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The renal pelvis

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Mammals and birds are the only vertebrates known to produce a concentrated urine by means of renal medullary countercurrent systems. These two countercurrent systems, however, exhibit functional and anatomical differences which appear to be related to the fact that mammals are ureotelic while birds are uricotelic. In mammalian kidneys, urea accumulation in the medulla plays an important role in the concentrating mechanism. In bird kidneys, there is no accumulation of urea in the medulla. The mammalian renal medulla is surrounded by a muscular, funnel–shaped pelvic wall, leaving an elaborate urinary space between the renal medulla and the inside of the pelvic wall, while the bird renal medulla is surrounded by tight sheets of connective tissue leaving no space for the urine to contact the renal medulla. The mammalian renal pelvis makes it possible for urine to contact the epithelial covering of the inner and outer medulla, and the peristaltic contractions of the muscular pelvic wall exerts a rhythmic pumping action on the renal papilla. The functional significance of these two aspects of the renal pelvis have in recent years become the focus of attention by some renal physiologists.

Anatomical relationship between renal pelvic urinary space and the renal medulla

At this point clarification concerning terminology is necessary. In a multipapillate kidney, such as the human kidney, each papilla is surrounded by a funnel shaped "calyx" which corresponds to what we call the pelvis in the uni-papillate kidney. In multipapillate kidneys the "pelvis" is a compartment between the calyces and the ureter, which is not present in uni-papillate kidneys. Since the pelvis of uni-papillate kidneys is an extension of the ureter it has been referred to as the ureter by some authors (1). In the kidneys of cats, dogs and several other mammals the inner medulla forms a crest rather than a papilla. The elaborate pelvic extensions of the dog kidney have sometimes mistakenly been referred to as calyces (2). In cross–sections of mammalian kidneys the pelvis appears to surround the inner medulla only, and to have a simple funnel shape. Casts of the pelvic space [3–6] however, reveal the presence of a series of leaf–like extensions, which have been termed fornices and secondary pouches [6, 7]. They have been shown to reach into the outer medulla as far as the cortico-medullary border [5]. Fornices and secondary pouches are found in all types of kidneys, crest–type, uni- and multi-papillate kidneys. There is an enormous variation in the extent of pelvic fornices and secondary pouches, which range from the most elaborate forms seen in the giraffe [4] and sand rat [8] to a simple funnel devoid of pelvic extensions; the latter is found in kidneys with no inner medulla [6].

The anatomy of the renal pelvic space has been described in some detail by Sheehan and Davis in the rabbit [7], by Kaisling et al in the sand rat [8] and by Lacy and Schmidt–Nielsen in the hamster [9]. The pelvic tissue, which is continuous with the ureter, forms two septa which enclose the entire inner medulla (corresponding to the calyx in humans). Each septum has a scaffolding of spokes which radiate toward the cortex from the septum and are inserted into the substance of the kidney. Between these spokes the outer margin of the septum is free and has a semilunar edge, behind which the secondary pouches extend downward toward the hilum between the septum and the renal parenchyma [7] (Figs. 1 and 2). The smooth muscle layer of the ureter is continued as a large sheet of longitudinal fibers under the epithelium along the entire inner face of the septum toward the fornices and along the lateral (fornical) edge of the septum, the muscle becomes continuous with the "levator anguli fornicis" [7]. In the rabbit Gosling and Dixon showed that an external layer of circular or obliquely running muscle fibers intermingle with the muscles of the inner layer. The muscle cells of the outer layer are associated with many adrenergic nerves [10]. At the pelvic–ureteric junction the outer layer ends abruptly, leaving the ureter devoid of a similar layer [10]. These distinguishing features indicate that the renal pelvis may perform different functions from the upper ureter [10]. On the outside of the muscle layer the main substance of the septum is almost entirely fat containing the renal vessels, nerves and lymphatics [7].

Peripelvic columns project into the pelvic space between the fornices (Fig. 3). The renal parenchyma of the peripelvic columns and of the fornices and secondary pouches facing the urinary space is outer medullary tissue, both inner and outer stripe [9, Fig. 2].

