

Evolution of the Kidney

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Abstract

Aim of the work: This article will elucidate the extraordinary parallels between the evolution of the kidney from provertebrates to man. In invertebrates, the excretory structures are classified into three types included contractile vacuoles in protozoa, nephridia (flame cell system) in most invertebrate animals and Malpighian tubules (arthropod kidney) in insects. While, in vertebrates, there are three distinct excretory organs formed in succession during the development of the vertebrate kidney, they are called pronephros, mesonephros and metanephros.

Conclusion: From this review, it can be concluded that the important factors in the evolution of the basic structure and function of the vertebrate kidney appeared associating with body fluid- regulation, involving the maintenance of a constant water and salt content of the body. As the evolution of the vertebrate kidney illustrates how pronephric, mesonephric and metanephric kidneys are represented successful evolutionary responses to the surrounding environmental pressures.

Keywords: Development of kidney; Pronephros; Mesonephros; Metanephros; Opisthonephros; Archinephros; Flame cells; Contractile vacuoles; Malpighian tubules

Introduction

Evolution of the kidney is a hot topic for many researches and biologists as there is no better place to see the impact of evolutionary pressures on organ development than in the kidney and to study the ability of human metanephroi to differentiate after transplantation into functional mature nephrons [1].

Aim of the work

All vertebrates have kidneys like the human kidneys, they are made of many nephrons. However, there are many differences in the structure and function of various vertebrate kidneys that adapt them to the environment in which the animals live. This article will elucidate the extraordinary parallels between the evolution of the kidney from provertebrates to man.

The Excretory structures in Invertebrates and Vertebrates

The excretory system regulates the chemical composition of body fluids by removing metabolic wastes and retaining the proper amount of water, salts and nutrients. The invertebrate excretory structures are classified in according to their marked variations in the morphological structures into three types included contractile vacuoles in protozoa, nephridia (flame cell

system) in most invertebrate animals and Malpighian tubules (arthropod kidney) in insects [2].

There are three distinct excretory organs formed in succession during the development of the vertebrate kidney, they are called pronephros, mesonephros and metanephros. The **pronephros** is the most primitive one and exists as a functional kidney only in some of the lowest fishes and is called the **archinephros**. The **mesonephros** represents the functional excretory organs in anamniotes and called as **opisthonephros**. The **metanephros** is the most caudally located of the excretory organs and the last to appear, it represents the functional kidney in amniotes [2-4].

Invertebrate excretory structures

Contractile vacuole: The contractile vacuole presents in the protozoa (Figure 1A), do not be considered as a true excretory organ, as ammonia and nitrogenous wastes left the cell by diffusion, while the contractile vacuole is a true organ for water and salt balance. In amoeba proteus, the excess water is collected in fine and many vesicles surrounding the membrane of the contractile vacuole. These vesicles are emptied their contents into the vacuole. This vacuole is moving inside the cytoplasm for a time until it reaches a certain size where it is then passes up through the plasma membrane and empties its contents into the surrounding

medium through a small pore in the plasma membrane. When the water is expelled from it, it starts to refill immediately [2].

Nephridia (Flame cell system): In most of the invertebrates, excretory organs are called nephridia or nephridial tubules. There are two types of nephridia, the first is protonephridium and the second is metanephridium. **The protonephridium** had a blind tubule system, it is present in many invertebrates such as flatworms. At the end of each blind tubule of the nephridium is a ciliated flame cell (Figure 1B). The fluid enters the system through the flame cells and then passes down through the tubule where some ions and molecules are reabsorbed. The wastes are expelled outside through excretory pores on the body surface [2-4]. **The metanephridium** or called true nephridium has an open tubule system which is surrounding by a vascular network. It is present in some invertebrate such as the earthworm. In the earthworm, each nephridial tubule occupies two adjacent segments. The tubule is connected to the coelom at one end by a ciliated funnel, or **nephrostome**, and at the other end is opened to the exterior by an excretory pore called **nephridipore**.

In amphioxus (primitive chordates), there is a series of excretory tubules opened into the atrium or pericardial space. Each lies on the outer dorsal side of the secondary gill bar. They were apparently of ectodermal origin, has no connection with the coelom and are composed of numerous flame cells called “**solenocytes**” which collected wastes. The solenocytes are attached to the walls of blood vessels and are bathed by coelomic fluid. Those belonging to a given tubule entered a common excretory canal, which in turn is opened into the atrium through a small excretory pore, is called a nephridipore [2,3].

