Preliminary investigations of the digestive processes of the white-tailed rat *Mystromys albicaudatus* (Smith 1834)

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The possibility of pregastric fermentation or amylolytic digestion in the bilocular stomach of *Mystromys albicaudatus* was examined. Measurements of various digestive parameters (pH, stomach size and ingesta passage rates) and analyses of gut contents (volatile fatty acid concentration and amylase activity) revealed that gastric fermentation is unlikely, but that the forestomach acts as an amylase reservoir. Large populations of amylase-producing bacilli, located on fornical papillae, contribute significantly to high alpha amylase activity in the fornix. Examination of the natural food preferences of the white-tailed rat showed that the rodent selects a diet rich in starch, glycogen and protein. The bilocular stomach of *M. albicaudatus* is well adapted to efficiently digest these dietary components with carbohydrate digestion occurring in the keratinized fornix and protein digestion in the glandular antrum.
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Die moontlikheid dat pregastriese fermentasie en amilolitiese vertering in die tweekamermaag van *Mystromys albicaudatus* voorkom, is ondersoek. Meting van verskeie spysverteringsparameters (pH, maaggroote en voedseldeurgangstempo), en chemiese analise van die maaginhoud (vlugtige vetsuurkonsentrasie en amilase-aktiwiteit) het aan die lig gebring dat fermentasie in die maag onwaarskynlik is, maar dat die voormaag dien as 'n amilase-reservoir. Groot bevolkings amilase-vervaardigende basille, wat voorkom op papille in die fornix, dra betekenisvol by tot hoë alfaämilase-aktiwiteit in die fornix. Ondersoek van die natuurlike voedselvoorkeur van die witstertrot het getoon dat hierdie knaagdier 'n dieet uitsoek wat ryk is aan stysel, glikogeen en proteïene. Die tweekamermaag van *M. albicaudatus* is goed aangepas om hierdie voedselkomponente doeltreffend te verteer. Koolhidraatvertering vind plaas in die verhoringde fornix en proteïenvertering in die klieragtige antrum.
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A previous study of the gastric morphology of the white-tailed rat, *Mystromys albicaudatus*, revealed a bilocular hemiglandular stomach with a papillated, keratinized fornix (forestomach) separated from a glandular antrum (hindstomach) by a pregastric pouch (Maddock & Perrin 1981). The fornical papillae differ structurally and functionally from those of the rumen. Whereas rumen papillae are important in absorption, those of *M. albicaudatus* increase surface area for the attachment of symbiotic bacteria.

The aim of the present study was to investigate the feeding habits and digestive processes of *M. albicaudatus*, to explore the possibility of pregastric amylolysis or fermentation, and to provide an overview of the feeding strategy of this cricetid rodent. *M. albicaudatus* is a medium-sized rodent (75 – 100 g) whose relict populations are endemic to the Southern Savanna Grassland and the South West Cape biotic zones (De Graaff 1981). No information is available about its food under natural conditions.

Three major hypotheses have been advanced to explain the trend of increased cornification and concomitant glandular reduction in small mammalian herbivores. Bensley (1905) suggested that the physical consistency of the ingested food constituted a sufficient selective pressure favouring cornification of the stomach lining. However, many taxa (including the Chiroptera and Insectivora) digest abrasive foods but do not exhibit a similar trend in cornification (Myrcha 1967; Rouk & Glass 1970). Vorontsov's (1962) hypothesis equates a shift from a protein/lipid diet to a predominantly cellulose diet with a reduction in the highly acidic glandular antrum and increased sacculation of the stomach (to permit the existence of symbiotic cellulolytic bacteria). However, the presence of such organisms in the forestomach of a rodent has yet to be firmly documented. Studies on gastric symbionts taken from the fornical papillae occurring in the giant rat, *Cricetomys gambianus*, have demonstrated fermentation of glucose, hydrolysis of starch and the proteins casein and gelatin, but not the fermentation of cellulose (Camain, Quenum, Kerrest & Goueffon 1960).

