

Comparative renal morphology of some southern African otomyine rodents

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The kidney structure of 21 individual otomyine rodents representing six southern African taxa from localities with differing climatic profiles was studied by means of light microscopy. Variation in the data was accounted for primarily by relative cortex and medulla proportions. The kidneys of *Otomys angoniensis* Wroughton, 1906, *O. irroratus* (Brants, 1827) and *O. sloggetti robertsi* Hewitt, 1927 displayed mesic adaptation, and those of *O. unisulcatus* F. Cuvier, 1829, *Parotomys brantsii* (A. Smith, 1834) and *P. littledalei* Thomas, 1918 xeric adaptation, reflecting species-specific patterns of geographic distribution across southern African rainfall gradients. Neither mesic nor xeric renal characters appear optimally expressed in the species considered, and it is postulated that feeding habits and behavioural adaptations play a significant role in the water economy of otomyine rodents.

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Introduction

The physiology and anatomy of the mammalian kidney have been comparatively well studied, although more attention has been paid to arid adapted than to mesically adapted species (inter alia Sperber 1944, Schmidt-Nielsen 1964, MacMillen and Lee 1969, Marsh *et al.* 1978, Fyhn 1979, Rickart 1989). The range of urine concentrating potentials is particularly high among the rodents (Schmidt-Nielsen and O'Dell 1961, Fyhn 1979). Mesically adapted rodents have little ability to conserve urinary water (e.g. the North American mountain beaver *Aplodontia rufa* cannot elevate urine osmolality above 770 mOsm; Nungesser and Pfeiffer 1965). In contrast, many desert rodents concentrate the urine to levels unmatched by other mammals (e.g. the Australian hopping mouse *Notomys alexis* can achieve a urine concentration of 9370 mOsm; MacMillen and Lee 1967, 1969).

Anatomically, increases in kidney medulla width (especially of the inner medulla) and in the number of long-looped nephrons, as well as the appearance of secondary renal pyramids, are typically associated with high urinary concentrating abilities

(*inter alia* Sperber 1944, Schmidt-Nielsen 1964, Pfeiffer 1968, Moffat 1975, Fyhn 1979).

The murid subfamily *Otomyinae* (i.e. the vlei rats *Otomys* and the whistling rats *Parotomys*; Meester *et al.* 1986) is widely distributed across the primarily east-west southern African rainfall gradient (Davis 1974, Skinner and Smithers 1990), with representatives occurring in both the wettest and driest habitats. Hence, the subfamily is well suited to the study of adaptive variation and evolutionary trends in respect of kidney structure.

The present histological study was undertaken to describe and compare the kidneys of six southern African otomyine taxa: *Otomys angoniensis* Wroughton, 1906, *O. irroratus* (Brants, 1827), *O. sloggetti robertsi* Hewitt, 1927, *O. unisulcatus* F. Cuvier, 1829, *Parotomys brantsii* (A. Smith, 1834) and *P. littledalei* Thomas, 1918. These otomyines fall into broad mesophilic (*O. angoniensis*, *O. irroratus*, *O. s. robertsi*; Skinner and Smithers 1990) and xerophilic (*O. unisulcatus*, *P. brantsii*, *P. littledalei*; Davis 1962, Skinner and Smithers 1990) categories. On this basis, it was hypothesized that the otomyines display a continuum of renal structural adaptation, from extreme mesic adaptation on the one hand (cf *Aplodontia rufa*; Nungesser and Pfeiffer 1965) to extreme xeric adaptation on the other (cf *Notomys alexis*; MacMillen and Lee 1967, 1969). It was expected that the kidneys of the demonstrably mesophilic *O. irroratus* (*inter alia* Perrin 1981) would most closely approach the mesically adapted extreme, and those of *P. littledalei* (which does not occur in areas where rainfall exceeds 200 mm p.a.; see Skinner and Smithers 1990) the xerically adapted extreme.

