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A qualitative analysis of the kidney structure of Meliphagid honeyeaters from wet and arid environments

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ABSTRACT

The qualitative ultrastructural renal anatomy was examined in 4 species of honeyeater (parvorder Corvi) inhabiting 2 distinctly different environments. The kidneys of the wet zone New Holland honeyeater *Phylidonyris novaehollandiae* and little wattlebird *Anthochaera lunulata* were compared with those of the arid zone white-fronted honeyeater *Phylidonyris albifrons* and spiny-cheeked honeyeater *Acanthogenys rufogularis*. The size and structure of glomeruli were similar between species. In all species, except in *P. novaehollandiae*, the proximal tubule cells contained wide intercellular spaces filled with basolateral cell membrane interdigitations. Medullary nephron tubules were arranged in a sequential manner in all species. Thick and thin limbs of Henle were separated by the collecting ducts and extended the entire length of the medulla, a situation not found in muscicapid passerines. This tubular arrangement is not entirely consistent with the proposed single-effect countercurrent multiplier theory. The thin limb of Henle consisted of only one epithelium type, which had wide intercellular spaces. The thick limb of Henle consisted of 2 types of epithelial cells, each having narrow intercellular spaces, but with varying degrees of cell membrane infoldings. The ultrastructural morphology of the limbs of Henle in honeyeaters differed from those of muscicapid passerines. The ultrastructure of the distal nephron was similar in each species studied. All of the above nephron characteristics are considered to enable honeyeaters to absorb a large proportion of solutes and water from the glomerular filtrate.

INTRODUCTION

Passerine birds have evolved from 2 separate radiations, the parvorder Muscicapae, whose extant members are represented mainly by northern hemisphere species, and the parvorder Corvi, whose members are represented by southern hemisphere species (Sibley & Ahlquist, 1985; Sibley et al. 1988). Most studies on avian kidney morphology have concentrated on muscicapid passerines (Johnson & Mugaas, 1970; Nicholson, 1982; Nicholson & Kendall, 1983; Goldstein & Braun 1986; Warui, 1989), with only one study (Johnson & Skadhauge, 1975) examining briefly 2 species of corvid passerines. It is possible that due to their different evolutionary backgrounds, passerines from the 2 radiations may have different renal morphologies.

Australian honeyeaters are distributed widely throughout the continent, inhabiting vastly different environments. Some species are restricted to arid climates, while others inhabit more temperate climates (Blakers et al. 1984). Osmoregulatory demands are quite different for birds inhabiting such environmental extremes due, in part, to variations in diets (Braun, 1980). Arid zone honeyeaters feed predominantly on insects (Pyke, 1980) which, whilst restricted in the amount of water, contain high levels of sodium (31.5–65.0 mmol/l) and potassium (25.2–44.3 mmol/l) (Chapman, 1969; Wigglesworth, 1972; Nicolson & Worswick, 1990). Dietary restrictions coupled with the limited availability of water in arid Australia means that arid zone honeyeaters face the problem of water conservation. In contrast, most wet zone honeyeaters have a predominantly nectarivorous diet (Pyke, 1980), which contains a large quantity of water but small quantities of sodium (3.4–9.8 mmol/l) and potassium (18.7–24.7 mmol/l) (Hiebert & Calder, 1983; Nicolson & Worswick, 1990). These birds must filter large amounts of liquid yet extract the limited quantity of available ions. Strategies for either water or solute retention may require differences in kidney nephron structure.

