

Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system***

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Summary. A review is made of the ruminant digestive system in its morphophysiological variations and adaptations relating to foraging behaviour, digestive physiology, to interactions between plants and ruminants and to geographic and climatic diversity of ruminants' ecological niches. Evidence is provided for evolutionary trends from an extreme selectivity mainly for plant cell contents and dependence upon a fractionated fore- and hindgut fermentation, to an unselective intake of bulk roughage subjected to an efficient plant cell wall fermentation, mainly in the forestomachs. The review is based on detailed comparative morphological studies of all portions of the digestive system of 65 ruminant species from four continents. Their results are related to physiological evidence and to the classification of all extant ruminants into a flexible system of three overlapping morphophysiological feeding types: concentrate selectors (40%), grass and roughage eaters (25%) and intermediate, opportunistic, mixed feeders (35%). Several examples are discussed how ruminants of different feeding types are gaining ecological advantage and it is concluded that ruminants have achieved high levels of digestive efficiency at each evolutionary stage, (including well-documented seasonal adaptations of the digestive system) and that ruminant evolution is still going on. Deductions made from the few domesticated ruminant species may have, in the past, biased scientific evaluation of the free-ranging species' ecology. The main threat to a continuous ruminant evolution and diversity appears to be man's neglect for essential ecological interactions between wild ruminants and their specific habitats, which he alters or destroys.

Key words: Wild ruminants – Digestive system – Morphophysiological adaptation Evolutionary trends Plant-herbivore interactions

Our growing scientific knowledge of the nutritional physiology of ruminants is documented in a vast number of publications annually, and every five years more than 600 researchers from all over the world meet in a different place to review and present new results. They discuss highly specialised aspects of physiology, metabolism, nutrition, biochemistry and digestive problems of these remarkable mammals – yet very few of them or of the thousands of others who deal scientifically with ruminants appear to be concerned that almost all of their results, their methods and models are based on merely two out of 150 species of extant ruminants. These two are sheep and cattle. Much fewer physiological and nutritional data available refer to the goat and far fewer still to the Asiatic water buffalo. Compared to all this, experimental data on wild African bovids, Eurasian cervids or American deer (let alone such oddities as the pronghorn "antelope", the giraffe or the musk ox – all of which are ruminants) cannot even be regarded as minimal. However, each new study on ruminants other than cattle, sheep and goats shakes the established ruminant image. It is different, though similar.

Ruminants are animals important to man. Some species are bioindicators of the first order in polluted human environments. More species are living barometers of man's inability to understand and handle ecological interactions and most, if not all ruminant species can benefit nutritionally from what man cannot digest.

Because they convert apparently indigestible carbohydrates and chemically trapped or protected proteins into nutritious and useful products, they deserve more than one approach. Ruminants are late-comers in evolution. Their stomach is a phylogenetic peak of complexity, not only compared with our own digestive tract.

But it is wrong to define ruminants simply as specialised fermentation machines which break down cellulose after chewing the cud.

Their digestive physiology is not based on an "all or nothing" principle and none of them is "primitive", although embryological evidence strongly suggests that roe deer or white-tailed deer, dik-diks or muntjac, kudu or moose are "older", earlier and still inefficient in breaking down cellulose. It will be shown, that ruminant evolution in the light of today's 150 living species is certainly "a bush, not a ladder" (Gould 1986). It has produced a fascinating array of animal forms ranging from 3 kg to over 1000

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**Dedicated to Professor Dr. Dr. h.c. Dietrich Starck on the occasion of his 80th birthday

Abbreviations: *bw* body weight; *CS* concentrate selector; *DFC* distal fermentation chamber (distended caecocolon); *GR* grass and roughage eater; *IM* intermediate (mixed) feeder; *PFC* proximal fermentation chamber (ruminoreticulum/forestomachs); *RR* Ruminoreticulum; *SCFA* Short-chain fatty acids (acetic, butyric, propionic acid set free by rumen bacteria); *SE* Surface enlargement (absorptive mucosa)

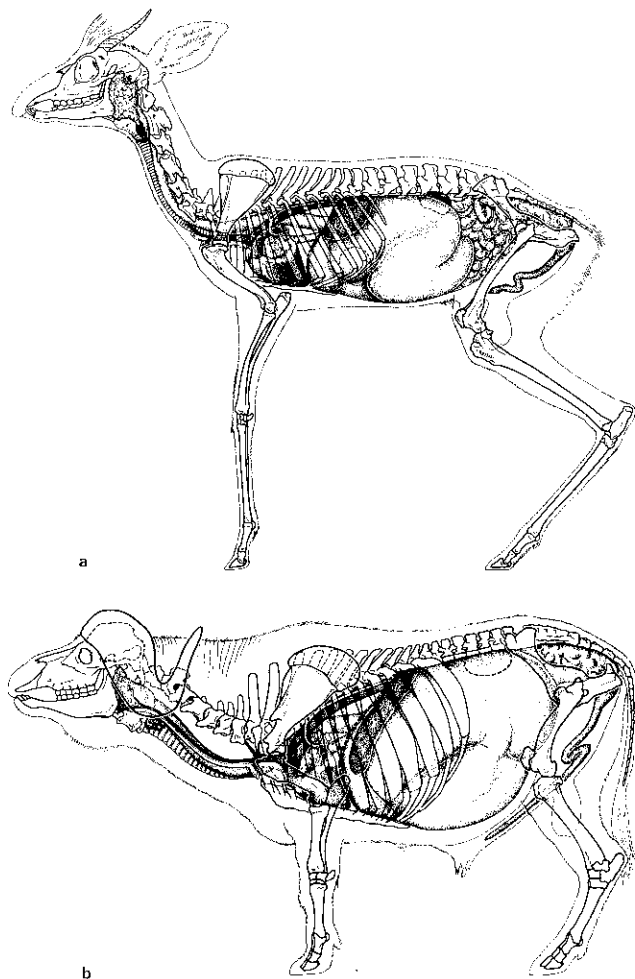


Fig. 1a, b. Comparison of ruminant extremes scaled to equal size irrespective of weight: Günther's dik-dik (a), 3–4 kg, early evolved concentrate selector; African buffalo (b), 800–1000 kg, late evolved grass and roughage eater; note relative dimensions of forestomach (from Hofmann 1973, redrawn)

(Fig. 1); living in torrid climates without surface water intake; surviving on ice and snow-covered high mountains; many are very stationary, even territorial and aggressive, others form spectacular herds and migrate over hundreds of miles (Fig. 5). Several species will simply die (and have died again and again in captivity, including zoos) when they are fed only what domestic ruminants are content with. Yet, as individuals they are highly adaptable as far as climate, habitat or even food plant communities are concerned, as translocations have shown.

Behaviour, climate, habitat pressure and ecological opportunity have influenced remarkable ruminant diversity in which all of them have retained two important genetic features:

1. a complicated morphophysiological master plan of the ruminant digestive system which permits astounding variations resulting in a series of regressive and progressive changes along the alimentary canal;
2. an incredible flexibility of morphophysiological adaptations, which extends to the level of the individual animal, i.e. the versatility of the individual as it adapts to changing diet and to changing nutrient requirements encompassing a good portion (not all!) of evolutionary history

as well as it includes cyclic, seasonal adaptations (photo-periodic or climatic) to changes of forage availability.

Thus ruminants cannot be understood if our only source of information (and deductive generalisation) are the four domesticated species, or wild species treated like them.

My starting point as a comparative anatomist was the beauty and the richness of *forms* in harmony with highly complicated *functions*. After investigating so many ruminant species in detail from macrolevel to ultrastructure, one cannot help being impressed by the fact that evolutionary forces obviously have achieved remarkable shifts and changes of digestive *functions and efficiency* in parallel array, yet the basic ruminant *structural design* has been retained in all its adaptive modifications. On what evidence are such ideas based?

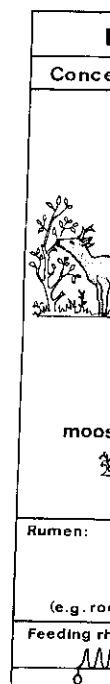
Selectivity is a key to ruminant adaptation and survival

The East Africa where I worked continuously for a decade is a centre of ruminant/bovid evolution (35 wild species!). Europeans are used to a comparatively poor spectrum of only nine of which six species predominantly eat grass (Fig. 2). The ubiquitous roe deer (25–30 kg) was long known by hunters to “sample forbs, flowers and leaves like a botanist”, but hardly ever grass. Very choosy, obviously. So were, according to Kenya hunters and farmers, the tiny dikdiks (3–5 kg), the bushbuck (35–50 kg), the bipedally browsing renyuk (30–45 kg) and the greater and lesser kudu (180–300 and 80–100 kg). Little observation was required to confirm the few early references that not only these “browsers”, but most of the “grazers” were also “choosy”, quite unlike cattle. Several species, like the huge gregarious eland antelope (400–600 kg) or Grant's and Thomson's gazelles (40–70 and 15–25 kg) and especially the widely distributed impala (40–70 kg) were obviously able to *switch* from “browsing” to “grazing” according to season or nomadic overgrazing. The savannah plains nourished up to 10 different “grazers” in large herds *without* any detrimental effect comparable to overstocking/overgrazing from cattle, sheep (and goat). First anatomical studies, accompanied by botanical analyses of forage plants and rumen contents, focusing initially on the complicated quadrilocular *stomach* (three compartments of the forestomach and one glandular portion) very soon revealed a very close structure-function-food relationship which led us to propose *three ruminant feeding types* (Hofmann and Stewart 1972) and to declare the conventional terms “grazer” and “browser” insufficient if not misleading for the entire suborder *Ruminantia* (Fig. 3).

