

# Chapter II

## Development of the Mesodermal Organs in Vertebrates

### II.1. Subdivisions of the Mesoderm

There are 4 subdivisions of the mesoderm:

1. The **Notochord** develops into the centrum of the vertebral column.
2. The **Paraxial Mesoderm**: In the head, this mesoderm forms some of the muscles of the head, and part of the skull. In the trunk, the paraxial mesoderm gives rise to the somites.
3. The **Intermediate Mesoderm** arises as a thin stalk of mesoderm connecting the paraxial mesoderm to the lateral plate mesodermal. It will give rise to the urinary system and parts of the genital system.
4. The **Lateral Plate Mesoderm** splits into 2 layers, the somatic mesoderm and splanchnic mesoderm, with a coelom in between. The viscera will be suspended in the coelomic cavity.

### II.2. Fate of the Somites

In the trunk, the paraxial mesoderm gives rise to the somites. The somites develop a central cavity, the **myocoele**. The somites flatten in shape so the myocoele changes from a spherical shape to a narrow slit. The inner and outer walls of the somite have different fates.

1. The *outer wall* is much thinner than the inner wall and will become the dermal layer of the skin; therefore it is called the **dermatome**.
2. The *dorsal part of the inner wall* of the somite is the source of the somatic muscles, and is called the **myotome**.
3. The *ventral part of the inner wall* of the somite is called the **sclerotome**.

The sclerotome breaks up into mesenchyme cells, which migrate to take position around the notochord and neural tube, where they form the body (centrum) and arches of vertebrae and ribs. During its development, the vertebral column passes through three phases:

1. 1st phase - is the notochord alone
2. 2nd phase - is a cartilage model of the vertebrae
3. 3rd phase - is after the cartilaginous skeleton is replaced by bone

### II.3. Vertebral Development

Originally the sclerotomes are segmental because they are part of the somites. When the sclerotomes break up and their mesenchyme spreads out as a continuous sheet, the segmentation is lost. Nodules of cartilage, **arcualia**, then form out of the mesenchymal sheet. The proximal parts of all four arcualia spread around the surface of the notochord and contribute to the **body of the vertebra**. The arcualia usually form in groups of two pair. One pair forms dorso-laterally to the notochord and the other pair ventro-laterally. The dorsolateral pair grow out dorsally along side the spinal cord. They unite above the spinal cord to form the **neural arch** of the vertebra. The ventro-lateral pair in the caudal

region grow downward and unite below the caudal vein to form the **hemal arch**. In the cervical and thoracic region the ventral-lateral pair give rise to lateral outgrowths which are the rudiments of the ribs in thoracic region.

## 11.4. The Development of the Urinary System

The Development of the Urinary System is from the **Intermediate Mesoderm**. In the vertebrates there are 3 main types of kidneys:

1. The **Pronephros** (head kidney) is functional in adult cyclostomes and a few fishes. It serves as a functional kidney in larval fishes & larval amphibians, but degenerates & is replaced by the mesonephros in adults.
2. The **Mesonephros** (middle kidney) is functional during the fetal life of reptiles, birds and mammals.
3. The mesonephros is then replaced by a new organ, the **Metanephros** (hind kidney) which is the third type of kidney.

All 3 kidney types are organs composed of units known as **uriniferous tubules**. These arise from the **nephrotomes** (*Gr. nephros = kidney & tome = to cut*). The nephrotomes connect the somites to the lateral plate mesoderm, which surrounds the coelom.

## 11.5. General Structural Features of the Kidney

The uriniferous tubules connect with the coelom by way of ciliated funnels, **nephrostomes** (*Gr. nephros = kidney & stoma = mouth*). The uriniferous tubules connect with each other and to the exterior by the **Pronephric duct**. In all 3 types of kidneys there is a tuft of blood vessels, the **Glomerulus(-i)** associated with the uriniferous tubules. This arrangement is essential to filter the blood of impurities. The glomerulus may invaginate into the wall of the uriniferous (renal) tubule, forming an **internal glomerulus**. In this case, the renal tubule grows around the glomerulus and forms a structure called **Bowman's capsule**. In other cases the glomerulus invaginates into the coelom, near the nephrostome. These are referred to as **external glomeruli**.