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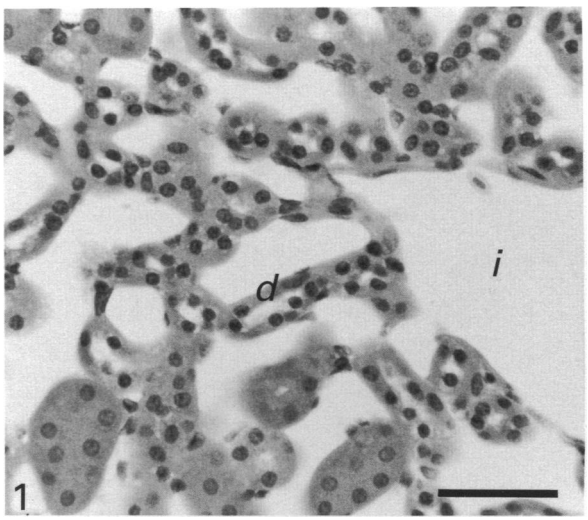
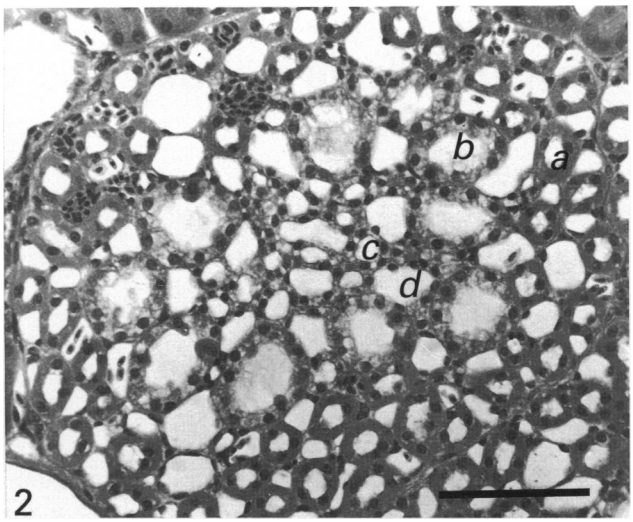
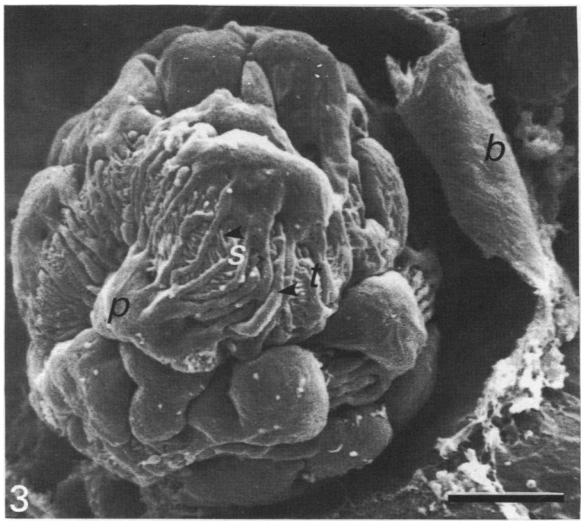
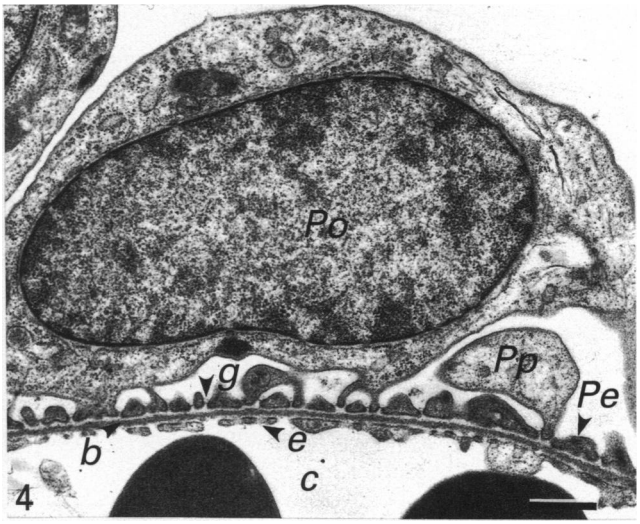
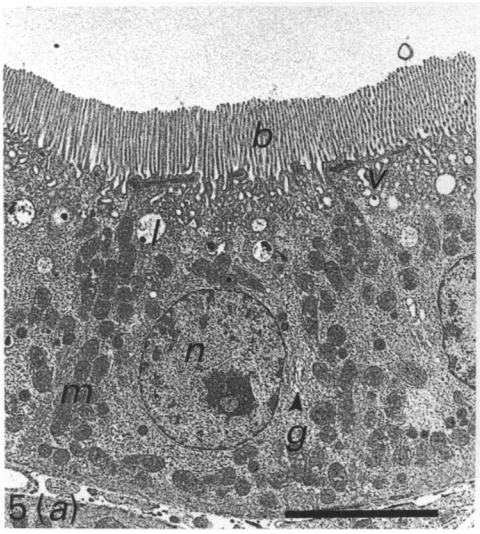










