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THE GLOMERULAR DEVELOPMENT OF THE VERTEBRATE KIDNEY IN RELATION TO HABITAT

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Some twenty-five species of fishes, belonging to twelve families, are known to possess nearly or completely aglomerular kidneys (Marshall, 1929, and this paper). It has been suggested that this aglomerular condition is related to the peculiar water cycle associated with a marine habitat (Smith, 1930). In fresh water a large quantity of pure water is absorbed probably by way of the oral membranes, and excreted in large part, if not entirely, by the kidneys; whereas, in sea water a relatively small quantity of sea water with its contained salts is absorbed from the gastro-intestinal tract, and a large fraction of the absorbed water is excreted extra-renally. Thus a persistent oliguria relative to fresh-water forms occurs in marine fish, and this oliguria is held to be the cause of the glomerular degeneration.

In this view glomerular development should be related to water excretion in the vertebrates generally, and we wish to present evidence in this paper that such is the case. This evidence takes the form of three arguments: (1), that the protovertebrate kidney was aglomerular and that the glomerulus was evolved as an adaptation to a fresh-water habitat, (2) that in the lower vertebrates the extent of glomerular development is related to the quantity of water normally excreted by the organism and (3) that in the mammals (and possibly to some extent in lower vertebrates) the primitive water-excreting function of the glomerulus has been secondarily diverted to a filtration-reabsorption system designed to excrete waste products without the loss from the body of excessive quantities of water.

The Protovertebrate Kidney

The only information available on the nature of the protovertebrate kidney is that which may be obtained from the embryonic development of the lower vertebrates. There are no essential differences in the development of the pronephros of the cyclostomes, fishes and Amphibia, but we may suppose that the cyclostomes approach most closely to the primitive condition. Of these the developmental history is best known in the case of *Petromyzon* which has been studied by Wheeler (1899), Hatta (1900–01) and Inukai (1929). Additional information on the vertebrate pronephros is given by Felix in Hertwig's Handbuch (1906).

The pronephros of the lamprey at an early stage consists of six tubules on either side, formed from mesoderm and opening by means of nephrostomes into the unsegmented body cavity just behind the branchial region. In a later stage some of the tubules at the cranial and caudal end degenerate while the remainder (according to Inukai from 3 to 6 pairs) develop and function for a considerable time during the larval period. These pronephric tubules communicate with the pericardial cavity, which at about this time has been cut off from the peritoneal cœlom. Hatta regards the segmental duct as being formed by a series of abortive pronephric tubules in about twelve somites lying posterior to the eighth somite. After the formation of paired tubules, further development of the pronephros consists in the lengthening and convolution of the tubules, and the formation of a blood supply and glomerulus.

The blood vessels which supply the pronephros acquire definite form in a comparatively late stage of development. The glomerulus or glomus is lobulated, supplied by at least three branches of the aorta and hangs free in the pericardial cavity.

Hatta comes to the conclusion that in the ancestors of *Petromyzon* the pronephros once extended over all the body segments from the branchial to the cloacal region, the tubules opening to the exterior in each segment. The tubules of the posterior region were later converted into the segmental duct which first opened to the exterior and then into the cloaca.

In teleosts, where several originally distinct pronephric tubules have fused to form the pronephric chamber and a single tubule, the glomerulus is evolved after the separation of the pronephric chamber from the cœlom has taken place. Therefore, the pronephric tubule is aglomerular and unconnected with the cœlom for a considerable time during development (Emery, 1882; Felix, 1906). The glomerulus is here an inner glomerulus and consists of an invagination of a capillary tuft into the dilated end of the tubule which forms the pronephric chamber. Besides this condition and that observed in *Petromyzon,* there is a third and more usual type of pronephric development where the glomerulus is formed by a more or less complete abstraction of the true body cavity with an outer glomerulus or glomus in a pronephric chamber. Of these three types it would appear that that of the lamprey is the most primitive. Here, the glomerulus is quite distinct, separate from, and formed much later than the pronephric tubules.

That the glomerulus was developed after and secondarily to the pronephric tubules in the early vertebrates is certainly suggested by the above discussion. It is borne out by many other considerations. In invertebrates, nothing resembling a glomerulus occurs, but we find as excretory organs various types of tubules with glandular epithelium. The mesonephros of teleosts is stated to be aglomerular in young embryos (Audigé, 1910). In certain mammals (*e.g.,* rat and mouse) the mesonephros never develops glomeruli (Bremer, 1916). In most vertebrates the mesonephros is usually first formed of segmental tubules connected to the cœlom by nephrostomes. Later the glomerulus develops and we have a tubule containing a typical Malpighian body with its glomerulus, but still connected to the body cavity by a nephrostome, as in the adult Urodeles. However, the tubule in these forms usually loses its connection with the cœlom (Widersheim, 1906). Borcea (1906) states that in the development of the mesonephros of certain elasmobranchs (*e.g., Raia*) the segmental tubules lose their connection with the body cavity before the formation of glomeruli, thus paralleling the development of the pronephros of teleosts.

We may infer, then, that at some period the protovertebrate kidney was aglomerular and that it probably consisted of a series of tubules communicating with the cœlom by means of nephrostomes, the tubules either opening separately to the exterior or opening into a common duct. The tubules extended over a greater portion of the body than is the case with the pronephros at present. The tubules were not simple conduits, but their epithelium was glandular in structure and they may have both reabsorbed substances from the cœlomic fluid passing through them and added to this fluid by secretion. That secretion was a function of the primitive tubules is suggested by the fact that the tubular epithelium is derived from cœlomic epithelium and by the fact that crystals have been found in the lumen of the blind pronephric tubule of the embryo trout before the glomerulus has developed (Nussbaum, 1886.)

