THE DEVELOPMENT OF THE MESONEPHROS OF THE PINK SALMON, 

ONCORHYNCHUS GORBUSCHA (WALBAUM).

by

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ABSTRACT

The development of the kidney of the pink salmon was traced from the earliest stages to the year-old fingerling. The development of the pronephros has been treated separately.

The mesonephros develops from the intermediate cell mass of the twelfth to the thirty-ninth segments. Differentiation of the unsegmented intermediate cell mass closely follows segmentation of the somites. The vascular strand is established beneath the hypochord by migration of cells from the intermediate mesoderm of either side. A solid cylindrical duct rudiment forms as a fold of the dorsolateral aspect of the mass on either side. Mesonephrogenic material separates as a narrow bridge of cells passing from one duct to the other between the cardinal vein and the aorta. Primary mesonephrogenic rudiments appear as condensations of the bridge cells closest to the ducts. Tubule rudiments are formed by elongation of the condensations. The free end of each tubule rudiment dilates to form a thin walled Bowman capsule whose lumen later extends into the tubule rudiment and finally opens to the duct. A glomerulus develops in the Bowman capsule as a solid invagination of cells from the vascular strand. This mass of cells subsequently becomes vascularised. Differentiation of the tubule into regions follows the appearance of the glomerulus. Secondary and subsequent tubule generations are
are similarly formed but open into previously formed primary tubules. The intertubular spaces become filled with myeloid tissue richly supplied with blood sinuses. The myeloid tissue is derived from the vascular strand. Three pairs of corpuscles of Stannius appear early in development as outgrowths of the segmental duct epithelium. Smaller unpaired corpuscles appear later to make the total number twelve.

The fully differentiated nephron has five regions:

1. a Bowman capsule and glomerulus
2. a short neck segment which opens directly from the Bowman capsule
3. a segment characterised by its low columnar epithelium and high brush border
4. a segment with tall columnar cells and a low brush border
5. a segment of low simple columnar cells.

Several nephrons enter a collecting tubule. At least three generations of tubules open to the segmental duct by way of a common collecting duct formed by modification of the primary collecting tubule.

Involution of the pronephros commences at about the time the fry normally enter the water at the river mouth. Retention in fresh water does not appear to affect the time of onset of involution. The pronephric region becomes very richly permeated with blood sinuses and may serve as a blood storage organ in older fish.
In the oldest specimens studied arterial blood is supplied by paired arterioles in the intersegmental septa. Venous blood from the tail passes directly into a large median vein which passes anteriad in the kidney tissue. This vein originates as the right postcardinal vein in the young embryo. The left postcardinal does not develop posterior to the pronephros. Portal blood from the dorsal and ventral musculature reaches the kidney by way of venules in the myosepta. In the posterior region two large median arteries (arteria primitiva mesenterica) pass through the kidney to the hind gut. In the pronephric region the large median coeliaco-mesenteric artery passes through the kidney to supply the viscera.

Glomerular counts made on samples taken from fresh and salt water over a period of two months suggest that the increased osmotic concentration of the marine environment has the effect of retarding the rate of development of new glomeruli in a logarithmic relation to length.
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I. INTRODUCTION

It has been suggested that the kidney is primarily an osmoregulatory organ and that its excretory role in higher vertebrates is secondarily acquired (Marshall and Smith, 1930; Smith, 1951). The secondary nature of renal excretion is especially apparent in the fish since the majority of metabolic wastes are lost extrarenally through the gill membranes, (Smith, 1928).

Evolutionary modification of the teleost kidney has involved particularly the degree of development of the glomerular apparatus. It was thought that a study of the kidney of the anadromous Pacific Salmon would prove of interest in this respect. Changes in the kidney structure during development were anticipated such as would facilitate adaptation to the dual osmotic environment of a migratory fish. This study includes:-

1. A descriptive account of the development of the mesonephros.

2. A study of the structure of the fully differentiated mesonephric nephron.

3. A consideration of some of the physiological aspects of osmoregulation viewed in the light of histological observations.
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III. LIFE HISTORY OF THE PINK SALMON

The Onchorhyncids are anadromous fishes which spend the earlier part of their life in fresh water. Pinks spawn in fresh water in the early fall. The alevins hatch after about sixty days incubation in gravel beds at stream head waters. Early the following spring the fry migrate seaward. Maturity is attained at the end of two years when the adults return to the streams from which they emerged, spawn and die.

Pinks are the smallest of the Pacific Salmon. Their young are readily identified by the absence of parr marks. Adults are identified by:

1. The number of rakers on the first gill arch (26-34)
2. The number of rays in the anal fin (13-17)
3. The number of scales on the lateral line (170-229).

Metamorphosed males are further identified by their very large dorsal hump (Clemens and Wilbee, 1946).

Pinks were chosen for this study because their rapid development makes them particularly suitable for developmental study.
IV. HISTORICAL REVIEW

A. The Study of the Kidney in Fish

In the late nineteenth and early twentieth centuries emphasis was placed on descriptive studies of renal development in fish. The account by Price (1897, 1904) of the development of the kidney of *Bdellostoma stouti* is one of the classic illustrations of the primitive mode of renal development. Accounts of teleost kidney development were published by Rosenberg (1867), Emery (1882), Brook (1887), McIntosh and Price (1887), Swaen and Brachet (1899, 1901) and Felix (1906). More recent studies by Stroer (1933), Maschkowzeff (1934), Kindahl (1938) and Moghe (1945) are available. A brief review was compiled by Moghe (1947).

Embryological studies encouraged speculation over the evolutionary origin of the three vertebrate kidney regions. Two major theories were proposed:–

1. that the pronephros, mesonephros and metanephros as described by Lankester (1877) were three distinct non-homologous organs developed in chronological succession along the trunk. This theory received strong support from German authors of the time, and particularly from Felix (1906).

2. that the three regions were serially homologous areas of a single primitively metameric archinephros which extended the entire length of the trunk. Audige (1910) referred to the entire vertebrate kidney as a mononephros while Price
(1904) applied the term holonephros to the serially homologous pro- and mesonephroi of *Bdellostoma*.

Descriptive work on lower craniates (Brauer, 1902–Hypogeophis) and later experimental studies (Boyden, 1926 and Gruenwald, 1942–chick; Cambar, 1948–Anura) confirmed the homologous nature of the three kidney regions. Goodrich (1930) discussed the evolution of the higher vertebrate kidney from a primitive archinephros. Fraser (1950) reviewed the question of the homology of the three vertebrate kidney regions. She emphasised the artificiality of the terms pro-, meso- and metanephros which imply some distinction between the three regions. She recommended that the entire vertebrate kidney be regarded as a holonephros and that the terms pro-, meso- and metanephros be retained for convenience of description only. Gerard (1954) distinguished between pro-, meso- and metanephroi in teleosts on the basis of their anatomical and histological structure. Audige (1910) had also described the separate caudal kidney of some teleosts as metanephroi. Fraser, however, preferred to restrict the term to the adult kidney of Amniotes. She pointed out that pro- and mesonephroi are distinguishable only in the young of animals that have a prolonged larval life and that the difference was a matter of size and complexity only.

More recent work on teleost kidneys has been concentrated on the histology and physiology of the nephrons. Huot (1897, 1902 in Marshall, 1929) first reported the existence of agglomerular kidneys in certain species of lophobranchs. Guitel
(1906) established the agglomerular condition of some Gobiescoides. Audige (1910) reviewed the then available material on the histology of the teleost kidney and reported an agglomerular kidney in another lophobranch, *Lophius piscatorius*. Further reports of agglomerular kidneys have since been published by Verne (1922), Edwards (1929), Nash (1931), Grafflin (1937, a).

