Comparative morphology of the digestive system of 19 species of Southern African myomorph rodents in relation to diet and evolution

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Trends in digestive system-morphology have been examined in 19 species of Southern African myomorph rodents. Structure was related to function, diet, and evolution. Characters related to an ancestral proteinaceous diet, and specialized characters associated with herbivory, were recognized. All stomachs were of the unilocular hemiglandular type with increasing degrees of cornification of the corpus, although the stomach of *Saccostomus compestris* approached the bilocular discoglandular condition. Those of *Thallomys paedulcus* and *Mystromys albicaudatus* were highly modified in containing numerous papillae in the corpus, possibly associated with gastric fermentation. The most complex caeca, of the herbivorous Otomyids, possessed numerous haustra and internal papillae probably associated with caecal microbial fermentation.

S. Afr. J. Zool. 1980, 15: 22 – 33

Daar is gelyk na tendense in die morfologie van die spysverteringskanaal in 19 spesies van Suid-Afrikaanse myomorfe knaagdiere. Die struktuur het verband gehou met funksie, dieet, en evolusie. Kenmerke wat verband hou met 'n voorouerlike proteienagtige dieet, en gespesialiseerde kenmerke geassosieerd met 'n plantaardige dieet kon herken word. Al die mae was van die eenholtige halfklieragtige tipe met 'n liggaam wat toenemend verhoring, alhoewel die maag van *Saccostomus campestris* neig na die dubbelholtige skyfklieragtige toestand. Die mae van *Thallomys paedulcus* en *Mystromys albicaudatus* was hoogs gemodifiseer en die liggaam het 'n groot aantal papillae bevat, wat heelwaarskynlik te doen het met gastriese gisting. Die meer ingewikkelde caeca het voorgekom by die plantvretende Otomyidae en hier het die groot aantal Laustra en inwendige papillae heelwaarskynlik iets te doen met mikrobiese gisting in die caecum.

S.-Afr. Tydskr. Dierk. 1980, 15: 22 – 33

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Received 8 May 1979; accepted 7 September 1979

Amongst the mammals, the rodents are the most diversified order, and include the greatest number of species and individuals. Two families, the Cricetidae and the Muridae, dominate the present African fauna. The more recent Murids are confined to the Old World whereas the older Cricetids also show great diversity in the New World. Highest densities and diversity of Murids occur in central and east Africa (Misonne 1969) and the relatively recent southern range extension from Zambia to the Cape primarily colonized savanna. The African Cricetidae are certainly in a regressive position in comparison with the Muridae (Misonne 1969). Most of them have developed extreme specialization and are now scansorial or fossorial, or have resorted to dry steppes (gerbils), or marshes (otomyids). Such adaptations have allowed them to survive in competition with the Murids, that have not extensively invaded xeric and mesic grassland or tropical rain forest.

A major factor influencing the outcome of competitive interaction between these two large families is their reproductive strategies. Although members of both families typically produce several litters per season, Murids are characterized by a larger litter size (> 5,3) than the Cricetids (< 4,5) (French, Stoddart & Bobek 1975). Both families have similar pregnancy rates, but Murids are typically shorter lived and experience greater changes in density. These characteristics suggest a greater rate of population turnover and hence genetic recombination and rapid adaptation in the Murids. The extant African Cricetids have offset these reproductive limitations by long-term adaptation and specialization through evolutionary time. They arose in North America in the early Oligocene and soon developed an extensive geographical range and wide adaptive radiation. Africa was brought into communication with the Palearctic land mass in the early Miocene, and owing to increasing aridity in the Pliocene many areas of south-eastern Europe and Africa developed into steppe or savanna (Kurten 1971). In Africa the invasion by Murids from south-east Asia was associated with the transition from woodland to savanna. Both rodent families were subjected to similar environmental changes, and Cricetids were subjected to increased competition from Murids. Coexisting Murid and Cricetid faunas developed in complex or heterogeneous habitats due to competition and character divergence. To increase species packing, diversity increased and many muroids became increasingly modified to herbivory, as a result of expanding grassland ecosystems. Herbivory arose from the omnivorous habits of the ancestral muroid stock (Landry 1970; Vorontsov 1962).

Diet changed from being largely proteinaceous (insects and seeds) to one of complex polysaccharides of plants (grasses and herbs: Vorontsov 1961, 1962). Associated with this change in diet were modifications of the anatomy and physiology of the digestive system, and the behaviour of the rodents. The transition from high-calorific hard-to-get seeds and insects to low-calorific easy-to-get vegetation led to an increase in the total volume of food consumed, and changes in gut morphology and physiology (Vorontsov 1961, 1962). Seasonal abundance of insects and seeds might have caused rodents depending on those resources to be r-selected, with wide ranges (to locate sparse trophic resources) and specific activity patterns, and perhaps torpidity to overcome winter. Herbivores exploiting relatively constant food supplies might have developed K selection, localized feeding areas (territory or colony) and continuous activity patterns.

Assuming a shift in diet from omnivory (Landry 1970) or granivory/insectivory (Vorontsov 1962) to herbivory, certain morphological adaptations of the gastro-intestinal tract have been predicted (Vorontsov 1961, 1962, 1967). Tuberculous molars become flattened and laminate to facilitate grinding of the fibrous diet. Attrition causes hypsodonty and open-rooted molars allow for constant growth. The total length of the digestive tract increases. The simple unilocular glandular stomach becomes more complex due to cornification of the fornix ventricularis and corpus, sacculation, and a shift and localization of the gastric glands to a region between the corpus and antrum, to form the bilocular discoglandular stomach through the intermediary of a compound (glandular and cornified) unilocular hemiglandular condition. The relative length of the small intestine decreases while that of the caecum and colon increases to facilitate the microbial digestion of complex polysaccharides. Caecum volume increases by the formation of haustra (sacculations), grooves and folds. The colon becomes coiled and develops internal spiral ridges to increase surface area. With a decreased protein content of the diet the original eight liver lobes reduce to six. Continuous feeding on low calorific food requires constant secretion of small amounts of bile, and the gall bladder is lost.

Few studies have examined the adaptive radiation of the gastro-intestinal tract of rodents in relation to feeding habits. Vorontsov (1957, 1962, 1967) has made an extensive study of predominantly Palearctic muroids, particularly the Microtines, and Carleton (1973) has examined the New World Cricetinae. Since no studies have been made on the morphology of the digestive system of Southern African rodents, the current research was initiated. The purpose of this preliminary study was to examine the gut morphology of a series of rodents ranging from granivore/insectivore through omnivore to strict herbivore and to relate structure to function in terms of digestive processes, feeding habits and evolution.

Table 1 Taxonomic relationship of the rodents studied in connection with digestive system morphology (after Meester & Setzer 1971)

ORDER RODENTIA

SUBORDER MYOMORPHA

FAMILY BATHYERGIDAE

Cryptomys hottentotus (Roberts 1924) Hottentot mole-rat

SUPERFAMILY MUROIDEA

FAMILY CRICETIDAE

SUBFAMILY CRICETINAE

Mystromys albicaudatus (A. Smith 1834) White-tailed rat

SUBFAMILY GERBILLINAE

Desmodillus auroculariss (A. Smith 1834) Namaqua gerbil
Tatera brantsii (A. Smith 1836) Highveld or Brant's gerbil
Tatera leucogaster (Peters 1852) Bushveld gerbil

SUBFAMILY DENDROMURINAE

Steatomys pratensis (Peters 1846) Fat mouse

SUBFAMILY CRICETOMYINAE

Saccostomus campestris (Peters 1846) Cape pouched mouse

SUBFAMILY OTOMYINAE

Otomys angoniensis (Wroughton 1906) Angola vlei rat
Otomys irroratus (Brants 1827) Vlei rat

FAMILY MURIDAE

SUBFAMILY MURINAE

Lenothrix-Parapodemus Division
Thallomys paedulcus (Sundevall 1846) Black-tailed tree rat
Acomys spinosissimus (Peters 1852) Spiny mouse

Arvicanthis Division
Aethomys chrysophilus (De Winton 1897) African bush rat
Aethomys namaquensis (A. Smith 1834) Namaqua rock rat
Lemniscomys griselda (Thomas 1904) Single-striped field mouse
Rhabdomys pumilio (Sparrman 1784) Four-striped field mouse

