The browser wars (1968-2004) – and beyond

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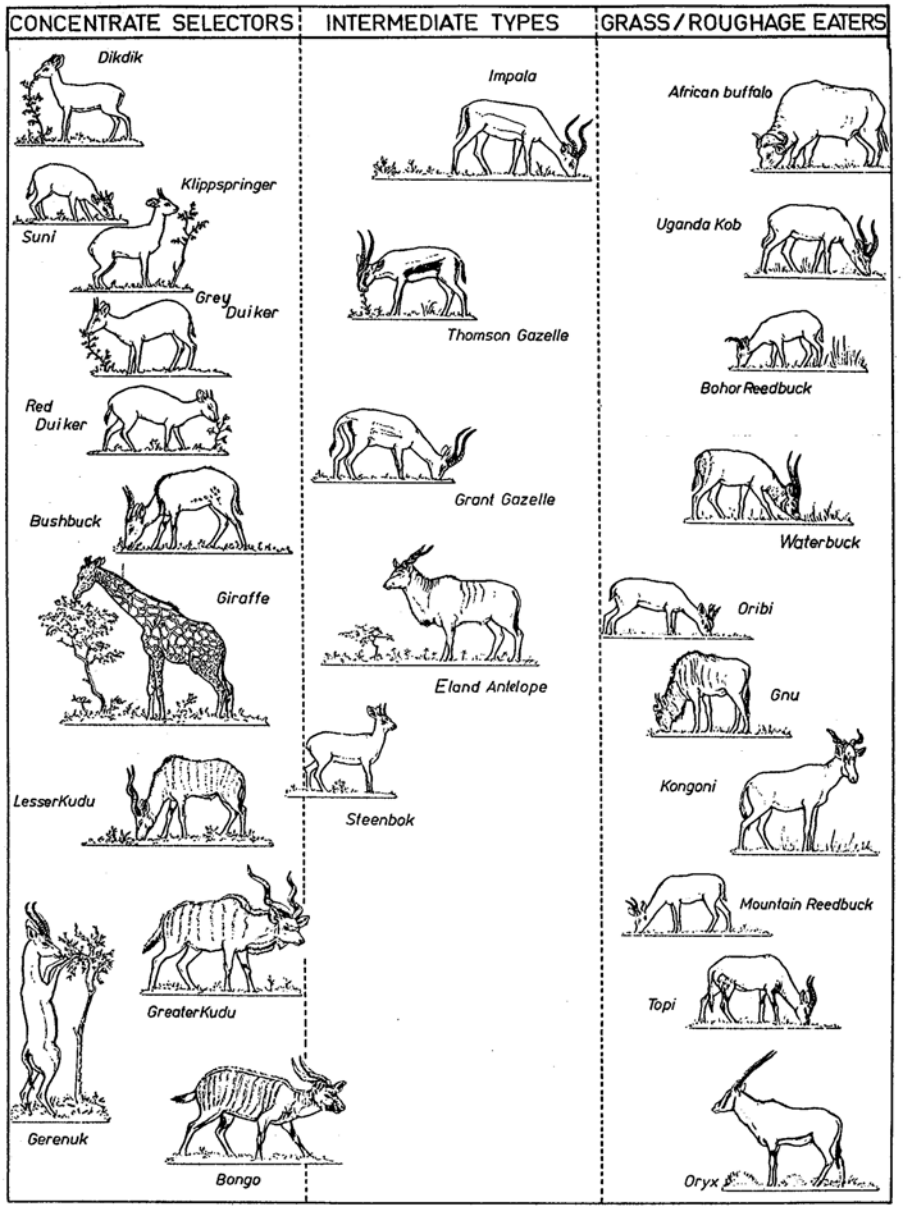
Prague 2019

University of Zurich[UZH]

Clinic of Zoo Animals, Exotic Pets and Wildlife

Comparative approaches



from Hofmann (1989)

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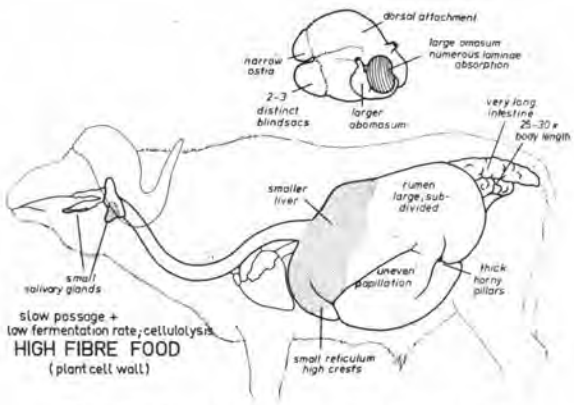

Fig. 1: The African buffalo, a non-selective roughage grazer.

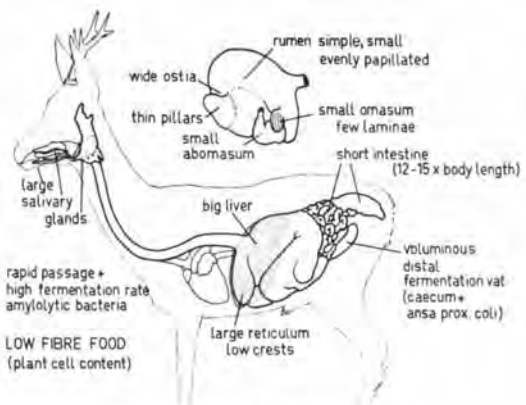

Fig. 2: The roe deer, a concentrate selector.

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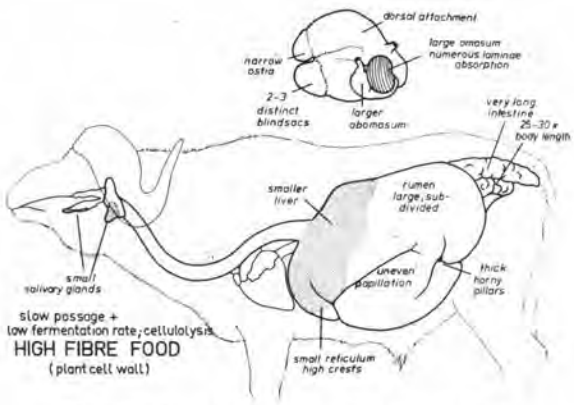

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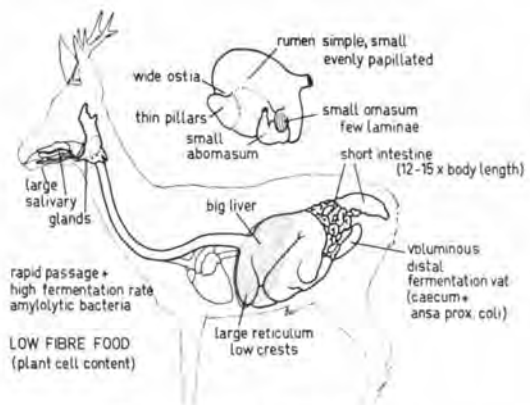

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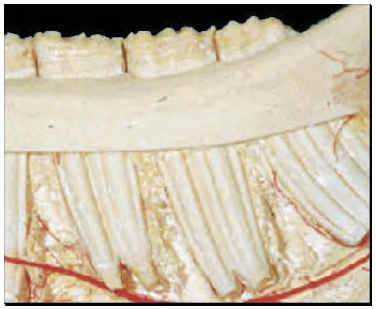
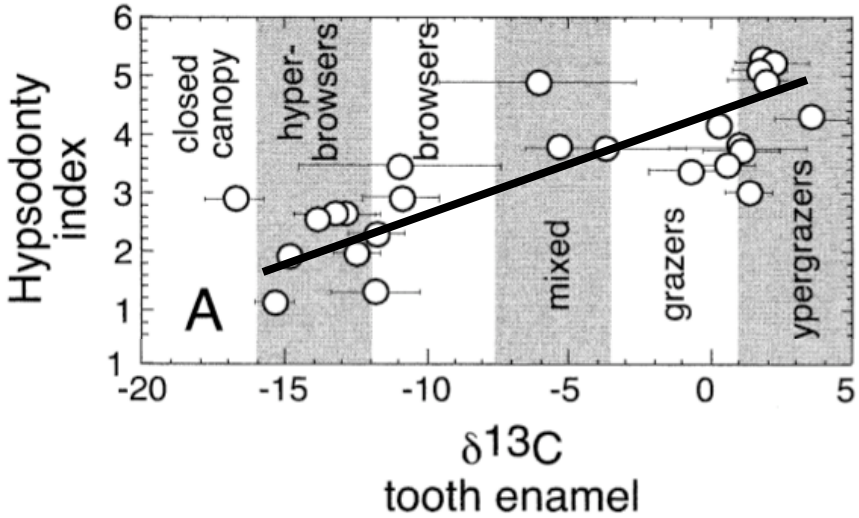
Form and Function

- the probably oldest approach to biology: linking form and function

Form and Function

- An evident link: hypsodonty index and grass consumption





from Cerling et al. (2003)

Form and Function

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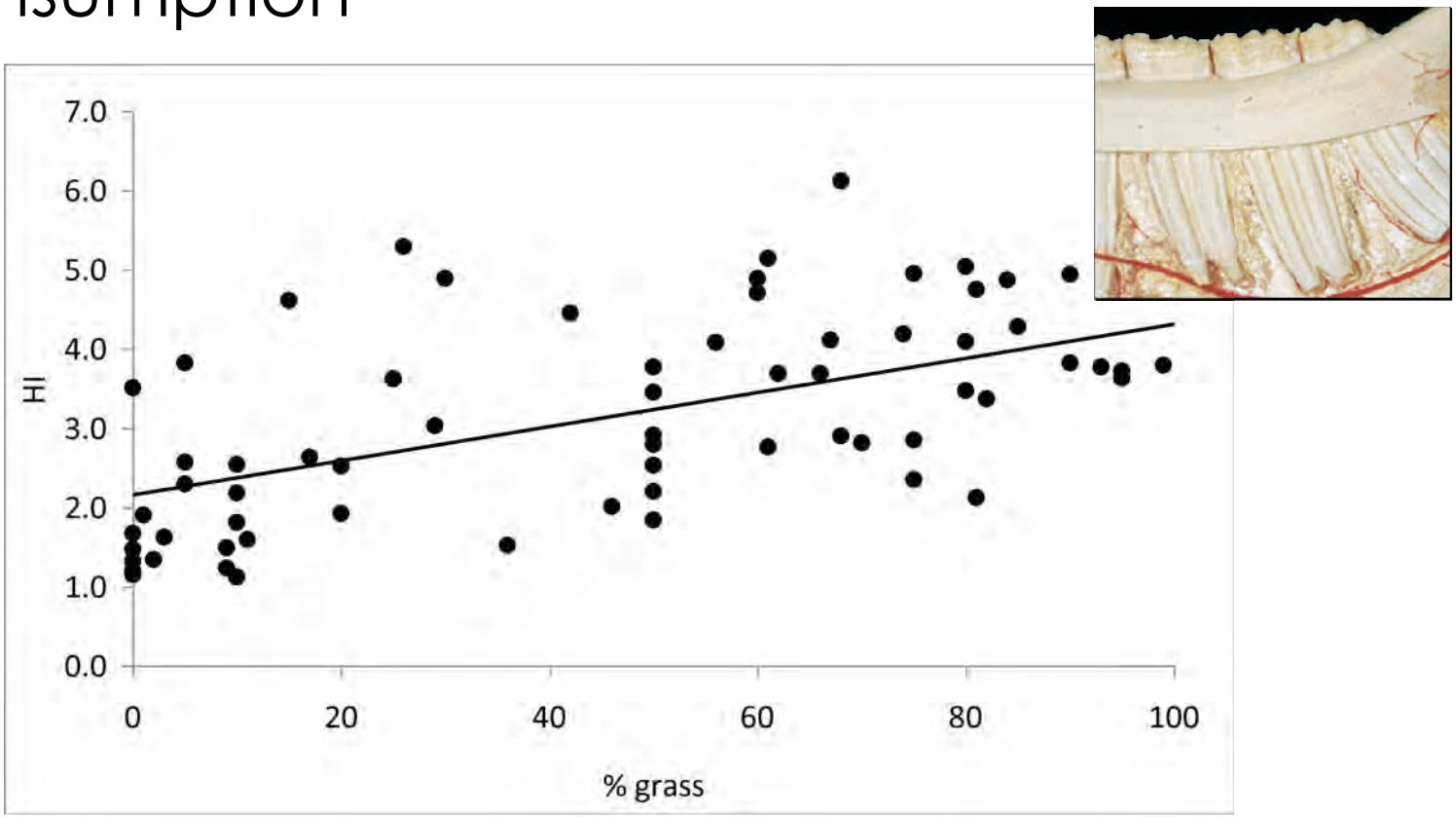

Own evaluation

Form and Function

- Conclusion: diets of grazers must be more abrasive

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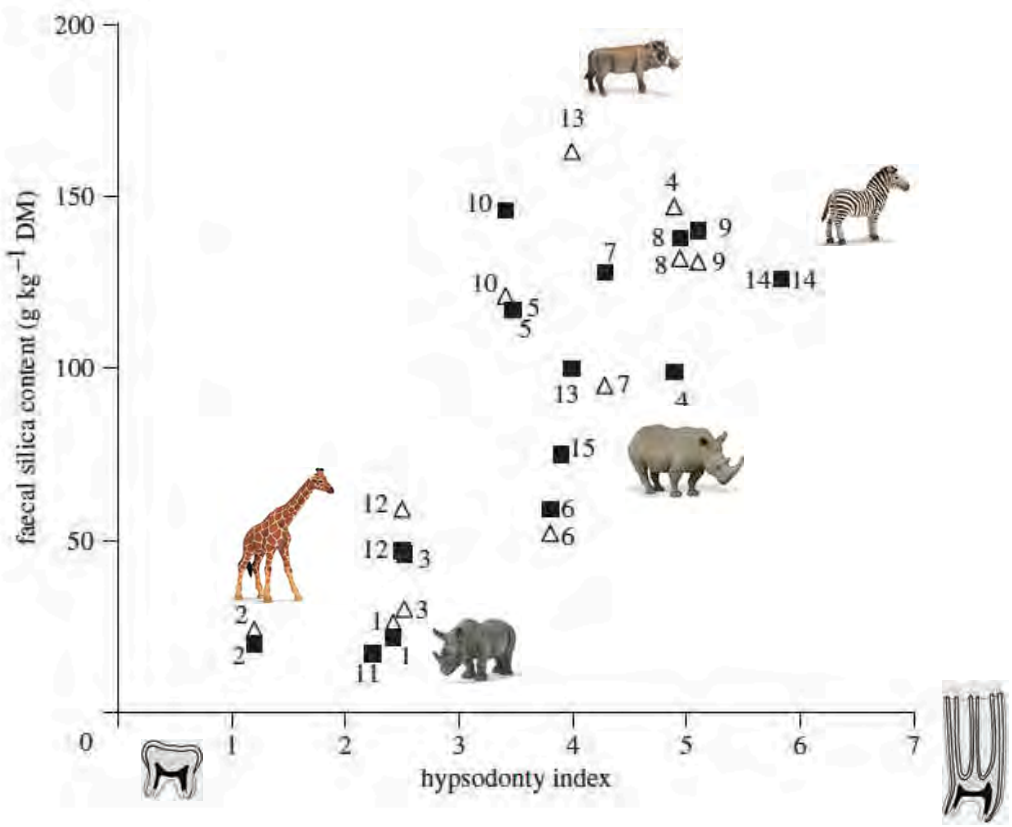
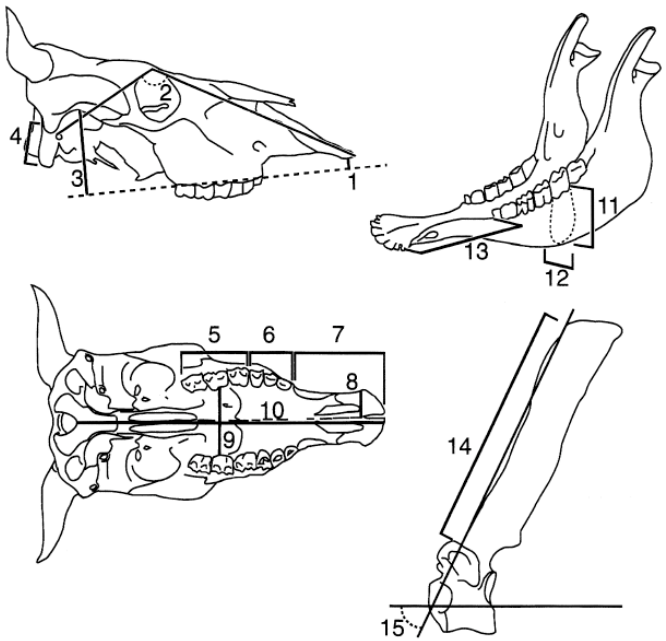
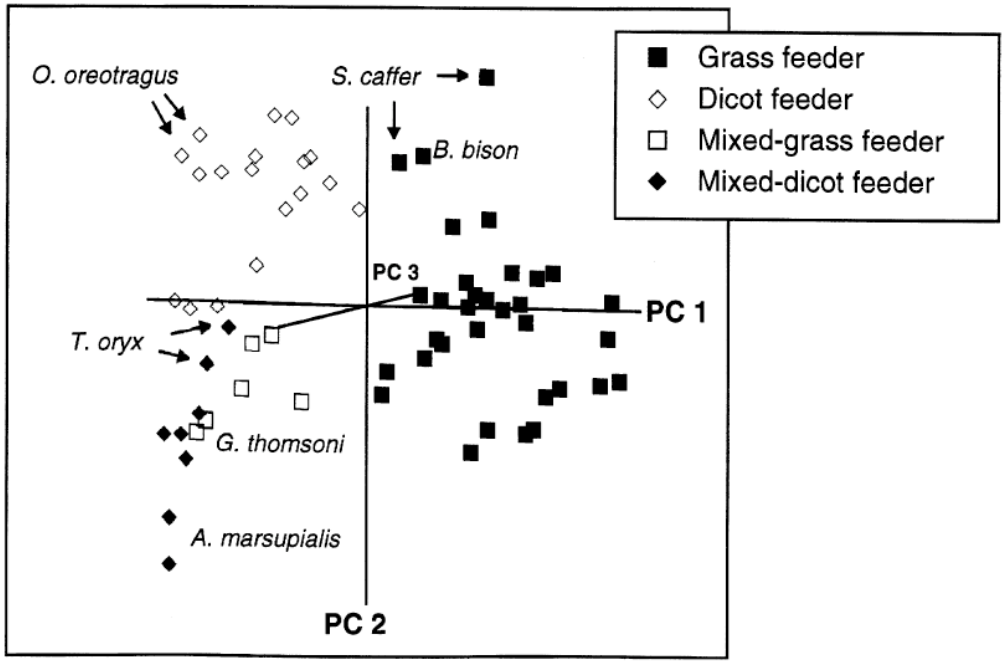


Hummel et al. (2011)

Form and Function

- Often, the pattern may be obvious but the underlying cause (function) is not





from Spencer (1995)

The Comparative Method

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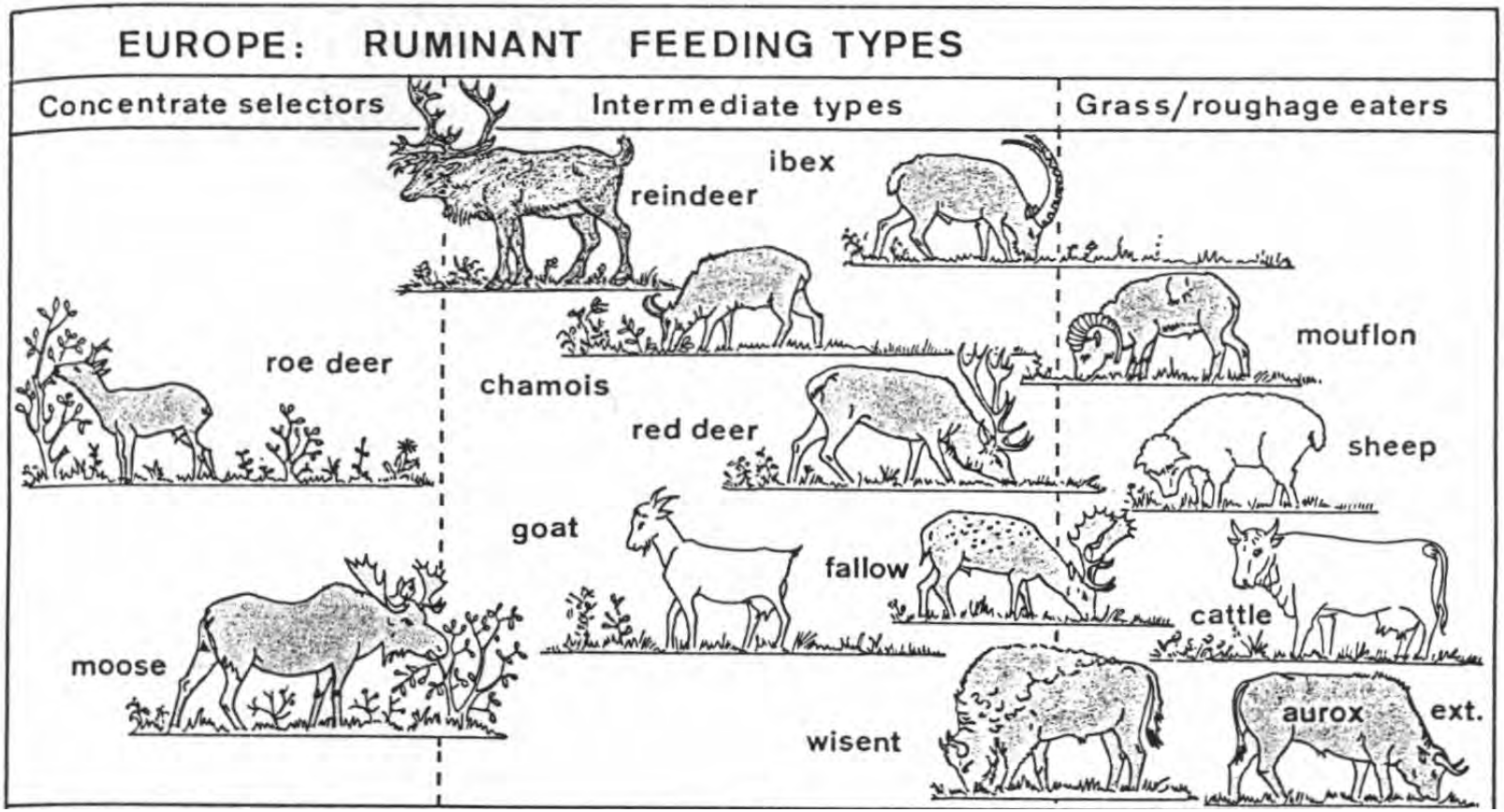
  (i.e. we determine convergence)
- '*because...*'

  ... and we assume a function

  ... and we use words to label our findings

Don ‘t believe names, think for yourself

- **What is a ‘concentrate selector’?**



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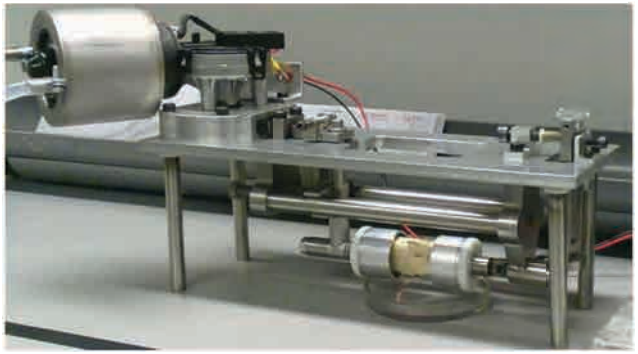
Convergence is not a proof of function (only circumstantial evidence).

Mechanical modelling of tooth wear

Aleksis Karme[1,†], Janina Rannikko[1,†], Aki Kallonen[2], Marcus Clauss[3] and Mikael Fortelius[1]



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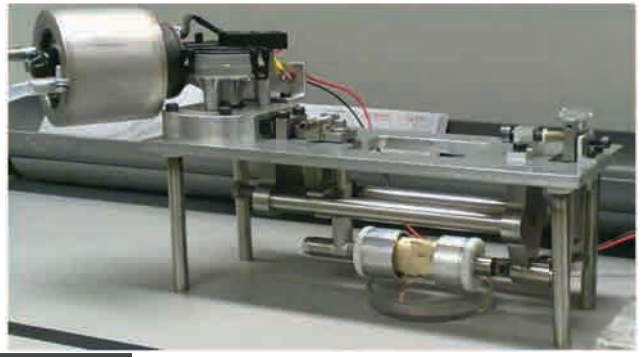

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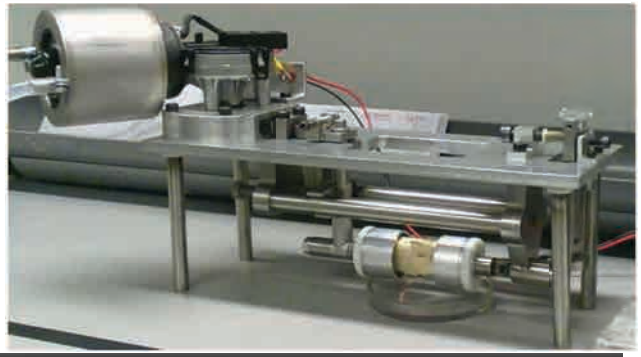
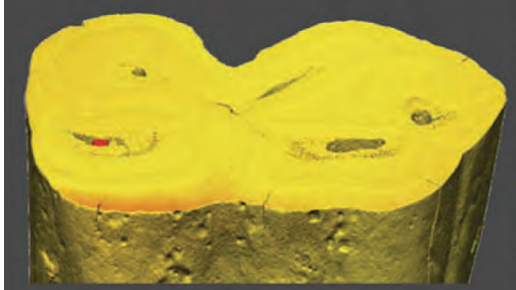
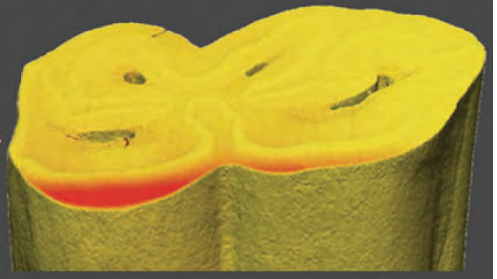
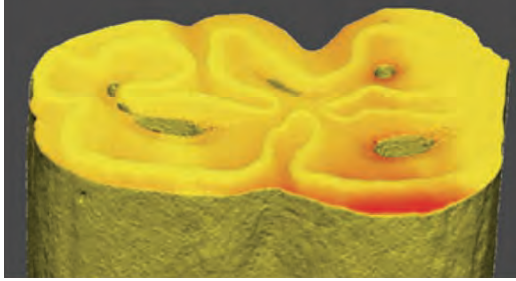




lucerne, L
height change
0.003 mm
wear rate per year
0.18 mm
lifespan (12 cm)
658 years

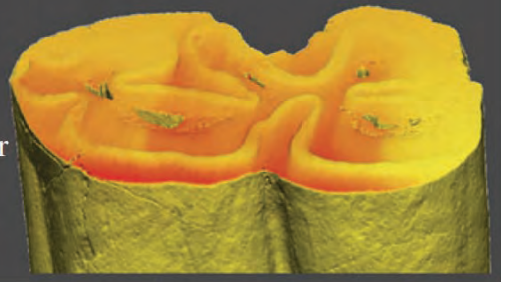
grass, G
height change
0.060 mm
wear rate per year
4.1 mm
lifespan (12 cm)
29 years





grass + rice, GR
height change
0.067 mm
wear rate per year
4.5 mm
lifespan (12 cm)
27 years

GR + sand, GRS
height change
0.134 mm
wear rate per year
9.0 mm
lifespan (12 cm)
13 years



the browser wars

The term "browser wars" is the name given to the competition for dominance in the web browser marketplace - the struggle between Internet Explorer and Netscape Navigator during the late 1990s, and the growing threat which Mozilla Firefox poses to Internet Explorer from 2004 onward.

(Wikipedia)

But why is the web-browser called “browser”?

browser = animal that eats (mainly) browse?

especially as opposed to

grazer = animal that eats (mainly) grass?

Did you know that there are 'grazing' and 'browsing' mites?

Siepel H, de Ruiter-Dijkman EM (1993)
Feeding guilds of oribatid mites based on their carbohydrase activities.
Soil Biol Biochem 25:1491–1497

Did you know that there are 'grazing' and 'browsing' carnivorous fish?

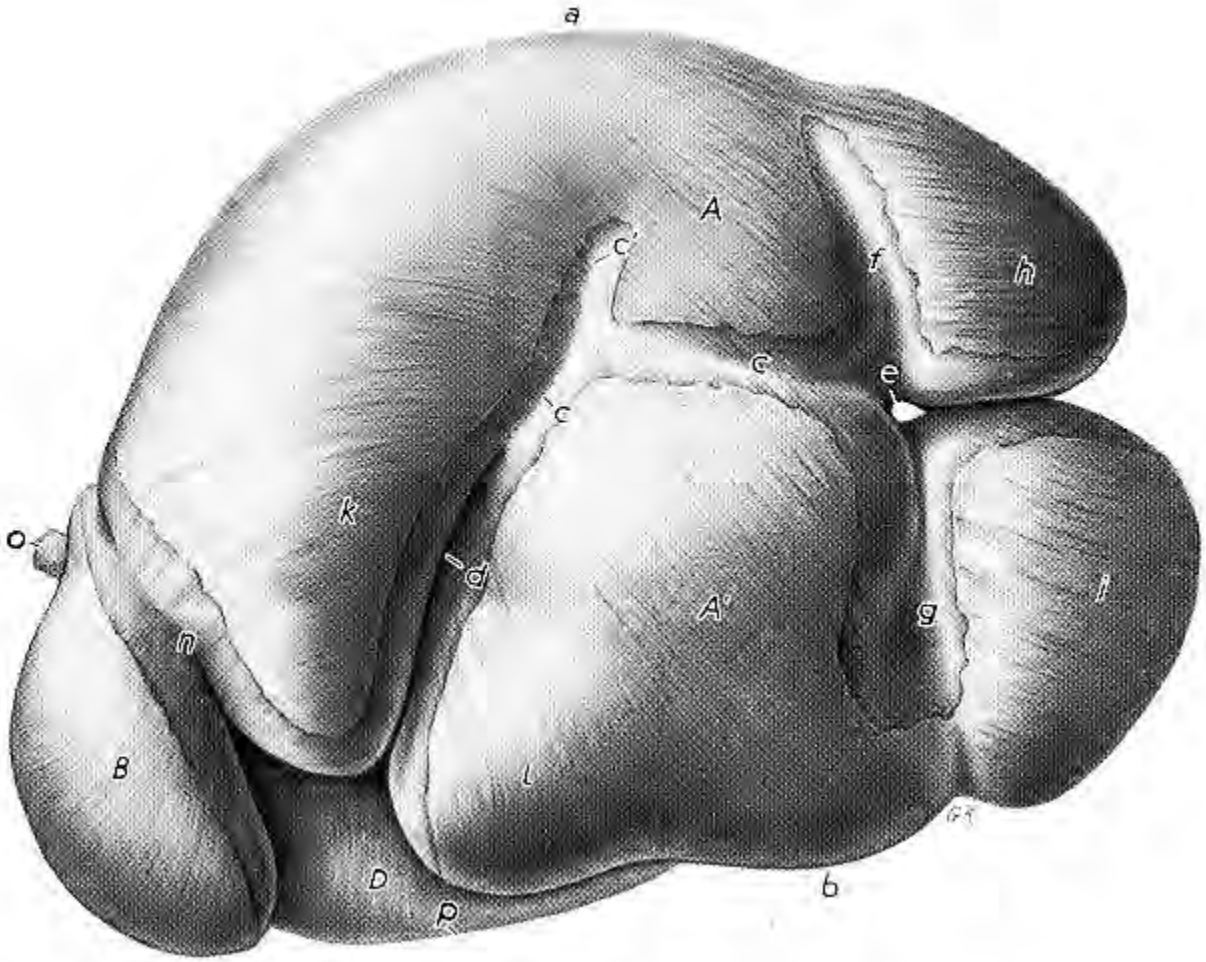
Lechanteur YARG, Griffiths CL (2003)
Diets of common suprabenthic reef fish in False Bay, South Africa.
Afr Zool 38:213–227

Coupled with Hofmann's term "concentrate selector", the word "browser" has become a synonym for an organism selectively feeding on highly digestible material.

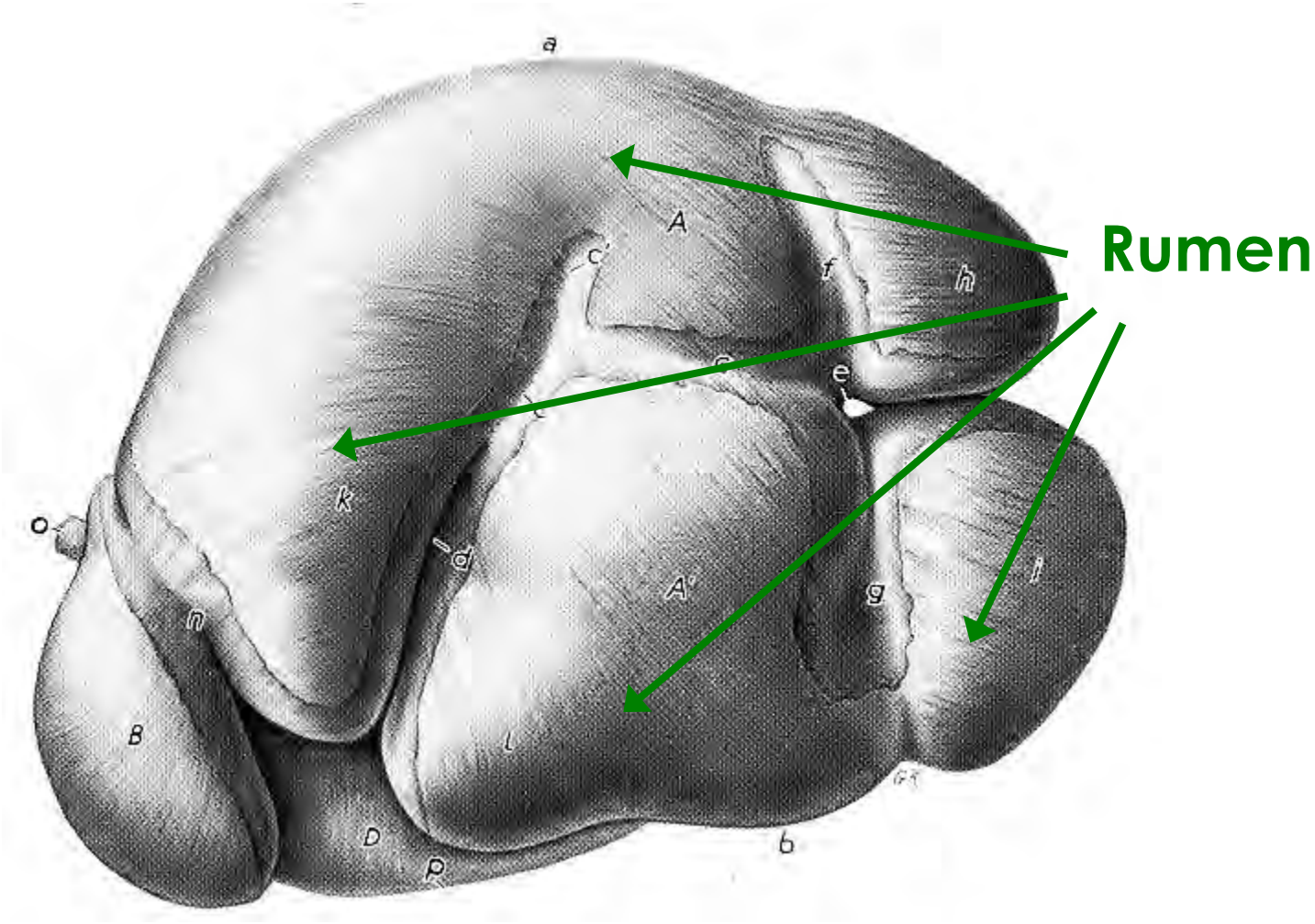

OEKOSOFT
OKAPI
ORACLE
OEKOSOFT
OKAPI

until 1970:

All ruminants are similar and function as cattle and sheep do.



(from Nickel-Schummer-Seiferle 1967)



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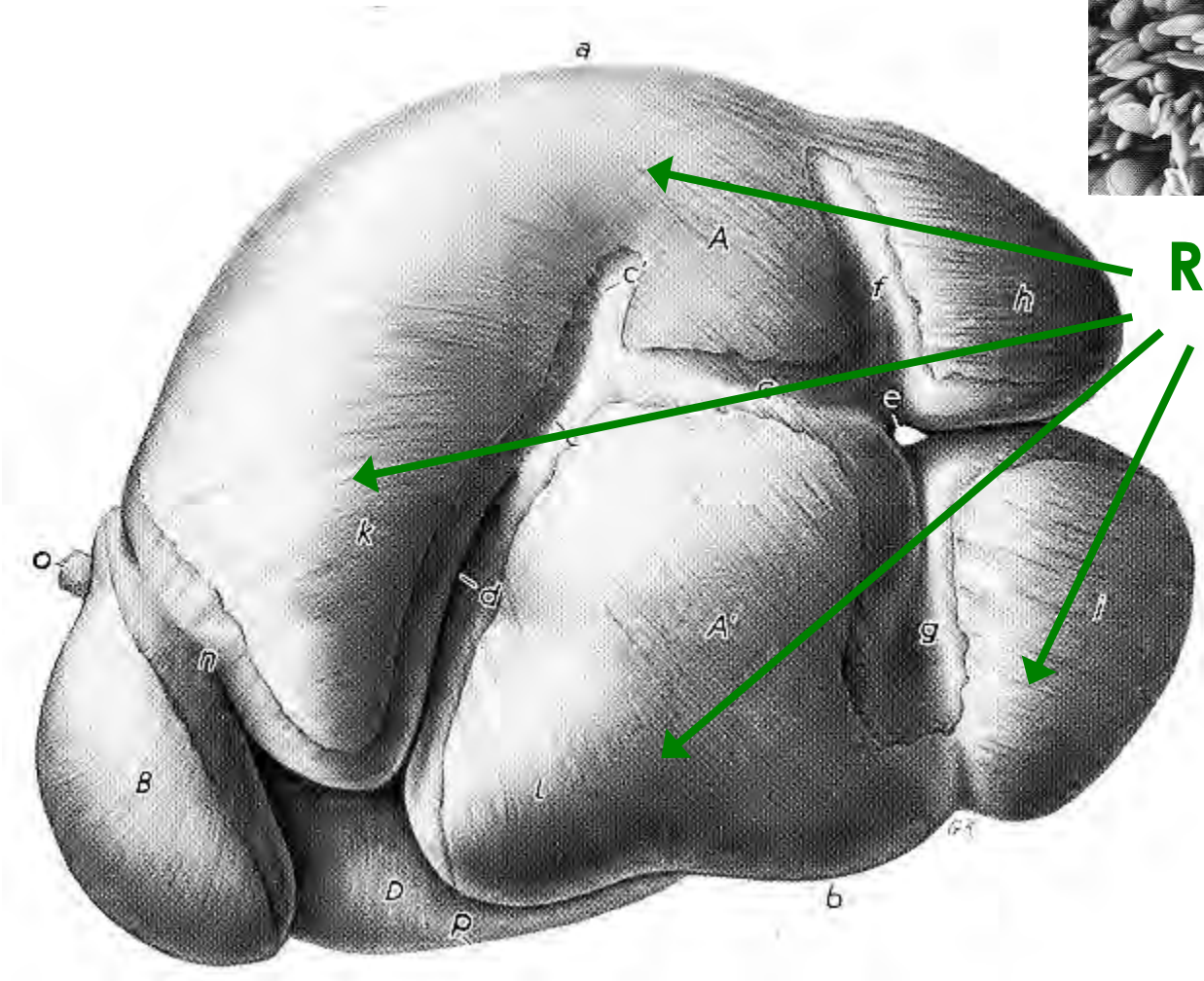
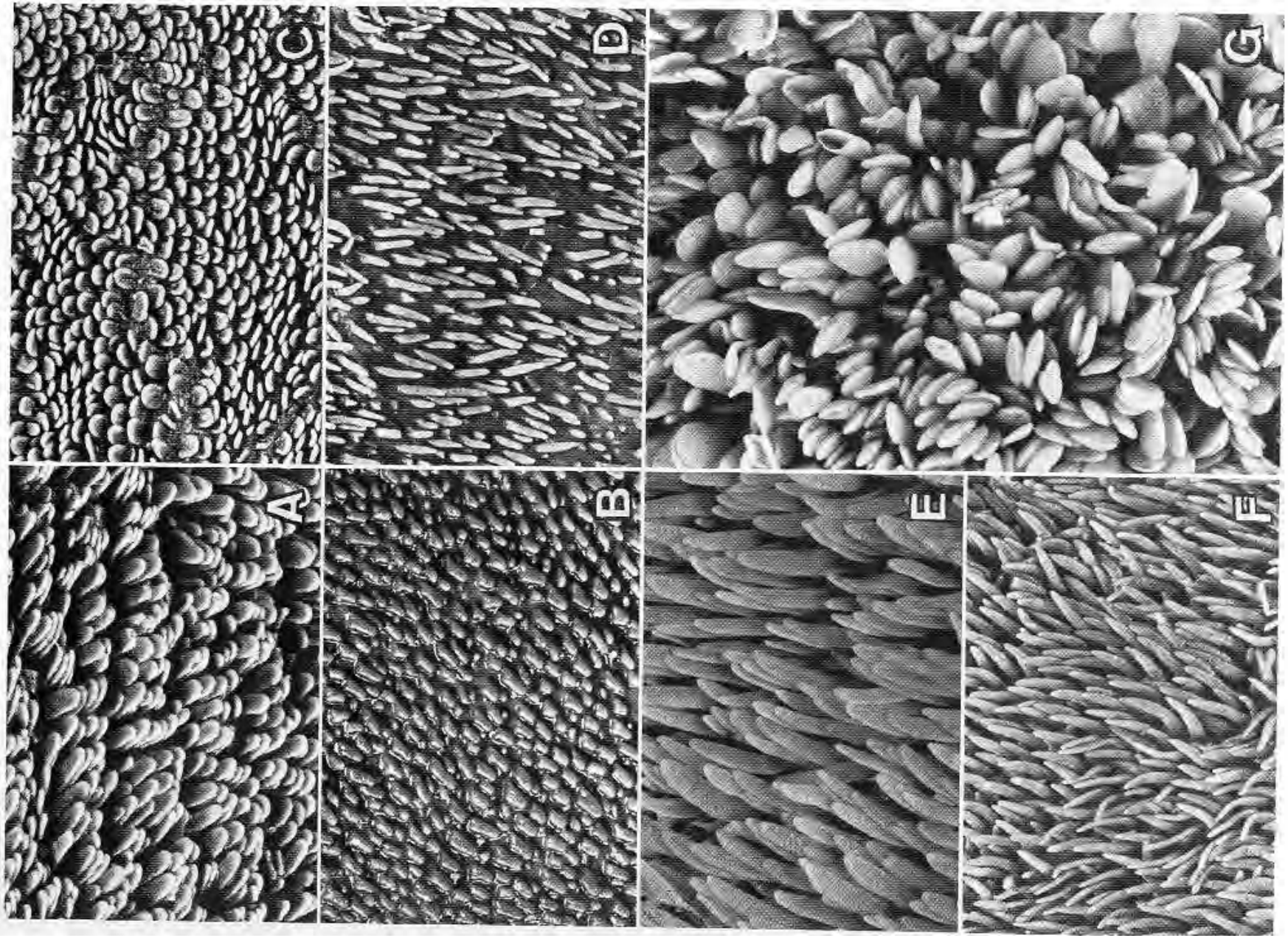
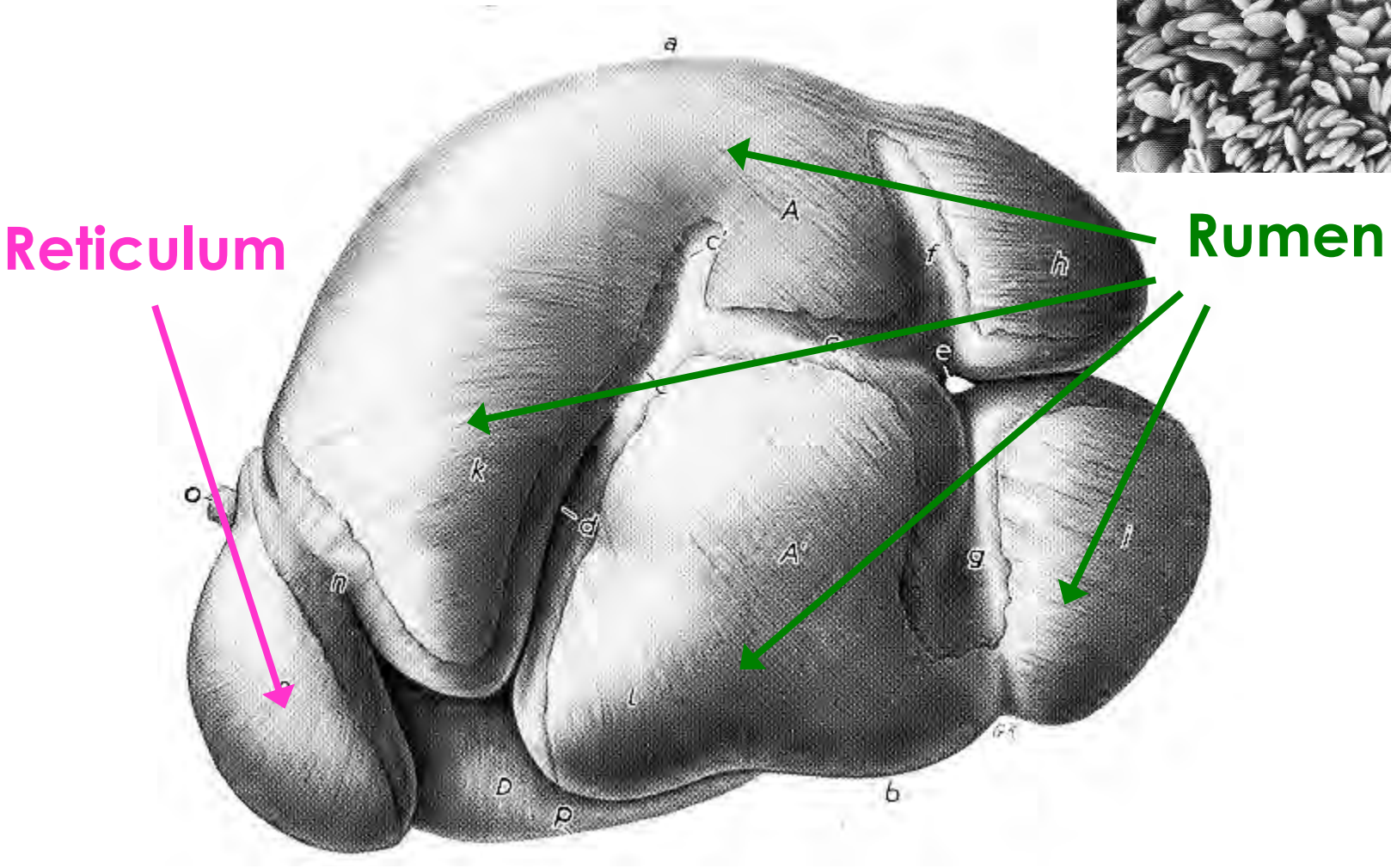


Rumen

(from Nickel-Schummer-Seiferle 1967)



(from Hofmann & Schnorr1982)



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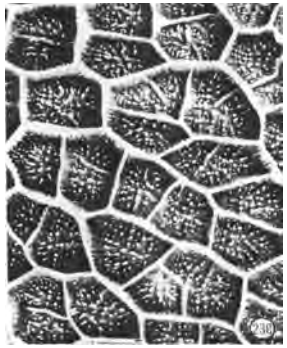
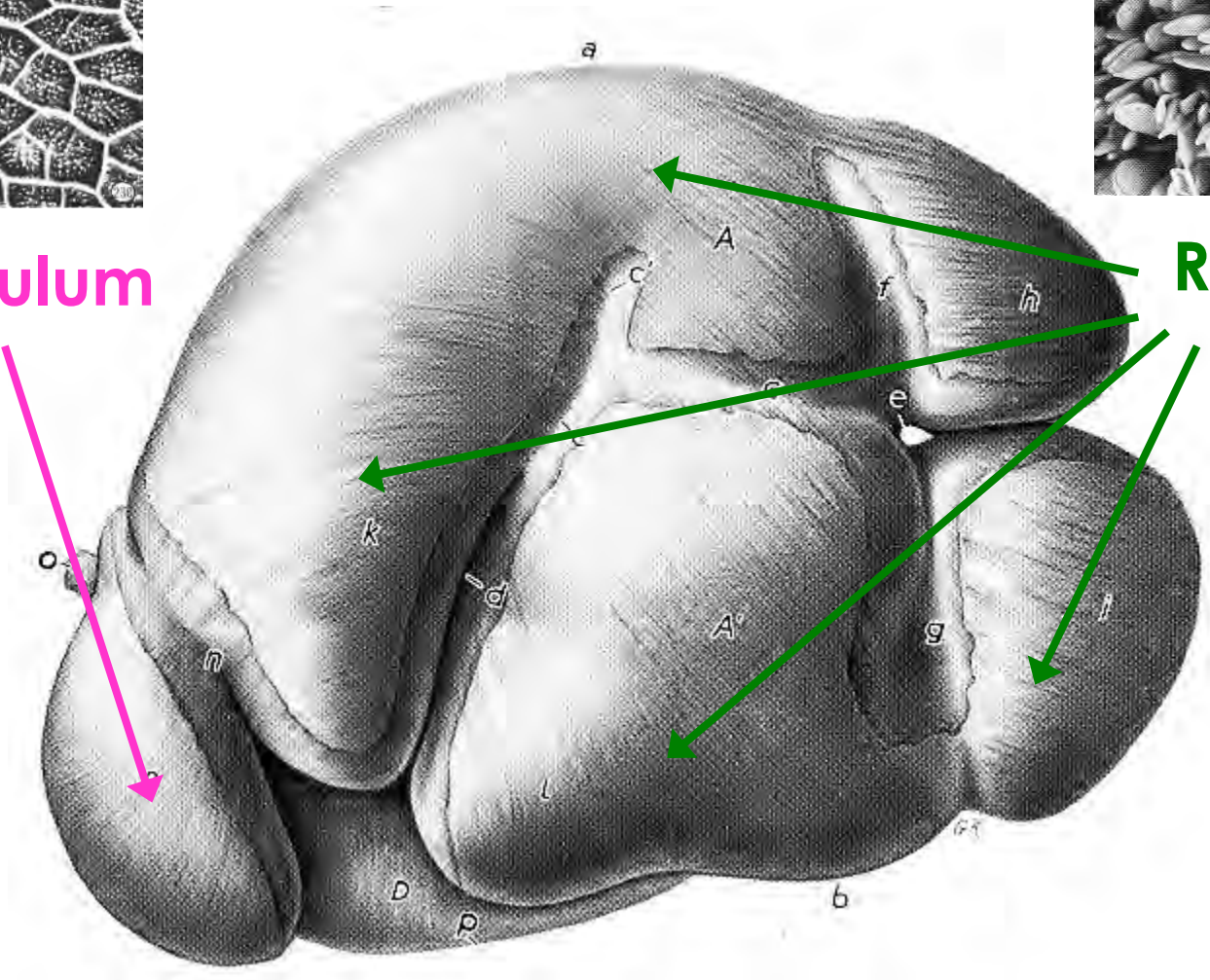


Reticulum

Rumen



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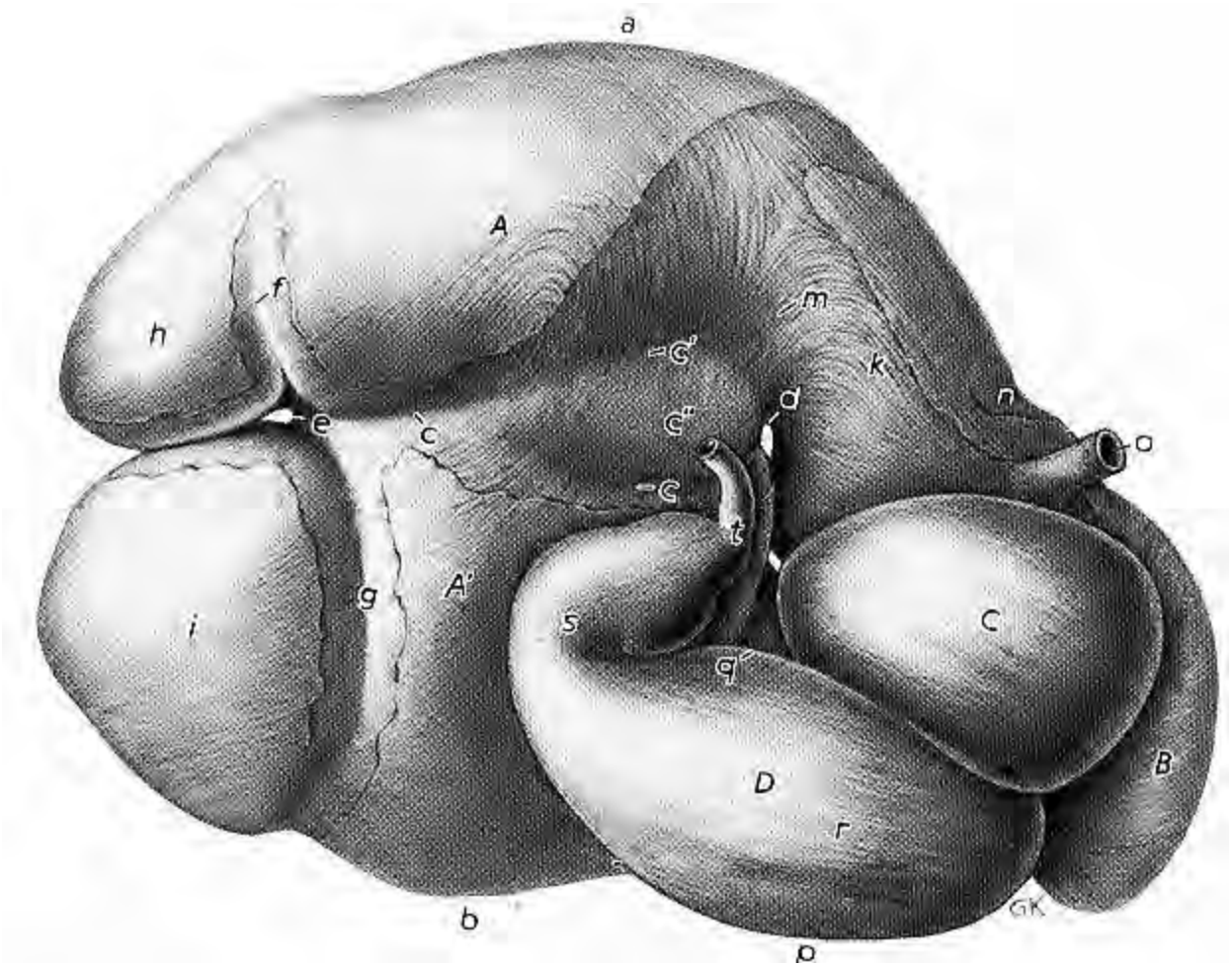

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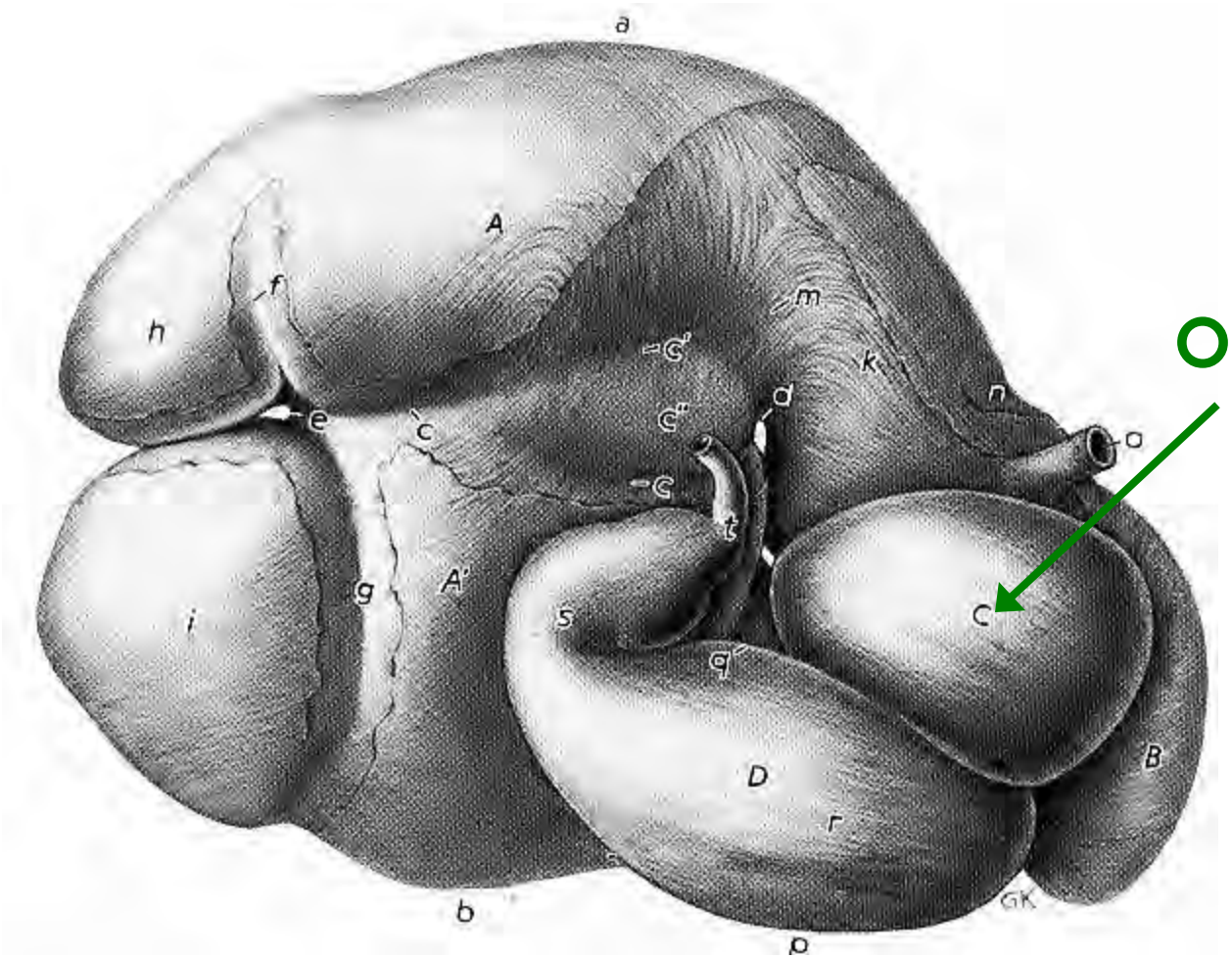
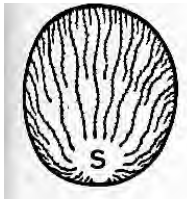
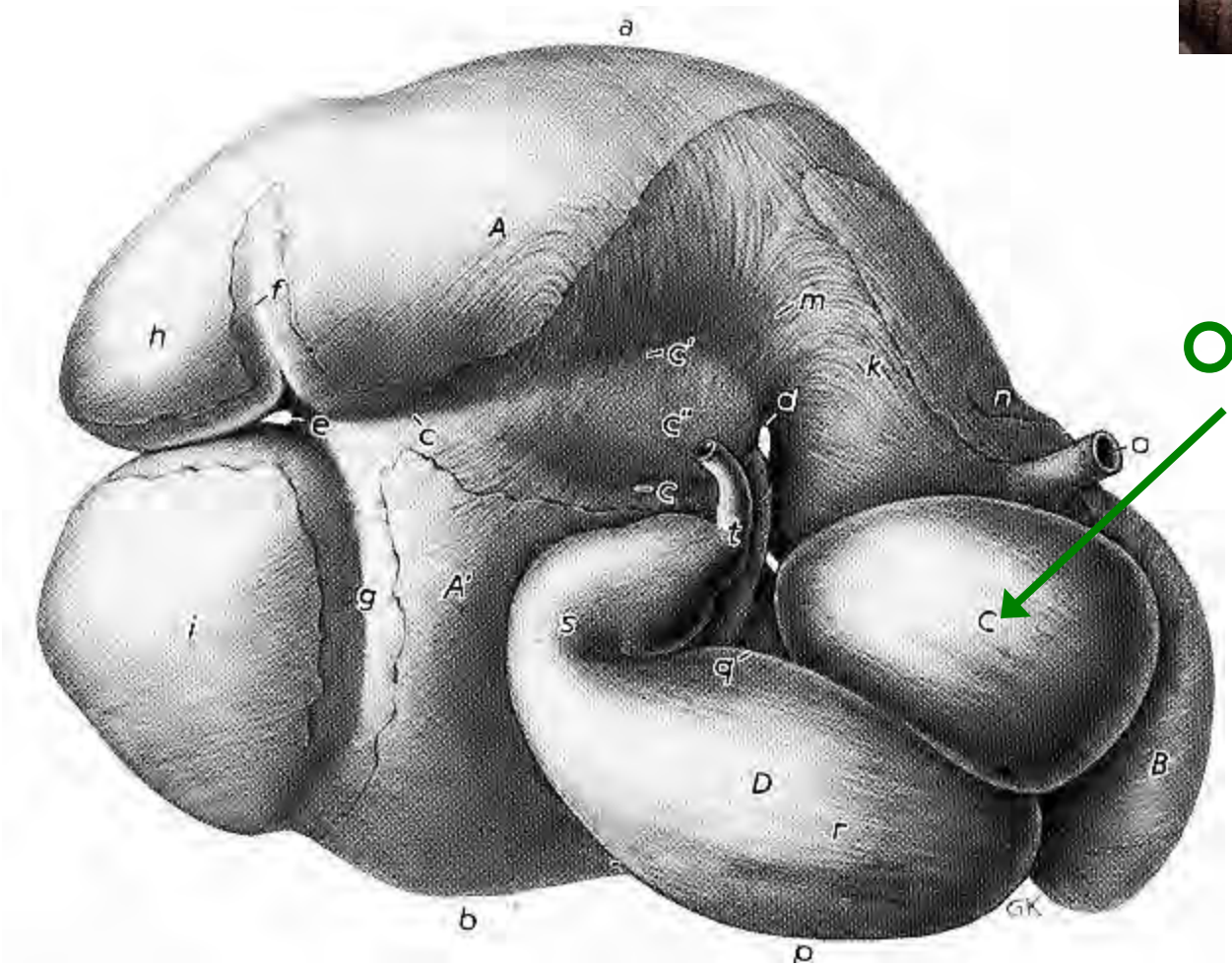


