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FUNCTIONAL ASPECTS OF RENAL GLOMERULI BASED ON SCANNING ELECTRON MICROSCOPY OF CORROSION CASTS, WITH SPECIAL EMPHASIS ON REPTILES AND BIRDS

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Abstract

The glomerular complexity of several species of birds and reptiles is investigated in this study by scanning electron microscopy of vascular corrosion casts. Comparing these results with those of a freshwater teleost and a mammalian species, a trend towards small, simple glomeruli of the avian type, beginning with large, well vascularized glomeruli resembling the type found in fish, can be observed in reptiles.

A close correlation between glomerular size and habitat can be established comparing related species having a similar physiological mode of renal function.

Entirely different from this sauropsidian evolutionary line of development is the highly complex, large differentiation of the mammalian glomerulus.

KEY WORDS: Corrosion casting, scanning electron microscopy, ultrastructure, glomerulus, kidney, urogenital system, reptiles, birds, fish, mammals.

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Introduction

Comparisons of the development of renal glomeruli in different vertebrates using the light microscope (e.g., Marshall and Smith, 1930) have a number of technical limitations (low resolution, tissue shrinkage during processing, ...). Only a small number of glomeruli have been studied in detail (e.g. Vilter, 1935; Bargmann, 1937), and the natural variability of glomerular structure has been neglected altogether.

Scanning electron microscopy (SEM) of vascular corrosion casts offers an excellent opportunity for studies on glomerular morphology and allows both a higher resolution and the investigation of a large amount of specimens within a reasonable time. Although several studies on non-mammalians exist, most of the previous work was carried out on mammalians (for a detailed review see Lametschwandtner et al., 1984).

We selected several reptilian and avian species, differing in their ecology and systematic position, to study the differentiation of renal vascular structures in this type of kidney. These results were compared with those of rats and freshwater bony fish.

Materials and Methods

The following species were used for the preparations: fish - six Tenches (Tinca tinca, Linné 1758); reptiles - nine Pond Slider turtles (Pseudemys scripta, Wied 1839), five Hermanns Tortoises (Testudo hermanni, Gmelin 1789), one Common Iguana (Iguana iguana, Linné 1758), four Peloponnes Wall Lizards (Podarcis peloponnesiaca, Bibron and Bory 1833); birds - nine mallards (Anas platyrhynchos, Linné 1758), seven doves (Streptopelia roseogrisea, Sundevall 1857); mammals - six laboratory rats (Rattus norvegicus, Berkenhout 1769) strain Him:OF1/Swiss.

All animals were anaesthetized with pentobarbital i.p. (10mg/100g BW; Nembutal; Serva; FRG) and received an anticoagulant (0.1/0.2ml heparine - less/more than 500g BW; 5000I.E./ml Immuno; Austria) approximately 30 minutes

before preparation. After preparation of the heart, a disposable polyethylene catheter (ø 0.5x1.0mm; Braun-Melsungen; FRG) was ligated into the aorta near the heart. In reptiles the catheter was placed into the left aortic branch, while the right aortic branch was only ligated immediately before perfusion. For small species (e.g., lizards) the catheters were mechanically drawn to the appropriate diameter. The vascular system was rinsed of blood by a Tyrode-solution adjusted to the specific pH, osmolarity and body temperature of the animals (see e.g., Spector, 1956); a peristaltic pump (PA-SF 2; Ika; FRG), calibrated according to the mean cardiac output rate of the specimen, was used. The preparation desk and rinsing solution were heated by a bath-heater (D8; Haake; FRG). Immediately after onset of the perfusion, the posterior caval vein was cut near the heart. When the outflowing liquid appeared free of blood, the casting resin was injected through the same catheter with a "Record"-syringe in a mechanical press (modified construction after Lametschwandtner et al., 1976) until the liver-sinusoids appeared macroscopically completely injected. Mercox-B1 (Japan Vilene Co.; Japan) diluted with 20% methyl-methacrylate monomer (Fluka; Switzerland) according to Ohtani and Murakami (1978) or pre-polymerized methyl-methacrylate prepared after Murakami (1971) in the modification according to Lametschwandtner and Simonsberger (1975) was used as casting resin. The catheter and the posterior caval vein were clamped after the injection, and in situ polymerisation was allowed either at room temperature for 24 hours or in a 60°C water bath overnight. Maceration was carried out in daily changes of 10% KOH. The casts were washed in tap and distilled water and dried in a desiccator with silica gel blue.

