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Scope and Method of Study: This report was undertaken as a study of the information available concerning the evolution of the nephron and related research. The sources of information used in this study are (1) scientific journals and periodicals and (2) books.

Findings and Conclusions: The material relative to the subject was scant. The theory was discussed extensively in the philosophical articles but almost ignored during the discussions following actual research. There seems to be little supporting evidence for the theory because of the magnitude of the work needed to support such a broad theory.

ADVISER'S APPROVAL L. Herbert Bruneau.

A CONSIDERATION OF THE EVOLUTIONARY SIGNIFICANCE OF THE NEPHRON

BY

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CHAPTER I

INTRODUCTION

The idea that the development of the nephron is apropos to the most widely accepted theory of evolution first came to the author's attention in connection with a course in High School Biology, the blue version of the Biological Science Curriculum study as produced at the 1961 Summer Writing Conference. Under the topic, "The Evolutionary Significance of the Nephron," the hypothesis is presented as follows:

> The ancestors of the chordates came from the sea. The excretory system which the inverbrates inherited from their marine ancestors consisted of a series of tubules which opened into the body cavity. The migration from salt to fresh water required structural as well as functional adaptations. By the time the truly fresh-water fishes evolved, the nephron was fully developed. This is most important since chordate tissues and body fluids contain salts and organic compounds in higher concentrations than the surrounding water. This would cause water to be absorbed from a fresh-water environment (See Figure 1). The evolution of the glomerular kidney as a device for the excretion of excess water from the body constitutes but one in a large number of adaptive changes which arose in response to the requirements for living in fresh water.
>
> The story of water conservation has been different among the marine fishes (See Figure 2). For instance, the cartilaginous fishes, such as sharks, skates, rays, like some of the primitive fresh-water fishes, produce urea as a by-product of protein breakdown. Urea is a waste compound that is soluble in water. Urea can be excreted as a soluble waste in ruine. Instead of getting rid of urea as other vertebrates do the cartilaginous fishes reabsorb it through the kidney tubules. In this way, the concentration of urea is maintained at a high level. Such a level raises the osmotic pressure of the fish blood above that of the sea water. Thus, the

tendency of water movement into the fish through the gills is sufficient to serve the normal water needs of the fish without the necessity of swallowing salt water.

The marine bony fishes do not conserve metabolic urea. The osmotic pressure of the blood is not as high as the osmotic pressure of the sea water. Thus, water normally tends to leave the animal. Replacement water can only be obtained by drinking sea water. Every gulp of water that the fish drinks is accompanied by salt. This creates a problem of salt disposal. Fortunately, salt is excreted from the blood through the gills leaving water available for the body tissues and for urine formation. If the fish were to excrete large volumes of urine, it would be necessary to drink more salt water. This is not a problem, for urine formation in bony fishes is maintained at a low level. How? This is possible since the glomeruli in many marine fishes are usually degenerate. The glomeruli was completely absent in a few older ancestral groups. Such modifications in glomeruli cut down filtration which is important for the conservation of water. Excretion of waste and excess substances takes place through the tubules.

Certain changes in excretory devices are also necessary for life on land. The first truly terrestrial animals were the reptiles. As we have discussed, a problem of land-dwelling animals is the conservation of water. We have studied the action of a typical mammalian kidney, so let us look at another adaptation necessary for life on land. The reptiles and birds have evolved a somewhat different excretory mechanism for the maintenance of a normal water content. In both groups of animals the glomeruli are degenerate. There are only a few channels of blood supply making up the glomerulus. This, of course, restricts the surface of transport tissue available for filtration. Thus, the volume of urine excreted is small. The end product of protein breakdown in these animals is not water-soluble urea. If this was the case, large amounts of urine would have to be formed. Protein breakdown in most birds and reptiles is different in that uric acid is the chief end product. What is different about uric acid? Basically, the most important property of this compound is the fact that it is almost insoluble in water. When urine is formed in the tubules of reptiles and birds, the uric acid crystallizes (becomes solid) leaving the water free to be reabsorbed. Excretion in such animals occurs with very little loss of water. The droppings of birds contain fecal matter, a suspension of uric acid crystals, and very little water.

These have been just a few examples of adaptations of organisms for survival in various environments. Many such adaptations have evolved for the proper maintenance of the constancy of the internal environment in changing external environments (See Figure 3).[1]

These exciting ideas inspired further study into the history and development of the hypothesis. In pursuit of this study, the entire scope of evolving life required review. In considering the relationship of nephric evolution, focus was set on the origin of the vertebrates, whose beginning was really the start of life itself. How and where the fossils of organisms were located became historically important in tracing the path of development. The function and structure of the nephrons of living organisms who resemble the fossils contributed to the unfolding picture. Finally, the strange parallels between periods in individual embyronic development and the historic complexity of the evolving nephron appeared to be closely related.

However, the broad assumptions and ever increasing exceptions also demand inquiry. There seems to be no simple solution to the problem. The future is filled with the challenge to inquire, to see, to know, and understand.

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[1] J. J. Schwab and M. Grant, (eds.), High School Biology Blue Version. American Institute of Biological Sciences, Biological Sciences Curriculum Study, 1961. University of Colorado. Hereafter referred to as B.S.C.S.

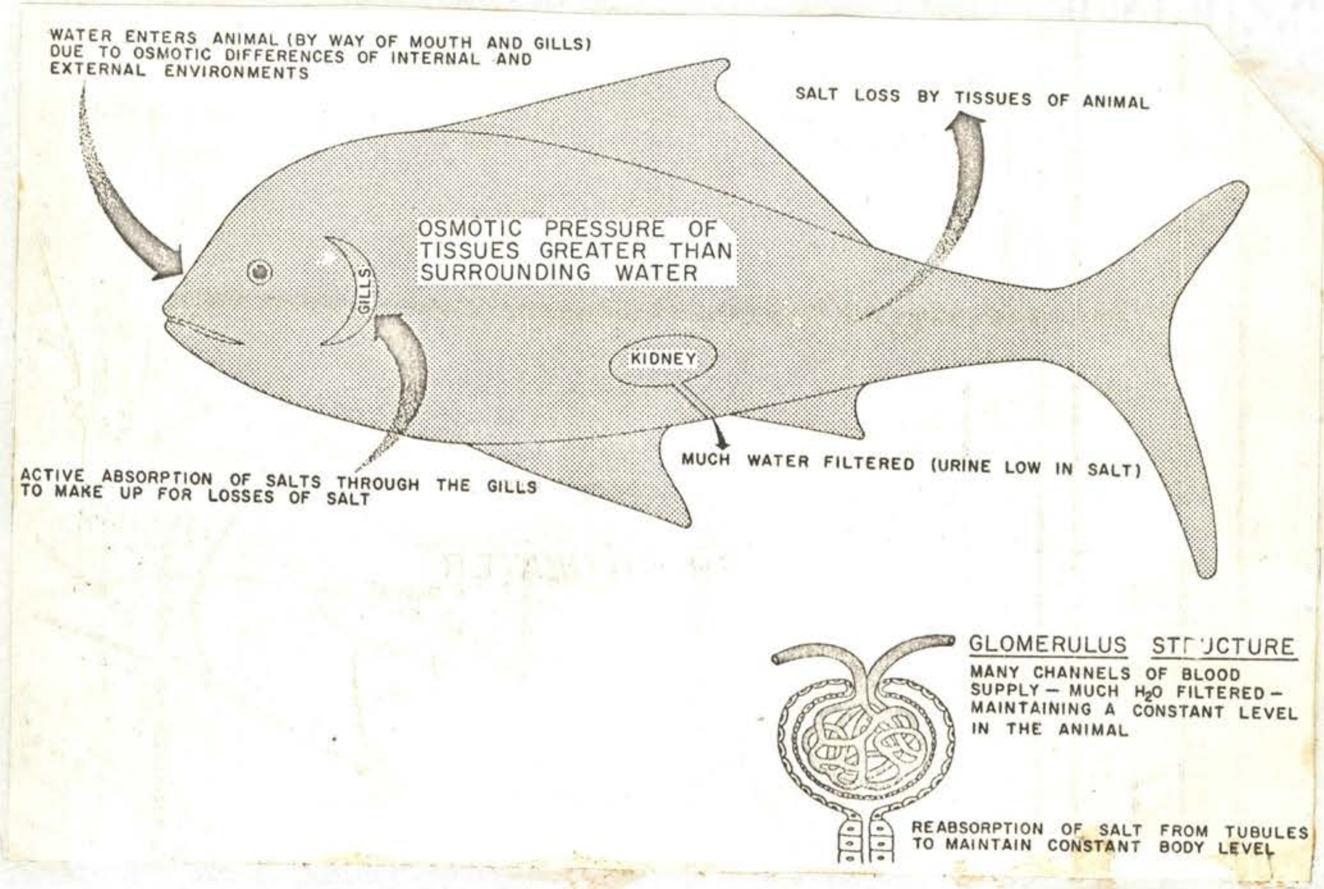


Figure 1. Basic excretory adaptations of fish living in a fresh-water environment. (After B.S.C.S.)

