FEEDING HABITS OF MOUFLON (OVIS AMMON MUSIMON) AND CHAMOIS (RUPICAPRA RUPICAPRA) IN RELATION TO THE MORPHOPHYSIOLOGICAL ADAPTATION OF THEIR DIGESTIVE TRACTS.

Reinhold R. Hofmann, Department of Comparative Anatomy of Domestic and Wild Animals, Vet. Anatomy Institute and AKWJ, Justus Liebig University, Giessen, F. R. Germany.

ABSTRACT

The European wild ovids and caprids are highly differentiated ruminant species which are adapted to a feeding cycle based on short montane or very short alpine vegetation periods. They can vary rumen and caecal volume and show extremes of ruminal papillary development or regression all related to seasonal food intake variation and changing plant digestibility. Mouflon are selective grass eaters, ibex selective grass and forb eaters while chamois are intermediate: they are extreme concentrate selectors from June to October but are coping well with high fibre feeds from November to May.

INTRODUCTION

There are two species of caprids (ibex and chamois) and one species of wild sheep (mouflon), which have survived in densely populated, industrialized central Europe. Two of these became almost extinct earlier this century but have been reintroduced and recently built up in many places. All three species are being hunted under strictly controlled conditions, which permitted collection of samples for morphophysiological studies of their digestive tract.

The uniquely rich bovid fauna of East Africa (Hofmann 1969 and 1973) served to establish a comparative grouping of these ruminants, based originally on stomach structure and feeding habits of 29 species. Three feeding types, termed "concentrate selectors", "grass and roughage eaters" and "intermediate" or "mixed feed eaters" were established also for, so far, 23 further ruminant species in Europe, Africa, North America and Asia (Hofmann 1983) and the criteria were extended to anatomical characteristics of all portions of the digestive system. They reflect physiological variations and specialization as first noted by Hungate (1959), extended by Hoppe (1977 and 1983) and recently summarized by Kay et al (1980) and by Van Soest (1982). Specific information on chamois digestive physiology has been provided by Drescher-Kaden (1976 a) and on their anatomical adaptation by Hofmann (1982). Morphophysiological data

Fig. 1: Mouflon ram and sheep during the rut in Central Germany (phot. J. Behnke)

Fig. 2: Young chamois billy, October; Bavarian alps (phot. W. Henkel)

on mouflon were also published by Drescher-Kaden (1976 b) while stomach anatomy and mucosa characteristics of mouflon were established by Geiger et al (1977), their salivary glands were described by Saber and Hofmann (1984), their intestine by von Trott (1983).

METHODS AND MATERIAL

This survey paper summarizes a series of comparative morphological studies which were carried out on 18 free ranging chamois, 3 ibex and 21 mouflon in western and southern Germany, Austria and Switzerland, collected in their natural habitat. In most cases, the digestive system was exenterated and preserved in stages with 10% formalin (4% formaldehyde), either via the esophageal and intestinal lumen or via the blood vascular system. All heads investigated were perfused via the carotid artery while one chamois and two mouflon were preserved in toto in a natural standing position by infusion as described by Hofmann (1966) (Figure 3). For detailed methodical descriptions, the literature cited may be referred to. The morphological results are based on subadult (2-3 years) and adult male and female animals. Chamois weighed 16-34 kg eviscerated (approx 21-46 kg live weight), shoulder height 70-75 cm. Mouflon weighed 16-30 (22-45) kg, standing only 60-65 cm at the shoulder. Ibex weighed 24 (subadult female), 36 (male 4 years) and 76 kg (male 10 years). Of the latter species, only limited sampling (mainly stomach material) was possible. Abbreviations used in this paper are CH for chamois, MF for mouflon and IB for ibex.

RESULTS

The salivary glands are best developed in CH and least in MF. The parotid gland is flat and wide in CH (0,16 - 0,19% of body weight) but flat and narrow in MF (0,06 - 0,08%), where it does not cover the mandibular gland as in CH (Figure 4). Sublingual and ventral buccal glands are better developed in CH than in MF. Total salivary gland weight amounts to 0,22 - 0,30% in CH but only to 0,11 - 0,12% of body weight in MF. Detailed measurements and descriptions are given by Saber and Hofmann (1984).

Stomach shape is similar in all three species. The rumen of MF shows a clearer subdivision than that of IB and CH, but in all three species a relatively small dorsal blindsac is matched by a long and spacious ventral blindsac. Ruminoreticular capacity varies greatly according to season; it ranges in MF from 7,5 to 11,5 litres; in CH from 3,5 litres (rut) to 11,3 litres. During the vegetation period, MF have a relatively greater ruminoreticular capacity than CH (10,2 - 11,5 litres vs 7,6 - 8,9 litres). MF show maximal capacity in late summer and fall, CH in late winter/early spring.

Size sequence of stomach compartments is in all three species rumen - abomasum - reticulum - omasum. The most striking difference is showing in the size of the omasum, which is relatively best developed in MF and least in CH (20 - 25% smaller) (Figure 5).