Carleton (1973) has argued that a decrease in fundic gland complement could serve to protract the action of salivary amylase and thereby enhance starch digestion. The extent of glandular reduction may reflect the relative intensities of selection which favour the hydrolysis of protein (by fundic glands) versus the carbohydrate (by salivary amylase) fraction of available foods. Such extended salivary amylase activity could effectively increase the utilization of the starch content of seeds or the glycogen content of arthropods in a diet. However, he did not suggest that gastric symbionts may be an important source of amylase activity in the rodent forestomach (Peters 1973; Krishnamurti, Kitts & Smith 1974).

The validity of these theories to the digestive processes of *M. albicaudatus* was tested by examining various parameters associated with pregastric fermentation and/or amylolysis; that is, ingesta passage rate, gastric pH, stomach weight, fermentation (volatile fatty acid (VFA) production) and amylase activity. Since the feeding habits of *M. albicaudatus* were poorly known, a food preference study was initiated.

Materials and Methods

Stomach weight and pH

Thirteen adult *M. albicaudatus* were killed with chloroform anaesthesia and the full and empty stomach weights recorded. Fornical and antral stomach contents were removed, diluted 1/9 (v/v) with double distilled water and their pH measured with a Beckman 3500 digital pH meter.

Rate of passage of ingesta

Rate of passage is the time taken for undigested residues from a given meal to be voided in the faeces; the stained-particle method (Kobt & Luckey 1972) was used to estimate this value. Commercial rat pellets (the normal laboratory diet of *M. albicaudatus*) were ground to powder, and boiled in a 5% aqueous solution of crystal violet for one hour (Kindel 1960). Next morning the stained food was washed in running water, air-dried in an oven, and 50 g of it was mixed with 150 g of rat pellet powder and made into biscuits. Methyl cellulose (1%) was used as a binder.

Five laboratory-reared *M. albicaudatus* were starved for 34 h and then given 2 h access to the stained food (17h00 to 19h00). The time of ingestion (time zero) of the stained meal was taken as 18h00 and at 19h00 the marked food was replaced with untreated rat pellets.

Total faecal excrement was collected from 1 h after time zero and at intervals not exceeding 1 h for the next 96 h. Faeces were dried at 60 °C, crushed to powder and the number of stained particles per 0,1 g faeces counted under a dissecting microscope; allowing more than one particle count to be made per sample. The number of stained particles excreted per unit time was expressed as a percentage of the total. Cumulative totals were plotted against time to give excretion curves (Castle 1956); excretion times for 5%, 50%, 90% and 100% of the marker, and mean retention time of food in the gut were calculated from the curves.

Volatile fatty acid analysis

The concentrations of acetic, propionic and butyric acids in the fornical and antral stomach of *M. albicaudatus* were determined by gas chromatography. Adult rats were killed with chloroform anaesthesia at 08h00 since the gut was full after feeding activity the previous night. Fornical and antral contents were weighed and VFAs extracted with ether; 100 ml of solution were concentrated to 5 ml using a one-metre Vigreux fractionation column.

Samples of the concentrate (1 μl) were injected into a Perkin-Elmer gas chromatograph containing a one-metre glass column (3 mm internal diameter) packed with 10% Supelco 1200 plus 1% H_3PO_4 on chromosorb AW 80–100 mesh. The injection block was maintained at 220 °C, the manifold at 215 °C and the column at 95 °C. A Hitachi model QPD 54 recorder was used. This technique eluted acetic, propionic and butyric acids in under 10 min and the concentrations of the acids were determined by comparison of the curves obtained for test samples with the area of peaks recorded for standards of each acid.

Food preferences

The feeding trials were designed to indicate the categories of foods (Table 1) preferred by *M. albicaudatus* rather than the rodents' preference for individual food items. Since this rodent is endemic to the eastern Cape savanna, a selection of plants available to the rat under natural conditions was collected from the Albany district. The plants were identified and categorized (Table 1) by Palmer (1981).