The epithelium covering the *septum and the extensions* facing the urinary space is continuous with the lining of the ureter and the bladder and is a transitional epithelium with a low permeability to urea and water [12, 13]. In contrast, the epithelium covering the *inner medulla* and facing the pelvic space is remarkably similar to the epithelium of the papillary collecting ducts [9, 14, 15]. The cells are columnar near the tip and become flattened toward the base of the papilla [9, 15]. As in collecting duct cells, the intercellular spaces show complex interdigitations and are dilated in antidiuresis and closed in

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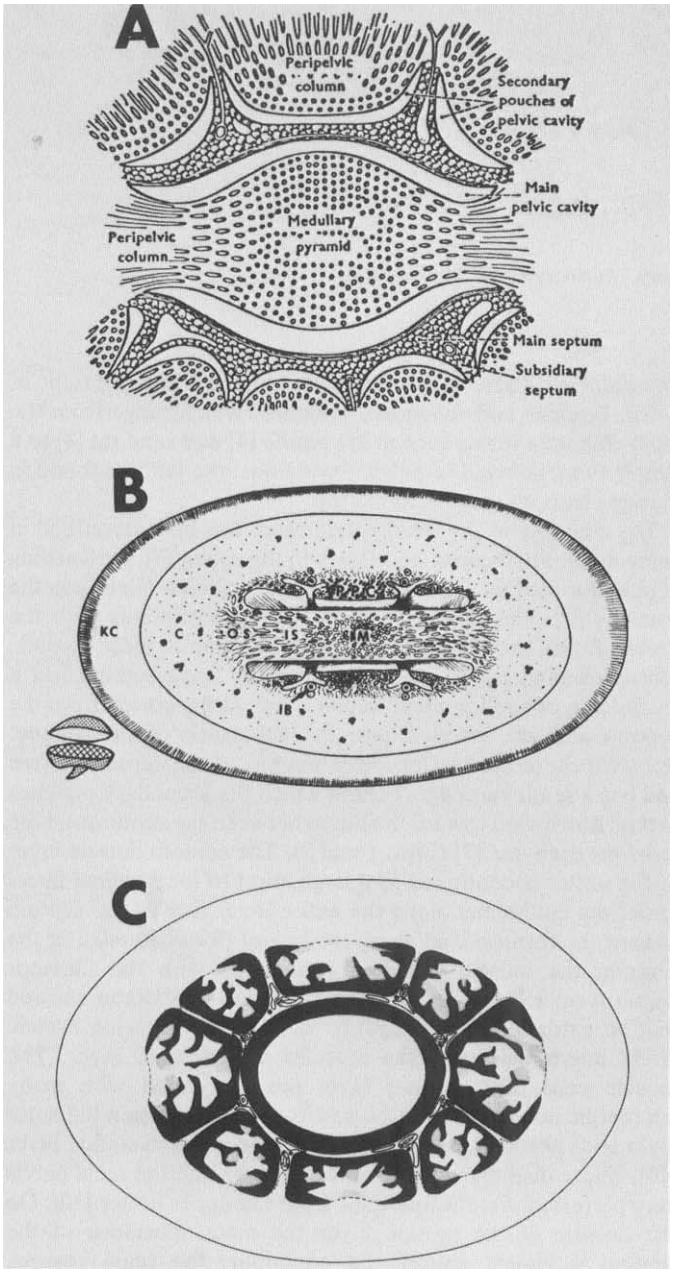

Fig. 1. *Horizontal sections of kidneys.* Drawings showing horizontal (transverse) sections of rabbit, hamster and sand rat kidneys. **(A)** Rabbit kidney. The main septum is seen on each side of the medullary pyramid (inner medulla). The subsidiary septa radiate from the septum toward the cortex and are inserted into the renal parenchyma. The secondary pouches which are part of the urinary space are seen behind the main septum. The peripelvic columns (outer medullary tissue) reach into the secondary pouches. Reprinted from Sheehan and Davis [7] with permission. **(B)** Hamster kidney. The small diagram to the left indicates where the section was made. This section is made above the main septum which can therefore not be seen in the diagram, but the peripelvic columns (outer medulla) are seen to reach into the urinary space around the inner medulla. Reprinted from Lacy and Schmidt–Nielsen [5] with permission from the journal. **(C)** Sand rat kidney. In this section the main septum (white) completely surrounds the renal papilla in the center. As in the section from the rabbit the subsidiary septa are seen radiating toward the cortex. The peripelvic columns are not smooth as in the rabbit and hamster, but are indented where capillary bundles are surrounded by urinary space (black). Reprinted from Kaissling et al [8] with permission.

