

## MORPHOPHYSIOLOGICAL SPECIALIZATION AND ADAPTATION OF THE MOOSE DIGESTIVE SYSTEM

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**ABSTRACT:** During comparative studies of 66 ruminant species considering feeding habits and multiple morphological criteria along the digestive tract, moose specimens from one Swedish and two Finnish populations were studied. Data were evaluated relative to body mass. Focal points of specialisation in the head section were salivary glands, tongue and palate; furthermore all four stomach portions with the comp. small proximal fermentation chamber (PFC) and the large intestine with its relatively large distal fermentation chamber (DFC). Total salivary gland weight is changing from c.0.18% of BW in winter/spring to 0.30 in summer/autumn of which the parotid shows a swing from 0.09 - 0.13 (winter) to 0.14 - 0.18 (summer). The mobile free end of the tongue is at 36% above feeding type average, combined with a short torus linguae. Ruminoreticular capacity (41 l, range 30-72 l) is utilized at only 50-55%, omaso-abomasal capacity is 1:9 - 1:11 to ruminoreticular capacity. Rumen mucosa is evenly papillated but its surface regionally and seasonally differently enlarged, Pilae ruminis comparatively weak. Omasum extremely small, offers merely 1/5 of the absorptive surface of sheep or 1/3 of red deer omasum. All stomach ostia are comp. wide facilitating rapid food passage. Abomasal fundic mucosa is almost 100% thicker than average mucosal thickness of 14 grazing ruminant species. DFC volume is at 10-12% of PFC volume typical for concentrate selectors, unusual is the ratio of small to large intestinal length (60-76 : 40-45%). The spiral colon is almost 30% of total intestinal length. The functional implications of these findings for moose digestion and nutrition are discussed. Moose are seasonally adaptable concentrate (foliage) selectors depending on forage plant diversity.

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Renecker (1987) has shown with a wealth of hard data and comparative experimental evidence, that moose with their large body mass are not simply browsers like many small or medium sized ruminants, but their digestive strategy contradicts the "Bell-Jarman-Principle". It states that body size and social behaviour of ungulates is a function of the quality and quantity of the food resources that they exploit, and it contends that body size is the mechanism which determines interspecies differences in diet selection depending on the limitations of quality and quantity of forage resources (quotation from Renecker, 1987).

With patchy physiological and less morphological data available by then, Hofmann (1985) characterized moose, on the base of its commonly known feeding behaviour pattern and a few anatomical observations, as a large concentrate selector (CS) within the ruminant feeding type system as proposed by Hofmann

and Stewart (1972).

Since then, several American and European authors have reported on moose nutrition and energetics, on foraging behaviour and seasonal adaptations (Haukioja *et al.* 1982; Renecker 1987; Renecker and Hudson 1986; Risenhoover 1986; Risenhoover and Maas 1987; Nygren and Hofmann 1987; Vivas and Saether 1987; Hjeljord 1987; Schwartz *et al.* 1987; Risenhoover 1989), while Schwartz *et al.* 1988 and Renecker and Hudson 1990 provided data on the digestive kinetics of moose.

In a morphophysiological survey of ruminant digestive adaptations, Hofmann (1989) discusses the ecological significance of moose foraging and digestive strategies comparatively.

This paper summarises the morphological results accumulated from Northern European moose specimens studied in comparison

with the digestive system of 65 other ruminant species, amongst those 15 species of Cervidae.

### MATERIAL AND METHODS

We investigated 34 moose of both sexes from one Swedish and two Finnish populations with a body weight range from 189 to 366 kg.

For fixation and preparation methods of entire animals, heads, organs or parts thereof (gross and microscopic anatomy, electron microscopy, morphometric techniques) we refer to Hofmann (1966, 1973), Schmuck (1986), Ludwig (1986), Thomé (1990), Werner (1990) and, in this volume, to Hofmann and Nygren (1991). A series of 10 late foetuses and juveniles up to 2 months p.p. were additionally used for stomach development studies.