The cœlom seems to have been the original excretory organ, being connected with the exterior by means of pores, (*c.f.,* abdominal pores of cyclostomes and elasmobranchs) or by tubules opening into the cœlom by means of nephrostomes. Felix (1906) says, " als primitivestes Harnorgan haben wir fraglos die Leibeshohle selbst anzusprechen." The excretory function of the primitive cœlomic epithelium is indicated by the connection of both pronephros and mesonephros with its cavity, by the existence of abdominal pores in cyclostomes and elasmobranchs, and by the composition of the cœlomic and pericardial fluids of the latter (Smith, 1929b).

With the development of glomeruli, the nephrostomal connection of the tubule with the cœlom is usually abolished. The nephrostomes draining the cœlom may be secondarily diverted to empty into the venous system (Amphibia), into lymphoid spaces (elasmobranchs) or they may disappear completely.

Ever since Bowman published his original theory of urinary secretion in 1842 the glomerulus has been assigned the rôle of eliminating most of the water of the urine. All subsequent theories have taken this premise as their starting point. When this developmental and functional evidence is coupled with the evolutionary history of the lower vertebrates it appears probable that the glomerulus was evolved in response to the need for an easy means to excrete large quantities of water.

There is much evidence in the geological nature of the strata in which the early fossil vertebrates are found to indicate that these animals were inhabitants of fresh or slightly brackish water (Chamberlain, 1900; Barrell, 1916; O'Connell, 1916; Kiâer, 1924; Geikie, 1903; Woodward, 1900; Grabau, 1921; Hussakof and Bryant, 1918; Patten, 1912; Stromer, 1920). The subject presents many palæontological and geological difficulties and must still be considered a controversial one. According to Barrell (1916) with slight extensions based on the observations of other palæontologists and geologists, it would appear that the Silurian and Devonian ostracoderms and fishes were inhabitants of the continental rivers and fresh-water lakes. From some unknown relatives of these fresh-water forms there were evolved the Devonian elasmobranchs, dipnoans and ganoids and later the Carboniferous Amphibia. The elasmobranch fishes migrated to the sea toward the middle or late Devonian and, though frequently invading fresh water in subsequent times, this sub-class is predominantly marine today. The ganoid fishes may have invaded the sea to some extent in the Devonian, but so far as those forms which were ancestral to the recent teleosts are concerned, the permanent assumption of a marine habitat appears to date more properly from Carboniferous or even Mesozoic times. Judging in part from the historical record and in part from the life habits of the recent fishes, it would appear that the recent dipnoans, ganoids and many primitive teleosts have had a more or less continuous fresh-water history since the early Palæozoic period, while the recent marine teleosts may be assumed to have lived in pelagic or deep ocean waters only through Mesozoic and Tertiary time.

The composition of the sea in past ages is unknown, but it may be inferred that the salinity in the Devonian period was at least half, if not three-quarters, of what it is at present. It is certain that the salinity of the ocean waters throughout the Tertiary has been great enough to impose upon the marine teleosts the same osmotic restraints in regard to the absorption and excretion of water and salts that characterize this habitat today.

When these separate lines of evidence are brought side by side it is a logical deduction that the glomerulus was evolved in some early Palæozoic chordate to enable the organism to excrete readily the large quantity of water which was absorbed along the osmotic gradient existing between its blood and its fresh-water environment. This glomerulus represented simply an advantageous juxtaposition of the blood-vascular system to the already existing tubular system draining the excretory cœlom.

So long as the organism remained in fresh water (dipnoans, ganoids and teleosts) or in intimate dependence upon it (Amphibia), this excretory arrangement persisted; but with the secondary assumption of a marine habitat (teleosts) where the osmotic gradient was reversed and the water excretion reduced, or with the assumption of terrestrial life in which water conservation became a necessity (arid-living reptiles and birds), the organism no longer needed and could no longer economically use this primitive water-excreting mechanism. There was thus a need to either (*a*) discard or reduce the glomeruli or (*b*) amend their primitive function by adding distally a more efficient mechanism for the reabsorption of water. The first process appears to be occurring in the marine teleosts and in the reptiles. In the mammals and possibly to some extent in the birds, on the other hand, the addition of the loop of Henle has permitted the reabsorption of water against the osmotic pressure of the metabolites in the urine; consequently in these the glomeruli, although still very active as filters, have become secondarily incorporated into a filtration-reabsorption system which permits the excretion of waste products without the excretion of excessive quantities of water.

In substantiation of this thesis we wish to present here a description of the glomerular development in some fresh-water and marine fishes and in a few other vertebrates. No attempt has been made to interpret the structure of the kidney in larval forms because nothing is known at present about their water excretion or osmotic relationships. The marine cyclostomes and elasmobranchs possess blood which has about the same osmotic pressure as sea water, and such limited knowledge as we have of these animals indicates that the water cycle in them is quite different from what it is in the marine teleosts. Until more information is available on these points we cannot expect to fit these sub-classes into the present hypothesis.

