QUALITATIVE AND QUANTITTATIVE STRUCTURAL CHARACTERISTICS OF THE TELEOSTEAN KIDNEY

A thesis submitted to the University of Nairobi in part fulfillment for the Degree of Master of Science (Veterinary Anatomy)

by

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1993

DECLARATION

I hereby declare that the work reported in this thesis was done by me. Except where reference is made this work is original and has not been submitted before for a higher degree.

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ACKNOWLEDGMENT

I would like to thank the University of Nairobi Dean's Committee for their generous financial contribution that enabled me to make this study. I am grateful to my supervisors Dr. C. N. Warui and Dr. S. Kisia for reading and criticizing this work. My thanks also to Dr. T. Chokwe and Mr. J. Musyoka for their assistance in collecting the fish, Mr. J. Mavulu for his help in microscopy and Mr. J. Gachoka for his advice in photography.

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DEDICATION

This thesis is dedicated to my wife and sons.

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ABSTRACT

The kidneys of four freshwater teleost fish *Oreochromis niloticus*, *Micropterus salmoides*, *Cyprinus carpio* and *Clarias mossambicus* and one marine teleost, *Chanos chanos*, representing Perciformes (*O. niloticus* & *M. salmoides*) Ostariophysi (*C. carpio*, & *C. mossambicus*) and Salmoniformes (*C. chanos*) were studied for qualitative and quantitative characteristics using materials fixed *in situ* by perfusion via the bulbous arteriosus into the entire renal arterial system. The kidneys of *O. niloticus*, *M. salmoides* and *C. carpio* were partially fused and those of *C. mossambicus* and *C. chanos* were completely fused. Partial or complete venous portal systems were present in all the species except *O. niloticus*. The renal lobule was centered around the intralobular artery and duct and delimited by efferent veins.

The nephron of the fishes consisted of a renal corpuscle, the neck, proximal I, proximal II and distal segments and the collecting tubule-collecting duct system. These parts of the nephric tubule were distinguished on the basis of their staining reactions and histological and ultrastructural characteristics. Intrarenal heamopoietic tissue was absent in the Perciformes teleosts but was abundant in the Ostariophysi and Salmoniformes. Interrenal tissue in the head kidney was arranged in cords around branches of the posterior cardinal

vein.

Rodlet cells have been described in the proximal tubule of the blackbass.

Kidney volume per gram body weight ranged from 2.2-6.13 mm^3/g and was well correlated with body weight, the correlation coefficient (r) was 0.96. The allometric equation relating kidney volume (V_k) to body weight (W) was $V_k = 3.236W^{0.977}$. The mean (±S.D.) values for the volume proportions of uriniferous tissue, total vascular space (all blood vessels and capillaries), ureter and its ducts and connective tissue were 52.56±14.93%, 29.59±2.20%, 4.04±2.44% and 2.43±0.83% respectively; however, renal haemopoietic tissue formed 31.62±4.38% in the kidneys of 3 species namely *C. carpio, C. mossambicus* and *C. chanos*). The absolute volumes of the main components of the teleostean kidney namely the uriniferous tissue (V_{ut}) and the total vascular space (V_{tvs}) were strongly correlated with body weight and the allometric equations and correlation coefficients relating these parameters were: $V_{ut} = 1.102W^{1.077}$, r = 0.97 and $V_{tvs} = 1.197W^{1.025}$, r = 0.96 respectively.

The fish were divided into three categories each with two groups with contrasting characteristics; (1) percoid and ostariophysian, (2) fish with and without intrarenal haemopoietic tissue and (3) freshwater and marine fish. In

each category Student's t-test was used to assess the differences between kidney weight per gram body weight and those between the respective volume proportions of renal corpuscles, uriniferous tissue, total vascular space and renal tubules. The differences between the values of all parameters, except the kidney volume per gram body weight and the volume proportions of renal tubules in freshwater and marine fish, in the two groups of each category were significant ($P < 0.05$).

These results show that the quantitative characteristics of the teleost kidney are influenced by the order, habitat and distribution of intrarenal haemopoietic tissue.

CHAPTER 1

INTRODUCTION

I. GENERAL INTRODUCTION

The qualitative and quantitative structural characteristics of the teleostean kidney have been examined in this study. Table 1 shows the species studied, their common names, orders, families, identifying characteristics, and the habitats from which they were obtained. Teleosts are aquatic vertebrates and in contrast to the land vertebrates they have a special problem in maintaining a constant concentration of dissolved salts in their internal environment. Water availability and salt concentration vary greatly in the diverse aquatic habitats that present day teleosts inhabit. The diversity in the habitats has resulted in structural, physiological and behavioral adaptations among the teleosts in order to thrive in each habitat.

The kidney has been studied because it contributes substantially to the maintenance of a proper balance of the internal environment (homeostasis). Secondly, the kidney is the key osmoregulatory organ in the vertebrates, and has been held as a central pre-adaptation that allowed the spectacular radiation of vertebrates as a whole. Moreover, it has been reported that only the kidneys of about 100 teleost species out of the more than 20,000 recent teleosts have been studied (Hickman & Trump, 1969); more work on the teleost kidney is therefore necessary. In addition the kidney is usually affected in many diseases of teleosts (Hinton *et al.*, 1976; Harrison &

Richards, 1979; Elger & Hentschel, 1983); thus it is necessary to establish the structure of the normal teleost kidney. This study aims at examining the structure of teleostean kidney both qualitatively and quantitatively for comparison with those of other vertebrates.

II. QUALITATIVE AND QUANTITATIVE STRUCTURAL CHARACTERISTICS OF TELEOSTEAN KIDNEYS

A. Qualitative structure

1. Embryology and Gross Anatomy

The embryological development and the gross anatomy of the teleostean kidney have been investigated by several authors and it is presently accepted that the definitive teleostean kidney is mesonephric (Audige, 1910). Kerr (1919 cited by Youson & Mcmillan, 1971a) proposed the term opisthonephros for the kidneys of lower vertebrates because the kidneys originate from the whole of the nephrotomic plate which represents both the embryonic mesonephros and the nephrogenic material that forms the metanephros in higher vertebrates.

The teleostean kidney is invariably retroperitoneal and usually lies behind the swim bladder closely applied to the dorsal body wall. Edwards (1928) and Ogawa (1961, 1962) studied the shapes and the patterns of blood supply of the kidneys of several freshwater and marine teleosts and established that fish kidneys are elongated and vary in shape, size, symmetry and the degree of fusion according to species.

The variations in kidney shape and extent of fusion of right and left kidneys has been interpreted on the basis of the evolutionary level of the respective family. The kidney has been divided into the head and trunk kidneys on the basis of their location along the body (Ogawa, 1961, 1962; Singh & Srivastava, 1979; Mok, 1981). These authors also classified the kidneys into five types according to the shape and extent of fusion and noted that kidneys of freshwater fish are either completely fused or partially fused. However, some marine species belonging to the family Lophidae have separate kidneys. Hentschel & Elger (1987) reported that the kidneys of an elasmobranch of Potamotrygon species and a polypteriformes, *Polypterus senegalus* Cuvier also have separate kidneys.

The kidneys of teleosts are organised around the posterior cardinal vein (Edwards, 1928, 1930; Hickman & Trump, 1969) which is the main vein that drains venous blood from the posterior parts of the body into the heart.

The arterial supply to the teleostean kidney is effected by branches of intercostal arteries which are lateral branches of the dorsal aorta (Hickman & Trump, 1969; Anderson & Anderson, 1976; Elger *et al.*, 1984b). Complete absence of renal arteries has been reported in the aglomerular kidneys (Audige, 1910; Edwards, 1930).

The venous system of the teleostean kidney shows considerable variation (Edwards, 1928; Gerard, 1954; Hickman & Trump, 1969; Hentschel & Elger, 1987; Hentschel, 1991) and

two general forms have been described. In many teleosts the venous system has both afferent and efferent veins. The caudal vein on entering the caudal part of the kidney breaks up into a capillary network and forms the main afferent vein of the kidney. The intercostal veins also contribute to the renal portal system as they break into capillaries on entering the kidney. In these species the kidney is drained mainly by the posterior cardinal vein. In relatively few teleosts the caudal vein continues along the medial border of the right kidney as the right posterior cardinal vein which receives major tributaries from the caudal and cranial parts of the kidney and small tributaries from the right kidney. In these fishes the intercostal veins drain directly into the right posterior cardinal vein and the kidneys lack a renal portal system.

The ureter usually runs the whole length of the kidney and receives several ureteral (primary) branches at intervals along its length (Edwards, 1928; Hickman & Trump, 1969). In elasmobranchs, there are many secondary ureters along the mesial tissue of the kidney.

It appears, therefore, that many aspects of the gross anatomy of the fish kidney have been examined; however, comprehensive studies on the external form showing the relationships between the blood vessels, the ureter and ureteral ducts and the renal parenchyma have apparently only been made on the marine dogfish, *Scyliorhinus caniculus* (Hentschel, 1991).

2. Histology of the teleost kidney

Microscopic observations on the teleostean kidney have shown that zonation of the renal tissue does not occur in members of the class Teleostei, whereas zonation occurs in fishes from many other classes, for example, the petromyzons, elasmobranchs, chimeroids and the dipnoans. Furthermore, structures analogous to the loops of Henl'e which occur in mammalian and avian kidneys are lacking (Bulger & Trump 1968; Hickman & Trump, 1968a; Wendelaar Bonga, 1973; Hentschel, 1977a; Ottosen, 1978; Elger *et al.*, 1984b; Hentschel & Elger, 1987; Hwang & Wu, 1987). The teleostean kidney consists of renal tubules, ureteral and collecting ducts, renal corpuscles and blood vessels embedded in a stromal framework of loose haemopoietic tissue; however, the haemopoietic tissue is absent in some species.

Glomerularism and aglomerularism have been reported in both freshwater and marine teleosts (Edwards, 1930; Nash, 1931; Marshall & Smith, 1930; Grafflin, 1937; Ogawa, 1962; Bulger, 1965; Von Mollendorf, 1935; Hickman & Trump, 1969; Dobbs & De vries, 1975; Hentschel & Elger, 1987, 1989; Oguri, 1989). These studies have also shown that on the basis of the size, number, and the ultrastructural characteristics the glomerulus is less well developed in the marine teleosts with relatively few exceptions especially among the euryhaline species.

Hentschel & Elger (1987) have suggested that a common nomenclature for the nephrons of all vertebrates, and

especially for all the fishes may not be possible in view of the wide variations in the form and length of the nephrons and nephronal parts. However, studies on the topographical, microscopical and embryological characteristics of teleostean kidneys have established a basis for comparative histological studies of fish kidneys (Bulger & Trump, 1968; Hickman & Trump, 1969; Hentschel & Elger, 1987). It is generally accepted that the nephron components of fish include the renal corpuscle, the neck segment, the proximal tubule segments I & II, the intermediate segment and the distal segment. Interestingly in most gnathostomous fish the collecting tubule-collecting duct systems are derived from the nephron anlage (Hentschel & Elger, 1987) and are therefore considered to be parts of the nephron. The most consistent renal component is the proximal tubule which has been reported in all vertebrates (von Mollendorf, 1935; Beyenbach, 1985; Hentschel & Elger, 1987). The other renal components are either present or absent depending on species. The ureter or the homologous archinephric duct are present in all species.

B. Quantitative structural characteristics of the teleost kidney

Comprehensive data on the quantitative structural characteristics of fish kidneys are generally scarce. The available data includes the measurements of kidney length and weight, the number, area and size of glomeruli, the renal tubule length, and the height of the epithelium in the tubules

and collecting ducts, the size and volume of mitochondria and lysosomes and the surface density of basal cell infoldings (Edwards, 1928; Marshall & Smith, 1930; Nash, 1931; Olivereau & Olivereau, 1971; Wendelaar Bonga, 1972; Hwang & Wu, 1988). The length proportions of the tubular segments have been reported for the American eel, *Anguilla rostrata* , toadfish, *Opsanus tau* , Southern flounder, *Paralichthyes lethostigma* and the plaice, *Pleuronectes platessa* (Grafflin, 1937; Bulger, 1965; Ottosen, 1978).

It is therefore clear that more studies on the quantitative structural characteristics of the fish kidney need to be made in order to provide comprehensive data for comparison of renal structure among the fishes, comparison with other vertebrates, and also to give an insight on the relationship between kidney structure and function. Such data would also throw light on the extent to which kidney function is complemented by extra-renal organs such as the gills, the liver, the intestines and the rectal gland.

III. OBJECTIVES OF THE STUDY

The objectives of this study are as follows:

i. To device a procedure for applying stereological methods for the quantitative analysis of the fish kidney.

ii. To study the qualitative structure of the fish kidney in order to find out whether the renal parenchyma is organised into lobules.

iii. To describe the ultrastructure of the fish kidney.

iv. To obtain quantitative data on the fish kidney and compare such data in fish with contrasting characteristics of body size, habitat, and order.

v. To describe the structure-function relationships in fish kidneys by comparing the quantitative data and the known functional characteristics of fish kidneys.

vi. To compare the structural characteristics of fish kidneys with those of other vertebrates.

CHAPTER 2

LITERATURE REVIEW

I. HISTORICAL BACKGROUND OF STUDIES ON THE FISH KIDNEY

The fish kidney has been studied from as early as 1851 when Hyrytl reported the morphology of fish urogenital organs. Several early twentieth century renal morphologist reported renal structure of the Myxini (Conel, 1917), Petromysontia (Wheeler, 1899; Regand & Policard, 1902; Krause, 1923), Elasmobranchii (Krause, 1923), Teleostei (Audige, 1910). These studies laid the foundation for studies on renal structure among the fishes. The study by Audige (1910) covered developmental, gross anatomical and histological aspects of the teleostean kidney. This author reported that the teleost kidney was mesonephric and was aglomerular in the young embryo. Kerr (1919 cited by Youson & McMillan, 1971a) described the kidney of most lower vertebrates as an opisthonephros. Between 1920 and 1940 many scientists reported on structural and functional aspects of fish kidneys. Some of the most remarkable reports are those by Edwards (1928, 1930, 1935); Marshall & Smith (1930); Nash (1931) Edwards & Schnitter (1933); and Grafflin (1937). Most of the literature on teleost kidney has been comprehensively reviewed by Fange, 1963; Hickman & Trump, 1969; Beyenbach, 1985; and Hentschel & Elger, 1987.

II. THE QUALITATIVE, QUANTITATIVE AND FUNCTIONAL CHARACTERISTICS OF FISH KIDNEYS

A. Qualitative structure of fish kidneys

Kidneys from many species representing all the classes of fish have been studied and the simplest kidney is that of the Myxini (hagfishes) which are among the earliest vertebrates. In this group the kidney consists of a paired anterior pronephros (Holmgren, 1950) and the caudal definitive kidney (mesonephros) consisting of segmentally arranged large renal corpuscles and paired archinephric ducts. The renal corpuscle is connected to the archinephric duct by a short neck segment. Fange (1963) described the kidney as atubular due to the absence of a segmented renal tubule. The ultrastructural characteristics and functions of the archinephric duct are similar to those of the proximal tubule in other vertebrates (Fange, 1963; Ericsson, 1967; Ericsson & Trump, 1969; Heath-Eves & McMillan, 1974). The microvasculature of the kidney consists of the afferent arterioles from the dorsal aorta to the glomeruli, the efferent arterioles and the peritubular capillaries (Hentschel & Elger, 1987). A renal portal system is absent (Capreol & Sutherland, 1968).

The kidneys of Petromyzontia (lampreys) are paired elongated straps with a triangular cross-sectional configuration and show highly organised structures such as the glomus and the tubular loops (Wheeler, 1899; Gerard, 1954; Youson & McMillan, 1970a & b, 1971a-c; Ooi & Youson,

1977; Logan *et al.*, 1980a & b). Each renal strap of the paired elongated kidneys has a large glomus of capillary loops formed by fusion of glomeruli instead of the individual renal corpuscles seen in other vertebrates. Several nephrons arise from the glomus. The uriniferous tubule, therefore, consists of a glomus (equivalent of renal corpuscle) a ciliated neck segment (Gerard, 1954), a brush bordered proximal tubule which is divided into two depending on cytological detail (Youson & Mcmillan,1970b), a distal segment, and a collecting tubule-collecting duct system which occurs mainly on the ventral zone of the kidney and drains into the archinephric duct (Youson & McMillan, 1971a). The glomus is supplied with blood by renal arteries via short afferent arterioles (Youson & McMillan, 1970a; Logan *et al.*, 1980a). The ultrastructure of the glomus resembles that of the renal corpuscle in that it has podocytes whose pedicels rest on a basement membrane. The filtration barrier resembles that in other vertebrates. The peritubular circulation derives entirely from the efferent arterioles and a portal system is lacking (Hentschel & Elger, 1987).

The elasmobranch kidney has been widely studied particularly with regard to the role it plays in the retention of high concentrations of urea and trimethylamine oxide (TMAO) in the marine elasmobranchs (Smith, 1936; Kempton, 1943, 1962; Borghese, 1966; Bulger, 1967; Forster, 1967; Hickman & Trump, 1969; Schmidt-Nilsen *et al.*, 1972; Payan *et al.*, 1973). The kidneys are elongated strap-shaped organs which are

separated anteriorly and fused caudally in sharks (Hentschel 1988, 1991; Hentschel & Elger, 1987). The anterior part shows metameric arrangement but such arrangement is not apparent in the caudal part. The kidney also shows two zones, a lateral bundle and mesial tissue (Hentschel & Elger, 1987; Hentschel, 1990). The skate kidneys, on the other hand, are two separate flat rounded bodies which are roughly bean shaped and located in the caudal part of the body cavity (Elger & Hentschel, 1982, 1983, Hentschel & Elger, 1987a; Lacy & Reale, 1985a, b). The kidneys do not show any zonation (Hentschel & Elger, 1987).

Information on the structure of the nephron in the elasmobranchs is given in the reports by Kempton (1943, 1953, 1962), Nash (1931), Hickman & Trump, (1969), Lacy & Raele (1985b), Hentschel & Elger (1987) and Elger & Hentschel (1982). These authors have reported the presence of an exceptionally long nephrogenic tubule that runs through the different zones of the kidney (Kempton, 1940; Hentschel, 1987, 1988, 1991). The nephron segments distinguished on the basis of their staining properties (Hickman & Trump, 1969), histochemistry (Hentschel & Meyer, 1982) and fine structure (Lacy *et al.*, 1975; Hentschel & Elger, 1987; Lacy & Reale 1986) are the renal corpuscle, neck segment, proximal segment I & II, intermediate segment, distal segment, and these drain into a system of collecting tubules and collecting ducts which open into the ureter. In addition, the marine elasmobranchs possess a countercurrent arrangement between

the proximal and distal parts of the renal tubule which is lacking in freshwater elasmobranchs (Hentschel & Elger, 1987).

The arterial supply to the kidney is by ventral branches of intercostal arteries which penetrate into the renal tissue from the dorsal side and give rise to small arteries and arterioles (Hickman & Trump, 1969; Hentschel & Elger, 1987). A renal portal system is present and the afferent veins are the caudal vein and the intercostal veins and efferent veins are the right (large) and left (small) posterior cardinal veins (Hentschel & Elger, 1987).

The renal structure of chimeras (Holocephali) is not well known; however, examination of the kidney of one species, *Hydrolagus colliei*, (Stanley, 1963; Hickman & Trump, 1969) showed absence of intrarenal haemopoietic tissue and a glomerular nephron with a neck segment, bisegmental proximal tubule and a distal tubule with cells containing many mitochondria.

The structure of kidneys in representative species of the group Osteichthyes has been reported for several species (Hickman & Trump, 1869; Hentschel & Elger 1987).

The kidneys of the primitive bony fishes, Polypteriformes, have been studied Hentschel & Elger (1987). In these species the left and right kidneys are separate and elongated and show zonation of renal tissue in cross-sections. The uriniferous tubules consist of the renal corpuscles (arranged in longitudinal rows on the ventral third of the kidney), neck

segments, unisegmental proximal tubules with endocytic apparatus along the whole length, and ciliated intermediate and distal segments whose basal and lateral membranes interdigitate. Collecting tubules open into collecting ducts which in turn drain into the archinephric duct. The collecting tubules and collecting ducts have principal and intercalated cells which are devoid of microvilli. The renal tissue is supplied by small arteries from the intercostal arteries which are branches of the dorsal aorta. In these fishes a renal portal system has yet to be demonstrated.

Hentschel & Elger (1987) reported that the kidneys of Chondrostei (sturgeons) are elongated strap-shaped organs in which the renal tissue does not show zonation. The nephrons consist of renal corpuscles, proximal segments I & II, and distal segments drained by collecting tubule-collecting duct systems which open into the ureter. Ciliated cells are found at the beginning of the proximal tubule I and at the end of proximal tubule II suggesting the presence of the neck and intermediate segments. The blood vascular supply of the sturgeon kidney has apparently not been studied.

The available reports on the structure of the kidney of Holostei (De Smet, 1963 cited by Hentschel & Elger, 1987) show that the nephron consists of a renal corpuscle, neck segment, bisegmental proximal tubule and a distal segment. The collecting tubule-collecting duct system has yet to be clearly identified.

Reports on more than 100 teleostean species whose kidneys have been studied (Hickman & Trump, 1969) show that the kidneys differ in the shape, the pattern of blood supply and the symmetry. The renal blood vascular supply differs in different teleostean orders (Hickman & Trump,1969) and all teleosts have a venous renal portal system (Hentschel & Elger,1987). The typical teleostean nephron consists of a renal corpuscle, a ciliated neck segment, a proximal segment I (with low columnar cells, high microvillus brush border, basal nuclei, apical endocytic vesicles and vacuoles and numerous lysosomes), proximal tubule II (with high columnar cells, central nuclei, lower brush border, numerous mitochondria and small apical vesicles), an intermediate segment and a distal segment with low columnar cells and extensive basolateral invaginations of the basolateral membrane. (Hickman & Trump, 1969; Hwang & Wu, 1987; Hentschel & Elger, 1987). The nephrons are drained by a system of collecting tubules and ducts which have principal and intercalated cells in many species.

The only available information on the renal structure of Crossoptergii is on the coelacanth, *Latimeria chalumnae* (Millot & Anthony, 1973; Lagios, 1974). The kidney is glomerular and shows zonation of renal tissue. The renal tubule has a proximal segment, intermediate segment, and is drained by the collecting ducts. Like the marine elasmobranchs, the coelacanth blood contains a high concentration of urea and TMAO (Griffith *et al.*, 1974).

However, a countercurrent system similar to that of elasmobranch has not been described in the coelacanth kidney. Thus, the coelacanth and the mangrove frog (*Rana cancivora*) are the only two ureosmotic (build up high concentration of TMAO in blood plasma) vertebrates without a renal countercurrent system (Hentschel & Elger, 1987).

The renal structure of Dipnoi (lungfishes) has been reviewed by Hickman & Trump (1969) and Hentschel & Elger (1987). The kidneys are paired elongated organs which are fused caudally in some species. The renal tissue shows zonation and contains islets of haemopoietic tissue, and pigment cells. The blood vascular supply consists of arteries and a venous renal portal system. The nephron consists of a renal corpuscle, neck segment, bisegmental proximal tubule, intermediate and distal segments and these open into the collecting tubule-collecting duct system which drains into the ureteral ducts and the ureter.

It is apparent that renal structure differs considerably between the lower fishes (Myxini) and the higher fishes (Teleostei and Dipnoi). This difference is characterized by an increase in the number of nephron segments along the phylogenetic tree. The disparities in the number of nephron segments that have been observed among the various classes (groups) of fish have been explained on the basis of evolution and the environmental factors in the habitat of the fish (Hickman & Trump, 1969; Hentschel & Elger, 1987).

B. Quantitative structural characteristics of fish kidneys

Among the vertebrates, the quantitative renal structural characteristics have been investigated in mammals, (Sperber, 1944; Dunnill & Halley, 1973; Abdalla & Abdalla, 1979; Seyer-Hansen, Hansen & Gundersen, 1980; Schiller *et al.*, 1980; Schiller & Tiedmann, 1981; Pfaller, 1982) and in Aves, (Poulson, 1965; Johnson & Mugaas, 1970; Johnson & Ohmart, 1972, 1973; Johnson & Skadhauge, 1975; Skadhauge, 1981; Warui & King, 1985; Warui, 1984, 1989). These studies have demonstrated that renal structure and function are well correlated and that the structure of the kidney is greatly influenced by body size and environmental factors.

The fish kidney structure has been investigated quantitatively by relatively few authors (Edwards, 1928; Marshall & Smith, 1930; Nash, 1931; Bulger, 1965; Olivereau & Olivereau, 1971; Wendelaar Bonga, 1973; Ottosen, 1978; Hentschel, 1982). These studies have emphasized the morphometric renal parameters and it is therefore necessary to apply stereological methods (Weibel, 1979) to the quantitative analyses of the fish kidney.

C. Renal function in fish

The physiology of fish kidney has been reviewed by Hickman & Trump (1969); Hardisty (1979); Rankin & Davenport (1981), Nishimura & Imai (1982); Rankin *et al.* (1983); Beyenbach (1985). The fish kidneys contributes to

extracellular fluid homeostasis by regulating either the excretion or reabsorption of water and divalent and monovalent ions, and also regulates the acid-base balance by excreting organic acids. In glomerular kidneys, the renal tubules also reabsorb filtered glucose and other macromolecules. The nephrons of higher fishes contribute a wider range of functions than those of the lower fishes. The kidneys of Myxini which are isosmotic regulators do not handle magnesium, calcium and phenol red; consequently these are excreted by the liver. The kidneys of teleosts, on the other hand, regulate these substances. The uriniferous tubules of the aglomerular teleosts mainly excrete divalent and monovalent ions and in fishes other than the Myxini and elasmobranchs the kidney contributes only marginally to the excretion of nitrogenous waste. The kidneys of marine elasmobranchs and Latimeria, in addition, are capable of concentrating urea and TMAO to very high levels in blood.

The above differences in the functional characteristics of the kidneys are reflected in the renal structure in the various classes; thus giving the impression of a good correlation between structure and function. As an example, the kidneys of the marine elasmobranchs possess a countercurrent system between the proximal tubules and the distal tubules and this arrangement is lacking in all other fish so far studied. This countercurrent system is associated with retention of urea and TMAO.

Environmental factors also play an important role in determining the renal function in fish. According to the model of Evans (1979) and Eddy (1982) fish in the freshwater habitat the fish are hyperosmotic relative to the environment, and thus there is a general influx of fluids into the body. The role of the kidney as a hyperosmoregulator is to rid the body off excess water and to conserve salts. Consequently, the kidney in the freshwater habitat exhibits a high glomerular filtration rate, net tubular fluid secretion and high tubular reabsorption of monovalent ions culminating in the production of a large volume of dilute urine.

The marine fish, on the other hand, are hyposmotic to their environment except the Myxini which are isosmotic and the elasmobranchs which are hyperosmotic. Marine fish are therefore faced with the problem of water scarcity and high salt loads. Such fish restrict the water loss by lowering the glomerular filtration rate, retaining water via net tubular reabsorption, obtaining water by increasing their drinking rates and excreting salts through the kidney and gills. Although a urine concentrating structure like the loop of Henl'e is lacking in teleost fish, the formation of hypertonic urine has been observed in isolated perfused tubules and in the intact kidney of winter flounders (Beyenbach, 1982; Elger *et al.*, 1987). The excretion of hypertonic urine has been attributed to net tubular reabsorption and secretion of divalent ions and organic substances (King *et al.*, 1982). The voided urine is little and relatively highly concentrated. Thus

depending on the habitat a fish may place a premium on water conservation and salt secretion or water elimination and salt conservation.

The morphological correlates to some specific renal functions have been described, for example the marine fish which have low glomerular filtration rates have poorly developed renal corpuscles (Edwards, 1930; Nash, 1931; Wendelaar Bonga, 1973; Beyenbach, 1985; Hentschel & Elger, 1987). The extreme conditions reflecting poor development of renal corpuscles are the aglomerular and pauciglomerular states. These states occur in fish with sedentary habits in very cold habitats (Hickman & Trump, 1969; Dobbs & De Vries, 1975; Elger & Hentschel, 1981). In addition, Brown *et al.*, (1978) and Hentschel & Kaune (1980) proposed that anuria which occurs on adaptation to sea water leads in the long term to glomerular degeneration due to disuse. This lends support to the principle of symorphosis which states that there are no superfluous structures in the body; that is structure correlates with function.

Mammals have countercurrent exchange and multiplier systems to facilitate water conservation, but on the other hand, fish as well as other non-mammalian vertebrates exhibit glomerular antidiuresis (Dantzler, 1982). Glomerular antidiuresis enables the fish to cope with higher osmolarities since not all the salts or wastes can be eliminated on less filtrate. This glomerular antidiuresis occurs due to intermittent glomerular filtration (Foster, 1942; Brown *et al.*,

1978, 1980; Elger *et al.*, 1984a). During glomerular antidiuresis, renal arterial flow is greatly compromised and the venous renal portal system supplies blood and nutrients (Beyenbach, 1985)

CHAPTER 3

MATERIALS AND METHODS

I. BIOLOGICAL MATERIALS AND FIXATION OF THE KIDNEYS

Twenty seven male and female adult fish were caught by a gill net or line hook from Sagana Fisheries, Masinga dam, Lake Naivasha, and the Indian Ocean. The fish obtained from the Indian Ocean were fixed at the site of collection, but those from the other sites were transported in polythene bags containing aerated water to the Department of Veterinary Anatomy, University of Nairobi. These fish were maintained in an aquarium for about one or two days before they were sacrificed and the kidneys fixed.

Prior to dissection each fish was immobilized by a sudden blow on the head (Brown *et al.*, 1980), weighed and placed in a dorsal recumbency on an M-shaped trough (Elger *et al.*, 1984a). A ventral midline incision extending from a point two centimeters cranial to the pelvic fins and on to the anal opening was made, and part of the lateral body wall on either side was excised in order to adequately expose the peritoneal cavity of the abdominal coelom. Further dissection of the abdominal cavity was avoided to prevent the disruption of renal blood vessels before the kidneys were adequately fixed. The pericardial part of the coelom was opened to expose the three chambered heart and the ventral aorta. For each fish the pumping action of the heart gave an indication that the fish was alive.

The kidneys were fixed *in situ* by gravitational perfusion through the blood vessels. A canula was inserted through the ventricle and the bulbus cordis into the ventral aorta and anchored by a ligature (which also served to prevent back-flow of the fixative) placed at the junction between the ventricle and the bulbus cordis. The canula was connected to a gravity flow device at a height of 80-100 cm of water (Elger *et al.*, 1984b). The sinus venosus was then cut open to act as drainage point for the fixative and to prevent the build up of pressure to unphysiological levels. Prior to the infusion of the fixative, the vascular system was flushed with physiological saline (Wolf, 1963) at a pressure of 80-100 cm water for 10 minutes. Fixation was done at the same pressure with 2.5% glutaraldehyde in 0.15 M phosphate buffer, pH 7.2 for 30 minutes. The abdominal viscera were subsequently removed to expose the dorsal aspect of the peritoneum which was then excised to expose the retroperitoneal swim bladder and the trunk kidneys which were closely applied to the dorsal body wall. The kidneys were removed *in toto* by careful dissection which involved the cutting of intercostal arteries and veins and undermining along the dorsal surfaces. The dissection was extended beyond the pericardio-peritoneal septum to expose the head kidneys which were removed together with the trunk kidneys, rinsed in 0.15 M phosphate buffer and weighed.

II. MEASUREMENT OF BODY WEIGHT, BODY SURFACE AREA AND KIDNEY PARAMETERS

The body weight of each fish was measured directly on an electronic balance and the body surface area for each fish was calculated by the formula of Rubner (1924) which states that:

Area (in cm2) = $K. \sqrt[3/2]{g}$

where K is a constant equal to 9 in fishes and g is the body weight in grams.

