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Particularities in forestomach anatomy, physiology and biochemistry of camelids compared to ruminants

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SUMMARY - The independent development of forestomach fermentation and rumination of ruminants and camelids is reflected by remarkable differences of forestomach anatomy and histology. Large proportion of the forestomach epithelium in camelid consists of columnar surface epithelium and deep tubular glands. Motility of the forestomach in camels is different from ruminants although the mechanism of rumination resembles each other. The biochemical pattern of microbial fermentation is generally similar between ruminants and camelids although concentrations of short chain fatty acids in the forestomach contents are always higher in camels. The superior adaptability of camels to harsh grazing conditions on both, heterogenous thornbush savannah pastures and on homogenous grassland may be explained by the better water economy and the more flexible adaptation strategies of camels. On heterogenous pasture camels successfully select plants of higher digestibility. On homogenous grassland where selection is mostly restricted during dry seasons, camels are able to achieve very long retention times of feed particles in their forestomach and thereby improve the microbial utilization of slowly digestible fibrous plant constituents.

Key words: Dromedaries, microbial digestion, motility, grazing.

RESUME - "Particularités de l'anatomie, de la physiologie et de la biochimie du pré-estomac des camélidés comparé avec celui des ruminants". Les particularités des fermentations dans le pré-estomac et de la rumination chez les camélidés, découlent des différences importantes anatomiques et histologiques. Une grande partie de l'épithélium du pré-estomac est constituée de glandes tubulaires séparées par un épithélium collinaire. La motilité du pré-estomac des dromadaires est différente de celle du rumen alors que les mécanismes de rumination sont similaires. Les fermentations microbiennes sont semblables entre les ruminants et les camelins, bien que la concentration en acides *gras volatils est plus élevée dans le pré-estomac. Une meilleure adaptation des dromadaires au pâturage dans les parcours pauvres de la savane comme dans les pâturages, s'explique par une économie plus grande d'eau et une souplesse plus grande des dromadaires sur les pâturages pendant la saison sèche ; les dromadaires augmentent leur temps de rétention des aliments dans le pré-estomac, favorisant l'utilisation microbienne des parois végétales.*

Mots-clés : *Dromadaires, digestion microbienne, motilité, pâturage.*

Introduction

The Camelidae (the old- and the new-world camelids) developed independently of the ruminants; ruminants developed more recently in the evolutionary process than camelids. Both, Camelidae and Ruminantia have large forestomachs with extensive microbial fermentation.

Anatomy

The forestomach of ruminant camelids consists of three different sections (Fig. 1). In ruminants we differentiate between the rumen, the reticulum and the omasum followed by the HCl- secreting abomasum. In camelids, the forestomach consists of a large compartment 1 (C1) that is divided by a strong transversal muscular ridge into a cranial and a caudal portion. The relatively small compartment 2 (C2) is not completely separated from C1. Compartment 3 (C3) which originates from C2, is situated at the right side of C1. C3 is a long, tube like form, intestine-like organ. HCl is produced only in the comparatively small hindstomach. The ventral regions of C1 and C2 are formed by glandular sac areas, which are particularly prominent between the strong rip-muscular ridges in the caudal C1.

Histology

In camelids, unlike as in ruminants, only the dorsal parts of C1 and C2 are made of a squamous keratinized epithelium. The ventral parts of C1, C2 and the whole inner surface of C3 are, instead, lined by a columnar surface epithelium and deep tubular glands. This region mucosa appears, in light microscopy, similar to the cardia region of the abomasum of the ruminants. The morphology of the regions mentioned above has been previously described in the llama and guanaco by light and electron microscopy (Cummings *et al.*, 1972; Luciano *et al.*, 1979).

In camelids, the epithelium lining the surface areas of the mucosa is composed by about 40 µm high columnar cells having a prominent oval nucleus located in the basal third (Fig. 2). The fine structure is comparable to that found in the corresponding regions in llama and guanaco (Luciano *et al.*, 1979). The main characteristics of these cells are a brush border membrane formed by tiny microvilli, a well developed golgi apparatus and numerous secretory granules (mainly packed together between the golgi and the apical plasma membrane). The mitochondria are elongated, slender and with a dense matrix; they fill wide cytoplasmic areas in the upper region in the cell where several dense bodies can also be seen. The lateral plasma membrane is extremely infolded, the intracellular space is very variable in width. These characteristics indicate that the cells have absorptive functions and furthermore that they, like in the llama and guanaco, probably secrete mucosubstances.