### RESULTS

**HEAD PORTION:** By comparison, moose have a particularly wide mouth; the ratio head length to unilateral mouth width is 3.78 - 3.86 : 1 (similar to giraffes and several small concentrate selectors). The facial muscles serving the lips are highly differentiated, especially *M.levator labii maxillaris* which terminates upon a penicillar tendon system (Meinertz 1956), completed by *M.caninus* and *M.depressor labii maxillaris* which originate together from the facial tuber. The buccinator muscle, however, is relatively weak. The masseter muscle comprising of two overcrossing main portions attaches in an extremely compact manner onto a very small mandibular surface area. Its total relative weight, however, is around 0.20 % of body weight (BW) as in all other ruminant species irrespective of feeding type (Axmacher and Hofmann 1988).

The salivary glands (Fig.1) are extremely adaptable to changing forage quality and availability throughout the year. Our relatively small sample points to a total salivary gland weight in winter of c. 0.16 - 0.18 / of BW

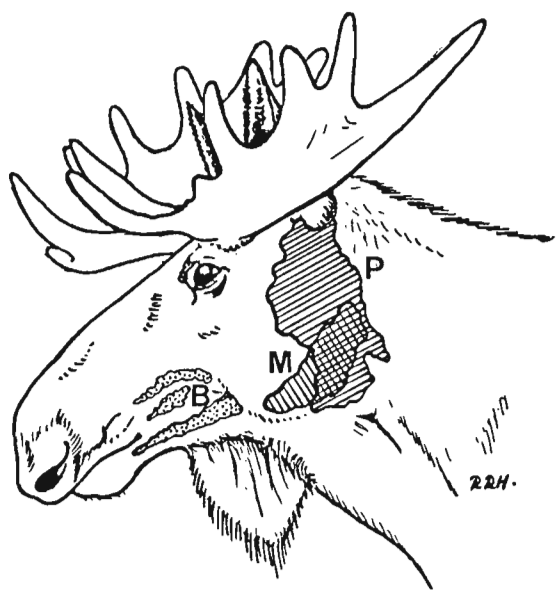


Fig. 1. Moose salivary glands in situ: B = buccal glands, dotted (dorsal, middle and ventral); M = mandibular gland, oblique-vertically hatched; P = parotid gland, oblique-transversely hatched, partly overlying M.

and an average total salivary gland mass of c. 0.23 - 0.28 % in summer (with calves up to 0.30 % of BW). The serous parotid gland is always largest and shows an adaptive "swing" from 0.09 in autumn (rut) to 0.13 in winter, but is up to 0.14 - 0.18 of BW over summer. Microscopically (Thomé 1990), the moose parotid has at 6.5 a very small percentage of connective tissue and at 9.0 % a relatively high proportion of blood vessels, about 13 % of the glandular tissue consists of striated ducts, 84.5 % of end pieces. The mandibular gland has 40 % serous and 60 % mucous cells. 16 % of the glandular tissue consists of striated ducts. In the sublingual (monostomatic) gland, there are at 16.4 % in moose two times more serous end pieces than in grass eating species. The highly developed ventral buccal gland has a much higher proportion of serous glandular end pieces, especially in its caudal portion, than grazers (similar to roe deer, Hofmann 1976).

The oral mucosa thickens and cornifies

mainly in exposed areas. The buccal mucosa carries densely placed conical papillae, some of which are bi- or tritubercular.

The **hard palate** (Fig.2) is particularly long and narrow. The ratio of the rugated rostral portion to the dental plate is at 1 : 6.2 to 1 : 9.0 similar e.g. to giraffe and roe deer, i.e. it is significantly shorter than in all grass eating ruminant species. Moose have two rows of *rugae palati* (18 + 19 to 23 + 22) with aborally directed papillae.

