The digestive tract of *Macroscelides proboscideus* and the effects of diet quality on gut dimensions

A.C. Spinks* and M.R. Perrin

Department of Zoology and Entomology, University of Natal, Pietermaritzburg, 3200 South Africa

Received 21 October 1994; accepted 1 March 1995

The digestive anatomy of the round-eared elephant shrew, *Macroscelides proboscideus*, was investigated. The gut combines features indicative of both insectivory and herbivory. The stomach is a unilocular glandular sac. The caecum is an elongate blind-ending pouch, and houses a diverse microflora. The colon is well developed (25% of gut length). Digestive anatomy supports Kerley's (1995) contention that *M. proboscideus* is a true omnivore. The gut dimensions of *M. proboscideus* responded to differences in food quality, animals fed a high fibre diet exhibiting greater caecal capacity than those fed a low fibre diet. This hindgut plasticity is likely to compensate for short-term changes in food quality.

Aspekte van die gastro-intestinale anatomie van die ronde-oorklaasneus *Macroscelides proboscideus*, is ondersoek. Die dermkanaal kombineer eienskappe van beide insek- en plantvreters. Die maag is 'n enkel, klieragtige sak. Die sekum is 'n verlengde, blindeindigende holte en huisves 'n verskeidenheid van mikroflora. Die kolon is goed ontwikkel (25% van die lengte van die dermkanaal). Die gastrointestinale anatomie ondersteun Kerley (1995) se mening dat *M. proboscideus* 'n ware omnivoor is. Die grootte van die spysverteringskanaal weerspieël verskille in voedselgehalte. Diere wat 'n hoë veseldieet gevoer is, het 'n groter sekale volume as diere op 'n lae veseldieet. Hierdie plastisiteit van die derm kompenseer vir korttermyn veranderings in voedselgehalte.

*To whom correspondence should be addressed at: Department of Zoology, University of Cape Town, Private Bag, Rondebosch, 7700 South Africa

Elephant shrews (Family: Macroscelidae) are endemic to Africa, occurring in a range of habitats from desert to forest (Grizmek 1990). Although likely to have originated from a herbivorous ancestor (Patterson 1965), the majority of extant species have commonly been regarded as insectivorous (Woodall 1987; Skinner & Smithers 1990). However, on reviewing available dietary data, Kerley (1995) suggested that elephant shrews are far more omnivorous than previously thought. Most species consume fruit, seeds and herbage in addition to insects (Kerley 1995).

The round-eared elephant shrew, *Macroscelides proboscideus*, is restricted to the south-western parts of southern Africa (Skinner & Smithers 1990), and together with *Elephantulus brachyrhynchus* ingests significantly more plant material than the other elephant shrew species (Kerley 1995). Kerley (1989, 1995) described *M. proboscideus* as a true omnivore, after observing that foliage constituted approximately 42% of its diet. Consumption of plant material increased from 40% in summer to 70% in winter (Kerley 1989). The utilization of a diet so high in fibre is likely to pose acute digestive challenges to *M. proboscideus*.

Short-term responses of the gastrointestinal tract (GIT) to diet quality (fibre content) have been demonstrated in a number of rodent species (Brownlee & Moss 1959; Gross, Wang & Wunder 1985; Green & Millar 1987; Woodall 1989; Hammond & Wunder 1991). Prairie voles, *Microtus ochrogaster*, and water voles, *Arvicola terrestris*, fed a high fibre diet have significantly larger and heavier GITs (especially caeca) than those fed a low fibre diet (Gross *et al.* 1985; Woodall 1989; Hammond & Wunder 1991).

The aims of the present study were to describe the anatomy, histology and microflora of the digestive tract of *M. proboscideus* in relation to dietary habits, and to perform a preliminary investigation of the effects of diet fibre content on gut dimensions.

