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KIDNEY STRUCTURE INVESTIGATIONS USING SCANNING ELECTRON MICROSCOPY
OF CORROSION CASTS - A STATE OF THE ART REVIEW

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Abstract

The corrosion casting technique using acrylic resins in the scanning electron microscope (SEM), was originally developed to investigate renal microvascular structure and is now also successfully used in studies on various other organs. However, in the last two decades nearly 100 papers have been published on the renal vascular anatomy of various taxa of vertebrates or on pathomorphological structures of kidneys, using this technique. Analyzing these works, trends and developments in this field can be summed up as follows: The majority of studies are anatomical works on the vascular system of kidneys from all vertebrate classes. In addition, experimental pathological investigations, mostly done using rodents, and documentation of pathologically altered renal structure form another large part of the publications covered in this review. Perspectives for future research on renal systems using this versatile method may be derived from this survey.

Introduction

The microcorrosion casting technique using acrylic resins in the scanning electron microscope (SEM) was initially developed to investigate the renal vascular system of the rat (Murakami, 1971). Subsequently, a notable number of studies applied this technique in morphological studies on the kidney in other vertebrates and in investigations on renal pathology and pharmacological processes. A number of methodological and general aspects of this technique have been reviewed recently (Gannon, 1978; Murakami, 1978; Hodde and Nowell, 1980; Lametschwandtner et al., 1984; Ditrich and Splechtna, 1987b; Christofferson and Nilsson, 1988;). The kidney is not only a "classical" organ for comparative anatomical investigations and considerations on vertebrate phylogeny but also responds to numerous diseases with structural alterations. Hence, a survey of the data obtained using this method to study renal structures may be helpful in determination of the present state of the art and future perspectives. New data on several species of bony fish, snakes and the Axolotl (Ambystoma mexicanum) have been included for a better demonstration of the adaptive variability of renal structures.

Material and Methods

A standard protocol for renal vascular casting has recently been described in detail (Ditrich and Splechtna, 1987b). In short: anaesthesia, preparation of the injection site (usually the heart) and flushing the vascular bed with Tyrode-solution should be carried out, meeting the specific anatomic and physiologic properties of the animal as closely as possible. Thus, the vascular bed should reflect the in vivo state as close as possible. The more technical parameters (resin - composition, injection technique, curing, maceration, rinsing,

Key Words: Corrosion Casting; Kidney; Vertebrates; Scanning Electron Microscopy; Blood Vascular System

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trimming and drying of the cast, mounting, coating and observation) should be kept constant to facilitate comparisons of the obtained data. Members of all classes of vertebrates except Agnatha, including embryological material (Ditrich and Splechtna, 1989), have been cast successfully with the standard technique applied in our lab.

Literature Survey

For a survey of the literature in the field the following data banks have been checked: Biological Abstracts, Medline, ISI and Dissertation Abstracts. The obtained entries have been supplemented by references kindly provided by colleagues and the collection of pertinent literature of the authors.

The search strategy for literature retrieval was as follows: Search Set:

- #1 SCANN? ELECTRON? MICROSCOP?
- #2 CORROSIO?
- #3 CAST?
- #4 REPLICA?
- #5 UROGENITAL SYSTEM

- searching for files that fit the following specifications: having #1 and #5 and (#2 and/or #3 and/or #4) as entries listed in either the title or abstract, dating back from 1969 on. (Truncation symbol "?" represents any, or no extension to the stem word.)

However, CAST and REPLICA are ambiguous expressions, as several studies on mineral sediments in the kidney as well as freeze fracture studies were listed in addition to the targeted works. Additionally, studies on adrenals, urinary bladder, etc., are included in the search set on UROGENITAL SYSTEM. These studies were later excluded. However, in order to get a search result that covers the literature in this field as complete as possible, the search structure was initially not further restricted. Works on corrosion casts studied by other means than scanning electron microscopy (clearing techniques, light microscopy, etc.) were also generally excluded.

A crude division into disciplines (as there obviously are overlaps) shows that more than half of the studies cover general morphological aspects of the renal vascular system (Fig.1A). Nearly 3/4 of the files that matched the specifiers deal with mammals (Fig.1B) while the other vertebrate-classes have been studied less.

Anatomical nomenclature of renal vessels is quite complex and synonyms are numerous, depending on the specific topological relations. In this paper, an attempt is made to keep the terminology

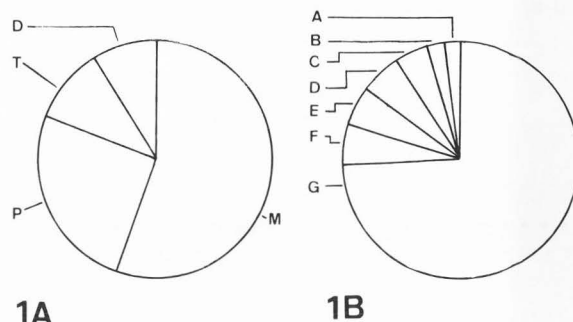


Fig.1A: Diagram of the general fields of application of the corrosion casting technique. Note that the classification has been made according to the main results of the paper. "Morphology" (M - 55%) includes also works on vascular details (cushions, etc.), "Pathology" (P - 25%) covers all aspects, including experimental and pharmacological studies. "Development" (D - 9%) includes pre- and postnatal topics of vascular differentiation while "Technique" (T - 11 %) represents all methodological works with kidneys as a test model.