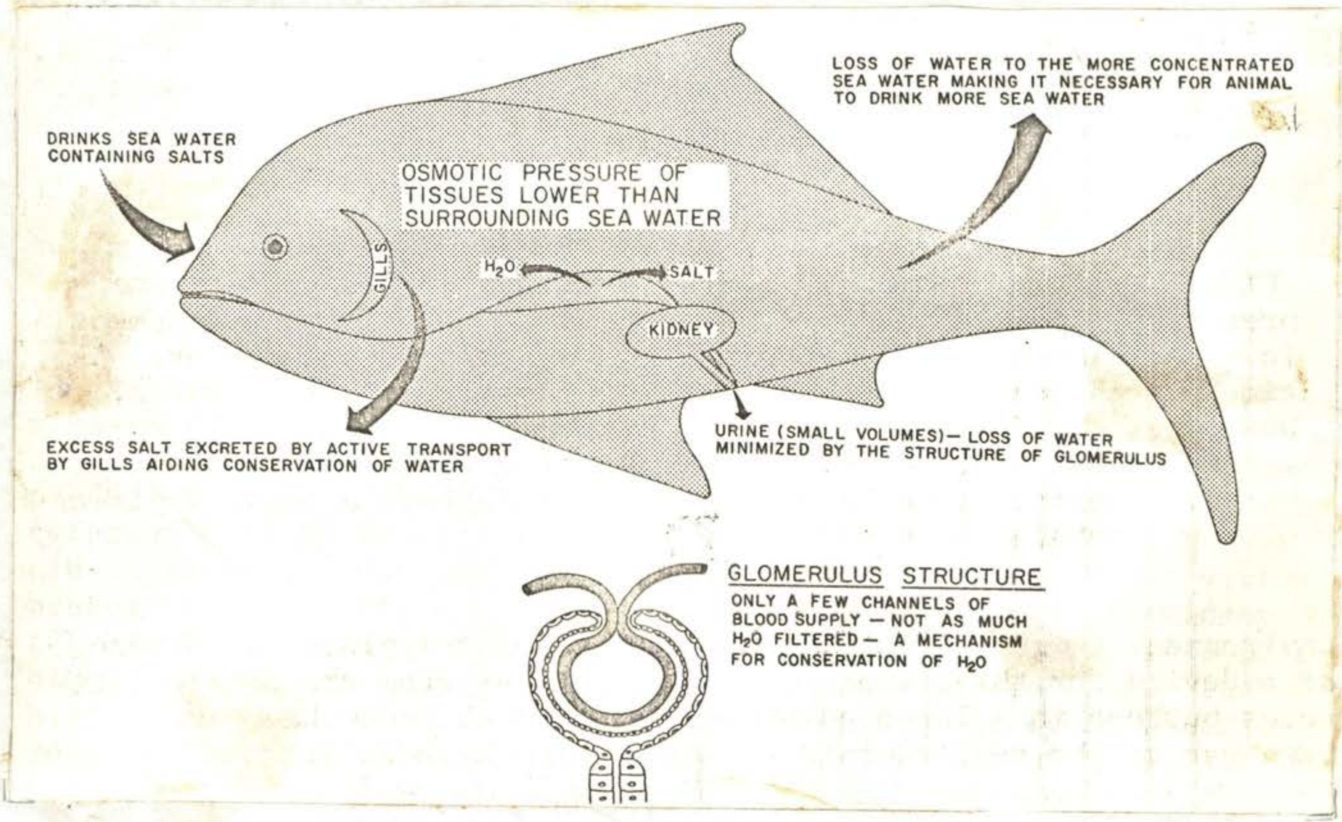
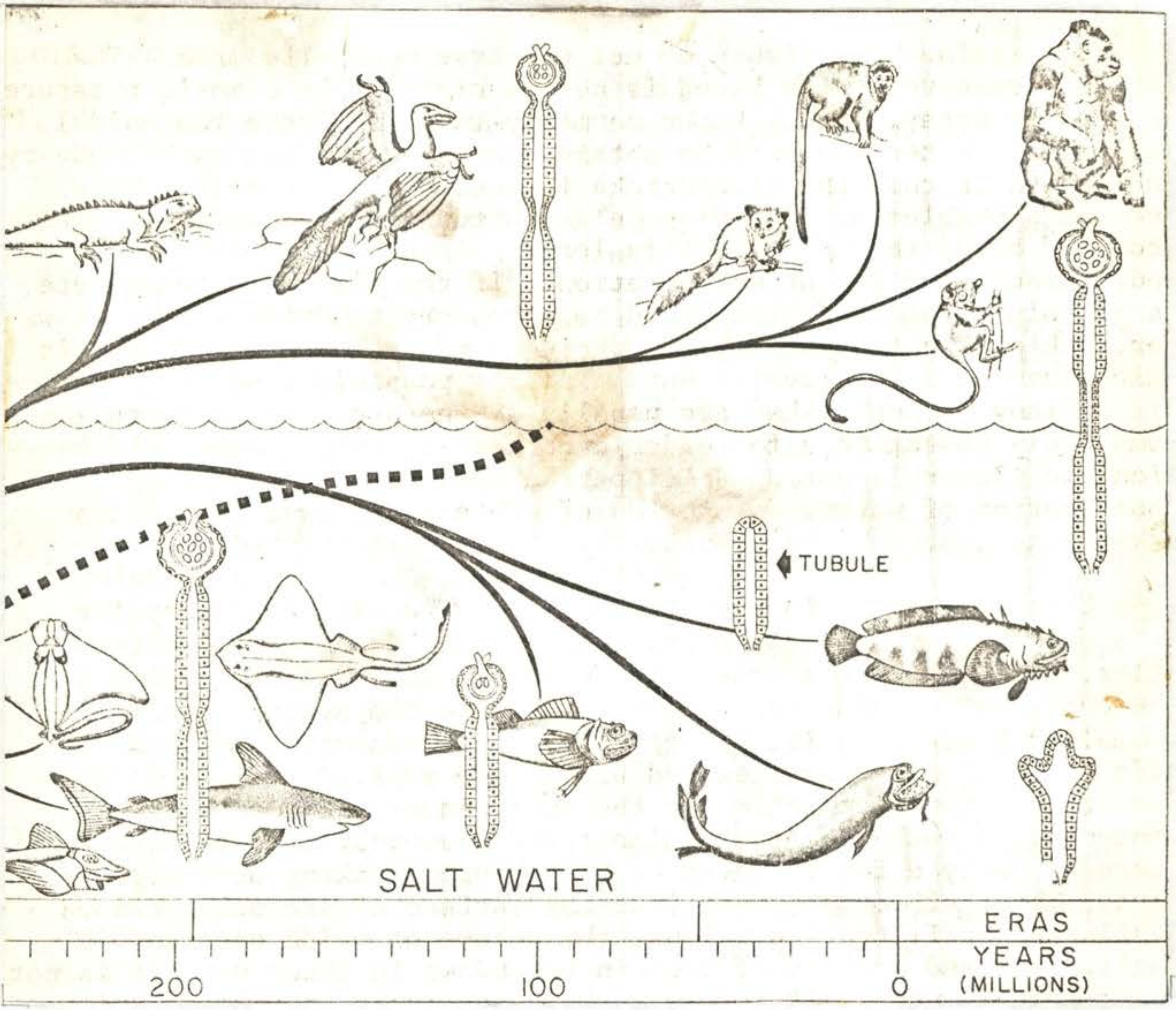


Figure 2. Basic excretory adaptations of fish in a salt-water environment. (After B.S.C.S.)



