Gut morphology of the Otomyine rodents: an arid-mesic comparison

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In this article we examine the gut morphology of the only three arid-occurring otomyine rodents; Brants' whistling rat, *Parotomys brantsii*, Littledale's whistling rat, *Parotomys littledalei* and the Karoo bush rat, *Otomys unisulcatus* and relate this to the semi-arid environment in which they are endemic. All three otomyine rodents display a gastro-intestinal system well suited to a wholly herbivorous diet, with a well-developed caecum and relatively long large intestine. Despite the broad similarity in the gross gastro-intestinal anatomy between the species examined in this study and their mesic-occurring otomyine counterparts, the results suggest an elongation of the large intestine, with a concurrent reduction in the size of the small intestine in the arid-occurring species. We argue that this trend may be related to water conservation and is supported by the distribution of the three species, with *P. littledalei*, which occurs in the most arid areas of the three, having the longest large intestine.

Six species of otomyine rodent are currently recognised within the southern African subregion (Meester *et al.* 1986). These can be divided into two broad groups, one inhabiting the more mesic eastern areas of the subregion and the other occurring in the drier western areas (Skinner & Smithers 1990). The species which have been studied are all known to be exclusively herbivorous (Nel & Rautenbach 1974; Curtis & Perrin 1979; Du Plessis, Kerley & Winter 1991; Monadjem 1997; Jackson 1998), their diets consisting entirely of plant material including shoots, stems, leaves, grasses and flowers as well as geophytes. Insects and seed material, which are typical components of the diets of many rodents, are conspicuously absent from the diet of the Otomyinae. Together with the mole-rats, these are probably the only truly herbivorous rodents occurring in southern Africa (Perrin & Curtis 1980). Furthermore, the gastro-intestinal tract (GIT) of the Otomyinae exhibits a high degree of specialisation to their herbivorous lifestyle, including a large and complex caecum, and a well-developed large intestine. Perrin and Curtis (1980) suggest that the GIT of the Otomyinae is the most specialised of any South African herbivorous rodent.

Whilst data on the gastro-intestinal morphology of the Otomyinae are available for two species occurring in mesic areas within southern Africa, namely the vlei rat, *Otomys irroratus*, and the Angoni vlei rat, *O. angoniensis*, no comparable data are available for any of the three arid-occurring species; the Karoo bush rat, *O. unisulcatus*, Brants' whistling rat, *Parotomys brantsii* and Littledale's whistling rat, *P. littledalei*. The diets of *O. unisulcatus* and *P. brantsii* are known to be strictly herbivorous, whilst the sparse data available for *P. littledalei* suggests they too are strict herbivores (Du Plessis 1989; Skinner & Smithers 1990; Du Plessis *et al.* 1991; Jackson 1998; N. Coetzee & T. Jackson unpublished data). Given their common ancestry as well as the similarity in their feeding habits, the arid-occurring Otomyinae are likely to posses a gut morphology which is similar to their mesic counterparts, being well adapted to their herbivorous lifestyle.

Although arid-occurring, *P. brantsii* and *O. unisulcatus*[1] apparently exhibit poor physiological adaptations to the arid areas they inhabit; both species exhibit a higher metabolic rate than predicted for body mass, a low 'lower critical temperature' and symptoms of heat stress at 31°C (Du Plessis 1989; Du Plessis, Erasmus & Kerley 1989). In this respect they differ from sympatric rodent species such as the hairy-footed gerbil, *Gerbillurus paeba*, short-tailed gerbil *Desmodillus auricularis*, and Namaqua rock mouse, *Aethomys namaquensis*, all of whom appear physiologically well suited to the desert environment (Buffenstein 1984a; 1984b; Buffenstein & Jarvis 1985; Buffenstein, Campbell & Jarvis 1985). Field observations suggest that *P. brantsii* copes behaviourally with the thermoregulatory constraints of the arid areas they inhabit, by occupying a burrow and being largely crepuscular (Nel & Rautenbach 1974; Jackson *in press*). However, no information exists to suggest how these species may cope with the potentially more severe problems of water conservation in arid environments.

