

## Kidney of the Sumatran Rhinoceros, *Dicerorhinus sumatrensis*

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**ABSTRACT** The kidney of *Diceros sumatrensis* has the rhinocerotid form and lobation. The ureter divides intrarenally into two fibromuscular conduits which receive, at separate loci, the terminal collecting ducts of the lobes. The kidney is 67% cortex. Total renal mass is 0.46% of body mass. There are about 34 lobes and 23 primary orifices at the conduits. Glomeruli are relatively small and of the same size across the cortex. They number about 14.6 million in one kidney but the glomerular mass is relatively low. Unlike other rhinocerotid species, the kidney of *D. sumatrensis* lacks interlobar septa. The interlobar arteries nevertheless enter the renal parenchyma as in the other rhinoceroses, i.e., between the cortices of adjacent lobes rather than in the common mammalian manner between cortex and medulla. Thus, internal "perforator" arteries pass from cortical periphery to interior giving off cortical twigs on their way to the corticomedullary border, along which they branch while releasing centrifugal arteries back toward the cortical periphery. The arcuate veins are wide centrally where they enter the paraconduital veins. The latter form prominent central anastomoses between the large interlobar veins. © 1993 Wiley-Liss, Inc.

*Dicerorhinus sumatrensis* is the smallest of the five existing species of rhinoceros (Flower and Lydekker, 1891; Osborn, 1898). Of the three Asiatic species, it is the only one with two horns. Unlike the others, it is partly covered with hair. Osborn (1898), partly from the study of rhinocerotid skulls by Flower (1876), remarked that *D. sumatrensis* is the most primitive living rhinoceros. In the nineteenth century, *D. sumatrensis* extended throughout the tropical rain forests of southeast Asia (Anderson, 1872; Pfeffer, '68), but it now appears to be on the verge of irretrievable extinction (Hutchinson and Ripley, '54).

Some of the anatomy of *Dicerorhinus sumatrensis* was described by Bell (1793), Beddard and Treves (1889), and Hubback ('39). The only known statements on the kidneys of *D. sumatrensis* are by Home (1821): "The Kidneys are conglomerate and rather longer than common," and by Garrod (1873) for an aged female: "The kidneys are flattened and oval in form. One is 6 inches broad by 9 inches long. They are nearly equal in size and together weigh 10 lbs. The hilum is linear and on the inferior surface, not at the margin. They are lobulated externally, but not so much as in Seals." Availability of excellent kidneys of this rare rhinoceros and a recent study of the kidneys of three other rhinocero-

tic species (Maluf, '87, '89a, '91a) prompted this investigation.

### MATERIALS AND METHODS

The intact right kidney was that of a normally nourished preadult female *Dicerorhinus sumatrensis* (No. 30915) which died from acute peritonitis caused by torsion of the large colon apparently secondary to a large lipoma at the ileocolic junction. Necropsy was on day of death. The kidney was received frozen from San Diego. Before use it was thawed in a refrigerator at about 4°C. Sections of the left kidney, which had been fixed in buffered 4% aqueous formaldehyde, were used for some of the histological examinations. A portion of kidney of an adult female *D. sumatrensis* (No. 92-53), fixed in 4% formaldehyde, was received from Cincinnati. The above numerals are the necropsy numbers.

After the intact kidney was thawed, it was measured and the ureter, renal artery, and renal vein were cannulated and repeatedly perfused gently with small amounts of 10% aqueous formaldehyde totalling 700 ml. Width of the renal vein (Fig. 4, RV) necessitated applying a purse-string suture through its wall around a wide cannula to prevent leakage. The kidney was returned to the refrigerator and radiographs (see below) taken the following morning. After injection of the

pigments (see below), the kidney was refrozen and cut midcoronally, i.e., medial border to lateral border, with a long, thin, flat knife. The entire hilum, being ventromedial, was retained with the ventral coronal half.

Some structures were measured on the coronally cut surfaces and the latter inspected with the dissecting microscope using fiberoptic illumination. The kidney was dissected using a pair of watch-maker's forceps, a straight ophthalmic scissors, and a curved dull probe. A fine geometrical divider with set-screw was used for measurements.

For radiography, the kidney was placed about 5 cm above the cassette. A radiopaque liquid (60% Hypaque® meglumine of Winthrop Pharmaceuticals, a water-clear solution of organically bound iodine) was injected into the ureteral (for pyelogram), arterial, and venous cannulae and radiographs taken in that sequence. Past experience guided the volumes injected: 44 ml for the ureter, 20 ml for the artery, and 25 ml for the vein. The volume for the ureter, producing the pyelogram (Fig. 9), nevertheless resulted in filling of infundibula and terminal collecting ducts. It is practically impossible to avoid this flux into wide terminal collecting ducts (Maluf, 1991a).

The renal artery and vein were injected with aqueous acrylic emulsions (Winsor and Newton®) that had been diluted to the consistency of thin cream: cobalt blue (oxides of cobalt and chromium) into the vein and cadmium red (cadmium sulpho-selenide) into the artery. These tissues were injected immediately after radiography and this proved valuable during dissections. The red pigment did not pass the afferent arterioles to reach the glomeruli. Intralobular and arcuate veins were well injected. No pigment entered the medullae.

Paraffin-embedded tissue was sectioned at 5  $\mu$ m intervals. Stains for the right kidney (No. 30915) and for the portion of kidney from the Cincinnati specimen (No. 92-53) were modified Masson's ('29) trichrome (cf. Luna, '60) to differentiate smooth muscle from collagen, Verhoeff's stain ('08) for elastin, and periodic acid-Schiff (Sheehan and Hrapchak, '80) for glomerular capsules. Pieces of the left kidney (No. 30915) had been fixed at necropsy time in buffered neutral 4% aqueous formaldehyde. Sections of these were stained with hematoxylin and eosin. Careful measurements of tissues fixed in 10% aqueous formaldehyde (right kidney), before and after histological sectioning, indicated shrinkage of less than 10%.

Glomerular measurements were from the histological sections of the left kidney. Only the largest glomeruli were selected as these likely had been cut through their meridian. The average of two diameters of the spheroidal glomeruli was taken: the longest diameter and the diameter at right angle to it. The volume of a sphere in  $\text{mm}^3$  was multiplied arbitrarily by the density value of 1.060 to obtain its mass in mg.

The entire cranial half of the dorsal coronal half of the right kidney was saved for measurement of mass of cortex and of medulla. This was cut transversely into sections of less than 10 mm. Cortex was distinguished from medulla by texture and by separation of the two regions by arcuate vessels which were colored by the injected pigments. The pieces were mopped carefully with absorbent paper and weighed to the nearest milligram.