However, such fresh-water forms gave rise to animals which returned to the sea. Note the earliest nephrons are composed of tubules. The latest nephrons of land animals have a complex glomerulus and tubules made of two segments. (After B.S.C.S.)

CHAPTER II

ORIGIN OF THE VERTEBRATES

Any understanding of the significance of the nephron in the evolutionary theory must begin with the origin of life. Many broad assumptions must be made to explain the development of organisms prior to the appearance of the nephron. This may be illustrated by quoting Homer Smith:

> Speculation on the origin of life can be deferred until more knowledge is available about the chemistry of the ancient seas. There need have been nothing unique about the circumstances attending its birth except that protoplasm spun itself out of sunlight and the available stuffs of water and air, and operated according to the laws of thermydynamics--with only this to distinguish it from sea, wind, and rain: that by favorable contatenation of molecular forces it automatically became organized in such a manner as to preserve and reproduce itself.[1]

In making this statement, Mr. Smith assumes many things: (1) life came from non-living material in the ancient seas, (2) the form was autotrophic in nature, (3) the environment was different from today, and (4) the form of life was protoplasmic in nature. These ideas are widely accepted as true. However, while scientists have been thinking of this idea which is actually spontaneous generation, other plausible ideas have been expressed. For example, Preyer's imaginative approach toward explaining life changes the basic assumption.

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[1] Homer Smith, From Fish to Philosopher (Boston: Little, Brown and Co., 1953), p. 23.

He regards the whole earth as a mighty living organism and all living things as only bits of that living mass. Therefore nothing actually ceases to exist but is altered in relation to the whole living mass.[1]

Another example of imaginative thinking is the hererotroph hypothesis championed by Oparin.[2] This heterotrophic material, whatever its form, gave rise to the autotrophs and other complex unicellular organisms. This idea that the first living organism obtained its energy directly from the non-living environment seems more credible since the discovery of bacteria whose energy source is the flow of electrons.

The first forms of life were of necessity soft-bodied, so do not exist in fossil form. These organisms probably were as numerous and diverse as protozoa today--perhaps more abundant because of their favorable environment provided by the ancient seas. From these arose the first fossilized forms found in the rock formations of the Cambrian period. Through parallel, though independent forms, the diversified Cambrian organisms evolved. These organisms registered their presence on this planet because they produced shells of chitin, a substance quite similar to the nitrogeneous material insects produce today. From these early beginnings, the million or more species of living animals making up the presently described world populations have evolved with the vertebrates,

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[1] B.S.C.S., p. 77.

[2] *Ibid.*, p. 79.

crowned by man, as the superior creatures. The vertebrates make up only about 25,000 species, most of which are water dwellers.

Historically, the first meager traces of vertebrates were found in the rocks of the Ordovician period (see Figure 4). Some archaic fishes appear in the rock formation of the following Silurian period. These fossils indicate that the beginning of vertebrate existence is correlated to the great geological disturbances that occurred during the late Cambrian period.

The fossils found in the Old Red Sandstone in the British Isles, since 1900, have been considered by geologists as being from fresh water. These beds are thought to have originated from huge torrential rivers draining the mountain areas of the Devonian continent as extremes of dry seasons and torrential rains alternated. These extremes inundated the land with rapid erosion, mud rivers, and mineral decomposition. This rock and sand-laden water lends credence to the idea that the survival of the early fishes was due to their armour-like exterior. For only an armour could endure the constant abrasion of the miriads of water borne sand particles.[1]

Near the end of the Devonian period, the first aldn vertebrates appeared as the continents leveled and the swamps formed. Amphibia were abundant during the Carboniferous period.

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[1] Smith, op. cit., p. 29 and A. S. Romer and Grove, "Habitat of Early Vertebrates," American Midland Naturalist, XVI (1935), 805-856.

GEOLOGIC TIME SCALE

ERA	SYSTEM AND PERIOD	SERIES AND EPOCH	SOME DISTINCTIVE FEATURES	YEARS BEFORE PRESENT
CENOZOIC	QUATERNARY	RECENT	Modern man	11 thousand
		PLEISTOCENE	Early man; northern glaciation	½ to 2 million
	TERTIARY	PLIOCENE	Large carnivores	13 ± 1 million
		MIOCENE	First abundant grazing mammals	25 ± 1 million
		OLIGOCENE	Large running mammals	36 ± 2 million
		EOCENE	Many modern types of mammals	58 ± 2 million
		PALEOCENE	First placental mammals	63 ± 2 million
MESOZOIC	CRETACEOUS		First flowering plants; climax of dinosaurs and ammonites, followed by extinction	135 ± 5 million
	JURASSIC		First birds, first mammals; dinosaurs and ammonites abundant	181 ± 5 million
	TRIASSIC		First dinosaurs. Abundant cycads and conifers	230 ± 10 million
PALEOZOIC	PERMIAN		Extinction of many kinds of marine animals, including trilobites. Southern glaciation	280 ± 10 million
	CARBONIFEROUS	PENNSYLVANIAN	Great coal forests, conifers. First reptiles	310 ± 10 million
		MISSISSIPPIAN	Sharks and amphibians abundant. Large and numerous scale trees and seed ferns	345 ± 10 million
	DEVONIAN		First amphibians and ammonites; fishes abundant	405 ± 10 million
	SILURIAN		First terrestrial plants and animals	425 ± 10 million
	ORDOVICIAN		First fishes; invertebrates dominant	500 ± 10 million
	CAMBRIAN		First abundant record of marine life; trilobites dominant	600 ± 50 million
	PRECAMBRIAN		Fossils extremely rare, consisting of primitive aquatic plants. Evidence of glaciation. Oldest dated algae, over 2600 million years; oldest dated meteorites 4500 million years	

Reptiles first appeared at this time but became common during the later Permian period. This time merged with the "age of reptiles." The Triassic period produced the first dinosaurs, turtles and ichthyosaurs. Reptiles dominated on the land, in the sea, and in the air during Jurassic time. (Traces of these animals are found the world over--as far north as Lat. 78 06' N. which is twelve degrees from the North Pole.[1]) The first birds appeared at this time along with a few archaic mammals. The Cretaceous period, which began with a dominance of reptiles, is marked by the extinction of the large reptiles. This "time of the great dying," when all living creatures seem to have been decimated, may have been the result of a shift in the earth's crust which changed the weather, seas, swamps, and vegetation all over the world. This hypothesis set forth by J. W. Durham is the result of studies of the earth's changing magnetic fields conducted by S. K. Runcorn and associates.[2]

The age of mammals represents a very short period of geologic time, but it is by far the most important to man. During this Cenozoic era, the recovery of animal life from its previous devastation was marked by change, a change generated by the complexities of evolution which produced the varied groups that inhabit the land today. Apparently the population of the seas was not affected as much because the evolution in

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[1] Edwin H. Colbert, "Dinosaurs of the Arctic," Natural History, April, 1964, p. 22.

[2] J. W. Durham, "The Drifting Continents," Natural History, April, 1962, pp. 30-39.

marine life has been less radical.