THE GLOMERULAR DEVELOPMENT IN ADULT VERTEBRATES

In examining different animals we have used the following criteria in judging glomerular development:

1. Reduction in the number of glomeruli and presence of aglomerular tubules (here the extreme stage is an aglomerular kidney).
2. Very small size of the glomeruli.
3. Lack of good vascularization in the glomerular tuft, whether due to the presence of excessive amounts of connective tissue or to lack of capillary branching.

When only one of these conditions occurs one cannot draw definite conclusions, but if two or all conditions are present, it seems safe to conclude that glomerular development is poor.

The Higher Fishes.—Our observations have been most extensive in the heterogeneous group of teleostean fishes. We have collected a large series of data here in order to test our hypothesis.

The kidney of teleosts has not been extensively or intensively studied. It appears that wide variations in its structure can occur. What is known at present of the structure of its renal tubule has been summarized in a recent paper (Marshall, 1930). The long paper by Audigé (1910) is the most complete on teleost kidneys. Following Hyrtl (1851), Audigé divides the kidney into an anterior, middle, and posterior kidney. He further states that the posterior kidney is a metanephros, has well developed large glomeruli with branching capillary tufts, and that no aglomerular tubules occur; that the middle kidney has none, few, or many glomeruli, which are small and consist of a single coiled capillary; and that the anterior kidney in most adult forms consists entirely of lymphoid tissue. On this basis one can divide the teleosts into two groups, those with and those without a posterior kidney. We made such a division from all the data we could collect from the literature. Although in general the marine teleosts fell into the group without posterior kidney (poor glomerular development);

and the fresh-water fish into that with posterior kidney (good glomerular development), there were many exceptions. Our subsequent histological study of sections from the kidneys of many teleosts convinced us that a classification on the basis of the examination of sections was much more accurate than the above, and hence we omit this preliminary classification.

We have divided the higher fishes into four groups on the basis of glomerular development as shown from a study of sections of the kidney. These are as follows:

Group I. Kidneys having frequent glomeruli which are medium or large and invariably well vascularized. This group presents extremely good glomerular surface.

Group II. An intermediate group. Kidneys may have frequent glomeruli which are very small, or may have few glomeruli which are small or fair sized. Kidneys never have both frequent and medium sized glomeruli.

Group III. Kidneys having infrequent glomeruli which are small, poorly vascularized and which may show signs of degeneration. This group presents extremely poor glomerular surface.

Group IV. Aglomerular kidneys. In this group are included *Lophius,* where the very few glomeruli present are non-functional in the adult (Grafflin, 1929), and several species described by Guitel (1906) in which a single large glomerulus occurs in the persistent pronephros, but in which the remainder of the kidney (mesonephros) is aglomerular.

There would appear to be little error involved in placing a species into groups I and IV, but some selection is necessary to determine whether a species should go into group II or III and to a less extent as to whether it should go into group I or II. Any questionable case has been put in the intermediate group II, so that it is possible that some species in group II should have been in group I or III.

The following table gives the groups as defined above and the average size of the renal corpuscles in sections of kidney fixed and treated in the same way.[1] The habitat of the species studied is given in

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[1] Measurements of the size of the renal corpuscle in fixed sections are undoubtedly too small due to shrinkage. Another objection to measuring glomeruli in sections is the difficulty of always measuring a section cut through the middle. This error will affect the larger glomeruli more than the smaller. Distortion of the shape of a Malpighian body also occurs in sections. This has led us to average the two diameters measured in ten corpuscles and give a single figure as representing the size. Using our measurements only to indicate whether the glomeruli are small, medium or large would seem to be justified in spite of the many unknown factors which must be considered in comparing different animals. We have worked only with adult animals.

TABLE I

Glomerular Development and Habitat of Higher Fishes

Species	Family	Common Name	Habitat	Size of Renal Corpuscle in Micra
Group I				
Protopterus æthiopicus Heckel	Lepidosirenidæ	Lung-fish	F	153
Polypterus senegalus Cuvier	Polypteridæ		F	89
Amia calva Linnaeus	Amiidæ	Bowfin	F	82
Plecostomus plecostomus (Linnaeus)	Loricaridæ		F	73
Cyprinus carpio Linnaeus	Cyprinidæ	Carp	F	82
Carrassius auratus (Linnaeus)	Cyprinidæ	Goldfish	F	62
Catostomus commersonii (Lacépède)	Cyprinidæ	Sucker	F	60
Ameriurus nebulosus (LaSueur)	Siluridæ	Catfish	F	99
Morone americana (Gmelin)	Serranidæ	Silver perch	E	63
Ambloplites rupestris (Rafinesque)	Centrarchidæ	Bass	F	86
Enneacanthus gloriosus (Holbrook)	Centrarchidæ	Sunfish	F	76
Perca flavescens (Mitchill)	Percidæ	Perch	F	102
Salmo gairdneri Richardson	Salmonidæ	Trout	E	60
Salvelinus fontinalis (Mitchill)	Salmonidæ	Trout	E	75
Umbra limi (Kirtland)	Esocidæ	Mud minnow	F	106
Esox lucius Linnaeus	Esocidæ	Pickerel	F	81
Anguilla rostrata LaSueur	Anguillidæ	Eel	E	104
Gymnothorax funebris Ranzani	Murænidæ	Moray	M	112
Myoxocephalus octodecim (Mitchill)	Cottidæ	Sculpin	M	81

TABLE I (*Continued*)