The **tongue** (Fig.3) is adapted to the slender palatine shape, its short *torus linguae* functionally opposes the unrugated caudal portion of the palate. The mobile free end of

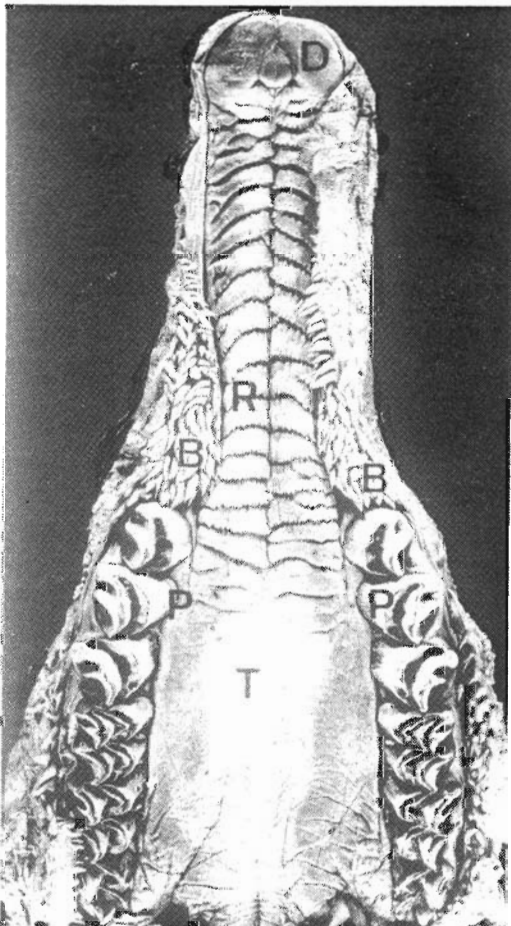


Fig. 2. Hard palate of a moose cow, ventral aspect. B, buccal papillae; D, dental plate; P, premolars; R, rugae palati (rugated portion); T, unrugated portion of palate, opposite *Torus linguae*.

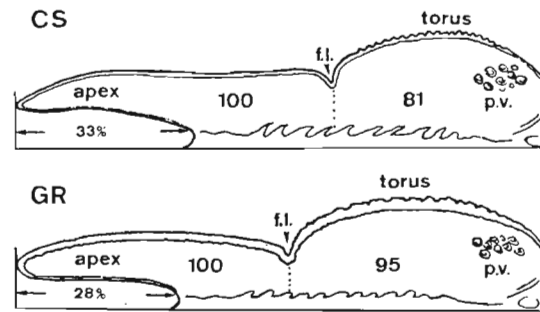


Fig. 3. Comparison of CS tongue (above) with GR tongue (below) as a schematic side view; f.l., fossa linguae; p.v., papillae vallatae. Values for moose are, from left to right: 36 %, 100, 80 (from Hofmann, 1989).

the tongue is at 36 % of the total lingual length well above the average of most other concentrate selectors (33 %) and significantly above most grass eaters, except cattle. The ratio corpus portion to caudal torus is at 1 : 0.80 below CS average. The filiform papillae and fungiform papillae are species-specific, the latter contain more taste buds than in most other CS. There are 40 *papillae vallatae* (18 right and 22 left), which is well above the CS average of 27, but they are very poorly equipped with taste buds - only two per section, as opposed to an average of 11.26 in 14 concentrate selectors investigated (Schmuck 1986).

Moose **cheek teeth** (premolars, molars) are relatively short, narrow and conical; their pointed enamel tubercels (Fig.2) make them well suited for puncture crushing of dicot plant material, less for grinding fibrous monocots sideways. Judging from changes in food particle size, moose do not chew intensely during summer and autumn when they can afford to be "wasteful" and to pass lignified material rapidly, but ruminate intensely for particle size reduction in winter (Nygren and Hofmann 1990).