Materials and methods

Animals used in the study were livetrapped at the localities detailed in Table 1, and were held captive for periods up to three weeks before sacrifice. They were maintained on a diet of grass (mainly *Panicum maximum*), cabbage, carrot and Epol rabbit pellets. Water was provided *ad libitum*, although the animals were never observed to drink.

In terms of standard taxonomic measurements (Skinner and Smithers 1990), all animals were adult when sacrificed. Body mass, the mass of the paired kidneys cleared of external fat, and head-body length were recorded immediately after sacrifice. Condylbasal skull length was measured following standard morphometric procedures once the skulls had been cleaned.

The kidneys were fixed in 10% buffered formalin for 3–6 days. Thereafter, they were sequentially cleared in alcohol and xylene, embedded in paraffin wax, and sectioned to 8 μm in both the transverse (right kidney) and sagittal (left kidney) planes; the sections were mounted and stained with haematoxylin and eosin (after Humason 1979).

The following structures were measured or counted using a Zeiss 2730 photomicroscope and optical micrometer: maximum kidney width; width of the inner and outer medulla and cortex (sagittal section); and number of glomeruli per 10^{-2} mm in both sagittal and transverse section. The number of nephrons represented per section was estimated by counting all visible glomeruli, and the number of long-looped nephrons by counting only those glomeruli in the juxtamedullary (sub-cortical) region, where the longest loops originate (Moffat 1975, Bulger and Dobyas 1982). In all cases, a minimum of 10 kidney sections containing the area cribrosa (approximately along the kidney midline) were

Table 1. Sample size (*n*) and locality data of the *Otomys angoniensis*, *O. irroratus*, *O. s. robertsi*, *O. unisulcatus*, *Parotomys brantsii* and *P. littledalei* populations represented in the study. Altitude and rainfall: South African localities – nearest weather station (Weather Bureau 1984), Aus – White 1983, Oxbow – Killick 1978. Veld type: Aus – White 1983, all other localities – Acocks 1988.

Species	<i>n</i>	Locality/grid reference	Environmental parameters		
			Mean annual Altitude (m)	Rainfall (mm)	Veld type and number
Mesophilic					
<i>O. angoniensis</i>	5	Hazelmere, Natal 29°34'S, 31°01'E	104	926	Coastal forest thornveld, 1
<i>O. irroratus</i>	5	Stutterheim, Cape 32°34'S, 27°26'E	809	759	Dohne sourveld, 44b
<i>O. s. robertsi</i>	3	Oxbow, Lesotho 28°46'S, 28°39'E	2591	1277	<i>Themeda-Festuca</i> alpine veld, 58
Xerophilic					
<i>O. unisulcatus</i>	5	Victoria West, Cape 31°24'S, 23°09'E	1256	253	Central upper Karoo, 27
<i>P. brantsii</i>	2	Springbok, Cape 29°40'S, 17°53'E	162	214	Namaqualand broken veld, 33
<i>P. littledalei</i>	1	Aus, Namibia 26°40'S, 16°16'E	1470	< 100	Sparse succulent vegetation, 74 (Namib desert)

examined, and mean values for all parameters were calculated for each animal. The presence of secondary renal pyramids was noted.

Principal components analysis (NTSYS; Rohlf 1988) was carried out on the correlation matrix obtained from the following five variables: kidney mass scaled to condylobasal skull length; inner and outer medulla and cortex widths expressed as percentages of total kidney width; and number of long-looped nephrons expressed as percentages of total glomeruli (sagittal section). These variables were chosen on the basis of reported physiological significance, as outlined above, by examining a correlation phenogram representing the data for all variables and each individual animal. The data set used in the principal components analysis was arcsine transformed because variables expressed as percentages are subject to statistical disadvantages such as non-normal distributions (see Pimentel 1979, Sokal and Rohlf 1987).

