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Effects of diet on the gastric papillae and microflora of the rodents *Mystromys albicaudatus* and *Cricetomys gambianus*

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Diets high in soluble sugar concentration cause an increase in number and hypertrophy of gastric papillae, and a dominance of filamentous bacilli in the associated symbiotic microflora in two species of rodent. Fibrous diets do not stimulate the growth of papillae but trigger a change in the microbial community which becomes dominated by cocci. Intermediate diets are associated with regular papillae and a mixed gastric microflora. The results support an amylolytic reservoir, rather than a cellulose fermentation hypothesis for the symbiosis. The responses of *C. gambianus* (and its microflora) are more complex than those of *M. albicaudatus* which suggest multiple functions, including the possible detoxification of secondary plant compounds. Protein digestion and amino acid requirements require urgent attention. The rodent-bacteria symbiosis has important consequences for nutritional niche definition and the competition and coexistence of herbivores.

Diëte met 'n hoë oplosbare suikerinhoud veroorsaak 'n toename in aantal, sowel as hipertrofie van die maagpapille in twee knaagdierspesies. Hierdie effekte gaan gepaard met 'n oorheersing van die simbiotiese maagmikroflora deur draadvormige basille. Veseldiëte stimuleer nie die groei van maagpapille nie, maar het wel 'n verandering in die mikrobiese gemeenskap tot gevolg, wat deur kokkusvormige bakterieë oorheers word. Tussendiëte gaan gepaard met normale maagpapille en 'n gemengde maagmikroflora. Die resultate dui op 'n amilolitiese opgaring eerder dan 'n sellulosegisting-hipotese ter verduideliking van die simbiose. Die reaksie van *C. gambianus* (en sy mikroflora) is meer ingewikkeld as dié van *M. albicaudatus*, wat op veelvoudige funksies dui, insluitende die moontlike ontgifting van sekondêre plantsamestellings. Proteïnevertering en aminosuurbehoeftes verg dringend aandag. Die simbiose van knaagdiere en bakterieë het belangrike gevolge vir voedselnisdefinisie en die kompetisie en medebestaan tussen plantvreters.

Trends in digestive system morphology have been examined in many species of southern African myomorph rodents (Perrin & Curtis 1980). Structure was related to function, diet and evolution. Characters related to an ancestral proteinaceous diet, and specialized characters associated with herbivory, were recognized. A detailed study of the gastric morphology of the white-tailed rat *Mystromys albicaudatus* revealed a sacculated stomach with a papillated, keratinized forestomach (corpus) separated from a distal glandular hindstomach (antrum) by a pregastric pouch; it was defined as the bilocular hemiglandular condition (Maddock & Perrin 1981). The anatomy of the stomach of the giant rat *Cricetomys gambianus*, a cricetomyine, shows many parallels with that of *M. albicaudatus*, a cricetine (Perrin & Kokkinn 1986); both possess forestomach papillae and adherent symbiotic bacteria.

The major function of the forestomach papillae in *M. albicaudatus* is for the attachment of the symbiotic bacteria (Maddock & Perrin 1981). The possibility of pregastric (forestomach) fermentation or amylolysis in this species was examined by quantifying various digestive parameters (pH, ingesta passage rate) and analysing stomach contents (for volatile fatty acid concentration and amylase activity) (Perrin & Maddock 1983a, b). Results revealed that gastric fermentation of cellulose is unlikely and suggested that the forestomach acts as an amylase reservoir. Populations of amylase-producing bacilli located on gastric papillae contribute significantly to high alpha amylase activity. Similarly, studies on gastric symbionts taken from *C. gambianus* have demonstrated fermentation of glucose, hydrolysis of starch, casein and gelatin, but not the fermentation of cellulose (Camain, Quenum, Kerrest & Goueffon 1960).

The anatomical division of the stomach of African cricetids equates with a physiological division with microbial carbohydrate degradation in the forestomach preceding proteolytic digestion in the hindstomach (Camain *et al.* 1960; Maddock & Perrin 1981). Amylolysis appears to be a significant function of microbial activity but it is unlikely the sole or even the primary function since hosts can secrete amylase intrinsically.

Results to date support Carleton's (1973) amylolytic reservoir theory rather than Vorontsov's (1962) fermentation theory. Since hosts secrete amylase directly they could theoretically prevent an energy drain to the microbial trophic level (Perrin & Maddock 1985). The microbial-mammal gastric symbiosis can no longer be explained by a unitary hypothesis and should be viewed from the perspective of the multidimensional trophic niche (Kinnear, Cockson, Christensen & Main 1979; Kinnear & Main 1979). The holistic nutritional niche concept is a significant development and suggests niche expansion for hosts with symbionts. However, Perrin (1985) has suggested that the reciprocal constraints and benefits of microbe and mammal will lead to coevolutionary adaptations representing niche shifts and diversification causing niche specialization (reduction) rather than niche expansion.

The purposes of the present investigations are to quantify the effects of diets differing in quality (proximate chemical composition) and palatability (toxin concentration) on the growth (abundance and height) of gastric papillae in *C. gambianus* and *M. albicaudatus*; and to record subjectively changes in gastric microflora (relative abundance and apparent species composition) in relation to diet in the same subjects. Resulting data should help to confirm or refute the amylolytic reservoir hypothesis, identify secondary functions, and demonstrate whether both subject species exhibit similar responses. It is hypothesized that hypertrophy of papillae and the growth and dominance of bacteria species (morphological types) will occur on diets that provide optimal or preferred substrates; while an inability to neutralize toxins present in the diet would likely cause death of bacteria and possibly the atrophy of papillae.

C. gambianus is a large (~1 kg), nocturnal and semi-fossorial rodent, widely distributed in the non-arid regions of tropical and sub-tropical sub-Saharan Africa. It selects an omnivorous diet containing a high proportion of seeds, fruits and vegetable matter (Ewer 1967; Ajayi 1977; De Graaff 1981). *M. albicaudatus* is a medium-sized (80 – 110 g) terrestrial, nocturnal rodent occurring in the Southern Savanna Grassland and the South West Cape biotic zones (De Graaff 1981). It prefers insects, seeds and fruits to plant material, but will eat herbage, preferring herbs to shrubs or grasses (Perrin & Maddock 1983a).

