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-log-log slope relating number of glomeruli per kidney to body-mass. Neonatal rhinos at term have mature 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-
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, \( \frac{4}{3} \pi r^3 \), in which \( \pi \) 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; Schweiggert-Seidel, 1865; Kunkel, 1930; Ryland, 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 cm³, or 40.3 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 Gilson-type pipette. The internal diameter of the tip is 404 N.S.R. MALUF

**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 33a and b; 57a and b; and 73a 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**

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<td>A</td>
<td>arcuate vessel</td>
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<td>AA</td>
<td>arcuate artery</td>
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<td>AV</td>
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<td>Cx</td>
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<td>DM</td>
<td>divergence of medullae</td>
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<td>ILV</td>
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<td>IM</td>
<td>internal medulla</td>
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<td>IN</td>
<td>orifice of infundibulum</td>
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<td>IN, IN₂</td>
<td>orifices of primary, secondary and tertiary</td>
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<td>INLV</td>
<td>intralobar vein</td>
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<td>gap in interlobar septum</td>
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<td>OM</td>
<td>outer medulla</td>
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<td>P</td>
<td>pelvis proper</td>
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<td>P₁</td>
<td>cephalic conduit of pelvis</td>
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<td>P₂</td>
<td>caudal conduit of pelvis</td>
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<td>RA</td>
<td>renal artery</td>
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<td>S, S₁, S₂, S₃</td>
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<td>terminal collecting ducts</td>
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<td>TM</td>
<td>tubus maximus</td>
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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, P1) 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.
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.
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 interlobular arteries and veins enter and leave, respectively, the lobes close to the pelvis proper and to the two pelvic conduits.

HISTOLOGY

Renal 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 spheroidal. 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 log10N = 0.59 log10M + 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 = 1,585M0.59, 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 M = 0.55 × 108 per kidney. The 16-month-old 154.1-kg Tapirus bairdii has 12,444 glomeruli per gm of cortex and 4.0 × 106 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. 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 maxi

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. 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 infundibula, 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.

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1The 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; Vacek 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.
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 \( \mu m \) in diameter. The wall of a single vein, 284 \( \mu m \) in diameter and in the same cross-section, can vary in thickness from a few micrometers to muscular bundles 50 to 80 \( \mu m \) 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 \( \mu m \) in diameter has a wall 43 to 60 \( \mu m \) 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 \( \mu m \). In the larger arcuate arteries, the circular-oblique muscle coat (media) is 103 to 172 \( \mu m \) thick and the longitudinal muscle bundles 43 to 86 \( \mu m \) thick.

Intralobar veins

The diameter of an intralobar vein adjacent to a renal calyx varies between 95 and 3,000 \( \mu m \). Its wall consists of an admixture of muscle and collagen fibers and is 29 to 86 \( \mu m \) 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 \( \mu m \)). 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.

Intralobar arteries

Intralobar arteries, between cortex and calyx, vary in outer diameter between 500 and 675 \( \mu m \).

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 \( \mu m \) 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 \( \mu m \). The glomeruli are uniformly distributed; their number, in tiers along the cortex is about 13. The cortex cortices is 17 \( \mu m \), or the width of a single proximal tubule.
TABLE 1. Average diameter (in µm ± standard deviation) of glomerular capsules (see Methods) in one- and two-day-old male R. unicornis

