QUANTITATIVE AND ORGANIZATIONAL FEATURES OF THE AVIAN RENAL MEDULLA

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Studies of water and salt metabolism in a number of avian taxa have demonstrated considerable variation in saline tolerance, the ability to produce a concentrated urine, and survival without drinking water (Batholomew and Cade 1963; Cade et al. 1965; Smyth and Bartholomew 1966; Greenwald et al. 1967). Presumably these differences should, at least in part, be related to variations in renal medullary organization. The avian renal medulla, consisting of a series of medullary lobules, is organized much differently than its mammalian counterpart. Each medullary lobule is associated with one or more cortical lobules and contains collecting ducts, loops of Henle, and capillaries. From the distal to the proximal end of a medullary unit (using the ureter as the point of reference) the collecting ducts are gradually reduced in number by dendritic fusion. Proximally, the remaining collecting ducts fuse to form ureteral branches which drain directly into the ureter. Earlier diagrams and descriptions (Sperber 1960; Poulson 1965) have over-simplified the configuration of individual medullary lobules and their arrangement as a system within the kidney. That this system is often tortuous and elaborate has not been recognized. This lack of understanding probably relates to the fact that one can be easily misled when studying the medullary system in sectioned materials.

MATERIALS AND METHODS

We have devised an india ink injection procedure which allows the direct visualization of the entire medullary system of an intact kidney. To accomplish this, one removes the synsacrum (kidneys and ureters in situ) from a freshly killed bird, and then (under suitable magnification) frees the ureters posteriorly from adjacent connective tissue. One can introduce a fine hypodermic into a ureter, and with the aid of an assistant, administer a retrograde injection which fills the collecting ducts. The injected kidneys are hardened and dehydrated in alcohol, dissected free from the synsacrum, and cleared in methyl salicylate.

From such preparations (fig. 1) the number of medullary lobules per kidney, their lengths, and configurations were readily determined. Distally, a medullary unit arises as a flower-like mass of collecting ducts which converge from adjacent cortical lobules to form an organized structure bounded by a delicate connective tissue sheath (figs. 1a, 2). Length measurements were made with an ocular micrometer in a dissecting microscope. They represent the distance (either curved or straight; see below) from the point of initial collecting duct convergence to a proximal level (close to the ureter) where only a few large collecting ducts and the longest loops of Henle remain. Within a species there tends to be a direct relationship between the length of medullary units and the relative complexity of their configuration. Each medullary unit was assigned to one of four categories (S, C_1, C_2, and C_3) descriptive of its shape. A lobule designated S is relatively straight or only slightly curved, and would not be encountered more than once in any transverse section passing through its length. Types C_1, C_2, and C_3 represent progressively greater distal curving, such that the three types are J-shaped, U-shaped, and S- or W-shaped, respectively. Some C_3 units were twisted upon themselves to form configurations more bizarre than suggested here. In transverse sections, the same C_1 unit would be encountered twice in some sections, a C_2 unit would be found twice in most sections, and a C_3 unit would, in many sections, be seen three or four times.

As an adjunct to the injection studies, quantities of cortex and medulla were determined from a representative group of serially sectioned kidneys. Outline drawings of the projected images of every fourth transverse 10 μ section were traced on paper. Each tracing showed the boundary of the section plus outlines of medulla and conspicuous blood vessels within. The drawings were cut apart (blood vessels were eliminated from consideration) and the relative percentages of cortex and medulla determined by weighing the pooled cut-outs from a given kidney.

Siller and Hindle (1969) argue that the term "lobe" has been misused in most descriptions of avian kidney morphology. As an alternative, they urge that the term "division" be applied in this context. Their suggestion appears valid, and has been adopted in this paper.