Methods for counting of glomeruli have been described (Maluf, '89b, '91a,b). Briefly, a few grams of central cortex of the right kidney are weighed and gradually disintegrated with 7.4 N (27%) HCl at room temperature. The resultant suspension is diluted with 0.9% NaCl to known volume and the number of glomeruli in 50 0.010 ml aliquots, taken up with a calibrated Gibson pipette (Rainin Instruments, Woburn, MA), was recorded.

Tissues were macerated only for study of the medulla (Maluf, '91a,b). Thin slices, including both cortex and medulla, were immersed in 7.4 N HCl until the tissue became soft enough that it could not be grasped. The acid was drained and the tissue washed carefully with 0.9% NaCl. Fine (4-0) steel entomological pins fitted into needle-holders served for dissection.

## RESULTS

### General

The kidneys of the four species of Rhinocerotidae have characteristics quite peculiar to the family. They consist of numerous, closely juxtaposed lobes, all of which are present at the surface. The terminal collecting ducts of the lobes drain into a cranial and a caudal fibromuscular conduit (Fig. 9, P<sub>1</sub>, P<sub>2</sub>), which apparently result from bifurcation of the ureter within the renal sinus. The conduits may branch into infundibula and, thus, receive the drainage of more lobes than the number of orifices at the conduits (Maluf, '87, '91a).

The kidney of *Dicerorhinus sumatrensis* is flat dorsoventrally (Figs. 2-3, Table 1). The cranial and caudal poles CF and CD are contiguous medially (Figs. 1, 2, 4) and are sup-

TABLE 1. *Dicerorhinus sumatrensis*. General data<sup>1</sup>

Age (years) and sex	ca. 8; F
Body mass (kg) <sup>2</sup>	630
Kidney	Right
Mass of kidney (g)	1,541
Mass of both kidneys (g)	2,891
Renal mass percent of body mass	0.46
Length of kidney (mm)	270
Greatest width of kidney (mm)	150
Greatest thickness of kidney (mm)	50
Length of hilum (mm)	82
Distance of greater curvature of kidney to pelvic conduit (mm)	35.9 ± 3.5 (n = 12)
Distance of lesser curvature of kidney to pelvic conduit (mm)	37.8 ± 3.8 (n = 6)
Average distance to pelvic conduit (height of lobes) (mm)	36.9 ± 3.7 (n = 18)
No. of lobes/kidney	ca. 34

<sup>1</sup>Data in Tables 1—5 are for *D. sumatrensis* No. 30915.

<sup>2</sup>Body mass of a fully grown adult *D. sumatrensis* is reported as 800–1,000 kg (Burton, '62; Nowak, '91). Macdonald ('84) puts it at 800 kg maximally. The adult female at Cincinnati was about 800 kg but had been losing weight owing to illness evidenced by jaundice.

ported in this manner by strong perirenal fascia, which makes the kidney tightly C shaped. The hilum is ventromedial (Figs. 1, 2, 4; Table 1). After removal of the perirenal fascia, lobation becomes most evident at the lateral border (Fig. 3) and at the caudal half of the medial border (Fig. 2). There is no strictly longitudinal sulcus along either border (Figs. 2, 3). Fat occurs at the hilum and within the renal sinus where it surrounds the blood vessels and ureter before these enter the parenchyma.

Sulci between lobes are indistinct at the ventral (Fig. 1) and dorsal surfaces. Unlike the cortices of adults of three other species of rhinoceros (Maluf, '87, '89a, '91a), the cortices of adjacent lobes are not separated by interlobar septa. This was confirmed by use of the dissecting microscope and by histological sections. Only one example of an interlobar septum was found. Thus, the cortices of adjacent lobes of *Dicerorhinus sumatrensis* are fused into a continuous mass. Cortical partitions or plicae corticales (Heidenhain, '37) separate the medulla of every lobe (Fig. 5C), as they do in the kidneys of humans (Bertin, 1774)<sup>1</sup> and oxen.

The pyelogram (Fig. 9) displays lobation similar to that of three other species of rhinoc-

eros which, however, have prominent interlobar septa (Maluf, '89a, '91a, and unpublished). Terminal collecting ducts of apparently every lobe are evident owing to influx of the radio opaque solution. The subsequent midcoronal cut of the kidney confirmed the pyelogram.

All lobes appear at the renal surface, which includes the renal sinus. Absence of interlobar septa, however, makes an exact count of lobes uncertain. The pyelogram (Fig. 9) and the coronal cuts nevertheless indicate about 34 lobes.

The kidneys of preadult *Dicerorhinus sumatrensis*, stripped of extraneous fascia, are large relative to its body mass (Table 1). Fraction of renal mass of adult body mass of various mammalian species nevertheless tends to vary inversely with body mass (Maluf, unpublished).

#### Ureter and pelvic conduits

The muscular ureter (Figs. 1, 2, U; Table 2), enters the renal hilum equidistant between the cranial, T, and the caudal, B, extremities of the kidney. Within the renal sinus, the ureter crosses the lobes of the lesser curvature (Figs. 4, 9–12, U). It deviates cranially and expands slightly (Fig. 9, U) before bifurcating into a cranial, P<sub>1</sub>, and a caudal, P<sub>2</sub>, conduit. The outer half of the muscular layer (Table 2) is composed of thick circular bundles (Fig. 16) which, when viewed under higher power (×400), are seen to consist chiefly of longitudinal and oblique muscle fibers (Fig. 17). The inner half is composed mainly of circular and oblique fibers and some longitudinal ones. The muscular bundles are interspersed with collagen fibers; elastic fibers are scant or absent. The portion of the ureter within the renal sinus has a thinner muscularis than the hilar portion (Table 2).

The pelvic conduits course centrally throughout the curvature of the kidney. Thus, the distance from the greater curvature of the kidney to the pelvic conduits is equal to that of the lesser curvature to the conduits. Because the lobes usually end at the conduits (Fig. 5), this distance defines the average height of the lobes (Table 1). The conduits are also equidistant from the dorsal and ventral surfaces of the dorsoventrally flat kidney.

The wall of the pelvic conduits (Table 2) is lined by urothelium (Fig. 13) and is composed almost entirely of closely packed longitudinal and oblique muscle fibers (Fig. 14), as it is in the three other species of rhinoceros.

<sup>1</sup>Bertin (1744), in a classical paper, named the cortical partitions, between the medullae of the human kidney, *cloisons* and never *colonnes*. Obviously, these are not columns (circular pillars) but developmentally cortical folds (*plicae corticales*) which enclose the medulla of every lobe (Heidenhain, '37). The Latin term appropriately could be *partitio renalis* (renal partition) or *loculus renalis* (renal compartment). The common current latinization, *columnae renales Bertini*, is not only incorrect anatomically but deprives Bertin of his nationality.

