

Comparative gastric anatomy of *Cricetomys gambianus* and *Saccostomus campestris* (Cricetomyinae) in relation to *Mystromys albicaudatus* (Cricetinae)

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The gastric anatomy of two African cricetomyines is described and compared with that of the only African cricetine. The stomach of *C. gambianus* is more specialized than that of *S. campestris* and shows many parallels with that of *M. albicaudatus*. Both cricetomyines possess an oesophageal groove system which is absent from the cricetine, while *C. gambianus* and *M. albicaudatus* have forestomach papillae supporting vast colonies of symbiotic bacteria that are not found in *S. campestris*. Specializations in gastric anatomy are discussed in relation to phylogeny, using taxonomy to distinguish between apomorphic and plesiomorphic characters, convergence and divergence. Complex gastric adaptations can be explained only by increased digestive efficiency, while the symbiotic association with numerous autochthonous bacteria implies coevolutionary adaptation.

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Die maaganatomie van twee Afrika-spesies van die Cricetomyinae word beskryf en vergelyk met die van die enigste Afrika-spesie van die Cricetinae. Die maag van *C. gambianus* is meer gespesialiseer as die van *S. campestris* en toon 'n aantal ooreenkomste met die van *M. albicaudatus*. Albei Cricetomyinae besit 'n slukdermgroefstelsel wat ontbreek by die lid van die Cricetinae, terwyl *C. gambianus* en *M. albicaudatus* papillae in die voormaag besit wat groot kolonies van simbiotiese bakterieë ondersteun; hierdie bakterieë ontbreek by *S. campestris*. Spesialiserings van die maaganatomie word bespreek met betrekking tot filogenie, met behulp van taksonomie om tussen apomorfe en plesiomorfe kenmerke, konvergensie en divergensie te onderskei. Komplekse maagaanpassings kan slegs deur 'n verhoging in spysverteringsdoeltreffendheid verduidelik word, terwyl die simbiotiese assosiasie met taryke inheemse bakterieë koevolusionêre aanpassing impliseer.

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Comparative studies of gastric anatomy in myomorph rodents have demonstrated evolutionary trends (Vorontsov 1962; Perrin & Curtis 1980) including radiation, encompassing the unilocular-glandular, bilocular-hemiglandular and bilocular-disco-glandular grades of organization (Carleton 1973); parallelism of corpal papillae in a cricetomyinid, bathyergid and cricetinid (Camain, Quenum, Kerrest & Goueffon 1960; Rahm 1976; Maddock & Perrin 1981) and innovation in the form of corpal diverticula in a folivorous murid (Perrin & Maddock 1985).

The giant rat *Cricetomys gambianus* has a complex gastric anatomy with a non-glandular forestomach lined with filiform papillae covered with symbiotic bacteria capable of fermentation of glucose (Camain *et al.* 1960). Maddock & Perrin (1981) subsequently described the gastric anatomy of the white-tailed rat *Mystromys albicaudatus*, which has many parallels with that of *C. gambianus*, and concluded that the function of symbiotic bacteria attached to gastric papillae is to elevate alpha amylase activity and aid starch/glycogen degradation. It is suggested that *C. gambianus* and *M. albicaudatus* have evolved parallel adaptations, since each species belongs to a different sub-family of rodents: *C. gambianus* is a cricetomyine while *M. albicaudatus* is a cricetine. The hypothesis is tested by employing a detailed comparative investigation of the gastric anatomy of *C. gambianus* and the other African cricetomyine, the pouched mouse *Saccostomus campestris*, and equating results with what is known of *M. albicaudatus* (Maddock & Perrin 1981). *S. campestris* lacks gastric papillae but shares many common gastric, anatomical features with *C. gambianus*, but also possesses certain plesiomorphic characters (e.g. little sacculatation of the stomach, and an indistinct pregastric pouch) with *M. albicaudatus* but which are well developed in *C. gambianus*.

Cricetomys gambianus is a large (± 1 kg) cricetomyine rodent, widely distributed in the non-arid regions of tropical and sub-tropical Africa. It is a nocturnal, burrowing rodent with an omnivorous diet, containing a high proportion of seeds, fruits and vegetable matter (Ewer 1967; Ajayi 1977; De Graaff 1981). *Saccostomus campestris* is a medium-sized (40–70 g) cricetomyine rodent found throughout southern Africa except in the coastal arid/desert zones of SWA/Namibia and the S.W. Cape, and the Southern Savanna Grassland biotic zone (De Graaff 1981). It is exclusively terrestrial, largely solitary and nocturnal, and eats predominantly the seeds of a diversity of plant species (De Graaff 1981).

Materials and Methods

Stomachs, including 10-mm lengths of oesophagus and

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duodenum, were dissected from five freshly killed adult *C. gambianus* and *S. campestris* and placed on ice to retard autolysis. Tissues for electron microscopy were cut from the stomach wall immediately after dissection and fixed in 5% buffered glutaraldehyde at 4°C. To prevent distortion only small incisions in the stomach wall were made; stomachs were placed in Bouin's fixative for 24 h. After fixation stomachs were bisected sagittally and preserved in 70% ethanol; one half was used for gross morphological analysis and the other for histological studies.

A dissecting microscope was used to examine the shape and dimensions of the stomachs which were recorded photographically. The myology of the oesophageal and pyloric regions received particular attention. Composition of the tunica muscularis of the gastric epithelium was examined, and the distribution, abundance and dimensions of papillae were recorded.

Tissues representative of each histological zone of the stomach were removed by dissection, embedded in paraffin wax and sectioned at 7 µm; selected sections were photographed to record cell types and spatial histological arrangements. Haematoxylin and eosin (Humason 1967) was used for preliminary examination of the gastric epithelium while the Periodic Acid-Schiff (PAS) reaction was used to demarcate areas of mucin secretion (Humason 1967) and the Ayoub-Shklar stain to verify the presence of keratin in the corpal epithelium (Ayoub & Shklar 1963).