Over the past 20 years, detailed comparative studies of *all* portions of the digestive system from lips to anus of so far – 65 ruminant species from four continents, carried out by myself, several co-workers and eight graduate students have substantiated and extended earlier observations and functional hypotheses (Hofmann 1968, 1973).

Discussion and co-operation with interested comparative physiologists and nutritionists has resulted in establishing a morphophysiological history of ruminant evolution which now permits us to place any existing (and several extinct) ruminant species within a *flexible system of overlapping ruminant feeding types*. For their majority, *selectivity* is the key factor in several strategies of adaptation to changing forage quality and availability.

It sounds logical that a dikdik in the semi-arid African



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In discussing the system, the author as a biologist is forced to functional analysis during...

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EUROPE: RUMINANT FEEDING TYPES

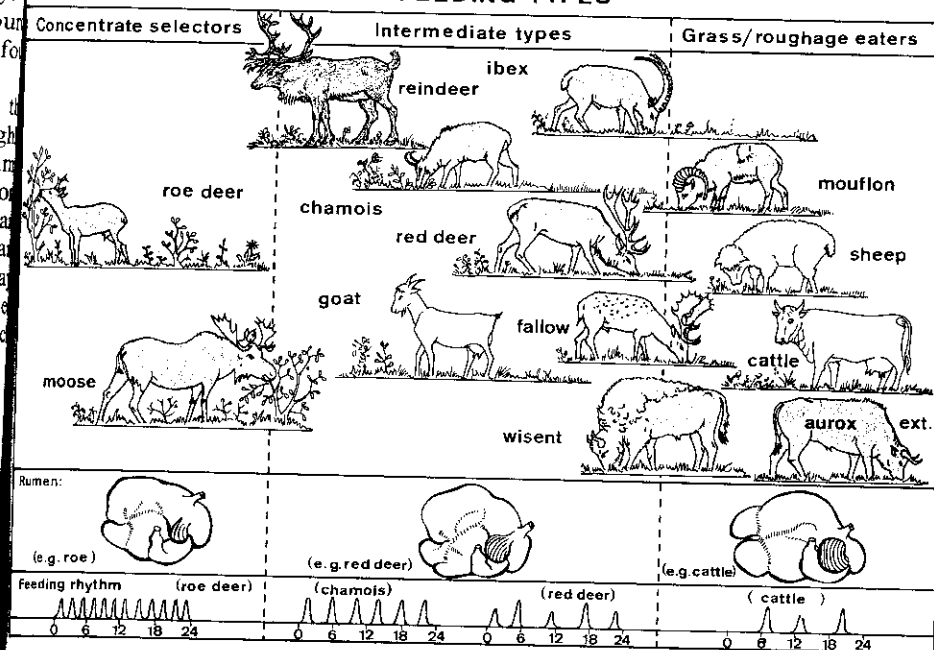


Fig. 2. European ruminants according to feeding type (shaded), domesticated species white; the further to the right, the better a species' adaptation to digest plant cell wall/fibre in its RR; the more to the left, the more plant cell contents are selected for. Note changes in diurnal feeding frequency (from Hofmann 1976, redrawn)

bush savannah has developed a survival strategy different from that of a roe deer in the Bavarian Alps. But it can be shown that similar functional events and essential seasonal adaptations have induced *homologous* structural variations of the digestive tract of tropical as well as of Northern species. In this, the evolutionary pathway of ruminants can be backtracked to what I believe are truly *formative* elements of the "typical" ruminant system.

In discussing the design of the mammalian respiratory system, Taylor and Weibel (1981) introduced *symmorphosis* as a biological principle which states that "no more structure is formed and maintained than is required to satisfy functional needs; this is achieved by regulating morphogenesis during growth and during maintenance of structures".

This is certainly pertinent to the ruminant digestive system; but due to its *multiple* functions and its essential adoption of *microorganisms* as cellulolytic enzyme producers, it presents a much more exciting and multifaceted story.

Of approximately 150 ruminant (I refrain from taxonomic discussions on species/subspecies status) including six domesticated species, only about 25% fall into the feeding type "grass and roughage eaters" (GR) which are characterized on free range by adaptations to forage rich in *plant cell wall*, i.e. structural carbohydrates (e.g. cellulose), in short: fibrous food. Cattle, sheep, water buffalo and banteng belong to this group. The GR circadian rhythm is distinguished by a few long feeding periods, followed by a few long ruminating and resting periods.

More than 40% of the extant ruminant species, however, are equipped with a digestive system far less suited to optimise plant fibre digestion. They are perfectly adapted to processing easily digestible forage rich in accessible *plant cell contents* (solubles). Their extremely pronounced selective talent is based primarily on olfactory cues. Since they thrive on natural "high-quality" diets, I have termed this group "concentrate selectors" (CS).

Their typical morphophysiological adaptation is manifested in several structural characteristics along the digestive


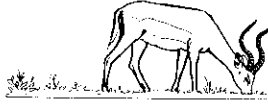
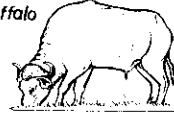




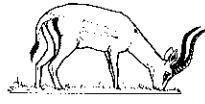

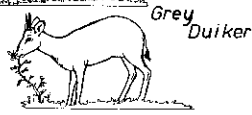
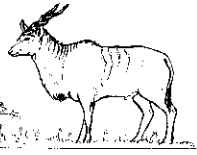




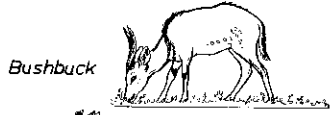
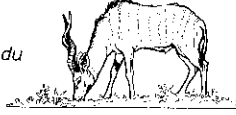
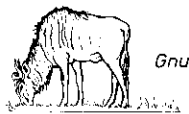
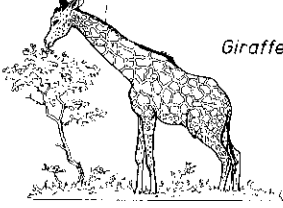
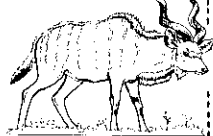


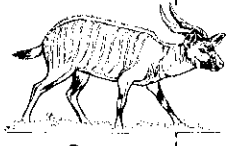

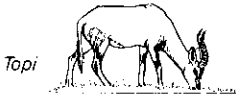
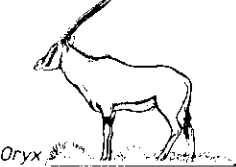
tract. There is *no* domesticated species amongst them. The CS circadian rhythm in the growing season of the vegetation is dictated, as will be reasoned, by *frequently repeated* periods of feeding, usually alternating with short (intermittent) rumination periods.

About 35% of all ruminant species are morphophysiological *intermediate* (IM) between the two formerly mentioned extreme types. All of them practise a marked degree of forage selectivity. They choose a *mixed diet* but avoid fibre as long and as much as possible. Their way of foraging is opportunistic. They show remarkable shortterm or seasonal anatomical adaptations to changes in forage quality, within periods of about two weeks. Like concentrate selectors (CS), these IM ruminants can increase food intake two or three fold when food is plentiful to meet peaks of nutrient requirements corresponding to changes in metabolism. Those controlled by greater seasonal fluctuations of forage quality (examples: impala antelopes in dry or rainy-growing seasons; Eurasian red deer/American wapiti in winter or growing seasons) adjust their productive activities such as lactation, juvenile growth and adult fattening/energy reserve deposits to occur when the pasture is at its best (Kay 1985). When forage plants lignify these animals switch to "browse" or falling fruit and seeds ("autumn mast") and finally reduce metabolism and food intake as they, like CS, cannot digest fibrous forage as well as GR. The domestic goat and red deer (Fig. 4) belong to this IM type.

Modern man, by grain feeding, is ignoring ruminant evolution

There is no doubt, man has domesticated predominantly such ruminant species which can easily, by evolutionary adaptation, utilize fibrous low-quality diets (v. Engelhardt et al. 1985) unfit for human consumption. It appears anti-biological if not immoral that much of to-days ruminant livestock production in affluent countries is based on grain feeding. This unfortunate "counter-evolution" is still af-

I.AFRICA: RUMINANT FEEDING TYPES

CONCENTRATE SELECTORS	INTERMEDIATE TYPES	GRASS / ROUGHAGE EATERS
 <i>Dikdik</i>	 <i>Impala</i>	 <i>African buffalo</i>
 <i>Klipspringer</i>	 <i>Thomson Gazelle</i>	 <i>Uganda Kob</i>
 <i>Suni</i>	 <i>Grant Gazelle</i>	 <i>Bohor Reedbuck</i>
 <i>Grey Duiker</i>	 <i>Eland Antelope</i>	 <i>Waterbuck</i>
 <i>Red Duiker</i>	 <i>Steenbok</i>	 <i>Oribi</i>
 <i>Bushbuck</i>	 <i>Lesser Kudu</i>	 <i>Gnu</i>
 <i>Giraffe</i>	 <i>Greater Kudu</i>	 <i>Kongoni</i>
 <i>Gerenuk</i>	 <i>Bongo</i>	 <i>Mountain Reedbuck</i>
		 <i>Topi</i>
		 <i>Oryx</i>

fecting even the feeding management of zoos and wildlife reserves. In the majority groups of CS and IM (75% of all *Ruminantia*), however, there are a number of species with a considerable potential for a less intensive but ecologically beneficial utilisation by man especially on marginal land.