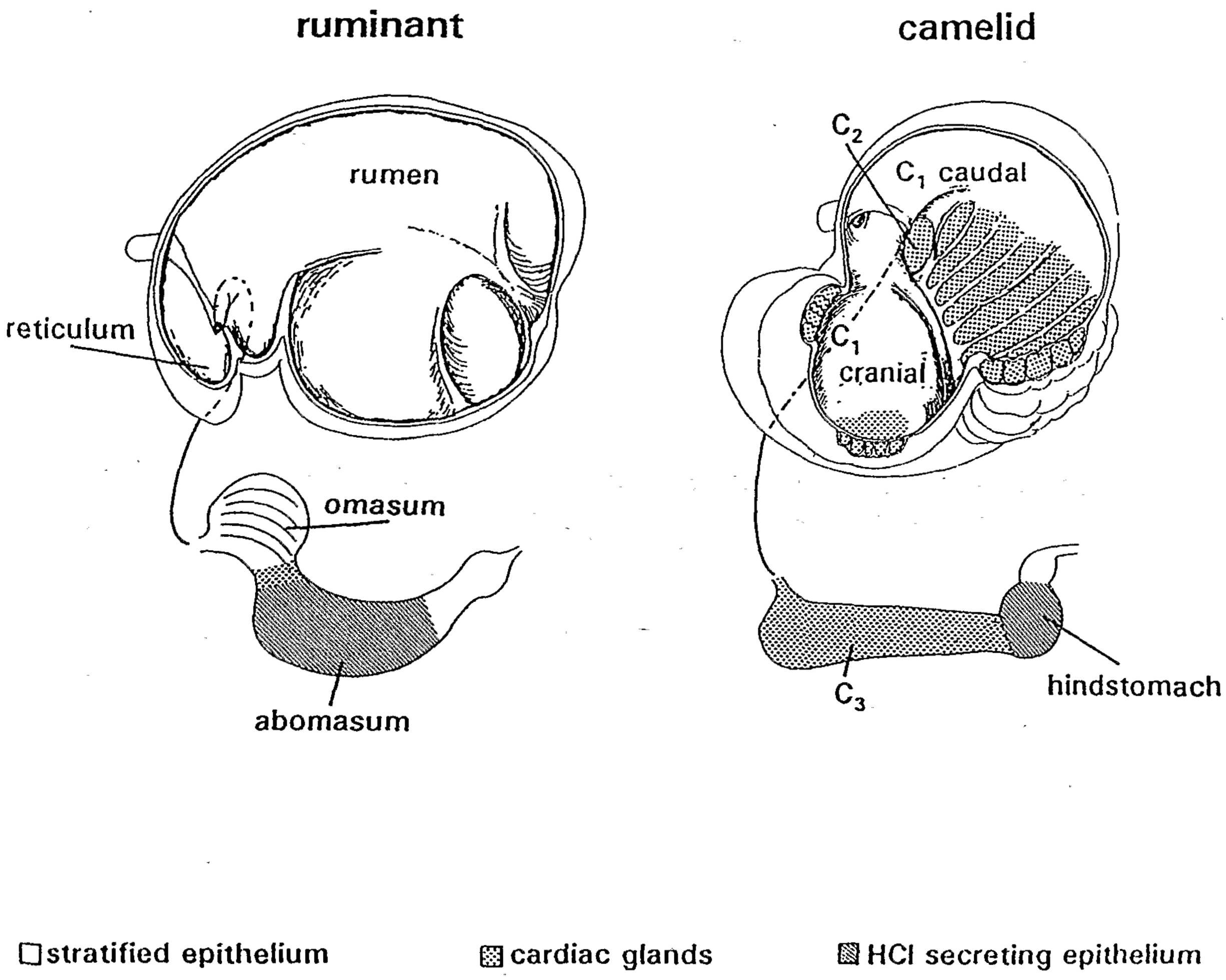

Fig. 1. Comparison of forestomach compartments in Ruminantia and in Camelidae.

The epithelial cells on the glands are cuboidal and produce two morphologically different types of granules (Fig. 3). One type is of variable diameter (from 300 to 800 nm) and pale content, the other type of granules is small (from 160 to 300 nm) and electron dense. These two types of granules can be located either separately in different cells or together in the same cell (Fig. 3). Endocrine cells occur mainly at the base of the glands. Moving cells, especially eosinophilic granulocytes, can be often seen intraepithelially.

Forestomach motility, rumination and eructation

Motility events related to the mixing of forestomach contents. The passage of digesta from the forestomach, rumination and eructation are well known in ruminants. In ruminants, two contraction sequences are generally differentiated. The primary cycle is initiated by a double reticular contraction, during which the digesta passes through the reticular-omasal orifice followed by a contraction of the cranial, dorsal and ventral sac of the rumen. This contraction sequence leads to an effective mixing of the forestomach contents. The secondary cycle starts with a contraction of the rumen dorsal sac, during which the eructation occurs followed by a contraction of the ventral sac.