Materials and Methods

Each experimental group comprised four adult individuals of either *C. gambianus* or *M. albicaudatus*; there were four groups of *C. gambianus* and six of *M. albicaudatus*. One group of each species was placed on one of four artificial diets, namely rat cubes, drought (antelope) cubes, crushed maize or dried lucerne. The two remaining groups of *M. albicaudatus* were fed natural diets of *Acacia nilotica* or *Dichrostachys cinerea* leaves respectively; unfortunately no other specimens of *C. gambianus* were available for experimentation.

Subjects were provided with the test diet (and water) *ad libitum* for 10 consecutive days, and were caged individually in an animal house at 20°C with a 14L : 10D photoperiod. Prior to treatment, rodents were maintained on rat cubes under the same conditions.

Following treatment, individuals were sacrificed by chloroform anaesthesia and placed on ice to retard autolysis. Stomachs (including approximately 10 mm of oesophagus and duodenum) were removed and samples of the forestomach taken for papillae counts or scanning electron microscopy. Blocks of tissue with an area of 1 cm^2 were punched from the stomach wall, placed beneath a stereomicroscope, and the number of papillae on them were then counted. Each papilla was separated by careful dissection and its height determined using an eyepiece micrometer. Additional blocks of tissue were fixed in 5% cold buffered glutaraldehyde for a minimum of 12 h, and critical-point dried (Anderson 1951) for scanning electron microscopy (SEM).

The proximate analyses of artificial diets for crude fat (Soxhlet), crude protein (Kjeldahl), crude fibre and total soluble carbohydrate were determined using standard techniques (Allen, Grimshaw, Parkinson & Quarmby 1974). The concentrations of total polyphenols and condensed tannins in *A. nilotica* and *D. cinerea* were determined using the butanol HCl (Bates Smith) and Jerumanis (CSIR) methods respectively.

Results

Proximate analyses

The results of the chemical analyses of the artificial diets are presented in Table 1. Diets differed only slightly in energy content but markedly in other parameters. Maize had a high soluble sugar content but was low in fibre and moderate for protein. Lucerne had high protein, soluble carbohydrate and fibre concentrations. Like lucerne, drought cubes had a high fibre content, but a low soluble carbohydrate and only a moderate protein concentration. Protein content was high in rat cubes but the levels of soluble carbohydrate and fibre were low. Two of the diets were high or low in fibre and soluble carbohydrate, and protein levels varied considerably. *Acacia nilotica* had high concentrations of polyphenols but no condensed tannins whereas *D. cinerea* contained some tannins but fewer polyphenols (Table 2).

Table 1 Proximate composition of the artificial diets

Diet	Carbohydrate (%)	Protein (%)	Fibre (%)	Energy (kJ g^{-1})	*n*
Crushed maize	7,40	9,8	1,61	17,56	4
Dried lucerne	7,23	17,2	15,41	17,95	4
Drought cubes	2,67	12,9	16,38	18,33	4
Rat cubes	4,20	20,8	4,82	17,69	4

Table 2 Concentrations of toxins in natural diets

Diet	Total polyphenols (%)	Condensed tannins (%)
Acacia nilotica	28	0,0
Dichrostachys cinerea	16	3,5

Papillae

Structural changes to the papillae are concerned with the growth (hypertrophy) or degradation of the keratinized stratum corneum or lamina epithelialis of the mucosa. In

Figure 1 Bisected stomachs of subjects maintained on a diet of rat cubes. (a) *C. gambianus* (×0,77) (b) *M. albicaudatus* (×2,58).

particular, surface layers of keratin are sloughed off while whole papillae may be lost owing to structural weaknesses developing at papillae bases with pressure from ingesta flow above. The form of the lamina propria mucosae may alter its configuration slightly but its structure is apparently constant when papillae are lost or regenerate. The lamina muscularis mucosae is not involved in such structural changes but a more precise investigation is required.

Diets have a marked effect on the form and abundance of gastric papillae in *C. gambianus* and *M. albicaudatus* (Figures 1 – 4). Maize diets produced the highest densities of papillae in each subject species while the papillae were of average height (Table 3). The next most dense populations of papillae were found in animals fed lucerne, and this held for both subject species. While the density of papillae in *C. gambianus* fed lucerne approached the density recorded for subjects fed maize, this was not so for *M. albicaudatus* where the density of papillae in lucerne-fed subjects was only half that of maize-fed subjects. Lucerne-fed *C. gambianus* had by far the longest papillae of any treatment group. The height of papillae differed highly significantly between each treatment group of *C. gambianus*, whereas papilla length changed only marginally in *M. albicaudatus* (Table 3) but was short on the lucerne diet.

Lowest densities of papillae were encountered in *C. gambianus* fed drought cubes and *M. albicaudatus* fed rat cubes. However, papillae were long in *C. gambianus* fed drought cubes; the shortest papillae in the species were recorded in

