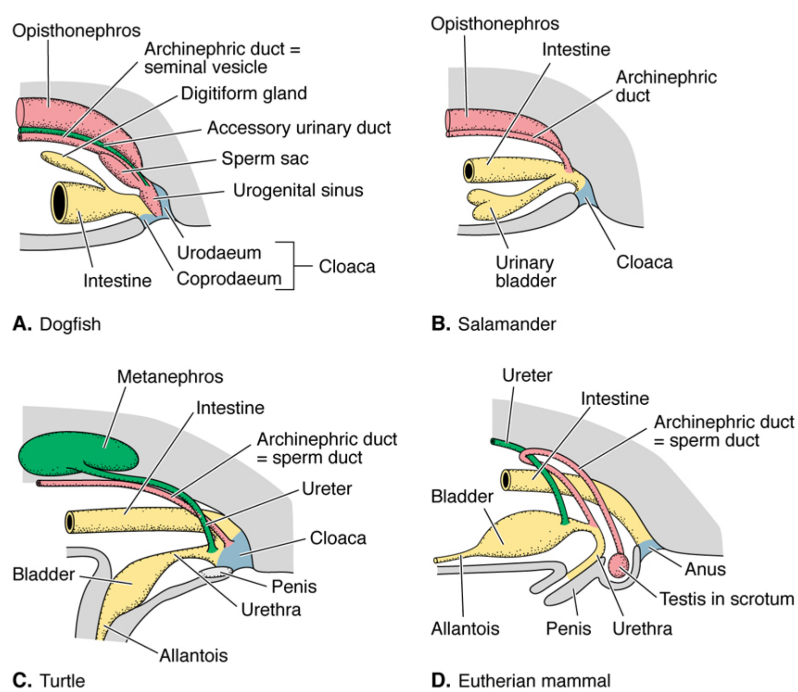
Most ions and molecules that are needed by the body are reabsorbed in the proximal tubule.

The intermediate portion and the loops of Henle play a key role in producing a concentration gradient of salt that is used to reabsorb water from the collecting ducts that connect to the ureters. The distal tubule is a site primarily used for active secretion of some unwanted salts.

This leaves water, salts, and nitrogenous wastes in the filtrate that passes down the archinephric duct.

Urinary Bladder

Before being excreted, urine is often stored in specialized regions of the urogenital system. The primary reason for this is most likely for water and salt balance. Urine in the bladder can often be concentrated further if water reabsorbtion is required by the animal or salt can be reabsorbed as required.



In fishes, urine is usually stored within the ends of the urinary ducts where they join the cloaca or open to the outside. A urinary bladder of this sort is mesodermal and noncloacal in origin. It is found among the elasmobranchs and most teleost fishes.

In tetrapods, the urinary bladder arises as an outpocketing of the cloaca. Urine flows from the urinary ducts into the cloaca and then into the bladder.

In mammals, the ureters empty directly into the urinary bladder.

In tetrapods, a urinary bladder is present in amphibians, turtles, most lizards, ostriches and all mammals.

It has been lost in snakes, some lizards, crocodilians and all birds except ostriches.

Evolution of the Vertebrates

Fresh Water or Sea Water Origins?

While the blood of marine invertebrates is isosmotic with sea water, the blood of marine vertebrates in only roughly 1/3 the concentration of sea water.

The vertebrate kidney is designed to filter large volumes of fluid and is not well designed, in most vertebrates, to reabsorb it.

Hence, the vertebrate kidney seems better designed for life in fresh water than in sea water - it is better for forming dilute urine than concentrated urine.

This led early anatomists and physiologists such as Homer Smith to argue that vertebrates must have evolved in fresh water.

They argued that as vertebrates moved into sea water they had to then evolve mechanisms to deal with excess salt excretion and water retention (such as drinking sea water, salt glands, and gills for salt secretion - or in some instances elevating the osmotic concentration of body fluids by retaining special ions.

The early fossil record also seemed to support these hypotheses.

Currently, the fossil record supports a marine origin for the vertebrates. Vertebrate style kidneys are also found amongst invertebrates - within the crustacea.