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Kidney of the Great Indian Rhino *Rhinoceros unicornis*, Linnaeus

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ABSTRACT **The kidney of *R. unicornis* has almost 80 closely apposed lobes, all appearing peripherally. Every lobe, almost enclosed by a collagenous septum, resembles a deformed truncated cone. The pelvis proper is a small pouch which divides into a cephalic and a caudal urothelial-lined fibromuscular conduit. The terminal collecting ducts of every lobe open into a tubus maximus. This is lined by cuboidal cells and otherwise has no wall. There is no papilla. All lobes finally empty through the 18 primary infundibular orifices at the pelvic conduits. A primary fibromuscular infundibulum typically yields a secondary one supplying an adjacent lobe. Two or three lobes can use a common tubus maximus by "convergence" of their medullae.**

Tubus maximus, terminal collecting ducts and deep outer medulla are embraced by a fibromuscular calyx which is the peripheral extension of an infundibulum and is fused to the outer medulla. There is thus no vault between medulla and calyx. Large intralobar veins are fused to the outer wall of the calyx. The possible significance of this is discussed.

The cortex is the only part of a lobe which has contact with infundibulum, pelvic conduits, or pelvis proper.

The kidney has about 16 million glomeruli which form 5.8% of the adult's cortical mass. Many adult mammals, from mouse to rhinoceros, fit into the $\log_{10}$-$\log_{10}$ slope relating number of glomeruli per kidney to body-mass. Neonatal rhinos at term have mature glomeruli throughout the cortex. The small size of the glomeruli and the large number per field allow 16 million in an 118-gm kidney.

INTRODUCTION

The Great Indian rhinoceros has been known in the west since the striking drawings by Albrecht Dürer in 1515 (Parsons, 1743) notably the ink drawing in the British Museum, London, and the woodcut in the Albertina, Vienna (Waetzoldt, 1936). In Dürer's time, this animal ranged throughout the grassy jungles of India from Assam and Nepal through the Punjab (Lydekker, 1894).

Knowledge of the kidneys of the rhinoceros is at best sketchy (see Discussion). The writer's initial assumption was that the small pelvis divides into two tubi maximi and that the terminal collecting ducts (of Bellini) open directly into these, as in another perissodactyl, the horse. The actual situation is different and more complicated.

MATERIALS AND METHODS

Material

The left kidney was that of a young and adequately nourished female *R. unicornis*, 3-½ years old and weighing 1,057 kg. She had an infected fracture of the right metatarsus and a comminuted fracture of the left acetabulum from assaults by the large male. Autopsy was on day of euthanasia. Both kidneys appeared normal and were refrigerated. *R. unicornis* may attain 2,000 kg in weight (Brehm, 1922; Grzimek, 1968) and more rarely 4,000 kg (Burton, 1962; Walker and Paradiso, 1975), the female being smaller.

The one-day-old male *R. unicornis* showed no gross or histological abnormality. He weighed 55 kg; both kidneys weighed 235.75 gm or 0.43% of body-mass. The two-day-old male *R. unicornis* died from necrotizing colitis. He weighed 48.6 kg; the two kidneys weighed 344 gm or 0.71% of body-mass. These specimens were from the Zoological Society of San Diego through the kindness of the pathologist, Marilyn P. Anderson, D.V.M., Ph.D. Glomerular count of an equine kidney was made possible courtesy of R.I. Genovese, D.V.M., Randall Veterinary Hospital, Cleveland, who supplied a frozen normal kidney of a 3-year-old horse weighing about 455 kg.

Counting of Lobes and Dissection

The kidney was thawed in an icebox. It was then stripped of superficial connective tissue, measured, and weighed. The numerous lobes were numbered with tempera color. Drawings were made according to careful measurements of all aspects. The ureter and vessels were perfused with buffered 10% formalin. The kidney was then cut in the coronal plane with a long, flat knife and immersed in the formalin for several days.

Dissection was done under a microscope using fiberoptic illumination, watchmaker's forceps, a small scalpel, razor blades, an overhead blower, and latex gloves. Importance of dissection in identifying infundibular orifices, infundibula, and calyces, and in establishing relationships, cannot be over-emphasized.

Histological Sections

Sections were cut at a thickness of 4 μm and stained separately with Masson's trichrome and Weigert's elastin stain. Formalin and passage through alcohol and xylol did not shrink the glomerular capsules appreciably. Thus, the average of two diameters of the spheroidal glomerular capsules of adult *R. unicornis*, in thin, hand-

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cut slices of the formalin-fixed kidney, was 191.6 μm ± 15.8 S.D. In histological sections, the averaged diameters were 194 μm ± 10.8. For the horse, the measurements were 205 μm ± 19.8, and 200.7 μm ± 10.7, respectively.

In comparing sizes of glomerular capsules throughout the cortex, large ones were selected and the two diameters averaged. Typically, maximal diameters needed display of a tubular or vascular pole.

Volume of Glomerular Capsule

In *R. unicornis*, glomerular capsules are about the same size throughout the cortex, even in the newly born at term. Volume of a glomerular capsule is that for a sphere, $4/3\ \pi r^3$, in which π is 3.14 and r is half the averaged diameter.

Number of Glomeruli

Method I. Four rectangular slabs were cut from mid-cortex by razor blades, blotted carefully with filter paper, and weighed to the nearest milligram. The slabs, 121, 153, 154 and 236 mg, were placed in the specimen block so that sections were cut parallel with one of their two broad surfaces. Frozen sections were cut 100-μm thick as was done formerly (Maluf, 1981). With the known mass of the cortex (see below), the total number of glomeruli could be calculated.

Method II is essentially that used by Baer et al. (1978), and depends upon relative resistance of the glomerular capsule to strong hydrochloric acid and to maceration (Henle, 1862; Schweigger-Seidel, 1865; Kunkel, 1930; Rytand, 1938). Thus, 3,055 mg of cortex are macerated in 40 cc of 28% HCl (7.4 N) in a 100-cc Erlenmeyer flask. Assuming the cortex has a specific gravity of 1,060, the total volume is 40 + 2.88 cc, or 42.88 cc. After about 3 hours in a bath at 37°C, the tissue is spatulated against the container and then, if soft, triturated with a 5-cc pipette with Gilson attachment (Rainin Instruments, Woburn, MA). If timing in the bath is right, there will be no gross fragments after a few minutes of trituration. Aliquots of 0.010 cc are drawn up into a calibrated Gilson-type pipette. The internal diameter of the tip is about 575 μm, thus considerably wider than the glomeruli. The 0.010-cc droplet is delivered onto a slide and counts made under the microscope using transmitted light. The number of glomeruli per droplet ranged between 9 and 12 (average 10.6 ± 0.8 S.D.). Counts by both methods were close, giving 14,080 and 14,889 glomeruli per gram of rhino cortex. Method II was used for the horse, which yielded 15,806 glomeruli per gram of cortex.

Size of Cortex and Medulla

About six contiguous half-lobes were excised from a coronal half. Under the dissecting microscope, the cortex was pared off with a scalpel and fine scissors. The pieces were blotted thoroughly on filter paper and weighed on a delicate beam-balance.

RESULTS

Gross Anatomy

General

The kidney is C-shaped (Figs. 1, 2, 5, 6) and weighs 1,480 gm. The cephalic and caudal poles approximate each other medially. Thus, the kidney is as broad (17.0 cm) as it is long (16.8 cm). Its width is 8.9 cm (Figs. 3, 4). The cleft separating the poles is 9 cm long (Figs. 1, 2, 5–8). The poles are separable at the cleft, thus allowing display of the sinus (Figs. 7, 8). Assuming both kidneys are equal, their sum is 0.28% of the body-mass. Superficial areolar fascia which covers the kidney is not fixed to the interlobar furrows. There is no fat deep to this. The renal capsule is translucent and can be stripped freely from the surface but is fused to the interlobar septa; it is moderately stretchable at right angles to its parallel fibers. The six perforating vessels, 0.5 to 3 mm in diameter, issue through interlobar septa.

On the ventral surface, 42 lobes are evident (Fig. 1); on the dorsal, 49 lobes (Fig. 2); on the medial, 41 lobes (Fig. 3); and on the lateral, 45 lobes (Fig. 4). By complete count there are 78 lobes, which includes lobes 33*a* and *b*; 57*a* and *b*; and 73*a* and *b*. All lobes appear at the surface. The interlobar furrows are distinct although, in general, superficial. The interlobar septa are visible grossly. There are two deep furrows. These are parahilar. The ventral one occurs between lobes 59 and 60 (Figs. 1, 4); the dorsal one between lobes 35 and 48 (Figs. 2–4).

The lobes are apposed compactly (Figs. 5, 6, 9–11), unlike the looseness in oxen. Interlobar septa separate the cortices. Typically, three lobes meet along a septum which appears as a point in cross-section (Figs. 1–4, 9–11). The corner or angle formed by the lobes, and depicted by their septa, is typically 120°. The septa of three lobes thus inevitably form 360° in cross-section. So compact is this formation that, at a meeting of three lobes, one or two of these often form an acute angle of as little as 60°. These angles are neatly accentuated by the interlobar septa.

Abbreviations

A	arcuate vessel
AA	arcuate artery
AV	arcuate vein
C	cortex
CX	calyz
DM	divergence of medullae
F	base of valve
IL	interlobar vessel
ILA	interlobar artery
ILV	interlobar vein
IM	internal medulla
IN	orifice of infundibulum
IN_1, IN_2, IN_3	orifices of primary, secondary and tertiary infundibula
INLA	intralobar artery
INLV	intralobar vein
IS	gap in interlobar septum
L	lumen
M	medulla
MR	medullary ray
OM	outer medulla
P	pelvis proper
P_1	cephalic conduit of pelvis
P_2	caudal conduit of pelvis
RA	renal artery
RC	renal capsule
RV	renal vein
S, S_1, S_2, S_3	interlobar septa
TD	terminal collecting ducts
TM	tubus maximus
U	ureter
V	vein

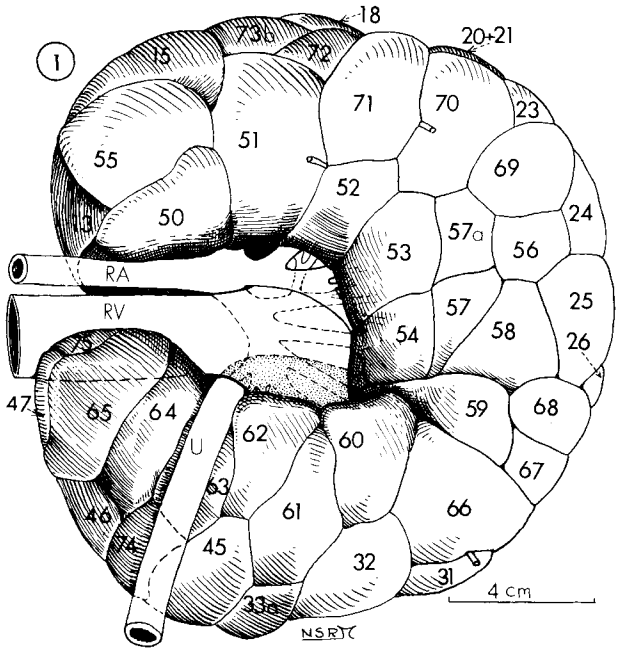


Fig. 1. Ventral aspect of left kidney. Branches of the renal artery that extend dorsal to the renal vein are in broken lines. The major ventral fissure is para-hilar between lobes 59 and 60. Two vessels issue through interlobar septa.

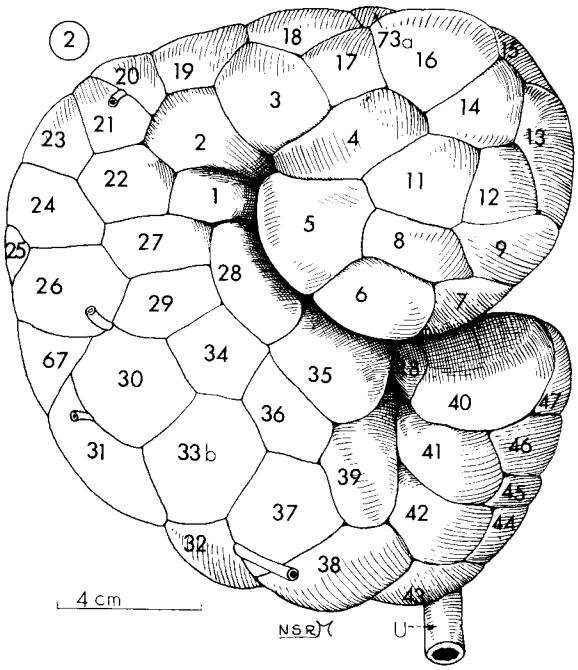


Fig. 2. Dorsal aspect of left kidney. The major dorsal fissures are between lobes 35 and 40 and between lobes 1 and 5; the latter is a deep cleft 9 cm long. One vessel issues through an interlobar septum.