Glutaraldehyde-fixed (2 mm by 2 mm) pieces of papillated or cornified corpal epithelium for scanning electron microscopy (SEM) were critical point dried (Anderson 1951), osmicated, coated with gold-palladium and viewed in a JEOL JSM/VS scanning electron microscope. Secondary fixation and embedding of the tissues for transmission electron microscopy (TEM) were prepared according to the method of Cross (1979). Sections were cut on an LKB mark 3 ultramicrotome and stained with uranyl acetate and lead citrate (Cross 1979).

Results

Morphology

The stomachs of *C. gambianus* and *S. campestris* are divided by a grenzfalte (corpopyloric fold) forming a non-glandular corpus (forestomach or pars oesophagea) and a glandular antrum (or hindstomach) (Figures 1 and 2). The forestomach in *C. gambianus* is large relative to the hindstomach, and to that of *S. campestris*. The stomach is U-shaped and receives the oesophagus medially on the lesser curvature (curvatura ventriculi minor) in both species: it is markedly sacculated in *C. gambianus* and the antrum is bilobed. The corpus (corpus ventriculi) comprises an elongated fornix ventriculi which in *C. gambianus* contains numerous, irregularly orientated, filiform papillae projecting into the gastric lumen. A small sub-oesophageal, pregastric pouch (PGP) is barely discernable in *S. campestris* but clearly evident in *C. gambianus*. The elongated antra are produced by the absence or small size of the incisura angularis in *C. gambianus* and *S. campestris* respectively; a conspicuous pyloric pouch is present in both species (Figures 1 and 2).

The antrum of *C. gambianus* is bipartite comprising distal pyloric pouch and proximal fundus. The areas immediately adjacent but distal to the grenzfalte contain cardiac glands, the antra contain only fundic glands (particularly in the proximal chamber of the antrum of *C. gambianus*) and the pyloric pouches contain pyloric glands. The superior (pars superior) duodenum is ascending in both species and the pyloric sphincters have more extensive musculature on the

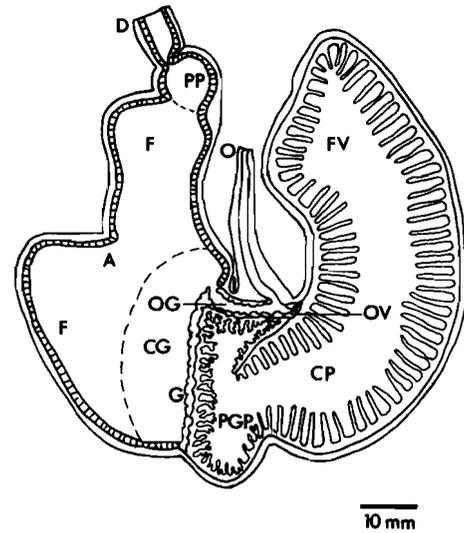


Figure 1 Drawing of a bisected stomach of *C. gambianus*. A = antrum, CG = cardiac glands, CP = corpus, D = duodenum, F = fundus, FV = fornix ventriculi, G = grenzfalte, O = oesophagus, OG = oesophageal groove, OV = oesophageal valve, PGP = pregastric pouch and PP = pyloric pouch.

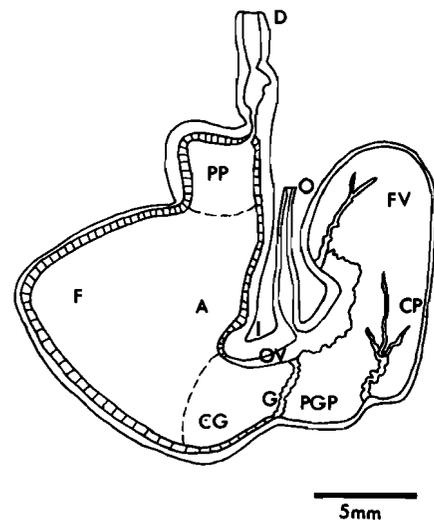


Figure 2 Drawing of a bisected stomach of *S. campestris* (labelling as in Figure 1, I = incisura angularis).

greater curvature giving an asymmetrical appearance. The PGP epithelium of *C. gambianus* differs from that of *M. albicaudatus* since it is papillated; however, the papillae are short and tufted and dissimilar from those of the fornix ventriculi (Figure 1). Neither the corpal nor the PGP epithelia of *S. campestris* are papillated.

The gastro-oesophageal junction contains striated and smooth muscle and shows considerable complexity, particularly in *C. gambianus*. The distal oesophagus dilates to form a sub-oesophageal vestibule which is surrounded by sphincteric musculature (Figure 3). The oesophageal continuation of the vestibule (on the gastric side of the sphincter) forms an oesophageal groove (Figure 4) which leads to the antrum, and forms the anterior end of the grenzfalte. On either side of the oesophageal groove (beneath the oesophageal orifice) are two cornified flaps which form the oesophageal valve.

Proposed passage of digesta through the stomach of *C. gambianus*

Interpretation of anatomical data with inductive reasoning

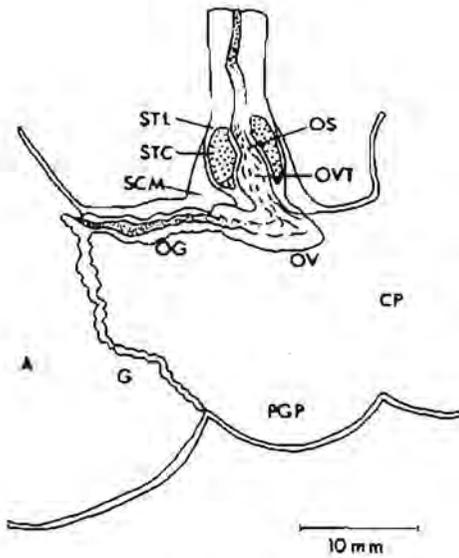


Figure 3 Drawing of the distal oesophagus: stomach junction in *C. gambianus*. A = antrum, CP = corpus, G = grenzfalte, OG = oesophageal groove, OS = oesophageal sphincter, OV = oesophageal valve, OVT = oesophageal vestibule, PGP = pregastric pouch, SCM = smooth circular muscle, STC = striated circular muscle, STL = striated longitudinal muscle.