Before going into some details of how ecology and physiology are reflected in the structure of ruminant digestive systems, I should like to remind the reader of some basic

"ruminant problems". Such problems, almost inevitably refer to the domestic GR sheep and cattle. They have been unfortunately, applied to other ruminants and thus have also biased comparative research.

When only microbial fermentation rates and the ensuing host-beneficial production of short-chain fatty acids (SCFA) are considered, metabolic laws can explain the smaller ruminants will have to balance their comparatively higher energy requirements by eating more food of a high



Fig. 4. Red deer feeder, with topography. sum; Re = ret

nutritional deer, most are CS, but and the Asia quite a few large CS (e 180–1000 kg of cellulose weight (Fig.



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Fig. 3. African ruminants investigated according to feeding type (see legend of Fig. 2); from Hofman 1973

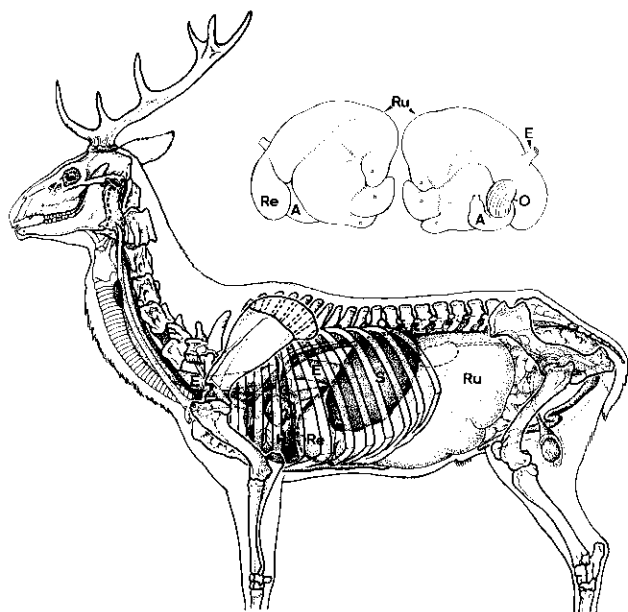


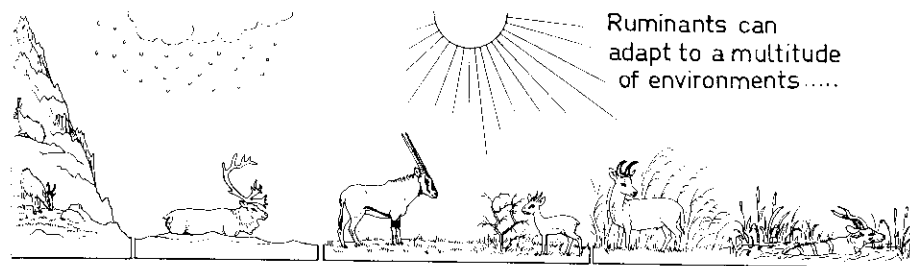
Fig. 4. Red deer as example of an intermediate, opportunistic mixed feeder, with stomach in situ and isolated. *Cervus elaphus*. Organ topography. A=abomasum; E=esophagus; H=heart; O=omasum; Re=reticulum; Ru=rumen; S=spleen

nutritional value (Prins et al. 1984; Van Soest 1982). Indeed, most *smaller* ruminants under 40 kg body weight (bw) are CS, but some, such as the small African oribi (12–20 kg) and the Asiatic blackbuck (30–40 kg) are selective GR and quite a few are IM. More important: there are several *very large* CS (e.g. greater kudu, bongo, moose, giraffe, i.e. 180–1000 kg). Prins et al. (1984) have shown that the rate of cellulose digestion is lowest in CS, *irrespective* of body weight (Fig. 5).

Ruminants being anaerobic forestomach fermenters, have the principal handicap that "energy is in excess but protein is limiting" (Hungate 1985) but they can utilize cellulose, hemicellulose and pectin. It is considered uneconomic, to feed high concentrations of protein to (domestic) ruminants, as it is either lost to the ruminal microbes or expelled unused ("ruminal escape"). On the other hand, it has been shown that CS of small body size are unable to cover their energy requirements sufficiently from SCFA produced in the ruminoreticulum. There is evidence to suggest that *none* of the CS and IM can do so; perhaps not even the smaller GR, and yet: they all survive ...

A further handicap (?) of ruminants: the size of their forestomach fermentation chamber (rumen+reticulum), the flow rate of digesta and food retention time in relation to microbial activity, especially that of cellulolytic bacteria, in the rumen. For cellulolysis, there must be sufficient time for the delay of ingesta, i.e. the ruminoreticulum must be voluminous. Ruminants chew the cud for longer or shorter periods, depending on feeding habits in order to *reduce plant particle size* which, in turn, enables ruminal microbes to gain access to structural (plant cell wall) carbohydrates. But there is a *selective retention* of feed particles (in the GR sheep down to 0.5 mm!) which *limits new food intake*. A bottleneck opening between the rumino-reticulum and the third forestomach, i.e. the laminated *omasum*, appears to control the gradual outflow. In addition, the ruminoreticular fermentation system is based on a "steady state" (pH near neutral point) depending on the balance between SCFA production, continuous buffer – carbonate *saliva influx* and SCFA *absorption* in its acid form via papillary surface enlargements of the ruminal lining (nonglandular mucosa) defined as "dilution rate".

Thus, the common line of thinking centres on a forestomach fermentation system, for which *soluble* carbohydrates "rarely form a major constituent of ruminant diets, but



Extremes of habitat, climate, seasons and change of fibre content

Snow cover – low temperature vertical + horizontal migration • desert – heat load lack of surface water • swampy reed – subaquatic shoots

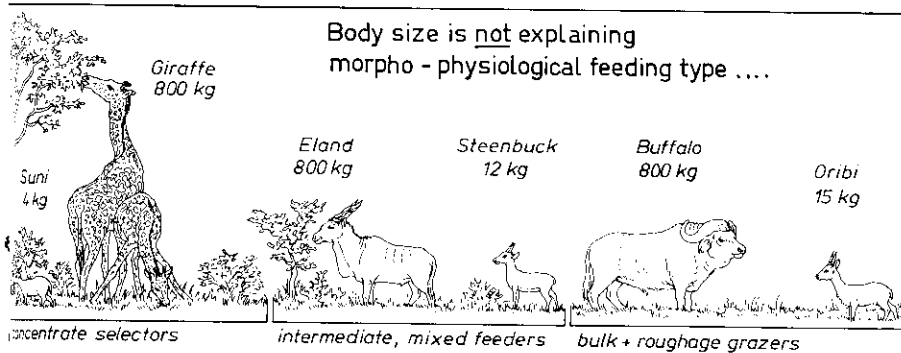


Fig. 5. Ecological diversity and size differences of ruminants have influenced their adaptive range

they do form an important carbohydrate source in fresh grass" (Sutton 1986) and in which valuable nutrients, especially proteins in excess of requirements for microbial growth should be protected from loss (i.e. from degradation during ruminal fermentation) by management methods. In this context, Ørskov (1986) refers to the *ventricular groove* which by-passes the rumenoreticulum in the milk-sucking phase. Although it is *not* regressing (Hofmann 1969) but highly developed in all *adult* ruminants, Ørskov et al. (1970) have shown that, in domestic ruminants, its by-pass function can be retained as a conditioned reflex only if the animal is trained from birth. But, carbohydrates which can be digested *post-ruminally* are "utilized more efficiently since the inevitable rumen fermentation losses in heat and methane production are avoided" (Ørskov 1986). In cattle feeding, *chemical* protection of feeds using formaldehyde and tannin is practiced widely on the principle that the protection achieved at *rumen* pH (6–7) is reversed at the low pH levels encountered in the hydrochloric acid secreting *abomasum*. Does all this apply to our 75% "alternative" ruminants of the CS and IM feeding types?

Cattle are not superior, they are different: all shoots of the "bush" are efficient

The digestion of soft, juicy dicot plant material must have been of primary and long-lasting importance for the evolving ruminants, before and when the grasses spread in the miocene. However, in many foliolate plants they encountered, besides resistant cell walls, *chemical repellents*, e.g. phenolic compounds, tannins etc. which were originally defending the plant against phylogenetically older insects (Cooper and Owen-Smith 1985); an important plant-herbivore-system interaction. As these compounds affect the fibre-splitting microbial key enzyme *cellulase* negatively if eaten excessively and consequently reduce the spectrum of nutritious forage, these plant signals must have induced early ruminant reactions. Only when *grass* became the main food resource, such adaptations were rendered redundant: most grasses lack secondary compounds.