The Kidney volume was measured by the fluid displacement method of Scherle (1970). This method is based on the Archimedes principle that a floating body displaces its own volume of fluid (Fig 1). If the fluid is water, with a specific gravity equal to one, the volume is equal to the weight increase shown on the balance when an organ is freely suspended in the water. In this study, it was assumed that the specific gravity of 2.5% glutaraldehyde in 0.15 M phosphate was equal to one and kidney volume was read directly as the weight increase on the balance. In all the species pilot studies on the kidneys had shown that the head part does not contain renal tissue but contains tissue homologous to that of adrenal gland. Therefore, in measuring the kidney volume, the head part of the kidney in each fish was cut at the level of the pericardio-peritoneal septum, and only the volume of the trunk and tail parts of the kidney was estimated. In addition, the catfish lateral renal lobes were excluded.

After measuring the volume each kidney was immersed in 2.5% glutaraldehyde in 0.15 M phosphate buffer for at least 12

hours. The kidneys were not cut into smaller blocks because they were relatively thin and flattened dorso-ventrally, and it was assumed that they would be adequately penetrated by the fixative; however, in the common carp two incisions were made on either side of the C-shaped parts of the trunk kidneys (Fig. 11) to allow adequate penetration by the fixative.

III. TISSUE SAMPLING AND PROCESING FOR LIGHT AND TRANSMISSION ELECTRON MICROSCOPY AND MORPHOMETRY

In each fish the kidney was sampled by the stratified random method. The right and left kidneys in all the fishes were either partially or completely fused, and thus they were considered as one organ and cut into eight equal blocks which were subsequently processed for paraffin sectioning. Two technically adequate and equally spaced sections from each block were used for stereological analysis. For each fish one whole kidney was processed for serial paraffin sections in order to study the qualitative structural characteristics. In processing for paraffin sections the tissues were routinely washed in running tap water, dehydrated in ethanol, and cleared in methyl benzoate. The tissues were then infiltrated and embedded in paraffin wax. Sections seven microns thick were cut on a Leitz rotary microtome and prepared for light microscopical examination. The sections were stained with Harris's haematoxylin and Gomori's trichrome and then counterstained with 1% alcian blue.

For electron microscopy the tissues were cut into small blocks, thoroughly rinsed in cold 0.15 M phosphate buffer and post fixed in buffered osmium tetraoxide for 4 hours. After a second rinse in buffer the tissues were block stained with uranyl acetate for 30 minutes with a subsequent rinse in buffer. The tissues were then dehydrated via ethanol and propylene oxide and infiltrated and embedded in epon 812. Semithin sections were stained with toluidine blue and ultrathin sections with uranyl acetate and lead citrate. The thin sections were examined under the electron microscope Philips 301.

Tissue shrinkage due to processing was assessed by measuring the length of a block of tissue before processing and the length of the same phase on a stained section. The linear shrinkage factor (fs) was calculated using the formula of Weibel (1979) which states that,

$$fs = ls/lo$$

where ls and lo are some characteristic lengths in the shrunken

and the original tissue block.

In this study the linear shrinkage factor was 0.88.

1V. STEREOLOGICAL ANALYSIS

Stereology differs from morphometry in which the direct measurements of the parameters of gross specimens, tissue elements on sections or photomicrographs of tissue sections are made without reference to their three-dimensional

structure. Stereology, on the other hand, uses probes which allow the extrapolation of information on the three dimensional characteristics of organs or tissues from two dimensional objects, for example sections. Stereological methods have been described in detail by Elias, Henning & Elias (1961), Weibel (1979), and Aherne & Dunnill (1982). These methods have been adopted for the teleostean kidney in this study.

In stereological analysis of tissues the component analyzed should be present in adequate numbers, be identifiable on sections and have similar shape and size at different locations within the tissue. The component should also be randomly distributed within the organ or tissue since the distribution of a component within the tissue reference space determines the type of probe to be used.

The volume densities of the teleostean renal components were estimated using the point counting method described by many authors, (see for example Chalkley, 1943; Aherne, 1967; Weibel, 1979). Point counting is based on the Delesse principle of 1847 which states that, if random points are superimposed on a given section of tissue or that of any other composite structure, the number of points (P) falling on profiles of a particular test component (a) divided by the total number of points in the test system falling onto the section (Pt) is a good estimator of the areal density (AA) and volume density (VV) of component a within the reference area or

volume of the test system. This can be represented by the expression:

Pa/Pt= AA(a) = VV(a)

Figure 2 shows how the point counting was performed. The kidney sections were analyzed at two levels to estimate the volume densities of the renal components. The first level of sampling was done at a magnification of x 100. Fifteen sections from the fused right and left kidneys of each species were completely analysed field by field using an eyepiece graticule to estimate the volume densities of the main components of the kidney. The main components of the kidney are shown in figure 4. These included the parenchyma/uriniferous tissue which comprised of nephrons (renal corpuscles, neck, proximal I & II and distal segments and collecting tubule-collecting duct system). The other components, together grouped as non-parenchyma, were the blood vessels larger than capillaries, intrarenal haemopoietic tissue, ureter and its ducts and connective tissue. Ureter and its ducts had distinct fibrous walls.

The second level of sampling was done at a magnification of X 400 using the same eyepiece graticule to estimate the volume proportions of the components of the parenchyma shown in Figure 5. Five sections from the fused right and left kidneys were selected by a stratified random method from the sections used at the first level of sampling. This involved the determination of a spacing interval by dividing the total number of sections in the sample by the number of sections

required. In this case there were fifteen sections of each kidney and five sections were required; therefore the spacing interval was 15/5 = 3.

Proximal tubules were the tubular profiles made up of tall columnar cells with apical brush border and non-metachromatic cytoplasm. The distal tubules were the tubular profiles lined by low columnar cells with metachromatic cytoplasm but lacking a brush border. Neck segments were the tubular profiles of low columnar/cuboidal cells with luminal cilia. Collecting tubules and small ducts were the profiles with low columnar cells, metachromatic cytoplasm and little amount of connective tissue coat.

The sufficient number of points or sections to be counted for each component was arrived at by plotting a cumulative mean graph in which it was found out that by the fifteenth and fifth section or more at the first level and second levels of sampling respectively the volume proportion of each renal component had a standard error of ± 5% of the mean.

Diameters of renal corpuscles, glomeruli, and proximal and distal tubules were measured at a magnification of X 400 using an eyepiece micrometer (Olivereau & Olivereau, 1971; Hwang & Wu, 1988). Renal corpuscle and glomerular diameters were measured from renal corpuscles sectioned through the vascular pole and the beginning of the neck segment. The maximum and minimum diameters of each renal corpuscle, glomerulus and the profiles of proximal and distal tubules were measured and the average values for every pair of

measurements used to compute the mean values. Due the difficulty in locating renal corpuscles sectioned through the median plane only fifteen renal corpuscles were measured for each species. For the tubular diameters five sections were used for each species. The data obtained in the study was statistically analyzed by logarithmic regression based on the equation that Log Y = a + b logW which when rearranged become $Y = aW^b$ where Y is the variable, W is the body weight in grams, b is the slope of the regression line and a is the Y value for W = 1. In addition the Student's t-test was carried out for purposes of determining the level of significance between values of renal parameters in fishes with contrasting characteristics (Table 6).

Stereology requires that the reference space be known because the volume of a given component is a proportion of an identifiable compartment of the organ. The teleost kidney was therefore compartmentalized into a hierarchy of reference space as show in Fig. 3.

CHAPTER 4

RESULTS

I. QUALITATIVE OBSERVATIONS ON THE STRUCTURE OF THE TELEOSTEAN KIDNEY

A. External form of the kidney

1. General remarks

The external configuration of the kidneys and the main blood vessels which relate to the kidney in each of the five teleost species examined are shown in figures 9, 10, 11, 12 and 13 for tilapia (*Oreochromis niloticus*), the blackbass (*Micropterus salmoides*), the common carp (*Cyprinus carpio*), the catfish (*Clarias mossambicus*) and the milkfish (*Chanos chanos*) respectively. It is apparent from the figures that the external form of the kidney differed considerably among these teleosts; however, several characteristics especially the colour, topographical relationships, general location and the extent of the kidney along the vertebral column were similar in the fishes. Thus in all the species the kidneys were paired elongated dark-red organs occupying a retroperitoneal position in the dorsal parts of the abdominal and pericardial coelomic cavities (Fig. 6, 7, 8). In each fish the kidneys were related cranially to the heart and caudally to the urinary bladder or urogenital sinus. Laterally, they were related to the lateral body musculature and ribs. Dorsally, the kidneys were closely applied to the dorsal body wall and ventrally they abutted on the swim bladder or peritoneum (Fig. 7, 8). On the caudo-

ventral aspect they were closely related to the corpuscles of Stannius.

All the kidneys examined had smooth ventral surfaces and grooves/indentations on the dorsal aspect. The dorsal indentations were caudally directed and corresponded to the ribs. In mature fish the grooves formed on the dorsal surface of the kidney by the proximal ends of adjacent ribs were quite deep and made the removal of the kidneys in toto quite difficult. The kidneys in situ conformed to the contour of the coelomic cavity; in species with a deep coelomic cavity the kidneys were curved ventrally, but in species with a shallow body cavity they were more or less straight.

For descriptive purposes and based on its close relationship to specific bones of the vertebral column, each kidney in some of the teleosts could roughly be divided into three regions namely the head , trunk, and tail parts of the kidney. These parts are subsequently referred to as the head kidney, the trunk kidney and the tail kidney respectively. The head kidney was an expanded roughly pyramidal cranial part located in the pericardial cavity and corresponding to the first and the fourth vertebrae. It was more dark-red than the rest of the kidney. The trunk kidney was the region corresponding to the fifth vertebra (i.e. the level of the pericardio-peritoneal septum) and extending to the level of the seventeenth vertebra. It appeared as an elongated strap and occupied most of the dorsal part of the abdominal coelom. The tail kidney was the tapering dorso-ventrally flattened flap of renal tissue

extending from the level of the seventeenth to the nineteenth vertebrae.

Two major blood vessels, the dorsal aorta and the posterior cardinal vein, were located between the left and right kidneys in each species (Fig. 9-13). Caudal to the seventeenth vertebra, the two vessels were contained in a heamal arch which extends throughout the whole tail region of the fish. The posterior cardinal vein and the dorsal aorta formed the border between the right and left kidney even in fused kidneys. The dorsal aorta and the posterior cardinal vein supplied and drained the kidney via branches of intercostal arteries and short renal veins respectively. Furthermore, intercostal veins supplied the kidney with venous blood but some drained directly into the posterior cardinal vein (Fig. 9-13).

In all the species each kidney was drained by a ureter located on the ventro-lateral aspect. The primary tributaries of the ureter were located in the cranial part of the trunk kidney, at the level of pericardio-peritoneal septum, and the mainstream ureter then coursed caudally to drain into the urinary bladder in males or urogenital sinus in females. The width of the ureter increased towards the caudal end as it received additional tributaries from the kidney.

2. Detailed morphology

It is apparent that relatively few of the gross structural characteristics of the kidneys in the teleost species examined

were similar. It is therefore convenient to describe the detailed gross anatomy of the kidneys of each species alone.

a. Morphology of the tilapia kidney

The right and left kidneys of tilapia (Fig. 9) occupied a region in the dorsal part of the coelomic cavity corresponding to the first and on to the eighteenth vertebral bones. Caudal to the fourteenth vertebra the left and right kidneys were fused together forming a compact organ. This union was to a large extent effected by a bridge of renal tissue which extended between the the ventro-medial borders of the kidneys, and covered the ventral surface of the posterior cardinal vein; however, the extreme caudal parts of the kidney (especially the tail kidneys) were completely fused. The two kidneys thus appeared as one V-shaped organ with two cranial expansions forming the head kidneys. The unfused cranial two-thirds of the trunk kidneys resembled a flattened ribbon and showed a distinct metameric arrangement of the renal tissue. The metameric arrangement was less distinct in the fused caudal part of the trunk kidneys and the tail kidneys (Fig. 9) and absent in the head kidneys.

The cross-sectional profiles of the tilapid trunk and tail kidneys were roughly triangular with an apex formed by the lateral border and the base by the medial border. The cross-sectional form of the head kidney was an irregular polyhedron with rounded edges.

The dorsal aorta coursed ventral to the vertebral column along the dorsal mid-line and in the fused region of the kidneys it ran along the dorso-medial borders of the left and right kidneys. Intercostal arteries branched from the dorsal aorta at regular intervals and supplied ventral branches to the kidneys. The head stream of the posterior cardinal vein was the caudal vein which emerged from the tail region caudal to the kidney. It coursed ventral to the dorsal aorta along the dorso-medial borders of the kidneys but, within the fused part of the trunk kidneys (Fig. 9) the posterior cardinal vein changed course and assumed a position ventro-medial to the kidneys. The posterior cardinal vein continued its cranial course along the ventro-medial border of the right kidney and received numerous tributaries from both the left and right kidneys.

Each kidney was drained by a ureter which emerged from the renal parenchyma in the caudal parts of the trunk kidney and coursed caudally on the ventro-lateral surface of the kidney to drain into the urinary bladder in males and the urogenital sinus in females In the cranial parts of the trunk kidney the ureter was completely embedded in renal parenchyma; however, cross-sections of the kidney showed that it coursed close to the lateral border of the kidney.

b. Morphology of the blackbass kidney

The right and left kidneys of blackbass corresponded to the length of coelomic cavity between the first and eighteenth

vertebral bones. The caudal one third of the two kidneys was united by a bridge of renal tissue on the ventro-medial surfaces of the two kidneys and around the walls of the posterior cardinal vein. The tapering caudal extremity of the kidney ended in two relatively short tails (Fig. 10). Thus the whole kidney was roughly V-shaped with two cranial expansions forming the head kidneys. The unfused cranial two thirds of the trunk kidney resembled a flattened ribbon and showed metamerism which was less distinct in the head and tail parts of the kidney. The cross sectional profiles of the blackbass trunk and tail kidneys were triangular (Fig. 14) and those of the head kidney were irregular polyhedrons.

The arterial supply to the blackbass kidney was through 7-10 intercostal arteries from the dorsal aorta. The intercostal arteries were caudo-laterally directed and gave off ventral branches which supplied the kidneys as the intra-renal arteries. Within the renal parenchyma the intra-renal arteries gave rise to the intermediate and terminal arterioles (Fig 16).

The venous drainage of the blackbass kidney (Fig. 10) was mainly shared between the posterior cardinal vein and the caudal vein. The posterior cardinal vein emerged from a large venous sinus located on the ventro-medial aspect of the fused parts of the kidney and coursed cranially along the ventro-medial border of the right kidney receiving tributaries from the cranial parts of the kidney along its course. Venous tributaries from the cranial parts of the left kidney formed an

accessory posterior cardinal vein which drained into the posterior cardinal vein.

The caudal vein emerged from the tail region and coursed along a dorsomedian groove between the fused tail kidneys, but at the level of the caudal part of the trunk kidney the vessel bifurcated into the right and left caudal veins. Each of these vessels coursed cranially along the dorsal surface of the respective kidney receiving tributaries from the kidney and also draining many of the ipsilateral intercostal veins. The right caudal vein joined with the posterior cardinal in the head part of the kidney before draining into the sinus venosus, but the left caudal vein opened independently into the sinus venosus. Some of the intercostal veins entered the renal parenchyma and had no direct connection with either the caudal vein or the posterior cardinal vein. These vessels probably constitute a renal afferent (portal) system of the blackbass.

The ureter of each kidney was located along the lateral border of the kidney and followed a zig-zag course corresponding to the indented lateral border of the the trunk kidney. Some parts of the ureter were located ventral to the tips of the renal segment, but all along its course to either the urinary bladder or urogenital sinus the ureter was not embedded within the renal tissue.

c. Morphology of common carp kidney

The common carp kidneys (Fig. 11) differed considerably from those of other the species studied. Each kidney could on the basis of the relationship to the vertebral column and appearance, be divided into three main regions namely the head, trunk, and tail kidneys. The head kidneys were located within the pericardial part of the coelom in the region corresponding to the first four bones of the vertebral column. The metamerically arranged trunk kidneys occurred in the abdominal part of the coelom in the region corresponding to the pericardio-peritoneal septum and on to the seventeenth vertebral bone. The caudal part of the kidney was laterally expanded to form a voluminous part of the kidney. The tail kidney was flattened dorso-ventrally and extended to the level of the nineteenth vertebra.

The caudal parts of the left and right kidneys were completely fused. Owing to the fusion the laterally expanded voluminous renal masses resembled a crescent with a concave ventral surface and a convex dorsal surface (Fig. 11). The unfused parts of the trunk kidneys showed metameric arrangement of renal tissue which was absent in the head kidneys and the fused caudal parts of the kidneys. The cross-sectional form of each kidney was roughly polygonal in the head kidney and triangular in the trunk and tail kidneys.

The dorsal aorta coursed between the right and left kidneys and supplied them via ventral branches of intercostal arteries. The caudal vein emerged from the tail region and

drained into a venous sinus located on the ventral aspect of the crescent-shaped part of the trunk kidney. Venous tributaries from the caudal parts of the kidneys drained into the sinus. The left and right posterior cardinal veins emerged from the sinus and coursed cranially on the ventral surfaces of the left and right kidneys respectively. Each of these vessels received tributaries from the kidney and also drained the intercostals.

In each kidney the ureter formed in the cranial parts of the trunk kidney and coursed caudally within the renal tissue close to the lateral border of the kidney. A short part of the ureter could be observed extending from the metameric part of the trunk kidney to the laterally expanded parts (Fig. 11); however, the ureter mainly emerged from the kidney at the caudal border of the crescent-like part of the trunk kidney and coursed caudally along the lateral border of the tail kidney to either the urinary bladder or urogenital sinus.

d. Morphology of the catfish kidney

The right and left kidneys of the catfish were fused along the whole of their medial borders giving the anomalous appearance of one organ (Fig. 12). The fusion was effected by two bridges of renal tissue which enclose the posterior cardinal vein and join the dorso-medial and ventro-medial borders of the kidneys. The kidney corresponded to the region between the fourth and nineteenth vertebral bones. Each kidney had a triangular cross-sectional profile and the kidney

as a whole had a triangular configuration with lateral lobes embedded in the lateral thoracic musculature. The kidney had a wide cranial end and a tapering caudal end (Fig. 12). The lateral renal lobes, were connected to the main kidney by vasculature and scanty parenchyma. Metamerism was evidenced by presence of shallow grooves on the dorsal kidney surface even though the whole lateral margin appeared even and rounded. The dorsal renal indentations were less prominent than in the other species studied.

The dorsal aorta coursed along the ventral surfaces of the vertebral bones between the two kidneys and branched into intercostal arteries that supplied the kidney via short ventral branches. The posterior cardinal vein continued from the caudal vein and coursed along a deep groove on the dorsomedian surface of the fused tail and trunk kidney; however, at the level of the sixteenth vertebra the posterior cardinal vein penetrated the renal parenchyma and emerged on the ventral surface of the kidney. The posterior cardinal vein continued its cranial course between the right and left kidneys and received intercostal veins and several small tributaries from the kidneys (Fig. 12).

In each kidney the ureter emerged on the ventral surface in the caudal part of the trunk kidney (Fig. 12) and continued caudally into the urinary bladder or urogenital sinus. Transverse sections of the kidney showed that the ureter originated from the cranial parts of the trunk kidney and coursed caudally close to the medial border of the kidney.

e. Morphology of the milkfish kidney

The left and right kidneys of the marine milkfish were fused medially (Fig. 13) and did not have lateral lobes nor head kidneys. The kidney corresponded to the region between the fourth and nineteenth vertebral bones. The cross-sectional profile of each kidney was triangular, and the fused kidneys assumed a triangular configuration with a cranial base and a caudal apex. Metamerism of kidney tissue was evidenced by dorsal grooves. The dorsal aorta was situated ventral to the vertebral column and supplied the kidney via several intercostal arteries. The posterior cardinal vein which coursed between the right and left kidneys cranially deviated to the right of the vertebral column. The ureter originated from the cranial parts of the kidney and coursed caudally to the urinary bladder or urogenital sinus. In its course along the kidney the ureter was completely embedded in the renal tissue.

B. Structural organization of the renal lobule

The kidneys of tilapia, blackbass and common carp consisted of 9-13 segments/mesomeres which were less pronounced in the fused caudal parts of the kidneys. In the catfish and milkfish evidence of similar segmentation/metamerism was the presence of grooves on the dorsal aspect of the kidneys. A renal segment (mesomere) (Fig. 14) was supplied by a branch from the intercostal artery

and occasionally by a direct branch from the dorsal aorta and drained by a short tributary of the posterior cardinal vein. It was drained by a ureteral duct and supplied by an intercostal vein in specimens with a portal system. In the absence of a portal system, the intercostal veins drained directly into the posterior cardinal vein.

The intercostal artery and vein and the primary branch of ureter ran alongside each other in the same plane. The secondary branch of the ureter and the renal branches of the intercostal vein entered the renal parenchyma in the same plane and got closer and closer as they went deeper into the kidney parenchyma. At the finer levels, the most consistent observation was that the collecting duct and arterioles were usually together (Fig. 15) and were occasionally accompanied by a venule. In the close vicinity of the duct and arteriole were renal corpuscles which were usually supplied by short afferents from branches of the renal artery. The greater majority of the venous profiles occurred alone and such profiles were largely surrounded by renal tubules. All the veins and venules surrounded mainly by tubular profiles were tributaries of the posterior cardinal vein which was also largely surrounded by renal tubules. The venules and veins accompanying the ducts and arterioles were traced to the intercostal vein and were therefore afferent veins.

The renal lobule (Fig. 15) is organized around the intrarenal artery, and the associated collecting duct and the occasional afferent vein. These structures thus formed the axis of the

C. The nephron

In the species studied the nephrons consisted of the renal corpuscles, the neck segments, the proximal tubule segments I & II, the distal segments and the collecting tubule-collecting duct system.

1. The renal corpuscle

The renal corpuscles were topographically located around the collecting ducts and terminal arterioles (Fig. 16) but some were occasionally encountered at the periphery of the kidney bulging into the abdominal coelom. In the blackbass and the tilapia renal corpuscles frequently occurred in clusters of three to five members (Fig. 18).

The renal corpuscle (Fig. 19) consisted of an anastomosing glomerular capillary network within a double walled glomerular (Bowman's) capsule. The glomerular capillaries originated from a short afferent arteriole, a branch of a terminal arteriole or intra-renal artery. There were usually 4-5 anastomosing capillary loops all of which joined to form the efferent arteriole which emerged from the renal corpuscle at the same point as the afferent arteriole. The point of entry of the afferent arteriole and exit of the efferent arteriole occurred at the vascular pole of the renal corpuscle. Almost directly opposite the vascular pole was the urinary pole, the point where the Bowman's space was continous with the renal tubular lumen. The wall of the Bowman's capsule consisted of an inner visceral epithelium made up of podocytes embracing

the fenestrated glomerular capillary endothelium (Fig. 20). The podocytes had a large cell body with trabeculae which had primary, secondary and tertiary processes. All these processes had pedicels (foot processes) which interdigitated extensively with each other leaving small gaps bridged by filtration slit membranes (Fig. 21) The outer layer of the Bowman's capsule, the parietal epithelium, consisted of squamous cells which were continous with the cuboidal cells of the neck segment. Between the visceral and parietal epithelia was the Bowman's space or urinary space and between the capillary loops were few mesangial cells.

2. The neck Segment

The neck was the shortest part of the nephron in all the teleost species examined. In tilapia the lumen of the neck segment was markedly constricted (Fig. 22a) and almost occluded by the cilia. This marked constriction of the lumen was not observed in the neck segments of the other species. This segment continued from the urinary pole of the renal corpuscle and had low cuboidal epithelium which increased in height towards the proximal segment I. The neck cells (Fig. 22b) had apical cilia in all the species studied but no brush border; however, few short luminal microvilli were present. Nuclei were centrally located and mitochondria were few and perinuclearly located. The cytoplasm of the cells showed alcian blue metachromasia and contained free ribosomes and

rough endoplasmic reticulum and few apical endocytic vesicles or tubules.

3. The proximal tubule

The proximal tubule was the longest part of the nephron in the fishes examined and in histological sections was represented by a relatively large number of tubular profiles. The tubule consisted of tall columnar epithelial cells with non-metachromatic cytoplasm, central nuclei and prominent apical microvilli which formed a distinct brush border (Fig. 23, 24). The brush border was alcian blue and periodic acid schiff (PAS) positive. The structural characteristics of the proximal tubule in all the fishes varied along its length and two different parts of the tubule namely the proximal segment I and II could be distinguished (Fig. 5, 25).

Rodlet cells were observed in the blackbass proximal tubule (Fig. 26a, b). These elongated ovoid cells were often in direct contact with the lumen of the tubule to which they opened through a pore. The cells were interposed between the columnar cells with which they formed apical junctional complexes (tight junctions). The cells had large basal nuclei and peripherally modified cytoplasm with fibrillar strands (Fig. 26a-d). The rest of the cytoplasm contained large ovoid crystalline structures (rodlets) with variable electron density, numerous vesicles and apically located mitochondria. These cells showed variation in relation to the typical proximal tubule cells. Some cells were in close contact with

the basal membrane of the proximal tubule; others were in contact with the apical membranes of the columnar proximal tubule cells and protruded into the tubule lumen through pores (Fig. 26c). The cells abutting the basement membrane of the proximal tubule had large nuclei and no crystalline inclusions (Fig. 26d), whereas those abutting the lumen had numerous crystalline inclusions (Fig. 26a-c). Presumably, therefore, the location of these cells varies with their age, the young cells being closer to the basement membrane of the tubule and the mature ones (which appeared to be detaching from the typical proximal tubule cells) being close to the luminal surface.

a. Proximal Segment I

The proximal segment I continued abruptly from the neck segment and was characterized by tall columnar cells with well developed luminal brush border (Fig. 24). The microvilli were long and slender and relatively more tightly packed than in the subsequent segments. Cilia were often seen in the tubule lumen. The characteristic proximal tubule columnar cell cytoplasm stained lightly with eosin and contained numerous large and small vesicles, tubules and many lysosomes below the brush border (Fig. 23). Mitochondria were numerous and located along the lateral cell membrane and around the nucleus. In the basal cytoplasm mitochondria were closely apposed to invaginations of the cell membrane which were extensively folded in the blackbass. Junctional

complexes consisting of tight junctions, and desmosomes characterized the the apical intercellular spaces (Fig. 27).

b. Proximal Segment II

In all the specimens studied the transition from the proximal segment I to proximal segment II was gradual and marked by reduction in the luminal diameter, the relative density and height of brush border microvilli and the relative number of endocytic vesicles in the cytoplasm of the tubule cells. In histological sections profiles of proximal segment II were more numerous than those of proximal segment I suggesting that the proximal segment II was the longest part of the proximal tubule (Fig. 5). The cells of the proximal segment II proper (Fig. 25) were columnar but lower than in proximal segment I and had relatively less well developed brush border, dense acidophilic cytoplasm and few vesicles. The apical cytoplasm contained granular and smooth endoplasmic reticulum, lysosomes and multivesicular bodies. Mitochondria were present in all the parts of the cytoplasm except the region immediately below the brush border. The cell membranes formed many perpendicularly oriented basal infoldings which contained mitochondria. Tight junctions and desmosomes were invariably present in the apical intercellular spaces.

4. Distal tubule

The distal tubule was located between the proximal tubule and the collecting tubule-collecting duct system and the transition from proximal tubule segment II to distal tubule was gradual. Profiles of the distal tubule were irregularly intermixed with those of the proximal segments and collecting tubules and ducts. The distal tubule consisted of low columnar cells with metachromatic cytoplasm, centrally located nuclei and few short microvilli (no brush border) (Fig. 28). Mitochondria were numerous and large and most of them were basal to the nucleus in the basal cell membrane infoldings which were very extensive (Fig. 29, 30). The cells were held together by junctional complexes comprising of long zonula occludens (Fig. 31) and small desmosomes (Fig. 29). Due to the low columnar cells the luminal and outer tubular diameters were small. The area of transition between the proximal tubule and distal tubule has in some species acquired unique characteristics such as cilia and has been described as an intermediate segment. However an intermediate segment was not observed in any of the species investigated. Frequently, the terminal part of the distal tubule described below as the collecting tubule, returned to the vascular pole of its parent renal corpuscle. In the catfish, principal and intercalated/dark cells were observed in the late distal nephron (Fig. 32a, b).

5. The collecting tubule-collecting duct system

The collecting tubule-collecting duct system was well developed in the freshwater species studied. The transition from the distal segment to the collecting tubule occurred gradually. The low columnar epithelium of the distal tubule gradually became surrounded by a discontinuous layer of smooth muscle cells to become the collecting tubule. The collecting tubule cells had metachromatic cytoplasm and basally located nuclei. The tubules subsequently joined to form small collecting ducts (Fig. 33) with more muscular layers and fibrous connective tissue elements. Both the muscular and connective tissue elements increased distally such that the ureteral ducts (not part of collecting tubule-collecting duct system) were surrounded by a thick fibromuscular sheath (Fig. 16, 33) which contained capillaries. The collecting ducts were usually accompanied by arterioles which supplied renal corpuscles with short afferent arterioles. Cells of the collecting ducts were columnar with few short microvilli, central nuclei and numerous apical and basal mitochondria in the metachromatic cytoplasm. The luminal cell border had alcian blue positive deposits and granules containing stainable material were present in the apical cytoplasm. Cell membrane infoldings were found in the basal cytoplasm.

In the common carp the collecting duct had relatively taller columnar epithelial cells and much thicker connective tissue sheath compared to the rest of the species studied. The

blackbass collecting tubule-collecting duct system was extensively branched whereas that of the marine milkfish was least branched.

D. Juxtaglomerular cells

The juxtaglomerular apparatus was poorly developed in all the fish studied. In the juxtaglomerular region smooth muscle cells on the walls of arterioles stained intensely with Gomori's trichrome, Harris's hematoxylin and alcian blue. The intensely staining cells occurred predominantly on the walls of the afferent and terminal arterioles but they were also seen on the walls of efferent and intermediate arterioles (Fig. 34a). These cells are modified smooth muscle cells termed juxtaglomerular cells and they are known to secrete renin in higher vertebrates. The juxtaglomerular cells were observed in the five species studied. Under the electron microscope these cells were demonstrated mainly in the tunica media of arterioles or small arteries (Fig. 34b, c) and contained large electron lucent nucleus, numerous granules, well developed granular endoplasmic reticulum and Golgi apparatus.

E. Renal interstitial tissue

Among the fishes studied the kidneys of all, except the percoid, species contained abundant peritubular tissue (Fig. 35). This tissue contained a wide variety of cells which included mainly haemopoietic, lymphoid pigment and interrenal cells (Fig. 36)

F. Interrenal gland (Head kidney)

The head kidney contains the interrenal gland which is the adrenal gland homologue in fishes. In the fishes studied it appeared as an irregular polyhedron between the last gill slit and the fifth vertebral bone. The interrenal gland cells were found surrounding small or medium sized branches of the posterior cardinal vein (Fig. 37 & 38) and formed into cords which were widely dispersed in the head kidney. The rest of the areas of the gland were occupied by lymphoid and haemopoietic tissue, phagocytic cells and numerous mast cells.

G. The Ureter

The large collecting ducts joined to form secondary branches of the ureter which in turn drained into primary branches which opened into the ureter at varying intervals. These tributaries of the ureter were characterized by columnar cells with metachromatic cytoplasm and basal nuclei (Fig. 39). They were surrounded by a thick fibromuscular coat which had a blood vascular supply. The ureter increased in diameter caudally as it received primary ureteral branches and this increase was characterized by increase in the calibre of the ureteral wall. In all the species studied the epithelium of the ureter did not vary along its length and was low columnar in blackbass, tall columnar in tilapia and catfish, pseudostratified columnar in milkfish and

pseudostratified columnar with goblet cells in common carp (Fig. 40 & 41)). The luminal surface of the ureteral epithelium had alcian blue positive deposits.

