# Digestive secretions in camels

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*SUMMARY - The digestive secretions of both old world and new world camels are considered.*

*The salivary glands closely resemble those of cattle and sheep both morphologically and physiologically. Evidently, as in the Ruminantia, they provide almost all of the fluid and alkali needed to maintain favourable conditions for microbial digestion in the forestomach. The glandular epithelium of the camel's forestomach does not seem to have an important role in this respect except in that its free permeability to volatile fatty acids allows exchange of fatty acids for bicarbonate, as occurs also across the squamous keratinised epithelium of the Ruminantia.*

*Little is known of the secretions and digestive processes of the hindstomach and intestines.*

*A large part (up to about 90%) of the urea formed in the camel's body may be hydrolysed in the gut. This provides and endogenous source of nitrogen for microbial protein synthesis.*

*The forestomach contains about a quarter of the water in the whole body. It serves as a substantial and dynamic reservoir, releasing water during dehydration and accommodating it when a thirsty animal takes a huge drink to allow gradual rehydration of the tissues.*

*Key words: Dromedary, secretion digestive.*

RESUME - «La sécrétion digestive chez les chameaux». Les sécrétions digestives des chameux du vieux monde et du nouveau monde sont étudiées.

Les glandes salivaires ressemblent de près de façon morphologique et physiologique à celles des bovins et des moutons. Evidemment, comme pour les Ruminants, elles produisent presque tout le fluide et toutes les bases nécessaires pour maintenir des conditions favorables pour la digestion microbienne pour les préestomacs. L'épithelium glandulaire du préestomac du chameau ne semble pas avoir un rôle important dans ce contexte, à part sa perméabilité aux acides gras volatiles permettant l'échange de bicarbonate à la place d'acides gras comme cela se produit à travers l'épithelium squameux kératinisé des Ruminants.

Les sécrétions et les actions digestives des postestomacs et de l'intestion sont peu connues.

Une grande partie (jusqu'à environ 90%) de l'urée formée dans le corps du chameau peut être hydrolysée dans son tube digestif. Ceci produit une source endogène d'azote pour la synthèse des protéines microbiennes.

Les préestomacs contiennent environ un quart de l'eau du corps entier. Ils remplissent le rôle de réservoirs importants et dynamiques, relâchant l'eau pendant la déshydratation et l'accumulant lorsqu'un animal assoiffé s'abreuve rapidement, permettant de cette façon une réhydratation graduelle des tissus.

Mots-clés: Dromadaire, secretion digestive.

## Introduction

This paper briefly reviews what is known of the digestive secretions of camels in relation to nutrition and environment. Both old world camels, the dromedary (Camelus dromedarius) and Bactrian camel (C. bactrianus), and new world camels, the llama (Lama glama), guanaco (L. guanicoe), alpaca (L. pacos) and vicuna (Vicugna vicugna), are considered as much of the work on digestive physiology has been conducted on the latter group.

By feeding behaviour and by the structure and function of their digestive tract, the camels as a group are adapted to both browsing and grazing, able to select a high-quality diet when it is available but also able to survive on low quality fibrous roughages (ENGELHARDT et al., 1986a & b). Their long neck and their mobile and divided upper lip allow them to browse shrubs up to 3 m. above the ground, selecting leaves from among twigs and thorns. Unlike the Ruminantia the camels possess incisor teeth in the upper jaw as well as the lower jaw but the significance of this difference for the selection and chewing of food requires further study. The camels are, besides, physiologically adapted to arid conditions, the hot deserts of North Africa and Western Asia (dromedary), the cold deserts of Central Asia (Bactrian camel), and from the coastal deserts to the cold altiplano of South America (guanaco, llama, alpaca and vicuna). Often they must subsist on poor dry fibrous forage though at other seasons new green herbage may be abundant. Their long legs, endurance and resistance to

dehydration allow them to forage in a much wider circle around watering points than cattle or sheep.

## Salivary glands

The salivary glands have an important role in relation to the moistening and swallowing of newly ingested food and for the maintenance of oral hygiene, but this has not been studied in the camels. The saliva of some species contains important amounts of digestive enzymes. NASR (1959) detected some amylolytic activity in the dromedary's parotid gland and also in mixed saliva, the latter due in part to microbial contamination.