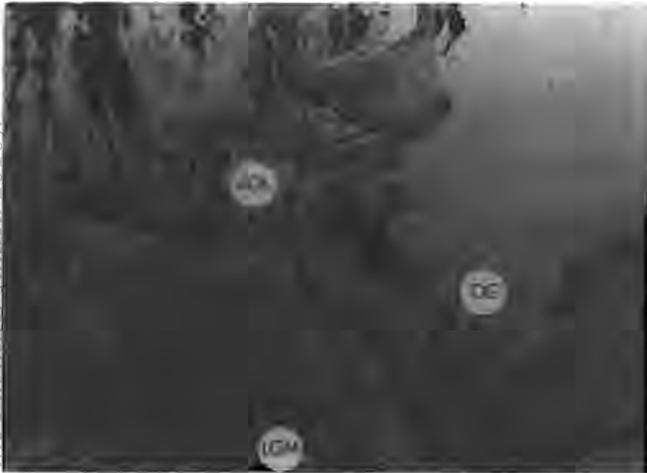


Figure 4 A histological section through the oesophageal groove of *C. gambianus*. AOL = aboesophageal limb, LGM = longitudinal groove muscles, OG = oesophageal groove.

suggests that digesta is likely routed through the stomach of *C. gambianus* as follows. Control of digesta flow into and out of the stomach is regulated by the sphincteric sub-oesophageal (pouch) myology, and the structure of the pyloric pouch and pylorus musculature respectively. Regulation of digesta flow between the corpus and antrum is governed by constrictions of the tunica muscularis on either side of the pregastric pouch, the grenzfalte, and the oesophageal groove (Figures 1 and 3). The oesophageal groove/valve system permits differential passage of digesta from the oesophagus to either the corpus or antrum.

Digesta enters the stomach through the oesophageal sphincter and passes into a small, muscular sub-oesophageal vestibule. The combined action of the sphincter and the sub-oesophageal vestibule musculature forces the digesta either through the oesophageal valve to the corpus, or if the valve is closed, directly along the oesophageal groove to the antrum

(Figure 5). Contraction of the longitudinal groove muscles (in concert with the stratum circulare of the incisura angularis) closes the oesophageal groove (Figure 5), thereby effectively extending the reach of the oesophagus into the boundary of the fundic and cardiac chambers of the antrum. This route would likely be followed by proteinaceous (insect) food in the adult or by milk in neonates. (Oesophageal grooves were well developed in all individuals and did not degenerate in adults; their function is therefore not solely concerned with the routing of milk in juveniles.)

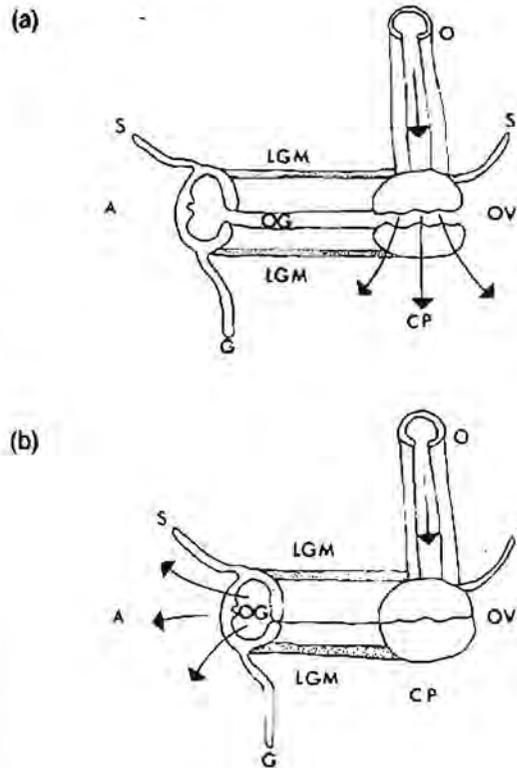


Figure 5 Diagram to illustrate the operation of the oesophageal groove system: (a) oesophageal groove and valve disengaged, digesta passes to the corpus, (b) groove muscles contracted with valves and groove engaged, food passes to the antrum. A = antrum, CP = corpus, G = grenzfalte, LGM = longitudinal groove musculature, O = oesophagus, OG = oesophageal groove, OV = oesophageal valve, S = stomach wall.

Digesta leaving the PGP is forced over the grenzfalte by exaggeration of the corpal PGP constriction (stratum circulare contraction) and relaxation of the antral PGP constriction (stratum longitudinale contraction). Similar constrictions induced by the tunica muscularis control digesta flow between the proximal and distal antrum and the pyloric pouch. With a concentration of muscle on the greater curvature, the pyloric sphincter functions by a milking action and contractions progress from proximal to distal. The presence of numerous muscular valves and a complex myology suggests a regular and controlled digesta flow through the stomach.