II. QUANTITATIVE OBSERVATIONS

A. Body weight and surface area and kidney volume

The mean (± S.D.) body weight, body surface area, kidney volume, kidney volume per gram body weight and kidney volume per square centimeter of body surface area for the individual species are shown in Table 2. The blackbass was the largest fish with a mean body weight of 442.6 ± 119.94 g and the milkfish was the smallest with a mean body weight of 17.86 ± 6.17 g. The mean body surface area ranged from 60.90 ± 14.17 cm^2 in the milkfish to 526.05 ± 173.39 cm^2 in the common carp. The mean kidney volume ranged from 42.00 ± 13.04 mm^3 in the milkfish to 1854 ± 1021.5 mm^3 in the common carp. The kidney volume (Vk) showed a direct relationship with the body weight (W) and the correlation coefficient (r) and the allometric equation for this relationship were 0.96 and $Vk = 0.51W^{0.977}$ respectively. The mean kidney volume per gram body weight ranged from 2.22 ± 0.07 mm^3/g in the blackbass to 6.13 ± 0.71 mm^3/g in the catfish whereas the kidney volume per square centimeter of body surface area ranged from 0.68 ± 0.006 mm^3/cm^2 in the milkfish to 3.35 ± 0.72 mm^3/cm^2 in the common carp. There is apparently no clear relationship between either the values

for kidney volume per gram body weight or those for kidney volume per square centimeter of body surface area and size of the fish.

B. Volume proportions of the components of the kidney

1. The volume densities and absolute volumes of the main components of the kidney

Table 3 shows the mean (± S.D.) volume proportions and absolute volumes of the main components of the kidney namely the uriniferous tissue, blood vessels larger than capillaries, ureter and ureteral ducts, intrarenal haemopoietic tissue and connective tissue. The mean percentage volume proportion of the uriniferous tissue was highest in the tilapia (72.52 ± 1.61%) and lowest in the milkfish (36.23 ± 0.99%). The absolute volume of uriniferous tissue (Vut) was well correlated with body weight (W) and the correlation coefficient (r) for this relationship was 0.97. This relationship was fitted by the allometric model: $Vut = 0.042W^{1.077}$.

In all the species the volume proportions of blood vessels larger than capillaries were greater than 20% of the total kidney volume. The values were lowest in the common carp (21.93 ± 1.36%) and highest in the blackbass (24.88 ±1 21%). The absolute volume of the total vascular space (Vtvs) (blood vessels and capillaries) was well correlated with body weight and the correlation coefficient and allometric equation

relating these parameters were, r = 0.96 and Vtvs = $1.197W^{1.025}$ respectively.

Ureter and ureteral ducts were best developed in the blackbass in which they formed 8.20 ± 0.41% of the total kidney volume and least developed in the catfish in which they occupied 1.59 ± 0.18% of the kidney volume.

Intrarenal haemopoietic tissue was found in all the species studied except in the percoid species (tilapia and blackbass). The mean volume proportion of haemopoietic tissue was highest in the milkfish (34.22 ± 1.11%), but in the ostariophysian teleosts namely the catfish and the common carp the haemopoietic tissue formed 28.73 ± 1.64% and 28.90 ± 2.01% of the total kidney volume respectively. The connective tissue formed 1-4% of the total kidney volume and the mean values ranged from 1.37 ± 0.17% in the milkfish to 3.60 ± 0.74 % in the common carp.

2. The volume proportions of the components of the uriniferous tissue expressed in relation to renal parenchyma

Table 4 shows the mean (± S. D.) values for the volume proportions of the components of the uriniferous tissue (i.e parts of the nephron, collecting tubule-collecting duct system and the peritubular capillaries). The mean volume proportions of the renal corpuscles differed considerably among the species. The percoid teleosts (tilapia and blackbass) had high volume proportion of renal corpuscles, and the mean values

were 4.06 ± 0.51% in tilapia and 5.74 ± 0.29 % in blackbass. The ostariophysian teleosts had relatively lower mean values (i.e. 3.55 ± 0.95% in the carp and 3.39 ± 0.48% in the catfish); however, the marine milkfish (belonging to the family Salmonidae) with a mean proportion of 2.11 ± 0.38% had the lowest proportion of renal corpuscles among the species. The absolute volumes of the renal corpuscles (Vrc) were well correlated with body weight and the correlation coefficient (r) was 0.94. The allometric equation relating these parameters was $Vrc = 0.0038W^{1.536}$.

The neck segment in all the species studied formed less than 1% of the renal parenchyma. The mean volume proportion was lowest in the milkfish and highest in common carp the values being 0.18 ± 0.07% and 0.95 ± 0.29% respectively.

The proximal tubule, which was bisegmental, formed the largest proportion of renal parenchyma in all the species. In the freshwater teleosts the mean volume proportions ranged from 58.96 ± 1.87% in the blackbass to 62.8 ± 2.21% in the tilapia and in the marine milkfish the proximal tubule had a much higher volume proportion and formed 73.74 ± 2.82% of the parenchyma.

The mean volume proportions of the distal segment in the freshwater teleosts and ranged from 15.51 ± 1.25% in the common carp to 18.15 ± 191% in the catfish. In the milkfish the distal tubule constituted only 7.83 ± 1.29% of the renal parenchyma.

Like the distal tubule, the collecting tubule-collecting duct system constituted a larger proportion of the renal parenchyma in freshwater fish than in the marine fish. In the freshwater teleosts investigated the mean values ranged from 5.10 ± 1.76% in the tilapia to 6.55 ± 1.16%.in the catfish. The milkfish collecting tubule collecting duct system formed only 3.5 ± 1.04% of the parenchyma.

The mean volume proportions of capillaries in the teleost kidney were relatively high in all the fishes investigated. The mean values were lowest in tilapia in which the capillaries formed 9.96 ± 1.4% of the renal parenchyma and highest in common carp in which they formed 14.57 ± 0.26% of the parenchymal volume.

3. The volume proportions of the uriniferous tissue components expressed in relation to the kidney as a whole

Table 5 shows the mean (± S. D.) volume proportions of the uriniferous tissue components expressed in relation to the volume of the kidney as a whole. The mean volume proportions of renal corpuscles ranged from 3.7 ± 0.18% in the blackbass to 0.76 ± 0.12% in the milkfish. Among the freshwater teleosts the mean values for the proportions of renal corpuscles were relatively higher in the percoid species (i.e. 3.7 ± 0.18% in the blackbass and 2.94 ± 0.38% in the tilapia) than in the ostariophysian fish (i.e. 1.47 ± 0.39% in the common carp and 1.44 ± 0.20% in the catfish) and the

difference between the mean absolute values in the two groups was significant.

The neck segment formed a relatively small volume proportion of the kidney. The highest was 0.43 ± 0.24% in the blackbass and the lowest was 0.07 ± 0.03% in the milkfish.

The proximal tubule constituted a higher percentage of the kidney in the percoid fish (45.50 ± 1.60% in tilapia and 37.51 ± 1.19% in the blackbass). In the ostariophysian and salmonid teleosts, whose kidneys had abundant intrarenal haemopoietic tissue, the proximal tubule comprised 24.48 ± 0.73%-26.75 ± 1.02% of the kidney.

The volume proportion of the distal tubule in the whole kidney ranged from 2.84 ± 0.47% to 12.80 ± 2.43% in the milkfish and the tilapia respectively. It was high in the percoid teleosts and medium in the ostariophysian teleosts (whose species from both groups were studied were freshwater).

The values of the volume proportions of the collecting tubule-collecting duct system showed similar trends as for the distal tubule. The percoid teleost had the highest proportion (3.70 ± 1.28% in tilapia and 3.55 ± 0.81% in blackbass), the ostariophysian teleosts intermediate values (2.49 ± 0.30% in common carp and 2.80 ± 0.49% in catfish) and the marine milkfish (salmonid) the lowest value (1.27 ± 0.38%).

The proportion of the capillaries ranged from 4.52 ± 0.41% in the milkfish to 8.50 ± 1.02% in the blackbass.

C. Comparison of renal parameters in groups of fish with contrasting characteristics

Table 6 shows the comparison of the mean (± S.D.)values for kidney volume per gram body weight and the volume proportions of the renal corpuscles, uriniferous tissue, tubules and total vascular space in groups of fish with contrasting characteristics using the Student's t-test. These parameters were compared in: 1, percoid fish and ostariophysian fish; 2, fish with haemopoietic tissue and fish without haemopoietic tissue; 3, freshwater fish and marine fish.

The kidneys were significantly larger in the ostariophysian fish than in the percoid fish, $P<0.001$. It is also apparent that fish with abundant peritubular haemopoietic tissue had relatively larger kidneys than those without the haemopoietic tissue, $P<0.02$. However, the kidney volume was not significantly different between freshwater and marine fish.

The volume proportions of renal corpuscles was relatively higher in the percoid fish than in the ostariophysian fish, $P<0.001$, and in fish without peritubular haemopoietic tissue compared to those with the haemopoietic tissue, $P<0.001$. In addition the freshwater fish had relatively higher volume proportions of renal corpuscles than the marine fish, $P<0.02$.

The volume proportions of the uriniferous tissue were significantly higher in percoid fish than in the ostariophysian fish, $P<0.001$ and in fish without peritubular haemopoietic tissue ($P<0.001$) than in those with the haemopoietic tissue.

There was no significant difference between the volume proportions of the renal tubules in freshwater and in marine fish.

The volume proportion of the total vascular space were relatively higher in the percoid fish than in the ostariophysian fish, $P<0.02$, and in fish without peritubular haemopoietic tissue than fish with the haemopoietic tissue, $P<0.001$. However there was no significant difference in the volume proportions of the total vascular space between the freshwater and marine fish.

D. Diameters of the renal corpuscle, glomerulus and proximal and distal tubules

The mean diameters of renal corpuscles ranged from 37.44 μm in the milkfish to 69. 32 μm in the blackbass (Table 7). It varied directly with body size but not proportionately.

Glomerular diameter was largest in the tilapia (52.73 ± 8.36 μm) and smallest in the milkfish (31.07 ± 6.48 μm). The glomerulus formed 68-79% of the renal corpuscles in all the species studied. The proximal tubule was generally wider than the distal tubule in all the species studied and ranged from 37.50 ± 11.10 μm in blackbass to 48.87 ± 14.60 μm in common carp. The distal tubule diameter in turn ranged from 26.43 ± 7.90 μm in common carp to 32.43 ± 7.03 μm in tilapia.

CHAPTER 5

DISCUSSION

1. COMMENTS ON THE METHODS

A. The sample of the teleosts

Twenty seven male and female teleost specimens from five species representing the orders Perciformes, Cypriniformes, Siluriformes and Salmoniformes (Table 1) were examined in this study. The fish were caught at random from their habitats, and those studied were selected on the basis of maturity of the gonads. The size at maturity varied greatly especially in the tilapia which shows precocious breeding (Fryer & Iles, 1972). A specimen could not be considered immature merely on the basis of its size because some relatively small specimens were found to have fully developed and functional gonads. Maturity in the catfish is reached at 13 cm total body length (Clay, 1977) and all the catfish specimens investigated in this study were more than 13 cm in length and had mature gonads. In all the other species the maturity of the fish was based only on the examination of gonads.

Among the male and female specimens studied no sexual dimorphism was observed. However, sexual dimorphism in the fish kidney has been reported in the stickleback, *Gasterosteus aculeatus* (Wendelaar-Bonga, 1973, 1976; Hentschel & Meyer, 1979;) and in the African lungfish, *Protopterus dolloi* (Codier, 1937). Hentschel (1979) reported that there is no direct

anatomical connection between the kidney and testis in the stickleback as in the pars sexualis of male elasmobranchs, amphibians and reptiles. In species exhibiting sexual dimorphism different sampling methods would have been necessary for the kidneys of males and females.

Among the fishes there are 18,007 teleost species (about 96% of known living fishes) belonging to 31 orders, 415 families and 3869 genera (Nelson, 1970). Thus the five teleost species examined in this study represent only a small sample of the entire population of teleosts. On the other hand comprehensive quantitative data on the teleost kidney is quite scarce, and thus the preliminary observations made in this study could in future be expanded to give a comprehensive knowledge of the structural-functional relationships of the teleost kidney.

B. The influence of fixation, volumetry, tissue processing and sampling on the qualitative and quantitative structural characteristics of the teleostean kidney

1. Fixation

Tissue fixation may be effected either by perfusion or immersion of the tissue in a suitable fixative. Previous assessment of the advantages of immersion and perfusion fixation in the kidneys of rats (Maunsbach, 1966) and in those of birds (Warui, 1985) showed that perfusion fixation was advantageous when compared to immersion fixation because

fixative infused through the vasculature disperses evenly throughout the tissues, and thus fixes the whole organ uniformly. In addition, the fixative probably also passes the glomerular filter and fixes the tubules and ducts from the inside. It is likely that lack of fixation from the inside as would be expected in immersion fixation leads to the collapse of the proximal tubules and the widening of the extracellular spaces commonly observed in immersed kidney tissues (Fig. 42). The changes observed in immersed kidneys are not acceptable in quantitative studies because they contribute errors in the estimation of the proportions of the components affected by the fixation artefacts. In this study the teleost kidneys were therefore fixed by perfusion to ensure adequate fixation of all the tissues components.

Previous studies have reported the fixation of the teleost kidney via the dorsal aorta after decapitation (Marshall, 1930; Elger *et al* , 1984b), the bulbus arteriosus (Hinton, 1975; Hentschel, 1977a, 1978) and via the posterior cardinal vein (Ottosen, 1978). Perfusion fixation via the bulbus arteriosus was found to be the most suitable because the kidney as a whole is fixed evenly by infusion of the entire arterial system (Fig. 43). Decapitation to expose the dorsal aorta usually destroys the head kidneys and their blood vessels, and fixation through the caudal vein results in collapse of proximal tubule and widening of extracellular space (Fig. 44). The perfusion of blood vessels with saline prior to perfusion fixation creates an artefact (i.e blood vessels without blood cells) but at the

same time lessens the development of other fixation artefacts which may result from the possible reaction between haemoglobin and the fixative.

Shrinkage due to fixation with 2.5% glutaraldehyde in 0.15 M phosphate buffer was not assessed, but was assumed to be minimal because the fixative has a low osmolarity. Thus, the volume of the fixed kidneys was considered to be similar to the volume of the fresh kidneys and formed the basis for calculating the absolute volume of each of the renal components. This absolute volume was considered to represent the actual volume of the component before fixation.

2. Volumetry

The measurement of kidney volume by the water displacement method (Scherle, 1970) was necessary because of the irregular form of the teleostean kidney. In measuring the kidney volume the kidney was immersed in fixative and it was assumed that the specific gravity of the fixative was close to that of water. This could be a source of error; however, the error is likely to be small because the difference in kidney volume obtained by displacement of fixative and displacement of water was negligible. The error that could have resulted from determining the volume of wet kidneys was reduced by mopping the kidney surface with adsorbent papers.

The inclusion of extrarenal tissue such as the corpuscles of stannius, fat and the peri-renal connective tissue or the loss of renal tissue during removal of the kidney could have

introduced errors in the measured total kidney volume. However, these errors were minimized by trimming the kidney free off all extrarenal tissue before measuring the volume and removing the kidney as intact as possible.

3. Tissue processing

Processing of tissues for paraffin sections requires dehydration with ethanol and infiltration of the tissues with molten wax (Temp. 57°C). These procedures cause considerable shrinkage of tissues in contrast with resin embedding which only causes minimal shrinkage (Weibel & Knight, 1964). Weibel (1979) suggested that in morphometric studies, shrinkage resulting from fixation and processing procedures should either be controlled or assessed. As pointed out by Maunsbach (1966) and Warui (1985) the shrinkage during paraffin embedding and sectioning may affect the structural components of the teleostean kidney in a similar manner.

The Gomori's trichrome, Harris's haematoxylin and alcian blue staining technique used in this study was appropriate because it facilitated the identification of renal tubular components on the basis of the staining reactions, and this together with the histological and ultrastructural characteristics of the components were completely adequate for the identification of the parts of the renal tubules. Alcian blue was first used with the picric acid stain (PAS) by Mowry & Morard, 1957) to demonstrate acid muco-polysaccharides in

the kidney. Subsequently the suitability of the PAS method for simultaneous demonstration of glycogen, neutral glycoproteins, sialylated glycoconjugates and sulphated glycoconjugates in fish kidneys has been reported (Hentschel, 1979). Using the same method, Hentschel & Finkdenstadt (1980) were able to distinguish most of the segments of the renal tubule in the rainbow trout, *Salmo gairdneri*. In the present study the combination of alcian blue, Gomori's trichome and Harris's haemotoxylin staining has been found to be suitable for distinguishing the renal components in fish kidneys. The method has an added advantage since Gomoris trichrome also stains the muscle cells, the juxtaglomerular cells and connective tissue components in the walls of the ducts, ureter and blood vessels.

Edwards (1928) observed that maceration of vascular casts may not be necessary in studying renal vasculature in fish. Anderson & Anderson (1976) and Hentschel (1977b, 1990) used vascular casting with and without maceration and obtained good results. In this study serial sectioning and vascular casting were adequate in studying renal vascularisation in teleosts.

4. Tissue sampling

The stratified random sampling method was used to sample the kidney because the elongated form of the teleostean kidney necessitated taking samples at predetermined intervals along the whole kidney. The teleostean kidney is not characterized

by zonation as seen in tetrapods, dipnoans, elasmobranchs and lampreys. Zonation occurs due to a preferential arrangement of tissue components and differences in the distribution of the structural components; and thus special considerations, especially in the sampling techniques and type of grid to be used are necessary. Transverse sections of each kidney examined in this study showed all the renal components as one phase. The adequate sample of tissue sections for morphometry was based on a pilot study in which cumulative mean plots showed that analysis of fifteen (first level of sampling) and five (second level of sampling) or more sections in each case was required to determine the volume proportion of each renal component with a standard error below ± 5% of the mean.

Point counting directly on a section under a microscope was preferred to counting on microphotographs overlaid with a graticule because some of the renal components were identified on the basis of the colour reaction. Colour could not be appreciated on black and white prints and colour prints would have been very expensive to produce; moreover, the sections were usually small enough to be completely analysed by about the tenth field.

The randomness and representativeness of the sample was strictly observed because it is impractical to quantitatively analyse a whole kidney section by section. Furthermore, lack of randomness would make the sample unrepresentative and render the quantitative data useless since stereological

principles are based on randomness of composition of the tissue and the sample (Weibel, 1979).

C. Statistical methods

In the statistical analysis of the quantitative data the mean values and standard deviations were computed for some of the parameters and compared with those reported for other fish and tetrapods. By comparing the mean values of the parameters obtained in this study and those of other vertebrates it was possible to demonstrate the significant quantitative differences between renal structure in fishes from the same class, and also between teleostean kidneys and those of other vertebrates. Correlation coefficients were calculated to show the relationships between the renal parameters and the body weight of the fish and allometric equations for the relationships given for purposes of estimating renal parameters in fishes of known body weight.

The Student's t-test was used to determine the level of significance of the differences between the mean values of renal parameters of fish with contrasting characteristics.

II. THE QUALITATIVE STRUCTURAL CHARACTERISTICS OF THE TELEOST KIDNEY

A. The gross Anatomical characteristics

The macroscopic observations made on the teleost kidneys in this study were in many ways similar to those previously reported by other investigators. The elongated form, the retroperitoneal position, and the differences in the extent of fusion of the right and left kidneys noted in this study have previously been reported (Edwards, 1928; Nash, 1931; Ogawa, 1962; Hickman & Trump, 1969). In the tetrapods, the normal left and right kidneys are separate, whereas in teleosts there is usually some degree of fusion. The kidneys of the teleosts studied fell into class I (complete fusion) and class III (fusion of caudal one third) described by Ogawa (1962). It appears therefore that among the fishes so far studied the only kidneys which resemble those of normal tetrapods by being unfused are those of Latimeria and skates (Hentschel & Elger, 1987).

The correlation of kidney shape with body shape has been observed in the skate and in *Lophius piscatorius* (Hentschel, 1988) in which the flat shape of the kidneys was associated with the extreme dorso-ventral compression of the whole body. In this study the elongated form of the teleostean kidney is probably only partially explained by the elongated form of the teleostean body since other vertebrates with elongated body forms for, example reptiles, have relatively compact kidneys (Davies, Schimidt-Nielsen & Stolte, 1976;

Dantzler & Braun, 1980). The kidneys of the species studied occupied a region in the coelomic cavity corresponding to 60-65% of the vertebral column length and more than 85% of the length of the dorsal part of the abdominal cavity. Anderson & Anderson (1976) have previously reported that the trout mesonephros occupies about 80% of the length of the dorsal part of the body cavity. The elongated form of the teleostean kidney can probably be better explained in terms of the embryological development of the fish ophisthonephros. In vertebrate embryology, the renal, gonadal and interrenal tissues derive in varying proportions from mesodermal blocks, known as nephrogenic blastema which could extend from the level of the second postotic somite to some distance behind the anus (Chester-Jones, 1987). Among the three embryonic kidneys, the mesonephros corresponds to the longest region of the nephrogenic cord (somites 9-26) while the pronephros and metanephros occupy somites 7-14 and 26-28 respectively. In teleosts, for example *Tilapia zilli*, (Khalil & Agamy, 1981) the mesonephros lies behind the pronephric region from the fifth to eighteenth body segment. The observations made in this study agree with these fundamental facts of renal embryology. The trunk and tail kidney, both constituting the mesonephros, occupied the region corresponding to the fifth and nineteenth vertebrae and the head kidney occupied the region behind the last gill slit to the fifth vertebra, a region that is equated to the pronephros.

The head kidney, which increases the kidney weight, is unique to fish though it has been reported absent in some species. Among the species investigated in this study the catfish and the milkfish did not have a head kidney; the catfish, however, had lateral renal lobes which were similar in structure to the head kidney. Previous workers have reported the presence of renal tissue, lymphoid tissue with pigment and haemopoietic cells, thyroid follicles, intramesonephric gland and tubule corpuscles and adrenomelanogenic tissue in the head kidney (Baker-Cohen, 1959; Sharma, 1968; Hickman & Trump, 1969; Shrivastava, 1969; Peter, 1970; Anderson *et al.*, 1983);. The head kidney has been described by several authors to contain interrenal gland or the adrenal homologue (AH) in fish (Haider & Pandey, 1980; Battacharyya *et al.*, 1981; Chester-Jones 1981, 1987;). The head kidneys examined in the present study contained tissue resembling that of the adrenal gland (i.e. cortical and chromaffin cells), lymphoreticular tissue, giant macrophages and pigment cells.

The external segmentation (metamerism) of the renal tissue observed in the teleostean kidneys has been reported in other fish, Marshall (1928), and suggests that the fish kidney consists of repeating units of renal tissue. The renal mesomere has apparently only been described in detail in the dogfish, (*Scyliorhinus caniculus*) in which the mesomere has been considered to represent a renal lobule (Hentschel, 1991). Similarly the grossly visible repeating units of renal tissue in

reptilian kidneys have been described as renal lobules (von-Mollendorf, 1930; Davies & Schmidt-Nielsen, 1967). In mammals such as the bovine the grossly visible divisions (reniculi) of the kidney are termed renal lobes because they consist of several lobules. In the present study the mesomere was considered to be the renal lobe. On the basis of the presence or absence of afferent veins to the kidney two types of renal lobules have been described in this study. In one case the lobule is centered around an artery, collecting duct and an afferent vein and in the other case it is centered around an artery and collecting duct. This arrangement of the components of the renal lobule described in this study differs markedly from that of elasmobranchs (Hentschel, 1991), reptiles (Von Mollendorf, 1930; Davies & Schmidt-Nielsen, 1967), birds (Sperber, 1960; Poulson, 1965; King & Mclelland, 1985) and mammals (Kaissling & Kriz, 1979) due to the location of the axes and peripheral limits of the lobules. The axes and peripheral limits of the lobule have not been defined in the elasmobranchs, but in the reptiles the tributaries of the branches of the renal vein and branches of the renal artery lie in the axis and the branches of the portal vein and collecting ducts mark the peripheral extent of the lobule. In birds the intralobular efferent vein and the intralobular artery to the lobule lie in the axis and the collecting ducts and perilobular afferent veins are at the periphery. In mammals the collecting ducts are axial and the vessels peripheral. Kaissling & Kriz (1979) observed that the actual lobule in mammalian kidneys

cannot be easily delimited in histological sections and that the concept most suitable for explaining the architecture and functional morphology of the kidney and that which is most appropriate for comparative anatomical descriptions should be adopted. The lobule centered about a vascular axis, therefore, appears to be a suitable model for explaining renal architecture in teleosts.

Previous reports on renal vasculature in fish (Hickman & Trump, 1969; Anderson & Anderson, 1976; Elger *et al.*, 1984b) indicate that the arterial supply is by branches of segmental arteries or direct renal arteries. The observations made in this study were consistent with these reports. Hickman & Trump (1969) have reported that the efferent arterioles enter the peritubular capillary bed immediately after emerging from the renal corpuscle, whereas Elger *et al.*, (1984b) noted that the efferent arterioles entered the muscular sheaths of the collecting ducts in the rainbow trout (*Salmo gairdneri*). Examination of serial sections in the present study showed that the efferent arteriole entered the peritubular capillary bed immediately after emerging from the renal corpuscle.

Observations on the venous system in this study showed that the main efferent vein draining the kidney was the posterior cardinal vein as reported earlier by Marshall (1928), Hickman & Trump (1969) and Hentschel & Elger (1987). However, conflicting reports exist on the presence or absence of the afferent (portal) veins of the teleost kidney. Moore (1933) studied freshwater pikes and perches and reported the

presence of a partial portal system comprising of the intercostal veins, but in the review of observations on the structure of the kidneys of more than 100 teleost fish (Hickman & Trump, 1969) most freshwater species lack a venous afferent system. On the other hand, Hentschel & Elger (1987) reported that all teleosts possess a renal portal system. In the present investigation the renal portal system was absent in tilapia, but present in the catfish, common carp, milkfish and blackbass. The renal portal system is well developed in fishes and amphibians and regresses in reptiles and is absent in the mammals (Beyenbach, 1985). The absence of the renal portal system noted in the tilapia is characteristic of kidneys of Myxini, Petromyzontia, Polyteriformes and some other freshwater teleosts; thus, the kidneys of these species resemble those of mammals (Hentschel & Elger, 1987). These observations make it difficult to draw correct general statements describing the structure of the renal venous system of teleost and lower vertebrates.

Many authors have attempted to explain the functional significance of a well developed venous afferent (portal) system in fish kidneys. Hoar (1966) suggested that the portal system permits renal function independent of glomerular blood flow. In addition, Springthorpe (1971) suggested that the well developed renal portal system in fish and other lower vertebrates was due to their low blood pressure and since nephron function and efficiency of excretion and

osmoregulation depend on a good supply of blood to the peritubular capillaries, the portal system serves to increase the blood flow to the peritubular region. Beyenbach (1985) further suggested that the portal system ensures renal tubular function in periods of decreased renal arterial flow during glomerular antidiuresis, and thus supported the suggestion by Hoar (1966). Furthermore, venous blood may still possess adequate nutrients owing to the low metabolic rates in the poikilotherms and may be a source of nutrients to the fish kidney. This suggestion is supported by the existence of aglomerular fish kidneys (Nash, 1931; Grafflin, 1937; Hickman & Trump, 1969; Dobbs *et al.*, 1974; Hentschel & Elger, 1989) which do not have an arterial supply, and are presumably supplied with nutrients by the afferent veins. The presence of the portal system in all the species studied except the tilapia highlights the importance of the system in renal function of teleosts. Moreover, the greater proportion of the renal vasculature in all the species studied comprised of veins.

The ureter in fish is a mesonephric duct and may run along the lateral border of the kidney or within the renal parenchyma depending on species (Edwards, 1928; Hickman & Trump, 1969). Similar observations were made in this study. The course of the ureter along the whole length of the kidney noted in this study, is similar to that described in birds (King & Maclelland, 1985) and amphibians (Huber, 1917), but differs from that of mammals. It is also similar to the course of the mesonephric duct along the developing mesonephros. In

contrast this arrangement differs from that in the elasmobranchs in which several secondary ureters have been observed adjacent to the mesial renal tissue (Hentschel, 1991).

B. The Microscopic characteristics

The detailed light microscopic structure and ultrastructure of the teleost kidney, especially the nephron and the collecting and ureteral duct system have recently been reviewed and common principles for nomenclature of the tubule segments have been established (Hickman &Trump, 1969; Hentschel & Elger, 1987). Moreover, these reviews indicate that the species differences in the segmentation of the renal tubule are quite remarkable and have apparently led to the proposals by Anderson & Loewen (1975) and Hentschel & Elger (1987) that general remarks on the segmentation of the renal tubule should be carefully evaluated because renal structure in one teleost is not necessarily similar to that of other teleosts.

In the present study observations on the kidney of tilapia (*O. niloticus*) showed a nephron consisting of a renal corpuscle, neck segment, bisegmental proximal tubule and distal tubule draining into a collecting tubule-collecting duct system which is consistent with reports by Jirge (1971) and Hwang & Wu (1987) on the kidney of another tilapid *Oreochromis mossambicus*. The ultrastructure reported in this

study conforms with that reported for related teleosts (Hickman & Trump, 1969; Hentschel & Elger, 1987).

Few reports are available on the renal structure in species of the genus micropterus. Moore (1933) studied the kidney of the small mouthed bass (*Micropterus dolomieu*) and reported the presence of compound renal corpuscles supplying many nephrons and Hickman & Trump (1969) reported that such renal corpuscles do not occur in the large mouthed bass (blackbass). Observations on the blackbass kidney in the current investigation showed clusters of renal corpuscles consisting of as many as five members, and each renal corpuscle had its own renal tubule and afferent arteriole. Furthermore, it has been shown in this study that the other components of the nephron are the neck segment, the bisegmental proximal tubule and a distal tubule opening into the collecting tubule-duct system.

The ultrastructural features of the blackbass nephronal segments were basically similar to those of other vertebrates. However, unique cells were seen in the proximal tubule of this species. Similar cells have previously been described as parasites in tissues of cyclostomes, elasmobranchs, teleosts and frogs (Thelohan, 1892). Due to the thick wall and sporozoite-like inclusions Languese (1906) named them *Rhabdospora thelohani*. Subsequent authors, probably because of coming across the cells incidentally, associated their function with the organ they were studying. Consequently the cell has been termed osmoregulatory, glandular, blood

granulocyte, mucous and endocrine cell (Barber & Westermann, 1986). Maina, 1990 described the cells in *Oreochromis alcalicus* the only completely aquatic ureotelic teleost (Randall *et al* , 1989; Wood *et al.*, 1989) and presumed their function to be urea secretion. Having previously been called a variety of names such as pear-shaped cell, feliaceous cell and rod cell, the cell is currently called a rodlet cell (Bullock, 1963).

In their recent paper Barber and Westermann (1986) showed that in teleosts the DNA of the rodlet cell is similar to the DNA of teleost cells whereas that of the rods was different. They concluded that the rodlet cell was of teleost origin and that the rods were parasitic. Furthermore the thick peripheral wall of the cell has been shown to be actin and myosin (Desser & Lester, 1975; Barber & Westermann, 1986). Desser & Lester (1975) showed immature and mature stages of the cell and suggested that the inlusions (rods) are synthesized by the cell and the muscular wall eventually squeezes them through the thin apical region. These authors suggested that the cells eventually slough off to be replaced by new cells from below. Observations made in this study also suggest continous maturation of the cells from the base to the apex of the proximal tubule. This is supported by the observation that the cells in contact with the base of the tubule had large nuclei but no apical pores or crystalline inclusions (rodlets) whereas those in contact with the tubule lumen had apical pores, many rodlets and appeared to be

detaching from the adjacent cells. The wide intercellular spaces between the rodlet cells and adjacent proximal tubule cells observed in this study may be an indication that the cell is contracting or sloughing off. In addition, the occurrence of cells without rodlets observed in this study supports the previous suggestions that rodlet cells are teleost cells with a wide distribution (Mattey *et al.*, 1979). However, the absence of rodlets in a cell could be due to the random nature of sectioning whereby it is possible to miss the rods. The occurrence of these cells in the gills, kidney and the gastrointestinal tract of teleosts suggests that these cells (if they are normal) may have some osmoregulatory function.