Species	Family	Common Name	Habitat	Size of Renal Corpuscle in Micra
Group II				
Copeina guttata (Steindachner)	Characidæ		F	48
Astanyx sp.	Characidæ		F	50
Centropristis striatus (Linnaeus)	Serranidæ	Sea bass	M	52
Hæmulon album Cuv. and Val.	Hæmulidæ	Grunt	M	34
Hæmulon album Cuv. and Val.	Hæmulidæ	Grunt	M	64
Holocentrus ascensionis (Osbeck)		Squirrel fish	M	39
Gadus callarias Linnaeus	Gadidæ	Cod	M	37
Melanogrammus æglefinus (Linnaeus)	Gadidæ	Haddock	M	38
Hemitripterus americanus Gmelin	Cottidæ	Sea Raven	M	65
Chilomycterus schœpfi (Walbaum)	Diodontidæ	Spiny box fish	M	59
Caranx ruber (Bloch)	Carangidæ	Jack	M	33
Sphyræna barracuda (Shaw)	Sphyrænidæ	Barracuda	M	35
Strongylura raphidoma Ranzani	Sphyrænidæ	Hound fish	M	46
Tautoga onitis (Linnaeus)	Labridæ	Tautog	M	56
Scomber colias Gmelin	Scombridæ	Tinker mackerel	M	48
Cryptacanthodes maculatus Storer	Cryptacanthodidæ	Wrymouth	M	94
Pseudopleuronectes americanus (Wal.)	Pleuronectidæ	Flounder	M	50
Poronotus triacanthus (Peck)	Triglidæ	Butter fish	M	51
Stenotomus chrysops (Linnaeus)	Sparidæ	Porgy	M	51
Chætodipterus faber (Broussonet)	Chætodipteridæ	Spade fish	M	40
Balistes vetula Linnaeus	Balistidæ	Trigger fish	M	41
Sebastes marinus (Linnaeus)	Scorpænidæ	Rose fish	M	44

TABLE I (*Continued*)

Species	Family	Common Name	Habitat	Size of Renal Corpuscle in Micra
Group III				
Argyropelecus hemigymnus Cocco	Stomiatidæ		M	
Chauliodus sloanei B. and S.	Stomiatidæ		M	
Gonostoma bathyphilum (Vaillant)	Stomiatidæ		M	
Gonostoma grande (d?)	Stomiatidæ		M	
Strongylura notatus (Poey)	Belonidæ	Needle fish	M	39
Strongylura sp.	Belonidæ	Bill fish	M	37
Cypselurus heterurus (Rafinesque)	Exocœtidæ	Flying fish	M	30
Teuthis hepatus Linnaeus	Teuthidæ	Brown tang	M	27
Sphæroides maculatus (B. and S.)	Tetradondidæ	Puffer	M	38
Lactophrys bicaudalis (Linnaeus)	Ostrociidæ	Shell fish	M	26
Group IV				
Syngnathus dumerilii (Kaup)	Syngnathidæ	Pipe fish	M	None
Syngnathus acus Linnaeus	Syngnathidæ	Pipe fish	M	"
Siphonostoma sp.	Syngnathidæ	Trumpet fish	M	"
Nerophis lumbriciformis (Willoughby)	Syngnathidæ		M	"
Entelurus anguineus (Kaup)	Syngnathidæ		M	"
Hippocampus brevirostris Storer	Syngnathidæ	Sea horse	M	"
Hippocampus guttulatus Cuvier	Syngnathidæ	Sea horse	M	"
Lepadogaster gouanii Bris. de Ban.	Gobiesocidæ		M	"
Lepadogaster bimaculatus (Pennant)	Gobiesocidæ		M	"
Lepadogaster candolli Risso	Gobiesocidæ		M	"
Lepadogaster macrocephalus (d.?)	Gobiesocidæ		M	"
Chorisochismus dentex (Pallas)	Gobiesocidæ		M	"
Gastrostomus bairdi Gill and Ryder	Saccopharyngidæ		M	"
Pterophryne histrio (Linnaeus)	Antennariidæ	Mouse fish	M	"
Opsanus tau (Linnaeus)	Batrachidæ	Toad fish	M	"
Lophius piscatorius Linnaeus	Lophiidæ	Goose fish	M	"

the third column, *F* indicating fresh water, *M* marine and *E* euryhaline (where the fish can live in fresh or salt water). The evidence for the aglomerular nature of the kidneys of group IV is given by Marshall (1929) and that for placing the first four fish in group III by Nusbaum-Hilarowicz (1923). The kidneys of all the remaining fish have been examined in the course of this study.[2] The microphotographs of typical fields in cross sections of the kidney given at the end of this paper illustrate fairly well the differences between these groups (Plates I, II and III).

The relationship of habitat to glomerular development is brought out forcibly by the extremes represented in groups I and IV.

The fishes of group IV are aglomerular and thus represent the extreme condition which we imagine to result from a very low water excretion, namely, the complete absence of all filtering surface as typified by the glomerulus, and the presence only of tubular tissue of a high, cuboidal and secretory nature. The fish included in this group are all marine, and even related species do not migrate into fresh water except in rare instances which we may believe represent secondary invasions of fresh water. (The Syngnathidæ have representatives in Panama which may occasionally be found in brackish to fresh-water streams). They are all end-products or terminal members in the evolution of specialized Teleostei. The Saccopharyngidæ are abyssal or deep water forms, though occasionally the latter may invade brackish water. The remaining families are littoral or pelagic forms, and though some of them (*Opsanus*) may normally invade brackish waters, none is known to migrate into strictly fresh water.