Results

Kidney size was highly variable between species (Table 2), with the mean mass of the kidneys of *O. s. robertsi* only 32% that of *P. littledalei*. Three measures of relative kidney size (Table 2) showed that the kidneys of xerophilic species (*O. unisulcatus*, *P. brantsii* and *P. littledalei*) were larger than those of mesophilic species (*O. angoniensis*, *O. irroratus* and *O. s. robertsi*). Kidney mass scaled to body mass was a poor indicator of relative kidney size: in captivity, all species other than *O. s. robertsi* accumulated much body fat, although fatness was individually variable. Kidney mass scaled to head-body and condylobasal skull length provided a more realistic indicator of relative kidney size (Table 2).

Table 2. Mass of the paired kidneys, and kidney mass relative to other measurements, of *Otomys angoniensis*, *O. irroratus*, *O. s. robertsi*, *O. unisulcatus*, *Parotomys brantsii* and *P. littledalei*. Sample sizes and localities as in Table 1. Two SE given in brackets.

Species	\bar{x} kidney mass (g)	Body mass (g)		Head-body length (mm)		Skull length (mm)	
		\bar{x}	Relative kidney mass	\bar{x}	Relative kidney mass	\bar{x}	Relative kidney mass
Mesophilic							
<i>O. angoniensis</i>	1.21 (0.14)	115.8 (12.6)	1.05	150.6 (12.9)	0.80	38.2 (0.5)	3.17
<i>O. irroratus</i>	1.76 (0.09)	172.3 (27.4)	1.02	181.3 (12.3)	0.97	41.4 (0.8)	4.25
<i>O. s. robertsi</i>	0.96 (0.07)	102.3 (16.4)	0.94	156.7 (8.8)	0.61	38.4 (1.2)	2.50
Xerophilic							
<i>O. unisulcatus</i>	1.88 (0.12)	117.6 (10.9)	1.60	151.4 (5.0)	1.24	36.0 (0.9)	5.22
<i>P. brantsii</i>	1.75 (0.15)	112.0 (1.0)	1.56	156.5 (5.5)	1.12	37.3 (0.8)	4.69
<i>P. littledalei</i>	3.00 –	107.0 –	2.80	154.0 –	1.95	40.0 –	7.50

Diagrammatic representations of sagittal sections in the midline of the kidneys of the six otomyines appear in Fig. 1. Mesophilic species had the kidney medulla width narrower than xerophilic species, with cortex width displaying an opposite trend. The ratio of inner medulla width to cortex width increased from mesophilic (*O. angoniensis* = 1.22, *O. irroratus* = 1.21, *O. s. robertsi* = 1.08) to the xerophilic group (*O. unisulcatus* = 3.56, *P. brantsii* = 3.01, *P. littledalei* = 3.42; Fig. 1).

Secondary renal pyramids were present in the kidneys of *O. unisulcatus* and the two *Parotomys* species. No clear mesic-xeric trend was observed in respect of the density of glomeruli in either the transverse or sagittal planes, although the