In view of the recent demonstration that the DNA of the rods (parasites) is different from that of the rodlet cells (Barber & Westermann, 1986) it is possible that the unique structure of the rodlet cells is a result of tissue changes on some specific teleost cell which is selectively invaded or infected by the rodlets. The striking feature about these cells is their occurrence in a variety of teleost tissues (gills, gastrointestinal tract, kidney, heart and skin) and in teleosts in diverse habitats. This has been explained on the basis that rodlet cells are normal cells with a wide distribution in different tissues (Morrison & Odesse, 1978) or infected tissue cell (Barber & Westermann, 1986).

Both the tilapia and the blackbass belong to the group Percomorpha which is the most recent group of fish that has evolved (Hentschel & Elger, 1987). Percomorpha is also the

largest and most varied of all fish orders with about 1257 genera and 6880 species. In contrast to the general assumption that all fish kidneys contain haemopoietic tissue (Hickman & Trump, 1969; Ottosen, 1978), the percoid fish examined here do not have profuse peritubular haemopoietic tissue, and thus they resemble the reptilian, avian and mammalian kidneys. The absence of the haemopoietic, lymphoid or intertubular tissue observed in tilapia, *O. niloticus*, in this study has been reported for a related tilapia species *Tilapia zilli* (Khalil & Agamy, 1981). Furthermore, the absence of nephrons in the head kidney of a tilapia species, *Saratherodon mossambicus* has been previously reported (Agarwal & Jahu, 1989)

Cyprinoidea (carplike fish) are stenohaline freshwater fish and the morphology of their kidneys has been reported for the common carp, *Cyprinus carpio* (Reichle, 1959; Hickman & Trump, 1969); the goldfish, *Carassius auratus gibelio* (Nash, 1931; Edwards & Schnitter, 1933; Ogawa, 1961b, 1962; Hentschel, 1978, 1987; Elger *et al.*, 1984b, Hentschel & Elger, 1987; Elger & Hentschel, 1981; Sakai, 1985) and for the cyprinid *Danio malabaricus* (Edwards 1935). These studies have reported that the cyprinid nephron consists of a large renal corpuscle, neck segment, bisegmental proximal tubule, a variably present intermediate segment and a distal tubule emptying into a collecting duct system. The microscopic examination of common carp kidneys confirmed the presence

of all the above nephronal segments except the intermediate segment.

Observations on the kidney of the silurian catfish showed a uriniferous tubule consisting of a renal corpuscle, ciliated neck segment, bisegmental proximal tubule and a distal tubule emptying into the collecting tubule-collecting duct system. This is consistent with previous histological observations (Ogawa, 1959; Hickman & Trump, 1969; Kendall & Hinton, 1974; Hentschel & Meyer, 1982; Hentschel & Elger, 1983, 1987).

The cyprinids (carps) and the silurids (catfishes) have been classified together into the group Ostariophysi (Regan, 1929). In addition to the presence of similar segments in their nephrons the kidneys of the ostariophysian fish studied contained abundant intertubular tissue,.which apparently contributes substantially to their relatively larger kidneys (Table 2). The intertubular tissue in these species consisted of haemopoietic, interrenal, reticular, phagocytic, and mast cells . Similar cells have been reported in the common carp (Zapata, 1979).

The histology of the kidney of the salmonid milkfish, *Chanos Chanos* has not previously been reported except for the development of the kidney in an unidentified Chanos species (Holstvoogd, 1936). The renal structure of salmonids has, however, been reported (Newstead & Ford, 1960; Ogawa, 1962; Hentschel and Finkenstadt, 1980 Elger & Hentschel, 1986; Hentschel & Elger, 1987) and the nephron has been shown to

consist of the renal corpuscle, proximal segment I and II, distal segment and collecting tubule-collecting duct system . The nephron of the marine milkfish examined in this study showed a compact renal corpuscle, proximal tubule, distal segment and a collecting duct system.

It appears, therefore, that the parts of the nephronal tubules in the kidneys of the teleosts studied are similar to those found in the mesonephros of mammalian embryos due to the absence of the medullary loop (loop of Henl'e) (De Martino & Zamboni, 1966; Tiedemann, 1979; Wettstein & Tiedemann, 1981). However, the definitive kidneys (metanephros) of birds and mammals differ considerably from those of the teleosts. On the one hand, the mammalian and avian renal tubules have medullary loops (Henle's loops) which are absent in the teleostean kidney. On the other hand, zonation (i.e the spatial separation of the distal tubule from the proximal tubule and collecting tubule), which is characteristic of the tetrapod kidney is absent in the teleostean kidney. Zonation, however, is seen in the kidneys of other classes of fish namely the petromyzons, marine elasmobranchs, polypterids, Latimeria and the dipnoans and provides evidence of the basic similarity of these kidneys to the tetrapod kidney. This apparent difference between the architecture of the teleostean kidneys and those of other lower vertebrates has been explained on the basis of the differences in the line and level of evolution (Hentschel & Elger, 1987). Taking into account that the kidneys of tetrapods are zonated and have multisegmental

nephrons, these authors drew an evolutionary line embracing the primitive lampreys via the polyterids and dipnoans to the amphibians. Teleosts and elasmobranchs are viewed as side branches of this line, and this could explain the apparent difference in nephron specializations and renal architecture in these classes. The teleostean kidneys also differ from the mammalian and avian kidneys in that the kidneys lack a countercurrent exchange system. Among the fishes a countercurrent system has only been described in elasmobranchs (Hentschel, 1988; Hentschel & Elger, 1987; Hentschel, 1991) and it functions in the maintenance of a high concentration of urea and trimethylamine oxide (TMAO). Hentschel & Elger (1987) suggested that the basic similarity between the elasmobranch opisthonephros and the mammalian and avian metanephroi is the result of convergent evolution.

The nephron parts described in the teleosts in the present study occur in the kidneys of other fishes and in those of tetrapods, but some of the parts are absent in some members of the lower vertebrate classes. The proximal tubule has been described in all the vertebrates with glomerular kidneys (Maunsbach, 1973) and its presence in these kidneys is considered to be an indication of the conservative nature of evolution (Edwards & Schnitter, 1937; Beyenbach, 1985). In all the specimens, the proximal tubule had a characteristic brush border which reflects absorptive function. The morphological differentiation of the brush-bordered proximal tubule into the initial part with apical vesicles and an

adjoining part without apical vesicles was observed in all the species studied; similar differentiation has been reported in the kidneys of the other glomerular teleosts (Hickman & Trump, 1969) and in those of elasmobranchs (Lacy & Reale, 1981; Elger & Hentschel, 1983; Hentschel, 1991). The nephrons of all the teleosts investigated were glomerular but aglomerular tubules have previously been reported among freshwater and marine fish (Hickman & Trump, 1969; Hentschel & Elger, 1987; Oguri, 1989).

Previous studies have demonstrated that the structural and functional characteristics of the glomerulus are basically similar throughout the vertebrates despite the considerable variation of the glomerular filtration rate among the vertebrates (Stanley *et al.*, 1985). In addition, De Martino & Zamboni (1966) observed that the glomeruli of the sea water carp resembled those of the human embryo. Observations in the present study showed relatively large and highly vascularised glomeruli in freshwater species and more compact glomeruli with narrow capillaries in the sea water milkfish. In addition the renal corpuscle in the freshwater species studied was characterized by a glomerular capillary endothelium with many large fenestrae, large and many podocytes offering an extensive surface area and few mesangial cells. These observations agree with the suggestions of Hickman & Trump (1969), Hentschel (1977) and De Ruiter (1980) that the relatively more vascular glomeruli are typical of freshwater teleosts. The structural

characteristics of the renal corpuscle in the fishes studied were similar to those of other vertebrates which conforms with the observations by Stanley *et al.*, (1985).

The distal tubule is either present or absent in the nephron and has been reported absent in many marine fishes (Hickman &Trump, 1969; Hentschel & Elger, 1987). In this study the marine species examined had a relatively low volume proportion of distal tubules suggesting that this part is poorly developed. The ultrastructural observations on the teleost distal tubule indicate that the baso-lateral interdigitating processes are relatively more extensive than in other vertebrates. It is therefore conceivable that inspite of the relatively low volume proportions of distal tubule in the teleosts the extensive interdigitating processes may provide an equal or even larger surface area than that of other vertebrates. A large distal tubule surface area is particularly necessary in freshwater teleosts which secrete large volumes of dilute urine in an attempt to rid the body off the high load of osmotic water influx from the hyposmotic environment.

The juxtaglomerular apparatus has apparently not been described in fish kidneys; however, juxtaglomerular cells have been reported in freshwater and marine fish (Hentschel, 1977a, Oguri, 1979, Elger *et al.*, 1984b). The absence of juxtaglomerular cells has also been reported in Stringrays and primitive bony fishes (Oguri, 1986) and in cyclostomes and marine elasmobranch (Nishimura *et al.*, 1970; Oguri *et al.*, 1970; Crockett *et al.*, 1973). Subsequently cyclostomes and

elasmobranchs have been shown to lack a renin-angiotensin system (RAS) (Nishimura & Bailey, 1982). However, recent studies by Henderson *et al.*, (1981) and Hazon *et al.*, (1989) have demonstrated components of the renin-angiotensin system in the elasmobranch kidney which may be an indication of the presence of juxtaglomerular cells. In this study juxtaglomerular cells were demonstrated in terminal arteriole and afferent arterioles of all the species studied.

In the species studied the head kidney, which represents the cephalad part of the mesonephros, contained the interrenal, haemopoietic, pigment and lymphoid cells. This conforms with the previous reports on composition of the head kidney, (see Hickman & Trump, 1969; Chester-Jones, 1980). The interrenal/adrenal tissue was organized into cords and fell into types II and III according to the classification of Chester-Jones (1980). It was also observed that most of the cells in the interstitium of the kidneys of the catfish and common carp were similar to those in the head kidney. It is therefore conceivable these cells belong to the same groups as those of the head kidney.

Unlike mammals, birds and reptiles in which the ureteral epithelium is transitional, that of the teleosts studied was columnar or pseudostratified columnar. The presence of mucin secreting cells and goblet cells in the epithelium of the ureter and ureteral ducts observed in the kidneys of teleost in the present study has been reported in uricoteles and freshwater teleosts (Liu, 1962) but not in the marine fish. The goblet

cells observed in the ureter and large ureteral ducts in the common carp have previously been reported (Lui, 1962; Trump, 1968; Hentschel & Elger, 1987). These cells secrete protective mucus against the voluminous highly toxic and soluble ammonotelic urine of freshwater fish. Liu (1962) proposed that protection of the epithelium is not necessary in marine teleost since they secrete low volumes of urine and much of their waste nitrogen is converted to the non-toxic TMAO. In uricoteles goblet cells may be accounted for by the need for protection of the ureteral epithelium from the semi-solid and relatively toxic urine. Ureotelic animals do not have ureteral goblet cells because they secrete less toxic fluid urine.

The presence of goblet cells in the large collecting ducts of the common carp probably indicates a close embryological relationship with the archinephric duct (ureter) in which similar cells are found. However, in most gnathostomous fish, the collecting tubules and small collecting ducts are derived from the nephron anlage (Hentschel & Elger, 1987), and are therefore considered to be parts of the nephron. Hentschel & Elger (1987) have, in addition, suggested a possible homology between large collecting ducts and secondary ureters which are found in the caudal part of the kidney in some teleosts, and in elasmobranch and amphibian opisthonephroi.

III. BASIS FOR STRUCTURAL-FUNCTIONAL CORRELATION IN FISH KIDNEYS

A. The relationship between the qualitative structural features and functional characteristics

It is generally accepted that function is either correlated or consistent with structure. The nephron is, in general, the basic structural and functional unit of the fish kidney as in other vertebrates. The structural differentiation of the nephron could probably be correlated with function and may therefore form a basis for the interpretation of the mechanisms involved in renal function. The kidneys of vertebrates, in their osmoregulatory roles, have favoured ultrafiltration of blood together with the modification of the filtrate by reabsorptive and secretive processes. The renal corpuscles are the filtering devices and filtration is favoured by the relatively high blood pressure in the glomerular capillaries and the negative pressure within the glomerular capsular space. In addition, the plasma oncotic pressure is higher in the glomerular capillary blood than in the glomerular capsular space. These two physiological forces lead to a net filtration pressure into the glomerular capsular space. In fish the arterial blood pressures are low and this is reflected in the low glomerular capillary hydrostatic pressure which result in low glomerular filtration rate.

The morphological features that favour filtration include the thin barrier formed by the fenestrated glomerular capillary endothelium and the large surface area provided by

the highly anastomotic glomerular capillaries and the foot processes of the podocytes. Glomerular development in fish appears to be influenced by the habitat. Hickman &Trump, (1969) reported that the glomeruli in freshwater fish are relatively better developed than those of sea water fish, and subsequently glomerular filtration rate is relatively higher in these fish than in sea water fish (Holmes & McBean, 1963). Moreover, glomerular intermittency and recruitment are considered to be mechanisms for the regulation of kidney function according to the habitat (Forster, 1973; Elger *et al.*, 1984a). Renal function leads mainly to the formation of dilute urine in freshwater fish and water conservation and salt secretion in marine fish. Aglomerularism in fishes has been associated either with sedentary habits or the need to prevent the loss of anti-freeze glycoproteins.

The neck segment is a primitive part of the nephron that has been discarded in many higher vertebrates. It is present in nephrons of many lower vertebrates and serves to propel the glomerular filtrate along the nephron. For this function it has long motile cilia. The relatively low blood pressure in poikilotherms, compared to that of homeotherms, leads to low filtration pressure in the renal corpuscle and thus the need for mechanical propulsion of the glomerular filtrate along the nephron. The propulsive action of the cilia in the neck segment is apparently lost with the disappearance of the cilia in the renal tubules of homeotherms which have relatively high blood pressure. The proximal tubule provides a leaky

epithelium capable of selective reabsorption and secretion. The luminal microvilli (brush border) increase the surface area for reabsorption and secretion and the lateral interdigitations of the cell membrane increase the surface area for trans-cellular exchange. The vesicles observed in the cell cytoplasm are evidence of secretory, endocytotic and exocytotic activity. The secretion and reabsorption involves both the solutes and fluids. Due to its significance the proximal tubule is the major tubule segment in both freshwater and marine fishes. In some aglomerular teleosts, for example the toadfish (*Opsanus tau*) the proximal tubule is the site for urine formation by active secretion (Bulger, 1965).

The distal tubule selectively reabsorbs solutes, and thus dilutes the filtrate. The surface area of the distal tubule cells is greatly increased by basolateral interdigitating processes. The selective permeability of the distal tubule has been attributed to the selective barrier properties of the basal lamina. The collecting tubule-collecting duct system also contributes to the dilution of urine. However the major function of the distal nephron (i. e. the distal tubules, collecting tubules and collecting ducts) and the archinephric duct is to provide a pathway for conveying the urine to the ureter. The contraction of the smooth muscle in the walls of these tubules and ducts and the ureter provides the propulsive force which moves urine into the bladder or urogenital sinus. However, Nishimura & Imai (1982) and Logan *et al.* (1980b)

have demonstrated that the entire distal nephron, the archinephric duct and the bladder contribute to the dilution of tubular fluid in the freshwater rainbow trout (*Salmo gaidneri*) and in the lamprey (*Lampetra fluviatilis*). Furthermore, goblet cells in the collecting ducts and the archinephric duct secrete mucin which lubricates and protects the epithelium against the injurious effects of the toxic urine. This protection is mostly required by the freshwater teleosts which produce copious amounts of toxic ammonotelic urine.

B. The relationship between the quantitative structural characteristics and function

The quantitative structural characteristics of fish kidney appear to be well correlated with function which is to a large extent influenced by the habitat. In the freshwater habitat there is a high osmotic influx of water into the fish body. This influx requires an elaborate system to rid the body off the excess water and at the same time to conserve the filtered salts. Previous studies on marine and freshwater teleosts have shown a relatively better developed filtration surface in the freshwater fish (Edwards, 1930; Nash, 1931; Ogawa, 1962; Hickman & Trump, 1969; Wendelaar-Bonga, 1972; Ottosen, 1978; Stanley *et al.*, 1985) and an inverse relationship between glomerular size and tonicity of environment (Black, 1957). Furthermore it has been shown by allometric plots that fishes have relatively lower number of glomeruli than mammals and birds (Stanley *et al.*, 1985). A

well developed filtration surface is characterized by numerous and/or large renal corpuscles, and an extensive glomerular capillary network with highly fenestrated endothelium. Fish have also been shown to have relatively fewer capillary fenestrations and thicker basal laminae than mammals (Bulger & Trump, 1968). In this study however, the glomerular capillary endothelium in the freshwater fish studied was was highly fenestrated (Fig. 20). On the other hand, filtration in the glomerular capillaries is selective and active, and thus physiological factors such as the oncotic and hydrostatic pressures of blood must be taken into account when comparing filtration rates in vertebrates. The propulsive role of the cilia in the neck segment may not be essential to renal function and for this reason several fish (Hickman & Trump,1969) and most higher vertebrates (Beyenbach, 1985) have discarded the neck segment. The proximal tubule has been reported to be the major renal tubular compartment in the kidneys of all vertebrates (Beyenbach, 1985; Hentschel & Elger, 1987). Among the fishes, Ottosen (1978) reported that in the marine flounder, the proximal tubule forms 90% of the total tubular length. Bulger (1965) reported that the proximal tubule is the sole nephron component in the toadfish, *Opsanus tau*. The presence of the proximal tubule in relatively high proportions in the kidneys of all fishes irrespective of the species or habitat is evidence of the importance of this nephronal component in renal function. The modification of the tubular fluid by

reabsorption and secretion occurs in the proximal tubule irrespective of species or habitat.

In order to produce a large volume of dilute urine, high glomerular filtration rate (well developed renal corpuscles) combined with low water permeability in the distal nephron are necessary. Hickman & Trump (1969) and Hentschel & Elger (1987) have reported that the distal nephron is relatively better developed in freshwater teleosts. The distal nephron is absent in some marine species, e.g the toadfish (Bulger, 1965). In the report on the marine flounder, (*Pleuronectes plattessa*) Ottosen (1978) indicated that the distal nephron formed less than 3% of the total tubular length. Thus the distal nephron is of little functional significance in the marine habitat and has been discarded by stenohaline salt water fish (Hentschel & Elger, 1987).

All fish require excretory pathways for urine; consequently the ureter and its ducts are usually present in fish kidneys. However, due to the role the ureter and the ducts play in urine dilution (Nashimura & Imai,1980b) and the protective role of the mucus from the goblet cells, it constitutes a greater volume proportion of the kidney in freshwater species. Freshwater species need to dilute urine and require protection from the resulting large volumes of toxic ammonotelic urine.

A structural gradient characterized by the increase in epithelial cell height and volume of mitochondria along the uriniferous tubule has been demonstrated in the anadromous stickleback, *Gasterosteus aculeatus* in freshwater

environment (Wendelaar Bonga, 1973). This structural gradient along the uriniferous tubule is associated with a parallel physiological gradient (decrease in concentration of tubular fluid) which occurs only in fish in a freshwater habitat.

IV. COMMENTS ON QUANTITATIVE PARAMETERS OF THE FISH KIDNEYS

A. Factors which influence the quantitative parameters of fish kidneys

In the reviews on fish renal morphology, Hickman & Trump (1969) and Hentschel & Elger (1987) noted a general increase in the number of renal tubule segments from the lower fishes to the higher fishes and on to the tetrapods and explained the discrepancies on the basis of divergent evolution. It is likely that among the fishes renal structure may be influenced by the phylogenetic level of the class. In the class Teleostei, the qualitative and the quantitative structural characteristics appear to be also influenced by the order. The volume densities of the renal components of the percoid fishes (the tilapia and the blackbass) differed significantly from those of the ostariophysian fishes (the catfish and carp) and the salmonids (milkfish) (Table 6). The difference could be attributed to the abundant peritubular haemopoietic tissue in the ostariophysian and salmonid fishes which was absent in the percoid fishes.

The freshwater teleosts, in which the main renal function apparently is water excretion, have relatively high renal corpuscle and distal nephron volume densities whereas the marine teleosts (in which the kidneys are mainly divalent ion regulators and water conservers) have relatively low renal corpuscle and distal nephron volume densities. Elger *et al.*, (1984) reported that more than 90% of the glomeruli disappeared in *Carassius auratus gibelio* when adapted to 15% sea water. Furthermore, it has also been reported that glomeruli decrease in size when freshwater fish are raised in sea water (Olivereau & Olivereau, 1971; Wendelaar Bonga, 1973; Hwang & Wu, 1988)). Marine elasmobranchs (Hentschel & Elger, 1987) and the hagfishes (Fange, 1963) are isosmotic regulators and thus their renal structures are markedly different from those of other marine fish. It seems, therefore, that the habitat determines the quantitative renal parameters of teleosts by influencing their renal function.

The quantitative parameters of the kidney are also influenced by the age of the fish. Nephrogenesis in the definitive kidneys is characteristic of growing elasmobranch and teleost fish (Hentschel, 1991); therefore quantitative analysis of the juvenile fish kidney gives unrepresentative data. Furthermore, quantitative studies on the human kidney have reported that some renal parameters, especially the number of renal corpuscles, increases from the young to the adult and then decreases with advancing age (Moffat, 1975). It

is therefore necessary to study adult fish specimens to obtain representative quantitative data for any given species.

B. Kidney size and body weight

The teleostean kidney volume increased with body weight. The correlation coefficient between kidney volume and body weight was 0.96. Previous studies (Edwards 1930; Nash 1931) in which the correlation between body size and kidney weight was examined showed similar trends to those found in this study.

The data on kidney volume per gram body weight showed that all the teleosts examined had more than 2 mm^3 of kidney tissue per gram body weight. This data also showed that closely related species in similar habitats had approximately similar values for kidney volume per gram body weight. The ostariophysian fish which have intrarenal haemopoietic tissue had relatively higher values for kidney volume per gram body weight than the Perciformes fish which do not possess the intrarenal haemopoietic tissue. It can therefore be inferred that the haemopoietic tissue is more dense than renal tissue and therefore contributes more to the kidney weight. It is also likely that haemopoietic tissue in the ostariophysian fish kidneys occupies space that would have otherwise been occupied by renal tissue, and thus these kidneys have necessarily got to be larger in order to contain adequate renal parenchyma.

The significantly lower kidney volume per unit body weight in the marine teleost (milkfish) compared to the values for the freshwater teleosts with similar renal structure may be attributed to the influence of habitat. Hickman & Trump (1969) reported that renal function in marine fishes is highly complemented by the extra-renal organs and it is therefore in order for marine species to have relatively smaller kidneys. Edwards (1930) reported a kidney weight/body weight ratio of 2 g/kg body weight in *Lophius piscatorious*. This value is similar to the values noted in this study for tilapia, blackbass and milkfish. The relationships between kidney weight and body weight reported by Nash (1931) in the catfish and the common carp are relatively higher than the values obtained for these fish in the present study. The discrepancy between the values reported by Nash (1931) and those obtained in this study is probably due to the inclusion of the weights of the head kidneys and lateral renal lobes by Nash (1931), whereas these components were excluded in the calculations in the present investigation. It was necessary to exclude the head kidneys of the common carp and lateral renal lobe of the catfish because they do not contain any uriniferous tissue.

The teleostean kidney forms a much smaller percentage of the body weight than in other vertebrates. In birds kidney volume per gram body weight ranged from 4.23 mm^3/g in the turkey to 16.56 mm^3/g in the common starling (Warui, 1989) and these values are much higher than those for the fish examined here. The relatively smaller kidneys in fish may be

an indication of the high level of complementation of renal function by extrarenal organs, for example the gills.

C. Analysis of the quantitative structural characteristics of the fish kidney

1. Comparison of the volume proportions of the main components of the fish kidneys and those of other vertebrates

The main components of the fish kidney are the uriniferous tissue, blood vessels larger than capillaries, ureter and ureteral ducts, haemopoietic tissue and connective tissue (Table 3). The percoid teleosts examined in this study had relatively higher volume proportions of uriniferous tissue than the other fish investigated. This seems to be contributed by the absence of haemopoietic tissue in their kidneys and the presence of haemopoietic tissue in the kidneys of the other fish. Haemopoietic tissue occurred in the kidneys of the ostariophysian and salmonid fishes, however, there was a significant difference ($P<0.001$) between the volume proportions of the uriniferous tissue in the two groups. This difference may be accounted for on the basis of the differences in their habitats; the ostariophysian fishes were freshwater forms, whereas the salmonid fishes were sea water forms. The relatively low value for the volume proportion of uriniferous tissue in the marine fish could also support the possibility of supplementation of renal function by extra-renal organs. This agrees with the suggestion by

Hickman & Trump (1969) that renal function is highly supplemented by extrarenal organs in the marine fishes. Furthermore, the mean values for the volume proportions of uriniferous tissue in the fish kidneys examined in this study are much lower than the mean value (81%) in perfused kidneys of the domestic fowl reported by Warui & King (1985). This provides further evidence that renal function in fishes could be complemented by extra-renal organs such as the gills, liver and intestines. Renal function is complemented to a lesser degree in mammals by the skin and respiratory system and the nasal glands in avian species.

The blood vessels larger than capillaries comprised 22-26% of the total volume of the fish kidney, and these values are relatively higher than the range of 11-15% reported for birds (Warui, 1989). This disparity is probably explained by the inclusion of the posterior cardinal vein, which is homologous to the caudal vena cava and is closely related to the fish kidneys and was sampled as part of renal blood vessels. Moreover, the presence of numerous afferent intercostal veins, the caudal vein and numerous wide efferent veins contributed greatly to the relatively high volume proportions of large blood vessels.

The mean volume proportions of the ureter and ureteral ducts were much higher in the fishes (1.6-8.2%) compared to those reported in birds (Warui, 1989). In birds other than the domestic fowl, this component formed less then 1% of the total kidney volume (Warui, 1989). The relatively high volume

proportion of ureter and ureteral ducts in the fish kidney may be explained on the basis that the ureter was either embedded in the renal parenchyma or along the lateral border of the kidneys, and thus the whole ureter was sampled for morphometry. In reptiles, birds and mammals, a large part of the ureter lies outside the kidney parenchyma.

2. The volume proportions of the components of the uriniferous tissue in relation to renal function

Since the description of the renal corpuscle and its function as a filter by Bowman (1842), two theories on the origin of the renal corpuscle have been proposed. Smith (1953) proposed that the glomerulus arose as a regulatory device in the freshwater vertebrates to rid the body off water entering from the hypotonic environment. This theory was contested by Robertson (1957) who suggested that the glomerulus arose as an ion regulating device which also provided a useful pre-adaption to the ancestral sea vertebrates which migrated to freshwater (Wendelaar-Bonga, 1973). Despite these differing views quantitative studies on marine and freshwater teleosts have showed that the renal corpuscles are relatively better developed in freshwater fish than in the marine fish (Edwards, 1930; Nash, 1931; Ogawa, 1962). In the anadromous stickleback renal corpuscles are better developed when in freshwater than in sea water. The observations in this study agree with these previous reports since the volume density of renal corpuscles was quite high in

fresh water species (tilapia, blackbass, common carp and catfish) compared to the marine species. A high volume of functional renal corpuscles is likely to ensure a high glomerular filtration rate in the freshwater habitat. Among the freshwater species studied the volume density of renal corpuscle varied with the order. However, the absolute volumes of renal corpuscles were similar in freshwater fish of approximately equal sizes. It was noted that the volume density of renal corpuscles could be high in a kidney with a relatively large number of renal corpuscles as in the blackbass or with relatively large renal corpuscles as in the common carp. The volume density of renal corpuscles may be well correlated with the filtration surface in a fish kidney; however, the effective filtration surface is also influenced by the branching of the glomerular capillaries and the thickness of the the filtration barrier (Bulger & Trump, 1968; Wendelaar Bonga, 1973).

The percentage proportions of the renal corpuscles in the fish kidneys were relatively lower than the value reported for the domestic fowl (4.81%) by Warui & King (1985). The number of renal corpuscles and consequently their volume density is much higher in mammalian kidneys (Smith, 1951) than in fish kidneys (Nash, 1931). However, Abdalla & Abdalla (1979) suggested that the number of renal corpuscles does not directly influence the capacity for excreting urine with a high electrolyte concentration.

The neck segment comprised less than 1% of the renal parenchyma in all the teleost investigated. This could be an indication of the relatively low contribution by this nephronal component to renal function in fishes. The neck segment has, in fact, become redundant in evolution and is absent in kidneys of most mammals. Previous quantitative analyses on the renal tubules of fish indicate that the neck segment is poorly developed. The neck segment forms 8% of the length of the renal tubule in *P. lethostigma*, 0.07% in *Anguilla rostrata* and 3% in *Pleuronectes platessa* (Grafflin, 1937; Bulger, 1965; Bulger & Trump, 1969; Ottosen, 1978)

The proximal tubule is the most developed renal tubular segment in marine and freshwater fishes and indeed in all the vertebrates (Beyenbach, 1985). This is because the proximal tubule contributes substantially to the reabsorptive and secretory functions of the renal tubules in all vertebrates. The quantitative analyses in this study have shown that the proximal tubule is a major component of renal parenchyma contributing 59-74% of parenchyma in the kidneys of all the species studied (Table 4). This conforms with previous quantitative studies in which the proximal tubule as a proportion of the nephron formed 79.5%, in *Anguilla rostrata*, 100% in *Opsanus tau*, 87% in *P. lethostigma* and 90% in *Pleuronectes platessa* (Grafflin, 1937; Bulger, 1965; Bulger & Trump, 1965; Ottosen, 1978).

The volume proportion of the proximal tubule in tilapia (45.50%) expressed in the kidney as a whole was close to the

46.29% reported for the kidney of the domestic fowl (Warui & King, 1985). However, the values for the other fishes studied (Table 5) were much lower than that of the domestic fowl. The variations in the proportions of proximal tubules in fish kidneys could be an indication of the influence of the order, the presence or absence of haemopoietic tissue and habitat on the quantitative structure of fish kidney. In fish the proximal tubule is the only invariably present part of the renal tubule, and is therefore the best indicator of the influence of order, qualitative structure and habitat on the quantitative structural characteristics of the fish kidney.

The distal nephron dilutes urine and would therefore be expected to be better developed in freshwater fish because it preferentially reabsorbs solutes. This has been confirmed in qualitative studies (Hickman & Trump, 1969; Hentschel & Elger, 1987) and also in the quantitative studies on *Anguilla rostrata* (Grafflin, 1937), the toadfish (Bulger, 1965), *P. Lethostigma* (Bulger & Trump 1965), and *Pleuronectes platessa* (Ottossen 1978). The quantitative data on the distal nephron in this study (Table 4) supports the view that the distal nephron is better developed in the freshwater teleosts. Furthermore, the basal membrane infoldings appear to be more extensive in fish than in other vertebrates.

The volume density of the peritubular capillaries was relatively higher in fish with a renal portal system, and was generally more than 11% of the parenchyma in most species investigated. The relatively low proportion (less than 10%) in

tilapia may be attributed to the absence a renal portal system in this species. Peritubular capillaries enhance renal function by supplying nutrients to the tubule cells and facilitating the exchange of solutes and fluid between the tubules and blood. The capillaries therefore form an important component of renal parenchyma and were well developed in all the fishes investigated. In perfused kidney of the domestic fowl the peritubular capillaries comprised 9.09% of the total kidney volume (Warui & King, 1985). This value is much higher than those of all the fish species examined in this study.