Twenty-four *M. proboscideus* were captured near Beaufort West (22°36'E, 32°20'S) in January 1992. Four subjects, used to examine gut morphology and anatomy of wild individuals, were sacrificed within one week of capture. The remaining 20 animals were divided into two equal groups. Throughout the five month experimental period both groups were provided with water and a high protein cereal (Pronutro^R, 20% protein, 15% fibre on a dry basis) *ad libitum*. Dietary fibre content was varied by supplementing Group 1's diet with insects (mealworms: *Tenebrio molitor*) and Group 2's diet with grass (kikuyu: *Pennisetum clandestinum*, 26% crude fibre). Consumption of the diets was confirmed visually for Pronutro^R and mealworms, and by the presence of grass fibre in the faeces of Group 2.

One animal from each group was killed every two weeks by carbon dioxide asphyxiation. Each animal was weighed, the GIT was dissected out and measurements were made in water, to minimize stretching (Chivers & Hladik 1980). Stomach, small intestine, caecum and colon lengths, and gastric and caecal capacities, were determined. The pH in the stomach, small intestine and caecum was measured using a single glass probe electrode.

For scanning electron microscopy (SEM) gastric and caecal tissues (3mm × 3mm) were fixed in buffered glutaraldehyde, postfixed in 2% osmium tetroxide and critical point dried. Specimens were coated with gold palladium and viewed with a Hitachi S-570 scanning electron microscope.

The stomachs and caeca were preserved in Bouin's fixative, and then sagitally bisected; one half was used to examine gross morphology and the other for histology. Histological sections were stained with haemotoxylin and eosin. Descriptions use the terminology of Langer (1985; 1988).

The stomach is a simple unilocular glandular sac (Figure 1), constituting only 5,1% of the total GIT length (Table 1). The oesophagus enters the stomach medially on the lesser

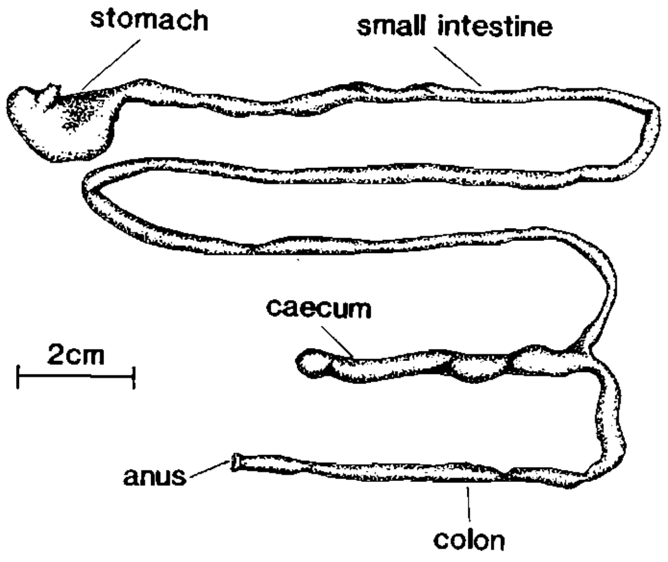

Figure 1 Drawing of the digestive tract of *M. proboscideus*, showing the various regions.

Table 1 Measurements of body mass, GIT dimensions and GIT pH in *M. proboscideus*

	Measurement			
Parameter	x	SE (n)	%GIT	pH (n)
Body mass (g)	34,9	2,4 (4)	–	–
Lengths (mm)				
Stomach	16,6	0,7 (4)	5,1	2,3 (2)
Small inestine	182,5	4,3 (4)	56,5	6,5 (2)
Caecum	43,3	4,3 (4)	13,4	7,4 (2)
Colon	80,4	4,1 (4)	25,0	–
Volumes (ml)				
Stomach	152,7	32,5 (4)	–	–
Caecum	371,0	33,8 (4)	–	–

curvature, adjacent to the corpus. Sinistral to the corpus, the fundus extends laterally, forming a small conical expansion. The voluminous antrum extends dextral to the corpus, opening into a clearly defined pyloric pouch. The large antrum and conspicuous pyloric pouch are produced by the absence of the incisura angularis. The pyloric pouch leads to the duodenum via a well developed pyloric sphincter. Numerous rugae line the gastric wall.