**STOMACH PORTION:** At birth, the **ruminoreticulum** (Fig.4) already shows its characteristic shape: a high but relatively short rumen added to by a large reticulum. All

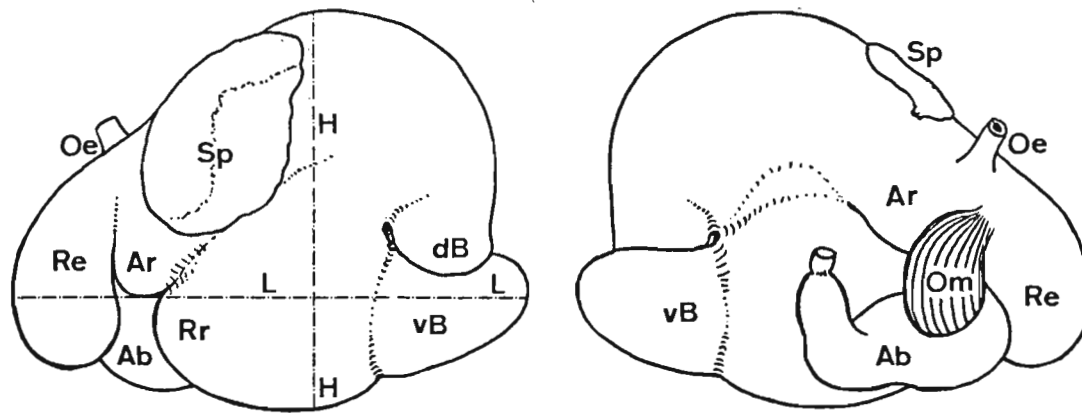


Fig. 4. Moose stomach, moderately filled (exenterated), left and right aspect. Ab, Abomasum; Ar, Atrium ruminis; dB, dorsal blindsac of rumen; H, height measure line; L, length measure line; Oe, Oesophagus (cut off); Om, Omasum; Re, Reticulum; Rr, Recessus ruminis; Sp, Spleen; vB, ventral blindsac of rumen.

linear dimensions of the three forestomach compartments increase allometrically from birth to mature age about sixfold; ruminoreticular capacity, however, increases about 250 x (from c. 150 ml to an average total capacity of 41 l, range 30 - during rut -, to 72

l, early November).

The moose rumen rarely extends over the median plane to the right side, its blindsacs do not reach the pelvic inlet as in grazers (Fig.5). The ruminal blindsacs are evenly wide at their base but the ventral blindsac has more than