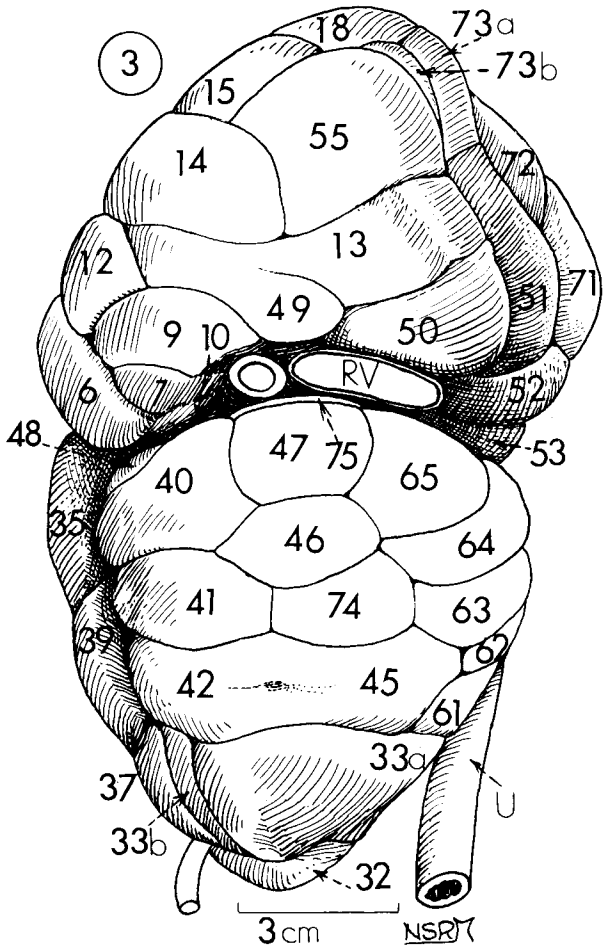


Fig. 3. Medial aspect of left kidney. Forty-one lobes are visible: 19 at the cephalic pole and 22 at the caudal pole. At the caudal pole, a vessel issues through an interlobar septum.

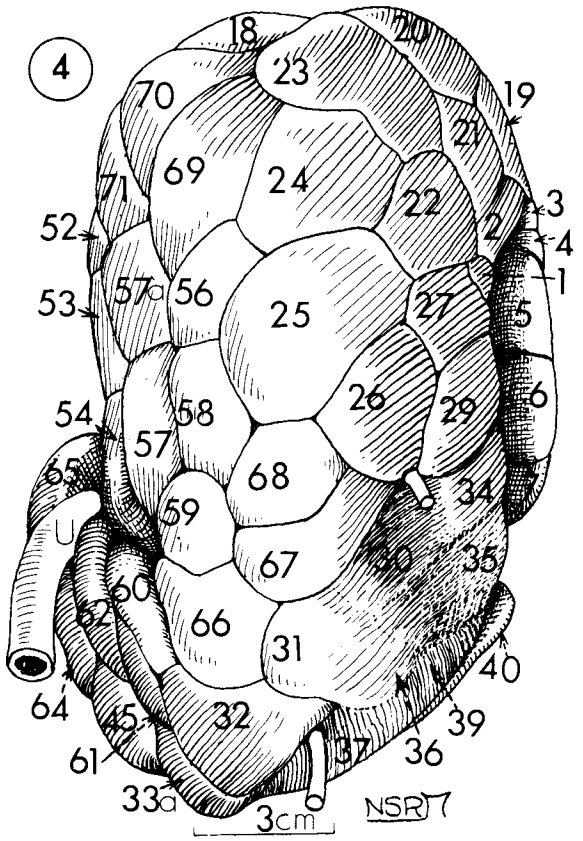


Fig. 4. Lateral aspect of left kidney. Owing to foreshortening, interlobar septa at the dorsal aspect of the caudal pole are not discernible. Two perforating vessels emerge at interlobar septa.

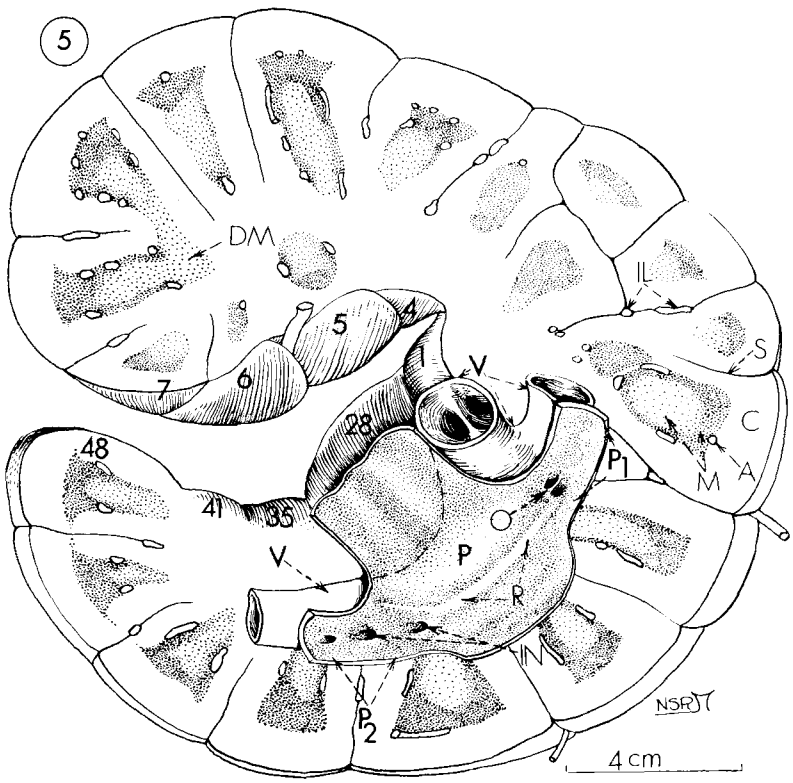


Fig. 5. Ventral surface of dorsal coronal half of left kidney. Only the lobes bounding the renal sinus are labeled. Part of the pelvis is in the ventral half (Fig. 6). Interlobar septa are shown as close to the pelvis as possible without destroying part of the specimen precociously. The cortices are clear; the medullae are stippled. Darker zones of the medullae probably represent vasculature of the outer medulla. Orifices of the infundibula, which are 2 to 3 mm in diameter, are depicted somewhat larger than the scale; orifice labeled "O" is shown in Fig. 13.

Beneath the surface there are, not infrequently, gaps in the septa. These allow parts of adjacent cortices to fuse. Interlobar septa do not intercept the medullae.

The lobes are truncated cones with their broad bases at the surface and their sides deformed by adjacent lobes. Length of a lobe ranges between 20 and 40 mm (Figs. 5, 6). Their greatest width is at the periphery, and is between 1.5 and 5 cm.

Cortex and medulla

The cortex has a mean width of 7.5 mm. It tends to be wider at the surface than at the interlobar septa. It is about 75.3% of the renal mass and thus weighs 1,114 gm. Length of the medulla equals that of a lobe minus peripheral width of the cortex (Figs. 5, 6). Greatest width of the medulla is about 24.5 mm.

Pelvis and ureter

The pelvis proper is a small pouch which measures 31 mm at its lateral border. It occupies the renal sinus between lobes 1 and 35 dorsally (Fig. 5) and 53 and 60 ventrally (Fig. 6) where it bridges the gap between the two pelvic conduits. Its lateral wall is thickened as a ridge (Fig. 5). It divides into two conduits: cephalic (Figs. 5, and 6, P_1) and caudal, which are 10.8 and 7.5 cm long, respectively. Since the pelvis proper is in the caudal half of the kidney, its length can be added to that of the caudal conduit. Thus, the entire pelvis of the caudal half of kidney equals that of the cephalic half.

Each conduit is almost circular in cross-section, has an outer diameter of 10 mm, and a wall thickness about 0.75 mm. The conduits end bluntly at the length of a lobe from the periphery of each pole (Fig. 6). The entire pelvis has a smooth and silky internal surface. The pelvis proper is soft and pliable. The conduits, on the other hand, have an arterial consistency.

The pelvis proper and the two conduits are loosely adherent to the adjacent renal cortices. Renal vessels, nerves, and areolar fascia intervene; but the medullae contact neither pelvis proper nor its conduits (Figs. 19–25).

The ureter courses on the ventral surface of the caudal pole (Figs. 1–4). Within the sinus, the ureteral wall is less than 1 mm thick. It thickens as it leaves the renal hilus (Fig. 7). Its outer diameter is then 11 mm and the thickness of its wall about 3 mm.

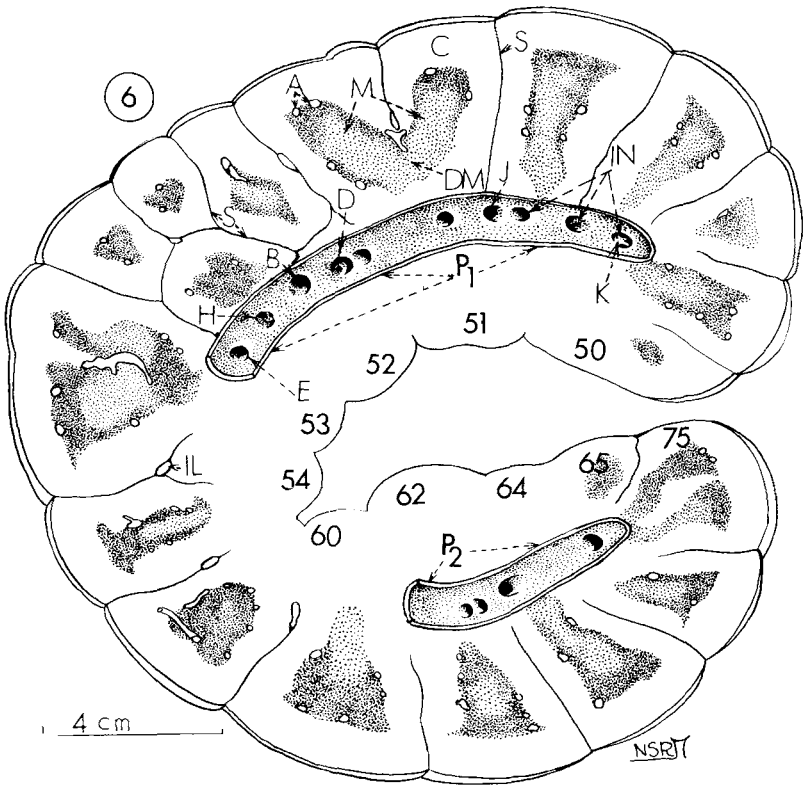


Fig. 6. Dorsal surface of ventral coronal half of left kidney. Only lobes bounding the renal sinus are labeled. Part of the pelvis is in the dorsal half (Fig. 5). Interlobar septa are shown as close to the pelvis as possible without destroying part of the specimen precociously. The conduits of the pelvis are shown slit open and spread transversely. Orifices of the infundibula (labeled B, D, E, H, J, and K), which are 2 to 3 mm wide, are depicted somewhat larger than the scale.

Infundibular orifices

Along the cephalic and caudal conduits of the pelvis, but not the pelvis proper, there are 18 orifices (Figs. 5, 6), every one 2 to 3 mm wide. Eleven are in the cephalic conduit and seven in the shorter, caudal conduit. They are the only final outlets of the lobes. No terminal collecting duct (of Bellini) opens directly into the pelvis proper nor into its conduits.

An orifice typically is guarded by a single flap-valve (Figs. 20, 22–24). The valves are disposed transversely along the conduits with no preference as to direction (Fig. 6). They may resist back-flow of urine during straining.

Since there are 78 lobes, there are 4.3 lobes per orifice. Every orifice typically leads into an infundibulum into which a secondary orifice usually opens and leads into a secondary infundibulum. The latter can give origin to a tertiary. A sample of a primary infundibulum and its branches is shown in Figure 18, which was dissected from primary orifice *K* of Figure 6.

Some of the primary orifices are shown in Figures 12 to 17. Variations are evident. Upon stretching a primary orifice with fine forceps, a secondary orifice usually becomes visible within the primary infundibulum (Figs. 12, 14, 16, 17).

Infundibula, calyces, and tubi maximi

The primary orifices communicate with their respective infundibula, which are of variable size (Figs. 21–24) and which receive the contents of one or more calyces.

Close to the infundibula are large interlobar arteries and veins (Fig. 18). Intimately associated with the calyces are large intralobar veins (Figs. 21–25; see below).