Rattus Division
Praomys natalensis (A. Smith 1834) Multi-mammate mouse
Rattus rattus (Linnaeus 1758) House rat
Mus minutoides (A. Smith 1834) Dwarf mouse

SUPERFAMILY GLIROIDEA

FAMILY MUSCARDINIDAE

Graphiurus murinus (Desmarest 1822) African doormouse

Methods

Specimens for examination were collected either locally in the Albany district of the eastern Cape Province by snap-trapping, or from museum collections. Freshly killed or preserved specimens of 19 species of Southern African myomorph rodents with varying feeding habits were examined from several localities (Table 1). The mass and measurements of all specimens were determined (Table 2) and their alimentary canals dissected. The lower jaw was removed by severing the masseter muscles, and the molar teeth were drawn with the aid of a camera lucida fitted to a Wild M5 stereomicroscope. The liver and digestive tract from the oesophageal/stomach junction to the anus were then removed. The number of liver lobes and the presence or absence of a gall bladder was noted. A liver lobe that was clearly divided into two lobes was regarded as two lobes to correspond with Vorontsov (1962). Wet stomach mass was determined and the stomach dissected along its plane of symmetry from oesophagus to duodenum, and the contents removed and examined beneath a stereomicroscope. Identified items were used to validate the feeding habits of the rodents listed in Table 2, which were based on a literature survey. Samples were nonrandom and too small to permit a thorough description of feeding habits, in relation to seasonal and locality variation. In most species stratified

Table 2 Size and feeding habits of the rodent analyzed with regard to gut-morphology. Mean values and standard deviations are included for weight and head/body length data

Species	Locality	Sample size	Body weight (g)	Head and body length (mm)	Feeding habits
Cryptomys hottentotus	Eastern Cape	2	80,6 ± 22,8	123,5 ± 9,2	Bulbs, roots, aloe leaves (1, 5, 7)
Mystromys albicaudatus	Transvaal	2	172,1 ± 6,9	180,5 ± 7,8	Seeds, vegetable matter (1, 7)
Desmodillus auricularis	Transvaal	1	86,2	120,0	Seeds, locusts (1), seeds of grasses and annuals (1, 3, 7)
Tatera brantsii	Natal	4	147,0 ± 22,0	154,0 ± 10,2	Seeds, vegetable matter (1, 3, 5, 7, 9)
Tatera leucogaster	Natal	4	99,0 ± 16,9	140,0 ± 5,4	Seeds, vegetable matter (1, 3, 5, 7, 9), bulbs and grass roots (5)
Steatomys pratensis	Rhodesia	1	31,5	83,0	Seeds, insects, bulbs, sometimes grass (5)
Saccostomus campestris	Rhodesia	2	82,9 ± 46,4	132,0 ± 18,4	Seeds, fruit, insects (1, 3, 5, 6, 7)
Otomys angoniensis	Rhodesia	2	104,2 ± 29,3	151,5 ± 14,8	Grass, leaves, stems (10)
Otomys irroratus	Eastern Cape	7	93,0 ± 31,9	150,4 ± 15,4	(1, 5, 6, *pers. obs.*)
Aethomys chrysophilus	Rhodesia and Transvaal	8	89,0 ± 16,6	132,6 ± 10,6	Seeds, fruit, leaves, buds, roots (1, 5)
Aethomys namaquensis	Eastern Cape	7	46,8 ± 18,1	108,4 ± 15,3	Seeds, fruit, leaves, buds, roots (1, 5)
Acomys spinosissimus	Rhodesia	2	17,2 ± 2,2	76,5 ± 0,7	Seeds, flowers, leaves, insects (5)
Lemniscomys griselda	Rhodesia	3	54,9 ± 3,8	113,7 ± 4,2	Vegetable matter, seeds (1, 7), grass, seeds, insects (5)
Mus minutoides	Rhodesia and Eastern and Western Cape	4	4,7 ± 2,1	60,0 ± 6,8	Vegetation, arthropods (5, 6, 8)
Praomys natalensis	Eastern Cape	5	36,9 ± 11,9	104,0 ± 7,0	Seeds, insects, plants (1, 5, 6)
Rattus rattus	Eastern Cape	2	105,2 ± 15,7	159,5 ± 4,9	Seeds, plants, insects (1, 5, 6)
Rhabdomys pumilio	Eastern Cape	7	46,2 ± 10,3	110,3 ± 6,2	Green vegetation (1, 5, 6), seeds (4), seeds, insects, greens (*pers. obs.*)
Thallomys paedulcus	Rhodesia	1	55,2	115,0	Seeds, plants, occasionally insects (1), buds, roots, Acacia gum (5)
Graphiurus murinus	Eastern Cape	1	20,9	86,0	Insects, fruits, seeds, birds, eggs (2, 5, 8)

1 = Roberts 1851.
2 = Meester & Setzer 1971.
3 = Smithers 1971.
4 = Brooks 1974.
5 = Kingdon 1974.
6 = Delany 1975.
7 = Walker 1975.
8 = Hewitt 1931.
9 = Shortridge 1934.
10 = Davis 1973.

squamous and cuboidal glandular regions of the gastric mucosa were easily distinguishable with the aid of a stereomicroscope. The approximate zonation of these two epithelia were mapped using simple but precise measurements. Where there was any uncertainty as to stomach morphology, histological slides were prepared. Tissues were fixed, cleared and then embedded in paraffin wax. Sections (10 μm) were cut, mounted, and stained with haematoxylin and counterstained with eosin. The purpose of these slides was to distinguish between (cuboidal) glandular and stratified squamous (cornified) gastric mucosa cells for comparative purposes rather than to examine any one tissue in great detail.

After removal, the intestines were measured on a clean flat surface to the nearest millimetre. The lengths of the small (duodenum, jejunum, ileum) and large (colon, rectum) intestines and the caecum were later expressed as a percentage of the total length of the gut (small and large intestine plus caecum). All digestive tracts, including caeca, were fixed in 10% formalin, and slit open longitudinally and the circumference at four equidistant points along their length was measured using a Wild M5 stereomicroscope and micrometer eyepiece, to estimate a mean diameter. The number of haustra projecting from the greater curvature of the caecum, and the number of spiral loops within the colon were counted. The proportion of the colon containing spiral folds, and their incidence per unit length were recorded.

Ranking of the data

In order to demonstrate adaptation of the rodent gut to omnivory or herbivory it was necessary to develop a ranking system and define some terms. Three arbitrary ranking categories were selected based on the results from Vorontsov (1962), and were applied to the variables measured or examined:

1 = ancestral or omnivorous condition, unspecialized for herbivory.
2 = transitional or intermediate form.
3 = advanced with reference to herbivorous adaptations.

I Molar tooth pattern

1 = numerous sectorial cusps, brachyodont.
2 = several bunodont cusps in an irregular pattern.
3 = flattened occlusal surface, with transverse lophs or ridges, hypsodont and open rooted.

II Total length of gut (excluding oesophagus) as a ratio to head and body length

$1 = < 4{,}5, \quad 2 = 4{,}5 - 6{,}0, \quad 3 = > 6{,}0$

III Ratio of stratified squamous to glandular epithelium of the stomach

$1 = 0, \quad 2 \leq 1, \quad 3 = > 1.$

IV Number of liver lobes

$1 = 8, \quad 2 = 7, \quad 3 = < 7.$

V Gall bladder

1 = always present, 2 = present in some individuals,
3 = always absent.

VI Ratio of length of small to large intestine (plus caecum)

$1 = > 2, \quad 2 = 1 - 2, \quad 3 = < 1.$

VII Caecum length as a percentage of total gut length (excluding oesophagus)

$1 = <10, \quad 2 = 10-15, \quad 3 = >15.$

VIII Number of caecal haustra

$1 = 0, \quad 2 = 1-10, \quad 3 = >10.$

IX Number of loops of the large intestine

$1 = 0-1, \quad 2 = 2-8, \quad 3 = >8.$

X Food category as determined from the literature (Table 2)

I = insectivore: predominantly insect-eating
G = granivore: predominantly seed-eating
G/I = granivore/insectivore: consuming large amounts of insects and seeds
G/O = granivore/omnivore: seed-eaters with a tendency towards mixed feeding
O/H = omnivore/herbivore: mixed feeders with a tendency to herbivory
H = herbivore: diet solely of herbage (graze and/or browse)
B = herbivore: diet predominantly of bulbs, roots and tubers.