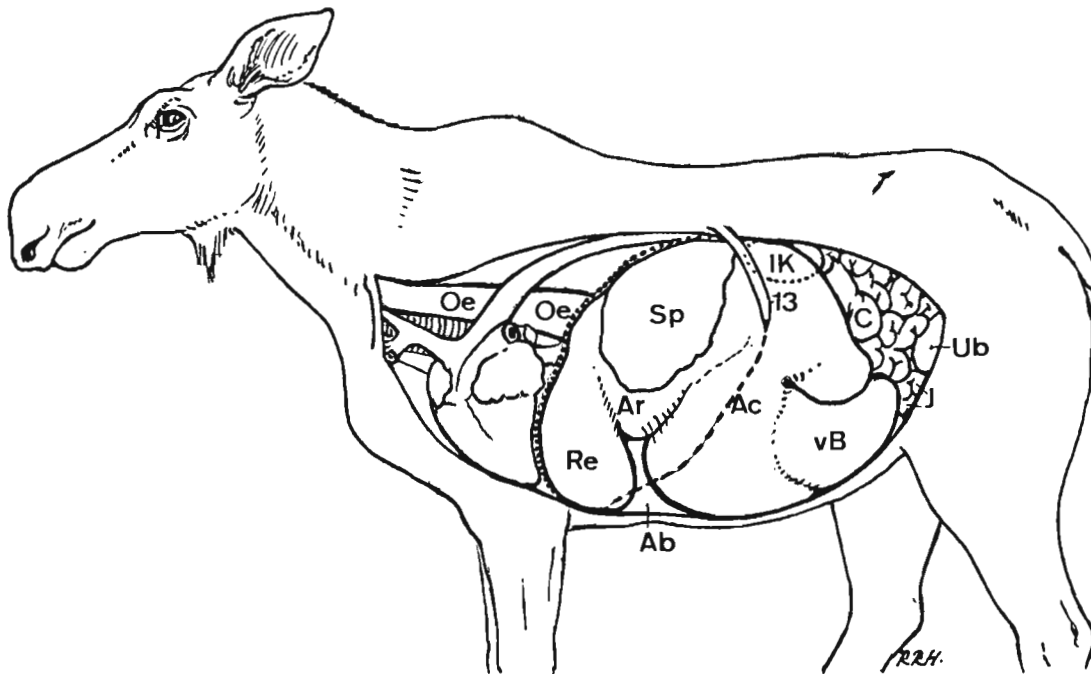


Fig. 5. Moose viscera in situ, left aspect. Ab, Abomasum; Ac, Arcus costarum (interrupted line); Ar, Atrium ruminis; C, Caecum; J, Jejunum; IK, left Kidney; Oe, Oesophagus; Re, Reticulum; Sp, Spleen; Ub, Urinary bladder; vB, ventral blindsac of rumen; 13, last (left) rib; dotted line: diaphragm.

twice the length of the dorsal one. As observed in many other CS (Hofmann 1973, 1989; van Hoven & Boomker 1985), moose seldom use more than 0.60 of their ruminoreticular space, i.e. fresh contents are c. 20 - 35 kg of semiliquid mass. As a general rule, the liquid level is just below the reticulo-omasal orifice, which marks the end of the reticular groove.

Morphological evidence (Hofmann 1973, 1984) strongly supports the suggestion, that ruminants are maintaining their *sulcus ventriculi* throughout life since it does not become atrophic or reduced. Hence it can be safely assumed, that also adult moose are using their well developed reticular groove (length 15.5 - 18 cm) to bypass saliva-diluted soluble nutrients (released in the mouth by puncture crushing from leaves and fruit), directly into the abomasum.

The ruminal mucosa is amply characterised in this volume (Hofmann and Nygren 1992). There is no unapillated area, even the relatively thin/weak ruminal pillars carry (short) papillae. During summer, they enlarge the mucosal surface up to 21 x, in winter up to 11.5 x i.e. a reduction of c. 50 %. All internal openings are relatively wide facilitating rapid food passage, e.g. *ostium intraruminale* and ruminoreticular opening. The "ruminants' bottleneck", the reticulo-omasal orifice, can be regulated (widened) for rapid passage (Ehrlein and Hill 1969; Hofmann 1984; Renecker 1987); its resting size is already c. 3 x 2 cm. Its claw-like papillae fall off when nutrition becomes poorer.

The **reticulum** is capacious; it is lined by a crested cornified mucosa with basically undivided reticular cellulae. The crests are at 1.9 - 3.2 mm very low; they and the bottom of the cellulae are studded with regularly spaced, pointed horn papillae. Towards the cardia, the crests show gradual transitions into absorptive papillae, similarly on the ruminoreticular fold.

The **omasum** (Fig.4) as in all CS in re-

lation to body mass, is comparatively small and distinguished by its unusually elongate shape (already preformed at birth); its length is more than twofold its height, ratio 1 : 2.17. Werner (1990) has shown in his comparative study of the omasum of 17 ruminant species, that an adult moose (CS) of 280 kg offers about the same internal (mucosal) surface as the omasum of sheep, a grass and roughage eater (GR) of only 50 kg BW (n = 3). The total absorptive surface area amounts to only 1820 cm<sup>2</sup> (range n = 3: 1.740 - 2.038), which is extremely small compared to cattle (33.380 - 42.010 cm<sup>2</sup>) of only about double the body mass of moose. 92.5 % of all moose omasal surfaces are provided by 12 + 11 laminae of 1st and 2nd order, while 21 omasal folds of 3rd order are contributing the rest, added to by 26 low crests along the omasal curvature. Accordingly, moose have at 20 mm relatively narrow interlaminal recesses. Particularly wide, however, is the omasal-abomasal orifice, which is at 98 - 103 mm exactly as long as in cattle.