Omasum

(from Nickel-Schummer-Seiferle 1967)



Omasum



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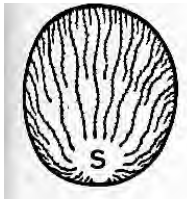
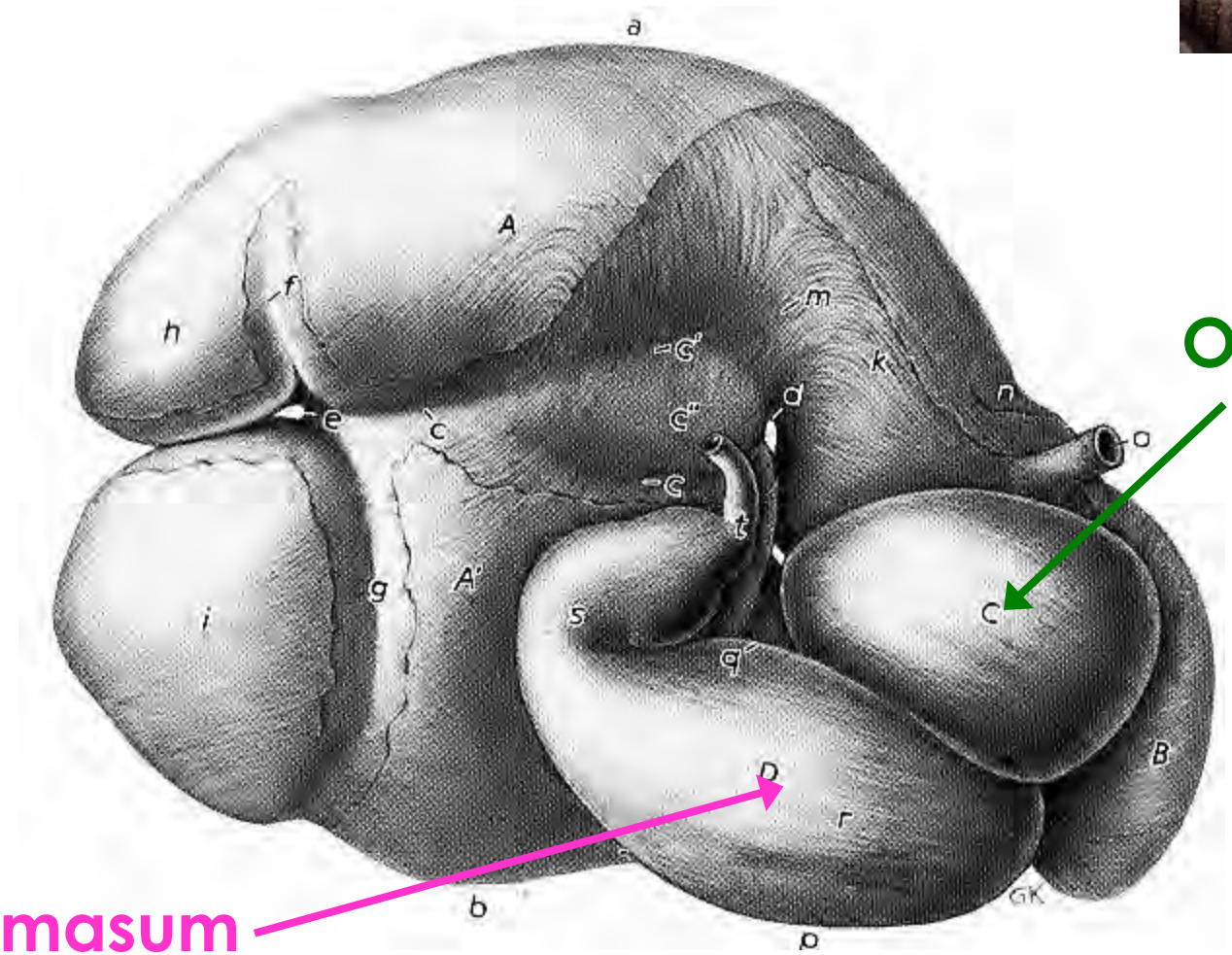
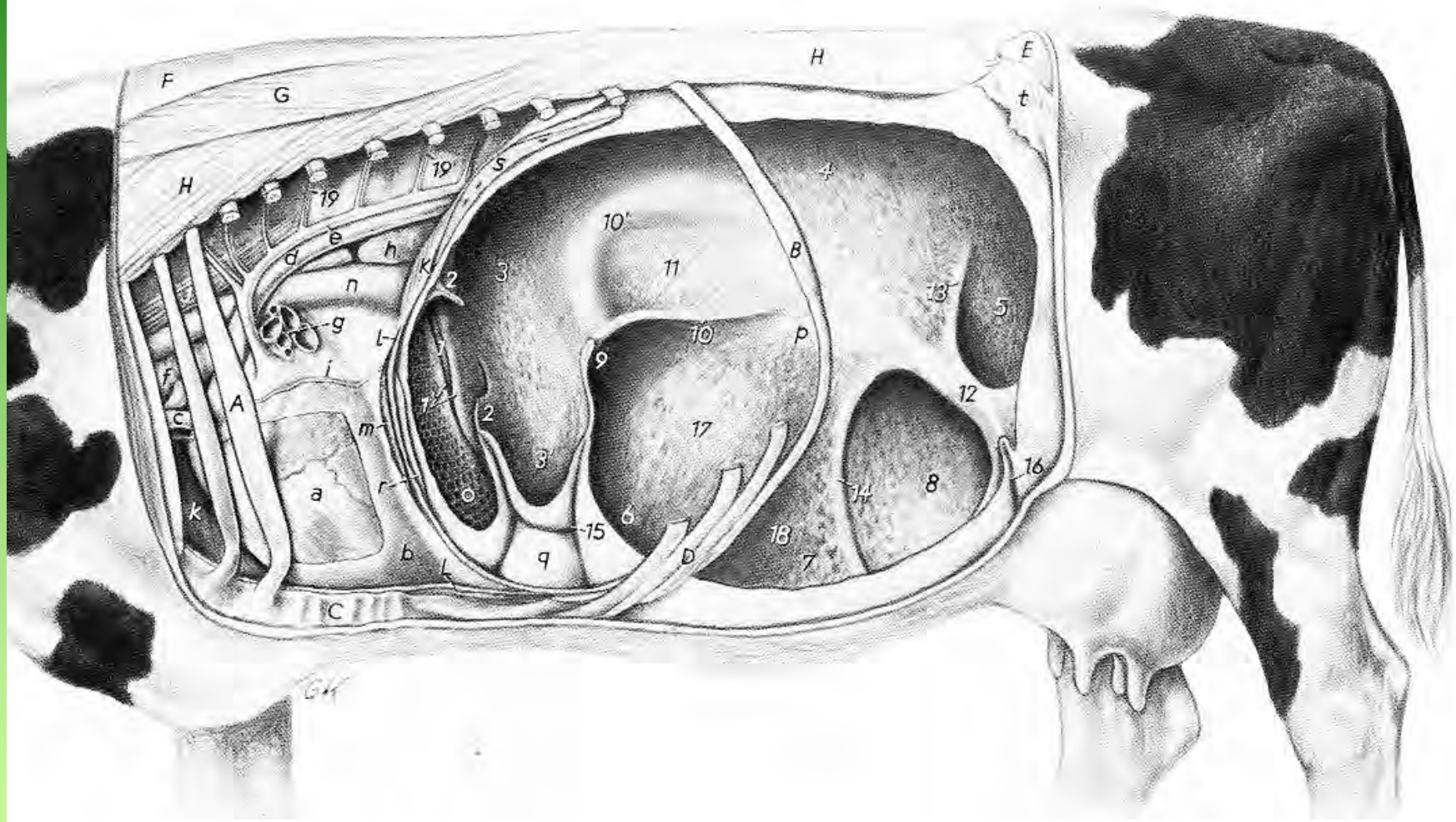




Omasum

Abomasum

(from Nickel-Schummer-Seiferle 1967)



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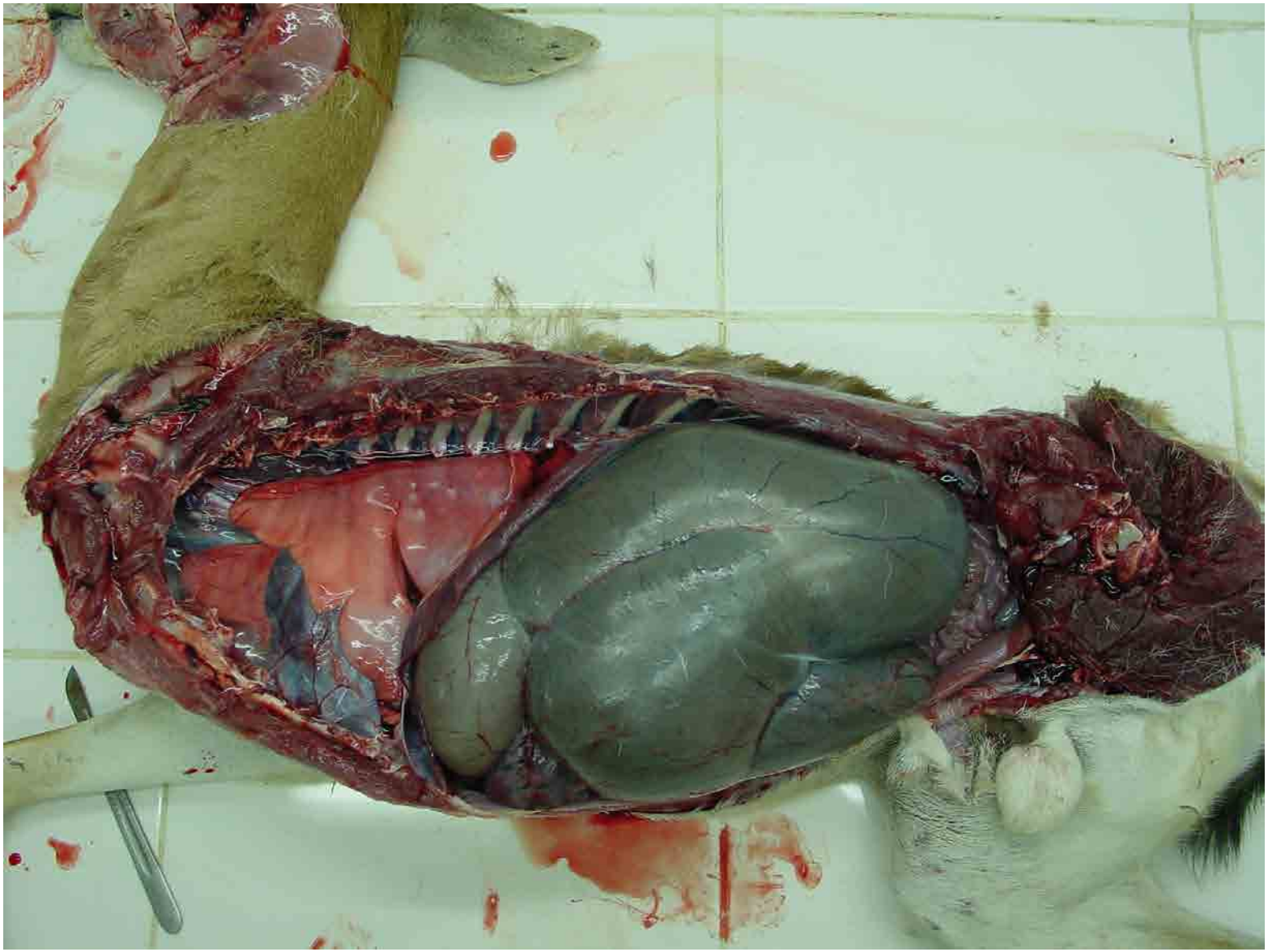
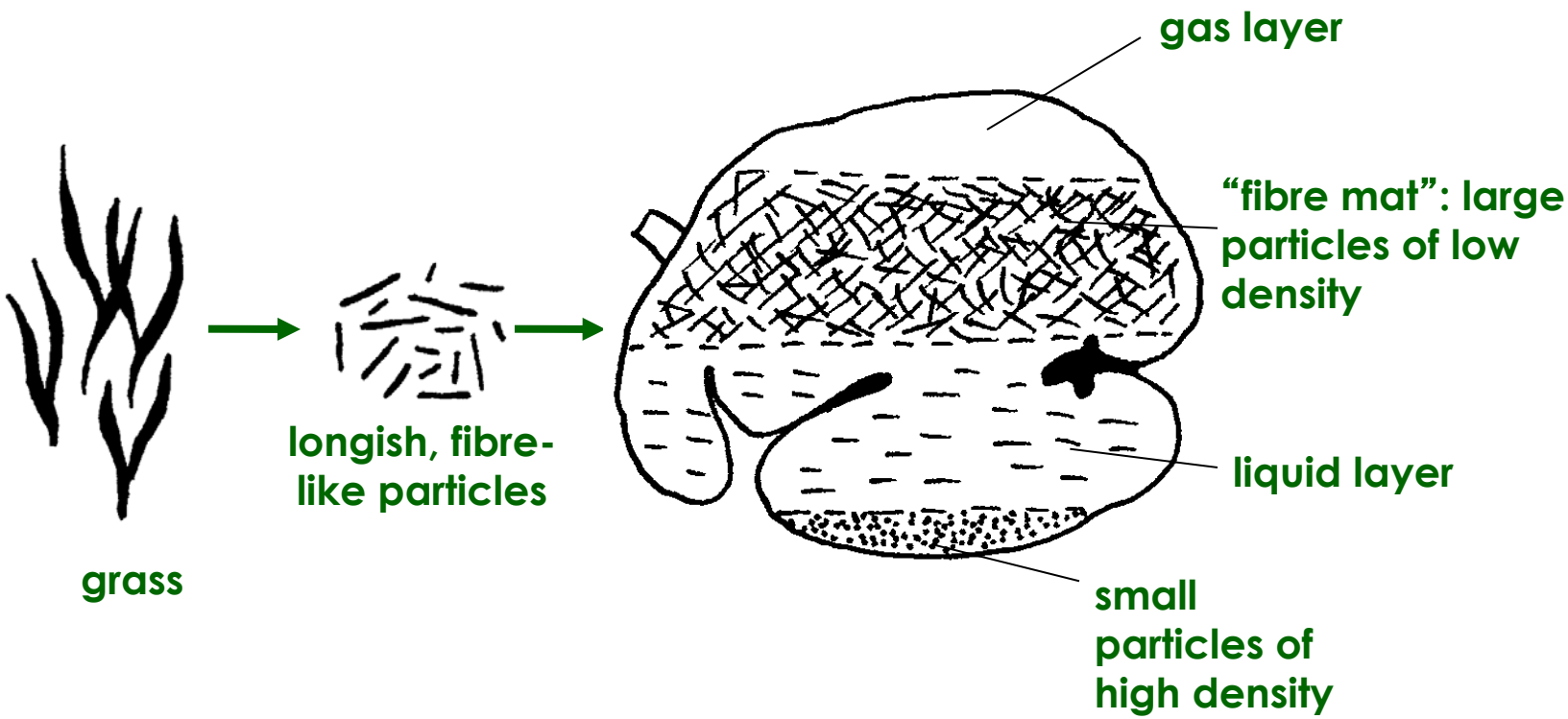


Stratification of rumen contents: 'cattle-type'



from Clauss et al. (2003)

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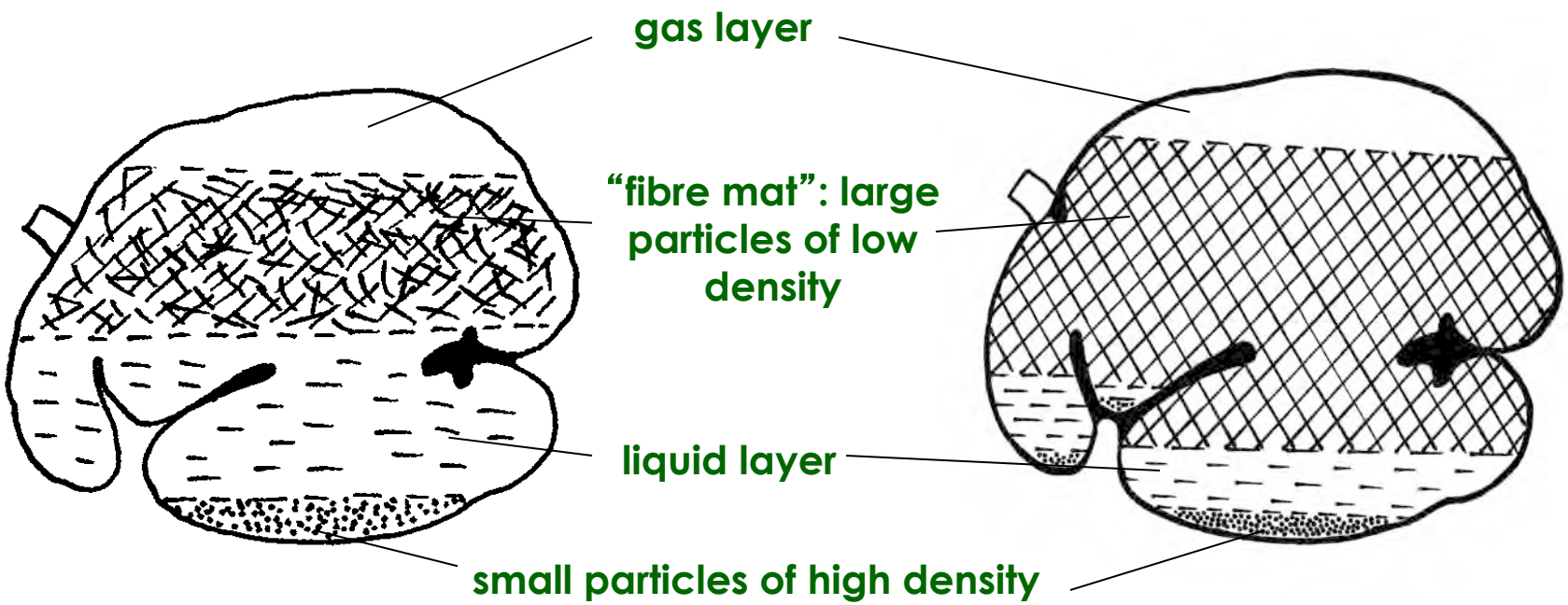

from Hummel et al. (2009)

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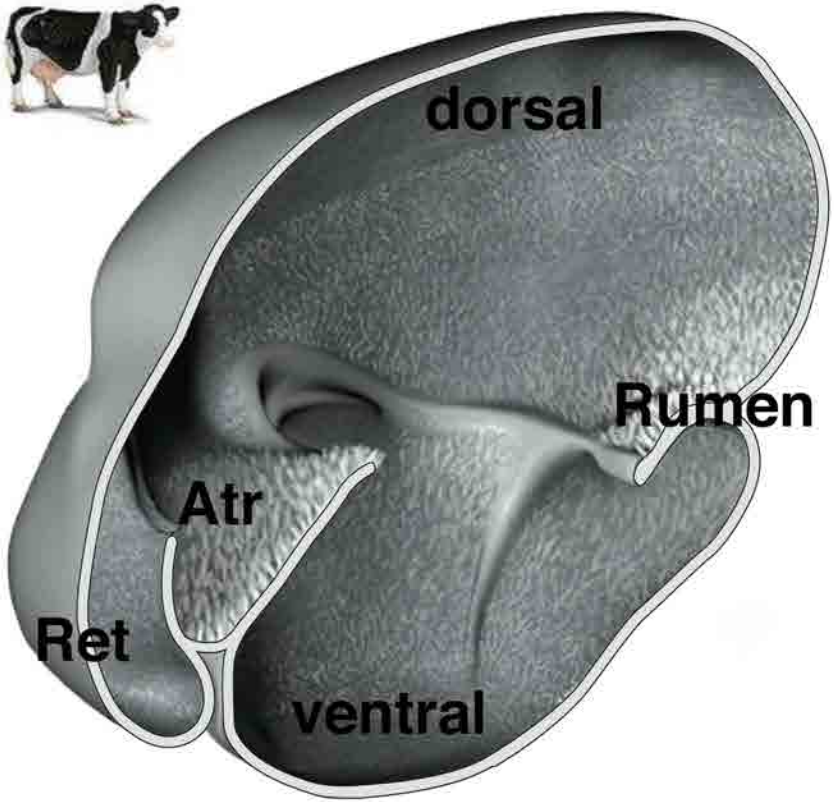
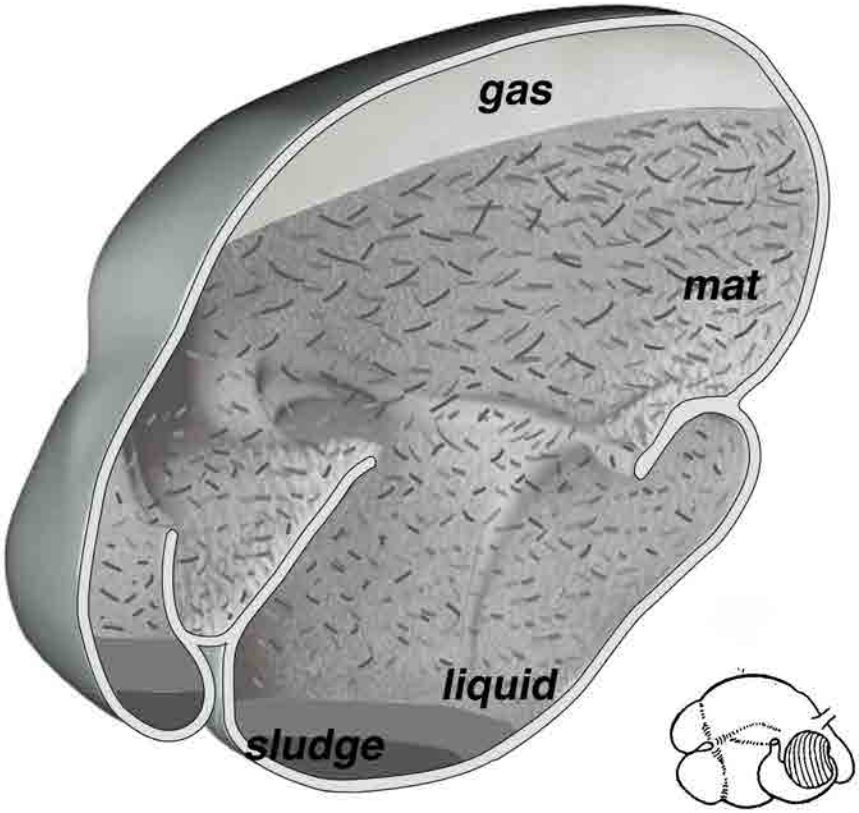


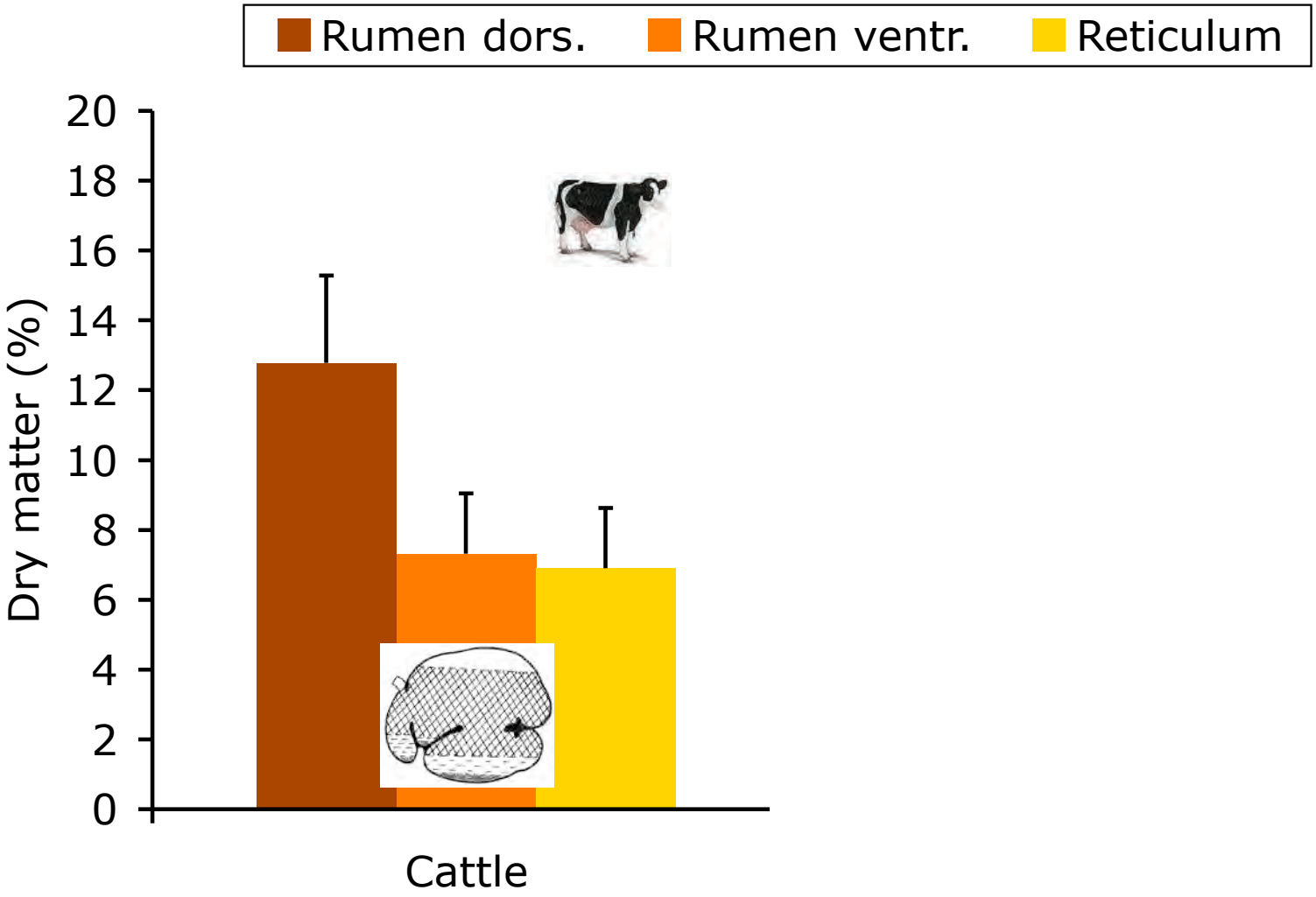


from Clauss et al. (2010)

Rumen of addax - a grazer

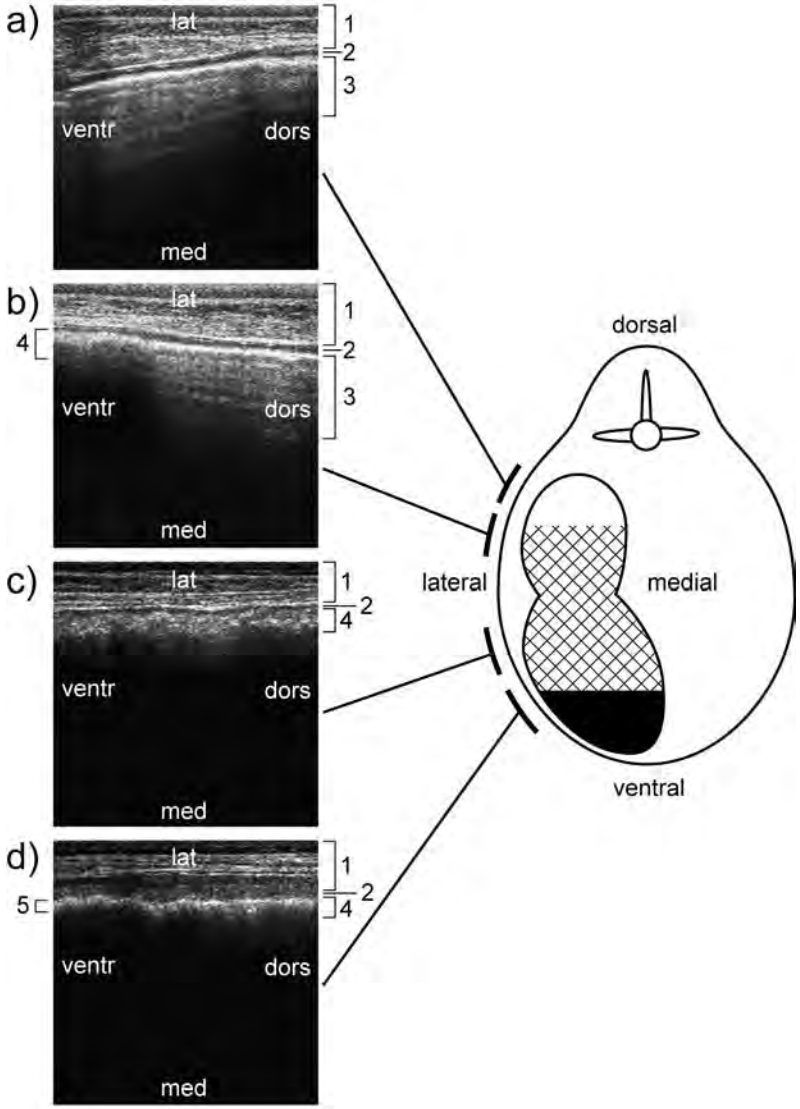
from Clauss et al. (2009)

Stratification of rumen contents

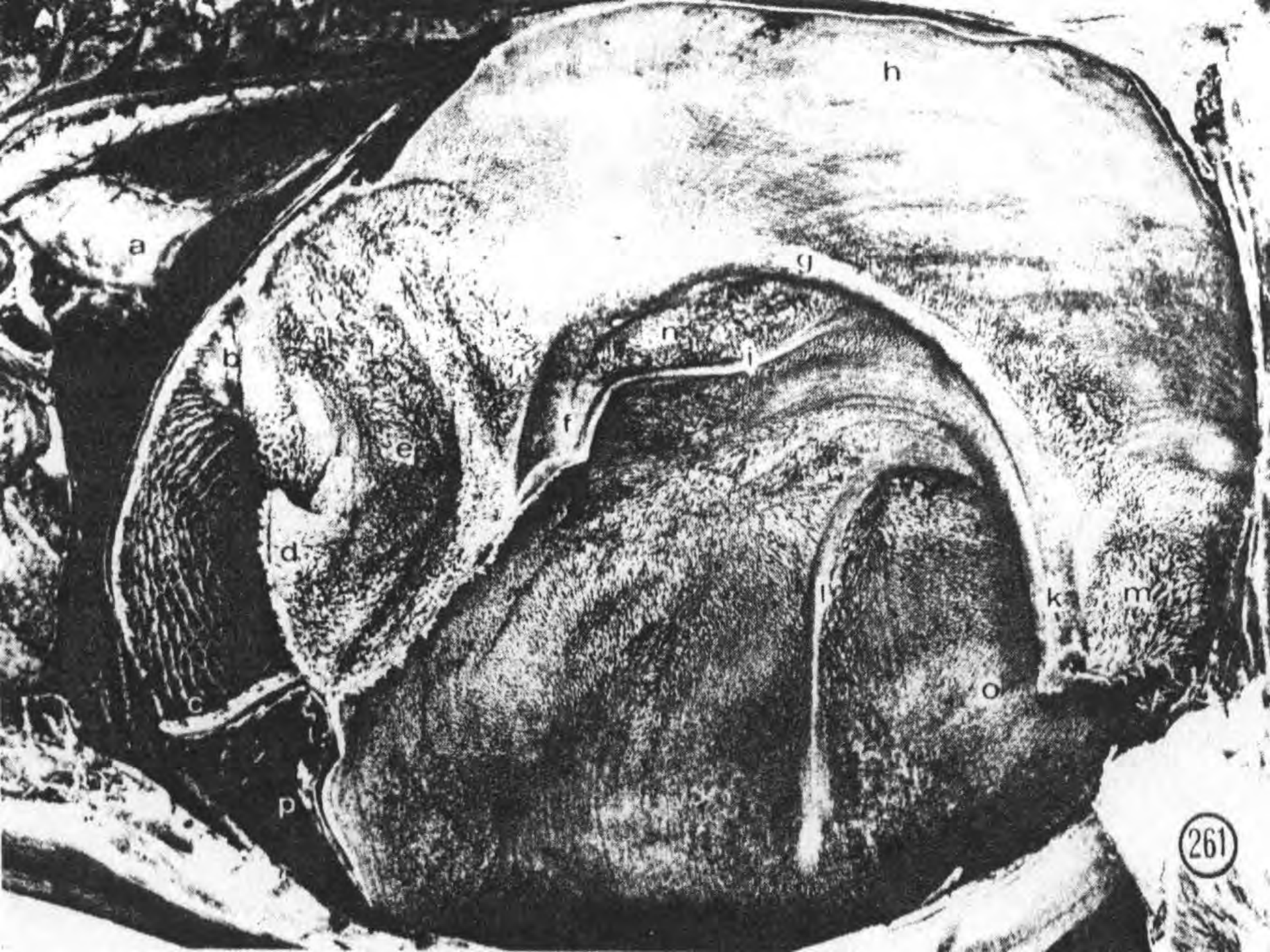


from Clauss et al. (2010)

Testing stratification by ultrasound - cattle



from Tschuor & Clauss (2008)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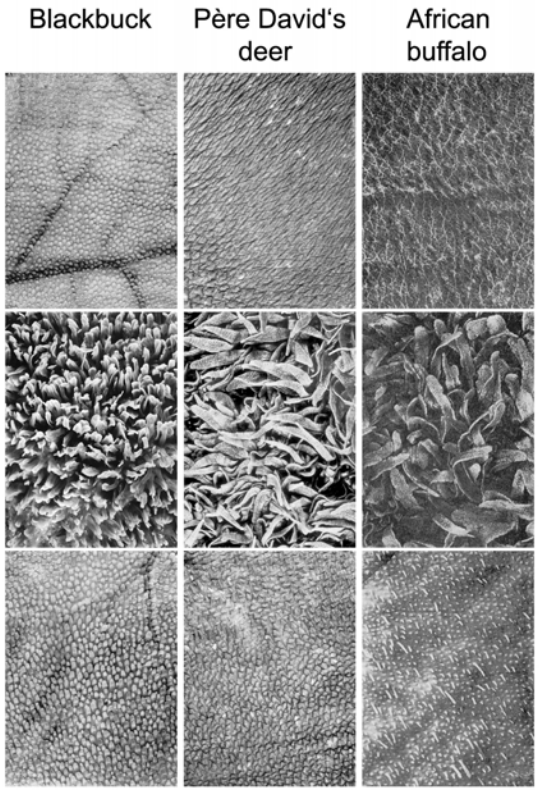
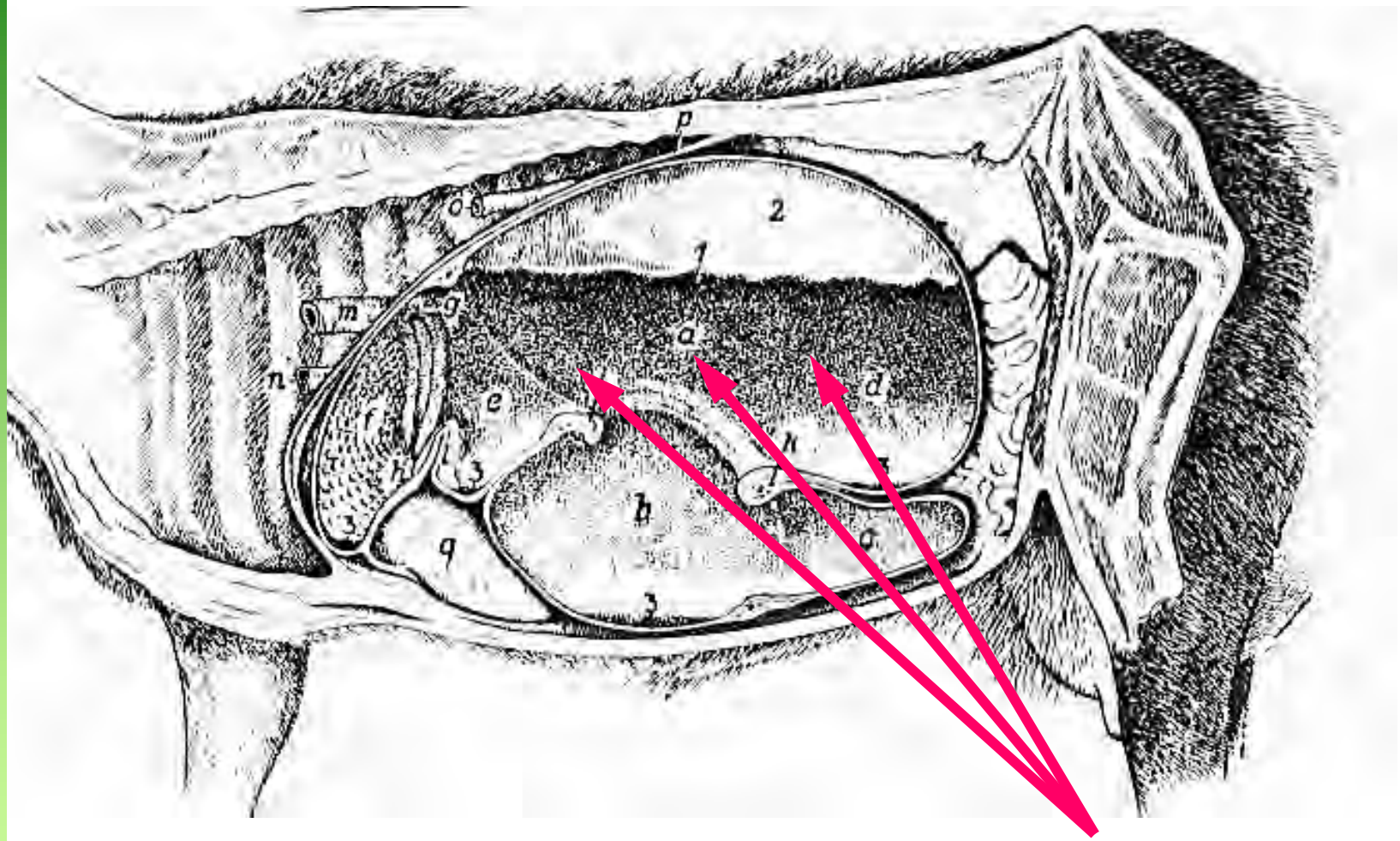
Stratification and rumen papillation



from Clauss, Hofmann et al. (2009)

Digestion and Sorting



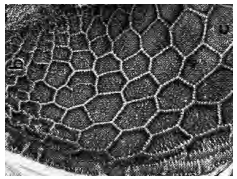
Rumen: Fermentation

(from Grau 1955)

Digestion and Sorting

Reticulum: Sorting

Rumen: Fermentation



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Reticulum: Sorting

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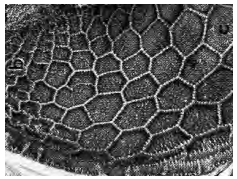
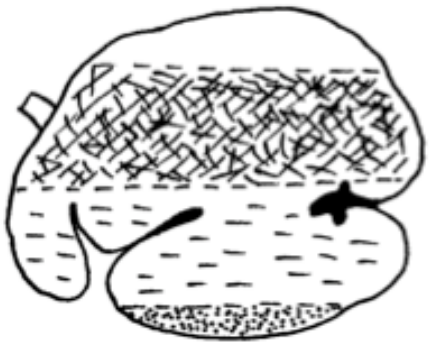


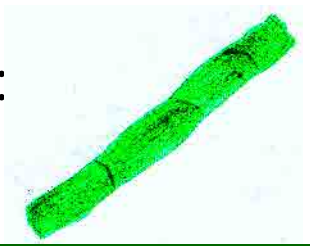
(from Grau 1955)

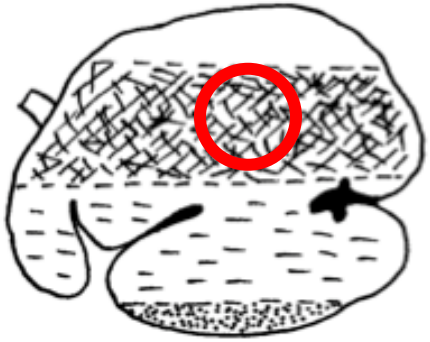
Functional density of particles



Functional density of particles

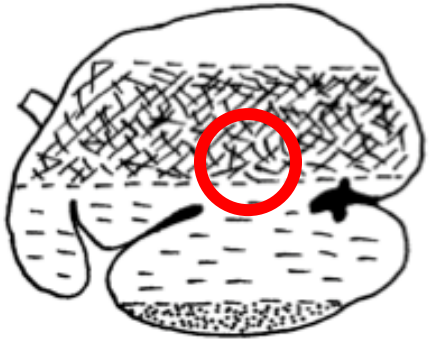
un-fermented ingesta particle:
entangles in fibre mat



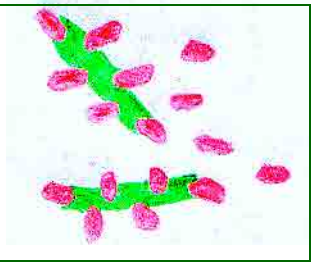


Functional density of particles

un-fermented ingesta particle:
entangles in fibre mat

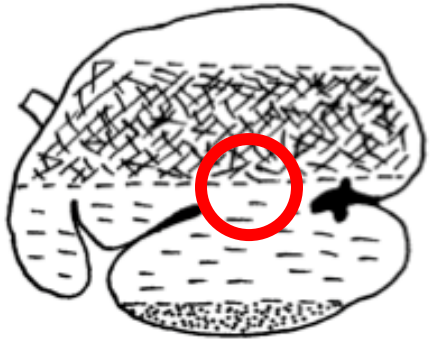


size reduction by rumination/
attachment of bacteria

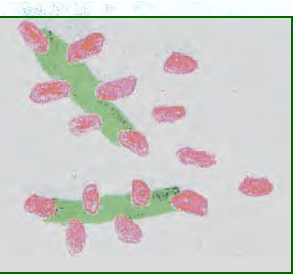


Functional density of particles

un-fermented ingesta particle:
entangles in fibre mat



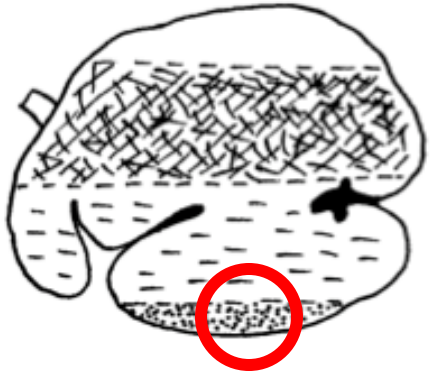
size reduction by rumination/
attachment of bacteria



fermentation activity = gas production
=> adhesion of gas bubbles
=> updrift/low density

Functional density of particles

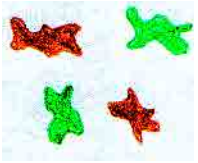
un-fermented ingesta particle:
entangles in fibre mat



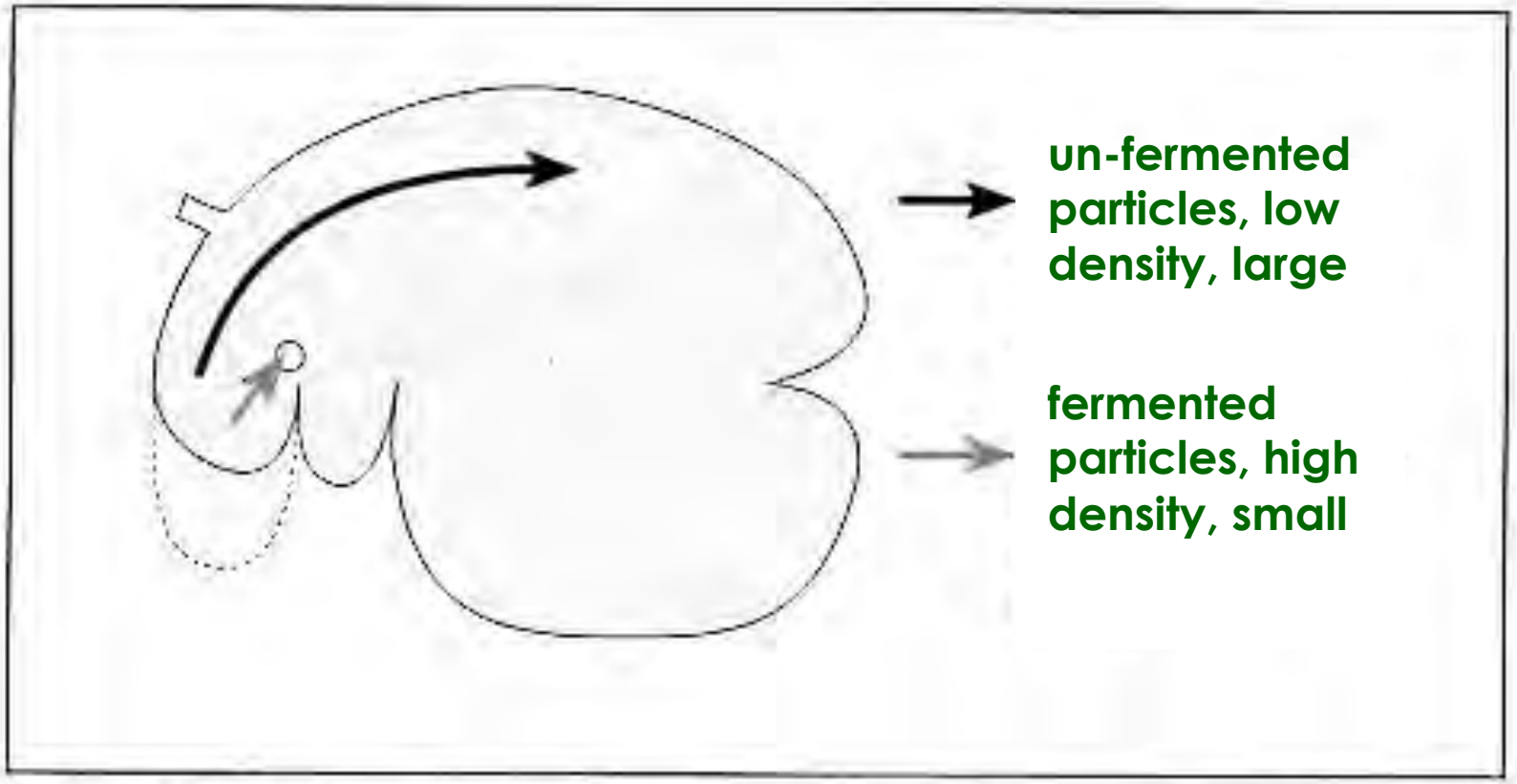
size reduction by rumination/
attachment of bacteria

fermentation activity = gas production
=> adhesion of gas bubbles
=> updrift/low density

fermented ingesta particles:
high density

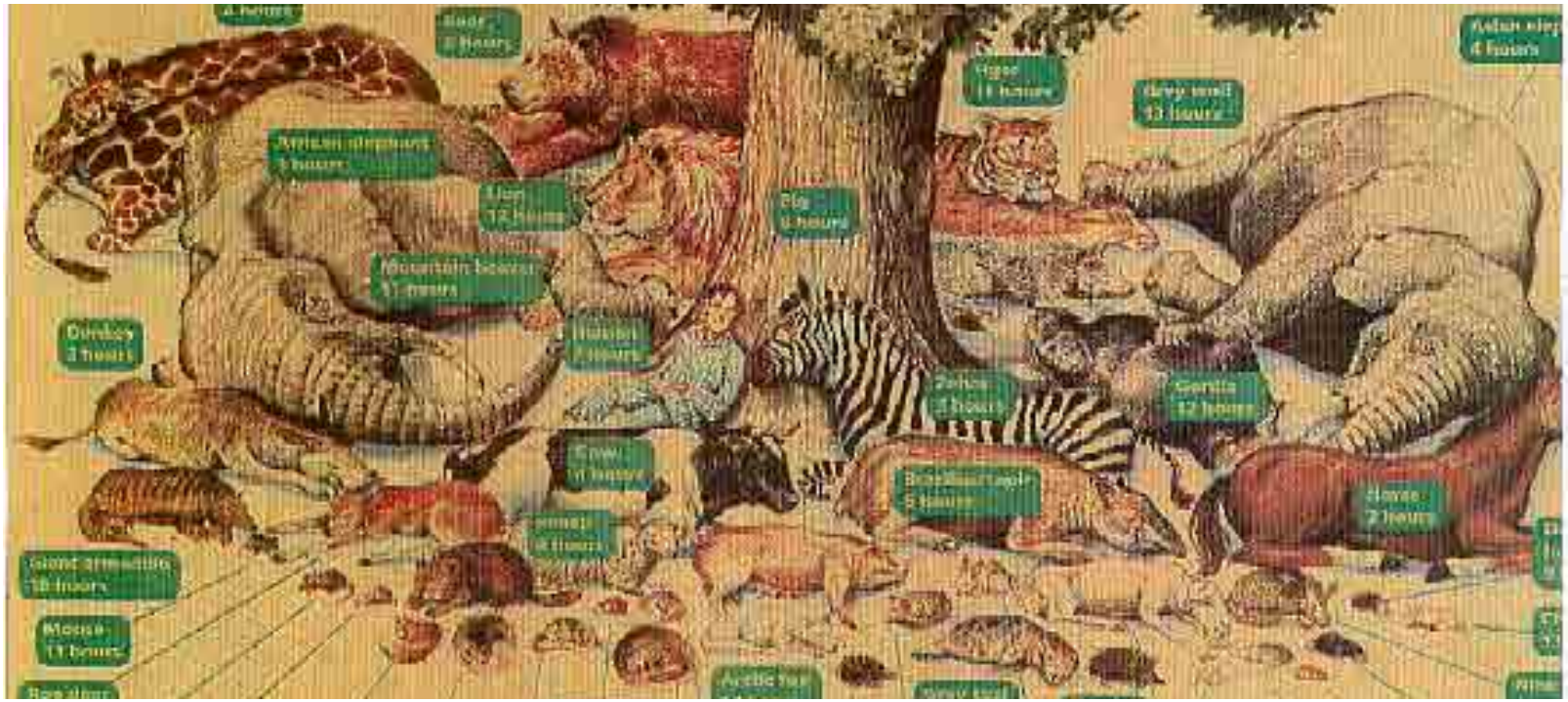


Sorting in the reticulum

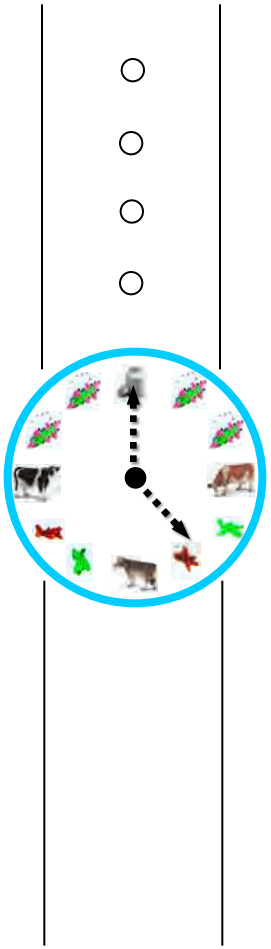


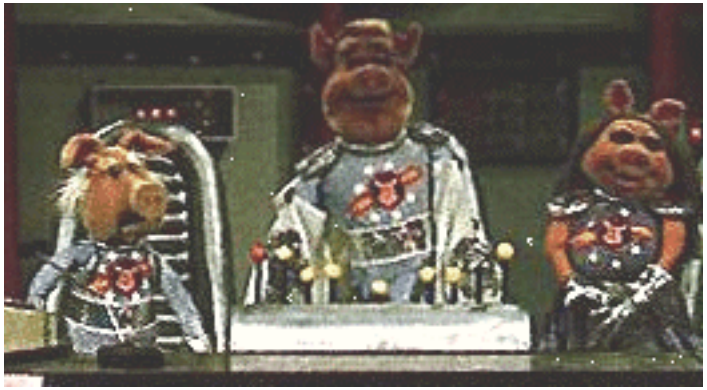
(from von Engelhardt & Breves 2000)

Ruminants always rest in sternal recumbency



Fine mechanics at highest level

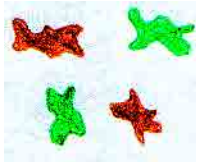




(there may be pigs in space, but no sheep on the moon!)

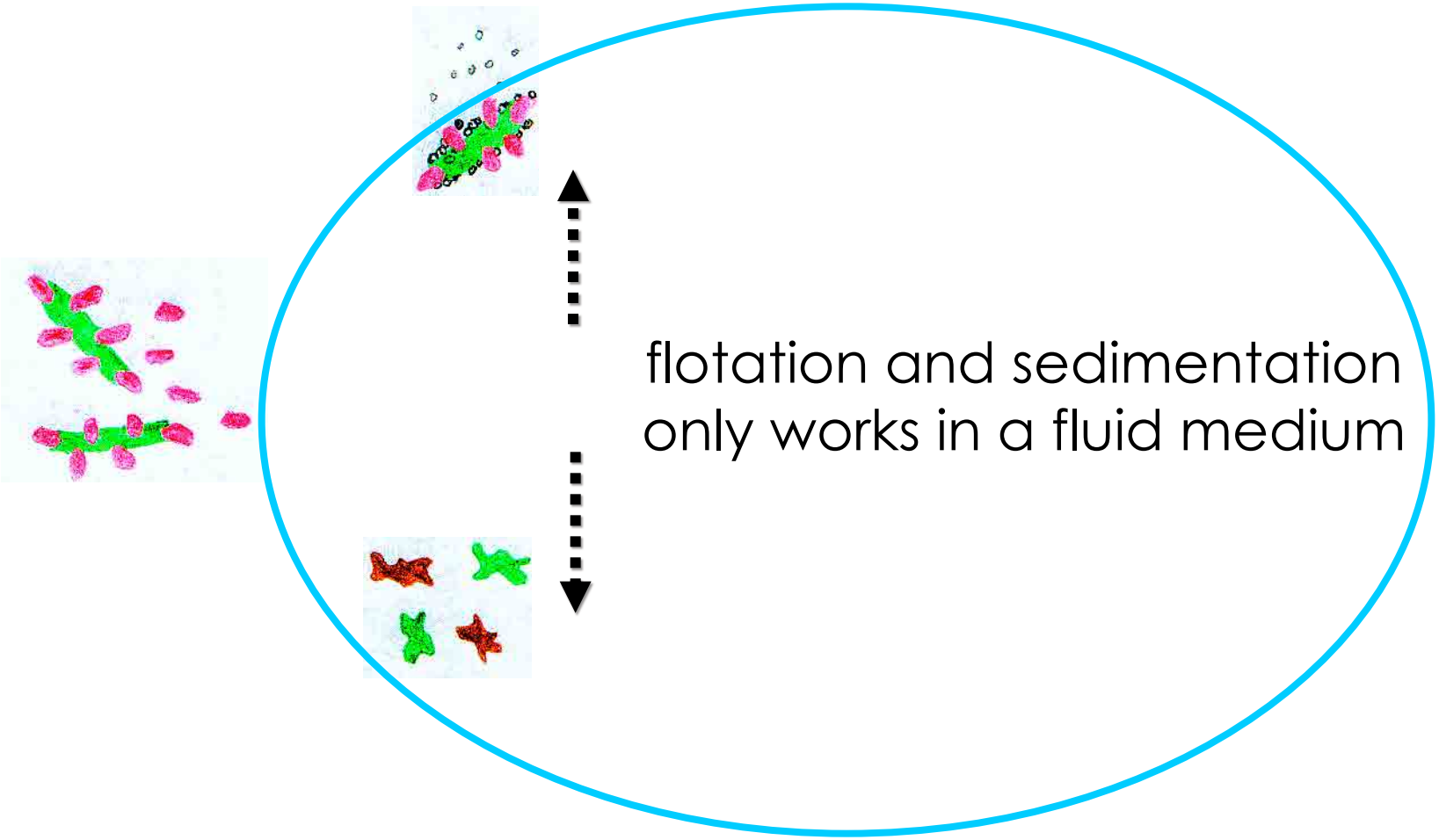
Sorting by density ...

fermentation = gas production
gas adhesion = updrift



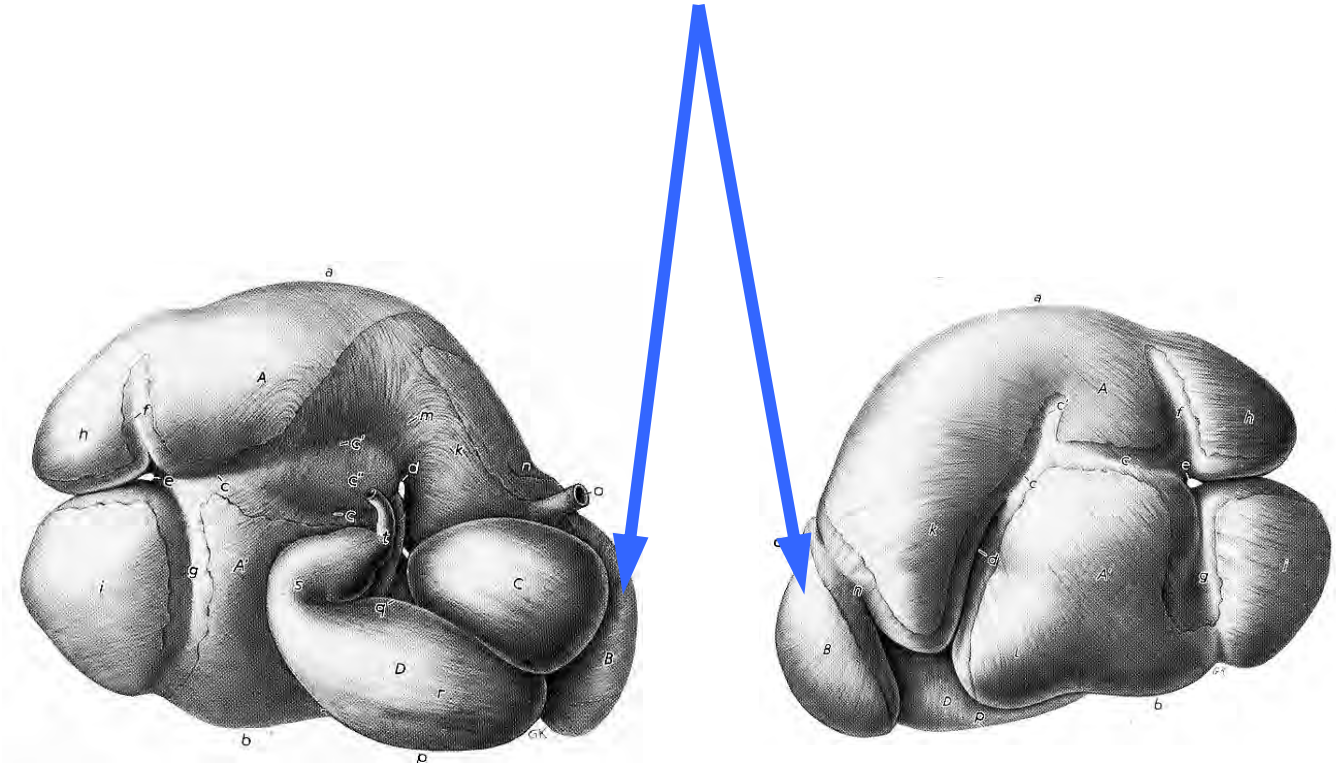
fermented particle
no gas bubbles = high density

Sorting by denisty ...



the fluid must be removed ...

high moisture content in the reticulum

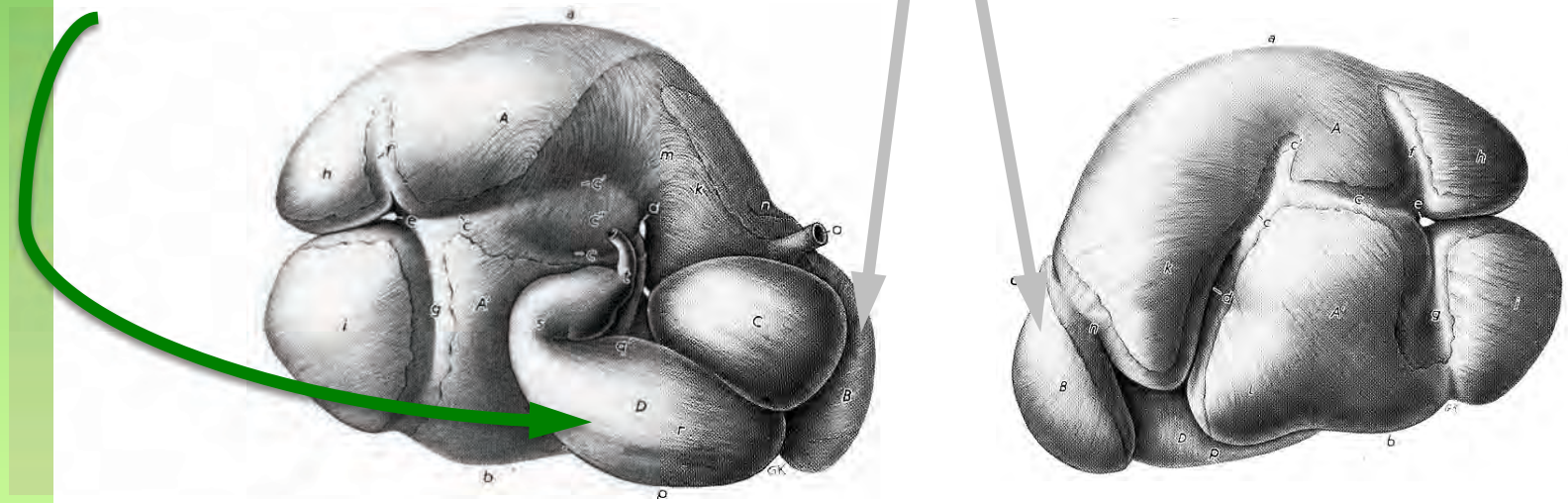


(from Nickel-Schummer-Seiferle 1967)

the fluid must be removed ...

high moisture content in the reticulum

it would be difficult for the abomasum to work against the dilution



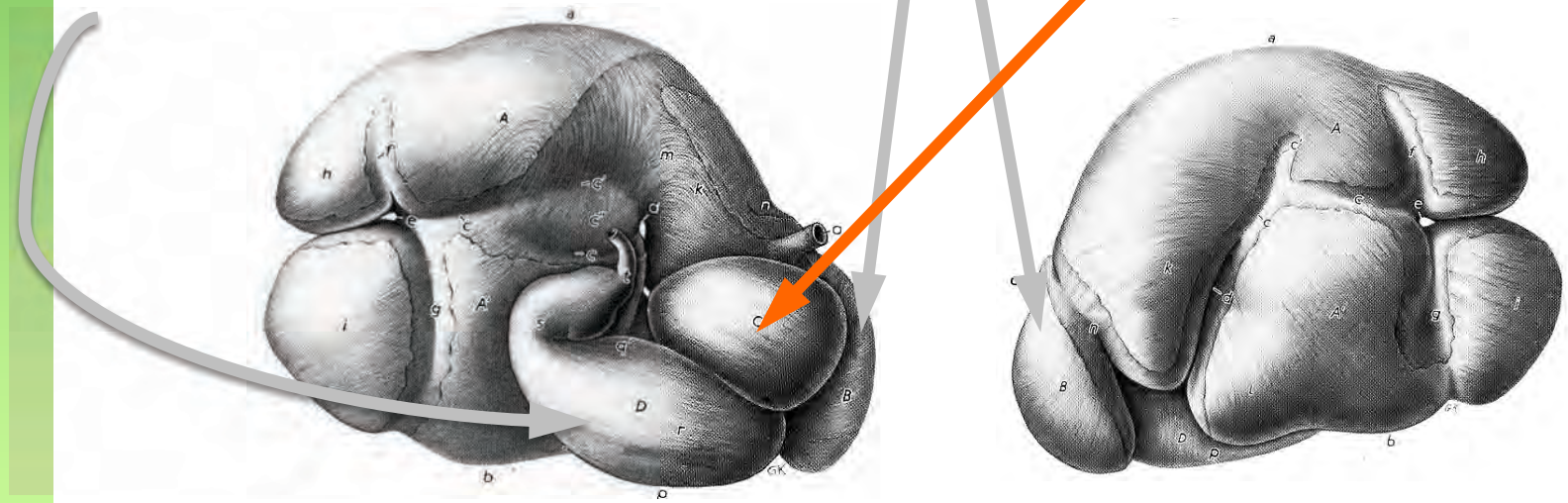
(from Nickel-Schummer-Seiferle 1967)

the fluid must be removed ...

high moisture content in the reticulum

it would be difficult for the abomasum to work against the dilution

therefore the omasum removes fluid



(from Nickel-Schummer-Seiferle 1967)

until 1970:

All ruminants are similar and function as cattle and sheep do.