Table 1 Foods comprising the various feeding categories recognized during the feeding trials

Feeding category	Definition	Food group	Group number
Graminivore	Grass eating	Grass stems and leaves	1
Granivore	Seed eating	a) Grass seeds	2
		b) Seeds of herbs and shrubs	5
Folivore	Eating leaves and soft stems	a) Herbs	3
		b) Shrubs	4
Frugivore	Fruit eating	Fruits of herbs and shrubs	5
Insectivore	Insect eating	Insects	6

In the absence of wild-caught individuals, eight laboratory-reared *M. albicaudatus* were used as subjects. To introduce the rats to a 'natural' diet, they were offered a selection of indigenous plants (in addition to rat pellets) for five days before the trials. Food preferences were determined using the cafeteria test (Drozdz 1975). Samples from each food group (Table 1) were placed in the cage at the start of each three-day trial period, and the percentages of each food item consumed were estimated daily, and categorized as follows.

Class I: Preferred. 50% or more consumed on the first day of the test. These species would be taken most readily in the wild.

Class II: Palatable. 30–40% consumed on the first day or more than 50% taken in total after three days. These species are less palatable than those of Class I, but would be likely to form a substantial part of the natural diet.

Class III: Unpalatable. 10–20% taken on the first day or 30–50% taken in total over the three-day period. This food would only be eaten if species of the above two classes were not available.

Class IV: Inedible. None eaten on the first day and less than 30% taken in total after three days, or 10% taken on the first day, but thereafter not touched. These species are not likely to be consumed in the wild or would only be selected in cases of extreme food shortage. They may contain unpalatable toxins or physical defence mechanisms.

The food preferences were ranked linearly for all food items tested (Table 3). Mann-Whitney U tests were employed to determine preferences between food groups. These tests are based on the sequencing of dietary preferences and are semigraphical and non-parametric.

Amylase activity

Adult *M. albicaudatus* were killed by chloroform anaesthesia. Fornical, antral and duodenal contents were removed, diluted 1/9 (v/v) with double distilled water and centrifuged. Alpha amylase activity was determined using Merckotest (Merck, Darmstadt, West Germany) and a procedure modified after Street & Close (1956). Further dilution was determined by experimentation. Absorption was measured with a Beckman 25 digital spectrophotometer and enzyme activity expressed in international units (U = μl/min/ml of culture at 37 °C). To determine if the papillae bacilli produced amylase, enzyme activity of the fornical contents with and without papillae (bacilli) was measured.

General

The relative stomach weights, gastric pH's and VFA concentrations of various herbivores were extracted from the literature to facilitate comparisons with *M. albicaudatus*.

Results

Relative stomach weight

The stomach contents of *M. albicaudatus* constituted approximately 3% of total body weight. Animals with foregut fermentation have larger stomachs and their contents range from 6,6% (for *Setonix brachyurus*: Moir, Somers & Waring 1956) to 17% (for *Presbytis cristatus*: Bauchop & Martucci 1968) of body weight, while ruminants have intermediate values (8 – 15%: Hungate, Phillips, MacGregor, Hungate & Beuchner 1959). Mean relative value for foregut fermenters is about 13%, which is considerably higher than that recorded for *M. albicaudatus*.

pH

The pH values of the fornical and antral samples were 4,57($\pm$0,46; $n = 10$) and 2,67($\pm$0,39; $n = 9$) respectively. Separation between the non-glandular and glandular regions was effective to the extent that the difference in fornical and antral pH was highly significant ($p < 0{,}001$). The fornical pH of *M. albicaudatus* was lower than that of known foregut fermenters (pH about 6), while the glandular stomachs of all herbivores investigated (including *M. albicaudatus*) were similarly acid (pH about 2,6).

Rate of passage of ingesta

Percentages of 5, 50, 90 and 100 of the stained particles were voided in the faeces 4,4 ± 1,1; 11,7 ± 4,3; 19,5 ± 4,3 and 34,1 ± 4,7 h after ingestion respectively. The rodents passed 50% of the marker after about 12 h at a rate of 4,3%/h and voided the main mass (75%) of test food in 15,8 h (Figure 1). The final 10% of the marker was eliminated slowly at approximately 0,7%/h and the mean retention time was 12,1 ± 3,2 h.