3. Parameters of the renal corpuscle in relation to renal function in fish

The freshwater teleosts had relatively larger renal corpuscles and higher renal corpuscle volume proportions than the marine teleost. The renal corpuscles in the freshwater teleosts were highly vascularised as indicated by the much larger proportions (diameters) of glomerular capillaries compared to the valuesfor the glomerular capsular space. The higher renal corpuscle volume proportion and the large glomerular diameters in the freshwater fish may suggest that a large filtration surface is essential in the freshwater environment and conforms with previous observations by Hickman & Trump (1969). However, Wendelaar Bonga (1973), demonstrated in the anadromous stickleback that the mesangial cells were thicker and the capillary fenestrations fewer when reared in sea water. This might indicate that a

large filtration surface may not necessarily be correlated with a high glomerular filtration rate. The glomerulus of the freshwater fishes examined in this study appeared to have many fenestrations and few mesangial cells an indication of a surface adapted for high filtration rate.

The glomerular diameter in fish increased directly with body size. The values obtained for the catfish and the carp were close to the values given by Nash (1931) and Elger and Hentschel (1981). The renal corpuscle diameter is a factor of the corpuscular volume; a large diameter implies a higher volume. Furthermore, although it is unlikely that capillary filtration surface is a simple function of glomerular diameter, it is conceivable that a large filtration area may contribute significantly to glomerular filtration rate in fish which have low ultrafiltration pressure.

CONCLUSIONS

A qualitative and quantitative study of the structural characteristics of four freshwater teleost and one marine teleost species belonging to the orders Perciformes, Ostariophysi and Salmoniformes has been made and the results obtained showed the following:

1. Perfusion fixation through the heart results in uniformly fixed kidneys suitable for stereological analyses, and in sections stained with Gomori's trichrome, Harris's haematoxylin and alcian blue the different parts of the renal tubules can be distinguished on the basis of their staining characteristics.

2. The teleost kidneys lie retroperitoneally in the dorsal part of the body coelomic cavity and are either partially or completely fused. The renal tissue shows metameric arrangement which is an indication of organization of the tissue into repeating structural units or lobules. The renal lobule is organized around an intralobular artery (branch of intrarenal artery), a collecting duct and an afferent vein in teleosts with a venous renal afferent (portal) system. In teleosts without a venous renal afferent system the lobule is centered around an intralobular artery and a collecting duct. The efferent veins formed the peripheral limits in all the lobules.

3. The teleost kidney is not zonated (i.e lacks cortical and medullary zones) and the renal tissue contained abundant peritubular haemopoietic tissue in some of the species. The

parts of the nephron identified on the basis of the staining reactions and the light and electron microscopic characteristics were: the renal corpuscle, neck segment, proximal segments I and II, and the distal segments. The nephrons are drained by the collecting tubule-collecting duct system into the ureter which is embedded in the renal parenchyma to variable extents.

4. The juxtaglomerular apparatus was poorly developed. The only component of a typical juxtaglomerular apparatus observed was the juxtaglomerular cells in the tunica media of the terminal, afferent and efferent arterioles. These cells were apparently not associated with the distal tubule.

5. Volume proportions and absolute volumes of the main renal components and also the volume proportions of the components of the uriniferous tissue in the teleost kidney were determined by point counting. The mean (± S.D) values for the volume proportions of uriniferous tissue, blood vessels, ureter and it's duct, haemopoietic tissue, and connective tissue, ranged from 36 03 ± 1.67 - 72.52 ± 1.73%, 21.93 ± 1.36 - 25.59 ±1.12%, 1.59 ± 0.18 - 8.20 ± 0.41%, 0 - 34.22 ± 0.74%, and 1.37 ± 0.17 - 3.60 ± 0.74% in all the species respectively; those for the proportions of the uriniferous tissue components expressed in the kidney as a whole ranged as follows: renal corpuscles, 0.76 ± 0.12-3.70 ± 0.38% neck segment, 0.07 ± 0.03-0.43 ± 0.12%, proximal segment, 26.75 ± 1.02 - 45.50 ± 1.60%, distal segment, 2.84 ± 0.47 - 12.80 ± 2.43%, collecting tubules and ducts, 1.27 ± 0.38 - 3.70 ± 1.28%.and capillaries,

4.52 ± 0.41 - 8.50 ± 1.02%. There was good correlation between body weight (W) and the renal parameters and the allometric models for the relationships between; (a) the body weight and kidney volume (V_k); (b) body weight and volume of the uriniferous tissue (V_{ut}); (c) body weight and volume of the total vascular space (V_{tvs}) and (d) body weight and volume of the renal corpuscles (V_{rc}) were $V_k = 3.236W^{0.977}$, $V_{ut} = 1.102W^{1.077}$, $V_{tvs} = 1.197W^{1.025}$, and $V_{rc} = 0.0038W^{1.536}$. The teleostean renal parameters were influenced by the body size, habitat and order.

6. The quantitative data gave the impression of a good structure-function correlation. The fresh water teleosts had relatively higher volume proportions of renal corpuscles, distal tubules and collecting tubule-collecting duct system than the marine teleosts. This observation is consistent with the previously noted higher glomerular filtration rates and the production of dilute urine in the fresh water teleosts.

7. Many aspects of the qualitative structural features of the teleostean kidney were similar to those of other vertebrates. The notable differences observed in this study were: i, the absence of cortico-medullary zonation; ii, the presence of peritubular haemopoietic tissue; iii, the presence of a ciliated neck segment and a bisegmental proximal tubule; iv, and the absence of a juxtaglomerular apparatus.(only juxtaglomerular cells were observed); v, presence of rodlet cells in the proximal tubule.

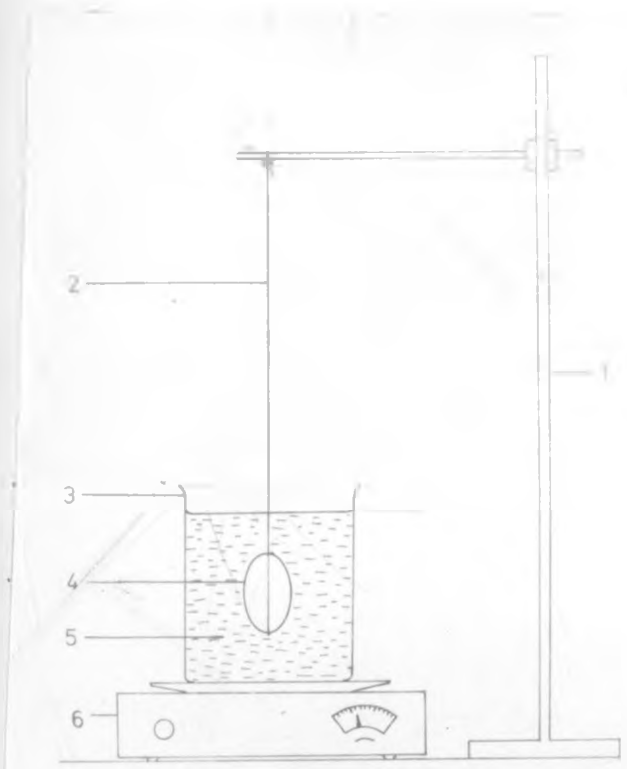

Fig. 1: Diagram of the apparatus used in the measurement of kidney volume by water displacement. The apparatus include: 1, clamp stand; 2, thread; 3, beaker; 4, kidney; 5, water; 6, balance.

Fig. 2: Light micrograph of the blackbass kidney overlaid with a quadratic lattice to illustrate how point counting to estimate the V_v of renal components was done. As an example, the total number of points on the section are 176, and those falling on the renal corpuscles are 11. Therefore the V_v of renal corpuscles on the field overlain by the lattice is equal to 11/176 = 6.25%.

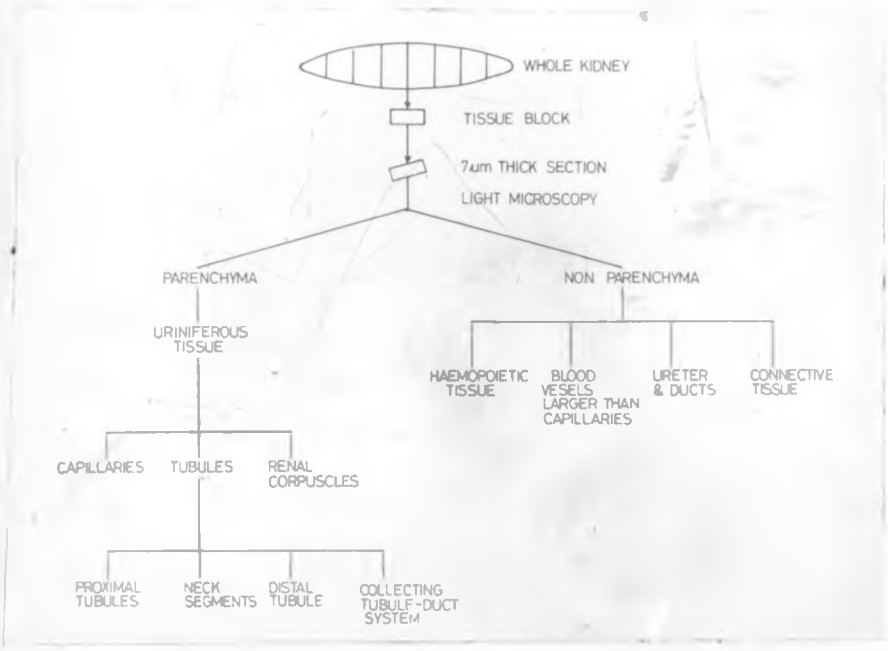

Fig. 3: Diagram showing the sampling of the teleostean kidney. The kidney was sampled at two levels, first at X 100 to quantify the main components (parenchyma and non-parenchyma), and then at X 400 for the components of parenchyma.

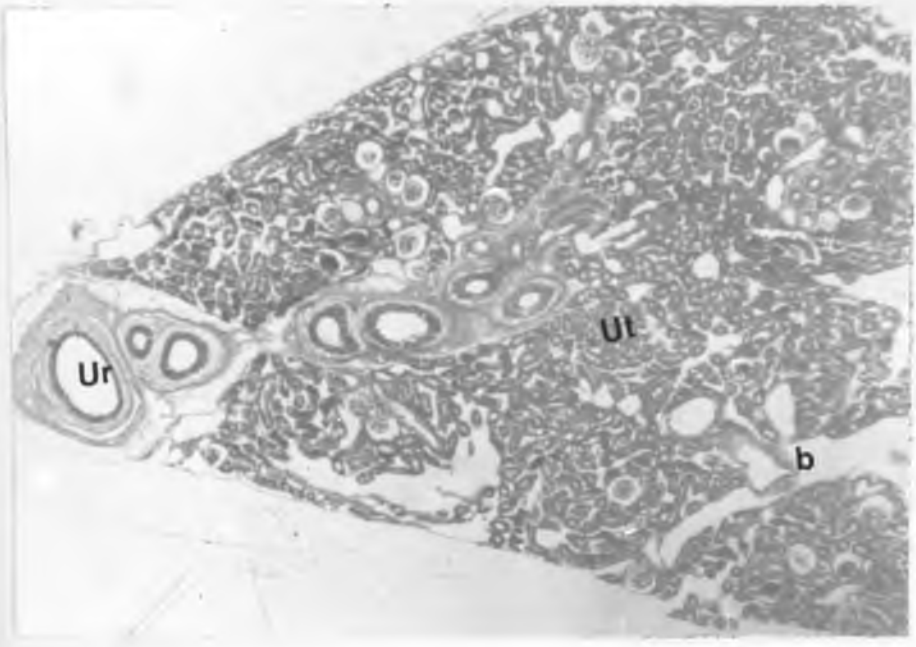

Fig. 4: Part of a section of kidney of the blackbass showing some of the components of the kidney sampled at the first level. Ut, uriniferous tissue; b, blood vessels largrer than capillary; Ur, ureter. X 100.

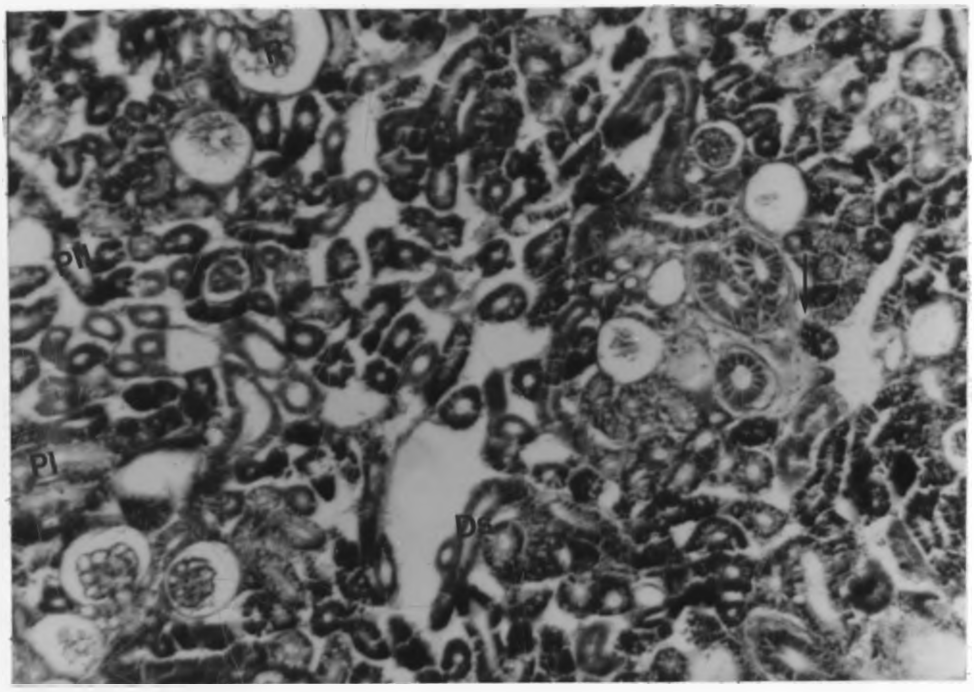

Fig. 5: Light micrograph of part of the kidney of the blackbass stained with Gomori's trichrome, Harris's haematoxylin and alcian blue showing the components sampled at the second level. PI, proximal segment I, PII; proximal segment II; Ds, distal segment; arrows, capillaries; R, renal corpuscles. X 400.

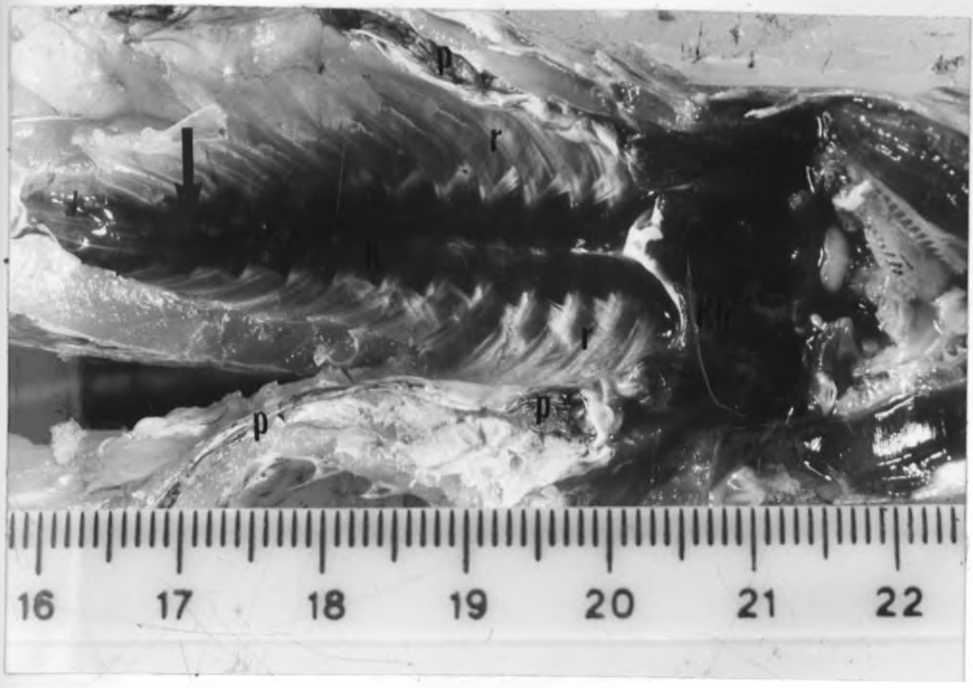

Fig. 6: Ventral view of the opened coelomic cavity of tilapia showing the paired kidneys in a retroperitoneal position along the vertebral column . The kidneys are closely applied to the dorsal body wall. The head kidney lies behind the gills and is separated from the rest of the kidney by the pericardio-peritoneal septum. The trunk kidney shows a characteristic metamerism and the mesomeres correspond to the ribs. The kidneys are supplied by branches of the dorsal aorta and drained by the right posterior cardinal vein. K, kidney; Kh, head kidney; P, peritoneum; r, ribs; curved bold arrow, pericardio-peritoneal septum; short bold arrow, renal mesomeres; long bold arrow, posterior cardinal vein; long arrows, dorsal aorta.

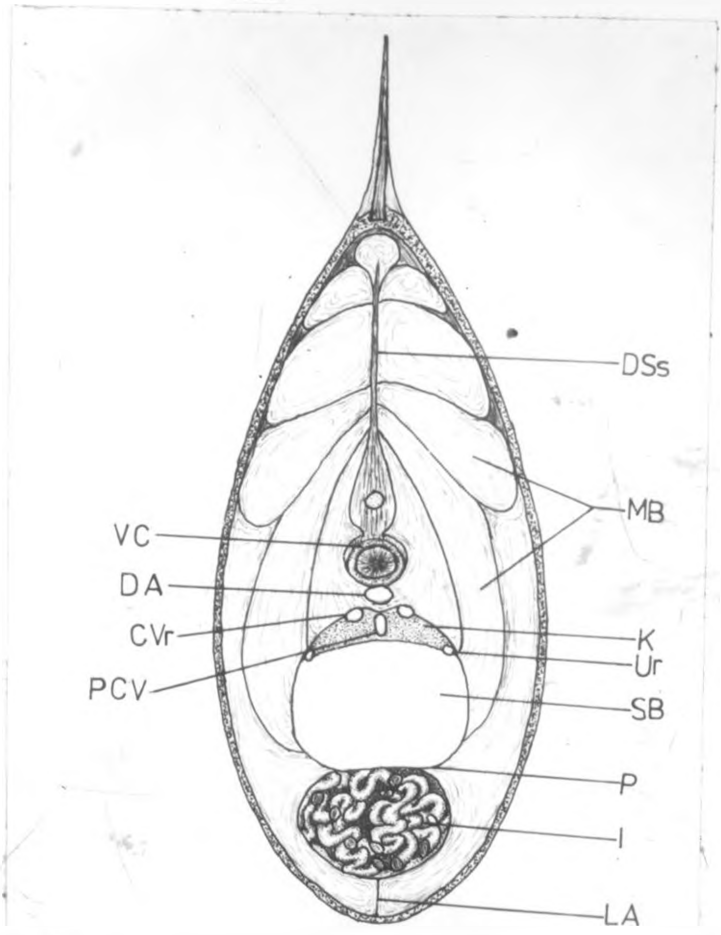

Fig. 7: Cross section through the abdomen of the blackbass showing the relationship of the kidneys to the rest of the abdominal viscera. The peritoneum divides the coelomic cavity into a ventral compartment containing visceral organs e.g intestines and a dorsal compartment containing the swim bladder and the kidney. K, kidney; LA, linea alba; I, intestines; P, peritoneum; Sb, swim bladder; CVr, right caudal vein; PCV, posterior cardinal vein; Ur, ureter; DA, dorsal aorta; VC, vertebral column; MB, muscle bundles; DSs, dorsal longitudinal septum.

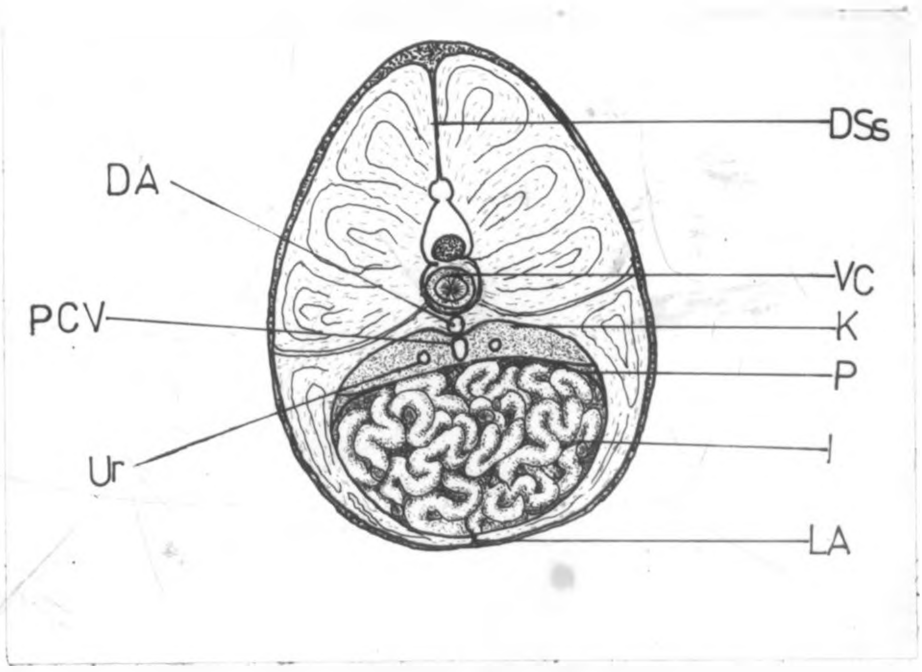

Fig. 8: Cross section through the body trunk of a catfish similar to figure 5 highlighting the absence of a swim bladder. The kidney is immediately dorsal to the peritoneum. K, kidney; P, peritoneum; DA, dorsal aorta; PCV, posterior cardinal vein Ur, ureter; I, intestines; VC, vertebral column; DSs, dorsal longitudinal septum; LA, linea alba.

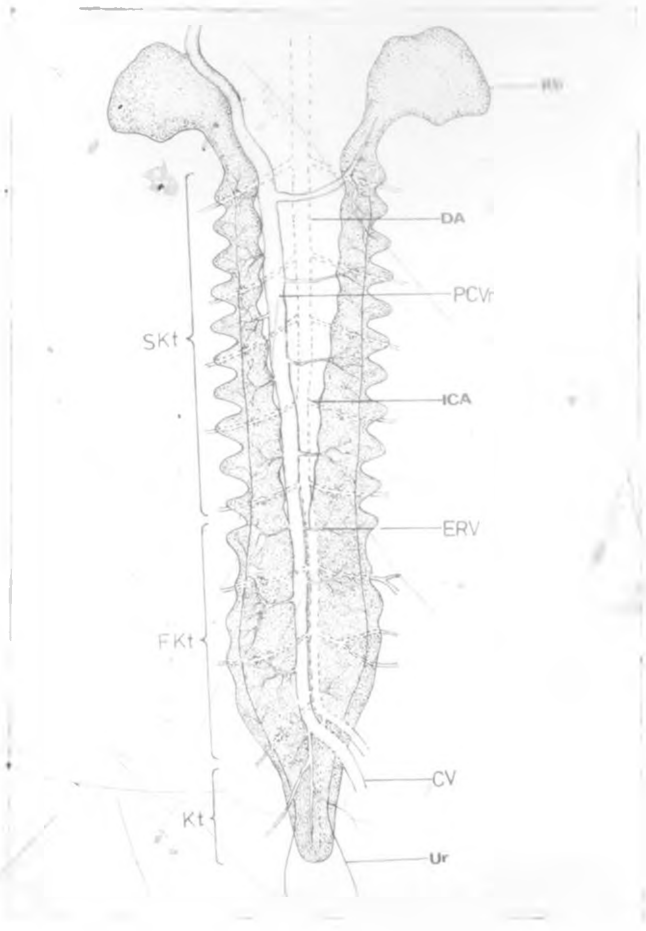

Fig. 9: Free hand sketch of the paired kidneys of tilapia showing the right and left kidney, kidney divisions and associated blood vessels. In this species there is no renal venous (afferent) portal system. Kh, head kidney; SKt, unfused part of the trunk kidney; FKt, fused part of the trunk kidney; Kt, tail kidney; DA, dorsal aorta; PCVr, right posterior cardinal vein; CV, caudal vein; ICA, intercostal arteries.

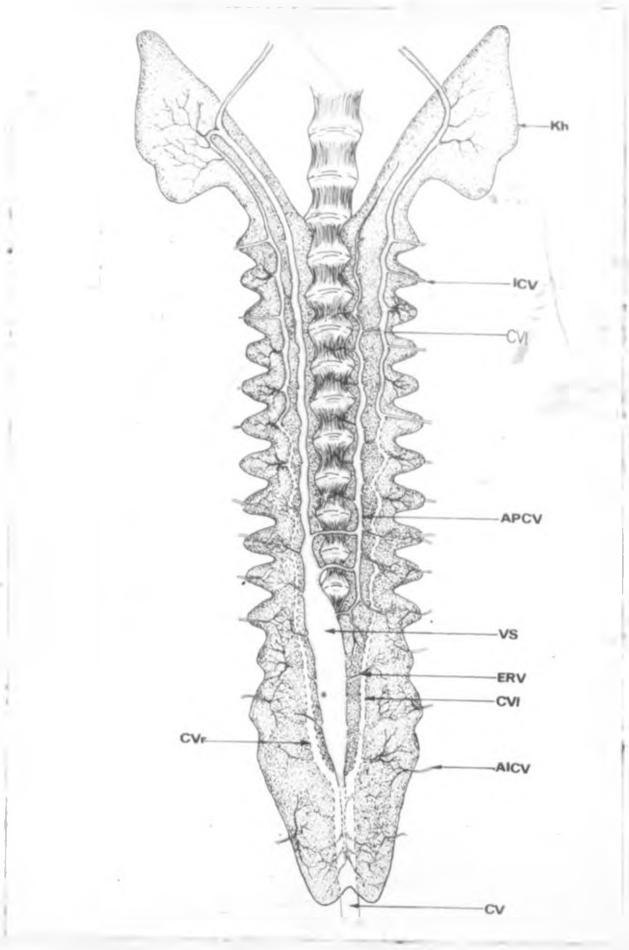

Fig. 10: Ventral view of the paired blackbass kidneys showing their configuration and venous drainage. These kidneys resemble those of the tilapia but end abruptly in two short bifurcations rather than a long tail as in tilapia. The arterial supply is similar to that of tilapia. The venous system differs considerably from that of tilapia. CV, caudal vein; CVr, right caudal vein; CVl, left caudal vein; AICV, afferent intercostal vein; ERV, efferent renal vein; VS, venous sinus; APCV, accessory posterior cardinal vein; Kh, head kidney.

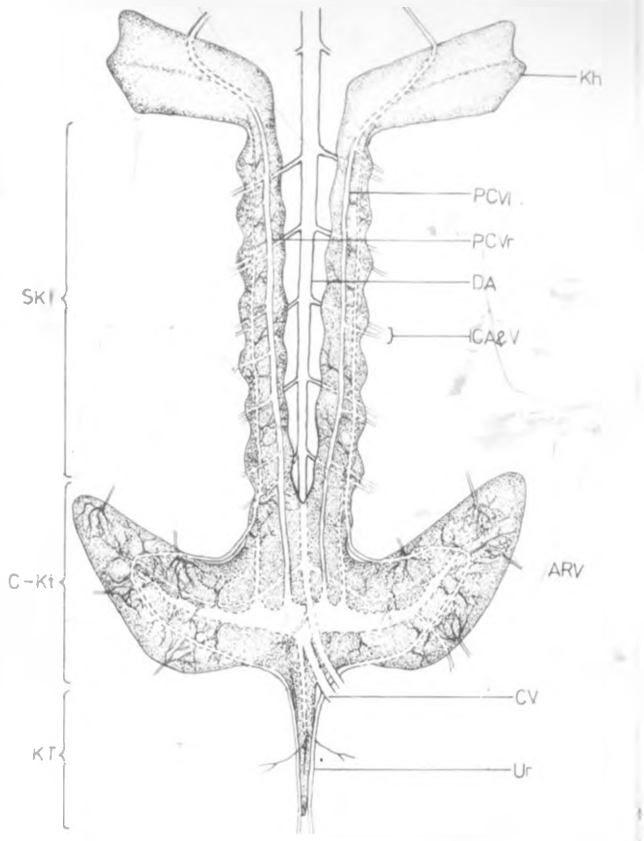

Fig. 11: Ventral view of the kidneys of the common carp showing their configuration and blood vascular supply. Kh, head kidney; SKt, unfused part of trunk kidney; C-Kt, C-shaped part of trunk kidney; KT, tail kidney; CV, caudal vein; ARV, afferent renal vein; ICA & V, Intercostal artery and vein; DA, dorsal aorta; PCVr, right posterior cardinal vein; PCVl, right posterior cardinal vein; Ur, ureter.

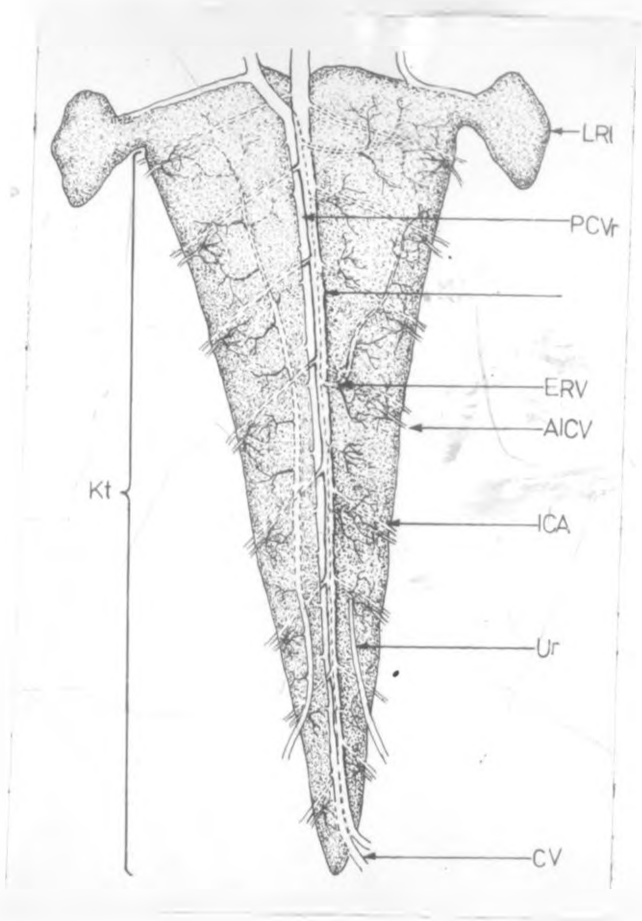

Fig. 12: Ventral view of the kidneys of the catfish showing the blood vascular supply and the fusion of the right and left kidneys into a single wedge shaped organ. Kt, trunk kidney; LRl, lateral renal lobe; CV, caudal vein; ICA, intercostal arteries; AICV, afferent intercostal veins; ERV, efferent renal veins, DA, dorsal aorta; PCVr, right posterior cardinal vein; Ur, ureter.