The discovery of the common occurrence of the agglomerular tubule in teleosts stimulated interest in the comparative physiology of agglomerular and glomerular tubules. The demonstration (Grafflin, 1933) that the kidney of the daddy sculpin (*Myxocephalus scorpius*), in which the tubules behaved physiologically as if agglomerular, was in fact glomerular was of particular interest. Studies of various species by Edwards (1928), Grafflin and Eisenberg (1934) and Smith were reported.

Attempts have been made to correlate the degree of glomerular development with the osmotic concentration of the environment (Marshall and Smith, 1930; Nash, 1931; Edwards, 1933; Grafflin, 1937, a). More recently attention has turned to the evolutionary significance of the vertebrate kidney and especially of the glomerular apparatus (Smith, 1953).

B. Osmoregulation in Teleosts

It is claimed that, owing to its importance in osmoregulation, evolutionary modification of the kidney had to precede all other modifications of the vertebrates (Smith, 1953). Marshall and Smith (1930) and Grafflin (1937, b) have attempted
to correlate the degree of development of vertebrate nephrons, and particularly of the glomeruli, to the osmotic environment in which the animals live. Nash (1931) calculated the area of glomerular filtration surface per unit area of body surface of different fresh water and marine teleosts. These authors all concluded that, in general, fish from fresh water environments possessed many well vascularised glomeruli while those from marine environments tended to have reduced areas of glomerular filtration or, in extreme cases, to be aglomerular. In the entirely aglomerular tubule associated simplification of the renal tubules was invariably found (Edwards, 1929; 1935). Smith (1953) considered the aglomerular condition to be the natural result of prolonged adaptation of a species to a marine environment.

1. Renal Physiology.

Nussbaum (1887, in Gerard, 1936) obtained almost total cessation of urine flow when the glomerular neck of the Amphibian nephron was ligatured. Bensley and Steens (1928), however, found continued excretion of dilute urine after a similar operation. Gray (1930), as a result of Bensley and Steens' experiments and his own observation that the mesonephric tubules in Triton vulgaris frequently were not open to the Bowman capsule, denied any excretory or osmoregulatory role of the glomerulus. He postulated a role in the resorption of dissolved substances from the coelomic fluid by way of the open peritoneal funnels.

Wearn and Richards (1924), by chemical analysis of micropipette samples from the Bowman capsule, demonstrated that
the glomerular fluid was of approximately the same composition as deproteinised blood serum. Their results strongly supported Nussbaum's theory of glomerular filtration. Wearn and Richards (1924) and Gerard and Cordier (1934) demonstrated by the same technique the occurrence of tubular resorption of glucose and sodium chloride in the proximal section of the uriniferous tubule and of water in the distal section of the Amniote tubule. Tubular resorption of water has not been demonstrated in teleosts (Gerard, 1936).

Gerard and Cordier (1934), Gerard (1936) and Singer (1933) were able to demonstrate tubular excretion of vital dyes in tubules whose glomerular necks were ligated. Their results were supported by studies of Grafflin and Eisenberg (1934) with fluorescent materials. In the agglomerular tubule all excretion, including that of water, must occur by active processes in the tubule walls. Marshall (1930) showed that, with the exception of glucose which is excreted only by the glomerulus, the agglomerular tubule of marine teleosts excreted a urine of approximately the same composition as that excreted by glomerular tubules of marine teleosts. Grafflin (1937, a) pointed out that all gradations from the glomerular to the completely agglomerular kidney were found in animals from both marine and fresh water environments. He observed that the uniformly brush-bordered agglomerular tubule was able to perform most of the functions of glomerular tubules. Grafflin (1937, b) suggested that the ability to adapt to a wide range of osmotic conditions was a function of extrarenal factors associated with osmoregula-
tion. He apparently considered chloride regulation by means of the chloride cells of the gills to be of more importance in osmoregulation than water regulation by means of the glomerulus. Smith (1953) strongly emphasised the role of the glomerulus in osmoregulation.

2. Chloride Balance.

The role of the gills in chloride uptake in fresh water teleosts has been demonstrated (Keys, 1931). Bevelander (1932) claimed that chloride uptake occurred through the general gill epithelium. Burns and Copeland (1950) and Copeland (1948) described specialised cells in the gill epithelium and well vascularised areas of the oral epithelium which showed a high degree of eosinophilia and stained strongly with a silver technique. The authors concluded that these were chloride secreting cells similar to the gastric parietal cells and that they were responsible for the chloride uptake observed by Keys. Krogh (1939) was unable to detect measurable chloride uptake in the fresh water adapted eel but observed chloride absorption in other teleosts including Fundulus. Wikgren (1953) found in the lamprey a dynamic equilibrium between active uptake and diffusive loss of salts from the gills in fresh water acclimatisation.

Marine teleosts constantly drink sea water to replace water lost by exosmosis. The contained chloride, which is absorbed from the intestine with the water, is removed from the blood by active excretion in the gill region (Black, 1951). Copeland (1950) was able to demonstrate reversal of function in
the chloride cells of *Fundulus* when transferred from fresh to salt water and back. Getman (1950) described a similar reversal in *Anguilla*. Both authors described cytological changes in the chloride cells which accompanied the reversal of function. Keys and Wilmer (1932) and Black (1951) emphasised the importance of reversibility of chloride cell function to the osmoregulation of euryhaline teleosts. Black suggested a quantitative relationship between degree of euryhalinity and rate of reversal of chloride cell function. Getman (1950) and Keys (1933) observed that chloride secretion began in the species studied only after the body fluids had become rather concentrated. These authors considered that adaptability of the chloride cells was primarily responsible for the maintenance of homeostasis in teleosts.


It is generally accepted (Smith, 1953; Florkin and Morgulis, 1952) that fishes evolved from the protovertebrate salt stock only after migration from fresh to salt water had been initiated. In fresh water the protovertebrates were subject to osmotic flooding owing to their relatively concentrated body fluids. To maintain homeostasis it was necessary:

a) to exclude from the body as much water as possible. This was achieved with the evolution of the impervious armour of the Ostracoderms (Florkin and Morgulis, 1952).

b) to eliminate osmotic water which penetrated the permeable gill and oral membranes. This was made possible by
the introduction of a glomerular ultrafilter into the glomerular protovertebrate nephridium (Smith, 1953). The absorptive function of the nephridial epithelium, which was responsible for resorption of useful solutes from the coelomic fluid, was retained in the glomerular tubule of fishes for the resorption of materials from the glomerular filtrate. A high rate of glomerular filtration together with active tubular resorption enabled the early fish to excrete osmotic water while retaining essential chloride.

c) to obtain chloride from the environment against an adverse diffusion gradient. This was achieved by active chloride absorption in the gill and oral regions at the expense of respiratory energy. Considerable amounts of chloride were also obtained from the food.