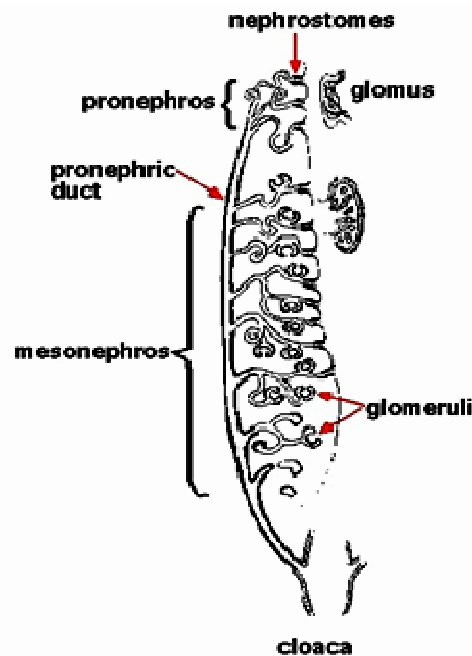


Fig.11.1. General Structural Features of a kidney

## 11.6. Development of the Pronephros

The functional pronephros of lower vertebrates consists of paired pronephric tubules, arranged segmentally. These arise as buds from the nephrotome. The ends of the pronephric buds grow back and unite with each other, forming the pronephric duct. The other end of the pronephric tubules opens into the coelom by way of a funnel shaped nephrostome. Near the nephrostome an arterial tuft, the glomerulus, projects into the coelom. Since the glomerulus is covered only with a thin epithelium, wastes filter out of the blood into the coelom. From there the wastes are carried into the ciliated nephrostome and then eventually to the exterior via the pronephric duct.

## 11.7. Mesonephric Kidney Development

The mesonephros develops from the nephrotomes as does the pronephros. However, in all but a few lower vertebrates, the mesonephros does not develop directly from the nephrotomes. Instead the nephrotomes dissociate into a mass of mesenchyme, referred to as the **nephrogenic cord**. The mesenchyme cells of the nephrogenic cord then aggregate into vesicles. These are solid at first but soon hollow out. Each vesicle then begins to elongate, forming a tubule. One end of the tubule connects with the pronephric duct. The other end of the tubule forms a Bowman's capsule around a glomerulus. The glomerulus is supplied with blood from a branch coming from the aorta. The duct (in the region of the mesonephros) is referred to as the **mesonephric duct**. The mesenchymal nephrogenic cord will develop into mesonephric tubules only if the mesonephric duct is present. Therefore, the mesonephric duct induces the formation of the mesonephric tubules.

## 11.8. Gross Anatomy of the Mammalian Kidney

The innermost region, the **pelvis**, is an expanded portion of the ureter. The pelvis subdivides to form **calyces (calyx) major & minor**. Surrounding the pelvis is the **medulla**, which is divided into triangular wedges, the **pyramids**. The pyramids have a striated appearance. The outer layer of the kidney is the **cortex**, which is granular in appearance. Urine passes from the pelvis into the **ureters**, which carry urine to the **bladder**. Urine then passes to the outside through the **urethra**.