Histology

The arrangement of gastric tissues of *C. gambianus* and *S. campestris* conforms to the mammalian pattern (Figure 6). Generally the tunica muscularis is thicker in the corpus (where it supports a keratinized or papillated epithelium) than in the antrum. However, the muscular walls of the distal antra and pyloric pouches are thicker than those of the proximal antra

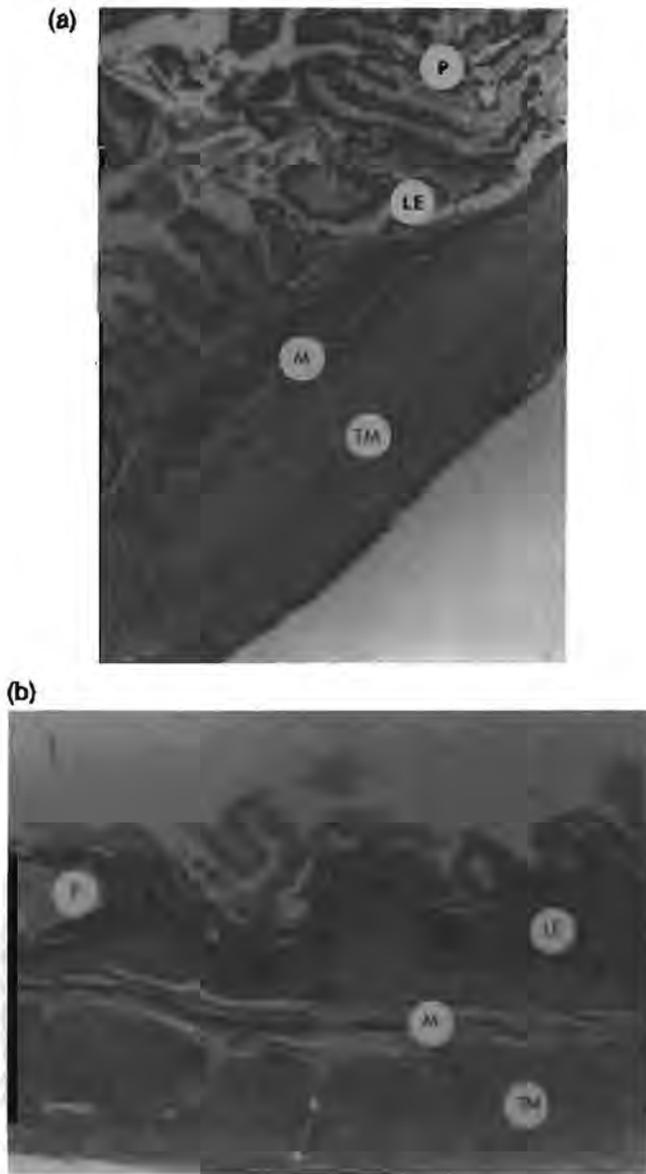


Figure 6 Arrangement of the gastric tissues in (a) *C. gambianus* and (b) *S. campestris*. M = mucosa, LE = luminal epithelium, TM = tunica muscularis. The epithelium of *C. gambianus* is papillated (P) while *S. campestris* possesses a folded (F) epithelium.

in both species. Striated circular muscle of the distal oesophagus is thicker in the region of the vestibule but does not extend beyond the incisura angularis, where it is replaced by smooth muscle. Striated longitudinal muscle penetrates the outer smooth muscle layers of the stomach so that a transitional region of both smooth and striated fibres occurs at the gastro-oesophageal junction (Figure 3).

Submucosae of loose connective tissue with some nerve fibres and blood vessels maintain a constant thickness in the antra but are enlarged in the corpus (Figure 6), while fine reticular connective tissues with elastin fibres constitute the lamina propria. The muscularis mucosa forms a ribbon of tissue comprising two layers of muscle cells in opposition. The corpus is lined by stratified, squamous epithelium and displays a stratum germinativum, granulosum and corneum (Figure 7). The stratum lucidum is absent from the corpal epithelium while the stratum corneum is hypertrophied giving rise to numerous filiform papillae in *C. gambianus* (Figure 8). Keratinization of the papillae forms through a keratohyalin stage. The corpal epithelium of *S. campestris*, unlike that of

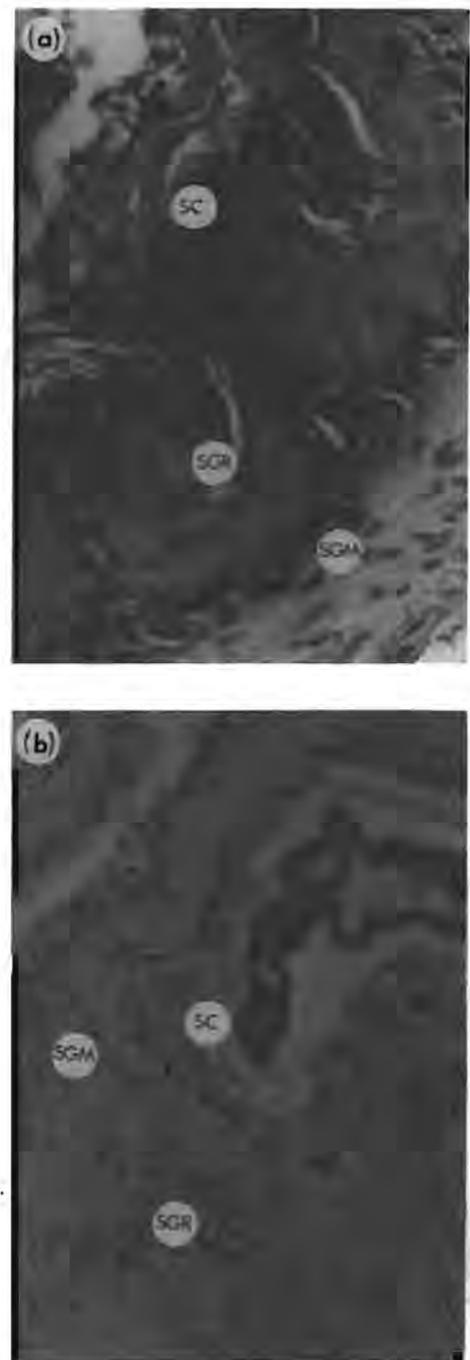


Figure 7 Stratified folded corpal epithelium of *S. campestris* (a) longitudinal section, (b) cross-section. SC = stratum corneum, SGM = stratum germinativum, SGR = stratum granulosum.