Their later return to sea water exposed the ancestral fish to osmotic dehydration. Excessive glomerular filtration became a liability. The evolution of the urea retention habitus made unnecessary any modification of the elasmobranch nephron (Smith, 1936). Teleosts, however, underwent long term modifications which made useful in water conservation an organ formerly specialised for water elimination. Modification involved primarily reduction of the glomerular filtration rate. With the reduced urine flow active excretion by the tubular epithelium became of more significance. Reversibility of the chloride cell function presumably made possible the initial colonisation of the new environment.
C. Structure of the Teleost Kidney

1. Anatomy.

The definitive kidney of most teleosts is the mesonephros. Audige (1910) showed the presence of a hind kidney with a distinct duct system in several species. Some species possessed functional tubules in both mid and hind kidneys while some possessed tubules only in the hind kidney. In the adult teleost the fore kidney was usually entirely degenerate. Tubules and glomerulus were replaced by myeloid tissue.

Teleosts are more varied in their renal anatomy and histology than any other taxonomic group. Audige (1910) described two distinct forms of adult kidney:

1) mononephric kidneys such as were found in the genus Cyclothone (Owen, 1938). A single very large median glomerulus projected on either side into a nephric chamber from which a single uriniferous tubule led into the duct of that side. Gerard (1954) considered the mononephric nephron to be a neotenous condition in Cyclothone. A similar mononephric fore kidney was found in all species of adult Lepadogaster, sometimes in conjunction with a functional polynephric mid kidney.

2) polynephric kidneys, located in the mid or hind kidney region. They consisted of many nephrons entering a pair of ducts which emptied into the cloaca.

Gerard (1953) found four fairly representative arrangements of the kidney in teleosts:
1) fore and mid kidneys in the adult. The fore
kidney might (a) be mononephric (e.g. Lepadogaster), (b) have
no nephrons, but consist of a mass of myeloid tissue (e.g. Barbus) (c) possess both a typical mononephric unit and a
group of glomerular nephrons (e.g. Fundulus)

2) fore kidney degenerate; mid and hind (post cloacal)
kidneys both with functional tubules (e.g. Auguilla)

3) fore kidney a mass of myeloid tissue. Mid and
hind kidneys with functional tubules (e.g. Apola)

4) mid kidney only in the adult (e.g. Lophius, Opsanus).

Gerard found the hind kidney to be typically a com­
 pact mass which was located in a post cloacal diverticulum of
the coelom. Arterial circulation was supplied by one or two
medial arteries. In those forms where the hind kidney was pre­
sent but aglomerular no arterial circulation was found (Hippo­
campus - Edwards, 1929). A pair of ducts which developed as
buds of the Wolffian ducts drained the hind kidney. The mid
kidney was often an elongate organ, tapering posteriad, which
extended most of the length of the trunk. There was generally
no outward sign of metamerism. The separation of right and
left kidneys was also obscured but Edwards (1928) showed by
injection of the Wolffian ducts that there was no connection
between the nephrons of the two sides in the species studied
by him. The kidney was well supplied with wide venous sinuses
around which myeloid tissue was packed.
Audige (1910) described three principal arrangements of the venous circulation in the mesonephros:

1) blood from the caudal vein reached the kidney by way of a true portal system. The right post cardinal was better developed than the left but both persisted and extended far posteriad in the kidney to receive blood from the renal portal veins (figure 1).

2) a portal vein existed only on the left while the right post cardinal was continuous with the caudal vein (figure 2).

3) the right post cardinal alone persisted to the adult stage in the trunk region. It was continuous with the caudal vein and passed anteriad through the mesonephros. In the pronephric region the left cardinal existed as a short branched vessel receiving blood from the sinusoids (figure 3). A type of portal system was formed by the intersegmental veins from the dorsal and ventral body wall which drained into the kidney sinusoids. Arterial blood reached the mesonephros by way of arterioles in the intersegmental connective tissue.

2. Histology.

Structure of the nephron.

Li Kowt Tchang (1923), Marshall and Smith (1930) and Viltner (1935) reported the presence of an avascular core of dense syncitial tissue in the avian glomerulus. Nash (1931) reported modifications in the glomeruli of marine teleosts
relative to those of fresh water species. He observed in particular reduction of vascularity and the presence of quantities of fibrous material scattered through the glomerular tissue. He interpreted the presence of quantities of fibrous matter as an indication of degeneracy. Grafflin (1929) observed hyaline degeneration in the centre of the pseudo-glomerulus of *Lophas piscatorius*. The core lacked capillaries, cells, or fibres, and in cases of extreme degeneration was filled with granules. Arterial vascularisation was limited to the peripheral areas of the pseudo-glomeruli. In the common sculpin (*Myxocephalus octodecemspinous*) Grafflin (1937, c) found considerable variability in size, degree of vascularity, degree of lobulation and cellularity of the glomerulus. Scattered groups of connective tissue cells were common, but no fibrous core was reported. In a few glomeruli the centre was occupied by a large fluid-filled cyst. The glomeruli of the daddy sculpin (*Myxocephalus scorpius*) (Grafflin, 1933) showed more advanced degeneration. Distortion of the Bowman capsules was common. Four stages of degeneration were found:

1) glomeruli consisted of a few nuclei in a large mass of syncitial tissue

2) glomeruli were without nuclei or fibres and consisted of a mass of green caseous matter

3) glomeruli consisted of a mass of structureless membranes

4) the peripheral region of the glomerulus was
vascular but the centre was filled by a large cyst.

In all cases the glomeruli were connected to tubules whose necks were closed.

Grafflin (1937, d) observed great variability in the size and degree of lobulation of the glomeruli of the catadromous common eel (*Anguilla rostrata*). In larger glomeruli avascular connective tissue masses occupied some of the lobules but no central cores were found. Some glomeruli were found to possess two distinct vascular tufts, each with an afferent and an efferent arteriole. My observations of the involuting pronephric glomerulus of *O. gorbuscha* indicated that glomerular degeneration was accompanied by invasion of the glomerulus by fibrous connective tissue.

Edwards (1937) found no juxtaglomerular structures in association with teleost glomeruli. In other vertebrates he found either a plaque, a disc, or both.

Edwards and Schnitter (1933) remarked that a tubule segment cytologically equivalent to the brush bordered proximal convolution of the mammalian nephron was common to the nephrons of all vertebrates. The aglomerular tubules of some marine teleosts were uniformly brush bordered over their whole length. One or more such tubules entered a common collecting ductule. Glomerular tubules were of variable structure but were always more complex than were aglomerular tubules. Edwards (1933, 1935) found up to five segments in the glomerular teleost tubule:

1) the glomerular neck (first minor segment). The squamous epithelial cells of the Bowman capsule changed grad-
ually to the columnar laterally compressed cells of the neck segment. If the tubules of a given species possessed an intermediate segment, the glomerular neck was invariably ciliated; if not, it was never ciliated.

2) the first major segment. According to Edwards, the cells of this segment were low columnar with a high well-defined brush border at least one third the height of the cells. Their large ellipsoidal nuclei were basally located. The cytoplasm was faintly basophilic. Numerous short rod like mitochondria were concentrated toward the base of the cells (Cowdry and Covell, 1928).

3) the second major segment, which usually preceded the second minor segment. Tall columnar cells with a low brush border characterised this region of the tubule. The round nuclei were basally located. Thread-like mitochondria were distributed throughout the eosinophilic cytoplasm. The mitochondria - cytoplasmic ratio was considerably lower in this segment (Cowdry and Covell, 1928).

4) the second minor segment, or intermediate segment, was absent in many species. If present, it was invariably of ciliated tall columnar laterally compressed cells.

5) the third major segment resembled the distal convolution of the mammalian tubule. Its cells were low columnar with central nuclei and basophilic cytoplasm. The lumen of this region of the tubule was large.
Several tubules drained into a collecting tubule characterised by its columnar epithelium and very narrow lumen which increased in diameter further along its length.