It is difficult to plot the course of vertebrate ancestry, so speculation is rampant and such hypothesis as have resulted have produced few positive results.[1] The annelid worms have been considered extensively. They are bilaterally symmetrical and are active animals with a central nervous system which is composed of a brainlike mass at the anterior end of the body, and a longitudinal nerve cord. Here the difficulties begin since almost nothing else fits except that the nephridia of the earthworm resembles the vertebrate nephron more than any other invertebrate excretory organ. (See Figures 5 and 6.) Arachnids have been considered with similar results. Echinoderms have been suggested but not seriously considered as direct ancestors, but are certainly near relatives. Obviously numerous assumptions must be made because the wide gap remains unbridged. Apparently, then, "the best place to start the evolution of the vertebrate is in the imagination."[2]

Homer Smith suggested a hypothetical provertebrate. This was an elongated spindle-shaped, bilaterally symmetrical organism with a stiffened but flexible axial rod. The axial rod supported muscles that produced strong lateral movements of the body which propelled it through the water. It possessed a "brain" and gonads, probably fed on the bottom of

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[1] A. S. Romer, The Vertebrate Body (Philadelphia: W. B. Saunders Co., 1956), chapter 5.

[2] Smith, *op. cit.*, p. 26.

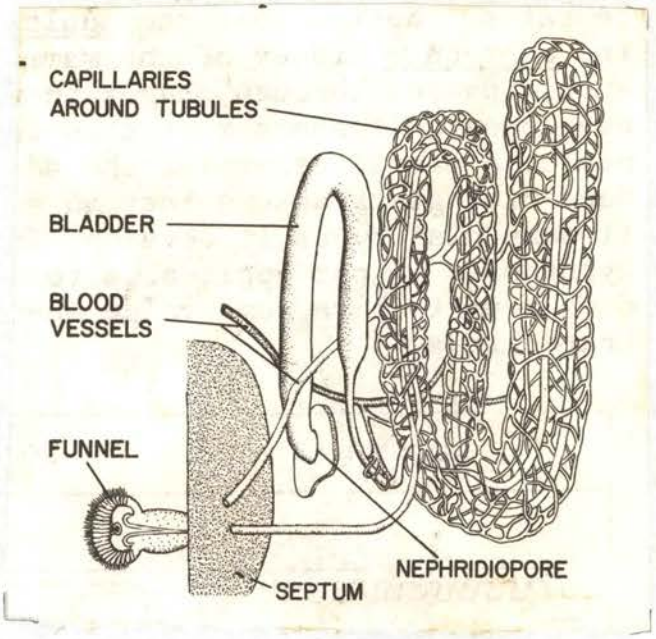

Figure 5. Nephridia in the earthworm. (After B.S.C.S.)

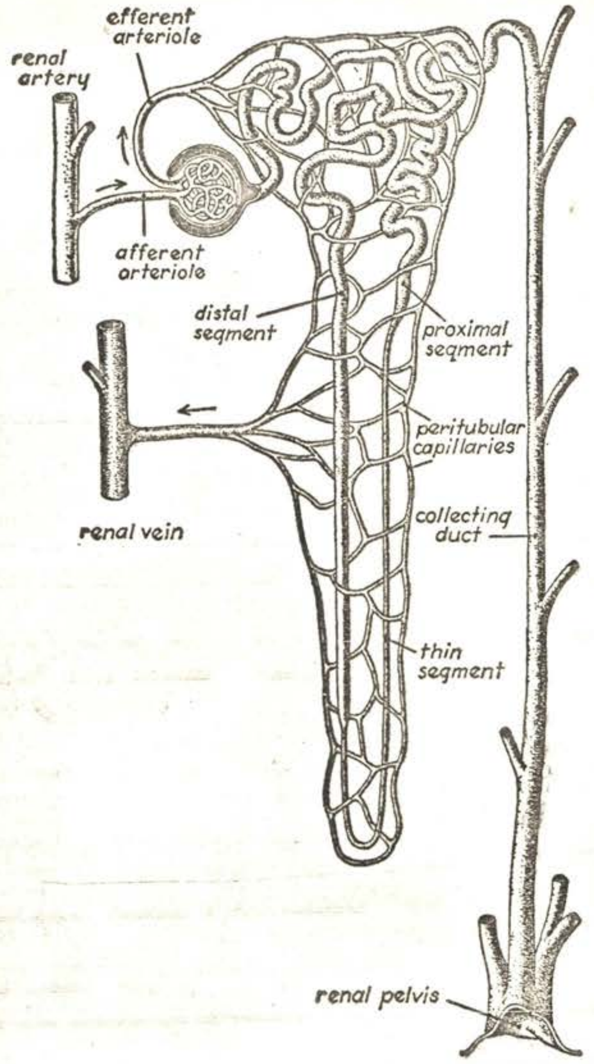

Figure 6. Diagrammatic representation of the mammalian nephron. (After Smith)

streams through a jawless mouth and had some type of urinary opening connected to a nephron. With this organism, imaginative though it is, one can begin the long development up the ladder of time. However, one must exercise caution. The place of origin should be considered. Scientists agree this place is water but disagree as to whether the water was salty or fresh. The hypothetical protovertebrate can give no clues to that early existence, so the evidence must come from the first primitive fish.

The home of these early heavily armored creatures have been proposed by many to be fresh water. Prosser wrote:

> The history of fishes represent a migration from fresh water to salt water. . . the kidney arose in fresh water protovertebrates as an organ which gets rid of water and in no fish is the kidney of primary importance in the excretion of mitrogenous wastes.[1]

Virginia Black agreed: "Paleontological and anatomical evidence indicates that fishes first evolved in fresh water. . . . Kidney structure favors osmotic regulation in a fresh water medium."[2]

Kent assumed a fresh water origin when he expressed the opinion: "the vertebrate kidney appears to have been designed primitively as a water eliminating mechanism."[3]

Romer and Grove presented a lengthy argument favoring

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[1] C. L. Prosser, Comparative Animal Physiology (Philadelphia: W. B. Saunders Co., 1950),

[2] V. S. Black, in The Physiology of Fishes, edited by M. E. Brown (New York: Academic Press, n.d.), I, 164.

[3] G. C. Kent, Jr., Comparative Anatomy of the Vertebrates (New York: Blackiston Co., Inc., 1954), p. 398.

the fresh origin hypothesis while Smith stated: "The fact that the theater of the evolution of the early vertebrate was in fresh water."[1]

The above mentioned authors discuss the development of the nephron as from the fresh water origin. However, in a later work, Prosser and Brown expressed a modified view. In the second edition of Comparative Animal Physiology, the following statement appears:

> The origin of vertebrate animals is obscure. All prochordates are marine, and the phylum chordate doubtless arose from marine ancestors. Amphioxus has protonephridial excretory organs. . . . Fresh water origin of fish is suggested by the dilute blood of all modern bony fish and the low salt content of the blood of cartilaginous fish, and also by the glomerular kidney which is well adapted for excreting a hypoosmotic urine.[2]

Dineley has conjectured from his fossil study that the early fishes spent part of their life cycle in the sea or at least along the shallows near shore and later moved into fresh water.[3] J. D. Robertson is not so indefinite. He ardently maintains that the early home of the vertebrates was marine. Quoting E. J. Conway and G. E. Hutchison, he states that the Cambrian seas had the same relative composition as today so the stresses on the early vertebrates were practically the same as the stresses in today's environment. He suggested a real need for re-examination of paleontological data to ascer-

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[1] Smith, op. cit., p. 33.

[2] C. L. Prosser and F. A. Brown, Jr., Comparative Animal Physiology (Philadelphia: W. B. Saunders Co., 1961), p. 27.

[3] D. L. Dineley, "Armor-plated and Jawless Devonian Fish," Natural History, August-September, 1964, p. 51.

tain the true nature of the primitive environment. He inferred there have been extensive errors made in data evaluation which in turn have produced erroneous assumptions. He noted that the internal medium of cyclostomata is the same as sea water so this may very well be the primitive trait derived from marine chordate ancestors. In his opinion, the glomerular kidney probably existed as a marine trait that was easily adapted to fresh water and as a filter it does not depend on osmotic gradient but on hypostatic pressure in the blood capillaries. Thus, he unequivocally denied the nephron's development as having begun in fresh water and declared the origin of the vertebrates to be the sea.[1]

Salt water origin or fresh water origin seems to be the main point of disagreement. Data are interpreted either to prove the aglomular or glomerular nephron as the primitive structure. No author offered any explanation as to why the difference in direction of nephric evolution has developed. However, all authors agreed that the development of the nephron is quite important in the story of evolution.