Fig. 2. Glandular mucosa of the ventral region of compartment 1. x 400; bar: 50 µm.

In camels, two basic contraction sequences (A- and B-contractions) have been observed (Heller *et al.*, 1986b; Engelhardt *et al.*, 1992). A-sequences start with a contraction of C2 followed by a contraction of the caudal C1 about 4 sec later. B-sequences begin with a contraction of the cranial C1 followed by C2 and caudal C1. B-sequences last for about 9 sec (Fig. 4). The flow of digesta through the canal between C2 and C3 occurs during contraction of C2. The canal relaxes shortly before each C2 contraction. During eating and rumination forestomach motility is frequent (about 100 A- and B-sequences per hour). During the resting periods long pauses in motility (up to 20 min) may occur.

Rumination in camels, as in ruminants, is initiated by a deep inspiration during which the glottis remains closed. These results in a decline of pressure in the chest part of the oesophagus. After contraction of the cranial C1, contents are sucked into the oesophagus. This is followed by an antiperistaltic wave toward the mouth cavity. Eructation of gas from the forestomach of camels, occurs during a contraction of the caudal C1 during the B-sequence. When eructation occurs, additional short contraction of the dorsal C1 is seen at the end of the caudal C1 contraction. The eructation is accompanied by a pressure increased in the chest part of the oesophagus. Forestomach motility in camels results in an effective mixing of fluid and particles. The direction of digesta movement within compartment 1 and compartment 2 is shown in Fig. 5.

Biochemical aspects of digestion in the forestomach of camelids and ruminants

The basic principles of microbial digestion in the forestomach are similar in both groups. However, certain quantitative aspects may show differences. Two aspects of interest will be mentioned briefly.

Adaptation to low protein diets

When protein contents in feed of camelids is low with sufficient available energy for microbial growth, recycling and use of endogenous urea-N is high. Renal urea excretion is low under these conditions. Ninety to 96% of total urea turnover was recycled into the gastrointestinal tract of llamas compared to 47% under control conditions (Engelhardt *et al.*, 1978; Hinderer, 1978). In camels, a decrease in dietary protein from 13.6 to 6.1% was associated with an increase in urea recycling from 47 to 86% (Emmanuel *et al.*, 1976), increasing to 92% when low-nitrogen desert hay was given (Mousa *et al.*, 1983). Read (1925) and Schmidt-Nielsen *et al.* (1957) demonstrated that pregnant camels on a low protein diet excrete only little urea. The return of urea from blood into the forestomach, is beneficial only under nitrogen shortage conditions. If the recycled urea-N cannot be incorporated into microbial protein, ammonia will be absorbed back into the blood and must be resynthesized into urea. To prevent this futile circulation of urea, it would be advantageous to regulate the amount of urea-N recycled according to the rate of microbial utilization of urea-N in the forestomach. In experiments with llamas, utilization of urea-N was highest on a low protein, isocaloric diet (78%) compared to 10% on a control diet that approximated maintenance requirements (Engelhardt, 1978; Hinderer, 1978). The mechanisms involved in the control of urea recycling are not well understood.

Fig. 3. Base of a tubular gland in the ventral region of compartment 1. The apical region of the cells is filled by rather large granules with pale contest. This type of granule is at place intermingled with another, small and electron dense (arrows). EC: endocrine cell. x 6000; bar: 1 µm.

Short-chain fatty acids (SCFA)

The total concentrations of SCFA in camels were 40-90% higher than in ruminants

(Fig. 6) (Lechner-Doll *et al.*, 1991b). Differences in feeding behaviour of camels, cattle, sheep and goats (Rutagwenda *et al.*, 1990a) indicated considerable differences in microbial activity in the forestomach. Concentrations of SCFA showed only small seasonal variations. No differences were found between sheep and goats, although goats selected a diet of significantly higher digestibility in the dry season than sheep (Lechner-Doll *et al.*, 1991b). The fluid volumes and flow rates as well as acetate concentrations, pools, outflow and production rates in the forestomach of camels are summarized in Table 1. In this Table green season and an extreme dry situation are compared. An almost three fold increase in acetate production rate was measured in the green season compared to the dry season. The absorption of acetate from the forestomach increased correspondingly. The acetate concentration in the forestomach fluid, on the other hand, did not differ significantly. This indicates that acetate concentrations do not reflect the considerable higher SCFA production in the green season.