In relation to other elephant shrew species (Woodall 1987), the post-gastric GIT of *M. proboscideus* is characterized by a short small intestine (56,5% of GIT, Table 1), a long, voluminous caecum (13,4% of GIT, Table 1) and a long colon (25% of GIT, Table 1). The GIT morphometrics determined in this study differ marginally from those of Woodall (1987) (shorter small intestine, longer caecum and colon), but this may merely reflect GIT plasticity.

The caecum is an elongate, unilocular, blind-ending pouch, extending from the ileocolical orifice (Figure 1). It has a simple structure, with numerous transverse muscular folds lining the walls of the corpus caeci. It shows no haustration.

A typically mammalian gastric tissue plan was observed, consisting of a well developed glandular mucosa underlain by a submucosa of loose connective tissue and the muscularis externa. The mucosal lining is histologically divisible into three regions *viz.* cardiac, fundic and pyloric. There was no evidence of gastric keratinization, or significant development of the muscularis externa. The caecal tissue arrangement is regular, comprising a well developed glandular layer, a submucosa and an external muscle layer. The pH of the stomach was highly acidic, while most of the GIT was slightly alkaline (Table 1).

Few bacteria were observed on the gastric epithelium, although fungal hyphae and spores were present in the pylorus and fundus, as well as in the caeca of most animals. The caecal epithelium was densely covered with a diverse bacterial community. Cocci (1–2 μm) and rods (2–7 μm) comprised the major component of the microbial communities, which also included spirochaete (3–5 μm, Figure 2a) and atypical cocci (1,5 μm, Figure 2b). On a few occasions a seliberia bacterium (3 μm, Figure 2c) was noted. The final morphotype observed was an unidentified bacterium, with peculiar striations in its plasma membrane (1–1,5 μm, Figure 2d).

These results suggest that the GIT of *M. proboscideus* combines features indicative of both insectivory and herbivory. Gastric morphology and microstructure concur closely with those of *E. myurus* (Allison 1948), and are more typical of an insectivore than an omnivore. The lack of keratinization or development of gastric musculature precludes its functioning in the mechanical preparation of abrasive foods.

In foregut fermenters, a voluminous gastric fermentation chamber accommodates microbial communities that degrade cellulose (Bauchop 1978). The simple unilocular stomach of *M. proboscideus* is not specialized for such a function. Furthermore, the absence of gastric microflora and the low pH negate a fermentatory role for the stomach. This suggests that the stomach of *M. proboscideus* functions primarily in the initial digestion of high energy, easily digestible soluble carbohydrates and protein.

In his investigation of GIT morphometrics of seven elephant shrew species, Woodall (1987) concluded that the digestive tract dimensions reflected an insectivorous diet. However some variation in caecal dimensions between species was recognized, in particular *M. proboscideus* had a longer colon and longer caecum than the *Elephantulus* species. These differences were attributed to variation in water conservation needs or dietary quality. Although the gut dimensions obtained in this study differed marginally from those of Woodall (1987), the basic pattern was maintained. Scheick & Millar (1985) demonstrated that colon length indicated the degree of herbivory, with species consuming more plant material having relatively longer colons. Hence, the long colon of *M. proboscideus* may be an indication of its retention of a degree of ancestral herbivory (Kerley 1995).