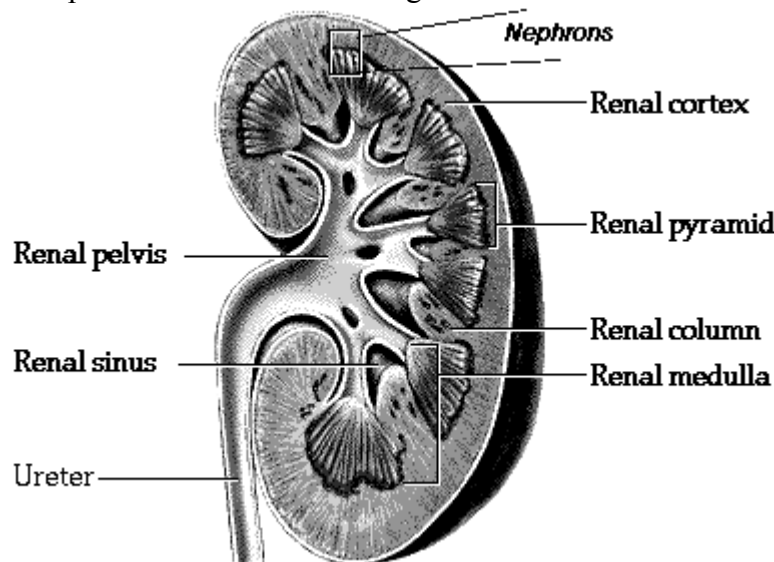


Fig.11.2. Gross Anatomy of the Mammalian Kidney

## 11.9. Microscopic Anatomy of the Kidney

The functional unit of the kidney is the **nephron** (1¼ million in each human kidney). They resemble funnels with long convoluted stems. The proximal end forms a double-walled cup, **Bowman's capsule**, which surrounds a cluster of capillaries, the **glomerulus**. Extending from the Bowman's capsule is a renal tubule which is divided into several sections: the **proximal convoluted tubule**, the **loop of Henle** and finally, the **distal convoluted tubule**. The distal convoluted tubules empty into **collecting tubules**, which then empty into the pelvis of the kidney.