Two major problems exist. The literature is incomplete, and sometimes inadequate and anecdotal. The classification of trophic niches does not differentiate between changes in diet in time and in space. (A species can be insectivorous at one season but omnivorous at another, or a species can feed predominantly upon seeds although seeds may constitute 40 or 100% of its diet). Nevertheless, the scheme is thought to be acceptable at the present state of knowledge of rodent feeding habits in most areas of Africa.

Results

The major characters involved in assigning the degree of adaptation to a herbivorous diet are presented in Table 3 (relative proportions of the alimentary canal) and Table 4 (modification of the associated organs and large intestine). Absolute intestinal measurements, which may be of secondary importance, are presented in Table 5. Table 6 reports the overall degree of specialization and individual species rankings sequentially.

The teeth of *Graphiurus murinus* (Fig. 1) were distinctive among all the species studied in that there was a decrease in the number of cusps, flattening of the crown, and a matrix of alternating enamel ridges and dentine troughs. The teeth of *Cryptomys hottentotus* (Fig. 1) were simple with no cusps and a flat occlusal surface, but with a large surface area. Few transverse ridges or lophs were present although the species is totally herbivorous.

Within the Cricetidae there was a marked change in occlusal configurations of the molar teeth, from those of *Mystromys albicaudatus* to those of *Otomys irroratus* and *O. angoniensis*. There was a transition from molars with many sectorial or piercing cusps to ones that are flattened with a series of transverse lophs (Fig. 1). In this series there was also a tendency for increased size and dentine exposure, and hypsodonty. Trends within the pattern of molar teeth of the Muridae also showed a shift from multicusped tubercular teeth (*Aethomys namaquensis* and *Thallomys paedulcus*) to more flattened crowns (*Rattus rattus*) (Fig. 1) but there were no specialized adaptations to herbivory. In the series of Murids examined, none exhibited laminated, hypsodont, open-rooted molars. Generally, the Murids exhibited changes typical of a shift from granivory to omnivory but not to complete herbivory, as was observed in the Cricetid molars.

The stomach structure of all 19 species studied was of the unilocular-hemiglandular type described by Carleton (1973) (Fig. 2). This is a single-chambered stomach in which the

Table 3 Measurements of gastro-intestinal tract that are indicative of an adaptation to herbivory. Mean values and standard deviations are included

Species	Relative length of intestine as % total hindgut length			Ratio of hindgut to head/body length	Ratio of small intestine to colon and caecum	Caecum weight as % body weight	Stomach weight as % body weight (range)
	Small	Caecum	Large				
Cryptomys hottentotus	62,7 ± 0,5	29,1 ± 1,6	8,2 ± 0,7	5,4 ± 0,7	1,7 ± 0,04	10,5 ± 1,2	0,5 – 3,7
Mystromys albicaudatus	53,1 ± 0,1	6,6 ± 0,0	40,3 ± 0,1	4,9 ± 0,6	1,1 ± 0,0	1,0 ± 0,1	1,7 – 2,9
Desmodillus auricularis	65,0	7,3	27,7	4,8	1,9	0,9	0,4 – 2,0
Tatera brantsii	63,8 ± 2,3	8,0 ± 1,7	28,2 ± 2,1	5,6 ± 0,6	1,8 ± 0,2	1,7 ± 0,3	0,5 – 4,3
Tatera leucogaster	61,3 ± 1,6	8,6 ± 0,9	30,1 ± 0,7	5,0 ± 0,6	1,6 ± 0,1	1,3 ± 0,1	0,4 – 2,7
Steatomys pratensis	74,9	7,9	17,2	4,1	3,0	1,6	0,5 – 8,2
Saccostomus campestris	52,4 ± 1,5	12,9 ± 0,0	34,7 ± 1,6	5,7 ± 0,2	1,1 ± 0,02	4,0 ± 0,8	0,7 – 1,9
Otomys angoniensis	42,0 ± 0,1	20,2 ± 0,6	37,8 ± 0,5	4,3 ± 0,4	0,7 ± 0,0	4,9 ± 2,3	0,8 – 1,5
Otomys irroratus	42,2 ± 2,1	18,4 ± 4,0	39,4 ± 2,3	5,6 ± 0,9	0,7 ± 0,1	11,1 ± 5,9	1,0 – 8,0
Aethomys chrysophilus	58,2 ± 1,3	11,1 ± 1,2	30,7 ± 1,4	5,0 ± 0,4	1,4 ± 0,1	2,8 ± 1,7	1,0 – 6,1
Aethomys namaquensis	64,4 ± 3,5	11,4 ± 2,2	24,2 ± 3,0	5,3 ± 0,3	1,8 ± 0,3	4,2 ± 2,2	0,8 – 6,8
Acomys spinosissimus	71,8 ± 0,4	7,0 ± 0,2	21,2 ± 0,6	4,7 ± 0,1	2,6 ± 0,1	2,5 ± 0,2	0,2 – 0,8
Lemniscomys griselda	54,3 ± 3,6	10,6 ± 2,0	35,1 ± 4,4	3,9 ± 0,2	1,2 ± 0,2	2,4 ± 0,4	0,7 – 8,7
Mus minutoides	72,1 ± 1,7	5,8 ± 1,3	22,1 ± 1,4	4,3 ± 1,3	2,6 ± 0,2	1,0 ± 0,8	0,5 – 10,4
Praomys natalensis	73,4 ± 1,4	6,0 ± 0,4	20,6 ± 1,8	5,5 ± 1,1	2,7 ± 0,2	2,9 ± 0,5	0,9 – 5,7
Rattus rattus	80,1 ± 0,4	3,7 ± 0,1	16,2 ± 0,5	7,5 ± 0,8	4,0 ± 0,1	1,4 ± 0,3	1,4
Rhabdomys pumilio	58,7 ± 2,0	11,1 ± 2,2	30,2 ± 1,4	4,5 ± 0,6	1,4 ± 0,1	3,9 ± 2,0	0,7 – 6,7
Thallomys paedulcus	50,9	16,3	32,8	5,3	1,0	4,4	3,5
Graphiurus murinus	53,5	0,0	46,5	3,7	1,1	0,0	1,4

Table 4 Features of the digestive system that are indicative of an adaptation to herbivory

Species	Ratio of stratified squamous to glandular gastric epithelium	No. of caecal haustra	No. of spiral loops of colon	% of colon lined with spiral folds	No. of liver lobes	Gall bladder
Cryptomys hottentotus	0	19	0	0	6	Yes
Mystromys albicaudatus	1,8	0	0	25	5	No
Desmodillus auricularis	1,1	0	2	30	7	No
Tatera brantsii	0,8	0	2	23	7	Yes
Tatera leucogaster	0,9	0	2	22	7	Yes
Steatomys pratensis	1,9	0	2	31	6	No
Saccostomus campestris	0,8	0	2	14	6	No
Otomys angoniensis	0,2	22	4	39	7	No
Otomys irroratus	0,2	31	4	53	7	No
Aethomys chrysophilus	1,4	0	2	21	7	No
Aethomys namaquensis	0,8	0	2	30	7	No
Acomys spinosissimus	1,5	0	1	22	5	Yes
Lemniscomys griselda	1,5	0	3	32	7	No
Mus minutoides	1,1	0	0	31	6	No
Praomys natalensis	0,6	0	0	32	7	No
Rattus rattus	0,7	0	1	43	7	No
Rhabdomys pumilio	0,8	3	4	41	7	Yes
Thallomys paedulcus	1,3	0	4	34	5	Yes
Graphiurus murinus	0	–	0	0	7	Yes

incisura angularis barely extends beyond the oesophageal opening. The stomachs of *Graphiurus murinus* and *Cryptomys hottentotus* (Fig. 3) are wholly glandular and contain no stratified squamous epithelia. They can be described as unilocular glandular (or simple unilocular) stomachs. Seven of the nine Murids possessed an unspecialized unilocular hemiglandular (or compound unilocular) stomach, with both stratified squamous and cuboidal glandular epithelia. The area of stratified squamous epithelium increased only marginally in the series *A. spiniosissimus, A. chrysophilus, A. namaquensis, L. griselda, M. minutoides, R. pumilio* and *R. rattus*. The stomach of *P. natalensis* was more complex and consisted of two distinct regions, and that of *T. paedulcus* possessed a fornix ventricularis distinctly demarcated by an incisure lined with papillae. In the Cricetidae, a wider range of adaptations was evident. Only the gerbils,