Kempton (1943) reported extreme elongation of the neck segment of the elasmobranch nephron. Its cells were cuboidal with depressed basal nuclei. The entire length was heavily ciliated. It was believed that this special segment was related to the resorption of urea from the urine.

Grafflin (1937, c) observed numerous ciliated cells in the second major segment of the nephron of the common sculpin. Edwards (1929) found the entire length of the first and second major segments in Muraena was uniformly ciliated. He noted that only the first major segment was common to all vertebrate nephrons and that this was the only segment occurring in aglomerular tubules. He concluded that the glomerulus acted as the stimulus for cytological differentiation of the tubule but that functional differences were not attributable to the presence of the glomerulus.

D. The Development of the Kidney

1. Nomenclature.

The entire kidney develops from the mesodermal material located between the somite and the lateral plate. This material was called by Balfour (1877) the intermediate cell mass. Primitively, the mass becomes segmented and arranged into somatic and splanchnic layers. The narrow cavity between the layers is continuous ventrally with the splanchnocoele and dorsally with
the myocoele. The area nearest the somite dilates to form a conspicuous coelomic chamber or nephrotome which encloses a nephrocoele (Ruckert, 1888). The connection with the myocoele is lost very early in development. The connection with the splanchnocoele is reduced to a narrow peritoneal funnel and peritoneal canal by ingrowth of cells from either end of the nephrotome. Dilation of the nephrotome and flattening of its epithelium forms a Bowman capsule.

Early in the development of the kidney amoeboid cells migrate from the medial surface of the intermediate cell mass, and later of the nephrotomes, along the entire trunk. These cells form beneath the hypochord a darkly staining mass which Maschkowzeff (1929) called the venous strand. The strand gives rise not only to the cardinal veins, as was supposed by Maschkowzeff, but also to the aorta, glomeruli, myeloid tissue and certain skeletal elements (Fraser, 1950). Accordingly the strand is referred to as the vascular strand ("masse vasculaire") as suggested by Swaen and Brachet (1902).

The medial wall of the Bowman capsule is invaded by a vascular tuft, the glomerulus, which is supplied with arterial blood from the aorta.

A solid outgrowth (rudiment of the uriniferous tubule) of the dorsal wall of the early nephrotome becomes elongated, cavitated and opens from the nephrocoele by a nephrostome. Goodrich (1930) prefers the term nephrocoelostome to differentiate it from the nephrostome of Amphibian pronephroi but Fraser (1950) has pointed out the homology of the structure in Amphibia
and other vertebrates. Fraser describes two types of glomerulus:

1) **Internal glomerulus**, entirely enclosed in a Bowman capsule.

2) **External glomerulus** which projects into a diverticulum of the general coelom. McEwen (1949) applies the term glomus to this structure. Fraser's nomenclature is preferred since it emphasises the homology of the two types of glomerulus.

Emery (1882) described the appearance of mesonephrogenic condensations in a narrow band of cells passing from one segmental duct to the other between the aorta and the cardinal. Hall (1904) found a similar condition in *Rana*. Hall called the bridge mesonephric blastema and the condensations blastulae. Moghe (1945) referred to a similar bridge of cells in *Thynnichthys* as bridge cells and to the mesonephric rudiments simply as condensations.

2. The development of the segmental duct.

In the primitive animals *Bdellostoma* (Price, 1899, 1904) and *Hypogeophis* (Brauer, 1897) each of the segmentally placed uriniferous tubules grows posteriorly to unite with the next tubule. A duct is formed along the length of the trunk by the union of the tubules. The free end of the most posterior tubule grows actively ventrad to enter the cloaca. It is believed (Goodrich, 1930) that the segmental ducts of the early vertebrates were similarly formed by union of segmental contributions.

The segmental duct is formed in Elasmobranchs by
active growth from the anterior region. A small knob of tissue develops from the intermediate mesoderm just posterior to the heart. From the knob a solid rod of cells grows posteriad to the cloaca. The rod later becomes tubulated and opens at the anterior end to the coelom. Mesonephric rudiments form and later open to the duct (Bates, 1914).

Maschkowzeff (1926) found the segmental duct of *Acipenser* (Chondrostei) to be formed as a thickening of the dorsal aspect of the intermediate cell mass in each segment. The thickening later becomes folded off as a solid rod which in turn acquires a lumen. Union with the cloaca is accomplished by active growth.

In *Polypterus* (Kerr, 1907 in Moghe, 1947) the segmental duct is formed posterior to the pronephros by "bodily conversion and fusion of segmental nephrotomes".

McIntosh and Price (1887) and Brook (1887) claimed that the segmental duct of teleosts is formed as a thickening of the ectoderm from which the duct later becomes separated. Swaen and Brachet (1899, 1901) described a dorso-lateral cleavage of the intermediate cell mass which sets aside a solid mass of tissue. Later, the mass of tissue acquires a lumen which the authors claimed is lined partly with somatic and partly with splanchnic mesoderm and therefore is the morphological equivalent of the coelom. Swaen and Brachet suggested that the tubule and pronephric chamber differentiate from the anterior end of the duct. Stroer (1930) found that the duct in *Perca* forms as a fold of the dorsolateral aspect of the intermediate
mesoderm in each segment after formation of the pronephric chamber.

Recent experimental studies (O'Connor, 1935 on Amphibia; Cambar, 1948, Gruenwald, 1942, on birds) show that the duct is formed in less primitive animals by union of the free ends of the fore kidney rudiments and active growth posteriad of the last rudiment to the cloaca. There are no significant segmental contributions of material. The supposed segmental origin of the teleost segmental duct is yet to be tested experimentally.

3. Development of the mesonephros in teleosts.

The intermediate cell mass appears early in development as a loose triangular mass of tissue lateral to the somites and medial to the lateral plate (Brachet, 1935 - *Salmo trutta*). Separation from the somite occurs very early but the connection with the lateral plate is retained longer. Formation of the vascular strand commences soon after separation from the somites. Swaen and Brachet (1899) described the appearance of the vascular strand prior to differentiation of the intermediate cell mass in *S. trutta*. Maschkowzeff (1929) showed their conclusion to be based on erroneous interpretation of the prolonged attachment of intermediate cell mass and lateral plate. Nephrotomes are said not to appear during the development of the teleost kidney (Fraser, 1950). Felix (1897), however, described the appearance of segmental structures in the pronephric region of *S. trutta* and Stroer (1932) referred to a "nephrotome" in *Perca*.

Nussbaum (in Moghe, 1940) described the origin of
mesonephric rudiments as outgrowths of the duct epithelium. Felix (1906) described a similar origin of primary agglomerular mesonephric tubules in _S. trutta_. He claimed that the primary tubules are later replaced by permanent tubules of unknown origin. Maschkowzeff (1934) traced the origin of the permanent mesonephric tubules to condensations of mesonephric mesenchyme developed from the intermediate cell mass in _S. trutta_. He did not comment on Felix's description of the origin of primary tubules. Brachet (1935) observed the appearance of hemispherical evaginations of the duct epithelium similar to those described by Felix. He traced their further development and found that they separate from the duct, round up and migrate out into the kidney tissue. In later stages they become lobulated and well vascularised. He considered them to be the rudimentary corpuscles of Stannius.