The forestomach mucosa shows typical variations related to evolutionary adaptation and thus genetically determined feeding type while changes are related to seasonal influences caused by changing forage quality.
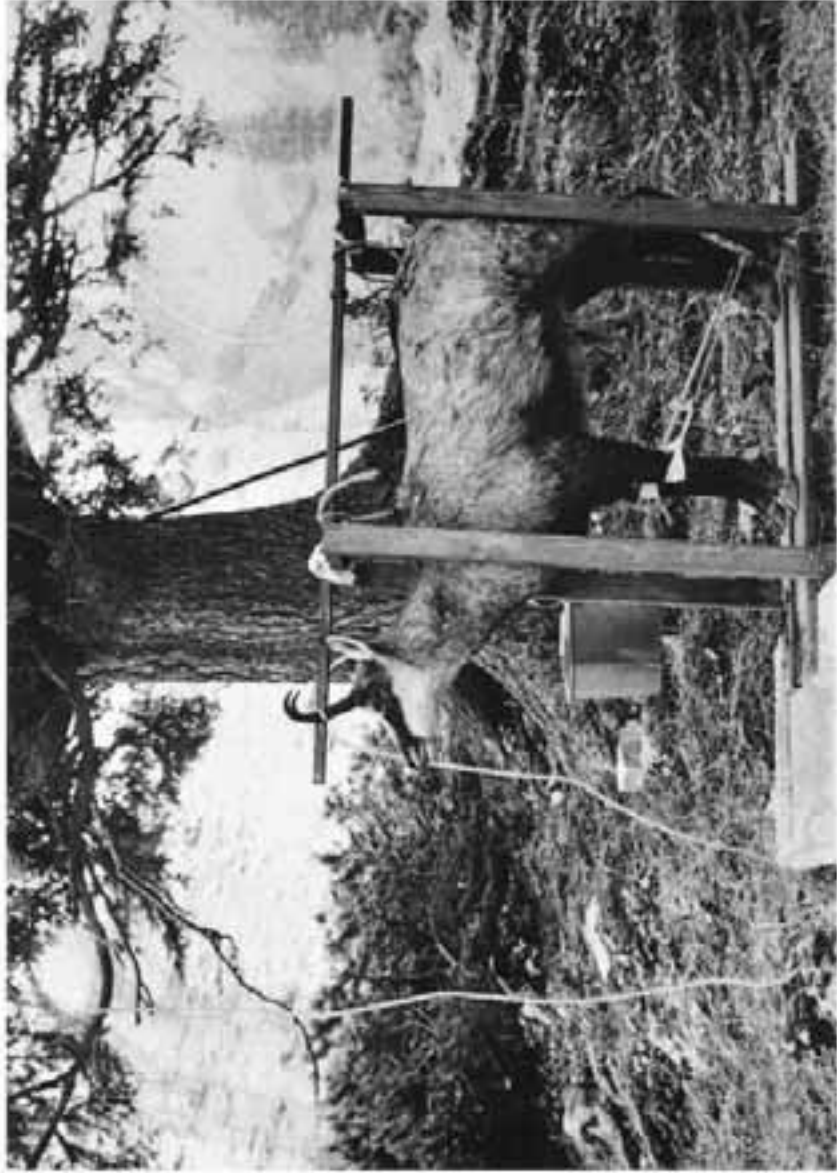
Fig. 3: A six year old chamois billy preserved with formalin after neck shot at c. 3200 ft., September; Austrian alps.