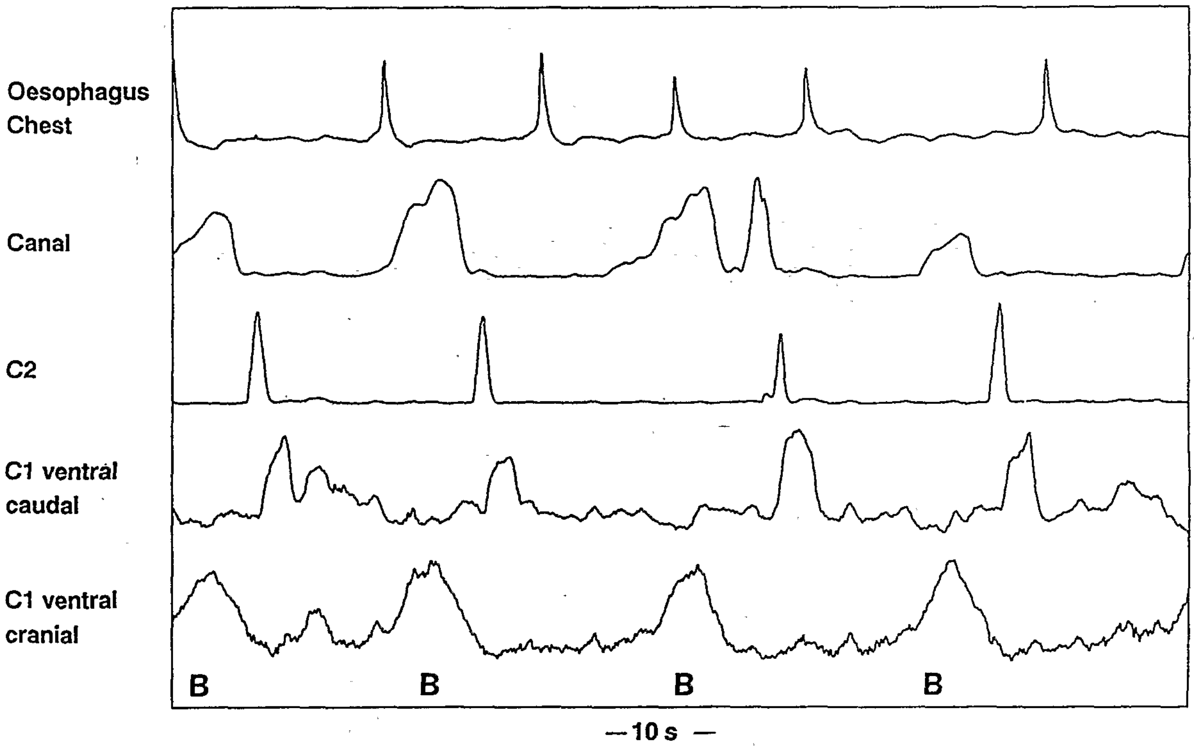

Fig. 4. Pressure recordings in the forestomach and in the oesophagus of a camel. Four B-sequences (C1 cranial, canal, C2, C1 caudal) are shown.

The flow rates of fluid from the forestomach, relative to body weight, did not differ between camels and ruminants (Lechner-Doll *et al.*, 1990). Turnover of fluid (as a percentage of fluid volume per hour leaving the forestomach) was faster in the green than in the dry season in all species, and higher in camels than in other species (Table 2). This may contribute to the low differences in SCFA concentrations between seasons, and may mask the higher production of SCFA expected during the green season. Different fluid turnover rates also make inter-species comparison difficult.