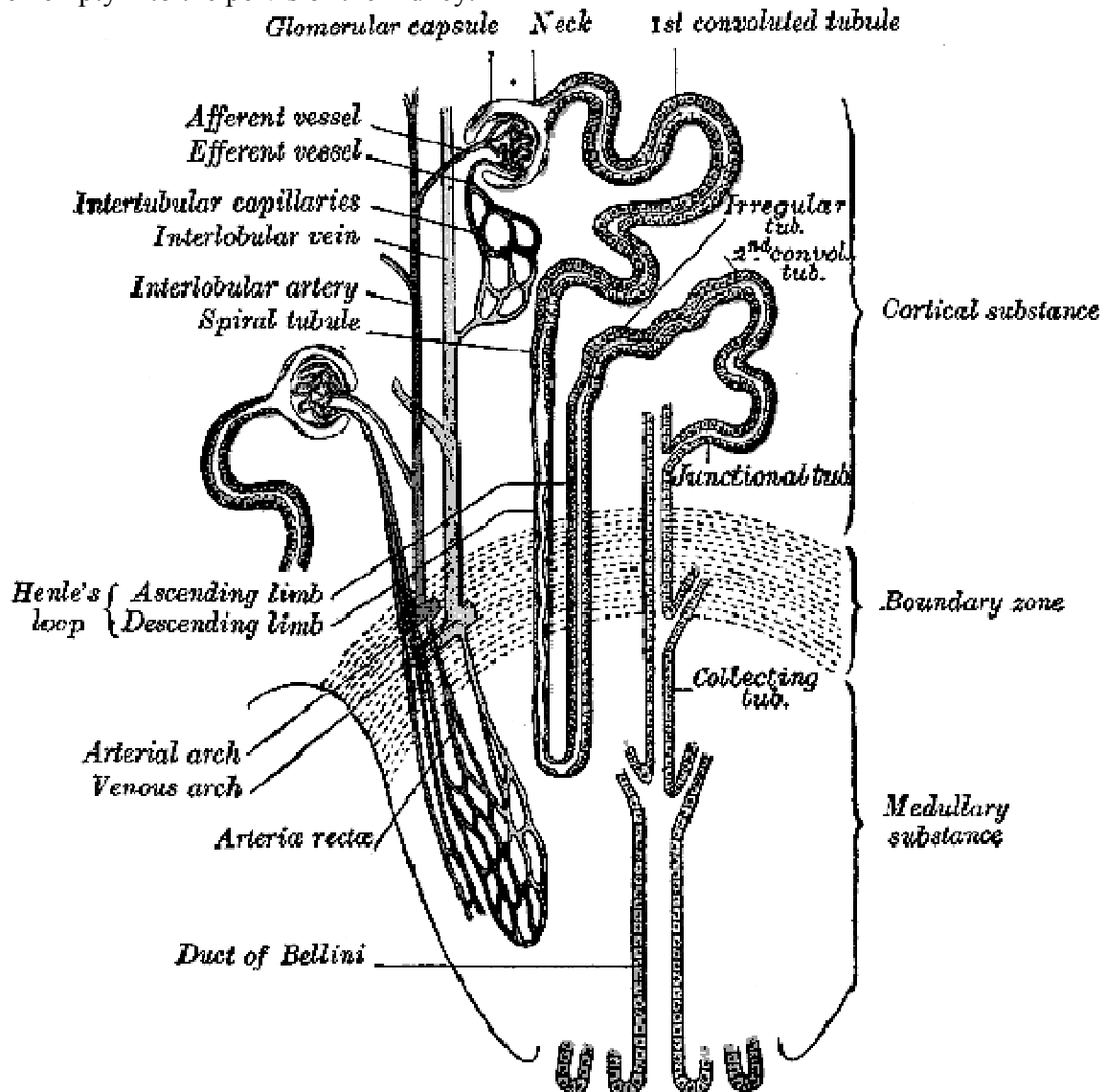


Fig.11.3. Microscopic Anatomy of a mammalian kidney (Nephron)

## 11.10. Development of Metanephros

The **metanephros** develops from the **nephrogenic cord** in the **cloacal** region. The metanephros, like the mesonephros, does not develop a duct of its own to remove the urine it excretes; the metanephros uses the mesonephric duct. A **ureteric bud** forms, near to where the mesonephric duct joins the cloaca. As the ureteric bud grows out and becomes the ureteric stem; the **mesenchymal metanephrogenic tissue** accumulates

around it. The ureteric stem expands to form the renal pelvis and then bifurcates to form two major calyces, from which secondary branches form. After branching repeatedly the collecting tubules are eventually formed.

The **metanephrogenic** material, surrounding the collecting tubule, is solid at first, but then hollows out to form secretory tubules (the future nephrons). One end of the developing secretory tubule becomes the Bowman's capsule, which comes into contact with a tuft of capillaries, the glomerulus. The other end of the secretory tubules attach to the collecting tubules. With further development, complete nephrons are formed with a Bowman's capsule at one end and the other end connected to the collecting tubule. Some fishes and amphibians have a mesonephric kidney which shows characteristics of a metanephros at its posterior end. This is frequently referred to as an **opisthonephros**. The opisthonephros is like the metanephros in the following traits: a complete absence of nephrostomes and the nephric tubules join to large collecting ducts which are outgrowths of the mesonephric duct.

## **11.11. The Lateral Plate Mesoderm**

The **Lateral Plate Mesoderm** splits into 2 layers, the **somatic mesoderm** and **splanchnic mesoderm**, with a **coelom** in between. The viscera will be suspended in the coelomic cavity. There are specific structures which develop from lateral plate mesoderm:

1. Anteriorly, the heart and pericardial cavity.
2. Posterior to the heart, the coelomic space becomes pleural cavity, for the lungs.
3. Most posteriorly, the coelomic space becomes peritoneal cavity, which houses the stomach, intestines, digestive glands and the part of the gonads.