Fig.1B: Diagram of the relative percentages of studies covering the different vertebrate classes. A - Agnatha (2.2%); B - Chondrichthyes (2.2%); C - Osteichthyes (4.5%); D - Amphibia (5.6%); E - Reptilia (5.6%); F - Aves (5.6%); G - Mammalia (74.2%).

as constant as possible. Only the most common synonyms are employed. Sizes of glomerular casts are given as their mean values for comparative purpose only. The inherent difficulties regarding morphometry of corrosion casts in comparing renal structures of different species, as outlined earlier (Ditrich and Splechtna, 1987b) should be taken into account considering these values. Two values for a species represent the mean diameters from vascular to urinary pole x perpendicular axis (ovoid glomeruli). Glomerular diameters taken in our laboratory represent the mean of pooled values from measurements taken randomly in all directions on a cast glomerulus. Small deviations from our older published data are therefore likely to occur as no distinction was made for structural anisotropy (ovoid glomeruli) in this paper.

Agnatha (Cyclostomata)

When renal morphology is a criterium, neither Myxine glutinosa (Atlantic Hagfish) (Albrecht, et al., 1978) nor Lampetra fluviatilis (River Lamprey) (Logan et al., 1980 - light microscopical data) can be regarded as evolutionary "basal" vertebrates. This

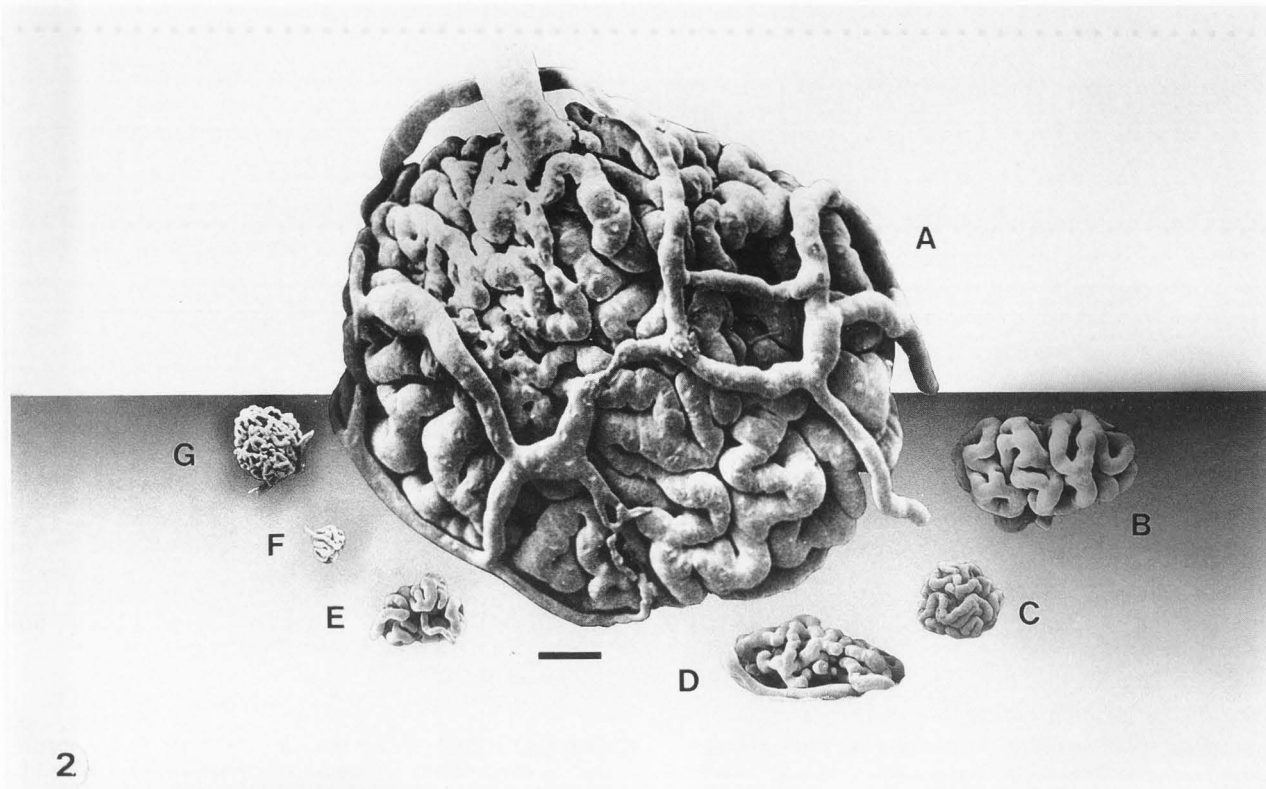


Fig.2: Mount of glomeruli from all vertebrate classes in the same magnification. A - Myxine glutinosa (Agnatha); B - Scyliorhinus canicula (Chondrichthyes); C - Conger conger (Osteichthyes); D - Ambystoma mexicanum (Amphibia); E - Python regius (Reptilia); F - Gallus domesticus (Aves); G - Rattus norvegicus (Mammalia); Note the comparatively large size and capillary diameter of M. glutinosa and the ovoid forms of S. canicula and A. mexicanum. bar: 100 μ m.

is true for the gross anatomy of the kidney, as the left kidney and (post-) cardinal vein are more strongly developed than the right one, as well as for numerous vascular details. The intrarenal vascular system is dominated by a large suprarenal sinus which opens into the cardinal vein. The dorsal part of the kidney is formed of lympho-endothelial and haematopoietic tissue, only the ventral part serves an excretory function. The adult glomeruli are probably the product of fusion of several glomeruli and therefore extremely large (Fig.2A). They are arranged medially in a single cavity formed by fusion of Bowman's capsules and supplied by branchings from the aorta and (more frequently) from the

(inter-) segmental arteries. Numerous nephric funnels open into this cavity. A portal supply in the kidney is lacking. The efferent glomerular arterioles form an anastomosing peritubular network before being drained by the suprarenal sinus. This highly specialized anatomical situation does not suggest a position at the basis of vertebrate kidney phylogeny.