Malpighian tubules (Arthropod kidney): The insects have a special excretory system which is formed of Malpighian tubules and rectal glands (Figure 1C). The Malpighian tubules are thin, delicate, convoluted and blind. They have no blood supply. The body fluids are drawn into the tubules by osmosis due to the large concentrations of potassium inside these tubules, and then the body fluids are passed back into the body and reabsorbed by the rectal glands. While the nitrogenous wastes emptied into the insect’s gut. This excretory system conserved water and is suitable for insects which lived in a dry environment [2] (Figure 1).

Evolution of the vertebrate kidney

Evolution of the vertebrates is a fascinating story viewed in terms of the external osmotic environment in which various classes evolved. Fresh water, marine and terrestrial habitats possessed different problems for the maintenance of internal water balance and the excretion of nitrogenous wastes. The evolution of the kidney in vertebrates illustrates how pronephric, mesonephric and metanephric kidney, represent successful evolutionary responses to these environmental pressures. So many variations in the evolution of the kidney are correlated with these environmental factors. Variations in the structure of the vertebrate kidney from fish to man are primarily in the nature of alterations in number, complexity, arrangement and location of the kidney tubules [5,6].

Embryological origin: The kidney in all vertebrate is originated from the intermediate mesoderm. The mesoderm which will form the kidney was called nephrogenic mesoderm. The kidney as a whole is made up of two elements, the kidney duct and the kidney tubules. The kidney tubules called nephrons, they are evolutionary modifications of the nephridia and they are the kidney’s functional units. The development of the kidney is somewhat complex in that two or three different kidneys (depending on species) formed in temporal and spatial sequence. The first, most anterior and largest to develop is the pronephric kidney. The second kidney to form is the mesonephric kidney. In birds, reptiles and mammals, a third kidney developed posterior to the mesonephros, called the metanephric kidney [3-6].

Effect of environment on the nephron structure and function: The components of the nephron in higher vertebrates and man are the glomerulus, the Bowman’s capsule, the proximal convoluted tubule, the loop of Henle and the distal convoluted tubule. The glomerulus filters the blood. The Bowman’s capsule also filters the blood and their cells (podocytes) prevent the passage of the large molecules as blood proteins and blood cells to the Bowman’s space. The proximal convoluted tubule reabsorbs water, salts, glucose and amino acids. Loop of Henle reabsorbs water and small molecules. The distal convoluted tubule secretes H₂ ions, potassium and certain drugs [5,6].

However, there are three types of nephrons in different species of vertebrates. The first type is presumably the most primitive, found in amphibians, fresh water, bony fishes and elasmobranchs, there is a renal corpuscle of good size and hence a high water output. The second type was that found in many marine teleosts and in reptiles, the corpuscle is small or absent with shortening of the renal tubule, hence increases salt excretion and water conservation (water output is low). The third type is seen in mammals and in a less extreme form, in birds. The glomerulus is large, but there is interjected into the middle of the convoluted tubule, a long slim extra- segment, the loop of Henle. This slim segment appeared to be a powerful resorption

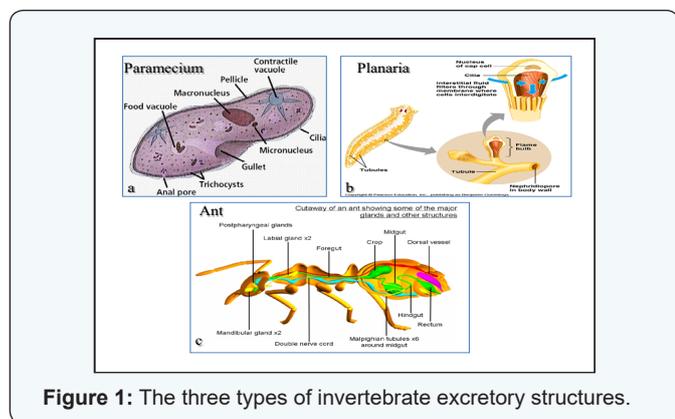


Figure 1: The three types of invertebrate excretory structures.

of water, hence despite a plentiful output at glomerulus, relatively little water reached the bladder [5]. The distribution of the three types of nephrons among vertebrates is correlated with the environmental factors. These variations can be explained as followed:

I. The first type is present in early fresh water vertebrates. Such an animal lived in a medium more dilute than its own fluids and hence is in danger for overdilution of these fluids by osmosis through the surface of the body and of the gut. To prevent this, large amount of water should be eliminated and this is afforded by the presence of a large corpuscle.