Dissection of the casts was done either with two razor blades, with a sliding microtome after embedding in polyethylene glycol (Ditrich, 1984), or after "ice-embedding" (Lametschwandtner et al., 1984) using a diamond mini-cutting disc. Super-sonication of casts in distilled water under microscopical control (35kHz; Transsonic T 460; Elma; FRG) for 5 to 12 minutes allowed visual-isation of larger, concealed vessels by removal of dense capillary zones. The trimmed casts were mounted with double-sided self adhesive tape and coated with gold in a "Hummer JR" sputter coater (6-7kV, 10-12mA, 7-10min.). A "JEOL JSM-35 CF" and a "Cambridge Mark 2A Stereoscan" at an acceleration voltage of 5-10kV were used for the investigation. All measurements were taken with the "JEOL" instrument, which had previously been calibrated for correctness of the magnification display and been checked for spherical aber-ration using standardized test specimens.

For measurements of capillary networks, micrographs were overprinted with a "multipurpose stereologic test grid" (e.g., Pinto and Brewer, 1974) (Fig.1). For the exact form and size of complex three-dimensional structures, stereo-photogrammetric "contour maps" were drawn from pairs of stereo-micrographs (tilt-angle 5°) with an "Autograph A6" (Wild; FRG) analyzer (Ditrich and Splechtna, 1985) (Fig.2).

Results

For quantitative investigations on casts of glomerular blood vessels, complete replication of the renal vascular system is essential. Besides more indirect methods (e.g. embedding and taking sections as controls) several criteria can be applied to check the completeness of the casts directly:

+) Endothelial impressions, indicating a sufficient injection pressure, and replication of the glomerular mesangial channel system should be present (Fig.3A). The latter, however, is poorly visible in unfractured glomeruli of some types (mammalians) and may be absent in others.

+) The venous portal supply to the kidney and consequently the full extent of the peritubular capillary plexus should be replicated (Fig.1). This pertains only to non-mammalian kidneys (portal kidneys), but proves that the casting medium has passed the capillary zones beyond the arterial supply of the kidney and returned in sufficient quantities to the kidney by the renal portal veins.

+) Blind-ending vessels should be absent at least in the glomerulus.

Those renal vascular casts filling these criteria were used for determination of glomerular parameters. The glomeruli used for further investigations, providing they were not partly concealed by other vessels, were selected at random from the surface of the dissected casts. The average diameters of the different glomerular casts are given in Table 1.

The freshwater fish Tinca tinca exhibits a well vascularized, rather large glomerulus (Fig.4) (hereafter referred to as "basic type"). The turtles Pseudemys scripta and Testudo hermanni (Fig.5A) show significantly ($P<1\%$;$n=163$) different glomerular sizes. P. scripta, as a freshwater species, resembles the basic type of T. tinca in glomerular size and morphology. The average diameter of the glomerulus of T. hermanni is about 60% larger than that of P. scripta. This is only partly due to the larger diameter of the single glomerular capillaries (P. scripta: 7-10µm; T. hermanni: 15-23.6µm), as more capillary loops are usually visible on the surface of the glomerulus of T. hermanni. The average glomerular diameter of the lacertilians Iguana iguana (Fig.5B) and Podarcis peloponnesiaca (Fig.3B) do not statistically differ from the basic type. However, especially in I. iguana, glomeruli resembling the avian glomerular type, regarding their complexity, can be found.