The Ruminant

EAST AFRICAN MONOGRAPHS IN BIOLOGY

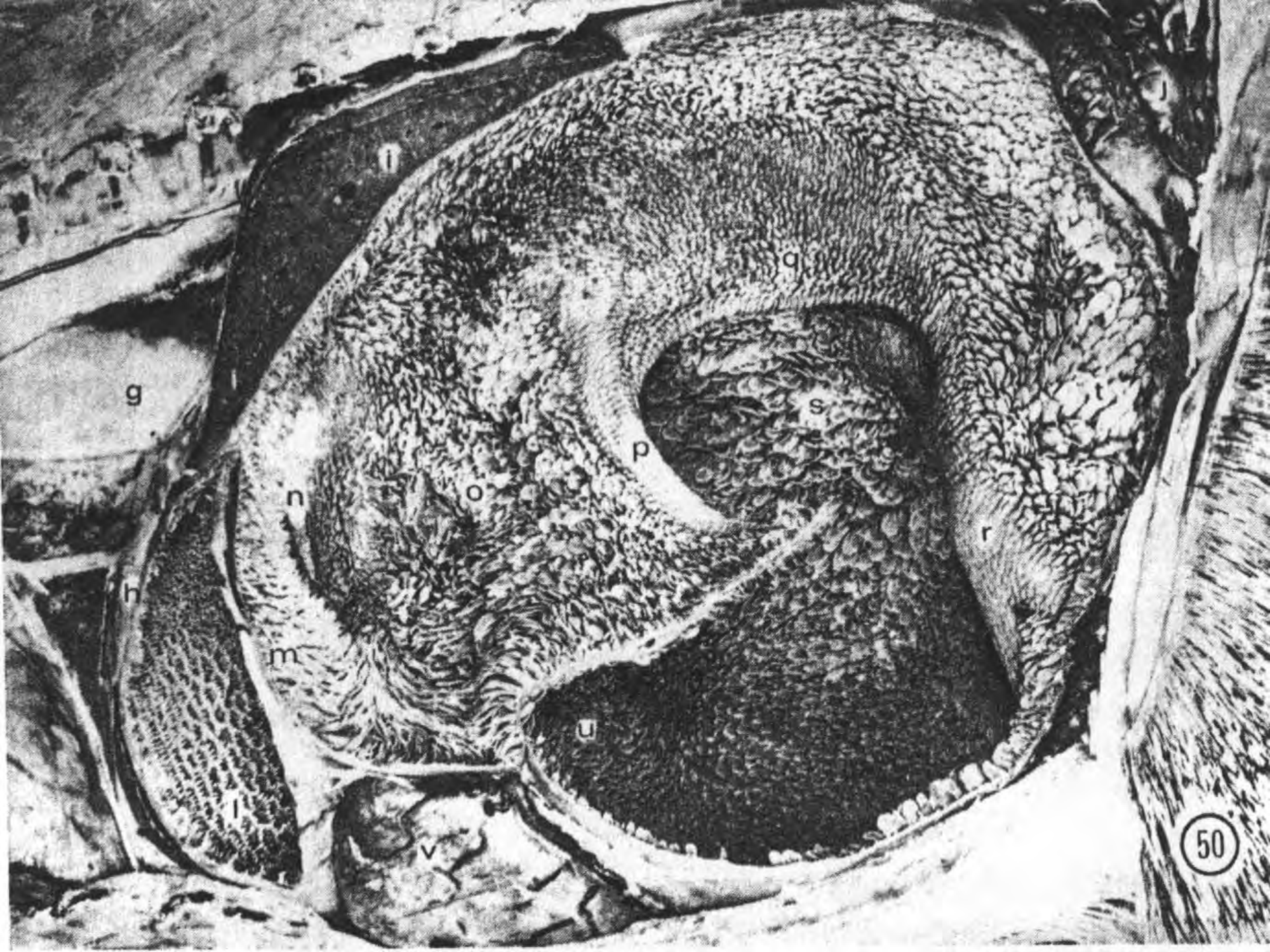
VOLUME 2

Stomach

Stomach Structure and Feeding Habits of East African Game Ruminants

R. R. HOFMANN,
Dr. med. vet. (Giessen), Professor of Veterinary Anatomy, Histology and Embryology.

EAST AFRICAN LITERATURE BUREAU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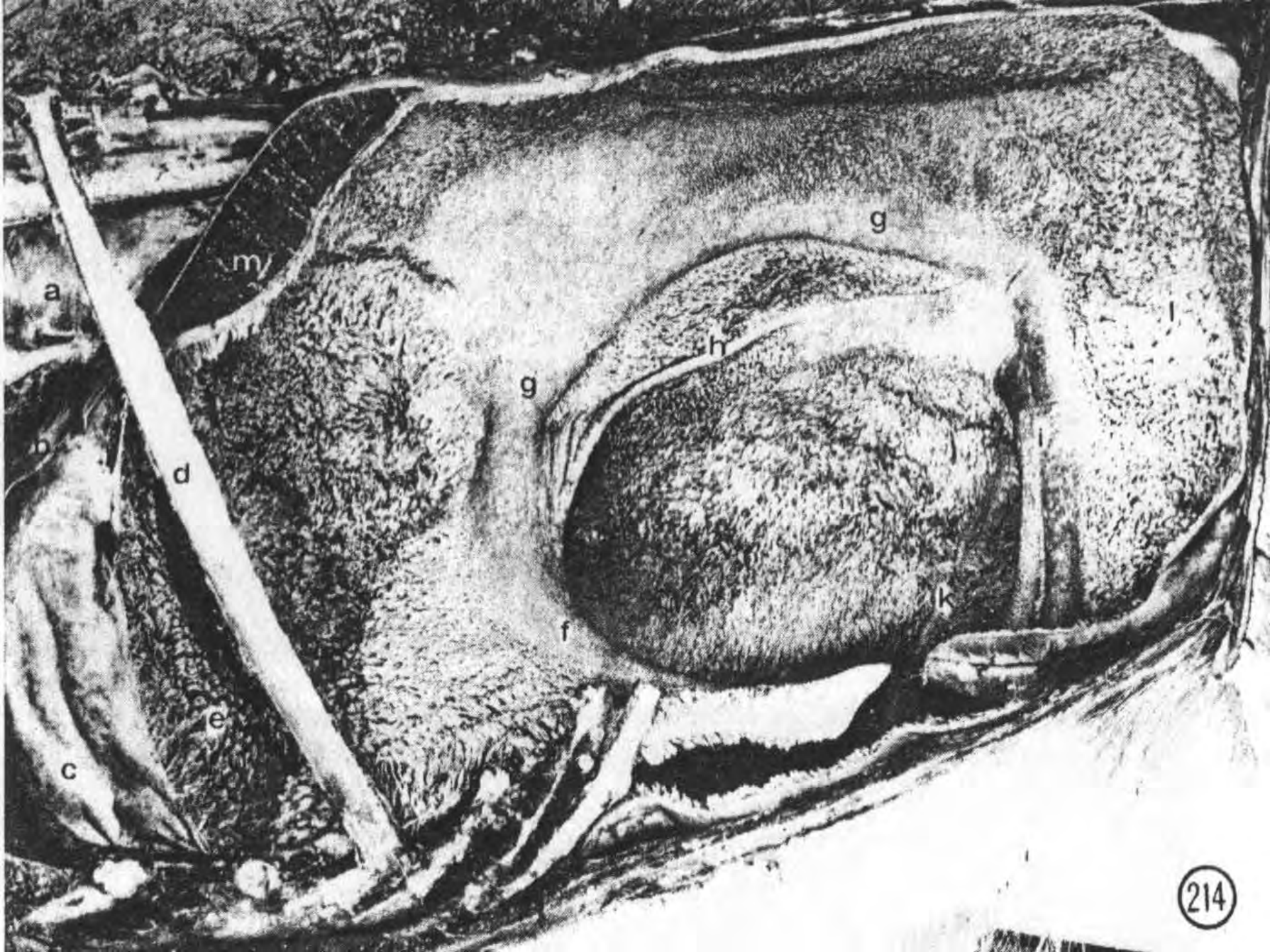
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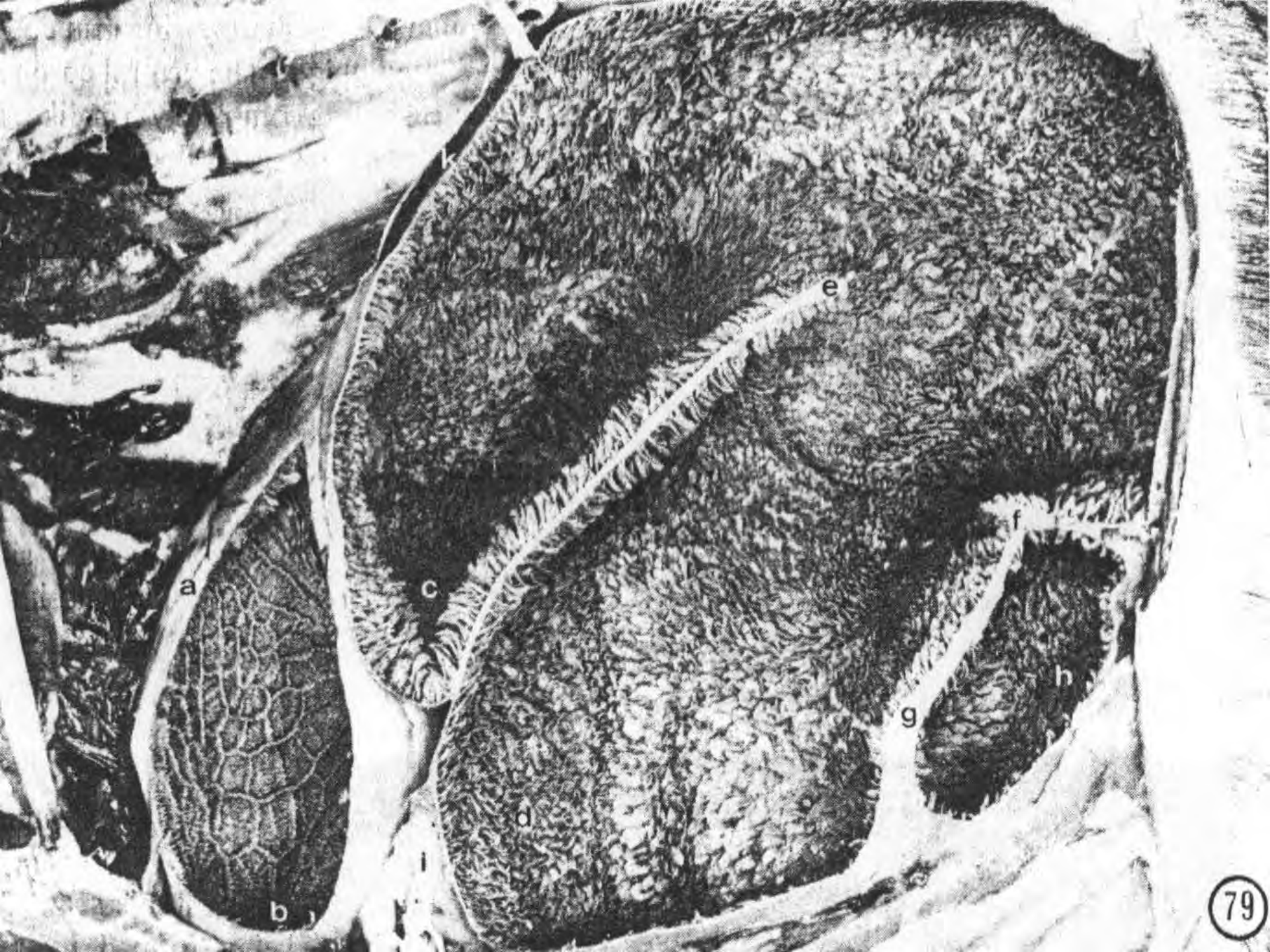
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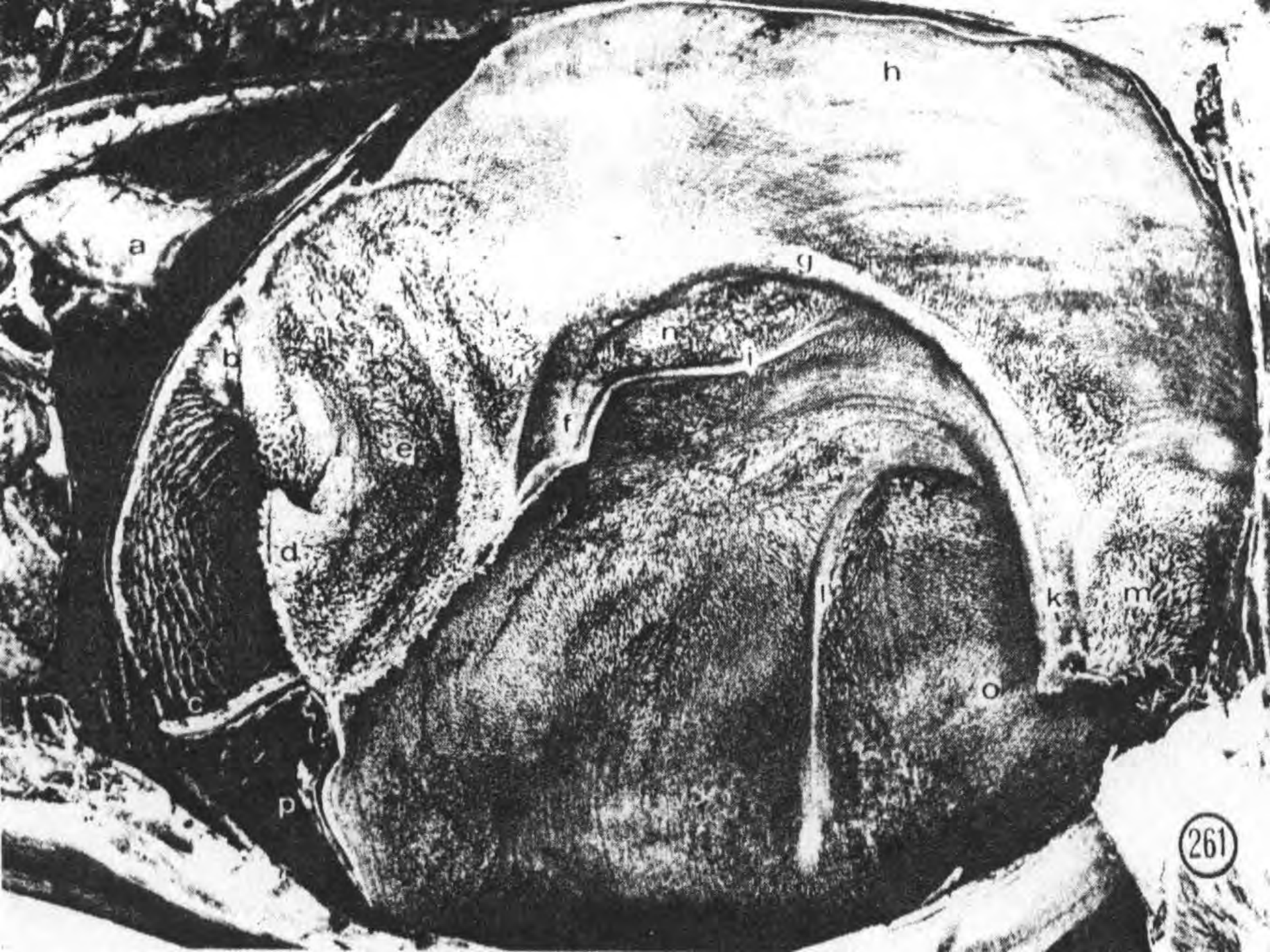
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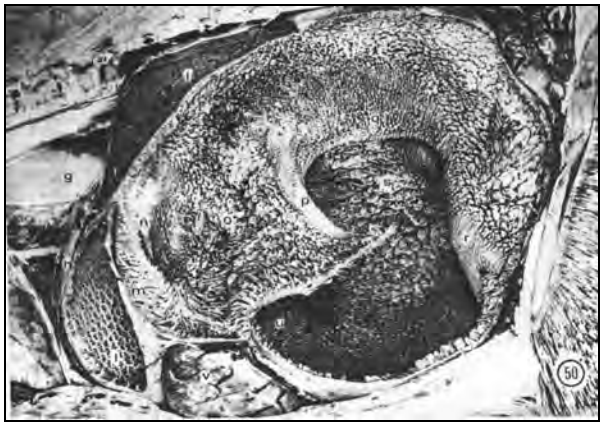
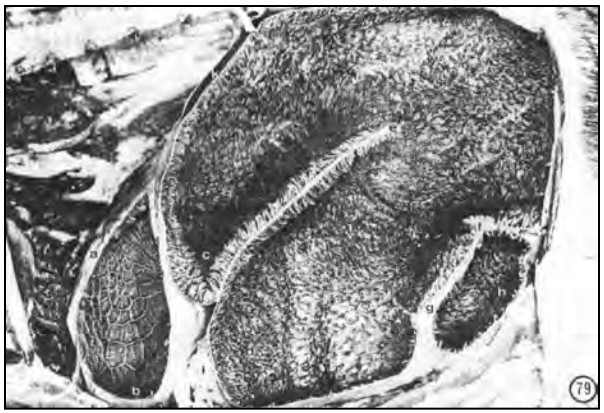
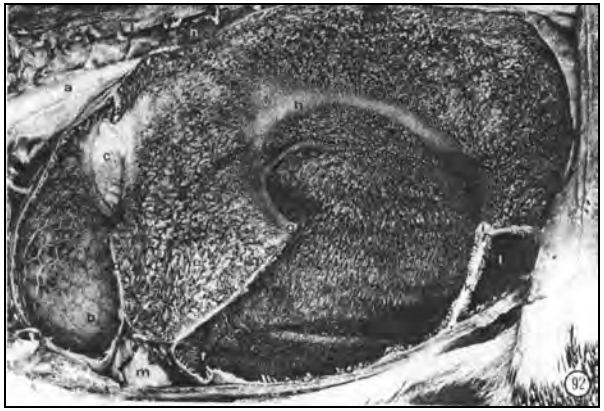
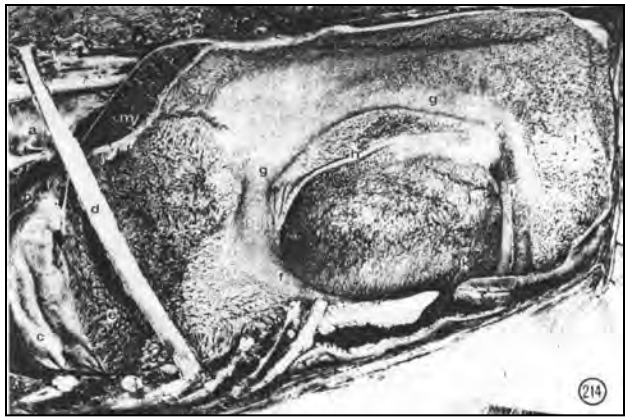
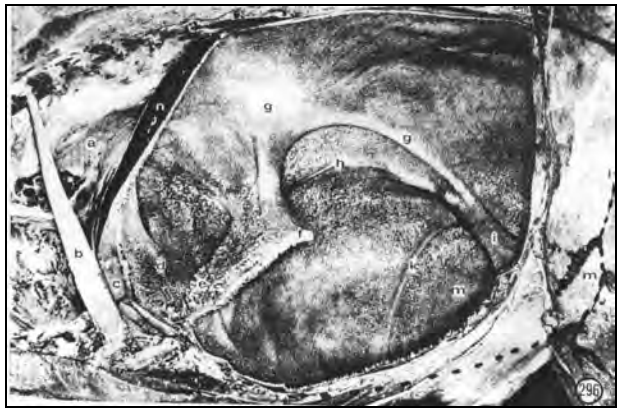
BROWSER





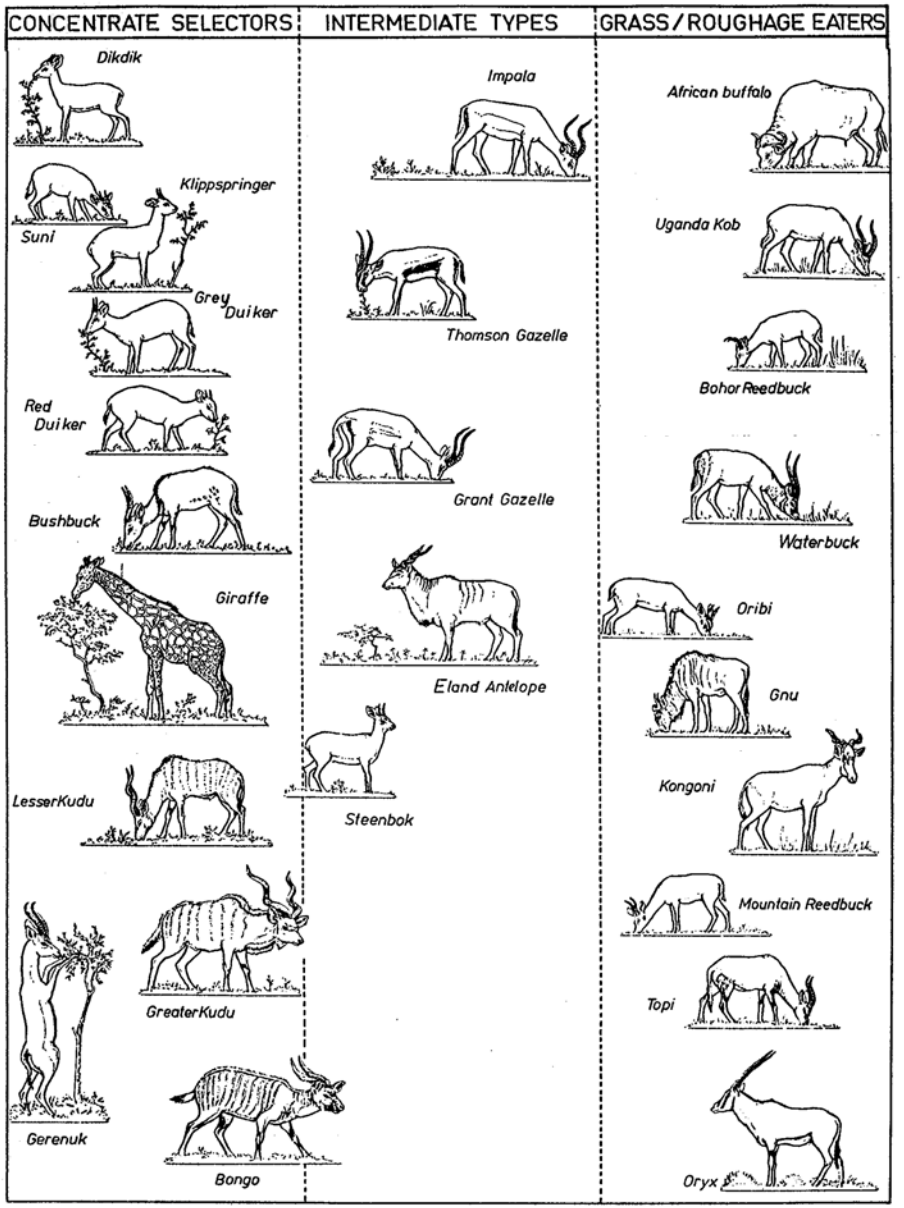






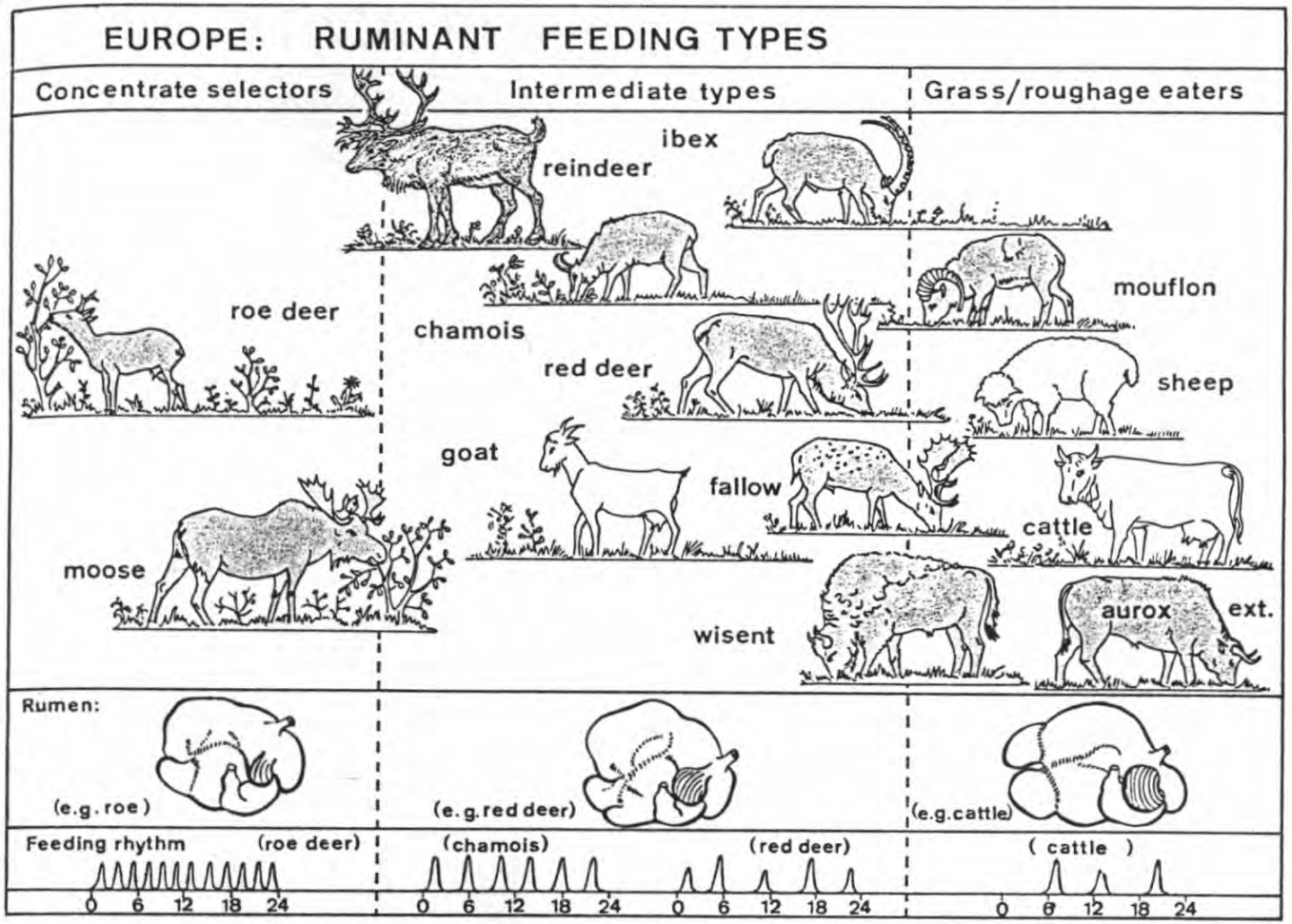
GRAZER

Ruminant feeding types (Hofmann)



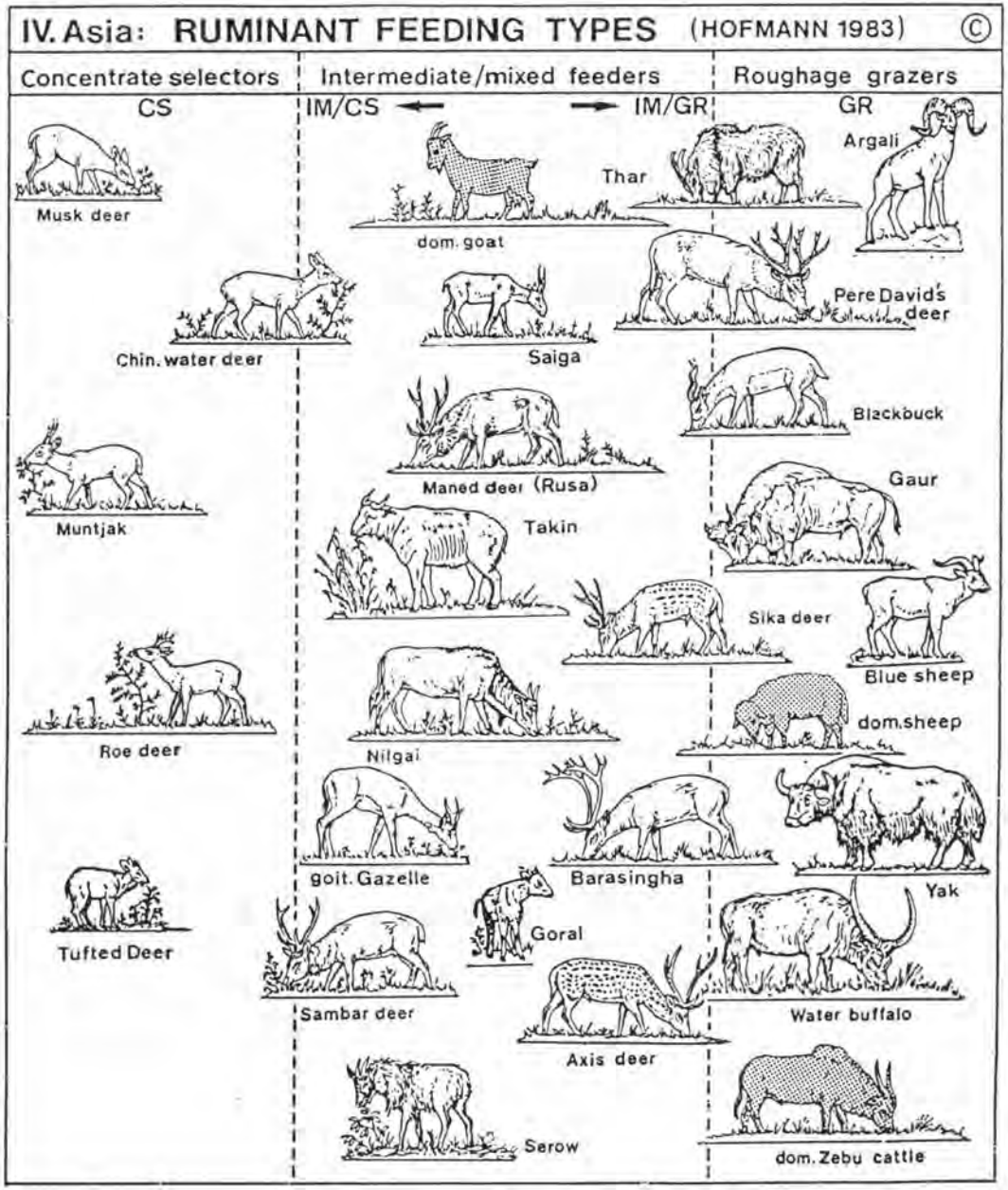
from Hofmann (1989)

Ruminant feeding types (Hofmann)



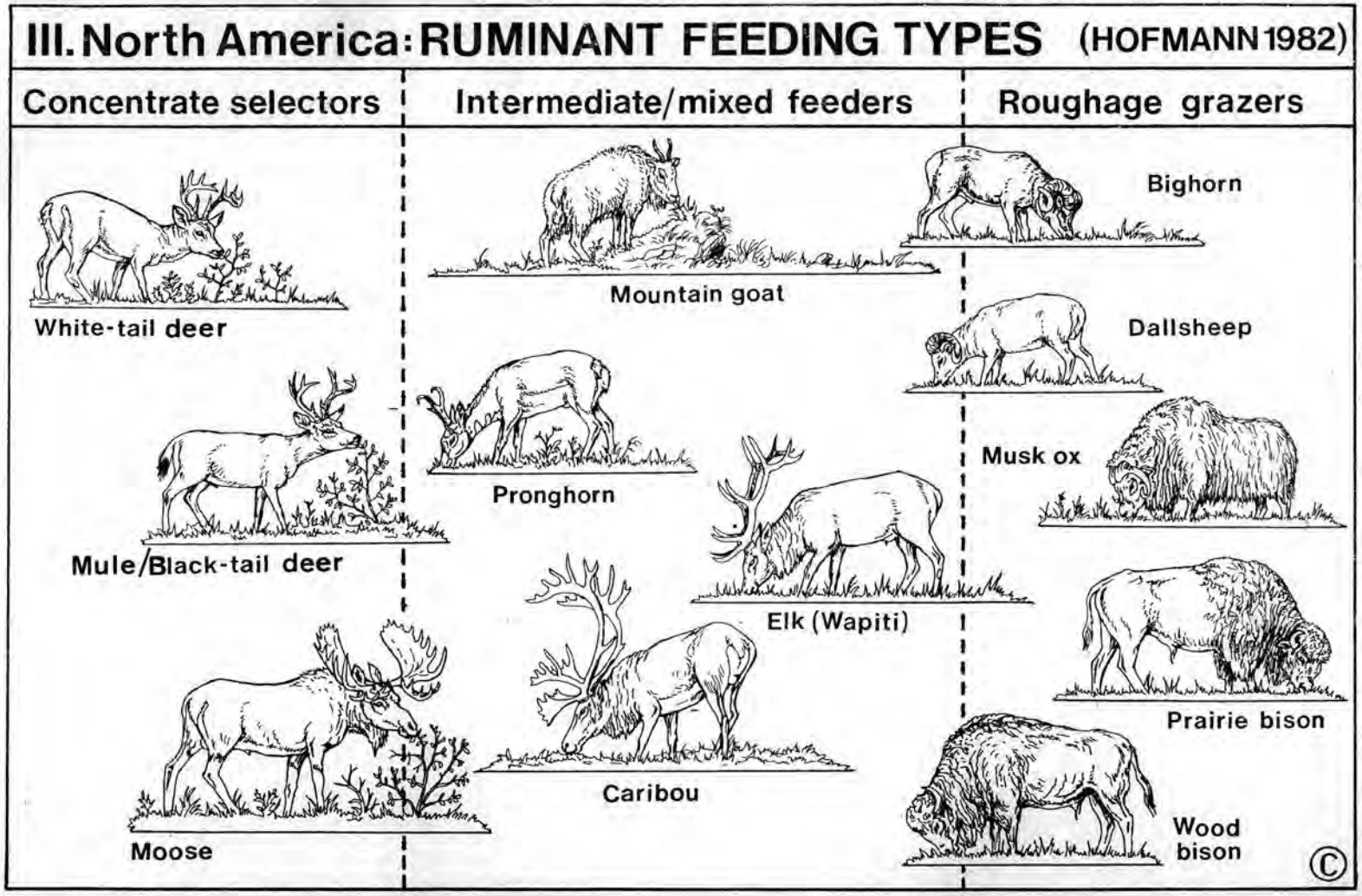
from Hofmann (1989)

Ruminant feeding types (Hofmann)



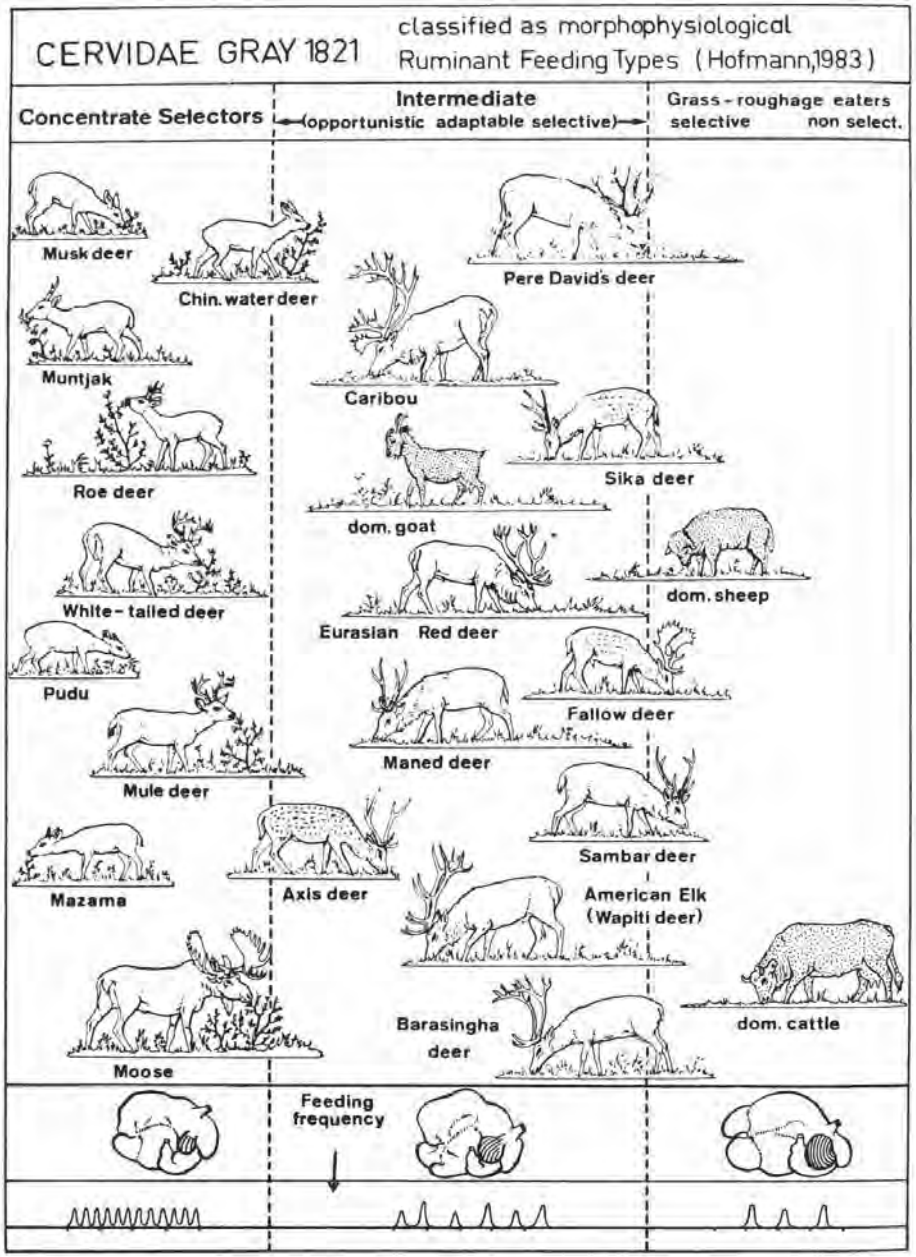
from Hofmann (1991)

Ruminant feeding types (Hofmann)



from Hofmann (unpubl.)

Ruminant feeding types (Hofmann)



from Hofmann (1985)

Oecologia (1989) 78:443–457

7003

Oecologia

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

R.R. Hofmann

Institut für Veterinär-Anatomie, -Histologie und -Embryologie, Abteilung Vergleichende Anatomie der Haus- und Wildtiere, Justus-Liebig-Universität Giessen, D-6300 Giessen, Federal Republic of Germany

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

* Supported by German Research Community grant DFG Ho 273/6

** 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 acis (acetic, butyric, propionic acid set free by rumen bacteriae); *SE* Surface enlargement (of absorptive mucosa)

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.

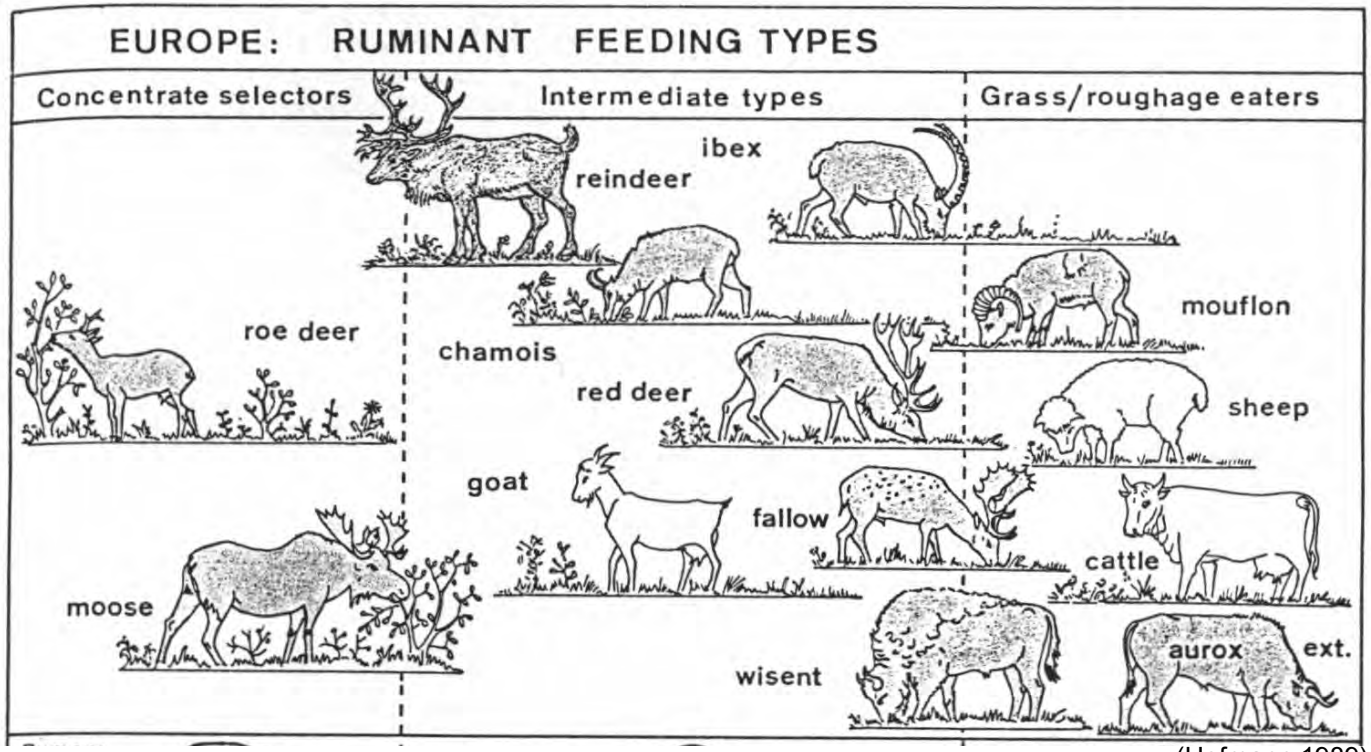
Because they convert apparently indigestible carbohydrates and chemically trapped or protected proteins into nutritious and useful products, they deserve more than *one* approach. Ruminants are late-comers in evolution. Their stomach is a phylogenetic peak of complexity, not only compared with our own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

> 460 citations
(and counting)

Ruminant feeding types (Hofmann)

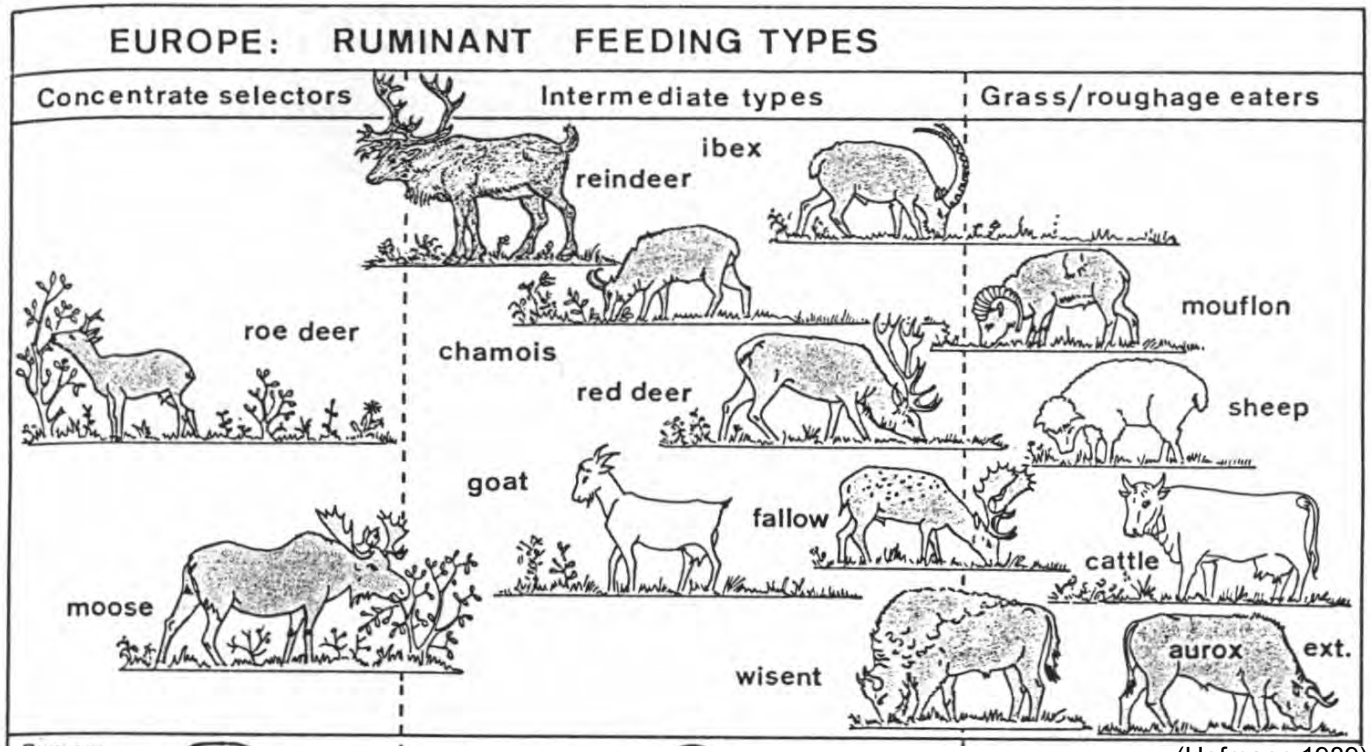


(Hofmann 1989)

dicot ⟷ **monocots**

'browser' 'grazer'

Ruminant feeding types (Hofmann)



(Hofmann 1989)

dicot ⟷ **monocots**

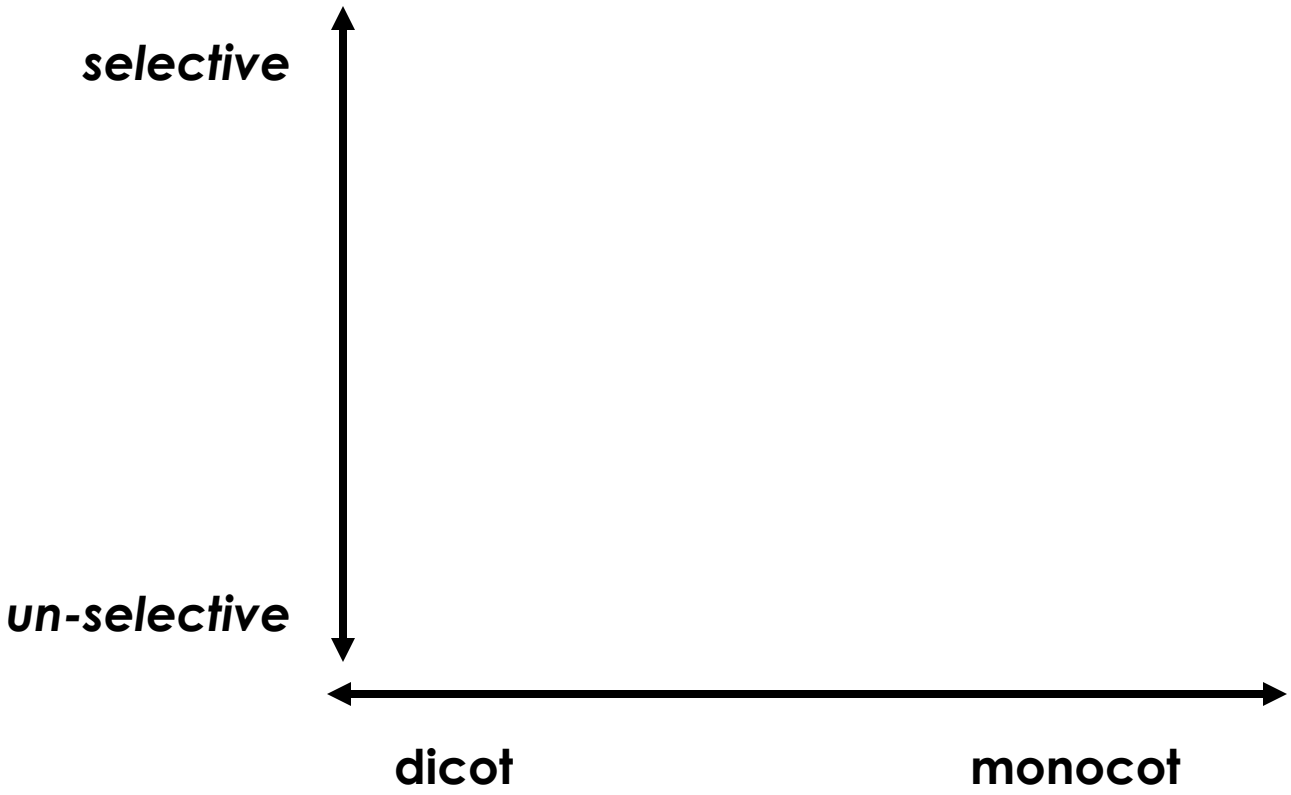
'browser'
"selective"?

'grazer'
"un-selective"?

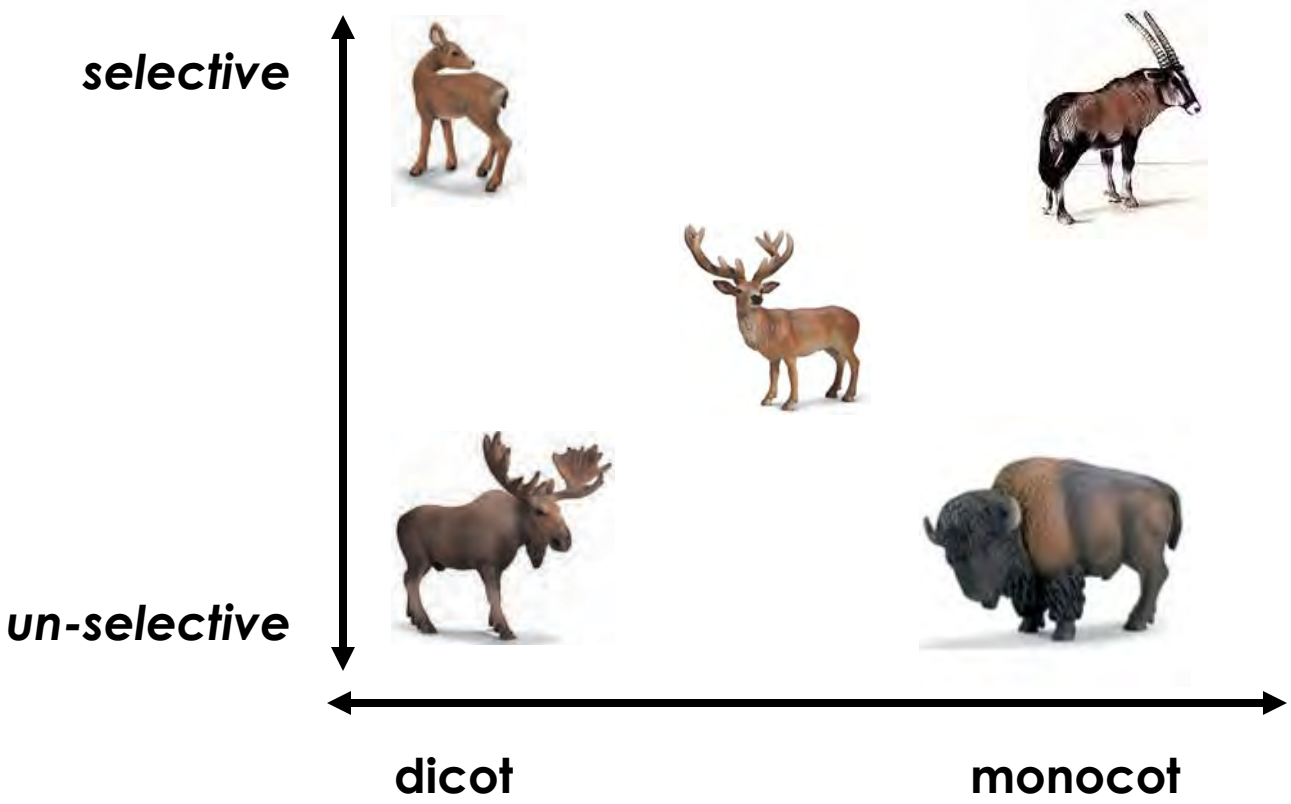
Feeding types

dicot ⟷ **monocot**

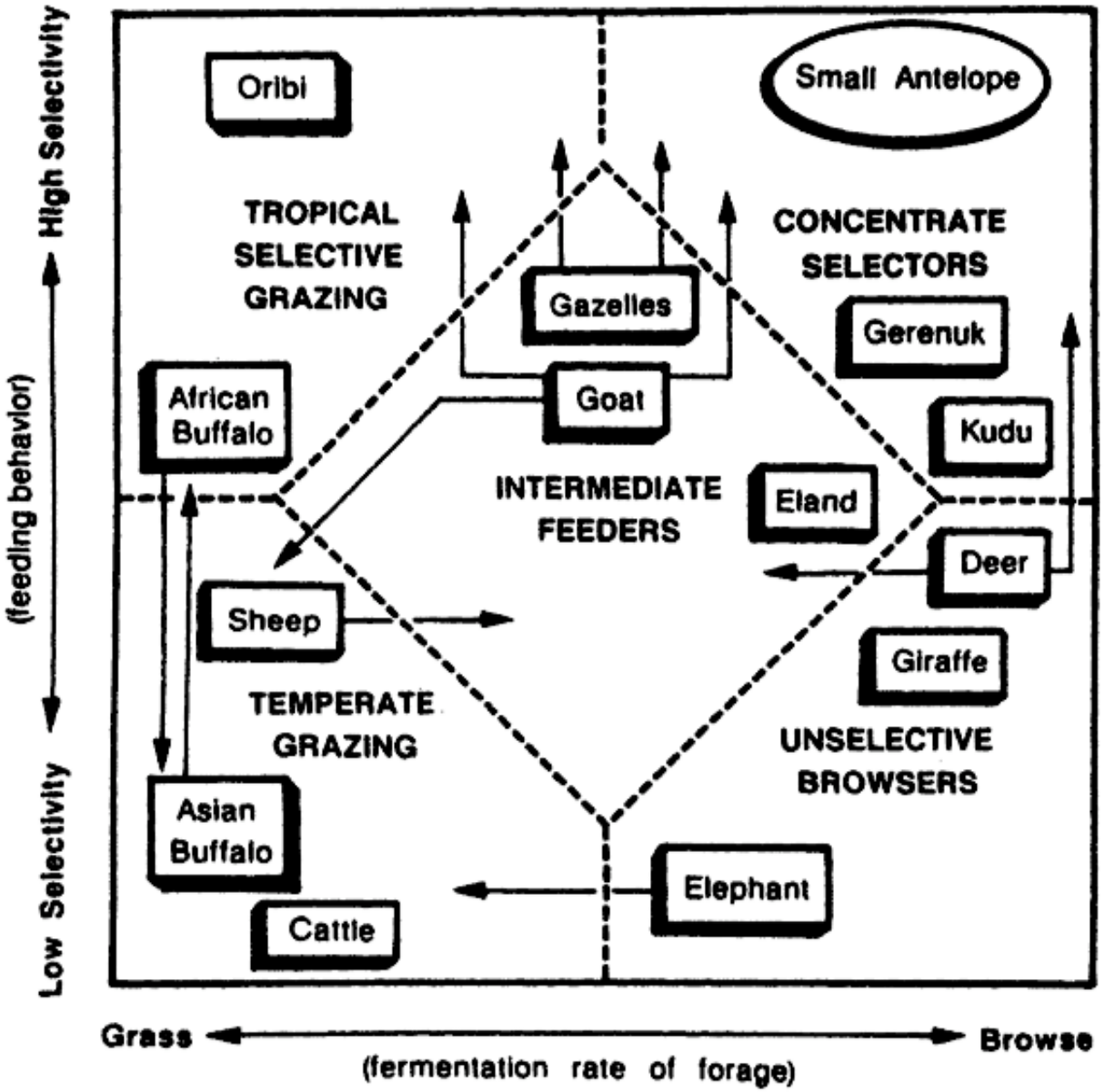
Feeding types



Feeding types

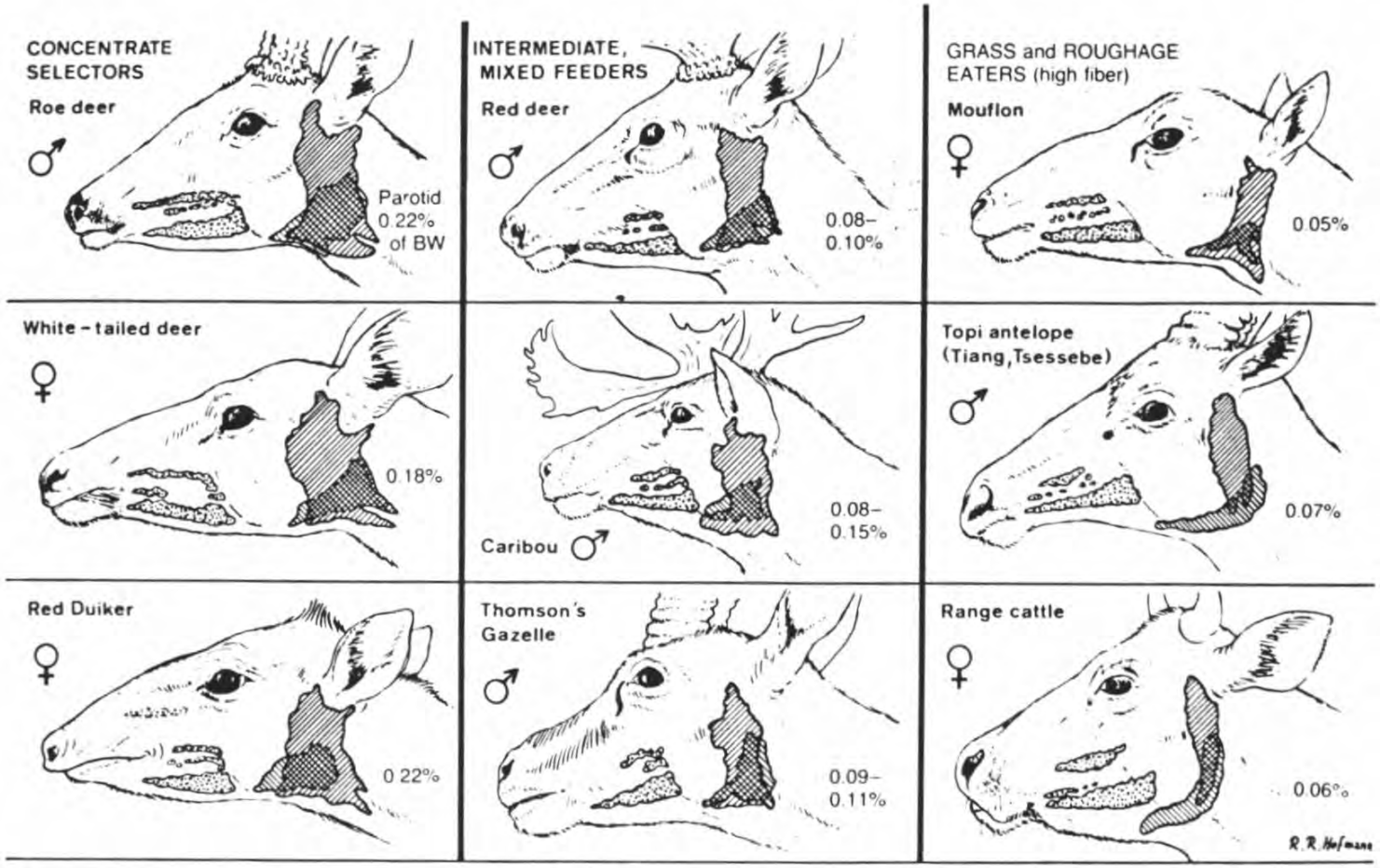


Feeding types



from Van Soest (1996)

Ruminant feeding types (Hofmann)



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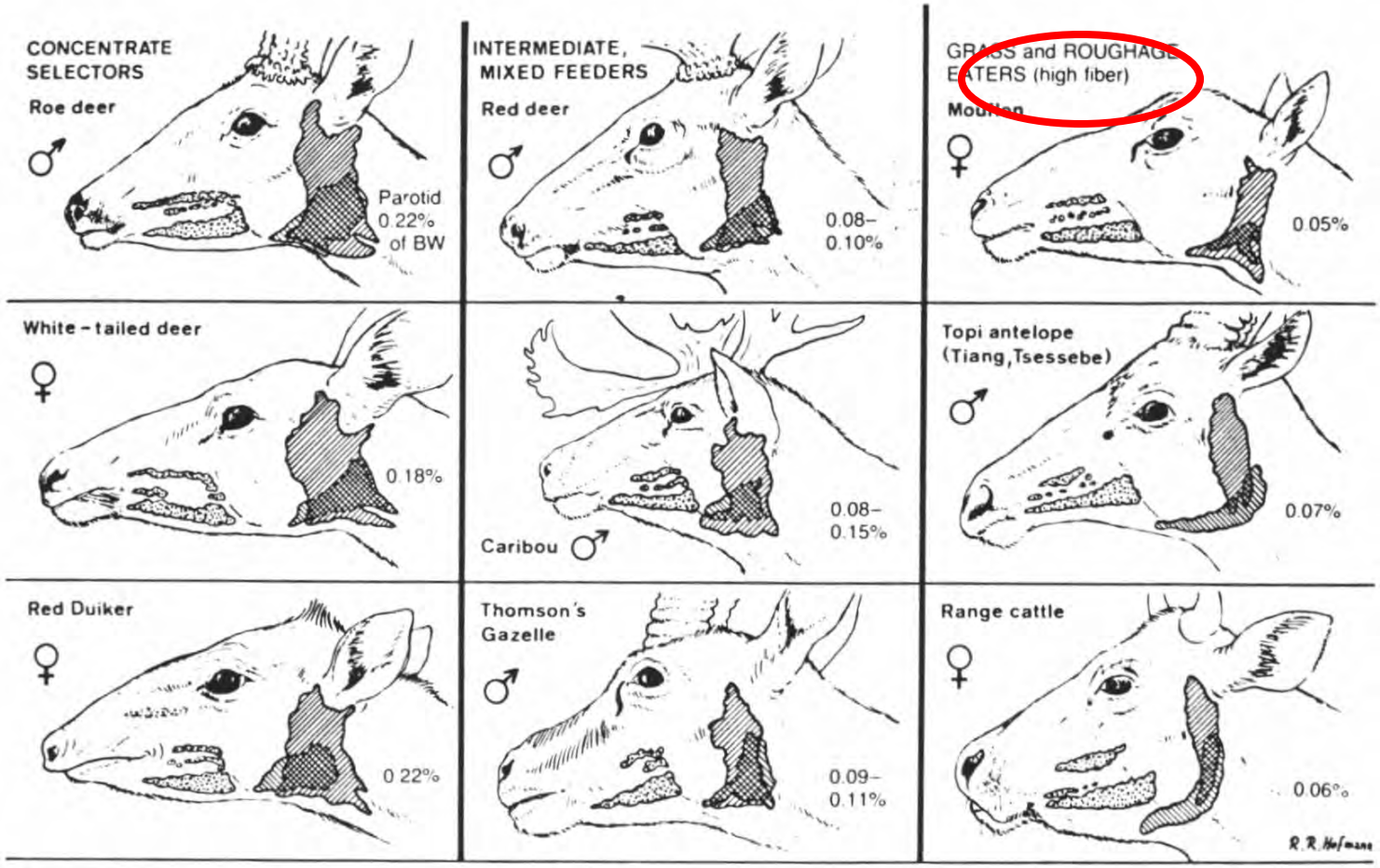
Ruminant feeding types (Hofmann)



from Hofmann (1989)

Ruminant feeding types (Hofmann)

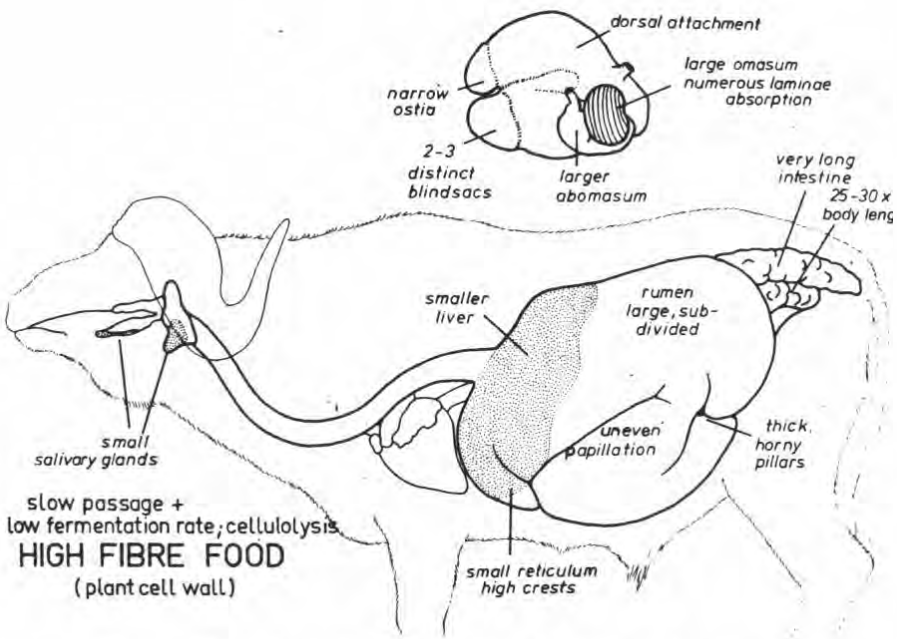


Fig. 1: The African buffalo, a non-selective roughage grazer.