The fishes of group I represent the primitive condition which we imagine existed in the Palæozoic ganoids which were ancestral to all the Teleostei, marine and otherwise. In these the glomeruli are numerous, large, with very flat capsular epithelium and the capillary tuft is finely divided by branching. Here the filtering surface is obviously extensive. These species are with two exceptions (*Myoxecephalus* and *Gymnothorax*) either exclusively fresh-water or euryhaline forms. *Ameriurus, Myoxocephalus, Gymnothorax* and *Plecostomus* are relatively highly specialized forms; the others are primitive types. The Loricaridæ, Siluridæ, Cyprinidæ and Characidæ belong to the Ostariophysi, which is typically a continental and fresh-water order. *Amia* is a primitive ganoid and *Protopterus* and *Polypterus* represent the two most ancient types of surviving fishes.

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[2] The specimens of *Protopterus* and *Polypterus* were collected by H. W. S. in Africa through the favor of the John Simon Guggenheim Memorial Foundation.

In contrasting these groups we note that the members of groups III and IV consist of aglomerular or nearly aglomerular fish, of a generally specialized type, which are exclusively marine; group I consists of well glomerularized fish, of a generally primitive type, which are with few exceptions exclusively fresh-water or which occasionally enter fresh water. It is perhaps significant that all the abyssal marine forms which have been studied fall into groups III or IV while the continental and pelagic forms fall into groups I and II. An abyssal habitat may be taken as evidence of a long marine history. It is to be expected that aglomerular kidneys would more probably occur in fishes which had been marine for a long period of time. The fact that the aglomerular forms are in other respects specialized rather than primitive is in accord with general principles of evolution.

Between the extremes of fresh-water or primitive marine fish, on the one hand, and highly specialized marine fish on the other, it is to be expected that there would occur every degree of glomerular development. That such is the case is shown by the character of the fish which we have placed in the intermediate groups II and III. Group III consists of fish with greatly reduced glomerular development; the glomeruli are small, poorly vascularized and very infrequent. These fish are all marine and specialized forms. They approach quite closely to the members of group IV in general character and in glomerular development. It is possible that among these fish some of the few remaining glomeruli are non-functional.

The members of group II are intermediate in glomerular development and heterogeneous in character. They are mostly marine, and include specialized as well as more generalized forms. It is, of course, in this group that the need of a more quantitative expression of glomerular development is most pressingly felt, but this gap in our knowledge is not the only deficiency; we have no information as to how long these fish have been marine or to what extent they may have migrated from salt to fresh water, or *vice versa,* in the course of teleostean evolution. Without such information a quantitative interpretation of this group is practically impossible.

It may be noted that some instances of secondary invasion of fresh water are clearly evident. Thus in the sub-order Apodes the Saccopharyngidæ, Murænidæ and most of the Anguillidæ are marine; but the common eel, *Anguilla rostrata,* lives in fresh water and only returns to the sea to spawn. It may be inferred, then, that a fresh-water habitat is relatively recent for this species. The deep-sea *Saccopharyngida, Gastrostomus bairdi,* is aglomerular; while *Anguilla* shows the typical fresh-water development of the glomeruli. It is probable that the fresh-water Percidæ and Centrarchidæ and the brackish-water Pleuronectidæ, Tetradondidæ and Cottidæ represent forms derived from marine stocks and secondarily entering fresh-water.

Until more is learned, both about the physiology of these forms and their evolutionary history, a closer interpretation than that attempted above is clearly impossible.

Amphibia.—A large amount of work has been done on the kidneys of the Amphibia, yet there is no evidence that aglomerular tubules ever occur in this class. The glomeruli appear to be numerous, well vascularized and the capsule has a low epithelium. This is in line with the close ecological dependence of the Amphibia on fresh water.

The largest glomeruli of all animals occur in the Urodeles (Hyrtl, 1863). Steinbach (1927) gives measurements of the size of glomeruli from sections of several species of Amphibia. These vary from 86 to 217 micra. Using our technique, we find for the average size of the glomerulus in *Rana catesbeiana,* 115 micra; *Bufo americanus,* 92 micra; *Plethodon cinereus,* 145 micra; *Siren lacertina,* 211 micra; and *Necturus maculosus,* 308 micra.

There are some Amphibia which burrow and remain underground during the drought season (North Central Australia). Sweet (1907) states that these forms take in large quantities of water by the mouth and skin before estivating and excrete and store it in the urinary bladder. The water is reabsorbed from the bladder into the abdominal cavity during estivation and passed by the nephrostomes (of which these species have an exceptionally large number) into the renal veins; in this way the water is used over and over again. This absorption of water from the urinary bladder is in line with the recent observation of Steen (1929) that, when exposed to dry air, frogs may reabsorb all the water from the urinary bladder. Sweet states that in one of these burrowing species (*Chiroleptes alboguttatus*) the glomeruli are very few in number and remarkably small.

But as a class the amphibians are provided with good glomerular surface. It is difficult to compare the separate species because of the wide variation in the size of the animal and of the size of the glomerulus. We have not attempted any quantitative analysis within this class.