Intraspecific studies have shown that rodent gastro-intestinal morphology is labile. For instance, individuals that are subject to low or high fibre diets (Gross, Wang & Wunder 1985), insectivorous or vegetarian diets (Spinks & Perrin 1995; Corp, Gorman & Speakman 1997), or different temperature regimes (Koteja 1996) show differences in their gastro-intestinal morphology. Similarly, several workers have recognised the importance of the hindgut in water resorption, and suggest that directional changes in the relative size of the large intestine of small mammals reflect adaptive variation in water conservation needs (Laange & Staaland 1973; Katz 1973; Woodall 1987). Thus, we would predict that the otomyine

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** Present address: Department of Physiology, University of the Western Cape, Bellville 7535, South Africa species occurring in xeric areas should exhibit a directional response with regard to gastro-intestinal morphology, especially in relation to adaptations for water conservation.

In this study we examine aspects of the gastro-intestinal morphology of the three arid-living otomyine rodents of southern Africa in relation to phylogenetically related species from more mesic habitats. We predict that all three species should show a similar gut morphology to that of the mesic-living Otomyinae, which is well adapted to an herbivorous lifestyle. However, we also predict a directional modification of their gastro-intestinal morphology, associated with the arid and semi-arid habitats in which they occur and related to inter-habitat differences in water conservation requirements.

The three arid-occurring otomyine rodents examined in this study were collected from Goegap Nature Reserve (29°37' S, 17°59' E), in the Northern Cape Province, South Africa. Animals were trapped in the middle of the summer, during February 1998 and again in April 1998. At this time food availability in the area, judging by the search effort of individual *P. brantsii*, is lowest (Jackson 1998). Individuals were trapped using a double-ended trap (50×12×12 cm), baited with the succulent *Augea capensis*. In total 14 *P. brantsii*, (14 males, $x \pm \mathrm{SD}=144.4 \pm 16.9$ g) eight *P. littledalei* (four males, 134.3 ± 14.4 g; four females 85.0 ± 5.6 g) and seven *O. unisulcatus* (four males, 143.3 ± 6.0 g; three females, 85.7 ± 17.9 g) were used in this study.

Immediately upon capture, animals were euthanased by inhalation of ether and the entire GIT was removed. The GIT was fixed in 10% buffered formalin for 24h and then stored in 70% ethanol for later examination. It was assumed that any size changes in the tissue examined, resulting from fixation, would be constant across all samples. GITs were cleared of surrounding adipose and connective tissue, blotted to remove excess fixative, and weighed to the nearest 0.1 g (including gut contents). Tracts were separated into stomach, small intestine, caecum and large intestine, and the length of each section was measured on a clean flat surface to the nearest 1.0 mm. Caecal capacities were estimated using the formula for the volume of a cylinder *i.e.* $\pi r^2 l$, where r = average caecal radius (calculated as the mean of three measurements taken along the length of the caecum) and l = caecal length. All sections were also weighed, and the empty mass of the stomach and caecum was also determined. The number of caecal haustra was assessed.

Preliminary analysis revealed that parasites were restricted to the small intestine of all species examined. Thus, the density of parasites present in the small intestine was estimated on a nominal scale of 0–3, where 0 = no parasites, 1 = low parasite load, 2 = moderate parasite load, and 3 = high parasite load.

Regression analysis revealed a significant correlation between gastric, small and large intestine morphometrics, and body mass. Consequently body mass was introduced as a covariant during subsequent analysis of these parameters. In contrast none of the caecal measurements correlated significantly with body mass. Accordingly these parameters were not standardised relative to body mass. Interspecific differences in gut morphometry were tested using either multifactorial analysis of variance (MANOVA) or one-way analysis of variance (ANOVA) (Zar 1996). Differences in parasite load were tested using a Kruskal-Wallis ANOVA (Zar 1996). Results for parasite loads have been tabulated according to the modal value.