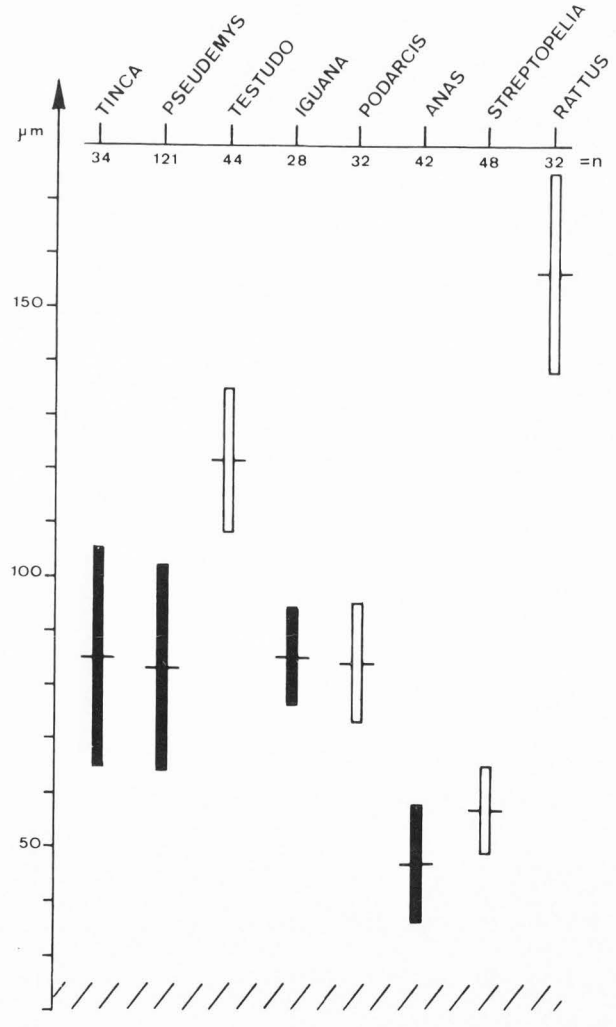
Examination of the cut surfaces of casts (Fig.1) indicates that the peritubular capillary network in reptiles and birds from more arid habitats is more developed than in those from humid or freshwater habitats. In P. scripta, the peritubular capillary plexus covers 15-35% of the cut surface, while in the second species (T. hermanni) this value was 40-60%. This difference was most distinct in turtles, but the investigated lacertilians and birds showed a similar trend. However, statistical confirmation

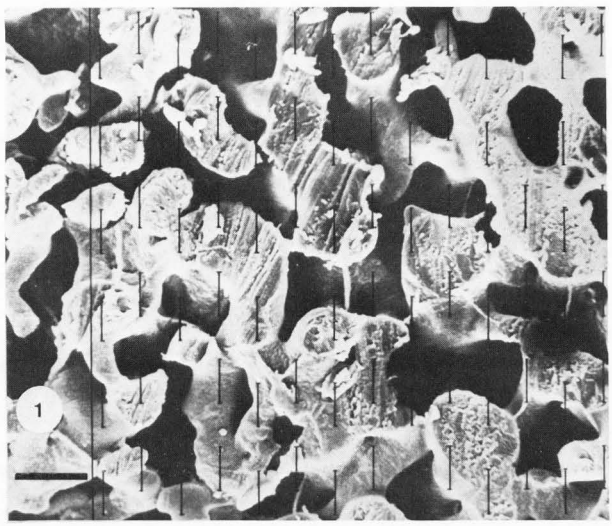
Fig.1: Sectioned peritubular capillary zone of Pseudemys scripta overprinted with a "multipurpose stereological test grid" for quantification of the relative extent of this compartment. Bar = 50µm.

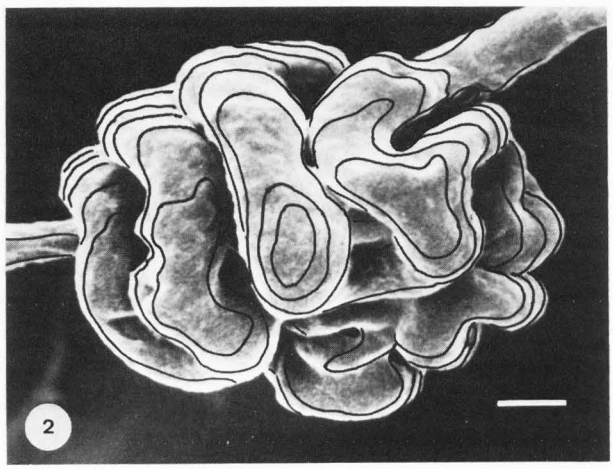
Fig.2: Cast of the ovoid type of glomeruli of Streptopelia roseogrisea. The stereophotogrammetric "contour map", derived from a stereo pair, is drawn over the micrograph to demonstrate the three dimensional structure of the specimen. Bar = 10µm. Each layer corresponds to 5µm.

Table 1

The bars represent the mean glomerular diameters ± their standard deviation. The values for n indicate the total number of measurements for each species, pooled from all investigated animals. Open bars refer to species from terrestrial or arid habitats, the full bars refer to species from humid or freshwater biotopes. The hatching indicates the hypothetical minimum-size.