Chondrichthyes (Elasmobranchii)

The kidney of sharks shows several features which may be regarded as rather basic. The kidney is supported by renal arteries that branch from the (inter-) segmental arteries or the aorta and by the cardinal veins that give rise to the peritubular renal portal system. The latter is drained by branches of the subcardinal veins, collecting the portal venous blood. Arterial blood from the glomerular efferent arterioles and from non-glomerular arterioles that join the peritubular system directly is also drained via the subcardinal tributaries. The outer shape of the kidney is a cranially tapered band in sharks and more compact, "bean-shaped", in rays and skates. Elasmobranchs are slightly hypertonic (or nearly isotonic) to their environment via reabsorption of urea from their urine into the blood. Their net nitrogen excretion is strongly supported by ammonia diffusion from the

gills. The main renal function in these animals is excretion of hypotonic urine (water) whereas excretion of electrolytes appears less intensive. Sodium chloride (in marine forms) is mainly excreted by rectal glands and by chloride cells of the gills, thus assisting the kidney.

The glomeruli are large, effective "water glands" (Fig.2B) about 230 μm in diameter in Scyliorhinus canicula (Dogfish) and up to 150 x 350 μm . (ovoid glom.) in Raja erinacea (Little Skate) (Hentschel, 1988). Several afferent glomerular vessels are formed by dichotomous ramifications of the intrarenal arteries, and the nephrons accordingly form groups (bundles - Hentschel, 1988), which may have functional significance in forming a countercurrent mechanism for urea conservation (Hentschel, 1988). Compared to most other vertebrate classes, elasmobranchs show conspicuously prominent sculpturing of the cast vascular surfaces (endothelial impressions). Arterial cushions and sphincter-like structures can be found on the casts (Green, 1986). The presence of the latter suggest that individual regulation of glomerular perfusion takes place. This was already tested in the dogfish by catecholamine perfusion. A decrease in the number of filtering nephrons (perfused glomeruli) was found after adrenaline administration, while the single nephron glomerular filtration rate increased (Green, 1986).

Osteichthyes

Bony fish are a vertebrate class with very heterogeneous ancestry. Renal morphology varies in this class from the basic pattern described above for elasmobranchs to numerous highly diversified forms. Agglomerular kidneys (e.g., some seahorses and seaneedles - Syngnathidae) or unpaired, compact renal forms (e.g., eels - Anguillidae) (Fig.3) can be regarded as highly evolved. The conditions of fresh water vs. marine habitats strongly influence renal construction. However, using corrosion casting and SEM, only studies on fresh water species have been published up to now. Salmonids (Salvelinus fontinalis - Brook trout - Anderson and Anderson, 1976; Salmo gairdneri - Rainbow trout - Anderson and Anderson, 1976; Brown, 1985) and a cyprinid (Tinca tinca - Tench - Ditrich and Splechtna, 1986, 1987b) have a relatively similar renal vascular pattern, generally comparable with sharks.

Glomerular size varies from 51.1 x 68.2 μm (ovoid glom.) in S. gairdneri (Brown, 1985) to 81.9 μm T. tinca (Ditrich and Splechtna, 1986) and is 101.8 μm in Anguilla anguilla (Eel). The latter, however, can be compared with a

relative closely related marine fish, Conger conger (Conger Eel - avg. Glom. diam.: 115.7 μm) (Fig.2C), that has statistically significant ($p < 1\%$) larger glomeruli. However, our initial observations also indicate that glomerular number is by far larger in the fresh water eel. Similar to Chondrichthyes, the dominant function of the kidney of bony-fish is handling of the body water with respect to the environment. The other renal functions are mainly performed by the gills (ammonia diffusion; NaCl - secretion/absorption). Consequently, a change in the hydration status of an individual, like migrating from sea to fresh water, must result in drastic physiological and anatomical adaptations. The mechanisms involved remain to be studied in detail. Due to the highly adaptive radiation and different origins of the class Osteichthyes, a large number of questions remains to be answered. Studies on Chondrosteian, Holosteian and Brachiopterygian species may allow new insights in renal phylogeny.

Amphibia

Urodels and anurans exhibit a different intrarenal distribution of blood vessels compared to the fish type, although the general scheme is basically similar. The kidney is shorter and caudally more compact. The medio-lateral orientation of the nephrons, present in most fish, changed to a dorsoventral pattern. The lower abdominal and extrarenal vasculature changed according to the formation of hindlimbs. The portal blood is distributed from dorsal branches (V. caudalis + Vv. iliaca communes + Vv. dorsolumbares = renal portal veins \rightarrow Vv. ren. afferentes = Vv. ren. advehentes) to the peritubular vascular system and the efferent drainage (Vv. renales efferentes = Vv. ren. revehentes = Vv. subcardinales \rightarrow V. cava posterior) is situated ventrally. The glomeruli are located either in the ventral half (e.g., Bufo bufo - Common Toad) or on the ventral surface (e.g., Bombina variegata - Fire-Bellied Toad - Lametschwandtner et al., 1978) of the kidney, being supplied by renal (urogenital) arteries. The latter follow the course of the efferent veins, arising from the aorta. This pattern is shown by anurans (Morris and Campbell, 1978; Lametschwandtner et al., 1978; Ohtani and Naito, 1980) and by the salamander (S. salamandra - Ditrich and Splechtna, 1987b). However, a different urodelan species, Ambystoma mexicanum (Axolotl) shows a vascular arrangement that is more fish-like (Fig.4). Average glomerular size in amphibians is generally large, reflecting the conditions of their habitat. In the neotenic, fully aquatic axolotl it is

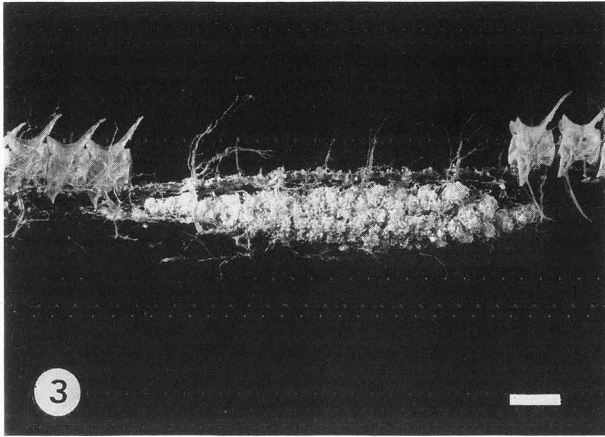


Fig.3: Macrophoto of the kidney of the eel (*Anquilla anguilla*) -lateral view. The kidney has developed to an unpaired, compact organ dorsally to the cloaca. bar: 10 mm.