## **11.12. Development of the Heart in Vertebrates**

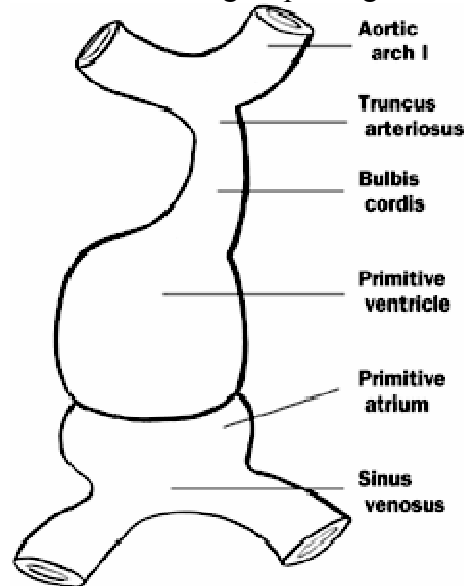
In the gill region the lateral plate mesoderm converges toward the mid-ventral line. At the same time, some mesenchymal cells converge along the mid-ventral line; these form the rudiment of the **endocardium**, which is the endothelial lining of the heart. The endocardial cells form the endocardial tube, which lies along the mid-ventral line of the embryo. The lumen of the endocardial tube is the future cavity of the heart. The endocardial tube bifurcates at both ends. The 2 **ventral aortae** are formed at the anterior end. The 2 **vitelline veins** are formed at the posterior end. While the endocardial tube is forming, the left & right **lateral plates** move underneath the endocardial tube and unite. Where they unite a septum is formed, the **ventral mesocardium**. It soon disintegrates. The visceral layer of the lateral plate mesoderm then surrounds the endocardial tube. Where the visceral mesoderm unites dorsally a **dorsal mesocardium** forms. It also degenerates later. A **pericardial cavity** now surrounds the heart. At first, the pericardial cavity is continuous with the coelom, but later it becomes a separate cavity. The pericardial cavity is lined with lateral plate mesoderm. The **parietal layer** of the lateral plate forms the **pericardium** (*viz.* the sac around the heart). The **visceral layer** adheres to the endocardial tube, and differentiates into the **myocardium** (*viz.* the muscle layer of the heart).

The heart at first is a straight tube and then it folds upon itself in a characteristic manner, becoming roughly S-shaped. In addition to folding the heart constricts in some areas and expands in others. This divides the heart into **four chambers**:

1. The **sinus venosus** lies posteriorly and receives blood from the veins.

2. The **atrium** develops at the tip of the first inflection of the heart.
3. The **ventricle** develops from the straight part between the two inflections.
4. The **conus (truncus) arteriosus (or bulbus cordis)** develops from the part running forward from the 2nd inflection.

Before the heart divides into chambers it begins pulsing with a regular rhythm.



*Fig.11.4. Primitive Heart*

### **11.13. Fetal and Adult Circulation in Mammals**

In air breathing vertebrates, the atrium and ventricle may become divided into left & right atria and left & right ventricles. This is accomplished by the formation of septa across the atrium and ventricle. Trace the **adult circulation** from the inferior and superior venae cavae to the dorsal aorta. In the **embryo**, gas exchange takes place in the placenta, not the lungs. Consequently, the embryo has three right-to-left shunts, to route most of the blood around the lungs:

1. **Foramen ovale**, between the atria, which closes at birth
2. **Interventricular foramen** between the ventricles, which begins closing by 7th week of development.
3. **Ductus arteriosus** is a duct from the pulmonary trunk to the aorta; this closes at birth and remains as the **ligamentum arteriosum**.

Failure of the foramen ovale, the interventricular foramen or the ductus arteriosus to close results in mixing of oxygenated & un-oxygenated blood. The condition is referred to as blue baby.

Blood vessels form from aggregations of mesenchyme cells, called **angioblasts**. The angioblasts form a thin epithelium surrounding a cavity (which is the future lumen of the blood vessel). This epithelium becomes the endothelium of the blood vessel; the outer layers of the blood vessels are added much later in development. The blood vessels are originally laid down as a network. Those blood vessels through which the most blood is channeled develop into arteries & veins. Those with the least blood flow remain as capillaries or degenerate. New blood vessels are also produced by sprouting outgrowths from those blood vessels already present. There are certain preferred locations in the embryo for the **angiogenesis** (development of blood vessels); these are between the

endoderm and visceral mesoderm and around the kidneys.