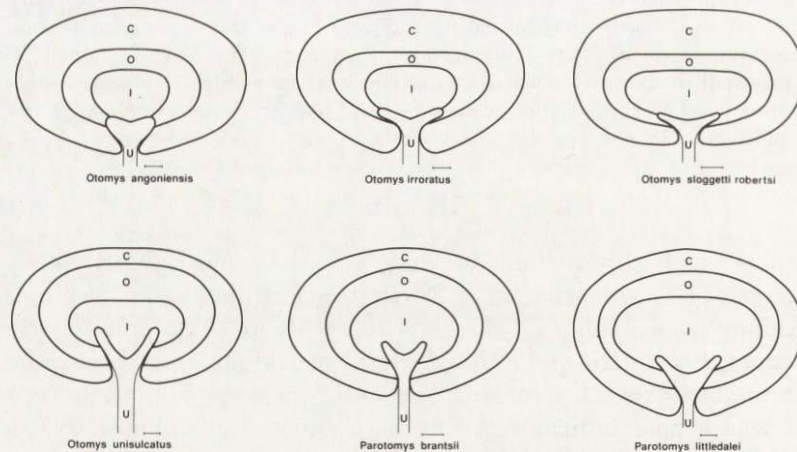


Fig. 1. Diagrammatic representation of sagittal sections in the midline of the kidneys of *Otomys angoniensis*, *O. irroratus*, *O. s. robertsi*, *O. unisulcatus*, *Parotomys brantsii* and *P. littledalei*. C – cortex, I – inner medulla, O – outer medulla, U – ureter. Scale lines represent 1 mm.

Table 3. Density of glomeruli per 10^{-2} mm, and number of glomeruli in sagittal section, in the kidneys of *Otomys angoniensis*, *O. irroratus*, *O. s. robertsi*, *O. unisulcatus*, *Parotomys brantsii* and *P. littledalei*. Sample sizes and localities as in Table 1. Two SE given in brackets.

Species	\bar{x} glomeruli per 10^{-2} mm		\bar{x} glomeruli per section		
	Transverse section	Sagittal section	Total	Long-looped nephrons	% long-looped nephrons
Mesophilic					
<i>O. angoniensis</i>	12.3 (0.4)	7.6 (1.2)	279 (10)	26 (2)	9.3
<i>O. irroratus</i>	16.7 (1.3)	13.2 (1.9)	381 (7)	33 (3)	8.7
<i>O. s. robertsi</i>	17.3 (1.2)	8.7 (0.7)	323 (18)	17 (2)	5.3
Xerophilic					
<i>O. unisulcatus</i>	14.3 (1.4)	11.9 (0.5)	269 (9)	41 (4)	15.2
<i>P. brantsii</i>	17.3 (1.8)	7.9 (1.0)	297 (5)	52 (2)	17.5
<i>P. littledalei</i>	19.6 -	7.9 -	315 -	67 -	21.3

percentage of long-looped nephrons was higher in xerophilic than in mesophilic species (Table 3).

Eigenvector loadings for the first three principal components from the principal components analysis are given in Table 4. Whereas the first two principal components accounted for 92.28% of the total variance, the third component only accounted for a further 5.55% of the variance. Consequently, only components one and two were considered in the analysis.

The first principal component was responsible for 78.82% of the observed variance, and was characterised by eigenvector loadings having mixed signs, which is indicative of a bipolar or 'shape' vector (Pimentel 1979). High eigenvector

Table 4. Eigenvector matrix of a five-variable principal components analysis of the kidneys of *Otomys angoniensis*, *O. irroratus*, *O. s. robertsi*, *O. unisulcatus*, *Parotomys brantsii* and *P. littledalei*.

Variables	Vectors		
	I	II	III
$\frac{\text{Kidney mass}}{\text{Skull length}} \%$	0.847	-0.468	0.197
$\frac{\text{Inner medulla width}}{\text{Total kidney width}} \%$	0.901	-0.386	-0.099
$\frac{\text{Outer medulla width}}{\text{Total kidney width}} \%$	0.840	0.490	0.205
$\frac{\text{Cortex width}}{\text{Total kidney width}} \%$	-0.957	-0.190	-0.124
$\frac{\text{Long loops}}{\text{Total glomeruli}} \%$	0.889	0.169	-0.414

loadings represent variables that contribute strongly towards a particular principal component, and variation in the first principal component is thus largely explained by an inverse relationship between relative cortex and inner medulla widths (eigenvector loadings of -0.957 , 0.901 respectively; Table 4). As in the first principal component, the second principal component was bipolar, variation being explained by the inverse relationship of relative kidney mass and outer medulla width (-0.468 and 0.490 respectively; Table 4).