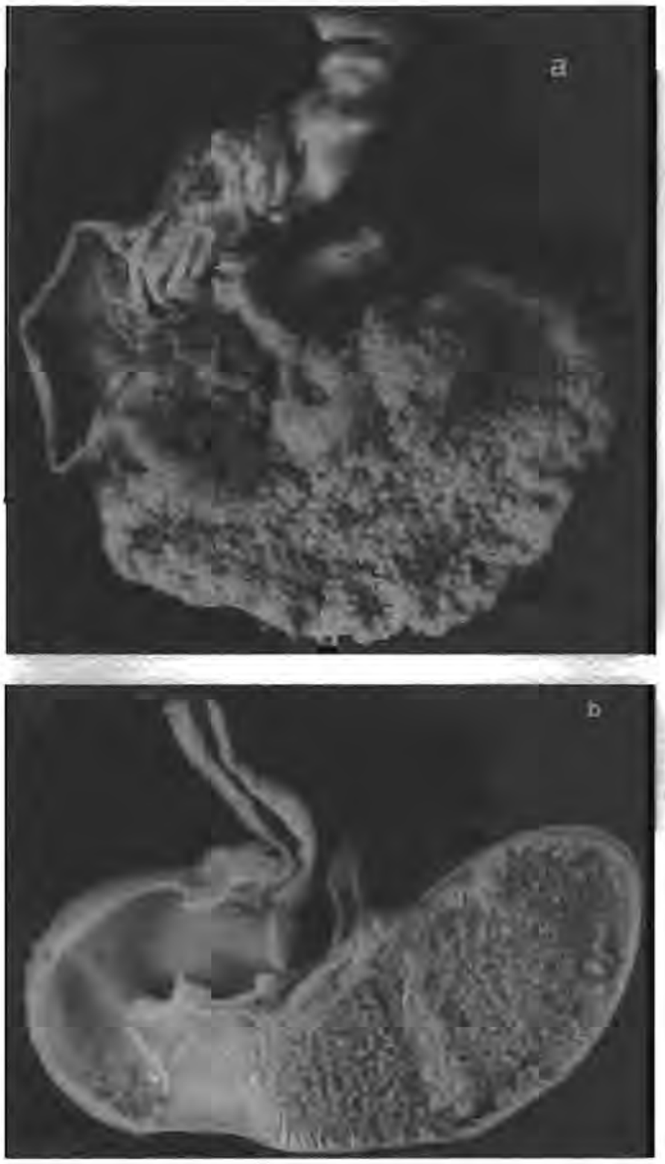

Figure 2 Bisected stomachs of subjects maintained on a diet of crushed maize. (a) *C. gambianus* (×1,1) (b) *M. albicaudatus* (×2,2).

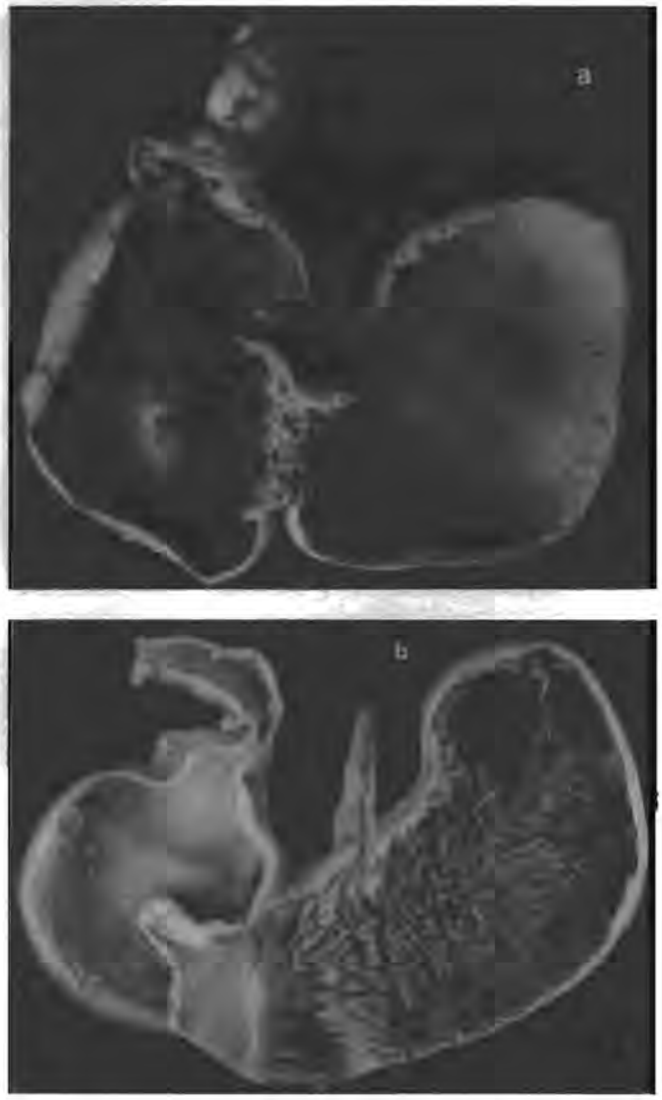

Figure 3 Bisected stomachs of subjects maintained on a diet of drought cubes. (a) *C. gambianus* (×0,79) (b) *M. albicaudatus* (×2,16).

Table 3 The response of forestomach papillae to different diet treatments

Species	Parameter of the papillae	Crushed maize	Dried lucerne	Drought cubes	Rat cubes	*F*	*P*
C. gambianus	Density	156,8 ± 11,6	119,7 ± 22,9	58,8 ± 11,6	92,7 ± 10,1	37,3	<< 0,01
	Height	0,19 ± 0,03	0,43 ± 0,02	0,33 ± 0,07	0,15 ± 0,02	112,0	<< 0,01
M. albicaudatus	Density	129,0 ± 62,7	63,0 ± 19,5	55,1 ± 14,7	47,2 ± 11,1	6,6	< 0,01
	Height	0,19 – 0,28	0,23	0,32	0,30	–	