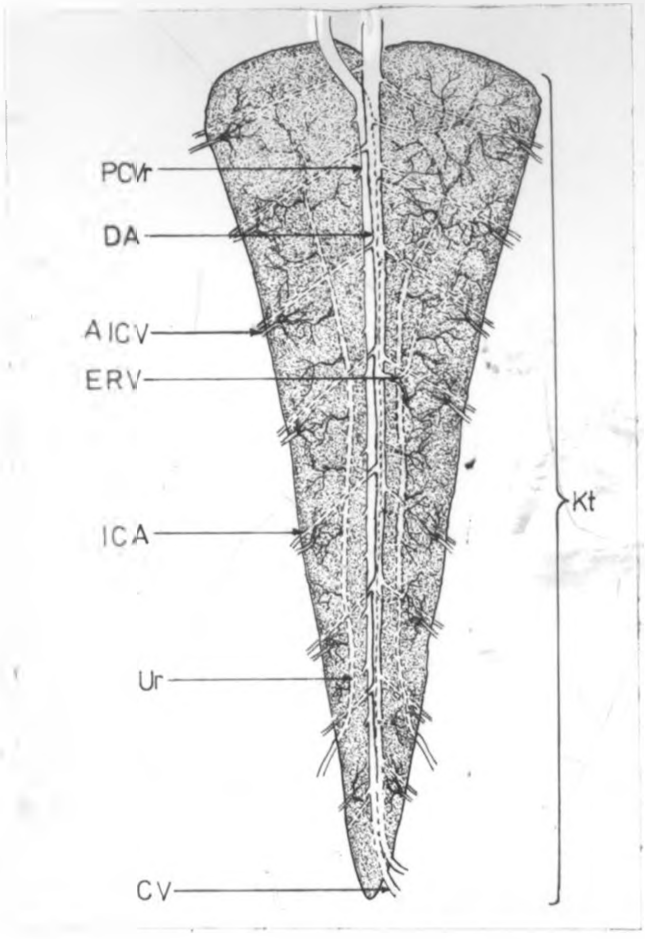

Fig. 13: Ventral view of the kidneys of the milkfish showing their configuration and blood vascular supply. The kidneys resemble those of the catfish but lack lateral renal lobes. Kt, trunk kidney; CV, caudal vein; ICA, intercostal artery; ERV, efferent renal vein; AICV, afferent intercostal vein; DA, dorsal aorta; PCVr, right posterior cardinal vein; Ur, ureter.

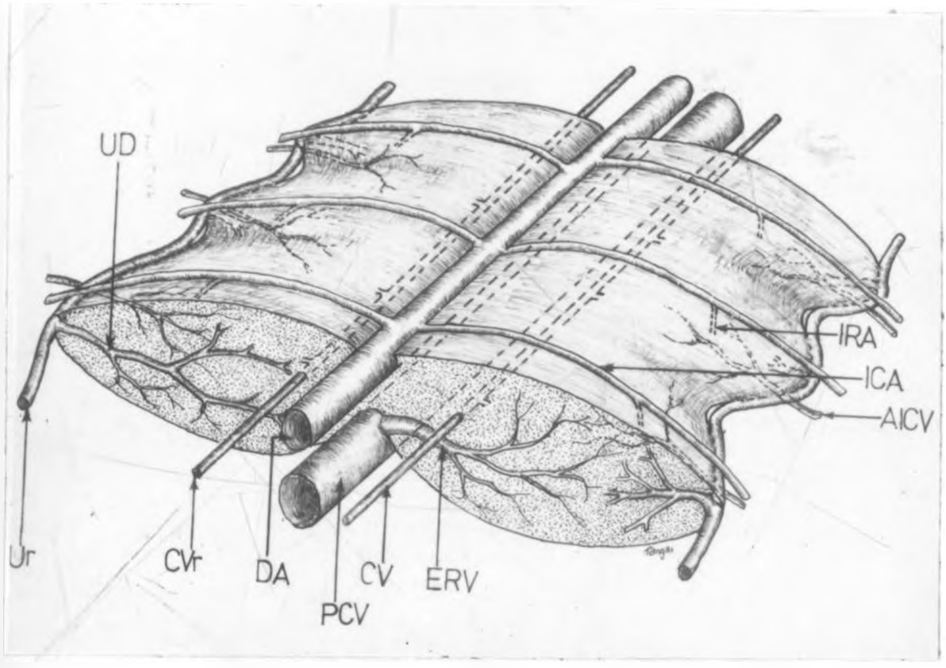

Fig. 14: Section through a kidney of the blackbass showing three mesomeres and the interelations of arteries, veins and the ureteral branches within the mesomere. M, mesomere; Ur, ureter; UD, ureteral duct; CVr, right caudal vein; DA, dorsal aorta; PCV, posterior cardinal vein; CVl, left caudal vein; ERV, efferent renal vein; AICV, afferent intercostal vein; ICA, intercostal artery; IRA, intrarenal artery.

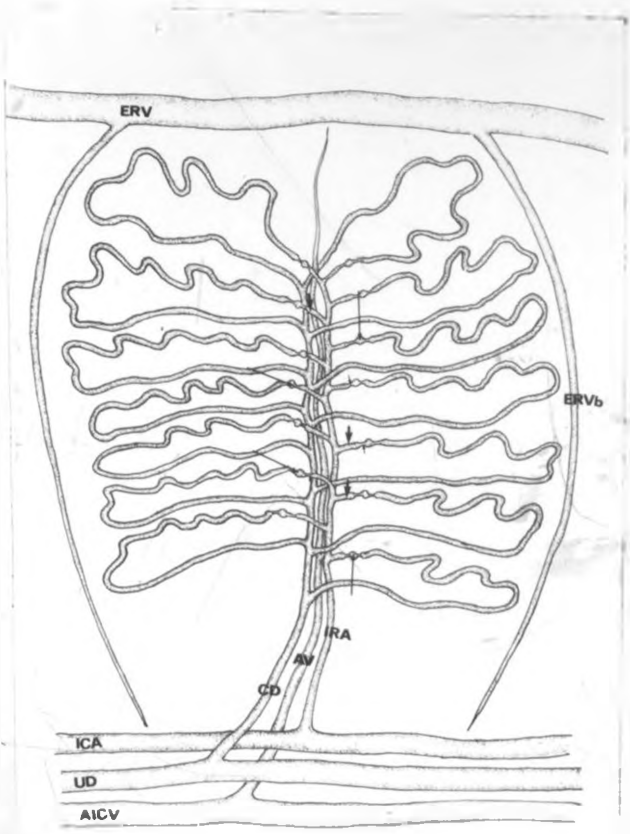

Fig. 15: Free hand drawing of the renal lobule of the teleost showing the disposition of blood vessels, ureteral duct system and the nephrons. AICV, afferent intercostal vein; UD, ureteral duct; CD, collecting duct; ICA, intercostal artery; IRA, intrarenal artery; short arrows, afferent arterioles; long arrows, renal corpuscles; ERV, efferent renal vein; ERVb, efferent renal vein branch.

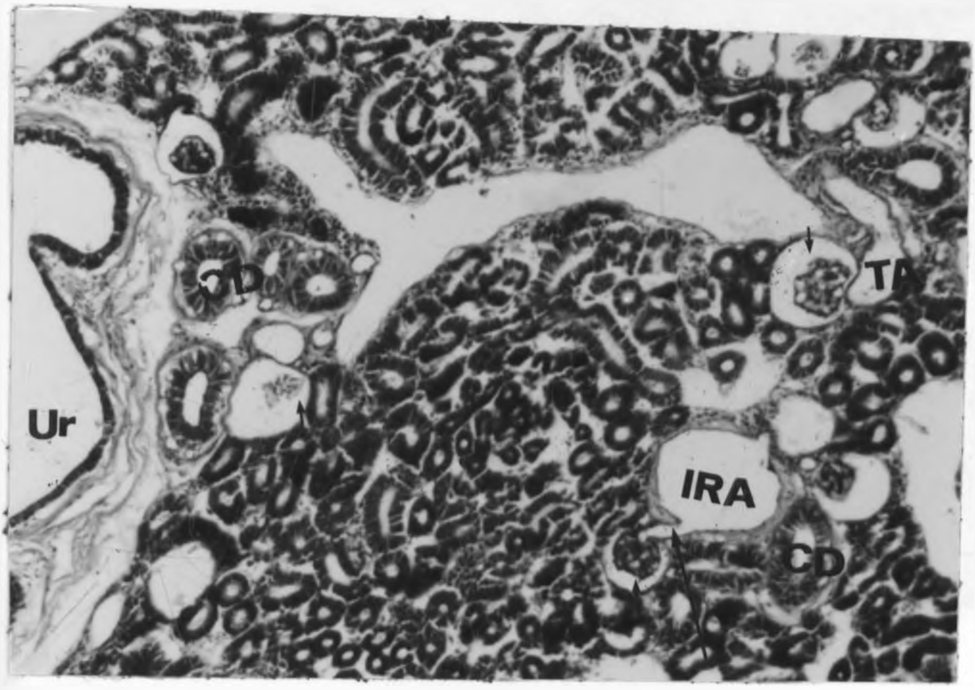

Fig. 16: Part of a section of the kidney of the blackbass showing an afferent arteriole arising from the intrarenal artery. The intrarenal artery is accompanied by a collecting duct and renal corpuscles are adjacent to the intrarenal artery or terminal arteriole. The ureter is at the periphery of the organ and is lined by cuboidal/low columnar epithelium which becomes tall columnar in the collecting ducts. IRA, intrarenal artery; CD, collecting duct; TA, terminal arterial; long arrow, afferent arteriole; short arrows, renal corpuscles; Ur, ureter; X125.

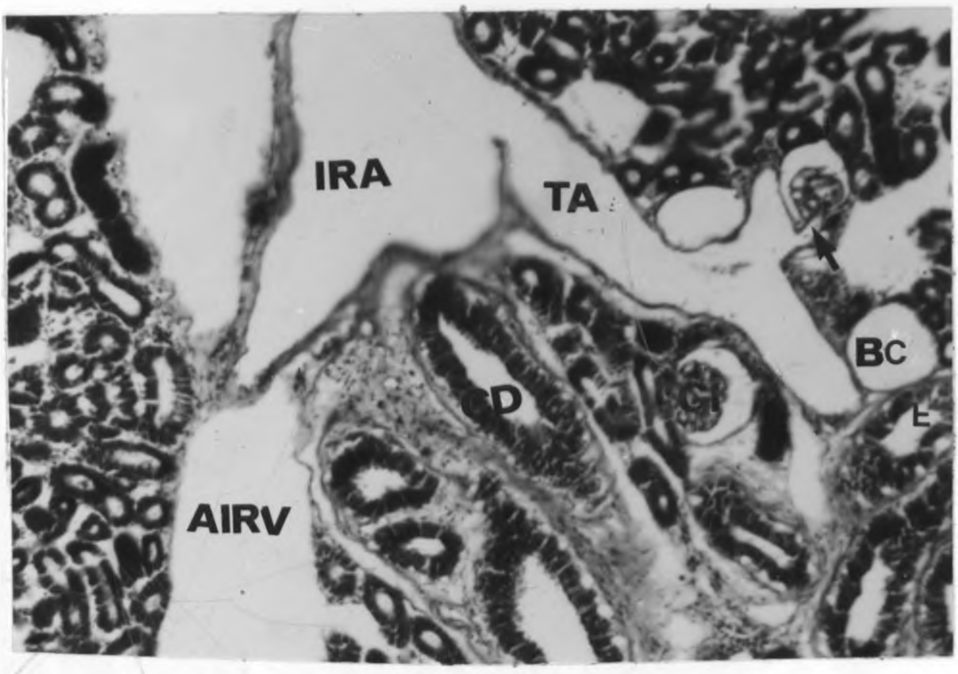

Fig. 17: Light micrograph of part of the blackbass kidney showing the vascularisation. The intrarenal artery (IRA) gives off a terminal arteriole (TA) which gives rise to a short afferent arteriole (bold arrow) to the glomerulus (Gl). There is a general decrease in thickness of the wall of the artery towards the arteriole. The artery is usually accompanied by a collecting duct (CD) and afferent intrarenal vein (AIRV). Arrows, neck segments; BC, Bowman's (glomerular) capsule). X 310.

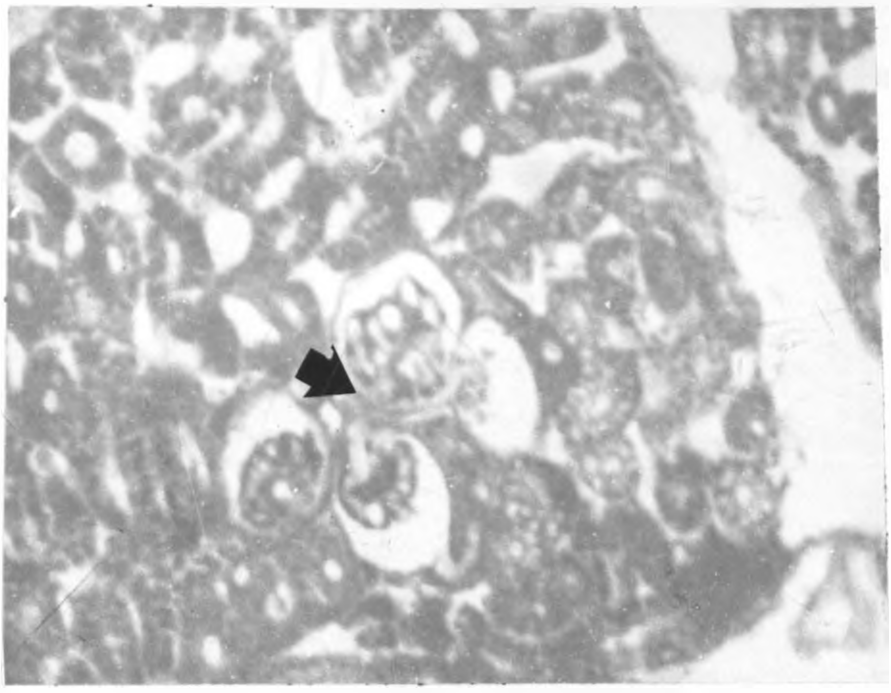

Fig. 18: Light micrograph of kidney of blackbass illustrating a cluster of renal corpuscles (short bold arrow). X 310.

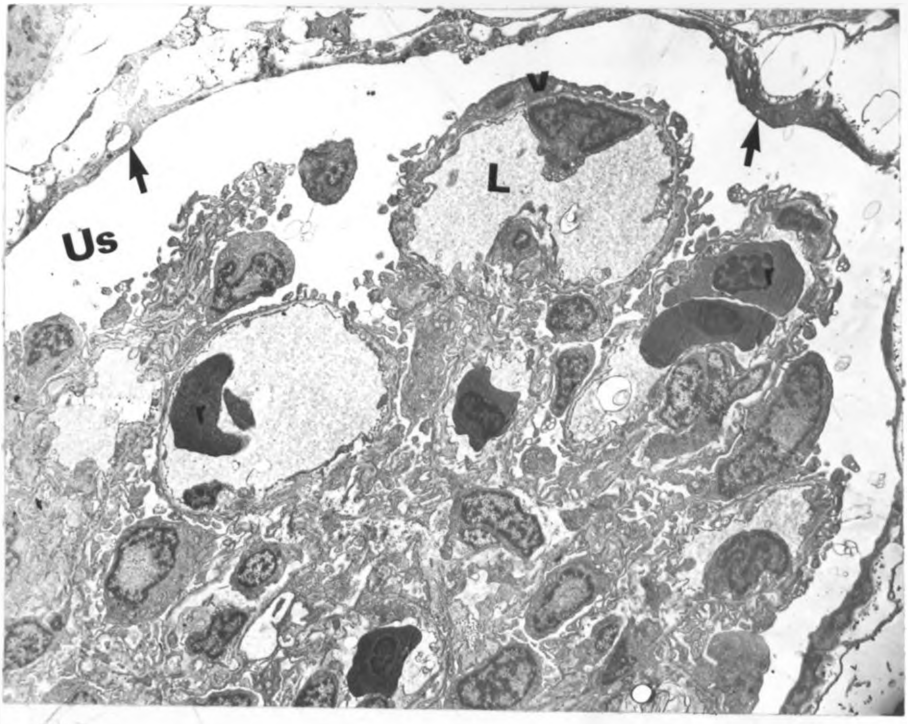

Fig. 19: Electron micrograph of a part of a renal corpuscle of tilapia. L, glomerular capillary lumen; Us, urinary space; arrows, parietal epithelium; v, visceral epithelium composed of podocytes; r, red blood cell. X 1900.

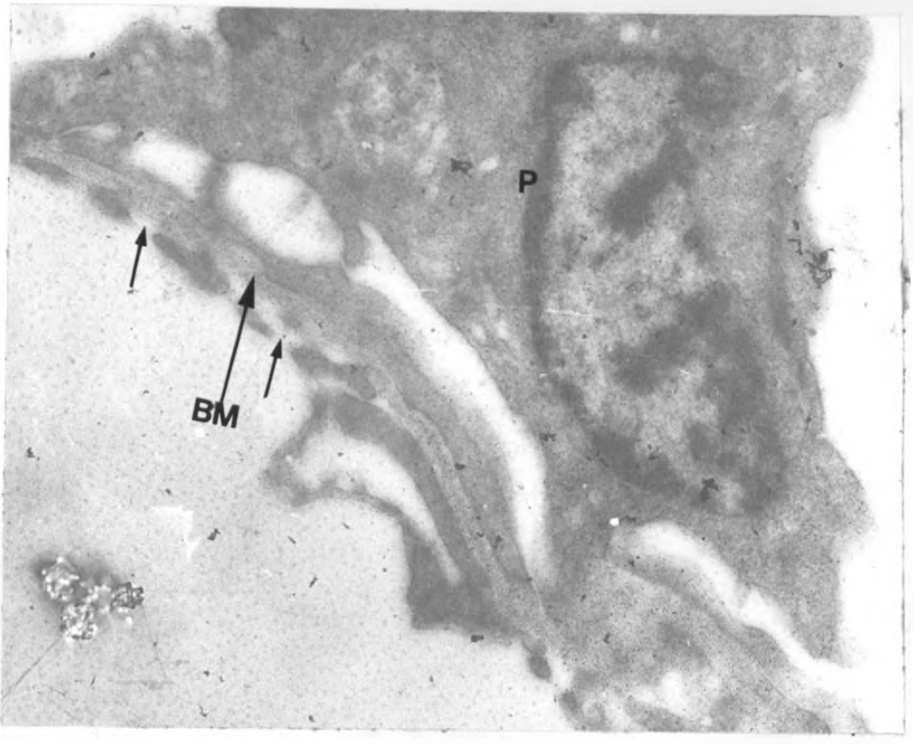

Fig. 20: Electron micrograph of part of the glomerulus showing fenestrated capillary endothelium (arrows). The basement membrane has a prominent lamina densa. P, podocyte; BM, basement membrane. X 19000.

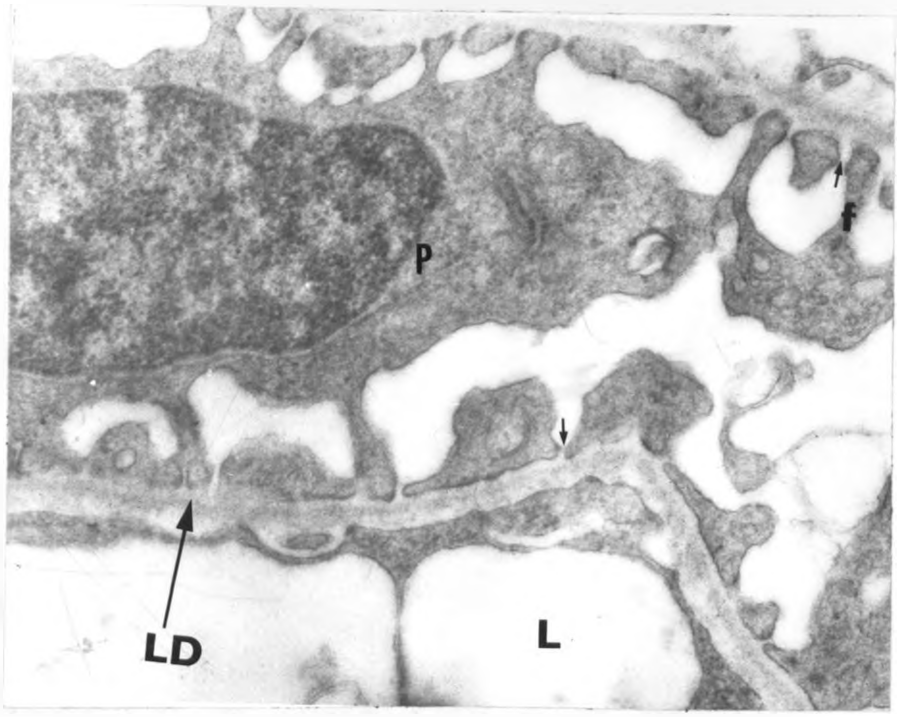

Fig. 21: Electron micrograph of a podocyte lying between two glomerular capillaries. The podocyte has many foot processes which interdigitate to form narrow pores bridged by filtration slit membranes. The basement membrane has a prominent lamina densa. P, podocyte; L, lumen; f, foot processes; LD, lamina densa; arrows, filtration slit membranes. X 19000.

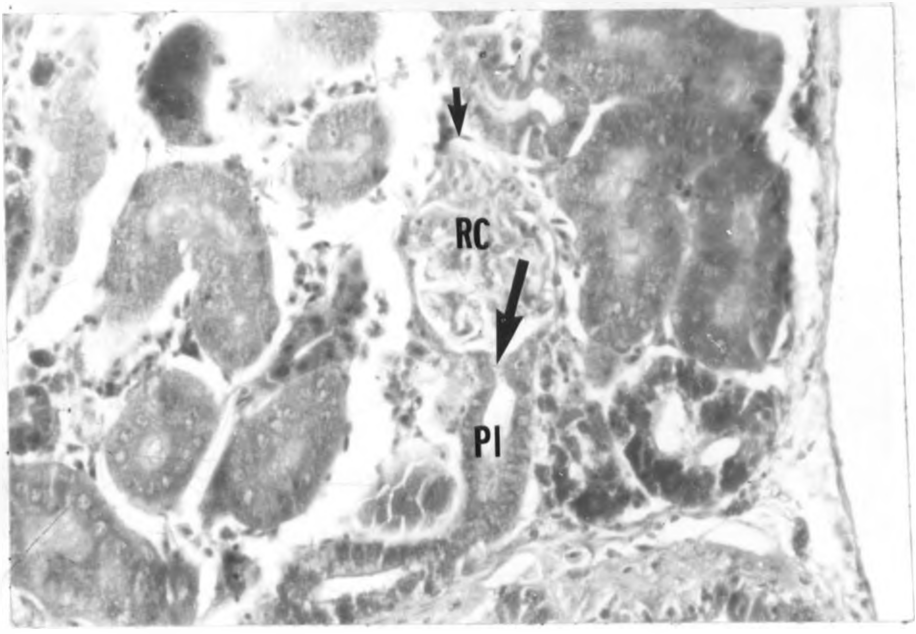

Fig. 22a: Light micrograph of the kidney of tilapia showing part of the nephron. RC, renal corpuscle; short arrow, urinary pole; long arrow, vascular pole; PI, proximal segment I. X 390.

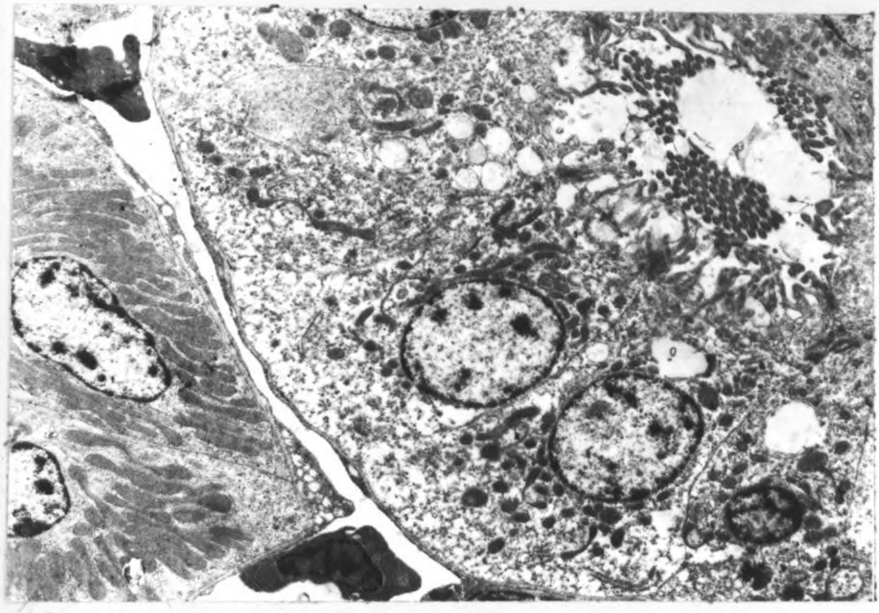

Fig. 22b: Electron micrograph of a tilapia neck segment showing the high cuboidal cells, central nucleus, perinuclear mitochondria, and luminal cilia. X 3400.

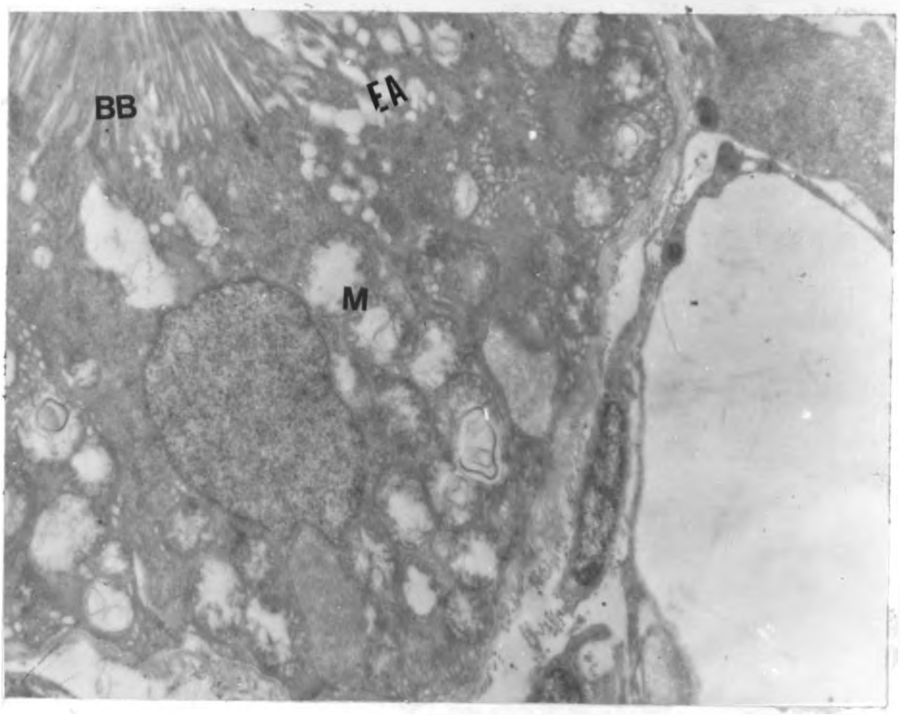

Fig. 23: Electron micrograph of the cells of the proximal tubule of tilapia showing a well developed microvilli brush border (BB), e xtensive endocytic apparatus (EA) and numerous mitochondria (M). X 4500.

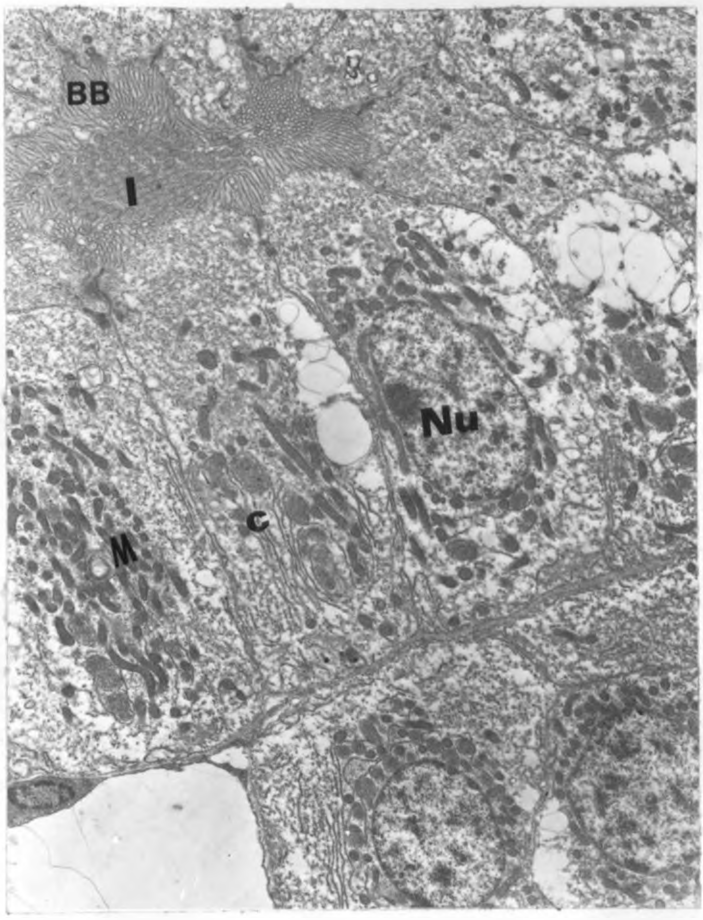

Fig. 24: Electron micrograph of proximal segment I of tilapia showing tall columnar cells (c) with central nuclei (Nu), numerous mitochondria (M) around the nucleus, well developed brush border (BB) and cilia (I) from the preceding neck segment are seen in the lumen. X 3400.

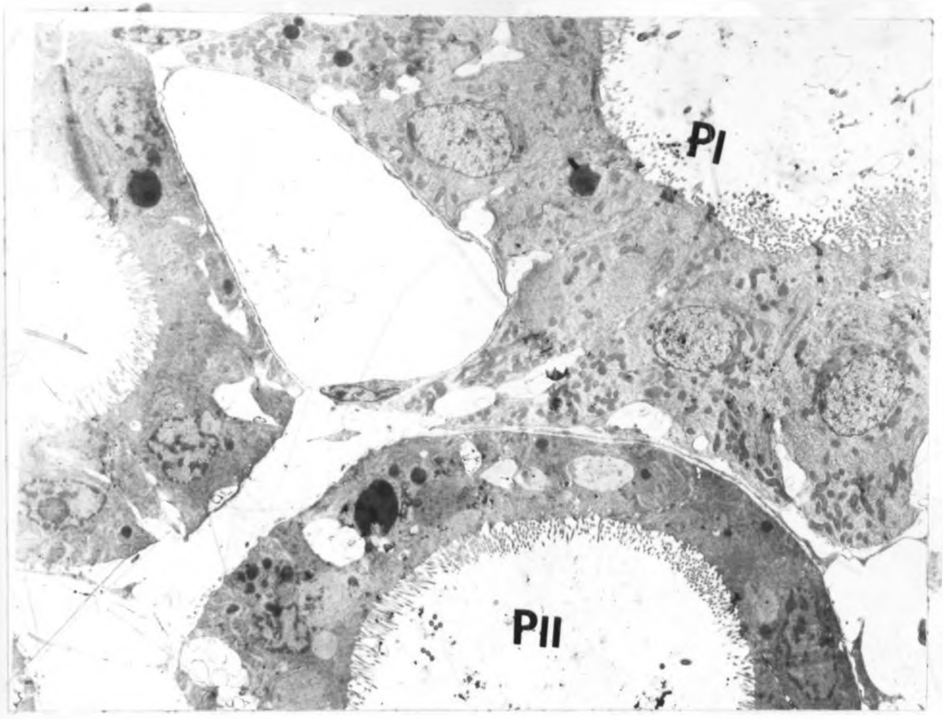

Fig. 25: Electron micrograph of a portion of the kidney of the blackbass showing proximal segment I (PI) and proximal segment II (PII). x 2500.