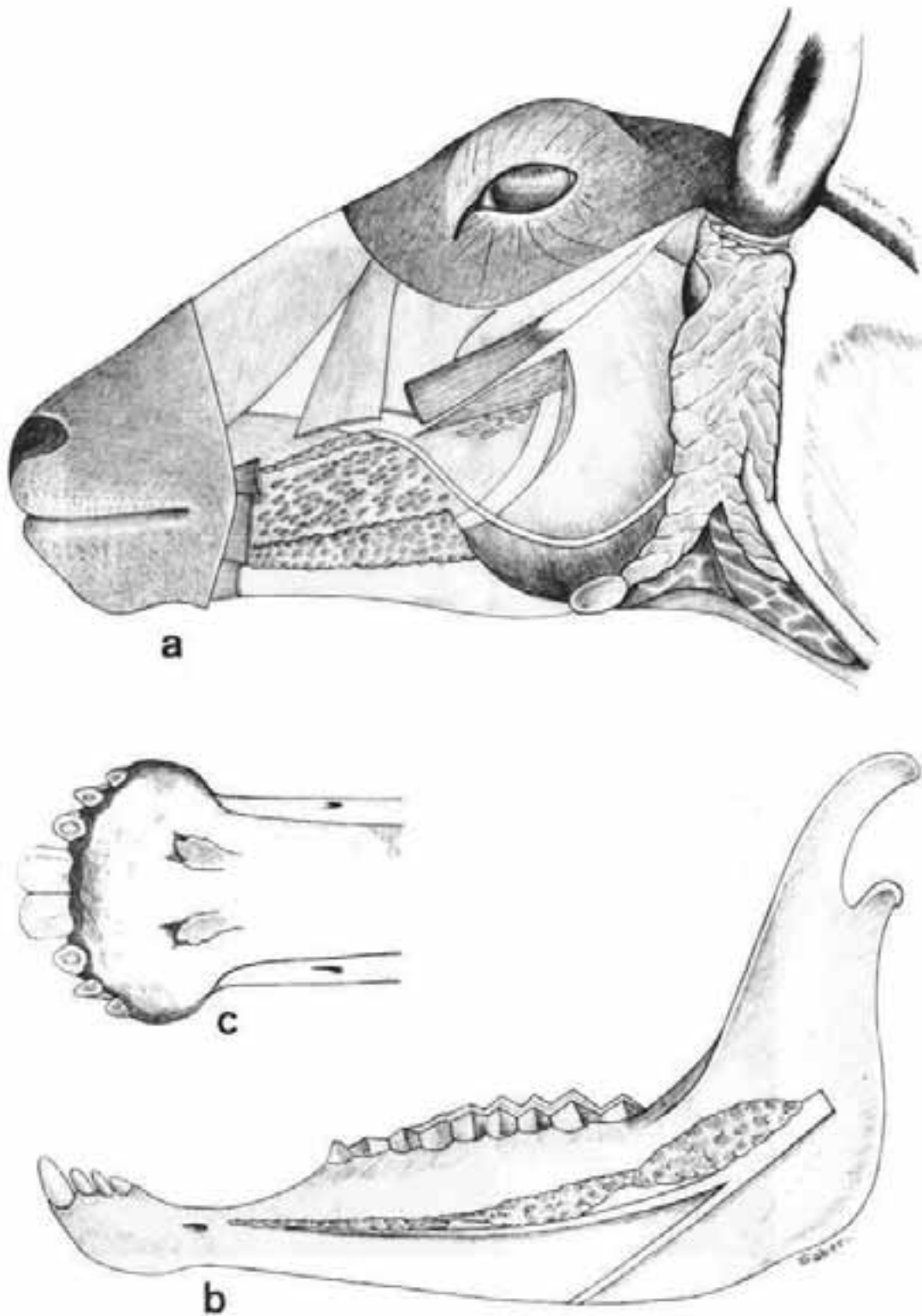
Fig. 4: Dissections showing (a) salivary glands of an adult
mouflon sheep (from SABER and HOFMANN, 1984). Buccal
glands left, parotid gland upper right, mandibular
gland lower right and (b) the sublingual glands at
the mandible and (c) the opening of mandibular and
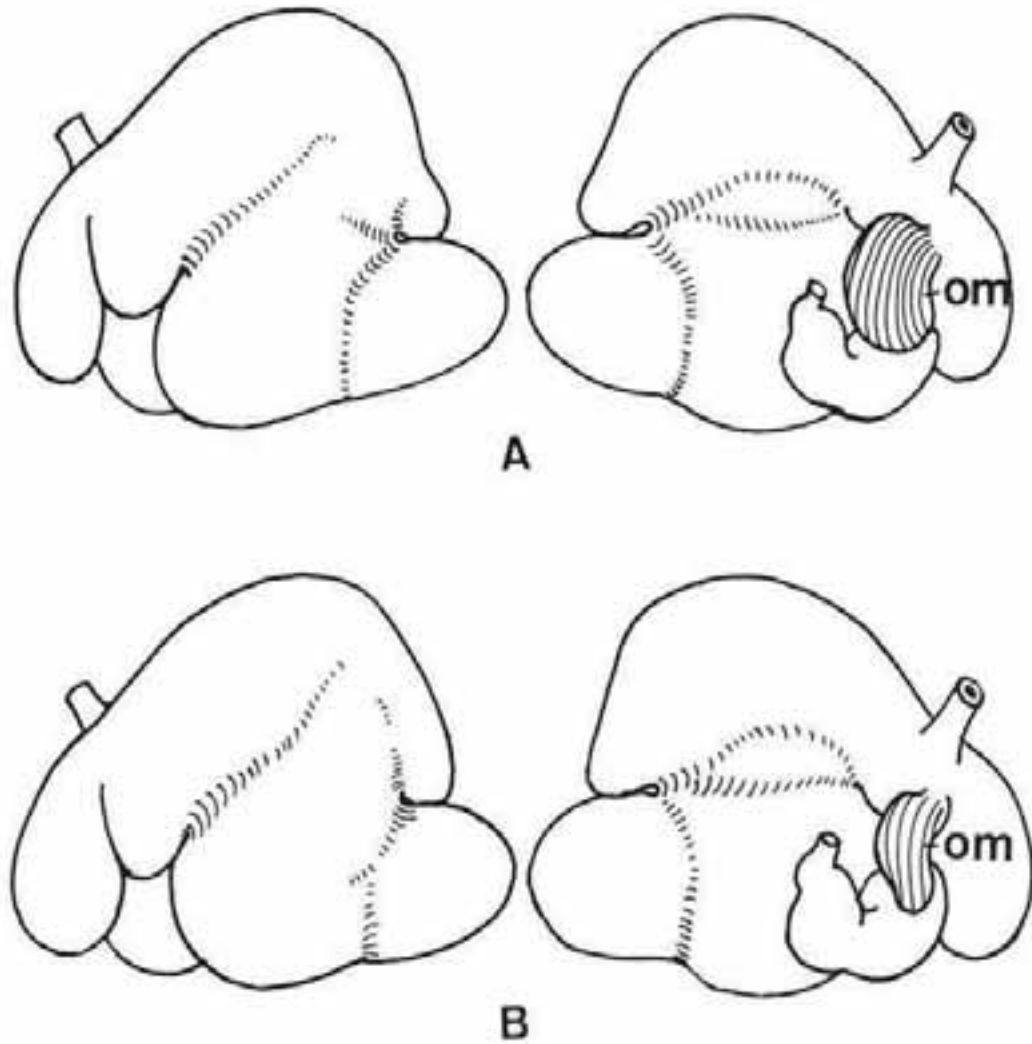sublingual ducts below the tongue (caruncula sub-
lingualis).