The second main function of salivary secretion in ruminant animals is the regulation of digestion in the forestomach. The gross and microscopic anatomy of the salivary glands of the dromedary has been described by many authors (see ENGELHARDT & HÖLLER, 1982). Recently NAWAR & EL-KHALIGI (1975) gave a detailed description of the parotid, the largest of the salivary glands, showing that its histochemical appearance changes with the feeding cycles as it passes from phases of rest to activity and then exhaustion. In its innervation and morphology and in the control and composition of its secretion the dromedary's parotid so closely resembles that of the Ruminantia as to suggest homology (HOPPE et al., 1975; KAY et al., 1980). HOPPE et al. (1975) studied two young dromedaires, weighing about 160 and 180 kg. When freely watered and consuming 4-5 kg. of hay daily, the secretion rate of a single parotid was 12-21 l/day. STEPANKINA & TASHENOV (1958) recorded a flow of 20.8 l/day from the fistulated parotid of an adult dromedary, and BHATIA et al. (1986) reported flows of 9.2-11.7 l/day from single parotids of two adult dromedaries (body weights not reported), given roughage plus pelleted concentrate diets. All three sets of authors found that saliva flowed most rapidly during feeding and rumination, though a continuous flow was observed at all times, as in bovids.

In a llama weighing 75-95 Kg. ENGELHARDT & SALLMAN (1972) collected mixed saliva by aspiration from the oral side of an oesophageal balloon (which may itself have stimulated salivary secretion). A flow declining from 679 to 379 ml/h. was observed. Mixed saliva was collected at the cardiac orifice of a llama via a large rumen cannula by ECKERLIN & STEVENS (1973); the flow rate between was 235 ml/h. In five alpacas weighing about 63 kg., ORTIZ et al (1974) found a single cannulated parotid to secrete at about 140 ml/h. before feeding, 202 ml/h. while feeding on hay, and 159 ml/h. an hour after food was removed.

The salivary flow rates recorded in all these studies on camels are similar to or perhaps slightly more than would be expected in sheep and cattle, allowing for body weights and experimental conditions (KAY, 1966).

During rumination camels chew alternately on the left and then the right side of the mouth, transfering the bolus from side to side after each bite. The Ruminantia, in contrast, chew the bolus for more prolonged periods on a single side. We have noted (P. P. HOPPE; R. N. B. KAY & G. M. O. MALOIY, unpublished) that in ruminating dromedaries each bite produced a continuous jet of saliva from the ipsilateral parotid but little flow from the contralateral gland. Alternation of chewing therefore allows both glands to contribute equally to ensalivation of the ruminated bolus, perhaps resulting in more efficient utilisation of parotid secretory capacity than in the Ruminantia.

The parotid saliva of camels, like that of bovids, is strongly buffered with bicarbonate and phosphate and is approximately isosmotic with plasma. Mixed saliva has a similar composition (table 1).

The parotid glands of the dromedary weigh about 0.5 g/kg. body weight, as in other ruminants adapted to feeding on coarse roughages (KAY et al., 1980). Ruminants selecting rich and digestible diets have parotids which are about three times heavier than this. The relative small glands of the camel seem appropriate, for the slowly-digested diet must not be flushed from the forestomach until it has undergone prolonged microbial fermentation and there is no need for rapid secretion of alkali into the forestomach at mealtimes when fermentation follows a slow and continuous course.

HOPPE et al. (1975) briefly describe the other salivary glands of the dromedary. The mandibular gland is less than half the size of the parotid. It secretes rapidly during feeding, slowly during rumination and not at all at other times. Its secretion is hypotonic and weakly buffered. As in the bovids, its function is evidently to moisten and lubricate newly ingested food. Inferior molar glands resembling the parotid are present in the dromedary, as in bovids, and abundant sheets of mucous glands line the cheeks, palate and pharynx where they are well placed to lubricate the swallowed bolus. The sublingual glands are small.

## Gastric secretion - forestomach

In the Ruminantia the compartments of the forestomach in which food is held during microbial digestion, the rumen, reticulum and omasum, are lined by a stratified keratinous epithelium that is devoid of glands. The salivary glands therefore serve as the only secretory tissue meeting the needs of the forestomach. They provide the bulk of the liquid that keeps the fermenting food in fluid suspension (drinking water is of subsidiary importance) and the alkaline salts needed to neutralise part of the volatile fatty acids (VFA) produced.

The camels forestomach is quite different. Although it is divided into three parts, carrying the neutral names compartments 1, 2 and 3, which are analogous in function to the rumen, reticulum and omasum respectively, it differs anatomically in many respects from the forestomach of the Ruminantia. Compartment 1 is not papillated nor strongly subdivided by muscular pillars like the rumen, compartment 2 is not lined by the honeycomb structure of the reticulum, and compartment 3 is not globular and filled with laminae

like the omasum. Instead compartments 1 and 2 possess many deep and muscular saccules lined by a smooth mucous epithelium and the tubular compartment 3 has longitudinal folds also lined by a mucous epithelium (see HANSEN & SCHMIDT-NIELSEN, 1957; CUMMINGS et al., 1972; RÜBSAMEN & ENGELHARDT, 1979).