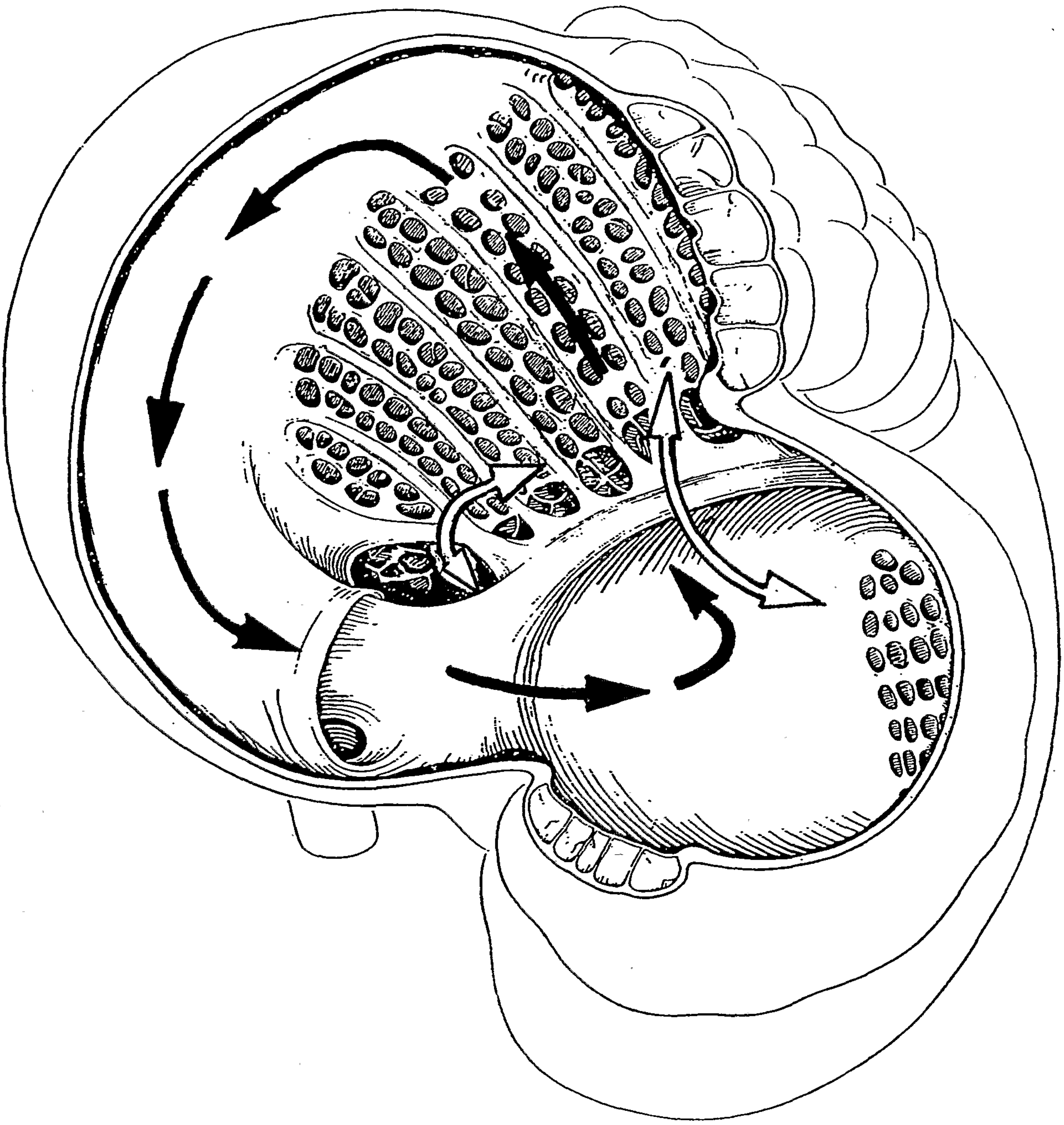

Fig. 5. Digesta movements in the forestomach. Black arrows: slow circulation of the solid digesta; open arrows: exchange of fluid and small particles between the ventral region of C1 and between C2 and caudal C1.

In conclusion, concentrations of SCFA in the fermentation chambers do not reflect production rates. Species differences and variations in dilution rates, rumen fluid volume and absorption rates influence SCFA concentrations more than production rate.