Whereas most small insectivores lack a caecum (Scheick & Millar 1985), elephant shrews retain a functional caecum (Woodall & Mackie 1987). In *M. proboscideus* caecal structure is ideally suited to retard the passage of digesta, thereby enabling the degradation of complex plant polysaccharides. The transverse muscular folds running along the caecum possibly represent a specialization allowing for the mixing and movement of caecal contents (McBee 1971; Bruorton & Per-

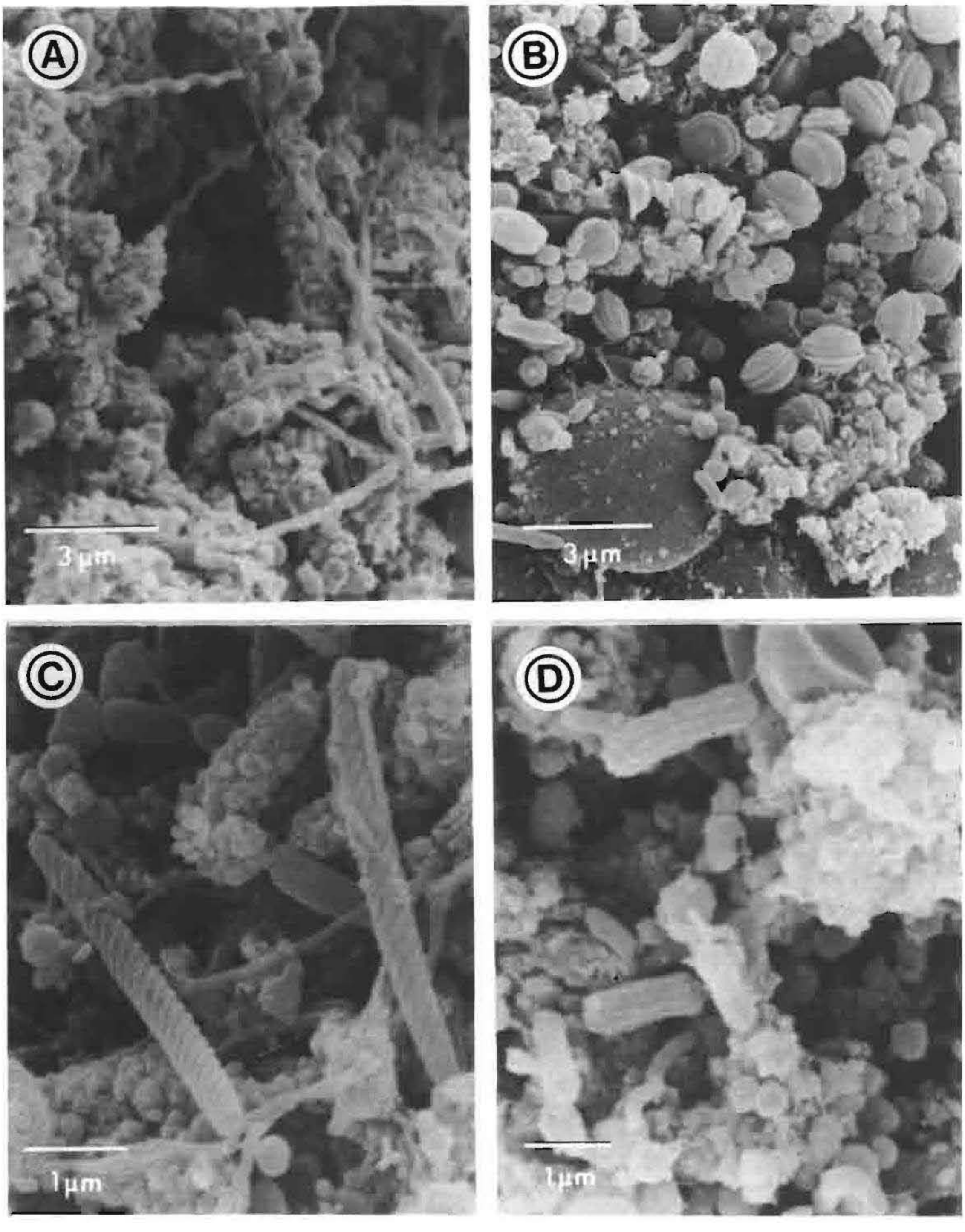

Figure 2 Scanning electron micrographs of the microflora present in the caecum of *M. proboscideus:* a – spirochaeta; b – atypical coccus; c – seliberia; d – striated bacterial morphotype.

rin 1988). This would aid the fermentation process (Bruorton & Perrin 1988).