C. gambianus, is vascular (Figure 9).

The length, size and distribution of the papillae within the corpus of *C. gambianus* is variable (Figure 1). In some specimens there was an apparent gradation in size from the fornix ventriculi to the pregastric pouch (where papillae were short and sparse) while others possessed randomly distributed patches devoid of papillae and long papillae occurred in the pregastric pouch. Recent studies indicate that such differences are attributable to changes in diet composition and quality.

The grenzfalte and oesophageal groove are lined by stratified squamous epithelium that is keratinized and partly folded. Grenzfalten arise from a single thin fold in the mucosa; the basal region of which is invaded by smooth muscle cells from the muscularis mucosa. Although the oesophageal grooves have U-shaped cross-sections, the ab-oesophageal limb is

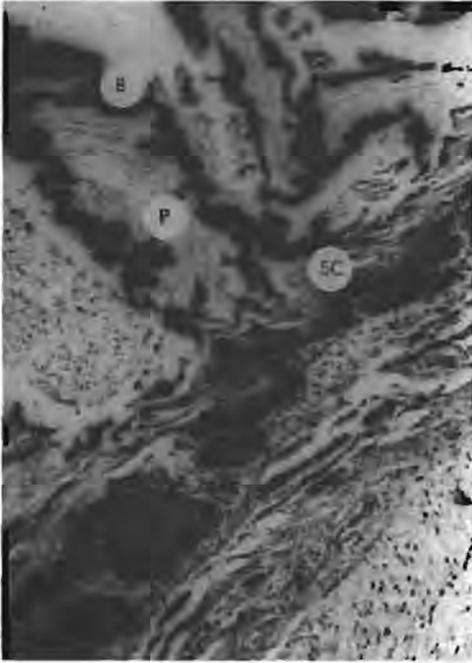


Figure 8 Corpal epithelium of *C. gambianus*. B = bacteria, P = papillae, SC = stratum corneum.

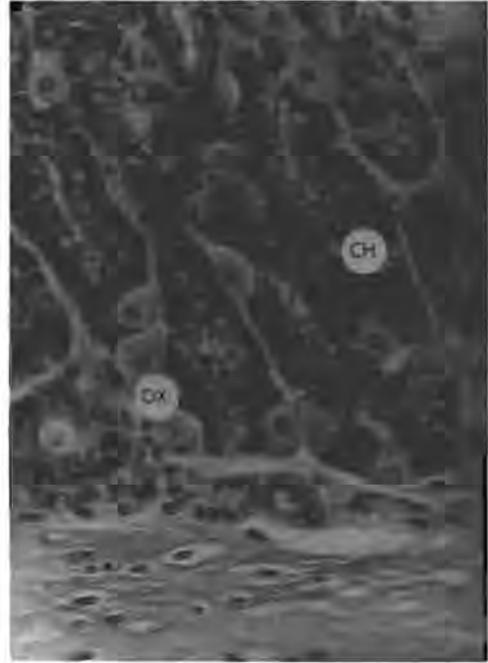


Figure 10 Fundic glands of *C. gambianus*. CH = chief cells, OX = oxyntic cells.

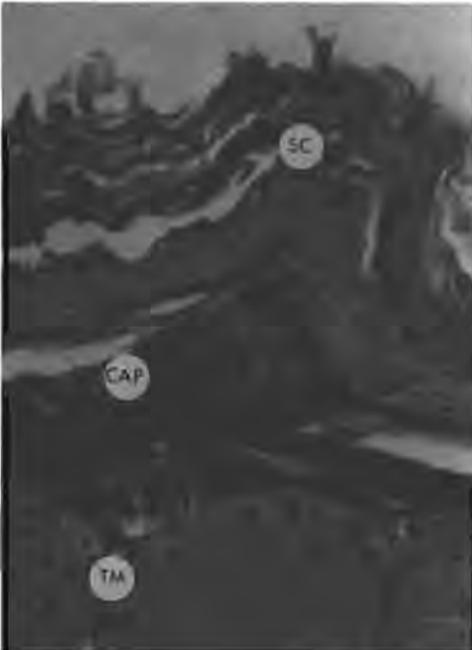


Figure 9 Vascular corpal epithelium of *S. campestris*. CAP = capillary, SC = stratum corneum, TM = tunica muscularis.

enlarged (Figure 4). It is underlain by a conspicuous block of muscles which run parallel to the groove; here named the longitudinal groove muscles. Sections of the oesophageal valve revealed striated muscle fibres indicating that, like the oesophagus, its action is under voluntary control.

Histochemistry

The presence of mucin in the lumen of cardiac and pyloric glands, but only in the foveolae of fundic glands, was demonstrated by a positive PAS reaction. Chief (parietal) and oxyntic cells were clearly differentiated in the fundic glands by haematoxylin and eosin stains (Figure 10). The keratinous

nature of the corpal stratum corneum and papillae was evident from the brilliant red reaction to the Ayoub-Shklar stain (Figure 11). Haematoxylin and eosin stains demonstrated the absence of nuclei from the stratum corneum but demonstrated the presence of keratohyalin granules in the stratum granulosum (Figure 7).



Figure 11 Base of a keratinous papilla from *C. gambianus*. B = bacteria, K = keratin, PC = plant cells, SGM = stratum germinativum.