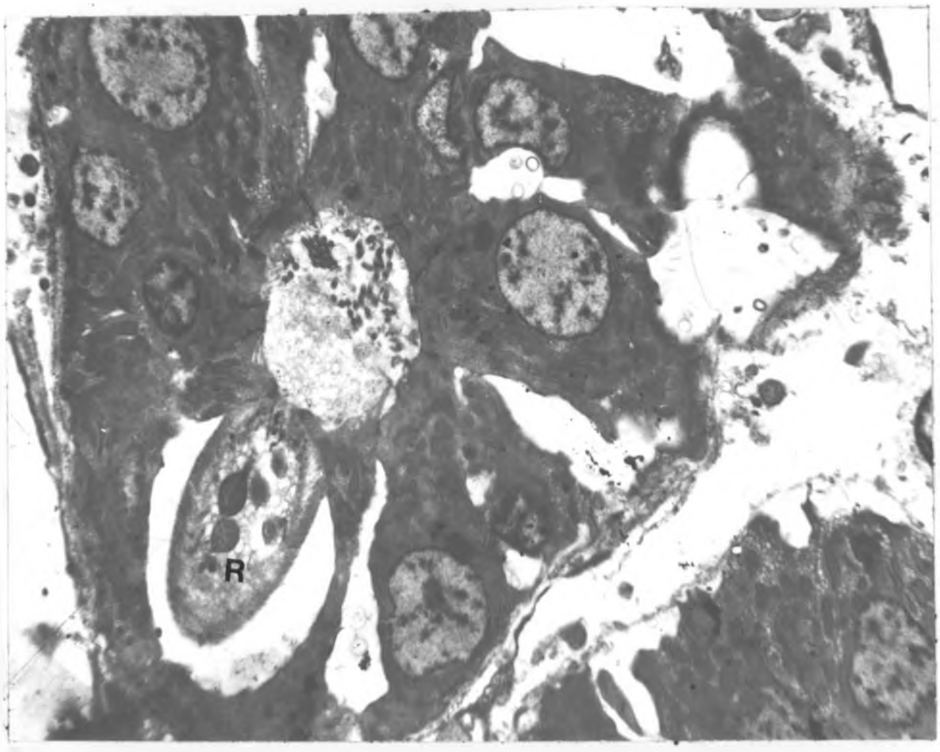

Fig. 26(a). Electron micrograph of the proximal tubule showing the location of a rodlet cell (R) in relation to the other proximal tubule cells. X 2500.

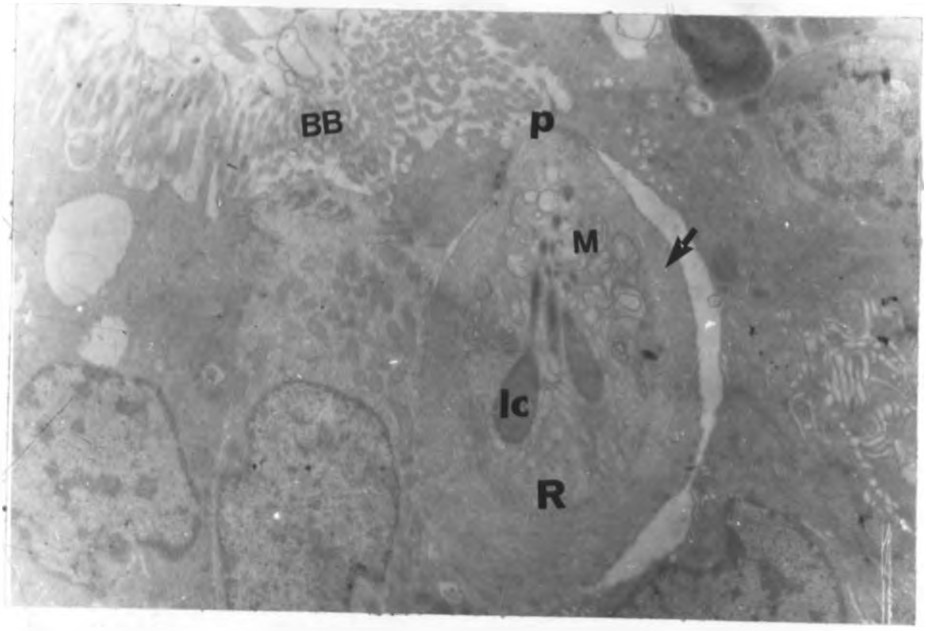

Fig. 26(b): Electron micrograph of the proximal tubule of the blackbass showing a rodlet cell (R) interposed between the columnar cells of the proximal tubule which have a brush border (BB). The rodlet cell contains several apical mitochondria (M) and opens at the apical pore (p). The cell has large crystalline inclusions (rodlets) (lc) and a thick fibrillar peripheral cytoplasm (arrows). X 5700.

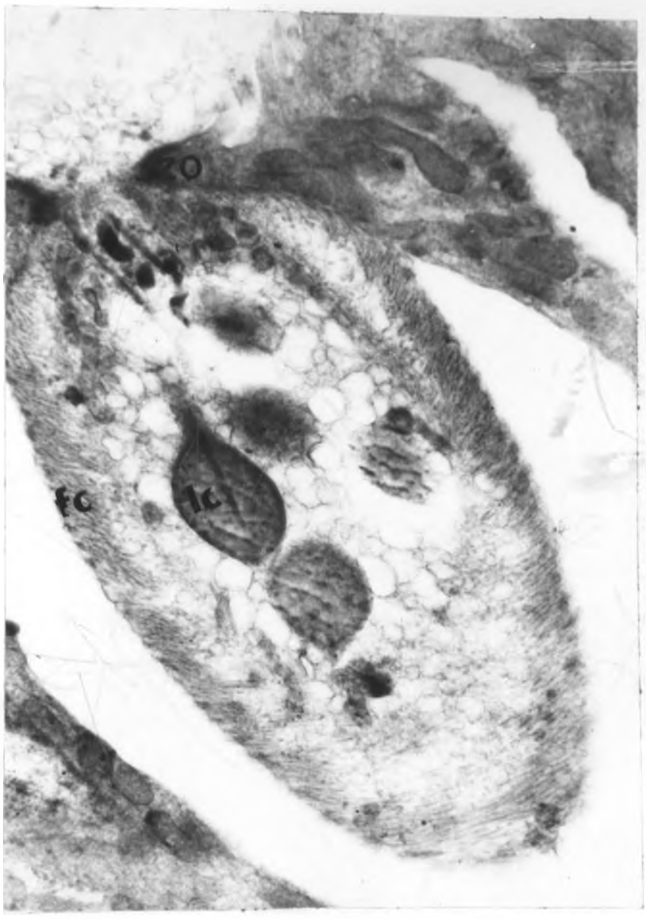

Fig. 26(c): Electron micrograph showing a higher magnification of a rodlet cell. The cell appears to be detaching from adjacent cell. fc, fibrillar peripheral cytoplasm ZO, zonula occludens; lc, crystalline inclusions (lc). X 9100.

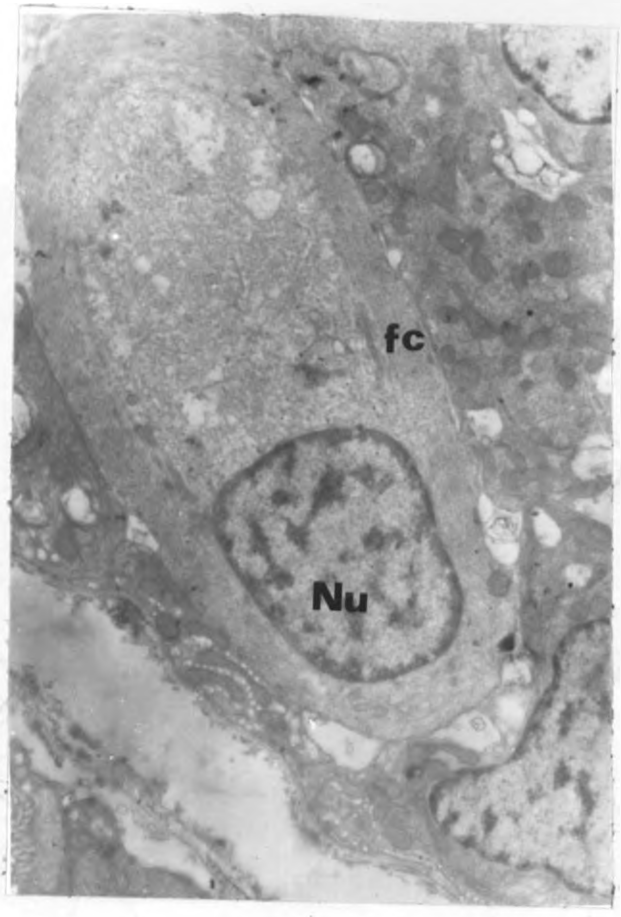

Fig. 26(d): Electron micrograph showing a rodlet cell which is ovoid in shape and has a large basal nucleus (Nu) and thick fibrillar peripheral cytoplasm (fc). This is presumably a young cell because it is close to the basement membrane and does not have either an apical pore or crystalline inclusions. X 9100.

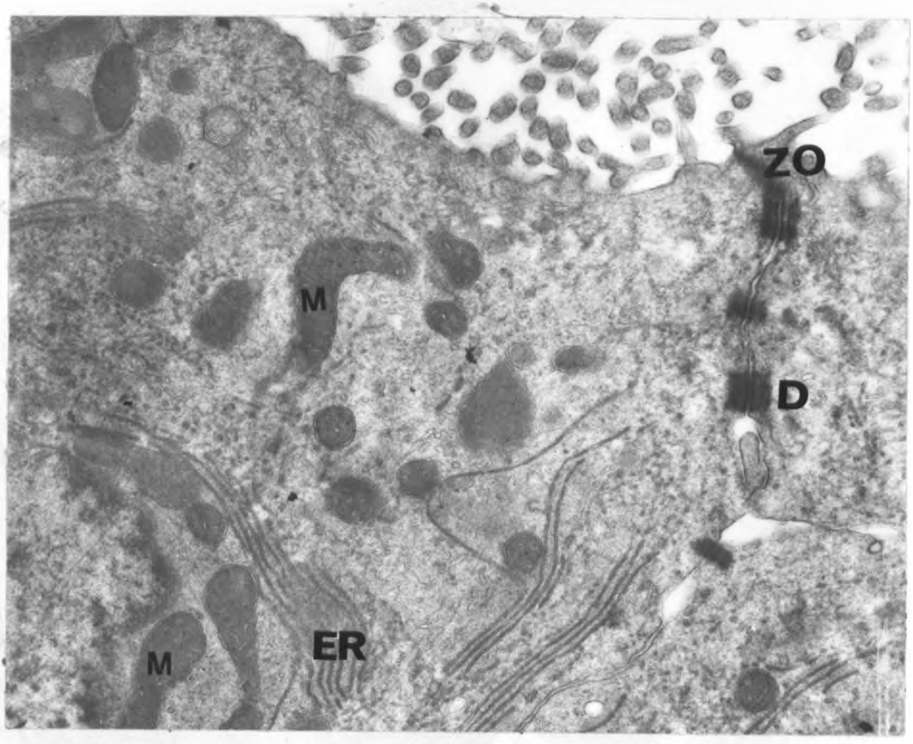

Fig. 27: Electron micrograph showing the junctional complexes in the apical region of the lateral border of two adjacent proximal tubule II cells. The zonula occludens (ZO) occurs at the apex of the cells and desmosomes (D) occur below the tight junctions in the apical one third of the cells. M, mitochondria; ER, endoplasmic reticulum. X 15000.

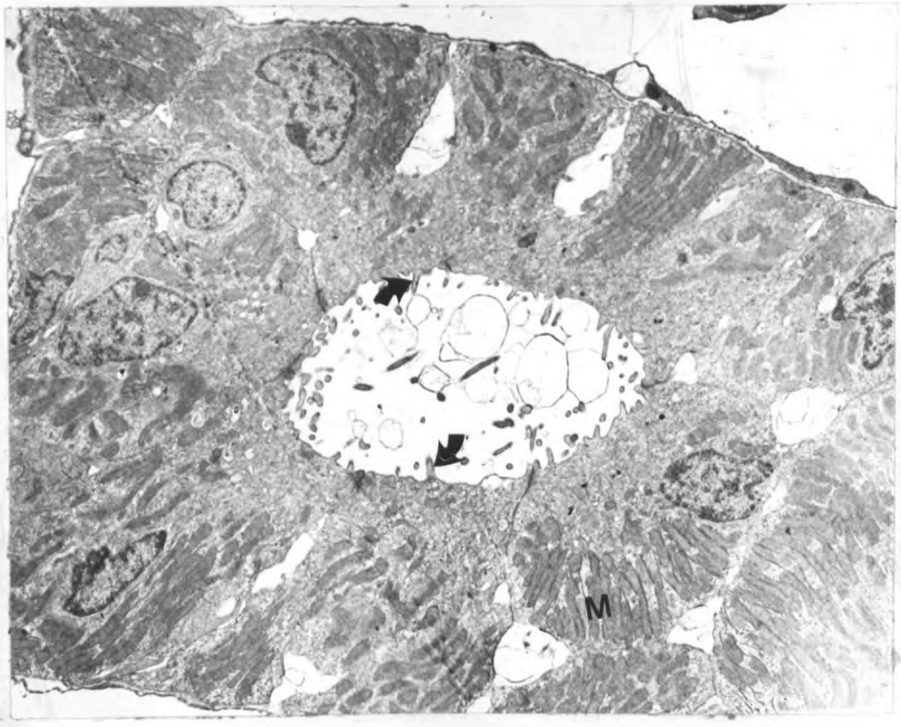

Fig. 28: Electron micrograph of the early distal tubule of tilapia illustrating few luminal microvilli (arrows) and numerous perpendicularly arranged mitochondria (M). X 1900.

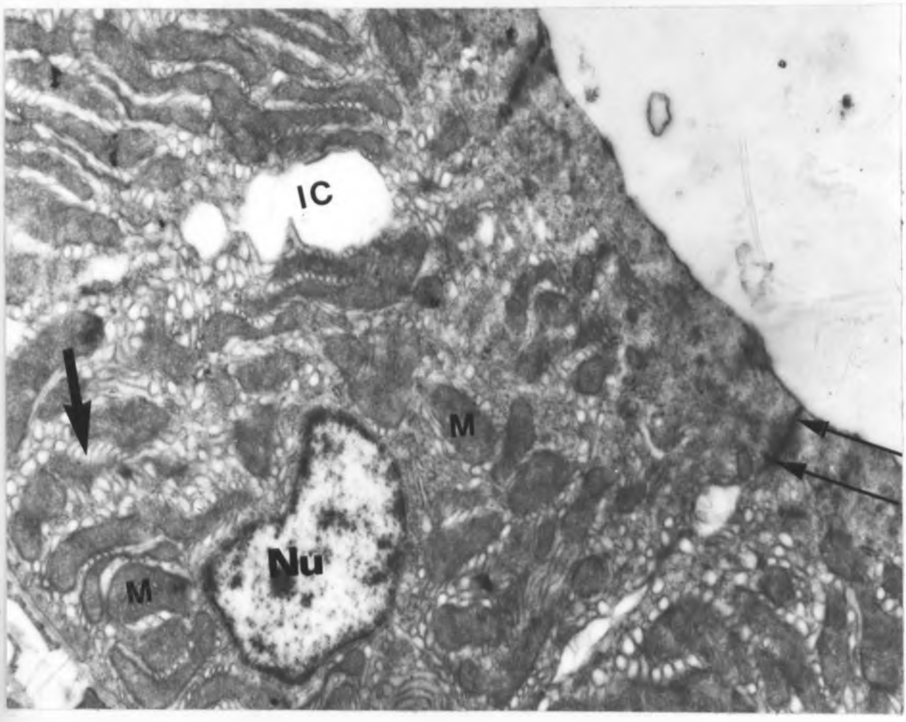

Fig. 29: Electron micrograph of the cells of the distal tubule of tilapia showing extensive basal and lateral infoldings of the cell membrane (bold arrows) and large mitochondria (M) contained in the membrane infoldings. The cells are apposed together by junctional complexes (arrows) in the apical region. Nu, nucleus; IC, intercellular space. X 7100.

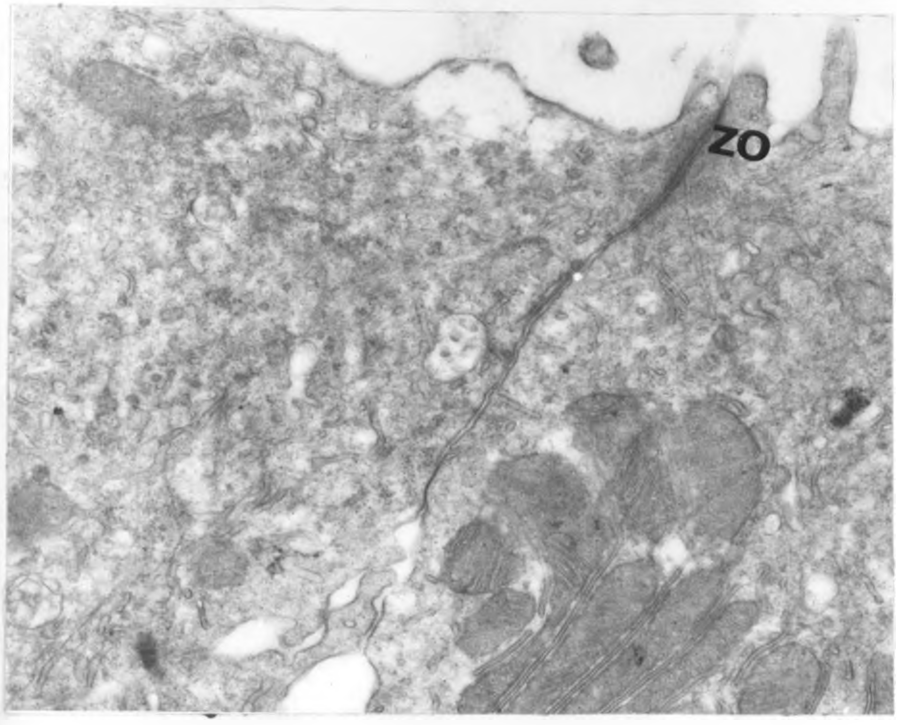

Fig. 30: Electron micrograph showing the junctional complexes in the lateral membranes of two adjacent distal tubule cells. The junctional complex consists of a long zonula occludens (ZO). X 15000.

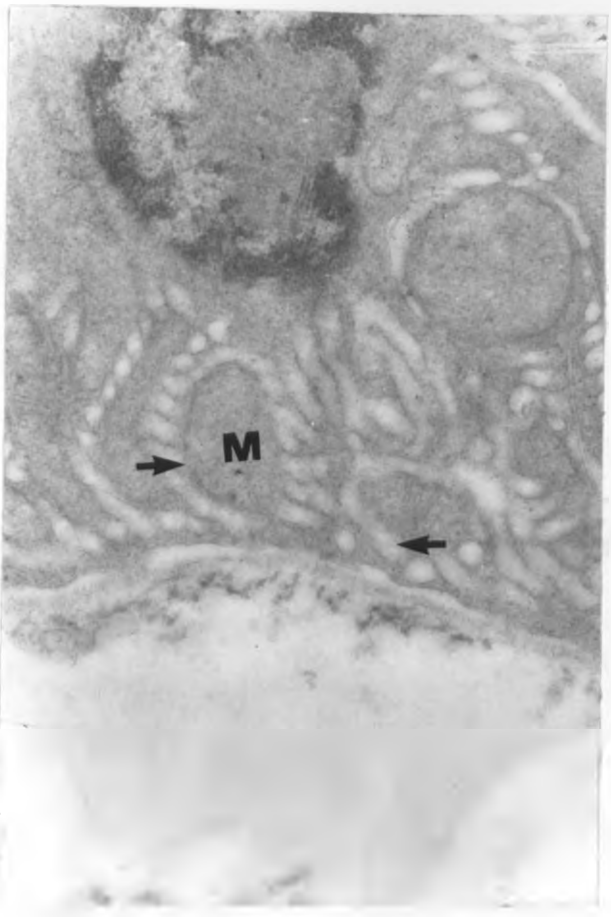

Fig. 31: Electron micrograph of part of distal tubule of blackbass showing extensive basal membrane infoldings (arrows) containing mitochondria (M). X 19000.

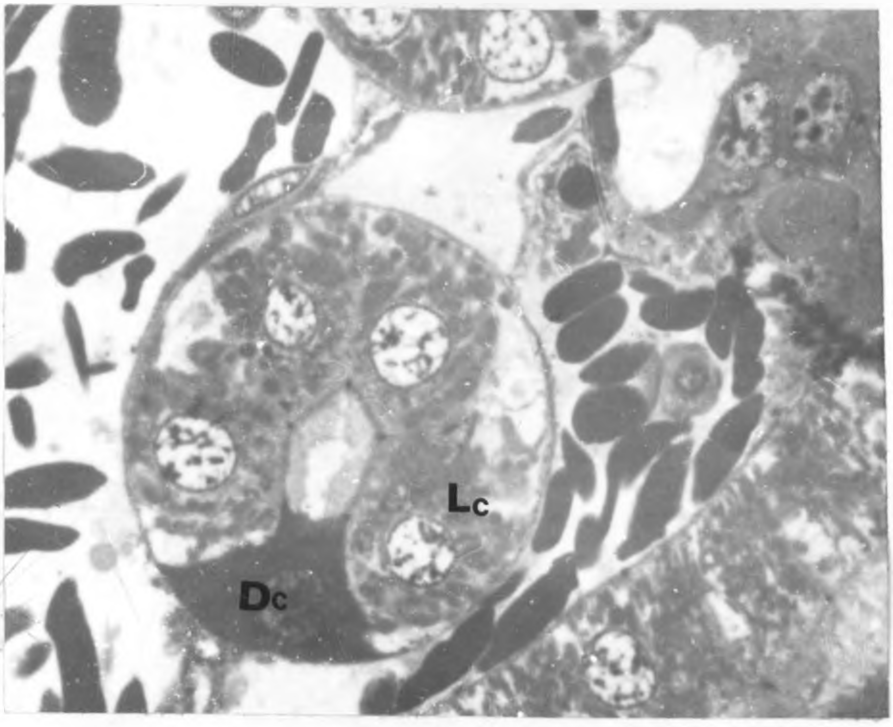

Fig. 32(a): Light micrograph of the late distal tubule of the common carp showing a dark cell (Dc) and a principal cell (Lc). X 1500.

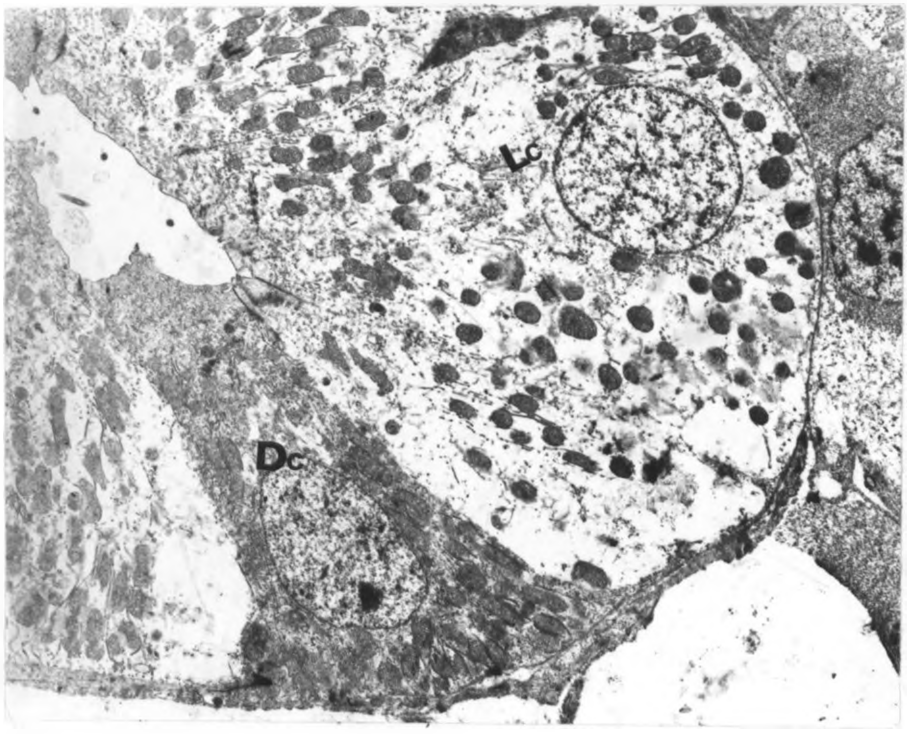

Fig. 32(b): Electron micrograph of the late distal tubule of the common carp showing two types of cells namely a dark cell (Dc) and a principal cell (Lc). X 2500.

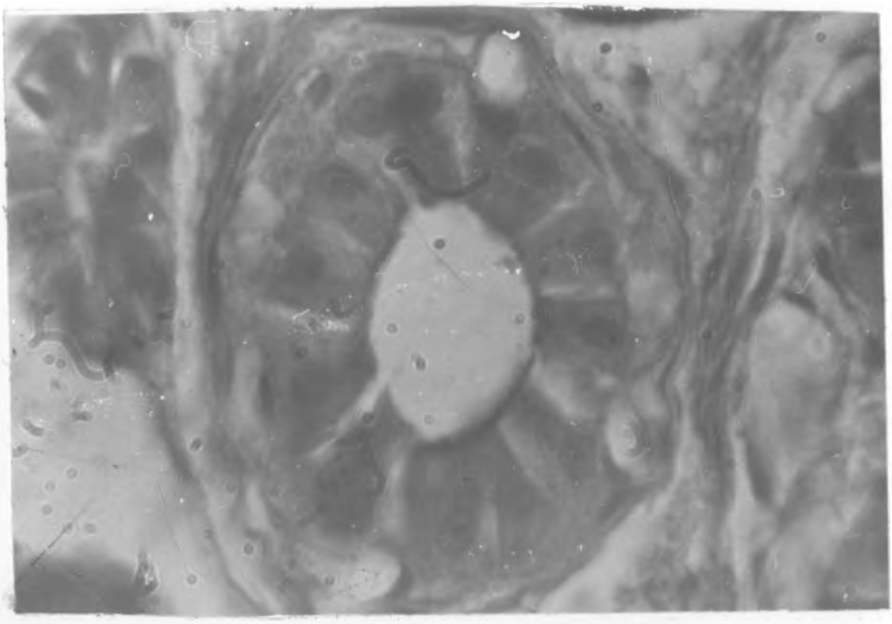

Fig. 33: Photomicrograph of the collecting duct of the blackbass. The cells lining the duct are columnar and have basal nuclei and mucin deposits on the luminal border. The epithelium is surrounded by a fibromuscular coat which is vascularised. X 625.

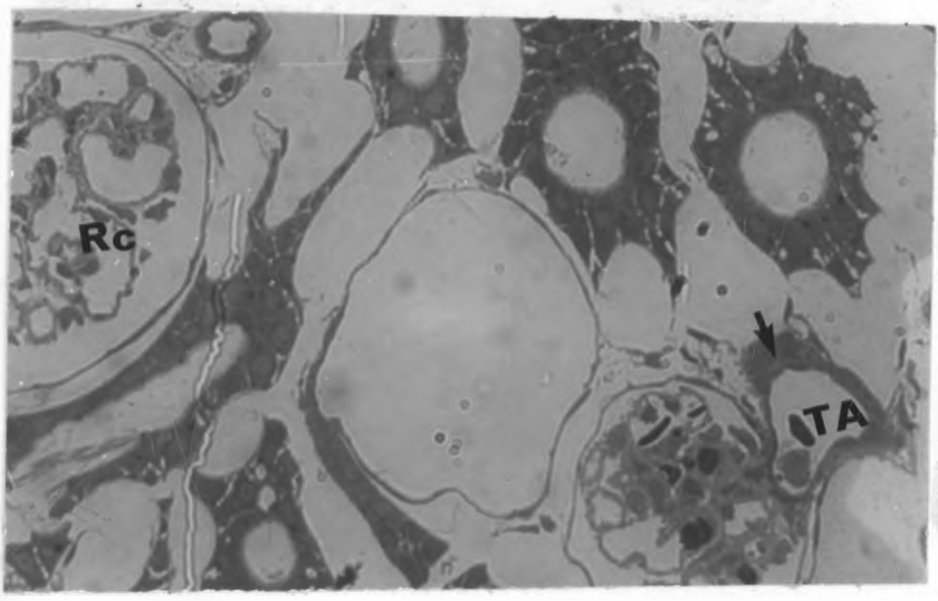

Fig. 34(a): Part of a section of the kidney of the blackbass showing the location of a juxtaglomerular cell (arrow) on the wall of a terminal arteriole (TA). Rc, renal corpuscle. X 625.

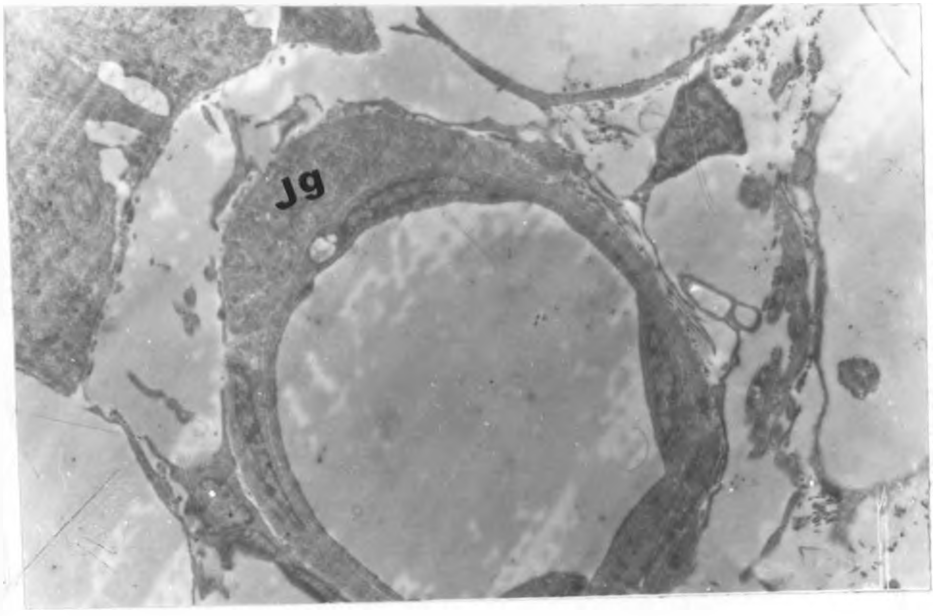

Fig. 34(b): Electron micrograph of a terminal arteriole in the kidney of the blackbass showing a juxtaglomerular cell (Jg). X 3400.

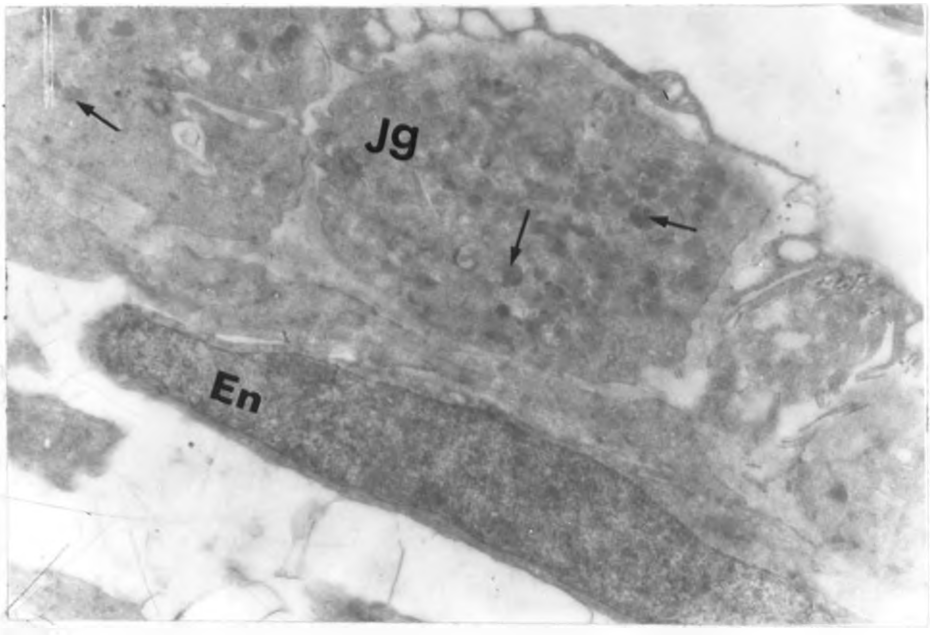

Fig. 34(c): Wall of a terminal arteriole of the blackbass showing a juxtaglomerular cell (Jg) with numerous granules (arrows) and an elongated endothelial cell (En). X 3900.