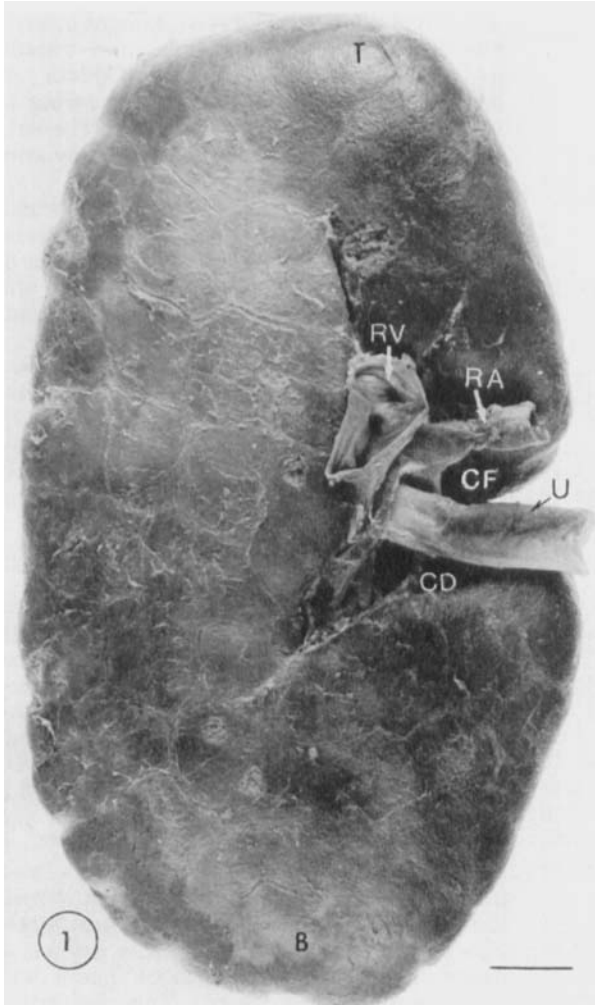
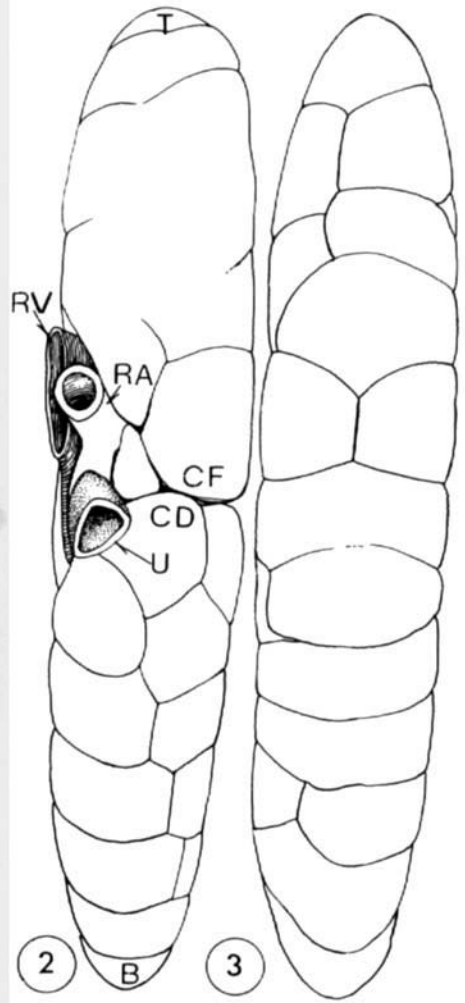


Fig. 1. *Dicerorhinus sumatrensis* (No. 30915). Ventral aspect of right kidney. Perirenal fascia has been removed and hilar structures have been clarified by dissection. CD, caudal pole; CF, cranial pole; RA, renal artery; RV, renal vein; U, ureter. Bar = 22.7 mm.

Fig. 2. *Dicerorhinus sumatrensis* (No. 30915). Medial border of right kidney showing contiguity of cranial



(CF), and caudal (CD) poles. Hilar structures are at the ventromedial border. B, caudal extremity of kidney; RA, renal artery; RV, renal vein; T, cranial extremity of kidney; U, ureter.

Fig. 3. *Dicerorhinus sumatrensis* (No. 30915). Lateral border of right kidney.

Unlike the ureter there is very little admixture of collagen fibers among the muscle fibers.

The conduits are enveloped loosely by areolar fascia, through which pass interlobar arteries, interlobar veins, and nerves. The central portions of the cortical partitions (of Bertin), covered with a thinned renal capsule, are imbedded in this areolar fascia and may contact the conduits unless blood vessels and nerves interpose (Fig. 5).

Lengths of the pelvic conduits, measured by a malleable ruler, are indicated in Table 2. Because the ureter deviates cranially (Figs. 9–12, U) the cranial conduit,  $P_1$ , is shorter than the caudal one,  $P_2$  (Fig. 9). The internal diameter of the conduits diminishes as the conduits extend to the cranial and caudal poles of the kidney (Table 2, Fig. 9). Estimated capacity of the conduits is based on their total length and approximate average diameter of 7 mm (Table 2). The amount of

TABLE 2. *Dicerorhinus sumatrensis*. Data for ureter and pelvic conduits

Cranial crest of kidney to ureter at hilum (mm)	135
Caudal crest of kidney to ureter at hilum (mm)	135
Ureter, distended, at hilum, outer diam. (mm)	17
Thickness of ureteral tunica muscularis at hilum ( $\mu\text{m}$ )	538
Thickness of ureteral tunica propria at hilum ( $\mu\text{m}$ )	563
Thickness of urothelium, stretched ( $\mu\text{m}$ )	5.7
Thickness of ureteral wall at renal sinus ( $\mu\text{m}$ )	190
Thickness of ureteral muscularis at sinus ( $\mu\text{m}$ )	120
Thickness of wall of pelvic conduit ( $\mu\text{m}$ )	348
Internal diam. of pelvic conduit (mm)	5.5 to 8
Length of cranial conduit (mm)	173
Length of caudal conduit (mm)	240
Capacity of both conduits ( $\text{cm}^3$ )	16
No. of primary orifices at conduits	23
Diam. of the orifices (mm)	$4.2 \pm 1.0$ (n = 8)

contrast solution ( $44 \text{ cm}^3$ ) infused during pyelography through the hilar ureter distended the entire kidney slightly, although most of the volume was taken up by the large and distensible proximal stump of the ureter.