Fig. 5: Stomach shape and compartment relations in (A) mouflon
and (B) chamois. Note relative size differences of
omasum (om) on right aspect.

The reticular mucosa is most differentiated in MF where higher secondary and tertiary crests are much more pronounced than in CH where spike-like papillae are dominating the reticular cellulae with mainly primary crests.

The ruminal mucosa of MF shows a heteromorphic distribution of papillae which is typical for all grass and roughage eaters. This is similar in IB and extremely variable in CH. Its ruminal mucosa looks evenly papillated as in all concentrate selectors during the short alpine vegetation period but resembles the uneven pattern of grazing ruminants in winter and early spring (Figure 6).

The average surface enlargement factor (SEF) of the ruminal mucosa ranges in MF from 2,6 on the dorsal ruminal wall to 8,6 in the atrium ruminis; in CH from 3,6 on the dorsal ruminal wall to 16,5 in the atrium ruminis. SEF maxima in MF were 20,6, in CH 35,3. Generally, CH offer a greater mucosal surface area for the absorption of solubles and fermentation products, but seasonal variations are much more extreme than in MF. The dorsal ruminal mucosa ("roof of rumen") of CH shows maximal surface enlargement in September/October before the rut: SEF 10,6 on average, up to 12 in optimal cases. It drops dramatically at the beginning of the rut with its minimal food intake about late October/early November to 6,4 and finally even to 2,6 or 1,69 when food intake is reduced to old grass reappearing under melting snow. Average SEF as calculated from four "indicator regions" of the rumen (Hofmann and Saber, in press) range from 14 (20) over 2,5 to 4,5 before it rises again with the onset of a new vegetation period (Figure 7).

The omasal mucosa shows a lower degree of differentiation in CH than in MF. There are basically only two sizes of elongate, narrow laminae while there are three sizes of laminae omasi in MF which have much less long, claw-like papillae than in CH.

The abomasal mucosa shows little differences macroscopically, but there are seasonally varying differences in the microstructure which have not yet been sufficiently evaluated. CH appear to have more parietal cells during their "concentrate period" producing more hydrochloric acid.

MF have a relatively smaller liver (1,1 - 1,2% of body weight) than CH (1,7 - 1,8).

MF have a relatively longer intestine (total length c. 2100 cm) than CH (c. 1680), in relation to very similar body lengths. The proportion of the small intestine to the large intestine is 3,8:1 in MF and 3,1:1 in CH. The average volume of the caecum which is the main portion of the distal fermentation chamber is 310 ml in MF but 630 in CH. There is, however, a striking change of capacity in the chamois' caecum and proximal colon which occurs parallel to the rumen volume changes. During the rut, caecal volume has at 220 ml the annual low, while it reaches 850 or even 1030 early in spring, when old fibrous food only is available. During the vegetaton period, the caecal volume is around 500 - 700 ml. There are, finally, indications of seasonal variations also of the intestinal mucosal microstructure, which are related to seasonally changing forage quality as found in roe deer by Lackhoff (1983). A comparative study is under way.