The apex and sides of a tubus maximus receive the terminal collecting ducts. There is no papilla. The infundibular and calyceal walls are protrusions of the pelvic conduits. Distance between an infundibular orifice and a corresponding calyceal rim is about 5 mm. The calyx is adherent to the outer medulla and thus embraces the medulla including the tubus maximus and the latter's terminal collecting ducts (Figs. 20–25).

The internal diameter of a calyx and its infundibulum varies between 3.5 and 8 mm; its outer diameter between 4 and 8.5 mm.

Fusion of lobes

Medullae of two or more lobes "converge" not infrequently or, embryologically speaking, diverge. This can occur upstream of the calyces (Figs. 5, 6, 9, 34) or within the calyces (Figs. 30, 31, 35). Minor fusion of adjacent

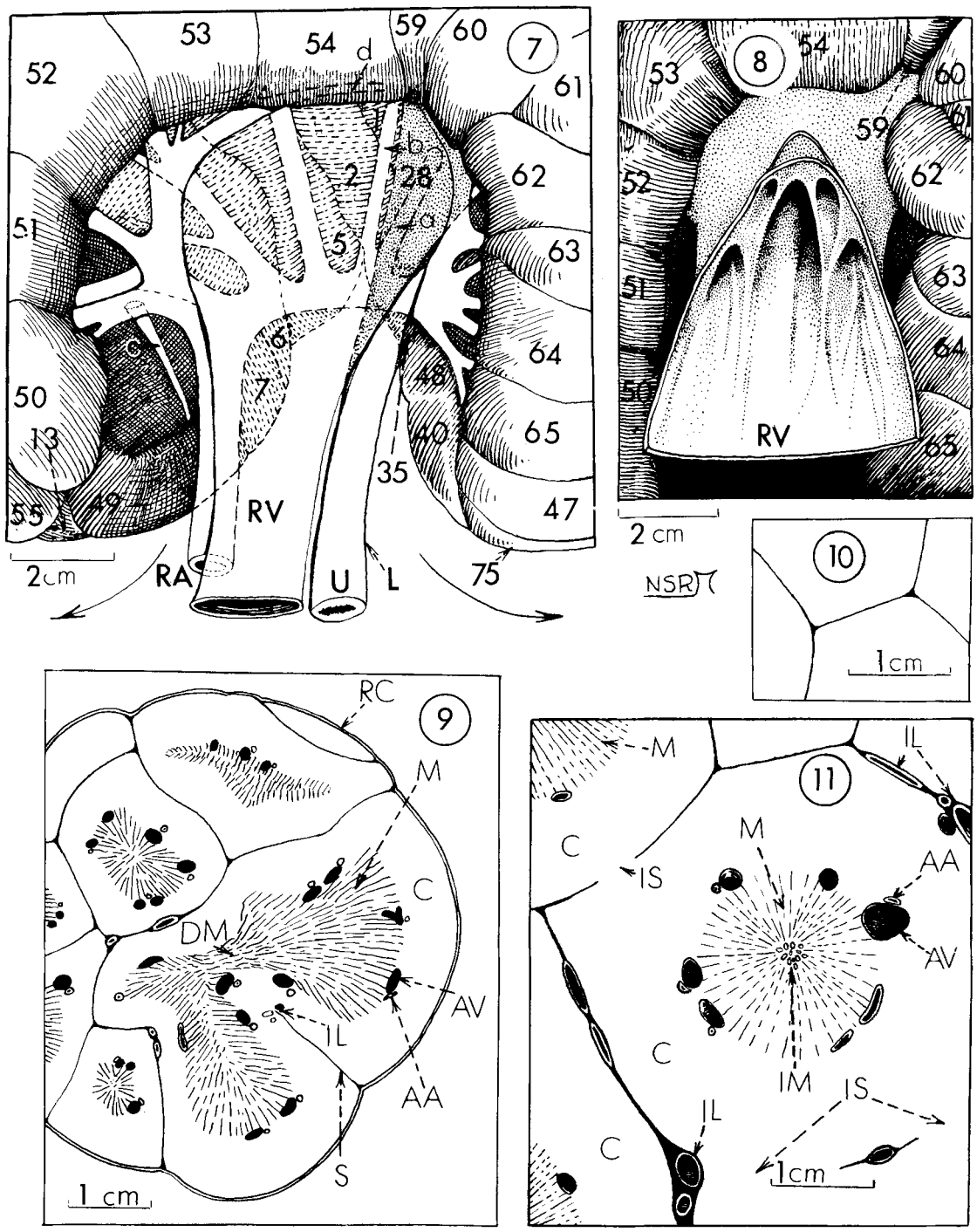


Fig. 7. Ventral aspect of hilus and sinus of left kidney. The poles are being spread apart, as indicated by the unbroken arrows. The cephalic pole is on the left. The renal vein is capacious and occupies a large part of the sinus. The branches of the renal artery which extend dorsal to the renal vein and ureter, and enter the kidney at the dorsal lobes of the sinus, are shown by broken lines. Thus, artery *a* enters between lobes 28 and 35; artery *b* enters between lobes 1 and 2. The dorsal branch of the renal artery is wider than the ventral and supplied a larger territory. L, level at which ureteral wall thickens.

Fig. 8. Ventral aspect of renal sinus. The enormous renal vein is slit open after removing its enveloping fascia. Orifices of primary tributaries are evident. An especially large tributary issues dorsally. Every orifice has a pseudovalve. Cephalic pole of the kidney is on the left. The main ventral fissure is between lobes 59 and 60.

Fig. 9. Superficial coronal cut through cephalic pole showing arrangement of interlobar septa.

Fig. 10. Paramedian coronal cut through cephalic pole showing meeting of interlobar septa. Three lobes, in cross-section, meet at one point. Angles between the septa are typically nearly 120°. There need be no vessel at lines of meeting of the lobes.

Fig. 11. Paramedian coronal cut through cephalic pole showing cross-section of a lobe. Interlobar septa separate adjacent cortices but never medullae. Interlobar septa are often interrupted allowing renal tubules to enter the gaps. Arcuate veins tend to be central to corresponding arcuate arteries.

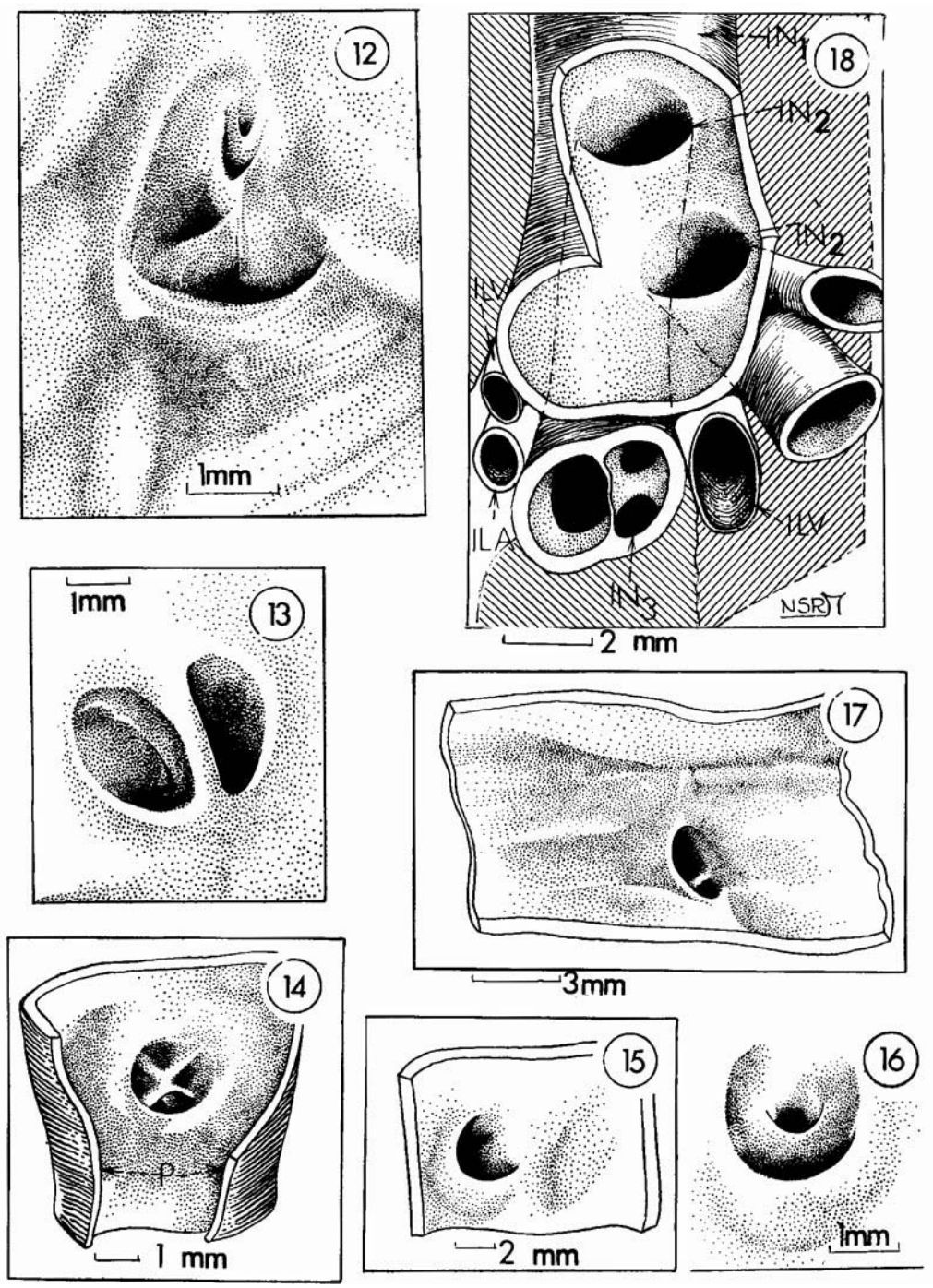


Fig. 12. A double orifice of separate infundibula; about 2 mm wide when not stretched. This is orifice *B* of Figure 6. The separate orifices are supplied with flap-valves, probably not fully competent, made of connective tissue with no muscle and lined by layered cuboidal cells.

Fig. 13. Binary infundibular orifices. These are *O* of Figure 5; are the most central of the orifices of the cephalic conduit of the pelvis; and are on the ventral wall of the conduit. Each orifice is about 2.2 mm in greatest diameter.

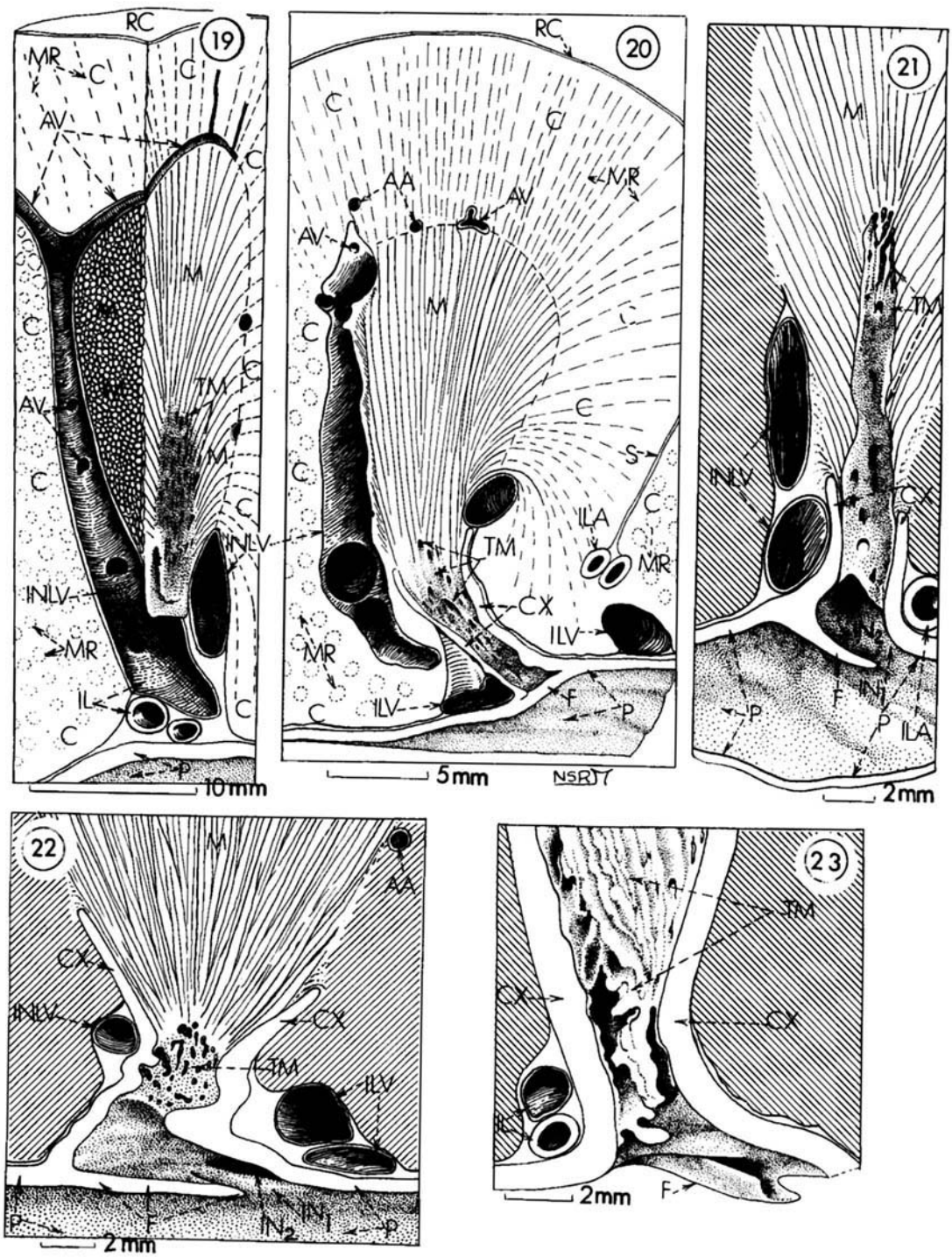
Fig. 14. Infundibular orifice *H* in Figure 6. The flap would direct urine centrally but, probably more importantly, it would resist back-pressure upon abdominal straining. Three secondary infundibula open through this.