Table 5 Measurements of the gastro-intestinal tract of rodents examined with regard to gut-morphology. All values are means and the standard deviation has been included for total length of the gut

Species	Mean width of caecum (mm)	Width of small intestine (mm)	Width of large intestine (mm)	No. of spiral folds in large intestine	Width of folds (mm)	Height of fold (mm)	Total length of gut (mm) excl. oesophagus
Cryptomys hottentotus	23,8	13,8	11,0	0	–	–	663 ± 37
Mystromys albicaudatus	–	10,0	9,0	50	–	–	884 ± 146
Desmodillus auricularis	12,0	–	–	29	–	–	577
Tatera brantsii	22,1	10,9	12,3	32	0,31	1,00	776 ± 61
Tatera leucogaster	22,5	9,9	12,0	28	0,19	0,65	770 ± 83
Steatomys pratensis	15,6	9,0	8,7	18	0,20	0,48	343
Saccostomus campestris	27,8	13,3	18,6	16	0,10	0,78	743 ± 68
Otomys angoniensis	31,6	17,5	13,0	116	0,19	0,78	653 ± 3
Otomys irroratus	25,3	13,0	14,6	169	0,26	0,75	832 ± 104
Aethomys chrysophilus	25,1	13,5	14,5	42	0,15	0,54	670 ± 76
Aethomys namaquensis	18,3	9,5	10,7	33	0,30	0,72	568 ± 86
Acomys spinosissimus	16,2	7,9	9,0	15	0,20	0,40	362 ± 12
Lemniscomys griselda	26,2	12,3	14,9	56	0,14	0,51	449 ± 38
Mus minutoides	7,7	8,0	5,7	15	0,23	0,29	242 ± 40
Praomys natalensis	13,0	8,1	8,2	27	0,27	0,60	126 ± 140
Rattus rattus	–	–	–	47	–	–	1 194 ± 107
Rhabdomys pumilio	18,4	11,0	10,8	47	0,24	0,60	500 ± 90
Thallomys paedulcus	22,0	11,5	8,7	48	0,28	0,88	615
Graphiurus murinus	–	10,0	9,0	0	–	–	318

Table 6 The degree of specialization of the major organs concerned with an adaptation towards herbivory. Arbitrary ranking has been used as outlined in the text. Species are listed in order of their adaptedness to herbivory

Species	Feeding category	Teeth	Gut length	Stratified squamous: glandular cuboidal epithelium	Liver	Gall bladder	Small intestine: large intestine	Caecum size	Caecal haustra	Colic spiral loops	Mean rank
Graphiurus murinus	G/I	2	1	1	2	1	2	1	1	1	1,3
Praomys natalensis	O	1	2	2	2	3	1	1	1	1	1,6
Tatera brantsii	O	2	2	2	2	1	2	1	1	2	1,7
Tatera leucogaster	O	2	2	2	2	1	2	1	1	2	1,7
Acomys spinosissimus	G/I	2	2	3	3	1	1	1	1	1	1,7
Mus minutoides	O	2	1	3	3	3	1	1	1	1	1,8
Rattus rattus	O	2	3	2	2	3	1	1	1	1	1,8
Steatomys pratensis	G/I	2	1	3	3	3	1	1	1	2	1,9
Aethomys namaquensis	O/H	1	2	2	2	3	2	2	1	2	1,9
Rhabdomys pumilio	O	1	2	2	2	2	2	2	2	2	1,9
Mystromys albicaudatus	G/O	2	2	3	3	3	2	1	1	1	2,0
Aethomys chrysophilus	O/H	1	2	3	2	3	2	2	1	2	2,0
Lemniscomys griselda	O/H	2	1	3	2	3	2	2	1	2	2,0
Thallomys paedulcus	O	1	2	3	3	1	2	3	1	2	2,0
Cryptomys hottentotus	B	3	2	1	3	1	2	3	3	1	2,1
Desmodillus auricularis	G/I	3	2	3	2	3	2	1	1	2	2,1
Saccostomus campestris	G/I	3	2	2	3	3	2	2	1	2	2,2
Otomys angoniensis	H	3	1	2	2	3	3	3	3	2	2,4
Otomys irroratus	H	3	2	2	2	3	3	3	3	2	2,5

1 = primitive or unspecialized; 2 = intermediate; and 3 = specialized.

D. auricularis, T. leucogaster and *T. brantsi,* possessed a typical unilocular hemiglandular stomach. In *O. irroratus* and *O. angoniensis,* a narrow strip of stratified squamous epithelium extended from the corpus to half way along the greater curvature of the stomach. *M. albicaudatus* possessed corpal papillae similar to those of *T. paedulcus* but their distribution extended almost along the whole length of the stratified squamous region of the stomach. The glandular region in *S. pratensis* has become extremely reduced and confined to the antrum. The stomach of *Saccostomus campestris* was unique in possessing three distinct regions, with glandular tissue only occurring in the corpus and not in the antrum. It appears to be approaching the bilocular-discoglandular condition although no incisura angularis was present.

The rodent caecum is a blind sac-like structure at the junction of the small and large intestines; it may contain haustra and papillae (Fig. 4) and leads into the spiral loop(s) of the colon. Both Murids and Cricetids demonstrated a similar range of structural adaptations from simple to complex. *G. murinus* was the only species without a caecum, whereas *C. hottentotus* possessed the largest, which contained 19 haustra. The proximal part of the colon was dilated or sacculated but contained no spiral loops. The simplest caecum with a straight colon occurred in the Cricetid, *M. albicaudatus.* Simple caeca also occurred in the Murids, *Mus minutoides* and *Praomys natalensis,* but the proximal part of the colon was looped. In *Tatera brantsi* and *T. leucogaster* the caecum was greatly elongated and folded. Broad sac-like caeca occurred in both Murids (*Acomys spinosissimus*) and Cricetids (*Steatomys pratensis*). There were also marked differences in the degree of dilation of the proximal end of the colon as is exemplified by *A. spinosissimus* and *A. namaquenis.* Two spiral colic loops occurred in *Tatera* sp., *S. pratensis, D. auricularis* and *Aethomys* sp., three in *L. griselda* and four in *T. paedulcus.* The most complex Murid caecum encountered was that of *Rhabdomys pumilio* which possessed several haustra and colic loops. Those of the Cricetids *O. irroratus* and *O. angoniensis* were more elaborate. They had two rows of haustra, numerous caecal papillae, and four colic loops. The adaptations of *Otomys* appeared to parallel those of *Cryptomys.*

It appears that a wider range of adaptations occur in the Cricetidae than the Muridae with reference to dentition, and gastric and caecal morphology. This might in part be due to the fact that only a few species were examined, and that five sub-families were represented for the Cricetidae (Table 1) but only one for the Muridae. However, three of the four Murid divisions were represented in the samples. The classification of rodents used in this study was taken from Meester and Setzer (1971). Recent palaontological studies (Pocock 1976) suggest however that the Otomyids are not Cricetids but Murids.