ECKERLIN & STEVENS (1973), using a llama, showed that after the stomach had been isolated and its contents replaced by a saline solution, moderate amounts of bicarbonate appeared in exchange for chloride. Secretions collected into absorbent sponges placed in the saccules contained about 50 m. molar bicarbonate and 10 m. molar phosphate. The authors suggested that these secretions may provide «an important supplementary mechanism for buffering the VFA by-products of cellulose digestion».

A different opinion has been formed by ENGELHARDT and his colleagues in studies on llamas and guanacoes. Water, sodium and VFA were found to be absorbed in large quantities from compartements 1 and 2, especially from the sacculated parts, VFA absorption occuring much faster than from the reticulo-rumen of sheep and goats (ENGELHARDT & SALLMANN, 1972). Compartment 3 of the llama, like the omasum, was also found to absorb water, sodium and VFA readily (ENGELHARDT et al., 1979). In studies using Pavlov pouches prepared from the sacculated part of compartment 1 it was shown that bicarbonate accumulated in exchange for VFA on an almost equimolar basis, the rate being dependent on pH (RÜBSAMEN & ENGELHARDT, 1978). Thus the bicarbonate appeared·as the result of an absorptive process, not as a result of a digestive secretion. While some mucus could be isolated from the fluid in the Pavlov pouch (RÜBSAMEN & ENGELHARDT, 1979) it was thought it «has mainly protective functions but adds little to the overall buffering capacity» (ENGELHARDT & HÖLLER, 1982).

If this is correct, then despite the great differences in epithelial morphology between camels and the Ruminantia, both groups show the same dependence on the salivary glands to provide fluid and alkali for the fermenting digesta in the forestomach.

## Gastric secretion - hindstomach

Compartment 3 is a long tubular organ leading rather imperceptibly to a short hindstomach. The oral portion of the hindstomach has a folded epithelium through which pass long tubular glands lined with cells resembling the parietal cells, chief cells, endocrine cells and mucus cells of the fundus of the stomach in monogastric animals (LUCIANO et al., 1980; DOUGBAG & BERG, 1981). The unfolded epithelium of the aboral portion resembles that of the pyloric antrum in monogastric animals. Although no obvious sphincter divides compartment 3 from the hindstomach the contents of the two organs are effectively separated. In the llama the pH of the contents of compartment 3 averaged 6.35 whereas intense acidification occurred in the hindstomach (ENGELHARDT et al., 1979). Hindstomach contents in the grazing dromedary registered pH 3.6 (MALOIY, 1972a).

## Intestinal digestion

TOOFANIAN & ALIAKBARI (1977) infused various sugar solutions (10%, w/v) into dromedaries through a cannula placed in the proximal small intestine and recorded the subsequent elevation in blood glucose concentration as an index of digestion and absorption. Lactose infusion produced almost as great a response as a mixture of glucose and galactose, indicating substancial lactase activity in the intestine. Infusions of maltose and sucrose with appropriate controls indicated low maltase activity and very low sucrase activity. We can find no other physiological information concerning the digestive secretions of the intestine, pancreas or liver in camels.

## Secretion of urea into the digestive tract

A substantial fraction of the urea formed in the liver passes back into the lumen of the gut, either as a component of digestive secretions or by diffusion through the gut wall. It is then rapidly hydrolysed to ammonia and carbon dioxide by microbial urease. In the forestomach this ammonia may be utilised for microbial protein synthesis. When the supply of dietary nitrogen is limiting microbial synthesis and there is adequate energy as digestible carbohydrate the endogenous urea nitrogen promotes additional microbial activity and protein synthesis, thus increasing the amount of microbial protein passing to the intestine for digestion. When the protein content of the diet given to dromedaries was decreased from 13.6 to 6.1% the fraction of the urea entry rate that was degraded rather than excreted in the urine increased from 47 to 86% (EMMANUEL et al., 1976). Experiments on the llama summarised by ENGEL-HARDT & SCHNEIDER (1977) and ENGELHARDT (1978) show that diets low in protein and adequate in fermentable energy are associated wtih the recycling of about 90% of endogenous urea to the gut. With such diets, dehydration in camels (as in other herbivores) leads to further reduction in urinary urea excretion (SCHMIDT-NIELSEN et al. 1957) making a still larger fraction of urea available for return to. the gut. However, when dietarty nitrogen is not limiting to microbial activity the ammonia produced from endogenous urea in the gut is simply reabsorbed and converted back to urea in the liver, a futile and energy-wasting cycle.

