Session 4 Comparative herbivore nutrition

Anatomical and nutritional adaptations in African rodents

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Anatomical and nutritional adaptations were studied in four African rodents (*Cricetomys gambianus, Mystromys albicaudatus, Thallomys paedulcus* and *Saccostomus campestris*). The stomachs of all species are markedly sacculated with a highly modified corpus containing either numerous papillae or several diverticula and a 'grenzfalte' separating the corpus from a glandular antrum. Scanning electron microscopy revealed that the corpal papillae were colonized by numerous bacteria and were associated with a high α-amylase activity. Values for pH, volatile fatty acids and retention time suggest that little ruminant-like fibre digestion occurs in the stomach.

Anatomiese en voedingsaanpassings is bestudeer by vier Afrikaanse knaagdiere (*Cricetomys gambianus, Mystromys albicaudatus, Thallomys paedulcus* en *Saccostomus campestris*). Die mae van al die spesies is opvallend gesakkuleer met 'n hoogs gewysigde korpus wat of talryke papille of verskeie divertikula bevat en 'n 'grenyfalte' wat die korpus van 'n klieragtige antrum skei. Skandeerelektronmikroskopie het aan die lig gebring dat die papille van die korpus gekoloniseer is deur talryke bakterieë en dit is ook die setel van sterk α-amilase aktiwiteit. Waardes vir pH, vlugtige vetsure en retensie tyd dui daarop dat die veselvertering wat in die maag plaasvind baie min ooreenkoms toon met dié in die grootpens.

Keywords: Herbivore, rodent, stomach, digestion, fermentation, amylolysis, symbionts, bacteria

Introduction

Fermentation of fibrous foods contributes significantly to the energy requirements of many herbivores, but since energy requirements increase with decreasing body mass, small herbivores are faced with increased requirements and decreased fermentation capacities (Parra, 1978). Hence, total fermentation in small herbivores should be greater relative to mass than in large species. This problem can be overcome by small species selecting easily fermentable foods, although precise selectivity for a high quality/low fibre diet would render fermentation unnecessary. The high energy cost of passing food through an additional, microbial, trophic level should negate the advantages gained by foregut fermentation, which, however, has been recorded in several small mammals (Parra, 1978).

Few studies have examined the adaptive variations of the gastro-intestinal tract of rodents (Vorontsov, 1962; Carleton, 1973) and none have concentrated on African species until the present investigations of bizarre gastric morphology and physiology were initiated, with the above points in mind.

Materials and Methods

The subjects of study were the giant rat (*Cricetomys gambianus*), the white-tailed rat *(Mystromys albicaudatus)*, the black-tailed tree rat, *(Thallomys paedulcus)* and the pouched mouse *(Saccostomus campestris)*. Stomachs dissected from each species were cleaned of contents and fixed in Bouin's solution, and the pH of the corpora and antra were recorded. Gross morphology was examined through a stereomicroscope. General purpose tissue stains were used to examine the glandular antra, and specific histochemical stains for the non-glandular corpora (Maddock & Perrin, 1981).

Tissues for electron microscopy were fixed in 5% buffered glutaraldehyde; those for SEM were critical point dried. TEM sections were stained with uranyl acetate and lead citrate.

Rate of digesta passage was determined by the stained particle method. Concentrations of volatile fatty acids (acetic, propionic and butyric) in the corpus and antrum of *M. albicaudatus* were determined using gas chromatography. α-Amylase activity was quantified using a Merckotest reagent kit. Food preferences were determined using a cafeteria test.

Results

Gross morphology

The stomachs of all species are markedly sacculated (Figures 1 and 2) with a highly modified corpus containing either numerous papillae or several diverticula, and a grenzfalte separating the corpus from a glandular antrum. In all species, the oesophagus enters the stomach medially on the lesser curvature above a small pregastric pouch. The fornices of *M. albicaudatus* and *C. gambianus* contain numerous, irregularly orientated filiform papillae (Figure 1). In *T. paedulcus,* many diverticula lead outwards from the fornix (Figure 2) to act as small reservoirs for digesta. A pyloric pouch, and zonation of the gastric glands, is evident in each species. Except in *M. albicaudatus* an oesophageal groove leads either, to the antrum at the anterior end of the grenzfalte, or, towards the corpus to form a pair of cornified oesophageal valves.

Histology

A typical mammalian gastric tissue plan is observed: generally, the tunica muscularis is thickened in the corpora. The corpora are lined by stratified, squamous epithelia and display characteristic strata germinativum, granulosum and corneum; the last being markedly hypertrophied in *C. gambianus* and *M. albicaudatus* to form numerous filiform papillae. The papillae differ from those of ruminants since they are poorly vascularized, and lack connective tissue cores and swollen cells superficially.