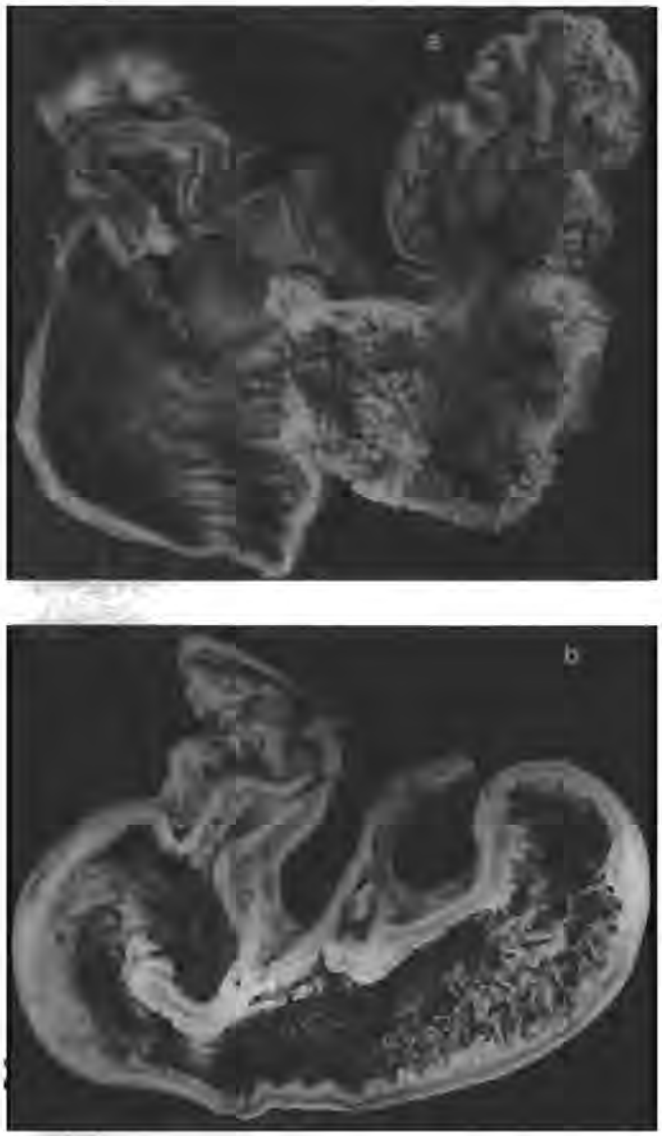

Figure 4 Bisected stomachs of subjects maintained on a diet of lucerne. (a) *C. gambianus* (× 1,14) (b) *M. albicaudatus* (× 2,31).

subjects maintained on rat cubes. *C. gambianus* fed on rat cubes had moderate densities of papillae, while *M. albicaudatus* maintained on drought cubes possessed papillae with a density similar to that of the same species maintained on lucerne or rat cubes.

In summary, each diet had a significant effect on the density of papillae in *C. gambianus* but only a maize diet had a significant positive response in *M. albicaudatus*. Papilla height was little affected by diet in *M. albicaudatus* but significantly affected by each treatment in *C. gambianus*. Changes in papillae density were not linearly correlated with changes in papilla height in *C. gambianus*, for example, highest density was associated with relatively short papillae. However, both rodent species appeared to respond (and do well) on maize diets, and *C. gambianus* on lucerne also. Neither species reacted positively on drought cube or rat cube diets.

Microflora

In general the microflora responded similarly to diet treatments in both species, the only exception being the loss of the microflora in *M. albicaudatus* when fed lucerne. Differences were apparent in the microbial community in terms of species (morphological types) composition and spatial arrangement (Table 4) but microbial biomass was always high (except for *M. albicaudatus* on lucerne).

On a nutritionally-balanced rat cube diet, the microflora of *C. gambianus* contained similar numbers of cocci and filamentous bacilli (Figure 5) in a patchy, non-stratified spatial arrangement (Figure 6). On the same diet, the microflora of *M. albicaudatus* comprised a lower density of filamentous bacilli (Figure 7) surmounted by much smaller numbers of cocci (Figure 8).

The maize diet yielded almost pure cultures of elongate filamentous bacilli in palisade formation in *C. gambianus* (Figure 9) and *M. albicaudatus*, although small numbers of cocci could be found between the filaments and food (starch) granules.

Figure 5 *C. gambianus* on a rat cube diet: cocci and filamentous bacilli (× 2000).

Table 4 Summary of microflorae: effects of diet treatments

Diet	Parameter	*C. gambianus*	*M. albicaudatus*
Rat cubes	Bacterial community	Diverse	Predominantly filamentous
	Spatial arrangement	No clear stratification	Vertically stratified
Crushed maize	Bacterial community	Filamentous dominant	Filamentous dominant
	Spatial arrangement	Vertical, palisade	Vertical, palisade
Drought cubes	Bacterial community	Cocci dominant	Cocci dominant
	Spatial arrangement	Disordered	Disordered
Dried lucerne	Bacterial community	Diverse	Destroyed
	Spatial arrangement	Patchy; irregular strata	Destroyed

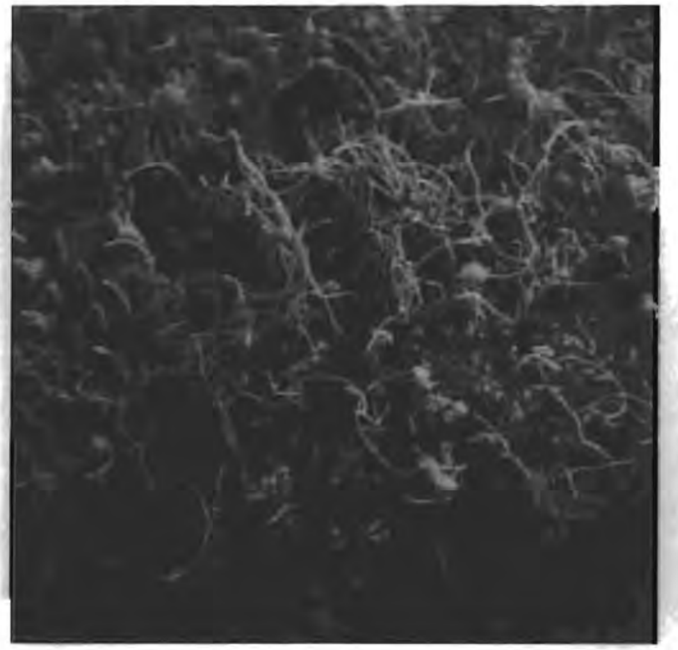

Figure 6 A patchy, non-stratified bacterial community (×800): *C. gambianus* on a rat cube diet.