Fig. 15. Infundibular orifice *J* of Figure 6. When cut across at right angle to its semi-lunar valve, it is found to lead to an infundibulum 4 mm long (tubus maximus) which receives terminal collecting ducts on a slant.

Fig. 16. Compound orifice leading to two infundibula, each supplied with a valve and located on the ventral wall of the cephalic conduit. The valves overlap each other. The infundibulum of each orifice is short and receives, on an irregular flat surface, the terminal collecting ducts. This is orifice *D* in Figure 6.

Fig. 17. Infundibular orifice *E* of Figure 6. It is on the dorsomedial wall of the cephalic conduit and has two openings. Its valve directs the flow centrally.

Fig. 18. A primary infundibulum from orifice *K* in Figure 6. It is dissected toward its secondary and tertiary branches. The renal cortex is cut in two planes and is depicted by the diagonal hatching.


19
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2mm
22
IN2
IN1
2mm
23
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lobes occurs through gaps in interlobar septa (Figs. 11, 32, 34).

Blood vessels

A conspicuous feature of the renal sinus and hilus is the wide renal vein (Figs. 7, 8). Enveloped by an areolar fascia, it overlaps the ureter ventrally within the sinus. It is thin, translucent, and 30 mm wide when flat. It has large tributaries, especially a major one dorsally. At their ostia, the tributaries have delicate single flap-valves (Fig. 8). The valves may be competent enough to resist back-pressure during straining. The large dorsal tributary bifurcates, medial to and alongside the pelvis (Fig. 5), into major branches to both poles. These receive large short interlobar veins which, in turn, receive wide intralobar tributaries (Figs. 19, 21, 22, 25, 32, 33, 35). The intralobar veins course between cortex and medulla receiving arcuate veins. As they leave their lobes, the intralobar veins are adherent to the respective calyces. Possible significance of this and of the large size of the intralobar veins is indicated in the Discussion.

The renal artery (Figs. 7, 8) is 11 mm in outer diameter with a wall 2-mm thick. It courses dorsal to the renal vein and soon divides into a primary branch, 8 mm in outer diameter, ventral to the vein and a branch, 9 mm in outer diameter, dorsal to the vein and ureter (Fig. 7). Secondary branches can be traced as interlobar arteries 3 to 4 mm in outer diameter. Thus, artery *a* enters between lobes 28 to 35; artery *b* between lobes 1 and 28; artery *c* between lobes 49 and 7; and artery *d* between 1 and 2.

The interlobar arteries and veins enter and leave, respectively, the lobes close to the pelvis proper and to the two pelvic conduits.

HISTOLOGY

Renal and Capsule and Interlobar Septa

The renal capsule is about 130 μm thick. It consists of collagen bundles in parallel. It has no muscle but has numerous fine fibroblasts which may be mistaken for muscle because of staining red with Masson's. Elastic fibers are restricted to the outermost two or three collagen bundles. Capillaries are not evident.

The interlobar septa are continuous with the central collagenous bundles of the renal capsule. They have no muscle but have fine elastic fibers along the collagen bundles. Maximal width of an interlobar septum is 300 μm; this is usually at the renal capsule. Beneath the surface, the septa often taper and disappear or cease abruptly, allowing gaps of variable distance (Figs. 11, 32, 34). Through these interruptions, renal tubules enter leaving no evidence of a boundary between adjacent cortices.

Cortex

The cortex cortices is about 225 μm wide, capable of accommodating 4 or 5 proximal renal tubules in cross-section. The outer diameter of the proximal tubule is 46–60 μm; that of the distal tubule 32–46 μm. Cells of the proximal tubule are high cuboidal and about 16 μm tall; those of the distal tubule are cuboidal and 12 μm tall. The outer diameter of a collecting duct in the medullary rays at the cortico-medullary border is 34–36 μm. There the medullary rays are 300–375 μm wide and 450–750 μm apart.

Glomeruli

There are tiers of 7 to 11 glomeruli between renal capsule and medulla in sections 4 μm thick and perpendicular to the periphery. The glomerular capsules are basically spheroidal, with lateral and polar distortions equally distributed. In slices of the fixed kidney obtained by razorblade, the glomerular capsules are quite spherical. The number of glomeruli per gram of renal cortex is 14,080 and that in the entire cortex is 15,612,520 by method I. These numbers are 14,889 and 16,603,442 by method II. The average is 16,107,981 glomeruli per kidney.

Relationship of number of glomeruli per kidney to body-mass of several adult eutherian mammals and an opossum is shown in Figure 43. The adult range between mouse and rhino is expressed by $\log_{10}N = 0.59 \log_{10}M + 3.2$, in which 0.59 is the slope; 3.2 the intercept; N is number of glomeruli per kidney; and M is total body-mass of adult in grams. The arithmetical expression is $N = 1,585M^{0.59}$, which shows that increase in number of glomeruli per total body-mass diminishes exponentially with body-mass. The black circles in Figure 43 are the writer's for okapi (Maluf, 1981), tapir, horse, and Indian rhino. The 3-year-old 455 kg horse has 15,806 glomeruli per gram of cortex and 5.55×10^6 per kidney. The 16-month-old 154.1-kg *Tapirus bairdi* has 12,444 glomeruli per gm of cortex and 4.0×10^6 per kidney.

Average diameter of glomerular capsules (see Methods) is the same throughout the cortex of the adult *R. unicornis*: peripheral 194 μm (S.D. 10.8; n=6); mid-cortical 194 μm (S.D. 4.5; n=6); juxtamedullary 181 μm (S.D. 11.2; n=6). Measurements from another section yielded similar results.

The fraction of the cortical mass occupied by the glomeruli is 5.8% and of the whole kidney is 4.4%. The glomerular fraction of cortical mass in twelve unrelated species of adult and sub-adult eutherian mammals,

Fig. 19. Longitudinal cuts through a renal lobe in two planes at right angles to each other. Note large intralobar vein between cortex and medulla. This vein is receiving a number of relatively large arcuate veins along its course. The medullary rays of the cortex on the left face are circles because they are cut at right angles to their direction.

Fig. 20. Longitudinal cut through a renal lobe. Note the large intralobar veins (2.5 mm wide) and that the cortex is the only part of the lobe which contacts the pelvis (pelvic conduit). The medullary rays of the cortex, at peripheral left and right, are represented as circles as they are cut at a right angle to their direction. The large 2.3 mm orifice of a tributary of the intralobar vein, at the calyceal rim, is noteworthy.

Fig. 21. Longitudinal cut through part of central end of a lobe. The cortex, represented by oblique hatching contacts the renal pelvis (pelvic conduit).

Fig. 22. Longitudinal cut through part of central end of a lobe. The cortex is represented by oblique hatching. The tubus maximus here is short and broad. Note that the cortex but not the medulla contacts the renal pelvis.

Fig. 23. Longitudinal cut thorugh part of central end of a lobe. The cortex (oblique hatching) is the only part of the lobe which contacts the renal pelvis.

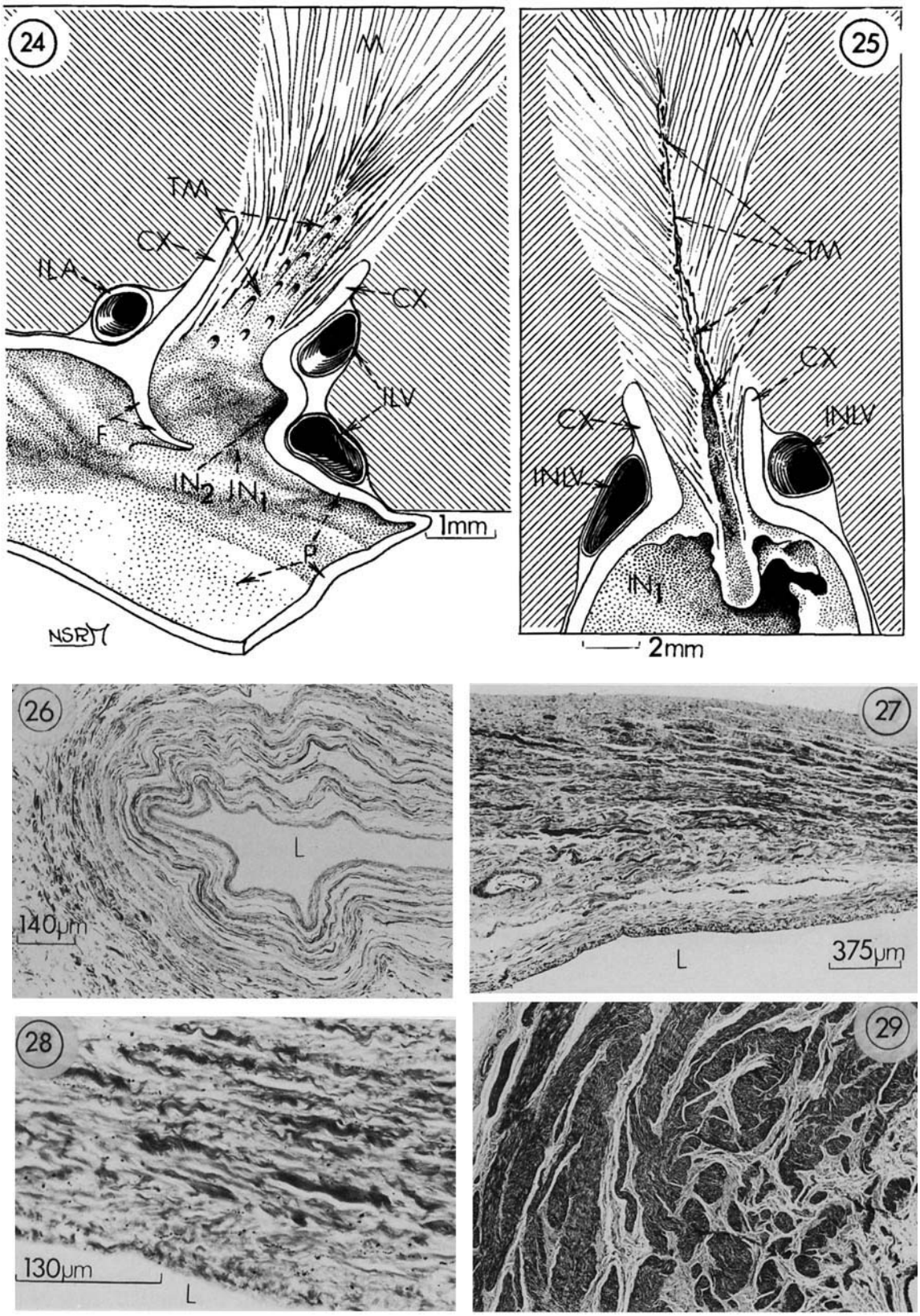


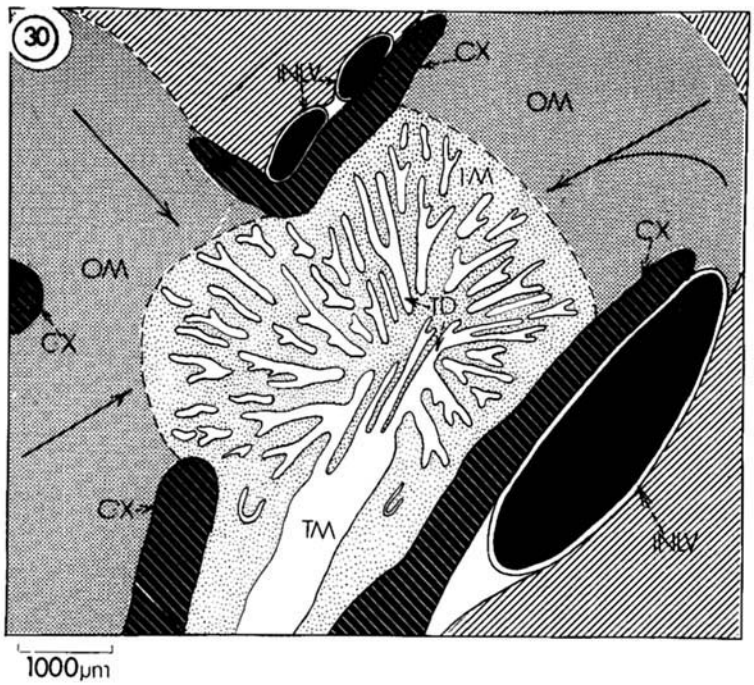
Fig. 24. Longitudinal cut through part of central end of a lobe. Cortex (represented by oblique hatching) is attached to the pelvis by strong areolar fascia.