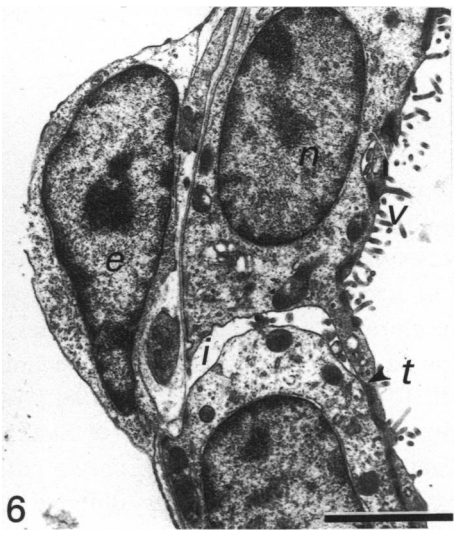


Fig. 1. Histological section of the kidney of *Acanthogenys rufogularis*. Note the concentric arrangement of distal tubules around the intralobular vein. *d*, distal tubules; *i*, intralobular vein. Haematoxylin-eosin. Bar, 50 μm.

Fig. 2. Histological section of a medullary cone in the kidney of *Phylidonyris albifrons*. Note the arrangement of tubules. *a*, thick ascending limb of Henle; *b*, collecting duct; *c*, thin descending limb of Henle; *d*, capillary. Haematoxylin-eosin. Bar, 250 μm.

Fig. 3. Electron micrograph of a glomerulus in *Phylidonyris albifrons*. *b*, Bowman's capsule; *p*, podocyte; *t*, trabeculae (arrowed); *s*, secondary process (arrowed). Bar, 10 μm.

The avian kidney is unique amongst vertebrates in that the cortex and medulla are arranged in a series of cones which are distributed and oriented randomly (Braun & Dantzler, 1972; Dantzler & Braun, 1980). The avian kidney has both looped (i.e. with a loop of Henle) as well as loopless nephrons. A number of anatomical features have been correlated with the ability to produce a hyperosomotic urine including the number of cones (Braun, 1980), the length of the loop of Henle (Goldstein & Braun, 1989) and the percentage and relative thickness of the renal medulla (Schmidt-Nielsen & O'Dell, 1961; Heisinger & Breitenbach, 1969). However, these variables have been inconsistent in predicting renal concentrating ability (Johnson, 1974; Jamison, 1987; Beuchat, 1990). Urine is thought to be concentrated by the movement of sodium chloride from the thick to the thin limb of Henle, without the accompaniment of water. This increases the osmotic concentration in the medullary interstitium and allows reabsorption of water from the collecting duct (Nishimura et al. 1989). The ability to conserve ions and/or water may be correlated with the structure of the nephron. Previous ultrastructural studies have concentrated on the nephron anatomy of the domestic fowl *Gallus domesticus* (Siller, 1971; Hodges, 1974) and very few studies have been undertaken on other species (Nicholson, 1982; Morild, Bohle & Christensen, 1985; Braun & Reimer, 1988).

In a previous paper (Casotti & Richardson, 1992), the quantitative anatomy of 4 honeyeater species was examined. It was found that arid zone honeyeaters had a higher percentage and absolute volume of renal medulla, whilst wet zone honeyeaters had a higher percentage and absolute volume of cortex. In the current study, the qualitative renal ultrastructure of the same species, the New Holland honeyeater *Phylidonyris novaehollandiae*, little wattlebird *Anthochaera lunulata*, white-fronted honeyeater *Phylidonyris albifrons* and spiny-cheeked honeyeater *Acanthogenys rufogularis*, was examined. The aim was to identify, by both light histology and electron microscopy, anatomical differences between wet and arid zone species consistent with a need to conserve either ions or water, respectively.

MATERIALS AND METHODS

Honeyeaters were collected in Western Australia, under licence, using mist nets. The renal anatomy of exclusively wet versus arid zone honeyeaters was compared qualitatively. The kidneys of *P. novaehollandiae* and *A. lunulata* were compared with those of *P. albifrons* and *A. rufogularis*. Six birds of each species were used in this study.

Captured honeyeaters were killed in the field with an overdose of sodium pentobarbitone administered intraperitoneally. Heparin was added to the barbiturate to prevent blood coagulation. Whole body perfusions were done by an injection through the left ventricle of half-strength Karnovsky fixative (1.5% glutaraldehyde, 0.8% paraformaldehyde, 0.066 M phosphate buffer), osmolality 320 mOsm/kg H_2O. The kidneys were dissected free from the retroperitoneum and stored in half-strength Karnovsky fixative for 72 h.