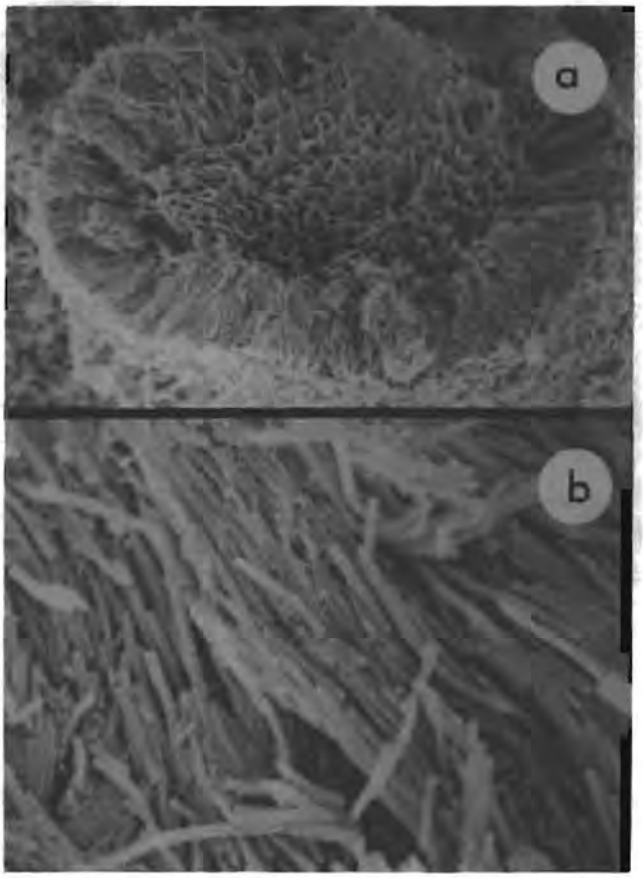

Figure 7 (a) Cross section of a papilla (×340) showing (b) filamentous bacteria in palisade formation (×3400): *M. albicaudatus* on a rat cube diet.

Figure 8 Superficial cocci on a foundation of filamentous bacteria (×2600): *M. albicaudatus* on a rat cube diet.

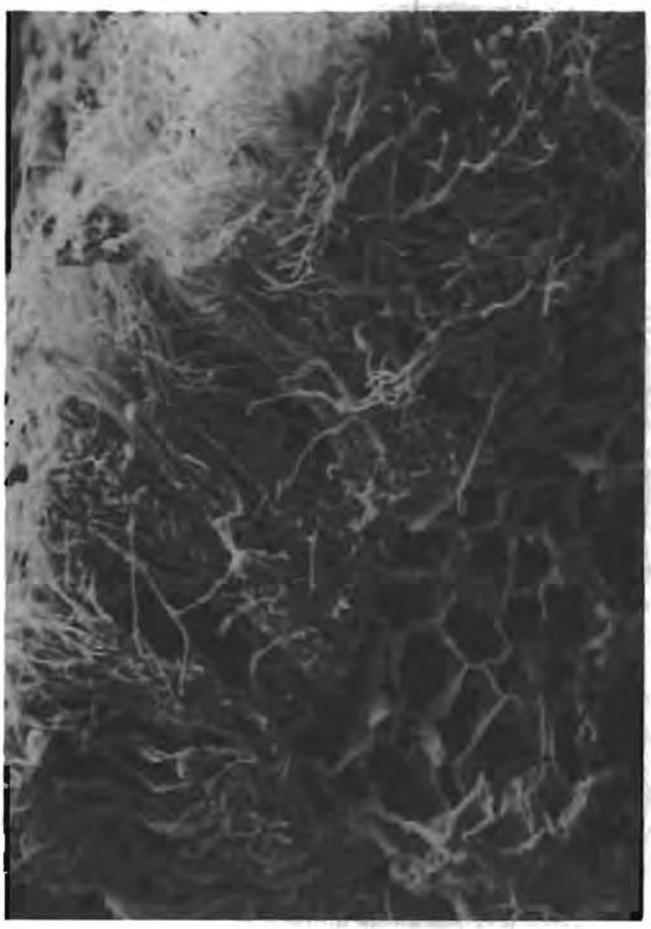

Figure 9 Cross section of a papilla with numerous elongate filamentous bacteria (×600): *C. gambianus* on a maize diet.

Cocci and lesser numbers of cocco-bacilli dominated the microbial communities of both subject species when maintained on the drought cube diet (Figure 10). There was little evidence of an aggregated or stratified distribution (Figure 11) and very few filamentous bacilli were evident.

A diverse microflora was present on the surface of papillae

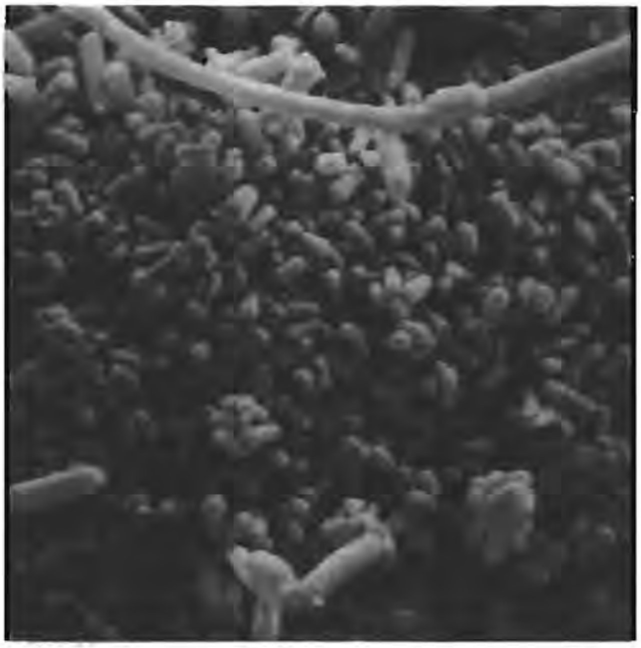

Figure 10 A population of cocci (×4400): *C. gambianus* on a diet of drought cubes.