The scatter of the first and second component scores for each animal is illustrated in Fig. 2. The first principal component clearly acted as a 'habitat' vector, separating the species into mesically and xerically adapted subsets. The second

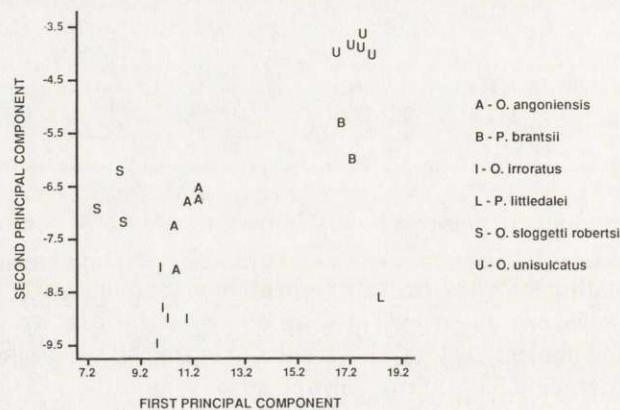


Fig. 2. Scattergram of the first two components of a five-variable principal components analysis of the kidneys of *Otomys angoniensis*, *O. irroratus*, *O. s. robertsi*, *O. unisulcatus*, *Parotomys brantsii* and *P. littledalei*.

principal component appears to have acted as a 'species-partial habitat' vector, with a perfect grouping by species of individuals of xeric origin along the gradient of environmental moisture (see Table 1). Species-specific separation of mesophilic species was less definite, with overlap between individual *O. angoniensis* and *O. irroratus*.

Discussion

The urine concentrating ability of the mammalian kidney is determined primarily by the proportions of the cortex and medulla (*inter alia* Schmidt-Nielsen and O'Dell 1961). It was therefore predictable that the relative width of these areas was mainly responsible for separating the kidneys of the otomyines considered here into comparatively mesically adapted (*O. angoniensis*, *O. irroratus*, *O. s. robertsi*) and xerically adapted (*O. unisulcatus*, *P. brantsii*, *P. littledalei*)

types. This relationship (i.e. mesophilic species with a larger cortex and smaller medulla, and the opposite in xerophilic forms) probably accounted for the bipolar ('shape') nature of the first principal component, which is very often a 'size' vector in morphometric analyses (Blackith and Reyment 1971).

Lack of a clear species-specific grouping of *O. angoniensis* and *O. irroratus* according to a mesic-xeric trend could be interpreted as contradicting the idea that a habitat factor partially determined the second principal component (Fig. 2). It is likely, however, that renal overlap between *O. angoniensis* and *O. irroratus* (Fig. 2) was determined by dietary and other ecological similarities between them (De Graaff 1981, Skinner and Smithers 1990). Furthermore, differences in the observed grouping patterns (i.e. xerophilic species discrete; mesophilic species partially overlapping; Fig. 2) may indicate that selection for renal modification is less severe in respect of mesophilic than xerophilic otomyines.

There is no consensus as to the precise physiological role of the two medullary regions of the mammalian kidney (see Fyhn 1979), but the ratio of inner medulla to cortex width (IM/C) is thought to provide a reliable index of urine concentrating potential: low and high IM/C ratios respectively indicate the production of dilute and concentrated urine (Fyhn 1979). IM/C ratios of the mesophilic otomyines (1.08–1.22) were predictably low. Comparison with other mesically adapted rodents is impossible because, as far as we are aware, no suitable data are available in, or can be extrapolated from, the literature. The comparatively low IM/C ratios of the xerophilic otomyines (3.01–3.56) indicate that the urine of these species is significantly less concentrated than that of extreme arid adapted rodents such as *N. alexis* (IM/C = 6.60; extrapolated from MacMillen and Lee 1969) and *Psammomys obseus* (IM/C = 5.45; extrapolated from Sperber 1944). However, secondary renal pyramids facilitate additional urine concentration (Pfeiffer 1968), and the presence of these structures in the kidneys of *O. unisulcatus* and both *Parotomys* species probably increases their urine concentrating potential. Clearly, detailed physiological studies are required to resolve questions raised here in respect of otomyine water metabolism.