Fig. 25. Longitudinal cut through a part of another renal lobe. Note the large intralobar veins between calyx and cortex. These veins are fused with the calyceal wall.

Fig. 26. Cross-section of an arc of the caudal conduit of the pelvis. Collagen and muscle fibers are interspersed almost equally. Both fibers are mainly circular; elastic fibers are sparse. There is less muscle than in the calyces or the infundibula.

Figs. 27 and 28. Increasing magnification of cross-sections through the wall of pelvic conduits. The part toward the lumen is especially collagenous. There are numerous capillaries but sparsely scattered arterioles. Masson's trichrome with yellow-green filter.

Fig. 29. Transverse section of ureter distal to renal hilus. The periphery is at the upper left hand corner and the lumen at the lower right. Circular muscle bundles of the outer half are especially prominent. Collagen is interspersed between muscle fibers. Masson's trichrome with yellow-green filter.



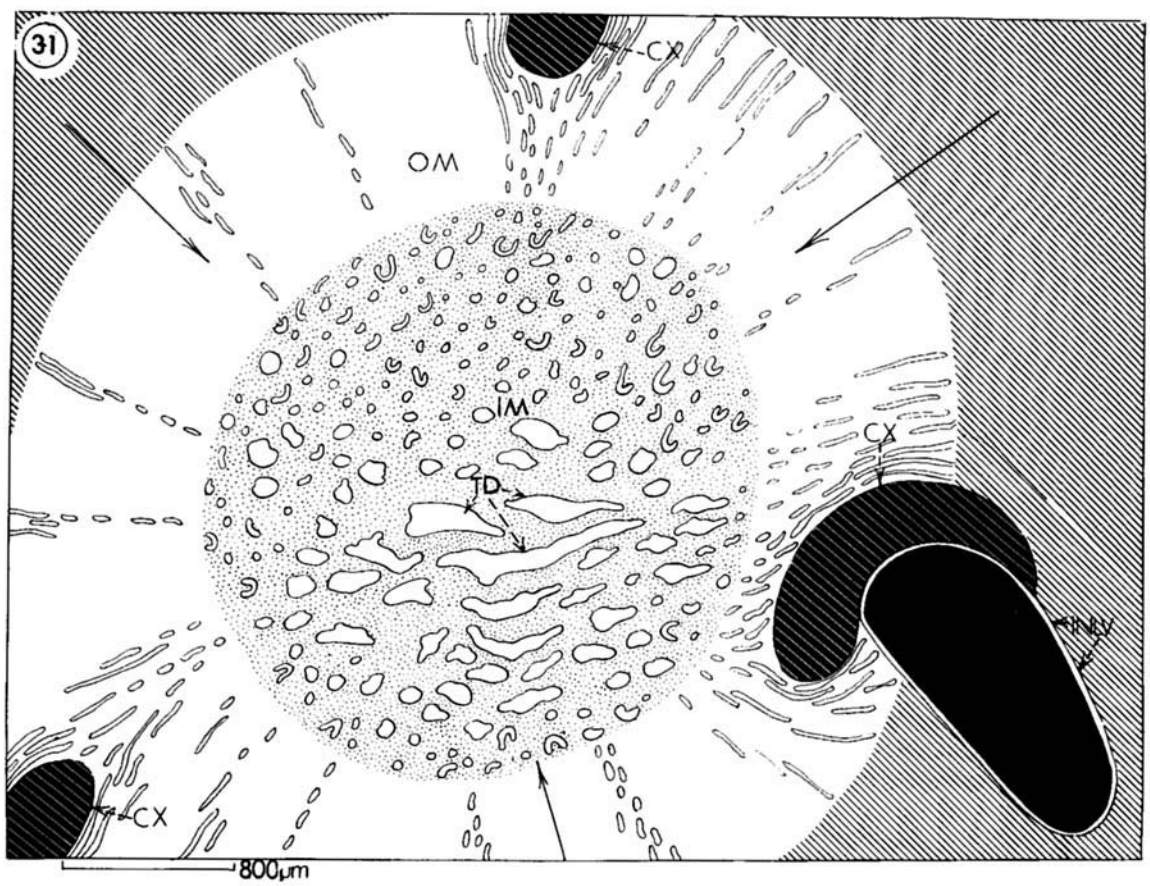


Fig. 30. Regional drawing to scale of a longitudinal section through a tubus maximus which receives the flow from the medullae of three renal lobes (unbroken arrows). Cortices are shown by oblique hatchings; the outer medullae are stippled heavily; and the inner medulla is stippled lightly.

Fig. 31. Regional drawing to scale of transverse section through inner medulla and terminal collecting ducts. The inner medulla receives flow from the outer medullae of three lobes (unbroken arrows). The cortices are indicated by oblique hatching.

ranging from mouse to rhinoceros, averages 5.02% ± 1.21 S.D. (calculated from data of Hollatz, 1922; Kunkel, 1930; Denzer, 1935; Tischer, 1976; Maluf for tapir, horse, rhino, manatee, and dog).

Medulla, including the tubi maximi

The outer medulla varies in width between 860 and 3,000 μm and the inner medulla between 1,750 and 4,000 μm (Figs. 30–33, 34, 35). Counts of parallel medullary tubules per unit field indicate only a slight difference between deep outer medulla and peripheral inner medulla. This suggests that most medullary loops are long. Outer diameter of a long loop is 14 to 18 μm.

The subterminal and terminal ducts at the tubus maximus range between 95 and 258 μm in outer diameter (Figs. 30, 31, 35) and, like the tubus maximus, consist of cuboidal cells. In some lobes, the terminal ducts are much wider and lined by flattened cells, suggesting dilatation (Figs. 32, 33).

The tubus maximus varies in size. That shown in Figure 35 is 470 to 650 μm wide. It consists of an apparently single layer of cells, 15 μm tall and 7 μm wide, which is surrounded by an extensive interstitium containing capillaries, terminal collecting ducts, segments of narrow medullary loops, and interstitial cells. The outer medullae of two or three lobes can "converge" toward a common inner medulla and tubus maximus (Figs. 5, 6, 9, 30, 31, 34, 35). This is one way that 18 orifices of the pelvis can accommodate 78 renal lobes; another is by secondary and tertiary infundibula as described above.

Infundibula and calyces

An infundibulum is an evagination of a pelvic conduit (Figs. 18, 19, 21, 22, 24, 25) and likewise is lined by urothelium.[1] The walls of an infundibulum extend peripherally as a calyx (Figs. 20–25, 30, 31). The thickness of the wall of a primary infundibulum, measured in sections perpendicular to the wall, is 645 to 774 μm; that of the calyceal wall is 430 to 1,000 μm.

Walls of the infundibulum and calyces are similar, consisting of striking amounts of smooth muscle interspersed with collagen bundles (Figs. 36–38) and well supplied with capillaries and fine elastic fibrils (Fig. 39). As tubules of the outer medulla enter a calyx, they cross over the calyceal rim on their way to the inner medulla (Figs. 30, 31, 33, 36, 37).

The calyx is adherent to the outer medulla. The inner medulla, embraced by the outer medulla, drains into the tubus maximus. Thus, there is no vault between calyx and medulla.

At the calyceal rim, the muscle fibers run mostly circularly. Thus, in a longitudinal section of a calyx, these fibers are cut across (Figs. 36, 37). On the other hand, the muscle fibers along the calyceal stalk run parallel with the long axis (Fig. 38). The possible function of the calyceal musculature is treated in the Discussion.

Pelvis proper and its two conduits

Thickness of the pelvic walls varies between 675 and 1,250 μm. The conduits are thicker and stiffer than the pelvis proper. The walls are largely collagen bundles and muscle in almost equal amounts. The muscle fibers are mostly circular and oblique. Next to the multilayered urothelium is a collagenous layer, about 60 μm wide, which contains capillaries (Figs. 26, 27). Arteries, about 80 μm in outer diameter with prominent internal elastic lamina, occur among the muscle fibers especially near the periphery.

The flap-valve, extending across most of the infundibular orifices, is about 146 μm thick at base and 60 μm at free margin. It consists mainly of fibers of collagen and muscle laced with fine fibrils of elastin. These, together with the capillaries, tend to run from base to free margin.

The cortex is the only zone which contacts infundibulum, pelvis proper, or pelvic conduit. Exchange of substances between cortex and pelvic urine is probably prevented by the thick collagenous wall of infundibulum and pelvis (Figs. 19–23).

Ureter

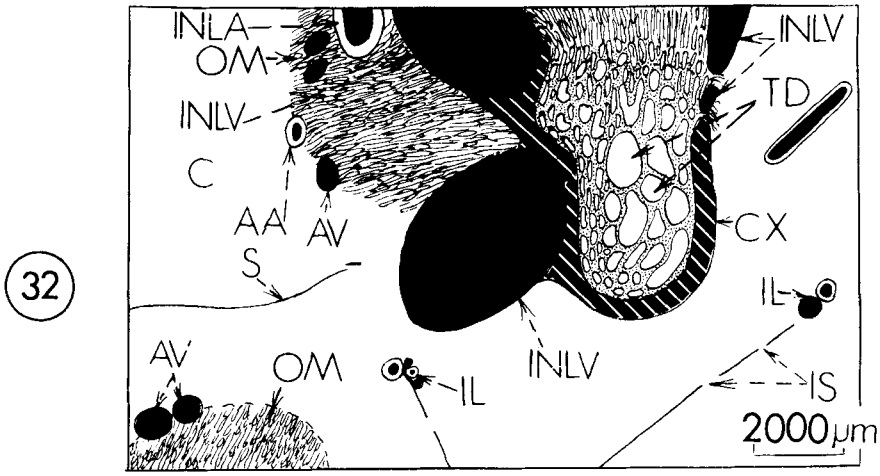
The lamina propria approximates 625 μm in thickness. Collagen is densest next to the typical urothelium where it contains numerous capillaries. In cross-section, an empty segment of ureter displays 14 major and 28 minor folds. Muscle comprises most of the ureter (Fig. 29) and, unlike the lamina propria, does not enter the folds. Most of the muscular fibers run in a circular and oblique manner and occupy the outer two-thirds; those nearest the lumen are longitudinal or oblique. This arrangement of muscle fibers presumably changes at the caudal end of the ureter. Judging by muscle mass, the extra-hilar portion of the ureter is incomparably more powerful than pelvis proper or pelvic conduits.

[1]The term "urothelium" is believed to have originated about forty years ago in the Department of Pathology of Columbia-Presbyterian Hospital, New York City. This epithelium forms the lining of renal pelvis, ureter, urinary bladder, and proximal urethra. It has characteristic properties even though it is of mesodermal origin in renal pelvis and ureter and endodermal in bladder. Classically, it is called "transitional" " . . . because morphologically it occupies a position between simple and stratified epithelium. It is the characteristic lining of the urinary passages . . . and is not found elsewhere in the body" (Clark, 1958). By special fixation and electron microscopy, however, it has acquired histological and histochemical characteristics (Walker, 1958; Vaçek and Schuck, 1960; Peachey and Rasmussen, 1961; Leeson, 1962; Hicks, 1965). it is a barrier, although not completely so (Maluf, 1953, 1955; Levinsky and Berliner, 1959), to free diffusion of water and is resistant to contact with urine.

Fig. 32. Regional drawing to scale of a nearly transverse section through inner medulla and terminal collecting ducts. The notable feature here is the large intralobar veins fused to the calyx. The cortices of three lobes are evident. Note that the interlobar septa are interrupted.

Fig. 33. Regional drawing to scale of a nearly transverse section through inner medulla and terminal collecting ducts. This is a variant of the preceding figure. The inner medulla receives flow from the outer medulla of at least two lobes. A notable feature is the large intralobar veins fused to the calyx.