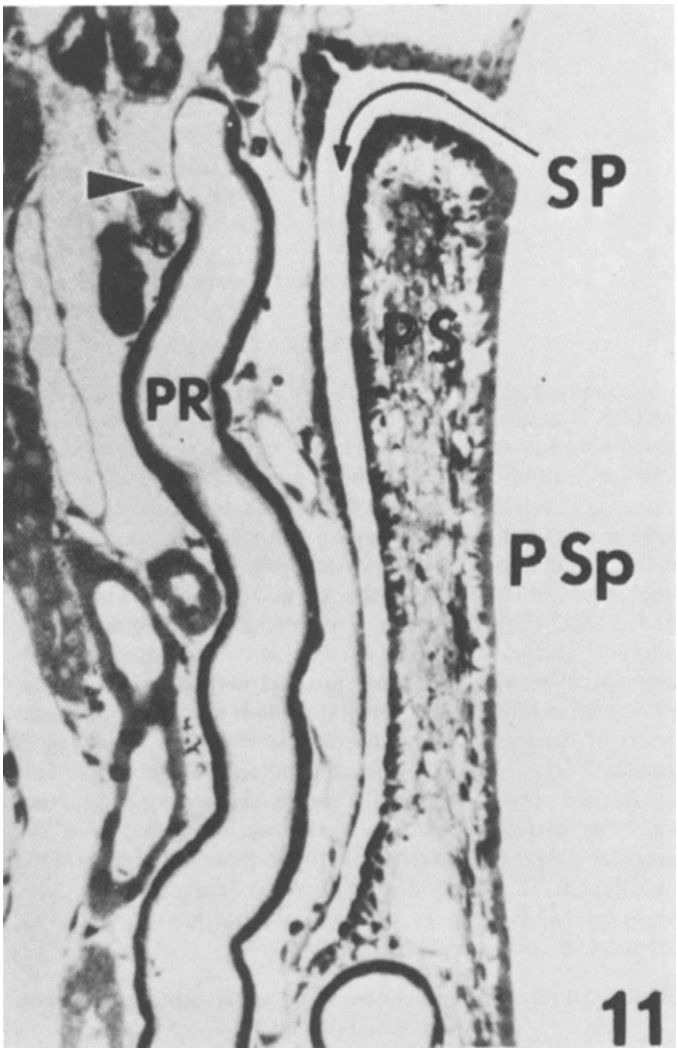

Fig. 2. *Pelvic septum from a hamster kidney.* Light micrograph of pelvic septum (P Sp) and a secondary pouch (SP). Outer stripe of outer medullary tissues faces the urinary space, note proximal tubule (PR). Reprinted from Lacy and Schmidt–Nielsen [5] with permission from the journal.

diuresis [14]. The epithelium covering the *outer medulla* facing the pelvic urinary space is thin and consists of cells ranging from squamous to low cuboidal [9, 15, 16]. It has two cell types: cells that form the mucosal epithelial surface and contact the basal lamina, and cells which are darkly stained and confined to the basal region. There are striking similarities between this epithelium and that of the toad urinary bladder which may indicate similar permeability characteristics of the two epithelia, including a similar response to antidiuretic hormone [9].

Directly under the thin epithelium covering the outer medulla (fornices, secondary pouches, and peripelvic columns) the most abundant structures are capillaries. In the hamster about 60% of the structures are capillaries, with fenestrated capillaries outnumbering continuous capillaries [9]. In the sand rat, *Psammomys obesus* [8], the peripelvic columns are far more elaborate than in the hamster. The most interesting feature in the sand rat is that the vascular bundles of the inner stripe of the

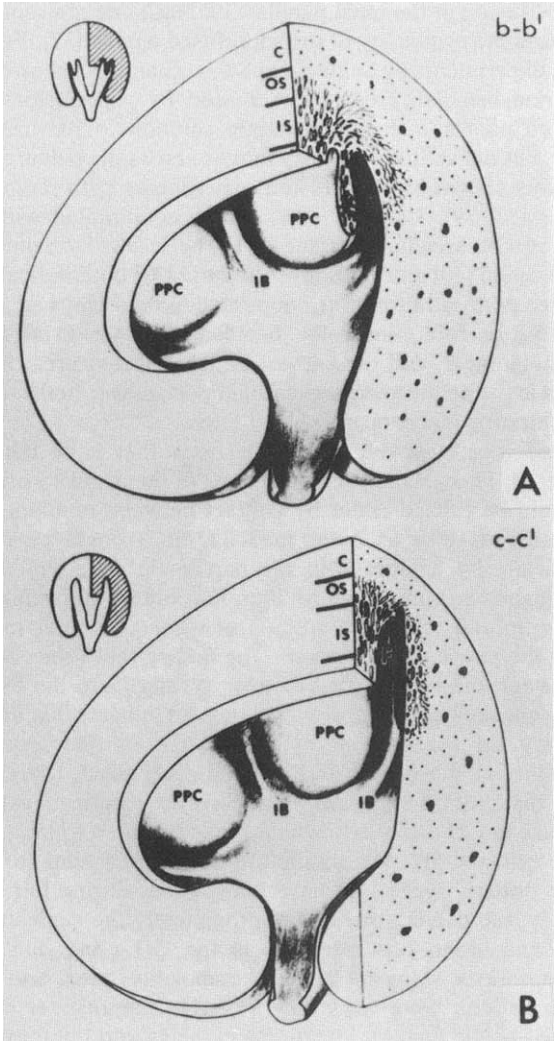

Fig. 3. *Sections through hamster kidney*. Two sections through hamster kidney illustrate the peripelvic columns (PPC). In **B** the fornix reaching up to the cortex can be seen. Reprinted from Lacy and Schmidt–Nielsen [5] with permission.

outer medulla are almost completely surrounded by the urinary space [8]. Thus, the possibility for exchange of solutes and water between pelvic urine and the vascular bundles is maximized by the pelvic extensions.