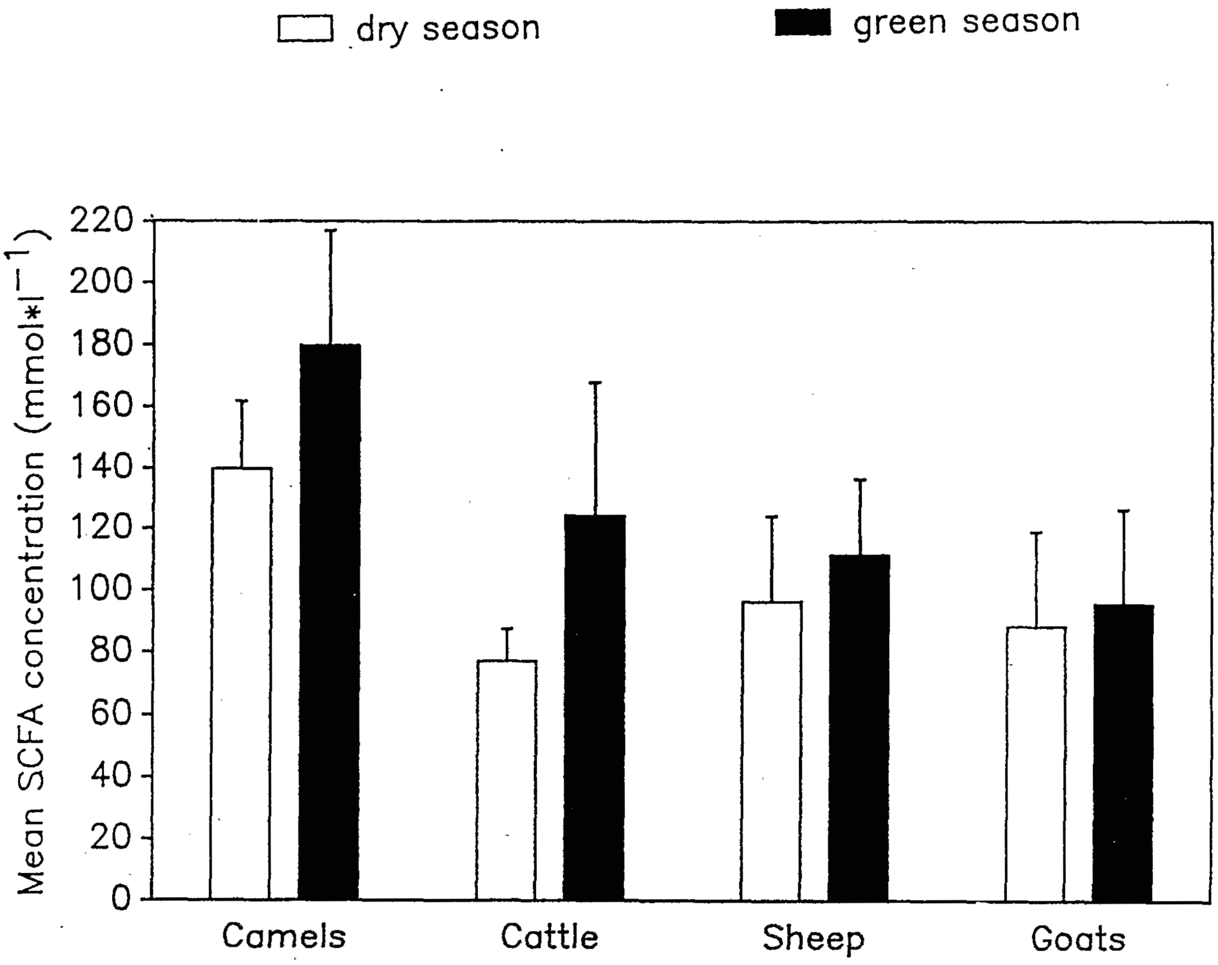

Fig. 6. Concentration of short-chain fatty acids in forestomach fluid of camels, cattle, sheep and goats grazing on a thornbush savannah in Northern Kenya.

Table 1. Fluid volumes, flow rates of fluid, acetate concentrations, acetate pools, outflow rates and production rates in $C_{1/2}$; the camels were weighing 420-515 kg in the green and 450-560 kg in the dry season about 1 year later (from Höller *et al.*, 1989; Lechner-Doll *et al.*, 1991b)

	Green season	Dry season
Fluid volume (l)	38.9 ± 2.1	39.8 ± 2.0
Flow rate of fluid (l h^{-1})	6.1 ± 0.7	3.7 ± 0.8
Acetate concentration (mmol l^{-1})	122.0 ± 6.2	111.4 ± 1.0
Acetate pool (mol)	4.74 ± 0.37	4.48 ± 0.37
Acetate outflow rate (mmol h^{-1})	743 ± 90	415 ± 82
Acetate production rate (mmol h^{-1})	2234 ± 722	816 ± 178

Mechanisms for adaption of camelids and ruminants to harsh grazing conditions

We shall discuss, in this respect, two aspects: (i) adaptation on a heterogenous thornbush savannah; and (ii) adaptation to feeding conditions where no selection of higher quality feed plants are possible.

Table 2. Turnover of forestomach fluid in the dry and in the green season (from Lechner-Doll *et al.*, 1991b)

	Season	Camels	Cattle	Sheep	Goats
Fluid turnover (% of fluid volume h^{-1})	Dry	9.6	6.9	6.2	6.8
	Green	13.6	10.8	10.8	9.4

On a thornbush savannah we have estimated the feeding behaviour of camels, cattle, sheep, goats and donkeys. In parallel, the dry matter disappearance from nylon-bags was estimated for the plants eaten by the various animals. From this dry matter disappearance rates we differentiated between poor quality, medium quality, and high quality feed (Rutagwenda *et al.*, 1990b). Fig. 7 shows the estimated percentage of plants (monocotyledons or dicotyledons) respectively low, medium and high quality plants during the dry and the green season. During the green season, cattle selected 40-50% of poor and medium quality plants which were almost exclusively monocotyledons. Camels, on the other hand, did feed 50% of their feeding time on good and 50% on medium quality plants, exclusively dicotyledons. Goats, like camels, were able to select good and medium quality feed. Sheep were somewhere intermediate between cattle and camels. During the dry season, cattle depended on poor quality monocotyledons more than 80%, 20% were of medium quality (mainly monocotyledons). Camels and also goats selected 80-90% good or medium quality dicotyledons.