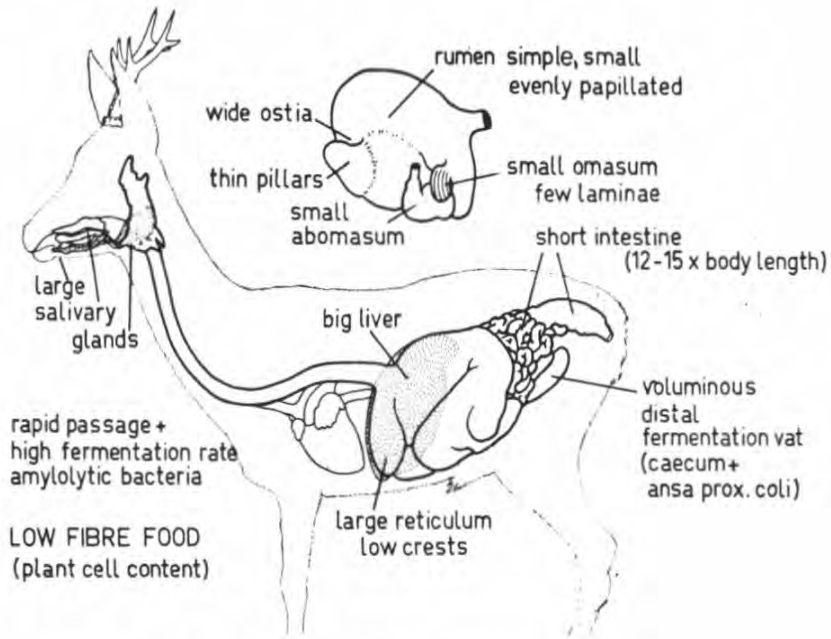


Fig. 2: The roe deer, a concentrate selector.

from Hofmann (1989)

Ruminant feeding types (Hofmann)

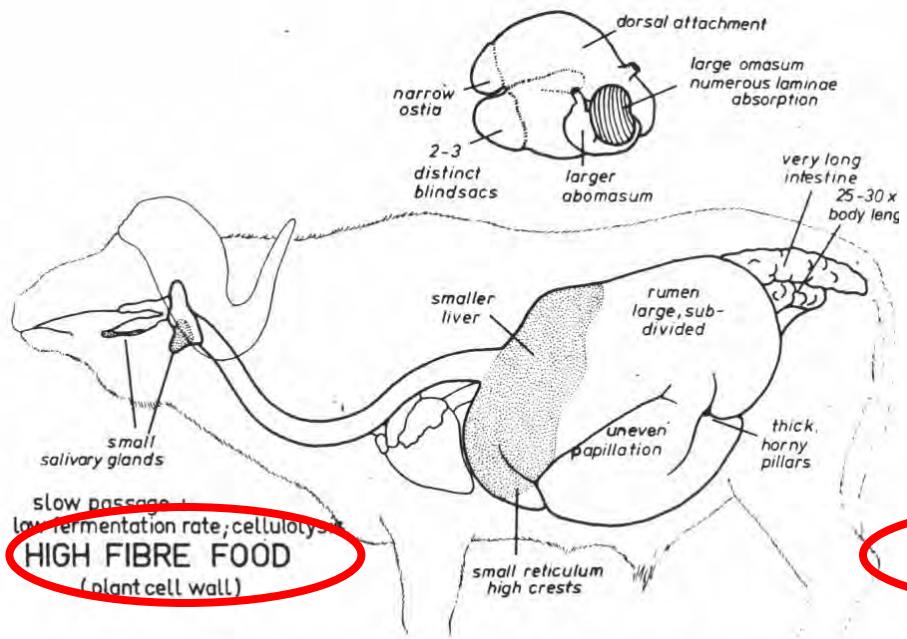


Fig. 1: The African buffalo, a non-selective roughage grazer.

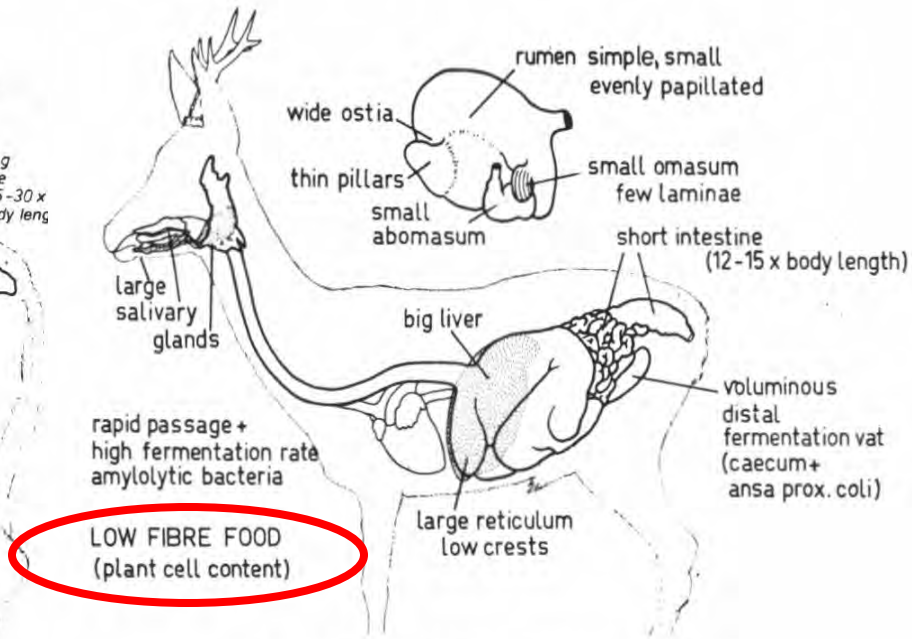


Fig. 2: The roe deer, a concentrate selector.

from Hofmann (1989)

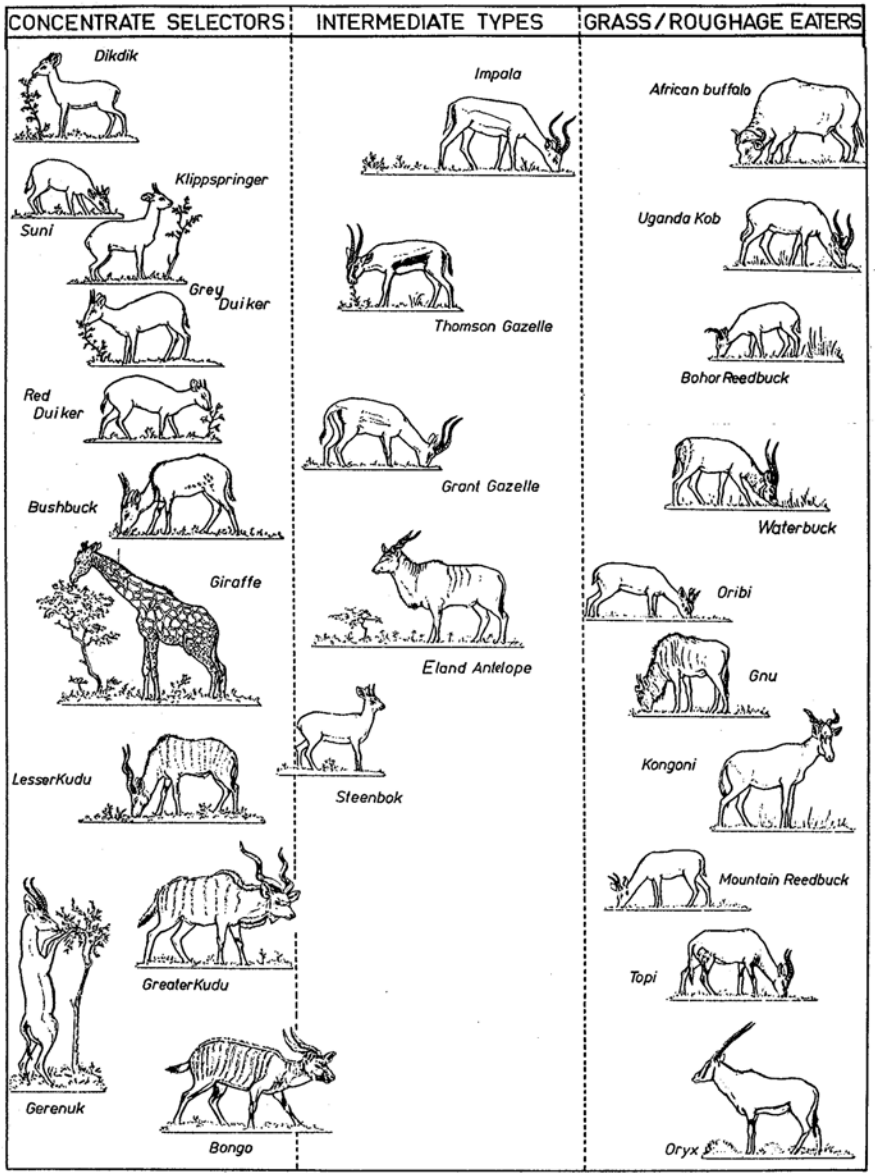
Do diets of grazers and browsers really differ?

Species	Crude fiber (% dry matter)	NDF (% dry matter)
Giraffe (*Giraffa camelopardalis*)	-	50-70
Okapi (*Okapia johnstoni*)	-	43-48
Moose (*Alces alces*)	20-45	50-70
White-tailed deer (*Odocoileus virginianus*)	-	35-50
Buffalo (*Syncerus caffer*)	30-40	-
Waterbuck (*Kobus ellipsiprymnus*)	30-40	-

from Clauss & Dierenfeld (2008)

Do diets of grazers and browsers really differ?

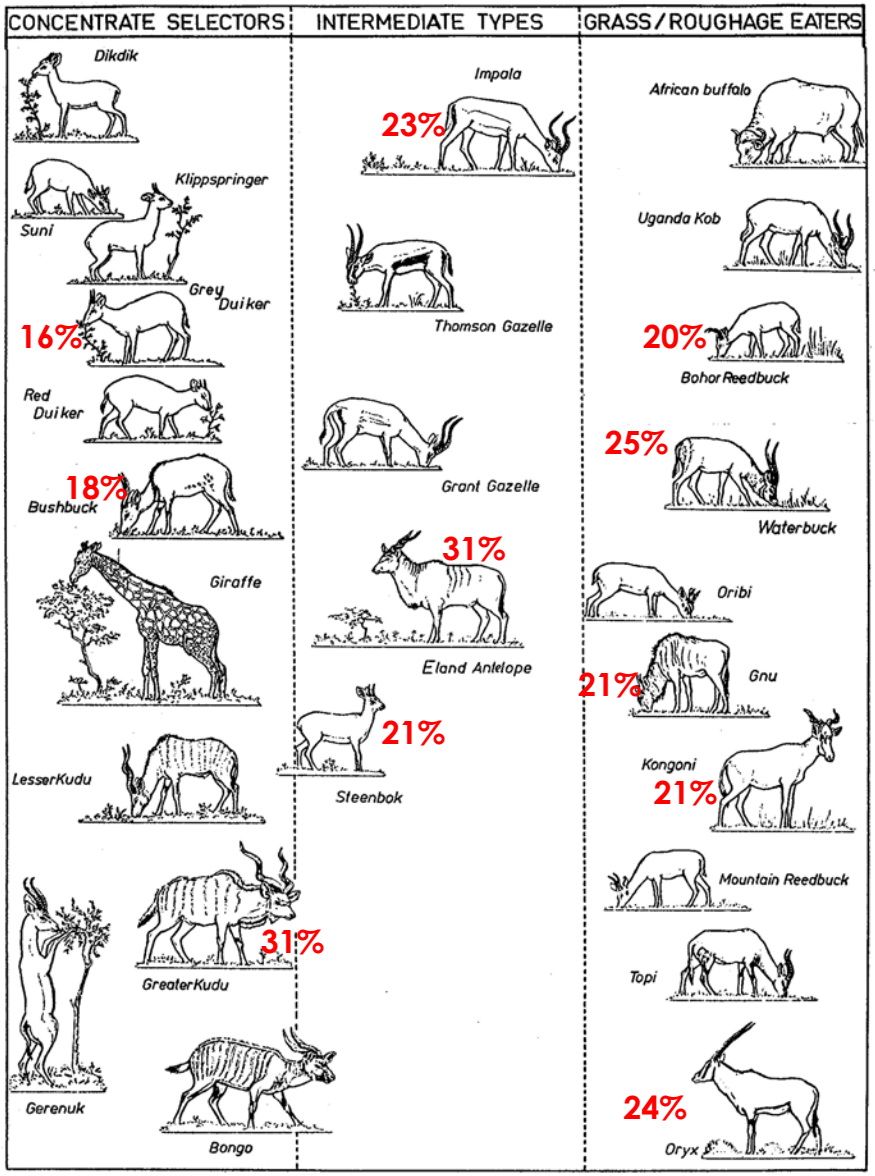
Crude fibre in rumen contents (%DM)



from Hofmann (1989) and Woodall (1992)

Do diets of grazers and browsers really differ?

Crude fibre in rumen contents (%DM)



from Hofmann (1989) and Woodall (1992)

Crude fibre in rumen contents
(Drescher-Kaden & Seifelnasr 1977)

(%dry matter)

Crude fibre in rumen contents
(Drescher-Kaden & Seifelnasr 1977)

(%dry matter)

20 % Area 1 20 %

Crude fibre in rumen contents
(Drescher-Kaden & Seifelnasr 1977)

(%dry matter)

20 %	Area 1	20 %
24 %	Area 2	34 %

Differences between grass and browse

	Sugar	Starch	Pectin	Hemi-cellulose	Cellu-lose
	[% DM]	[% DM]	[% DM]	[% DM]	[% DM]
Grass	5-15	1-5	1-2	15-40	20-40
Browse	5-15	-	6-12	8-12	12-30

from Robbins (1993)

Don‘t lose perspective !

Don‘t lose perspective !

is slower than ...

Don‘t lose perspective !

a slow car ?

Don‘t lose perspective !

Don‘t lose perspective !

contains less alcohol than

...

Don‘t lose perspective !

an alcohol-free beverage ?

Don‘t lose perspective !

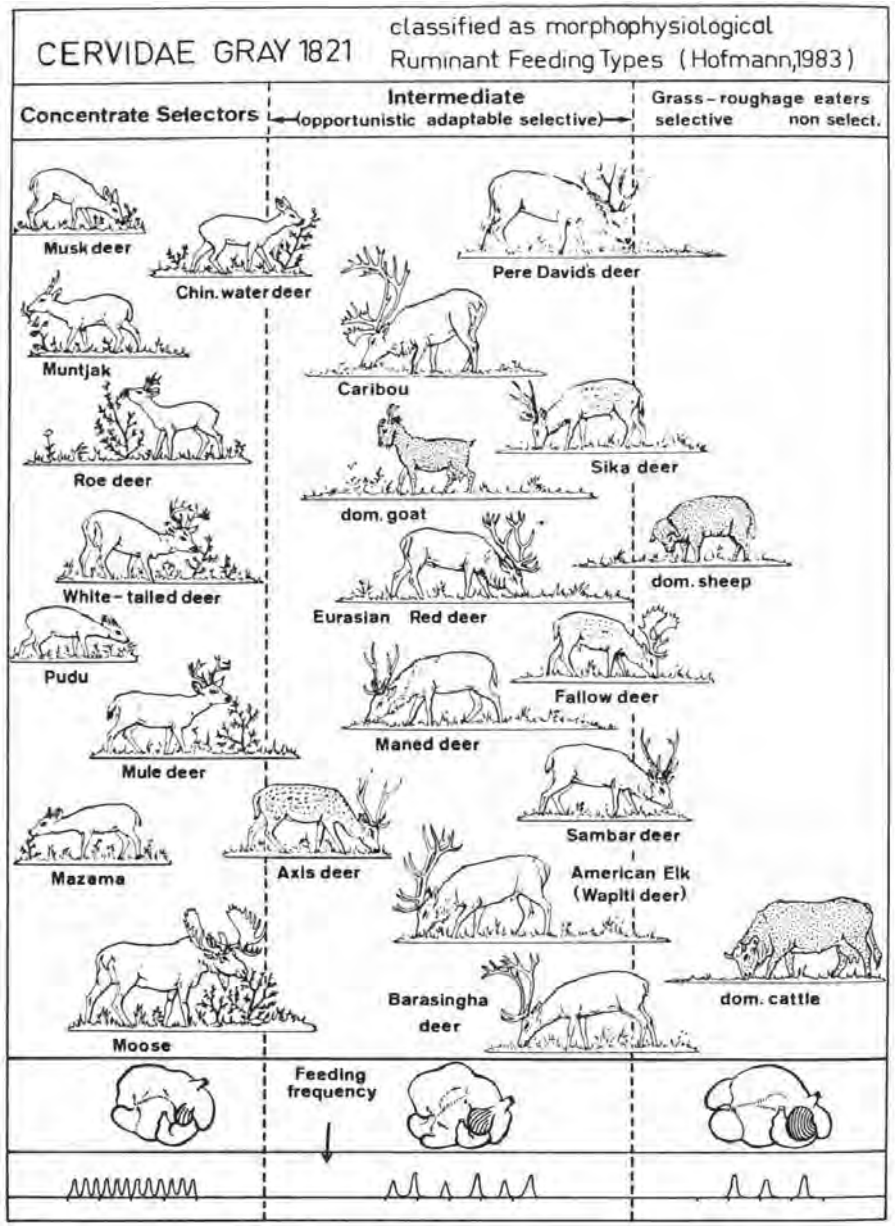
Don‘t lose perspective !

eats a diet of lower fibre content than ...

Don‘t lose perspective !

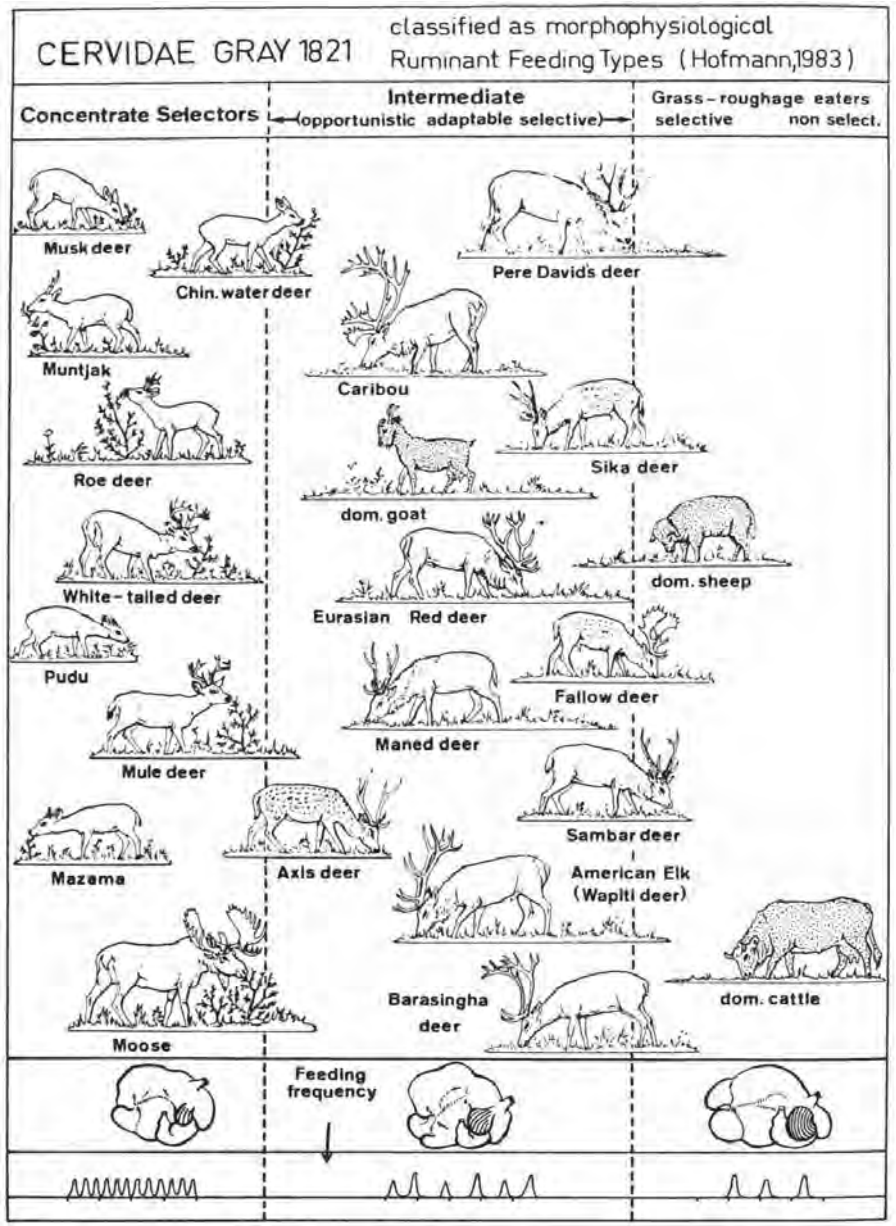
a ‘concentrate-selector?’

Ruminant feeding types (Hofmann)



from Hofmann (1985)

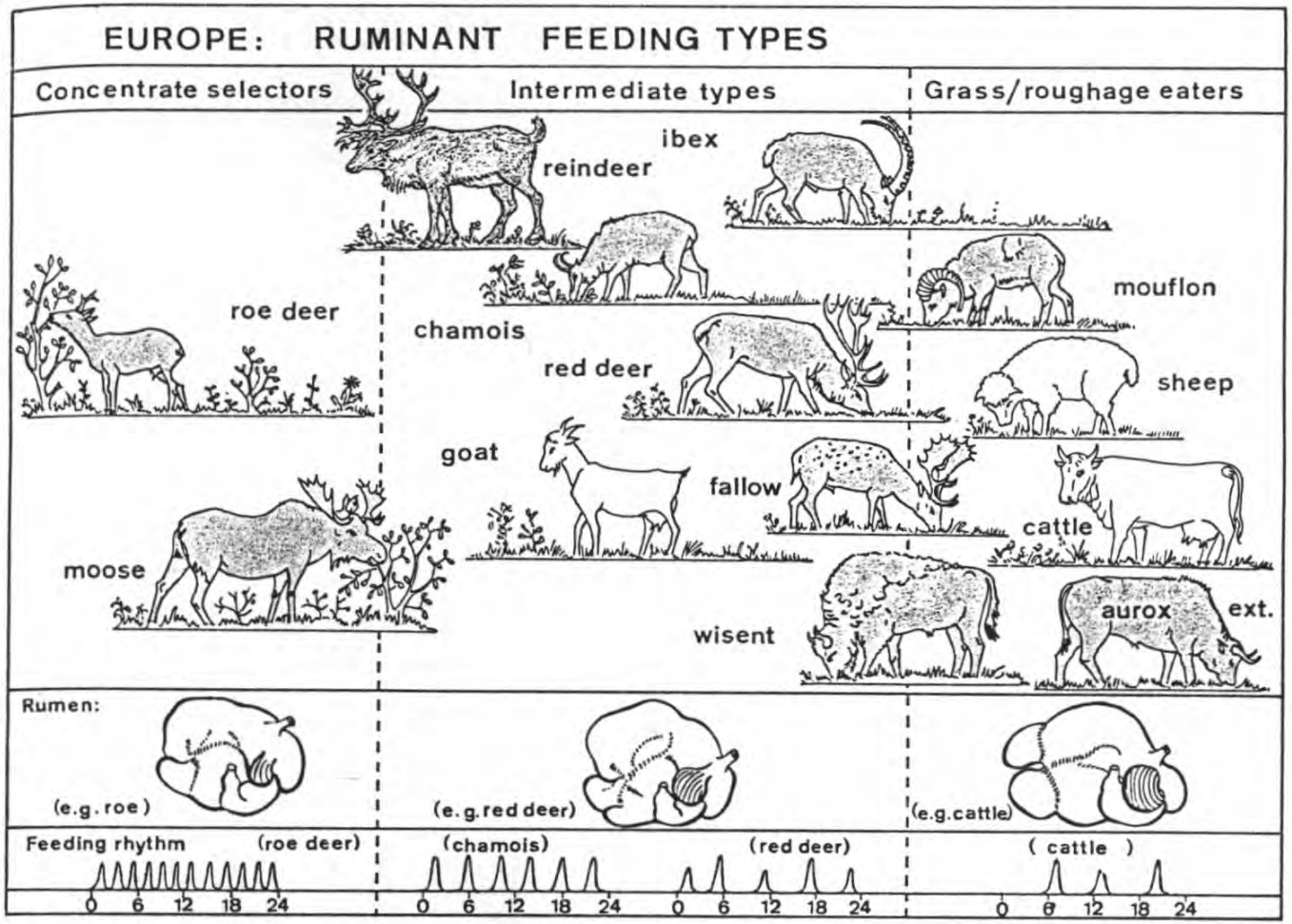
Ruminant feeding types (Hofmann)



"... based on anatomical and dietary observations ..."

from Hofmann (1985)

Ruminant feeding types (Hofmann)



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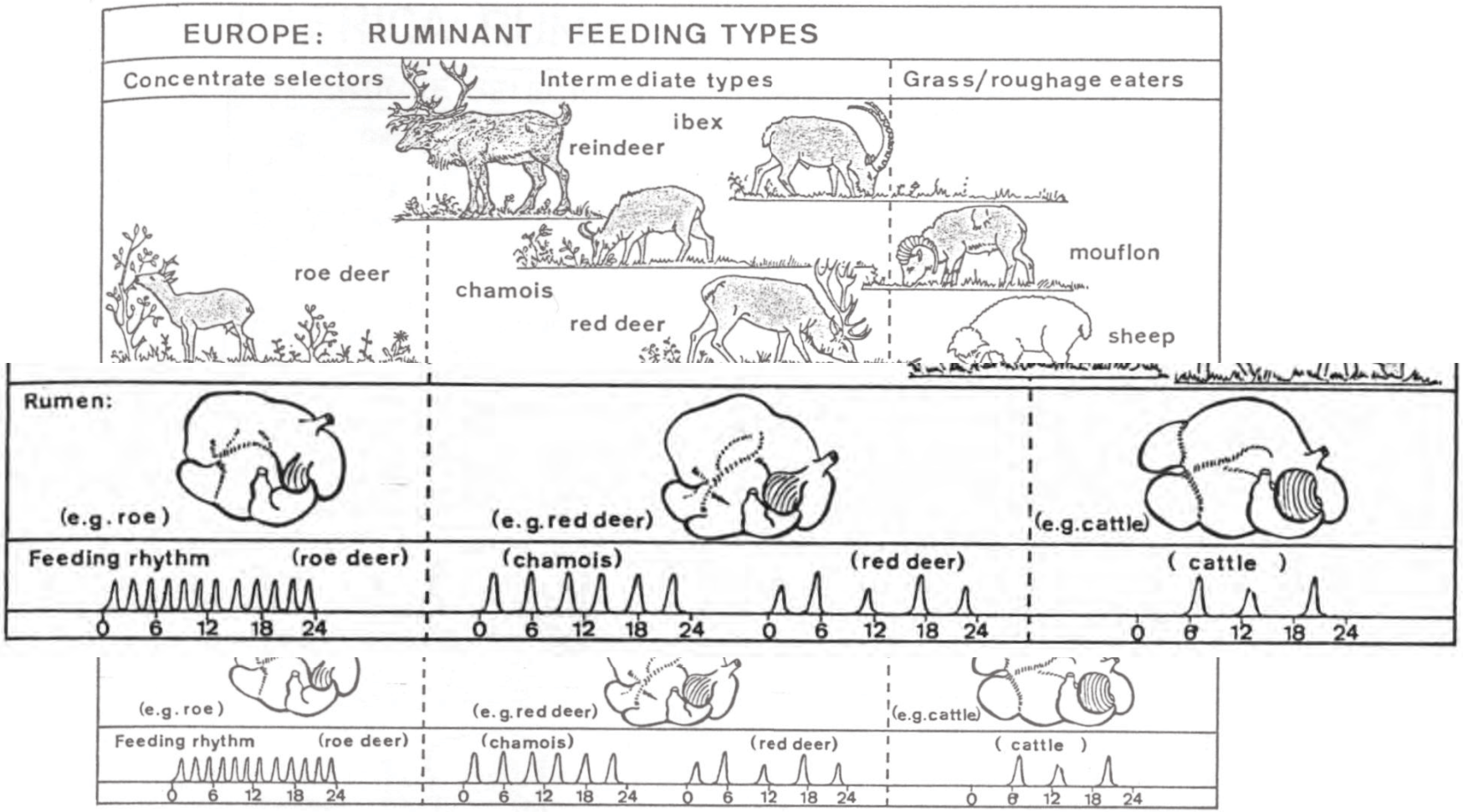

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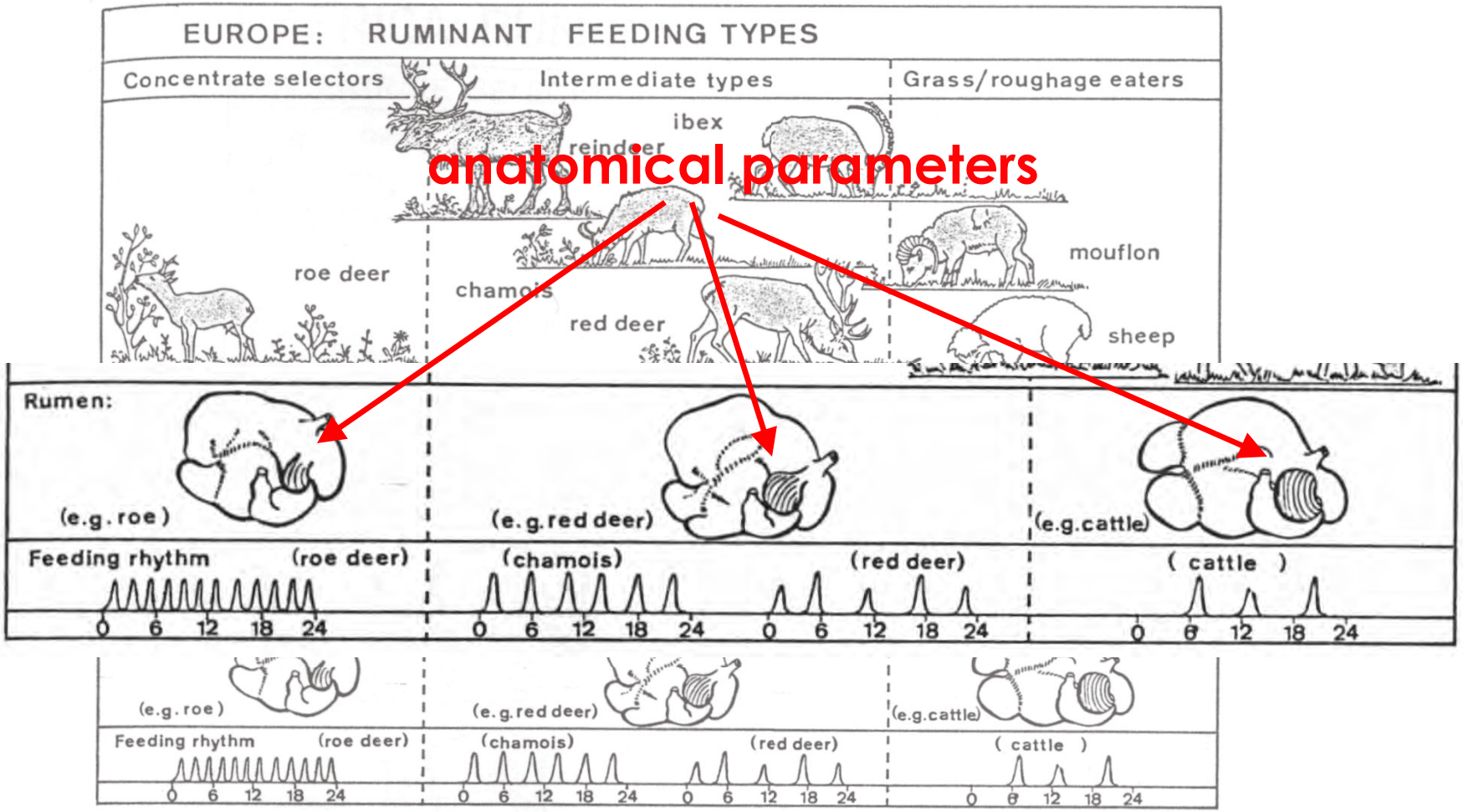

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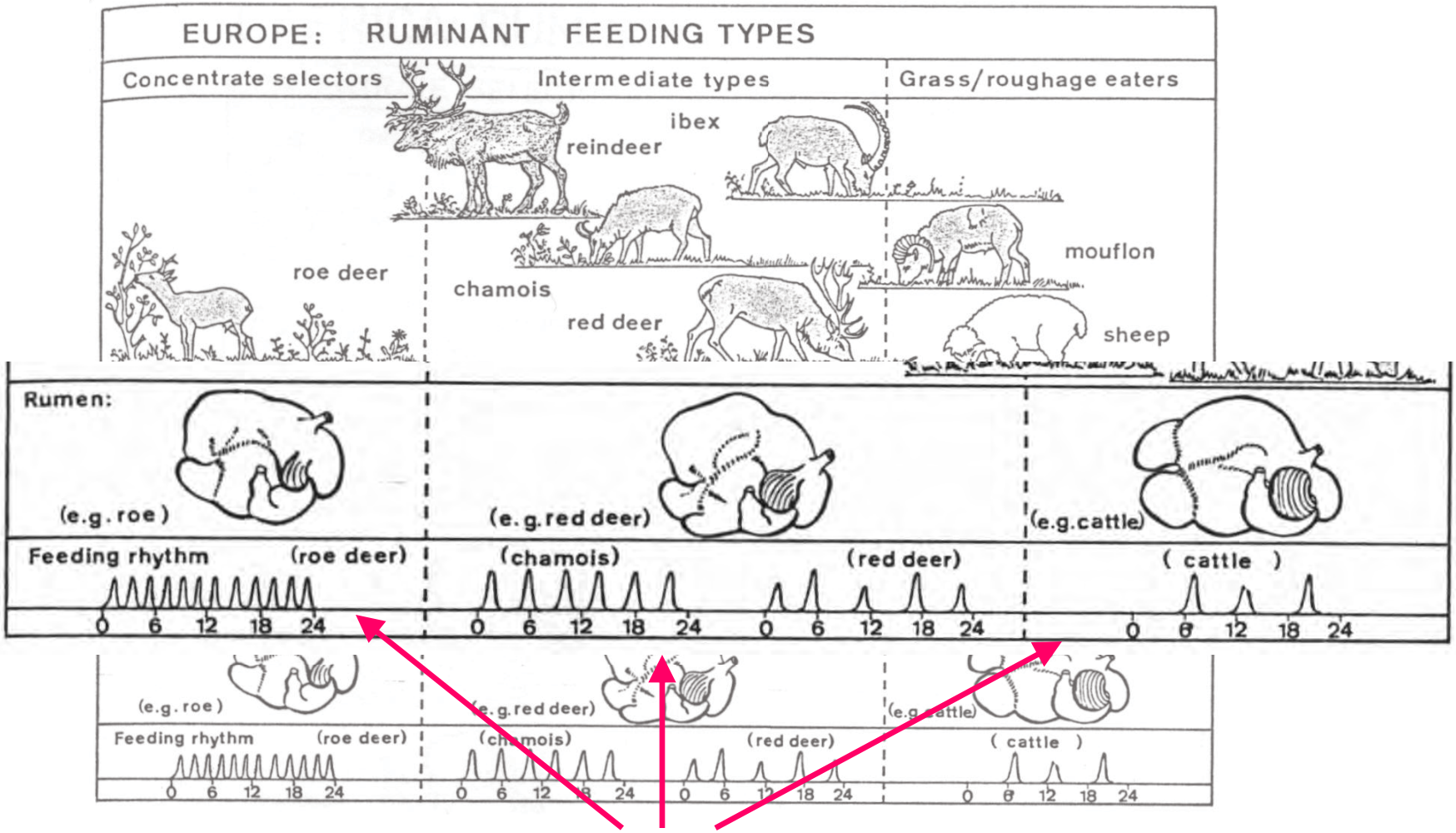


behavioral parameters

from Hofmann (1989)

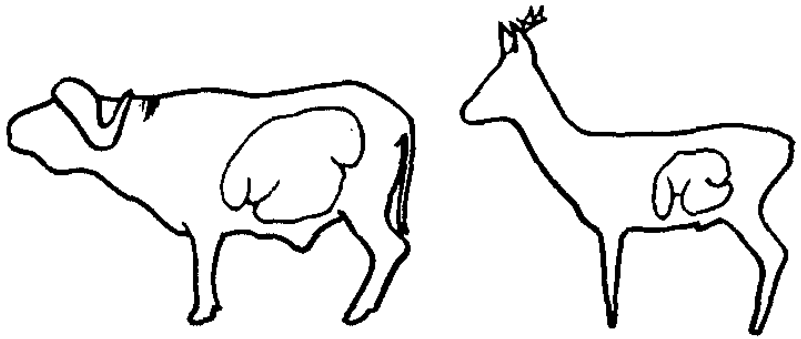
Feeding bout frequency

Table 3. Reported number of daily feeding bouts in different free-ranging ruminant species

Species		Season	Feeding bouts/day	Source
Browser				
Roe deer	*Capreolus capreolus*	Winter/summer	6–13	Cederlund (1981)
White-tailed deer	*Odocoileus virginianus*	Winter	5	Ozoga & Verme (1970)
Mule deer	*Odocoileus hemionus*	Winter	5–6	Carpenter (1976)
Moose	*Alces alces*	Winter/summer	5–8	Risenhoover (1986); Cederlund, Bergström & Sadbergen (1989); Renecker & Hudson (1989); Van Ballenberghe & Miquelle (1990)
Greater kudu	*Tragelaphus strepsiceros*	Winter/summer	5	Owen-Smith (1998)
Giraffe	*Giraffa camelopardalis*		5	Pellew (1984)
Grazer				
Mouflon	*Ovis ammon musimon*	Winter/summer	2–5	Langbein, Scheibe & Eichhorn (1997); Moncorps *et al.* (1997)
Muskox	*Ovibos moschatus*	Winter	3–4	Jingfors (1982)
Bison	*Bison bison*	Summer/autumn	3–5	Hudson & Frank (1987)
African buffalo	*Syncerus caffer*	Autumn/winter	3	Ryan & Jordaan (2005)

from Hummel et al. (2006)

Differences between grazers and browsers: anatomy ... and physiology?

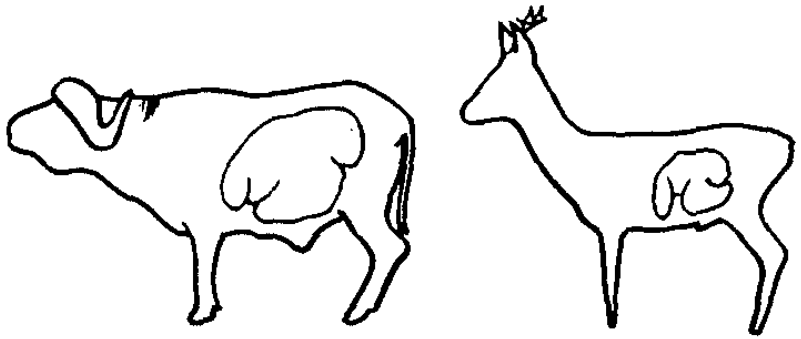


	Grazer or roughage eater	*Browser or concentrate selector*
	(buffalo)	(roe deer)
Rumen size	+	−
Rumen pillars	+	−
Rumen papillae	−	+
Reticulum	−	+
Omasum	+	−
Parotid salivary glands	−	+
Food retention time	+	−
Fermentation rate	−	+
Cellulolytic bacteria	+	−
Protozoa (diversity)	+	−

+, relatively bigger or more developed
−, relatively smaller or less developed

from Kay et al. (1984)

Differences between grazers and browsers: anatomy ... and physiology?



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	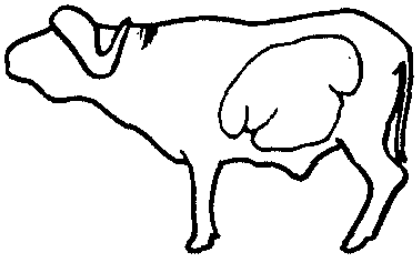	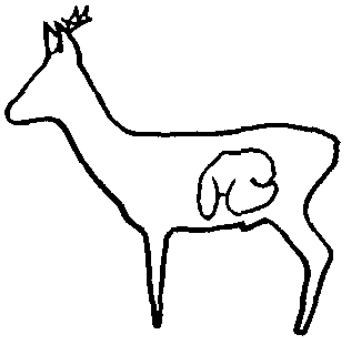
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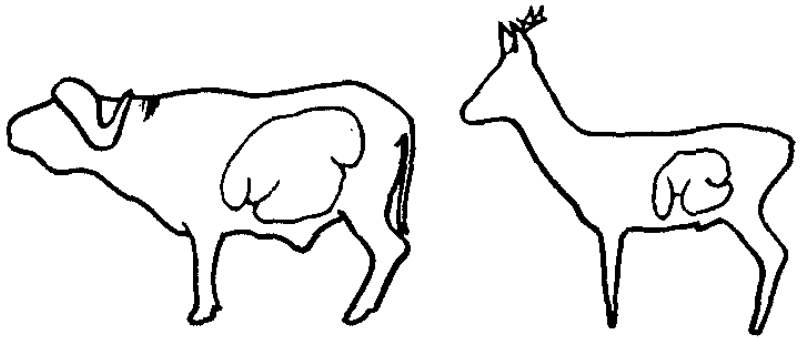

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	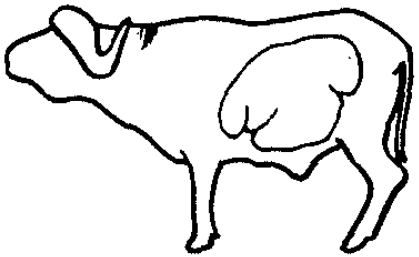	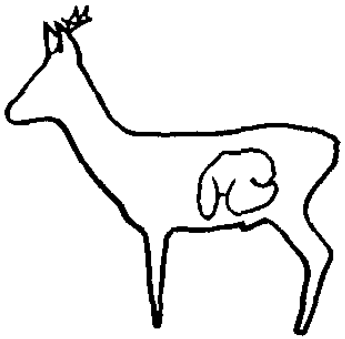
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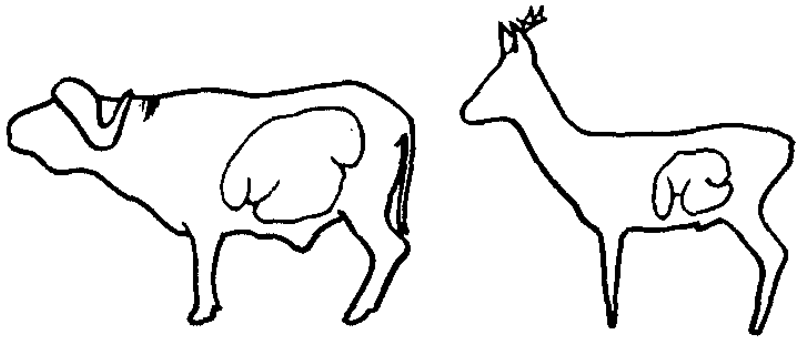

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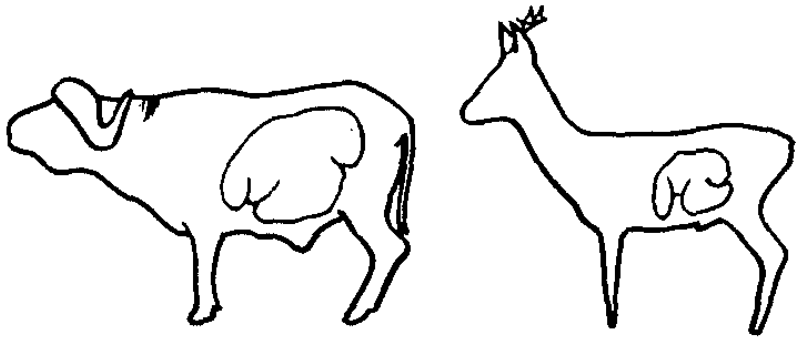

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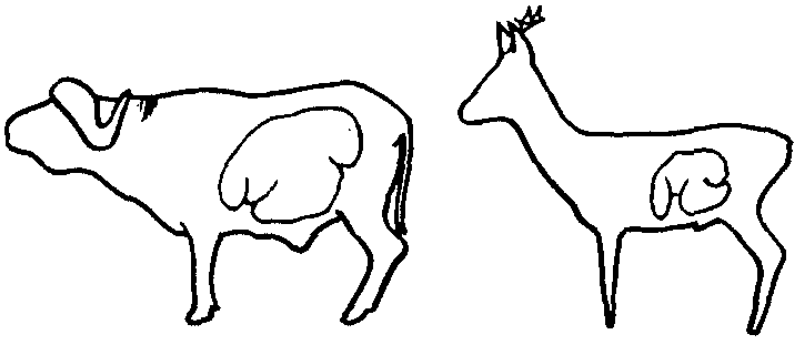

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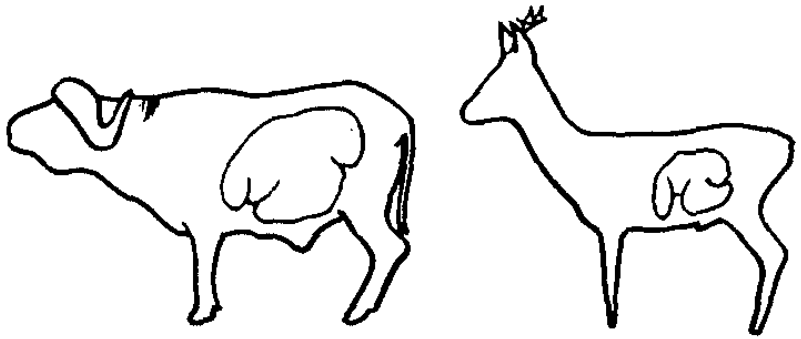

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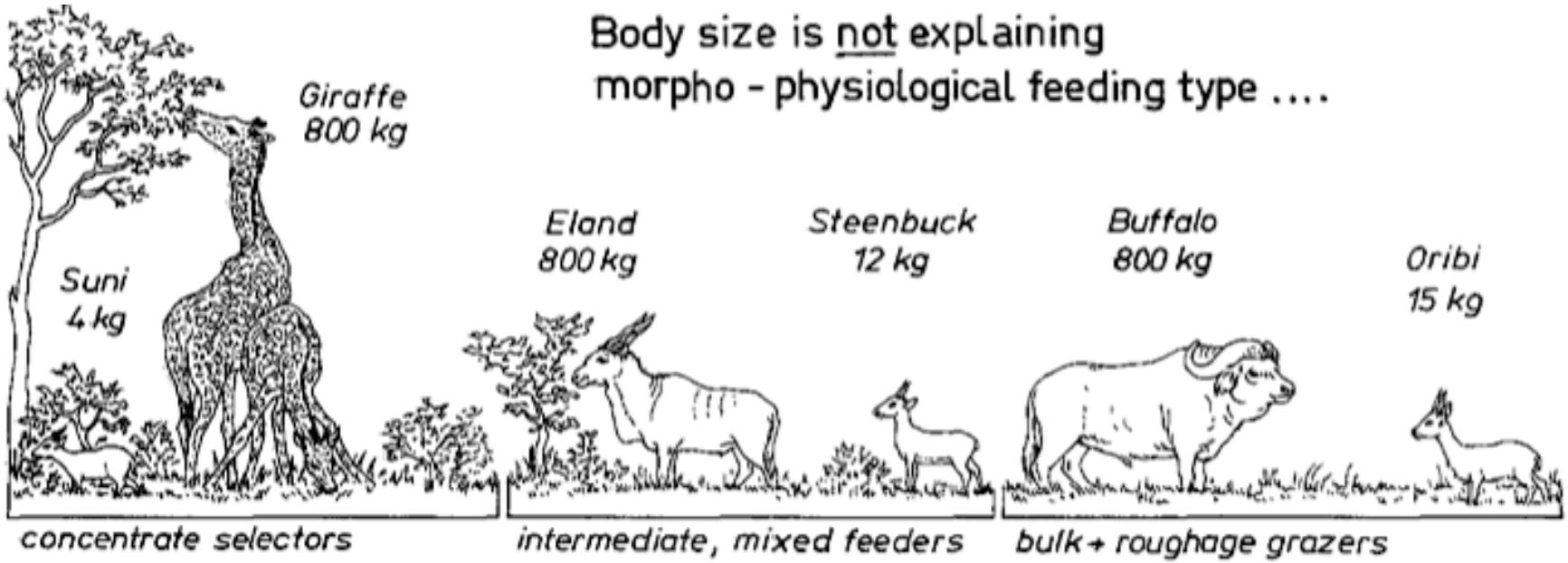
Protozoa (diversity)	+	−

+, relatively bigger or more developed
−, relatively smaller or less developed

from Kay et al. (1984)

Pyhsiological postulates based on anatomical observations without experimental data!



from Hofmann (1989)

Additionally, Hofmann claimed that the most influential factor for all physiological processes – body size – was less important than the feeding type classification!

Oecologia (1994) 98:167–175

ORIGINAL PAPER

Iain J. Gordon · Andrew W. Illius

The functional significance of the browser-grazer dichotomy in African ruminants

Received: 24 February 1994 / Accepted: 12 April 1994

Abstract The allometric relationships for the fermentation rate of dry matter, the total energy concentration of volatile fatty acids (VFAs), the energy supplied from VFA production and the mass of the digesta contents within the rumen or caecum and proximal colon (hindgut) were used to test whether the digestive strategies of grazing and browsing African ruminants differ. The wet and dry mass of the contents of the rumen and hindgut were allometrically related to body mass (BM). These relationships did not differ between browsing and grazing ruminants. The fermentation rates in the rumen were strongly allometric and the intercepts of the relationships did not differ between browsers and grazers. The fermentation rates in the hindgut were not allometrically related to BM and did not differ between ruminants with different feeding habits. Likewise, the total energy concentration of the VFAs in the rumen and hindgut showed no allometric scaling and did not differ between browsing and grazing ruminants. The energy supplied by VFA production in both the rumen and hindgut of African ruminants scaled at around 0.8 with BM. Only in the case of the energy supplied by VFAs in the rumen were there significantly different intercepts for browsing and grazing ruminants. The energy supplied by VFA production in the rumen was inadequate to meet the energy requirements for maintenance of browsers and small grazers. The retention time of digesta in the alimentary tract was positively related to BM although there was no difference in the allometric relationships for grazers and browsers. The results of these analyses suggest that, after controlling for the effects of body mass, there is little difference in digestive strategy between African ruminants with different morphological adaptations of the gut.

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Key words Feeding habits · Rumen · Digestive strategy · Allometry · Retention time

Introduction

African ruminants have diversified to fill a wide variety of ecological niches and vary considerably in body mass and the type of diet consumed (Sinclair 1983). Body mass (Bell 1971; Jarman 1974), feeding facilitation (Bell 1971), competitive exclusion (Murray and Brown 1992; Illius and Gordon 1993) and predation (Sinclair 1985) have been hypothesized as the primary ecological pressures shaping the community structure of African ruminants. Hofmann and Stewart (1972) and Hofmann (1973, 1989) suggested that the major dichotomy separating species of ruminants is in their adaptations for consuming a bulk/roughage diet of primarily grasses (grazers) or a concentrate diet of browse or forbs (browsers).

The differences in the proportions of structural carbohydrates in grasses and browse are seen as leading to differences in the structure and function of the digestive tract of grazing and browsing ruminants. Forages consist of cell contents which are wholly digestible (van Soest 1982), digestible cell wall and an indigestible residue (predominately lignin). For any given phenological stage, browse has higher levels of cell solubles and lignin but lower levels of holocellulose (cellulose and hemicellulose) than grasses (McDowell et al. 1983; Demment and van Soest 1985). Consequently, browse has higher levels of the rapidly fermenting soluble component than grasses. However, because of the higher lignin content in the cell wall of browse, the absolute digestibility of browse tends to be lower (White and Trudell 1980). Therefore, browsers are expected to have a digestive system adapted for the rapid excretion of the highly lignified, less digestible cell wall fraction, whereas grazers have adaptations to slow down the passage of plant material in the rumen, thereby increasing the extent of digestion of the less lignified cell wall component. Hofmann (1973) demonstrated anatomical adaptations of the ali-

Oecologia (1995) 103:208–213

ORIGINAL PAPER

2007

Charles T. Robbins · Donald E. Spalinger
Wouter van Hoven

Adaptation of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid?

Received: 15 November 1994 / Accepted: 18 February 1995

Abstract As a result of pioneering work of Hofmann (1973, 1989), nutritional ecologists classify ruminants into three feeding-type categories: browsers ("concentrate" feeders), grazers, and intermediate or mixed feeders. Hofmann proposed that these feeding types result from evolutionary adaptations in the anatomy of the digestive system and that one consequence is shorter retention of the digesta in the rumen of browsers, and thus a decreased efficiency of fiber digestion relative to that of grazers. We examined the hypotheses that (1) fiber digestion of browsers is lower than that of grazers, (2) salivary gland size is larger in all browsers than in grazers, (3) the browser's larger salivary glands produce larger volumes of thin serous saliva than those of grazers, and (4) thus, browsers have higher liquid passage rates than do grazers. We found that the extent of fiber digestion is not significantly different between browsers and grazers, although fiber digestion is positively related to herbivore size. In general, salivary gland size is approximately 4 times larger in browsers than grazers, but some browsers (e.g., greater kudu) have small, grazer-sized salivary glands. Resting (non-feeding or ruminating) saliva flow rates of mule deer (browser) and domestic sheep and cattle (grazers) were not significantly different from each other. Finally, ruminal liquid flow rates were not different between feeding types. We conclude that many of Hofmann's nutritional and physiological interpretations of anatomical differences amongst ruminants are not supportable.

Key words Ruminants · Browsers · Digestion · Foraging · Saliva

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Introduction

Ruminants occupy a diverse array of feeding niches throughout the world. Although they feed on plants of widely divergent physical and chemical compositions (e.g., lichens, grasses, and woody stems), ecologists classify ruminants into one of three general feeding categories, comprising grazers, browser/concentrate feeders, and intermediate feeders. These categories reflect the predilection of the animals for consuming grasses, browses/herbs/fruits, or a mixture of both, respectively (Hofmann 1973, 1989).

In a classic work, Hofmann (1973) examined the foraging preferences of these groups in relation to their digestive anatomy, and concluded that general digestive system adaptations correspond to the ecological role of the animal. He hypothesized that grazing ruminants are better adapted for consuming slowly digested plant fiber (typical of grasses and sedges) than are browsing ruminants because grazers have larger rumens, and the structure of the rumen and omasum retards the passage of food to the lower tract. Conversely, browsers have smaller and less complex rumens and omasums, and they have larger parotid salivary glands that produce a copious, serous saliva to help buffer the rapidly digestible ("concentrate") diet and aid in the passage of foods from the rumen. These differences have led Hofmann (1989, p. 453) to suggest that "all [browsers and intermediate] species cannot digest fibre as well as grazers".

Hofmann's nutritional and ecological interpretations have been a powerful abstraction of ruminant function, influencing the way that nutritionists and ecologists view ruminant evolution and behavior, and the organization and composition of herbivore communities (McNaughton and Georgiadis 1986; Owen-Smith 1991). However, until recently, Hofmann's hypotheses have not been rigorously tested. In the first major attempt to test Hofmann's ideas, Gordon and Illius (1994) concluded that there is no significant difference in digestive kinetics (fermentation rate, daily VFA (volatile fatty acid) (VFA) production, and mean total tract retention time of food)

Oecologia (2000) 125:82–84

Stephen S. Ditchkoff

A decade since "diversification of ruminants": has our knowledge improved?

Received: 11 October 1999 / Accepted: 6 April 2000

Abstract In his landmark 1989 paper, R.R. Hofmann classified ruminants into three categories based upon digestive anatomy and preferred forages, and proposed that divergence of feeding strategies among ruminants is a result of morphological evolution of the digestive tract. Because of the hypothetical nature of these views and the ingrained beliefs that they challenged, several papers were published that reported tests of Hofmann's predictions. The consensus among these papers was that Hofmann's predictions were inadequate. I describe the experimental evidence that has been put forth in opposition to the ruminant diversification hypothesis and contend that we have failed to adequately test Hofmann's predictions.

