

# Gastric anatomy and histology of an arboreal, folivorous murid rodent: The Black-tailed tree rat *Thallomys paedulus* (Sundevall, 1846)

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## Abstract

A study of the gastric anatomy of *Thallomys paedulus* revealed a sacculated stomach, with a proximal keratinised forestomach (corpus) leading to an apical fornix ventricularis, that possesses several diverticula and a distal glandular hindstomach (antrum). A pregastric and a pyloric pouch occur proximal to the bordering fold (grenzfalte) and the pyloric sphincter respectively. The stomach is one of the most complex yet described for a rodent but can be categorised as bilocular hemiglandular, and has certain parallels with the stomachs of some African cricetid rodents. An oesophageal valve and groove may allow for alternate pathways of digesta flow and/or regurgitation. Keratin squames sloughed from the luminal surface of the corpus and the diverticula of the fornix ventricularis provide a microhabitat for numerous symbiotic bacteria.

## Introduction

Recent comparative anatomical studies of gastro-intestinal tracts of African rodents have demonstrated not only marked structural diversity (PERRIN and CURTIS 1980) and some unique adaptations (MADDOCK and PERRIN 1981), but also a need to revise current hypotheses of rodent gastric evolution and digestive physiology. Previous reviews of rodent gastric morphology, particularly of Palaearctic muroids (VORONTSOV 1962) and New World cricetids (CARLETON 1973), have suggested a fundamental dichotomy of structure and function. Radiation from the unilocular wholly glandular stomach has produced the present-day evolutionary continuum of diversity, with varying degrees of glandularisation, keratinisation, sacculatation and microbial symbiosis within the stomach that cannot be represented by a simple dichotomy (PERRIN in press a). The original simple ideas require critical reappraisal to develop and deepen our shallow understanding not only of gastric anatomy but of rodent evolution and herbivory. This necessitates a full description of several atypical morphological adaptations found in certain herbivorous African rodents. The purpose of the present paper is to describe the gross anatomy, histology and microflora of the stomach of the black-tailed tree rat, *Thallomys paedulus*, in relation to that of other African muroids and its feeding biology.

*T. paedulus* prefers dry environments and occurs in the South West Arid and Southern Savanna woodlands but is absent from the Grassland subzone of southern Africa (DE GRAAFF 1978). They are nocturnal, arboreal murids that live in small communities usually associated with large untidy nests of twigs located in *Acacia* trees. They feed largely on *Acacia* seeds, young *Acacia* leaflets, young pods of *A. erioloba* and the outer green coating

of *A. tortolis* pods, but also consume young leaves of Witgat *Boschia albitrunca* and the epidermis of Buffalo-thorn *Ziziphus mucronata* (DE GRAAFF 1981).

## Materials and methods

Ten *T. paedulus* were killed by chloroform anaesthesia and placed on ice to retard autolysis. The stomach including 10 mm of distal oesophagus and proximal duodenum were removed by careful dissection. Small pieces (2 mm × 2 mm) of tissue were removed from selected areas of the ventral half of the stomachs for ultrastructural studies, and fixed in 5 % buffered glutaraldehyde at 4 °C for a minimum of 24 h. Whole stomachs with their contents were placed directly into Bouin's fixative for 24 h.

One stomach was bisected along its sagittal plane and photographed. Dorsal halves of the stomachs were used to examine gross morphology including the presence and position of sacculations, and diverticula. Tissues were taken from particular regions of the forestomach (corpus) and hindstomach (antrum) to facilitate study of their histological structure and arrangement. Paraffin-embedded tissues were sectioned at 7 microns, stained and mounted; selected sections were photographed.

Haematoxylin and eosin (H & E) was used as a general tissue stain (HUMASON 1967) and was supplemented with two histochemical stains. The Ayoub-Shklar (A-S) stain (a modified Mallory's stain) was used to demonstrate the presence of keratin (AYOUB and SHKLAR 1963) and the Periodic Acid Schiff (P.A.S.) reaction was used to confirm mucus (polysaccharide) secretion (HUMASON 1967). Tissue used for scanning electron microscopy (S.E.M.) was critical point dried (ANDERSON 1951), osmicated, coated with gold palladium, and examined with a JEOL JSM/VS scanning electron microscope.

## Results

### Gross morphology

The stomach of *T. paedulus* is U-shaped and markedly compartmentalised (Fig. 1). The nonglandular forestomach is considerably enlarged and consists of a cornified corpus and a blind-ending fornix ventricularis. The glandular antrum is separated from the corpus by a constriction and a bordering fold of tissue, the grenzfalte. The antrum comprises a large sacculated fundus, a cardiac region, and a pyloric pouch (Fig. 1).

The oesophagus enters the dextral side of the lesser curvature of the corpus, which comprises a horizontal and a vertical arm, the latter terminating in the apical fornix ventricularis (Fig. 1). On the gastric side of the oesophageal sphincter, a pair of cornified flaps form an oesophageal valve (Fig. 2). Short, opposing oesophageal grooves lead from the oesophageal valve into the antrum, cranial and distal to the grenzfalte.

The mucosa on the lesser curvature of the horizontal arm of the corpus is deeply and regularly folded to form a series of furrows leading to the ascending arm and fornix ventricularis respectively (Fig. 1). On the greater curvature, the sinistral region of the mucosa is elaborately convoluted to form a series of transverse folds and ridges. A particularly large fold forms the boundary with the ascending arm and is designated the corpal valve (Fig. 1). On the posterior side of the corpus there is a small sub-oesophageal or pregastric pouch (Fig. 3) that forms a boundary with the grenzfalte; its mucosal surface is finely folded.