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[1] J. D. Robertson, "Habitat of the Early Vertebrates," <u>Biological Review</u>, XXXII (1957), 156-187.

CHAPTER III

ANATOMICAL STRUCTURE AND EVOLUTION

The anatomical structure of the kidney has been cited as evidence supporting evolution. It is necessary for this discussion to assume that vertebrates originated in fresh water.

In most vertebrates the regulation of the internal environment is controlled largely by the kidney. The delicate balance of salts and water must be kept relatively constant to allow the completion of the chemical processes necessary for the continuing functions of complicated nerves, organs, glands, and muscles of the vertebrate body. Any marked variation in the body fluid will hinder these delicate operations. The most important constituents of the body fluids of all vertebrates are water and sodium chloride. The control of these and the other functions of excretion and osmoregulation are ordinarily closely related and are performed by the same structure.[1]

In fish, the structures which control the internal environment are the gills and kidneys. The gills function efficiently in salt ion absorption and excretion. In salt water fish, the gills excrete salts; in fresh water species,

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[1] Romer, op. cit., chapter IV.

salt ions are absorbed by the gills, especially during long periods of fasting such as occur when the fish is spawning or migrating.[1]

Water balance is maintained by the kidney. Fresh water fish are continually absorbing water osmotically because their body fluids are more concentrated than their immediate environment. This water enters the body through the gill and oral membranes as the fish take in food and oxygen. A small amount of water is also absorbed through the body surface. This excess water is removed by the excretory mechanism of the kidney.[2]

The structural unit of the vertebrate kidney is the minute tubule or nephron. Since no fossil remains of the early vertebrates contain any soft tissue, the evolution of the kidney must be reconstructed from similar living forms. In reconstructing this sequence, one assumes that living organisms which resemble the fossil forms furnish reasonably accurate data concerning the structure and the functions of the nephron. In the protovertebrate, each body segment had its own nephron which consisted of a renal corpuscle, a tubule surrounded by capillaries, and a duct through which water passed from the celomic cavity. In some embryos, a primitive type tubule develops with a ciliated funnel opening from the celomic cavity into the tubule. A typical glomerulus is

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[1] Black, <u>op. cit.</u>, p. 165.

[2] C. L. Prosser, (ed.), <u>Comparative Animal Physiology</u> (Philadelphia: W. B. Saunders Co., 1950),

sometimes present but lies within the celomic cavity. However, the glomerulus is often absent altogether. Originally, these tubules may have simply drained off excess fluid and accumulated waste from the celomic cavities with the glomerulus coming as a later development.

In adult kidneys, three general types of nephric units are found in existing vertebrates today.[1] The first type, typical of amphibians, fresh water bony fishes and elasmobranchs, has a large renal corpuscle capable of high water output. (If the fresh water origin hypothesis is correct and the vertebrates did need to excrete large amounts of water, this large corpuscle would be considered primitive.) The osmotic behavior of frogs has been extensively studied and the water equivalent to thirty-one per cent of the body weight can enter and be excreted every twenty-four hours. Perhaps this large corpuscle with its well developed vascularized glomerulus has been the factor that has limited the habitat of the amphibian. All fresh water fish have glomerular kidneys and excrete a hypotonic urine.[2]

The second type of nephron which is found in marine teleosts and reptiles has a small corpuscle or no corpuscle at all so water excretion is limited.[3] This is an effective variation that conserves water whether the medium is salty sea

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[1] Romer, op. cit., p. 295.

[2] C. L. Prosser and F. A. Brown, Jr., Comparative Animal Physiology (Philadelphia: W. B. Saunders Co., 1956), p. 27.

[3] Romer, loc. cit.

water or dry land. (The presence of aglomerular organisms can be used as evidence that structures no longer needed tend to disappear during evolution.) The existence of this type tubule has led investigators to conclude that glomeruli are active filters for water, salts and other substances which enter the kidney tubule from the glomeruli but may be reabsorbed or excreted later. A few aglomerular fishes have left the sea to reinvade brackish water, but how these forms maintain water balance in fresh water has not been studied. Tubular excretion of these organisms includes nearly all the important constituents of urine, creatinine, creatine, urea, uric acid, magnesium, calcium, etc. The aglomular kidney cannot excrete sugars but it can excrete against higher pressure than the blood. These substances are carried by active transport. Reptiles can excrete uric acid in a fine crystaline form so need only small amounts of water to excrete sodium chloride.

The third type structure is that seen in mammals and birds (see Figure 7).[1] The glomerulus is large and filters excessive quantities of substances from the blood plasma which passes on to the convoluted tubule where extensive reabsorption takes place. In land dwelling organisms, much of the water is also reabsorbed. The remaining product is a concentration of water and nitrogenous wastes that are excreted as urine. The main area for water reabsorption appears to be the loop of Henle (see Figure 8 c). Those mammals with the longest loop

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[1] Ibid.

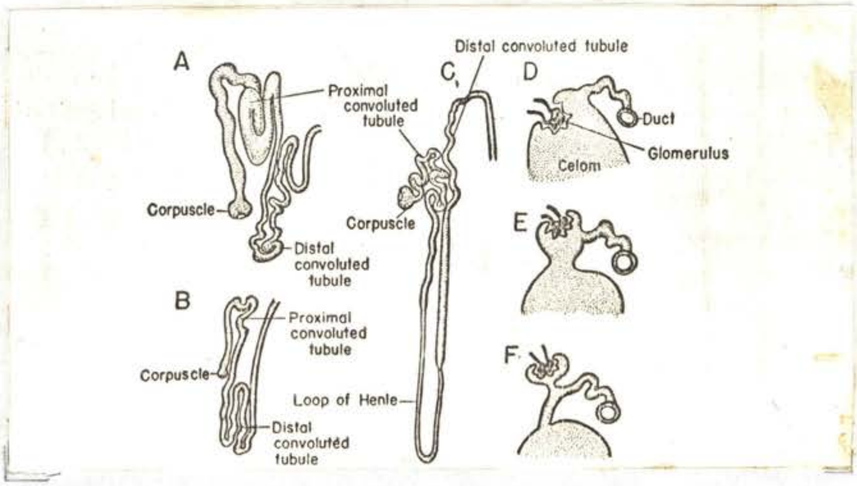

Figure 7. Tubule types. A to C, the three major types common in adult vertebrates. A, presumably the most primitive, with corpuscle of good size, found in elasmobranchs, fresh-water bony fishes, amphibians. B, corpuscle reduced or absent, characteristic of salt-water teleosts, reptiles. C, corpuscle large; a loop of Henle inserted; found in mammals, birds. D to F, primitive tubule types found in lower vertebrates, principally in the embryo, and perhaps illustrating the early evolution of kidney tubules. D, tubule runs from celom to kidney duct; glomerulus, if present in celom, not associated with tubule. E, special small celomic chamber formed for glomerulus. F, this chamber has become the capsule of a renal corpuscle; tubule still connects with celom; closing the celomic opening leads to more progressive tubule type. (After Romer)