Microbial caecal fermentation is well documented in small mammals (McBee 1971). The caecal epithelium of *M. proboscideus* exhibited a dense and diverse bacterial community. This suggests, together with the observed caecal morphology, that the caecum functions as a fermentation vat. Although fermentation is an important function of the caecal microflora, there is little evidence of it being the primary function (McBee 1971). In addition to facilitating fermentation, the microflora of *M. proboscideus* may also perform several supplementary nutritive functions [e.g. vitamin synthesis, neutralizing allelochemicals (McBee 1971; Bauchop 1978)].

With a decline in food quality or quantity, animals must consume more food or assimilate it more efficiently in order to meet energy and nutrient demands (Gross *et al.* 1985). However, without changes in GIT morphometrics, increased intake reduces retention time, thereby depressing digestibility and ultimately the efficiency of nutrient extraction (Milton 1981; Gross *et al.* 1985).

Sibly (1981) postulated an inverse relationship between gut capacity and food quality, which is supported by the

Table 2 Comparative body mass and GIT morphometric data for *M. proboscideus* offered a low fibre (Group 1) or high fibre (Group 2) diet

	Group 1 (n = 10)		Group 2 (n = 10)	
Parameter	x	SE	x	SE
Body mass (g)	39,6	2,2	41,3	1,4
Lengths (mm)				
Stomach	16,7	0,7	18,3	0,6
Small intestine	200,8	12,4	196,9	13,8
Caecum	36,6	2,4	42,8	1,9
Colon	86,1	4,1	85,7	5,1
Volumes (ml)				
Stomach	144,3	16,9	311,2	92,7
Caecum	243,70	51,0	424,4*	61,4

* = significant at $p < 0,05$ level, Students t test

responses of *M. proboscideus* to differences in diet composition. Group 2 exhibited a greater caecal volume than Group 1 (Table 2, $p < 0,05$), possibly related to greater fibre consumption. Increased caecal capacity would facilitate digesta retention, aiding microbial fermentation and the assimilation of fibrous forage (Gross *et al.* 1985; Bruorton & Perrin 1991).

The stomach, small intestine and colon exhibited no response to dietary manipulation (Table 2). Scheick & Millar (1985) found that caecal and colon morphometrics best indicated the amount of fibre in the diet of small mammals, whilst small intestine morphometrics were a poor indicator of diet composition. The colon of *M. proboscideus* comprises a substantial portion of the GIT (25%), and consequently modification of this region may be unnecessary. Furthermore, if the round-eared elephant shrew practices coprophagy, which is common in herbivorous small mammals (McBee 1971), this may augment colonic absorption of hindgut products.

Kerley's (1995) contention, based on dietary data, that *M. proboscideus* is more omnivorous than previously thought, is supported by this study. The digestive tract combines features indicative of insectivorous and herbivorous diets, and is wholly adapted to a mixed diet. Moreover, the plasticity of the hindgut is likely to compensate for short-term changes in food quality.

Acknowledgements

Nigel Bennett, Jenny Jarvis, Sioban Munro and Justin O'Riain are thanked for critically reviewing earlier drafts of the manuscript. This study was funded by a research grant from the Foundation for Research Development.

References

ALLISON, A.C. 1948. The stomach in South African insectivora, with notes on the organization of mammalian gastric glands. *J. Anat.* 82: 249–261.

BAUCHOP, T. 1978. Digestion of leaves in vertebrate arboreal folivores. In: The ecology of arboreal folivores, (ed.) G.G. Montgomery. Smithsonian Institute Press, Washington D.C.

BROWNLEE, A. & MOSS, W. 1959. Changes in size of the gastrointestinal tract, liver and kidneys of the laboratory rat at different live weights and on different dietary regimes. *Bri. Vet. J.* 115: 225–234.