The ascending arm of the corpus possesses a series of large folds, mainly orientated longitudinally, which connect with the very complex structure of the fornix ventricularis (Fig. 1).

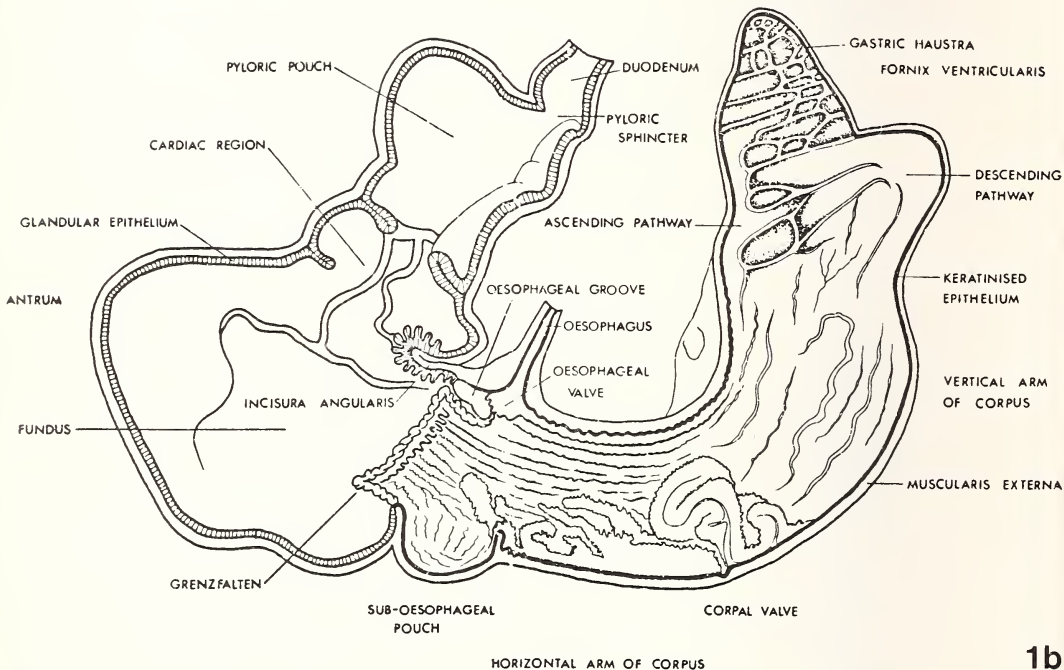
The fornix contains an internal spiral pathway which ascends to an apical point. Numerous diverticula lead outwards from the internal pathway (Fig. 4) and act as small reservoirs for ingesta. A descending pathway of cornified mucosa leads from the basal region of the fornix, in the form of a duct, to the vertical arm on the greater curvature of the corpus.

The antrum is a glandular sac originating immediately distal to the grenzfalte. The



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Fig. 1. a: Photograph of a bisected stomach of *T. paedulcus* illustrating gross morphology. A = antrum, C = corpus, D = duodenum, F = fundus, F.V. = fornix ventricularis, G = Grenzfalte, I.A. = incisura angularis, O = oesophagus, P = pyloric pouch, and S = sub-oesophageal pouch or pregastric pouch; b: Fully-labelled drawing of a bisected stomach of *T. paedulcus* to demonstrate its gross anatomy



1b

presence of a very small incisura angularis (Figs. 1 and 3) maintains a broad contact between the large sacculated fundus and the smaller cardiac region of the antrum. Large folds occur in the mucosal wall of the cardiac stomach. A clearly-defined and enlarged pyloric pouch (Fig. 5) is evident which empties into a vertically ascending duodenum through the pyloric sphincter (Fig. 5). A larger sphincteric muscle mass occurs on the lesser curvature of the stomach.