The total number of orifices (Fig. 5, OR) at the conduits, including those at the terminal ends of the conduits and including both coronal halves of the kidney is less than the number of lobes. The orifices occur at all surfaces of the conduits along the greater and lesser curvatures. They are nearly circular in shape with pores up to  $375 \mu\text{m}$  wide, at which the terminal collecting ducts open (Fig. 6). Every orifice has a partial operculum (Fig. 8, O) that is directed to favor flow of urine toward the ureter. The thickness of the operculum is about  $114 \mu\text{m}$  at its base; it is composed of longitudinal and oblique muscle fibers, contains very little connective tissue, and is lined by urothelium. Some orifices lead to short infundibula (Fig. 11, IF) and some receive more than one lobe, thus accounting for the excess number of lobes.

#### Cortex

The cortex comprises 67% of the renal parenchyma (Table 3). It extends centrally along the sides of the medulla of a given lobe toward the pelvic conduits, being separated from the conduits by a thin renal capsule, areolar fascia, interlobar vessels, and nerves (Fig. 5, C). There are essentially no interlo-

bar septa and the cortex is continuous throughout the kidney.

The average size of glomeruli is constant from periphery of the cortex to the juxtamedullary border (Table 3). Number of glomeruli per kidney in *Dicerorhinus sumatrensis* (Table 3) is within the range of the other species of rhinoceros (Maluf, '87, '91a). The glomeruli of *D. sumatrensis* (No. 30195) are, however, small (Fig. 15). Thus the mass of glomeruli per unit mass of cortex or of kidney is relatively low (Table 3). In the kidney of the adult female from Cincinnati (No. 92-53), most of the glomeruli appear essentially normal. Diameters here are  $198.7 \mu\text{m} \pm 22.3$  (n = 18) for glomerular capsules and  $197.8 \mu\text{m} \pm 7.8$  (n = 18) for glomerular tufts. Assuming this animal has the same number of glomeruli as No. 30195 and that the mass of its renal parenchyma is 67% cortex, then its glomerular mass is 3.11% of renal mass and 4.64% of cortex. Both values are rather low and this probably is due to the relatively small glomeruli.

#### Medulla

The medulla is divided into lobar compartments by the cortical partitions (Fig. 5, M) and comprises one third of the renal parenchyma (Table 4).

The ratio of width of cortex to length of medulla (i.e., across the length of a lobe) is 0.25 (Table 4, Fig. 5, M). This linear ratio is misleading because the cortical mass is actually more than double the medullary mass. This can be demonstrated by modelling any lobe in Figure 5 as a conic frustum. The volume of such a frustum is given by the formula (Camm, '60):  $C = \frac{1}{12} \Pi h (D^2 + Dd + d^2)$ ; here C is the volume, h the height, D the greater diameter, and d the lesser diameter. The volume of lobe minus volume of medulla equals volume of cortex. Taking an exemplary lobe L from Figure 5, the volume of lobe =  $1,877 \text{ mm}^3$  and of the medulla =  $469 \text{ mm}^3$ . Therefore the volume of its cortex =  $1,408 \text{ mm}^3$ , which is 75% of its lobar volume or mass.

The average length of the medullae is 24 mm and of the outer medullae, with the vascular bundles, is about 9 mm. This would imply that the longest thin medullary loops (Henle) reaching the areae cribrosae measure about 15 mm. Thick loops occur between 4,000 and 9,000  $\mu\text{m}$  from the cortico-medullary border.

Terminal collecting ducts at the areae cribrosae vary in diameter (Table 4). Those

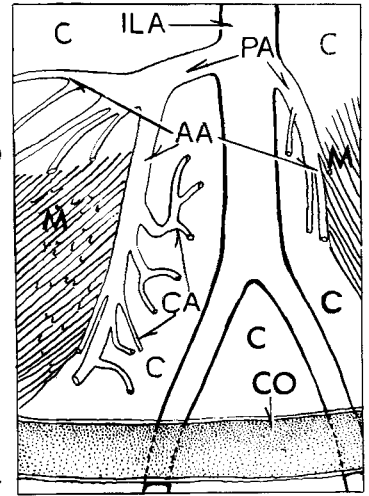
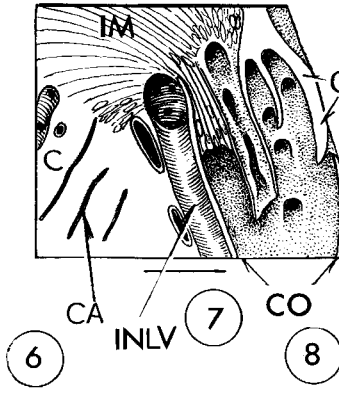
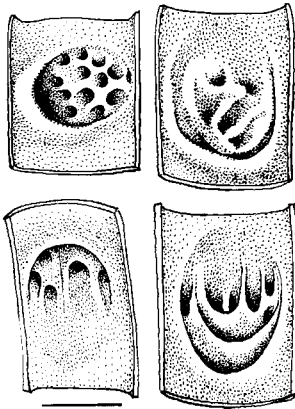
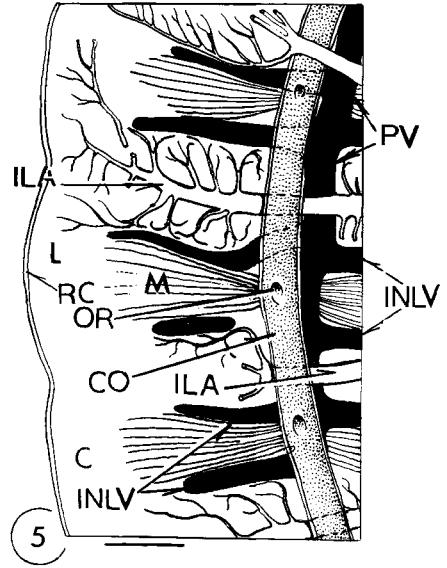
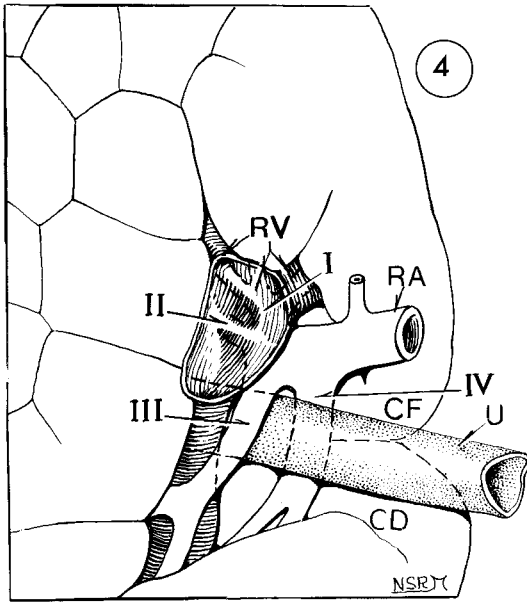


Fig. 4. *Dicerorhinus sumatrensis* (No. 30915). Hilum of right kidney. Ureter is stippled; renal vein and tributaries are striped; renal artery and its branches are white. The four early branchings of the renal artery are indicated by Roman numerals I to IV; branches I and II are obscured by overlying renal vein. CD, caudal pole; CF, cranial pole; RA, renal artery; RV, renal vein. I-IV, the primary branches of the renal artery. Bar = 20 mm.