Key words Concentrate selectors · Intermediate feeders · Roughage eaters · Rumen bypass · Ruminant diversification

Early attempts to explain variation found in feeding strategies of free-ranging ruminants classified individual species as "browsers" or "grazers" based upon types of forage consumed. Though an important step in understanding the complexities of ruminant nutrition, Hofmann and Stewart (1972) recognized that feeding strategies of ruminants could not simply be classified into two categories, and proposed three categories (i.e., bulk and roughage eaters, selectors of concentrate forages, and intermediate feeders) based upon stomach structure and feeding ecology. Hofmann (1984) later documented variation in all portions of the digestive anatomy among the three categories of his system of ruminant classification. The dynamic interactions among body size, fermentation and passage rates, and energetic requirements, and their influence on dietary strategy formed the basis for these early classifications.

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In a landmark paper, Hofmann (1989) expanded upon the concepts proposed by Hofmann and Stewart (1972) and Hofmann (1984) by providing a working hypothesis of the functional and morphological basis for diversity in ruminant feeding strategies. Hofmann (1989) proposed that feeding strategies ranged from nonselective intake of bulk roughage and efficient fermentation in the forestomach, to selectivity for concentrate forages (high in plant cell content) with increased post-ruminal digestion. This hypothesis challenged many beliefs regarding digestion in free-ranging ruminants and proposed that we reexamine the manner in which ruminant herbivores obtain nutrients from the environment.

Because of the magnitude of Hofmann's hypothesis, several papers (Gordon and Illius 1994, 1996; Robbins et al. 1995) were published describing tests of his predictions. These researchers examined components of Hofmann's hypothesis and concluded that they did not find support for morpho-physiological adaptations to diet type within classes of ruminants. They attributed differences in digestive function to body mass or food characteristics. As a result, the consensus has been that Hofmann's hypothesis regarding gut morphology and function in classes of ruminants is inadequate (Robbins et al. 1995; Illius 1997). However, upon critical examination of both Hofmann's hypotheses and subsequent critiques, I contend that we have not adequately tested Hofmann (1989). Although scientifically sound, the studies of Gordon and Illius (1994, 1996) and Robbins et al. (1995) did not completely examine components of the ruminant diversification hypothesis and therefore should not be considered to support or refute Hofmann (1989).

Hofmann (1989) proposed variations on the traditional theme of foregut fermentation in the ruminant. In addition to suggesting that hindgut fermentation may play an important role in some ruminant animals, he also commented on postruminal digestion of soluble components of the diet after rumen bypass via the reticular groove (Hofmann 1989, p. 448). While post-ruminal fermentation had previously received some attention (Van Soest 1982), selective bypass of the rumenoreticular

Oecologia (2001) 129:498–508
DOI 10.1007/s004420100768

F. Javier Pérez-Barbería · Iain J. Gordon
Andrew W. Illius

Phylogenetic analysis of stomach adaptation in digestive strategies in African ruminants

Received: 19 March 2001 / Accepted: 25 June 2001 / Published online: 31 July 2001

Abstract The stomach morphology of 28 species of artiodactyls that differ in feeding style (browser, mixed feeder, grazer) was analysed using a multivariate approach and phylogenetic correction in order to test whether stomach morphology was correlated with feeding style when body mass was controlled for. A total of 25 morphological traits of the stomach were used in the analysis. After the effects of body mass and phylogeny on stomach morphology were taken into account, there was no significant grouping of species according to feeding style. When information about the feeding style of each species was included in the analysis, the set of morphological traits separated the mixed feeders from the other two feeding styles, but grazers and browsers had similar morphological features. Most of the variance in stomach morphology was explained by body mass and a lesser proportion by phylogeny. The main morphological features that have previously been proposed as being adaptations in grazing species, namely, lengthening of the retention time of ingesta to achieve an increase in their fibre digestion capability by means of a larger relative stomach capacity, a greater subdivision of chambers and smaller openings, are not supported by the findings of this study. Thus, there is no consistent evidence to support a significant adaptive effect of stomach morphology to different diets in the Artiodactyla.

Keywords Allometry · Body mass · Comparative method · Feeding styles · Gut morphology

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Introduction

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A recurrent problem which arises when studying the differences in the morphology or function of the digestive system, in relation to Hofmann's classification, is the possible confounding effect of body mass (Gordon and Illius 1994; Robbins et al. 1995; Iason and Van Wieren 1998). After controlling for body mass, Gordon and Illius (1994) found that there were no differences in wet

The Ruminant Stomach

EAST AFRICAN MONOGRAPHS IN BIOLOGY

VOLUME 2

Stomach Structure and Feeding Habits of East African Game Ruminants

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Dr. med. vet. (Giessen), Professor of Veterinary Anatomy, Histology and Embryology.

EAST AFRICAN LITERATURE BUREAU

Oecologia (2001) 129:498–508
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F. Javier Pérez-Barbería · Iain J. Gordon
Andrew W. Illius

Phylogenetic analysis of stomach adaptation in digestive strategies in African ruminants

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Abstract The stomach morphology of 28 species of artiodactyls that differ in feeding style (browser, mixed feeder, grazer) was analysed using a multivariate approach and phylogenetic correction in order to test whether stomach morphology was correlated with feeding style when body mass was controlled for. A total of [illegible] morphological traits of the stomach were used in the analysis. [illegible] the effects of body mass and phylogeny on stomach morph[illegible]y were taken into account, there was no significant group[illegible] of species according to feeding style. When information [illegible]ut the feeding style of each species was included in the a[illegible]lysis, the set of morphological traits separated the mix[illegible] feeders from the other two feeding styles, but grazer[illegible] and browsers had similar morphological features. Most of the variance in stomach morphology was explained by body mass and a lesser proportion by phylogeny. The main morphological features that have previously been proposed as being adaptations in grazing species, namely, lengthening of the retention time of ingesta to achieve an increase in their fibre digestion capability by means of a larger relative stomach capacity, a greater subdivision of chambers and smaller openings, are not supported by the findings of this study. Thus, there is no consistent evidence to support a significant adaptive effect of stomach morphology to different diets in the Artiodactyla.

Keywords Allometry · Body mass · Comparative method · Feeding styles · Gut morphology

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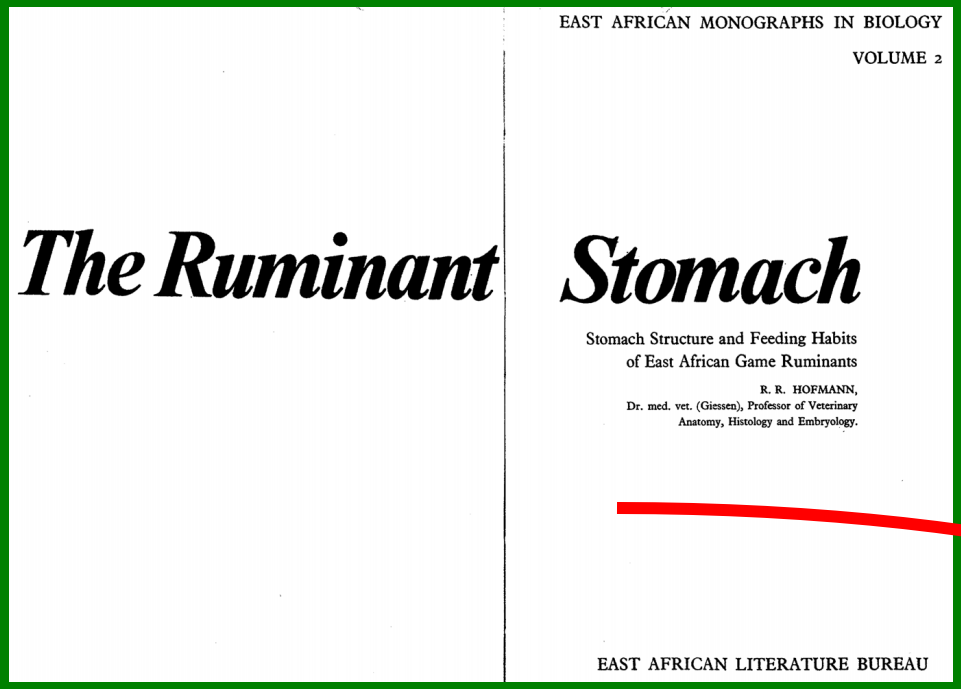

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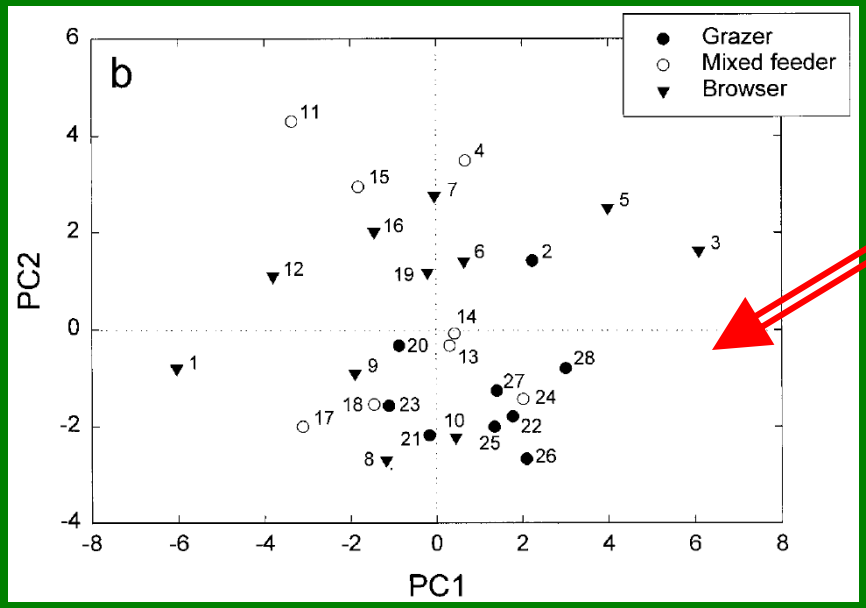

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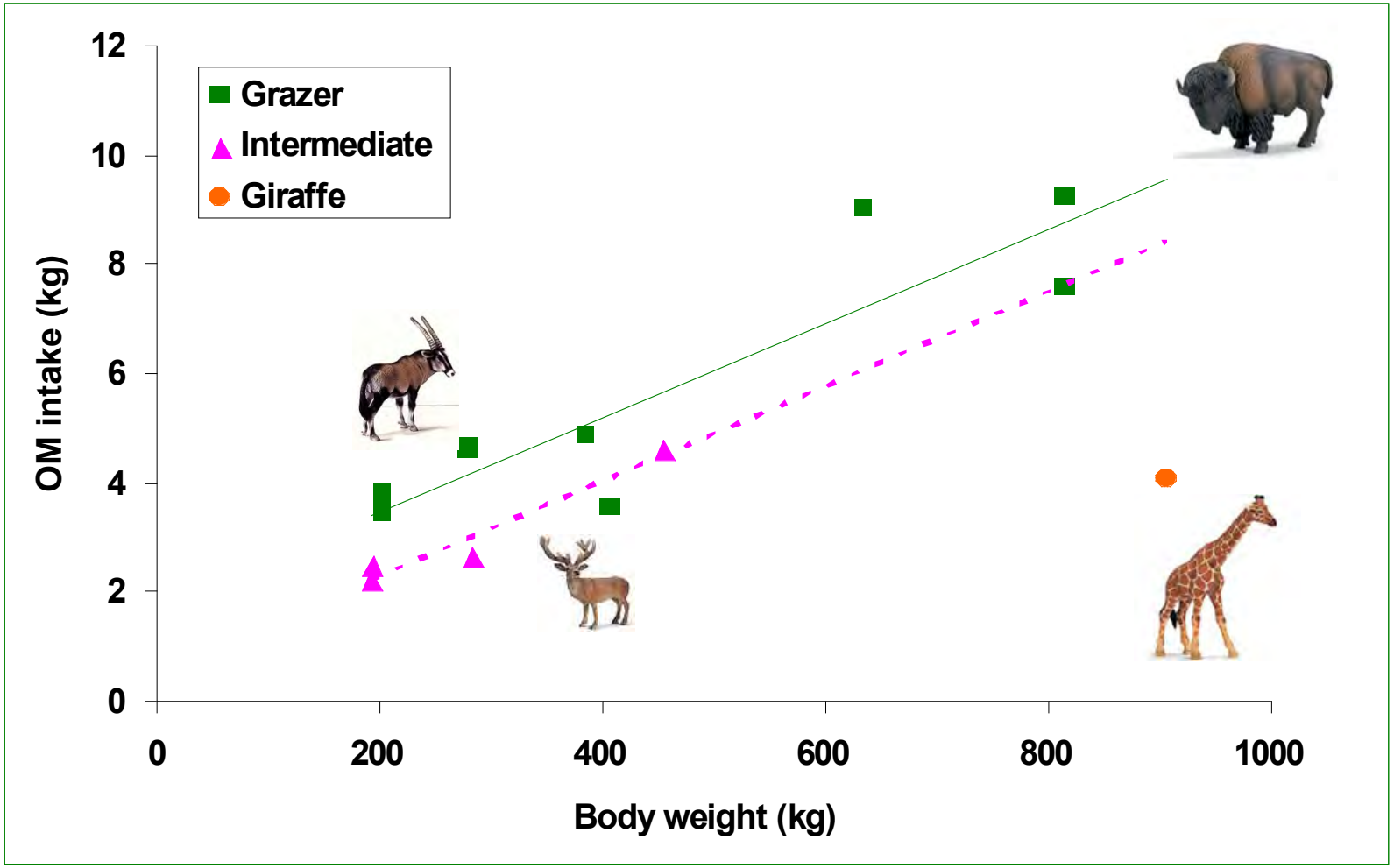

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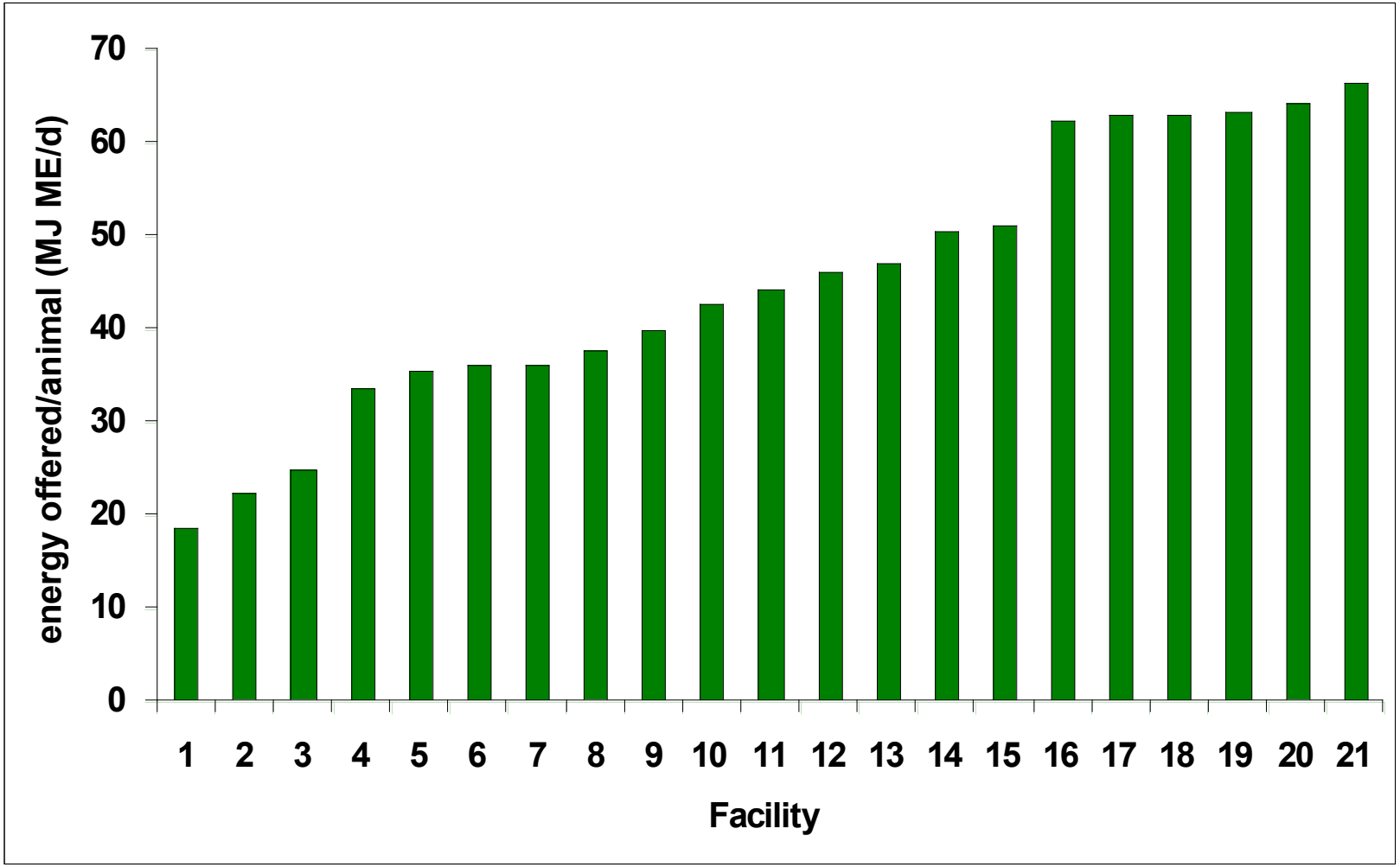
Moose study: energy offered as concentrates



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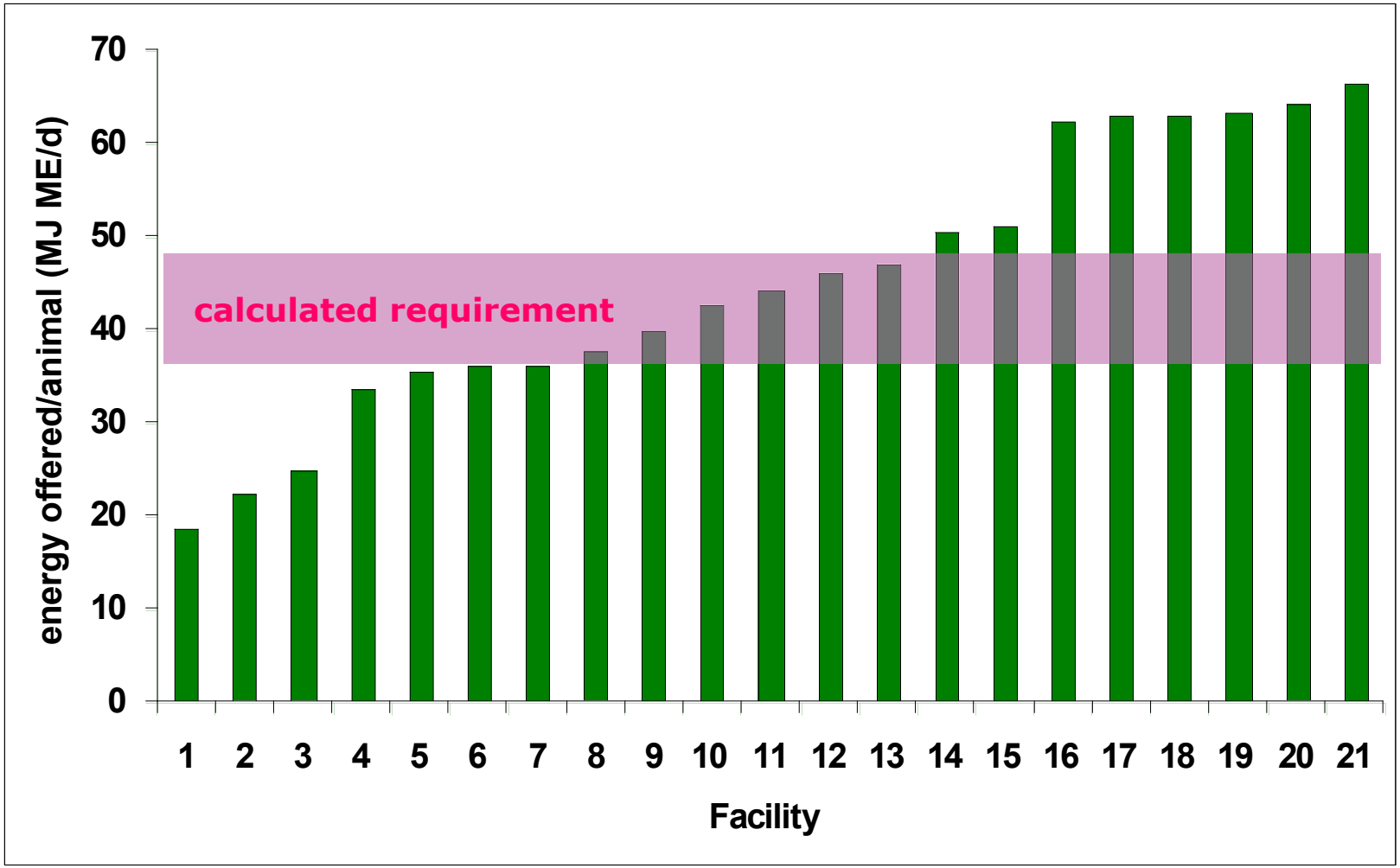

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Problems with hay acceptance

Giraffe Fox (1938), Gradwell (1976), Kloeppel (1976), Altmann (1978), Gorgas et al. (1978), Brancker (1980), Foose (1982), Franz et al. (1984), Gutzwiller (1984), Hofmann and Matern (1988), Matern and Kloeppel (1995)

Moose Baines (1965), Landowski (1969), Heptner and Nasimowitsch (1974), Bo and Hjeljord (1991), Schwartz (1992), Schwartz and Hundertmark (1993), Shochat et al. (1997)

Mule deer Cahart (1943), Doman and Rasmussen (1944), Nagy et al. (1969), Schoonveld et al. (1974)

Roe deer Dissen (1983)

Chinese water deer Hofmann et al. (1988)

Duiker Cowan (1982), Luginbuhl et al. (1991), Van Soest et al. (1995)

Reindeer Eriksson and Schmekel (1962), Kurkela (1976), Valtonen et al. (1983)

Eland Hofmann (1973, p. 40), Miller et al. (2010)

Kudu Miller et al. (2010)

Oecologia (1994) 98:167–175

ORIGINAL PAPER

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The differences in the proportions of structural carbohydrates in grasses and browse are seen as leading to differences in the structure and function of the digestive tract of grazing and browsing ruminants. Forages consist of cell contents which are wholly digestible (van Soest 1982), digestible cell wall and an indigestible residue (predominately lignin). For any given phenological stage, browse has higher levels of cell solubles and lignin but lower levels of holocellulose (cellulose and hemicellulose) than grasses (McDowell et al. 1983; Demment and van Soest 1985). Consequently, browse has higher levels of the rapidly fermenting soluble component than grasses. However, because of the higher lignin content in the cell wall of browse, the absolute digestibility of browse tends to be lower (White and Trudell 1980). Therefore, browsers are expected to have a digestive system adapted for the rapid excretion of the highly lignified, less digestible cell wall fraction, whereas grazers have adaptations to slow down the passage of plant material in the rumen, thereby increasing the extent of digestion of the less lignified cell wall component. Hofmann (1973) demonstrated anatomical adaptations of the ali-

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species (8 browsing, 7 intermediate and 11 grazing species of ruminant). In all 99.6% of the variance was explained by a model including the body mass of the species and the food type. Mean retention time was allometrically related to body mass (Fig. 4; exponent 0.22; $F_{1,23} = 88.1$, $P<0.001$). The food type also significantly added to the regression model: animals which were fed alfalfa hay had shorter retention times than did those fed grass hay (intercepts: alfalfa = 15.1 h, grass = 17.6 h; $t = 2.98$, $P<0.01$). After controlling for body mass and food type no other parameter was significant (i.e. feeding type: $F_{2,23} = 2.88$, NS). Thus from the limited data set available there was no difference in the mean retention times in the gut between browsing, grazing and intermediate feeders of ruminants after accounting for variation due to body mass and food type.

Discussion

Comparison with other studies

Much has been written on the relationship between digestive function and feeding habits in ruminants but only two other studies (Demment and Longhurst 1987; Maloiy and Clemens 1991) have adopted the allometric approach to compare the scaling factors involved in ruminants with different feeding habits. From studies using less controlled analyses (Prins and Geelen 1971; Hofmann 1973, 1989; Kay et al. 1980), it was concluded that browsers have a lower rumen capacity than grazers. However, the results of the present study indicate that, whilst there is a significant difference in the relationship for the wet rumen contents of browsers and grazers using the Hofmann classification there is no significant difference using the dietary classification. For the dry rumen contents there was no significant difference in the allometric relationship with body mass for species which consume different diets. The previous studies measured either rumen volume or only wet rumen contents, combined the data from animals shot in different seasons (and therefore varying in diet and intake) and did not employ an estimate of body mass net of gut contents. These potential sources of bias are minimized in the present data set, which thus provides a more reliable guide to trends in rumen wet and dry matter load. Comparative studies have found differences in the relative sizes of the organs of alimentary tract of browsers and grazers. Hofmann (1989) found that the small intestine and hindgut were larger in browsing ruminants than in grazers. However, using allometric analyses we found no difference in the wet or dry masses of material in the hindgut of browsers as compared to grazers.

As found in other studies (Hungate et al. 1959; Hoppe 1977a; Maloiy et al. 1982), the fermentation rate within the rumen scales negatively with body mass. It has previously been assumed that this is due to larger species consuming a poorer quality diet. Gordon and Illius (submitted) have shown that this may not a valid conclusion.

It has been assumed that, within a given body mass range, browsers would have a higher fermentation rate in the rumen than grazers because they consume a diet which is higher in rapidly fermented cell solubles (see above and Hofmann 1989 for a review), although this assumption has not previously been examined quantitatively. The assumption is not supported by the data set used in this study which shows no significant difference between browsers and grazers in the relationship between rumen fermentation rate and body mass. Similarly, despite the absence of a quantitative test, it has been assumed that the molar proportions of propionate and thus the energy concentration of the VFAs produced within the rumen would be higher relative to body mass in small species and in browsers than in grazers, due to the higher cell solubles content of their diet (Hoppe 1977a). Again, the data set shows that there is no significant effect of body mass on total energy concentration of VFAs produced and there is also no effect of feeding habits. Other studies support this: Clemens et al. (1983) found that acetate:propionate ratio in the rumen did not differ between browsing, intermediate or grazing East African ruminants (n = 4, 5, 7 respectively) and concluded that body mass has more influence than feeding habits on rumen fermentation rate and the ratio of VFAs present. Maloiy and Clemens (1991) found no difference in caecal VFA composition due to feeding habits. Murphy et al. (1982) showed that the stoichiometry of VFA yield from forage rations gave a limited range in VFA proportions as compared to the starch-based diets upon which previous assumptions may have been based. Thus forages cannot apparently provide high propionate yields typical of a starch-based concentrate diet (cf. Hofmann 1989).

The data presented above suggest that small species and particularly those consuming browse-dominated diets are less able to meet their energy requirements from rumen fermentation alone than are larger species, especially grazers. Other studies also find that the fermentation in the rumen does not supply all the energetic requirements of the animal. For example, Allo et al. (1973) found that the percentage contribution of VFAs from the rumen to meet maintenance energy costs is 60–90% in sheep (*Ovis aries*) and 20–45% in black-tailed deer (*Odocoileus hemionus*). Stewart et al. (1958) present a figure of 37% in goats (*Capra hircus*) and van Hoven and Boomker (1981) give 67% for the black wildebeest (*Connochates gnou*). In a broad comparative study, Prins et al. (1984) found that few species of ruminants were able to meet twice their maintenance energy requirements (assumed to be the requirements for a free-living animal) from VFA production in the rumen. This was particularly the case for small browsers.

It is widely held that food particles flow through the rumens of browsers faster than through the rumens of grazers (e.g. Hofmann 1973, 1989; Demment and Longhurst 1987; Kay 1987). This assumption is primarily based on differences in the comparative anatomical structure of the rumen and omasum of grazing and brow-

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It has been assumed that, within a given body mass range, browsers would have a higher fermentation rate in the rumen than grazers because they consume a diet which is higher in rapidly fermented cell solubles (see above and Hofmann 1989 for a review), although this assumption has not previously been examined quantitatively. The assumption is not supported by the data set used in this study which shows no significant difference between browsers and grazers in the relationship between rumen fermentation rate and body mass. Similarly, despite the absence of a quantitative test, it has been assumed that the molar proportions of propionate and thus the energy concentration of the VFAs produced within the rumen would be higher relative to body mass in small species and in browsers than in grazers, due to the higher cell solubles content of their diet (Hoppe 1977a). Again, the data set shows that there is no significant effect of body mass on total energy concentration of VFAs produced and there is also no effect of feeding habits. Other studies support this: Clemens et al. (1983) found that acetate:propionate ratio in the rumen did not differ between browsing, intermediate or grazing East African ruminants (n = 4, 5, 7 respectively) and concluded that body mass has more influence than feeding habits on rumen fermentation rate and the ratio of VFAs present. Maloiy and Clemens (1991) found no difference in caecal VFA composition due to feeding habits. Murphy et al. (1982) showed that the stoichiometry of VFA yield from forage rations gave a limited range in VFA proportions as compared to the starch-based diets upon which previous assumptions may have been based. Thus forages cannot apparently provide high propionate yields typical of a starch-based concentrate diet (cf. Hofmann 1989).

The data presented above suggest that small species and particularly those consuming browse-dominated diets are less able to meet their energy requirements from rumen fermentation alone than are larger species, especially grazers. Other studies also find that the fermentation in the rumen does not supply all the energetic requirements of the animal. For example, Allo et al. (1973) found that the percentage contribution of VFAs from the rumen to meet maintenance energy costs is 60–90% in sheep (*Ovis aries*) and 20–45% in black-tailed deer (*Odocoileus hemionus*). Stewart et al. (1958) present a figure of 37% in goats (*Capra hircus*) and van Hoven and Boomker (1981) give 67% for the black wildebeest (*Connochates gnou*). In a broad comparative study, Prins et al. (1984) found that few species of ruminants were able to meet twice their maintenance energy requirements (assumed to be the requirements for a free-living animal) from VFA production in the rumen. This was particularly the case for small browsers.

It is widely held that food particles flow through the rumens of browsers faster than through the rumens of grazers (e.g. Hofmann 1973, 1989; Demment and Longhurst 1987; Kay 1987). This assumption is primarily based on differences in the comparative anatomical structure of the rumen and omasum of grazing and brow-

species (8 browsing, 7 intermediate and 11 grazing species of ruminant). In all 99.6% of the variance was ex-

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	Body mass	Dry mass of rumen contents (D_R; kg DM)	Fermentation rate in the rumen (F_R; moles VFA kg DM^{-1} d^{-1})	Energy content of VFAs (E_R; kJ mol^{-1})	Energy production from the rumen (P_R; kJ d^{-1})	Reference [a]
Browsers						
Nesotragus moschatus	3.7	0.05	8.61	1096.4	406.0	7
Rhynochotragus kirki	4.8	0.05	8.70	1169.4	437.5	7
Raphicerus campestris	10.5	0.12	8.57	1228.0	1086.2	4
Sylvicapra grimmia	13.0	0.20	8.18	1094.0	1540.0	4
Tragelaphus scriptus	27.0	0.28	6.97	1147.6	2624.3	4
Litocranius walleri	33.6	0.56	5.08	1072.7	2624.3	5
Antidorcas marsupialis	37.1	0.60	4.02	1219.3	2434.6	1
Aeypyceros melampus	43.5	1.00	3.41	1077.5	4654.8	1
Gazella granti	49.0	0.66	7.26	1081.2	4455.4	3
Tragelaphus strepsiceros	145.0	2.70	3.32	1117.4	8609.0	1
Giraffa camelopardalis	702.5	12.84	3.21	1078.2	38218.6	5
Grazers						
Gazella thomsoni	18.0	0.32	7.96	1070.7	2436.4	3
Aeypyceros melampus	51.0	0.59	7.12	1141.4	6072.7	3
Damaliscus korrigum	114.0	1.94	5.15	1221.4	10496.1	2
Alcelaphus buselaphus	120.0	2.08	4.93	1105.8	9750.9	2
Connochaetes gnou	127.2	2.59	3.15	1220.3	8427.3	6
Oryx beisa	174.3	5.26	4.53	1127.0	23117.0	5
Connochaetes taurinus	217.5	5.26	3.70	1133.1	18787.8	1, 2
Kobus defassa	229.3	4.44	3.63	1066.6	14767.8	5
Syncerus caffer	807.0	22.85	3.32	1134.5	73971.2	1
Intermediate feeder						
Taurotragus oryx	458.8	10.24	3.66	1106.6	35667.3	5

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	Body mass (kg)	Dry mass of hindgut contents (D_C; kg DM)	Fermentation rate in the hindgut (F_C; mol VFA kg DM^{-1} d^{-1})	Energy content of VFAs (E_C; kJ mol^{-1})	Energy production from the hindgut (P_C; kJ d^{-1})
Browsers					
Rhynochotragus kirki	5.5	0.04	1.47	1374.4	76.4
Nesotragus moschatus	6.0	0.03	1.55	1276.6	51.0
Raphicerus campestris	9.5	0.04	1.68	1170.7	60.9
Litocranius walleri	46.0	0.13	2.06	1052.3	242.4
Gazella granti	55.0	0.06	1.60	1227.1	108.1
Giraffa camelopardalis	625.0	2.07	1.18	1206.3	2530.3
Grazers					
Gazella thomsoni	23.5	0.03	1.51	1178.9	42.9
Redunca fulvorufula	25.5	0.04	1.51	1114.8	70.7
Aeypyceros melampus	62.0	0.09	1.63	1146.9	146.3
Damaliscus korrigum	129.0	0.23	1.51	1125.6	333.3
Alcelaphus busalaphus	138.0	0.26	1.16	1158.4	302.8
Oryx beisa	188.5	0.74	1.53	1124.7	1102.5
Connochaetes taurinus	206.5	0.70	1.36	1139.7	922.4
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Gazella granti	49.0	0.66	7.26	1081.2	4455.4	3
Tragelaphus strepsiceros	145.0	2.70	3.32	1117.4	8609.0	1
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Connochaetes gnou	127.2	2.59	3.15	1220.3	8427.3	6
Oryx beisa	174.3	5.26	4.53	1127.0	23117.0	5
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DIGESTIVE PHYSIOLOGY OF EAST AFRICAN WILD RUMINANTS

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(*Received* 18 *January* 1983)

Abstract—1. The physiology of digestion of wild ruminants in their natural habitat was determined. The study consisted of fifty-one adult male animals representing sixteen species.

2. While diet and body weight were both related to the gastrointestinal composition, body weight appeared to be the more influential factor.

3. Reticulo-rumen and caecal-colon composition, relative to abomasal and small intestinal composition, showed the greater species, diet and body weight effects.

4. The buffalo, oryx and gerenuk were somewhat more unique in gastrointestinal composition than were other species of wild ruminants, and were deserving of special consideration.

INTRODUCTION

With the continued studies of both domestic and wild ruminants, knowledge of reticulo-rumen physiology is rapidly expanding. Comparative information and, to a lesser extent, post-ruminal digestion studies have not been as fruitful. Furthermore, quantitative information derived from studies of different species is difficult to compare, owing to the variation in technique. The present investigation allowed for an intensive, comparative study without the variance due to technique. In addition, these animals were studied in their natural habitat, thus providing a more realistic comparison of wild ruminants.

MATERIALS AND METHODS

Fifty-one adult, male animals representing 16 species of East African wild ruminants were used in the study. These included: five Kirk's dik-dik (*Madoqua kirki*), two suni (*Nesotragus moschatus*), three giraffe (*Giraffa camelopardalis*), three gerenuk (*Litocranius walleri*), three eland (*Taurotragus oryx*), four Grant's gazelle (*Gazelle grati*), two steenbok (*Raphicerus campestris*), four impala (*Aepyceros melampus*), four Thomson's gazelle (*Gazella thomsoni*), three buffalo (*Bubalus caffer*), two waterbuck (*Kobus ellipsiprymnus*), three wildebeest (*Connochaetes taurinus*), three hartebeest (*Alcephalus buselaphus*), three topi (*Damaliscus lunatus*), three mountain reedbuck (*Redunca fulvorufula*), and four oryx (*Oryx gazella*). All animals were collected from their natural habitat in conjunction with wildlife management programs. Field analysis and sample collection were begun immediately after sacrifice and generally completed within 1 hour after the death of the animal. Body weights of the animals were taken as those reported for the average species weight (Hofmann, 1973).

The abdominal cavity of each animal was opened immediately after death. Urine and blood samples were collected and refrigerated. Ligatures were used to tie off the oesophagus at the cardia and the large bowel at the rectal–anal junction, and the gastrointestinal tract removed. The gastrointestinal tract of each animal was further separated by ligatures into six selected segments. These consisted of the reticulo-rumen, abomasum, small intestine, caecum, and proximal and distal halves of the colon. Total contents were removed from each segment, weighed, and a representative sample refrigerated for later analysis. Additional samples were strained through cheese cloth, the supernatant acidified with concentrated H_2SO_4 (approx 0.5 ml per 20 ml sample), and refrigerated for later analyses of volatile fatty acids.

The dry matter content was determined by drying a portion of each sample to a constant weight in a forced-air oven at 105°C. Samples of whole gut contents were centrifuged and the supernatant collected for laboratory analysis. The osmolality of the supernatant fraction was determined on a laboratory osmometer, the sodium and potassium concentrations by flame photometry, and the chloride concentration was determined with the aid of a chloridometer. The lactic acid concentration of each sample was determined by the methods of Barker and Summerson (1941). Volatile fatty acid concentrations were determined by the steam distillation method of Markham (1942), and by partition chromatography of short chain fatty acids.

Data were subject to analysis of variance, Duncan's Multiple Range test, and regression analysis for determination of significant differences (Steel and Torrie, 1960).

RESULTS

The series of Tables 2–8 present the analytical data for seven parameters measured in this study. Tables are further divided according to species, major and sub-feeding groups, and weight of the animal. Table 1 presents the live weight, food selection and mean weight of gastrointestinal contents, by species and for the six primary gut segments.

The percent dry matter within the reticulo-rumen showed considerable variability for the species investigated, ranging from a low of 10.5% (suni) to 21.8% (oryx) (Table 2A). However, when comparing sub-feeding groups, dry region grazers' reticulo-rumen dry matter was significantly greater ($P < 0.05$) than other groups (Table 2B). The intermediated feeders also appeared to have a higher dry matter value than most browsers or grazers. Abomasal

habits assessed from diet composition in the rumen (data from Clemens et al. 1983; Clemens and Maloiy 1983; Maloiy and Clemens 1991; Clemens pers. comm.).

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The abdominal cavity of each animal was opened immediately after death. Urine and blood samples were collected and refrigerated. Ligatures were used to tie off the oesophagus at the cardia and the large bowel at the rectal–anal junction, and the gastrointestinal tract removed. The gastrointestinal tract of each animal was further separated by ligatures into six selected segments. These consisted of the reticulo-rumen, abomasum, small intestine, caecum, and proximal and distal halves of the colon. Total contents were removed from each segment, weighed, and a representative sample refrigerated for later analysis. Additional samples were strained through cheese cloth, the supernatant acidified with concentrated H_2SO_4 (approx 0.5 ml per 20 ml sample), and refrigerated for later analyses of volatile fatty acids.

The dry matter content was determined by drying a portion of each sample to a constant weight in a forced-air oven at 105°C. Samples of whole gut contents were centrifuged and the supernatant collected for laboratory analysis. The osmolality of the supernatant fraction was determined on a laboratory osmometer, the sodium and potassium concentrations by flame photometry, and the chloride concentration was determined with the aid of a chlorindometer. The lactic acid concentration of each sample was determined by the methods of Barker and Summerson (1941). Volatile fatty acid concentrations were determined by the steam distillation method of Markham (1942), and by partition chromatography of short chain fatty acids.

Data were subject to analysis of variance, Duncan's Multiple Range test, and regression analysis for determination of significant differences (Steel and Torrie, 1960).

RESULTS

The series of Tables 2–8 present the analytical data for seven parameters measured in this study. Tables are further divided according to species, major and sub-feeding groups, and weight of the animal. Table 1 presents the live weight, food selection and mean weight of gastrointestinal contents, by species and for the six primary gut segments.

The percent dry matter within the reticulo-rumen showed considerable variability for the species investigated, ranging from a low of 10.5% (suni) to 21.8% (oryx) (Table 2A). However, when comparing sub-feeding groups, dry region grazers' reticulo-rumen dry matter was significantly greater ($P < 0.05$) than other groups (Table 2B). The intermediated feeders also appeared to have a higher dry matter value than most browsers or grazers. Abomasal

Table 3B. Mean (±SEM) volatile fatty acid concentration (mmol/l) as observed at various sites along the gastrointestinal tract of the major and sub-feeding groups

Food selection	Section of tract: Reticulo-rumen	Abomasum	Small intestine	Caecum	Proximal colon	Distal colon
MAJOR GROUPS*						
Browsers	149.7[a]	13.1	14.0	65.1	65.8[a]	52.7
	(7.4)	(2.1)	(3.5)	(5.9)	(5.9)	(7.8)
Intermediate	131.2[ab]	18.7	12.8	66.9	59.2[a]	51.8
	(8.0)	(3.0)	(1.4)	(4.6)	(4.7)	(5.2)
Grazers	115.0[b]	15.2	16.4	52.5	44.3[b]	44.7
	(10.9)	(2.5)	(4.0)	(5.4)	(5.0)	(5.3)
SUB GROUPS						
Fruit and dicotyledon	148.6	13.4	11.7	66.1	68.3	51.6
(Browsers)	(6.4)	(2.5)	(3.4)	(5.9)	(7.4)	(10.2)
Trees and shrub	122.3	12.5	19.4	62.6	59.9	55.2
(Browsers)	(17.1)	(4.5)	(9.2)	(16.5)	(10.5)	(13.7)
Prefers browse	130.6	21.4	13.4	72.4	62.4	57.5
(Intermediate)	(10.1)	(3.9)	(1.9)	(5.3)	(6.6)	(5.7)
Prefers graze	131.8	16.0	12.1	61.4	56.0	46.1
(Intermediate)	(13.0)	(4.7)	(2.1)	(7.2)	(6.8)	(8.5)
Fresh grass	89.3	12.3	11.8	42.1	37.8	36.7
(Grazers)	(15.3)	(2.2)	(4.1)	(3.3)	(6.5)	(9.4)
Roughage	101.8	10.3	5.8	41.2	33.7	46.9
(Grazers)	(4.6)	(1.6)	(1.8)	(3.7)	(4.6)	(8.0)
Dry region	183.5	29.0	42.8	90.6	74.0	54.9
(Grazers)	(9.1)	(1.2)	(6.3)	(5.0)	(5.3)	(11.1)

*Values within a column with unlike superscripts are statistically different at the 0.05 level of significance.

lationship between the weight of the animal and reticulo-rumen VFA concentrations (Table 3C). However, this relationship is less clear when comparing the individual mean values for weight groups. Abomasal and small intestinal VFA concentrations were considerably lower than that of the reticulo-rumen contents. VFA concentrations within the animal's caecum were 1/3–1/2 that observed within the forestomach (33.2–90.6 mmol/l). While no significant difference was noted, browsers and intermediate feeders generally had higher caecal VFA values than grazers. VFA concentrations tended to decrease from caecum to distal colon for most species, and feeding groups. VFA concentration and feeding group were significantly ($P < 0.005$) related within the proximal colon. Concentrations were noted to increase with the ingestion of more browse.

Reticulo-rumen lactic acid concentrations were less than 5% of that for VFA's. Lactic acid concentrations remained low throughout the entire gastrointestinal tract of all species (Table 4A). Caecal and colonic lactic acid concentrations were significantly higher ($P < 0.05$) in browsers and intermediate feeders than in grazers (Table 4B). There was also a significant negative relationship between lactic acid concentrations and an increase in body weight for the caecum and colonic segments of the tract (Table 4C).

Reticulo-rumen osmolality ranged from 232 mOsm

Table 3C. Mean (±SEM) volatile fatty acid concentration (mmol/l) as observed at various sites along the gastrointestinal tract of the seven weight groups of wild ruminants

Weight group	Section of tract: Reticulo-rumen	Abomasum	Small intestine	Caecum	Proximal colon	Distal colon
Less than 20 kg	143.8*	16.6	10.7	69.9	66.7	55.6
	(6.4)	(2.9)	(2.7)	(0.3)	(7.4)	(8.6)
20–50 kg	118.3	10.7	13.3	54.6	43.7	48.5
	(8.8)	(1.9)	(3.8)	(4.0)	(5.1)	(9.9)
51–100 kg	147.2	19.5	14.4	67.7	58.8	53.0
	(11.3)	(5.6)	(1.9)	(7.5)	(6.7)	(6.4)
101–150 kg	101.6	8.3	3.2	33.2	30.8	42.0
	(6.9)	(1.9)	(0.1)	(3.9)	(4.4)	(4.3)
151–200 kg	163.8	26.7	34.8	80.4	69.5	53.0
	(20.9)	(5.8)	(9.3)	(10.9)	(6.0)	(8.8)
201–300 kg	111.5	14.6	11.3	44.1	45.6	26.8
	(6.7)	(2.2)	(4.7)	(1.8)	(5.9)	(2.9)
More than 300 kg	79.4	13.8	13.6	56.1	52.4	37.5
	(15.0)	(2.3)	(3.4)	(9.8)	(12.0)	(9.4)

*Regression analysis ($P < 0.01$); $Y = 151.26.8X$.

habits assessed from diet composition in the rumen (data from Clemens et al. 1983; Clemens and Maloiy 1983; Maloiy and Clemens 1991; Clemens pers. comm.).

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"No difference in ingesta retention time between the feeding types.

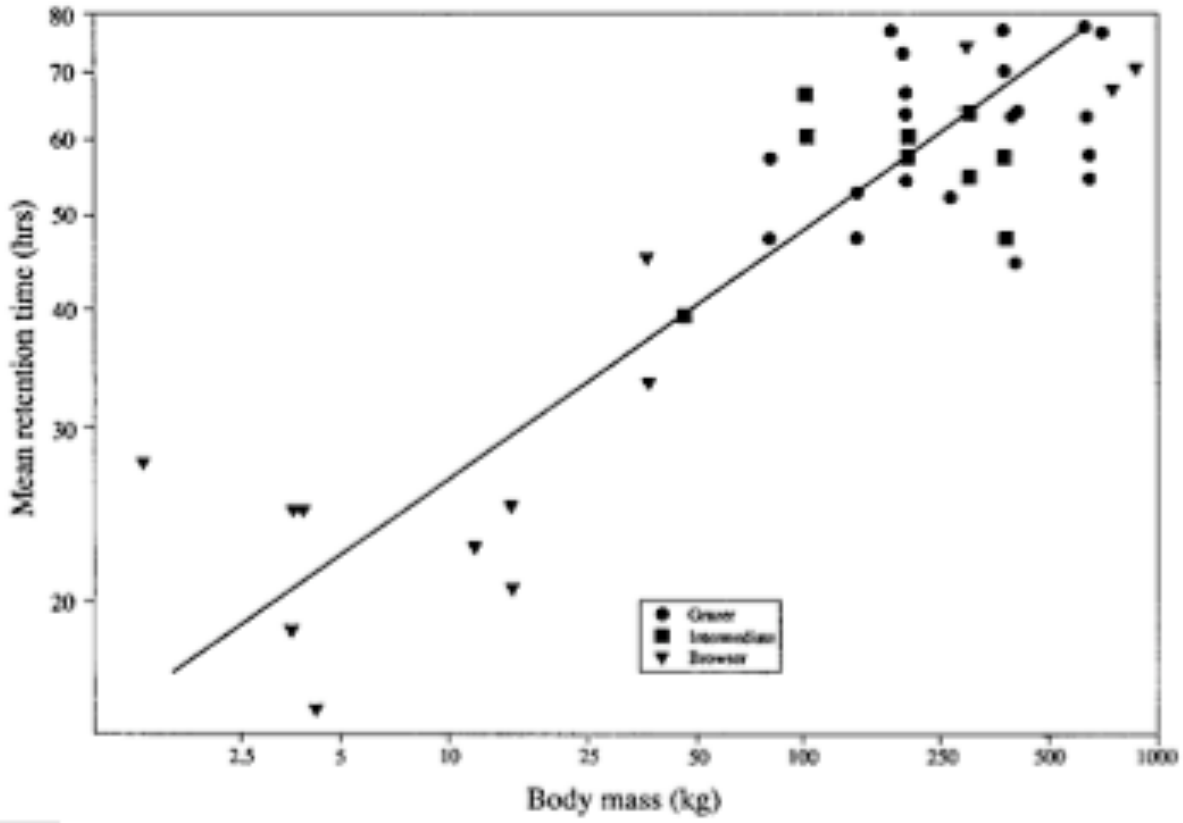
All differences in ingesta retention can be explained by body weight."

according to Gordon and Illius (1992, 1994)

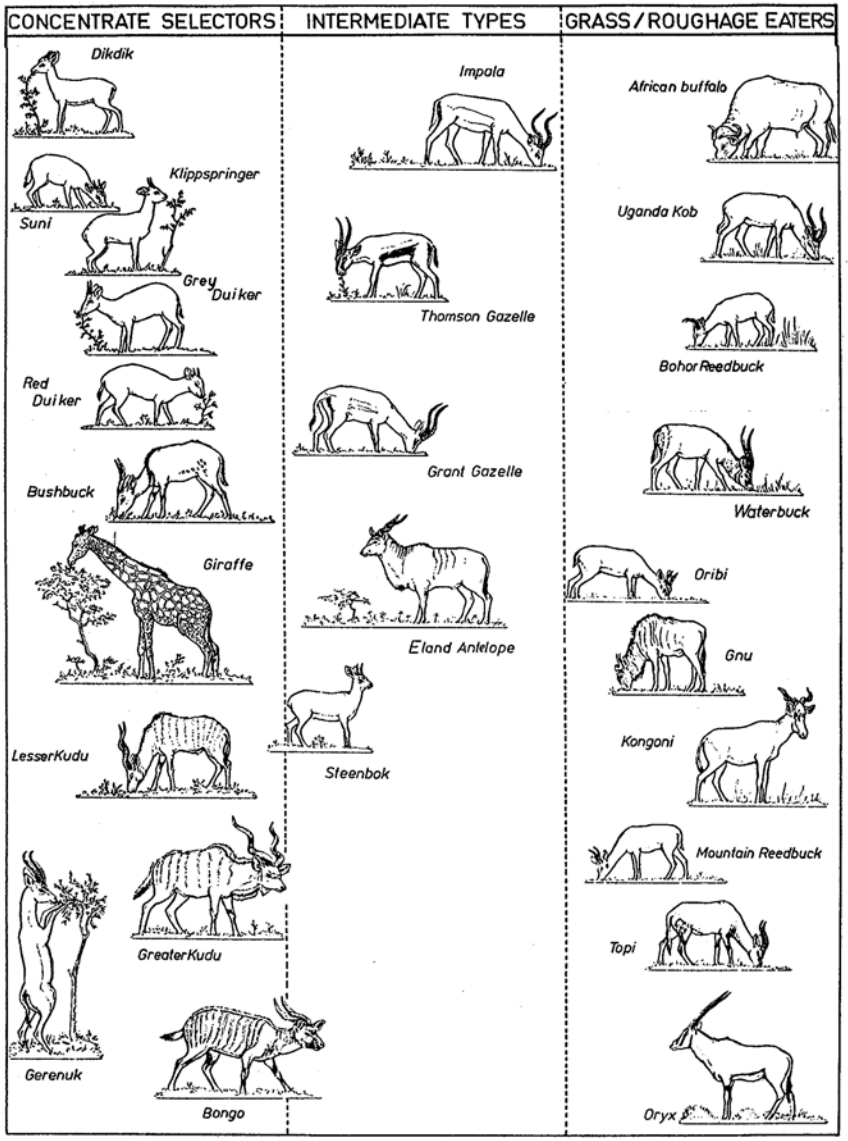
Mean retention time (particles) = 15.3 * $BM^{0.251}$

„for all feeding types“

From Illius & Gordon (1992); no particle size given; data e.g. from Foose (1982)



Ruminant feeding types (Hofmann)



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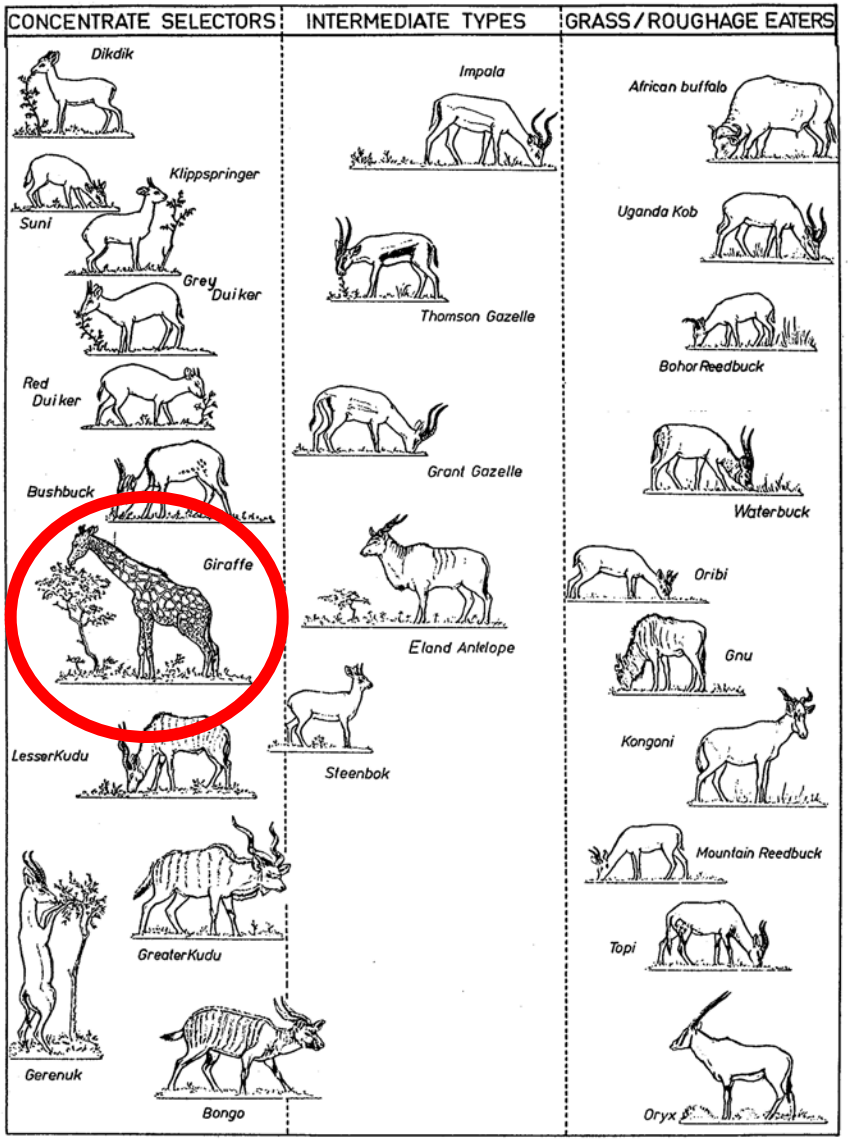

from Hofmann (1989)

Illius & Gordon 's (1992) equation reliably predicts retention time in grazers

Species	BM (kg)	MRT (h)	
		calculated	measured
Mouflon	33	37.3	36.0
Mountain sheep	90	47.3	51.0
Cattle	450	71.0	74.0

data from Udén et al. (1982), Baker & Hobbs (1987), Behrend et al. (2004)

Illius & Gordon ‘s (1992) equation overestimates retention time in browsers

Species	BW (kg)	MRT (h)	
		calculated	measured
Roe deer	20	32.5	23.6
Okapi	210	58.6	42.1
Giraffe	1000	90.7	48.2

data from Clauss et al. (1998), Clauss and Lechner-Doll (2001), Behrend et al. (2004); particle size < 2 mm

Oecologia (1995) 103:208–213

ORIGINAL PAPER

2007

Charles T. Robbins · Donald E. Spalinger
Wouter van Hoven

Adaptation of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid?

Received: 15 November 1994 / Accepted: 18 February 1995

Abstract As a result of pioneering work of Hofmann (1973, 1989), nutritional ecologists classify ruminants into three feeding-type categories: browsers ("concentrate" feeders), grazers, and intermediate or mixed feeders. Hofmann proposed that these feeding types result from evolutionary adaptations in the anatomy of the digestive system and that one consequence is shorter retention of the digesta in the rumen of browsers, and thus a decreased efficiency of fiber digestion relative to that of grazers. We examined the hypotheses that (1) fiber digestion of browsers is lower than that of grazers, (2) salivary gland size is larger in all browsers than in grazers, (3) the browser's larger salivary glands produce larger volumes of thin serous saliva than those of grazers, and (4) thus, browsers have higher liquid passage rates than do grazers. We found that the extent of fiber digestion is not significantly different between browsers and grazers, although fiber digestion is positively related to herbivore size. In general, salivary gland size is approximately 4 times larger in browsers than grazers, but some browsers (e.g., greater kudu) have small, grazer-sized salivary glands. Resting (non-feeding or ruminating) saliva flow rates of mule deer (browser) and domestic sheep and cattle (grazers) were not significantly different from each other. Finally, ruminal liquid flow rates were not different between feeding types. We conclude that many of Hofmann's nutritional and physiological interpretations of anatomical differences amongst ruminants are not supportable.

Key words Ruminants · Browsers · Digestion · Foraging · Saliva

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Introduction

Ruminants occupy a diverse array of feeding niches throughout the world. Although they feed on plants of widely divergent physical and chemical compositions (e.g., lichens, grasses, and woody stems), ecologists classify ruminants into one of three general feeding categories, comprising grazers, browser/concentrate feeders, and intermediate feeders. These categories reflect the predilection of the animals for consuming grasses, browses/herbs/fruits, or a mixture of both, respectively (Hofmann 1973, 1989).

In a classic work, Hofmann (1973) examined the foraging preferences of these groups in relation to their digestive anatomy, and concluded that general digestive system adaptations correspond to the ecological role of the animal. He hypothesized that grazing ruminants are better adapted for consuming slowly digested plant fiber (typical of grasses and sedges) than are browsing ruminants because grazers have larger rumens, and the structure of the rumen and omasum retards the passage of food to the lower tract. Conversely, browsers have smaller and less complex rumens and omasums, and they have larger parotid salivary glands that produce a copious, serous saliva to help buffer the rapidly digestible ("concentrate") diet and aid in the passage of foods from the rumen. These differences have led Hofmann (1989, p. 453) to suggest that "all [browsers and intermediate] species cannot digest fibre as well as grazers".

Hofmann's nutritional and ecological interpretations have been a powerful abstraction of ruminant function, influencing the way that nutritionists and ecologists view ruminant evolution and behavior, and the organization and composition of herbivore communities (McNaughton and Georgiadis 1986; Owen-Smith 1991). However, until recently, Hofmann's hypotheses have not been rigorously tested. In the first major attempt to test Hofmann's ideas, Gordon and Illius (1994) concluded that there is no significant difference in digestive kinetics (fermentation rate, daily VFA (volatile fatty acid) (VFA) production, and mean total tract retention time of food)

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Charles T. Robbins · Donald E. Spalinger
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Adaptation of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid?

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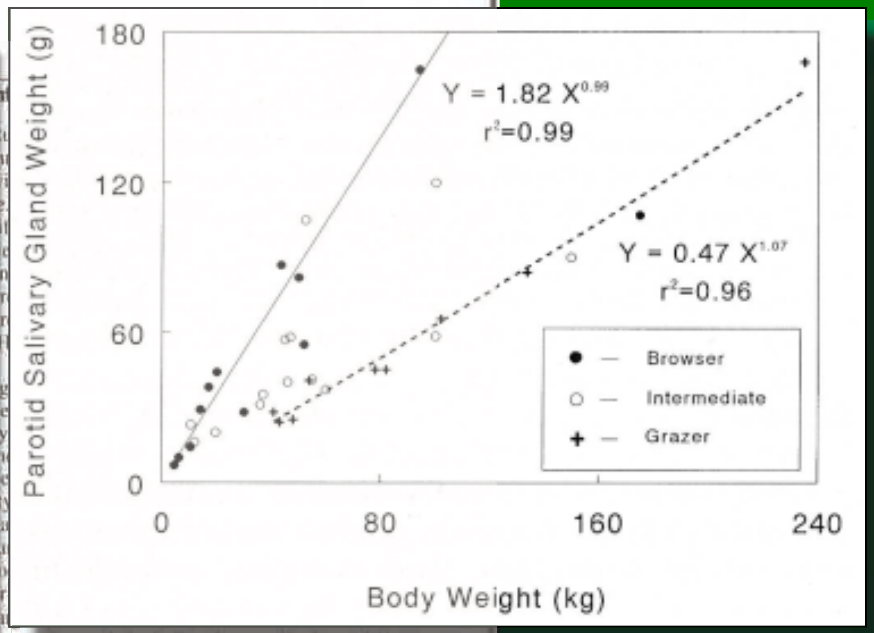
1989, p.449). We tested that statement by dissecting the salivary glands (parotid, mandibular and buccal) of five browsers [greater kudu (*Tragelaphus strepsiceros*), bushbuck (*T. scriptus*), nyala (*T. angasii*), giraffe, and common duiker (*Sylvicapra grimmia*)], five grazers [common reedbuck (*Redunca arundinum*), red hartebeest (*Alcelaphus buselaphus*), blesbok (*Damaliscus dorcas*), black wildebeest (*Connochaetes gnou*), gemsbok (*Oryx gazella*)], and two intermediate feeders [springbok (*Antidorcas marsupialis*) and impala (*Aepyceros melampus*)] killed during culling operations in South African game parks. Additionally, salivary gland and body weights were obtained for mule deer, black-tailed deer, white-tailed deer and moose (*Alces alces*) (browsers), domestic goats, fallow deer (*Cervus dama*), axis deer (*C. axis*), and mountain goats (*Oreamnos americanus*) (intermediate feeders), and domestic sheep and cattle (grazers) in the United States. The parotid lymph node was removed from all parotid



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Stephen S. Ditchkoff

A decade since "diversification of ruminants": has our knowledge improved?

Received: 11 October 1999 / Accepted: 6 April 2000

Abstract In his landmark 1989 paper, R.R. Hofmann classified ruminants into three categories based upon digestive anatomy and preferred forages, and proposed that divergence of feeding strategies among ruminants is a result of morphological evolution of the digestive tract. Because of the hypothetical nature of these views and the ingrained beliefs that they challenged, several papers were published that reported tests of Hofmann's predictions. The consensus among these papers was that Hofmann's predictions were inadequate. I describe the experimental evidence that has been put forth in opposition to the ruminant diversification hypothesis and contend that we have failed to adequately test Hofmann's predictions.