Fig. 34. Longitudinal cut through parts of three adjacent lobes as seen through the dissecting microscope. The medullae of two lobes fuse. Arcuate veins tend to be central to arcuate arteries of their association and to be considerably wider.


32
INLA
OM
INLV
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AA
AV
S
INLV
TD
CX
IL
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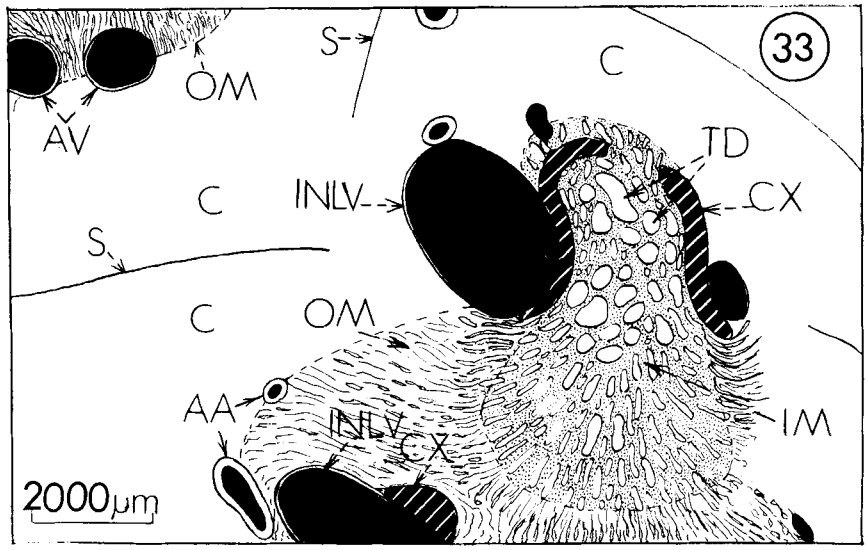
IS
2000μm


33
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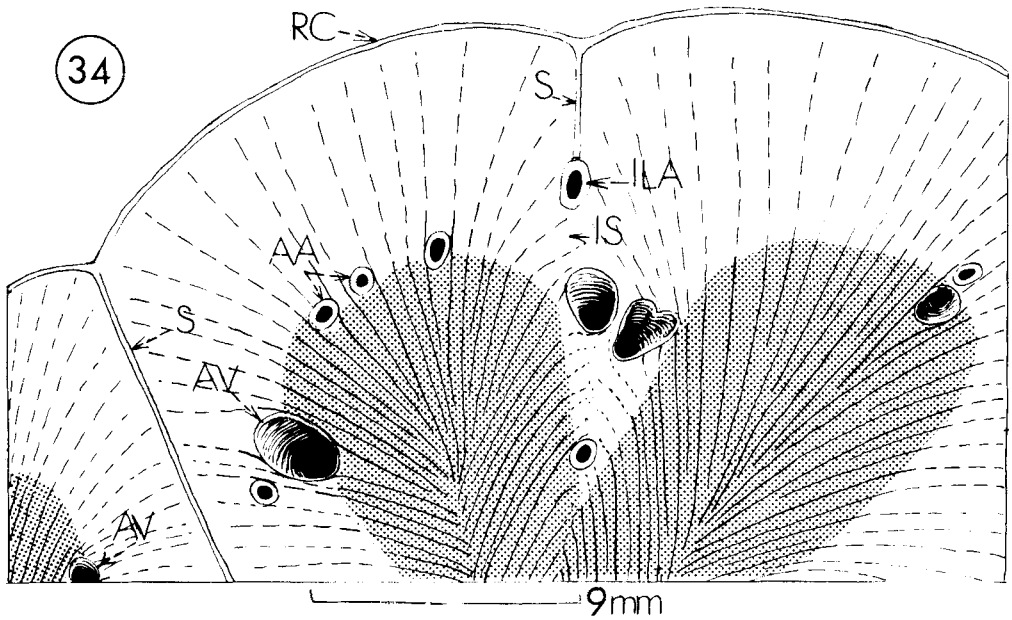
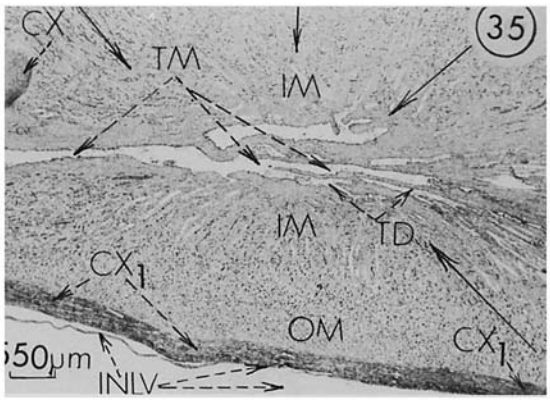
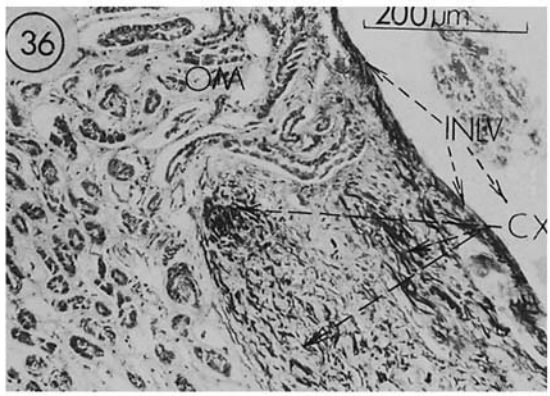
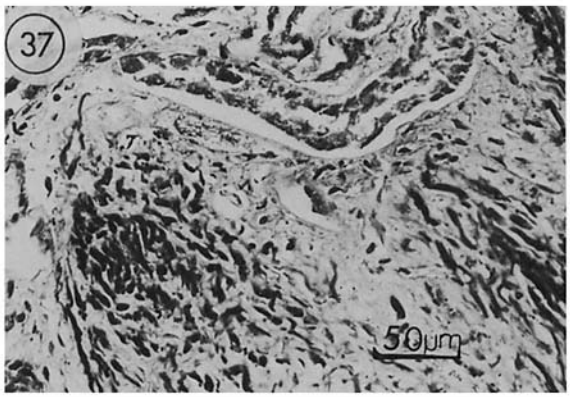
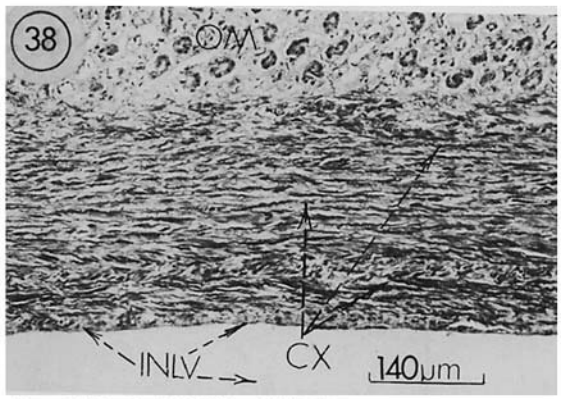

34
RC
S
ILA
IS
AA
S
AV
AV
9mm

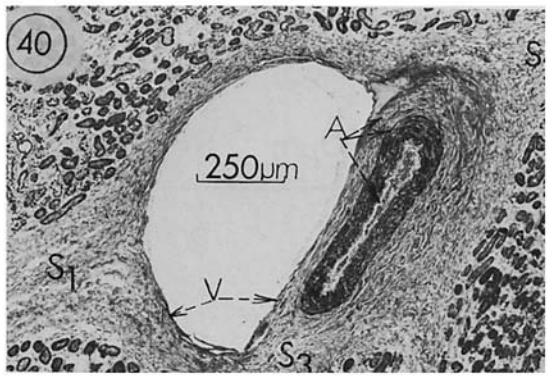

35
CX
TM
IM
IM
TD
CX1
OM
CX1
50µm
INLV

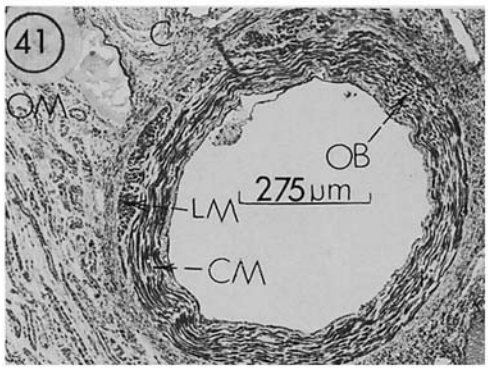

36
200µm
OM
INLV
CX

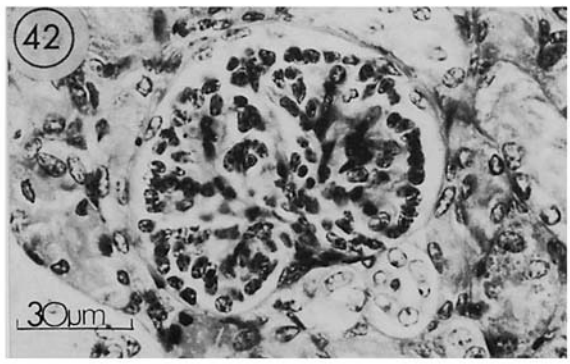

37
50µm


38
OM
INLV
CX
140µm


39
275µm


40
S
A
250µm
S1
V
S3


41
C
OM
OB
275µm
LM
CM


42
30µm

Arcuate vessels

Veins at the cortico-medullary border tend to be nearer the center of a lobe than the associated arteries. This relationship is not as striking or regular as in the rat (Fourman and Moffat, 1971; confirmed by the writer). Most arcuate veins are wider than the arteries and apparently more numerous (Figs. 11, 32, 33, 40). Arcuate veins range between 32 and 1,575 μm in diameter. The wall of a single vein, 284 μm in diameter and in the same cross-section, can vary in thickness from a few micrometers to muscular bundles 50 to 80 μm thick. These discrete bundles run obliquely and longitudinally. Otherwise, muscle fibers course obliquely and circularly throughout the thin wall. Collagen fibers and fragments of elastic fibers seem to be mixed uniformly with the muscle fibers. A vein as large as 774 μm in diameter has a wall 43 to 60 μm thick and can lie directly against the renal tubules with practically no adventitia.

An arcuate artery, on the other hand, has a discrete muscular layer of nearly uniform thickness consisting of circularly and obliquely arranged muscle fibers (Fig. 41) without striking collagen admixture. Such an artery also has bundles of longitudinal muscle externally (Fig. 41), which is confirmed by sections parallel to its length. Arcuate arteries, measured across their media, range in diameter from 43 to 795 μm. In the larger arcuate arteries, the circular-oblique muscle coat (media) is 103 to 172 μm thick and the longitudinal muscle bundles 43 to 86 μm thick.

Intralobar veins

The diameter of an intralobar vein adjacent to a renal calyx varies between 95 and 3,000 μm. Its wall consists of an admixture of muscle and collagen fibers and is 29 to 86 μm thick. At the calyx, the intralobar vein is fused to the wall of the calyx (Figs. 30–33, 35, 36). In Figure 35, the intralobar vein has become partially detached from the calyx. In Figure 38, the wall of the intralobar vein is indistinguishable from that of the calyx, has an identical composition of muscle and collagen fibers, but is much thinner than the calyceal wall. Combined thickness of both walls is thus largely that of the calyceal wall (215 to 645 μm). The thicker calyceal walls belong to calyces receiving the medullae of more than one renal lobe (Figs. 30, 31, 35). The possible significance of fusion of calyx with wall of a large intralobar vein is discussed below.

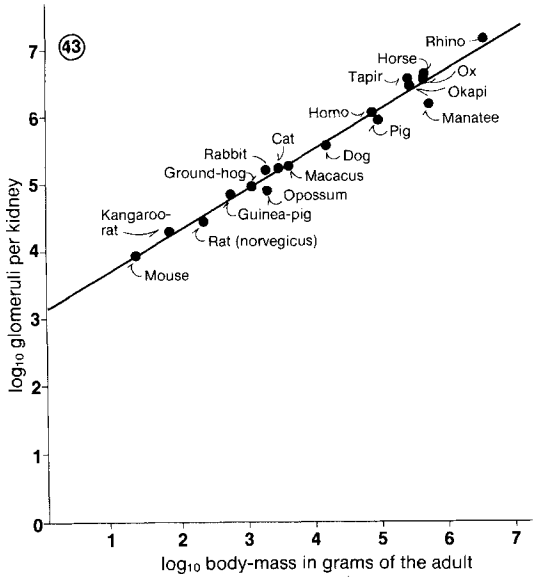


Fig. 43. Relation of body-mass to number of glomeruli in one kidney. Data for okapi (2.5×10^6 glomeruli per kidney), *Tapirus bairdi* (4.0×10^6), and Great Indian rhino (16.1×10^6) are from animals not fully grown and thus have been related to expected body-mass of the mature adult (250 kg for okapi; 263 kg for tapir; and 3,000 kg for rhino). Manatees and opossum have an exceptionally low number of glomeruli. Data for okapi, tapir, horse, rhino, and manatee are the writer's. The other plottings, except for kangaroo-rat from Rytand (1938) and for man, are calculated from the data of Kunkel (1930).