BRUORTON, M.R. & PERRIN, M.R. 1988. The anatomy of the stomach and caecum of the samango monkey, *Cercopithecus mitis erythrarchus* Peters, 1852. *Z. Säugetierkunde* 53: 210–224.

BRUORTON, M.R. & PERRIN, M.R. 1991. Comparative gut morphometrics of vervet (*Cercopithecus aethiops*) and samango (*C. mitis erythrarchus*) monkeys. *Z. Säugetierkunde* 56: 65–71.

CHIVERS, D.J. & HLADIK, C.M. 1980. Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. *J. Morphol.* 166: 337– 386.

GREEN, D.A. & MILLAR, J.S. 1987. Changes in gut dimensions and capacity of *Peromyscus maniculatus* relative to diet quality and energy needs. *Can. J. Zool.* 65: 2159–2162.

GRIZMEK, B. 1990. Elephant shrews. In : Grizmek's encyclopedia of mammals, (ed.) B. Grizmek. McGraw-Hill Publishing Co., New York.

GROSS, J.E., WANG, Z. & WUNDER, B.A. 1985. Effects of food quality and energy needs: changes in gut morphology and capacity of *Microtus ochrogaster. J. Mamm.* 66: 661–667.

HAMMOND, K.A. & WUNDER, B.A. 1991. The role of diet quality and energy needs in the nutritional ecology of a small herbivore, *Microtos ochrogaster. Physiol. Zool.* 64: 541–567.

KERLEY, G.I.H. 1989. Diet of small mammals from the Karoo, South Africa. *S. Afr. J. Wildl. Res.* 19: 67–72.

KERLEY, G.I.H. 1995. The round-eared elephant shrew *Macroscelides proboscideus* (Macroscelidae) as an omnivore. *Mammal Rev.* 25: 37–42.

LANGER, P. 1985. The mammalian stomach: structure, diversity and nomenclature. *Acta Zool. Fennica* 170: 99–102.

LANGER, P. 1988. The mammalian herbivore stomach. Comparative anatomy, function and evolution. Gustav Fischer Verlag, Stuttgart.

McBEE, R. H. 1971. Significance of intestinal microflora in herbivory. *Ann. Rev. Ecol. Syst.* 2: 165–176.

MILTON, K. 1981. Food choice and digestive strategies of two sympatric primate species. *Am. Nat.* 117: 496–505.

PATTERSON, B. 1965. The fossil elephant shrews (Family Macroscelidae). *Bull. Mus. Comp. Zool.* 133: 295–335.

SCHEICK, J.O. & MILLAR, J.S. 1985. Alimentary tract measurements as indicators of diets of small mammals. *Mammalia* 49: 93–104.

SIBLY, R.M. 1981. Strategies of digestion and defecation. In: Physiological ecology. An evolutionary approach to resource use, (eds) C.R. Townsend & P. Calow. Blackwell Scientific Publications, Oxford.

SKINNER, J.D. & SMITHERS, R.H.N. 1990. The mammals of the southern African subregion. University of Pretoria Press, Pretoria.

WOODALL, P.F. 1987. Digestive tract dimensions and body mass of elephant shrews (Macroscelididae) and the effects of season and habitat. Mammalia 51: 537–545.

WOODALL, P.F. 1989. The effects of increased dietary cellulose on the anatomy, physiology and behaviour of captive water voles, *Arvicola terrestris* (L.) (Rodenda: Microtine). *Comp. Biochem. Physiol.* 94(A): 615–621.

WOODALL, P.F. & MACKIE, R.I. 1987. Caecal size and function in the rock elephant shrew, *Elephantulus myurus* (Insectivora, Macroscelididae), and the Namaqua rock mouse, *Aethomys namaquensis* (Rodentia, Muridae). *Comp. Biochem. Physiol.* 87(A): 311–314.