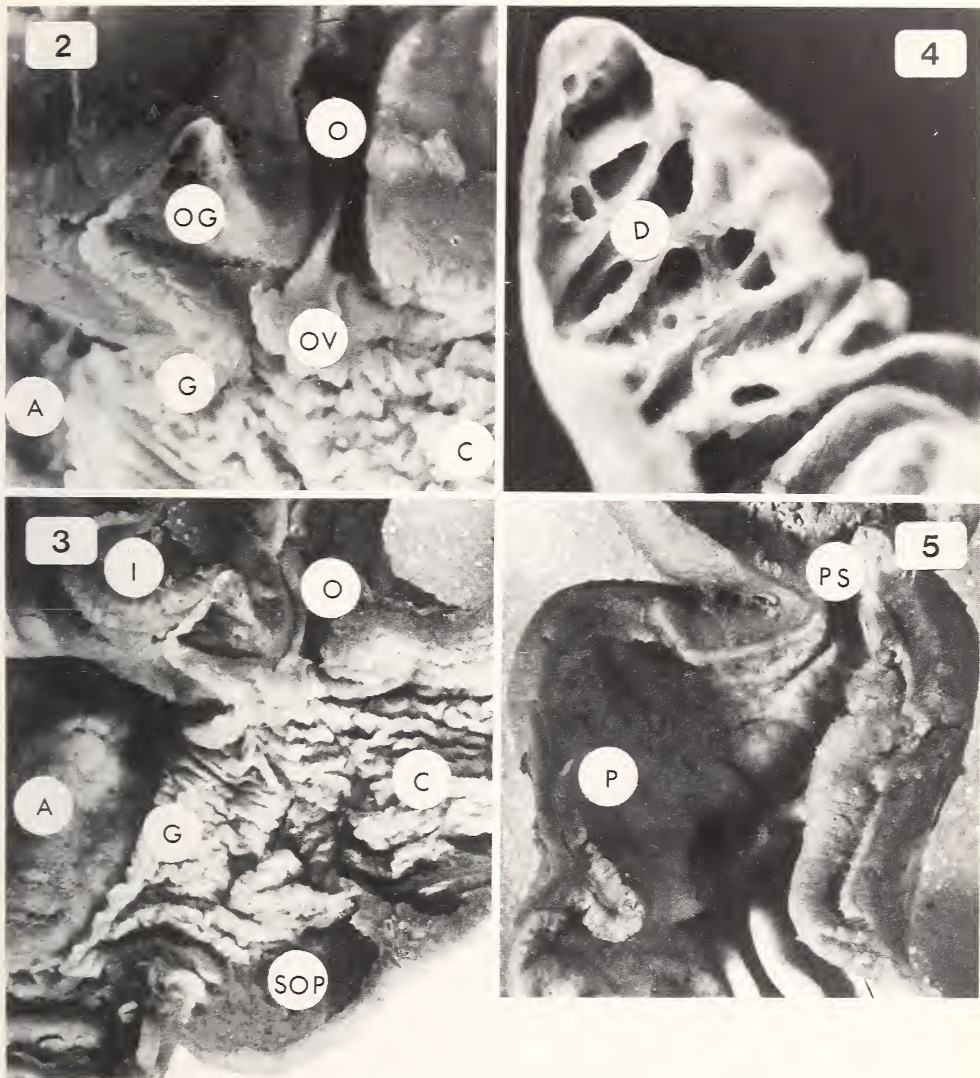


Fig. 2. A photograph showing the opening of the oesophagus (O), past the oesophageal valve (O.V.) and oesophageal groove (O.G.) into the corpus (C), and past the Grenzalte (G) into the antrum (A). – Fig. 3. The dextral region of the horizontal arm of the corpus showing the relative positions of the oesophagus (O), incisura angularis (I), suboesophageal pouch (S.O.P.), Grenzalte (G), corpus (C) and antrum (A). – Fig. 4. A photograph showing diverticula (D) leading off the spiral lumen of the fornix ventricularis. – Fig. 5. A photograph of the pyloric pouch (P), which leads into a vertically ascending duodenum through the pyloric sphincter (P.S.)

### Histology

A typically mammalian gastric tissue plan (DEARDEN 1969) was observed (Fig. 6). Although the epithelium appeared hyperplastic (Fig. 7), there was no pathological hyperplasia, only a retardation of desquamation. The tunica muscularis, which was markedly thicker in the cornified forestomach (Fig. 8), consisted of a thin stratum circulare and a

thick stratum longitudinale. The stratum circulare was well developed at the pylorus and considerably expanded in the fornix ventricularis and oesophageal sphincter.

The submucosa was markedly reduced in the antrum but extensively developed in regions of the forestomach, particularly the fornix ventricularis (Fig. 9). Small blood vessels and loose connective tissue were evident in the corpal submucosa (Fig. 9), but the fornix was markedly vascular (Fig. 6) and contained much connective tissue and extensive bands of smooth muscle (Fig. 9). The muscularis mucosa formed a definite but intermittent band of tissue in the fornix ventricularis (Fig. 6), while elsewhere in the forestomach it was a fine but clear and regular ribbon comprising two layers of muscle cells in opposition. In the antrum it was reduced in thickness. The inner of the two layers of the muscularis mucosa supplied strands of smooth muscle to the lamina propria (Fig. 10).

Loose connective tissue containing elastin fibres mainly constituted the thin lamina propria which varied only slightly in thickness; in the corpus owing to the folding of the epithelium, and in the antrum between adjacent layers of glandular tissue.

The antrum which is lined by a simple columnar mucus-secreting epithelium was divisible into three regions typical of mammalian gastric mucosa, namely fundic, cardiac and pyloric glandular regions. Fundic glands, with mucoid neck cells lining the upper regions of foveolae, and chief (zymogenic) and parietal (oxyntic) cells at the body and fundus of the foveolae (Fig. 10), occurred throughout the fundus (Fig. 1). Cardiac glands comprising simple, columnar, mucus-secreting cells were only found adjacent to the grenzfalte, while the branched, mucus-secreting pyloric glands were located distally within the antrum, in the pyloric pouch.

The corpus and fornix ventricularis were lined throughout by stratified, squamous epithelia. Three layers characteristic of mammalian epidermis (JARRETT 1973), that is the strata germinativum, granulosum and corneum were clearly identifiable (Fig. 11), unlike the stratum lucidum which was either greatly reduced or absent. The folded, multi-layered, keratinised epithelium (Fig. 7) which lined the corpus provided an extensive surface area for trapping ingested food particles, and microhabitats for bacterial colonisation (Fig. 12).

The diverticula of the fornix ventricularis possessed a multi-layered stratum corneum (Fig. 13), not only lining its lumen, but also filling its centre with a core of regularly-stratified, keratinous sheets. The outer layers tended to fracture and become interspersed with ingesta and bacteria (Fig. 14). Plant fragments lodged between the epithelial tissues of the fornix ventricularis were surrounded by aggregations of bacteria (Fig. 15).

The grenzfalte and corpal valve were keratinised folds of mucosa containing the submucosa and some smooth muscle fibres of the muscularis mucosa.