This indicates that the ability to select high quality feed is an important strategy of camels and goats in order to adapt to the dry season.

Adaptation strategies when only poor quality feed is available, have to be different. Camels are also successfully kept on grassland where the possibility to select high quality feed is very restricted. Table 3 gives an overview of the seasonal changes of some characteristics of the diet selected on such a grassland. Under these conditions, camels may be confronted exclusively with slowly digestible fibrous material. The camels are able to increase their forestomach volume considerably and, thereby, achieve a much longer retention time of feed particles in their forestomach (Fig. 8). This prolongation of the microbial digestion leads to an improvement of the slow utilization of fibrous material (Lechner-Doll *et al.*, 1991a).

Camels, in contrast to most ruminant species, are able to take advantages of both strategies of adaptation - selective feed intake if there is a choice to select, and utilization of slowly digestible cell wall constituents if no feed of better quality is available.

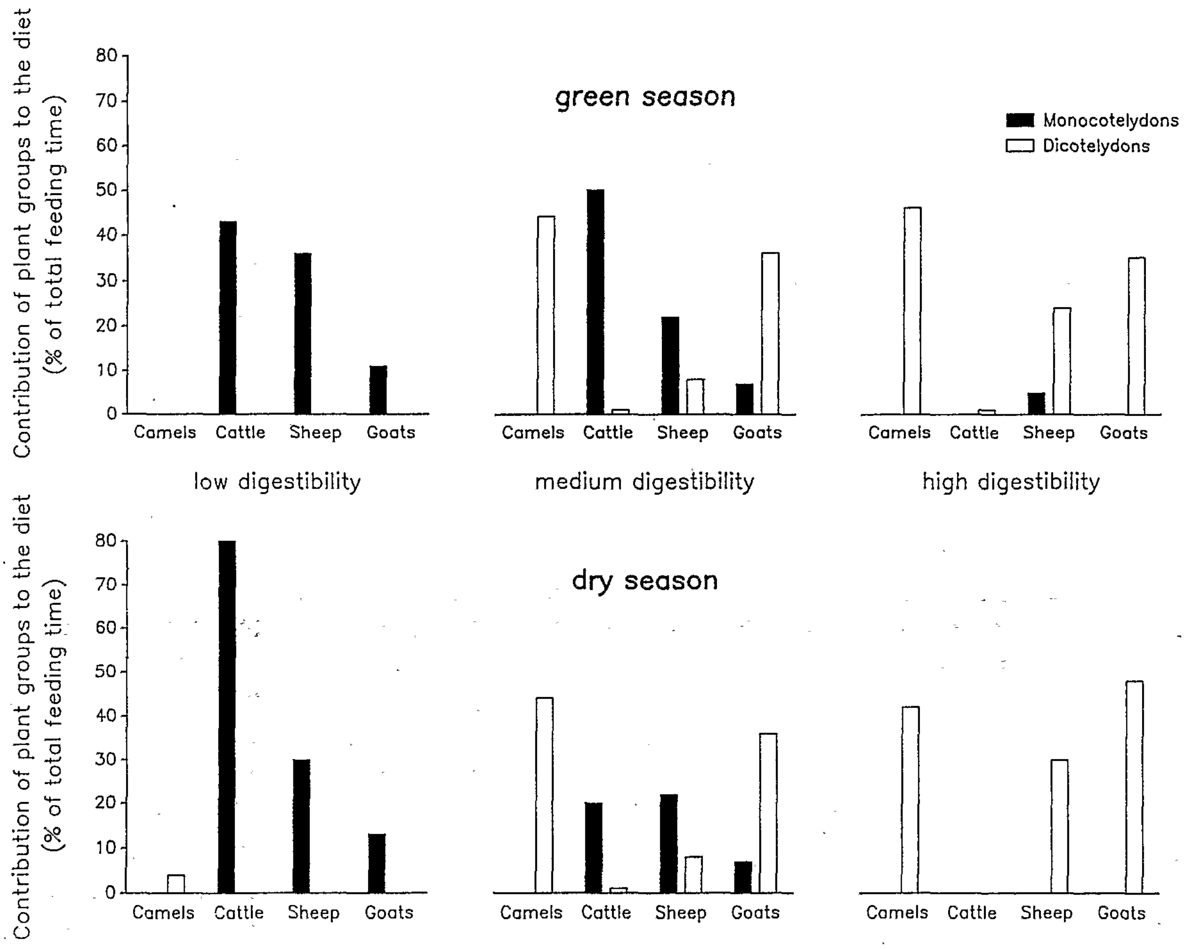

Fig. 7. Contribution of plant groups to the diet selected by camels and ruminants from a thornbush savannah. Plants were grouped into low, medium and high digestibility.