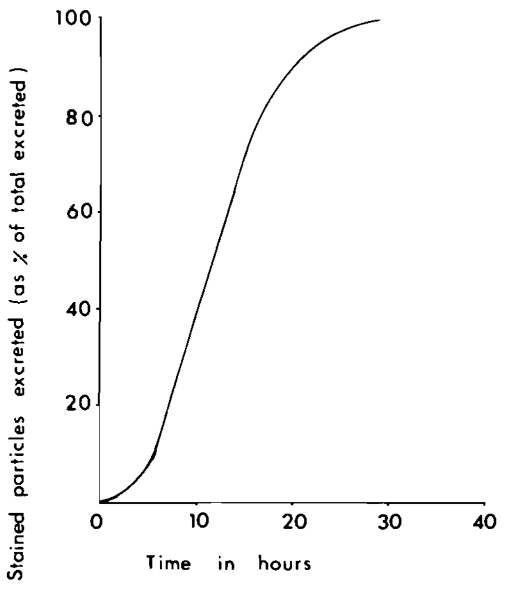

Figure 1 Mean excretion curve for stained particles excreted by *M. albicaudatus*.

Volatile fatty acid analysis

Results of the VFA determinations are presented in Table 2. Generally the quantities of acetic, propionic and butyric acids were similar in the fornix and antrum. Gastric VFA concentrations were low in *M. albicaudatus* compared with those of known PGF mammals.

Table 2 Volatile fatty acid (VFA) concentrations (mean ± S.D.) in the stomach of *M. albicaudatus* (mM/g dry ingesta)

	Volatile fatty acid concentration		
Region	Acetic acid	Propionic acid	Butyric acid
Fornix	$0{,}031 \pm 4{,}8 \times 10^{-3}$	$0{,}012 \pm 3{,}4 \times 10^{-3}$	$0{,}021 \pm 7{,}0 \times 10^{-3}$
Antrum	$0{,}029 \pm 0{,}015$	$0{,}016 \pm 7{,}3 \times 10^{-3}$	$0{,}026 \pm 0{,}012$

Total VFA concentration in the gastro-intestinal tract was 0,189

Food preferences

Results for the food preference trials are presented in Table 3 and Figure 2. *M. albicaudatus* exhibited a statistically significant preference for insects ($p < 0{,}001$), and fruits and seeds ($p < 0{,}001$) over other foods. Grass seeds were mostly inedible although *Eragrostis curvula* seeds were an exception and were eaten. Grasses were inedible and the leaves and stems of shrubs and herbs were unpalatable. A slight preference was shown for herbs over shrubs. The test showed that *M. albicaudatus* selects a diet rich in protein and starch and can be classified as a granivore/insectivore.

Amylase activity

An important finding of this analysis was the high amylase

Table 3 Food preferences of *M. albicaudatus*

Food Group (See Table 1)	Food class (See text)	Ranking (Most preferred = 1 least preferred = 37)
Grass stems and leaves		
Melica racemosa	IV	34
Elionurus agenteus	IV	32
Eragrostis curvula	IV	31
Panicum maximum	IV	29
Sporobolus sp.	IV	27
Heteropogon contortus	IV	33
Setaria sp.	IV	21
Grass seeds		
Cymbopogon sp.	IV	28
Setaria sp.	II	15
Digitaria sp.	IV	22
Elionurus agenteus	IV	37
Eragrostis curvula	I	5
Herbs		
Clutia sp.	II	12
Helichrysum rosum	IV	35
Anthrospermum sp.	III	19
Crassula lycopoides	III	17
Stachys aethiopica	IV	24
Asparagus africanus	II	14
Elitropappus rhinoceratus	IV	26
Shrubs		
Grewia robusta	IV	25
Portulacaria afra	III	18
Diospyros dichrophylla	III	20
Rhigozum obovatum	II	13
Lycium campanulatum	I	9
Hypoesta verticillata	IV	23
Rhus sp.	IV	36
Scutia myrtina	IV	30
Fruits and seeds		
Maytenus capitata	I	8
Asparagus africanus	I	11
Grewia robusta	II	16
Acacia karoo	I	6
Scutia myrtina	I	4
Rhus sp.	I	7
Insects		
Tenebrionid beetles	I	1
Tenebrio molitor	I	10
Mimorista pulchellalis	I	2
Periplaneta americana	I	3