Overall, the mass or length of the gastro-intestinal tracts of all three arid-occurring species did not differ significantly (Table 1). However, there were species-specific differences in the importance of its various components. In all species examined, the stomach was a simple unilocular sac and exhibited very little gross anatomical specialisation. However, the empty stomach mass differed significantly between all species, being largest in *O. unisulcatus* and smallest in *P. littledalei* (Table 1). There were no marked differences in the morphometry of the small intestine. The only notable feature of the small intestine was the presence of a large number of parasites (Cestoda: Cyclophyllidae) in *P. brantsii*, whilst similar parasites were only found at low numbers, or were entirely absent from the small intestine of both *P. littledalei* and *O. unisulcatus*. All three species possess the complex caecum characteristic of the Otomyinae, with a double row of deep haustra running along the greater curvature from the ileum to its blind end. The caeca of each species were also characterised by numerous caecal papillae. The smaller caeca of *O. unisulcatus* and *P. littledalei* may be more complex structures than that of *P. brantsii*, both having a greater number of caecal haustra (Table 1). Whilst the caecal length did not show significant inter-specific variation ($p = 0.06$), the volume and full mass of the caecum of *P. brantsii* was significantly greater than the other two species, indicative of a greater volume of food present (Table 1). The large intestine was longer in *P. littledalei* than the other two species. Additionally, it was heavier than *O. unisulcatus*, but not significantly so relative to *P. brantsii* (Table 1). An interesting observation was the presence of several distinct, raised patches, with numerous villi on the free surface, in the hindguts of all the species examined (1 in the caecum, 2–3 in the large intestine). Histological examination revealed dense aggregations of lymphoid tissue associated with these patches. Johnston, Davies and Davies (1958) describe analogous structures in the human small intestine, ileum and appendix, and Wheater, Burkitt and Daniels (1987) suggest these aggregations of lymphoid tissue in the hindgut of humans serve for protection from ingress of micro-organisms. It seems plausible that the patches serve a related function in the caecum and large intestine of the otomyine rodents, which are likely to contain dense populations of bacteria.

The gastro-intestinal tract of the arid-adapted Otomyinae is similar to those of mesic otomyine species which have previously been examined (Perrin & Curtis 1980). All possess a large, complex caecum as well as a relatively big large intestine suggesting a tendency towards herbivory within the subfamily. Schiek and Millar (1985) in their investigation of the alimentary tract dimensions of 35 species of North American small mammals, concluded that the relative lengths of the large intestine and caecum were the best indicators of herbivory. The occurrence of herbivory in the three study species is further supported by field observations which indicate that their diets consist exclusively of plant material, including leaves, stems, flowers and geophytes (Du Plessis *et al.* 1991; Jackson 1998; T. Jackson unpublished data).

Table 1 Comparative gastro-intestinal morphology of *P. littledalei*, *P. brantsii* and *O. unisulcatus*. Values expressed as mean ±SD, tested using ANOVA, MANOVA or Kruskal-Wallis ANOVA (parasite load). For probabilities: * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$

Variables	*P. littledalei*	*P. brantsii*	*O. unisulcatus*	Probability
Total gut:				
mass (g)	18.4 ± 5.7	24.7 ± 4.7	19.4 ± 6.8	ns
length, excl. stomach (mm)	574 ± 45	594 ± 44	542 ± 87	ns
length, incl. stomach (mm)	601 ± 48	620 ± 45	571 ± 90	ns
Stomach:				
length (mm)	27.3 ± 5.4	26.2 ± 3.1	28.6 ± 6.1	ns
mass, full (g)	4.8 ± 2.7	5.5 ± 1.8	5.4 ± 3.6	ns
mass, empty (g)	0.8 ± 0.1^{a}	1.3 ± 0.1^{b}	1.4 ± 0.4^{c}	***
Small intestine:				
length (mm)	211± 22	245 ± 23	234 ± 38	ns
mass, full (mm)	3.6 ± 0.8	4.8 ± 1.9	4.1 ± 1.7	ns
parasite load	Low^{a}	High^{b}	Low^{a}	***
Caecum:				
length (mm)	71 ± 3	79 ± 8	71 ± 11	ns
mass, full (g)	5.7 ± 2.2	9.2 ± 2.0	6.4 ± 2.0	**
mass, empty (g)	1.2 ± 0.4	1.5 ± 0.2	1.5 ± 0.4	ns
volume (cm^3)	5.9 ± 1.4^{a}	10.1 ± 2.0^{b}	7.1 ± 2.1^{a}	***
haustra (n)	29.3 ± 4.8^{a}	22.9 ± 2.6^{b}	27.9 ± 4.2^{a}	***
Large intestine:				
length (mm)	293 ± 29^{a}	270 ± 26^{b}	237 ± 46^{b}	**
mass (g)	4.0 ± 1.3^{a}	4.3 ± 1.2^{ab}	2.7 ± 1.0^{b}	*

The relative contribution of the large intestine to the length of the gastro-intestinal tract (excluding the stomach) was significantly greater for *P. littledalei* than for the other two species (Table 2). Conversely the small intestine was relatively shorter in *P. littledalei* than for *P. brantsii* or *O. unisulcatus* (Table 2). However, the caecum appeared to contribute an equal length to the gastro-intestinal tract in all three species (Table 2), even though its volume was greater in *P. brantsii*.