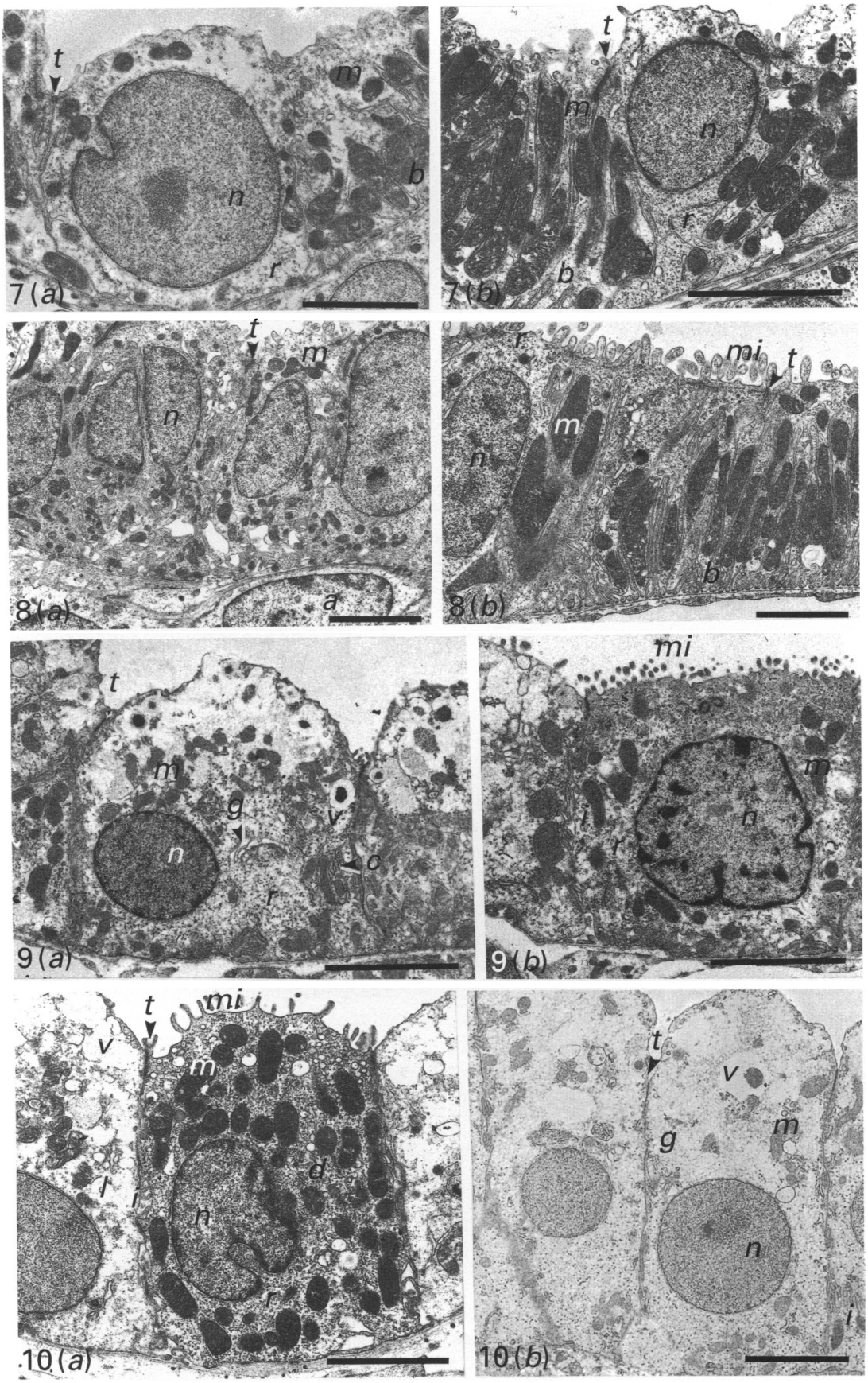
For the purpose of this study, the anatomy of both kidneys were assumed to be identical. The right kidney was processed routinely for light microscopy. It was placed in 10% neutral buffered formalin, then through a series of graded alcohols, chloroform and eventually into paraffin wax. Ten transverse parallel interrupted serial sections were taken at equal intervals along the length of the kidney. At each of the 10 levels, two 5 μm sections were cut. One was stained with haematoxylin and eosin, the other with periodic-Schiff (PAS)-Alcian Blue (pH 2.5). The latter stain was essential to distinguish cortical collecting tubules from distal tubules (Nicholson, 1982). The maximum diameters of 100 renal corpuscles, 50 from the peripheral cortex and 50 juxtamedullary, were measured on sections using a compound microscope fitted with an eye-piece micrometer.