Rosenberg (1867) thought that the mesonephric rudiments are aggregations of cells either from the ventral wall of the aorta or from "parietal" cells located in the walls of the cardinal veins. Emery (1882) described the appearance of mesonephric condensations in a bridge of cells which passes between the aorta and cardinal vein from one duct to the other. He thought that the bridge originated from the peritoneal epithelium.

Hall (1904) found in _Rana_ a similar bridge of mesonephrogenic cells in which mesonephric rudiments formed by condensation. He traced the origin of the mesonephrogenic bridge to the intermediate cell mass. Gray (1930) verified his con-
clusion in a different species of *Rana*.

Moghe described the appearance as condensations of the mesonephrogenic bridge cells of hemispherical caps of cells closely applied to the ducts. He traced the origin of the bridge cells to the region of the intermediate cell mass closest to the somite. This is the region from which nephrotomes develop in those species where mesonephric nephrotomes form (Fraser, 1950). Brachet (1935) and Felix (1906) described the elaboration of the mesonephrogenic condensations in *Salmo trutta*. The hemispherical condensations become closely applied to the ducts. Rapid cell division results in elongation of the rudiments. The end of the newly formed cylinder of cells penetrates the wall of the segmental duct and, after tubulation, becomes open to the duct. The free end of the tubule dilates to form a Bowman capsule which is later invaginated by a glomerulus. Moghe described a similar situation in *Thynnichthys*, but reported that the glomerulus and capsule are formed independently of the tubules as condensations of the cells of the mesonephrogenic bridge. The condensations grow to large solid spherical masses which become attached to the tubule and subsequently become hollow. The glomerulus appears as a solid mass of basophilic cells which invaginates the wall of the Bowman capsule. Gray (1930) found that the tubules in *Rana* form by elongation and tubulation of the mesonephrogenic condensations. As a result of more rapid division of the laterally located cells, the developing tubules curl ventro-medially around the duct. At the free end, division occurs exclusively in a tangential plane and results in the
formation of a large thin walled capsule. The area of the wall opposite the tubule mouth is invaginated by a solid mass of cells derived from the mesonephric bridge. Vascularisation of the mass by an arterial shoot completes the development of the glomerulus. Andige (1910) remarked that all mesonephric tubules are initially agglomerular. Felix (1906) and Moghe (1945) observed the formation of secondary and tertiary mesonephric tubules which open into the connecting segment of previously formed tubules. Gray (1933) pointed out that no secondary tubules can form in *Triton* since the entire mesonephrogenic mass differentiates into primary vesicles. In this species, rudiments are formed by fragmentation of the mass rather than by condensation of cells as in *Rana*. Secondary generations are formed in *Rana*.

Peritoneal funnels, which Gray reported in the mesonephros of *Rana* and *Triton*, were not observed by Felix, Brachet, Moghe or Maschkowzeff in the mesonephroi of teleosts.

4. The development of the Corpuscle of Stannius.

Garrett (1942) reviewed the available literature on the development and structure of the corpuscle of Stannius. When originally reported by Stannius the corpuscle was thought to be the homologue of the mammalian adrenal cortex (interrenal). More recent research located both suprarenal and interrenal bodies in the anterior region of the teleost kidney. It is now believed that the corpuscle of Stannius is unrelated to the adrenal system. Its function is unknown but apparently endocrine. The corpuscles have been reported only in teleosts and holostean
ganoids. Up to fifty pairs are reported in Holostei; one pair in most teleosts. In the catfish, a single corpuscle is formed by fusion of the two members of a pair. Salmonids commonly possess three or four pairs.

Garrett (1942) discussed the origin of the corpuscles of Stannius in *Amia calva* as paired outgrowths of the duct epithelium prior to the appearance of mesonephric condensations. Their cells are early differentiated from those of the duct by their very palely stained cytoplasm. The outgrowths appear in regions where the cardinal sinusoids are closely applied to the ducts.

The rudiments increase greatly in size and acquire a slit like lumen. At this stage they have the appearance of early mesonephric rudiments (cf. Felix, 1906). At about the time of separation from the ducts fibrous trabeculae carrying arterial capillaries invade the tissue of the corpuscles and subdivide them to lobules. Finally the developing corpuscles are forced away from the ducts into the kidney tissue where they increase considerably in size, vascularity and degree of lobulation.
V. MATERIALS AND METHODS

A. Materials

Eggs of the pink salmon (*Onchorhyncus gorbuscha*) were collected at Cultus Lake in November, 1953, and artificially fertilised before transportation to the University hatchery. They were maintained in fresh water tanks at temperatures which ranged from 12.5°C in November through 5°C in January to 15°C in August. Hatching began on the fiftieth day after fertilization. The alevins were fed on a mixture of canned salmon and Pablum. Samples were taken every hour in the early stages. Thereafter, the intervals were increased to two weeks for the latest stages of the series sampled. This fresh water series was continued until August, 1954. Migrating fry were trapped in April, 1955 as they entered the sea at Port John, B.C., and were held in salt water pens in the bay. These specimens were sampled weekly at first, but later bimonthly until November 1955. Further sea water specimens were obtained during their migration into the Pacific in July and August of 1955. A second series was maintained at the University hatchery during the fall and winter of 1955. In the late spring of 1956 they were transferred to the Vancouver Public Aquarium and divided into salt and fresh water populations which were sampled weekly.

B. Methods

1. Fixation.
(a) General histological detail.

Eggs and fry were fixed whole in Bouin's fluid or in Smith's formal bichromate. These fixatives gave rather poor preservation of cytological detail. They proved adequate for demonstration of general histological structure. Smith-fixed material hardened less during subsequent treatment and was found more satisfactory for yolky material. Fry and fingerlings collected in the field were fixed in Bouin's.

(b) Mitochondria and brush borders.

Regaud's fixative (Krajian, 1940) was found to give very satisfactory preservation of mitochondria and brush borders. The material was fixed four days in Regaud's followed by post-chroming for 10 days in 3 percent potassium bichromate. The kidney was partially dissected out of the freshly killed animal to aid penetration of the fixative.

2. Embedding and sectioning.

Material was embedded in a 50:50 mixture of 50-53°C m.p. and 54-56°C m.p. tissuemat. The mixture was found to be most satisfactory for the summer conditions under which much of the work was performed. Routine methods were followed for tissues not containing yolk. Whenever possible, embryos were dissected off the yolk prior to embedding. Where this was not possible either the Peterfi double embedding technique (Pantin, 1948) or the method of clearing with terpineol from 90% alcohol was employed. The kidney was dissected out of older embryos before embedding. The need for decalcification was thereby avoided.
Yolk-containing blocks were trimmed down to the yolk on one side and soaked 24 hours in softening agent prior to sectioning. Material for demonstration of general structure was cut at 10 µ, that for demonstration of mitochondria at 5 µ. Sections were adhered to slides with Mayer's albumen. In the case of yolk-containing sections it was necessary to coat the adhered sections with a 0.5% solution of celloidin in 50% ether-alcohol immediately after dewaxing to prevent their becoming detached. The celloidin was then removed with acetone prior to clearing the stained sections.

3. Staining.

(a) Bulk staining.

Bulk staining with Grenacher's borax carmine was tried to simplify glomerular counting. The attempt was unsuccessful owing to heavy uptake of stain by the kidney tubules and myeloid tissue. Staining of thick sections (40 microns) was also unsuccessful.

(b) General histological detail.

Heidenhain's iron haematoxylin was used for demonstration of general detail owing to its good photographic properties. For general purposes no counterstain was used. Counterstaining with eosin was used for demonstration of acidophila in the cells of the gill and renal epithelium. Heidenhain's azan was used for demonstration of the fine structure of the glomeruli.