These features of the renal pelvic space make it tempting to postulate that exchange of urea and water between urine and outer medulla serves an important function in the mammalian renal concentrating mechanism. Pfeiffer, noting certain characteristic differences between pelvises of mammals, divided them into two types. Type I pelvis is an uncomplicated, slightly expanded ureteral ending, while type II is an extensive pelvis with the features discussed above. In contrast to kidneys with a type II pelvis, kidneys with a type I pelvis have no inner medulla and urea does not accumulate in the outer medulla and does not enhance the osmotic ceiling of the urine [6]. This would suggest that urea accumulation in the outer and inner medulla of kidneys with type II pelvis is facilitated by the pelvic extensions. Attempts to correlate ability to concentrate the urine with size and elaboration of the pelvic space in kidneys with type II pelvis have, however, failed to yield any conclusive answers [3]. Desert rodents with high urinary concentrating ability show a great variability in the extent of their pelvises. Thus, the pocket mouse which can concentrate the urine up to 7500 mOsm/kg H_2O [17] has only modest pelvic extensions [3, 17]. The sand rat with extensive fornices and secondary pouches has a far greater pelvic surface area than that of the hamster and gerbil [18], although the concentrating ability of the three species is about the same. Among three species of hedgehogs, the one with the most prominent fornices is the one with the poorest concentrating ability [19]. Attempts to correlate nitrogen intake with the shape of the pelvises have been equally unsuccessful. Thus, elaborate pelvises are found in herbivores such as camel, giraffe, dugong, sand rat (*Psammomys*), and sheep, but are also present in carnivores such as dog, tiger, leopard, and cat [3, 4]. Consequently, urea production shows no correlation to the size of the renal pelvic urinary space. There appears to be another possible explanation for the role of the fornices which will be discussed later.

Peristalsis of the renal pelvis

The muscular pelvic wall exhibits peristaltic contractions which have been studied in a number of mammals both in vitro and in vivo. As early as 1880 Henle [20] proposed that the calyx milks the papilla, a notion which was vigorously disputed by Narath [20]. Peristalsis is initiated by a pacemaker situated in the uppermost parts of the pelvic septum [2, 11, 21–25]. In multipapillate kidneys peristalses of the calyces are not synchronized and each has its own intrinsic rhythm [11, 25]. The frequency of peristalsis (per min) is under normal conditions 4 to 6 in pig [26], 20 to 30 in hamster, and 40 to 50 in rat [27]. Sections of the pelvic wall have their own intrinsic peristaltic rhythm which is slower than the pacemaker rate [2, 21, 25]. Thus, there is coupling as the rhythm of the lower sections is driven by the pacemaker. The frequency of pelvic peristalsis is constant and independent of urine flow rate [21, 27], but electric myogenic activity increases in the pelvic muscles during abruptly–rising urine flow rate [26]. Ureteral peristalsis is coupled to pelvic peristalsis but at a lower frequency which depends on urine flow rate. Only during osmotic diuresis is there a 1:1 ratio between pelvic and ureteral activity [24].

The intra pelvic pressure generated by the peristalsis and exerted on the papilla is about 5 mm Hg [26, 28, 29]. The renal papilla has no smooth muscle and no intrinsic contraction; therefore movements of the papilla are strictly driven by the pelvic wall.

Studies of the effect of hormones on peristalsis of the ureter have shown that its activity is affected by histamine, antihistamine, serotonin, and bradykinin [30]. In the isolated rabbit pelvis which has a spontaneous rhythm of 4 to 5/min, neither tone nor motility were affected by acetylcholine, esserine, carbachol, histamine, caerulin, angiotensin, bradykinin, prostaglandin, or cyclic AMP. However, catecholamines increased the rate and force of pelvic contraction. A response to nerve stimulation, mediated through alpha-adrenoreceptors, could be elicited [31]. Peristalsis can be abolished in vivo by blocking smooth muscle contraction or by the application of xylocaine [Morita, personal communication, 32]. Epinephrine increases pelvic contraction rate and force in man [33].

In addition to the indirect assessment by use of implanted electrodes or pressure transducers, pelvic peristalsis can be observed directly in vivo in rodents with a long renal papilla extending beyond the cortex at the hilum. In anesthetized hamsters following removal of pelvic fat, peristalsis of the pelvic wall can be observed and filmed through the microscope. As the wall contracts the papilla is stretched and its cross-sectional area reduced by as much as 36%. In the hamster, peristaltic waves move over the papilla with a linear velocity of 1.6 mm/sec. At the moment the wave has passed over the tip of the papilla, the tip moves upward on the the average about 300 μm.