<table>
<thead>
<tr>
<th></th>
<th>Peripheral</th>
<th>Midcortical</th>
<th>Juxtamedullary</th>
</tr>
</thead>
<tbody>
<tr>
<td>One-day-old</td>
<td>76.6 ± 3.53</td>
<td>82.6 ± 5.46</td>
<td>81.6 ± 7.85</td>
</tr>
<tr>
<td>(n = 5)</td>
<td>(n = 5)</td>
<td>(n = 5)</td>
<td></td>
</tr>
<tr>
<td>Two-day-old</td>
<td>92.1 ± 12.9</td>
<td>86.0 ± 11.3</td>
<td>98.0 ± 15.5</td>
</tr>
<tr>
<td>(n = 12)</td>
<td>(n = 7)</td>
<td>(n = 7)</td>
<td></td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Measurement or Calculation</th>
<th>1-day-old rhino</th>
<th>2-day-old rhino</th>
<th>Adult female rhino (3½ yrs)</th>
<th>Human adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>Volume of glomerular capsule (mm³)</td>
<td>0.000268</td>
<td>0.000408</td>
<td>0.00382</td>
<td>0.00359</td>
</tr>
<tr>
<td>Ratio of adult to neonatal glomerular mass</td>
<td>14.25</td>
<td>9.34</td>
<td>—</td>
<td>13.4² (ratio to 1-day rhino)</td>
</tr>
<tr>
<td>Mass of both kidneys (gm)</td>
<td>235.75</td>
<td>344.0</td>
<td>2,960</td>
<td>300.0</td>
</tr>
<tr>
<td>Ratio of adult to neonatal renal mass</td>
<td>12.6</td>
<td>8.6</td>
<td>—</td>
<td>1.27² (ratio to 1-day rhino)</td>
</tr>
<tr>
<td>Number of glomeruli (no. per field at 35 X)</td>
<td>150 ± 8.1</td>
<td>132 ± 11.2</td>
<td>13.56 ± 3.1</td>
<td>11.6 ± 1.5</td>
</tr>
<tr>
<td>(n = 6)</td>
<td>(n = 6)</td>
<td>(n = 25)</td>
<td>(n = 8)</td>
<td></td>
</tr>
<tr>
<td>Ratio of density neonatal/adult</td>
<td>11.1</td>
<td>9.7</td>
<td>—</td>
<td>12.9¹ (ratio to 1-day rhino)</td>
</tr>
<tr>
<td>Width of cortex (µm)</td>
<td>1,750</td>
<td>2,250</td>
<td>6,250</td>
<td>5,000</td>
</tr>
<tr>
<td>Ratio of width of cortex adult/neonatal</td>
<td>3.57</td>
<td>2.78</td>
<td>—</td>
<td>2.86 (ratio to 1-day rhino)</td>
</tr>
<tr>
<td>Cortex % of renal mass</td>
<td>—</td>
<td>—</td>
<td>75.3</td>
<td>70.0</td>
</tr>
<tr>
<td>Glomerular mass % of cortex</td>
<td>—</td>
<td>—</td>
<td>5.83</td>
<td>4.71</td>
</tr>
<tr>
<td>Mass of glomeruli per kidney (gm)</td>
<td>4.57</td>
<td>6.96</td>
<td>65.08</td>
<td>4.95</td>
</tr>
<tr>
<td>Ratio of glomerular mass adult/neonatal</td>
<td>14.18</td>
<td>9.35</td>
<td>—</td>
<td>1.08¹ (ratio to 1-day rhino)</td>
</tr>
<tr>
<td>Glomerular mass % of single kidney</td>
<td>3.88</td>
<td>4.05</td>
<td>4.4</td>
<td>3.3</td>
</tr>
<tr>
<td>Body-mass (gm)</td>
<td>55,000</td>
<td>48,636</td>
<td>1,057,000</td>
<td>70,000</td>
</tr>
<tr>
<td>Mass of kidneys as % of body-mass</td>
<td>0.43</td>
<td>0.71</td>
<td>0.28</td>
<td>0.43</td>
</tr>
<tr>
<td>Diameter of prox. tubules (O.D.) (µm)</td>
<td>34</td>
<td>41</td>
<td>48.4</td>
<td>67</td>
</tr>
<tr>
<td>Ratio of diameter prox. adult/neonatal</td>
<td>1.4</td>
<td>1.2</td>
<td>—</td>
<td>1.97¹ (ratio to 1-day rhino)</td>
</tr>
<tr>
<td>Diameter of distal tubules (O.D.) (µm)</td>
<td>18.5</td>
<td>24</td>
<td>28</td>
<td>54</td>
</tr>
<tr>
<td>Ratio of diameter dist. tubule (adult/ neonatal)</td>
<td>1.5</td>
<td>1.17</td>
<td>—</td>
<td>2.9¹ (ratio to 1-day rhino)</td>
</tr>
<tr>
<td>Diameter of glomerular capsule (µm)</td>
<td>80.0</td>
<td>92.0</td>
<td>194.0</td>
<td>200.0</td>
</tr>
<tr>
<td>Ratio of diameter of glomerular capsule (adult/neonatal)</td>
<td>2.43</td>
<td>2.11</td>
<td>—</td>
<td>2.5¹ (ratio to 1-day rhino)</td>
</tr>
</tbody>
</table>

¹Data 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 a periphery. About 14 pm thick. As in the adult, the septa form gaps between the gen fibers. The interlobar septa are collagenous and extend medullary border and about 450 pm apart at the periphery 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 growth, as shown by increase in glomerular and tubular mass, evidently progressed (Table 2).

**DISCUSSION**

**Kidney of Rhinoceroses**

Thomas (1801) noted that “the kidneys [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; Potier, 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 calices divides into a pair of calices minores. The last are described as funnel-like invaginations which receive flat papillae (“flaecher Papillae renales”). Hyrtl’s minor calyces may be synonymous with the infundibula of this paper. His casts would not show the important medullary-adherent calyces.

Garrod (1873) remarked that the kidneys of an aged Sumatran rhino, *Ceratotherium sumatrensis*, are nearly equal in size and “are lobulated externally.” In *Rhinoceros sondaicus* (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 renuli. This conception is supported by my finding the kidneys of a *Diceros bicornis* embryo to be strongly lobated. They appear to be typical renuli 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 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; Jameson, 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 tubes 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 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 sinus at the base of the cetacean skull shown by Fraser and Purves (1954, 1960).

**Urine**

Renal osmotic power of rhinoceri is unknown. 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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