RESULTS AND DISCUSSION

Based upon information from the literature, the taxa studied (table 1) can be categorized as to their relative efficiency in water economy. The inability of salt marsh races of the Song Sparrow to maintain weight when drinking saline solutions in excess of 50 per cent sea water (Bartholomew and Cade 1963) implies that the inland race used in this study (*Melo-*

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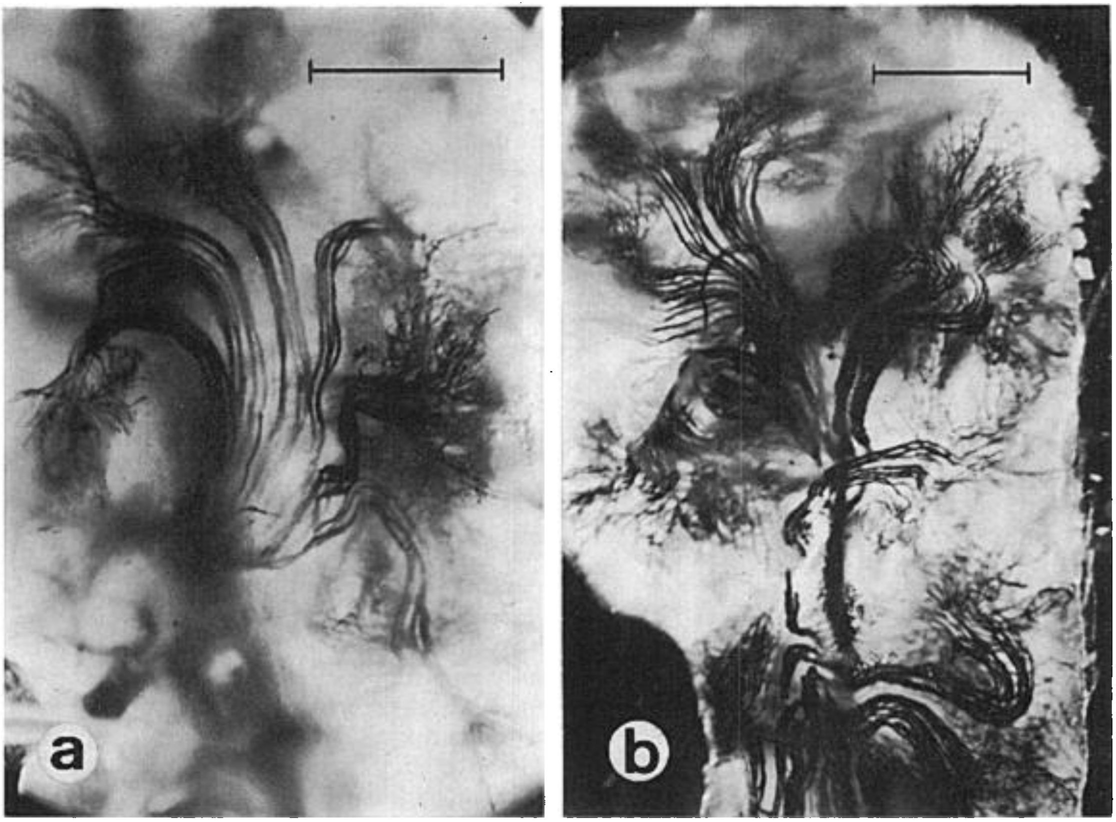

FIGURE 1. (a) Several medullary lobules (each shown by a cluster of injected collecting ducts) in the posterior division of a Budgerigar kidney. Note the flower-like mass of collecting ducts converging from surrounding cortex at the distal end of each lobule. (b) A portion of the medullary system in the anterior and middle divisions of a House Finch kidney. Configurational variation of lobules is evident in both photographs. Scale lines equal 1 mm.