The left kidney of 3 birds per species were processed routinely for transmission electron microscopy. The tissue was cut into 1 mm^3 blocks, postfixed in 1% Dalton's osmium tetroxide, washed in a series of graded alcohols, then infiltrated with propylene oxide and embedded in epon resin. Sections were cut to a thickness of 90 nm and stained with uranyl acetate and lead citrate. After carbon-coating, the specimens

Fig. 4. Electron micrograph of a podocyte (*Po*) and glomerular filtration membrane from *Acanthogenys rufogularis*. *b*, glomerular basal lamina (arrowed); *c*, capillary; *e*, fenestrated endothelium (arrowed); *g*, glomerular slit membrane (arrowed); *Pe*, pedicel; *Pp*, secondary podocyte process. Bar, 1 μm.

Fig. 5. Electron micrographs of a proximal tubule in *Anthochaera lunulata* (*a*) and *Acanthogenys rufogularis* (*b*). Note differences in the intercellular spaces and cell membrane infoldings. *b*, brush border; *g*, Golgi apparatus (arrowed); *i*, interdigitated infoldings of the cell membrane; *l*, lysosome; *m*, mitochondria; *n*, nucleus; *v*, apical vesicle. Bars 5 μm (*a*) and 1 μm (*b*).

Fig. 6. Electron micrograph of a descending limb of Henle cell epithelium in *Acanthogenys rufogularis*. *e*, capillary endothelial cell; *i*, intercellular space; *n*, nucleus; *t*, junctional complex (arrowed); *v*, microvilli. Bar, 5 μm.



Figs 7–10. For legends see opposite.

were viewed in a Philips 301 transmission electron microscope. The remaining tissue was processed routinely for scanning electron microscopy. The tissue was cut into 3 mm^3 blocks, postfixed in 1% Dalton's osmium tetroxide, washed in a series of graded alcohols and infiltrated with amyl acetate. The tissue was then critical point dried, mounted onto stubs and sputter-coated with gold. The specimens were viewed in a Philips 501 scanning electron microscope.

RESULTS

Unless stated otherwise, the renal anatomy was identical in wet and arid zone honeyeaters. Within the cortex, most nephron tubules were distributed randomly, except for the glomeruli which occurred most commonly in the peripheral cortex and the majority of distal tubules which were clustered around the intralobular veins (Fig. 1). Within the medulla, nephron tubules had an orderly distribution along the entire length of the cone. Thick ascending limbs of Henle were restricted to the periphery of the medullary cone and surrounded a ring of collecting ducts, which in turn surrounded a cluster of thin descending limbs of Henle (Fig. 2).

As there were no differences in the ultrastructural anatomy at any segment between looped and loopless nephrons, the following descriptions are for both nephron types.

Renal corpuscle

In all species, renal corpuscles varied in size. Those situated in the peripheral cortex had a diameter of approximately 30 μm and those in a juxtamedullary position had a diameter of approximately 40 μm. The renal corpuscle consisted of a centrally located glomerulus encapsuled within Bowman's capsule (Fig. 3). The glomerulus consisted of a tightly packed central core of mesangial cells, surrounded by capillary loops, the walls of which were composed of a fenestrated endothelium (Fig. 4). Surrounding this was a 3-layered glomerular basal lamina, surrounded by a layer of pedicels separated by the glomerular slit membrane (Fig. 4). Podocytes surrounded the capillaries and branched into trabeculae, secondary processes and pedicels (Figs 3, 4).

Proximal tubule

The proximal tubule was connected directly to the urinary pole of the glomerulus and consisted of a cuboidal epithelium. The cytoplasm contained a central nucleus, numerous mitochondria in the basal three-quarters of the cell, Golgi apparatus and rough endoplasmic reticulum (Fig. 5*a*). The apical one third of the cell contained a layer of lysosomes and above this a layer of apical vesicles and apical pits. The luminal surface area was enhanced by a 2 μm thick layer of microvillus brush border (Fig. 5*a*). Adjacent cells were joined by junctional complexes.

Narrow and wide intercellular spaces were found between cell membranes. Where wide intercellular spaces were present, adjacent cells were approximately 1 μm apart and filled with fine, microvillus-like, interdigitated infoldings of the cell membrane (Fig. 5*b*). The occurrence of this type of intercellular space varied between honeyeater species. In *P. novaehollandiae*, intercellular spaces were narrow and infoldings were absent (Fig. 5*a*). In *P. albifrons* and *A. lunulata*, both types of intercellular spaces occurred, while in *A. rufogularis* only wide intercellular spaces with interdigitated infoldings were present (Fig. 5*b*).