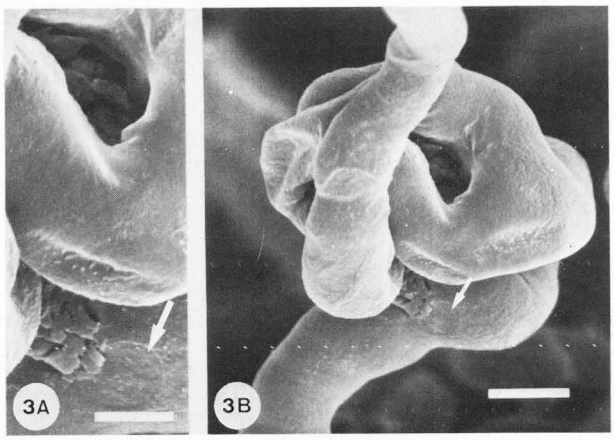


Fig.3: Cast of a glomerulus of Podarcis peloponnesiaca. A: Detail showing casted mesangial channels between capillaries and at the vascular pole as well as impressions of endothelial cells (arrow). Bar = 10µm.
B: General view of the same glomerulus as in Fig.3A. Bar = 20µm.

is extremely difficult, as comparisons of intrarenal capillary areas are possible only for corresponding zones in species with a similar intrarenal anatomy.

The glomeruli of the investigated birds were generally the smallest and consisted of few (sometimes only two) capillary loops. As in the two turtle species, a correlation of larger glomeruli with lower water uptake could be established. The average glomerular diameter of Anas platyrhynchos (Fig.5C) is about 20% smaller than that of Streptopelia roseogrisea (Fig.2). Detailed stereophotogrammetrical investigations on the glomeruli of both species showed a continuous transition from round to ovoid forms, the latter sometimes elongated up to 60% when compared with the glomerular diameter measured from the vascular to the urinary pole.

The glomerulus of Rattus norvegicus is clearly different from those described above; it has a very large diameter and a high number of capillary loops (Fig.5D).

Discussion

Our findings on T. tinca are very similar to the description of the glomerulus of the teleost Salmo gairdneri (Anderson and Anderson, 1976). According to the results on several other freshwater teleosts based on light microscopy (e.g., Marshall and Smith, 1930) or transmission electron microscopy (e.g., Bonga, 1973; deRuiter, 1980; for comparative data see also Bargmann, 1978; Rouiller, 1969), the renal corpuscle of freshwater teleosts may be regarded as "basic", showing a well-developed, relatively large capillary network that functions efficiently as a "water gland" in removing the excess water taken up from the environment.

As most amphibians face similar conditions, their glomeruli should be of similar structure. Descriptions of several anuran species, based on corrosion casts (Lametschwandtner et al., 1978; Naito, 1984), indicate that these glomeruli are generally large and well-vascularized. Urodelan glomeruli are probably the largest of all Gnathostomata (Marshall and Smith, 1930; - light microscopical data). Amniota, however, are predominantly confronted with the problem of water conservation.

The turtle T. hermanni, inhabitating arid zones, unexpectedly shows a larger and more complex glomerulus than the freshwater species P. scripta. This may be explained by the fact that the less soluble main excretion product of T. hermanni (uric acid) requires more primary filtrate to be transported in the renal tubules than the main excretion product of P. scripta (urea). The higher glomerular surface, however, is compensated by a lower number of glomeruli in T. hermanni (H. Ditrich, - submitted for publication), resulting in a smaller glomerular surface per kidney volume than in P. scripta. Similar, though less distinct, was the correlation between the glomerular diameters of the two investigated birds.

The results on the lacertilians P. peloponnesiaca and I. iguana show that, although environment and nutrition differ, the resulting differences in their water uptake are probably too small to be statistically confirmed on the basis of glomerular diameter. However, a reduction of size and complexity can be observed; average-sized glomeruli of these two species often show less branchings and capillaries than, e.g., chelonian glomeruli of similar size.

Reports on other lacertilian glomeruli (Bargmann, 1937; Anderson, 1960), based on sections, also indicate simplification of the glomerular structure within this group. The glomerulus of the snake Thamnophis sirtalis is reported to consist of only one or two simple convoluted loops (Peek and McMillan, 1979). This tendency towards glomerular reduction together with predominance of uricotelism within reptilian evolution leads to the development of the avian excretory system. While mammalian evolution led to the well-studied, large, highly complex glomerular type (Murakami, 1971; Spinelli, 1974; Pinto and Brewer, 1974; ...) and to the development of Henle's loop for reabsorption of most of the large amount of primary filtrate, the evolution of the avian nephron led to a different functional mode.