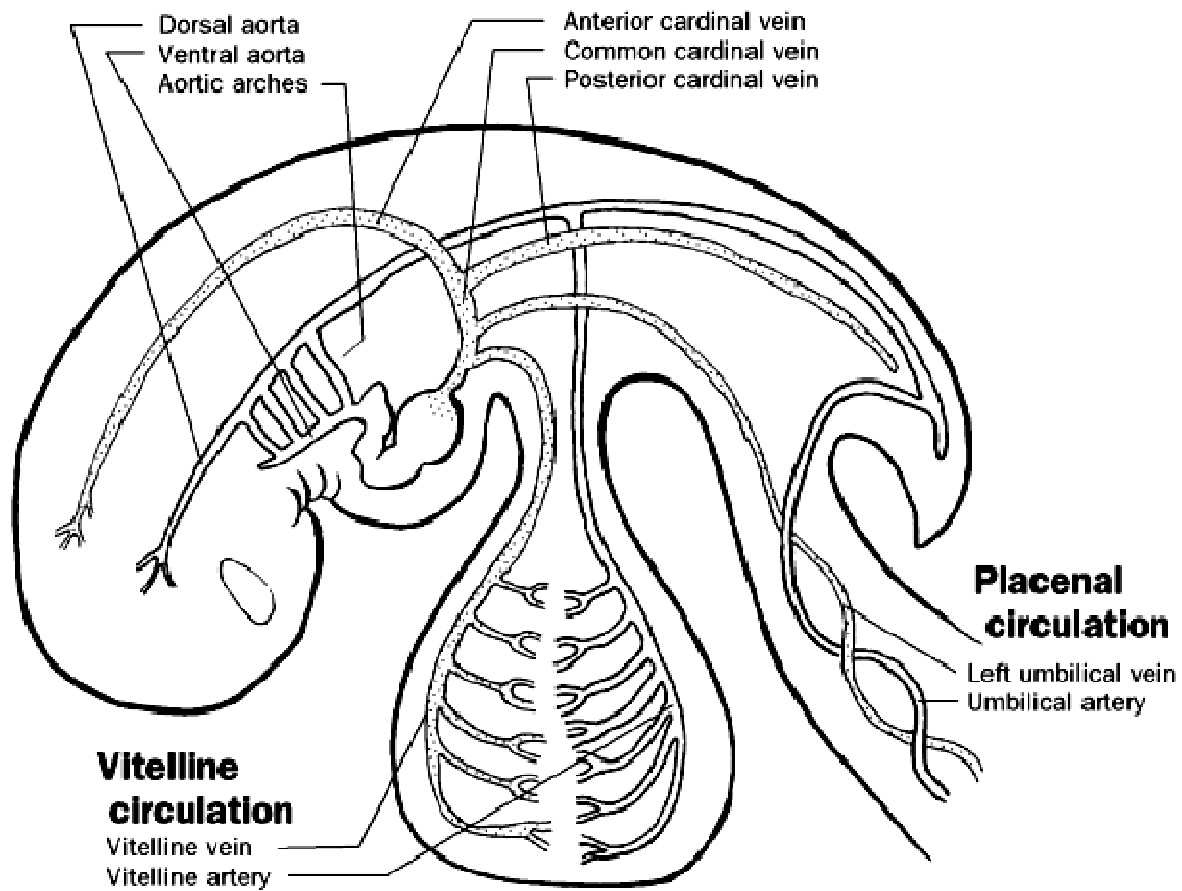


Fig.11.5. The three embryonic circulations

## 11.14. Development of the Reproductive Organs

The components of the reproductive system arise from different tissues. Because the gonads develop from **lateral plate mesoderm** it will be discussed here. In vertebrates, the gonads develop from **germinal ridges**, a pair of longitudinal mesodermal thickenings, that develop in the posterior half of the body from the upper edge of the visceral layer of the lateral plate mesoderm. They develop just medial to the mesonephros. The germinal ridges contain two types of cells. Most of the cells are very similar to the other cells of the peritoneal epithelium. The other type of cells, the **primordial germ cells**, are larger and round. These will develop into the gametes. The **primordial germ cells** migrate to the germinal ridge from other locations:

1. In chickens the primordial germ cells are produced originally in the extraembryonic endoderm, well in front of the head of the embryo.
2. In frogs, they originate from the endodermal cells.
3. In urodeles, they originate from the lateral plate mesoderm.
4. In mice and men, they originate in the endoderm of the hindgut.

As the germinal ridges bulge into the coelom, they form a hollow space within, which is originally filled with loose mesenchymal tissue. This loose mesenchymal tissue is partially replaced by compact strands of cells which migrate from the mesonephrogenic tissue into the gonad. These strands of cells are the **primitive sex cords**. The primitive sex cords constitute the **medulla** of the gonad. The thickened epithelium of the germinal

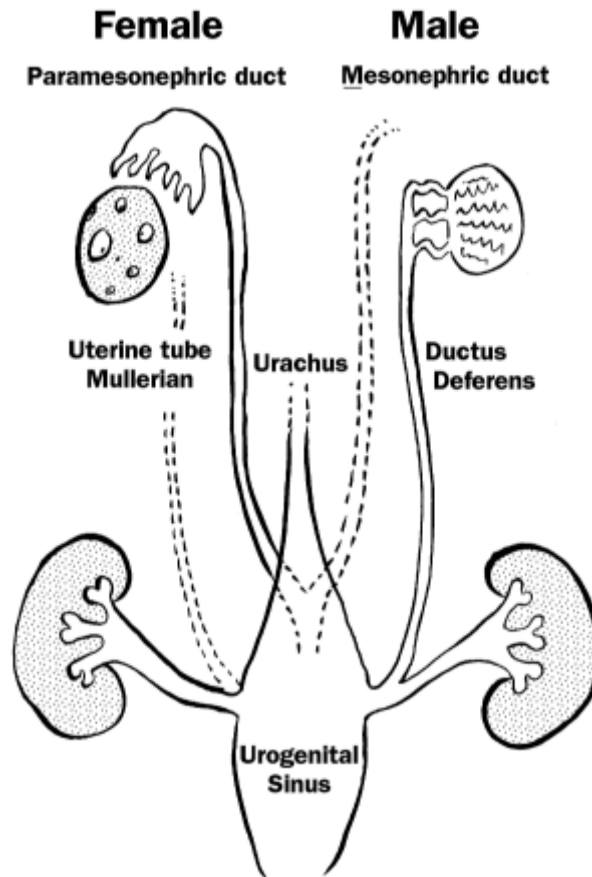
ridge forms the outer layer of the gonad, called the **cortex**. The connection between the gonad and the peritoneal wall constricts and the gonad becomes suspended from the peritoneal wall by a mesentery. This mesentery is the **mesorchium** in males and the **mesovarium** in females. Up to this point the gonads are indifferent, that is, there is no difference in appearance between the male and female gonad. In males, the primordial germ cells migrate from the cortex and enter the primitive sex cords of the medulla. The primitive sex cords then are transformed into the **seminiferous tubules**. Therefore, the medulla in the testis is the functional part while the cortex thins and becomes an epithelial layer covering the testes. In the female, the medulla of the gonad is reduced and the sex cords are reabsorbed. The primordial germ cells remain in the cortex and the cortex expands to become the functional part of the ovary.