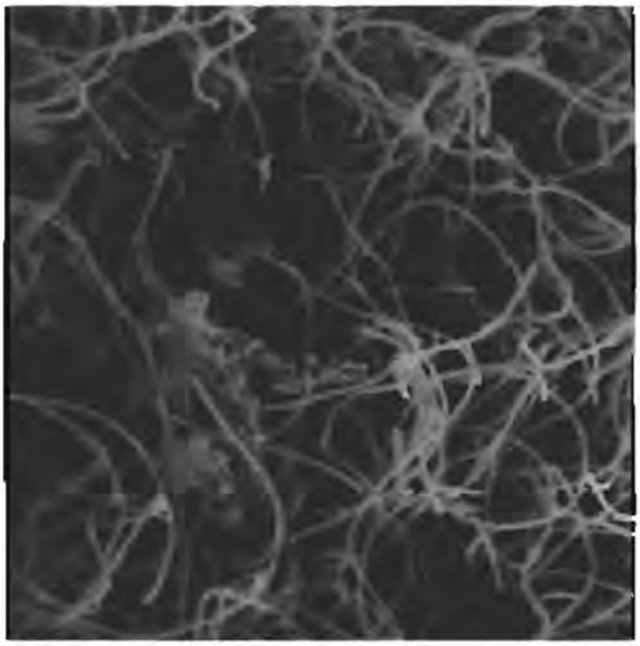

Figure 12 Coiled elongate filamentous bacilli (×1100): *C. gambianus* on a diet of dried lucerne.

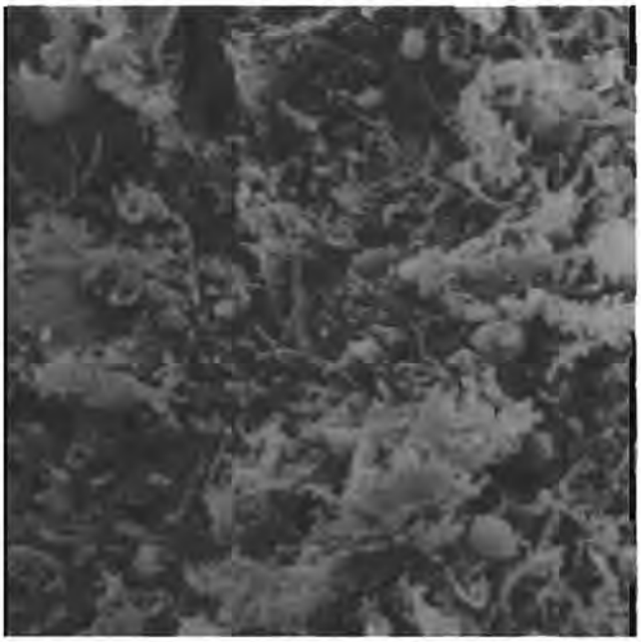

Figure 11 A disordered community of bacteria (×1500): *M. albicaudatus* on a diet of drought cubes.

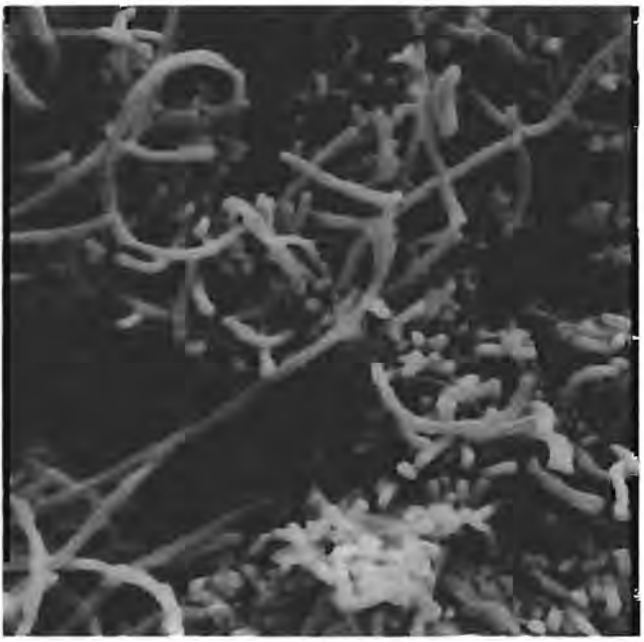

Figure 13 Clusters of cocci between filaments (×2200): *C. gambianus* on a diet of dried lucerne.

in *C. gambianus* fed lucerne; the microbial populations of coiled elongate filamentous bacilli (Figure 12) and short cocci (Figure 13) were patchy and stratification was irregular. There was an intimate association between food material and microorganisms (Figure 14) in *C. gambianus*. In *M. albicaudatus* the microflora was destroyed and the keratinous surface of the papillae was devoid of bacteria (Figure 15).

The *D. cinerea* diet had an antibiotic effect on the gastric microflora of *M. albicaudatus* in that the keratinized forestomach was cleansed of all bacteria. In one subject returned to a rat cube diet for one week and then sacrificed there was evidence of microbial recolonization (Figure 16). A similar but less drastic response was recorded for the *A. nilotica* diet. Microbial biomass was reduced and filamentous bacilli were lost from the community.

Discussion

The four diets, comprising a balanced control (rat cubes), a high starch/low fibre diet (maize), a low starch/high fibre diet (drought cubes) and a semi-natural diet (lucerne), represent treatments that were used to test previous hypotheses of gastric function in rodents, that is forestomach fermentation (Vorontsov 1962) or amylolysis (Carleton 1973). Responses to treatments were recorded by quantifying changes in density and height of gastric papillae and their associated symbiotic microflora in two subject species.

Figure 14 Association between food and bacteria (× 1650): *C. gambianus* on a diet of dried lucerne.