Intralobar arteries

Intralobar arteries, between cortex and calyx, vary in outer diameter between 500 and 675 μm.

Nerve bundles

Nerve bundles occur strikingly among the interlobar and arcuate vessels. They stain light purple with Masson's trichrome. A typical such bundle with its perineurium is 130 μm in diameter.

Kidneys of newly born *R. unicornis*

Gestation of 19 months (Walker and Paradiso, 1975) allows the one-day-old *R. unicornis* to have essentially mature glomeruli throughout the cortex. The glomerular tufts are lobulated, which indicates some maturity (Gruenwald and Popper, 1940; Hall, 1955; MacDonald and Emery, 1959), and maculae densae are present. Glomerular capsules are almost equal in diameter throughout the cortex (Table 1). Relative maturity at birth is of survival value to a mammal which must stay on the move.

The average width of the cortex is 1,875 μm. The glomeruli are uniformly distributed; their number, in tiers along the cortex is about 13. The cortex cortices is about 17 μm, or the width of a single proximal tubule.

Fig. 35. Photomicrograph of longitudinal section through the nearly terminal part of a lobe showing the tubus maximus. The thin-walled intralobar vein, *INLV*, is partly detached from the thick-walled muscular calyx, *CX*.

Fig. 36. Photomicrograph of rim of a calyx sectioned longitudinally with part of adjacent intralobular vein and related outer medulla. Note typical crossing over calyceal rim by tubule of outer medulla. Masson's trichrome with yellow-green filter.

Fig. 37. Greater magnification of calyceal rim of Fig. 36 showing the dark, transversely cut, muscle fibers.

Fig. 38. Photomicrograph of longitudinal section of stalk of calyx with adjacent outer medulla and large intralobar vein fused to calyceal wall. Masson's trichrome with yellow-green filter accentuating the red-stained muscle fibers which run longitudinally in the stalk.

Fig. 39. Photomicrograph of longitudinal section of calyceal stalk showing direction of elastic fibers. Weigert's elastin.

Fig. 40. Photomicrograph of transection of an interlobar artery and vein at the meeting of three lobes. Interlobar septa are just in the picture. Masson's trichrome.

Fig. 41. Photomicrograph of an almost perfect cross-section of an arcuate artery showing the circular (CM), obviously spiral (OB), and longitudinal (LM) muscle fibers. Masson's trichrome.

Fig. 42. Typical glomerulus, from mid-cortex, of a one-day-old *Rhinoceros unicornis.*

TABLE 1. Average diameter (in μm $\pm$ standard deviation) of glomerular capsules (see Methods) in one- and two-day-old male *R. unicornis*

	Peripheral	Midcortical	Juxtamedullary
One-day-old	76.6 $\pm$ 3.53 (n = 5)	82.6 $\pm$ 5.46 (n = 5)	81.6 $\pm$ 7.85 (n = 5)
Two-day-old	92.1 $\pm$ 12.9 (n = 12)	86.0 $\pm$ 11.3 (n = 7)	98.0 $\pm$ 15.5 (n = 7)

TABLE 2. Measurements and calculations of renal structures in kidneys of neonatal and adult *R. unicornis* and of adult *Homo sapiens*

Measurement or Calculation	1-day-old rhino	2-day-old rhino	Adult female rhino (3½ yrs)	Human adult
Volume of glomerular capsule (mm^3)	0.000268	0.000408	0.00382	0.00359
Ratio of adult to neonatal glomerular volume	14.25	9.34	—	13.4[1] (ratio to 1-day rhino)
Mass of both kidneys (gm)	235.75	344.0	2,960	300.0
Ratio of adult to neonatal renal mass	12.6	8.6	—	1.27[1] (ratio to 1-day rhino)
Number of glomeruli (no. per field at 35 ×)	150 $\pm$ 8.1 (n = 6)	132 $\pm$ 11.2 (n = 6)	13.56 $\pm$ 3.1 (n = 25)	11.6 $\pm$ 1.5 (n = 8)
Ratio of density neonatal/adult	11.1	9.7	—	12.9[1] (ratio to 1-day rhino)
Width of cortex (μm)	1,750	2,250	6.250	5,000
Ratio width of cortex adult/neonatal	3.57	2.78	—	2.86 (ratio to 1-day rhino)
Cortex % of renal mass	—	—	75.3	70.0
Glomerular mass % of cortex	—	—	5.83	4.71
Mass of glomeruli per kidney (gm)	4.57	6.96	65.08	4.95
Ratio of glomerular mass adult/neonatal	14.18	9.35	—	1.08[1] (ratio to 1-day rhino)
Glomerular mass % of single kidney	3.88	4.05	4.4	3.3
Body-mass (gm)	55,000	48,636	1,057,000	70,000
Mass of kidneys as % of body-mass	0.43	0.71	0.28	0.43
Diameter of prox. tubules (O.D.) (μm)	34	41	48.4	67
Ratio of diameter prox. adult/neonatal	1.4	1.2	—	1.97[1] (ratio to 1-day rhino)
Diameter of distal tubules (O.D.) (μm)	18.5	24	28	54
Ratio of diameter dist. tubule (adult/ neonatal)	1.5	1.17	—	2.9[1] (ratio to 1-day rhino)
Diameter of glomerular capsule (μm)	80.0	92.0	194.0	200.0
Ratio of diameter of glomerular capsule (adult/neonatal)	2.43	2.11	—	2.5[1] (ratio to 1-day rhino)

[1]Data for the human kidney are for comparison with those of the kidney of the neonatal rhino (see text).

Cortical medullary rays are about 250 μm apart at the medullary border and about 450 μm apart at the periphery.

The renal capsule is 14 μm thick and consists of collagen fibers. The interlobar septa are collagenous and about 14 μm thick. As in the adult, the septa form gaps which allow fusion of adjacent cortices. The cortices of three lobes meet along a septum typically forming 120°angles with one another.

The kidney of a newly born rhino has no nephrogenic zone. Thus, the 118-gm kidney contains the adult quota of about 16 million glomeruli. This is accomplished as follows (Table 2): 1) The volume of the glomerular capsule of the neonate is 14 times smaller than that of the adult; 2) the number of glomeruli per unit area of cortex is 11 times greater than in the adult; if translated into three dimensions, the difference would be still more; and 3) the width of the cortex is relatively greater in the neonate.

To convert from volume to mass, one multiplies by 1.060, the assumed specific gravity of tissue. The total mass of glomeruli in a kidney equals the volume of a glomerulus × number of glomeruli × 1.060. This value is 4.57 gm for the one-day-old rhino and 6.97 gm for the two-day-old rhino (Table 2). The mass of glomeruli per 100 gm of kidney is almost the same for neonates (3.88 and 4.05 gm) and adult (4.4 gm) (Table 2).

Although the 118-gm kidney of a one-day-old rhino is smaller than a normal adult human kidney of 150 gm, the former has over twelve times the number of nephrons. This is possible because of the small volume of the neonatal rhino glomerulus (13.4 times smaller than in the human adult) and the greater number of glomeruli per unit area of cortex in the neonatal rhino (11.6 times greater than in the human adult). Thus, 100 gm of kidney of one- and two-day-old rhinos and of the human adult have almost the same mass of glomeruli (Table 2).

An interesting feature is that growth of the kidney in a neonate apparently continues in spite of retarded body-mass. Thus, body-mass of the two-day handicapped rhino was 6 kg below that of the one-day rhino. Yet renal growth, as shown by increase in glomerular and tubular mass, evidently progressed (Table 2).

DISCUSSION

Kidney of Rhinoceros

Thomas (1801) noted that "the kidnies [of *R. unicornis*] were large and considerably flattened: they were lobulated, but their lobes did not appear as distinct as those of the same gland belonging to the bear: probably as the animal advances in life, this appearance may be altogether lost. . . ." In the fetal ox (Petit, 1924), renal lobes increase in number during development and can reach thirty. In the horse, an animal which does not have discrete renal lobes, the cortex becomes lobed during early fetal life and smooths out as the fetus grows (Schurian, 1925). During human fetal growth, renal lobes increase in number and size (Toldt, 1874; Heidenhain, 1937; Löfgren, 1949; Potter, 1972) and smooth out with further growth. The cortex of the domestic pig undergoes no lobation during development (unpublished data), even though its kidney has both papillae and calyces and is 86% cortex (Hollatz, 1922).

Owen (1862) described the kidneys of *R. unicornis* as "lobulated." He noted that the ureter divides into two canals and that "into this canal the common trunk of the radiating 'tubuli uriniferi' from the several lobes open without forming any valvular protuberance or 'mammilla'." The drawing by J. Erxleben of Owen's coronal cut (his Fig. 3 but mislabeled Fig. 2) indicates every lobe has its own orifice into the pelvic "canals." Owen (1862, 1868) did not indicate how the collecting ducts open into the pelvis and did not mention branchings of the pelvic conduits.

Hyrtl's (1870, 1872) observations were confined to casts of the pelvis by a viscous mass (Hyrtl, 1873). In Plate II of Hyrtl (1870, 1872), Figures 2 and 3 for horse and for "*Rhinoceros africanus*" should have their labels exchanged. He reported bifurcation of the rhino ureter into a cephalic conduit ("der obere Ast") and a shorter caudal conduit. He noted that each conduit branches into two calices majores and that each of the four c. majores divides into a pair of calices minores. The last are described as funnel-like invaginations which receive flat papillae ("flächer Papillae renales"). Hyrtl's minor calyces may be synonymous with the infundibula of this paper. His casts would not show the important medulla-adherent calyces.

Garrod (1873) remarked that the kidneys of an aged Sumatran rhino, *Ceratorhinus sumatrensis*, are nearly equal in size and "are lobulated externally." In *Rhinoceros sondaicus* Desm., of Java, Beddard and Treves (1890) noted merely that the "kidneys showed slight indication of lobulation." The kidneys of an *R. unicornis*, which died in 1905, thirteen years after Owen's death, are described in "Owen's Catalogue" of the Hunterian Museum (O.C. 1217) as having its "surface marked by connective tissue partitions but the lobulation does not extend below the surface except in so far as is indicated by the collection of urinary ducts into bundles or pyramids for the drainage of local areas. . . . Upon the wall of the main channel and its branches are numerous perforated areas through which the constituent collecting ducts of the medullary pyramids communicate with the cavity of the pelvis." The "perforated areas" are not described further. Sperber (1944) wrote (p. 365) that "Thus it would seem most probable that the Rhinoceros kidney is also composed of renculi. This conception is supported by my finding the kidneys of a *Diceros bicornis* embryo to be strongly lobated. They appear to be typical renculi kidneys but their inner structure is not so differentiated as to allow of any definite conclusion." Evidently, the rhinoceros kidney needs clarification.

Hyrtl and the Tubus Maximus

In his 1870 and 1872 papers, which are identical, Hyrtl originated the term "tubus maximus" for the duct receiving the terminal collecting ducts (of Bellini) along its course. He applied the term only to the kidneys of an elephant and gave no histological data. Strangely, he did not designate the fore and rear extensions ("vordere und hintere Verlängungscanal") of the equine renal pelvis as tubus maximus; nor did he use the term for the rhinoceros kidney.

The term "tubus maximus" is precise provided it is applied to a supreme collecting duct lined by collecting duct epithelium and with no definitive wall. The cephalic and caudal extensions of the equine renal pelvis qualify eminently since they have no definitive wall and

are lined by cuboidal epithelium similar to that of the equine terminal collecting ducts (unpublished data). On the other hand, the pelvic conduits of the rhinoceros kidney do not qualify since they have a definitive fibromuscular wall and are not penetrated by terminal collecting ducts. The receptacle for the terminal collecting ducts which empties into an infundibulum in the rhinoceros qualifies as a tubus maximus. The primary and secondary extensions of the diminutive pelvis of the pygmy hippopotamus, which has a lobated kidney, receive terminal collecting ducts and have an epithelial lining but no definitive wall (Maluf, 1978). They are thus primary and secondary tubi maximi.