II. The second type is present in marine teleosts where high salinity of the surrounding medium is present. In this type, water should be conserved and much salt eliminated. So the glomeruli are frequently reduced or absent. The aglomerular kidney is present in seahorses and pipefishes [7]. So water output consequently reduced, further salts and wastes are excreted by the cells of the gills membranes and rectal glands as well as by the kidneys. The terrestrial vertebrates, lived in a dry environment have the same problems as a marine fish, water should be conserved. In modern reptiles, this is accomplished by reduction in size of the renal corpuscles with a consequent decrease in water output.

III. The third type is present in birds and mammals. These animals developed a different method of conservation of water. There is a normal glomerulus of large size and consequent high water output. The complex tubule and the presence of loop of Henle result in absorption of much of the water, the product is a relatively concentrated urine [5,6].

Types of developing vertebrate kidney (Figure 2):

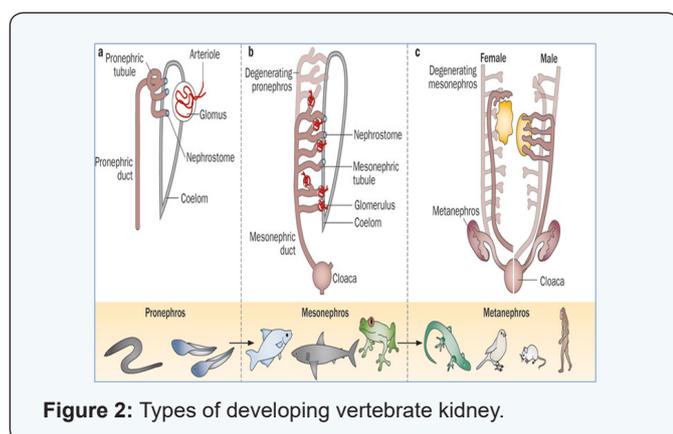


Figure 2: Types of developing vertebrate kidney.

Archinephros: The primitive vertebrates possess an excretory organ which is referred to as an archinephros or holonephros. This is consisted of a pair of archinephric ducts located on the dorsal side of the body cavity and is extending the length of the coelom. Each duct is joined by a series of segmentally arranged tubules, one pair of tubules to a segment. At its other end, the tubule is opened into the coelom by a ciliated, funnel-shaped, peritoneal opening called the nephrostome. Also another

structure formed in connection with each tubule, it was also called external glomerulus, a small knot or cluster of capillaries interposed within the course of an arteriole and located in close proximity to the nephrostome. Tissue fluids, exuded at the glomeruli, are passed in the coelom and hence the nephrostomes into the kidney tubules and finally through the archinephric ducts to the outside [8].

The Anamniote kidney: The developing kidney in an amniotes differentiated in two stages: pronephros and opisthonephros.

Pronephros: The pronephros is actually consisted of a varying number of anteriorly located pronephric tubules together with a pair of archinephric ducts (which called here pronephric duct). The tubules and ducts lay in the dorsolateral mesoderm on either side of the mesentery that supported the gut. The tubules were segmentally arranged, connected with the near pronephric duct at its anterior end. The outer end of the tubules opens into the coelom by means of nephrostomes. The nephrostome and the part of the tubule near it are ciliated. Most forms are possessed internal glomeruli. These are knots of interarterial capillaries, each surrounded by a double wall structure called Bowman's capsule, the two together are known as renal or Malpighian corpuscle. Sometimes, several glomeruli united to form a large glomus. In some cases, pronephric tubules expanded so as to form pronephric chambers or one large pronephric chamber. The pronephros was degenerated soon after it have been formed [2,3,5,6].

Opisthonephros: Since the pronephros in most cases is a transient structure, the opisthonephros is served as the adult kidney in lampreys, most fishes and amphibians. In many accounts, the term mesonephros is used in describing what they are here calling the opisthonephros. Biologists have realized that the opisthonephros of cyclostomes, fishes and amphibians is not quite comparable to the mesonephros of embryonic amniotes even though the two are structurally similar in many ways.

It is important to mention that the opisthonephros of anamniotes actually extended over a region which in amniotes would form the mesonephros and metanephros. In forms possessed an opisthonephros, there is a general tendency toward a concentration of kidney tubules toward the posterior end of the organ. The anterior portion frequently losses its significance as an excretory organs and in the male, may became part of the reproductive system. Furthermore, the connection of the kidney tubules with the coelom is lost in most case and the presence of renal corpuscles with internal glomeruli being typical [6,8].

Structure of the opisthonephros

Each tubule differentiated into a narrow neck at the end of the renal corpuscle, followed in turn by secretory and collecting portions. The collecting portion connected with the archinephric duct. The secretory part of the tubule forms two loops named the proximal and distal convoluted segments or tubules [3,9].