### Histochemistry

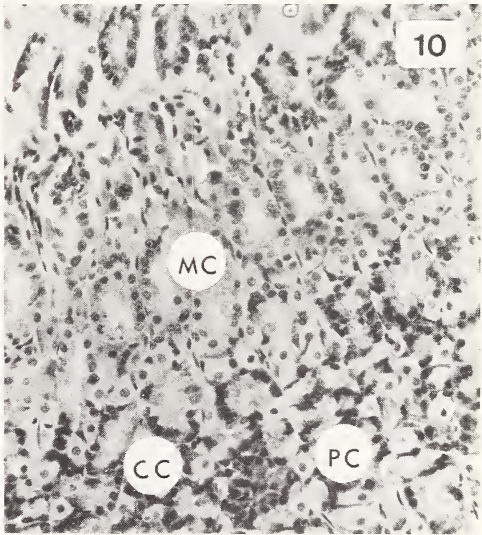
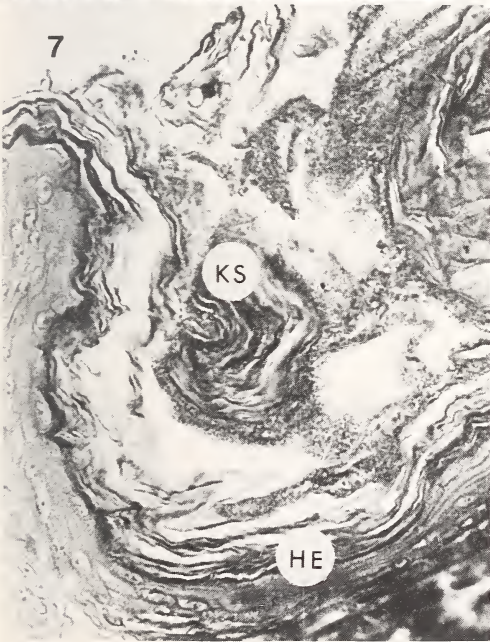
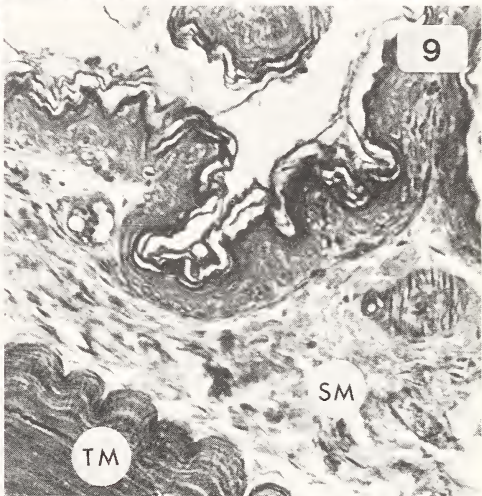
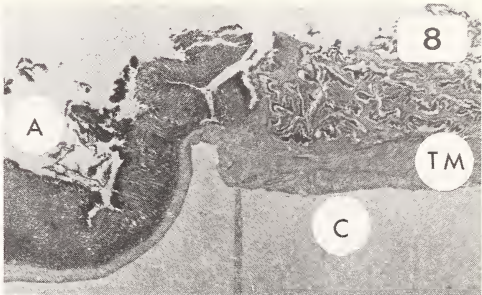
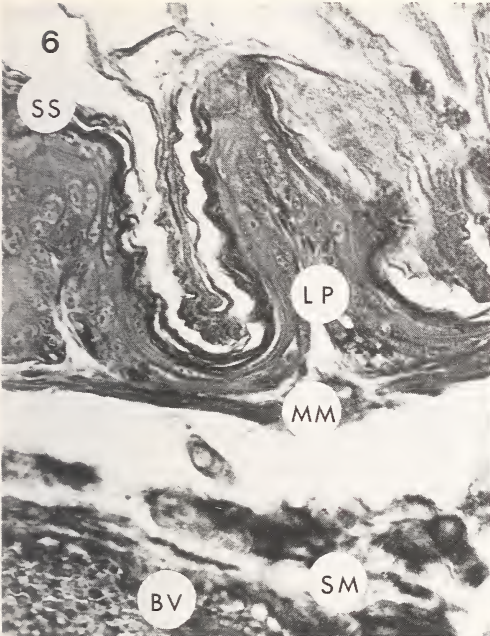
Haematoxylin and eosin stain demonstrated the absence of nuclei from the stratum corneum, and the presence of keratohyalin granules in the stratum granulosum (Fig. 11) which is indicative of complete, "soft" keratinisation. The ubiquitous occurrence of keratin in the surface epithelium of the corpus and fornix ventricularis was verified by its diagnostic brilliant red reaction to the Ayoub-Shklar stain (Figs. 6 and 7).

The surface and foveolar cells of the cardiac glands, but only the foveolar cells of the

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*Fig. 6.* A typically mammalian gastric tissue plan was observed. SM = submucosa (containing a blood vessel, B.V.), M.M. = muscularis mucosa, L.P. = lamina propria and S.S. = stratified squamous epithelium. – *Fig. 7.* Hyperplastic epithelium (H.E.) showing the loss of keratinous squames (K.S.) surrounded by ingesta and bacteria. – *Fig. 8.* A photograph showing the transition from the glandular antrum (A) to the keratinised corpus (C): note the marked change in thickness of the tunica muscularis (T.M.). – *Fig. 9.* The submucosa (S.M.) and tunica muscularis (T.M.) were extensively developed in the fornix ventricularis. – *Fig. 10.* A section of the fundic glands showing chief cells (C.C.), parietal cells (P.C.) and mucoid neck cells (M.C.)





fundic glands, were stained bright pink with PAS reagent (Fig. 8) owing to mucus secretion. Bacteria in the corpus were very deeply stained by PAS (Fig. 8) indicating the presence of a mucopolysaccharide capsule.