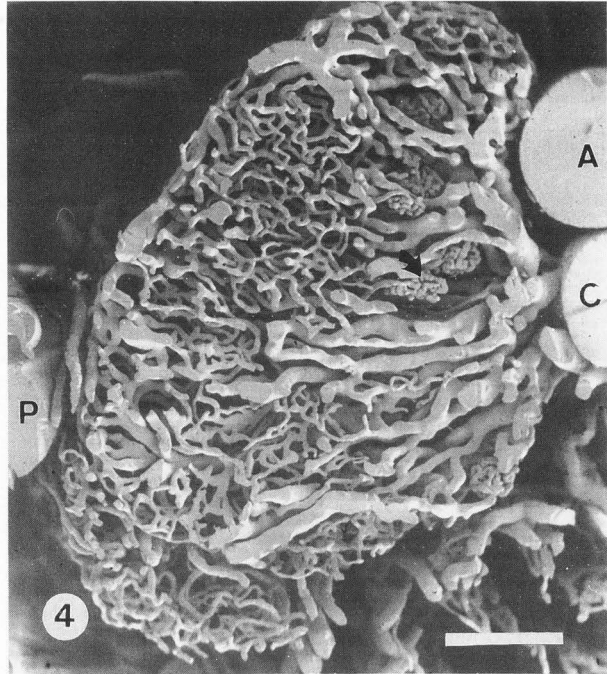


Fig.4: Cranial view of the right kidney of the Axolotl (*Ambystoma mexicanum*). The peritubular capillary bed is supplied by branches from the portal vein (P) while the glomeruli (arrow) receive arterial blood from the aorta (A). The efferent glomerular arterioles fuse with the peritubular system about half way towards the periphery and the whole blood is drained via the posterior caval vein (C). bar: 500 μ m.

235 μ m (Fig.2D) and in the terrestrial salamander 222 μ m (Ditrich and Splechtna, 1987b, 1988). In anurans glomerular size ranges from 201 μ m in *Bufo bufo* (Ditrich and Splechtna, 1987b, 1988) to about 70x110 μ m to 60x70 μ m (ovoid glom.) in *Bufo marinus*. The smaller glomeruli in the latter species are located more superficial (ventral) than the larger ones (Morris and Campbell, 1978). Ohtani and Naito (1980) described an increase in glomerular diameter from medial to lateral, the smallest being situated closest to the aorta. As far as known, all non-mammalian species are capable of developing nephrons during their entire life. The postmetamorphous development of glomeruli has been described by Naito (1984). Interstitial vessel coil, dilate and form vascular buds (sprouts) which later anastomose and develop to glomerular capillaries.

As amphibians can be regarded as the first, though temporary, inhabitants of terrestrial environments, their kidney structures adapted to this habitat. In addition adaptive mechanisms, like physiologic variability of the ammonia/urea relation in the urine and extra-renal mechanisms for water and salt regulation (cloaca, urinary bladder, skin) largely contribute to the ability of coping with the demands of terrestrial life. Moreover terrestrial biotopes require more functional plasticity, as stronger oscillations in the relevant parameters for kidney function are more likely to occur (hibernation, spawning, ...). Intrarenal morphologic equivalents of controlling

mechanisms (sphincters, etc.) can therefore be expected to be more prominent than e.g., in a stenohaline fresh water fish. However, a comparative study on this problem remains to be carried out.

Reptilia

Several mechanisms contribute to the capability of reptiles to inhabit a large variety of biotopes, most of them exceeding the scope of this paper (e.g., amnion, egg-shells, strong epidermal keratinization, ...). Shifting the relative proportions of nitrogenous waste products (ammonia, urea, uric acid) depends on the environmental parameters and allows precise alignment of a species (less commonly, also of an individual) to the environmental water supply. Renal anatomy reflects this physiologic adaptation at the tubular, as well as the vascular level. This was initially tested by comparing *Chrysemys (Pseudemys) scripta* (Red Eared Turtle), a fresh water inhabitant and *Testudo hermanni* (Greek Land Tortoise), living

in an arid biotope. Surprisingly, the more arid living species T. hermanni, had larger ovoid glomeruli (111.1 x 131.6 μm) than the water living C. scripta (83.1 μm). However, considering also glomerular number, it was found that the filtering surface per kidney volume is roughly 1/4 smaller in T. hermanni than in C. scripta, i.e., there are less, though bigger glomeruli. Also the peritubular capillary system, being responsible for tubular uric acid secretion, is about double as dense in T. hermanni than in P. scripta (Ditrich, 1984; Ditrich and Splechtna, 1986, 1987 a,b). Similar trends have been observed comparing the snakes Eunectes noteus (Anakonda - avg. Glom. diam.: 59.1 μm), living in fresh water and Python regius (Ball Python - avg. Glom. diam.: 124.3 μm) (Fig.2E), living in bushlands. A comparison between two lizard species, Iguana iguana (Common Iguana - avg. Glom. diam.: 72.1 μm) and the mediterranean Podarcis peloponnesiaca (Peloponnes Wall Lizard - avg. Glom. diam.: 76.9 μm) failed to show significant differences, although their environment and nutrition differ (Ditrich and Splechtna, 1987b).