Limbs of Henle

The thin descending limb of Henle arose abruptly from the proximal tubule as it entered the medulla and consisted of a cuboidal epithelium. The cytoplasm contained a basal nucleus, a few mitochondria,

Fig. 7. Electron micrographs of the 2 types of cuboidal epithelial cells in a thick ascending limb of Henle. (*a*) A proximal segment in *Anthochaera lunulata* and (*b*) a distal segment in *Phylidonyris novaehollandiae*. *b*, basal labyrinth; *m*, mitochondria; *n*, nucleus; *r*, polyribosomes; *t*, junctional complex (arrowed). Bar, 5 μm.

Fig. 8. Electron micrographs of (*a*) a macula densa and (*b*) a distal tubule in *Phylidonyris novaehollandiae*. *a*, granular cell (the portion shown did not contain granules); *b*, basal labyrinth; *m*, mitochondria; *mi*, microplicae; *n*, nucleus; *r*, polyribosomes; *t*, junctional complex (arrowed). Bar, 5 μm.

Fig. 9. Electron micrographs of the epithelium of a cortical collecting tubule in *Phylidonyris albifrons* showing (*a*) a principal and (*b*) an intercalated cell. *c*, cisternae of rough endoplasmic reticulum; *g*, Golgi apparatus; *i*, interdigitated cell membrane infoldings; *m*, mitochondria; *mi*, microplicae; *n*, nucleus; *r*, free ribosomes; *t*, junctional complex; *v*, mucopolysaccharide vesicle. Bar, 5 μm.

Fig. 10. Electron micrographs of (*a*) a dark cell in the proximal segment of a collecting duct in *Anthochaera lunulata* and (*b*) cells of a papillary duct in *Phylidonyris albifrons*. *d*, dark cell; *g*, Golgi apparatus; *i*, interdigitated cell membrane infoldings; *l*, light cell; *m*, mitochondria; *mi*, microplicae; *n*, nucleus; *r*, free ribosomes; *t*, junctional complex (arrowed); *v*, mucopolysaccharide vesicle. Bar, 5 μm.

lysosomes and free ribosomes (Fig. 6). The apex of each cell was covered with short microvilli. Wide intercellular spaces up to 750 nm wide, occurred between adjacent cells culminating apically in junctional complexes (Fig. 6). The thick ascending limb of Henle consisted of a cuboidal epithelium which varied in ultrastructural appearance along its length. The cytoplasm of the proximal portion contained a central nucleus, mitochondria enveloped within a basal membranous labyrinth and free ribosomes (Fig. 7*a*). The cytoplasm of the distal portion was similar but contained numerous elongated mitochondria, enveloped within a complex basal membranous labyrinth and numerous polyribosomes (Fig. 7*b*). Adjacent cells of the thick ascending limb of Henle terminated at junctional complexes.

Macula densa and distal tubule

The distal tubule was in intimate contact with the renal corpuscle of a nephron, forming the macula densa and juxtaglomerular apparatus. The nuclei of the macula densa cells were packed closely together and the cytoplasm contained smaller mitochondria, distributed and oriented irregularly, compared with distal tubule cells (Fig. 8*a*). Cells with relatively few organelles but with occasional electron-dense granules were present between the glomerulus and the macula densa.

The distal tubule consisted of a cuboidal epithelium. The cytoplasm contained a central nucleus surrounded by elongate mitochondria located within a basal labyrinth of the cell membrane (Fig. 8*b*). Other organelles included the Golgi apparatus, rough endoplasmic reticulum, lysosomes, free ribosomes and polyribosomes (Fig. 8*b*). Adjacent cells were connected by close intercellular spaces terminating apically at junctional complexes. The cell luminal surface bulged apically into the lumen and contained few microplicae.

Cortical collecting tubule

The cortical collecting tubule consisted of a cuboidal epithelium which contained principal and intercalated cells, the ratio of these cell types appeared to be similar between species. The cytoplasm of each principal cell contained a basal nucleus, a few mitochondria, Golgi apparatus, ribosomes, cisternae of rough endoplasmic reticulum, and numerous mucopolysaccharide vesicles in the upper one third of the cell (Fig. 9*a*). The mucopolysaccharide stained positive with Alcian Blue and PAS. The cell membrane contained infoldings which terminated apically at junctional complexes. The cytoplasm of each intercalated cell contained a central nucleus, numerous mitochondria and free ribosomes (Fig. 9*b*). Interdigitating infoldings extended into the cytoplasm from the cell membrane. The cell luminal surface was flattened and covered with a layer of microvilli (Fig. 9*b*).