Extant CS (and many IM), however, have retained these features: in their specific habitats they prefer and utilise most of the *plant cell contents* of their chosen dicot forage plants, which are usually higher in protein than monocots. They do so *in addition* to the phylogenetically "new" benefit of a forestomach fermentation of *cell wall* carbohydrates, although this is as yet exceeded by *amylolytic* fermentation. Hoppe et al. (1983) were able to show that the small dikdik and suni antelopes select food with high amounts of plant cell contents but very low in fibre. Their relatively *small* rumen, after *frequent* feeding and rumination, shows a ratio of amylolytic: cellulolytic activity as 5:1 and high fermentation rates, *fast absorption* and a fast turnover. Unlike cattle or sheep, they harbour hardly any *protozoa*: their ingesta move faster than these can reproduce. Only 40–60% of the cellulose, which they essentially engulf, is digested: there *must* be other pathways of digestion, since undigested cell wall components are passed out of the rumenoreticulum *quickly*. Obviously, no bottleneck effect, no miniature sheep. Is this a special case for extremely low body weight? Roe deer (CS) weigh about six times more than a dikdik and white-tailed deer 10–15 times more; they still function much more like a dikdik and not so much like sheep.

As far as *structure* is concerned, CS are clearly *different*

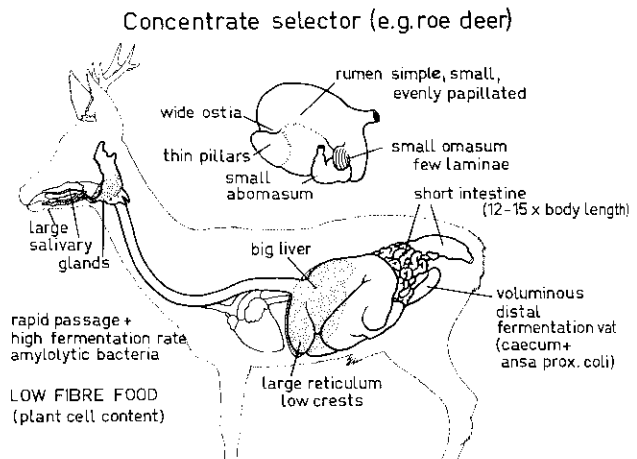


Fig. 6. Type example of a concentrate selector (roe deer) showing morphophysiological characteristics common to all ruminants belonging to this feeding type: from Hofmann 1985

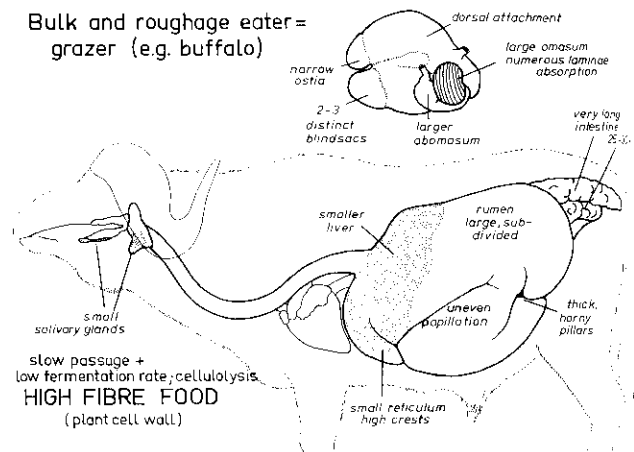


Fig. 7. Type example of a grass and roughage eater (buffalo); see legend of Fig. 6: from Hofmann 1985

from GR in *all* physiologically important portions of their digestive tract (Figs. 6 and 7).

The following descriptions are strictly comparative and based on a wealth of statistically tested research results which have confirmed that *feeding ecology* and *diet* is the *primary* adaptive factor in ruminant evolution while body weight/size is secondary. This *does* permit one to compare species ranging from 3–1000 kg. Most of the supporting data cannot be included here. They are contained in two earlier monographs (Hofmann 1969, 1973), several recent reviews (Hofmann 1985, 1988a, b) and in a new comprehensive monograph (Hofmann, unpublished work).

When we have recognized *selectivity* as a key factor, we have first to consider the *prehensile organs* and how they became adapted, in the three feeding types, to food intake. These are *lips*, *tongue*, lower *incisor* teeth (the upper ones are missing in all ruminants) and the *dental pad* at the rostral end of the *hard-palate*.

All CS have a relatively larger *mouth* opening, permitting the sideways stripping of twigs or the gnawing of inflorescences and fruit, while GR have shorter (rigid) *lips* and a small mouth opening. This does not contradict Jamies (1986) findings of significant differences in the incisor ro-

CONCENTRATE SELECTORS

Roe deer



White-tailed deer



Red Duiker



Red Duiker



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The lips, rough labial adapted to glandular lining of the, icantly thin which select when comp buccal pap cornification

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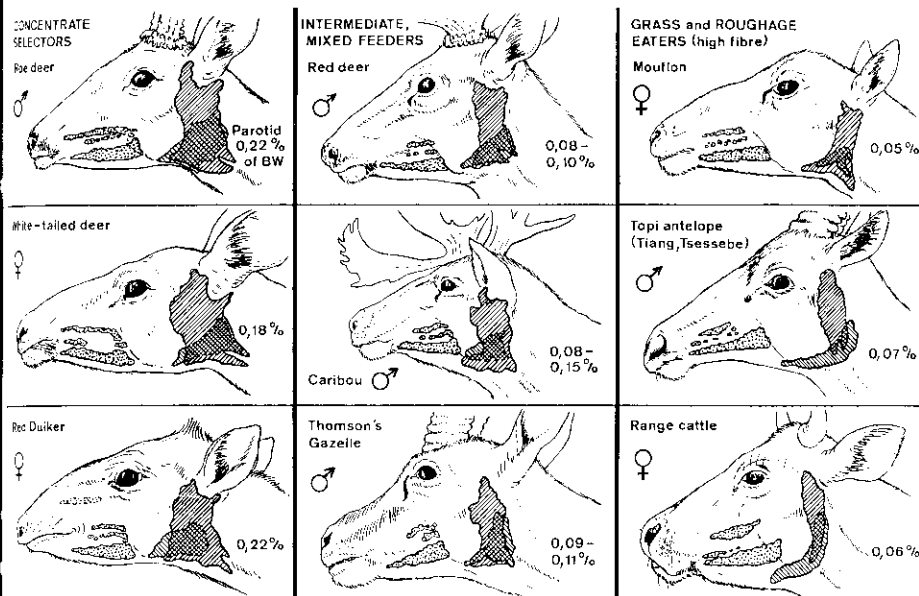


Fig. 8. Comparative topographic representation of the salivary glands (from left to right: buccal, mandibular, parotid) in 9 ruminant species of 3 feeding types and the relative weight of the parotid. All salivary glands (incl. sublingual, not shown) regress with increasing adaptation to plant cell wall digestion, most distinctly the parotid, for functional reasons. From Hofmann (1988)

width of "browsing" and grazing species and the latter group's faster food intake at a time; a smaller mouth opening prevents grass losses during plucking.

The lips of CS (and IM) contain considerably more *serous* labial glands; the latter decrease in species more adapted to grazing. In GR, there are relatively few *mucous* glandular lobules only. The stratified squamous epithelial lining of the mouth cavity also covering the tongue, is significantly *thinner* and *less cornified* in CS and in those IM which select non-fibrous (soft) forage as long as available, when compared with GR. The latter have fewer (more rigid) buccal papillae, i.e. their mouth is properly protected by cornification against grass and roughage.

All ruminant *tongues* are distinguished by a hump, the *torus linguae*. Its pressing interaction with the hard palate may be a functional compensation for the incomplete dentition. According to Schmuck (1985) CS have, in relation to total lingual length, the shortest torus but GR the longest. On the other hand, CS have at c. 33% the longest free-mobile portion of the tongue, GR at c. 28% the shortest. White-tail deer, kudu, muntjac or gerenuk with their short torus make good use of the long mobile tip of their "soft" tongue in cautiously selecting forb and foliage, the extreme being the giraffe. Among GR, cattle, like other bovinæ, and Pere David's deer have an exceptionally short torus and a relatively long tip of their heavily cornified tongue; they are *unselective* grazers, using it for tearing off grass bundles.

Crompton (1987) ascribes to the anterior part of the tongue the fine control of its motor modification which deforms it in response to food stimuli.

The tongue is also the site of taste receptors, and no herbivore group has so many *gustatory papillae* as ruminants, especially the circumvallate of which man has only few. There is an obvious relationship between the number of *taste buds* (receptor organs) in these papillae and feeding behaviour: while CS and IM already show many, GR have c. 50% more which they obviously need to test the constituents of the grass layer for palatability; for them the primary *olfactory* selectivity of the two former groups has become impracticable and uneconomic.

With its functional relationship to the tongue, the *palate* as its counterpart exhibits a feeding type surface pattern, which appears to be related to functional differences in sorting out and transporting either fibrous grass or soft foliage, flowers or fruit and seeds; its more or less papillated rugae direct forage either to be crushed between the cheek teeth or to be passed on to the pharynx.

Salivary glands are indicators of selectivity and dietary niche

In considering the main *salivary glands* (parotid, mandibular, sublingual and ventral buccal, Fig. 8) we are approaching the *preruminal focal point* of multifarious parallel ruminant feeding type evolution. In forestomach fermenters, they principally function as constantly secreting *buffer* producers because ruminal bacteria (especially cellulolytes) ferment and multiply best in fluid suspension ("dilution rate") only around pH 6.5, but these bacteria set SCFA free, which tend to lower this pH value.