Key words Concentrate selectors · Intermediate feeders · Roughage eaters · Rumen bypass · Ruminant diversification

Early attempts to explain variation found in feeding strategies of free-ranging ruminants classified individual species as "browsers" or "grazers" based upon types of forage consumed. Though an important step in understanding the complexities of ruminant nutrition, Hofmann and Stewart (1972) recognized that feeding strategies of ruminants could not simply be classified into two categories, and proposed three categories (i.e., bulk and roughage eaters, selectors of concentrate forages, and intermediate feeders) based upon stomach structure and feeding ecology. Hofmann (1984) later documented variation in all portions of the digestive anatomy among the three categories of his system of ruminant classification. The dynamic interactions among body size, fermentation and passage rates, and energetic requirements, and their influence on dietary strategy formed the basis for these early classifications.

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In a landmark paper, Hofmann (1989) expanded upon the concepts proposed by Hofmann and Stewart (1972) and Hofmann (1984) by providing a working hypothesis of the functional and morphological basis for diversity in ruminant feeding strategies. Hofmann (1989) proposed that feeding strategies ranged from nonselective intake of bulk roughage and efficient fermentation in the forestomach, to selectivity for concentrate forages (high in plant cell content) with increased post-ruminal digestion. This hypothesis challenged many beliefs regarding digestion in free-ranging ruminants and proposed that we reexamine the manner in which ruminant herbivores obtain nutrients from the environment.

Because of the magnitude of Hofmann's hypothesis, several papers (Gordon and Illius 1994, 1996; Robbins et al. 1995) were published describing tests of his predictions. These researchers examined components of Hofmann's hypothesis and concluded that they did not find support for morpho-physiological adaptations to diet type within classes of ruminants. They attributed differences in digestive function to body mass or food characteristics. As a result, the consensus has been that Hofmann's hypothesis regarding gut morphology and function in classes of ruminants is inadequate (Robbins et al. 1995; Illius 1997). However, upon critical examination of both Hofmann's hypotheses and subsequent critiques, I contend that we have not adequately tested Hofmann (1989). Although scientifically sound, the studies of Gordon and Illius (1994, 1996) and Robbins et al. (1995) did not completely examine components of the ruminant diversification hypothesis and therefore should not be considered to support or refute Hofmann (1989).

Hofmann (1989) proposed variations on the traditional theme of foregut fermentation in the ruminant. In addition to suggesting that hindgut fermentation may play an important role in some ruminant animals, he also commented on postruminal digestion of soluble components of the diet after rumen bypass via the reticular groove (Hofmann 1989, p. 448). While post-ruminal fermentation had previously received some attention (Van Soest 1982), selective bypass of the rumenoreticular

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F. Javier Pérez-Barbería · Iain J. Gordon
Andrew W. Illius

Phylogenetic analysis of stomach adaptation in digestive strategies in African ruminants

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Abstract The stomach morphology of 28 species of artiodactyls that differ in feeding style (browser, mixed feeder, grazer) was analysed using a multivariate approach and phylogenetic correction in order to test whether stomach morphology was correlated with feeding style when body mass was controlled for. A total of 25 morphological traits of the stomach were used in the analysis. After the effects of body mass and phylogeny on stomach morphology were taken into account, there was no significant grouping of species according to feeding style. When information about the feeding style of each species was included in the analysis, the set of morphological traits separated the mixed feeders from the other two feeding styles, but grazers and browsers had similar morphological features. Most of the variance in stomach morphology was explained by body mass and a lesser proportion by phylogeny. The main morphological features that have previously been proposed as being adaptations in grazing species, namely, lengthening of the retention time of ingesta to achieve an increase in their fibre digestion capability by means of a larger relative stomach capacity, a greater subdivision of chambers and smaller openings, are not supported by the findings of this study. Thus, there is no consistent evidence to support a significant adaptive effect of stomach morphology to different diets in the Artiodactyla.

Keywords Allometry · Body mass · Comparative method · Feeding styles · Gut morphology

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Introduction

The feeding habits of some ungulates in a natural habitat were, to our knowledge, first defined by Van Zyl (1965), but it was Hofmann who classified African ruminants into three feeding styles according to morphological adaptations of the digestive system (Hofmann 1973, 1989), as related to differences in diet composition (Hofmann 1968, 1984, 1988; Hofmann and Stewart 1972; Hofmann et al. 1995). Hofmann's categorisation of feeding styles has been extensively used in grazing ecology (Owen-Smith 1982; Gordon and Illius 1988, 1994, 1996; McNaughton 1991; Van Wieren 1996). Differences in stomach morphology between species that differ in diet triggered subsequent studies on other parts of the digestive system, for example, morphological adaptations of the organs involved in the selection (lips, muzzle: Janis and Ehrhardt 1988; Pérez-Barbería and Gordon 2001a) and the processing of food (teeth, jaws, jaw muscles: Fortelius 1985; Axmacher and Hofmann 1988; Janis 1988; Pérez-Barbería and Gordon 1999a, 2001a) and also in behavioural variables (activity time: Mysterud 1998; Pérez-Barbería and Gordon 1999b; home range: Mysterud et al. 2001; habitat use: Pérez-Barbería et al. 2001b). Based on Hofmann's (1973) classification, it has been assumed that grazing species achieve a greater extent of digestion of fibre in comparison with browsing species by means of food retention in the rumen, large stomach capacity, higher degree of stomach compartmentalisation and smaller openings between the rumen and omasum. However, a statistical relationship between the differences in stomach morphology, described by Hofmann (1973), and diet composition has not yet been demonstrated.

A recurrent problem which arises when studying the differences in the morphology or function of the digestive system, in relation to Hofmann's classification, is the possible confounding effect of body mass (Gordon and Illius 1994; Robbins et al. 1995; Iason and Van Wieren 1998). After controlling for body mass, Gordon and Illius (1994) found that there were no differences in wet

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Table 2 The data set used in this study comes from Hofmann (1973).

Variable no.	2	3	4	5	6	7	8	9	10
Species name									
Giraffa camelopardalis	750.0	105.0	16.0	144.1	2.0	104.5	24.5	24.0	19
Syncerus caffer	750.8	107.0	12.0	176.0	12.0	156.8	16.5	49.5	23
Tragelaphus strepsiceros	213.5	45.8	4.4	75.7	3.5	181.3	30.5	33.5	28
Tragelaphus oryx	420.0	53.0	6.5	171.0	2.3	80.0	40.0	42.5	44

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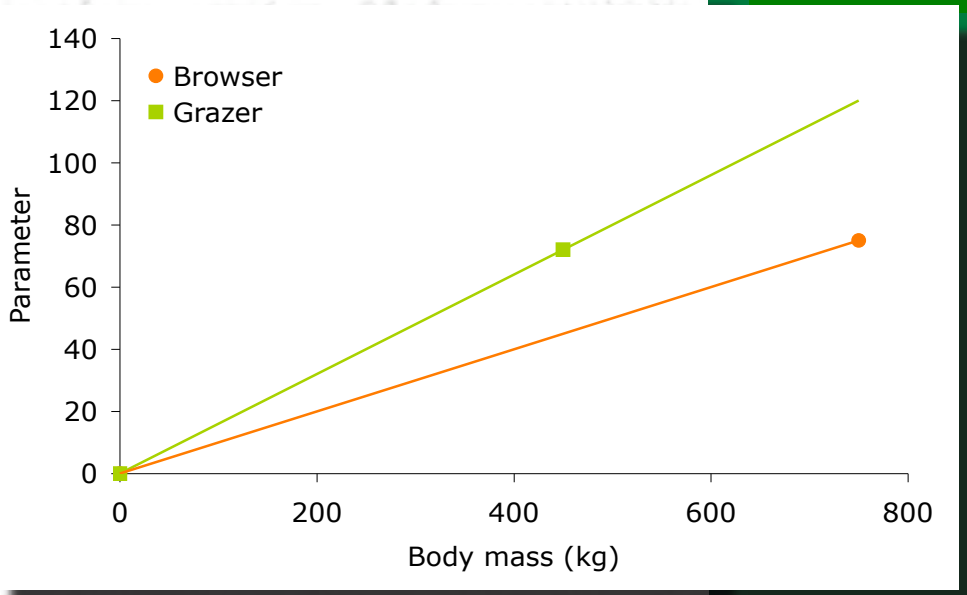

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The evolution of phylogenetic differences in the efficiency of digestion in ruminants

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This study investigates, for the first time (to our knowledge) for any animal group, the evolution of phylogenetic differences in fibre digestibility across a wide range of feeds that differ in potential fibre digestibility (fibre to lignin ratio) in ruminants. Data, collated from the literature, were analysed using a linear mixed model that allows for different sources of random variability, covariates and fixed effects, as well as controlling for phylogenetic relatedness. This approach overcomes the problem of defining boundaries to separate different ruminant feeding styles (browsers, mixed feeders and grazers) by using two covariates that describe the browser–grazer continuum (proportion of grass and proportion of browse in the natural diet of a species). The results indicate that closely related species are more likely to have similar values of fibre digestibility than species that are more distant in the phylogenetic tree. Body mass did not have any significant effect on fibre digestibility. Fibre digestibility is estimated to increase with the proportion of grass and to decrease with the proportion of browse in the natural diet that characterizes the species. We applied an evolutionary model to infer rates of evolution and ancestral states of fibre digestibility; the model indicates that the rate of evolution of fibre digestibility accelerated across time. We suggest that this could be caused by a combination of increasing competition among ruminant species and adaptation to diets rich in fibre, both related to climatically driven environmental changes in the past few million years.

Keywords: browser; grazer; phylogeny; evolution; digestibility; diet

1. INTRODUCTION

Despite considerable efforts in the analysis of the comparative anatomy of the digestive tract of ungulates, research has hitherto failed to demonstrate any relationship between differences in morphology and digestive efficiency between species, other than at a gross level (Robbins 1993). We offer a novel analysis that controls for confounding effects and highlights the flexibility of digestive adaptation in ruminants.

Previous research in this area demonstrates a number of weaknesses. The first weakness is the question of continuous versus discrete variables. Hofmann (1968, 1973) and Hofmann & Stewart (1972) described the stomach morphology of a number of species of African ruminants and using this information classified species into three groups (i.e. concentrate selectors, intermediate, and bulk and roughage eaters). Concentrate selectors (i.e. browsers) were the species whose diet mainly contained browse; bulk and roughage eaters (i.e. grazers) were species in which grass was the main component of the diet, and the third group, intermediate (i.e. mixed feeders), consumed a mixture of browse and grass, depending upon the habitat or season. Hofmann & Stewart (1972) and Hofmann (1973) pointed out that their stomach classification coincided with the main dietary habits of the ruminant species. However, Hofmann's later papers (1985, 1988) established a composite criterion of species classification '...based on typical structures of the digestive tract ... and/or on feeding behaviour/forage selection' (Hofmann 1985, p. 398). This may be the cause of confusion in the literature as to the criteria used to classify species, almost entirely based on dietary habits but frequently linked with the stomach classification of Hofmann (1973) (see Iason & van Wieren 1999; Pérez-Barbería & Gordon 1999*a*, 2000, 2001; Brashares *et al.* 2000; Gagnon & Chew 2000; Pérez-Barbería *et al.* 2001*a*). As a result, the relationships that many studies find between the variables studied—dietary classification and stomach morphology—are confounded by circular argumentation (Pérez-Barbería *et al.* 2001*a*).

Hitherto, ruminant species have been classified into dietary groups using discrete boundaries based on information on stomach morphology or dietary habits (Axmacher & Hofmann 1988; Gordon & Illius 1988, 1994, 1996; Janis & Ehrhardt 1988; Spencer 1995; van Wieren 1996, Iason & van Wieren 1999; Pérez-Barbería & Gordon 1999*a*,*b*, 2000, 2001; Brashares *et al.* 2000; Gagnon & Chew 2000; Pérez-Barbería *et al.* 2001*a*). However, stomach morphology and dietary habits are continuous variables and they should be treated as such.

A second weakness of previous work has been an underemphasis on phylogeny. Phylogeny has been demonstrated to be a significant factor in explaining the variability in a number of morphological traits (Pérez-Barbería & Gordon 1999*a*, 2001; Pérez-Barbería *et al.* 2001*a*) and behavioural variables (Pérez-Barbería &

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The evolution of phylogenetic differences in the efficiency of digestion in ruminants

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This study investigates, for the first time (to our knowledge) for any animal group, the evolution of phylogenetic differences in fibre digestibility across a wide range of feeds that differ in potential fibre digestibility (fibre to lignin ratio) in ruminants. Data, collated from the literature, were analysed using a linear mixed model that allows for different sources of random variability, covariates and fixed effects, as

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We expect that

(iii) species adapted to consuming different diets will differ in the efficiency with which they digest fibre when body mass has been taken into account;

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Oecologia

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

R.R. Hofmann

Institut für Veterinär-Anatomie, -Histologie und -Embryologie, Abteilung Vergleichende Anatomie der Haus- und Wildtiere, Justus-Liebig-Universität Giessen, D-6300 Giessen, Federal Republic of Germany

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

* Supported by German Research Community grant DFG Ho 273/6

** 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 acis (acetic, butyric, propionic acid set free by rumen bacteriae); *SE* Surface enlargement (of absorptive mucosa)

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 todays' 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

Explaining a putative contradiction

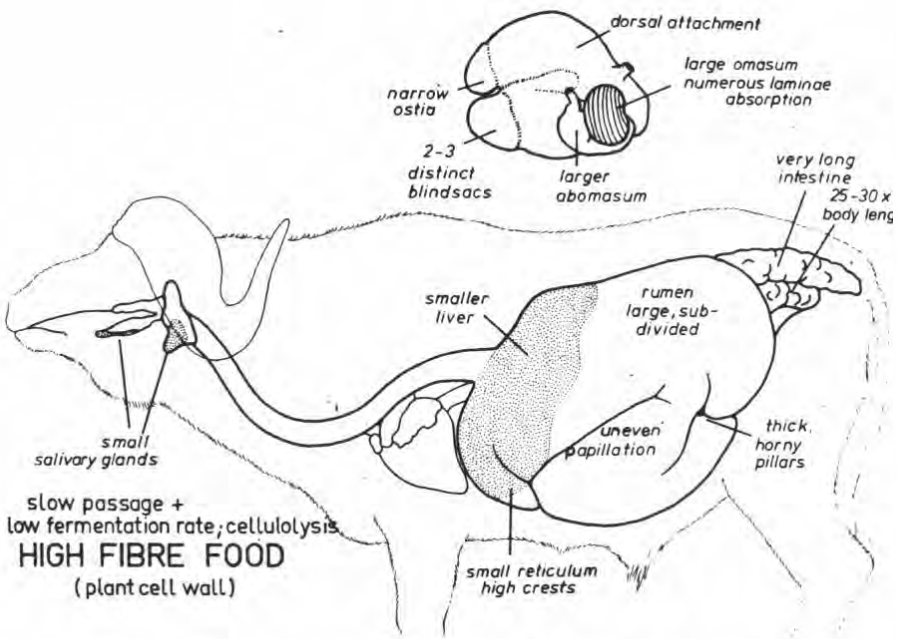
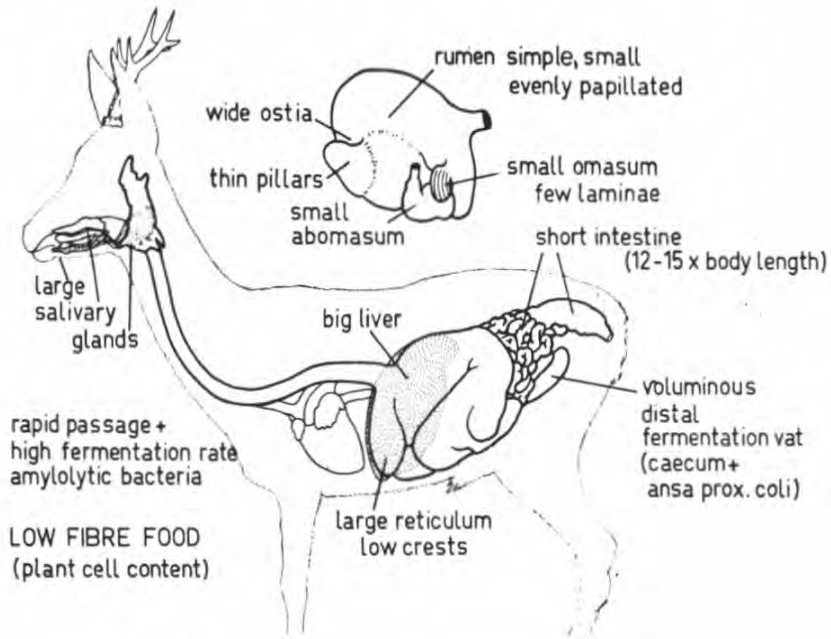


Fig. 1: The African buffalo, a non-selective roughage grazer.



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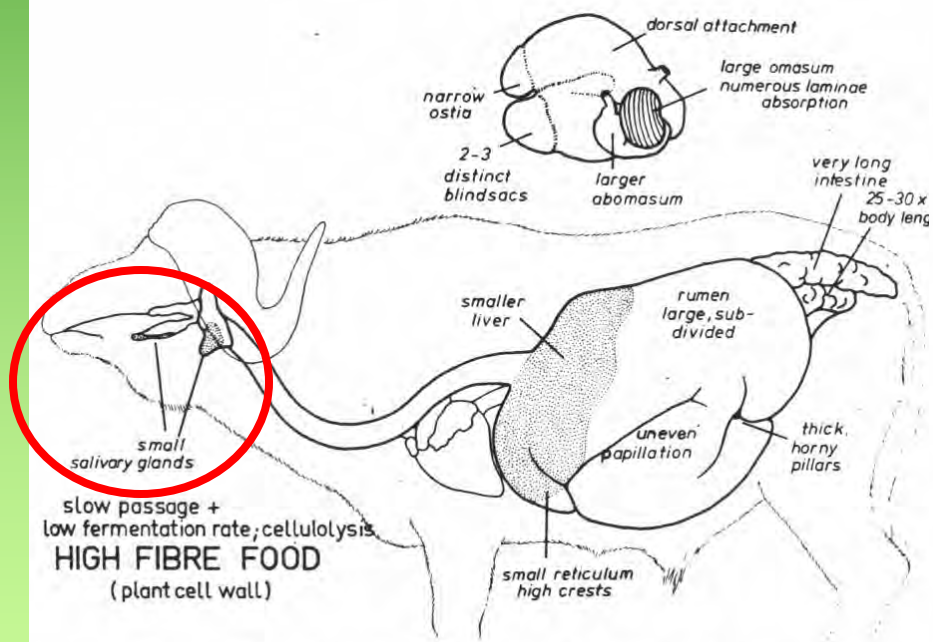

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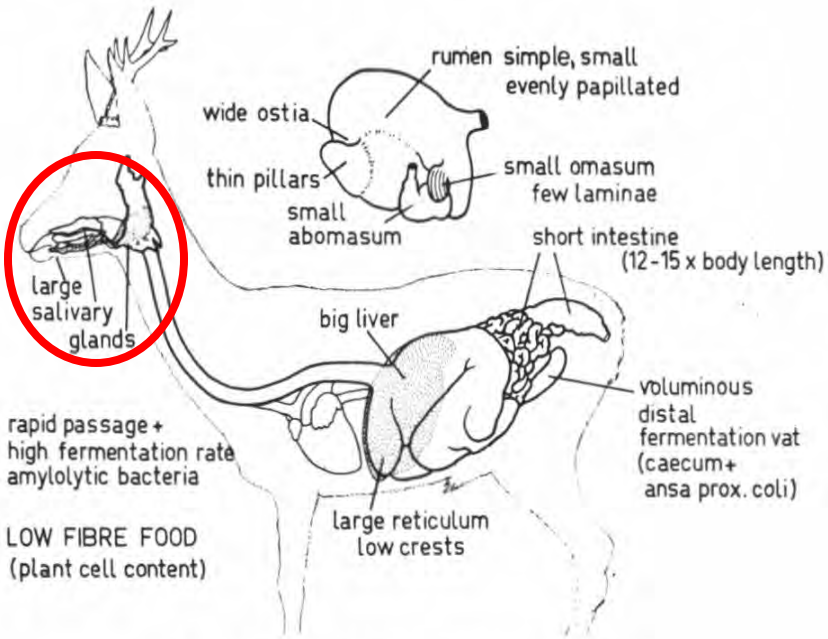

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Explaining a putative contradiction

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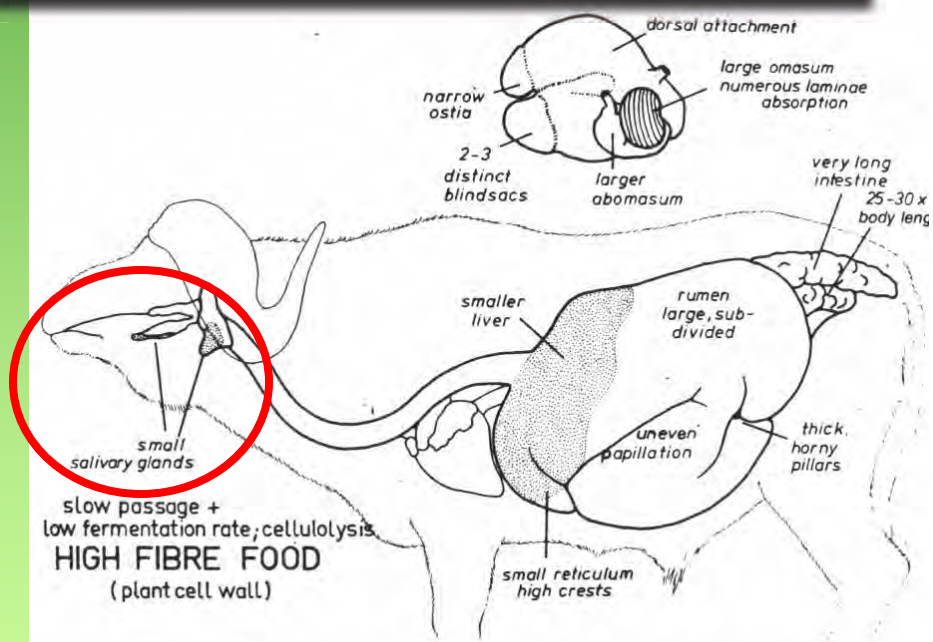
But there is another, third reason for much more (and more serous) saliva production in CS and IM: it is a



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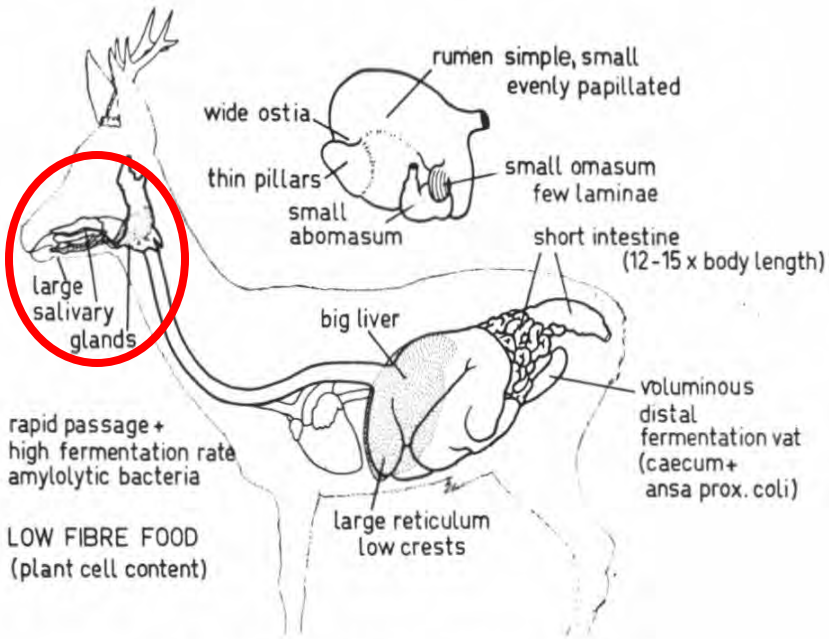

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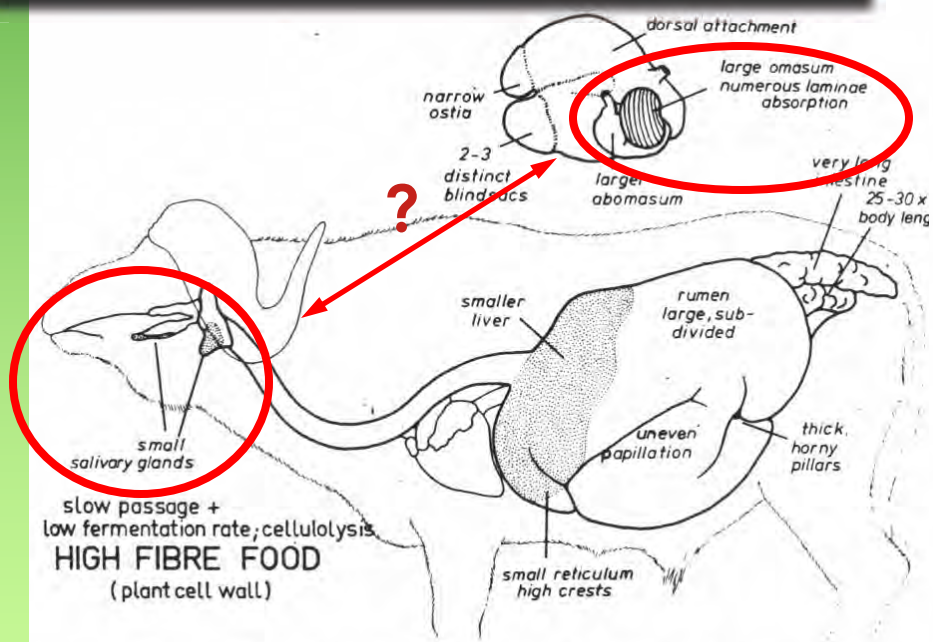

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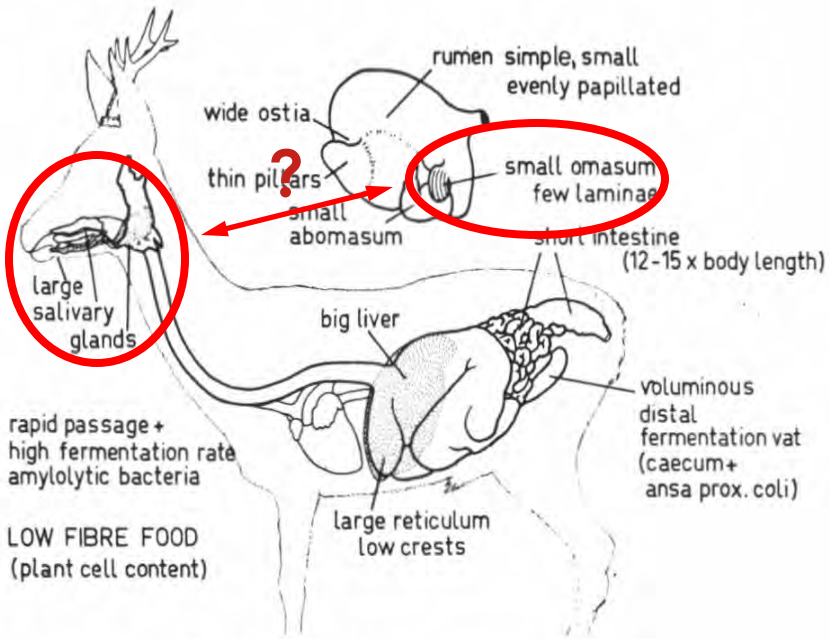

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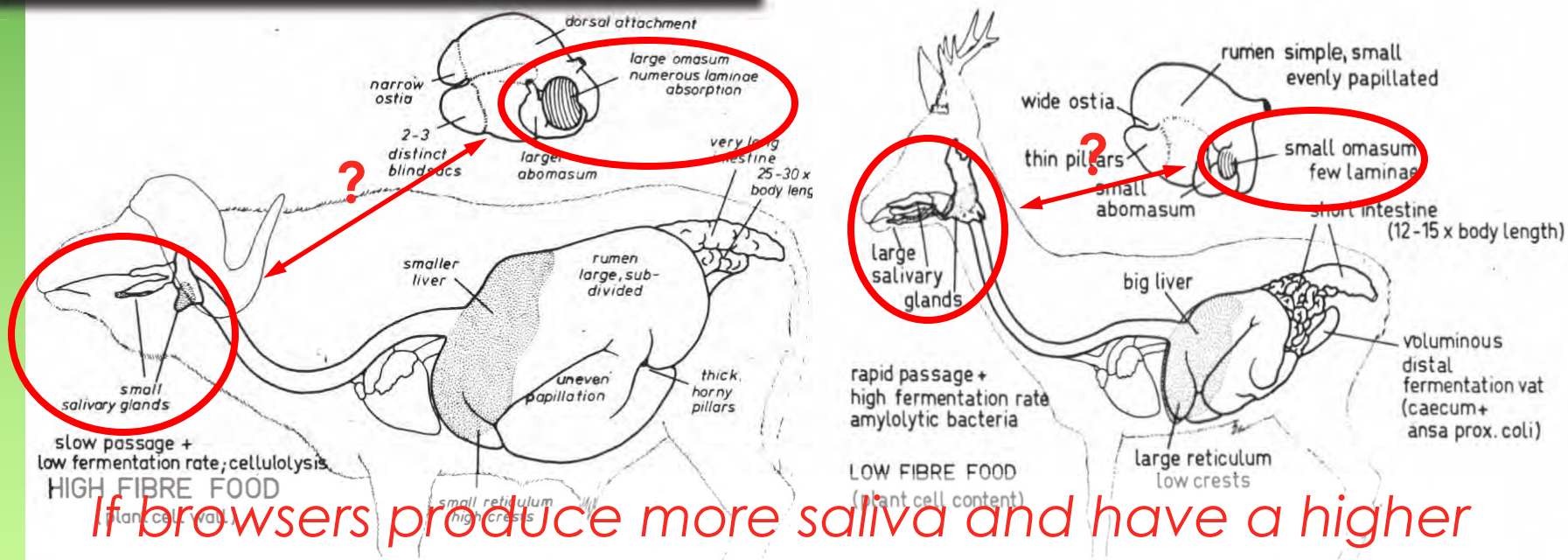
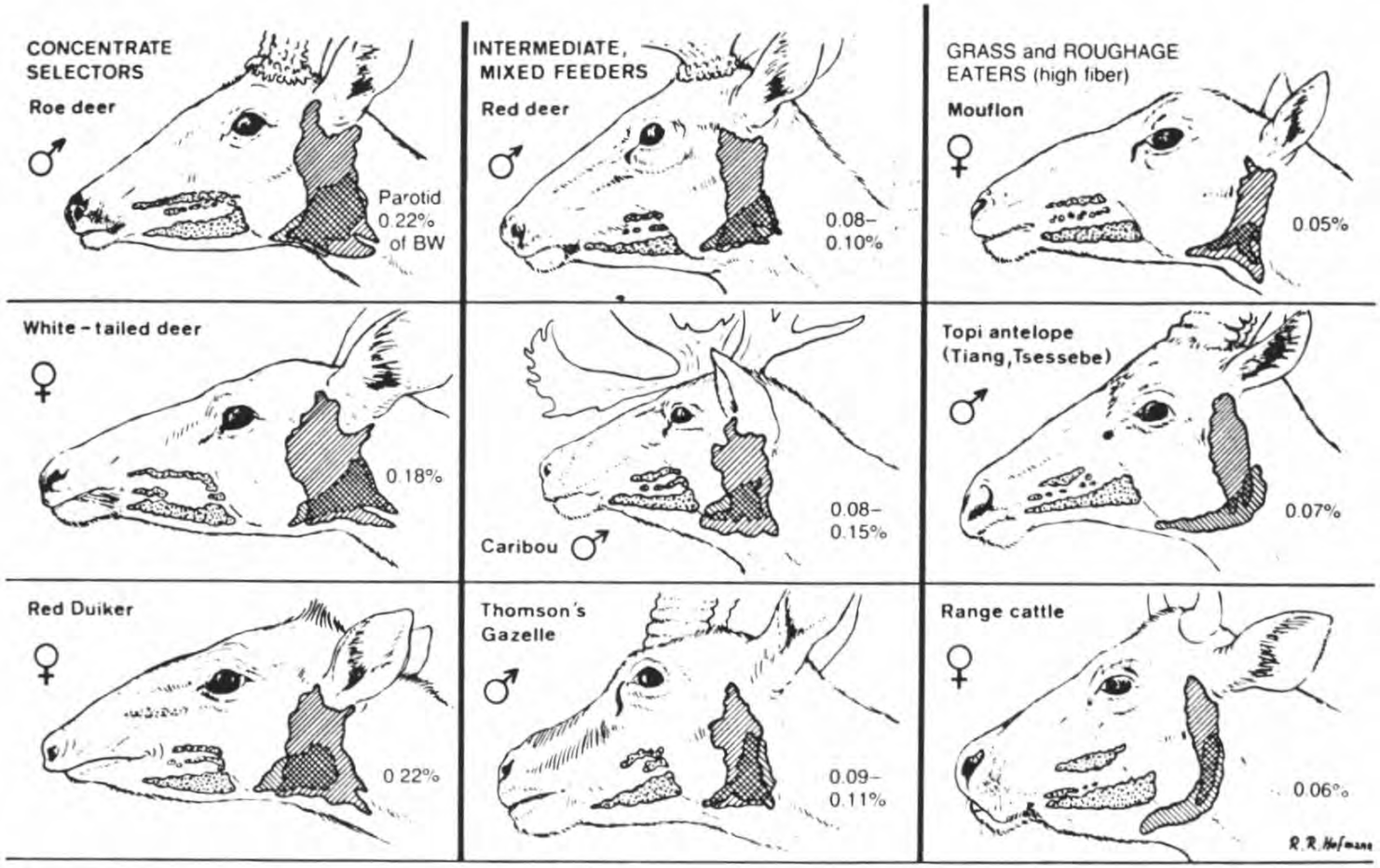


If browsers produce more saliva and have a higher fluid throughput through the rumen, why don't ***they*** *have the larger omasa?*

from Hofmann (1989)

Different salivary gland size



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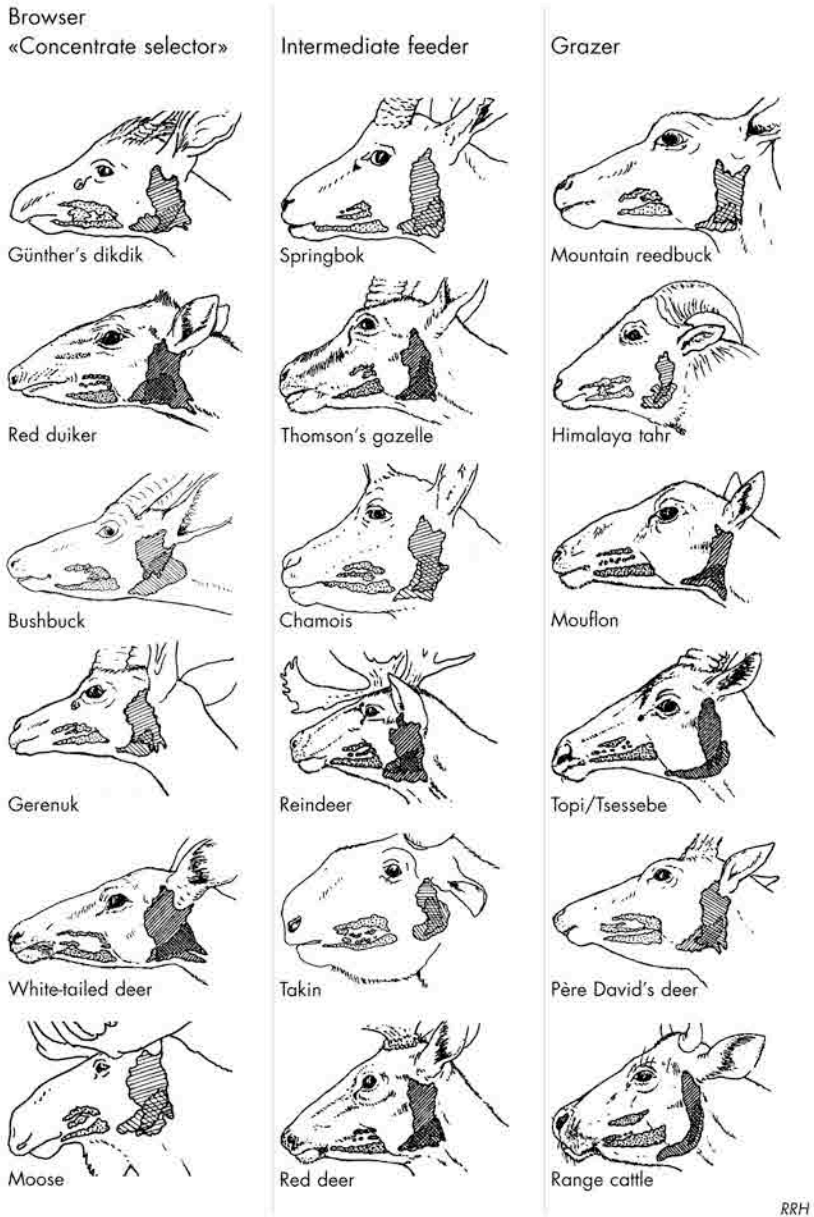

from Hofmann et al. (2008)

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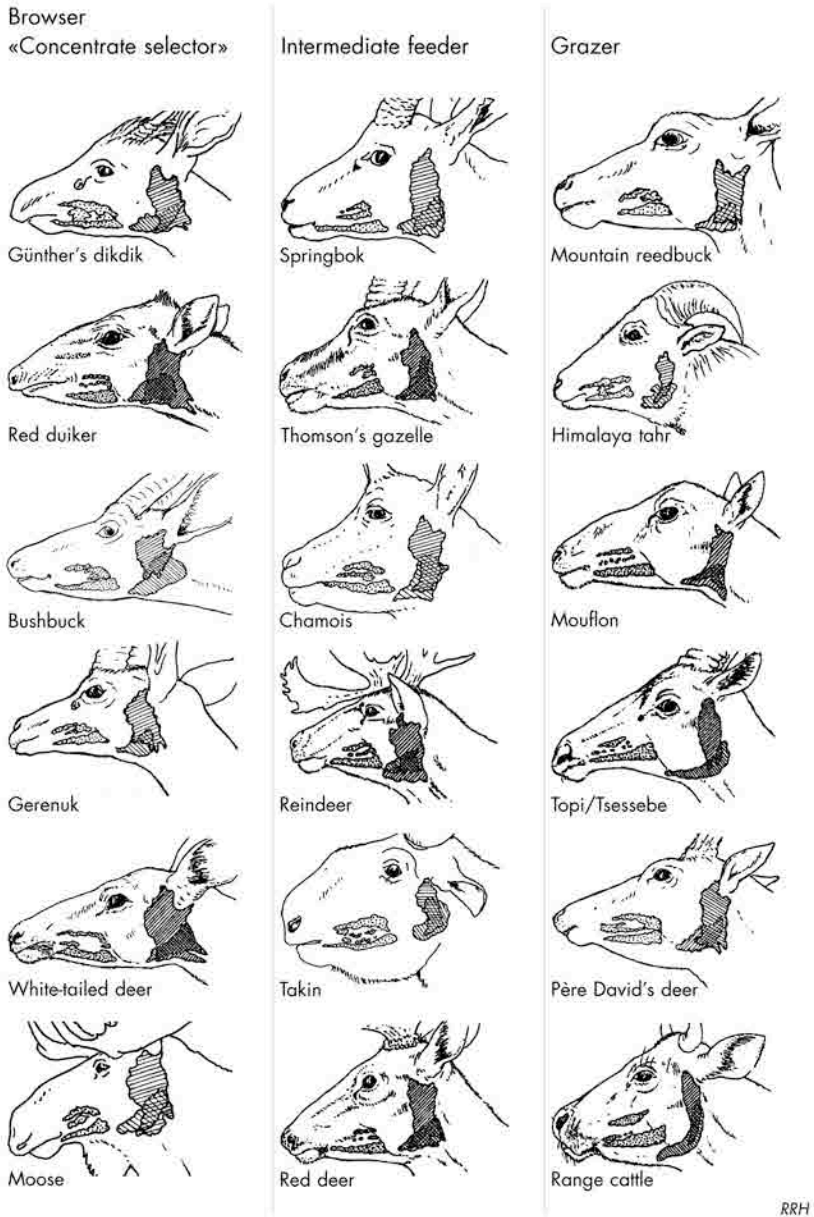

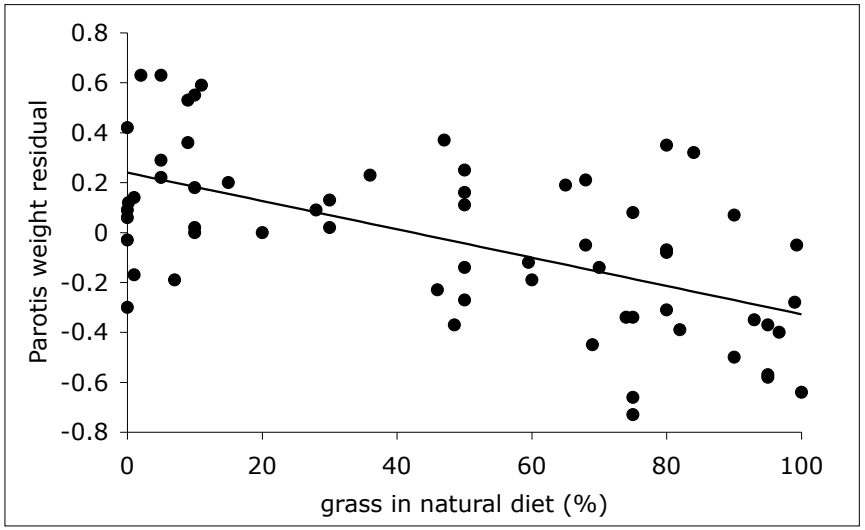

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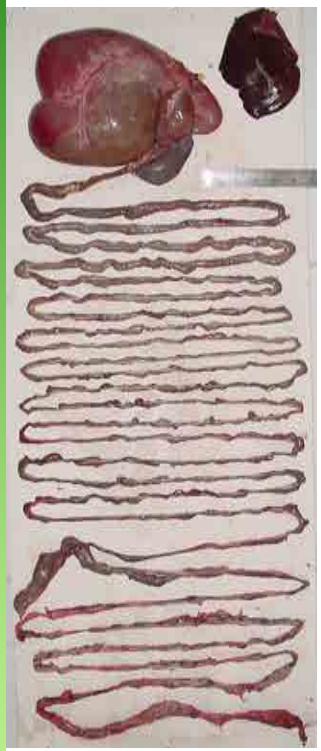

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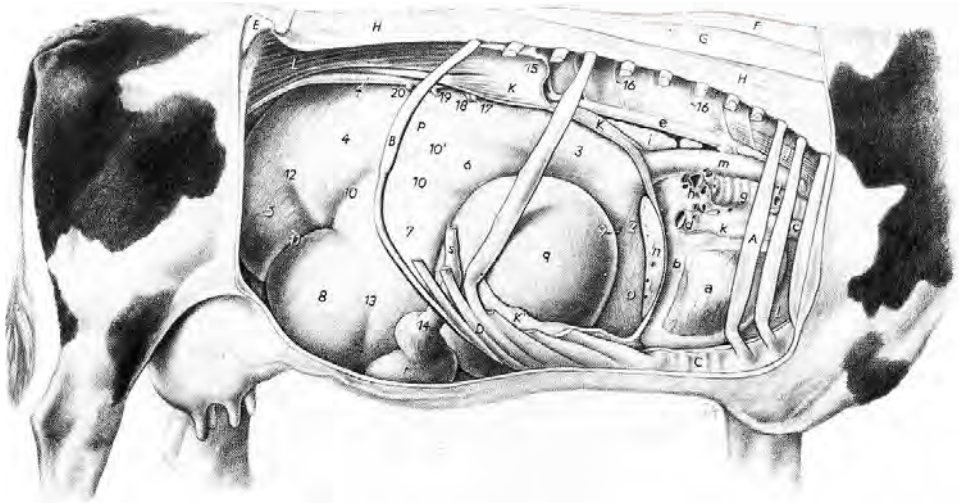

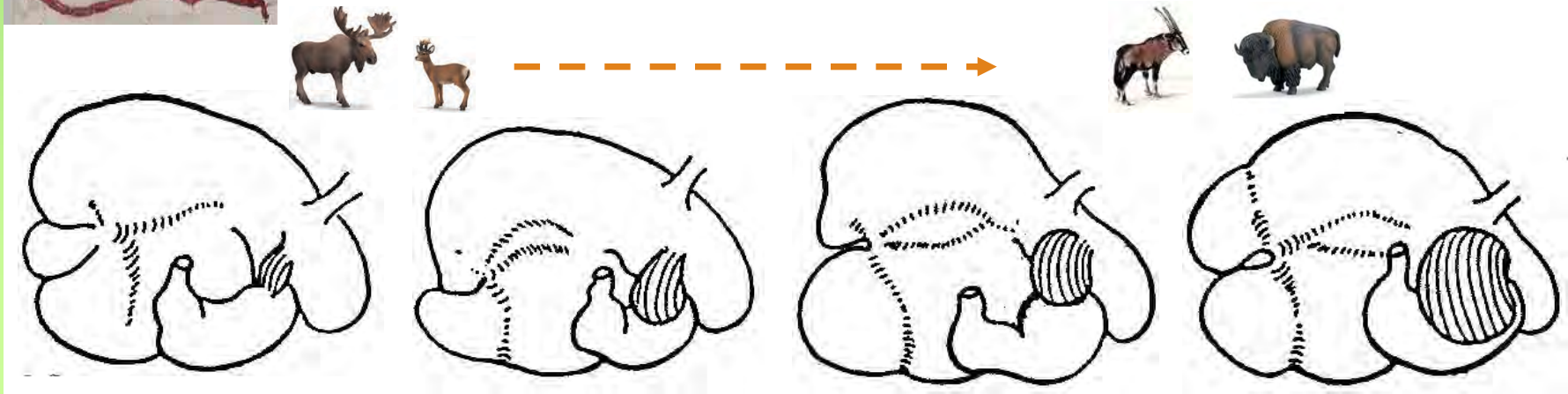

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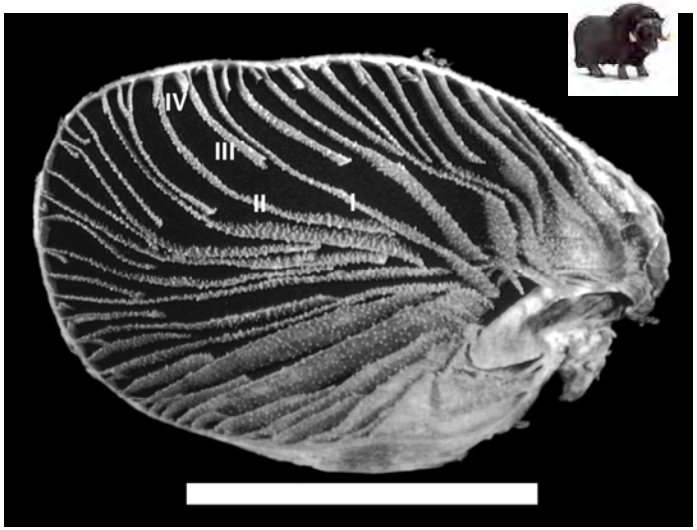

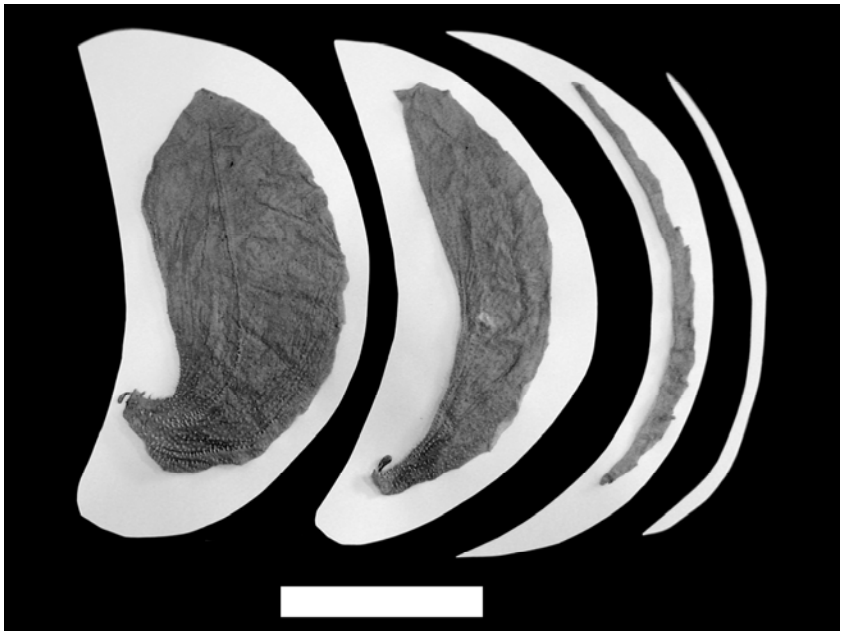

from Clauss, Hofmann et al. (2006)

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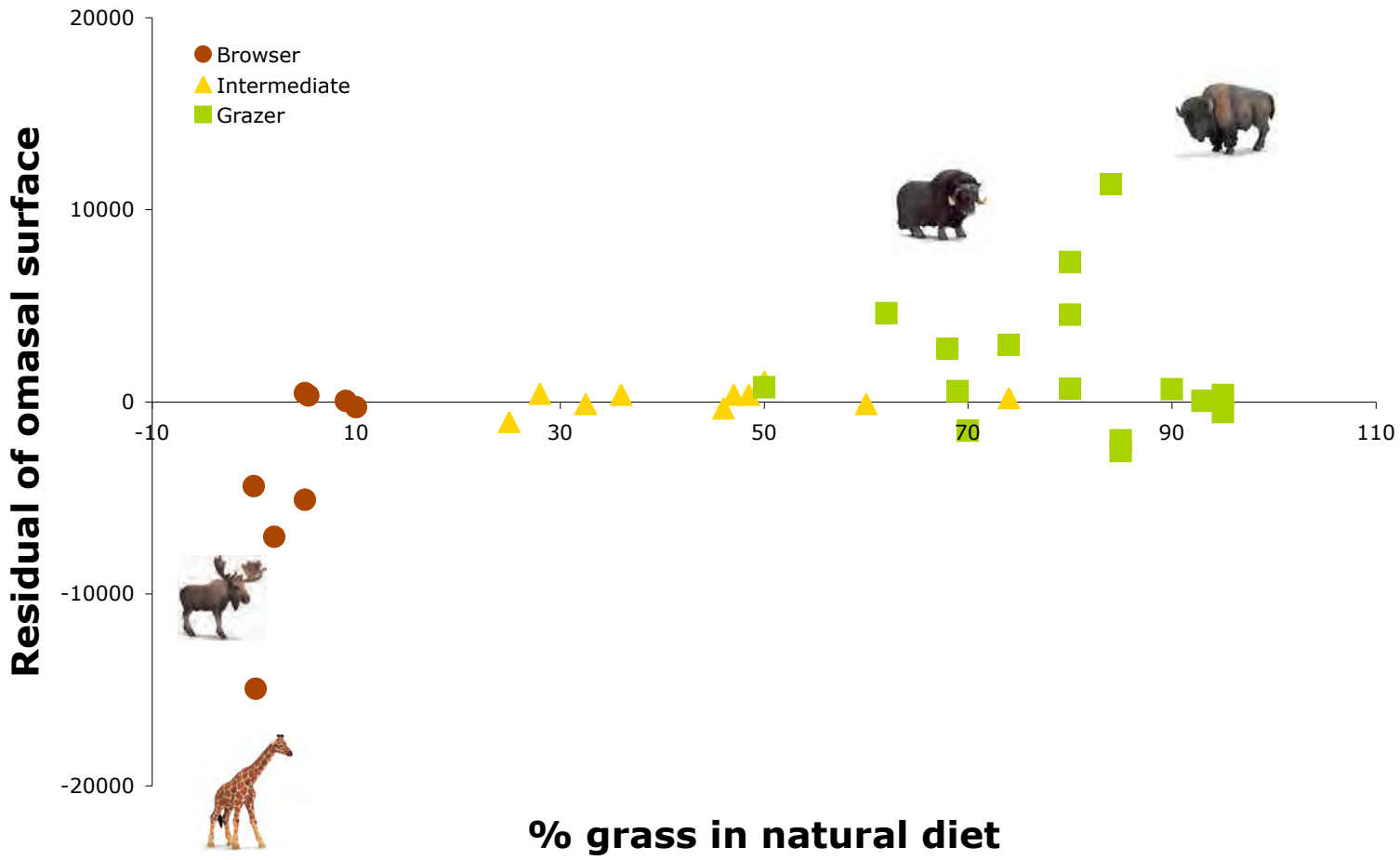

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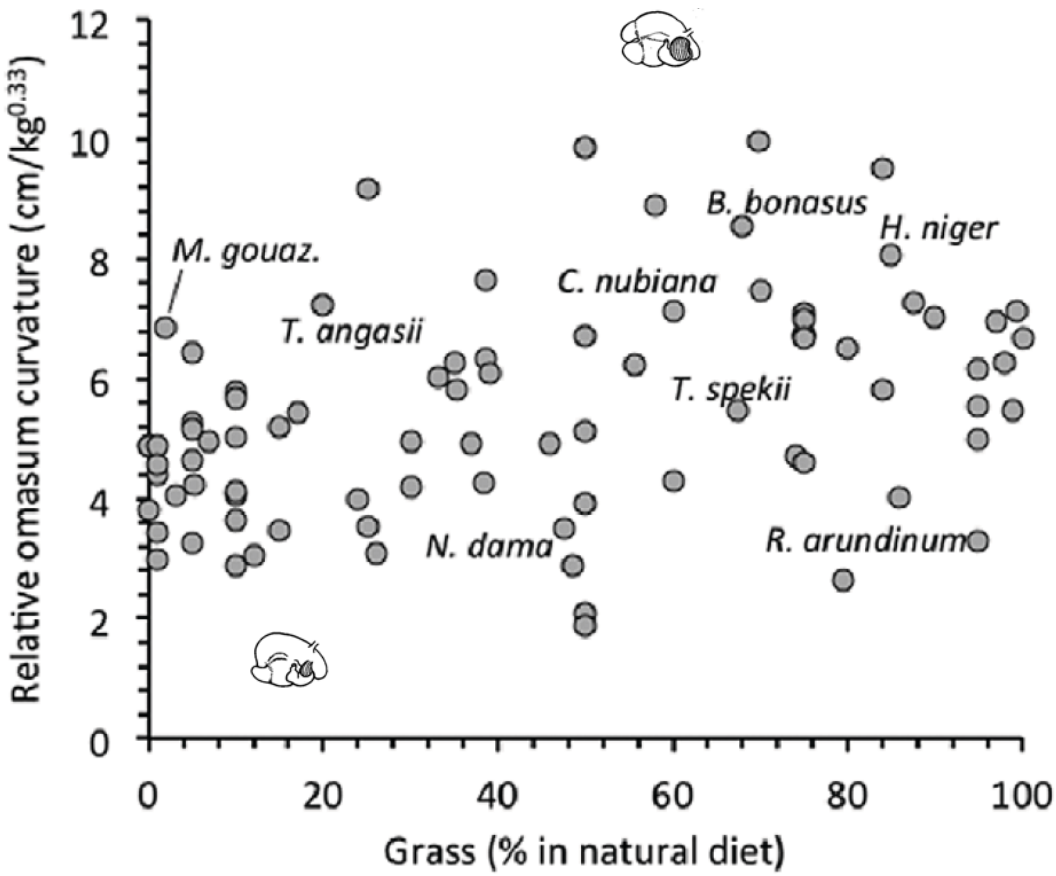

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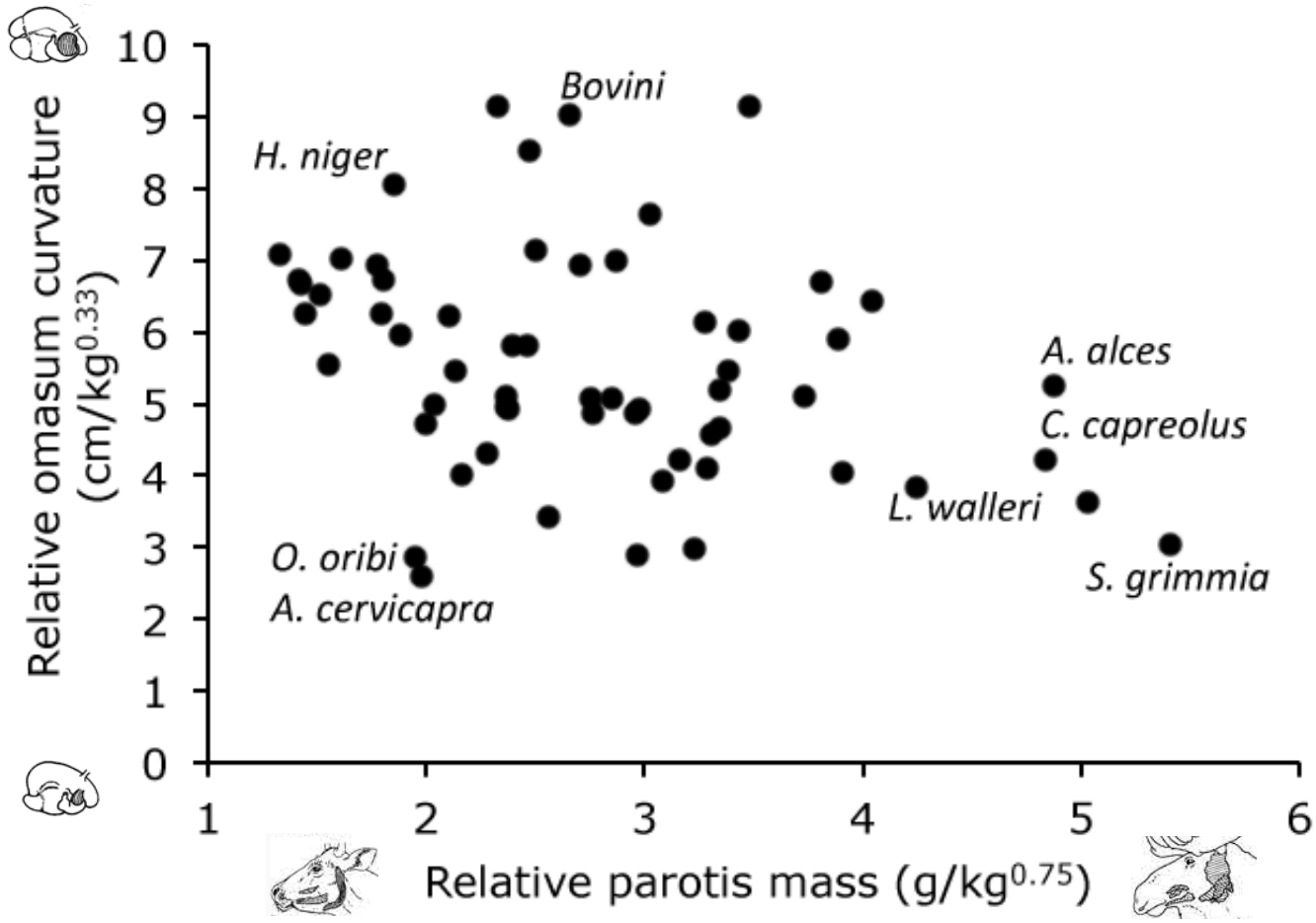

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Our growing scientific knowledge of the nutritional physiology of ruminants is documented in a vast number of publications annually, and every five years more than 600 researchers from all over the world meet in a different place to review and present 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 todays' 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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7003

Oecologia

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

R.R. Hofmann

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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. Evi-

a shorter retention time of ingesta. At the end of long grazing periods the maximally filled GR ruminoreticulum shows a *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 connec-

only 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

* Supported by German Research Community grant DFG Ho 273/6

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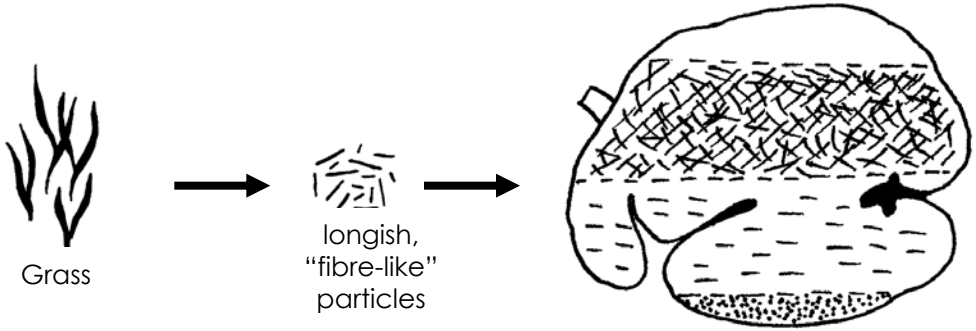
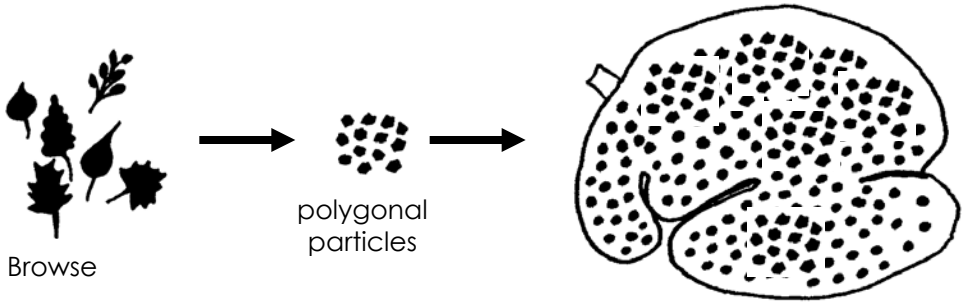
Grazer