The Amniote kidney

In reptiles, birds and mammals including humans, three types of kidneys are recognized, pronephros, mesonephros and metanephros. These are appeared in succession during embryonic development, but only one, the metanephros is persisted to become the functional adult kidney. Mesonephros and metanephros are actually represented different levels of the opisthonephros of the anamniotes, the metanephros being the equivalent of the posterior portion. In all forms, an anteriorly located pronephros is present during early stages of development, but it is soon degenerated and the more posterior mesonephros then is developed. The duct of the pronephros is persisted to become the duct of mesonephros. This is actually the same as the archinephric duct. The mesonephros is persisted for a time and then is degenerated. In the meantime, the metanephros developed from the region posterior to the mesonephros. Portions of the mesonephros persisted to contribute to the reproductive system in the male or to remain as mere vestigial structures, without any apparent function in female [10].

Pronephros: The pronephros in amniotes is formed in a manner similar to that of anamniotes. Segmentally arranged pronephric tubules appeared in the intermediate cell mass in some of the anterior segments of the body. They are first solid structures, but they soon are hollowed out, one end established a connection with the coelom. The tubules are appeared in succession in a cranio-caudal direction. A variable number of such tubules are formed in different species. **In the chick**, for example, 10 or 11 pronephric tubules are formed on each side from the 5th to the 15th or 16th segment, the last tubule is enlarged caudally and established a connection with the cloaca. Thus, a long pronephric duct is formed, the anterior end of which is connected to a series of tubules with coelomic connections. The tubules soon are disappeared, in fact, the anterior tubules may degenerate before the posterior ones even formed. External glomeruli may or may not form. So, **in mammals**, pronephric tubules are appeared only as the merest of vestiges. Hence, the pronephric duct can scarcely be said to be formed as the result of fusion of tubules. Nevertheless, it is appeared in the nephrotome region, first as a solid cord which grow back to the cloaca, hollowing out to become a typical pronephric duct [4,10].

Mesonephros: The mesonephros of amniote embryos have essentially the same structure as the kidneys of fishes and amphibians except that nephrostomes are rudimentary in most birds and seldom appeared in mammals. **In embryonic chick**, the mesonephros reaches its peak of development at the 11th day of incubation, halfway through embryonic life. **In mammals**, it reaches its peak earlier at the 9th week of gestation. **In a human fetus**, it is appeared after 4 weeks of embryonic life (20- somites stage). A wave of differentiation is occurred along the nephrogenic mesoderm, so that even before the last mesonephric tubules at the caudal end of the series has been formed, the earliest ones at the anterior end has been already involuted. The result is

that at peak development of the human mesonephros, there are about 30 functioning renal corpuscles, although as many as 80 have been formed by that time. The mesonephroi of various species of mammals differ in the number of mesonephric tubules formed. Those in man, cats and guinea pigs are relatively small as compared with the mesonephroi of rabbits [4,10].

Fate of Mesonephros: Although the mesonephros is basically an embryonic kidney in amniotes, it functions for a short time after birth in reptiles, monotremes and marsupials. In the meantime, a new kidney to be used by the amniotes the rest of life, the metanephros, is in the process of development. When the metanephros took over the functions of a kidney, the mesonephros involuted and only remnants remained after birth [10].

Mesonephric remnants in adult amniotes: Small remnants of the mesonephroi are remained in both sexes after the metanephroi involuted. In mammals, the remnants consisted of groups of blind tubules known as the paradidymis and the appendix of the epididymis located near the epididymis and as the epooporon and paroophoron near the ovary. The mesonephric ducts remained as sperm ducts in male amniotes, but they are involuted in females and thus remained only as short, blind Gartner's ducts coursing in the mesentry of the oviducts [10,11].

Function of mesonephric tubules: The function of mesonephric tubules much like the nephrons of the adult kidney. A filtrate of blood from the glomerulus enters the capsule and flow into the tubule, where selective resorption of ions and other substances are occurred. A major difference between the mesonephric kidney and the permanent kidney of higher vertebrates is the relative inability of the mesonephros to concentrate urine. This is related to the elongated structure of the mesonephros and the absence of a well developed renal medulla, a structural adaptation of land animals to preserve water by concentrating it through an elaborate countercurrent exchange mechanism.

*Such a fluid conserving mechanism was not needed by the embryo which lived in a bath of amniotic fluid, just as preservation of body water was not a problem for the mesonephric kidney of fishes and aquatic amphibians [10].