The glomerular mesangial channel system extending through the core of the glomerulus is comparatively strongly developed in reptiles. It has been observed in turtles (Ditrich, 1984, 1985; Ditrich and Splechtna, 1987a) and in lizards (Ditrich and Splechtna, 1986) where it forms a lacuneous system of matrix gaps that allows access for mesangial cells to macromolecular substances circulating in the plasma.

An additional evolutionary change in reptiles was the development of the renal lobule as an intrarenal structural and functional subunit. The basic pattern shows a central artery supplying the glomeruli and a central vein draining the blood. At the periphery of the lobule, numerous portal branches distribute the blood into the peritubular capillary system. The latter receives additional blood from the glomerular efferent arterioles at a distance towards the center of the lobule. The three-dimensional structure of the lobule itself and their arrangement in the kidney varies according to species. While the pattern is quite complicate in turtles and several species of lizards, other lizards and especially snakes show a simple, fan-like lobule in a more or less serial order. Therefore even tubular polyacryl-injections are useful (Fig.5), as separating the brittle casts of intertwining tubules can be accomplished for snake kidneys.

The extrarenal vascular system of reptiles differs in several aspects from the amphibians pattern described above.

The arterial input arises from a variable number of renal and adreno-renal-genital arteries that branch off the aorta (occasionally also from the Aa. iliaca), enter the kidney medially and branch dichotomous to form the intralobular arteries. The renal portal vein is situated at the ventral or ventromedian surface of the kidney. It is formed by a split of the caudal vein that takes up a number of small veins from the cloacal region including the larger hypogastric vein at each half. The iliac vein joins in the renal portal vessel not caudally from the kidney as in amphibians, but at its ventral surface. The situation of the efferent veins is similar to amphibians. This scheme varies according to the specific anatomical situation (e.g., apod lizards, snakes) of the respective species.

The implications of the different ontogenetic development of the amniote kidney (induction by the cranially growing ureter and thus an "inversion" of the direction of renal differentiation) will not be discussed here.

Aves

The avian renal anatomy resembles that of reptiles in many aspects. Each kidney can roughly be divided into three parts. Arterial supply arises from an anterior renal artery branching directly from the aorta and from two large branches of the sciatic artery supplying the median and caudal division. The renal portal vein is formed by confluence and subsequent splitting of coccygomesenteric and the right and left hypogastric vein. Along its way at the ventral kidney surface, the ischiadic vein joins and numerous branches are given off to supply the peritubular capillary system (interlobular veins). The iliac vein anastomoses with the portal vein at the border between median and cranial lobe with a large valve (Fig.6). This valve, if closed enhances portal supply to the cranial and median division, while when open, allows bypass of the iliac blood into the renal efferent vein. The latter fuses with the controlateral branch to form the posterior caval vein (for details see e.g., Siller, 1971; 1983; Akester, 1984).

The construction of the renal lobes differs from reptiles, in that each lobule contains several intralobular arteries that run parallel to the intralobular vein at about half way towards the periphery of the lobule. Short afferent glomerular arterioles branch off the intralobular arteries, usually also in the direction towards the interlobular (afferent) veins. The glomeruli of birds are generally simple in structure and small (Siller, 1971; - neoprene cast of the fowl), although size and complexity increase from the

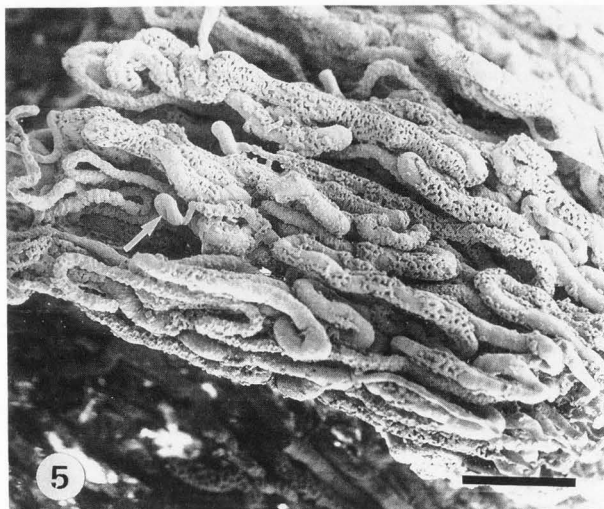


Fig.5: Tubular injection of a group of nephrons in the snake *Python regius*. Note the parallel orientation and the differences in surface structure that are due to the different regions of the tubules. Bowman's capsules appear as blind ending buds (arrow). bar: 200 μ m.

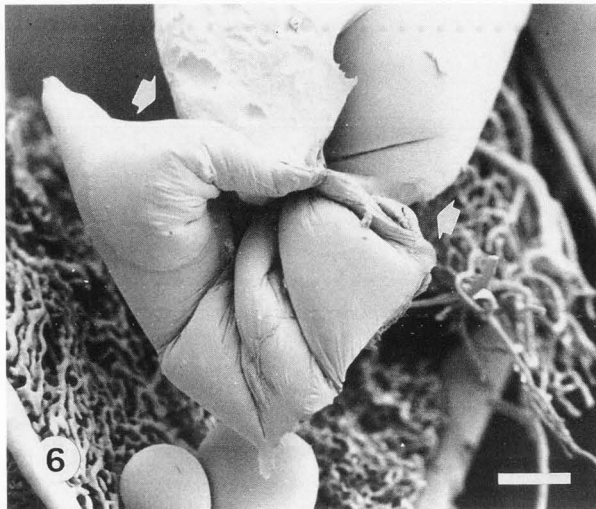


Fig.6: Portal valve of the mallard (*Anas platyrhynchos*) at the border between the external and common iliac vein. The latter, however, was not injected due to the constricted state of the valve. The site of the main constrictor muscles is marked by arrows. bar: 200 μ m.