The **abomasum** (at birth 130 % of the three forestomach portions) increases its capacity into adult age only 12 - 25 x (from 200 ml to c. 2.4 - 5.1 l). The adult ratio omasum/abomasum : ruminoreticulum is variable from 1:9 - 1:11.

There are 13 - 15 low spiral folds enlarging the fundic (proper gastric) glandular mucosa 5 - 6 x. At 1146 µm, this mucosa is much thicker than the average mucosal thickness calculated from 12 CS species (873 µm) and about twice the mucosal thickness of grazers of similar body mass. Moose have also very deep gastric crypts (Axmacher, 1987). It was estimated that they can produce c. 100 % more gastric HCl than comparable grazers. The pyloric mucosa is 1460 µm thick.

**POST-GASTRIC PORTION:** The moose **intestine** (Fig.6), situated in the supraomental recess and occupying most of the right half of the abdominal cavity is 16 - 21 x body length; its average total length is 43.7 m (range 35.9-

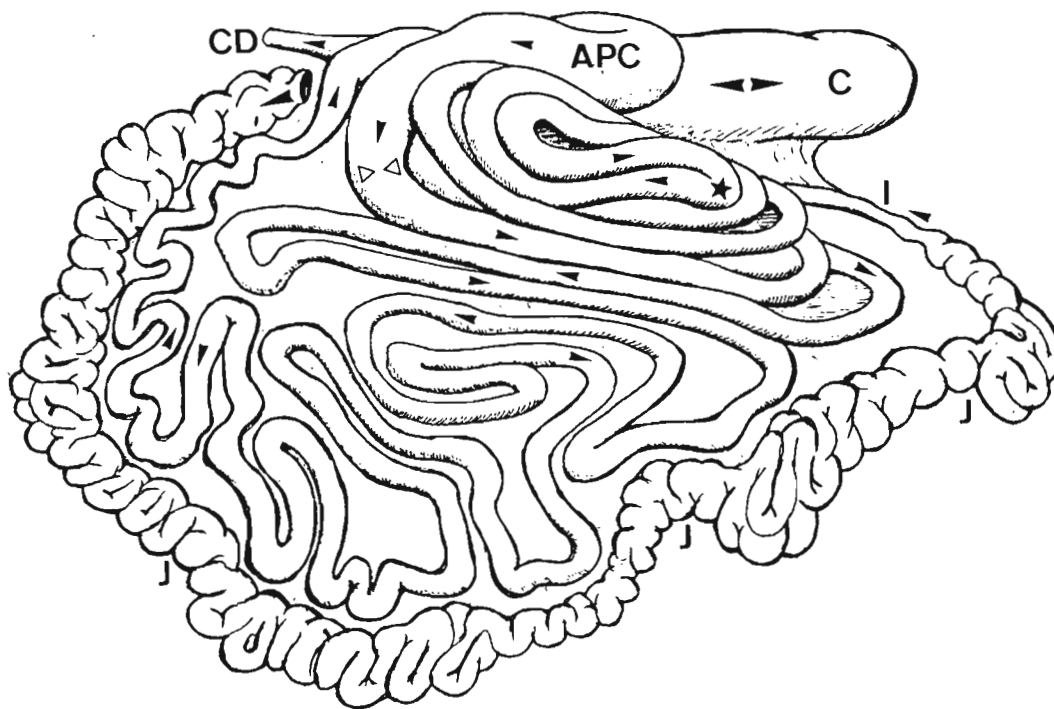


Fig. 6. Moose intestine, exenterated (modified from Westerling, 1975).