Fibre „mat"/ „raft"
Stratification

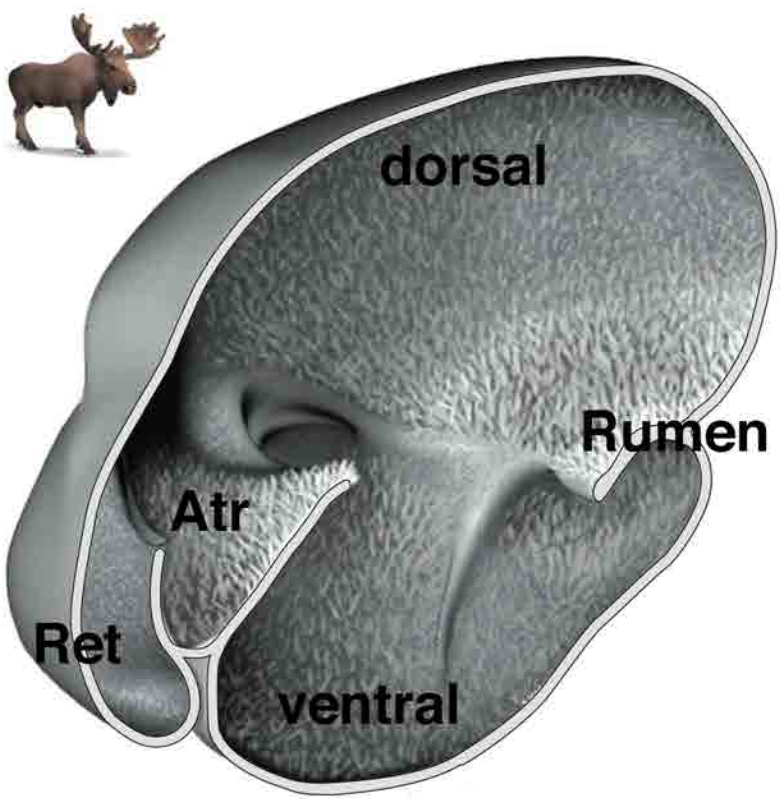
Browser

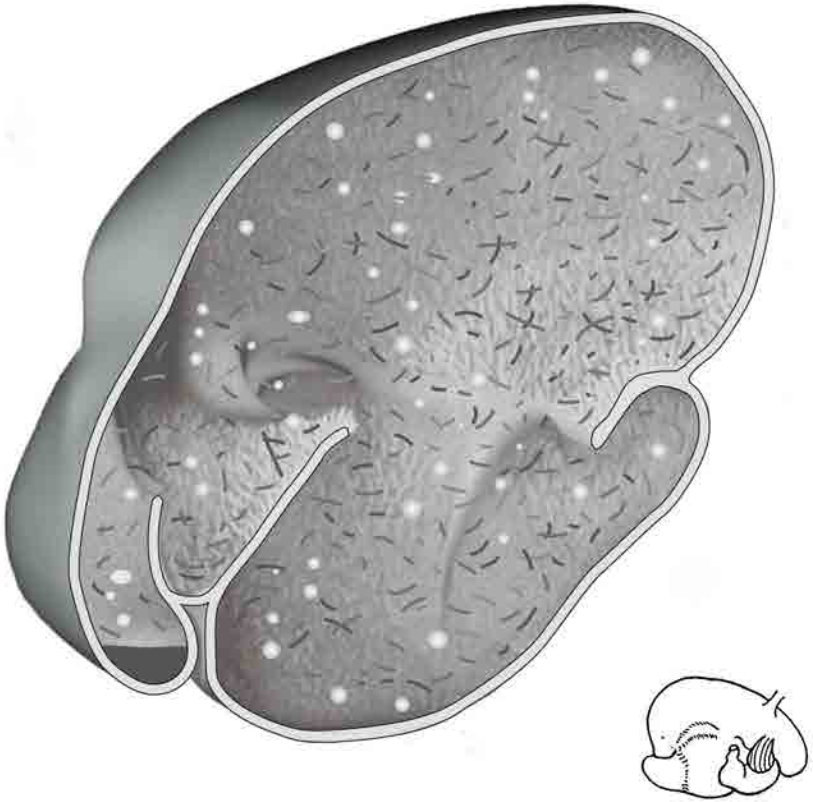


No fibre „mat"/ „raft"
No stratification

from Clauss et al. (2003)

No stratification of rumen contents: 'moose-type'





from Clauss et al. (2010)

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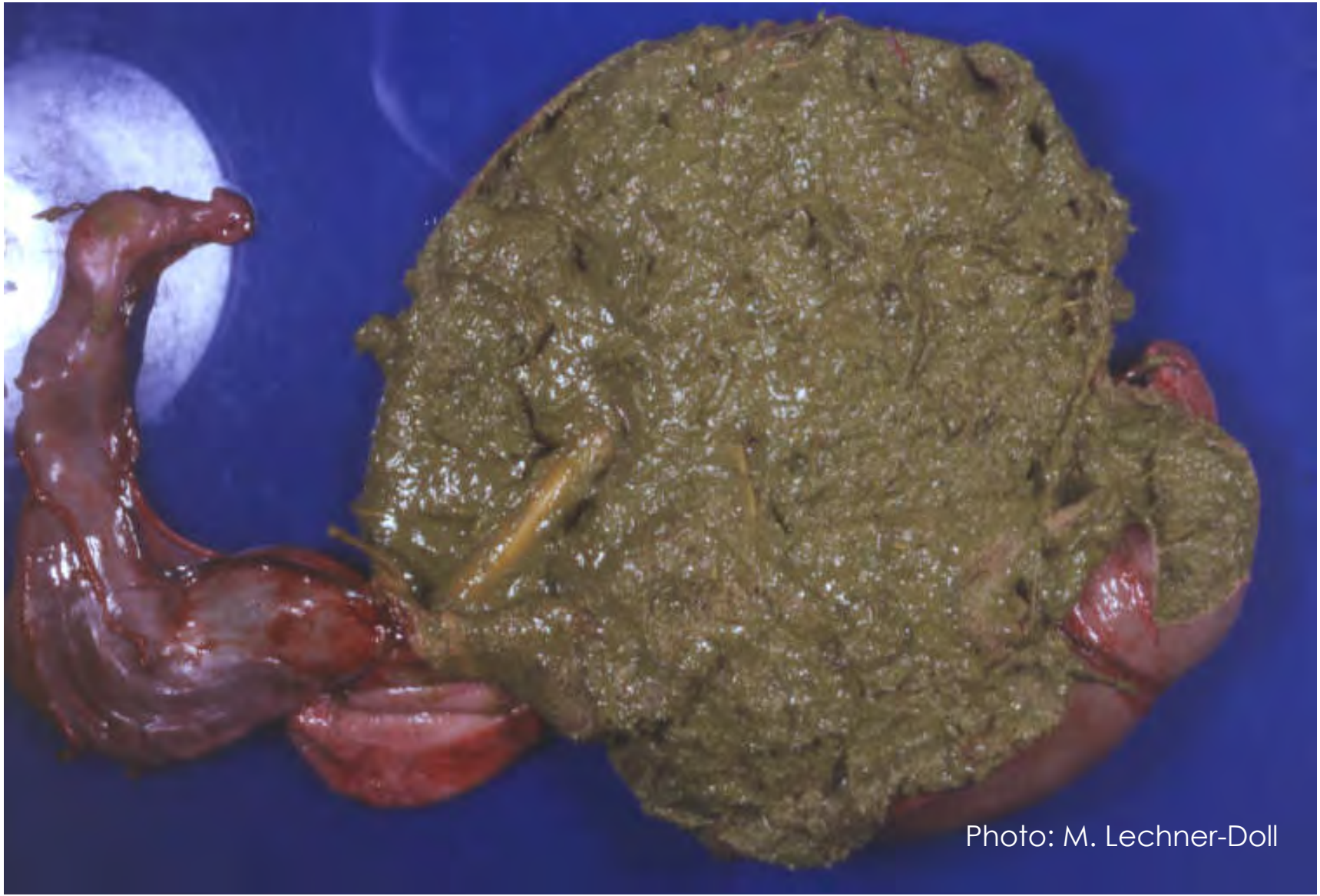
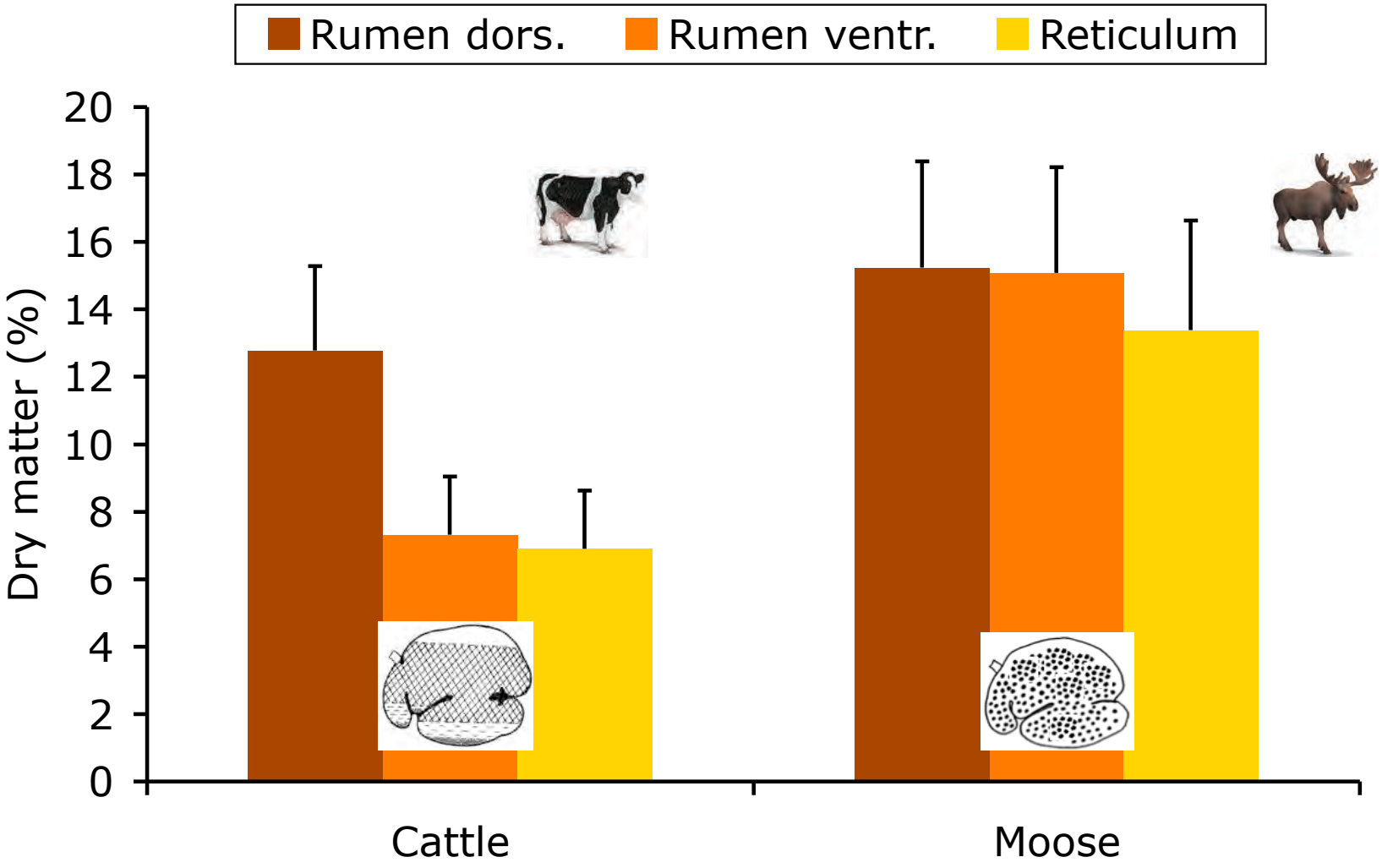
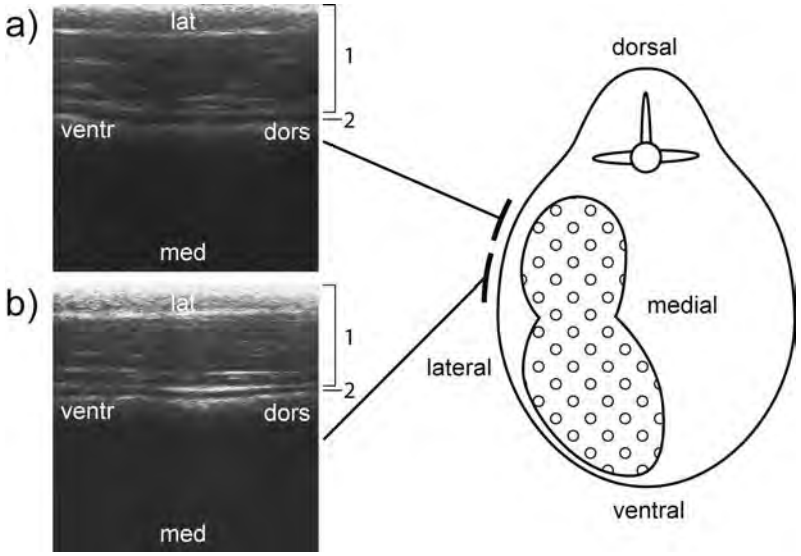


Stratification of rumen contents



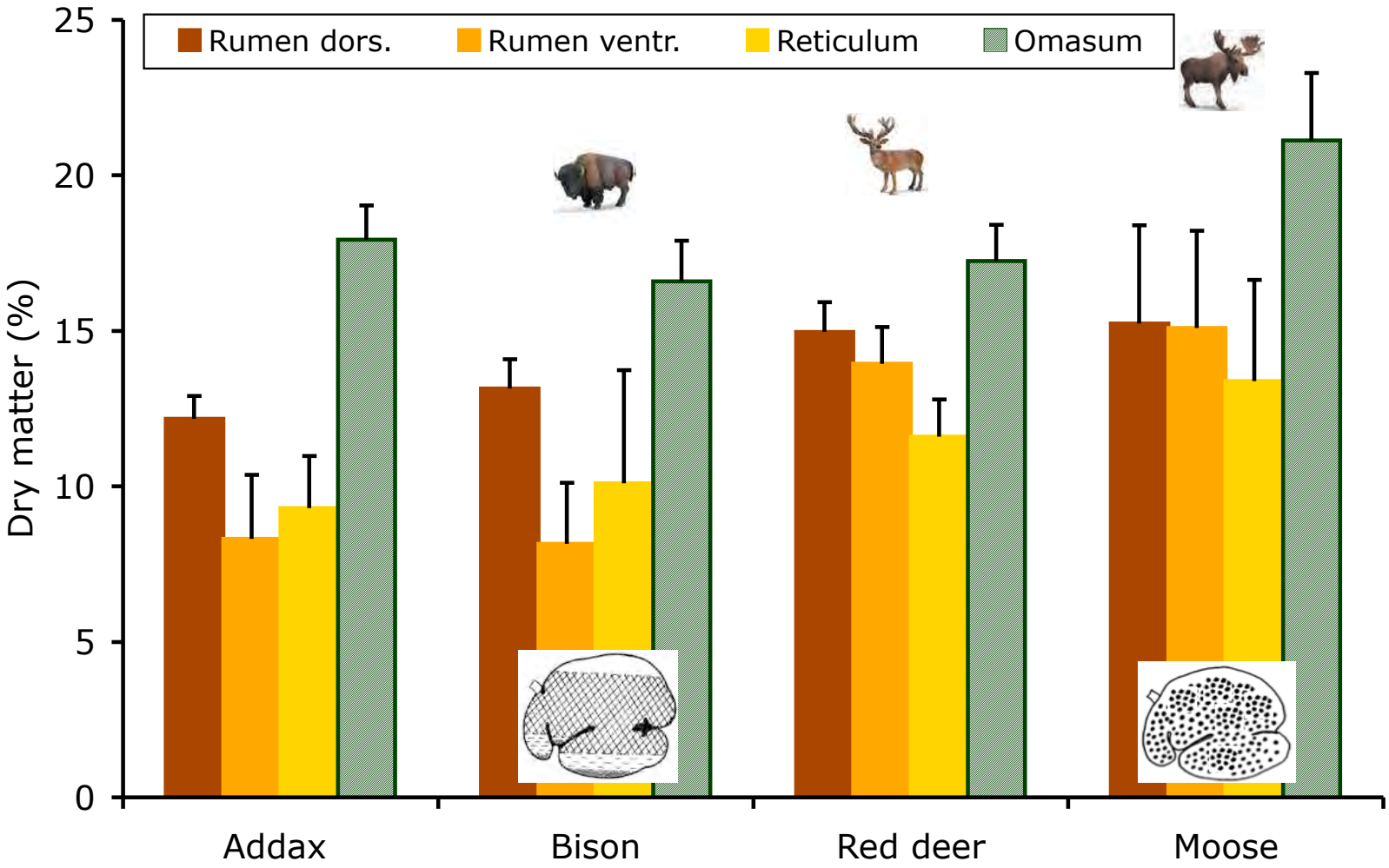
from Clauss et al. (2010)

Testing stratification by ultrasound - moose



from Tschuor & Clauss (2008)

Testing stratification by dry matter content



from Clauss et al. (2009)

Testing stratification by rumen morphology

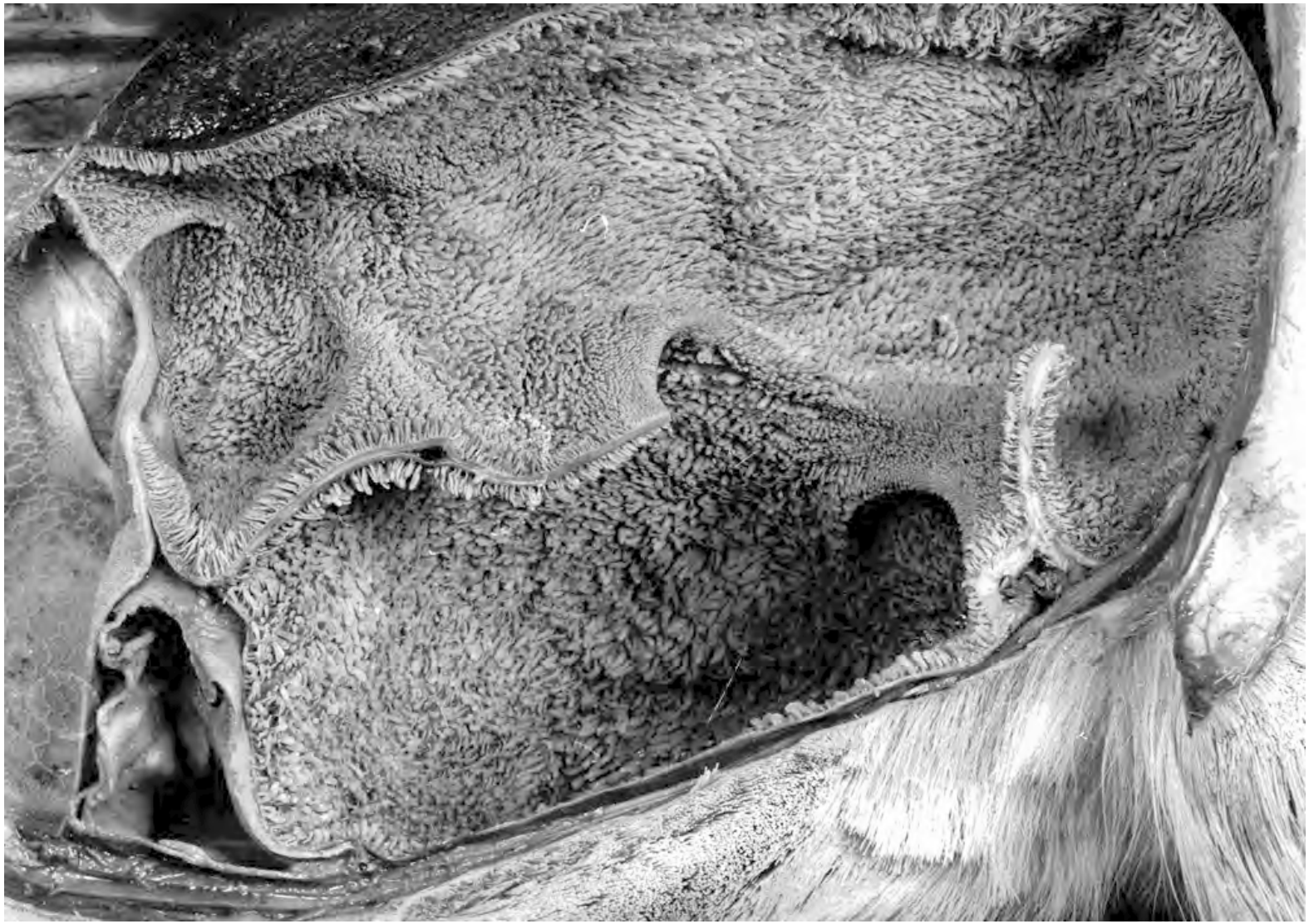
-Rumen papilla growth is stimulated by volatile fatty acids

-Differences in ruminal papillation should indicate differences in rumen contents stratification (e.g., a gas accumulation (CO_2, methane) will displace volatile fatty acids

Testing stratification by rumen morphology

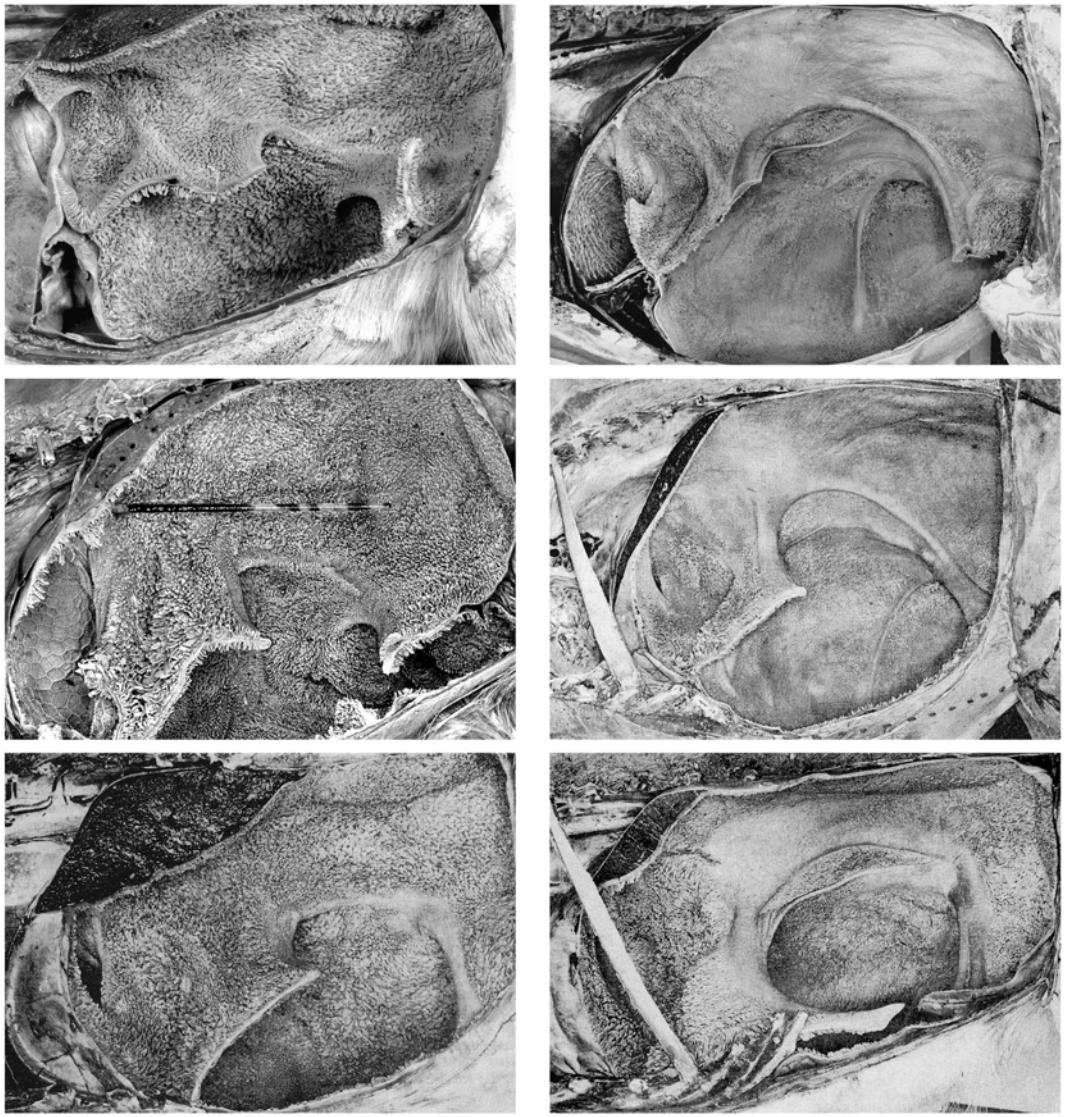
from Clauss, Hofmann et al. (2009)

Testing stratification by rumen morphology



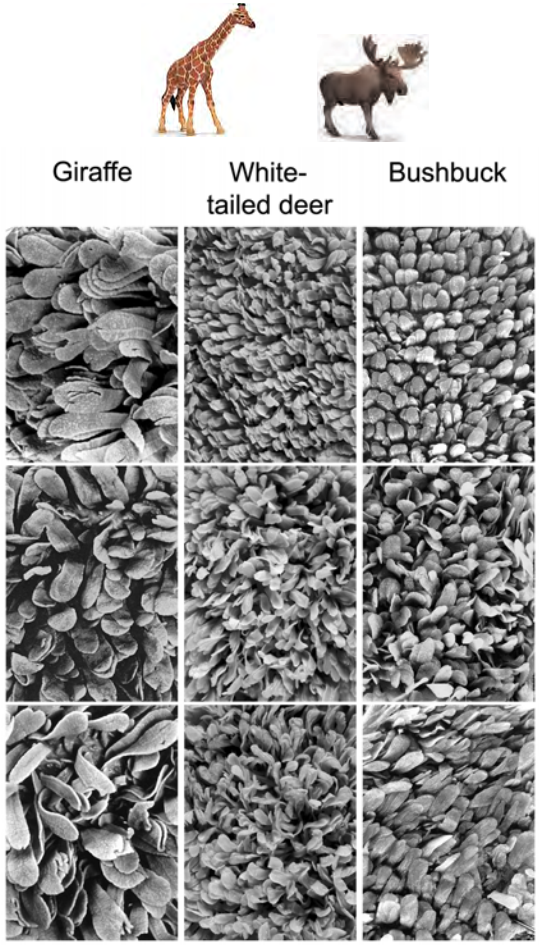
from Clauss, Hofmann et al. (2009)

Testing stratification by rumen morphology



from Clauss, Hofmann et al. (2009)

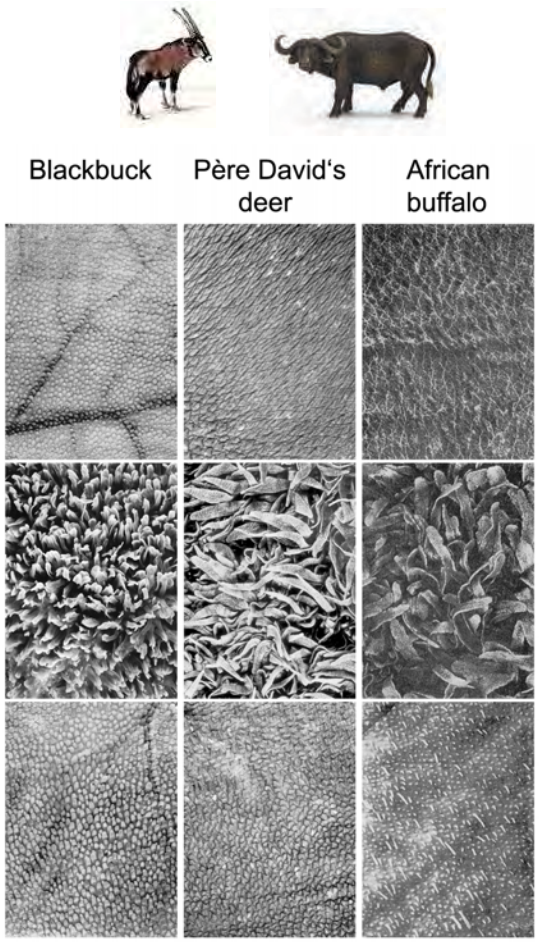
Stratification and rumen papillation



dorsal

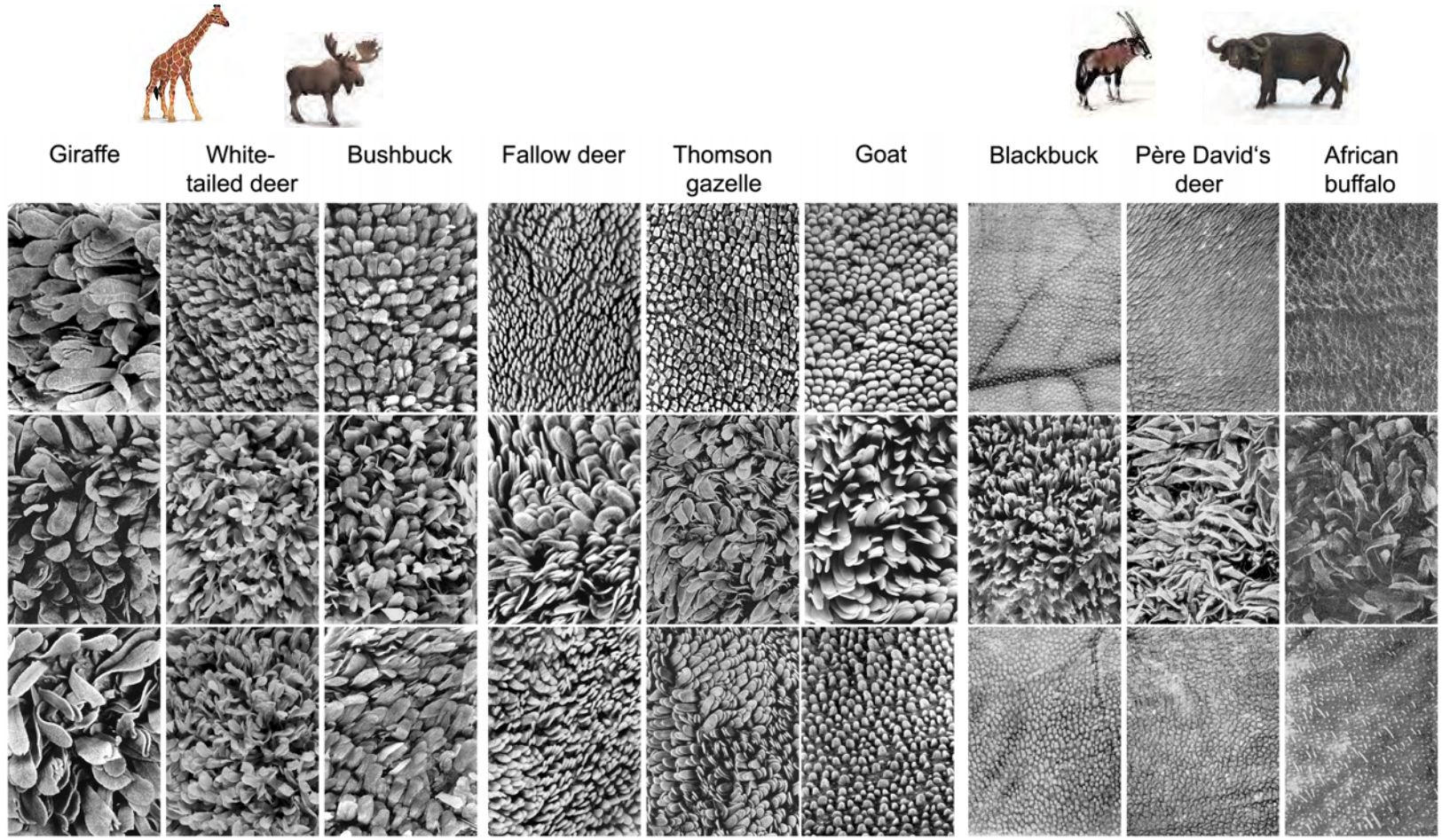
Atrium

ventral



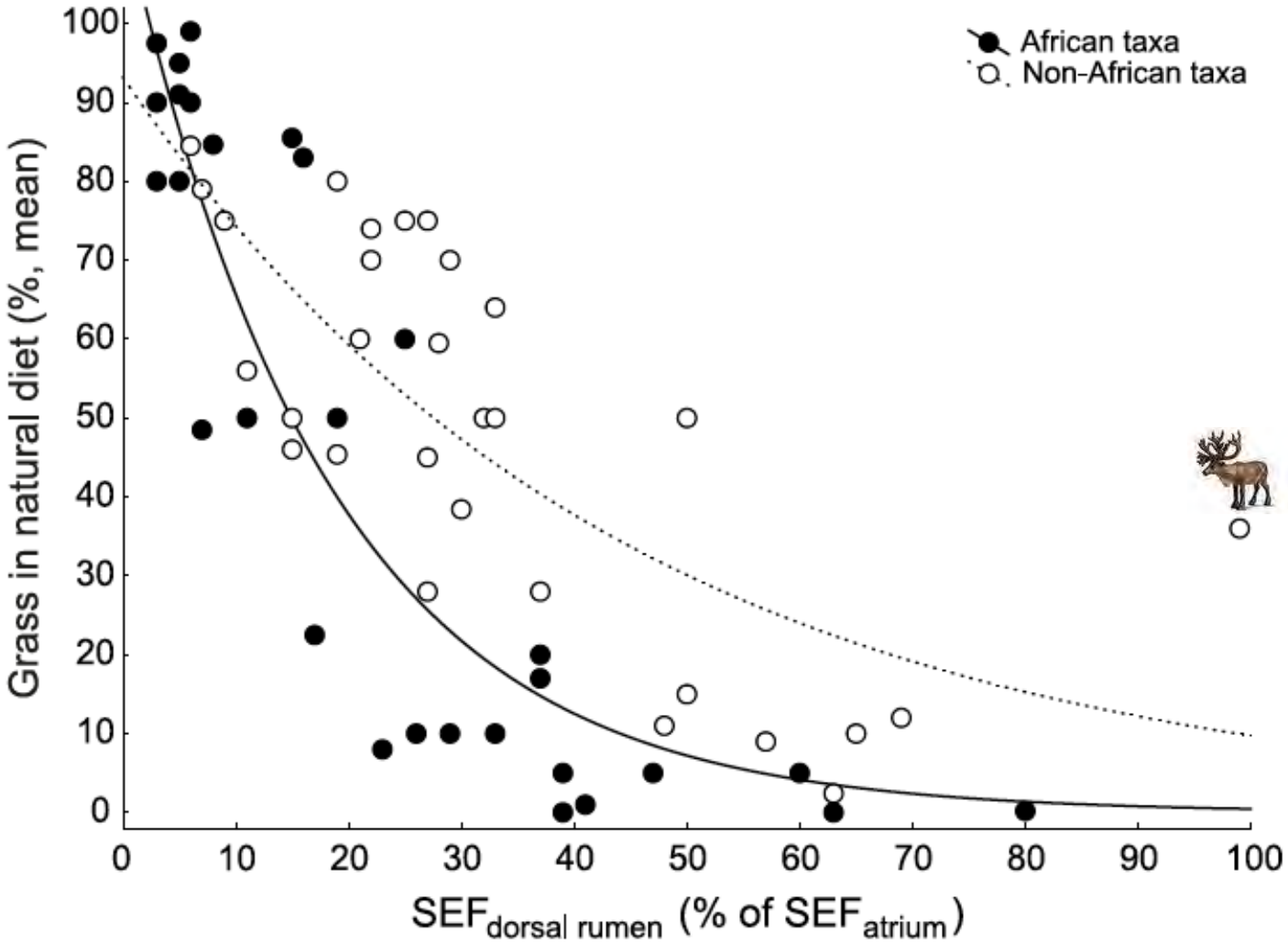
from Clauss, Hofmann et al. (2009)

Stratification and rumen papillation



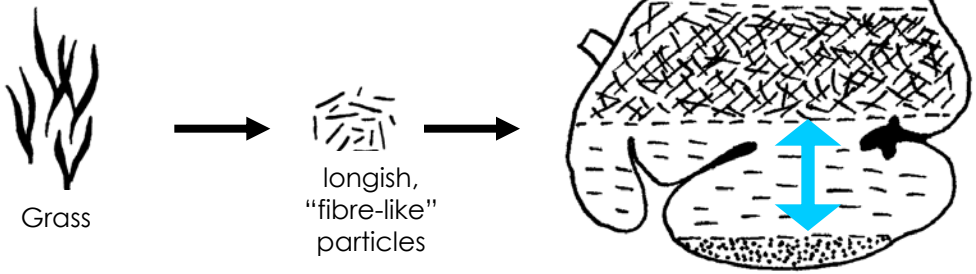
from Clauss, Hofmann et al. (2009)

Stratification and rumen papillation



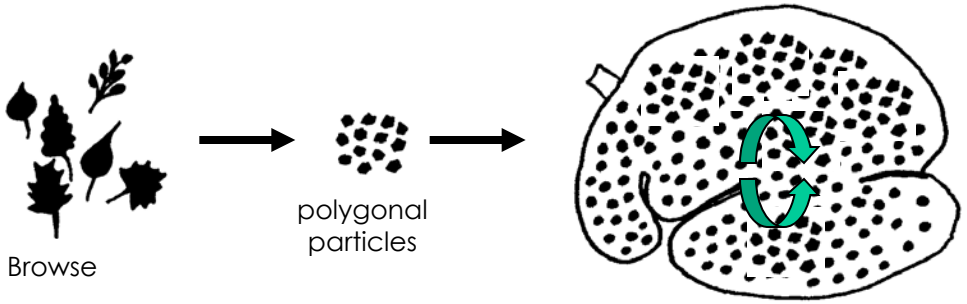
from Codron & Clauss (2010)

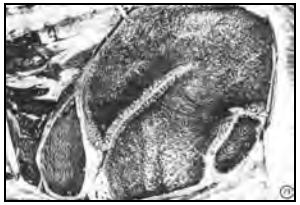
Grazer



Low viscosity fluid: Separation due to flotations/sedimentation; clear separation of gas dome

Browser

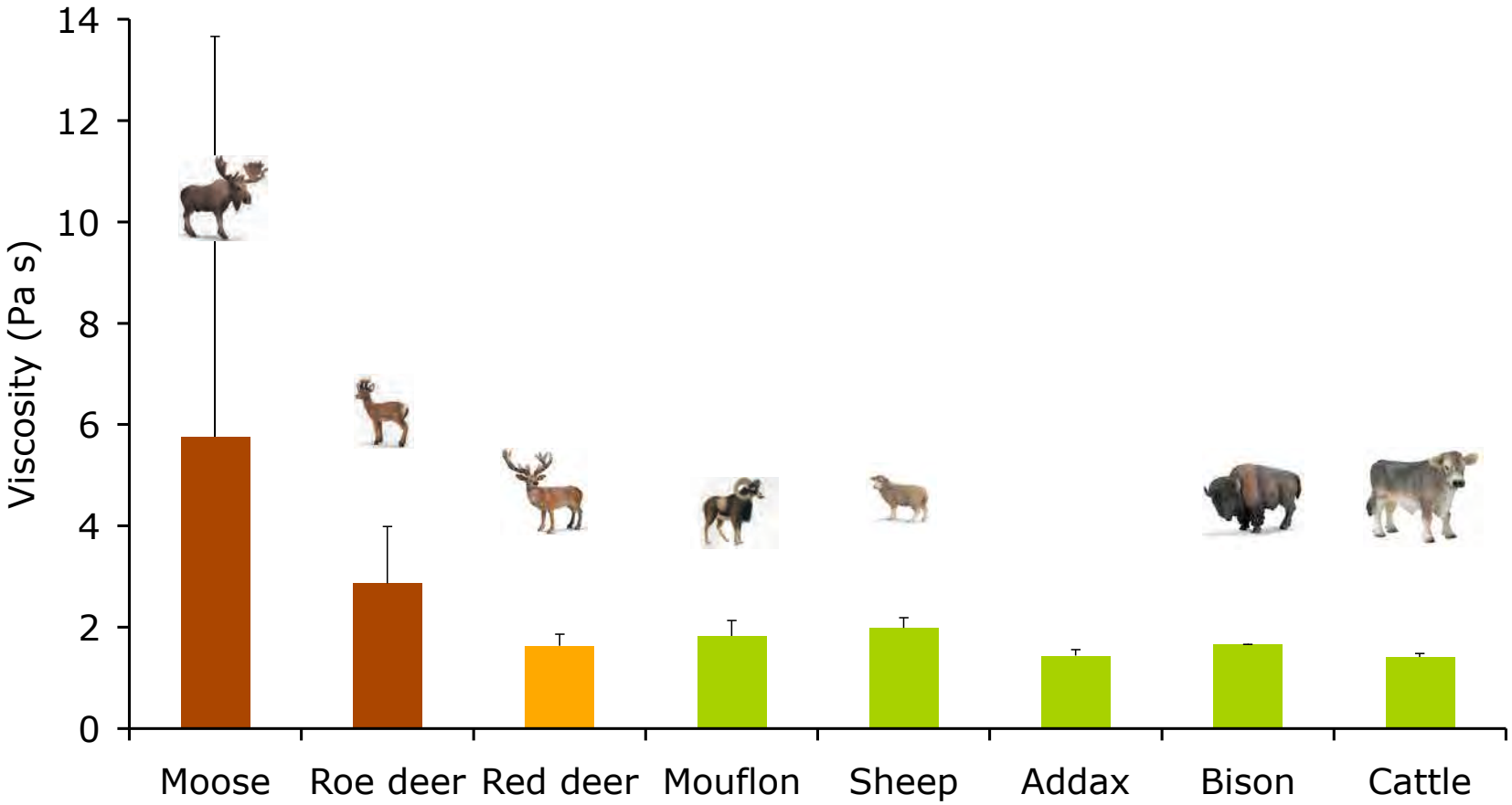




High viscosity fluid: Separation due to flotation/sedimentation less possible; gas bubbles distributed evenly in the contents

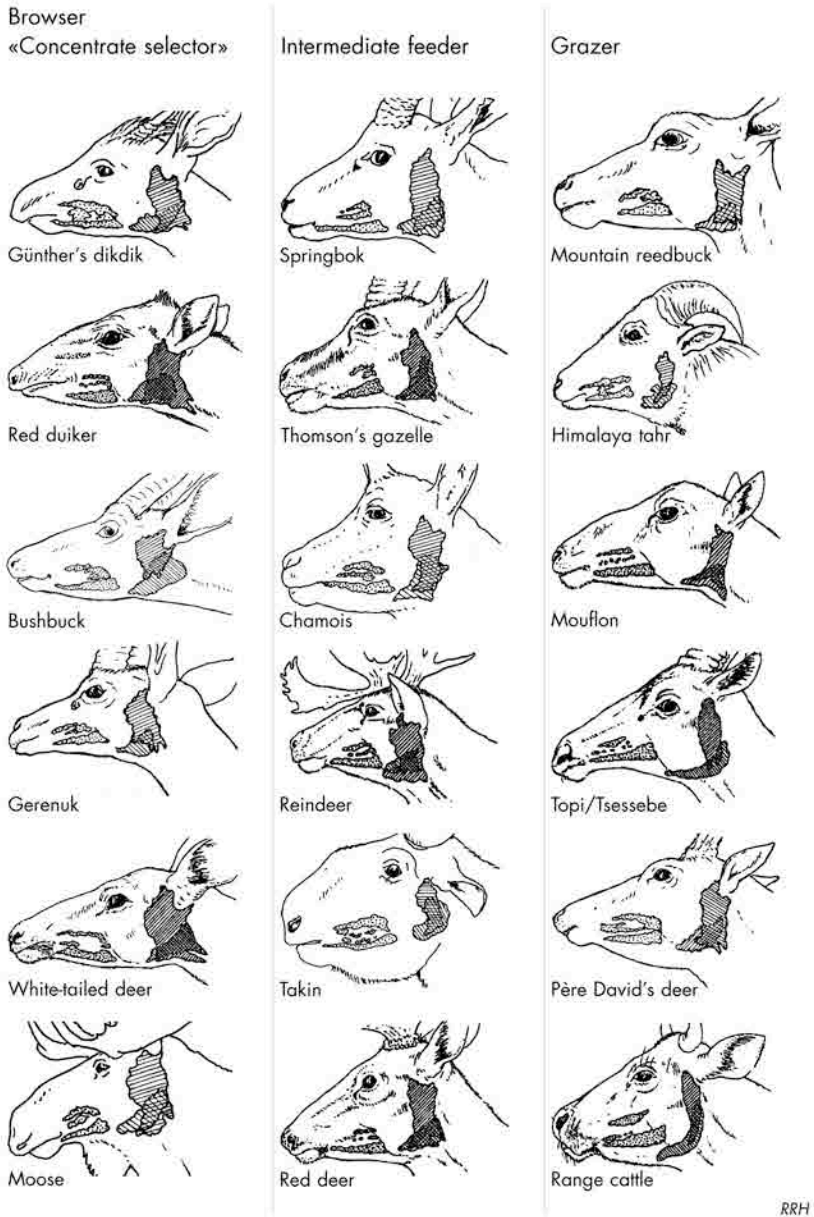
from Clauss et al. (2003)

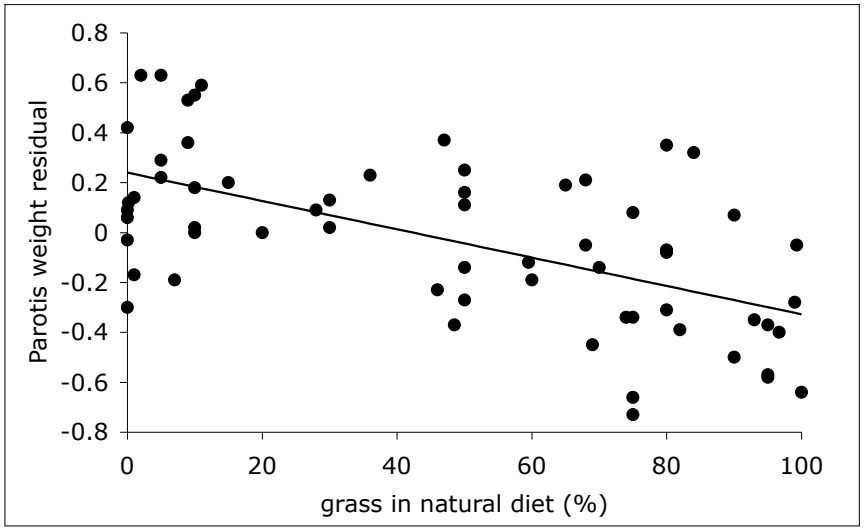
Rumen fluid viscosity



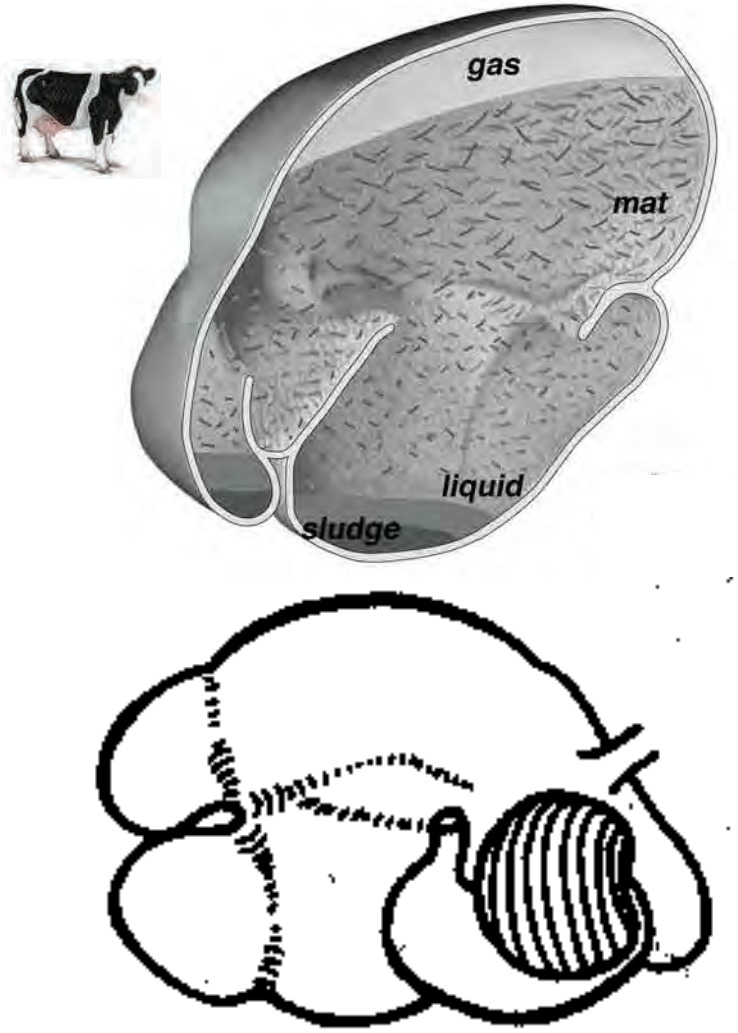
from Hummel et al. (2009) and Clauss et al. (2009ab)

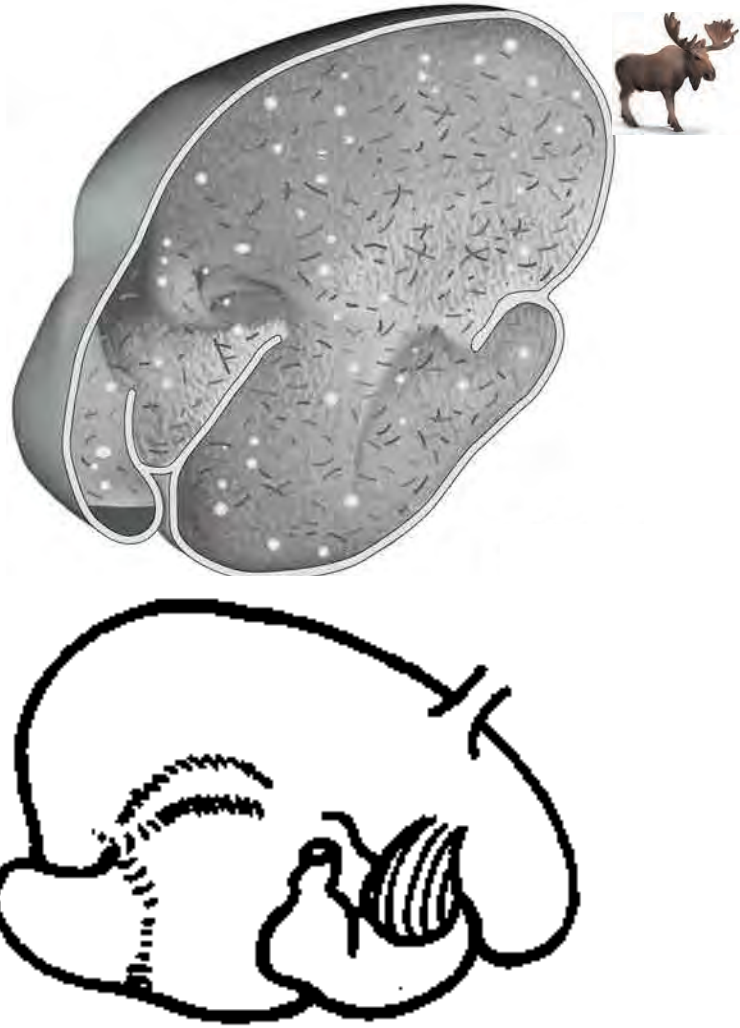
Different salivary gland size





from Hofmann et al. (2008)



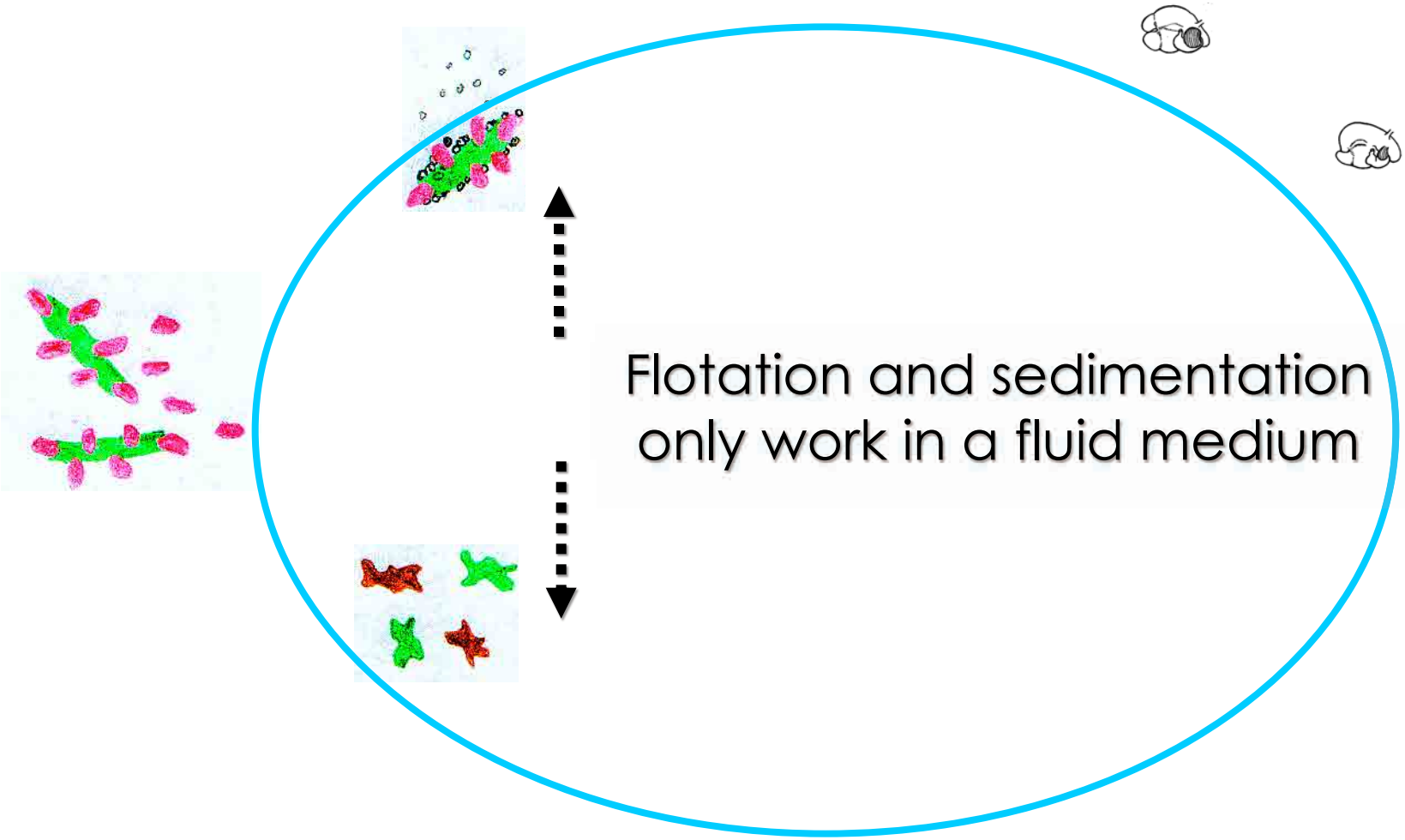


large omasum – high water absorption capacity

small omasum – lower water absorption capacity

from Hofmann (1973, 1992)

Sorting by density …



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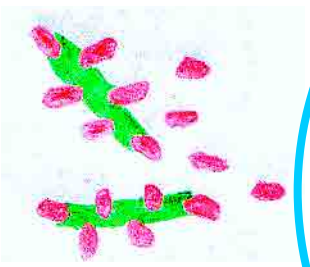


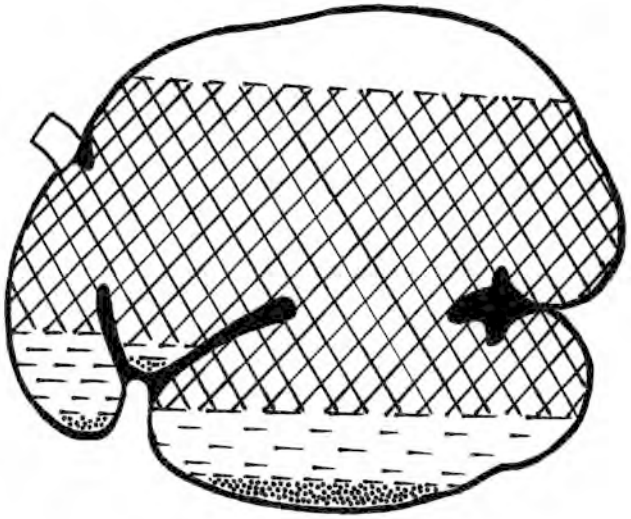
Flotation and sedimentation only work in a fluid medium

Indication for a difference in sorting mechanism between browsers and grazers?

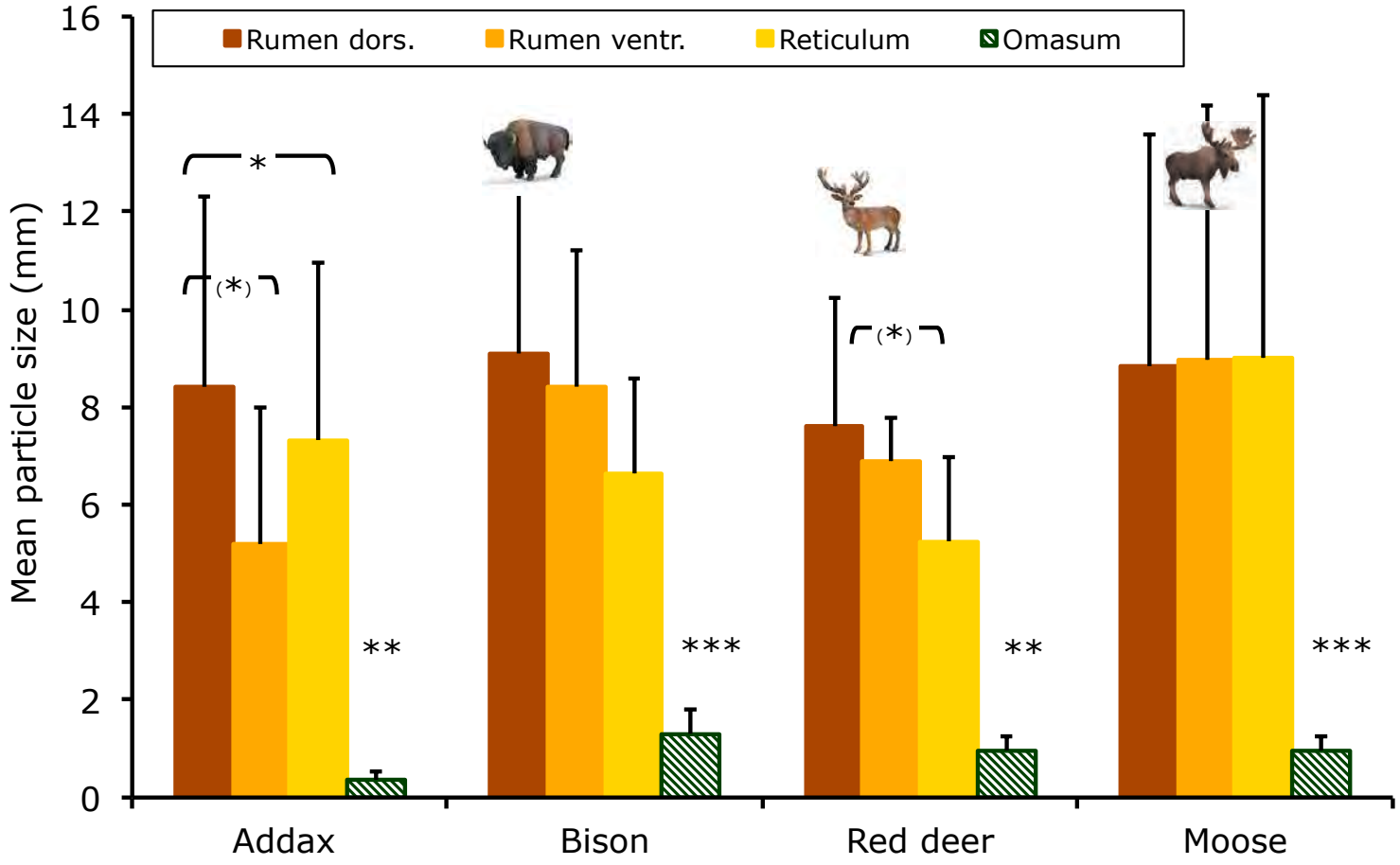
Why a higher fluid throughput?

- First hypothesis:

  A high fluid throughput ensures a fluid, low viscosity medium in the rumen - stratification, building of a mat, 'filter-bed effect' – more efficient particle retention



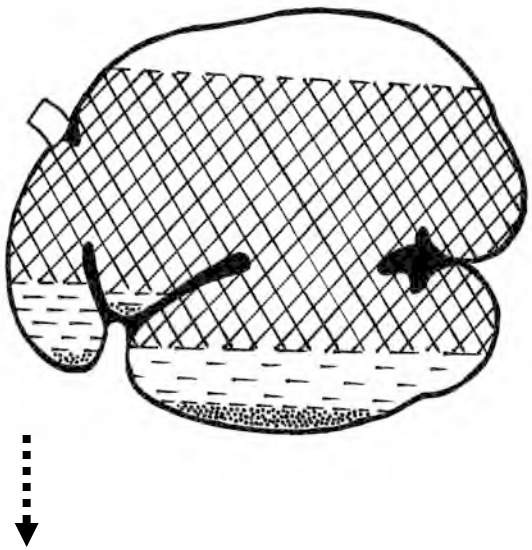
Differences in RR contents stratification could mean ...

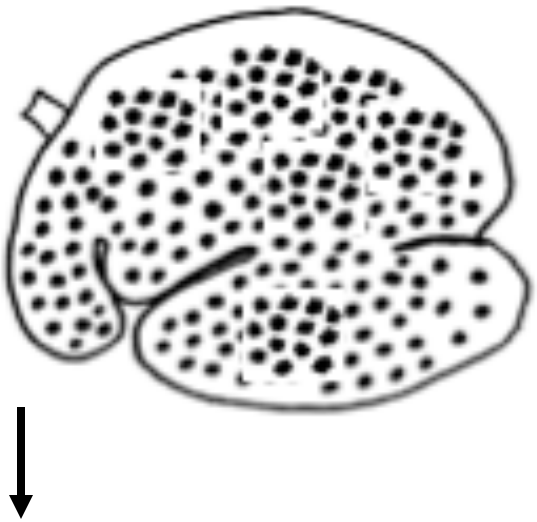


... not only the reticulum, but the whole rumen helps with sorting particles in grazers!

from Clauss et al. (2009)

Differences in RR contents stratification could mean ...