Calyceal System of the Rhinoceros

At the calyceal rim, the muscle fibers run transversely; in the calyceal stalk they course longitudinally. Embraced by the medulla-adherent calyx are the central ends of the outer and inner medullae and at least the terminal end of the tubus maximus. There is no papilla. Only in the tubus maximus can urine contact the medulla. The rhino kidney has no vaults between calyx and medulla and has no way whereby the outer medulla can contact the pelvic urine. This is unlike the rat and other rodents in which both papilla and a large area of outer medulla, the latter forming large fornices, are exposed to pelvic urine (Bankir and de Rouffignac, 1985). Hypotheses applicable to murine papilla and medullary fornices (Schütz and Schnermann, 1972; Bonventre et al., 1980; Oliver et al., 1982; Bargman et al., 1984; Jamison, personal communication) thus may not be extended to mammals in general.

The calyceal rim presumably can squeeze the terminal ducts and tubus maximus while the calyceal stalk shortens: a "milking" action. This may be the effector end of a reflex induced by the conspicuous nerve bundles among the interlobar vessels.

Muscles of the human calyx were described by Henle (1873) who found that they extend from renal pelvis, within the calyceal wall, onto the collagen fibers of the adventitia surrounding arcuate arteries at the corticomedullary border. He illustrated the circular fibers ("Ringfasern") at the fornices. "That the contraction exerts pressure on the papilla, which contributes to the emptying of the tubules coursing through the papilla, leaves no room for doubt" (Henle, 1873). Wassink (1921) noted peristaltic waves of calyces and pelvis of the hypertrophied pelvis of a freshly excised dilated human kidney. Haebler (1922a,b,c) observed waves of contraction of the feline renal pelvis and described muscle fibers in the pelvis of various domestic mammals. He initiated the term "milking renal calyces." Steinhausen (1964) and Reinking and Schmidt-Nielsen (1982) observed in hamsters urine in papillary collecting ducts propelled by pelvic peristalsis, which also coincided with discontinuous flow of blood in the papillary vasa recta.

Narath (1951) objected to the milking hypothesis because "the musculus sphincter papillae is a delicate structure; it is very unlikely that it is able to exercise sufficient pressure to express the papilla, and the papilla is quite a rigid organ." In the rhinoceros, large intralobar veins are fused to the calyceal wall. This may allow the ring muscles of the calyceal rim to contract freely. Venous inflow would allow temporary expansion of the venous space between calyx and renal cortex. In man, ox, and elephant (unpublished data), large intralobar veins occur at the calyces. Analogy exists with the reciprocal relationship between pneumatic and venous sinuses at the base of the cetacean skull shown by Fraser and Purves (1954, 1960).

Urine

Renal osmotic power of rhinoceri is unkown. The Asiatic species live in grasslands and forests; the African species are subject to heat and intermittent drought. The only urinary analyses appear to be those of *R. unicornis* by Vogel (1817). Dry solids were 2.19% of the turbid yellowish urine. The content of urea and ammonium did not approach that of Carnivora. No sodium was reported, probably because there was very little in the diet. There was calcium, magnesium, potassium, silicon, and iron on one side and chloride, carbonate, phosphate, sulfate, and benzoic acid on the other. Quantitative data are lacking.

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LITERATURE CITED

Baer, P.G., G. Bianchi, and D. Liliana 1978 Renal micropuncture study of normotensive rats before and after development of hypertension. Kidney Internat., *13*:452–466.

Bankir, L., and C. de Rouffignac 1985 Urinary concentrating ability: insights from comparative anatomy. Am. J. Physiol., *249*:R643–666.

Bargman, J., S.L. Leonard, E. McNeely, C. Robertson, and R.L. Jamison 1984 Examination of transepithelial exchange of water and solute in the rat pelvis. J. Clin. Invest., *74*:1860–1870.

Beddard, F.E., and F. Treves 1890 On the anatomy of the Sondaic rhinoceros. Trans. Zool. Soc. Lond., *12*:183–198.

Bonventre, J.V., R.J. Roman, and C. Lechene 1980 Effect of urea concentration of pelvic fluid on renal concentrating ability. Am. J. Physiol., *239*:F609–618.

Brehm, A., ed. 1922 Brehm's Tierleben. Die Säugetiere. 3rd ed., Vol. 12. Bibliographisches Institut Leipzig. (This volume edited by L. Heck and J. Hilzheimer).

Burton, M. 1962 Systematic Dictionary of Mammals of the World. T.Y. Crowell, New York, 307 pp.

Clark, W.E. LeG. 1958 The Tissues of the Body, 4th ed. Clarendon Press, Oxford, 415 pp.

Denzer, H. 1935 Vergleichend messende Untersuchungen an Säugernieren. Würzburg, Richard Mayr, Ph.D. thesis, 33 pp.

Fourman, J., and D.B. Moffat 1971 The Blood Vessels of the Kidney. Blackwell Scientific Publ., Oxford, 161 pp.

Fraser, F.C., and P.E. Purves 1954 Hearing in cetaceans. Bull. Brit. Mus. (Natural Hist.), *2*:103–114.

Fraser, F.C., and P.E. Purves 1960 Hearing in cetaceans. Evolution of the accessory air sacs and the structure and function of the outer and middle ear in recent cetaceans. Bull. Brit. Mus. (Natural History), *7*:1–140.

Garrod, A.H. 1873 The visceal anatomy of the Sumatran rhinoceros. Proc. Zool. Soc. Lond., pp. 92–104.

Gruenwald, P., and H. Popper 1940 The histogenesis and physiology of the renal glomerulus in early postnatal life: Histological examina-

tion. J. Urol., *43:*452–458.
Grzimek, B., ed. 1968 (English ed. 1972) Animal Life Encyclopedia. Van Nostrand Reinhold, New York, Vol. 13, 566 pp.
Haebler, H. 1922 Zur Funktion der Nierenkelche. Z. Urol. Chir. *8:*315–316.
Haebler, H. 1922 Ueber die nervöse Versorgung der Nierenkelche. Z. Urol., *16:*377–384.
Hall, B.V. 1955 The organization of the renal glomerulus into indepedent lobular systems of intercommunicating anastomosing capillaries. Anat. Rec., *121:*433 (abstr.).
Heindenhain, M. 1937 Synthetische Morphologie der Niere des Menschen. E.J. Brill, Leiden, 270 pp.
Henle, J. 1862 Zur Anatomie der Niere. Dieterichschen Buchhandlung, Göttingen, 33 pp.
Henle, J. 1873 Handbuch der Eingeweidelehre des Menschen. 2nd ed. F. Vieweg u. Sohn, 926 pp (pp.300–335).
Henle, J. 1966. 1st ed. of above; not seen.
Hicks, R.M. 1965 The fine structure of the transitional epithelium of rat ureter. J. Cell Biol., *26:*25–48.
Hollatz, W. 1922 Das Massenverhältnis von Rinde zu Mark in der Niere des Menschen und einiger Säugetiere und seine Bedeutung für die Nierenformen. Z. Ges. Anat., I. Abt., *65:*482–494.
Hyrtl, J. 1870 Das Nierenbecken der Säugethiere und des Menschen. Kaiserlich-Königlichen Hof-und Staatsdrückerei, Wein, 36 pp.
Hyrtl, J. 1872 Das Nierenbacken der Säugethiere und des Menschen. Denkschr. Akad. d. Wissensch. Wien; math–naturw. Klasse, *31:*107–140.
Hyrtl, J 1873 Die Corrosions-Anatomie und ihre Ergebnisse. Wilhelm Braunmüller, Wien, 253 pp.
Kunkel, P.A., Jr. 1930 The number and size of the glomeruli in the kidney of several mammals. Bull. Johns Hopkins Hosp., *47:*285–291.
Leeson, C.R. 1962 Histology, histochemistry and electron microscopy of the transitional epithelium of the rat urinary bladder in response to induced physiological changes. Acta Anat., *48:*297–315.
Levinsky, N.G., and R.W. Berliner 1959 Changes in composition of the urine in ureter and bladder at low urine flow. Am. J. Physiol., *196:*549–553.
Löfgren, F. 1949 Das topographische System der malpigischen Pyramiden der Menschenniere. Hakan Ohlssons Boktryckerei, Lund, 200 pp.
Lydekker, R., ed. 1894 The Royal Natural History. F. Warne & Co., London, Vol. 2, 583 pp. (p. 467).
Maluf, N.S.R. 1953 Absorption of water urea, glucose and electrolytes through the human bladder. J. Urol., *69:*396–404.
Maluf, N.S.R. 1955 Further studies on absorption through the human bladder. J. Urol., *73:*830–835.
Maluf, N.S.R. 1978 Anatomy of the kidneys of a newly born pigmy hippopotamus, *Choeropsis liberiensis* Morton. Z. Vet. Med., C. Anat. Histol. Embryol., 7:28–48.
Maluf, N.S.R. 1981 Kidney of a juvenile okapi, *Okapia johnstoni.* Am. J. Anat., *161:*257–279.
MacDonald, M.S., and J.L. Emery 1959 The late intrauterine and postnatal development of human renal glomeruli. J. Anat., *93:*331–341.
Narath, P.A. 1951 Renal Pelvis and Ureter. Grune & Stratton, New York, 429 pp.
Oliver, R.E., D.R. Roy, and R.L. Jamison 1982 Urinary concentration in the papillary collecting duct of the rat. J. Clin. Invest., *69:*157–164.
Owen, R. 1862 On the anatomy of the Indian rhinoceros (*Rh. unicornis*, L.) Trans. Zool. Soc. Lond., *4:*31–58.
Owen, R. 1868 On the Anatomy of Vertebrates. Vol. III. Mammals. Longmans, Green, London, 915 pp.
Parsons, J. 1743 A letter from Dr. Parsons to Martin Folkes, Esq., president of the Royal Society, containing the natural history of the rhinoceros. Philos. Trans. Roy. Soc. Lond., pp. 523–54.
Peachey, L.D., and H. Rasmussen 1961 Structure of the toad's urinary bladder as related to its physiology. J. Biophys. Biochem. Cytol., *10:*529–553.
Petit, G. 1924 Remarques sur la morphologie comparée du rein due boeuf et du rein, du buffle. Arch. Anat. Histol. Embryol., *3:*493–501.
Potter, E.L. 1972 Normal and Abnormal Development of the Kidney. Year Book Medical Pub., Chicago, 305 pp.
Reinking, L.N., and B. Schmidt-Nielsen 1982 Peristaltic flow of urine in the renal papillary collecting duct of hamsters. Kidney Internat., *20:*55–60.
Rytand, D.A. 1938 The number and size of mammalian glomeruli as related to kidney and to body weight with methods of their enumeration and measurement. Am. J. Anat., *62:*507–520.
Schurian, W. 1925 Ueber Form- und Lageveränderungen der Nieren an Pferdefeten. Anat. Anz., *59:*522–528.
Schütz, W., and J. Schnermann 1972 Pelvic urine composition as a determinant of inner medulla solute concentration and urine osmolarity. Pflüg. Archiv, *334:*154–166.
Schweigger-Seidel, F. 1865 Die Nieren des Menschen und der Säugethiere in ihrem feineren Baue geschildert. H:Buchhandlung des Waisenhauses, Halle, 88 pp.
Sperber, J. 1944 Studies on the mammalian kidney. Zool. Bidrag., *22:*219–231.
Steinhausen, M. 1964 In vivo-Beobachtungen an der Nierenpapille von Goldhamstern nach intravenöser Lissamingrün-Injektion. Pflügers Arch., *279:*195–213.
Thomas, H.L. 1801 An anatomical description of a male rhinoceros. Philos. Trans. R. Soc. London, pp. 145–152.
Tischer, C.C. 1976 Anatomy of the kidney. In: The Kidney, Vol. I. B.M. Brenner and F.C. Rector, eds. Saunders, Philadelphia, Chap. 1.
Toldt, C. 1874 Untersuchungen über das Wachstum der Nieren des Menschen und der Säugethiere. Sitzungsber. der kaiserl. Akad. Wissensch. Wien. math.-naturwiss. Classe. III Abt. *69:*1–27.
Vacek, Z., and O. Schuck 1960 Histology and histochemistry of the transitional epithelium of the rat bladder in response to experimental filling. Anat. Rec., *136:*87–96.
Vogel, Prof. 1817 Analyse des Urins vom Rhinoceros und vom Elephanten. J. Chemie Physiol., *19:*156–165.
Waetzoldt, W. 1936 Dürer und seine Zeit. 3rd ed. Phaidon Verlag, Wein, 592 pp.
Walker, B.E. 1958 A comparative study of transitional epithelium with the electron microscope. Anat Rec., *130:*385; abstract.
Walker, E.P., and J.L. Paradiso eds. 1975 Mammals of the world. 3rd ed. Johns Hopkins Univ. Press, Baltimore, Vol. 2, p. 1351.
Wassink, W.F. 1921 Ueber Peristaltik des Nierenbeckens. Nederlandsch. Tijdschrift voor Geneeskunde, *65:*29–31.