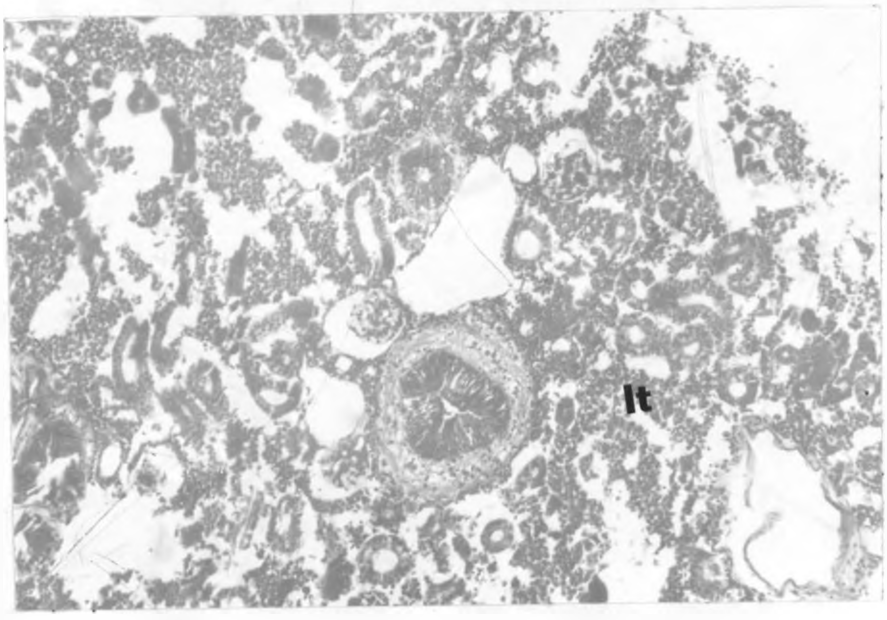

Fig. 35: Light micrograph of part of the kidney of the common carp showing abundant interstitial tissue (It). X 125.

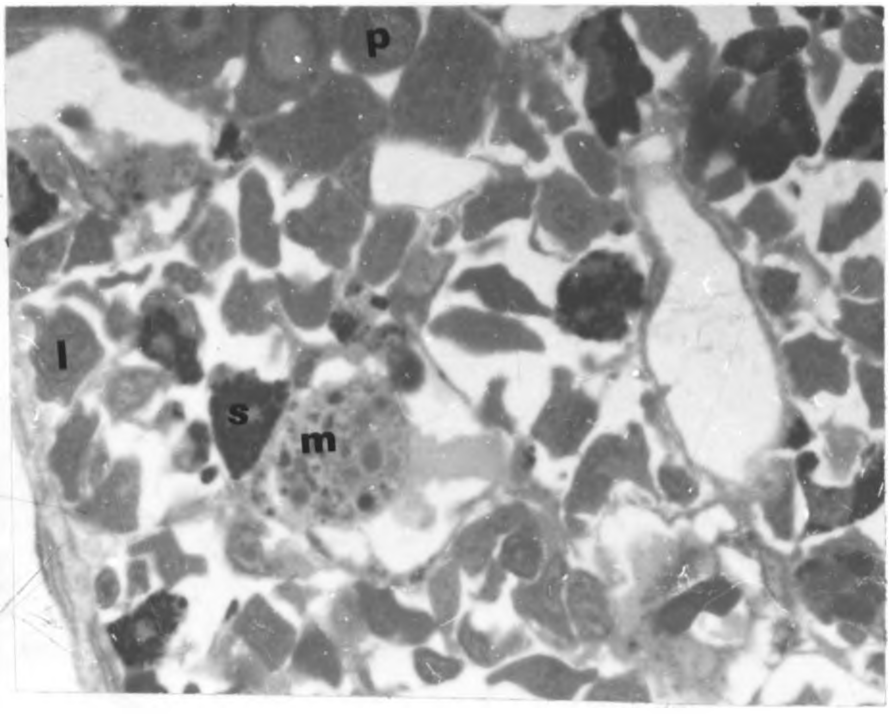

Fig. 36: Light micrograph of part of a section of the kidney of the catfish showing the cellular components of the intrarenal heamopoietic tissue. m. macrophage; l, lymphocyte; p, plasma cell; s, mast cell. X 1500.

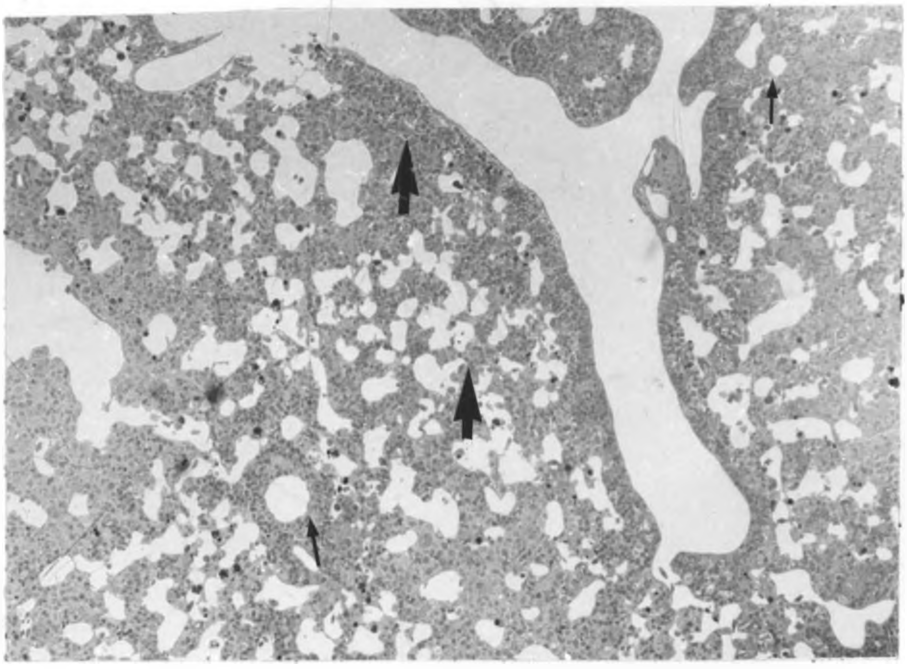

Fig. 37: Section from the head kidney of the blackbass showing the absence of renal tissue. The organ consists of interrenal tissue organised around branches of the posterior cardinal vein (short arrows) and haemopoietic tissue (bold arrows). X 125.

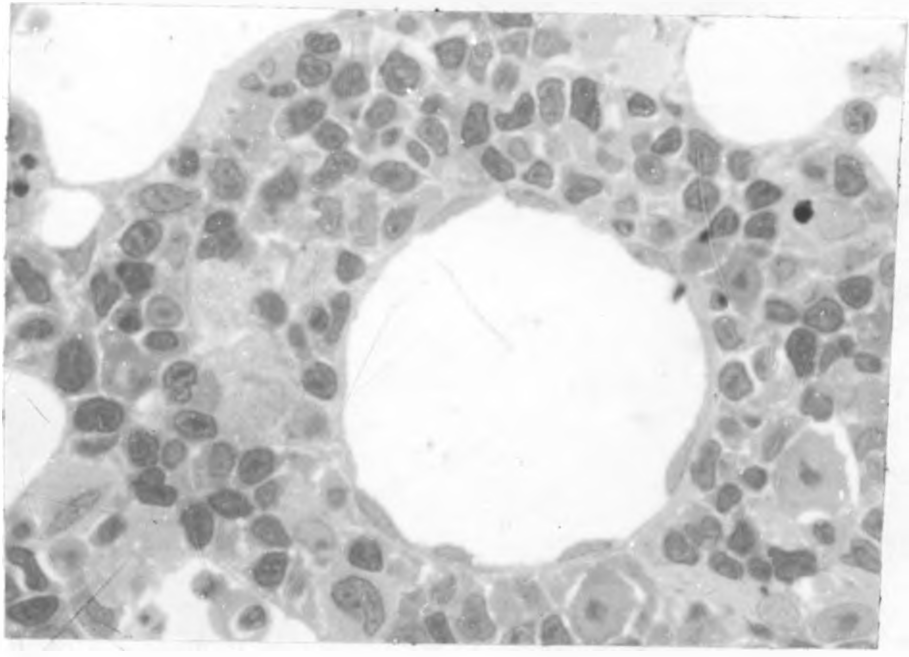

Fig. 38: Photomicrograph of a tributary of the posterior cardinal vein and the interrenal tissue around it. The tissue consists of cortical and chromaffin cells. X 1500.

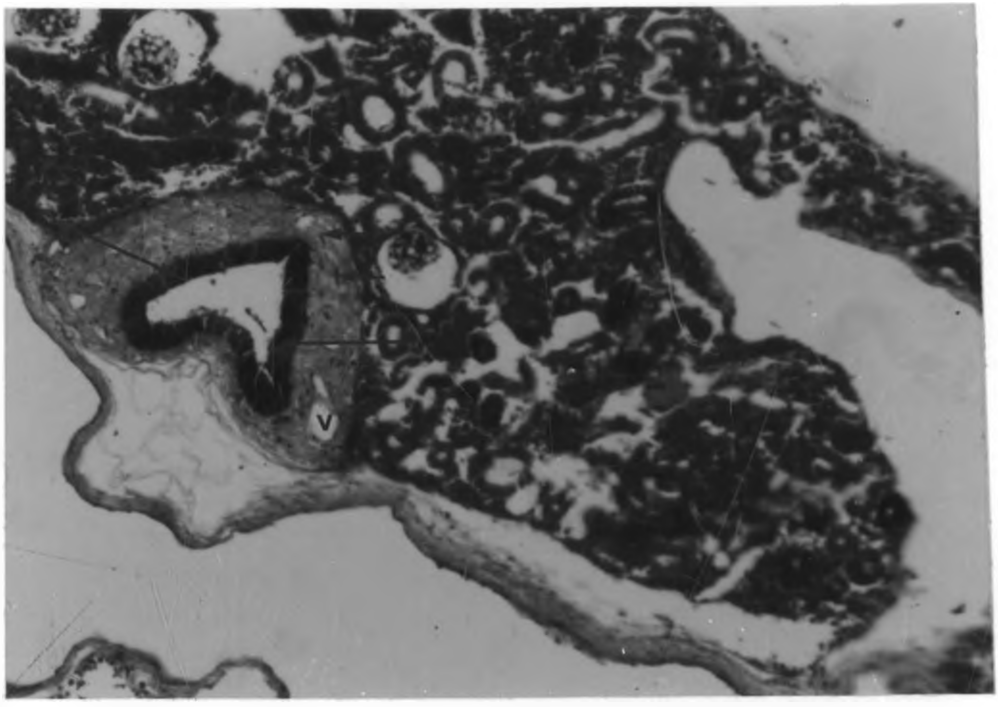

Fig. 39: Part of a section from the kidney of the common carp (stained with Gomori's trichrome, Harris's hematoxylin and alcian blue) showing an ureteral duct with a thick fibrous wall containing smooth muscle cells (small arrows) and blood vessels (V). The columnar epithelium contains goblet cells (long arrows). X 125.

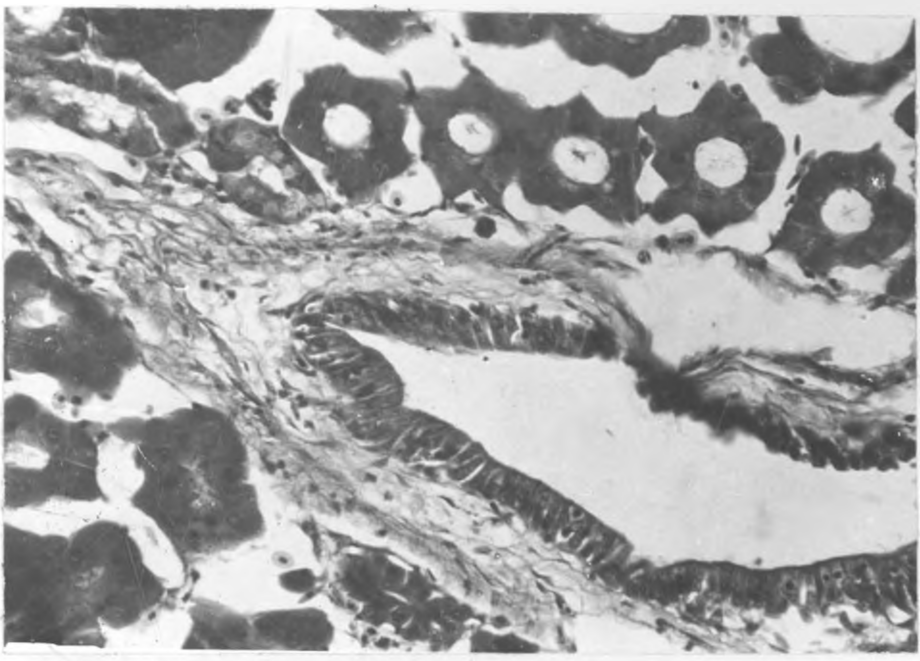

Fig. 40: Part of a section of the tilapia kidney showing the columnar epithelium of the ureter, and the relatively thick fibromuscular coat of connective tissue forming the wall of the ureter. X 390.

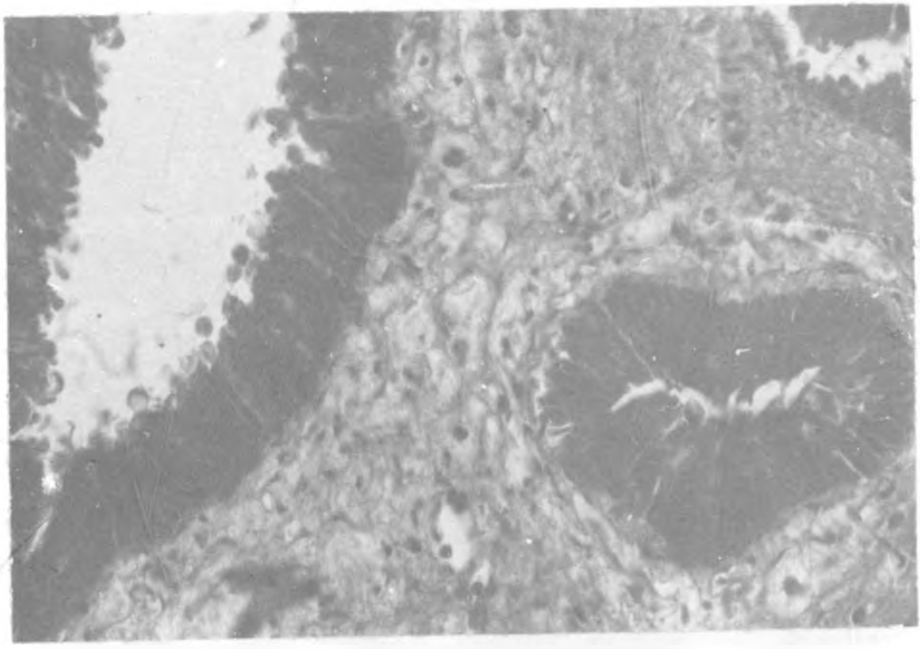

Fig. 41: Section through the ureter of the common carp showing the psuedostratified columnar epithelium X 390.

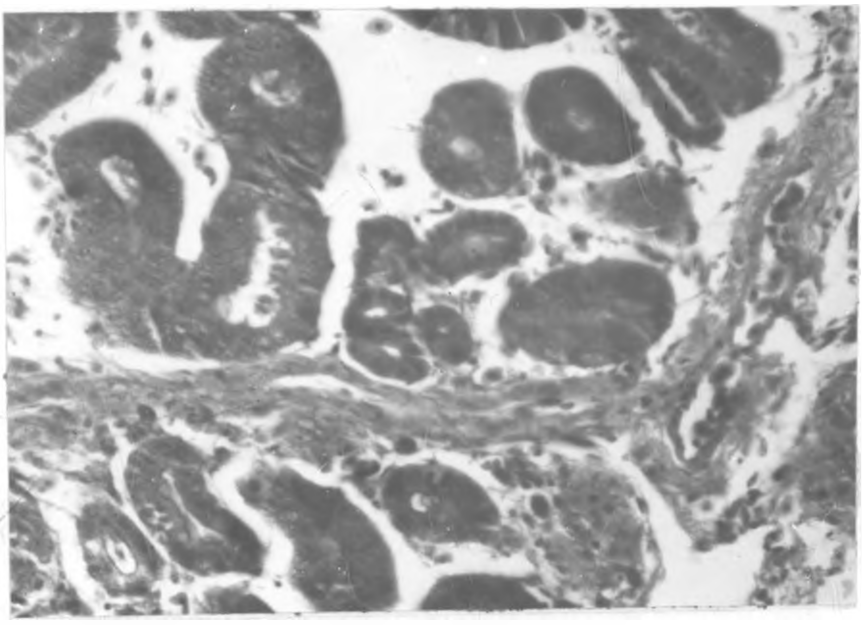

Fig. 42: Light micrograph of part of a section of the kidney of the tilapia fixed by immersion illustrating collapse and swelling of proximal tubules. Note the blood cells in the blood vessels. X 390.

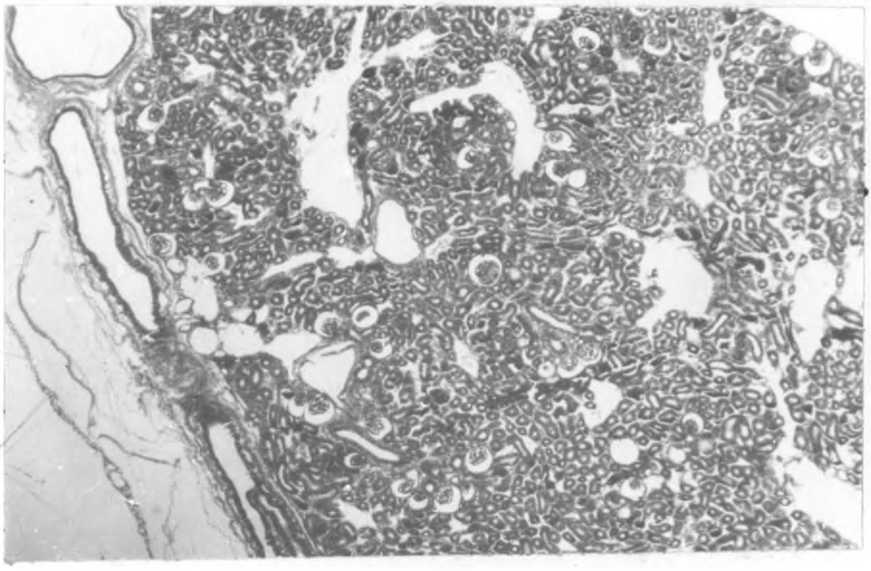

Fig. 43: Light micrograph of part of a section of the kidney of the blackbass fixed by perfusion via the arterial system showing well preserved tissue with patent tubules and blood vessels without blood cells. X 60.

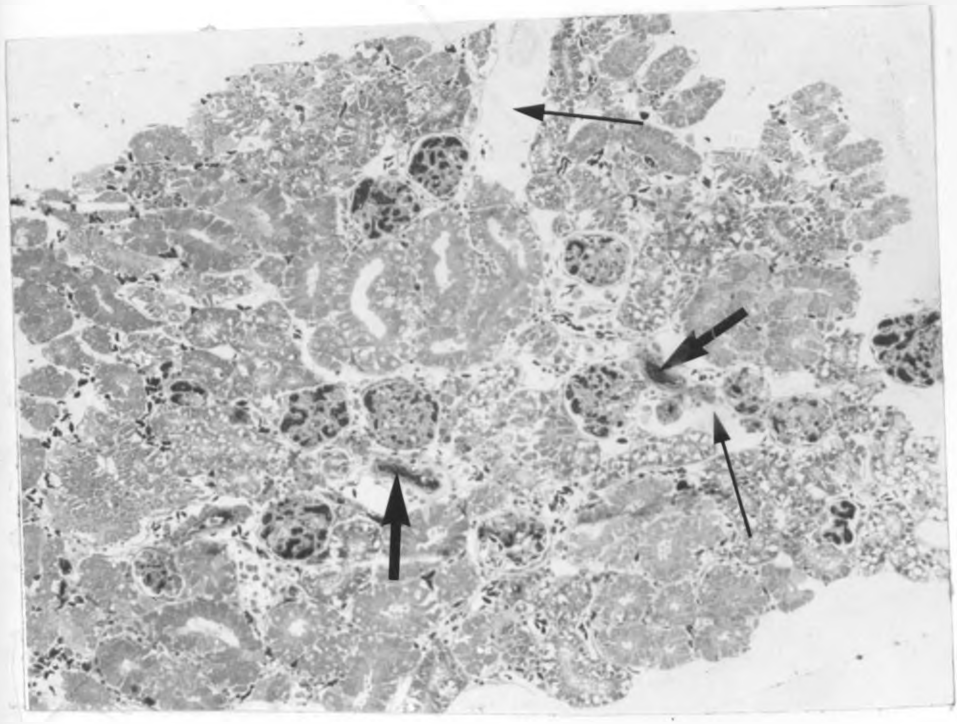

Fig. 44: Light micrograph of part of a section of the kidney of tilapia fixed by perfusion via the tail vein. The venous system (long arrows) is clear of blood but the arterial system (short bold arrows) still contains blood. Renal tissue is not adequately preserved. X 310.

T A B L E S

Species	Common name	Order	Family	collection site	Identification
Oreochromis niloticus	Tilapia	Perciformes	Cichlidae	Sagana Fisheries (Freshwater)	One pair of nostrils, dorsal fin spinous and long-based, caudal ends of dorsal and anal fins pointed
Micropterus salmoides	Blackbass	Perciformes	Cichlidae	Lake Naivasha (Freshwater)	Body fairy slim, dorsal and anal fins have spines, dorsal fin has a soft part continous with spinous part.
Cyprinus carpio	Common carp	Cypriniformes	Cyprinidae	Masinga dam (Freshwater)	Elongate body form covered by cycloid scales, barbels present at corners of the mouth, pharyngeal teeth present, swimbladder two-chambered, Weberian apparatus present.
Clarias mossambicus	Catfish	Siluriformes,	Clariidae	Masinga dam (Freshwater)	Streamlined body, Weberian apparatus present, no spines on long dorsal fin and anal fin, barbels occur at the corners of the mouth, possesses a labyrinthic organ, liver and kidney have lateral lobes.
Chanos chanos	Milkfish	Salmoniformes	Salmonidae	Indian Ocean (Marine)	Body and fins streamlined and symmetrical, body covered with small smooth cycloid scales, paired pectrol fins directly posterior to the head, caudal fin well developed.

Table 1: Species studied, their common names, Order, Family, collection site and identifying characteristics.

Species	n	Body weight (g)	Body surface area (cm^2)	Kidney volume (mm^3).	V_k/Bwt (mm^3/g)	V_k/BSa (mm^3/cm^2)
Tilapia *(O. niloticus)*	6	86.98 ± 17.80	176.24 ± 24.36	248.00 ± 72.21	2.83 ± 0.34	1.39 ± 0.23
Blackbass *(M. salmoides)*	6	442.69 ± 119.94	520.34 ± 93.84	978.30 ± 278.3	2.22 ± 0.27	1.86 ± 0.23
catfish *(C. mossambicus)*	5	75.69 ± 41.44	157.12 ± 57.80	466.00 ± 262.3	6.13 ± 0.71	2.81 ± 0.63
Common carp *(C. carpio)*	5	439.47 ± 247.11	526.05 ± 173.39	1854.00 ± 1025	4.24 ± 0.97	3.35 ± 0.72
Milkfish *(C. chanos)*	5	17.86 ± 6.17	60.90 ± 14.17	42.00 ± 13.04	2.38 ± 0.14	0.68 ± 0.06

Table 2: Mean (± S.D.) values for body weight (Bwt) (g), body surface area (BSa) (cm^2), kidney volume, kidney volume per gram body weight (V_k/Bwt) and kidney volume per square centimeter of body surface area (V_k/BSa) of the teleosts examined in the present study.

Species	n	Uriniferous tissue		Blood vessels		Ureter and its ducts		Haemopoietic tissue		connective tissue	
		V_V(%)	Absol. vol.	V_V(%)	Absol. vol.	V_V(%)	Absol. vol.	V_V(%)	Absol. vol.	V_V(%)	Absol. vol.
Tilapia	6	72.52 ± 1.73	180.19 ± 52.39	22.57 ± 1.45	56.10 ± 16.86	2.84 ± 0.49	7.15 ± 2.68	0.00	0.00	2.07 ± 0.38	5.24 ± 2.17
Blackbass	6	64.43 ± 1.43	629.33 ± 176.64	24.88 ± 1.21	243.66 ± 69.73	8.20 ± 0.41	80.73 ± 26.14	0.00	0.00	2.48 ± 0.43	24.48 ± 8.27
Common carp	5	41.42 ± 1.63	757.80 ± 406.06	21.93 ± 1.36	414.94 ± 253.32	4.20 ± 0.50	78.69 ± 45.70	28.90 ± 2.0	526.34 ± 22.18	3.60 ± 0.74	70.39 ± 53.90
Catfish	5	42.89 ± 1.43	201.98 ± 118.78	24.1 ± 1.36	112.56 ± 63.62	1.59 ± 0.18	7.46 ± 4.43	28.73 ± 1.64	131.60 ± 69.27	2.70 ± 0.35	12.42 ± 7.15
Milkfish	5	36.03 ± 1.67	15.11 ± 4.55	25.59 ± 1.12	9.49 ± 5.32	2.78 ± 0.59	1.17 ± 0.83	34.22 ± 1.11	15.65 ± 3.86	1.37 ± 0.17	0.58 ± 0.06

Table 3: Mean (± S.D.) values for the percentage(V_V%) volume densities and absolute volumes(absol. vol.) of the main components of the kidney. The uriniferous tissue comprised of the nephron and blood capillaries, blood vessels included all the blood vessels larger than capillaries, ureter and its ducts included the ureter and its primary and secondary ducts, heamopoietic tissue consisted of all the interstitial tissue.

Species	n	Renal corpuscles (%)	Neck segment (%)	Proximal segment (%)	Distal segment (%)	Collecting tubules and ducts (%)	Capillaries (%)
Tilapia	6	4.06 ± 0.51	0.45 ± 0.15	62.80 ± 2.21	17.67 ± 3.36	5.10 ± 1.76	9.96 ± 1.40
Blackbass	6	5.74 ± 0.29	0.67 ± 0.37	58.96 ± 1.87	16.83 ± 0.86	5.58 ±1.27	11.85 ± 2.06
Common carp	5	3.55 ± 0.95	0.95 ± 0.29	59.36 ± 1.77	15.51 ± 1.25	6.04 ± 0.74	14.57 ± 0.26
Catfish	5	3.39 ± 0.48	0.83 ± 0.24	59.42 ± 2.22	18.15 ± 1.91	6.55 ± 1.16	12.16 ± 1.05
Milkfish	5	2.11 ± 0.38	0.18 ± 0.07	73.74 ± 2.82	7.83 ± 1.29	3.50 ± 1.04	12.75 ± 1.15

Table 4 : Mean (± S.D.) values for the percentage volume proportions of the components of uriniferous tissue components expressed in renal parenchyma.

Species	n	Renal corpuscles (%)	Neck segments (%)	Proximal segments (%)	Distal segments (%)	Collecting tubules & ducts (%)	Capillaries (%)
Tilapia	6	2.94 ± 0.38	0.33 ± 0.11	45.50 ± 1.60	12.80 ± 2.43	3.70 ± 1.28	7.21 ± 0.9
Blackbass	6	3.70 ± 0.18	0.43 ± 0.24	37.51 ± 1.19	10.71 ± 0.55	3.55 ± 0.81	8.50 ± 1.02
Common carp	5	1.47 ± 0.39	0.39 ± 0.12	24.48 ± 0.73	6.40 ± 0.52	2.49 ± 0.30	6.04 ± 0.32
Catfish	5	1.44 ± 0.20	0.35 ± 0.10	25.37 ± 0.95	7.75 ± 0.81	2.80 ± 0.49	5.19 ± 0.53
Milkfish	5	0.76 ± 0.12	0.07 ± 0.03	26.75 ± 1.02	2.84 ± 0.47	1.27 ± 0.38	4.52 ± 0.41

Table 5: Mean (± S.D.) values for the percentage volume proportions of the components of the uriniferous tissue expressed in the kidney as a whole.

Groups	No. of fish	K.vol./Bwt (mm^3 /g)	Renal corpuscles Vv (%)	Uriniferous tissue V_V (%))	Tubules V_V (%)	Total vascular space V_V (%)
Percoid	12	2.56 ± 0.40	3.32 ± 0.49	68.46 ± 4.48	57.61 ± 5.10	31.48 ± 1.49
Ostariophysian	10	5.18 ± 1.11	1.46 ± 0.29	41.66 ± 1.67	28.73 ± 1.36	35.08 ± 1.78
		(P<0.001)	(P<0.001)	(P<0.001)	(P<0.001)	(P<0.02)
With haemopoietic tissue	15	4.25 ± 1.63	1.24 ± 0.43	39.85 ± 2.86	33.64 ± 2.63	28.19 ± 1.43
Without haemopoietic tissue	12	2.56 ± 0.40	3.32 ± 0.49	68.46±4.48	57.61 ± 5.10	31.48 ± 1.49
		(P<0.02)	(P<0.001)	(P<0.001)	(P<0.001)	(P<0.001)
Freshwater	22	3.75 ± 1.55	2.47 ± 1.03	56.28 ± 14.06	47.37 ± 12.11	30.23 ± 1.98
Marine	5	2.38 ± 0.15	0.76 ± 0.12	36.23 ± 0.99	30.75 ± 1.22	27.16 ± 0.91
		(P>0.05)	(P<0.02)	(P<0.05)	(P>0.05)	(P>0.02)
Mean for all fish	27	3.50 ± 1.49	2.16 ± 1.45	52.56 ± 14.93	44.27 ± 12.75	29.59 ± 2.20

Table 6 : Comparison of the mean (± S.D.) values for kidney volume per gram body weight and volume proportions of renal corpuscles, uriniferous tissue, tubules and total vascular space in groups of fish with contrasting characteristics. The percoid group includes the tilapia and the blackbass and the ostariophysian includes the catfish and the common carp. Tubules comprised of the proximal and the distal tubules and the total vascular space comprised of the blood capillaries and blood vessels larger than capillaries.

Species	n	Renal corpuscle diameter (µm)	Glomerular diameter (µm)	Proximal tubule outer diameter (µm)	Distal tubule outer diameter (µm)
Tilapia	6	66.42 ± 9.59	52.73 ± 8.36	45.99 ± 16.77	32.43 ± 7.03
Blackbass	6	69.32 ± 6.92	47.02 ± 6.40	37.50 ± 11.10	26.86 ± 6.73
Common carp	5	65.76 ± 5.43	47.64 ± 7.85	48.87 ± 14.60	26.43 ± 7.90
Catfish	5	63.14 ± 7.07	44.10 ± 6.76	42.52 ± 10.68	30.55 ± 7.47
Milkfish	5	37.44 ± 6.73	29.07 ± 6.48	----------	----------

Table 7: Mean (± S.D.) values for the diameters of renal corpuscles , glomerulus, and proximal and distal tubules of the species studied.

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