When I first observed much bigger parotids in African CS, like gerenuk or kudu, I was content that slowly fermenting roughage eaters like buffalo or sheep could well suffice with "small" glands to keep the steady state in a big ruminoreticulum (RR) with long food retention times and a slow fluid turnover rate, while CS with high fermentation rates and a more rapid flow through a smaller RR (shorter retention) obviously required more buffer to protect them from a detrimental lowering of rumen pH. The total salivary gland weight as a percentage of body weight (on average of all species investigated) is c. 0.36 in CS, 0.26 in IM and only 0.18 in GR. *Parotid* weight of CS, again irrespective of body size, is more than three times that of GR as Kay (1987) recently confirmed. This means, salivary glands have *regressed* as ruminants increased fibre digestion. The question arises, do CS and IM then need so much more saliva for buffering purposes? Because as will be seen, all these selective species also have a much denser, evenly distributed rumen papillation than GR. This results in a greater internal surface enlargement facilitating *faster absorption* of SCFA; hence: little danger of pH depression.

First of all, these bigger glands supply more *diluting*



Fig. 9. Male gerenuk, an extremely selective East African CS, feeding on young acacia leaves. The bipedal position permits cautious plucking with the tongue and lips to avoid excessive release of tannin, the plant's deterrent. Moderate amounts of tannins obviously can be neutralised by the species' serous saliva (very large parotid, see Fig. 8)



Fig. 10. During drought periods, selective CS and IM species (here: female impala) avoid the plentiful lignified sundried indigestible grass and rather bite acacia bushes down to stumps, in spite of their tannin contents

liquid, which reduces retention time (as observed). Secondly, CS produce a much higher proportion of thin, proteinaceous *serous* saliva (all glands open into the mouth cavity) to carry away much of the *soluble* plant cell contents set free by *puncture crushing* of dicots (GR grind fibrous food sideways). There is reason to believe that *some* of these nutrients (e.g. sugars) are absorbed already *in loco*, while more solutes are washed, together with excessive serous saliva, down the *ventricular groove* into the *abomasum*. This would lead to a certain loss of salivary bicarbonate and to CO_2 formation in reaction to the acidic gastric juice. It would, however, initially explain the considerable *surplus of HCl-producing parietal cells* which Axmacher (1987) found in all CS and IM abomasa in comparison with GR. With reference to the accepted principle of symmorphosis, we can assume that wild ruminants *regularly* use their perfectly retained by-pass (Sulcus reticuli) to "save" a good proportion of their soluble nutrients which, as from the abomasum, are subjected to a monogastric-type of digestion. Many CS feed with their head positioned as in milk sucking; they need no training as domesticated sheep.

But there is another, third reason for much more (and more serous) saliva production in CS and IM: it is a *counter-adaptation* to overcome the plants' chemical defenses. The phenolic compounds produced by plants form insoluble complexes with protein (tanning effect). Provenza and Malechek (1984) observed in goats (IM) with oesophageal fistulas browsing on blackbrush, that c. 50% of the tannins had disappeared already before swallowing – there is good reason to believe that much of it was bound by excessive serous saliva. Moreover, as protein feed protec-

tion experiments have shown, the undigestible tannin-protein complex will be dissolved in the acidic *abomasal* environment – this would be a vital second reason for so much more HCl-production in that thicker abomasal mucosa of selective ruminants. They obviously practice, with this particular adaptation, their own protein feed protection! But they practice it with caution (Fig. 9): no shaking, no pulling or plucking when they feed on tannin-producing plants which are said to release more of this bitter, adstringent chemical on rough treatment. Although foresters claim this, browsing wild species do *not* kill plants by *excessive* harvest; they seem to "know" that they can neutralise some, but *not* any amount of these chemical compounds. Drought (or winter starvation) conditions, however, may upset this co-evolutionary balance (Fig. 10): impala and gazelles would rather bite down bitter acacia bushes to stumps, to the limit of their superior salivary apparatus, than take sundried, lignified grass which they *cannot* digest. With Kay (1987) we have reasons (and data) to believe that winter or dry season reduced forage intake causes salivary *cell atrophy* and subsequently gland weight loss; but ecologically reduced functional demands have determined the regression of the salivary glands from CS via IM to GR already during evolution – obviously in reaction to the increasing importance of grass in the diet.

The ruminant stomach attained its functional potential in small steps

In backtracking ruminant evolution, it helps to remember Haeckel's phylogenetic/ontogenetic law by looking at em-



Fig. 11. Ruminant species illustrating the relative size of the head and neck, WTD

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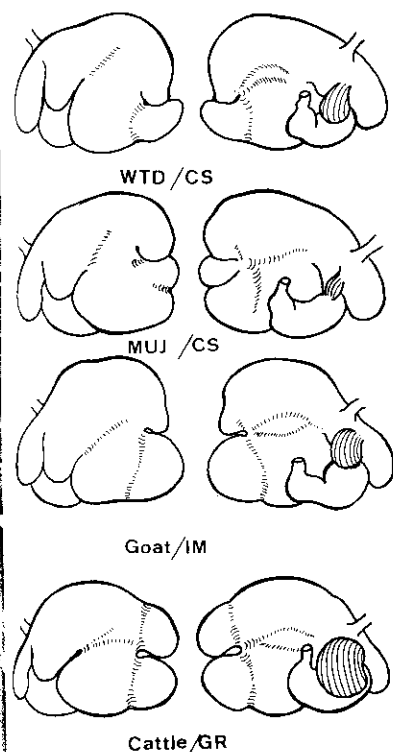


Fig. 11. Ruminant stomachs of two wild and two domesticated species irrespective of actual size; note extreme differences in relative size of omasum (striated/laminated) between CS (white-tailed deer, WTD and muntjac, MUJ), IM and GR ruminants

embryological steps comparatively. Perissodactyls and Artiodactyla older than tragulids and ruminants have a widened initial stomach portion (fundus). It provides in ruminants – after passing ontogenetically through this phase – the formative material for the big *ruminoreticulum*, i.e. the proximal fermentation chamber. This mammalian fundus is distinguished by a special (internal oblique) *muscle layer* which finds its most luxurious development in ruminants as powerful pillars, arches and folds subdividing the rumen – but not at once. Moose or giraffe are very big CS ruminants, yet their rumen musculature is much weaker (only half the relative thickness) than that of a buffalo. It is, however, perfectly adapted to the dicot forage CS select.

The other embryological indicator of evolutionary sequence, besides increased rumen subdivision and thicker pillars, is the *omasum*. It is the phylogenetic newcomer which morphophysiological separates ruminants from tragulids and camelids, which also chew the cud. The early omasum was little more than a strainer sieve, according to Bost (1970) a “flood gate”, preventing unchewed leaves or fruit to enter the glandular abomasum – as can be seen in those “persisting” early ruminants like duikers, muntjacs etc. In scaling down the stomach outlines of all species investigated evenly, irrespective of actual size or bw, we receive clear answers: the smallest omasum belongs to CS, the biggest to unselective GR (Fig. 11).

It has been shown already that the CS stomach has lesser relative weight and capacity, less subdivision and larger openings, all of which facilitates a faster passage rate, a shorter retention time of ingesta. At the end of long grazing periods the maximally filled GR ruminoreticulum shows stratification of ingesta according to specific weight and

particle size with lighter, longer parts floating above. CS normally do *not* fill their rumen above the “bottleneck” outlet to the omasum (reticulo-omasal orifice) and their better diluted mass of short-broken dicot material does *not stratify*. Their relatively larger *reticulum* is in wide connection with their relatively smaller, dorsally unattached *rumen* (complete contractions possible). Both are instrumental in a fast turnover of ingesta. This forces most CS into an almost oscillating feeding cycle – as long as easily digestible, rapidly fermenting forage rich in plant cell contents is available. CS of Northern climates had to solve a survival problem in winter.

As mentioned, the rumen of CS is *evenly* papillated: total surface enlargement (SE) is greater than in GR, in particular on the dorsal ruminal wall (Fig. 12).

The principal function of ruminal papillae is to *absorb SCFA* (via their subepithelial capillary and venule network) which are either metabolized *in loco* or transported into the liver for gluconeogenesis (the reconstitution of sugar typical of ruminants). I first observed in East African impalas (IM) over several dry and rainy seasons how papillary size, SE and vascular development were linked to forage quality. Later in Central Europe, we were able to confirm the same *cyclic principle* in roe (CS) and red deer (IM) under winter and summer conditions. Japanese research workers (Tamate; Sakata; Amasaki) substantiated our deductions by showing that SCFA, especially increasing amounts of propionate and butyrate which stimulate ruminal blood flow, are increasing the mitotic rate of the papillary epithelium and induce the formation of new papillae or more subepithelial capillary loops and nets, all of which enlarge the ruminal mucosal surface and enhance absorption (Fig. 13). Conversely, towards dry season or winter, following a decline in digestibility (or availability) of forage plants, peripheral blood flow in the rumen papillae is reduced, cornification increased and thus the papillary SE becomes reduced again, a cyclic morphophysiological process. Here again: the *principal* layout of papillation is there in any ruminant; in adaptation to forage selected, available or provided by man, it appears to react within limits set by evolutionary selection. Late bovine fetuses show a dense but short rumen papillation on the dorsal ruminal wall, where papillae are lacking (undeveloped) in the adult. All GR show this *heteromorphic* distribution of papillae: it reflects the stratification pattern of their fibrous forage.