spiza melodia juddi) is even less efficient. Compared to the House Finch (*Carpodacus mexicanus*), the Nevada Savannah Sparrow (*Passerculus sandwichensis nevadensis*) can tolerate slightly greater salinity (0.40 as opposed to 0.25 M NaCl), but nonetheless is relatively unspecialized (Bartholomew and Cade 1958; Cade and Bartholomew 1959). In contrast to the above taxa, the Zebra Finch (*Taeniopygia castanotis*), Black-throated Sparrow (*Amphispiza bilineata*), and salt marsh Savannah Sparrow (*P. s. beldingi*) display considerable saline tolerance and/or the ability to withstand long periods without drinking water (Cade and Bartholomew 1959; Poulson and Bartholomew 1962; Oksche et al. 1963; Smyth and Bartholomew 1966). The Budgerigar (*Melopsittacus undulatus*) can be regarded as intermediate with respect to the extremes described above. It is intolerant to saline solutions exceeding 0.3 M NaCl, but is capable of living for extended periods without drinking water (Cade and Dybas 1962; Greenwald et al. 1967).

Renal histology in the House Finch and in two races of the Savannah Sparrow (*P. s. beldingi* and *P. s. brooksi*) was studied by Poulson (1965), who concluded that there was a direct relationship between the number of Henle's loops and relative capacity to concentrate urine. Poulson used the mean number of medullary lobules in representative transverse sections as an index to the number of Henle's loops present. Subsequently, McNabb (1969) employed the same technique in a comparative study of three species of quail. An inherent assumption of this approach is that a given medullary unit be counted only once per section wherein it occurs. The extensive curving and configurational variation demonstrated in the present study (table 1) indicate that this is not a valid assumption.

Nonetheless, Poulson's concept of a direct relationship between the number of Henle's loops and urine concentrating ability tends to be supported by this work. The kidneys of salt marsh Savannah Sparrows are large in proportion to body weight and contain an

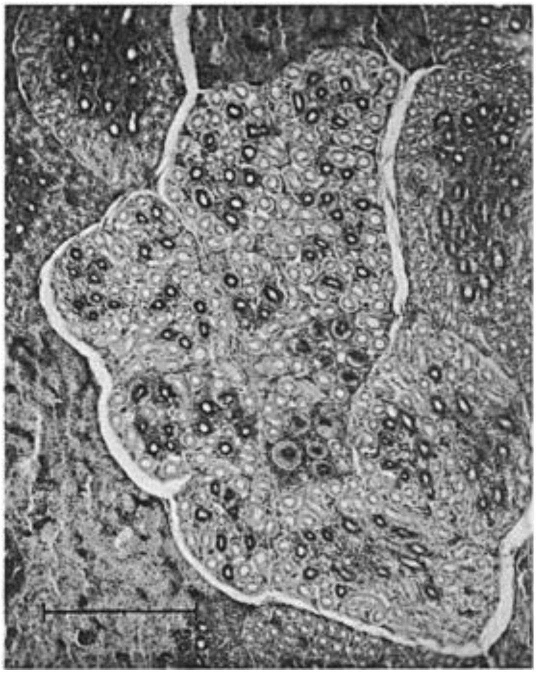

FIGURE 2. A group of closely packed medullary lobules in a salt marsh Savannah Sparrow kidney. Each lobule is defined by a central cluster of collecting ducts, and is lightly coated by connective tissue. A common sheath of connective tissue (partially separated from adjacent cortex) surrounds the entire complex. The tissue was fixed in AFA, then stained in alcian blue, followed by hematoxylin and eosin. Scale line equals 0.25 mm.

abundance of medullary units (table 1). When equivalent quantities of kidney tissue from the other taxa are compared to the latter, one sees a relatively sharp contrast in the number of medullary units per kidney (index to number of Henle's loops) between the least efficient (table 1:a, b, c) and most efficient (table 1: e, f, g) forms. Assuming equal density of cortical and medullary tissues, the quantity of cortex per medullary lobule can be calculated from the data in table 1. Such calculations approximate a two- to three-fold difference between the kidneys of the two groups. In the less efficient forms each medullary lobule drains 1.6 to 1.9 mg of cortex, with corresponding values in the efficient group ranging from 0.6 to 1.1 mg. Hence, an abundance of medullary lobules, with each draining a relatively small quantity of cortex, suggests that the kidneys of taxa e, f, and g of table 1 contain a high proportion of medullary nephrons. Such a relationship is consistent with the high urinary chloride levels (maxima of 960 and 703 mEq/liter, respectively) in salt marsh Savannah Sparrows and Black-throated Sparrows (Poulson and Bartholomew 1962, Smyth and Bartholomew 1966). Similar data are lacking for the Zebra Finch; however it is pertinent that Calder (1964) noted relatively dry excreta from water-restricted birds of that species.