Fig. 6: Stomach of a six year old chamois in situ, opened from the left side. From left to right: heart, 6th rib, reticulum 8th rib, spleen cut surface; heavily papillated dorsal and ventral ruminal sac, above 13th rib; right below entrance into ventral blindsac. Specimen as in Fig. 3.
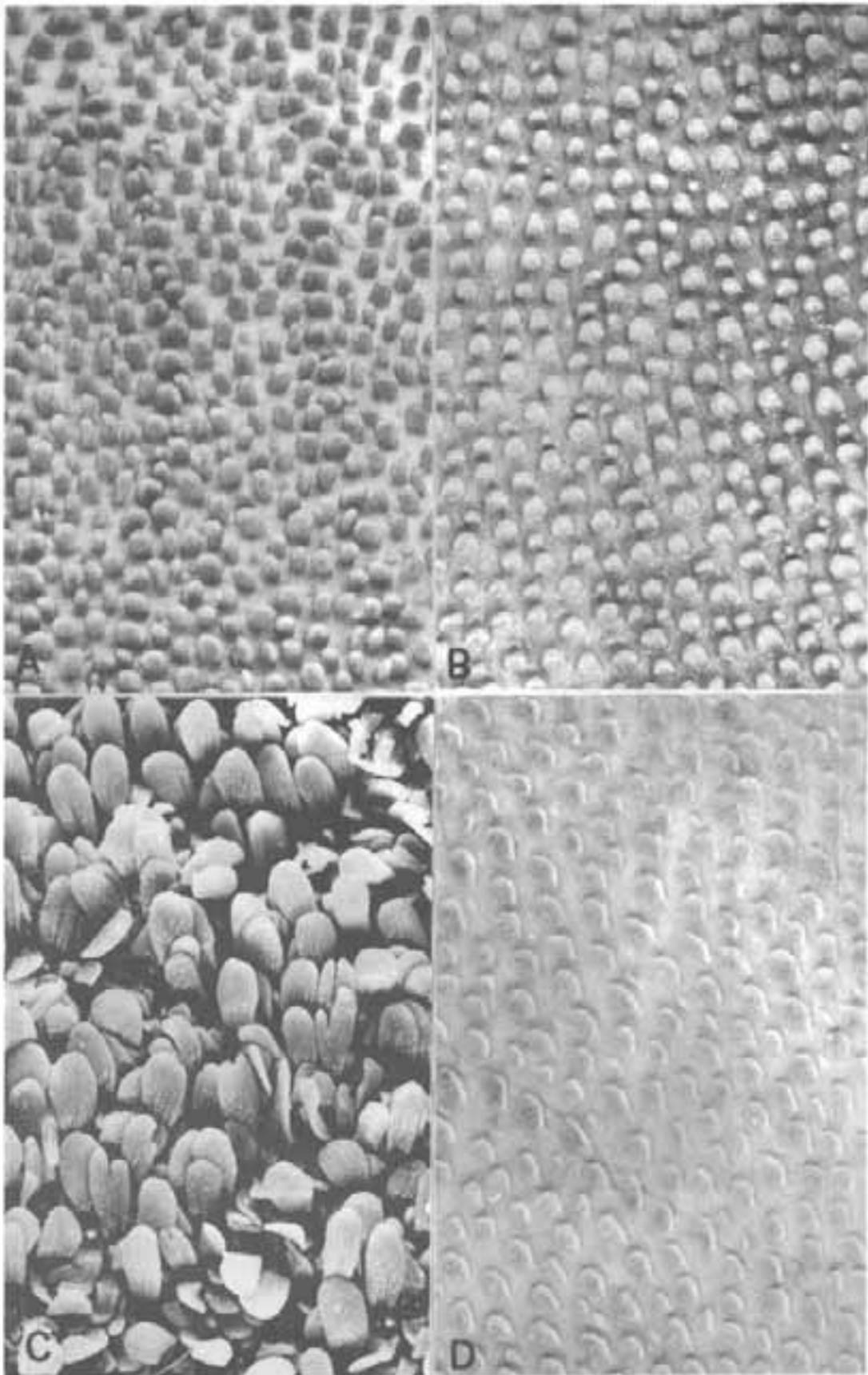
Fig. 7: Mucosa samples from the centre of the dorsal ruminal wall of
mouflon (A) under summer, (B) under winter feeding conditions;
of chamois (C) in summer, (D) in late winter. Little SEF changes
in mouflon, extreme changes in chamois.

DISCUSSION

According to the morphological criteria established (Hofmann 1973 and 1983) the European wild sheep shows the typical evolutionary adaptation within the group of grass and roughage eaters and resembles thus the domestic sheep and, presumably, also other sheep species. It has relatively small salivary glands with a parotid quite dissimilar from concentrate selectors like roe deer (Ramisch 1978), gerenuk or duiker (Hofmann 1973). It has a relatively capacious ruminoreticulum with a distinct subdivision for delayed food passage and an uneven distribution of ruminal papillae. There is only little surface enlargement on the dorsal and ventral wall of the rumen. The margin of seasonal variation through mucosal response and reconstruction (Hofmann et al, 1976; Sakata et al. 1980) is relatively narrow. Main absorption from predominantly slow cellulolytic processes occurs at mid-level of the rumen where papillation is dense and the SEF always higher. The reticular mucosa is subdivided and well suited to separate coarse fibrous food from broken down particles. The medium sized omasum is well developed and offers already a considerable additional mucosal surface for absorption. The liver is relatively small while the intestine is extremely long. The proportion of the large intestine, as calculated by Drescher-Kaden (1976 a,b) and von Trott (1983) is at 19-20% small when compared with ruminants of the concentrate selectors' or intermediate group. This is mainly due to a much smaller caecum. Chamois, on the other hand, which are taxonomically close to the North American mountain goat, show all morphological signs of an intermediate, opportunistic ruminant utilizing a mixed diet but selecting whenever possible for cell content rather than for cell wall, i.e. fibre (Figure 9). This has obviously led to a digestive strategy much different from wild sheep which are well capable to digest poor fibrous food throughout the year. The cyclic changes induced by the limitation of the alpine forage availability are much more dramatic both anatomically and physiologically than in sheep as was shown by Hofmann (1982). Chamois have an extremely high food intake combined with extreme selectivity, optimal nutrient utilization and rapid converson into fat. Their gastro-intestinal tract undergoes remarkable changes of capacity both in the reticulorumen and the caeco-colon. While this distal fermentation chamber is 1:30 in sheep, it is 1:10 in chamois during the vegetation period. While the reticulorumen of CH is at 8-9 litres very capacious at that time, a drastic reduction down to one third occurs during the rut, with only a moderate increase in the subsequent period of moderate food intake and reduced activity during winter. But obviously as a direct result of exhausted energy reserves in late winter and early spring when only poor fibrous food is available, a drastic increase in capacity (from 5 to 10 or 11 litres) is used to compensate lack of nutrient contents by increased intake, which requires adjustment of passage regulating structures.