Metanephros

The metanephros is found only in amniotes and human, arising posterior to the mesonephros on each side and is more compact than the latter organ. It comes from a level which is corresponded to the most posterior portion of the opisthonephros of the anamniotes. The development of the metanephros begins with the appearance of a tiny bud-like outgrowth from the mesonephric duct just cephalic to the point where the duct opened into the cloaca. The outgrowth, is called the metanephric diverticulum. This diverticulum is pushed into the posterior portion of the intermediate mesoderm, which is condensed around the diverticulum like a cap to form the metanephric blastema.

Thus, the metanephric kidney had a dual origin, the metanephric diverticulum, which gives rise to the ureter, the renal pelvis and the collecting duct system and the intermediate mesoderm from which the tubular units of the kidney arose [11-13].

Differentiation of the metanephric tubules

The metanephric blastema organize the metanephric tubules, they commence as S-shaped tubules. The upper arm of each tubule grows toward and finally opens into a collecting tubule. The lower arm is invaginated by a developing glomerulus to become a Bowman's capsule. The mammalian metanephros exhibits a greater organization than that of lower amniotes. The organization is the result of the formation of a long thin, U-shaped loop of Henle interposed between the proximal and distal convoluted tubules. As the loops of Henle elongated, they grow away from the surface of the kidney and toward the renal pelvis. The kidney therefore consisted of a cortex in which are concentrated the renal corpuscles and a medulla which consists of the hundreds of thousands of loops of Henle and common collecting tubules.

The loops of Henle and collecting tubules give the medulla a striated appearance in frontal section. They are aggregated into one or several conical lobes (pyramids), depending on the species. The pyramids are tapered to a blunt apex (renal papilla), projecting into the renal pelvis and are surrounded by extensions (the calyces) of the pelvis. Each collecting tubule drains a small number of metanephric tubules and then empties into the renal pelvis near the end of the papilla.

The metanephric tubules of reptiles have no loop of Henle, and those of birds have only a very short equivalent segment. So reabsorption of water in reptiles and birds also are occurred in the cloaca, into which the ureters are opened. The glomeruli in reptiles and birds are reduced in size and exhibited only two or three short vascular looped within Bowman's capsules [11-13].

Comparative anatomy of metanephros: The comparative anatomy of metanephros in amniotes are described [3,6,14].

In reptiles, the kidneys are restricted to the posterior half of the abdominal cavity and are usually confined to the pelvic region. They are generally small and compact but their surfaces are lobulated. They are elongated or slender in shape.

In birds, the kidneys were situated in the pelvic region of the body cavity and the two frequently united at their posterior ends. They are flat-shaped. Their surface is lobulated, deep fissures between the lobules are present, serving for the passage of the branches of the renal veins.

In mammals and human, the typical kidneys are compact bean-shaped attached to the dorsal body wall. They are retroperitoneal. The ureter leaves the medial side at a depression called the hilum. At this point, a renal vein also leaves the kidney and a renal artery and nerves enter it. The metanephros is surrounded by a capsule

of connective tissue under which lie the cortex.

Lobulation of vertebrate kidneys

Many metanephric kidneys are lobulated as in reptiles, birds and others, each lobe consisted of clusters of many tubules. Lobulation is occurred also in human infants but later is disappeared during the first year after birth. Varying degrees of lobulation, however, on occasion, persisted through life [4].

Arterial supply of the vertebrate kidneys

In reptiles and birds, the arterial blood supply to the metanephric kidney, is via a series of two or more renal arteries of segmental origin. In mammals, there is usually a single renal artery, but it very often bifurcated before reaching the kidney. Upon entering the kidney of mammals, the renal artery divides into numerous branches which passed radially toward the cortex as interlobar arteries. At the base of the cortex, the interlobular arteries give off arcuate arteries which arch along the base of the cortex more or less parallel to the surface of the kidney. From the arcuate arteries arise tiny interlobular arteries which in turn, give off afferent glomerular arterioles terminating in glomeruli. Emerging from each glomerulus is an efferent arteriole which passes directly to a capillary bed surrounding the tubule. Emerging from the capillaries are arcuate veins. The kidney is drained by one or several renal veins.

The kidney of reptiles and monotremes is similar to a slight degree, to that of birds, also has an afferent venous supply via a renal portal system. The portal vessels terminate the same peritubular capillary beds as do the efferent glomerular arterioles [3,11].

Conclusion

From this review, it can be concluded that the important factors in the evolution of the basic structure and function of the vertebrate kidney appeared to have been associated with body fluid – regulation, involving the maintenance of a constant water and salt content of the body. As the evolution of the vertebrate kidney illustrates how pronephric, mesonephric and metanephric kidneys are represented successful evolutionary responses to the surrounding environmental pressures.

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