### Scanning electron microscopy

SEM revealed the relationship between the keratinous squames of the stratum corneum, ingesta, and bacteria (Fig. 16) within the diverticula of the fornix ventricularis. The stratification and sloughing of keratin was clearly displayed (Fig. 17). Superficial squames trapped ingesta, and both the epithelium and food particles were covered in a dense layer of cylindrical cocco-bacilli (Fig. 18). The bacteria appeared homogeneous in their external morphology (Fig. 19) although more than a single autochthonous species may be present.

## Discussion

### General

The extreme complexity of gastric morphology of *T. paedulcus* rivals that of the hystricomorph *Capromys melanurus* (DOBSON 1884) which has the most complicated stomach within the Rodentia. The stomach is bilocular and hemiglandular (MADDOCK and PERRIN 1981) but does not tend to the discoglandular condition (CARLETON 1973). The bilocular arrangement which also occurs in the cricetid *Mystromys albicaudatus* (MADDOCK and PERRIN 1981) is believed to be plesiomorphic and is absent from the two cricetomyinids *Cricetomys gambianus* and *Saccostomus campestris* (PERRIN and KOKKIN in press). Several adaptations, including the development of an oesophageal valve and an oesophageal groove; diverticula in the fornix ventricularis; the reciprocal restriction of gastric, glandular epithelium and the consequent elongation of the gastric glands; and a keratinised *grenz-falte*, are indicative of evolution towards a digastric physiology.

The complexity of the stomach of *C. gambianus* approaches that of *T. paedulcus* but its morphology, histology and ultrastructure differ in many detailed respects (CAIMAN et al. 1960). The divergent phylogenies of these rodents which represent different (sub) families indicate independent evolutionary histories for the development of digastric digestion and their coevolution with symbiotic (amylolytic/fermentative) bacteria. The diversity of stomach forms (PERRIN and CURTIS 1980) within the polyspecific Rodentia precludes the possibility of a single lineage leading to the complex digastric condition.

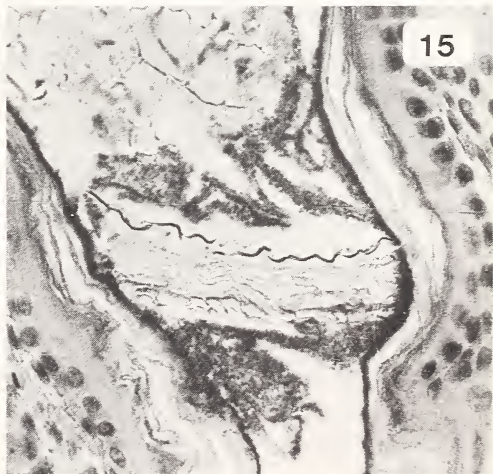
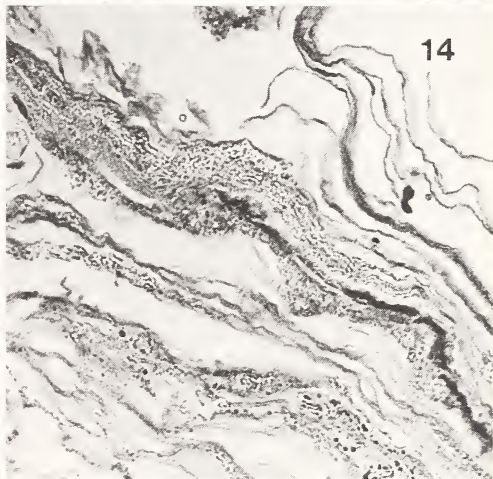
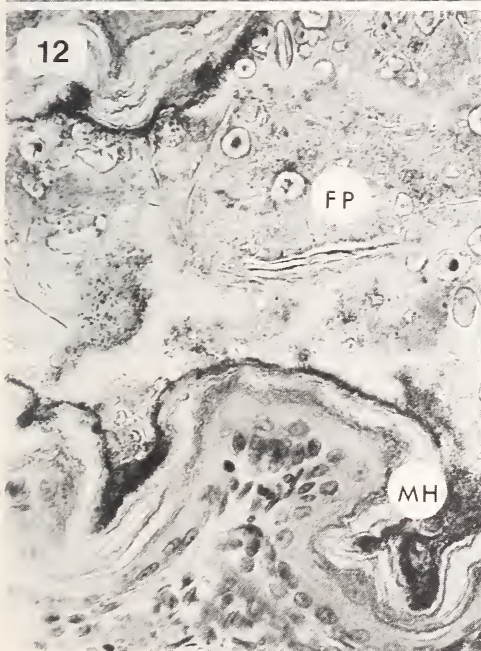
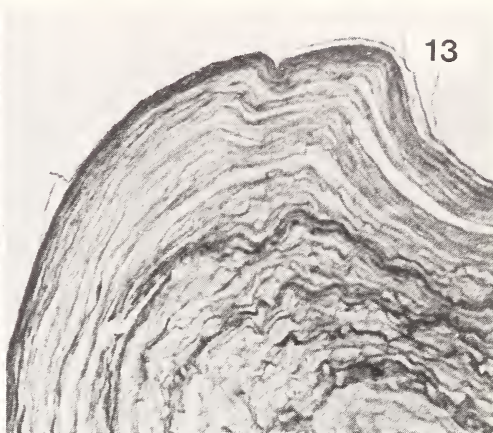
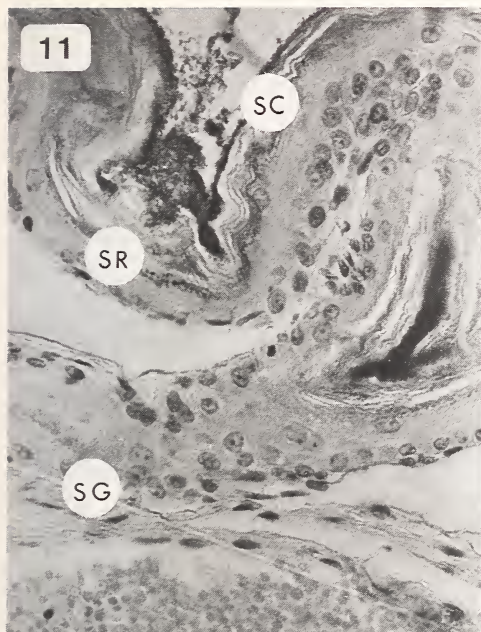
### Histology