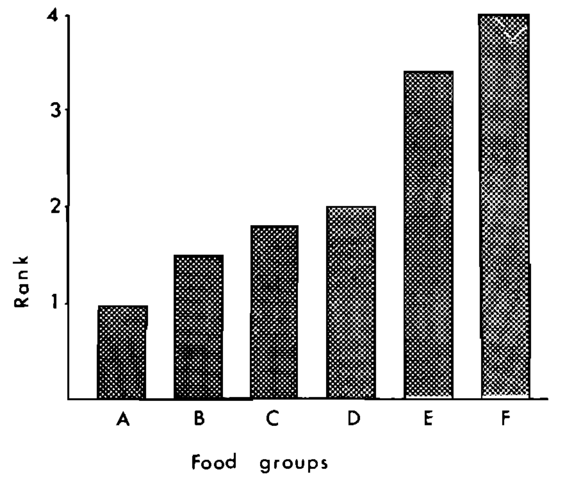

Figure 2 Preferences shown by *M. albicaudatus* for the six food groups used in the study. A = grasses, B = grass seeds, C = herbs, D = shrubs, E = fruits and seeds, F = insects.

Table 4 Alpha amylase activity (mean ± S.D.) in various regions of the gut of *M. albicaudatus* (μl/min/ml sample) Sample size in parentheses

Fornix		Antrum	Duodenum
Contents	Contents + papillae		
4 402 ± 5 592 (11)	12 692 ± 6 458 (7)	40 (4)	2 989 ± 3 412 (10)

activity afforded by the papillae bacilli. This was revealed by the high activity of the fornical contents plus papillae and bacilli (total amylase activity) compared to that of the fornical contents alone (Table 4). Amylase activity was negligible in the antrum, probably because acidic conditions denatured the enzyme. Enzyme activity was lower in the duodenum than in the fornix. A feature of the results is their wide variability.

Discussion

Fermentation of fibrous foods contributes significantly to the energy requirements of many large mammalian herbivores; however, energy requirements increase with decreasing body size (Kleiber 1961), and so small herbivores are faced with increased requirements but decreased fermentation capacities (Parra 1978). Thus total fermentation in small herbivores should be greater, relative to body weight, than in larger pregastric fermentation mammals (Hungate, *et al.* 1959). This problem might be overcome by small mammals (i.e. weighing less than 5 kg) selecting easily fermentable foods (Bauchop 1978), although precise selectivity for high quality/low fibre food might render fermentation unnecessary. Selection for starchy (seed, tuber, insect) foods, rather than fibrous food, would necessitate protracted amylolysis. The high energy cost of passing food through an additional, microbial trophic level may negate the advantages gained by a foregut fermentation strategy in small herbivores (Janis 1976; Parra 1978), while microbial amylase secretion could be exploited without any such limitation, and form part of a co-evolved symbiosis.

However, pregastric fermentation has been recorded in several small mammals (Moir 1968; Hofmann 1973; Bauchop 1977), thereby contradicting theory (Parra 1978; Janis 1976). Evidently the advantages gained from foregut fermentation can outweigh resultant energy losses. Thus the possibility of pregastric fermentation in *M. albicaudatus* could not be ignored in this investigation.

Fermentation of fibrous food takes considerable time, necessitating food retention in the region of microbial fermentation (Parra 1978). Kostelecka-Myrcha & Myrcha (1964) compared ingesta passage rates of the granivorous bank vole *Clethrionomys glareolus* and the herbivorous common vole *Microtus arvalis*. Food passage through the granivore (non-fermenter) was significantly faster than through the herbivore (fermenter). *M. albicaudatus*, that passes food through its gut 10 h faster than the similarly sized *M. arvalis*, therefore possesses a similar digestive strategy to *C. glareolus*, with a rapid ingesta passage maximizing non-fibrous, starch/protein digestion.

Associated with a slow passage rate in PGF mammals is an increase in volume of the fermentation chamber (Hungate *et al.* 1959; Bauchop 1977). *M. albicaudatus* has an anatomically complex stomach (Maddock & Perrin 1981) but its size is small for a rodent which is expected to utilize pregastric fermentation. Therefore, neither ingesta passage rate nor stomach size of *M. albicaudatus* suggests that foregut fermentation contributes significantly to its energy requirements. Amylolysis, unlike fermentation, does not necessitate such adaptations.