Similarly impressive and further evidence for this adaptive strategy is the clearly cyclic transformation of the ruminal absorptive mucosa which shows a potential swing of the SEF of 1:7; f.i. during optimal forage availability chamois have an absorptive surface available which is more than seven times larger than during periods of need. Morphological signs of this nature are much more reliable than stomach content analyses which merely inform about a fraction of the animals' year. CH are from the beginning of the alpine vegetation period (after 2-3 weeks of transformation) between June and October, extremely efficient concentrate selectors. They turn fibre digesters during winter and are capable of bridging the dangerous gap between the exhaustion of
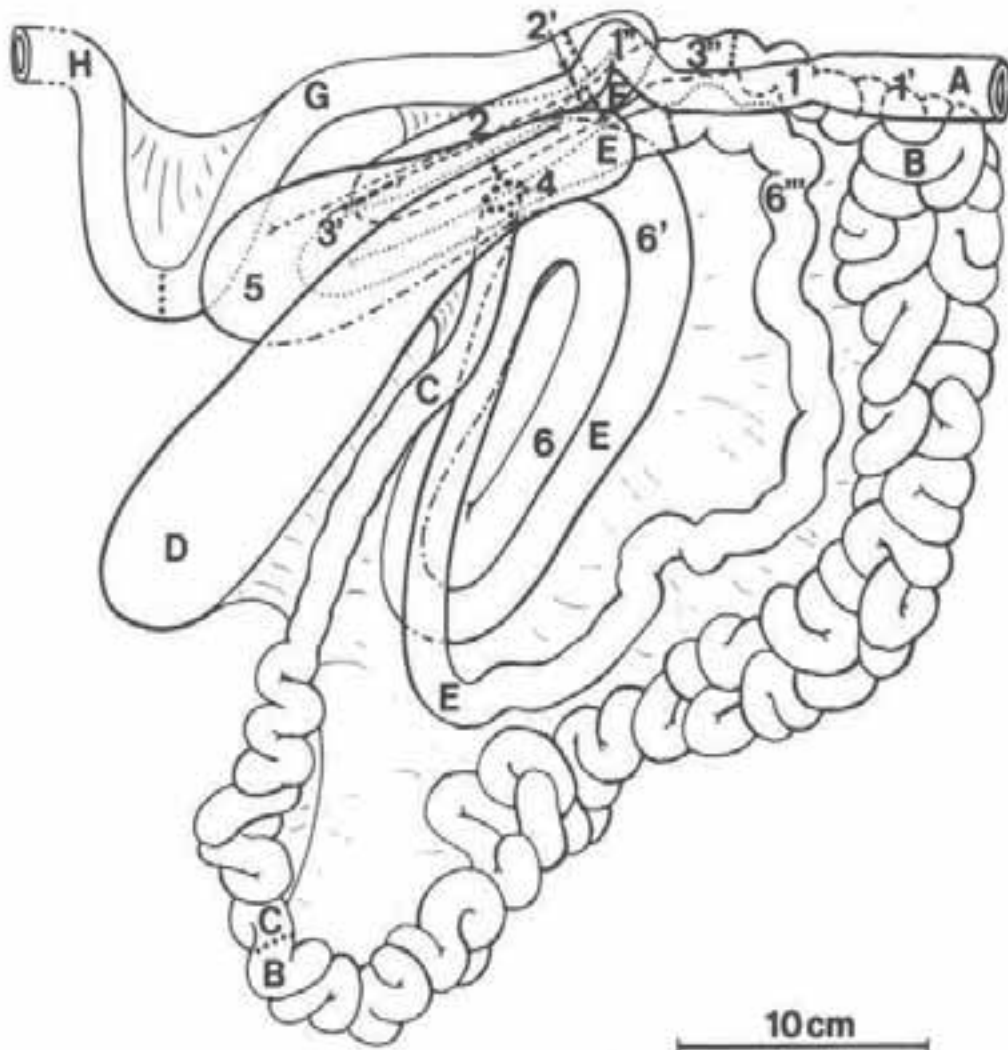
Fig. 8: Schematic diagram of the intestine of mouflon, right aspect. (A) duodenum, (B) jejunum, (C) ileum, (D) caecum, (E) Colon ascendens, (F) Colon transversum, (G) Colon descendens, (H) rectum; 5 widened ansa proximalis coli (part of distal fermentation chamber), 6 spiral colon; from W. von TROTT zu SOLZ, 1983.