Reptiles.—The glomeruli of reptiles are peculiar in that the center of the glomerular tuft consists of connective tissue with capillaries only on the outside (Regaud and Policard, 1903–04; Cordier, 1928). In addition to this peculiarity, the Malpighian corpuscle is rather small. Bowman (1842) gives the diameter of the glomerulus of the tortoise as 106 micra, and of the boa constrictor as 63 micra; Hüfner (1866) gives for *Testudo græca* and *Emys europoea,* 110 micra; Regaud and Policard (1903–04) give for the Ophidia, 110 x 90 and 80 x 60 micra; and Hoffman (1890) gives for the Saurians 45 to 52 micra. Zarnik (1910) reports measurement of the glomeruli of the longest tubules of several species of reptiles from macerated preparations, but since they cannot be taken as average values, they are of no assistance to us here.[3] Cordier (1928) reports the average size of the glomerulus in the Chelonians as 50 micra, in the Ophidians as 80 micra and in the Lacertilians as 50 micra. He made careful reconstructions of the glomeruli of these forms and came to the conclusion that the capillary is never an unbranched vessel as stated by Regaud and Policard (1903–04); but the filtering surface of the glomerulus in Chelonians is fairly good and in Ophidians and Lacertilians extremely poor. Cordier clearly recognizes that this difference is related to the elimination of water. He finds from sections that the decrease in filtering surface of the glomerulus of snakes and lizards is not compensated for by increased number, and relates the poor glomerular development of the former to their solid or semi-solid excrement; and the much better development in Chelonians, to their fluid urine.

Table II summarizes our observations on a few species.

TABLE II

Glomeruli of Reptiles

Scientific Name	Common Name	No. Renal Corpuscles	Size in Micra	Vascularity of Tuft
Pseudemys sp.	Slider Terrapin	Frequent	63	Fair
Caretta caretta (Linnaeus)	Sea Turtle	"	91	"
Alligator mississippiensis (Daudin)	Alligator	"	—	"
Boa imperator Daudin	Boa Constrictor	Infrequent	71	Poor
Liopeltis vernalis (Harlan)	Grass Snake	"	59	"
Phrynosoma cornutum (Harlan)	Horned Toad	"	51	"

Two distinct groups of reptiles can be established: one with fair glomerular surface and fluid urine (Chelonia and Crocodilia); the other with very poor glomerular surface and solid or semi-solid urine (Lacertilia and Ophidia). It is in this last group that Regaud and Policard (1903–04) and Zarnik (1910) have found blind diverticula or

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[3] As a rule no statement is given as to how the measurements were made (sections, macerated tissue, or fresh material). This probably accounts for many of the wide discrepancies in the figures. The size of the animal from which the kidneys were removed would also be an important factor.

aglomerular tubules. Microphotographs of sections from kidneys of the terrapin, horned toad, and boa constrictor are given at the end of this paper (Plates III and IV).

Birds.—In the bird's kidney we find the beginning of the loop of Henle. Many tubules occur without the loop, however, and these have a short intermediate segment similar to that of reptiles. Many other tubules show transitional stages (Huber, 1917; Feldotto, 1929). The glomeruli of birds' kidneys are stated to be the smallest known; they are, however, no smaller than some occurring in marine teleosts. The capillary loop of the glomerulus is described by some observers as unbranched and by others as only slightly divided. Bowman (1842) states that the " Malpighian vessel is a coiled ampulla "; Hyrtl (1863) says that in spite of the extremely small size of the glomerulus, the vessel is not simple but divides in the smallest glomeruli into 2, and in the largest into 7 or 8 branches. Standfuss (1908) also remarks on the small number of capillary loops in the glomeruli of birds.

Bowman gives the diameter of the glomerulus of the parrot as 59 micra and Hüfner (1866) gives for the dove 44 x 35 micra. Von Mollendorff (1922) has measured the glomeruli of several birds in macerated preparations. He finds average diameters of 48 micra for the pigeon, 38 micra for the ring-sparrow, 28 micra for the house-sparrow, and 24 micra for the finch. We have examined sections of the kidneys of the chicken and pigeon, and find the average diameter of the Malpighian bodies to be 70 micra in the former and 50 micra in the latter. A curious fact about the glomeruli of these birds, which so far as we know has not been noted before, is that the central part of the glomerular tuft resembles the reptilian glomerulus in its lack of capillaries. There is, however, instead of connective tissue a central core of dense syncytial-like tissue. A microphotograph of a section from a chicken kidney is given (Plate IV).

It is obvious that the bird's kidney shows glomerular degeneration, as indicated by the very small size and poor vascularization of the glomeruli, and by the replacement of the central portion of the tuft by syncytial tissue. It is improbable that increased number of glomeruli can offset this reduction in filtering surface.

Mammals.—So far as is known, the tubules of mammalian kidneys are supplied with large, well vascularized glomeruli. Bowman (1842) gives the average size of the glomerulus of a number of mammals ranging from 100 micra in the mouse to 362 micra in the horse. Many subsequent observers give measurements for different species (See Vimtrup, 1928, and v. Mollendorff, 1929). Thus the smallest mammalian glomerulus can be considered large in comparison with those occurring in many marine teleosts, reptiles and birds.