kidney surface towards the basis of the lobule. Reptile- and mammalian types of nephrons, the latter having short loops, are associated with the respective glomeruli. However, although the reptile type truly resembles e.g., lizard nephrons, the glomerulus of the "mammalian type" is not equivalent to the mammalian structure. In *Streptopelia roseogrisea* (dove), typical round (reptilian type) glomeruli have a diameter of 56.6 μ m while the ovoid ("mammalian") type averages 50.9 x 67.4 μ m (Ditrich and Splechtna, 1985). Comparing glomerular size and intrarenal vascularization of this species living in arid biotopes (pooled data avg.: 59.6 μ m) with the well hydrated *Anas platyrhynchos* (mallard - avg. Glom. diam.: 42.8 μ m), a similar trend as described above for turtles and snakes became evident (Ditrich and Splechtna, 1986, 1987b). Mean glomerular diameter is 63 μ m in *Gallus domesticus* (fowl - Fig.2F), in chicken embryos, however, an entirely different renal morphology, resembling amphibians in many aspects, is present. Glomerular size in the embryonic kidney of the chicken is approx. 160 μ m, but only a small number of these can be found at the ventral surface (Ditrich and Splechtna, 1989). Further studies may concentrate on adaptive mechanisms in ecological specialists (desert, marine birds) and on the perinatal renal development.

Mammalia

Studies on mammals are represented by nearly 3/4 of the matching citations. The nomenclature for the (mammalian) kidney has been standardized recently (Kritz and Bankir, 1988). Initially, corrosion casts in SEM have been used to study the glomerular morphology of the rat (Murakami, 1971). Further methodological developments used the kidney, mostly in rats, as a model system. A number of casting resins have been tested for suitability for SEM studies on microvascular morphology (see for example Gannon, 1978). At present most commonly polyacrylic resins are used (methyl-methacrylate, Mercox, Technovit, Plastogen G, Tensol No.7, etc.); in addition polyesters (e.g., Batsons No. 17), polystyrols (e.g., Tardoplast SL), silicone-rubbers (e.g., Microfil) and latex mixtures (Neoprene, Vultex, Cementex, etc. -see also e.g., Lee, 1972; Bielke et al., 1976), and other plastics have been applied with varying success. Osmification of the specimens (Murakami, et al., 1973) reduces charging during observation and allows further dissection of an object without additional sputtering, even inside the SEM using a micromanipulator (Yoshida et al., 1986). Softening of casts by immersion in warm ethanol (Murakami, 1971) gives access to otherwise hidden structures. Cracking (Noda, et al., 1975) or cutting (Murakami, 1978) of kidneys embedded in ice or polyethylenglycol (Ditrich, 1984) allows a

more precise orientation of the desired cutting plane and trimming of vessels of strongly different diameters, thus minimizing fractures in the brittle capillary areas. Observation of uncorroded, injected tissue allows correlation of the vascular patterns with otherwise lost perivascular structures like e.g., the glomerular basement membrane (Castenholz, 1983).

The value of morphometry of casts, i.e., the problem of vascular dilatation during injection, versus polymerization shrinkage remains to be investigated in detail. Also, opinions about using perfusion fixation before injections are still controversial. As outlined earlier (Ditrich and Splechtna, 1987b), comparable data can be obtained if the method is kept as simple and constant as possible, however, systematic studies on the questions mentioned above would be of great value.

Ontogeny & Morphology

The gap between the non-mammalian renal structures and the mammalian kidney can partly be bridged by embryological studies. The development of the cranial part of the opisthonephros (mesonephros) has been studied in pig embryos (Tidemann and Egerer, 1984). This embryonic kidney has several features in common with the corresponding structure in chicken. There are few (about 50) glomeruli that are extremely large (up to 750 μm = triple the diameter of the adult) supplied by dichotomous branches of ventrally situated renal arteries. The general intrarenal vascular and tubular orientation also is similar to the cranial part of the chicken embryo opisthonephros or of anuran amphibians, although a venous portal supply is lacking in mammals. The prospective adult kidney (caudal part of the opisthonephros = metanephros) follows a different pattern that still proceeds its development after birth, especially in insessorial mammals (e.g., rodents). However, well developed glomeruli can already be found in human fetuses (Hitomi et al., 1987). Studies on the maturation of the highly structured intrarenal system of mammals have mainly been carried out in rats. Glomerulogenesis begins with the penetration of an interstitial vessel loop into the vesicle that will develop into Bowman's capsule. This vessel splits longitudinally into the prospective glomerular lobes that later develop sprouts and split further to form glomerular capillaries (Kazimierczak, 1976, 1980a, 1980b; Kazimierczak et al., 1984). The development of the cortical vascular system proceeds from juxta-medullary towards the kidney surface by induction of metanephrogenic blastema

differentiation by the growing ureter bud. Two types of vascular sources have been described: arterial vessels that supply the developing glomeruli and venous sinusoids that give rise to the peritubular and efferent vessels (Kazimierczak, 1978).