Physiological observations

Effect of pelvic peristalsis on fluid movement in the renal pelvis

The anatomical structures of the renal pelvis as well as the rhythmic contractions of the muscular septum and its fornical extensions indicate that urine may be brought in close contact with inner and outer medullary tissue. This raises the general question of what physiological functions such contact may serve. The first specific questions to be answered are: 1) under what physiological conditions does urine contact the various regions of inner and outer medulla facing the pelvic urinary space? 2) What effect does this contact have on the osmolality and solute concentrations of urine and papillary tissue? To answer the first question, fluid movement within the pelvis was studied in anesthetized hamsters and rats in vivo when the urine was colored by the intravenous infusion of the dye lissamine green, first introduced in renal studies by Steinhausen [34]. The following observations were made. When the urine leaves the ducts of Bellini at the tip of the papilla (when the pelvic wall is intact), it does one of three things: 1) it flows directly down the ureter; 2) it contacts the tip of the papilla briefly by fanning out around the papilla tip (tip refluxes); or 3) it refluxes up over the entire inner medulla and reaches all of the fornices and secondary pouches (full pelvic refluxes) [27].

During constant urine flow (independent of flow rate) urine flows directly down the ureter after leaving the ducts of Bellini. Tip refluxes occur sporadically during constant or falling urine flow. During a tip reflux, the urine after leaving the duct of Bellini briefly fans out and covers the lower 50 to 100 μm of the papilla before flowing down the ureter. However, full pelvic refluxes do not occur during constant urine flow. Full pelvic refluxes are induced only when the rate of urine flow increases faster than 0.05 μl/min^2. They continue for several minutes after the flow is no longer increasing. Full refluxes may be induced by rising pressure in the ureter, but are not caused simply by mechanical effects on the ureter [27].

Exchange of solutes and water between urine and renal medulla and its effect on concentrating and diluting ability

Removal of the renal pelvis from the part of the renal papilla extending beyond the cortex causes the osmolality in collecting duct (CD) urine to decrease to approximately half its initial value [35]. This dramatic decrease takes place within 10 to 15 minutes of exposure [1, 36] and is primarily due to a decrease in urea concentration of the renal tissue [37] which causes the decrease in the CD osmolality [38].

Superfusion of the renal papilla with NaCl and urea solutions enhances the osmolality of the superfused papilla [37]. Furthermore, experiments by Schutz and Schnermann [34] showed that the urine osmolality can be increased by superfusion of an exposed papilla with hyperosmotic solutions. That urea and water, but not sodium, actually moves across the pelvic epithelium was shown by superfusion experiments with radioactive solutes [37, 39]. Labeled urea quickly equilibrated within 10 minutes with urea in the tissue [37]. The results by Schutz and Schnermann [40] and by Bonventre et al [38] both indicate that the urea concentration in the superfusion fluid plays an important role in determining the osmolality of the urine in the collecting ducts; and the authors concluded that urea concentration in the pelvic urine serves an important role in the urinary concentrating mechanism.

There are, however, other questions that have not been answered. Theoretically, enhancement of the papillary osmolality could be caused either by contact between refluxing urine and inner as well as outer medulla, or it could be caused specifically by contact with the papilla tip. The superfusion experiments do not distinguish between contact of the fluid with papilla tip and the entire surface of inner and outer medulla facing the pelvic urinary space. The finding that urine, at least in hamster and rat, was never seen to reflux into the fornices during constant or falling urine flow would indicate that only the papillary tip exchange is of importance for increasing the osmolality of the papilla [27]. On the other hand, Oliver et al found that cutting the ureter just below the papilla tip caused a decrease in CD osmolality which they attributed to lack of full pelvic refluxes [1]. Micropuncture samples of fluid from the pelvic urinary space [41] have shown that during full pelvic refluxes, the pelvic urine had approximately the same composition and inulin concentration as the CD urine, but when visible refluxes were not present, osmolality, urea, and inulin concentrations were very low [1, 41]. Bargman et al [42] sampled pelvic fluid by inserting a catheter into the fornix and found lower urine–to–plasma (U/P) osmolality and inulin ratios in the fornices than at in the CD. They concluded that refluxing urine is diluted in the pelvis by abstraction of water from the papilla and possibly addition of urea to the renal parenchyma [42]. This is possible, however, the data are not conclusive, since the introduction of the pipette into the fornix could cause some reflux.