It is in the mammalian kidney that the loop of Henle attains for the first time its full development. This fact is significantly associated with the marked hypertonicity which mammalian urine can exhibit in comparison with the blood plasma (Crane, 1927) and suggests that the glomerular function in these animals has been almost completely modified from its primitive water-excreting function. It is interesting to note that in the primitive *Echidna,* the kidney resembles that of the reptile as much as that of the higher mammals, and that here the glomerular development is stated to be less than in other mammals of the same size (Zarnik, 1910). Much more work, however, will have to be done before mammals can be compared in a quantitative way with other animals or among themselves.

DISCUSSION

The idea that the development of the glomerulus is an adaptation to water excretion by the kidney agrees well with the facts which we have presented.

In the diversified group of higher fishes, we find convincing evidence of the influence of a marine habitat on the development of the glomerulus. In the snakes and lizards as well as the birds, where water conservation is so important that a solid or semi-solid urine is eliminated, the unquestionable reduction in glomerular surface is entirely in accord with what might be predicted.[4] The good glomerular development of the fresh-water fishes and the Amphibia is quite in line with the general thesis. Difficulties arise in attempting to compare different animals with one another in a quantitative way. It is essential to know the number of glomeruli in the kidneys, and also the surface area presented by the capillaries of an average glomerulus. One can obtain the number by accurate counts, but there is no accurate method for obtaining the surface area of a glomerulus and more particularly of the variable capillary tuft. It appears to be generally true that the smaller the glomerulus, the less the capillary tuft is broken up by branching, but the amount of space in the glomerular tuft not occupied by capillaries also seems quite variable in different animals. The recent careful investigation of the surface of a human

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[4] In the reptiles and birds the urine coming from the ureters is fluid, and the final reabsorption of water takes place in the cloaca. Quite different figures have been given for the ureteral urine flow of the bird, none of which has been determined under strictly normal conditions. Gibbs (1928, 1929*b*) finds that extremely concentrated urine may come from the fowl's ureters. The fact that the ureteral urine is always extremely concentrated as regards waste products when compared to the urine of fresh-water fish and Amphibia, may be taken as supporting our hypothesis.

glomerulus by Vimtrup shows how erroneous are the estimates of glomerular surface used by Putter (1926) and von Mollendorff (1922).

Even with the number of glomeruli in a kidney determined, there is no exact method of correlating the number in different animals of widely varying size. No data exist to show on what basis such a comparison should be made. All one can do at present is to compare the number of glomeruli in the kidneys of animals of approximately the same size on the basis of body weight and then judge the relative glomerular surface by the average diameter of a glomerulus. An attempt at a more quantitative comparison of glomerular surface is in progress for fish, reptiles and birds of various sizes, and a further quantitative interpretation will be deferred until this work has been completed. For mammals (von Mollendorff, 1929) and Amphibia (Steinbach, 1927) the number and size of the glomeruli have already been determined for many species.

In conclusion, it may be remarked that the relative amounts of a substance eliminated by the glomerulus and tubule will depend on the glomerular development of the animal. If we accept the filtration theory of glomerular function, it is obvious that in eliminating water through the glomerulus, diffusible plasma constituents must also be eliminated and excreted unless reabsorbed by the tubule.[5] Looking at this problem from the standpoint of secretion by the tubule, it is clear that where a large amount of fluid is eliminated by the glomerulus, the secretory function of the tubule will be minimal, but where small amounts are eliminated in the case of poor glomerular development, secretion by the tubule will be maximum. This agrees fairly well with what we know about secretion by the tubule in different classes of vertebrates. Thus, in mammals, it has been supposed that filtration by the glomerulus and reabsorption by the tubule play a major rôle in the production of the urine, and that secretion exists only as a relic of a primitive process (Mayrs, 1924; Marshall, 1926). On the other hand, in birds there is now rather conclusive evidence (Mayrs, 1924; Gibbs, 1929*a*) that secretion plays a major rôle in the elimination of uric acid by the kidney. That secretion by the tubule also will play an important rôle in excretion by the reptilian kidney can be safely predicted. In Amphibia and fresh-water fish, where secretion by the tubule may be small, special conditions must be employed to demonstrate it. On the other hand, tubular elimination or secretion is easily proven in marine teleosts (Marshall, 1930). Just how much secretion by the tubule will take place in a kidney would appear, then, to depend on

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[5] Of course, some reabsorption of water and concentration of urinary constituents takes place in the tubule of the lower vertebrates.

the amount of filtrate elaborated by the glomeruli and hence on glomerular development and activity.

SUMMARY

Evidence is presented for the view that the glomerular development of the kidneys of vertebrates is related to water excretion. The protovertebrate kidney was at one stage probably aglomerular and the glomerulus was evolved as an adaptation to a fresh-water habitat. In the lower vertebrates remaining in fresh water (dipnoans, ganoids and fresh-water teleosts) and in those still in intimate dependence on it (Amphibia), the glomerular development is good; but with the secondary assumption of a marine habitat (marine teleosts) or with the assumption of terrestrial life in which water conservation becomes a necessity (arid-living reptiles and birds) the glomerular development is extremely poor. In the mammals (and possibly to some extent in lower vertebrates) the primitive water-excreting function of the glomerulus has been secondarily diverted to a filtration-reabsorption system designed to excrete waste products without the loss from the body of excessive quantities of water. The relative importance of tubular secretion in any kidney will, on this view, depend upon the extent of glomerular development.