After testing four homologue indicator regions of rumen mucosal changes in several bovid and cervid species over several tropical and Northern seasons (impala, Thomson gazelle, topi, chamois, roe, red, sika and Chinese water deer and moose) we are able to link these results to our multidisciplinary study of a big herd of fistulated nomadic goats (IM) and sheep (GR) in Northern Kenya (Schwartz et al. 1987; Hofmann et al. 1987). It has provided invaluable data: free ranging goats are highly selective with a greater harvesting efficiency, lower dry matter intake of higher quality, faster feed passage rates, larger absorptive surface and faster SCFA uptake than sheep. There are strong indications that goats regularly *bypass* soluble nutrients from fresh dicot plants. Several of their preferred food plants (acacias and dwarf bushes) contain *tannins*. Goats deposit maximally 15% fat, sheep up to 40% during the green seasons – they subsequently loose much weight when grass becomes increasingly lignified in the dry season. Our mucosal studies in this context confirm that there is a *wide* reac-

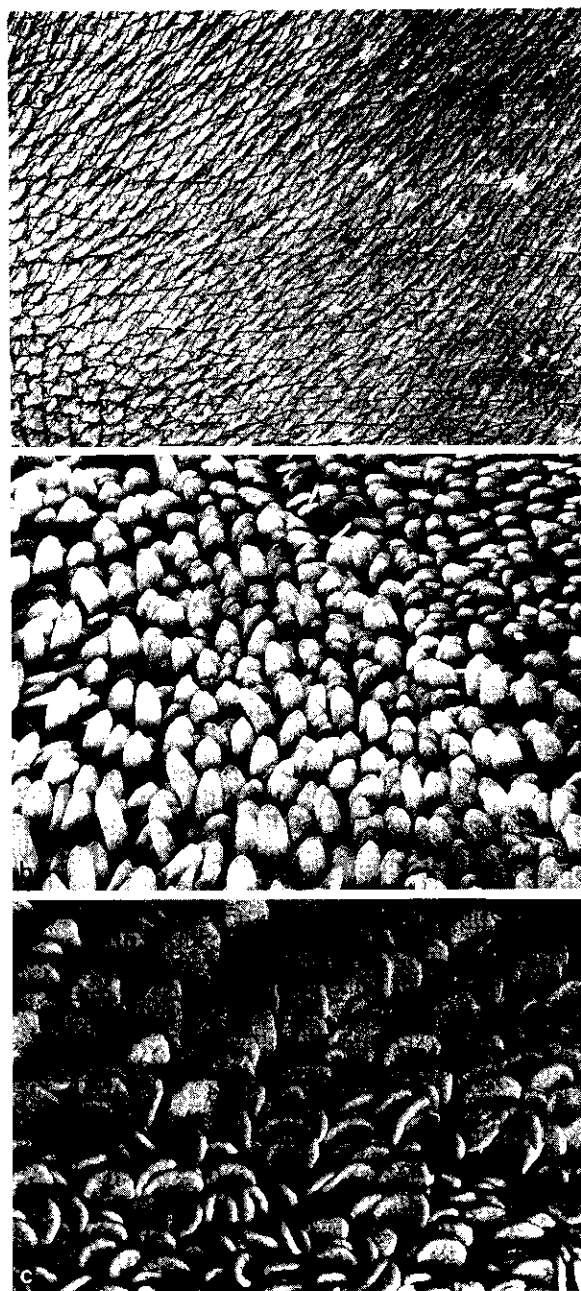


Fig. 12a–c. Identical rumen wall samples (mid dorsal) of a Pere David's deer (GR), b Pronghorn antelope (IM) and c Gervuik (CS). The absorptive surface enlargement differs according to differences in fermentation rate or food stratification in that rumen region from 0 (a) via $5.2 \times$ (b) to $7.5 \times$ (c)

tive “swing” of ruminal SE-variation in GR through mucosal response and reconstruction between the green and the dormant plant season (the main factor of morphological change being expressed in papillary length and in number). In CS and IM computation dates of SE stay closer together – they select similar forage qualities during dry and green conditions. This they cannot do in Northern climates to such an extent; hence they either migrate (like caribou or saiga antelopes) to better feeding grounds and/or they reduce activity, food intake and metabolism – after adding at least 15% of bw to their fat deposits during the fall, when most plants provide fruits and seeds. Alpine chamois

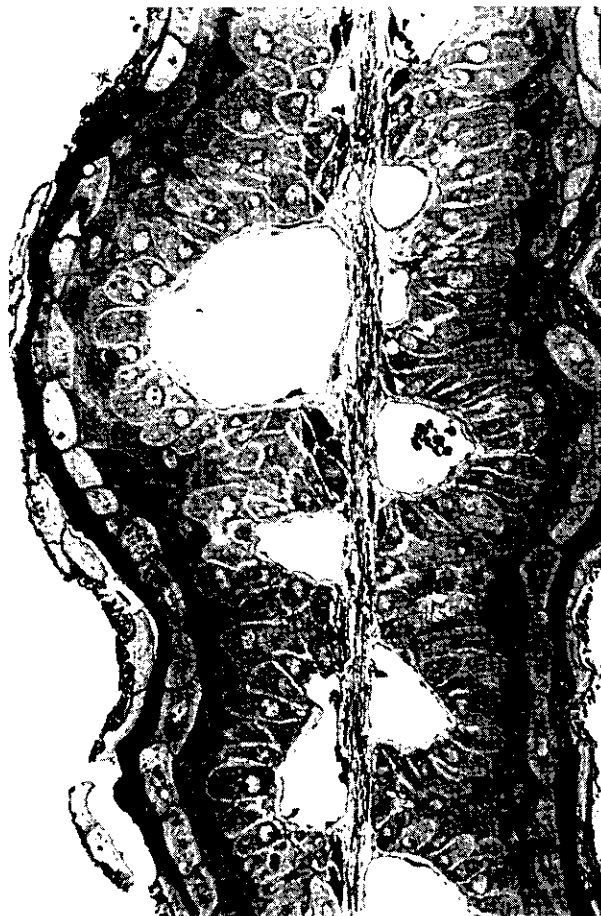


Fig. 13. Histological cross section of a dikdik rumen papilla during the green season showing enlarged venules (optically empty spaces) and reduced surface epithelial cell layers facilitating rapid absorption of SCFA. $\times 373$

(IM) like many cervids, reduce food intake during their late fall/early winter rut to almost nothing (c. 30 g per day!) after they have behaved, between May and October, like extreme CS, with all morphophysiological consequences (15–20% of bw as fat deposit). Their rumen mucosa in summer (lavishly enlarged 20–30 times by densely placed papillae) reacts in the rut dramatically: its overall SE drops by a factor of 7! Thereafter, the chamois rumen looks like that of a dry season nomadic sheep – these relatively small (25–40 kg) animals switch to become highly efficient roughage eaters. SE stays low, but ruminoreticular capacity increases between the rut and April up to 300%. Peak capacity (long retention) coincides with the annual quality low of available “old” forage and with fat depletion (Hofmann 1984); I assume the taxonomically and ecologically similar American mountain goat is using the same strategy.

Similar-sized roe deer (CS) are unable to digest low quality fibrous food. They reach maximal rumen capacity and papillary SE during maximal forage intake in the fall – unless they inhabit conifer plantations which leave them no chance. In late February, after 2–3 months of photoperiodically reduced forage intake and inactivity, their rumen SE is down by 30–50%, while fat deposits help them to survive; this is almost identical to what happens in the big moose.

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Moose contradict the body size rule

What becomes of all those undigested structural carbohydrates (especially hemicelluloses forming the "skeleton" of dicot forbs and foliage) which are rapidly expelled from the CS forestomach system? "Ruminal escape" must not be a dead loss, and it certainly differs from domestic GR in its *critical particle size*, where it is only 0.5–1.0 mm. Our recent investigations of Finnish moose (Nygren and Hofmann 1988) strengthen earlier assumptions that the fast forestomach turnover of CS and many IM is facilitated by an *intermittent widening* of the "bottleneck" reticulo-omasal orifice. It is guarded in CS by long claw-like papillae (rudiments in GR) which cornify and fall off, when selection becomes uneconomic with digestible forage rare.

Moose, the biggest cervid, have a relatively small and "simple" CS ruminoreticulum and also a small omasum. But in comparison to bacterial dimensions and plant cell wall structures, they are big. Still: poor cellulolysis in the growing season; cell solubles of forbs and leaves provide 50–75% of forage dry matter from spring to autumn while cellulose is below 20% even in the Canadian winter (Renecker 1985). We found moose pass many food particles over 4 mm, some up to 8 mm! They occur randomly in all portions of the tract beyond the RR. Maximal passage of coarse particles >4 mm coincides with greatest selectivity for plant cell contents: from June to September. In the Northern winter, moose cannot afford to be selective. Rumination and retention time must then be increased and critical size reduced for cellulolytic bacterial activity. Fortunately, they can rely on their *distal fermentation chamber* as will be seen. Thus, the specific strategy of this big CS parallels the cyclic changes of its Northern environment; its size does *not* make it a GR! In this it resembles a similar-sized African bovid CS, the greater kudu, which also can better afford than small species to include food types of lower quality in their foliage diet (Owen-Smith 1985) and they also make good use of their second fermentation chamber to survive dry seasons, even droughts.