Ultrastructure

SEM revealed the papillae of *C. gambianus* to be elongate, club-shaped structures with characteristic longitudinal invaginations (Figure 11). These invaginations, and desquamating

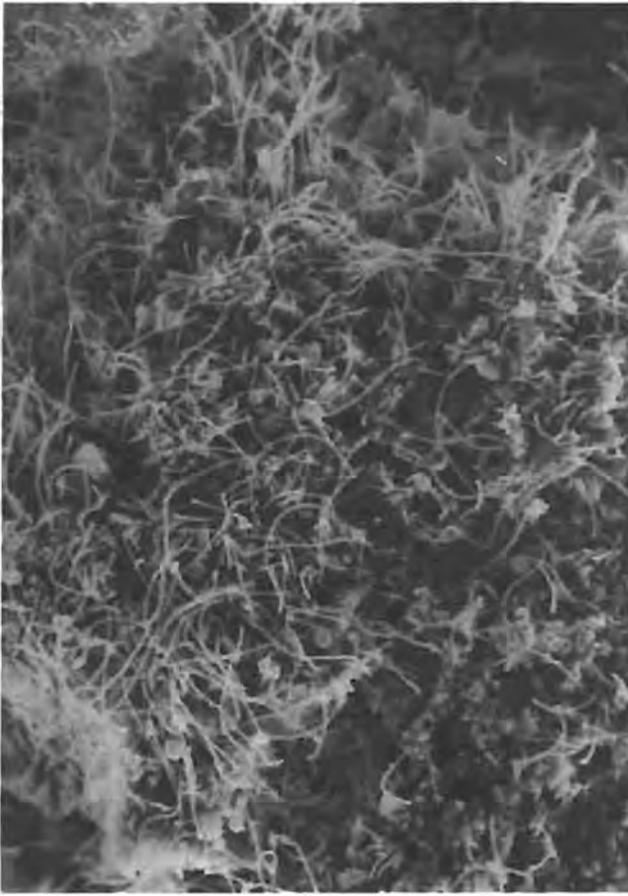


Figure 12 Surface of a papilla from *C. gambianus* covered by a diverse microflora.



Figure 14 Sessile cocco-bacilli and cocci from *C. gambianus*.

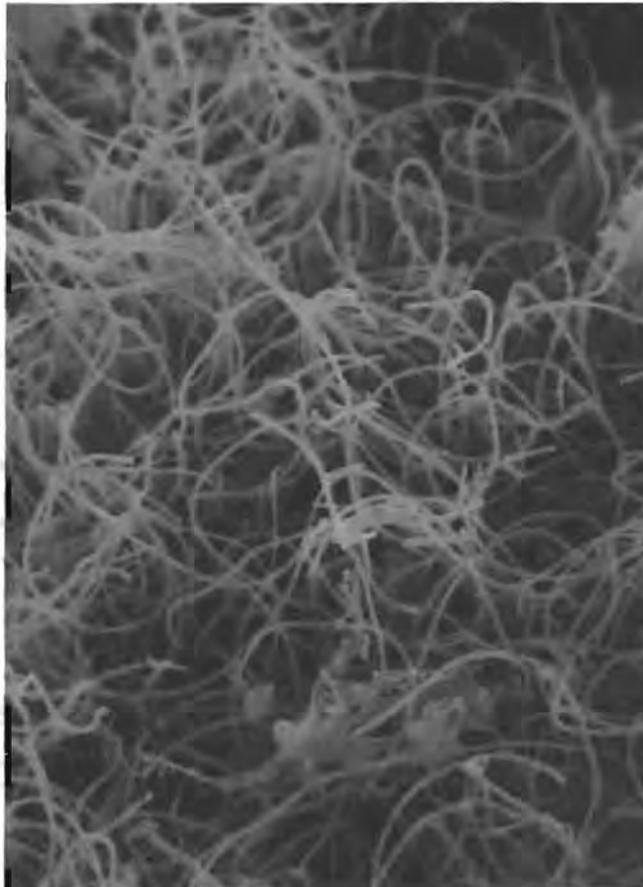


Figure 13 Superficial (luminal) filamentous bacilli from *C. gambianus*.

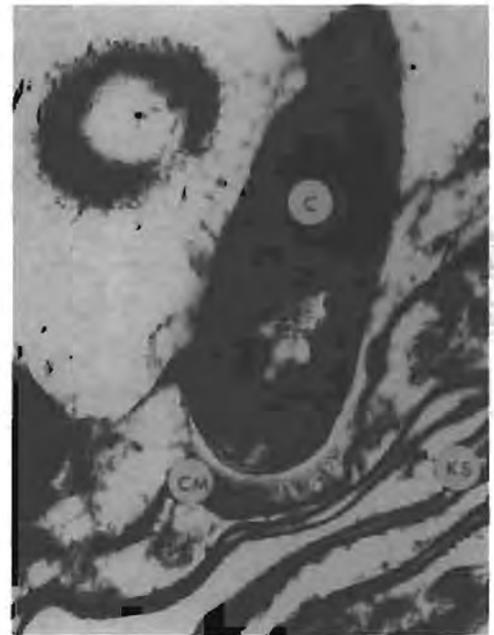


Figure 15 Cocci attached to keratinous squames by a capsular membrane.

keratinous squames sloughed from the papillae, were covered by a dense microbial flora (Figure 12) except in the zone bordering the *grenzfalte*. The stratified bacterial community of *C. gambianus* comprised superficial (luminal) filamentous bacilli (Figure 13), which overlaid sessile cocco-bacilli and cocci (Figure 14) that were attached to the keratin by a capsular

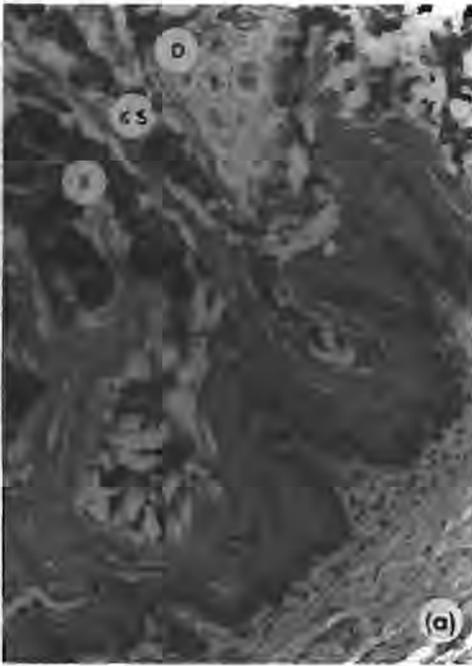


Figure 16 Close association between digesta, bacteria and sloughed keratin: (a) flat fornical epithelium, (b) folded corpal epithelium.