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REFERENCES

Audigé, J., 1910. *Arch. de Zool. expér. et gén.*, 5me Sér., **4**: 275.
Barrell, J., 1916. *Bull. Geol. Soc. Amer.*, **24**: 387.
Borcea, I., 1906. *Arch. de Zool. expér. et gén.*, 4me Sér., **4**: 199.
Bowman, W., 1842. *Phil. Trans. Roy. Soc., London,* page 57.
Bremer, J. L, 1916. *Am. Jour. Anat.*, **19**: 179.
Chamberlain, T. C., 1900. *Jour. Geol.*, **8**: 400.
Cordier, R., 1928. *Arch. de Biol.*, **37**: 1.
Crane, M. M., 1927. *Am. Jour. Physiol.*, **81**: 232.
Emery, C., 1882. *Arch. Ital. Biol.*, **2**: 135.
Feldotto, A., 1929. *Zeitschr. f. mick-anat. Forschung,* **17**: 353.
Felix, W., 1906. *Hertwig's Handbuch der Entwick. der Wirbeltiere,* **3**: 81.
Geikie, C., 1903. Text-book of Geology, Chap. 2, page 995. London.
Gibbs, O. S., 1928. *Am. Jour. Physiol.*, **87**: 594.
Gibbs, O. S., 1929a. *Am. Jour. Physiol.*, **88**: 87.
Gibbs, O. S., 1929b. *Science*, **70**: 241.
Grabau, H., 1921. Text-book of Geology. Chap. 2. Historical Geology. Page 591. New York.

GRAFFLIN, A. L., 1929. *Am. Jour. Anat.*, **44**: 441.

GUITEL, F., 1906. *Arch. de Zool. expér. et gén.*, 4me Sér., **5**: 505.

HATTA, S., 1900–01. *Jour. College Sci., Imp. Univ. Tokyo,* **13**: 311.

HOFFMANN, C. K., 1890. Brouns Klassen und Undnungen des Tierreichs. Reptilien.

HUBER, G. C., 1917. *Anat. Rec.,* **13**: 305.

HÜFNER, C. G., 1866. Zur vergleichenden Anatomie und Physiologie der Harncanälchen. Inaug. Diss. Leipzig.

HUSSAKOF, L., AND BRYANT, W. L., 1918. *Bull. Buff. Soc. Nat. Sci.*, page 12.

HYRTL, J., 1851. *Denk. Kais. Akad. des Wissen. Math-Natur. Classe,* **2**: 27.

HYRTL, J., 1863. *Sitzungsber. Math-Natur. Classe der Kais. Akad. des Wissen.,* **47**: 146.

INUKAI, T., 1929. *Zeitschr. f. mikr-anat. Forschung,* **19**: 139.

KIÄER, J., 1924. The Downtonian Fauna of Norway. I. Anaspida. *Videnskapsselskepets Skrifter, I. Mat.-Natur. Klasse,* Bind I, No. 6.

MARSHALL, E. K., 1926. *Physiol. Rev.,* **6**: 440.

MARSHALL, E. K., 1929. *Bull. Johns Hopkins Hosp.,* **45**: 95.

MARSHALL, E. K., 1930. *Am. Jour Physiol.,* **94**: 1.

MAYRS, E. B., 1924. *Jour. Physiol.,* **58**: 276.

VON MOLLENDORFF, W., 1922. *Munch. Med. Woch.,* **69**: 1069.

VON MOLLENDORFF, W., 1929. *Bethe's Handbuch der Norm. u. Path. Physiologie,* **4**: 183.

NUSBAUM-HILAROWICZ, 1923. *Comp. Sci. Monaco,* **65**: 1.

NUSSBAUM, M., 1886. *Arch. f. mikr. Anat.,* **27**: 442.

O'CONNELL, M., 1916. *Bull. Buff. Soc. Nat. Sci.,* **11**: 93.

PATTEN, W., 1912. The Evolution of the Vertebrates and their Kin. Philadelphia.

PUTTER, A., 1926. Die Drei-drüsentheorie der Harnbereitung. Berlin.

REGAUD, Cl., AND POLICARD, A., 1903–04. *Arch. d'Anat. micros.,* **6**: 191.

SMITH, H. W., 1929a. *Jour. Biol. Chem.,* **81**: 727.

SMITH, H. W., 1929b. *Jour. Biol. Chem.,* **81**: 407.

SMITH, H. W., 1930. *Am. Jour. Physiol.,* **93**: 480.

STANDFUSS, R., 1908. *Arch. f. mikr. Anat.,* **71**: 116.

STEEN, W. B., 1929. *Anat., Rec.,* **43**: 215.

STEINBACH, G., 1927. *Zeitschr. f. Zellforsch.,* **4**: 382.

STROMER, A., 1920. *Sitz. Math. Phy. Klasse, K. B. Akad. Wiss. Munchen,* Vol. 9.

SWEET, G., 1907. *Proc. Roy. Soc. Victoria,* **20**: 222.

VIMTRUP, B. J., 1928. *Am. Jour. Anat.,* **41**: 123.

WHEELER, W. M., 1899. *Zool. Jahrbuch., Abt. Anat.,* **13**: 1.

WIDERSHEIM, R., 1906. Vergleichende Anatomie der Wirbeltiere. Jena.

WOODWARD, A. S., 1900. *K. Svenska vet.-akad. Bihang till Handlingar,* Bd. 26, Afd. 4, No. 10.

ZARNIK, B., 1910. *Jen. Zeitschr. f. Naturwissen.,* **46**: 113.