Marsh and Martin sampled ureteral and ducts of Bellini urine in hamsters. When they found no difference in filtered water and urea present between the two sites, they concluded that urea reabsorption across the surface of the papilla is negligible in the hydropenic state [43]. A similar conclusion was reached by Knepper and Sands from their measurements of urea permeability of CD epithelium in rats and rabbits and papillary epithelium in rabbits [44].

During rising urine flow, when full pelvic refluxes occur, urine osmolality is normally falling. The fall in urine osmolality preceeds the fall in renal medullary osmolality, therefore, the urine being swept up into the fornices has a lower osmolality than the papillary tissue. The osmolality of the outer medullary tissue facing the urinary space in the peripelvic columns and fornices is not known. But it is likely that the capillaries and ascending vasa recta (fenestrated capillaries), right under the epithelium, are carrying blood with a high osmolality from the

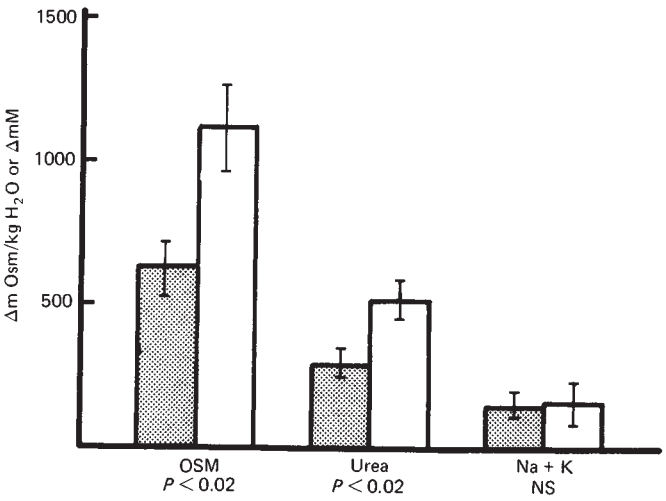

Fig. 4. *Effect of full pelvic refluxes during increasing urine flow upon papillary solute concentrations.* Difference (mean ± SE) in osmolality (mOsm/kg H_2O), urea (mM), and Na + K (mM) concentrations between the renal papilla and urine in refluxing (▨) and nonrefluxing (□) kidneys. Reprinted from Schmidt–Nielsen [39] with permission.

papilla. From experiments on hamsters designed to determine the effects of full pelvic refluxes during rising urine flow, it appears that refluxes serve to reduce the osmolality and urea concentration of the renal medulla. The urine flow was increased from 5 to 50 μl/min at a rate of increase just below the rate causing full refluxes. Then refluxes were mechanically induced for 20 minutes in the experimental kidney, while the other kidney served as a control. The osmolality and urea concentration decreased significantly faster in the kidney with induced pelvic refluxes than in the kidney without refluxes [Fig. 4, 39 and unpublished data].

Effects of pelvic peristalsis on fluid movements in the renal papilla

In the CD, fluid movements can be observed through the pelvic wall when the urine is colored. Steinhausen in 1964 introduced the technique of intravenous injection of the dye lissamine green which, following filtration in the glomeruli, causes tubular fluid and urine to become intensely green. In hamsters with the pelvis opened, but not removed, Steinhausen observed a rhythmic flow of urine in one or several CD which he suggested was caused by the peristaltic contraction of the pelvis [34]. In our studies, the renal pelvis was left intact and lissamine green was infused continuously. The transilluminated renal papilla of rats and hamsters (and other rodents with a long papilla) was observed through the transparent pelvic wall, from which only the fat had been removed. It was found that urine in all CD flows intermittently. Not only does the flow stop, as observed by Steinhausen, but the CD empty and their walls collapse during each peristaltic wave [45, 46]. Urine moves through the papillary CD in boluses with a linear velocity of 1.6 mm/sec. The length of the urine bolus varies with urine flow rate (as in the ureters). At low flow rates, the CD may be empty as much as 95% of the time [45]. At a higher urine flow rates the boluses are longer and the contact time increased. The leading edge of the urine in the CD moves with a lower linear velocity (the velocity of urine formation) than the trailing edge of the urine, which is being pushed with the velocity of the peristaltic wave (independent of urine flow rate). Thus, paradoxically, the average velocity is increased and contact time between CD urine and CD wall is reduced at very low compared to higher urine flow rates [45, 47].

Papillary blood flow and fluid flow in loops of Henle are also affected directly by the peristaltic contractions. Measurements showed the capillary flow to be stopped 30% of the time [39]. Verification of the in vivo observations was obtained from papillae fixed through the renal pelvic wall during the pelvic contraction. When fluid flow was stopped (by tightening a snare around the papilla) and the papilla fixed at the end of the contraction the pelvic wall was tight around the papilla [46]. Light and electron microscopy showed that CD were all closed, so were loops of Henle and vasa recta [46]. The intercellular spaces between the CD and papillary epithelial cells were closed. This appearance was seen from about 50 μm from the tip to 600 to 700 μm from the papilla tip. At the tip capillaries full of blood were seen. When the snare was tightened during the early relaxation of the pelvic wall (which occurs 1/2 sec after the end of the contraction), capillaries and loops of Henle were wide open. The intercellular spaces between CD cells and between papillary epithelial cells were also wide open [46]. Morphometric analysis showed volume of CD cells and papillary epithelial cells to be greater in the papillae with contracted than in those with relaxed pelvises [46].