Differences in the kidneys examined partially support the hypothesis upon which the study was based, namely that renal morphology would reflect the relative aridity of the habitats of the free-living *Otomys* and *Parotomys* populations. In neither mesophilic nor xerophilic otomyines was the degree of medullary development as marked as anticipated, however. Kidneys of the mesophilic otomyines are, particularly as regards the degree of medullary development, dissimilar to those rodents occupying permanently moist habitats; similarly, the kidney medulla widths of the xerophilic otomyines was less exaggerated than in many other arid adapted rodents (Sperber 1944, Schmidt-Nielsen 1964, Nungesser and Pfeiffer 1965, Fyhn 1979). Otomyine kidneys therefore appear comparatively conservative, and may be respectively categorized as 'intermediate mesic-adapted' and 'intermediate xeric-adapted' types, although for convenience, 'intermediate' is hereafter omitted.

Selection for renal modification reflects the interaction of rates of water gain and urinary and pulmocutaneous water loss (*inter alia* Schmidt-Nielsen 1964, Ingram and Mount 1975). Moreover, kidney structure and function must be adapted to the most arid and desiccating (i.e. simultaneously hot and dry) conditions likely to be encountered by a species. None of the otomyines drink water except under conditions of food deprivation (i.e. *O. irroratus*; Willan and Hickman 1986). All otomyines are strict herbivores (see below), and the conservatism of their kidneys may mainly reflect the similarity of diets, although a complex of interrelated climatic and behavioural factors appears also to influence renal adaptation, as set out below.

Climate

Rainfall is the most significant underlying determinant of renal structure (Ingram and Mount 1975). This factor (Table 1) apparently determines the broad division into mesically and xerically adapted otomyine kidney types.

The present results indicate a lower degree of mesic adaptation of the kidneys of *O. irroratus* than of *O. angoniensis*, but this relationship may not apply universally to these two species. The *O. irroratus* used here represent an area of comparatively moderate rainfall (Table 1), and were collected in a grassland that was drier than the moist, often marshy, preferred habitats of this species (Davis 1973, Willan and Meester 1989). Conversely, the *O. angoniensis* Hazelmere locality is situated in the Natal coastal region where rainfall (Table 1) and humidity (Weather Bureau 1984) are higher than would be expected elsewhere within the distributional range of this species, at least in southern Africa (Skinner and Smithers 1990). It is therefore probable that the kidneys of *O. irroratus* from typically moist localities exceed the degree of mesic adaptation of *O. angoniensis* from areas other than the Natal coast.

All three xerophilic otomyine species are represented within the west coast fog zone of southern Africa (De Graaff 1981, Skinner and Smithers 1990), and it seems likely that the fog has allowed extension of their range into habitats where rainfall is low. The effects of dew and fog on the biota of the west coast of southern Africa are well documented: some plants use fog as a water source (Seely and Louw 1980), while mammals may lick dew and condensed fog off solid objects such as rocks (Louw and Seely 1982). The water requirements of *O. unisulcatus* and the two *Parotomys* species may therefore be supplemented by fog water, probably indirectly as a result of individuals feeding on fog-dependent plants.

Feeding habits

The otomyines are all specialist herbivores that feed more or less exclusively on green plant material (*inter alia* Roberts 1951). Irrespective of relative environmental aridity, therefore, the water content of their food falls within a comparatively narrow range, selecting for reduced renal variation in the subfamily.

The feeding habits of arid adapted mammals may be such that extreme renal physiological, hence morphological, modification is unnecessary. For example, the pack rat *Neotoma lepida* feeds largely on succulent plant material (cactus), and does not have the kidneys extensively modified despite the aridity of its desert habitat (Schmidt-Nielsen 1964). Similarly, all three xerophilic species feed on succulent herbaceous plants when available (Skinner and Smithers 1990, Vermeulen and Nel 1988, Brown and Willan 1991). Furthermore, *O. unisulcatus* feeds arboreally on the highly hydrated shoots and leaves of shrubs and small trees (Brown and Willan 1991).