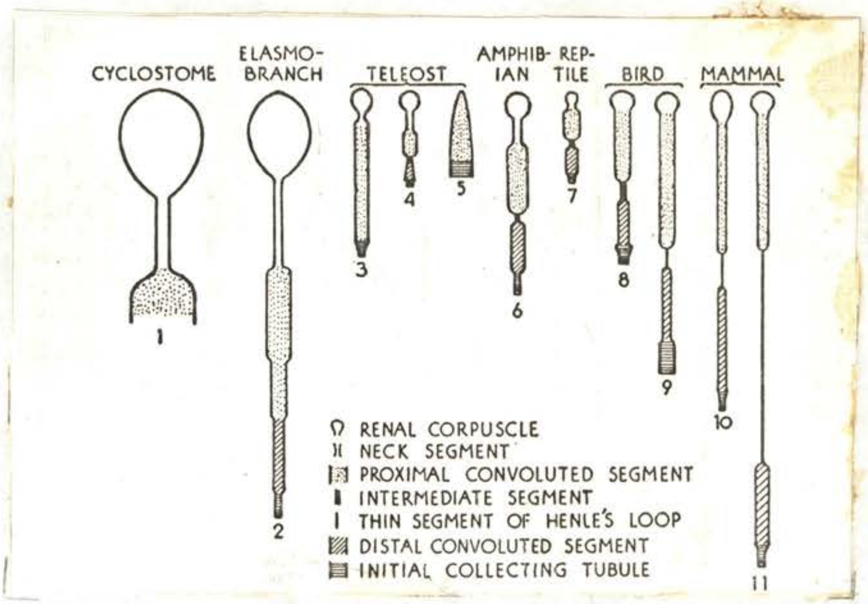

Figure 8. Diagram of kidney tubules of various vertebrates, all reduced on the same scale, to show the relative size of the components in the different groups. The glomeruli are at the upper end in each case, and the tubules are represented as if straightened out. The glomeruli are well developed in most groups and of enormous size in cyclostomes and elasmobranchs, but of reduced dimensions in reptiles, and are done away with in some marine teleosts (5). All have a proximal convoluted segments of the tubule; an intermediate segment, followed by a distal convoluted tubule, appears in some fishes and is present in all land forms. The intermediate segment becomes the loop of Henle in birds (in part) and mammals; this loop may be much elongated in the latter group. 1, Hagfish; 2, skate; 3, sculpin; 4, catfish; 5, toadfish; 6, frog; 7, painted turtle; 8 and 9, chicken; 10 and 11, rabbit. (After Marshall, Kepton, from Prosser.)

of Henle can produce the most concentrated urine.[1] Water absorption continues past Henle's loop, however, for if need arises, some water is absorbed from the bladder.

The above discussion leads to a reasonable conclusions that the large glomerulus is a primitive trait that arose to control the water pressure in the evolving vertebrate as he invaded fresh water. After a stay in fresh water, some teleosts returned to the sea where the glomeruli deteriorated or disappeared altogether thus enabling the fish to adjust to the new environment. Quite independently, the elastmobranchs also returned to the sea but retained their glomeruli and at the same time changed the body fluid concentration by adjusting to a high content of the usually toxic material, urea. The amphibians remained in fresh water, because any degree of salinity above their blood concentration is apparently toxic to them. In contrast, the reptiles lost the large glomeruli and excrete protein wastes as uric acid as do birds. The latter however have developed the convoluted tubule with Henle's loop.

So the evolution of the nephron can be observed by thus examining the anatomical structures as they progress from the simple to the complex.

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[1] Prosser, loc. cit.

CHAPTER IV

EMBRYONIC DEVELOPMENT AND EVOLUTION

Embryonic development may be used to support the hypothesis that the history of the nephron illustrates evolution. The basis for this chapter may well be considered a variation of Ernest Haeckel's idea that an organism recapitulates its evolutionary history during its embryonic development. Although this hypothesis has only limited application, it does point up the fact that some of the evolutionary process does remain during the growth of the embryo.[1] Witschi gives three modifying factors that blur the evolutionary picture in ontogeny: "(1) secondary adaptations at the embryonic level, (2) recapitulation of obsolete adaptive characters, and (3) reduction of nonfunctional characters."[2] In spite of the limitations, it is in the embryonic evolution that is considered here.

In 1908, Morgan wrote (concerning evolution and adaptation) about a new area of investigation, the nephridia. He felt this was too soon to draw any conclusions but gave the following generalization:

> In sharks and bony fishes, the nephridia lie at the anterior end of the body cavity. In the amphibia there

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[1] E. Witschi, Development of Vertebrates (Philadelphia: W. B. Saunders Co., 1956), p. 6.

[2] *Ibid.*, p. 7.

> is present in the young tadpole a pair of nephridial organs, the head-kidney, also another pair in the anterior end of the body cavity. Later these are replaced by another pair of organs, the permanent mid-kidneys, that develop behind the head kidney. In reptiles, birds and mammals, a third nephridial organ, the hind-kidney, develops later than and posterior to the mid-kidney, and becomes the permanent organ of excretion. . . . The anterior end of the kidney develops first, then the middle part, and then the most posterior. The anterior part disappears in the amphibian, the anterior and middle parts in the birds and mammals so that in the latter group the permanent kidney is the hind-kidney alone.[1]

In 1950, Fraser wrote:

> The motion put forward, mainly by German workers, and above all by Felix (1906), that the vertebrate excretory system was made up of three sets of organs, the pronephros, the mesonephros and the metanephros, which were laid down all along the trunk and succeeded one another in time, has long ago been shown to be mere hypothesis for which no real proof has ever been forthcoming.[2]

Fraser continued to explain that the mesonephron and metanephron are not separated in the lower vertebrates so the terms should be omitted, and that the continuous structure which acts as the functional kidney be designated as opisthonephros. He thought that perhaps the problem developed because there has been too much reliance on the careful examination of a large number of embryos and young from one order of the vertebrates. So with some modification, the ontogeny of the vertebrates furnishes a guide to study evolutionary history.

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[1] T. H. Morgan, Evolution and Adaptation (New York: The Macmillan Company, 1908), p. 78.

[2] E. A. Frazer, "The Development of the Vertebrate Excretory System," Biology Reviews, XXV (1950), 163.

The primitive kidney or holonephros must first be considered. Perhaps the young hayfish represents the nearest approximation to the ideal holonephros (see Figures 9 and 10). Its kidney has a single tubule for each trunk segment. This structure produced a long kidney on each side of the body with a duct gathering the urine from the series of segmentally arranged units. This duct is called the archinephric duct. These structures are of mesodermic origin, having formed from the anterior and backward. Each tubule is joined to the duct as they develop toward the posterior end. When the last tubule has been formed, the archinephric duct continues to grow until it unites with the cloaca. Above this level, the simple segmental arrangement is lost when a variable and often high number of tubules may develop from each segment.[1]

The first formed part of the kidney called pronephros is short lived in many vertebrates, but in some fishes and amphibians it becomes highly specialized and is termed the head-kidney because of its position. The myxinoids have an embryonic holonephros, as stated above, but the intermediate region deteriorates in the adult.[2] In most bony fishes the pronephric tissue is replaced by lymphoid tissue. However, the pronephros function in those species which have aglomerular mesonephroi.

The opithonephros in lower vertebrates give rise to the

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[1] Romer, op. cit., p. 297 and Kent, op. cit., p. 400.

[2] Libbie H. Hyman, Comparative Vertebrate Anatomy Chicago: University of Chicago Press, 1942), p. 391.

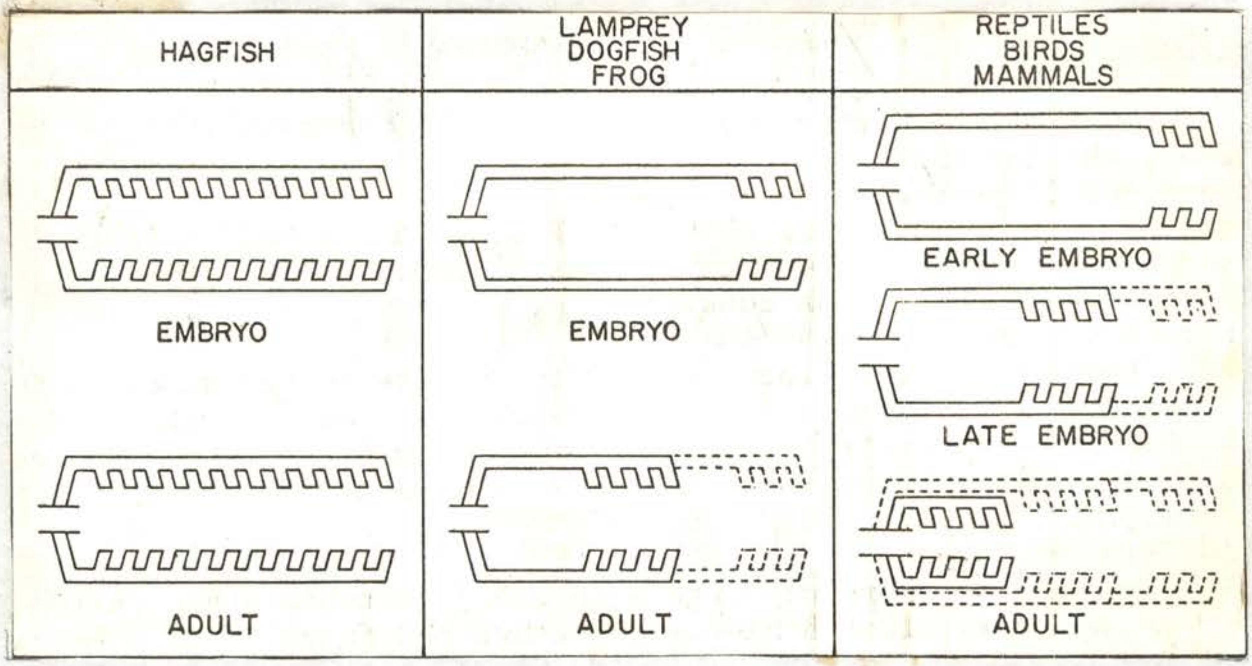

Figure 9. The kidney system of vertebrates. The dotted lines indicate embryonic structures that degenerate during development. (After B.S.C.S.)