The simplest construction of the mammalian kidney is represented by the unilobar (unipapillary = unipyramidal) type, present in monotremes, some marsupials, edentates, bats, insectivores, several species of rodents (e.g.: rats, mice) and carnivores (cats). The rat kidney has been extensively investigated. Initially, morphological aspects of the glomeruli have been studied, demonstrating that Malpighi's original concept of the glomerulus being composed of anastomosing capillary loops has been correct. The glomerular lobes (lobules) arise from splitting of the afferent arteriole. Each lobe consists of a more or less independent vascular plexus that is connected to other lobes by few small vessels. The lobular vessels reunite near the vascular pole with those of the other lobes to form the efferent arteriole. Although glomerular flow is clearly arterial, the impressions of endothelial nuclei are ovoid, thus resembling venous vessels (Murakami, 1971, 1972, 1978; Spinelli, 1974; Fujii et al., 1975; Fujii and Fujibayashi, 1976; Povalii, et al., 1980; Murakami et al., 1985a; for details see Kikuta and Murakami, 1989). Double glomerular afferent (Murakami et al., 1971) and efferent (Murakami, 1976) arterioles have been found as rare anomalies, probably without functional significance. "Plastic strips" (term after Anderson and Anderson, 1978) have been found near the vascular pole as a vestige of juxtaglomerular cells. Endothelial cushions are found as flow dividers mostly at branch points of larger cortical arteries (arcuate / cortical radiate artery / afferent arteriole) (Casellas et al., 1982). Data on glomerular size may differ slightly between different authors, probably due to different animal strains and preparation details. However, Gattone and Evan (1986) found a glomerular diameter of 159 μm (Batson's No. 17) in the outer cortex of Wistar Kyoto rats after prefixation and our measurements (Ditrich and Splechtna, 1986, 1987b) gave a mean diameter of 156 μm in supravitaly Mercox injected Sprague Dawley rats (HIM:OFA-SD) (Fig. 2G). These values are in surprising agreement, although they were obtained with different protocols.

The anatomy of the unipapillary kidney can essentially be found in all textbooks of anatomy. The supply of the medullary vascular bundles (arterial

Renal Casting Review

vasa rectae) is derived from the efferent vessels of the juxtamedullary glomeruli and from (aglomerular) descending branches of the arcuate (interlobar *) arteries. The vascular bundles consist of a dense capillary plexus that appears to differ in source between the innermost part of the inner stripe and the rest of the cortex (Yamamoto et al., 1984a). Direct arteriovenous connections bypassing the glomeruli also have been described for the cortex (Casellas et al., 1981; Casellas and Mimran, 1981a, 1981b), supplying additionally the cortical peritubular capillaries. The unipapillary type of kidneys was also studied in the cat (Marais 1987, 1988). With the exception, of size, no essential differences to the rat have been described.

In many artiodactyles (e.g., sheep) and some carnivores (e.g., dog) instead of a renal papilla a crest is formed. Canine kidneys have mainly been used as controls or for comparative purposes (Spinelli, 1974; Anderson and Anderson, 1976; Zhang et al., 1986, Zhen et al., 1986). The average glomerular diameter in dogs is 253 μm (Anderson and Anderson, 1976). Signs of the juxtglomerular apparatus and of smooth muscle cells of the afferent vessel have been observed as "plastic strips" on casts (Rosenbauer, 1980; Zhang et al., 1986). Juxtamedullary nephrons with an afferent arteriole arising directly from the arcuate artery have been found in the rabbit kidney (Ojeda et al., 1986). However, it is not yet clear if these are functionally different to other mammalian nephrons.

In man, several primates, pigs, kangaroos and some carnivores, a polylobular kidney of the compact type is found. Here, structural subunits (lobes) separated by connective tissue (Bertini's columns) can be discerned that independently form papillae projecting into the renal calyces. Special attention has been paid to the occurrence of double efferent arterioles in man (Murakami et al., 1985b). The human glomerular tuft shows no substantial differences to rats (Murakami, 1978, 1985a; Kikuta and Murakami, 1989) nor does the monkey glomerulus (Nopanitaya, 1980; Unehira, 1981). The renal system of pigs is anatomically similar to human kidneys (Hah and Yoon, 1982) and should therefore prove to be a suitable model for experimental pathology and surgical works (Russel et al. 1981). The reported finding that the glomeruli in the left kidney of pigs are smaller than in the

*) The term "interlobar" seems not appropriate for an unilobar kidney.

right one (Ohtsuka et al., 1982) remains to be explained.

A highly evolved type is the polylobular loose or renculi kidney, developed e.g. in cows, pinnipedians, whales and bears. In this type, the lobes are more or less independent, each resembling a unilobular kidney. The Black Bear's (*Ursus americanus*) renal system has recently been studied in detail (Anderson, et al., 1988). In addition to the anatomical aspects, the strong development of filtration regulating structures, i.e., the juxtglomerular apparatus and muscular sphincters (cast as "plastic strips") on the afferent arterioles are a striking feature. These may be of special importance during winter-sleep when renal function is low.

Summarizing the publications dealing mainly with renal vascular morphology it can be stated that the basic components (distribution of larger vessels, capillary networks, glomeruli) and some cast surface details (cushions, "plastic strips", endothelial nuclei) are well described, mostly in rats. Future studies might cover special adaptations like hibernating or desert animals and the renal system of several interesting species like *Echidna aculeata* (the ant-hedgehog) or whales and seals. Works on embryological material should further clarify the developmental course of the vasculature in the different parts of the mammalian opisthonephros.

Pathology, Experimental Pathology & Pharmacology

For studying alterations of the renal vasculature a three-dimensional image is expedient in addition to the commonly applied sectioning techniques (Andrews, 1978). Gerontological alterations of the human renal vasculature involve increased glomerular capillarization and complexity in the more cortical layers and features of degeneracy in juxtamedullary glomeruli (Hitomi et al., 1987).

The vasculature in the human clear cell carcinoma (Bugajski et al., 1989) shows at its periphery the characteristics of strong angiogenesis (sprouts). Especially veins are induced to form capillary networks during tumor proliferation. Centers with relatively few, degenerating vessels apparently represent necrotic areas. This process of vascular degeneration seems to be caused by the increasing intratumoral hydrostatic pressure, among other factors. A corresponding animal model (Shah-Yukich and Nelson, 1988) shows striking similarities. Flattening, endothelial proliferations and fusion in addition to displacement of preexisting vessels are the most prominent pathomorphological vascular consequences. The

polycystic kidney model in rabbits exhibits different alterations. In this case, numerous vascular malformations, like inhibited differentiation and glomerular degeneration, can be observed (Ros et al., 1985). However, pathogenesis in this model seems less linked with vascularization than in the tumors described above.