O. angoniensis feeds mainly on grasses and fine reeds (Skinner and Smithers 1990), and *O. irroratus* (Davis 1973) and *O. s. robertsi* (Willan 1990) on most of the grasses and herbaceous species present in a given area. The water content of these plants declines during the dry season, at least in the *O. irroratus* habitats (Schulz 1953, Brown 1988). The intermediate rather than extreme mesically adapted kidneys of *O. angoniensis*, *O. irroratus* and *O. s. robertsi* apparently reflect an ability to concentrate the urine when the need arises (e.g. winter).

Domiciles, hoarding and sociality

Underground nesting is a common adaptation to water conservation among xerophilic small mammals, substantially reducing pulmocutaneous water loss (Ingram and Mount 1975). Communal nesting further reduces pulmocutaneous water loss (Baudinette 1972, Fyhn 1979), and increases the moisture content of stored food, especially of hygroscopic plant material (Schmidt-Nielsen 1964).

O. unisulcatus (Vermeulen and Nel 1988, Brown and Willan 1991) and both *Parotomys* species (De Graaff 1981, Skinner and Smithers 1990) nest communally in underground burrows. In addition, *O. unisulcatus* (Vermeulen and Nel 1988, Brown and Willan 1991) and *P. littledalei* (Roberts 1951) construct an insulating lodge above the burrow system. Comparatively high relative humidities (50–95%) have been recorded in the burrows of *P. brantsii* (Bolwig 1958); high relative humidities presumably also occur in the burrows of the remaining xerophilic otomyines.

Circadian activity

Mammalian activity patterns often vary according to local climatic conditions (Ashby 1972). Most arid adapted rodents are nocturnal, limiting pulmocutaneous water loss by restricting above-ground activity to periods when temperatures are lowest and relative humidities highest (Schmidt-Nielsen 1964, Ingram and Mount 1975). The *Otomyinae* are mainly diurnal (Roberts 1951), but *O. unisulcatus* (Brown and Willan 1991) and *P. brantsii* (Nel and Rautenbach 1974), and probably *P. littledalei*, tend toward crepuscularity during hot weather, thereby minimizing pulmocutaneous water loss.

Evolutionary considerations

The subfamily *Otomomyinae* is widespread in sub-Saharan Africa but, like the majority of southern African otomyines (see Skinner and Smithers 1990), extra-limital forms are confined to comparatively moist regions (see Misonne 1974). Apart from the xerophilic species referred to here, the otomyines therefore comprise an essentially mesophilic taxon. *Prototomys*, the Pliocene ancestor of the modern *Otomomyinae* (Pocock 1976), was apparently adapted to moist habitats, and, like extant otomyines, probably fed on green plant material (Taylor *et al.* 1989). There is evidence that *Prototomys* was ecologically analogous to *O. irroratus* (Willan 1990), and it is therefore likely that the kidney structure of *Prototomys* was similar to that of the extant mesophilic otomyines. If this is so, selection for increasing renal efficiency among the ancestors of the extant xerophilic otomyines occurred from a base of mesic adaptedness, with renal modification accompanying secondary phylogenetic divergence which occurred in response to the aridification of western southern Africa during the late Pliocene (Taylor *et al.* 1989).

The closer phenetic relationship in terms of kidney morphology between *O. unisulcatus* and *P. brantsii*, with *P. littledalei* more distant from them (Fig. 2), closely parallels the results of protein electrophoresis (Taylor *et al.* 1989). The validity of otomyine generic taxonomy was questioned on the basis of this study (Taylor *et al.* 1989), but the present results have no readily identifiable phylogenetic or taxonomic significance.

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