The pronounced muscular structure of the corpal wall of *T. paedulcus* suggests that mechanical preparation of food may occur in the corpus. Indeed the complex myology suggests a mechanism considerably more advanced than that present in either of the digastric rodents *M. albicaudatus* (MADDOCK and PERRIN 1981) or *C. gambianus* (CAIMAN et al. 1960). Although the corpal mucosa is keratinised it is highly vascular, and differs in this most important respect from *M. albicaudatus* (MADDOCK and PERRIN 1981). This vascularisation may be suggestive of nutrient absorption from the stomach.

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*Fig. 11.* A section of the corpal epithelium showing the stratum germinativum (S.G.), stratum granulosum (S.R.) and the stratum corneum (S.C.). – *Fig. 12.* The folded corpal epithelium provided an extensive surface area for trapping food particles (F.P.), and microhabitats (M.H.) for bacterial colonisation. – *Fig. 13.* A core of regularly stratified, keratinous sheets taken from the lumen of a diverticulum of the fornix ventricularis. – *Fig. 14.* Keratinous squames interspersed with ingesta and bacteria. – *Fig. 15.* Plant fragments lodged between the epithelial tissues of the fornix ventricularis were surrounded by aggregations of bacteria







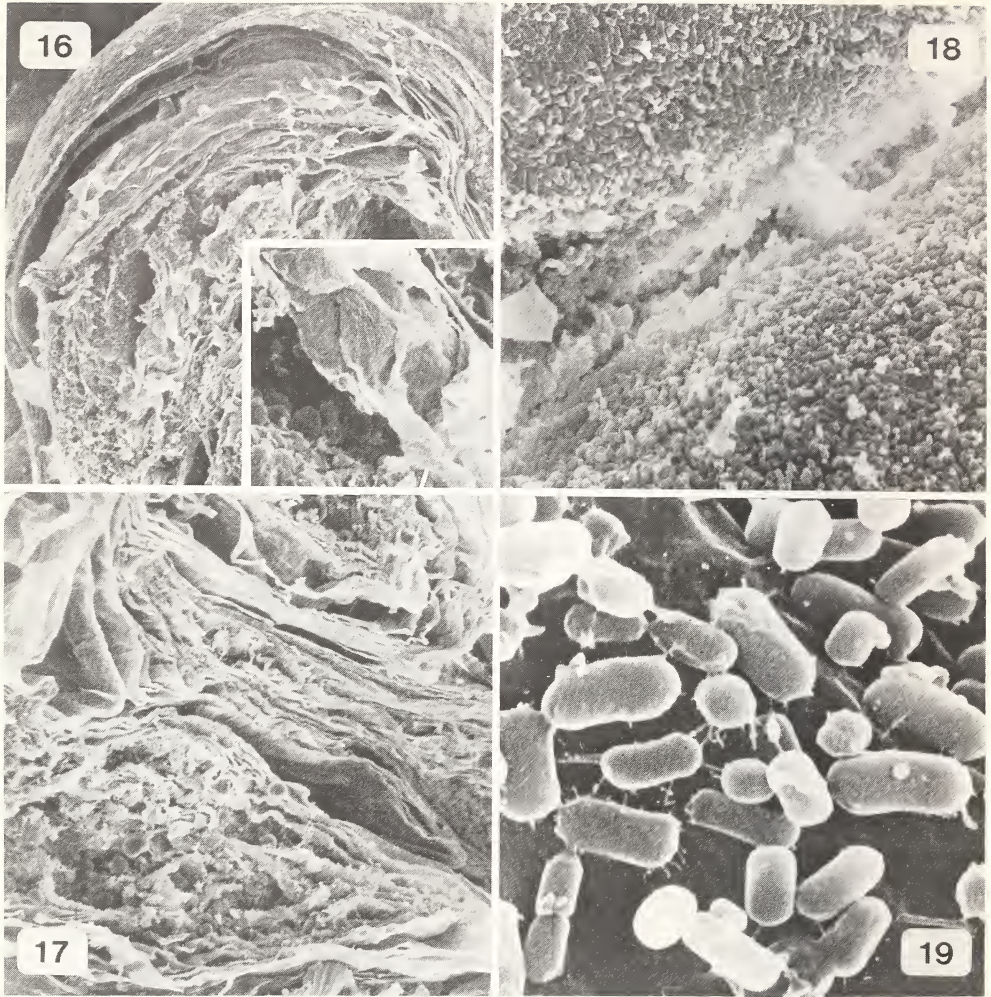


Fig. 16. Matrix of keratinous squames and ingesta within the diverticula of the fornix ventricularis. The insert shows the surface structure of a squame. – Fig. 17. Stratification and sloughing of keratin. – Fig. 18. A dense layer of bacteria coating the stratum corneum (of the corpus). – Fig. 19. Cylindrical cocco-bacilli on the surface of sloughed keratin