With increasing evolutionary adaptation to fibrous food, the *omasum* of IM and GR became not only bigger; its booklike structure is *more differentiated* (size orders and number of laminae increase) in comparison with the simple, small sieve-cum-transfer pump of CS. It obviously has gained a new function based on its considerable SE: effective *absorption of water and electrolytes* during the slow passage of thoroughly fermented, evenly broken down plant fibre residues. But in CS? Their small omasum cannot absorb much. Their much diluted, quickly passed ingesta (enriched with rapidly reproducing amylolytic bacteria and frequently with tannin-protected salivary and plant proteins) arrive in smaller or bigger gushes in a well-prepared *abomasum*. In animals of comparable body weight, be they small or large, the CS abomasal mucosa is always 100% *thicker* than in GR and by 50% thicker in IM (Axmacher 1987). Since the proportion of HCl-producing parietal cells is 20% of the mucosal tissue in all ruminants irrespective of feeding type, the greater thickness of the mucosa is providing CS and IM with so much more HCl per surface unit from more parietal cells – what for?

1. to *neutralise* copious alkaline saliva carrying by-passed soluble nutrients via the ventricular groove (which ends here as sulcus abomasi);

2. to *kill/disrupt* ruminal *micro-organisms* (to be digested as protein)
3. to provide a *suitable pH* for pepsin activity;
4. to *dissolve* Ca–P-plant absorption salts and complexes (abundant in foliage);
5. to *break up* tannin-protein complexes or otherwise (e.g. terpenes) "protected" proteins in adaptation to plant self-defence mechanisms; and
6. to *macerate* and *break down hemicellulose bonds* of dicot ingesta necessarily escaping ruminal fermentation (revealed as a principle by Ulyatt et al. 1975).

An abomasal microstructure so significantly different in the three feeding types (statistically tested in 36 species) implies *essential* digestive adaptations.

Wild GR presumably use potential No. 1 when foraging on fresh grass, No. 2 and 3 regularly, to a lesser regular extent also No. 4 and 6, but for them No. 5 has become *redundant*. Since, however, the abomasal mucosa has *regressed* 100% in GR, this function *must* have been of great adaptive importance to CS.

Carried-over hindgut fermentation rounds up the story

Traditionally, ruminant research has focussed on the complicated *stomach*, which in GR so efficiently digests up to 80% of forage carbohydrates. This had led many to neglect the so-called "lower tract" (small and large intestine) as Van Soest (1982) remarks plaintively: "... although it is relatively simple, it would appear that it is more important than is ordinarily realised". He emphasizes, that more *hemicellulose* escapes rumen fermentation than cellulose: much of it is digested in the lower tract. The final portion of the ruminant digestive system, as will be shown, is "better" adapted to this function in CS (summary in Fig. 14).

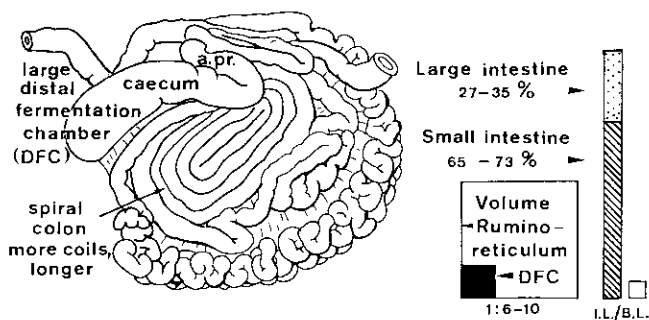
In an evolutionary sense, CS and IM have *not yet* discarded hindgut fermentation. Their lower tract incorporates decisive functions as they practice successfully a *fractionated fermentation* of plant matter; some in the proximal (PFC), some in the distal fermentation chamber (DFC). Even GR have retained it, though smaller, as an option in need. Hoppe et al. (1983) point to small capacity, hence low efficiency of the caecum of their dikdiks, miniature CS ruminants, but still its dry season bacterial activity (rising from 23 to 40% of RR fermentation rate) compensates in part low winter/dry season fermentation rates of the rumen. We saw roe deer, chamois and moose considerably increase their DFC in winter – e.g. chamois from 220 ml in the rut to almost 1000 ml in April.

A giraffe (CS), in spite of its relatively big RR (mean 105 l) would be unable to survive on acacia browse if it could not rely on the SCFA/energy production of its voluminous caeco-colonic DFC (c. 10–18 l capacity!). This principle holds also for kudu, moose or gerenuk, for mule deer or pronghorn antelope etc. Prins et al. (1984) provide convincing physiological data of this compensatory effect for the CS and IM energy balance, as all these species cannot digest fibre as well as GR. Hence, the *ratio small: large intestine* which is so strikingly different in the two extreme feeding types CS and GR not only in length, but particularly in volume, provides the morphological clue for this diversion.

Hindgut fermentation has been the main herbivorous digestive strategy in most monogastric ungulates that evolved *before* the ruminants. But they all have haustra,

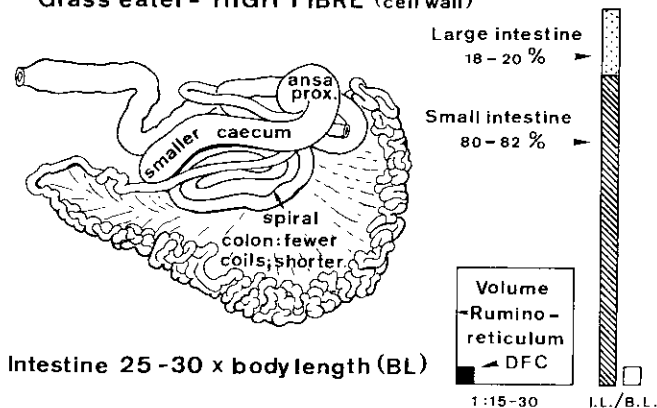
Intestine: evolutionary + functional adaptation

Concentrate selector- LOW FIBRE (cell content)



Intestine 12-15 x body length (BL)

Grass eater- HIGH FIBRE (cell wall)



Intestine 25-30 x body length (BL)

Fig. 14. Ruminant intestinal structure (from Hofmann 1985, modified)

taeniae and mucosal folds to compartmentalize their hindguts for more efficient forage retention and cellulolysis, as Langer (1987) recently reviewed. Not so ruminants; they use the *spiral colon*, which follows the widened but smooth DFC portion at reduced width, as a principle delay mechanism. No surprise, therefore, that it is relatively longer in all CS and IM – for two reasons. In addition to the propulsion action the tight concentric coils must have a congesting effect upon the preceding voluminous DFC gut portions, after which they tighten more or less abruptly. This device achieves the necessary retention time for cellulolysis. Secondly, the longer spiral provides sufficient *surface and time* for water and electrolyte absorption – a function which the small omasum of CS and many IM is *not* (yet) able to perform. It is obvious that the much more differentiated, big omasum of GR is combined with a smaller DFC and a shorter i.e. reduced spiral colon.

I would not, however, base my reasoning on macro-measurements only, had not Ludwig (1986) provided convincing complementary data of *hindgut microstructure* of 30 ruminant species: GR have the thickest hindgut *musculature*, CS the weakest; in selective ruminants of the temperate zones, this musculature is reduced with less winter forage intake. In CS, there are considerably more (and more distended, absorptive) submucosal *blood vessels* in the DFC than in the spiral colon, also the structure (length, width, goblet cell proportion) of the *intestinal crypts* differs signifi-

cantly between feeding types. This is resulting in a typical surface enlargement factor, while the percentage of the average number of crypts shows (in 30 species) *no* adaptive variations related to feeding type or season! Again: the principal blueprint is there, but differentiation is favouring *hindgut nutrient absorption* significantly in those (CS and IM) species, which apparently have not yet perfected their rumen functions.

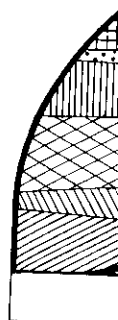
However, these selective ruminants perfectly utilise the rich spectrum of dicot forage plants by implementing a *complex combination* of digestive sites and avenues: very little oral absorption, a little by-pass of soluble nutrients – set free in the mouth (after selective food prehension) by differently structured teeth and differently arranged masticatory muscles (attached to a differently shaped mandible, Stöckmann 1979). Much plant cell content fermentation (by amylolytic bacteria) but far less cellulolytic fermentation occurs in the small rumen with its greater absorptive surface. Much ruminal escape material is properly prepared by a better developed abomasal mucosa. It is not a coincidence but systematic evidence of symmorphosis, that we found salivary gland tissue *and* fundic abomasal mucosa to be developed or reduced in almost exactly the same proportion: c. 100% in GR, 150 in IM and 200% in CS, and the bigger the rumino-reticulum (PFC), the smaller the hindgut (DFC) and vice versa.

If we finally consider that CS with their superior faculty for plant and bacterial *protein digestion* have up to 100% more *liver tissue* to body weight than GR and that – again – all IM species show most of these features “halfway” developed or reduced, we can conclude safely: *ruminant evolution is going on* in 150 species, as a bush with many impressive branches.

Cattle with their wild bovine relatives have reached, so far, the most efficient digestion of low quality fibrous forage, finally very largely performed in a huge ruminoreticulum. All other extant ruminants demonstrate that this was achieved *in stages*. The basic structural design remains highly variable but is *optimized* in *each* evolutionary stage. Morphophysiology changes with environmental pressure due to a greater *genetic plasticity* of *soft tissues* – fossil bones and teeth do not easily render such information. Our comparative studies of so many different extant ruminant species luckily permit us to group them into those *overlapping* feeding types (Fig. 15).