Effect of pelvic peristalsis on the concentrating mechanism

Since peristalsis affects flow in all of the papillary structures it seemed likely that it would influence concentrating ability. Thus, Reinking and Veale [48] found that the concentrating defect observed following removal of the pelvic wall could be partly restored by cyclical mechanical compression of the exposed papilla. It seems logical that fluid reabsorption in the papillary collecting CD should be dependent on flow velocity [49]. However, fluid reabsorption, at low urine flow rate, estimated in the terminal CD in hamster [47] and rat [1] during normal pelvic peristalsis was still high. In spite of the high fluid velocity, about 50% of the fluid entering the last mm of the CD is reabsorbed. Oliver, Roy and Jamison found that paralysis of the pelvic wall with verapamil for 5 to 30 minutes had no effect on urine flow, osmolality, GFR, or inulin U/P in collecting duct urine [1]. However, paralysis of pelvic muscle (for one hour) was found to lower osmolality and sodium concentration of the papillary tissue significantly [32]. In the latter case the decrease in sodium content of the renal papilla may have been due to the increase in blood flow of the papilla caused by the paralysis.

Chuang et al [36], found a 40% increase in papillary blood flow following removal of pelvic wall and attributed the decrease in urinary osmolality to the increase in blood flow. Since the increase in blood flow and decrease in osmolality could be prevented by inhibition of prostaglandin synthesis, they suggested that exposure of the papilla causes an alteration in papillary prostaglandin synthesis. An alternative explanation is that the mechanical effect of the peristalsis which stops blood flow for 30% of the time is responsible for the lower papillary blood flow when the pelvic wall is intact.

Summary and conclusion

The facts gathered in recent years about the mammalian renal pelvis show that it influences the solute concentration in the papilla as well as the flows in capillaries tubules and CD. While it seems quite clear that the role of the renal pelvis is somehow linked to the role that urea plays in the mammalian concentrating mechanism, the available facts are not sufficient to form a comprehensive hypothesis for the functional significance of the pelvis. The difficulties lie in the complexity of the interactions between several physiological effects of the peristalsis and refluxing of the urine. Nevertheless, I shall in the following attempt to present my own interpretation of the facts.

Exchange between pelvic urine and renal medulla

Exchange with outer medulla in fornices (diluting and/or concentrating effect). The issue of contact between urine and outer medullary tissue and significance of the pelvic extension is currently subject to alternative interpretations. As mentioned earlier, comparative anatomical data showed no correlation between size and proliferation of pelvic extensions and concentrating ability. Furthermore, in the hamster and rat full refluxes which bring the urine in contact with the outer medulla were not observed during constant or falling urine flow when urea accumulation takes place. To the contrary, they were seen during rising urine flow (falling urine and papillary osmolality). Data indicate that urine refluxing into the fornices during falling urine osmolality serves to reduce the amount of urea in the renal medulla. Thus, the pelvic refluxes may serve to shorten the time it takes for a water diuresis to develop following a large intake of water. This feature may be particularly significant for certain animals from arid regions. Desert mammals can be divided into those who can live entirely without drinking water and those who tolerate severe dehydration but must drink periodically. Animals in the former group, such as desert rodents living on dry food only, show very high concentrating ability but may die from water intoxication when given a water load [50, 51]. These animals do not have large fornices [3]. On the other hand, mammals from the latter group (such as the camel, giraffe, lion, tiger and other large animals from arid regions) may at times take in huge amounts of fluid and therefore have to be able to dilute the urine promptly [50, 51]. Also the sand rat takes in large amounts of fluid with its diet of succulent plants, which may have highly variable solute content. Most of these mammals are known to have large pelvic extensions [3, 4].

The alternative hypothesis that a small amount of urine contacts the outer medulla during constant and falling urine flow, however, cannot be excluded since a thin film of colored urine may not be visible. Therefore, the hypothesis presented by Bargman et al that papillary osmolality is enhanced by countercurrent exchange between refluxing pelvic urine and renal medulla may be equally valid [42]. Further anatomical and physiological data are needed before these issues can be resolved.