Individual characteristics

Family BATHYERGIDAE: *Cryptomys hottentotus*

This highly specialized fossorial species feeds on roots, bulbs and tubers (Roberts 1951; Kingdon 1974) and occasionally some invertebrates (Walker 1975). The molars are flat-topped and hypsodont but have no transverse lophs for grinding coarse vegetation. This is possibly because bulbs and tubers do not contain elaborate cellulose cell walls, silica bodies or structural lignin which are abundant in woody stems and leaves. Functional compensation among different organs is seen, as *Cryptomys* has characters ranging from primitive to specialized. The stomach is a simple single-chambered glandular sac although the caecum is

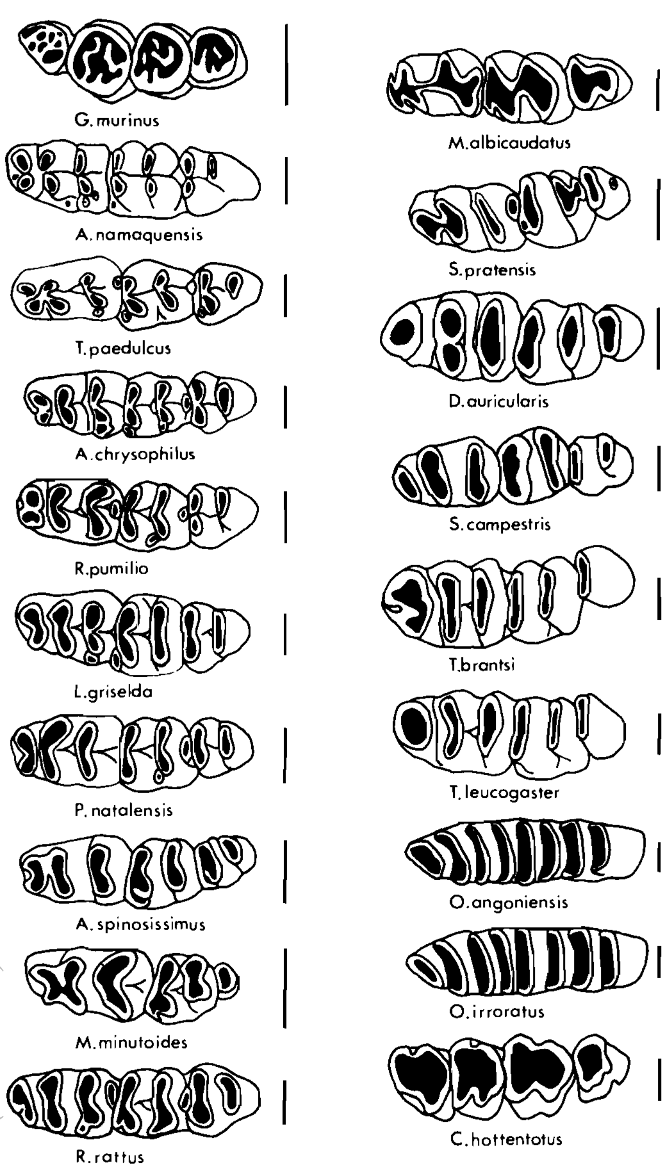

Fig. 1 Occlusal surface of the molar teeth of the lower left jaw of several rodents showing decrease in cusp number and development of transverse ridges. The Muscardinae and Muridae (left) are shown separately from the Cricetidae and Bathyergidae (right). Scale lines represent 1 mm. Dentine exposure is indicated by black shading.

complex, with several large haustra. In the caecum, two parallel rows of small papillae form a canal running from the small to the large intestine (Fig. 5). The colon is not looped and contains no internal spiralling. The ratio of small to large intestine is higher than expected for a herbivore; but the number of liver lobes has been reduced to only five, indicative of a reduced protein intake. The lack of extensive physical mastication by the teeth might be compensated for by the enzymatic action of caecal micro-organisms. The gall bladder is retained.

Family CRICETIDAE: *Mystromys albicaudatus*

The digestive system of *M. albicaudatus* indicates an omnivorous diet. The species is described as eating seeds and vegetation (Roberts 1951; Walker 1975). The teeth are cusped, not flattened and the lengths of the small and large intestines are typical of an omnivore. Reduction in the number of liver lobes and absence of a gall bladder indicate a decrease in protein intake but prolonged feeding, possibly a trend away from granivory. The small caecum and lack of spiral loops in the colon are primitive characteristics not suggestive of herbivory. Nevertheless, increased spiral ridges within the colon may partially compensate for the lack of spiral loops. The stomach has a large area of cornified epithelium with numerous large papillae which may serve to anchor symbiotic bacteria (*unpubl. data*).

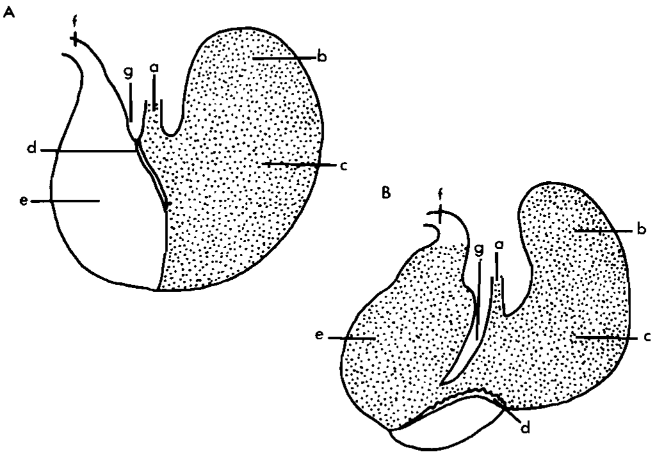

Fig. 2 Generalized diagrams of (A) unilocular-hemiglandular and (B) bilocular-discoglandular stomachs of muroid rodents. (After Carleton 1973). Stippling represents statified squamous epithelium and clear areas represent glandular epithelium. a = distal end of oesophagus, b = fornix ventricularis, c = corpus, d = bordering fold, e = antrum, f = proximal end of duodenum, and g = incisura angularis.

Desmodillus auricularis

Since *D. auricularis* is a granivore occasionally taking insects (Hewitt 1931; Roberts 1951; Smithers 1971; Walker 1975) its diet is proteinaceous, and it must be a forager. Its molar teeth show transverse but bunodont occlusal ridges, and its stomach is of the typical unilocular hemiglandular type. The small simple caecum with its lack of haustra reflects the ancestral type. Fine villi lining the caecum may be concerned with water reabsorption. This species has few specializations for herbivory, and must avoid competition through some other mechanism.

Tatera brantsi and *T. leucogaster*

The gut morphology of these two species is very similar and they are therefore considered together. Both species are adapted to their opportunistic habits and omnivorous diets (Shortridge 1934; Roberts 1951; Smithers 1971; Kingdon 1974; Walker 1975). They have none of the specialized characters typical of herbivores and the only primitive characters are the presence of a gall bladder and a small, simple caecum. These general feeders have few trophic specializations but are adapted to xeric habitats, often where fire is a significant environmental factor, which may reduce competition.

Steatomys pratensis

S. pratensis is essentially granivorous but will take some insects and vegetation (Kingdon 1974). The teeth are distinctly ridged, and owing to cusp reduction (Delany 1975) approach a laminate condition. Many characters suggest a high protein content diet. These include a short gut, small caecum and a long small intestine. The decreased number of liver lobes and loss of a gall bladder are atypical of a seed-eater, but may in some way be related to the pronounced lipid storage in this species (Kingdon 1974) and/or its partial torpidity (Petter 1966).