Fig. 5. *Dicerorhinus sumatrensis* (No. 30915). Dissection of dorsal surface of mid-coronal cut of kidney showing part of pelvic conduit (CO), interlobar arteries (ILA), arcuate (intralobar) veins (INLV), and paraconduital vein (PV). The conduit is stippled; the veins are black; the arteries are white. The paraconduital vein(s) drain into the large interlobar veins (Figs. 11, ILV, 12). C, cortex; L, a lobe; M, medulla. Bar = 6.9 mm.

Fig. 6. *Dicerorhinus sumatrensis* (No. 30915) Areae cribrosae of orifices at lumen of pelvic conduits. An operculum only partially covers every orifice. Bar = 3.4 mm. Fig. 7. *Dicerorhinus sumatrensis* (No. 30915). Longitudinal cut through a single orifice of the pelvic conduits showing area cribrosa and its relations. C, cortex; CA, centrifugal artery; CO, pelvic conduit; IM, inner medulla; INLV, intralobar veins; O, operculum. Bar = 2.6 mm.

Fig. 8. *Dicerorhinus sumatrensis* (No. 30915). Dissection of an interlobar artery (ILA), showing arterial supply to two adjacent renal lobes. AA, arcuate artery; C, cortex; CA, centrifugal arteries; CO, pelvic conduit; ILA, interlobar artery; M, medulla; PA, "perforating artery." Bar = 5.0 mm.

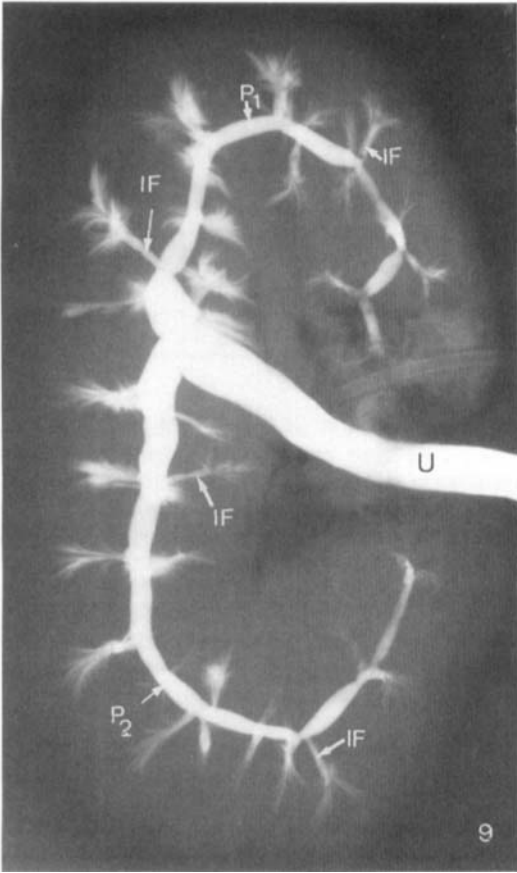


Fig. 9. *Dicerorhinus sumatrensis* (No. 30915). Pyelogram of right kidney. Contrast medium has fluxed into collecting ducts at the areae cribrosae. IF, infundibulum; P<sub>1</sub>, P<sub>2</sub>, cranial and caudal pelvic conduits, respectively; U, ureter. Bar = 23.5 mm.

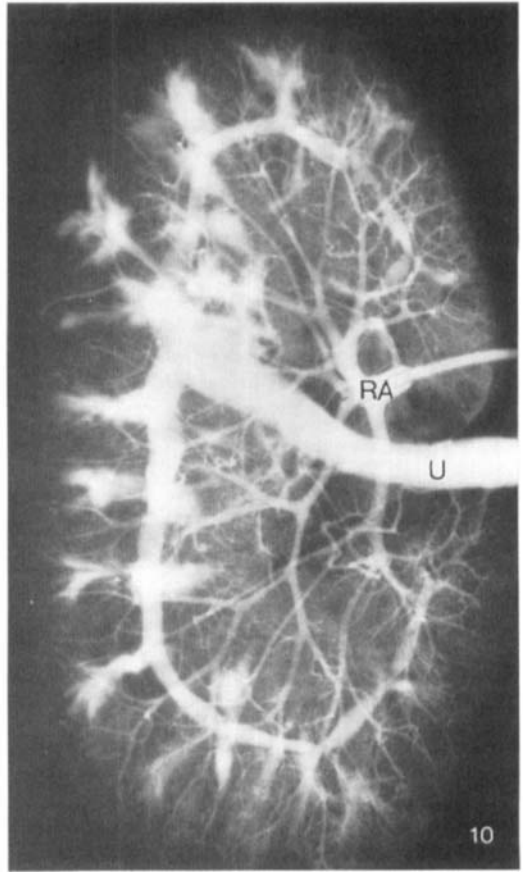


Fig. 10. *Dicerorhinus sumatrensis* (No. 30915). Arteriogram superimposed on pyelogram of right kidney. RA, renal artery; U, ureter. Bar = 23.5 mm.

with large diameters include the terminal pores at the flat or slightly concave areae cribrosae (Figs. 6, 7).

#### Vasculature

At the hilum, the renal artery (Figs. 4, 10, RA) gives off four major branches (Fig. 4, I–IV), which bifurcate twice within the renal sinus and become interlobar arteries (Figs. 5, ILA, 10). The latter arteries (Table 5), usually enter the renal parenchyma between the cortices of adjacent lobes (Figs. 5, 8, ILA). In *Dicerorhinus sumatrensis*, the interlobar arteries take the same course as in the other rhinoceroses (see Discussion) but have no interlobar septum through which to pass (Figs. 5, 8, ILA). The “internal perforating” arteries of *D. sumatrensis*, while supplying

the cortex with direct twigs, continue to the corticomedullary (C-M) border; here they become branching arcuate arteries parallel with the C-M border and give off branches centrifugally (Fig. 8, CA).