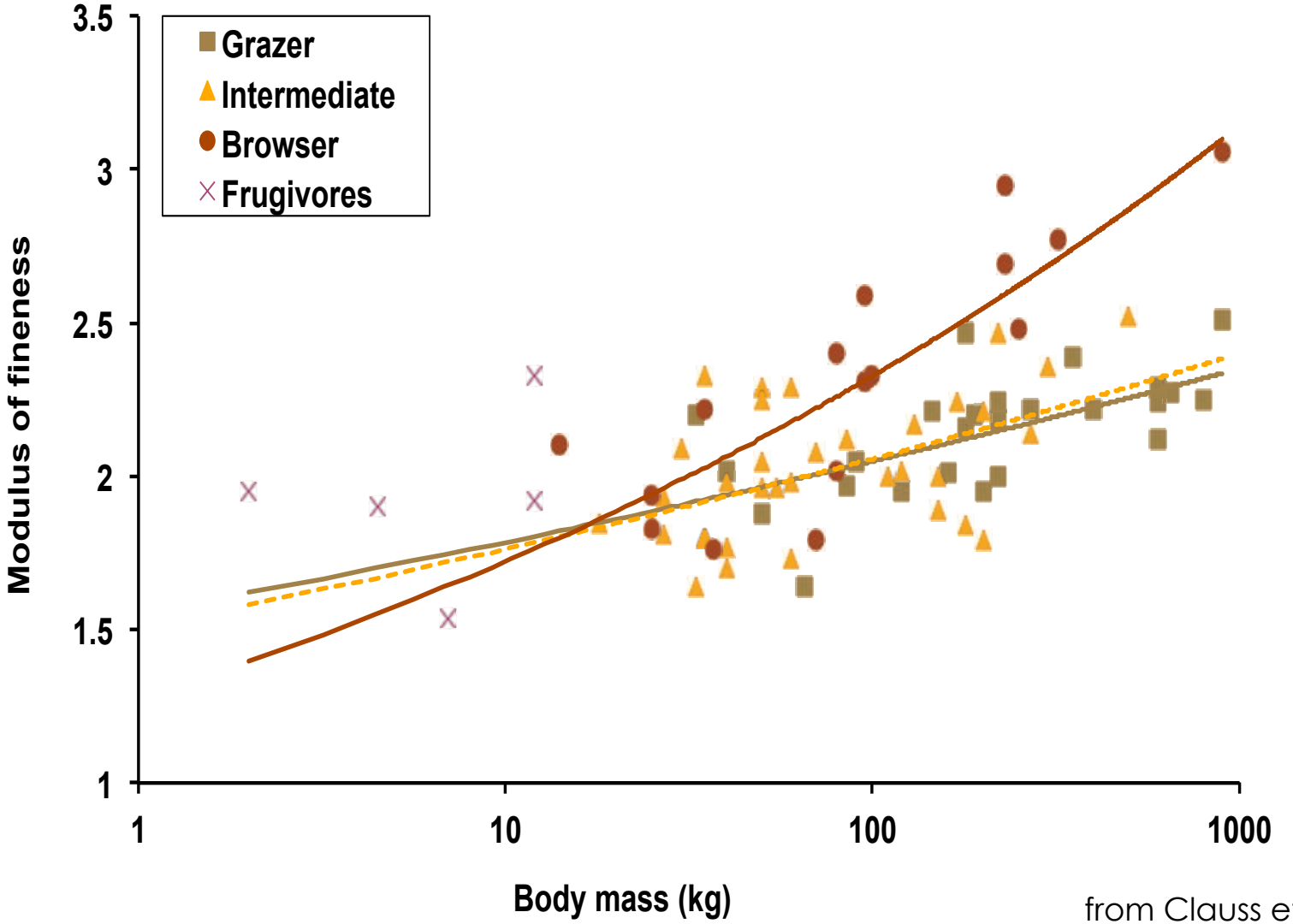




only small particles escape the rumen

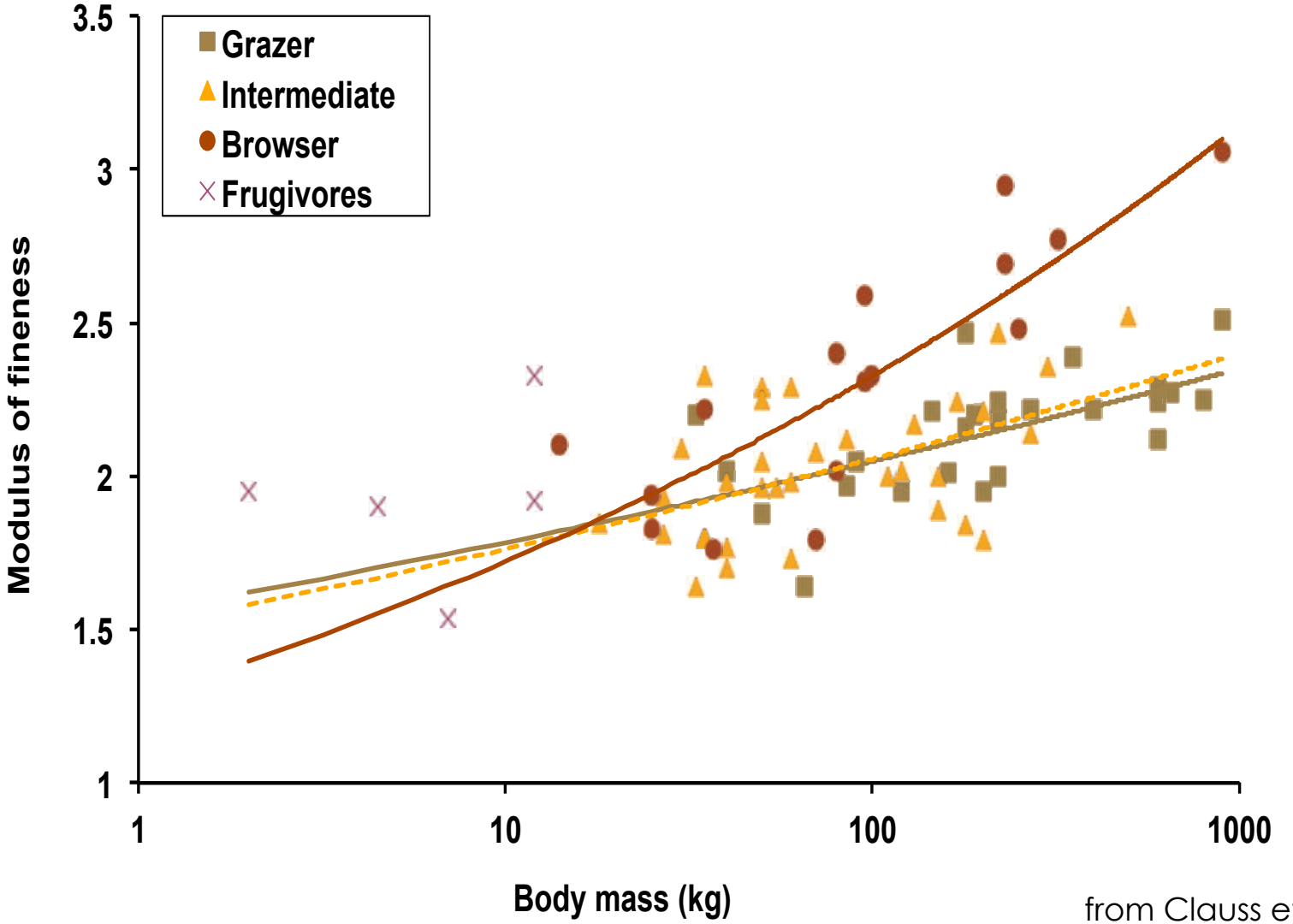
escape of larger particles possible

Faecal particle size in captive wild ruminants



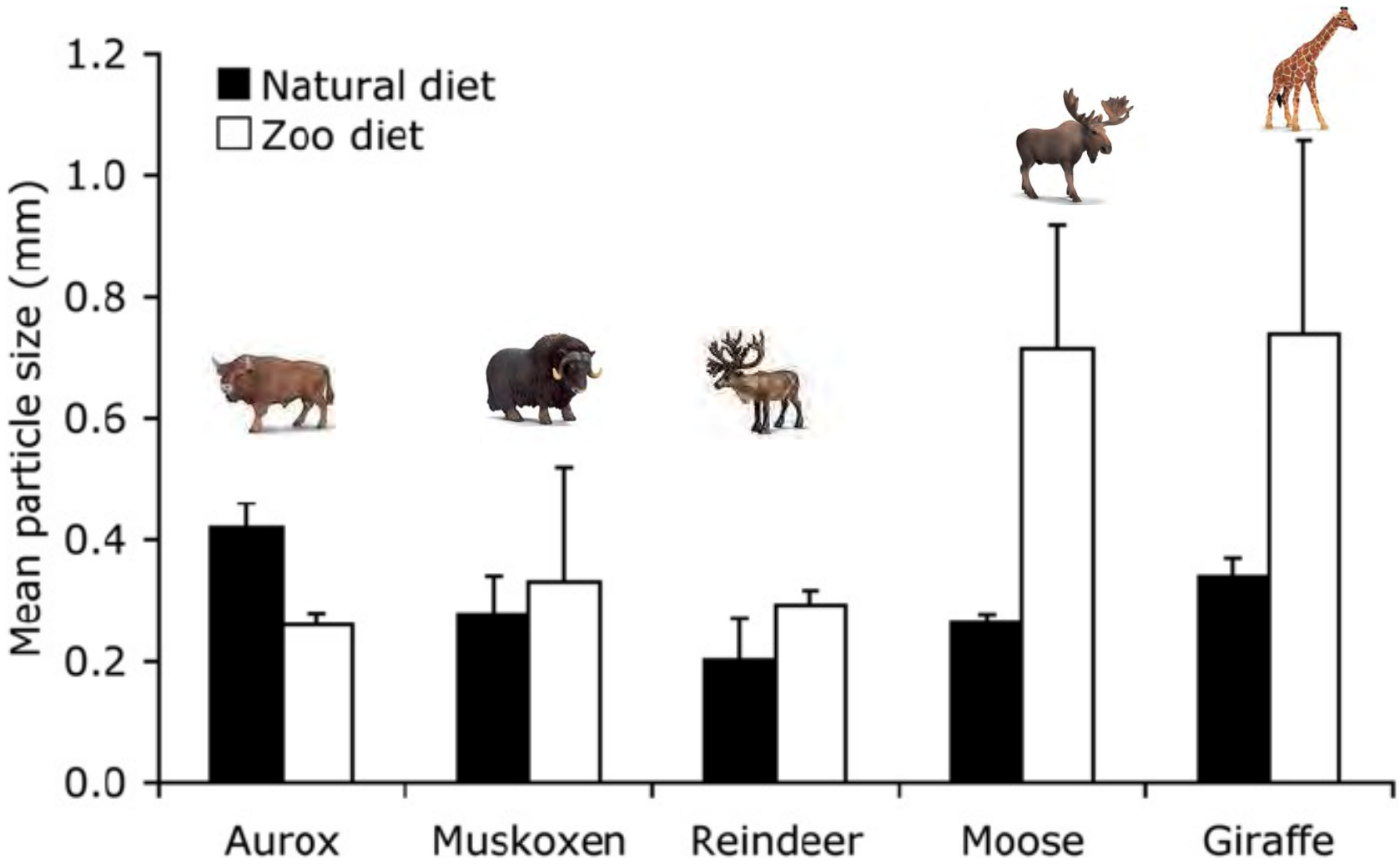
from Clauss et al. (2002)

Faecal particle size in ***captive*** wild ruminants



from Clauss et al. (2002)

Faecal particle size in ruminants



from Lechner et al. (2010)

Does digestion type influence the ‘filter-bed effect’?

from Lechner et al. (2010)

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from Lechner et al. (2010)

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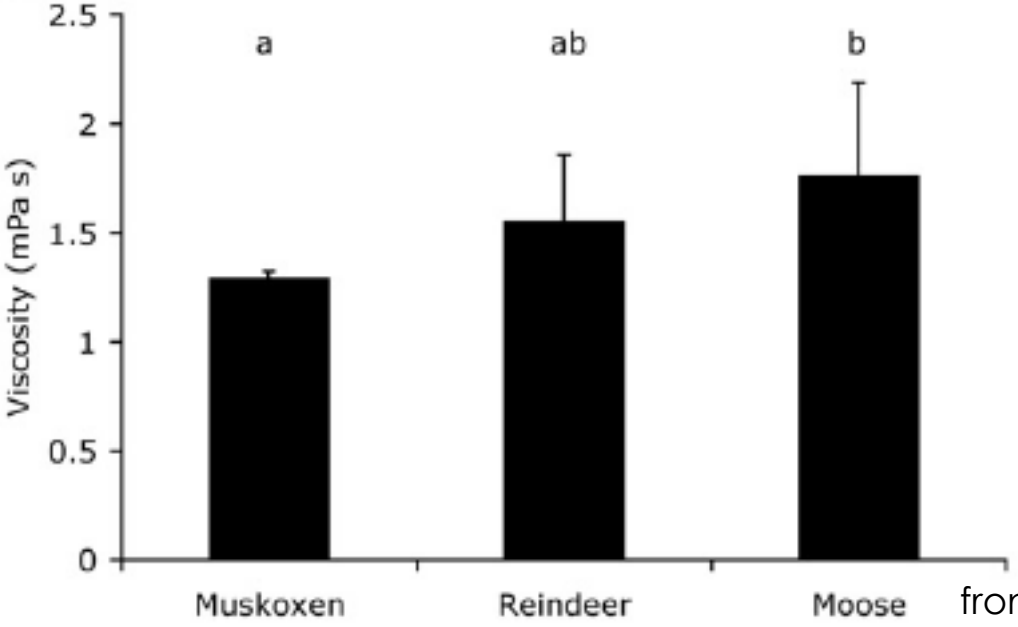
from Lechner et al. (2010)

Does digestion type influence the 'filter-bed effect'?







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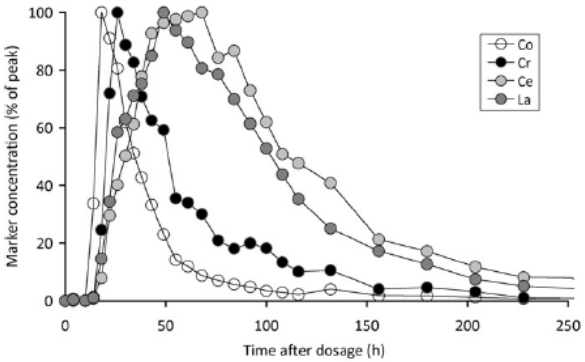
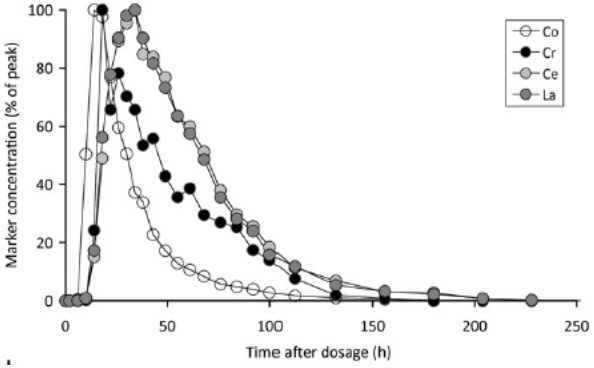
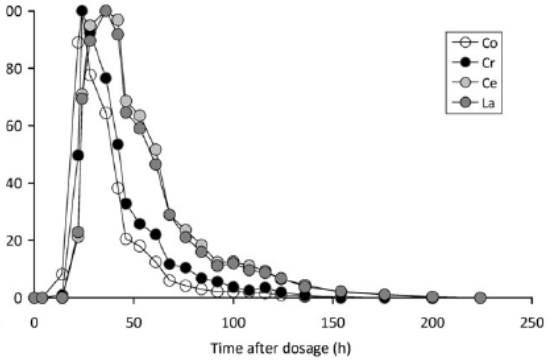
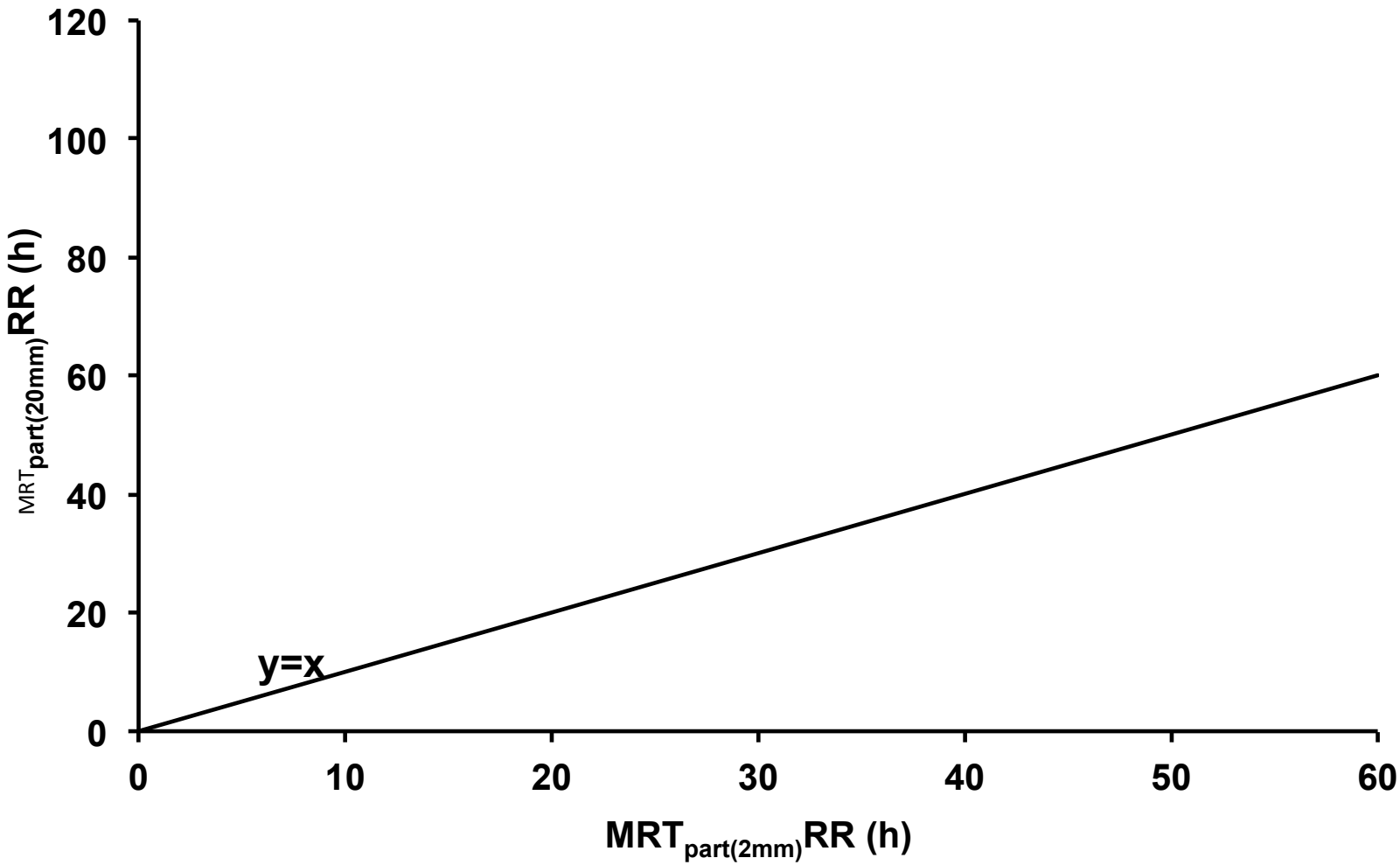






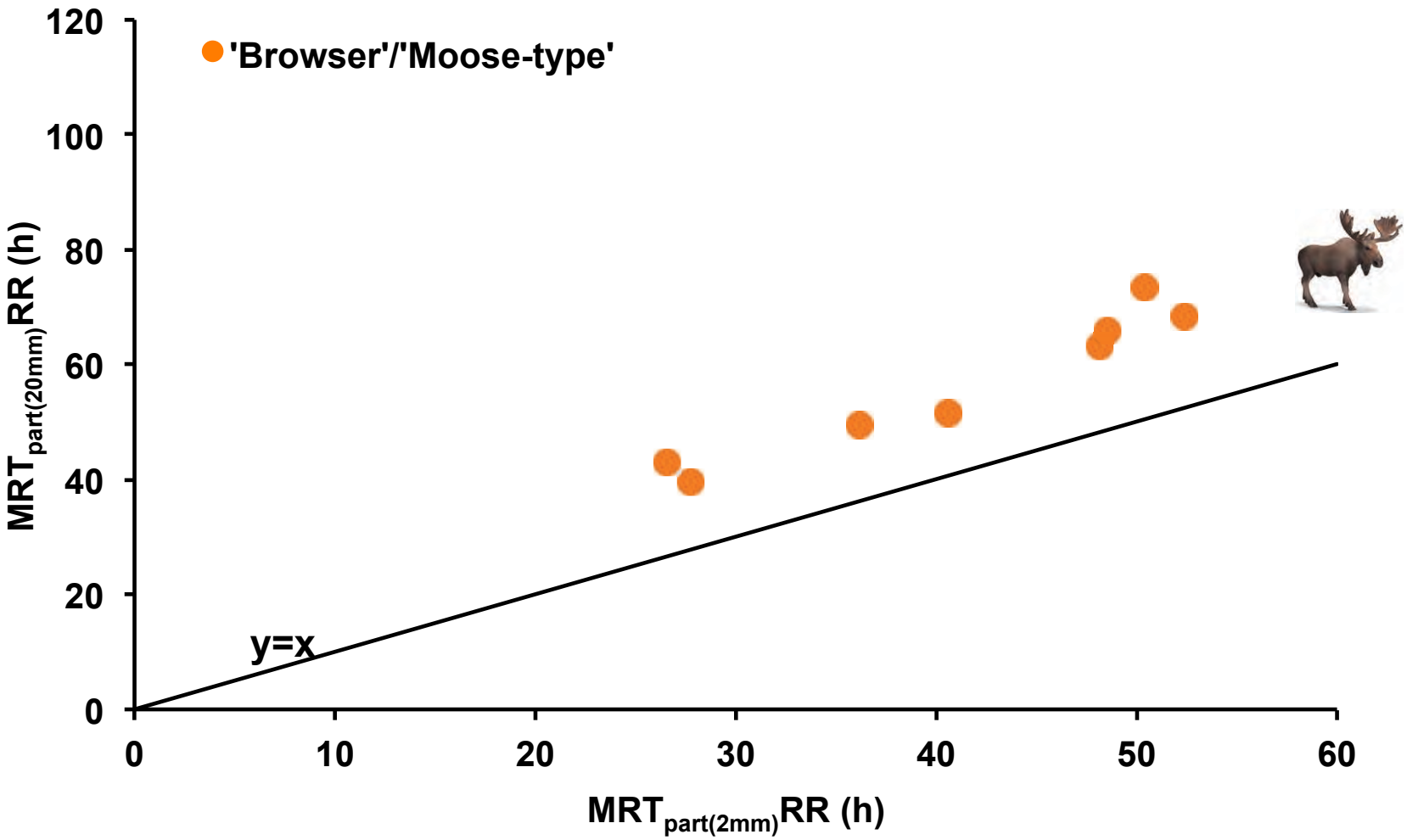
from Lechner et al. (2010)

No difference in sorting mechanism



from Clauss et al. (2010)

No difference in sorting mechanism



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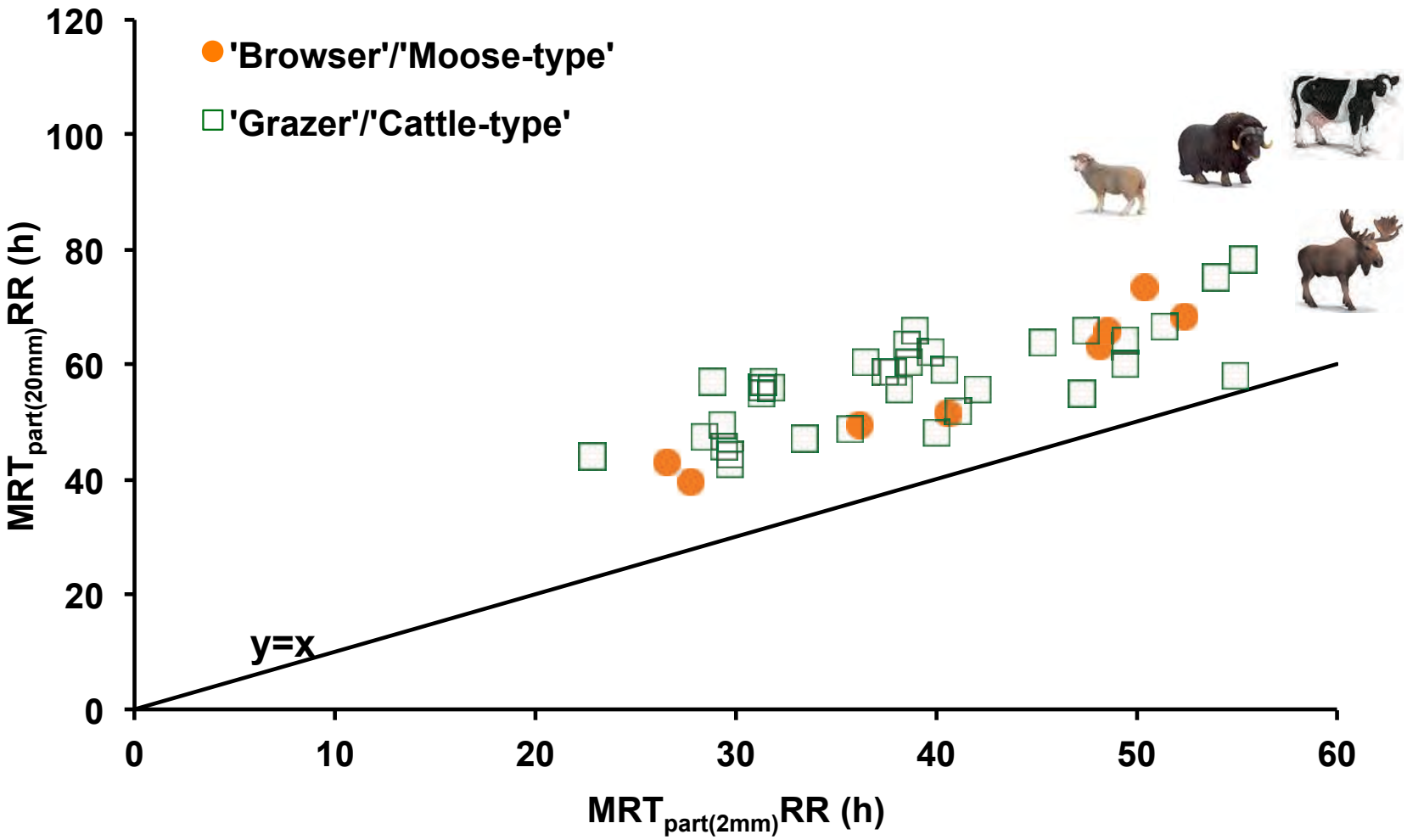

from Clauss et al. (2010)

Differential passage of fluids and different-sized particles in fistulated oxen (*Bos primigenius* f. *taurus*), muskoxen (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*): Rumen particle size discrimination is independent from contents stratification

Isabel Lechner [a], Perry Barboza [b], William Collins [c], Julia Fritz [d], Detlef Günther [e], Bodo Hattendorf [e], Jürgen Hummel [f], Karl-Heinz Südekum [f], Marcus Clauss [a,*]

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Particle size
Viscosity
Fluid throughput

ABSTRACT

Ruminant species differ in the degree that their rumen contents are stratified but are similar insofar that only very fine particles are passed from the forestomach to the lower digestive tract. We investigated the passage kinetics of fluid and particle markers (2, 10 and 20 mm) in fistulated cattle (*Bos primigenius* f. *taurus*), muskoxen (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*) on different diets. The distribution of dry matter in the rumen and the viscosity of rumen fluids suggested that the rumen contents were more stratified in muskoxen than moose. Correspondingly, as in previous studies, the species differed in the ratio of mean retention times of small particles to fluids in the reticulorumen, which was highest in cattle (2.03) and muskoxen (1.97–1.98), intermediate in reindeer (1.70) and lowest in moose (0.98–1.29). However, the ratio of large to small particle retention did not differ between the species, indicating similarity in the efficiency of the particle sorting mechanism. Passage kinetics of the two largest particle classes did not differ, indicating that particle retention is not a continuous function of particle size but rather threshold-dependent. Overall, the results suggest that fluid flow through the forestomach differs between ruminant species. A lower relative fluid passage, such as in moose, might limit species to a browse-based dietary niche, whereas a higher relative fluid passage broadens the dietary niche options and facilitates the inclusion of, or specialization on, grass. The function of fluid flow in the ruminant forestomach should be further investigated.

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Chapter 6

The digestive system of ruminants, and peculiarities of (wild) cattle

Marcus Clauss and Reinhold R. Hofmann

Cattle are members of the Ruminantia, which represent the most successful group of extant large herbivores in terms of species diversity. Ruminants have a multi-chambered forestomach, similar to other foregut fermenters like kangaroo, hippos, peccaries or sloths (Langer 1988); this means that plant material is partly digested by symbiotic microbes before the whole digesta – which includes the partly digested diet and the microbes – is passed on to the lower digestive tract where the herbivore's own enzymes further digest this mixture. Because microbial protein is a major component of this mixture, foregut fermenters produce a set of specific enzymes in their glandular stomach and small intestine that help break down microbial cells, so that their protein can be used (Pacheco et al. 2007). Functional ruminants – the phylogenetic ruminants as well as the camelids – combine simple foregut fermentation with peculiar sorting mechanisms that assure that larger digesta particles are regurgitated and re-masticated (ruminated). This process of rumination is an obligatory physiological feature, facilitates a more efficient particle size reduction (Pritz et al. 2009), higher digestive efficiencies (Foose 1982) and potentially also higher food intake levels than observed in non-ruminant foregut fermenters (Clauss et al. 2010a).

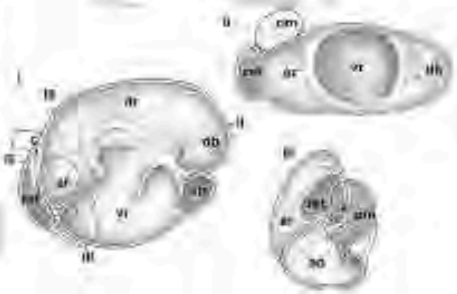

Figure 6.1 Schematic presentation of the ruminant forestomach modified from Hofmann (1973). (I) view from the left side into the reticulorumen with the dorsal rumen (dr), ventral rumen (vr), the dorsal and ventral blind sacs (dh, vh), the atrium ruminis (ar) and the reticulum (ret). Note the remnants of the ventral rumen groove, through which, in suckling ruminants, milk is diverted directly from the cardia (c) into the caecum (ab) (ab-caecum); this groove is structurally maintained in all adult ruminants. In fetal via the omasal canal into the abomasum. Food is digested by symbiotic microbes in the rumen compartments and sorted, according to density, in the reticulum. The numbers that lead to views II and III are indicated. (II) view from the top of the reticulorumen, through the transverse orifice from the dorsal to the ventral rumen; this orifice is flanked by muscular ridges called 'rumen pillars'; note the omasum (om) which is not opened in this view. (III) view from within the forestomach towards the front, displaying the atrioventricular orifice that links the atrium ruminis and the reticulum, and the inside of the omasum with its laminae, and the abomasum (ab). Digesta is passed from the reticulum either back into the atrium ruminis, on to the omasum, where most water is removed, and from there to the abomasum, where digestion by the animal's own enzymes is initiated.

Ruminant digestive anatomy and physiology

The ruminant stomach consists of four compartments – three representing the forestomach complex, and the last representing the glandular stomach ('abomasum'), the equivalent of the stomach of monogastric animals (Hofmann & Schnorr 1982). The three forestomach compartments are, in the sequence of the digestive process, the rumen, the reticulum and the omasum (Figure 6.1). From the outside, the rumen and the reticulum form a unit – a large fermentation chamber with several sub-compartments, including the dorsal and the ventral rumen, the dorsal and ventral rumen blindsacs, the atrium ruminis and the reticulum. The whole complex is often referred to as the reticulorumen (RR). The reticulum is the most cranial part of the RR. On the right side of the RR, the omasum is a distinct structure. In contrast to the RR, which has a consistency of the digesta it contains, the omasum is more solid to the touch, and ball- or bean-shaped. The omasum leads to the abomasum, which in turn leads to the small and then the large intestine.

Due to the economic relevance of domestic ruminants, an enormous amount of research has been published on detailed functions of the ruminant gastrointestinal tract (GIT) in relation to digestion and absorption. Without doing this body of research justice, the function of the different parts of the ruminant digestive tract can be crudely summarized as follows.

Ecology, Evolution and Behaviour of Wild Cattle: Implications for Conservation, ed. M. Melletti and J. Burton. Published by Cambridge University Press.

Grazers vs. browsers: where are we?

What is the relevance of the 'cattle-type' forestomach anatomy/physiology? To what diet is it really linked?

Ruminant questions

- What is the success of the buffalo/cattle-type anatomy/physiology?

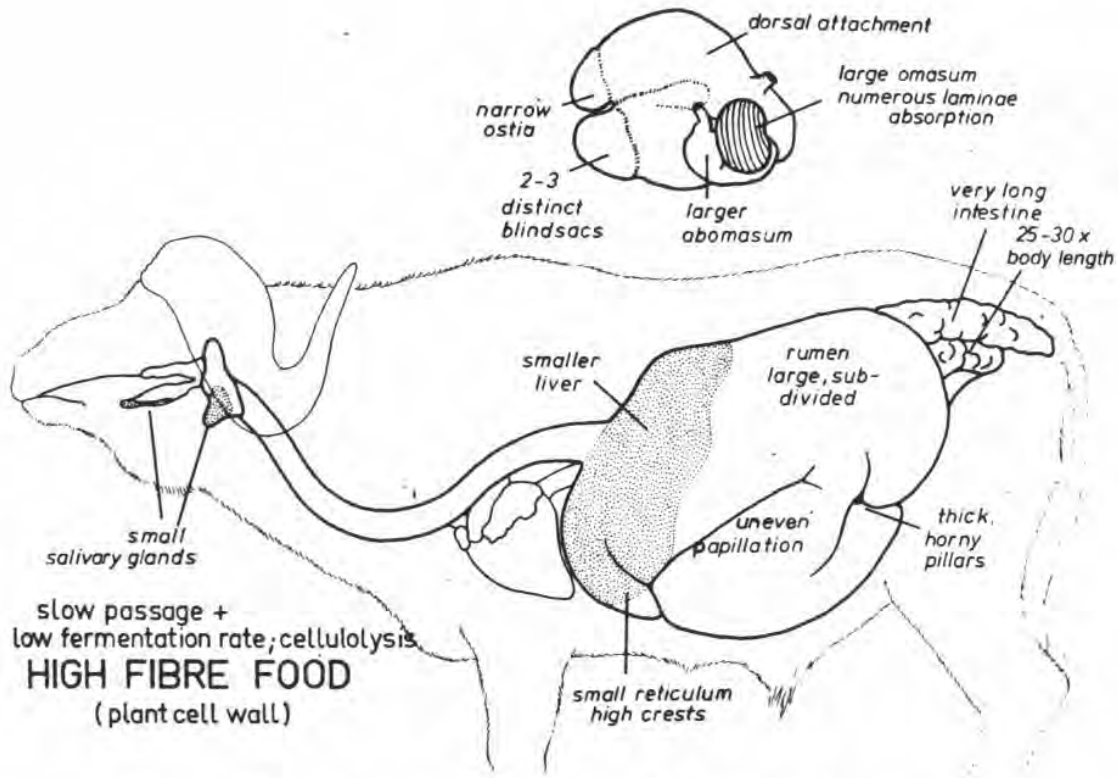

Fig. 1: The African buffalo, a non-selective roughage grazer.

from Hofmann (1989)

Ruminant questions

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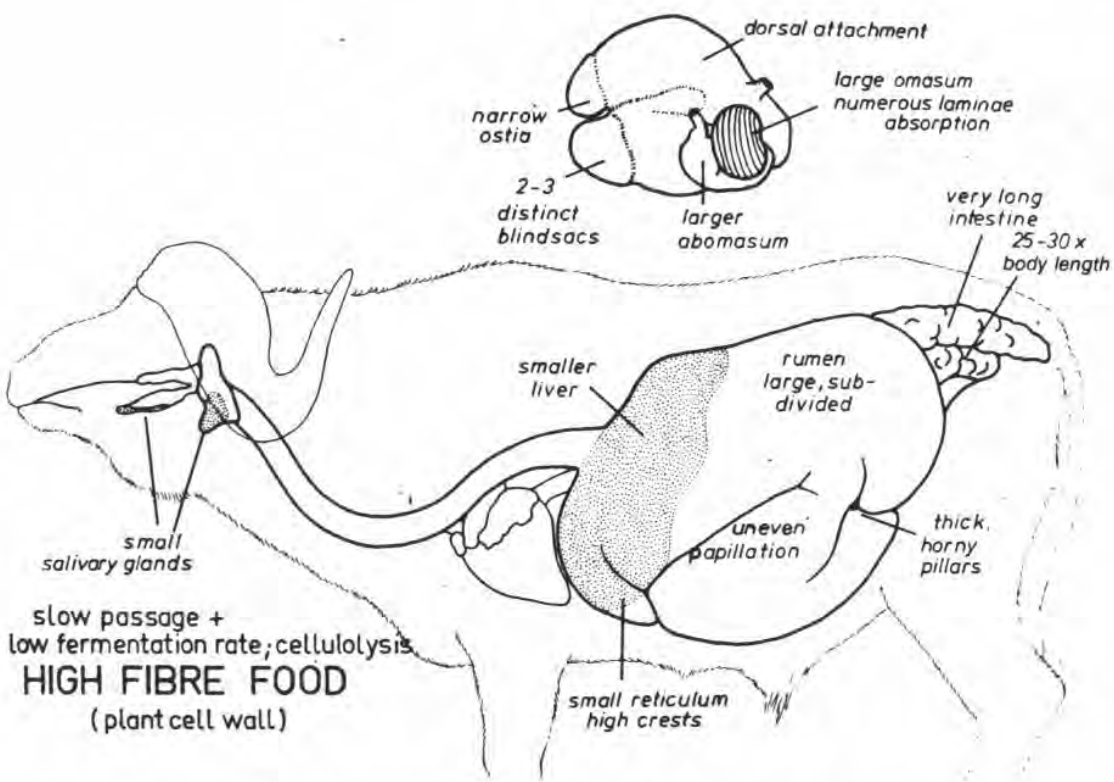

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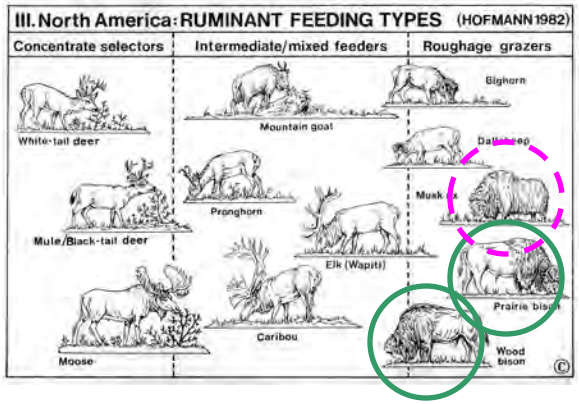
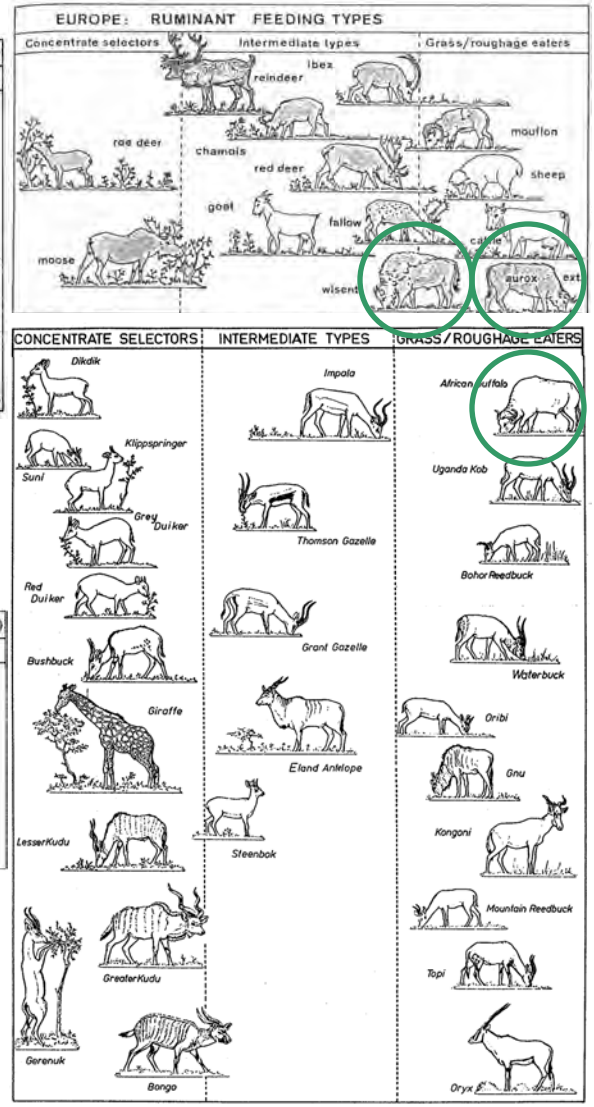
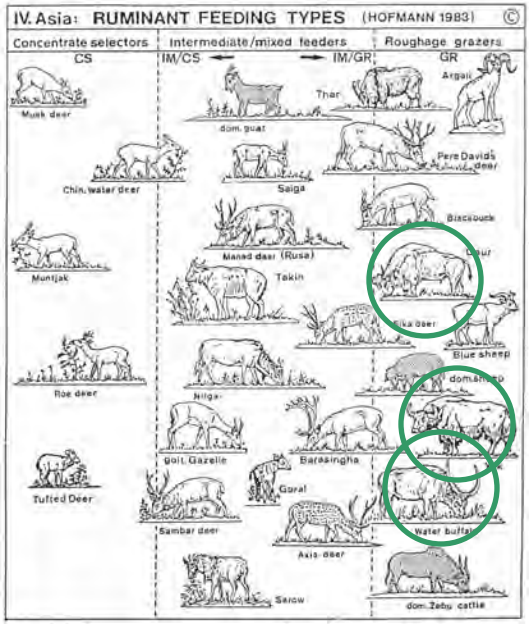
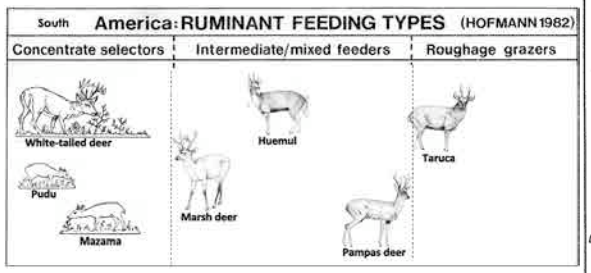
Ruminant feeding types (Hofmann)









from Hofmann (1989, 1991, unpubl.) and Geist (1999)

Ruminant questions

- What is the success of the buffalo/cattle-type anatomy/physiology?

- Not a typical "grazer" adaptation but one that evidently also facilitates mixed feeding/browse diets:

  African buffalo - Red forest buffalo

  Plains bison - Wood bison - Europ. Bison

  Yak - Gaur - Banteng

  Muskoxen

Form & Function

- The strategy of
  - Distinict contents stratification
  - High rumen fluid throughput
  - Large omasum

... *does not increase particle sorting efficiency*

... *but it might:*

- Enhance harvesting of forestomach microbe populations?

Why a higher fluid throughput?

- ~~First hypothesis:~~

  ~~A high fluid throughput ensures a fluid, low viscosity medium in the rumen - stratification, building of a mat, 'filter-bed effect'~~

- New hypothesis:

  A high fluid throughput increases microbial harvest from the forestomach - microbes are washed out faster, more energy used for microbial growth than microbial maintenance

New hypothesis

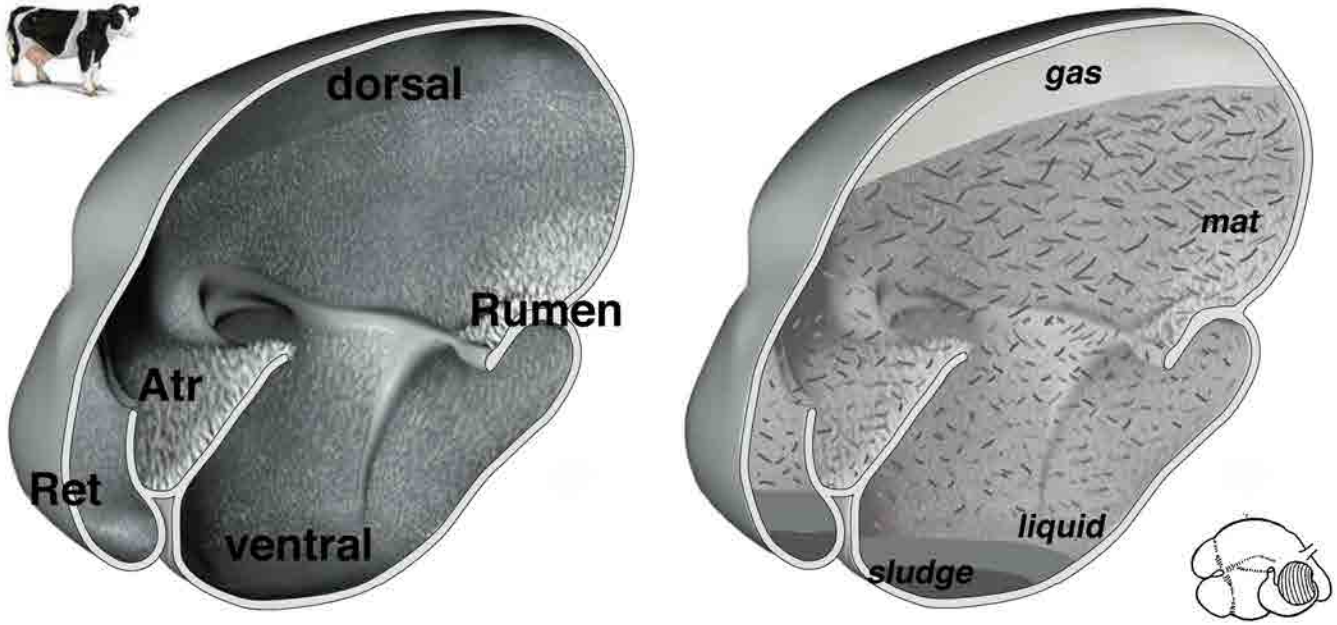
- Extreme browsers need saliva with high amount of tannin-binding proteins (=viscous saliva, production limited)

  ⇒ 'moose-type physiology'

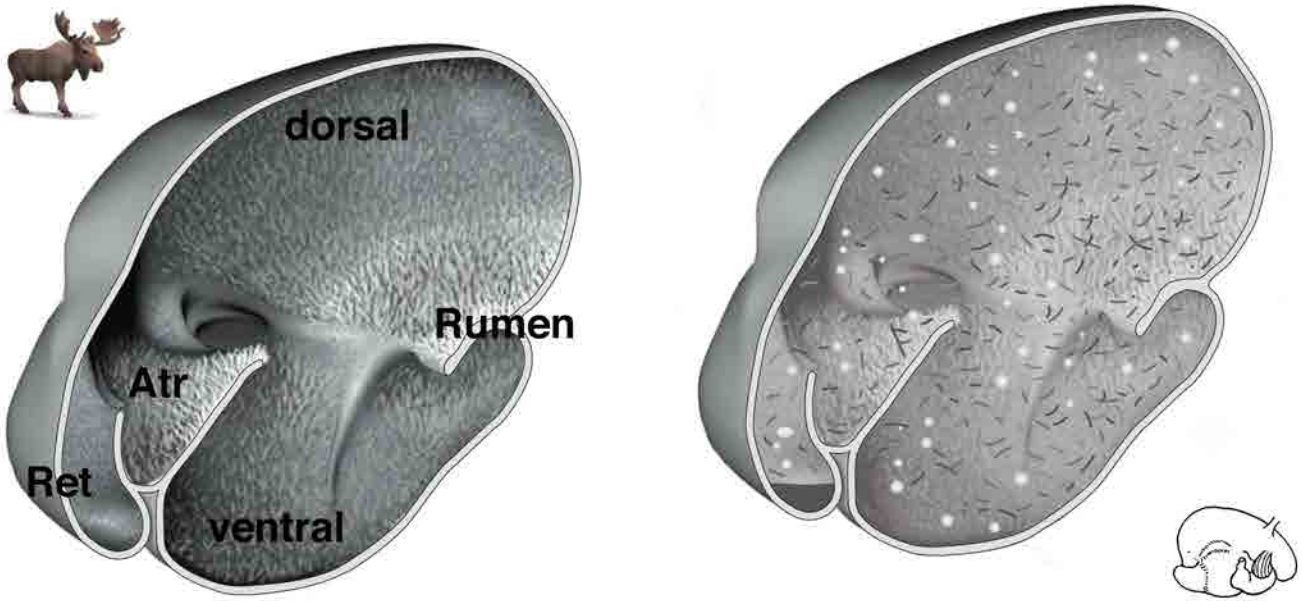
  ⇒ can live on grass, but not as efficient as 'cattle-type'

- Due to bacterial harvest, 'cattle-type' are more efficient in all other diet niches (mixed feeding and grazing) that do not depend on salivary defences

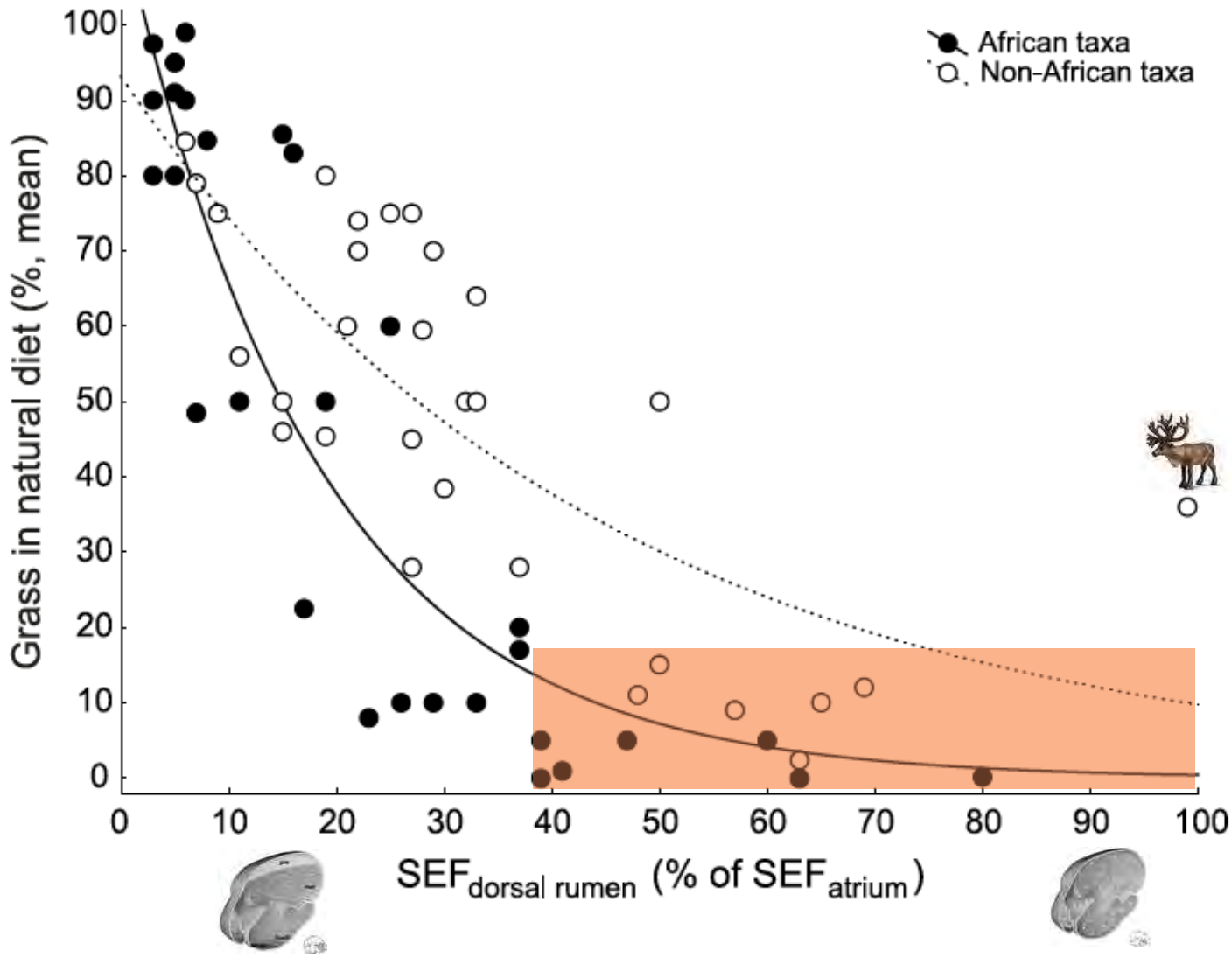
‘cattle-type’ (grazer?/universalist)



‘moose-type’ (non-grazer/browser)



Stratification and rumen papillation



from Codron & Clauss (2010)

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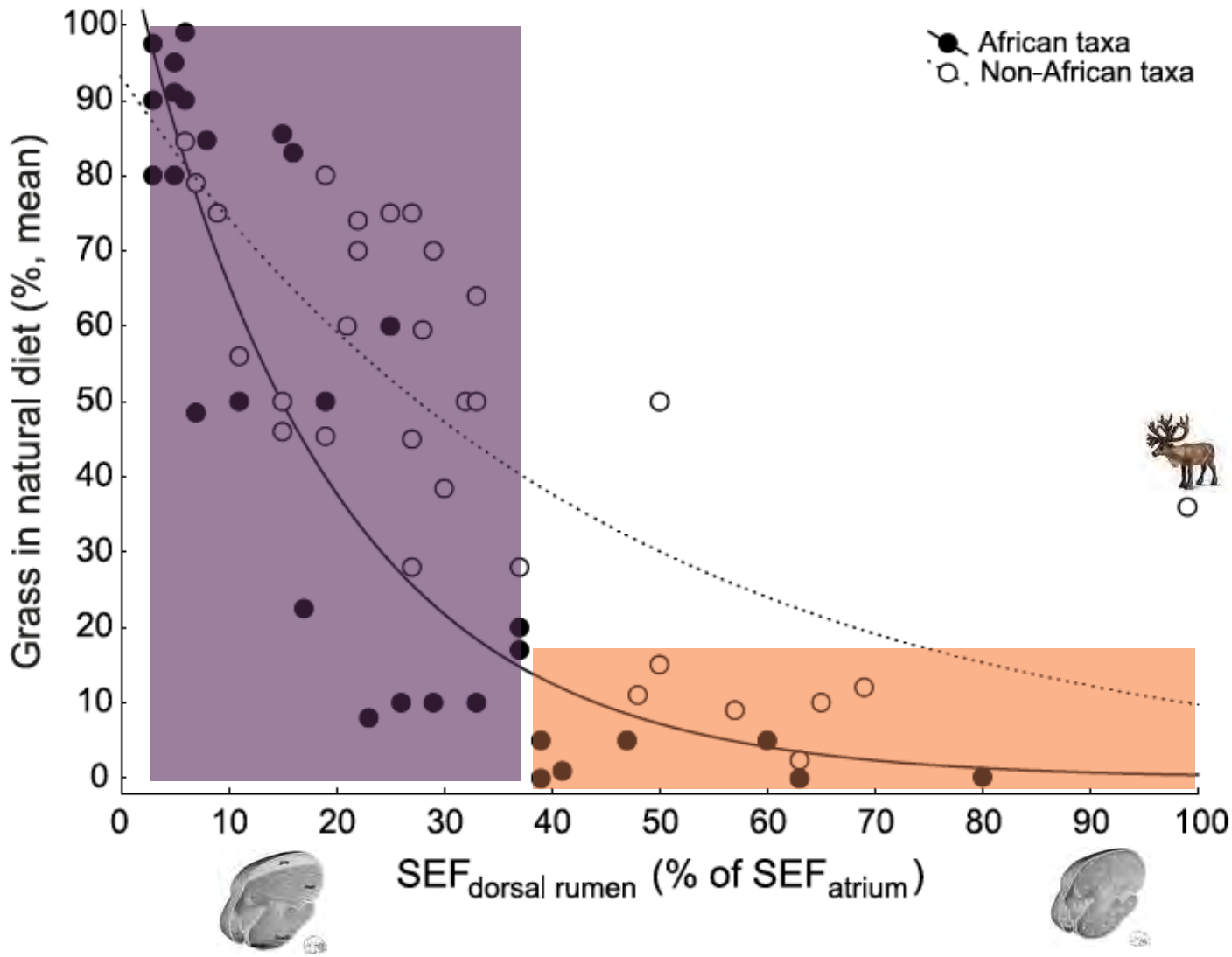

from Codron & Clauss (2010)

Attempts to increase rumen fluid throughput

- Continuous infusion of artificial saliva in fistulated animals
- Feeding of mineral salts
- Offering of isotonic fluids instead of drinking water?

Chalupa (1977) Manipulating rumen fermentation. J Anim Sci 46, 585
Harrison & McAllan (1980) Factors affecting microbial growth yields in the reticulo-rumen. In Digestive physiology and metabolism in ruminants (eds. Ruckebush & Thivend), p 205, MTP Press, Lancaster
Croom et al. (1993) Manipulation of gastrointestinal nutrient delivery in livestock. J Dairy Sci 76, 2112

Attempts to increase rumen fluid throughput

EFFECTS OF A SALIVARY STIMULANT, SLAFRAMINE, ON RUMINAL FERMENTATION, BACTERIAL PROTEIN SYNTHESIS AND DIGESTION IN FREQUENTLY FED STEERS[1]

M. A. Froetschel[2], H. E. Amos[2], J. J. Evans[3], W. J. Croom, Jr.[4] and W. M. Hagler, Jr.[5]

J. Anim. Sci. 1989. 67:827–834

With SF administration, as much as 13% more bacterial protein exited the rumen, resulting in a 16.5% linear improvement ($P < .1$) in the efficiency of ruminal bacterial protein production per 100 g of OM fermented.

These results demonstrate a positive relationship between salivation and ruminal bacterial protein synthesis and suggest that feed utilization by ruminants may be improved by pharmacological stimulation of salivary secretions.

Sequence of hypotheses

Soft tissue variation and forestomach physiology is linked to

diet fibre content

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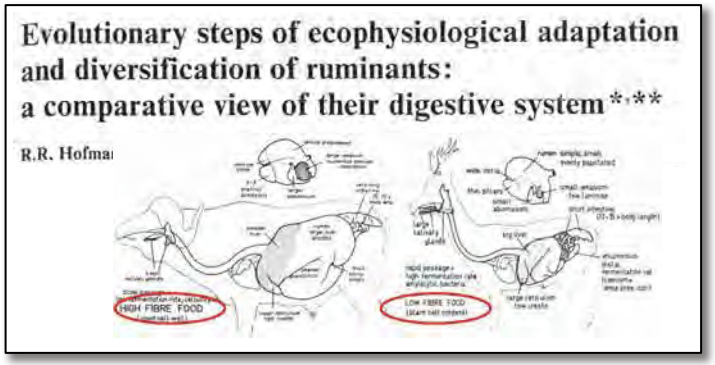

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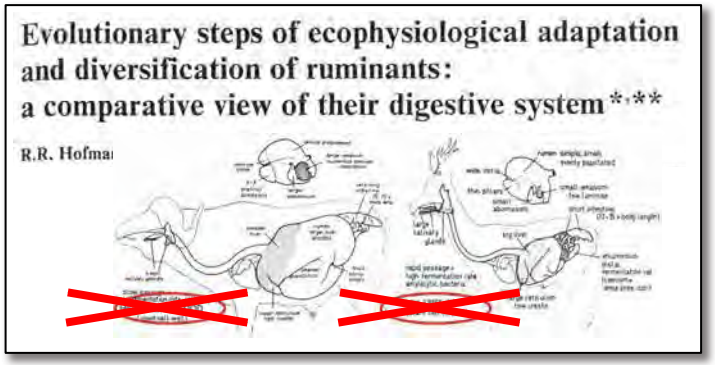
Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system*,**

R.R. Hofma

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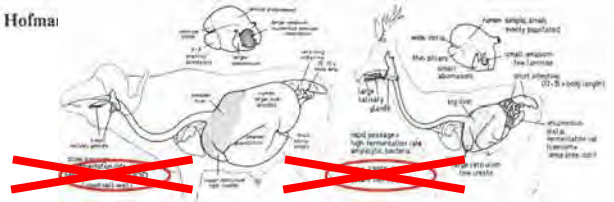

RR stratification enhancement for better fibre use

Ruminant diversification as an adaptation to the physicomechanical characteristics of forage. A reevaluation of an old debate and a new hypothesis

Marcus Clauss, Matthias Lechner-Doll and W. Jürgen Streich

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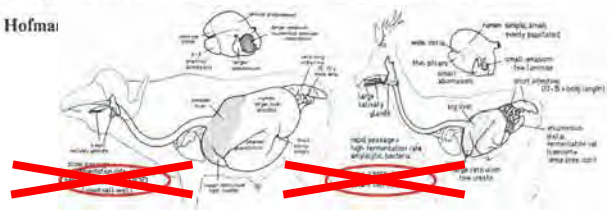

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Differential passage of fluids and different-sized particles in fistulated oxen (*Bos primigenius* f. *taurus*), muskoxen (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*): Rumen particle size discrimination is independent from contents stratification

Isabel Lechner [a], Perry Barboza [b], William Collins [c], Julia Fritz [d], Detlef Günther [e], Bodo Hattendorf [e], Jürgen Hummel [f], Karl-Heinz Südekum [f], Marcus Clauss [a,*]

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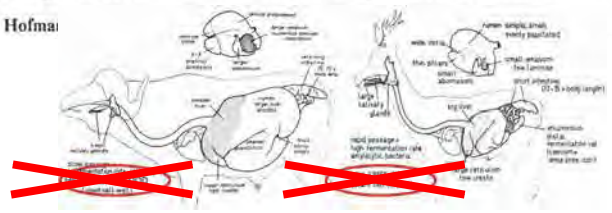

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difference in salivary defence and potential for RR microbial harvest

... the browser wars are over!

Gordon IJ, Prins HHT (eds) (2008) The ecology of large mammalian herbivore browsing and grazing. Springer, Heidelberg

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with a foreword by R. R. Hofmann