APC, Ansa proximalis coli; C, Caecum (APC + C = distal fermentation chamber, DFC); CD, Colon descendens; I, Ileum; J, Jejunum. Arrows indicate flow of ingesta; asterisk: ansa centralis, turning point of spiral colon coils.

56.9) which appears to vary with season, perhaps more so with forage preference. It is unusual, even amongst CS, in its extreme ratio of small to large intestine length. This ranges from 59 : 41 to 67.3 : 32.7; in the majority of cases measured, it is 63 : 37. The comparable ratio of grazers is 81:19! The average small intestine length is 27.6 m (range: 22.2 - 34.7), the average large intestine length is 16.0 m (range 13.5 - 22.2).

Moose have a particularly long spiral colon (29 % of total intestinal length) which forms 3-4 irregularly placed centripetal and 3-4 centrifugal turns (Westerling 1975) as a relatively narrow gut portion. Besides being a long absorptive passage tube, it provides a backstop mechanism (Hofmann 1985, 1990) into the distal fermentation chamber (DFC). It comprises of the much widened *caecum-cum-ansa proximalis coli* (Fig.6). The caecal capacity varies seasonally or according to for-

age selected from c. 1200 - 2300 ml; similarly, ansa proximalis capacity varies from 1400 to 2700 ml and it more or less abruptly tightens to lead into the spiral colon. The average combined capacity of the DFC amounts to 3920 ml (range 2500 - 6400). The ratio PFC (ruminoreticulum): DFC (caecocolon) is 10 - 12 : 1 in moose, with the lowest values in July and the highest in November. It is peculiar, that moose have a very thin DFC mucosa: it is only 167  $\mu\text{m}$  as compared to 618  $\mu\text{m}$  in roe deer in the ansa proximalis coli (Ludwig 1986) and 335.5  $\mu\text{m}$  in the caecum (roe deer: 663.4). Accordingly, the surface enlargement by Lieberkühn's crypts is only 8.4 x in moose but 17.2 x in roe deer. Seasonal micro-changes are to be expected but have not yet been investigated in moose.

The liver finally is situated to the right of the median plane, mostly in the intrathoracic portion of the abdomen. It is relatively large as

in all CS. At 2850 - 6360 g it is clearly related to individual body weight but seasonal variations are almost certain. The average percentage of BW is 1.62 % (range 1.33 - 2.20), in calves it is usually around 2 %. Due to its absolute size, the moose liver tissue is slightly richer in connective tissue than that of smaller CS species (lobular demarcations well visible) but less than in cattle (Liedtke 1989).

### DISCUSSION AND FUNCTIONAL CONCLUSIONS

In the head portion of their digestive system, moose show extreme adaptive variations of the structures facilitating selective food prehension (highly mobile lips and long mobile tip of the tongue for grasping even small leaves or berries) combined with an unusually wide mouth for rapid intake of large quantities of suitable forage. Mandibular shape, angulation and surface area combine with very compact masseter muscles to form a masticatory apparatus which is better suited for puncture crushing of dicot material rich in plant cell contents (soluble nutrients), than for grinding down fibrous food (plant cell wall, i.e. cellulose). The teeth are built accordingly.

Moose have at least twice the relative mass of saliva producing tissue available which cattle and other grazers rely on, and the proportion of serous saliva is considerably higher in moose. They obviously use their mainly serous saliva rich in carbonates and specific proteins not only for buffering the VFAs in the rumen, but also to dilute rumen contents and to bypass soluble nutrients released in the mouth during mastication (which would be lost, otherwise, to the ruminal bacteria). Their strategy to propel undigestible fibrous or lignified food, especially browse material, rapidly through their stomach system (in order to provide space for new intake) requires much diluting liquid, while salivary carbonates are neutralised by excessive HCl produced in a thick abomasal mucosa. To what extent moose use their constantly released

serous saliva also to overcome secondary plant compounds (polyphenolic complexes, tannins, conifer terpenes etc.) is not clear. Their ability to consume larger quantities of pine needles and other coniferous material is pointing into that direction.