Exchange with papillary tip (concentrating effect). The urine leaving the ducts of Bellini and bathing the papilla tip through tip refluxes would have much the same effect upon urea recycling as urea reabsorbed from the papillary collecting ducts. It could enhance the delivery of urea to the tip of the countercurrent system and thus insure a urea gradient with the highest concentration at the tip of the papilla. It is, however, difficult to imagine that this effect could be quantitatively important compared to the reabsorption from the CD [44, 45].

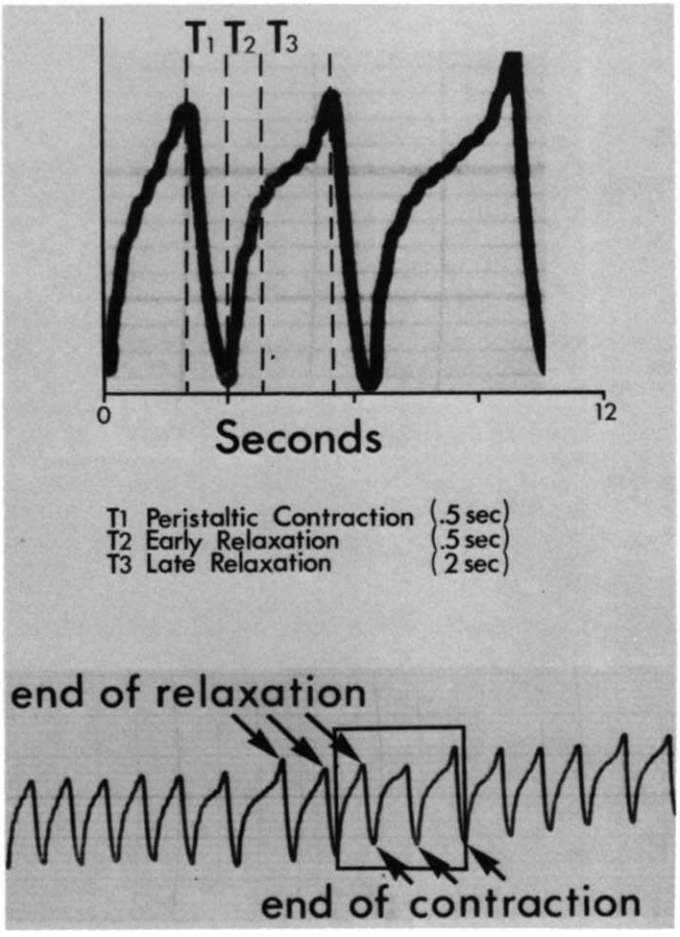

Fig. 5. *Fiber optic recordings made on papilla during contractions of the renal pelvic wall.* The upper recording illustrates the three phases (T_1, T_2, T_3) of contraction–relaxation in the papilla and corresponds to the delineated area in the lower recording. T_1. Peristaltic contraction (0.5 sec). Bolus moves through CD (velocity 97 mm/min). Fluid absorption from CD lumen to CD cells. Blood flow stops and vessels empty. Loop of Henle flow stops and tubules empty. T_2. Early relaxation (0.5 sec). No flow in CD. Blood flow in vasa recta and fluid flow in loops of Henle resume. Fluid moves from CD cells into intercellular spaces (open), interstitium, and ascending vasa recta along the CD. T_3. Late relaxation (2.0 sec). Flow in CD resumes in the later part during this period (velocity about 28 mm/min). Normal flow in capillaries and loops of Henle (reprinted from Schmidt–Nielsen [39] with permission).

Direct effect of peristalsis on concentrating mechanism

The effect of peristalsis on the papilla involves all of the papillary structures (Fig. 5). The longer the renal papilla the greater the milking effects can be expected to be. *Blood flow*, which is stopped for 30% of the time during normal peristalsis, is increased when the pelvic wall is removed. This would also occur when the pelvic wall is paralysed. According to the models of the countercurrent system a higher blood flow would result in increased removal of papillary solutes and, therefore,

a lower solute concentration of the papilla [in agreement with recent findings, 32]. *Flow in the loops of Henle* appears to be affected in a fashion similar to that of the blood flow and may have the same effect on papillary solutes. However, what is not taken into account in this discussion, for lack of data, is the hydrostatic effect upon the fluid in these structures as peristalsis forces some of the fluid toward the bend of the loops.

Flow in CD is greatly affected by the pelvic wall. In papillae with intact pelvic walls the linear velocity of CD urine is increased and the contact time between CD urine and CD epithelium is reduced compared to papillae not exposed to the peristalsis. At this time, no ready explanation is available for the physiological findings by Oliver, Roy and Jamison that paralysis of the pelvic wall did not change any of the urinary parameters measured during the first 20 minutes of paralysis [1]. It would seem that a combination of several papillary changes (including the increased contact time between CD urine and papillary epithelium) may have resulted in the overall lack of net change in the measured parameters.

Acknowledgment

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