Epithelial stratification, with keratohyalin granules in the stratum granulosum, indicates that the epithelium of the forestomach has undergone orthokeratinisation (SPEARMAN 1977). The epithelium has a unicellular basal layer and relatively thin epithelium paralleling phase one type epidermis (BULLOUGH 1975).

#### Gastric diverticula

The gastric diverticula of *T. paedulcus* are unique, and homologous structures have not been recorded; similar analogous structures are uncommon in mammals although herbivory is widespread. MOIR (1968) has listed three general strategies to accommodate bulky foods and microbes in herbivorous mammals: elongation of the stomach, widening of its cross-sectional diameter, and sacculation. The fornix of *T. paedulcus* is elongated and

contains many diverticula but neither its sectional area nor its volume is greatly enlarged; the stomach is complex but is unlikely to accommodate bulky foods.

The gastric diverticula of *T. paedulcus* are markedly more complex than those of pigs (Sisson and Grossman 1964), and superficially resemble (i) the proximal, funnel-shaped spiral groove of the macropod forestomach (Moir et al. 1956), which is also lined with non-glandular stratified squamous epithelium (Griffiths and Bartin 1966); (ii) the right gastric caecum and diverticulum of the three-toed sloth *Bradypus tridactylus* (Grasse 1956); and (iii) the glandular sac areas ("water cells") of the tylopod (Hansen and Schmidt-Nielsen 1957; Bohlken 1960) "rumen".

### Oesophageal valve

The presence of an oesophageal valve and groove indicates that either there are two alternative routes of digesta flow through the stomach, that regurgitation occurs, or that both mechanisms are operative. These structures guard entrances to the microbial community of the corpus and the glandular antrum, whose functions are markedly different. Microbial fermentation and/or amylolysis of fibrous foods would of necessity precede antral and duodenal digestion, indicating initial digesta flow to the corpus and fornix ventricularis. However, the direct routing of proteinaceous food to the antrum would be advantageous to the host; to accelerate protein digestion by gastric pepsin and to prevent its utilisation by the microbial flora. Regurgitation might facilitate the efficient digestion of fibrous materials by permitting remastication and the lysis of plant cell walls. The operation of a similar oesophageal groove system found in *C. gambianus* has been described (Perrin and Kokkinn in press).

Control of ingesta flow between the horizontal and vertical arms of the corpus of *T. paedulcus* is likely regulated by the action of the extensive tunica muscularis and the corpal valve. The routing of food through the fornix ventricularis must be a very complex process involving numerous antagonistic muscles in the muscularis mucosa and tunica muscularis.

Once in the antrum ingesta passes from the fundus through the cardiac region into the pyloric pouch. Passage to the duodenum must be controlled by the operation of the pyloric sphincter and the musculature of the pyloric pouch. Inferred muscle action at the pyloric sphincter suggests a nearly symmetrical arrangement and circular action (Dearden 1969).

Regurgitation, if present, would initially involve confining the ingesta to the horizontal arm of the corpus by the combined action of the corpal valve and grenzfalte. Contraction of the corpal musculature would then eject the ingesta through the open oesophageal valve into the oesophagus: reversed peristalsis would return the partially digested food to the buccal cavity. Regurgitation has not been observed in captive animals, and it seems likely that the oesophageal groove functions solely in the differential passage of digesta to the corpus or antrum.

### Microbiology

Since the autochthonous bacteria of *T. paedulcus* are capable of attaching to food particles in addition to the corpal mucosa, they are most probably not space limited as are the symbiotic bacteria on the corpal papillae of *M. albicaudatus* (Maddock and Perrin 1981) and *C. gambianus* (Perrin and Kokkinn in press). Restriction of microbes to the surface of papillae limits their association and interaction with the digesta, while pelagic forms benefit from direct communion with the food source. There is no evidence to propose a stratified community of coexisting bacteria as occurs on the surface of gastric papillae in *C. gambianus* (Perrin and Kokkinn in press). The autochthonous, symbiotic bacteria of *T. paedulcus*, *M. albicaudatus* and *C. gambianus* appear morphologically dissimilar. Filamentous bacilli form part of a stable community in *C. gambianus*, but if present, are allochthonous to *T. paedulcus* and *M. albicaudatus*. Cocco-bacilli predominate in *T.*



*paedulcus* and *M. albicaudatus* and are abundant in *C. gambianus*. The composition of the bacterial community changes with diet composition and quality (PERRIN in prep.).