(c) Mitochondria.
Altmann's acid fuchsin aniline (Krajian, 1940) counterstained with methyl green gave excellent results.

4. Glomerular counts.

It was found that, with the exercise of a reasonable amount of caution, accurate counts (4%) could be obtained by counting glomeruli in every fifth section in the larger fish. In the smaller fish, each section was studied.
VI. OBSERVATIONS

A. The structure of the fully differentiated kidney.

1. Anatomy.

The definitive kidney is a mesonephros. It is an elongate organ extending from the twelfth to the fortieth segment. In its early development it is distinctly bilobate but by the time the fish is a year old the lobes are obscured along most of the length of the kidney. The fore kidney region (fourth to twelfth segments) is flattened and tends to be bilobate. The post cardinal veins pass out of the kidney in the fifth segment at which point the kidney tissue grows ventrolaterally along the veins as they pass around the anterior end of the liver. The right cardinal vein is continuous with the caudal vein in the fortieth segment. It enters the dorsal aspect of the kidney in the thirty-eighth segment and passes anteriad in the centre of the kidney tissue. Opposite the sixteenth somite it curves to the right before entering the region of the fore kidney (figure 4). The entire fore kidney is permeated by a network of venous sinusoids. Blood from the right postcardinal passes direct to the right common cardinal. Blood drains from the sinusoids into the right and left postcardinal veins. Patches of well-vascularised interrenal tissue (figure 5) are distributed throughout the pronephric region. Arterial blood reaches the interrenal tissue from arterioles which develop only after occlusion of the main pronephric arteriole.
Paired intersegmental renal veins drain blood from the kidney tissue into the cardinal vein (figure 5). Portal blood from the dorsal and ventral body walls reaches the kidney sinusoids by way of intersegmental venules which enter the lower angles of the kidney. Arterial blood reaches the kidney from paired arterioles which enter at the dorsal angles opposite alternate segments. Two median arteria primitiva mesenterica pass through the kidney tissue to supply the swim bladder and hind gut. The median coeliaco-mesenteric artery passes through the fore kidney to supply the anterior viscera. The lower angles of the kidney are usually indented corresponding with the myosepta.

The Wolffian ducts pass posteriad along the lower surface of the kidney to the thirty-ninth segment where they unite prior to passing ventrad to the cloaca. The common duct enters a bladder-like distention (figure 25) but no sphincter is present.

2. Histology.

The excretory role of the kidney is performed by a number of non-metameric renal units made up of several glomerular tubules and a collecting duct. The collecting ducts discharge into the segmental ducts on either side. Each unit comprises several nephrons with:

a) glomerulus and Bowman capsule. The capsule is a wide dilation of the free end of the tubule. It is lined with simple squamous epithelium which undergoes a gradual transition
to the laterally compressed columnar epithelium of the neck segment. The glomerular pole is usually diametrically opposite the tubular pole. The well developed glomerulus is an ellipsoidal mass, about 70 microns X 50 microns, composed of arterial capillaries among which are distributed connective tissue cells and fibres. The whole structure is enclosed by the epithelium of the Bowman capsule which is reflected into the glomerular tissue around the capillaries (figure 8). The smaller glomeruli are usually almost entirely avascular. The centre of many larger glomeruli is taken up by a vesicle.

b) a short neck segment of low simple columnar laterally compressed cells with elliptical nuclei basally located in the cells (figure 8).

c) a first major segment of low columnar weakly basophilic cells with a high brush border at least one quarter the height of the cells. The spherical nuclei are basally located (figure 9). Granular mitochondria are concentrated in the basal region of the cell (figure 10). The lumen of the tubule is rather wide throughout the length of this segment.

d) a second major segment of taller columnar cells with a low brush border (figure 12). Rodlike mitochondria are distributed throughout the cell (figure 11). The tubule lumen is narrow in this segment.

e) a third major segment of low columnar unbordered cells with spherical basally placed nuclei. The tubule lumen
is very wide (figure 13).

No intermediate segment is found in *O. gorbuscha*.

A collecting duct of tall columnar epithelium (figure 14) drains into the segmental duct (figure 15), also of tall columnar epithelium.

The intertubular spaces are packed with myeloid tissue permeated by a rich net of venous sinusoids. Post glomerular blood apparently enters the sinusoids since no capillary nets are to be found associated with the tubules.

In the twenty-seventh to the twenty-ninth segments large ellipsoidal highly lobulated corpuscles of Stannius appear. The corpuscles are richly vascularised. Between six and twelve corpuscles are found.

B. The Chloride Cells of the Gills.

In the eight month old sea water acclimatised specimen the "chloride" cells appear as weakly acidophilic cells located in the gill epithelium and in well vascularised areas of the mouth. However, an eight month old embryo of the fresh water series (67 mms) also showed weak acidophilia of certain cells in the gill and oral region.

C. The Development of the Mesonephros.

3.33 mms. 16 somites

The pronephros of this embryo has commenced to differentiate. The nephrotomes of the sixth and seventh segments,
from which the definitive pronephric chamber develops, are fused together and open over their whole length to the coelom. The tubule rudiment, or pronephric fold, appears as a thickening of the dorso lateral surface of the fused nephrotomes. This is continuous in the eighth and ninth segments with a solid uniform rod of cells (duct rudiment) which formed as a fold of the intermediate cell mass in this region. The vascular strand appears as a darkly staining mass of cells beneath the hypochord in the fourth to the seventh segments. Posterior to the ninth segment the intermediate cell mass is an undifferentiated unsegmented triangular mass of cells between the somite and the hypomere (figure 16). Differentiation of mesoderm has not proceeded beyond the sixteenth segment.

4.4 mms. 23 somites

The duct rudiment is set aside in the anterior mesonephric segments as a solid cylinder which forms as a fold of the dorsolateral surface of the intermediate cell mass (figure 17). In the pronephric region the duct is becoming hollow. Migration of cells from the medial surface of the intermediate cell mass has established the vascular strand in the more anterior mesonephric segments.

7.4 mms.

The pronephros is well formed with large pronephric chambers and single median glomerulus. Convolution of the pronephric tubule has commenced. The segmental ducts are complete to the level of the cloaca where they unite and pass ventrally
to enter the cloaca. A narrow band of palely stained mesonephric bridge cells derived from the intermediate cell mass stretches uninterrupted the length of the mid kidney from one duct to the other between the aorta and the post cardinal vein (figure 18 - 5.24 mms.). The aorta has differentiated from the intermediate cell mass along the length of the trunk. Ventrolateral to it on the right is located the right post cardinal vein which is continuous caudally with the caudal vein and anteriorly with the pronephric portal system. Proliferation of myeloid tissue has commenced from the vascular strand tissue just posterior to the pronephric chambers.

From the dorsal surface of each duct in the twenty-fifth to the twenty-seventh segments rudimentary corpuscles of Stannius appear as palely-stained hemispherical outgrowths of the duct epithelium (figure 27).

16.66 mms.

Condensations of cells of the mesonephrogenic bridge nearest the ducts form hemispherical caps of basophilic cells which become closely applied to the ducts (figure 19). In this embryo three such condensations are apparent on the left and two on the right located in the posterior region of the mid-kidney. The corpuscles of Stannius are separated from the ducts by this time as large ellipsoidal bodies (figure 28).

19.05 mms.