The fornical diverticula of *T. paedulcus* possess a multilayered corneum, where lumenal keratinous squames fracture and become interspersed with digesta and bacteria. In *T. paedulcus* and *S. campestris* only, the lamina is markedly vascular.

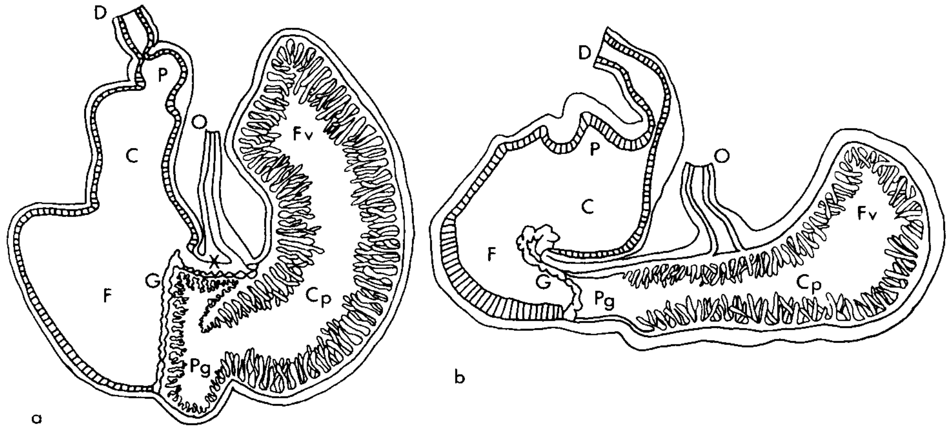

Figure 1 Semi-diagrammatic drawings of the bisected stomachs of (a) *Cricetomys gambianus* and (b) *Mystromys albicaudatus*. C = cardiac chamber, Cp = corpus, D = duodenum, F = fundic chamber, Fv = fornix ventricularis, G = grenzfalte, O = oesophagus, P = pyloric pouch, Pg = pregastric pouch, X = oesophageal groove.

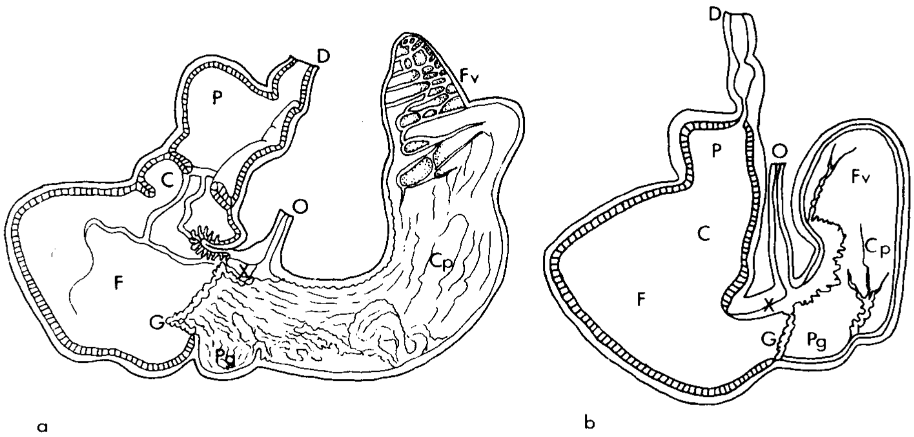

Figure 2 Semi-diagrammatic drawings of the bisected stomachs of (a) *Thallomys paedulcus* and (b) *Saccostomus campestris*. C = cardiac chamber, Cp = corpus, D = duodenum, F = fundic chamber, Fv = fornix ventricularis, G = grenzfalte, O = oesophagus, P = pyloric pouch, Pg = pregastric pouch, X = oesophageal groove

The grenzfalten and oesophageal grooves are lined by keratinized, stratified squamous epithelia, and are underlain by the longitudinal groove musculature. Sections of oesophageal valve reveal striated muscle fibres, indicating voluntary control.

The antrum of each species contains fundic glands, with mucoid neck cells lining upper regions, while distinctive chief and parietal cells occupy the body and fundus of the foveolae.

Scanning electron microscopy

SEM revealed the corpal papillae to be completely covered by numerous bacteria. In *C. gambianus* the papillae possess characteristic longitudinal invaginations and squames that are covered by a dense, stratified and speciose microbial flora. Similar papillary microhabitats in *M. albicaudatus* are colonized only by sessile (cocco-) bacilli. In *T. paedulcus* diverticular epithelia and digesta are covered by cylindrical cocco-bacilli, anchored by filiform extensions of the glycocalyx.