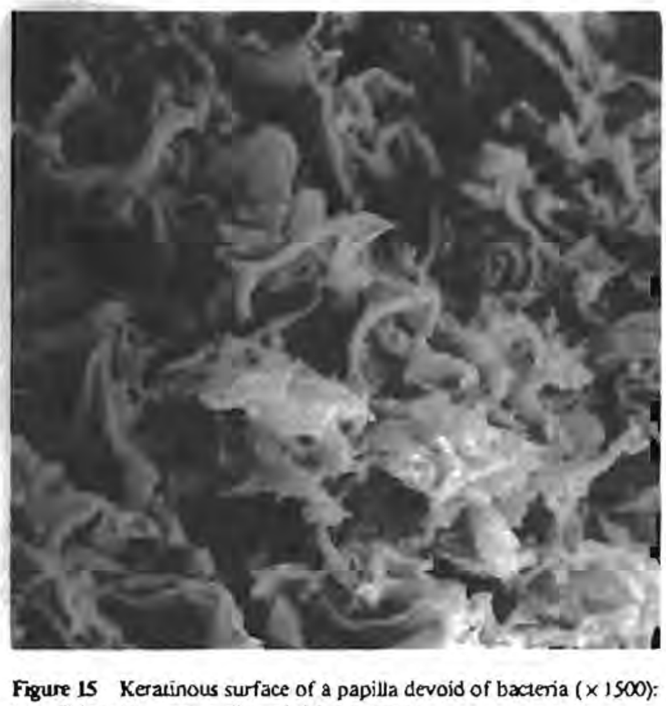

Figure 15 Keratinous surface of a papilla devoid of bacteria (× 1500): *M. albicaudatus* on a diet of dried lucerne.

Papillae

The high densities of papillae on a starchy maize diet in both subjects support the amylolytic reservoir theory; which is substantiated by the low density of papillae when soluble sugar concentrations were low. Brownlee (1956) has shown that roughage is not a factor influencing the development of rumen papillae; papillae growth is determined by the availability of high-energy, absorbable fractions of digestion. Lucerne also has a high soluble sugar concentration and many papillae were present in the forestomach of *C. gambianus* maintained on this diet, further corroborating the hypothesis. However, the density of papillae in *M. albicaudatus* did not increase on this diet. This might be explained by the high fibre content of lucerne having a negative effect on papillae development since the protein content of this diet is high. The lesser response of the papillae in numbers and size to the high soluble sugar fraction in dried lucerne, much of which contributes pentoses and pentosans associated with hemicellulose, could be due to the fact that the low pH of the forestomachs also inhibits the growth of *Butyrivibrio* and *Ruminococcus* which are pH sensitive below pH 7 (Mackie, Gilchrist, Robberts, Hannah & Schwartz 1978). These are the bacteria which attack hemicelluloses and their constituent sugars. (An alternative explanation implicating toxins is considered later.)

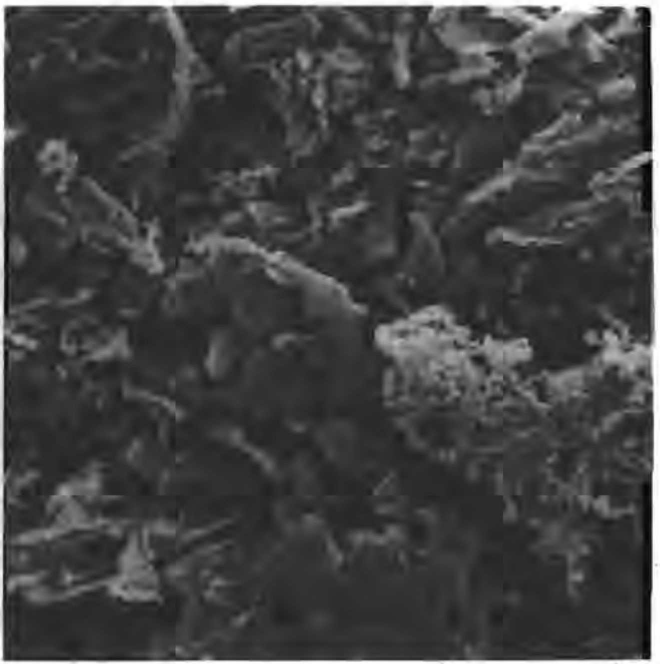

Figure 16 Bacterial recolonization of a papilla in *M. albicaudatus* (× 1150).

Previous studies that analysed volatile fatty acid concentration and amylase activity of *M. albicaudatus* demonstrated that large populations of amylase-producing bacilli located on forestomach papillae contribute to high amylase activity (Perrin & Maddock 1983a). Since papillae increase the surface area for the attachment of the symbiotic bacilli, an increase in the density of papillae likely increases the production of microbial amylase thereby enhancing starch digestion. The fact that the growth and activity of cellulolytic bacteria diminish rapidly below pH 7 supports the hypothesis that acidic forestomachs, of the two species of rat investigated, act as amylase reservoirs and not organs of cellulose fermentation (Mackie *et al.* 1978).

The roles of bacterial carbohydrases in aiding digestion in rodent hosts have been considered (Peters 1973; Krishnamurti, Kitts & Smith 1974) but rarely established or documented. In *M. albicaudatus* and *C. gambianus* the forestomach apparently functions for the rapid and efficient digestion of soluble sugars, facilitating almost immediate energy release or subsequent hepatic storage. Similarly, in *Rattus norvegicus* the forestomach acts as a carbohydrate store supplementing the liver's reserves (Peters & Gaertner 1973; Gaertner & Pfaff 1979).

Drought cubes appear to reduce the abundance of papillae in *C. gambianus*, which can be attributed to a low availability of soluble sugars; (the protein content of the drought cube diet is higher than that of the maize diet). The positive response of papillae in this species on a lucerne diet is therefore probably and largely attributable to the high soluble sugar concentration and not to the high fibre concentration. This argument is supported by the previous work of Camain *et al.* (1960) which suggests that *C. gambianus* has a limited ability to digest cellulose. Studies of crude fibre tolerance by *C. gambianus* have shown that with increasing dietary concentration of fibre, feed intake and protein assimilation efficiency is remarkably reduced; although high fibre rations can be tolerated (Faturoti, Tewe & Ajayi 1982). It is possible in the smaller species *M. albicaudatus* that the presence of a fair amount of fibre in the diets of drought cubes and dried lucerne increases the rate of passage to the extent where micro-organisms cannot establish and maintain themselves in the forestomach, but this requires further experimentation.