The renal vein (Figs. 1, 2, 4, RV) is large and thin walled, and lies ventral to the renal artery. Its wide tributaries define the extent of the renal hilum (Fig. 4). Within the renal sinus its tributaries receive wide interlobar veins (Figs. 11, ILV, 12). The latter drain the wide paraconduital veins (Figs. 5, 11, 12, PV) which course along the pelvic conduits. In the radiograph shown in Figure 11, the paraconduital veins are partially obscured by the pelvic conduits. The arcuate veins course between cortex and medulla, in the typical mammalian manner, and enter the paraconduital

TABLE 3. *Dicerorhinus sumatrensis*. Data for cortex

Renal capsule, thickness ( $\mu\text{m}$ )	113
Cortex percent of renal parenchyma	67.1
Peripheral thickness of cortex (mm)	$6.1 \pm 1.4$ (n = 21)
Diam. of peripheral glomerular capsules ( $\mu\text{m}$ )	$161.1 \pm 8.6$ (n = 6)
Diam. of mid-cortical glomerular capsules ( $\mu\text{m}$ )	$153.0 \pm 13.0$ (n = 6)
Diam. of juxtamedullary glomerular capsules ( $\mu\text{m}$ )	$157.7 \pm 5.8$ (n = 6)
Average diam. of glomerular capsules ( $\mu\text{m}$ )	$157.3 \pm 9.1$ (n = 18)
Mass of a glomerular capsule (mg)	0.00216
No. of glomeruli/low power field of cortex at $35 \times$ (diam. of field $\sim 2,560 \mu\text{m}$ )	$12.9 \pm 1.4$ (n = 18)
No. of glomeruli/kidney	14,558,720
Mass of glomeruli (g)/kidney	31.4
Mass of glomeruli percent of cortex	3.04
Mass of glomeruli percent of kidney	2.04
Cortex corticis, thickness ( $\mu\text{m}$ ) (essentially absent)	< 60

veins. Centrally the arcuate veins are quite large and hence may be termed intralobar (Table 5; Figs. 5, 7, INLV).

Scattered minute blood vessels perforate the renal capsule, especially at the dorsal surface. There are no subcapsular stellate veins and no external perforating vessels of large or moderate size.

#### DISCUSSION *Comparative*

Each of the three families of Perissodactyla has a distinctly characteristic renal collecting system. The terminal collecting ducts of the non-lobed smooth kidney of the Tapiridae all open at a medullary crest (Maluf, '91b). The Equidae (horses, zebras, and asses) are generally larger than tapirs and have larger non-lobed kidneys. The relatively small

TABLE 4. *Dicerorhinus sumatrensis*. Data for medulla

Medulla % of renal parenchyma	32.9
Length of medulla (mm)	$24.4 \pm 4.2$ (n = 17)
Width of medulla, widest (mm)	$11.0 \pm 4.2$ (n = 17)
Ratio of width of cortex/length of medulla	0.25
Length of outer medulla (mm)	9
Terminal collecting ducts, outer diam. ( $\mu\text{m}$ )	61 to 374
Thick medullary loops, outer diam. ( $\mu\text{m}$ )	35
Thin medullary loops, outer diam. ( $\mu\text{m}$ )	17.4
Distance between limbs of a loop ( $\mu\text{m}$ )	8 to 87

TABLE 5. *Dicerorhinus sumatrensis*. Data for vasculature

Renal artery, outer diam. (mm)	14
Renal artery, inner diam. (mm)	10
Wall-thickness of renal artery ( $\mu\text{m}$ )	1,536
Thickness of media of renal artery ( $\mu\text{m}$ )	1,280
Interlobar arteries, outer diam. (mm)	1.8 to 3.5
Renal vein, diam. (mm)	22
Interlobar renal veins, diam. (mm)	4 to 10
Paraconduital renal vein(s), diam. (mm)	2.5 to 5
Intralobar (i.e., proximal arcuate) renal vein, diam. (mm)	2.5 to 3.2
Distal arcuate renal veins (mm)	To 1.2

medullary crest of the Equidae is extended cranially and caudally as a relatively wide *tubus maximus* at which the terminal collecting ducts open. In addition the equid kidney acquires more length by tending to become C shaped. The Rhinocerotidae are still larger mammals and have multilobed C-shaped kidneys. The terminal collecting ducts of every lobe open at localized *areae cribrosae* and/or *tubi maximi* at the cranial and caudal fibromuscular conduits. The latter can branch into primary and secondary infundibula and thus receive the *areae cribrosae* and/or *tubi maximi* of additional lobes (Maluf, '87, '91a). These fibromuscular conduits, which result from an intrarenal bifurcation of the ureter, are characteristic of the rhinocerotid kidney.

The kidney of the smallest living rhinoceros, *Dicerorhinus sumatrensis*, is distinctly lobed but has essentially no interlobar septa. On the other hand, the considerably larger kidneys of the great Indian rhinoceros, *Rhinoceros unicornis* (Maluf, '87), the broad-lipped African rhinoceros, *Ceratotherium simum* (Maluf, '89a), and the hook-lipped African rhinoceros, *Diceros bicornis* (Maluf, '89a, '91a), have interlobar septa which extend, with some interruptions, peripherally from the renal capsule to the base of every lobe adjacent to the pelvic conduits. Interlobar septa add to stability of a large kidney but preclude venous anastomoses between adjacent lobes.

The cortices of contiguous lobes of *Dicerorhinus sumatrensis* are fused, thus forming a continuous cortical mass as in the kidney of humans and oxen and as the central portions of adjacent lobes of manatees (Maluf, '89a). Yet the interlobar arteries of *D. sumatrensis* have the rhinocerotid characteristic of coursing between the cortices of contiguous lobes rather than entering the renal parenchyma



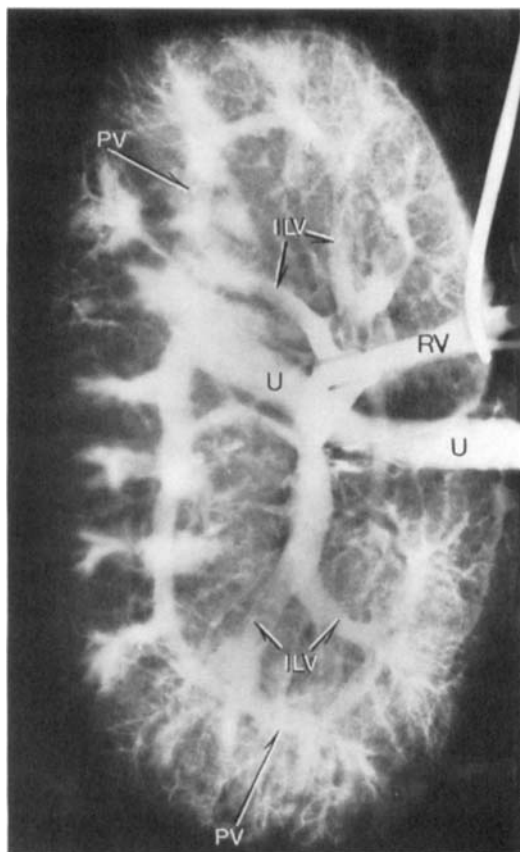


Fig. 11. *Dicerorhinus sumatrensis* (No. 30915). Phlebogram superimposed on arteriogram and pyelogram of right kidney. IF, infundibulum; some infundibula extend from an area cribrosa; ILV, interlobar veins. Bar = 23.5 mm.