Comparing the gut morphology of the arid-occurring Otomyinae to the published data for mesic-occurring species (Table 2), it is apparent that the large intestine, which is relatively longer in the arid-occurring species, is a more important feature of the gastro-intestinal tract than in the mesic species. Additionally, the caecum is reduced in relative size, as is the small intestine. Consequently, the large:small intestine ratio is greater in the arid than the mesic Otomyinae. Furthermore, *P. littledalei*, whose range includes the most arid regions occupied by any of the Otomyinae, has the greatest large:small intestine ratio, whilst *O. unisulcatus*, whose range does not extend into such arid areas as the two *Parotomys* species, has the lowest large:small intestine ratio of these arid-occurring species.

Despite the general accord in gross anatomy of the GIT of mesic and arid-occurring Otomyinae, there is apparently a

Table 2 Relative length of different sections of the hindgut of *P. littledalei*, *P. brantsii* and *O. unisulcatus*, expressed as a percentage of total hindgut length (excluding the stomach). Values for arid-occurring species expressed as mean ±SD a, b indicate significantly different groups, tested using KW ANOVAs and non-parametric multiple comparisons. For probabilities: *** = $p<0.0005$.

Variables	Mesic-occurring species		Arid-occurring species			Probability
	O. irroratus†	*O. angoniensis*†	*P. littledalei*‡	*P. brantsii*‡	*O. unisulcatus*‡	
Small intestine	42.2	42.0	36.7 ± 2.8^{a}	41.2 ± 1.1^{b}	43.2 ± 3.3^{b}	***
Caecum	18.4	20.2	12.4 ± 1.9	13.3 ± 1.5	13.2 ± 2.3	ns
Large intestine	39.4	37.8	50.9 ± 2.1^{a}	45.4 ± 1.0^{b}	43.6 ± 2.6^{b}	***
Large:small intestine ratio	0.93	0.9	1.4^{a}	1.1^{b}	1.01^{b}	***
Number of caecal haustra	31	22	29^{a}	23^{b}	28^{a}	***

Source: † Perrin & Curtis (1980); ‡ this study trend towards an increase in the relative importance of the large intestine in the arid-occurring species. Woodall (1987) attributed variation in the hindgut dimensions of seven elephant shrew species to differences in water conservation needs or dietary quality. Thus the relatively larger large intestines of *P. littledalei*, *P. brantsii* and *O. unisulcatus* may serve either to improve water economy or to enhance digestive efficiency on low quality/high fibre forage. The later explanation is unlikely, however, since we would predict an increase in relative caecal size in addition to increased large intestine size to improve digestion of low quality foods. Moreover, the diets of the mesic-occurring species are also known to include high fibre forage. Thus it seems more likely that the increase in the relative contribution of the large intestine in the arid-occurring Otomyinae is an adaptation to improve water retention in the xeric areas they inhabit. Several workers have highlighted the functional involvement of the hindgut in water conservation in rodents, suggesting that the large intestine is a crucial site for water resorption (Laange & Staaland 1973; Katz 1973; Woodall 1987). This proposed functional involvement of the large intestine in water conservation in the arid-occurring otomyine rodents is supported by the fact that *P. littledalei*, whose range covers the most arid regions receiving less than 100 mm of rainfall per annum (Werger 1978, Lovegrove 1993), has the greatest large:small intestine ratio. We speculate that the distribution of *P. brantsii* and *O. unisulcatus* into areas receiving such low rainfall may be more limited than that of *P. littledalei*, partly accounting for the occurrence of this species along the Namibian coast well beyond the limits of *P. brantsii* and *O. unisulcatus*.

Whilst our study provides the first published information on the GIT anatomy of the arid-occurring otomyine rodents, there is clearly a need for further comparative physiological studies to help explain the differences in the distribution of these three arid-occurring species. The results of our study suggest that *P. littledalei* may well be marginally better adapted to an arid environment than either *P. brantsii* or *O. unisulcatus*, or in fact any other otomyine rodent.

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Notes

1. No physiological data are available for *P. littledalei*.

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