Collecting duct

The collecting duct consisted of a proximal segment and a distal papillary duct. The proximal segment consisted of a columnar epithelium which contained light cells and dark cells (Fig. 10*a*). The cytoplasm of each light cell contained a basal nucleus, a few mitochondria, rough endoplasmic reticulum, numerous mucopolysaccharide vesicles and free ribosomes. The cell membrane contained interdigitated infoldings between narrow intercellular spaces which terminated apically in junctional complexes (Fig. 10*a*). The cytoplasm of each dark cell contained a central nucleus, numerous mitochondria and free ribosomes (Fig. 10*a*). The luminal surface was covered with few short microvilli. The papillary duct consisted of a columnar epithelium, the cells of which contained a basal nucleus, Golgi apparatus, a few mitochondria and cisternae of rough endoplasmic reticulum (Fig. 10*b*). Apically situated mucopolysaccharide vesicles stained positive with Alcian Blue and PAS. Close intercellular spaces were lined with few interdigitated infoldings of the cell membrane which terminated apically at junctional complexes. The cell luminal surface bulged apically into the lumen (Fig. 10*b*).

DISCUSSION

Of the few qualitative studies of the passerine nephron structure, all have been of northern hemisphere birds of the parvorder Muscicapae (Johnson & Mugaas, 1970; Nicholson, 1982; Nicholson & Kendall, 1983; Goldstein & Braun, 1986). The current study is the first qualitative description of the kidney ultrastructure of Australo-Papuan species of the parvorder Corvi and has found that kidney ultrastructure differed between muscicapid and corvid passerines, but not between corvid honeyeaters from different environments. The latter was surprising given that within the Meliphagidae, diets vary, with wet zone species feeding predominantly on nectar, whilst arid zone species feed predominantly on insects (Pyke, 1980). In a previous paper (Casotti & Richardson, 1992), we found that the kidneys of wet zone

honeyeaters contained a higher proportion of cortex whilst arid zone honeyeaters contained a higher proportion of medulla. Given the different environmental and dietary restrictions, the renal concentrating ability of birds may vary (Braun, 1980). For the honeyeaters, this change would be the result of differences in the proportions of cortex and medulla rather than ultrastructural differences within the nephron tubules.

The current study found that the nephron organisation of the kidneys was identical in the species studied. Within the cortex, the majority of distal tubules surrounded the intralobular vein, an arrangement which has also been found in the kidneys of *G. domesticus* (Morild, Bohle & Christensen, 1985). In honeyeaters, the nephron tubules were arranged in an orderly manner for the entire length of the medulla, with the ascending and descending limbs of Henle being separated by the collecting ducts. This situation differs from the pattern of arrangement reported in muscicapid passerines, where tubules were arranged in an orderly manner only in the superficial areas of the medulla, and randomly deeper within the medulla (Johnson & Mugaas, 1970; Johnson, 1979; Goldstein & Braun, 1986; Nishimura et al. 1989). The functional significance of the ordered medullary tubule arrangement in passerines is unknown. The separation of the thick and thin limbs of Henle by the collecting ducts appears to complicate the current theory on the production of a concentrated urine in birds (Nishimura et al. 1989). In this theory, sodium chloride is transported actively from the ascending limb of Henle and passively into the descending limb of Henle. A close association between the descending and ascending limbs may facilitate the exchange of sodium chloride. In this manner, a single solute maintains a high medullary interstitial osmolality, essential for water reabsorption along the distal nephron.

Wet zone honeyeaters with a predominantly nectar diet need to filter a greater volume of fluid than do arid zone species with a predominantly insect diet. Studies have shown that freshwater fishes which must filter a large volume of fluid, had larger glomeruli than did salt water fishes which filter comparatively smaller volumes (Hickman & Trump, 1969). However, in honeyeaters, despite the different volumes of fluid filtered, the size of the renal corpuscles were similar in all species. The ultrastructure of the proximal tubule in *P. novaehollandiae* showed narrow intercellular spaces and simple basolateral interdigitations, compared with the other 3 species which had wide intercellular spaces and complex basolateral interdigitations. However, given that all species have the same phylogenetic origin, and that *A. lunulata* occupied the same niche as *P. novaehollandiae*, these differences cannot be explained. It is accepted that wide intercellular spaces coupled with extensive cell membrane infoldings are a characteristic of cells that have a high ion and water reabsorption capacity (Rhodin, 1963). For example, the gecko *Hemidactylus* sp. with elaborate infoldings of the cell membrane reabsorbed 80% of all filtered water and ions under hydrated conditions, whilst the horned lizard *Phrynosoma cornutum* and the Galapagos iguanid lizard *Tropidurus* sp. with no cell membrane infoldings, reabsorbed approximately 50% of the filtered water and ions (Roberts & Schmidt-Nielsen, 1966).