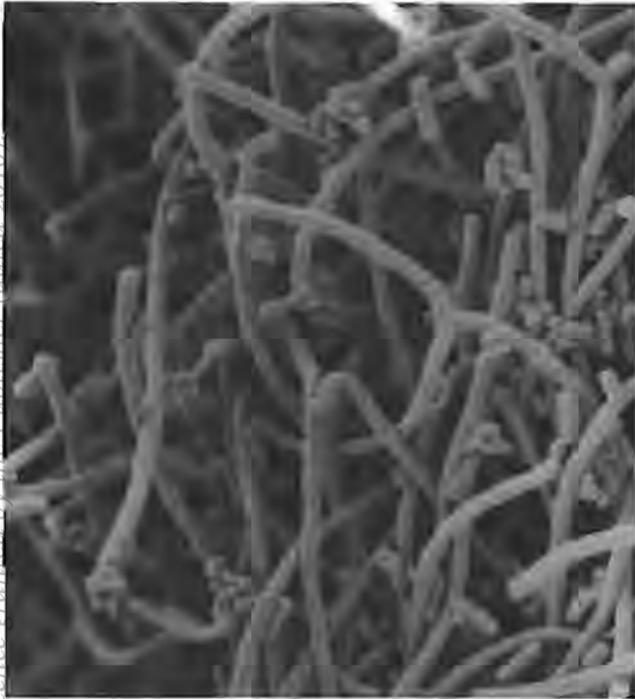


Figure 17 Filamentous bacteria overlying cocci and cocco-bacilli in the forestomach of *S. campestris*.

membrane (Figure 15).

There is an intimate association between digesta, keratinous squames sloughed from the stratum corneum and bacteria in the forestomach of *S. campestris* (Figure 16). The microflora of *S. campestris* paralleled that of *C. gambianus* since it comprised filamentous bacteria overlying cocci and cocco-bacilli (Figure 17) although its biomass was assessed subjectively to be less.

Discussion

Classification of rodent stomach complexity depends on which criteria are used for its evaluation. Carleton (1973, 1981) used

the extent to which the glandular epithelium is reduced while Vorontsov (1962) used the extent of sacculatation. The stomach of *C. gambianus* is more highly specialized than that of *S. campestris* (Table 1) but on the basis of glandularization and sacculatation both must be categorized as unilocular hemiglandular. Although the stomach of *C. gambianus* possesses several distinct chambers, the absence of a pronounced incisura angularis results in the anomalous unilocular categorization. The stomach of *M. albicaudatus* is clearly bilocular which is interpreted as the apomorphic state.

Although the discoglandular (apomorphic) condition (Carleton 1981) is not achieved in *C. gambianus* the distribution of fundic and cardiac glands has increased relative to that of the pyloric glands (and to the situation in *S. campestris*), thereby implying such a tendency (Bensley 1905). The position and area occupied by fundic and cardiac glandular epithelia in *C. gambianus*, the presence of elongated fundic glands (Luthje 1976) and the fact that the grenzfalten are keratinized and non-glandular in both species (Bensley 1905), are indicative of trends towards the digastric stomach type. Complexity of gastric morphology in *C. gambianus* rivals that of the hystricomorph *Capromys melanurus* (Dobson 1884) and the murid *Thallomys paedulcus* (Perrin & Maddock 1983b, 1985).

A major feature characterizing the gastric anatomy of the two cricetomyines is the presence of an oesophageal groove system which is absent from the cricetine *M. albicaudatus*. Its occurrence in *S. campestris* suggests that control of digesta flow predated the origin of papillae in the cricetomyines. Hence the absence of an oesophageal groove in *M. albicaudatus* represents a different phylogenetic history (or secondary loss). Assuming the oesophageal groove directs digesta differentially in adults (and not only milk in neonates), and knowing the functions of the corpus and antrum of *M. albicaudatus* to be amyolytic and proteolytic respectively, then the latter explanation of secondary loss is untenable.

The complex anatomy of the stomach of *C. gambianus* suggests a dichotomy of functions, with carbohydrate digestion predominating in the corpus and proteolytic degradation in the antrum (Camain *et al.* 1960; Perrin & Maddock 1983a).

Table 1 Comparison of *C. gambianus*, *S. campestris* and *M. albicaudatus*, with particular reference to gastric morphology

	<i>C. gambianus</i>	<i>S. campestris</i>	<i>M. albicaudatus</i>
Sub-family	Cricetomyinae	Cricetomyinae	Cricetinae
Range	(Sub) tropical	Southern Africa	Southern savanna
Habitat	Mesic savanna/woodland	Wide tolerances (but not deserts)	Grassland or bushveld
Mass	1,0–1,5 kg	40–70 g	75–110 g
Diet	Tubers, seeds and vegetables	Seeds and insects	Seeds and insects
Stomach	Unilocular hemiglandular	Unilocular hemiglandular	Bilocular hemiglandular
Sacculation	Exaggerated	Present	Present
Grenzfalte	Present	Present	Exaggerated
Incisura	Very small	Very small	Exaggerated
Oesophageal grooves	Well developed	Present	Absent
Fornix	Large	Elongated	Extended
Papillae	Numerous	Absent	Numerous
Pyloric pouch	Present	Present	Indistinct
Pregastric pouch	Distinct	Indistinct	Present
Bacteria	Diverse and stratified community. Sessile cocci & cocco-bacilli; superficial filamentous bacilli		Simple community of predominantly sessile bacilli
Bacterial function	Ferments glucose, hydrolyses amidon, casein & gelatine. Reduce nitrates to nitrites	Unknown	High amylase activity for starch & glycogen degradation

Microbial amylolysis of fibrous foods would of necessity precede antral and duodenal digestion, indicating initial digesta flow to the fornix ventriculi. However, if the food is proteinaceous it is advantageous to the host for it to be routed directly to the antrum; to accelerate protein digestion and prevent microbial utilization.