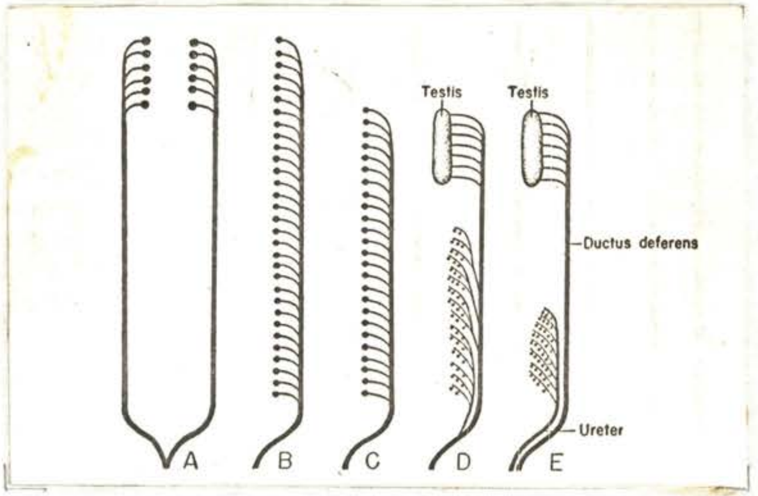

Figure 10. Diagrams of kidney types. A, Pronephros (embryonic); B, theoretical holonephros (each trunk segment with a single tubule), much as in a young hagfish or apodous amphibian; C, primitive opisthonephros; pronephros reduced or specialized, tubules segmentally arranged, as in hagfish. D, Typical opisthonephros: multiplication of tubules in posterior segments, test is usually taking over anterior part of system, trend for development of additional kidney ducts (most anamniotes). E, Metanephros of amniotes: an opisthonephros with a single additional duct, the ureter, draining all tubules. In A, both sides of the body are invluded; in B to E, one side only. (After Romer)

functional kidney. In the lamprey, dogfish and frog, the anterior tubules cease to function in the adult and are replaced by the next posterior tissue. This produces segmented pairs of tubules with a peritonial funnel and a renal corpuscle opening into the pronephric duct. However, these produce many tubules so the segmental arrangement is lost and the kidney of the adult lamphreys, fishes, and amphibians has arisen. There are many variations of this development as the posterior enlarges and the anterior end is reduced. The more the posterior end expands, the more like the complex kidney of the amniotes it becomes.

In amniotes, as the mesoderm is undergoing differentiation, the pronephros starts forming at the end of the head where the neck will be and at the same time the archinephric duct grows rapidly back to the cloacal region as in the anaminotes (see Figure 11 A). These tubules function only briefly and then degenerate.[1] This is in contrast to the amphibian pronephros which functions throughout the larval stage. Differentiation continues posteriorly to form a second nephric structure, the mesonephros, which functions for most of the embryonic life. To distinguish between a pronephros and mesonephros is only possible when the young has a larval stage that requires a functioning excretory mechanism early in its life. This is logical on functional grounds for all three parts appear to be sectionally specialized areas of the more

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[1] Romer, op. cit., p. 299.

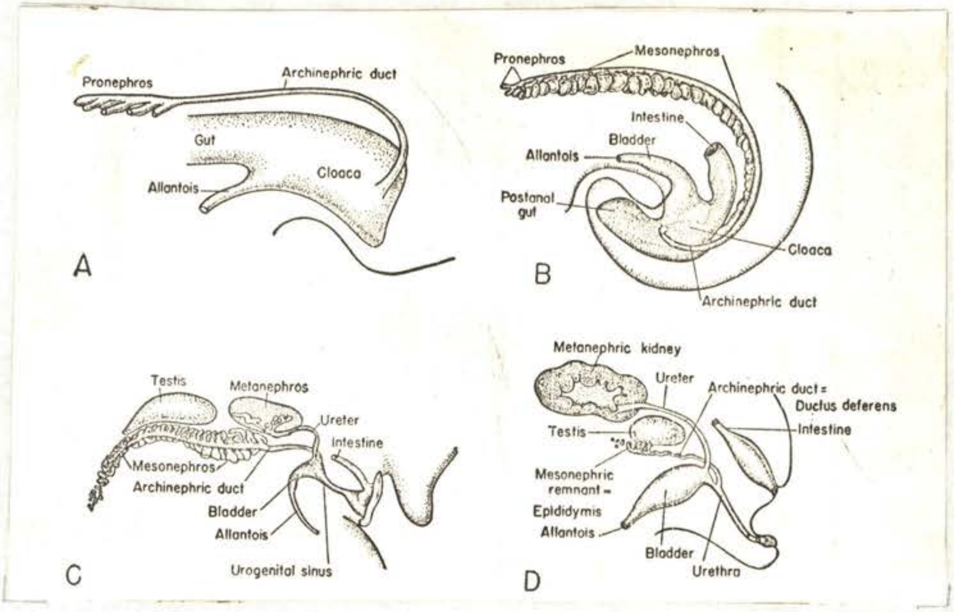

Figure 11. Diagrams to show formation of the metanephros of an amniote (male) embryo as seen from the left side. A, Pronephros and duct formed; B, mesonephros partly formed; C, pronephros reduced, posterior part of mesonephros functional, ureter formed, and metanephros beginning to differentiate; D, definitive stage; mesonephros reduced, and tubules and duct utilized only for sperm transport; metanephros, the functional kidney. (After Romer)

primitive holonephros. Amniotes which develop within the body of the parent do not need to use the anterior part of the excretory system so they appear as vestigial structures with gradually increasing complexity which pass into the fully formed tubules that develop into the metanephros.[1]

While the pronephros are rudimentary, often without glomeruli, the later mesonephric tubules are well formed. As development continues, these degenerate and the more complex metanephros begins functioning.

The metanephros forms the mature kidney. The large number of kidney tubules are drained into a newly formed duct, the ureter, which budded from the old archinephric duct and replaced it in function. The most complex kidney is a specialized type which tends toward posterior concentration and the formation of a definitive ureter. This ureter formation readily distinguishes the mesonephros from the metanephros in the amniote. The number of kidney tubules is fantastic--up to 30,000 in reptiles; 200,000 in fowl; 20,000 in a mouse; and millions in large mammals.[2] Thus, the kidney tends to become more compact and more efficient as it moves up the evolutionary ladder (see Figure 12).

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[1] Frazer, op. cit., p. 164.

[2] Romer, op. cit., p. 290.