Saccostomus campestris

This species is a partially insectivorous granivore (Delany 1975; Walker 1975) with bunodont molars possessing

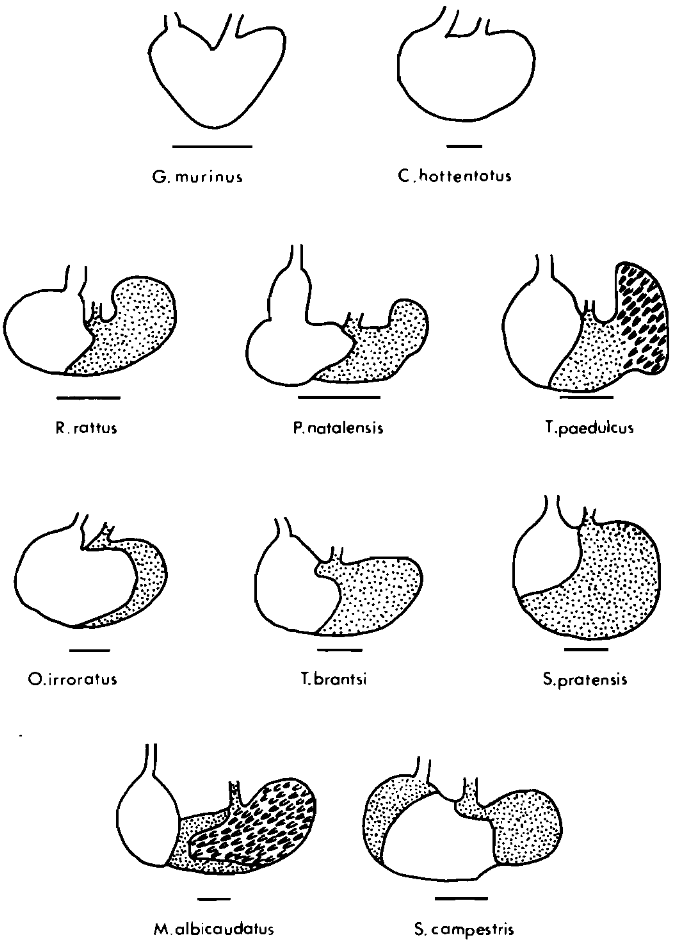

Fig. 3 Comparative stomach morphology of several rodents showing increasing cornification of the corpus. Stippling represents stratified squamous epithelium and clear areas represent glandular epithelium. Scale lines represent 10 mm. The first line shows a Muscardinid and a Bathyergid, the second line Murids and third and fourth lines Cricetids. Note the presence of papillae in *T. paedulcus* and *M. albicaudatus.*

several transverse lophs. It is adapted for a proteinaceous diet and the presence of a simple caecum without haustra is a conservative character. The stomach has the most advanced structure of all the species studied. It is the only one having three distinct regions that approach the bilocular discoglandular condition. The highly cornified corpus leads into a glandular fundic region, and thence to a nonglandular pyloric region. Stratified squamous epithelium comprises less than half of the gastric lining; this may be associated with the presence of cheek pouches which are used for temporary food storage. The liver lobes are reduced in number.

Otomys irroratus and *O. angoniensis*

These species are wholly herbivorous (Roberts 1951; Davis 1973; Kingdon 1974; Perrin *In press*), and the most advanced of all the species studied with respect to herbivorous specializations. Except for the total length of the gut and the number of spiral colic loops, these two species possess the same high degree of adaptation to herbivory. The teeth bear transverse lophs and the caecum is large and complex. This compensates for the apparently little specialized stomach where the band of cornified epithelium is extremely small, yet very elastic. The caeca have a double row of deep haustra running along the greater curvature from the ileum to its blind end. A groove runs from the ileum opening along the caecum to the colon. The caeca contain numerous papillae and the colon of each species has four tight loops with internal ridges that are large and closely packed.

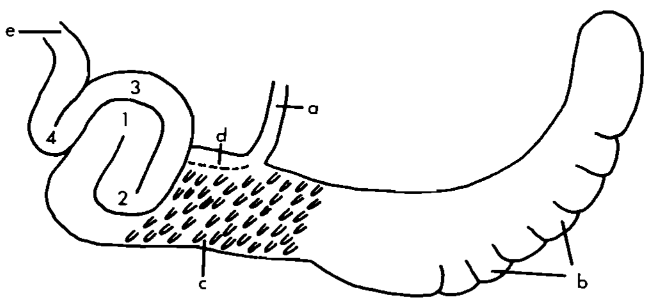

Fig. 4 Generalized diagram of a rodent caecum and proximal colon. a = distal end of small intestine, b = haustra, c = papillae, d = groove running from small intestine to colon, e = proximal end of colon, and 1 – 4 = spiral loops of the large intestine, or colic loops.

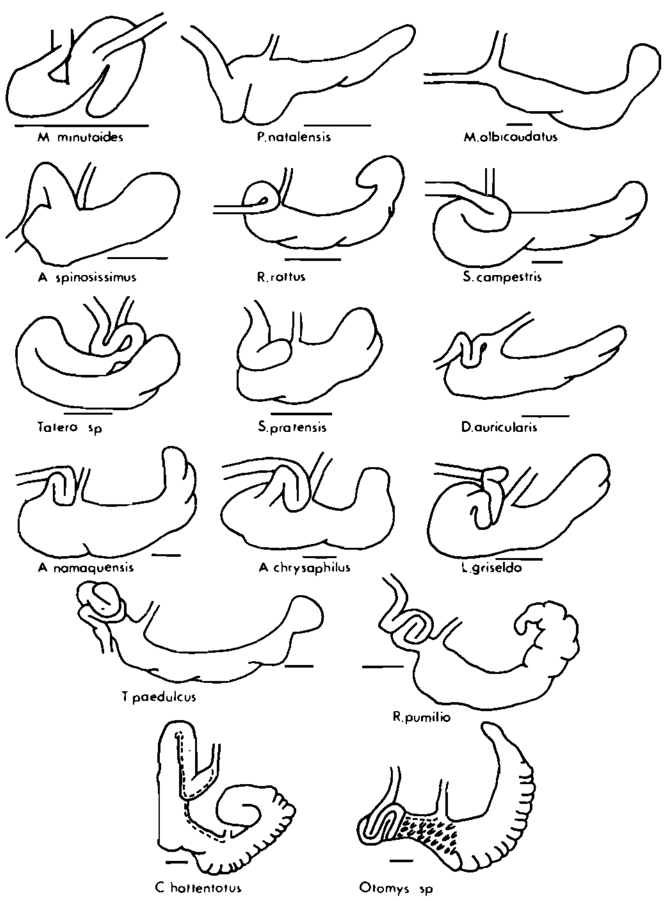

Fig. 5 Caecum and proximal colon morphology of several rodents, showing increasing complexity with the addition of colic loops, haustra and papillae. Scale line represents 10 mm.

Family MURIDAE: *Aethomys chrysophilus* and *A. namaquensis*

These two species which may be regarded as omnivores (Roberts 1951) or generalized herbivores (Kingdon 1974), are virtually identical in their degree of adaptation. Both possess unilocular hemiglandular stomachs and multicusped molar teeth of the ancestral type. The caeca are large, which, together with the loss of a gall-bladder, may be indicative of a tendency towards herbivory.

Acomys spinosissimus

This species feeds predominantly on seeds and insects (Vesey–Fitzgerald 1966; Kingdon 1974), but is opportunistic and will also take vegetation and other invertebrates. It shows primitive characteristics in intestinal and caecal morphology and the retention of a gall bladder, which might be expected from its feeding habits. Its proteinaceous diet is also reflected in the total length of the gut and tooth structure. The ratio of stratified squamous to glandular epithelium in the stomach is particularly high, reflecting the advanced condition. As *A. spinosissimus* inhabits arid regions (Kingdon 1974) this may be an adaptation to allow for temporary food storage.

Lemniscomys griselda

As with various other omnivores, *L. griselda* has characters ranging from primitive to specialized. The total length of the gut is short and the caecum lacks haustra. The dentition is characteristic of a generalized Murid. The ratio of stratified squamous to glandular epithelium in the stomach is high and there is no gall bladder. This agrees with Kingdon's (1974) grouping of *Lemniscomys* with the herbivorous Murids. Yet, the morphology of the caecum and large intestine lend support to the omnivorous tendencies of this species as described by Roberts (1951) and Walker (1975).

Mus minutoides

In the length of the gut and structure of the caecum and colon, this species is primitive, but the teeth reflect a transition from granivory to omnivory, or possibly herbivory owing to loph formation, as does the ratio of stratified squamous to glandular epithelium of the stomach. Decrease in the number of liver lobes and lack of gall bladder are specialized characteristics. This species appears to be omnivorous (Hewitt 1931; Delany 1975; Kingdon 1974), and possesses both ancestral and advanced characters. It probably avoids competition from other generalized feeders by its extremely small size.

Praomys natalensis

This versatile species, often commensal with man, is an opportunistic feeder (Kingdon 1974). It has a high small intestine to large intestine ratio, a small caecum and only one colic loop, which are primitive features. Its dentition is typical of an omnivorous Murid, and its only advanced feature is the loss of the gall bladder.