While the number of Henle's loops appears

TABLE 1. Summary of quantitative features in the avian renal medulla.

Species	% medulla	Range in no. medullary units/kidney: Actual	Wt.[a] relative	Length of units[b] Mean mm: A	M	P	% units curved[b]: A	M	P	T[c]	Kidney wt.[d]: $\bar{x}$ g	% body wt.	n
a. *Melospiza melodia juddi*	7.2	57–62	76–83	1.6	1.2	1.4	20	53	35	9	0.225	1.1	13
	5–5[e]	5–6[e]		55[f]	29[f]	68[f]							
b. *Passerculus sandwichensis nevadensis*	9.7	55–60	79–86	1.6	1.3	1.5	32	88	60	17	0.209	1.2	18
	4–4	8–11		34	26	109							
c. *Carpodacus mexicanus*	12.7	55–63	69–79	2.0	1.5	1.8	45	85	68	31	0.239	1.2	5
	3–3	5–7		76	47	113							
d. *Melopsittacus undulatus*	13.3	60–68	76–86	2.6	2.1	2.6	57	100	93	58	0.238	0.7	12
	4–6	4–5		51	27	129							
e. *Taeniopygia castanotis*	11.0	40–45	116–130	1.8	1.5	1.7	68	100	93	68	0.104	1.0	16
	3–6	5–9		65	35	88							
f. *Amphispiza bilineata*	15.4	60–65	124–134	2.2	1.9	2.2	58	100	96	65	0.146	1.1	12
	5–6	6–8		48	35	48							
g. *Passerculus sandwichensis beldingi*	22.2	180–195	180–195	1.7	1.6	1.7	62	80	68	51	0.302	1.6	6
	5–5	6–6		206	107	299							

[a] In proportion to the weight of *P. s. beldingi* kidneys.
[b] Values refer to the anterior (A), middle (M), and posterior (P) kidney divisions, respectively.
[c] Per cent of total curved units falling in C_2 and C_3 categories (see text).
[d] Weights represent both kidneys after fixation in AFA; 100 × pooled kidney wt. (g)/pooled body wt. (g); final no. = sample size.
[e] Number of birds followed by no. of kidneys evaluated.
[f] Number of medullary lobules measured in each division.

to have major significance in kidney efficiency, the possible effects of variation in length and configuration of medullary lobules should not be overlooked. Several points can be made. First, relatively short medullary units lacking extensive curving (as indexed by the low proportion of C_2 and C_3 lobules) are typical among less efficient forms (table 1:a, b, c). Second, although the Budgerigar has small kidneys (in proportion to body weight) without abundant medullary units, the latter are long and extensively curved (table 1, fig. 1a). Perhaps these features are related to the ability of Budgerigars to survive for lengthy periods without drinking water (Cade and Dybas 1962). Third, the absolute lengths of medullary units in kidneys of the Zebra Finch and Black-throated Sparrow are somewhat misleading. Relatively speaking, these units are long since they are contained within very small kidneys (table 1). This situation resembles efficient mammalian concentrators (i.e., desert rodents) which in relation to kidney dimensions display a thick renal medulla. In absolute terms, the thickness of the latter is often much less than in poor concentrators (Sperber 1944). Fourth, perhaps elaborate curving (high proportions of C_2 and C_3 units) represents only a concomitant of increasing length or abundance of medullary lobules (table 1:d, e, f, g). On the other hand, it produces an intricate arrangement of counter-current systems (each clad only lightly in connective tissue) which seems worthy of further study. Of a related nature is the fact that as length and/or abundance of medullary units increase, there is a much greater degree of interlobular association. This often brings adjacent medullary units together over most of their length, forming extensive masses of closely packed medullary tissue (fig. 2). While a prominent connective tissue coat surrounds each mass (Poulson 1965), the individual medullary units within are ensheathed very lightly. Thus, differences in the length, configuration, and arrangement of medullary lobules may have functional significance especially when viewed against a background of potential variation in hemodynamics and the efficiency of transport processes.