The glomeruli found in birds are probably the smallest and simplest of all amniotes. Although the minimal-glomerulus (consisting of one simple loop; hypothetical diameter about 20-25µm) was not found in this study, some glomeruli of A. platyrhynchus approach this limit. A simple (minimal-) glomerulus, however, has been described for chicken (Pak Poy and Robertson, 1957) using transmission electron microscopy. The dimorphism (round/ovoid) shown by avian glomeruli (Siller and Hindle, 1969; Braun and Dantzler, 1972; Ditrich and Splechtna, 1985) may be correlated with the differing nephron types (with/without "Henle's loops") and functional properties in maintaining the osmolarity of the blood constant (Braun and Dantzler, 1972).

The excretion of uric acid and urates seems closely connected with the differentiation of the peritubular venous portal capillary plexus. The results of physiological studies on tubular excretion (Dantzler and Schmidt-Nielsen, 1966; Sykes, 1971; Dantzler, 1982a, b) correspond to the extent of the peritubular capillaries.

Beginning with the "basic type" of strongly filtrating glomeruli in teleosts, our study shows the two strategies in glomerular development that have evolved to meet the requirements of terrestrial life. Corrosion casting offers an excellent opportunity for investigating renal vascular differentiation, including quantitative aspects. The problem of inaccuracy due to methodology (e.g., varying injection pressure, polymerisation shrinkage, optical distortion in the SEM, ...) can be minimized by standardizing the procedure to the greatest extent possible.

More studies on species from different biotopes will be needed to explain the full range of capacity of the renal system of the sauropsids.

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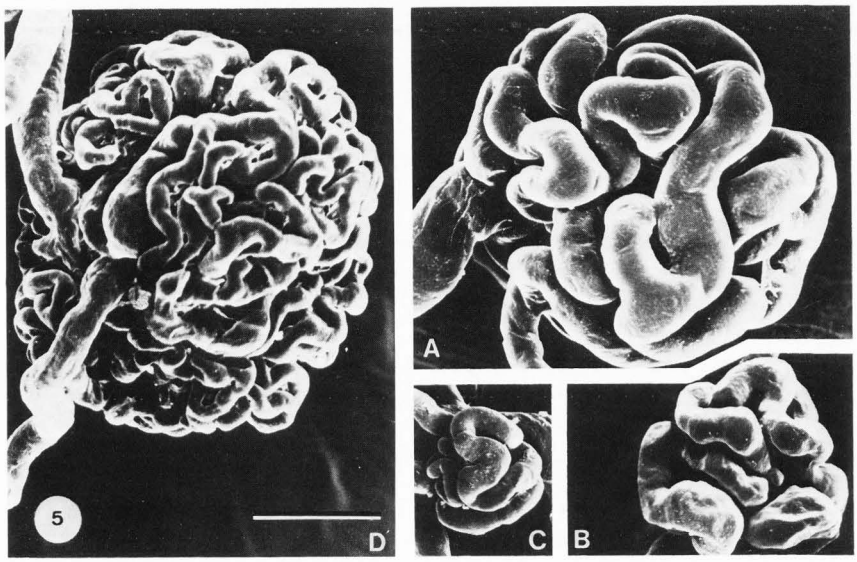
Fig.4: Terminal artery of Tinca tinca giving rise to numerous glomeruli. Bar = 100µm.

Fig.5: Casted glomeruli of:
A: Testudo hermanni showing a relatively large, complex vascular differentiation.
B: Iguana iguana reduced in size and capillary number when compared with Fig.5A.
C: Anas platyrhynchus showing a simple structure similar to the reptiles in Figs. 3B and 5B but with a considerably smaller diameter.
D: Rattus norvegicus representing the mammalian type.
Bar = 50µm (for all figures).



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Discussion with Reviewers

O.Ohtani: Your vascular corrosion casts appear to represent the dilated vessels. Why didn't you apply perfusion-fixation prior to the casting medium?

Authors: We have compared the casts of prefixed and unfixed glomeruli of rats and found no marked differences in their morphology, providing that the fixation quality was optimal. Under suboptimal conditions casts frequently appeared wrinkled and/or incomplete. Introducing several additional parameters to the casting procedure (like fixation medium, duration, temperature, pH, osmolarity, ...) raises the problem of keeping these parameters either constant (to assure comparability) or adequate to the specific properties of the different species (to assure optimal fixation). Regarding size measurements, prefixed tissue will not reflect the in vivo size due to fixation-derived tissue shrinkage, a difficult factor to quantitate in glomerular structures. Although dilation has occurred to some extent with our procedure, we regard omitting prefixation as more closely representing the in vivo situation and as being more easily reproducible when using different species.