Concentrate selectors	Intermediate types	Grass/roughage eaters
roe deer	ibex	mouflon
moose	chamois	sheep
	red deer	cattle
	goat	aurox
	fallow	
	wisent	ext.

Rumen:

(e.g.roe)   (e.g.red deer)   (e.g.cattle)

Feeding rhythmus : (roe deer)   (chamois)   (red deer)   (cattle)

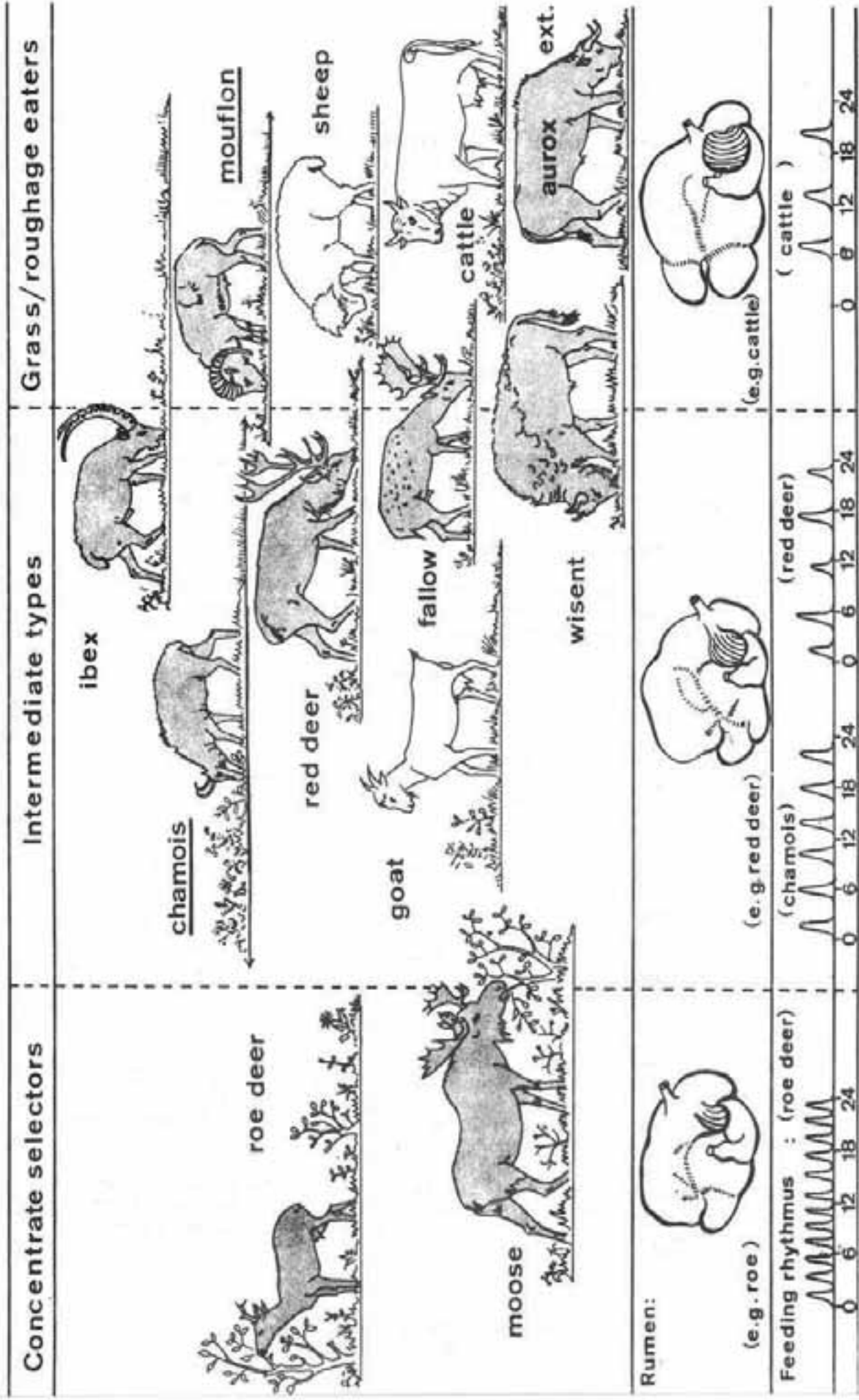0 6 12 18 24   0 6 12 18 24   0 6 12 18 24   0 6 12 18 24

Fig. 9: The European ruminant species in their typical position after evolutionary adaptation to the available vegetation according to feeding habits and morphophysiological specialization of their digestive tract. The further a species is placed to the right, the greater its capability to digest cell wall (fibre; cellulose). (HOFMANN, 1976)

fat deposits and the arrival of new vegetation by maximal intake of low quality forage - a fact which up to now only equids were reputed to do.

Although merely initial work has started on North American species taxonomically related to these European species (Figure 9) it can be stated that the mountain goat will occupy the position similar to that of chamois while the various North American sheep species (Bighorn, Stone, Dall) can be placed in a very similar position as mouflon. This will be verified by detailed studies and published in due course.