Table 3. Characteristics of the diet selected by camels from the Butana grassland (Sudan) (Abbas, unpublished)

	Dry season	Green season
Dicotyledons in the diet (% TFT)	9.7	80.6
Monocotyledons in the diet (% TFT)	90.3	19.4
Mean ME of diet (MJ per kg of DM)	5.2	8.6
Mean pot. digestibility (% of DM)	58.1	77.6

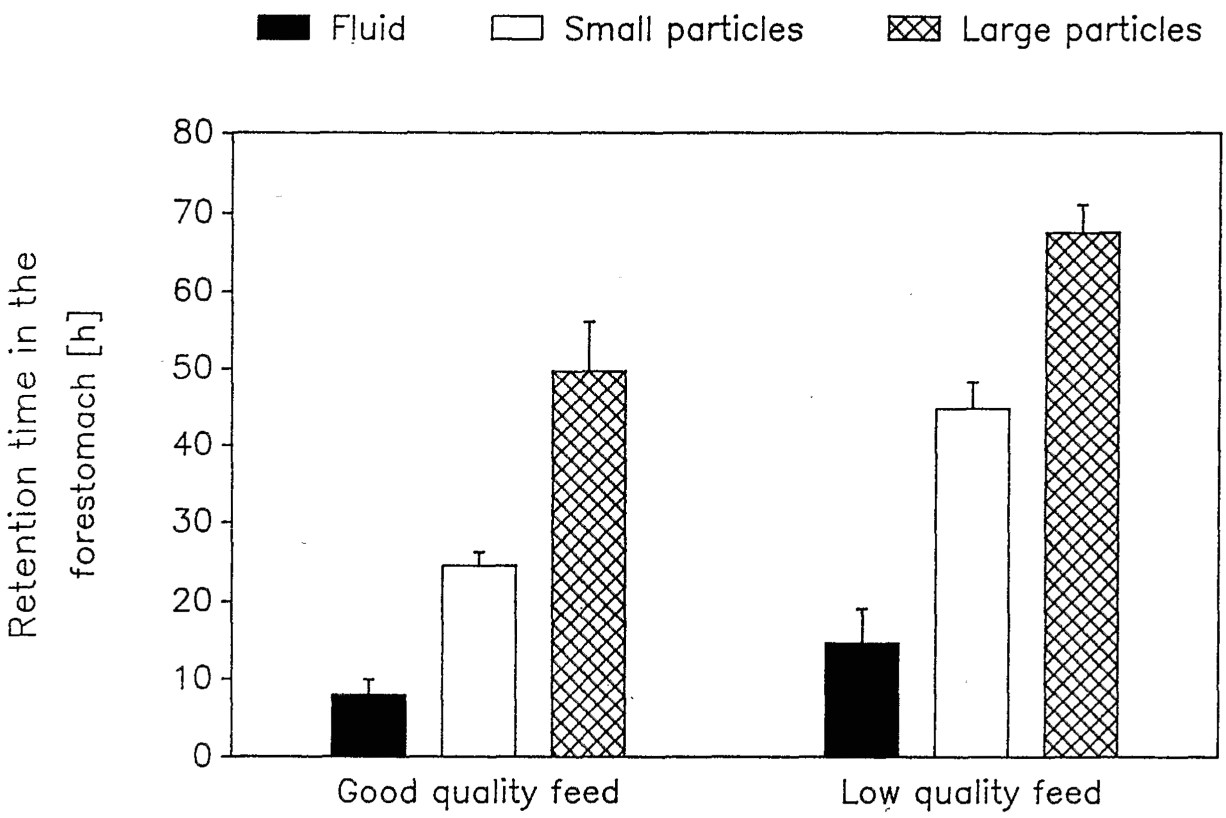

Fig. 8. Retention time of fluid and particles in the forestomach compartments 1 and 2 of camels grazing a green season pasture and fed indoors a fibrous diet *ad libitum* (Heller *et al.*, 1986a).

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