Glomerular alteration is a frequently encountered response to a number of diseases. Local constrictions and loss of glomerular capillaries have been described in the chronic phase of rat Masugi nephritis (Takizawa et al., 1979). The procainamide induced model of Lupus erythematosus shows irregular constrictions and dilatations of glomerular vessels (Lee, 1974). A moderate decrease of glomerular vessel diameter has been observed in experimental toxemia of pregnancy after constriction of the postrenal aorta (Fukuda et al., 1987).

Hypertensive renal changes have been experimentally induced (Lee, 1972; Lee et al., 1972; Gattone and Evan, 1986) and have been studied in spontaneously hypertensive rat strains (Gattone et al., 1983a; Gattone and Evan, 1986). An initially narrow, or by the experimental procedure constricted distal glomerular afferent vessel is the main location of vascular resistance associated with elevated blood pressure. The constriction of the afferent glomerular arteriole is partly counteracted by renal denervation (Gattone et al., 1984). It can be shown experimentally that ischemic renal changes involve circulatory defects in the outer medulla (Yamamoto et al., 1984b), reduction of glomerular size (Gattone and Sale, 1986) and strong arteriolar constrictions which initially reduce glomerular perfusion in the glycerol model in rats (Gattone et al., 1983b; Gattone and Evan, 1986).

Angiotensin II administration is reported to cause numerous constrictions in specific locations of smaller cortical (radial) arteries and the distal afferent glomerular arteriole (Wilson and Heptinstall, 1984; Wilson, 1986) as well as contraction of the glomeruli (Weinberger et al., 1986).

The extent of recovery of renal function after ureter obstruction has been studied in dogs. The amount of nephrons that remain permanently damaged increases with the duration of impediment, due to arteriolar constriction (Leahy et al., 1989). The pathomorphological changes include an overall reduction of the cortex and a decrease in size of the remaining glomeruli (Amselgruber et al., 1989). Vascular, especially glomerular degeneration is also an important

feature of radiation damage in the kidney. Leakage and fusion of glomerular capillaries can be observed already one week after administration of 100 rad (Nelson et al., 1984; Dodd and Berry, 1987). Hydronephrosis likewise results in glomerular atrophy, glomerular size decreases to 40 - 90 μm in rats and the radial peritubular capillary plexus orientation is lost (Ninomiya and Nakamura, 1988). Similar glomerular changes, though less intense, can be found in the 5/6 nephrectomy model of chronic renal failure, probably as a result of hyperfiltration (Gattone and Evan, 1986).

Concluding Remarks

Investigations on the renal vasculature have been carried out for centuries using dissection, maceration and isolation techniques as well as reconstruction of light microscopical serial sections. Injections with wax, india ink, silicone rubber, etc. and clearing or corrosion of the specimen proved to be highly valuable tools for visualizing most of the renal vessels. However, the resolving power of these techniques has often not been adequate for unequivocal resolution of microvascular details; e.g., the pattern of glomerular capillaries was a matter of discussion until the works of Murakami and others demonstrated the now accepted glomerular model (see Kikuta and Murakami, 1989). Summarizing the studies of the last years, a trend towards usage of ready-to-use casting resins (Batsons No.17, Mercor, ...), either with or without prior perfusion fixation, can be observed. Considering the distribution of the studies carried out so far, it can be stated that a number of animal groups, especially the highly adaptive and diverse class of bony fish did not yet receive the proper attention.

The glomeruli of all vertebrates, as far as investigated, consist of anastomosing loops. However, large interspecific differences exist with respect to the development of the renal corpuscles. The theoretically minimum, one single looped capillary, has not yet been documented with corrosion casts. This may be explained by the data on glomerular development, as longitudinal splitting of a vessel seems to be the onset of glomerular formation. It should be kept in mind that there is evidence that most vertebrates with the exception of mammals seem capable of forming glomeruli during their entire life span. Thus the aspects of postnatal adaptation of renal function must also be considered in studies on non-mammals. Erythrocyte size probably determines the minimal diameter of capillaries,

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although erythrocytes are deformable to some extent. The renal portal vein, that is present in all vertebrates except mammals and cyclostomes should not be underestimated in its role for nitrogen excretion. When evaluating the performance of an excretory system glomerular number, the extent of the peritubular vascular network and the physiological determinants of an animal should be studied in addition to glomerular size. A better understanding of the adaptations of vertebrates to their different environments during evolution might result from this approach.

A theoretic discussion on the phylogeny of the kidney, i.e., the justification for the termini Pro-, Meso-, Metanephros versus Pro- and Opisthonephros versus Holonephros would exceed the scope of this paper. However, corrosion casting studies might contribute substantially to answer these traditional questions.

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Discussion with Reviewers

D.B. Jones: The narrow segment of the efferent arteriole of the kidney is thought by some to contribute to vascular resistance in the rat. (Fretschner et al., 1990). Is there evidence in other species of a narrow segment of the efferent arteriole of the kidney ?

Authors: This article describes in detail the flow regulating properties of specialized, mainly endothelial cells in rats. The efferent arteriole is also generally smaller in diameter than the afferent arteriole in non-mammalian species. A similar specialized area for luminal constriction, however, has not been apparent in the species we studied. Also no explicit statement on the existence of such a structure has been found in the literature. Discrete impressions at the cast surface of the efferent arteriole can be observed in various locations, esp., at the joint with peritubular portal vessels. Whether such structures are homologous or functionally similar to the narrow segment of the efferent arteriole in rats is a question to be answered by future studies.

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