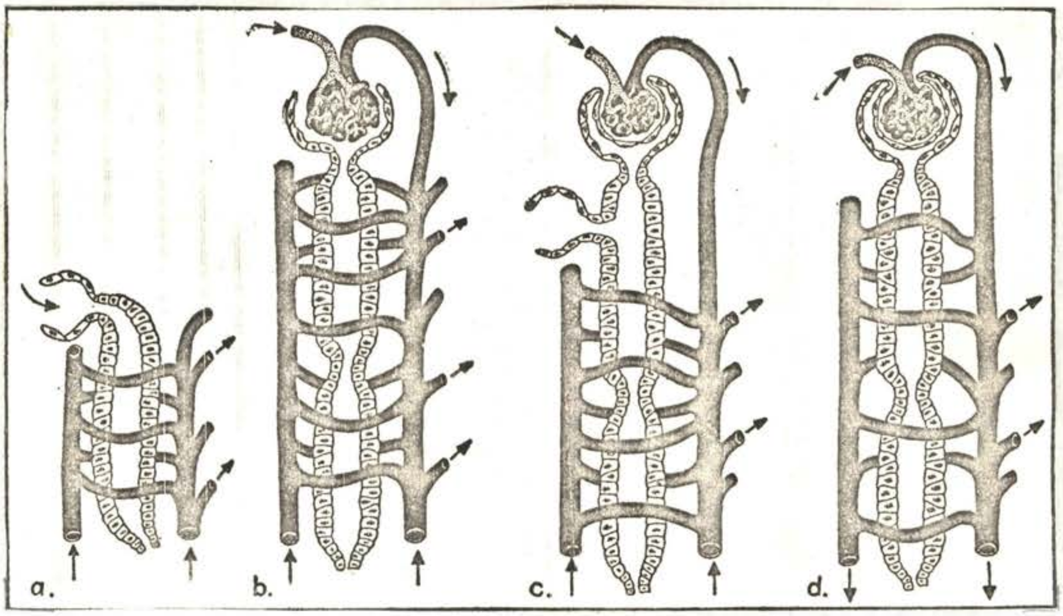

Figure 12. Four stages in the evolution of the vertebrate nephron. (a) In the protovertebrate the renal tubule drained the coelom or body cavity by means of an open mouth or coelomostome. (b) The glomerulus was evolved in the earliest vertebrates as a device to excrete water, and was at first only loosely related to the coelomostome. (c) Later the glomerulus became sealed within the end of the tubule, the coelomostome persisting in some species. (d) In the higher vertebrates, the coelomostome has disappeared entirely, leaving the typical vertebrate nephron.

The primitive blood supply to the protovertebrate tubule persists as the "renal-portal system" through the fishes, amphibia, reptiles and birds (a to c); but disappears in the mammals (d), leaving the tubules supplied only by postglomerular blood. (After Smith)

CHAPTER V

SOME UNANSWERED QUESTIONS

The discussion so far has been deliberately limited to the regulation of water by the nephron because that seems to be its primary function. However, if the nephron arose as a water regulating mechanism and osmotic principles apply, some consideration should be given to euryhaline vertebrates and how these species meet the need for water regulation.

One answer can be that some diadomous fish are not truly euryhaline but are able to migrate because of hormonal activity which changes the fish physiologically so it can live in the changed environment.[1] Since some die after breeding, the hormone reversal may have ended leaving the poor fish in the wrong environment.

Many fish can live in either fresh or salt water. Methods used to meet the changing environment seem to be as diverse as the species involved. King salmon enter fresh water and soon have a twelve per cent dilution of blood, indicating an adjustment to living with a changed internal environment. Young eels migrate because of possible pituitary secretion while the adult eel depends on the salt secreting cells in the gills to help it survive in salt water. (In fresh water no salt is secreted and the glomerular kidney

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[1] Black, <u>op. cit.</u>, p. 193.

functions as a typical fresh water kidney.) The sickleback migration may be the result of thyroid activity. Thus, internal regulators appear to be the factor affecting adjustment.[1]

Two other factors help in the adjustment when the switch in medium is made. One is the reduced permeability of the body surface due to slime or scales or a tough skin. An example is the eel which absorbs little water or salt because of the excretion of a heavy slime layer. Scales and tough skin in other organisms likewise reduce absorption or loss of water. Another factor in medium adjustment is salt excretion by the gills. This seems to be a major adjustment for salt water inhabitants. Much work needs to be done in this area.[2]

In these euryhaline fish, the body apparently resorts to mechanisms other than the nephron to meet any change in the water concentration of the environment. Any generalization concerning the evolution of the nephron from these and the myriad of other examples produced by researchers seems remote and any definite conclusions would appear ad hoc.

One important function of the nephron in mammals is the excretion of nitrogenous wastes. Perhaps a pattern exists in the excretion of nitrogen waste by the nephron as it evolves in the vertebrate that will be evident as data accumulate.

Waste nitrogen is excreted in many forms--the three

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[1] Prosser and Brown, op. cit., p. 29.

[2] Black, op. cit., p. 198.

most important are ammonia, urea and uric acid. Ammonia is highly toxic and must be excreted immediately. Urea is also toxic but less so than ammonia and more toxic than uric acid. The pattern of excretion is related to the amount of water available. The more water available, the more toxic the excreted form of nitrogen. Thus, the tadpole of a frog in a watery environment excretes more ammonia; in the adult form the environment is drier so more urea is excreted. Fresh water fish excrete ammonia and some urea. Of this, the kidney excretes very little because most wastes diffuse out through the gills.[1]

Marine teleosts retain nitrogen in the form of trimethylamine oxide in order to solve their osmotic problems. Some of this is excrete along with urea--again mostly through the gills. Elastmobranchs retain urea in their blood but excrete any excess via the gills. Mammals excrete urea through the kidneys in a highly concentrated form. This is possible because the convoluted tubule is impermeable to urea for most of its length. Some mammals (ungulates) retain urea for synthesis.

Reptiles and birds excrete uric acid and thus conserve water. Their urine is a semisolid mass of crystals. There are combinations of these various major forms of nitrogen excretion with a continuous range and mixed quantity that are not pertinent here.

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[1] Prosser and Brown, op. cit., p. 28.

From this brief outline of nitrogen excretion there seems to be no close correlation between nitrogen excretion and nephron evolution. The same lack of parallel exists with salt ion balance and nephric function. The extensive work of osmoregulation common to the mammalian kidney apparently has no consistent evolutionary pattern leading up to this climactic organ. Data accumulated are incomplete--almost infintesimal compared to the vast amount needed to substantiate the hypothesis.

The varied interpretation of available data also is confusing. The problem of nitrogen excretion as presented above was questioned by Homer Smith, a man devoted to research concerning renal excretion. He maintained that most nitrogen is excreted as urea or uric acid in all vertebrates. He particularly disagreed with the idea that excreted ammonia is waste from protein metabolism.[1] The problem of evaluating research and interpretation of facts gleaned is gargantuan.

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[1] Smith, op. cit., p. 82.

CHAPTER VI

SUMMATION AND CONCLUSIONS

The theory of evolution has been accepted as a logical explanation of life as it existed in the past and as it exists today. The appearance of new species following periods of violent geological change has supported the idea that adaptability results from genetic changes in existing organisms. (Further support is given by the lack of change in marine life where the environment has remained more constant.) One organ of adaptation developed by animals is the nephron. The evolution of the nephron has been considered a small but important bit of evidence that the theory of evolution is indeed fact.

The nephron arose as a water regulating mechanism. The primitive assumption was that the early vertebrates arose in fresh water and the glomerular nephron was the primitive organ. However, this has been questioned extensively, so the primitive structure may be the aglomerular nephron. The efficiency of the glomerular mechanism for facilitating the removal of water could be evidence that this type is primitive. The value of the nephron as evidence in supporting the theory of evolution is not established because of the strong disagreement on the primitive structure and the resulting pattern of development. However, as data accumulate, a more precise picture of the evolving organ is expected to unfold.

The limitations embodied in the idea that embryonic development parallels the evolutionary process indicate that this idea needs extensive investigation by experimental biologists. Since ancestral history is not recapitulated exactly but is subject to variation, ontogeny is not infallible. However, the fascinating similarities will continue to challenge the inquisitive mind until a pattern does emerge.

No conclusion concerning the importance of the nephron's development in the evolutionary picture can be made at this time because of the limited data avilable from the experimental theater. Indeed, now is the time for all scientists to refuse to accept theories as facts and to examine ideas with originality and perserverance.

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