The pronephros of this embryo has attained its peak development. The pronephric chamber and glomerulus have attained
their maximum length of 400 μ. The uriniferous tubule is highly convoluted and cytological differentiation into two regions has occurred. Fifteen mesonephric blastulae are apparent, nine on the right and six on the left. Most of the new blastulae are added anterior to those present in the 10.95 mm. embryo. Elongation of the more posterior rudiments has commenced. More rapid cell division in the lateral aspects causes the forming tubules to curve around the ducts in a medio-ventral direction. The proximal ends of the solid tubule rudiments are fused to the ducts. The mesonephric bridge is obscured by myeloid tissue, proliferated from the vascular strand. Myeloid cells have begun to fill the spaces between the post cardinal vein, ducts and tubules. The corpuscles of Stannius are becoming penetrated by arterioles direct from the aorta which follow connective tissue trabeculae into the corpuscular stroma. No other arterial blood supply to the mesonephros has developed.

19.80 mms.

Forty-six mesonephric rudiments appear, the new ones being added anterior to those observed at 19.05 mms. Of the forty-six only the most anterior are unelaborated. The remainder show varying degrees of tubular development. In the first formed rudiments the free end is dilated into a wide Bowman capsule (figure 20). The lumen of the capsule extends into the tubule in some cases and some tubules are open to the ducts. Ten such rudimentary capsules are apparent.

20.41 mms.

The antitubular aspect of some of the newly formed
Bowman capsules is invaginated by a solid mass of lightly staining cells, the rudiments of the mesonephric glomeruli (figure 21). There is as yet no sign of vascularisation of the glomeruli nor of arterial blood supply to the mesonephros. There are seventeen rudimentary glomeruli in this specimen.

20.9 mms.

Thirty-one incipient glomeruli are apparent. The epithelium of the expanded Bowman capsules is squamous changing gradually to tall columnar at the point from which the tubule leaves. The cells of the neck segment are very basophilic and laterally compressed. The remainder of the tubule is unbordered tall columnar weakly basophilic epithelium. The duct is of low columnar epithelium. The corpuscles of Stannius appear as large ellipsoidal masses of vascularised tissue located dorso-laterally to the ducts.

26.9 mms.

Arterial blood is supplied to the mesonephros by paired mesonephric arterioles which enter through the inter-segmental connective tissue of each segment. Venous blood from the dorsal and ventral myosepta enters the four corners of the trapezoid mesonephros. The larger glomeruli in the posterior regions are becoming vascularised (figure 22). Mesonephric rudiments extend anteriorly to the twelfth segment on the left though the more anterior rudiments are not elaborated. The area between the tenth (last pronephric) and twelfth segments never shows any development of kidney structures. Glomerular tubules
extend only as far as the twentieth segment at this time. Development of rudiments in the right lobe extends only to the sixteenth segment since anterior to this the lobe is filled by the very large right post cardinal vein. Fifty-five mesonephric glomeruli are found in this specimen.

28.58 mms.

Secondary mesonephric condensations identified by the deep basophilia of their cells are starting to appear closely applied to the primary tubules. The more posterior primary glomeruli are large and quite vascular (figure 23). Their tubules are differentiated into (1) neck segment; (2) first major segment of low columnar cells with a low brush border and large ellipsoidal basally located nuclei; (3) second major segment of tall columnar cells with a low brush border and smaller spherical nuclei; (4) third major segment of low columnar unbordered cells and a connecting segment of tall columnar cells. The duct epithelium is now tall columnar. This specimen possesses seventy-six glomeruli. The more posterior glomeruli are highly vascular and apparently functional.

29.78 mms.

Incipient secondary Bowman capsules are commencing to appear by this time though differentiation of the secondary tubules has not yet occurred (figure 24). One hundred and twelve primary and nine secondary glomeruli appear. Occlusion of the pronephric arteriole has commenced.

35.0 mms.
Mesonephric glomeruli extend as far as the sixteenth segment on the left. Secondary condensations are as far anteriad as the twenty-sixth segment. Posteriorly, no tubules appear behind the thirty-eighth segment at which point the ducts leave the kidney. Myeloid tissue extends to the level of the cloaca (segment forty). Further new primary condensations and secondary condensations appear in the posterior regions of the mid kidney.

The pronephric arteriole is partly occluded and the glomerulus shows reduction of vascularity. In a second specimen the artery is entirely occluded and the glomerulus reduced in length to 210 microns by invasion of its anterior and posterior ends with fibrous connective tissue. The nephrostomes are partly closed by ingrowth of cells from its epithelium.

49.6 mms.

The pronephric artery is completely occluded. The glomerulus is much reduced in size and its vascularity reduced by a core of fibrous connective tissue. Degeneration of the tubular borders has commenced. There has been little change in the mesonephros beyond an increase in the size and vascularity of the already formed glomeruli, addition of new primary and secondary glomeruli and the appearance of new condensations. The total number of glomeruli is now three hundred and sixty-nine. The corpuscles of Stannius are large and highly lobulated with a very rich arterial supply (figure 29).

67 mms.

The mesonephros is becoming typically trapezoid in
cross section (figure 26). One thousand mesonephric glomeruli were counted in one specimen, twelve hundred and ten in another. Masses of very vascular palely stained interrenal tissue appear scattered throughout the pronephric region (figure 30). The pronephric chambers are open, but the glomerulus is very vesicular and degenerate in appearance. The entire kidney is richly permeated with blood sinuses.

D. Comparison of Marine and Fresh Water Series.

There is no significant difference in the histology of glomeruli or tubules in specimens taken from fresh or salt water. No agglomerular tubules are apparent even in the most anterior mesonephric region. Occlusion of the pronephric arteriole commences at the same stage of development in both series. Glomerular counts indicate a rather larger number of glomeruli in fresh water fish than in marine fish of a given size.
VII. DISCUSSION

The prolonged attachment of the teleost intermediate cell mass to the lateral plate has caused considerable confusion in the interpretation of the early phases of teleost kidney development. The origin of the mesonephric blastema from the intermediate cell mass in teleosts was established only in 1934 (Maschkowzeff, 1934). During the course of the present investigation it was found that the mesonephric blastema in the pink salmon was derived from that portion of the intermediate cell mass nearest to the somite.

The development of the Bowman capsule is somewhat different than that of any species hitherto reported. In general the Bowman capsule is reported as arising as a distention of the already hollow tubule. Moghe (1940) reported the origin of Bowman capsules in Thynnichthys as separate condensations of the mesonephrogenic bridge cells. These condensations subsequently became attached to the already formed tubule and opened to it. In the pink salmon the Bowman capsule develops as a distention of the tubule rudiment prior to its tubulation. The cavity of the Bowman capsule subsequently extends into the tubule rudiment and finally breaks through into the lumen of the segmental duct. The glomerulus forms as a separate condensation apparently of vascular strand cells. Vascularisation of the glomeruli prior to their connection with the aorta by capillaries developed in situ has been reported in birds (Davies in Fraser, 1950) but this is apparently the first time that it has been observed in
teleosts.