Rattus rattus

This introduced Eurasian species has a worldwide distribution and diverse feeding habits; it is also commensal with man in Africa and may be in competition with the previous species (Kingdon 1974). The characteristics of this species' gut morphology reflect its omnivorous diet. The dentition is unspecialized and typical of an omnivore. The great length of the gut may be associated with herbivory but the ratio of small to large intestine reflects (opportunistic) proteinaceous feeding, as does the small caecum and single colic loop.

Rhabdomys pumilio

This rodent has been variously described as a granivore (Brooks 1974) and a herbivore (Roberts 1951; Kingdon 1974; Delany 1975). Recent studies suggest that it is an opportunistic omnivore whose diet varies seasonally (Perrin *In press*) and that it is definitely not a herbivore (Curtis & Perrin 1979). In all characteristics, with the possible exception of the dentition, the digestive tract is typical of an omnivore. There is no character which reflects a herbivorous specialization. The caecal haustra are small and not apparent in all specimens. Similarly, gall bladders occur only in some individuals. This is indicative of polymorphism or changing adaptation.

Thallomys paedulcus

This omnivore is almost monophagous and feeds on the seeds, fruits, flowers and leaves of Acacias (Kingdon 1974). It has a range of characters, from the primitive multi-cusped teeth (similar to the Miocene *Parapodemus* stock, Misonne 1969) and presence of a gall bladder, to the advanced features of a large caecum and a reduced number of liver lobes. The caecum contains no haustra and the stomach is highly cornified. This species avoids competition in being arboreal and by its specialized (restricted) feeding habits.

Family MUSCARDINAE: *Graphiurus murinus*

The diet of *G. murinus* consists of proteinaceous insects, seeds and fruits (Meester & Setzer 1971; Kingdon 1974; Walker 1975). The teeth are brachyodont with few pointed cusps but many shallow ridges. They are unlike those of most insectivores but are typical of the Muscardinae (Vorontsov 1962). The lack of a caecum and the presence of a single chambered glandular stomach are indicative of a proteinaceous diet. The liver consists of seven large lobes and a gall bladder is present. In most characteristics *G. murinus* shows the primitive characteristics of a species feeding on a nutritious diet.

Discussion

The molar teeth of the Muridae are typically cuspidate, whereas those of the Cricetidae tend to develop transverse lophs, sometimes with cusp reduction, hypsodonty and a flattened occlusal surface. These taxonomic relationships tend to mask changes in adaptation to diet composition. Similarly, the ratio of small to large intestine is greater among the Murids than the Cricetids. In all other characteristics the degree of specialization appears to vary equally among the two distinct families. Thus is appears that parallel specializations have occurred independently in both families, or were present in an ancestral form.

Both *C. hottentotus* and *G. murinus* possessed a unilocular wholly glandular stomach although their feeding habitats are distinct. Yet most Eurasian members of the Bathyergidae and Muscardinae also lack gastric cornification. The gastric anatomy in these two families is rather regular and demonstrates little adaptive radiation at the morphological level. It is not unrealistic to suggest tentatively that the ancestral type was wholly glandular, and that cornification has developed secondarily, as has sacculation of the stomach (Carleton 1973).

Tooth structure is partially dependent on phylogeny (Misonne 1969) and only appeared to become adapted to herbivory in specialists, notably the Otomyids; indicating a long-term evolutionary development. It appears that the multi-cusp trituberculate molars of ancestral insectivores and granivores are pre-adapted for omnivory. The laminate, hypsodont molars of *Otomys* sp. with flat crowns and open roots are clearly an adaptation to a fibrous diet. (Age is a factor which can influence the interpretation of the cusp pattern of the occlusal surface of molars, but was circumvented here by using young specimens).

The suggestion of Vorontsov (1962) that the number of liver lobes reduces with adaptation away from a proteinaceous diet is not upheld, and future studies might examine changes in liver mass. None of the species studied has the eight-lobe liver described by Vorontsov (1962) as the primitive condition. Reduction of liver lobe number was not apparent in the herbivorous Otomyids but occurred in *C. hottentotus* and several partially insectivorous granivores and omnivores. Similarly elongation of the alimentary tract from duodenum to anus does not appear to be indicative of herbivory. However changes in length should be considered in relation to dilation or diameter of the gut. The herbivore *O. angoniensis* has a particularly short large intestine although with a greater diameter than *O. irroratus*. In future studies total surface area of the gut should be computed, making allowance for dilation and villous morphology (Barry 1976, 1977).

The unilocular-hemiglandular stomach is believed to be a primitive condition from which the more complex bilocular discoglandular form evolved (Carleton 1973). These complex multi-chambered stomachs of highly adapted species (Vorontsov 1962, Carleton 1973) were not encountered in this study. The unilocular hemiglandular type occurred with several varying degrees of cornification. A complex compound stomach occurred in *S. campestris* which approached the bilocular discoglandular condition in that only the corpus was glandular but there was no deep incisura angularis to produce sacculation. Particularly interesting are the extensive papillae occurring in the fornix ventricularis of *T. paedulcus* and the corpus of *M. albicaudatus*. These cornified structures greatly increase the surface area of the corpus, which in most muroids is smooth (Carleton 1973). The papillated fornix of *T. paedulcus* is partially separated from the corpus by a constriction. Similar gastric papillae have been reported in *Cricetomys gambianus* (Camain *et al.* 1960) where micro-organisms ferment glucose to produce acetylmethyl carbinol, hydrolyze starch and the proteins casein and gelatin, reduce nitrate, but do not ferment cellulose.

Increased gastric cornification might be an adaptation to harsh, abrasive foodstuffs (Bensley 1902; Horner, Taylor & Padykula 1961). The abrasive nature of food, however, does not appear to have adverse effects on the stomach of the mole-rat *C. hottentotus* or the beaver, *C. canadensis* (Nasset 1953), both of which consume rough diets and possess completely glandular stomachs. Lagomorphs, which have a totally glandular stomach (Bensley 1902), also ingest many abrasive foods including grasses, sedges, twigs and bark (Todd 1927; Dalke 1942). Thus, it is unlikely that the mechanical action of the food has resulted in increased gastric cornification.

Vorontsov (1962) suggested that increased cornification may be an adaptation to a herbivorous diet by forming a fermentation chamber in which symbiotic organisms may degrade complex polysaccharides. This seems feasible in *C. gambianus* (Camain *et al.* 1960) and possibly *T. paedulcus* and *M. albicaudatus*. Carleton (1973) listed a number of difficulties in fully accepting Vorontsov's (1962) hypothesis, in that gastric sacculation does not approximate that of a ruminant; there is no anatomical division of glandular and cornified areas; and the theory does not explain the cornification of the pyloric region of the stomach. However, gastric fermentation may have evolved differently within the Rodentia, and has certainly developed along several independent lines within the Mammalia, and is known to occur in bradypodid edentates (Jeuniaux 1962), colobine primates (Kuhn 1964) and macropodid marsupials (Moir, Somers & Waring 1956).

Carleton (1973) questioned the development of gastric and caecal fermentation chambers in a single individual and Moir (1968) has suggested an inverse relationship between gastric and caecal adaptation to herbivory. Stomach fermentation is more advantageous as it occurs prior to the site of protein digestion. In *T. paedulcus* which possesses a papillated unilocular hemiglandular stomach, the caecum is large but without haustra. It is unlikely that two fermentation chambers should develop unless they operate in a functionally different manner.

Carleton (1973) suggested that a reduction of glandular epithelium might result in decreased hydrochloric acid secretion, an increased gastric pH, prolonged salivary amylase activity at pH7, and increased carbohydrate digestive efficiency. Selection may have favoured those individuals which could better utilize starch of seeds or glycogen of arthropods than protein. Thus, the extent of glandular reduction might reflect the relative intensities of selection favouring hydrolysis of protein (fundic glands) on the one hand or carbohydrates (salivary amylase) on the other (Carleton 1973). This would explain the highly cornified stomachs of species such as *D. auricularis* and *S. pratensis*, and the wholly glandular stomach of *C. hottentotus*.