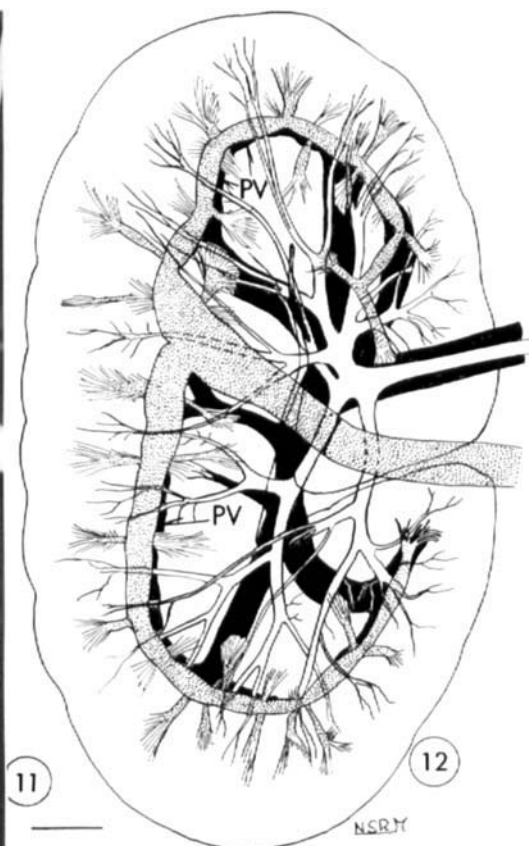
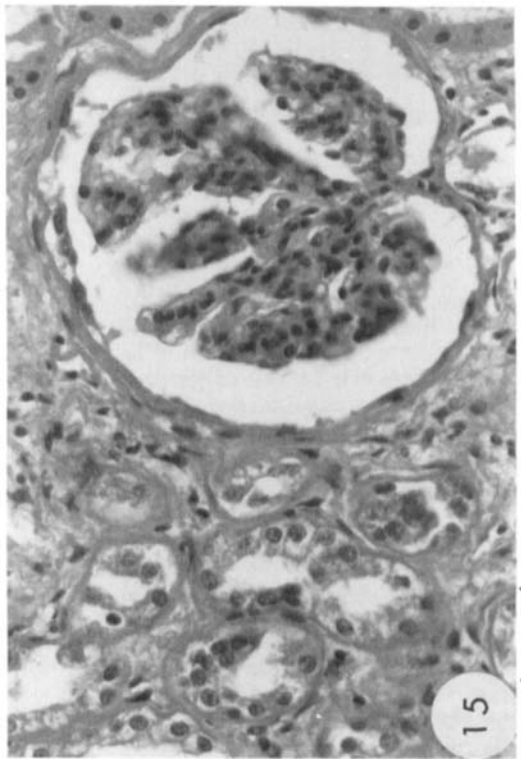
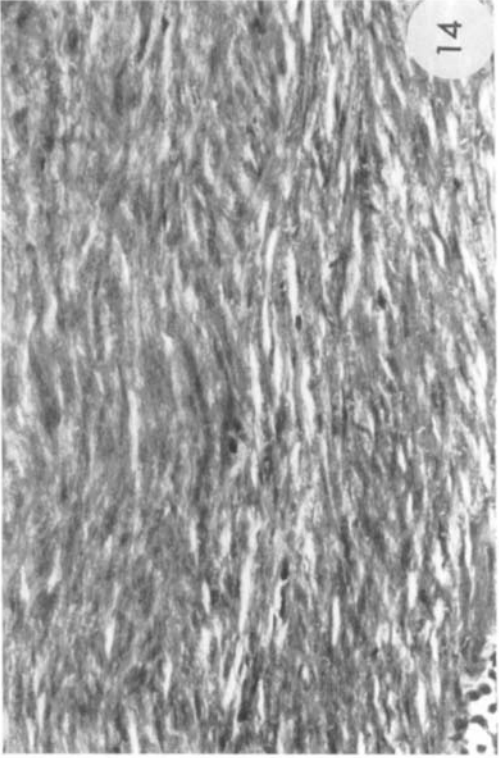
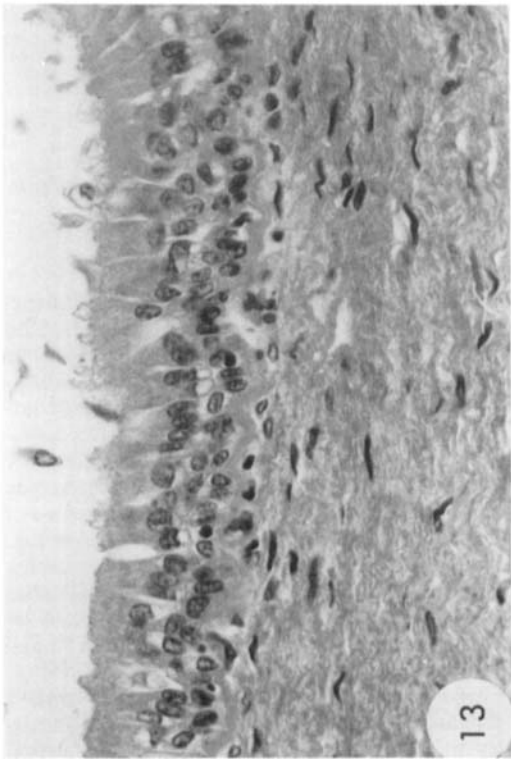


Fig. 12. *Dicerorhinus sumatrensis* (No. 30915). Tracings of the pyelogram (stippled), arteriogram (white), and phlebogram (black) superimposed on each other to define relations which were confirmed by dissection. PV, para-conduital vein.

between cortex and medulla in the common mammalian manner (Bertin, 1744; Henle, 1873; Gérard, '11; Ljungvist and Lagergren, '62; and others). In the other rhinoceroses (*Rhinoceros unicornis*, *Diceros bicornis* and *Ceratotherium simum*), the interlobar arteries pass through the interlobar septa and supply internal perforator arteries to the adjacent cortices necessarily through the septa (Maluf, '89a, '91a). In *D. sumatrensis* branches of the interlobar arteries similarly pass between contiguous cortices but, in doing so, have no septum to perforate. They are designated internal "perforators" here to indicate homology with similar arteries of the other rhinoceroses.