It is acknowledged that mammals exhibiting pregastric fermentation have a high digestibility of crude fibre, but *M. albicaudatus* lose weight and die when maintained on medium to high fibre content diets (Maddock 1981). This suggests that microbial pregastric fermentation of structural plant carbohydrates in the fornix of *M. albicaudatus* is minimal, but does not preclude the likelihood of amylolysis.

Only a very limited amount of fermentation was suggested by the low concentrations of VFAs found in the forestomach of *M. albicaudatus*. If the fornix (and its symbionts) evolved to maximize utilization of fermentation products, absorption through its epithelium would produce low gastric VFA concentrations. However, VFAs cannot be absorbed through the keratinized non-vascular fornix (Maddock & Perrin 1981). Since bacteria cannot survive the highly acidic conditions of the antrum, and since mammals do not possess cellulases, the similar and low concentrations of VFAs in the fornix and antrum probably result from a dietary source, or from low-level liberation in the fornix and transfer to the antrum.

The high level of amylase activity in fornical contents inoculated with bacteria-covered papillae strongly suggests that their major function (benefit to the host) is amylolysis. This result is corroborated by data from all other parameters investigated. The wide variability of amylase activity recorded may have resulted from differences in degree of individual stomach fullness, as amylase activity decreases with forestomach emptying. However, a broad range of enzyme activity may persist when stomach fullness is standardized (Kunstyr, Peters & Gaertner 1976).

M. albicaudatus selected a concentrate-rich diet of fruits, seeds and insects, which is presumed to be indicative of the rodent's natural diet. Since fermentative processes are not required to digest such foods, the diet of the white-tailed rat does not necessitate the use of a foregut fermentation process.

The sacculated stomach of *M. albicaudatus* favours the growth of a specific microflora (Maddock & Perrin 1981). Fornical pH at 4,6 is acidic for the growth of fermentative microbes (Hungate 1966) but within the minimum range of amylase activity (Peters & Gaertner 1973). Bacilli established on papillae in the fornix of *M. albicaudatus* enter into a symbiotic association with the host and production of bacterial alpha amylase aids starch digestion. Papillae increase the area of attachment sites for the amylase-producing bacilli; so in the absence of papillae, bacterial numbers and amylase activity would decrease.

The secure attachment of bacilli to the papillary epithelium (Maddock & Perrin 1981) imposes serious restraints on applying Vorontsov's (1962) gastric fermentation theory to *M. albicaudatus*. Since microbial attachment to the ingesta is required during efficient fermentation processes, fermentative microbes are often free-living (Hungate 1968). Obviously only limited mixing with food can occur with bacilli attached to fornical papillae. However, secretions (of microbial amylase) can readily mix with the ingesta while bacteria remain in microhabitats protected from disturbance by ingesta flow. Carleton (1973) suggested that increased muscular action in the non-glandular regions of the rodent stomach results in more efficient mixing of food particles. Mixing of fornical amylase and food is likely in the forestomach of *M. albicaudatus* because of its extensive tunica muscularis (Maddock & Perrin 1981).

In *R. norvegicus*, the forestomach acts as a carbohydrate store supplementing the liver's reserves (Peters & Gaertner 1973; Gaertner & Pfaff 1979). In *M. albicaudatus*, the fornix is seen as a region for the rapid and efficient digestion of starch and glycogen, facilitating either almost immediate energy availability or eventual hepatic storage.

This study clearly rejects Vorontsov's (1962) pregastric fermentation theory to account for gastric complexity, increased cornification and concomitant glandular reduction in *M. albicaudatus*, and supports a modification of Carleton's (1973) gastric amylolytic reservoir theory. The fornix is seen as an amylolytic reservoir where prolonged salivary amylase digestion occurs, supplemented by the production of alpha amylase by large numbers of symbiotic bacilli located on papillae. The roles of bacterial carbohydrases in aiding digestion in rodent hosts have been considered (Peters 1973; Krishnamurti *et al.* 1974) but rarely documented; high amylase activity has for example been reported in the forestomach of *R. norvegicus* (Kunstyr *et al.* 1976). However, *M. albicaudatus* has a higher amylase activity than *R. norvegicus*, emphasizing its potential for carbohydrate digestion.

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