The autochthonous bacterial flora may serve several beneficial functions in ruminant-like animals (BAUCHOP 1978). Short-chain volatile fatty acids are liberated by microbial fibre degradation, and urea derived from host protein catabolism can be converted to microbial protein in the fermentation organ, which may aid water conservation and supplement a low protein food source. Many vitamins are synthesised by gastric microorganisms which increases availability to the host (BAUCHOP 1978). The gastric bacterial flora adapts rapidly to allelochemicals which may enable the host to utilise otherwise unpalatable foods and to colonise new nutritional niches (KINEAR et al. 1979; KINNEAR and MAIN 1979; PERRIN in prep. a). A primary function of the microflora of *M. albicaudatus* is  $\alpha$ -amylase synthesis and carbohydrate degradation but not fibre fermentation (PERRIN and MADDOCK 1983a, b).

### Conclusion

The evolution of complex gastric morphology including diverticula in *T. paedulcus* can only be explained by increased digestive efficiency, while the high density of bacteria in intimate association with the forestomach mucosa in healthy animals suggests a symbiotic relationship, together implying a coevolutionary adaptation. Thick keratinisation of the diverticular and corpal stratum corneum does not resemble pathological hyperkeratosis (SPEARMAN 1977) and it seems most unlikely that the bacteria are parasitic. The highly vascular lamina propria of the diverticula mucosa is indicative of nutrient absorption, and strongly supports a hypothesis of bacterial symbiosis since the corpal mucosa is non-secretory. This conclusion, if correct, suggests that bacterial enzymes are utilised to initiate the digestive process, and that some of the products of degradation are absorbed into the capillaries of the lamina propria. Such a pathway of nutrient uptake is unavailable to the digastric rodents *M. albicaudatus* (MADDOCK and PERRIN 1981) and *C. gambianus* (PERRIN and KOKKINN in press) since their corpal papillae are non-vascular.

An understanding of the mechanisms and processes of this symbiotic relationship will only be gained by studies of digestive physiology and microbial function (PERRIN 1983a, b). In most rodents with a bilocular hemiglandular stomach, pregastric fermentation exceeds caecal fermentation (HOOVER et al. 1969; SAKATA and TAMATE 1976). It is speculated that protein-rich bacteria are digested in the stomach of *T. paedulcus* but other digestive strategies are possible (EHLE and WARNER 1978).

It is widely believed that the forestomach-microbial system of pregastric fermenters has evolved to utilise fibrous plant materials, but there are now many exceptions to this view (HOFMANN 1973). KINNEAR et al. (1979) have shown that the pregastric microbial-mammal symbiosis results in nutritional niche expansion for pregastric fermenters by allowing them to satisfy their nutritional requirements from unnutritious foods. The argument is extended to include competitive interactions with non-pregastric fermenters where it has been demonstrated that pregastric fermenters are inherently inferior when competing for nutritious food. It is reasoned that in order to avoid the consequences of their competitive inefficiencies, pregastric fermenters must be occupying expanded (unnutritious) nutritional niches which exclude other herbivores with different alimentary systems (KINNEAR et al. 1979). This new approach has been applied to current studies of digestive physiology and niche occupation of *T. paedulcus* and other African rodents with complex gastric anatomy and physiology, and critically evaluated (PERRIN 1985, PERRIN in prep.).

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### Zusammenfassung

*Anatomie und Histologie des Magens eines arboricolen, folivoren Vertreters der Muridae:*

*Die Schwarzschwänzige Baumratte Thallomys paedulcus (Sundevall, 1846)*

Anatomische Untersuchungen am Magen von *Thallomys paedulcus* ergaben ein gekammertes Hohlor-gan mit einem proximalen keratinisierten Vormagen (corpus), der in einen apicalen Fornix ventricularis führt. Dieser ist mit verschiedenen Divertikeln ausgestattet und geht in einen distalen drüsenreichen Hauptmagen (antrum) über. Eine prägastrische Aussackung findet sich proximal zur Grenzfalte, eine Pylorusaussackung vor dem Sphincter. Dieser Magen ist für Rodentia äußerst kompliziert gebaut und kann als bilocular und hemiglandular bezeichnet werden. Er hat einige Gemeinsamkeiten mit Mägen afrikanischer Cricetidae. Eine oesophageale Falte und Furche läßt die Vermutung zu, daß alternativer Durchlaß von Nahrungsbrei und/oder Regurgitation möglich sind. Keratinschuppen, die von der Lumenoberfläche des Corpus und der Divertikel des Fornix ventricularis abgestoßen werden, ermöglichen ein Mikrohabitat für zahlreiche symbiontische Bakterien.

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## Postnatal physical development of the Water mongoose (*Atilax paludinosus*)

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### Abstract

The physical postnatal development of captive-bred *Atilax paludinosus* is described. Data indicate a litter size of two to three young. At birth the eyes and ears are closed and the animals are fully furred. The sequence of tooth eruption and weaning age are discussed. Comparisons with other Herpestinae indicate similar rates of development.

### Introduction

Water mongooses are solitary, nocturnal viverrids about which very little is known. SMITHERS (1983) remarks on the scarcity of information available on the reproduction of *Atilax*; apart from ZUCKERMAN's (1953) report on their breeding season and FRESE's (1981) record of births in the Berlin Zoo, little detail has been recorded. The remaining information concerning this species is presented in general references (SHORTRIDGE 1934; HINTON and DUNN 1967; DORST and DANDELOT 1970; ROSEVEAR 1974; KINGDON 1977; ROWE-ROWE 1978; STUART 1981; SMITHERS 1983). POCOCK (1916) describes some of the external characteristics of *Atilax* and DÜCKER (1965) has included some details regarding their biology in her text on viverrids.

This study describes the postnatal physical development of water mongooses in captivity, and compares it with the rate and pattern of development in other Herpestinae.

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