The trials with *M. albicaudatus* suggest that amylolysis is a major function of bacterial symbionts. Unlike the graded response in papillae density in *C. gambianus* to changes in diet, papillae number in *M. albicaudatus* was only significantly increased on the starchy maize diet. This suggests that amylolysis may be more important in affecting papillae density than low protein content, or that the two processes are linked. It has been shown that the hamster *Mesocricetus auratus* (which has a complex forestomach containing numerous micro-organisms) can use non-amino nitrogen sources for the synthesis of microbial protein which is then harvested by the host (Moir 1964).

It is probable that protein-rich bacteria are digested by *M. albicaudatus* and *C. gambianus*, although *R. norvegicus* and *Mus musculus* do not obtain protein from a gastric bacterial source (Gaertner & Pfaff 1979). The densely papillated forestomachs of African cricetids (which maintain dense bacterial communities) are grossly different from those of laboratory murids. Similar conclusions were drawn by Sakata & Tamate (1976) and Hoover, Mannings & Sheerin (1969) when studying the cricetine *M. auratus*.

Matsumoto (1955) has demonstrated changes in body weight and nitrogen balance indicative of a nutritive effect of urea on nutrition in *M. auratus*, whilst Hoover *et al.* (1969) demonstrated pregastric fermentation and volatile fatty acid production. Further research by Banta, Warner & Robertson (1975) suggested substantial forestomach alteration of protein quality so that *M. auratus* is buffered against changes in the quality of dietary protein. Parallel processes are likely in *C. gambianus* and *M. albicaudatus* and this will be the subject of a subsequent study.

Microflora

Rodents normally harbour an extensive gastric bacterial flora that plays an essential role in the development and well being of its host. In dissimilar animal taxa, similar types of micro-organisms can be found on comparable gastric epithelia (Savage 1972). Certain components of the flora are always present in large and approximately constant numbers (Dubos, Schaedler, Costello & Hoet 1965); e.g. lacto-bacilli and anaerobic streptococci are extremely numerous in the stomach. The micro-organisms are highly adapted to growth on gastric epithelia and associations are often stable (Savage 1972). The mechanisms involved in the stable interactions are obscure, but may involve nutritional and environmental factors, microbial interference, and specific macromolecular interactions between microbial surfaces and mammalian epithelia. This makes the observed short-term changes in microbial community structure in *C. gambianus* and *M. albicaudatus* that much more significant.

Although species identification of anaerobic gastric bacteria from rodents are difficult (Schaedler, Dubos & Costello 1965), different morphological categories can be recognized easily using scanning electron microscopy. The microflora on the forestomach papillae in both subject species maintained on maize was dominated by elongate filamentous bacilli whilst on a diet of drought cubes cocci were very abundant in each species. It is difficult not to suggest a correlation between a starchy diet and a preponderence of filamentous bacilli, or between a fibrous diet and a microbial community dominated by cocci. Whilst the cocci occur in disordered clusters, the filamentous bacilli are present in palisade formation which is often associated with biochemical exchange between conspecifics, or competition for space.

Savage & Blumershine (1974) have argued that close association is an important factor in the structure and stability of gastro-intestinal microbial communities, and metabolic products of one microbial type are known to be used as nutrients by other types in natural environments (Hungate 1966). Products of bacterial metabolism may be absorbed through the mammalian epithelium or transferred between bacteria (Hoskins 1968). The intimate associations between gastric symbionts in cricetid rodents may facilitate biochemical exchange of considerable complexity.

On the rat cube diet, which had similar concentrations of soluble sugars and crude fibre, the microbial community was mixed and contained both filaments and cocci in each subject species. (Although the microflora of the forestomach of *M. albicaudatus* was mixed, filamentous bacilli were more abundant than cocci, which may suggest the predominance of amylolysis over other secondary microbial functions.) Together with the results on papillae density and height, it appears that *C. gambianus* has a more complex response to changes in diet, which may be indicative of multiple functions of the microflora/symbiosis.

The arguments mentioned above predict a diverse microflora on a lucerne diet high in soluble sugars and crude fibre. This response was observed in *C. gambianus* but not in *M. albicaudatus* where the microflora was destroyed. This difference in species-specific response was unexpected and cannot be attributed to differences in proximate composition because the range of concentrations of soluble sugars, protein and crude fibre of lucerne were within the ranges of values for the other diets.

This suggests perhaps that the lucerne contained a chemical toxin or microbial/fungal agent which resulted in the antibiotic effect in *M. albicaudatus* (but not in *C. gambianus*). This implies that *C. gambianus* may be able to detoxify specific secondary compounds or counter the invasion of allocthonous micro-organisms. Studies of the comparative toxicity and metabolism of pyrrolizidine alkaloids in ruminants and non-ruminant herbivores have demonstrated marked species-specific differences (Cheeke 1984). It is therefore possible that the different responses observed in *M. albicaudatus* and *C. gambianus* are the result of species-specific reactions.

When fed natural diets containing polyphenols, or polyphenols and condensed tannins, the microflora of *M. albicaudatus* was lost. This indicates that secondary compounds can adversely affect the microbial symbionts of this species, its digestive efficiency and perhaps its competitive ability. It is most unfortunate that *C. gambianus* were not available for parallel studies, since if this species can in fact deal effectively with noxious chemicals (or micro-organisms) then it has a great ecological advantage over its competitors; in that its nutritional niche is expanded or shifted to include plant foods not palatable to other herbivores (Kinnear & Main 1979; Kinnear *et al.* 1979).

In summary, the responses of forestomach papillae (host) and gastric bacteria (symbionts) to changes in diet in two species of rodent suggest that the symbiosis operates to optimize amylolysis and not cellulose fermentation. However, changes in the composition of the bacterial community suggest that an alternate function is served when the concentration of soluble sugar is low and that of crude fibre is high. These might include limited fermentation following acclimation to a fibrous diet or changes in protein digestion; an area that requires immediate attention. Although amylolysis is a likely function of gastric symbionts in both rodents, it appears that the microflora of *C. gambianus* may serve a number of functions, one of which may include the neutralization of plant or bacterial toxins. The symbiosis has very important consequences not only for digestive physiology but also for competition and coexistence of herbivores.

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