LITERATURE CITED

Drescher-Kaden, U. 1976 a. Berechnungen über den Energiegewinn aus der Vergärung der Naturäsung im Pansen des Gamswildes. Tagungsberichte 2. Internat. Gamswild-Treffen Bled, Hrsg. S. Valentincic; 158-165.

Drescher-Kaden, U. 1976 b. Untersuchungen am Verdauungstrakt von Reh, Damhirsch und Mouflon. Mitt. 1: Gewichtserhebungen und Kapazitätsmessungen...Zschr. Jagdwiss. 22: 184-190.

Geiger, G., R. R. Hofmann, R. König. 1977. Vergleichend-anatomische Untersuchungen an den Vormagen von Damwild (Cervus dama) und Muffelwild (Ovis ammon musimon). Säugetierkd. Mitt. 25: 7-21.

Hofmann, R. R. 1966. Field and laboratory methods for research into the anatomy of East African game animals. E. A. Wildlife Journal 4: 115-138.

Hofmann, R. R. 1969. Zur Topographie und Morphologie des Wiederkäuermagens im Hinblick auf seine Function (nach vergleichenden Untersuchungen an Material ostafrikanisher Wildarten). Zentralblatt f. Vet. Med.: 180pp., Berlin und hamburg.

Hofmann, R. R. 1973. The Ruminant Stomach (Stomach Structure and Feeding Habits of East African Game Ruminants), Vol. 2 East African Monographs in Biology, 364 pp. E.A. Lit. Bureau, Nairobi.

Hofmann, R. R. 1982. Zyklische Umbauvorgänge am Verdauungsapparat des Gamswildes (Rupicapra rupicapra L. 1758) als Ausdruck evolutionärer Anpassung an extreme Lebensräume. Allg. Forst Zeitschrift 37 Nr. 51/52, pp. 1562-1564.

Hofmann, R. R. 1983. Adaptive changes of gastric and intestinal morphology in response to different fibre contents in ruminant diets, pp. 51-58 in: Proceed. Internat. Symposium Dietary Fibre in Human and Animal Nutrition, Ed. L. Bell, G. Wallace, Royal Society of New Zealand, Wellington.

Hofmann, R. R., G. Geiger, and R. König, 1976. Vergleichend-anatomische Untersuchungen an der Vormagenschleimhaut von Rehwild (Capreolus capreolus) und Rotwild (Cervus elaphus). Z. Säugetierkunde 41: 167-193.

Hofmann, R. R. and Saber, A. S. (in press). Rumen mucosal morphology as an index of nutritional status in wild and domestic ruminants.

Hoppe, P. P. 1977. Rumen fermentation and body weight in African ruminants; in: Proc. 13th Internat. Congr. Game Biologists, pp. 141-150. Ed. T. J. Peterle, Wildl. Soc. Washington, D. C.

Hoppe, P. P., 1983. Strategies of digestion in African herbivores; in: Proc. Symposium on Herbivore Nutrition in the Tropics and Subtropics; Pretoria.

Hungate, R. E. 1959. Microbial Fermentation in certain Mammals. Amer. Assoc. for the Advancement of Science; 130: 1192-1194.

Kay, R.N.B., W. von Engelhardt, and R. G. White. 1980. The digestive physiology of wild ruminants, in: Digestive Physiology and Metabolism in Ruminants. Eds.: Y. Ruckebusch and P. Thivend. Lancaster: MTP Press: 743-761.

Lackhoff, M. 1983. Vergleichende histologische und morphometrische Untersuchungen am Darm von Rehwild (Capreolus capreolus, Linne 1758) und Buschschliefer (Heterohyrax syriacus). Med. Vet. Diss. Univ. Giessen.

Ramisch, W. 1978. Topographische und funktionelle Anatomie der Kaumuskeln und der Speicheldrüsen des Rehes, (Capreolus capreolus Linne, 1758), 104pp. Heft 3 der AKWJ-Schriftenreihe. Ferd. Enke Verlag, Stuttgart.

Saber, A. S. and R. R. Hofmann, 1984. Comparative anatomical and topographic studies of salivary glands of red deer (Cervus elaphus), fallow deer (Cervus dama) and mouflon (Ovis ammon musimon) Ruminantia; Cervidae, Bovidae. Gegenbaurs Morph. Jahrb.,Leipzig 130: 273-286.

Sakata, T., K. Hikosaka, V. Shiomura and H. Tamate, 1980. The Stimulatory Effect of Butytrate on Epithelial Cell Proliferation by Insulin; Differences between in vivo and in vitro studies. In cell proliferation in the gastrointestinal tract (Ed. Appleton, Sunter, Watson), Pitman Medical Ltd: 123-137.

von Trott zu Solz, W. 1983. Vergleichend-anatomische Untersuchungen des Darmes von Rotwild (Cervus elaphus Linne), Damwild (Cervus dama Linne) und Muffelwild (Ovis ammon musimon), einschließlich der assoziierten Strukturen, 139 pp. Heft II der AKWJ-Schriftenreihe. Ferd. Enke Verlag, Stuttgart.

Van Soest, P. 1982. Nutritional ecology of the ruminant. O & B Books, Inc. Corvallis, Or. 373 pp.