## **11.15. Development of the Genital Ducts**

Both sexes develop a new duct, the **paramesonephric (Müllerian) duct**, which runs from the coelom to the cloaca. In **males** the paramesonephric duct has no function and degenerates, but the **mesonephric (Wolffian) duct** becomes the **vas deferens**. In **females**, the **paramesonephric** duct becomes the **oviduct, uterus & vagina**, but the mesonephric duct has no function and degenerates. The development of the genital ducts is controlled by sex hormones released from the gonads. In amphibians, reptiles and birds the mesonephric ducts and ureters (*which carry excretory products*), and the genital ducts (*which carry gametes*) open into the posterior section of the gut called the **cloaca**. Therefore, the cloacal opening serves as the exit for urine, gametes & feces. In mammals, the cloaca becomes divided into a posterior channel for feces and an anterior channel for urine and gametes. In early mammalian embryos the cloaca is a widened portion of the hindgut. A **cloacal membrane** prevents the cloaca from opening to the exterior. Ventrally, the cloaca gives off the **allantoic stalk** (to the umbilicus). Laterally, the mesonephric ducts join the cloaca. A mass of mesenchymal cells, the **urorectal or cloacal septum**, grows back dividing the cloaca into a ventral **urogenital sinus** & a dorsal **rectum**. The perforation of the ventral part of the original cloacal membrane forms the **opening of the urogenital sinus**. The perforation of the dorsal part of the cloacal membrane forms the **anus**. The external surface of the wall between the two openings is the **perineum**. Recall that, in addition to the mesonephric ducts, 2 other pair of ducts develop, which drain into the urogenital sinus. The two **ureters**, which originate by budding off the mesonephric ducts, migrate cranially and open into the urogenital sinus independently. Secondly, the **paramesonephric ducts** drain into the cloaca. The terminal sections of the paramesonephric ducts partially fuse. The upper portion of the urogenital sinus, which receives the ureters and allantoic stalk, expands to form the **urinary bladder**. The portion of the urogenital sinus just below the bladder narrows to form the **urethra**. The external opening of the urogenital sinus is flanked on both sides by the genital folds. Ventrally, these folds join and form a median outgrowth, the **genital tubercle**, which is the rudiment of the **phallus**. Up to this point, the embryo represents the indifferent conditions; (it is not possible to differentiate the sexes). In the **male mammalian embryo** the **seminiferous tubules** attach to the mesonephric duct by way of the **mesonephric tubules**, which are converted into the **rete testis** and the **epididymis**. *The rete testis is a meshwork of tubules; the epididymis is a highly convoluted tubule, which is the main storage area for the sperm. It is 6 to 7 meters long in humans.* The **mesonephric duct** is converted into the **vas deferens**. Also, in the male, the



**paramesonephric ducts degenerate**, the **rudiment of the phallus** grows and becomes the **glans penis**, the **genital folds** fuse forming the **base of the penis** and the enclosed **urogenital sinus** forms the **urethra of the penis**. In the **female** the **terminal portions of the paramesonephric ducts** fuse to form the **uterus and vagina**. The upper parts of the paramesonephric ducts form the oviducts (Müllerian ducts, fallopian tubes, uterine tubes). These **DO NOT** connect to the ovary. The female **mesonephric duct** in amniotes degenerates when the mesonephric kidney ceases operation. The **rudiment of the phallus** grows slightly and becomes the **glans clitoris**. The **genital folds** do not fuse and form the **labia minora**. The **posterior portion of the urogenital sinus** widens and forms the **vestibulum**, which is a longitudinal cleft into which the vagina & urethra open independently.



*Fig.11.6. Adult persistence of embryonic ducts in the genitourinary system*

## **11.16. The Development of Paired Limbs**

Paired limbs are complex structures, which are derived from several sources, mainly the lateral plate mesoderm, the epidermis & the somites. First, the somatic layer of the lateral plate thickens. The cells of these thickenings then break off and attach to the inner surface of the epithelium. The epithelium then thickens and protrudes from the side of the body, forming the limb bud. It consists of a thickened epithelial covering and an internal mass of densely packed mesenchyme. The limb buds then grow out and differentiate.

Extra limb buds can be induced by transplanting the epidermis of another limb bud onto the side of a host embryo. The ear vesicle, olfactory sac and other organ rudiments will also induce a limb to form if transplanted into the side of a young embryo.