As examples of their specific feeding type, ruminant species on free range overlap much in the same way as their ecological niches are overlapping and because they are subjected to seasonal changes within their environment. They must overlap in order to retain a wide range of adaptive tolerance. Species belonging to different feeding types show different limitations within their adaptive range. Ecophysiological specialisation was an evolutionary advantage; when left undisturbed in its niche, any of these ruminant species (and several of them together, especially in East Africa) thrives in its environment and appears to be in balance with the vegetation it consumes. Ruminant digestion, being based on a complicated, multi-faceted and interdependent chain-system of functional structures, can fail, however, easily. If ecosystems are destroyed by man, if plant succession is grossly interfered with, if animal populations are treated not as a sum of living individuals but as abstract figures, this highly developed ruminant system of plant digestion and energy conversion may even turn into an anti-

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Ruminant morpho-physiological feeding types

(Co-evolution of plants and herbivores)

Plant cell contents + dicot cell wall + monocot cell wall (fibre)

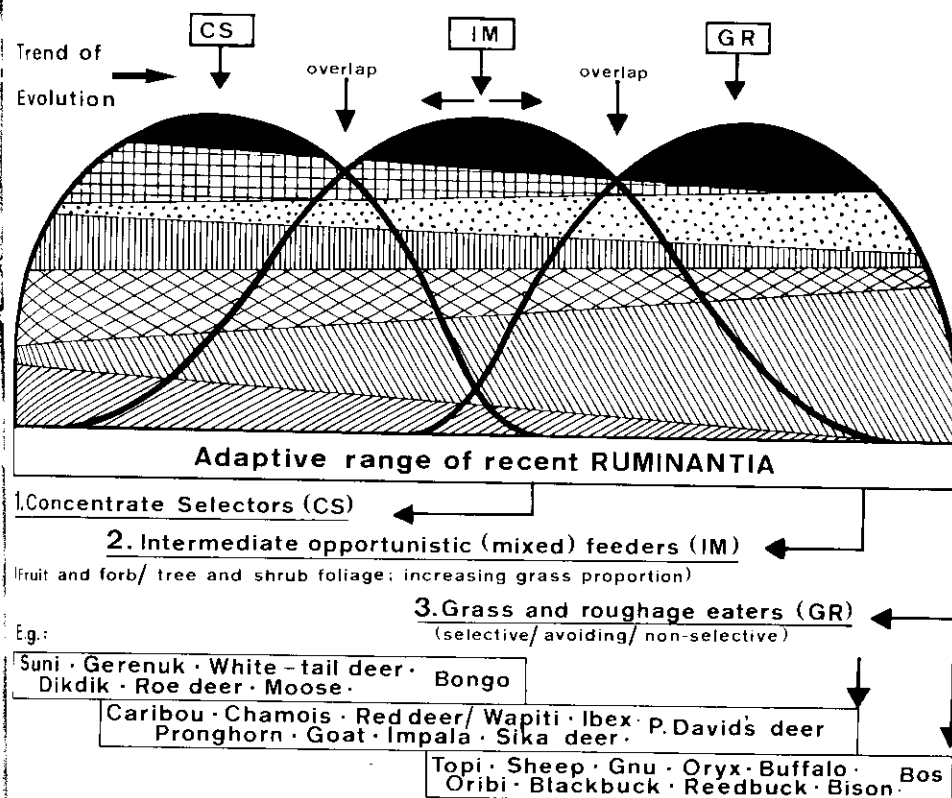


Fig. 15. Schematic representation of ruminant specialisation, with adaption to their feeding plants, during evolution. While the basic structural and functional design is retained, the increasing ability to digest plant cell wall carbohydrates (trend to the right) causes *regression* of some, but *development* of other components of the digestive system and changes of feeding strategy. Overlapping morphophysiological criteria ensure the retention of *safeguards* (e.g. for nutritional bottle-necks) and a wide adaptive range. Separating limitations are found on both ends of the range. Intermediate species can *switch* seasonally from one strategy to the other. [Patterns in text box] Selectivity for plant cell contents; [Pattern] Fibre digestion (cellulolysis) in rumen; [Pattern] HCl-producing tissue in abomasum; proportion of salivary gland tissue of b.weight; postruminal (caecocolic) fibre digestion; [Pattern] ruminal amyolysis, possibly bypass of solubles (retic. groove); [Pattern] effective food passage delay structures and mechanisms; total intestinal length; [Pattern] papillary surface enlargement on dorsal ruminal wall; [Pattern] rumino-reticular capacity and weight relative to b.weight; Ref. Hofmann and Stewart 1972; Hofmann 1973, 1976, 1983, 1984; Van Soest 1982; Hofmann and Schnorr 1982

ecological destruction device: overgrazing, plant species reduction.

Ruminants as a well-defined group of herbivorous mammals show many signs of a still ongoing evolution. Man has domesticated three or four or five species; while they keep him alive, he tends to forget the important majority of non-domestic ruminants. Hence, the only real threat to a continued ruminant evolution is *man* with his arrogance born of ignorance. May we learn in time to refrain from interfering ...

Specialisations of ruminant digestive structures in physiological order:

- buccal papillae (enlarging and protecting oral mucosal surface)
- dental pad (rigid mucosal cushion, upper jaw, in place of incisors)
- gugac palati/palatine ridges (covered by cornified epithelium)
- corus linguae (elevated back portion of tongue with heavily cornified epithelium and mechanical papillae)
- ventral buccal gland (serous buffer-secreting salivary gland covered by buccinator muscle fibres)
- elenodont cheek teeth (with cementum-filled enamel folds and cups, in CS more tuberculate for crushing, in GR more crested for grinding)
- ventricular groove (bypassing the PFC, connecting stomach cardia as reticular, omasal and abomasal portions, with the abomasum)

- reticulum/honeycomb (first forestomach portion below cardia, non-glandular, with mucosal crests forming open cellulac; mixing and particle separating functions)
- rumen/paunch (main forestomach portion, subdivided by muscular pillars into 5-6 portions including two caudal blindsacs; non-glandular, mucosal surface more or less enlarged by papillae or protected by keratinisation)
- rumen papillae (variable mucosal surface enlargements furnished with dense vascular network of capillaries and venules; epithelium transformed into absorptive cell layers with ultrastructural barrier and keratinized balloon cells which house ruminal bacteria when broken)
- omasum/manyplies (third nonglandular forestomach portion with two physiological compartments: omasal canal for direct transfer between reticulum and omasum, and interlamina recesses between few or several orders of mucosal laminae, providing more or less absorptive surface)
- reticulo-omasal orifice ("bottleneck" opening, guarded by clawlike horn papillae in CS and IM or blunt cones in GR; selective passage of small/ruminated plant particles, the more or less rapid outflow of which determines new food intake in RR)
- abomasum (only glandular stomach without cardiac glands; proper gastric glandular region enlarged by high spiral folds, mucosa varies in thickness (according to feeding type) but not in microscopic composition)
- colon ascendens (modified in initial ansa proximalis coli, morpho-physiologically combined with widened caecum to form DFC; subsequently modified as spiral colon/ansa spiralis with abruptly reduced diameter and finally forming ansa distalis all of which prolong ingesta passage for absorption)

*Ruminant species mentioned in the text,
with feeding type sign*

cattle (*Bos primigenius taurus dom.*) GR
sheep (*Ovis ammon dom.*) GR
goat (*Capra hircus dom.*) IM
water buffalo (*Bubalus bubalis dom.*) GR
pronghorn antelope (*Antilocapra americana*) IM
giraffe (*Giraffa camelopardalis*) CS
musk ox (*Ovibos moschatus*) IM
roe deer (*Capreolus capreolus*) CS
white-tailed deer (*Odocoileus virginianus*) CS
dik-diks (*Madoqua spp.*, *kirkii*, *guentheri*) CS
muntjacs (*Muntiacus muntjak*) CS
greater kudu (*Tragelaphus strepsiceros*) CS
lesser kudu (*Tragelaphus imberbis*) CS
moose (*Alces alces*) CS
bushbuck (*Tragelaphus scriptus*) CS
gerenuk (*Litocranius walleri*) CS
eland antelope (*Taurotragus oryx*) IM
Grant's gazelle (*Gazella granti*) IM
Thomson's gazelle (*Gazella thomsoni*) IM
Impala antelope (*Aepyceros melampus*) IM
banteng (*Bibos javanicus*) GR
wapiti (*Cervus elaphus canad.*) IM
oribi (*Ourebia oribi*) GR
blackbuck (*Antelope cervicapra*) GR
bongo (*Taurotragus euryceros*) CS/IM
suni (*Nesotragus moschatus*) CS
Pere David's deer (*Elaphurus davidianus*) GR
duiker spp. (*Sylvicapra spp.*, *Cephalophus spp.*) CS
red deer (*Cervus elaphus*) IM
topi (*Damaliscus lunatus*) GR
chamois (*Rupicapra rupicapra*) IM
sika deer (*Cervus nippon*) IM
Chinese water deer (*Hydropotes inermis*) CS/IM
Saiga antelope (*Saiga tatarica*) IM
mountain goat (*Oreamnos americanus*) IM
mule deer (*Odocoileus hemionus*) CS

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