Medullary characteristics differ somewhat in each kidney division (table 1). The cranial portion of the anterior division generally contains a series of relatively straight medullary lobules which converge at the apex of the ureter. Hence the proportion of curved units is lower here than elsewhere. Medullary lobules in the anterior and posterior divisions are

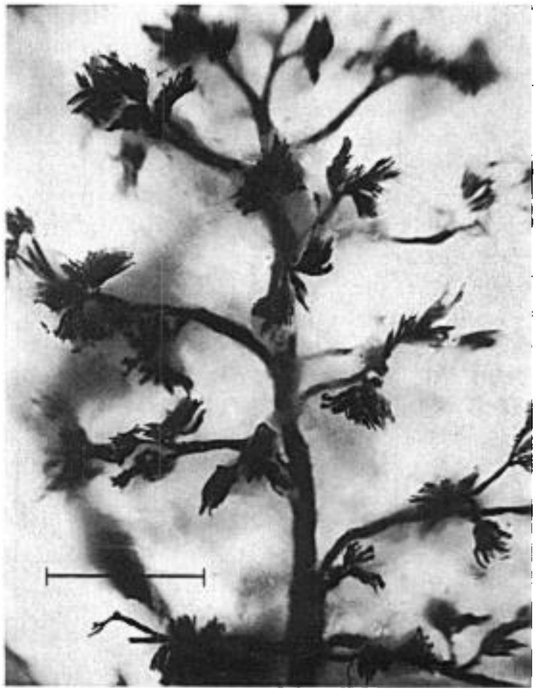

FIGURE 3. The anterior division of an injected coot kidney. Medullary lobules are clustered at the ends of long ureteral branches. Scale line equals 3 mm.

essentially equal in length and distinctly longer than those in the middle division. However, the latter contains the greatest proportion (up to 100 per cent) of curved units. All injected passerine kidneys showed three regions of medullary-ureteral association separated by unbranched segments of ureter. This further substantiates the concept that passerine kidneys are composed of three divisions, a feature often obscure externally (Johnson 1968).

Preliminary observations on the injected kidneys of several non-passerine species indicate further variation. For example, cormorant (*Phalacrocorax auritus*), Blue-winged Teal (*Anas discors*), and coot (*Fulica americana*) kidneys contain short (1.5 mm or less), straight, medullary lobules set in clusters at the ends of long ureteral branches (fig. 3). One would infer that there is a low proportion of medullary nephrons in these forms. In relation to its size, the Mourning Dove (*Zenaidura macroura*) kidney contains relatively short (about 2 mm), straight, medullary units which are few in number (approximately 45 per kidney) but greater in diameter than the passerine units studied.

SUMMARY

This report presents quantitative information on the renal medullae of seven taxa which vary in kidney efficiency. Most of the data were

obtained by a procedure (injection followed by clearing) which offers considerable potential in further studies of avian kidney organization. Per unit of kidney cortex, medullary lobules are two to three times more abundant in effective water conservers. This supports the concept of a direct relationship between the abundance of Henle's loops and urine concentrating ability.

However, there are also other variables of potential significance which should be evaluated further. Examples include: (1) Zebra Finch and Black-throated Sparrow kidneys which in relation to their size contain long medullary units, a feature similar to efficient mammalian concentrators; and (2) a greater degree of interlobular association notable in the medullae of more effective concentrators.

Extensive ureteral branching terminating in relatively short medullary lobules was found in several non-passerine species.

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