In honeyeaters, the ultrastructure of the descending limb of Henle is less complex than those found in the Syrian hamster *Mesocricetus aureatus*, which contained 3 different types of epithelial cells (Bachmann & Kriz, 1982) and the desert rodent *Psammomys obesus* (Barrett et al. 1978*a*, *b*) and Gambel's quail *Callipepla gambelii* (Braun & Reimer, 1988), in which 2 different types of epithelial cells were found. In contrast, the descending limb in honeyeaters had a single type of epithelial cell which resembled the type 2a epithelia in *M. aureatus*, the type 2 epithelium in *P. obesus* and the type B cells in *C. gambelii*. The wide intercellular spaces and few mitochondria in the thin limb of Henle epithelium are typical of a leaky epithelium which transport solutes passively (Braun & Reimer, 1988). In contrast, the epithelial cells of the thick limb of Henle in honeyeaters contained more mitochondria and individual cells were separated by narrow intercellular spaces. This ultrastructural morphology is similar to that found in *C. gambelii* (Braun & Reimer, 1988). However, in honeyeaters, the degree of cell membrane infolding increased distally along the segment, whereas in *C. gambelii* it decreased.

The macula densa in honeyeaters was not as well developed as in mammals, in not possessing taller cells with a basally located Golgi apparatus, but resembled closely those macula densa cells found in *G. domesticus* (Morild, Mowinckel, Bohle & Christensen 1985), *C. japonica* (Ogawa & Sokabe, 1971) and the common starling *Sturnus vulgaris* (Nicholson, 1982). No lacis cells were present in honeyeaters as has been reported in most avian studies thus far (Sokabe et al. 1969; Ogawa & Sokabe, 1971; Sokabe & Ogawa, 1974; Wideman et al. 1981). The ultrastructure of the distal tubule in honeyeaters was similar to that described in other avian species (Siller, 1971; Nicholson, 1982).

There was no difference in the epithelial ultrastructure of the cortical collecting tubule amongst wet and arid zone species. Previous studies have found

that both the principal and intercalated cells secrete potassium and reabsorb water, sodium and other ions (Grantham et al. 1970; Hansen et al. 1978; Evan et al. 1980; Stanton et al. 1984). Nicholson (1982) showed in *S. vulgaris* that the intercalated cells may undertake both potassium and water reabsorption. In the current study, the infoldings in the cell membrane of the cortical collecting tubules suggests the potential for substantial ion and water reabsorption. The principal cells secrete mucus to prevent uric acid precipitation, hence preventing blockage along the tubules of the distal nephron (Guzsal, 1970; Peek & McMillan, 1979). Since uric acid is a means of excreting solutes with minimal water loss, it might be expected that arid zone honeyeaters would have more principal cells and hence produce more uric acid than wet zone honeyeaters as a water conservation strategy. However, in this study, the number of principal cells appeared to be similar between species.

In all honeyeaters studied, the number of dark cells appeared to decline towards the papillary duct, a pattern also found in *S. vulgaris* (Nicholson & Kendall 1983) and in the kidneys of some mammals (Stanton et al. 1981). The collecting duct cell ultrastructure is typical of cells that absorb water passively into the interstitium (Jamison & Kriz, 1982).

The ultrastructure of the honeyeater kidney suggests that they have the capacity to absorb a large quantity of solutes and water from the glomerular filtrate. The proximal tubule contained wide intercellular spaces lined with interdigitated infoldings in all species, except in *P. novaehollandiae*. The medullary tubule organisation differed from muscicapid passerines, as did the ultrastructure of the thin limb of Henle which contained only one type of epithelial cell and the thick limb of Henle two epithelial cell types. As few differences were found in the ultrastructure of the nephron between wet and arid zone honeyeaters, possible differences in the urinary concentrating ability of species from different zones may simply be the result of differences in the proportion of cortex and medulla.

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