Reference to the table (figure 6) indicates a rather higher number of glomeruli in fresh water than in marine specimens of comparable length. The logarithmic regression curves (figure 7) and "t" values calculated for the regression coefficients indicate that there is significant difference in the rate of development of glomeruli in marine and fresh water fish. The lower figures for the marine series may be, in part, a result of a temporary retardation of the rate of development of glomeruli relative to length, perhaps associated with the abrupt transfer from fresh to salt water. The experiment as performed here is not entirely satisfactory since the fish ceased to thrive when maintained in fresh water past the time of their normal migration. It is suspected that a species of the Pacific salmon which remains truly euryhaline for a prolonged period might prove more satisfactory for an experiment of this type. The present results should be viewed with caution since no attempt was made to assess the effect of the different temperatures of the fresh water and marine series on the rate of appearance of glomeruli.
VIII. CONCLUSIONS

1. The development of the mesonephros in the pink salmon closely parallels that of teleosts described by other authors.

2. The mesonephros is glomerular during its development. Since glomeruli continue to develop following the transfer from fresh to salt water it seems likely that the mesonephros of the adult will be glomerular. No aglomerular tubules were observed even in the oldest specimens studied. No significant difference in the size of glomeruli developed in salt or fresh water was observed.

3. It appears that the increased osmotic concentration of the marine environment has the effect of retarding rate of development of glomeruli.

4. The demonstration of "chloride" cells in the gills of O. gorbuscha is unconvincing.
IX. LITERATURE CITED


76. 1953. From Fish to Philosopher. Little, Brown and Co., Boston.


PLATE I  ANATOMY

Venous drainage of the teleost mesonephros.

Figure 1  True portal system in adult.

Figure 2  Left portal vein only in adult.

Figure 3  Right post cardinal only in adult — no true portal system.

*cv  caudal vein
*pcv_l  left post cardinal vein
*pcv_r  right post cardinal vein
*pv  portal vein
*c  common cardinal

*adapted from Audige, (1910).
PLATE II  ANATOMY

Figure 4  Ventral view of entire kidney of 65 mms. fingerling.

b  bladder
pcv<sub>l</sub> left post cardinal vein
pcv<sub>r</sub> right post cardinal vein
sd  segmental duct
ugp  urogenital papilla

Figure 5  Transverse section of mesonephros of 65 mms. fingerling. (idealised).

a  aorta
pcv  post cardinal vein
ra  renal arteriole
rv  renal vein
v  portal vein
TABLE - PHYSIOLOGY

**Figure 6** Tabular representation of glomerular counts in fresh and salt water series.
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<th>No. Glomeruli</th>
<th>Length</th>
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</table>
Figure 7  Graphical representation of relationship of number of glomeruli to length in fresh and salt water series (Regression lines).

Regression Equations

1. F.W.

\[ Y = 2.36X - 1.12 \]

\[ t_{dif} = 0.048 \]

2. S.W.

\[ Y = 2.44X - 2.43 \]
PLATE IV  HISTOLOGY

**Figure 8** Glomerulus and capsule of fully differentiated nephron. Heidenhain haematoxylin.

x 800

- a arteriole
- bc Bowman capsule
- e epithelial cell nucleus
- ns neck segment

**Figure 9** Transverse section of first major segment. Heidenhain haematoxylin.

x 800

- b brush border
PLATE V  HISTOLOGY

**Figure 10** Transverse section of first major segment stained for mitochondria. Altmann acid fuchsin.

x 800

**Figure 11** Transverse section of second major segment stained for mitochondria. Altmann acid fuchsin.

x 800
PLATE VI  HISTOLOGY

Figure 12  Transverse section of second major segment. Heidenhainn Haematoxylin.

x 800

Figure 13  Transverse section of third major segment. Heidenhainn Haematoxylin.

x 800

s  secondary condensation
PLATE VII  HISTOLOGY

Figure 14  Transverse section of collecting duct.  
Heidenhain Haematoxylin.  
x 800

Figure 15  Transverse section of segmental duct.  
Heidenhain Haematoxylin.  
x 600
Figure 16 Transverse section of 3.45 mm embryo through sixteenth segment to show triangular intermediate cell mass.

\[ x \times 350 \]

- ch notochord
- ent entoderm
- icm intermediate cell mass
- lp lateral plate
- n neural keel
- s somite

Figure 17 Transverse section of 4.4 mm embryo through twentieth somite to show separation of duct rudiment and vascular strand.

\[ x \times 350 \]

- d duct rudiment
- m mesonephric bridge rudiment
- vs vascular strand
PLATE IX  EMBRYOLOGY

**Figure 18** Transverse section of 5.24 mm embryo to show localisation of structures derived from the intermediate mesoderm.

x 125

a  aorta  
ch  notochord  
g  gut  
mb  mesonephrogenic bridge  
pcv  post cardinal vein  
sd  segmental duct

**Figure 19** Transverse section of left lobe of kidney of 16.66 mm embryo to show mesonephric condensation.

x 700

a  aorta  
mb  mesonephric bridge  
mc  mesonephric condensation  
pcv  post cardinal vein  
sd  segmental duct
Figure 20  Transverse section of kidney of 19.05 mm alevin to show early stage in development of the Bowman capsule.

x 350

bc  Bowman capsule
go  gonad
mt  myeloid tissue
sb  swim bladder
sd  segmental duct
tr  tubule rudiment

Figure 21  Transverse section of kidney of 19.8 mm alevin to show incipient glomerular invagination.

x 700

bc  Bowman capsule
gt  glomerular rudiment
tr  tubule rudiment
PLATE XI  EMBRYOLOGY

**Figure 22** Section of Bowman capsule and avascular glomerular invagination of 19.8 mm alevin.

x 800

bc  Bowman capsule
gr  avascular glomerulus
mt  myeloid tissue
ns  neck segment of tubule

diagram:

**Figure 23** Transverse section of kidney of 26.9 mm fry to show beginning vascularity of glomerulus.

x 700

c  capillary containing erythrocyte
gl  glomerulus
sd  segmental duct
t  tubule
Figure 24  Transverse section of kidney of 28.58 mm fry to show well-formed glomeruli.

x 400

bc  Bowman capsule

gl  glomerulus

mc2  secondary mesonephric condensation

sd  segmental duct

t  tubule

Figure 25  Transverse section of kidney of 29.78 mm fry to show secondary Bowman capsule.

x 400

bc2  secondary capsule

sd  segmental duct

t  primary tubule

t2  secondary tubule
**PLATE XIII  EMBRYOLOGY**

**Figure 26** Typical transverse section of kidney of 64 mm fingerling.

x 200

- a arteriole
- gl glomerulus
- pcv post cardinal vein
- sd segmental duct
- t tubule

**Figure 27** Longitudinal section of 20.9 mm alevin to show bladder like distention of ducts.

x 100

- a anus
- b bladder
- g gut
- m mesonephros
- sd segmental duct
- sdc common urinary duct
- ugp urogenital papilla
PLATE XIV  CORPUSCLE OF STANNIUS

Figure 28  Longitudinal section of segmental duct in 7.4 mm embryo to show rudiment of corpuscle of Stannius.

x 800

c  corpuscular rudiment
ep  epithelium of duct
l  lumen of duct

Figure 29  Transverse section of right lobe of kidney in 9.54 mm embryo to show separation of corpuscle from duct.

x 400

c  corpuscle
pcv  post cardinal vein
sd  segmental duct
PLATE XV  CORPUSCLE OF STANNIUS

Figure 30  Frontal section of corpuscle of Stannius in 59 mm fingerling.

x 100

c  capillary
cap  capsule
t  fibrous trabeculum
PLATE XVI  INTERRENAL TISSUE

Figure 31  Transverse section of part of pronephros in 100 mm fingerling to show arrangement of interrenal tissue.

x 50

c  capillary net
it  interrenal tissue
mt  myeloid tissue
s  blood sinusoid