O.Ohtani: The numbers of the glomerula also shows interspecies differences. Do you have any data on the numbers of the glomerula in each species you examined, in addition to the sizes of the glomerula?

Authors: We presently have results only on the two chelonian and avian species (H. Ditrich - submitted for publication); the remaining species are still being investigated. We use histological sections for quantifying glomerulus number per kidney area and have found interesting differences. In the kidney tissue of Pseudemys scripta, for example, about four glomeruli (nephrons) can be found in the same volume occupied by one (though larger) glomerulus in Testudo hermanni. We plan to continue our research in this field in order to explain these features in more detail.

D.B.Jones: Do you find any correlation between the weight of the species studied and the glomerular size?

Authors: We examined this question only in the two turtle species and in mallards, as only here we had the range from juvenile to adult animals. No correlation between glomerular diameter and body weight has been statistically determined, possibly because of the low number of species studied. The data given in this study are derived only from adult animals.

A.P.Evan: Did the authors find the diameters of individual glomerular capillaries to vary between species? This difference could also influence filtration area.
Authors: The diameters of the individual glomerular capillaries vary strongly between the species (compare Fig.5). This seems to be predominantly a function of erythrocyte size in the different animals; this factor probably determines the smallest diameter of glomerular capillaries. We found this diameter to be quite variable, but usually within the range of the diameters of the vas afferens and vas efferens.

D.B.Jones: I suggest that since this paper is published in the English language that the spelling glomerulus and glomeruli be used.
V.H.Gattone: I prefer the term glomerulus (pl. glomeruli) to glomerulum (glomerula).
Reviewer IV: All dictionaries that I am aware of use the masculine Latin form "glomerulus (i)".
Authors: The use of the form "glomerulum (-a)" was criticized by the majority of the reviewers of the initial manuscript (as a minor point) and therefore changed. However, the Latin stem "glomus" (pl. glomera) is neutral and its diminutive "glomerulum" did not change its gender. Information obtained from philologists indicate that as a "terminus technicus" the form "glomerulus" is acceptable, though "glomerulum" is more correct.

Reviewer IV: What do you mean by the statement that mesangial channel system "is poorly visible in unfractured glomerula of some types (mammalians) and may be absent in others?" This is not clear. If it is absent or cannot be seen, how can its presence be a criterion for the completeness of the casts?
Authors: Its presence usually indicates a good cast, its absence does not necessarily mean a bad one.

Reviewer IV: The suggestion that a higher filtration rate per glomerulus in T. hermanni compared with P. scripta is required for urate secretion may be correct, but there is often much urate in P. scripta urine and urea actual requires more water to be excreted. Urate precipitates can apparently move through the tubules with little trouble. Therefore, I doubt this explanation. Moreover, how does it fit with differences for bird species? Both avian species eliminate urate primarily. If anything, ducks have to get rid of more ammonia, a process that requires a higher urine output. Why do they not have larger glomeruli? Or does diameter mean anything?
Authors: In turtles, uric acid usually precipitates only in the bladder but not in the tubules, in the other uricotelic species, as far as investigated in this study, the main precipitation occurs in the cloaca. For ducks also more, though smaller glomeruli can get them rid of ammonia.

Reviewer IV: I really cannot see how you can say that the glomeruli get smaller and simpler with greater uricotelism in view of your discussion immediately above about the chelonians. This is not clear. I do not think that the trends are this simple. You certainly need to document the structural differences in a more thorough and, if possible, quantitative fashion. Henle's loop in mammals has nothing to do with the "reabsorption of most of the large amount of primary filtrate." Most can be reabsorbed without loops of Henle.

You speak of the possible difference in avian glomeruli depending on the types of nephrons sampled. However, you do not indicate which nephrons you studied. I believe that you are only looking at the reptilian type. The larger mammalian-type glomeruli appear to be more complex.
Authors: Smaller and simpler refers to the general trend in sauropsids. T. hermanni, as a basic form, is not representative for this trend on its own. Henle's loop is generally known to be the principal site of urine concentration and water reabsorption in mammals. Fig. 2 is a very typical example of a "mammalian-type" avian glomerulus.