Digesta passage

The oesophageal groove/valve system permits differential passage of digesta from the oesophagus to either the corpus or antrum, and may allow regurgitation for prolonged mastication.

The complex gastric anatomy suggests a dichotomy of functions; for microbial fermentation/amylolysis to predominate in the corpus, and for proteolytic degradation to occur in the glandular antrum.

Digestion

Some preliminary data concerning gastric function in *M. albicaudatus* are presented (Table 1). Stomach contents constitute approximately 3% of body mass, while the mean value for foregut fermenters averages 13%. Corpal pH at 4,6 is significantly higher than antral pH at 2,7, but lower than 6,0, which is the typical pH recorded in regions of microbial fermentation in other herbivores. Rats void 75% of ingesta in 16 h with a mean retention time of 12 h; this is not indicative of fermentation.

Similar quantities of acetic, propionic and butyric acids are produced in the corpus and antrum of *M. albicaudatus*. Gastric VFA concentrations are low compared with herbivores known to have active fermentation (Parra, 1978), suggesting that extensive fermentation is absent. Mammals exhibiting pregastric fermentation have a high digestibility of crude fibre (Parra, 1978), yet, *M. albicaudatus* lose

Table 1 Some aspects of digestion in *Mystromys albicaudatus*

Appearance of stained particles and retention time (R) (h) (Mean ± S.D.)				
5%	50%	90%	100%	R
4,4 ± 1,1	11,7 ± 4,3	19,5 ± 4,3	34,1 ± 4,7	12,1 ± 3,2

VFA concentrations (mM/g dry ingesta × 10^{-3}) (Mean ± S.D.)					
	pH	Acetic	Propionic	Butyric	Total
Corpus	4,6	31 ± 5	12 ± 3	21 ± 7	64
Antrum	2,7	29 ± 15	16 ± 7	26 ± 12	71

α-Amylase activity (μmol/min/ml) (Mean ± S.E.)		
Corpus		Duodenum
Contents only	Contents and papillae	Contents only
4402 ± 1686	12692 ± 2440	2989 ± 1079

weight or die when maintained on artificial diets containing more than 27% crude fibre.

An important finding is the high amylase activity afforded by the papillae bacilli; revealed by the high activity of the corpal contents plus papillae and bacilli, relative to that of the corpal contents alone.

M. albicaudatus shows a clear preference for insects, and fruits and seeds of various herbs and shrubs, while leaves and stems of grasses, and shrubs and herbs are unpalatable. Thus *M. albicaudatus* selects a diet rich in protein and starch that does not necessitate elaborate foregut fermentation.

Discussion

These data negate the applicability of Vorontsov's (1962) pregastric fermentation theory to *M. albicaudatus* and support a modification of Carleton's (1973) gastric amylolytic reservoir theory. The corpus is an amylolytic reservoir where prolonged salivary amylase digestion occurs, supplemented by α-amylase production by large numbers of symbiotic bacilli located on papillae.

Studies by Camain, Quenum, Kerrest and Goueffon (1960) on the biochemical characteristics of corpal bacilli from *C. gambianus* have demonstrated fermentation of glucose (but no reference is made to degradation of more resilient polysaccharides) and hydrolysis of starch, casein and lecithin. Further data and quantification are required, although some carbohydrate breakdown is evident. The diet of *C. gambianus* comprises fruits, seeds, tubers and vegetables, but not herbage, suggesting perhaps that amylolysis would be more beneficial than fermentation.

Data collected on *M. albicaudatus* and *C. gambianus* do not suggest ruminant-like fibre fermentation, although the situation might be different for *T. paedulcus,* which is a specialist arboreal folivore feeding of the fibrous leaves, seeds and pods of *Acacias*. Fibre digestion would appear to be of considerable adaptive value, for which there is substantial morphological evidence, i.e. an elaborate oesophageal groove system, unique fornical diverticula to localize particular biochemical activities (yet to be elucidated), and a vascular fornix for nutrient absorption; while the extensive corpal tunica muscularis suggests mechanical degradation of the digesta. Bacterial attachment to food particles allows for direct enzymatic attack on the particulate substrate and preferential utilization of the resultant products of digestion.

It is hypothesized that the evolution of bizarre gastric morphology and microbial symbiosis can be explained by increased digestive efficiency, an expanded nutritional niche and increased competitive ability.

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