The number of lobes exceed the number of orifices at the conduits in *Dicerorhinus suma-*

*trensis* and in three other species of rhinoceros (Maluf, '87; '91a; and unpublished). The kidney of *Diceros bicornis* and *Rhinoceros unicornis* shows significantly more branching of infundibula than that of *D. sumatrensis*. Associated with this is the greater number of lobes in *D. bicornis* and the markedly greater number in *Rhinoceros unicornis* (Maluf, '87 and unpublished). Average size of glomeruli is constant across the renal cortex. *Dicerorhinus sumatrensis* thus resembles *Rhinoceros unicornis* (Maluf, '87), *Diceros bicornis* (Maluf, '91a) and *Ceratotherium simum* (unpublished). This also applies to the neonatal *R. unicornis* and *Diceros bicornis* and to the newly born at term of *C. simum* (personal observations). Relative renal maturity in the newly born rhinoceros is associ-



Figures 13-17

ated with its ability to scamper soon after birth (Bartlett, 1873, for *D. sumatrensis*).

The medulla of *Dicerorhinus sumatrensis* is about a third of the renal parenchyma (Table 4). This is of the same order as in adults of the African hook-lipped rhinoceros, *Diceros bicornis* (Maluf, '91a). In the adult and neonatal Indian rhinoceros, *Rhinoceros unicornis* (Maluf, '87 and unpublished), and in the adult broad-lipped rhinoceros, *Ceratotherium simum* (personal observations), the medulla is nearly a fourth of the renal mass.

### Veins

In the rhinoceroses, e.g., *Dicerorhinus sumatrensis* and *Diceros bicornis*, the paraconduital veins (Figs. 5, 11, PV; Fig. 12), which are large and central, form prominent anastomoses between interlobar veins (Figs. 5, 11, ILV; Fig. 12). Peripherally, across the cortical *partitio renales*, anastomoses are relatively inconspicuous. In *Homo sapiens* the analogy is similar: major anastomoses between the interlobar veins occur centrally, at the level of the calyces adjacent to the fornices (v. Lenhossék, 1876; Hauch, '04; and others). Hunter (1794, p. 184) had already observed that intrarenal anastomoses occur "in very large trunks because a vein is easily compressed, and the blood has a ready passage into another."

None of the four species of rhinoceros studied, including *Dicerorhinus sumatrensis*, have subcapsular stellate veins. Three patterns of

subcapsular renal veins have been distinguished (von Möllendorff, '30; Kazzaz and Shanklin, '51). In the simplest pattern there are no superficial veins running parallel with the renal capsule and the veins begin near the renal capsule and pass perpendicularly inwards through the cortex to empty into the arcuate veins. This pattern occurs in rats, hedgehogs, guinea-pigs, sheep, oxen, and rhinoceros. In the second pattern, subcapsular stellate veins exist but connect inwardly with the arcuate veins, e.g., humans, dogs (von Möllendorff, '30; Kazzaz and Shanklin, '51; von Kügelgen et al., '59), and okapis (Maluf, '81). In the third pattern, confluent prominent subcapsular veins avoid the medulla and empty into the renal vein(s) at the hilum, e.g., in felines, hyenas, and seals as first reported by Hunter (1794, pp. 183-184) who noted that "the veins in the kidneys of the cat kind and hyaena have the veins, in part, passing along the surface in the external membrane." Possible adaptive significance of these different patterns is uncertain (Ulfendahl, '62a,b; Nissen, '65, '66a,b).

### Question of exchange between pelvic conduits and renal parenchyma

The rhinocerotid kidney lacks papillae, medullary crest, and fornices. Its terminal collecting ducts open at a giant collecting duct (tubus maximus) and/or at a flat or concave area cribrosa which opens at the pelvic conduits. These conduits have a thick compact muscular wall which probably precludes significant transmural exchange. Retrograde pyelograms, done by gentle instillation of radiopaque solution into the ureter, indicate that flux into the terminal collecting ducts is difficult to avoid. Pyelotubular reflux may occur in the living normal rhinocerotid kidney during contraction of the pelvic conduits. This seems to be the only route whereby definitive urine might recontact renal parenchyma. Experimental evidence indicates that intermittent pyelotubular reflux, secondary to incompetent ureterovesical valves, does not injure kidneys provided the urine remains sterile (King and Idriss, '67; Lenaghan et al., '72; Newman et al., '74; Danforth et al., '80; James et al., '81). Nevertheless it is not clear how reflux of urine could increase excretion of urea or other solutes (Oliver et al., '82).

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The frozen right kidney of *Dicerorhinus sumatrensis* (No. 30915) was provided cour-

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Fig. 13. *Dicerorhinus sumatrensis* (No. 30915) Longitudinal section of luminal portion of pelvic conduit of left kidney showing urothelium and adjacent muscular wall. Hematoxylin and eosin. Bar = 52  $\mu$ m.

Fig. 14. *Dicerorhinus sumatrensis* (No. 30915) Longitudinal section of muscular wall of pelvic conduit of right kidney showing closely packed longitudinal and oblique muscle fibers. Masson's trichrome; Kodak green filter 58. Bar = 174  $\mu$ m.

Fig. 15. *Dicerorhinus sumatrensis* (No. 30915) Glomerulus of left kidney. Hematoxylin and eosin. Bar = 33  $\mu$ m.

Fig. 16. *Dicerorhinus sumatrensis* (No. 30915) Cross-section of peripheral part of muscular wall of ureter showing circularly disposed bundles. Masson's trichrome; Kodak green filter 58. Bar = 116  $\mu$ m.

Fig. 17. *Dicerorhinus sumatrensis* (No. 30915) Cross-section of peripheral part of muscular wall of ureter indicating that longitudinal and oblique muscle fibers constitute a large part of the circular bundles. Masson's trichrome; Kodak green filter 58. Bar = 35  $\mu$ m.

tesy of M.P. Anderson, chief pathologist to the San Diego Zoological Society, the necropsy having been done by B. Rideout. Histological sections of the left kidney of this animal were courtesy of Anne Sawyers, assistant in pathology. Portions of the kidney of *D. sumatrensis* (No. 92-53) were kindly supplied by M. Campbell of the Cincinnati Zoological Society. The radiographs were done in the Roberts and Wendt Animal Hospital, Cleveland, with the help of Anthony T. Lesh. Histological sections of the right kidney were by Stephen D. Sindely and photography by Michael D. Thomas and Ken I. Kondo. Michael S. Simonson, at Case Western Reserve Medical Center, provided facilities.

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