The increased area of cornified epithelium may simply be an adaptation for temporary food storage. The cheek pouches of *S. campestris* probably serve such a function, but are not present in most muroids. *M. albicaudatus* has lost its cheek pouches (Kingdon 1975) but possesses a large cornified stomach. Energy can be stored over longer periods as body fat (*S. pratensis*) or by cacheing seeds (*Beamys hindei*) (Kingdon 1974). It is likely that there is no single causal factor in the evolution of stomach complexity and that in different families different selective pressures may have resulted in a diversity of stomach forms for various functions and diets.

The ratio of small to large intestine was lowest in the herbivorous Cricetids studied, is typical of herbivory, and appears late in an evolutionary transition. Nevertheless, Barry (1977) has shown that the relative lengths of the intestines are not always an accurate indication of the relative absorptive surface area of the gut, whereas villous morphology appears to be correlated with feeding habit and may be altered by changes in diet (Barry 1976); this approach would be of value in future studies.

The structure of the caecum in many of the species studied was very simple, and the most complex caeca occurred in the vegetarian *Otomys* sp. and *C. hottentotus* and in no other species. They are diagnostic of herbivory, and probably occur late in an evolutionary sequence or transition.

Many herbivorous rodents have an enlarged caecum where symbiotic bacteria degrade cellulose (McBee 1971). The beaver *C. canadensis* is able to utilize micro-organisms to hydrolyze dietary cellulose and release metabolizable volatile fatty acids (Currier, Kitts, & McCowan 1960). Various studies have shown that volatile fatty acids liberated in the caecum of rodents are utilized for growth and maintenance (Johnson & McBee 1967; Yang, Manoharan, & Young 1969; Yang, Manoharan & Michelsen 1970). It seems probable on anatomical grounds that fermentation of complex carbohydrates occur in the caeca of *Otomys* sp. and *C. hottentotus*. Fermentation can be aided by coprophagy, which occurs in *O. irroratus*. It is important in vitamin metabolism (Kulwich, Struglia, & Pearson 1953) and can function to provide a protein source from caecal micro-organisms, as occurs in ruminant digestion (Hungate, Mah, & Simesen 1961; Johnson & McBee 1967). Some rodents appear to be polygastric, and the golden hamster, *Mesocricetus auratus*, can utilize urea as a substitute for feed protein (Matsumoto 1955). The extent of such physiological mechanisms in *O. irroratus* or other species examined here is unknown, but warrants further investigation.

Gut morphology did not always reflect dietary habits accurately and several species reported to be predominantly granivorous, *D. auricularis*, *S. campestris* and *S. pratensis*, possessed several characters regarded as transitional towards herbivory. These somewhat anomalous results can be explained by a changing diet, phylogeny, or functional compensation (Vorontsov 1962). The paucity of detailed quantitative food studies presents a major practical obstacle to correlations of gut morphology and diet. The idea that rodents are fundamentally herbivorous has been negated by Landry's (1970) extensive survey of rodent species that consume animal matter. Landry (1970) suggested that rodents may have been primitively omnivorous, later becoming specialized towards an insectivorous or herbivorous diet, and Vorontsov (1962) acknowledges that a reversed direction of specialization may have occurred.

It is evident that the degree of specialization of various organs within the digestive system is not always equivalent (Fig. 6), probably due to functional compensation (Vorontsov 1961, 1962). For example, *C. hottentotus* and *Otomys* sp. have a simple stomach which may be compensated for by dentition and a large and complex caecum. The teeth of *A. namaquensis* are of an ancestral granivorous type which may be compensated for in a transition towards omnivory or herbivory, by a specialized stomach and reduced liver size. The principle of functional compensation depends on the phylogenetic variability of organs within a system (Vorontsov 1961, 1962) and involves modified organs rapidly intensifying their functions to compensate for slower rates of adaptation of other organs. Even narrowly adapted herbivores do not possess extreme degrees of specialization in all portions of their digestive system. Should living conditions change, the generalized organs may develop in the opposite direction from that in which the specialized organs were developing. Thus, the compensated organ may become the compensating one, and provides a means for the continual adaptation of the species. Vorontsov (1961) was unable to find a single case of synchronous transformation of all organs within a species. This asynchronous transformation of organs may be due to selective pressures acting differentially on random mutations.

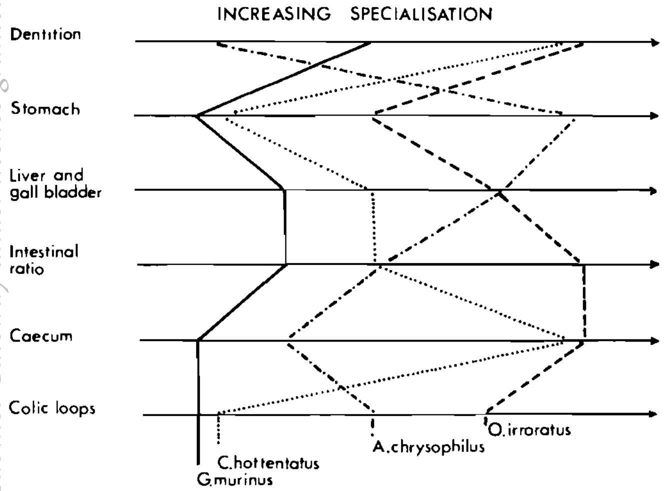

Fig. 6 Scheme of variation in the rates of transformation of various organs in the digestive system of four rodents (after Vorontsov 1961). The left side represents extreme degrees of adaptation to a high-protein diet whereas the right side represents extreme degrees of adaptation to a cellulose diet. Much of the variability in adaptation is believed to be due to functional compensation (see text).

This brief survey has attempted to correlate gut morphology with feeding habits in several species of Myomorph rodents. Trophic differences were evident, but more information is required to define each species' ecological niche. An indication of some species habitat orientation or adaptation to variables not associated with feeding was briefly outlined in the species characteristics. Gerbils are often associated with xeric habitats and possess adaptations for water conservation, whereas Otomyids are often confined to riparian or mesic habitats. Most Bathyergids are fossorial and feed on subterranean vegetation whereas *T. paedulcus* is arboreal and closely associated with *Acacia* woodland. Extreme seasonal change in food availability may have led to torpidity in dormice, lipid storage in *S. pratensis* and a major shift in diet in *R. pumilio* (Perrin *In press*). Other species may avoid competition by their size (*M. minutoides, C. gambianus*) or rates of increase (*P. natalensis*).

It would be premature and incorrect to conclude by stating that gut morphology was directly correlated with diet in either Murid or Cricetid rodents. Certainly such tendencies are apparent, but more extensive and detailed research is essential to validate such an hypothesis. The ideas of Vorontsov (1962) that stimulated this work appear to require revision, particularly with references to the development of a cornified and sacculated stomach. The argument of Carleton (1973) that the cornified stomach evolved to enhance carbohydrate digestion rather than to provide for a gastric microbial fermentation chamber (or to resist abrasive foods) is valid. Caecal hypertrophy and fermentation probably developed along several lines and is more common than gastric fermentation in small mammals (McBee 1971). The latter may have developed in species with reduced caeca, but with a stomach modified for carbohydrate digestion. It is clear that a reappraisal of the criteria used in assessing adaptation to herbivory is required. Difficulties will persist because of functional compensation, polymorphism and the continual changes of natural selection. Different individuals of *R. pumilio*, for example, either possess or have lost either gall bladders and/or caecal haustra. More detailed studies of many species feeding habits are required, with reference to food preferences in time and space.

It is concluded that the colonizing African Murids are more generalized feeders than the older resident Cricetids, which show several specialized adaptations to herbivory in terms of gastric and caecal morphology, but compete effectively because of their r-selected reproductive strategies (French *et al.* 1975).

Acknowledgements

We should like to thank the following people for supplying rodent specimens: Mr K.M. Adams, National Museum, Bulawayo, Mr J. David, University of Cape Town, Mrs H. Koegh, South African Institute for Medical Research and Miss L. Scott, University of Natal, Pietermaritzburg. Financial support from the CSIR and Rhodes University is acknowledged. We thank Miss A. Rennie for typing this paper.

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