Epithelial stratification, with keratohyalin granules in the stratum granulosum, typifies the mammalian condition (Jarrett 1973) and indicates that the corpal epithelium has undergone 'soft' keratinization (Matoltsy 1975; Spearman 1977). Keratinization of the papillae in *C. gambianus* is by physiological hyperkeratosis, as in *M. albicaudatus* (Maddock & Perrin 1981), and generates squames and invaginations suitable for bacterial colonization. The extensive stratum corneum of the papillae is produced by a high mitotic rate in the basal cells, and resembles phase two type epidermis (Bullough 1975).

Papillae play an integral role in the attachment of symbiotic bacteria in *C. gambianus* and *M. albicaudatus*, but owing to the presence of keratinization and the absence of vascularization are not absorptive, unlike the papillae of ruminants (Lavker, Chalupa & Dickey 1969). [Rodent gastric papillae differ from those of the rumen in lacking a connective tissue core, or swollen cells in the superficial layers (Hofmann 1973).] The folded keratinized corpal epithelium of *S. campestris* is vascular [like that of the gastric diverticula of *T. paedulcus* (Perrin & Maddock 1985)] and may function in the absorption of metabolites resulting from amylolysis. This might appear anomalous since *C. gambianus* and *M. albicaudatus* are advanced in many characters but do not possess a vascularized corpus. The most parsimonious explanation is that the absence of a vascularized corpus is beneficial and apomorphic. This paradox is resolved if one assumes different utilization of the gastric microbes by species with or without a vascular gastric mucosa. It is hypothesized that rodent hosts with a vascular mucosa absorb simple fatty acids and alcohols from the degradation of carbohydrate while species with a non-vascular mucosa harvest gastric microbes in the antrum and/or duo-

denum to obtain protein. Since protein is more limiting than carbohydrate in rodent diets, the latter adaptation is more valuable. (Since keratinization of the fornix ventriculi is unlikely to be conducive to effective absorption, its presence must be attributable to a conflicting adaptive force, such as ingestion of abrasive foods.)

Pallisade attachment of papillary cocci and cocco-bacilli in *C. gambianus* suggests surface area for attachment may be limiting (while the outermost bacilli maintain a holdfast by virtue of their highly elongated filamentous shape) which implies corpal papillae have evolved to provide attachment sites for symbiotic bacteria. However, the presence of autochthonous bacteria associated with digesta may facilitate biochemical exchange and symbiosis. The relatively low density of bacteria in the forestomach of *S. campestris* suggests that their contribution to host digestion and metabolism is less than in *C. gambianus* and *M. albicaudatus*. However, the folded, stratified nature of the keratinized corpal epithelium in *S. campestris* itself provides an increased surface area over a flat non-stratified epithelium, and therefore represents an intermediate condition. It appears that the establishment or origin of a symbiotic microflora does not require corpal papillae but may be associated with the development of a folded, keratinized corpal epithelium. (The temporary reduction in papillae and bacteria in the pregastric pouch of *C. gambianus* is likely caused by a reduced pH, triggered by a backflow of hydrochloric acid over the grenzfalte from the fundus.)

Symbiotic bacteria serve several functions in ruminant-like animals (Bauchop 1978) and in *C. gambianus* are known to ferment glucose (liberating alcohols), hydrolyse amidon, casein and gelatine and reduce nitrites to nitrates (Camain *et al.* 1960). The possibility exists that there is a complex succession of biochemical interactions between the various micro-organisms and rodents investigated. The primary function of corpal bacilli of *M. albicaudatus* is elevated amylase activity that serves for starch and glycogen degradation (Perrin & Maddock 1983a), but ancillary functions are anticipated (Perrin & Maddock 1985). Examination of ingesta from the antrum of

C. gambianus reveals the presence of fragments of papillae lost from the corpus, which may represent an avenue for the digestion and utilization of sessile symbionts.

The evolution of gastric sacculation, glandular zonation, corpal papillae and oesophageal grooves in African cricetomyine rodents can only be explained by increased digestive efficiency, while the symbiotic association with numerous autochthonous bacteria implies coevolutionary adaptation. The presence of a well-developed incisura angularis which produces the bilocular stomach in *M. albicaudatus* (but which is absent from the cricetomyines), and the common occurrence of oesophageal grooves in *C. gambianus* and *S. campestris* (but its absence from *M. albicaudatus*) are explained on the basis of different phylogenies. The presence of corpal papillae in *C. gambianus* represents divergence from *S. campestris* and convergence with *M. albicaudatus*. It is suggested that the absence (loss) of corpal vascularization in species with a papillated forestomach may be associated with the cropping of symbionts to yield microbial protein in the antrum and small intestine. Many features are constant and common to the three species studied here, including the presence of a grenzfalte, cornified corpus, glandular antrum, and the structure of the fundic, cardiac and pyloric glands, the stratified keratinized epithelium and the oesophageal grooves. The major interspecific, qualitative difference is the absence of corpal papillae from *S. campestris* while most other differences like the degree of development of the pregastric pouch, are quantitative.

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