Moose like other selectors of easily digestible forage with concentrated nutrients, are preselecting their food by olfaction which explains the rather poor development of taste receptors on their tongue. Torus linguae, palatine ridges and papillae plus densely placed, large buccal papillae all provide in the oral cavity an efficient forage transport system. It is adapted to the type of plant material which moose are plucking and which they crush (for sap release) before swallowing and rumination. Given the food which wild moose select from a diverse vegetation, and their body size, their ruminoreticulum is absolutely big, but it is relatively small in comparison with similar sized grazers. It occupies not even the left abdominal half completely. This proximal fermentation chamber has a relatively weak muscular wall, hence it is poorly adapted to move fibrous monocot plant material around. It is lined by a densely papillated, greatly enlarged absorptive mucosa which is well adapted to higher fermentation rates (efficient absorptive removal of VFAs to prevent acidosis).

While wide openings in and between the various compartments of the forestomach system make the moose stomach unsuitable for efficient (slow) cellulolysis as observed in grazers, they facilitate a quick turnover of high quality, concentrate forage, i.e. rapid passage of large particles of undigestible plant parts and of "ruminal escape" material broken down further on in the tract.

The capacious reticulum with its cornified, pointed papillae separates broken down and fermented food particles from larger plant parts still requiring rumination; on contraction its mucosal relief retains unchewed foliage which is prevented from entering the

omasal canal by claw-like papillae. The small alpine omasum with its relatively small absorptive surface appears to suffice in completing VFA absorption, but would absorb too few minerals and too little water (as is the case in grazing ruminants with a much bigger, multilaminated omasum). It appears to be, however an efficient muscular transfer pump, a function enhanced by its elongate shape.

The abomasum receives liquid gushes containing relatively big plant particles (mostly < 4 mm, but many up to 8 or 10 mm!) and numerous ruminal bacteria, which die off in the excessive HCl and are digested, as a constant source of endogenous nitrogen, *in loco*. More HCl is bound by salivary carbonates arriving here via the ventricular groove and the macerating effect of the abomasal HCl upon foliage hemicelluloses must be considerable.

Moose have a slightly longer intestine than most other concentrate selectors, but there is no other ruminant in this or other feeding type groups with a similar long large intestine portion: 37 - 41 % of the total length! Since moose also have a particularly long spiral colon (almost one third of the total length) and since their DFC can take about 4 litres of fermentable plant material, i.e. more than a roe deer's rumen capacity, one can safely assume that hindgut fermentation (especially of hemicelluloses broken down in the abomasum) plays a vital role in moose digestion. Hence they heavily rely on a fractionated forestomach-cum-hindgut fermentation (Hofmann 1989), totally unlike cattle and other grazers. This is apparently more so in autumn - perhaps to recover rut energy losses, by fully utilising all morphophysiological avenues to extract nutrients from fresh plant material before winter reduces forage diversity. The relatively high surface enlargement factor (SEF) which wild moose retain in their rumen over winter supports the assumption that even then, by first choice, they select nutritious, digestible plant material, while the

particle reduction to less than 1 mm, achieved by more intensive rumination (Nygren and Hofmann 1990), suggests that also more cellulolysis occurs than in summer, which the absolute size of both the rumen and the caecocolon would permit them to achieve.

Thus, all morphological data and their functional interpretation support and complement Renecker's (1987) conclusions. Moose are not simply large "browsers" but seasonally highly adaptable large concentrate (foliage) selectors relying on plant diversity in low, middle and higher strata of Northern habitats - this is why neither monoculture commercial forests nor artificial feeding (e.g. in Zoos) can easily satisfy moose forage requirements.

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