Urea nitrogen can similarly be converted to microbial protein in the fermenting contents of the large intestine. Here however there is little opportunity for absorption of amino acids except in coprophagous animals and so the bulk of the protein will be excreted in the faeces. As less water is needed to excrete nitrogen as microbial protein in the faeces than as urea in the urine the faecal route of excretion offers some advantage to desert animals.

## The forestomach as a water reservoir

In grazing ruminants, the volume of water in the gut (mostly in the forestomach) accounts for about a quater of total body water and the volume of digestive secretions (mostly saliva) secreted daily is equal to about a half of body water. The gut thus provides a substantial and dynamic reservoir of water. To what extent do herbivores make use of this reservoir?

Camels, cattle, sheep, goats and donkeys that were dehydrated until they had lost 20% of their initial weight tended to desiccate and make hyperosmolar the contents of all parts of the digestive tract, and the camel showed much the same ability as other species in this respect (MALOIY et al., 1978); it is not clear how far reduced food intake will have contributed to the response. Sheep deprived of both food and water rapidly reduce the water content of the reticulorumen so that the water absorbed meets requirements and delays signs of dehydration for a day or two (HECKER et al., 1964). HOPPE et al (1976) studied two dromedaries that were gradually dehydrated over 20 days to 28% weight loss. Their food intake declined rapidly after 4 days, the volume of saliva secreted daily by a single parotid fell from about 15 l before dehydration to 3 l when fully dehydrated, the volume of water flowing through the forestomach fell from about 56 to 9 l daily and the water content of the forestomach from about 26 to 11 l. STEPANKINA & TASHENOV (1958) found the secretion rate of a fistulated parotid fell from 20.8 l/d. in a fully hydrated dromedary to 0.6 l/d. after 12 days of dehydration. It is not known how far the changes seen by HOPPE et al. (1976) were due to dehydration itself, and how far to the consequent fall in food intake; nonetheless, water absorption from the forestomach accounted for about a third of the weight lost during dehydration, thus helping to delay tissue and extracellular dehydration to a useful extent.

When these two animals were allowed to drink freely they consumed enough in 12 min to rehydrate themselves fully. Plasma osmolality and packed cell volume began to decline gradually an hour later but fell little below normal values and next day much of the water drunk was still present in the forestomach. Evidently by storing the water the forestomach avoided the ill-effects of over-rapid rehydration seen in monogastric animals and allowed the gradual rehydration and readjustment of body fluid compartments. Sheep that are dehydrated and rehydrated in a similar manner respond in much the same manner (T. SUGAWARA, K. KATOH & R. N. B. KAY, unpublished)

so it seems that the camel is not alone in exploiting the opportunities offered by its forestomach reservoir.

Many studies have been made of the ability of the camel to respond to heat and dehydration by adaptations of behaviour, heat balance, and the hormonal and renal mechanisms regulating fluid distribution and conservation; (SCHMIDT-NIELSEN, 1964; SIEBERT & MACFARLANE, 1971; MALOIY, 1972 b; YAGIL & ETZION, 1979). The interplay between dehydration and nutritional physiology needs futher study. To what extent can food intake be maintained in face of dehydration and attendant declines in digestive secretions and gut fluids? To what extent are these responses of the digestive system a consequence of declining food intake rather than dehydration itself? What is the influence of infrequent watering on retention and digestion of poor forages and on the ranging behaviour and the intake selection of food by grazing camels? A start has been made (ENGELHARDT et al., 1986a, b) but much remains to be done.

## Table 1

### THE COMPOSITION OF SALIVA
### IN VARIOUS CAMELS AND THE SHEEP
### (m. equiv/1)

| | $Na^+$ | $K^+$ | $HCO_3^=$ | $HPO_4^=$ | $Cl^-$ |
|---|---|---|---|---|---|
| **Parotid saliva** | | | | | |
| Alpaca (ORTIZ et al., 1974) | 165 | 13 | 122 | 33 | — |
| Dromedary (HOPPE et al., 1975) | 152 | 24 | 119 | 9 | 16 |
| Sheep (KAY, 1966) | 170 | 13 | 112 | 48 | 11 |
| **Mixed saliva** | | | | | |
| Llama (ECKERLIN & STEVENS, 1973) | — | — | 144 | 18 | — |
| Guanaco (ENGELHARDT & SALLMANN, 1973) | 148 | 7 | — | — | 29 |

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